CHAPTER 1-1
INTRODUCTION

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CHAPTER 1: INTRODUCTION

"Man is placed in the middle between two infinities - the infinitely great and the infinitely little - both of which are incomprehensible to him." (from Pascal, in Crum 1976)

Figure 1. Bryophytes, forming their own communities on a microscale. Photo by Janice Glime.

Thinking on a New Scale

When Simon Levin (1992) presented his Robert H. MacArthur Award Lecture (presented to the Ecological Society of America August 1989), he began his abstract with the statement "It is argued that the problem of pattern and scale is the central problem in ecology, unifying population biology and ecosystems science, and marrying basic and applied ecology." He pointed out the need to interface phenomena that occur on "very different scales of space, time, and ecological organization." It is time that the scale be broadened to examine the role of bryophytes in ecosystem processes. While the scale is small, the role can at times be crucial. This treatment attempts to place bryophytes into the context of current ecological theory, to place the scale in perspective, and to raise important questions related to their behavior relative to current ecological theories.

In this treatise, we shall begin by examining the intricacies of the life styles and development of the bryophytes so that we may set forth on an informed and directed pathway toward filling our knowledge gaps.

Although bryophytes have provided a variety of uses for millennia, use in horticulture, fuels, and massive oil spill cleanups are only now beginning to threaten their existence. These ancient uses as well as new uses in medicines, pollution monitoring, and gardening place urgency on understanding their place in ecosystems – what they contribute, what they need, and how they got there.

Several factors have been important in legitimizing this new field. First, lack of taxonomic descriptions for many taxa, particularly in the new world, made ecological work all but impossible. With the publication of regional floras dealing with Europe, many parts of Asia, the Antarctic, and most of North America, those interested in bryology could begin asking more sophisticated questions. More recently, the tropical, African, and South American bryophyte floras are becoming sufficiently well known to permit study of their ecological relationships as well.

About the time our expertise in taxonomy reached an acceptable level, international attention was turning to problems of atmospheric contaminants and their effects on ecosystems of the world. Observations in Japan, Europe, and North America indicated that cryptogams (especially lichens and bryophytes) were among the most sensitive. The classical experiments with the peppered moths revealed that their color phase shift was related to the death of lichens on the trees due to industrial pollutants. Then, bryologists began documenting loss of bryophytes on the trees. Thus, bryophytes emerged as tools to indicate impending damage to ecosystems. Moss bags served as collectors of heavy metals and provided early warning systems of high accumulations. Aquatic mosses were used in transplant studies to assess river conditions. I have found more than 300 research papers dealing with aquatic bryophytes and pollution, and many more probably exist in publications not yet catalogued.

The field of bryophyte ecology has existed for as long as anyone has observed bryophytes and been curious about their requirements and growth. However, as a formal science, this is a young field. Scattered formal efforts have been made over many years, but these were mostly by taxonomists who made ecological observations as they described species, or by general plant ecologists who encountered the bryophytes in their study areas. Within the last 20-25 years, however, more papers have been published on bryophyte ecology than in all prior history. Now there are those scientists who specialize in the field of bryophyte ecology.

More recently, international interest in diminishing species diversity has resulted in "redlists" of threatened taxa. In the United States there have been many requests from the National Park Service and the U. S. Forest Service for bryological surveys, preferably with ecological studies accompanying them. As they began to understand that assemblages of species tell us more about a given site than a single species or physical measurements, foresters began to include bryophyte species in habitat classification systems and management plans. For example, at Pictured Rocks National Lakeshore, the National Park Service considered locations of unusual and endangered mosses in planning for construction of a road. These same governmental units are raising questions about dangers of moss harvesting and are seeking input on growth rates and replacement times in order to set reasonable harvest limits.

Despite all this new and exciting attention directed at mosses and liverworts, we still know very little about the role of bryophytes in the ecosystem, and we especially know very little at the species level. The information that has been published has been widely scattered in the literature and is often immersed inconspicuously in studies dealing primarily with **tracheophytes** (those plants with lignified vascular tissue). Collecting such literature is a lengthy and arduous task, although computer search engines have facilitated this job enormously. Additionally, at least three national journals regularly publish lists of current bryological literature, and these journals have also made efforts to locate older literature of significance to bryologists. Such bibliographies are making it possible to develop a picture of the role of bryophytes in the ecosystems of the world.

Adaptations to Land

Bryophytes are generally considered the first land plants, and likewise the first true plants. The algae most likely preceded them on land. (I won't try to defend the Chlorophyta as the first land plants, although some are now considered plants by some botanists.) Both of these groups exist on land as **gametophytes** (Figure 2), unlike their seed plant counterparts that exist as **sporophytes** with their gametophytes imbedded deep within **sporophyte** (Figure 3-Figure 4) tissues. The nature of these two generations, one producing gametes and existing with one set of chromosomes (**gametophytes**) and the other producing spores and existing with two sets of chromosomes (**sporophytes**) will be discussed later.

Figure 2. Moss ***Schistidium apocarpum*** showing capsules of the sporophyte and leafy gametophyte. Photo by J. C. Schou (Biopix), through Creative Commons.

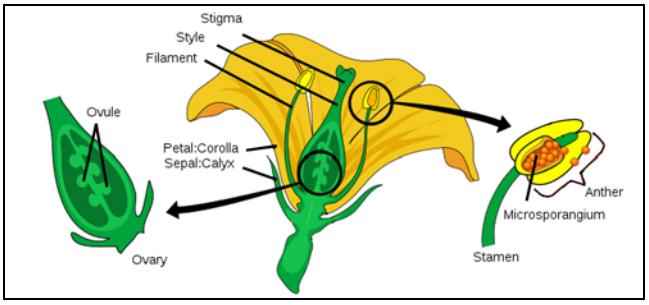

Figure 3. Flower diagram showing locations of sporophyte reproductive parts. Modified from drawing by Mariana Ruiz, through public domain.

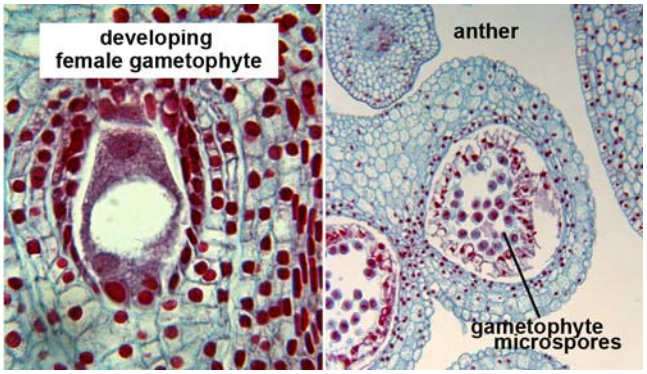

Figure 4. *Lilium* gametophytes showing developing female gametophyte inside ovule on left and developing male gametophytes (microspores) in anther on right. Photos by D. L Nickrent, through fair use license for educational use.

The most obvious change needed in the move to land is that of obtaining and maintaining water. This is not just a need for fertilization, but also a need in surviving daily life. Proctor (2007), in discussing our intellectual impediments to the consideration of gametophytes, challenges us to think about the reasons for their success. He points out that in the course of plant evolution, two strategies developed to cope with periods of low water. **Tracheophytes** (Figure 5) developed a water-conducting system that transports water from the roots in the soil to the leaves where water is constantly lost, an **endohydric** system (Figure 6). This not only brings a continuous supply of water for most plants under most conditions, but it also brings nutrients and plant metabolites such as hormones. Gametophytes, on the other hand, lack this organized system, although bryophytes do have vascular tissue in the center of the stems of many genera, but with few exceptions this system does not connect directly with the leaves. Rather, bryophytes suspend their metabolism when water is unavailable, being controlled by movement of an external water supply (**ectohydric**), and often maintaining a water supply in capillary spaces at the bases of leaves or among spaces of a tomentum, paraphyllia, or rhizoidal covering.

Figure 5. ***Geranium maculatum***, an example of the sporophyte of a tracheophyte. Photo by Janice Glime.

Figure 6. Xylem and phloem, the conducting cells of tracheophytes. The cells with red bands (stained) are **tracheids**. Photo by Spike Walker, Wellcone Images, through Creative Commons.

Proctor (2007) points out that minimizing water loss in bryophytes is regulated by boundary-layer resistances and energy budgets (see also Gates 1980; Proctor *et al*. 2007; Monteith & Unsworth 2013). For these small plants, the "intricacy of form" lies within this laminar boundary layer, a space where water vapor and CO_2 are able to move, albeit slowly, by molecular diffusion. This degree of intricacy may affect capillary storage, water movement, gas exchange, and CO_2 uptake.

Evidence in the past few decades indicates that the ancestor to the land plants, *i.e.*, to the bryophytes, was a member of the Coleochaetales, now placed in the Streptophyta, possibly *Coleochaete* (Figure 7; Graham, *et al*. 2012). This group of researchers experimented with two species of *Coleochaete*, normally an aquatic alga, to determine its ability to grow and reproduce in humid rather than aquatic environments. But to be truly terrestrial, this alga also needed to survive desiccation. And, to link it to ancestral fossils, it needed to produce degradation-resistant remains like those Cambrian fossils.

Figure 7. ***Coleochaete***, a likely ancestor of bryophytes. Photo by Yuuji Tsukii, with permission.

The land form of ***Coleochaete***, grown by Graham *et al*. (2012), did not look like its aquatic progenitors. Rather, it took on a form that had one-cell-thick lobes, was hairless, and formed hemispherical clusters. Furthermore, the chemically resistant cell walls did indeed resemble those of certain lower Palaeozoic microfossils that had remained a mystery. When these terrestrial forms were returned to water, they produced typical asexual zoospores and normal germlings. Even after several months of desiccation they retained their green coloration and structural integrity.

Bryo-ontogeny

An antithetic ballad, attempted free translation by Willem Meijer from the Dutch version of poet -bryologist Victor Westhoff in Buxbaumiella 40, August 1996 page 45.

As a toddler I am called protonema
A thread or thallus like structure without mom or pa
just creeping onwards without aim or thema
until I start to differentiate

and all sorts of tissues intercalate;
to anchor me to the soil I am using rhizoids
upwards I carry budding stems crowned with phylloids
those are kind of leaflets with or without dentation
they carry me to the realms of temptation
they call that the arrival of puberty
what makes me suffer during life
now I know emotion as a plant
because in my body swells a perianth,
makes me aware which fate awaits me
I can now supply some progeny
soon an antheridium is in the make
which makes sperm for a newborn baby embryo
from the egg cell of an archegonium.
Without much of a brake
my stomach becomes gradually rounder
and I am becoming the new founder
of the next generation.
A sporogonium grows in my body, a column, swank ,
poor of chlorophyll but provided with a strong will
producing my progeny in the spore sacks,
to follow up my hanky panky with phylogeny,
resulting in another phase with no resemblance
with the haploid plant.
That makes me a good moss after all, with a life that raises
me above the monotonous existence of people , pigs, dogs and cats
so tame and all the same just like a lion, a cub and a calf .
So our existence is always half by half.
We always look with amazement what the purpose is of the seta,
like an obelisk so full with admiration
for the godly gift of creation
with the change of generation.

Contributed by Wim Meijer, Bryonet 3 September 1999

Minimum Size

In our consideration of scale, let's consider the minimum size needs for bryophytes vs tracheophytes, especially seed plants. Raven (1999) suggests that a minimum size exists for a seed to succeed, and that such a minimum would be about 5 µg, the mass needed to become photosynthetically self-sufficient and to maintain its internal water content. This makes the assumption that the seedling must at the same time be able to contact the soil to obtain water and to extend into the air to obtain light. This latter need for water and light Raven suggests would require a minimum height of about 5 mm. If this is indeed true, then it is already obvious that some bryophytes, through **poikilohydry** (state of hydration controlled by external environment), have circumvented the need for 5 mm of height as there are a number of species that live with a shorter stature independently of any spore or seed.

Raven further estimated that for a seedling to succeed independently, it must attain 1.6 µg to permit it to reach this size and house the xylem tissue needed for its survival. He then stated that a spore with a radius less than 100 µm (thus a weight less than 4 µg fresh mass) will not reliably produce a gametophyte or succeed to produce a sufficiently large sporophyte to succeed. If we carry this need to plants with dominant gametophytes, *i.e.* bryophytes, then poikilohydric photosynthesis would be essential before the plant was large enough to become **homoiohydric** (state of hydration controlled by internal mechanisms). Thus, it is not just for fertilization, as we often read, but for the very survival of small plants that external water is needed, *i.e.* a poikilohydric strategy. It appears that **homosporous** (Figure 8) plants (having only one kind/size of spore) such as the bryophytes have greater desiccation tolerance in their gametophytes than do those of **heterosporous** (Figure 9) plants (bearing two genetically determined kinds of spores, generally large female and small male spores).

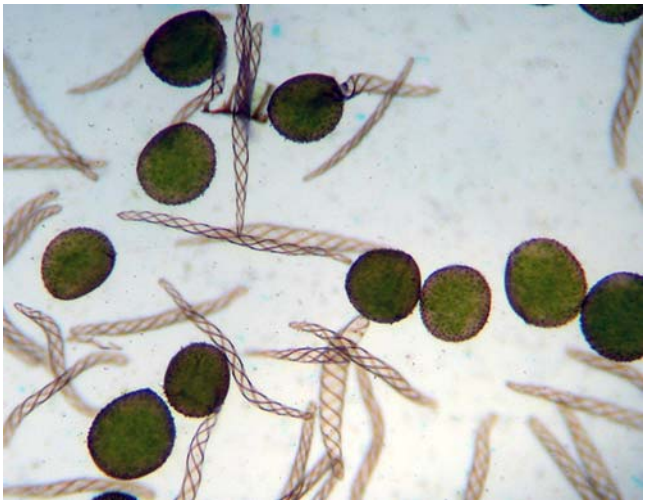

Figure 8. ***Conocephalum conicum*** spores & elaters, an example of **homospory** in liverworts. Photo by UBC Botany Website, with permission.

Figure 9. *Selaginella* strobilus showing small, male spores (left side) and large female spores (right side), a condition of **heterospory**. Photo by Ross Koning, with permission.

Proctor (2010) considers it infeasible for evolution and natural selection to produce a tracheophyte *de novo*. Rather, these must have evolved from a poikilohydric strategy. The drive toward tracheophytes could very likely have arisen from the limitations of two essential resources, water and CO_2. Whereas having air spaces within the leaves is common among tracheophytes, it is rare among bryophytes. Nevertheless, we find that a number of modern bryophytes also have such adaptations: **Marchantiales** (thallose liverworts; Figure 10), **Polytrichaceae** (haircap mosses; Figure 11), and sporophytes of **Bryophyta** (mosses; Figure 12) and **Anthocerotophyta** (hornworts; Figure 13) in particular.

Figure 10. ***Marchantia polymorpha*** with antheridiophores (male) and archegoniophores (female) on different plants. Note the thallus at the base. Photo by Robert Klips, with permission.

Figure 11. ***Polytrichastrum formosum***, a species that creates air spaces within the leaves by bending the leaf over stacks of cells (lamellae). Photo by James K. Lindsey, with permission.

Figure 12. ***Coscinodon cribrosus*** capsules (sporophytes) showing internal space. Photo by Michael Lüth, with permission.

Figure 13. ***Phaeoceros laevis*** showing sporophytes that contain interior spaces. Photo by Bob Klips, with permission.

Although the early atmosphere most likely provided higher levels of CO_2 (~10X; Berner 1998 in Proctor 2010) than our present-day environment, an epidermis, seen in many thallose liverworts, would protect against both mechanical damage and water loss. The development of the epidermis, followed by increasing cuticle development on both epidermal and non-epidermal plants, most likely marked the beginnings for a greater need for CO_2.

The complexity required to maintain a tree simply would not work to maintain a plant that is 100 times smaller and has a volume one millionth that of a tree (Proctor 2010). This smaller size necessarily means that the bryophyte as a plant has less interaction with the atmosphere, although its surface to volume ratio is greater, creating more area for interaction per unit volume. The non-linear nature of the bryophyte surface can create eddy diffusion that permits exchange between the bryophyte and its surroundings, but this can be minimized by the tightness of the lower portions of the plant. The selection pressures of strength and movement of gases and water in a tracheophyte leaf provide no constraint on the bryophyte. Thus, slow molecular diffusion is sufficient for heat and mass transfer in bryophytes. The one-cell-thick leaves of most bryophytes present two surfaces for diffusion of CO_2 into the leaf and directly to the cells that need it. Thus, being small has its advantages, albeit requiring quite different strategies.

Do Bryophytes Lack Diversity?

Early in 2011 Bryonetters questioned why bryophytes seem to lack extensive genetic diversity despite their long evolutionary history. I question the assumption that they lack diversity and argue that they have considerable diversity. For example, ***Ceratodon purpureus*** has an estimated leafy plant genome size of 240-270 Mbp, whereas the mustard plant *Ababidopsis thaliana* has only 100 Mbp (Lamparter *et al.* 1998). When we read about evolution among groups of plants or animals, most of the discussions center on morphological characters. But for these early land plants, biochemical characters may have been more important. Consider their abilities to withstand cold, heat, and desiccation or to deter herbivory and disease. The rate of genetic change in bryophytes has been as rapid as in tracheophytes. Wyatt (1994) pointed out that having a dominant gametophyte suggests that genetic variation should be low. However, he notes that isozyme data refute

that assumption, indicating that bryophytes display a range of variation like that of the diploid tracheophytes. Furthermore, having only one set of chromosomes permits the organism to express every gene innovation without the overriding effect of a complementary dominant gene. Asexual reproduction permits new genes, if not lethal, to be reproduced in populations without the need for compatibility in sexual reproduction.

One restriction to morphological diversity is the limitation of size. The bryophyte sporophyte size is limited by lack of structural support due to lack of true lignin. These sporophytes furthermore rely on non-lignified gametophytes for physical support and nutrition and are no doubt confined by genes that work best for the gametophytes.

But being small can be advantageous. Miniaturization has been a strategy that has permitted lycopods and horsetails to survive as water became more and more limited. In animals, miniaturization is typically accompanied by simplification or loss of morphological structures. For example, tropical miniature frogs have lost their teeth, have fewer toes, and have a reduced laryngeal apparatus. These structures simply don't fit in the smaller organism. Lack of space may cause whole organ systems to disappear, sometimes through crowding that alters embryonic development. In beetles, flies, and wasps, miniature organisms have evolved feather wings as an apparent response to that miniaturization.

While flowering plants were responding to the evolution of insects by evolving a multitude of adaptations to insect pollination, bryophytes were evolving a multitude of secondary compounds that protected them from herbivory from the ever-increasing insect herbivores. This was a necessity due to their slow growth and small size, while at the same time costing energy that might otherwise have been diverted to growth and complexity.

Nevertheless, one must wonder why some bryophytes with horizontal growth structure, thus negating the need for support, have not developed a greater morphological diversity. Perhaps they have "limiting genes" that restrain their growth rates or freeze their diversification with age. Gerson (1972) showed that the mite ***Eustigmaeus*** (as *Ledermuelleria*) ***frigida*** was unable to reproduce when fed bryophytes, suggesting that some sort of inhibitor was present. Such an inhibitor could permit the diversion of energy to making secondary compounds for defense.

But let's consider other alternatives to this bryophyte strategy. What would be lost if they became larger or more morphologically diverse? Would they still be able to develop from fragments if they had more specialized structures? It appears not, if we consider how rarely fragmentation of leaves of most seed plants can result in a new plant. For these gametophytic plants, this could be a very limiting loss.

The "Moss"

The term "moss" has a multitude of meanings in English, and even in other languages, the term referring to this group of plants likewise has multiple meanings. In Japanese, the word is "*koke*" (left) and means not only members of the Bryophyta, but also any of the small plants. Thus plants suitable for plantings under a bonsai tree are *koke*.

Beware also of Spanish moss (*Tillandsia usneoides*, a member of the pineapple family; Figure 14) and Irish moss (*Chondrus crispus*, a red marine alga; Figure 15). I was enticed to visit the Virgin Islands, where the locals insisted there were lots of mosses hanging from the trees, only to find Spanish moss.

Figure 14. ***Tillandsia usneoides***, known as Spanish moss, is a moss look-alike. Photo by Alfred Osterloh, through Creative Commons.

Figure 15. ***Chondrus crispus***, named Irish moss. Photo by Seaweed Collections Online, through Creative Commons.

In his *Mosses in English Literature*, Sean Edwards (1992) has this to say: "The word moss has always been used to refer to boggy ground as well as to the plants themselves, and both aspects of the word almost certainly have the same origin in northern European languages (Bradley 1908). Quotations that refer clearly to boggy ground have been excluded, but see the section *Stagnation and barrenness*. Onions (1966) says that the first “formal” reference in English to moss meaning the plant rather than boggy ground, is found in the 12th century; this may refer to the '*Durham Plant-Name Glossary*' (1100-1135), but see Aelfric (993-996)."

"It is to be expected that the word moss should include all bryophytes (as it does in other European languages), although only Saint Winefride's Moss (Caxton, 1485) can be identified as a liverwort. Moss may also be used loosely to encompass algae and mould, as well as other moss-like plants such as Iceland Moss (a lichen) and Spanish Moss (a flowering plant, see Longfellow, Townsend). Grey moss probably usually refers to lichen (Clare; Longfellow; Masefield; Spenser), but generally quotations that are clearly not referring to bryophytes have been omitted."

There is no doubt that in usage by Robert Burns in Scotland and northern England the word moss refers to bogs and is based on the Danish word *mose*, meaning bog (Jim Dickson, Bryonet 4 November 2010; Simon Laegaard, Bryonet 5 November 2010). But in Danish, the word referring only to bryophytes is *mos*. In English, Moss is used in place names, such as Flanders Moss and Lenzie Moss, again meaning a boggy place (Jim Dickson, Bryonet 4 November 2010).

In German, the word for the bryophyte is *Moos*, but in Bavaria, Austria, Switzerland, and South Tyrol (Italy) the same word also means flat boggy peatland (Michael Häusler, Bryonet 4 November 2010). Such use often shows in the names of places, reminiscent of their past, but often long-gone mossy habitat.

What's in a Name?

Discussions about names, cladistics, priorities, and use of numbers to designate a taxon remind me of a conversation between Alice and a gnat in Lewis Carroll's *Through the Looking Glass*, Chapter 3:

'What sort of insects do you rejoice in, where YOU come from?' the Gnat inquired.
'I don't REJOICE in insects at all,' Alice explained, 'because I'm rather afraid of them — at least the large kinds. But I can tell you the names of some of them.'
'Of course they answer to their names?' the Gnat remarked carelessly.
'I never knew them do it.'
'What's the use of their having names' the Gnat said, 'if they won't answer to them?'
'No use to THEM,' said Alice; 'but it's useful to the people who name them, I suppose. If not, why do things have names at all?'
'I can't say,' the Gnat replied.

We need names to communicate; without communication, there is no purpose for science. So while I might see the utility of using numbers to designate relationships among taxa, they are not a suitable way to communicate in other contexts. I think that both the lay public and the scientific community will agree with me that species names must remain with us, no matter how efficient the number system may be for phylogenetic purposes.

But the naming system is fraught with problems. As we learn more about organisms, we find they have been placed in a genus where they have no close relatives. Or their birth certificates that provide a legitimate name and description, after being lost for a long time, resurface with an earlier name that has priority. These problems we must continue to deal with, and we have made provisions in our nomenclatural code to do so.

But in our attempts to clean up our naming, and to be consistent with conventions recently adopted by the zoologists, we have begun to erode long-standing concepts of higher taxonomic levels. I discovered to my horror that the bryophytes have been moved to the umbrella of Equisetopsida! This has stripped a very workable system in the plant kingdom of its two highest taxonomic levels for the bryophytes! I suppose it is my 50 years of understanding the Bryophyta that makes this idea so repugnant to me, but in this treatise, and elsewhere, I refuse to subscribe to that system and will continue to use Bryophyta as a phylum.

Perhaps I am as stubborn as Humpty Dumpty, again quoting from Lewis Carroll's *Through the Looking Glass*:

"When I use a word," Humpty Dumpty said in rather a scornful tone, "it means just what I choose it to mean – neither more nor less." "The question is," said Alice, "whether you can make words mean so many different things." The question is," said Humpty Dumpty, "which is to be master – that's all."

I am not so stubborn as to ignore all recent (think 50 years) name changes. I fully support breaking the traditional bryophytes into three, or perhaps four, phyla (divisions). And I fully support the standardizations of names for the higher taxonomic levels. Hence, I will not be using some of the traditional names because they have been replaced with names that follow the type concept to the very top of the classification (except perhaps kingdom). To bring you up to speed, here are the type-based names for phylum and class with their proper endings:

Phyla/Divisions

I shall use the term phylum (pl. phyla) throughout, in this case being consistent with terminology used for animals. The terms division and phylum are equally correct for plants. The division names I am using are not a new concept. Following the type concept in higher levels of classification was proposed while I was still a graduate student (see Cronquist *et al.* 1966). But it is only now reaching relatively consistent usage in bryological publications.

Marchantiophyta (Figure 8): liverworts only, previously class Hepaticae in the phylum Bryophyta; more recently also called Hepatophyta, but that name does not follow the type concept; classes include **Marchantiopsida** (Figure 8) and **Jungermanniopsida** (Figure 16)**.**

Anthocerotophyta (Figure 13): hornworts, previously named Anthocerotae as a class of liverworts in Bryophyta; now has one class, **Anthocerotopsida**.

Bryophyta (Figure 11-Figure 12): mosses only, previously class Musci in the phylum Bryophyta; has six classes currently: **Takakiopsida** (Figure 17), **Sphagnopsida** (which may be considered a separate phylum, the **Sphagnophyta**; Figure 18), **Andreaeopsida** (Figure

19), **Andreaeobryopsida** (Figure 20), **Polytrichopsida** (Figure 11), and **Bryopsida** (comprising more than 95% of the species; Figure 12).

Sphagnophyta (Figure 18): Considered by Crum (2001) to warrant a separate phylum, but still considered by most authors as a class of **Bryophyta** (**Sphagnopsida**) in the **Bryophyta**; two genera only - ***Sphagnum*** (Figure 18) and ***Ambuchanania*** (Figure 21).

Figure 16. ***Porella vernicosa***, a member of the Jungermanniopsida. Photo by Masanobu Higuchi, with permission.

Figure 17. ***Takakia lepidozioides***, a member of phylum **Bryophyta**, class **Takakiopsida**. Photo by Rafael Medina, through Creative Commons.

Figure 18. ***Sphagnum fallax*** with capsules, a member of **Sphagnopsida**. Photo by J. K. Lindsey, with permission.

Figure 19. ***Andreaea cf mutabilis*** with capsules, a member of **Andreaeopsida**. Photo by Niels Klazenga, with permission.

Figure 20. ***Andreaeobryum macrosporum***, member of **Andraeaobryopsida**. Photo from University of British Columbia, Botany website, with permission.

Figure 21. ***Ambuchanannia leucobryoides***, a member of Sphagnopsida. Photo by Lynette Cave, with permission.

Role of Bryology

Bryologists have a role today that far exceeds that of any prior time in history. Organizations and individuals interested in protecting the environment have realized that we know little about the contributions of the groups of small organisms, plant or animal or microscopic organism, to diversity, either in their own right or in stabilizing the diversity of larger organisms. Ecosystem biologists are realizing that bryophytes may have a major role in nutrient cycling, water retention, and water availability.

Physiologists and even medical scientists are realizing the potential of the bryophytes in understanding gene function and in producing needed proteins. Global climate modellers are realizing that massive peatlands make substantial contributions to the modification of global temperatures and water movement. And everyone involved is realizing that we know very little about this fascinating and important group of organisms. The time is now!

Summary

Scale is a major evolutionary driver for bryophytes, bringing both successes and constraints. Small size, coupled with slow growth, make them susceptible to destruction by herbivory, but their evolution of a myriad of secondary compounds have rendered them inedible or undesirable by many would-be herbivores.

Small size and lack of lignified vascular tissue have enhanced the selection for physiological means of drought survival, including metabolic shutdown and the ability to revive with a minimum or at least sustainable level of destruction.

The role of bryophytes in the ecosystem, a largely overlooked field of study, may be significant despite their small size. ***Sphagnum*** alone may be the genus that sequesters the most carbon of any genus on Earth. And their role in housing small organisms that ultimately increase the diversity of their predators could be vital. Ecologists are increasingly recognizing that even at their small scale they are important contributors to the ecosystem and can no longer be ignored.

Although there is ultimately a minimal size to house the essential contents of a eukaryotic cell, bryophytes seem to lack the minimal size needed to house the photosynthetic and water transport needs of a seedling. A spore less that 100 μm in diameter can provide sufficient energy for a new bryophyte to get started.

Water is clearly needed by bryophytes, but rather than maintaining hydration, they are able to become metabolically inactive, exercising an ectohydric strategy that holds water in capillary spaces while they dry slowly. Being small itself seems to be a strategy to conserve water, as seen in the miniature of lycopods and horsetails.

Bryophytes seem to lack morphological diversity, but they nevertheless exhibit as much genetic diversity as do tracheophytes, expressing it in a biochemical diversity that protects them against desiccation, heat, cold, and herbivory.

As we learn more about the evolutionary relationships of the bryophytes, we find it convenient to change the names of the groups where we place them. The group once known as the **Bryophyta** has now been accepted by most bryologists to be three phyla (divisions): **Marchantiophyta**, **Anthocerotophyta**, **Bryophyta**. But we may still see further divisions, particularly into Sphagnophyta or Takakiophyta. So despite the inconvenience of keeping track of the names and their equivalencies, the names will keep changing, keeping us on our toes as we learn by these changes.

Acknowledgments

I am grateful to Anne Stoneburner for a conversation decades ago on the diversity of bryophyte genetics. Michael Proctor, a constant source of information and guidance, has been an inspiration for this volume. And Nancy Slack has kept me encouraged through her friendship, research, collaboration, and most importantly, her invitation to the first Andrews Foray, where I learned that bryophyte identification can stump even the world-renowned experts. Thank you to John Steel for reporting several typos to me. I appreciate Jan Galkowski for numerous discussions by email and for alerting me to comprehensive references on biophysical ecology. Llo Stark reviewed the chapter and made valuable suggestions.

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CHAPTER 2-1
MEET THE BRYOPHYTES

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CHAPTER 2-1
MEET THE BRYOPHYTES

"The beauty there is in mosses must be considered from the holiest, quietest nook." Henry David Thoreau. Natural History of Massachusetts. 1842. Photo by Janice Glime.

Definition of Bryophyte

Before we can further consider these small organisms in any context, we all need to speak the same language. In the 1600's, Jung considered mosses to be aborted plant fetuses (Crum 2001)! Today, bryophytes occupy a position within the Plant Kingdom and may even be considered to have their own subkingdom. Recent genetic information is causing us to rethink the way we classify bryophytes, and more to the point of this book, what we consider to be a bryophyte.

The hornworts (Figure 1), sharing their small size and independent, dominant gametophyte and dependent sporophyte with the mosses and liverworts, have been considered by most systematists now to be in a separate **phylum** (*i.e.* division), the **Anthocerotophyta** (Shaw & Renzaglia 2004). Most bryologists also now agree that the liverworts should occupy a separate phylum, the **Marchantiophyta** (previously known as Hepatophyta, Hepaticophyta, and class Hepaticae; Figure 2). This leaves the mosses as the only members of **Bryophyta** (formerly known as the class Musci; Figure 3). Together, the mosses, liverworts, and hornworts are still considered by the English name of **bryophytes**, a term having no taxonomic status and to be used in its broad sense in this book. Some have suggested for them the subkingdom name **Bryobiotina**.

Figure 1. ***Anthoceros agrestis***, a representative of **Anthocerotophyta**. Photo by Bernd Haynold through Creative Commons.

Figure 2. ***Marchantia polymorpha*** thallus with antheridiophores (male) and archegoniophores (female), a representative of **Marchantiophyta**. Photo by Robert Klips, with permission.

Figure 3. ***Bryum capillare*** with capsules, representing the type genus of **Bryophyta**. Photo by David Holyoak, with permission.

Nomenclature

The **type concept** of naming has dictated the current names for these phyla. It follows the premise that the first named taxon within a category becomes the type of that category. Hence, ***Bryum*** (Figure 3) is the type genus in the family **Bryaceae**, and as the first named genus [along with many others at the same time in Hedwig (1801)] in its order, class, and phylum/division, it is the type all the way to the top, giving us the name **Bryophyta** for the mosses. By the same premise, ***Marchantia*** (Figure 2) became the base name for **Marchantiophyta** and ***Anthoceros*** (Figure 1) for **Anthocerotophyta**.

It was necessary to define a starting date for bryophyte names to avoid finding older publications that would predate and force changes in names. Linnaeus (1753), who first organized the binomial system of names for organisms and provided the names for many common animals and plants, had little understanding of bryophytes. He put *Potamogeton* (an aquatic flowering plant; Figure 4) and ***Fontinalis*** (an aquatic moss; Figure 5) in the same genus. Hence, the publication by Hedwig (1801) became the starting point for moss names. Linnaeus recognized and named ***Marchantia*** and did not include any incorrect placements as liverworts, so his 1753 publication is recognized as the starting date for liverworts.

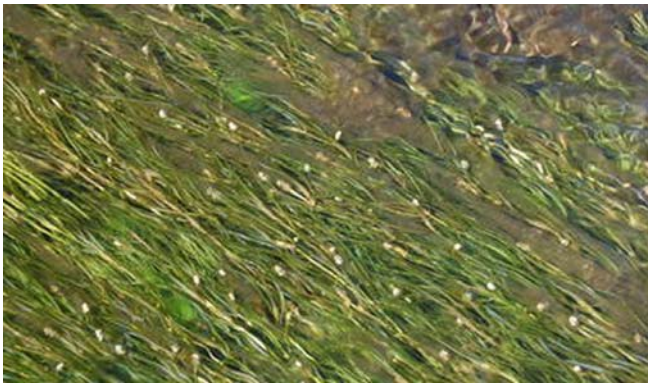

Figure 4. *Potamogeton turionifer*, in a genus that was originally included in the moss genus ***Fontinalis***. Photo by C. B. Hellquist, through Creative Commons.

Figure 5. ***Fontinalis antipyretica***, looking superficially similar to the *Potamogeton* species in the above image. Photo by Andrew Spink, with permission.

The term bryophyte was coined centuries ago when all three groups were in the same phylum, and moss, liverwort, and hornwort served to distinguish the **Musci**, **Hepaticae**, and **Anthocerotae**, respectively. Once the type concept came into use for higher categories, ***Bryum*** was the type for the mosses and hence the basis of the name **Bryophyta**. Thus, it kept its old phylum name and **Marchantiophyta** became the liverwort phylum based on ***Marchantia*** as the type (see Stotler & Crandall-Stotler 2008). So we are sort of stuck with the old meaning of bryophyte and new meaning of **Bryophyta**.

Recently the name **Sphagnophyta** has come into occasional usage, with Howard Crum (2001; Séneca & Söderström 2009) as a primary proponent of its rank as a phylum/division. Although there are a number of unique characters in this group, this separation has not yet received widespread acceptance.

What Makes Bryophytes Unique?

Among the world of plants, the bryophytes are the second largest group, exceeded only by the Magnoliophyta – the flowering plants (350,000 species). Comprised of 15,000 (Gradstein *et al.* 2001) – 25,000 species (Crum 2001), they occur on every continent and in every location habitable by photosynthetic plants. Of these, there are currently 7567 accepted binomials for liverworts and hornworts (Anders Hagborg, pers. comm. 23 February

2017). And, one could argue that bryophyte gametophytes are among the most "elaborate" of any phylum of plants (Renzaglia *et al*. 2000).

Bryophytes seem all the more elaborate because of their small size. Some bryophytes are only a few millimeters tall and have but few leaves, as in the mosses ***Ephemeropsis*** (Figure 6) and ***Viridivellus pulchellum*** (Crum 2001). The more common ***Buxbaumia*** (Figure 7) has a large capsule on a thick stalk, but only a few special leaves protect the archegonia; the plant depends on its protonema (and later the capsule) to provide its photosynthate. The liverwort thallus of ***Monocarpus*** (Figure 8) is only 0.5-2 mm in diameter. At the other end of the scale, the moss ***Polytrichum commune*** (Figure 10) can attain more than half a meter height in the center of a hummock and ***Dawsonia superba*** (Figure 10) can be up to 70 cm tall with leaves of 35 mm length (Crum 2001) and be self-supporting. ***Fontinalis*** species (Figure 10), supported by their water habitat, can be 2 m in length.

Figure 6. ***Ephemeropsis trentepohlioides***, one of the very small mosses. Photo by David Tng <www.davidtng.com>, with permission.

Figure 7. ***Buxbaumia aphylla***, known as Aladdin's lamp or bug-on-a-stick moss, is a moss dependent upon its protonema for energetic support of the sporophyte, which sports a thick stalk and robust capsule. Originally, its lack of leaves caused scientists to consider it to be a fungus. Photo by Michael Lüth, with permission.

Figure 8. ***Monocarpus sphaerocarpus***, a liverwort with a tiny thallus 0.5-2 mm in diameter. Photo by Helen Jolley, with permission.

Both green algae (Chlorophyta) and other members of the plant kingdom share with the bryophytes the presence of **chlorophylls *a*** and ***b***, **xanthophyll** and **carotene,** storage of photosynthate as **true starch in plastids**, sperm with **whiplash flagella**, and **cellulose cell walls**. But bryophytes and other members of the plant kingdom possess **flavonoids** (a group of pigments that absorb UV light), whereas only some members of the charophytes among the algae possess these. The unique thing about the mosses and liverworts among members of the plant kingdom is that all the vegetative structures, the leaves (or thallus), stems, and **rhizoids** (filamentous structures that anchor the plant), belong to the **1*n*** (**gametophyte**) generation, having just one set of chromosomes to dictate their appearance and function. By contrast, the analogous structures are **sporophytic** (**2*n***) in the non-bryophytic plants (**tracheophytes**), with the gametophyte becoming smaller and smaller as one progresses upward in the phylogeny of the plant kingdom. In fact, in the bryophytes, the **sporophyte** is **unbranched** and arises from archegonia located on the gametophyte (Figure 9)! The gametophyte **lacks secondary growth** and **meristematic tissues**, growing new tissue instead from a **single apical cell** (Crum 1991).

Figure 9. ***Bryum alpinum*** showing sporophyte attached to the gametophyte. Photo by Michael Lüth, with permission.

Graham and Wilcox (2000) suggest that the alternation of generations progressed from presence of egg and sperm

to retention of zygotes on the parent, resulting in embryos. The plant subkingdom **Bryobiotina** (bryophytes) is separated from the Kingdom Protista by the presence of **multicellular sexual reproductive structures** protected by a **jacket layer** (**antheridia** for sperm and **archegonia** for eggs), as opposed to unicellular antheridia and oogonia in the algae, and the presence of an **embryo** (Figure 15), the forerunners of which can be found in the charophytes (Kingdom Protista; Graham *et al.* 1991; Mishler 1991).

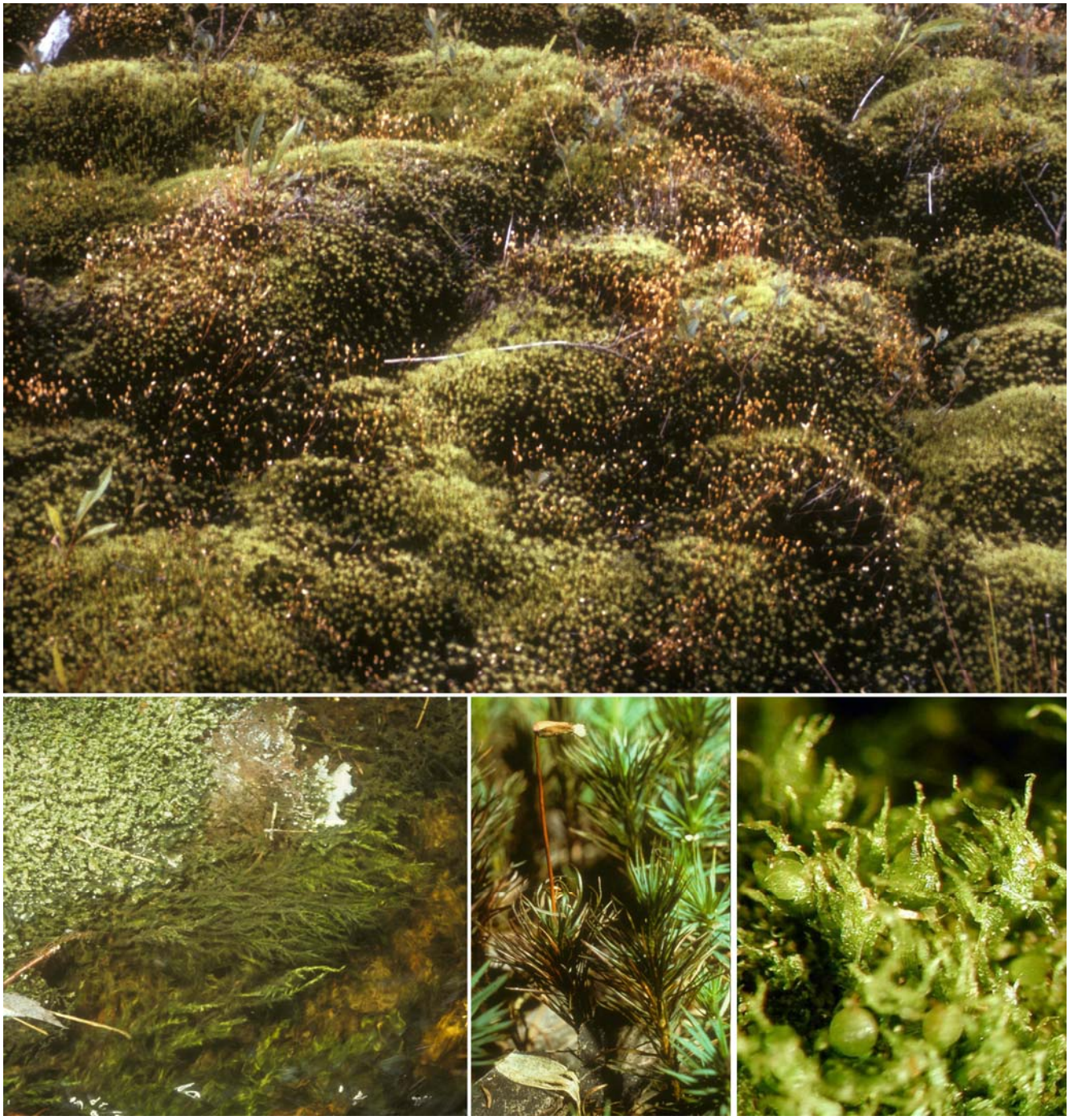

Figure 10. Bryophytes vary in size from the large ***Polytrichum commune*** (**upper**), ***Fontinalis novae-angliae*** (**left**), and ***Dawsonia superba*** (**middle**) to the minute ***Ephemerum minutissimum*** (**right**). Photos by Janice Glime; ***Ephemerum*** by Michael Lüth, with permission.

Who are the Relatives?

Their nearest algal relatives appear to be members of the **Charophyta** (Figure 11). Although the charophyte reproductive structure is still only a single cell, that cell is surrounded by corticating cells (Figure 11) that give the egg and **zygote** multicellular protection. Nevertheless, the zygote fails to develop further until leaving its parent. In the green alga ***Coleochaete*** (Figure 12-Figure 13), however, the female reproductive organ becomes surrounded by overgrowths of cells from the thallus following fertilization, and the zygote divides (Figure 14), becoming multicellular. In bryophytes, this embryo remains attached to the gametophyte plant body and continues to develop and differentiate there (Figure 15). Recognition of these similarities to those of embryophytes has led to many studies that have revealed other similarities between charophytes and bryophytes. Less obvious among these, and perhaps of no ecological significance, is the presence of **spiral motile sperm bodies** with **anterior whiplash flagella** (Figure 16), a trait shared with nearly all tracheophyte groups and these same few charophyte algae (Duckett *et al*. 1982). In the bryophytes, these sperm are **biflagellate**, as they are in several other groups.

Figure 11. ***Chara*** antheridia (red) and oogonia (brown) showing the surrounding cells (**corticating cells**) that begin to resemble the multicellular antheridia and archegonia of bryophytes. Photo by Christian Fischer, through Creative Commons.

Figure 12. ***Coleochaete*** thallus. Photo by Yuuji Tsukii, with permission.

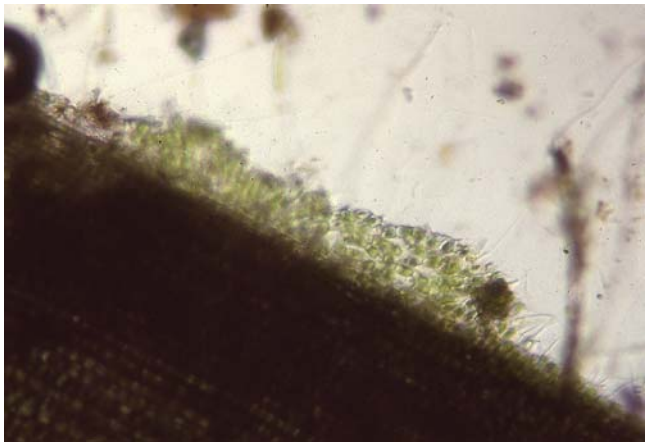

Figure 13. ***Coleochaete*** thallus from a side view on a vascular plant. Photo by Janice Glime.

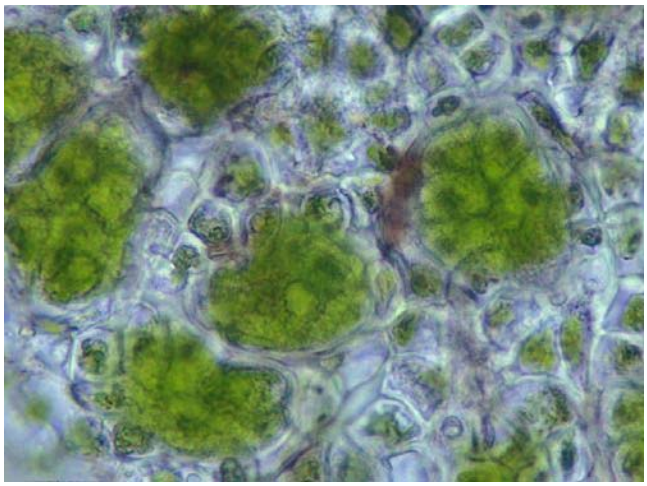

Figure 14. ***Coleochaete conchata*** with dividing zygotes. Photo by Charles F. Delwiche. Permission pending.

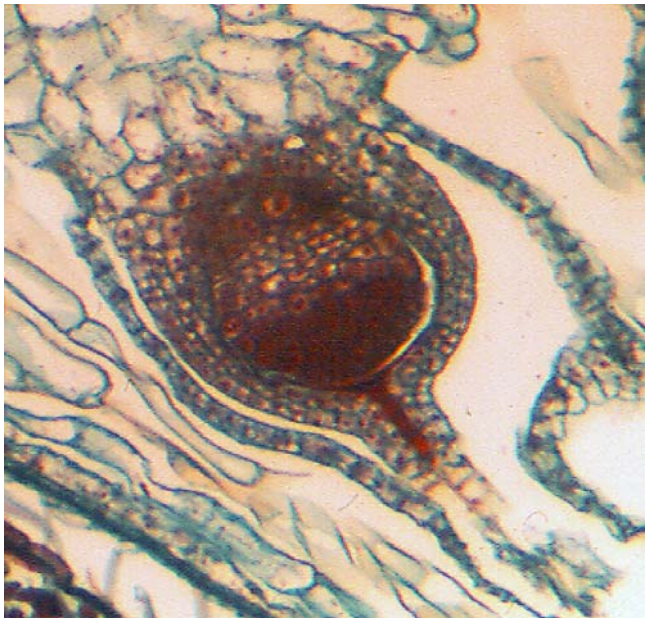

Figure 15. ***Marchantia*** (Phylum **Marchantiophyta**, Class **Marchantiopsida**) archegonium with embryo attached to parent gametophyte tissue. Photo by Janice Glime.

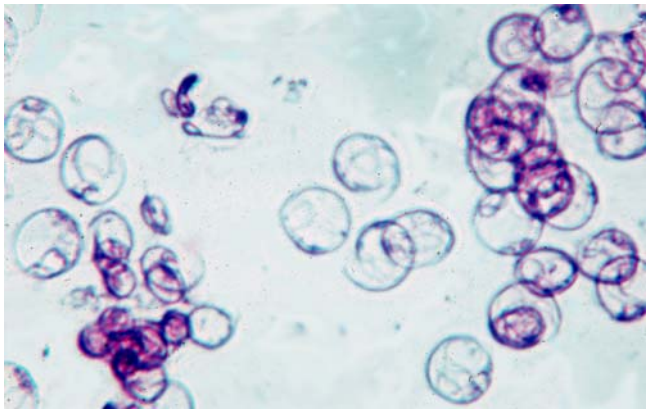

Figure 16. Stained sperm of Bryophyta, having spiral body and two flagella. Photo by Janice Glime.

One advancement with implications for land colonization, visible through transmission electron microscopy, is the presence in both bryophytes and charophytes of a layer on the outside of gametophyte cells that resembles early developmental stages of the **cuticle** of tracheophytes (Cook & Graham 1998). The sporophyte was already known to possess one (Proctor 1984). Although bryophyte gametophytes were considered to lack a cuticle or possess one only as thin as that on the interior cells of tracheophyte mesophyll (Proctor 1979), Cook and Graham (1998) showed that all three relatively primitive bryophytes tested [***Monoclea gottschei*** – thallose liverwort (Figure 17), ***Notothylas orbicularis*** – hornwort (Figure 18), and ***Sphagnum fimbriatum*** – peatmoss (Figure 19)] have an osmophilic layer on their outer walls. The nature of this layer in these bryophytes and in the charophyte *Nitella gracilis* suggests that some features of a plant cuticle existed when bryophytes first arose. Those taxa that are mostly **endohydric** (having most water movement occurring within the plant) were recognized earlier to have at least a thin leaf cuticle (Lorch 1931; Buch 1945), and in some species this cuticle seems to be similar to that of tracheophytes (Proctor 1979). This may account for the difficulty of getting such endohydric mosses as ***Plagiomnium*** (Figure 20) and ***Polytrichum*** (Figure 21) to rehydrate. Yet the **ectohydric** taxa (those that move and gain their water across the plant surfaces above ground) seem to lack such protection from water loss (Proctor 1979), not surprisingly, since that which would keep water in would also keep water out.

Figure 17. ***Monoclea gottschei***, a thallose liverwort with an osmophilic layer on its outer walls. Photo by Filipe Osorio, with permission.

Figure 18. ***Notothylas orbicularis***, a hornwort with an osmophilic layer on its outer walls. Photo by Michael Lüth, with permission.

Figure 19. ***Sphagnum fimbriatum***, a peat moss with an osmophilic layer on its outer walls. Photo by David T. Holyoak, with permission.

Figure 20. ***Plagiomnium cuspidatum*** dry, with a waxy coating that makes it difficult to rehydrate it. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 21. ***Polytrichum piliferum*** in a dry state. Water is slow to penetrate these leaves with a thin waxy coating. Photo by Janice Glime.

Two Branches

It appears that once those algae ventured onto land to survive outside a water medium, two different journeys began, at least 450 million years ago (Stackelberg 2006). At that point, the bryophytes diverged from the **polysporangiate plants** [having multiple sporangia on a single sporophyte and including *Aglaophyton* (Figure 22), which lacks tracheids]. The polysporangiate plants soon gave rise to the **tracheophytes**. Nevertheless, approximately half the bryophyte genes are the same as those of tracheophytes. Some of these genes, however, are no longer used and remain as fossil genes, never to be turned on by modern bryophytes. Experiments now at the Missouri Botanical Garden and other places are attempting to unravel the phylogeny of bryophytes by turning on the latent genes to discover what that will do to the morphology and function (Zander 2006). Hopefully this will help us identify their closest relatives. The bryophytes (**Bryobiotina**) share with the tracheophytes the development of an **embryo** within a **multicellular reproductive organ** (Figure 23), a covering of **sporopollenin** on their spores, and the presence of **flavonoids**.

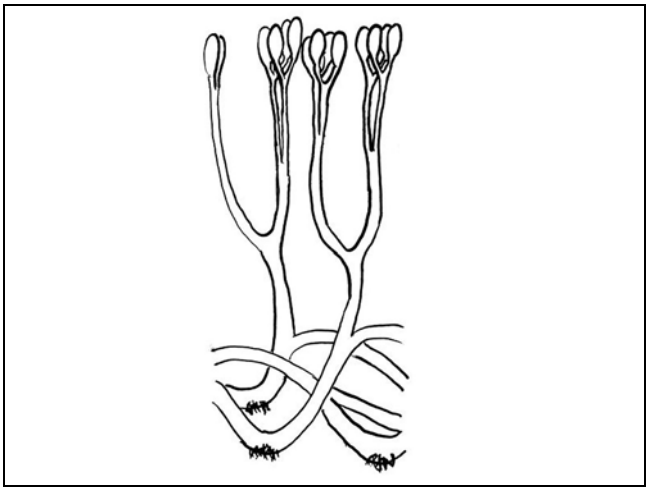

Figure 22. ***Aglaophyton*** reconstruction. Drawing by Griensteidl, through Creative Commons.

Figure 23. Multicellular archegonia nestled at the tip of the moss ***Orthotrichum pusillum***. Photo by Bob Klips, with permission.

Limitations of Scale

Limited by Scale – and No Lignin

When thinking about bryophytes, one necessarily has to think on a new scale from the more familiar way of looking at **tracheophyte** (traditionally called "vascular plant") vegetation. One contribution to their small size is their lack of **lignin** (Hébant 1977), limiting their size to that which their nonlignified tissues can support. Note that the presence or absence of lignin in bryophytes is still controversial. Downey and Basile (1989) found evidence for it in sporophytes of the thallose liverwort ***Pellia epiphylla***, and lignin-like compounds occur in some peristomes (Crum 2001), but conclusive gametophyte evidence seems still to be lacking. Siegel (1969) reported true lignin in ***Dawsonia*** and ***Dendroligotrichum***, which Hébant (1974, 1977) questioned. Edelmann *et al*. (1998) found evidence for a lignin-like substance in the cell walls of the moss ***Rhacocarpus purpurascens***, but some of the specific peaks expected with lignin were absent. Erickson and Miksche (1974) likewise found phenolic cell wall contents but showed that lignin was definitely absent in six species of mosses and two liverworts. Many bryophytes possess phenolic compounds similar to lignin. The problem, at least in part, is the absence of a clear definition of lignin. In bryophytes, the "lignin-like" compounds are polyphenolics that are most likely tri-hydroxybenzene derivatives (Wilson *et al*. 1989), whereas those of tracheophytes are polymers of phenylpropenols and have different precursors. The bryophyte polyphenolics do not even seem to be ancestral precursors of the tracheophyte lignins (Savidge 1996).

In 2011, Espiñeira *et al*. suggested that the syringyl lignins, known from some liverworts, were at first "developmental enablers" and only later became

strengthening compounds in tracheids. Lewis (1980) suggested that it was the ability of boron to avoid sequestration in carbohydrate complexes that made it available to catalyze the lignin pathway and later, germination of pollen. Groundwork for this dichotomy between tracheophytes and non-tracheophytes depended on genetic selection for sucrose as a carbohydrate storage product in Chlorophyta because sucrose forms only weak bonds with borate, unlike those of other algal sugar groups.

Being without lignin imposes other limits on plants as well. It means they have no tracheids or vessels, hence lack the type of conducting system known in those plants we will call **tracheophytes**, or more traditionally, those known as vascular plants. This implies that bryophytes lack true leaves, hence making it more appropriate to call their photosynthetic extensions **phyllids** (but few bryologists do, choosing to call them leaves). The bryophytes are more appropriately termed **non-tracheophytes** (rather than non-vascular plants) because many do indeed have vascular tissue, possessing **hydroids** (Figure 24) that confer much the same function as xylem, but lack tracheids or vessels. And some, probably many more than we have detected, have **leptoids** (Figure 24), the moss version of phloem. Many moss stems possess what we often term a **central strand** (with or without hydroids, but with elongate cells) that functions in conduction, and because of its greater density of smaller cells may also provide support. But for the leafy liverworts, even these gametophytic conducting elements seem lacking.

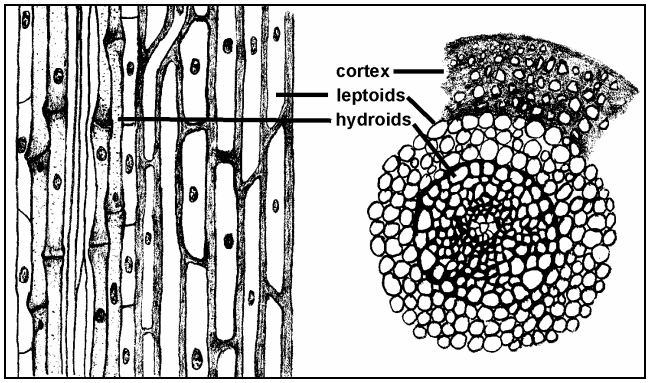

Figure 24. Longitudinal and cross sections of a stem with hydroids and leptoids, typical of taxa such as the Polytrichaceae. Drawings by Margaret Minahan, with permission.

The lack of a sophisticated tracheid conducting system limits or slows the movement of water within the plant, and the lack of roots, substituted in most bryophytes by the non-vascular **rhizoids** (Figure 25-Figure 27), makes obtaining water from beneath difficult to impossible, although they may help in obtaining nutrients from a larger soil volume, as well as slowing the process of desiccation. With these structural limitations, many bryophytes are necessarily **desiccation tolerant** (unlike most people's perception), an advantage replaced in most tracheophytes by drought avoidance.

Limited by Scale – Forced to Be Simple

Niklas (1997) suggests that maintaining hydration necessarily imposes a small size on bryophytes. But this could be a question of the chicken or the egg. Being small prevents bryophytes from having a complex conducting system, and lacking a complex conducting system keeps them from attaining great size. Bonner (2004) demonstrates that in general larger entities, whether they are organisms or societies, have a greater division of labor. In plants, this is manifest in a greater variety of cell types. Thus, smaller organisms are necessarily simpler.

Hedenäs (2001) studied 439 mosses to determine the types of characters that differed most. Two complex functions seem to dominate their structural differences: characters related to water conduction and retention, and characters related to spore dispersal. If we consider what might be most important when structural diversity is limited, success of these two attributes would seem to be paramount.

Figure 25. ***Fontinalis*** showing leaves (phyllids) with a clump of rhizoids at the node. Photo by Janice Glime.

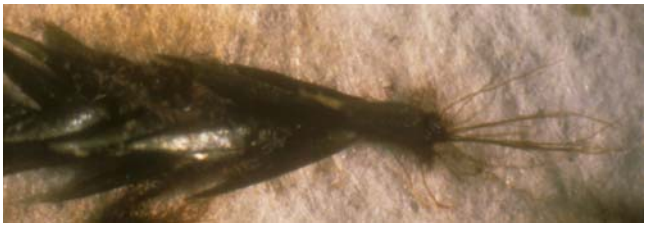

Figure 26. ***Fontinalis*** plant with rhizoids attached to paper towel. Photo by Janice Glime.

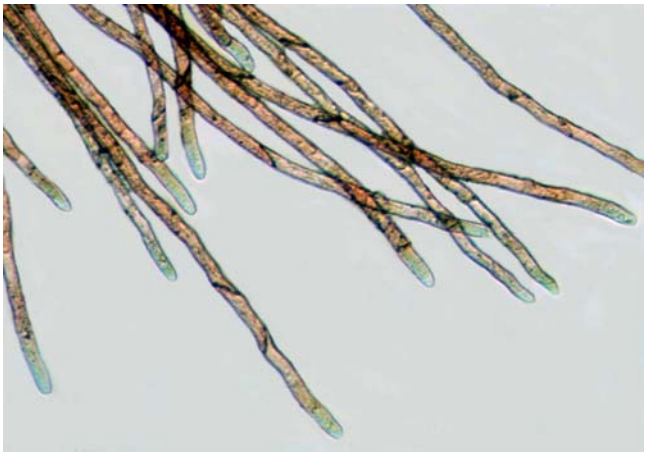

Figure 27. Microscopic view of rhizoids of the brook moss, ***Fontinalis***, showing multicellular structure and diagonal crosswalls. Photo by Janice Glime.

Limited by Scale – Needing to Swim

One might suggest that getting a sperm to an egg without windborne pollen necessarily limits the size of a gametophyte on land. This suggestion certainly could be supported by the total absence of large terrestrial gametophytes in any plant group. Since the sperm must find a film of water in which to swim, and cannot swim very far, it must rely on short stature and various splashing mechanisms in order to reach the female reproductive structures, especially when they occur on another plant. Such a limit is supported by the small size of all gametophytes in the plant kingdom.

Limited by Scale – and Housing an Embryo

But does the life cycle have anything to do with size? Raven (1999) contends that it does. The algae have a minimum size determined by that which can house the genome, the smallest being about 0.65 µm in diameter, but lacking a nucleus. With the addition of both a cell membrane and nuclear membrane, a minimum size of 0.95 µm is required (Raven 1999). This lower size limit has implications for a minimum size of spores, with even larger requirements for impervious walls and extracellular decorations. But the bryophytes have added to these minimum requirements an **embryo** (Figure 28), the structure that separates them exclusively from the Kingdom Protista. To qualify as an embryo, the **zygote**, that new cell that results from sexual union of sperm and egg, must remain inside the reproductive organ of its parent and divide, developing into the initial stages of the new generation by mitotic divisions (Figure 28). Hence, this necessarily means a larger size, with at least a one-cell-thick container around the embryo. The structural organization necessary to define an embryo requires that these organisms be at least 100 µm in diameter for both life cycle generations (**1*n* gametophyte** and **2*n* sporophyte**) (Raven 1999).

On the other end of the scale, some marine algae attain the size of a giant sequoia, reaching 60 m in length and weighing more than 100 kg (Raven 1999). In their watery environment, it would seem their only constraint is the mechanical stress of such a large size being tossed about by the action of waves. But once on land, new constraints are imposed – not only is support necessary, but also plants need a means to distribute water and other substances. The bryophytes, like the algae, are predominantly **poikilohydric**. That is, their state of hydration is controlled by the environment; they cannot control it internally. It is this trait that makes it necessary for them to 1) live where they are constantly moist, 2) complete their life cycle to the production of dormant spores before the season becomes dry, or 3) be desiccation tolerant. For some "mysterious" reason, primarily poikilohydric, desiccation-tolerant embryophytes are unable to sustain a body size greater than 1 m tall (Raven 1999). Their **homoiohydric** (state of hydration controlled by internal mechanisms in plant) tracheophyte counterparts are able to maintain their homoiohydric status through such features as gas spaces, stomata, cuticle, internal water-conducting system, and water and nutrient uptake structures, structures that Raven (1999) estimates require a height of at least 5 mm.

Figure 28. Young embryo of the liverwort ***Marchantia polymorpha*** showing early multicellular stage enclosed within the archegonium. Photo modified from Triarch by Janice Glime.

Thus, it is with this necessary smallness in mind that we must envision the ecological role of the bryophytes. As we explore possible adaptations of bryophytes, we will see that size will indeed play a role in the structural adaptations available and that while constrained in size, physiological and biochemical adaptations abound. Even with their vascular limitations, bryophytes, and mosses in particular, can occupy large surface areas on rocks, soil, logs, and tree trunks. In boreal zones, they can virtually form the substrate around lakes. And they can spread vegetatively to occupy a large area from the minute beginnings of a single branch, a single spore, or a single fragment. If the genetics were known, perhaps it is some moss that is truly the largest "single" organism clone in the world!

Higher Classifications and New Meanings

"We need to keep firmly in mind that biological classification is a human construct, to be adopted for the uses we find most compelling in light of current understanding" (Mishler 2009). Hence, there has been a continuing battle for systematists to attain the stability needed for ease of communication and the changes needed as new knowledge shows our old concepts to be in error. Those of us who have already been through change during the early stages of our careers are reticent to re-organize our minds around a new set of names and relationships presented late in our professional lives. Nevertheless, as scientists we recognize the importance of being objective, critical thinkers, challenging and improving on existing ideas.

Chase and Reveal (2009) argued that current classification of bryophytes is not compatible with the APG III classification (Angiosperm Phylogeny Group III system) and suffers from inflated taxonomic ranks. They kindly stated that this problem was especially true for angiosperms. BUT, they further stated that if the major algal clades are considered classes, then all land plants, INCLUDING BRYOPHYTES, should be included in one class: the Equisetopsida! This system is primarily based on molecular taxonomy and does not yet seem to have entered widespread use among the bryologists. No one likes to see their group diminished, and this demotes the bryophytes from a subkingdom to three subclasses: **Anthocerotidae**, **Bryidae**, and **Marchantiidae**.

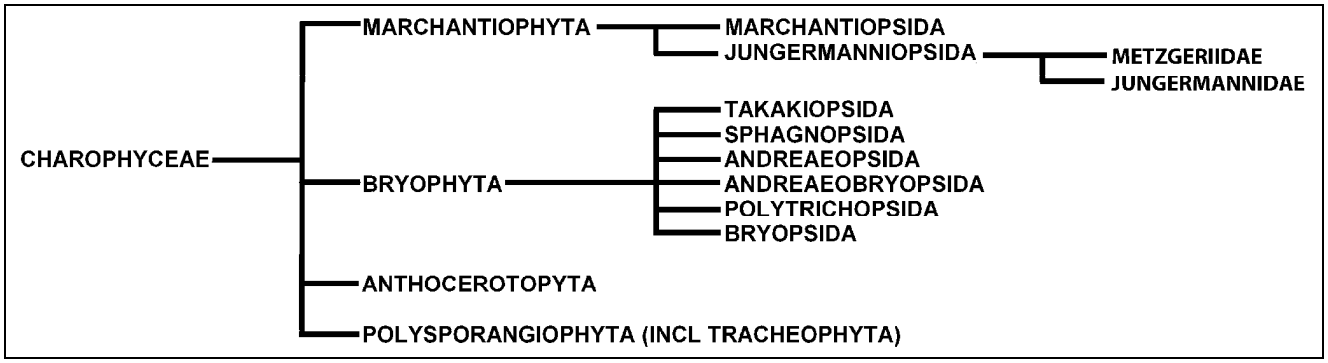

Figure 29. Schematic representation of the **Bryobiotina** phyla and classes related to other members of the Plant Kingdom (**Polysporangiophyta**), based on Shaw & Goffinet 2000.

New Meanings for the Term Bryophyte

Perhaps all this discussion of Equisetopsida vs using Bryophyta as a phylum will go away if the new PhyloCode (PhyloCode 2010) is widely adopted by the scientific community. Among the principles defined by this code, number 4 states "Although this code relies on the rank-based codes [i.e., International Code of Botanical Nomenclature (ICBN)]... to determine the acceptability of preexisting names, it governs the application of those names independently from the rank-based codes. Item 6 in the Principles states that "This code will take effect on the publication of *Phylonyms: a Companion to the PhyloCode*, and it is not retroactive. The PhyloCode is online at <http://www.ohio.edu/phylocode/>. The printed version and the Companion Volume will be published by UC Press. For a detailed example of a Phylocode-style classification in bryology see Fisher *et al*. 2007. Here are the names that will be applied in *Phylonyms* for the clades relating to the bryophytes:

Viridiplantae
- Chlorophyta (most of the former green algae)
- Charophyta (some of the former green algae and land plants)
  - Phragmoplastophyta (Coleochaete + Chara + embryophytes)
    - Streptophyta (Chara + embryophytes)
      - Embryophyta (land plants)
        - Hepaticae
        - Musci
        - Anthocerotae
        - Tracheophyta (etc.)

This appears to be a long step backwards, but one can argue that it lends stability in a field that is constantly changing how it views relationships. Brent Mishler reported to Bryonet, 30 January 2010, that the group of authors for these names in *Phylonyms* chose to "apply the traditional names **Hepaticae**, **Musci**, **Anthocerotae** specifically because of their long use. And, the lack of a rank-based ending is a bonus. We did not use **'Bryophyta'** or **'Bryopsida'** anywhere, because of the ambiguity people have mentioned."

This brings us back to our earlier discussion of the term "bryophyte." Mishler states that he does agree with Jon Shaw that "bryophyte" (small "b") is a useful term for talking about plants with a somewhat similar biology, like "prokaryote," "invertebrate," or "algae," but there is no room for it in formal cladistic classification.

But not all bryologists are enamored with cladistics. I am still wary of them because I do not think we know enough about the genetic structure to adequately interpret the data, at least in some cases. As Richard Zander put it on Bryonet (31 January 2012), there are two ways it can be wrong – bad theory and lack of adequate sampling. "Bad theory means cladistics is not the way to analyze evolution because it just clusters end members of a tree, with no discussion of what the nodes of the tree mean, *i.e.,* totally ignoring macroevolution." Inadequate sampling has been a problem of molecular systematics, but this is being rectified by time and continuing research on more and more species, making the interpretation more reliable.

As a teacher, and for my own learning, I find grouping things to be invaluable. The molecular-based classification of genera into families (see Shaw & Goffinet 2000) has made more natural groupings and thus made it much easier to understand the relationships, permitting one to place something new into a group (genus, family) and thus more easily discover its identity. Until now, our International Code of Botanical Nomenclature has guided our naming of both species and higher categories.

These rules of nomenclature are laid out in The International Code of Botanical Nomenclature (McNeill *et al*. 2006), renamed in 2011 to the International Code of Nomenclature of Algae, Fungi, and Plants (Miller *et al*. 2011). These rules are reviewed and modified as needed every six years at the meeting of the International Botanical Congress. Of note are changes in 2011 to permit taxon descriptions in **English** or in Latin and to permit electronic publication of descriptions and names of new taxa in specified types of electronic journals and books (See Penev *et al*. 2010).

Differences within Bryobiotina

Within the **Bryobiotina**, there are distinct differences among the phyla and classes. Those morphological differences will be discussed in the next chapter, but from an evolutionary perspective, one must also consider the biochemical evidence, which will play a major role in their ecological capabilities. Those **Marchantiophyta** that possess oil bodies synthesize **mono-**, **sesqui-**, and **diterpenes** as their **terpenoids**, as do some

Anthocerotophyta, whereas Bryophyta produce **triterpenes** (Crum 2001). All of these more closely resemble the terpenoids of tracheophytes rather than those of algae. Marchantiophyta commonly have **flavonoid glycosides**, whereas only about one-fourth of the Bryophyta do. **Lunularic acid**, acting as a growth regulator and dormancy factor, occurs in all orders of Marchantiophyta, but in no Bryophyta or algae. Members of Anthocerotophyta lack lunularic acid and have a different pathway for the **degradation of D-methionine** from that of Marchantiophyta. And ***Sphagnum*** seems to be a non-conformist all around, with a complete acetylization of D-methionine, a process differing from that of other mosses and all liverworts, and its flavonoids also differ from those of other **Bryobiotina** and from tracheophytes as well. **Bryophyta** have **ABA**; **Marchantiophyta** do not. Even the cell wall components differ between mosses and liverworts, with mature moss (**Bryophyta**) cell walls staining with aceto-orcein, but not liverwort (**Marchantiophyta**) cell walls (Inoue & Ishida 1980).

As you will see, morphological evidence, coupled with this biochemical evidence, has led Crum (2001) to create the phylum **Sphagnophyta** (Figure 19). Nevertheless, when data from morphological, developmental, anatomical, ultrastructural, and nucleotide sequence characters have been used together, they have supported the concept of a **monophyletic** origin (single origin) for the Bryophyta, including ***Sphagnum*** (Rykovskii 1987; Newton *et al.* 2000).

Perhaps the bigger question that remains to be answered is whether the bryophytes are truly the first and most primitive land plants, or if they are instead derived from other land plant embryophytes by reduction. In any case, it appears that they were derived independently from the tracheophytes as we know them (Hébant 1965). Their absence of lignin to protect them from UV light and other aspects of their simple structure suggests they would have been unable to survive on land until the development of larger plants to provide shade and maintain moisture. Raven (2000) suggests that such protective compounds, common throughout the rest of the plant kingdom, may have been lost by reduction. Rather, based on their CO_2 affinities through use of **RUBISCO** (enzyme that catalyzes carbon fixation in plants), it would appear that all the **embryophytes** (*i.e.* all members of plant kingdom) may have evolved under the influence of the high levels of atmospheric CO_2 present in the late Lower Palaeozoic.

Infraspecific Taxa

Bryologists recognize several types of infraspecific taxa. These include **subspecies**, **varieties**, and **forms**. Wikipedia (2016) states that in botanical nomenclature, **variety** (abbreviated var.; in Latin: *varietas*) is a taxonomic rank below that of **species** and **subspecies** but above that of **form**. In addition to these, one can find the terms race, microspecies, and cryptic species.

Darwin (1859) struggled with defining a **species**, and it hasn't gotten any easier with our much greater understanding of evolution. But these terms are useful in our understanding of ecology.

While generally a **species** is a group of potentially interbreeding organisms, isolated reproductively from other units considered to be species, that is not a practical definition because we do not have the resources to determine it each time we find an organism. On the other hand, genetic variation and founder populations may look different from their parent populations. In attempting to indicate differences among our study locations, we are forced to apply one of the above terms to distinguish our organisms.

These differences in appearance can lead us to falsely naming different varieties as different species, while on the other hand a similar appearance may hide differences in functionality that result from physiological varieties. Both morphological and physiological differences result from genetic variations. Molecular techniques are helping us to delineate some of these microspecies or cryptic species, and some of our seemingly same species are revealing their differences through these techniques. Hence, we are left with the task of indicating these differences in our studies.

It is therefore useful to understand the current differences among these infraspecific terms. The term **subspecies** is generally used to define populations that are disconnected, *i.e.*, are **allopatric**. The assumption is that these allopatric populations have been disconnected for some time and now differ genetically. They may be unable to interbreed if they are re-connected, but they currently are unable to interbreed due to geography. A subspecies is exemplified in ***Acrolejeunea securifolia*** (Figure 30). This species has four allopatric subspecies, each differing from the others by 1-2 morphological characters (Gradstein 1975). Their morphs are located in eastern Malesia, Australia, New Caledonia, and French Polynesia.

Figure 30. ***Acrolejeunea securifolia***, a species with several subspecies. Photo by John Braggins, with permission.

A **variety** has a genetic difference that can occur within a population or between populations. It is presumed that the varieties are able to interbreed. It differs from a **form** in that a variety has inherited traits, whereas a form is modified by its environment and its trait differences are not inherited. Generally, a variety is **sympatric**, *i.e.*, occurs within overlapping distributions.

This leaves us with **microspecies** and **cryptic species**. As the term **cryptic species** implies, the characters are hidden and cannot be identified by a field bryologist. They are species that cannot interbreed, but that cannot be recognized as morphologically different. These include genetic differences that are expressed as differences in physiology and biochemistry and can be identified as differences by using molecular techniques. Cryptic species

are exemplified in the desiccation-tolerant ***Grimmia laevigata*** (Figure 31) (Fernandez *et al*. 2006). This is a cosmopolitan species, occurring on every continent except Antarctica and occupying bare rock in a broad range of environments. To do this, it includes variants that survive extremes of very high temperatures, prolonged desiccation, and high UV B. These differences are the result of multiple alleles.

Figure 31. ***Grimmia laevigata***, a species with cryptic species distinguished by physiological differences. Photo by Hermann Schachner, through Creative Commons.

A **microspecies** has a genotype that is perpetuated by **apomixis**, a trait exhibited by a number of bryophyte species. Hence, a microspecies is a small population with limited genetic variability. But bryophytes complicate this by having many species that rely largely on asexual reproduction, but that are also capable of sexual reproduction. ***Fontinalis*** (Figure 5) species are typical of this strategy, relying largely on fragmentation, but capable of having sexual reproduction. ***Pohlia*** is even more complex, having species with bisexual gametophytes, unisexual gametophytes with no specialized asexual propagules, and unisexual gametophytes with specialized asexual propagules. Shaw (1999) screened 50 populations representing eleven species. Using isozyme analysis, he determined that the seven propaguliferous species are less distinct from one another than are the four non-propaguliferous species.

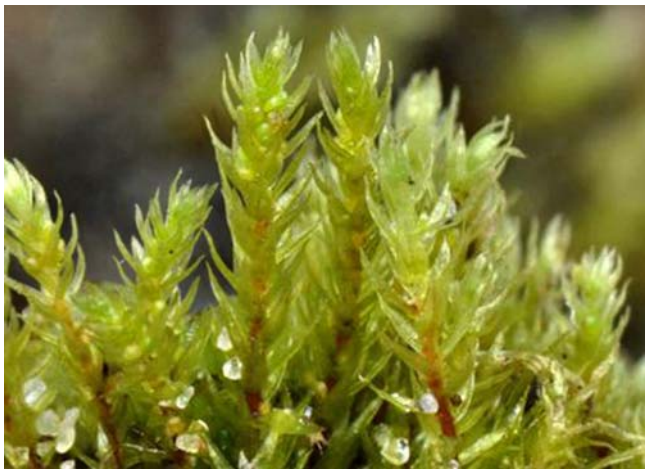

Figure 32. ***Pohlia bulbifera*** with bulbils in upper leaf axils. Photo by J. C. Schou, through Creative Commons.

The use of barcoding is an attempt to remove subjectivity from identification and to provide a tool for those not trained in the taxonomic group, while exposing the crypto- and microspecies. However, identification of species by genetic markers is a young science and many caveats remain (Naciri & Linder 2015). Only when large and multiple populations have been barcoded can we reliably determine species boundaries. We must understand the range of variability within a species, and ideally understand what can breed with what. This is further complicated by the large number of species that can reproduce without having genetic mixing, *i.e.*, those reproducing asexually.

Given that differences in habitats can result in both selection pressures against certain traits, and differences in form resulting from environmentally influenced expression of physiological and morphological traits, ecologists are able to contribute to our understanding of species by their detailed observations of these expressions as they relate to habitat.

Summary

Traditional bryophytes are classified into three phyla (Marchantiophyta = liverworts, Bryophyta = mosses, and Anthocerotophyta = hornworts) and can be placed in the subkingdom Bryobiotina. The bryophytes (**Bryobiotina**) share with the tracheophytes the development of an **embryo** within a **multicellular reproductive organ**, a covering of **sporopollenin** on their spores, and the presence of **flavonoids**. Bryophytes have **chlorophylls *a*** and ***b***, store their photosynthate as **true starch** (but may also use oils and lipids). They have spiral sperm bodies with two flagella.

Bryophytes differ from tracheophytes in having a dominant gametophyte supporting a dependent sporophyte. They **lack meristematic tissue**, **lignin, tracheids** (but have **hydroids** with similar function), and **sieve cells** (moss **leptoids** are similar enough to sieve cells that some biologists consider them to be such). The expected consequences of lack of lignin are not only small stature, but also lack of tracheids and vessels, hence the term **non-tracheophytes**.

Some biochemical differences support creation of the phylum **Sphagnophyta**, but others interpret total characters to support monophyletic origin of **Bryophyta**, including ***Sphagnum***, but not liverworts or hornworts. Some researchers consider that **Bryobiotina** may have been derived from tracheophytes by reduction and loss of lignin.

Infraspecific taxa include subspecies (geographically separated), varieties (genetically determined morphological differences with interbreeding), **forms** (environmentally determined), **cryptic species** (non-interbreeding with no morphological differences), and **microspecies** (having genotypes perpetuated by apomixis).

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CHAPTER 2-2
LIFE CYCLES: SURVIVING CHANGE

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CHAPTER 2-2
LIFE CYCLES: SURVIVING CHANGE

Figure 1. ***Dicranum majus*** showing leafy gametophyte and attached sporophyte. Photo by Michael Lüth, with permission.

The General Bryobiotina Life Cycle

Perhaps one could explain most of plant and animal ecology by explaining all the factors that contribute to and control the life cycle and development of individuals of a species. These interwoven abilities and responses to signals determine who arrives, who survives, and who leaves any given community. It is in this context that plants and animals are able to contend with the changing seasons – they have programmed into their life cycle the means by which to escape when the going gets rough. Thus, it is appropriate that we continue our discussion of bryophyte ecology with a thorough understanding of the limits imposed upon a species by its developmental processes and life cycle. For bryophytes, these limits affect different stages and in different ways from those same limits on the lives of the **tracheophytes** (lignified plants).

As Niklas (1976) points out, plants "oscillate between morphological and biosynthetic adaptive impasses." For bryophytes, the limitations imposed by the lack of lignin prevented them from accomplishing significant size and thus limited their morphological development. However, they have achieved tremendous variety in their biochemical development, often having capabilities rare or unknown in tracheophytes. This development is manifest in their biochemical protection from interactions with other organisms, including herbivores, bacteria, and fungi, as well as their ability to survive desiccation, temperature extremes, and low light levels unavailable to tracheophytes in caves and deep water. In addition, their unique biochemically driven life cycle strategies and physiological behaviors permit them to occupy a wide variety of niches – even those polluted with sulfur or heavy metals. It is indeed true that bryophytes have tremendous genetic diversity (see Krazakowa 1996), expressed in their highly variable and rich biochemistry. It appears that our definition of a species as being reproductively isolated is inadequate for representing the variety of biochemical forms that exist among bryophytes. May Father Hedwig save us from those who want to identify them by numbers!

Fortunately for the systematists, the life cycles differ among the phyla and classes in the anatomy of their specific reproductive structures and the environmental and biochemical controls that regulate them. But bryophytes have in common the characteristic of retaining the zygote within an archegonium, separating them from all algae.

Dominant Generation

One of the ways that plants manage to survive as "immobile" organisms, yet are able to survive the severe changes of seasons, is by having different life cycle stages that are adapted to different conditions. As we progress through the protist and plant kingdoms, we see that most green algae (Chlorophyta), especially in freshwater, spend most of their time in the water and most of them have only one set of chromosomes (**1*n***). Although there is much disagreement about evolutionary pathways among photosynthetic organisms, all evolutionary biologists seem to agree that this **life strategy** came first, with both invasion of land and dominant **2*n*** organisms coming later. (The **dominant generation** refers to the most conspicuous and generally the most long-lived generation.) This 1*n* stage is termed the **gametophyte generation** (1*n* or **haploid** generation that reproduces by gametes in plants) because the generation ends when it produces **gametes** (sexual reproductive structures that have one set of chromosomes and must unite with another of the same species but opposite strain to continue the life cycle) that join to form the 2*n* **zygote** (2*n* cell resulting from fusion of male and female gametes, *i.e.* from fertilization; Figure 2). Hence, the zygote is the first structure of the 2*n* stage or **sporophyte generation** [**diploid** (2*n*) generation that reproduces by **meiospores** in plants; Figure 2]. The **meiospores** in many bryophytes are able to survive many years in a dry state, thus permitting at least some taxa to live in habitats that only occasionally get moisture.

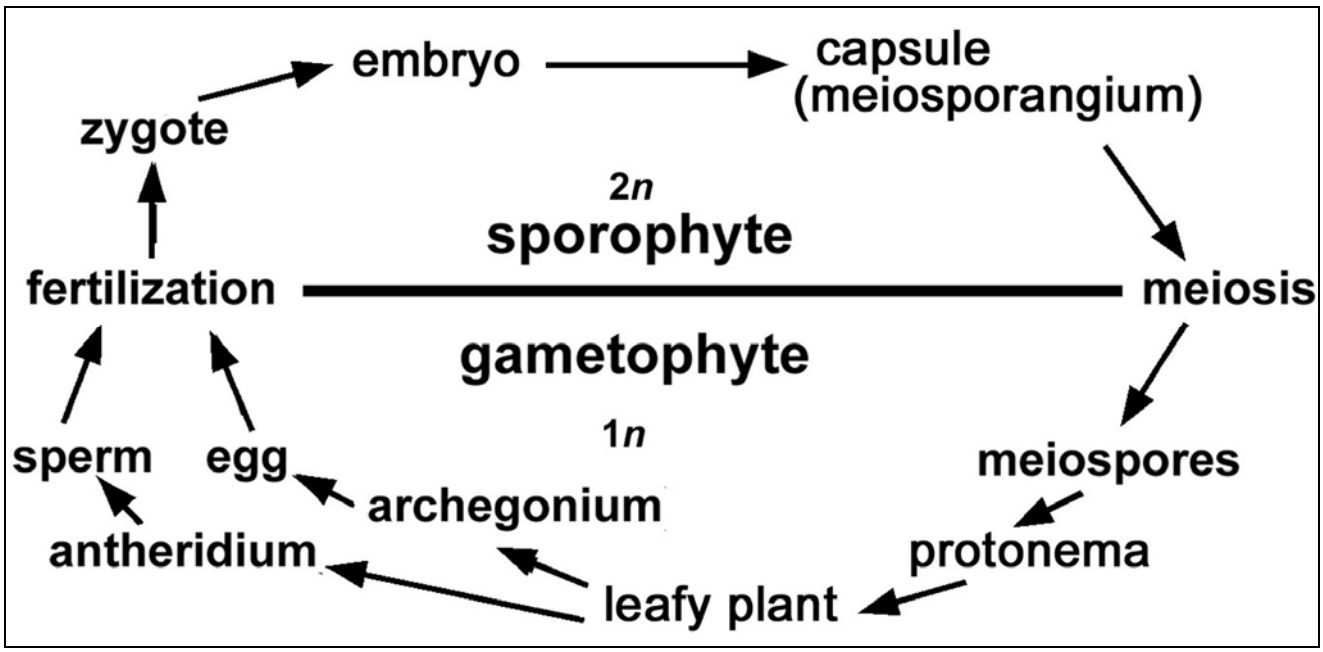

Figure 2. Basic sexual life cycle of a bryophyte. Gemmae or other propagules, not shown here, can occur on the leafy plant or on the protonema (pl. **protonemata:** alga-like, usually filamentous, stage that develops from spores of bryophytes), giving rise to the same generation as its origin. Diagram by Janice Glime.

The Life Cycle

The dominant **1*n*** condition (the **nuclear condition**, referring to having 1 **set** of chromosomes, where *n* represents the number of chromosomes in a complete set) begins as a **spore** (reproductive cell that develops into plant without union with another cell, usually 1-celled; Figure 3), produced by **meiosis** (reduction division; nuclear process in which each of four daughter cells has half as many chromosomes as parent cell; produces spores in bryophytes and other plants), hence a **meiospore** (Figure 3-Figure 4). Linnaeus observed these spores and considered this "fine powder" to be of the same sort as the "dust" liberated from anthers of flowers (Farley 1982). Indeed he was close, although the pollen grain (dust) is already a mature gametophyte in the flower, having divided a few times within the spore wall, whereas the spore of the moss or liverwort is the very first cell of that generation.

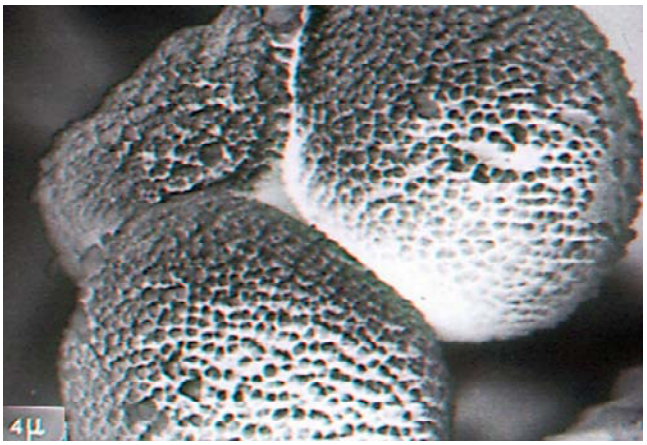

Figure 3. SEM of tetrad of meiospores of aquatic moss ***Fontinalis squamosa***, with fourth spore hidden beneath. Photo by Janice Glime

Figure 4. ***Fontinalis squamosa*** spore germination. Photo by Janice Glime.

Bryophytes differ in their life cycle behavior in another way as well. They have two gametophyte phases with very different **life forms** and often very different requirements for growth. Prior to development of a leafy shoot (or thalloid plant body in many liverworts), they exist in a **protonema** stage (*proto* = first; *nema* = thread; Figure 5-Figure 10) that develops from the germinating spore (Figure 4). In most mosses, this protonema is truly the "first thread," forming a mat of green filaments (Figure 8-Figure 10), but in most liverworts (Figure 5-Figure 6) and **Sphagnopsida** (Figure 7) it becomes more thalloid after a few cell divisions.

Figure 5. Young thalloid protonema of the thallose liverwort ***Cyathodium***. Photo courtesy of Noris Salazar Allen.

Figure 6. Thalloid protonema of liverwort ***Sphaerocarpus texanus***. Photo from Plant Actions through Eugenia Ron and Tom Sobota, with permission.

Figure 7. ***Sphagnum*** protonemata on a branch of ***Sphagnum***. Photo by Andras Keszei, with permission.

Figure 8. Threadlike protonema of the moss ***Funaria hygrometrica***. Photo by Janice Glime.

Figure 9. Moss ***Grimmia orbicularis*** protonema. Photo from Plant Actions through Eugenia Ron and Tom Sobota, with permission.

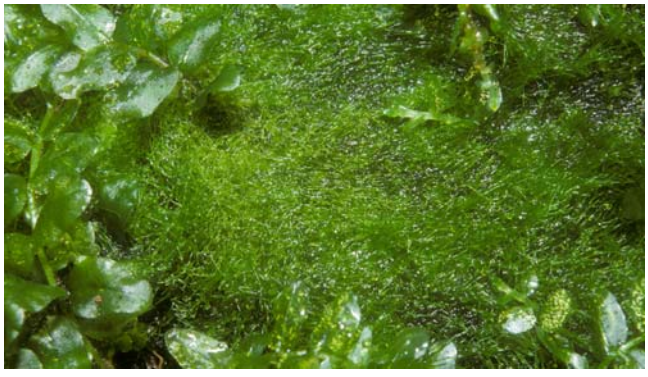

Figure 10. Protonemata of the moss ***Plagiomnium*** sp. Photo by Janice Glime.

These protonemata produce **buds** (Figure 11-Figure 12) and grow into thalloid (thallose liverworts) or leafy plants. These plants are **haploid** (containing one set of chromosomes; 1*n*); thus they are the **gametophyte generation** of the life cycle.

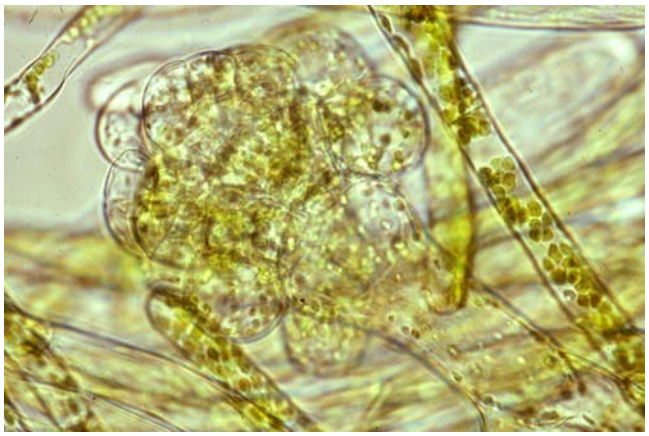

Figure 11. Moss ***Funaria hygrometrica*** protonemal bud. Photo by Janice Glime.

Figure 12. Moss protonema with bud. Photo by Janice Glime.

The mature gametophytes are the leafy plants you see (Figure 13-Figure 19). They produce **antheridia** (sing. **antheridium**; male gamete containers; sperm-containers; Figure 20-Figure 27) and **archegonia** (sing. **archegonium**; multicellular egg-containing structures that later house embryo; Figure 31-Figure 37) on the same or different plants, depending on the species. Antheridia can number up to several hundred in ***Philonotis***, but a much smaller number is typical (Watson 1964). Archegonia are generally few, but can reach as many as 20-30 in ***Bryum***.

Figure 13. Leafy liverwort ***Porella navicularis*** male branches. Photo from botany website at the University of British Columbia, with permission.

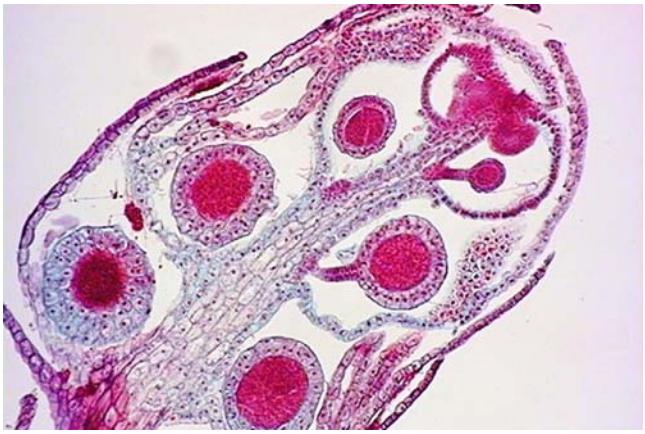

Figure 14. Leafy liverwort ***Porella*** antheridia in antheridial branch. Photo by Paul Davison, with permission.

Figure 15. ***Porella navicularis*** female with arrow indicating perianth. Photo from botany website at the University of British Columbia, with permission.

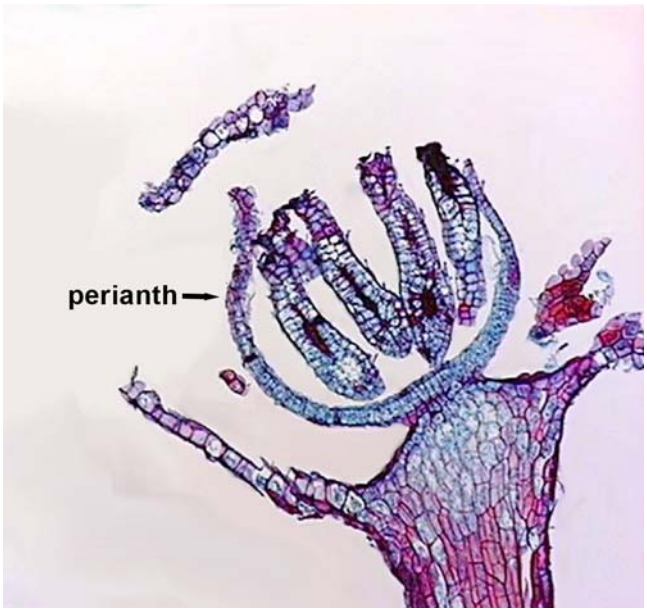

Figure 16. ***Porella*** archegonia in perianth. Photo by Paul Davison, with permission.

Figure 17. ***Bryum capillare*** males with antheridia in a splash platform. Photo by Dick Haaksma, with permission.

Figure 18. ***Polytrichum juniperinum*** males with antheridial splash cups. Photo by David Holyoak, with permission.

Figure 19. ***Polytrichum ohioense*** female showing lack of any special structures at the stem tips, but tight leaves looking somewhat budlike. Note that unopened male splash cups can be seen around the periphery of the clump at the right. Photo by Janice Glime.

The **antheridium** consists of a layer of cells, the **sterile jacket**, surrounding the **spermatogenous** cells (Figure 21), *i.e.*, those that divide to form the **spermatocytes** (sperm-containing cells). If you remember that this is the gametophyte generation and, therefore, already in the haploid state, you will realize that the **sperm** (Figure 27-Figure 30), produced in large numbers within an **antheridium** and released as a mass (Figure 28), and the **egg** (non-motile female gamete that is larger than motile sperm), produced singly within an **archegonium**, must be produced by **mitosis** (ordinary cell division).

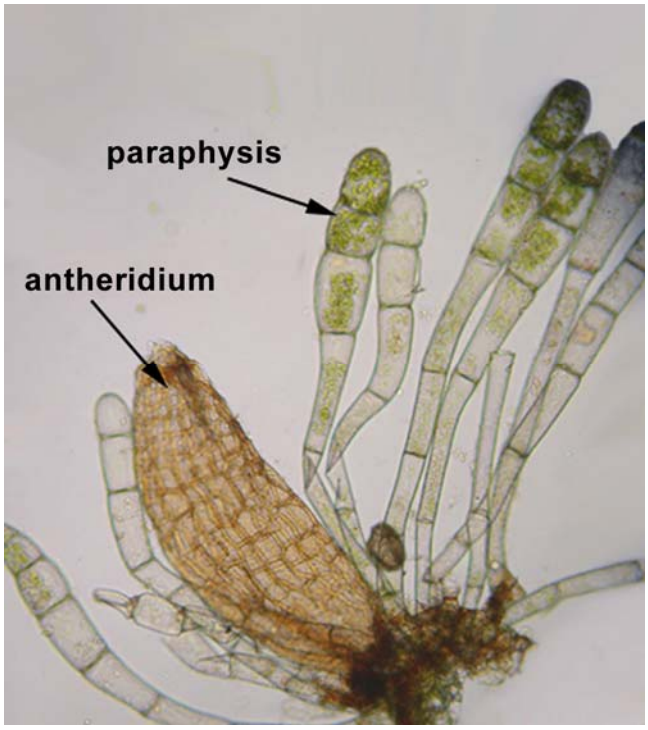

Figure 20. ***Plagiomnium insigne*** antheridium and paraphyses. Photo from Botany 321 website at the University of British Columbia, with permission.

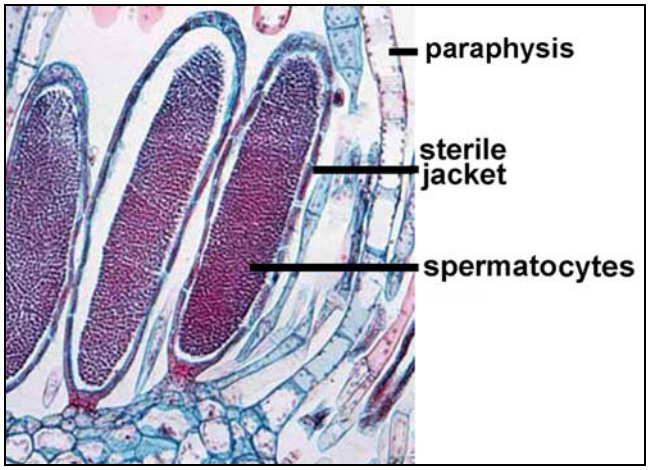

Figure 21. Moss **antheridia** showing **spermatocytes** that have been formed by the **spermatogenous tissue**. Photo by Janice Glime.

Figure 22. Thallose liverwort, ***Androcryphia confluens***, with brown **antheridia** along stem. Photo by George Shepherd, through Creative Commons.

Figure 23. ***Andreaea nivalis* antheridium**. Photo from botany website at the University of British Columbia, with permission.

Figure 24. ***Bryum capillare* antheridia** and **paraphyses** at the base of a leaf. Photo by Dick Haaksma, with permission.

Figure 25. ***Fissidens bryoides* antheridia** on a special branch. Photo by Dick Haaksma, with permission.

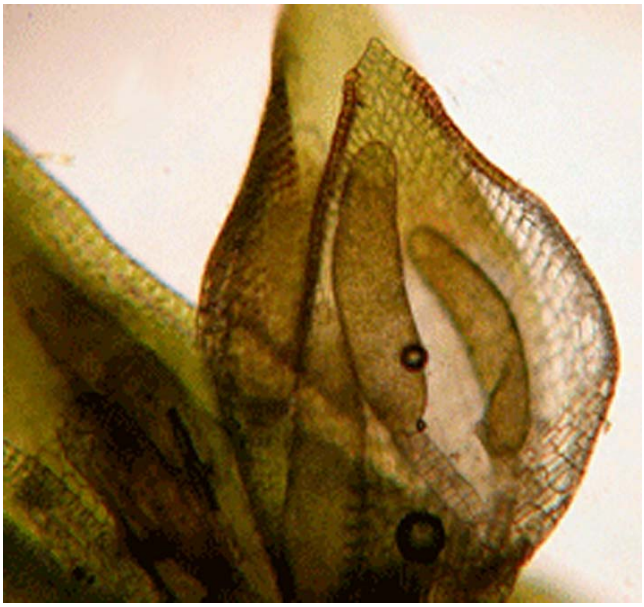

Figure 26. ***Orthotrichum pusillum* antheridia** nestled among leaves. Photo by Bob Klips, with permission.

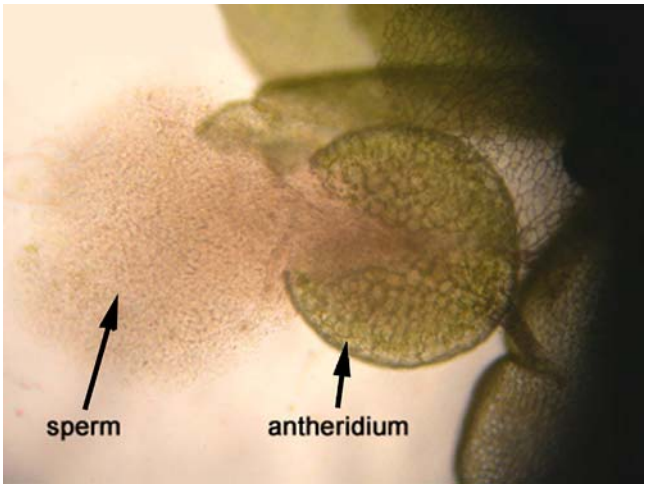

Figure 27. ***Porella navicularis*** **antheridium** releasing **sperm** as a mass. Photo by Jonathan Choi from Botany 321 website at the University of British Columbia, with permission.

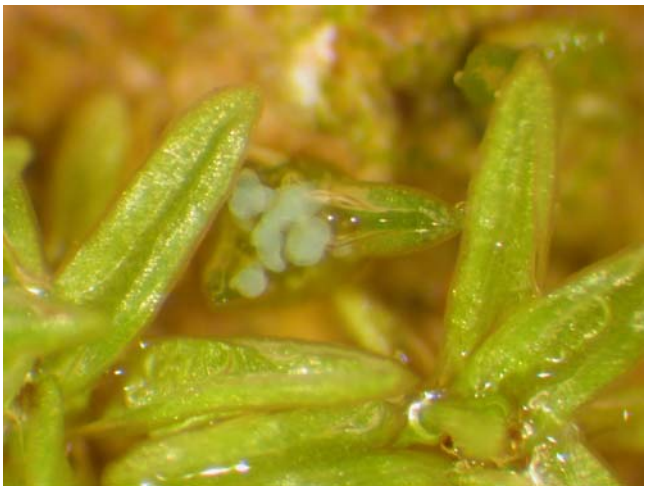

Figure 28. ***Aloina ambigua*** sperm release in packages. Photo courtesy of Llo Stark.

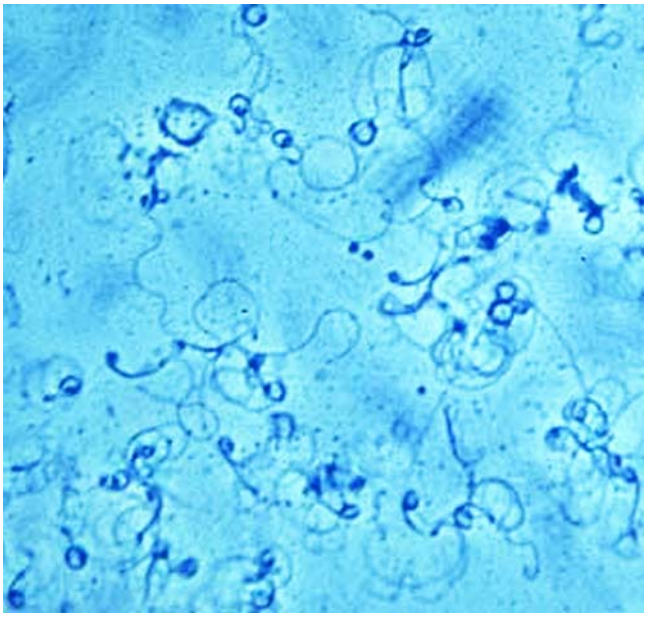

Figure 29. ***Marchantia polymorpha*** **sperm**. Photo from Botany 321 website at the University of British Columbia.

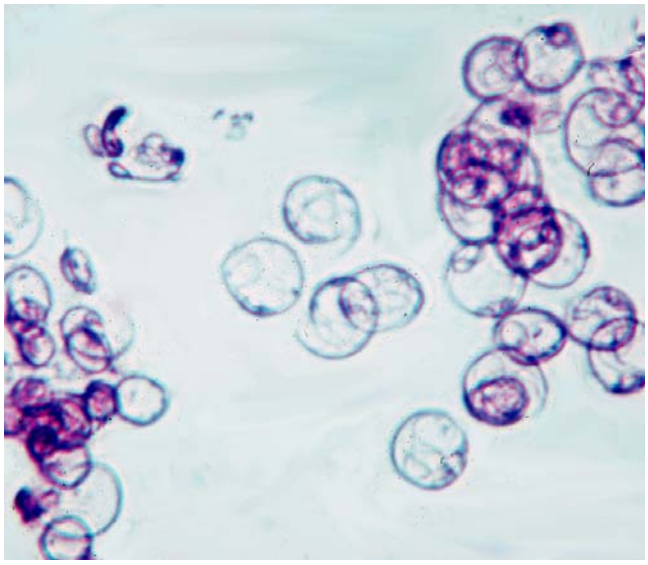

Figure 30. Stained bryophyte **sperm**. Photo by Janice Glime.

It is then the task of the **sperm** (Figure 29-Figure 30), with its two **flagella**, to find a film of water within which to swim to the awaiting egg in the **archegonium** (Figure 31-Figure 37). This is facilitated, most likely in all cases, by the presence of a chemical gradient produced by the archegonium and serving as an attractant (Figure 34). The archegonium is shaped like a flask with a **neck** (Figure 31), albeit a short one in some taxa. This neck has an outer layer of cells and a middle layer, the **neck canal cells** that disintegrate prior to fertilization, leaving this area as the **neck canal** (Figure 31). It is this disintegration that releases the chemicals that attract the sperm, and the cellular remains provide a fluid medium in which the sperm can swim. This fluid exudes from the archegonium (Figure 34) and can serve as a chemical gradient. Yet it appears that the ability of the sperm to advance any great distance by means of its flagella may be unlikely, if ***Riccardia pinguis*** is at all representative. Showalter (1926) found that when sperm of that species were placed at one end of a 1 x 0.5 cm pool, the majority still remained at that end of the pool an hour later, retaining motility up to 6 hours. Cronberg *et al*. (2008) showed the timescale of sperm deterioration (Figure 38).

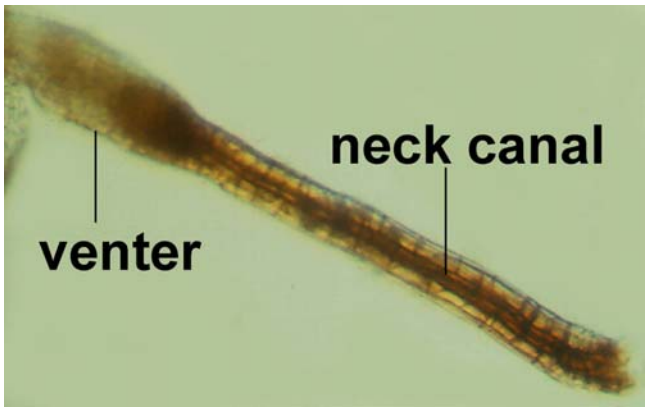

Figure 31. **Archegonium** of ***Fontinalis dalecarlica*** showing entry pathway (**neck canal**) for the sperm. Photo by Janice Glime.

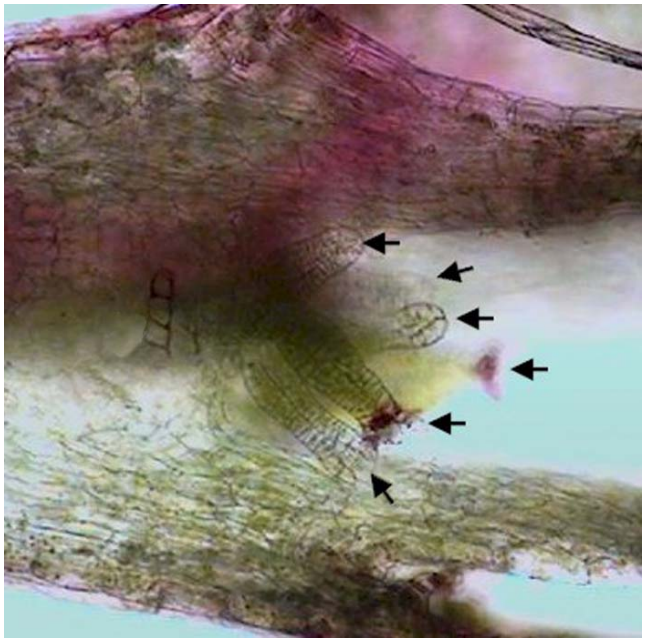

Figure 32. Terminal **archegonia** (arrows) of leafy liverwort ***Jungermannia evansii***. Photo by Paul Davison, with permission.

Figure 33. Immature archegonia of leafy liverwort ***Lophocolea cuspidata***. Photo from Botany 321 website at the University of British Columbia, with permission.

Figure 34. ***Aloina ambigua*** showing archegonial exudate. Photo courtesy of Llo Stark.

Figure 35. ***Pleurozium schreberi*** archegonia with two developing embryos, on short side branch. The large one is likely to be the only one to mature. Photo by Janice Glime.

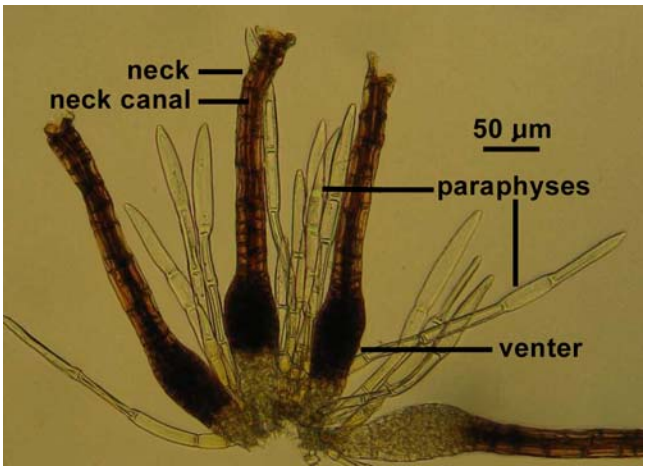

Figure 36. Moss ***Zygodon intermedius*** archegonia with paraphyses. Photo by Tom Thekathyil, with permission.

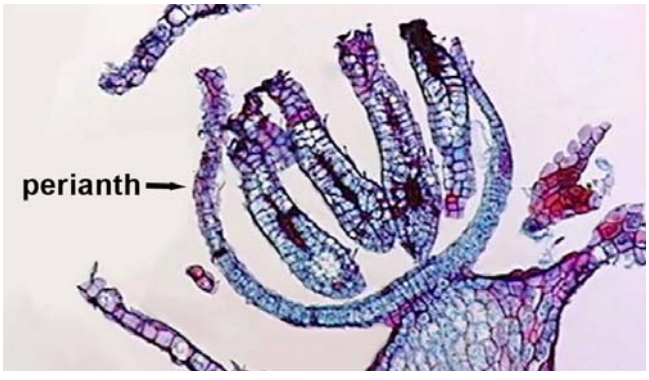

Figure 37. ***Porella*** archegonia in perianth. Photo by Paul Davison, with permission.

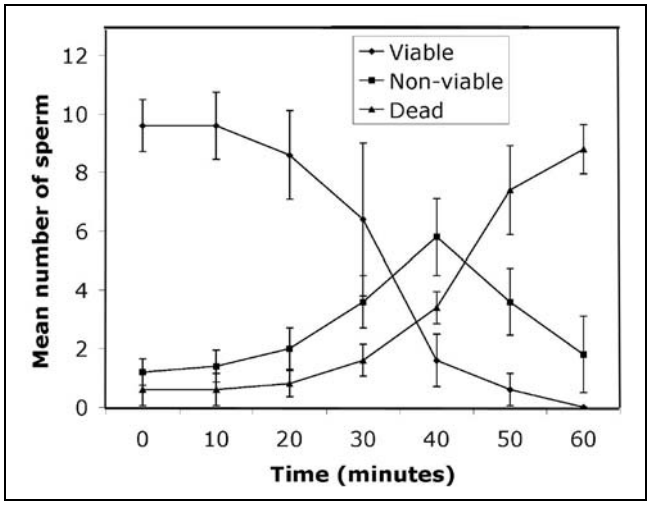

Figure 38. Time lapse of sperm release in ***Bryum argenteum***. Modified from Cronberg, Hans Berggren, & Rayna Natcheva 2008.

But that does not mean that all species have such short sperm longevity. In their experiments with the **paroicous** (having archegonia and antheridia on same branch) ***Pohlia nutans*** (Figure 39-Figure 40), a widespread moss that tolerates the high temperatures of geothermal areas and the extremes of the Antarctic, Rosenstiel and Eppley (2009) found that 20% of the sperm were still viable after 100 hours in DI or rainwater. They furthermore found that longevity was not affected by 22-60ºC, but at 75ºC it was significantly shortened. Dilution reduced viability. This longevity is much longer than anticipated, but it may not be representative of bryophytes with more narrow ecological distributions.

Figure 39. ***Pohlia nutans*** **perigonia** (modified leaves around antheridia in bryophytes). This species is usually **paroicous**. Photo by Michael Lüth, with permission.

Figure 40. ***Pohlia nutans*** with capsules, a widespread moss from geothermal areas to the Arctic. Photo by Michael Lüth, with permission.

It appears to be typical for sperm to be shed within their spermatocyte cells as a mass, being squeezed out of the antheridium by the swelling tissues (Figure 41-Figure 43). Both **paraphyses** (sterile filaments among the reproductive organs; Figure 20-Figure 24) and the **antheridium** (Figure 20-Figure 27) itself, swell. Then the spermatocytes drift to the top of the splash apparatus. It seems usual that the sperm do gain distance from the antheridium when they reach the surface of the surrounding water, especially in a splash cup, and break away from their enclosing spermatocyte cell membrane (Muggoch & Walton 1942). At that point, the sperm seem to disperse readily across the surface of the water, hopefully facilitating their dispersal in splashing raindrops. Yet, this leaves them to fend for themselves once they reach the surface upon which they land, hopefully that of a female plant or near a female organ. Could it be that they are programmed to avoid wasting energy unless they are within the liquid from a female plant or near a female organ?

Figure 41. ***Bryum argenteum*** releasing sperm masses from antheridia. Photo by Nils Cronberg, Hans Berggren, & Rayna Natcheva, with permission.

Figure 42. ***Bryum argenteum*** antheridium with initial explosive sperm mass release. Photo by Nils Cronberg, Hans Berggren, & Rayna Natcheva, with permission.

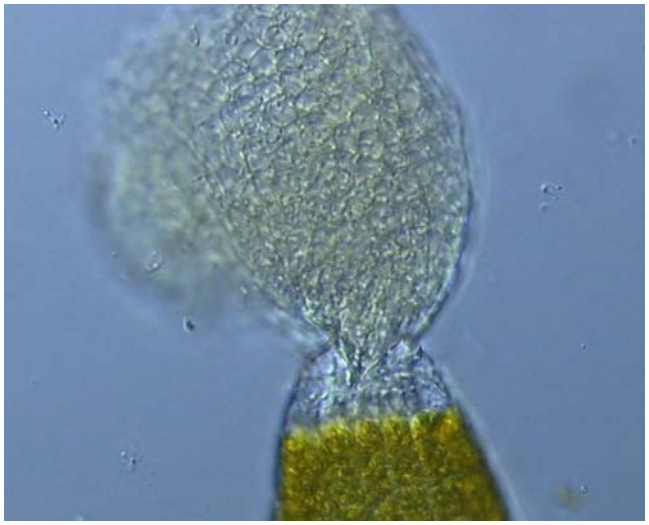

Figure 43. ***Bryum argenteum*** antheridium with final sperm mass release. Photo by Nils Cronberg, Hans Berggren, & Rayna Natcheva, with permission.

To put this in perspective, compare a study on corn (*Zea mays*) sperm where the researchers were attempting to improve sperm longevity (Zhang *et al*. 1992). By adjusting sucrose concentrations, using six sugars, ten buffers, five *p*H levels, and three membrane protective agents, they screened for the best combination. By adding 0.55 M galactose and performing other fine-tuning, they improved longevity to 72 hours with 70% viability. This was to keep a sperm alive that would normally travel in the protection of a pollen tube and female gametophyte tissue. For the bryophyte sperm, normal travel is in the harsh and unpredictable environment. In some ways, this might predict that the bryophyte sperm is tolerant of a wider range of conditions, but should we really expect it to live longer?

We know little about the ability of the archegonial fluid to attract the sperm, but it appears that **sucrose** may be one of the factors, perhaps the only one, involved (Kaiser *et al.* 1985; Ziegler *et al*. 1988). These researchers found that in the moss ***Bryum capillare*** (Figure 44), once the neck canal cells of the archegonium had disintegrated, the leaves and the archegonia contained less than 20% of the sucrose found in the intact neck region. There was virtually no fructose in the intact archegonium, but the glucose concentration rose after the receptive period ended.

Figure 44. ***Bryum capillare*** with capsules. Photo by David Holyoak, with permission.

Once the sperm reaches the **venter** of the archegonium (the bulbous base of the flask; Figure 45), it penetrates the egg and together they form the **zygote** (Figure 46), the first 2*n* cell of the sporophyte. Unlike an alga, the bryophyte retains its zygote in the female **gametangium** (archegonium) and when conditions are right the zygote divides, forming the **embryo** (young plant still contained in archegonium). This embryo continues dividing (Figure 47) and then specializing, forming eventually a **foot**, **stalk**, and **capsule** (sporangium; spore-container of mosses and liverworts; Figure 47) with a **cuticle** (water-protective layer; Crum 2001), which together constitute the **mature sporophyte** (Figure 48-Figure 58).

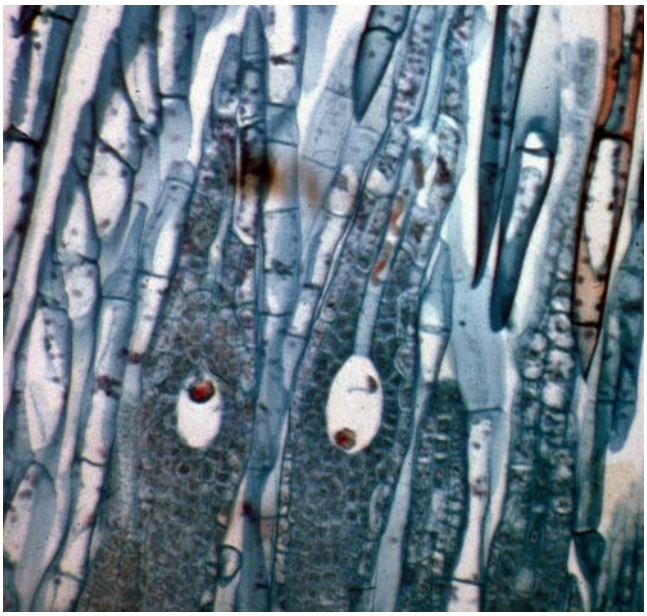

Figure 45. Moss ***Polytrichum*** archegonia. The archegonium on the right has an egg in the bottom of the venter and a biflagellate sperm near the neck. Two more sperm are in the neck canal of the archegonium on the right. Photo from botany teaching collection, Michigan State University, with permission.

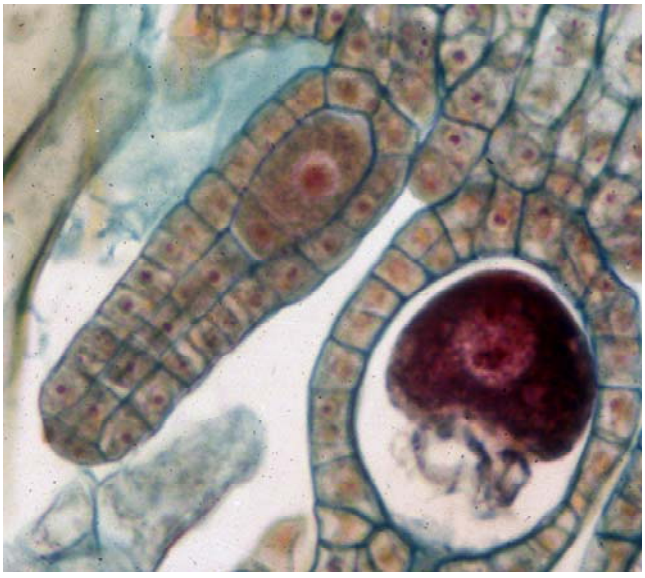

Figure 46. Thallose liverwort ***Marchantia polymorpha*** fertilization. Archegonium on left is young and neck canal cells have not broken down yet. The egg cell is in the swollen venter. On the right is an egg that is fusing with the sperm during fertilization. Photo from botany teaching collection at Michigan State University, with permission.

Because the base of this sporophyte is still firmly anchored in the gametophyte tissue, the sporophyte is at least partially a parasite on the gametophyte, gaining at least some of its nutrition through a joining tissue called the **haustorium**. Being contained in the gametophyte, the zygote necessarily competes for energy, as well as space, with other zygotes or embryos, and thus it is not surprising that multiple capsules are rare. Notable exceptions occur in the mosses ***Dicranum*** (Figure 1), ***Plagiomnium*** (Figure 59), ***Rhodobryum*** (Figure 60), and ***Mittenia plumula***, with as many as nine capsules in ***Plagiomnium insigne*** (Figure 59) (Crum 2001).

Consideration of the sporophyte as a parasite on the gametophyte is controversial. Some botanists find this to be an obvious interpretation, but others are adamantly opposed to such a label. Part of this reasoning against the relationship as parasitic is because most sporophytes, at least in mosses, are photosynthetic until the spores near maturity. They also argue that the fitness of the gametophyte is tied to the fitness of the sporophyte with, in at least some monoicous species, the same genome. Llo Stark (pers. comm. 25 February 2023) has also found that the strategy for desiccation tolerance can change shortly after fertilization, changing from constitutive protection to inducible protection. He suggests that this could cause the release of sugars that are moved to the sporophyte. The same dilemma of terminology applies to the human embryo, but the case against calling it a parasite in bryophytes seems stronger due to the photosynthetic ability of many sporophytes, at least in Anthocerotophyta and most Bryophyta.

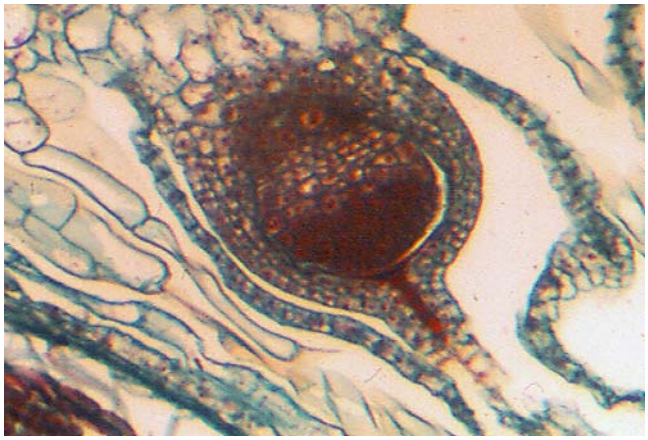

Figure 47. Thallose liverwort ***Marchantia polymorpha*** embryo in archegonium, showing development of the **foot**, **seta**, and **sporogonium**. Note the red-stained **neck canal** of the archegonium. Photo by Janice Glime.

When **meiosis** occurs and spores begin development, the supply of nutrition from the gametophyte may be cut off due to material that is deposited in the spaces within the cell walls of the haustorium (Wiencke & Schulz 1978). Water, however, still moves from the gametophyte to the sporophyte.

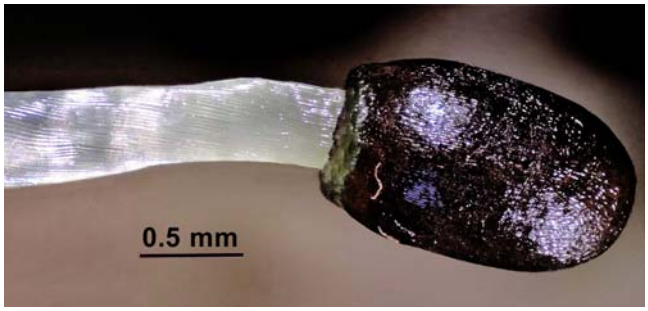

Figure 48. Liverwort ***Blasia pusilla*** capsule and stalk. Photo by Walter Obermayer, with permission.

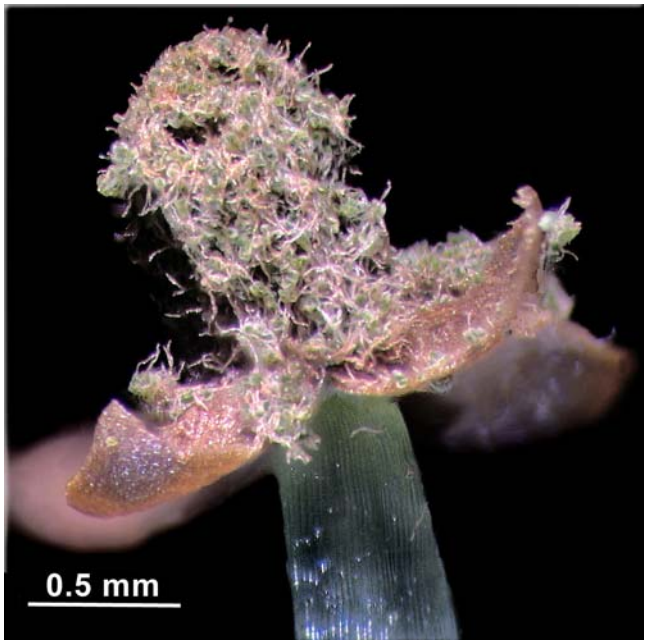

Figure 49. Liverwort ***Blasia pusilla*** open capsule showing spores and elaters. Photo by Walter Obermayer, with permission.

Figure 50. Liverwort ***Lophocolea cuspidata*** capsule with elongated seta. Photo from Botany 321 website at the University of British Columbia, with permission.

Figure 51. Moss ***Orthotrichum stramineum*** capsule with calyptra. Photo by Des Callaghan, with permission.

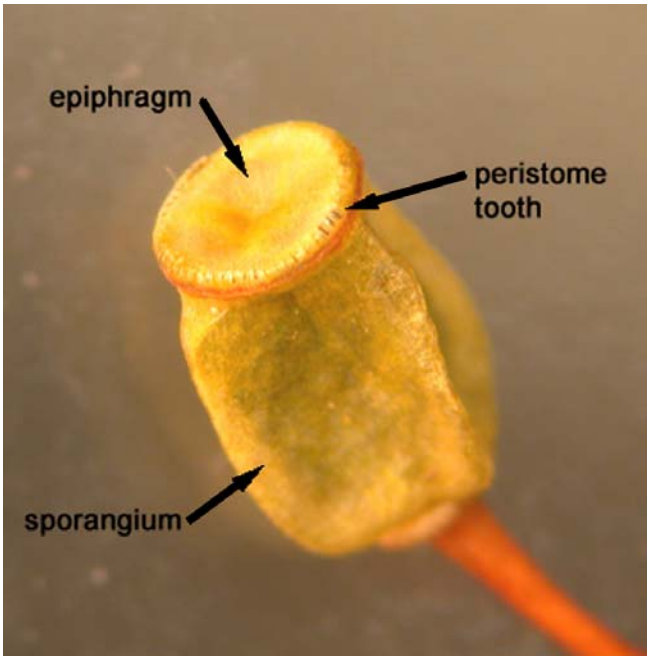

Figure 52. ***Polytrichum commune*** capsule. Photo from Botany 321 website at the University of British Columbia, with permission.

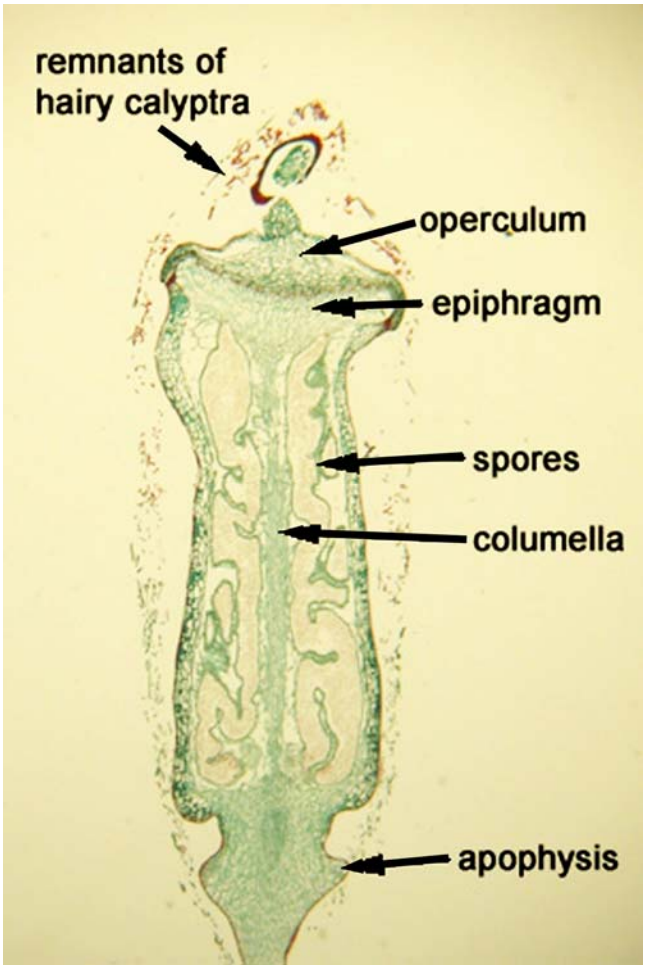

Figure 53. ***Polytrichum commune*** capsule longitudinal section. Photo from Botany 321 website at the University of British Columbia, with permission.

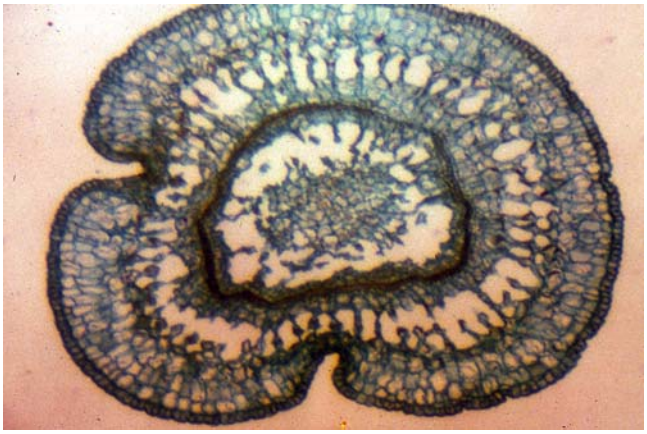

Figure 54. ***Polytrichum*** capsule cross section. The blue center is the columella. The dark circle around it is the developing sporogenous tissue. Photo by Janice Glime.

Figure 55. ***Bartramia pomiformis*** showing leafy gametophytes and sporophyte capsules. Photo by Janice Glime.

It is this dependence on the gametophyte that makes the sporophyte unique among photosynthetic organisms. On the one hand, it differs from algae by being retained within the archegonium; on the other it differs from the remainder of the plant kingdom by being dependent on the gametophyte. Furthermore, it lies within the protection of the gametophyte tissue through a great part of its development, although less so in the **Bryophyta**. This protection shelters it from selection pressures of the environment and could therefore slow the evolution of this generation (Crum 2001). It is this greater stability of sporophyte characters that makes them seemingly more useful for deriving classification within the **Bryobiotina** (bryophytes).

The details of the foregoing structures differ among the phyla of **Bryobiotina** and in many cases form the basis for separating the phyla. These are best understood by examining each phylum and class in greater detail.

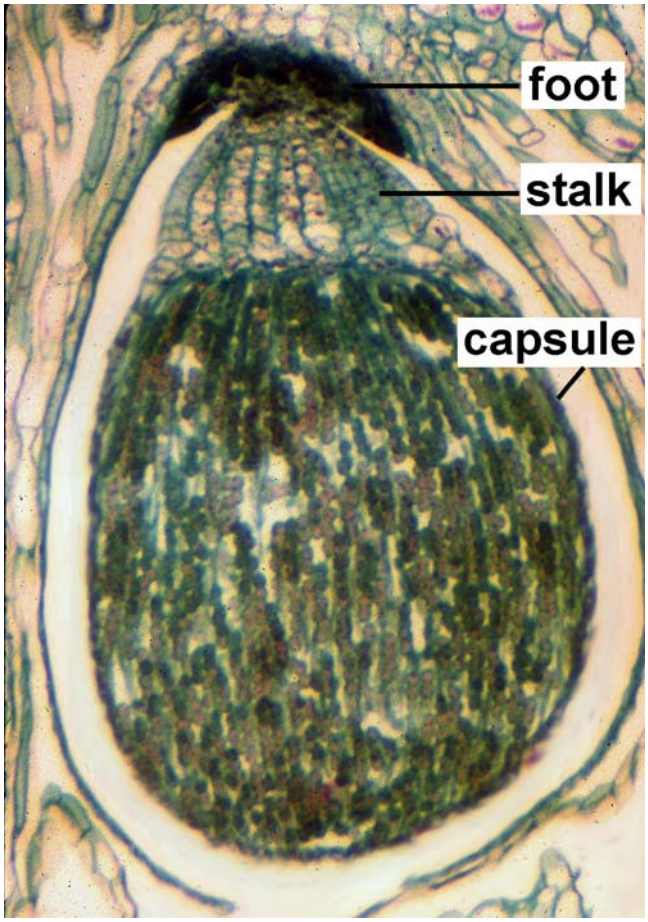

Figure 56. Mature sporophyte of thallose liverwort ***Marchantia polymorpha*** showing **foot**, **stalk**, and **capsule**. Photo modified from botany teaching collection, Michigan State University, with permission.

Figure 57. ***Gigaspermum repens*** capsule showing spores. Photo by David Tng, with permission.

Figure 58. Longitudinal section through mature ***Fontinalis squamosa*** capsule, showing green spores. Photo by Janice Glime.

Figure 59. ***Plagiomnium insigne*** **sporophytes**, illustrating multiple sporophytes on one shoot. Photo from Botany 321 website at the University of British Columbia, with permission.

Figure 60. ***Rhodobryum roseum*** with multiple capsules from one shoot. Photo by Michael Lüth, with permission.

Life Cycle Controls

For life cycles to work effectively in their environments, they need controls that respond to environmental cues. Without these, they cannot respond to differences in the weather between years, to changing climate, or to dispersal to other parts of the world. Among these, response to photoperiod and temperature provide effective cues that the season is changing and it is time to initiate a life cycle stage (Newton 1972).

For example, in ***Mnium hornum*** (Figure 61) there is an endogenous rhythm that coincides approximately with the seasonal cycle (Newton 1972). Short days delay gametangial production, but when 7.25-hour days are maintained, neither 10 nor 20°C is capable of completely suppressing the gametangia. Newton interpreted this to mean that the short days of winter maintain coordination with the seasons. In ***Plagiomnium undulatum*** (Figure 62), archegonial induction responds to long days (7.25-12 hours at 10°C). Males are also long-day plants, but in addition they require a diurnal temperature fluctuation.

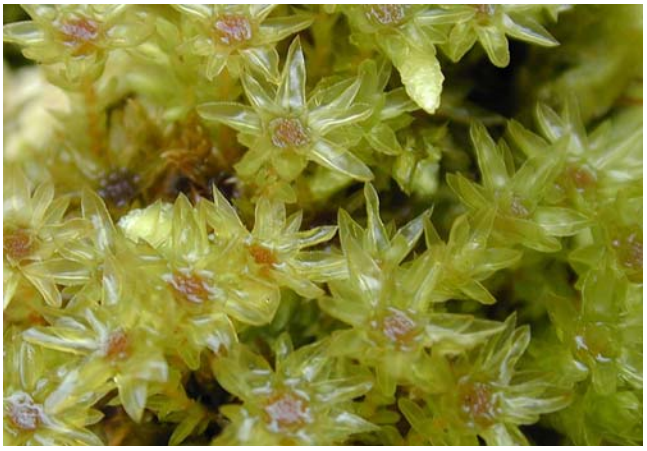

Figure 61. ***Mnium hornum*** showing antheridia that cease production in response to short days. Photo by Michael Lüth, with permission.

Figure 62. ***Plagiomnium undulatum*** with **antheridia** that respond to long days and diurnal temperature fluctuations. Photo by Jan-Peter Frahm, with permission.

Generation Time

The concept of generation time is well known even to the layperson. We know that in humans it means the time from birth to becoming a parent, and for the population we average the data from everybody. I like the Wikipedia definition: The average difference in age between parents and offspring when the population is at the stable age distribution. For plants, it seems the best definition is one complete life cycle. Llo Stark (Bryonet 20 February 2014) agrees with this implied spore-to-spore definition, but he suggests expanding it to include shoot fragment or fragment of a protonema as the starting point instead of a spore. For example, he and John Brinda have found that it takes only 5-6 months for a shoot fragment of ***Aloina ambigua*** (Figure 63) to produce viable spores. In this rapid cycle, only 40 days are required for the sporophyte to develop. On the other hand, Stenøien (Bryonet 21 February 2014) suggests that the average length of time required to replace an individual is a workable definition of generation time. But Lars Hedenäs (Bryonet 21 February 2014) cautions us that we rarely know what this means in any specific case.

Figure 63. ***Aloina ambigua***, a moss with a short generation time of only 5-6 months. Photo by Hermann Schachner, through Creative Commons.

But do we have information for many, or even any, bryophytes on the amount of time required to progress from spore or fragment germination to spore production? This is easy for annual bryophytes, but for perennials, few have been grown from spore to mature capsule and field observations would be based mostly on colonists because spores are an important part of their life strategy. And some bryophytes further complicate this by rarely or never producing capsules, forcing us to guess based on gametangial maturation time. However, once fertilization occurs, sporophyte maturation can proceed rapidly as in the annuals, or take 15 months as in some ***Polytrichum*** (Figure 64) species.

Figure 64. ***Polytrichum commune*** sporophytes, in 4 cases covered by the gametophyte calyptra. Photo by Michael Lüth, with permission.

Even "annuals" might cause problems. For example, ***Buxbaumia*** (Figure 65-Figure 66) is usually considered an annual because the sporophyte lasts only one year and there is no leafy gametophore. But Hancock and Brassard (1974) found that despite the annual disappearance of the sporophyte, the protonema remained for several years.

Figure 65. ***Buxbaumia aphylla*** with mature capsules. Photo by Jan-Peter Frahm, with permission.

Figure 66. ***Buxbaumia aphylla*** with capsule wall peeled back and interior exposed. The greenish ground cover is caused by protonemata that will survive the winter and form new plants. Photo by Janice Glime.

Let us take an example first given by Hans Stenøien and carried further by Lars Hedenäs (Bryonet 21 February 2014). If a moose walks across a bog and kills a ***Sphagnum*** (Figure 67) shoot, the empty space created will most likely be filled by an expanding neighboring shoot. The probability is high that the neighbor originated by branching from the now dead shoot. This means the same individual survives despite the death of one of its shoots. Do we know anything about the frequency of this happening?

Figure 67. ***Sphagnum capillifolium***, a moss that spreads by branches. Photo by David Holyoak, with permission.

To these comments, Lars Hedenäs (Bryonet 20 February 2014) adds that many bryophytes reproduce sexually numerous times during their lifetimes, perhaps for hundreds of years. Note that this can occur while the lower parts of the plants are dying so that it may be more typical for only 4-5 years of growth to remain alive. How do we treat these long-lived taxa? Do we take the average of the first to last reproduction, or do we use the first?

And how do we treat the asexual "generations?" Hedenäs points out that these clones may block the establishment of new introductions due to lack of space.

If we consider genetic change in terms of generations, the issue has even more complications. As Richard Zander (Bryonet 20 February 2014) points out, genetic change may be more the result of point mutation than of recombination. And these may be passed on through fragmentation or **ramets** (physiologically distinct organism that is part of group of genetically identical individuals derived from one progenitor; individual of clone).

By now it is clear that generation time in bryophytes cannot be defined as it is in humans (Brent Mishler, Bryonet 20 February 2014). In fact, Guy Brassard (Bryonet 20 February 2014) reminds us that it is an animal term. As Mishler concludes, "maybe there is no reasonable concept of generation time in mosses!" Rod Seppelt (Bryonet 20 February 2014) agrees: "I rather like the suggestion that 'generation time' is nonsensical in bryophytes." At the very least, we need to define the term whenever we use it in order to make clear what we mean by it. In that case, we should consider the suggestion of Hans Stenøien (Bryonet 20 February 2014): "The length of a generation could be defined as the average time it takes to replace an individual (a shoot or a ramet) in a stable population. This could be done by sexual or vegetative means, by residents or immigrants. Bog systems can be quite dynamic, and many shoots die and are replaced from time to time (because mosses do what they do, competition *etc.*)."

Rod Seppelt (Bryonet 2 January 2022) has suggested what might be the shortest "generation time" for a bryophyte. When in Alaska, he found a population of ***Riccia cf. cavernosa*** (Figure 68) on a floodplain about a week after the water receded. These were very small plants, suggesting their origin from spores rather than dormant thalli. It was late autumn, and a new submersion was imminent due to upstream rains. He collected more plants about two weeks later and found mature spores in the thalli. He estimated that these plants went from spore to producing mature sporangia in just 2-3 weeks!

Figure 68. ***Riccia cavernosa***, a species that can apparently complete its life cycle in less than 3 weeks on a floodplain. Photo by Richard Orr, with permission.

Importance

So why is it important to understand generation time of a bryophyte? The question about the length of a generation was raised by Jon Shaw who wanted to know the generation time in ***Sphagnum*** (Figure 67). As Hans Stenøien and Richard Zander summarized on Bryonet (21 February 2014), understanding generation times (and population sizes) enables us to use population genetic models to infer the action of evolutionary processes. Likewise, phylogenetic models enable us to infer evolutionary relationships. From these, we can infer migration rates and divergence time between lineages.

Longevity and Totipotency

Bryophyte longevity can be difficult to define because unlike most other plants, they die at the bottom and continue growing at the tip. Furthermore, they may seem dead, yet still be capable of life. For example, I have boiled ***Fontinalis*** (Figure 69) for two weeks, replaced it in its native stream, and found a few new leaves on one stem tip a year later, whereas all the original leaves were brown or gone.

Figure 69. ***Fontinalis dalecarlica***, a species that can survive two weeks of boiling because of its totipotency. Photo by J. C. Schou, through Creative Commons.

This capability of "coming back to life" is in part the result of **totipotency** – the ability of any cell of the organism to dedifferentiate and then differentiate into a new plant. We have seen this regeneration many times in the growth from fragments, to be discussed in other chapters, especially in Dispersal.

We know that ***Sphagnum*** (Figure 67) continues growing for hundreds of years, but only the recent few years of growth seem to be alive. But is that really true?

Recent studies in polar regions suggest that parts of some bryophytes can retain life for 1500 years under ice (LaFarge *et al*. 2013; Roads *et al*. 2014). Working in the Arctic, LaFarge *et al*. (2013) were able to grow new gametophytes from two species of buried bryophytes: ***Aulacomnium turgidum*** (Figure 70) ~400 years old and ***Bartramia ithyphylla*** (Figure 71) ~460 years old.

Figure 70. ***Aulacomnium turgidum***, a species found buried in Arctic ice cores. Photo by Michael Lüth, with permission.

Figure 71. ***Bartramia ithyphylla***, a moss found in ice cores from the Arctic. Photo by Michael Lüth, with permission.

Then Roads *et al*. (2014) found new growth of ***Chorisodontium aciphyllum*** (Figure 72-Figure 73) in Antarctic cores at 138 cm, a layer they interpreted to be ~1500 years old! They found that after 55 days the ***Chorisodontium aciphyllum*** grew *in situ* at the base of their ice core at 110 cm. Protonemata developed on the rhizoids at the base in 22 days. (See also Miller 2014; Zimmer 2014).

Figure 72. ***Chorisodontium aciphyllum*** showing the extensiveness of a mat. Photo through Creative Commons.

Figure 73. ***Chorisodontium aciphyllum*** showing upper live green parts and lower dead or dormant parts. Photo through Creative Commons.

Summary

The traditional bryophytes (Subkingdom **Bryobiotina**) are classified into three phyla (**Marchantiophyta** = liverworts, **Bryophyta** = mosses, **Anthocerotophyta** = hornworts).

Bryophytes have a dominant gametophyte (1*n*) generation that limits their ability to store recessive alleles. The life cycle involves a **protonema** that develops from the germinating spore, becoming thalloid in most liverworts and Sphagnopsida, but becoming a branched thread in most other mosses. The protonema produces **buds** that develop into leafy gametophores. Mosses in the Bryopsida, but not liverworts or ***Sphagnum***, can produce multiple **upright gametophytes** from one protonema, and therefore from one spore.

Gametophores produce **archegonia** and/or **antheridia** and the zygote divides to form an **embryo** that develops within the archegonium. Sporophytes remain attached to the gametophyte and produce spores by meiosis.

Acknowledgments

I appreciate the comments and suggestions of Karla Werner, who offered a beginner's perspective. Noris Salazar Allen offered constructive criticisms on the taxonomic descriptions and reviewed an early draft. Peter Convey and Catherine La Farge entered an email discussion with me on their own finds and concerns about available data on the ice core finds. Thank you to Llo Stark for improving the wording in several parts of the chapter.

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CHAPTER 2-3
MARCHANTIOPHYTA

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CHAPTER 2-3
MARCHANTIOPHYTA

Figure 1. ***Symphogyna podophylla*** (Phylum **Marchantiophyta**, Class **Jungermanniopsida**, subclass **Metzgeriidae**) in New Zealand, showing dorsiventral orientation of the thallus and dependent sporophyte. Photo by Janice Glime.

Distinguishing Marchantiophyta

Both the leafy and thallose liverworts are placed in the phylum **Marchantiophyta** (variously known as Hepatophyta, Jungermanniophyta, Hepaticae, and Hepaticopsida), an often inconspicuous group with about 5000 species (Gradstein *et al*. 2001), or as Crum (1991) put it, up to 10,000, "depending on who says it and when," because so many species names described from different parts of the world have proved to be synonyms.

Because of the long tradition of considering these to be bryophytes, liverworts (and hornworts) are still lumped into that group for a vernacular name instead of creating a new name that is unfamiliar to everyone. As a phylum, **Marchantiophyta** are distinguished from the phylum **Bryophyta** by their **dorsi-ventral orientation** (Figure 1, Figure 12), **unicellular rhizoids** (Figure 2), **inoperculate capsules** [*i.e.* lacking a lid (Figure 3), although there are a few exceptions], **absence of a columella** in the center of the capsule (Figure 4), and **no stomata** in the capsule. They possess a **seta** (stalk on the capsule), as do mosses, but it elongates **after** development of the capsule (Figure 11-Figure 12), whereas in mosses it elongates first, then develops the capsule. The spores, as in mosses, are all produced simultaneously by **meiosis** (Figure 5). The capsule, unlike that of most mosses, dehisces typically by **splitting into four valves** (Figure 6), but not in the class Marchantiopsida, revealing spores mixed with **elaters** (thickened elongate cells with spiral wall thickenings that twist in response to drying; Figure 6-Figure 7).

Figure 2. ***Fossombronia*** rhizoids. Note that these rhizoids are unicellular, and the ones in this genus are purple by nature. Photo by Paul Davison, with permission.

Figure 3. ***Marchantia polymorpha*** archegonial head showing inoperculate capsule in lower right. Photo by George Shepherd through Creative Commons.

Figure 4. Capsule, lacking cell wall, of ***Marchantia polymorpha***. Photo from Michigan State University Botany Department teaching collection, with permission.

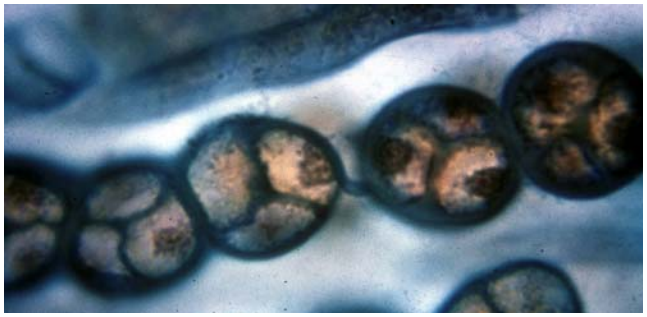

Figure 5. ***Marchantia polymorpha*** spore tetrads and one elater (upper) before spiral thickenings form. Photo from botany teaching collection at Michigan State University, with permission.

Elaters

Elaters are notably absent in the thallose liverworts **Ricciaceae** and **Sphaerocarpales** (***Sphaerocarpos***, ***Riella***), although sterile cells exist in the latter. Elaters respond to changing moisture conditions, most likely rather suddenly upon the first splitting of the capsule, and twist and turn among the spores as they dry. When the capsule opens, the elaters are filled with water, but as the capsule dries, so do the elaters. This causes the thin areas of the elaters to be pulled inward, distorting them. As the space between the thickenings is pulled in, the spirals tighten until the entire elater becomes a tight, twisted helix. Physical forces keep trying to untwist them, but adhesion of water inside the elater cell wall resists this extension, creating tension. When the tension of the water column finally breaks, the elater extends to its original shape so violently that it springs free of the capsule, scattering spores as it does so. The pressure in the cellular water just prior to its release can be as high as 200-300 atmospheres in ***Lophozia*** (Figure 8). In the tiny ***Cephaloziella*** (Figure 9), spores can travel up to 4-5 cm (Douin 1914 in Schuster 1966) and in ***Tritomaria quinquedentata*** about 2.5 cm (Meylan in Schuster 1966).

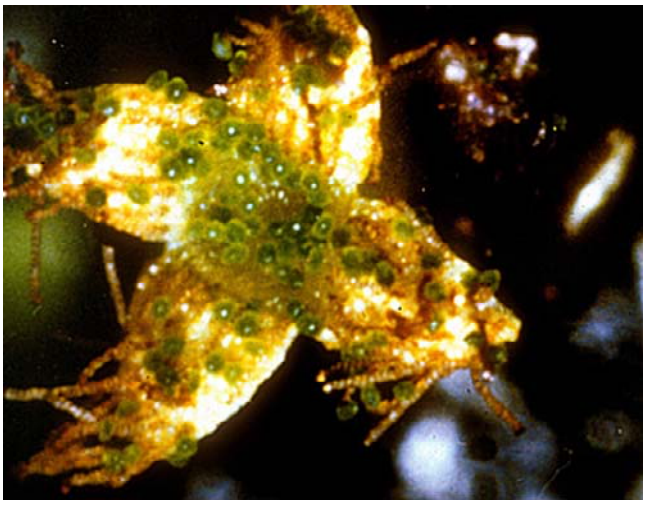

Figure 6. Open valvate capsule of the leafy liverwort ***Frullania kagoshimensis*** (Class **Jungermanniopsida**) showing spores and elaters and no columella. Photo by Zen Iwatsuki, with permission.

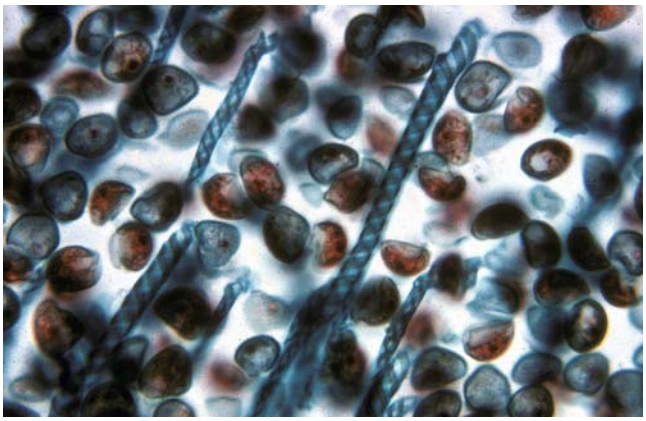

Figure 7. Spores and elaters with spiral thickenings from ***Marchantia polymorpha*** (**Marchantiopsida**). Photo from botany teaching collection at Michigan State University, with permission.

Figure 8. ***Cephaloziella hampeana*** with closed (black) and open (brown) capsules, a genus in which spores can travel 4-5 cm. Photo by David T. Holyoak, with permission.

Figure 9. ***Lophozia incisa*** with capsules, a species whose capsules open after building up pressure of 200-300 atmospheres. Photo by Tab Tannery, through Creative Commons.

In the leafy liverwort ***Frullania dilatata*** (**Jungermanniopsida**), elaters attach to the capsule wall at both ends (Schuster 1966). When the capsule opens, the elaters are stretched, creating tension. Most likely further drying contributes to the tension until the inner ends suddenly release (see Figure 6), providing a springboard from which spores are catapulted 1-2 cm above and out of the capsule. However, Schuster felt that most of the contribution of the elaters in this case is to loosen the spore mass.

In ***Marchantia*** (Figure 10), elaters twist and untwist, based on moisture changes. The capsules do not open along four distinct lines of dehiscence (compare Figure 10 to Figure 14), but rather open irregularly into short lobes that bend back. Elaters twist as they dry and become entangled (Figure 10). When an elater becomes free of the others, it does so with a sudden movement that throws spores from the capsule, although the elater generally remains (Ingold 1939 in Schuster 1966). In other liverworts, such as ***Pellia*** (Figure 11-Figure 13), the spiral thickenings are not so thick and the movements are too subtle to accomplish much dispersal (Schuster 1966). Rather, release of pressure at the time of dehiscence seems to be responsible for at least some dispersal. However, even the subtle movement of elaters may serve to loosen spores from each other, making dispersal easier when something disturbs the stalk and capsule (Figure 14). (See chapter on dispersal.)

Figure 10. ***Marchantia polymorpha*** archegoniophore showing unopened capsule on right and open capsule on left with elaters emerging. Photo by George Shepherd through Creative Commons.

Figure 11. ***Pellia epiphylla*** (**Jungermanniopsida**) with young capsule emerging from perianth, before seta elongation. Photo through Biopix, through Creative Commons.

Figure 12. ***Pellia epiphylla*** (**Jungermanniopsida**) with capsules on elongated setae, from southern Europe. Photo by Michael Lüth, with permission.

Figure 13. ***Pellia epiphylla*** (**Jungermanniopsida**) with capsule wall peeled back and elaters exposed. Photo by Malcolm Storey from <www.discoverlife.org>, through Creative Commons.

Figure 14. ***Noteroclada confluens*** (**Jungermanniopsida**) elaters and spores. Photo by George Shepherd through Creative Commons.

Leafy or Thallose?

The Marchantiophyta can be divided into two classes (Figure 40), the **Marchantiopsida** (thallose liverworts; Figure 15 & Figure 18) and **Jungermanniopsida**, the latter with two subclasses, the **Metzgeriidae** (mostly thallose liverworts; Figure 41), and the **Jungermanniidae** (mostly leafy liverworts; Figure 47 & Figure 49). One could argue that these two classes should actually be separate phyla (Bopp & Capesius 1996), but most modern systematists disagree (Crandall-Stotler & Stotler 2000). Based on 18S rRNA genes for all bryophytes tested, the **Marchantiopsida** are clearly separated from the **Jungermanniopsida**, but the latter are in the same clade as the **Bryophyta**! Furthermore, the orders **Metzgeriales** and **Jungermanniales** are indicated on the same branch. I will leave these arguments for the future and describe the two classes of **Marchantiopsida** and **Jungermanniopsida** as comprising the **Marchantiophyta**.

Figure 15. ***Preissia quadrata*** (**Marchantiopsida**), a thallose liverwort, showing antheridiophores. Photo by Janice Glime.

Class Marchantiopsida

Thallus Construction

The **Marchantiopsida** possess a thallus that is dichotomously forked (Figure 12) and generally has pores (Figure 16-Figure 18). The thallus is several cells thick and the upper (**dorsal**) tissue is loose, resulting from internal air spaces (Figure 18-Figure 20). The lower (**ventral**) surface usually has two kinds of **rhizoids** (Figure 19, Figure 21-Figure 22), **smooth** ones and those with "**pegs**" (protrusions inward from the cell wall), and usually has scales (Figure 22). The capsule dehisces irregularly (Figure 13), or less commonly by means of an operculum of thin-walled cells, as in ***Cyathodium***.

Figure 16. ***Marchantia chenopoda*** pores. Photo by George Shepherd through Creative Commons.

Figure 17. ***Marchantia chenopoda*** pores. Photo by George Shepherd through Creative Commons.

The thallus in Marchantiopsida has some resemblance to the leaf of a tracheophyte. The air chambers have stacks of photosynthetic cells (Figure 18) that resemble the spongy mesophyll of a tracheophyte leaf. The pores permit gas exchange into and out of these photosynthetic cells.

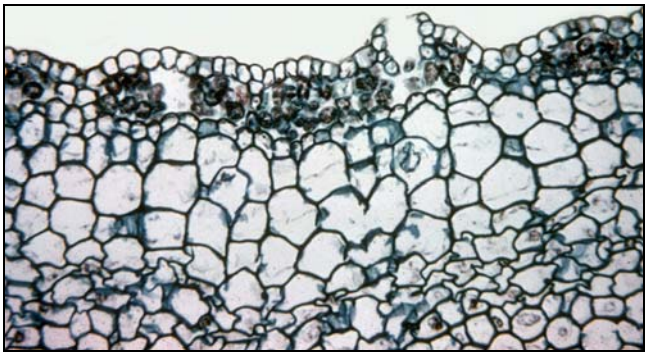

Figure 18. Cross section of thallose liverwort ***Marchantia polymorpha*** (**Marchantiopsida**) showing the internal air chambers, pores, and fragments of rhizoids. Note stacks of cells in internal air chambers, somewhat resembling the spongy mesophyll of a tracheophyte leaf. Pores are surrounded with rings of cells 4-5 cells high that can, as a group, curve and close pores in a manner somewhat resembling that of guard cells in leaves. Photo from botany teaching collection, Michigan State University, with permission.

Figure 19. **Marchantiopsida** thallus showing multiple layers, rhizoids, and dorsiventral orientation. Photo by Smith through Wikimedia Commons.

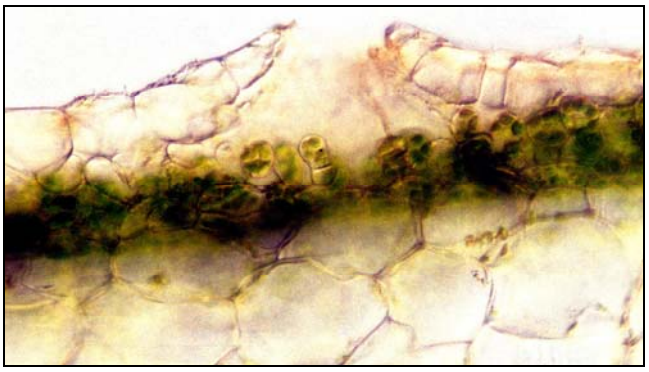

Figure 20. ***Marchantia polymorpha*** thallus pore. Photo by George Shepherd through Creative Commons.

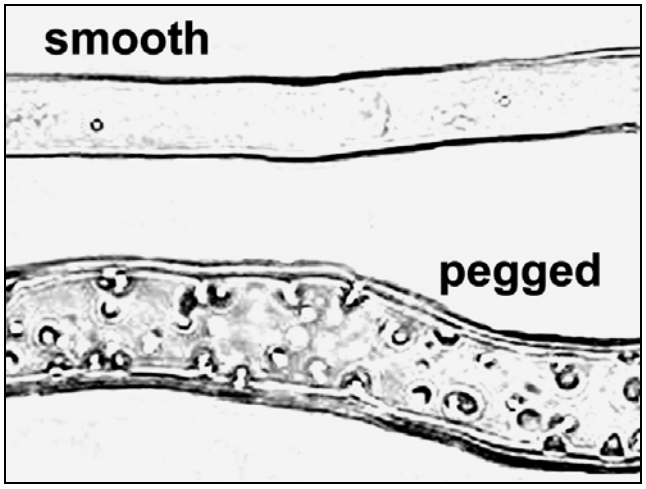

Figure 21. Smooth and pegged rhizoids of ***Conocephalum conicum*** in the Class **Marchantiopsida**. Photo with permission, modified from web site of Paul Davison, <www2.una.edu/pdavis/bryophytes.htm>, with permission.

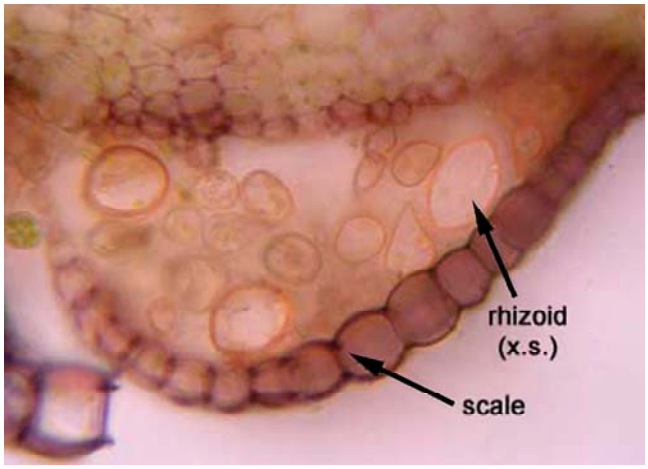

Figure 22. ***Marchantia polymorpha*** cross section showing ventral surface with scale and rhizoids. Photo from University of British Columbia website, with permission.

Sexual Structures

Members of the **Marchantiopsida** may have the archegonia imbedded in the thallus, as in ***Ricciocarpos*** (Figure 23), or raised on an umbrella-like **archegoniophore** (Figure 24-Figure 25), as in **Marchantiaceae.** Likewise, the antheridia may be imbedded in the thallus, as in ***Ricciocarpos*** (

Figure 23), or imbedded in a splash platform atop an **antheridiophore** (Figure 26, Figure 28-Figure 29), as in ***Marchantia***. The archegoniophore and antheridiophore are made by the infolding of the thallus. The "suture" along the vertical surface, and often scales and rhizoids, can be seen along the stalk where they stick out from the stalk (Figure 25). Such elevation of antheridia within a **splash platform**, the **antheridial head**, in ***Marchantia*** presumably permits the sperm to be splashed away from the parent to land on the archegonial head that is just beginning to develop and is not yet elevated significantly (Figure 27-Figure 31). Once the sperm are in the vicinity of the archegonia, the archegonium attracts them with a protein (Harvey-Gibson & Miller-Brown 1927).

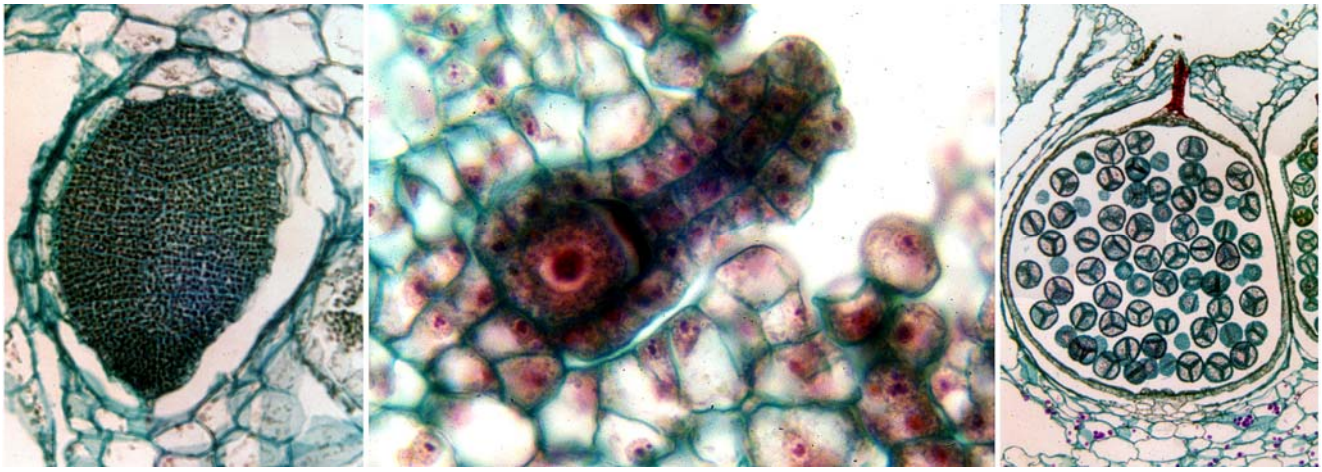

Figure 23. Reproductive structures of ***Ricciocarpos natans*** (Class **Marchantiopsida**). **Left: Antheridium** imbedded in thallus. **Middle: Archegonium** imbedded in thallus. **Right: Spore tetrads** (following meiosis) in sporophyte imbedded within the thallus and still within the archegonial wall. Photos modified from Triarch.

Figure 24. ***Marchantia polymorpha*** **archegoniophores**. Photo by Janice Glime.

Figure 26. **Antheridiophores** of ***Marchantia polymorpha*** elongating. Photo by Des Callaghan, with permission.

Figure 25. ***Marchantia polymorpha*** **archegoniophore** showing scales and rhizoids along the stalk. Photo by Janice Glime.

Figure 27. Antheridiophores and developing **archegoniophores** on thalli of ***Marchantia polymorpha***. Note the "button" heads just beginning on some thalli. Photo by Bob Klips, with permission.

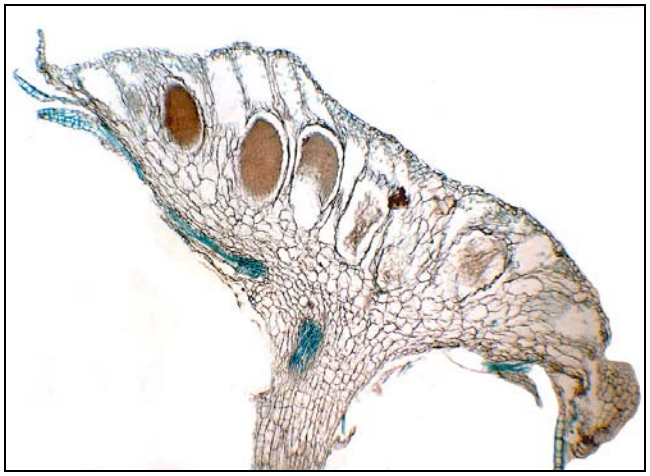

Figure 28. ***Marchantia polymorpha*** antheridial head. Photo by George Shepherd through Creative Commons.

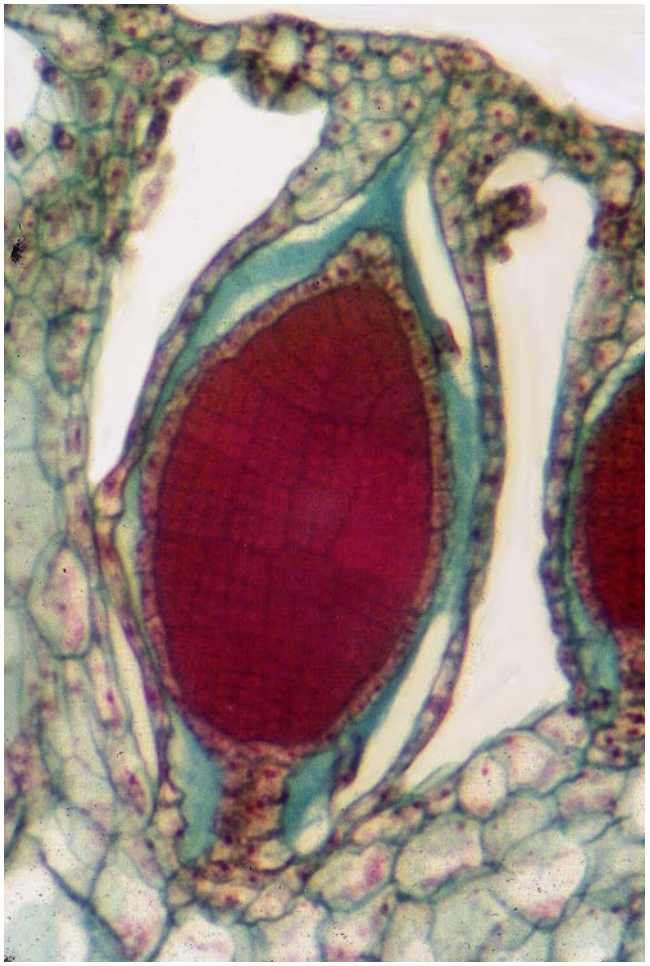

Figure 29. ***Marchantia polymorpha*** antheridium opening to the upper surface of the antheridial head. Photo from Michigan State University teaching collection, with permission.

In ***Marchantia***, this sexual expression is under the control of a small Y chromosome in the male, with no X chromosome, and a single X chromosome in the female (Lorbeer 1934). The life cycle of ***Marchantia*** is summarized in Figure 39.

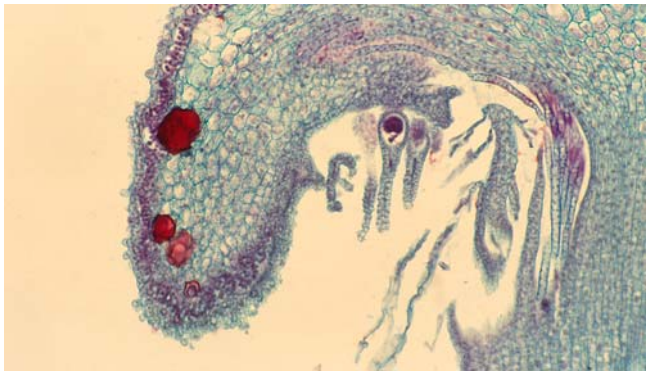

Figure 30. **Archegonial head** of ***Marchantia polymorpha*** with archegonia hanging down from the under side. Photo by from Plant Actions through Eugenia Ron Alvarez, with permission.

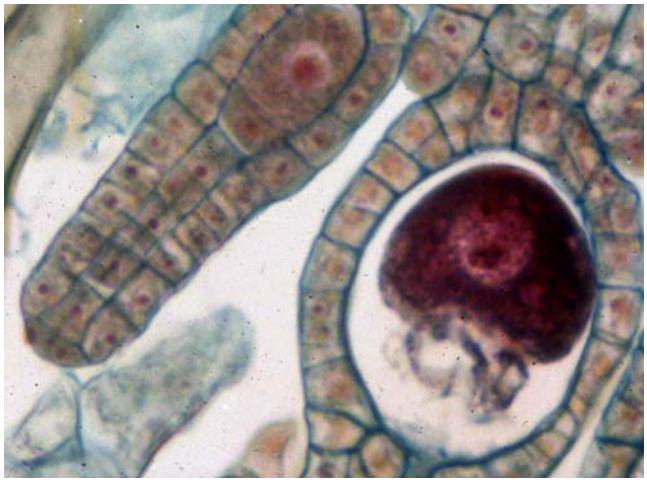

Figure 31. ***Marchantia polymorpha*** archegonia. **Left** archegonium has unfertilized egg; **right** archegonium has zygote. Photo by Janice Glime.

Sperm Dispersal

But just how far can these tiny sperm travel? Showalter (1926) found that the sperm of ***Riccardia pinquis*** could swim at a rate up to one centimeter in one hour, but more often it was considerably slower. Furthermore, their maximum swimming endurance time was only six hours.

Duckett and Pressel (2009) found that classical knowledge of ***Marchantia*** fertilization did not always fit reality. Following a fire, ***Marchantia polymorpha*** (Figure 27) spread rapidly. Both gemmae and sexual reproduction are most likely responsible. Rather than relying entirely on splash from antheridiophores, the sperm are actively discharged from the antheridial heads to as much as 15 cm above it (Shimamura *et al* 2008). Duckett and Pressel found that every archegoniophore in this large patch had achieved fertilization, some of which were several decimeters from the nearest male. Some archegonial heads bore as many as 30-50 sporophytes with more mature ones near the ends of the arms and younger ones nearer the central stalk. Dye splashed on the antheridial heads landed up to 30 cm away, hardly explaining the distances at which some archegonia were fertilized, more than 90% of the dye solution was readily absorbed by the antheridial heads. The dye quickly moved to the ground level (within

minutes). Within an hour the dye had spread throughout the rhizoids of the entire 10 cm diameter colony. Upward movement to archegonial heads was a bit slower but nevertheless reached the heads in 30-60 minutes.

As early as 1950, Benson-Evans observed the remarkable dispersal of spermatozoids from ***Conocephalum conicum*** (Figure 32). She found that they are "vigorously" dispersed into the air through an ejection mechanism, but also that mites, known as dispersal vectors in other Marchantiales, were probably not involved. She found that the dry antheridia, such as those following a hot day, would eject the spermatozoids in a fine mist that occurred in regular puffs. If these plants were put into direct sunlight, the activity increased enough that the packets of sperm were visible to the unaided eye.

Shimamura *et al*. (2008) have successfully filmed <http://www.youtube.com/watch?v=ALGDLzWcvnU> the remarkable dispersal of **sperm** from the antheridia (Figure 32) of ***Conocephalum conicum*** (Figure 32). In ***Conocephalum***, there is no splash platform, and instead the sperm are ejected from the antheridium in a cloud that rises into the air several centimeters (Shimamura 2008), a phenomenon originally described by Cavers (1903), and again by Muggoch & Walton (1942) and Benson-Evans (1950). In Hiroshima, Japan, these sperm are typically dispersed in April to May. Shimamura (pers. comm. 2008) relayed to me that they were able to detect many airborne sperm on a sunny day after a rain shower. After a week of dry, sunny conditions, sperm were dispersed following a rainy day, resulting in most of the mature antheridiophores being empty. In the lab, antheridia can be persuaded to release their sperm by misting them. The intense lighting for photography also seemed to help. Initially, the sperm in these droplets are non-motile. Touching the droplets causes them to swim (Masaki Shimamura, Bryonet 3 January 2008), suggesting that these might be packets that must be broken for the sperm to begin swimming (Muggoch & Walton 1942) (see Figure 80).

Figure 32. ***Conocephalum conicum*** males showing **antheridial heads**. The polygon shapes delineate the internal chambers and the tiny dot visible in the middle of some is the pore. Photo by John Hribljan, with permission.

At this stage, the archegoniophore has not extended and the archegonia are near the main thallus (Figure 33), making transfer of sperm easier. As in our traditional understanding of ***Marchantia***, the archegoniophore elongates following fertilization (Figure 34) and the capsules form on the underside of the archegonial head (Figure 35-Figure 37), extending from the archegonial wall. Des Callaghan has provided us with a film of liverwort sperm swimming <http://youtu.be/Jdh8flxvZgk>, demonstrating how they are able to reach the archegonia. Splashing can bring them close to the archegonia, but they must swim to reach the archegonial neck and enter it.

Figure 33. ***Conocephalum conicum*** showing young **archegoniophores**, probably before they are mature enough for fertilization. Photo by Dick Haaksma, with permission.

Figure 34. ***Conocephalum conicum*** **archegoniophores** with elongated stalks. Photo by Janice Glime.

Figure 35. ***Conocephalum conicum*** (**Marchantiopsida**) **archegoniophores** with capsules. Photo by Hermann Schachner through Wikimedia Commons.

Figure 36. Mature archegonial head of ***Conocephalum salebrosum***, showing capsules. Photo by Barry Stewart, with permission.

Figure 37. ***Conocephalum conicum*** capsules on ventral side of archegonial head. Photo by Hermann Schachner through Wikimedia Commons.

Like ***Marchantia*** (Figure 18, Figure 20), ***Conocephalum*** has a spongy photosynthetic layer in the thallus (Figure 38). The life cycle for ***Marchantia*** applies equally well to ***Conocephalum***, except for the lack of an antheridiophore, and is illustrated in Figure 39. Sexual structures of ***Cyathodium spruceanum*** (**Marchantiopsida**) are illustrated in Figure 46. Examples of species of **Marchantiopsida** and **Jungermanniopsida** are in Figure 40.

Figure 38. Cross section of thallus of ***Conocephalum conicum*** showing photosynthetic cells. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

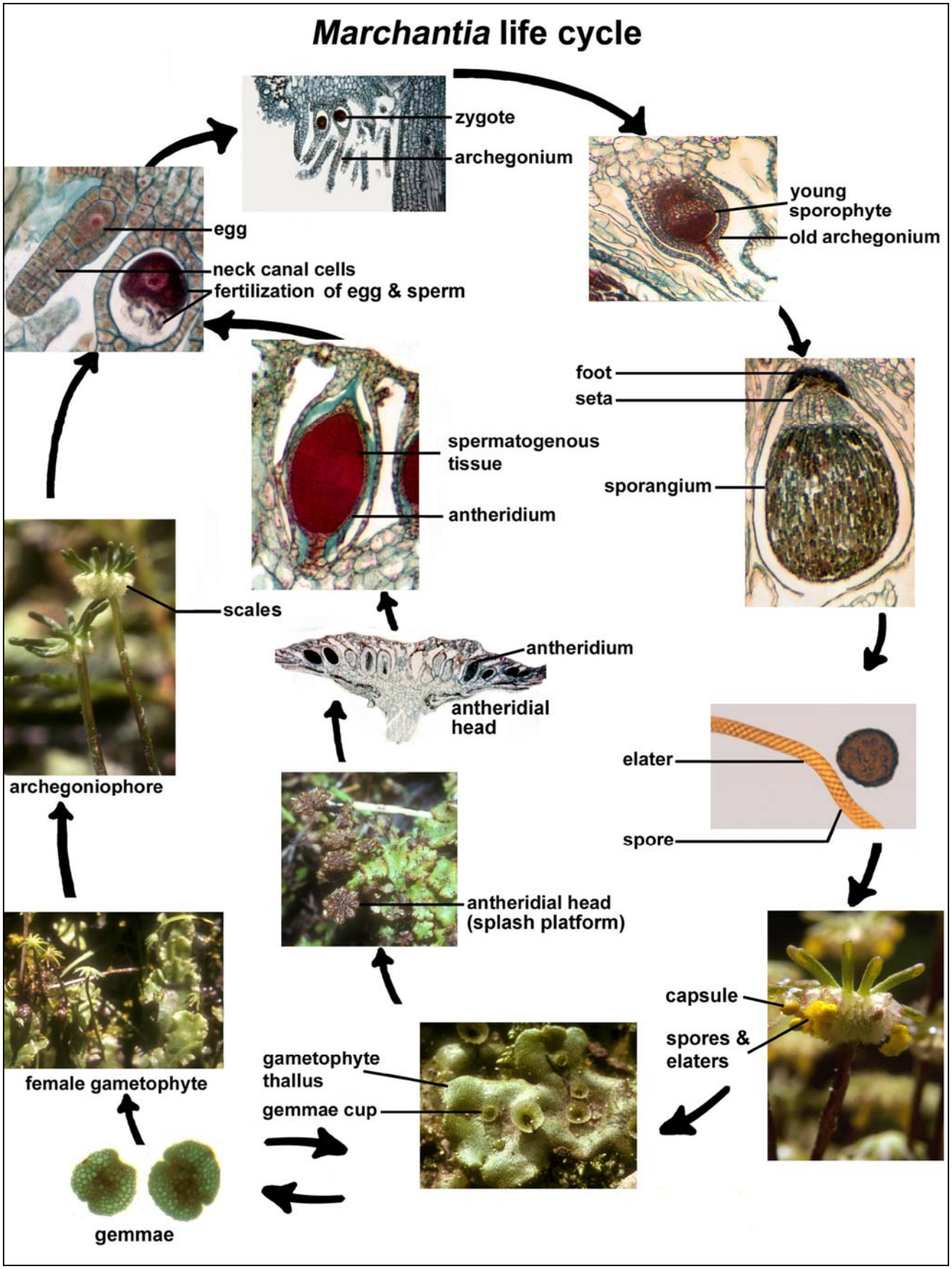

Figure 39. Life cycle of ***Marchantia polymorpha***, showing dominance of the gametophyte generation. Photos by Janice Glime, photomicrographs from botany teaching collection of Michigan State University, and spore and elater modified from photo by Noris Salazar Allen.

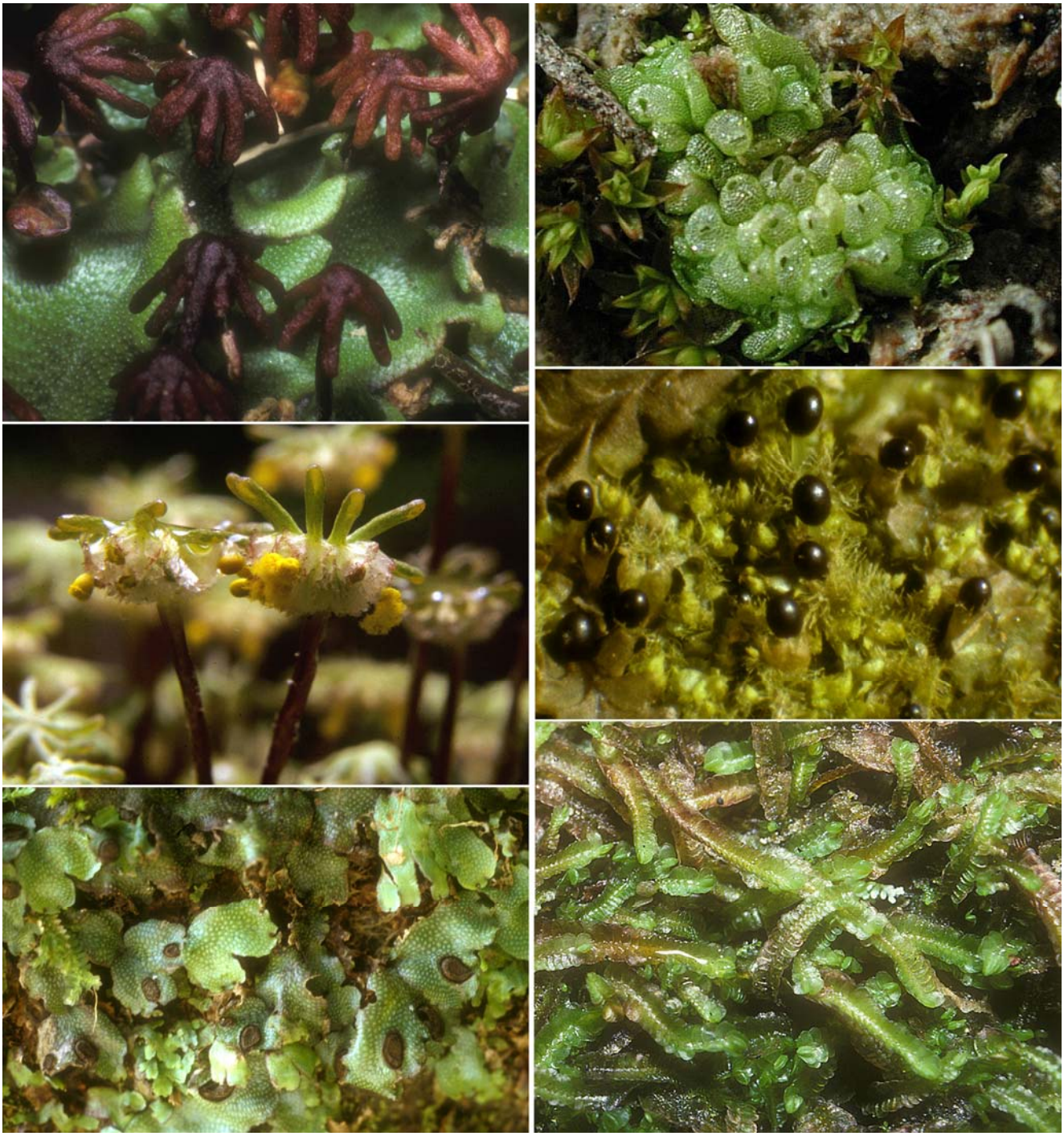

Figure 40. Examples of **Marchantiophyta**. **Left: Marchantiopsida** – **left upper:** ***Marchantia polymorpha*** with archegoniophores; **left middle:** mature sporophytes hanging from archegoniophores of ***Marchantia polymorpha***; **left lower:** ***Conocephalum conicum*** showing antheridial patches on the thallus. **Right upper:** ***Sphaerocarpus texanus*** thallus (**Marchantiopsida**) with involucres surrounding archegonia; **right middle:** ***Blepharostoma trichophylla*** (**Jungermanniopsida**), a leafy liverwort with finely divided leaves and protruding sporophyte capsules; **right lower:** ***Odontoschisma prostratum*** (**Jungermanniopsida**), a leafy liverwort. Photos by Janice Glime; upper right photo of ***Sphaerocarpus texanus*** by Michael Lüth, with permission.

Class Jungermanniopsida

Jungermanniopsida lack dichotomous forking, internal air spaces, dorsal pores, ventral scales, and pegged rhizoids. They may be ribbon-like, thallose, or leafy. Many have oil bodies (isoprenoid essential oils). The role of oil bodies is unclear, but they may help to prevent desiccation damage or to protect against UV light. Yet, those seem like strange functions if the oil bodies disappear upon drying. On the other hand, species that typically live in dry habitats seem less subject to oil body disappearance. Goebel and Balfour (1905) suggested that they are the source of the unique odors found in many of the liverworts, particularly the thallose taxa. The **Jungermanniopsida** are divided into two subclasses: **Metzgeriidae** and **Jungermanniidae**.

Metzgeriidae

Plants in the subclass **Metzgeriidae** (Figure 41-Figure 45) are thalloid or ribbon-like, except that some members of ***Fossombronia*** (Figure 44) appear leafy, while having only one initial cell instead of 2-3 as in other members (Renzaglia 1982). But despite their thalloid nature, other features seem to place the **Metzgeriidae** within the **Jungermanniopsida**. They lack true dichotomous forking (although pseudodichotomies occur), and their tissues are solid, lacking internal air spaces. They also **lack dorsal pores** and **ventral scales**, and the **rhizoids** are all smooth, and never in clumps as in **Jungermanniidae**. Cells often have **oil bodies** (Figure 50), although these disappear upon drying.

Figure 41. Thallose liverwort ***Metzgeria conjugata*** in the Class **Jungermanniopsida**, subclass **Metzgeriidae**. Photo by Michael Lüth, with permission.

Figure 42. ***Metzgeria furcata*** thallus cross section. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 43. Neotropical ***Metzgeria***. Photo by Michael Lüth, with permission.

Figure 44. ***Fossombronia husnotii***, a "leafy" liverwort in the **Jungermanniopsida**, subclass **Metzgeriidae**. Some members of this genus appear thallose (but ruffled), and their single apical initial and developmental pattern suggest a transition between the two growth types within the **Jungermanniopsida**. Photo by Michael Lüth, with permission.

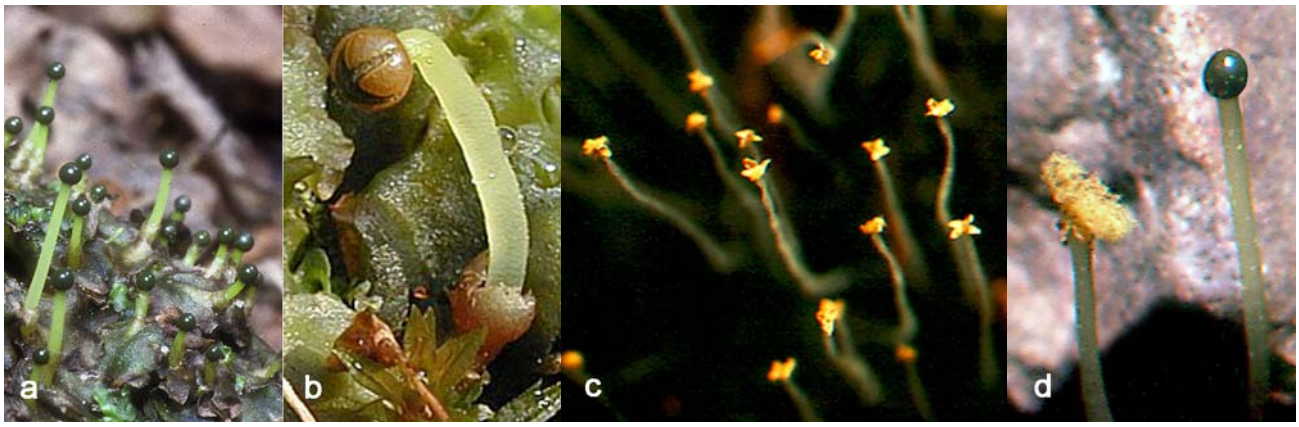

Figure 45. ***Pellia***, a thalloid liverwort in the class **Jungermanniopsida**, subclass **Metzgeriidae**. Note the watery, colorless setae with the globose, inoperculate capsules. **a:** undehisced capsules and setae. **b:** capsule splitting into four valves. **c:** dehisced capsules showing four valves. **d:** dehisced capsule (left) looking fuzzy due to elaters and undehisced capsule (right). Photos a, c, & d by Janice Glime. Photo b by Michael Lüth, with permission.

Figure 46. ***Cyathodium spruceanum*** (**Marchantiopsida**). **Left:** male plants; R = male receptacles. **Right:** female plants; ES = sporophytes; arrows = involucres. Photos courtesy of Noris Salazar Allen.

Jungermanniidae

Members of the subclass **Jungermanniidae** are leafy and usually branching. These are the leafy liverworts. They often have reduced underleaves (Figure 47) that at least in some cases can develop into a third row of normal leaves if the plant is supplied with an ethylene inhibitor (Basile & Basile 1983). The leaves are never more than one cell thick, never have a costa or rib, and unlike the mosses, are often toothed or lobed (Figure 48-Figure 49). The leaves typically have oil bodies (Figure 50), membrane-bound, terpene-containing organelles unique to liverworts, in all their cells, although these usually disappear upon drying.

Figure 47. ***Calypogeia integristipula*** (Class **Jungermanniopsida**) showing the dorsiventral orientation of the plant and the underleaves. Photo by Michael Lüth, with permission..

Figure 48. ***Bazzania trilobata***, a leafy liverwort in the Class **Jungermanniopsida**. Note the two stolons on the ventral side. Photo by Janice Glime.

Figure 49. ***Bazzania trilobata***; note the two-ranked leaves and top-bottom (**dorsi-ventral**) orientation. Photo by Janice Glime.

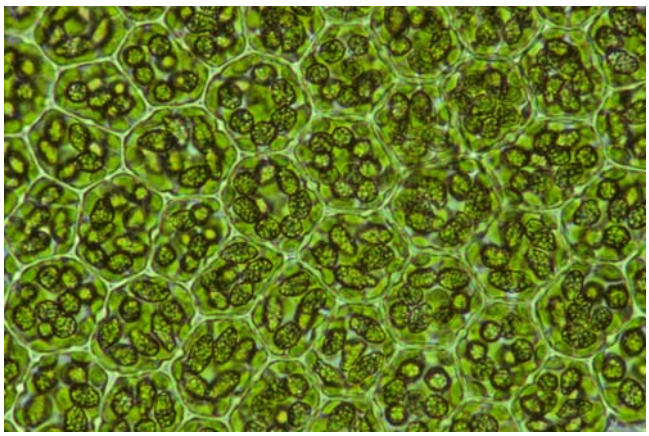

Figure 50. Leaf cells of the leafy liverwort ***Frullania davarica*** (**Jungermanniopsida**). Note the oil bodies resembling bunches of grapes and the numerous small chloroplasts clumped around the periphery of cells. Cell walls also have **trigones** (swellings in the walls). Photo by Zen Iwatsuki, with permission.

In the leafy liverworts, the leaf may be folded to create a pocket or pouch (**lobule**; Figure 51), usually on the lower side, but the smaller lobe may occur on the upper side in such genera as ***Scapania*** (Figure 52). Rhizoids, unlike those in the **Metzgeriidae**, usually occur in clumps at bases of underleaves (Figure 53).

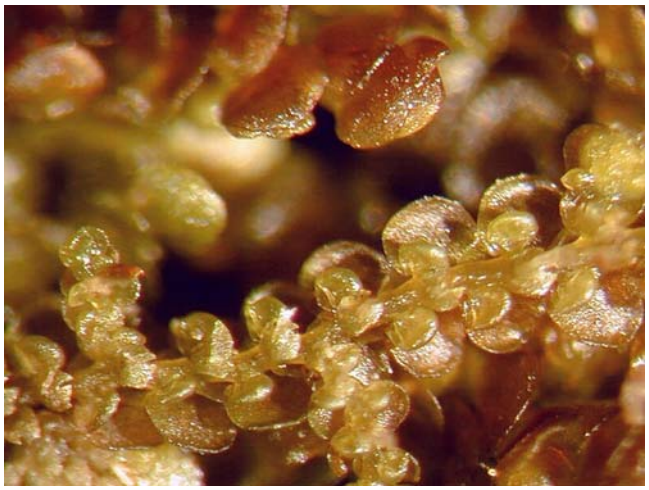

Figure 51. ***Frullania dilatata*** (Class **Jungermanniopsida**), a leafy liverwort showing the ventral (under) side of the stem with hood-shaped lobules under each leaf and underleaves on the stem. Photo by Michael Lüth, with permission.

Figure 52. ***Scapania gracilis*** showing leaves folded up to the dorsal side. Photo by Jan-Peter Frahm, with permission.

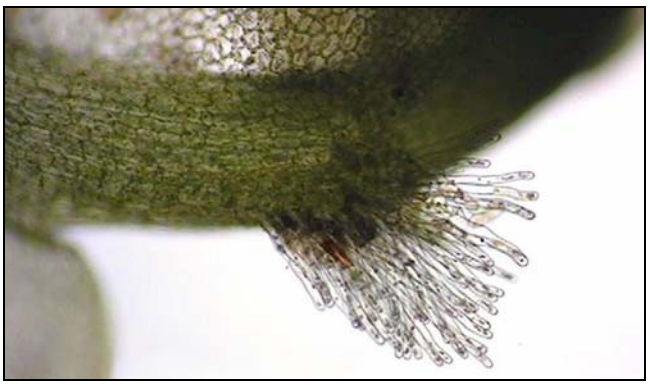

Figure 53. ***Chiloscyphus polyanthus*** with a clump of rhizoids at the base of the underleaf. Photo by Paul Davison, with permission.

In all the bryophyte phyla, the spore is a **meiospore** (produced by meiosis and therefore 1*n*; Figure 54-Figure 56). These structures can be variously decorated and their size and decorations can contribute to their dispersal ability. Germination (Figure 56) in liverworts is apparently inhibited inside the capsule, thus occurring only after capsule **dehiscence** (splitting apart) and spore dispersal (Figure 57-Figure 59).

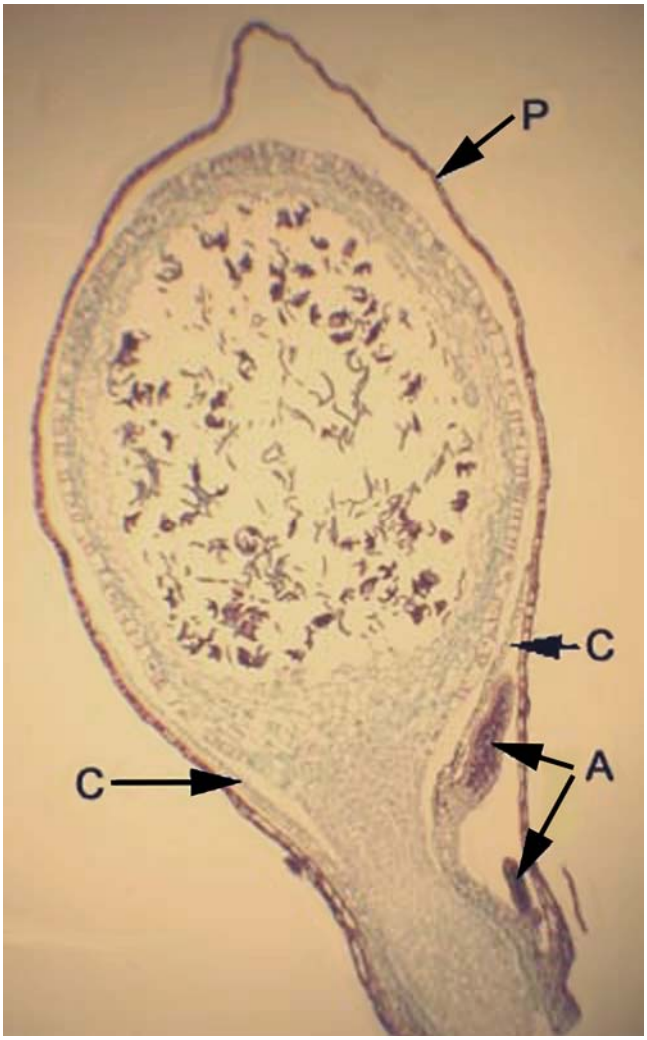

Figure 54. ***Porella navicularis*** capsule with meiospores and elaters. Photo from University of British Columbia website, with permission.

Figure 55. ***Noteroclada confluens*** (Metzgeriidae) meiospores and elaters. Photo by George Shepherd, through Creative Commons.

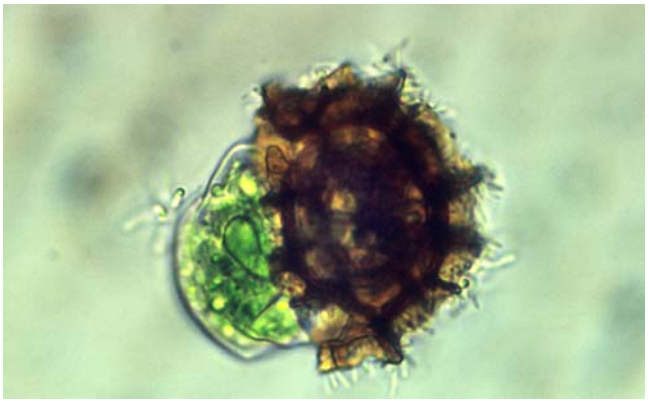

Figure 56. ***Fossombronia angulosa*** protonema emerging from spore. Photo by Plant Actions through Eugenia Ron Alvarez, with permission.

Figure 57. ***Lophocolea*** capsule. Photo by George Shepherd, through Creative Commons.

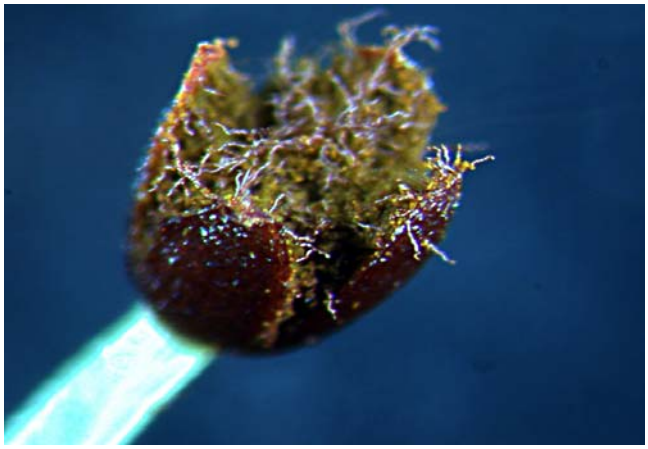

Figure 58. ***Lophocolea*** capsule dehiscing. Photo by George Shepherd, through Creative Commons.

Figure 59. ***Lophocolea*** capsule fully open into four valves. Photo by George Shepherd, through Creative Commons.

The spore, once finding a suitable condition of moisture and lighting, germinates (Figure 56-Figure 61). Here, the liverwort **sporeling** differs from that of most mosses. In liverworts the protonema is variable, even within orders, with the protonema ranging from **filamentous** to **thalloid**, but mostly forming only a few cells (Figure 64-Figure 61).

In the leafy liverworts ***Frullania moniliata*** and ***Drepanolejeunea***, as in all **Porellales**, the protonema is formed within the spore (**endosporic**); in ***Cephalozia otaruensis*** it is an **ectosporic** filamentous protonema; in most of the liverworts it is **ectosporic** (developing outside the spore) and thalloid (Figure 61-Figure 65) (Nehira 1966).

Liverworts differ markedly from mosses not only in most species having a thalloid rather than filamentous protonema (exceptions in some Cephaloziaceae), but in producing only one upright plant per protonema. Furthermore, unlike many mosses, they never produce protonemal **gemmae** or other protonemal **propagules** (Schofield 1985) and rarely reproduce by fragments (Crum 2001). [See Glime (1970) for a new plant produced by a fragment in ***Scapania undulata*** (Figure 66)]. Nevertheless, in all bryophytes the sporeling is quite different in structure and appearance from the mature gametophyte that will develop from it.

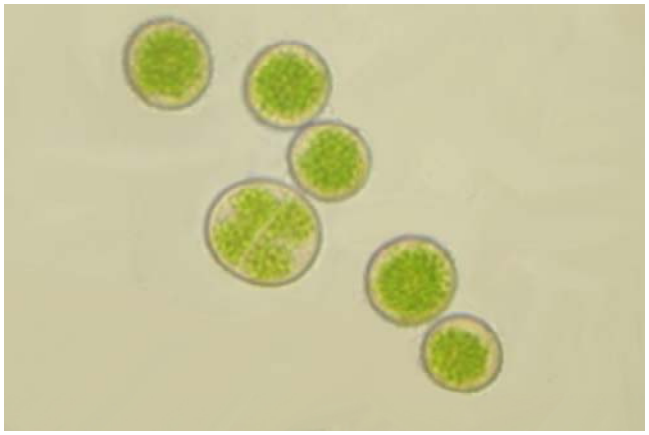

Figure 60. ***Radula recubans*** spores and protonema. Photo by Adaíses Simone Maciel da Silva, with permission.

Figure 61. ***Radula recubans*** protonema. Photo by Adaíses Simone Maciel da Silva, with permission.

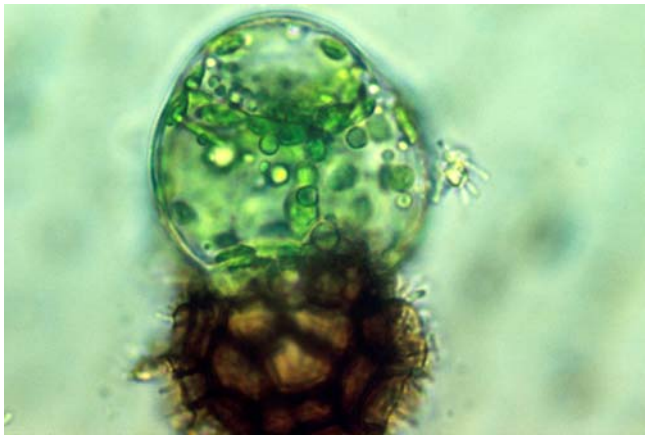

Figure 62. ***Fossombronia angulosa*** protonema. Photo by Plant Actions through Eugenia Ron, with permission.

Figure 63. ***Fossombronia caespitiformis*** protonema. Photo by Plant Actions through Eugenia Ron, with permission.

Figure 64. ***Sphaerocarpus texanus*** protonema. Photo by Plant Actions through Eugenia Ron, with permission.

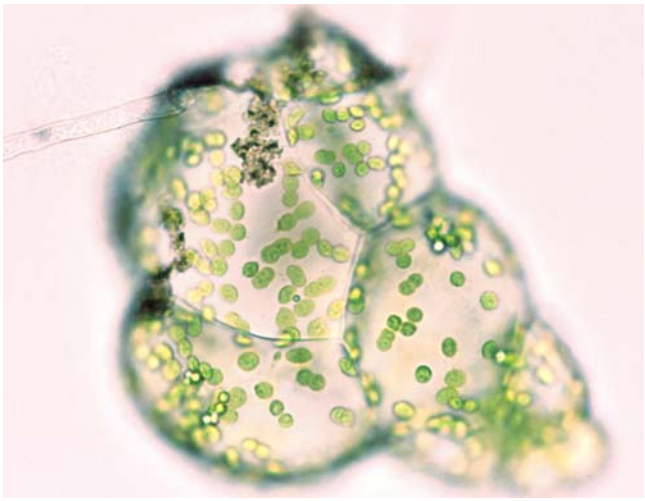

Figure 65. Thalloid protonema of the thallose liverwort ***Cyathodium foetidissimum***. Photo courtesy of Noris Salazar Allen.

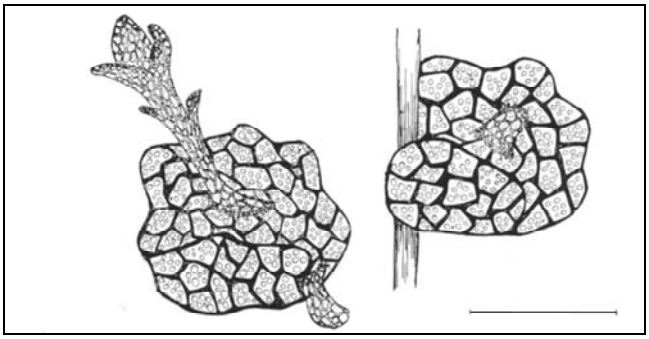

Figure 66. ***Scapania undulata*** showing young plant and two beginnings of plants from leaf fragments. Drawings by Flora Mace from Glime 1970.

But what links the thallose liverworts to the leafy ones? Steenbock *et al*. (2011) reported an interesting find from Vancouver Island, British Columbia, Canada. In the Eocene flora, they found a liverwort unlike any currently known, either as fossils or extant. This liverwort had three-ranked leaves arranged in a spiral, with the underleaves **larger** than the lateral leaves. The rhizoids were in fascicles associated with all three ranks of leaves. These and other characters caused them to name a new family, the Appianaceae, based on the name of the type locality at the

Appian Way. This arrangement of leaves is reminiscent of the leaf arrangement in ***Haplomitrium*** (Figure 67-Figure 68). The genus ***Treubia*** (Figure 69) is yet another unusual liverwort (Anonymous 2010) and appears to be one of the basal groups among liverworts. This liverwort might be described as a thallus with leaves. It is intermediate between thallose and leafy liverworts and is most closely related to ***Haplomitrium***.

Figure 67. ***Haplomitrium gibbsiae*** plants demonstrating the three-ranked leaves in this family. Photo by Jan-Peter Frahm, with permission.

Figure 68. ***Haplomitrium hookeri*** showing young capsules. Photo by David Holyoak, with permission.

Figure 69. ***Treubia lacunosa***. Photo by Jan-Peter FFrahm, with permission.

Within the Jungermanniopsida, the **gametophore**, or mature gametophyte, can be either of two forms, depending on the family. The thalloid form has a blade-like appearance and usually produces its antheridia and archegonia within the thallus. The leafy liverworts produce their antheridia (Figure 70-Figure 73) and archegonia (Figure 74-Figure 79) along branches.

Figure 70. ***Porella navicularis*** antheridial branch. Photo from Botany 321 University of British Columbia website, with permission.

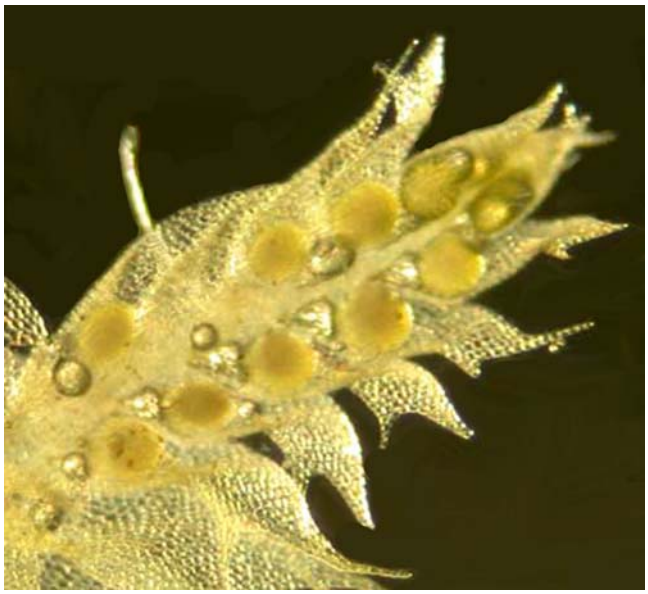

Figure 71. ***Lophocolea cuspidata*** male branch showing location of antheridia among leaves. Photo from Botany 321 at University of British Columbia website, with permission.

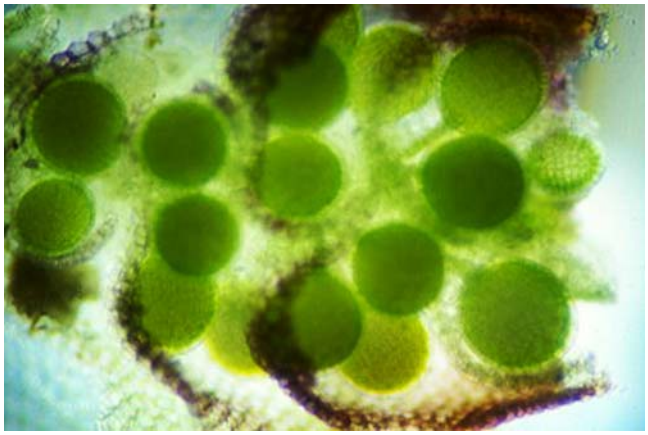

Figure 72. ***Lophozia capitata*** antheridia. Photo by Paul Davison, with permission.

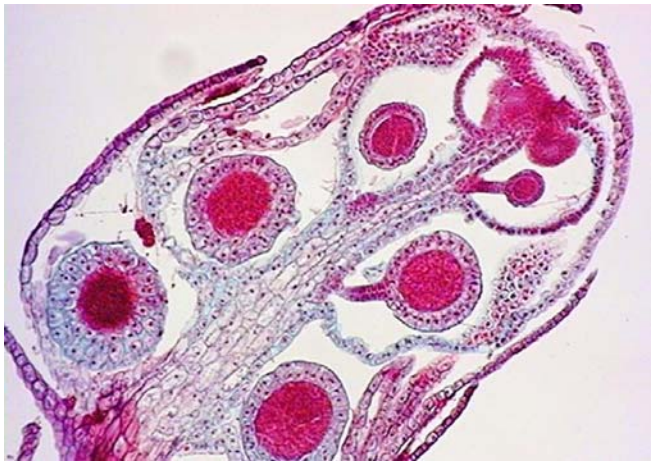

Figure 73. ***Porella*** sp. branch showing location of antheridia. Photo by Paul Davison, with permission.

Figure 74. ***Lophocolea cuspidata*** in its log habitat. Photo from Botany 321 at University of British Columbia website, with permission.

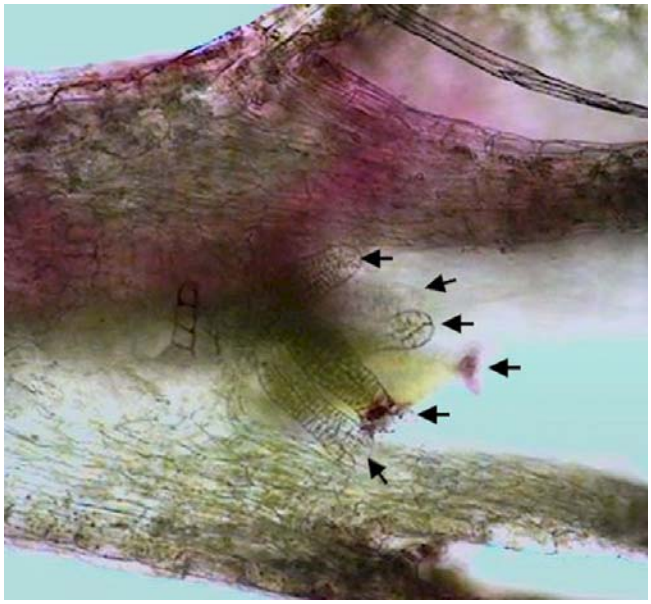

Figure 75. ***Jungermannia evansii*** archegonia at leaf base. Photo by Paul Davison, with permission.

Figure 76. ***Lophocolea cuspidata*** archegonia. Photo from Botany 321 at University of British Columbia, website, with permission.

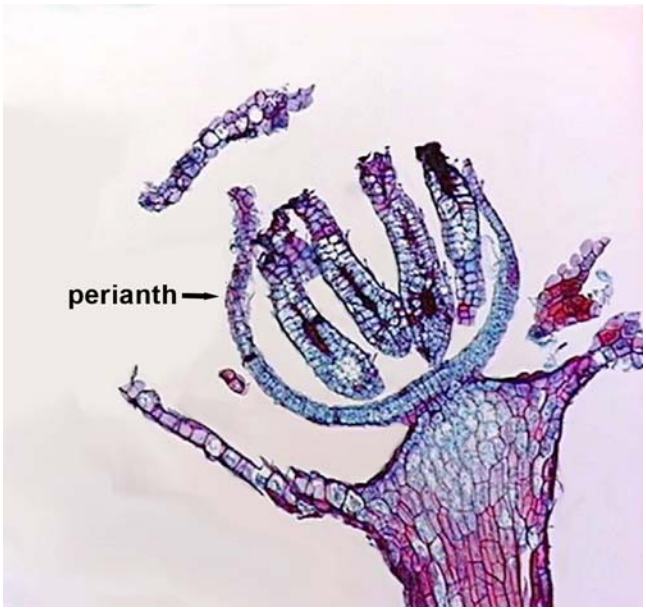

Figure 77. ***Porella*** archegonia in perianth. Photo by Paul Davison, with permission.

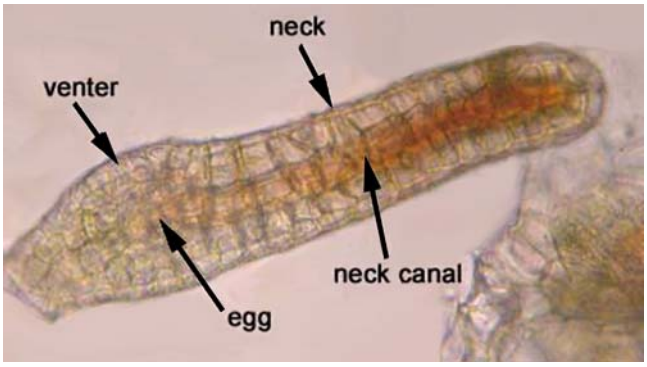

Figure 78. ***Porella navicularis*** archegonium. Photo by Jannah Nelson through Botany 321, University of British Columbia website, with permission.

Figure 79. ***Pellia epiphylla*** archegonium. Photo by Plant Actions through Eugenia Ron Alvarez, with permission.

Mucilage filaments usually occur among the gametangia (Schofield 1985), presumably helping them to retain water and to help squeeze the antheridia when it is time for sperm to emerge.

Once reaching a female plant, the biflagellate sperm presumably swim, in all cases, to the archegonium. In some genera, for example the thallose ***Aneura*** (**Marchantiopsida**), it may take several hours for the sperm to travel a mere 10 mm (Showalter 1925 in Walton 1943). In fact, in many taxa, it is the **spermatocytes** (cells that become converted into sperm), prior to sperm release, that travel across the thallus by means of surface tension over the free water surface (Figure 80). This is at a much faster rate of 20 mm per minute (Muggoch & Walton 1942).

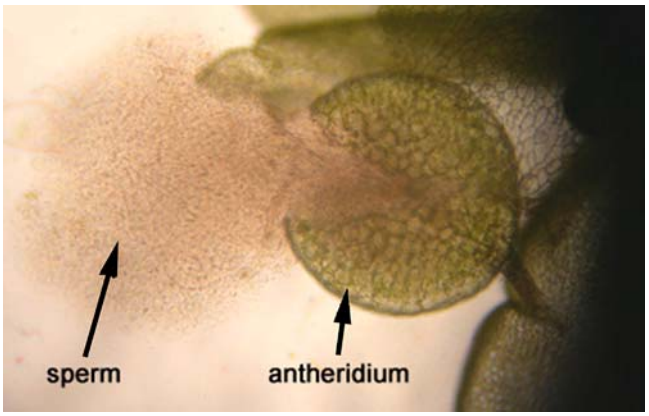

Figure 80. ***Porella navicularis*** (**Jungermanniopsida**) antheridium expelling sperm. Photo by Jonathan Choi, through Botany 321 University of British Columbia website, with permission.

By contrast to these earlier observations of Muggoch and Walton (1942), in ***Pellia***, the emerging **spermatocytes**, in this case housing the sperm within a membrane, emerge from the dehiscing antheridium in grey masses. These masses spread rapidly across the wet surface, breaking apart as they reach the surface, with sperm emerging in about 15 seconds. It takes only 15 seconds for these spermatocytes to reach the archegonial **involucre** (protective sheath of tissue of thallus origin surrounding single antheridium, archegonium, or sporophyte; Figure 81). Another 15 minutes is required for the free sperm to emerge from the spermatocyte. Thus, the sperm disperse and are ready to enter the archegonia in little more than 15 minutes from the time of antheridial dehiscence. Such rapid movement could not be achieved by the slow-swimming sperm, which would require hours to achieve the same distance, often failing to reach their destination before the necessary water was gone.

Figure 81. ***Pallavicinia lyellii*** (**Metzgeriidae**) showing filamentous fringe of the involucre where archegonia are located on the thallus. **F** denotes female gametophyte; **M** denotes male gametophyte. Photo by Noris Salazar Allen, with permission.

Following fertilization, the stalk supporting the archegonial head elongates and elevates the archegonial head several cm above the thallus where the capsule enlarges. This is of little advantage, it would seem, until the sporophytes are mature and the spores ready for dispersal. When the spores are mature, the capsules (sporangia) split (with very few exceptions having a lid), revealing the spores and **elaters** (in **Marchantiophyta**, elongate one-celled structures with two spiral thickenings and associated with spores).

In **Jungermanniidae**, the antheridia are not imbedded, but occur at the bases of leaves, whereas the archegonia are at the ends of stems or branches, surrounded by a **perianth** (Figure 82), and that is again surrounded by an **involucre** of two **bracts** and often a **bracteole**, all of which are often joined. The capsule develops inside the **perichaetium** (modified leaves that surround the archegonia), but ultimately sits atop an elongate, **hyaline** (colorless), delicate **seta** (stalk; Figure 83-Figure 85) that soon withers away. The capsule itself opens by four valves and usually contains **elaters**.

Figure 82. ***Frullania*** sp. perianth. Photo by George Shepherd, through Creative Commons.

Figure 83. ***Porella navicularis*** with young sporophyte emerging, through Botany 321 University of British Columbia website, with permission.

Figure 84. ***Lophocolea cuspidata*** perianth and developing sporophyte. Photo through Botany 321 University of British Columbia website, with permission.

By contrast to the mosses, liverworts lack a split-off **calyptra** (covering of capsule formed from upper part of torn archegonial wall) and the capsule matures while it is still immersed among the protecting leaves. As the capsule (sporangium) expands, the archegonial wall is ruptured and remains at the base of the sporangial stalk. In contrast to the **Marchantiopsida** taxa that may have thalloid stalks supporting the archegonia and ultimately the capsules (*e.g.* ***Marchantia***), and the sporophyte stalk remains small and is typically not visible among elevated scales and thallus, in the Jungermanniopsida the sporophyte stalk is conspicuous. In leafy taxa (**Jungermanniidae**) and other thalloid taxa this sporangial stalk elongates only after the capsule matures. The stalk elongates (in leafy liverworts) by rapid (3-4 days) elongation of the watery stalk (**seta**) cells (Bold *et al.* 1987) and extends the capsule away from the plant (Figure 85), using turgor pressure within the delicate cells to maintain this position. This **seta** supports and extends the capsule of most mosses and liverworts.

Figure 85. ***Lophocolea heterophylla*** with mature sporophytes. Photo by David Holyoak, with permission.

The spores are all of equal maturity and all ready for dispersal at the same time (Schofield 1985). Once the spores are shed, the deliquescent stalk soon collapses and the capsule disintegrates.

Liverworts frequently produce **gemmae** that occur on leaves of leafy liverworts (Figure 86-Figure 91) or on the thallus of thallose taxa (Figure 92). These permit the plants to reproduce asexually in places where sexual reproduction is unsuccessful. As will be discussed in a later chapter, this is especially important when the sexes are on separate plants. These gemmae are often useful for taxonomic purposes because they have a variety of shapes and colors.

Figure 86. ***Tritomaria exsecta*** (**Jungermanniidae**) showing gemmae on leaf tips (**light brown**; see also Figure 87). Photo by Michael Lüth, with permission.

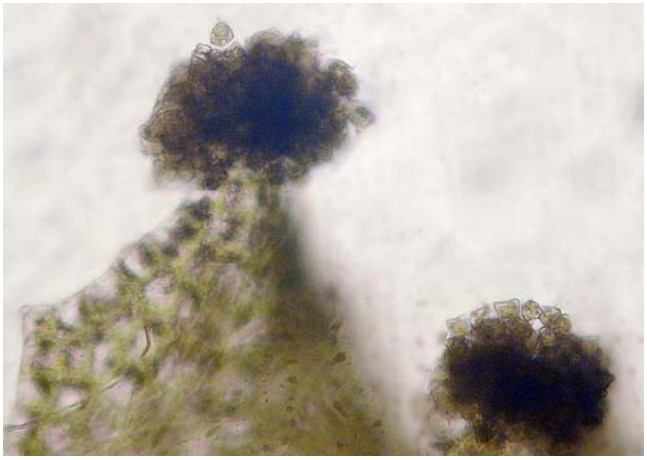

Figure 87. Microscopic view of ***Tritomaria exsectiformis*** leaf tips with gemmae. Photo by Michael Lüth, with permission.

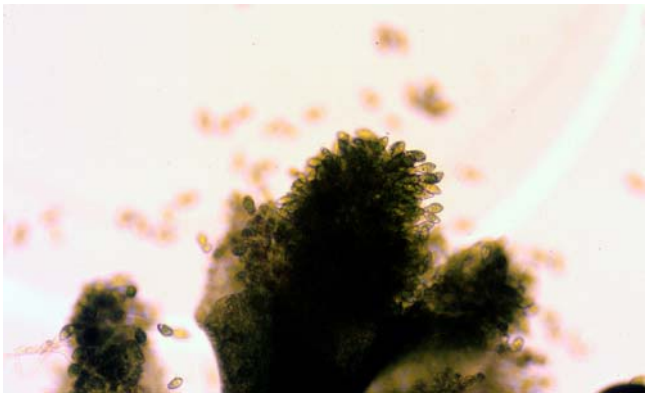

Figure 88. ***Scapania aspera*** gemmae on leaf tips. Photo from PlantActions through Eugenia Ron Alvarez, with permission.

Figure 89. ***Anastrophyllum hellerianum*** with terminal leaf gemmae. Photo by Des Callaghan, with permission.

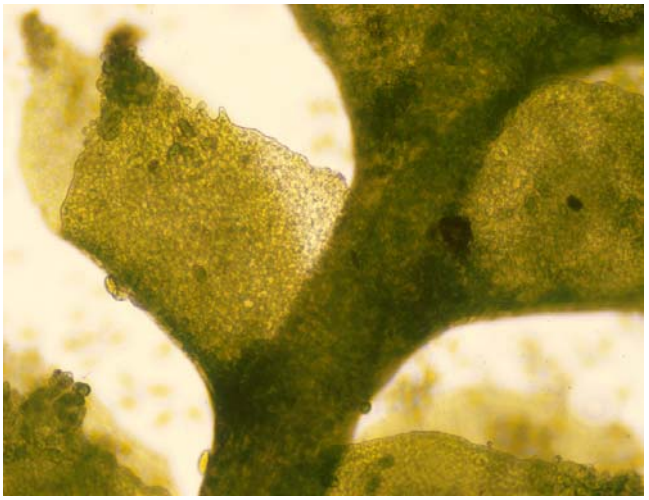

Figure 90. ***Scapania aspera*** with gemmae on leaves. See Figure 91. Photo from PlantActions through Eugenia Ron Alvarez, with permission.

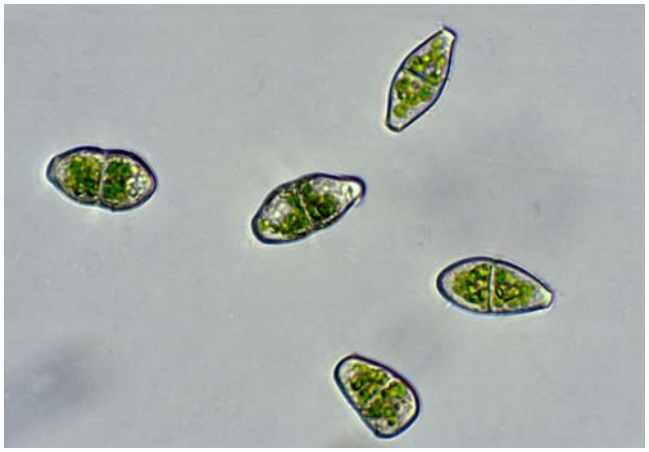

Figure 91. Gemmae of ***Scapania aspera***. Photo from PlantActions through Eugenia Ron Alvarez, with permission.

Figure 92. Arrow indicates gemmae on the thallus of ***Blasia pusilla*** (Metzgeriidae). Photo by Michael Lüth, with permission.

Summary

Marchantiophyta are distinguished from the phylum Bryophyta by their **dorsi-ventral orientation**, **unicellular rhizoids**, **inoperculate capsules**, **absence of a columella**, and **no stomata** in the capsule. Marchantiophyta are generally considered to have two classes: **Marchantiopsida** (thallose liverworts) and **Jungermanniopsida**, including **Metzgeriidae** (thallose liverworts) and **Jungermanniidae** (leafy liverworts).

Marchantiophyta have a dominant gametophyte generation with a dependent, short-lived sporophyte. The life cycle involves a **protonema** that develops from the germinating spore, becoming thalloid or globose in most liverworts. The protonema produces a **bud** that develops into a **leafy** or **thallose plant**.

Gametophytes produce **archegonia** and/or **antheridia** and the **embryo** develops within the archegonium.

Sporophytes remain attached to the gametophyte and produce **spores** by **meiosis**. Marchantiophyta produce spores from the sporophyte only once, *i.e.* simultaneously. These spores are dispersed, in most genera, by **elaters** that are produced among the spores and that have spiral thickenings, causing them to twist as moisture changes.

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I appreciate the comments and suggestions of Karla Werner, who offered a beginner's perspective. Noris Salazar Allen offered constructive criticisms on the taxonomic descriptions and helped with the proof reading. Rob Gradstein suggested clarifications and Christine Cargill provided important information and references. Eugenia Ron Alvarez and Tomas Sobota secured permission for me to use images from the PlantActions website and to obtain the original images. Norbert Stapper helped me get an email address needed to obtain permission to use an image. George Shepherd has made many wonderful images available through Creative Commons. As in most of these chapters, images from Michael Lüth and Des Callaghan have been invaluable. Noris Salazar Allen has provided me with several morphological images. Wilf Schofield helped me to obtain permission to use images from the Botany Website at the University of British Columbia. Heino Lepp of the Australian National Herbarium shared his preliminary website information on elaters with me, helping me to find original sources on their mechanisms of dispersal. Thank you to Llo Stark for alerting me to errors and formatting problems in this chapter.

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CHAPTER 2-4
BRYOPHYTA – TAKAKIOPSIDA

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CHAPTER 2-4
BRYOPHYTA – TAKAKIOPSIDA

Figure 1. Mt. Daisetsu from Kogan Spa, Hokkaido, Japan. The foggy peak of Mt. Daisetsu is the home of ***Takakia lepidozioides***. Photo by Janice Glime.

Figure 2. Hunting for ***Takakia*** in its typical damp, high elevation or foggy habitat. Photo with permission from <http://www.botany.ubc.ca/bryophyte/LAB8.htm>.

Phylum Bryophyta

Bryophyta, *sensu stricto* (in their narrowest sense), are the mosses. These comprise, roughly, 13,000 species worldwide (Crum 2001), but with many tropical taxa likely to be as yet undiscovered, the number could be much higher. Three classes have been recognized traditionally, the **Bryopsida**, **Andreaeopsida**, and **Sphagnopsida** (Crum 1991). However, as more evidence from genetic and biochemical relationships have become available, and the interesting genus ***Takakia*** has produced sporophytes in our presence, further division seems justified. Buck and Goffinet (2000) define six classes: **Takakiopsida**, **Sphagnopsida**, **Andreaeopsida**, **Andreaeobryopsida**, **Polytrichopsida**, and **Bryopsida**. Recent cladistic analyses using morphological, developmental, anatomical, ultrastructural, and nucleotide sequencing data supports placement of these classes into a single phylum (Newton *et al*. 2000).

Class Takakiopsida

Takakia seems to be among the most primitive of mosses, possessing many characters similar to those of the liverworts, and is the only known genus of its class, having two species [***T. ceratophylla*** (Figure 6-Figure 23), ***T. lepidozioides*** (Figure 24-Figure 35)]. Its **leaves in groups of fours**, often fused at the base (Figure 5, left), made it immediately stand out as unique. ***Takakia*** was actually discovered in the Himalayas in 1861 by Mitten (Renzaglia *et al*. 1997), but it was described as a species of liverwort in the genus ***Lepidozia***, ***L. ceratophylla***. Then it was forgotten for nearly a century. When it was again discovered high in the mountains of Japan, Sinske Hattori sent it to specialists around the world. The phycologists looked and decided it was not one of theirs, and eventually it produced multicellular archegonia, supporting their claim. The pteridologists concluded it was not a reduced fern, nor a lycopod or other tracheophyte cryptogam. It seemed the more likely choices were mosses and

liverworts. Although its 3-dimensional structure seemed a bit out of place, it seemed most like a liverwort, and there it stayed for several decades (Hattori & Inoue 1998; Hattori & Mizutani 1958). But eventually, its **slime papillae** (Figure 4), its **leaves in 3 rows** (Figure 5), its **simple oil bodies** – not granular as in liverworts, its **archegonia** (Figure 3) sometimes on a **pedestal**, and its archegonial **neck cells** in **6 vertical rows** began to raise questions. Its chromosome number was 4 or 5, unlike the typical 10 in liverworts and even higher numbers in most mosses.

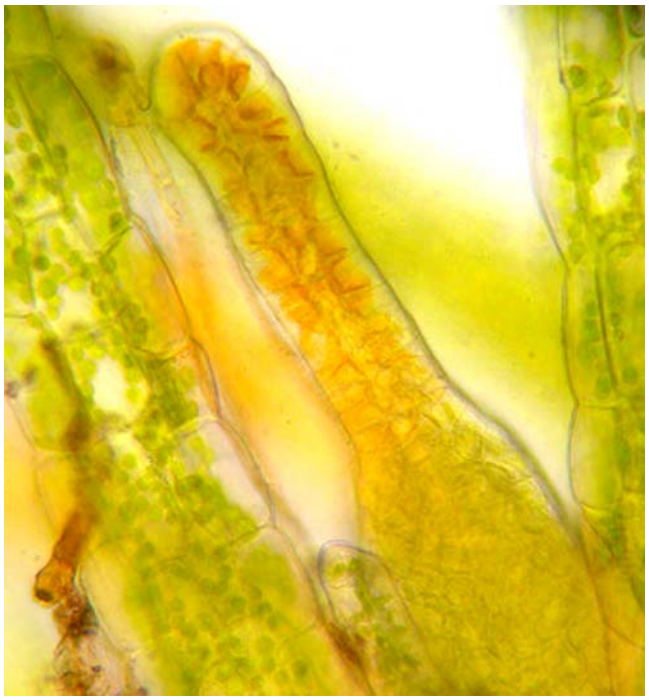

Figure 3. Archegonium of ***Takakia lepidozioides***. Photo with permission from <www.botany.ubc.ca/ bryophyte/LAB8.htm.>.

Then, at one of its former collection sites, it produced capsules (Smith 1990; Smith & Davison 1993)! And there was the proof. Although not too distant from a liverwort capsule, it **dehisced spirally** in a single valve (Figure 5, right), and **no elaters** emerged. Indeed, aside from its **filamentous, divided leaves**, it had much in common with ***Andreaea***, a moss. The spiral line of dehiscence splits and twists, creating a more efficient spore dispersal (Renzaglia *et al*. 1997; Higuchi & Zhang 1998).

Figure 4. Slime papilla of ***Takakia lepidozioides***. Photo with permission from <http://www.botany.ubc.ca/bryophyte/LAB8.htm>.

In trying to resolve the phylogenetic position of ***Takakia***, Schuster (1997) referred to it as "one of a handful of isolated and unique plants." It is like the Monocleales of the liverworts in its longitudinal suture of the capsule and its "feeble conducting strand" of the sporophyte. Its lobed leaves are like those in the Jungermanniales of the liverworts. The leafless horizontal stolons, slime papillae, massive secretions of mucilage, orange antheridia nestled among leaves of all three rows (Figure 5, middle), and absence of rhizoids are characters like those of the Calobryales among the liverworts. Its capsule with 3-4-5 layers and thickened epidermal cells with thin inner cells and its absence of stomata and air spaces resemble ***Symphogyna*** in the Metzgeriales, also a liverwort.

Figure 5. ***Takakia***. **Left:** vegetative plant of ***Takakia lepidozioides*** showing filamentous leaves. **Middle:** leafy plant of ***Takakia ceratophyllum*** with young capsule. **Right:** dehiscing capsule of ***Takakia ceratophyllum*** showing spiral split and exposed spores. Note single suture that splits, hence a single valve. Photo permissions on left from www.botany.ubc.ca/ bryophyte/LAB8.htm; photo in middle from website of the Hattori Botanical Laboratory; photo on right from Ken McFarland, Mosses website, through fair use.

Some of its characters are unlike those of either mosses or liverworts. The antheridia of ***Takakia*** lack perigonia or any structure to surround them, and likewise the archegonia lack perichaetial leaves or any modified surrounding structures.

But it clearly has moss characters as well. The calyptra ruptures distally and is carried by the sporophyte on an elevated capsule. The capsule differentiates and sporogenesis occurs after the seta elongates. The sporophyte is persistent, and the capsule lacks elaters and operculum, but it has a "feeble" **columella** (mass of sterile tissue in center of capsule). Hence, as is often the case in the bryophytes, the gametophyte and the sporophyte tell different stories. In this case, the gametophyte is most like the Marchantiophyta, but the sporophyte is clearly more like members of the Bryophyta. Looking so much like a liverwort, yet also much like a moss, this apparently primitive plant seems an appropriate link between these two major groups.

The genus is distributed in western North America (Queen Charlotte Islands) and central and eastern Asia (Himalayas and mountains of China and northern Japan). The known locations all have cool climates where fog is often present to keep this strange moss moist.

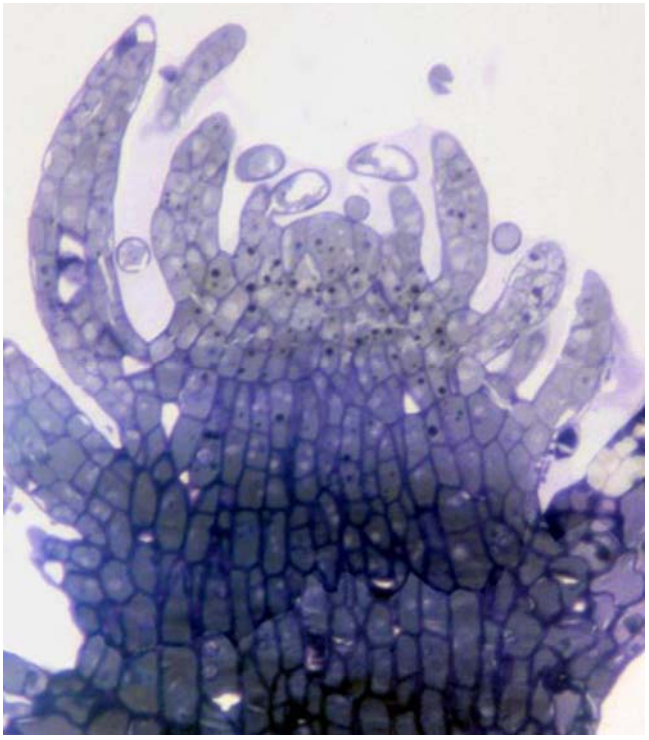

Figure 6. ***Takakia ceratophylla*** longitudinal section of stem tip. Photo by Karen Renzaglia, with permission.

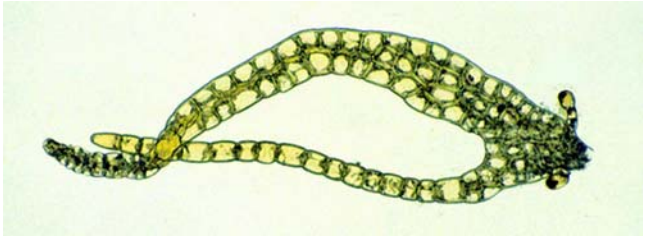

Figure 7. ***Takakia ceratophylla*** leaf. Photo by Karen Renzaglia, with permission.

Figure 8. ***Takakia ceratophylla*** stem stripped of leaves to reveal the antheridia. Photo by Karen Renzaglia, with permission.

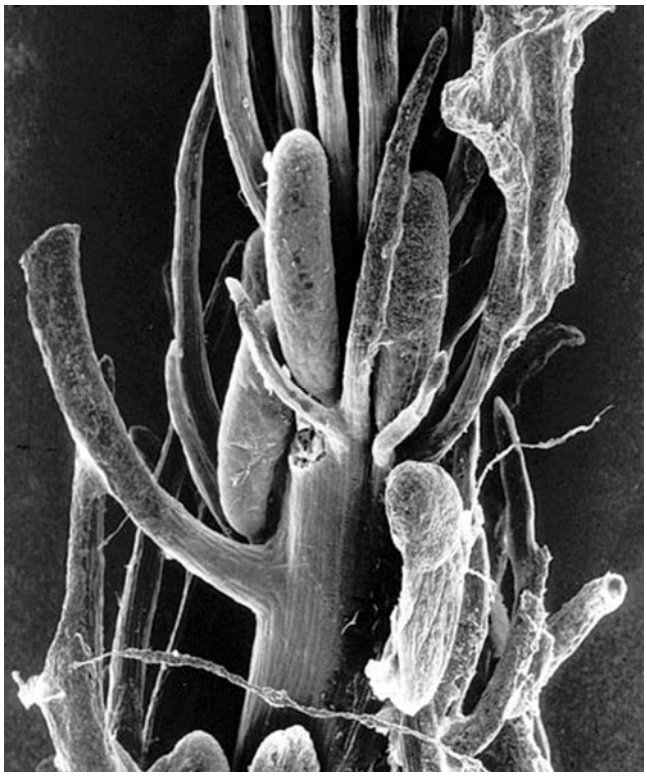

Figure 9. SEM of ***Takakia ceratophylla*** stem stripped of leaves to reveal the antheridia. Photo by Karen Renzaglia, with permission.

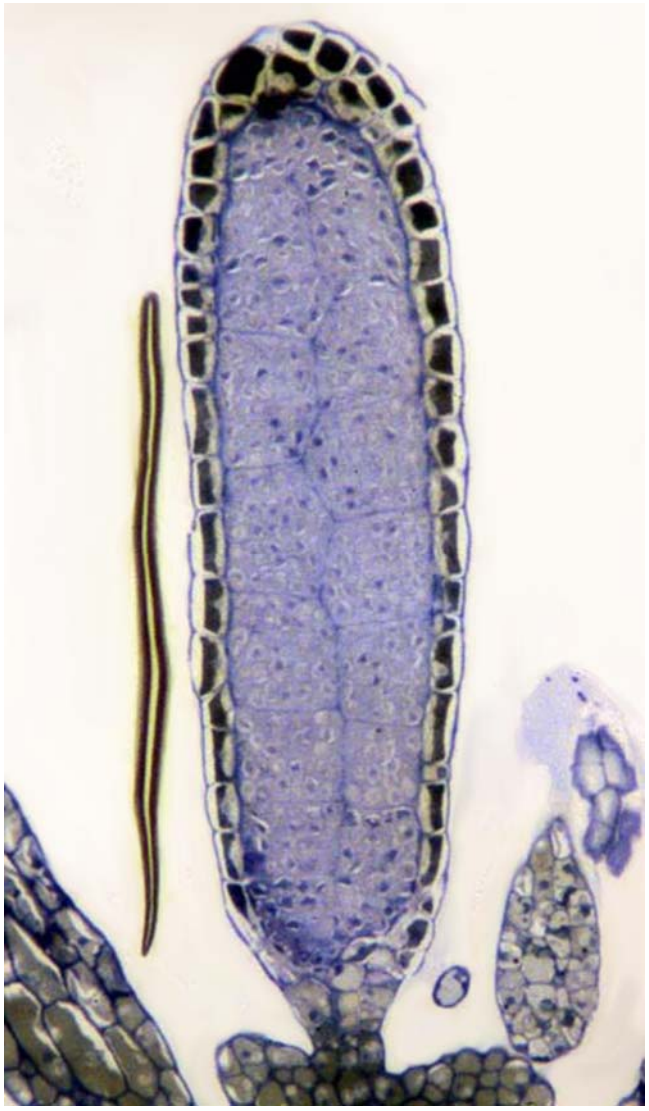

Figure 10. ***Takakia ceratophylla*** antheridium. Photo by Karen Renzaglia, with permission, and modified by Janice Glime.

Figure 11. ***Takakia ceratophylla*** seta and aborted archegonia. Photo by Karen Renzaglia, with permission.

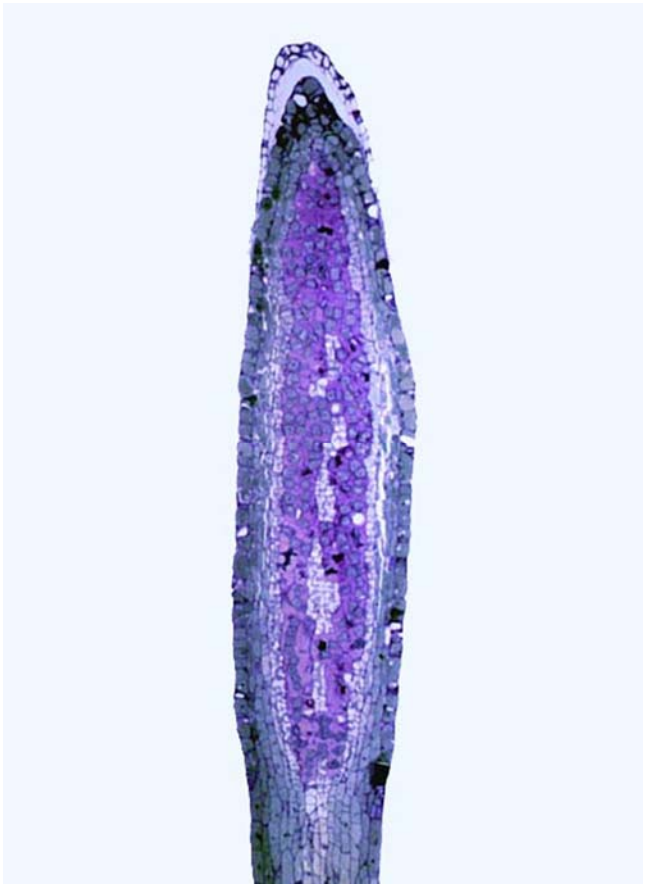

Figure 12. ***Takakia ceratophylla*** longitudinal section of immature capsule and calyptra with glimpses of the columella. Photo by Karen Renzaglia, with permission.

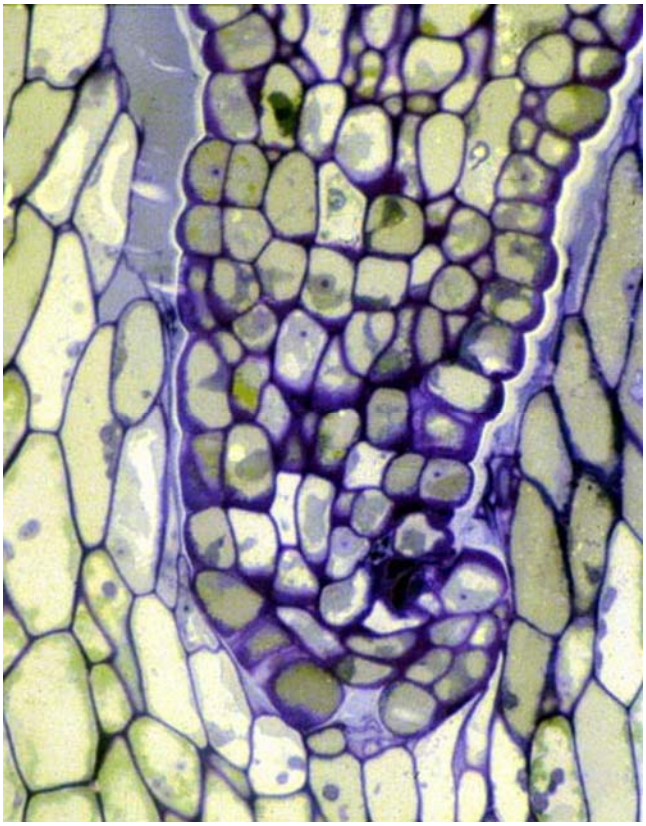

Figure 13. ***Takakia ceratophylla*** sporophyte with hooked foot. Photo by Karen Renzaglia, with permission.

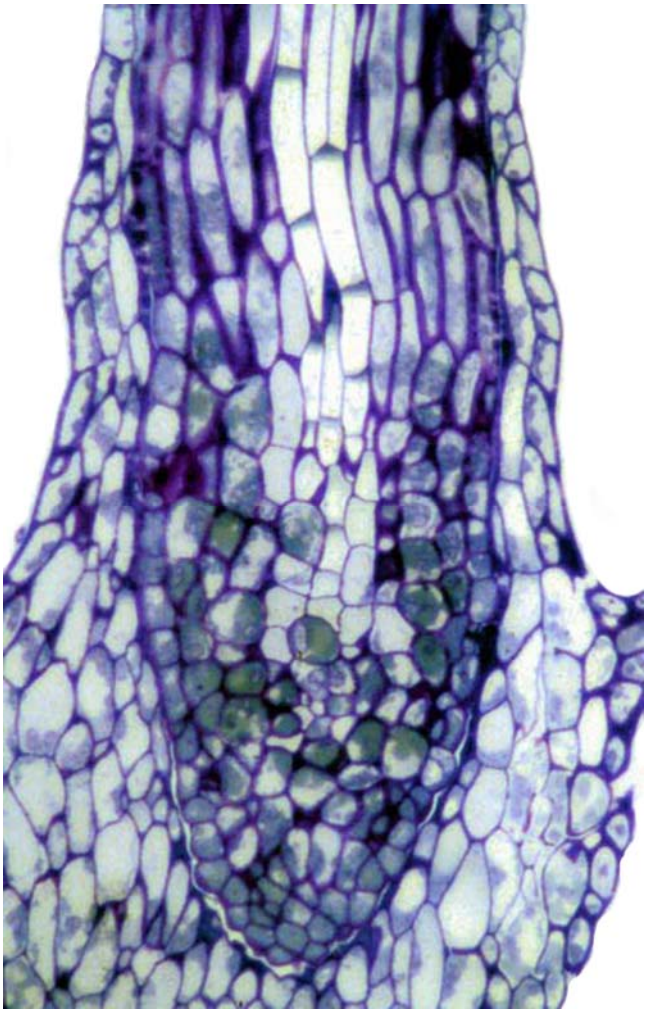

Figure 14. ***Takakia ceratophylla*** sporophyte foot. Photo by Karen Renzaglia, with permission.

Figure 15. ***Takakia ceratophylla*** epidermal cell of foot with wall ingrowths. Photo by Karen Renzaglia, with permission.

Figure 16. ***Takakia ceratophylla*** with immature capsule. Photo by Ken McFarland, through fair use.

Figure 17. ***Takakia ceratophylla*** with capsules. Photo by Ken McFarland, with permission.

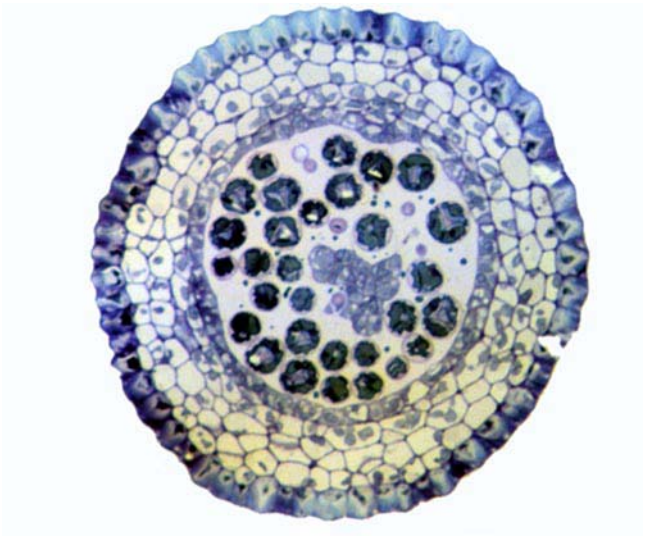

Figure 18. ***Takakia ceratophylla*** sporophyte cross section showing columella and tetrads of spores. Photo by Karen Renzaglia, with permission.

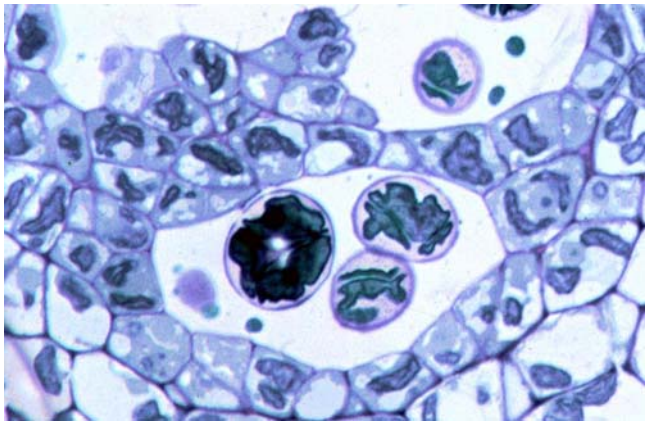

Figure 19. ***Takakia ceratophylla*** sporophyte cross section showing chambers with tetrads of spores. Photo by Karen Renzaglia, with permission, and modified by Janice Glime.

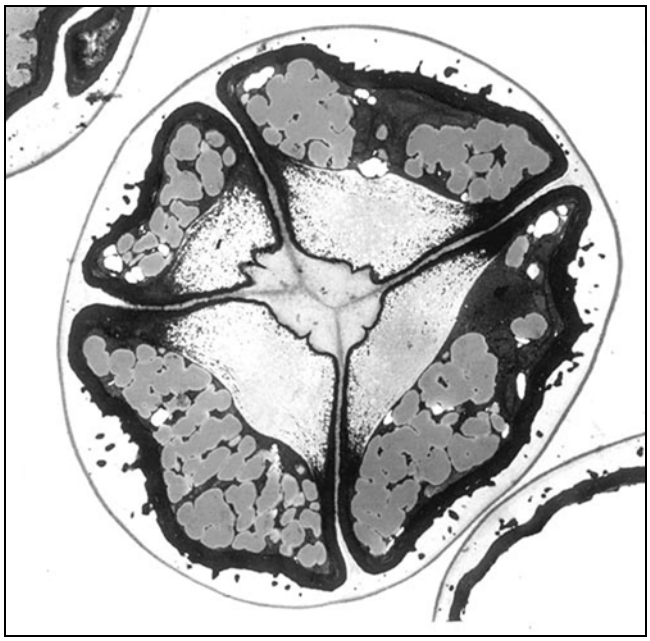

Figure 20. ***Takakia ceratophylla*** TEM of tetrad of spores. Photo by Karen Renzaglia, with permission.

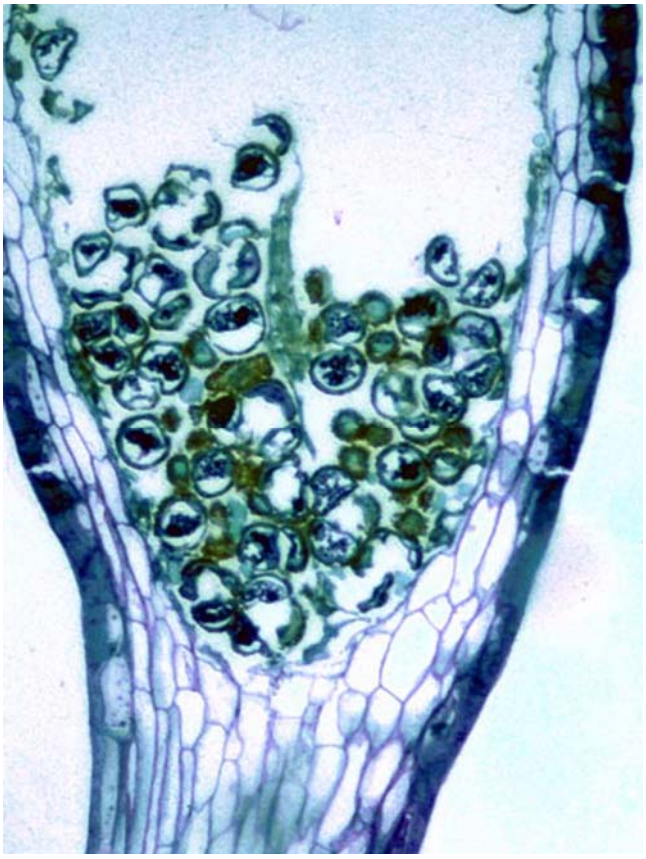

Figure 21. ***Takakia ceratophylla*** sporophyte longitudinal section showing spores. Photo by Karen Renzaglia, with permission.

Figure 22. ***Takakia ceratophylla*** with dehisced capsules. Photo by Karen Renzaglia, with permission.

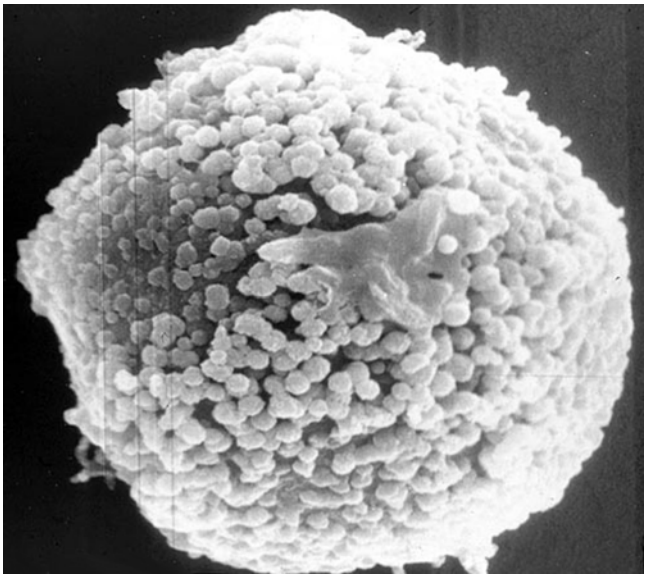

Figure 23. ***Takakia ceratophylla*** spore SEM. Photo by Karen Renzaglia, with permission.

Figure 24. ***Takakia lepidozioides*** habitat in Hokkaido, Japan, where this species can be found on Mt. Daisetsu. Photo from website of the Herbarium of the University of Hiroshima, with permission.

Figure 25. ***Takakia lepidozioides*** cave in Hokkaido, Japan, where this species can be found on Mt. Daisetsu. Photo from website of the Herbarium of the University of Hiroshima, with permission.

Figure 26. ***Takakia lepidozioides*** growing on rock in Japan. Photo from website of the Herbarium of Hiroshima University, with permission.

Figure 27. ***Takakia lepidozioides*** showing connecting rhizomes. Photo from the Herbarium of Hiroshima University, with permission.

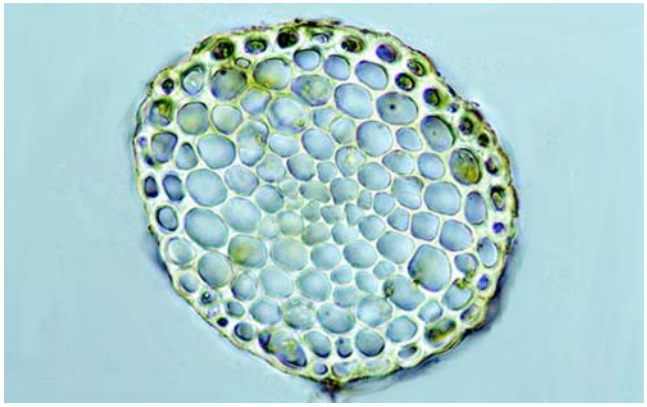

Figure 28. ***Takakia lepidozioides*** stem cross section. Photo from the website of the Herbarium of Hiroshima University, with permission.

Figure 29. ***Takakia lepidozioides*** leaf cross section. Photo from the website of the Herbarium of Hiroshima University, with permission.

Figure 30. ***Takakia lepidozioides*** rhizome tip with mucous cells. Photo from the website of the Herbarium of Hiroshima University, with permission.

Figure 31. ***Takakia lepidozioides*** tip of young rhizome. Photo from the website of the Herbarium of Hiroshima University, with permission.

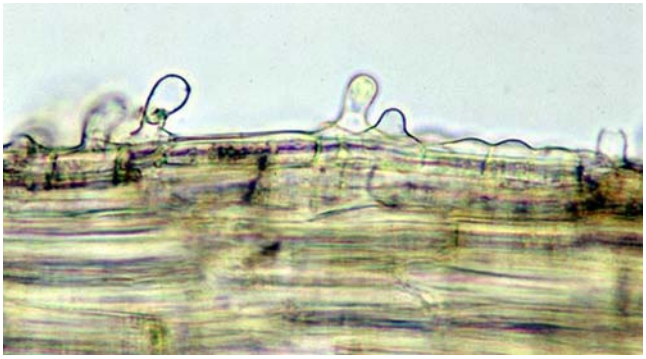

Figure 32. ***Takakia lepidozioides*** mucous cells on stem. Photo from the website of the Herbarium of Hiroshima University, with permission.

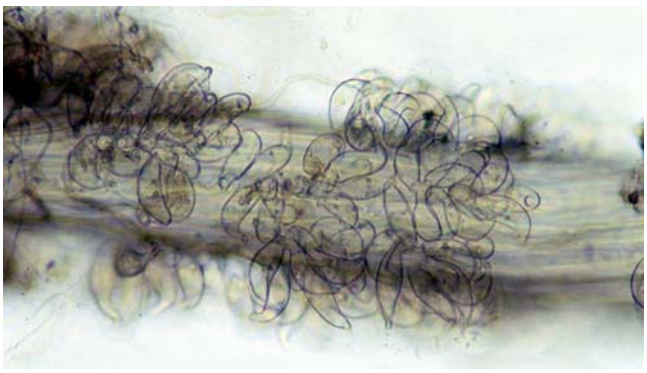

Figure 33. ***Takakia lepidozioides*** slime papillae. Photo from the website of the Herbarium of Hiroshima University, with permission.

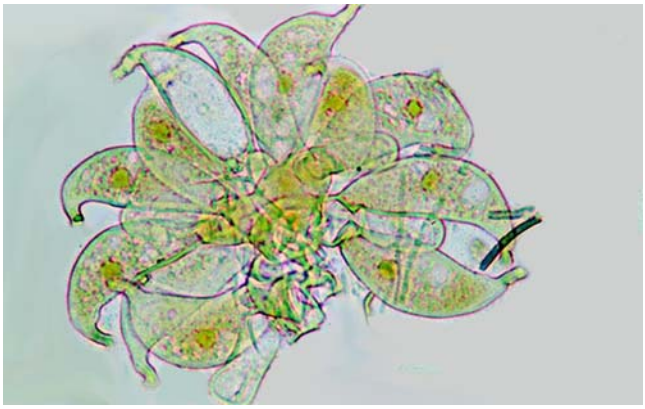

Figure 34. ***Takakia lepidozioides*** mucous cells on stem. Photo from the website of the Herbarium of Hiroshima University, with permission.

Figure 35. ***Takakia lepidozioides*** mucous cells on stem. Photo from the website of the Herbarium of Hiroshima University, with permission.

Summary

Bryophyta can be considered to have six classes: **Takakiopsida**, **Sphagnopsida**, **Andreaeopsida**, **Andreaeobryopsida**, **Polytrichopsida**, and **Bryopsida**. **Gametophores** of Bryophyta, including Takakiopsida, produce **archegonia** and/or **antheridia** and the **embryo** develops within the archegonium.

In **Takakiopsida**, as in all Bryophyta, **sporophytes** remain **attached** to the gametophyte and produce **spores** by **meiosis**. Bryophyta, hence **Takakiopsida**, produce spores from the sporophyte only once. Takakiopsida have **capsules** that split spirally into valves.

Acknowledgments

I appreciate the comments and suggestions of Karla Werner, who offered a beginner's perspective. Noris Salazar Allen offered constructive criticisms on the taxonomic descriptions and helped with the proof reading of an early version. Karen Renzaglia and Hironori Deguchi kindly gave me permission to use their many web images. Llo Stark helped me improve the clarity.

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CHAPTER 2-5
BRYOPHYTA – SPHAGNOPSIDA

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CHAPTER 2-5

BRYOPHYTA - SPHAGNOPSIDA

Figure 1. ***Sphagnum papillosum*** with capsules. Photo by Janice Glime.

Class Sphagnopsida – the peat mosses

The class **Sphagnopsida** is very different from other members of **Bryophyta** (*sensu stricto*). It certainly is worthy of its own class, and some agree with Crum (2004) that it is likewise worthy of its own phylum, the **Sphagnophyta**. Certainly its morphological differences play a major role in its unusual ecology. Until recently it was composed of only one genus (***Sphagnum***; Figure 1), but now the family **Ambuchananiaceae** (one genus, ***Ambuchanania***) has been described from Tasmania, and possesses rhizoids. The only other member of **Sphagnopsida** with rhizoids is ***Sphagnum*** (=***Flatbergium***) ***novo-caledoniae*** (Figure 2-Figure 4), an **epiphyte** (Iwatsuki 1986; plants that grow on another plant without deriving nutrients from it) that grows in or near rivers (IUCN 2013).

Figure 2. ***Sphagnum*** (=***Flatbergium***) ***novo-caledoniae***. This species is an endemic to New Caledonia and is the only ***Sphagnum*** species known to produce rhizoids. Photo by Louis Thouvenot, with permission.

Figure 3. ***Sphagnum novo-caledoniae*** showing its habitat that is often on riverbanks. Photo by Juan Larrain, with permission.

Figure 4. ***Sphagnum novo-caledoniae*** rhizoids. Photo by Louis Thouvenot, with permission.

Sphagnaceae

Of all the Bryobiotina, ***Sphagnum*** is best known to the layperson because of its formation of peat and use in horticulture. The class Sphagnopsida is distinguished by **leaves** that are **one cell thick** and mostly possessing two types of cells – **photosynthetic cells** that possess chloroplasts and that form a network arrangement, and **hyaline** (colorless) **cells** that are dead at maturity, have one or more **pores** (giving access to the environment), and hold water (Figure 44). These hyaline cells form transparent patches among the network formed by the photosynthetic cells and may be equal in height to those cells or may surround them on the top (inner leaf surface) or on both surfaces. This arrangement seems to correlate well with the ability to avoid desiccation because the hyaline cells provide a reservoir of water to the photosynthetic cells. Those species typically occupying drier habitats generally have more of the hyaline cell surrounding the photosynthetic cell. These hyaline cells are usually strengthened by bar-like thickenings (**fibrillae**, Figure 44) in the cell walls, making them look superficially like many cells instead of the single long cell that they are. These leaves never possess a **costa** (moss version of a midrib).

The branches in Sphagnopsida occur in **fascicles** (bunches) along the stem, usually with some descending branches close to the stem (helping in capillary movement of water) and some extending outward. The stems have a wood-like cylinder that may be brittle or soft. The most readily distinctive feature is the arrangement of young branches in a tight **capitulum** (Figure 45), the result of branch production and elongation without the elongation of the stem. As older portions of the stem elongate, new branches form and the capitulum is maintained. This gametophyte can reproduce by fragmentation, often bifurcating at the apex to produce two capitula.

This large genus can be divided into two groups based on the large, succulent-looking leaves vs the small leaves on more narrow branches. But this grouping did not work well phylogenetically, so instead nine sections were recognized. These were recently reorganized into subgenera based on 11,704 nucleotide sequences from the nuclear, plastid, and mitochondrial genomes (Shaw *et al*. 2010):

Subgenus *Sphagnum* is characterized by tightly or loosely imbricate, hood-shaped (**cucullate**) branch leaves and large, tongue-shaped (**lingulate**) or fan-shaped stem leaves (> 1 mm long) (Figure 5-Figure 12).

Subgenus *Rigida* is the other group with cucullate branch leaves but is separated by small (< 1 mm long), triangular stem leaves and somewhat (or not) **squarrose** (spreading at right angles) branch leaves (Figure 13-Figure 14).

Subgenus *Cuspidata* has a pronounced difference between hanging branches and spreading branches, usually with hanging branches longer and more slender than spreading branches; stem leaves are much smaller than branch leaves and usually hang downward on the stem; colors vary but are never red; they are typical in wet mineral-rich depressions, submerged or near the water level (Figure 15-Figure 24).

Subgenus *Subsecunda* has flexuose hanging and spreading branches that are very similar, about the same length, or with few or no branches; stem leaves are much smaller than branch leaves and usually hang downward on stems; plants are various colors but never red (branches and stems sometimes pinkish) (Figure 25-Figure 29).

Subgenus *Squarrosa* has distinctly squarrose branch leaves and large (1-1.5 mm long) lingulate stem leaves (Figure 30-Figure 31).

Subgenus *Acutifolia*

Section *Acutifolia*, like Subgenus ***Cuspidata***, has a pronounced difference between hanging branches and spreading branches, usually with hanging branches longer and more slender than spreading branches; they differ from ***Cuspidata*** in having stem leaves nearly the same size as branch leaves or larger and usually upright on stems; plants are various shades of green, brown, or red (Figure 32-Figure 41).

Section *Polyclada* is monotypic and lacks the cucullate leaf structure, being distinguished by having six or more branches per fascicle and a dense, rounded capitulum (Figure 42).

Section *Insulosa* has toothed branch leaves and pores in hyaline cell ends (Figure 43).

Figure 5. ***Sphagnum divinum*** (Subgenus ***Sphagnum***). Photo by David Holyoak, with permission.

Figure 6. ***Sphagnum centrale*** (Subgenus ***Sphagnum***). Photo by Michael Lüth, with permission.

Figure 7. ***Sphagnum cristatum*** (Subgenus ***Sphagnum***). Photo by Jan-Peter Frahm, with permission.

Figure 8. ***Sphagnum austinii*** (Subgenus ***Sphagnum***). Photo by Des Callaghan, with permission.

Figure 9. ***Sphagnum papillosum*** (Subgenus ***Sphagnum***). Photo by David Holyoak, with permission.

Figure 10. ***Sphagnum imbricatum*** (Subgenus ***Sphagnum***). Photo by Jan-Peter Frahm, with permission.

Figure 11. ***Sphagnum affine*** (Subgenus ***Sphagnum***). Photo by Jan-Peter Frahm, with permission.

Figure 12. ***Sphagnum palustre*** (Subgenus ***Sphagnum***). Photo by Michael Lüth, with permission.

Figure 13. ***Sphagnum compactum*** (Subgenus ***Rigida***). Photo by Jan-Peter Frahm, with permission.

Figure 14. ***Sphagnum strictum*** (Subgenus ***Rigida***). Photo by Jan-Peter Frahm, with permission.

Figure 15. ***Sphagnum riparium*** (Subgenus ***Cuspidata***). Photo by Jan-Peter Frahm, with permission.

Figure 16. ***Sphagnum tenellum*** (Subgenus ***Cuspidata***). Photo by David Holyoak, with permission.

Figure 17. ***Sphagnum pulchrum*** (Subgenus ***Cuspidata***). Photo by Des Callaghan, with permission.

Figure 18. ***Sphagnum fallax*** (Subgenus ***Cuspidata***). Photo by David Holyoak, with permission.

Figure 19. ***Sphagnum angustifolium*** (Subgenus ***Cuspidata***). Photo by Michael Lüth, with permission.

Figure 20. ***Sphagnum majus*** (Subgenus ***Cuspidata***). Photo by Michael Lüth, with permission.

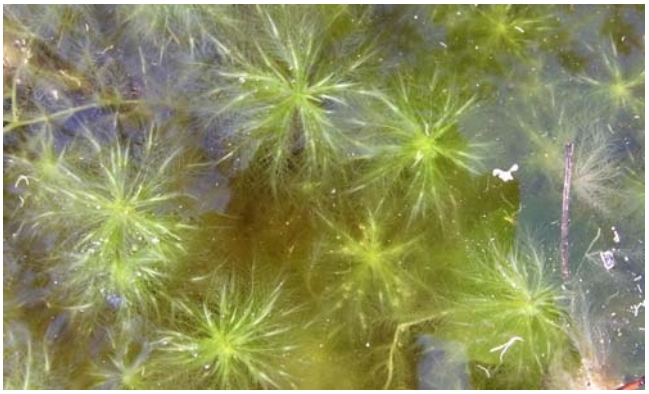

Figure 21. ***Sphagnum trinitense*** (Subgenus ***Cuspidata***). Photo by Blanka Aguero, with permission.

Figure 22. ***Sphagnum mendocinum*** (Subgenus ***Cuspidata***). Photo by Adolf Ceska, with permission.

Figure 23. ***Sphagnum cuspidatum*** (Subgenus ***Cuspidata***). Photo by Michael Lüth, with permission.

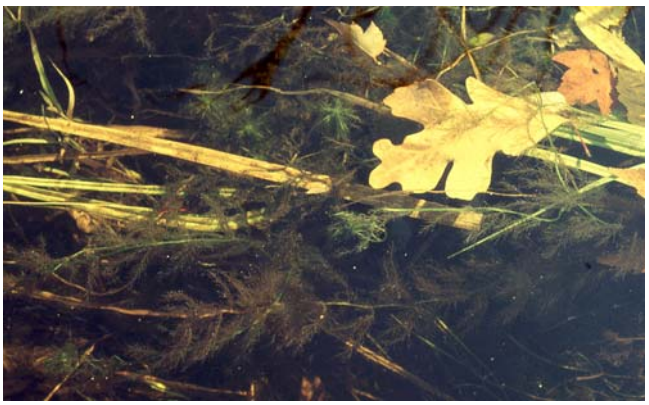

Figure 24. ***Sphagnum torreyanum*** (Subgenus ***Cuspidata***). Photo by Janice Glime.

Figure 25. ***Sphagnum pylaisii*** (Subgenus ***Subsecunda***). Photo by Jan-Peter Frahm, with permission.

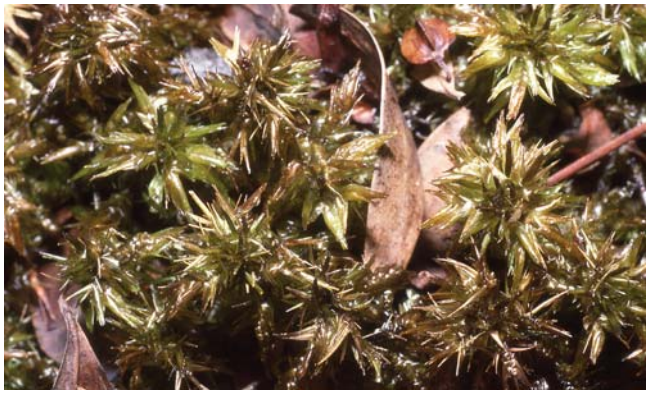

Figure 26. ***Sphagnum macrophyllum*** (Subgenus ***Subsecunda***). Photo by Janice Glime.

Figure 27. ***Sphagnum subsecundum*** (Subgenus ***Subsecunda***). Photo by Michael Lüth, with permission.

Figure 28. ***Sphagnum contortum*** (Subgenus ***Subsecunda***). Photo by Michael Lüth, with permission.

Figure 29. ***Sphagnum platyphyllum*** (Subgenus ***Subsecunda***). Photo by Michael Lüth, with permission.

Figure 30. ***Sphagnum squarrosum*** (Subgenus ***Squarrosa***). Photo by Dick Haaksma, with permission.

Figure 31. ***Sphagnum teres*** (Subgenus ***Squarrosa***). Photo by Michael Lüth, with permission.

Figure 32. ***Sphagnum quinquefarium*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). Photo by Jan-Peter Frahm, with permission.

Figure 33. ***Sphagnum fimbriatum*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). Photo by Jan-Peter Frahm, with permission.

Figure 34. ***Sphagnum girgensohnii*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). Photo by Janice Glime.

Figure 35. ***Sphagnum russowii*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). Photo by Michael Lüth, with permission.

Figure 36. ***Sphagnum arcticum*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). Photo by Michael Lüth, with permission.

Figure 37. ***Sphagnum meridense*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). Photo by Jan-Peter Frahm, with permission.

Figure 38. ***Sphagnum warnstorfii*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). This species can turn blue in a basic *p*H. Photo by Michael Lüth, with permission.

Figure 39. ***Sphagnum fuscum*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). Photo by Michael Lüth, with permission.

Figure 40. ***Sphagnum balticum*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). Photo by Michael Lüth, with permission.

Figure 41. ***Sphagnum capillifolium*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). Photo by David Holyoak, with permission.

Figure 42. ***Sphagnum wulfianum*** (Subgenus ***Acutifolia***, Section ***Polyclada***). Photo by Jan-Peter Frahm, with permission.

Figure 43. ***Sphagnum aongstroemia*** (Section ***Insulosa***). Photo by Dale Vitt, with permission.

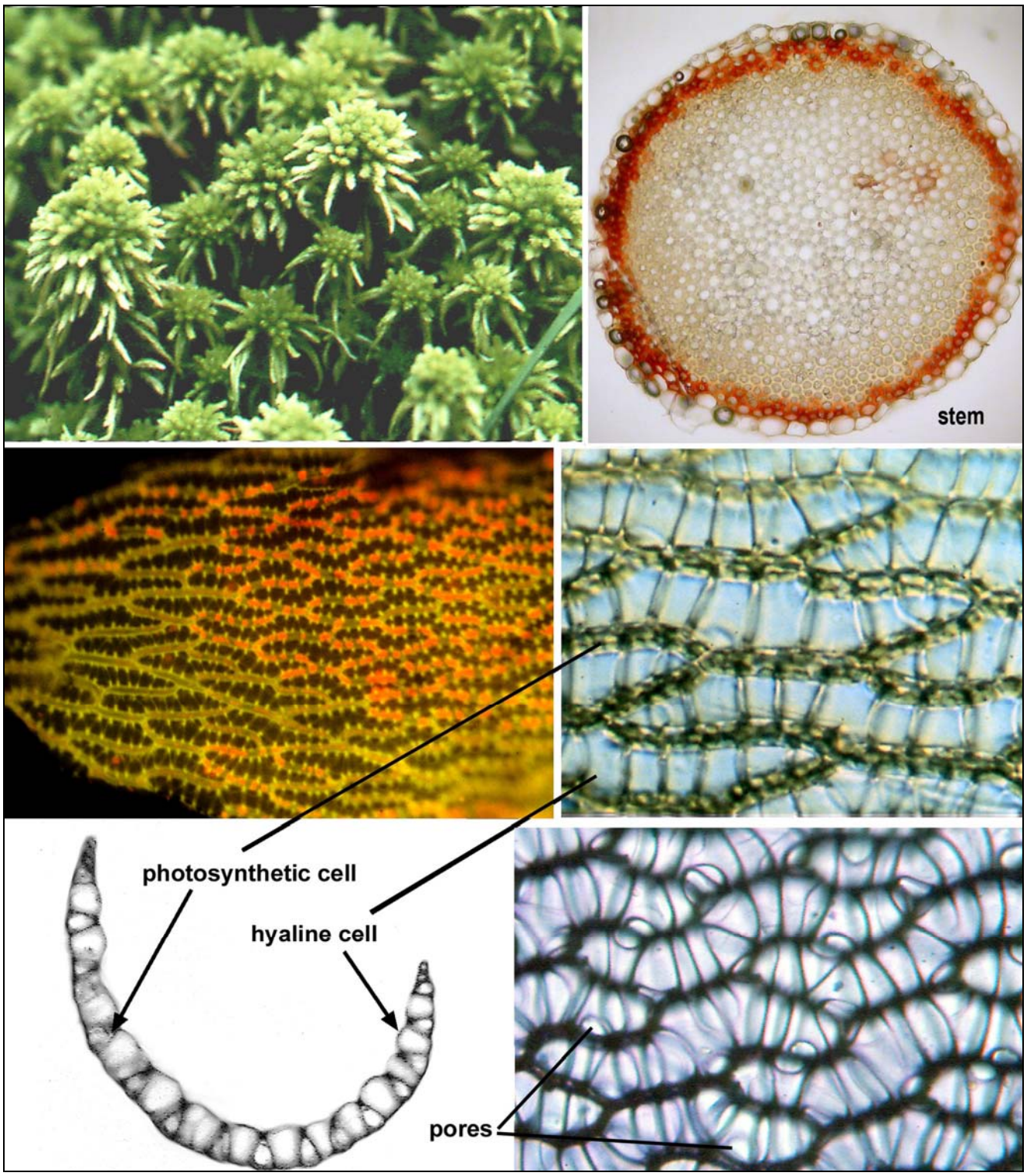

Figure 44. Vegetative characters of ***Sphagnum***, Class Sphagnopsida. **upper left:** ***Sphagnum wulfianum*** capitula; **upper right:** cross section of stem showing hyaline cells of interior and outer layer (photo by David Tng, with permission); **middle left:** leaf showing pattern of hyaline and photosynthetic cells illuminated by UV light; red areas indicate chlorophyll fluorescence; **middle right:** portion of leaf showing photosynthetic and hyaline cells (note fibrillae on hyaline cells); **lower left:** cross section of leaf showing hyaline cells that nearly enclose the photosynthetic cells; **lower right:** methylene-blue-stained portion of leaf showing pores in hyaline cells. Photos by Janice Glime, except as noted.

Figure 45. ***Sphagnum fimbriatum*** showing capitulum where archegonia will arise. Photo by Janice Glime.

The **antheridia** are nearly globose (Figure 46) and are nestled among the leaves near the tips of the capitulum branches, usually endowing those tips with a reddish color (Figure 47). The **archegonia** are terminal on short branches near the center of the capitulum.

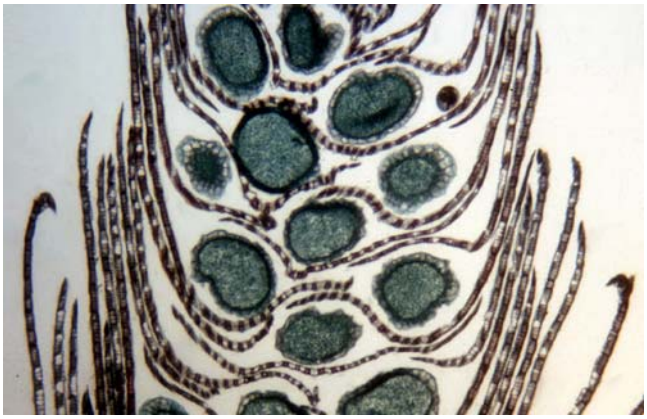

Figure 46. Globose ***Sphagnum*** antheridia nestled among the leaves of a capitulum branch. Photos by Janice Glime (**top**) and Yenhung Li (**bottom**), with permission.

Jennings (1915) and Bryan (1915 in Jennings 1915) recognized the unique character of ***Sphagnum***. They described a globose antheridial head that began development in August, before the September initiation of the archegonia. They discovered that some of the oldest archegonia matured by 25 October, whereas others did not mature until spring. But the uniqueness was the structures. The archegonia have a stalk, thick venter, and a narrow, twisted neck, all characteristic of mosses. But their inactive cover cell, intercalary growth of the archegonia, and the small number of canal cells (8-9) are characteristic of liverworts.

Figure 47. Antheridial branches in the capitulum of ***Sphagnum***. Red coloration is from the antheridia. Photo by Janice Glime.

Sphagnum* capsules** (Figure 48), or sporangia, are rarely seen in many of the species, but some fruit abundantly. Nevertheless, one must be lucky to see them because they, like the liverwort sporophytes, are **short-lived**. They develop from fertilized eggs (**zygotes**) in the capitulum (Figure 45). As these develop embryos, they likewise form a **foot**, **stalk**, and **capsule** (Figure 48), but the stalk does not elongate. Instead, it remains with its foot, embedded in gametophyte tissue. ***Sphagnum is much like the liverworts in that its stalk matures after the capsule is mature, but in ***Sphagnum***, this watery stalk (**pseudopodium**, pl. **pseudopodia**) is part of the gametophyte generation, not the sporophyte (Figure 48). It soon disintegrates, as do the liverwort stalks.

The capsule does not split as in liverworts and the **Takakiopsida**, **Andreaeopsida**, and **Andreaeobryopsida** in the **Bryophyta**, but instead possesses an **operculum** (lid; top part of capsule of mosses that comes off for spore dispersal) that is shed prior to spore dispersal (Figure 48), as in the **Bryophyta** classes **Bryopsida** and **Polytrichopsida**. However, unlike most members of the latter two classes, it lacks a **peristome** (set of teeth-like appendages around the opening of capsule; Figure 48). The **columella** (Figure 48), that central mass of sterile tissue that is like a column in **Bryopsida** and **Polytrichopsida**, is globose in ***Sphagnum***, protruding like a knob into the center of the capsule without reaching its top. **Elaters are lacking**, a characteristic shared with all other **Bryophyta** (*sensu stricto*).

Within the capsule, meiosis occurs, producing the spores. When the spores are mature, the **operculum** (Figure 48) is shed explosively when the capsule shrinks and compresses the gases, dispersing nearly all the spores in one blast of 4-6 atmospheres of pressure (Crum 2004; see Chapter 4-9). In fact, bryological folklore claims that one can hear the explosions when the sun and moisture are just right to cause the capsules to explode. No extant sphagnologist seems to have actually heard this, but following a ***Sphagnum*** field trip at an international meeting in Great Britain, one of the bryologists was startled

to hear ping...ping-ping...ping-ping-ping while he was sitting in bed reading. He had put his ***Sphagnum*** with capsules under the bed lamp to dry, and so it had, with capsules shrinking and exploding. The pings were opercula hitting the metal shade on the lamp!

It appears that ***Sphagnum*** is prolific in its spore production, with mean number per capsule ranging from 18,500 in ***Sphagnum tenellum*** to 243,000 in ***S. squarrosum*** (Sundberg & Rydin 1998) and **source strength** (estimated original number of spores in capsules that dehisced during experiment) ranging 8-90 million spores (Sundberg 2005). And these spores seem to disperse quite well, with only 2-14% of those dispersed remaining within the parent colony. Being large helps. The larger capsules dispersed a greater percentage of spores, had a smaller percentage trapped within the parent colony, and thus dispersed more spores to greater distances.

In the presence of moisture and light, and at least some nutrients, particularly phosphates (see Sundberg & Rydin 2002; Claeys 2017), the spores germinate to form a short thread. This thread soon, however, divides in more than one direction to form a **thalloid protonema** (Figure 48), as in most liverworts. A similar thalloid protonema is present also in other bryophytes such as ***Andreaea*** (Bryophyta class Andreaeopsida) and would be more appropriately called a **sporeling**. Like the liverworts, and unlike the other mosses, each protonema produces **only one bud**, thus only one mature gametophyte.

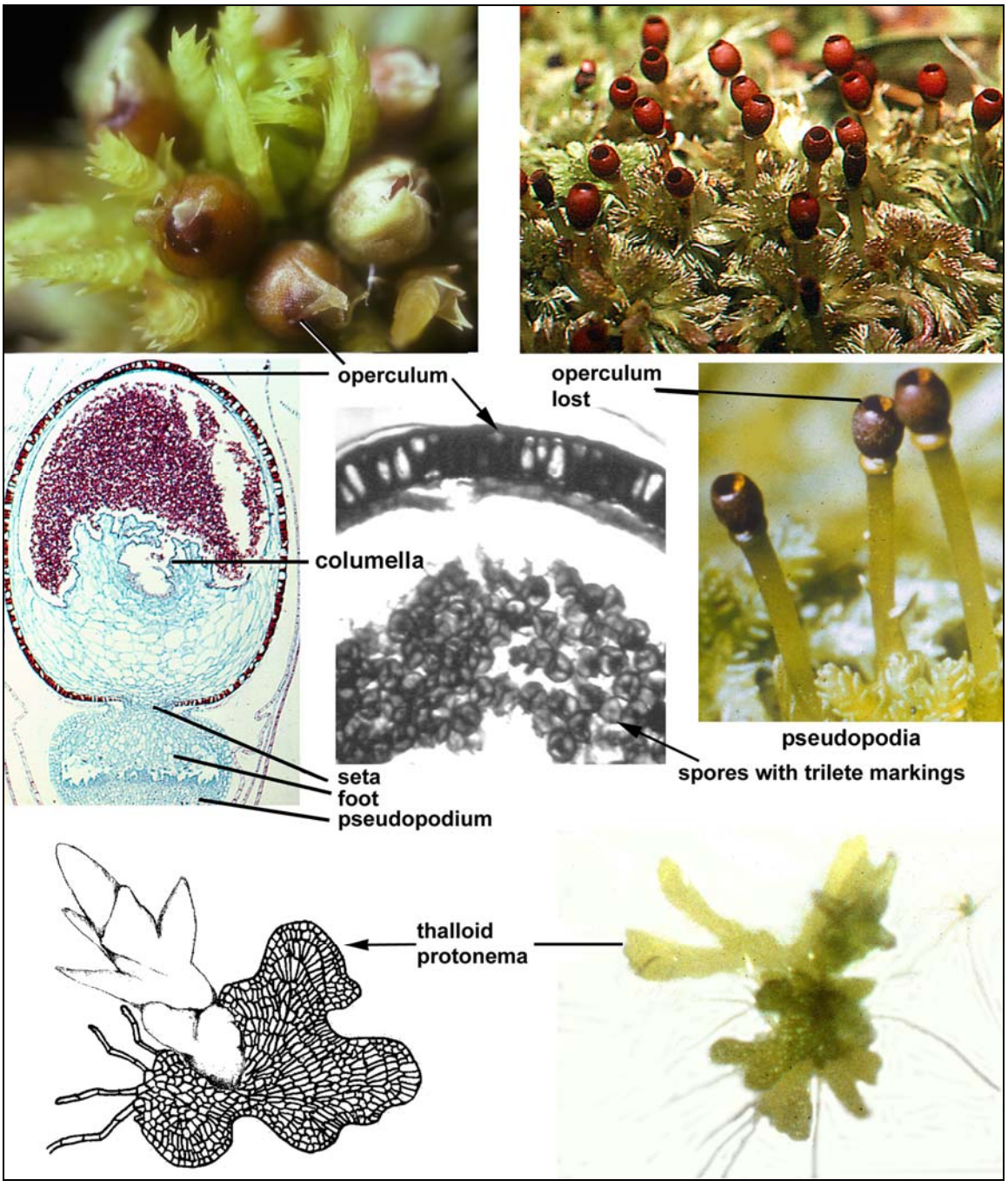

Figure 48. ***Sphagnum*** life cycle stages. Upper left photo by Zen Iwatsuki; others by Janice Glime. Protonema drawing by Margaret Minahan and Noris Salazar Allen, with permission.

Flatbergiaceae (= Sphagnaceae?)

Shaw (in Shaw *et al*. 2010) separated this family morphologically from **Sphagnaceae** by its efibrillose leaves. It is currently monotypic, with only the species ***Flatbergium sericeum***. Currently, however, both Tropicos and The Plant List (Kew) consider this genus to belong in the **Sphagnaceae**. A second species is implicated for the family (Devos *et al*. 2016), based on molecular data. This would transfer ***Sphagnum novo-caledoniae*** to ***Flatbergium novo-caledoniae*** (Figure 49).

Figure 49. ***Flatbergium novo-caledoniae***. Photo courtesy of Kjell Flatberg.

Ambuchananiaceae

Not many of us get to describe a new order. And certainly no one was expecting one in the **Sphagnopsida**! (Shaw 2000; Buchanan 2008). But this organism, this moss, was certainly something new! – ***Ambuchanania leucobryoides*** (Figure 50).

Figure 50. ***Ambuchanania leucobryoides*** showing similarity to some species of ***Sphagnum***. Photo by Lynette Cave, with permission.

Excerpts from correspondence with Rod Seppelt

"We knew it from two localities in south western Tasmania. Alex Buchanan found it in acid gravelly sand outwash near the coast. Heathy vegetation, very low nutrient status soils. The plants were mostly buried in the sand, only the top few mm showing."

"When I first saw the material I kept trying to put it in **Leucobryaceae**. Same habit, hence the epithet. Initially I thought I saw a peristome. The leaves did not fit anything in **Leucobryaceae**. Then the penny dropped – it had no peristome. The position of the archegonia also started to ring bells."...

"So, no protonema is, as yet, known. We have a second locality, inland, from acid, low nutrient, peat amongst button grass moorland (*Gymnoschoenus*, which is a tussock sedge, not a grass). Alex spotted it amongst the base of some *Isolepis* material (pressed) that had been brought into the Tasmanian Herbarium for incorporation."

"Leaf morphology. Yes, it does have chlorophyllose cells and hyaline cells. The thickenings on the walls of the hyaline cells are a bit weird... Norton Miller first asked me if I thought of describing it as a second genus in Sphagnaceae."

"Ultimately, Howard Crum wrote to say that he was so convinced that it was so different from ***Sphagnum***, but within the **Sphagnales**, that it required a separate genus ***Ambuchanania***, new family **Ambuchananiaceae**. Incidentally, Jon Shaw has managed to get some DNA sequencing (incomplete) but he concurs that it is not ***Sphagnum***, although (I believe) happy to see it remain in the Sphagnales."

An endemic of Tasmania, ***Ambuchanania leucobryoides*** occurs in sandy washes known as "daisy pans" derived from Precambrian quartzite (Johnson *et al*. 2008). ***Ambuchanania*** has been collected at two relatively inaccessible, high elevation localities in western Tasmania (Yamaguchi *et al*. 1990).

Now, this strange, yet somewhat familiar genus resides not just in a new family, but a new order, the **Ambuchananiales** (Shaw 2000; Shaw *et al.* 2003). It differs from ***Sphagnum*** in **lacking fascicles**, being **sparsely branched**, and **lacking the "wood" cylinder** of the stem. Its **leaves** are **partially bistratose** but have those telltale **hyaline** and **photosynthetic cells** (Figure 51-Figure 52). It is anchored by **rhizoids**, a character found in ***Sphagnum*** only in one epiphytic species. Its **archegonia** are located **terminally** on stems and its **capsules** are **cylindrical**, and likewise perched on an elevated **pseudopodium**.

Figure 51. ***Ambuchanania leucobryoides*** leaf showing hyaline and photosynthetic cells. Photo by Lynette Cave, with permission.

Figure 52. ***Ambuchanania leucobryoides*** leaf cross section showing hyaline and photosynthetic cells. Photo by Lynette Cave, with permission.

In addition, the genus ***Eosphagnum*** has been added to the **Ambucananiaceae**, an older species that has been reclassified (Shaw *et al*. 2010). This genus has the single species ***E. rigescens*** (an older name for ***E. inretortum***; Figure 53) (Shaw *et al*. 2016).

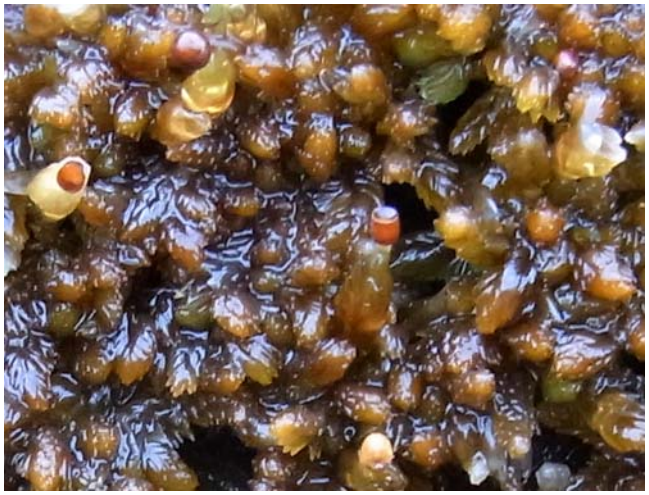

Figure 53. ***Eosphagnum rigescens*** with capsules. Photo courtesy of Blanka Aguero.

Summary

The **Sphagnopsida** are in the **Bryophyta**, although some researchers put them in a separate phylum, the **Sphagnophyta**. Only four genera are known, a large genus – ***Sphagnum***, ***Ambuchanania*** and ***Eosphagnum*** – monotypic genera in a separate order, and ***Flatbergium***.

Sphagnopsida have a **dominant gametophyte** generation with leaves that have a network of **hyaline** and **photosynthetic cells**. Gametophores produce **archegonia** and/or **antheridia** in the **capitulum** and the **embryo** develops within the archegonium.

Sporophytes remain attached to the gametophyte and produce **spores** by **meiosis**. The stalk supporting the ***Sphagnum*** sporophyte is a deliquescent extension of the gametophyte (**pseudopodium**) and it develops after the **capsule** is mature. **Sphagnopsida** lack teeth in the capsule but have an **operculum**, which the capsule sheds explosively.

The life cycle involves a **protonema** that develops from the germinating spore, becoming **thalloid** in ***Sphagnum***, whereas it becomes a branched thread in true mosses. The protonema produces one **bud** that develops into a leafy **gametophore**.

Acknowledgments

I appreciate the comments and suggestions of Karla Werner, who offered a beginner's perspective. Noris Salazar Allen offered constructive criticisms on the taxonomic descriptions and helped with the proof reading. I appreciate Rod Seppelt's correspondence that added human interest to this story. Louis Thouvenot took pictures of ***Flatbergium*** (=***Sphagnum***) ***novo-caledoniae*** for me so I could illustrate rhizoids. Lynette Cave answered my call for pictures of ***Ambuchanania*** and notified me of an error in the text. Jon Shaw helped me update the nomenclature and classification for the **Sphagnopsida**. Blanka Aguero provided me with images of ***Eosphagnum***. Llo Stark provided a valuable review of the chapter.

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CHAPTER 2-6

BRYOPHYTA - ANDREAEOPSIDA, ANDREAEOBRYOPSIDA, POLYTRICHOPSIDA

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CHAPTER 2-6

BRYOPHYTA - ANDREAEOPSIDA, ANDREAEOBRYOPSIDA, POLYTRICHOPSIDA

Figure 1. ***Andreaea rupestris*** with open capsules. Photo by Michael Lüth, with permission.

Andreaeopsida – The Granite Mosses

This is a small, cool-climate class of **siliceous-**rock-dwelling mosses (Schofield 1985), again with only one genus, but with approximately 100 species. They are typically **blackish** or **reddish**, **brittle**, and **short** (Figure 1). One can recognize them by rubbing one's hand across them and discovering small fragments stuck to the hand. This no doubt has dispersal potential.

The leaves are but **one cell thick** (Figure 2), but some species have a multiple cell thickness in the center, forming a **costa** (Figure 3). The arrangement of leaves is multi-ranked and the stem typically has colored cell walls (Figure 4). Unlike most mosses, they have a **thalloid protonema**.

Of ecological significance, ***Andreaea*** is **autoicous** (having male and female reproductive organs in separate clusters on the same plant; Figure 5-Figure 7). This ensures there will be others around to accomplish fertilization.

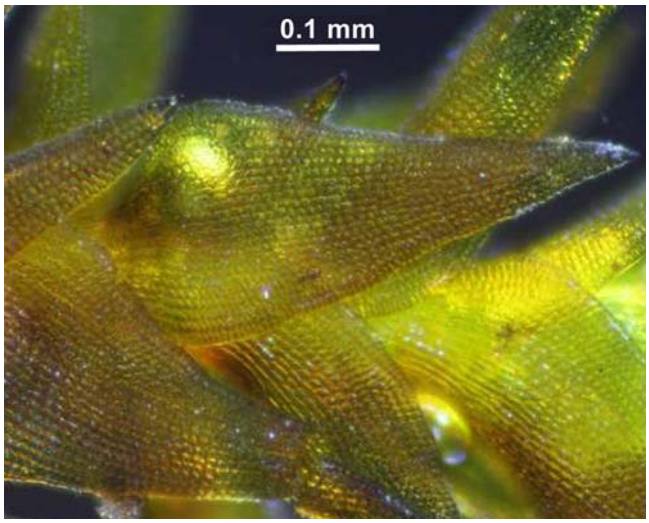

Figure 2. ***Andreaea mutabilis*** leaves with no costa. Photo by Tom Thekathyil, with permission.

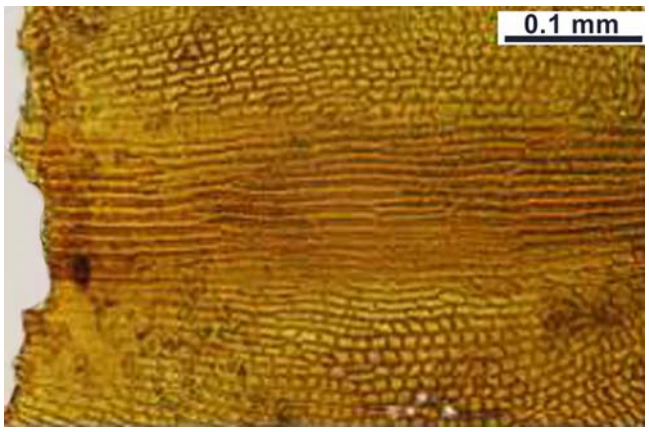

Figure 3. ***Andreaea subulata*** leaf showing costa. Photo by Tom Thekathyil, with permission.

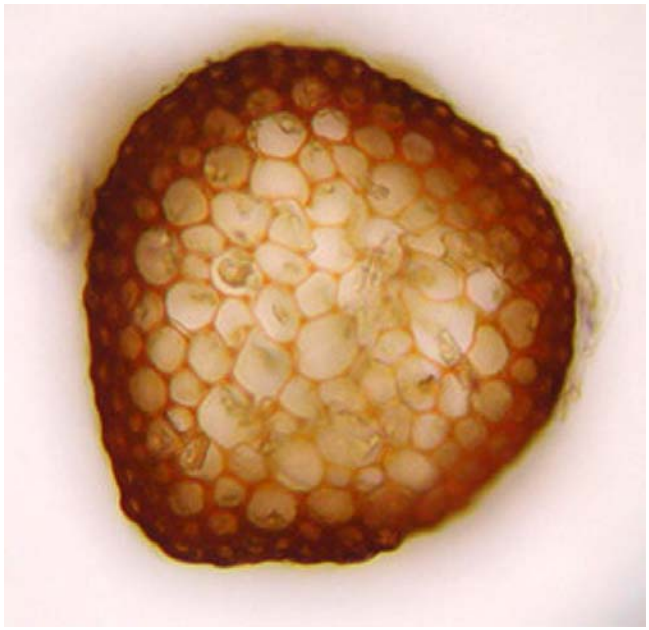

Figure 4. ***Andreaea*** stem cross sections. Photo from website of Botany Department, University of British Columbia, with permission.

Figure 5. ***Andreaea nivalis*** perigonium. Photo from website of Botany department, University of British Columbia, with permission.

Figure 6. ***Andreaea nivalis*** perigonium crushed to reveal paraphyses. Photo from website of Botany Department, University of British Columbia, with permission.

Figure 7. ***Andreaea nivalis*** antheridium. Photo from website of Botany department, University of British Columbia, with permission.

The capsule is reminiscent of liverworts, opening in **four valves**, but having the tips remaining **attached** to each other, making it look like those paper lanterns we made as children for Halloween (Figure 8). Unlike the liverworts, it **lacks elaters**. And unlike most liverworts and Bryopsida, it **lacks a seta** and has a gametophyte **pseudopodium**, a character in common with **Sphagnopsida**, a stalk produced at capsule maturity from the gametophyte tissue.

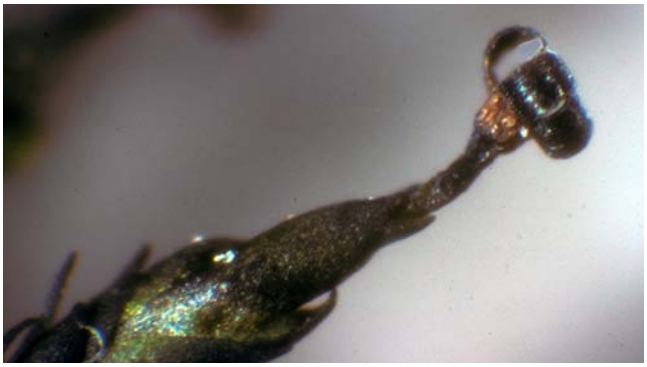

Figure 8. ***Andreaea rupestris***, Class **Andreaeopsida**, gametophyte with sporophyte showing four valves of capsule and pseudopodium of gametophyte. Photo by Janice Glime.

Andreaeobryopsida

This class likewise is comprised of a single genus, ***Andreaeobryum*** (Figure 9), which has been considered by most to belong to the Andreaeopsida, but recently separated in the treatment by Buck and Goffinet (2000). It differs in being **dioicous** (having male and female reproductive organs on separate plants) and possessing a **seta**. Its **calyptra** is larger, **covering the capsule**, and the capsule is **valvate**, but unlike the Andreaeopsida, the apex erodes, so the **valves are free**, not joined at the apex. The distribution is narrow, restricted to the northwestern part of Canada and adjacent Alaska, where it grows on calcareous rocks, contrasting with the acidic granite preference of ***Andreaea*** (**Andreaeopsida**).

Figure 9. ***Andreaeobryum macrosporum*** with valvate capsules. Photo from Biology 321 Course Website, UBC, with permission.

Polytrichopsida

With bryophytes, the determination of primitive or advanced often depends on the generation being examined. The gametophyte may have changed considerably while some set of characters of the sporophyte remained constant. And of course, the reverse can be true. The **dioicous** condition (male and female reproductive organs on separate plants) that characterizes **Polytrichopsida** is considered to be primitive (Longton & Schuster 1983), with the **monoicous** condition (male and female reproductive organs on the same plant) that is so frequent in **Bryopsida** typically being derived by doubling of the chromosome number. Likewise, **nematodontous peristome teeth** (having evenly thickened walls and whole dead cells lacking eroded walls; Figure 10) of **Polytrichopsida** would seem to be an earlier development than the **arthrodontous** (having 1-2 rings of separated teeth with differentially thickened walls; Figure 11) condition of **Bryopsida**.

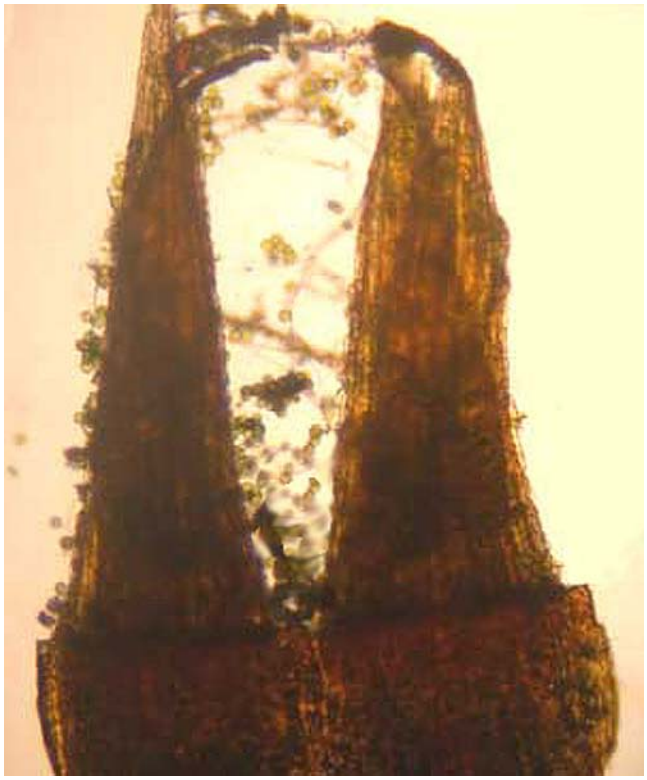

Figure 10. **Nematodontous** peristome teeth of ***Tetraphis pellucida*** (**Polytrichopsida**). Note the separation at the tips and absence of thickenings. Photo from Biology 321 Course Website, UBC, with permission.

Figure 11. Capsule with **arthrodontous** teeth. Note the projections along the edges. Photo by Laurie Knight, with permission.

All members of the class **Polytrichopsida** possess an elongate sporophyte **seta** (Figure 12), supporting an **operculate peristomate** capsule (Figure 13), and a **columnar columella**, characters that are more advanced than in **Sphagnopsida** but typical in **Polytrichopsida**. Spores are produced by meiosis in a single event in **sporogenous** tissue that surrounds the columella (Figure 14-Figure 15).

Figure 12. ***Polytrichum juniperinum*** with capsules and seta. Photo by Ralph Foster, through Creative Commons.

Figure 13. ***Polytrichum commune*** capsules with some showing reddish operculum. Photo by Kristian Peters, through Creative Commons.

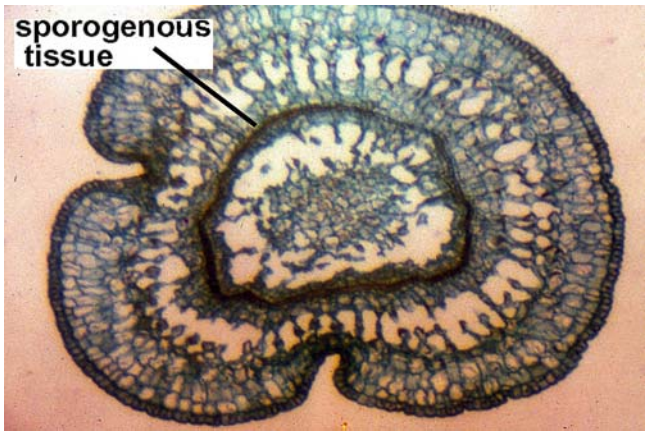

Figure 14. Cross section of immature ***Polytrichum*** capsule showing sporogenous tissue. Photo by Janice Glime.

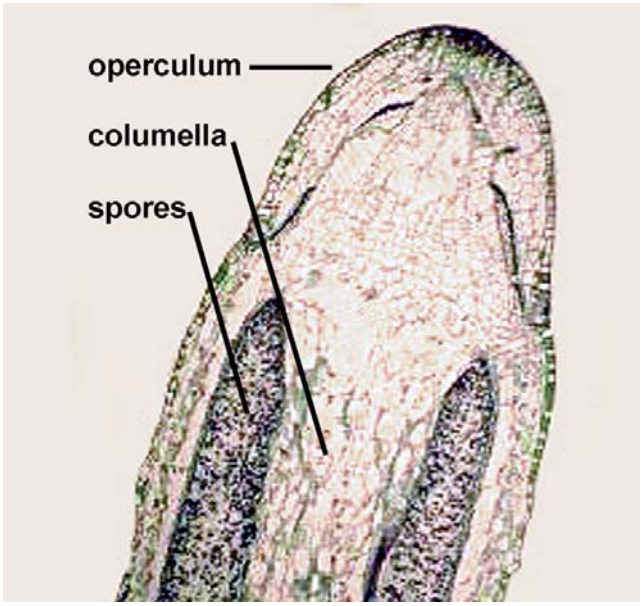

Figure 15. Longitudinal section of ***Polytrichum*** capsule. Photo by Janice Glime.

The moss gametophyte is often very specialized, being characterized by stems with a **central strand**, reaching its peak in **Polytrichaceae** (Figure 18), with the presence of **hydroids** (water-conducting cells) and **leptoids** (sugar-conducting cells). The leaves of the class are **all costate** (having a midrib-like structure; Figure 16-Figure 17).

Figure 16. ***Atrichum undulatum*** leaves showing costa. Photo by Bernd Bäumler, through Creative Commons.

Figure 17. ***Atrichum undulatum*** excised leaves showing costa. Photo by Hermann Schachner, through Creative Commons.

Polytrichaceae

In many ways, this family looks like a tracheophyte wanna-be. It attains a greater height than the typical moss and can even stand alone to nearly half a meter in the case of ***Dawsonia longifolia*** (Figure 19). ***Polytrichum commune*** (Figure 20) likewise attains similar heights, but only with the support of other individuals, forming a hummock. Even in the cold climate of Macquarie Island, ***P. juniperinum*** reaches hummock heights of 30 cm (Rod Seppelt, pers. comm. 16 March 2007).

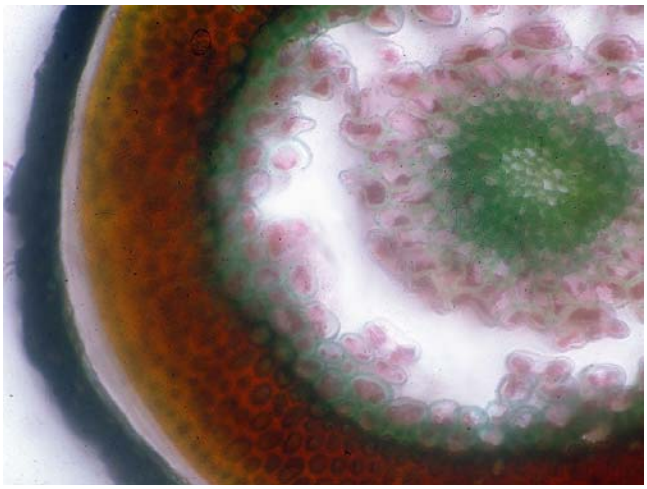

Figure 18. Cross section of a ***Polytrichum*** stem showing green **hydroids** in center and larger **leptoids** surrounding them. Photo by Izawa Kawai, with permission.

The genus ***Dawsonia*** has many unresolved species, some of which have been moved to a different genus. Even the well known ***D. superba*** (Figure 19) has been merged into ***D. longifolia***. ***Dawsonia longifolia*** *s.l.* is a native of New Zealand, Australia, and Papua New Guinea and breaks the height record for upright mosses. It grows up to 48 mm in a year and in this study ranged 6-38 cm tall (Green & Clayton-Greene 1981). This compares well with known growth rates of ***Polytrichum commune*** of 3-5 cm in one growing season (Figure 21) (Sarafis 1971). It occurs in a temperate climate and its growth tracks available moisture and temperature. Its sperm dispersal is aided by an antheridial splash cup, with sperm known to reach females 1.5-2 m from the males in the field, but experimental tests showed they could splash to heights up to 3.3 m in the lab (Clayton-Greene *et al*. 1977)! Ligrone *et al*. (2002) showed that ***Dawsonia*** responded differently to antibodies used to label the arabinogalactan proteins in the water conducting cells (WCC), suggesting that their chemical structure differed from that of other mosses tested. On the other hand, ***Dendroligotrichum*** (Figure 22) and ***Polytrichum*** demonstrated a strong reaction in the leptoids (Figure 18; Figure 23) of the stem. These three genera differed in other marker reactions as well, supporting the uniqueness of the **Polytrichopsida**.

Antibodies against varied carbohydrate epitopes of arabinogalactan proteins gave different results. The 'arabinogalactan proteins (AGP)' antibody labelled the WCCs in all mosses, except ***Dawsonia***, whilst no labelling was observed in hepatics.

Figure 19. ***Dawsonia longifolia*** from New South Wales, Australia. Photo by Janice Glime.

Figure 20. ***Polytrichum commune*** with capsules. Photo by George Shepherd, through Creative Commons.

Figure 21. ***Polytrichum commune*** 2-year growth in Europe. Photo by Michael Lüth, with permission.

Figure 22. ***Dendroligotrichum dendroides***. Photo by Jan-Peter Frahm, with permission.

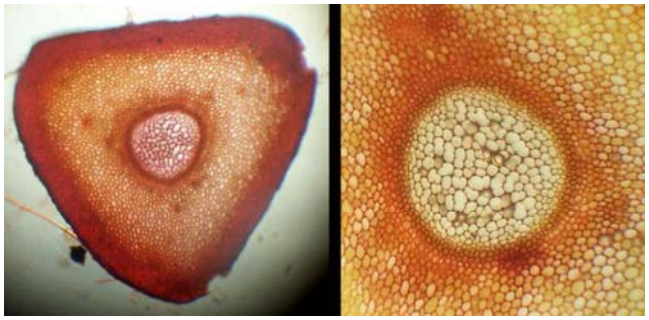

Figure 23. ***Dendroligotrichum dendroides*** stem cross section showing hydroids and leptoids. Photo by Juan Larrain, with permission.

The **Polytrichaceae** lead the way to complexity with their unusual leaf structure, possessing vertical **lamellae** (vertical tiers of cells like the pages of an open book; Figure 24-Figure 26) that provide an interior somewhat resembling that of a maple leaf. In fact, in the genus ***Polytrichum***, some members have the outer portion of the blade folded over the lamellae (Figure 27-Figure 28), creating an internal chamber resembling palisade mesophyll surrounded with epidermis. The **cuticle** (in this case, a waxy, water-repellant covering on the outer surface of the leaf; Proctor 1979) of ***Polytrichum*** is more developed than in most other bryophytes, and ***Polytrichum*** seems to repel water from its leaves rather than to absorb it (Figure 27), a phenomenon that may prevent the spaces among the lamellae from flooding that would block access of CO_2 to the chloroplasts within. Its rhizoids function not only for anchorage, but also seem to facilitate external water movement.

Figure 24. ***Polytrichum ohioense*** leaf lamellae in surface view. Photo by John Hribljan, with permission.

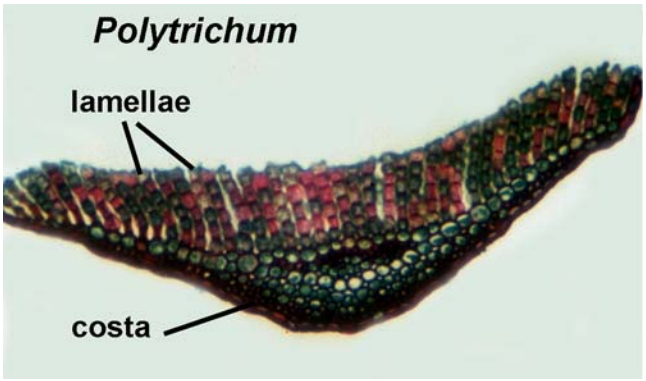

Figure 25. Stained leaf cross section of ***Polytrichum*** showing vertical lamellae. Photo by Janice Glime.

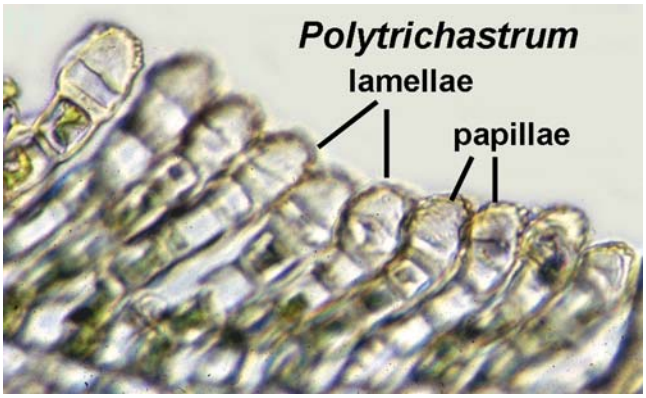

Figure 26. Hand section of ***Polytrichastrum alpinum*** leaf showing lamellae with papillose terminal cells. Photo by Janice Glime.

Figure 27. ***Polytrichum juniperinum*** with waxy leaves and lamina that rolls over the lamellae. Photo by Janice Glime.

Figure 29. Male plants of ***Polytrichum juniperinum*** with antheridial splash cups. Photo by Janice Glime.

Figure 28. ***Polytrichum juniperinum*** leaf cross section showing lamellae and edges of leaf folded over them. Photo by John Hribljan, with permission.

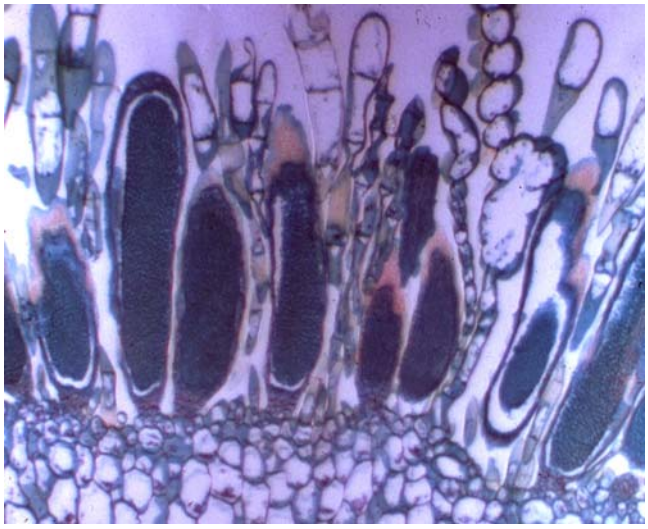

Figure 30. ***Polytrichum*** antheridial head showing paraphyses and antheridia. Note space where mucilage collects between the dark sperm tissue and the sterile jackets of the antheridia. Photo by Janice Glime.

In some mosses, like ***Polytrichum***, the antheridia are in splash **cups** or **platforms** (rosette of leaves from which reproductive units such as sperm, gemmae, or spores can be splashed by raindrops; Figure 29), and when the **sperm** (male reproductive cells; male gametes) are mature, the antheridium (Figure 30) swells and bursts during a rainy period. The bases of the antheridia, in taxa such as ***Polytrichum*** and ***Atrichum*** (Figure 37), collect fluid between the sperm tissue and the antheridial jacket (Figure 30) (Bold *et al*. 1987). When the cells at the tip of the sterile jacket open, the antheridial jacket contracts. At this time, the fluid at the bottom acts as a hydraulic ram and forces the sperm out of the antheridium. Once in the open water of the splash cup, the sperm are splashed from the cup. Hopefully, some of these sperm will splash near the tip of a female plant (Figure 31) and will begin swimming toward the archegonium (Figure 32).

Figure 31. Female plants of ***Polytrichum ohioense*** showing the tight leaves at the apex where archegonia are housed. To the right of the female plants, the yellow swollen tips are male plants with unopened antheridial splash cups. Photo by Janice Glime.

Figure 32. Archegonia nestled among terminal leaves of ***Polytrichum***. Photo from Michigan State University botany collection, with permission.

But it appears that the sperm of ***Polytrichum commune***, and perhaps others, may have some help in this process from another source (Harvey-Gibson & Miller Brown 1927). A variety of invertebrates visit the male splash cups once they are fertile and get the mucilage with sperm stuck on their bodies. While visiting the plants, the insects lap up the mucilage and lick the saline crystals that form on the margins of the perichaetial leaves. The same insects, bodies and limbs smeared with mucilage in which sperms were abundant and motile, likewise appear on female plants. Now, can someone show whether the red color of splash cups (Figure 29) in several members of this family have the ability to attract any dispersal agents?

After fertilization, the zygote divides to form an **embryo** within the **archegonium**. Eventually this sporophyte embryo tissue forms a **foot**, **seta**, and **capsule**. The capsule develops within the **calyptra** (Figure 33-Figure 35), which is the expanded archegonium. The calyptra is essential for normal development in most mosses, and a split on one side can cause asymmetrical development. In the case of ***Polytrichum***, the calyptra is very hairy (Figure 35), earning the moss the name of haircap moss or goldilocks moss. If it is removed early in development, the capsule will not develop properly.

Eventually the **calyptra** (Figure 35) is shed, exposing the capsule. Then the **operculum** (lid) must come off to permit spore dispersal. In this family the capsule has 64 short teeth joined by a membrane (**epiphragm**) that covers the capsule like skin on a drum (Figure 36). These small spaces permit spores to escape the capsule a few at a time, providing maximum chances for some escaping under the right conditions for dispersal and establishment.

Figure 33. ***Polytrichum piliferum*.** Young sporophyte with **calyptra** (old archegonium) on top. Photo by Janice Glime.

Figure 34. **Seta** (stalk) of sporophyte with calyptra removed, showing that the capsule has not yet begun to develop. Photo by Janice Glime.

Figure 35. Capsules of ***Polytrichum*** at maturity, still covered with the calyptra. Photo by Janice Glime.

Figure 36. Epiphragm of ***Polytrichum***. Photo by Laurie Knight <http://www.flickr.com/photos/laurie-knight>, with permission.

Figure 37. ***Atrichum undulatum*** with antheridial splash cups, another member of the **Polytrichaceae**. Photo by Janice Glime.

Tetraphidaceae

Tetraphis (Figure 38), also in the **Polytrichopsida**, looks more like a typical moss than do other **Polytrichopsida**, with thin, 1-cell-thick leaves and a costa (Figure 38-Figure 39). ***Tetraphis*** is unique among mosses in having **gemmae** (Figure 40-Figure 42) arranged in splash cups at the tips of the stems when sexual reproduction is not in season, arguably a primitive remnant. These gemmae are asexual bits of plant material that can grow into a new plant. Its most unusual character is that its protonemata are not threads, but rather flaps (Figure 43). Antheridia are borne terminally on the leafy plants (Figure 44), as are the archegonia. The capsule (Figure 45) has only four long, unjoined, nematodontous teeth (Figure 10, Figure 46).

Figure 38. ***Tetraphis pellucida*** showing thin leaves with a **costa**. Photo by Des Callaghan, with permission.

Figure 39. ***Tetraphis pellucida*** leaf cross section showing 1-cell-thick lamina and multicellular costa. Photo from botany website, University of British Columbia, with permission.

Figure 40. Leafy gametophytes of ***Tetraphis pellucida*** with gemmae cups on top. Photo by Janice Glime.

Figure 41. Gemma cup with gemmae of ***Tetraphis pellucida***. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

Figure 42. ***Tetraphis pellucida*** gemmae, asexual means of reproduction. Photo by Jessica Budke, with permission.

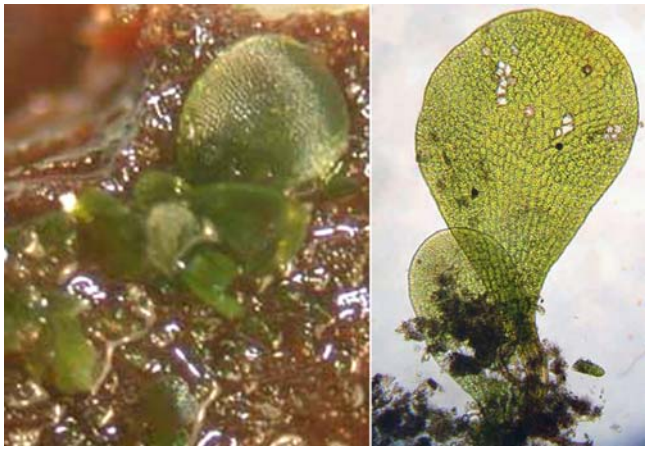

Figure 43. Protonemal flaps of ***Tetraphis pellucida***. Photos from University of British Columbia Biology 321 Course Website, with permission.

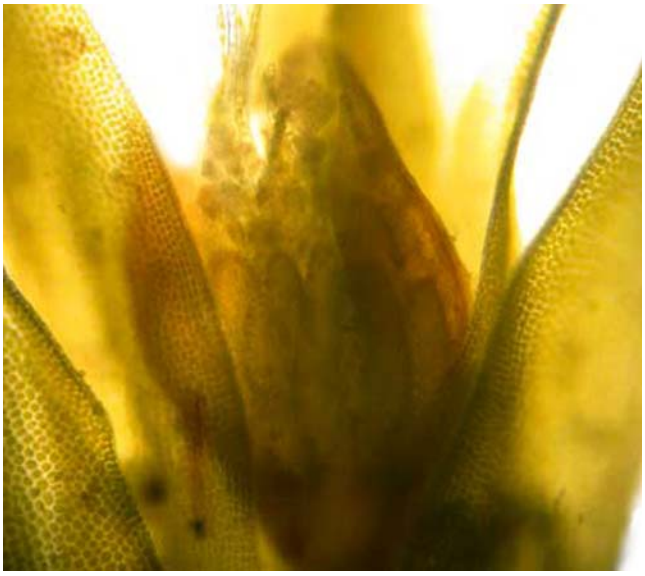

Figure 44. Leaves and antheridia of ***Tetraphis pellucida***. Photo from UBC Biology 321 Course Website, with permission.

Figure 45. Capsules of ***Tetraphis pellucida*** showing calyptra with capsule exposed in the lower third. Photo by Janice Glime.

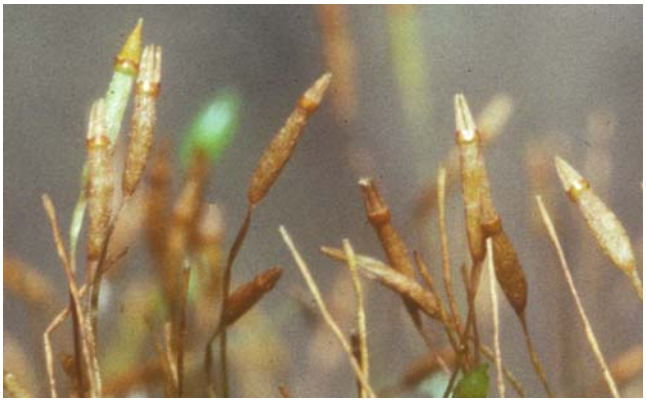

Figure 46. Capsules of ***Tetraphis pellucida***, lacking calyptra and **operculum** (lid), exposing the 4 peristome teeth. Photo by Janice Glime.

Buxbaumiaceae – Bug on a Stick

Buxbaumia (Figure 47-Figure 51) is one of the strangest of all mosses. It lacks any leafy stem at all (Figure 47). Its archegonia and antheridia arise directly from the protonema. Hence, its capsules (Figure 49) arise directly from this persistent protonema (Figure 47). They all tend to orient in the same direction (Taylor 1972), most likely in response to the predominant direction of light. Its capsules, although possessing teeth (Figure 50), more typically split across their broad, flattened surface, hence exposing the spores (Figure 51) (Koch *et al*. 2009). Koch and coworkers demonstrated that in ***Buxbaumia viridis*** (Figure 47) this capsule surface is covered with "massive" wax layers that have embedded and superimposed platelets and granules on them. When these waxy layers peel back, the epidermis peels with them.

Figure 47. ***Buxbaumia viridis*** sporophyte and protonema. Photo by Bernd Haynold, through Wikimedia Commons.

The ***Buxbaumia*** capsule interior is chambered and spongy, somewhat like a spongy mesophyll of Magnoliophyta. It typically occurs with tiny, black leafy liverworts such as ***Cephalozia*** (Figure 52). Campbell (1918) had considered this moss to be saprophytic, exhibiting almost no chlorophyll, but Mueller (1975) demonstrated dense chlorophyll in the protonema and considered that to be the primary photosynthetic organ, one that persists throughout the life of the moss. The protonema is not a good competitor, so you can find it after forest fires, on soil banks, on roadsides, and other places that are not very hospitable to plants that could easily overgrow the photosynthetic protonemata. The capsule (Figure 47-Figure 49) is rather unusual, with its broad, flattened side and a rounded side. This strange shape has earned it a number of common names, including humpbacked elves, elf-cap moss, Aladdin's lamp, and bug on a stick.

Figure 48. ***Buxbaumia aphylla*** on a soil bank with all capsules pointing the same direction. It has been suggested that common habit is advantageous to maximize light absorption by the photosynthetic capsule. Photo by Janice Glime.

Figure 49. Unopened capsule of ***Buxbaumia aphylla***, illustrating flat side with beaked operculum that has earned it the common names of bug-on-a-stick and Aladdin's lamp moss. Note the absence of a leafy gametophyte, but the presence of other mosses. Photo by Adam Gordon through Creative Commons.

Figure 50. ***Buxbaumia piperi*** capsule showing diminished peristome teeth. Photo from botany website at the University of British Columbia, with permission.

Figure 51. ***Buxbaumia aphylla*** (Class **Polytrichopsida**) showing flat side of capsule peeled back to expose the spores and spongy interior. Photo by Janice Glime.

Figure 52. ***Cephalozia bicuspidata***, member of a genus of tiny liverworts that often occur with ***Buxbaumia aphylla***. Photo by Kristian Peters, through Wikimedia Commons.

In ***Buxbaumia aphylla***, Hancock and Brassard (1974a) found that almost all elements that occurred in the protonema also occurred in the sporophyte, suggesting they were transported internally. Hancock (1973) also suggested that its protonemata were perennial. In northern climates, this is advantageous because the capsules are very susceptible to mortality from sudden early frosts. Normally, the capsules form in fall and overwinter as green capsules (Hancock & Brassard 1974b). They complete development and disperse their spores early in spring, then disappear.

Diphysciaceae

Diphyscium (Figure 53-Figure 60) is distributed mostly in the northern hemisphere (Milne & Klazenga 2012). Its three genera have been reduced to one (Magombo 2002; Goffinet 2012), which has an asymmetrical capsule (Figure 57-Figure 60) of similar shape to that of ***Buxbaumia*** and lacks a leafy female stem except for perichaetial leaves (Figure 60), but the male plant of this genus has large, strap-shaped leaves and leads an independent and separate existence (Figure 53-Figure 56). The capsule opening is quite small and the teeth extrude like a wisp of hairs (Figure 60). The perichaetial leaves are unusual, having a long, excurrent costa and often being fimbriate on the margins (Figure 59-Figure 60). As in ***Buxbaumia***, the capsule shape is responsible for several common names – nut moss, powder gun moss, grain of wheat moss. It shares the phototropic behavior of ***Buxbaumia*** by having its capsules all oriented in one direction with their flat sides facing the direction of the light (Figure 57-Figure 59).

Figure 53. Male plant of ***Diphyscium foliosum*** showing strap-shaped leaves. Photo by Hermann Schachner, through Creative Commons.

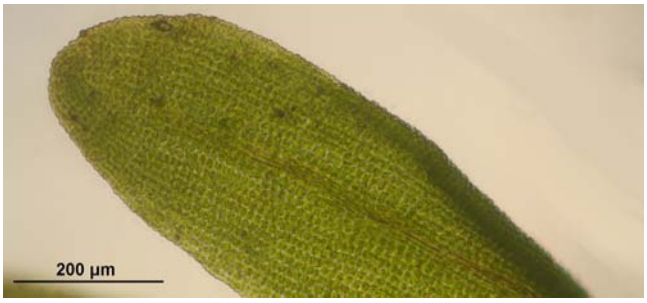

Figure 54. Leaf of male plant of ***Diphyscium foliosum*** showing weak costa and rows of cells. Photo by Hermann Schachner, through Creative Commons.

Figure 55. Male plant of ***Diphyscium foliosum*** showing antheridia. Photo modified from botany website and University of British Columbia, with permission.

Figure 56. Cross section of leaf of male plant of ***Diphyscium foliosum*** showing multiple layers and extensive papillae. Photo by Hermann Schachner, through Creative Commons.

Figure 57. ***Diphyscium foliosum*** female plants with young sessile capsules surrounded by perichaetial leaves. These are clumped here among male plants with green, strap-shaped leaves. Photo by Janice Glime.

Figure 58. **Upper:** ***Diphyscium foliosum*** female plants with young sessile capsules among male plants. Photo by Janice Glime. **Lower:** Mature female ***Diphyscium foliosum*** plants with capsules showing peristome teeth. Photo by Michael Lüth, with permission.

Figure 59. Capsules and perichaetial leaves of ***Diphyscium foliosum***. Photo by Michael Lüth, with permission.

Figure 60. ***Diphyscium foliosum*** female plant with perichaetial leaves and capsule showing small opening and peristome teeth. Photo by Jan-Peter Frahm, with permission.

Summary

Bryophyta can be considered to have six classes: Takakiopsida, Sphagnopsida, Andreaeopsida, Andreaeobryopsida, Polytrichopsida, and Bryopsida, differing most consistently in capsule structure. Gametophores of **Andreaeopsida**, **Andreaeobryopsida**, and **Polytrichopsida** produce **archegonia** and/or **antheridia** at the apex and the **embryo** develops within the archegonium.

Sporophytes remain attached to the **gametophyte** and produce **spores** by **meiosis**. These classes, and all Bryophyta, produce spores from the sporophyte only once.

Takakiopsida, **Andreaeopsida**, and **Andreaeobryopsida** have capsules that **split** into valves, but lack elaters. **Sphagnopsida** lacks valves and has an **operculum** that is shed at dispersal time, but lacks peristome teeth. In capsules of **Polytrichopsida** and **Bryopsida**, an **operculum** usually covers **peristome** teeth that often aid dispersal, contrasting with liverworts wherein the capsule splits into four valves with elaters that possibly facilitate spore movement. **Polytrichopsida** have **nematodontous** peristome teeth; **Bryopsida** have **arthrodontous** peristome teeth. All other classes of Bryobiotina lack peristomes. **Andreaeobryopsida** is **dioicous** (two sexes on separate plants) and possesses a **seta** (stalk of capsule), whereas **Andreaeopsida** is **monoicous** (both sexes on same plant) and lacks a seta.

Acknowledgments

I appreciate the comments and suggestions of Karla Werner, who offered a beginner's perspective. Noris Salazar Allen offered constructive criticisms on the taxonomic descriptions and helped with the proof reading. Heino Lepp alerted me to the invertebrate dispersal of sperm by his 3 September 2006 contribution to Bryonet. Llo Stark provided valuable suggestions on the chapter.

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CHAPTER 2-7
BRYOPHYTA – BRYOPSIDA

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CHAPTER 2-7
BRYOPHYTA – BRYOPSIDA

Figure 1. ***Aulacomnium androgynum*** with asexual gemmae on a modified stem tip. Photo by Michael Lüth, with permission.

Bryopsida Definition

By far the largest class of Bryophyta (*sensu stricto*) (84% of families) (Goffinet *et al*. 2001) and ~98% of the species, the class **Bryopsida** (formerly Musci) (Figure 1) is unquestionably the most diverse. Their evolution by both advancement and reduction makes circumscription difficult, with nearly every character having exceptions. It appears that the only unique and consistent character among the Bryopsida is its peculiar peristome of **arthrodontous teeth** (the lateral walls of the peristome teeth are eroded and have uneven thickenings; Figure 2).

This arrangement of teeth has implications for dispersal – the teeth form compartments in which spores are trapped. The outer surface is **hydrophilic** (water loving, hence attracting moisture) whereas the inner layer has little or no affinity for water (Crum 2001), causing the teeth to bend and twist as moisture conditions change. Whether this aids or hinders dispersal, and under what conditions, is an untested question. Yet even this character does not hold for some taxa; some taxa lack a peristome. And all other characters, it would seem, require the adjectives of most or usually.

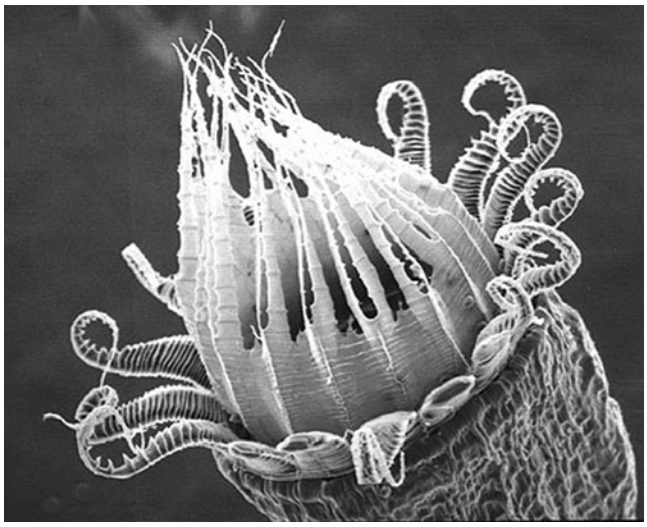

Figure 2. Electron micrograph of the arthrodontous peristome teeth of the moss ***Eurhynchium praelongum***. Photo from Biology 321 Course Website, UBC, with permission.

Chromosome Numbers

Known chromosome numbers in bryophytes range widely. The assumption is that the basic number is 9 and that all other numbers are derived from that basis by loss of chromosomes, chromosome fusion, chromosome breakage, addition of chromosomes through fertilization, polyploidy, and complications during meiosis. The lowest number is 3, ranging from 4 to 10 in the **Anthocerotophyta**, where 5 is the most common (Przywara & Kuta 1995). In the **Marchantiophyta**, the number ranges (3)4 to 48 with most species having n=8 or 9. In the **Bryophyta**, the number ranges 4 to 72(96) with chromosome numbers of n=10 and 11 being most common. In 1983, the highest reported number in pleurocarpous mosses was that of ***Stereophyllum tavoyense*** – 44 (Verma & Kumar 1983).

Przywara and Kuta concluded that polyploid numbers are n>10 in **Anthocerotophyta** and **Marchantiophyta** and n>9 in **Bryophyta**, although they consider the basic numbers in those groups to be 5, 9, and 7 respectively. They report 0% polyploids among the **Anthocerotophyta**.

There have been suggestions that polyploidy permits some polar tracheophytes to survive the extreme conditions, so it would be interesting to examine that correlation in bryophytes. One must also ask if the severe climate causes greater ploidy, or if having greater ploidy makes those species more fit to succeed. But in her study on bryophytes of Signey Island in the Antarctic, Newton (1980) found that there was no increase with latitude in polyploidy number among the 13 moss and 6 liverwort species there. However, she did conclude that it warranted further investigation, particularly in ***Bartramia patens***, ***Brachythecium austrosalebrosum***, ***Pohlia nutans***, ***Tortula robusta***, and ***Riccardia georgiensis***.

The interest in chromosome number has been superseded by an interest in mapping chromosomes and identifying the functions of genes. Information on nuclear, chloroplast, and other cellular DNA is helping us to understand relationships among the bryophytes. Chromosome numbers, however, still give us useful information on ways that new species have been created (see, for example, Ramsay 1982; Newton 1989).

Spore Production and Protonemata

As in all bryophytes, the spores are produced within the capsule by meiosis. In the **Bryopsida**, once germinated (Figure 3), they produce a **filamentous protonema** (first thread) that does not develop into a thalloid body. This germination process (Figure 4) can be rapid (1-3 days in ***Funaria hygrometrica***) or lengthy, involving a long dormancy period.

Figure 3. Germinating spore of ***Fontinalis squamosa***. Photo by Janice Glime.

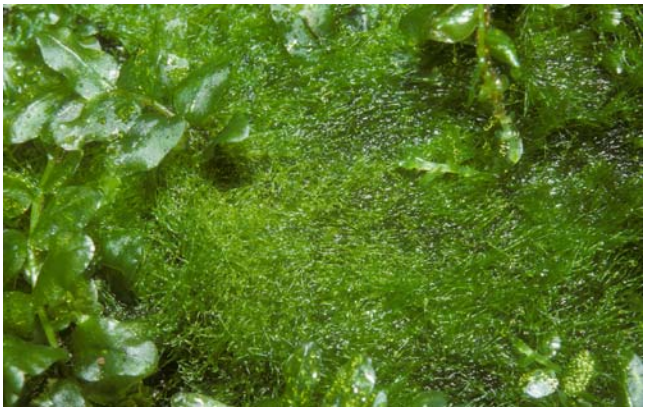

Figure 4. Protonemata among leafy plants of ***Plagiomnium***. Photo by Janice Glime.

Many mosses differentiate their protonemata into **chloronema** and **caulonema** (Figure 5-Figure 6). The **chloronema**, meaning light green thread or chlorophyll thread, is the first part of the protonema to form when the spore germinates. The **caulonema**, meaning stem thread, is the portion that develops later, but not in all mosses, and that gives rise to the upright **gametophores**, or leafy plants. The caulonema differs from the younger parts of the protonema, the chloronema, in having longer cells with slanting cross walls, usually brownish cell walls, and fewer, less evenly distributed, smaller spindle-shaped chloroplasts. The chloronema exhibits irregular branching, whereas the caulonema exhibits regular branching.

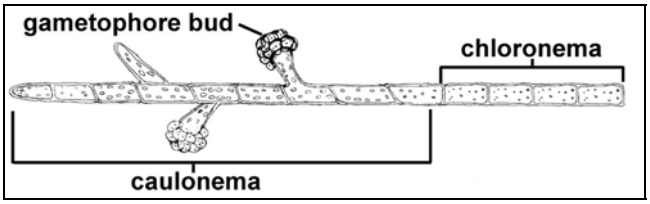

Figure 5. Protonema of moss such as ***Funaria hygrometrica*** with differentiated caulonema and chloronema. Drawing by Noris Salazar Allen, with permission.

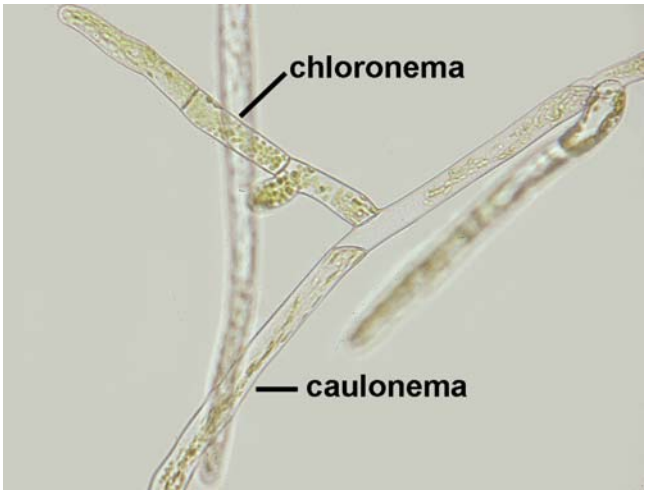

Figure 6. Protonema of ***Funaria hygrometrica*** showing chloronema (short cells with perpendicular walls and dense chloroplasts) and caulonema (long cells with diagonal cross walls and more dispersed chloroplasts). Photo by Janice Glime.

Gametophore Bud

As the protonema continues to develop and produce buds (Figure 7-Figure 9), the mosses and liverworts again differ. In liverworts, the bud is produced by the apical cell, hence ending further growth of the protonema and accounting for its single gametophore. In mosses, on the other hand, the bud originates from a cell behind the apical cell, hence permitting the apical cell to continue to divide and the protonema to continue to grow. The result is that moss protonemata produce many buds and upright plants (Figure 10). This provides the possibility for somatic mutations to arise, affording genetic variation among the leafy plants.

Figure 7. Moss protonema with young bud. Photo by Chris Lobban, with permission.

Figure 8. Protonema (caulonema) and young developing bud of the moss ***Funaria hygrometrica***. Photo by Martin Bopp, with permission.

As the bud develops, **rhizoids** (Figure 9, Figure 102) form, functioning largely in anchorage, but at least in some mosses, also functioning in moving water and nutrients from substrate to moss. This may be especially important as the atmosphere dries and the rhizoids help to maintain a humid substrate.

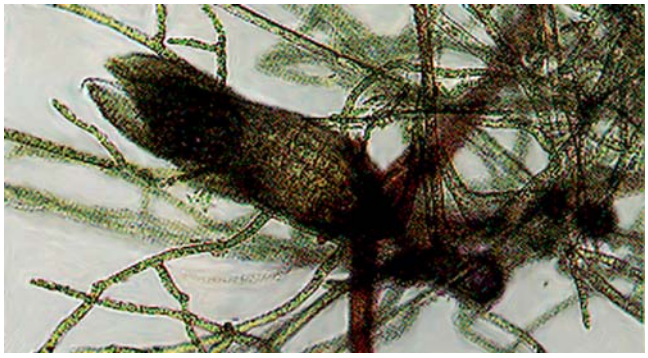

Figure 9. Moss protonema with developed bud. Brown threads are rhizoids. Photo by Janice Glime.

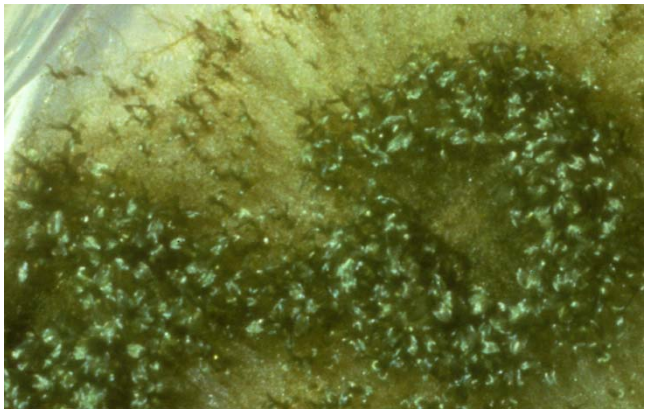

Figure 10. Leafy buds on the protonemata of ***Funaria hygrometrica*** forming a doughnut shape. Each of these circles of buds is the result of one spore. The hole in the middle is the area where the protonemata is in the chloronema stage and does not produce buds. Photo by Janice Glime.

Gametophores

The bud develops into the upright (or horizontal) **gametophore**. These plants are leafy **haploid** (1*n*) plants; thus, they are the **dominant gametophyte generation** of the life cycle. The stem may have a **central strand** (Figure 11), or lack it (Figure 12); this strand may or may not have **hydroids**.

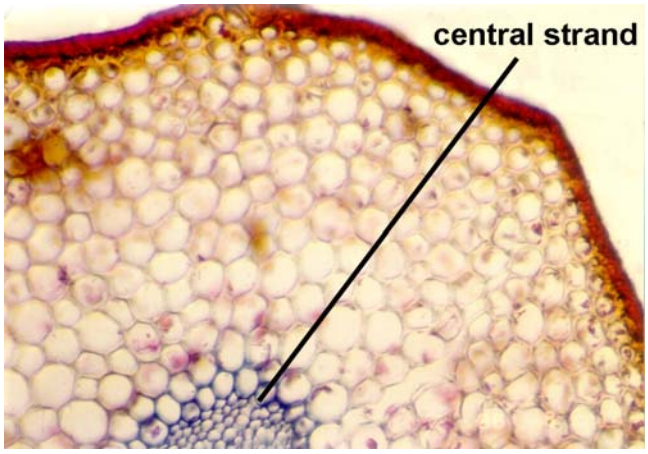

Figure 11. Stem cross section of ***Rhizogonium*** illustrating central strand of hydroids. Photo by Isawa Kawai, with permission.

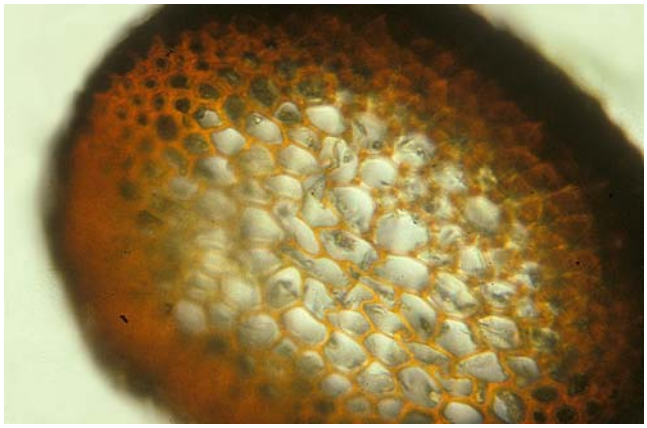

Figure 12. Cross section of stem of the brook moss ***Fontinalis dalecarlica*** showing absence of central strand and conducting tissues. Photo by Janice Glime.

Their leaves, more accurately known as **phyllids** (but rarely called that), are usually in **more than three rows** (Figure 13), but there are exceptions with two (Figure 14) or three rows (Figure 15). Typically they are one cell thick, but there are modifications on this scheme that are expressed in some mosses by leaves folded over on themselves, creating a pocket in the genus ***Fissidens*** (Figure 14), or alternating **hyaline** (colorless) and photosynthetic layers as in ***Leucobryum*** (Figure 16-Figure 18), or just multiple layers of tissue, sometimes in patches.

Figure 13. ***Brachymenium*** from the Neotropics, illustrating that leaves arise in more than three rows. Photo by Michael Lüth, with permission.

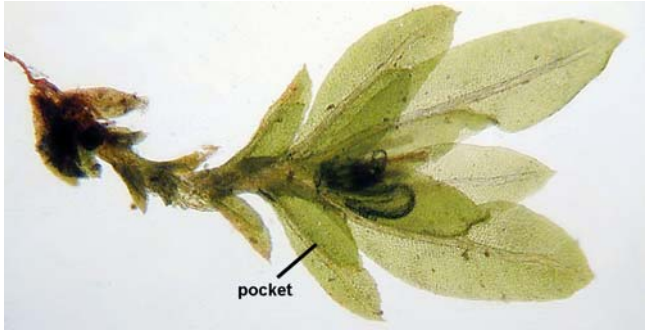

Figure 14. Pockets in leaf of ***Fissidens arnoldii***. Note the leaves in two rows. Photo by Michael Lüth, with permission.

Figure 15. ***Fontinalis antipyretica*** showing keeled leaves. Photo by Li Zhang, with permission.

Figure 16. ***Leucobryum glaucum***, a moss that gets its name from its whitish appearance due to hyaline cells surrounding the photosynthetic cells. Photo by Ralf Wagner <www.drralf-waner.de>, with permission.

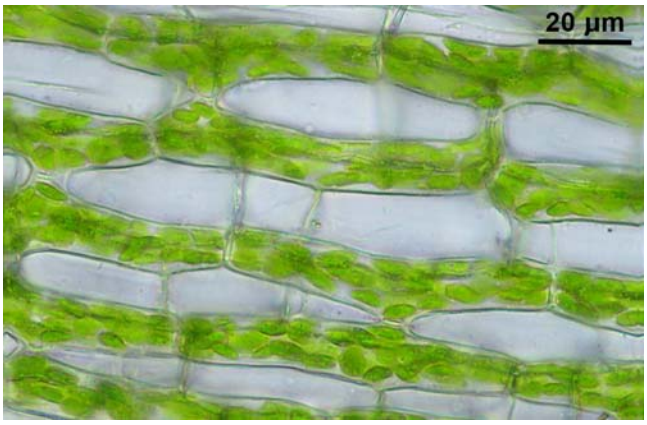

Figure 17. Hyaline and chlorophyllous cells of ***Leucobryum glaucum*** leaf. Photo by Ralf Wagner <www.drralf-wagner.de>, with permission.

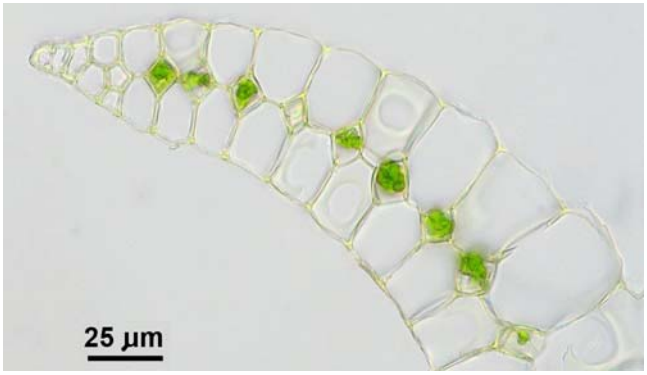

Figure 18. ***Leucobryum glaucum*** leaf cells. Photo by Ralf Wagner <www.drralf-wagner.de>, with permission.

Some leaves may have borders (Figure 19-Figure 20) which likewise can be one or more layers thick. These leaves often have a multi-layered **costa** (Figure 19, Figure 21) in the center, or double (Figure 22), or even triple costa. The **costa** itself (Figure 23) consists of long, narrow cells that offer support and seem to function in moving water more quickly than their wider and often shorter neighboring cells.

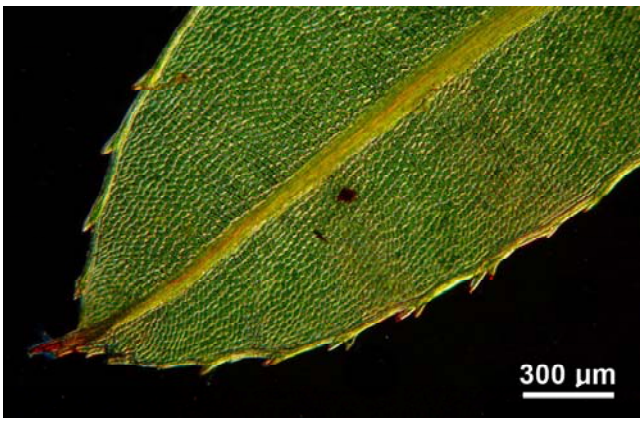

Figure 19. ***Mnium spinosum*** leaf showing border and costa. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 20. ***Mnium spinosum*** leaf cells, costa, and border. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 21. Cross section of Bryopsida leaf showing one cell thick lamina (blade) portion and thickened costa. Photo by Janice Glime.

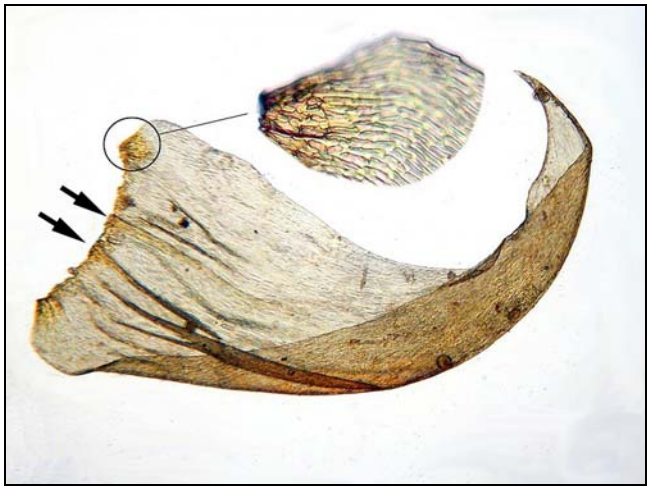

Figure 22. ***Caribaeohypnum polypterum*** leaf showing double costa. Photo by Michael Lüth, with permission.

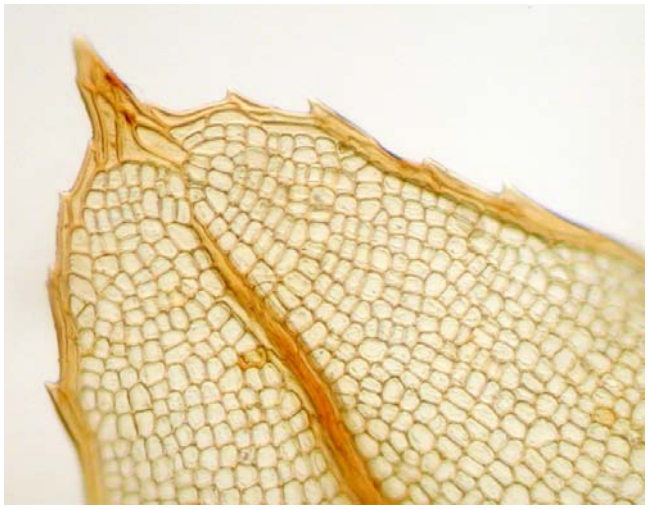

Figure 23. ***Mnium marginatum*** showing elongate costa cells compared to short lamina cells. Photo by John Hribljan, with permission.

Location of Sex Organs

Based on the branching patterns and location of sexual organs, the Bryopsida have traditionally been divided into two major groups, although there are good arguments for additional groupings. The **acrocarpous** mosses (Figure 24) are generally those upright mosses with terminal sporangia. They usually are unbranched or sparsely branched. **Pleurocarpous** mosses (Figure 25), by contrast, produce their sporangia on short, specialized lateral branches or buds and typically are prostrate, forming freely branched mats. The truly pleurocarpous mosses appear to represent a single monophyletic clade (Buck & Goffinet 2000; Buck *et al*. 2000a, b; Cox *et al*. 2000) and may be an adaptation to forming mats of continuous growth in mesic conditions (Vitt 1984). Those mosses that bear sporophytes terminally on short, lateral branches form a special category of pleurocarpous mosses termed **cladocarpous**. The branching patterns and positions of sporangia determine not only the **growth form**, but also influence success of fertilization, availability of water, and ability to spread horizontally across a substrate.

Figure 24. ***Barbula unguiculata***, an **acrocarpous** moss. Setae originate at the apex of the previous year's growth. Photo by Michael Lüth, with permission.

Figure 25. ***Neckera urnigera***, a **pleurocarpous** moss showing the origin of the setae on short side branches. Photo by Michael Lüth, with permission.

The upright or sprawling stems of the gametophyte produce **antheridia** (sperm-containers; Figure 26) and **archegonia** (egg-containers; Figure 28). In mosses, antheridia and archegonia may be located at the end of the main stem (Figure 29), at the ends of lateral branches, or along the main stem, either at the ends of very short branches (Figure 30) or nearly sessile (Figure 103). One can determine the position of archegonia most easily by finding the base of the seta. Often the chloroplasts of the antheridial jacket cells are converted into chromoplasts as the antheridia mature, causing the characteristic red-orange color (Figure 29) (Bold *et al.* 1987).

Sperm Dispersal

Crawford *et al*. (2009) found that there seemed to be no evolutionary support for a relationship between asexual reproduction and the separation of the sexes. Hence, they reasoned that the evolution of the sexual system is influenced by mate availability and gamete dispersal.

Release of Sperm from the Antheridium

The release of the sperm from the antheridium is an interesting phenomenon. In ***Mnium hornum*** (Figure 31), within about four minutes of placing water into an antheridial cup, dehiscence will occur (Muggoch & Walton 1942). The **spermatocytes** (cells in which sperm have differentiated) emerge in a banana-shaped packet (Figure 27, Figure 33) into the water surrounding the antheridium, usually within 4-10 minutes.

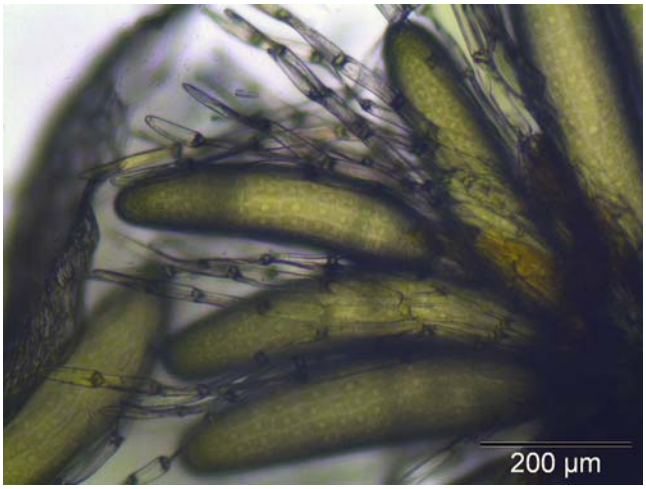

Figure 26. ***Hypnum cupressiforme*** paraphyses and antheridia. In this species, antheridia occur long the stem. Photo by Kristian Peters, with permission.

Figure 27. ***Aloina ambigua*** sperm release, looking like white, gelatinous clouds. Photo courtesy of Llo Stark.

Figure 28. Pleurocarpous moss ***Pleurozium schreberi*** showing archegonia on short branch along stem. Photo by Janice Glime.

Then, when (or if) that packet connects with the water-air interface, the sperm spread apart rapidly to form a surface layer of regularly spaced sperm (Muggoch & Walton 1942). This movement of sperm emerging from an antheridium is shown in a film by Serge Hoste <http://users.pandora.be/serge.hoste1/>. This spreading suggests that some substance with a low surface tension might be present in the sperm packet because the mass spreads much like an oil spill. The behavior suggests that there is a small amount of fat present in the sperm mass.

Figure 29. ***Ptychostomum capillare*** showing antheridial head of male plants. Photo by Michael Lüth, with permission.

Figure 30. ***Racomitrium didymum*** showing seta, hence archegonium, arising on a short branch. Photo by Michael Lüth, with permission.

Figure 31. ***Mnium hornum*** male splash cups. Photo by David T. Holyoak, with permission.

Cronberg *et al*. (2008) filmed various stages in the life cycle of ***Bryum argenteum***. They found that this species expels its sperm in a mass (Figure 32-Figure 37). The upper cells of the antheridium are expelled and the sperm mass is released. This is a rapid occurrence, followed by a slower activity of sperm escaping from the mass. The sperm have a density close to that of water and thus are easily transported by moving water. When the sperm mass reaches the air surface, the mass disintegrates almost instantly as the mass and surface tension of water react. The surface tension causes a passive dispersal of the sperm for ~2 cm. After 30 minutes, about half the sperm are dead. All are dead after 60 minutes. This might differ in nature where the water chemistry is different.

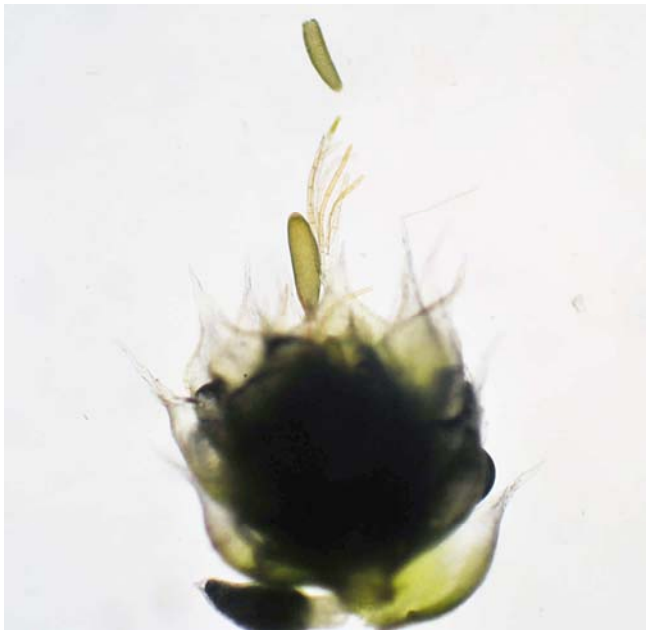

Figure 32. ***Bryum argenteum*** antheridia with antheridia and sperm masses being released. Photo by George Shepherd through Creative Commons.

Figure 33. ***Bryum argenteum*** releasing sperm masses from submerged antheridia. Photo by Nils Cronberg, Hans Berggren, & Rayna Natcheva, with permission.

Figure 34. ***Bryum argenteum*** antheridium with initial explosive sperm mass release. The upper cells of the antheridium are also expelled. Photo by Nils Cronberg, Hans Berggren, & Rayna Natcheva, with permission.

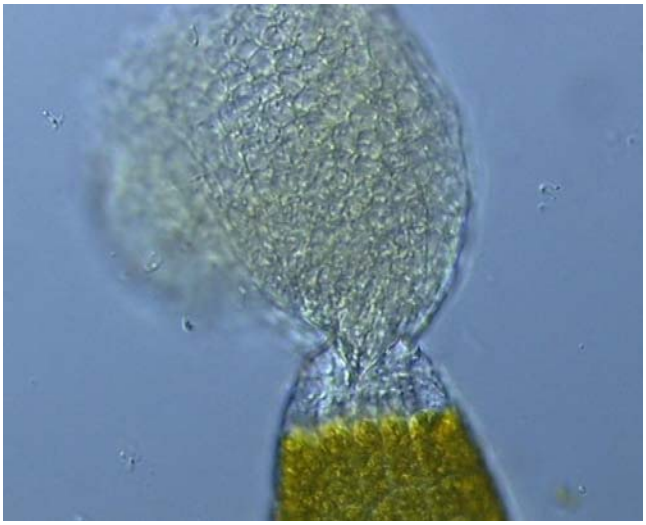

Figure 35. ***Bryum argenteum*** antheridium with final sperm mass release. A few sperm have already left the sperm mass. Photo by Nils Cronberg, Hans Berggren, & Rayna Natcheva, with permission.

Figure 36. ***Bryum argenteum*** perigonium with spent antheridia. Photo by George J. Shepherd through Creative Commons.

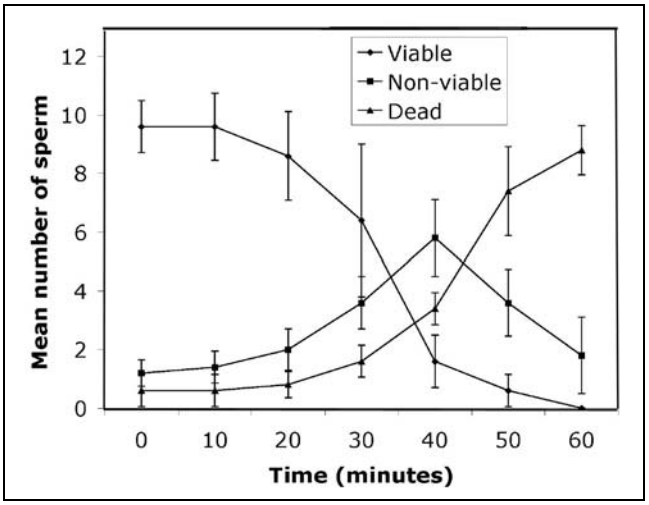

Figure 37. Time lapse of sperm release and viability in ***Bryum argenteum***. Modified from Cronberg *et al*. 2008.

Llo Stark has provided us with a time sequence of the release of the sperm packets in ***Aloina ambigua*** (Figure 38-Figure 40).

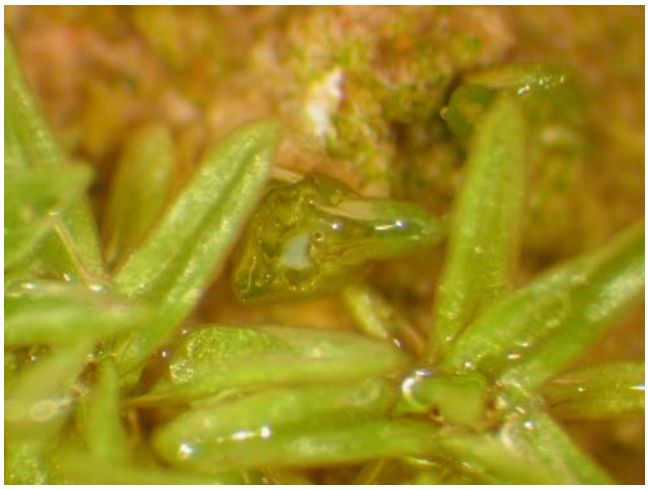

Figure 38. ***Aloina ambigua*** early sperm packet release into the cup formed by the perigonial leaves. Photo courtesy of Llo Stark.

Figure 39. ***Aloina ambigua*** sperm packet release into the perigonium. Photo courtesy of Llo Stark.

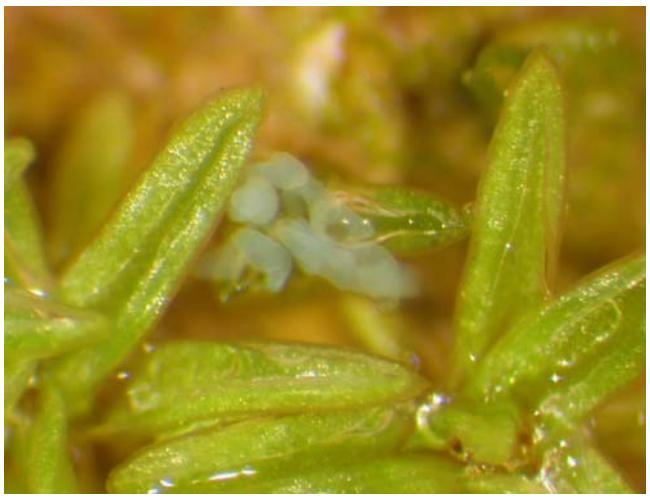

Figure 40. ***Aloina ambigua*** with distended sperm packets. Photo courtesy of Llo Stark.

Dispersal to the Archegonium

Some bryophytes seem to have no special means of dispersing their sperm, relying on the water film that surrounds the bryophytes when it rains. Others have developed splash cups or splash platforms that aid in the dispersal of sperm. Andersson (2002) filmed the splashes on splash cups in the moss ***Plagiomnium affine*** (Figure 41). Andersson observed that water fills the splash cup capillary spaces among the antheridia and paraphyses up to the bottom of the cup. He determined that for a striking raindrop to have the space needed to develop, the diameter of the drop should be 1 mm or less, a size common in most rain showers. The impact of the drop causes the ripe antheridia to rupture, causing the spermatozoids to reach the bottom of the splash cup through the capillary spaces created by the heads of the paraphyses. The drop of rain incorporates water from the bottom of the splash cup, thus including the spermatozoids that are entering the cup. These droplets can travel 100 mm or more as they rebound from the cup, thus effecting fertilization of nearly all female gametangia within about 80 mm. Since the fertilization period in southwestern Sweden lasts about three weeks, this is usually sufficient time for one or more appropriate rainfalls to occur and facilitate dispersal.

Figure 41. ***Plagiomnium affine*** splash cups. Photo by Peter Gigiegl. Permission pending.

Duckett and Pressel (2009) demonstrated that falling raindrops on the antheridiophores of the liverwort ***Marchantia polymorpha*** were not very effective, so the even softer splash platforms of mosses may be even less effective, or certainly not any better. Measurements from fertilized females to nearest male have provided us with some estimates, as for example that of ***Plagiomnium ciliare*** (Figure 42) for 5.3 cm (Reynolds 1980). But Reynolds did find that artificial rainfall could splash over 10 cm and concluded that measurements to nearest male most likely underestimated the distances sperm could travel from a splash cup or platform.

Figure 42. ***Plagiomnium ciliare*** with splash platforms. Photo by Robert Klips, with permission.

Figure 43. ***Polytrichum commune*** males with splash cups. Photo by Li Zhang, with permission.

Until somewhat recently we have assumed that in most bryophytes sperm reached the archegonia by splashing or swimming from the antheridia to a landing spot, then swimming the remainder of the way. Closer observation by recent researchers indicates that such an inefficient and unsafe method may not be the case for some bryophytes, and that we should examine others more closely for secrets in their sperm dispersal. Muggoch and Walton (1942) considered the presence of fat in the sperm mass to be a widespread phenomenon, perhaps true of all mosses, and that it was important in permitting insects to carry sperm to female plants. However, there seem to be few observations of such insect dispersal except in ***Polytrichum*** (Class **Polytrichopsida**; Figure 43) and ***Ptychostomum capillare*** (syn. = ***Bryum capillare***; **Bryopsida**; Figure 29).

The idea that invertebrates may disperse sperm is not entirely new. Harvey-Gibson and Miller-Brown (1927) observed various invertebrates visiting the fertile shoots of ***Polytrichum commune*** (Figure 43). As the invertebrates crawled about the male splash cups, they picked up mucilage and sperm. The researchers then observed that the same insects would appear on female plants with abundant sperm smeared on their bodies and legs in the mucilage. The invertebrates seemed to consider mucilage to be a source of food as they "greedily" lapped it up and also licked at saline crystals on the perichaetial leaf margins.

It appears that ***Ptychostomum capillare*** (Figure 29) may indeed be fertilized, at least some of the time, by animals. When covered by a fine net to discourage winged insects and other creatures, females were not fertilized, but when the net was removed, fertilization occurred 2 m(!) from the nearest males (Gayat 1897). However, it is difficult to rule out the possibility of raindrops in this case, or even squirrels, for that matter. Raindrops are likely to trap the mucilage with its sperm load in the tiny capillary spaces of the net. The success of fertilization would depend on the success of these drops getting bounced from one plant to another, and that bounce would surely be inhibited by such a filter to diminish the impact and retain the mucilage.

Observations on ***Bryum argenteum*** (Figure 44-Figure 45) are more conclusive. Cronberg *et al*. (2006), in an experiment in which male and female plants were separated by 0, 2, and 4 cm, demonstrated that help from such agents as invertebrates are essential. These treatment distances were combined either with no animals, or with mites (Acarina: ***Scutovertex minutus***; see Figure 46) or springtails (Collembola: ***Isotoma caerulea***, Figure 47) (Cronberg *et al*. 2006; Milius 2006). After three months, those females in contact with male plants (0 cm) produced sporophytes. Those without this contact (2 or 4 cm) and without either animal group produced no sporophytes. But those housed with springtails or with mites produced numerous sporophytes, with springtails being the more effective conveyor. Springtails are more mobile than mites, and in this experiment, more sporophytes were produced at greater distances when springtails were available as dispersal agents.

Figure 44. ***Bryum argenteum*** males. Photo by George Shepherd, through Creative Commons.

Figure 45. ***Bryum argenteum*** with sporophytes, signalling successful fertilization. Photo by George Shepherd, through Flickr Creative Commons.

Figure 46. ***Scutovertex sculptus***; ***Scutovertex minutulus*** is a mite that facilitates sperm dispersal in some bryophytes. Photo by Matthew Shepherd, through Creative Commons.

Figure 47. ***Isotoma caerulea***, a springtail that is instrumental in fertilizing ***Bryum argenteum***. Photo by Katrina Hedlund, with permission.

But how do these springtails find the mosses? Flowers provide odors and colors to attract their pollinators. It appears that these mosses also have a way to attract their dispersal agents. When springtails and mites were given choices of plants with mature gametangia vs those that were sterile, fertile plants were chosen over non-fertile ones about five times as often (Beckman 2006) in the cases of both male and female mosses and by both arthropod organisms. Cronberg *et al*. (2006) suggest that fertile plants may attract the invertebrates with sucrose (Pfeffer 1884), starch, fatty acids, and/or mucilage (Harvey-Gibson & Miller-Brown 1927; Paolillo 1979; Renzaglia & Garbary 2001). Ziegler *et al*. (1988) demonstrated the presence of sucrose in the archegonium exudate of ***Ptychostomum capillare*** (Figure 29). Llo Stark has captured images of this exudation in ***Aloina ambigua*** (Figure 48-Figure 50).

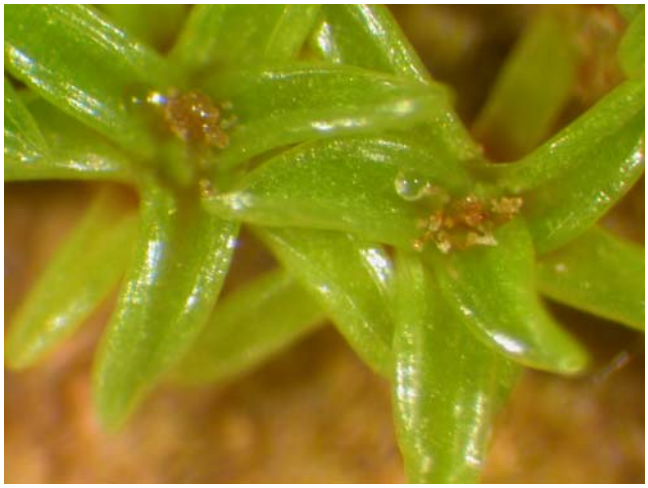

Figure 48. ***Aloina ambigua*** archegonium exudate. Photo courtesy of Llo Stark.

Figure 49. ***Aloina ambigua*** archegonia with one showing exudate. Photo courtesy of Llo Stark.

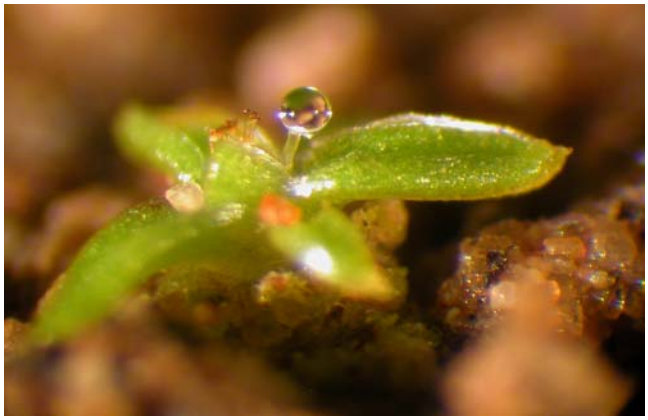

Figure 50. ***Aloina ambigua*** showing archegonium exudate. Photo courtesy of Llo Stark.

A small flurry of research followed this exciting finding (Cronberg 2012). Both ***Bryum argenteum*** (Figure 45) and ***Ceratodon purpureus*** (Figure 51) sperm are transported by tiny springtails (***Folsomia candida;*** Figure 52) (Rosenstiel *et al*. 2012). Rosenstiel and coworkers (2012) used ***Ceratodon purpureus*** to examine what attracts sperm dispersers. They found that this moss species produces volatile compounds – some of those secondary compounds that have evolved tremendous varieties in bryophytes. They were able to demonstrate that some, perhaps many, of these compounds attracted the springtail ***Folsomia candida*** (Figure 52). The volatile compounds are sex-specific (Figure 53) and definitely increase the rate of fertilization, even when splashing water is provided to facilitate sperm transfer (Figure 54). Although fertilization rates were about the same in treatments of water spray alone and springtails alone, the presence of both more than doubled the rate of using either alone.

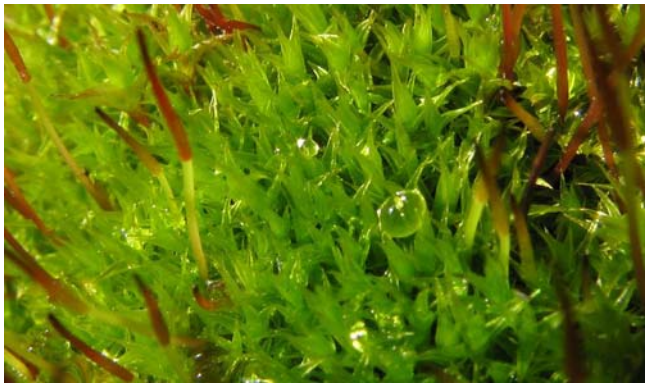

Figure 51. ***Ceratodon purpureus*** showing water drops that could facilitate fertilization. Photo by Jiří Kameníček, with permission.

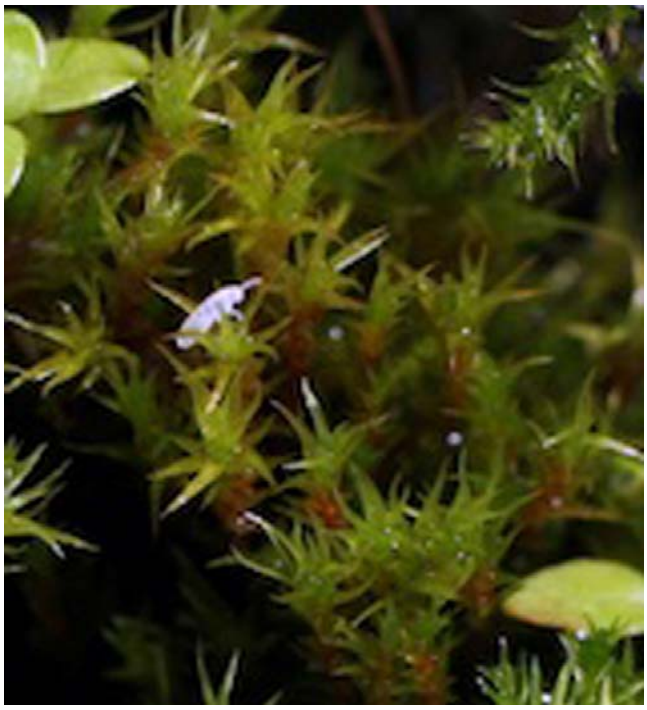

Figure 52. ***Folsomia candida*** (Collembola) on ***Ceratodon purpureus***. Photo by Erin Shortlidge, with permission.

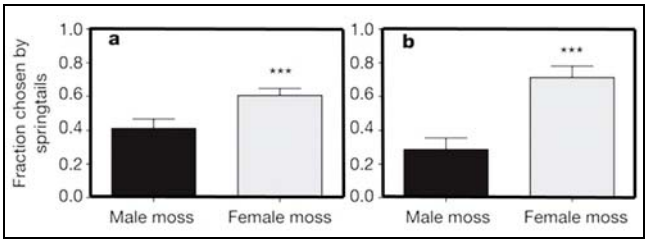

Figure 53. Sexual preference of the springtail ***Folsomia candida*** on ***Ceratodon purpureus***. **a.** Petri dishes with 24 assays, 491 springtails. **b.** Samples in an olfactometer with 10 assays, 276 springtails. Vertical lines represent standard error of the mean. *** denotes $p<0.0001$. Modified from Rosenstiel *et al*. 2012.

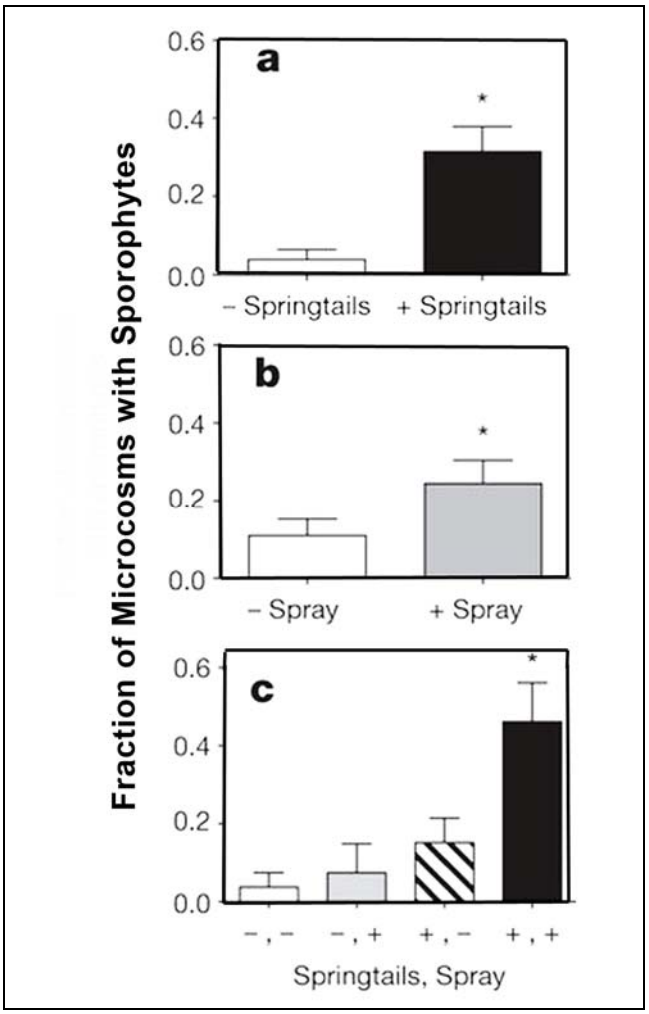

Figure 54. Effect of the springtail ***Folsomia candida*** vs water spray treatment on fertilization success of ***Ceratodon purpureus*** and ***Bryum argenteum*** in 108 microcosms. Vertical lines represent standard error of mean. * denotes significantly different, $p<0.05$. Modified from Rosenstiel *et al*. 2012.

Splash cups and splash platforms help to launch the sperm in many acrocarpous taxa, with spreading upper leaves serving to facilitate the launch. Richardson (1981) estimated that raindrops could splash these sperm only about 5 cm in small mosses, but up to 2 m in large ones. In mosses without antheridial splash cups or platforms, dispersal distances are typically short. Pleurocarpous mosses are not arranged in such a way as to offer much of a boost to raindrops containing sperm. In ***Hylocomium***

splendens (Figure 55), sperm have a long distance record of only 11.6 cm (Rydgren *et al*. 2005).

Figure 55. ***Hylocomium splendens*** in autumn. Photo by Petr Brož, through Wikimedia Commons.

Insect dispersal of sperm is not unique to ***Ceratodon purpureus*** (Figure 52). Ignatov (1921) reported that the luminous moss, ***Schistostega pennata*** (Figure 56), has several kinds of visitors who facilitate sperm dispersal. This species is **cladoautoicous** (male and female reproductive structures on separate stems, connected only by the protonema; Figure 57-Figure 59). Thus, the sperm must be dispersed to a different stem. In addition to movement in a drop of water when the antheridium bursts (Figure 60), in the Moscow Province of Russia this dispersal is facilitated by a variety of small arthropods, including mites in the families **Damaeidae** (*e.g.* ***Damaeus lengersdorfi***, Figure 61, Figure 62) **Oribatulidae** (*e.g.* ***Oribatula tibialis***, Figure 63-Figure 64), **Astegistidae** (*e.g.* ***Furcoribula furcillata***, Figure 65), and **Ceratozetidae** (*e.g.* ***Melanozetes mollicomus***, Figure 66), and springtails ***Orchesella bifasciata*** (Figure 67) and ***Entomobrya nivalis*** (Figure 68) in the family **Entomobryidae**. The arthropods use the antheridial contents as food. This activity is facilitated by the barely hidden antheridia of ***Schistostega pennata***, unlike those of most mosses that are well protected by perigonia.

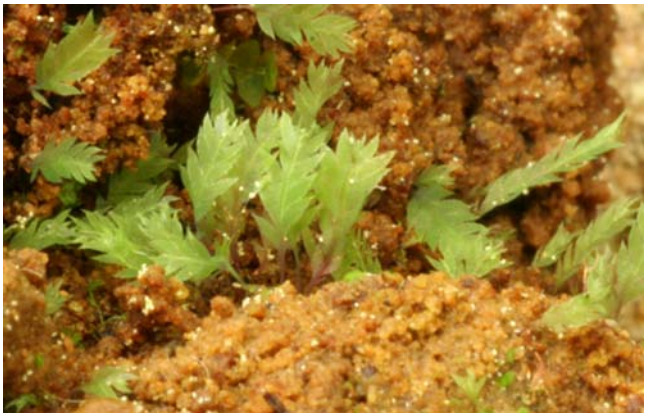

Figure 56. ***Schistostega pennata*** showing individual stems. Photo by Martine Lapointe.

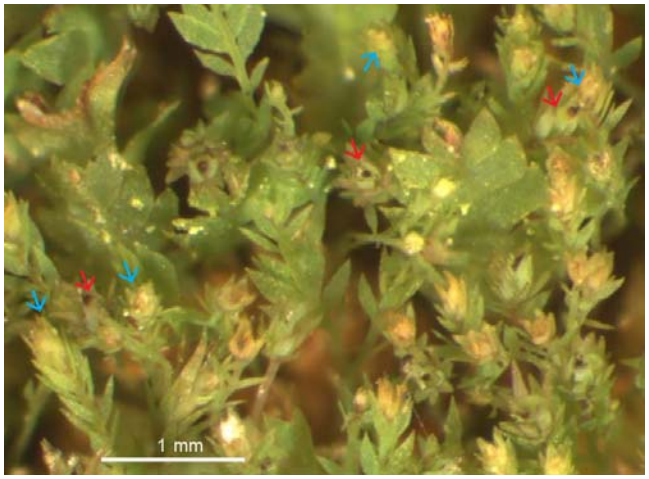

Figure 57. ***Schistostega pennata*** male (**blue**) and female (**red**) plants. Photo by Misha Ignatov, with permission.

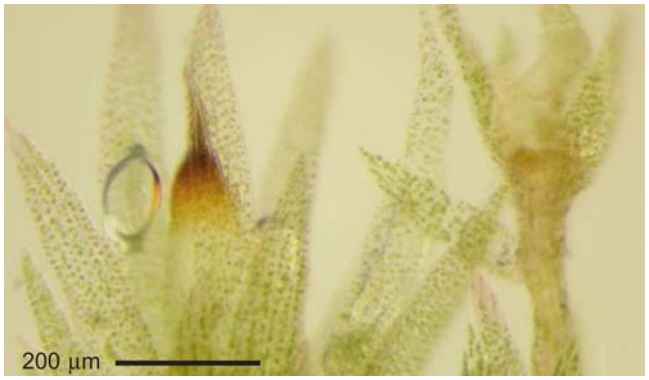

Figure 58. ***Schistostega pennata*** female (**left**) and male (**right**) plants. Photo by Misha Ignatov, with permission.

Figure 59. ***Schistostega pennata*** male plants showing antheridia. Photo by Misha Ignatov, with permission.

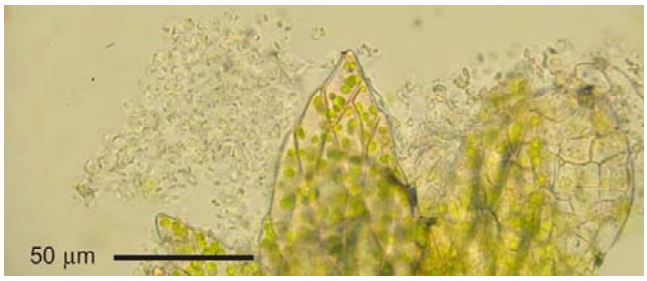

Figure 60. ***Schistostega pennata*** antheridia dispersing sperm. Photo by Misha Ignatov, with permission.

Figure 61. ***Schistostega pennata*** with young mite of ***Damaeus lengersdorfi*** approaching antheridia and eating contents. Photo by Misha Ignatov, with permission.

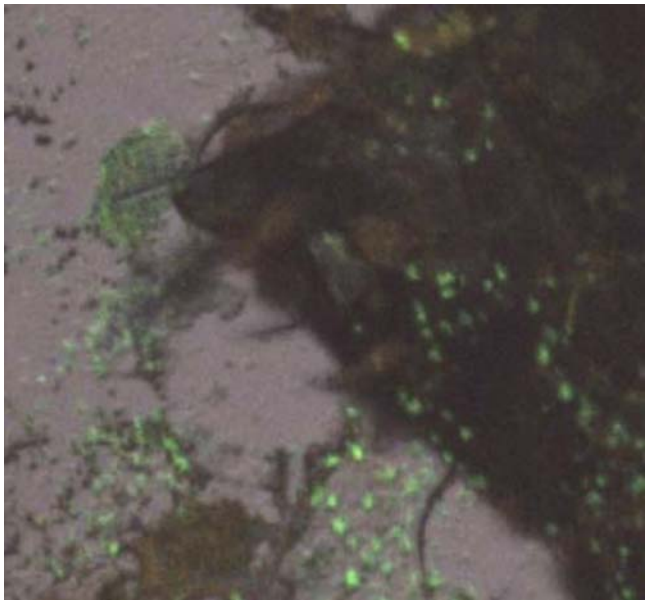

Figure 62. ***Damaeus lengersdorfi*** with sperm (with green DAPI stain) after visiting ***Schistostega pennata***. Photo by Misha Ignatov, with permission.

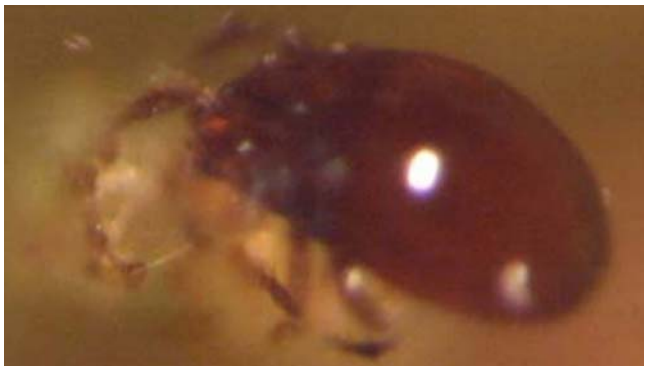

Figure 63. The mite ***Oribatula tibialis*** feeding on ***Schistostega pennata*** antheridia. Photo by Misha Ignatov, with permission.

Figure 64. ***Oribatula tibialis*** from ***Schistostega pennata***. Photo by Misha Ignatov, with permission.

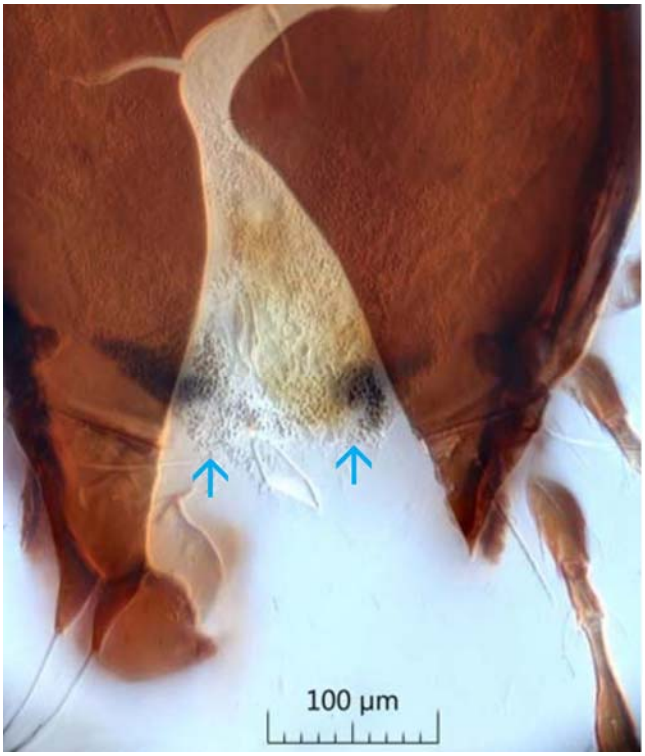

Figure 65. ***Furcoribula furcillata*** esophagus with sperm (**dark**) and **ovate** spores from ***Schistostega pennata***. Photo by Misha Ignatov, with permission.

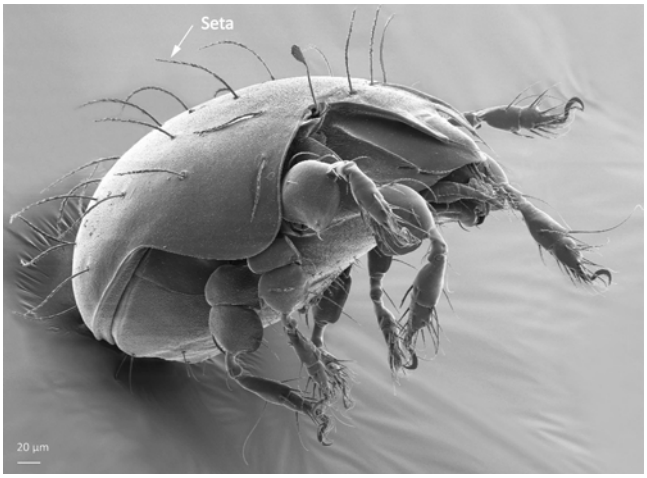

Figure 66. ***Melanozetes mollicomus***, a mite known to feed on antheridia of ***Schistostega pennata***. Photo by Anna Seniczak, through Creative Commons.

Figure 67. ***Orchesella bifasciata***, a springtail that feeds on antheridia of ***Schistostega pennata***. Photo by Arne Fjellberg, through Creative Commons.

Figure 68. ***Entomobrya nivalis***, a springtail that feeds on antheridia of ***Schistostega pennata***. Photo by Ben Armstrong, through Creative Commons.

Anderson (2000) managed to catch the dispersal of ***Plagiomnium affine*** (Figure 41) on video to see the effectiveness of the splash platform of that moss. Although many drops will miss the tiny platform completely, a few manage full hits. Impact causes a "crown" of water to form, like dropping a rock into a lake. The capillary spaces between the antheridia and adjoining **paraphyses** (sing. **paraphysis:** sterile filaments located among reproductive organs; Figure 69, Figure 101, Figure 103) fill with water.

The impact of the drop causes the swollen antheridia to burst, releasing the swimming sperm. For the splash to be effective in making the crown, the diameter of the drop should be 1 mm or less, a common size in most rain showers. The rim of the crown has small droplets that are propelled away by the action. Since these droplets include water from within the splash platform, they also contain the sperm and thus propel them away from the plant. These droplets can travel 100 mm or more and manage to fertilize most of the females within 80 mm. The dioicous liverwort ***Marchantia*** has a splash platform that performs a similar function.

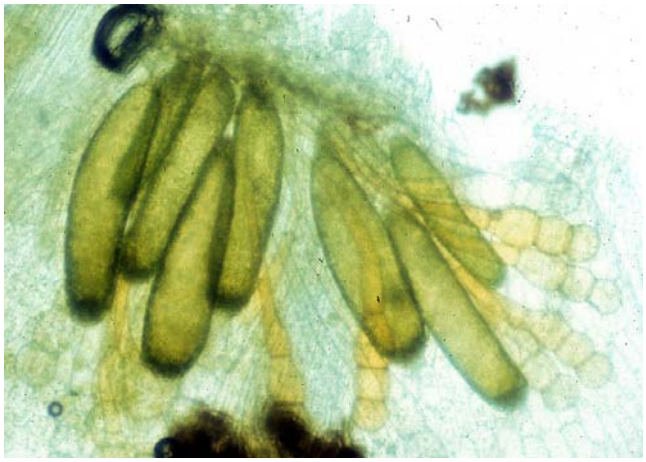

Figure 69. Mature **antheridia** and **paraphyses** of the moss ***Rhizomnium*** sp. Photo by Janice Glime.

Splash cups and platforms seem to be rare in monoicous taxa [exceptions include species of ***Brachymenium*** (Figure 70) and ***Rosulabryum*** (Figure 71) per John Spence], suggesting fertilization is accomplished with close neighbors. For most **Bryopsida**, however, there is no antheridial splash cup or platform, so seemingly sperm must swim all the way.

Figure 70. ***Brachymenium*** sp. showing splash platform. Photo by Michael Lüth, with permission.

Figure 71. ***Rosulabryum laevifilum*** with splash platform. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

However, other things can create splash. Jonathan Shaw (pers. comm.) has considered that ***Funaria. hygrometrica*** (Figure 72) has wide-spreading bracts surrounding the antheridia and the flexible nature of these bracts permits them to bend back and create an effective cup from which sperm in that species might be splashed. Angela Newton (pers. comm.) has suggested that platform surfaces among the more dendroid and shelf-forming taxa could be viewed as water-trapping mechanisms that would promote surface flow and dripping to the next level down as a mode of transporting sperm between individual plants or parts of plants. One complication in this arrangement is that the complex texture would act to trap water drops rather than encouraging them to splash out and away. However, in some of the plants with large smooth leaves, these leaves might act as springboards, but Newton considered that in such a case the water drops would be unlikely to carry sperm, although they might carry the smaller kinds of vegetative propagules. Nevertheless, sperm that had gotten as far as a leaf might benefit from this splash as well.

Figure 72. ***Funaria hygrometrica*** males showing splash apparatus. Photo by James K. Lindsey, with permission.

Now it would seem that monoicous taxa might not need a partner since they have one built in. For example, ***Desmatodon randii*** and ***D. urainicus*** are both self-compatible when grown from a single spore (Lazarenko & Lesniak 1972; Lazarenko 1974). ***Desmatodon randii*** retained vigorous fertility for 15 generations of self crossing in the lab (Lazerenko 1974). On the other hand, it also gave rise to a spontaneous **apogamous** (development of sporophyte without gamete union) haploid line that continued the line vegetatively.

The suggestion of selfing is even supported by the scarcity of splash platforms in monoicous taxa. And in desert habitats, the monoicous condition prevails, presumably due to the scarcity of water for sperm dispersal (Stark 1983). Nevertheless, means exist to ensure at least some cross fertilization in monoicous taxa (Longton & Miles 1982; Ramsay & Berrie 1982). Such means include having antheridia placement below the archegonia on the same stem (Longton & Miles 1982) or on different stems or branches, and differences in timing of maturity of male and female gametangia. Despite the greater opportunity for selfing, Lefebvre (1969) found evidence in the **Plagiotheciaceae** that not only do monoicous species have a wider distribution, they also have greater phenotypic variability than that found in dioicous species in the family.

Longton and Miles (1982) suggest that the greater distance between male and female gametangia in **autoicous** (male & female gametangia in separate clusters) species provides a greater opportunity for out-crossing. But a close neighbor is likely to be part of the same clone or grown from a spore from the same parent. Nevertheless, this permits mutations to be remixed and passed to a new generation and thus provide at least some genetic mixing.

Lazarenko and Lesniak (1972) found that ***Physcomitrella patens*** from wild strains was self compatible, but certain mutant strains were self incompatible. On the other hand, they found that monosporic cultures of ***Desmatodon cernuus*** were sterile when grown in 24-hour light (these are long-day plants preferring 16 hours daylight), demonstrating the importance of environmental conditions, especially in new locations.

Ashton and Cove (1977) have also demonstrated possible mechanisms of compatibility by using mutants. They have shown that many **auxotrophs** (requiring an additional nutrient) of ***Physcomitrella patens*** are self-sterile. They obtained a diploid strain by aposporus regeneration from a hybrid sporophyte and the progeny accomplished self-fertilisation. Outcrossing would most likely supply the right genes to complement the missing one(s), but half the forthcoming spores would still be expected to carry the mutation. There would be a quick selection against the mutants in the next generation of gametophytes if the missing or mutant gene was needed by the gametophyte. The big advantage for monoicous taxa is that their nearest neighbors can always provide gametes of the opposite sex. (See fuller discussion in Chapter 3-4 of this volume.)

Whereas flowering plants frequently rely on animals, especially insects, to transport their male gametophytes, and ultimately the sperm, to the female reproductive organ, this seems rarely to be the case in bryophytes. Surprisingly, until recently it appears that the only documented case of such animal transport of sperm was in ***Polytrichum commune*** (Polytrichopsida; Figure 73), which has well-developed splash cups (Figure 73) for the purpose of sperm dispersal. Nevertheless, it was in this species that Harvey-Gibson and Miller-Brown (1927) found motile

sperm on the bodies of small arthropods (flies, leafhoppers, mites, spiders, and springtails) on both male and female reproductive inflorescences. Schofield (1985) suggests that mucilage produced in both the **perigonia** (modified leaves enclosing male reproductive structures; Figure 74) and **perichaetia** (modified leaves enclosing female reproductive structures; Figure 75) sometimes attract invertebrates.

Figure 73. ***Polytrichum commune*** antheridial splash cups. Photo by Michael Lüth, with permission.

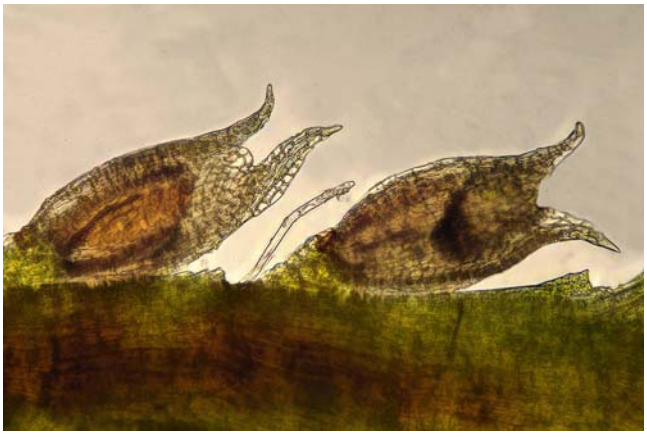

Figure 74. ***Fissidens bryoides*** antheridia along stem where they are surrounded by **perigonia**. Photo by Dick Haaksma, with permission.

Figure 75. ***Polytrichum commune*** female showing tight perichaetial leaves at the tips of plants. Photo by Michael Lüth, with permission.

Clayton-Greene *et al*. (1977) used laboratory tests to determine the distance sperm could travel from the large moss ***Dawsonia longifolia*** (=***D. superba***) (Figure 76). Field investigations indicated that this species uses a splash cup mechanism. Field data of sporophyte production indicated that capsules seldom develop on females located more than 1.5-2 m from any male. They found similar results in the lab when they dropped water from a height of up to 3.3 m. In experimental heights ranging from 150 to 330 cm, travel distances ranged from 105 to 230 cm, indicating that height of water drop positively affects dispersal distance. But in the smaller ***Polytrichum ohioense*** (Figure 77), sperm in experiments only landed up to 61 cm from the source when water was dropped from ~1 m (Clayton-Greene *et al*. 1977). Clayton-Greene *et al*. suggested that smaller drops could act like an aerosol spray and float in air, achieving greater distances.

Figure 76. Female ***Dawsonia longifolia*** (=***D. superba***). Photo by Jan-Peter Frahm, with permission.

Figure 77. ***Polytrichum ohioense*** males with new growth from old splash cups. Photo by Janice Glime.

One might expect that many antheridia burst as they and their surrounding **paraphyses** (Figure 78) swell from a desiccated state to a hydrated state during early minutes of a precipitation event. Could it be that the same external capillary forces that carry water rapidly to other parts of the plant could move sperm, thus reducing the energy requirements for getting these tiny cells to their destinations? Or are these forces to be reckoned with, forcing the sperm to swim against a current?

Figure 78. Antheridia and paraphyses of ***Rhizomnium*** sp. Photo by Janice Glime.

If sperm swim so slowly, how do they ever reach their goal in the absence of an accurate splash? One aid to this dispersal in at least some bryophytes is that the antheridia release fatty materials that cause a rapid dispersal of sperm upward in a continuous film of water (Muggoch & Walton 1942). But apparently this mechanism is not available to all bryophytes, nor are conditions always suitable for it to work.

If animal dispersal is so rare, then how, in this vast world, does an unintelligent sperm find an archegonium and an egg? Fortunately for the moss, the archegonium at this time has dissolved the **neck canal cells** (entry canal through neck to egg in base of archegonium; Figure 79; Figure 103) leading down to the **egg** in the venter (Figure 79), and the resulting liquid provides a chemical attractant for the sperm.

Meanwhile, the egg exudes mucilage into the cavity of the venter (Lal *et al*. 1982). When the canal opens, the liquid exudes from the opening of the neck (Figure 48-Figure 50), creating a chemical gradient. The sperm follows the concentration gradient toward the archegonium and finally swims down the **neck canal** (Figure 79) of the archegonium to the egg. The exact nature of this liquid is unknown, but it seems that sugars (Harvey-Gibson & Miller-Brown 1927) and sometimes boron are necessary. It seems also likely that something specific, perhaps a protein, might guide the sperm to the correct species. Otherwise, it would seem that in spring, when so many species are producing sexual structures, some of these sperm would find their way into the wrong archegonium – or perhaps they do!

Gayat (1897 in Clayton-Greene *et al*. 1977) experimented with ***Ptychostomum capillare*** (Figure 29) and found that when the plants were covered with a fine net, female plants located 2 m from males had no fertilization, but when the net was removed, giving insects access to the females, these same plants did have fertilization. Harvey-Gibson and Miller-Brown (1927) found that in ***Polytrichum commune*** (Figure 73-Figure 75) the paraphyses (Figure 79) of both males and females exuded mucilage, but contained no sugar. These gametangial areas were "constantly" visited by oribatid mites, two species of **Collembola** (springtails), a small midge (**Diptera**), a leaf hopper (**Cicadidae**), an aphid, and a spider. They found that the insects "greedily" lap the mucilage and their body parts become smeared with the mucilage excretion. This adhering mucilage contains actively motile sperm. These sperm-carrying invertebrates were also located on female plants.

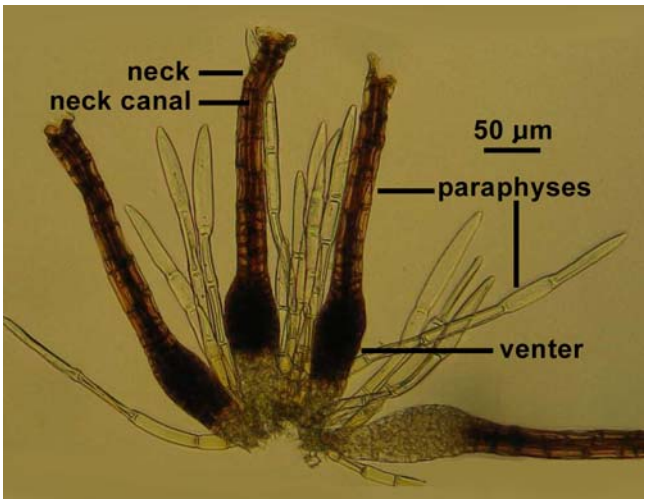

Figure 79. Archegonia of ***Zygodon intermedius***. Photo by Tom Thekathyil, with permission.

Archegonial Reception

Cronberg *et al*. (2008) described the opening of the archegonium in ***Bryum argenteum*** (Figure 44) as sudden. The top of the archegonium ruptures and the upper cells fold outward, creating a small funnel leading to the neck canal (*e.g.* Figure 80-Figure 81). At the same time, the archegonium releases a fluid.

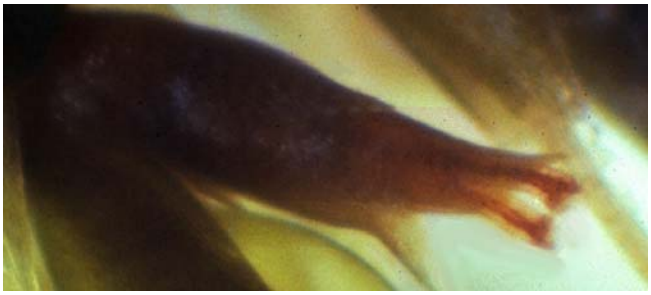

Figure 80. Archegonia of the moss ***Fontinalis dalecarlica***, showing the funnel-like tip. Photo by Janice Glime.

Figure 81. ***Rhodobryum roseum*** perichaetium showing archegonium with funnel tip (arrow). Photo by George J. Shepherd, through Creative Commons.

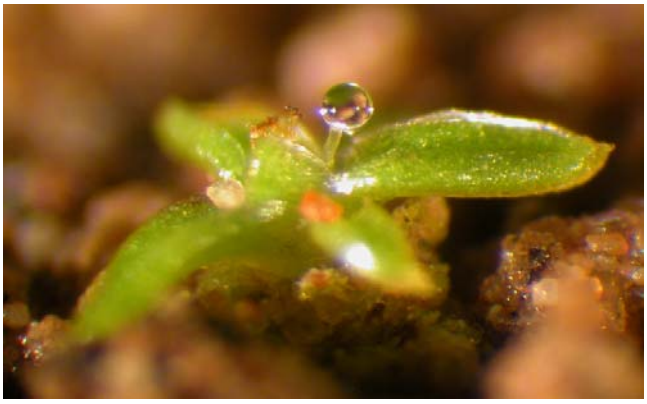

Figure 82. ***Aloina ambigua*** showing archegonial exudate. Photo courtesy of Llo Stark.

Sexual strategies are covered in Chapter 3-1 of this volume.

Embryo Development

When a sperm reaches and fertilizes an egg, the resulting **diploid** (having two sets of chromosomes; 2*n*) **zygote** begins dividing by **mitosis** to form an **embryo** that starts to stretch the archegonium (Figure 83). But the archegonium cannot stretch indefinitely, and as the embryo gets larger, the archegonium finally tears. Here, mosses and liverworts differ. In most mosses, part of the archegonium remains perched on top of the developing **embryo** (young sporophyte). This separated piece of archegonium is the **cap** you often see on top of the capsule and is now called a **calyptra** (Figure 103). So the calyptra is a 1*n* covering over the 2*n* capsule.

The emerging embryo grows into the sporophyte of the moss. The mature sporophyte has a **capsule** and **stalk** (**seta**), with a **foot** embedded into the gametophyte tissue (Figure 84). **Meiosis** occurs in the mature capsule, producing haploid (1*n*) spores, as in all plants. Note that this is a major difference from meiosis in animals, which results in gametes. These spores are dispersed from the capsule by wind (or in a few cases – *e.g.* Splachnaceae – by insects) and grow into new gametophytes.

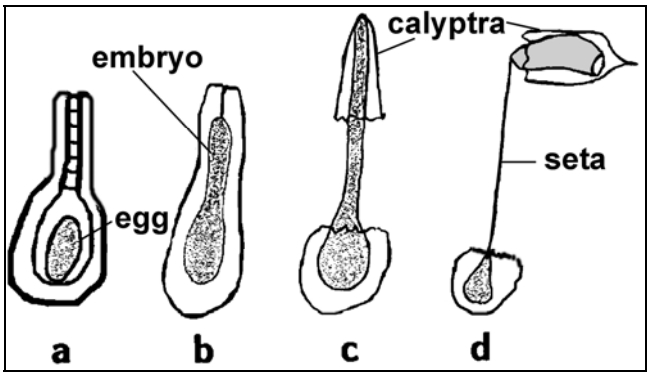

Figure 83. Development of calyptra of a moss. **a.** egg in archegonium, with neck canal cells not yet disintegrated. **b.** archegonium after fertilization and early development of embryo, showing elongation of archegonium as embryo grows. **c.** elongated seta with calyptra perched on top of it before capsule has developed. **d.** mature capsule with calyptra and fully elongated seta. **c & d** indicate remains of venter of archegonium at base of sporophyte. Drawings by Janice Glime.

Figure 84. ***Aloina rigida*** with stalk and capsule and with foot imbedded in gametophyte tissue. Photo by Michael Lüth, with permission.

The **calyptra** (Figure 85) that covers the capsule of mosses most likely plays multiple roles. We know that in many species, normal development ceases if the calyptra is removed (Paolillo 1968; French & Paolillo 1976a, b). One could assume that it provides protection from UV light and other environmental influences, as well as changing the internal environment, and that these influences are important in shaping the further development of the capsule, as will be discussed in another chapter.

Capsule Development

In mosses, once the calyptra (Figure 85) has been shed, the **operculum** (lid) of the capsule is exposed (Figure 86). As a result of this exposure, the environment is considerably changed for remaining development. Gas exchange could be easier, moisture relations can change, and the constraining effect of the size and shape of the capsule might change.

Figure 85. ***Polytrichum*** sp. with calyptra covering the capsule. Photo by George Shepherd, through Creative Commons.

Figure 86. ***Polytrichum*** sp. capsule with calyptra removed, showing operculum. Photo by George Shepherd, through Creative Commons.

The exposed operculum must come off before the spores can be dispersed. The **dehiscence** of the operculum is usually facilitated by drying of the capsule that causes it to shrink and compress the contents. This creates a distortion that forces the operculum to pop off, at least in some species. But a few are **cleistocarpous** (indehiscent; lacking a regular means of opening; Figure 87), thus lacking an operculum (Figure 89). Capsules in these taxa open by irregular breakage of the capsule. Llo Stark (pers. comm. 22 March 2023) describes this in ***Physcomitrella patens*** as highly fragile capsule walls that break up very quickly after the capsules are mature.

Figure 87. ***Pleurophascum grandiglobum*** with cleistocarpous capsules. Photo by Yordle Ziggs, through Creative Commons.

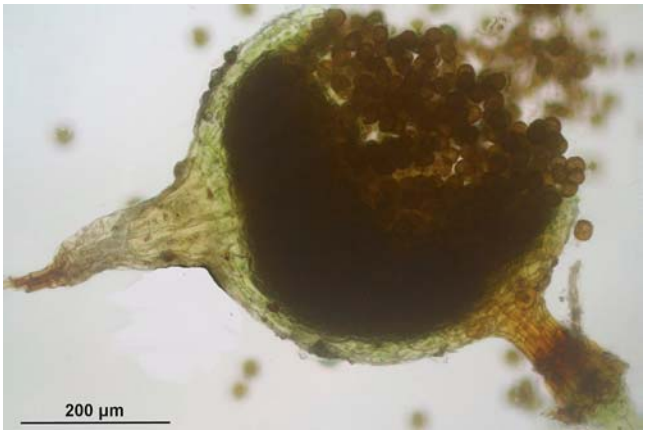

Figure 88. ***Physcomitrella patens*** cleistocarpous capsule opening. Photo by Hermann Schachner, through Creative Commons.

Just under the lid of most moss capsules you will find the **peristome teeth** (in mosses, fringe of teeth around opening of capsule, involved in spore dispersal; Figure 90-Figure 98). These are usually **hygroscopic** (responding to humidity changes) and may flex back and forth in response to moisture changes to aid in gradual dispersal. In most cases, these function best as the capsule is drying, but in some taxa moisture actually facilitates dispersal. Perhaps their best role is in preventing the spores from all exiting the capsule at the same time, as happens in the liverworts and ***Sphagnum*** and most likely also in the mosses with valvate capsules. They often form spaces between the teeth, creating a salt shaker appearance (Figure 96). The sporophyte capsule usually has a **columella** (Figure 93, Figure 97) that is columnar like those in Polytrichopsida, providing structure. Most mosses also have an **annulus** (Figure 91) just below the peristome. This annulus aids in dehiscence of the operculum.

Figure 89. ***Pleurophascum grandiglobum*** showing capsules with no operculum. Photo by Niels Klazenga, with permission.

Figure 90. Moss peristome. Photo by Laurie Knight, with permission.

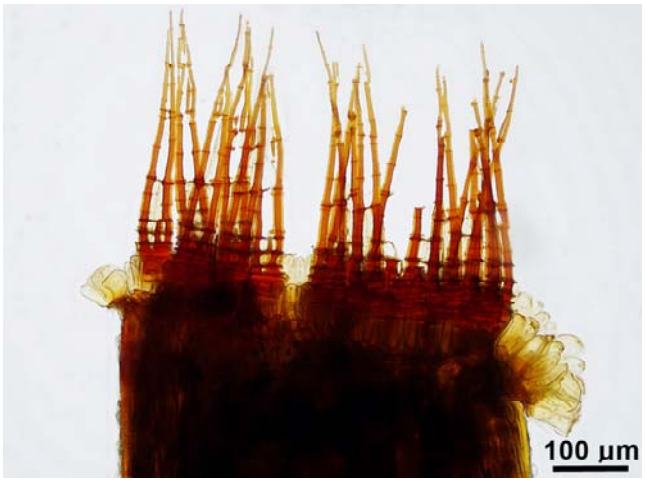

Figure 91. ***Ceratodon purpureus*** peristome with annulus peeling back at its base on each side. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 92. ***Schistidium rivularis*** sporophyte view showing operculum dehiscence. Photo by Betsy St. Pierre, with permission.

Figure 93. ***Schistidium rivularis*** sporophyte showing operculum dehiscence with columella still attached. This continued attachment is unusual. Photo by Betsy St. Pierre, with permission.

Figure 94. ***Schistidium crassipilum*** open capsules with teeth spreading. Photo by Jan-Peter Frahm, with permission.

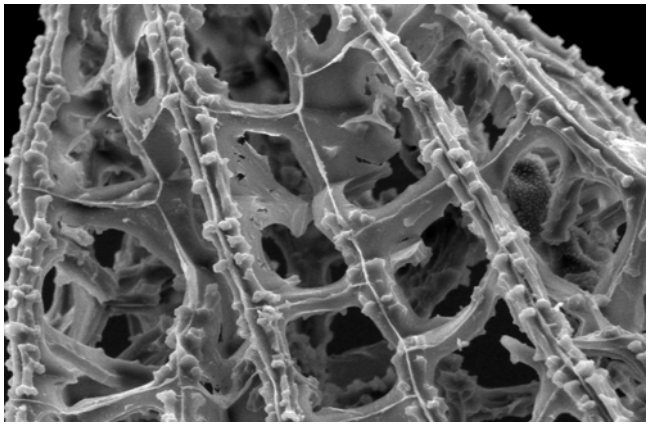

Figure 95. SEM of ***Fontinalis*** peristome illustrating the elaborate lattice structure. Note a few spores nestled within it. Photo by Misha Ignatov, with permission.

Figure 96. **Perfect peristome** showing inner (endostome) and outer (exostome) peristome with spores. Photo by George Shepherd, with permission.

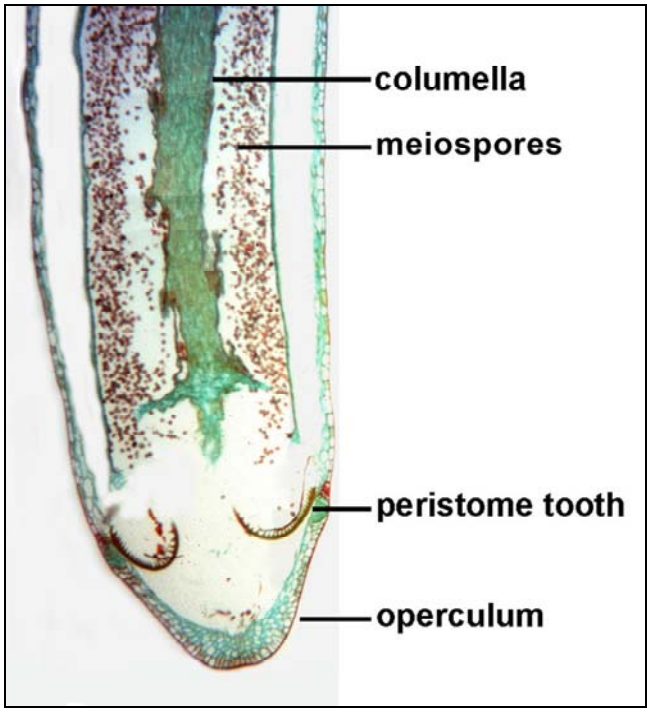

Figure 97. Section of ***Mnium*** capsule. This capsule actually hangs down, so teeth are on the bottom of the picture. Photo by Janice Glime.

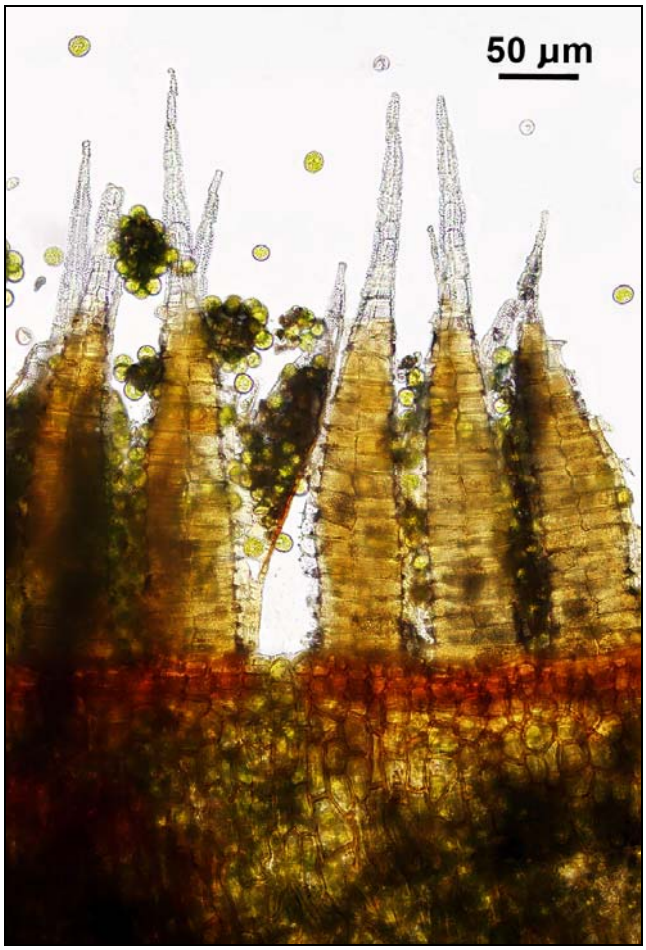

Figure 98. ***Rosulabryum laevifilum*** peristome and spores. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

A very recent study by Zanatta *et al*. (2018) has revealed that some mosses are **xerochastic** (and others are **hygrochastic (hydrochastic; hydrochastique**). That is, some peristome teeth flex and open as the surrounding moisture decreases (**xerochastic**) and others respond and open in response to increasing moisture (**hygrochastic**). In their study of 16 species, they found that all nine species with **perfect peristomes** [having both **endostome** (inner peristome) and **exostome** (outer peristome); Figure 96] exhibited xerochastic behavior, opening at around 90% RH upon drying, but initiating closing (exostome teeth bending inward toward endostome) around 50-65% RH as humidity increased. On the other hand, five species with specialized peristomes displayed hygrochastic behavior, opening as RH increased and closing as it decreased. Opening started at about 70% RH; closing started when humidity decreased below about 94%. But ***Pseudoamblystegium subtile*** possesses a specialized peristome while exhibiting xerochastic behavior. Behavior of the peristome in ***Orthothecium rufescens*** could not be classified as it was unclear whether teeth were clearly closing or opening. In three species, the humidity initiating position changes was dependent on age. These interesting observations need to be expanded to many more species from a wide range of habitats to determine if there is any relationship to habitat.

Unlike the valvate capsules of liverworts and some moss classes, the sporophytes of the Bryopsida are photosynthetic (Figure 99). The same pigments often occur in both generations: chlorophylls *a* and *b*, carotene, lutein, violaxanthin, and zeaxanthin (Freeland 1957). Even the ratio of chlorophyll *a* to *b* is approximately the same – about 2.5:1 (Rastorfer 1962). Nevertheless, the gametophyte contains a higher chlorophyll concentration than does the sporophyte and the ratio of photosynthesis to respiration is likewise higher in the gametophyte. Despite its photosynthetic abilities, the sporophyte still depends on the gametophyte for some of its carbohydrates (Krupa 1969).

Figure 99. ***Bryum gemmiferum*** capsules showing photosynthetic green immature capsules and darker ones with maturing spores. Photo by David Holyoak, with permission.

The stages of the life cycle are summarized in Figure 100 and Figure 101. Structures involved in the life cycle and in general morphology are illustrated in Figure 102-Figure 105.

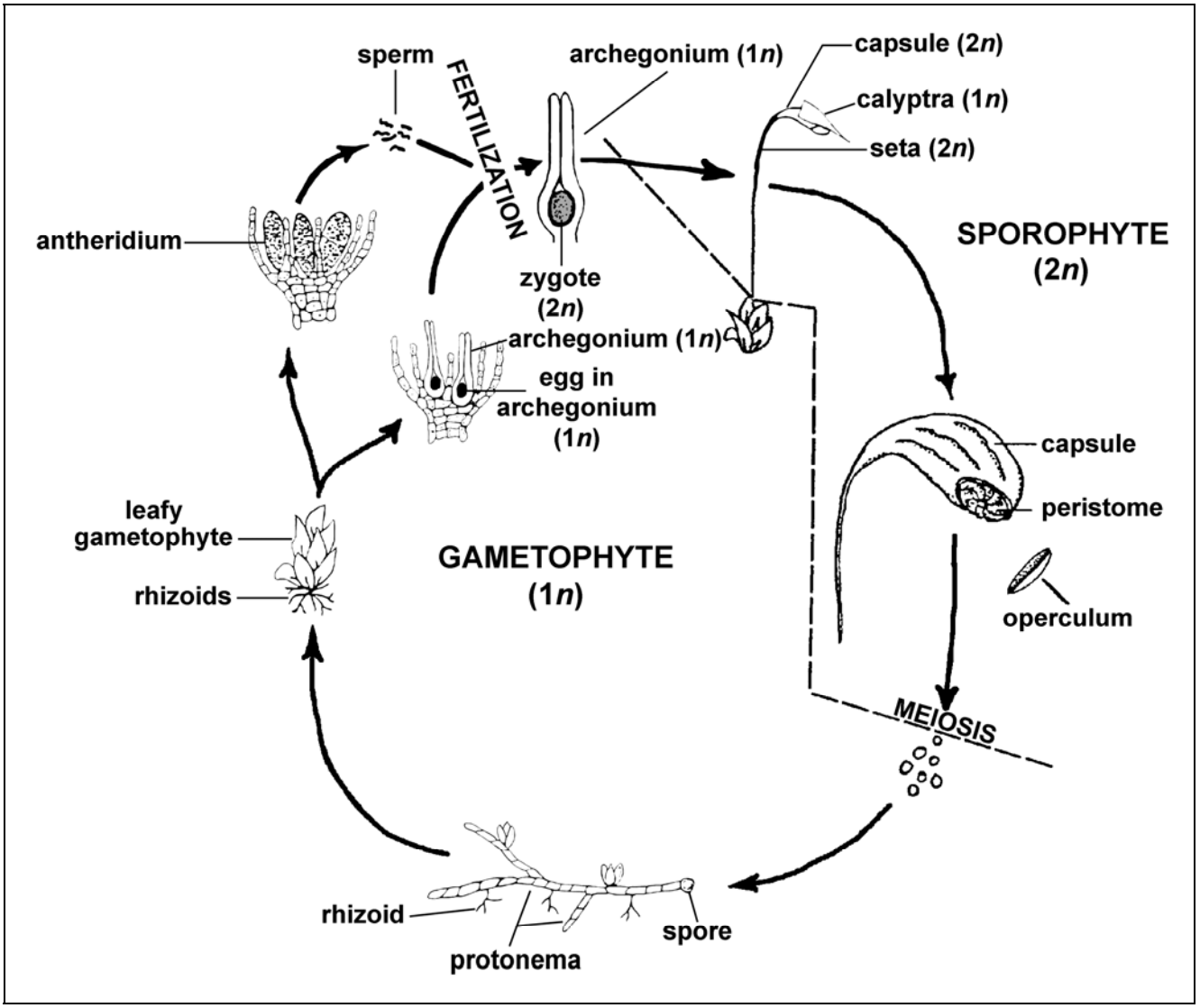

Figure 100. Life cycle of the moss ***Funaria hygrometrica***. Drawn by Shelly Meston, with permission.

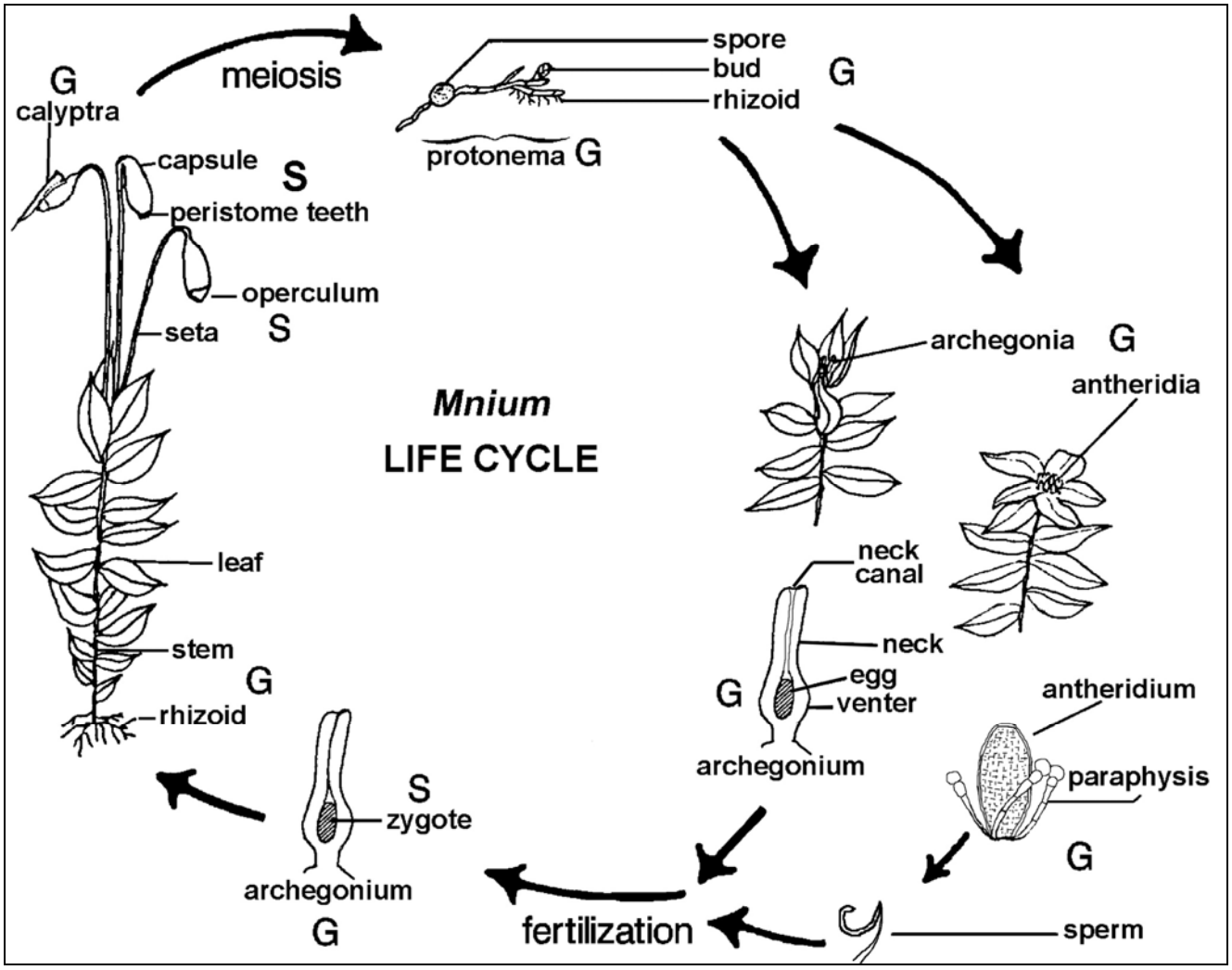

Figure 101. Life cycle of a moss such as ***Mnium*** (Bryopsida). **G** represents Gametophyte; **S** represents Sporophyte. Drawings by Allison Slavick, Noris Salazar Allen, and Janice Glime, with permission.

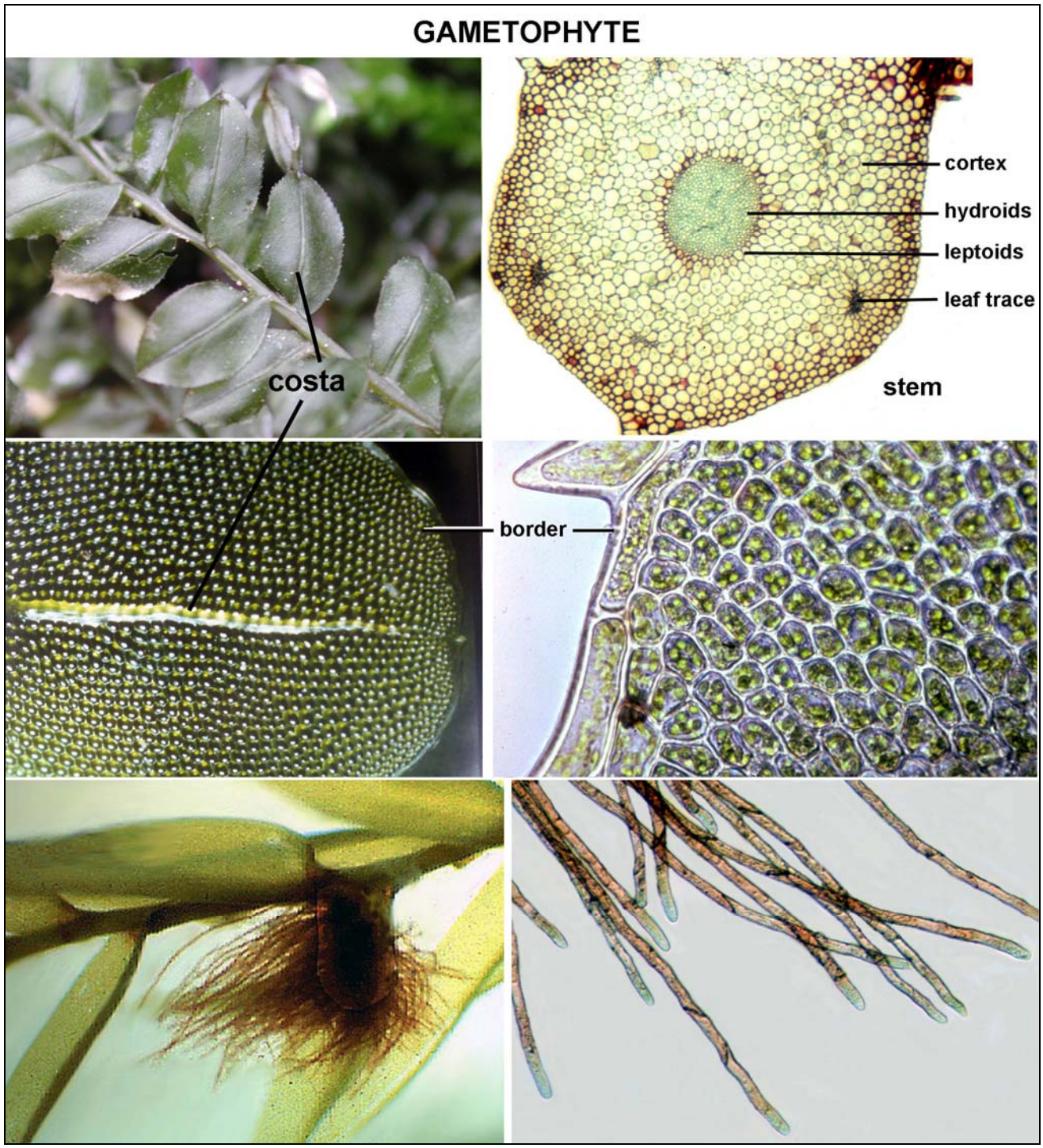

Figure 102. Vegetative characters (gametophyte) of Class Bryopsida. **Upper Left:** ***Plagiomnium medium*** stem and leaves. Photo by Michael Lüth, with permission. **Upper right:** ***Plagiomnium*** stem cross section showing central strand of hydroids. Note smaller darkened areas in stem cortex that are leaf traces. Photo by Janice Glime. **Middle Left:** Leaf of ***Rhizomnium*** illustrating a border, small, roundish cells, and a distinct costa. Tip of leaf lacking a costa, illustrating elongate cells and undifferentiated apical leaf cells. Photo by Zen Iwatsuki, with permission. **Middle Right:** Portion of ***Plagiomnium*** leaf showing border. Photo by Janice Glime. **Lower Left:** ***Fontinalis*** stem, leaves, and tuft of rhizoids. Photo by Janice Glime. **Lower Right:** Microscopic view of rhizoids showing single cell thickness and diagonal cross walls. Photo by Janice Glime.

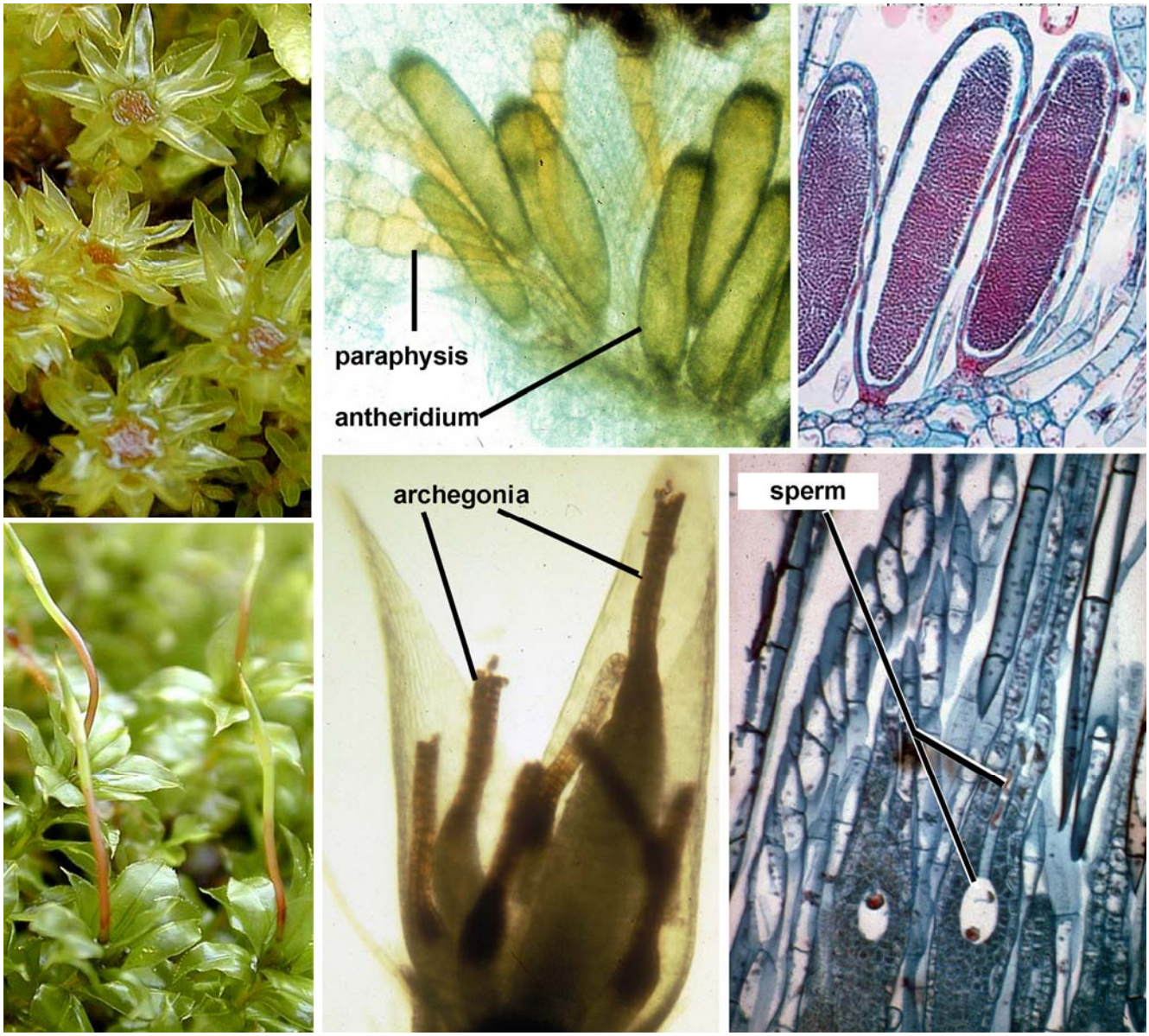

Figure 103. Sexual reproduction of mosses. **Upper row** shows male reproductive parts. Splash platforms (**left**) of ***Mnium hornum*** in which antheridia may be located, or they can be among ordinary leaves (**center**); among the antheridia are paraphyses (**center** and **right**) that help in retaining water and in forcing sperm out of the antheridia at maturity. **Lower row** shows female reproductive parts. Perichaetial leaves and young sporophytes of ***Plagiomnium cuspidatum*** (**left**), archegonia from leaf bases of ***Pleurozium schreberi*** (**center**), and a section of archegonia (**right**) with sperm in the neck canal. Plant photos by Michael Lüth, with permission; photomicrographs by Janice Glime.

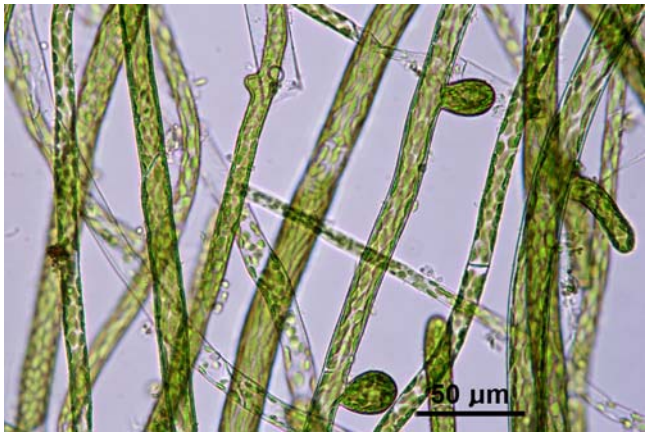

Figure 104. Moss protonemata. Photo by Jan Fott, with permission.

Figure 105. Moss protonema. Photo by Jan Fott, with permission.

Summary

The **Bryopsida** is the largest and most diverse class of **Bryophyta**. In **Bryopsida**, as in **Polytrichopsida**, an **operculum** usually covers **peristome** teeth that often aid dispersal. **Bryopsida** have **arthrodontous** peristome teeth, separating them from the **Polytrichopsida**, which have **nematodontous** teeth. All other classes of **Bryobiotina** lack peristomes.

The life cycle of **Bryopsida** involves a **protonema** that is usually threadlike and develops from the germinating spore, developing numerous **buds** and **gametophores**. Gametophores produce **archegonia** and/or **antheridia**. Sperm escape as a mass when the antheridium bursts. In some species, arthropods facilitate transfer of sperm from the antheridium to the archegonium. The **embryo** develops within the archegonium.

Sporophytes remain attached to the gametophyte and produce **spores** by **meiosis**. As in all Bryophyta, **Bryopsida** produce spores from the sporophyte only once. A **perfect peristome** has two rows of teeth and seems to respond to drying by opening the teeth. The **specialized peristomes** tested generally respond to drying by closing the teeth.

Vegetative reproduction is common among bryophytes. **Bryophyta** can reproduce by **fragments** as well as specialized asexual structures and thus add a new dimension to life cycle strategies.

Acknowledgments

I appreciate the comments and suggestions of Karla Werner, who offered a beginner's perspective. Noris Salazar Allen offered constructive criticisms on the taxonomic descriptions and helped with the proof reading and life cycle diagrams. Betsy St. Pierre has been taking pictures for me and contributed several for this chapter. Llo Stark kindly offered his images of archegonial exudate and sperm packet release; he also has provided a review and valuable comments on this chapter.

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Summary

The traditional bryophytes are classified into three phyla (Marchantiophyta, Bryophyta, Anthocerotophyta) that can be placed in the subkingdom Bryobiotina. **Anthocerotophyta** (hornworts) differ in having a sporophyte that is shaped like horn and continues to grow at the base as spores mature and are dispersed at the apex.

Anthocerotophyta have a **dominant gametophyte** generation. Gametophytes produce **archegonia** and/or **antheridia** and the **embryo** develops within the archegonium.

Sporophytes remain attached to the gametophyte and produce **spores** by **meiosis** over a prolonged period of time, with the youngest spores at the base. **Pseudoelaters** are produced along with the spores, but are formed by mitosis and remain 2*n*. **Capsules** split longitudinally and peel backward from the tip.

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CHAPTER 2-8
ANTHOCEROTOPHYTA

Figure 1. ***Notothylas orbicularis*** thallus with involucres. Photo by Michael Lüth, with permission.

Anthocerotophyta

These plants, once placed among the bryophytes in the Anthocerotae, now generally placed in the phylum **Anthocerotophyta** (hornworts, Figure 1), seem more distantly related, and genetic evidence may even present them as more like ferns as we understand them better (Hori *et al*. 1985; Sherman *et al*. 1991; Nickrent *et al*. 2000; Knoop 2004; Groth-Malonek 2005). Yet other chemical evidence places them close to the liverworts (Hanson *et al*. 1999); they lack isoprene emission, as do liverworts, whereas mosses and ferns possess it. However, such characters may prove to be retained or lost adaptively and contribute little to phylum level relationships.

The hornworts are divided into two classes (Stotler & Crandall-Stotler 2005), a concept supported by molecular data (Frey & Stech 2005). **Anthocerotopsida** is the largest and best known of these, with two orders and three families. The second class is **Leiosporocerotopsida**, a class with one order, one family, and one genus. The genus ***Leiosporoceros*** differs from members of the class **Anthocerotopsida** by having the Cyanobacterium ***Nostoc*** in longitudinal canals. In the other hornworts, the ***Nostoc*** colonies are scattered in discrete globose colonies (Villarreal A. & Renzaglia 2006).

As in other Bryobiotina, the gametophyte in the Anthocerotophyta is the dominant generation, but then, there are a few ferns in which the gametophyte might also be considered dominant. Hornworts differ from Marchantiophyta in having typically only **one chloroplast per cell** in the thallus, **lacking oil bodies**, and possessing a **pyrenoid** (a proteinaceous body serving as a nucleus for starch storage and common in green algae) (Figure 2).

Figure 2. Hornwort cells showing single chloroplast, doughnut-shaped pyrenoid in center, and absence of oil bodies. Photo by Chris Lobban, with permission.

Some **Anthocerotophyta** have interesting adaptations to help them get the most from their environmental resources. The **pyrenoid**, present in many taxa, has a concentration of Rubisco, and this permits it to concentrate CO_2 (Hanson *et al*. 2002). Furthermore, the thallus typically has colonies of ***Nostoc*** (Figure 3-Figure 5), a member of the Cyanobacteria, embedded within the tissues and providing a conversion of atmospheric nitrogen into a form the hornwort can use. This fixed nitrogen is transferred from the gametophyte thallus to the sporophyte. Furthermore, if the gametophyte happens to be grown in the dark, and the sporophyte is illuminated, it can transfer the photosynthate to the gametophyte (Bold *et al*. 1987). And that sporophyte can have twice the photosynthetic carbon fixation of the gametophyte (Thomas *et al*. 1978)!

Figure 3. Probably ***Megaceros*** with ***Nostoc*** colonies. Photo by Chris Lobban, with permission.

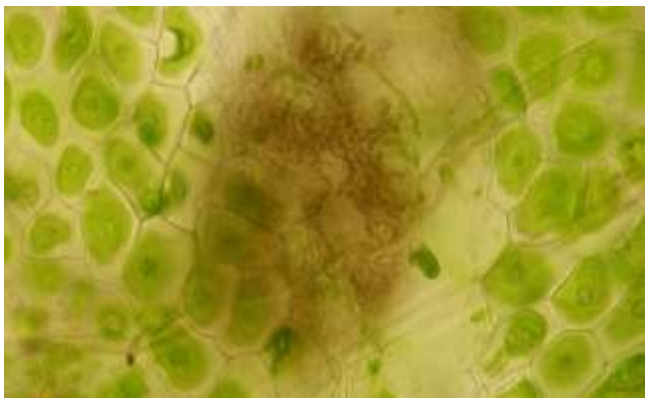

Figure 4. ***Nostoc*** (brown cells) in hornwort. Photo by Chris Lobban, with permission.

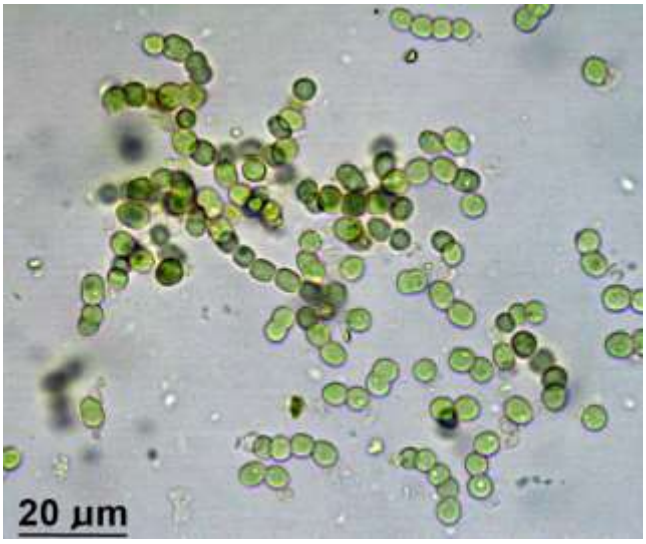

Figure 5. ***Nostoc*** from ***Anthoceros agrestis***. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

At least some members have associated fungi. Ligrone (1988) reported fungi in association with ***Phaeoceros laevis***. The fungus colonized the parenchyma cells except at the growing tips of the thallus and epidermal cells. The infected cells increased their cytoplasmic contents, but the chloroplast lost starch and the pyrenoids disappeared. The chloroplast became branched and these branches intermingled with the arbuscular fungal hyphae.

The sporophyte is like that of ***Sphagnum*** in **lacking a sporophyte stalk** (seta) on the capsule (Figure 6) and like the Bryophyta in having a **columella** (Figure 7-Figure 8) that is not in liverworts. The capsule also has **stomata** surrounded by two kidney-shaped **guard cells** (Figure 9), characters shared with Bryophyta. Instead of elaters, they have **pseudoelaters** (arising from division of a pseudoelater mother cell and outnumbering spores; Figure 10) of one, two, or four cells, usually with **no spiral thickenings** [except ***Megaceros*** and ***Dendroceros*** (Renzaglia 1978)] (Figure 11). The pseudoelaters probably provide nutrition, at least initially, but at maturity they twist, contributing to dehiscence and dispersal (Renzaglia 1978).

Figure 6. ***Phaeoceros*** showing gametophyte thalli at base and horn-like sporophytes. Photo by Janice Glime.

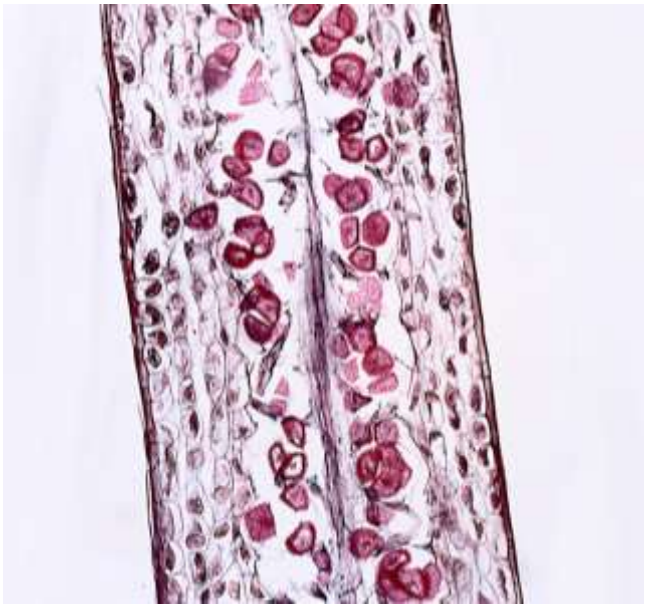

Figure 7. ***Anthoceros*** sporophyte longitudinal section showing spores and spore tetrads. Note central columella. Photo by George Shepherd, through Creative Commons.

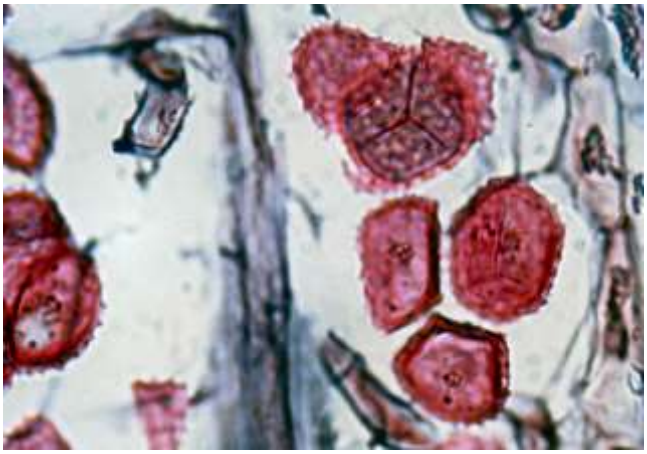

Figure 8. ***Anthoceros*** sporophyte longitudinal section showing spores and spore tetrads. Note central columella. Photo by George Shepherd, through Creative Commons.

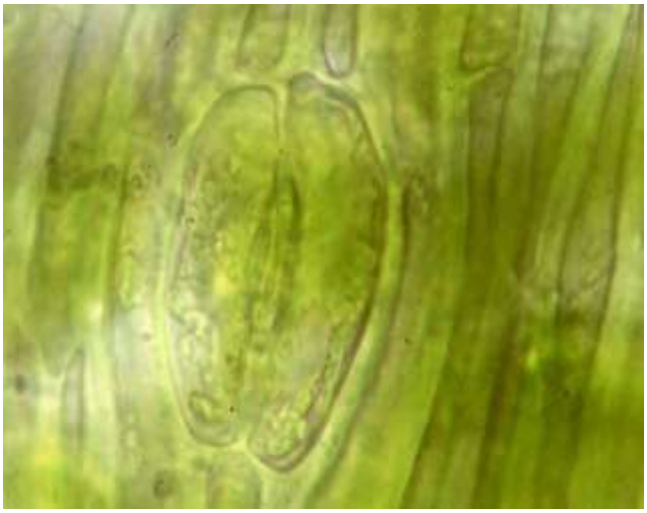

Figure 9. Stoma and guard cells on sporophyte of ***Anthoceros angustata***. Photo by Hironori Deguchi from <www.digital-museum.hiroshima-u.ac.jp>, with permission.

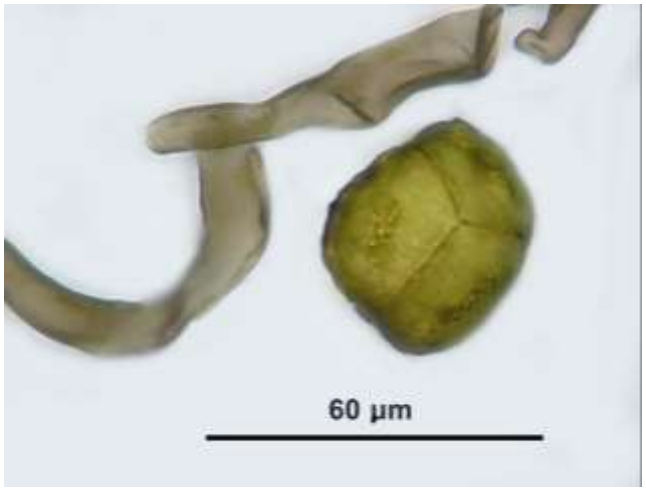

Figure 10. ***Phaeoceros*** spore and pseudoelater. Photo by David H. Wagner, with permission; scale modified by Janice Glime.

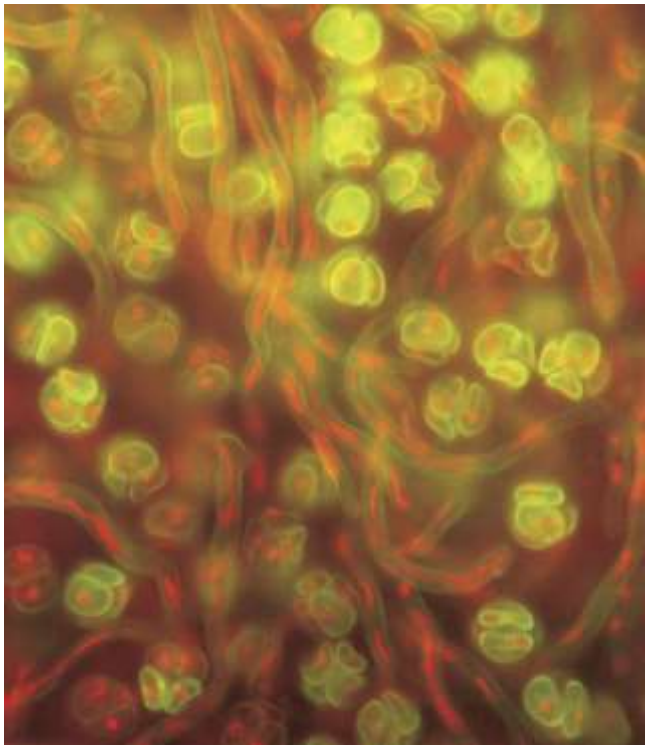

Figure 11. ***Leiosporoceros dussii*** spores and pseudoelaters using fluorescence microscopy. Note the absence of spiral thickenings in the elaters. Photo by Andrew Blackwell, and Juan Carlos Villarreal A., Southern Illinois University, with permission.

Meiosis is **continuous**, occurring at the base of the capsule, causing the tip of the sporophyte to have more mature spores than the base (Figure 12-Figure 14), a feature unique to the Anthocerotophyta. Dispersal results as the **capsule splits** into valves from the top down (Figure 25), and consistent with its development, this peeling back of the capsule occurs slowly over time, retaining the lower spores while dispersing the upper ones. The valves twist in response to moisture changes, perhaps aiding in dispersal. The **spores mature progressively** from top to bottom of the capsule (Figure 13) as the capsule splits and **continues**

to grow at its base, unlike any other Bryobiotina (Figure 26).

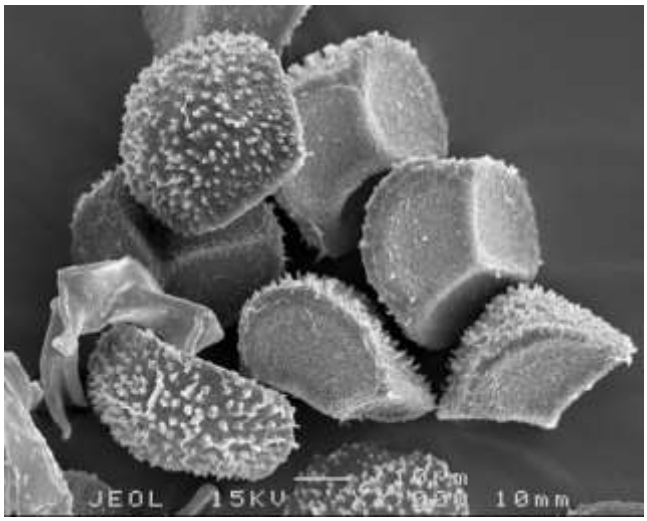

Figure 12. SEM of ***Phaeoceros carolinianus*** meiospores. Photo by Christine Cargill at Trin Wiki.

Figure 13. Hornwort sporophyte foot in gametophyte tissue. Note that basal portion of the sporophyte contains sporogenous tissue; those above have undergone meiosis. Oval area at the base of the sporophyte is the foot, imbedded in the gametophyte. Photo by Michael W. Clayton. Permission pending

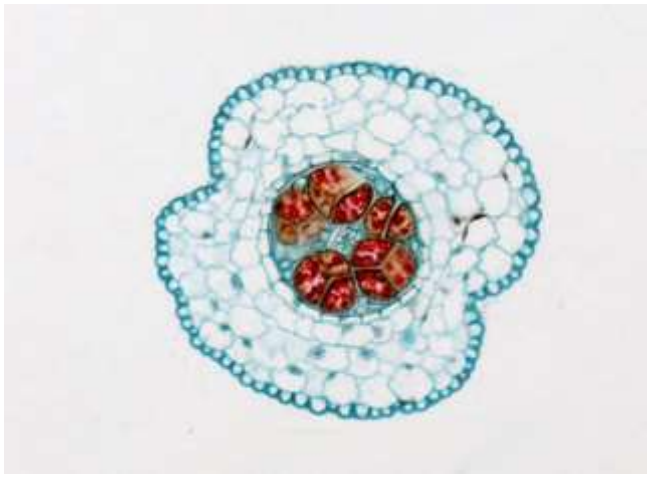

Figure 14. ***Anthoceros*** sporophyte cross section, showing meiospores and columella. Photo from Botany 321 website at University of British Columbia, with permission.

Dendroceros is a tropical genus that is unusual among the Anthocerotophyta by growing on tree bark and leaves. Furthermore, it produces multicellular green spores (Figure 15) (Schuette & Renzaglia 2010). Schuette and Renzaglia suggest that the precocious development of the spore, resulting in **endospory**, permits it the time and resources necessary to survive the desiccating habitat where it lives.

Figure 15. ***Dendroceros tubercularis*** endospores. Photo by Karen Renzaglia, with permission.

Spores in **Anthocerotophyta** germinate to form a short **protonema** that does not remain threadlike, but gets areas that are more three-dimensional, resembling a tuber (Figure 16).

Figure 16. ***Anthoceros dichotomus*** protonema. Photo from Plant Actions through Eugenia Ron Alvarez, with permission.

The mature gametophyte thallus resembles that of a club moss (Lycopodiophyta) in that the **antheridia** may occur in groups within a chamber (Figure 17-Figure 23). The archegonia are likewise embedded within the thallus, again like those of the club mosses. The structure of the archegonium is illustrated in Figure 24.

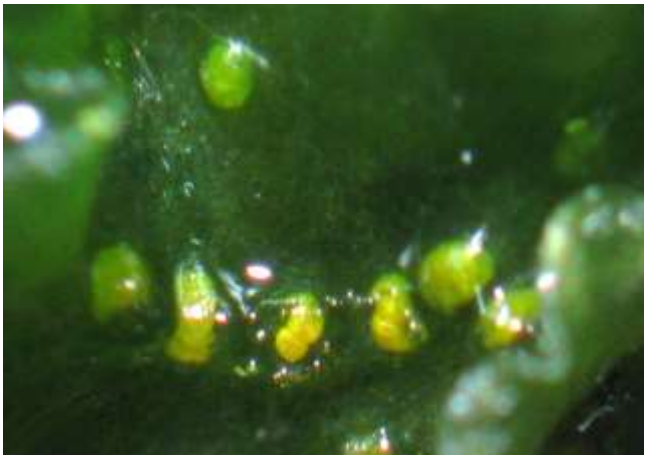

Figure 17. Hornwort **antheridia**, illustrating the clustering. Photo by Tom Thekathyil, with permission.

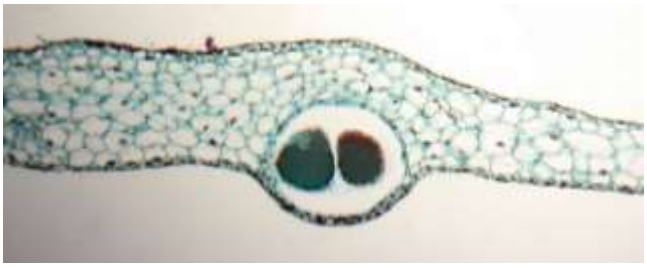

Figure 18. **Antheridia** in thallus of hornwort. Photo from Botany 321 website at University of British Columbia, with permission.

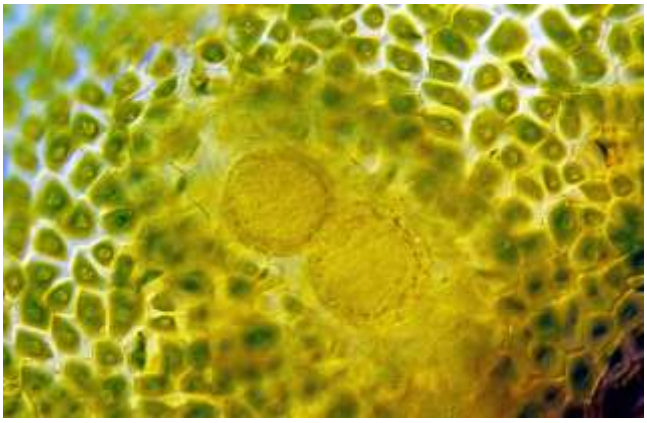

Figure 19. ***Phaeoceros*** gametophyte with **antheridia**. Photo by George Shepherd, through Creative Commons.

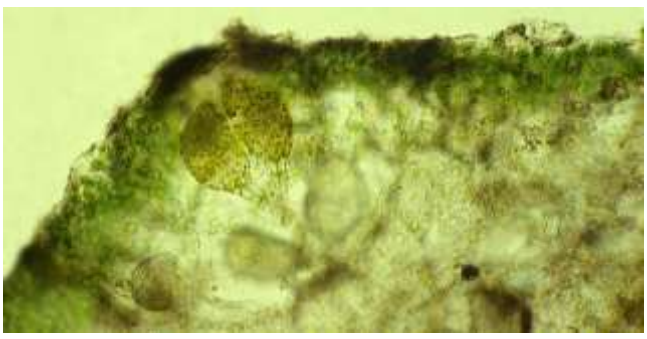

Figure 20. ***Anthoceros punctatus*** **antheridia**. Photo from Plant Actions website through Eugenia Ron Alvarez, with permission.

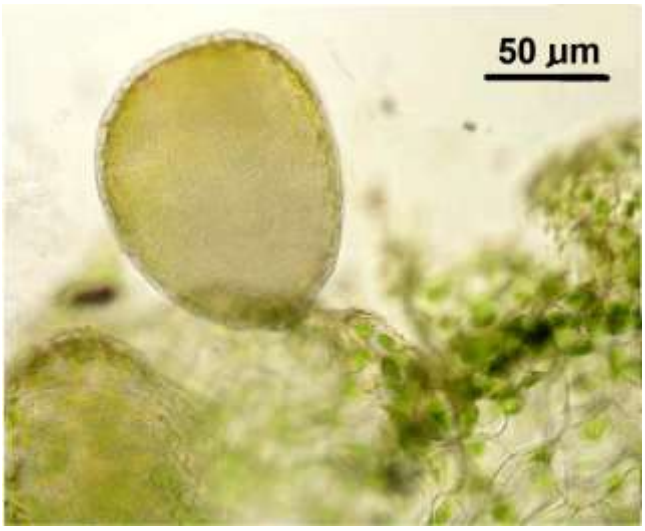

Figure 21. **Antheridium** of a hornwort. Photo by Hatice Ozenoglu Kiremit, with permission.

Figure 22. **Antheridia** of a hornwort dispersing its sperm. Photo by Hatice Ozenoglu Kiremit, with permission.

Figure 23. Antheridium of hornwort (probably ***Phaeoceros carolinianus***) expelling sperm. Tom Thekathyil (pers. comm. 17 September 2009) reported that sperm were still alive several hours later. Photo by Tom Thekathyil, with permission.

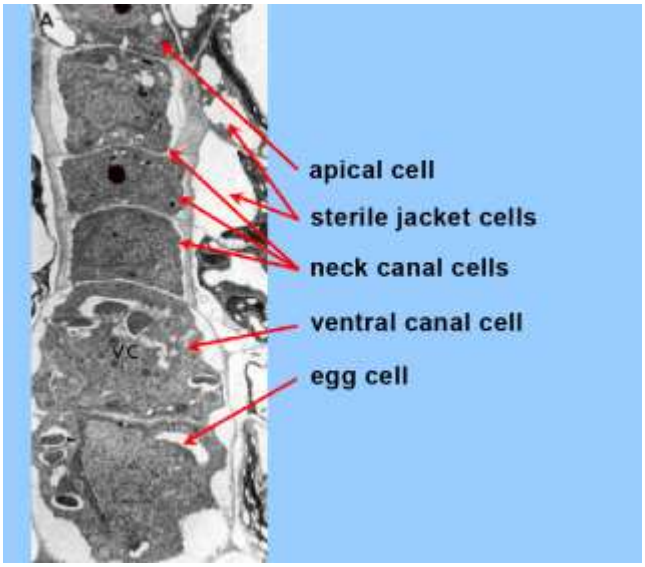

Figure 24. Hornwort archegonium. Photo from Science Land Plant website at Southern Illinois University, with permission.

Figure 25. ***Phaeoceros oreganus*** sporophytes showing the splitting tips of mature capsules. Photo by Li Zhang modified in Photoshop.

Figure 26. Anthocerotophyta – hornworts. **Upper left:** ***Anthoceros bulbicosus*** thallus and undehisced sporophyte. **Upper right:** cleared section of gametophyte thallus, collar, and hornlike sporophyte. **Lower left:** Cross section of ***Anthoceros*** thallus. Although the sporophyte is complex, the gametophyte is quite simple, perhaps indicating reduction. Note the lack of specialized tissues and absence of air chambers. **Lower right:** Older sporophyte of ***Phaeoceros carolinianus*** showing yellow color near tips of sporophyte due to mature spores. Upper left and lower right photos by Michael Lüth; upper right and lower left photos by Janice Glime.

Table 1. Comparison of the phyla of Bryobiotina. Amplified from Crandall-Stotler (1996) and Gradstein *et al.* (2001).

Character	Marchantiophyta	Bryophyta	Anthocerotophyta
Protonema	Mostly globose or thalloid, forming one bud; no gemmae	Filamentous, forming many buds; may produce gemmae	Globose, forming one bud; no gemmae
Gametophyte form	Leafy shoot or thallus; thallus simple or with air chambers; dorsi-ventral	Leafy shoot	Simple thallus; dorsi-ventral
Branches	Developing from leaf initial cells or inner stem cells, rarely stem epidermis	Developing from stem epidermis	
Leaf origin	2 initial cells (1 in Calobryales & Metzgeriales)	1 initial cell	
Leaf arrangement	Leaves in two or three rows, ventral row usually of different size	Leaves usually in spirals	Not applicable
Leaf form	Leaves unistratose, divided into 2+ lobes, no costa	Leaves unistratose in most, undivided, costa present in some	Thallose
Leaf/thallus cells	Usually isodiametric, have trigones; numerous chloroplasts	Often elongate, rarely possess trigones; numerous chloroplasts	No trigones; 1-4 large chloroplasts
Special organelles	Complex oil bodies often present	Simple, small oil bodies or none	Single plastids with pyrenoids
Gemmae	Common on leaves	Common on leaves, stems, rhizoids, or protonemata	Absent
Water conducting cells	Present only in a few simple thalloid forms	Present in both gametophytes and sporophytes of many	Absent
Rhizoids	Hyaline, one-celled	Brown, multicellular	Hyaline, one-celled
Gametangial position	Apical clusters (leafy forms) or on upper surface of thallus	Apical clusters	Sunken in thallus, scattered
Paraphyses	Usually lacking; often have mucilage filaments	Usually associated with antheridia & archegonia	Lacking
Growth of sporophyte	Apical	Apical	Grows continuously from basal meristem
Stomata	Absent in both generations, but pores present on some gametophyte thalli	Present on sporophyte capsule	Present in both sporophyte and gametophyte
Seta	Hyaline, elongating just prior to spore release, rigid when turgid, deliquescent	Photosynthetic, emergent from gametophyte early in development in Bryopsida & Polytrichopsida, rigid due to cell structure, persistent; not elongating in Sphagnopsida – pseudopodium present	Absent
Calyptra	Ruptures & remains at base of seta, lacks influence on capsule shape	Ruptures & persists at apex of seta & capsule, influences capsule shape	Lacking
Capsule	Undifferentiated, spherical or elongate; jacket uni- or multistratose; often with transverse or nodular thickenings	Complex with operculum, theca and neck; jacket multistratose; lack transverse or nodular thickenings	Undifferentiated, horn-shaped; jacket multistratose
Sterile cells in capsule	Spirally thickened elaters	Columella	Columella and pseudoelaters
Capsule dehiscence	Into 4 valves; spores shed simultaneously	At operculum & peristome teeth in Bryopsida & Polytrichopsida, spores shed over extended period; valvate in Takakiopsida, Andreaeopsida, & Andreaeobryopsida; lacking peristome in Sphagnopsida	Into 2 valves; spores mature & shed over extended period
Chemistry	Monoterpenes, sesquiterpenes, & diterpenes; lunularic acid	Triterpenes; ABA	Terpenoids(?)

CHAPTER 3-1
SEXUALITY: SEXUAL STRATEGIES

JANICE M. GLIME AND IRENE BISANG

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CHAPTER 3-1
SEXUALITY: SEXUAL STRATEGIES

Figure 1. Depiction of the ***Marchantia*** sexual life cycle in a chalk drawing by Gerald W. Prescott. Photo by Janice Glime.

Expression of Sex

Understanding sexuality is fundamental to understanding evolution, and by extension, to understanding the ecology of species. The topic of sexual expression has led to interesting discussions for many centuries and still perplexes us. On Bryonet, 14 February 2016, Ken Kellman asked several pertinent questions that remain with incomplete answers. His questions included the role of auxins or other hormones in the **perigonium** (leaves surrounding male reproductive structures) and **perichaetia** (leaves surrounding female reproductive structures) formation. How does **polyploidy** (condition of multiple sets of genes) relate to separate sexes? How many totally asexual species are there? (In California Kellman is aware that only ***Dacryophyllum falcifolium*** is never known to form gametangia). And some species are sexual in Europe, but not in North America, *e.g.* ***Hennediella stanfordensis*** (Figure 2), or male in Europe and female in North America, *e.g.* ***Syntrichia pagorum*** (Figure 3).

Figure 2. ***Hennediella stanfordensis***, a species that is sexual in Europe but not in North America. Photo by Martin Hutten, with permission.

Figure 3. ***Syntrichia pagorum***, a species that is male only in Europe, female only in North America, and both sexes occur in Australia. Photo by Michael Lüth, with permission.

But it turns out that Ken Kellman's example from California is only a drop in the bucket – many species in Europe are not known to reproduce sexually, including ***Bryoerythrophyllum caledonicum***, ***B. ferruginascens*** (Figure 4), ***Bryum dixonii***, ***Campylopus gracilis*** (Figure 5), ***Didymodon maximus*** (Figure 6), ***Ditrichum plumbicola*** (Figure 7), ***Leptodontium gemmascens*** (Figure 8), ***Pohlia scotica***, ***Thamnobryum cataractarum*** (possibly a form of ***T. alopecurum***), and ***Tortella limosella*** (Christopher Preston, Bryonet 15 February 2016). To these, Misha Ignatov (Bryonet 15 February 2016) added ***Limnohypnum muzushimae***, a rare pleurocarpous species in Kamchatka, Kurils, and Japan. Johannes Enroth, Bryonet 16 February 2016) added ***Caduciella mariei***, a species that occurs in eastern Africa, SE Asia, Queensland, and New Britain; it seems to reproduce only by caducous branch leaves. Liverworts include ***Mastigophora woodsii*** (Figure 9), ***Plagiochila norvegica***, ***Riccia rhenana*** (Figure 10), ***Scapania nimbosa*** (Figure 11), ***Herbertus borealis*** (Figure 12), ***H. norenus***, ***Lophozia wenzelii*** (Figure 13-Figure 14), ***Protolophozia herzogiana***, ***Anastrophyllum alpinum*** (Figure 15), and ***Marsupella arctica*** (Jeff Duckett, Bryonet 15 February 2016). But as Nick Hodgetts pointed out (Bryonet 16 February 2016), some may reproduce by sexual union only rarely and "bryologists are unfortunately likely to miss the event!"

Figure 4. ***Bryoerythrophyllum ferruginascens***, a species not known to reproduce sexually. Photo by David T. Holyoak, with permission.

Figure 5. ***Campylopus gracilis*** showing caducous tips by which it reproduces. Sexual plants are unknown. Photo by Michael Lüth, with permission.

Figure 6. ***Didymodon maximus***, a species for which sexual structures are unknown. Photo by Rory Hodd, with permission.

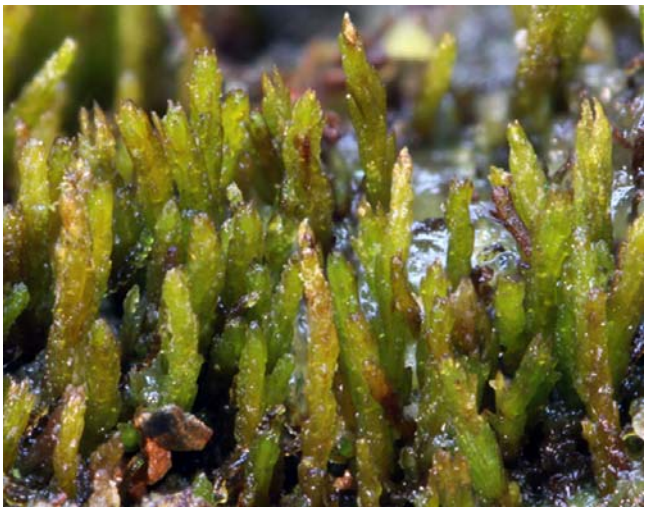

Figure 7. ***Ditrichum plumbicola***, a species for which sexual plants are unknown. Photo by Des Callaghan, with permission.

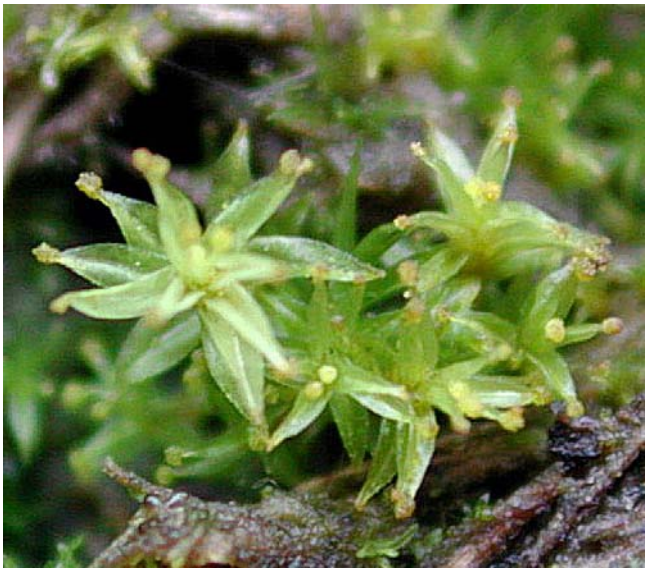

Figure 8. ***Leptodontium gemmascens*** with gemmae, a species with no known sexual plants. Photo by Michael Lüth, with permission.

Figure 9. ***Mastigophora woodsii***, a species for which sexual structures are unknown. Photo by Des Callaghan, with permission.

Figure 10. ***Riccia rhenana***, a liverwort for which there are no known sexual plants. Photo by Štěpán Koval, with permission.

Figure 11. ***Scapania nimbosa***, a species that is unknown in a sexual state. Photo by Michael Lüth, with permission.

Figure 12. ***Herbertus borealis***, a species with no known sexual plants. Photo by Jan-Peter Frahm, with permission.

Figure 13. ***Lophozia wenzelii***, a species with no known sexual plants. Photo by Michael Lüth, with permission.

Figure 14. ***Lophozia wenzelii*** with water trapped in leaves. No sexual plants are known in this species. Photo by Des Callaghan, with permission.

Figure 15. ***Anastrophyllum alpinum***, a species in which sex organs are unknown. Photo by Michael Lüth, with permission.

Unisexual and Bisexual Taxa

Jesson and Garnock-Jones (2012) attempted to provide a single classification of functional sex that could be used for all land plants. They divided the strategies into three categories: sporophyte (and gametophyte) **dimorphic** (having two forms); sporophyte-**cosexual** and gametophyte-dimorphic; gametophyte (and sporophyte) cosexual (having both sexes). Bryophytes exhibit only the latter two of these, always having sporophytes that are cosexual and never dimorphic. The gametophyte is always dimorphic in seed plants. [Note that in seed plants, the female gametophyte is embedded in the sporophyte tissue and the male gametophyte is a pollen grain; hence gametophyte sexes are always on separate gametophyte individuals.] Despite this simplistic approach, Jesson and Garnock-Jones consider that there are many variations within these three categories and that closer examination should reveal that bryophytes have as many variations in strategy as do more complex seed plants.

In bryophytes, it is the gametophyte (1*n*, **haploid**) plant that exhibits the **bisexual** (**monoicous**) trait. To the seed-plant botanist, the terms monoecious and dioecious are familiar, referring to having male and female organs on one sporophytic individual or on separate individuals, respectively, but the terms are legitimately restricted to sporophytes (Magill 1990). The counterpart to these terms for bryophytes, applied to the gametophyte, are **monoicous** and **dioicous**. Nevertheless, the sporophyte terms are often applied, as are the terms leaf and stem, but the oicy terms emphasize important differences in bryophyte sexuality (Zander 1984; Allen & Magill 1987; Magill 1990). Their root words are the same, derived from the Greek móνος (mónos), single, or δι- (di-), twice, double, and οἶκος (oîkos) or οἰκία (oikía), house. In other words, one house for sperm and egg on one plant (**monoicous**) or two houses for sperm and egg on different plants (**dioicous**).

Bryophytes have an unusually high number of **dioicous** taxa (male and female gametangia on separate individuals) among green land plants. Ramsay and Berrie (1982) reported that about 42% of bryophyte genera are exclusively dioicous, 49% of the genera include both dioicous and monoicous species, and only 9% are exclusively monoicous. Hedenäs and Bisang estimated roughly 60% of all bryophyte species are dioicous. Villarreal and Renner (2013a) estimated 57% in mosses and somewhat higher in liverworts (68%), although McDaniel and Perroud (2012) consider them to be about equal. This may differ somewhat by geographic distribution, but more careful analysis is needed. By contrast, in seed plants only 4-6% of the species are dioecious (Renner & Ricklefs 1995; de Jong & Klinkhamer 2005) and the sex ratio is more likely to be male-biased (Sutherland 1986; Delph 1999; Barrett *et al*. 2010).

Cross fertilization in monoicous **Bryophyta** is insured in many species by having differences in maturity times of male and female gametangia. Other furtherance of outcrossing is accomplished by the placement of gametangia on the plants. Bryophytes exhibit all sorts of arrangements of sexual organs on their **monoicous** species (having male and female gametangia on same individual), providing them with various strategies for outbreeding. These include having male and female gametangia on separate stems or branches and having male gametangia below female gametangia on the same branch or stem. When male and female organs are on separate individuals (Figure 1), outbreeding is ensured whenever sexual reproduction occurs; opportunities for fertilization decrease and opportunities for genetic variation increase.

One of the major problems for dioicous species is that one sex may arrive in a new location without the other, as seems to be the case of ***Syntrichia pagorum*** (Figure 3) in North America (female only) and Europe (male only). ***Didymodon nevadensis*** (Figure 16) is endemic in North America, occurring on the gypsiferous ridges of Nevada and only female plants are known (Zander *et al*. 1995). Llo Stark (pers. comm. 28 March 2023) considers that males have become extinct here. Nevertheless, with a variety of vegetative reproductive means, the species can persist.

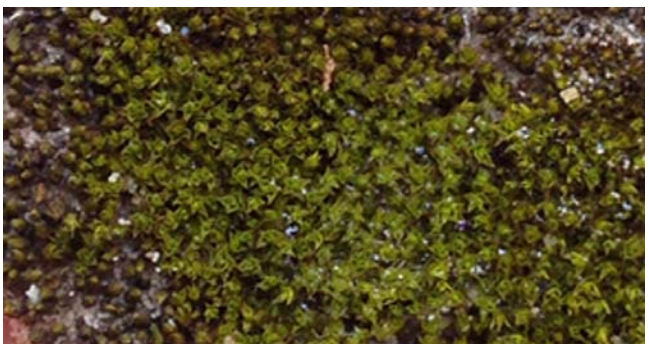

Figure 16. ***Didymodon nevadensis***. Photo by Theresa Clark, with permission.

Among the bryophytes, it is well known that many taxa with separate sexes never produce capsules [*e.g.* ***Sphagnum*** (Cronberg 1991)], presumably due to absence of the opposite sex or to inability of the sperm to reach the female plant and its reproductive structures successfully. For example, in a population of ***Cyathophorum bulbosum*** (Figure 17) in New Zealand, where male plants were located nearly a meter above the females, sporophytes existed in several developmental states, but on a nearby bank the entirely female population was completely barren (Burr 1939). In studies by Grebe (1917) on 207 German mosses and Arnell (1875) on 177 Scandinavian mosses, 200 of the 220 taxa that seldom produced capsules were dioicous. So one must ask what is the genetic mechanism that underlies the sexual differences in these unisexual taxa (taxa having only one sex on an individual; **dioicous**) and just what permits these unisexual taxa to persist?

Sex Chromosomes

Bryologists are the proud discoverers of **X** and **Y** sex chromosomes (Figure 18) in plants (Anderson 2000), first discovered in the liverwort genus ***Sphaerocarpos*** (Figure 19) (Allen 1917, 1919, 1930). And it is fitting that one of the first sex markers in bryophytes was likewise found in ***Sphaerocarpos*** (McLetchie & Collins 2001), although this was predated by identifying the tiny X and Y chromosomes in the female and male liverwort ***Marchantia polymorpha*** (Figure 20-Figure 21) (Okada *et al.* 2000; Fujisawa *et al.* 2001). These researchers have determined that the Y chromosome of the dioicous ***Marchantia polymorpha*** has unique sequences that are not present on the X chromosome or on any autosomes. Note that these individual haploid plants each have only one sex chromosome. To emphasize differences between **haploid** and **diploid** sex determination, the haploid single sex chromosomes have recently been distinguished as **U** (female) and **V** (male) chromosomes (Bachtrog *et al.* 2011; Olsson *et al.* 2013).

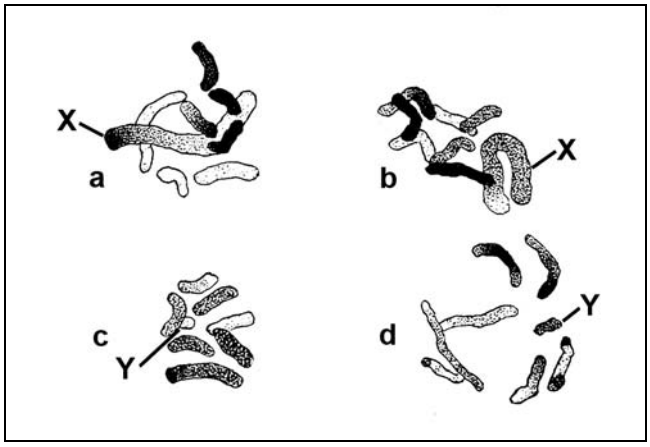

Figure 18. Chromosomes of ***Sphaerocarpos donnellii***. **a** & **b**: Chromosomes from female gametophyte. **c** & **d**: Chromosomes from male gametophyte. From Allen 1919.

Figure 19. ***Sphaerocarpos michelii***, member of the genus where X and Y sex chromosomes were first discovered. Photo by Jan-Peter Frahm, with permission.

Figure 17. ***Cyathophorum bulbosum***, a species that can readily be fertilized when males are above females, but not when females are isolated on a nearby substrate. Photo by Niels Klazenga, with permission.

Figure 20. ***Marchantia polymorpha*** male with antheridiophore, first bryophyte species in which sex markers were found and unique sequences found on males that were not present on females. Photo by David T. Holyoak, with permission.

Figure 21. ***Marchantia polymorpha*** females with archegoniophores, the first bryophyte species in which sex markers were found. Photo by Janice Glime.

But the presence of sex chromosomes does not mean that all bryophytes have separate sexes, or even that all bryophytes have sex chromosomes, so we must ask what determines the sexual differentiation. Ramsay and Berrie (1982) discussed the mechanisms of sex determination in bryophytes, including physiological and genetic regulation of sexuality. They considered that genetic sex is determined at the spore stage, but Bachtrog *et al.* (2011) consider that it is determined at meiosis. Even within the same genus, some bryophytes may be **unisexual** (Figure 22-Figure 25), others **bisexual** (having both sexes on the same individual; monoicous) (Figure 26-Figure 30). Clearly we need more research to discover how some of these determinations are made.

Figure 22. Clonal colony of male ***Philonotis calcarea***. Note innovation branches below the male splash cups. Photo by Michael Lüth, with permission.

Figure 23. A dioicous species, ***Philonotis calcarea***, showing antheridial splash cups. Photo by David T. Holyoak, with permission.

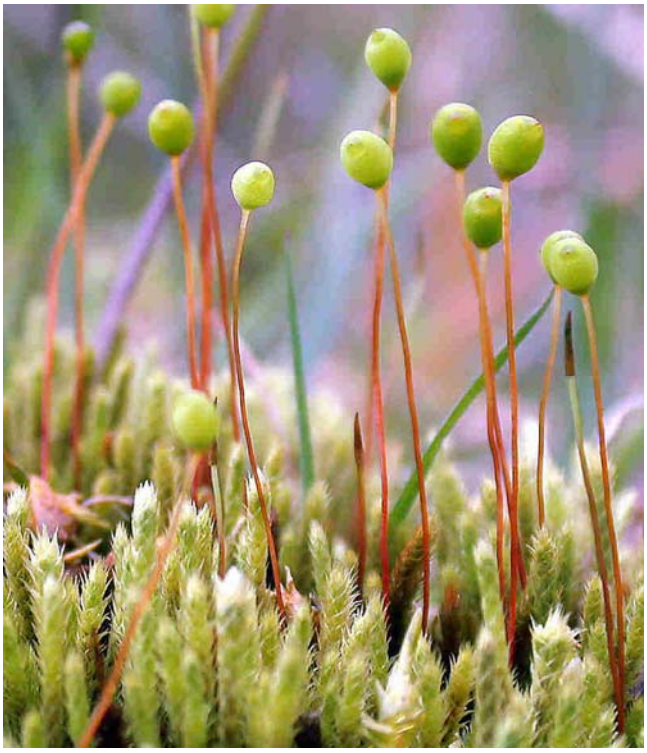

Figure 24. Female plants of the dioicous ***Philonotis calcarea***, distinguishable by their sporophytes. Photo by David T. Holyoak, with permission.

Figure 25. Colony of non-expressing or female plants of the dioicous ***Philonotis calcarea***. Archegonia are hidden among **perichaetial leaves** at the tip of the plant and are often difficult to distinguish without destroying the tip of the plant. Photo by David T. Holyoak, with permission.

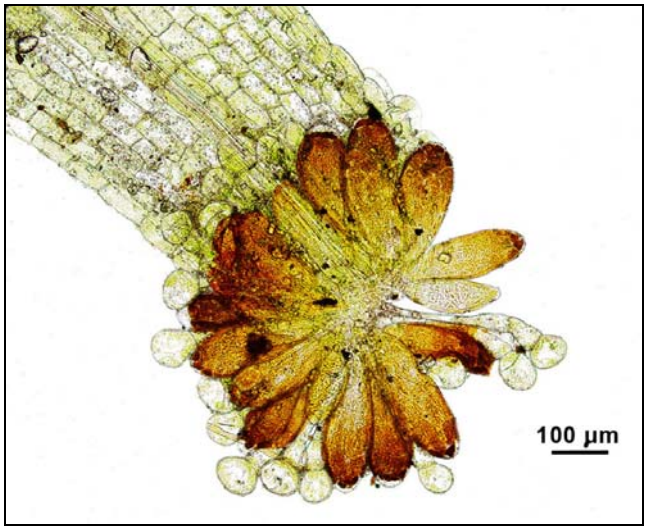

Figure 26. **Antheridia** of ***Funaria hygrometrica***. This is a special case of monoicous termed **autoicous**. Both male and female gametangia are on the same plant, but in separate places. Here the antheridia are at the base of a leaf. The white-knobbed structures with them are **paraphyses**. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Renner *et al*. (2017) reported a different combination of sex chromosomes. In ***Frullania dilatata*** (Figure 28), there are two U chromosomes and one V chromosome. In ***Plagiochila asplenioides*** (Figure 29), there are one U chromosome and two V chromosomes. They discuss the many things we don't understand in bryophyte sexual genetics. There is a lack of high-throughput sequencing, quantification, or *in situ* study of repetitive DNA, organellar DNA, or transposable elements. The causes of size differences in U and V chromosomes is unknown. Even though heterochromatin was first discovered in bryophytes, its role in sex regulation of these organisms remains unknown. The only sequencing of sex chromosomes is that of the V chromosome in ***Marchantia polymorpha*** (Figure 20-Figure 21), a species with 8 autosomes and 1 sex chromosome.

Figure 27. ***Frullania dilatata*** on tree trunk, a species with two U chromosomes and one V chromosome. Photo by Claire Halpin, with permission.

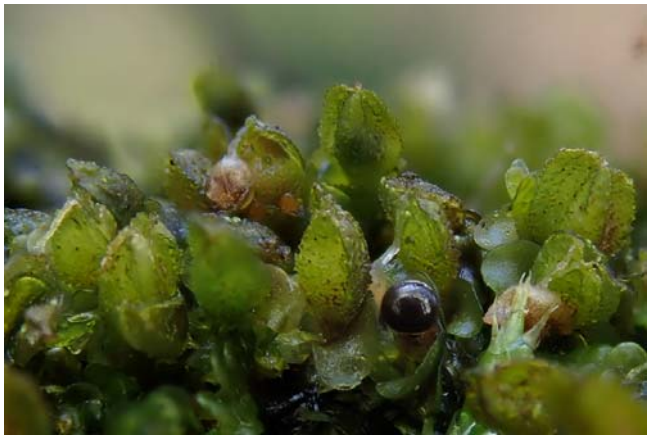

Figure 28. ***Frullania dilatata*** (**lower** with capsules), a species with two U chromosomes and one V chromosome. Photos by Claire Halpin, with permission.

Figure 29. ***Plagiochila asplenioides***, a species with one U chromosome and two V chromosomes. Photos by Claire Halpin, with permission.

An Unusual Y (=V) Chromosome

An active "Y"-chromosome-specific gene has been unknown in plants, although mammals such as humans do have specific genes on the Y chromosomes (Okada *et al.* 2001). But Okada *et al*. found that the bryophytes, or at least ***Marchantia polymorpha*** (Figure 20-Figure 21), have at least one such gene. This gene is unique and is expressed specifically in the male sex organs.

Since that earlier discovery, Yamato *et al*. (2007) have identified 64 genes on the V (male) chromosome of ***Marchantia polymorpha*** (Figure 20-Figure 21). Of these, 14 occur only in the male genome and have been linked exclusively to expression in reproductive organs. Although their individual functions are still not known, this relationship suggests that they participate in the reproductive functions of the male. Additional genes (40 genes) on the V chromosome are expressed in both male sexual organs and male thalli, suggesting that they have cellular functions unrelated to reproduction.

Figure 30. ***Funaria hygrometrica*** with both undeveloped and nearly mature capsules on female plant portions. Photo by Robert Klips, with permission.

Figure 31. ***Orthotrichum pusillum***, an **autoicous** species with capsules. Photo by Robert Klips, with permission.

Gametangial Arrangement

There are multiple configurations of gametangia among the various bryophytes. The monoicous condition of sexuality among mosses can be further divided into **autoicous**, **paroicous**, and **synoicous**. In the **autoicous** condition, the male and female gametangia are in separate clusters, as in ***Orthotrichum pusillum*** (Figure 31-Figure 33). In the **paroicous** condition, the male and female gametangia are in separate groupings but in a single cluster, as they are in a number of species of the liverwort ***Lophozia*** (Figure 34) (Frisvoll 1982). The **synoicous** condition is one in which the male and female gametangia occur intermixed in the same cluster, as in ***Micromitrium synoicum*** (Figure 35), a condition unusual enough to be used in the specific name. Whereas archegonia in acrocarpous mosses are always terminal, pleurocarpous mosses grow horizontally, and the female and male sex organs occur at the apex of specialized short branches, **perichaetia** and **perigonia**, respectively. In dioicous taxa, antheridia of acrocarpous mosses are in various positions, whereas archegonia are terminal. The same arrangements into perichaetia and perigonia is true for both monoicous and dioicous species.

Figure 32. ***Orthotrichum pusillum***, an autoicous species showing antheridia. Photo by Robert Klips, with permission.

Figure 33. ***Orthotrichum pusillum***, an **autoicous** species showing archegonia. Photo by Robert Klips, with permission.

Figure 34. ***Lophozia excisa***, a **paroicous** species. Photo by Michael Lüth, with permission.

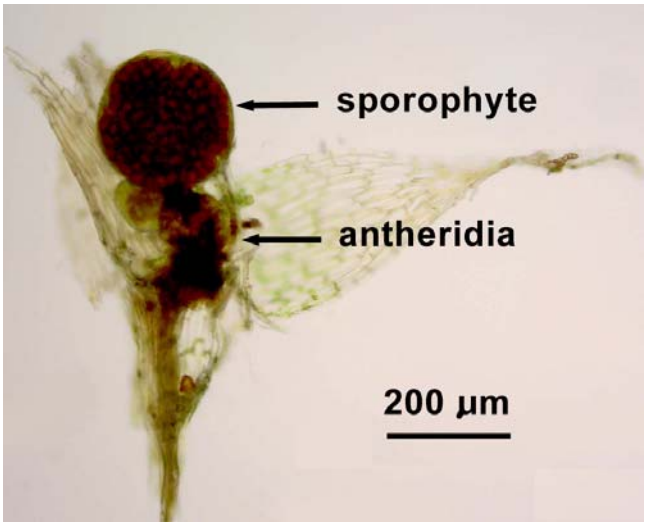

Figure 35. ***Micromitrium synoicum*** with male and female gametangia among the same bracts (**synoicous**). Photo from Duke University, through Creative Commons.

In **Jungermanniopsida**, the antheridia are arranged behind the growing point (Figure 36-Figure 38). In most of the leafy **Jungermanniopsida** the archegonia occur in perianths (Figure 36, Figure 39) that may be terminal on stems and branches or located along these. In the **Metzgeriales** (**Jungermanniopsida**), the archegonia appear along the midrib of the thallus, thus permitting continued apical growth (Figure 40). In the **Marchantiopsida** the antheridia occur in clusters on the thallus (Figure 41) or elevated on a stalk (Figure 42), with similar arrangements for archegonia (Figure 42-Figure 43). In **Anthocerotopsida** the antheridia are imbedded in the thallus (Figure 44-Figure 45) and archegonia are single and surrounded by involucres (Figure 44).

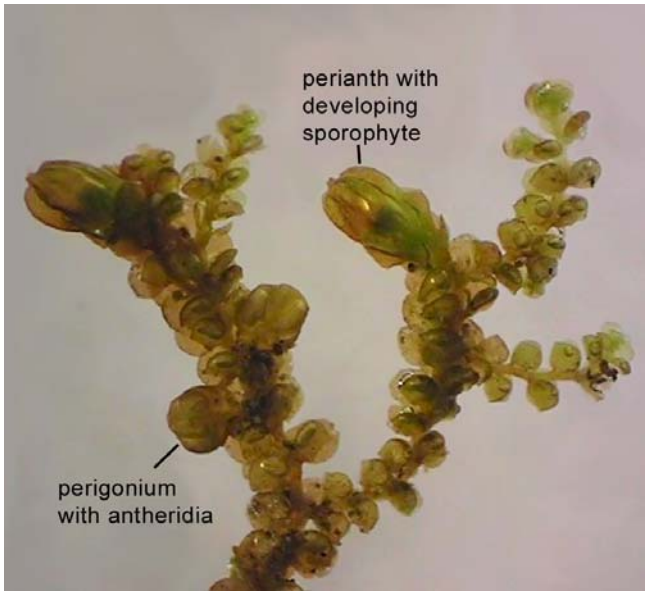

Figure 36. Arrangement of **perianth** with archegonia and **perigonium** with antheridia in the monoicous leafy liverwort ***Frullania oakesiana***. Photo by Paul Davison, with permission.

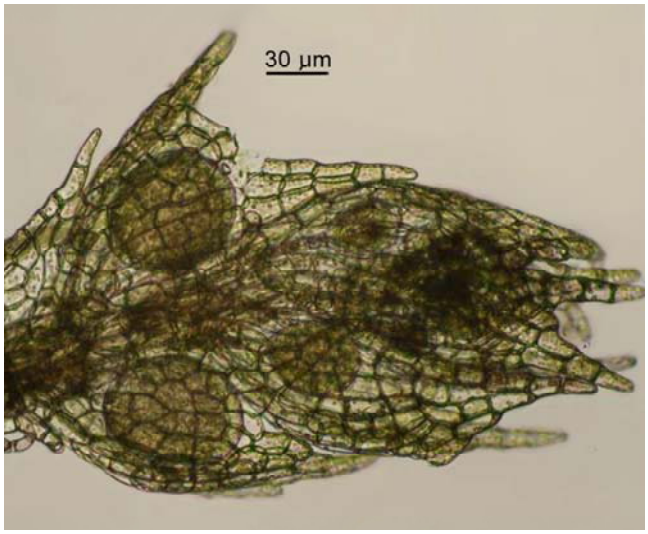

Figure 37. Antheridial arrangement on the leafy liverwort ***Kurzia***. Photo by Tom Thekathyil, with permission.

Figure 38. ***Pellia endiviifolia*** with antheridia on the thallus in positions not at the apex. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 39. **Perianth** of the leafy liverwort ***Frullania*** (**Jungermanniopsida**) in its terminal position. Photo by George Shepherd, through Creative Commons.

Figure 40. ***Symphogyna brasiliensis*** (**Metzgeriales**) showing subapical position of archegonia, hidden in this case by fimbriate scales. Photo by George J. Shepherd through Creative Commons.

Figure 41. ***Conocephalum conicum*** antheridia in clusters on the thallus (arrow). Photo by Malcolm Storey, through Creative Commons.

Figure 42. ***Marchantia polymorpha*** showing flat-topped antheridiophores with antheridia embedded in them and archegoniophores with fingerlike arms with archegonia on the undersides. Photo by Robert Klips, with permission.

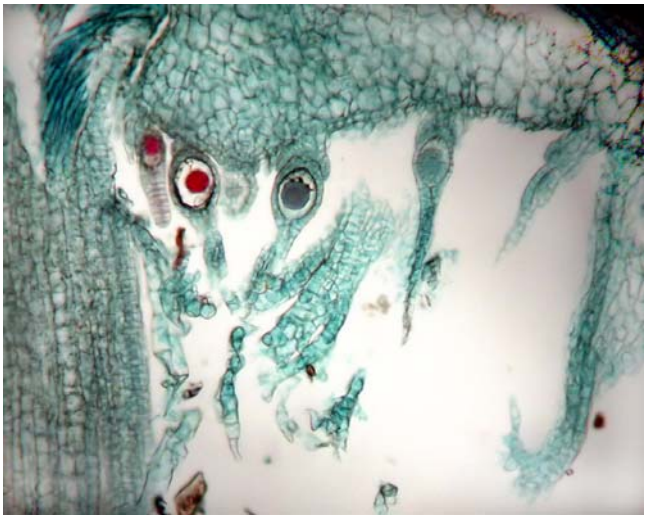

Figure 43. Arm of archegoniophore head of ***Marchantia polymorpha*** with archegonia hanging down. Photo by George Shepherd, through Creative Commons.

Figure 44. ***Notothylas orbicularis*** (**Anthocerotopsida**) with involucres that surround archegonia and pouches that contain antheridia (see insert). Photo by Paul Davison, with permission.

Figure 45. **Antheridia** in the pocket of a hornwort (**Anthocerotopsida**), expelling sperm. Photo by Hatice Ozenoglue Kiremit, with permission.

Origin of Bisexuality in Bryophytes

As already noted, the number of dioicous species of bryophytes is greater than the number of monoicous species (Hedenäs & Bisang 2011), with 68% of liverworts, 57% of mosses, and 40% of hornworts being dioicous (Villarreal & Renner 2013a). Longton and Schuster (1983) recognized 205 liverwort taxa as dioicous, 112 as monoicous in New Zealand. In Guatemala, 161 taxa are dioicous compared to 145 monoicous. Une (1986) found 613 (62.2%) of the bryophyte species in Japan were dioicous and 356 (36.2%) were monoicous. This prevalence of dioicous taxa is an unusual situation among plants and raises questions about its significance. The switch to monoicy has previously been suggested to be a derived character in bryophytes (but see below under Monoicy as a Derived/Advanced Character?), and in many genera it drives speciation through doubling of some or all of the chromosomes. One must then ask, how do so many dioicous taxa survive and spread?

Monoicy as a Derived/Advanced Character?

Ando (1980) suggested seven reasons to consider monoicy as advanced over dioicy in bryophytes, based on concurrent knowledge on bryophyte systematics, distributions, and life histories:

1. Frequently the strain with the haploid chromosome number is dioicous and the monoicous one is diploid.
2. Monoicous taxa seem to have more limited distribution, despite their higher frequency of producing sporophytes and spores.
3. Bryophytes of specialized, more recent habitats such as on decaying wood or living leaves of tracheophytes include many monoicous taxa.
4. Taxa with small gametophytes are more commonly monoicous.
5. Most annual bryophytes are monoicous, e.g. Ephemeraceae, Funariaceae, and Splachnaceae.
6. More advanced groups such as Marchantiales and Anthocerotophyta include many monoicous taxa. [This statement does not fit with 2016 thinking about the phylogenetic position of these groups.]
7. Monoicous taxa have several means to prevent self-fertilization and may have evolved by hybridization.

This suggested direction of evolution is in line with the recent study in hornworts, discussed below, which revealed a transition rate from dioicy to monoicy that was twice as high as in the opposite direction (Villarreal & Renner 2013a, b). Devos and coworkers (2011) consider genetic history in their treatise on the evolution of sexual systems in the mostly epiphytic liverwort genus ***Radula*** (Figure 46). They also found that shifts from dioicy to monoicy in that genus occurred multiple times, with some epiphytes having facultative shifts.

However, recent studies using modern comparative phylogenetic analyses and large scale phylogenies of mosses (McDaniel *et al*. 2013) and liverworts (Laenen *et al*. 2016) found that transitions in sexuality are biased towards dioicy. Furthermore, they found that there seem to be higher rates of diversification among the monoicous moss taxa than among the dioicous ones. In liverworts,

bisexuality evolved multiple times. It is nonetheless associated with certain clades in the liverwort tree, which suggests that it might be a response to environmental conditions (Laenen *et al.* 2016). The distinct phylogenetic signal in sexual systems across the liverwort phylogeny contrasts with the high lability of sexual systems in mosses and hornworts. McDaniel and coworkers (2013) suggest that dioicy works best when separate sexes derive some advantage in their different morphologies.

Figure 46. ***Radula complanata*** growing epiphytically and exhibiting numerous sporophytes. Photo by David Holyoak, with permission.

One might look for these dioicy advantages in genera such as ***Diphyscium*** (Figure 47) where males and females have very different morphologies, or in those taxa with **dwarf males** (See Dwarf Males in Chapter 3-3). But even more likely are sexual differences in physiology – phenomena that have barely been explored (see discussions for ***Syntrichia caninervis*** and ***Marchantia inflexa*** in section on Environmental and Geographic Differences in Chapter 3-2).

Figure 47. ***Diphyscium foliosum*** females with capsules surrounded by perichaetial leaves and photosynthetic males (green leaves in foreground). Photo by David T. Holyoak, with permission.

It seems that it still remains for us to unravel the selection pressures and evolutionary processes behind this dioicous phenomenon, but this unravelling is promising with current molecular techniques. It is likely that further phylogenetic analyses as well as the thorough study of genome evolution will shed light on the evolution of sexual systems in bryophytes (Crawford *et al.* 2009; Laenen *et al.* 2016; McDaniel & Perroud 2012; McDaniel *et al.* 2013; Villarreal & Renner 2013a, b).

Multiple Reversals

The hornworts (**Anthocerotophyta**) are unique in many ways, and among these are their sexual systems. Villarreal and Renner (2013a, b) contend that hornworts underwent numerous transitions between dioicy and monoicy, with a transition rate from dioicy to monoicy that was twice that from monoicy to dioicy. But a seemingly strange occurrence is that monoicous groups of hornworts have higher extinction rates. This might be explained by the fact that in the hornworts, diversification rates do not correlate with higher ploidy levels as they do in some mosses (*e.g.* Lowry 1948 for **Mniaceae**). Rather, in hornworts polyploidy in monoicous taxa is rare, occurring in only one (***Anthoceros punctatus***, Figure 48-Figure 49) of 20 species that have been assessed (Villarreal & Renner 2013a). Crawford *et al*. (2009) consider the evidence for simultaneous transitions in chromosome ploidy numbers and sexual systems to be inconclusive in mosses as well. And in liverworts, only about 5% of the species are polyploid whereas 30-40% of the species are monoicous (Fritsch 1991 in Laenen *et al*. 2016).

Figure 48. ***Anthoceros punctatus*** with sporophytes. Photo by Des Callaghan, with permission.

Villarreal and Renner (2013a) examined the sexual systems of 98 of the 200 known species of hornworts. Knowing that a relationship between dioicy and small spores exists in mosses, they looked for a similar relationship in hornworts. Using Bayesian techniques, they found at least a weak support for this correlation in hornworts. More to the point, they showed that the sexual system depends on spore size, but that the reverse relationship is not true. They reasoned that dioicous species would be more successful with small spores by providing dense carpets of gametophytes for reproduction. It would seem that this character also permits them to occupy their disturbed and ephemeral habitats where they can thrive without competition.

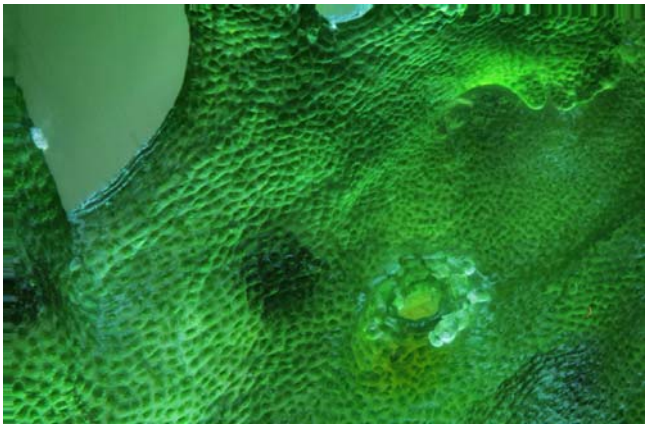

Figure 49. ***Anthoceros punctatus*** antheridial pit. Note the bluish *Nostoc* colony to the left of the antheridial pit. Photo by Des Callaghan, with permission.

The Monoicous Advantage

The effects of these oicy differences on bryophyte ecology and biology are impressive for this gametophyte-dominant group. As in other plants, monoicous species might appear at a competitive advantage, as all individuals in a population can potentially produce offspring. Moreover, monoicous species in general also reproduce by spores more frequently than do dioicous taxa (Longton & Schuster 1983), although this is not always the case. In 1950, Gemmell published vice-county records for the sexual condition of British mosses, using Dixon's The Student's Handbook of British Mosses, and supported the concept that mosses with the monoicous condition are more successful at producing capsules than those of the dioicous condition (Figure 50). Although a much higher percentage (97% compared to 58% in dioicous taxa) of the monoicous group has capsules frequently (Figure 50), presumably because of greater opportunity for fertilization, the dioicous group occupies a greater proportion of the vice-county observations compared to the number of monoicous species (Figure 51).

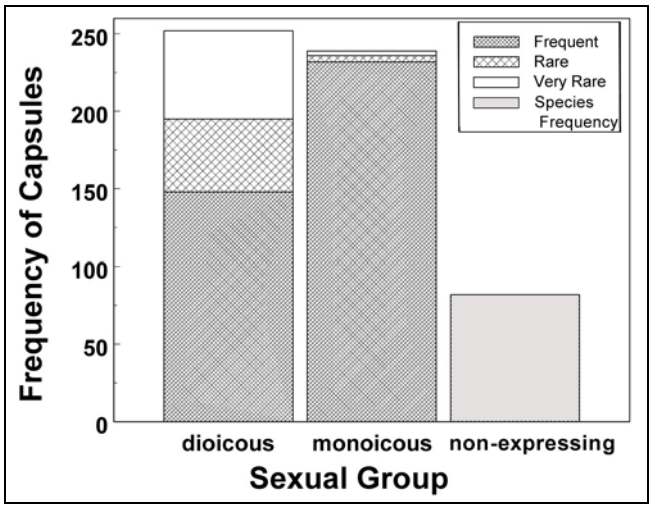

Figure 50. Frequency of producing capsules in dioicous and monoicous mosses and frequency of non-expressing species in vice-counties of Great Britain. The total number of species is 573, and the bars represent the relative frequency of the three types. Based on table in Gemmell 1950.

Heegaard (2001) illustrates the problem of dioicy in ***Andreaea*** (Figure 52-Figure 55). Both monoicous and dioicous species occur in western Norway, permitting us to compare genetically similar sibling taxa from a limited geographic range. The only dioicous species, ***Andreaea blyttii*** (Figure 52), had a lower percent (38%) of sporophytes on cushions bearing **perichaetia** (leaves surrounding archegonia) than did the three monoicous taxa (60-86%). Nevertheless, even among monoicous taxa, ***A. nivalis*** (Figure 53) and ***A. obovata*** var. ***hartmannii*** (Figure 54) rarely produced capsules. The production of capsules in monoicous ***A. rupestris*** var. ***rupestris*** (Figure 55) was highly correlated with the environment, with one group having capsule production that was strongly correlated with altitude and slope, corresponding with **perichaetial** development, and a second group where there was no correlation with perichaetial development, but sporophyte production correlated with gradients of flushing and snow cover. Yet another group produced sporophytes throughout its environmental range. Coordination between the sexes for timing of formation and maturation of the sexual structures, influenced by the environment, could add to the problems of both monoicous and dioicous taxa.

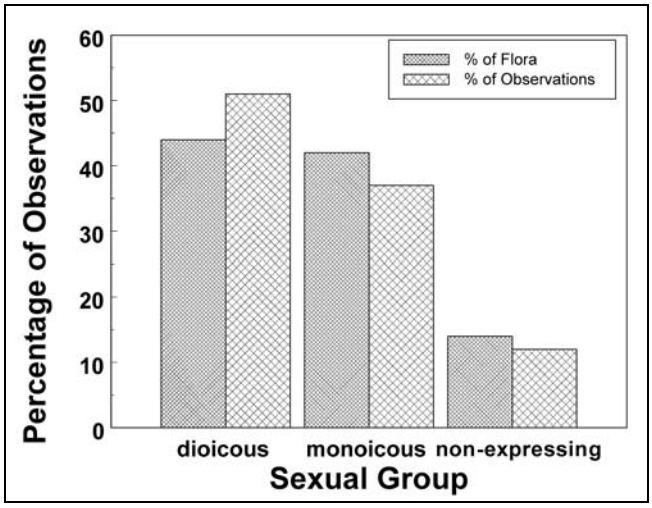

Figure 51. Effect of sexual group on relative frequency of bryophytes in British vice-counties. Total number of species is 573. Percent of flora was obtained by dividing number of species in the category by total number of species. Percent of observations was obtained by dividing total number of vice-county observations by number of species in the category and converting to percent. Based on table in Gemmell (1950).

Figure 52. ***Andreaea blytii*** at Khibiny Mountains, Apatity, Murmansk. Photo by Michael Lüth, with permission.

Figure 53. ***Andreaea nivalis*** in Europe. Photo by Michael Lüth, with permission.

Figure 54. ***Andreaea obovata*** (the dark-colored moss) at Akisko, Sweden. This population lacks capsules, as indicated by the smooth black color. Photo by Dale Vitt, with permission.

Figure 55. ***Andreaea rupestris*** with capsules. Photo by Michael Lüth, with permission.

In comparing taxa that commonly produce capsules, Longton and Schuster (1983) reported only 22 British dioicous mosses, compared to 134 monoicous taxa, commonly have capsules; 154 dioicous taxa rarely or very rarely have capsules, compared to 12 monoicous taxa. It is apparent, then, that factors other than sexual reproduction contribute to the success of dioicous taxa.

Nishimura and Une (1989) examined sporophyte production in **pleurocarpous** mosses (horizontally growing taxa with reproductive organs on short side branches; Figure 56) of the Hiruzen Highlands in Japan. Out of 22 **autoicous** (monoicous with antheridia and archegonia in different clusters) species, 20 produced sporophytes (91%). However, out of 49 dioicous species, including 5 with **dwarf males** (**phyllodioicous** – see Dwarf Males in Chapter 3-2), only 27 produced sporophytes (55%). Studies like this suggest that there is a sexual reproductive advantage to being monoicous. But they still beg the question of better survival.

One possible consequence of being dioicous and spreading to new locations is the total absence of sporophytes for some species in part of their geographic range. This appears to be the case for the entire genus of ***Sphagnum*** in California, USA (Carl Wishner, Bryonet 14 August 2012; Norris & Shevock 2004). McQueen and Andrus (2007), in Flora of North America vol. 27, report that most, if not all, of the species known from California are dioicous. Yet, for the typically dioicous ***Sphagnum russowii*** (Figure 57), Shaw *et al.* (2012) report that some specimens are apparently monoicous. The common presence of sporophytes for some California species [*e.g.* ***S. capillifolium*** (Figure 58), ***S. angustifolium*** (Figure 59)] when they occur elsewhere suggests that there may be a **founder principle** at work (Carl Wishner, Bryonet 14 August 2012) wherein only one sex arrived to colonize a particular location. This was also suggested for ***S. palustre*** (Figure 60) in Hawaii where sporophytes are not known to occur (Karlin *et al.* 2012). But without genetic evidence, we cannot rule out the possibility of a climate that is not suitable for expression of one of the sexes or that makes the two sexes mature at different times.

Herbarium records are frequently the basis for descriptions of bryophytes and frequency of sporophytes. One must view herbarium collection records for such factors as male:female ratios and sporophyte production with caution, however, due to collection bias. As Harpel (2002) demonstrated for bryophytes collections for the western U.S., bryologists are more likely to collect the unusual, creating a bias toward over-collecting the rarer species and those with capsules, while ignoring the common.

Figure 56. ***Plagiothecium denticulatum***. Photo by Bob Klips, with permission.

Figure 57. ***Sphagnum russowii*** in Europe. Photo by Des Callaghan, with permission.

Figure 58. ***Sphagnum capillifolium*** in Chile, showing capsules. Photo by Juan Larrain, with permission.

Figure 59. ***Sphagnum angustifolium*** in Europe. Photo by Michael Lüth, with permission.

Figure 60. ***Sphagnum palustre*** in Europe. Photo by Michael Lüth, with permission.

Stark (1983) suggests that monoicy is advantageous in the desert because of limiting water supplies. However, when he tested the hypothesis in the field in New Mexico, USA, he was unable to support the hypothesis (Stark & Castetter 1987). As found by others, Stark and Castetter found patterns of monoicy correlation with sporophyte production. Nevertheless, Stark considers that at the species level, monoicy provides advantages in the desert habitat.

Or the Dioicous Advantage?

To their potential detriment, monoicous taxa frequently experience **selfing** (being fertilized by sperm from the same plant; see Reproductive Barriers in Chapter 3-4), despite having neighbors that can produce gametes of the opposite sex (Eppley *et al.* 2007). This results in significantly fewer heterozygous fertilizations than that found in dioicous taxa. Furthermore, these monoicous near-neighbors typically belong to the same clone, produced through vegetative reproduction, or have developed from spores from the same parent. This results in a deficiency of heterozygous sporophytes among monoicous taxa. Could it be that the heterozygous condition might itself drive the "mistakes" that result in having two sex chromosomes in one spore, resulting from a misalignment of chromosomes during meiosis? This would drive the bryophytes toward monoicy.

As suggested for the California ***Sphagnum*** species (see The Monoicous Advantage above), total absence of the opposite sex in dioicous taxa can force species to survive vegetatively in many isolated regions and margins of distribution. Because of the success of **vegetative propagation** (reproduction by asexually produced pieces or branches of the plant) (Figure 61-Figure 62), entire single-sex populations of dioicous taxa may exist and expand over large areas without ever producing capsules. Such is often the case with aquatic taxa like ***Fontinalis*** (Figure 63) and in parts of its distribution for ***Pleurozium schreberi*** (Figure 64) (Longton & Greene 1969).

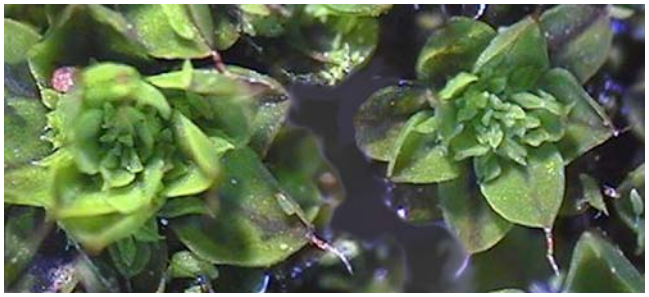

Figure 61. ***Syntrichia pagorum*** exhibiting **gemmae**. These are one means of asexual reproduction. Photo by Paul Davison, with permission.

Figure 62. **Gemma** of ***Syntrichia pagorum***, illustrating its very papillose cells. Photo by Bob Klips, with permission.

Figure 63. ***Fontinalis duriaei*** showing its flowing growth of a single clone. It is unlikely a female in this position would ever get fertilized and produce capsules unless a male clone became intermixed. Photo by Janice Glime.

Figure 64. ***Pleurozium schreberi***, seen here with capsules in Baraga County, Michigan, USA, is barren northward in Ontario where apparently only one sex exists. Photo by Janice Glime.

As a result of being dioicous it may be possible to harbor more genetic variation than that of monoicous species. Both mating systems permit species to reproduce asexually by **ramets** (individual members of clone, arising vegetatively), but the greater percentage of species with asexual diaspores permits those dioicous species to carry non-functional or non-lethal genes as potential pre-adaptations without the selection step that often occurs during failed pairing in meiosis.

Shaw (1991) found that the monoicous moss ***Funaria hygrometrica*** (Figure 30) never had heterozygous sporophytes for 14 allozyme loci, *i.e.*, it had a high level of heterozygote deficiency. The dioicous moss ***Polytrichum juniperinum*** (65), on the other hand, had extremely high levels of heterozygosity based on six allozyme loci (Innes (1990).

In short, monoicous taxa do not always gain the advantages of cross-breeding, although their chances for cross-breeding may in some cases be equal to or greater than that of dioicous taxa. This cross-breeding opportunity assumes that spores of another genotype of a monoicous taxon have equal chances of germinating and growing near that taxon compared to spores of a dioicous taxon growing close enough for fertilization of a plant of the opposite sex of that taxon.

65. ***Polytrichum juniperinum***, a dioicous moss shown here with prolific capsule production. Photo by Daniel Mosquin, through Creative Commons.

In fact, the opportunities for cross fertilization in monoicous taxa should be greater than those of dioicous taxa because any spore of the species that germinates near another of the same species should be able to cross with it, whereas the dioicous taxon must have a pair of sexes. On the other hand, if the archegonia of a monoicous taxon lack any protection against self-fertilization, their own sperm have the greater chance of reaching them due to the shorter distances. Thus, taxa of both mating systems have opportunities for different individuals nearby to fertilize them. At present we do not have enough data to generalize about the numbers of cross-fertilizations that occur in monoicous taxa. Due to the higher number of total successful fertilizations, monoicous taxa have much better

dispersal through spores, increasing the possibility of a different genotype nearby and providing it a source of cross-fertilization. The likelihood of cross-fertilization with a different genotype in both sexual strategies is complicated by arrival times, competition, leakage of inhibitory substances, and the degree of self-incompatibility (See Chapter 3-4 in this volume). But dioicous taxa have the advantage of more frequent asexual reproduction and guaranteed mixing of genes when they do reproduce sexually, creating the variability for the species to survive throughout environmental changes.

Origins of Polyploidy

The monoicous condition in mosses may be the result of **polyploidy** (in bryophyte gametophytes, having more than one complete set of chromosomes). Polyploidy is a common occurrence among plants, being rare only among the gymnosperms (Ahuja 2005). Bryophytes seem to have multiple avenues by which to become polyploids. This increase in ploidy is often considered to make the monoicous condition possible by providing an extra set of chromosomes. But in this group where sex chromosomes have been identified in at least some species, the understanding of how all of these possible origins work is complex. See Monoicy as a Derived/Advanced Character? above and examples below.

Sporophytes from Fragments

It is still unclear how the majority of monoicous taxa arose. We know that it is possible in the lab to grow 2*n* (**diploid**) protonemata and leafy gametophores from bits of sporophyte tissue, producing monoicous plants (Crum 2001). Marchal and Marchal (1907, 1909, 1911) grew nineteen species of diploid moss gametophytes from setae in the lab. Since then, many others have succeeded in producing diploid moss gametophytes without spores (Crum 2001). Lorbeer (1934) induced diploid gametophytes from capsules and setae in 52 species of liverworts. But this development of sporophyte tissue into a gametophyte has been observed only once (***Funaria hygrometrica***, Figure 26-Figure 30) in nature (Brizi 1892; Crum 2001).

Sporophytes have also been developed from gametophyte tissues. The first was produced as outgrowths from 2*n* leaves and stem tips of ***Tortula acaulon*** (=*Phascum cuspidatum*) (Marchal & Marchal 1911; Springer 1935). These were initially misinterpreted by Marchal and Marchal as asexual reproductive structures, but later Springer (1935) interpreted them as apogamous sporophytes. These seemed to be the result of altered, mostly dry, conditions. However, these pseudosporophytes failed to produce normal capsules and never produced spores. More recently El-Saadawi *et al*. (2012) discovered what appears to be an apogamous sporophyte – one that lacks any evidence of an archegonium at its base, in ***Fissidens crassipes*** subsp. ***warnstorfii*** (Figure 66). It likewise never produced spores. It originated at the base of the stem, whereas this species normally produces its sporophytes at the apex.

It is unlikely that these vegetative anomalies have contributed much, if any, to the creation of monoicous taxa. On the other hand, the accidental fusion of haploid gametophyte cells other than gametes can result in capsules with at least some viable spores. This suggests that cases might exist where cells join but remain as gametophyte, possibly becoming polyploid monoicous plants.

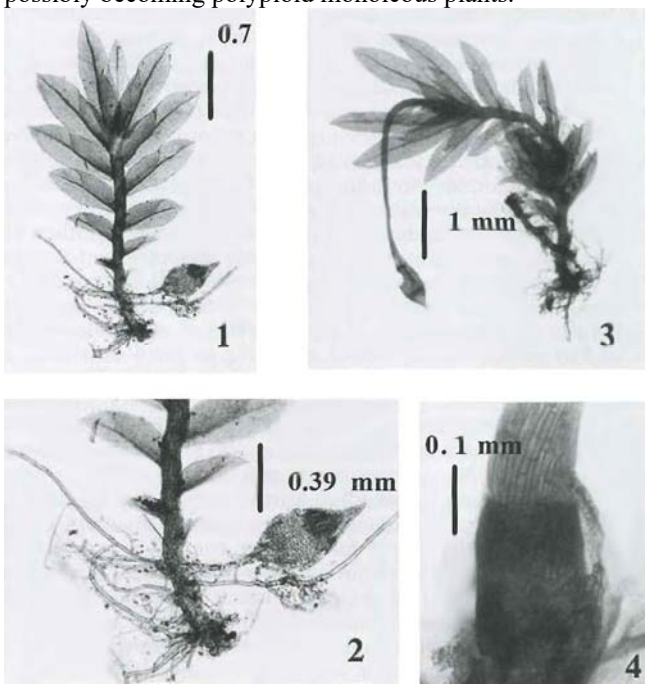

Figure 66. ***Fissidens crassipes*** showing an apogamous sporophyte (**1 & 2**) compared to a normal sporophyte (**3**) and the vaginula at the base of the normal sporophyte (**4**), but absent on the apogamous sporophyte. Photo from El-Saadawi *et al*. (2012). Permission pending.

Genome Doubling in Mosses

Genome doubling seems to occur commonly in mosses [76% polyploidy (Przywara & Kuta 1995)], but seemingly less often so in hornworts (Villarreal & Renner 2013a) and liverworts [10% (Newton 1983); 5% (Fritsch 1991 in Laenen *et al.* 2016) (this can include ancient polyploidism and subsequent chromosome loss). Polyploidy might be coupled with a change in sexual system from dioicous to monoicous, but not necessarily so (Jesson *et al.* 2011). Both **autopolyploidy** (self-doubling of chromosomes within a single bryophyte) and **allopolyploidy** (**hybridization**) are known to be present among bryophytes in nature (Natcheva & Cronberg 2004; see also 3.4, Hybridization).

Autopolyploids – Although **autopolyploidy** was once considered the primary source of polyploidy in mosses (Boisselier-Dubayle & Bischler 1999), this may not be the case. Košnar *et al*. (2012) were able to use genetic markers to demonstrate autopolyploid origin of several lineages in

the ***Tortula muralis*** (Figure 67) complex, making them the first group of mosses in which autopolyploidy was demonstrated with molecular markers. Google Scholar, when searched for bryophyte autopolyploidy, listed mostly allopolyploidy references. In one species that does exhibit autopolyploidy, ***Targionia hypophylla*** (Figure 68), its triploidy seems to actually be a combination of autopolyploidy and allopolyploidy (Boisselier-Dubayle & Bischler 1999).

Figure 67. ***Tortula muralis*** with capsules. Photo by Derek Christie, with permission.

Figure 68. ***Targionia hypophylla*** showing black marsupial pouches that house the archegonia and sporophytes. Photo by Martin Hutten, with permission.

Allopolyploids – allopolyploids can be achieved by **hybridization** (crossing of non-identical genomes, as in a different strain or species) and has been demonstrated in a number of bryophyte species. For example, Wyatt *et al*. (1988, 1992) showed that ***Plagiomnium medium*** (**Mniaceae**; Figure 69) arose from a cross between ***Plagiomnium ellipticum*** (Figure 70) and ***Plagiomnium insigne*** (Figure 71-Figure 72), resulting in **allopolyploids** (having two or more complete sets of chromosomes that derive from more than one species). Not only did it happen, but it happened multiple times! ***Plagiomnium cuspidatum*** (Figure 73-Figure 75) is likewise an allopolyploid, but one of its parent species is unknown (Wyatt & Odrzykoski 1998). ***Cinclidium stygium*** (Figure 76) (*n*=14), also a member of **Mniaceae**, is a monoicous polyploid closely related to ***C. arcticum*** (Figure 77) and ***C. latifolium*** (Figure 78), both having *n*=7 (Wyatt *et al.* 2013). ***Cinclidium stygium*** appears to have an **allopolyploid** origin from these two close relatives. Also ***Cinclidium subrotundum*** (Figure 79) is a monoicous polyploid (*n*=14) that exhibits strong evidence for allopolyploidy, having 7 fixed heterozygous loci out of 17 scored (Mogensen 1973).

Figure 69. ***Plagiomnium medium***. Photo by Jan-Peter Frahm, with permission.

Figure 70. ***Plagiomnium ellipticum*** Khibiny Mountains, Apatity, Murmansk. Photo by Michael Lüth, with permission.

Figure 71. ***Plagiomnium insigne*** male splash cup. Photo from Botany 321 website, UBC, with permission.

Figure 72. ***Plagiomnium insigne*** female with sporophytes. Photo from Botany 321 website UBC, with permission.

Figure 73. ***Plagiomnium cuspidatum*** females with sporophytes. Photo by Michael Lüth, with permission.

Figure 74. ***Plagiomnium cuspidatum*** showing males with black centers containing antheridia and females with green centers. This arrangement fits the dioicous condition discussed by Andrews (1959), not the more typical synoicous condition known for the species. Photo by Betsy St. Pierre, with permission.

Figure 75. ***Plagiomnium cuspidatum*** showing female reproductive structures on left and male splash cup on right. Photo by Betsy St. Pierre, with permission.

Figure 76. ***Cinclidium stygium*** with capsules, a species with *n*=14. Photo by Misha Ignatov, with permission.

Figure 77. ***Cinclidium arcticum*** (*n*=7), a close relative of ***C. stygium*** (*n*=14). Photo by Michael Lüth, with permission.

Figure 78. ***Cinclidium latifolium*** from Spitzbergen, a species with *n*=7. Photo by Michael Lüth, with permission.

Figure 79. ***Cinclidium subrotundum*** from Spitzbergen. Photo by Michael Lüth, with permission.

In cases when monoicous taxa are polyploids developed from dioicous taxa, we could hypothesize that the monoicous taxa should have more variability and thus better survival. Natcheva and Cronberg (2004) report that the spontaneous hybridization among bryophytes is sufficient to have a significant evolutionary significance, with the many allopolyploid taxa supporting this contention. (See Chapter 3-4, Sexuality: Reproductive Barriers and Tradeoffs).

Relationship of Polyploidy and Monoicy in *Atrichum*

In an ***Atrichum undulatum*** (**Polytrichaceae**, Figure 82) complex from a study in New Brunswick, Canada, monoicous plants were either diploid or triploid, with the number of monoicous individuals increasing as the number of triploids increased (Figure 80; Jesson *et al*. 2011). Many diploid populations, on the other hand, were dioicous (Figure 81). Jesson and coworkers found that male and female gametophytes were represented by haploid, diploid, and triploid individuals (Figure 81). Perley and Jesson (2015) examined the association between polyploidy and sexual system further in the genus, including species of different ploidy-levels. In the haploid state, this genus has either a female **U** chromosome or a male **V** chromosome. Using genetic markers, they determined that certain gene sequences are consistent with independent **allopolyploid** origins of **diploid** (2 sets of chromosomes) and triploid (3 sets of chromosomes) species. In the **triploid *Atrichum undulatum*** (Figure 82-Figure 84), and possibly the diploid ***A. altecristatum*** (Figure 85-Figure 86) as well, hermaphroditism appears to be a result of allopolyploidy. However, in the diploid ***A. crispulum*** (Figure 87), this allopolyploid event did not result in the hermaphrodite condition. This tells us again that the creation of monoicy (hermaphroditism) is more complex than simply doubling the chromosome number. (See more in Chapter 3-4, Reproductive Barriers: Selfing and Hybrids.)

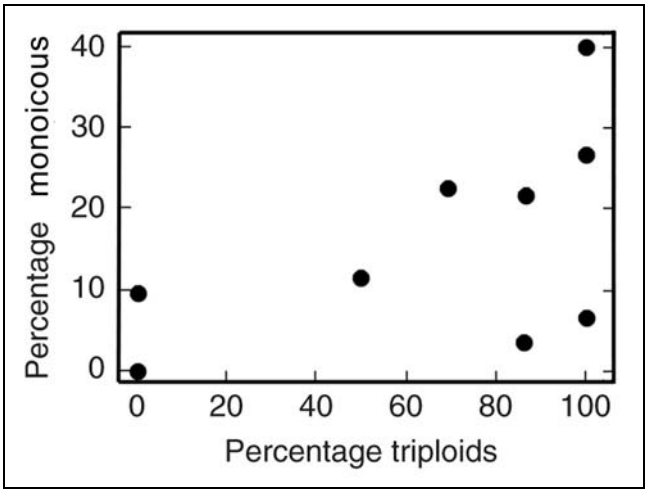

Figure 80. Relationship between percentage of triploid individuals and monoicism in 21 randomly sampled populations of the ***Atrichum undulatum*** complex in New Brunswick, Canada. Five populations were not sampled for ploidy determination. Eight populations exhibited no hermaphrodites and no triploids. Modified from Jesson *et al*. 2011.

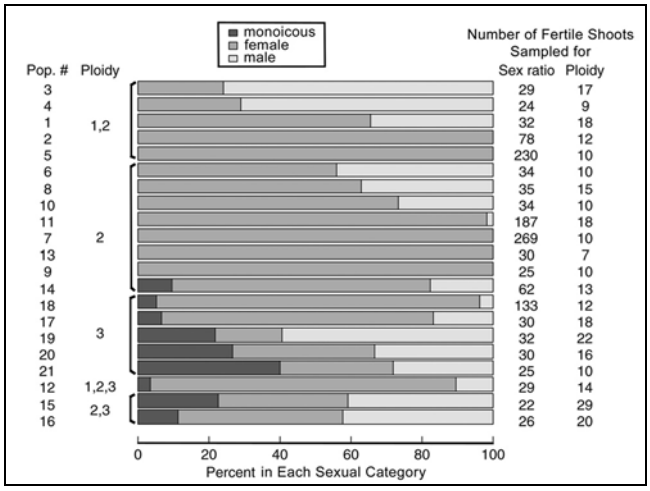

Figure 81. Percentage of individuals in each of three sexual categories in 21 populations of the ***Atrichum undulatum*** complex in New Brunswick, Canada. Column on right indicates the number of individuals in random samples for determining sex ratio and those used for determining ploidy. Modified from Jesson *et al.* 2011.

Figure 82. Female plants representative of the ***Atrichum undulatum*** complex, a group of taxa that may be monoicous or dioicous. Photo by Janice Glime.

Figure 83. ***Atrichum undulatum*** males. Photo by Janice Glime.

Figure 84. ***Atrichum undulatum*** females with capsules. Photo by Andrew Hodgson, with permission.

Figure 85. ***Atrichum altecristatum*** males. Photo by Bob Klips, with permission.

Figure 86. ***Atrichum altecristatum*** capsules. Photo by Bob Klips, with permission.

Figure 87. ***Atrichum crispulum*** capsules. Photo by Robert Klips, with permission.

Pseudodioicy

As its name implies, **pseudodioicy** is a condition which appears to have separate sexes, but in fact they originate from one plant with separate sexual branches. The best known examples of the pseudodioicous condition typically arise when a male branch breaks off or becomes separated by decay. However, that male branch typically remains in proximity of the original plant, which often appears to be only female. The second type is more difficult to observe and can arise when male and female buds from a protonema become separated, causing separate plants to form.

The first record of pseudodioicy I could find is that of Barnes (1887). He noted the condition in ***Fissidens closteri*** (Figure 88), ***F. incurvus*** (Figure 89), and ***F. pallidinervis*** (Figure 90). He described ***F. closteri*** as male gemmiform, attached to the female by rhizoids or separate. For ***F. incurvus***, he writes "male gemmiform, at the base of stems from which they sometimes separate." For ***F. pallidinervis***, he hedges and says "probably pseudodioicous."

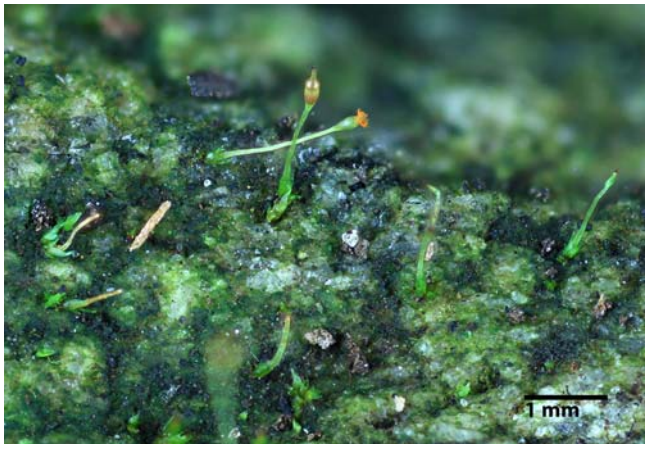

Figure 88. ***Fissidens closteri***, a species with pseudodioicy. Photo by Ken McFarland and Paul Davison, with permission.

Figure 89. ***Fissidens incurvus***, a species with pseudodioicy. Photo by Jan-Peter Frahm, with permission.

Figure 90. ***Fissidens pallidinervis*** with capsules, a species with pseudodioicy. Photo by Frederick B. Essig, with permission.

Fissidens seems to have the most recorded observations of the pseudodioicous condition. Hill (1907) reported that ***F. minutulus*** (Figure 91) had male "flowers" that form little stems among the rhizoids of fertile plants. As the plants age, the connection with the parent plant ceases to exist. Hill suggested that male organs may start in the leaf axils of fertile stems as buds, later becoming independent. Whittier and Miller (1967) described ***Fissidens mangarevensis*** (Figure 92) from the Society Islands as sometimes being pseudodioicous, but they found no antheridia to verify that.

Figure 91. ***Fissidens minutulus***, a species with pseudodioicy. Photo by Jan-Peter Frahm, with permission.

Figure 92. ***Fissidens mangarevensis***, a species with pseudodioicy. Photo by Yang Jia-dong, through Creative Commons.

The fascinating cave moss ***Schistostega pennata*** (Figure 93) likewise can be pseudodioicous (Mežaka *et al*. 2011). Jeff Duckett (pers. comm. 3 December 2019) tells me he has confirmed this in freshly collected material. Hill *et al*. (1994) describe it as pseudodioicous with male and female plants arising separately from the same protonema. Thus, this species fits the second type of pseudodioicy. It is likely that this separation occurs frequently in species with male and female buds on one protonema, but it is difficult to document, and it is likely that these species have been treated as dioicous, as is the case for ***S. pennata*** in Crum's 1983 description.

Other cases of pseudodioicy have been reported in both leafy and thallose liverworts. Some of these are guesses, based on finding what appear to be both autoicous and dioicous plants, as in the leafy liverwort ***Lophonardia jamesonii*** (Vána & Watling 2004).

Several thallose liverworts become pseudodioicous when the thallus decays from its base and leaves male and female gametangia in separate thalli. Such is the case for ***Reboulia hemisphaerica*** (Figure 94) (Puglisi *et al*. 2018). In this species the branches can also be easily separated by age, but also during preparation. ***Mannia californica*** (Figure 95) can produce its gynoecia on ventral branches, but at least in Japan, terminal autoicous female branches occur (Borovichev *et al*. 2014). Decaying thallus bases make the species appear to be dioicous, but they are in fact pseudodioicous. Among Canadian specimens of ***Metzgeria conjugata***, Brinkman (1931) found several pseudodioicous specimens in this monoicous species. Borovichev *et al*. (2012) described pseudodioicous plants of ***Sauteria alpina*** (Figure 96) from Russia, earlier described from Greenland by Schuster (1992).

Figure 93. ***Schistostega pennata*** capsules, a species with pseudodioicy. Photo by Martin Hutten, with permission.

Leafy liverworts also exhibit this trait among several species. ***Cephaloziella crassigyna*** can be found in an autoicous or pseudodioicous state (Beveridge *et al*. 2017). Watson (1913) reported that Macvicar considered ***Cephalozia lammersiana*** as pseudodioicous; the taxonomic affinities of the species were unclear, but it does seem to represent the condition in some specimens of ***Cephalozia***.

Figure 94. ***Reboulia hemisphaerica*** male and female reproductive structures. Branches with only one of these can become separated through thallus decay. Photo by Bob Klips, with permission.

Figure 95. ***Mannia californica*** showing thallus fragments with archegoniophores. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University (permission from Russ Kleinman & Karen Blisard).

Figure 96. ***Sauteria alpina***, demonstrating decay of older parts of the thallus that can separate branches with female reproductive structures from those of male structures. Photo by Hermann Schachner, through Creative Commons.

Polyploidy and Spore Size

Stebbins (1950) concluded that cell size of constant-form cells such as spores was the best indicator of hybridization and polyploidy in plants. We know from studies in ferns that polyploidy can result in larger cells (Lawton 1932). Subsequent studies indicated a similar relationship in spores size in ferns (Hagenah 1961; Wagner 1966; Schneller 1974). Kott and Britton (1983) suggested that spore size could be used to characterize a species as long as at least 20 spores were measured.

But Britton (1968) found that such a correlation does not seem to exist in the fern genus *Dryopteris*, a finding later corroborated by Wagner (1971) for the same genus. Other factors contribute to selection for spore size, making the ploidy relationship unreliable in at least some cases. For example, Carlquist (1966) demonstrated that small spore size increases likelihood of spore dispersal to greater distances, whereas on islands spore size increases because of absence of suitable habitat at greater distances. Barrington *et al*. (1986) noted the absence of statistical data and statistical analyses in studies of spore size-ploidy relationships. Voglmayr (2000) demonstrated, using 138 different moss taxa, that variation in DNA contents has a much lower range of variation than that of tracheophytes (12-fold compared to 1000-fold). However, the possible correlation of spore size and ploidy level does not seem to be explored in bryophytes.

So what evidence do we have that bryophytes exhibit any relationship of larger spores in polyploid individuals? I decided to examine the possibilities in the **Mniaceae**, a family known to have polyploid species. I was not surprised to find a complicated relationship (Table 1).

Although these data suggest possibilities, they do not supply the necessary link between spore size and chromosome number. Furthermore, as Des Callaghan reminded me, descriptions often fail to indicate true variation. Spore sizes vary a lot; he recommended a mean of 50 spores (10 spores from a capsule and five capsules from different populations).

Table 1. Comparison of spore size with number of chromosomes in several genera of **Mniaceae** in the Great Lakes region of North America (from Crum 1983).

Species	Spore Size	Number of Chromosomes
Mnium stellare	20-29 µm	n=6 + m, 7
Mnium lycopodioides	19-29 µm	n=6
Mnium marginatum	22-32 µm	n=12
Mnium thomsonii	20-31 µm	n= 6, 8
Mnium spinulosum	28-21 µm	n=8
Plagiomnium cuspidatum	24-31 µm	n=6, 12
Plagiomnium drummondii	18-24 µm	n=6
Plagiomnium affine	26-29 µm	n=6
Plagiomnium medium	24-29 µm	n=12
Plagiomnium rostratum	22-33 µm	n=7, 12, 14, 21
Pseudobryum cinclidioides	31-40 µm	n=6,7
Rhizomnium punctatum	29-41 µm	n=6, 7; 2n=14
Rhizomnium pseudopunctatum	28-48 µm	n=13-14

Variation within a species can be enormous. For example, within ***Cinclidium stygium*** (Figure 76), spore size may range from 31-68 µm within the same capsule, with a ploidy number of n=14 (Crum 1983). Mogensen (1981) demonstrated that multiple spore sizes can occur in the same capsule in mosses, and Glime and Knoop (1986) showed that in ***Fontinalis squamosa*** (Figure 97) two spore sizes can be present in the same capsule (Figure 98-Figure 99), apparently resulting from arrested development and progressive death of spores. The latter phenomenon can make more space for the remaining spores and perhaps permit them to develop to a larger size before leaving the capsule.

This leaves us with little to suggest whether more chromosomes, *i.e.* a higher ploidy number, would result in larger spores in bryophytes, adding this to the many questions still unanswered about bryophytes.

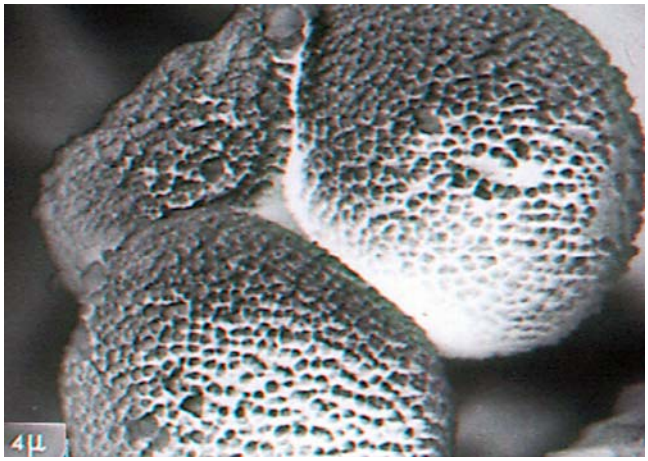

Figure 99. ***Fontinalis squamosa*** tetrad showing abortion already beginning. Photo by Janice Glime.

Figure 97. ***Fontinalis squamosa*** at Cwm Idwal National Nature Reserve. Photo by Janice Glime.

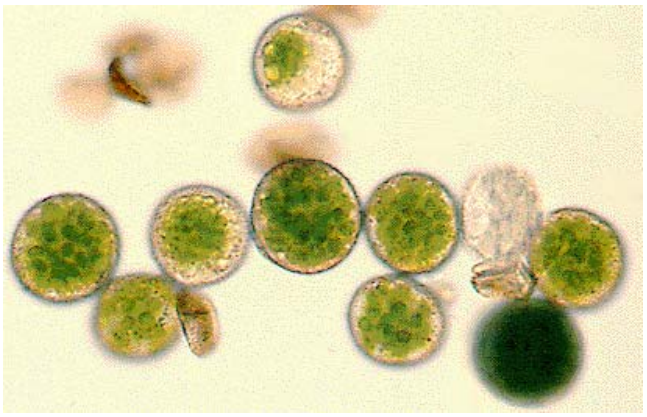

Figure 98. ***Fontinalis squamosa*** spores showing healthy, green spores, pale, aborting spores, and small, aborted spores. Photo by Janice Glime.

Cross Fertilization

Certain mixing of genes results from cross fertilization, a condition widely accepted among botanists as providing genetic variability and greater chances for the species to survive changing conditions. For sexual reproduction to be successful, the sperm must reach the egg. For bryophytes, this could be an easy task in **synoicous** taxa (monoicous with antheridia and archegonia in same cluster), but quite difficult in dioicous taxa. (See above in The Monoicous Advantage.)

Some bryophytes can alter their life cycle depending on the density of the population – a strategy reminiscent of maple (*Acer*) trees. The moss ***Tetraphis pellucida*** reproduces asexually with gemmae at low densities and has a female-biased sex ratio (Kimmerer 1991). As the density increases, there is an increase in sexual reproduction and sporophyte production. The proportion of males also increases as the population size increases, but this greater density also causes the onset of senescence. The strategy is beneficial to a species such as this that lives in unstable or short-lived environments.

Sperm Dispersal

Sperm transfer is a problematic aspect of fertilization for bryophytes. It must be accomplished wihin the life of the sperm, keep the sperm hydrated, and find an archegonium of the right species at the right maturity stage. A good release mechanism can start the sperm on their journeys.

The release of sperm in bryophytes is not a simple bursting of the antheridial wall with swimming sperm free to travel their own way. Rather, it typically occurs as the release of **spermatocytes** as a mass (Muggoch & Walton 1942). Meanwhile, as water accumulates at the base of the antheridium, it pushes this mass outward and away from the antheridium. As the spermatocytes reach the air-water interface, they spread apart rapidly to form a regular spaced arrangement on the surface. Muggoch and Walton concluded that this spreading and spacing correlated with the presence of fat from the spermatocyte mass. As the fat

lowers the surface tension, the spermatocytes gain their freedom and spread. In some bryophytes, such as ***Sphagnum*** and some liverworts, fats seem to be absent and surface spreading likewise is absent. Muggoch and Walton further concluded that it is the surface spreading that makes the sperm susceptible to dispersal by invertebrates in dioicous taxa – a rather astute observation so long before we had actual proof that invertebrate dispersal occurs.

Once freed, the sperm are able to swim rapidly, and if they are near enough they may be attracted to the female gamete chemotactically. Pfeffer (1884) found chemotaxis involved in sperm locating archegonia of ***Marchantia polymorpha*** (Figure 43) and ***Radula complanata*** (Figure 46). Lidforss (1904) found that the proteins albumin, hemoglobin, and diastase were each able to attract sperm of ***Marchantia polymorpha*** to a capillary tube that contained them. Chemotaxis of sperm still needs clear verification and some studies suggest there is no chemotaxis (Showalter 1928). Diversity among the species is likely, but it leaves us with the question of how the sperm finds the archegonium if no attractant is present.

Walton (1943) observed the spreading of sperm in the monoicous thallose liverwort ***Pellia epiphylla*** (Figure 100-Figure 101). In his observations, archegonia were only 5-10 mm from antheridia. Whereas freed sperm in the dioicous liverwort ***Aneura*** (Figure 102) took several hours to travel only 10 mm, those in many moss and liverwort taxa spread rapidly by surface tension over free water at a rate of ~20 mm per minute. Walton found that ***Pellia epiphylla*** sperm behaved like these fast-moving moss and liverwort sperm, extruding in grey masses into water, breaking apart when they reached the surface, and dispersing over the wet surface rapidly. Once released, they were able to reach archegonial involucres in only ~15 seconds. The more lengthy process was emergence of sperm from spermatocytes, which required ~15 minutes. Walton concluded that if the sperm had to swim it would require several hours, but that the surface tension carried them rapidly to their destination. This leaves us with the question of how transfer is accomplished in dioicous taxa with longer distances to traverse.

Figure 100. ***Pellia epiphylla*** with antheridia (brown). Photo by Des Callaghan, with permission.

Figure 101. ***Pellia epiphylla*** with sporophyte. Photo by Malcolm Storey, through Creative Commons.

Figure 102. ***Aneura pinguis*** with capsules, indicating successful sperm transfer. Photo by Jan-Peter Frahm, with permission.

Sperm Travel Distances

One reason for the observed genetic variability in bryophytes is that cross-fertilization may extend greater distances than we had supposed (Table 2). Anderson and Lemmon (1974) considered the maximum distance for sperm to travel in acrocarpous mosses to be 40 mm, with a median dispersal distance of about 5 mm. Pleurocarpous mosses were assumed to have even shorter dispersal distances due to the total lack of splash cups or platforms (see below under Splash Mechanisms) (Anderson & Snider 1982). But as seen in Table 2, known (implied?) distances range up to 230 cm.

Reynolds (1980) found that splashing water on the platforms of the moss ***Plagiomnium ciliare*** (Figure 103) indicated greater travel distance (50+ cm) than that to the nearest male (5.3 cm). In the thallose liverwort ***Marchantia chenopoda*** (Figure 104), fertilization distances seem to range 0.7-65 cm (Moyá 1992), a range that suggests microhabitat factors may play a role in dispersal distance. Differences in dispersal mechanisms

can account for wide ranges. Earlier chapters on **Marchantiophyta** and **Bryophyta** have discussed these mechanisms, including splash cups and platforms, flowing water, and arthropods.

Table 2. Maximum known distances for sperm dispersal. Those in bold have splash cups or splash platforms. Distances mostly from Crum 2001.

Splachnum ampullaceum	5-15 mm	Cameron & Wyatt 1986
Breutelia arcuata	2.5 cm	Bedford 1940
Weissia controversa	4 cm	Anderson & Lemmon 1974
Climacium dendroides	7 cm	Bedford 1938
Pleurozium schreberi	10 cm	Longton 1976
Plagiomnium affine	10 cm	Andersson 2002
Atrichum angustatum	11 cm	Wyatt 1977
Abietinella abietina	12 cm	Bisang *et al.* 2004
Anomodon viticulosus	25 cm	Granzow de la Cerda 1989
Hylocomiadelphus triquetrus	34 cm	Bisang *et al.* 2004
Plagiomnium ciliare	50 cm	Crum 2001
Polytrichastrum ohioense	60 cm	Brodie 1951
Marchantia chenopoda	65 cm	Moyá 1992
Polytrichum juniperinum	75 cm	Longton 1976
Ptychostomum (=*Bryum*) *capillare*	200 cm	Gayet 1897
Dawsonia longifolia	230 cm	Crum 2001
epiphytes	2-5 m	Longton & Schuster 1983
Marchantia polymorpha	9 m	Pressel & Duckett 2019

Figure 103. ***Plagiomnium ciliare*** showing male splash cups and horizontal (plagiotropic) branches. Photo by Robert Klips, with permission.

Figure 104. ***Marchantia chenopoda***, with males on **left** and females on **right**. Female archegoniophores elongate after fertilization. Photos by Janice Glime.

Maggot and Walton (1942) demonstrated experimentally that some bryophyte sperm can move 0.1-0.2 mm per second and continue movement for several hours, suggesting they could swim for 35 cm. Rosenstiel and Eppley (2009) and Shortlidge *et al.* (2012) provided further evidence of the possibility of greater sperm dispersal distances based on longevity (see below under Sperm Longevity).

Explosive Help in Thallose Liverworts

As discussed in Chapter 2-3 on **Marchantiophyta**, ***Conocephalum conicum*** (Figure 105) releases its sperm into a mist that makes them airborne (Benson-Evans 1950; Shimamura *et al.* 2008; see Chapter 2-3), suggesting that this could result in greater dispersal distances. Benson-Evans (1950) describes her experience with dried males of this species in the lab, the result of a hot week-end. Upon rewetting, the plants emitted a fine mist. She paid little attention to this until she noticed that "the mist was being emitted from the antheridial heads in regular puffs. Removal into direct sunlight increased the activity and the particles which were being ejected were visible to the naked eye, so that the puffs were obviously composed of distinct granules." A similar "explosion" is known from a number of other Marchantiales taxa (Peirce, 1902; Cavers 1903, 1904a, 1904b; Andersen 1931; Benson-Evans 1950).

Figure 105. ***Conocephalum conicum*** antheridia. Photo by Janice Glime.

Sperm Dispersal Vectors – After Release

Water has been presumed to be the primary dispersal vector in bryophytes. But interesting mechanisms accompany this water dispersal and still others rely on other organisms to accomplish the task.

I have suggested (Glime 1984) that species of the dioicous aquatic moss ***Fontinalis*** could accomplish fertilization when females are wet but above the water level in streams or lake margins. In streams, this would typically be on emergent rocks, and emergent rocks can create water spray. Once released the sperm could then travel in these drops of water to land on the moist female plants. The timing of their gametangial maturation in autumn when plants are often emergent supports this hypothesis. And if splash from the stream is not effective, autumn rains splashing on emergent males could accomplish the mission.

Splash Mechanisms

Bryologists have been interested in the use of splash mechanisms in bryophytes for dispersal of sperm. Clayton-Greene *et al.* (1977) found that both field studies and lab tests support the hypothesis that antherozoids of ***Dawsonia longifolia*** (= *D. superba*; Figure 106) are dispersed by a splash mechanism. They found that females up to 1.5 m from males were fertilized, a distance only slightly less than the distance travelled by water drops released at 3.3 m above the splash cups.

Figure 106. ***Dawsonia longifolia*** male plant with splash cup. Photo by Allan Fife, with permission.

Andersson (2002) used a more sophisticated approach by making a video of splashes of rain on the splash platforms of the moss ***Plagiomnium affine*** (Figure 107). He discovered that a crown forms upon impact of water. Small droplets are propelled away from the rim of this crown. For this to be effective, the diameter of the drop should be 1 mm or less to permit the crown to form, a size common in most showers. Upon impact of the drop, the antheridia rupture. Water fills the capillary spaces between the antheridia and the paraphyses, permitting the spermatozoids to reach the bottom of the splash cup. When the crown forms, it incorporates water from the bottom of the splash cup and hence includes the spermatozoids. These entrapped spermatozoids are ultimately released from the splash cups as the small droplets propel away from the splash cups. Such droplets are known to travel more than 100 mm, fertilizing most of the females within an 80 mm radius.

Among the best known splash platforms among bryophytes is that of ***Marchantia polymorpha*** (Figure 20-Figure 21). But Duckett and Pressel (2009) inform us that the widely told dispersal story is not entirely correct. Traditional description since the accounting by Goebel (1905) has been that fertilization occurs when the archegoniophore stalks are still young and short, at which time the archegonial necks still point upward. The antheridiophores, developing first, tower over these, permitting sperm to travel downward by splashing or dripping during rainfall. But it is likely that the sperm actually disperse as they do in ***Conocephalum conicum*** (Figure 105), discharging into the air up to 15 cm above the antheridial heads (see Sperm Dispersal by the Bryophyte above). This can explain why both Parihar (1970) and Crum (2001) reported that the archegonia continued to be fertilized after the stalk elongated. Furthermore, when female thalli were placed in dye, the coloring reached archegonial heads in 30-60 minutes (Duckett & Pressel 2009), suggesting that capillary action and surface tension movement could carry the water and accompanying sperm from the antheridial splash cups upward to the archegonial heads and archegonia.

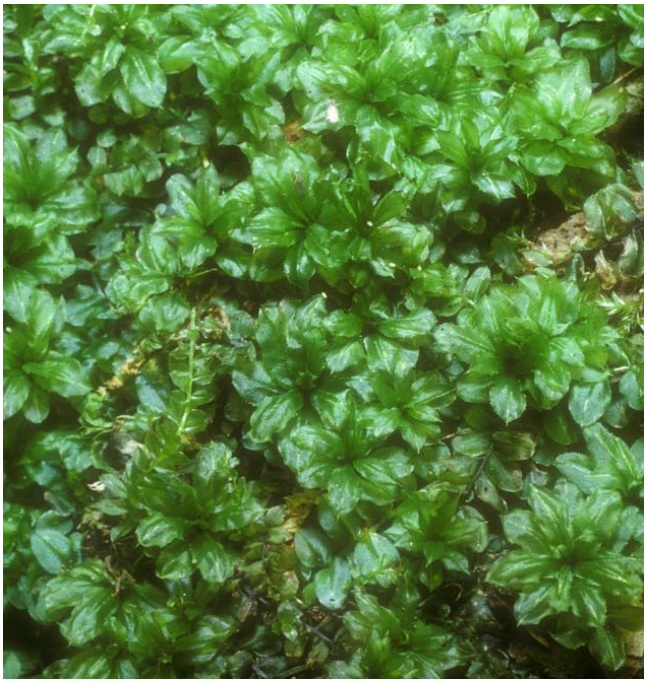

Figure 107. ***Plagiomnium affine*** showing splash platforms of male plants. Photo by Janice Glime.

The splash mechanism in the dioicous ***Fontinalis*** (Figure 108) requires a suitable location within a rapid stream. When female plants are elevated above the water and male plants or their rock substrate are obstructing flow to create splash, sperm may be able to go about 2 m (personal estimate based on distance between male plants and females with capsules) in a rocky stream. This takes advantage of the splashing of rapid water, whereas when the antheridia and archegonia are under water, the highly diluted sperm will be swept away, most likely never being able to enter the neck of an archegonium (Goebel 1905).

Figure 108. ***Fontinalis dalecarlica*** with immature, green capsules. This clump is located in a rapid stream where rocks are covered with this species. Photo by Janice Glime.

Invertebrate Dispersal

Clayton-Greene *et al.* (1977) reported on the use by Gayet (1897) of netting over ***Rosulabryum capillare*** to demonstrate that some outside force was needed for fertilization. With fine nets over the plants, fertilization failed, but when the netting was removed, fertilization occurred over distances of 2 m. Although this may suggest that invertebrates were denied access, hence being prevented from fertilizing the females, it does not eliminate the possibility of the netting affecting the splashing of raindrops.

As early as 1927, Harvey-Gibson and Miller-Brown found that the paraphyses (Figure 26) of both males and females in ***Polytrichum commune*** (Figure 109) exuded a mucilage, but that mucilage did not contain any sugars. Nevertheless, **oribatid mites**, **springtails** (**Collembola**), **midges** (**Diptera**), **leaf hoppers** (**Cicadellidae**), **aphids**, and **spiders** visited these structures and lapped up the mucilage. Their body parts carried the mucilage, and thus they might easily have carried the sperm. But this possibility seemed to be ignored by most bryologists until recently.

Figure 109. ***Polytrichum commune*** with capsules. Photo by David Holyoak, with permission.

Cronberg *et al.* (2006) experimentally demonstrated that **springtails** and **mites** were able to transport sperm over distances of up to 4 cm, but it is possible that under the right circumstances transport could be much farther. Rosenstiel *et al.* (2012) also described one of the more remarkable cases of sperm dispersal in the mosses ***Bryum argenteum*** (Figure 110-Figure 111) and ***Ceratodon purpureus*** (Figure 112). These species can have their sperm dispersed from male to female by the springtail ***Folsomia candida*** (Figure 112). Rosenstiel and coworkers showed that the springtails chose significantly more female mosses than male mosses in ***Ceratodon purpureus*** (Figure 113) and that their presence facilitated fertilization (Figure 114). This preference was supported by verifying that the volatile compounds differed between the two sexes in ***C. purpureus*** (Figure 115-Figure 116).

Figure 110. ***Bryum argenteum*** mixed females and males. Note the open brown tips where antheridia are located. Photo by George Shepherd, through Creative Commons.

Figure 111. ***Bryum argenteum*** perigonium, a collection of antheridia that attract invertebrates to facilitate transfer of sperm. Photo by George J. Shepherd, through Creative Commons.

Figure 112. Springtail ***Folsomia candida*** on ***Ceratodon purpureus***, possibly bringing sperm to the archegonia. Photo by Erin Shortlidge, with permission.

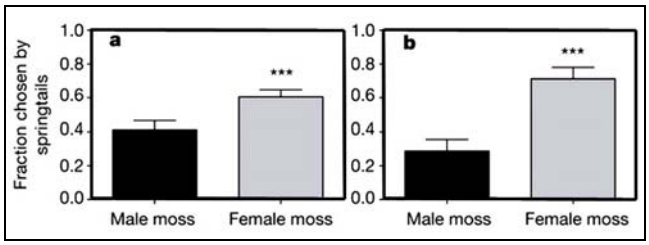

Figure 113. Visits to ***Ceratodon purpureus*** males and females by the springtail ***Folsomia candida***, a showing mean and error bars. n=24 assays, 491 springtails. b represents male vs female samples in an olfactometer; n=10 assays; ***P<0.0001. Redrawn from Rosenstiel *et al.* 2012.

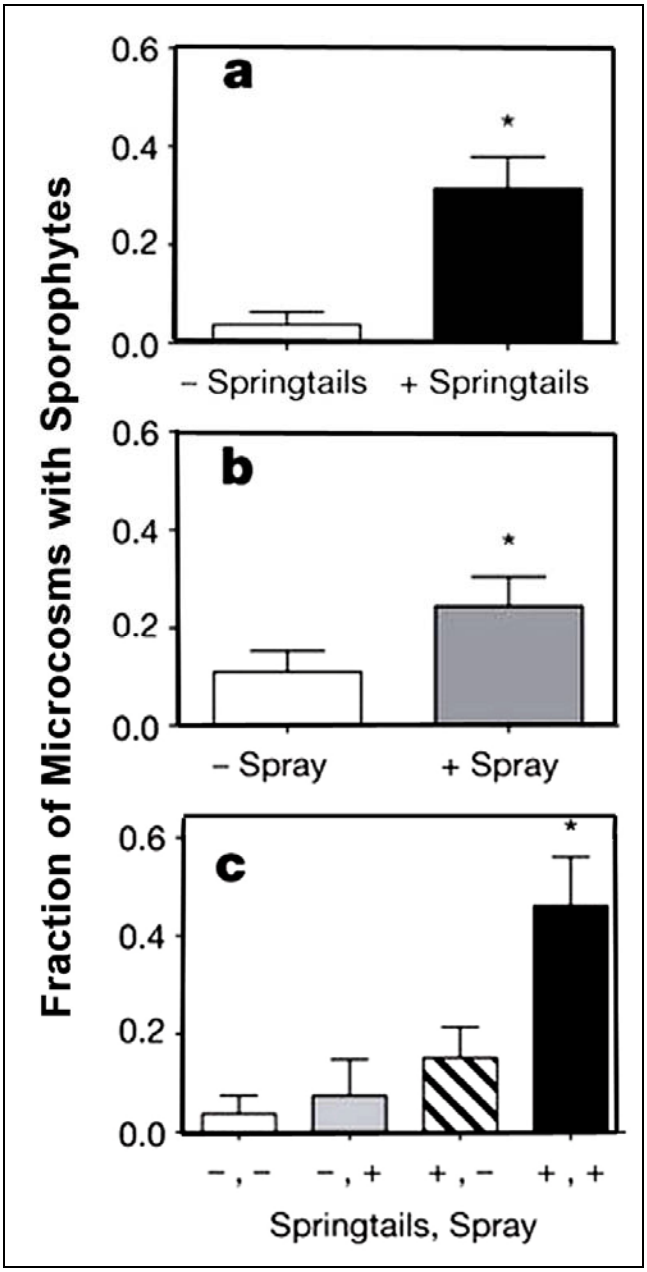

Figure 114. Effect of spray and the springtail ***Folsomia candida*** presence on sporophyte production in ***Ceratodon purpureus*** / ***Bryum argenteum*** microcosms, showing mean and error bars. + and – represent presence or absence of **springtails** or water spray; n=108 microcosms; *P<0.05. Redrawn from Rosenstiel *et al.* 2012.

Sperm Longevity

Few studies have included the life of the sperm or experimented with conditions necessary for their survival. It has always been assumed that sperm had a short life span and were unable to survive desiccation. However, Rosenstiel and Eppley (2009) experimented with sperm from geothermal populations of the **paroicous** (having reproductive organs beside or near each other) moss ***Pohlia nutans*** (Figure 117-Figure 118) and found that this is not the case, at least for this ubiquitous species. Sperm in this species were not affected by temperatures between 22 and 60°C and only showed increased mortality at temperatures above 75°C. Dilution also contributed to their mortality (Figure 119), suggesting that they might protect each other. Moreover, within their safe temperature range 20% survived for more than 200 hours (Figure 120). If this trait has been retained in a paroicous moss, we are likely to find some surprisingly tolerant and long-lived sperm in dioicous bryophytes.

Shortlidge *et al*. (2012) demonstrated that in ***Bryum argenteum*** (Figure 110-Figure 111), ***Campylopus introflexus*** (Figure 121), and ***Ceratodon purpureus*** (Figure 112) some of the sperm were able to survive environmental desiccation for extended periods of time. The tolerance seemed to be independent of both species and dehydration conditions. Furthermore, the addition of sucrose during drying improved their recovery. Despite the lack of variation among species, there was considerable variability among individuals within a species.

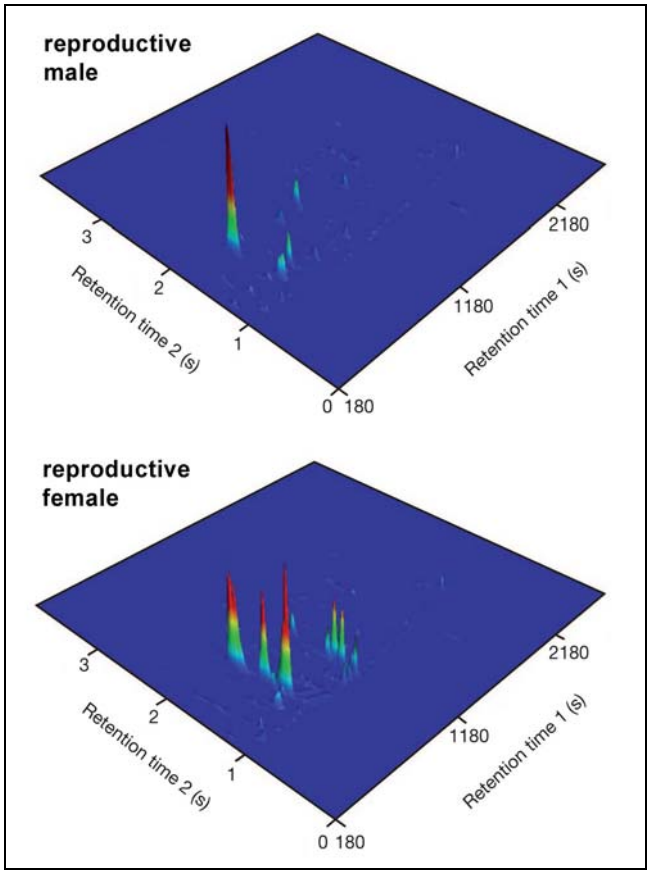

Figure 115. Comparison of profiles (two-dimensional GC3GC–TOFMS chromatograms) of volatile compounds in a male and a female shoot of reproductive ***Ceratodon purpureus***. Colors indicate relative measures of compound abundance; red indicates compounds that are greater than 50% of the largest individual peak area. Modified from Rosenstiel *et al.* 2012.

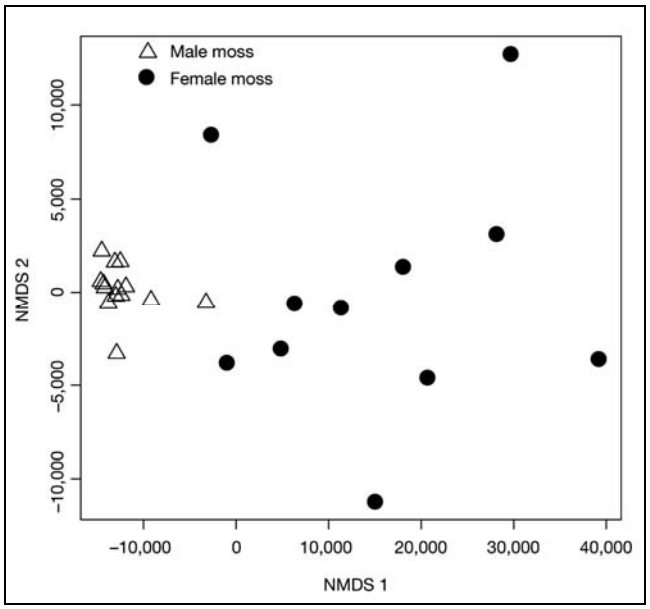

Figure 116. Differences in volatile gas composition from reproductive male and female individuals of the moss ***Ceratodon purpureus*** using non-metric multidimensional scaling (NMDS). This graph shows that there are significant sex-specific differences in VOC composition (P=0.001). Each symbol represents one individual moss plant. Modified from Rosenstiel *et al.* 2012.

Figure 117. ***Pohlia nutans*** plants showing apex where antheridia and archegonia occur together. Photo by Petri Kuhno, through Creative Commons.

Figure 118. ***Pohlia nutans*** in the Khibiny Mountains, Apatity, Murmansk. Photo by Michael Lüth, with permission.

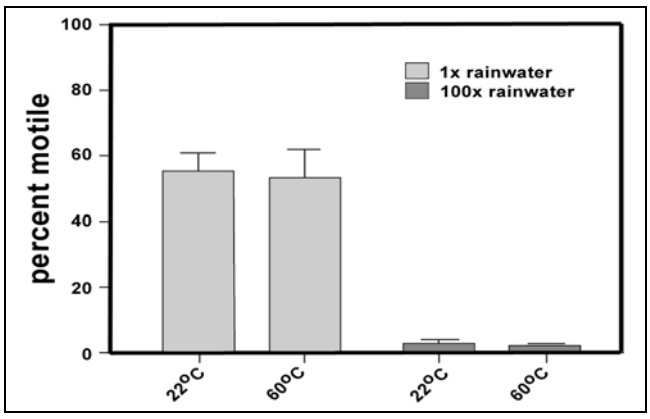

Figure 119. The mean percent of motile (live) ***Pohlia nutans*** sperm vs dilution in rainwater for 96 hours at 1x (no dilution) and 100x dilution at 22°C and 60°C. Redrawn from Rosenstiel and Eppley 2009.

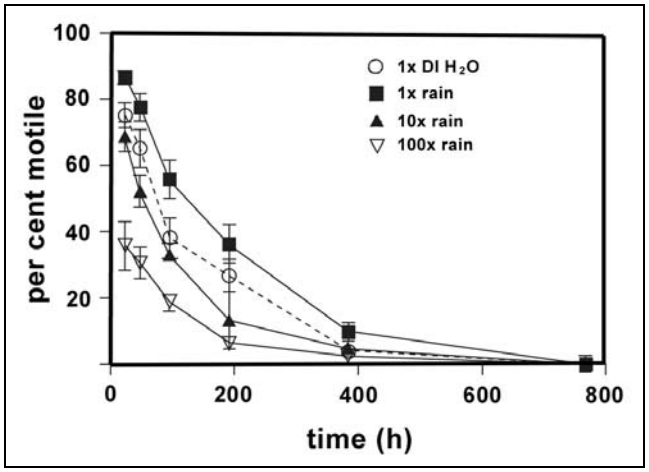

Figure 120. The percent of motile (live) ***Pohlia nutans*** sperm in 40 µl DI or rainwater as they diminish through time. Rainwater created a series of dilutions. Open circles, 1x DI H2O; filled squares, 1x rain; filled triangles, 10x rain; inverted triangles, 100x rain. Redrawn from Rosenstiel and Eppley 2009.

Figure 121. ***Campylopus introflexus*** with water drops. Such drops can greatly aid fertilization. Photo by Michael Lüth, with permission.

Stark *et al*. (2016) revealed that moss antheridia are desiccation tolerant. Noting that free-living sperm are partially desiccation tolerant, they hypothesized that the mature antheridia should also be tolerant. They further hypothesized that rehydration to partial turgor or full turgor before immersion in water is required for full recovery from the damaging effects of desiccation. They cultured ***Bryum argenteum*** until it produced mature perigonia with antheridia, then dried them slowly over ~36 hours, equilibrating them with 50% relative humidity. To test their hypothesis, they prehydrated them in a saturated atmosphere or rehydrated them in saturated media in a range of times from 0 to 1440 minutes. Following these treatments they immersed them in sterile water. When they were prehydrated for at least three hours before their immersion, the antheridia functioned like those of the controls that had not been dried. They found that prehydration did not improve on the recovery compared to rehydration. After three hours of rehydrating before immersion, the antheridia have full recovery.

Factors for Successful Fertilization

Multiple factors contribute to the successful fertilization of bryophytes, including sex expression of both sexes, distance to nearest mate, suitable sperm dispersal mechanism (see above), and appropriate weather conditions, especially temperature and water availability. But assessing the relative importance of multiple factors in a single study has rarely been done. Rydgren *et al.* (2006) used generalized linear modelling (GLM) to assess three factors for the dioicous perennial moss ***Hylocomium splendens*** (Figure 122). They found that most sporophytes (up to 85%) were located within 5 cm of a male, with the longest distance measured being 11.6 cm. But year was an even better predictor of success than distance, attesting to the importance of weather and probably past history, although female segment size as well as distance to closest male were both highly significant. They emphasized the importance of using multiple factors as predictors of reproductive success.

Figure 122. ***Hylocomium splendens*** with capsules. This dioicous species forms colonies with only one sex, hence not producing sporophytes from fertilization by its neighbors. Photo by Janice Glime.

Bisang *et al.* (2004) took the distance question further to see if increasing the availability of mates would increase the success of fertilization. They selected two dioicous pleurocarpous mosses, ***Hylocomiadelphus triquetrus*** (=*Rhytidiadelphus triquetrus*; Figure 123) and ***Abietinella abietina*** (Figure 124) and transplanted individual male shoots into non-sporophyte-bearing female colonies.

Figure 123. ***Hylocomiadelphus triquetrus*** with capsules. Photo by David T. Holyoak, with permission.

Figure 124. ***Abietinella abietina*** in Europe. Photo by Michael Lüth, with permission.

They determined that the number of sporophytes produced depended on the distance from the male mate, *i.e.* spermatozoid source. Furthermore, differences between species were evident, with ***Hylocomiadelphus triquetrus*** (Figure 123) being more successful than ***Abietinella abietina*** (Figure 124). They estimated that in ***H. triquetrus*** the maximum fertilization distance was 34 cm, considerably more than the 3-6 cm previously reported (Riemann 1972). Bisang *et al.* (2004) found that in ***H. triquetrus*** the number of female reproductive branches significantly affected the number of sporophytes. By contrast, in ***A. abietina*** the number of female reproductive branches per plot did not affect sporophyte production. Both species were mate limited.

As one might expect, for both species, when male plants were uphill from female branches, the number of sporophytes was significantly greater than when their positions were reversed, presumably because the sperm were able to travel farther, possibly carried or splashed down the slope by rain (Bisang *et al.* 2004). In ***Hylocomiadelphus triquetrus*** (Figure 123), a mean of 40 sporophytes per plot (n=25 plots) occurred on sloping substrata compared to 22 on horizontal surfaces. Upslope distances for this species had a mean of 6.2 cm above transplanted males (max=16 cm) and 10.2 cm downslope (max=34 cm). In ***Abietinella abietina*** (Figure 124), the downslope distances (mean=3.3 cm) were also significantly greater than upslope (mean=1.9 cm) distances, but in this species both the distance travelled and the successful production of sporophytes (mean=2.4 per plot) were considerably less than in ***H. triquetrus***. Genes matter.

Figure 125. ***Anomodon viticulosus*** in a seepage area of England. Photo by Janice Glime.

Granzow de la Cerda (1989) demonstrated movement of sperm in seepage water by transplanting male ***Anomodon viticulosus*** (Figure 125) to a position at least 25 cm above female plants, a move that resulted in production of sporophytes.

Multiple Fertilizations

Wyatt *et al*. (2022) used isozyme markers to estimate incidence of multiple paternity in the dioicous, haploid, leafy liverwort ***Porella platyphylloidea*** (Figure 126). They found that 12.6% of the plants were non-sex-expressing, 13.4% were females without sporophytes, 31.9% were males, and 42% were females with sporophytes. The sex ratio was female biased at 1.74:1. Using the criterion that only females with two or more sporophytes with different genotypes had experienced multiple paternity, they estimated 57% of female plants had been fertilized more than once. Plants on the lower parts of trees were significantly larger, but the larger size of females seemed to account for this difference.

Figure 126. ***Porella platyphylloidea***, a species in which a female can be fertilized by multiple males. Photo by Suzanne Cadwell, through Creative Commons.

Summary

The liverwort genus ***Sphaerocarpos*** was the first genus in which sex chromosomes were known in plants. Many bryophytes possess sex chromosomes (**X** & **Y** chromosomes, or designated **U** & **V** to refer to their haploid condition) which may play a role in sex

determination. Bryophytes can be **monoicous** (bisexual) or **dioicous** (unisexual). Gametangia in monoicous bryophytes can be **autoicous** (♂ & ♀ gametangia in separate clusters), **paroicous** (♂ & ♀ gametangia in separate groupings but one cluster), or **synoicous** (♂ & ♀ gametangia intermixed in same cluster). **Monoicy** may have arisen through **hybridization** and **polyploidy**. Transitions from monoicy to dioicy and vice versa have happened multiple times. There seem to have been more changes from monoicy to dioicy than the reverse in mosses, whereas the opposite was the case in hornworts, but this pattern appears to depend on those taxa included in the study and is not a settled relationship. McDaniel *et al*. suggested that dioicy works best when there are advantages to both sexes for being separate.

At least some antheridia can tolerate desiccation, but survival is improved by rehydration before submersion. Sperm dispersal begins with bursting of the antheridium, often accompanied by movement with surface tension of water drops. In thallose liverworts, sperm are often expelled explosively into the air. Sperm dispersal is usually accomplished by movement through a water film or by splashing and is sometimes aided by gravity. But some species have their sperm dispersed by invertebrates, including insects and mites. Dispersing sperm are known to survive as much as 200 hours and travel distance is known up to 230 cm. Travel distance and weather seem to be the most important factors in determining the success of fertilization in bryophytes.

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CHAPTER 3-2
SEXUALITY: SEX RATIO AND SEX EXPRESSION

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Figure 1. ***Marchantia polymorpha*** developing archegoniophores and antheridiophores on separate thalli. Photo by Bob Klips, with permission.

Sex Ratio

We tend to expect the number of males and females to be about equal (Figure 1), as they are in humans, but many plants and animals have not evolved that way. In bryophytes, it has seemed that mature populations of dioicous species were typically female-biased (Bisang & Hedenäs 2005), and this bias is often huge (but see When Males Are Dominant below). Sex ratios are likely to affect fertilization and thus sporophyte frequency. For example, in ***Syrrhopodon texanus*** (Figure 2) in the USA central plains, males are very rare (Reese 1984). However, wherever males are found, there are also females bearing sporophytes. These sex ratio imbalances can result from a number of factors, including developmental factors, age, environment, weather, neighbors, and genetic factors.

Figure 2. ***Syrrhopodon texanus*** in North Carolina, USA. Photo by Janice Glime.

The Bryophyte Female Bias

Stark (2002) reports, based on literature values, that 20 out of 30 species of dioicous bryophytes in those reports have a female bias; 5 have a male bias, and the other 5 seem to have no bias. Bisang and Hedenäs (2005; Bisang, pers. comm. December 2014) reviewed the expressed sex ratios in 143 taxa of dioicous bryophytes (89 mosses, 54 liverworts) based on their own studies and literature data. They used both herbarium specimens and field patches as one category (1) and field studies of individual shoots or thalli (2) as a second. Their study provides us with a cautionary warning that methods can skew the study. They found that for category 1, 85% had a female bias, whereas for category 2, 82% had a female bias. In herbarium studies, the exact bias may be slightly obscured by the tendency of bryologists to collect plants with capsules whenever possible. This is further complicated by the clonal nature of bryophytes, so that it is likely that one small patch is all one clone.

Spore Sex Ratios

In a **dioicous** species, the expectation for a **sporogenous** (giving rise to spores) cell at the onset of meiosis is that it will have one set of chromosomes containing a male chromosome and one set containing a female chromosome. If all proceeds normally during meiosis, a sporogenous cell will produce 4 daughter cells, 2 female and 2 male. But often things do not proceed "normally."

Spore sex ratio has been examined in only a few species so far, by means of cytological evidence (Allen 1919; Newton 1972) or by cultivating plants from spores to sexual maturity (Allen 1919; McLetchie 1992; Shaw & Gaughan 1993; Shaw & Beer 1999; Stark *et al.* 2010). Newton (1972) and Allen (1919) argued for unbiased spore sex ratios in ***Plagiomnium undulatum*** (Figure 4) and ***Sphaerocarpos donnelli***, based on segregation patterns. Also Stark *et al.* (2010) recounted a 1:1 spore sex ratio in ***Bryum argenteum***, while ignoring the portion of late-germinating spores. Large fractions of non-germinated spores are also reported for the species investigated in the other cultivation studies, which makes it difficult to assess the actual spore sex ratios in these. This also holds true for the study of the meiotic sex ratio variation in the moss ***Ceratodon purpureus*** (Figure 3), using a PCR method (Norrell *et al*. 2014). Spore viability varied strongly among sporophytes (0.04 to 0.69) in 9 subsamples each from 11 sporophytes; overall, 63% of the spores did not germinate. Among the germinated spores, the sex ratio at the completion of meiosis was variable, more often female-skewed (proportion of males 0.17-0.72, overall mean 0.41), but not related to spore viability. In contrast, McDaniel *et al*. (2007) found that the EC-NY population cross of ***Ceratodon purpureus*** had a male-biased sex ratio. They suggested that this was caused by lethal genetic interactions between the sex-linked loci and those of the pseudo-autosomal loci. Nothing like having your genes fight with each other!

While most of the attempts to reveal spore sex ratio so far included easily cultivated ruderals that rapidly express sex in the laboratory, Bisang *et al.* (2017) recently investigated the rarely sexually reproducing perennial dioicous moss ***Pseudocalliergon lycopodioides*** (Figure 8). They used single-spore cultures from field-collected sporophytes, and a molecular sex-associated marker to determine the sex of individual sporelings. They achieved a near-complete or complete spore germinability. In line with cytological evidence in the species mentioned above, spore sex ratio was balanced. However, it differed strongly from the female-skewed adult genetic sex ratios observed in the regional natural populations where the sporophytes were collected, as well as from the sex ratio in the European population established on the basis of a herbarium collection survey (Bisang *et al.* 2013; see also below, Genetic vs Expressed Adult Sex Ratio).

Provided that the observed sex ratios in ***Ceratodon purpureus*** (Figure 3) correspond to the actual sex ratios in the entire spore population, Norrell *et al.* (2014) may conclude that the noted variability in viability and sex ratio is due to genetic variations within populations. As spore viability and sex ratio were not related, factors other than **sex ratio distorters** (cytoplasmic element such as infection may replace nuclear gene as sex-determination mechanism; see Taylor 1990) may account for sex ratio variation. In this case, and in the case of even spore sex ratios as in ***Drepanocladus lycopodioides*** (Figure 8) that differ from adult sex ratio biases, other possible causes need to be explored, for example sexual dimorphism in life histories or in eco-physiological requirements, which selectively favor females. Norrell *et al.* (2014) further suggested that the sex ratio might be affected by genetic conflict over meiotic segregation and that this affects the fitness variation in the species.

Figure 3. ***Ceratodon purpureus***, a species in which the sex ratio differs among populations. Photo by Michael Lüth, with permission.

Genetic vs Expressed Adult Sex Ratio

Are females truly more abundant, as suggested when counting populations or individuals with sexual structures? Even in female-biased populations male bryophyte plants can be more abundant among non-sex-expressing plants than many counts of plants forming sexual organs would indicate. It is crucial to separate an observed sex ratio pattern into its two elements, namely 1) genetic sex ratio, and 2) differential sex expression among sexes. Knowledge of both components is necessary to understand the underlying mechanisms of sex ratio variation, and to determine when and how observed sex ratio biases are established during the life cycle.

Genetic sex ratios have been studied in relatively few bryophytes to date, and both agreement and differences exist between phenotypically expressed and genetic sex ratios. Newton (1971) pioneered the genetic approach by comparing plants of ***Plagiomnium undulatum*** (Figure 4) with large **heterochromatin bodies** with those having smaller bodies, using heterochromatin body size as a sexual marker. She found that among 239 non-expressing plants examined (34 gatherings) the ratio was 6.5 females to 1 male, but when only the 156 sex-expressing plants in bisexual populations were considered, the ratio was only 3.9♀:1♂. Newton concluded that using only fertile plants underestimates the abundance of male plants. She determined that the non-expressing males of ***Plagiomnium undulatum*** were rarer than non-expressing females, but not as rare as in the expressing male to female ratio. Using this ratio change, Newton suggested a lower sex expression rate for males than for females. This could also suggest a narrower range of environmental conditions in which sex expression is able to occur. Newton (1972) demonstrated in ***P. undulatum*** that the environmental conditions for production of antheridia were more restricted than those needed for production of archegonia. However, she could find few differences between the sexes for the environmental parameters she tested. In at least some taxa male plants may be less fit, surviving in a narrower range of conditions than do females. The balance of conditions is complicated in bryophytes by the fact that antheridia typically take longer to develop than do archegonia, thus requiring different conditions to initiate them and needing to survive for a longer time under a greater range of conditions.

Figure 4. ***Plagiomnium undulatum***, a species where antheridial expression requires a narrower set of environmental conditions than those required for archegonial expression. Photo by David T. Holyoak, with permission.

Cronberg *et al.* (2003) used electrophoresis to identify **genets** [genetic individual that develops from the zygote and produces **ramets** (any physically and physiologically independent individual plants, whether sexually produced or derived by vegetative reproduction) of the same genotype vegetatively] in ***Plagiomnium affine*** (Figure 5), reducing the number of plants with unknown sex to 10%. At the ramet level, the overall sex ratio had a slight female bias, but at the genet level it was close to 1:1. Cronberg *et al.* (2006) found a sex ratio in five plots of ***Hylocomium splendens*** (Figure 27) to be female biased at the ramet level (2.6 female to 1 male), but it was male biased at the genet level (1 female to 3 males).

Figure 5. ***Plagiomnium affine***, a species that invaded European forests multiple times. Photo by Hermann Schachner, through Creative Commons.

More recently, cultivation approaches and novel techniques of molecular sex markers have been used to reveal genetic sex ratios (see below, Sex Expression and the Shy Male Hypothesis).

Causes of Female Bias

There have been many efforts to explain this female bias (Longton & Schuster 1983; McLetchie & Puterbaugh 2000; Crowley *et al.* 2005; Bisang *et al.* 2006; Rydgren *et al.* 2010; Stark *et al.* 2010; Horsley *et al.* 2011, and many more), to date usually the expressed female bias. In fewer cases the underlying genetic sex ratio has been approached. We ask, if it is real, what evolutionary forces drive a female bias? Henceforth we present a number of studies that have examined bryophyte sex ratios, its variation, and discuss possible explanations for the observed patterns.

Sex Expression and the Shy Male Hypothesis

As already mentioned, our methods so far are usually indirect, such as using capsules, perichaetia, and perigonia to assess sex, and few studies involve a direct count that provides a ratio under field conditions. In most cases to date, we are unable to determine the sex of plants not producing sexual organs. Several factors could cause a disproportionate phenotypically expressed sex ratio. Might males take more time to develop and express sexual maturity? Or is the unbalanced observed sex ratio merely a consequence of differential sex expression, as Newton (1971) suggested for ***Plagiomnium undulatum*** (see above; Figure 4)?

Hedenäs *et al.* (2010) examined the question of sex ratio in non-expressing females of ***Pseudocalliergon trifarium*** (=***Drepanocladus trifarius***) (Figure 6) using a new technique of genetic sex-targetting markers. They estimated the European population sex ratio to be 1.93:1 (female:male) (Hedenäs *et al.* 2010). There were no

significant differences among expressed, non-expressed, and population sex ratios, and thus no differences in expression rates between the sexes.

Figure 6. ***Pseudocalliergon trifarium***. Photo by Andrew Hodgson, with permission.

The "**shy male hypothesis**" suggests that males express sex less frequently than do females (Stark *et al.* 2010). Those individuals that have no sexual structures are often referred to as "sterile," but sterile implies that they are incapable of producing sexual organs. The preferable terminology, therefore, is "non-expressing" or "non-sex-expressing" (Bowker *et al.* 2000).

Using ***Bryum argenteum*** (Figure 7), Stark *et al.* (2010) tested both the "shy male" hypothesis and the hypothesis that sex ratios of sporelings are biased (for the latter, see above, Spore Sex Ratios). They used both sex-expressing and non-expressing collections from the field and shoots grown from spores in the lab. Field collections revealed a greater than 80% female bias among 154 collections in the USA, with male expressions being even more rare (as little as 2%) in arid habitats of the Mojave Desert and California chaparral. They grew non-expressing shoots from mixed-sex populations until they reached sexual expression and found that the ratio of males to females did not differ significantly from that of sexually expressing field populations. Hence, the "shy male hypothesis" lacks support in ***Bryum argenteum***. Populations grown in the lab from spores, on the other hand, had a 1:1 sex ratio. This leads us to the conclusion that in this species there are factors between sporeling and mature gametophyte that differentially affect the two sexes.

Using herbarium samples from a wide geographic range, Bisang and Hedenäs (2013) assessed the sex ratio in expressing and non-expressing ***Pseudocalliergon lycopodioides*** (Figure 8), using a sex-associated molecular marker to identify the sex of non-expressing plants. They determined that the true genetic population sex ratio (non-expressing plants included) was the same (2.6:1 female bias) as that when non-expressing plants were not included, thus refuting the "shy male" (non-expressing male) hypothesis also in this species. This distinct female genetic sex ratio bias in the adult population differs from the balanced spore sex ratio (see above, Spore Sex Ratios; Bisang *et al.* 2017). As in ***Bryum argenteum*** (Figure 7), biased population sex ratios in ***Pseudocalliergon lycopodioides*** seem to arise at life cycle stages after spore germination. In any case, simply refuting the "shy male" hypothesis in a species does not answer our question regarding the unequal adult sex ratio.

Figure 7. ***Bryum argenteum***, a species with 80% females in montane and disturbed habitats in western USA and up to 98% females in native lowland desert and chaparral, but with a 1:1 ratio of plants grown in the lab from spores. Photo from India Biodiversity Portal, through Creative Commons.

Figure 8. ***Pseudocalliergon lycopodioides***, a moss with a 2.6:1 female-biased sex ratio among both non-expressing and fertile plants. Photo by David T. Holyoak, with permission.

Eppley *et al*. (2018) set out to understand the origin of biased sex ratios in ***Ceratodon purpureus*** (Figure 3). They started with equal populations of male biased and female biased sex ratios to test the hypothesis that male-biased populations would become female-biased and that stress could increase the transition. After 18 months there was no significant change in the originally female-biased populations. However, the male-biased populations became more female. This provides concrete evidence that sex ratio change can occur during the gametophyte generation. Furthermore, sporophytes were produced only in female-biased populations. Eppley and coworkers suggested that females in male-biased populations may have invested energy in producing ramets, thus increasing the number of females. They noted that these results, combined with previous work, indicate that both the gametophyte and the sporophyte operate in determining the sex ratio in ***Ceratodon purpureus***. Yes, for than one mechanism exists in a single species!

Brzyski *et al*. (2013) cultivated ***Marchantia inflexa*** (Figure 9) from different environments. In contrast to ***B. argenteum*** (Figure 7), they found that in the roadside habitat the males were 4.7 times more likely to express sex than were females, despite the better growth for females in that habitat.

Figure 9. ***Marchantia inflexa*** thallus, a liverwort where males and females have different environmental stressors. Photo by Scott Zona, with permission.

Germination Patterns and Spore Mortality

But if we examine what might explain such a biased expressed ratio, we know that meiosis in a dioicous plant such as ***Sphaerocarpos texanus*** (Figure 10), known to have X and Y chromosomes (now called **U** and **V**), should result in an equal number of male and female spores, as found in *Bryum argenteum* (see above). Nevertheless, also McLetchie (1992) found numbers that support female dominance in sex expression of the liverwort ***Sphaerocarpos texanus***. In both the field and in culture, ***Sphaerocarpos texanus*** produces a greater number of pure female clumps, followed by mixed sexes and then pure males. McLetchie interpreted this to mean that males have a lower survival rate than females, both before germination and while growing. The first loss of males, leading to an unequal germination rate, assumedly results from unequal survival and germination capability of spores. This abortion can start immediately after meiosis (Figure 11). These differences can result from a difference in allocation of resources to male and female spores, leading to reduced viability and germination success in the males (McLetchie 1992). McLetchie (1992, 2001) also found that there was a sex-specific determination at germination in ***Sphaerocarpos texanus***, with more female than male germinations. Could it be, as suggested by Schuster (1983) for ***Sphaerocarpos*** (Figure 10), that small spores become male plants and that their poor nutrient conditions as spores give them an inferior start in life, causing them to die soon after producing sperm?

McLetchie (1992) suggests that even after germination, males may have inferior competitive ability or be more susceptible to unfavorable environmental conditions. In mixed clumps, females may provide added protection that permits more males to survive, and both benefit from the increased sexual reproductive success.

Figure 10. ***Sphaerocarpos texanus*** showing female population. Photo by Michael Lüth, with permission.

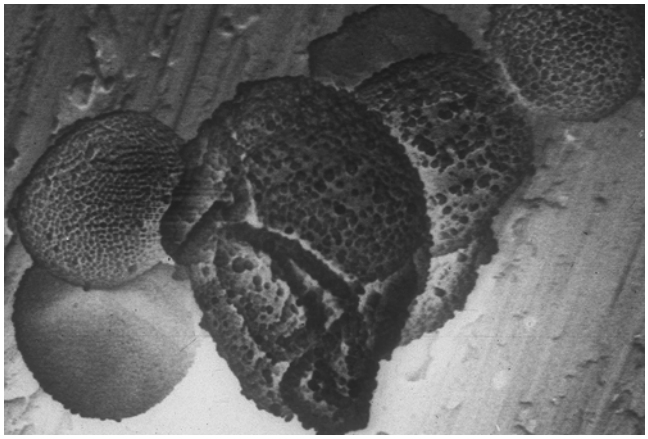

Figure 11. SEM image of spores of ***Fontinalis squamosa*** showing abortion of two spores in the tetrad. Photo by Janice Glime.

Even where spores are retained in tetrads and thus travel together, as in ***Riccia*** (Figure 12), females of ***Riccia frostii*** (Figure 13) outnumber males (Pettet 1967). In this case, at least one factor is greater mortality of males under conditions of rapid desiccation. In ***Cryptothallus*** (Figure 14), where sex is determined by sex chromosomes, females outnumber the males 5:1 (Shaw 2000). It appears in this genus that some spores of the tetrad are inviable.

Figure 12. ***Riccia sorocarpa*** spore tetrads ready for dispersal. Photo by Des Callaghan, with permission.

It would be helpful to know the number of males and females at all life cycle stages to elucidate further the causes of biased sex ratios. Modern molecular techniques (see *e.g.* Pedersen *et al.* 2006; Bisang *et al.* 2010; Bisang & Hedenäs 2013) or cultivation methods (*e.g.* Stark *et al.* 2010) make this possible, albeit very time-consuming.

Figure 13. ***Riccia frostii***. Photo by Rosemary Taylor, with permission.

Figure 14. ***Cryptothallus mirabilis*** producing sporophytes from its subterranean mycorrhizal thallus. Photo by Michael Lüth, with permission.

Environmental and Geographic Differences

Bell (1980) stressed the importance of life history in understanding evolutionary theory. Although he focussed on animals, his principles can apply to bryophytes. He posited that "once reproductive costs are introduced, reproduction will be optimized rather than being merely maximized. The 'survival cost' is the decrease in the rate of adult survival which accompanies a given increase in fecundity." Sex ratio can be influenced by these life history principles.

In the Bisang and Hedenäs (2005) study, expressed sex ratio variation not only occurred among species, but also within species. The latter variation was related to geographic region, elevation, year, substratum, and plant/clone maturity. It was interesting that Bisang and Hedenäs did not find a direct relationship between the sex ratio and the proportion of sporophytic samples or shoots across species. This suggests that the bryophytes may have evolved to optimize the sex ratio for the conditions where they grow. But Bisang and Hedenäs contend that the "data do not support a generalization that the most strongly female-biased sex ratios among dioicous bryophytes occur in 'extreme environs.'" Rather, they suggest that phylogenetic history may explain at least some of the species-wide sex ratios better than current habitat conditions (Bisang *et al.* 2014).

It is likely that both phylogenetic history and extreme environments play a role in determining sex ratio, depending on the species and location. Stark *et al.* (2001) provide supporting data that the greatest departure from a 1:1 sex ratio in mosses is seen in the extreme desert environment (high temperatures and extreme drought) and always leads to male rarity. In fact, there are four species in the Mojave desert that are known there only from females (Llo Stark, pers. comm. 28 March 2023).

In ***Marchantia inflexa*** (Figure 9), habitat seems to play a strong role in the performance of the sexes (Brzyski *et al.* 2013). Females had both higher growth rates and more asexual reproduction among road-collected plants whereas males tended to have better growth and asexual reproduction (but not significantly) in river-collected plants.

Environmental differences can occur even within short distances. Although the sexes of ***Marchantia inflexa*** (Figure 9) are spatially separated within populations, they overlap in habitat use and their distributions are not correlated with an environmental gradient (Fuselier & McLetchie 2004). Males collected on the island of Trinidad tend to occur in a wider range of light conditions than do females (Fuselier & McLetchie 2002, 2004). Groen *et al.* (2010a), using five locations in Trinidad, found that males in ***M. inflexa*** occur where there is more tree-canopy openness than that found in locations where females occur. Groen and coworkers (2010a, b) also found that males of this species had lower chlorophyll *a* to *b* ratios compared to females, the opposite of what one would predict for plants in more open areas. On the other hand, in populations from Grangier County, Tennessee, USA, Fuselier (2004) found that laboratory-grown and field-grown males showed little difference in their responses to moisture and light levels.

Fuselier and McLetchie (2002) tested the influence of selection on asexual and sexual fitness components in ***Marchantia inflexa*** (Figure 9) using a field study on natural selection. They grew replicates of female and male genotypes from Trinidad under two different light environments in a greenhouse. Not only did they find that the timing for the onset of asexual reproduction and the determination of size of the plant during early development were under sex-specific selection in low light, but for females, there was also an apparent cost for plasticity in the timing of their asexual reproduction in high light. Selection pressures favoring asexual fitness tended to favor monomorphism (both sexes looked the same) rather than sexual dimorphism. But if the female morphology was expressed, then selection acted on sexual fitness rather than on morphology, hence favoring females.

McLetchie and Puterbaugh (2000) also explored the relationship of male and female numbers, using the thallose liverwort ***Marchantia inflexa*** (Figure 9) in Trinidad. They found that among 209 individual patches of this liverwort along a stream, 83% were not expressing sexual characters at all, 9% had both male and female thalli, and the remainder were 4% all male and 4% all female. In bisexual patches, the proportion of males ranged 22-80%. This is hardly an image of sexual dominance by either sex and is one of the examples of infraspecific variation mentioned by Bisang & Hedenäs (2005). Furthermore, when gemmae from non-sex-expressing field collections were planted, the resulting ratio of plants was 10 females to 8 males.

But in those 209 patches of ***Marchantia inflexa*** (Figure 9), the role of environment in affecting sex expression began to emerge (McLetchie & Puterbaugh 2000). Those patches with the lowest canopy openness, *i.e.* less light, exhibited less sex expression. And, growth patterns of male and female plants differed. The female plants grew faster and produced more meristematic tips, but they had lower levels of asexual reproduction (gemmae) than did the male plants. In fact, asexual reproduction was negatively correlated with the number of meristematic tips (see also 3.4, Reproductive Trade-off). This suggests that the female plants might be more competitive through more rapid growth and soil coverage, but male plants might have greater ability to disperse and occupy new ground. And, this behavior could lead to large numbers of single-sex patches and biased sex ratios among mature, sex-expressing plants.

In the Mojave Desert of southern Nevada, USA, the female-biased desert moss ***Syntrichia caninervis*** (Figure 15) is a dominant moss in the blackbrush (*Coleogyne ramosissima*) community. Bowker *et al.* (2000) demonstrated that microhabitat can play a major role in sex expression in this xerophytic dioicous moss. On one 10-ha site, sex-expressing female ramets dominated males 14:1 (890 samples). In this harsh environment, it is not surprising that 85% of the ramets did not show sexual expression during their entire life span. Demonstrating responses similar to those of ***Sphaerocarpos texanus*** (Figure 10), ***Syntrichia caninervis*** showed more sexual expression in shaded sites, where there was more moisture and plants were taller. Predictably, ramet height was positively correlated with soil surface moisture in more exposed sites. Male ramets were restricted to shaded sites, whereas female ramets and populations occurred in both shaded and exposed locations. There were no mature sporophytes in the ramets sampled, and only 3% of the populations overall had any mature sporophytes. Among the reasons for the success of females are their greater ability to produce biomass and to produce new protonemata and shoots from detached leaves that have experienced desiccation (Figure 16-Figure 17), an inevitable event in this habitat (Stark *et al.* 2005). In this case it appears that there is a strong selection pressure, based on available moisture, against males in some environments and that females are more tolerant of exposed, desiccating conditions.

Figure 15. ***Syntrichia caninervis***. Photo by John Game, through Creative Commons.

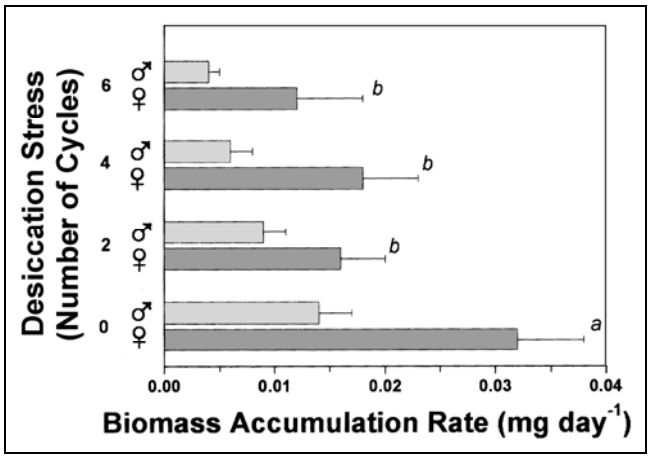

Figure 16. Effect of varying numbers of desiccation cycles on biomass accumulation rates in males and females of ***Syntrichia caninervis*** leaves. Values are means (n=20) ± 1 SE. Cycles with different letters are significantly different (P<0.05, Tukey's multiple comparison). Graph modified from Stark *et al.* (2005).

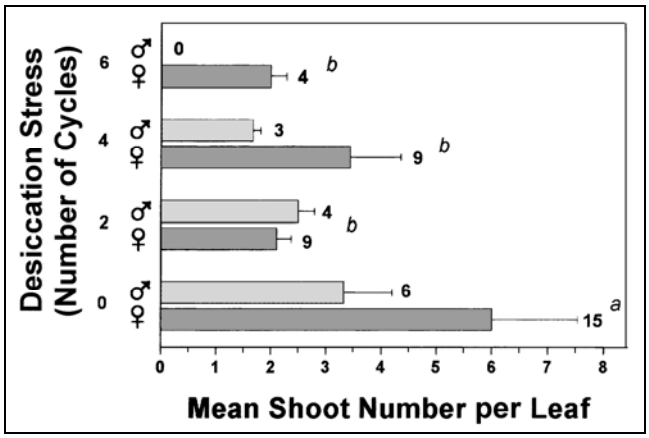

Figure 17. Shoot production from regenerating leaves of males and females of ***Syntrichia caninervis*** subjected to varying numbers of desiccation cycles. Values are means (n=20) ± 1 SE. Cycles with different letters are significantly different (P<0.05, Tukey's multiple comparison); data were log-transformed before analysis. Graph modified from Stark *et al.* (2005).

Sex-expressing males of ***Syntrichia caninervis*** (Figure 15) are restricted to higher elevations in the Mojave Desert where they are tucked under shrubs (Stark *et al.* 2005). Female plants, on the other hand, have no such habitat restriction and are relatively widespread along the elevational gradient. Whenever only one sex is expressed, it is always the female. Stark *et al*. (2005) found that the greatest stress results from rapid drying cycles (Figure 16). The plants need 72 hours to deharden after a gradual drying event. In their desert habitat, they experience 40-70°C temperatures in a dry condition, but may experience 30-40°C while still hydrated. Differential abilities to handle such stress can have severe effects on sex ratios.

Blackstock (2015) investigated sex expression rate, sporophyte frequency, and sex ratios of the dioicous liverwort ***Frullania tamarisci*** (Figure 18) in western Britain, comparing woodland populations with exposed coastal colonies. Whereas the former were highly fertile, the coastal population exhibited a distinct female sex ratio bias, spatial segregation of the sexes, and male scarcity, which appear to limit sporophyte formation.

Figure 18. ***Frullania tamarisci***, a species in which habitat affects the sex ratio. Photo by Hermann Schachner, through Creative Commons.

As seen in the moss genus ***Macromitrium*** (Figure 19), both geographic and ecological differences are present (Une 1985). Dwarf males (see Chapter 3-3, Dwarf Males, in this volume) of the isosporous species ***M. gymnostomum*** and ***M. japonicum*** are widely distributed in Japan, whereas normal males are rare and occur only in low altitudes and latitudes on the Pacific Sea side of Japan. Experimental results suggest that this difference is due to suppression of growth of males at low temperatures, whereas females and dwarf males are less affected by the cold.

Hassel *et al*. (2005a) compared mountain and lowland populations of ***Pogonatum dentatum*** (Figure 20) in Fennoscandia. They found differences in age of maturation, with females in the lowlands producing spores in their second year, whereas those in the mountains required three years. Nevertheless, both populations produced sex organs in the second year.

Figure 19. Neotropical ***Macromitrium*** sp. with capsules. Photo by Michael Lüth, with permission.

Fisher (2011) examined differences between sex ratios at the edges vs the centers of distributions in ***Syrrhopodon involutus*** (Figure 21). In this species, she found that female sex expression was significantly lower at the margins than in central areas of the species complex. Furthermore, the margins had a higher proportion of non-sex-expressing individuals. On the other hand, the proportion of male-expressing plants did not differ significantly between marginal and central areas. Nor did the percentage of female-expressing successfully producing sporophytes plants differ between margins and the centers of distribution. Fisher concluded that this indicates the availability of males constrains sporophyte production for this species in both the margins and the centers of distribution. Could it also mean that the two sexes are more likely to differ genetically on the margins?

Figure 20. ***Pogonatum dentatum*** in Norway. Photo by Michael Lüth, with permission.

Figure 21. ***Syrrhopodon involutus***. Photo by Jan-Peter Frahm, with permission.

The only study so far that explores the association between genetic adult sex ratio and environmental factors was conducted with the wetland moss ***Pseudocalliergon trifarium*** (Figure 6), a species that rarely produces sexual structures or sporophytes (Bisang *et al.* 2015). In a total of 277 shoots representing 214 locations, Bisang and coworkers determined sex using a female-targetting molecular marker. They found that the sexes did not differ in shoot biomass. The sexes were randomly distributed and environmental factors associated with the localities of the two sexes did not differ. Nevertheless, the sex ratio had a strong female bias of 28:1! In this case, the environment does not appear to be the cause of the biased genetic sex ratio.

When Are Some Males More Stress Tolerant?

Loss of males due to stressful environments is not true for all species. Cameron and Wyatt (1990) found that males of ***Splachnum*** are able to survive in more stressful habitats than are females. Using experimental cultures, they found that for ***S. ampullaceum*** (Figure 22), ***S. rubrum*** (Figure 23-Figure 24), and ***S. sphaericum*** (Figure 25), low light and low *p*H favored production of males over females, whereas good nutrition seemed only to affect ***S. ampullaceum***. Nevertheless, the sexes are highly clumped and the sex ratio is typically 2:1 female to male.

Figure 22. ***Splachnum ampullaceum*** with sporophytes in southern Europe. Photo by Michael Lüth, with permission.

Figure 23. ***Splachnum rubrum*** males, which are more abundant than females in this species when provided with low light, low *p*H, and good nutrition. Photo by Dick Haaksma, with permission.

Figure 24. ***Splachnum rubrum*** with capsules on Isle Royale, Michigan, USA. This is a species where males are favored over females by low light, low *p*H, and good nutrition. Photo by Janice Glime.

Figure 25. ***Splachnum sphaericum*** with capsules, a species where males are favored over females by low light, low *p*H, and good nutrition. Photo through Creative Commons.

Other Differences between Populations

Even within a species complex (based on isozyme analysis), the ratios can vary in size and bias. For example, in the liverwort ***Aneura pinguis*** (Figure 26) complex, in one cryptic species there were equal frequencies of males and females, in one male plants numbered more, and in a third female plants were more numerous (Buczkowska *et al.* 2006). In ***Ceratodon purpureus*** (Figure 3) cultivated from spores to maturity, the sex ratio is also heterogeneous (Shaw & Gaughan 1993), but a female bias occurred in more than half of the eleven studied populations.

Figure 26. ***Aneura pinguis*** with perianths and one black capsule. Photo by Dick Haaksma, with permission.

Another possibility might be that dispersal and germination success differ between male and female propagules, causing more females to colonize. Such a difference would not present itself in experiments on germination of spores from individual capsules or other propagules because these would not have been subjected to the stresses of long-distance dispersal. Males and females would then not arrive and / or establish together and long periods of time may elapse before both sexes are present. And these sexes may represent different cryptic species. Using allozyme electrophoresis, Cronberg (2002) showed that ***Hylocomium splendens*** (Figure 27) presented 103 haplotypes in a sample of 694 shoots on 10 Baltic islands. The number of clones, sex expression, and sporophyte frequency increased, and sex ratios became more balanced with the age of the islands.

Figure 27. ***Hylocomium splendens***, a moss with many haplotypes in Europe. Photo through Wikimedia Commons.

Frequency and Timing of Sex Expression

Functional sex ratio is dependent on the frequency with which it is expressed and whether sequential sex changes ever occur. Do males express sex only once, or do they continue to do it year after year? Likewise, are females able to repeat their high-cost sexual endeavors?

Zoologists have named two strategies of sexual frequency as **iteroparity** and **semelparity.** The story behind the term **semelparity** helps one to remember its meaning. *Semel* comes from the Latin *semel*, meaning once, a single time. *Parous* is derived from *pario*, meaning to beget. The origin seems to be in Greek mythology, where Semele, daughter of Cadmus and Harmonia, was the mortal mother of Dionysus by Zeus. In the myth, Semele asked Zeus to reveal himself as his true entity. Because he had promised to grant her a boon, he could not break his promise, revealing himself as the lightning bolts he represented, and that cause any human that views them to incinerate. Hence, Semele could bear a child only that once, then died.

The terms semelparity and iteroparity have been applied to plants, as for example the century plant that blooms only once, then dies, certainly an example of semelparity. But the terms are rarely used for bryophytes. Hassel *et al*. (2005a) used it in relation to the populations of ***Pogonatum dentatum*** (Figure 20) in the mountains vs lowlands of Fennoscandia to describe their differences in sexual parity. Among mountain females, 41% of the shoots branched following reproduction the first time, a condition known as **iteroparous** (having sexual crossing in iterations, *i.e.*, successive years). On the other hand, the lowland female populations did not produce branches, thus being unable to produce sexual organs the next year, a behavior one could call **semelparous** (having sexual crossing only once), assuming it never produces such innovations. On the other hand, new plants might arise from rhizomes.

More likely representatives of semelparity are the **Splachnaceae** (Figure 28-Figure 29). As they mature, their habitat changes. They produce capsules and their substrate is no longer able to support the early stages of the life cycle, nor do they produce additional sporophytes in subsequent years.

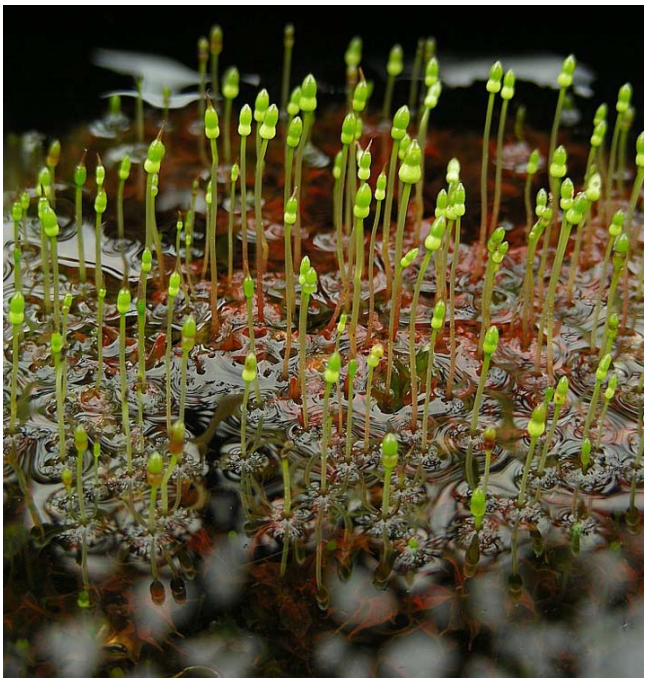

Figure 28. ***Splachnum rubrum*** females with young sporophytes. Photo by Michael Lüth, with permission.

Figure 29. ***Splachnum rubrum*** females with mature capsules. Photo by Michael Lüth, with permission.

Among **pleurocarpous** plants, both males and females continue to produce ramets or side branches where new gametangia can form, making them **iteroparous**. But what is the general case in **acrocarpous** mosses? Observations of clumps suggest that individual sporophytes are produced annually, but do these come from the same branches or from new plants formed within the clump? For example, in ***Weissia*** spp. (Figure 30) most shoots are **unisexual** (only male or female) during a given reproductive cycle (Anderson & Lemmon 1973, 1974). To answer these questions we must understand the differences in growth habits among the bryophytes.

Figure 30. ***Weissia controversa*** with capsules. Photo by J. C. Schou, with permission.

Branching Patterns and Gametangial Location

Among mosses there are two overall branching patterns: **sympodial** for **acrocarpous** mosses and **monopodial** for **pleurocarpous** mosses (with some exceptions). **Sympodial** growth is growth in the absence of apical dominance, *i.e.*, apical growth is terminated (in acrocarpous mosses it is terminated by the gametangia) and the main axis produces branches by innovations or produces ramets at the base. **Monopodial** growth is growth with apical dominance wherein new apical stem and leaf tissue continues to be added. In pleurocarpous mosses, the primary axis produces side branches where the gametangia develop, while the primary axis continues growth. In acrocarpous mosses, growth appears at first to be monopodial, but once gametangia occupy the apex, new growth of that axis ceases. (See Mishler & De Luna 1991 for a discussion of branching in mosses.)

The family **Polytrichaceae** exhibits both of these branching patterns, often in the same species. In ***Polytrichum*** (Figure 31), we know that new growth originates in the antheridial splash cup and that new splash cups are produced in successive years on the primary axis. In his studies on ***Pogonatum dentatum*** (Figure 20), Kristian Hassel (pers. comm. 24 January 2014) found that both male and females were able to produce innovations just below their gametangia, but this behavior seemed to be affected by the environment. Furthermore, in Scandinavia he found that production of innovations varied among species in **Polytrichaceae** as well as between males and females. For example, Hassel never observed innovations on shoots of ***Polytrichum commune*** (Figure 31) that had sporophytes, but in ***Polytrichastrum alpinum*** (Figure 32) and ***Pogonatum urnigerum*** (Figure 33) such innovations are common. Males of these species usually produce new antheridial splash cups on the primary axis year after year, reliably enough that these have been used as growth markers. In the genus ***Atrichum*** (Figure 59-Figure 61), sex expression occurs via branching (Linley Jesson, unpubl., pers. comm. 25 January 2014).

Figure 31. ***Polytrichum commune*** with capsules, a species where innovations apparently do not occur. Photo by David T. Holyoak, with permission.

Figure 32. ***Polytrichastrum alpinum***. Photo from Botany Department, University of British Columbia, Canada, with permission.

Figure 33. ***Pogonatum urnigerum*** males with splash cups. Photo by David T. Holyoak, with permission.

But it appears that among **acrocarpous mosses** in the **Bryopsida**, the formation of archegonia at least terminates the apical growth, requiring subapical innovations for further extension of that gametophore. For example, in ***Philonotis*** (Figure 34), new male inflorescences can appear on innovations in successive years. Mishler and Oliver (1991) reported that female gametangia terminated growth of annual innovations in the dioicous acrocarpous moss ***Syntrichia ruralis*** (Figure 35). Bisang and Ehrlén (2002) have observed perichaetia terminating each annual innovation of female stems of ***Dicranum polysetum*** (a species with dwarf males; Figure 36-Figure 38). ***Tortella rigens*** (Figure 39) females have similar innovations, although the perigonia could not be located (Lars Hedenäs, pers. comm. 23 January 2014). The multiyear behavior in males seems to be less obvious, although the **Polytrichaceae** demonstrate the possibility for growth to continue apically, even when a splash cup is present (Figure 40).

Figure 34. ***Philonotis fontana*** with antheridia and innovations. Photo by Michael Becker, through Creative Commons.

Figure 35. ***Syntrichia ruralis*** with sporophytes arising from archegonia that terminate its apical growth. Photo by Peggy Edwards, with permission.

Figure 36. ***Dicranum polysetum*** showing multiple sporophytes in one apex. The apical production of archegonia stops growth of that apex (see Figure 37). Picture by Janice Glime.

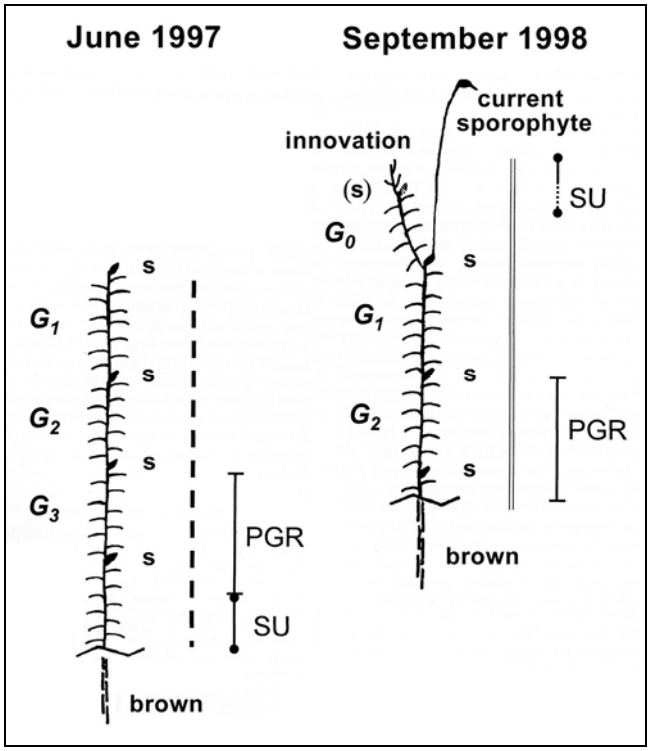

Figure 38. Representation of unbranched plant of ***Dicranum polysetum*** indicating locations of shoot sections and reproductive structures. G_x indicates annual growth interval, with G_0 indicating current year's growth as innovation. Note that the innovation is just below the apex where the sporophyte emerges from the sexual structure. **s** indicates location of sexual organs, in this case perichaetia. **Brown** portions are at the base and move progressively upward as the stem grows. **SU** indicates summer growth; **PGR** indicates proximal green portion. **Broken line** on **1997 drawing** indicates green gametophyte; **thin double line** on **1998 drawing** indicates the green gametophyte at the time of the G_1 sporophyte maturation. Modified from Bisang & Ehrlén 2002.

Figure 37. ***Dicranum polysetum*** tomentum and innovations. Photo by Walter Obermayer, with permission.

Figure 39. ***Tortella rigens***, a species with female innovations, growing or exposed rock. Photo by Michael Lüth, with permission.

Figure 40. ***Polytrichum juniperinum*** with new growth arising from the splash cups. Photo by Janice Glime.

Also those acrocarpous mosses that have horizontal growth forms much like those of pleurocarpous taxa do produce antheridia and archegonia in multiple years, but usually not at the original apex. In fact, it is the innovations, growing horizontally, that make them look pleurocarpous. This group includes such taxa as ***Racomitrium*** (Figure 41), ***Hedwigia*** (Figure 42) (Sean Edwards, pers. comm. 23 January 2014), and some members of the **Orthotrichaceae** (Figure 43). For example, Arno van der Pluijm (pers. comm. 23 January 2014) tells me that his search for males of the dioicous acrocarpous ***Zygodon*** (***Zygodon viridissimus***, Figure 43) in **Orthotrichaceae**) in old herbarium collections revealed male plants with multiple male buds on the same stem. He found that one or two innovations can develop directly below the perigonium, make a new perigonium, then branch again. He was able to observe up to five generations of male buds in 19th century collections. This family has members that often appear to be pleurocarpous, with predominantly horizontal growth like that of ***Macromitrium*** (Figure 19).

Figure 41. ***Racomitrium heterostichum*** with capsules. Photo by Jan-Peter Frahm, with permission.

Figure 42. ***Hedwigia ciliata*** with capsules. Photo by Robert Klips, with permission.

Figure 43. ***Zygodon viridissimus*** var ***viridissimus*** with capsules. Photo by David T. Holyoak, with permission.

In **thallose liverworts**, the apex typically continues to grow or divides to produce two branches for the succeeding year. For example, in perennial ***Riccia*** (Figure 44-Figure 45) species, the apex continues growing, and if fertilized, leaving successive sporangia to mature – and decay – behind (Rod Seppelt, pers. comm. 23 January 2014). Similarly, in Australia populations of fertilized ***Lunularia cruciata*** (Figure 46) produce white scale-like conical structures on the upper surface of the thallus. These enclose fully developed sporangia with spores and elaters as well as the **carpocephalum** (sporangial receptacle in most thallose liverworts). When autumn rains arrive, the stalks suddenly elongate to elevate the mature sporangia. It appears that in thallose liverworts, growth continues at the apex following gametangial formation and new gametangia later arise near the new apex.

Leafy liverworts have a growth pattern in which most species have terminal perianths surrounding the archegonia and sporophytes, but with antheridia in leaf axils along the branches. This pattern permits the male branches to continue growing at the apex, but alas, the female has a terminator in the presence of the perianth and archegonia, whether it is terminal on the stem or terminal on a branch. Hence, only new branches can form subsequent archegonia.

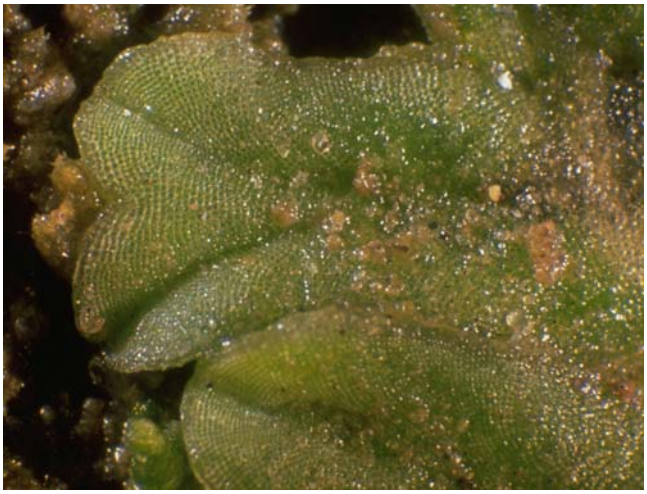

Figure 44. ***Riccia glauca*** showing apices where growth occurs (at end of rib). Photo by Jan-Peter Frahm, with permission.

Figure 45. ***Riccia glauca*** spores showing their location behind the apex. Photo by Rick Haaksma, with permission.

Figure 46. ***Lunularia cruciata*** with archegoniophores and young sporophytes. Note the scales at the base of the archegoniophores. Photo by Ken-Ichi Ueda, with permission.

It is likely that we should find examples where bryophytes expend so much energy on capsule development that they must wait a year or more to provide enough energy for another sexual endeavor. A negative relationship between sporophyte production and future perichaetia initiation was actually demonstrated in ***Dicranum polysetum*** (Figure 36-Figure 38) (Bisang & Ehrlén 2002; see also Chapter 3.4, Reproductive Trade-off). If we are to use growth increment markers such as splash cups, we need to understand this relationship lest we underestimate the age of the plants.

Protogyny and Protandry

Protogyny, the maturation of female reproductive structures before those of the male, and **Protandry**, the maturation of male reproductive structures before those of the female, are not commonly reported in the bryophytes [but see for example Lackner 1939; Crum 1972 for ***Atrichum undulatum*** (Figure 59-Figure 58) and ***Funaria hygrometrica*** (Figure 47); Longton & Schuster 1983; Stark 2002]. That does not mean they are effectively absent or even rare. One of the problems in identifying maturation of the male and female sexual organs at different times is that this may occur even in different years and give the appearance of having the two sexes on separate plants. Deguchi (1978) sums this up well in his study of ***Grimmia*** (Figure 48): "When successive branchings, including subfloral innovations, continue, and lower, older branches are decomposed in time, the upper newer branches, with different sexual organs, appear to be of different individuals. This circumstance often leads bryologists to a misunderstanding of the sexuality."

Figure 47. ***Funaria hygrometrica***, a monoicous annual shuttle species that produces prolific capsules with long-lived spores, shown here growing on fresh charcoal. Photo by Janice Glime.

Figure 48. ***Grimmia affinis***, a species that produces mature antheridia and archegonia at different times. Photo by Michael Lüth, with permission.

Ken Kellman (Bryonet 17 April 2014) excitedly reported the discovery of a plant that had been thought to be dioicous, but that in reality was synoicous and protogynous, an undescribed species of ***Bryum*** (***Gemmabryum***). The antheridia are produced after the archegonia have senesced. As he aptly pointed out, this is an effective mechanism to prevent selfing in monoicous species, while retaining the advantage of a clone that contains both sexes and achieves adequate spore dispersal for later mixing of genes.

This discovery by Kellman brought other Bryonetters to report their observations. Brent Mishler (Bryonet 18 April 2014) reported that in ***Syntrichia princeps*** (Figure 49) mature archegonia are present while antheridia in the same inflorescence are just beginning their development. We can't be certain whether this is maturing of archegonia first, or if the antheridia of that year have already matured and disintegrated, but one would assume that since they are in the same inflorescence this is protogyny. Stark (1985) likewise found evidence of brief protogyny in both species of ***Forsstroemia*** (Figure 50) in Virginia, USA. The monoicous ***Phaeoceros carolinianus*** (Figure 51) is an example of a typically protandrous hornwort.

Figure 49. ***Syntrichia princeps***, a species that exhibits protogyny. Photo by Jan-Peter Frahm, with permission.

Figure 50. ***Forsstroemia trichomitria***, a protogynous moss. Photo by Misha Ignatov, with permission.

Figure 51. ***Phaeoceros carolinianus*** with sporophytes, a protandrous hornwort. Photo by Hermann Schachner, through Creative Commons.

Age-related Differences

Could differences be due to fewer males expressing sex in their lifetimes, or do they take longer to reach sexual maturity? Since antheridia frequently require a longer time to develop than do archegonia (Clapham & Oldroyd 1936; Miles *et al.* 1989; Stark 1997, 2002; Milne 2001), it seems logical that males might require more maturity before they produce their first antheridia.

In ***Anastrophyllum hellerianum*** (Figure 52), Pohjamo and Laaka-Lindberg (2004) found that a **threshold size** exists not only for sexual reproduction, but also for asexual reproduction. Stark *et al*. (1998) also report a threshold size for sex expression in ***Syntrichia caninervis*** at 2.1 mm height; this usually is reached at about 6 years. This threshold could account for a large number of non-expressing plants in some populations and some species might even exhibit a different threshold for male and female expression.

Figure 52. ***Anastrophyllum hellerianum*** with gemmae. Photo by Michael Lüth, with permission.

Sexual Plasticity

It seems that bryophytes may have their own version of the alligator and crocodile story. In these reptiles, and some other animals, the temperature during development of the embryo determines the sex. At high temperatures ca 34°C all the hatchlings are males and when it is ca 30°C, all are female (Woodward & Murray 1993). In this case, there are no sex chromosomes, so temperature during incubation is a crucial factor in sex determination. The

planktonic microcrustacean *Daphnia* is dependent on environmental triggers for sex determination of its progeny (Innes & Dunbrack 1993; Tessier & Cáceres 2004).

Bisexual through Ramets and Rhizautoicy

Dioicous plants may not always be what they seem. Stark and Delgadillo (2001) became curious when the Mojave Desert moss ***Aloina bifrons*** (Figure 53), reputedly dioicous, appeared frequently with sporophytes. This was most unusual for a xerophytic, dioicous moss. Upon further investigation, they found that **ramets** (individual members of a clone) (Figure 54-Figure 55) of the same clone could on some individual ramets bear **perichaetia** (modified leaves enclosing archegonia) (Figure 56) and on others bear **perigonia** (modified leaves enclosing antheridia) (Figure 57), but that underground these ramets were connected by single rhizoids, rhizoid strands, or masses of rhizoids (Figure 54-Figure 55). In an experimental approach, Stark & Brinda (2013) recently confirmed **rhizautoicy** in this species, *i.e.* the sexual condition of separate male and female shoots connected by protonemata (Crandall-Stotler & Bartholomew-Began 2007) (or rhizoids), often beneath the substrate surface. Such a strategy, apparently from a single spore, would increase the probability of fertilization while permitting a somewhat greater chance for somatic variation between the sexes.

Figure 53. ***Aloina bifrons***, a dioicous species with frequent sporophytes. Some individuals can bear both archegonia and antheridia. Photo by Martin Hutten, with permission.

Figure 54. Seven **ramets** from one individual of ***Syntrichia caninervis***. Photo courtesy of Llo Stark.

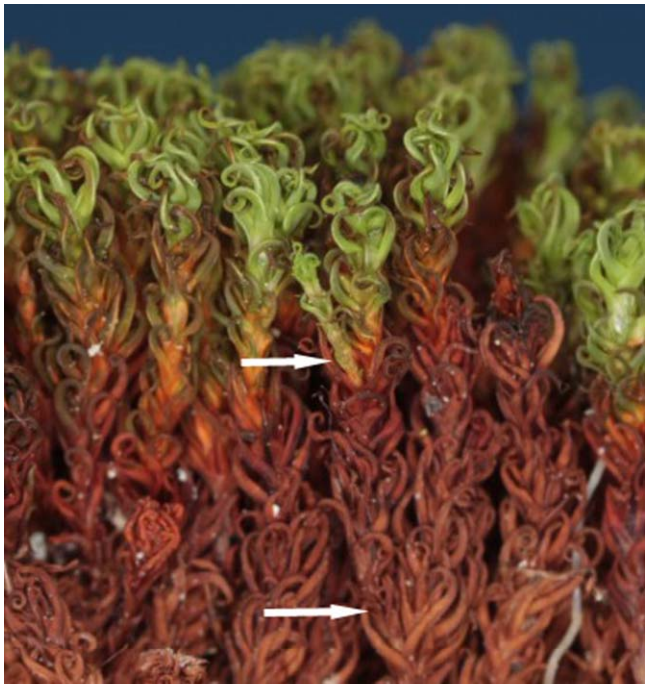

Figure 55. ***Bryoerythrophyllum rubrum* ramets**. Examples of branching is indicated by arrows. Photo by Jan-Peter Frahm, with permission.

Figure 56. ***Diphyscium foliosum*** females with capsules and **perichaetial leaves**. This species is dioicous (the male and female sexual organs occur on separate individuals), with photosynthetic males with leaves and females that consist of only a protonema and perichaetial leaves that surround the archegonia and subsequent sporophyte. Photo by David Holyoak, with permission.

One example of possibly environmentally determined sex in bryophytes is that of ***Splachnum ampullaceum*** (Figure 22). In this species a protonema from a single spore can produce both male and female shoots (Cameron & Wyatt 1990), fitting the definition of rhizautoicy. The spores are bisexual, but the individual gametophores are unisexual. Therefore, it appears that selection against female-expressing plants is determined later in the developmental stage, although field conditions might cause quite different responses from those in the lab. What is it that determines the sex in these gametophores? Could density of the population in the dung habitat influence sexual differentiation or survival in this functionally dioicous moss? Or could presence of external hormones in the dung habitat influence sexual differentiation or survival? Such factors as ethylene concentrations,

regulated by population density or other environmental factors, could alter the sex ratio. For example, in the flowering plant *Cucurbita texana*, an injection of ethylene into the stem resulted in a greater proportion of female-expressing flowers (Krupnick *et al.* 2000). It is possible that bryophytes, like flowering plants (Lebel-Hardenack & Grant 1997), have environmental means of sex determination. But, alas, it seems we know little about the ability of a single protonema to produce gametophores of different sexes and what might control those differences.

Figure 57. **Perigonial leaves** and antheridia of ***Diphyscium foliosum***. Photo from Botany 321 website at the University of British Columbia, with permission.

How common is rhizautoicy in bryophytes? Is this a facultative trait that responds to absence of the opposite sex? Does it involve genetic mutations on the branches, or suppression of genes? And what environmental stimuli are involved in triggering the formation of each sex? Does the environmental trigger cause a physiological response that changes the sex of a newly developing ramet? What is the role of hormone concentration in determining sex expression? Do these rhizautoicous plants retain their sex, or can they switch from year to year based on their stored energy or growing conditions or even age? Is rhizautoicy involving rhizoid connections really the same phenomenon as the production of separate male and female gametophores produced from a single protonema in ***Splachnum ampullaceum***?

Sex Reversal

This brings us to attempting to answer the question of sex change in bryophytes. Do bryophytes behave like the Jack-in-the-pulpit (*Arisaema triphyllum*) and remain non-expressing until they have sufficient energy, then change sex in a pattern determined by their sizes? This species does not flower when it is small, produces males flowers when somewhat larger, and produces female flowers in its largest size range (Bierzychudek 1982). Hence, as these perennial plants increase or decrease in size from year to year, they also may change sex.

This model would seem only to work for perennials with underground overwintering structures like the Jack-in-the-pulpit, but consider another scenario. Annual growth of an innovation after sporophyte production can decrease due to energy transfer to the sporophyte, as seen in ***Dicranum polysetum*** (Figure 36-Figure 38) (Bisang & Ehrlén 2002). Then the new branch would represent the shorter "plant." In ***D. polysetum*** sporophyte development reduced the probability of development of future perichaetia and/or reduced the mass of new perichaetia. In short, it exhibited an energy tradeoff much like the Jack-in-the-pulpit, but there is no sex change involved.

Is there evidence that any bryophytes can change sex in response to stored nutrients or nutrient availability? Crum (1976) reports that ***Atrichum undulatum*** (Figure 59-Figure 58) behaves this way in Michigan, USA. He observed that this species does not produce male and female gametangia on the same plant at the same time, but that at least some populations produce antheridia the first year and archegonia the next (Braithwaite 1887-1905; Dixon 1924; Nyholm 1954-1969; Smith 1978). Thank you to Bryonetters, we can cite further personal observations to shed light on this matter. Linley Jesson, in response to my question on Bryonet in January 2014, shared her observations that in ***Atrichum*** (**Polytrichaceae**; Figure 59-Figure 61), because new innovations arise after sex expression, sex indicators remain over 2 or sometimes 3+ years. In triploid ***Atrichum undulatum*** (Figure 59-Figure 58) and diploid ***Atrichum altecristatum*** (Figure 60-Figure 61; or possibly ***A. undulatum***) it appears that sequential sex expression occurs. Often the first gametangia produced are male and in the next year either female or both gametangia appear. The age of reproduction in both sexes certainly needs further investigation.

Figure 58. ***Atrichum undulatum*** with capsules. Photo by Michael Lüth, with permission.

This leaves us with two pieces that we have not been able to connect in bryophytes. ***Dicranum polysetum*** (Figure 36-Figure 38) demonstrates the tradeoff due to energy cost, with innovations behaving like the subsequent year of growth from the Jack-in-the-pulpit rhizome. ***Atrichum undulatum*** (Figure 59-Figure 58) demonstrates the ability to change sex in subsequent years. But we lack

the link to demonstrate that energy/nutrient availability cause a change to the less costly sex.

Figure 59. ***Atrichum undulatum*** males with splash cups. Photo by Janice Glime.

Figure 60. ***Atrichum altecristatum*** showing male splash cups. Photo by Robert Klips, with permission.

Figure 61. ***Atrichum altecristatum*** in its first year of invasion. There was no evidence of sexual structures. Photo by Eric Schneider, with permission.

Dan Norris, in his discussion on Bryonet (2 May 2003), helps to answer this question. He expressed his observations on the variability of sexual type within species: "I find myself very skeptical about published data on dioicy and monoicy. As I write my own manual of California mosses with all descriptions based upon observation of actual specimens, I have found too many contradictions to published reports... I have found the **Polytrichaceae** is so often male in early few years of its life and female later. Too many presumed **cladautoicous** (having archegonia and antheridia on different stems of the same plant) specimens can only be guessed as such because actual connections of the stems cannot clearly be demonstrated...The frequency of sporophytes is hardly a reliable indication of sexuality; ***Orthotrichum lyellii*** (Figure 87) in my California region seems to be dioicous, as universally reported, but nearly all bunches of the plant – bunches I first thought to be clones – contain both sexes and are almost always with sporophytes."

Even in the well-known dioicous ***Polytrichum*** (Figure 40) and ***Atrichum*** (Figure 59-Figure 58), both archegonia and antheridia can occur on the same plant, either mixed together or in separate locations, a condition known as **polyoicous** or **heteroicous** (Vitt 1968). We have much to learn about sex determination in bryophytes!

Mechanisms of Labile Sex Expression

Korpelainen (1998) compared the **lability** (flexibility) of sex expression among the plant phyla and found that while it exists in all the major plant phyla, it is the rule only among homosporous ferns. Furthermore, most of the plants that have labile sex expression are perennials with long life cycles. She found that environmental stresses such as low light, nutrition, unfavorable weather, and too much or too little moisture often favor male expression. Unfortunately, we know little of these mechanisms in bryophytes.

In the monoicous ***Tetraphis pellucida*** (Figure 63-Figure 62), density affects sex expression, with male shoots dominating when densities are greater (Kimmerer 1991). Selkirk (1979) found that nitrate levels affected sexual expression in ***Riccia duplex*** (Figure 64), but she did not show differences between male and female expression. In ***Riccia rhenana*** (Figure 65), some clones produced archegonia in both soil and nutrient solutions, whereas others did not produce any sexual structures during the same six-month cultivation period, suggesting that either they differed genetically or that their past history (*e.g.* age, environmental conditions, time since last production of sporophytes) affected their ability to respond.

Figure 62. ***Tetraphis pellucida*** with capsules. Photo by Bob Klips, with permission.

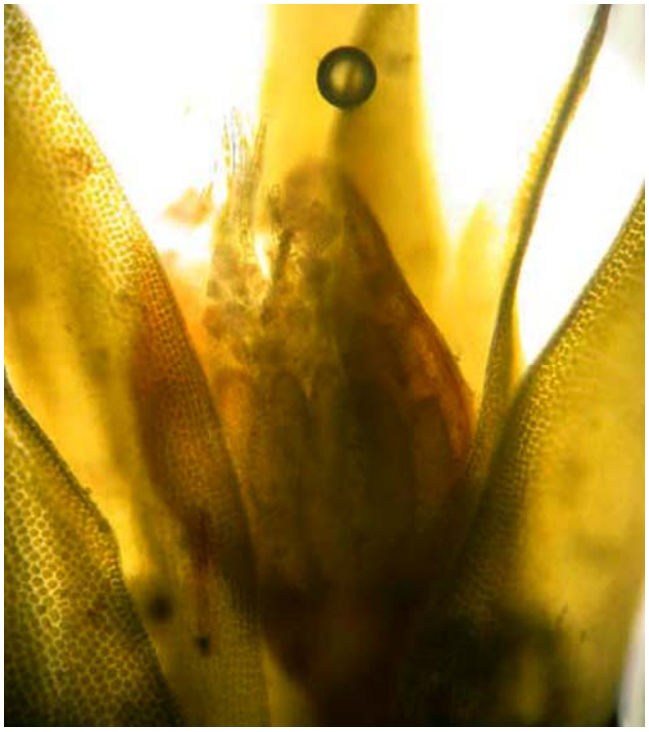

Figure 63. ***Tetraphis pellucida*** antheridia. Photo from Botany Department UBC, with permission.

Figure 64. ***Riccia duplex***, a species in which nitrate affects sexual expression. Photo by Michael Lüth, with permission.

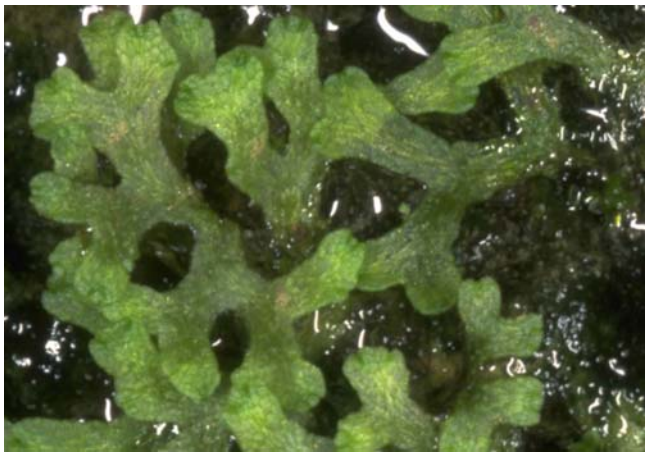

Figure 65. ***Riccia rhenana***, a species for which sexual expression is not affected by nitrates. Photo by Jan-Peter Frahm, with permission.

Hormones undoubtedly contribute to sex expression and we might expect their concentrations to be subject to environmental conditions. When experimenting with the mostly vegetative liverwort ***Riccia crystallina*** (Figure 66), Chopra and Sood (1973) found that **gibberellin** and **ethrel** enhanced antheridial formation, whereas **glycocel** enhanced archegonial formation. In the dioicous ***Bryum argenteum*** (Figure 7), Bhatla and Chopra (1981) stimulated expression of male gametangia with **auxin** and **gibberellin**, whereas these same hormones inhibited development of female gametangia. Instead, **cytokinins** stimulated the development of female gametangia, slightly inhibiting development of gametangia in male clones. Studies such as these suggest that hormones could control sex expression either by genetic control or environmental control on gene expression. Furthermore, gaseous hormones such as **ethylene** or fungal exudates such as **gibberellin**, present in the environment, could influence sexual expression, differing between years and environments and causing the differences and changes in sexual expressions that have been observed in some species.

Figure 66. ***Riccia cf crystallina***, a species in which **gibberellin** and **ethrel** enhance antheridial formation, whereas **glycocel** enhances archegonial formation. Photo by Michael Lüth, with permission.

We cannot overlook the importance of hormonal interactions on development (see Chapter 5-1 of this volume, Ecophysiology of Development: Hormones). In their experiments with ***Bryum argenteum*** (Figure 7), Bhatla and Chopra (1981) showed that **IAA** and **cytokinin** could counteract each other's individual hormonal inhibitory effects on the female and male clones, respectively. **ABA**, known as a stress hormone, inhibited both sexual expression and vegetative growth in this species, with sexual induction in the female being more sensitive. In addition to interactions, concentrations are important in developmental control.

Plasticity vs Genetic Differentiation

Transplant experiments can be used to help us understand plasticity that permits environmentally induced changes vs genetic characters that may prevent living in some environments. Hassel *et al.* (2005b) used ***Pogonatum dentatum*** (Figure 67) transplants to demonstrate such plasticity. They found that vegetative growth was greater in the mountain areas than in lowland areas. Furthermore, reproductive investment was greater in

the lowland areas. But lowland plants tended to produce larger sporophytes than those from the mountain when grown in the same environment, suggesting a genetic difference between the two populations. What is interesting is that the transplanted shoots often outperformed the native ones by growing larger and producing larger sporophytes. They suggested that plasticity may have permitted the range expansion of ***P. dentatum***.

Figure 67. ***Pogonatum dentatum***. Photo by Michael Lüth, with permission.

Using reciprocal transplants, Hedderson and Longton (2008) likewise found both genetic variation and plasticity in life history traits in upland and lowland sites of several other **Polytrichaceae**: ***Pogonatum aloides*** (Figure 68-Figure 69), ***Polytrichum commune*** (Figure 31), and ***P. juniperinum*** (Figure 40, Figure 70). These differences were apparent in male reproductive effort and investment in vegetative shoots by females. Variation included tradeoffs between number and size of spores and between vegetative reproduction and spore production.

Is There an Asexual Role for Males?

Is it possible that male bryophytes may have more vegetative reproductive success while females have the primary sexual reproductive role? A sexually reproducing female bryophyte needs to nurture the developing sporophyte (see Chapter 3-4, Reproductive Trade-off). Reproductive output may be increased if the female individual is large, increasing fitness by permitting that female to occupy more space and obtain more light, and possibly more water and nutrients. But a male may be able to maintain the population, and enlarge it, through asexual means.

Figure 68. ***Pogonatum aloides*** males. Photo by David Holyoak, with permission.

Figure 69. ***Pogonatum aloides*** females with capsules. Photo by Michael Lüth, with permission.

Figure 70. ***Polytrichum juniperinum*** males showing old antheridial splash cups (**arrows**) with new growth and splash cups above that previous apex. Photo by Jan-Peter Frahm, with permission.

As discussed above (Genetic vs Expressed Sex Ratio), in ***Marchantia inflexa*** (Figure 9) the growth patterns of males and females differ, with the females in some habitats producing more meristematic tips, but the males producing more gemmae (Brzyski *et al*. 2013), giving the females more coverage in the immediate area and more chance for long-distance dispersal through spores, but giving males more opportunity to spread locally away from the immediate clump.

Among mosses in Great Britain about 18% (Longton 1992) to 29% (Hill *et al.* 1991, 1992, 1994) produce specialized vegetative propagules, and there are significantly more of these in dioicous mosses than in monoicous taxa (Longton 1992; During 2007). Among Belgian and Dutch liverworts, 69% of the dioicous species produce vegetative propagules, compared to 54% for monoicous taxa (During 2007). Such a strategy of asexual reproduction in males could be cost effective in dioicous taxa, permitting the females to put energy into producing spores while males could maintain the local population through asexual means (see *e.g.* Laaka-Lindberg *et al.*

2000). Even if both sexes produce vegetative propagules, this may be suppressed while sexual reproductive processes occur. In ***Marchantia polymorpha*** gemma cup (Figure 71) production ceases while it is producing sexual reproductive structures (Terui 1981).

Recently, Pereira *et al.* (2016) noted in Amazonian **Calymperaceae** that gemmae-bearing shoots produced fewer gametangia than shoots without gemmae, although both sexual and asexual reproduction were positively related to monthly precipitation amounts. Likewise, in his assessment of life cycle strategies, During (2007) concluded that there is a negative correlation between processes and structures (such as propagules and sexual structures) that serve the same functions in the life of the bryophyte.

Figure 71. ***Marchantia polymorpha*** with gemmae cups. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Stieha *et al*. (2014) confirmed that in ***Marchantia inflexa*** (Figure 9), male plants produce gemmae more quickly and prolifically than do females. Nevertheless, this is not necessarily an indication of a greater role for asexual reproduction in males. Once gemma cups are produced, male plants of this species increase production of gemmae to week 4 and stop at about week 9. Female plants, on the other hand, have stable production of gemmae during the first three weeks of cup existence, increasing sharply in week 4, then declining in subsequent weeks. On the other hand, male gemmae suffer greater desiccation effects, resulting in greater gemmae mortality than that of female plants. But once gemmae are dispersed (about 20 cm per minute in light rain), they have a high survival rate if they remain moist and are critical for maintaining both sexes.

Differential survival may account for the observed sex imbalance (see above in Germination Patterns and Spore Mortality; Environmental and Geographic Differences). And it appears this could diminish the role of males in asexual reproduction. Newton (1972) demonstrated the loss of young males from leaf regeneration in ***Mnium hornum*** (Figure 72) and ***Plagiomnium undulatum*** (Figure 73-Figure 74) where none of these survived desiccation, but 77% of the leaf regenerates from females did survive.

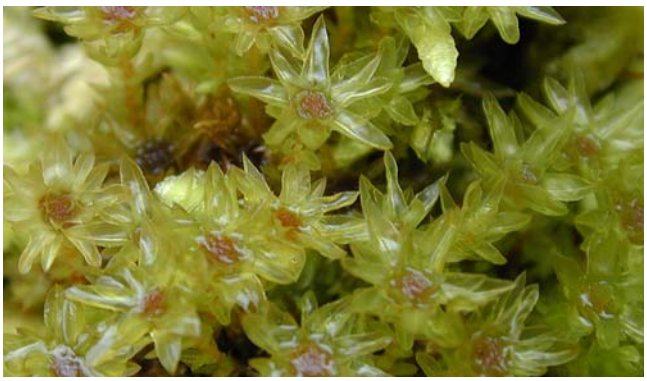

Figure 72. ***Mnium hornum*** males at Bretagne, France. Photo by Michael Lüth, with permission.

Figure 73. ***Plagiomnium undulatum***, a species in which male regenerants are more likely to die than those of females. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 74. ***Plagiomnium undulatum*** with antheridial splash cups. Photo by Jan-Peter Frahm, with permission.

When Males Are Dominant

But we must remember that females are not always the dominant sex. In her 1972 study Newton showed that isolated spores of ***Plagiomnium undulatum*** (Figure 73-Figure 74) had a sex ratio of 4.1♀:1♂, changing little to 3.5♀:1♂ in the first protonemal buds, but in the same family ***Mnium hornum*** (Figure 72) had a ratio of 0.89♀:1♂, becoming more skewed in favor of males (0.45♀:1♂) in the first protonemal buds. Other examples exist of expressed male dominance in some populations within a species. This could be an advantage in species where differences in stress tolerance favor males. And

having more males increases the chances for some of the sperm reaching eggs.

Laaka-Lindberg (2005) found that only 8% of the females were sex-expressing whereas 17% of the males were sex expressing in the leafy liverwort ***Lophozia ventricosa*** var. ***silvicola*** (Figure 75), with a female to male sexual ratio of 0.61:1. Furthermore, the timing of gametangia production and conditions needed for development differed between the males and females. This timing in females varied among years, suggesting that the environmental signals differed between the sexes. Such timing differences could cause a mismatch between male and female maturation that could reduce fertilization.

Figure 75. ***Lophozia ventricosa*** from Europe. Photo by Michael Lüth, with permission.

Alvarenga Pereira *et al*. (2013) found a highly male-biased condition (0.43 ♀:1 ♂ at ramet level, n=604) in the epiphyllous moss ***Crossomitrium patrisiae*** (Figure 76) in the Brazilian Atlantic rainforest. In this study of 797 ramets, a high rate of 76% were expressing sexual structures. This species had an extremely high rate of sporophyte production, with 40% of all female ramets, and 74% of female ramets occurring in mixed colonies bearing sporophytes. For this species, arriving and establishing on a new leaf, a short-lived habitat, is a necessity for the species to continue, and this is best achieved by spores that can more easily become airborne than many larger vegetative propagules. Low levels of abortion and high investment in sporophyte maturation provide this species with the dispersal units to survive in this ephemeral habitat.

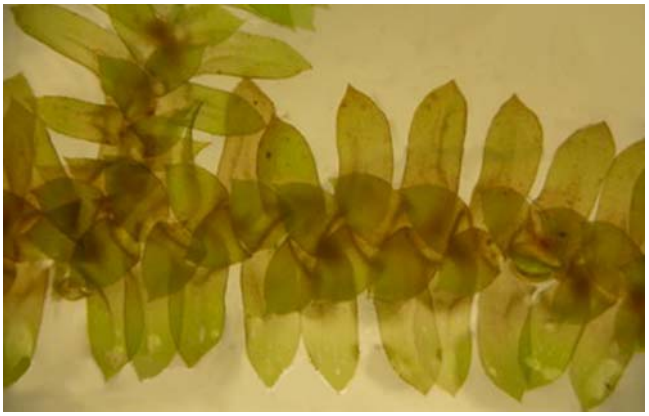

Figure 76. ***Crossomitrium patrisiae*** habit in Costa Rica. Photo by Michaela Sonnleitner, with permission.

Also the aquatic liverwort ***Scapania undulata*** (Figure 77) exhibits a clearly male-skewed expressed sex ratio (Holá *et al*. 2014). The authors suggest that the high production of males is a strategy to overcome sperm dilution and ensure fertilization over longer distances in water.

Figure 77. ***Scapania undulata*** with capsules, a species with more males than females. Photo by Michael Lüth, with permission.

Maintaining Sexual Dimorphism in a Population

What factors might maintain the balance of males to females to retain the dioicous character in a bryophyte species? We have seen many cases of male suppression, some so strong that they could lead to male extinction in some populations, at least when we look at sex-expressing plants. Maintenance of both sexes is important for fitness and evolution. We find that the same factors that separate the environments of males and females might contribute to the continuation of both sexes. That is, some years and conditions may favor one sex, whereas other years and modified conditions may favor the other. For the slow-growing bryophytes, this slows competition between the sexes and prevents rapid extinctions.

Marchantia inflexa (Figure 9) demonstrates the complex way in which sexual expression might occur. In this as in many other bryophyte species, it is common for males to be rare. Single-sex populations, especially of females, are common (Garcia-Ramos *et al*. 2002). In the USA, only single-sex populations are known, but in tropical sites, populations with both sexes occur. Spread of both sexes by clonal growth and vegetative propagules is common. Garcia-Ramos and coworkers found that in ***Marchantia inflexa*** seasonal disturbances (desiccation) delay the elimination of males within the patch, whereas large scale disturbances permit re-establishment by spores. It is these large-scale disturbances that permit both sexes to coexist at a **metapopulation** level (*i.e*. group of partially isolated local populations of same species, but connected by migration). In this species, isolated clonal populations seem independent of sexual reproduction, but at the landscape scale, sexual reproduction is crucial for re-establishment by spores.

Fuselier and McLetchie (2002) explored the question of what maintains sexual dimorphism, using ***Marchantia inflexa*** (Figure 9) as a model system. They suggested that there is sex-specific selection, as already seen for ***Syntrichia caninervis*** (Figure 15) (Stark *et al.* 2005) and discussed above for this species (Environmental and Geographic Differences), causing one sex to be favored over the other under certain stressful conditions. When the habitats of the sexes do not overlap, the sex with the higher cost of sexual reproduction should experience higher mortality in the more stressful habitats (Lloyd & Webb 1977; Charnov 1982; Bierzychudek & Eckhart 1988; Fuselier & McLetchie 2002). Whereas habitat specialization can lead to difficulty in obtaining mating success, it leads to a wider habitat range for the species, albeit by separating males and females. In this case, the species must be maintained by asexual reproduction. Fuselier and McLetchie (2002) reasoned that such a strategy would favor males with a high degree of asexual reproduction, but females with a low asexual reproduction.

In ***Marchantia chenopoda*** (Figure 78), Moyá (1992) found that there was a large female bias, even when the population seemed to be relying on its abundant sporophytes. The **selective forces** acting on asexual vs sexual fitness can act in opposition and may help to explain the persistence of sexual dimorphism and the smaller number of males.

Figure 78. ***Marchantia chenopoda*** in Puerto Rico, a dioicous species. **Upper:** male population; **Lower:** female population. Photos by Janice Glime.

Sexual dimorphism may occur at the clump level while seemingly absent at the shoot level. Moore *et al*. (2014) found that when 25 male and 25 female shoots of ***Bryum argenteum*** were cultured, no differences in water-holding capacity could be ascertained between the sexes. However, when 1 cm^2 samples were saturated with water and then centrifuged to remove external water, the female clumps retained more water per unit of clump area. The researchers suggested that this water retention ability could favor greater growth of females and contribute to a female bias in expressed sex ratio.

Season and Sex Expression

Those of us in the temperate and arctic climates expect bryophytes to be dormant in the winter and that many species will take advantage of rainy or melting periods in spring for fertilization. But not all species conform to those expectations (Arnell 1878, 1905). In the majority of species in temperate regions, phenology of fertilization and sporophyte formation are clearly seasonal, and differ among families and habitats.

Capsules take varying periods to mature, some taking more than a year, so those can be found almost year-round, albeit on different species (Milne 2001). In the tropics, a seasonal cold period is absent, but precipitation may cause seasonality. Maciel-Silva and Marques Válio (2011) examined the effects of season on bryophyte sexual expression in Brazilian tropical rainforests. They found that many of the species exhibited sexual expression continuously over the 15-month study in both the sea level and montane sites.

Seasons did, however, affect the length of time required for gametangia to mature in the tropics (Maciel-Silva & Marques Válio 2011). Male gametangia typically matured by the end of the dry season, providing sperm when the rains were present, presumably facilitating their dispersal during the following rainy season. Female gametangia, on the other hand, were receptive over the entire period, even having many mature before the start of the rainy season. This strategy would assure that females were ready at any time the rains came, allowing for year-to-year differences. It is interesting that the male gametangia took longer to develop and that many aborted. This scheme also maximizes the dispersal of spores, permitting them to mature near the end of the dry season when conditions are best for dispersal; rains will soon follow to induce germination.

If seasons are indeed important, then there should be differences between sea level and montane reproductive cycles at the same latitude, in this case the Brazilian Atlantic rainforest. Maciel-Silva *et al.* (2012) found that species at sea level produced more sexual branches and had a more strongly female-biased sex ratio than did the montane populations. There were more frequent fertilizations among the montane populations, but ultimately, the number of successful sporophytes was about the same at the two elevations. Fertilization occurred mostly during the rainy season of October to December. Moreover, monoicous species exhibited a higher reproductive performance in terms of number of sexual branches, fertilization, and sporophyte formation. The authors concluded that both the breeding system and the

environment influenced the sexual expression and mating strategies.

But even when sex is expressed in plants within proximal distance suitable for fertilization, that sporophyte production might not occur (Bisang & Hedenäs 2008). This is the case in ***Pseudocalliergon trifarium***, based on transplantation experiments. Even when the archegonium was present, it was never swollen, and no sporophytes became evident. Instead, the archegonia withered. Although ***Rhytidiadelphus triquetrus*** had sporophytes in 100% of the transplant plots that made both sexes available, ***Abietinella abietina*** produced them in only 41% of the plots, and ***Pseudocalliergon trifarium*** in none! Although we can postulate potential causes for the lack of sporophyte development, we lack the kind of evidence needed to support such hypotheses.

Role of Asexual Reproduction in Dioicy

By now it should be clear that dioicous bryophytes suffer from lack of sexual reproduction in many populations. On the other hand, asexual reproduction can maintain the population and help it spread. But is specialized asexual reproduction more common among dioicous taxa?

It appears that among British mosses, asexual propagules are common among dioicous colonists (Longton 1992), but this relationship does not exist among the liverworts (Longton 1997). Rather, among the British liverworts the production of asexual propagules is not related to sexuality (monoicous vs dioicous).

In examining the Japanese flora, Une (1986) found support for the concept of vegetative success in the relationships of specialized vegetative reproduction. Of the 111 moss taxa that produced **asexual diaspores** (any structures that become detached and are dispersed) (Figure 79), 86 were dioicous (77.5%), whereas only 11 (9.9%) were monoicous. A further phenomenon in this story is the presence of more asexual propagules in the erect-growing dioicous mosses than in the prostrate (creeping) taxa. Could it be that these rarely sporulating but upright taxa take advantage of vegetative propagules to facilitate movement "in search" of the opposite sex?

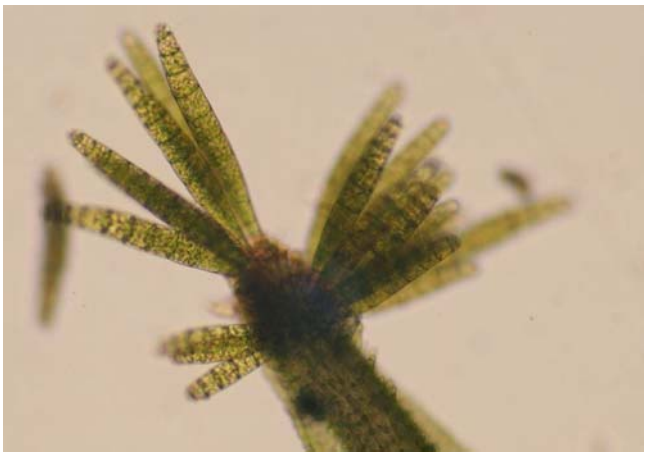

Figure 79. ***Calymperes erosum*** with gemmae on the leaf tip. Photo by Li Zhang, with permission.

Similarly, During (2007) was able to show that among bryophytes in Belgium and The Netherlands, dioicous taxa more commonly had vegetative propagules than did monoicous ones. But among the mosses, this relationship only held true for acrocarpous species; the pleurocarpous taxa were able to achieve significant expansion by clonal growth, thus negating much of the advantage of vegetative propagules. During suggested that the tradeoff between propagules and vegetative growth seen in the liverwort ***Marchantia inflexa*** (Figure 80) might be a common phenomenon among bryophytes. He found that negative correlations generally occur between processes and structures that serve the same functions in the life of the bryophyte, suggesting that vegetative diaspores and sexual organs compete for the same energy reserves. A more detailed discussion of asexual reproduction follows.

Gemma-bearing Dioicous Taxa

We have previously mentioned (Chapter 3-1, Or the Dioicous Advantage?) the importance of asexual propagules in dioicous taxa. To the examples cited above, we can add that of 715 species of mosses examined in eastern North America, 13% have some obvious means of specialized asexual reproduction (Crum 2001). Of these, 76% are dioicous, 19% monoicous, 5% of unknown sexuality. Old data from Germany (Correns 1899) indicated that of 915 species, 12% had true gemmae, with 86% of these dioicous and 14% monoicous.

Longton (1992) indicated that producing asexual propagules in many dioicous moss taxa provided them with a safety net, permitting reproduction under conditions when sexual reproduction was not possible. Such a strategy permitted them to survive in marginal habitats and in years when the weather was unfavorable to fertilization due to drought or frost (Longton 1990). Furthermore, it appeared that a greater number of rare taxa relied on asexual reproduction – not surprising due to the greater ease of dispersal of spores (Schuster 1988; Miles & Longton 1990; Söderström & Herben 1997; Bolker & Pacala 1999).

Figure 80. ***Marchantia inflexa***. Photo by Scott Zona, through Wikimedia Commons.

The moss genus ***Aulacomnium*** is known for special brood bodies (Figure 81-Figure 82). In most species, these are comprised of reduced and thickened leaves in a cluster on stalks at the tips of plants (Figure 81-Figure 82). However, in ***Aulacomnium heterostichum*** (Figure 83), sporophytes are common and these brood bodies were overlooked until 1991 when Imura *et al.* reported them from Japan. In this species, brood bodies are on a terminal stalk, but the individual propagules are not thickened as in other ***Aulacomnium*** species and only slightly modified from the leaves (Figure 84). It is likely that brood bodies have been overlooked in other bryophyte taxa as well, particularly rhizoidal tubers and protonemal gemmae.

Protonemal gemmae predominate among the **Pottiaceae**, even when the plants are expressing gametangia. ***Dicranella heteromalla*** produces chloronemal gemmae with well defined tmema cells (Duckett & Matcham 1995). The tiny ***Ephemeropsis*** produces protonemal gemmae on its leaf substrate (Pressel & Duckett 2009). Duckett *et al*. (2004) found propagules on protonemata in species where they were previously unknown, including ***Ditrichum cornubicum***, ***Saelania glaucescens***, ***Seligeria carniolica***, and ***Zygodon gracilis***. And the aquatic moss ***Fontinalis antipyretica*** produces protonemal gemmae (Ares *et al*. 2014).

Figure 81. Brood body production in dioicous ***Aulacomnium androgynum***. Photo by Michael Lüth, with permission.

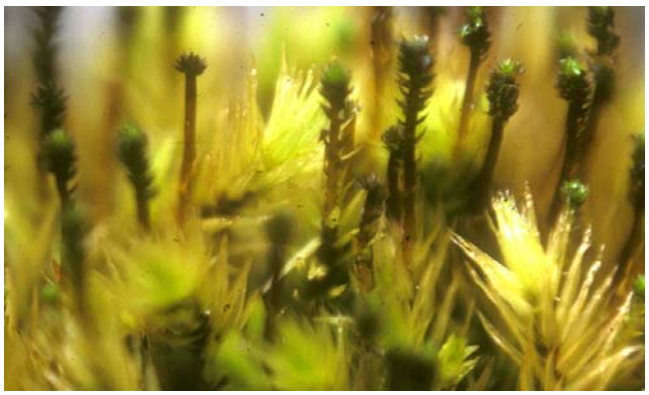

Figure 82. ***Aulacomnium palustre*** with brood bodies. Photo by Zen Iwatsuki, with permission.

Figure 83. ***Aulacomnium heterostichum***, a monoicous moss with abundant sporophytes. Photo by Janice Glime.

Figure 84. ***Aulacomnium heterostichum*** in Japan, with brood bodies (arrows). Photo by Janice Glime.

Spores, Asexual Propagula, and Rarity

There seems to be a distinct correlation between spore size and asexual propagules, with plants having small spores being more likely to have propagula (Longton & Schuster 1983; During 2007). If having small spores means having more of them, such a species would seem to have the best of all worlds, with a good chance for long-distance dispersal through spores, and colony expansion through readily sprouting propagula. Its price would be in lower viability of small spores compared to large ones.

The possibility to self-fertilize would suggest that sexual reproduction should be more frequent in the monoicous condition, with the possibility of cross fertilization with sister plants in the same clone, if not on the same plant. Longton (1997, 1998) agrees. He predicts that at least among the colonists, fugitives, and annual shuttle species (all inhabiting newly available substrata; Figure 47), the trend toward monoicy will be accompanied by an increased reproductive effort, decrease in life span, and decrease in the age of first reproduction. To facilitate such a strategy, he predicts that the life cycle will have substantial **phenological** (timing of events) flexibility and that the success of establishment from spores will increase. He suggests that the specialized asexual propagules that are common among dioicous colonists compensate for their more limited sexual reproduction.

To sum up what we know now, it appears that species that rarely produce capsules are more likely themselves to be rare (Miles & Longton 1990; Söderström 1992; Laaka-Lindberg 2000). Monoicous species produce capsules much more frequently than do dioicous species, with the

distance between archegonia and antheridia being a limiting factor (Longton & Schuster 1983; Wyatt & Anderson 1984; Longton 1990; Laaka-Lindberg 2000; Bisang *et al.* 2004). Even monoicous species may become rarer in severe habitats where weather conditions may prevent even short-range dispersal of sperm to egg (Laaka-Lindberg 2000). Asexual propagules are more common among dioicous moss species. (See Chapter 4-7, Adaptive Strategies: Vegetative vs Sexual Diaspores, for more information on asexual vs sexual reproduction.)

Why Are Liverworts Different?

Laaka-Lindberg (2000) found that the relationship between rarity and presence of asexual vs sexual strategy differs markedly between British mosses (Longton 1992) and liverworts. Whereas only 18% of the mosses produce asexual propagules, 46% of the liverworts do (Longton 1992), a group that is 68% dioicous (Villarreal & Renner 2013). And, unlike the mosses, production of asexual propagules in liverworts is not linked to the dioicous condition, but is nearly equal to that in the monoicous condition. The researchers warn us, however, that the ephemeral nature of liverwort sporophytes could create a bias in herbarium data since liverworts are more likely to be collected in sterile condition than are non-sporophytic mosses with persistent capsules elsewhere in the population. This could also increase the collected representation of propaguliferous plants among liverworts compared to mosses. There also seems to be less evidence of fragmentation success in leafy liverworts (see, for example, Miller & Howe Ambrose 1976).

Nevertheless, the long-identified association between dioicy and the ability to produce vegetative propagules in mosses in different regions and at different scales has recently also been challenged by Laenen *et al.* (2015). The authors applied comparative phylogenetic methods with 303 out of 382 liverwort genera currently recognized globally. They were unable to find a correlation between dioicy and the formation of vegetative propagules. They did not compare 'rarity' with reproductive system, but used size of geographic ranges. Interestingly, the production of vegetative propagules was positively correlated with range size, but sexual system and spore size were not. This suggests that asexual reproduction may play a more important role than hitherto thought in long-range dispersal of liverworts, and calls for further investigation of the spatial genetic structure of bryophyte populations in relation to their mating systems.

Laaka-Lindberg *et al.* (2000) concluded that those British liverwort taxa that produce neither spores nor vegetative propagules tend to be rare (Figure 85). Rarity of capsule production does correlate with rarity of the species, with those failing to produce spores being three times as likely to be rare. Monoicous taxa have a higher proportion with sporophytes than do dioicous taxa, but among those species of both mating systems that do produce capsules, there is greater rarity among the monoicous taxa. This suggests that there is a fitness price for selfing or sibling crosses due to suppression of genetic variation that would be available through outcrossing. Data are needed to support this hypothesis.

The production of asexual propagules is not related to rarity in British liverworts, with propagules occurring as often in common species as in rare ones (Laaka-Lindberg *et al.* 2000). It is interesting that whereas there are few liverwort taxa in which sporophytes are unknown anywhere (Figure 85), there are many taxa in which vegetative propagules are unknown (Figure 86), and the frequency of those lacking such propagules is twice as great among dioicous liverworts as among monoicous liverworts, although the proportion is about the same in both (Figure 86) (Laaka-Lindberg *et al.* 2000). Spores are more likely to provide long-range dispersal, but among seeds Thompson *et al.* (1999) concluded that the best predictor of range among British plants was diversity of habitats used. It is likely that this is true for bryophytes as well.

Could it be that liverworts, rather than using specialized asexual means as a safety net, more frequently are opportunistic, having occasional sexual reproduction, but gaining the advantages of both means of reproduction (Green & Noakes 1995; McLellan *et al.* 1997)? Their horizontal growth habit, producing ramets, permits them to expand on their substrate without having to reproduce. Asexual reproduction, including ramification, is suggested to require less energy, particularly on the part of females, and therefore may be useful under stressful conditions (Longton & Schuster 1983; Newton & Mishler 1994). This concept is supported by greater occurrence of species with asexual propagation in arctic and alpine areas than in the tropics (Schuster 1988). In stable environments, maintenance will permit survival of the population, but in habitats subject to frequent disturbance, dispersal of progeny is essential (Schuster 1988; Söderström 1994) and may even depend on delay through dormancy (McPeek & Kalisz 1998).

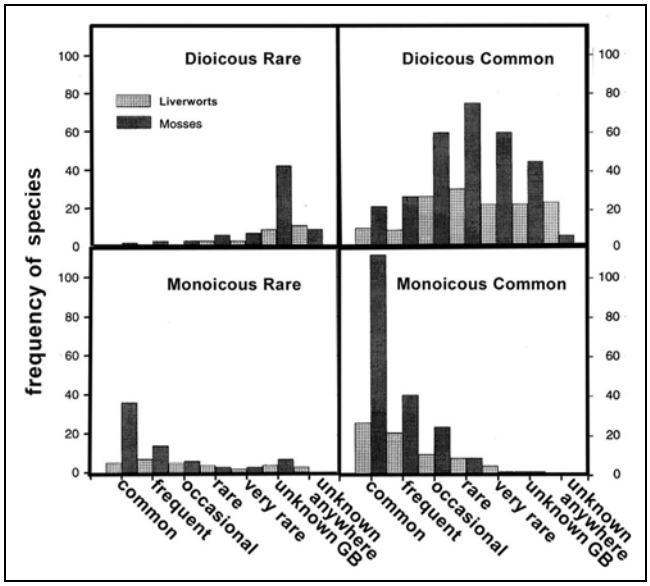

Figure 85. Comparison of frequencies (seven classes) of sporophyte production for mosses and liverworts in four sexuality groups within Britain. Modified from Laaka-Lindberg *et al.* 2000.

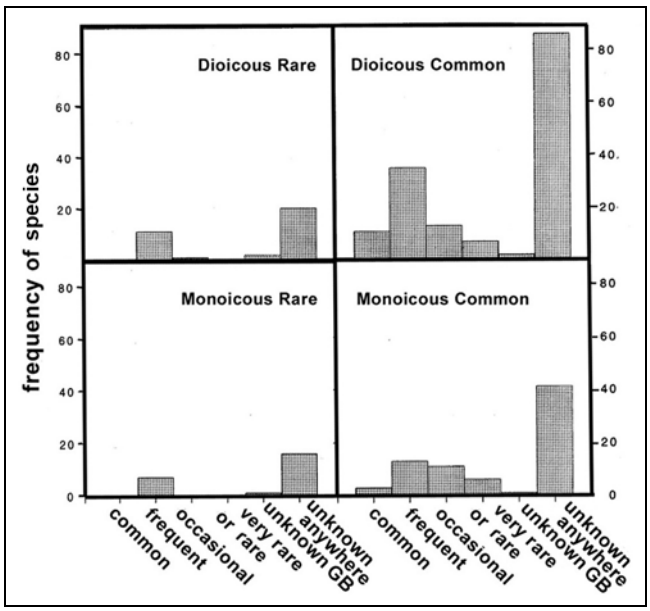

Figure 86. Comparison of frequencies (six classes, rare and very rare combined) of asexual reproductive structures for liverworts in four sexuality groups within Britain. Modified from Laaka-Lindberg *et al.* 2000.

Are Epiphytes a Special Case?

For epiphytic species such as the presumed dioicous ***Orthotrichum lyellii*** (Figure 87), the same tree needs to be colonized by both sexes to facilitate sexual reproduction. Norris (see Sex Reversal above) finds that colonies frequently have both sexes. Fortunately, sperm can be washed downward considerable distances by rainfall, facilitating fertilization. The presence of numerous gemmae permits this species to spread vegetatively and the gemmae may help it to become established on its vertical substrate, increasing chances for both sexes to survive. But this begs the point Norris tried to make about sexual expression (see Sex Reversal above). We need to be cautious about generalizations and look closely for variability due to age relationships, habitat expressions, or hidden connections.

Figure 87. ***Orthotrichum lyellii***, an epiphytic dioicous species. Note brown gemmae on leaves. Photo by Michael Lüth, with permission.

Smith (1982) reported that the proportion of monoicous taxa among those restricted to bark greatly exceeds that among mosses in general. Devos and coworkers (2011) found that the mostly epiphytic liverwort genus ***Radula*** (Figure 88) exhibits evidence of shifts from dioicy to monoicy multiple times as new species arose, with some epiphytes having facultative shifts. It is interesting that they found no correlation between asexual gemmae and either dioicy or strict epiphytism in ***Radula***. Rather, the obligate epiphytes tend to disperse by whole gametophyte fragments, avoiding the protonemal stage that is more susceptible to the ravages of rapid changes in moisture. The former is in line with findings of Laaka-Lindberg (2000) for British liverworts and by Laenen *et al.* (2015) for liverworts at the global scale (see above, "Why Are Liverworts Different?").

Figure 88. ***Radula complanata*** growing epiphytically and exhibiting gemmae. Photo by J. C. Schou, with permission.

As a result of their dispersal by fragments and often the absence of successful sexual reproduction, many epiphytes may have a special problem in maintaining the species due to lack of genetic variability. Because of the limited success of establishment on the vertical substrate of tree trunks and vertical rocks, these substrates often have only one clone and therefore only one sex in dioicous taxa. Hence, in the frequent absence of sexual reproduction, reproduction is accomplished by clonality or possibly selfing or among siblings. This may result in a lack of genetic diversity, as exemplified by ***Leucodon sciuroides*** (Figure 89) in Europe (Cronberg 2000). Glaciated areas had lower genetic diversity, as might be predicted for an area of lower age. Furthermore, the unglaciated populations from the Mediterranean region reproduce sexually, whereas the younger and more isolated populations from glaciated areas reproduce asexually, leading further to lack of genetic variability. This lack of variability may contribute to the disappearance of epiphytic populations under stress of air pollution and climate change.

Figure 89. ***Leucodon sciuroides*** on tree bole in Europe. Photo by Dick Haaksma, with permission.

Summary

Many species exhibit a strongly female-biased phenotypically expressed sex ratio that likewise is in some cases genetic and in others possibly due to varying responses of sex expression to environmental conditions. The "**shy male**" hypothesis lacks support in explaining most of this female bias. Examples of distinct male bias in expressed sex ratios also exist. Sex ratios based on genetic information on non-expressing plants is known for a very limited number of species.

Some species, perhaps more than we realize, have sexual plasticity. That is, they have different sex expressions in different years, possibly dependent on age or available energy resources. This can be due to hormonal expressions of the same or neighboring plants.

When sexual reproduction fails, asexual reproduction by specialized propagules can compensate, and this is especially true for dioicous mosses at the same scales. In addition, clonal growth and fragmentation can help the species spread. Because of the energy cost of producing sporophytes, males may exhibit higher vegetative performance. A modelling study suggests that disturbance level (weather, pollution, fire, etc) affects sexes differentially, hence maintaining both sexes in the long term. Epiphytes are frequently isolated on a tree with only one sex present. Although there seems to be no correlation between epiphytism and asexual propagules, there is a greater proportion of monoicous taxa among epiphytes than in general.

Acknowledgments

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CHAPTER 3-3
SEXUALITY: SIZE AND SEX DIFFERENCES

JANICE M. GLIME AND IRENE BISANG

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CHAPTER 3-3
SEXUALITY: SIZE AND SEX DIFFERENCES

Figure 1. ***Plagiomnium*** producing male splash cups as it grows amid ***Thuidium delicatulum***. Photo by Janice Glime.

Sex-related Differences in Gametophores

For most bryophytes, secondary sexual characteristics are subtle and are noticed only by the most observant. Fuselier and Stark (2004) consider size, morphology, physiology, reproductive investment, and stress response all to be expressed among sexual differences in bryophytes. Une (1985 a, b) with the moss ***Macromitrium*** and Fuselier and McLetchie (2004) with the thallose liverwort ***Marchantia inflexa*** (Figure 3) have shown that males and females of the sex-expressing individuals of these species can respond differently to stress. Even at the spore stage, size and morphology are traditional characteristics used to determine **anisospory** (two spore sizes) and **anisogamy** (size, shape, or behavioral differences in gametes) in bryophytes as well as in algae. For bryophyte gametophytes, reproductive investment has been shown to differ between antheridia and archegonia in some species (*e.g.* Stark *et al*. 2000; Horsley *et al*. 2011), but not in others (Bisang *et al*. 2006).

Shaw and Gaughan (1993) noted non-reproductive differences between the sexes in the moss ***Ceratodon purpureus*** (Figure 2). Among 160 single-spore isolates representing 40 sporophytes from one population, female gametophytes outnumbered males by a ratio of 3:2 at the time of germination. The resulting female gametophytic clones formed significantly more biomass, and individual female shoots were more robust than in male clones. On the other hand, male clones produced more numerous stems. Shaw and Gaughan suggest that this strategy may permit the females to provide more nutritional support for the sporophytic generation.

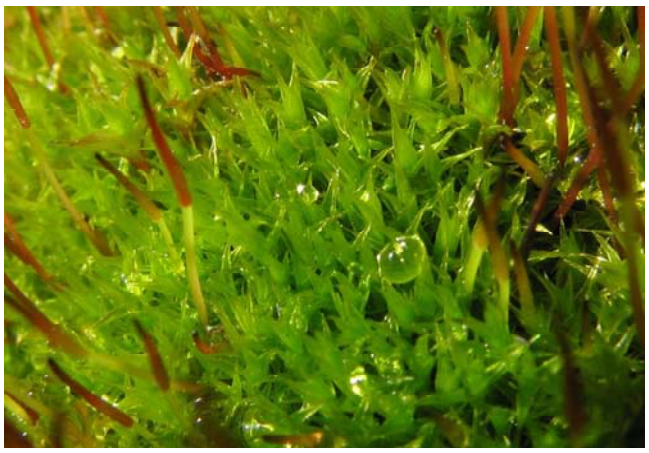

Figure 2. ***Ceratodon purpureus*** with young sporophytes. Photo by Jiří Kameníček, with permission.

Even in ***Ceratodon purpureus*** (Figure 2) that lacks **dwarf males** (see below under Dwarf Males) and where sex is chromosomally determined, sexes differ in size and in maturation rate, a character that Shaw and Beer (1999) suggest may prove to be widespread among bryophytes.

Even factors related to photosynthesis can differ between sexes. In their study Groen *et al*. (2010) found that females of ***Marchantia inflexa*** (Figure 3) had higher chlorophyll *a*:*b* ratios. And in the same study they found that females had a negative relationship between thallus thickness and gross photosynthesis whereas males did not, but they were unable to explain that negative relationship. Finally, differences between sexes in physiological traits may also occur at the clump level, as recently demonstrated in ***Bryum argenteum*** (Moore *et al.* 2016). Female clumps held more water and included more robust shoots than male clumps.

Figure 3. ***Marchantia inflexa***, a species in which photosynthetic factors differ between males and females. Photo by Scott Zona, with permission.

Size and Sex Differences

"Why is the world full of large females?" (Lewin 1988). Particularly among insects, fish, amphibians, and reptiles, females are larger than males (Lewin 1988). Darwin explained this as the need of the species to produce a large number of eggs, a concept known as the fecundity-advantage model. Shine (1988) feels the concept is flawed in that evolution should maximize lifetime reproductive success, not instantaneous reproductive success. He suggests that the fecundity-advantage model implies one large reproductive effort late in life, thus subjecting the female to great energy costs, and would only be of benefit when energy resources are non-limiting. With that in mind, it is interesting that mammals that must carry their young within do not generally have larger females than males. It is also the case in seed plants that are dioecious; only the female must bear the fruits. Yet it is not typical among seed plants for the female plant to be larger.

Bryophytes present an interesting contrast here. No other group of plants or algae is characterized by the need for the gametophyte to persist through the entire development of the sporophyte (there are individual exceptions, such as the fern *Botrychium*). In bryophytes, the female must supply the energy to support the developing sporophyte. Indeed, some bryophytes do have larger females than males [*e.g.* the liverworts ***Cryptothallus*** (Figure 4), ***Pallavicinia*** (Figure 5), ***Pellia*** (Figure 6-Figure 8), ***Riccia*** (Figure 9), and ***Sphaerocarpos*** (Figure 10)]. There are also a number of mosses with **dwarf males** [male plants that are considerably reduced in size relative to female plants, usually occurring on leaves (Figure 14) or in the tomentum of female plants, *e.g.* ***Micromitrium*** (Figure 11)] – about 60 genera already identified by Fleischer (1900-23, 1920). Females smaller than males are rare, with the non-sexual part of ***Diphyscium foliosum*** (Figure 12) being a notable exception.

Figure 4. ***Cryptothallus mirabilis*** with young capsules. This is a genus with females larger than males. Photo by David Holyoak, with permission.

Figure 5. ***Pallavicinia levieri***, in a genus with females larger than males. Photo by Li Zhang, with permission.

Figure 6. ***Pellia endiviifolia*** males with reddish antheridial cavities and females in center; females are the larger sex. Photo by David Holyoak, with permission.

Figure 7. ***Pellia endiviifolia*** with antheridia. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 8. ***Pellia endiviifolia*** with antheridium cross section and spermatocytes. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 9. ***Riccia sorocarpa***, a genus with females that are larger than males. Photo by Michael Lüth, with permission.

Figure 10. ***Sphaerocarpos*** sp., a species in which females are larger than males. Photo by David T. Holyoak, with permission.

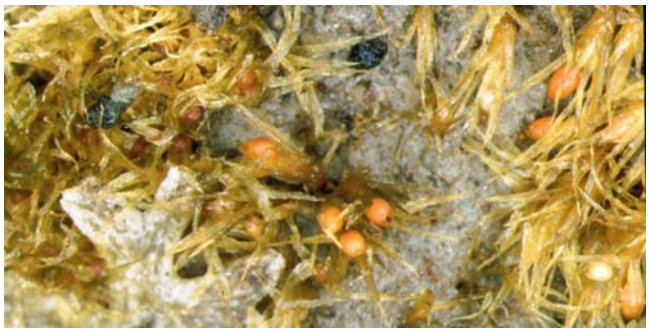

Figure 11. ***Micromitrium tenerum*** with capsules, a genus with females that are larger than males. Photo by Jan-Peter Frahm, with permission.

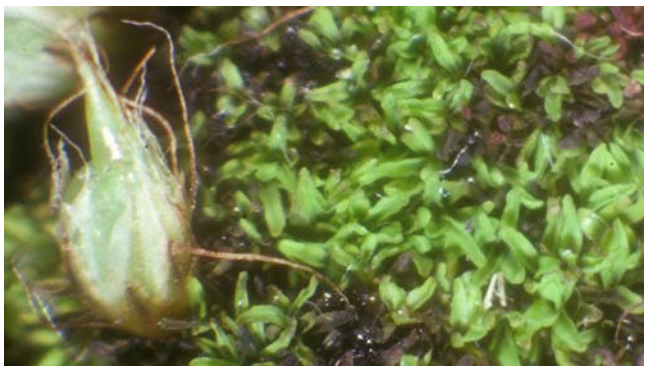

Figure 12. ***Diphyscium foliosum*** female (**left**) with only perichaetial leaves visible and reduced vegetative gametophyte; male plants are to its **right**, showing conspicuous leafy plants. Photo by Janice Glime.

Dwarf Males

Dwarf males are a notable exception to the observation that there is little, if any, size difference between males and females among most bryophytes. Even early publications on bryophytes recognized examples of sharp size distinctions (Bruch *et al.* 1851-1855; Limpricht 1895-1904; Fleischer 1920). Dwarf males occur in approximately 60 genera and 22 families (Rosengren & Cronberg 2015); estimations suggest that they occur in 10-20% of all moss species (Hedenäs *et al*. 2011). Where spores germinate on the leaves (**phyllodioicy**; Figure 13-Figure 18) or other parts of the female, some species produce **dwarf males** (**nannandrous males**) whose primary function is to produce sperm (Crum 1976). This production of dwarf males is unique to bryophytes among land plants [but is present in some species of the green alga *Oedogonium* (Figure 19) in Oedogoniaceae (Maier & Müller 1986)].

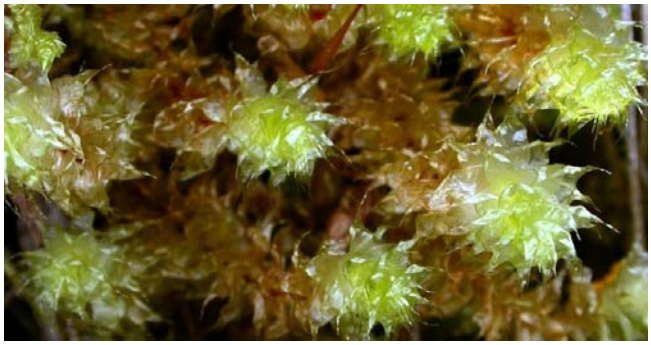

Figure 13. ***Ptychomnion aciculare***, a species that produces dwarf males. Photo by David Tng, with permission.

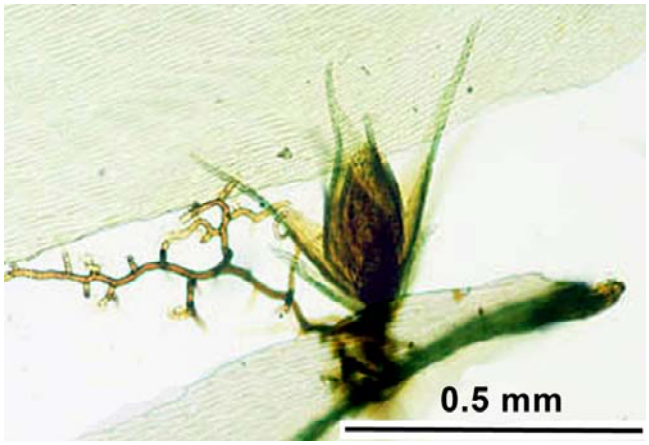

Figure 14. ***Ptychomnion aciculare*** with dwarf male on leaf. Photo modified from one by John Braggins, with permission.

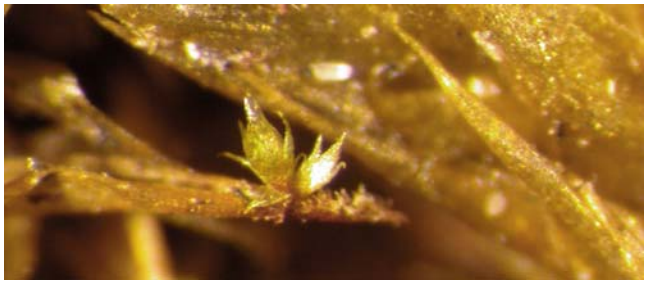

Figure 15. ***Acroporium stramineum*** dwarf male on leaf of mature female. Photo courtesy of Lars Hedenäs.

Figure 16. ***Isothecium alopecuroides*** dwarf male on leaves. Photo courtesy of Lars Hedenäs.

Figure 17. ***Isothecium alopecuroides*** dwarf male. Photo courtesy of Lars Hedenäs.

Figure 18. ***Eurhynchium angustirete*** dwarf males on female plant. Photo courtesy of Lars Hedenäs.

Figure 19. *Oedogonium* sp. with enlarged oogonium (female gametangium) and two dwarf males curved toward the oogonium. Photo by Janice Glime.

Although dwarf males have been known for many decades in some genera, their widespread occurrence among many more genera has been overlooked (Hedenäs & Bisang 2011). This is especially true for facultative dwarf males. Hedenäs and Bisang (2011, 2012) estimate that 25-44% of the dioicous pleurocarpous moss species exhibit dwarf males, with about 75% of these producing them **facultatively**, *i.e.*, the species has the ability to form both normal-sized and dwarf males. The underlying mechanisms (discussed below under How Do Facultative Males Develop) are currently unresolved in most cases, although at least some seem to produce normal males on a non-moss substrate and dwarf males on a moss substrate. Nearly 60% of the 1737 species in the total data set investigated by Hedenäs and Bisang are dioicous. Of the 178 species reported to produce dwarf males, 113 are considered to form obligate dwarf males. When they examined in detail a subset of 162 species, 72 produced observable dwarf males, but only 18 of these had obligate dwarf males. Hedenäs and Bisang (2011) reason that these dwarf males are likely to be overlooked when counting male presence.

This **phyllodioicous** strategy has been repeated in at least 27 separate families of mosses (Fuselier & Stark 2004), including both acrocarpous (Schellenberg 1920; Ramsay 1979; Yamaguchi 1993; Une & Yamaguchi 2001; Hedenäs & Bisang 2004) and pleurocarpous species (Une 1985a; Goffinet 1993; Hedenäs & Bisang 2011). Hedenäs and Bisang (2011) found dwarf males in 22 pleurocarpous families.

Even when we find dwarf males, we can't be certain of the sex unless they have gametangia. For example, Fleischer (1900-23) suggested a strategy for ***Trismegistia brauniana***, wherein spores that germinate on leaves of normal females all develop into dwarfs – both male and female. But these were non-expressing dwarfs, so there was no way for Fleischer to determine if there were really females (Lars Hedenäs, pers. comm. 4 April 2013).

The dwarf male strategy may increase fitness for the species by saving space and conserving resources. A sexually reproducing female bryophyte needs to nurture the developing sporophyte. Fitness of the reproductive output may be increased if the female individual is large, permitting that female to occupy more space and obtain more light, and possibly more water and nutrients. Males, on the other hand, need only produce sperm and do not sacrifice nutrients and energy to a developing embryo.

Vollrath (1998) referred to the condition of dwarf males associated with females as being short of true parasitism. Although the females provide a kind of room and board for the males, the males provide sperm to the females. But we are unaware of any evidence that the females provide nutrition. Rather, they provide a safe habitat that offers protection from desiccation and a short route to the egg.

Revisiting the Sex Ratio

Realization that 10-20% of the pleurocarpous moss species worldwide produce functional dwarf males requires re-examination of our data on sex ratios (Hedenäs & Bisang 2011) (discussed in Chapter 3-2). Using herbarium specimens of five Macaronesian species as models, Hedenäs and Bisang (2012) examined the effect of adding these newly recognized dwarf males to the calculation of sex ratio. If dwarf males were not counted, male availability was reduced by 51-61%, with that reduction increasing to 74-76% for sporophyte-producing plants. As one might expect, presence of sporophytes was positively correlated with presence of dwarf males. Hence, in those species with dwarf males, the sex ratio at the specimen level was balanced if dwarf males were counted, but strongly female biased if they were not.

Dwarf males in *Homalothecium lutescens*

Rosengren and co-workers (2014) examined the nanandrous sexual system in the pleurocarpous moss ***Homalothecium lutescens*** (Figure 20) in grassland habitats in southern Sweden and on the Baltic island Öland. These detailed studies, covering both ecological and genetic aspects, greatly advanced our knowledge on the conditions for and consequences of male dwarfism in mosses. ***Homalothecium lutescens*** has facultative dwarf males, but large males are extremely rare in this species (Wallace 1970; Rosengren *et al.* 2014 and references therein). In one of the study sites, dwarf males were almost exclusively found on sporophytic shoots (Rosengren *et al.* 2014). Investigating 90 colonies from three localities, Rosengren and Cronberg (2014) found that dwarf male density was positively related to colony moisture (two localities).

Figure 20. ***Homalothecium lutescens***, a species with facultative dwarf males. Photo by Michael Lüth, with permission.

In addition, fertilization frequency was positively affected by dwarf male density, but also by canopy cover in one locality (Rosengren & Cronberg 2014). Their findings suggest that nannandry reduces the problem of short fertilization distances in bryophytes, but that the presence of water is still critical. In terms of genetic affinity, dwarf males are most closely related to their host shoot, then to neighbors within their colony of 0.5m^2, and finally, to plants in the remaining population (Figure 21) (Rosengren *et al.* 2015). This means that spores giving rise to the dwarf males are at most commonly produced by the mother shoot or by a shoot in the close vicinity. Occasionally, however, dwarf males seemed even to originate from outside the host population, *i.e.* from another of the four study populations within a radius of 60 m^2. The researchers conclude that although dwarf males have in general local origin, sporadic dispersal to greater distances happens. These events contribute to the gene flow across populations and to the accumulation of genetic diversity within a population. Overall, the levels of genetic diversity were comparable between dwarf males and females within each population (Rosengren *et al.* 2015).

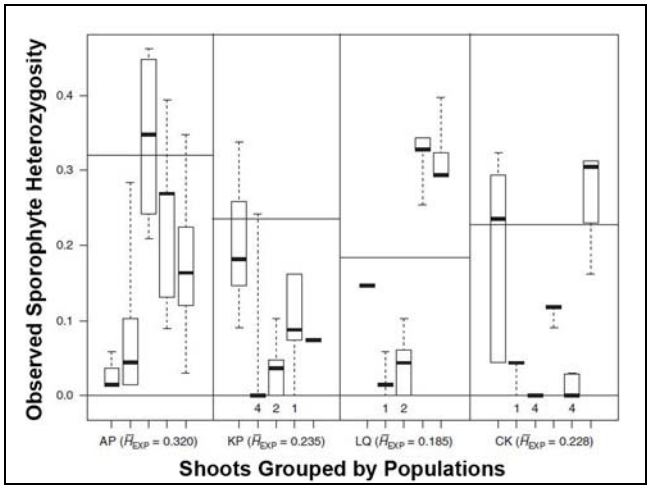

Figure 21. Inbreeding vs outcrossing in ***Homalothecium lutescens*** from four populations in Sweden. Each box represents the lower and upper quartile of 4-6 sporophytes on a single female shoot. The thick horizontal lines within boxes represent the median and whiskers denote the total range of data (minimum and maximum values outside the quartiles). Horizontal lines across each population section represent the mean H_{exp} (mean expected sporophyte heterozygosity over all loci, based on male and female allele frequencies). Sporophytes falling below that line could be considered inbred, with a few exceptions. Numbers below the y=0 line represent the number of sporophytes on the shoot that are homozygous in all loci, *i.e.* probably self-fertilized or inbred. Modified from Rosengren *et al.* 2016.

Rosengren *et al.* (2016) also genotyped sporophytes, female host shoots, and dwarf male plants in these populations. The high proportion of entirely homozygous sporophytes confirms frequent mother-son mating. Nevertheless, 23% of sporophytes exhibited a higher heterozygosity level than the expected population mean, which gives evidence of occasional fertilizations by non-host males (Figure 21). Further, almost 60% of the sporophytes were sired by distinct fathers (Rosengren *et al.* 2016). The extent of **polyandry** (multiple male parents) in bryophytes is poorly understood, but Szövény *et al.* (2009) also reported prevalent multiple paternity (polyandry) among sporophytes in ***Sphagnum lescurii*** (Figure 22).

Figure 22. ***Sphagnum lescurii***, a species that has multiple paternity of its sporophytes. Photo by Bob Klips, with permission.

In an *in vitro* experimental approach by sowing spores from three species [***Homalothecium lutescens*** (Figure 20), ***H. sericeum*** (Figure 23), ***Isothecium alopecuroides*** (Figure 16-Figure 17) on shoots of ***H. lutescens***, Rosengren and Cronberg (2015) noted distinct differences in germinability of the sown spores among the three species (Figure 24). While no dwarf males were formed from spores of the distantly related ***I. alopecuroides***, both ***H. lutescens*** and ***H. sericeum*** spores developed into dwarf males (Figure 25). The latter points to a possible pathway for hybridization between the two species (Rosengren & Cronberg 2015).

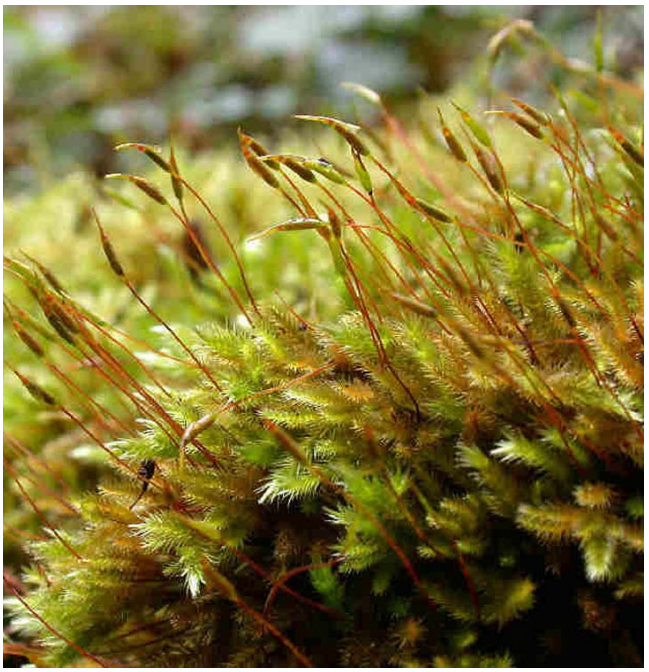

Figure 23. ***Homalothecium sericeum*** with capsules, indicating successful fertilization. Photo by David Holyoak, with permission.

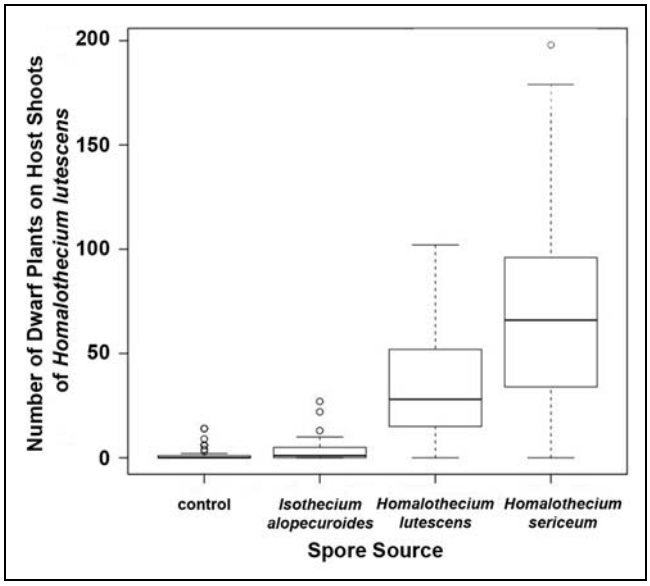

Figure 24. Total number of dwarf plants of each source species on ***Homalothecium lutescens*** 10 months after sowing spores of three species on ***H. lutescens*** (n-46). Redrawn from Rosengren & Cronberg 2015.

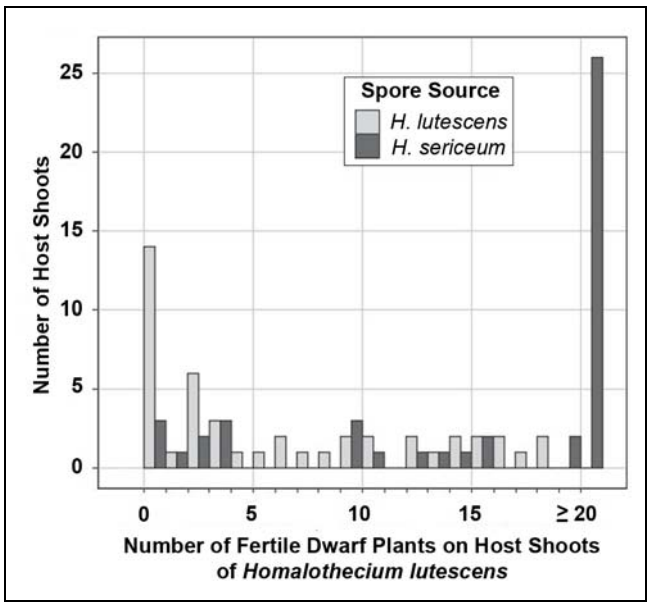

Figure 25. Number of fertile dwarf male-expressing plants of ***Homalothecium lutescens*** and ***H. sericeum*** that germinated from spores placed on ***Homalothecium lutescens***. Redrawn from Rosengren & Cronberg 2015.

What Is the Role of Vegetative Propagules?

As noted above, some species of the alga *Oedogonium* (Figure 19) (Chlorophyta) have a similar dimorphism in the size of the filaments, whereupon a male spore produces a dwarf male when it germinates upon a female (Rawitscher-Kunkel & Machlis 1962). However, if a male spore develops away from a female, it will grow into a larger filament and produce asexual spores that again have the opportunity to locate a female and form a dwarf male, a possible strategy that has apparently received no consideration among bryophytes.

I (Glime) became curious as to a similar relationship between vegetative propagules (since asexual spores do not exist in bryophytes) and facultative dwarf males in bryophytes. That is, do vegetative propagules develop into normal-sized male plants when establishing on "ordinary" substrate away from a female, but form minute males on a female individual, as has been observed for spores in some species (see below). Would the non-dwarfed males then produce vegetative propagules that might develop dwarf males if they were to land on a female? Bryonetters brought me several examples, predominantly in the genus ***Dicranoloma*** (Figure 26-Figure 27). But species bearing both dwarf males and gemmae in Asia and Australia [***D. bartramianum***, ***D. dicarpum*** (Figure 26), ***D. platycaulon***, ***D. leichhardtii*** (Figure 27)] do not produce gemmae in New Zealand (Milne 2000; Pina Milne and Allan Fife, pers. comm. 9 January 2014). In southeastern Asia, Malesia, and Oceania, ***D. braunii*** has the most frequent and conspicuous gemmae and produces dwarf males (Niels Klazenga, pers. comm. 8 January 2014). But this still begs the question, do gemmae that land on females produce dwarf males, and do those that land on soil continue to produce gemmae-producing non-sex-expressing plants?

Figure 26. ***Dicranoloma dicarpum***, a moss with both dwarf males and gemmae. Photo by Tom Thekathyil, with permission.

Figure 27. ***Dicranoloma leichhardtii***, a moss with both dwarf males and gemmae. Photo by Niels Klazenga, with permission.

Several other examples exist. ***Platygyrium repens*** (Figure 28) produces brood branches and sometimes produces facultative dwarf males (Lars Hedenäs, pers. comm. 8 January 2014). Many species of ***Garovaglia*** (**Ptychomniales**) have both dwarf males and produce filamentous gemmae, with ***G. elegans*** (Figure 29)

producing gemmae rather frequently (Neil Bell, Bryonet 8 January 2014). But despite these examples, Pedersen and Newton (2007) found no correlation between the evolution of dwarf males and the filamentous gemmae in the order **Ptychomniales**.

Figure 28. ***Platygyrium repens*** with bulbils clustered at the branch tips. Photo by Dick Haaksma, with permission.

The problem with trying to interpret these observations is that if a non-expressing individual has propagules, we have been unable to tell if it is a male or a female. Hence, it is difficult to assess the importance of vegetative propagation in males that developed away from a female. Do bryophyte male propagules in any species behave as do nannandrous species of *Oedogonium*, reproducing asexually until they land on a female? Do the gemmae of asexual (sterile) male plants of some species develop into dwarf males if they land on a female substrate? Fortunately, we now have genetic means to identify sex of non-sex-expressing plants using DNA markers. As markers become available in more species, we may be able to answer these questions more easily.

Figure 29. ***Garovaglia elegans*** with capsules. Photo by Li Zhang, with permission.

For my *Oedogonium* comparison to work for bryophytes, we need evidence that asexual propagules, *e.g.* gemmae or bulbils, produced by male plants, are able to germinate on females and produce dwarf males. Tamás Pócs (pers. comm. 14 January 2014) kindly pointed me to his publication (Pócs 1980) on the liverwort ***Cololejeunea borhidiana*** (Figure 30) as a new species. He illustrates a dwarf male, complete with antheridia, developing from a gemma from this species (Figure 30), a much smaller version than a male that develops into a normal-sized plant (Figure 31). This is the only evidence that dwarf males exist among liverworts, and is the only evidence we know of a dwarf male developing from an asexual propagule. The complete story for this species is not known and we have no evidence that the spores ever form dwarf males. However, it suggests the possibility that an asexual strategy for males that fail to land on a female might exist among some bryophytes. ***Cololejeunea borhidiana*** is **epiphyllous** (growing on leaves of other plants), and the ability to produce vegetative plants until a gemma reaches a female to induce formation of a dwarf male could be very advantageous for a species that occupies a somewhat short-lived substrate that is difficult to reach and colonize. But was it a female that stimulated this gemma to become a dwarf male, or was it the current environmental conditions? And is this an isolated occurrence, with dwarf males otherwise unknown in liverworts? Knowledge of gemmae of any bryophyte developing into dwarf males seems to be otherwise lacking, so we cannot measure its importance among the bryophytes. In the case of ***Cololejeunea borhidiana***, we don't know if the gemma came from a male or a female plant. If the nannandrous *Oedogonium* strategy does exist among some bryophytes, it presents an interesting adaptation that could be quite beneficial in difficult habitats.

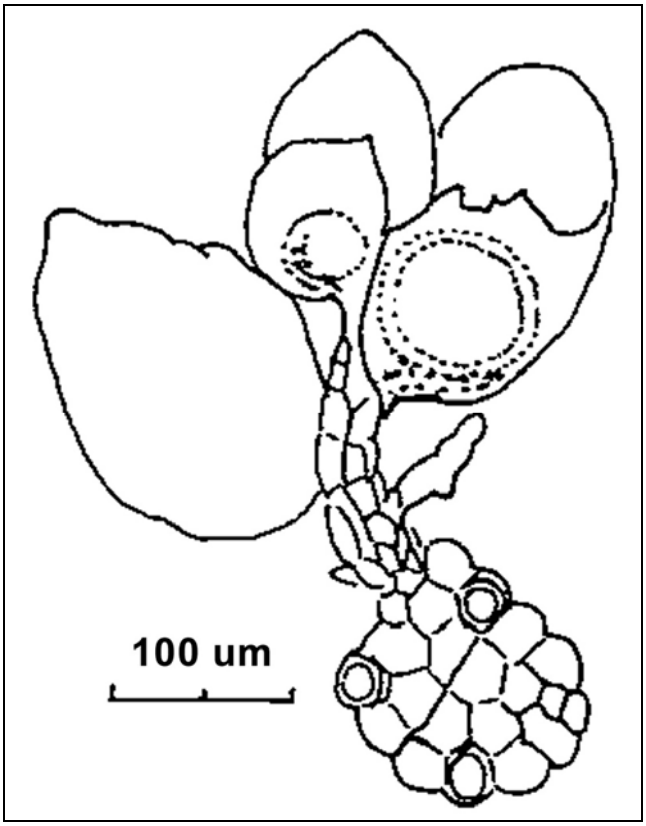

Figure 30. ***Cololejeunea borhidiana*** dwarf male developing from a gemma. Drawing by Tamás Pócs, with permission.

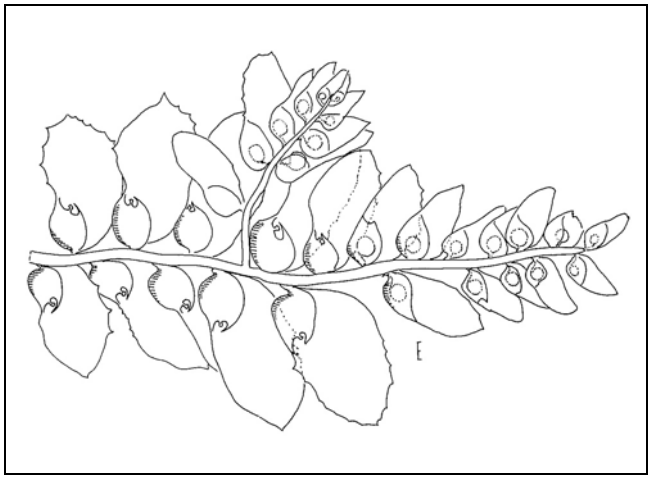

Figure 31. ***Cololejeunea borhidiana*** normal male developing from a gemma. Drawing by Tamás Pócs, with permission.

How Do Facultative Males Develop?

Dicranum has a well-established record of dwarf males. Based on a literature review, Pichonet and Gradstein (2012) estimate that such dwarf males occur in about 20% of the ***Dicranum*** species, with most species being obligately nannandrous. However, in at least two species, ***D. bonjeanii*** (Figure 32) and ***D. scoparium*** (Figure 38), both normal-sized and dwarfed males occur. In this genus, the environment seems important to control male plant size.

Figure 32. ***Dicranum bonjeanii*** showing the dense tomentum that provides a habitat for dwarf males. Photo from Frullania Data Portal, through Creative Commons.

One must ask how a spore can become a full-sized male on soil or other substrate, but when it lands on a female of its own species, it develops into a dwarf. This facultative behavior may support the suggestion of Loveland (1956) that the dwarfism on leaves of the same species was the result of some chemical interaction with the substrate leaf. For example, in ***Trachybryum megaptilum*** (Figure 33) normal-sized males never have dwarf males on them (Wallace 1970), suggesting that the female has some sort of chemical, most likely hormonal, control over expression of the dwarf male – or could it be that the male plant prohibits germination of the male spore.

Figure 33. ***Trachybryum megaptilum***, a moss that may have several hundred dwarf males growing on the female. Photo by Martin Hutten, with permission.

Hormones – Hormonal suppression seems to account for the development of males in a number of taxa (Loveland 1956; Wallace 1969, 1970). In fact, some species prevent growth of males among females, but those spores fortunate enough to germinate away from a female become males (Crum 2001). This would seem to be maladaptive for purposes of fertilization but reduces competition for resources between the sexes.

In the moss genus ***Dicranum*** (Loveland 1956), ***D. drummondii*** (Figure 34), ***D. sabuletorum*** (Figure 35), ***D. polysetum*** (Figure 36-Figure 37), and ***D. scoparium*** (Figure 38) (Preston & Mishler 1997) and in other dimorphic bryophyte species, spores cultured on agar produce normal-sized males, suggesting hormonal control of plant size that is determined by the female. Briggs (1965) provides further evidence in this genus, with those species that have a variety of sizes of males only producing dwarf males in culture when they are grown near females.

Figure 34. ***Dicranum drummondii*** from Europe, a species that produces normal-sized males on agar, but produces dwarf males on female plants. Photo by Michael Lüth, with permission.

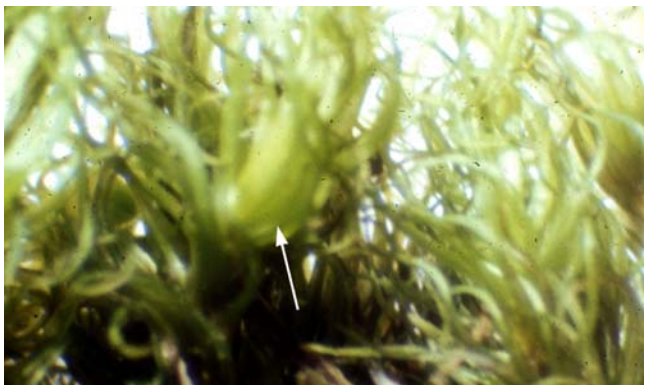

Figure 35. ***Dicranum sabuletorum*** dwarf male (**arrow**) growing on a female plant. Photo by Janice Glime.

Figure 36. ***Dicranum polysetum***, showing tomentum where dwarf males often develop. Photo by Robert Klips, with permission.

Figure 37. ***Dicranum polysetum*** dwarf males on the tomentum of a female. Photo courtesy of Lars Hedenäs.

In ***Leucobryum***, ***L. glaucum*** (Figure 39) and ***L. juniperoideum*** (Figure 40) males can be dwarf to full size (Blackstock 1987). Dwarf males form on the tomentum of ***L. bowringii*** and ***L. juniperoideum*** (Figure 40), but normal males also form on non-***Leucobryum*** substrates (Une & Yamaguchi 2001). Furthermore, Une and Yamaguchi found that dwarf ***Leucobryum*** males removed from the female and grown on a different substrate grew into tall male plants. Suggesting physiological differences between the sexes, males of these ***Leucobryum*** species, particularly normal males, are restricted to lower altitudes and latitudes in Japan, but females are not. This is also the case in some ***Macromitrium*** species (Figure 41) (Ramsay 1979; Une 1985c).

Figure 38. ***Dicranum scoparium*** with dwarf male in Norway. Photo by Michael Lüth, with permission.

Figure 39. ***Leucobryum glaucum*** with tomentum (at arrow) and what appears to be a dwarf male. Photo by Aimon Niklasson, with permission.

Figure 40. ***Leucobryum juniperoideum***, a moss that gets dwarf males on its tomentum. Photo by Jan-Peter Frahm, with permission.

Figure 41. ***Macromitrium*** from the Neotropics. Photo by Michael Lüth, with permission.

There seem to be a number of possible hypotheses to explain ways that hormones from the female could influence the sizes of males.

1. The spore must land and probably germinate before the female produces the "hormone" that determines the size, with the spore or germling serving as a stimulant. Hence, the "hormone" would act on the protonema. This would be like a response to a fungus or herbivory that stimulates production of a secondary compound in seed plants and similar to the response of the alga *Oedogonium* that produces its oogonium after the spore lands on the filament (Rawitscher-Kunkel & Machlis 1962).
2. The "hormone" from the female is highly volatile and thus only works when the spore/protonema/young plant is in direct contact with the plant that provides it. Ethylene could do this.
3. The "hormone" is rendered inactive by contact with soil (binding by soil). That, however, would not explain the epiphytic ***Macromitrium***, assuming bark does not have the binding properties known for soils.
4. The level of "hormone" is too weak anywhere but on the female plant.
5. Similar to 4, but the "hormone" is water soluble and is soon washed away elsewhere, but is continually produced on the female.
6. Similar to 1; there is some sort of complementation between male and female plant – both must be present for the female to produce the "hormone."

Heinjo During (Bryonet 27 February 2009) suggested that the variation in sizes of males may in some cases relate to the **distance from females** (possibly related to hypotheses 2, 4, & 5). He has observed this size variation in ***Leucobryum*** (Figure 39-Figure 40). A possible explanation for this observation is that a hormone gradient exists, but it is also possible there is a male size gradient due to an environmental gradient away from the female colony in this cushion-former. The colony could create this gradient through such factors as moisture retention, nutrient usage, or *p*H alteration.

During (Bryonet 27 February 2009) reports that ***Garovaglia*** (Figure 29) seems to lack those intermediates, with males being either full size (similar to the size of females) on a non-leaf substrate, or dwarf when sitting on a female leaf. During suggests that a lack of intermediates, as in ***Garovaglia***, indicates that dwarfing is genetically fixed and not dependent on effects of female neighbors. One possible explanation is that the large ***Garovaglia*** males are mutants in which the dwarfing is inactivated. We can also consider that if a certain level of hormones is required for dwarf males to develop in a species, a hormonal gradient away from the female could reach a threshold at a certain distance from the female, with those farther away and beyond the threshold becoming full-sized males.

Inhibitors – Absence of dwarf males on older parts of mosses suggests that emission of some inhibitor, perhaps the gaseous hormone **ethylene**, may suppress germination, thus being adaptive by avoiding the waste of energy and resources on a part of the plant too far from apical female reproductive organs for fertilization success. Alternative explanations might be that the stimulant hormone has been leached out of older parts and is not being replaced, or that growth conditions, especially with respect to light, are unfavorable.

Nutrient Considerations – Rod Seppelt (Bryonet 1 March 2009) suggested another possibility – a nutritional limitation. He suggested that when the spore germinates on a moss leaf, it could be at first rain after a dry period. At this time, the moss would leak nutrients due to membrane damage during desiccation. This would provide the nutrients needed for the male plant to start growing, but once the membranes were repaired in the substrate leaf, the nutritional source would be gone, hence limiting the further growth of the male, causing it to be a dwarf. Those spores on soil would obtain nutrients from the soil and the male gametophyte plant could grow to a full size. I have observed this in flowering plants. In one of my early attempts at gardening I grew poppies in very poor soil. Instead of growing to 60 cm tall, they were only 3-4 cm tall, but nevertheless produced miniature flowers. However, Hedenäs and Bisang (2012) could find no support for this nutrient limitation hypothesis in the pleurocarpous mosses they examined. Rather, they observed that dwarf males are most common shortly after spore release, the dwarfs being dead and more difficult to detect during the period before spore maturation.

Genetically Obligatory Dwarfs – In Japanese ***Macromitrium*** (Figure 41), eight species are dimorphic, producing dwarf males (Une 1985a; 2009). In these **anisosporous** (**anisospory** – having 2 spore sizes in the same tetrad following meiosis, see also the section on Anisospory below) species the dwarf males are genetically determined, whereas in **isosporous** (one spore size) species the dwarfness is apparently regulated by hormones from the female plants, with the potential to develop into normal plants in absence of the hormones. In his experiments, Une found that the hormone **2,4-d** (an auxin – growth hormone) caused dwarf males to develop in the **isosporous** species, supporting the hypothesis that hormones produced by the substrate leaf are the factor determining the development into a dwarf male.

Andréa Pereira Luizi-Ponzo (Bryonet 2 March 2009) and her students examined dwarf male biology in ***Orthotrichum*** (Figure 42-Figure 45). They found that in all species that have dwarf males, there are two spore sizes (**anisospory**). In those that exhibit full-sized males, the spores are **isomorphic** (all the same in form and size; Figure 45). So far they have found no species with both dwarf males and full-size males that also exhibit anisospory.

Hedenäs and Bisang (2011) present evidence that the presence of male dwarfism is related to family membership, and that it does not correlate with geographic area. Such examples of dwarf male relatedness occur in the currently configured family **Miyabeaceae**: ***Homaliadelphus***, ***Miyabea***, ***Bissetia*** (Olsson *et al*. 2009). Olsson *et al*. have placed these three genera in the same family, **Miyabeaceae**, based on a molecular phylogenetic analysis. ***Homaliadelphus*** (formerly in **Neckeraceae**; Figure 46) produces normal-sized males or facultatively produces dwarf males, whereas ***Miyabea*** (formerly in **Thuidiaceae**) and ***Bissetia*** (formerly in **Neckeraceae**; Figure 47) produce obligatory dwarf males. ***Homaliadelphus*** has all the spores the same size, but those of the obligatory dwarf male genera ***Miyabea*** and ***Bissetia*** are of two distinct sizes.

Figure 42. ***Orthotrichum lyellii*** habit. This species exhibits **anisospory** and **dwarf males**. Photo by Malcolm Storey at Discover Life, through Creative Commons.

Figure 43. ***Orthotrichum lyellii*** with gemmae (brown structures on leaf margins). Photo by Michael Lüth, with permission.

Figure 44. ***Orthotrichum alpestre***, an isosporous species. Photo by Michael Lüth, with permission.

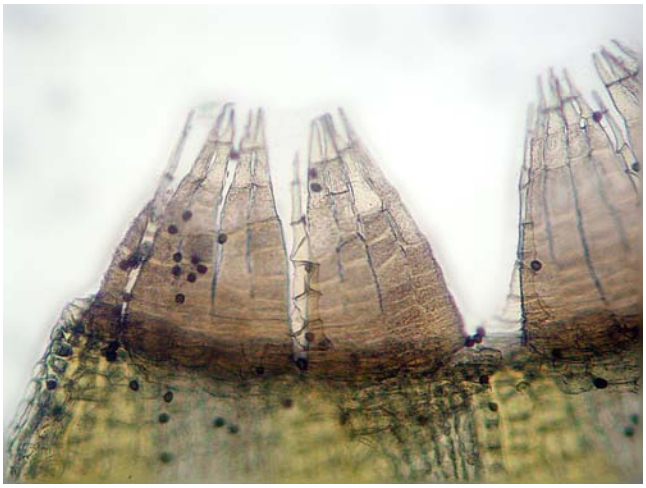

Figure 45. Peristome and spores of ***Orthotrichum alpestre***, an isosporous species. Photo by Michael Lüth, with permission.

Figure 46. ***Homaliadelphus sharpii***. Photo by Paul Redfearn, Ozarks Regional Herbarium, with permission.

Figure 47. ***Bissetia ligulata***, a species of obligatory dwarf males. Photo by Digital Museum Hiroshima University, with permission.

Neoteny vs Progenesis

These two conditions are easy to confuse because they have similar results. **Neoteny** is the condition of slowing down developmental growth (**somatic** or body cell), resulting in sexual reproduction that happens in what was ancestrally a juvenile morphologic stage. **Progenesis** is the condition of developmental growth at a normal rate, but the production of gametangia occurs at a faster rate, resulting in **paedomorphosis** (retention by organism of juvenile traits into later life), *i.e.*, reproduction also happens in what was ancestrally a juvenille morphologic stage. Mishler and DeLuna (1991) consider the development of dwarf males to be **progenesis**.

Dwarf males typically attach to the female by rhizoids (Johannes Enroth, pers. comm 29 December 2020) and at least in ***Garovaglia***#and#***Euptychium*** also protonemata (Heinjo During, Bryonet, 29 December 2020).

Neoteny and progenesis should not be confused with **sexual dimorphism** such as that found in ***Sphaerocarpus*** (Irene Bisang, pers. comm., 28 December 2020).

The Dwarf Male Advantage

So, we repeat the question here, what is the advantage to having a larger female? Lewin (1988) suggests that bigger females may produce more fit offspring; smaller males may have increased mobility (an animal bias but could be applied to small spores); females may survive longer after reaching sexual maturity and continue growing. Do these explanations apply to bryophytes?

For those species with small male spores and large female spores, the greater dispersal distance that correlates with small spore size could be an advantage, especially in species where asexual diaspores are produced by the males. This could eventually increase reproductive success by providing males with greater possibilities to reach females.

Among ***Dicranum majus*** (Figure 48) female plants with dwarf males, there was an 84% success rate in fertilization compared to 75% when including those identifiable females without dwarf males (Sagmo Solli *et al.* 1998). In the northern part of Lower Michigan, monoicous species of mosses achieve the same rate (75%; Rohrer 1982). Also in ***Homalothecium lutescens*** (Figure 20), fertilization rate was positively associated with dwarf male density (Rosengren *et al.* 2014, see above). The dwarf male mechanism seems to ensure fertilization success while wasting little on production of male plant tissue, thus avoiding competition with female plants for resources. Nevertheless, it appears that in some cases males must be reborn each year, as Sagmo Solli *et al.* (1998) were unable to find any males on female ***Dicranum majus*** parts more than one year old.

Figure 48. ***Dicranum majus***, a species with dwarf males from Bretagne. Photo by Michael Lüth, with permission.

So it appears that one strategy of energy conservation and assurance of having males nearby females that works for a number of genera is to dwarf any male that develops on a female plant (Wallace 1970) (see also below, evolutionary drivers). Wallace found that in ***Trachybryum*** (=*Homalothecium*) ***megaptilum*** (Figure 33) only one plant in 200 is a normal-sized male, whereas a single female may have several hundred dwarf male plants growing on her.

Some bryophytes make certain that sperm dispersal distance is absolutely minimal. ***Leucobryum martianum*** (Figure 49) produces rhizoidal heads (Salazar Allen 1989). Yamaguchi (1993) later reported that the characteristic rhizoid formation in ***Leucobryum*** occurs at the lower abaxial side of the inner perichaetial leaves. Young plants develop on this rhizoidal tomentum and this was originally considered a means of asexual reproduction. Further examination revealed that these young plants were actually dwarf males developed from spores, located conveniently close to the archegonia.

Figure 49. ***Leucobryum martianum***, a species with rhizoidal tufts on the inner perichaetial leaves where dwarf males grow. Photo by Jan-Peter Frahm, with permission.

Hedenäs and Bisang (2011) suggest that **evolutionary drivers** toward dwarf males in bryophytes may have included (1) competing selective pressures on cytoplasmic and nuclear genomes, (2) selection for reduced mate competition, in particular when resources are limited, and (3) selection for reduced fertilization distances. In many cases it is likely that combinations of these drivers existed. Furthermore, the associated niche shift of the males may provide them with a habitat that is both humid and nutrient-rich (but see above - nutrient considerations under How Do Facultative Males Develop? by Seppelt).

Dwarf males seem to be sensitive to microclimate, living shorter lives than the females of the species. This resultes in variation of male frequencies among years (Sagmo Solli *et al*. 2000; Rosengren & Cronberg 2014; Lang *et al*. 2021).

Lang *et al*. (2021) investigated the facultative dwarf males in ***Dicranum scoparium*** (Figure 38). They found that numbers of dwarf males differed greatly between sites. When present, the dwarf males usually outnumbered both females and normal males. Genetic variation was low within a locality. It was strongest between cushions for both females and normal males and within cushions of dwarf males. They found indications that inbreeding occurs some of the time.

Species Interactions

If females can inhibit the development of males of their own species through nutrition or hormonal control, can they likewise do this to other species?

Mishler and Newton (1988; Newton & Mishler 1994) experimented with interaction effects of moss leaves and leaf extracts on spore germination. They determined the effect of ***Dicranum scoparium*** (Figure 38) and four species of ***Syntrichia*** (previously in *Tortula*) on ***Syntrichia*** spore germination. Spores planted on agar or sand had normal germination and growth, but spores (either sex) of ***S. ruralis*** (Figure 50) and ***S. laevipila*** (Figure 51) that were planted on ***Dicranum scoparium*** or ***Syntrichia*** leaves either didn't germinate or germinated very slowly. ***Syntrichia princeps*** (Figure 52) germination was inhibited by extracts from leaves of its own species. Even a water extract of ***D. scoparium*** caused a significantly slower spore germination or resulted in significantly smaller plants than those grown with no extracts. At least in this case, it appears that when the inhibition of other species exists, it is to a degree that sexual maturity is not reached. What is puzzling is that in three of the species germination was inhibited by leaf extracts of their own species.

In contrast, spores of ***Homalothecium lutescens*** (Figure 22) and ***H. sericeum*** (Figure 23) both germinated on shoots of the former, but spores of the more distantly related ***Isothecium alopecurioides*** (Figure 16-Figure 17) did not (Rosengren & Cronberg 2015; see above). This suggests that the regulation of spore germination on host shoots is associated with the degree of relatedness between species. In contrast, spores of ***Homalothecium lutescens*** and ***H. sericeum*** both germinated on shoots of the former, but spores of the more distantly related ***Isothecium alopecurioides*** did not (Rosengren & Cronberg 2015; see above). This suggests that the regulation of spore germination on host shoots is associated with the degree of relatedness between species.

Figure 50. ***Syntrichia ruralis*** in Europe. Spore germination in this species is inhibited by extracts of both other members of its own genus and of ***Dicranum scoparium***. Photo by Michael Lüth, with permission.

Figure 51. ***Syntrichia laevipila*** with capsules in Europe. Spore germination in this species is inhibited by extracts of both other members of its own genus and of ***Dicranum scoparium***. Photo by Michael Lüth, with permission.

Figure 52. ***Syntrichia princeps***, a species for which spore germination is inhibited by both ***S. princeps*** and ***Dicranum scoparium***. Photo by Jan-Peter Frahm, with permission.

Spore Differences

Spore differences can account for male-female differences. Mogensen (1981) elaborated on the types of spores in bryophytes; note that these definitions refer to the species, not to individuals, and are based on spore size frequencies (SSF) and mean spore size frequencies (MSSF) across populations:

isospory – one SSF and MSSF; spore mortality none or only a few percent
ex.: ***Fissidens limbatus*** (Figure 53), ***Funaria hygrometrica*** (Figure 54-Figure 55), ***Mnium hornum*** (Figure 56); probably the most common type in bryophytes

[**heterospory** – large female and small male spores present [microspores produced in microsporangia and mega(macro)spores produced in megasporangia] – bryophytes have only one type of sporangium
ex.: not known in bryophytes]

pleurispory – 2 or more SSF grouped around 1-2 MSSF
ex.: ***Ditrichum difficile***

anisospory – SSF and MSSF grouped around 2 mean sizes in 1:1 ratio; probably in 2-3% of mosses
ex.: some ***Orthotrichum*** (Figure 42-Figure 43) & ***Macromitrium*** spp (Figure 41)

pseudoanisospory (= false anisospory) – SSF & MSSF grouped around 2 mean sizes, usually in 1:1 ratio; small spore fraction is aborted
ex.: ***Cinclidium*** spp. (Figure 64), ***Ceratodon purpureus*** (Figure 69), ***Rhizomnium magnifolium*** (Figure 66), ***Fissidens*** spp. (Figure 67), ***Macromitrium*** spp. (Figure 41)

amphispory – SSF & MSSF grouped around 2 mean sizes in varying ratios; small spore fraction is aborted
ex.: ***Pleurozium schreberi*** (Figure 57)

combispory – SSF & MSSF grouped around 3 or more mean sizes; may have aborted spores but also living spores in at least 2 sizes
ex.: ***Macromitrium*** spp. (Figure 41)

Figure 53. ***Fissidens limbatus*** from Europe. Photo by Michael Lüth, with permission.

Figure 54. ***Funaria hygrometrica*** with capsules. Photo by Li Zhang, with permission.

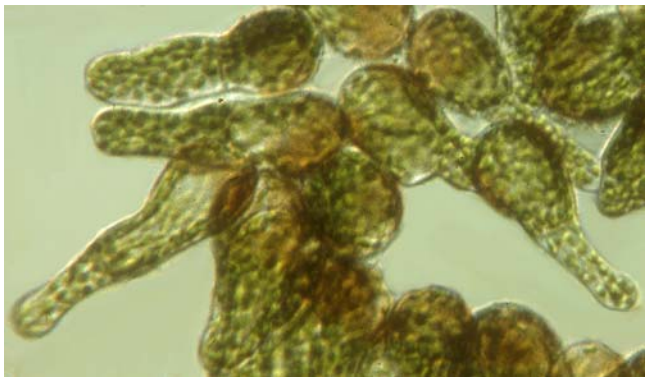

Figure 55. ***Funaria hygrometrica*** spore germination from isosporous spores. Photo by Yenhung Li, with permission.

Figure 56. ***Mnium hornum***. Photo by Andrew Spink, with permission.

Figure 57. ***Pleurozium schreberi*** growing on sand. Photo by Janice Glime.

Anisospory

The "big female" concept has been based on animals, but like so many other evolutionary concepts, the broader concept is applicable throughout living organisms. Haig and Westoby (1988) have applied this concept to the origin of heterospory in plants. But bryophytes are not quite there yet. Instead, they have evolved (in relatively few species) only to **anisospory** with some related variants.

Spores in bryophytes are always **homosporous** and generally **isosporous** (all the same size). **Heterospory** can be defined as bearing spores of distinctly different types; it is the condition when **microspores** are produced in microsporangia and **mega(macro)spores** in megasporangia. Micro- and megaspores differ in size and sex. Heterospory has evolved independently several times in vascular plants, but does not occur in bryophytes. Early diverging ferns are homosporous; several families of aquatic ferns are heterosporous. All bryophytes are homosporous in this sense, all seed plants are heterosporous, and in ferns both conditions exist.

Anisospory in bryophytes refers to a bimodal size difference between spores produced in the same sporangium (Magill 1990). In this case, meiosis results in a tetrad of two small spores that generally produce male gametophytes and two larger spores that produce female gametophytes (Ramsay 1979; Magill 1990).

Anisospory has been reported in a variety of mosses, not just in connection with male dwarfism as described above, with several explanations for their occurrence. But the usage of the term may not always be precise. Pant and Singh (1989) reported several possible cases of anisospory in liverworts: ***Targionia indica***, ***Targionia hypophylla*** (Figure 58), ***Cyathodium aureonitens***, and ***Cyathodium barodae***. They based this conclusion on the wide variations in size of spores, similar to those in the moss family **Orthotrichaceae**. They did not determine sex or viability, hence we cannot eliminate the possibility of **false anisospory**. Multiple spore sizes can occur in bryophytes as a result of unequal growth of the spores, or in some cases abortion of spores (Ramsay 1979). These cases do not have any known relationship to sex.

Figure 58. ***Targionia hypophylla*** with marsupium (black), a structure that houses the archegonia and sporophyte. Photo by Des Callaghan, with permission.

Support for the anisospory concept comes from some species with dwarf males (see paragraphs above). In several dioicous taxa [***Lorentziella***, some ***Macromitrium*** (Figure 41), including the former ***Schlotheimia*** (Figure 59)], small, yellow spores produce males and larger, green spores produce females (Ernst-Schwarzenbach 1938, 1939, 1944). But this differentiation in spore size seems to be rare among the bryophytes.

Alfayate *et al*. (2013) have recently provided irrefutable evidence of anisospory in two more genera – irrefutable because both sizes of spores germinated. In ***Leucodon canariensis*** (Figure 60) viable spores were of two classes - uni- or multicellular, medium-sized (26-48 µm) spores and multicellular, large (50-94 µm) spores. In ***Cryptoleptodon longisetus***, viable spores are likewise of two kinds in the same capsule, unicellular, small spores (11-24 µm) and medium-sized (26-35 µm) spores. Furthermore, in both species, germination was present within the capsules. Somewhat similar anisospory occurs in ***Brachythecium velutinum***, with both sizes germinating (Herguido & Ron 1990).

Figure 59. ***Macromitrium trichomitrium*** (=*Schlotheimia trichomitria*) with capsules. This dioicous genus has small and large spores and produces dwarf males. Photo by George J. Shepherd, through Creative Commons.

Figure 60. ***Leucodon canariense*** in habitat. Photo by Jonathan Sleath, with permission.

False Anisospory – Spore Abortion

Mogensen (1978a) described **false anisospory** (appearing to have two sizes, one chlorophyllous and one not), later (1981) referring to it as **pseudoanisospory**; false anisospory seems to be the terminology most used. Mogensen does not include any sex relationship for this condition.

In several species that exhibit **dimorphic** (having two forms) spores, one can find on closer examination that the small ones are dead (thus not implying a difference in sex) and satisfying the condition Mogensen (1978a) termed false anisospory. (Dimorphic does not imply that the size difference is genetically based.) He first reported aborted spores in ***Cinclidium*** (Figure 61-Figure 64) (Mogensen 1978a) and later in ***Macromitrium japonicum*** (=*M. incurvum*; Figure 65), ***Rhizomnium magnifolium*** (Figure 66), and ***Fissidens cristatus*** (Figure 67) (Mogensen 1978b). In ***Cinclidium arcticum*** (Figure 61-Figure 62) and ***C. stygium*** (Figure 63) 50% of the spores abort, whereas in ***C. subrotundum*** (Figure 64) only 11% abort. It is also known in ***Lorentziella imbricata*** (Figure 68) (Crum 2001). The result is that large, green, live spores cohabit the capsule with small, brown, dead ones.

Figure 61. ***Cinclidium arcticum*** with capsules. Photo by Michael Lüth, with permission.

Figure 62. ***Cinclidium arcticum***, a species in which 50% of the spores abort as the spores mature. Photo by Michael Lüth, with permission.

Figure 63. ***Cinclidium stygium***, a species in which a ~50% of the spores abort as the spores mature. Photo by Michael Lüth, with permission.

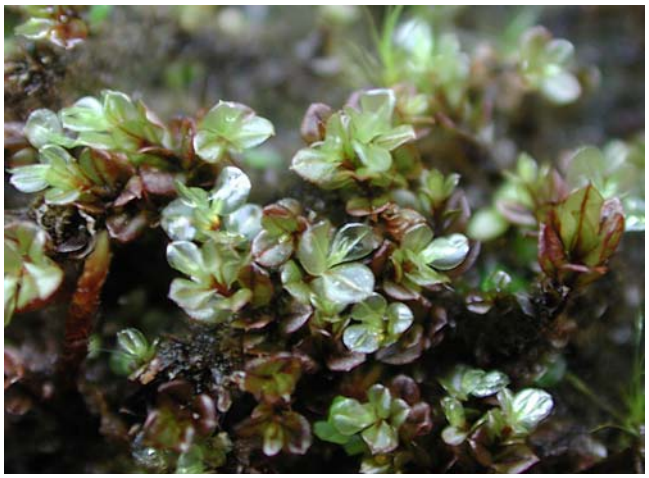

Figure 64. ***Cinclidium subrotundum***, a species in which only 11% of the spores abort. Photo by Michael Lüth, with permission.

Figure 65. ***Macromitrium japonicum***. Photo from Digital Museum of Hiroshima University, with permission.

Figure 66. ***Rhizomnium magnifolium*** from Europe, a species with false anisospory. Photo by Michael Lüth, with permission.

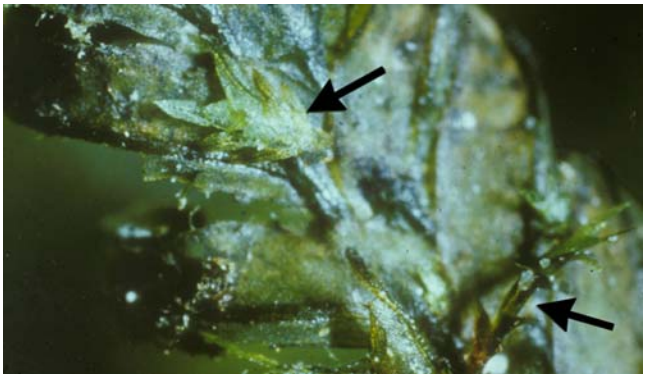

Figure 67. Dwarf males (arrows) on ***Fissidens cristatus***. Photo by Janice Glime.

Figure 68. ***Lorentziella imbricata***. Photo by Claudio Delgadillo Moya, with permission.

Mogensen (1978a, 1981) tracked the spore sizes of ***Cinclidium arcticum*** (Figure 61) as the capsule dried. He concluded that the columella serves as a reservoir of water (Mogensen 1978a). He demonstrated a range of spore sizes in a single capsule and that as the columella dries and shrinks, the smaller spores die first. A similar loss of smaller spores during maturation was present in ***Ceratodon purpureus*** (Figure 69) (Mogensen 1981). Premature drying can cause the operculum to be released before the spores reach their potential size, stopping their development (Mogensen 1981).

Figure 69. ***Ceratodon purpureus*** capsules. Photo by Hermann Schachner, through Creative Commons.

Glime and Knoop (1986) observed a similar phenomenon in the dioicous aquatic moss ***Fontinalis squamosa*** (Figure 70-Figure 75). Because its capsules are constantly wet in nature (Figure 70), it was possible to simulate their maturation conditions in the laboratory and examine the spores at various times during development (Figure 71). In that species, death did not occur to all spores simultaneously. At any point in time during development, large and small spores were present (Figure 72-Figure 75). However, small spores at later points in time were larger than small spores at earlier points in time. It was not clear whether the first degenerate spores disintegrated before larger ones appeared, or if different spores accomplished abortion at different developmental stages. Some already were abortive in their tetrads following meiosis (Figure 75). Glime and Knoop suggest that at least in ***Fontinalis squamosa***, spore abortion is a gradual and continual process as the capsule matures, and that it is determined either randomly or by location of developing spores in the capsule, rather than by genetic predetermination. This species is not known to have dwarf males. The smaller spores had a much lower germination rate.

Figure 70. ***Fontinalis squamosa*** var. ***curnowii*** with capsules, showing their tough structure. Note the perichaetial leaves that cover about half the capsule. Photo by David T. Holyoak, with permission.

Figure 71. Longitudinal section through capsule of ***Fontinalis squamosa*** showing the tightly packed spores. Photo by Janice Glime.

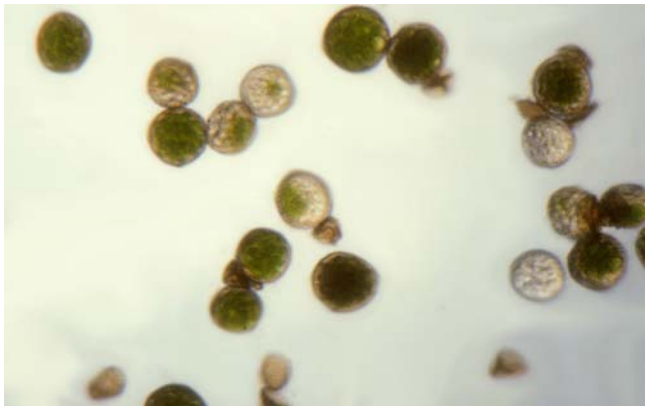

Figure 72. Spores of ***Fontinalis squamosa*** showing large, healthy green spores, smaller white dying or dead spores, and small brown spores that may be dead. These are not anisosporous because they are not of two sizes at the end of meiosis. Photo by Janice Glime.

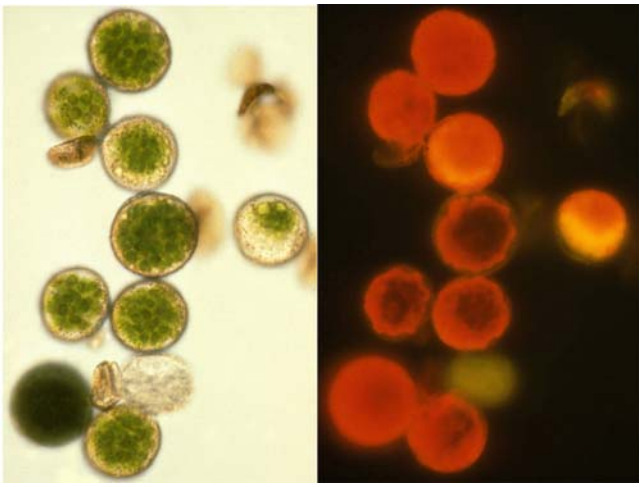

Figure 73. Normal and aborting spores of ***Fontinalis squamosa*** in white light (**left**) and the same spores fluorescing under ultraviolet light (**right**), showing red healthy spores and yellow or green dying spores. Note the lack of fluorescence in the small, deflated spores and the yellow edges of some that are beginning to abort. Smaller spores with no remaining chlorophyll are not visible in this image through fluorescence. Photo by Janice Glime.

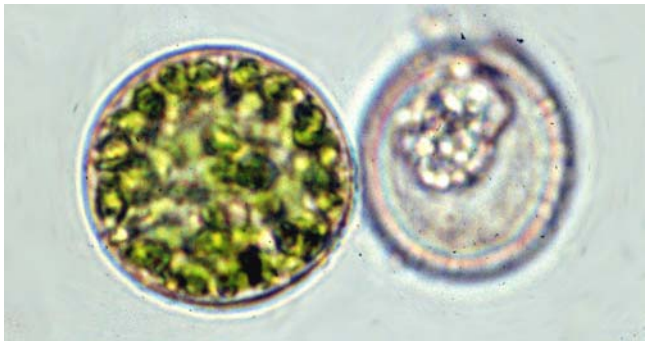

Figure 74. Normal (**left**) and smaller aborted (**right**) spores of ***Fontinalis squamosa***. Photo by Janice Glime.

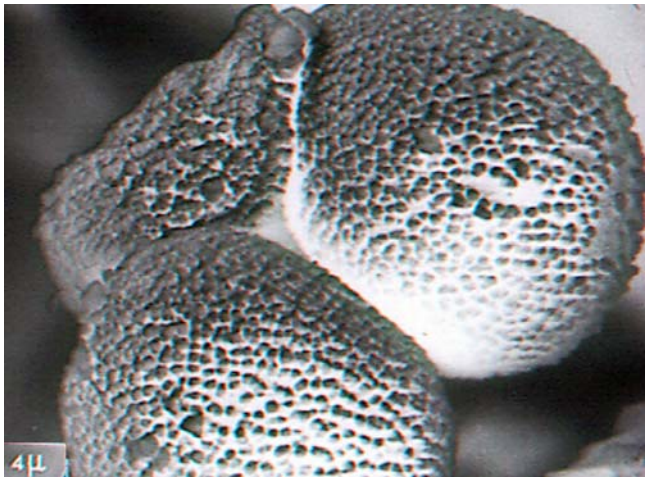

Figure 75. Tetrad of spores from ***Fontinalis squamosa***. Note one abortive spore. Photo by Janice Glime.

Zander (1972) reported a similar situation for ***Leptodontium viticulosoides*** var. ***viticulosoides*** (Figure 76). In this case, the seeming anisospory was actually a large, chlorophyllous spore and a small, non-chlorophyllous spore, *i.e.* false anisospory. The small spores were, as in most for ***Fontinalis squamosa*** (Figure 74), not viable. So I would add another possibility, although with absolutely no proof for ***Fontinalis*** or any other species. If the smaller spores in some species are indeed viable, they could produce a smaller gametophyte due to reduced starting nutrition. In this case, a leaf producing inhibitory substances would not be needed. However, such a function for small spores is not known for ***Fontinalis*** or any other bryophyte.

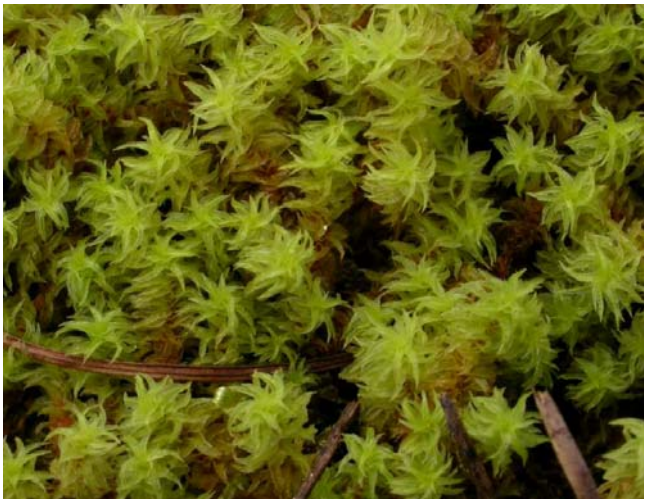

Figure 76. ***Leptodontium viticulosoides***. Photo by Li Zhang, with permission.

Rhizomnium punctatum (Figure 77), a species closely related to ***Rhizomnium magnifolium*** (Figure 66), provides further support for the hypothesis that false anisospory can result from the progressive abortion of spores during the stages leading up to spore maturity. This species exhibits false anisospory during early capsule development but in the mature capsule the spores are isosporous (Mogensen 1978b). Mogensen further points out that there is no correlation of spore size with the monoicous or dioicous condition, at least in his small sample of taxa.

Figure 77. ***Rhizomnium punctatum*** with capsules in Europe, a species in which mature spores are isosporous. Photo by Michael Lüth, with permission.

But not all capsules have the progressive abortion we have been describing. In ***Bryowijkia ambigua***, abortion

occurs in the tetrad stage, with two spores aborting and two presumably remaining viable (De Luna 1990). This brings to mind the image a spore tetrad from ***Fontinalis squamosa*** above (Figure 75) where one visible spore is likewise aborted in the tetrad stage. In the case of ***F. squamosa***, spore abortion may begin as early as the tetrad and continue throughout development, or it might be that I have misinterpreted the continual abortion throughout development. Nevertheless, as seen in Figure 78, three spores can abort in one tetrad, suggesting that the number of abortions is not a programmed event in the tetrad stage.

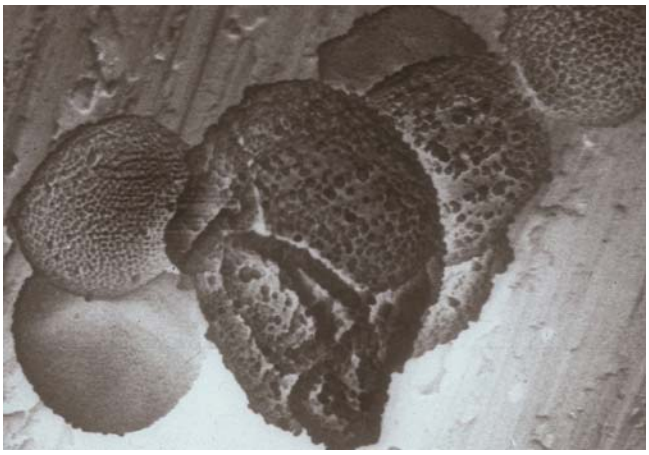

Figure 78. ***Fontinalis squamosa*** showing what to be three aborted spores in one tetrad. Photo by Janice Glime.

Figure 79. ***Bryowijkia ambigua***, a species in which spore abortion occurs in the tetrad stage. Photo by Li Zhang, with permission.

It is likely that abortion of some spores is the rule among bryophytes, and it would be interesting to investigate how widespread the process is. It might be that in seasons of low water or nutrient availability the abortion is more common. This would be an interesting topic to explore for both its control and its adaptive value. The number of studies of changes in spore size during sporogenesis are insufficient to make accurate generalizations. Mogensen (1981) suggests that the abortion is a selection against certain genotypes, and he (1978a) interpreted this phenomenon to be a genetic factor that is lethal to a fraction of the spores prior to vegetative growth of the spore. Without further detailed study we cannot rule out random abortion between the sexes or resource-related abortion, perhaps based on crowding, water availability, or nutrient availability.

Evolution of Spore Differences

In studying the evolution of heterospory in ferns, Haig and Westoby (1988) predicted that sporophytes would produce spores of a size that would maximize return in gametophyte fitness per unit investment. He postulated that the evolution of heterospory would occur in three steps:

1. a gradual increase of spore size in a homosporous population
2. the sudden introduction of smaller microspores
3. subsequent divergence in size and specialization of the two spore types.

This implies that larger spores would occur in those taxa that depend on stored reserves of the spore for successful reproduction. No surprises there. Their model predicts that because there are only minimal costs for male reproduction compared to that of female reproduction, larger food reserves would therefore evolve for female reproduction. Following this model, above some critical spore size, the population can be invaded by smaller spores that are predominately males (assuming that small spores travel farther?).

If one continues with this logic, it would then imply that the population would have few large females and more small males. A larger number of small males would increase chances of some of these males being near a female and strategically placed so that sperm can reach and fertilize the egg. Whenever male reproductive cells must travel by themselves to the female, many will be lost, literally unable to find the female, or perishing before the distance is accomplished. Hence, such a system will necessarily require many male gametes. In bryophytes, by having many small gametophytes, it would be possible for more gametophytes to occupy available small spaces near the female and offer more opportunities for successful fertilization.

The theory presented by Haig and Westoby (1988) would seem to make sense for the heterosporous ferns where the gametophyte is contained within the spore wall. And it makes sense for the seed plants where male gametophytes can travel reasonably long distances. But does this concept really work for evolution of anisosporous bryophytes where the sporophyte and sporangia have no sex distinction and the gametophyte is **exosporic** (develops outside the spore wall)? The number of male and female spores produced in the bryophyte case should be equal, dividing in a 1:1 ratio at meiosis, at least in the absence of sex ratio distorters. The model would only seem to be applied in bryophytes if size differentiation occurred after meiosis, during spore development. Then, it would require that being a small spore caused differentiation into a male while larger spores containing more stored nutrients became female. But unlike heterosporous ferns such as *Marsilea*, the bryophytes do not have gametophyte development and fertilization within the spore wall and the spore is not used to nourish the developing embryo. And to satisfy the Haig and Westoby model, the distinction in

spore size would have to favor few large spores and many small spores. This possibility cannot be ruled out, and there may be some support for it in ***Fontinalis*** (Figure 70-Figure 75), where a distinction between small and large spores occurs throughout spore development (Glime & Knoop 1986), but linkage of size, number, and sex has not been established.

Advantages of Anisospory and False Anisospory in Bryophytes

One must wonder if the progressive death of spores is a waste of energy, or a way of saving or even providing resources. Dead spores may serve a useful function by reducing the rate and extent of desiccation, and by reducing the drain of nutrients, until the remaining spores are larger and crowded, thus protecting each other. Finally, they could be a reservoir of nutrients readily available as they abort. It would be interesting to explore whether seasons of low water or nutrient availability increase the percent abortion.

Whereas the anisosporous condition seems to be favorable for dioicous taxa, the false anisosporous condition can occur in monoicous taxa (Mogensen 1981), but is not restricted to them. This leads us to consider the space-nutrient need as a possible selection factor for false anisospory.

New Methods

Our understanding of bryophyte sexuality should become increasingly easier with the development of molecular techniques. Pedersen *et al*. (2006) amplified DNA from nine mosses and one liverwort. This technique permitted them to obtain sufficient DNA from a single dwarf male of ***Dicranum scoparium*** (Figure 38). This will permit us to study genetic variation even in such small plants as dwarf males.

Summary

Males and females can differ in non-sexual ways, including size, biomass, branching, maturation rate, chlorophyll content, and photosynthetic rate and other physiological traits. Large female and small male plants (**dwarf males**) are known among bryophytes, but not the converse, except in non-sporophytic ***Diphyscium***. Most dwarf males develop on the leaves or tomentum of females of the species. Dwarf males are often missed in surveys and this omission can cause misleading results in sex ratio determination. Spores of some species develop dwarf males on females of the species but normal males on other substrates. Dwarfism can increase the success of fertilization while decreasing the competition for resources with the females.

Bryophytes are **isosporous**, but some species exhibit **anisospory**; some exhibit **false anisospory** due to abortion of spores. The anisosporous condition seems to present a potential advantage for fertilization when it is correlated with the presence of dwarf males. On the other hand, this strategy reduces the dispersal of the larger female spores compared to that of the smaller male spores. This is less of a problem if nearly all females get fertilized. Many **anisosporous** and **false anisosporous** conditions occur in species with no dwarf males (Mogensen 1981). This causes us to seek other explanations for their presence, including abortion related to water, space, and nutrient limitations within the capsule. The abortions can provide room for remaining developing spores while maintaining protection and resources for them.

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CHAPTER 3-4
SEXUALITY: REPRODUCTIVE BARRIERS AND TRADEOFFS

JANICE M. GLIME AND IRENE BISANG

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CHAPTER 3-4
SEXUALITY: REPRODUCTIVE BARRIERS AND TRADEOFFS

Figure 1. ***Funaria hygrometrica***, a monoicous species showing numerous capsules. Photo by Michael Lüth, with permission.

Reproductive Barriers: Selfing and Hybrids

Bryophytes are fundamentally different from tracheophytes by having a dominant haploid generation. Since many bryophytes can produce both antheridia and archegonia on the same plant (Figure 1), self fertilization (**selfing**) is likely to occur. Reproductive barriers to prevent selfing are important components of speciation. As long as genes are able to mix and appear in new offspring, the populations involved will be unable to become distinct species (Anderson & Snider 1982). When two species reside within centimeters of each other, they may receive sperm from the other species. We might expect some of the same mechanisms to prevent both selfing and hybridization.

Linley Jesson (pers. comm. 25 January 2014) used allozyme markers and successive innovations to measure selfing rates between individuals expressing one sex (in one year) and individuals expressing both sexes. Her (unpublished) work has shown extensive hybridization in the ***Atrichum*** (Figure 2-Figure 3) complex.

Selfing and Inbreeding Depression

Selfing in bryophytes can happen in two ways: intragametophytic and intergametophytic. **Intragametophytic selfing** is self-explanatory, where the crossing occurs between antheridia and archegonia on the same ramet (branch/gametophore), and can thus occur only

in unisexual bryophytes. Being **gametophyte** (haploid) and **monoicous** (having male and female reproductive organs on same gametophyte plant) means that all gametes are produced by mitosis, hence are identical. Therefore, any result of intragametophytic self-fertilization (sometimes also referred to as 'true self fertilization' or **autogamy**) results in a sporophyte that is homozygous for every trait!

Figure 2. Female ***Atrichum undulatum*** showing perichaetial leaves. Photo by Janice Glime.

Figure 3. Male ***Atrichum undulatum*** showing male splash cups. Photo by Janice Glime.

Intergametophytic selfing, therefore, is a specific type of inbreeding where mating occurs between separate gametophytes produced by the same sporophyte (Klekowski 1969; Krueger-Hadfield 2013). This is the only form of selfing that is possible in **dioicous** (male and female reproductive organs on separate gametophyte plants) bryophytes, where the two sexes are, by definition, on different plants. It is genetically comparable to selfing as the term is applied in heterosporous seed plants (see, *e.g.*, Shaw 2000). When meiosis occurs in a dioicous bryophyte sporophyte, some spores will give rise to female plants and some to male plants. Those will not be identical, due to independent assortment during meiosis, but will be siblings. When those siblings mate (**inbreeding**), those events in bryophytes are considered to be **selfing**. If one considers the event in flowering plants, meiosis occurs in separate male and female sporangia, and makes separate gametophytes, so the gametes, even from the same plant, are not identical and are no more closely related than bryophyte gametophytes developed from separate spores. Hence, whether spores develop enclosed within the sporophyte (flowering plants) or on the substrate (bryophytes), if they came from the same sporophyte and they cross, it is selfing.

Since inbreeding results from fertilization by close relatives such as siblings or in bryophytes between ramets of the same gametophyte, this may imply duplicating deficient genes or inheriting absence of genes. In tracheophytes, this typically results in decreased fitness. Some organisms are protected from this wasted energy and decreased fitness by having mechanisms to suppress inbreeding, such as different maturation times of male and female parts on the same individual. Others express the inbreeding depression in the offspring, typically by reduced fitness. But based on tracheophytes, we are accustomed to evaluating the effects of inbreeding in diploid organisms, not haploid generations such as the leafy bryophyte gametophyte. Nevertheless, inbreeding is an expected consequence of monoicous bryophytes with limited capacity for sperm dispersal.

Fortunately, at least some bryophytes have mechanisms to prevent self-fertilization (Ashton & Cove 1976), but Crum (2001) assumed that most were self-fertilized because the sperm and eggs mature at the same time on the same plant (but see Chapter 3-2 on Protogyny and Protandry in this volume). Ashton and Cove (1976) showed experimentally that among six strains of ***Physcomitrella patens*** all were self-sterile, but certain combinations were cross-fertile. In this case, the self-sterility resulted from mutations to the nicotinic acid and p-aminobenzoic acid genes. Hence, incompatibility can result from missing but necessary genes, and these are supplied by having an outside partner. Does this mean the incompatibility affects the embryo? But abortion later in sporophyte development is also possible. Nevertheless, Maciel-Silva and Válio (2011), examining bryophyte sexual expression in Brazilian tropical rainforests, found that monoicous species used strategies that increased their chances for out-crossing. For example, they produce unisexual branches as well as bisexual ones. It is further possible that self-infertility is widespread; we simply have not gathered the data needed to understand the extent of its distribution, as proposed by Stark and Brinda (2013). These authors suggest incompatibility after self-fertilization in a clonal line of the monoicous ***Aloina bifrons*** (Figure 4). They also refer to reports of self-incompatibility in ***Desmatodon cernuus*** and mutants of ***Physcomitrella patens*** (Figure 5). Modern DNA techniques should make it relatively easy to determine this.

Figure 4. ***Aloinia bifrons***, a monoicous species that seems to be self-incompatible. Photo by Martin Hutten, with permission.

Figure 5. ***Physcomitrella patens*** on soil. Photo by Michael Lüth, with permission.

Although truly self-fertilizing monoicous taxa pass on the full complement of genes to all their offspring, each sporophyte is in fact a separate **genet** (group of genetically identical individuals) that results from a single fertilization (Eppley *et al.* 2007). The sporophyte has no normal means of spreading vegetatively, so that genet cannot spread. Hedrick (1987) suggested that the complete homozygosity that results from intragametophytic selfing in monoicous bryophytes should select for extremely high inbreeding depression, but Eppley *et al.* (2007) considered that elimination of those (spores?) with deleterious alleles resulting from the inbreeding would remove those genotypes from the population and remove the inbreeding depression in future generations, hence favoring selfing. But dioicous species predominate, so we must examine the situation further.

Eppley *et al.* (2007) suggest that it is the level of intergametophytic selfing that maintains dioicy. If the level of selfing is low in dioicous bryophytes, accumulating deleterious alleles in the diploid stage would create a high cost for selfing through such effects as sporophyte abortion. Hence, the cost of selfing may maintain separate sexes. On the other hand, if selfing is high in both mating systems, deleterious genes would cause selection against both sexual strategies and select for monoicy due to higher fertilization rates. Eppley and coworkers found low or non-existent selfing in a mean of 41% of the sampled five dioicous species. If their reasoning is correct, this could explain the high level of dioicy in bryophytes when compared to flowering plants.

Selfing in bisexual bryophytes is evidenced by high F_{is} values (*i.e.*, a measure of heterozygote deficiency) observed in the sporophytic phase of all bisexual species investigated so far (Eppley *et al.* 2007; Hutsemekers *et al.* 2013; Johnson & Shaw 2015; Klips 2015; Rosengren *et al.* 2016). Using allozyme electrophoresis to estimate the deviations from expected heterozygosity, *i.e.* to estimate inbreeding, Eppley *et al.* (2007) estimated **selfing rates** for 10 species of New Zealand mosses. As one might expect, monoicous species had significantly higher levels of heterozygote deficiency (more selfing) than did dioicous species (inbreeding coefficient=0.89±0.12 and 0.41±0.11, respectively). An unexpected result, however, was to find that in two dioicous species [***Polytrichadelphus magellanicus*** (Figure 6-Figure 7) and ***Breutelia pendula*** (Figure 8)], there were significant indications of mixed mating or biparental inbreeding in a handful of populations.

Figure 6. ***Polytrichadelphus magellanicus*** females. Photo by Tom Thekathyil, with permission.

Figure 7. ***Polytrichadelphus magellanicus*** males with splash cups. One appears to be a female, possibly from the same clone. Photo by David Tng, with permission.

Figure 8. ***Breutelia pendula***. Photo by Tom Thekathyil, with permission.

The classical explanation for the success of dioicous plants, based on tracheophyte literature, is that inbreeding, a product of having both sexes on the same plant, decreases fitness. In that case, one might assume that bryophytes, like other plants, have some mechanism of inbreeding depression (Beatriz Itten, Bryonet 26 May 2005). That is, they have some lethal or deleterious allele that gets expressed, leading to death or greatly reduced success. If such a gene is expressed in the haploid gametophyte, it is eliminated, rather than depressed, due to death of the individual.

In an attempt to remedy the absence of experimental data, Taylor *et al.* (2007) tested inbreeding depression in a monoicous and a dioicous moss species. Somewhat contrary to expectations, inbreeding depression occurred in the dioicous ***Ceratodon purpureus*** (Figure 9); crossing between siblings of the opposite sex significantly reduced fitness in both seta length and capsule length out of the four traits they examined. By contrast, the monoicous ***Funaria hygrometrica*** (Figure 10) exhibited no evidence of inbreeding depression in seta length, spore number, capsule mass, or capsule length. Jesson *et al.* (2011) found that hermaphroditism (monoicy) increased selfing rates rather than depressing them in ***Atrichum undulatum*** (Figure 2-Figure 3). Furthermore, they failed to demonstrate significant inbreeding depression in monoicous individuals of this species.

Figure 9. ***Ceratodon purpureus*** with sporophytes in a mixed population of males and females. Photo by Christian Hummert through Creative Commons.

Szöveni *et al.* (2009) noted in dioicous ***Sphagnum lescurii*** (Figure 11) that sporophyte size was correlated with the level of heterozygosity, in line with the prediction of inbreeding depression. This species experienced multiple paternity among sporophytes of a single female, enabling preferential maternal support of the more heterozygous embryos, which suggested active inbreeding avoidance and a possible post-fertilization selection. In contrast, inbreeding depression did not appear to be common in either dioicous or monoicous species in a multi-population study of 14 ***Sphagnum*** species (Johnson & Shaw 2015), despite that monoicous species exhibited higher levels of inbreeding than dioicous ones.

Figure 10. ***Funaria hygrometrica*** in southern Europe. Photo by Michael Lüth, with permission.

Figure 11. ***Sphagnum lescurii*** with ***Thuidium delicatulum***. Photo by Bob Klips, with permission.

Although further research on inbreeding depression in bryophytes is necessary, the evidence above suggests that the effects of bryophyte inbreeding are mitigated by the rapid purge of deleterious mutations during the gametophytic stage (Taylor *et al*. 2007; Jesson *et al.* 2011; Johnson & Shaw 2015). In particular, bisexual species are thought to rapidly purge recessive deleterious mutations through intra-gametophytic selfing (*i.e.* merging of gametes produced by shoots from the same protonema and hence, originating from the same spore. (See also below, Hybrid Success.)

Flowering plants frequently have mechanisms to prevent selfing. Could it be that monoicy in bryophytes is so recent that bryophytes have not yet evolved mechanisms to discourage it, or is it that they don't need to depress selfing, as implied by some of the above-cited studies? The former seems unlikely in view of evidence of many reversals indicated above (see also Chapter 3-1 in this volume).

We can suggest possible mechanisms to prevent selfing. As mentioned above and in Chapter 3-2, these might include timing (antheridia and archegonia mature at different times), as well as mechanisms of self incompatibility during fertilization or development. Hypotheses for possible mechanisms include:

1. rejection of sperm with same genotype (reminiscent of autoimmune diseases)
2. need for gene complementation to develop
3. embryo abortion
4. failure at meiosis

However, it would seem that any post-fertilization mechanism (2-4) would be wasteful (but see Szövényi *et al*. 2009, above), so selection should be greater for those species that can reject their own sperm, hence still allowing for subsequent outcrossing.

Could it be, then, that bryophytes are different from other major plant groups? Patiño *et al*. (2013) consider that **Baker's law** – as the loss of dispersal power and the bias toward self-compatibility after immigration to islands – applies to bryophytes. To defend this assertion, they cite evidence that the proportion of monoicous taxa was significantly higher on islands, and that a significant proportion of continental species that are monoicous or dioicous are represented on oceanic islands only by monoicous populations. This argument assumes a Founder Principle in which few colonists arrived and contact with the opposite sex was impossible. But it is also true that monoicous populations from the continent would have a greater chance of arriving on the island due to the greater ease of fertilization and spore production on the mainland. The shifts in life history traits toward a greater proportion of species producing asexual propagules and smaller proportion of species producing spores point to the loss of long-distance dispersal ability of bryophytes on oceanic islands.

Reduced Fitness

One consequence of selfing can be reduced fitness. This is illustrated in ***Atrichum undulatum***. Populations in the ***Atrichum undulatum*** complex (Figure 2-Figure 3) contain females, males, and hermaphrodites, and hermaphrodites can have sex organs in close proximity or spatially separated across branches. In their experiments Jesson *et al*. (2012) found that there was significant selfing within gametophytes, whereas there was no significant selfing between siblings, supporting the importance of proximity for fertilization. But what is the price for this selfing? They found that sporophyte size did not differ between sibling (**intergametophytic**) and **intragametophytic** selfing, but other factors suggest reduced fitness for products of selfing. Sporophytes from females contained 29% more spores than those from monoicous (~30% selfed on same branch) individuals. When the cultures were stressed by supplying only tap water instead of a nutrient medium, only the progeny from females (*i.e.* non-selfed) survived on tap water after 6 months (Figure 12). Progeny of females transplanted onto tap water media had a greater photosynthetic capacity but higher non-photochemical quenching than did the monoicous individuals, causing these females to have photosynthetic rates similar to those of the monoicous progeny. These are weak effects of partial selfing, but under certain stressful conditions may result in lower survival among progeny that are the product of selfing.

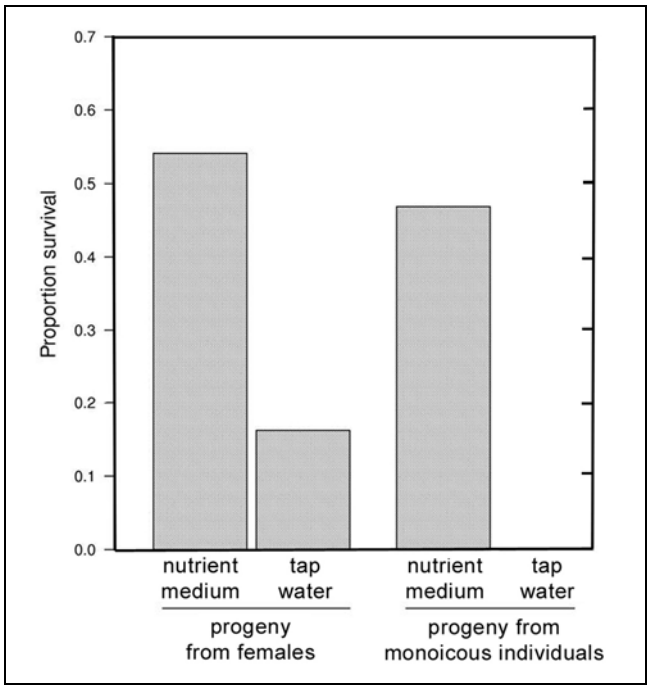

Figure 12. Proportion of culture plates with spores from females (n=39) compared to progeny of monoicous individuals (n=30) of ***Atrichum undulatum*** s.l. (Figure 2-Figure 3) germinating after 6 months on nutrient medium (Bold's basic media) vs tap water (stressful condition). Modified from Jesson *et al*. 2012.

Hybridization

Hybridization is the opposite of reproductive isolation. In the past, bryologists tended to consider hybridization in bryophytes to be unimportant (Andrews 1942; Vitt 1971; Smith 1978, 1979; Anderson 1980). But in fact, it seems to be widespread among bryophytes (Ruthe 1891; Nyholm 1958; Andrews & Hermann 1959; Crundwell & Nyholm 1964; Proskauer 1967; Ochi 1971; Delgadillo 1989; Schuster 1991; Ros *et al.* 1994; Natcheva & Cronberg 2004), often confounding attempts at cladistics when hybrids are among the data sets (Xu 2000).

It is interesting that among the bryophytes gametophyte hybrids seem only to exist in mosses, at least based on genetic information (Natcheva & Cronberg 2004). A number of hybrid liverwort species have been suggested, based on morphology, but so far few have been supported by genetic/molecular data – see, for example ***Targionia hypophylla*** (Figure 13) (Boisselier-Dubayle & Bischler 1999). Summarizing data, Natcheva and Cronberg concluded that moss hybrids usually occur among the "weedy" species with life history strategies of fugitive, annual, and short-lived shuttle or colonist, *i.e.*, species with life spans of only a few years.

Figure 13. ***Targionia hypophylla***. Photo by Ken-Ichi Ueda through Creative Commons.

Intergeneric Hybrids

Intergeneric Hybrids – It is even more interesting that within the **Polytrichaceae** there are apparent **intergeneric hybrids.** ***Polytrichastrum pallidisetum*** (Figure 14-Figure 15) and ***Polytrichastrum ohioense*** (Figure 16) both appear to have had one progenitor in ***Polytrichastrum*** and one in ***Polytrichum*** (Figure 43) (Derda & Wyatt 2000). ***Polytrichastrum sexangulare*** (Figure 17) appears to have had a species of ***Pogonatum*** (Figure 18) as one of its progenitors (but then, the mosses may classify themselves differently from the way we currently do and place themselves all in ***Polytrichum***).

Figure 14. ***Polytrichastrum pallidisetum*** with capsule. Photo by Štěpán Koval, with permission.

Figure 15. ***Polytrichastrum pallidisetum*** with capsules from Europe. Photo by Michael Lüth, with permission.

Figure 16. ***Polytrichastrum ohioense*** females. Photo by Janice Glime.

Figure 17. ***Polytrichastrum sexangulare***, a species produced by hybridization. Photo by Michael Lüth, with permission.

Figure 18. ***Pogonatum urnigerum*** with numerous capsules at Swallow Falls, Wales. Photo by Janice Glime.

Hybrid Success

Sphagnum (Figure 19-Figure 21) is a genus where polyploids are common (see also 3.1., Genome Doubling). Ricca *et al.* (2011) point out that we might expect all occurrences of polyploidization to result in instant sympatric speciation. But they cite several cases, *e.g.* ***S. lescurii*** (Figure 11), in which the resulting hybrid produces triploid sporophytes that are larger than those of the parents, but most of the spores are not viable. Furthermore, the spores that do germinate develop their sporelings more slowly. But such species are able to persist because of the pervasive vegetative reproduction. And some day in the future, some genetic error might enable successful spore reproduction.

Shaw *et al.* (2012) demonstrated **homoploid hybridization** (no change in chromosome number) and allopolyploidy in multiple species of ***Sphagnum***. In the ***S. fimbriatum*** (Figure 19) complex they found one species with diploid gametophytes. Based on plastid DNA sequences, all samples of the polyploid ***S. tescorum*** (Figure 20) share an identical haplotype with most samples of ***S. girgensohnii*** (Figure 21). Fixed or nearly fixed heterozygosity at ten microsatellite loci show that ***S. tescorum*** is an allopolyploid. Many other examples indicating the role of hybridization in creating species differences are known in this genus.

Figure 19. ***Sphagnum fimbriatum*** with capsules. Photo by David Holyoak, with permission.

Figure 20. ***Sphagnum tescorum*** in Alaska. Photo by Vita Plasek, with permission.

Figure 21. ***Sphagnum girgensohnii*** with open capsules. Photo by Janice Glime.

Flatberg *et al*. (2006) studied natural hybrids between haploid female ***Sphagnum girgensohnii*** (Figure 21) and diploid male ***S. russowii*** (Figure 22). These hybrids were discovered because when ***S. girgensohnii*** was in the presence of ***S. russowii***, large capsules formed. The spores from these crosses yielded viable spores that produced triploid protonemata and juvenile gametophores in culture. ***Sphagnum russowii*** is itself a hybrid of ***Sphagnum girgensohnii*** and ***S. rubellum*** (Figure 23). Not only were the capsules larger in the ***S. girgensohnii*** x ***S. russowii*** cross, but spores were larger as well. Nevertheless, spore germination from this hybrid was less than 5%, which is much less than when ***S. girgensohnii*** is crossed with others of its own species. Hence, while these hybrids may make a few super plants, the numbers of offspring are greatly reduced. Even so, through vegetative reproduction such a population could expand and grow.

Figure 22. ***Sphagnum russowii***. Photo by Blanka Shaw, with permission.

Figure 23. ***Sphagnum rubellum***. Photo by Jan-Peter Frahm, with permission.

It is fitting, then, to conclude that barriers to cross breeding among species are incomplete in the bryophytes and that evolution of new species through hybridization may occur somewhat frequently in this group. This suggestion is supported by the apparent lack of external barriers to cross fertilization and the nearly total absence of sperm vectors to help enforce same species selection.

When Barriers Are Needed – or Not

Eppley *et al*. (2007) conclude that for taxa that are colonizers and must be able to self-fertilize in repeated colonization events, being self-compatible is an evolutionary advantage. This permits them to establish and spread rapidly in a new location. This is also suggested by Baker's law, which was recently found to apply for bryophytes (Patiño *et al*. 2013; see above).

In seed plants, elaborate modifications help to ensure that the male gametophyte (pollen grain) will disperse and reach the appropriate female gametophyte, where it will release sperm and effect fertilization. Specialized behaviors of pollinators also ensure that self-pollination is minimal. Such specialized facilitators (**external isolating mechanisms**) are rare in bryophytes, but other environmental mechanisms exist. As in seed plants, reproductive isolation that prevents hybrids in bryophytes may also result from various **internal isolating mechanisms** or a combination of internal and external isolating mechanisms (Natcheva & Cronberg 2004).

In bryophytes, the spore is needed for dispersal, and being small permits a greater distance for that dispersal than that of many seed plant pollen grains. On the other hand, dispersal of the sperm of the bryophyte to the female reproductive organ lacks the protection and carrier capability of a pollen grain in tracheophytes and must get there by other means. As already discussed (Cross Fertilization in Chapter 3-1 of this volume), these gametes are motile and most of them must be transported in water or swim through a film of water. Thus, gene flow in bryophytes is affected by both gamete flow distances and spore dispersal distances. Anderson and Snider (1982) further contend that bryophyte establishment is more hazardous than that of seed and seedling establishment (see also Wiklund & Rydin 2004; Cleavitt 2005; Söderström & During 2005). These limitations make it advantageous to be bet-hedgers (having more than one strategy; see below) and permit at least some self-fertilization.

Effects of different reproductive barriers might be seen in the lack or scarcity of sporophyte formation. Bisang and Hedenäs (2008) transplanted males of the dioicous fen moss ***Drepanocladus trifarius*** (Figure 24) into the center of female patches. They could not observe any sporophytes in archegonia in the 'swollen venter stage.' Rather, the archegonia were withered or dehisced. Using a similar experimentation in forest habitats, the dioicous ***Rhytidiadelphus triquetrus*** (Figure 25) produced capsules freely, with 100% of the plots exhibiting sporophytes (Bisang *et al*. 2004). ***Abietinella abietina*** (Figure 26), on the other hand, had sporophytes in only 41% of the plots. Furthermore, these ***A. abietina*** sporophytes maintained their calyptrae and did not dehisce when they should have; 36% of the capsules aborted. These examples demonstrate that not only lack of one sex or spatial segregation of the sexes are responsible for lack of capsules in dioicous bryophytes, but multiple factors may have an influence and probably interact. ***Hamatocaulis vernicosus*** (Figure 27) fails to produce capsules in France; only embryonic sporophytes were observed in more than 12,000 studied archegonia from 45 localities (Pépin *et al*. 2013). A combination of factors related to sexual phenology and environment is required for sporophytes to be produced: sex expression of mixed-sex colonies, short distance between sexes, light grazing, and high water table.

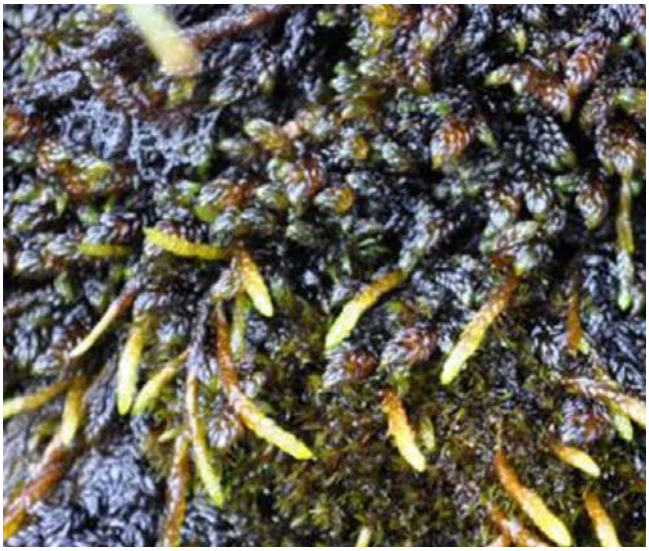

Figure 24. ***Drepanocladus trifarius***. Photo by Andrew Hodgson, with permission.

Figure 25. ***Rhytidiadelphus triquetrus***. Photo courtesy of Eric Schneider.

Figure 26. ***Abietinella abietina***. Photo by Janice Glime.

Figure 27. ***Hamatocaulis vernicosus***, a species that requires a limiting combination of environmental and sexual conditions to produce sporophytes. Photo by Des Callaghan, with permission.

Anderson and Snider (1982) summarized these differences and presented the reproductive barriers "used" by bryophytes. Bryophyte reproductive barriers can, as in seed plants, be divided into external and internal barriers (Anderson & Snider 1982).

External Barriers

Spatial or Geographic Isolation

For spatial or geographic isolation to occur, the distance between biotypes must be greater than the spore dispersal distance. That is more a theoretical limit than a practical one because spores can occasionally travel great distances through the atmosphere. Nevertheless, the greater the distance, the smaller the chance for genetically compatible biotypes to join. This same external barrier applies to sperm, which rarely travel more than a meter. However, as Anderson and Snider (1982) and much earlier Gayet (1897) suggested, it has by now been demonstrated that **mites**, **springtails**, and other small invertebrates can not only carry the sperm from male **perigonia** to female **perichaetia**, but in some cases facilitate much greater fertilization than in their absence (Cronberg *et al.* 2006; Rosenstiel *et al.* 2012; Bisang *et al.* 2016). Furthermore, we now know that some small portion of sperm are likely to survive even desiccation (Shortlidge *et al.* 2012), permitting survival during a much greater dispersal distance. Nevertheless, short-distance spatial separation is much more effective as an isolating mechanism among bryophytes than among tracheophytes.

Bryophytes, like tracheophytes, often exhibit incomplete isolation (Natcheva & Cronberg 2004). For example, some geographic races of the liverwort ***Sphaerocarpos texanus*** (Figure 28-Figure 29) are partly reproductively isolated whereas others are fully interfertile (Allen 1937). The hornwort ***Phaeoceros*** (Figure 30) has good reproductive isolation among species, but under some circumstances geographic races of ***Phaeoceros laevis*** (Figure 30) are able to interbreed (Proskauer 1969).

Figure 28. ***Sphaerocarpos texanus*** involucres of male plants, looking very much like archegonia! Photo by Paul Davison, with permission.

Figure 29. ***Sphaerocarpos texanus*** female. Photo by Martin Hutten, with permission.

Figure 30. ***Phaeoceros laevis*** with sporophytes. Photo by Bob Klips, with permission.

Ecological Isolation

A second external barrier is ecological isolation. In this case, the biotypes are confined to different habitats, making crossing unlikely. These differences were difficult to identify until recently because one had to do common garden or transplant studies to determine if perceived morphological differences were environmentally induced or genetically based. Such environmental plasticity differences have been especially noticeable for species that occur both in and out of water. And often transplanted populations did not succeed or looked different from any established field population. Now advances in the use of genetic markers permit us to identify different variants of a species. These may eventually be expressed as races, cryptic species, or microspecies, and if isolated long enough may evolve into separate species.

Ecological isolation in bryophytes is closely tied with spatial isolation because of the typical short distance of sperm dispersal. If they are close enough for the sperm to reach the archegonium, the microhabitat is not likely to differ much.

Seasonal Isolation – Gametangial Timing

In some locations, timing or climate can make one gender unable to complete its task. Seasonal isolation, as in pollination, can cause male and female gametangia to mature at different times (see Protogyny and Protandry in Chapter 3-2). Species that arrive by long distance travel may lack the necessary environmental triggers at the appropriate time to ensure that gametangia are coordinated. New arrivals may not be coordinated with established populations. Hence, if male and female propagules arrive at different times or from different places, they may be seasonally incompatible, a factor that can also isolate wind-pollinated members of the same genus among seed plants. This mechanism may be incomplete, working as an isolating mechanism in some years but not in others, depending on the weather.

We seem to have little verification of seasonal isolation in bryophytes. We do know that timing of male and female gametangial maturation can differ in monoicous bryophytes (Anderson & Lemmon 1973, 1974; Longton & Miles 1982; Shaw 1991). This mechanism can successfully isolate the eggs from being fertilized by sperm from the same plant (See Protogyny and Protandry in Chapter 3-2).

Speculation suggests that seasonal isolation is effective among several species of ***Sphagnum*** (Natcheva & Cronberg 2004). Other speculations include ***Weissia*** (Khanna 1960; Williams 1966), and the geographic races of ***Anthoceros*** (Proskauer 1969). A combination of phenology studies and genetic information revealing closely related **sympatric taxa** (having overlapping distributions) should reveal some examples.

Internal Barriers

In addition to external barriers, internal barriers may exist. Natcheva and Cronberg (2004) referred to these as reproductive isolation.

Gametic Isolation

Gametic isolation is a mechanism known from algae, animals, and tracheophytes, but it appears to be lacking, or perhaps simply unknown, in bryophytes. Wiese and Wiese (1977) define it in the green alga *Chlamydomonas* as nonoccurrence of initial contact between non-compatible gamete types. In other words, the opposite gene types such as sperm and egg cannot find or attract each other. In *Chlamydomonas*, gamete contact depends on molecular complementarity between **glycoproteinaceous** components. Parihar (1970) suggested that in bryophytes attractive substances such as sugars or proteins might help to guide the sperm to the archegonium and hence to the egg, but the importance and exact identity of such substances remains to be studied. (See Sperm Dispersal by the Bryophyte in Chapter 3-1.)

Natcheva and Cronberg (2004) found no studies to support the hypothesis that bryophytes produce substances to hamper or prohibit foreign sperm from entering the neck of an archegonium or to prevent penetration of the egg. In fact, Showalter (1926) showed that both moss and liverwort sperm [***Aneura*** (Figure 31), ***Sphaerocarpos*** (Figure 29-

Figure 28), ***Asterella*** (Figure 80), and ***Funaria*** (Figure 38-Figure 39)] were able to penetrate the egg cells of the liverwort ***Fossombronia*** (Figure 81). Duckett (1979; Duckett *et al.* 1983) even reported that sperm of ***Mnium hornum*** (Figure 32) were able to penetrate the egg cells of the tracheophyte ***Equisetum*** (Figure 33).

Figure 31. ***Aneura pinguis***, a possible sperm donor for the liverwort ***Fossombronia***. Photo by Li Zhang, with permission.

Figure 32. ***Mnium hornum*** males, potential sperm donors for such different taxa as *Equisetum*. Photo by David T. Holyoak, with permission.

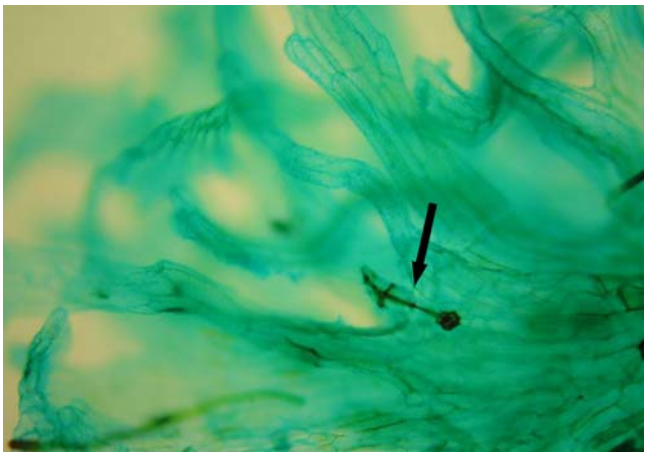

Figure 33. *Equisetum* prothallus with archegonium (**arrow**). Note the neck projecting from the gametophyte. Eggs of this species can be penetrated by sperm of other phyla, including the moss ***Mnium hornum***. Photo by Ross Koning, with permission.

Nevertheless, it does appear possible that the archegonium may attract and perhaps trap the sperm. In most cases, when the archegonium is mature and ready to receive the sperm, the neck canal cells and ventral canal cell disintegrate and exude a gelatinous matrix from the opening of the archegonial neck (Watson 1964). This has been considered the attracting substance, but others consider it a means of entrapment.

Since we know little about this entrapment in bryophytes, let's consider a well-known fern example. In the fern *Marsilea*, sperm reach the gelatinous matrix extruded by the archegonium when the neck canal opens. Once "entrapped" by the matrix, sperm are all directed toward the neck of the archegonium, which they enter, albeit slowly. Although Machlis and Rawitscher-Kunkel (1967) argue that these *Marsilea* sperm are trapped rather than attracted, it is significant that all sperm are clearly pointed toward the archegonial neck. Machlis and Rawitscher-Kunkel cite Strasburger (1869-1870) for a description of the massing of sperm at the opening of the neck canal in ***Marchantia polymorpha*** (Figure 34-Figure 35), suggesting that this likewise was entrapment in a gelatinous matrix surrounding the opening of the neck canal. Machlis and Rawitscher-Kunkel further cite Pfeffer (1884) as confirming observations of chemotactic responses of sperm to archegonia in the liverworts ***Marchantia polymorpha*** (Figure 34-Figure 35) and ***Radula complanata*** (Figure 36) and mosses ***Brachythecium rivulare*** (Figure 37), ***Funaria hygrometrica*** (Figure 38-Figure 39), and ***Leptobryum pyriforme*** (Figure 40). Alas, no substance he tested attracted the two liverwort sperm. Sperm of ***Brachythecium rivulare***, ***Funaria hygrometrica***, and ***Leptobryum pyriforme*** responded to sucrose, whereas the pteridophytes examined responded to malate. Parihar (1970) reported that sperm of the thallose liverwort ***Riccia*** (Figure 41) were attracted by proteins and inorganic sources of potassium.

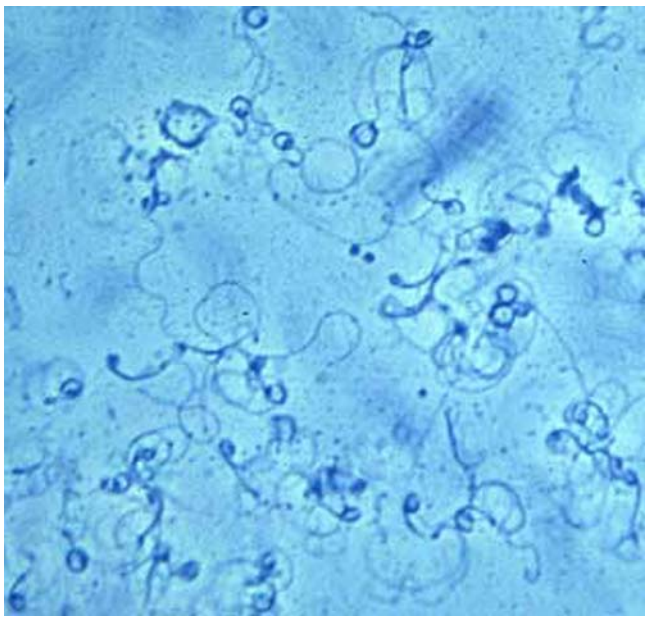

Figure 34. ***Marchantia polymorpha*** sperm swarming. Photo from Botany 321 website at the University of British Columbia, with permission.

Figure 35. ***Marchantia polymorpha*** with immature archegonium with neck canal cells intact (**left**) and archegonium venter with large purplish egg and sperm attached, penetrating the egg. When the neck canal cells break down, they exude a mucilage that attracts the sperm. Photo by Janice Glime.

Figure 36. ***Radula complanata*** with dehisced sporophytes. Photo by Michael Lüth, with permission.

Figure 37. ***Brachythecium rivulare***. Photo by David T. Holyoak, with permission.

Figure 38. ***Funaria hygrometrica*** males with splash cups. Photo by James K. Lindsey, with permission.

Figure 39. ***Funaria hygrometrica*** archegonia with emerging sporophytes covered by calyptrae. Photo by Andrew Spink, with permission.

Figure 40. ***Leptobryum pyriforme*** with capsules in Sweden. Photo by Michael Lüth, with permission.

Figure 41. ***Riccia sorocarpa***, a thallose liverwort that attracts its sperm by proteins and inorganic sources of potassium. Photo by Michael Lüth, with permission.

These early observations were somewhat hit or miss and did not clarify what substances in the archegonia had attractive powers. Furthermore, Showalter (1928) reported that in the thallose liverwort ***Riccardia*** (Figure 42) the collapsed cells of the archegonial neck played no role in attraction.

Figure 42. ***Riccardia latifrons*** with emerging capsules. This species does not seem to produce a sperm attractant when the archegonial neck cells disintegrate. Photo by Michael Lüth, with permission.

More recent compendia ignore the topic completely (Chopra & Bhatla 1990; Crum 2001; Vanderpoorten & Goffinet 2009). We find it hard to believe that the archegonia of bryophytes lack such attractants. But are they able to attract only specific sperm? Perhaps it is the clonal nature of bryophytes that decreases the likelihood of a foreign sperm finding the egg. Nevertheless, specialization occurs, as demonstrated by studies where invertebrates carry the sperm to archegonia that attract those insects (Rosenstiel *et al*. 2012).

Genetic Incompatibility

Stenøien and Såstad (2001) contend that bryophytes might experience inbreeding depression through genes that are silenced in the gametophyte phase but expressed in the sporophyte phase. Experimental evidence for this is beginning to emerge.

McLetchie (1996) found that in the dioicous liverwort ***Sphaerocarpos texanus*** (Figure 29-Figure 28), increasing inter-mate distance and decreasing male size reduced sporophyte production, thus suggesting sperm limitation. On the other hand, when three males and three females were mated in a factorial design resulting in nine unique crosses, sporophyte production was very low in some pairs of genotypes known to be fecund in other combinations. McLetchie suggested that genetic interactions may be responsible for some of the low levels of sexual reproduction in dioicous bryophytes. This would suggest that genes from a different population might be less compatible.

Genetic incompatibility was also suggested as one potential explanation for rare and incomplete sporophyte formation in dioicous ***Abietinella abietina*** (Figure 26) in a transplantation experiment (Bisang *et al.* 2004). But detailed data on the mechanisms in bryophytes are lacking. Natcheva and Cronberg (2004) could find no data indicating abortion of embryos in bryophytes and we are unaware of anything more recent. Nevertheless, Van Der Velde and Bijlsma (2004) found that up to 90% of the hybrid sporophytes from the crossing of ***Polytrichum commune*** (Figure 43) x ***Polytrichum uliginosum*** (=*Polytrichum commune* var. *uliginosum*; Figure 44) were aborted. Despite this poor reproductive performance, ***P. uliginosum*** has been considered to be a synonym of ***P. commune*** var ***commune*** (Kew 2014), but Kew currently lists it as ***Pogonatum uliginosum***.

Figure 43. ***Polytrichum commune*** 2-year growth. Photo by Michael Lüth, with permission.

Figure 44. ***Pogonatum uliginosum*** male plants with antheridial splash cups. Photo by Hermann Schachner, through Creative Commons.

Hybrid Sterility

Internal isolation among bryophytes is usually manifested by sterility of the hybrid sporophyte (Natcheva & Cronberg 2004). Nevertheless, hybrid sterility seems to be less important in bryophytes than in tracheophytes. There are numerous examples of presumed hybrids in mosses, in many cases being the mechanism of becoming monoicous. One consequence of fertilization from the wrong species is that the reproduction following that cross is unsuccessful. For example, sporophytes from these individuals typically produce many non-viable spores. But, since bryophytes are clonal, vegetative reproduction can lead to populations of ramets that are compatible with each other because all have the same number and type of chromosomes. There have also been a number of presumed interspecific hybrids noted in natural populations. Wettstein (1923) experimented with hybridization in the **Funariaceae** and was able to produce phenotypes that could also be observed in the field.

Bryophytes have two known types of **sterility barriers**: chromosomal sterility and developmental sterility. **Chromosomal (segregational) sterility** results from structural differences in chromosomes of the two parental species, causing disruption of pairing during meiosis and ultimately resulting in spores with incomplete chromosome sets or extra chromosomes. This type of sterility is known in pairing between ***Ditrichum pallidum*** males (Figure 45) and ***Pleuridium acuminatum*** (Figure 46, Figure 47), a case in which few spores formed and those that did aborted (Anderson & Snider 1982). The hybrid has intermediate characters of seta length, differentiated but indehiscent operculum, and spores of variable size (Andrews & Hermann 1959). Finally, Anderson and Snider (1982) reported almost a complete lack of chromosome pairing in hybrids between ***Pleuridium subulatum*** (Figure 48-Figure 49) (*n*=26) and ***P. acuminatum*** (Figure 47) (*n*=13).

Figure 45. ***Ditrichum pallidum*** with capsules, a species that hybridizes with ***Pleuridium subulatum***, producing hybrid sporophytes with intermediate characters but that do not function normally. Photo by Michael Lüth, with permission.

Figure 46. ***Pleuridium acuminatum*** with sporophytes. Photo by Jonathan Sleath, with permission.

Figure 47. ***Pleuridium acuminatum*** with capsules. Photo by Jan-Peter Frahm, with permission.

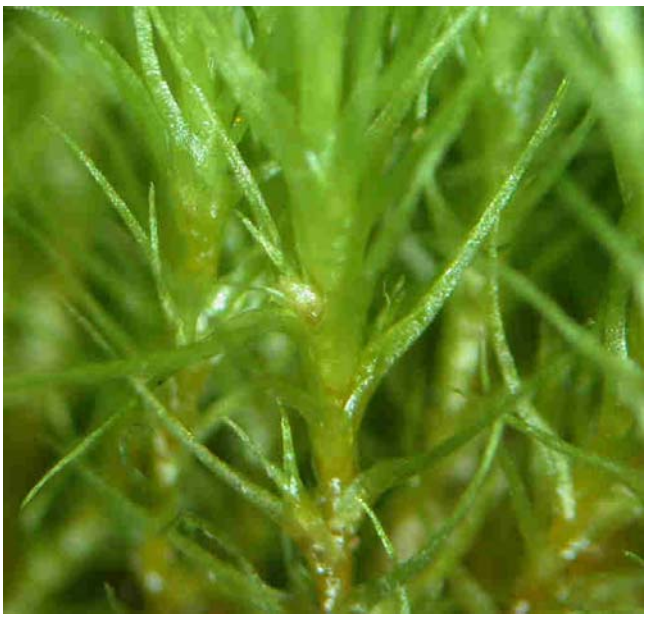

Figure 48. ***Pleuridium subulatum*** with axillary buds with antheridia. Photo by David Holyoak, with permission.

Figure 49. ***Pleuridium subulatum*** with capsules, a species that hybridizes with ***P. acuminatum*** but hybrids subsequently exhibit failure of chromosome pairing. Photo by Kristian Peters, with permission.

Consider that of the numerous spores formed in some species, it seems likely that there will be the occasional spore that gets the right set of chromosomes during pairing of meiosis. But wait, spores normally are protected by other spores, and as we have seen, those other spores die slowly as some continue to enlarge and reach maturity. Those other spores help to maintain moisture and may even provide nutrients as needed in the maturing capsule, so this massive abortion could explain why those normal spores generally are not able to reach maturity in a capsule lacking protection by other spores due to abortion during or immediately following meiosis.

Developmental sterility occurs when hybridization successfully produces a new plant, but it is developmentally different from its parents. Typically, these plants are sterile, producing what appeared to be normal tetrads of meiospores, but lacking viability. Wettstein (1923) suggested that one explanation was that the paternal set of chromosomes was unable to function in the maternal cytoplasm. There are other possibilities of incompatibility between the two sets of chromosomes – chromosomes that led to production of incompatible or lethal substances or that interfered with timing mechanisms.

These hybridization phenomena occur in nature as well as in the lab, as in the well known examples of hybrids between ***Astomum*** (Figure 50) and ***Weissia*** (Figure 51) (Nicholson 1905; Andrews 1920, 1922; Reese & Lemmon 1965; Williams 1966; Anderson & Lemmon 1972). These hybrids between ***Astomum*** (Figure 50) and ***Weissia*** (Figure 51) resulted in sporophytes that were intermediate in seta length, capsule shape, operculum being present but non-dehiscent, and presence of a rudimentary peristome (Nicholson 1905; Andrews 1920, 1922; Reese & Lemmon 1965; Williams 1966; Anderson & Lemmon 1972).

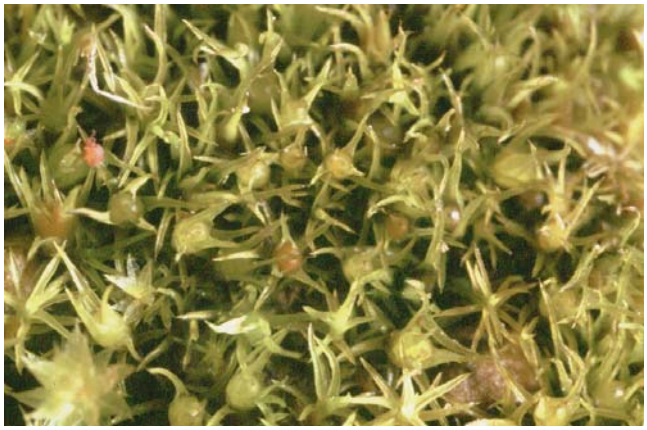

Figure 50. ***Astomum crispum*** with capsules, member of a genus that is able to produce hybrids. Photo by Jan-Peter Frahm, with permission.

Figure 51. ***Weissia muhlenbergianum*** with capsules, a species with chromosome numbers of *n*=13 and *n*=26. Photo by Bob Klips, with permission.

But if one tracks chromosome numbers in bryophytes, it becomes clear that some of these hybrids have succeeded in making new species (see 3.1, Genome Doubling in Mosses). Hence, from the basic chromosome number of 10 in bryophytes, we find that ***Weissia*** (=*Astomum*) ***muhlenbergianum*** (Figure 51) has a basic number of *n*=13 and *n*=26 (Reese & Lemmon 1965; Anderson & Lemmon 1972). It is interesting that all hybrids in these two genera occur with ***Astomum*** as the gametophyte female parent. Is that merely a problem of human perception of what constitutes the two genera?

In the cross of ***Weissia ludoviciana*** with ***W. controversa*** (Figure 52) and of ***W. muhlenbergiana*** (formerly placed in *Astomum*) (Figure 51) with ***W. controversa***, meiosis proceeded normally (Anderson & Lemmon 1972). But during the maturation and differentiation of the spores, abnormalities occurred, including spore abortion, failure to enlarge, retention in tetrads, and failure to develop chlorophyll.

Figure 52. ***Weissia controversa*** var. ***densifolia*** with capsules. Photo by Barry Stewart, with permission.

It is likely that many species experience both selfing and cross fertilization. These species necessarily either lack reproductive barriers or have barriers with incomplete effectiveness. For example, in the polyploid (*n*=18) monoicous liverwort ***Plagiochasma rupestre*** (Figure 53), both self fertilization and cross fertilization occur (Boisselier-Dubayle *et al.* 1996). Using two isozyme markers, Boisselier-Dubayle and coworkers determined that the two chromosome sets behave independently.

Figure 53. ***Plagiochasma rupestre*** with two archegoniophores. Photo by Michael Lüth, with permission.

Apomixis?

Ozlem Yayintas asked me if mosses have apomixis. That stopped me short. I understand it in seed plants – seeds are produced without fertilization due to a failure in meiosis. Dandelions have apomixis. But do bryophytes? If so, what would define it?

Hans Winkler (1908) defined **apomixis** as replacement of the normal sexual reproduction by asexual reproduction, without fertilization. Bryophytes certainly have lots of forms of asexual reproduction that fit his original definition. But as time passed, the definition narrowed and is often restricted to production of seeds without fertilization, a definition that cannot fit bryophytes. If we stay with Winkler's original definition, bryophytes have exhibited chromosome doubling through autoploidy, but they also have created sporophytes from gametophytes, fitting more closely with the seed definition (see Sporophytes from Fragments in Chapter 3-1 of this volume).

We turned to Google to see what others have said about apomixis in bryophytes. We found a 2013 study in which the researchers removed the KNOX2 gene and caused apomixis in a bryophyte (Elder 2013)! Sakakibara *et al*. (2013) deleted the KNOX2 gene in the moss ***Physcomitrella patens***, the bryophyte version of a lab rat, and caused it to develop gametophyte bodies from diploid embryos without meiosis. It may sound easy, but it is a lengthy process. The next step for the food world is to knock out that gene in hybrid food plants, create apomictic offspring, and have reliable seeds with the hybrid characters they want, representing two sets from the mother.

Vegetative Apomixis?

Terminology evolves as our knowledge evolves, and we find that some bryologists use the broader definition of Winkler (1908). This confuses those familiar with the seed plant definition. As suggested by Katja Reichel (Bryonet 21 February 2014), perhaps it is best not to define it for bryophytes, i.e., don't use it. She cites the ambiguity of the earlier definition by Åke Gustafsson (1946) that includes every form of asexual reproduction in plants, compared to Gustafsson's later definition as **agamospermy**, which means seed formation without fertilization. But Täckholm (1922) had already clearly defined apomixis in higher plants as being divided into two groups of phenomena: agamospermy and vegetative multiplication. Richards (1997) removed the vegetative form of apomixis in the chapter Agamospermy in his 2nd edition of Plant Breeding Systems, arguing that it is not a breeding system. No matter how we choose to define it, the damage has been done and confusion will continue to reign.

Reichel refers us to Goffinet and Shaw (2009) for a discussion of apogamy and apospory: a life cycle without sex and meiosis, where the term is avoided in a discussion where its use would be appropriate with the broader definition. Similarly, information on apomixis can be found in the discussion of asexual reproduction in mosses by Newton and Mishler (1994).

"But who knows," Reichel continues, "perhaps we just do not have enough data to find sporophytes producing 2n spores after a failed attempt at meiosis (this would, I think, be equivalent to 'diplospory' in seed plants) etc!" We agree with Reichel: "Since the frequency and importance of all this in nature appears to be largely in the dark and/or controversial, perhaps it's still more important to describe what is seen than to try to find the right box and label."

Reproductive Tradeoffs

When conditions are constant, we can expect either sexual or asexual reproduction to dominate, ultimately to the loss of the other (Brzyski *et al.* 2014). But conditions are not constant, and year-to-year or habitat variations can favor one reproductive system in some years and the other system in other years (Bengtsson & Ceplitis 2000; Bowker *et al*. 2000). That is, the relative fitness varies among years and habitats. For example, in ***Marchantia inflexa*** (Figure

54), females invested more in asexual reproduction in man-made environments relative to females in natural habitats, and relative to males in similar habitats (Brzyski *et al.* 2014).

Figure 54. ***Marchantia inflexa***. Photo by Scott Zona, with permission.

Cost of Sexual Reproduction

But what is the cost of producing a sporophyte, or more generally, of reproducing sexually? The basic assumption is that reproduction is costly, *i.e.* that a tradeoff exists between present reproduction and future performance (cost of reproduction) (Bell 1980; Williams 1996). Ehrlén *et al.* (2000) provided the first estimates of cost of sporophyte production, using the moss ***Dicranum polysetum*** (Figure 55) by experimentally manipulating sexual reproduction. They estimated that 74.8% of the total carbon allocation into top shoots during the study interval of about one year went to sexual structures in sporophyte-producing shoots. Shoots that aborted all sporophytes had significantly higher growth rates in the top shoots than did those with sporophytes. The difference in the mass of vegetative apical growth between control shoots and shoots in which sexual reproduction was manipulated was mainly because of different length increments. Mass per unit length was similar between groups.

In the same species, ***Dicranum polysetum*** (Figure 55), Bisang and Ehrlén (2002) found by examining patterns of growth and reproduction in shoots that females invest 16% of their productivity, as measured by photosynthetically active gametophyte biomass, into reproduction leading to sporophytes, but only 1.3% when eggs remain unfertilized, providing evidence of reproductive cost. Consequently, there is a negative correlation between development of mature sporophytes and annual shoot segment and innovation size. Sporophyte development further reduced the probability of future perichaetial development and mass of new perichaetia. It appears that the gametophyte and sporophyte must compete for limited resources within the plant.

Figure 55. ***Dicranum polysetum***, one of the few bryophytes producing multiple sporophytes from one gametophyte apex. Photo by Janice Glime.

Laaka-Lindberg (2001) explored biomass allocation in the leafy liverwort ***Lophozia ventricosa*** var. ***silvicola*** (Figure 65). She found that females allocated an average of 24% of their biomass to sexual reproduction whereas males allocated only 2.3%. Gametangial shoots had shorter stem length and modified branching patterns.

Costs for sporophyte formation were also demonstrated in other species, measureable as lower shoot elongation in ***Entodon cladorrhizans*** (Figure 56) (Stark & Stephenson 1983), less favorable size development and branching patterns in ***Hylocomium splendens*** (Figure 57) (Rydgren & Økland 2002, 2003), and decreased regeneration capacities in ***Pterygoneurum ovatum*** (Figure 58), ***Tortula inermis*** (Figure 59) and ***Microbryum starckeanum*** (Figure 60) (McLetchie & Stark 2006; Stark *et al.* 2007, 2009, and references therein). Stark *et al.* (2009) induced sporophytic abortion in ***Pterygoneurum ovatum***, and subjected plants to upper leaf removal and nutrition amendment treatments. The sexually reproducing plants were less likely or were slower to regenerate tissues or parts (protonemata or shoots). Nutrient amendment had no effect on ability or time of sexual reproduction or on the ability to regenerate clonally. Removal of leaves around the sporophyte base made the sporophytes slower to mature, less likely to mature, and smaller than those with their normal leaves remaining. Hence, there appears to be a cost in future development due to sexual reproduction.

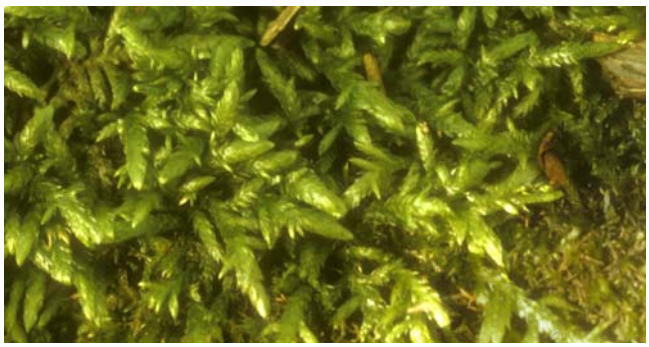

Figure 56. ***Entodon cladorrhizans***, a speciees in which shoot elongation is affected by sporophyte production. Photo by Janice Glime.

Figure 57. ***Hylocomium splendens***. Photo by Amadej Trnkoczy through Creative Commons.

Figure 58. ***Pterygoneurum ovatum*** with capsules. Photo by Hermann Schachner, through Creative Commons.

Figure 59. ***Tortula inermis*** with young sporophytes. Photo by Michael Lüth, with permission.

Stark *et al.* (2000) also found that males in ***Syntrichia caninervis*** (Figure 61) seem to invest more in antheridia than do females in archegonia. They made two assumptions and suggested that these may apply to other female-biased populations: 1) that male sex expression is more expensive than female; 2) that sexual reproduction is resource limited. This would give support to the "**cost of sex**" hypothesis, which predicts that the sex that is more expensive should be the rarer sex (Stark *et al.* 2000).

Figure 60. ***Microbryum starckeanum*** with sporophytes. Photo by Jonathan Sleath, with permission.

Figure 61. ***Syntrichia caninervis***. Photo by Proyecto Musgo, through Creative Commons.

Using the dioicous moss ***Drepanocladus trifarius*** (Figure 62), Bisang *et al.* (2006) asked whether the formation of sexual structures indeed incurred a cost in terms of reduced growth or future sexual reproduction. This species is female dominant but rarely produces sporophytes. The annual vegetative segment mass was the same among male, female, and non-sexual individuals, suggesting there was no threshold size for sexual expression. On the other hand, sexual branches in females exhibited higher mean and annual mass than did those in males, while branch number per segment did not differ from that of males. Females thus had a higher prefertilization reproductive effort (11.2%) than did males (8.6%). Nevertheless, these investments had no effect on vegetative growth or on reproductive effort in consecutive years. Therefore, a higher realized reproductive cost in males, suggested to occur in the desert moss ***Syntrichia caninervis*** (Figure 61) (Stark *et al.* 2000), cannot explain the unbalanced sex ratio in ***Drepanocladus trifarius*** (Figure 62).

Figure 62. ***Drepanocladus trifarius***. Photo by Andrew Hodgson, with permission.

Spore Size and Number

Spore size matters as well. During (1992) points out that when spores are small, bryophytes have the problem of juvenile mortality risk, but when they are large, the species has reduced dispersal potential. So it is not only a tradeoff in expenditure of parental energy vs providing offspring energy, or having many offspring vs few, but one of expanding the species to new areas vs staying put.

It would seem that having lots of large spores would overtax the female, whereas producing lots of small spores would provide ample opportunity to reach a suitable location for development of progeny. A compromise might be reached, but apparently has rarely been achieved by bryophytes, by having small male and large female spores. But is there further tradeoff to having lots of small spores? Noguchi and Miyata (1957) think there is. Their data indicate that mosses that produce abundant spores (implying mostly small ones) have a wide geographic range – the result of improved dispersal for tiny objects borne by wind, but the trade-off is reduced establishment success that restricts their habitats.

Where animals have had the evolutionary choice of producing many small offspring or few large ones and seed plants of producing many small seeds or few large ones, the bryophyte has a choice between producing spores of a small size in great numbers, larger spores but few in number, or producing no spores at all. For those taxa that produce no spores at all, we must assume that for most, either one sex is missing, or that they have spread beyond the range in which the proper signals and conditions permit them to produce spores. This usually means that fertilization cannot be accomplished. In these cases, vegetative means maintain the population and even permit it to spread to new localities, an option not available to most other groups of organisms.

Sexual vs Asexual Strategies

Sexual vs asexual strategies affect **metacommunity** (set of interacting communities which are linked or potentially linked by the dispersal of multiple, potentially interacting species) diversity (Löbel *et al.* 2009). In a study of Swedish obligate epiphytic bryophytes, forest patch size affected the species richness of monoicous species that reproduced sexually, whereas it did not affect the dioicous species that reproduced asexually. Löbel *et al.* found that it could take several decades for monoicous species to reach sexual maturity and produce spores. The researchers indicated that population connectivity in the past was more important for species richness in monoicous taxa than present connectivity. The difference in reproductive potential creates a tradeoff between dispersal distance and age of first reproduction. They suggested that this may explain the parallel evolution of asexual reproduction (primarily dioicous taxa) and monoicy for species that are able to live in patchy, transient habitats. Success in these conditions implies that relatively small changes in the habitat conditions could lead to distinct changes in the diversity of the metacommunity, wherein species using asexual reproduction may drastically decline as distances among patches increase, whereas those sexually reproducing species may decline as patch dynamics increase. (Sexual vs asexual strategies are discussed further in Chapter 4-7, Adaptive Strategies: Vegetative vs Sexual Diaspores, in this volume.)

Bet Hedgers

Bet hedgers are those species that use multiple strategies, often making each of those strategies less successful than they might be if all energy were concentrated on one of them. They are beneficial in unpredictable environments where one strategy is best in some years and another in different years or where disturbance may occur.

Specialized asexual reproductive structures such as gemmae require energy and thus compete with productions of sexual structures. But it seems that at least some, perhaps most, of the bryophytes are bet hedgers by maintaining both vegetative and sexual reproduction. They may reduce this competition for energy by temporal separation of the programmed asexual and sexual reproductive stages. For example, in the thallose liverwort ***Marchantia polymorpha*** (Figure 34-Figure 35), in which large archegoniophores and antheridiophores require considerable tissue production, the production of gemma cups and their asexual gemmae is timed so it does not coincide with development leading to sexual activity (Une 1984). In the moss ***Tetraphis pellucida*** (Figure 63-Figure 64), the terminal position of the gemmae and their splash cups precludes the simultaneous production of the likewise terminal reproductive structures.

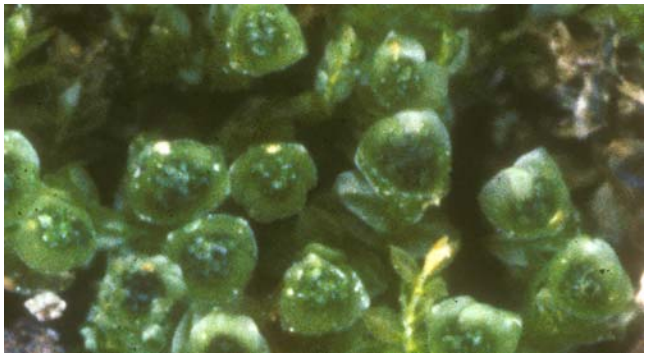

Figure 63. Top view of ***Tetraphis pellucida*** showing terminal gemma cups that prevent simultaneous development of reproductive structures. Photo by Janice Glime.

Figure 64. Side view of ***Tetraphis pellucida*** showing terminal gemma cups (and clusters that have lost their cup leaves) that prevent simultaneous development of reproductive structures. Photos by Michael Lüth, with permission.

Nevertheless, distinct tradeoffs between sexual and asexual reproduction have been detected. In studying biomass allocation of the leafy liverwort ***Lophozia ventricosa*** var. ***silvicola*** (Figure 65) Laaka-Lindberg (2001) found that sexual reproduction affected gemmae production. Female shoots averaged 800 gemmae, males 1360, and asexual shoots 2100, revealing a trade-off between sporophyte production (female sexual reproduction) and number of gemmae (asexual reproduction). In ***Marchantia inflexa*** (Figure 54), female sex expression was negatively associated with gemmae production under certain light conditions (Fuselier & McLetchie 2002). In agreement, ***Marchantia polymorpha*** ceases gemmae cup production during the period of producing sexual reproductive structures (Terui 1981). Pereira *et al*. (2016) reported a trade-off between pre-zygotic investment into gametangia and asexual reproduction, in terms of fewer gametangia in gemmae-producing shoots compared to barren shoots. Both the formation of gametangia and gemmae were in their turn positively associated with monthly precipitation. In contrast, Holá *et al*. (2014) suggested a minimal trade-off between sexual and asexual reproduction to occur in the aquatic liverwort ***Scapania undulata*** (Figure 66-Figure 67) as they found high gemmae production on male and female sex-expressing shoots.

Figure 65. ***Lophozia ventricosa*** showing gemmae on leaf tips. Photo by Jan-Peter Frahm, with permission.

Figure 66. ***Scapania undulata***, a male-biased dioicous liverwort. Photo by Hermann Schachner, through Creative Commons.

Figure 67. ***Scapania undulata*** gemmae. This species produces numerous gemmae at the leaf margins on both males and female plants. Photo by Paul Davison, with permission.

Whereas tracheophytes may often reproduce by bulbs, rhizomes, stolons, or other specialized bulky organs, bryophytes have the advantage that most can reproduce by tiny fragments (Figure 68) from any part of the gametophyte, and under the right conditions, sometimes even sporophyte parts, all of which can travel more easily than the bulky organs of a tracheophyte. This strategy is an effective fallback even for many successive years of spore production failure.

The Japanese and others have taken advantage of fragmentation to propagate their moss gardens, pulverizing mosses, then broadcasting them like grass seed (Shaw 1986; Glime pers. obs.). For some mosses, like ***Fontinalis*** species (Figure 69) (Glime *et al.* 1979) or ***Bryum argenteum*** (Figure 70) (Clare & Terry 1960), fragmentation may be the dominant reproductive strategy, and for those dioicous taxa where only one sex arrived at a location, or one or the other sex is not expressed, or sexes are spatially segregated, it is the only means.

Figure 68. ***Syntrichia caninervis*** protonemata produced from a leaf fragment. Photo courtesy of Llo Stark.

Figure 69. A clump of ***Fontinalis novae-angliae*** that has been scoured and broken loose from its substrate. Photo by Janice Glime.

Figure 70. ***Bryum argenteum*** showing large terminal buds that break off and disperse the plant. Photo by Janice Glime.

Growth vs Asexual Reproduction

Gemma cup number was negatively related to vegetative meristematic tips in ***Marchantia inflexa*** (Figure 54) (McLetchie & Puterbaugh 2000). Gemma production in ***Anastrophyllum hellerianum*** (Figure 71), on the other hand, did not affect shoot mortality (Pohjamo & Laaka-Lindberg 2004).

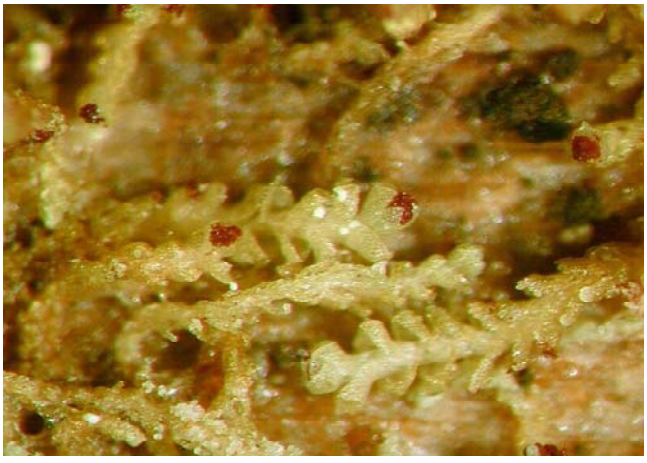

Figure 71. ***Anastrophyllum hellerianum*** with gemmae in Europe. Photo by Michael Lüth, with permission.

To test the tradeoffs in growth rate, asexual and sexual reproduction, and allocation to above and below-ground regenerative biomass, Horsley *et al.* (2011) cloned ***Bryum argenteum*** (Figure 70) for a growth period of 92 days, replicating each genotype 16 times, to remove environmental effects. There appeared to be three distinct ecotypes among the populations tested (representing 12 genotypes). It appears that the degree of sexual vs asexual reproductive investment is under genetic control. Furthermore, growth of the protonemata was positively correlated with both asexual and sexual reproduction. Asexual reproduction (Figure 72) was negatively correlated with shoot density, suggesting an energetic trade-off. None of these relationships appeared to be sex-specific. The sexes did not differ in growth traits, asexual traits, sexual induction times, or above- and below-ground biomass, but female sexual branches (Figure 73-Figure 75) were longer than those of males (Figure 76-Figure 77). Males produced many more perigonia (Figure 76) per unit area of culture media than the perichaetia produced by females, giving males 24 times the prezygotic investment. Horsley *et al.* considered that this strong sex bias in energy investment in male perigonia could account for the strongly female-biased sex ratio.

Figure 72. ***Bryum argenteum*** with terminal (1) and lateral (2) shootlets. Photo from Horsley *et al.* 2011.

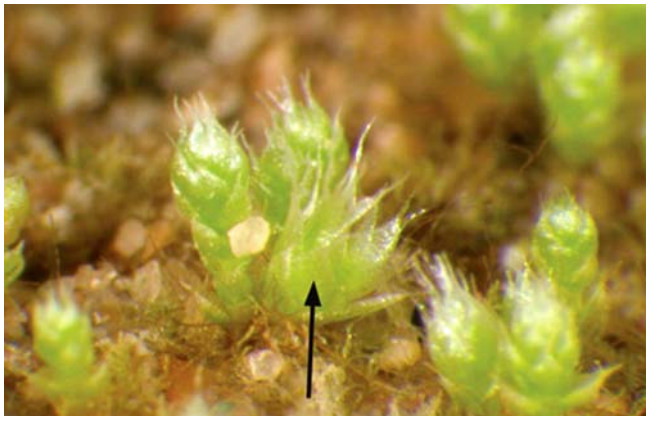

Figure 73. ***Bryum argenteum*** female plants. Photo from Horsley *et al.* 2011.

Figure 74. ***Bryum argenteum*** female plant with excised perichaetial leaves and archegonia. Photo modified from Horsley *et al.* 2011.

Figure 75. ***Bryum argenteum*** female (left) and male (right) plants, illustrating sexual dimorphism. Photo modified from Horsley *et al.* 2011.

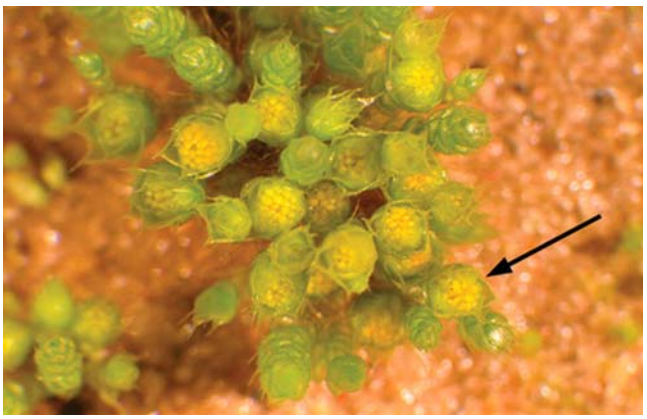

Figure 76. ***Bryum argenteum*** male plants, illustrating the numerous perigonia and antheridia present. Photo from Horsley *et al.* 2011.

Figure 77. ***Bryum argenteum*** male plant with excised perigonial leaves and antheridia. Photo modified from Horsley *et al.* 2011.

Significance of a Dominant Haploid Cycle

Longton (2006) provided evidence that dispersal of a spore is an extremely important aspect of bryophyte success in establishing new populations, whereas vegetative reproduction is more important for colony expansion and maintenance. Spores are 1*n* (**haploid**), and to be effective as a dispersal propagule, that body derived from the spore must have the characters needed for survival of the environment. This contrasts with those plants where it is a 2*n* (diploid) seed that gets dispersed. In the latter case, the 2*n* plant provides the needed environment for the development of the gametophyte, and the gametophyte is greatly reduced and resides mostly within the tissues of the

2*n* plant. Hence, those plants (bryophytes and non-seed tracheophytes) that disperse largely by spores must find a suitable habitat for their gametophytes (See chapter on Dispersal).

In bryophytes, the diploid stage is forever attached to the haploid stage and dependent at least partially upon it. Haig and Wilczek (2006) point out that the diploid stage has one set of nuclear genes in common with its haploid mother, in addition to obtaining resources from that mother; the paternal haploid genes are not in common with those of the mother. They explain that all of the "offspring's maternal genome will be transmitted in its entirety to all other sexual and asexual offspring that the mother may produce," but not all will have the genes of the father. Haig and Wilczek suggest that this will favor genomic imprinting and predict that a "strong sexual conflict over allocation to sporophytes" will occur. Furthermore, chloroplast genes are inherited from the mother, but there has been little or no assessment of the effect this has on physiological behavior or environmental needs of bryophyte species as they relate to sexual bias.

Ricklefs (1990) reminds us that, just as in the algae, the haploid (1*n*) plant has the ability to express its alleles in the generation where they first occur, whereas the diploid (2*n*) plants have the ability to mask deleterious recessive alleles. The haploid (1*n*) generation possesses "immediate fitness" if a favorable change occurs among the alleles, but is immediately selected against if the change is unfavorable, unless, of course, the trait is one not expressed in the gametophyte. This immediate expression is a tradeoff with the ability to mask genes that may be retained and beneficial in a different location or different point in time.

Zeyl *et al.* (2003) used yeast, with both haploid and diploid generations, to test the question of whether there is any advantage to being haploid. Based on their experiments, they argued that being haploid permits an organism to accumulate beneficial mutations rather than to avoid the effects of those that are deleterious. This is founded on the premise that even beneficial genes are masked in diploid organisms and thus provide no immediate advantage, if ever. Rather, the rate at which a beneficial gene increases in frequency in a haploid organism is far greater than in a diploid organism (Greig & Travisano 2003). Of course it is never the case that all genes are expressed simultaneously, or even that all genes are expressed during the lifetime of an organism. They are there to be turned on when the physiological state of the organism calls for them.

Zeyl *et al.* (2003) hypothesized that in small populations, the haploid organisms would lose their advantage. They reasoned that by having twice as many of each gene, diploid organisms may have an increased rate at which adaptive mutations are produced. Hence the supply of adaptive mutations would be reduced, rather than any reduction in the time required to fix them. By doubling the adaptive mutation rates (diploidy) the adaptive mutations become more important in small populations. When adaptive mutations are rare the rate of adaptation by diploid populations approaches a doubling of that found in haploid populations. In small populations, having two sets of chromosomes is an advantage if the adaptive mutations are dominant because they will be expressed and gain prominence through natural selection. But when the mutations are recessive, diploidy is a disadvantage because the mutations are not often expressed. In large populations, the extra genes (of the 2*n* state) would gain little advantage over the increased rate of expression of mutated genes.

Their experiments with haploid and diploid yeast (*Saccharomyces cerevisiae*) supported their hypothesis; in large populations, haploid populations adapted faster than diploid populations, but this was not the case when both populations were small (Figure 78) (Zeyl *et al.* 2003). They reasoned that a greater adaptation rate is not a general consequence of diploidy and does not, by itself, explain the prominence of diploidy in plants or animals. However, in their experiments they did not permit the yeast to mate, thus reducing the advantage of mixing in diploid organisms with chance mating of two beneficial or complementary mutations.

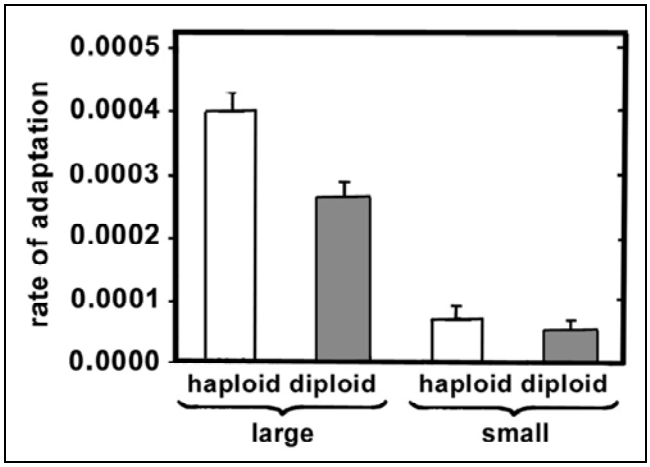

Figure 78. Rates of adaptation in large and small haploid and diploid populations of yeast. Bar length and 95% confidence interval was determined by slopes using linear regression of fitness on the generation number (n=5 pooled for 4 regressions). Ploidy was highly significant for large populations ($p<0.001$), but not for small populations ($p=0.35$). (2-tailed heteroscedastic t tests). Modified from Zeyl *et al.* 2003.

Would these experiments on one-celled yeast produce the same results if tried on multicellular bryophytes? There are genera, for example in the **Mniaceae**, in which some monoicous taxa possess a double set of chromosomes, apparently derived from a dioicous taxon with a single set. These would seemingly make appropriate experimental organisms for such testing. Our current molecular methods should make such an evaluation possible.

Having a dominant gametophyte has its limits, however. Longton and Schuster (1983) remind us that, unlike tracheophytes, once having achieved fertilization, the bryophyte is able to produce only a single sporangium that subsequently produces spores all at one time (except in **Anthocerotophyta**). On the other hand, tracheophytes (polysporangiate plants) produce many branches, hence many sporangia, and these may be produced on the same plant year after year, all resulting from a single fertilization. The closest behavior to this among the bryophytes is in **Anthocerotophyta**, a dubious bryophyte as noted earlier, where meiosis occurs on the same sporophyte over a period of time, with older spores at the apex and new ones produced at the base of the sporophyte (Schofield 1985).

But bryophytes are more **'polysporangiate'** than they might seem. Whereas they cannot produce multiple sporophytes from a single fertilization, pleurocarpous species do have multiple sporangia produced on a single gametophyte plant (Figure 79), each potentially with a different combination of genes. And most bryophytes are **perennial** (persisting for multiple years), thus in most cases sequentially accomplishing multiple fertilizations under multiple conditions and selection pressures. Furthermore, the meiotic events in multiple cells of sporogenous tissue, even though all in one sporophyte, result in different sortings of chromosomes, thus different combinations among the many spores produced.

Figure 79. ***Callicladium haldanianum*** showing multiple capsules from one plant. Photo by Misha Ignatov, with permission.

In diploid plants, on the other hand, the number of recessive alleles continues to increase until the effect of their expression is the same in the **homozygous diploid state** (both alleles for a trait are the same) as it is in their haploid state (Ricklefs 1990). This provides the diploid organism with a short-term advantage of maintaining steady state while sequestering alleles that may at a later date become advantageous due to changing environmental conditions. A further advantage to diploid plants is that heterozygous organisms (those having two different alleles for the trait) frequently are the most fit, in some cases due to complementation (two traits that complement or help each other), in others due to having more possibilities of possessing fit alleles. On the other hand, presence of two alleles can mask somatic mutations (*i.e.*, mutations in non-reproductive cells) that ultimately could result in a lack of coordination between cells. Perhaps this lack of masked genes is only a disadvantage for a large (complex) organism that must keep all its parts working together, whereas in organisms where there are few cell types to coordinate, the condition is less likely to be problematic, particularly in an organism where vegetative reproduction is often the rule and little other specialization occurs.

Immediate fitness of haploid organisms permits the few individuals possessing a trait to exploit a new situation, whereas the delayed fitness of diploid organisms that require a like partner is unlikely to permit these species to respond quickly to environmental change.

One complication to this scenario of haploid and diploid is that often haploid organisms are not pure haploids. In fact, it appears that **autopolyploidy** (having more than 1 set of homologous chromosomes in the gametophyte) has been a significant factor in bryophyte evolution (Newton 1984). Many, probably most, genes are identical in the two sets, but some differ, and possibly in rarer cases, an entire chromosome may differ. These cases of autopolyploidy result in **functional haploidy** (Cove 1983), albeit with twice as many alleles as were present in the parent species. But does meiosis subsequently separate them into the same identical sets after fertilization has joined these with a new doubled set? Wouldn't this be an opportunity for new combinations of alleles to have different homozygosity and heterozygosity?

Do Bryophyte Sexual Systems Affect Genetic Diversity?

Where do these strategies leave bryophytes in their genetic variation? Bryonetters questioned the lack of diversity in bryophytes (see also Glime 2011). Do their mating systems, and in some cases lack of them, affect their genetic diversity?

Most people think of diversity in terms of morphology. But genetic diversity may not be expressed as morphological diversity. Rather, differences in biochemistry may occur without our recognition. Recent studies using molecular and phylogenetic methods support the conclusion that bryophytes in fact have greater diversity than we has supposed, as evidenced by the genetic differences between geographically different populations (Shaw *et al*. 2011).

Although differences in form among closely related species of small organisms such as bryophytes are limited because of their small number of cells and small size, we are beginning to find that physiological variety is great. Stenøien and Såstad (2001) suggest that the mating system does not really matter in bryophytes in this respect. Rather, inbreeding can profoundly influence variation in the haploid generation. Furthermore, high levels of selfing are not a necessary consequence of being monoicous, as outbreeding is still possible, and even likely in some cases (see Reproductive Barriers above). Such mechanisms as different male and female gametangial maturation times would force outbreeding. Rather, the monoicous condition provides many other individuals nearby with whom genes can be exchanged, and it is possible that some of these have come from spores that represent a new combination of genes.

Whereas seed plants spend most of their lives with two sets of chromosomes ($2n$), they seldom express the mutations that arise because a second allele is present that still retains the old trait. For example, the absence of a gene to code for making a red pigment in the leaf might result in a green leaf in a species that would normally have a red leaf. Organisms with such hidden traits therefore have hidden changes that are retained in the population and that might at some future time be an advantage when conditions change. The ability to retain traits provides the plants with variability that might mean future success, but that do little for immediate fitness. In our pigment example, red pigment could protect the leaf against strong UV light, but if greenhouse gases and atmospheric exhaust

were to shield the Earth from UV light and reduce the light available for photosynthesis, being red might be less advantageous and a green leaf might then become beneficial for trapping more of the photosynthetically active portion of the spectrum.

Haploid bryophytes, on the other hand, cannot carry adaptive genes in a second set of chromosomes, but rather have immediate fitness or lack of fitness with the advent of a new gene. If these beneficial mutations occur in vegetative cells, they can be carried forward in clones or established in new colonies through fragmentation with no masking effects. Hence, if the bryophyte has a red pigment to protect it against strong UV light, it might not succeed in the shade, but those microspecies with no red pigments are immediately ready for the lower light levels. The individuals that do not have suitable genes may die, but those that have them are immediately fit.

Perhaps the answer to the paradox of genetic variation without cross fertilization does lie in asexual reproduction. It seems that asexual reproduction in bryophytes, unlike that of tracheophytes, may be a source of considerable variation (Mishler 1988, Newton & Mishler 1994). In addition to fragmentation, we know that bryophytes produce a variety of asexual propagules or gemmae (see Gemma-bearing Dioicous Taxa above and Chapter 4-10 of this volume) both above- and below-ground.

Clearly, producing gemmae or other propagules has served the dioicous taxa well. Growth by divisions of a single apical cell (instead of a meristematic region as in higher plants) can provide considerable genetic variation, with the fitness being determined almost immediately (Newton & Mishler 1994). Subsequent branches from this new growth, including gemmae and other propagules, and fragments that form new plants, would spread this new genetic variant. In some taxa, for example ***Lophozia ventricosa*** var. ***silvicola*** (Figure 65), the number of gemmae produced annually seems to outnumber the number of spores (Laaka-Lindberg 2000). Mishler (1988) suggested that sexuality is regressing in bryophytes with a concomitant increase in asexual reproduction, as later supported by During (2007) and others, particularly for dioicous bryophytes with high propagule production. Mishler feels that genetic variability is being maintained through somatic mutation, a suggestion by Shaw (1991) to explain variability in ***Funaria hygrometrica*** (Figure 10, Figure 38-Figure 39). The loss of sexuality is in sharp contrast to the suggestion of Longton (1997, 1998) that the monoicous condition will increase and with it the success of sexual reproduction.

If bryophytes can truly accomplish somatic mutations and make new plants, and they can derive new combinations from mating of autopolyploid plants, why then, are bryophytes still seemingly so primitive? Have they had a particularly slow evolution, with mutations providing little or no advantage? Some researchers have defended the position of slow evolution by referring to their small chromosome number (base = 9 or 10 in most, but 4 or 5 in some). Speculation suggests that their lack of structural support places severe limitations on the size bryophytes can support and the efficiency of water movement internally. This, in turn, limits the structural complexity they can support. However, recent biochemical evidence supports a genetic evolution as rapid as that of lignified plants (Asakawa 1982, 1988, 2004; Asakawa *et al*. 1979a, b, c, 1980a, b, 1981, 1990, 1991, 2012; Mishler 1988; Stoneburner 1990; Newton & Mishler 1994). That is to say, the rate of allele change and the number of isozyme differences found among species is as great as in their more complicated lignified relatives.

So where have all these genetic changes been expressed? One explanation is that the bryophytes harbor a tremendous variety of secondary compounds (Asakawa 1982, 1988, 2004; Asakawa *et al*. 1979a, b, c, 1980a, b, 1981, 1990, 1991, 2012), *i.e.* compounds that do not seem to have any direct role in any metabolic pathway. Their apparent role in antiherbivory, antibiotics, and protection from desiccation and light damage may be the secret to the continuing success of the bryophytes.

With an understanding of the life cycle, we can begin to understand the conditions that are required for the survival of an individual species. Yet, few studies have examined the requirements and responses of individual species throughout all the stages of their lives. Their absence on a given site may relate to climatic events during their juvenile life when they must bridge the stage between spore and leafy plant, when they are a one-cell wide protonema and fully exposed with no protection from desiccation or blazing sun, or when they arrive as other forms of propagules (Cleavitt, 2000, 2002a, b). In the coming chapters we will examine their growth patterns, the effects of their habitats on their phenology, and their ability to adjust to habitat variability.

The Red Queen Hypothesis

Nothing in the life of a species plays a more important evolutionary role than reproduction. The ability to retain non-expressed genes that may later be expressed and be beneficial permits organisms to be pre-adapted to sudden or gradual changes in their environment.

The terminology **Red Queen** derives from Lewis Carroll's *Through the looking-Glass*. The Red Queen explained to Alice the nature of Looking-Glass Land: "Now, here, you see, it takes all the running you can do, to keep in the same place." Van Valen (1973) saw coevolution as running to keep in the same place.

The **Red Queen Hypothesis** was first proposed by Van Valen (1973) as an evolutionary hypothesis that proposes that organisms must "constantly adapt, evolve, and proliferate not merely to gain reproductive advantage, but also simply to survive while pitted against ever-evolving opposing organisms in an ever-changing environment." Van Valen devised the hypothesis to explain constant extinction rates exhibited in the palaeontological record as a result of competing species on the one hand and the advantage of sexual reproduction by individuals on the other. The theory was developed to explain predator-prey and host-parasite interactions in the evolution of animals. If the prey developed more skill in avoiding the predator, the predator subsequently developed more skill in catching the prey. If a host developed immunity to a parasite, the parasite that survived was a more virulent or aggressive one. The theory expanded to explain other evolutionary drivers. In our context here, it emphasizes the importance of sexual reproduction in maintaining protection against changes in the environment, including predators and parasites.

An example of the workings of this concept can be illustrated by the snail *Potamopygrus antipodarum* (Jokela *et al*. 2009). When mixed asexual and sexual populations of this snail were cultured, the parasite population increased. The asexual snails were quickly reduced by the parasites, with some clones going extinct. Sexual populations, on the other hand, remained nearly stable over time, apparently adapting through genetic selection for the resistant genotypes that had been carried as a result of sexual mixing. Kerfoot and Weider (2004) supported the Red Queen Hypothesis by demonstrating a genetic relationship between changing predators and prey (*Daphnia*) through time using diapausing eggs of *Daphnia*, a parthenogenetic cladoceran. These eggs were derived from cores of sediment in Portage Lake from 1850-1997 and the eggs subsequently cultured to assess changes in characters. Clay and Kover (1996) tested the hypothesis in plant host-parasite interactions. They found that portions of the theory are supported, but not all.

At first this may not seem to apply to bryophytes, but consider the wide array of secondary compounds present among them. These compounds are known for their ability to protect the bryophytes from bacteria, fungi, and herbivores. This consideration can be considered as a parallel to the predator-prey or host-parasite relationships. As more herbivores evolved to attack the bryophytes, those bryophytes with the most protective array of secondary compounds were most likely to survive. But can it help to explain the persistence and re-introduction of the dioicous condition in bryophytes, as demonstrated for some animals (Morran *et al*. 2011)?

Sexual reproduction at the gene level permits sexually reproducing organisms to preserve genes that may be disadvantageous at present, but that may become advantageous under future conditions. This is somewhat complicated in bryophytes because of the dominance of the haploid gametophyte. But if the gene is not disadvantageous, or it is expressed only in the sporophyte, it could remain in the genetic line for centuries. If these genes code for secondary compounds that have been effective against predators, bacteria, fungi, or other dangers, they may be conserved in the genotype even if the danger is no longer present. And as new dangers arose, different secondary compounds would have been preserved in the genome, with the surviving bryophytes changing as the dangers changed. If the Red Queen Hypothesis applies, we should be able to see changes in the secondary compounds or the genome that relate to changes in the dangers. We can argue that the variability provided by the dioicous condition makes such changes possible to a greater extent than does the monoicous condition.

To our knowledge, there has been no test of the Red Queen hypothesis in bryophytes. Suitable fossils are scarce, but we should be able to test these ideas in ice cores that provide living organisms as much as 1500 years old (Roads *et al*. 2014)! By growing new organisms from fragments (see La Farge *et al*. 2013; Roads *et al*. 2014), we can compare the genes and also the potential responses to bacteria, fungi, or predators by looking at concentrations of secondary compounds using methods similar to those of Kerfoot and Weider (2004) for *Daphnia*.

Surviving in the Absence of Sexual Reproduction

Surviving unfavorable conditions is often a sexual function. In algae, **zygospores** (resting, resistant stage following fertilization) are the most common means of survival. In many invertebrate animals, including those living among bryophytes, the fertilized egg is likewise often the survival stage. Bryophytes do not use the fertilized egg to survive unfavorable conditions because that stage is dependent on the leafy haploid stage. Rather, many can produce sexual spores (meiospores) that survive during periods of drought and other unfavorable conditions. Spores are known to survive for long periods (See Chapter on Dispersal). Some species form persistent sporebanks that allow them to bridge unfavorable periods, then become active following disturbance. But bryophytes have many physiological means that permit them to survive without sexual reproduction.

As an alternative to spore survival, bud survival is important to some species. Haupt (1929) found that the thallose liverwort ***Asterella californica*** (Figure 80) survives hot, dry summers on banks and canyon sides in southern California as a leafy plant, but that only the ends of branches remain alive, starting new plants in autumn when sufficient moisture returns. In southern Illinois, ***Fossombronia foveolata*** (Figure 81) produces capsules in spring, but likewise survives the dry summer by means of its terminal bud, resuming growth in autumn and producing capsules a second time that year on the same plant (James Bray, pers. comm.).

These physiological mechanisms permit bryophytes to survive through vegetative reproduction for many years in the absence of sexual reproduction. And bryophyte species, unlike most tracheophytes, can survive for centuries without the intervening genetic mixing and resting stages afforded by sexual reproduction.

Figure 80. ***Asterella californica*** with archegoniophores and terminal buds that are able to survive drought. Photo by David Hofmann, through Flickr Creative Commons.

Figure 81. ***Fossombronia foveolata*** with young sporophytes and resistant terminal buds that can survive drought. Photo by Des Callaghan, with permission.

Bryophytes vs Seed Plants

The higher percentage of dioecy in bryophytes than in seed plants still begs explanation, and we have discussed possible explanations above and especially in Chapter 3.1. Could it in addition be that fragmentation, generally only available in poorly dispersed underground structures in seed plants, but available and easily dispersed from any part of the plant in bryophytes, might account for greater success of the dioicous condition among bryophytes?

Furthermore, since bryophytes are haploid-dominant, being dioicous provides immediate production of new genotypes as soon as sexual reproduction occurs, thus making selection for this strategy more rapid than in seed plants. Does this explain the high degree of dioicy among the early-diverging bryophyte group, where there has been considerable time to develop the best of the two strategies?

One answer may lie in short-distance dispersal of the male gametes, coupled with ease of vegetative reproduction in bryophytes. In seed plants, the male gametophyte (pollen grain) is more easily dispersed with less danger to its viability. There has been an enormous amount of evolution perfecting transfer by vectors, especially insects, among seed plants. While this would seem to improve dioecy fertilization success, it also provides for considerable outcrossing success for monoecy. It may also be the case that seed plants have more effective mechanisms for preventing successful self-fertilization. On the other hand, the vegetative ability to reach new locations is extremely limited in seed plants, although it can be quite effective over the short distance. For seed plants, long distance dispersal is almost entirely dependent on sexual reproduction. By contrast, many bryophytes can be dispersed considerable distances by both specialized vegetative diaspores and fragments (see for example Laenen *et al.* 2015), thus compensating for any lack of spores.

Summary

Monoicy (both sexes on same individual) frequently has arisen through **hybridization** and **polyploidy** (multiple sets of chromosomes). Barriers to hybridization and to **selfing** in bryophytes are poorly known. These include **external barriers** such as **spatial/geographic isolation**, **ecological isolation**, and **seasonal isolation**. **Internal barriers** include **gametic isolation**, **genetic incompatibility**, **hybrid sterility**, and **reduced fitness**. Nevertheless, hybridization seems to have played a major role in the evolution of monoicy due to lack of these barriers in many species.

Formation of gametangia and especially sporophyte formation incur reproductive costs measurable in reduced future vegetative and reproductive performance. Overall investment in sexual reproduction may vary among species, in some cases being greater in males and in others greater in females, depending on if assessed at the pre- or postfertilization stage.

Tradeoffs occur between dispersal ability of small spores and success of establishment of large spores. Fragments and vegetative diaspores are most successful at colonizing over short distances and are more likely to succeed than spores. Asexual reproduction can keep the species going for many years in the absence of sexual reproduction. Tradeoffs occur also among asexual reproduction, sexual reproduction, and vegetative performance. These tradeoffs vary among species.

The dominant haploid state of bryophytes limits their ability to store **recessive alleles**, but **autopolyploidy**, **somatic mutations**, **vegetative reproduction**, and **independent assortment** at meiosis contribute to genetic diversity. Despite their clonal nature, bryophytes still exhibit considerable genetic variation. This may be explained in part by the **Red Queen hypothesis**, a hypothesis that also might explain the persistence of evolution to a dioicous condition despite the difficulty of accomplishing sexual reproduction. Inbreeding depression may occur in monoicous bryophytes, but limited data suggest that it may be to a lesser degree compared to that of tracheophytes.

Bryophytes may lack the morphological diversity expressed by sporophytes in higher plants, but there is evidence that haploid plants and their diaspores can contain as much diversity as tracheophytes, often expressed in their biochemistry as a variety of secondary compounds rather than in morphology. They have life strategies that have survived since the beginning of land plants.

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CHAPTER 4-1

ADAPTIVE STRATEGIES: PHENOLOGY, WHAT DOES IT MEAN?

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CHAPTER 4-1

ADAPTIVE STRATEGIES: PHENOLOGY, WHAT DOES IT MEAN?

Figure 1. ***Hylocomium splendens*** emergent from the winter snow. Timing of reproduction must be such that sperm do not mature on a warm day in winter, only to be frozen by ensuing sub-freezing temperatures. Photo by Michael Lüth, with permission.

Phenology, defined by Stark (2002) as "the study of the timing of growth and reproductive events," is also used to refer to the series of events and includes changes of form and phenomena of an organism through time as they relate to climate and season. Classical studies in Europe have included branching architecture, timing of vegetative growth, gametangial initiation times, fertilization times, duration of sporophyte development, and time of spore liberation (Stark 2002). To these we can add nutritional status, population dynamics, fitness measures, spore dispersal patterns, interplay of sexual and asexual reproduction, **sexual dimorphism** (sexes look different), structural development, dormancy, and desiccation tolerance. Studying phenology permits us to understand interplay of plants with a constantly changing environment.

In the temperate forest, trees lose leaves in autumn, bloom and leaf out in spring, and store **photosynthate** (product of photosynthesis) in summer. These canopy phenological events have profound impact on smaller plants growing beneath them. Spring flowers bloom before leaves emerge on trees, taking advantage of a nearly full complement of sunlight. A few shade-tolerant species grow more slowly and take advantage of the tree canopy to protect them from bright light of summer. Other species use fungal partners to connect them with trees, taking advantage of canopy photosynthate that permits them to survive in low light. As these ground cover taxa enlarge through summer, bryophytes are impacted by light-depriving leaves of larger neighbors.

Bryophytes also must cope not only with a changing light and moisture regime resulting from the direct effect of changing seasons, but also with microclimatic changes resulting from changes in the tracheophytes around them. Their C_3 photosynthetic pathway (CO_2 is immediately put into photosynthesis, forming 3-C compound) permits them to take advantage of early light and moisture at snowmelt (Figure 1) when low temperatures prevent even other C_3 plants from having effective photosynthesis.

Bryophytes are limited in their occupancy of deciduous forests by the phenological event of leaf fall that fully blocks the light essential for their photosynthesis. Most forest bryophytes are perennials, yet, unlike their tracheophyte counterparts, most are unable to avoid the changing seasons by storing energy underground and losing their photosynthetic parts. As C_3 plants, they are able to photosynthesize at low temperatures as soon as the snow is gone, but they are likely to find the hot temperatures of summer to be detrimental. Furthermore, they require water to transfer their swimming sperm, rarely having an animal vector to carry these for them. Based on these constraints, we should expect that bryophytic phenological responses differ somewhat from those of their lignified vascular companions as the bryophytes take advantage of or avoid the changes provided by these companions.

One need only examine a few bryophyte floras to recognize that phenological events for mosses are poorly documented. Almost any flowering plant flora will include flowering dates, but bryophyte floras from Japan (Noguchi 1987-1994), the Nordic (Nyholm 1986, 1898, 1993), Michigan (Crum 2004), and the tropics (Gradstein *et al*. 2001) all fail to mention any season for any life cycle event, even the season of spore dispersal. Crum and Anderson (1981) occasionally include the season of spore ripening for the Eastern United States, but never any information on seasons for other events. In treating the genus ***Sphagnum***, for which both authors are world-renowned systematists, not a single species of the 42 described includes any phenological information. Conard (1947), in reporting the phenology of Iowa bryophytes, was able to find dates in the literature for presence of antheridia or archegonia for only 15 taxa out of 292. He was more successful in finding documentation of capsule production dates, locating it for all but 28 of the taxa that fruit in Iowa.

As the young field of bryophyte ecology began taking shape in the early 1970's, Longton (1974) suggested that the International Association of Bryologists and the British Bryological Society (Longton 1982) embark upon bryophyte phenology as a project. Perhaps because of British national pride, or because of the large number of good bryologists among the British society's mostly amateur membership, such a project had appeal to the BBS. It was a way for many people to contribute important information that could only be gained by such a wide undertaking. Through consorted efforts, they could define not only the phenology of a wide array of species, but could look at differences in patterns throughout the British Isles, comparing inland species with coastal, mountain and moor with valley and field.

Developing Consistency in Reporting

For comparisons among various studies and localities, a consistent way of examining and describing life cycle stages is necessary. Again, the British were the leaders, with a publication by Greene (1960) elucidating the stages. The British faithfully followed this nomenclature in making their reports. Slight modifications and refinements have made this system workable around the world.

Most researchers seem to recommend observing every two weeks to elucidate the phenology (Stark 1984). In general, the life cycle stages are arrested while the plants are dry, so it is possible to collect specimens periodically, then examine them later at one's convenience. The ability of bryophytes to continue their life cycle upon rehydration makes it possible to identify the stages after rehydration and even to photograph them. Nevertheless, one should exercise caution if high resolution is needed in defining dates because the ability to retain water may permit the bryophytes to continue development for a period of time. Mosses kept in plastic bags may continue growth for a month, elongating abnormally in the lower light of their new location. Dry mosses may shed the operculum prematurely, since drying itself is needed in most taxa to constrict the capsule and force the operculum off, occurring sooner in the dry lab than it would in nature with nightly dew to re-supply moisture.

When reviewing a series of dry collections, Stark (1984) recommends soaking the stems for a few minutes and removing the leaves on the upper 10-15 mm of the main stem, but not from the branches. This can be done with microforceps by holding the tip and pulling the leaves downward toward the base, being careful not to injure the gametangia in the process. Once leaves are removed, one can carefully remove a group of gametangia near the apex and place it in a drop of water on a slide. In **pleurocarpous** mosses (Figure 1), gametangia occur on side shoots, rather than at the stem apex where they occur in **acrocarpous** mosses (Figure 5). You can shorten the process by pressing the gametangia off with the side of a probe. In either case, use a cover slip and examine them with the compound microscope. Data should be recorded using one of the published systems of naming stages.

System of Naming

Fortunately for the British, and for bryologists everywhere, systems for scoring the developmental stages already existed. Greene made the "most significant" contribution to phenology (Stark 2002) when he suggested 20 stages (Figure 2), centering on the reproductive phases only, and omitting any presentation of the spore and protonema. He even recommended a method for preparing figures to illustrate the monthly changes (Figure 3).

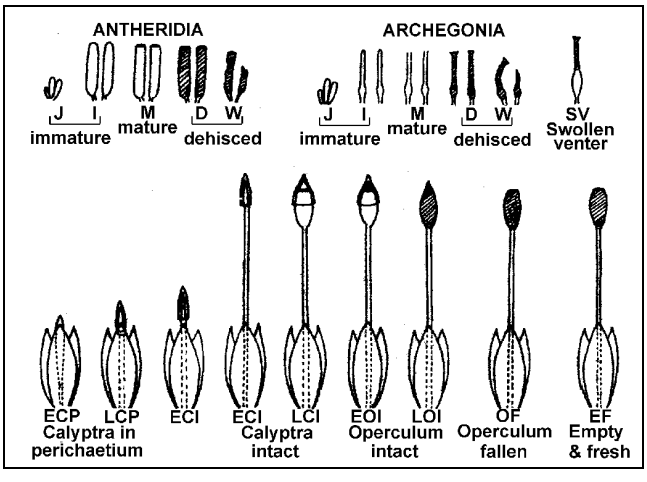


Figure 2. Maturation stages as represented by Greene (1960). **J** = juvenile, **I** = immature, **M** = mature, **D** = dehisced, **W** = withered archegonia or antheridia, **SV** = swollen venter, **ECP** = early calyptra in perichaetium, **LCP** = late calyptra in perichaetium, **ECI** = early calyptra intact, **LCI** = late calyptra intact, **EOI** = early operculum intact, **LOI** = late operculum intact, **OF** = operculum fallen, **EF** = empty and fresh.

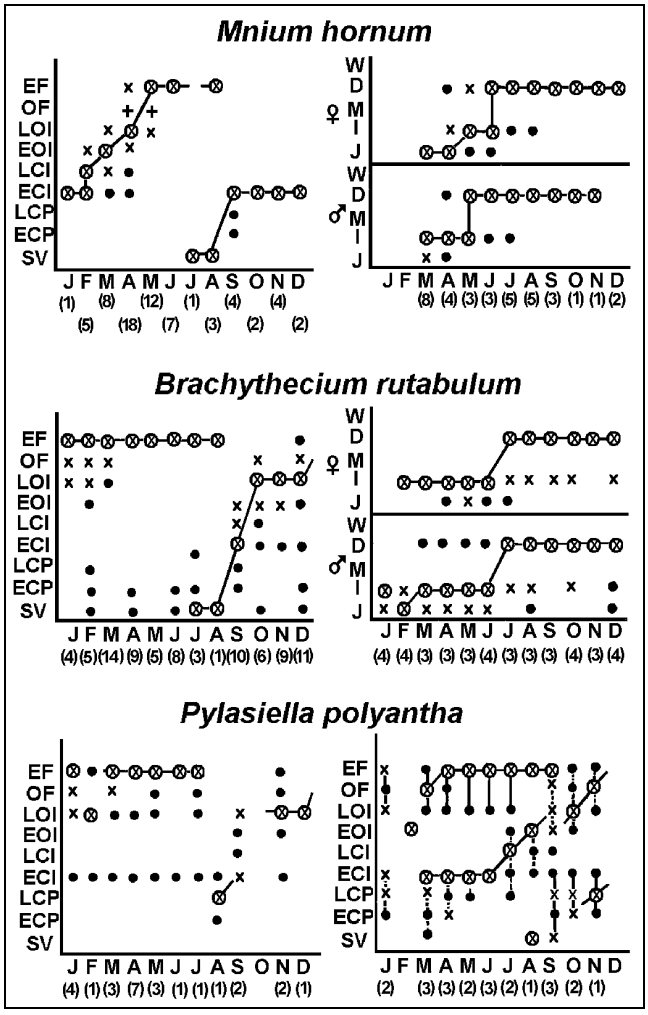
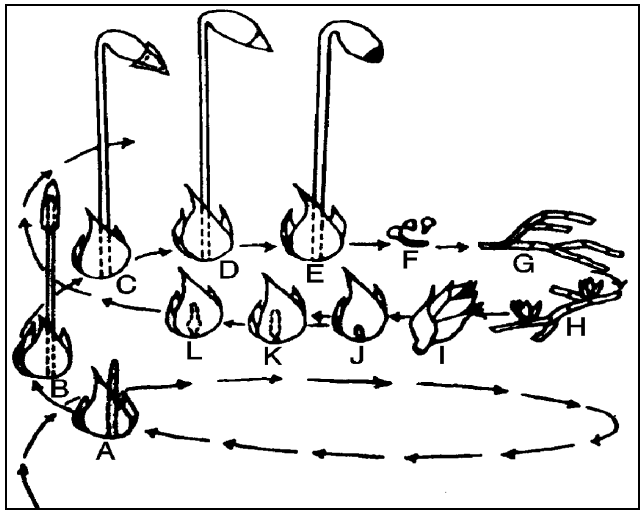


Figure 3. Sample figure given by Greene (1960) to illustrate the gametangial and capsular cycles of three species of moss. **Numbers in parentheses** indicate number of collections in which the majority state occurred. The **circled x** represents the state that was clearly the most abundant, **x** alone represents other stages that occurred as majority states in some collections, and a **solid circle** indicates present but never abundant. As in the previous figure, **SV** = swollen venter, **ECP** = early calyptra in perichaetium, **LCP** = late calyptra in perichaetium, **ECI** = early calyptra intact, **LCI** = late calyptra intact, **EOI** = early operculum intact, **LOI** = late operculum intact, **OF** = operculum fallen, **EF** = empty and fresh; **J** = juvenile, **I** = immature, **M** = mature, **D** = dehisced, and **W** = withered archegonia or antheridia.

Shortly thereafter, Forman (1965) developed a somewhat easier system by which researchers could make consistent descriptions related to phenological events. He decided that no two stages should be named separately unless they were morphologically distinct. Furthermore, the stages should be relatively easy to recognize without the use of a microscope. He defined the life cycle in 12 stages (Figure 4) for the purpose of describing the phenology and other events more precisely and in a standard fashion.

Forman (1965) decided that stages need not be delimited if they did not require any change in environmental conditions. For example, early and late stages of seta elongation are not separated because they occur as a continuous process independent of any environmental trigger. On the other hand, growth of the



A. **Embryonic calyptra**. (This corresponds with the development of the embryo following fertilization.) This stage commences with fertilization and terminates with the rupture of the gametophytic calyptra from the tissue beneath. The seta is not visible under the expanded neck cells of the archegonium.

B. **Seta with calyptra**. (This corresponds with the growth of the sporophyte from the embryo.) This stage commences when the seta becomes visible and terminates at the beginning of capsule expansion at the tip of the seta. A few plants lose their calyptras during this stage, but it is doubtful that these can eventually produce spores.

C. **Capsule green with calyptra**. (This corresponds with meiosis.) This stage ends either with the shedding of the calyptra or with the urn of the capsule beginning to turn brown. Meiotic divisions may occur from the latter portion of capsule expansion through the darkening of the operculum, depending upon the species.

D. **Capsule operculate and post-meiotic**. (This corresponds with spore maturation.) Since species appear differently in this stage, both green capsules without a calyptra and capsules at least partly brown with or without a calyptra are included here. This stage terminates with the dehiscence of the operculum.

E. **Capsule de-operculate**. (This corresponds with spore dispersal at the beginning.) This stage includes capsules containing spores, empty capsules in the year of maturation, and empty capsules from a previous year.

F. **Spore wall bulging**. (This corresponds with spore germination.) This stage terminates with the appearance of the cross wall of the first cell division.

G. **Protonema**. (This corresponds with growth of the protonema.) This stage begins with the two-celled structure as it emerges from the spore and terminates with the initiation of buds.

H. **Bud on protonema**. (This corresponds with the initiation of the leafy shoot.) This stage terminates with the beginning of rapid stem elongation.

I. **Juvenile stem**. (This corresponds with growth of the leafy shoot.) This stage terminates upon cessation of stem elongation and development. In practice two criteria have been used to identify this stage, namely, smaller leaves at the shoot tip plus a lighter green color in these leaves (indicating new growth). These two criteria may not be apparent in all species, in which case additional criteria should be found.

J. **Juvenile gametangium**. (This corresponds with the initiation of a sex organ.) Antheridia and archegonia are indistinguishable from each other at this stage. This stage ends when the sex can be determined.

K. **Antheridium**. (This corresponds with growth of the sex organ and differentiation of microgametes, *i.e.* sperm.)

L. **Archegonium**. (This corresponds with growth of the sex organ and differentiation of megagametes, *i.e.* eggs.) The presence of differentiated perichaetial leaves in some species will identify this stage from k.

Figure 4. Life cycle stages based on Forman (1965).

embryo within the perichaetium is likely to differ from growth of the seta because the developmental environment changes substantially once the seta emerges from the protective leaves. Forman conveniently chose the embryonic calyptra as the first stage (of course there is no beginning or end to a cycle), placing the protonema to gametophore stages (including production of gametangia) last, perhaps because these "later" stages are the most difficult and least likely stages to be observed.

Figure 5. ***Bryum pallescens*** showing terminal seta and capsule of an acrocarpous moss. Note that the capsule is protruding from last year's gametophyte while the growth for the current year is tall. Photos by Michael Lüth, with permission.

Stark (1984), in encouraging North Americans to join in collecting phenological data, recommended a modification of the systems of Longton (1979) and Greene (1960) for describing gametangia. It adds clarity and distinguishes between young, mature, and ruptured gametangia, distinctions that are important in taxa that have gametangial development interrupted by winter or a dry season:

1 = unruptured and less than 1/2 full length
2 = unruptured and more than 1/2 their full length
3 = green or hyaline with apices ruptured
4 = brown with apices ruptured
A = abortive; brown and unruptured

Stark later (2002) developed a system of fourteen events, but this system requires a 400x lens to distinguish the beginnings of gametangia before the gender is distinguishable, and while it provides more information, such requirements as determining that the theca contains fewer than half the spores makes the system rather impractical.

Imura (1994) reduced the number of stages to five in his study of ***Pogonatum inflexum***, but provided us with a graphical way of representing the sequence of events that is easy to produce and useful in understanding phenological relationships across multiple years (Figure 6). The degree of detail needed depends on the purpose, and certainly the representation by Imura serves a useful purpose to see the progression and overlap of events between years.

While the stages of the life cycle are similar for all bryophytes, the timing differs. This chapter will examine the major events and factors that control their timing. As demonstrated by Imura (Figure 6), these events include gametophyte growth, production of gametangia, fertilization, production of sporophytes, and dispersal of spores, as well as events that are more difficult to examine in the field – spore germination and development of gametophore buds.

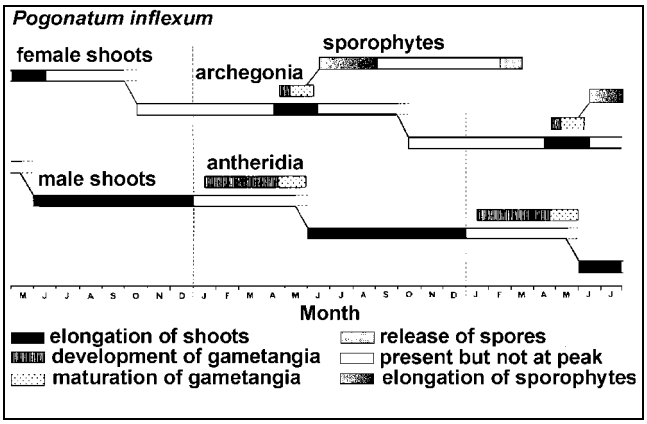


Figure 6. Annual sequence of events for ***Pogonatum inflexum*** on Miyajima Island, Japan. Redrawn from Imura (1994).

Summary

Phenology is defined by Stark (2002) as "the study of the timing of growth and reproductive events." The term is likewise used to refer to the series of events and includes changes of form and phenomena of an organism through time as they relate to climate and season.

The life cycle of a bryophyte can be described based on those stages that are **observably different**, are **discontinuous**, and require a **change in environmental conditions**. This definition presents us with the recognizable stages of **embryonic calyptra**, **seta** with calyptra, **green capsule** with calyptra, **operculate post-meiotic capsule**, **de-operculate capsule**, **spore** with bulging wall, **protonema**, protonema with **bud**, juvenile **stem**, **antheridium**, **archegonium**.

Acknowledgments

I appreciate the helpful comments of Heather Smith in giving me a student's perspective on this chapter. Linda Luster checked the literature citations, proofread, and checked for needed glossary entries.

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CHAPTER 4-2

ADAPTIVE STRATEGIES: PHENOLOGY, IT'S ALL IN THE TIMING

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CHAPTER 4-2

ADAPTIVE STRATEGIES: PHENOLOGY, IT'S ALL IN THE TIMING

Figure 1. ***Atrichum undulatum***, emergent from the snow, has already formed capsules, but must time the release of spores for a time favorable for their dispersal and germination. Photo by Michael Lüth, with permission.

Timing the Stages – Environmental Cues

It's all in the timing! Life cycles are the acrobatics of the plant world, and failure to time things correctly is just as deadly as missing your partner when swinging on the high wires. Timing determines when to germinate, when to release sperm, when to develop the sporophyte, and when to release the spores. This timing must be closely attuned to the climate of the area where the organism is growing and is a major factor in limiting the distributions of many species. In 1984, Taylor and Hollensen contended that there is "rarely any attempt to correlate life changes with time of year." However, where this ecophysiological information is lacking, there is no shortage of studies on dates of phenological events, despite their absence in most bryological manuals. In fact, the sheer numbers of studies are daunting and have caused the delay of this chapter. I will attempt to provide some of the implications of cause and effect through that available literature and examine how habitat and geography influence the timing.

Patterns

Stark (2002a) has compiled patterns of temperate zone phenology based on publications of a few bryophytes [***Pohlia*** (Figure 2) in UK, ***Ptychomitrium*** (Figure 3) in Japan, ***Grimmia laevigata*** (Figure 4) in Spain, ***Bryum argenteum*** (Figure 88) in UK, ***Polytrichum juniperinum*** (as ***P. alpestre***; Figure 5) in UK, ***Forsstroemia producta*** (Figure 6) in eastern USA]:

1. Antheridia initiate in autumn and winter, maturing the next spring and summer (duration several months)
2. Archegonia initiate and mature in the same spring and summer (duration several weeks)
3. Fertilization occurs in summer, lasting two weeks to several months.

Figure 2. ***Pohlia nutans*** with capsules, in a genus used to represent phenology of UK mosses. Photo by Bob Klips, with permission.

Figure 3. ***Ptychomitrium gardneri*** with capsules, in a genus used to represent phenology of Japanese mosses. Photo by Li Zhang, with permission.

Figure 4. ***Grimmia laevigata***, a species in a genus used to represent phenology of Spanish mosses. Photo by Sharon Pilkington, with permission.

Figure 5. ***Polytrichum juniperinum*** with antheridial splash cups, a species used to represent phenology of UK mosses. Photo by Ian Sutton, through Creative Commons.

Figure 6. ***Forsstroemia producta***, a species used to represent phenology of eastern USA mosses. Photo from Earth.com, with permission.

This pattern most likely works well for the many bryophytes that live in areas where they rely on spring rains for fertilization. But notable exceptions exist to these examples with their strongly temperate bias. For example, in Brazil the period of fertilization for ***Sematophyllum subpinnatum*** (Figure 7) extends throughout the entire year (de Oliveira & Pôrto 2001). In the desert, both gametangial initiation and fertilization in ***Trichostomum sweetii*** occur in the autumn and winter (Stark & Castetter 1995).

Figure 7. Epiphytic moss ***Sematophyllum subpinnatum*** in Brazil. Photo by Michael Lüth, with permission.

The sporophyte is dependent on moisture for its own development, but it fares best if it is dry for spore dispersal. Stark (2002a) considered that six generalized patterns prevail for sporophyte maturation:

1. Fertilization in spring and summer with continuous development; spore dispersal anywhere from early summer to the following spring; suitable for a mild climate.
2. Fertilization in summer; embryos overwinter & sporophyte matures the following spring or summer; spore dispersal over extended period; typical of areas with harsh winter; two cohorts may be developing at the same time.
3. Fertilization in summer (or spring) with continuous development to or just past meiosis; overwintering in meiotic/postmeiotic phase; spore dispersal winter-spring; known in south temperate of Northern Hemisphere.
4. Fertilization in winter/spring with embryos forming first winter; dormancy in summer; sporophyte maturation second winter; known in several desert species.
5. Annual species, sporophyte development within two months; fertilization at various times of year – flexible.
6. No pattern; events throughout the year

Zander (1979) reported patterns with taxonomic affinities. He examined spore maturation times in the **Pottiaceae** and showed that differences tended to group by suprageneric taxa. The **Trichostomoideae** mature primarily in spring, **Pleuroweisieae** in midyear, **Barbuleae** are bimodal, **Pottieae** primarily spring, but also summer and winter, **Cinclidotoideae** spring and summer, and **Leptodontieae** poorly known but mainly spring. He attributed the patterns to regional climate and the stress-tolerant nature of these taxa. He further considered that their **ruderal** (waste areas) habitat subjected them to competition from annual tracheophytes that forced them to take advantage of snowmelt water. He further concluded that spores of nearly all mid-latitude Pottiaceae taxa of variable, dry, lowland habitats mature in winter, spring, or early summer. Yet these taxa typically take 9 to 12 months for their sporophytes to mature. Perhaps this strategy permits the spores to germinate immediately while there is still available water, space, and light. Those species that occur in seepage areas or near waterfalls have summer or autumn maturation times instead, again suggesting that water is a driving force in sporophyte maturation times for the other taxa. Zander also found that non-endemic dioicous taxa in the Pottiaceae retain mature capsules slightly longer (mean 6.77 months) than do monoicous taxa (mean 5.55 months).

Growth

Growth is generally controlled by a combination of factors (light, temperature, nutrients, water), but in bryophytes, available water generally is the most important (Zehr 1979). Once moisture is available, the temperature must be sufficiently warm for the water to be in liquid form. Since bryophytes are C_3 plants, most function best at temperatures less than 25°C, so growth may cease during summer.

In temperate climates, growth generally seems to occur in spring and autumn, ceasing or at least diminishing in summer (Al-Mufti *et al.* 1977). For example, ***Atrichum undulatum*** (Figure 1) exhibits this type of growth in South Wales (Figure 27; Benson-Evans & Brough 1966). For other species, growth is predominately in spring, and autumn seems to be a time for elongation without biomass production (Rincon & Grime 1989; Figure 8). Other taxa, adapted to full sun, may be more productive in summer. This is the case in ***Polytrichum juniperinum*** (as ***P. alpestre***; Figure 9), which grows in June and July (Longton 1979). Interestingly, dry weight continues to increase until September, despite the greater increase in photorespiration with rising temperature, a topic that will be discussed in more detail in the chapters on photosynthesis and productivity.

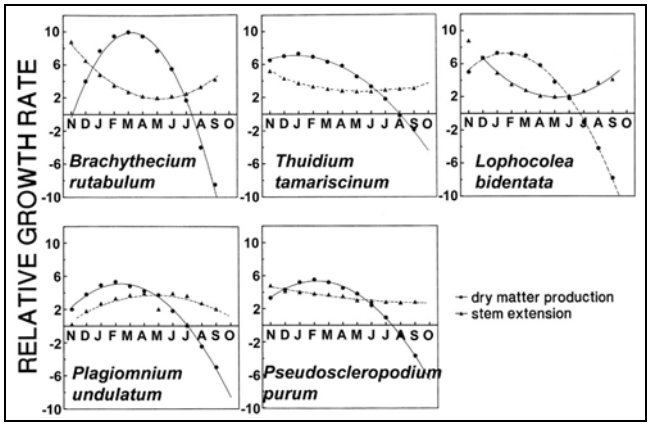

Figure 8. Comparison of relative growth rates in length and dry matter production in five bryophytes from calcareous grasslands. Redrawn from Rincon & Grime (1989).

Where winters are mild, growth may occur throughout the winter. In Japan Imura and Iwatsuki (1989) found that male plants of ***Trachycystis microphylla*** (Figure 10) elongate most rapidly from October until January, but interestingly, the female plants begin their rapid elongation in January and continue until June. In cases where this makes male plants taller than females during sperm dispersal stages, this could be an advantage for facilitating splash of sperm onto an archegonial inflorescence.

Figure 9. ***Polytrichum juniperinum*** with yellowish calyptrae emerging. Photo by Janice Glime.

Figure 10. ***Trachycystis microphylla***, a species in which male and female plants elongate at different times. Photo by Li Zhang, with permission.

Epiphytes may take advantage of decreased desiccation and temperature in winter. Pitkin (1975) found the greatest growth of ***Hypnum cupressiforme*** (Figure 11), ***Platygyrium repens*** (Figure 12), ***Neckera pumila*** (Figure 13), ***Isothecium myosuroides*** (Figure 14), and ***Homalothecium sericeum*** (Figure 15) in November to January in Oxfordshire, UK, corresponding to highest rainfall and mean temperatures below 10ºC at 15:00 hours. Trynoski and Glime (1982) suggested that the appearance of more bryophytes on the south side of trees at breast height in the Keweenaw Peninsula of Michigan, USA, could indicate ability to grow in winter when protection and moisture were available in the space between snow and tree trunk.

Figure 11. ***Hypnum cupressiforme*** in its epiphytic habitat. Photo by Dick Haaksma, with permission.

Figure 12. ***Platygyrium repens*** with bulbils, a species with most of the growth in November to January in Oxfordshire, UK. Photo by Claire Halpin, with permission.

Figure 13. Epiphytic habitat of ***Neckera pumila***. Photo by Jan-Peter Frahm, with permission.

Figure 14. ***Isothecium myosuroides*** on tree at Swallow Falls, Wales. Photo by Janice Glime.

Figure 15. ***Homalothecium sericeum***, a species with most of the growth in November to January in Oxfordshire, UK. Photo by Kristian Peters, through Creative Commons.

Furness and Grime (1982) show strong seasonal effects of temperature that help to explain the phenology of some bryophytes (Figure 16). These results are consistent with peaks of growth in spring and autumn in British tall herb communities. But they also show that different parts of the bryophyte can grow at different times and be favored by different temperatures. In ***Brachythecium rutabulum*** (Figure 17) growth of rhizoids peaks at 12ºC, branches at 15ºC, and stems at 20ºC.

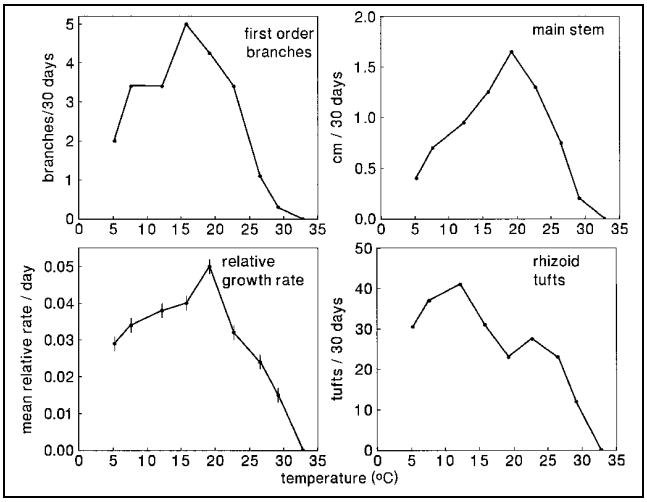

Figure 16. Effects of lab temperature on growth of branches, stems, and rhizoids of ***Brachythecium rutabulum*** (Figure 17) and relative growth rate among 9 growth temperatures under conditions of constant humidity. Redrawn from Furness & Grime 1982.

This difference in temperature, and thus timing of life processes, is consistent with observations on ***Fontinalis*** organs (Glime 1980, 1982, 1987b) and suggests that the bryophyte apportions its limited photosynthate to different activities at different times. This conserves energy and permits directing that energy into the needed structures. In ***Fontinalis***, we can presume that the timing is advantageous because the rhizoids (Figure 18) develop best at temperatures that coincide with the season when the moss is most likely to be stranded above water during low water (summer) and is therefore not likely to be dislodged by the motion of the water. The plants are typically "glued" to the rocks by their covering of sticky algae at this time. Furthermore, in ***Fontinalis*** (Figure 19) branching and growth follow the season of maximum runoff when fragments have been delivered to new substrata in the stream. Intact but damaged plants can also be replenished then (Glime *et al.* 1979; Glime 1980; Figure 20). Timing of gametangial production must permit the gametes to be splashed from plant to plant without having these structures submersed where they will be carried away by the moving water in streams.

Figure 17. ***Brachythecium rutabulum***. Photo by Michael Lüth, with permission.

Figure 18. ***Fontinalis antipyretica*** wound rhizoids. Photo by Janice Glime.

Figure 19. ***Fontinalis antipyretica***; at least some members of ***Fontinalis*** have maximum growth and branching during the season of maximum runoff. Photo by Claire Halpin, with permission.

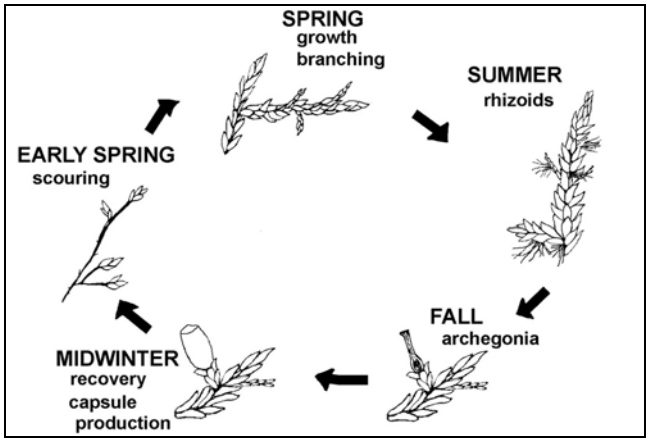

Figure 20. Phenological cycle of growth and reproduction in ***Fontinalis dalecarlica*** and ***F. novae-angliae***. Drawings by Janice Glime.

Many bryophytes, such as ***Eurhynchium praelongum*** (Figure 21), are relatively dormant in winter, resuming growth in spring (April) and continuing through August, with the main peaks in May and September (Benson-Evans & Brough 1966). The common boreal forest feather moss ***Pleurozium schreberi*** (Figure 22) grows little in winter, with growth from April to November (Longton & Greene 1969), but then one can't expect it to grow in the dim or absent light under snow.

Figure 21. ***Eurhynchium praelongum*** Bicton Common England. Photo by Janice Glime.

Figure 22. ***Pleurozium schreberi***, a moss that spends its winter under snow and resumes growth when the snow melts. Photo by Janice Glime.

In contrast, Mishler and Oliver (1991) found that **innovations** (new shoots; in acrocarpous mosses, a new branch) in the drought-tolerant ***Syntrichia ruralis*** (in the mountains of southern New Mexico, USA; Figure 23) appeared in midwinter, lengthening slowly throughout spring, but growing rapidly in late summer and completing growth by winter. Likewise, the chlorophyll concentration was higher in late summer and winter than it was in early summer, but there was no regular pattern of chlorophyll *a*/*b* ratios.

Figure 23. ***Syntrichia ruralis*** benefitting from the rain. Photo courtesy of Peggy Edwards.

Other species in these temperate climates lack seasonal growth peaks. Benson-Evans and Brough (1966) found that ***Funaria hygrometrica*** (Figure 54) initiated new leafy shoots continuously throughout the year in South Wales, reaching their maximum height of about 5 mm in 10 weeks (Figure 27). This results in numerous shoots that can quickly colonize bare ground.

Sphagnum most likely is controlled primarily by water availability, not by temperature. Lindholm (1990) demonstrated that the hummock species ***S. fuscum*** (Figure 24) could grow at most normal temperatures above 0ºC, but that moisture was the primary determinant in that range. Li (1991) found that 30-35ºC was optimum for growth of the hummock-dwelling ***Sphagnum papillosum*** (Figure 25) and ***S. divinum*** (Figure 26) when adequate water was available.

Figure 24. ***Sphagnum fuscum***, a hummock species that grows well at most temperatures above 0ºC, but that is water limited. Photo by Martina Poeltl, through Creative Commons.

Figure 25. ***Sphagnum papillosum***, a hummock species with optimum growth at 30-35ºC. Photo from Botany Website, UBC, with permission.

Figure 26. ***Sphagnum divinum***, a hummock species with optimum growth at 30-35ºC. Photo by Kjell Ivar Flatberg, through Creative Commons.

In South Wales, ***Atrichum undulatum*** (Figure 1) becomes dormant in late summer and begins growth again in January (Figure 27). Benson-Evans & Brough 1966). Different clones of this species can have different growth periods. In ***Funaria hygrometrica*** (Figure 54), growth can begin from new plants in any month of the year and is relatively continuous (Figure 27).

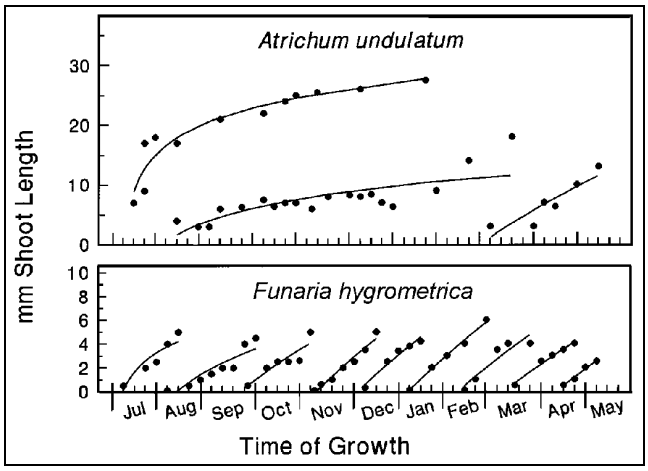

Figure 27. Contrast in vegetative growth periods for two bryophyte species in South Wales. ***Atrichum undulatum*** (Figure 1) becomes dormant in late summer and begins growth again in January. The three curves follow three different sets of plants. In ***Funaria hygrometrica***, growth can begin from new plants in any month of the year and is relatively continuous. Redrawn from Benson-Evans and Brough (1966).

The leafy liverwort ***Lophozia silvicola*** (Figure 28) seemed to exhibit no change in shoot density during the growing season (Laaka-Lindberg 1999). Measurements on liverworts are rare, and for the many very small species, very difficult.

Figure 28. ***Lophozia silvicola*** with gemmae, a species that does not seem to change shoot density during the growing season. Photo by Štěpán Koval, with permission.

One factor that may play a role in seasonal changes in growth is chlorophyll concentration. Valanne (1984) felt chlorophyll concentrations did not change seasonally. On the other hand, Raeymaekers and Glime (1986) found that

chlorophyll concentrations in ***Pleurozium schreberi*** (Figure 22) were slightly higher in summer than in early spring or late autumn. This is not surprising as the plants are shielded from light by snow in winter, thus being unable to replace chlorophyll. The heat and drought of summer can likewise reduce the ability to replace damaged chlorophyll. Habitats can affect the seasonal changes in chlorophyll content of bryophytes. For example, the forest species ***Brachythecium rutabulum*** (Figure 17) has seasonal chlorophyll changes (Kershaw & Webber 1986), increasing as the summer progresses and the light penetration decreases. Epiphytic bryophytes likewise respond to the decreasing light penetration through the canopy (Miyata & Hosokawa 1961). For the aquatic moss ***Fontinalis*** (Figure 29), both light intensity and temperature may play a role in the observed seasonality of chlorophyll content (Bastardo 1980).

Figure 29. ***Fontinalis antipyretica***, a moss that grows in cooler weather. Photo by Andrew Spink, with permission.

Growth in most bryophytes is limited by water availability, with light, nutrients, and temperature playing lesser roles. Most grow best at temperatures below 25ºC and go dormant above that. This puts most of their growth in temperate zones in spring and autumn, while permitting winter growth in warmer climates and summer growth in Polar Regions. Growth in mass can precede growth in length, and this may even be a general rule. Chlorophyll concentrations respond to changes in light intensity – a seasonal phenomenon.

Asexual Reproduction

The large number of propagule possibilities has already been discussed in the chapter on development. But what controls this production? In some species, these are so ever-present that they are used as taxonomic characters [***Plagiothecium*** (Figure 30-Figure 31), ***Pohlia*** spp. (Figure 32)]. In fact, they may be more common than we supposed, as noted by researchers on ***Orthotrichum*** (BFNA 2007; Figure 33). But such propagula require energy to produce and thus we should expect some seasonal differences that avoid other large-energy-requiring events. It is well known that ***Marchantia polymorpha*** (Figure 34) does not produce gemma cups while it is producing sexual reproductive structures. This is demonstrated by the suppression of gemma cup development during long-day conditions when archegoniophore development is occurring, but the addition of high sucrose concentrations can permit their development (Terui 1981). ***Tetraphis pellucida*** likewise does not have gemmae (Figure 35) and female gametangia or sporophytes (Figure 36) at the same time. Thus, we can in many cases surmise their phenology as those seasons when sexual reproduction is not occurring.

Figure 30. ***Plagiothecium cavifolium***, a species with brood bodies year-round. Photo by Bob Klips, with permission.

Figure 31. ***Plagiothecium cavifolium*** with axillary brood bodies that are present year-round. Photo by Bob Klips, with permission.

Figure 32. ***Pohlia annotina*** with bulbils that remain throughout the life cycle. Photo by Hermann Schachner, through Creative Commons.

Figure 33. Gemmae (dark spots on leaves) that are present throughout the life cycle on ***Orthotrichum obtusifolium***. Photo by Michael Lüth, with permission.

Figure 34. ***Marchantia polymorpha*** with gemmae cups and antheridiophores present on different plants. Photo by Claire Halpin, with permission.

Figure 35. ***Tetraphis pellucida*** with gemmae cups, a stage that does not co-occur with sexual structures. Photo by Stefan Gey, through Creative Commons.

Figure 36. ***Tetraphis pellucida*** with capsules, a stage in which gemmae cups do not form. Photo by Bob Klips, with permission. Note spent gemmae cups on left, topping plants with no sporophytes.

In liverworts, it appears that many taxa lack any seasonal absence of gemmae (Schuster 1988; Duckett & Renzaglia 1993), especially in the tropics (Schuster 1988). ***Lophozia silvicola*** (Figure 28) had gemmae throughout the sampling period of May to October in southern Finland, but their peak months were July through September (Figure 37; Laaka-Lindberg 1999; Laaka-Lindberg & Heino 2001).

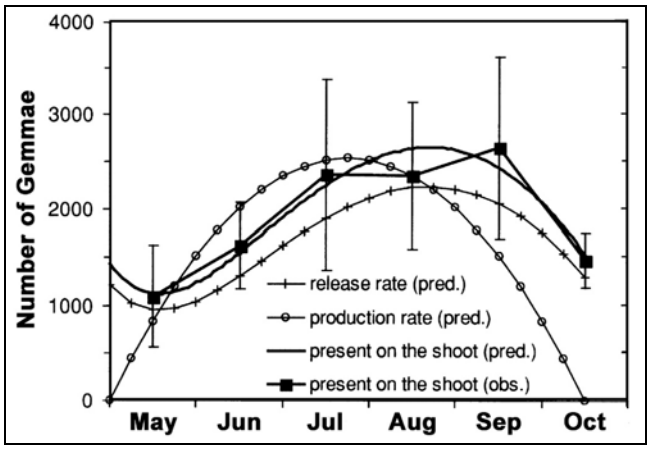

Figure 37. Model predictions (pred.) and observed behavior of gemmae from five colonies of ***Lophozia silvicola*** in southern Finland in 1997-1999. Redrawn from Laaka-Lindberg & Heino (2001).

Laaka-Lindberg (1999) found that gemmae of ***Lophozia silvicola*** (Figure 28) was highest in early spring, declining rapidly as the end of the growing season approached. Laaka-Lindberg and Heino (2001) suggested that there is a seasonal dormancy in gemmae of ***L. silvicola***. They modelled the effects of having two types of gemmae, dormant and non-dormant. Only the dormant gemmae could be expected to survive winter. This model fit well with data for southern Finland for this species and provided a mechanism for replacement of shoots lost to winter mortality. Success would be greatest if more dormant gemmae were produced at the end of the growing season.

Response to light intensity in some taxa suggests that at least some liverwort gemma production should be seasonal. Kumra and Chopra (1989) found that maximum

gemma cup production in ***Marchantia emarginata*** (Figure 38) occurred at continuous light at 4500 lux. However, this is an unlikely combination in nature, with full sun at ~70,000 lux and 24-hour light occurring only in Polar Regions.

Figure 38. ***Marchantia emarginata*** with gemmae. Photo by 楊玉鳳, through Creative Commons.

Laaka-Lindberg (2000) considered that gemmae most likely follow the same seasonal trends as vegetative growth. She reasoned that since gemmae are produced by mitotic cell divisions, albeit in specialized cells, they would be susceptible to the same environmental regulation of growth as normal gametophytic tissue. Since growth often is arrested during sexual reproduction, this is a reasonable possibility.

In west tropical Africa, two species of the moss genus ***Calymperes*** (Figure 39) exhibit distinct seasonal production of gemmae (Odu & Owotomo 1982). Reese (1984) found a striking seasonality in ***Syrrhopodon texanus*** (Figure 40), another member of the same family, with gemmae production increasing in August and peaking in September in the Gulf coastal plain. This follows the high rainfall season in July, which could be favorable to gemma production and establishment.

Figure 39. ***Calymperes tenerum*** with gemmae in a genus where at least some gemma production is seasonal. Photo by Damon Tighe, through Creative Commons.

Figure 40. ***Syrrhopodon texanus***, a moss with seasonal gemma production that peaks in September in the Gulf coast, USA. Photo by Janice Glime.

Aside from balancing the energy needs of sexual reproduction, the asexual structures generally do not have to wait for the right season, thus providing the plant with a more reliable means of reproduction.

Gametangia

Timing of gametangial production might well be the most important timing function a **cryptogam** (any plant with an independent gametophyte) could have. With only one cell layer of protection during development, gametes begin their existence in peril. Once released, the sperm have virtually no protection and must reach the egg in a film of water before effects of sun and winds render their required watery milieu non-existent. Furthermore, it is likely that they are susceptible to UV damage, lacking even a cell wall for protection. Gamete availability itself typically lasts only 1-2 weeks (Crum 2001), and even less in some species. Hence, mechanisms that position this development at a time most likely for success are essential for this step to reach fruition.

The timing mechanisms available to bryophytes have been studied extensively in, of course, the lab rat moss, ***Physcomitrella patens*** (Figure 41). Hohe *et al*. (2002) have determined that temperature, light intensity, and day length all impact the number of sporophytes produced, and thus by inference we must conclude also impact the success of the gametes. In this moss, the highest number of sporophytes resulted when the mosses were cultured at 15°C, 8:16 light:dark cycle at 20 μmol/m^2/s. Culture at 25°C or at 16-hour days drastically reduced the number of sporophytes, indicating that this species is adapted to reproducing under the conditions of spring in the temperate zone. As might be expected, growth diminished under conditions that favored reproduction. Hohe and coworkers even identified a MADS-box gene, PpMADS-S, that produced 2-3 times as much RNA under conditions that favored sporophyte development, suggesting its role in that development.

Figure 41. ***Physcomitrella patens*** with capsules; growth diminishes while capsules are maturing. Photo by Michael Lüth, with permission.

Laboratory experiments do not necessarily represent the real world. Day-night temperature differences may be critical, and certainly water is important. Maturation of reproduction must be timed to coincide with a season suitable for sperm transfer. For example, Odu (1981) showed that in four tropical African mosses, gametangia develop at the beginning of the rainy season. Sporophytes mature to coincide with the dry season.

Signals for timing of gametangial production are most likely a mix of direct responses to rainfall and other moisture sources and other cues, such as day length, that are generally good predictors of later environmental conditions. For example, we see in ***Sphagnum*** (Figure 42) that success of sporophyte production was positively related to the precipitation the previous summer and that summer droughts had a negative influence on gametangial formation (Sundberg 2002). Even after fertilization, however, drought has a negative effect on the sporophyte by drying it too soon before the spores are mature.

Figure 42. ***Sphagnum palustre*** with capsules. Photo by Andrew Hodgson, with permission.

In Scandinavia, this favorable season for gamete release appears to be spring (Arnell 1875), most likely taking advantage of "spring showers." Arnell (in Crum 2001) found that 15% of the taxa released gametes in January-March, 52% April-June (20% in May), 25% July-September, and 8% October-December. However, some taxa do not have a "season." Leitgeb (1868) found that ***Fontinalis antipyretica*** (Figure 29) formed antheridia from spring until autumn [although I found that archegonia matured in autumn and that numbers were greatest under short (6-hour) photoperiods (Glime 1984)].

In milder climates, such as California, USA, late autumn or winter months can provide the best season for successful fertilization. ***Fossombronia longiseta*** (Figure 43) has mature archegonia and antheridia there in November and December (Haupt 1929b).

Figure 43. ***Fossombronia longiseta***, a species that has successful fertilization in November and December in California, USA. Photo by D. L. Bowls, through Creative Commons.

In Japan, Deguchi and Yananose (1989) found that ***Pogonatum neesii*** (Figure 44) initiated its antheridia in early November, with maturity occurring in mid April. By late July they were all dead. Archegonia, on the other hand, matured only in early May.

Figure 44. ***Pogonatum neesii*** with capsules, a species that initiates antheridia in early November in Japan, with them maturing in mid April. Photo by Siddarth Machado, through Creative Commons.

Then there are bet hedgers. ***Dicranum majus*** (Figure 45) in central Norway can form gametangia in late autumn

or early spring, permitting fertilization in June and July (Sagmo Solli *et al*. 1998). It appears that this species has not fine-tuned its gametangial timing; mature antheridia are present all summer and autumn, but archegonia are available only in June and July.

Figure 45. Immature sporophytes of ***Dicranum majus***. Photo by Michael Lüth, with permission.

The initiation and maturation of sex organs of one sex before those of the other in a population may be a common phenomenon. Longton and Schuster (1983) contend that initiation of antheridia several months before archegonia in dioicous taxa results in their maturation at the same time. In the cases of ***Atrichum rhystophyllum*** and ***Pogonatum inflexum*** (Figure 46) in Japan, Imura (1994) found that shoot production of male plants preceded that of females by about four months (Figure 47). Likewise, antheridia production preceded that of archegonia, but antheridia took longer to develop. Similar differences occur in ***Atrichum androgynum*** (Figure 46), with antheridia beginning development in spring after the sporophytes reach maturity (Biggs and Gibson 2006). Archegonia begin development one month later. Development of the sporophyte takes 12 months, with spores being released in the spring. In four species of ***Ptychomitrium*** (Figure 3) in Japan, Deguchi and Takeda (1986) found that antheridia typically required 9 months whereas archegonia required only 1 month to develop, with both maturing in the June rainy season.

Figure 46. ***Pogonatum inflexum***, a species in which production of male shoots precedes that of female shoots by four months in Japan. Photo by Harum Koh, through Creative Commons.

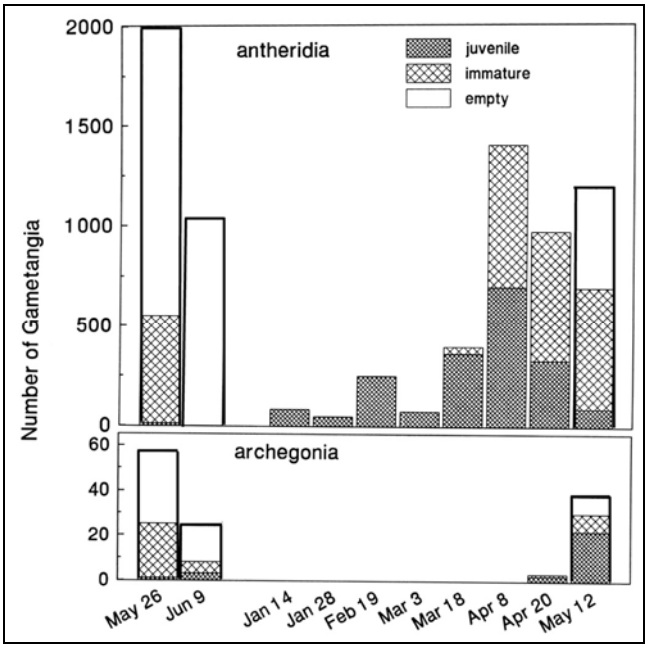

Figure 47. Maturation dates of antheridia and archegonia of ***Atrichum rhystophyllum*** at Miyajima Island, Japan, during 1987-1988. Samples included 1-10 individuals. Based on table by Imura (1994).

In the functionally dioicous ***Pleurozium schreberi*** (Figure 22) in Great Britain, perigonia (♂) begin development in August whereas perichaetia (♀) first occur in October (Longton & Greene 1969). Both overwinter and fertilization occurs in April-May. This results in maturation of the sporophyte by October with spores being shed January-April. Fertilization is delayed in more northern areas such as Scandinavia. On the other hand, Greene (1960) found that in ***Mnium hornum*** (Figure 48) antheridia mature about one month before the archegonia, perhaps insuring that sperm will be available when proper conditions for fertilization occur.

Figure 48. ***Mnium hornum*** from Europe. Photo by Michael Lüth, with permission.

When differences in initiation time occur, we can presume that different stimuli are needed to initiate the development. This is discussed briefly in the development chapter on gametogenesis, but it appears we know little about the signals for initiation when they differ for the two

gametangial types. One such signal is light intensity. In ***Riccia discolor*** (Figure 49), female clones developed gametangia maximally at 3500 lux continuous light at *p*H 5.5 (Gupta *et al*. 1991). However, male plants failed to produce antheridia at *p*H 3.5 or 5.5 at any light intensity in the experiment.

Figure 49, ***Riccia discolor***, a species in which light intensity signals time to develop female clones. Photo by Jan Ševčik, through Creative Commons.

The longer development time for antheridia is common. For example, in Australia ***Dicranoloma menziesii*** (Figure 50) and ***D. platycaulon*** **(**Figure 51**)** initiate their antheridia during winter and archegonia in the spring (Milne 2001). However, the archegonia mature in two months, whereas antheridia require 5-6 months. By contrast, a third species, ***D. billardierei*** (Figure 52), that is **sympatric** (occurring in the same geographic area) with these two, initiates its antheridia during late spring-summer and its archegonia in autumn. The result is that ***D. menziesii*** has fertilization in late summer, ***D. platycaulon*** in mid autumn, and ***D. billardierei*** in early winter. This separation of fertilization time permits these sympatric species to co-exist without the danger of interbreeding that could soon diminish the species distinctions. The sporophyte development is slow, requiring 18-24 months in ***D. billardierei*** and ***D. platycaulon***, but only 12 months in ***D. menziesii***.

Figure 50. ***Dicranoloma menziesii***, a species that initiates antheridia in winter and archegonia in spring. Photo by John Walter, through Creative Commons.

Figure 51. ***Dicranoloma platycaulon***, a species that initiates antheridia in winter and archegonia in spring. Photo by Emily Roberts, through Creative Commons.

Figure 52. ***Dicranoloma billardierei, a species that*** initiates its antheridia during late spring-summer and its archegonia in autumn. Photo by Michael Lüth, with permission.

Initiation of antheridia before archegonia may extend to monoicous taxa as well. Van der Wijk (1960) reported that 14 out of 18 mosses from the Netherlands initiated antheridia before archegonia; three of these 14 taxa were monoicous. The remaining 4 initiated archegonia in the same month as antheridia; one of these was monoicous. In his study, it was typical for antheridia to be initiated in the autumn with archegonia initiated the following spring. In ***Entodon cladorrhizans*** (Figure 56), a monoicous perennial, antheridia likewise initiate well before archegonia (Stark 1983).

Antheridia generally require longer to develop than archegonia. Therefore, male and female gametangia must time their development so that they both mature at the same time, and that maturity occurs at a time when water is available for fertilization. That fertilization period typically is less than one month. For many parts of the temperate zone, this means spring is the best season, with autumn being a second possibility, provided early frost is not a danger to the gametes or the embryo. In dry climates and the tropics, winter is usually the best season because of greater moisture.

Protandry and Protogyny

With the advent of the monoicous condition, bryophytes faced the problem of inbreeding. The solution to this is to have a mechanism to prevent that event. When there is no carrier organism involved, this can be accomplished in two ways. There can be some self-incompatibility mechanism involved, or the two types of gametangia can mature at different times.

Towle (1905) found protogynous timing in ***Atrichum undulatum*** (Figure 53), Egunyomi (1979) in ***Octoblepharum albidum*** (Figure 102). Longton and Schuster (1983) summarize several studies that indicate that **protandry** (maturation of antheridia before archegonia on same plant) and **protogyny** (maturation of archegonia before antheridia on same plant) are common among monoicous bryophytes, as in ***Funaria hygrometrica*** (Figure 54) and ***Atrichum undulatum*** (Figure 53). [***Atrichum undulatum*** is functionally dioicous, at least in Michigan, USA, *i.e.*, it does not produce male and female gametangia on the same plant at the same time, but it can, at least in some populations, produce antheridia the first year and archegonia the next (Crum 1976)]. This is similar to the sequential hermaphroditism seen in some animals such as the blue-headed wrasse. Interestingly, Crum (1976) reports that in North America ***F. hygrometrica*** produces **perigonia** first (housing antheridia), then **perichaetia** (housing archegonia), making them **protandrous**, but Benson-Evans and Brough (1966) report the same species in Great Britain as **protogynous** (having females mature first).

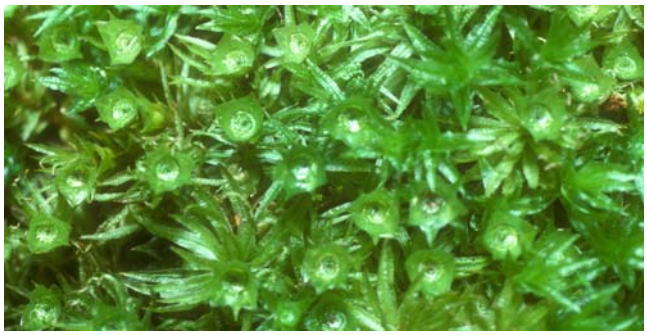

Figure 53. Male plants with splash cups on ***Atrichum undulatum***. Photo by Janice Glime.

Figure 54. ***Funaria hygrometrica*** with young sporophytes in Europe. Photo by Michael Lüth, with permission.

Even in the dioicous perennial moss ***Forsstroemia trichomitria*** (Figure 55), gametangial maturation is protogynous (Stark 1985). On the other hand, Greene (1960) was surprised to find that in perennial moss ***Brachythecium rutabulum*** (Figure 17) the intermixed archegonia and antheridia also had intermixed developmental stages for both gametangia, and that they both appeared to be produced year-round. But in ***Bryum argenteum*** (Figure 88), although archegonia and antheridia are produced at the same time in Reading, England, in north Wales antheridia typically begin development in November and archegonia in the following April (Miles *et al.* 1989).

Figure 55. ***Forsstroemia trichomitria*** with capsules, a species that develops female organs first. Photo by Jennifer Doubt, through Creative Commons.

Some monoicous mosses may benefit, or at least survive, with self-fertilization. In the Chihuahuan Desert, on ***Trichostomum planifolium*** each branch produces an average of 2 archegonia and 3 perigonia containing 6 antheridia, being at first protogynous, but then synchronous, and finally only male. Stark and Castetter (1995) found that fertilization among the gametangia on a single stem in this species appeared to be common.

Sporophyte Maturation

Degree of maturity of sporophytes may be reported in various ways, and the system of Greene (1960; see previous subchapter on phenology) seeks to straighten out these ambiguities. Some authors report the season for spores, which we may assume is the OF (operculum fallen) stage of Greene. Conard (1947), in his phenological study on Iowa herbarium specimens, considered the "perfect capsule" stage to include some opercula shed and others in place. The spike stage of Conard corresponds to the ECI (early calyptra intact) stage of Greene.

Energy Needs

Sporophytes require tremendous energy to mature. Stark and Stephenson (1983) have demonstrated the compensation for insufficient energy in the pleurocarpous ***Entodon cladorrhizans*** (Figure 56) through abortion of sporophytes, much like the abortion of fruits in *Asclepias* (milkweed). But it would seem that the best way to

provide sufficient energy would be to optimize time of development of the sporophyte. To this end, we will examine the timing of capsule production in several examples.

Figure 56. Gametophytes of the monoicous perennial ***Entodon cladorrhizans***. Photo by Janice Glime.

A common way to optimize energy is to avoid having two means of propagation at the same time. Thus, ***Tetraphis pellucida*** (Figure 35-Figure 36) produces capsules in spring (Figure 36), whereas gemmae with gemma cups (Figure 35) are produced after spores are shed. In ***Atrichum undulatum*** (Figure 1), spores are shed in March in Vermont (Figure 1), and new archegonia are present by early May (Towle 1905). As already noted, the antheridia were present earlier (mid April), but they do not compete for sporophyte energy in this dioicous species.

Optimizing Dispersal Time

Often, maturation of capsules is timed to take advantage of dry weather for dispersal. For example, in Nigerian populations of ***Octoblepharum albidum*** (Figure 102), capsules develop quickly from August to early December, when spore liberation begins, coinciding with the dry season (Egunyomi 1979). But natural phenomena are rarely so predictable. The difficulty in drawing generalizations about behavior based on either habitat or climate is exemplified by comparing ***Pylaisia polyantha*** (Figure 57) to ***Hypnum cupressiforme*** var. ***resupinatum*** (Figure 58) (Greene 1960), two species that have somewhat similar gross vegetative morphologies. Although both taxa are found on the bark of deciduous trees in the same areas in the British Isles, ***H. c.*** var. ***resupinatum*** begins its sexual cycle like ***P. polyantha***, with a swollen venter in July-August, but instead of the sporophyte requiring a year (or more), as in ***P. polyantha***, it soon completes its capsule development and loses its spores beginning in January. Although ***P. polyantha*** is monoicous and ***H. c.*** var. ***resupinatum*** is dioicous, it is difficult to imagine how this could affect development of the sporophyte. Similar differences occur in ***Ulota*** in Great Britain (Jones 1946). ***Ulota intermedia*** (Figure 59) capsules mature in July-August, ***U. crispa*** (Figure 60) in spring, and ***U. bruchii*** (Figure 61) in winter, suggesting that season of dehiscence may not be critical for these taxa in this particular location.

Figure 57. Dehisced sporophytes and seta spikes representing two cohorts present at the same time in ***Pylaisia polyantha***. Photo by Michael Lüth, with permission.

Figure 58. ***Hypnum cupressiforme*** var. ***resupinatum***, an epiphyte in the British Isles that begins sporophyte development in July-August and disperses spores in January. Photo by Claire Halpin, with permission.

Figure 59. ***Ulota intermedia*** with capsules that mature in July-August in Great Britain. Photo by Michael, through Creative Commons.

Figure 60. ***Ulota crispa*** growing epiphytically. ***Ulota intermedia*** and ***U. crispa*** have different capsule maturation dates in summer vs spring, respectively. Photo by Janice Glime.

Figure 61. ***Ulota bruchii***, a species where capsules mature in winter. Photo by Michael Lüth, with permission.

One pattern that seems to emerge is that in many terrestrial bryophytes spore dispersal may be timed for alternating moist and dry conditions. If moss spores do indeed depend on flexes of peristome teeth, then a season in which moisture conditions change from wet to dry frequently would be advantageous. Liverworts seem to be largely timed for the same benefit (Schuster 1966). On the other hand, perhaps the important timing is not dispersal as much as it is germination. Spore germination requires water, and if spores are to germinate immediately before being consumed or losing viability, a season of alternating wet and dry could be an advantage. While this latter explanation may have merit for some taxa, it seems that many bryophyte spores are viable for long periods in quite adverse conditions (van Zanten & Pocs 1981; During and ter Horst 1983; During 1986; van Zanten & Gradstein 1988; van Zanten 1992; During 1997; Frahm 2002).

In ***Sphagnum*** (Figure 42), if the capsule dries too soon, the spores are not mature and are forced out of the capsule before they are mature (Sundberg 2002). It appeared to be an advantage for these taxa to mature and have early spore dispersal in the drought-sensitive lawn species to avoid the risk of premature drying of the sporophyte during the summer droughts.

In ***Marchantia polymorpha*** (Figure 62), we have already seen that long days are important for development of the archegoniophore, causing it to reach its maximum height by mid summer when sporangia are mature and warm, dry conditions most likely optimize dispersal of the mature spores (Terui 1981). Thus, this liverwort has to time its gametophyte to carry out the function known for the sporophyte stalk of a moss, necessitating the expression of the trait in the gametophyte instead of the sporophyte generation. In its more tropical relative, ***Marchantia chenopoda*** (Figure 63), sporophytes mature earlier, in late spring to early summer (Moyá 1992), suggesting that temperature may be a signal.

Figure 62. ***Marchantia polymorpha*** with young and older archegoniophores. Photo by Claire Halpin, with permission.

Figure 63. ***Marchantia chenopoda*** females, Maraquez Mountain, Puerto Rico, 5 January 1991; in the tropics the sporophytes mature in late spring to early summer. Photo by Janice Glime.

Spring and Autumn Dispersal

The best overall picture of temperate zone sporophyte phenology seems to be that of Conard (1947) for Iowa, USA, bryophytes. He used herbarium specimens from the State University of Iowa and Grinnell College to determine the number of collections with sporophytes each month. Like gametangia, sporophytes exhibited two seasons of abundance. "Spikes," or setae with no capsule development, were present mostly in March - May and October - November (Figure 64). Capsules matured mostly May - June or October - November (Figure 64). However, these data lack details of timing, and as noted already, could possibly represent development that continued after the collecting date, and could have contained considerable collecting bias.

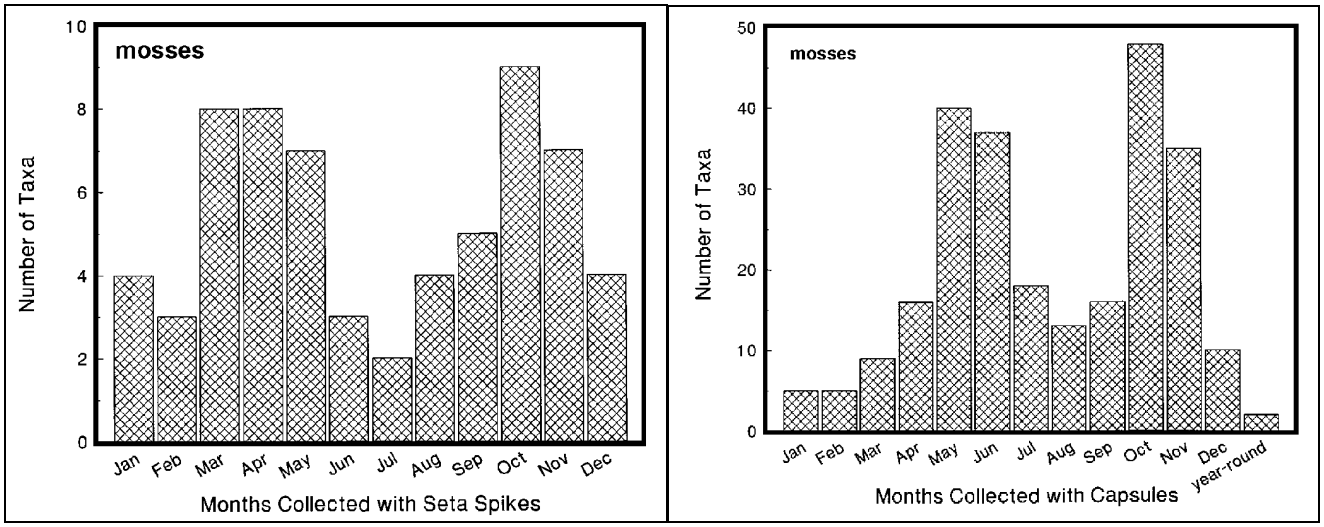

Figure 64. **Left:** Numbers of moss taxa with young setae ("spikes") per month among the 33 taxa that had spikes. **Right:** Numbers of taxa per month with capsules. Study based on 232 species of Iowa mosses in the herbaria at State University of Iowa and Grinnell College. Based on table from Conard (1947).

Lackner (1939) showed capsule and spore maturation times of 182 species in East Prussia. Capsules are present mostly from May to September, contrasting with the summer low reported by Conard (1947) for Iowa, USA. However, when these taxa are separated into those that do not delay capsule development and those that do, it is the ones that delay development that mature mostly in summer (Table 1; Hughes 1990); the others disperse spores mostly in spring (February - April). Previous work by Arnell (1875), as presented by Lackner (1939), on the beginning of capsule appearances for two locations in Europe are shown in Figure 65 and indicate that capsules began to form primarily from April to August in those locations. In these same areas and in Germany, Lackner shows spores ripening mostly in May through July, with other peaks (for East Prussia) in February and October (Figure 65).

Table 1. Phenology of (**a**) 35 species in which capsule formation is not delayed and (**b**) 42 species in which there is a lengthy delay. Table based on Lackner (1939) and modified from Hughes (1990).

		Number of species making response in each calendar month																				Total number of species
		J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	
Fertilization	(a)			1	4	12	11	6	1														35
	(b)		1	1	2	11	13	9	4	1													42
Swelling of capusule	(a)							4	16	8	6	1											35
	(b)														4	17	14	7					42
Spore shedding	(a)											1	3	1	12	10	5	2	1				35
	(b)																1	11	13	13	0	4	42

(a)

Anomodon viticulosus
Atrichum undulatum
Barbula unguiculata
Brachythecium albicans
B. populeum
B. rutabulum
B. velutinum
Bryum argenteum
Buxbauhmia aphylla
Climacium dendroides
Dicranella rufuscens
Dicranella sp.
Didymodon fallax
Discelium nudum
Entodon sp.
Eurhynchium hians
E. striatum
Fissidens bryoides
F. taxifolius
Hedwigia ciliata
Homalia trichomanoides
Homalothecium lutescens
Hylocomium splendens
Hypnum cupressiforme
Leucodon sciuroides
Phascum cuspidatum
Pogonatum urnigerum
Racomitrium heterostichum
Rhizomnium punctatum
Rhynchostegium murale
Rhytidiadelphus squarrosus
R. triquetrus
Schistidium apocarpum
Tetraphis pellucida
Thamnium alopecurum

(b)

Amblystegium serpens
A. subtile
Aulacomnium palustre
Bartramia ithyphylla
Bryum caespiticium
B. pallens
B. warneum
Calliergon cordifolium
Calliergonella cuspidatum
Ceratodon purpureus
Cratoneuron filicinum
Dicranum scoparium
Distichium capillaceum
Encalypta vulgaris
Helodium blandowii
Herzogiella striatella
Homalothecium nitens
Hygrohypnum luridum
Leptobryum pyriforme
Leptodictyum riparium
Mnium hornum
M. marginatum
Physcomitrium pyriforme
Plagiomnium affine
P. cuspidatum
P. medium
P. rostratum
P. undulatum
Plagiothecium cavifolium
P. curvifolium
P. nemorale
Pohlia nutans
Polytrichum commune
P. formosum
P. juniperinum
P. piliferum
Sanionia uncinata
Splachnum ampullaceum
Syntrichia ruralis
Syntrichia subulata
Tortula muralis
Warnstorfia fluitans

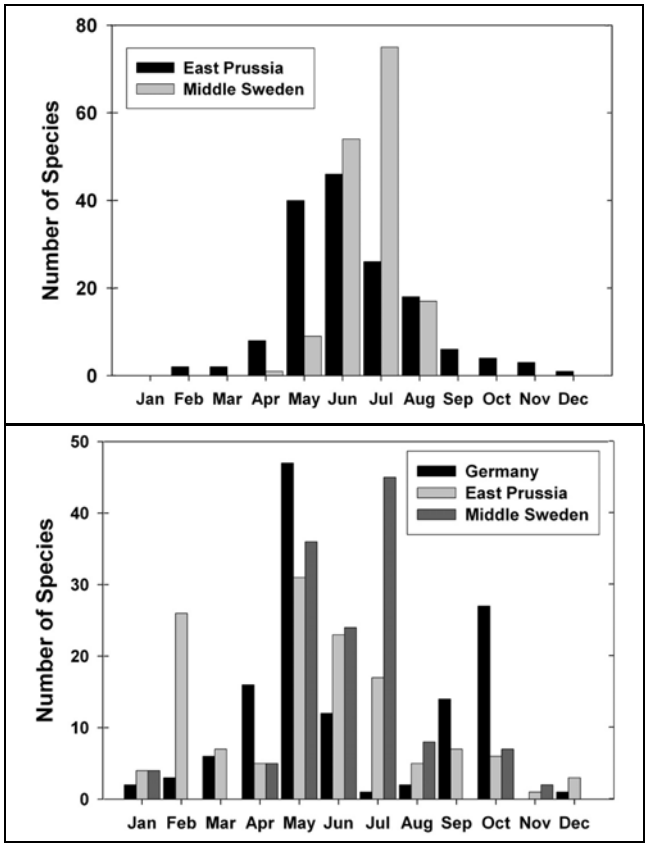

Figure 65. **Top:** Months of capsule appearance in two locations in Europe. **Bottom:** Months of spore ripening in three countries in Europe. Redrawn from Lackner (1939).

As in mosses, Conard (1947) found that the months with the greatest number of mature liverwort capsules were April - June and September - October (Figure 66). Bray (pers. comm.) found that ***Fossombronia foveolata*** (Figure 67) produces capsules in both spring and autumn on the same individuals, drying out in the summer and surviving by producing a dense terminal bud that seems to be protected by its dark, red-brown color. ***Fossombronia*** typically lives in places where it gets submerged part of the year and dried out another part, so it is not surprising that it has a life cycle much like some of the moss ephemerals.

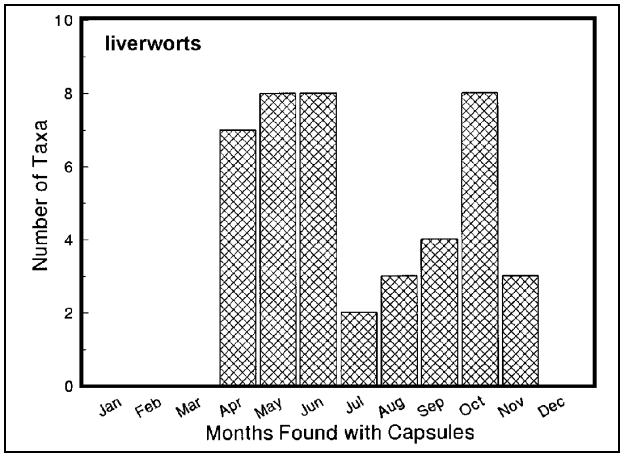

Figure 66. Numbers of liverwort taxa with capsules per month among 30 taxa with capsules out of 60 Iowa liverwort taxa (including Anthocerotopsida) in herbaria. Based on Conard 1947.

Figure 67. ***Fossombronia foveolata*** with capsules, a species that produces capsules in both spring and fall. Photo by Sharon Pilkington, with permission.

In the mild climate of California, USA, the thallose liverwort ***Asterella californica*** (Figure 68) occurs on moist banks and canyon walls, where its growth occurs autumn to spring and its capsules mature in April (Haupt 1929a). It dries out in summer and survives from tips of branches.

Figure 68. ***Asterella californica*** mature females with capsules ready to emerge. Photo by Peter J. Bryant, with permission.

Development Time

Sporophyte maturation can be a slow process, thus crossing multiple seasons. Grimme (1903) reported that in Germany he found the minimum time for sporophyte development to be that of ***Atrichum tenellum*** (4 months; Figure 69-Figure 70) and the maximum to be for ***Grimmia ovalis*** (24 months; Figure 71). Crum (2001) reports ***Polytrichum*** (Figure 72) to require 13 months and ***Dicranum*** (Figure 45) 17 months. These times differ with geographic location and may depend on such factors as length of growing season, temperature, and water availability. Many other variations occur, attesting to the fact that these sporophytes must withstand a wide range of conditions during their development, yet maintain a timing that is suitable for spore dispersal.

In addition to defining developmental stages, Greene (1960) suggested a scheme based on time required for development (Figure 74).

Figure 69. ***Atrichum androgynum***, a perennial species with a rapid sporophyte development. Photo by Niels Klazenga, through Creative Commons.

Figure 70. ***Atrichum tenellum*** capsules that are able to develop in 4 months. Photo by Hermann Schachner, through Creative Commons.

Figure 71. ***Grimmia ovalis*** with both immature and spent capsules that take 24 months to develop. Photo from Earth.com, with permission.

At least in the temperate zone, the spring and autumn maturation times may follow a long development, as found in ***Polytrichum*** (Figure 9, Figure 72) – 7-16 months in Scandinavia, 9-20 months in Sweden (Arnell 1905), and ***Forsstroemia trichomitria*** (Figure 55) – 17 months (Stark 1984), or 15 months for ***P. juniperinum*** (Figure 9, Figure 72) in the Antarctic (Longton 1972). In others, such as ***Mnium hornum*** (Figure 48, Figure 73), the seta emerges (Figure 73) in the autumn, remaining in that state throughout the winter, and continues development in early spring (Greene 1960). In Great Britain, this species has lost its opercula by early May.

Figure 72. ***Polytrichum juniperinum*** capsules with calyptra, a species in which capsules take 15 months to develop in the Antarctic; maturation time depends on location. Photo by Felipe Osorio-Zúñiga, with permission.

Figure 73. ***Mnium hornum*** with young sporophytes that are able to overwinter before completing development. Photo by Bob Klips, with permission .

categories of sporophyte development

6 months	– no resting stage (ex. ***Atrichum undulatum***)
10 months	– short winter resting stage (ex. ***Mnium hornum, Eurhynchium praelongum***)
14-18 months	– resting stage in winter, often persisting partly into next growing season (ex. ***Funaria hygrometrica***)

Figure 74. Scheme for representing sporophyte development. Based on Greene 1960; examples from Benson-Evans & Brough 1966.

The capsule cycle of the epiphytic ***Pylaisia polyantha*** (Figure 57) requires so much time for development that two generations of capsules are present at the same time, not only in Great Britain, but in many locations in both Europe and North America (Greene 1960). The venter is swollen in July to August, and the calyptra is retained for an entire year, falling in the next July. Capsule development continues, with the operculum falling early in the following year. In Great Britain, this species has lost its opercula by early May.

Winter Dispersal

Winter is a good time for capsule maturation to occur in mild climates where that is the moist season. In Great Britain, ***Brachythecium rutabulum*** (Figure 17) has lost its opercula by early May (Greene 1960). It continues development from its early calyptra stage in September on to an intact operculum with the operculum falling December to February. By March the capsules are empty. If it were to follow that timing in the Keweenaw Peninsula of Michigan, USA, its capsules would be imbedded in snow at the time of dispersal. In Japan, the thallose liverwort ***Mannia fragrans*** (Figure 75-Figure 76) has mature spores in early winter (Furuki 1992).

Figure 75. ***Mannia fragrans*** with emerging sporophytes. Photo by Samuel Brinker, through Creative Commons.

Figure 76. ***Mannia fragrans*** with nearly mature sporophytes, with mature spores in Japan occurring in winter. Photo by Botanical Wanderer, through Creative Commons.

Lackner (1939) found that ***Orthotrichum*** (Figure 86) species were notable exceptions to the spring and summer dispersals of bryophytes in his study. This epiphytic/saxicolous genus typically produced capsules in the winter months. Perhaps winter is good for mosses if they can avoid being covered by snow, although early frost causes mortality in young capsules of the soil-dwelling ***Buxbaumia aphylla*** (Figure 77-Figure 78) (Hancock & Brassard 1974). The result is that survival depends on the rapid maturation of the sporophyte in the autumn, permitting the capsules to be dormant during the winter.

Figure 77. Immature sporophytes of ***Buxbaumia aphylla*** in Michigan, USA. Photo by Janice Glime.

Figure 78. ***Buxbaumia aphylla*** mature capsules with one that has been damaged. Photo by Bernd Haynold, through Creative Commons.

Winter may also favor aquatic bryophytes, but for somewhat different reasons because the problems are quite different. Dispersal by air would seem to be nearly impossible when the environment is continuously moist or submersed. And, in fact, we have no direct evidence of the success of the spores of such submersed taxa as ***Fontinalis***.

Nevertheless, ***F. dalecarlica*** (Figure 79-Figure 80) and ***F. novae-angliae*** (Figure 81) produce capsules in autumn and mature them in winter, at least in New Hampshire, USA, with abrasion apparently serving as the primary means of opening the capsule (pers. obs.). The subsequent dispersal of the spores is pure conjecture, but since the peristome teeth are generally not exposed to air, one might suppose that water is the only available agent. It is interesting that the aquatic liverwort ***Scapania undulata*** (Figure 82-Figure 83) likewise produces its capsules in winter (Grainger 1947).

Figure 79. ***Fontinalis dalecarlica*** with developing capsules in late autumn. Photo by Janice Glime.

Figure 80. ***Fontinalis dalecarlica*** capsules that mature in winter in New Hampshire, USA. Photo by Janice Glime.

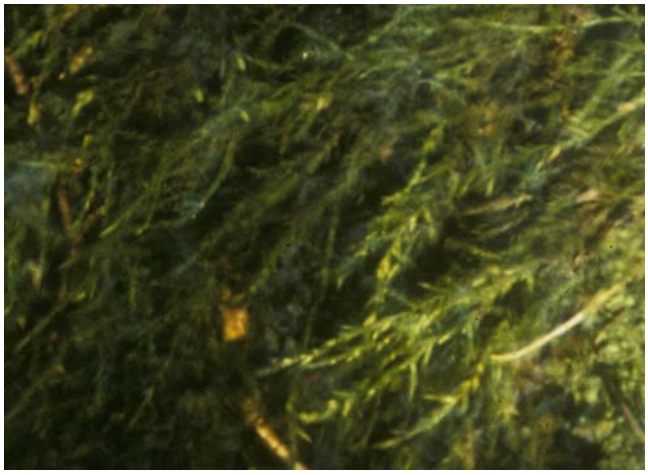

Figure 81. ***Fontinalis novae-angliae*** with young capsules in late autumn. Photo by Janice Glime.

Figure 82. ***Scapania undulata*** with its capsule in winter. Photo by Malcolm Storey <DiscoverLife>, with online permission.

Figure 83. ***Scapania undulata*** with dehiscing capsules. Photo by Malcolm Storey <DiscoverLife>, with online permission.

Elevation Effects

For those bryophytes not adapted for development during winter conditions, elevation provides evidence of the importance of temperature. For thirteen taxa growing at four elevations in the Eastern Pyrenees, Girona, Spain, those living at higher elevations have dormant sporophytes in the winter, completing their development early in the summer (Lloret 1987). Those that live at lower elevations have continuous development. Only one species among these, ***Schistidium confertum*** (Figure 84), is able to continue development at locations above 1800 meters.

Figure 84. ***Schistidium confertum*** with capsules, a species that is able to continue its development at elevations above 1800 m. Photo by Gordon Rothero, with permission.

One of the factors that can affect success of a sporophyte is the weather during development of pre-winter stages, as shown by the high mortality due to early frost in young sporophytes of ***Buxbaumia aphylla*** (Figure 77-Figure 78) in Newfoundland (Hancock & Brassard 1974). In this species, young capsules are formed in the autumn and remain green over the winter, maturing the following spring. By summer, little evidence of the capsule remains, although their thick setae are sometimes still present.

Fortunately, mosses are adaptable in their physiological responses, often resulting in physiological races in different parts of the world. Longton (1979), in comparing ***Polytrichum juniperinum*** (as ***P. alpestre***; Figure 9, Figure 72) populations at the more northern Churchill, Manitoba, Canada, site to those at Pinawa, Manitoba, found that the initiation of the LCP (late calyptra in perichaetium) stage began earlier in the autumn and that shift to the OI (operculum intact) stage occurred later in the spring at Churchill (Figure 85). However, the sporophyte development proceeded more quickly at Churchill during the growing season, surpassing that of the mosses at the Pinawa site, and compensating for the longer dormancy.

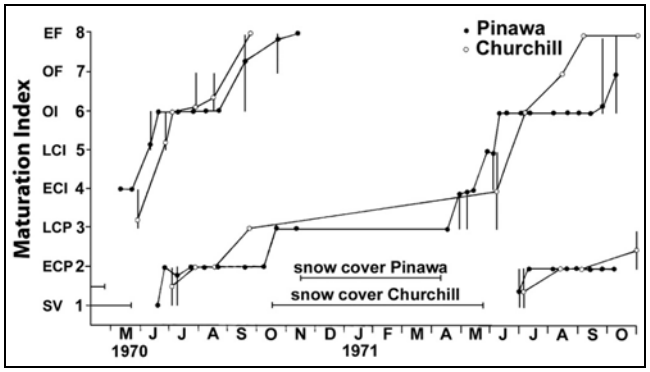

Figure 85. Comparison of sporophyte development of ***Polytrichum juniperinum*** in Pinawa and Churchill, Manitoba, Canada. Points represent the maturity indices with vertical bars indicating the range of stages present. Based on Longton (1979).

Spores and Protonemata

Spore dispersal is most advantageous if the air is dry and breezy, permitting the spores to travel long distances before becoming lodged within the minute crevices of the soil or other substrate. In fact, dryness usually initiates the shedding of the operculum, as illustrated by Johnsen (1969) for ***Orthotrichum anomalum*** (Figure 86). On the other hand, to mature, the capsule must have energy available, so these two factors must be included in the dispersal strategy to determine the season of dispersal. It may be this need for energy, then a dry season, followed by a suitable moist season, that some mosses disperse their spores in winter, *e.g.* ***Anomobryum julaceum*** (Figure 87) and ***Bryum argenteum*** (Figure 88) (Pedersen & Hedenäs 2002) and the liverwort ***Mannia fragrans*** (Figure 75-Figure 76) in Japan (Furuki 1992). In the seasonally dry interior of North America, ***Syrrhopodon texanus*** (Figure 40) has optimal spore release in October to March, followed by rain that peaks in July, then decreases rapidly to a low in November (Reese 1984). As we have already seen, one way to accommodate these needs for energy and the right moisture conditions is for the capsule to persist in a mature state, operculum intact, for months to years before initiating dispersal.

Figure 86. ***Orthotrichum anomalum*** with capsules. Photo by Claire Halpin, with permission.

Figure 87. ***Anomobryum julaceum*** with dry capsules that disperse spores in winter. Photo by David T. Holyoak, with permission.

Figure 88. Capsules on ***Bryum argenteum***. Photo by Michael Lüth, with permission.

Using herbarium specimens, Nishimura (1993) determined the dates of dispersal for mosses from the Hiruzen Highlands on the island of Honshu, Japan (Figure 90). He found 34 species that disperse spores in late autumn to early spring (late November to early April), 12 in late spring to summer (May to August), and 5 in autumn (September to November). ***Bryum argenteum*** (Figure 88) dispersed in both spring and autumn. ***Sematophyllum subhumile*** (Figure 89) was the only species that had no definite season of dispersal. Although herbarium specimens can introduce error because opercula tend to come off more easily under the dry conditions of the herbarium, the 551 specimens used in this study give us a general picture of events.

Figure 89. ***Sematophyllum subhumile*** with capsules, a species for which dispersal is not seasonal. Photo by Geoff Bryne, through Creative Commons.

Egunyomi (1979) found that capsules of ***Octoblepharum albidum*** (Figure 102) in Nigeria matured just in time for spores to be liberated during the dry season. Stark (2001a.) finds that most desert bryophytes release spores year-round, an advantage in a dry climate where rainfall is rare and not seasonal. On the other hand, spores in ***Pleurozium schreberi*** (Figure 22) in Britain are shed January-April when it is cool and relatively moist (Longton & Greene 1969). In a later study in Great Britain, Longton and Miles (1982) found that five mosses had fertilization in the period of April to July, but that sporophyte maturation time varied considerably. Spore liberation took place from six to twelve months later, spanning a variety of climatic conditions.

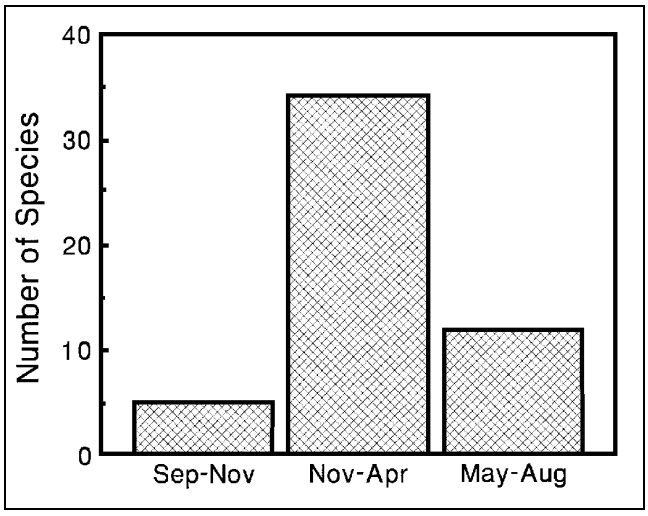

Figure 90. Seasons of dispersal in 51 species of mosses from the Hiruzen Highlands, Honshu, Japan. From data of Nishimura (1993).

To determine the availability of spores, Fenton and Bergeron (2006) studied the spore dispersal of ***Sphagnum*** (Figure 91) species in a black spruce (***Picea mariana***) forest (Figure 92) in Québec, Canada. Using spore traps, they determined the phenology of spore dispersal (Figure 93) for two years. Dispersal at these locations began in July, rose in mid August, and ended mid to late September, with peak dispersal near the beginning of September. The earlier dispersal than that of the study in Japan (Nishimura 1993) may be the result of the higher latitude.

Figure 91. ***Sphagnum fallax*** with capsules that disperse spores in July-August in Québec, Canada. Photo by James K. Lindsey, with permission.

Figure 92. Spruce peatland, where spore dispersal in Ontario begins in July, rises in mid August, and ends mid to late September, with peak dispersal near the beginning of September. Photo by Richard Norby, Oak Ridge National Laboratory, with permission.

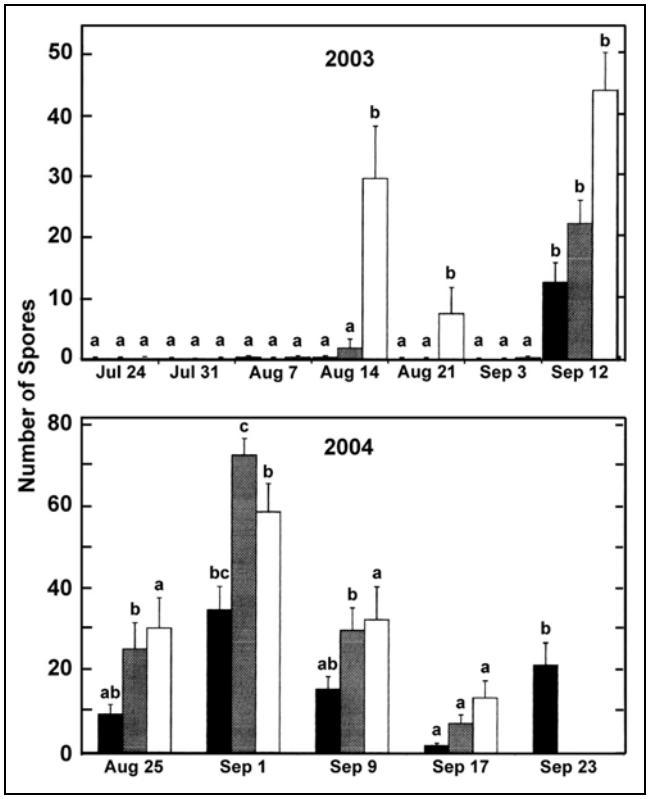

Figure 93. Number of spores collected in 20 spore traps at each of three sites in Québec, Canada. Vertical bars represent standard error. Different letters indicate those values that are significantly different within a site. Redrawn from Fenton & Bergeron (2006).

Although the time of spore dispersal is fairly well known, or at least available in herbaria, virtually nothing is known about the time of spore germination. Longton and Schuster (1983) comment that little is known about spore dormancy in liverworts and virtually nothing about the effect of day length on germination. This is due largely to the difficulty of locating this stage and, even if located, to identify even the genus, much less the species.

We can speculate on the importance of timing for spore establishment. Proctor (2000) pointed out that the need for water would limit the successful establishment of spores and their protonemata on rocks and bark to the lengthy wet season of autumn and winter in western Europe and whatever wet season elsewhere.

Even in taxa with persistent protonemata, *e.g.* ***Buxbaumia***, where sexual organs are produced directly on the protonema, field knowledge is lacking. After extensive study of ***Buxbaumia aphylla*** (Figure 77-Figure 78) spanning three years, Hancock and Brassard (1974) were unable to determine if the protonema persisted for more than one season or if the gametangia were produced the same season.

In most taxa, it is probably not necessary to couple suitable germination and protonema development conditions with those of dispersal. Spore viability can last from less than an hour in some epiphyllous and epiphytic liverwort taxa (Longton & Schuster 1983) to 50 years in other bryophytes (Sussman 1965), and probably longer in some taxa. Most spores probably have considerable longevity, as seen in several diaspore bank studies in the Netherlands (e.g. During 1986, 1990, During & ter Horst 1983, During *et al*. 1987). They even survive temperatures near absolute zero when dried and placed in vacuum tubes (Becquerel 1932). Van Zanten (1976) has shown that most taxa can survive desiccation for one year, with wet-frozen spores surviving better than dry-frozen ones. But for spores that fall near their parents and do not effect long-distance dispersal, immediate germination success will provide a better chance of establishing the next generation, particularly in overwintering annual taxa, by giving them an early start and a higher percentage of survival.

Protonemata can likewise survive considerable drying (Lipman 1936) and in some taxa such as ***Grimmia*** (Figure 4, Figure 71) may even require a drought period before advancing to the next stage (During, pers. comm.). In fact, Johnsen (1969) found that in ***Orthotrichum anomalum*** (Figure 86) watering during the dormant period (hot and dry) was detrimental. Thus it appears that germination should require more than just the right seasonal event, but rather a seasonal event coupled with the right environmental conditions to take things to the next stage. There seems to be no hope at present of generalizing about phenological events related to the protonemata based on any foundation in data.

Duration of Stages

Longton (1997, 1998) found that those bryophytes that have shorter life spans become reproductively active at a younger age and tend to have greater phenological flexibility. This strategy necessarily implies that each stage is short. This is especially true for the colonists, fugitives, and annual shuttle species to be discussed later in the life strategies chapter. For those taxa that stay longer, the stages may be longer, often depending on habitat characteristics, particularly availability of water.

Gametangia

One of the factors that is important in maintaining distinct species when more than one member of a genus cohabit a region is that their reproductive periods do not

overlap or that their means of dispersing gametes are mutually exclusive. Among three Australian species of ***Dicranoloma*** (Figure 50-Figure 52), all three species studied required 5-6 months for antheridia to mature, but only 2 for archegonia (Milne 2001), the longer time for antheridial development being typical for most mosses. Yet the timing for these three taxa was such that their periods of fertilization were mutually exclusive.

For ***Entodon cladorrhizans*** (Figure 56) growing in Pennsylvania, USA, the fertilization period lasts five weeks (Stark 1983). In the desert moss ***Syntrichia inermis*** (Figure 94), maturation of the antheridia takes one to several years due to the intervening dry periods that cause dormancy (Stark 1997).

Table 2 provides additional examples of maturation times, ranging from less than one month for some archegonia and three months for some antheridia to nearly one year for others.

Sporophytes

Ephemeral species have short-lived capsules that may last only a few weeks. Liverworts do likewise, with their deliquescent stalk soon withering away. Furthermore, the valvate capsules of liverworts shed all the spores at one time, whereas in mosses peristome teeth operate to extend dispersal over a longer period, providing the mosses with more opportunities to disperse under conditions favorable for greater dispersal or germination success. ***Sphagnum*** likewise has short-lived stalks, in this case a deliquescent pseudopodium (Figure 91) that develops from the gametophyte to extend the capsule away from the plant. It lacks teeth and disperses most of its spores in one explosive burst when the operculum is shed due to capsule drying and at least some of the time, internal gas expansion due to high temperatures.

Figure 94. ***Syntrichia inermis*** in its dry state beneath shrubs. Photo courtesy of Lloyd Stark.

But other mosses may have quite extensive periods of sporophyte development. In ***Dicranoloma***, ***D. billardierei*** (Figure 52) and ***D. platycaulon*** (Figure 51) required 18-24 months whereas those of ***D. menziesii*** (Figure 50) required only 12 (Milne 2001). ***Atrichum androgynum*** (Figure 46) likewise requires 12 months for sporophyte maturation (Biggs & Gibson 2006).

Table 2. Examples of times of initialization of gametangia, fertilization, and spore dispersal in bryophytes in the temperate zone.

	location	antheridia initialized	archegonia initialized	fertilization	spores dispersed	reference
Atrichum undulatum	UK	Jan-Feb	Apr-May	May-Jun	Jan-May	Miles *et al*. 1989
Polytrichum juniperinum (= *P. alpestre*)	UK	Sep-Oct	Mar-Apr	Jun	Jun-Jul	Miles *et al*. 1989
Bryum argenteum	UK	Oct-Nov	Apr-Jun	Apr-Jun?	Jan-May	Miles *et al*. 1989
Grimmia pulvinata	UK	most of yr	most of yr	most of yr	Apr-Jun	Miles *et al*. 1989
Tortula muralis	UK	anytime	anytime	anytime	Apr-Jun	Miles *et al*. 1989
Pellia epiphylla	UK	Jan-Jun	Jun	Jun	Mar-Jun	Clapham & Oldroyd 1936
Cephalozia	UK	Feb	Mar	May	?	Clapham & Oldroyd 1936
Marchantia polymorpha	UK	Mar-Apr	Mar-Apr	May	Aug	Clapham & Oldroyd 1936
Aplozia	UK	Apr	May	Jun	May	Clapham & Oldroyd 1936
Conocephalum conicum	UK	Apr-Jun	Jun-Jul	Jul	Mar-Apr	Clapham & Oldroyd 1936
Conocephalum conicum	MI, USA	Aug	Aug	Jun	Apr	Taylor & Hollensen 1984
Diplophyllum	UK	Dec	Jan	May	May	Clapham & Oldroyd 1936
Scapania	UK	Dec	Jan	May	May	Clapham & Oldroyd 1936

Mosses that depend on rainy periods may have very short periods for maturation of the sporophyte, attuned to dispersal at the end of the rainy season, as in ***Racopilum africanum*** (Figure 95), ***Fissidens weirii***, ***Thuidium gratum***, and ***Stereophyllum*** sp. (Figure 101) from SW Nigeria (Odu 1981). These mosses required 12 months from onset of gametangia to capsule maturity and dispersal, but sporophyte development itself is complete at the end of the rainy season (October-December), following gametangial development at the onset of the rainy season (March/April). Spore dispersal occurs during the dry season (November-April). The entire process requires 12 months. Other desert mosses can have very long maturation periods spanning several years with long dormancy periods intervening.

The soil-dwelling ***Syntrichia inermis*** (Figure 94), in the Mojave Desert, USA, requires about 21 months for sporophyte development, while being dormant for 18 of those months (Stark 1997). Span of operculum detachment may last up to 2.5 years, and capsules of the same cohort may disperse spores over a period of three years (Stark 2001a). In the same desert, the rock-dwelling ***Grimmia orbicularis*** (Figure 97-Figure 98) required only 3 months for its capsule to mature following meiosis, and its operculum dehiscence spanned only three weeks; spore release of the cohort lasted about six months (Stark 2001a).

Figure 95. ***Racopilum africanum*** with young sporophytes. In this species, gametangia develop at the onset of the rainy season and the sporophytes mature at the end of it. Photo by Jan-Peter Frahm, with permission.

Figure 96. ***Stereophyllum radiculosum***, one of the mosses where gametangia develop at the onset of the rainy season and the sporophytes mature at the end of it. Photo from Missouri Botanical Garden, with permission.

Figure 97. Rock-dwelling ***Grimmia orbicularis***. Photo by Michael Lüth, with permission.

The perennial moss ***Entodon cladorrhizans*** (Figure 56) requires six to nine months for the sporophyte to mature (Stark 1983).

Figure 98. Capsule of ***Grimmia orbicularis***. Photo by Michael Lüth, with permission.

Zander (1979) did an exhaustive study in the Pottiaceae of the north temperate zone of Europe, Asia, and North America, comparing dioicous and monoicous taxa. The **Pottiaceae** typically require 12-13 months for sporophyte development (Krieger 1915), but Zander found that the phenology of the two sexual conditions differed, with dioicous taxa having mature capsules over a slightly longer period of time than did monoicous taxa. Non-endemic dioicous taxa have a mean span of mature capsules of 6.77 months, whereas the non-endemic monoicous ones have only a 5.55-month mean. Among the 86 dioicous taxa studied, 12 have mature capsules spanning nine or more months, whereas only 5 of the 82 monoicous taxa exhibit this duration. He reasoned that this afforded dioicous taxa a better chance for dispersal, perhaps in part compensating for the smaller likelihood of fertilization. This compensation concept was further supported by finding that the monoicous taxa did not have a significantly wider distribution. Since the ratio of monoicous to dioicous taxa in **Pottiaceae** is similar to that of bryophytes as a whole, this study might be a model of mature capsule duration in monoicous vs. dioicous taxa. It would be interesting to determine if capsule duration can indeed compensate for the reputedly greater percent of species producing capsules among the monoicous taxa than among the dioicous ones (Gemmell 1950, Longton & Schuster 1983).

Winter Effects

In bryophytes, unlike the tracheophytes, embryos and gametangia are capable of surviving prolonged freezing of winter (Stark 1984). Continuous melt of snow during parts of the winter could facilitate fertilization of some bryophytes under the snow, but no broad-scale studies have examined this in areas where the phenomenon is likely, and while the gametangia might survive, one must question whether the sperm can swim and locate a female at near-freezing temperatures. Furthermore, while sperm can swim at speeds of 100-200 μm per second (Richards 1978), they require a chemical attractant to find the archegonium (Muggoch & Walton 1942), and cold temperatures might reduce the effectiveness of such an attractant. Even so, we know that the aquatic liverwort ***Scapania undulata*** (Figure

82-Figure 83) produces gametangia and accomplishes fertilization in winter (Grainger 1947).

On the other hand, Imura and Iwatsuki (1989) found that in ***Trachycystis microphylla*** (Figure 99) in Japan, antheridia production begins in January with sperm being released March to May. Archegonia production is delayed until March, but they are ready to accept sperm from April to July. The partitioning of energy among life cycle stages would appear to be complex in this species, with overlapping life cycle stages, since spores are released near the time of fertilization of the next generation. (Imagine sending one kid off to college while you are pregnant with the next!) Development of the sporophyte begins in May, and rapid sporophyte elongation occurs in October to November and again in February. Spores are released in April – apparently near the time sperm are released. One would think this delicate timing would require competing environmental conditions, wet for sperm and dry for spores. Since spring is a time of alternating sunshine and rain, these contrasting conditions are probably available.

Figure 99. ***Trachycystis microphylla***. Photo by Li Zhang, with permission.

One explanation for the success of overwintering antheridia as a strategy is that it may spread out the energy requirements over a longer period and give antheridia a chance to grow rapidly in spring, thus insuring that they precede the archegonia in maturity. Benson-Evans and Brough (1966) found that a cold period followed by warmer temperatures can induce more rapid maturation of sex organs if sufficient moisture is available, whereas low temperatures and drought retard development. In this case, the antheridia would receive the stimulation, but the archegonia, by delaying initiation until spring, would not. This advantage is consistent with the 10 out of 18 taxa examined by van der Wijk (1960) in which male gametangia overwintered; female gametangia in these were generally initiated in early spring. One must ask why it is the males that seem to overwinter, whereas females of the same species often delay initiating gametangia until spring. Is it because winter is in fact destructive, but male gametes are much more abundant than are female gametes and can therefore afford to sacrifice some in order to mature earlier? Is there some developmental reason why antheridia require a longer time to develop than do archegonia? Or is it a mechanism to increase protandry, thus ensuring at least some cross fertilization?

Despite the ability of gametangia to survive over winter, Arnell (1905) reported that most of the 33 German and Swedish taxa he studied had gametangial dehiscence in the summer, which suggests that fertilization must have occurred then as well. However, many parts of the world lack sufficient moisture in summer to ensure fertilization.

Huneck *et al*. (1984) determined that essential oils in the temperate leafy liverwort ***Bazzania trilobata*** (Figure 100) were highest in September and lowest in January, suggesting that perhaps these oils might be used for energy reserves during autumn and early winter. It is also possible that they offer a protective function to the cells during the period of freezing ant thawing in autumn.

Figure 100. ***Bazzania trilobata***, a species that has the most essential oils in September and lowest in January. Photo by John Garrett, through Creative Commons.

Geographical Differences within Species

Earlier studies by Richards (1959) indicate that seasonal behavior of bryophytes may vary in different climatic regions. The basic developmental pattern of gametangia and sporophytes may differ. Furthermore, lack of proper environmental signals, such as not reaching the necessary temperature at the necessary photoperiod, or inability of the plant to interpret the signals, can result in failure to produce gametangia or in failure of females to produce mature archegonia at a time when sperm are ready for release (Newton 1971, 1972, Longton 1972).

Even within a small geographic range, signals can come at a different time. For example, in North Wales, ***Bryum argenteum*** (Figure 88) begins development of antheridia before winter, in November, whereas archegonia develop in April (Miles & Longton 1987). In Reading, UK, both gametangia develop at the same time.

Some taxa have adopted different physiological responses in different parts of the world, as, for example, ***Lunularia cruciata*** (Figure 101), which seems to function as a long-day plant in Wales and a short-day plant in Israel (Longton 1974), but in much of the British Isles it is the climate that prevents this liverwort from producing an archegoniophore and capsules (Benson-Evans & Hughes 1955).

Figure 101. ***Lunularia cruciata***, a long-day plant in Wales but a short-day plant in Israel. Photo by David Holyoak, with permission.

Elevation has a strong effect on timing of the life cycle in the Eastern Pyrenees. Bryophytes at high elevations have arrested sporophyte development in the winter, with maturation occurring in the summer concurrent with the next fertilization. However, at lower elevations, there is a continuous progression of stages with no dormant period. ***Schistidium confertum*** (Figure 84), however, lives at elevations above 1800 m but, like lowland taxa, has no dormant period in winter.

The example of ***Funaria hygrometrica*** (Figure 54), as studied by Hoffman (1966), exemplifies the sorts of controls that determine the selection pressures affecting the maturation cycle. In that moss, Hoffman found that gametophytes appeared in early spring, with sporophytes maturing in June, but that maturation dates were progressively later at higher elevations. High light intensities contributed to more rapid gametophyte development, while a longer photoperiod resulted in larger stems and leaves. Thus, physiological controls adapt the bryophytes to their particular conditions and may be important factors in selection as bryophytes spread around the world. Whereas morphological variation between species is limited by small size, it is possible that bryophytes may have greater physiological variability than do tracheophytes, enabling individual species to occupy wider ranges of conditions than those of their tracheophyte counterparts. These adaptations permit bryophytes to conserve energy and to optimize it across time.

Seasonal Differences among Habitats

It is the sum total of the timing of all the life cycle stages that can adapt a bryophyte for a better rate of survival. As the seasons change, so do the selection pressures. Hence, we find that sperm dispersal is timed to coincide with a rainy season and spore dispersal with dry air. But these timing events differ considerably among habitats because the advantages of seasons vary among habitats.

Temperature, length of growing season, available moisture, and photoperiod all have effects on phenology. Studies on elevation can give us clues as to the effects of temperature, although gradients of these other variables exist as well. As already discussed, at low elevations of the Eastern Pyrenees, Spain, the life cycles follow a continuous progression of events with no dormant season (Lloret Maya 1987). By contrast, those living at higher elevations exhibit mature gametangia and accomplish fertilization in the first months of summer, with the sporophyte overwintering in a dormant state and maturing rapidly in early summer. If such differences exist in response to altitude, we might expect even greater differences among habitats of highly contrasting conditions. We shall examine the contrasts among the tropics, deserts, disturbed habitats, and wetlands as representatives of this spectrum.

Tropics

The rainy season is the primary governing factor in the phenology of many tropical mosses (Odu 1981). In four very different taxa of mosses [***Racopilum africanum*** (Figure 95), ***Fissidens glauculus***, ***Thuidium gratum***, and ***Stereophyllum*** sp. (Figure 96)], Odu found that gametangia develop at the onset of the rainy season (March/April), sporophytes develop later (October – December), and sporophyte maturation occurs at the end of the rainy season. In ***F. glauculus*** and ***T. gratum***, sporophytes developed immediately after fertilization, and within one month in ***R. africanum***, with all three producing mature capsules by the end of the rainy season (Odu 1982). Dispersal in these taxa begins at the end of the rainy season and continues into the dry season (November to April) (Odu 1981).

This same seasonal pattern existed in the herbarium specimens Odu examined (Odu 1982). The rainy season is likewise the best season for development of juveniles and gametangia for ***Octoblepharum albidum*** (Figure 102) (Pôrto & Oliveira 2002). The importance of humidity for ***O. albidum*** is underscored by its development of sporophytes one month earlier at sites in western Nigeria, with constantly high humidity, than at sites with lower humidity (Egunyomi 1979). Thus, gametangial timing must be set so that capsule maturation is completed in time to take advantage of dispersal in the dry season. Hence, archegonia mature during the rainy season and sporophytes begin developing while it is still rainy. It appears that these tropical bryophytes differ from temperate bryophytes in that their rapid cycle permits them to disperse spores during the next dry season and germinate when the rainy season returns.

Figure 102. ***Octoblepharum albidum*** on tree bark in Florida, USA. Photo by Janice Glime.

Initiation of archegonia and antheridia in some tropical taxa may occur throughout the year, as it does with ***Sematophyllum subpinnatum*** (Figure 103), nevertheless increasing in frequency during the rainy season (de Oliveira & Pôrto 2001). Although the most favorable season for fertilization is during the rainy season, it likewise can occur throughout the year in that species. Sporophyte development of ***S. subpinnatum*** usually begins later in the rainy season, reflecting the higher fertilization rates during that season.

Figure 103. ***Sematophyllum subpinnatum***, a moss that produces antheridia and archegonia throughout the year, from the Neotropics. Photo by Michael Lüth, with permission.

Deserts and Dry Habitats

Growth in winter is most likely typical in the desert. Stark (2001a, 2002c) suggests that phenology of bryophytes of the Mojave Desert, USA (Figure 104), contrasts sharply with that of other climatic regions, such as Nigerian savannah mosses, with phenological events tied almost solely to local rainfall events, which are rare and unpredictable. One adaptation to this unpredictable environment is that spore dispersal occurs over a long period. ***Grimmia orbicularis*** (Figure 97-Figure 98), a rock-dwelling species, retains operculate capsules for three months before its 3-week dispersal period (Stark 2001a). The entire clone, however, may disperse spores over a period as long as six months and within the area may last more than one year. This long dispersal period may also partially compensate for the very high rate of sporophyte abortion in these mosses following a summer rainfall that apparently uses up too many resources in repairing the cells (Stark 2001b). ***Syntrichia inermis*** (Figure 94, Figure 105), a soil-dwelling species, retains operculate capsules for eleven months, then disperses spores for up to 2.5 years, the clone dispersal lasting up to 3 years! Stark (2001a) concluded that the steeply inclined rock surfaces, supporting short, broad, inclined capsules, account for the more rapid rate of operculum shedding in ***Grimmia orbicularis*** (Figure 98).

Figure 104. Mojave Desert where ***Syntrichia inermis*** survives under shrubs and may be dormant for long periods. Photo courtesy of Lloyd Stark.

But one can learn a lot about what makes things work by stressing them to their limits. Deserts provide a good model for such stressful conditions. Stark (2002b) found that in the Mojave Desert, one population of ***Syntrichia inermis*** (Figure 105) initiated sporophyte development in 1995, but that the cohort remained dormant until early 1998. By that time, approximately 66% of the sporophytes had aborted. The remaining viable sporophytes of this group were considerably shorter and had less biomass than the previous cohort. In the next two years, sexual reproduction failed completely, apparently due to reduced winter-spring rainfall. On the other hand, it appeared to be heavy summer rainfall in 1997 that caused the abortion of many of the 1995 sporophyte cohort, with sporophyte numbers increasing again following 1998 summer rains. Stark suggested that the abortion may have been the result of rapid drying and high temperatures while the sporophytes were hydrated, causing membrane damage.

In dry habitats such as the desert, it is often easier to eke out a tiny bit of water in the winter than in the summer when the little rain that does fall evaporates almost before it lands. Hence, we should expect the phenology of desert bryophytes to be different from that of bryophytes in most other habitats. Mojave Desert populations of ***Syntrichia inermis*** (Figure 105) took an incredibly long time for antheridia to mature (Stark 2001a). Whereas the archegonia matured and became receptive in the same year, antheridia took one to several years to develop! Despite this long maturation time in which desiccation was a common state, the abortion rate was only 3-4% for either gametangium type. Not surprisingly, more than 90% of the plants were morphologically bisexual. And unlike their temperate and northern counterparts, their growth was in the winter, albeit only 1.4 mm per year. To take advantage of this cooler and more moist season, fertilization occurred in winter, and despite the frequent desiccation, 50% of the perichaetia bore embryos. These embryos remained dormant from spring until fall, resuming their growth once more in the cooler days of winter when the seta and capsule developed (Stark 2001a); sporophytes endure 18 or more months of dormancy during their development (Stark 1997). Spore dispersal, however, was delayed until late summer and early fall.

Figure 105. ***Syntrichia inermis*** with capsules in various stages of dispersal. Photo by Michael Lüth, with permission.

Syntrichia inermis (Figure 105) sets several bryophyte records through its phenological strategies to survive in the desert (Stark 1997). Considering the importance of reproductive development during the unpredictable and rare rainy periods, it is not surprising that it has the lowest known rates of stem elongation. It also has the longest known period required for antheridial maturation. Growth is greatly sacrificed to complete reproduction, presumably permitting the spores to remain dormant for long periods of time and to disperse over a wide range.

Syntrichia caninervis (Figure 107) also a resident of the Mojave desert, exhibits a sex ratio of roughly 7.9 female to 1 male to 3.1 non-expressing individuals (Stark *et al.* 2001). This large ratio of female to male may help to compensate for the 63% loss of developing sporophytes observed during three years of study. However, there is also partial, if not complete, compensation of sexes by the greater number of reproductive units on males than on females.

Herrnstadt and Kidron (2005) examined reproduction in ***Bryum dunense*** (Figure 106) in three different habitats in the Negev Desert, southern Israel. Despite differences in exposure, including exposed site, under shrub canopy, and partially shaded at foot of north-facing dune slope, all three populations initiated their gametangial development prior to the first winter precipitation. This suggests that the species are attuned to their environment by a signal such as declining day length or temperature. This prepared them for dispersal of both bulbils and sperm as soon as water was available.

Figure 106. ***Bryum dunense***, a species in the Negev Desert, Israel, that initiates gametangia prior to the first winter precipitation. Photo by Dror Melamed, with permission.

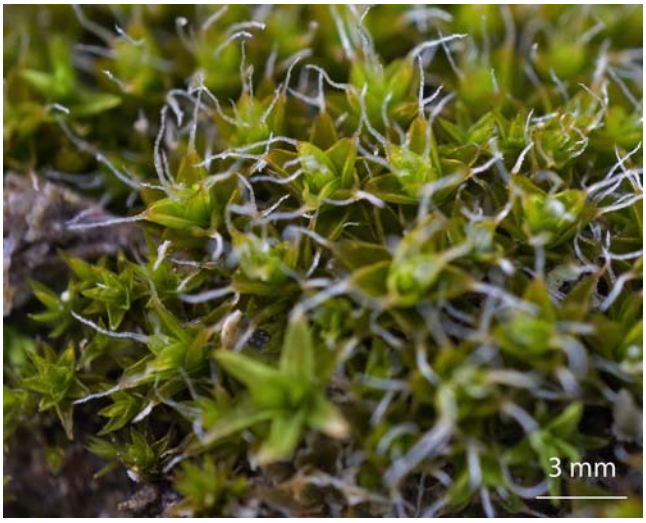

Figure 107. ***Syntrichia caninervis***. Photo from Proyecto Musgo, through Creative Commons.

In the dry mountains of southern New Mexico, USA, a close relative of several desert species, ***Syntrichia ruralis*** (Figure 108) grew, in this case by **innovations** (new shoots), in midwinter (Mishler & Oliver 1991). Female gametangia likewise were initiated in midwinter, causing cessation of growth in that innovation – a definite tradeoff. These female gametangia remained on the plants 6-9 months (December to June or even until August), during which no male gametangia were evident, and, of course, no sporophytes. But growth and structural development do not tell the whole story. In this species, the chlorophyll to dry weight ratio was higher in the late summer and winter than it was in early summer. One must pause to wonder what circumstance permitted the higher late summer values.

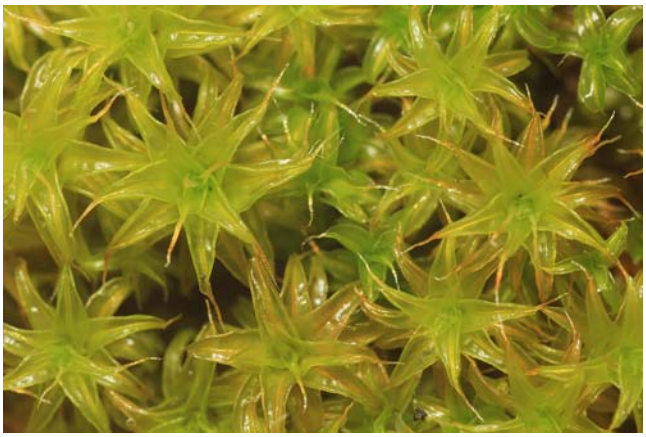

Figure 108. ***Syntrichia ruralis*** var. ***ruraliformis*** (Sand-hill Screw-moss). Photo by Barry Stewart, with permission.

When maturation of gametangia is an autumn event, it forces the young embryo to survive the winter. Haupt (1929b) found that the liverwort ***Fossombronia longiseta*** (Figure 43) in California, USA, had gametangia in the "best" condition in November and December, perhaps relating to the wetter weather in winter. The overriding importance of water is evidenced by ***Octoblepharum albidum*** (Figure 102) in Nigeria, where immature antheridia and archegonia are most abundant during July, the wettest month (Egunyomi 1979).

Moisture obviously is important in the regulation of season of growth. In the mountains of southern California, ***Asterella californica*** (Figure 109) grows on canyon sides and moist banks that become dry in summer. The liverwort dries out in summer (cf. Figure 110), surviving by terminal buds (Haupt 1929a). Bray (pers. comm.) found a similar survival mechanism in ***Fossombronia*** (Figure 111) in southern Illinois, permitting it to grow in fall through spring.

Figure 109. ***Asterella californica***, a liverwort that dries out in summer and survives by terminal buds. Photo by Peter J. Bryant, University of California, Irvine, with permission.

Figure 110. ***Asterella tenella*** with drying thallus and mature archegoniophore with open capsules. Photo by Janice Glime.

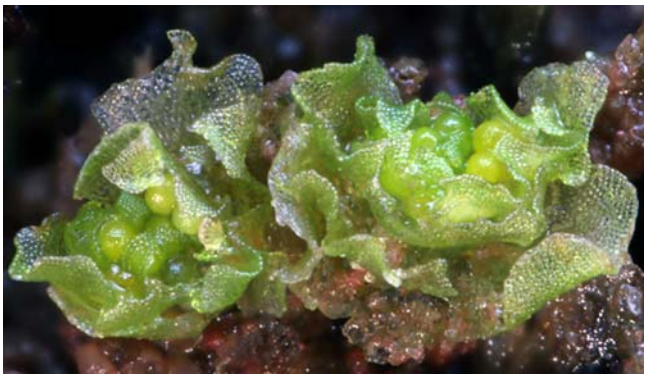

Figure 111. ***Fossombronia incurva***. Photo by Des Callaghan, with permission.

Trichostomum planifolium, a tiny **protogynous** (producing female organs before male organs) desert moss, has populations 20-50 years old (Stark & Castetter 1995). It solves the capsule drying problem by having fertilization in late fall with sporophytes maturing continuously until spring, when it disperses its spores. Completion of its entire sexual cycle during cooler months, coupled with extensive intra-stem fertilization, permits it to survive its desert habitat.

Bryophytes in deserts are very dependent on the annual moisture cycle for their life cycle. In the Nigerian desert, sexual cycles are short, occurring completely within the rainy season. In the Mojave Desert in southwestern USA, there is no rainy season, and rainfall events are unpredictable. In that regime, bryophytes have very long sexual cycles, sometimes taking several years to develop antheridia, several years for capsules to mature, and six months to disperse all the spores. Growth is mostly in winter, fertilization is in winter, and dispersal of spores occurs in late summer and early autumn. Some dry habitat thallose liverworts become dormant in summer, surviving as terminal buds while the remaining thallus dies.

Epiphytes

Epiphytes live in a habitat that is frequently dry, but unlike the desert, water is also frequently available. This alternate wet-dry microclimate brings its own set of problems. There can be relatively long periods of time when it is unsuitable for sperm transfer. The epiphyte ***Forsstroemia trichomitria*** (Figure 112) produces five sets of reproductive structures per year. This may be an adaptation to increase the chances of having the right weather (rain) to accomplish fertilization. Fertilization occurs in late summer through autumn, about four months duration. Both types of gametangia are produced at the same time. The sporophytes require 17 months for maturation, enduring two winters.

Figure 112. ***Forsstroemia trichomitria***, an epiphytic moss that produces five sets of gametangia each growing season. Photo by Misha Ignatov, with permission.

Savannah

Contrasting with mosses controlled by the rainy season, as in the tropics, or those of dry periods that can last years, mosses of the dry habitat of Nigerian savannah have much shorter sexual cycles than those of the desert, as noted by Makinde and Odu (1994) for four mosses, ***Archidium ohioense*** (Figure 113), ***Bryum coronatum*** (Figure 114), ***Fissidens minutifolius*** (Figure 115), and

Trachycarpidium tisserantii. Their entire sexual cycle, from production of gametangia to dehiscence of capsules, occurs during the rainy season. Protonemata and gametophytes develop in March-April; capsules mature and spores are dispersed in September-October. Nevertheless, spore discharge is somewhat difficult in the **cleistocarpous *A. ohioense*** and ***T. tisserantii*** compared to the other two species. (Cleistocarpous capsules have no operculum and must break apart without aid of lines of dehiscence to expel their spores.) Makinde and Odu suggest that this short maturation period may be advantageous in their savannah habitat.

Figure 113. ***Archidium ohioense***. Photo by Li Zhang, with permission.

Figure 114. ***Bryum coronatum*** in India, a moss that completes its entire sexual cycle during the rainy season in the savannahs of Nigeria. Photo by Michael Lüth, with permission.

Figure 115. ***Fissidens minutulus***, a generic relative of ***F. minutifolius*** – one of the mosses that completes its entire sexual cycle in the rainy season in the savannahs of Georgia. Photo by Jan-Peter Frahm, with permission.

Polar and Alpine

Ayukawa *et al*. (2002) investigated ***Polytrichastrum ohioense*** (Figure 116-Figure 117) in the Yatsugatake Mountains of Japan. They found mature antheridia from late May to early August and mature archegonia from late June to mid July, permitting fertilization to occur from late June to mid July. This timing of gametangial maturity avoided the occasional temperatures below 0°C in May. The longer period of sperm maturity permits variability in time of egg maturation and suggests that the two types of gametangia respond to different triggers. Sporophytes began showing at the end of June, became dormant for the winter, and began growth again in May. Spores were dispersed from mid July to mid August. Hence the 13-month sporophyte maturation included a 6-month resting period in winter.

Figure 116. ***Polytrichastrum ohioense***, sowing females with light geen tops on left and males with unopened golden splash cups on right. Photo by Janice Glime.

Figure 117. ***Polytrichastrum ohioense*** with immature capsules. Photo by Li Zhang, with permission.

Antarctic populations of ***Polytrichum juniperinum*** (as *P. alpestre*; Figure 5, Figure 9, Figure 72) behave quite differently (Longton & Greene 1967). The antheridia begin development in March and overwinter (May-October) with no further development. Development resumes after

snowmelt and most of the antheridia mature in December-early January. Archegonia, on the other hand, do not begin development until the end of November, but still reach maturity at the same time as the antheridia. Sporophyte development was much longer, beginning with fertilization in December and January but not completing development until mid-March the following year.

Clarke and Greene (1970) found somewhat different timing adaptations in populations of ***Pohlia*** (Figure 2) in the Arctic and sub-Arctic. In these populations, maturation was somewhat faster than for the same species in Britain.

Disturbed Habitats – Ephemerals

The ephemerals, or short-lived taxa, face some of the same problems as desert bryophytes. They are very dependent on climatological events to coordinate their phenological events. They often grow in areas that experience flooding during part of the year. Although the sequence of most life cycle events is poorly known in ephemerals, Crum (1976) provides us with information on when to expect to see these plants (capsules) in Michigan. We can suppose that during the remainder of the year the moss exists either as spores or as dormant protonemata, but in some cases absence is really a measure of lack of collecting inconspicuous non-fruiting upright gametophyte plants. Because of their tiny stature and non-mossy look of their habitats, these taxa are often overlooked by visiting bryologists in a hurry to get as many taxa as possible, so their presence may be much greater than would appear from collection records, and their sporophytic stage is probably over-represented in collections. By targetting such habitats, Kucyniak (1946) found numerous new or rare species in Québec (Jean Faubert, pers. comm.)

Spring and autumn seem to favor ephemerals when more moisture is available than in summer in most habitats, with a number of species visible all winter (Crum 1976 for Michigan, USA): ***Ephemerum crassinervium*** (Figure 118) late summer to early spring; ***Tortula acaulon*** (Figure 119) November to May; ***Microbryum floerkeanum*** (Figure 120-Figure 121) October to April; ***Acaulon*** spores mature in late autumn to spring [***A. triquetrum*** (Figure 122), ***A. muticum*** (Figure 123)]. Michigan spring ephemerals include ***Pleuridium subulatum*** (Figure 124), ***Tortula truncata*** (formerly in ***Pottia***; Figure 125), and ***Physcomitrium pyriforme*** (Figure 126), whereas ***Ephemerum cohaerens*** (Figure 127) appears in both spring and autumn. ***Pottia davalliana*** (Figure 128) appears in the autumn, but sometimes can be found in summer.

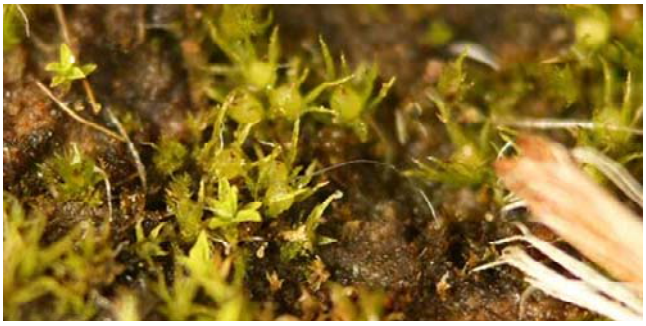

Figure 118. ***Ephemerum crassinervium***, an ephemeral moss that grows in the moisture from late summer to early spring. Photo by Bob Klips, with permission.

Figure 119. ***Tortula acaulon***, a species that is visible autumn through spring. Photo by David Holyoak, with permission.

Figure 120. ***Microbryum floerkeanum*** (inside red circle), an ephemeral that grows from October to April. Photo by Michael Lüth, with permission.

Figure 121. ***Microbryum floerkeanum***, an ephemeral that grows from October to April. Photos by Michael Lüth, with permission.

Figure 122. ***Acaulon triquetrum*** on sand; an ephemeral whose spores mature in late autumn to spring. Photo by Michael Lüth, with permission.

Figure 123. ***Acaulon muticum***, an ephemeral whose spores mature in late autumn to spring. Photo by Jan-Peter Frahm, with permission.

Figure 124. ***Pleuridium subulatum***, a moss of disturbed agricultural fields and roadsides. Photo by Michael Lüth, with permission.

Figure 125. ***Tortula truncata***, a Michigan, USA, spring ephemeral. Photo by Bob Klips, with permission.

Figure 126. ***Physcomitrium pyriforme***, a spring ephemeral in Michigan, USA, and elsewhere. Photo by Li Zhang, with permission.

Figure 127. ***Ephemerum cohaerens*** with perigonia, an ephemeral that appears in spring and again in autumn. Photo by Dick Haaksma, with permission.

It is not surprising that some ephemerals typically produce more than one generation of capsules in the same year. Gray (1935) found that ***Aphanorrhegma serratum*** (Figure 129) and ***Micromitrium tenerum*** (as ***Nanomitrium austinii***; Figure 130) have life cycles as short as 62-65 days in Florida, producing two or more sets of capsules per year. Between these cycles the moss is often buried by floods and silt. Gray surmised that since he always found both mature and immature capsules, these mosses must continuously produce capsules when growing conditions are suitable. Younger plants seem to be produced at the edge of older clumps.

Figure 128. ***Pottia davalliana***, an autumn ephemeral that sometimes also appears in summer. Photo by Michael Lüth, with permission.

Figure 129. ***Aphanorrhegma serratum***, a species that in Florida has a short life cycle of about two months and that completes that life cycle two or more times a year. Photo by Bob Klips, with permission.

Figure 130. ***Micromitrium tenerum***, a species that in Florida has a short life cycle of about two months and that completes that life cycle two or more times a year. Photo by Jan-Peter Frahm, with permission.

It appears that one strategy for these floodplain ephemerals is to produce some sort of survival structure. These may include very large spores, spores that remain in tetrads, and asexual structures that can remain in the mud for a prolonged period of time, then provide a good supply of energy to jumpstart the gametophyte plant when the mud becomes exposed to the sun. Members of the Marchantiopsida, especially members of the genus ***Riccia*** (Figure 131-Figure 132), seem especially adapted for such strategies (Kürschner & Parolly 1999).

Figure 131. ***Riccia sorocarpa*** in European floodplain. Photos by Michael Lüth, with permission.

Figure 132. ***Riccia beyrichiana*** showing folded up lobes that can close up as the plant dries. Photo by Jan-Peter Frahm, with permission.

Wetlands

One might expect that bryophytes growing in wetlands face few problems in dispersing their gametes and might instead time events so that capsules are not submersed or too humid. But Sundberg (2002) found that even in this "wet" habitat, rainfall of the previous summer had a strong effect on the number of capsules produced, suggesting that gametangia formation was improved under wetter conditions. In wetter peat pits, the amount of precipitation in spring of the same year seemed more important,

suggesting that greater precipitation increased sperm dispersal and fertilization. Spore dispersal in ***Sphagnum*** (Figure 91) is indeed facilitated by dry air, but summer droughts can cause premature drying, which negatively affects spore dispersal. At least some ***Sphagnum*** species grow best at higher temperatures, around 35°C (Li 1991), but it seems that growth might need to compete with spore production. All the species in Sundberg's study release their spores from the beginning of July to the end of August (summer in the North Temperate Zone), with up to a month difference in release times among the species present. Even in this wet habitat, there are dry seasons and wet seasons.

Aquatic

In aquatic habitats, winter may be the best growth period. Glime (1987b), found that in the Keweenaw Peninsula of Michigan, USA, where snow covers the ground about five months of the year, the lake and stream moss ***Fontinalis duriaei*** (Figure 133) takes advantage of its C_3 metabolism and begins new growth in November, continuing through winter, then accelerating from February to June, with little subsequent growth until cooler weather returns. Laboratory data on temperature effects on growth of six ***Fontinalis*** species suggest this is a general trend in the genus (Glime 1984, 1987a, b, c).

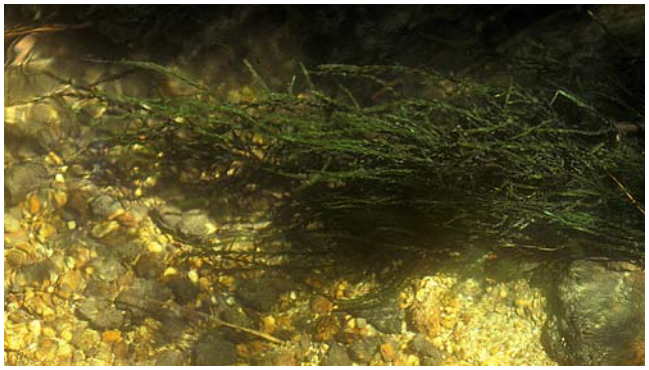

Figure 133. ***Fontinalis duriaei*** in Japan, a moss that begins its growth season in November. Photo by Janice Glime.

For populations of ***Fontinalis***, Glime (1984, 1987a) found that on Isle Royale and in the Keweenaw Peninsula of Michigan, USA, several species produced gametangia in September prior to resumption of growth. In this genus, autumn production of gametangia might be a means to facilitate movement of sperm in small puddles of water and on moist but not submerged mosses, reducing loss of sperm downstream due to strong currents. Once winter begins, these species of ***Fontinalis*** are completely submersed and this permits the development of the sporophyte in a fully hydrated state. ***Fontinalis*** species respond to photoperiod, having peak gametangia maturity in autumn and producing capsules in February. Temperatures soon become too warm in summer for aquatic bryophytes that generally remain hydrated, even when stranded above water. The easiest season for many of them to disperse sperm is autumn as water levels rise and dispersal is facilitated. Temperatures are cool enough for photosynthetic activity and the plant is almost guaranteed of remaining cool and hydrated following fertilization.

But the big surprise came when we found abundant capsules on ***Fontinalis dalecarlica*** (Figure 79-Figure 80) (Glime 1984) and ***F. novae-angliae*** (Figure 134) (Glime 1987c) in February in New Hampshire, USA. These capsules were abraded by spring runoff and had disappeared by the time the snow had melted. No wonder most bryologists think the genus almost never has capsules! No one is looking in midwinter. It appears that archegonia mature in the short days of September and the capsules are most likely the product of that fertilization season.

Figure 134. ***Fontinalis novae-angliae*** with capsules in February. Photo by Janice Glime

Summary

The life cycle of a moss can be described based on those stages that are observably different, are discontinuous, and require a change in environmental conditions. This definition presents us with the recognizable stages of embryonic calyptra, seta with calyptra, green capsule with calyptra, operculate post-meiotic capsule, de-operculate capsule, spore with bulging wall, protonema, protonema with bud, juvenile stem, antheridium, archegonium.

Growth requires sufficient moisture, nutrients, and light at a time when the temperature does not cause a high level of respiratory loss, below 25ºC for most shade-adapted taxa. Growth usually ceases in hot summers when the temperature is too high and carbon loss would be greater than carbon gain, and in cold winters when there is no free water and bryophytes go dormant. Optimal temperatures for elongation, bud formation, and rhizoid production may differ. Furthermore, increase in biomass may occur without increase in height. There is a trade-off between growth and reproduction so that growth diminishes or ceases during reproduction. Chlorophyll concentrations generally increase in response to decreasing light intensity, thus responding to seasonal changes.

Gemmae are more likely than other life cycle events to lack seasonal behavior, but their production may cease during sexual reproduction due to competition for energy.

Antheridia generally initiate before **archegonia** and require longer for development. Many will begin development, then become dormant during winter, resuming in spring to mature when archegonia, initiated

in spring, are also mature. Reproduction may be coupled with photoperiod, light intensity, and temperature, and these will most likely be coordinated to provide the reproductive bryophyte with the greatest possibility of sufficient water for fertilization. Nutrients and pH may also play a role in signalling onset of sexual reproduction.

Cross-fertilization in monoicous bryophytes is supported by **protogyny** and **protandry** in many taxa. In dioicous taxa, the perigonia (housing antheridia) are typically initiated first and mature at about the same time as perichaetia (housing archegonia).

Desert bryophytes may have multiple periods of dormancy interrupting any of the developmental stages. Some take advantage of cooler temperatures and greater availability of water in winter to accomplish fertilization. Aquatic bryophytes such as *Fontinalis* may have fertilization in autumn when water levels are rising, ensuring water for development, then produce capsules in winter when spring runoff can aid dispersal.

Sporophyte maturation of most taxa is timed for dispersal during the dry season and may last from only a few days to several years. For most temperate zone bryophytes, spring and autumn seem to be the best time for dispersal. Elevation generally meant that events start later in the year, but higher light levels and in some cases longer days, along with innate adaptations, may cause stages to mature in less time than at lower elevations.

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CHAPTER 4-3

ADAPTIVE STRATEGIES: PHENOLOGY, A *SPHAGNUM* CASE STUDY

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CHAPTER 4-3

ADAPTIVE STRATEGIES: PHENOLOGY, A *SPHAGNUM* CASE STUDY

Figure 1. *Sphagnum fimbriatum* with operculate capsules in midsummer. Photo by Janice Glime.

Sphagnum: A Case Study

The easiest way to understand any phenomenon is to examine an example. The detailed phenological study by Pujos (1992) of ***Sphagnum fimbriatum*** in Haute-Normandie and ***S. fuscum*** in Québec provides us with this opportunity.

Most of us think of ***Sphagnum*** as living in wet places, but in fact, its growing tips are often under drought conditions. As the water level falls in the summer, the tops of hummocks are dry, and in winter, the water is frozen, thus creating desiccating conditions. Consequently, the apex of the moss often lacks sufficient water to carry on photosynthesis. This results in considerable variation within the genus regarding the months of photosynthetic activity and growth. Hulme and Blyth (1982) found that species that live in hollows, such as ***S. cuspidatum*** (Figure 2) and ***S. auriculatum*** var. ***inundatum*** (Figure 3), had a longer growing season (10-12 months) than did hummock species such as ***S. papillosum*** (Figure 4), ***S. magellanicum*** (Figure 5), and ***S. capillifolium*** (Figure 6) (5-7 months).

For ***Sphagnum fimbriatum*** (Figure 7) in Haute-Normandie and ***S. fuscum*** (Figure 8) in Québec, it appears that despite their ability to grow best at the warm temperatures of summer, they become sexual in the cooler, probably wetter, conditions of fall (Pujos 1992).

Figure 2. ***Sphagnum cuspidatum***, a species of hollows and bog pools. Photo by Michael Lüth, with permission.

Figure 3. ***Sphagnum auriculatum***, a species of inundated areas. Photo by Janice Glime.

Figure 4. ***Sphagnum papillosum***, a hummock species. Photo by Michael Lüth, with permission.

Figure 5. ***Sphagnum magellanicum*** forming a hummock. Photo by Michael Lüth, with permission.

Figure 6. ***Sphagnum capillifolium capillifolium*** on top of a hummock. Photo by Barry Stewart, with permission.

Figure 7. ***Sphagnum fimbriatum*** habitat. Photo by Dick Haaksma, with permission.

Figure 8. ***Sphagnum fuscum***, a hummock species, in its vegetative state. Photo by Michael Lüth, with permission.

Gametangia

In both species studied, antheridial branches (Figure 9) appear first at the end of summer, with the antheridial stalk forming before the antheridium. Although the antheridium develops rapidly, **spermatogenesis** (formation of sperm) spans two months. Like so many other perennial

bryophytes, archegonial development begins somewhat later in Haute-Normandie, in September, requiring about one month for development.

Figure 9. Antheridial branches displaying typical red color. Photo by Janice Glime.

Fertilization

Perichaetial leaves grow much larger than other leaves and protect not only the archegonia, but the developing capsule as well. However, fertilization is delayed until February, at least in Normandie, occurring as the temperature first begins to increase at the end of winter. Archegonial neck cells break down and form mucilage at about the same time the antheridia dehisce. Fertilization of ***S. fimbriatum*** (Figure 10) in Normandie in 1991 occurred in March.

Figure 10. ***Sphagnum fimbriatum***. Photo by Dick Haaksma, with permission.

Embryogenesis (formation of embryo)

By early April, the embryo begins penetrating the branch beneath it and by the end of April mucilage completely surrounds the embryo. It is not until mid-May to June that **sporogenesis** (formation of spores, starting with meiosis) occurs and still another month passes before the pseudopodium (gametophyte extension that becomes a stalk to support the capsule) emerges with the capsule at its apical end (Figure 11).

Figure 11. Mature capsules of ***Sphagnum palustre*** with capsules still enveloped in perichaetial leaves before the pseudopodium elongates. Photo courtesy of Zen Iwatsuki.

Spore Release and Germination

Spores mature in July and changes in temperature and humidity cause the capsule to shrink, forcing the operculum off (Figure 12). Spores in both species germinate immediately after release (in the lab), producing a thalloid gametophyte and ultimately a single upright plant. But again, we know nothing of what happens in the field. Is there a dormancy, perhaps brought on by temperature or humidity, that delays the spore germination? How long does the protonema persist before the leafy plant develops? How long does it then take the leafy plant to reach sexual maturity?

Figure 12. Capsules after dehiscence and dispersal, with elongated pseudopodium, in ***Sphagnum palustre***. Photo courtesy of Zen Iwatsuki.

Summary

In *Sphagnum fimbriatum* in Haute Normandy, as in most mosses, antheridia appear first, in this case late summer, developing over two months. Archegonia begin development in September and require only one month. Fertilization occurs in February or March at the end of winter. The capsule is mature in mid-May to June and sporogenesis occurs, but the pseudopodium requires another month before it elevates the capsule. Spores are released in July and can germinate immediately, but field behavior is unknown.

Acknowledgments

I appreciate the helpful comments of Heather Smith in giving me a student's perspective on this chapter and of Heinjo During in critiquing this case study. Linda Luster checked the literature citations, proofread, and checked for needed glossary entries.

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CHAPTER 4-4

ADAPTIVE STRATEGIES: PHENOLOGY TRADEOFFS

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CHAPTER 4-4

ADAPTIVE STRATEGIES: PHENOLOGY TRADEOFFS

Figure 1. ***Hylocomium splendens*** with sporophytes and young shoot showing new growth of an unexpanded branch to their right. Photo by Janice Glime.

Tradeoffs

Just when you think you have solved all the problems, you discover that the solution has created a new problem. So it is with life, and so it is with optimizing the events in the life of a plant. Large spores give the plant a better start, small ones travel farther. Lots of spores give more chances for landing at a suitable time on a suitable spot, but their survival chances are lower. But what sorts of numbers are we talking about?

Finding this information is not easy, as few papers are written expressly for the purpose of comparing these numbers. We need a concerted effort to put together a representative list. A few are shown in Table 1.

In an organism where the male gamete must disperse without a very specific carrier and the female is stationary, we assume that more males are needed to service the females because many males will be unsuccessful. Rydgren and Økland (2003) stated that we still do not know if bryophytes exhibit reproductive costs (energy costs). Meager evidence suggests they do.

Table 1. Comparison of numbers of reproductive parts of bryophytes. This table is in no way representative.

Octoblepharum albidum	Pôrto & de Oliveira 2002
archegonia	6.7 per perichaetium
antheridia	13.4 per perigonium
Sematophyllum subpinnatum	de Oliveira & Pôrto 2001
archegonia	3-26 per perichaetium
antheridia	8-20 per perigonium
Sphagnum	Sundberg 2002
sporophytes	0.64-20 per dm^2
spores	16,000,000 per m^2
Trichostomum perligulatum	Stark & Castetter 1995
archegonia	2
antheridia	6
Cyathodium bischlerianum	Salazar Allen 2001
archegonia	1-2 per involucre
Plagiochila adianthoides	Johnson 1929
antheridia	22 per spike
sperm	25,000 per antheridium

Rydgren and Økland (2003) compared non-sporophyte-producing and sporophyte-producing sub-population of ***Hylocomium splendens*** (Figure 1) for five years. They found that indeed the plants with sporophytes had less size development of daughter segments, a lower branching frequency, and fewer new annual segments than those individuals with no sporophytes. This reduced development occurs primarily during the time when the capsule expands and spores are produced, suggesting that there is a significant cost for reproduction – a tradeoff.

However, if all the gametangia are accounted for, rather than individuals, this may not be the case. Stark and coworkers (2001), in examining the desert moss ***Syntrichia caninervis*** (Figure 2), found that when male and female expressing individuals were controlled for **inflorescence** (reproductive organ group) number, there were no significant differences in biomass between the sexes. Surprisingly, among those that were not expressing sexual traits, there was lower biomass, shorter total stem length, fewer branches, and shorter **ramets** (individual member of clone) than in sex-expressing males and females, and there were fewer ramets than there were sex-expressing female individuals. A threshold size seems to be necessary for sexual expression, accounting at least in part for size differences. In fact, for ***Syntrichia caninervis*** in this study, all individuals weighing more than 2.0 mg evidenced sexual expression. This biomass requirement supports the concept that more energy is needed for sexual expression, likewise supporting the expectation of a tradeoff between growth and reproduction.

Figure 2. ***Syntrichia caninervis***. Photo by John Game, through Flickr Creative Commons.

Tradeoffs with Spore Production

To understand the seasons of sexual reproduction, one needs to understand the tradeoffs within the growth cycle as well. First, there needs to be a sufficient energy supply for either a sexual or an asexual event, and while the formation of sex organs does not seem to produce as much biomass, it is a developmental stage that is costly in energy. Second, the production of gametangia may interfere directly with further growth. In acrocarpous mosses, the gametangia are terminal on the main stem (Figure 3), and once they develop, they inhibit the further development of the stem, at least for that season (Figure 4). Thus, vegetative growth, in acrocarpous taxa at least, may be strongly limited by time of gametangial production.

Figure 3. ***Polytrichum piliferum*** splash cups that effectively stop growth of the stem while they are functional. Photo by Janice Glime.

Figure 4. ***Polytrichum ohioense*** male stems with new growth extended from the splash cups. When the antheridia are developing, further growth of this apex is arrested. Photo by Janice Glime.

Pleurocarpous mosses, on the other hand, develop gametangia on lateral branches and these do not interfere with the growth of the main stems. This difference is further complicated by the fact that most (all?) pleurocarpous mosses are perennial, whereas many of the acrocarpous mosses are annual. Furthermore, one might suppose, the annuals are much more likely to produce capsules (and by implication, gametangia) to permit them to overwinter as spores, whereas many perennials persist by vegetative means only. But, we have very little direct field evidence to support or refute this supposition.

It might be interesting to compare seasons of vegetative growth vs gametangial season in acrocarpous vs pleurocarpous mosses and annuals vs perennials, but data on gametangia are scarce. Among the mosses in Conard's 1947 study, only 15 of the 232 taxa collected had gametangia.

Based on Conard's survey, it appears that peaks in gametangial production in liverworts occur during late spring and again in fall, at least among the 60 Iowa taxa (Figure 5). This is consistent with the report by Zehr (1979) that photoperiod is the dominant factor in gametangial formation in four of the five taxa he studied: ***Lophocolea heterophylla*** (Figure 6) is day neutral; ***Diphyscium foliosum*** (Figure 7), ***Atrichum angustatum***

(Figure 8), ***Trichocolea tomentella*** (Figure 9), and ***Nowellia curvifolia*** (Figure 10) are long-day plants. However, Zehr's sample size is small and Conard's samples may have been biased, since they were subject to seasons favorable for collecting (and collectors), and collectors may be selective in what they collect and keep, favoring plants with capsules over those without.

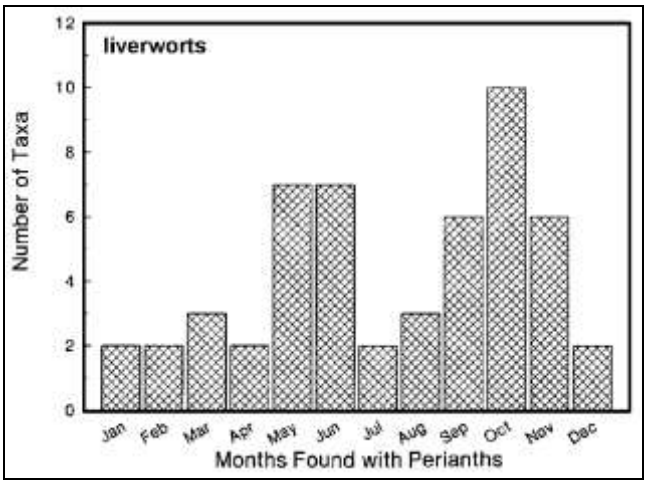

Figure 5. Numbers of taxa with perianths (leafy enclosure of liverwort archegonia) per month among the 30 taxa having perianths out of 60 Iowa liverwort taxa (including Anthocerotopsida) in the herbaria at State University of Iowa and Grinnell College. Based on table from Conard (1947).

Figure 6. ***Lophocolea heterophylla***, a day-neutral liverwort, on log. Photo by Janice Glime.

Figure 7. ***Diphyscium foliosum*** females, a long-day species. Photo by David Holyoak, with permission.

Figure 8. ***Atrichum angustatum***, a long-day moss. Photo by Bob Klips, with permission.

Figure 9. ***Trichocolea tomentella*** from Europe, a long-day liverwort. Photo by Michael Lüth, with permission.

Figure 10. ***Nowellia curvifolia***, a long-day liverwort, on a log. Photo by Jan-Peter Frahm, with permission.

It seems that the co-occurrence of fertilization and spore release is relatively common among bryophytes, as seen in the studies of Grimme (1903), Arnell (1905), Lackner (1939), Jendralski (1955), Greene (1960), and van der Wijk (1960). Based on his British experience, Greene (1960) stated that even before a **cohort** (group of individuals with same starting point) of capsules has dehisced, new gametangia are developing. To him, it was "clear" that when sporophytes develop slowly, fertilization may be effected before the previous generation of spores has been released. Likewise, David Wagner (pers. comm.) finds spore and sperm dispersal during the same season in the Northwestern United States. Stark (2001) points out that we have few definitive studies on the duration of spore

dispersal and that in some cases this may last an entire year, as it does with most desert bryophytes.

Two determining factors must be kept in balance to maintain a life cycle: the energy requirements and the growing conditions. For dispersal of sperm, clearly water is needed, and energy must be available leading up to sperm maturation. Spore dispersal is most often favored by dry weather, which as already pointed out, can alternate effectively with wet weather in spring. Spore dispersal itself is a mechanical process and presumably requires no energy. Spore maturation does, but dispersal can wait, being effected in most cases when the capsule dries out, forcing the operculum off. This process likewise might be presumed to require no energy. Therefore, energy requirements may be sufficiently spread over time so that the processes of gametangial maturation and spore/capsule maturation do not compete enough to be detrimental. Once these demands are met, it is beneficial for spores that lack dormancy to be dispersed when good growing conditions are close at hand. The alternating wet and dry conditions of spring would seem to be ideal for this. It remains for us to demonstrate that in fact this is so, since we know virtually nothing about spore germination and protonema development in nature for most species.

Geographic Differences

Both latitude and altitude create different climatic conditions. Inland conditions can be quite different from coastal conditions. The wide range of temperature and moisture created by these geographic conditions imposes strong selection pressures on the genes controlling the phenology of the organisms living there.

Some bryophytes seem to ignore winter, as does ***Schistidium apocarpum*** var. ***confertum*** (Figure 11) in the eastern Pyrenees (Lloret Maya 1987). This species, despite living above 1800 meters elevation, is not affected by winter conditions. However, other taxa in these mountains have mature gametangia and fertilization early in the summer with dormant winter sporophyte development followed by rapid maturation of the sporophyte in the first months of summer. At the same time, species living at lower elevations exhibit a continuous progression of stages with no dormancy. Only ***Schistidium apocarpum*** var. ***confertum*** behaves this way at high altitudes.

Figure 11. ***Schistidium apocarpum*** var. ***confertum*** growing on rock and exhibiting its typical abundant capsules. Photo by Michael Lüth, with permission.

Longton and Greene (1969) demonstrated a latitudinal difference in ***Pleurozium schreberi*** (Figure 12). In Great Britain, perigonial development begins in August. Antheridial development apparently is dormant in an immature stage through the winter. Archegonia are first evidenced by perichaetial development in October, but the archegonia likewise overwinter in an immature stage. In spring, both gametangia develop rapidly and fertilization ensues in April and May. The young sporophytes begin to emerge in May, but seta elongation is delayed until August. By October the operculum is in its mature stage, but spores are retained until January, with dispersal occurring January through April – a 9-12 month cycle. Thus, even in this maritime climate, winter is unsuitable for most developmental activities, although presumably winter growth is possible. In France, Finland, and North America, vegetative growth is arrested during the winter, resuming for the period of April to November.

Figure 12. The red-stemmed moss, ***Pleurozium schreberi***. Photo by Michael Lüth, with permission.

Measuring winter growth under the snow is difficult. One cannot remove the snow to measure the growth because that would alter the conditions, affecting subsequent measurements. Ideally, one could measure length or biomass just before the first snowfall and just after spring melt, but that is not as easy as it may seem. The first snowfall may only provide temporary cover, followed by a warm period. One cannot be there every day to ensure measurement on the one day that lies just before the permanent winter cover. And spring is not as easy to determine as it might seem. In many habitats, bryophytes are covered with water for a short period of time during and just after snowmelt. Furthermore, the snow may leave, but the air remain cold, or temperatures might rapidly climb to a balmy spring day when there is no more change of state from solid ice to liquid or gas as the snow melts. Predicting and being there and knowing that the patch you measure has just come out from the snow would require being a psychic.

For many bryophytes, those early days following snowmelt are the best time all year for growing as they take advantage of the open canopy and warm but not hot temperatures. But we know next to nothing about the ability of bryophytes to grow under the snow. Could they get enough light through thin layers of snow and enough moisture from partial melt to photosynthesize at times in the winter? Is there a possibility they begin their spring productivity two weeks before they are uncovered? And what about the epiphytes that rest within that funnel of air between the snow and the bark? Are they warm enough

and humid enough to continue photosynthesis throughout most of the winter? Trynoski and Glime (1982) suggest they might, based on finding more bryophytes and bryophyte biomass on the south side of the tree at breast height in Keweenaw County, Michigan, USA.

Longevity Tradeoffs

In 2009, Bryonetters asked "How long do mosses live?" In 2014, Bryonetter Wang Zhe asked about the **longevity** (length of life span) of bryophytes. There is no satisfactory answer to this question. True, some have very short life cycles, emerging from spores as flood waters recede and completing an annual life cycle within a few months. Others, like ***Sphagnum***, may live hundreds of years, dying at the bottom and growing at the top. Others challenge our definition of death, regaining photosynthesis after a long desiccation dormancy.

Thus, the first problem is to determine if the bryophyte is alive. In an organism that thrives on fragmentation, we are confounded by the possibility that a cell or cells remain alive and can under the appropriate conditions begin new growth, often to produce a new plant, a condition known as **totipotency**. In other cases, tissues may remain dormant for years, only to resume growth when getting the light and water they vitally need.

Guy Brassard responded to this query on Bryonet: "This is interesting in a rather odd way. Some years ago, when I was at Memorial University, I found a piece of ***Hylocomium splendens*** (Figure 1) that I had dried between the pages of a book some 20 years earlier. I put it on a damp paper in a Petri dish on a window ledge without hoping for anything to happen. But, much to my surprise, after about 2 or 3 weeks a NEW BUD appeared on the stem and proceeded to grow into a new branch. So there must have still been some live germ-plasm in the stem of that dried old specimen. If such a tiny piece could remain 'alive' for two decades inside the pages of a book (no water and essentially no light), this means that the time span for air-dried bryophytes retaining live tissue could be much longer (50? 100? years), and that most herbarium specimens are still 'alive' as well!"

This year I watched my moss garden emerge from under the snow after a long and especially cold winter. I was shocked to see that most of the mosses were brown and appeared to be dead. I resisted the temptation to replace them and watched. It took about a month, but green appeared, and most of the clumps now look fully green after a mild, bryophyte-favorable summer. How DO we recognize a dead bryophyte?

The second problem is to determine the age of the bryophyte. As already noted, some mosses have natural annual markers. ***Hylocomium splendens*** (Figure 1) is named stair-step moss because each year it produces a new primary branch. These stack up like stairs and can be used to determine the age of the moss. ***Polytrichum*** species have small sections of reduced leaves that mark the end of one year's growth and the beginning of the next (Figure 13). Male ***Polytrichum*** plants mark each year of growth with the antheridial splash cup (Figure 14-Figure 15). Petraglia (2007) reported ***Polytrichastrum sexangulare*** (Figure 16) in the Italian Alps as having shoots 9 years in age, with soil humidity apparently influencing longevity (Alessandro Petraglia, Bryonet 25 February 2009). On the other hand, ***Polytrichastrum formosum*** (Figure 17) in a Dutch forest has an estimated age of 80-100 years, based on the size of the **genets** (free-living individuals that develop from original zygotes, parthenogenetic gametes, or spores and that produce branches vegetatively during growth) (van der Velde *et al.* 2001). Other genera [*e.g.* ***Bryum*** *s.l.* (Figure 18), ***Schistidium*** (Figure 19), ***Zygodon*** (Figure 20)] have indentations (Rod Seppelt, Bryonet 25 February 2009) similar to those of female ***Polytrichum***. But does every plant produce sexual structures every year? How many years pass before the first sexual organs occur on the perennials? Do two rainy seasons cause two growth increments? Do drought interruptions cause growth increments?

Figure 13. ***Polytrichum commune*** showing growth interruptions (**arrow**). Photo by Michael Lüth, with permission.

Figure 14. ***Polytrichum commune*** male innovations, starting a new year of growth from the splash cup. Photo by James K. Lindsey, with permission.

Figure 15. ***Polytrichum juniperinum*** splash cups with new growth. Photo by Li Zhang, with permission.

Figure 16. ***Polytrichastrum sexangulare*** from southern Europe. Photo by Michael Lüth, with permission.

Figure 17. ***Polytrichastrum formosum***. Photo by David Holyoak, with permission.

Figure 18. ***Rosulabryum*** (=***Bryum***) ***billarderi*** showing three years of growth. Photo by Jan-Peter Frahm, with permission.

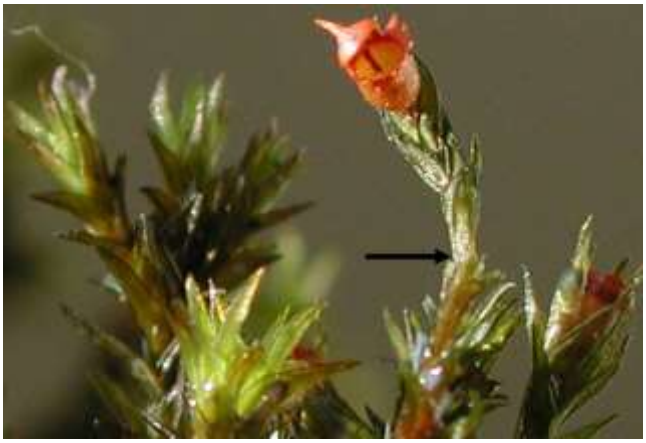

Figure 19. ***Schistidium rivularis*** showing growth increment (**arrow**). Photo courtesy of Betsy St. Pierre.

Figure 20. ***Zygodon dentatus*** showing growth increments (**arrows**). Photo by Michael Lüth, with permission.

Although this also seemed like a simple question, the answer is often not so simple. As Heinjo During and Martha Nungesser (Bryonet 25 February 2009) pointed out, a single **ramet** (stem/branch) may behave as an **annual** (living only one year), but the **genet** may exist for decades. This seems to be the case for ***Crossidium crassinerve*** (Figure 21) in the Mojave Desert, USA (Stark & Delgadillo 2003). The problem of genets seems to be further complicated by more extensive sexual reproduction than we often imagine, with males and females arising from one clone and reproducing within a distance of centimeters to several meters, as in ***Polytrichastrum formosum*** (Figure 17) (van der Velde *et al*. 2001).

Figure 21. ***Crossidium crassinerve***, a moss with annual ramets but perennial genets, from Europe. Photo by Michael Lüth, with permission.

As already noted, in ***Sphagnum***, some plants may be 100's of years old, but these plants keep dying at the bottom and growing at the top, so one must determine what portion of the plant is still alive before answering any question about its longevity. Yet, Dick Andrus (Bryonet 25 February 2009) found ***Sphagnum magellanicum*** (Figure 22) measuring 80 cm in Tierra del Fuego and reminded us of Clymo's opinion that ***Sphagnum*** from a meter or so down could be a 1000 years old. Despite looking old, new plants could be grown from fragments down a meter or more from the surface.

Figure 22. ***Sphagnum magellanicum***, a species that Clymo estimated could grow to be 1000 years old. Photo by Michael Lüth, with permission.

In the presumably annual ***Crossidium crassinerve*** (Figure 21), all is not what it seems to be. Stark and Delgadillo (2003) estimated that some of the stems were as much as 70 years old. Even the older portions were able to produce buds and protonemata in culture.

In the Antarctic, being frozen may suspend biological activity of bryophytes for even thousands of years (Miller 2014; Roads *et al*. 2014; Zimmer 2014). The moss ***Chorisodontium aciphyllum*** (Figure 23) was removed from a core sample of Antarctic permafrost (Roads *et al*. 2014). Samples from depths of 30, 110, 121, and 138 cm grew, suggesting that they had been preserved in permafrost that was subsequently overrun by a glacier. The stems removed from 110 cm showed evidence of growth *in situ* in ff days. Protonemata arose on rhizoids at the base of the core in 22 days. This older part of the core was estimated to be 1153-1697 years old.

Figure 23. ***Chorisodontium aciphyllum*** in Antarctica. Photo from Polar Institute, through Creative Commons.

LaFarge *et al*. (2013) found bryophytes emerging from the edge of the Arctic glacier on Ellesmere Island. The radiocarbon dating suggested they had been entombed by the ice during the Little Ice Age (1550-1850) AD. As these often blackened bryophytes emerged, some developed green stem tips or new lateral branches.

Tamás Pócs (Bryonet 18 September 2014) described longevity indicators in cushion-forming bryophytes like ***Leucobryum*** (Figure 24-Figure 26), **Dicranaceae** (Figure 27-Figure 29), and **Calymperaceae** (Figure 30) when living in seasonal climates. By examining the cushion in section, one can observe yearly layers, much like the annual rings of a tree trunk.

Figure 24. ***Leucobryum glaucum*** cushions. Photo by James K. Lindsey, with permission.

Figure 25. ***Leucobryum*** section showing layers. Photo by Lucas. Origin unknown.

Figure 26. ***Leucobryum glaucum*** clump section showing close view of growth layers. Photo by Walter Obermayer, with permission.

Figure 27. ***Campylopus introflexus*** (**Dicranaceae**) cushion. Photo by Michael Lüth, with permission.

Figure 28. ***Campylopus introflexus*** (**Dicranaceae**) growth increments exposed by eroding sand. Photo by Robin Stevenson, with permission.

Figure 29. ***Campylopus introflexus*** (**Dicranaceae**) indicating growth increments that form layers. Photo by Robin Stevenson, with permission.

Figure 30. ***Syrrhopodon involutus*** (**Calymperaceae**) showing layers. Photo by Jan-Peter Frahm, with permission.

How do you determine the age of an individual ***Sphagnum*** (Figure 31) that can give rise to all populations on the Hawaiian Islands (see Karlin *et al*. 2012)? How do we deal with mosses like ***Pleurozium schreberi*** (Figure 12) that spread horizontally, dying (?) at the base while continuing growth at the tips? Do we start over in aging them when a branch breaks off, becoming an independent plant?

Figure 31. ***Sphagnum fuscum*** showing two heads that share a base. Photo by J. C. Schou, with permission.

Richard Zander (Bryonet 18 September 2014) suggested that perhaps it is the diploid (sporophyte) stage that we should measure because it is important in repairing gene damage. He referred to the gametophyte as mostly immortal but genetically degrading.

New methods are making more accurate age determinations possible. Robinson *et al*. (2007) has used ANSTO to make rapid and accurate age determinations from small amounts of material. This technique uses a radiocarbon analysis to determine growth rates based on samples from different portions (5 cm segments) of the plants. They have indicated changes in the growth rates of ***Bryoerythrophyllum recurvirostre*** (Figure 32) in the Antarctic.

Figure 32. ***Bryoerythrophyllum recurvirostrum*** from southern Europe, a species with documented changes in growth rate. Photo by Michael Lüth, with permission.

There surely are tradeoffs between longevity and new plants, but such tradeoffs have not really been investigated. We have evidence that spores of at least some bryophytes, for example ***Dicranum scoparium*** (Figure 33), are unable to germinate when subjected to water extracts of their parents or other members of the same species (Mishler & Newton 1988; Newton & Mishler 1994). Hence, there is a tradeoff between asexual reproduction by ramets and sexual reproduction producing new clones. But which is best for the species? For evolution, sexual reproduction is usually best because it permits selection against plants with the weaker genomes. But the established genome is obviously adapted to that particular microenvironment.

Figure 33. ***Dicranum scoparium*** in Michigan, USA, showing what is most likely clonal growth because the adults inhibit the germination of spores. Photo by Janice Glime.

Control of Phenological Events

As implied by the above timing of life cycle stages, phenological events must have internal controls that are called into play by external phenomena. For example, ***Funaria hygrometrica*** (Figure 34) is under an intricate set of controls that determine where and when it germinates (Hoffman 1966). If it germinates where it is dark, it cannot complete its life cycle.

Figure 34. ***Funaria hygrometrica*** with developing sporophyte. Photo by Michael Lüth, with permission.

On the other hand, it does germinate over a wide range of both temperature and light intensities (Hoffman 1966). It fails to germinate without light, but can be stimulated to do so by supplying a source of carbon, particularly sugars, suggesting that the importance of light is to provide energy needed to power the process.

Funaria hygrometrica (Figure 34) produces its gametophytes in early spring, produces capsules in the early summer, and sheds its spores in July-September Hoffman 1966). It fails to germinate on soil treated with nutrients, but succeeds on soil from burned areas. If it

germinates where nutrients are too rich, other plants will be able to grow more easily, so competing plants may shade it before it is able to reach maturity. Humic acids inhibit germination (Raeymaekers, unpub. data.), perhaps accounting for its short life after invasion of a new area.

While it grows well on soil previously heated to temperatures of 200-300°C (sufficient to destroy litter and associated humic acids), ***Funaria hygrometrica*** (Figure 34) fails to grow on soil previously heated to greater than 300°C. At these high temperatures, N and P are released; addition of these two nutrients to soil previously heated to 600°C permits the moss to grow. Since the moss grows in open areas, it does not benefit from nutrients leached from the canopy, so it is not surprising that addition of K, Ca, and Mg (important canopy leachates) failed to benefit it. The controls at other stages of the life cycle of ***Funaria hygrometrica*** are less well known, but we do know a considerable amount about the kinds of internal and external controls that are available to mosses, and thus an entire chapter will be devoted to that discussion.

Although we know little about field development of protonemata, we know much about their physiology from laboratory studies, as discussed in the chapter on development. From these, we can surmise the importance of certain environmental controls. Certainly water and light are needed for spore germination. Kinugawa and Nakao (1965) found that photoperiod was important for both germination and protonemal development in ***Bryum pseudo-triquetrum*** (Figure 35). Both processes required a minimum of 12 hours light, although they could be fooled into thinking they had sufficient light by interrupting a long dark period with only 2 minutes of light.

Figure 35. ***Bryum pseudotriquetrum*** with antheridia. Photo by David Holyoak, with permission.

Timing of phenological events that bring antheridia and archegonia in the population to maturity at the same time is crucial to reproductive success. Yet different controls seem to guide these two developmental pathways. Hence, as some taxa expand into new geographic areas with different timing of day length, uncoupling of appropriate temperature from appropriate day length, and changes in seasonal moisture regimes, it is not surprising that some fail to produce capsules despite the presence of both sexes. Clearly phenology is an area requiring further study and may help us understand the success of bryophytes through the widespread areas where we find them. While their morphology has remained relatively unchanged, it appears that their ability to take advantage of seasonal events by a wide variety of phenological strategies, even within a species, may have been evolving rapidly.

Summary

There is a **trade-off** between growth and reproduction so that growth diminishes or ceases during reproduction. Growth also usually ceases in a cold winter when there is no free water and in summer when the temperature is too high and carbon loss would be greater than carbon gain. Optimal temperatures for elongation, bud formation, and rhizoid production may differ. Furthermore, increase in biomass may occur without increase in height. Reproduction may be coupled with photoperiod, light intensity, and temperature, and these will most likely be coordinated to provide the reproductive bryophyte with the greatest possibility of sufficient water. Nutrients and pH may also play a role in signalling onset of sexual reproduction.

Phenological events must not only coordinate with favorable climatic conditions, but they must coordinate with what is occurring among the other occupants of the ecosystem. For example, the non-competitive ***Funaria hygrometrica*** must grow in early spring, produce capsules in summer, and shed spores starting in July, permitting it to complete its life cycle before the arrival of other plants that compete for light and alter the nutrient regime. Following a fire, it takes advantage of the low nutrients before weathering, microbes, and other plants alter the soil and make it too nutrient-rich. Signals for initiation of life cycle stages often include photoperiod, and the required day length may differ between males and females of a species. Antheridia typically take longer to mature than do archegonia, thus requiring different signals to initiate in order to insure maturity at the same time.

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CHAPTER 4-5

ADAPTIVE STRATEGIES: GROWTH AND LIFE FORMS

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CHAPTER 4-5

ADAPTIVE STRATEGIES: GROWTH AND LIFE FORMS

Figure 1. ***Hypnodendron menziesii*** demonstrating the clonal growth and dendroid growth form that is possible in a humid climate such as that in New Zealand. Photo by Jan-Peter Frahm, with permission.

Growth Forms and Life Forms

Bates (1998) concluded that life form is a useful concept in bryophyte ecology because of the "exceptionally high dependence of bryophytes on transient external water supplies." He points out that for bryophytes it is not the individual that forms the ecological unit, but rather the clonal or colonial life form (Figure 1). The life form is so constructed as to minimize evaporative loss while maximizing photosynthetic light capture. For example, in the Taymyr Peninsula, Siberia, differences in life form can reduce evaporative rate by 5.3-46 times, depending on the species and site conditions (Vilde 1991).

Definitions

Meusel (1935) describes **growth form** as the overall character of a plant and explains it can only be determined by detailed morphological analysis. It is a purely morphological term, as opposed to **life form**, which is more encompassing and describes the result of life conditions, including growth form, influence of environment, and assemblage of individuals (Warming 1896; Mägdefrau 1982). **Life form** embodies all the selection pressures that are brought to bear upon a species, or in the words of Mägdefrau (1969), "the organization of a plant in correspondence with its life conditions." Hence, life forms are genetically determined. Growth forms are influenced by the environment.

If these **life forms** persist genetically, we tend to assume they have adaptive significance. Gould and Lewontin (1979) and Mishler (1988) warn us of the trap of this type of thinking. We must recall that selection works against those things that are not beneficial, and that it is a slow process, even slower for those things that convey only a slight disadvantage. Furthermore, such characteristics as life forms may simply carry an occasional advantage, an occasional disadvantage, or little difference from another life form. Correlation of life form with habitat, however, can be used as supporting evidence for the adaptive value of a given life form.

Early classification of **life forms** had little relevance for bryophytes. Dansereau (1957, in Ricklefs 1990) classified plant life forms into trees, shrubs, herbs, epiphytes, lianas (vines), deciduous, evergreen, and bryoids. Raunkiaer (1934) relied primarily on winter characteristics and based his system on bud position:

phanerophytes (*phanero* = visible) – large shrubs and trees, buds at tips of branches; moist, warm environments
chamaephytes (*chamae* = dwarf) – shrubs and herbs, buds near soil; cool, dry climates
hemicryptophytes (*hemicrypto* = half hidden) – die back to ground in winter; cold, moist
cryptophytes (*crypto* = hidden) – buds buried by soil; cold, moist
therophytes (*thero* = summer) – seeds; deserts, grassland

The classification of bryophytes into **acrocarpous** and **pleurocarpous** is somewhat analogous to Raunkiaer's system.

Mägdefrau (1969, 1982) considered that **life form** refers to the habit of the plant in harmony with its life conditions. Hence, life form includes growth form, the assemblage of individuals into formations, societies, or communities, and the influence of external factors. Life form is applied to communities, whereas growth form is applied to individuals. During (1979, 1992) stressed that life forms are linked to the life strategies of bryophytes.

Mishler (Bryonet 1996) takes a somewhat different approach by identifying three terms. He separates **architecture**, considering that to be the most fundamental expression of "internal" factors (genotype and development). This is determined by basic units of growth and their patterns of differentiation. **Growth form** is the middle condition, expressing a mixture of internal and external (environmental) factors and is expressed by the appearance of the stem in the habitat. **Life form** is likewise a mixture, but relies more heavily on external factors. It refers to the overall appearance of the whole colony. Mishler points out the importance of the hierarchical level we are examining – module, stem, or colony.

In response to the confusing array of definitions and uses of the terms life forms and growth forms in the literature, La Farge-England (1996) attempted to give a more precise definition, based on the early usage of the terms. She defined **life form** as "the structures and assemblage of individual shoots, branching pattern, and direction of growth, with modification by its habitat (*i.e.*, cushion, turf, dendroid, mat, pendant, *etc*.)." She emphasizes that the term **life form** applies to the **assemblage**. **Growth form**, by contrast, applies to the structures of the **individual shoot**, including direction of growth, combined with length, frequency, and position of branches. For example, a dense ***Grimmia*** (Figure 11) cushion is a life form that has responded to its xeric habitat and is a conglomerate of individuals. Its **growth form** would be erect stem, with variable numbers of branches, positioned along its stem (*i.e*. acrotonous or distally versus basitonous or proximally). Like Mishler, she asserts that **growth form** is really architecture of the individual shoot combined with the direction of growth.

Both Mishler and La Farge-England emphasize that the direction of growth does not necessarily imply perichaetial position. Mishler suggested that ***Hedwigia*** (Figure 2) is a good example of this uncoupling. It is an acrocarpous moss with a prostrate growth form like that of most pleurocarpous mosses.

Figure 2. ***Hedwigia ciliata*** showing terminal (acrocarpous) capsules (**top**; photo by Robert Klips, with permission) and horizontal growth form (**bottom**; photo by Janice Glime)..

Jargon of Life History

First, perhaps it is necessary to distinguish between **life history** (or life cycle) traits and **life forms**. As During (1979) points out, **holomorphy** (total form, Hennig 1966; the German ***Gestalt***) of plants resulting from their adaptations to their environments certainly relates to their **life strategies**. However, the **life strategy** refers to life cycle characteristics and their timing (treated in the next chapter), whereas **life form** refers to the morphological characters of individuals as well. La Farge-England (1996) points out the inconsistencies in the literature regarding the term **life form** and supports Barkman (1979) by defining it as "the overall organization of growth form, branching pattern, general assemblage of individuals, and modification of a population by the environment." **Growth form**, she reminds us, is "the structural architecture of the individual moss plant." But such architectures can be modified by the environment, hence merging life form and growth form (Tangney 1998). It would seem simpler to define one as the genetically programmed form and one as the environmentally modified form, but the muddle in the literature has crossed those lines with both terms. Thus,

even with the foregoing definitions, confusion in the use of terms will still be with us. I shall attempt to unravel their use in the literature presented here. Nevertheless, interpretation of their use should be done with caution.

Growth Forms

Since **growth form** is the simpler result of genetics, we should examine that first. Meusel (1935) applied the term growth form to individual shoots. It is therefore a purely morphological term expressing the architecture of the plant. As La Farge-England (1996) stated, the terminology of growth form, branching pattern, and position of perichaetia have been used inconsistently in the literature. This morass of literature makes it difficult to compare studies and to sort out the real meanings in nomenclature. After an extensive review of the literature and usage of the terminology, she recommended the following interpretations:

1. **Growth form** is distinct from **life form**.
2. Direction of growth does not necessarily imply perichaetial position; some **acrocarpous** mosses (having terminal perichaetia) grow horizontally, whereas some **pleurocarpous** ones (having perichaetia in lateral buds or on short side branches) grow erect.
3. **Cladocarpy** (Figure 3) is distinct from pleurocarpy, with perichaetia terminal on lateral branches and with juvenile leaf development similar to that on vegetative branches; perichaetial branches have lateral primordia that potentially develop subperichaetial branches. (It is defined in *Glossarium Polyglottum Bryologiae* as a type of pleurocarpy having sporophytes borne terminally on short lateral branches, as in ***Fontinalis***).
4. **Pleurocarpy** is defined as having perichaetia terminal on lateral innovations that appear sessile and swollen along supporting axes. Juvenile leaves are morphologically different from those of vegetative branches. Perichaetial innovations lack lateral branch primordia and thus do not produce subperichaetial branches. Pleurocarpy is restricted to **Hypnales**, **Hookeriales**, and **Leucodontales** (Figure 6d), including **Spiridentaceae** and **Racopilaceae**.

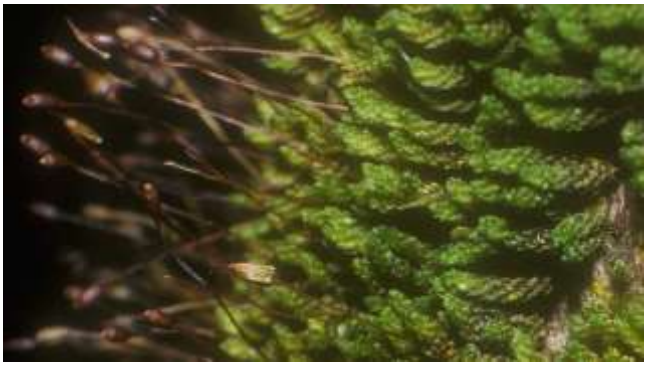

Figure 3. Cladocarpous branches of ***Macromitrium microstomum***. Photo by Janice Glime.

But traditionally, growth forms of mosses have been divided into those that are **acrocarpous** (Figure 4) and stand vertically (**orthotropic mosses**) and those that are **pleurocarpous** and lie horizontally relative to the substrate (**plagiotropic mosses**; Figure 6) (Meusel 1935). This of course leaves a few out of the scheme, as noted by La Farge-England. The orthotropic mosses can be further divided into the **protonema mosses** (Figure 5), with short or non-existent shoots that wither after the sporophyte is produced, and **turf mosses**, with upright shoots that bear new shoots after the sporophyte forms and subsequently bear further archegonia and more sporophytes; these new growths are the **innovations**. The **plagiotropic** mosses (Figure 6) include **thread mosses** (*e.g.* **Leskeaceae**, some **Amblystegiaceae**), with little difference between the main stem and lateral branches, **comb mosses** (*e.g.* **Hypnaceae**, **Brachytheciaceae**, **Meteoriaceae**), with a strong main shoot with many simple or branched lateral branches, and the **creeping-shoot mosses** (*e.g.* ***Leucodon***, ***Antitrichia***, **Climaciaceae**, **Hypnodendraceae**), with rhizomatous main shoots that give rise to upright main shoots.

Figure 4. Acrocarpous growth form exhibited by ***Oncophorus wahlenbergii***. Photo by Michael Lüth, with permission.

Figure 5. Protonema mosses. **Upper:** ***Pogonatum aloides***. **Lower:** ***Buxbaumia aphylla***. Photos by Michael Lüth, with permission.

The same species may exhibit more than one growth form. For example, in some populations ***Hylocomium splendens*** (Figure 7) exhibits **monopodial growth** (single central axis with apical growth) (Ross *et al*. 1998, 2001). However, some populations can continue by **sympodial growth** (growth produced by lateral buds just behind apex).

Figure 6. Plagiotropic, pleurocarpous, perennial mosses. **a & b.** creeping shoot mosses – ***Antitrichia curtipendula***. **c.** creeping shoot moss – ***Climacium dendroides***. **d.** creeping shoot moss – ***Leucodon brachypus*** var. ***andrewsianus***. **e.** thread moss – ***Amblystegium serpens***. **f.** thread moss – ***Leskea polycarpa***. **g.** comb moss –***Brachythecium reflexum***. **h.** comb moss – ***Hypnum sauteri***. **a, b, e-g** photos by Michael Lüth, with permission; **c, d** photos by Janice Glime.

In forest habitats of temperate to mid-arctic regions the growth if ***Hylocomium splendens*** (Figure 7) is primarily sympodial, creating the stair-step form that easily delineates annual growth (Ross *et al*. 2001). Higher nutrient availability promoted sympodial growth. In tundra and high arctic habitats, monopodial growth predominates and increments cannot easily be discerned. Transplant experiments demonstrated that these traits were plastic, but that natural variability was greater among those shoots in natural populations at transplant sites, indicating a genetic component as well as an environmental component to the differences, affecting both growth and life forms.

Figure 7. Weft life form of ***Hylocomium splendens***, exhibiting well-defined annual branching. Photo by Michael Lüth, with permission.

Ross *et al*. (1998) found that the sympodial ***Hylocomium splendens*** (Figure 7) plants had increasing stiffness with stem segment age and flexibility decreased with age up through four years, then declined. However, monopodial plants showed neither of these age effects and no increase in stem diameter with age. The sympodial stems had significantly more cellulose than their monopodial counterparts, providing them with a higher stress yield. The predominance of these two forms differs with habitat, with more northern populations lacking the sympodial branching that defines the annual increments. Økland (2000) further determined that reproductive capacity differs with stem position and age. The apical tips are subject to greater exposure and are less likely to have successful reproduction. Reproductive failure is greatest for older segments buried within the weft (44%), lowest for intermediate vertical positions (12%), and relatively high for the emergent segments. The greatest annual increment is likewise at this intermediate level (2-10 mm below the bryophyte surface) where there is still sufficient light but the loss of water is minimized.

Økland (2000) pointed out the importance of "growth form" in the way that pleurocarpous and acrocarpous bryophytes interact in competition. In our study on Isle Royale (Raeymaekers, Zhang, & Glime unpubl), the interaction between the acrocarpous ***Dicranum polysetum*** (Figure 8) and the pleurocarpous ***Pleurozium schreberi*** (Figure 8) differed from year to year, most likely depending on the precipitation patterns. In some years, ***D. polysetum*** increased in area and overran ***P. schreberi***, but in other years the reverse occurred. Økland suggested that the relationship of upper segments to lower ones represented **amensalism**, where the lower segments were harmed. Small segments were more easily buried. This relationship can play an important role in both infraspecific and interspecific interactions among bryophytes.

Figure 8. ***Pleurozium schreberi*** (diagonally at lower right) competing with ***Dicranum polysetum*** (upper left). Photo courtesy of Herschel Horton.

Life Forms

Literature on life forms and growth forms is confusing because different authors have used the terms in different ways, sometimes in reverse of the descriptions above. Even in the long-studied tracheophytes, the terms have often been used as if they are interchangeable. In studying loblolly pine trees, Haney *et al*. (1993) illustrated effects of density on "growth form" of loblolly pine tree shape (Figure 9). They found that in low densities, trees were shorter and had more branches. At medium density, they were taller, but branches were few in number. At high densities, trees were tallest and branches were still few. These environmental influences on tree form fit the more encompassing definition of life form described above by La Farge-England (1996). As expected, allocation of biomass changes relative to density (Table 1), resulting in a different form. Such mosses as ***Sphagnum*** and ***Climacium*** (Figure 13c) would be interesting tests of a similar form change in bryophytes. ***Climacium*** is known to change form, but it appears to be under both environmental and genetic control; effect of crowding was not studied (Shaw 1987).

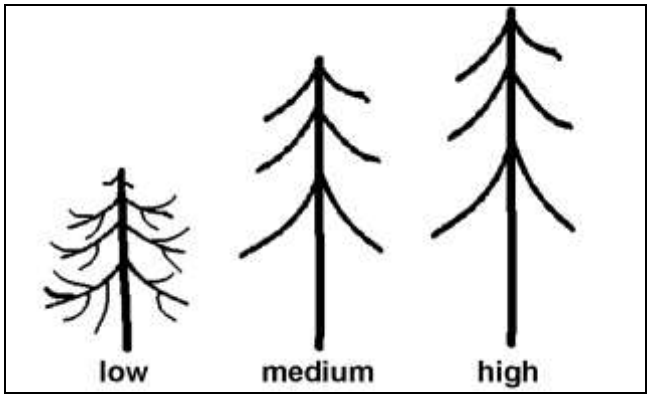

Figure 9. Illustration of forms in loblolly pine at different densities. Based on Haney *et al*. 1993.

Table 1. Allocation of biomass in trees of loblolly pine at three density levels. From Haney *et al.* 1993.

	low	medium	high
diameter (cm)	11.87	7.79	6.67
number of whorls	18	11	9
biomass (kg)	12	6.5	4.9
crown ratio	0.79	0.52	0.44
branches	50	27	21
branch length (m)	1.5	1.05	0.9

Bates (1998) raised the question "Is 'life-form' a useful concept in bryophyte ecology?" When he pointed out that most bryophytes are either clonal or colonial, he emphasized that it is these, not individual shoots, that are the functional units. The life form maximizes productivity and minimizes water loss, but it may also function to prevent photoinhibition or scavenge cloud water. Despite its usefulness in indicating moisture and light conditions, Bates considers life form to have limited use "as a framework in ecological studies." He also considers a major problem to be the inconsistent way the concept has been applied in the literature. Life forms also change, as pointed out by Warming (1896). Bates suggested that one interpretation of life form is to consider highly productive horizontal growth forms like that of ***Brachythecium rutabulum*** (Figure 10) to be an adaptation for **foraging** (horizontal growth that permits mosses to take wider advantage of nutrients and light; Bates 1998). Life forms do not evolve independently and are closely tied to the life cycle and reproductive traits. Nevertheless, Bates concluded that the concept was useful because of "the high dependence of bryophytes on external transient water supplies." However, the description of life form alone will provide insufficient understanding and will depend on knowledge of its relationship to other attributes of the life strategy.

Figure 10. Horizontal growth form of ***Brachythecium rutabulum*** that may be used for light-scavenging (foraging). Photo by Michael Lüth, with permission.

Age changes the life form and its effect on the physiology of ***Grimmia pulvinata*** (Figure 11) in a different way (Zotz *et al*. 2000). As discussed in the structural adaptations related to water, this moss forms cushions. As the cushion volume increases, so does the water volume. However, the surface area increases two-dimensionally as the volume increases three-dimensionally, causing a decrease in the surface area to volume ratio. This greatly enhances the water retention of the cushion as it enlarges. On the other hand, the CO_2 exchange decreased with size, again because of the reduced surface area. Lowered CO_2 exchange corresponded with lower rates of both net photosynthesis and dark respiration.

Figure 11. Cushion life form of ***Grimmia pulvinata***. Photo by Des Callaghan, with permission.

Nevertheless, life forms are often indistinct from growth forms. A plant is predisposed to a certain growth form, and despite neighbors or environmental conditions, it retains that growth form as part of its life form. In this sense, Mägdefrau (1982) lists ten life forms for bryophytes (Figure 12, Figure 13), to which I (Glime 1968) have added **streamer**.

Mägdefrau Life Forms

Annuals – pioneers; no vegetative shoots remain to carry on a second year; ***Buxbaumia*** (Figure 5), ***Diphyscium***, ***Ephemerum*** (Figure 13a), ***Phascum***, ***Riccia***

Short turfs – open mineral soils and rocks; regenerative shoots; form spreading turfs for only a few years; ***Barbula*** (Figure 13b), ***Ceratodon***, ***Didymodon***, ***Marsupella***

Tall Turfs – forest floors in temperate zones; can conduct water internally; very tall; persist by regenerative shoots; **Bartramiaceae**, **Dicranaceae**, **Polytrichaceae** (Figure 13c), ***Drepanocladus***, ***Herbertus***, ***Sphagnum***, ***Tomenthypnum***

Cushions – rocks, bark, Arctic, Antarctic, alpine; usually high light; grow upward and sideways; hemispherical; persistent for many years; ***Andreaea***, ***Grimmia***, ***Leucobryum*** (Figure 14), ***Orthotrichum***, ***Plagiopus***, no liverworts

Mats – rocks, bark, [on leaves (epiphyllous) in tropics]; plagiotropic and persistent for a number of years; **Lejeuneaceae**, most **Marchantiaceae**, ***Homalothecium***, ***Lophocolea***, ***Plagiothecium*** (Figure 13d), ***Radula***

Wefts – forest floor of temperate zone; hold considerable capillary water; grow loosely and easy to remove from substrate; new layer grows each year; **Brachytheciaceae**, **Hylocomiaceae** (Figure 7), ***Bazzania***, ***Ptilidium***, ***Thuidium***, ***Trichocolea***

Pendants – epiphytes, especially in tropical cloud forests; long main stem with short side branches; **Meteoriaceae** (Figure 13e), **Phyllogoniaceae**, some tropical ***Frullania*** (also spelled pendent, but in English usage, this is the adjective form)

Tails – on trees and rocks, shade-loving; radially leafed, creeping, shoots stand away from substrate; ***Cyathophorum***, ***Leucodon*** (Figure 6d), ***Spiridens***, some tropical ***Plagiochila***

Fans – on vertical substrate, usually where there is lots of rain; creeping, with branches in one plane and leaves usually flat; **Neckeraceae** (Figure 13f), **Pterobryaceae**, ***Thamnobryum***, some ***Plagiochila***

Dendroids – on ground, usually moist; main stem with tuft of branches at top; ***Climacium***, ***Hypnodendron***, ***Hypopterygium***, ***Leucolepis***, ***Pleuroziopsis*** (Figure 13g), ***Symphogyna hymenophyllum***

Streamer – long, floating stems in streams and lakes; ***Fontinalis*** (Figure 13h) (Glime 1968)

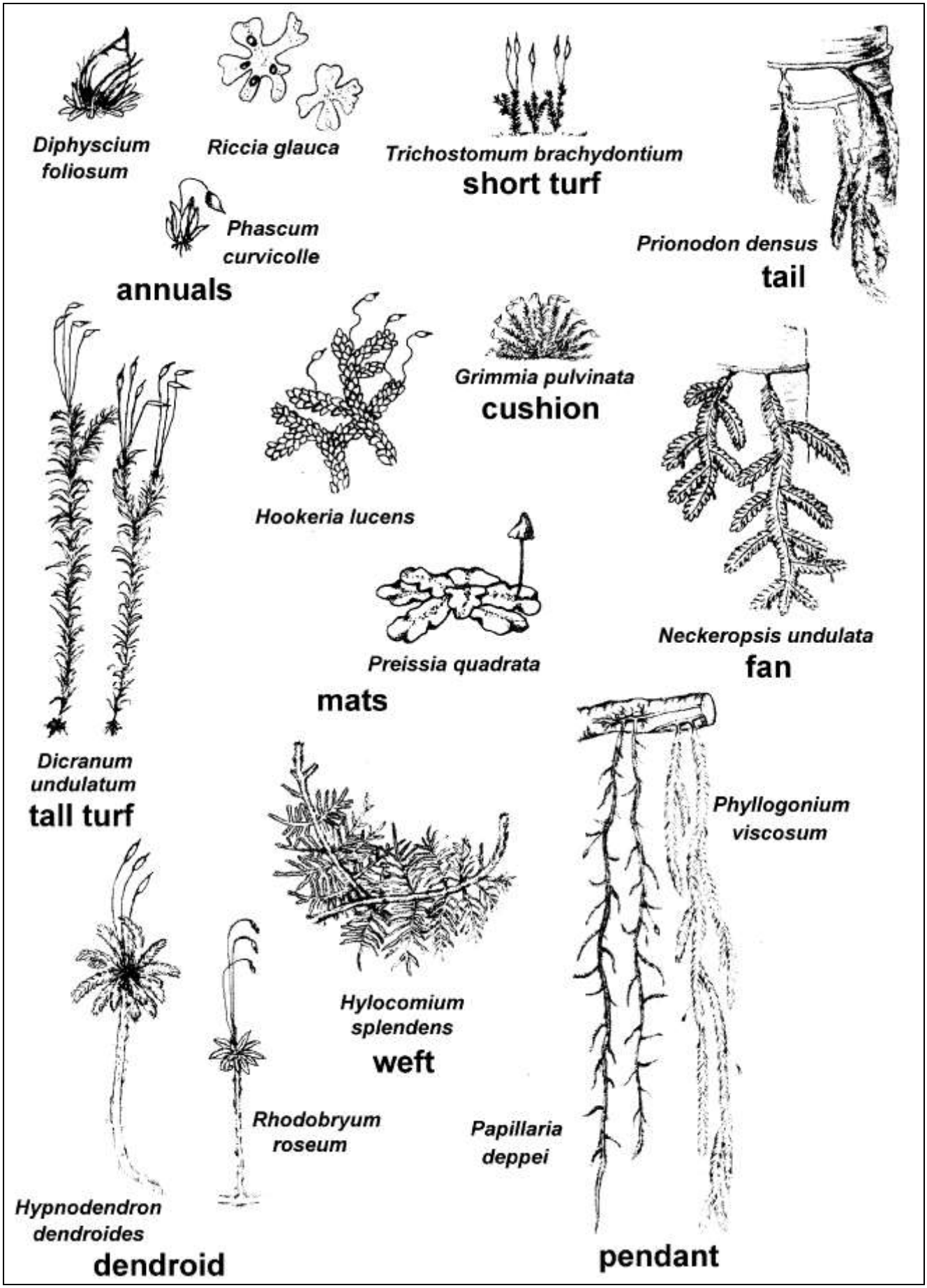

Figure 12. Life forms of mosses and liverworts, based on Mägdefrau 1969. Redrawn by Margaret Minahan.

Figure 13. Life forms of bryophytes. **a.** Annual – ***Ephemerum minutissimum***. **b.** Short turf – ***Barbula unguiculata***. **c.** Tall turf – ***Polytrichum formosum***. **d.** Mat – ***Plagiothecium curvifolium***. **e.** Pendant – ***Meteorium***. **f.** Fan – ***Neckera urnigera***. **g.** Dendroid – ***Pleuroziopsis ruthenica***. **h.** Streamer – ***Fontinalis antipyretica***. Photos by Michael Lüth, with permission; e & g by Janice Glime.

Environmental Influences on Life Form

These eleven forms may be further divided, as suggested by Horikawa and Ando (1952). As Mägdefrau (1982) points out, light and water are the predominant influences on life forms. Crowded shoots with dense foliage facilitate water movement and retention in areas with sufficient soil water, thus favoring **tall turfs**. **Mats**, **wefts**, **tails**, and **fans**, on the other hand, are unable to obtain water by capillary action, but depend on the capillary spaces to retain water and extend their periods of activity. **Pendants** (Figure 13e) are like laundry on the clothesline and are particularly susceptible to drying; hence they live in places with considerable rainfall or fog, assumedly directing the water to the growing tip. Mägdefrau (1982) cites his observations on mosses near waterfalls to support this assumption.

The **cushion** life form (Figure 14) is highly adapted for water conservation. Proctor (1980) found that the laminar flow patterns over moss cushions were consistent with the measured loss of water from surfaces of varying degrees of roughness. Water loss increased rapidly beyond a critical wind speed, at which the surface irregularities of the cushion could be related to boundary-layer thickness. The thickness of this boundary layer determines the rate of water loss, with thick layers reducing evaporation. Even cushions have turbulent flow as opposed to laminar flow (Rice *et al*. 2001), and the more deeply the air penetrates into the moss canopy, the more turbulent that flow and the greater the evaporation. Among the growth forms, we would expect cushions to have the least turbulence, with wefts and turfs creating more (Figure 15). Surface roughness increases conductance (Rice *et al*. 2001). However, Proctor (1980) found that hair-points of the leaves that project above the cushion surface reduce boundary layer conductance, for example, by about 20-35% in ***Syntrichia intermedia*** (Figure 16) and ***Grimmia pulvinata*** (Figure 11), hence serving as an adaptation to reduce water loss.

Figure 14. Cushions of ***Leucobryum glaucum*** in a mixed hardwood forest in the Keweenaw Peninsula of Michigan, USA. Photo by Janice Glime.

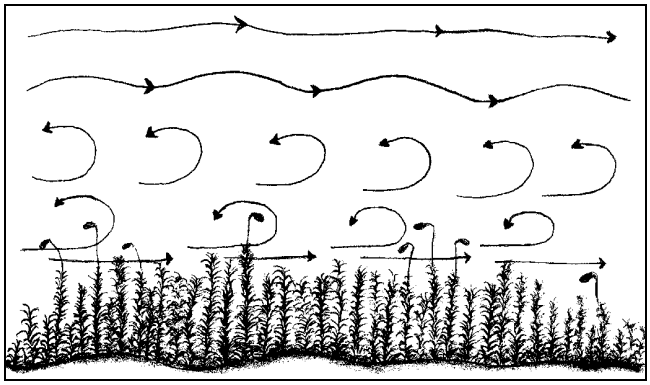

Figure 15. Diagram indicating turbulence and boundary layer as might be found above the irregular surface of a moss weft. Having all stems at the same height, as in a cushion, would reduce the turbulence. Drawing by Margaret Minahan.

Figure 16. ***Syntrichia intermedia***, a species with hair points that reduce boundary layer conductance. Photo by Michael Lüth, with permission.

Rice *et al*. (2001) have used wind tunnel experiments to examine effects of architectural features on boundary layer thickness and subsequent water balance of bryophytes. Using evaporation rates of ethanol, they were able to assess differences among 11 taxa having a variety of canopy structures. They accounted for 91% of mass transfer of water loss using models based on surface structure. Even the seemingly smooth surface of cushions behaved as turbulent flow rather than laminar flow boundary layers. Conductance increased with surface roughness, causing those species with greater roughness to have higher conductance rates at all wind speeds.

Water-holding capacity is often more important than obtaining water. In the Antarctic, dense rhizoids contribute to high water-holding capacity in ***Bryum algens*** (Lewis Smith 1988). In ***Schistidium antarcticum*** (Figure 17), the **turf** form has a high water-holding capacity, whereas the densely packed **cushion** form has a lower water content relative to its dry weight. Nevertheless, the rate of water loss is much more rapid in the turf form (Lewis Smith 1988). I am puzzled, however, by the more rapid water loss in the more tomentose form of ***Bryum algens*** than in the form with fewer rhizoids. I would have to conclude that water was held loosely among the rhizoids, contributing to the magnitude of weight loss, and was lost more easily, giving a higher percentage loss. A similar phenomenon could explain the differences between the water loss of the turf and cushion. Lewis Smith found that the reverse relationship holds if the water loss is expressed

relative to the initial water content instead of the dry weight, supporting my interpretation.

Figure 17. Cushions of *Schistidium antarcticum* on Macquarie Island in the Antarctic. Photo courtesy of Rod Seppelt.

Physical factors of the environment also contribute to life form in other ways. Once the growing apex reaches the surface of the **cushion** or exceeds the protection of a rock, it would be exposed to air movement where it would dry out. However, the ethylene concentration around the growing tip would also diminish. Whenever the moss slowed its growth and fell below its fellow cushion members, the higher ethylene concentration trapped within the cushion could again accelerate its cell elongation. Results with ***Fontinalis antipyretica*** (Figure 13h) suggest that ethylene in mosses reduces cell division but permits and perhaps enhances cell elongation (Figure 18) (Glime & Rohwer 1983). If it indeed acts this way, such a mechanism could be a sensitive and effective control mechanism that would maintain the cushion growth form necessary for maximum moisture retention (Kellomaki *et al*. 1978) and surface light. If, however, ethylene retards elongation as it does in most tracheophytes (Abeles 1973), **IAA** (indole acetic acid, a growth hormone) is probably the controlling factor. IAA is destroyed by light (Goodwin & Mercer 1983), so those branches getting more light would grow less, not to mention being retarded by desiccation, whereas those within the mat would be shaded and grow more, as an etiolation response. Mosses kept humid in a plastic bag in a place where little light reaches them produce narrow, etiolated shoots. In a terrarium, ***Dicranum scoparium*** (Figure 19), ***Pleurozium schreberi*** (Figure 8), and ***Brachythecium*** (Figure 10) all produce etiolated tips, presumably in response to low light (pers. obs.).

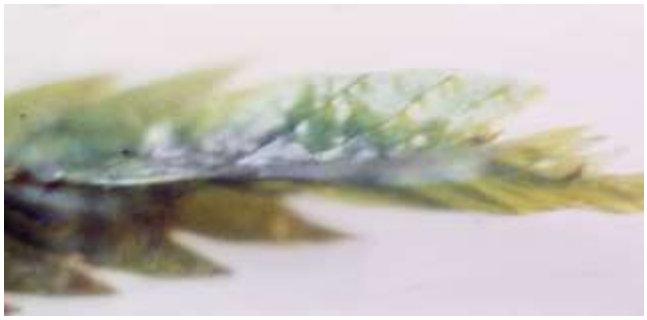

Figure 18. ***Fontinalis antipyretica*** leaves showing uneven growth effects of ethylene produced by application of ACC. Photo by Janice Glime.

Figure 19. ***Dicranum scoparium***, a species that becomes etiolated in very low light. Photo by Janice Glime.

Plants, including bryophytes, have specific mechanisms to combat light intensity changes. Species from open habitats respond to simulated shade with a large increase in stem elongation (Morgan & Smith 1981). This increase would carry the plant upward until it topped its competitors and could receive the needed sunlight. Lignified woodland species react much less or not at all; here the futile attempt to top the canopy would result in tremendous amounts of wasted energy. **Cushion** bryophytes, however, respond to shading by each other like species from open habitats. In nature we see rounded cushions of ***Leucobryum*** (Figure 14) and ***Dicranum*** (Figure 19), and we must wonder if the tall center plants and short border plants are merely a function of age. Yet when a clump is backed up against a rock, it is not as short on the rock side as it is on the other side, but rather it tapers down and away from the rock. Is it light intensity acting on IAA, exposure to desiccation, or ethylene concentration that maintains these cushions, or some combination of these?

In mangrove swamps, Yamaguchi and coworkers (1990) found that small, **appressed** liverworts, especially **Lejeuneaceae** and **Frullaniaceae** (Figure 20), predominated, whereas in more landward sites the larger **ascending** taxa such as ***Plagiochila*** (Figure 21) and pleurocarpous mosses were found. This distribution seems counter-intuitive unless the seaward sites were more subject to wind desiccation from buildup across the water, whereas the more landward ones were protected by the forest. Salt tolerance may enter the relationship as well, but this has not been explored.

Figure 20. ***Frullania tamarisci*** illustrating the compact growth form of the genus. Photo by Hermann Schachner, through Creative Commons.

Figure 21. ***Plagiochila*** sp. illustrating the loose growth form of this liverwort. Photo by Lin Kyan, with permission.

Birse (1957) showed that a normally monopodial dendroid ***Climacium dendroides*** (Figure 13c) can be induced to grow horizontally as a stolon when affixed to a substrate and supplied with ample moisture. It furthermore will reverse its direction of growth if turned upside down, yet, if placed in a moist pot, it will follow the substrate, growing down on the outside of the pot and ignoring gravity. If buried in sand, it will regenerate shoots that Birse *et al*. (1957) observed to grow up to the surface, then grow horizontally. She likewise observed that ***Thamnobryum alopecurum*** (Figure 22-Figure 23) exhibited growth forms ranging from simple branches in dripping water (Figure 22) to highly dendroid in very moist air (Figure 23).

Figure 22. Simple branching of ***Thamnobryum alopecurum*** in dripping water. Photo by David Holyoak, with permission.

Aquatic mosses such as ***Fontinalis*** (Figure 13h) do not fall easily into the above classification system. While most ***Fontinalis*** species hang in a pendent form similar to pendent epiphytes, their physiological relationship to their environment as a result of this growth form is quite different. The tip, instead of receiving water dripping down from the remainder of the plant, is immersed most of the year. This long form, which I have termed **streamer** (Glime 1968; Jenkins & Proctor 1985) is more likely a result than an adaptation. The persistent growth of this moss permits it to grow farther and farther from its substrate, but many branches stack upon each other to make a thick weft, but one that is not easy to remove from the substrate. In ***Fontinalis dalecarlica*** (Figure 24), rhizoids are generally restricted to bases of stems, and the long, persistent stems are extremely strong (Glime 1980). In ***F. novae-angliae*** (Figure 25), rhizoids can originate throughout the stems, especially on the stolons, making a firmer attachment to the substrate. It would be interesting to examine competition in these two taxa since they can occupy the same streams and even the same rocks.

Figure 23. Dendroid form of ***Thamnobryum alopecurum*** in moist air. Photo by Des Callaghan, with permission.

Figure 24. ***Fontinalis dalecarlica***, a species that produces rhizoids only at its base. Photo by Jan-Peter Frahm, with permission.

Figure 25. ***Fontinalis novae-angliae***, a species that forms rhizoids along its stems. Photo by Janice Glime.

Although many studies describe dominant life forms, these descriptions are rarely based on quantitative data. Kürschner (1994) used mean cover values to describe life

forms on basic rocks in nine communities in southern Germany on the northern border of the Schwaebische Alb. He found that communities subject to high light and temperature (photophytic and thermophytic) were dominated by cushions, short turfs, and perennial and short-lived colonists (life strategies discussed in the next chapter). As these graded into shady habitats, wefts and mats were more common, with perennial shuttle and perennial stayer life cycle strategies; reproduction was more "passive." Low light species (sciophytes) and aquatic species were perennial fan-formers with sexual reproduction.

Whereas growth form is important for water and light relations, we seldom speak of in relative to support. Nevertheless, with no lignin, bryophytes cannot grow very tall due to lack of support, utilizing cushion growth forms to provide support in some species, especially in ***Polytrichum*** and its close relatives. During *et al*. (2015) examined the relationship of support along an altitudinal gradient in northern Japan, using ***Pleurozium schreberi*** (Figure 8) and ***Pogonatum japonicum*** (Figure 26) as model organisms. ***Pogonatum japonicum*** had thicker stems, greater rigidity, and exhibited more effect with altitude than did ***P. schreberi***. Both exhibited thinner stems and greater stem flexibility with increasing altitude. To me this was a surprising result, based on the knowledge that in tracheophytes wind causes stems to thicken due to greater production of ethylene (Biro *et al*. 1980). I would expect greater winds at higher altitudes. This is an interesting observation that needs to be replicated in other species on other altitudinal gradients.

Figure 26. ***Pogonatum japonicum***, a species that exhibits thinner stems and greater stem flexibility with increasing altitude. Photo from Digital Museum, Hiroshima University, with permission.

Some stems can develop considerable stem stiffness and strength, as indicated by biomechanical tests (Frenzke *et al*. 2011). This is achieved by a dense hypodermal sterome "comparable with that of woody stems." With this strength, such mosses as ***Dendroligotrichum dendroides*** (Figure 27) are able to stand upright. Differences in stem strength are seen among the species of ***Fontinalis***, with ***F. dalecarlica*** (Figure 24) exhibiting considerable stiffness and strength that permit it to live where there is rapid flow. ***Fontinalis flaccida*** (Figure 28), on the other hand, has a flaccid stem that cannot withstand the strong flow, forcing it to lives in lakes and pools of streams. These differences can be observed as differences in the stems (Figure 29-Figure 30).

Figure 27. ***Dendroligotrichum dendroides***, a moss with a strong stem permitting it to stand upright. Photo by Felipe Osorio Zúñiga, with permission.

Figure 28. ***Fontinalis flaccida*** with perigonia, showing the thin stem for this species that is supported by water. Photo by Janice Glime.

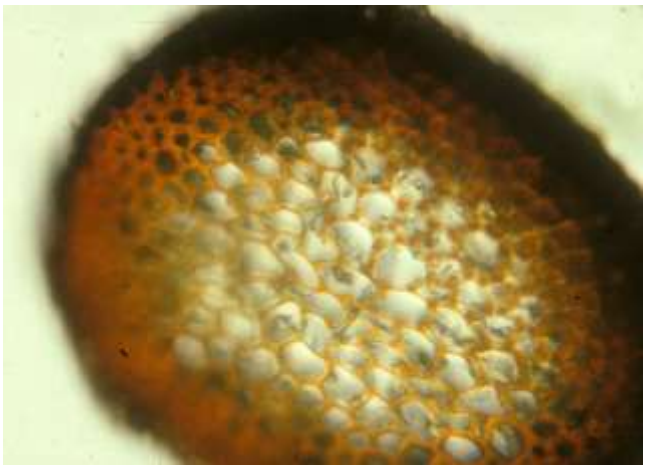

Figure 29. ***Fontinalis dalecarlica*** cs showing thick-walled cells in outer part of stem. Photo by Janice Glime.

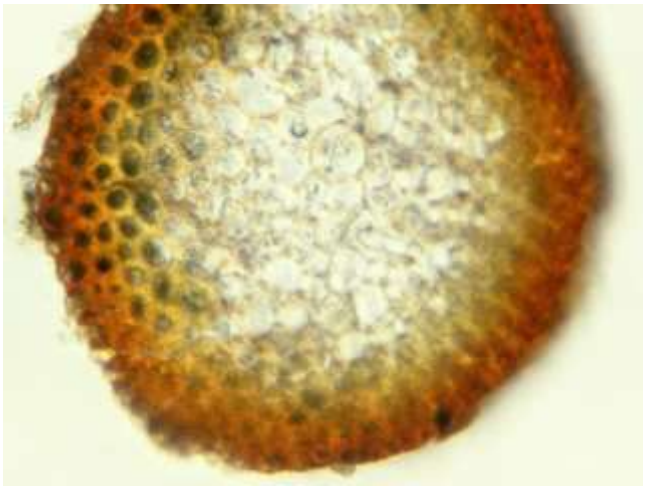

Figure 30. ***Fontinalis flaccida*** stem cs showing narrower stem and thinner cell walls, especially in the center of the stem. Photo by Janice Glime.

Physical Effects on Growth Form

Moss Balls

The strange phenomenon of moss balls was reported in 1912 by Dixon, who referred to them as "mosses growing unattached." Bryologists still remain fascinated by these strange organisms that grow in a ball and are mobile, so that at different times any part of the sphere may be exposed to sunlight or substrate. But bryologists are not the only ones fascinated by them. In Japan, a monument is dedicated to their preservation (Iwatsuki 1977).

In 1874, the United States sent an expedition to the Kerguelen Islands in the South Indian Ocean to observe the transit of Venus (Mägdefrau 1987). The surgeon of the expedition was also an amateur botanist and an avid collector. He brought back a "curious moss" that seemed "not to be rooted to another plant, but to be blown about by the wind indiscriminately," as described by the bryologist Th. P. James. Schimper later described these same mosses as having a size that varies between that of a cherry and a middle-sized potato. The smaller balls were ***Blindia aschistodontoides***, and the larger ones were formed by stems of ***Andreaea parallela*** by radiating from a central core of soil or a small pebble. Since then similar wind-formed balls have been found in Alaska, Iceland, Norway, on Mount Ontaka in Japan, and even at the high elevation tropics of Mount Kenya, Mt. Elgon, and Mt. Kilimanjaro in Africa.

Such balls in Arctic and alpine areas could result from **solifluction**. **Solifluction** is a slow creeping of fragmented material down a slope over impermeable material, due to the viscous flow of water-saturated soil and other surficial materials, particularly in regions underlain by frozen ground (not necessarily permafrost) acting as a barrier to downward water percolation. Its drift typically occurs at a rate of 1-10 cm per year (White 2001) in relatively cold regions when the brief warmth of summer thaws only the upper meter or two of loose earth materials above solid rock, which becomes waterlogged because the underlying ground remains frozen and therefore the water cannot drain down into it. Mosses could travel and tumble with it (Figure 31).

Figure 31. This moss, probably ***Grimmia ovalis***, has been termed a galloping moss due to its movement down its substrate. This behavior may be an example of solifluction. Photo by Wouter Bleeker, with permission.

Hedberg (1964) interpreted the African balls (***Grimmia ovalis***, Figure 31; Mägdefrau 1987) to form as a result of solifluction. Mägdefrau (1987) tested this hypothesis by experimenting with balls in Teleki Valley of Mount Kenya at 4200 m. The balls were marked and their locations sketched. When it was dry, there was no solifluction and the moss balls remained in place. However, when they experienced daily watering and frost at night, the balls rotated but held their positions. Rather, it appears that when ice crystals and ice needles form at night, they cause the mosses to be forced away from their substrate and broken off. These freed mosses are blown about continuously and thus grow in all directions, forming balls.

Mägdefrau (1987) observed that none of the mosses in balls had sporophytes, whereas those of the same species growing attached had plentiful sporophytes. He concluded that the growth of sporophytes is prevented by the rolling movement. It would seem likely that young setae and perhaps even archegonia at apices may be damaged by abrasion as they get beaten around over the rocky surface. When mosses lie for a longer period of time on one side, sporophytes develop on the edge of the disk.

On frozen Icelandic soil (Mägdefrau 1982) and Alaskan glaciers (Shacklette 1966; Heusser 1972; Iwatsuki 1976), dislodged mosses blow about across the surface, forming similar balls. During (1992) observes that this life form, which also includes lichen species, results in areas that have high winds and little vegetation.

Perez (1991) attributes the transport of ***Grimmia longirostris*** moss balls (Figure 32) in the Paramo de

Piedras Blancas of the Venezuelan Andes to needle ice activity. These balls had a high organic content (19%) and a collection of fine mineral grains (69%), a much higher fine grain than in the underlying mineral soils. This combination of organic content and fine grains affords the moss balls a much higher water retention capability than paramo soil, with water-holding capacity increasing with the size of the ball.

Figure 32. ***Grimmia longirostris*** solifluction moss balls in Ethiopia. Photo by Henk Greven, with permission.

At Tierra del Fuego, giant balls of ***Racomitrium lanuginosum*** form (Figure 33). Similar ***Racomitrium*** balls or hummocks form in Iceland (Figure 34). Examination of their interior revealed large clumps of grass. The ***Racomitrium*** had completely overtaken the grass.

Figure 33. These giant moss balls of ***Racomitrium lanuginosum*** have formed in the Tierra del Fuego. Could these be like the Iceland balls that form around clumps of grass, completely engulfing them? Photo by T. G. Allan Green.

Figure 34. ***Racomitrium*** hummocks in Iceland. Photo by Janice Glime

Wind and ice are not the only sources of creating moss balls. Action of waves can create similar assemblages (Figure 35-Figure 38). These strange assemblages of individuals have been reported from as distant places as Alaska (Iwatsuki 1976), Finland (Luther 1979), Japan (Iwatsuki 1956, 1977; Iwatsuki *et al*. 1983), and South America (Eyerdam 1967). Eyerdam found ***Fontinalis*** in balls up to 15 cm in diameter!

Figure 35. Moss balls of ***Warnstorfia fluitans*** var. ***kutcharokensis*** of Lake Kutcharo, Japan. Here m**oss balls are** being made by wave action. Photo by Janice Glime.

Figure 36. Row of moss balls of ***Warnstorfia fluitans*** var. ***kutcharokensis*** along the shore of Lake Kutcharo, Japan. Photo by Janice Glime.

Figure 37. Moss ball of ***Warnstorfia fluitans*** var. ***kutcharokensis*** with arrows indicating green, growing apices. Photo by Janice Glime

Figure 38. Side branch typical of many of the stems in these ***Warnstorfia fluitans*** var. ***kutcharokensis*** balls, creating the dense structure that makes the ball. Photo courtesy of Zen Iwatsuki.

In shallow water near lake shores in Hokkaido, Japan, ***Warnstorfia fluitans*** (Figure 39) attaches to small rocks (Iwatsuki 1956); once the rock is dislodged, wave action rolls the moss back and forth, causing it to lie first in one position, then another, with any protruding branches being broken off (Iwatsuki *et al*. 1983). These growths become extremely dense. As the mosses reach shallower water, wave action is even greater. Ultimately they may be deposited in great numbers along the beaches. Stress causes the production of ethylene, and ethylene can result in short, wide cells under stress conditions in higher plants (Abeles 1973). This could partly explain the short, but firm, branches in the moss balls.

Figure 39. ***Warnstorfia fluitans*** growing normally. Photo by Michael Lüth, with permission.

Even animals can create moss balls. In the Dutch wetland forest, it is foraging pheasants that turn the mosses upside down and initiate the upward growth that creates the ball (Wiegers 1983). Although ***Dicranum scoparium*** (Figure 19) and ***Mnium hornum*** (Figure 40) formed such balls, other upturned wetland taxa did not.

Adaptive Significance

Often the life form is a passive response to exposure; any protruding individual is more subject to desiccation and hence has a shorter period in which to be active for photosynthesis, thus reducing its growth rate below that of its shorter but hydrated neighbors. Although this is more commonly known in cushions, Perez (1991) found that the same phenomenon occurs in moss balls of ***Grimmia longirostris*** (Figure 32) in the Venezuelan Andes. This spherical life form holds more water than the soil, and larger balls hold more than small ones. In some cases, the form may be modified to accommodate the capture of cloud water or to avoid photoinhibition.

Figure 40. ***Mnium hornum*** forming cushion that could become a ball. Photo by Stepan Koval, with permission.

Mägdefrau (1935) found a clear relationship between life form and type of conduction. Dense tufts increase conduction, but there is considerable humidity difference within the tuft that suggests an important role in water retention (Zacherl 1956). When the air humidity is only 50% a few cm above the tuft, it can be as much as 90% within the tuft. Larger volumes are able to store more water, and volume increases more rapidly than surface area. Larger cushions have a greater volume of water per unit of surface area, thus losing less to evaporation than small cushions with a thinner boundary layer and greater proportion of surface area (Proctor 2000). Zotz *et al*. (2000) used ***Grimmia pulvinata*** (Figure 41) to demonstrate that the greater the size of the cushion, the more resistance it had to water loss. This size increase had no effect on the water-holding capacity on a dry mass basis, and the combination of these two factors contributed significantly to the length of the hydration period.

Figure 41. ***Grimmia pulvinata*** from southern Europe. Photo by Michael Lüth, with permission.

The cushion growth form (Figure 42) is important in decreasing the loss of water by reducing the turbulence of airflow (Figure 15). At low and even moderate wind speeds, the evaporative water loss from the cushion mimics that of a flat or rounded surface of the same area (Proctor

1984). This form is reminiscent of the tundra formations, where the cushions of seed plants not only impart resistance to moisture loss, but facilitate warming and protect from wind damage. The cushion shape presents a boundary layer that resists loss of moisture and permits wind to cross the plants with a minimum of disruption. Proctor (1979, 1980, 1982) found that the resistance to water loss extends the period of active metabolism after the precipitation stops. Nobuhara (1979) showed that ***Bryum argenteum*** (Figure 43) increased its water-holding capacity as the volume increased, with more than 100 shoots reducing the water loss to something very small.

Figure 42. ***Leucobryum glaucum*** cushions. Photo by Janice Glime.

Figure 43. ***Bryum argenteum*** in a large clump that helps to conserve water. Photo by Janice Glime.

The wind also can play a role in the formation of the cushion. As a branch, whether moss or tracheophyte, grows above the cushion, drying and wind action slow its growth and may even damage the terminal bud. Proctor (1980) demonstrated that when such surface irregularities reach the thickness of the boundary layer, there is a rapid increase in water loss at higher wind speeds. Thus, when a branch extends beyond the cushion, the other branches can catch up with it in growth before it is able to regain hydration and resume its growth, and if the terminal bud has been damaged, that growth may never occur.

Lewis Smith (1988) described the ability of dense turfs of ***Schistidium antarcticum*** (Figure 44) to hold strongly to their water content, but that the less densely packed shoots of cushions in xeric conditions could not maintain as high a water content as the turfs. Longton (1979a, b) drew a similar conclusion, noting that in Antarctica the plant size decreases as the shoot density increases; the shorter, more compact growth form could be adaptive to the cold, relatively dry habitats.

Birse (1957) found that in some cases the growth form of certain species of bryophytes is almost invariable, whereas in others variation occurs according to the conditions of the habitat. Birse (1958a), reported that as long as there was a constant ground water supply, a variety of growth forms could flourish, especially tall turf and dendroid forms. In the absence of ground-water supply, short turfs, round mats, and one dendroid species (***Climacium dendroides***, Figure 45) were the only forms to survive.

Figure 44. Growth of ***Schistidium antarcticum*** on Macquarie Island in the Antarctic. **Top:** The dense and well-hydrated turf surrounds ***Ceratodon purpureus*** growing in the crevices. **Bottom:** The uneven turf has exposed tops exhibiting dehydration. Photos courtesy of Rod Seppelt.

Figure 45. ***Climacium dendroides***, showing dendroid growth form. Photo by Michael Lüth, with permission.

For endohydric mosses, growth form is important in water retention. Longton (1979a) found variations in the

seasonal growth patterns of ***Hypnum cupressiforme***, and was able to relate these to water supply. Gimingham and Birse (1957) related growth form response to decreasing levels of moisture:

Relationship of Growth Form to Moisture

high moisture
dendroid & thalloid mats
rough mats
smooth mats
short turfs & cushions
low moisture

Dendroid mosses would seem to be particularly vulnerable to desiccation, with only a single stem in contact with the substrate and many exposed branches. Lorch (1931) found a correlation between the development of the central strand and the degree of branching, whereas the rhizome central strand became less developed, suggesting a greater importance for aerial water sources over soil sources as branching increased. Trachtenberg and Zamski (1979) supported these findings, re-affirming the importance of water absorption through the whole surface of the gametophyte and the utility of **apoplastic** transport.

Sollows and coworkers (2001) concluded that the colonial growth form of the leafy liverwort ***Bazzania trilobata*** (*i.e.* having branches lying on top of other branches; Figure 46) protected at least some inner shoots from the extreme exposures they experienced following clearcutting, avoiding the extinction of net photosynthesis observed in laboratory experiments following dehydration for 1-12 days. Likewise, it is likely that the overlapping leaves of this species afford additional water retention by creating capillary spaces.

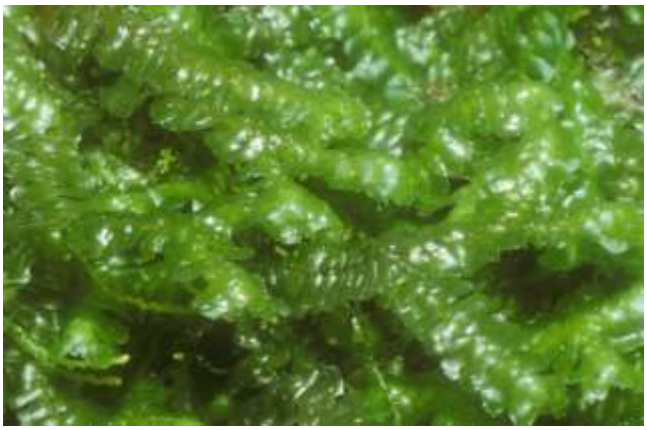

Figure 46. ***Bazzania trilobata***, illustrating the overlapping nature of the branches and leaves. Photo by Janice Glime.

Nakatsubo (1994) compared growth forms in the subalpine region in Japan and found that xeric species were indeed often **large cushions**, as well as **compact mats**. Mesophytic species, on the other hand, comprised **smooth mats**, **wefts**, and **tall turfs** on the coniferous forest floor. He demonstrated that the evaporative rate per dry mass was indeed much less in the xerophytic cushions and compact mats than in the mesophytic forms. While the evaporative rate and dry mass were closely correlated with the growth form, the evaporative rate per basal area was not necessarily smaller in xerophytic taxa.

Matteri and Schiavone (1988) demonstrated that some taxa, *e.g.* ***Polytrichastrum longisetum*** and to a lesser extent ***Bryum macrophyllum***, conserve their growth form but exhibit different life forms under different ecological conditions. During (1979) likewise related the growth form to the habitat. He found that ***Campylopus flexuosus***, ***Orthodicranum montanum***, and several other taxa form large turfs with almost no vegetative reproduction when living in moist, undisturbed environments, but when found in dry forests they consist almost entirely of dense cushions of easily detached branchlets.

But what empirical evidence do we have that the various growth forms and life forms actually afford any moisture advantage? Hanslin and coworkers (2001) demonstrated that increased shoot density of ***Dicranum majus*** (Figure 47) and ***Rhytidiadelphus loreus*** (Figure 48) actually had a negative effect on relative growth rate and green biomass, but that these were optimal at intermediate shoot densities in conditions of low relative humidity. It is likely that these species suffered a trade-off between light availability and moisture advantage at higher densities. In contrast, Bates (1988) found that ***Rhytidiadelphus triquetrus*** (Figure 49-Figure 50), likewise a boreal moss, had optimal growth when the colonies were most dense (1000 shoots dm^{-2}) (Figure 50). Apparently in this case the dense packing of the shoots gives the advantage of reduced water loss and outweighs the disadvantage of reduced irradiance.

Figure 47. ***Dicranum majus***, illustrating the dense colony that can reduce growth rate. Photo by David Holyoak, with permission.

Figure 48. ***Rhytidiadelphus loreus***, a species that benefits from the moisture of dense clumps but grows less. Photo by Malcolm Storey <www.discoverlife.org>, with online permission.

Figure 49. ***Rhytidiadelphus triquetrus*** demonstrating loose and dry plants. Photo courtesy of Eric Schneider.

Figure 50. ***Rhytidiadelphus triquetrus*** demonstrating dense and moist plants. Photo by Janice Glime.

Habitat Relationships

Certain growth forms seem to fare best in certain kinds of habitats (Proctor 1990). In the absence of direct physiological evidence, we can use the observed field relationships to form hypotheses concerning the best life form strategies.

Deciduous Woodlands

Proctor (1990) suggests that **large size** and **rapid growth** are important for woodland and grassland bryophytes to permit them to grow above the litter and surrounding vegetation. This life form permits them the competitive life strategy. Moist, shady habitats are more favorable for **smooth mats** and **small cushions**, but larger taxa occur as well, taking advantage of nutrients in throughfall and exposing more surface area for photosynthesis. In her study of British deciduous woodlands, Birse (1958b) found that **wefts** and **mats** predominated, responding primarily to light as a determinant of abundance.

In humid, montane **tropical** forests, **pendant** and **fan** forms provide the most surface area for interception of the limited light without sacrificing moisture in this humid climate (Proctor 1990). Furthermore, they are able to trap water from mist and clouds. However, the great exposure makes them vulnerable to air pollution.

Pine Woods

Using Proctor's principles as a guideline, then what should we expect in a pine forest where leaf litter is a minimal problem? Seim *et al*. (1955) examined a Jack pine forest (*Pinus banksiana*) in Itasca Park, Minnesota, USA, and found **wefts** and **mats** as the predominant growth forms, with **cushions** and **turfs** comprising most of the remaining taxa. Gimingham and Robertson (1950) likewise found predominately wefts in Northern Britain. However, in another study, Moul and Buell (1955) found the turf type to be predominant (84%) in a sandy coastal pine woods of New Jersey, as did Hamilton (1953) in the hills of central New Jersey, USA. In alpine regions of Japan, Nakatsubo (1994) found that mesophytic species consisted of **smooth mats**, **wefts**, and **tall turfs** on the coniferous forest floor.

Epiphytes

Horikawa and Nakanishi (1954) developed a key to the "growth" (actually life) forms of Japanese epiphytic bryophytes. In it they included **small cushion**, **large cushion**, **turf**, **fascicular** & **shrubby**, **dendroid**, **simple feather**, **branching feather**, **mat**, **carpet**, **hardly pressed mat**, **loosely pressed mat**, **epiphyllous**, **pendulous**. They pointed out that species will vary with growing conditions, causing the same species to be assigned to more than one type.

Peatlands

Some terrestrial and peatland bryophytes may solve the CO_2 problem by a cushion or other dense growth form (*e.g.* ***Sphagnum***) that provides CO_2 mostly from their own transpiration stream. In fact, ***Sphagnum*** seems to take advantage of CO_2 rising from deep in the peat, bringing up carbon stored there 1000 or more years earlier. Perhaps there is some advantage to having your living parts sitting on top of your dead parts!

Aquatic

Aquatic mosses such as ***Drepanocladus vernicosus*** rely on a water medium when submersed but benefit from close contact when emergent (Frahm 1978). Aquatic bryophytes are most constrained by CO_2. The **mat** form of ***Nardia compressa*** (Figure 51) and ***Scapania undulata*** (Figure 52) is beneficial in water below 0.1 m s^{-1} where its leaf-area index permits it to exploit the low boundary-layer resistance of high velocities without incurring a high drag. On the other hand, the **streamer** form of ***Fontinalis*** (Figure 13h) provides the most exposure (maximum surface area) in relatively quiet water of less than 0.01 m s^{-1} where boundary-layer resistance is high. Nevertheless, ***Fontinalis***, with the same streamer life form, occurs in very rapid and turbulent water of mountain streams. Perhaps the turbulence itself permits enough CO_2 to mix with the water for the moss to take advantage of its greater surface area.

In the Antarctic, aquatic mosses showed the greatest plasticity when submerged compared to being grown in the air (Priddle 1979). ***Warnstorfia sarmentosa*** (as ***Calliergon sarmentosum***; Figure 53) grew longer stems (longer internodes) and larger leaves in the water, whereas ***Sanionia uncinata*** (Figure 54) varied little from its terrestrial form.

Figure 51. ***Nardia compressa***, a leafy liverwort with a mat growth form that reduces drag of high water velocity. Photo by Jan-Peter Frahm, with permission.

Figure 52. ***Scapania undulata*** showing flattened branches and leaves that reduce the drag of rapid flow. Photo by Michael Lüth, with permission.

Figure 53. ***Warnstorfia sarmentosa*** exhibiting short leaves and internodes in its exposed position above the water. Photo by David Holyoak, with permission.

Figure 54. ***Sanionia uncinata*** forming a thick mat. Photo by Michael Lüth, with permission.

Deserts

It is significant that Frahm (1978) found only 9% of the bryophyte flora of the Sahara to be pleurocarpous. In the moist boreal forest, pleurocarpous is the dominant form. Pleurocarpous mosses expose much more surface area to the drying atmosphere; rather, in the dry desert, **small cushions** and **wefts** (loosely interwoven, ascending shoots capable of growing out of the sand are better adapted to the dry and shifting substrate.

Polar Regions

Longton (1979b, 1982) followed the life forms that Gimingham and Birse (1957) attributed to the polar regions in attempting to compare the Antarctic to other polar areas. He considered four Arctic bryophyte habitats: wetlands, mesic communities, polar deserts, and bryophyte-dominated habitats. He considered wetlands to be dominated by the **tall turf** life form, with lesser representation of **short turfs** such as ***Seligeria polaris*** (Figure 55) on small stones.

Figure 55. ***Seligeria polaris***, small, short turf moss on a pebble. Photo by Dale Vitt, with permission.

Mesic communities had a wider range of life forms than the wetlands, but the **tall turf** was still a dominant, with **short turfs** and **mat-forming** species also among the dominants. Although Longton (1979b) recognized five

habitat types among the mesic communities, these forms were generally common among all five mesic communities. However, in Iceland, the **weft** community joined the **tall turf** in prominence, along with mats of leafy liverworts. Furthermore, the birch woods there had abundant weft mosses.

Gimingham and Smith (1971) showed that the ***Polytrichum strictum*** (Figure 56) and ***Polytrichastrum alpinum*** (Figure 57) turfs lost water more slowly than ***Chorisodontium aciphyllum*** (Figure 58-Figure 59) and ***Sanionia uncinata*** in the same habitats, attributing this to the waxy cuticle on the former two. That ***P. alpinum*** loses only about 10% of its water when centrifuged suggests that most of its water is held internally compared to the 20% lost from ***Chorisodontium aciphyllum***.

Figure 56. ***Polytrichum strictum*** forming cushions in Alaska; this species has a waxy cuticle that helps to maintain moisture. Photo by Andres Baron Lopez.

Figure 57. ***Polytrichastrum alpinum***, a species in which surface wax helps to keep it hydrated. Photo by Europe 3 Michael Lüth, with permission.

Figure 58. ***Chorisodontium aciphyllum*** in Antarctica. Photo from Polar Institute through Creative Commons.

Figure 59. ***Chorisodontium aciphyllum*** in the Antarctic, a species that loses water more rapidly than its waxy counterparts.. Photo by Zicheng Yu through Public Domain.

The dry polar desert fellfields have **cushions** of both mosses and flowering plants, but other open areas have compact forms such as **mats**, **carpets**, and **short turfs** (Longton 1979b).

The bryophyte-dominated communities are those unsuitable for most tracheophytes (Longton 1979b). These include boulders, cliffs, musk ox dung, and hollows where snowmelt is late. The latter supports **large cushions** and **tall turfs** with small flowering plants rooted among them. The **liverwort *Anthelia juratzkana*** (Figure 60) is common here. **Small cushions** form on boulders, cliffs, and other rocky habitats. Rock crevices harbor **small mats** and **turfs**. **Large cushions** form on stony and marshy ground near permanent rivers and streams, with few bryophytes in the streams themselves. Where bryophytes do occupy streams, they are mostly **streamers** and **mats**.

Figure 60. Leafy liverwort, ***Anthelia juratzkana***, forming black mounds on the soil surface. Photo by Michael Lüth, with permission.

The most unique of the polar habitats are those enriched with nitrogen by animal dung that support dense communities of dung mosses (**Splachnaceae**). Bird perches and lemming burrows support short turfs of acrocarpous mosses (Longton 1979b). Soil fractures between the polygons (Figure 61) support short turfs of cosmopolitan taxa such as ***Bryum argenteum*** (Figure 43), ***Ceratodon purpureus*** (Figure 44), ***Funaria hygrometrica*** (Figure 62), and ***Marchantia polymorpha*** (Figure 63).

Figure 61. Tundra polygons from freeze-thaw cycles showing bryophytes in the lower areas. Photo by Spencer & Carole, through Creative Commons.

Figure 62. ***Funaria hygrometrica***, a species that in the polar regions can live in the fractures between soil polygons. Photo by Kurt Stueber, through Creative Commons.

Figure 63. ***Marchantia polymorpha***, a species that succeeds in the fractures between Arctic polygons. Image copyright by Stuart Dunlop <www.donegal-wildlife.blogspot.com>, with permission.

Racomitrium lanuginosum (Figure 33) forms extensive heaths resembling very large cushions in areas where it can gain water from the saturated atmosphere (Figure 34) (Longton 1979b). In areas with frequent precipitation as well as mist, ***Sanionia uncinata*** (Figure 54) forms moderately thick mats.

In the Antarctic, stones and gravel of nearly level ground support short turfs and cushions (Longton 1979b). In addition to these, calcareous substrata may have mats. Rock crevices have short turfs, small cushions, and mats.

Alpine

Alpine habitats seem to support mosses that resemble miniature tracheophyte growth forms. **Cushions** are common, but also **carpets** cover the dirt and provide protection from erosion. In studying the Ukrainian Carpathian Mountain alpine region, Ulychna (1970) included, in addition to these, bunches, dendroid, and interlacements, the latter two primarily in the transition into forest.

Studies Needed

While these growth and life form relationships to habitat seem to be well supported by field studies of species present, there has been little attempt to demonstrate that the proposed water relationships actually benefit the bryophytes. Transplant experiments need to be performed that compare the water loss of the various forms in a range of habitats, as well as their survival in this adult form without the need for surviving an establishment stage.

Summary

Growth forms are those genetically controlled characteristics of plants that determine their shape. These are manifest as **acrocarpous** with terminal perichaetia (including **protonema mosses** and **turf mosses**), **pleurocarpous** (**plagiotropic**, including **thread mosses**, **comb mosses**, and **creeping-shoot mosses**) with lateral perichaetia, **cladocarpous** with perichaetia terminal on lateral branches. **Life forms** encompass overall organization of growth form, branching pattern, general assemblage of individuals, and modification of a population by the environment.

The most widely used classification of **life forms** includes **annuals**, **short turfs**, **tall turfs**, **cushions**, **mats**, **wefts**, **pendants**, **tails**, **fans**, **dendroids**, and **streamers**. These can be subdivided, and a few others may exist in less well known habitats.

Growth forms and life forms of plants can aid in water retention by **reducing air resistance**, **increasing boundary layer thickness**, **providing capillary spaces**, and **protecting each other**. Thalloid forms protect one side of the plant at the expense of the other, but cuticular substances reduce the loss on the exposed side. Open growth forms (*e.g.* dendroid, rough mat, pendant) are more subject to water loss than compact, tight ones (*e.g.* smooth mat, short turf, cushion). The **cushion** form is able to provide the least surface exposure per unit of biomass and apparently has the lowest water loss rate. Conduction forms seem to

correlate with growth forms, with dense turfs increasing conduction as well as water retention.

Cushions and **moss balls** are formed as exposed shoots are broken off by force of wind, abrasion, and desiccation. Moss balls generally have a pebble at the center and arise in areas of wave action, wind on ice, solifluction (possibly), or other physical factors that tumble the moss.

Deciduous forests require large size and rapid growth such as wefts and mats to obtain enough light and avoid burial by litter. **Humid forests** support pendants and fans that can get moisture from fog and mist. **Pine forests** have wefts and mats, but also cushions, turfs, and smooth mats. **Epiphytes** include mostly appressed taxa such as smooth mats and small cushions, but a variety of other forms are possible in sufficient moisture. **Peatlands** take advantage of density to conserve moisture. **Aquatic** bryophytes are limited by availability of CO_2 and reduce the boundary layer resistance with **mats** or increase surface area with **streamers**. **Desert** mosses conserve water with small cushions and wefts. **Polar regions** support a variety of forms, depending on the habitat, with cushions predominating in habitats where tracheophytes also form cushions; turfs are common. **Alpine** bryophytes also benefit from the cushion form.

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CHAPTER 4-6

ADAPTIVE STRATEGIES: LIFE CYCLES

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CHAPTER 4-6

ADAPTIVE STRATEGIES: LIFE CYCLES

Figure 1. Strap-shaped leaves of males and capsules with perichaetial leaves of females of the dioicous moss *Diphyscium foliosum.* Photo by Michael Lüth, with permission.

Life Strategies

By now it must be obvious to you that to understand the life strategies of bryophytes, one must first understand the life cycle (*e.g.* Figure 1). Frahm and Klaus (2001) state that bryophytes are able to react quickly to such events as climatic fluctuations because of their short life cycle and ease of dispersal by spores. It is likely that when all other plant life has perished from some Earth catastrophe, it will be the bryophytes that persist, surviving as spores or other propagules until conditions return to safety and once again surrounding the earth due to their ability to travel great distances as "dust."

By definition, the life cycle includes reproduction. However, even such a widely used term has ambiguities. In bryophytes, we shall use this term to refer not only to the sexual reproduction that results from union of sperm and egg (ultimately resulting in spores produced by meiosis), but also to the multitude of **asexual** (vegetative) means by which bryophytes are able to make more, physiologically independent plants (Mishler 1988). This definition separates reproduction, which can permit relocation, from growth, which implies the increase in size of a physiological individual (Söderström 1994). On the other hand, growth can ultimately result in reproduction, as is the case when the plant branches and is physiologically connected, but later the branches separate and become physiologically independent. As you can see in Figure 2, the degree of reproduction by propagules depends on habitat. Among British habitats, short-lived habitats (wood, bark, farmland, dung) have the highest degree of propagular reproduction (that is, by vegetative means) (Herben 1994). On the other hand, the habitats with the greatest percent of the species are in the middle of the range of propagules.

Using the principle that extreme conditions might provide the best test of the limits of an organism, we learn that in the maritime Antarctic, bryophytes seem to have enhanced sexual reproduction (Lewis Smith & Convey 2002). This is contrary to the generally accepted belief that bryophyte fertility decreases toward the poles. Rather, 43% of the bryophytes (19 species) in Marguerite Bay and

47% of those on Alexander Island are known to produce capsules. But Lewis Smith and Convey attribute this to favorable microclimatic conditions. Nevertheless, in this extreme environment, the large majority of mosses with capsules were short, monoicous, acrocarpous taxa, suggesting that the predominance of dioicous taxa in more temperate climates may be possible because the environment is less stressful. In the more extreme environments of the Antarctic continent, the numbers of species producing capsules at similar latitudes (68-72°S) are much less (33%).

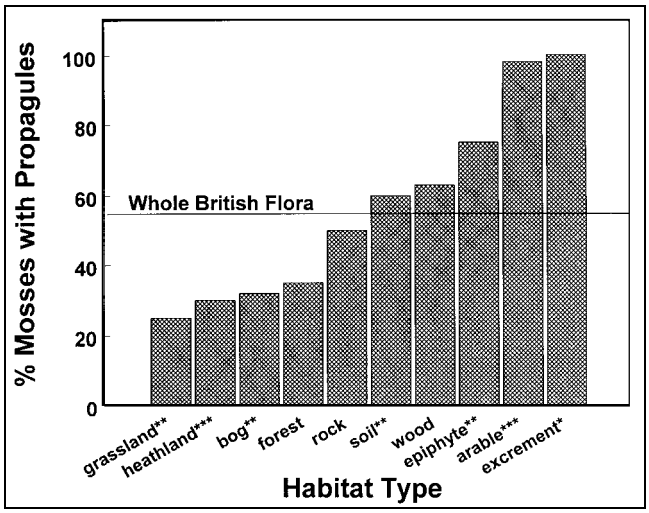

Figure 2. The percent of mosses that form spores or gemmae frequently or commonly in selected habitats of Great Britain. Asterisks indicate degree of significance (Chi-square test) when compared to the whole moss flora of Great Britain (* = P<.05, **=P<.01, ***=P<.001). Redrawn from Herben (1994), based on data from Smith (1978).

Although life cycle strategies are obviously important, especially in extreme habitats, life forms and growth forms may be more important. During and Lloret (1996) found that within individual sites in Spain, species with the same life strategy exhibited similar patterns, and that between locations, growth forms differed more than life cycle strategies.

Clonal Growth

At the mature end of the gametophytic cycle, bryophytes can form masses of related individuals, or clones. **Clones** can be defined as groups of individual plants created by fragmentation, viviparous bulbils, or apomictic seeds (Callaghan *et al.* 1992), whereas if gene flow is present the groups of plants are called **populations** (Harper 1977). In other words, clones have the same genetic makeup as the plant from which they were derived. In addition to these tracheophytic means, bryophytes create clones through multiple buds on the protonemata. But, as already discussed, somatic mutations render even these "clonal" derivations to be variable in genetic makeup.

Callaghan, *et al.* (1992) attribute to clonal growth the ability to sequester space and increase fitness of the populations. Among the benefits are persistence; spread of development and reproduction over time and environmental conditions; risk-spreading between **ramets** (individual members of clone) of the same type, thus increasing chances for survival of the genotype; protection of disadvantaged ramets that might later survive in the face of adversity; increased precision with the sequestering of space and dispersal of ramets; ability to monopolize resources for the benefit of the genotype. They furthermore include mobility, but I question whether this is much of a gain when compared to the alternative of wider distribution of propagules away from the parent.

One possibility that has barely been explored is the increase of genetic variability through production of these haploid genets. We had long assumed that the limited morphological development of the Bryophyta and Marchantiophyta reflected a limited genetic diversity, a case to be expected when the dominant generation is haploid and asexual reproduction is common. However, contrary to our expectations, moss populations are characterized by a high degree of isozyme variation, as shown for ***Ceratodon purpureus*** (Figure 3) (Shaw & Beer 1999). Cultivation of spores from one specimen of ***Drepanocladus*** (*Warnstorfia*) ***trichophyllus*** produced four distinguishably different morphologies (Sonesson 1966).

Figure 3. Color and leaf shapes of *Ceratodon purpureus*. **Top:** Green, broad leaf, hydrated form, **Middle:** Green, lanceolate leaf, hydrated form. **Lower:** Reddish dry form with capsules. Photos by Michael Lüth, with permission.

Velde and coworkers (2001) addressed this question of genetics of clonal relationships in ***Polytrichastrum formosum***. They determined that identical genotypes between spatially separated shoots were almost never present, whereas identical genotypes among **genets** (branching of gametophytes resulting from clonal growth of rhizomes) was extensive. However, this view of the genet has some problems. Scrosati (2002) pointed out that somatic mutations are predictably common, giving rise to genetic mosaics within any connected genet. To deal with this lack of genetic homogeneity, Scrosati suggested that **genet** should be defined as a "free-living individual that develops from one original zygote, parthenogenetic gamete, or spore and that produces ramets vegetatively during growth." Nevertheless, it appears that even in adjacent populations of spore-producing plants, genetic variation is minor. In another example, populations of ***Funaria hygrometrica*** (Figure 4) growing in close proximity on contaminated tailings of a copper mine displayed very low levels of genetic variability, but had extensive morphological plasticity (Shaw & Bartow 1992).

Figure 4. Crowded ***Funaria hygrometrica*** with its abundant capsules. Photo by Michael Lüth, with permission.

During and van Tooren (1987) attempted to explain this paradox of genetic diversity in vegetatively reproducing taxa. Referring to earlier views of bryophytes as evolutionary failures, they contended that bryophytes in fact have high genetic variability, yet maintain their populations almost entirely by asexual means. They suggest that even though sexual reproduction, when it occurs, results in huge numbers of spores, establishment from spores in the field seems to be very difficult. Rather, they suggest that "remarkably rapid fine-scale dynamics" of many bryophyte populations may account for their ability to maintain a high degree of genetic variability.

Itouga and coworkers (1999) provide data on genetic variability in the liverwort ***Conocephalum japonicum***. They consider both the species and populations to have low genetic diversity values of **Hes** (species genetic diversity) = 0.008 and mean **Hep** (population genetic diversity) = 0.008±0.003. Between populations diversity was likewise low with **Gst** (coefficient of genetic differentiation) = 0.062. They used this low diversity as an indication that reproduction by gemmae predominated over sexual reproduction by spores.

Velde and coworkers (2001) considered this strategy of producing clonal genets to be one that provided increased longevity for the genet that accompanies increased reproductive capacity. Nevertheless, they showed that male reproductive success in ***Polytrichastrum formosum*** is determined primarily on spatial distance from females. In fact, these populations achieved their success primarily through sexual reproduction, facilitated by the ability of sperm to disperse to distances measured in meters rather than mm or cm.

Foraging and Sharing

The reproductive advantages of ramets may be enhanced by other advantages found more recently, at least in tracheophytes. In seed plants, the ability to relocate photosynthate from plant parts in the light to shaded parts has been demonstrated (Kemball *et al.* 1992), while other plants are able to translocate resources through rhizomes and roots (Landa *et al.* 1992). This permits the ramets to take advantage of flashes of sunlight called **sunflecks**, and horizontal growth that permits such advantages has been termed **foraging** (Bates 1998). Ramets furthermore may have seasonal advantages as different parts become exposed to light at different times of the year. Even nutrient and moisture advantages may accrue if part of the plant receives sunlight while another part extends into moister or more nutrient-rich soil. Even in simpler plants like lycopods (*Diphasiastrum flabelliforme*), Lau and Young (1988) demonstrated that ramets that had been severed from their connecting ramets experienced 50% more mortality than unsevered ramets. Those ramets connected to shaded ramets were able to maintain higher water potentials, giving them the ability to take advantage of the sun in one ramet while maintaining high water potential through that supplied by another ramet.

In bryophytes, as in tracheophytes, we can expect advantages to the clonal habit. Living where their parents have lived increases the probability that the habitat is suitable, thus reducing wastage of propagules. A greater area of soil and atmospheric water is contacted by a clone, in some cases permitting a greater nutrient capture and the opportunity to provide needed water and nutrients to the growing tip. However, the ability to transport hormones, nutrients, and photosynthate is known for so few examples of bryophytes that we cannot generalize these benefits. In some tracheophytes, leaves on different parts of the plant and within the clone differ in morphology, permitting different environmental conditions to favor them. Such differentiation may be possible on rhizomatous taxa such as ***Climacium***, and some leafy liverworts exhibit different leaf morphologies on the same branch (*e.g.* ***Lophocolea heterophylla***, Figure 5), but no systematic investigation has explored this as a possible clonal advantage.

Figure 5. Heteromorphic leaves of ***Lophocolea heterophylla***. Compare the two leaves indicated by arrows. Photo by Janice Glime.

If indeed clonal transport such as that demonstrated in tracheophytes is possible in most bryophytes, nutrients could move internally from favorably placed ramets to those in less favorable positions in a patchy environment, benefitting the bryophytes in a competitive environment (Bates 1998). Bergamini and Peintinger (2002) likewise compared the bryophytes to tracheophytes, suggesting that their overall morphological responses to the differences in light levels approximated that of tracheophytes with stolons – a "spacer and branching strategy." But does this ability to share with less favorably placed ramets only work for bryophytes with internal conduction? Eckstein and Karlsson (1999) tested this hypothesis by comparing the movement of nitrogen in ***Polytrichum commune***, with well-developed internal conduction, with that of ***Hylocomium splendens***, with predominantly external conduction. Indeed, the labelled nitrogen pool in ***Hylocomium splendens*** moved from older segments to younger segments. In ***Polytrichum commune***, it disappeared from younger segments in autumn, presumably going to underground storage organs. Both of these examples support the hypothesis that ramets can provide sources of translocatable substances from one part of the clone to another, but we have few studies to permit us to assess the extent of this phenomenon among bryophytes, nor does this explicitly demonstrate the transfer from one ramet to another less favorably positioned. And could gametophytes such as those in Figure 6 transfer substances from one gametophore to another through the protonema?

Figure 6. Circular growth pattern of gametophores developing from a single spore of ***Funaria hygrometrica***. Photo by Janice Glime.

There need be no internal conduction to foster other types of advantages, however. For example, ***Sphagnum magellanicum*** is able to keep its neighbors moist through its efficient external conduction, and cushion mosses like ***Leucobryum*** (Figure 7) conserve moisture by growing in dense clones.

Implications for Reproduction

Perhaps there is a division of labor that provides a reproductive advantage among ramets of a clone that is independent of type of translocation. Stark *et al.* (2001) found that in the desert moss ***Syntrichia caninervis*** more mature ramets with larger size were more likely to reproduce than the smaller ramets, suggesting a division of labor that permitted smaller plants to conserve energy until they achieved a greater size. While this may be simply a function of age, it would permit the colony to have multiple reproductive strategies simultaneously, with larger ones reproducing sexually and smaller ones using only fragments or vegetative propagules.

Figure 7. Cushion of ***Leucobryum glaucum***. Photo by Janice Glime.

Many of the modes of reproduction of bryophytes result in clonal growth. Rarely does one see just a single bryophyte stem. Rather, clumps, cushions, tufts, mats, any number of growth forms, suggest that these are all siblings of an original single parent. In fact, even if only a single spore lands on the rock or soil, many plants arise, at least in mosses. The spore produces a protonema that branches, and in the case of the filamentous protonemata, the numerous branches can give rise to numerous upright gametophores. Knoop (1984) identifies two types of gametophore origin: ***Funaria*** type (Figure 6), developing gametophores on the caulonema only in a circular fashion around the spore; ***Polytrichum*** type, developing few gametophores near the germinated spore or even from the spore cell itself (Sood & Chopra 1973, Nehlsen 1979). Both result in several to many gametophores.

In ***Sphagnum*** a single spore produces a small thalloid protonema that gives rise to only one gametophore, thus resulting in populations when more than one spore germinates, and making one uncertain in any given clump of ***Sphagnum*** whether the clump is a clone derived from apical branching or a population derived from separate spores. However, if one considers that the branching of the **capitulum** contributes to a major portion of the mat growth, then, again, clonal behavior is at work. Furthermore, spores are likely to land on their own parents or siblings or cousins of the parent, and thus not be far removed from clonal relatedness.

Even gemmae can form circular arrangements of gametophores, as reported by Chopra and Rawat (1977) for ***Bryum***, or other arrangements of numerous gametophores, as in ***Physcomitrium sphaericum*** (Figure 8; Yoshida & Yamamoto 1982). Since these have arisen from one parent, they likewise produce clones. In ***Bryum bicolor***, numerous tubers and gemmae are produced early in the growth of the gametophore, permitting it to build up a large clone (Joenje & During 1977).

Density Effects

Colony density has varying effects on moss success. In ectohydric mosses, it is more likely that density will favor success and increase growth (During 1990; Økland & Økland 1996). But in ***Sphagnum*** (Clymo 1970) and ***Rhytidiadelphus triquetrus*** (Bates 1988) density is

detrimental to both branching and growth. Shoot mortality can increase, as in **Polytrichaceae** (Watson 1979), or decrease, as in ***Tetraphis pellucida*** (Kimmerer 1991), with density. Almost nothing is known of density effects on liverworts; Laaka-Lindberg (1999) showed that density had no effect on gemma production.

Figure 8. Clone of *Physcomitrium sphaericum*. Photo by Michael Lüth, with permission.

On the other hand, Kimmerer (1991), found that density was an important factor in asexual vs sexual expression in the acrocarpous ***Tetraphis pellucida*** (Figure 9). Gemmae were common in low-density colonies and the sex ratio was female-biased. High-density colonies, on the other hand, were more likely to have sexual reproduction and a greater proportion of males. She pointed out the advantage of this plastic strategy in unstable environments such as the rotting stump habitat of ***Tetraphis pellucida***, permitting the plants to expand by gemmae when the colony was not dense.

Figure 9. ***Tetraphis pellucida***. **Upper:** Uncrowded plants with gemmae on tips. **Lower:** Dense patch of plants with sporophytes. Photos by Michael Lüth, with permission.

Tradeoffs

Traditional life history theory holds that "maximizing reproductive value at each age is equivalent to maximizing fitness" (DeRidder & Dhondt 1992). However, in bryophytes, as in many species of seed plants, there is a negative correlation between sexual reproduction and asexual reproduction (Caswell 1985). On the other hand, in the clonal insectivorous flowering plant ***Drosera intermedia***, DeRidder (1990) found only limited evidence of a tradeoff between the two types of reproduction. DeRidder and Dhondt (1992) suggest that traditional theory may apply to the clonal ***D. intermedia***, whereas in many clonal species, it is an inappropriate theory because it was based on organisms (vertebrates) with only one mode of reproduction.

Ramets of one taxon, all from the same spore, seemingly competing for space and resources, seems like a maladaptive thing to do. However, the old safety in numbers adage may apply here. Multiple stems are less likely to dry out than a single plant. The colony can acquire a cushion shape as the middle members grow better due to moisture held by their neighbors. The edge members are slowed because if they too grow like the middle members, they are left with no protection from drought on the outer side. Hence, the adventurous stem that grows a bit taller is soon stopped by lack of moisture, and those on the edge are slowed the most because they lack a similar tall plant on the outside to protect them. For tracheophytes, Price and Hutchings (1992) also consider design constraints that limit vascular connections between some ramets, a consequence that should not be a problem for the ectohydric bryophytes. Could this, however, reduce the advantages for **endohydric** bryophytes, *i.e.* those relying significantly on internal conduction?

Perhaps one of the greatest benefits to ramets from a single spore of monoicous bryophyte taxa is availability of the opposite sex. Since in many cases, the male and female gametangia don't mature at exactly the same time on the same individual, gametangia of a neighbor are more likely to be receptive than other gametangia on the same plant. Such an opportunity is not so important to the tracheophytes because of their dependence on external pollinators that can readily visit nearby clumps of a different clone. Nevertheless, for the bryophytes, concomitant with the advantages of having nearby sexual partners are the tradeoffs in disadvantages of marrying your twin, in particular the loss of genetic diversity.

Like the tracheophytes, bryophytes must pay a price for the clonal habit. The advantage of being able to respond rapidly to environmental change is unlikely for the slow-growing bryophytes. Reduced recruitment from spores will make the clonal bryophytes vulnerable to permanent changes in the environment, and the connectedness makes the entire clone vulnerable to disturbance (*cf.* tracheophytes, Callaghan *et al.* 1992). The longevity of the clump in habitats like the Arctic make the probability of frost heave damage an eventuality in some habitats. Mosses seem less likely than tracheophytes to reap benefits from having only part of the clone disturbed. If part of a cushion is removed, the entire cushion is likely to dry out, whereas an intact cushion is able to keep its interior moist under most circumstances. In most cases, spread by spores in less clonal species may be a better

strategy, particularly for those that require fresh soil in open, disturbed areas. Thus, as their habitat changes, they have the means to move on to other suitable areas.

The trade-offs and benefits of clonal growth, contributing to increased bryophyte density, are hard to assess. The overwhelming presence of clonal growth suggests that it has its advantages for bryophytes, perhaps almost completely in the greater moisture retention.

r & K Strategies

Life cycles are basic to the survival of a species. Those that are annuals must usually survive the winter as spores. Those that are perennial must have other ways to survive the cold of winter. Still others may live where it is a dry season, not winter, that must be reckoned with. These differences in seasonal stresses are generally met by differences in life strategies.

Ramensky (1938) described three types of outcomes to the differences in life strategies as **violents** (aggressive species), **patients** (tolerant species), and **explerents** (non-competitive species that fill the spaces between others). Rabotnov (1975) added **pioneers** (species able to colonize substrata that are not yet suitable for other species). Meanwhile, MacArthur and Wilson (1967) introduced the concept of **r and K selection** as the extremes of a life cycle strategy continuum, and the western world seemingly ignored Ramensky and Rabotnov, generally only using the term "pioneer" among these. Although r and K strategies were largely described to fit animal concepts, many of the ideas can be applied as well to plants.

The **r-selected species** are characterized by a rapid growth rate, early reproduction, numerous, small offspring (spores or seeds in plants), and a high resource uptake; the **r** can be compared to the **r** (intrinsic growth rate) in the **logistic population model**. The **r strategist** is likely to be a short-stayer, adapted to disturbed or **ruderal** (field & wasteland) habitats where it is necessary to arrive quickly and mature before the habitat changes. By contrast, the **K-selected species** is characterized by slow growth rate, late reproduction, few, large offspring, and efficient use of resources; the **K strategist** optimizes for a high population density at the environment's carrying capacity (*cf.* the logistic model). The K strategist is likely to grow where the habitat is more stable, and it can be a long-stayer, eventually reaching considerable size (or cover). The K strategist is more likely to depend on asexual reproduction such as rhizomes and perennial habit whereas the r strategist is more likely to rely on seeds or spores and an annual habit with good dispersal.

Thus K strategists tend to be competitors; r strategists tend to be opportunists but not competitors. An r strategist is the more likely one to succeed on unstable, disturbed environments (sometimes a pioneer, sometimes an explerent), whereas the K strategist is the more likely one to succeed in more stable and predictable habitats (the patient or tolerant species and sometimes the violents or aggressive species).

Grime (1977) considered the **r strategist** to be **ruderal** (of field or wasteland) species that took advantage of disturbed habitats (Figure 10). The **K strategists** he considered to be the **stress tolerators** that were able to survive dry or cold periods as whole plants, the **perennial stayers**. Between those two he placed the competitors.

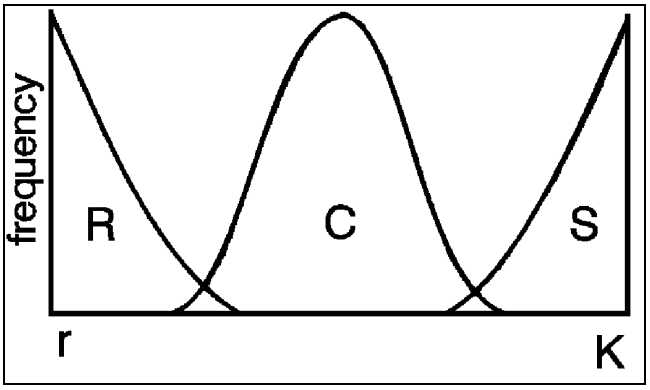

Figure 10. Frequency of ruderal (R), competitive (C), and stress-tolerant (S) species along an r-K continuum. Redrawn from Grime (1977).

Bet Hedgers

But between these two extremes are lots of possibilities for having some of the characteristics of each. Few species can meet all the criteria of either, and trade-offs abound to permit the organisms to meet the demands of their particular habitats. Plants that seem to have both good sexual reproduction and a means of vegetative reproduction are **bet hedgers**. Like the people to whom we refer as bet hedgers, these plants are "unwilling" to put "all their eggs in one basket." They use two strategies simultaneously so that they do not lose entirely. The price they pay is that they likewise never win entirely – at the ends of the spectrum, there is either an r strategist or a K strategist that is better adapted to the circumstances.

Production of gemmae among sexually capable species is one example of bet hedging. In the dry interior of North America, ***Syrrhopodon texanus*** (Figure 11) exhibits seasonal production of gemmae, arising in August (33% of specimens) and climaxing in September (50% of specimens) (Reese 1984). In this species, rarity of males makes this bet hedging a desirable strategy, although sporophyte-bearing females invariably occur when males are present.

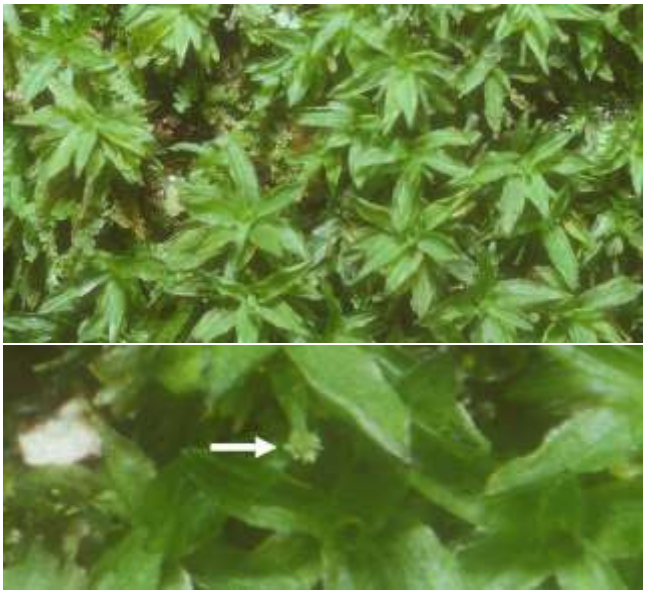

Figure 11. Gametophytes of ***Syrrhopodon texanus***. **Arrow** in lower picture indicates gemmae at leaf tip. Photo by Janice Glime.

Dedifferentiation Issues

It is somewhat difficult to consider bryophyte r and K strategists in the same way as that of seed plants. These two strategies rely heavily on three characteristics of the plant life cycle: arrival and persistence, establishment and growth to maturity in a developing community, and time taken for the species to reach critical life stages (During 1992). Bryophytes are problematic because they do not follow a consistent pathway from spore (propagule) → juvenile → immature individual → reproductive individual. They can revert, growing from a fragment into an adult, or growing from a broken tissue of a fragment into a protonema → juvenile → immature individual → reproductive individual. Bryophytes are able to **dedifferentiate** – return a cell to its embryonic (undifferentiated) state

Compared to most tracheophytes, most bryophytes would appear to be r strategists, utilizing many small progeny (spores) that travel great distances and having short life cycles, permitting them to move on to new locations easily. This may help to account for the widespread distribution of many bryophytes relative to that of seed plants. However, when compared to phanerogams, most bryophytes do not meet the requirement for rapid growth.

Since most species will fall between the two extremes of r and K, the first thing one must realize when trying to determine the r or K status of a species is that ascribing r or K must be done in the context of comparison. Thus, within bryophytes, both ends of the continuum exist, while most species have a mix of characters.

Although bryophytes typically produce large numbers of small spores, many taxa also can increase in numbers by stolons, rhizomes, and branching, qualifying them as K strategists, or long-term stayers. For example, Hedenäs and co-workers (1989) found that the invading moss ***Orthodontium lineare*** in Sweden had a high spore output, but that colonies had a clumped pattern that indicated strong neighborhood effects that permitted spread within a locality. Thus, within the bryophytes, as in tracheophytes, species can be divided into r and K strategists, but they are unlikely to meet all criteria of either, and many trade-offs exist (Stearns 1989). Instead, it appears that many of them are bet-hedgers, being prepared to take advantage of whatever comes along instead of being prepared with a single strategy.

To succeed, they must balance their energy expenditure between sexual reproduction and vegetative growth in a way that best permits them to survive. These strategies must of course be coordinated with their entire physiology and the methods by which each developmental stage is signalled.

The r Strategist

Like typical r strategists, bryophyte r strategists rely heavily on massive numbers, typically 50,000 per capsule, of small spores (10-15 µm) to get to a new location (Schofield 1985). For example, ***Funaria hygrometrica*** can arrive quickly on disturbed sites such as soil charred by fire or agricultural land. But should this be true in predictably disturbed sites such as flood plains? In flood plains one finds members of Archidiidae (Figure 12), a subclass of large-spored mosses, with spores usually 50-150 µm, large enough to be seen without a lens (Schofield 1985). Here it would appear to be advantageous to stay put by producing large, long-lived spores (Söderström 1994). It is likely that this stay-put strategy is available to many mosses and liverworts through spore longevity in soil banks.

Figure 12. A floodplain moss, ***Archidium alternifolium***. Photo by Michael Lüth, with permission.

The K Strategist

Our understanding of perennial stayers (K strategy) is limited by our ability to determine the age of an individual. To age a moss or liverwort is somewhat difficult because among the perennial ones, the bottoms typically die as the tops continue to grow. However, many mosses carry their own age markers (Hagerup 1935), as described in more detail in another chapter, much as trees can be aged by terminal bud scars while they are young. ***Polytrichum*** males can be aged by counting the number of splash cups along the stem, because a new year of growth will come from the cup in the following spring. Ulychna (1963) found ***Polytrichum commune*** with a mean age of 3-5 years, but dead parts in the hummocks ranged 15-17 years. Brunkman (1936) found ***Hylocomium splendens*** (Figure 13) up to 30 years old by counting the successive sets of branches that form like stair steps, each from a point near the apex of the old, but it is unlikely that the oldest parts were still live and functioning. Because most bryophytes do not require their lower parts to keep the upper parts of the plant alive, they could theoretically grow indefinitely in a location due to the growth of the tips. Such a phenomenon is approached in ***Sphagnum***, which will continue to grow as long as the habitat remains suitable.

Figure 13. ***Hylocomium splendens*** showing stairstep branching used for aging the moss. Photo by Janice Glime.

Spores, however, are not the only stage in which r and K strategies might be applied. One could also expect that

there would exist a trade-off between numbers of male and female gametangia. Just as some trees, such as maples (*Acer*) can adjust the number of male and female flowers based on tree crowding, one might look for regulation of numbers of male and female gametangia. In their studies of tropical bryophytes, Cavalcanti Pôrto and Moto de Oliveira (Moto de Oliveira & Cavalcanti Pôrto 2001; Cavalcanti Pôrto & Moto de Oliveira 2002) found that development of gametangia was responsive to rainfall. In the moss ***Sematophyllum subpinnatum***, the number of antheridia per perigonium was 8-20 while the number of archegonia per perichaetium was 3-26. For ***Octoblepharum albidum*** (Figure 14) mean number of antheridia per perigonium was 13.4 and of archegonia per perichaetium 6.7. Could moisture regime change these ratios?

Figure 14. ***Octoblepharum albidum***. Photo by Michael Lüth, with permission.

Just how do the r and K strategies of bryophyte gametangia line up? Fuselier and McLetchie (2004) considered this problem in ***Marchantia inflexa***. They found that females had a greater growth rate, but males had more asexual reproduction. Males were also more likely to be present in a high light regime (55% shade), where they began sexual development earlier; males in low light produced no sexual structures (McLetchie *et al.* 2002). Fuselier and McLetchie (2004) postulated that eventually, the greater female growth rate would result in a population of all females as they overgrew males. However, under a disturbance regime, more males would be successful. They found a female bias in sex expression, with many genetically male plants failing to express sexual traits.

The r and K strategies are at best a continuum. Individual species often do not meet the criteria completely. Evolution is imperfect and time is required to drive it toward perfection. Furthermore, the model predictions work only if the environment perfectly matches with the set of bryophyte characters predicted. In the Antarctic, extreme conditions would seem to test this r and K continuum to its limits. And there the imperfections of these predictions are evident. The disturbed nature of this volcanic habitat favors r-selected taxa that must arrive from considerable distances (Convey & Smith 1993). However, the difficulty of spreading during the short, cold growing season favors certain short-lived taxa with large spores. Five of the species that are widespread in the Antarctic have large numbers of small spores and are most likely long-distance colonists. Even the longer-lived taxa seem to defy the r & K model predictions, having a large investment in sexual reproduction.

Life Cycle Strategies

To combat all the insults of the environment that might be encountered in a global array of habitats and climates, a variety of strategies exist among both plants and animals. For bryophytes, the predominant controlling factor is available moisture, but we must consider that temperature is also a major contributor to the timing of life cycle events.

As we consider the life cycle strategies of bryophytes, we must keep in mind that they potentially expose all of their alleles to expression and selection through a considerable portion of their lives – as 1*n* gametophytes. All the variety in strategies discussed above come into play in permitting these tiny organisms to occupy the widest array of conditions of any group of plants. For the greatest number of species to survive across the greatest number of habitats, some have adapted to be **opportunists**, constantly moving from place to place, while at the other extreme are **perennial stayers**, finding a suitable place and remaining there for a long time. But because an individual bryophyte must stay in one place, it must have a life cycle that permits it to survive the onslaught of environmental fluctuations during the entire time it develops from protonema to leafy plant to fertilization to sporophyte to dispersal of spores.

The environment thus provides the major selection pressure on the life cycle strategies. Recognizing the instability of the environment, Stearns (1976) classified the environment into three main types (examples are mine):

1. having **long cyclic fluctuations**, with a period much longer than that of the generation time of the organism (*e.g.* fires)
2. having **short cyclic fluctuations**, with a period that is as long as or shorter than the generation time of the organism (*e.g.* seasons)
   a. cycle highly predictable
   b. start of cycle unpredictable
   c. start of cycle predictable, but conditions of growing season unknown
   d. start of cycle predictable, but conditions only partly known
3. having **random fluctuations**, *i.e.* not predictable (*e.g.* flash floods)

To survive in a fluctuating environment, the life cycle must prepare the bryophyte for the fluctuations. This means that at times it is advantageous to "run for your life" to other locations (produce spores), whereas under other, more favorable conditions it is best to sit still and keep your family together (reproduce vegetatively).

During (1979) has examined in detail the life cycle strategies of bryophytes in dealing with environmental conditions. In finding that most tracheophyte life cycle strategy systems either did not apply or were incomplete for the bryophytes, he devised a system of six strategies. He considered that bryophytes utilize three major trade-offs: few large spores vs. many small spores, survival of stressful season as spores (**avoidance**) *vs* survival as a gametophyte (**tolerance**), and life span that is negatively correlated with reproductive effort (for tolerants only) (During 1992). In addition, there is a usually tradeoff between sexual and asexual reproduction (Schofield 1981, During 1992). These considerations resulted in his organization of strategies based on life span, spore number and size, and reproductive effort (Table 1 and figures from During 1992; table slightly modified):

Table 1. Spore and life span characteristics of the various life cycle strategies for bryophytes as defined by During (1979).

Potential life span (yrs)	Spores: Numerous very light <20 µm	Spores: Few large >20 µm	Repro effort
<1	Fugitives	Annual shuttle	High
Few	Colonists		Variable
	Ephemeral	Short-lived shuttle	
	Colonists	Long-lived shuttle	
	Pioneers		
Many	Perennial stayers	Dominants	Low
	Competitive		
	Stress-tolerant		

The system of During has attributes that work as well for higher plants, and Frey and Hensen (1995) have proposed a modified system based on this one to be used for all plants. (Now how often do you see those tracheophyte folks copying a bryophyte idea?! Kudos to During!) They have expanded upon the original six strategies proposed by During to include nine: annual shuttle species, fugitives, kryptophytes, short-lived shuttle species, colonists, perennial colonists, perennial shuttle species, perennial stayers, and perennial stayers with diaspore years. Hürschner and Frey (2012) included geophytes and perennial shuttle species to the bryophyte list.

Fugitives (Figure 15), **colonists** (Figure 16), **annual shuttle species** (Figure 17), and **short-lived shuttle species** (Figure 18) are **r strategists** and all succeed in disturbed environments. The fugitive strategy is relatively rare, with ***Funaria hygrometrica*** being one of the few examples (During 1992). That many species require disturbance and therefore are relatively rare in any specific locality is usually overlooked in trying to conserve rare taxa. The very disturbance they need to persist is often prevented in an effort to maintain them! Noble and Slatyer (1979) attribute success following disturbance to plant strategies related to three factors: method of arrival (fugitives, colonists, annual shuttle species) or persistence at disturbed site (short-lived shuttle species); ability to become established and reach maturity in disturbed site; time needed to reach critical life cycle stage. These criteria are not intended to include those of taxa adapted to continuously disturbed or catastrophically disturbed habitats, but rather to those recurring events such as fire, flood, or treefall. The **perennial** bryophytes are **K strategists** (Figure 19, Figure 20) of stable habitats.

During (1992) added the category of **dominant** to accommodate taxa with large spores and long life expectancy, such as some ***Sphagnum*** species. It is a rare combination among bryophytes, whereas it is relatively common among trees. Other categories will surely be added as we gain understanding of tropical ecology and the adaptive strategies of bryophytes there (During 1992). One such category could develop based on **neoteny**, where juvenile characters are retained in adults, a condition that occurs among some species of ephemeral habitats such as living on leaves in the tropics (During 1992). In some taxa, such as ***Buxbaumia***, neoteny permits the species to avoid some life cycle stages, in this case the leafy gametophyte! La Farge-England (1996) has suggested the category of **protonema mosses** to encompass these few taxa (see chapter on life forms and growth forms). Others, such as ***Dicranum*** and ***Fissidens*** species, have **dwarf males** that develop on leaves of female plants, facilitating the transfer of sperm to the egg, a kind of male neoteny. (See chapters on sexuality and on the development chapter on gametogenesis for further discussion of dwarf males.)

Diaspore Banks

Disturbed habitats, whether the product of predictable natural phenomena or unpredictable events such as human intervention or volcanic eruptions, benefit from the bank of spores and asexual **diaspores** (any structures that become detached from parent plant and give rise to new individuals) stored in the soil out of reach of sun and sometimes even water. Major disturbances can bring these propagules to the surface where they can break dormancy and become established. We need only look at a recently disturbed bank in a forest, sloping deforested hillside, or crumbling streambank to recognize the importance of bryophytes in colonizing and often maintaining the surface integrity. Yet, as Ross-Davis and Frego (2004) pointed out, while these regeneration processes "may be critical to conservation of severely disturbed communities..., they are poorly understood." In an attempt to quantify this importance they sampled two grids in managed Acadian forests of New Brunswick, Canada. They identified 51 taxa in the aerial diaspore rain and buried diaspore banks. Of these, 36 represented species in the existing community of the Acadian forest. The composition of aerial diaspores was more similar to the existing community than to that of buried ones.

Tradeoffs

For bryophytes, the system of success strategies is complicated by the ability to reproduce from fragments, and in many cases the production of asexual propagules on the protonemata as well as on the leafy plant, leading During to his 1992 revision. One must keep in mind that bryophytes may be among the best dispersers in the world. Therefore, large spore size, as opposed to small ones with worldwide dispersal potential, may be a tradeoff of great magnitude. While many of these small spores will not survive the long distance travel due to UV radiation and other atmospheric hazards (see dispersal chapter later), many will survive significant local travel, with a few travelling for hundreds of kilometers.

Once the spores arrive, different attributes become important. The spore must have sufficient energy to survive until favorable conditions arise, and it must get the new protonema off to a good start with enough energy to survive in some very harsh environments. This has resulted in a correlation of spore germination patterns with habitat (Nehira 1987). Epiphytic and saxicolous species of both mosses and liverworts tend to have **endosporic** germination (*i.e.*, early development of several mitotic divisions within the spore wall; Figure 21), permitting them to be multicellular when they emerge from the protection of the spore. This would suggest that these species carry sufficient nutrients with them to supply their initial developmental nutrient needs. On nutrient-poor, **xeric** (dry) substrates such as rock and bark, internal development could insure protection during early, critical stages of development. However, most mosses have **exosporic** germination (first mitotic division occurs outside spore after rupture of spore wall).

Life Cycle Strategies
based on During (1979, 1992)

Fugitives

Fugitives – *species that live in unpredictable environments*

example: ***Funaria hygrometrica***
short life span; ephemeral or annual
high sexual reproductive effort; large percent of plant devoted to spore production
low age of first reproduction (first year)
spores small (<20 µm), very persistent and long-lived
no asexual reproduction
innovations absent
open turfs
rare in phanerogams (mustards?) and bryophytes; found among bacteria, algae, fungi

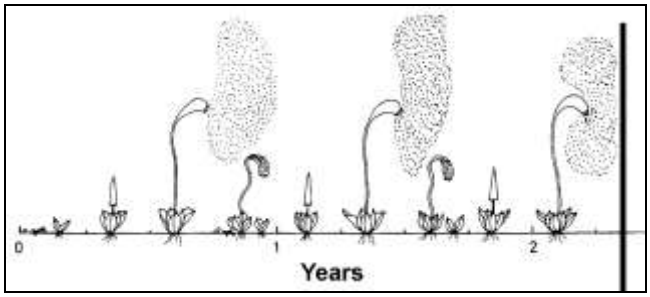

Figure 15. **Fugitive** strategy. From During (1979).

Colonists

Colonists (sensu stricto) – *species that live where habitat start is unpredictable, but lasts several years; secondary succession*

bryophyte examples: ***Bryum bicolor***, ***Bryum argenteum***, ***Ceratodon***, ***Marchantia***
short life span; (annual-) pauciennial-pluriennial
sporophyte late, somewhat rare in many; first sexual reproduction at least after 1 and usually 2-3 years
high reproductive effort
spores < 20 µm, persistent
innovations present
asexual in early life; first asexual reproduction in a few months
usually short turf
old field species like *Solidago*

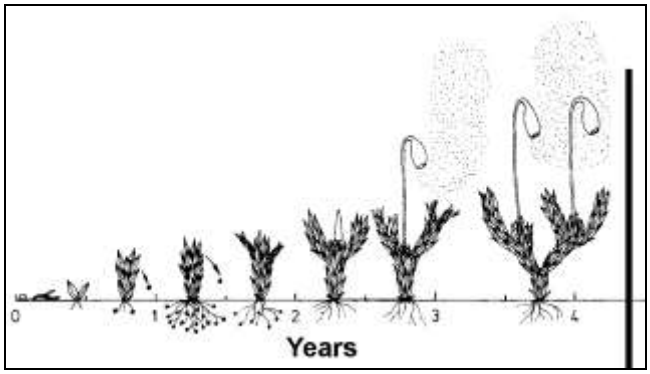

Figure 16. **Colonist** (*sensu stricto*) life cycle strategy. From During (1979).

Colonists

Colonists (ephemerals) – *gap-dependent species*

bryophyte example: ***Bryum erythrocarpum***
short life span; (annual-) pauciennial-pluriennial
first sexual reproduction in a few months
sexual reproduction rare
spores < 20 µm, persistent, numerous
high asexual reproductive effort by subterranean tubers on rhizoids
river flood plains, low areas submerged in spring, cultivated fields
usually short turf

Colonists (pioneers) – *species that live where habitat start is unpredictable and habitat lasts at least several years after disturbance; make habitat suitable for perennial stayers (Rabotnov 1975)*

bryophyte examples: ***Grimmia***, ***Schistidium***
long life span
slow growth
perennial
high reproductive effort
first sexual reproduction in a few years???
sexual reproduction low
asexual reproduction high
spores < 20 µm, persistent
river flood plains, low areas submerged in spring, cultivated fields
usually short turf

Shuttles

Annual Shuttle – *species that require small disturbances that last 1-2 years; survive severe stress periods*

bryophyte examples: ***Ephemerum***, ***Physcomitrium***, ***Fossombronia***
short life span; (ephemeral-) annual-pauciennial
sexual reproduction effort high and frequent
age of first reproduction < 1 year
spores large, 25-50 (-200) µm
survive by spores
capsules often immersed (short or no setae) (Longton 1988)
specialized asexual reproductive structures absent
innovations rare
open turf or thalloid mat
agricultural weeds, hoof prints, steep stream banks, dung
disturbed habitat species like *Brassica*

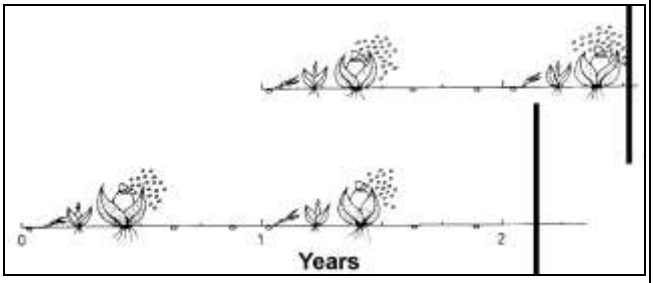

Figure 17. **Annual shuttle** life cycle strategy. From During (1979).

Short-lived Shuttle – *species that don't avoid periods of severe stress; habitat lasts 2-3 years*

bryophyte examples: ***Hennediella heimii***, ***Splachnum***, ***Tetraplodon***
life span several years, pauci-pleuriennial
sexual reproductive effort high; sporophytes more or less frequent
overall reproductive effort medium
ages of first reproduction 2-3 years
spores large, 25-50 (-100) µm
asexual reproduction rare
innovations present
short turf or thalloid mat

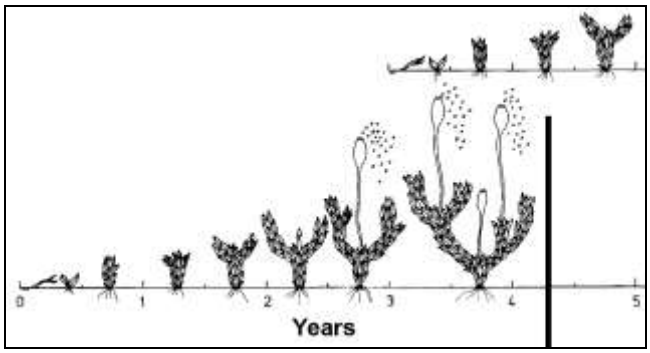

Figure 18. **Short-lived shuttle** life cycle strategy. From During (1979).

Perennial (Long-lived) Shuttle – *species that require stable environments, such as epiphytes, where end of habitat is predictable*

bryophyte examples: ***Orthotrichum***, **Marchantiales**
long life span; pluriennial, perennial
sexual reproduction effort moderate (During 1979) or low (During 1992)
age of first sexual reproduction high (>5yrs)
spores large (25-200 µm)
spore life span short
asexual reproduction effort moderate
innovations present
age of first asexual reproduction variable
cushion, rough mat, smooth mat, tuft
tracheophytes include bromeliads, *Betula*, *Populus*

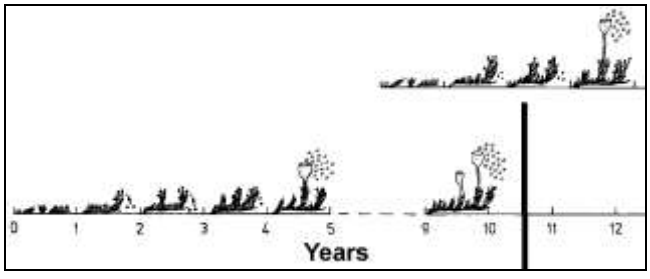

Figure 19. **Perennial long-lived shuttle** life cycle strategy. From During (1979).

Perennial Stayers

Perennial stayers (competitive) – *forest floor*

bryophyte examples: ***Brachythecium rutabulum***
long life span
perennials
rapid growth
sexual and asexual reproduction low or nearly absent
age of first reproduction several years
spores <20 µm
spore longevity variable
wefts, dendroids, mats, large cushions

Perennial stayers (stress-tolerant) – *fens, bogs, desert*

bryophyte examples: ***Sphagnum***, ***Syntrichia ruralis***
long life span; perennials
slow growth
sexual and asexual reproduction low or nearly absent
age of first reproduction several years
spores <20 µm
spore longevity variable
growth form plasticity
in deserts include acrocarpous taxa with long setae
tracheophytes include ericaceous shrubs

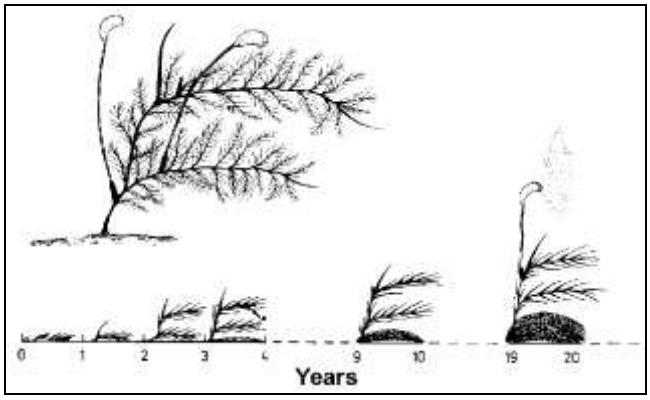

Figure 20. **Perennial stayer** life cycle strategy. From During (1979).

Dominants – bogs

bryophyte example: some ***Sphagnum***
long life span; perennial
sexual reproduction effort low
spores large (>20 µm)
asexual reproduction effort low
turf

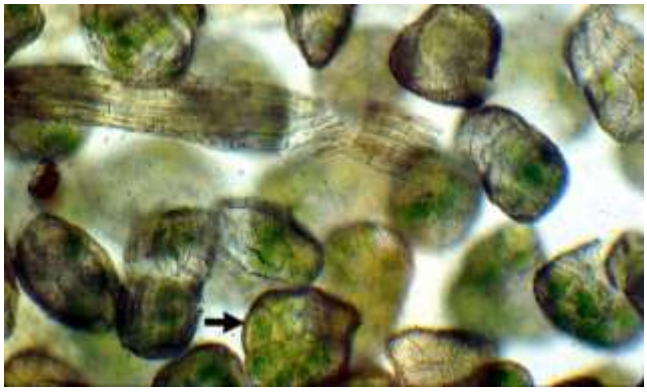

Figure 21. Endosporic development (**arrow**) in spores of the hornwort ***Dendroceros tubercularis***. Photo courtesy of Karen Renzaglia.

But spores are not the only way to travel. Fragments and propagules can carry the species to a new location, although the generally much larger size would usually limit distance considerably. Moss balls (see chapter on life form) along lake shores and on glaciers and snow banks serve as means of dispersing large units, including multiple plants. Landslides, rock movement in streams, trampling, and vehicle tires can carry fragments for some distance. For those producing asexual propagules, sexual reproduction and asexual propagules are usually not produced at the same time. Thus, investment in specialized asexual structures is indeed a trade-off. Taxa with annual life cycles, surviving unfavorable conditions as spores, rarely produce such specialized structures, investing their energy instead in the production of spores (During 1992).

We know little about the energy costs of producing spores and other propagules, and in particular know nothing of the effect of spore production on mortality (During 1992). There is evidence, however, that development of sporophytes slows the growth of the gametophytic plant in ***Scorpidium scorpioides*** (A. M. Kooijman & H. J. During, unpubl. data) and ***Plagiothecium undulatum*** (Figure 22; Hofman 1991), as well as in ***Dicranum polysetum*** mentioned earlier (Bisang & Ehrlén 2002). This tradeoff may be a general rule, as discussed in the chapter on sporophyte development.

Figure 22. ***Dicranum polysetum*** exhibiting its multiple setae per stem. Photo by Janice Glime.

Some characteristics of the life strategies may be interrelated. For example, Hedderson (1995) found that in the Pottiales the probability of producing capsules decreased with increased life expectancy and was negatively associated with asexual propagules. As discussed in the chapter on asexual propagules (brood bodies), these compete for energy with the production of capsules and generally do not occur simultaneously. It therefore follows that dioicous taxa in this group have more asexual propagules, corresponding with their lower likelihood of having sexual reproduction. Unlike sporophytes, asexual propagules were positively associated with life expectancy. On the other hand, size accounts for only a small, but statistically significant, proportion of the variation in life history traits in the Funariales, Polytrichales, and Pottiales (Hedderson & Longton 1996). Rather, characteristics related to water relationships were most important, accounting for 40-50% of the variation. It is interesting that the ability to take in and retain water coincides with monoicous taxa that are short-lived and produce few large spores, whereas those at the opposite end of the endo-ectohydric gradient have opposite characters. Spore number and spore size are strongly related to family, with most of the variation occurring among genera. Variation among species is moderate. Hedderson and Longton suggested the possibility of coevolution of water relations and life history in these orders.

Longton (1997) used the concept of life history strategies to predict character relationships. Colonists, fugitives, and shuttle species exhibit an earlier age for first reproduction as the longevity decreases. These strategies are accompanied by greater monoicy and reproductive effort (Longton 1997, 1998). Such species tend to have more plastic phenotypes and experience greater success at establishment by spores. Dioicous moss colonists, on the other hand, are more likely to produce asexual propagules, whereas such propagules are widespread among liverworts.

Generation Time

Generation time is one of the contributors to life cycle strategy, but we have no comprehensive study by which to label this function for bryophyte species in general. In order to meet the IUCN red list criteria, bryophytes mus be put into generation time categories. This is important because environmental changes may take longer to affect numbers of those species with a long life cycle than for those with a short one. Tomas Hallingbäck (Bryonet 9 January 2014) reports that in Sweden they have used templates of 10, 20, 50, and 100 years as the intervals for three generations. Since hard data are generally not available, the Swedes agreed upon approximate generation lengths and **life spans** and classified their species based on the potential life span of the gametophyte:

- 'short' (colonists s. str., fugitives) = 3 generations = 10 (*e.g.* ***Microbryum*** spp.)
- 'medium' (pioneer colonists, short-lived shuttle) = 3 generations = 20 years (*e. g.* a typical epiphyte like a ***Syntrichia***)
- 'long' (long-lived shuttle – perennial stayers) = 3 generations = 50 years (*e.g.* ***Hylocomium splendens***).
- For species rarely found with sporophytes, a generation time of 25 years was recommended

Habitat Studies

Occasionally a habitat study will describe the growth forms or life forms that dominate there. But quantitative studies to describe these are rare. However, a few examples from tropical habitats can serve to provide an understanding of their usefulness in giving a mental picture of the bryophyte cover in places we have never visited.

In the **Colombian cloud forest**, epiphytes are abundant due to the high moisture availability from the clouds and the infrequency of desiccation events. This type of climate supports growths of tall turfs and smooth mats as predominant growth forms on the trees (van Leerdam *et al*. 1990). On the other hand, the life strategies of bryophytes on trees on the **eastern Andean slopes** of northern Peru reflect the drier habitat. Colonists form short turfs of acrocarpous mosses, primarily in secondary forests suffering disturbance. In the **lowland** and **submontane forests**, perennial shuttle species and perennial stayers exercise low sexual reproductive effort and take advantage of the high humidity to accomplish high vegetative reproduction through both propagules and clonal growth (Kürschner & Parolly 1998a). ***Macromitrium*** (Figure 23) and ***Phyllogonium fulgens*** (Figure 25) have dwarf males resulting from small male spores compared to large female spores. (Dwarf males are discussed more thoroughly in the chapters on sexuality and gametogenesis.) ***Leptodontium viticulosoides*** (Figure 24) exhibits functional heterospory in which small spores are dispersed long distances and large ones only short distances. On the other hand, at high elevations **near timberline**, the perennial shuttle and perennial stayer species instead exercise a high sexual reproduction and produce numerous sporophytes. Similar altitudinal differences occur in Southeast Asia and Central Africa.

Figure 23. ***Macromitrium sulcatum***, member of a genus with small male spores and dwarf males. Photo by Manju Nair, through Creative Commons.

Bryophytes of the **tropical lowlands** have a very different character from these montane epiphytes, providing them with maximum water conservation in this much drier habitat. The mat life form encompasses species with water lobules, water sacs, and rhizoid discs (Kürschner & Parolly 1998b). This life form gives way to fans, wefts, dendroids, and pendants in the more humid **montane belt**. These forms serve as collectors to condense water vapor from the frequent fog and mist (**fog-stripping**; Figure 26). Deeply fissured or ciliate leaves and rill-like arrangement provide the fine wire-like surfaces needed for this water capture. The **tropical oreal** (high altitude) and **subandean belt** contrasts with this foggy area by having strongly contrasting diurnal conditions and supporting short-turf, tall-turf, and tail life forms with central strands, rhizoids, and rill-like leaf arrangements.

Figure 24. ***Leptodontium viticulosuides***, a species that has functional heterospory. Photo by Li Zhang, with permission.

Figure 25. Pendant ***Phyllogonium fulgens*** in Japan. Photo by Janice Glime.

Figure 26. "Fog-stripping" by thin leaves of ***Campylopus holomitrius*** in the mist from geothermal vents at Karapiti, New Zealand. Photo by Janice Glime.

Bryophytes of **arid habitats** are typically small and may include acrocarpous perennial stayers with small spores and long setae that aid in dispersal (Longton 1988). Annual shuttle species here are primarily ephemerals that avoid desiccation by going dormant as spores, develop rapidly to maturity following rain, and produce large spores in capsules that typically lack stalks and remain submersed among the perichaetial leaves; often these capsules lack peristomes and opercula and may be dispersed as whole capsules (see chapter on development of sporophytes). The perennial shuttle species are mostly thallose liverworts such as ***Riccia*** (Figure 27) that curl up and become dormant or survive as large spores. Fugitives may arrive, but generally are gone after 1-2 years, travelling to new sites as small spores.

Figure 27. ***Riccia sorocarpa***, showing curling leaves that facilitate survival of dry conditions. Photo from Botany website, UBC, with permission.

González-Mancebo and Hernández-García (1996) related life strategies to habitats along an altitudinal gradient in the Canary Islands. They found the following trends for the most abundant strategies:

higher elevations: colonists
rocks in driest forest: colonists, short-lived shuttle, long-lived shuttle
humid forest trees: long-lived shuttle, short-lived shuttle
humid forest soil: perennials
soil in shady, dry forest: perennials

These strategies seem to be determined by humidity conditions, substrate dynamics, and vegetation disturbance. Not surprisingly, the perennial life strategy had the lowest percentage of fertile species. The other strategies typically have approximately 70% fertility.

Summary

Bryophyte life strategies must be closely attuned to the water regime of their environment. They accomplish this fine tuning by using spores, fragments, and specialized asexual propagules during times when conditions are not suitable for the gametophyte. Furthermore, they attune their times of sexual reproduction to meet the availability of water. Secondary to the water schedule is the advent of disturbance for which some bryophytes are especially adapted (**opportunists**).

Bryophytes, especially mosses, are clonal organisms. All bryophytes are able to spread vegetatively through fragments and propagules. Perennial mosses also spread by branching (**ramets/genets**). Mosses, additionally, produce many upright gametophytes from the protonema developed from a single spore. Clones have the advantage of maintaining moisture, but have the disadvantage of being genetically identical. Bryophytes that grow horizontally have been considered **foragers** that are able to take advantage of a patchy environment to obtain nutrients, light from **sunflecks**, and even water in different parts of the plant. They are able, at least in some taxa, to transport these nutrients or the photosynthate to other parts of the plant. Sexual reproduction is favored when clones and clumps provide both sexes, and even in monoicous taxa the differences in maturation times among members of the clone become an advantage.

Density can work for and against bryophytes. At low densities, water loss is greater and sexual reproduction is less successful, favoring spread by spores at high densities. However, in some mosses, such as ***Polytrichum***, shoot mortality can increase with density, but in other taxa it can decrease.

There is a tradeoff between sexual reproduction and asexual reproduction, including branching and growth, as these events compete for energy.

Compared to tracheophytes, bryophytes are **r strategists**, but within the bryophytes there is an entire range from **r strategist** to **K strategist**. The **r strategists** rely on large numbers of small spores and a short life cycle (**opportunists**). **K strategists** rely on their clonal, perennial growth (**perennial stayers**) and often have only limited sexual reproduction or are strictly vegetative. But most bryophytes lie somewhere on the **bet hedger** line, producing spores sexually, but using fragments and asexual propagules during seasons when energy is not needed for sexual reproduction or spore production. Because of their ability to

dedifferentiate, bryophytes often spread by fragments of ordinary tissue.

Availability of water is the most important determinant of life cycle strategy. Endosporic development is more common on low water, low nutrient substrates like rock and bark. Disturbance is actually required for some species.

Bryophytes utilize three major tradeoffs: few large spores vs. many small spores, survival of stressful season as spores (**avoidance**) *vs* survival as a gametophyte (**tolerance**), and life span that is negatively correlated with reproductive effort. **Diaspore banks** permit bryophytes to survive untenable periods of time in a dormant state and begin growth when suitable conditions return. **Endosporic development** permits some bryophytes to get a head start in particularly short-lived periods of adequate moisture, such as deserts, floodplains, and vertical substrates.

Acknowledgments

Jean Faubert caught some serious inconsistencies in the r-K selection text and made valuable suggestions to improve this subchapter.

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CHAPTER 4-7

ADAPTIVE STRATEGIES: VEGETATIVE VS SEXUAL DIASPORES

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CHAPTER 4-7

ADAPTIVE STRATEGIES: VEGETATIVE VS SEXUAL DIASPORES

Figure 1. ***Marchantia polymorpha*** showing both vegetative diaspores (gemmae in splash cups) and umbrella-like archegoniophores where sporangia and sexual spores are housed. Photo by Michael Lüth, with permission.

Importance of Dispersal

Boedeltje *et al*. (2019) considered the vegetative diaspores of bryophytes to be of pivotal importance in colonization of new areas. These, however, are dependent on life history traits and habitat.

Diaspores

Diaspores are everywhere and some are ready to grow. In bryophytes, **diaspores** are spores and other propagules, including fragments, that function in dispersal (see Figure 1). These may be airborne, drop within the parent colony, or become buried in a diaspore bank in the substrate. Some even are dispersed by animals or water. They serve both to increase colony size and to invade new places.

Nevertheless, spread of many species is dispersal limited. Sillett *et al*. (2000) found that nine species of bryophytes had colonized branches of Douglas fir (*Pseudotsuga menziesii*) from 1995 to 1999, with relatively rapid colonization in all age classes. Nevertheless, when bryophytes were transplanted to Douglas fir trees, they became more frequent on inoculated branches than on ones not inoculated by the researchers. This suggests that these bryophytes were dispersal limited in colonizing the trees.

The importance diaspores is exemplified by the large number of bryophytes that occur on multiple continents. Of the 7567 accepted binomials for liverworts and hornworts, 2211 are found on more than one continent (Anders Hargborg, pers. comm. 23 February 2017). And of these, 20 are found on all 7 continents plus Oceania. Frey and Hensen (1995) considered dispersal of such importance that they proposed a life strategy system based on dispersal strategies. One strategy that differed from other systems was the **perennial stayers with diaspore years**. That is, some years have prolific reproduction, vegetative or sexual, whereas in other years these are more limited.

Sampling Methods

To fully understand the role of diaspores we must sample them. The methodology influences what we sample, so it is worthwhile to examine these first.

The most commonly used means of sampling spores and other diaspores in the atmosphere is to place open

Petri dishes with a common bryophyte nutrient agar in the field at various heights and distances from a known source for a species. For shorter distances, one can use **glass slides** coated with glycerine. The spores usually cannot be identified by themselves, unless one has considerable experience and a good set of pictures and/or samples for verification. Hence, they must be germinated and the developing protonemata must be coaxed to develop and produce gametophores. Even then, one cannot be certain that the ensuing growth form is representative, since the light is artificial, may be too low or too high, certain growth factors available in its environment may be missing, and nutrients may be at inappropriate levels.

Other traps can include filters or air funnels in strategic positions that catch microbiota carried by drafts and other wind patterns. Each of these methods has its drawbacks, in addition to the problems of culturing and identification. Contamination is certain, density is low, and local micropatterns in air movements may be more influential in what they record in some cases than major pathways.

Levetin *et al*. (2000) compared the **Tauber trap** (Figure 2-Figure 3) with the **Burkard volumetric spore trap** (Figure 4-Figure 5), the latter a trap used in Antarctica (Lewis Smith 1991). The Burkard volumetric spore trap is used primarily for collecting airborne pollen, whereas the Tauber trap is used primarily to analyze deposition. They found a strong correlation between the pollen trapping recorded by the Tauber traps and the cumulative sums of average daily airborne spores/pollen from collections with the Burkard spore trap. Peck (1972) used the Tauber trap to sample pollen in turbulent flow water and found that under those conditions the collection efficiencies for individual taxa vary with both size and weight of the grains and velocity of flow. Smaller grains were trapped less efficiently than larger ones. As the water speed increased, grain characteristics had less effect, but the trapping efficiency decreased.

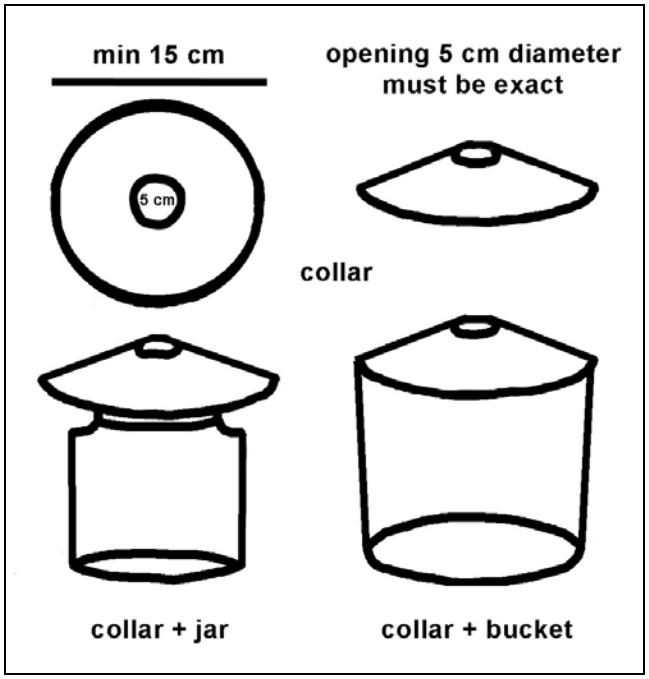

Figure 2. Tauber trap. Drawing based on Pardoe *et al*. 2010.

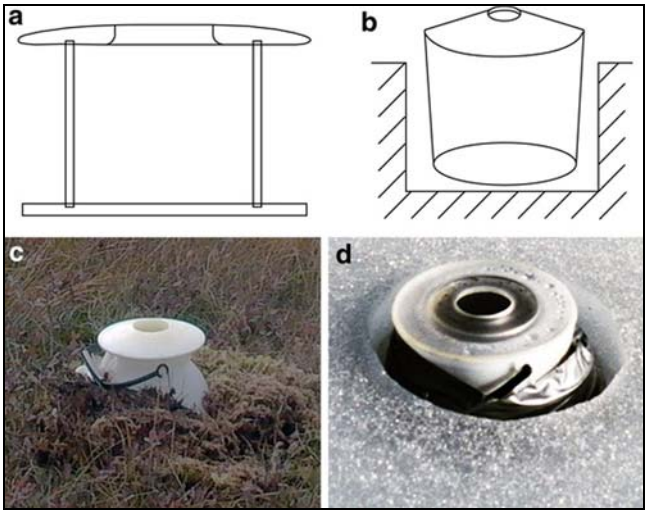

Figure 3. Tauber's original design (**a** & **c**) compared to the modification used with the Pollen Monitoring Programme (PMP) (**b** & **d**). Images from Pardoe *et al*. 2010, through Creative Commons.

Figure 4. Burkard volumetric spore trap. Photo by Burkard at <http://www.burkard.co.uk/7dayst.htm>, with permission.

More sophisticated samplers collect, filter, and concentrate the spores. One that has been used in bryophyte studies is the Rotorod sampler (Rotorod® Sampler 2009). This is a programmable instrument with a

timer that spins the head, bringing the pollen-collecting rods out by gravity. Its standard sampling is a 10% duty cycle, meaning that it samples for one minute out of every ten. A 5% duty cycle would collect for 30 seconds out of every ten minutes. Spores are collected on polystyrene rods pre-greased with silicone grease. To count the spores, the rod is placed in one of the deep grooves of a microscope stage adapter and a few drops of Calberla's stain applied. The rod is covered with a standard coverslip at the distal end of the rod and the spores are counted under a compound microscope at 400X. I am concerned that this rod is apparently intended to be used again and could easily have remnants of spores from a previous sampling, despite careful cleaning. A reticule can be used to aid in counting and to calibrate. The company has found that 400 spores are sufficient to get an accurate estimate of what is there.

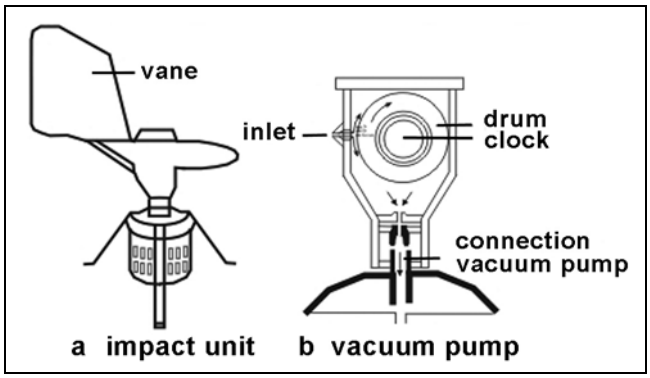

Figure 5. Burkard volumetric spore trap. Redrawn from Aerobiological Sampling, Universidad D Cordoba.

Nature provides her own traps that we can use, but these are varying pictures of time and not necessarily indicative of the present. In the Antarctic, snow provides an appropriate medium for analysis of deposition of diaspores (Lewis Smith 1991). And peatlands have been traditionally sampled for pollen as well as spores.

But not all evidence comes from trapping diaspores. Patterns of bryophyte distribution can help us to hypothesize the pathways and mechanisms. Lönnell (2011) summarizes indirect connections that can contribute to our understanding of dispersal:

1. genetic similarity between populations in different locations
2. successful colonization that can be connected through distribution patterns
3. diaspore longevity compared to species distribution
4. species composition with prevailing winds.

One problem with assessing the relative importance of asexual vs sexual reproduction is that we often misunderstand the mechanisms used by a species. Fritz (2009) demonstrated this for several pleurocarpous species. ***Pseudoscleropodium purum*** (Figure 6) and ***Pleurozium schreberi*** (Figure 7) are known for rarity of sporophytes, but Fritz found that genetic evidence of new gene combinations suggested that sexual reproduction followed by spore production was more common than suspected. This was further supported by finding frequent presence of both antheridia and archegonia.

Figure 6. ***Pseudoscleropodium purum*** with capsules in Bawsey Country Park, UK. Photo by Des Callaghan, with permission.

Figure 7. ***Pleurozium schreberi*** showing dying basal portion of stem that can result in the living portion becoming a separate plant, creating reproduction by cloning. Photo by Janice Glime.

Diaspore Banks or New Arrivals?

Leck and Simpson (1987) examined the spore bank in a Delaware River, USA, freshwater tidal wetland. Their samples came from rainwater, 0-2 cm, 4-6 cm, and 8-10 cm depth in high marsh, cattail, and shrub forest. These samples revealed 14 moss species and 2 liverwort species. The most common bryophyte was a species of ***Bryum***. The 0-2 cm samples had more species and greater densities, but no cover. The sample spores required longer germination times in culture than what is typical for seed bank spores and may explain the lack of cover on the tidal surfaces.

In a forested floodplain in Ohio, USA, McFarland and Wistendhal (1976) found six species of mosses, with ***Eurhynchium hians*** (Figure 8) being dominant. In this case, they considered low light levels and occasional flooding to promote protonemal growth. Samples of soil with plants and fragments buried under 10 cm of alluvium had good regrowth and appear to be important to the establishment of terrestrial mosses on these flood plains.

Diaspores for colonizing an area can arrive from elsewhere or be exposed from propagules that have been buried and dormant. In areas experiencing recolonization,

propagule sources can arrive quickly from **diaspore banks**, those buried propagules that have survived for long periods until such time as they are once again returned to a position with sufficient light and moisture to grow. In this case, travelling the distance means travelling down to a depth where they can survive until they once again experience a favorable location. This may mean not travelling too far so that they never again surface; in other cases, deeper is safer.

Figure 8. ***Eurhynchium hians*** in Europe. Photo by Michael Lüth, with permission.

Heinken *et al*. (2004) found three recolonization mechanisms at work in pine forest gaps in Central Europe. These were 1) advance of shoots from the edge of the gaps through clonal growth; 2) dispersal of detached individual shoots and clumps; 3) regeneration of what appeared to be dead stems from a soil diaspore bank. Each of the regenerating species seemed to be best at one of the strategies. Disturbance temporarily increased diversity as colonists succeeded on newly available ground before the perennial stayers were able to completely occupy the gap.

Arrival can account for differences in species dominance. In a boreal forest, ***Pleurozium schreberi*** (Figure 7) didn't show any diaspore limitation (Lloret 1994). ***Dicranum scoparium*** (Figure 9) cover was not influenced by proximity of its neighbors, but it did increase its colonization when the species was introduced by planting. In these forest sites, ***D. scoparium*** seemed to depend on the diaspore bank for its establishment. ***Hylocomium splendens*** (Figure 194), on the other hand, did depend on the presence of neighbors.

Activation conditions usually mean reaching not only sufficient moisture, but being exposed to light. Continued metabolic activity without light is certain death, but most species seem to have mechanisms to prevent germination until light is available. For example, diaspore banks of the forest floor can be activated for germination by disturbance that brings propagules into sufficient light and available moisture (Korpelainen *et al*. 2011). Such diaspore banks may be the source of rapid colonizers after forest harvesting (Caners *et al*. 2009), mining of peatlands (Poschlod 1995), or other soil/substrate disturbances.

Figure 9. ***Dicranum scoparium***. Photo by Janice Glime.

Even within the same habitat, the diaspore bank can differ based on the medium. In the bushland of western Australia, Biggs and Wittkuhn (2006) found 11 bryophytes in the soil and 13 in the litter. ***Tayloria octoblepharum*** var. ***octoblepharum*** (Figure 10) and ***Rosulabryum campylothecium*** (Figure 11) only occurred in soil diaspore bank samples and ***Lunularia cruciata*** (Figure 12), ***Fissidens serratus*** (Figure 13), ***Racopilum cuspidigerum*** var. ***convolutaceum*** (Figure 14), and ***Tortula antarctica*** (Figure 15) only occurred in litter samples. ***Bryum argenteum*** (Figure 16) and ***Rosulabryum billarderi*** (Figure 17) were present in soil samples from all nine floristic types (including various types of woodlands, shrublands, heath, and mobile dunes); ***Gymnostomum aeruginosum*** (Figure 18) occurred in litter from all nine floristic types. As in other studies discussed herein, the diaspore bank housed some species that rarely occurred above ground, *e.g.* ***Riccia*** (Figure 97) and ***Physcomitrium*** (Figure 20). Among the familiar taxa from studies in other parts of the world were ***Funaria hygrometrica*** (Figure 178) and ***Pohlia nutans*** (Figure 36) in these Australian diaspore banks.

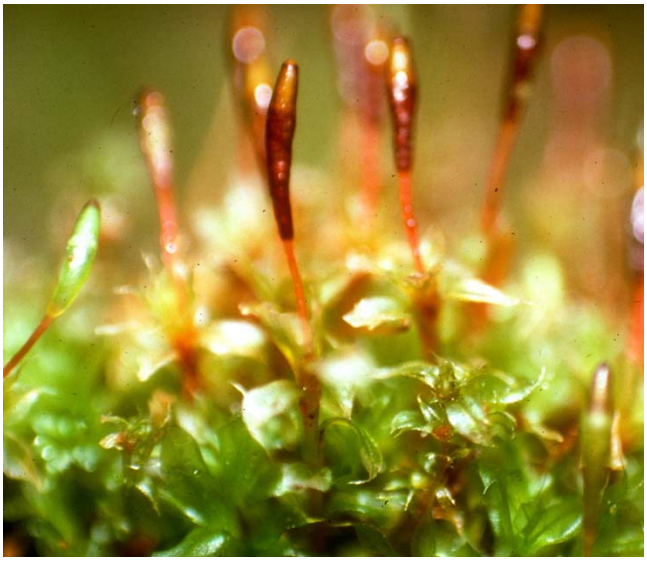

Figure 10. ***Tayloria octoblepharum*** with capsules. Photo by Janice Glime.

Figure 11. ***Rosulabryum campylothecium***, a species common in soil diaspore banks but not in litter. Photo from British Bryological Society website, with permission.

Figure 12. ***Lunularia cruciata*** showing gemmae. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 13. ***Fissidens serratus*** germinating bud. Photo by Tom Thekathyil, with permission.

Figure 14. ***Racopilum cuspidigerum***. Photo by Jan-Peter Frahm, with permission.

Figure 15. ***Tortula antarctica*** with capsules, a species for which spores occur in the litter but not in the soil of Australian bushland. Photo by M. Fagg, Australian National Botanic Gardens <www.anbg.gov.au>, with online permission.

Figure 16. ***Bryum argenteum*** males. Photo by George Shepherd, through Creative Commons.

Figure 17. ***Rosulabryum billarderi***. Photo by Tom Thekathyil, with permission.

Figure 18. ***Gymnostomum aeruginosum***. Photo by John Game, through Creative Commons.

During (2001) considers that species such as ***Micromitrium tenerum*** (Figure 19) and ***Physcomitrium sphaericum*** (Figure 20) that require "episodically suitable habitats" persist in the diaspore bank as spores. In Mediterranean habitats where conditions permit winter annuals to persist, a sporebank is likewise an important source. On the other hand, in temperate forests and grasslands, long-lived shoots (especially pleurocarpous mosses) are rare in the diaspore bank even if numerous on the surface, whereas the short-lived species are typically over-represented in the diaspore bank, often as asexual propagules, awaiting small-scale disturbance.

Figure 19. ***Micromitrium tenerum***, an ephemeral moss. Photo by Jan-Peter Frahm, with permission.

Figure 20. ***Physcomitrium sphaericum*** with protonemata, leaves, and capsules. Photo by Michael Lüth, with permission.

During (2001) considers that ruderal species often produce several types of propagules that are suitable for different conditions. One such species is ***Blasia pusilla*** (Figure 21), which has stellate gemmae (Figure 22-Figure 23) that have two auricles with the nitrogen-fixing Cyanobacterium ***Nostoc*** (Figure 24) and large amylochloroplasts in the gemmae. Its second type of gemma is ellipsoid or ovoid (Figure 25) and produced in flask-shaped structures (Figure 21-Figure 26). They are filled with starch, proteins, and lipids but lack ***Nostoc*** (Duckett & Renzaglia 1993). The stellate gemmae are produced throughout the growing season, but do not survive the winter cold. The ellipsoid gemmae are not released until late summer or autumn and do survive winter, germinating in the spring. These latter gemmae are suitable for the diaspore bank, but their presence there does not seem to be documented (During 2001). It is likely that other taxa with multiple diaspore types likewise have a division of labor.

Figure 21. ***Blasia pusilla*** showing flask-shaped stalks with gemmae on top. Photo by Dick Haaksma, with permission.

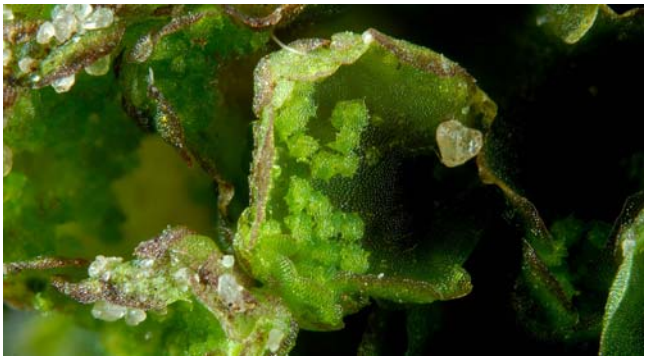

Figure 22. ***Blasia pusilla*** showing stellate gemmae. Photo by Dick Haaksma, with permission.

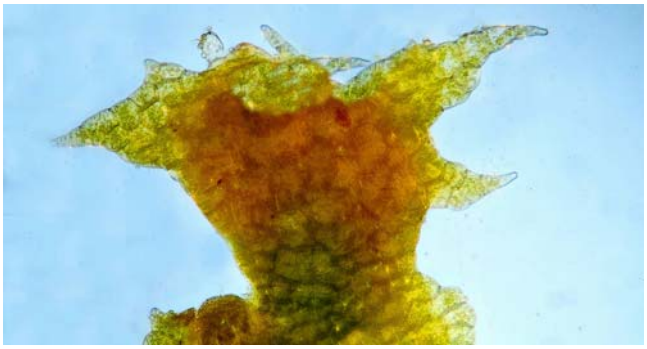

Figure 23. Stellate gemma of ***Blasia pusilla*** with ***Nostoc*** colonies. Photo by Dick Haaksma, with permission.

Figure 24. Thallus of ***Blasia pusilla*** with dark-colored ***Nostoc*** colonies. Photo by Walter Obermayer, with permission.

Figure 25. ***Blasia pusilla*** elliptical gemmae from the flask-shaped stalk. Photo by Dick Haaksma, with permission.

Figure 26. ***Blasia pusilla*** flask-shaped stalk with gemmae on top. Photo by Des Callaghan, with permission.

Species Differences

Not all diaspores enter the diaspore bank equally. Representation in diaspore banks is not necessarily a good indication of what grows at the surface. During (1997) found that species that were short-lived above-ground were usually over-represented in the diaspore bank, but perennial species tended to be absent or rare. These diaspore bank species tend to have large spores, but many are only represented by vegetative diaspores.

Lönnell (2011) reviewed dispersal literature and concluded that diaspore banks have little representation by even dominant pleurocarpous mosses, whereas the short-lived species that one can easily miss in the flora are common in the diaspore banks. This may account for the observations of Vitt (2006), who summarized previous studies and concluded that diaspore banks usually lack good representation of the extant community. Instead, he found that the species dominating the current community are generally rare or absent in the diaspore bank; rather, spores present in the diaspore bank represent pioneer species that are not present in more mature stages. This latter statement supports the conclusion of Lönnell (2011) that the short-lived species are the most common. Lönnell also found that larger diaspores are better represented than smaller ones. This latter strategy is useful for species that must await an opening, then accomplish their life cycle quickly before the competition arrives. During *et al*. (1987) demonstrated that even in diverse habitats in Spain, this bias holds true. They found tubers, gemmae, leaf fragments, and viable cells on decaying stems in the diaspore banks. Despite the mix of bryophytes growing on the surface, the diaspore bank was dominated by species with a colonist life strategy. On the other hand, Poschlod (1995) concluded that for disturbed (mined) peatlands, recolonization is from the diaspore bank.

During and ter Horst (1983) found 37 species in the diaspore bank of a chalk grassland. Among these the **acrocarpous** (having archegonia terminal on upright stems; mostly growing vertically) colonists were likewise the most frequent, despite dominance of **pleurocarpous** (having archegonia on short side branches; mostly growing horizontally) mosses and perennial liverworts on the surface. During (1990) suggested that high species diversity in chalk grasslands might be maintained by intermediate disturbances that cause a high turnover of species originating from the diaspore bank.

During and Moyo (1999; During 2003) found that in a Zimbabwean savannah, fire did not seem to harm the diaspore bank. Following disturbance by burning, only ***Exormotheca holstii*** (Figure 27), 2 ***Riccia*** spp (Figure 97), 2 ***Archidium*** spp (Figure 109) and ***Bruchia*** (Figure 28) emerged from soil samples near the surface in the middle of the rainy season (During & Moyo 1999; During 2003). Nevertheless, in soil samples representing the diaspore bank 11 liverworts and hornworts and 21 moss species were present. As seen in a number of other studies, taxa often were absent in the surface flora and appeared only when the right disturbance conditions occurred (During 2007). During and Moyo (1999) found that some rare species and even some species previously unknown for that region were conserved in the diaspore bank (During & Moyo 1999; Zander & During 1999).

Some species always seem to be there when the landscape is scoured for a road cut or for making a ski trail. Such is the case for ***Trematodon ambiguus*** (Figure 29). In fact, this species had been considered to be extinct in

Belgium and the Netherlands, but following large-scale disturbance it reappeared, apparently from a long-lived spore bank in the soil (During *et al*. 2006). The spores are somewhat large (~30 µm), not especially numerous in the capsule (~14,000), and emerged from soil samples taken at 0-3 cm.

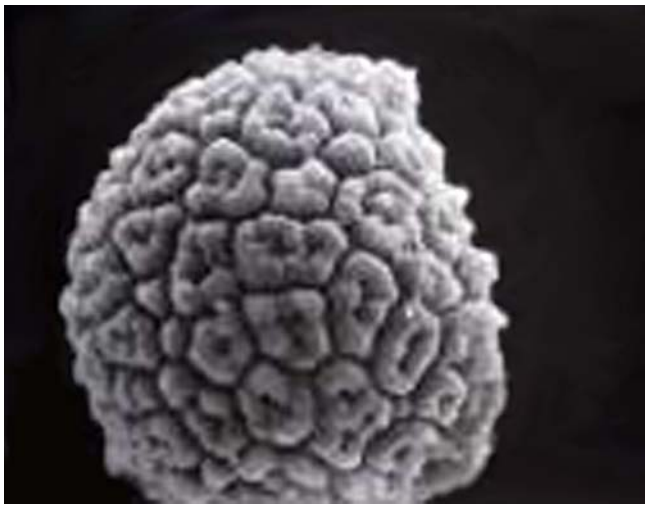

Figure 27. ***Exormotheca holstii*** spore, a propagule that can regenerate after fires in the Zimbabwe savannah. Photo by Laura Forrest, permission pending.

Figure 28. ***Bruchia flexuosa***, a species that can emerge from the diaspore bank after fire. Photo by John Game, through Creative Commons.

Figure 29. ***Trematodon ambiguus*** capsules in an exposed soil bank along a new ski trail in Houghton, MI, USA. Photo by Janice Glime.

While not all bryophytes enter the diaspore bank equally, neither do they emerge equally. In a different road-cut study, Hassel and Söderström (1998) found that two species of ***Pogonatum*** behaved differently. ***Pogonatum dentatum*** (Figure 30) was most likely to occur on roads only 0-4 years old, whereas ***P. urnigerum*** (Figure 31) was more likely along roads more than 4 years old. At least for ***P. dentatum***, frequency in the diaspore bank decreased with distance from parent colonies, suggesting that the diaspore bank is more important than diaspore rain.

Figure 30. ***Pogonatum dentatum***, a species that appeared along new road cuts. Photo by Michael Lüth, with permission.

Figure 31. ***Pogonatum urnigerum*** with capsules and young male splash cups (unopened). This species appeared along road cuts more than 4 years old. Photo by Michael Lüth, with permission.

Some tuber-bearing mosses (Figure 35) seem to be especially dependent on diaspore banks. They may be very common in the diaspore bank, but absent on the surface until the soil is disturbed (During 1995). Where they do occur on the surface, maintenance of that population seems to depend on occasional recruitment from the diaspore bank. Nevertheless, they can still exhibit clonal behavior because the tubers are deposited near the parent on relatively long rhizoids.

Arable Fields

In three cultivated fields of Switzerland, Bisang (1996) found ***Anisothecium staphylina*** (Figure 32), ***Dicranella schreberiana*** (Figure 33), ***Bryum rubens*** (Figure 34-Figure 35), ***Pottia*** sp (Figure 118), and ***Phascum*** sp (Figure 61) as common members of the soil diaspore banks. As is typical, some species were present in the diaspore bank but not

present among the flora of that field. Species of diaspores in these agricultural habitats varied most between localities.

Figure 32. ***Anisothecium staphylina***, a species that appears after disturbance of cultivated fields in Switzerland. Photo by Michael Lüth, with permission.

Figure 33. ***Dicranella schreberiana*** with capsules, a species common in diaspore banks of arable fields. Photo by Michael Lüth, with permission.

Figure 34. ***Bryum rubens*** growth habit, a species common in arable fields in Switzerland. Photo by Michael Lüth, with permission.

Figure 35. Rhizoidal tubers on ***Bryum rubens***. Photo by Jan-Peter Frahm, with permission.

Ponds and Lakes

One common bryophyte in the mud of ponds and lakes is ***Physcomitrium sphaericum*** (Figure 20). This species is not a regular member of the flora surrounding these water bodies because it requires conditions that are not present annually: exceptionally warm, dry summers (Furness & Hall 1981). In fact, the spores will germinate only in the range of 15-35°C. Its appearance under those suitable conditions is possible only because its spores remain viable in the mud for a long time.

Forests

The role of diaspore banks in various forested landscapes has been investigated through several studies. Caners *et al*. (2009) used mineral soil samples from mixed and coniferous stands of boreal mixed-wood forest in northern Alberta, Canada, to examine the role of these potential diaspore banks in reforestation after harvesting. Surprisingly perhaps, the composition of bryophyte species that were able to germinate related not to the forest types or harvesting intensity (measured by light regime), but to edaphic factors and, not surprisingly, to spatial proximity. Spatial proximity not only accounted for the species available, but also accounted for edaphic similarities. Nevertheless, light intensity had a significant influence on both the responses of individual species and on the species assemblages that arose.

In the boreal forest, Jonsson (1993) found 40 species, similar to the number found by During and ter Horst (1983) in chalk grasslands, of liverworts and mosses in the diaspore bank of an European *Picea abies* forest. The most abundant taxa were ***Pohlia nutans*** (Figure 36-Figure 37), ***Sphagnum*** spp. (Figure 47-Figure 52), and ***Polytrichum commune*** (Figure 88-Figure 89) / ***Polytrichastrum longisetum*** (Figure 38). In the boreal forest soil diaspore bank in southeastern Norway, Rydgren and Hestmark

(1997) found that ***Plagiothecium laetum*** agg. (Figure 39) and ***Polytrichum*** spp. (Figure 88-Figure 89) were the most frequent bryophytes germinating. Sean Robinson succeeded in growing new plants from a plant fragment of ***Pohlia nutans*** (Figure 37).

Figure 36. ***Pohlia nutans*** becoming established on sand. Photo by Des Callaghan, with permission.

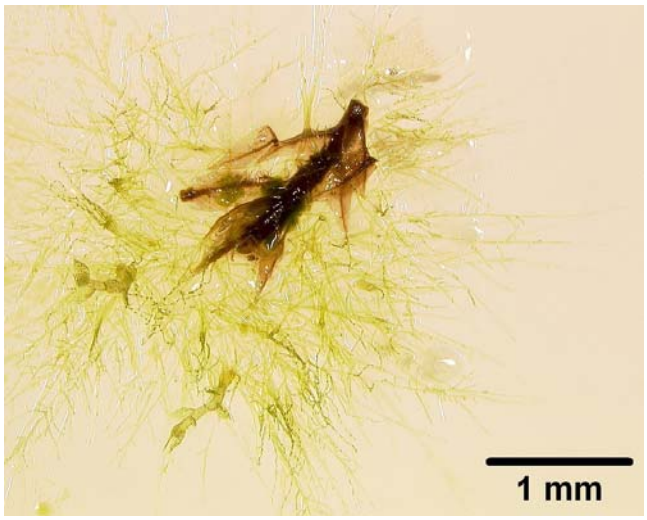

Figure 37. ***Pohlia nutans*** growth from fragments. Photo by Sean Robinson, with permission.

Figure 38. ***Polytrichastrum longisetum*** with capsules and mixed with ***Campylopus*** sp. Photo by David T. Holyoak, with permission.

Figure 39. ***Plagiothecium laetum***. Photo courtesy of Betsy St. Pierre.

Forest gaps benefit from diaspore banks. Palisaar and Poschlod (2001) found that both forest and windthrow areas have a predominance of long-lived species, but the colonist strategist predominates in the diaspore bank, ready to take advantage of large, sunny gaps.

Tropical forest diaspore banks have rarely been studied, but it appears that their composition follows different patterns from those of other forests and periodically disturbed habitats. In lab cultures of diaspore banks from Brazil, bark (68) and decaying wood (55) species dominated, compared to soil species (22) (Maciel-Silva *et al*. 2012). Mosses were more numerous in both species and number of shoots than liverworts. Monoicous species were more common than dioicous species. Species that produced sporophytes and those producing gemmae were well represented in the diaspore banks. The biggest difference was that the diaspore banks represented the growing vegetation rather well.

When culturing samples from the diaspore bank of three Malaysian mountain rainforests, Bisang *et al*. (2003) found germination of more liverworts than mosses, especially from the lower altitudes, contrasting with the results of Maciel-Silva *et al*. (2012). These liverworts [***Cincinnulus*** (as *Calypogeia*) ***argutus*** (Figure 40), ***Mnioloma*** (as *Calypogeia*) ***fuscum***, ***Lepidozia wallichiana*** (Figure 41), and ***Zoopsis liukiuensis*** (Figure 42)], were, as in the study of Maciel-Silva *et al*., common taxa growing in the area. Stem fragments that had lost their chlorophyll seemed to be the diaspores that gave rise to ***Isopterygium*** sp. (see Figure 43) and cf. ***Ectropothecium*** sp. (Figure 44), but for other taxa they were unable to identify the type of diaspore.

Figure 40. ***Cincinnulus argutus***, a species in tropical diaspore banks. Photo by Des Callaghan, with permission.

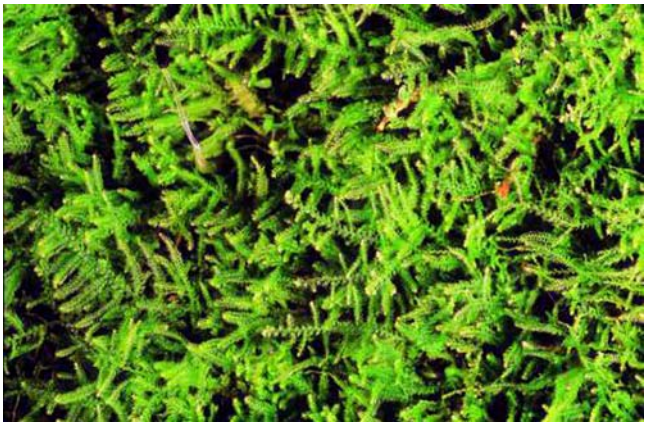

Figure 41. ***Lepidozia wallichiana***, a species in tropical diaspore banks. Photo by Jia-Dong Yang, through Creative Commons.

Figure 42. ***Zoopsis liukuensis***, a species in tropical diaspore banks. Photo by Rui-Liang Zhu, with permission.

Figure 43. ***Pseudotaxiphyllum elegans*** with gemmae, a species in tropical diaspore banks. Photo by Jan-Peter Frahm, with permission.

Figure 44. ***Ectropothecium perrotii***, a species in tropical diaspore banks. Photo by Jan-Peter Frahm, with permission.

Peatlands

In peatlands, recolonization is derived from diaspore banks and adjoining similar habitat. Sundberg and Rydin (2000) showed experimentally that 15-35% of ***Sphagnum*** spores could survive for 13 years when stored in humid conditions such as would be present in a peatland diaspore bank.

Campbell *et al*. (2003) found that in a regenerating Quebec, Canada, peatland, ***Polytrichum strictum*** (Figure 45) was widespread and its colonization showed no significant trends with distance from a living source. ***Pleurozium schreberi*** (Figure 46), ***Sphagnum capillifolium*** (Figure 47), and ***Sphagnum fuscum*** (Figure 48), on the other hand, only became frequent further from edges (> 20 m), suggesting that the right habitat conditions were absent at the edges. They explained the strong presence of ***Polytrichum strictum*** by the long fall times from capsule to substrate, coupled with its very small spores, facilitating its travel despite its low release height. Nevertheless, the diaphragm forces the spores out the sides, a position not conducive to aerial transport.

Figure 45. ***Polytrichum strictum*** with capsules in Europe, a species whose regenerating capacity does not seem to relate to distance from source. Photo by Michael Lüth, with permission.

Figure 46. ***Pleurozium schreberi*** in Michigan, USA. Photo by Janice Glime.

Figure 47. ***Sphagnum capillifolium***, a species that did not regenerate close to the edges of the peatland. Photo by David Holyoak, with permission.

Figure 48. ***Sphagnum fuscum*** in Alaska, USA, a species that did not regenerate close to the edges of the peatland. Photo courtesy of Andres Baron Lopez.

On the other hand, ***Sphagnum angustifolium*** (Figure 49), ***S. papillosum*** (Figure 50), ***S. cuspidatum*** (Figure 51), ***S. subsecundum*** (Figure 52), ***Pleurozium schreberi*** (Figure 46), ***Leucobryum*** sp. (Figure 53), and ***Chiloscyphus profundus*** (=*Lophocolea heterophylla*) (Figure 54) were present in the vegetation and absent in the measured diaspore rain of the regenerating peatland (Campbell *et al*. 2003).

Figure 49. ***Sphagnum angustifolium***, a species not detected in the diaspore rain of a regenerating peatland, but nevertheless present as a regenerant. Photo by Michael Lüth, with permission.

Figure 50. ***Sphagnum papillosum***, regenerating species absent from diaspore rain. Photo by Michael Lüth, with permission.

Figure 51. ***Sphagnum cuspidatum***, regenerating species absent from diaspore rain. Photo by Michael Lüth, with permission.

Figure 52. ***Sphagnum subsecundum***, a regenerating species absent from the diaspore rain. Photo by Michael Lüth, with permission.

Figure 53. ***Leucobryum glaucum*** with capsules. Note the broken leaves lying on the surface of the cushion. Photo by Janice Glime.

Figure 54. ***Chiloscyphus profundus***, a regenerating species absent from the diaspore rain of a peatland in Canada. Photo by Michael Lüth, with permission.

Poschlod (1995) conducted extensive studies comparing milled peatlands to natural raised bogs in the Bavarian foothills of the Alps. He found for those peatlands that recolonization apparently came entirely from diaspore banks, especially for ***Sphagnum*** species. That genus was entirely absent in the spore rain sampled. In particular, ***Sphagnum magellanicum*** (Figure 55), ***S. capillifolium*** (Figure 47), and ***Polytrichum strictum*** (Figure 45) occurred in the diaspore rain in at least one of the six sites studied.

Figure 55. ***Sphagnum magellanicum*** in Europe, a species that regenerates from diaspore banks. Photo by Michael Lüth, with permission.

Among the bryophytes in these peatland diaspore banks, Poschlod (1995) found six species of liverwort fragments. Of these, five of these are species that develop tubers. Furthermore, ***Cephalozia connivens*** (Figure 56) and ***Kurzia pauciflora*** (Figure 57) have subterranean shoot axes and ***Calypogeia*** (Figure 58) species have a shoot axis near the surface. Duckett and Clymo (1988) likewise found liverwort shoot axes in bogs in Great Britain and estimated that regeneration came from peat layers that were 25-60 years old. Based on studies by Clymo and MacKay (1987), they ruled out downwash into deeper layers.

Figure 56. ***Cephalozia connivens*** in Europe, a species that can persist in diaspore banks by its subterranean shoots. Photo by Michael Lüth, with permission.

Figure 57. ***Kurzia pauciflora*** in Europe, a species that can persist in diaspore banks by its subterranean shoots. Photo by Michael Lüth, with permission.

Figure 58. ***Calypogeia fissa***, a species that can persist in diaspore banks by its subterranean shoots. Photo by Hermann Schachner, through Wikimedia Commons.

Poschlod (1995) found all the ***Sphagnum*** species typical of raised bogs in the diaspore banks. Brown stems and branches of ***S. capillifolium*** (Figure 47) and ***S. cuspidatum*** (Figure 51) were able to regenerate from depths down to 15 cm. Peatland diaspore banks can be deep, with viable ***Sphagnum*** spores occurring as deep as 30 cm (Poschlod 1995). Poschlod (pers comm. 28 March 2013) concluded from this that the spores could survive more than two centuries!

Delayed Germination – Dormancy

Propagules may survive diaspore banks through dormancy (Hock *et al*. 2004). In two open grasslands in Hungary, gemmae of a species in the ***Bryum atrovirens*** complex (Figure 59) and ***Weissia controversa*** (Figure 60) exhibited dormancy. Likewise, dormancy seemed to be present in the spores of ***Tortula acaulon*** (=***Phascum cuspidatum***) (Figure 61). Hock *et al*. suggested that dormancy may be relatively common for diaspores of species living in habitats with short-term periods of unfavorable growing conditions.

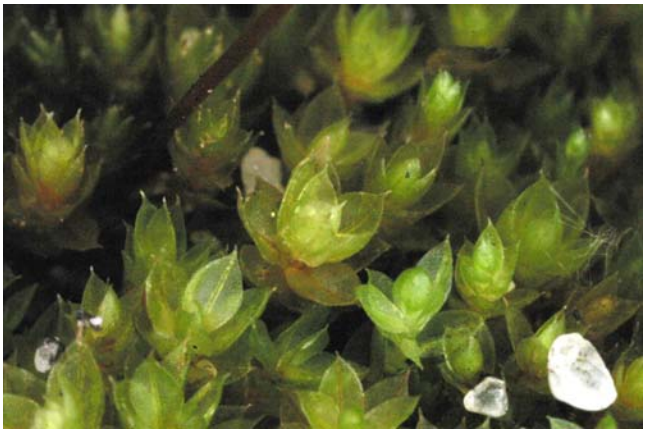

Figure 59. ***Bryum atrovirens*** aggregate. Photo by Jan-Peter Frahm, with permission.

Figure 60. ***Weissia controversa*** var ***controversa*** with capsules. Photo by David Holyoak, with permission.

Figure 61. ***Tortula acaulon*** (=*Phascum cuspidatum*) with capsules. Photo by David Holyoak, with permission.

It is interesting that initially the highest number of species in the boreal forest diaspore bank arose from the mineral soil (9.9 per sample), but after four years the reverse was true (Jonsson 1993), with more arising from the humus, suggesting that some species have a delay mechanism that does not permit them to germinate right away. Watson (1981) suggested that ***Polytrichum*** species had the option of chemical inhibition to facilitate dormancy. Such delay mechanisms are known from flowering plants and include such factors as immature embryos (not applicable to bryophytes), chemical inhibitors

that must be washed away or removed by digestive enzymes of an animal (not yet shown for bryophytes but possible), or the need for hormones or vitamins from a fungal or bacterial partner [known for development of the gametophore in ***Pylaisiella selwynii*** (Figure 62) and several other moss species (Spiess 1977, 1979; Spiess & Lippincott 1978; Spiess *et al*. 1971, 1972, 1973, 1976, 1981a, b, 1982, 1984a, b, c, d, 1986, 1990)]. I have cultured ***Fontinalis squamosa*** (Figure 63) that produced protonemal gametophore buds in the presence of contamination while the cultures that remained sterile produced no buds. What other examples of bryophytes are out there in nature where a living partner is needed to provide some growth factor necessary for development to continue – or even start?

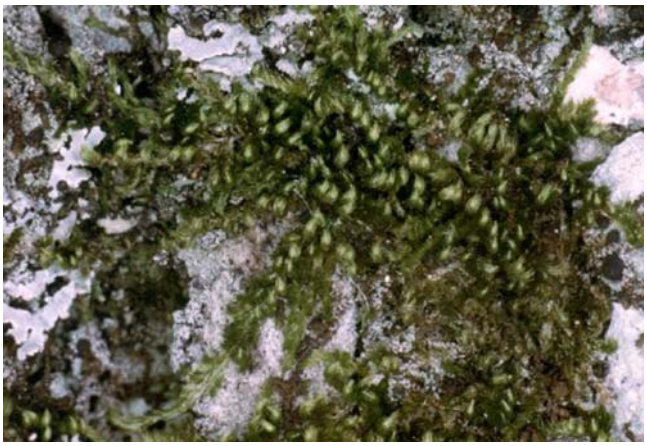

Figure 62. ***Pylaisiella selwynii*** on bark, a species that requires a bacterial partner to complete its development. Photo by Jan-Peter Frahm, with permission.

Figure 63. ***Fontinalis squamosa*** in Europe, a species that may require a bacterial partner to develop protonemal buds. Photo by Michael Lüth, with permission.

Other factors relating to delay of germination may be habitat condition or suitable weather. For example, in ***Sphagnum*** (Figure 47-Figure 52), dormancy may be conditional, depending on weather (Sundberg & Rydin 2000).

This leads us to ask what conditions are needed to break dormancy. Obviously, water is needed, and for continued success, light is needed. But water may be insufficient for continued development, so the spore needs a way to prevent germination when conditions are not likely to remain suitable. Mogenson (1981) suggested that spore surface sculpturing may serve to prevent small quantities of water from activating the spore by creating surface tension that prevents the water from penetrating the spore. However, this hypothesis seems not to have been tested.

Blasia pusilla (Figure 22-Figure 26) is one liverwort whose gemmae do not germinate right away when brought to the surface from a diaspore bank (During 2001). Gemmae of ***B. pusilla*** do not germinate until the spring after their production (Duckett & Renzaglia 1993), a phenomenon well known for seeds. This delay could be related to its storage of food reserves as protein, which is slower to metabolize than the starch or oils of other spores (Crum 2001). It seems likely to me that there are other bryophytes that have this delayed germination mechanism in spores or other propagules, especially in the **Anthocerotophyta** with their protein food reserves (Crum 2001). The leafy liverwort ***Lophozia ventricosa*** var. ***silvicola*** (Figure 64) changes its dormancy based on the time of production, with those gemmae produced in the spring germinating readily, but those produced later seem to lose germinability with time of production (Laaka-Lindberg 1999). A similar seasonal relationship is known for the forest floor tracheophyte *Melampyrum lineare*. If a propagule begins to convert its food reserves, loss of water could stop the process and prevent germination. This could only happen a few times before the reserves are used up, and a small propagule would lose its reserves sooner than a large one.

Figure 64. ***Lophozia ventricosa***. Photo by Hermann Schachner, through Creative Commons.

Asexual propagules likewise display dormancy. We have witnessed the effect of parents on inhibiting development of vegetative propagules, *e.g.* the absence of germination of ***Marchantia polymorpha*** gemmae (Figure 65) while they remain on the parent. There seem to be few species where either spores or vegetative propagules can germinate while still in contact with the parent, and many species, for example ***Funaria hygrometrica*** (Figure 178), are unable to germinate near their parents due to chemical inhibitors leached from the parent. Could there be biochemicals in the environment that must leach out before germination occurs in some species?

Even freshly produced spores may have dormancy (**innate dormancy**), as in ***Archidium alternifolium*** (Figure 66). This dormancy is broken slowly and the mechanisms for breaking it are unknown (Miles & Longton 1992). Germination was less than 65% and increased as the spores aged, up to 4 years. This delay suggests to me that there

may be a chemical inhibitor that is removed by leaching. In ***Sphaerocarpos texanus*** (Figure 67), spores are dormant when released, but dormancy is broken by fluctuating temperatures, typically 35/20°C and may even have dormancy/non-dormancy cycles resulting from temperature fluctuations (McLetchie 1999).

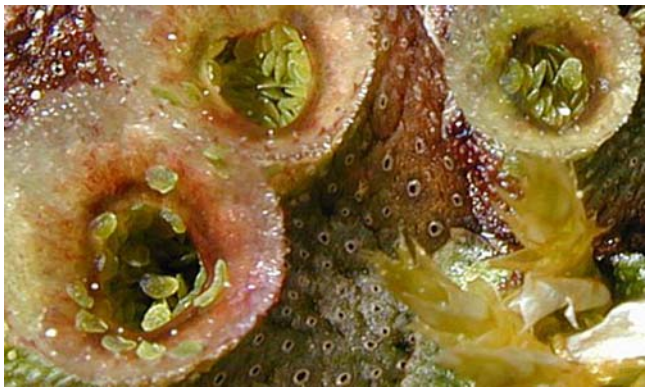

Figure 65. ***Marchantia polymorpha*** with gemmae. Photo by Michael Lüth, with permission.

Figure 66. ***Archidium alternifolium***. Photo by Michael Lüth, with permission.

Figure 67. ***Sphaerocarpos texanus*** on disturbed soil. Photo by Adolf Ceska, with permission.

Dormancy relationships seem to be complex, making them difficult to predict. Kobayashi and Yamamura (2000) found that inbreeding caused an increase in dormancy, perhaps through complementation. But the spores have only one set of chromosomes, so this logic seems to fail. And under some conditions inbreeding leads to decreased dormancy – a combination of genes where dormancy is poor to start with? We also know examples where longevity of female spores is longer than that of male spores [McLetchie 1992 for ***Sphaerocarpos texanus*** (Figure 67)]. How does dormancy affect longevity?

The seed bank houses a set of seeds that represent a non-random set of genotypes. That is, at the seed bank level, there is selection. There is evidence that there are correlations among suites of characters such as temperature of response and seed longevity. Such relationships need to be explored for bryophytes. Furthermore, risk of predation by animals and attack by fungi are strong selection factors for seeds, but these likewise have received inadequate attention for bryophytes.

Does Depth Matter?

Bisang (1996) compared germination of diaspores from above and below 25 cm for diaspores that were disturbed by regular ploughing to a depth of about 10-25 cm. In general, protonemata of mosses were less vigorous in soil samples from below 25 cm. Furthermore, ***Eurhynchium hians*** (Figure 8) and ***Riccia*** sp. (Figure 97) were present only to a depth of 15 cm.

Benefits of Diaspore Banks

Diaspore banks that have a store of recent species are likely to provide the soil/substrate characteristics required for the successful re-establishment from diaspore growth, once they are in a position to obtain sufficient light and moisture. On the other hand, light conditions may differ from those when the diaspores were deposited, and the species represented are often different from those on the surface (During & ter Horst 1983; During 1997). Furthermore, the species richness of the bryophytes may be influenced by the species composition of tracheophytes that has developed while the diaspores lay dormant (Aude & Ejrnæs 2005). For the short-lived shuttle species of agricultural landscapes, even the soil characteristics may have changed due to agricultural practices of fertilizing, a condition that can be detrimental to many bryophytes adapted to low nutrient conditions.

Tradeoffs

Diaspores, like any other novel solution, have their tradeoffs, although our understanding of these is very limited. During (2001) suggests that the lack of perennial bryophytes in the diaspore bank represents a tradeoff between adult longevity and diaspore longevity. Spore size is another potential tradeoff. Species with small spores such as ***Funaria hygrometrica*** (Figure 178) tend to have short viabilities in the soil (During 1987). During (2001) suggests that a similar tradeoff between dispersability and soil longevity could account for the scarcity of such weedy species as ***Marchantia polymorpha*** (Figure 1), ***Bryum argenteum*** (Figure 16), ***B. bicolor*** (Figure 68), and ***Ceratodon purpureus*** (Figure 69) in soil diaspore banks.

Nevertheless, Biggs and Wittkuhn (2006) found ***B. argenteum*** in the soil diaspore banks in all nine habitats in their study in western Australia. Could it be that this is a different microspecies?

Figure 68. ***Bryum bicolor*** with capsules, a species with good dispersability and poor diaspore longevity. Photo by Jonathan Sleath, with permission.

Figure 69. ***Ceratodon purpureus*** in southern Europe, a species with good dispersability and poor diaspore longevity. Photo by Michael Lüth, with permission.

Rather than small spores and good dispersal, During (2001) finds that the overall trend in diaspore banks is just the opposite. Those species that persist in the soil diaspore bank tend to have large spores (Jonsson 1993). This is a reasonable expectation because it would make it possible for these species to grow rapidly when they do germinate, taking advantage of the absence of competition from tracheophytes. Furthermore, many of these species have cleistocarpous capsules and short setae, making dispersal to any distance an unlikely event.

This presence of large spores in the diaspore bank is in contrast to that of seeds, where small seeds predominate. During (2001) suggests that seed predation on larger seeds and ease of dispersability of small spores may account for the difference in relationships. Furthermore, asexual diaspores are much more common among bryophytes.

Spores vs Vegetative Dispersal

All bryophytes require dispersal in some form to continue the species as its current habitat changes or disappears. Spores may be especially important for colonizing epiphytic habitats and other vertical habitats such as walls and cliffs, as well as being the primary source of propagules for forest clearings. Grime and coworkers (1990) contend that sporebanks are important in exploiting disturbed habitats, but even these sporebanks depend on aerial dispersal as well as local dispersal. These recolonization and new colonization events by spores are possible only because of the ease of dispersal of at least some of the spores.

Both spores and asexual diaspores provide the means by which bryophytes can reach new locations or spread in local ones. At some point, specialized asexual reproduction arose in photosynthetic organisms. Algae can make extensive use of fragmentation, and some algae have asexual spores. But bryophytes have developed specialized structures for their reproduction and never produce asexual spores, *i.e.*, they produce only meiospores.

We must ask then, what are the advantages of sexual vs asexual propagules, and under what circumstances? Newton and Mishler (1994) summarized our knowledge and pointed out that spores have a prerequisite of fertilization, and this process requires water. But spores usually disperse farther than vegetative propagules and germinate best in previously uncolonized substrates. Vegetative structures, on the other hand, can be produced even under stressful conditions, disperse well locally, and are more successful in germinating among existing colonies.

During (pers. comm. 5 January 2005), however, points out that in some cases, the role of spores in dispersal, particularly large spores, is very similar to that of asexual propagules, having short-range dispersal with greater chance of germination and establishment in a somewhat wider range of habitats. And if the species is **monoicous** (both sexes on same plant), it is likely that the spores resulted from selfing and thus have similar genetic makeup to that of any asexual diaspore that might be produced in the same species. Hence, there seems to be a trade-off in these species with large spores. There appears to be little advantage for them also to produce asexual structures for reproduction. This is especially true for annual shuttle species – these species may simply not have enough time to produce both, since many bryophytes typically do not have enough energy to produce sexual spores and vegetative diaspores at the same time, although they may ultimately be present at the same time.

Fritz (2009) tested the relative importance of asexual vs sexual reproduction in several species [***Pseudoscleropodium purum*** (Figure 6), ***Pleurozium schreberi*** (Figure 7), and ***Rhytidiadelphus squarrosus*** (Figure 70)] where sporophytes are considered to be rare. First, he found that sporophytes were apparently not so rare, using molecular data to demonstrate that the level of genetic diversity was that to be expected from spore dispersal. In these small populations, the genetic structure showed positive correlations between genetic diversity of a population and sporophyte occurrence. It appears that there may be an energy tradeoff at work here, because Fritz found that in these three species, clonal plants were present primarily in small patches up to 6 m^2 and were restricted to populations where both antheridia and archegonia, as well as sporophytes, were absent, or where only one sex of gametangia was present. This would be a good contingency strategy – that of a **bet hedger**.

Figure 70. ***Rhytidiadelphus squarrosus***. Photo by David Holyoak, with permission.

Pohjamo *et al*. (2006) compared spores and gemmae in the leafy liverwort ***Anastrophyllum hellerianum*** (Figure 71), where they are of equal size. Unlike the suggestion of During (pers. comm. 5 January 2005) that their dispersal distances would be equal, Pohjamo *et al*. found that dispersal distances differed, with gemmae travelling farther. Between 17.5 and 43.1% of the spores released and 0.64 and 4.8% of the gemmae available were deposited within 10 m of the central colonies. Rain had no effect on either dispersal pattern, but more gemmae were released on rainy days. This leaves us to wonder why gemmae travel farther. Perhaps their non-spherical shape causes them to be caught by the wind more easily, or to attach to animals more easily.

A number of species rarely produce capsules. If they likewise do not have any specialized reproductive structures, this presents a dispersal problem. But researchers continue to discover asexual means that were previously unknown or rarely described in floras. For example, despite the obvious presence of propagula in several species of ***Aulacomnium***, these are seldom mentioned for ***A. heterostichum*** (Figure 72), but can be quite abundant in some populations (Imura *et al*. 1991; Figure 72). Such was the case for ***Mnium stellare*** (Figure 73), a species that rarely produces capsules in Europe. However, in 2012, Hugonnot and Celle discovered that it reproduces by leaf **fragmentation**. This is not just random fragmentation, but rather the result of both splitting (**schizogeny**) and breaking (**lysogeny**). In **lysogeny**, there is partial cell disintegration that facilitates the fragmentation. They suggested that **schizogeny** was probably the result of hydration of the middle lamella. In ***Mnium stellare*** the fragility of the leaves seems to be greater when the leaves are hydrated, rather than when they are dry. Hugonnot and Celle verified these fragments as legitimate dispersal units by showing that they readily germinated on wet peat. Other species are already known for their leaf fragmentation abilities, *e.g.* ***Dicranum viride*** (Figure 74), ***D. fragilifolium*** (Figure 75), ***Tortella fragilis*** (Figure 76).

Figure 71. ***Anastrophyllum hellerianum*** gemmae that are the same size as spores in this species. Photo by Des Callaghan, with permission.

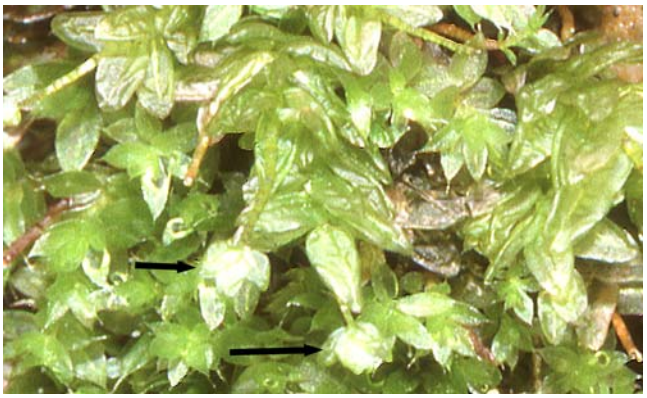

Figure 72. ***Aulacomnium heterostichum*** with propagules, indicated by the arrows. Note also the yellowish branch tips where these specialized leaves have been shed. Photo by Janice Glime.

Figure 73. ***Mnium stellare*** from the Khibiny Mountains, Apatity, Murmansk. Note the broken leaves at the arrows. Photo by Michael Lüth, with permission.

Figure 74. ***Dicranum viride*** showing broken leaves. Photo by Janice Glime.

Figure 75. ***Dicranum fragilifolium*** with broken leaf tips. Photo by Janice Glime.

Figure 76. ***Tortella fragilis*** with broken leaf tips. Photo by Michael Lüth, with permission.

Wang *et al*. (2012) used inter-sample sequence repeat markers and DNA sequences to investigate sexual vs asexual strategies in ***Hypnum plumaeforme*** (Figure 77) and ***Pogonatum inflexum*** (Figure 78). ***Hypnum plumaeforme*** reproduces primarily vegetatively. For this species, the genetic diversity among island populations was significantly greater than that among lakeside populations where the habitat became available and isolated 50 years earlier, suggesting greater isolation among the island populations. ***Pogonatum inflexum***, on the other hand, is frequently fertile, spreading primarily by spores. In this species there was no difference in genetic diversity between island and lakeside populations. Wang *et al.* (2012) considered this to be evidence that fragmentation of landscapes could increase genetic differentiation in species that have limited dispersal abilities, resulting in greater spatial differences in genetic structure.

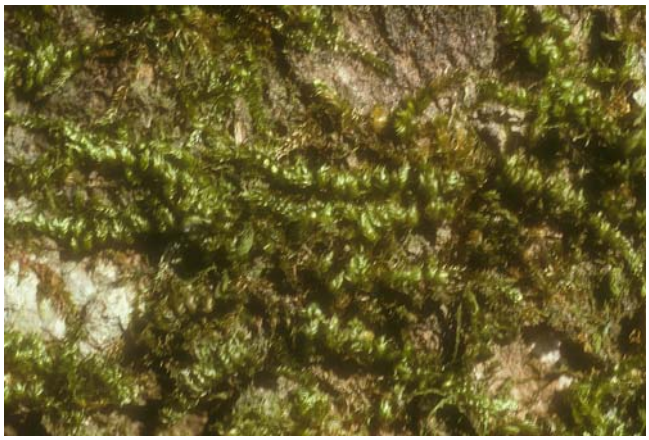

Figure 77. ***Hypnum plumaeforme*** on bark, a species that reproduces primarily vegetatively. Photo by Janice Glime.

Figure 78. ***Pogonatum inflexum***, a species that reproduces primarily by spores. Photo from the University of Hiroshima Digital Museum, with permission.

Understanding dispersal of bryophytes is complicated by their ability to disperse by more than one means. Furthermore, some species are not known to produce spores and others don't produce spores in some locations where only one gender is present. As an example, Bremer and Ott (1990) reported that nearly 40% of mosses in the Netherlands never or rarely produce spores. Nevertheless, the first bryophytes to colonize forests there are those that produce spores frequently, with those rarely producing spores [***Orthodicranum montanum*** (Figure 79), ***Rhytidiadelphus squarrosus*** (=*R. loreus*; Figure 80), ***Thuidium tamariscinum*** (Figure 81)] arriving 20 years later. In these forests, experiments suggest establishment from spores is very rare for perennial stayers. It is only in older forests that one can find species with large spores.

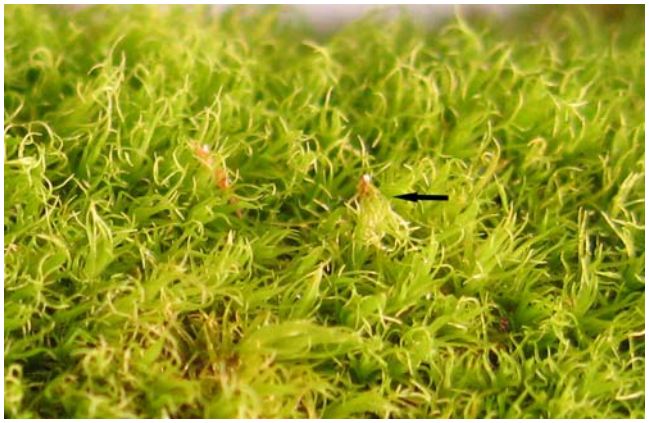

Figure 79. ***Orthodicranum montanum*** showing dislodged bulbil (**arrow**). This species can form entire colonies of bulbils or form larger gametophyte stems accompanied by these bulbils. Photo by Janice Glime.

Figure 80. ***Rhytidiadelphus squarrosus*** (=*R. loreus*) with capsules. Photo by David T. Holyoak, with permission.

Figure 81. ***Thuidium tamariscinum***, a moss that seldom produces capsules. Photo by Brian Eversham, with permission.

It is widely accepted that bryophyte spores are important for long distance dispersal to colonize newly available habitats (Newton & Mishler 1994). The time required, however, may be centuries or even millennia. Longton (1997, 2006) sums up the differences as one of spores being able to establish new populations more easily and asexual propagules being of major importance in colony expansion and maintenance.

Differences in Success

One question we might ask is why do some (actually many) bryophytes maintain both sexual and asexual reproductive propagules? Bengtsson and Ceplitis (2000) contend that for such a system to evolve and be maintained, the relative fitnesses of the sexual and asexual propagules must vary over the years. This would permit the most fit system to operate under the environmental conditions of that year. These conditions might be weather conditions, but they can also relate to competition, availability of bare soil, disturbance, herbivory, and other environmental factors. In this context, we might ask what hormonal changes occur in response to herbivory, or how does nutrient depletion affect asexual vs sexual reproduction? And if it is dry, will that stimulate asexual instead of sexual reproduction?

Frahm (2009) claims that there is no difference in effectiveness between sexual and vegetative propagation. He contends that the small size and weight of both spores and vegetative propagules would lead one to believe that both can be dispersed easily, thus supporting wide ranges for the species. Some species do have wide distribution, whereas others have very narrow ranges. And both of these categories include strictly vegetative reproducers and sexual (spore) reproducers. This disparity of ranges does not seem to relate to the abundance of propagules produced, with some species with high production of propagules demonstrating limited distribution and some sterile species having wide distribution (Frahm 2009).

But Callaghan and Ashton (2008) have arrived at a different conclusion for bryophytes in the British Isles. They found that among the 430 taxa there, range-size of both mosses and liverworts is significantly positively correlated with sporophyte production. But in seeming contradiction to this relationship, they found that **monoicous** (having both sexes on the same plant) moss species were rarer than **dioicous** (having the two sexes on different plants) species, suggesting that this rarity of monoicous taxa may be due to less fitness arising from self-fertilization.

Data on ***Octoblepharum albidum*** (Figure 82-Figure 83) demonstrate a different benefit than is typically attributed to gemmae. Their protonemata from gemmae grow faster than those from spores, most likely making their establishment more successful. On the other hand the spores produce more gametophytes. That is, one gemma produces one plant, but one spore produces many plants arising from multiple buds on a single protonema, at least for mosses.

It is not unusual for bryophytes to have more than one vegetative means of propagation. For example, ***Rhytidium rugosum*** (Figure 84-Figure 85) has three types of vegetative propagation: ramets (vegetative branches that separate by decay and disintegration when they are older; Figure 84); brood branches; and caducous branches (branches that easily break off as dispersal units; Figure 85). Pfeiffer *et al*. (2006) used AFLP fingerprinting to identify three clones from two plots, each having 2-15 samples with identical fingerprints. Presence of one clone in two plots indicates dispersal by vegetative diaspores. The close relationships between plots suggest that these plots were created through cloning, not spore dispersal.

Figure 82. ***Octoblepharum albidum*** with both capsules and gemmae (arrow). Photo by Li Zhang, with permission.

Figure 83. ***Octoblepharum albidum*** leaf with gemmae. Photo by Li Zhang, with permission.

Figure 84. ***Rhytidium rugosum*** showing dark bases of the ramet that will eventually decay and separate this piece (ramet) into a new plant. Photo by Michael Lüth, with permission.

Figure 85. ***Rhytidium rugosum*** demonstrating a dry branch that can easily be broken off (**caducous**) by a frisky squirrel. Photo by Michael Lüth, with permission.

Molecular data for ***Pseudoscleropodium purum*** (Figure 6) and ***Pleurozium schreberi*** (Figure 7) showed clonal reproduction [as in ***Rhytidium rugosum*** (Figure 84-Figure 85)] was an important part of their population dynamics (Fritz 2009). Fritz (2009) furthermore found possibilities for vegetative reproduction that had not yet been documented, including cloning, brood branches/branchlets, caducous shoot apices, and brood leaves (only in ***P. schreberi***).

Löbel *et al*. (2009) compared mating systems and concluded that larger asexual diaspores enjoyed higher establishment rates at the cost of shorter dispersal distances, whereas the small sexual spores sacrificed establishment rate to achieve greater dispersal distances, a concept supported by the ***Rhytidium rugosum*** (Figure 84-Figure 85) study (Pfeiffer *et al*. 2006). This is an interesting contrast to that of Pohjamo *et al*. (2006) for the leafy liverwort ***Anastrophyllum hellerianum*** (Figure 71) where the vegetative gemmae travelled farther.

Limits to Success

These inconsistencies based on propagule size and abundance lead us to the conclusion that the propagules of different species have different abilities to arrive and colonize in new locations, using attributes independent of size. As Frahm (2009) points out, it suggests that the germinating propagule is limited by narrow ecological niches, age of taxon, local extinction, or historical events such as ice ages. Caners *et al*. (2009) also found that microhabitat conditions determine the success of species once they arrive or get exposed from soil banks. **Edaphic** (soil) factors are especially important, as well as habitable space. Although successful species composition did not relate to forest type or harvesting intensity, Caners and coworkers found that light intensity had a significant influence on the success of individual species and thus has important management implications in reforestation. To further their assertion of the importance of soil, we might consider the conclusions of Bischler and Jovet-Ast (1981) that in the **Marchantiales** (Figure 1) morphological characters may not be important to survival and dispersal, but rather their adaptations are primarily "linked to biochemical and biophysical properties of the cell content."

With respect to soil characters, I must caution about an area of research that has received little attention. In a new location, differences in soil chemistry could cause morphological differences that could cause even an astute systematist to assume a different species. This can of course be sorted out by DNA fingerprinting, but there is little experimental evidence to address this question. A few studies have, however, demonstrated the plasticity of species under different environmental conditions. For example, Zastrow (1934) cultured a variety of species and showed that responses to water culture include loss of central strand, papillae, alar cells, and leaf border, as well as showing reduction in costa and chlorophyll. Alkaline conditions caused stem elongation between nodes compared to that in neutral and acid conditions. Buryová and Shaw (2005) cultured six populations of ***Philonotis fontana*** (Figure 86-Figure 87) under two light and two water regimes and observed that both light and water affected growth, but cell dimensions seemed unaffected. Responses differed not only according to treatment, but also showed genetic differences in their responses. But others have shown changes in the number of cell layers in the stem of ***Fontinalis*** (Figure 63) species (Sée & Glime 1984). Such plasticity makes tracking species dispersal pathways more difficult and our understanding is likely to remain under constant revision for some time to come as molecular data refute our earlier hypotheses.

Figure 86. ***Philonotis fontana*** in a wet habitat where it can become submerged. Leaves produced in these submerged conditions can be smaller and more widely spaced than those grown aerially. Photo by Michael Lüth, with permission.

Figure 87. ***Philonotis fontana*** showing brood bodies at the tip of the stem. Photo by Janice Glime.

In recent years, genetic/molecular methods are facilitating our understanding of the relative roles of asexual vs sexual means of reproduction in bryophytes (Shaw *et al*. 2002). For example, Derda and Wyatt (1990) measured 38 multilocus genotypes in populations of ***Polytrichum commune*** (Figure 88-Figure 89). They found that 69% of these genotypes were distributed evenly across the range of the species, with a mean genotypic diversity of 0.546 ± 0.042. This is a low value, coupled with potential for vegetative reproduction, and Derda and Wyatt used it to support the concept that spore-mediated gene dispersal in this species is limited. Van Zanten (1973) likewise asserted that dispersal of ***Dawsonia*** (Figure 90), another member of the **Polytrichaceae**, is limited due to the epiphragm that requires physical contact such as a raindrop to expel the spores.

Figure 88. ***Polytrichum commune*** with capsules. Photo by David Holyoak, with permission.

This chapter will consider each of these diaspore mechanisms and some examples of dispersal types among the bryophytes. Where possible (data are limited), we will examine what contributes to their success in getting established.

Figure 89. ***Polytrichum commune*** capsule showing epiphragm connected to teeth, forcing spores to exit the capsule from the sides. Photo by Michael Lüth, with permission.

Figure 90. ***Dawsonia longiseta*** with capsules. Photo by Niels Klazenga, with permission.

Figure 91. ***Polytrichastrum formosum***. Photo by Tom Thekathyil, with permission.

Which Strategy Accomplishes More?

In a model designed for Bryozoa, not bryophytes, Karlson and Taylor (1992) provided criteria for dispersal that would seem also to apply to bryophytes. Dispersal involves a tradeoff between energy spent on probable success of short distance dispersal and the energy lost to provide an expansion of the species through long-distance dispersal. "Using a procedure which minimizes the extinction probability for the lineage (hence maximizing survivorship of the genetic individual)," they predicted that "a high proportion of dispersed offspring should be associated with high numbers of asexual offspring, a low risk of mortality to offspring during dispersal, and high local survivorship of offspring."

One consequence of vegetative reproduction and dispersal might be a loss of genetic diversity. Van der Velde *et al*. (2001) used the genetic structure of ***Polytrichastrum formosum*** (Figure 91) to assess this genetic diversity in sexual vs asexual reproduction. They found that the levels of microsatellite variability were, on average, lower than those known for most other plant species. Nevertheless, genotypic diversity within the populations studied was high. They interpreted this as an indication that sexual reproduction is an important determinant of the within-population genetic structure of ***P. formosum***. Furthermore, Van der Velde *et al*. found no significant differences among microsatellite markers between populations or between regions (450 km in Denmark vs the Netherlands). They likewise interpreted this as evidence of sexual reproduction with high effective spore dispersal between populations, despite the well known ability of this species to reproduce clonally, supporting the interpretations discussed above for ***Pseudoscleropodium purum*** (Figure 6), ***Pleurozium schreberi*** (Figure 7), and ***Rhytidiadelphus squarrosus*** (Figure 70) (Fritz 2009). Members of the **Polytrichaceae** do not produce specialized asexual reproductive structures, and reproduction by fragments exists but is poorly known for most of the ***Polytrichum***/***Pogonatum***/***Polytrichastrum*** group (Figure 91).

The leafy liverwort ***Orthocaulis attenuatus*** (=*Barbilophozia attenuata*; Figure 92) provides another example of the tradeoffs. Korpelainen *et al*. (2011) found that diaspores of this species in the diaspore bank of a forest floor can be activated by disturbance. A disturbance as small as ant trails can favor the establishment of large gemmae over small spores for establishment. They found that these gemmae are effective at short distances, but not at mid-distances. For longer distances, spores are an effective means of dispersal. This short-distance gemmae dispersal provides compatible genotypes already adapted to this environment, but the tradeoff is the lack of genetic diversity and other problems attached to inbreeding.

Lost Energy

Production of sporophytes is a cost in energy. First, it costs energy to produce antheridia and archegonia. Then it costs energy to nourish the sporophyte to maturity. Production of spores likewise costs energy. Therefore, this costly process needs to afford a significant advantage for the species to succeed and survive with this strategy through evolution.

Figure 92. ***Orthocaulis attenuatus*** (=*Barbilophozia attenuata*), showing gemmae at the tips of some branches. Photo by Michael Lüth, with permission.

Nevertheless, some species seem to produce sporophytes to no avail. Unfavorable conditions for development may make vegetative dispersal more important than dispersal of spores. In Nigeria, the widespread ***Bryum coronatum*** (Figure 93) produces abundant sporophytes, but it appears that they have a large failure rate (Egunyomi 1982). Among those in the study, 42% remained undehisced even during the dry season when they normally discharge spores. Furthermore, 41% of the setae never developed capsules. Although the spore germination rate was 65-88%, protonemal growth was abnormal. The abundant production of axillary propagules is certainly important in those seasons, most likely frequent, when conditions during sporophyte development are less than ideal. This is a widespread species and sporophytes are most likely more important in other locations where conditions are more favorable for them.

Figure 93. ***Bryum coronatum***, a moss with a large failure rate for sporophytes in Nigeria. Photo by Jan-Peter Frahm, with permission.

As already mentioned, for species that produce large numbers of spores that travel great distances, most of those spores will not reach a suitable substrate and microclimate, hence contributing to the loss of energy.

Liverworts vs Mosses

Longton (1997) pointed out that the production of specialized asexual propagules is more common among (leafy) liverworts than among mosses. Gemmae are so common among leafy liverworts that their species often are identified by the structure and location of their gemmae. In the British liverwort flora, Laaka-Lindberg *et al*. (2000) found no association between production of asexual propagules and rarity, or with the monoicous vs dioicous condition. But those species that produce neither spores nor special asexual propagules are typically rare.

Habitat Differences

Disturbed Habitats

Disturbance can play a selective role for species that may be mediated by tradeoffs between dispersal rate and establishment success. Kimmerer (1993) found that ***Tetraphis pellucida*** (Figure 94-Figure 95) benefitted from frequent disturbance, whereas suppressed disturbance caused it to become out-competed by other bryophytes. Its competitor, ***Orthodicranum flagellare*** (Figure 96), is successful in colonizing gaps when there are other populations of the species nearby to contribute asexual brood branches. These germinate more rapidly than the gemmae of ***Tetraphis pellucida*** (Figure 94-Figure 95), making ***O. flagellare*** the better competitor.

Figure 94. ***Tetraphis pellucida*** gemmae in splash cups. Photo by Jan-Peter Frahm, with permission.

Flood plains, arable fields, and other regularly disturbed habitats are colonized by species that can lie dormant in diaspore banks during periods unsuitable for growth, or they must arrive quickly, colonize immediately, and complete their life cycles before the habitat is once again unfavorable. Such a habitat favors such species as thallose liverworts that can roll up their thalli, dry out, and resume growth from dormant terminal buds, as in ***Riccia*** (Figure 97). These are often invisible to the naked eye until those suitable growth conditions are provided, either in the field or in the lab. Kürschner and Parolly (1999) found that this community in Turkey consisted mostly of annual shuttle species and vegetative colonists that produced very large spores, retained spore tetrads, and/or produced asexual propagules, all of which survived in the diaspore bank during winter flooding and were able to re-establish the community quickly when the flood waters receded.

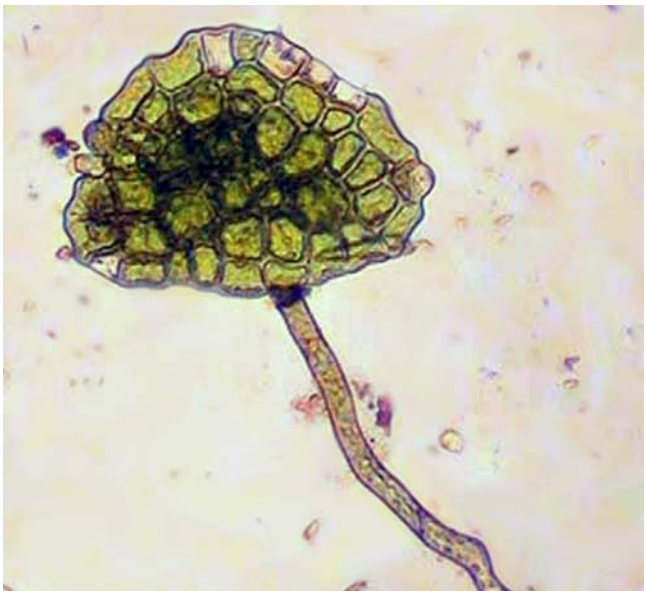

Figure 95. ***Tetraphis pellucida*** gemma germinating. Photo from UBC botany website, with permission.

Figure 96. ***Orthodicranum flagellare*** showing flagelliform branches that serve as propagules. Photo by Jan-Peter Frahm, with permission.

Figure 97. ***Riccia bischoffii*** var. ***ciliifera*** on drying mud. Photo by Jan-Peter Frahm, with permission.

Bijlsma *et al*. (2012) found ***Ephemerum cohaerens*** (Figure 98) and ***E. serratum*** var. ***rutheanum*** (Figure 99) in extensive beds where there was regular inundation and high flooding until May or early June, hence causing a setback to competing vegetation. They attributed the success of these species in these conditions to the flooding, life strategy, and soil characteristics. The large spores and tubers permitted these species to remain in the diaspore bank, whereas the rapid development of an extensive protonemal mat following the recession of flood waters gave them an establishment advantage. Their short life cycle permitted them to form plants in late summer and complete the life cycle to spore production in autumn.

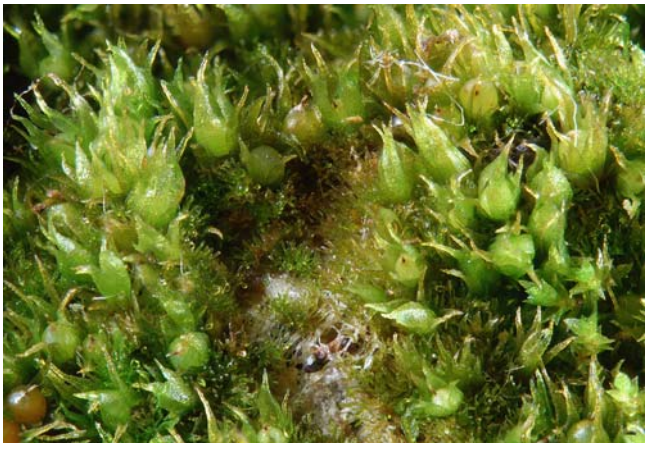

Figure 98. ***Ephemerum cohaerens*** with perigonia. Photo by Dick Haaksma, with permission.

Figure 99. ***Ephemerum serratum*** with capsules. Photo by David T. Holyoak, with permission.

Arable fields are a man-made habitat that favors certain bryophyte species. This can be a suitable habitat for some members of the **Anthocerotophyta**, but changes in agricultural practices can make the habitat unsuitable. Following years of hornwort-unfriendly agricultural practices, new eco-friendly practices returned in some areas of Europe. Bisang *et al*. (2009) compared the presence of this hornwort group before and after the eco-friendly practices were established in the Swiss plateau and found the return of ***Anthoceros agrestis*** (Figure 100) and ***Phaeoceros carolinianus*** (Figure 101-Figure 102). The re-establishment of these two species apparently resulted from spores that remained persistent in diaspore banks through the many years of unfavorable conditions.

Other disturbed habitat colonizers, like ***Marchantia*** (Figure 103), are frequent in the diaspore rain (Gaur & Kala 1984; Ross-Davis & Frego 2004) and arrive almost continuously, ready to take advantage of the low competition. ***Marchantia polymorpha*** is one of the colonizers after a forest fire (Graff 1936). In their experiments on buried propagules in an old-growth forest, Ingersoll and Wilson (1990) found that most (88%) of the gametophores emerging were from vegetative sprouts. There were significantly more vegetative sprouts in the undisturbed treatments. The number of emergents responded inversely to an increase in disturbance, with exposure to sun causing a significant decline in the six most abundant species. Vegetative structures with shallow burial were lost in the fire treatment.

Figure 100. ***Anthoceros agrestis*** with splitting sporophytes exposing spores. Photo by Michael Lüth, with permission.

Figure 101. ***Phaeoceros carolinianus*** on disturbed soil. Photo by Michael Lüth, with permission.

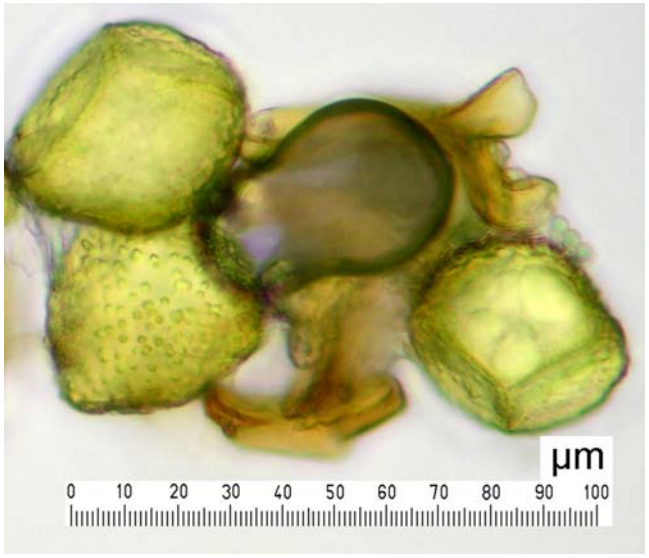

Figure 102. ***Phaeoceros carolinianus*** spores. Photo by David Wagner, with permission.

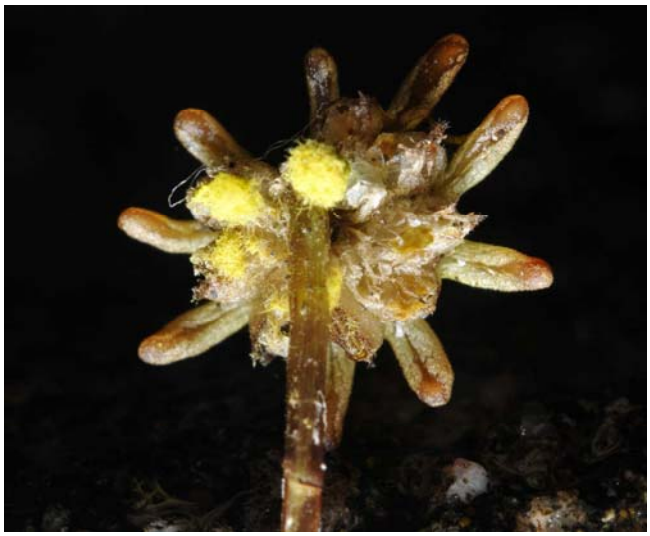

Figure 103. ***Marchantia polymorpha*** archegonial head showing spores and elaters. Photo by George Shepherd, through Creative Commons.

Unfortunately, our methods of determining what is in either diaspore banks or diaspore rain requires culturing, and this method is both time-consuming and incomplete, permitting us to identify the species if growth to a gametophore is successful, but often not permitting us to identify the dispersal structure that produced it. And we might not provide the right conditions for its successful development.

Epiphytes

Löbel and Rydin (2009) found that in epiphytic bryophytes, the conditions in the habitat influenced the production of sporophytes, but not that of asexual propagules. Furthermore, development of sporophytes had a negative effect on growth, whereas presence of asexual propagules did not. Further detriments to the sexual strategy arise from the need to reach a certain colony size before reproduction is effective; there is no threshold for the asexual reproduction. Thus, two sets of trade-offs arise: dispersal distance vs reproductive age and dispersal distance vs sensitivity to habitat quality. They considered that habitat turnover and connectivity may be more important selection pressures than species interactions.

The genus ***Radula*** (Figure 104), a leafy liverwort in which both monoicous and dioicous taxa exist, demonstrates a specific case for the advantages of asexual reproduction. In this genus that lives in a frequently dry environment, there was no correlation with either dioicy or epiphytism (Devos *et al*. 2011). Rather, there seems to have been a shift from sexual systems (dioicy to monoicy) among the facultative epiphytic taxa several times. Both facultative and obligate epiphytes in this genus produce gemmae equally, as well as dispersing gametophyte fragments. These asexual propagules may provide a pre-adaptive mechanism that permits the facultative epiphyte taxa to live on trees where frequent wetting and drying out are detrimental to the development of protonemata into buds and gametophores. Fragments and asexual propagules can skip this stage or use it only briefly before developing into a leafy plant. Devos *et al*. suggest that the larger size of these diaspores imposes a tradeoff by limiting dispersal distance.

Figure 104. ***Radula lindenbergiana*** with gemmae. Photo by Jan-Peter Frahm, with permission.

Peatlands

Peatlands are unique habitats, and they seem to do lots of things differently. Poschlod (1995) examined the relative importance of spores and fragments in the recolonization of milled peatlands in the Bavarian foothills of the Alps. He found that spores were relatively unimportant in the diaspore rain, but that fragments did

appear in the spore traps. In particular, branches and leaves of ***Sphagnum magellanicum*** (Figure 55), ***S. capillifolium*** (Figure 47), and ***Polytrichum strictum*** (Figure 45) were captured in the traps in most of the study sites. Furthermore, diaspore bank samples were placed in pots and cultivated for more than one year. In these pots, only three species germinated and grew: ***Betula*** (birch tree), ***Marchantia polymorpha*** (Figure 103), and ***Funaria hygrometrica*** (Figure 178).

The Antarctic

Harsh environments impose different selection pressures from the ones at play in more friendly environments. Lewis Smith and Convey (2002) offered evidence to refute the long-held hypothesis that bryophyte fertility decreases as latitude (and climate severity) increases. Using the maritime Antarctic (68-72° S lat) as an example, they demonstrated that a relatively high proportion of the bryophytes there were capable of producing sporophytes. At Marguerite Bay, 43% of the species (17 species of mosses, 2 of liverworts) were known to produce sporophytes; at Alexander Island it was 47% (16 species of mosses, 1 of liverworts). In more arid parts of the Antarctic continent, the number was less (33%). This is still considerably smaller than that found by González-Mancebo and Hernández-García (1996) for an altitudinal gradient in the Canary Islands, where most life cycle strategies had 70% fertility, with that of the perennial stayers being lower.

Not surprisingly, Lewis Smith and Convey (2002) found that most of the Antarctic fertile mosses in their study areas were short, monoicous acrocarpous species. For dioicous species, the problem arises of having both genders arrive on the island in sufficient proximity and having both mature at the same time under a different set of temperatures, day length, and moisture regime than at their source.

In this harsh Antarctic environment, spores were more abundant than bryophyte fragments in the Rotorod® samplers of Signy Island (Marshall & Convey 1997). Spore size did not seem to matter, with all five taxa occurring in samples 0.5-1 km from their nearest known sources. Nevertheless, the presence of spores was small compared to their represented ground cover and in comparison to the lichen propagules in the same samples. This extensive ground cover most likely resulted from vegetative spread after spore arrival.

Plasticity of Spore Size

Habitat may matter as well in determination of successful spore size and means of reproduction within a species. Hassel and Söderström (2003) compared the spread of ***Pogonatum dentatum*** (Figure 105) in the mountains vs lowlands in Fennoscandia. The lowland plants seem to have a tendency to produce more but smaller spores (statistically non-significant) compared to the mountain plants. Nevertheless, establishment in the mountains seems rarely to occur from either spores or leaves whereas these two methods are frequent in the lowland. On the other hand, the diaspore bank is more important in the mountains because of the more regular and shorter disturbance intervals there. The diaspores of ***P. dentatum*** are apparently too short-lived to survive the longer disturbance intervals in the lowlands.

Figure 105. ***Pogonatum dentatum***. Photo by Jan-Peter Frahm, with permission.

Seasons

In a study of airborne pollen and spores in Buenos Aires, Noetinger *et al*. (1994) noted that while spores are scarce throughout the year, they are mainly represented by the bryophytes, with the greatest densities in May to June. For seed plants, pollen density was dependent on phenology of the species, and densities corresponded with blooming seasons of the various groups. Latorre *et al.* (2008), in Mar del Plata city, Argentina, found an increase in pollen with an increase in temperature, reaching a maximum in early spring. Data differed among the trap types, with a negative correlation with wind using the Burkard trap and negative correlation with humidity using the Tauber trap. Data supporting such correlations with phenology and weather for bryophytes are meager. And some bryophytes retain their capsules for more than one year.

Marshall and Convey (1997) were surprised to find that spores were captured over a long time period on Signy Island in the Antarctic, including captures in the winter months. With availability of bare substrate, it is possible that spores could be redistributed from non-trapping surfaces throughout the year. Just what is going on during the seasons when most of us are not looking?

For ***Polytrichastrum ohioense*** (Figure 106) in the subalpine zone of the Yatsugatake Mountains, Central Honshu, Japan, capsules endure the winter in an immature stage, taking 13 months to mature and dispersing their spores in the following mid-July to mid-August (Ayukawa *et al*. 2002). In ***Racopilum africanum*** (Figure 107), ***Fissidens weirii*** (as ***Fissidens glauculus***), ***Thuidium gratum***, and ***Stereophyllum*** sp. (Figure 108) in southwest Nigeria, sporophytes develop and mature at the end of the same rainy season (Oct/Nov & Dec) as that for fertilization (beginning of rainy season) (Odu 1981). Spores from mature capsules of these species all dispersed during and after the dry season (Nov-Apr).

Figure 106. ***Polytrichastrum ohioense*** with capsules that take more than one year to mature. Photos by Bob Klips, with permission.

Figure 107. ***Racopilum africanum*** with developing sporophytes. Photo by Jan-Peter Frahm, with permission.

Figure 108. ***Stereophyllum radiculosum*** on bark. Photo by Scott Zona, through Creative Commons.

For ***Archidium ohioense*** (Figure 109), ***Bryum coronatum*** (Figure 93), ***Fissidens minutifolius***, and ***Trachycarpidium tisserantii***, also in southwest Nigeria, capsule dehiscence and spore dispersal occurred in September – October (Makinde & Odu 1994). But in this case, the stages of sporophyte development occurred during the rainy season, including capsule dehiscence and falling of the capsules themselves. Not surprisingly, they found that the spores did not discharge easily from the cleistocarpous capsules of ***A. ohioense*** or ***T. tisserantii***. In the Hiruzen Highlands of Japan, Nishimura (1993) found that dispersal dates for 34 species of mosses occurred in late autumn (late November) to early spring (early April); 12 occurred in late spring to summer (May to August) and 5 in autumn (September to November). One had no definite season and one had two dispersal seasons. In these examples, it appears that the season of dispersal is not random, but that conditions needed for one species may not be suitable for another. It is easy to understand that most small spores will benefit from dispersal when it is dry, permitting them to be carried by wind and air currents to new locations. For those with large spores that fall to the ground, a rainy season is beneficial for immediate germination and growth.

Figure 109. ***Archidium ohioense*** with capsules. Photo by Li Zhang, with permission.

Time of day matters and may help us to unravel the conditions favoring dispersal. For pollen, Pérez *et al*. (2003) found a maximum between 10:00 and 12:00 h, with a minimum at 18:00 h in Mar del Plata, Argentina. They suggested that optimal diurnal conditions for dispersal of arboreal pollen are high temperatures and low relative humidity. It is likely that this relationship could be applied on an annual scale and that it would also apply to bryophyte spores.

One seasonal advantage of asexual propagules is that they are generally produced throughout the growing season, whereas spores tend to be released during a limited time each year (During 2001).

Are These Adaptations?

Capsules and Setae

Setae develop first in **Bryophyta** and last in **Marchantiophyta** relative to the capsule. In either case, the elongated seta extends the spores farther above the plant (Figure 110), increasing the chances for them to be dispersed. Even in the **Anthocerotophyta**, where there are no setae, the elongate sporophyte matures from top down and dispels its spores from the top (Figure 100). Hence, we

might expect some differences in the length of the setae, with longer setae permitting spores to get farther from the parent bryophyte, and perhaps even hornwort sporophyte lengths, relative to dispersal needs. These may or may not correlate with characters of the capsule itself.

Figure 110. ***Pohlia nutans*** with nodding capsules and long setae. Photo by Michael Lüth, with permission.

We can list a number of differences among capsules that might contribute to their dispersal ability. Paramount among these is the means by which the capsule opens and dispels the spores. These will be discussed in some detail in the ensuing paragraphs, but one we might consider first is the drying of the capsule interior prior to spore expulsion. This process and its importance seem to lack experimentation except in ***Sphagnum*** (Figure 47-Figure 52), so some speculation is in order. Chater *et al.* (2011) have cited the regulation of stomatal behavior in photosynthetic organisms for 400 million years of evolution. Its role in leaves of tracheophytes is clear, but in bryophytes the sporophyte tissue is not in a leaf, and it is the sporophyte capsule that has the stomata (Renzaglia *et al.* 2000). However, it appears that as in the leaf, this tissue controls (perhaps permits is more appropriate) the loss of water. Recent evidence proposed by Duckett *et al.* (2010) suggest that we should consider the possible role of stomata in permitting the escape of moisture from the capsules of other mosses (Figure 111). Such drying leads to changes in capsule shapes and can contribute to the loss of the operculum, sometimes quite forcibly. This aspect of dispersal will be discussed in detail in another subchapter (4-9), but it may be helpful to keep this potential role in mind here as we examine dispersal strategies.

Habitat Differences

Spore capsules in mosses (but not in liverworts) seem to differ considerably among species, and many of these seem to fall into habitat categories. As Vitt (1981) points out, the function of the sporophyte is to produce and disperse the spores as efficiently as possible. In this role, selection pressures should shape the sporophyte into the most effective organ for its growing conditions. These selective pressures differ significantly among the major habitat classifications of hygrophytic, mesophytic, and xerophytic.

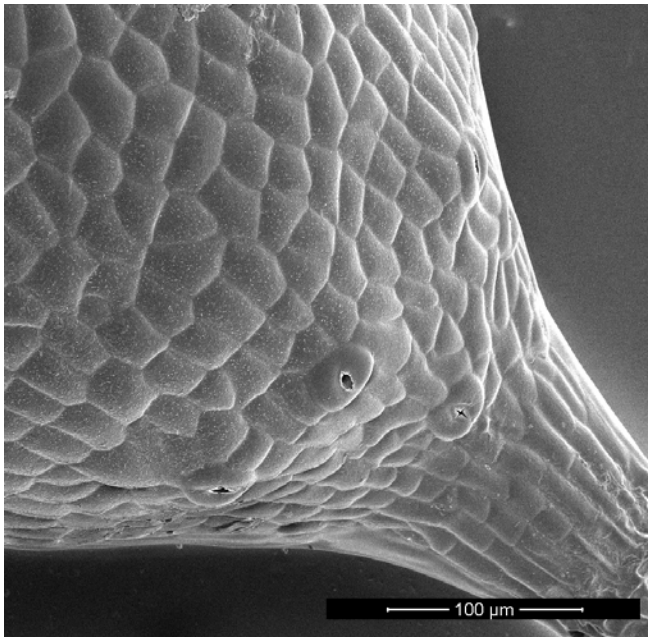

Figure 111. SEM of ***Physcomitrella patens*** stomata at base of capsule. Photo courtesy of Jeff Duckett and Silvia Pressel.

Xerophytes may be characterized by reduction of the sporophyte, including shorter seta length, broader and erect capsules, reduced or absent peristome including cleistocarpy, and large spores (Vitt 1981). These characters are often accompanied by a shortened life cycle that permits the xerophytes to avoid extended dry periods. As evidence, Vitt points out that this same group of adaptations has evolved in a number of unrelated mosses, including the acrocarpous genera ***Bryobartramia***, ***Viridivellus***, ***Sporledera*** (Figure 112), ***Goniomitrium*** (Figure 113), and pleurocarpous genus ***Gigaspermum*** (Figure 114). Others, including ***Encalypta brevipes*** (Figure 115), ***Ditrichum*** spp. (Figure 116), ***Funaria*** spp. (Figure 117), ***Pottia*** (Figure 118), ***Stegonia*** (Figure 119), ***Trematodon*** (Figure 120), and ***Weissia*** (Figure 121), lack the reduced life cycle but exhibit the other xerophytic adaptations.

Figure 112. ***Cleistocarpidium palustre*** (=***Sporledera palustris***) showing broad capsules. Photo by Jan-Peter Frahm, with permission.

Figure 113. ***Goniomitrium acuminatum*** subsp. ***enerve***, demonstrating the broad capsule typical of a xerophyte. Photo by David Tng <http://www.davidtng.com/>, with permission.

Figure 114. ***Gigaspermum repens***, demonstrating the broad capsule typical of a xerophyte. Photo by David Tng <http://www.davidtng.com/>, with permission.

Figure 115. ***Encalypta brevipes*** Khibiny Mountains, Apatity, Murmansk. Photo by Michael Lüth, with permission.

Figure 116. ***Ditrichum subulatum***, a species with an expanded capsule urn relative to others in the genus. Photo by Des Callaghan, with permission.

Figure 117. ***Funaria pulchella*** showing expanded capsule urn. Photo by Michael Lüth, with permission.

Figure 118. ***Pottia conica***, showing capsules with expanded urn. Photo by Jan-Peter Frahm, with permission.

Figure 119. ***Stegonia latifolia*** with slightly rounded capsule urns. Photo by Michael Lüth, with permission.

Figure 120. ***Trematodon longicollis***, a moss of disturbed banks. Note the long neck and expanded urn. Photo by Li Zhang, with permission.

Figure 121. ***Weissia controversa*** var. ***densifolia*** showing swollen urn. Photo by Barry Stewart, with permission.

Mesophytic taxa, on the other hand, can have amplified capsules, as in the entomophilous members of the **Splachnaceae** (Vitt 1981; Figure 199). Vitt lists other taxa exhibiting sporophytic amplification are some **Dicranaceae** (as polysety; Figure 122), **Mniaceae** (Figure 124), **Hypnodendraceae** (Figure 123), and ***Dawsonia*** [amplified peristome (Figure 126) compared to other **Polytrichaceae** (Figure 89)]. The mesophytic group, not faced with the extremes of habitat, has taken multiple routes that preclude a clear definition of adaptations. Vitt (1979, 1981) included elongate, straight setae; curved, horizontal to pendent capsules that are smooth, cylindric, and have well-developed peristomes as common characters of mesic forest floor mosses. Example taxa include ***Plagiomnium cuspidatum*** (Figure 124) and ***Timmia megapolitana*** (Figure 127).

Figure 122. ***Dicranum polysetum*** with polysetous capsules. Photo by Janice Glime.

Figure 123. ***Hypnodendron commutatum*** showing the large capsule. Photo by Janice Glime.

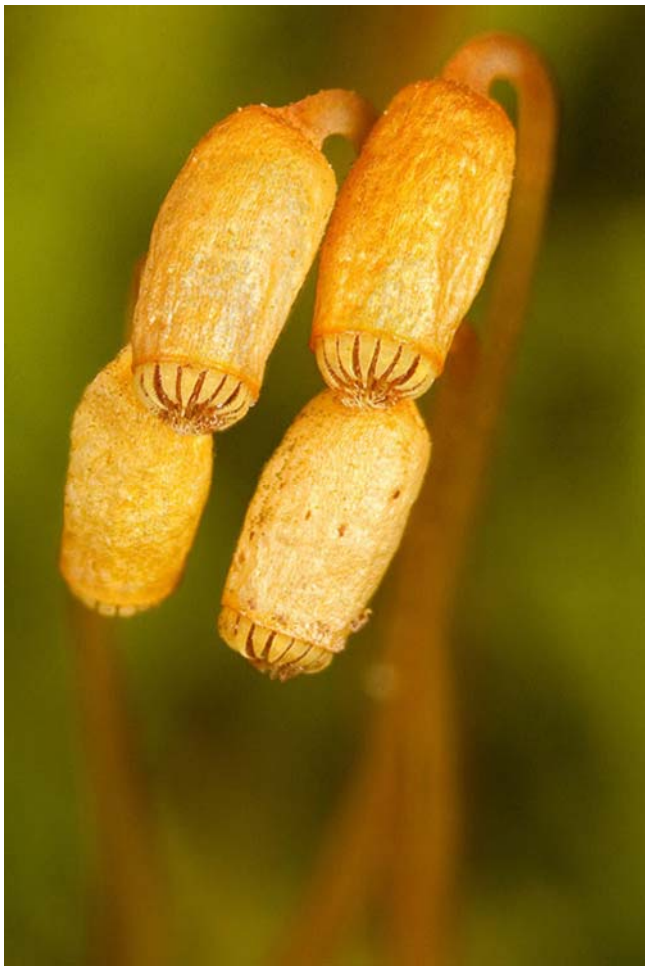

Figure 124. ***Plagiomnium cuspidatum*** illustrating the straight setae with smooth, cylindric, pendent capsules and well developed peristomes. Photo by Robert Klips, with permission.

Epiphytes usually have xerophytic adaptations, but these differ from those of the edaphic species because dispersal is a different problem for these elevated taxa. ***Cladomnion ericoides*** (Figure 125) provides a good example of epiphytic adaptations with its short, stout setae (permitting leaves and perichaetial leaves to protect the capsule from desiccation); erect, ribbed, ovate-oblong capsules; and sheathing perichaetial leaves (Vitt 1981).

Figure 125. ***Cladomnion ericoides*** from Pureora Forest, Taupo, NZ. Photo by Andy Hodgson, with permission.

Figure 126. ***Dawsonia longifolia*** capsule showing enlarged teeth. Photo from University of British Columbia Botany website, with permission.

Figure 127. ***Timmia megapolitana***. Photo by Jessica M. Budke, with permission.

Many epiphytic members of the **Isobryales** share similar features with other bryophytes of vertical surfaces: ***Haplohymenium*** (Figure 128), ***Andreaea*** (Figure 129), ***Fabronia*** (Figure 130), ***Grimmia*** (Figure 197), ***Tortula*** (Figure 131), ***Hedwigia*** (Figure 132), ***Orthotrichum*** (Figure 133-Figure 135), ***Ptychomitrium*** (Figure 136), ***Racomitrium*** *s.l.* spp. (Figure 137), and ***Tortella*** (Figure 76)**,** presumably adapting them to vertical substrates where humidity alternates between dry and wet periods and light intensity is higher (Vitt 1981). These habitat characteristics seem to favor the short, erect, ribbed capsules; short, stout

setae; reduced peristomes; and sheathing perichaetial leaves. Epiphytic ***Orthotrichum***, on the other hand, seems to have evolved from ribbed [*e.g.* mesophytic ***O. lyellii*** (Figure 133) or ***O. vittii*** (Figure 134)] to smooth [*e.g.* xerophytic ***O. pusillum*** (Figure 135)] capsules (Vitt 1981).

Figure 128. ***Haplohymenium triste*** with lichens on bark. Photo by Bob Klips, with permission.

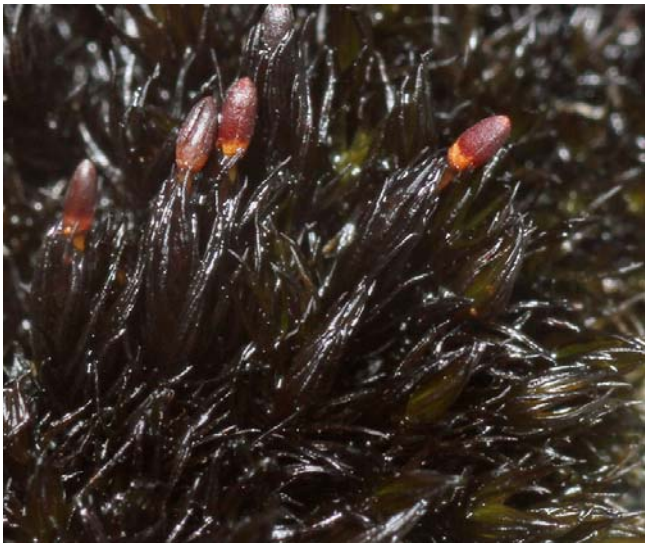

Figure 129. ***Andreaea rothii*** subsp. ***falcata*** showing valvate cylindric capsule. Photo by Barry Stewart, with permission.

Figure 130. ***Fabronia ciliaris*** with ovate capsules and short setae. Photo by Michael Lüth, with permission.

Figure 131. ***Tortula canescens*** capsules showing cylindrical shape and extended spiral peristome. Photo by Des Callaghan, with permission.

Figure 132. ***Hedwigia ciliata*** with short capsules on short setae and surrounded by perichaetial leaves. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 133. ***Orthotrichum lyellii*** with gemmae. Photo by Jonathan Sleath, with permission.

Figure 134. ***Orthotrichum vittii*** showing ribs on capsule. Photo by Jan-Peter Frahm, with permission.

Figure 135. ***Orthotrichum pusillum*** capsules. Note the nearly smooth (non-ribbed) surface of these capsules. Photo by Bob Klips, with permission.

Figure 136. ***Ptychomitrium polyphyllum*** showing short seta and cylindrical capsule. Photo by Malcolm Storey at Discover Life, through Creative Commons.

Figure 137. ***Bucklandiella affinis*** (=***Racomitrium affine***) with cylindric capsules, reduced peristome, and short setae. Photo by Michael Lüth, with permission.

Vitt (1981) considers two groups of mosses with submerged or emergent habits. Those with aquatic gametophytes and terrestrial sporophytes, often produced at times of low water levels, include, for example, ***Scorpidium*** (Figure 138), ***Hygrohypnum*** (Figure 139), ***Platylomella*** (as ***Sciaromium***; Figure 140), ***Drepanocladus*** s.l. (Figure 142), and ***Platyhypnidium riparioides*** (Figure 141). These taxa have sporophytes that align with mesophytic bryophytes from the forest floor. On the other hand, the aquatic mosses with aquatic sporophytes [*e.g.* ***Blindia*** (Figure 143), ***Fontinalis*** (Figure 144), ***Wardia*** (Figure 145), ***Scouleria*** (Figure 146)] tend to have reduced or absent peristomes; ovate or oblong, smooth, immersed capsules; enlarged perichaetial leaves; and thick or leathery **exothecial** (outer capsule wall) cells.

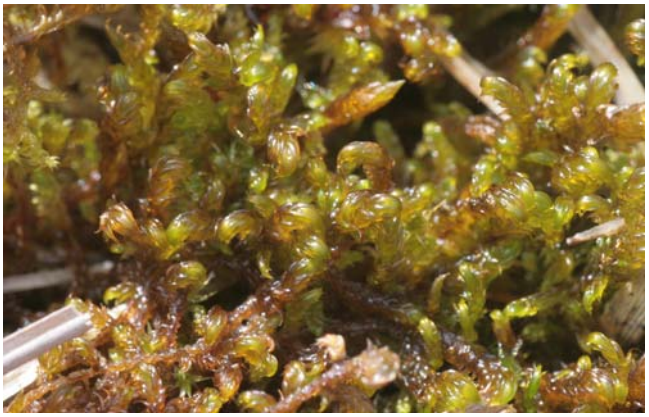

Figure 138. ***Scorpidium cossonii***. Photo by Hermann Schachner, through Creative Commons.

Figure 139. ***Hygrohypnum luridum*** with emergent capsules. Photo by Michael Lüth, with permission.

Figure 140. ***Platylomella lescurii***, a species that produces capsules at low water levels. Photo by Blanka Shaw, with permission.

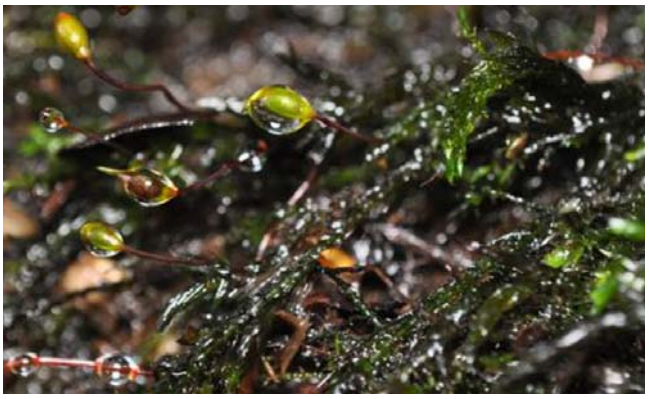

Figure 141. ***Platyhypnidium riparioides*** showing emergent capsules. Photo by Andrew Hodgson, with permission.

Figure 142. ***Warnstorfia*** (previously *Drepanocladus*) ***fluitans*** with capsules. Photo by Biopix, through Creative Commons.

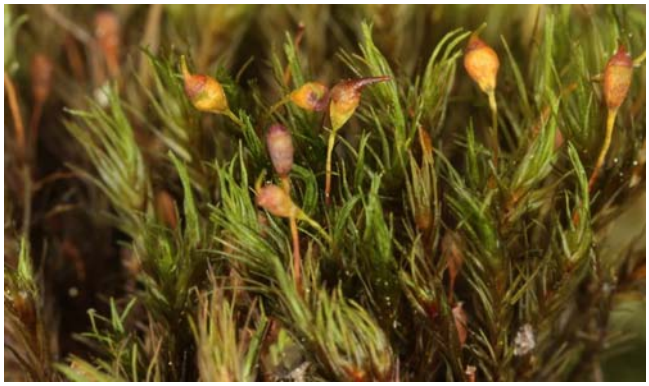

Figure 143. ***Blindia acuta*** showing ovate capsules common among submersed species. Photo by Jan-Peter Frahm, with permission.

Figure 144. ***Fontinalis squamosa***, member of a genus that produces submersed, ovate, thick-walled capsules that have short stalks and enlarged perichaetial leaves. Photo by David Holyoak, with permission.

Figure 145. ***Wardia hygrometrica*** from the southwest Cape of Africa, showing oblong capsules typical of submersed species. Photo by Des Callaghan, with permission.

Figure 146. ***Scouleria aquatica*** with a submersed capsule typical of aquatic species. Photo by Matt Goff <http://www.sitkanature.org/>, with permission.

Anisospory

Mogensen (1981) points out that having **anisospory** (unequal spore sizes, in this case) creates different dispersal potential between males (small spores) and females (large spores). One would presume that small spores will disperse farther, hence making it more likely that males establish as single-sex populations in distant places. It also seems that there is an advantage in the production of dwarf males from these anisosporous male spores because some of these will germinate on a female and thereby be close enough to accomplish fertilization. There is no equivalent advantage for the female spores to land on another member of the species because these are never known to produce dwarf plants that might somehow accomplish fertilization. Rather, in most cases, they will not germinate at all when landing on their own genotype.

Spores and Spore Walls

Liverworts and mosses differ in the number of layers in the spore wall (Mogensen 1981). Both have **intine** and **exine**. The **intine** (Figure 147) is the inner wall and possesses the aperture that is responsible for the breakup of the spore wall during germination. The **exine** is the outer wall and thus protects the spore from the environment. The **perine** is present only in moss spores and is laid down on the outer surface of the spore. It is not produced by the spore, but rather, the surrounding sporophyte deposits the perine (Figure 148) material on the spore walls. This perine is of taxonomic value and one might assume that it has environmental significance, but little information is available to provide us with such correlations.

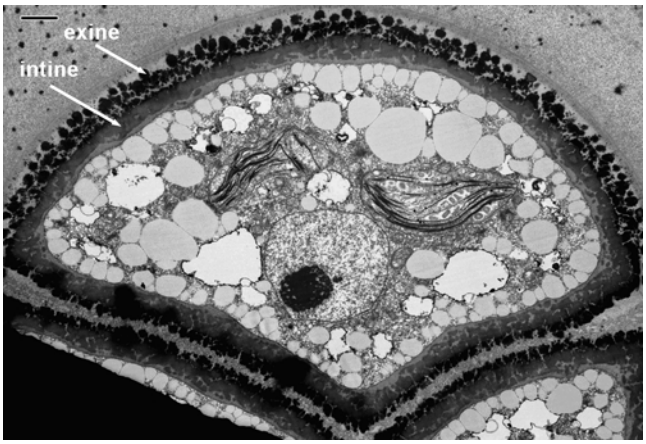

Figure 147. ***Andreaea rothii*** TEM of spore. Photo courtesy of Karen Renzaglia.

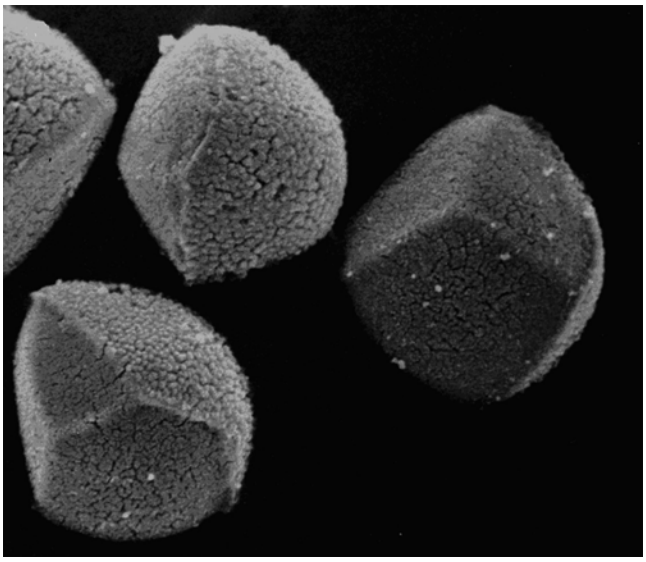

Figure 148. ***Andreaea rothii*** spore SEM showing papillae (perine layer) laid down by the sporophyte. Photo courtesy of Karen Renzaglia.

Some speculation is in order so that we can develop hypotheses about this perine layer (Figure 148). This layer causes air to be trapped in spaces around the surface of the spore. So one hypothesis is that the spores trap air that makes them lighter in weight per unit volume, permitting them to float. What are the advantages gained by spaces so small that cohesion of water molecules prevents them from entering those spaces? Does this potential repellence of water prevent inappropriate germination? And what difference does the pattern make? Or could it be that this layer provides a food source for potential dispersal agents that pass the spore through the gut unharmed at some new location or simply carry the spores like ants do seeds with elaiosomes? Does the layer have any food value? Does it make adherence easier for both dispersal and attachment to substrate?

Liverworts

Bischler and Jovet-Ast (1981) contend that adaptations in liverworts are primarily those of biochemical and biophysical properties of the cell content, hence making them more difficult to assess. Both the gametophyte and sporophyte produce specific **flavonoids** that may protect the developing gametes and spores from UV light (Suire & Asakawa 1980). They likewise synthesize secondary compounds that seem to deter predators and parasites. SEM images provided by William T. Doyle seem to provide evidence that they are also adapted by differences in the sculpturing of the spore wall (Figure 149-Figure 154).

Although liverworts lack a perine layer, spores of many species are not without decoration (Figure 149-Figure 154). Some of the leafy liverworts, *e.g.* ***Frullania chevalieri*** (Figure 152), have quite intricate and interesting patterns of papillae; others have deep sculpturing, as in ***Fossombronia*** (Figure 154).

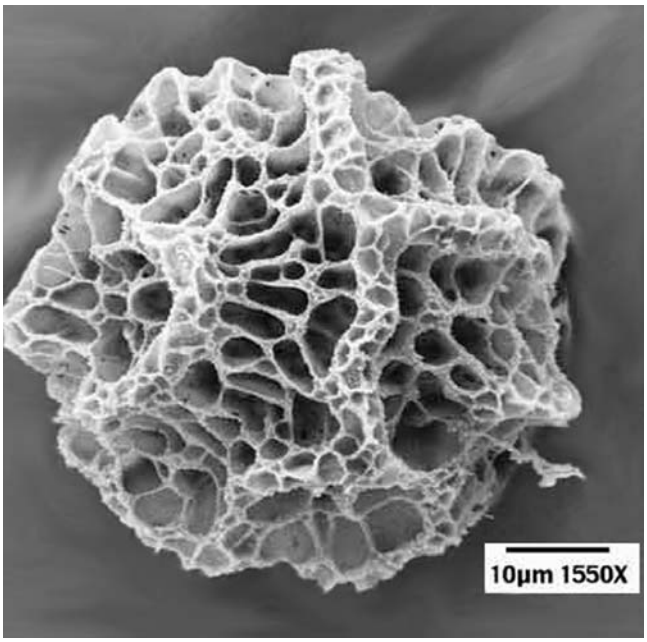

Figure 149. ***Targionia hypophylla*** distal spore wall SEM. Photo by William T. Doyle, with permission.

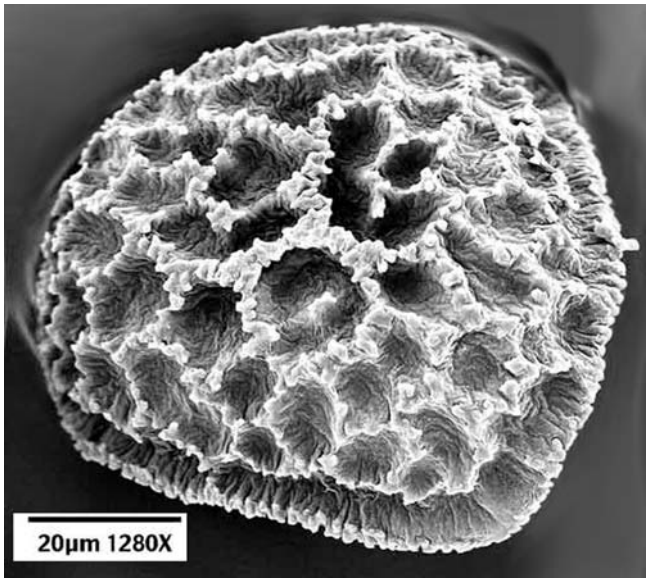

Figure 150. ***Riccia cavernosa*** distal spore wall SEM. Photo by William T. Doyle, with permission.

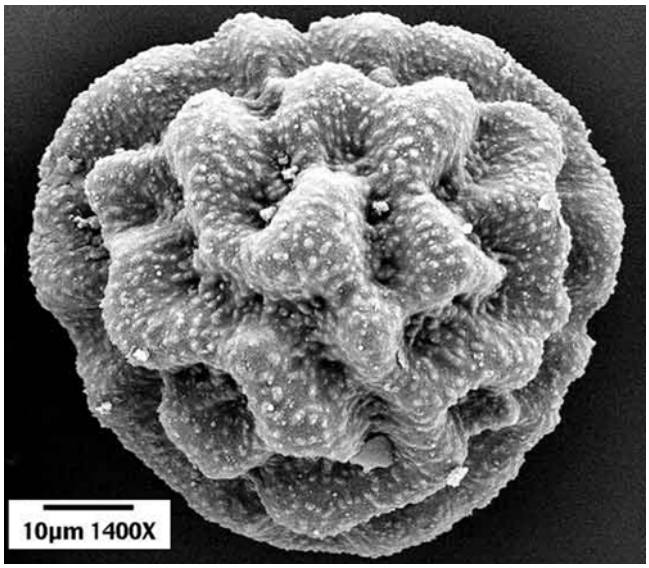

Figure 151. ***Mannia californica*** distal spore wall SEM. Photo by William T. Doyle, with permission.

Figure 152. ***Frullania chevalieri*** spore SEM showing the rosettes of papillae. Photo by Matt von Konrat, with permission.

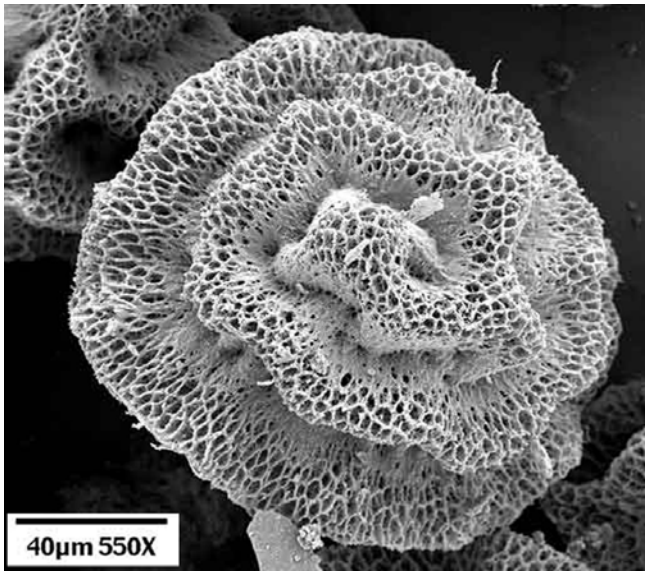

Figure 153. ***Asterella californica*** distal spore wall SEM. Photo by William T. Doyle, with permission.

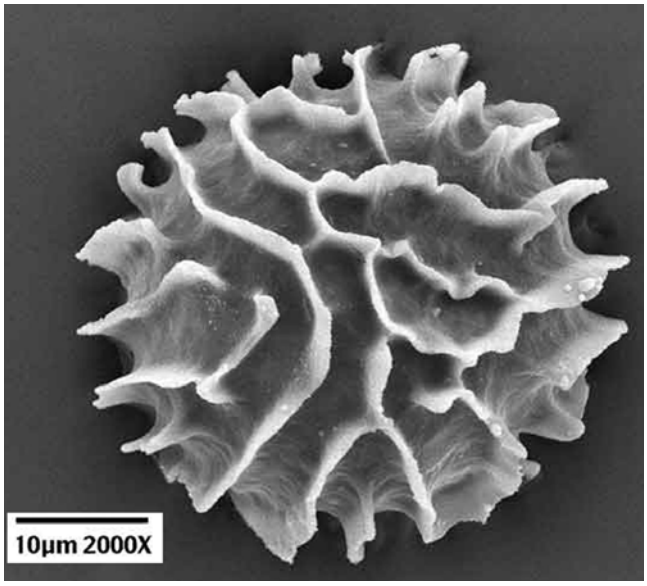

Figure 154. ***Fossombronia pusilla*** distal spore wall SEM. Photo by William T. Doyle, with permission.

But what is the overall indication of these sculpturings? Van Zanten and Gradstein (1988) found no significant difference between the spore sculpturing of transoceanic and endemic Neotropical liverwort species, with both smooth (Figure 155) and finely **verrucose** (covered with warts or wart-like projections) spores (Figure 152) in both groups. On the other hand, they found that there were significantly more strongly verrucose spores among endemic species than among transoceanic species, regardless of size. Furthermore, species with strongly verrucose spores (Figure 156) are typically hygrophytic and terrestrial (a combination for species that live where they are submersed for short periods of time), suggesting to van Zanten and Gradstein that this sculpturing might aid in short-distance dispersal overland by water movements during heavy rainfall. Such a strategy could be useful for ***Sphaerocarpos michelii*** (Figure 156).

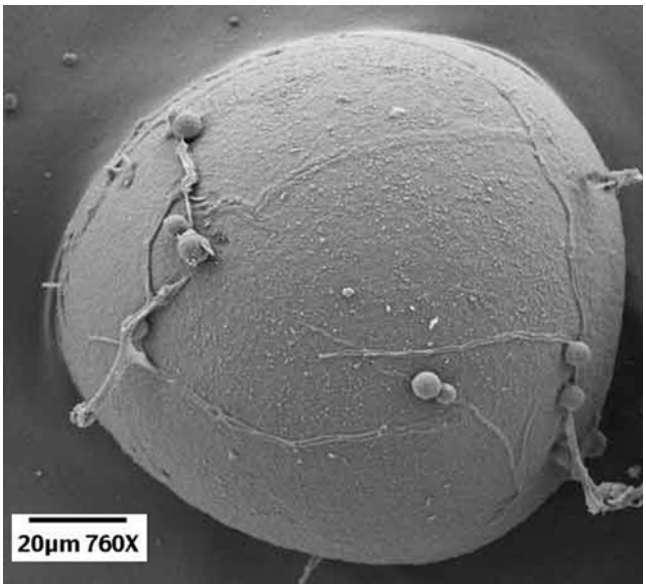

Figure 155. ***Geothallus tuberosus*** (Sphaerocarpaceae) spore SEM, a species of hot deserts. The large size and smooth surface are typical of spores that don't require adherence on their landing surfaces. Photo by William T. Doyle, with permission.

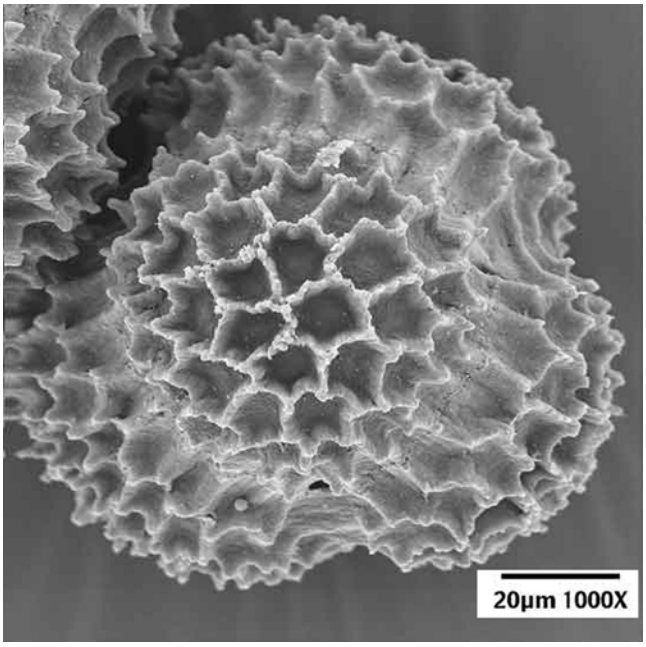

Figure 156. ***Sphaerocarpos michelii*** distal spore wall SEM. This species lives on damp soil of fallow fields, soils subject to seasonal flooding, and sandy soil of tall-grass prairies. Photo by William T. Doyle, with permission.

Bischler and Jovet-Ast (1981) attempted to assess reproductive adaptations for the **Marchiantiales**. This group is characterized by large spores with an ornamented exine (*e.g.* ***Asterella***; Figure 157). Few species of **Marchantiales** have specialized gemmae [*e.g.* ***Marchantia*** (Figure 1), ***Lunularia*** (Figure 158), ***Blasia*** (Figure 159) as exceptions], although these are common among leafy liverworts. The sporophyte is imbedded in or surrounded by gametophyte tissue, where it remains until the spores ripen. For many of the taxa, an archegoniophore is produced, hence raising the ensuing sporophyte above the thallus.

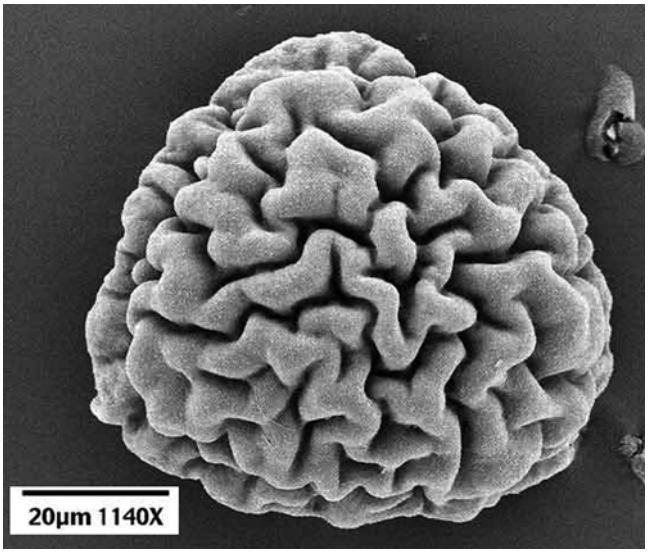

Figure 157. ***Asterella palmeri*** distal spore wall SEM, illustrating the highly decorated exine and large size. Photo by William T. Doyle, with permission.

Figure 158. ***Lunularia cruciata*** showing gemmae. Photo by Martin Hutten, with permission.

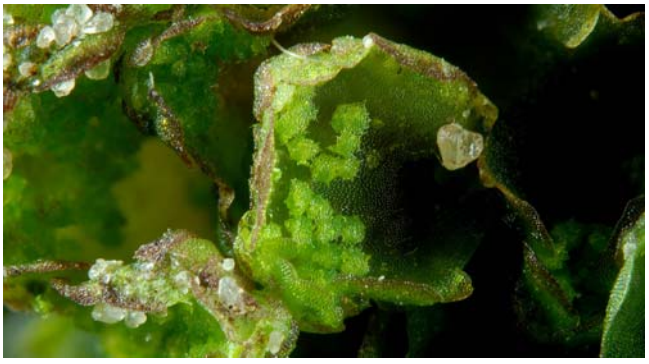

Figure 159. ***Blasia pusilla*** gemmae on the thallus surface. Photo by Dick Haaksma, with permission.

Elaters occur among the spores of both **Jungermanniales** and **Marchantiales**. These elongate structures twist in response to moisture changes and help in the dispersal in many of the taxa – or do they hinder it by entangling the spores (Figure 160) and forcing them to be dispersed as a mass? Little is known about the role of these elaters in dispersal – perhaps their primary role is in maintaining moisture in the capsule during spore development.

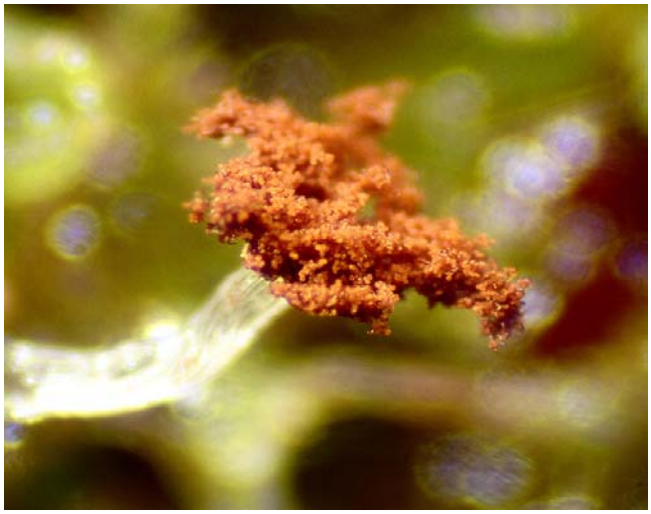

Figure 160. Open capsule of ***Jungermannia*** sp. showing spores and entangling elaters. Photo by George Shepherd, through Creative Commons.

Monoicous vs Dioicous

One interesting result of the study by van Zanten and Gradstein (1988) is that among the Neotropical liverworts they considered, monoicy vs dioicy made a difference in dispersal. Gradstein (1985) found that 57% of the endemic **Lejeuneaceae** (Figure 161-Figure 162) are monoicous. In the **Jubulaceae** (Figure 163), only one transoceanic species is dioicous. Van Zanten and Gradstein (1988) concluded that if the species had spores larger than 35 µm, then dioicism may create a serious reduction in its long-distance dispersal ability. They reasoned that for small spores there were better chances for transport by air currents, hence providing a greater chance for dioicous species with small spores to arrive near a partner of the opposite sex. To achieve the same opportunity for a partnership in species with larger spores would take a longer time. It is also important to recognize that the only dioicous species to achieve transoceanic dispersal in the Jubulaceae was ***Frullania ericoides*** (Figure 163), a species that is also the only one with gemmae. On the other hand, all the species in Lejeuneaceae that have gemmae are endemic.

Figure 161. ***Cheilolejeunea trifaria*** (**Lejeuneaceae**) from the Neotropics. Note the perianths, with a prominent one in the middle of the image. Photo by Michael Lüth, with permission.

Figure 162. ***Cololejeunea cardiocarpa*** (**Lejeuneaceae**) archegonia (**left**) and antheridia (**right**). Photo by Paul Davison, with permission.

Figure 163. ***Frullania ericoides***, the only transoceanic member of **Jubulaceae** among neotropical liverworts, and the only member of **Jubulaceae** with gemmae there. Photo by Paul Davison, with permission.

Ecological Adaptations

Not surprisingly, van Zanten and Gradstein (1988) found a positive correlation between Neotropical liverwort species range and xerophytic habitat. They found that correlation mainly related to large spore size. There was no similar relationship for species with small spores. Moreover, they found no relationship between spore drought tolerance and moisture level of the habitat. However, for sporelings there is a significant correlation with the average number of days for survival of desiccation, with 30 days for xerophytes, 25 for mesophytes, and 13 for hygrophytes. This suggestion that successful establishment may be more important than dispersal has appeared in other studies discussed herein.

Van Zanten and Gradstein (1988; Gradstein 2013) found that tropical lowlands have significantly more transoceanic species than at higher elevations. Most of these transoceanic species are members of the Lejeuneaceae and Jubulaceae, families with large, green spores. This requires some explanation since it is easier to get higher elevation species into the airstream, and large green spores suggest a need for immediate germination. But the lowland species are generally more widespread than are montane and alpine species, providing greater availability of these lowland species. Furthermore, this widespread habitat availability is in effect at the receiving end as well, creating greater opportunity for a "stepping stone" effect in regions where there are oceanic islands with large areas of relatively low elevation.

Persistent Protonemata

Some bryophytes retain their protonemata even after the leafy gametophores are well developed. These include ***Buxbaumia aphylla*** (Figure 164), ***Discelium nudum*** (Figure 165), various ***Ephemerum*** species (Figure 166-Figure 167), ***Fissidens exilis*** (Figure 168), ***Pogonatum pensilvanicum*** (Figure 169), ***Schistostega pennata*** (Figure 170) (Bob Klips, Bryonet 22 December 2021), ***Rhizomnium*** (Figure 171), ***Tetraphis*** (Figure 172) (Wolfgang Hofbauer, Bryonet 22 December 2021), ***Diphyscium*** (Figure 173) (Rob Gradstein, Bryonet 22 December 2021), ***Ephemeropsis*** (Figure 174), ***Cololejeunea metzgeriopsis***, ***Protocephalozia ephemeroides***, ***Radula aguirrei***, ***R. yanoella***, and ***Viridivellus pulchellum*** (Gradstein & Wilson 2008). ***Fissidens magnicellulatus*** from a damp, vertical soil bank in Zambia likewise has persistent protonemata (Bruggeman-Nannenga 2013). ***Mittenia*** (Figure 175), like ***Schistostega***, has persistent protonemata that reflect light when struck by it at right angles (Stone 1961).

Figure 164. ***Buxbaumia aphylla*** capsules with persistent protonemata. Photo by Janice Glime.

Figure 165. ***Discelium nudum*** masses of persistent protonemata. Photo by Andrew Hodgson, with permission.

Figure 166. ***Ephemerum recurvifolium*** showing capsule and protonemata. Photo by Rayna Natcheva, with permission.

Figure 167. ***Ephemerum rutheanum*** with attached protonema. Photo by Dick Haaksma, with permission.

Figure 168. ***Fissidens exilis*** with persistent protonemata. Photo by Jonathan Sleath, with permission.

Figure 169. ***Pogonatum pensilvanicum*** with protonemata and young sporophyte. Photo by Charlie Davis, through Creative Commons.

Figure 170. ***Schistostega pennata*** persistent protonema. Photo courtesy of Misha Ignatov.

Figure 171. ***Rhizomnium punctatum*** with persistent protonemata covering canyon wall, Hocking Hills OH, USA. Photo by Janice Glime.

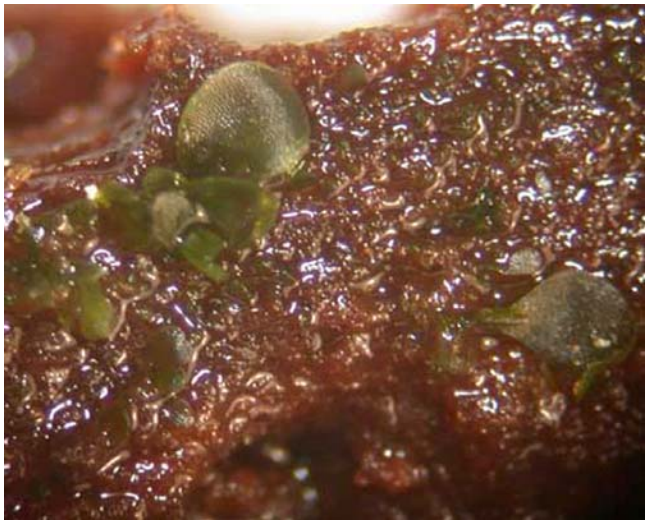

Figure 172. ***Tetraphis pellucida*** protonemal flaps on the persistent protonema. Photo from Botany Website, UBC, with permission.

Figure 173. ***Diphyscium foliosum***, in a genus with a persistent protonema. Photo by Michael Lüth, with permission.

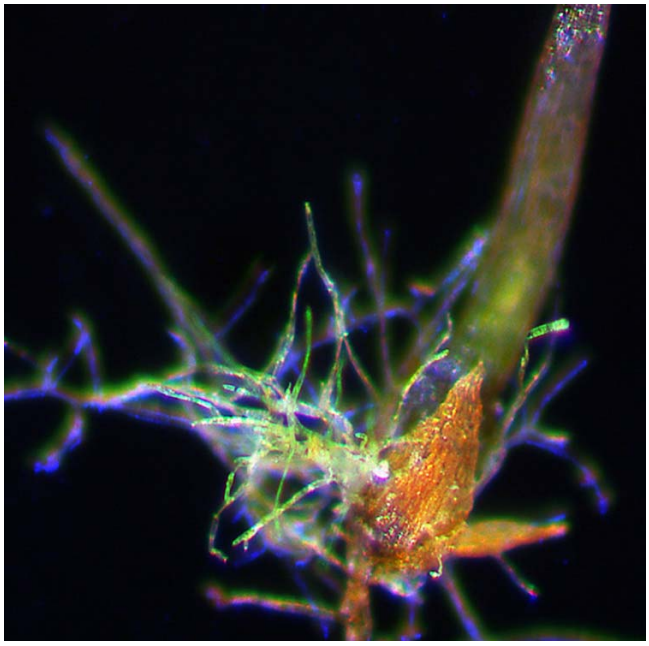

Figure 174. ***Ephemeropsis trentepohlioides*** leaves and persisttent protonema. Photo by Larry Jensen, with permission.

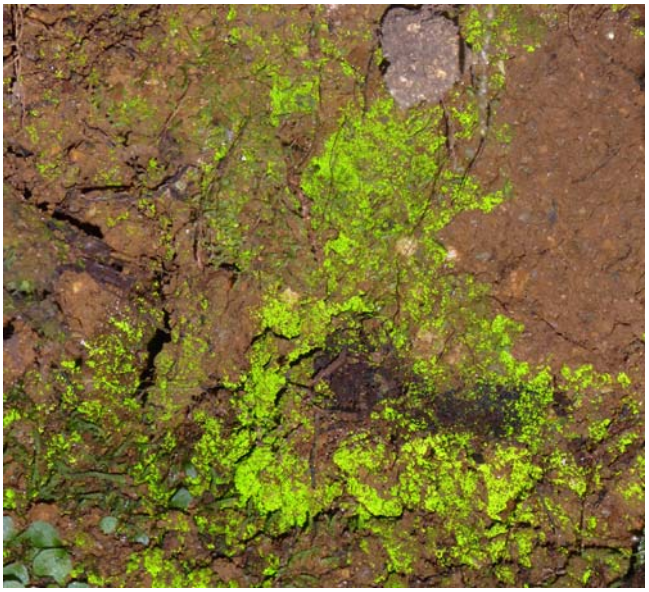

Figure 175. ***Mittenia plumula*** persistent protonemata. Photo courtesy of David Glenny.

When Furuki and Iwatsuki (1989) described the liverwort ***Mizutania*** as a new genus, they considered that the gametophyte thallus might actually be a persistent protonema.

Protocephalozia ephemeroides is a liverwort and consists of a mat of numerous branched filaments that give rise to very short, leafy sexual branches; it has been found only once – in 1854 in Venezuela (Gradstein & Wilson 2008). In ***Pogonatum*** (Figure 169), many species are represented by a mat of protonemata with only scattered leafy plants (Wyatt & Derda 1997). Protonemata in ***Ephemerum*** (Figure 166-Figure 167) produce long-lived tubers. Pressel *et al*. (2013) suggest that in their lake margin homes in the British Isles, these provide an alternative means of perennating that allows them to survive inundation when it occurs prior to sporophyte production.

In ***Rhizomnium punctatum*** (Figure 171), the protonemata are the dominant phase in the life cycle and remain persistent when leafy gametophores arise (Duckett & Ligrone 1994). Those produced by spores and those produced from excised leaf bases are the same. They produce gemmae on side branches and then secondary gemmae by proliferation. The gemmae germinate readily and the filaments are strongly adherent to solid objects. The protonemata are the dominant phase in the life cycle.

Stone (1985a) described an unusual persistent protonema in ***Archidium thalliferum*** in Australia. This protonema is cushion-shaped and thalloid, but composed of short-celled fillaments. The thalloid structure has differentiated layers with functions of protection, photosynthesis, and possibly storage. The upper layer of filaments is greyish-white and protects the chlorophyllose tissue beneath it. The middle portion provides dense chlorophyll concentrations with large spaces among the protonemal filaments that would facilitate photosynthesis much like a mesopyll. The basal portion has colorless cells and is rich in oils, possibly serving as a storage organ. The filaments break off easily and could potentially serve as propagules, but their ability to regenerate remains to be demonstrated. The rhizoids produce gemmae and both the

rhizoids and the gemmae store oil. Stone suggested that these and the oil-filled spores might remain viable for years when rainfall was insufficient for successful germination. Upright gametophores may remain buried within the cushion. ***Archidium minutissimum***, also in Australia, has persistent protonemata, but these do not form cushions and may be found on the ground or among the leaves (Stone 1985b).

Pursell and Allen (2017) found that the ephemeral ***Fissidens exilis*** (Figure 168), one of smallest species of ***Fissidens*** in eastern North America, grows from persistent protonemata on bare, usually disturbed soil. More recently, Kwon *et al*. (2019) found that ***Fissidens protonemaecola*** similarly produces a persistent protonema. The species occurs on shaded soil in Korea, where it produces small, bud-like shoots scattered on the protonemata. It is also known from China, Japan, and Taiwan.

Duckett and Pressel (2013) reported ***Discelium nudum*** (Figure 165) as a pioneer on unstable clay banks. It seems to persist or arrive as unicellular, colorless, starch-filled rhizoidal tubers (with up 20 µm diameter starch grains) *ca* 1 cm below the surface. These diaspores are exposed on new clay surfaces when winter causes leaves of the vegetation to disintegrate. The diaspores are both abundant and germinate rapidly, a reproductive strategy that gives the ***Discelium*** a competitive advantage. The persistent chloronemata lack gemmae, but their spread is rapid.

The **Ephemeraceae** typically occur in sunny or partly shaded areas on disturbed soil where they face little competition from mosses or larger plants. They appear as patches of green protonematal filaments with occasional tiny leafy gametophores. Their asexual reproduction is mostly by protonemal fragments, but rare thick-walled elongate, swollen protonematal segments may detach and persist on or in the soil.

In ***Bryum*** (Figure 176) species with persistent protonemata, protonemal gemmae and tubers are in greatest production in winter when sporophytes are still immature (Pressel *et al*. 2007). Protonemal gemmae arise within only weeks, whereas sporophyte formation takes at least a year. The most rapid protonemal production is evident in species in arable fields in autumn, and in these species the gemma production is transient. The persistent protonemata grow in places where leafy gametophores are unable to flourish. Pressel *et al*. suggested that this persistence was due to low irradiance. This behavior is similar to that of ***Dicranoweisia cirrata*** (Figure 177), wherein the gemmiferous protonemata form in conditions with high nutrients. In ***Bryum*** species, the spores are packed with lipids and are long-lived, whereas the gemmae are filled with starch and presumed to be short-lived.

Thus it appears that persistent protonemata provide different advantages in different species. Their ability to produce vegetative propagules seems to be common, providing a means of reproduction in habitats where spores might not succeed due to their smaller size and therefore smaller amounts of stored nutrients. But their nutrient strategies seem to differ. In species like ***Rhizomnium punctatum*** (Figure 171) the rock substrate is low in nutrients, whereas in fallow fields some ***Bryum*** (Figure 176) species persist as protonemata on a soil substrate rich in nutrients. Some of the persistent protonemata are present only in one or few species in a genus, whereas others characterize an entire order. Protonemal propagules have received insufficient attention in most bryophyte species, so overall statements as to the adaptive advantages of persistent protonemata with propagules would seem to be premature.

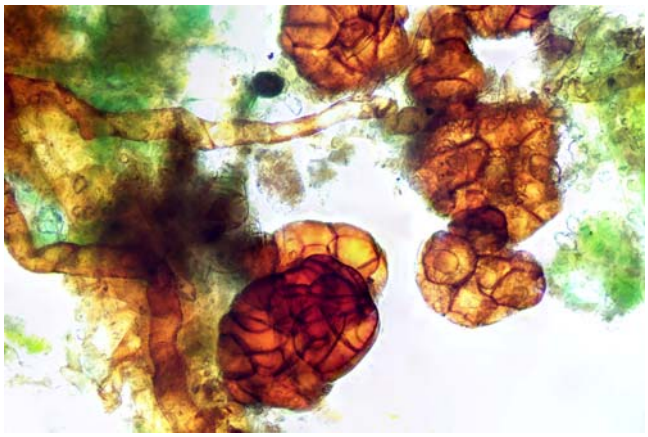

Figure 176. ***Bryum klinggraeffii*** tubers on the persistent protonemata. Photo by Claire Halpin, with permission.

Figure 177. ***Dicranoweisia cirrata***, a species with a persistent protonema. Photo from Biopix, through Creative Commons.

Who Is Travelling?

We seem to have a reasonable understanding of the algae that we are likely to encounter in diaspore rain, with genera like *Chlamydomonas* and *Chlorella* likely to show up in that translucent glass jar in which you are starting to root a plant. In fact, the water in most such glass jars will turn green before the plant has enough roots to put it in soil due to the arrival and successful colonization of *Chlorella*. But I was surprised to find we scarcely have similar information for bryophytes.

Ross-Davis and Frego (2004) examined the propagule rain in southeastern New Brunswick, Canada, forests that were managed for timber production. Using emergence, they identified 51 species in the aerial rain and soil propagule banks. Only 36 of these were extant species in the area sampled. The air-borne species were more similar to the extant vegetation than were the buried taxa, attesting to the readiness of the diaspore bank for changes in the conditions.

Anyone who has watched a disturbed area, peered at the cracks in the sidewalk, or investigated an area after a fire knows that one of the first bryophytes to arrive is often ***Funaria hygrometrica*** (Figure 178). To add to this list of habitats, this was the first moss to arrive and become established on the volcano Surtsey when it arose from the sea off the coast of Iceland (Schwabe 1974). This moss seemed to benefit from having its protonemata colonized by nitrogen-fixing Cyanobacteria, particularly members of the group ***Schizothrix*** (Figure 179)/***Plectonema*** and members of the **Nostocaceae**, particularly ***Anabaena*** (Figure 180).

Figure 178. ***Funaria hygrometrica*** on rocky substrate in southern Europe. Photo by Michael Lüth, with permission.

Figure 179. ***Schizothrix lenormandiana***. Photo from Cyanosite as freeware.

Figure 180. ***Anabaena*** sp., a common symbiont with some bryophytes. Photo by Janice Glime.

One test of the dispersal ability of bryophytes is to compare the spore rain with the extant species in the area. This will indicate those that are able to disperse there, but are unable to become established. This can be further tested by culturing the propagules to see if germination might be successful if different, and hopefully more appropriate, conditions are provided.

Certainly some species are more common in the diaspore rain than others. Leitao *et al.* (1996) and Santos *et al.* (1996) used agar traps to identify cryptogamic organisms from the atmosphere in Coimbra, Portugal. These included many non-bryophytes, but 75% of those collected were spores <25 µm (Santos *et al*. 1996). In addition to non-bryophytes [Cyanobacteria, Chromophyta (Ochrophyta), Chlorophyta, and Pteridophyta], Santos and coworkers isolated the liverworts ***Fossombronia angulosa*** (Figure 181-Figure 183) and ***Pellia epiphylla*** (Figure 184) and the mosses ***Leptodictyum riparium*** (Figure 185), ***Bryum dunense*** (Figure 186), ***Ditrichum*** sp. (Figure 187), ***Gymnostomum aeruginosum*** (=***G. calcareum***; Figure 188), ***Pottia*** sp. (Figure 189), and ***Trichostomum brachydontium*** (Figure 190). ***Bryum dunense*** forms axillary bulbils and ***Leptodictyum riparium*** is monoicous and produces abundant capsules.

Figure 181. ***Fossombronia angulosa*** with capsule, a species of liverwort found in agar traps. Photo by Des Callaghan, with permission.

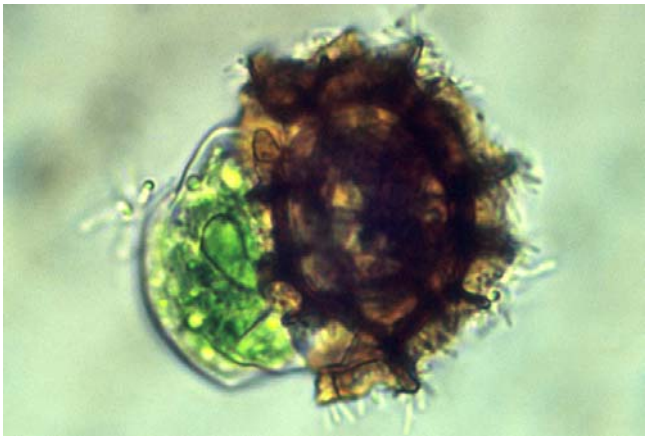

Figure 182. ***Fossombronia angulosa*** spore germination. Photo by Eugenia Ron and Tom Sobota, Plant Actions, with permission.

Figure 183. ***Fossombronia angulosa*** protonema. Photo by Eugenia Ron and Tom Sobota, Plant Actions, with permission.

Figure 184. ***Pellia epiphylla*** with sporophytes. Photo by Hermann Schachner, through Wikimedia Commons.

Figure 185. ***Leptodictyum riparium*** with capsules. Photo by Michael Lüth, with permission.

Figure 186. ***Bryum dunense***, one of the mosses distributing airborne propagules trapped in Coimbra, Portugal. Photo by Jan-Peter Frahm, with permission.

Figure 187. ***Ditrichum pallidum*** with capsules. Photo by Li Zhang, with permission.

Figure 188. ***Gymnostomum aeruginosum*** with capsules, a species found in the diaspore rain in Portugal. Photo by Hermann Schachner, through Wikipedia Commons.

Figure 189. ***Tortula modica*** (=***Pottia intermedia***) in Europe. Photo by Michael Lüth, with permission.

Figure 190. ***Trichostomum brachydontium*** showing dry (**left**) and wet (**right**). Photos by Michael Lüth, with permission.

Gaur and Kala (1984) tested what is in the spore rain compared to what is growing in the Himalayan alpine zone of India. They used adhesive-coated slides at 3600 m asl and identified spores of ***Marchantia*** (Figure 103), ***Conocephalum*** (Figure 191), ***Pellia*** (Figure 184), and ***Metzgeria*** (Figure 192) among the predominately fungal spores (65.5%) and flower pollen (23.9%). The liverworts in the spore rain were characteristic of the species growing in the area, so local dispersal could not be ruled out.

Figure 191. ***Conocephalum conicum*** with archegoniophores. Photo by Janice Glime.

Figure 192. ***Metzgeria decipiens*** spores and elaters. Photo by Tom Thekathyil at Blue Tier, with permission.

The most comprehensive study seems to be that of Ross-Davis and Frego (2004; Table 1). They examined the propagule sources of forest floor bryophytes in two mature mixed-wood forests in southeastern New Brunswick, Canada. The bryophyte communities in the two forest locations they studied revealed 36 bryophyte taxa. They found 51 taxa in the diaspore rain and diaspore bank. They furthermore found seasonal differences in the diaspore rain. Of the extant species present, 36% were absent in both the spore rain and the diaspore bank. Both communities were dominated by the feather mosses ***Pleurozium schreberi*** (Figure 193) and ***Hylocomium splendens*** (Figure 194), and these two species were present in both the spore rain and the buried diaspore bank. But the dominant taxon in the diaspore bank was ***Sphagnum*** (Figure 195), which was not present among the extant flora in either location. Up to 22 species from the diaspore bank were able to germinate after a six-hour culture. The aerial diaspore composition was 62% similar between the two locations, whereas the diaspore bank had only 34% similarity.

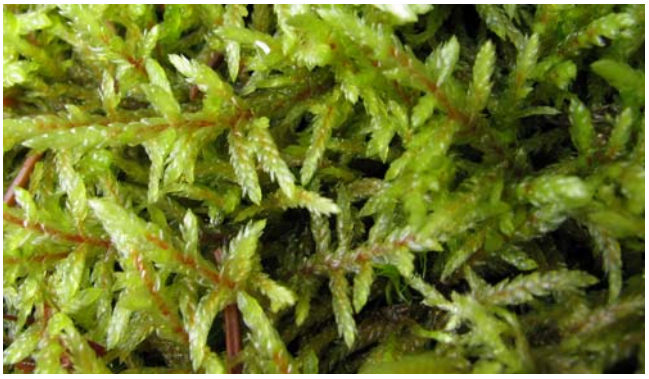

Figure 193. ***Pleurozium schreberi***, a species that appears in both diaspore banks and diaspore rain. Photo by Janice Glime.

Figure 194. ***Hylocomium splendens*** in autumn. Petr Brož, through Creative Commons.

Figure 195. ***Sphagnum*** protonemata and young plant. Photo by Andras Keszei, with permission.

Table 1. Bryophytes found in diaspore banks and aerial banks in southeastern New Brunswick, Canada. Diaspores were collected in two locations in mixed forest. Species that were in at least one of the diaspore samples at both locations are in **bold**. **DB** indicates buried diaspore bank. **DR** indicates aerial diaspore rain. Based on Ross-Davis & Frego 2004.

Amblystegium serpens	**DB**	**DR**	***Herzogiella striatella***		**DR**
Atrichum crispum	**DB**	**DR**	***Hypnum imponens***		**DR**
Atrichum spp.		DR	***Hypnum pallescens***		**DR**
Aulacomnium palustre		DR	*Hypnum* spp.		DR
Bazzania trilobata	**DB**	**DR**	*Isopterygiopsis pulchella*	DR	DB
Blepharostoma trichophyllum	DB		*Leptobryum pyriforme*	DB	DR
Brachythecium reflexum	DB		*Leptodictyum riparium*		DR
Brachythecium starkii	DB	DR	***Marchantia polymorpha***	**DB**	**DR**
Brachythecium spp.		DR	*Mnium stellare*	DB	
Bryum pallescens		DR	*Nowellia curvifolia*		DR
Callicladium haldanianum	DB	DR	*Philonotis fontana*	DB	
Campylium hispidulum	DB	DR	***Platydictya subtilis***		**DR**
Campylium stellatum	**DB**	**DR**	***Platygyrium repens***		**DR**
Cephalozia lunulifolia	DB		***Pleuridium subulatum***		**DR**
***Cephalozia* spp.**	**DB**	**DR**	***Pleurozium schreberi***	**DB**	**DR**
Cephaloziella spp.		DR	***Pohlia* spp.**	**DB**	**DR**
Ceratodon purpureus	**DB**	**DR**	*Polytrichum commune*	DB	
Chiloscyphus profundus (=*Lophocolea heterophylla*)		DR	***Polytrichum* spp.**		**DR**
			Pseudobryum cinclidioides	DB	
Dicranella rufescens	DB		*Ptilidium pulcherrimum*	DB	
Dicranum polysetum	DB		*Sanionia uncinata*		DR
Dicranum scoparium	DB	DR	***Sphagnum* spp.**	**DB**	
Ditrichum flexicaule	DB		*Syzygiella* (=*Jamesoniella*) *autumnalis*	DR	DB
Frullania oakesiana		DR			
Funaria hygrometrica		DR	*Thuidium delicatulum*		DR
Geocalyx graveolens	**DB**	**DR**			

But these studies are very local and tell us little about what species are most likely to be encountered in the atmosphere. There are certainly not enough studies to assess the types of characters that seem to contribute to

their presence. May I suggest, then, that the most likely entrants into the aerial realm are those diaspores (mostly spores) that are small, light weight, perhaps have surface waxes or papillae that increase their surface area and buoyancy without adding proportional weight, and have some means of getting away from the capsule and into the air stream, such as the explosive expulsion of spores from a ***Sphagnum*** capsule (see Chapter 4-9). Research by Sundberg (2012) on ***Sphagnum***, discussed in Chapter 4-8 under Everything is Everywhere, supports my last suggestion, but I have little support to offer for my other suggestions. They must also have a means to survive desiccation and protection against UV radiation. Testing these should provide for an interesting set of experiments. But first, we must find out what is in the spore rain around the world. This will be challenging because the concentrations are quite low. For example, Lewis Smith (1991) found no exotic bryophyte spores in the Antarctic air space, yet new volcanic land that was heated became colonized by species not known for more than 1000 km, suggesting that the diaspores are there in the diaspore rain but are too dilute to be sufficiently captured by our sampling methods.

Spore Dispersal Mechanisms

We might think of spore dispersal as having the same potential mechanisms as pollen dispersal, but some caveats exist. The flowers have carried the variety of dispersal agents to extremes, utilizing birds, bats, a variety of insects, water, gravity, and wind, and to a lesser extent, other mammals and invertebrate animals. To accomplish this great diversity, especially among the animal vectors, the flowers have spent tremendous energy in the production of attracting organs (the flowers themselves) that have colors, shapes, odors, and rewards that beguile their benefactors. Among the bryophytes, such extravagant expenditures of costly energy and biomass are rare, but some do exist (see subchapter 4-8).

For the seed plants, Hughes *et al*. (1994) concluded that plant growth form and stature can exclude certain dispersal modes. Since bryophytes generally are shorter in stature than their tracheophyte counterparts, we could expect all of them to exclude certain types of dispersal such as being eaten by large mammals. But some bryophytes could get around this problem by growing on trees, should any be suitable food for tall mammals. Their growth forms are such that they easily trap spores that pass by them, so the elevation of the capsule on a seta in most species seems necessary to reduce self-entrapment.

The third conclusion of Hughes *et al*. (1994) was that the availability of specific dispersal vectors seems to have no influence on dispersal mode. That conclusion needs some consideration, and dispersal vectors will be discussed in a later subchapter. But the wide range of dispersal vectors available to seed plants seems to have little similarity to the dispersal modes used by or even available to bryophytes in the same habitats, largely due to the small size of both the bryophyte plants and the propagules (Hughes *et al*. 1994).

Finally, Hughes *et al*. (1994) concluded that attributes of the physical environment rarely are important except indirectly through influencing plant stature and seed size. We have discussed above the meager evidence to support the influence of the physical environment on spore size in bryophytes; for example, it does seem that ephemeral habitats may have placed a selection pressure for larger spores [*e.g.* Bijlsma *et al*. 2012 for ***Ephemerum*** spp. (Figure 98)]. Living among other vegetation that can trap the spores, including forest canopies, may prevent them from getting into the air stream. I do wonder if bryophytes that live high on vertical surfaces (Figure 196) may be influenced in their success by the greater opportunity for wind carriage due to greater wind velocity, as shown for seeds by Greene and Johnson (1996). Perhaps there is a relationship to spore size and in some cases to the plant overall structure in such habitats.

Figure 196. ***Tortella fragilis*** at Khibiny Mountains, Apatity, Murmansk, demonstrating a vertical substrate at a high elevation where it might more easily become windborne. Photo by Michael Lüth, with permission.

Sporophyte Adaptations for Dispersal

Hedenäs (2001) elevated the role of dispersal in evolution and considered spore dispersal to be one of the two functions causing differences in character state frequencies among various environments. He considered such spore dispersal to be related to **shape** and **orientation of capsules**, **annulus**, **appearance of exostome** and **endostome**, **spore size**, **spore maturation time**, and **seta length**. One might ask if aquatic mosses in general have short or absent setae, as in ***Fontinalis*** (Figure 144), thus reducing the chance of drag dislodging the capsule before maturity, and do epiphytes truly more commonly have erect capsules?

Stark (2001) compared capsule adaptations of two Mojave Desert species of mosses. They differed both in morphology and in period of distribution. The ***Grimmia orbicularis*** capsule (Figure 197) is inclined, short, and broad, releasing its spores over about 6 months; its position on nearly vertical rock surfaces permits it to drop the opercula and liberate spores quickly. The ground-dwelling ***Syntrichia inermis*** (Figure 198) releases its spores from a single cohort of capsules over a period of three years. Dispersal of the operculum and spores is less certain for this soil-dwelling species, and the operculum detachment period can last up to 2.5 years.

Figure 197. ***Grimmia orbicularis*** from southern Europe, showing the short, broad, inclined capsule and the vertical substrate. Photo by Michael Lüth, with permission.

Figure 198. ***Syntrichia inermis*** growing on soil. Photo by Jan-Peter Frahm, with permission.

Crawford *et al*. (2009) found an evolutionary relationship between separate sexes and small spores, although this might be backwards since it appears that evolution in mosses tends to go from the dioicous condition to the monoicous one through doubling of the chromosome number (often through the failure of meiosis) or addition of a sex chromosome. Hence, we might consider that large spores are more common in monoicous taxa, a phenomenon that might result from the doubling of chromosome number.

Most bryophyte spores are wind dispersed, carrying many, probably most, to unsuitable habitats, but usually assuring that at least some will not land among their parents. Nevertheless, some bryophytes have evolved ingenious dispersal mechanisms. The simple bryophytes lack the resources to create such large and elaborate structures as flowers, but have, even so, in some cases (*e.g.* **Splachnaceae**, Figure 199) created highly visible and odiferous attractions to their dispersal vectors, as described in Chapter 4-9 of this volume. Nevertheless, most bryophytes seem to rely on wind and gravity as their primary dispersal agents. To this end, **mosses** have developed elaborate **peristome** teeth (Figure 200) that move in response to moisture changes and that tend to facilitate spore dispersal in dry air when the greatest opportunity for wind dispersal prevails (Bonnot 1978). The teeth are covered by an **operculum** (Figure 201) that seals the capsule and that is usually shed in response to drying and shrinkage of the capsule. It appears that this mode is highly successful, and the exceptions to wind dispersal are few.

Figure 199. ***Splachnum rubrum*** capsules displaying their showy hypophysis that attracts flies. Photo by Michael Lüth, with permission.

Figure 200. ***Brachythecium velutinum*** capsules showing double peristome. Photo by Dick Haaksma, with permission.

Figure 201. ***Brachythecium populeum*** capsules showing opercula. Photo by Des Callaghan, with permission.

One of the features of sporophytes that has fascinated my students is the twisting of the seta. When a dehydrated moss with sporophyte intact is hydrated, the seta of many species, *e.g.* ***Dicranella heteromalla*** (Figure 202), will gyrate in a spiral fashion, loosely coiling and uncoiling as its cells become hydrated, presumably unequally. Unfortunately, I have not observed that his has any effect on spore dispersal and must wonder if it is simply a consequence of the anatomy with no adaptive consequence at all. I am constantly reminded by the bryophytes that "all life has a twist in it."

Figure 202. ***Dicranella heteromalla*** with capsules and twisted setae that gyrate when the moisture changes. Photo by Biopix, through Creative Commons.

Sundberg (2005) examined capsule size in ***Sphagnum*** (Figure 203) to determine its possible role in dispersal distance. He tested four species of ***Sphagnum*** and found that the diameter of the capsule containing the spores was negatively correlated with the proportion of spores remaining in the capsule after dehiscence (5-16%), negatively correlated with those being deposited within the colony (2-14%), and negatively correlated with those being deposited between the colony edge and the outer sampled perimeter of 3.2 m (7-22%). These negative correlations imply that the larger diameter of the capsule somehow facilitates a greater dispersal distance.

Figure 203. ***Sphagnum fimbriatum*** with capsules that have lost their opercula. Photo by David T. Holyoak, with permission.

Thiers (1988) described morphological adaptations of the dispersal of liverwort propagules in the order **Jungermanniales** to their tropical habitat. These included **precociously** germinating spores (spores that germinate within the capsule; Figure 204-Figure 205), followed by a prolonged protonemal stage, and culminating in a **neotonic** life cycle (reproducing at an early developmental stage).

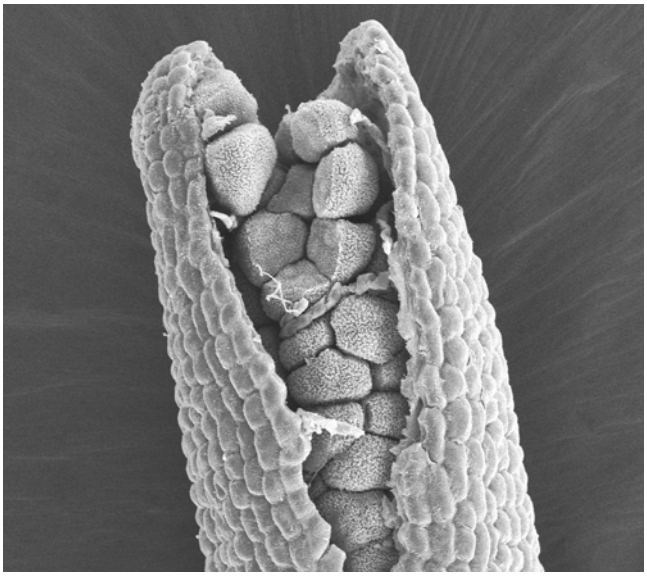

Figure 204. ***Dendroceros*** multicellular spores in capsule. Photo courtesy of Karen Renzaglia.

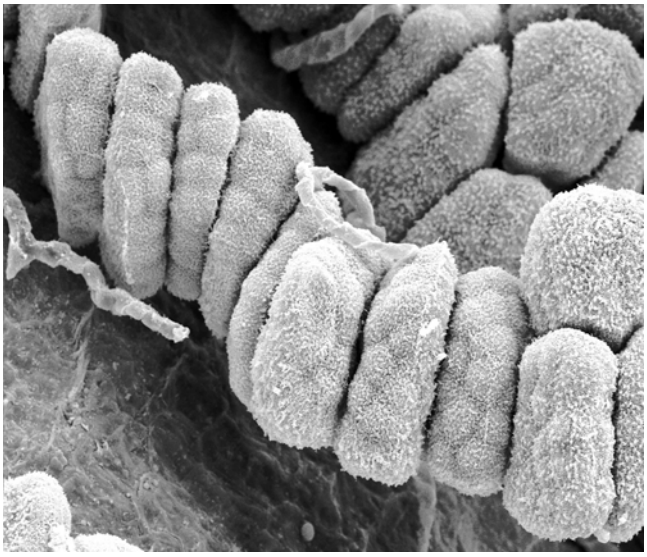

Figure 205. ***Dendroceros*** sp. (**Anthocerotophyta**) with stacks of multicellular spores, showing **precocious germination**. Photo courtesy of Karen Renzaglia.

Role of Peristome

The peristome teeth have various patterns of movement, with some resting inward and others resting outward. The structure of the teeth often causes uneven shrinkage as they dry, causing them to pulsate or even twist. Patterson (1953) described three behavior types for peristome teeth:

1. teeth wherein outer teeth either exclusively or predominately bend inward [***Ceratodon*** (Figure 206), ***Barbula*** (Figure 207), ***Pylaisia*** *s.l.* (Figure 208)]
2. teeth with outer teeth shrinking exclusively or predominately bending outward [***Grimmia*** (Figure 209), ***Orthotrichum*** (Figure 210-Figure 211), ***Dicranum*** (Figure 212)]
3. teeth that oscillate strongly as they change from shrunken to swollen states [***Amblystegium*** (Figure 213), ***Hypnum*** (Figure 214), ***Neckera*** (Figure 215), ***Bryum*** (Figure 216)]

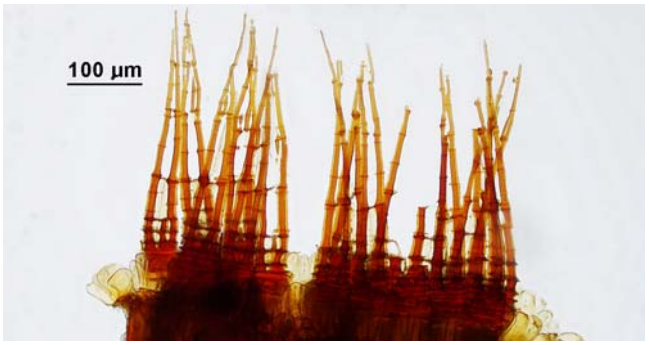

Figure 206. ***Ceratodon purpureus*** peristome, where teeth mostly bend inward. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

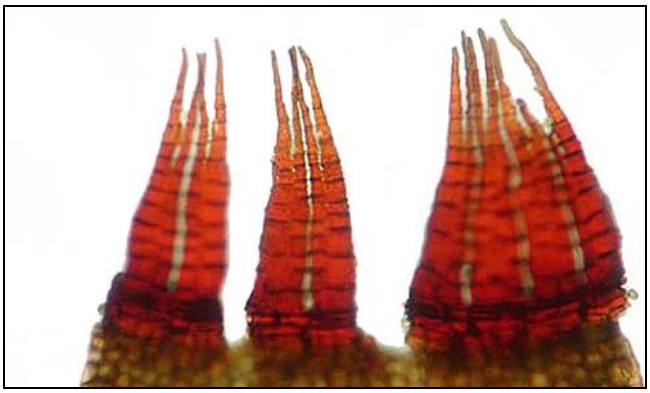

Figure 207. ***Barbula amplexifolia*** peristome from India, a species whose teeth bend inward. Photo by Michael Lüth, with permission.

Figure 208. ***Pylaisiella polyantha*** sporophytes showing teeth bending inward. Photo by Des Callaghan, with permission.

Figure 209. ***Grimmia ungeri*** with capsules showing outward-pointing teeth. Photo by Michael Lüth, with permission.

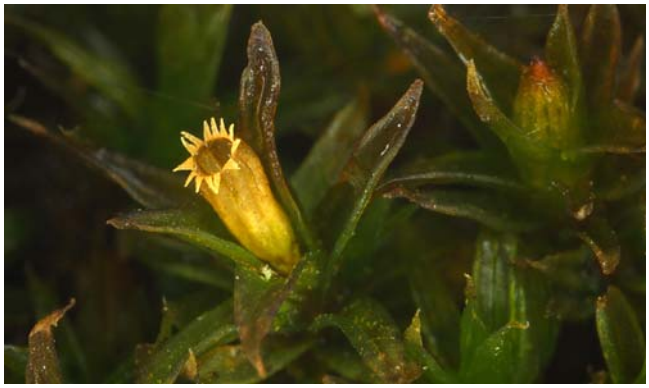

Figure 210. ***Orthotrichum diaphanum*** with capsules showing reflexed (outward-bending) teeth. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

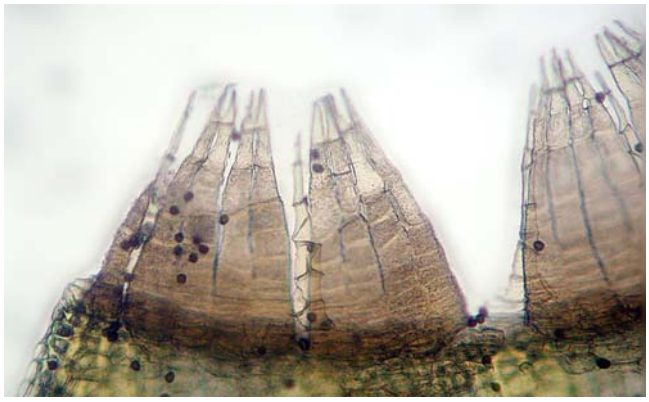

Figure 211. ***Orthotrichum alpestre*** peristome. Photo by Michael Lüth, with permission.

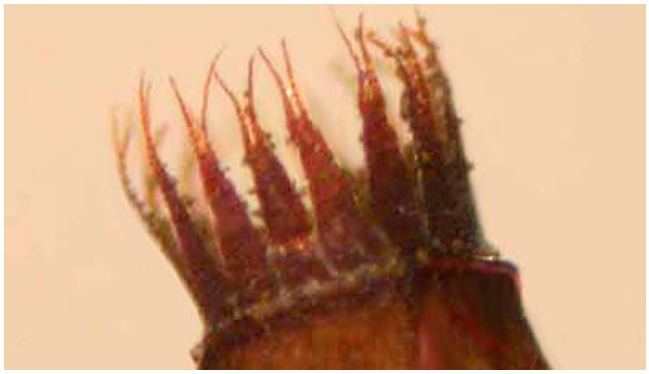

Figure 212. ***Dicranum scoparium*** peristome with teeth that bend outward upon drying. Photo from UBC botany website, with permission.

Figure 213. ***Amblystegium subtile*** with capsules showing teeth that flex as they change moisture states. Photo by Hermann Schachner, through Creative Commons.

Figure 214. ***Hypnum cupressiforme*** capsule showing peristome with teeth that flex as they change moisture states. Photo by Malcolm Storey, through Creative Commons on Discover Life.

Figure 215. ***Neckera pennata*** branch with capsule and teeth that oscillate in response to moisture changes. Photo by Dale A. Zimmerman, Herbarium, Western New Mexico University, with permission.

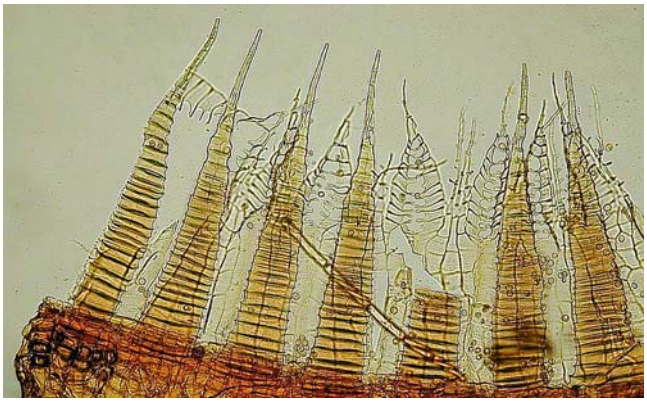

Figure 216. ***Bryum caespiticium*** peristome, with teeth that flex as they change moisture states. Photo by Michael Lüth, with permission.

Schnepf *et al*. (1978) described the movement of the outer peristome in the moss ***Racopilum intermedium*** (Figure 217). This movement arises from different swelling velocities of the outer plates and inner ridges of wall thickenings. These swelling differences arise from the suberin-like substances and wax lamellae enclosing the ridges. There is no suberin-like material in the plates.

Figure 217. ***Racopilum intermedium*** with capsules. Photo by Michael Lüth, with permission.

Estébanez *et al*. (2002) determined that strongly bound lipids, phenolics, and non-cellulosic polysaccharides were responsible for the movement of the teeth in ***Arctoa fulvella*** (Figure 218), ***Grimmia decipiens*** (Figure 219), ***Grimmia pulvinata*** (Figure 220), ***Schistidium rivulare*** (Figure 221), ***Bucklandiella sudetica*** (=***Racomitrium sudeticum;*** Figure 222), ***Ptychomitrium sinense*** (Figure 223), ***Glyphomitrium humillimum*** (Figure 224), and ***Venturiella sinensis*** (Figure 225).

Figure 218. ***Arctoa fulvella*** with capsules. Photo by Andrew Hodgson, with permission.

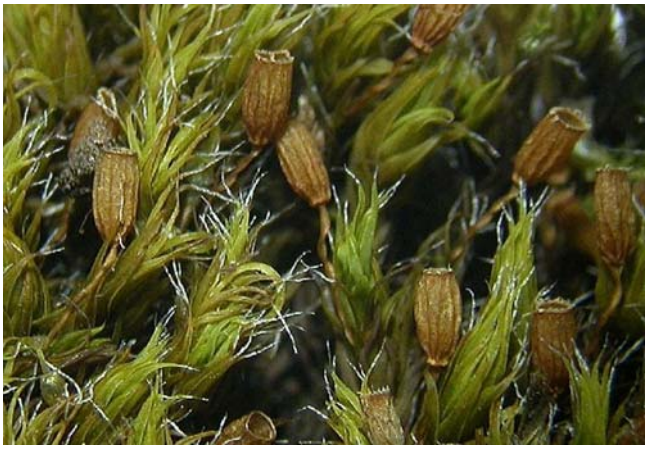

Figure 219. ***Grimmia decipiens*** with capsules. Photo by Henk C. Greven, Doorn, The Netherlands, with permission.

Figure 220. ***Grimmia pulvinata*** with capsules and teeth pointing outward. Photo by Michael Lüth, with permission.

Figure 221. ***Schistidium rivulare*** with capsule showing outward-pointing teeth and operculum attached by columella. Photo courtesy of Betsy St. Pierre.

Figure 222. ***Bucklandiella sudetica*** showing reflexed peristome teeth. Photo by Hermann Schachner, through Creative Commons.

Figure 223. ***Ptychomitrium sinense*** in dry state. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 224. ***Glyphomitrium humillimum*** with capsules. Photo by Okayama Prefectural Nature Conservation Center, permission pending.

Figure 225. ***Venturiella sinensis*** with capsules. Photo from Hiroshima University, with permission.

Takakia ceratophylla (Figure 226) has a dispersal mechanism that is unusual among mosses. The capsule has a spiral line of dehiscence. At maturity, when the capsule splits, this suture causes a spiral twisting that seems to help in spore dispersal (Higuchi & Zhang 1998). In many of the mosses, the annulus becomes modified as the capsule dries. For example, in ***Ludorugbya springbokorum*** the annulus rolls inwards, nearly covering the opening of the capsule (Hedderson & Zander 2007). Upon wetting, it rapidly everts, expanding the capsule opening. This exposes the two-sized spores within.

Figure 226. ***Takakia ceratophylla*** capsule showing spiral split. Photo by Ken McFarland, with permission.

Some bryophytes do not typically shed the operculum, but instead rely on disintegration of the capsule wall. ***Buxbaumia aphylla*** (Figure 227) seems rarely to shed the operculum (Glime & Liao, pers. obs.). Instead, the capsule cracks across its broad, flat upper face, peeling back to expose the spores (Figure 227). Eventually the tissue peels away, permitting the spores to escape. The protonema in this species produces sporophytes every year, and in Newfoundland, these sporophytes, which must overwinter to release the ripe spores in spring, can suffer high mortality from sudden frosts (Hancock 1973). ***Diphyscium*** (Figure 228) has a capsule with a similar small opening, but it does seem at least to shed the operculum. If it relies on the capsule splitting, I have not yet been able to observe it.

Figure 227. Capsules of ***Buxbaumia aphylla*** showing pealed away capsule wall on upper capsule. Photo by Janice Glime.

Figure 228. ***Diphyscium foliosum*** females with capsules showing shed operculum and teeth. Photo by Michael Lüth, with permission.

From my own observations, I concluded that ***Fontinalis*** (Figure 144) depends on abrasion for loss of the operculum. In spite of its beautiful lattice teeth, the operculum remains intact and winter-borne capsules become abraded by the silt load of melt waters. This abrasion removes sufficient tissue for spore dispersal to occur. In the absence of abrasion, the capsules seem to be so impregnated with phenolic compounds that the suture between the operculum and capsule body firmly glues them

together. But others have observed the beautiful teeth and spore dispersal, so my observations may only be of the unsuccessful capsules that remained after the others had dispersed their spores.

Cleistocarpy

In some mosses, the capsules have no peristome or operculum, a condition known as **cleistocarpy**. Such is the case for ***Archidium ohioense*** (Figure 109) and ***Trachycarpidium tisserantii*** (Makinde & Odu 1994). As already noted, these two species had poor spore release, compared to that of the two peristomate mosses, ***Fissidens ovatifolius*** (as *Fissidens minutulus*; Figure 229) and ***Bryum coronatum*** (Figure 93). All four species benefitted in their savannah habitat in Nigeria by having a rapid maturation cycle for their capsules.

Figure 229. ***Fissidens ovatifolius***. Photo by Jan-Peter Frahm, with permission.

In ***Archidium*** (Figure 109), the cleistocarpous capsule hides on a short seta among the leaves. At maturity, the capsule wall ruptures by decomposition, permitting spores to escape (Lönnell 2011). Lönnell suggests that this method of spore exposure and the large size of the spores are not supportive of wind dispersal and that use of another agent, perhaps water, is more likely. ***Riccia*** species likewise have large spores (Figure 230). Their presence in flood plains and other habitats that periodically get reasonably inundated with running water suggests that the same may be true for them.

Herrnstadt and Heyn (1988) have pointed out to us that a similar elaborate, complex, **sexine** (outer, sculptured layer of exine) spore wall pattern is common to a large percentage of the species that have cleistocarpous capsules or lack a peristome. These cleistocarpous species typically are small mosses, annual, terrestrial, and living in open habitats, particularly in the Mediterranean and adjacent arid regions. They furthermore have capsules that are immersed in the perichaetial leaves and possess large spores [(25) 30-40 µm]. Does this mean that this spore wall pattern has an adaptive value in arid regions?

Figure 230. ***Riccia sorocarpa*** showing the large, highly pigmented spores. Photo by Des Callaghan, with permission.

Summary

Diaspores include both spores and other propagules that serve in dispersal. These are typically sampled by exposed agar plates, glass slides with glycerine, or traps, including Tauber and Burkard traps.

Spores are usually smaller than vegetative diaspores and are therefore the most successful agents of long-distance dispersal in bryophytes, whereas vegetative means help the population to become established and spread once having arrived. But spores require fertilization as a prerequisite and therefore nearness of males and females. Vegetative diaspores continue in production under stressful conditions, but spores do not. Fragmentation is common in many species and seems only to require dry conditions; animals can help both in fragmenting and in carrying these propagules.

The success of dispersal and range size seems to be related to the abundance of sporophyte production. On the other hand, genetic information, at least for some species (especially **Polytrichaceae**), suggests that vegetative dispersal may be more important, even in species that produce abundant spores, perhaps due to spore dispersal limitations.

Dispersal success requires a tradeoff between energy spent on short-distance but energy-rich diaspores and energy wasted for a few of many spores produced that succeed in long-distance dispersal. Vegetative reproduction requires a tradeoff between likely success and loss of genetic diversity. Liverworts, as a group, seem to spend more energy on asexual reproduction than do mosses.

Disturbance can create conditions for vegetative growth, bring buried diaspores to the surface where they can germinate, and disperse propagules for short or long distances. Some species are especially adapted to

disturbances such as fires, floods, cold events, and even ants.

Diaspore banks are important for species that live in disturbed habitats. The spores of species that are regularly disturbed, such as floodplains, are typically large and these species may have rhizoidal tubers or other forms of rhizoidal propagules. For those that grow in areas of unpredictable disturbances, taxa that are easily dispersed, such as ***Funaria hygrometrica*** and ***Marchantia polymorpha***, are often important colonizers and can survive in spore banks as well as arriving through aerial dispersal. Representation in the diaspore banks often does not reflect the species at the surface, but rather has a strong bias toward acrocarpous species and species of early successional stages.

Peristome teeth in mosses, an **explosive capsule** in ***Sphagnum***, and **elaters** in liverworts help in dislodging spores and dispersing them. Other factors influencing dispersal are capsule size, shape, and orientation, annulus, exostome, endostome, spore size, maturation time, and seta length. Some rely on splitting of the capsule, including **cleistocarpy**. Strongly bound lipids, phenolics, and non-cellulosic polysaccharides contribute to peristome movement. Flood plain species tend to have large spores that permit a rapid life cycle. Dioicous species tend to have smaller spores, permitting them to travel farther on those occasions when sexual reproduction is successful. In some species, the spore size varies with altitude.

Maturation time can be important. For most spores, a dry atmosphere is favorable for longer distance dispersal. For vegetative propagules, some are favored by rain and others by dry wind.

It is likely that many species have spores that can survive years of dormancy, and some may survive hundreds of years while dry and in the dark. Those that start to germinate, then dry out again, will most likely die. Spores are also kept dormant by their parents, most likely due to chemicals from the parents.

Acknowledgments

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CHAPTER 4-8

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Figure 1. ***Conostomum tetragonum*** with capsules in the mountains of Norway where its spores become windborne more easily than those of bryophytes in the forest. Photo by Michael Lüth, with permission.

Diaspore Travel Distances

Although bryophyte spores are typically wind-dispersed, it appears that few actually travel very far. Most never actually become airborne (Wyatt 1977; Stoneburner *et al*. 1992). More typically, most of the spores fall within a meter or less (Crum 2001) of the capsule. It is likely that the bryophytes themselves act as spore traps, particularly for the neighboring plants of their own species. Pardoe *et al*. (2010), using mosses to compare trapping efficiencies, demonstrated that mosses serve as traps for pollen, suggesting that they should be traps for bryophyte spores as well.

But trapping spores and quantifying atmospheric spore rain is difficult at best, and the worldwide distribution of a number of taxa attests to the fact that these diaspores must at least occasionally travel great distances. There are tests of survivability for spores, but even less is known about vegetative diaspores.

Failure to Leave Home

Most spores will fall near the parent. In ***Tortula truncata*** (=***Pottia truncata***; Figure 2), 67% of the spores released fell within the parent clump and 70% within 2 m (Roads & Longton 2003). Further evidence of lack of gene flow to new locations is that there was little or no genetic variation within the individual clumps, but no genotypes were in common between the populations, suggesting that genes (including those in spores) from one population clump had not reached the other one. Sundberg (2005) found that for six species of ***Sphagnum*** (Figure 3), 8-32% of the spores that dispersed beyond the colony did not travel beyond the active release area of 3.2 m. Stoneburner *et al*. (1992) demonstrated this stay-at-home behavior experimentally for ***Atrichum angustatum*** (Figure 5). In that species, 94% of the spores were collected within 2 m of the colony center; 1% were found 15 m from the center. On the other hand, Miles and Longton (1990, 1992b) found

that more than 80% of the spores of ***Atrichum undulatum*** (Figure 6) and ***Bryum argenteum*** (Figure 7) travelled beyond their 2-m trapping distance.

Figure 2. ***Tortula truncata*** (=*Pottia truncata*) with capsules; most of the spores fall within the parent clump. Photo by Des Callaghan, with permission.

Figure 3. ***Sphagnum fimbriatum*** with capsules. Photo by David Holyoak, with permission.

Figure 4. ***Tortula acaulon*** (=***Phascum cuspidatum***) with capsules. Photo by Jan-Peter Frahm, with permission.

In ***Tortula acaulon*** (=***Phascum cuspidatum***) (Figure 4), 98% of the spores remained within the colony in this annual shuttle species (Roads & Longton 2006). This resulted in three of the five permanent quadrats having this species in them again in the second year. Many of the second-year colonies overlapped with the position of the first-year colonies, suggesting that spores fell close to home.

Figure 5. ***Atrichum angustatum*** with immature capsules; most spores apparently travel more than 2 m. Photo by Janice Glime.

Figure 6. Gametophytes and sporophytes of ***Atrichum undulatum***. Photo by Michael Lüth, with permission.

Figure 7. ***Bryum argenteum*** with capsules in Europe. Most spores are apparently able to travel more than 2 m. Michael Lüth, with permission.

Polytrichaceae

Atrichum undulatum (Figure 6) may not be a good example of dispersal distance in bryophytes due to its

presence of an epiphragm. This membrane, a characteristic of the **Polytrichaceae**, connects the 32 teeth and prevents spores from leaving from the top of the capsule, forcing them to leave between the teeth (Figure 8-Figure 9; see also Figure 61). Such a mechanism precludes the upward thrust that might be seen in some capsules where spores can travel upward directly. Rather, it is likely that spore dispersal in this species is facilitated by raindrops on the epiphragm, as is known for ***Dawsonia*** (Figure 10), limiting its dispersal (van Zanten 1973) both by the wet atmosphere and the horizontal ejection because they are not ejected high enough to reach the wind turbulence.

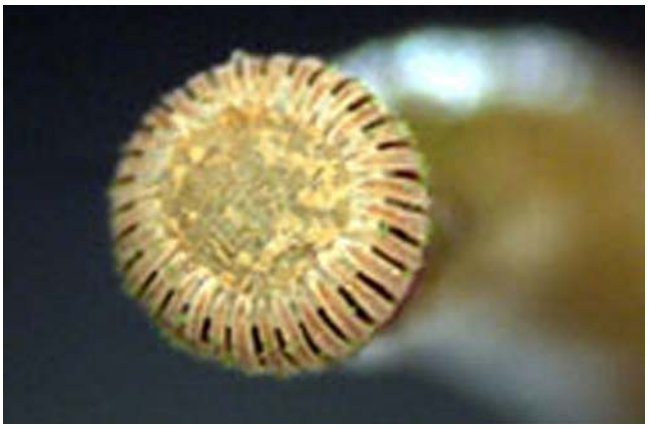

Figure 8. ***Atrichum undulatum*** showing epiphragm membrane extended across opening and attached to teeth like a trampoline. Photo from UBC website, with permission from Wilf Schofield.

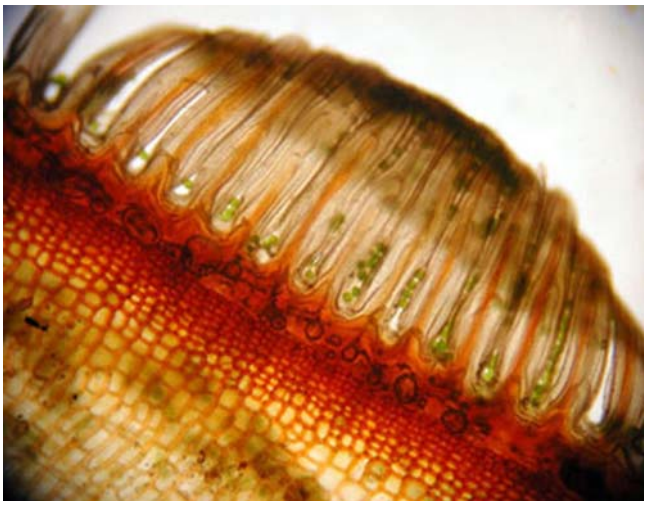

Figure 9. ***Atrichum undulatum*** with openings between peristome teeth showing spores. Photo from UBC website, with permission from Wilf Schofield.

Thus, based on limited data, it seems to be accepted that most bryophytes probably only disperse the majority of their spores within about 2 m (Table 1). But only a few spores need go farther to accomplish long-distance dispersal, and some species seem more able than others to accomplish this. Stoneburner *et al*. (1992) found that when air volume was increased, 4.5 million out of 25.8 million spores of ***Atrichum angustatum*** (Figure 5) from the colony reached the limits of their 15-m study area. Just think what would happen to spores caught in the updrafts of a forest fire or tornado!

Figure 10. ***Dawsonia longiseta*** with capsules. Photo by Niels Klazenga, with permission.

Table 1. Published maximum dispersal distances of bryophyte spores, based on direct measurements to traps. It is appropriate to consider that these spores will travel at least this far.

Sphagnum subtile	75-100 cm	McQueen 1985
Tetraphis pellucida	2 m	Kimmerer 1991
Bryum argenteum	>2 m	Miles & Longton 1992b
Atrichum undulatum	>2 m	Miles & Longton 1992b
Tortula truncata	>2 m	Roads & Longton 2003
Ptilidium pulcherrimum	2.5 m	Crum 2001
Atrichum angustatum	>15 m	Stoneburner *et al*. 1992

Evidence from a Road Cut

Miller and McDaniel (2004) used a novel method to estimate the distance and rate of dispersal that delivered new species to a new substrate. Using a highway construction site on Whiteface Mountain, New York, USA (Figure 11), they examined the bryophytes on concrete mortar there and found that it had increased the bryophyte diversity by 50% above that found on local rock substrata. The local and mortar bryophyte floras differed considerably. Many of these new species were typical of lower elevation forests, at least 5 km distant, where they were not on concrete. The new diversity suggested that these colonizers had arrived and established at the rate of at least one species per year during the 65 years since the highway construction. Miller and McDaniel concluded that for at least some bryophytes, dispersal over 5 km or more are routine events.

Figure 11. Whiteface Mountain, NY, with new-fallen snow at the summit. Photo from Wikimedia Commons.

Epiphytes

For epiphytes, dispersal must necessarily be more than a few meters for the species to survive natural die-off of forest trees, not to mention the ravages of harvesting. Snäll *et al*. (2003) found that the occurrence of the epiphyte ***Orthotrichum speciosum*** (Figure 12) in a fragmented forest landscape was most affected by shading, but also by connectivity to nearby tree patches, aspen (*Populus*) tree diameter, and forest vitality, suggesting that age of forest was a contributing factor, perhaps in providing more time for colonization. Furthermore, once either ***O. speciosum*** or ***O. obtusifolium*** (Figure 13-Figure 14) became established on a tree, the species remained there until the tree died. Local extinctions were entirely a function of the life of the host tree. Hedenäs *et al*. (2003) found that environmental variables seemed to have little influence on the epiphytes (including ***O. obtusifolium***) in a *Populus tremula* stand. Rather, asexually dispersing species were more common than sexually dispersing ones. Sexually dispersing species tended to be more aggregated than the tree species, whereas the asexually dispersing ones had a distribution similar to that of their host.

Figure 12. ***Orthotrichum speciosum*** with capsules. Photo by Michael Lüth, with permission.

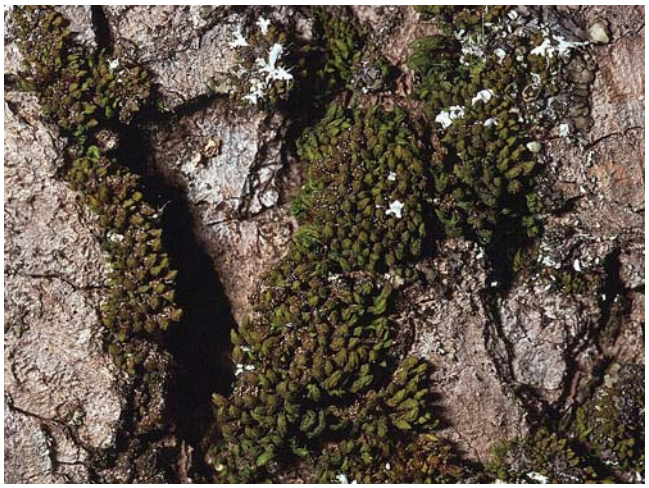

Figure 13. ***Orthotrichum obtusifolium*** on bark, a species that remains with its host tree until the tree dies. Photo by Michael Lüth, with permission.

Figure 14. ***Orthotrichum obtusifolium*** with gemmae on leaves. Photo by Michael Lüth, with permission.

The occurrence of ***O. obtusifolium*** (Figure 13-Figure 14) in the fragmented landscape was controlled by similar variables but with different relative importance. Unlike ***O. speciosum*** (Figure 12), colonization of ***O. obtusifolium*** was not affected by connectivity. Snäll *et al*. (2004a) found that there was significant kinship between individuals of both ***Orthotrichum speciosum*** and ***O. obtusifolium*** up to 350 m apart. Snäll and coworkers suggested that this indicated they were dispersal limited and might be threatened by current silvicultural practices. Nevertheless, this distance is superior to that of the species listed in Table 1, although it probably represents **stepping stone** dispersal, discussed below.

For the epiphyte ***Neckera pennata*** (Figure 15-Figure 16) the past history of its occurrence accounted for much of its current distribution, emphasizing the importance of nearby sources of diaspores (Snäll *et al*. 2004b). Snäll and coworkers (2004b) suggested that its dependence on connectivity, tree age, and tree diameter (a surrogate for tree age) indicate a restricted dispersal range for ***Neckera pennata***. Its primary distribution at heights of less than 1.6 m on the tree could also be a response to the restricted dispersal range.

Figure 15. ***Neckera pennata*** on bark of *Thuja occidentalis*. Photo by Janice Glime.

Figure 16. ***Neckera pennata*** branch with capsules, a species that seems to be dispersal limited. Photo by Jan-Peter Frahm, with permission.

Disturbed and Short-lived Substrata

One might assume that short-lived substrata would drive selection for species that have good dispersal capability. It appears that ***Ptilidium pulcherrimum*** (Figure 17) from rotting logs in the coastal peninsula of northern Sweden has a somewhat better dispersal than the epiphytes mentioned above where the tree substrate is stable for a longer period of time. Söderström and Jonsson (1989) found that only 43% of the spores of log-dwelling ***Ptilidium pulcherrimum*** produced remained within 2.5 m of the source, suggesting that 57% were able to travel far enough to reach logs at a greater distance than that.

Figure 17. ***Ptilidium pulcherrimum***, a log- and soil-dwelling species that relies on superior dispersal. Photo by Michael Lüth, with permission.

The soil-dwelling ***Atrichum angustatum*** (Figure 5) seems to be less adapted for dispersal than the log-dwelling ***Ptilidium pulcherrimum*** (Figure 17), with 94% of the spores of the former falling within 2 m of the colony center, and another 1% falling in the range of 15 m (Stoneburner *et al*. 1992). Hence, the soil-dwelling populations of ***P. pulcherrimum*** are prepared for dispersal to a greater distance as their habitat becomes uninhabitable. It is therefore not surprising to find it among the early colonizers of disturbed soil banks and other newly cleared soil in forests as well as on decaying logs.

Herben, *et al*. (1991), likewise using rotting logs, considered the number of spores needed to give rise to enough new colonies that a bryophyte species could persist in this system of temporary habitat patches. To answer this question, they studied the invasive moss ***Orthodontium lineare*** (Figure 18) in southern Sweden. This species invades rotting wood, and based on model simulations, its success depends primarily on spore transport and establishment. Disturbance rate, competition, and colony growth are of lesser importance.

Figure 18. ***Orthodontium lineare*** with numerous capsules that help it to be an invasive species. Photo by David Holyoak, with permission.

If a species thrives in a periodically disturbed habitat such as an arable field or floodplain, then it needs a means of surviving and distributing to suitable substrata when favorable growing conditions occur. But the most favorable circumstances typically are those where it currently exists, and although it is likely that nearby areas are suitable, many distant areas most likely are not. Hence, such species are often adapted for rapid colonization and short-distance dispersal. With these considerations in mind, it is somewhat surprising that diaspore banks in these habitats are typically dominated by spores, such as those of ***Physcomitrium sphaericum*** (Figure 19; During 1997). On the other hand, habitats with small scale but somewhat regular disturbances usually have species that mostly reproduce asexually.

Figure 19. ***Physcomitrium sphaericum*** with capsules, a common species in diaspore banks. Photo by Li Zhang, with permission.

In peatlands, disturbances from mining are large scale and recolonization occurs on a bank of peat. The disturbance exposes deep peat where propagules have collected for centuries (Poschlod 1995). Poschlod found that some ***Sphagnum*** spores can germinate from these older peats following disturbance that exposes them to light. He found that the species appearing after these disturbances are typical of the original vegetation, are represented in the diaspore bank, and are often absent in the diaspore rain. This was likewise true in a dry heath, where the dominant bryophyte re-colonizer was ***Campylopus pyriformis*** (Figure 20-Figure 21).

Figure 20. ***Campylopus pyriformis*** with abundant capsules. Photo by Jan-Peter Frahm, with permission.

Figure 21. ***Campylopus pyriformis*** showing detached leaves that can serve as propagules. Photo by Michael Lüth, with permission.

Richards (1988) considered all substrata useful for bryophyte colonization in tropical forests to be impermanent. He therefore considered it important for those species inhabiting such substrata to have efficient short-distance dispersal. The same will be discussed below (Spore Size and Number) for ***Archidium*** (Figure 22) species, with large spores, cleistogamous capsules, and poor dispersal ability.

Figure 22. ***Archidium alternifolium***. Photo by Andrew Spink, with permission.

Kubisch *et al*. (2014) summarized the importance of interacting factors in facilitating or preventing successful dispersal. Such factors include abiotic factors (wind, air currents) and adaptation to the new environment. They describe these as a "dynamic equilibrium of colonization and local extinction events." These principles should apply to bryophytes.

Long-Distance Dispersal (LDD)

For many bryophytes, there is at least indirect evidence that long-distance travel occurs. On Signy Island in the Antarctic, Marshall and Convey (1997) trapped spores of all five taxa of bryophytes at distances of 0.5-1 km from the nearest known sources, attesting to their ability to travel beyond a short distance. In this case, the spores were more abundant than bryophyte plant fragments in the trappings, and the representation of both was proportionately smaller than that of lichens.

A number of studies have demonstrated that typical bryophyte distance curves for spore dispersal are **leptokurtic** (Mogensen 1981). That is, they look like an exponential curve, but with a fat tail, *i.e.*, the numbers are greater close to the source and again at substantial distances than would be expected (Figure 23).

Lessons from Tracheophytes

Nekola and White (1999) took a comprehensive approach to evaluating the long-distance dispersal of bryophytes by comparing them to tracheophytes. They examined bryophytes in North American spruce-fir forests and Appalachian montane spruce-fir forests to estimate the rates of "distance decay." Predictably, the similarity of numbers compared to the source decreased significantly with distance. They found that the rate of similarity decay was 1.5-1.9 times as high for tracheophytes as for bryophytes, *i.e.*, bryophytes disperse farther. They considered that two factors cause distance decay: decrease in suitable habitat and limits to dispersal. Since the habitats were the same for both the bryophytes and the tracheophytes, it would imply that either the bryophytes have broader ecological amplitude for such factors as soil type, temperature, moisture, and day length, or they have greater dispersal ability. It is likely that both are true.

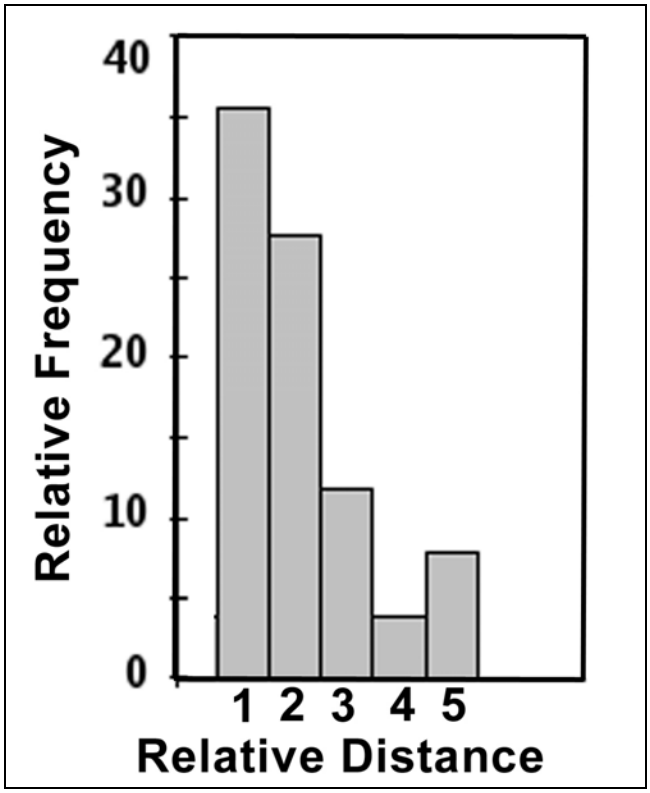

Figure 23. Hypothetical leptokurtic data graph showing asymmetrical distribution of data with a fat end on the right. Based on graph by Audrius Meskauskas through Wikimedia Commons.

Iwatsuki (1972) had a somewhat different perspective on the dispersal of bryophytes and their geographic isolation, particularly among the islands of eastern Asia. He considered the distribution of mosses to be comparable to that of tracheophytes and assumed that bryophytes lack an effective means of long-range dispersal. He also considered that bryophytes evolve very slowly, a factor that appears to be true for their morphology but not for their biochemistry and physiology (Glime 2011), and that this lack of evolution results in most moss species having wider ranges than the tracheophytes, *i.e.*, they have not evolved into new species. This perspective made sense based on our morphological understanding of species, but forty years later, with more recent techniques, we are learning that there are DNA differences and that many disjunct or distant populations represent microspecies that differ genetically, and presumably also biochemically. Hence, bryophytes have evolved to occupy somewhat different niches as they have spread to more distant lands. It seems that these wonderful plants have conjured up a million ways to confound us!

In support of Iwatsuki's 1972 premise, Mateo *et al.* (2013) examined the biogeographic regionalization of European bryophytes. They failed to support their first hypothesis, that regions defined for bryophytes would differ from those defined for other taxa due to the highly specific ecophysiology of the bryophyte group, thus adding credence to the suggestion of Iwatsuki. I'm not convinced that they have such a highly specific ecophysiology anyway. Mateo and coworkers concluded that their findings support a greater similarity between migration patterns of tracheophytes and bryophytes than previously considered. They did, however, find that bryophytes had a substantially lower optimal number of clusters and an absence of nested patterns within primary bryogeographic regions, supporting their second hypothesis. Nevertheless, they cautioned that there are so many regions lacking data that such conclusions are tentative until some of the assumptions and data gaps can be removed.

Certainly some records confirm that bryophytes have broader distributions than do tracheophytes. Jerry Jenkins (Bryonet 6 March 2013) has observed the colonization of his own farmland and second-growth forest in New York State, USA. This area has been invaded by about 100 bryophyte species and a similar number of tracheophytes. He has found a striking contrast in the distributions of the invading species of these two groups. Approximately half of the bryophytes are species known from two or more continents, whereas most of the tracheophytes are restricted to North America, and many to eastern North America. This leads us to examination of the concept that "everything is everywhere."

Everything Is Everywhere!

Baas-Becking (1934) formulated this hypothesis for micro-organisms, promulgating the notion that "everything is everywhere, but, the environment selects." This concept will be discussed later (Interactions volume) for protozoa and small animals. But is the concept applicable to bryophytes, where single-celled spores are among these small, airborne propagules?

The concept of everything is everywhere assumes that small propagules are able to travel the world over, but that once they arrive, they must locate in a suitable environment to survive. Santos-González (2007) discussed this concept for fungi, which, like the bryophytes, can spread by single-celled spores. It is easy enough to show for both fungi and bryophytes that the environment selects, but to demonstrate that everything is everywhere is more challenging. Not only must we demonstrate that air patterns are capable of distributing and redistributing bryophyte spores (and even asexual propagules) to all locations, but we must also demonstrate that they survive the journey. Such experimentation has rarely been attempted.

Bryophyte species are generally more widely distributed than those of tracheophytes (Pisa *et al*. 2013).

Lazarenko (1958) considered the remote transport of moss spores as doubtful in explaining the formation of discontinuous moss ranges. Rather, he, like Iwatsuki (1972), asserted that moss distribution has followed the same principles as that of tracheophytes, following continental drift theory. He uses radiation of species from two distribution centers of ***Syntrichia ruralis*** (Figure 24) to illustrate the role of the separation of the continents. He rejects the significance of long-distance transport to explain such patterns. While I agree that he has offered a plausible explanation, I do not agree that it is the only one, and I consider it possible that ***Syntrichia ruralis*** could have been transported from a northern location prior to the Ice Age to

both Europe and North America or been transported at some point in time from one of those continents to the other, perhaps when the species was young, then diverged into the various lineages of similar species, resulting in several degrees of differences. Such transport could have occurred by wind passage. Nevertheless, Lazarenko argues that the ranges of mosses show the same zonal regularities as seed plants. While that may be true, many bryophytes have much wider distributions than seed plants, suggesting a different or easier mode of dispersal. Most bryologists do consider that many bryophytes are capable of long-range dispersal, accounting for the presence of many species on both sides of the Atlantic Ocean and others at both poles. Van Zanten and Pócs (1981) considered it likely that long-distance transport was common for spores under 25 μm. On the other hand, they considered transport across the equator to be difficult, if not impossible.

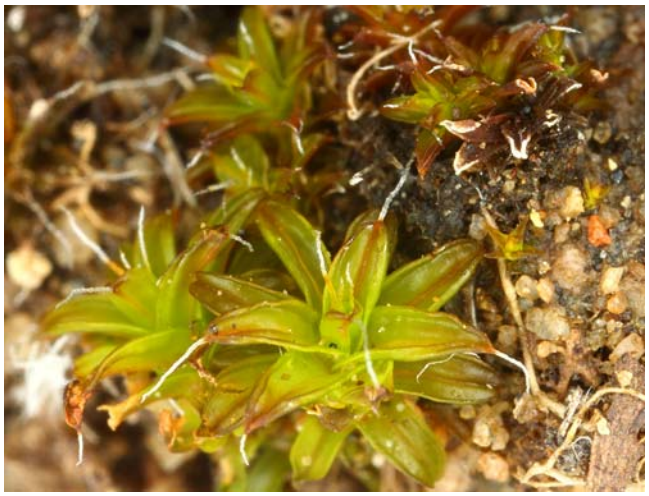

Figure 24. ***Syntrichia ruralis***. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Pisa *et al*. (2013) used ***Bryum argenteum*** (Figure 7) to demonstrate the Baas-Becking hypothesis. This species has a wide (**cosmopolitan**) distribution. They found that genetic diversity demonstrated environmentally driven genetic variation, with the greatest genetic diversity above 1900 m. There was a significant genetic variation correlation with elevation, but the genetic diversity did not correlate with geographic distance, supporting the concept of long-distance dispersal rather than stepping-stone distribution.

Spore Size and Range

One question that arises in dispersal is that of **effective size** of the dispersal unit. Because of their dominant haploid generation, bryophytes do not conform well to the general genetic models. Bengtsson and Cronberg (2009) investigated the size effect in bryophytes and found that the effective size corresponds well with the smallest size of scored individuals. When only a small number of sporophytes is produced by females in a male-dominated community, the decrease in effective size is most severe. They concluded that the **harmonic mean** (obtained by dividing number of observations by reciprocal of each number in series) of diploid sporophytes per individual gametophyte is the more relevant measure in determining minimal size needed for effective dispersal.

One way to test "everything is everywhere" and support or refute Lazarenko's assertion is to examine the correlation between spore size and species range. This correlation remains to be done on a broad scale. And this correlation might not be instructive if nearly all bryophyte spores are small enough to travel everywhere. As Schuster (1969) concluded, the evidence of distributions seen at our present point in time does not really permit us to distinguish ancient overland dispersal from more recent dispersal by spores. Delgadillo (1993) discussed this same problem in trying to explain the bryogeographic relationships between the Neotropical flora and that of Africa, areas that share about 334 taxa. These decisions are complicated by rapid evolution vs slow evolution. It is interesting that while the Afro-American liverworts number 74 species, these are all in one family, the **Oxymitraceae** (Figure 25) (Gradstein 2013). Nevertheless, these constitute about 5% of the Neotropical liverwort flora and 8% of the African liverwort flora. Gradstein treats these as primarily the result of long-distance dispersal.

Figure 25. ***Oxymitra incrassata*** (**Oxymitriaceae**), representing the only Afro-American liverwort family. Photo by Michael Lüth, with permission.

Distribution Stories

Schuster (1979) attempted to understand the distribution of liverworts in the Southern Hemisphere, where "old" families seem to predominate. He considered dispersal there to be the result of short-range or "step-wise" (referred to herein as "**stepping stone**") dispersal. This explanation relies on the separation of populations due to the fragmentation of Gondwanaland (Figure 26) and makes assumptions about the rate of speciation and efficiency of long-distance dispersal compared to the presumed geological background. Schuster (1982) explained the origin of plant groups in the southernmost Gondwanaland with the continental fragments (Figure 26) as "floating Noah's arks."

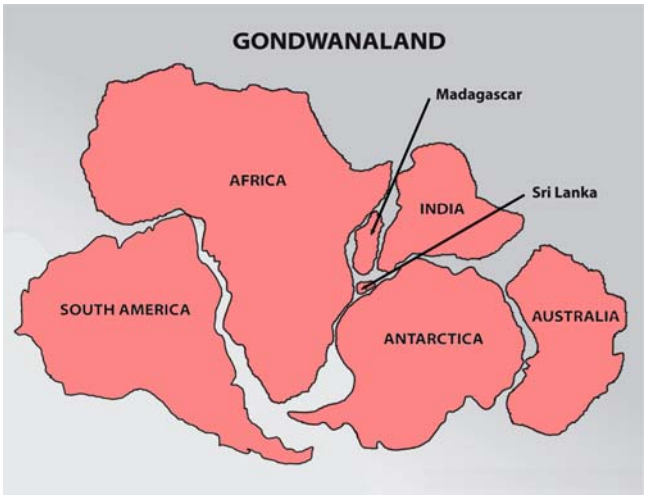

Figure 26. Gondwanaland breakup. Redrawn from Richard W. Hughes.

Ceratodon purpureus (Figure 27) arrived on one of the outer Aleutian Islands within less than a year of eruption (Rod Seppelt, Bryonet 11 March 2013). Surtsey was colonized by bryophytes by 1967 following the island's emergence from the sea off the Iceland coast in 1963 (Fridriksson & Magnússon 1992). However, the first vascular plant was found there in just two years after eruption, in 1965.

Figure 27. ***Ceratodon purpureus*** with capsules. Photo courtesy of Geralyn Merkey.

In New Zealand populations of ***Sphagnum plumulosum*** (= ***S. subnitens***; Figure 28), Eric Karlin, Jon Shaw, and Dick Andrus (Karlin *et al*. 2011) found that only two genetic signatures existed, representing two founding parents (Rogers 2011). In northwestern North America, they found 100% of the gene pool was derived from one individual! This means that to colonize the widespread areas in these two regions required considerable dispersal. They determined that this dispersal involved both vegetative fragments and spore dispersal. They also concluded that the spread of this species from Europe to North America and to New Zealand was by humans within the last 300 years, followed by non-human dispersal to reach their present ranges in those two regions.

Figure 28. ***Sphagnum subnitens*** with capsules. Photo by David Holyoak, with permission.

Island Colonization Stories

Surtsey, off the southeast coast of Iceland, provided a natural experiment in colonization following its volcanic emergence from the sea. The primary colonizers were mosses and lichens on the hardened lava and tracheophytes on ash. Colonization on Surtsey compared to Katmai in having few Cyanobacteria, but differed from Krakatau, where the primary colonizers were Cyanobacteria (Brock 1973). Tracheophytes arriving and becoming established were inversely proportional to the distance from the available source, the nearest being a rock 5.1 km away (Fridriksson 1987). However, distance to the mainland is more than 35 km.

Bryophyte invasion lagged behind that of tracheophytes. This may be the result of dispersal types, with most of the tracheophytes arriving with birds (Magnússon *et al*. 2009). Nevertheless, by 2008 on the block lava on the eastern part of the island, tracheophytes were still poorly represented. Instead, the lichen *Stereocaulon* and moss ***Racomitrium*** (Figure 29) predominated. By 1994, the Lesser Black-backed Gull invaded the southern barren lava and used the ***Racomitrium*** as nesting material. The effect of these birds in spreading the moss on the island is unknown.

The Northern Stockholm archipelago in the Baltic Sea can provide a test of dispersal and "everything is everywhere." Among the 19 islands, Sundberg *et al*. (2006) found 500 patches of ***Sphagnum*** in 19 species in 83 rock pools on 14 of these islands. The species richness on the islands correlated positively with island area and degree of shelter by surrounding islands, emphasizing the importance of habitat even when other locations might be more accessible. Supporting this habitat importance, they found that distance from mainland, connectivity, height, and age did not add to the predictability of the island flora. This suggests the importance of aerial dispersal over long distances. Furthermore, spore size did not add to the model, supporting my suggestion that most bryophyte spores might be small enough to be "everywhere." However, individual species did differ in the habitats they occupied, supporting the concept of "the environment selects." Species frequency (number of colonized islands and rock pools) was predicted primarily by spore output of the species on the mainland.

Figure 29. ***Racomitrium lanuginosum*** on rock. Photo by Janice Glime.

The choice of ***Sphagnum*** from these Baltic islands is a good one to support the Baas-Becking hypothesis. ***Sphagnum*** has no specialized asexual reproductive structures (Sundberg *et al*. 2006), although the importance of fragmentation in this genus is poorly known. Furthermore, only 2% of the ***Sphagnum*** patches on the islands produced sporophytes, and these were mostly on ***Sphagnum fimbriatum*** (Figure 30). Hence, we can be reasonably certain that there has been little or no stepping stone dispersal (discussed below) and that colonization is the result of spore dispersal from the mainland. Sundberg *et al*. concluded that the ***Sphagnum*** on the island is the product of centuries of colonization, but that it is not dispersal limited.

Figure 30. ***Sphagnum fimbriatum*** in Europe. Photo by Michael Lüth, with permission.

Reverse Colonization

For whatever reasons, ecologists have tended to consider islands to be the end of the journal for dispersal of species. But Bellemain and Ricklefs (2008) challenged that concept. They reasoned that if propagules could get to the island, their descendants could get from the island to the mainland. In most cases, we could expect their dispersal abilities to be as good as those of their ancestors. They supported this hypothesis with molecular phylogenies that revealed several examples of **reverse colonization** from islands to continents. But their work was based on animals. What does it mean for bryophytes?

Hutsemékers *et al*. (2011) addressed this question for spore-producing plants. They noted that arguments against reverse colonization focussed on the assumption that island colonizers lose their dispersal power and that back colonization is unlikely due to prior occupation of the niche. Using the Azores, Canary Islands, and Madeira, they found that the aquatic moss ***Platyhypnidium riparioides*** (Figure 31) does not lose its dispersal ability on the islands. This is not surprising since its primary means of dispersal is by fragments that travel downstream. They further found that mainland populations experienced a severe bottleneck during the last glacial maximum. Hence, instead of being dead ends for the propagules, these islands serve as major sources of biodiversity for postglacial recolonization of Europe, at least for this spore-bearing moss.

Figure 31. ***Platyhypnidium riparioides*** in a typical stream habitat. Photo by Hermann Schachner, through Creative Commons.

In the aquatic moss ***Platyhypnidium riparioides*** (Figure 31) there was a significant correlation between the strong genetic variation among populations at a regional scale and the genetic distances (Hutsemékers *et al*. 2010a). However, at a landscape scale, strong dispersal limitation seems to result different histories between southern and northern groups. Furthermore, ecological and genetic variation correlate, suggesting there is reproductive isolation among ecotypes.

Laenen *et al*. (2011) also supported the reverse colonization concept from nearby islands to Europe. They found that Macaronesia exhibited low rates of endemism for bryophytes. Using ***Radula lindenbergiana*** (Figure 32) as a model, they found that European populations share a common Macaronesian ancestor, supporting the view that this island served as a source to repopulate the species in Europe in the postglacial time. They further suggested that the reduced size of bryophytes could account for the diminished amount of morphological variation in these Macaronesian populations. They concluded that islands such as these could have served as refugia during glacial times.

Figure 32. ***Radula lindenbergiana***; European populations share a common Macronesian ancestor. Photo by Hermann Schachner, through Creative Commons.

I raised this question of reduced morphological variation many years ago and suggested that bryophytes diversified biochemically as they struggled to persist against the advances of herbivory, fungal attack, and competition with larger plants (Glime 2011). Laenen *et al*. (2014) suggested another explanation. They used statistical rate analysis with time calibration to support the hypothesis that both mosses and liverworts experienced bursts of diversification since the mid-Mesozoic. The current low number of extant species is the result of mass extinctions, with fossil finds not adequately representing their history.

Cronberg *et al*. (2006) explored the variation in the genetic clonal structure of the **dioicous *Hylocomium splendens*** (Figure 33). Using five 10x10 cm plots monitored for five years, they determined the allozyme haplotype of 157 ramets and those from an additional four neighboring plots. They found only four haplotypes within the plots. One female type occurred in all plots and one male type occurred in four plots. Genets were growing intermingled. Although sporophytes were abundant, they found no evidence of recruitment from spores. Their evidence suggests that clonal diversity within patches is determined by vegetative reproduction, in this case by branching and fragmentation. Among patches, sexual processes, *i.e.* production of spores, dominates diversity.

Figure 33. ***Hylocomium splendens***, a species that has little recruitment from spores. Photo by Daniel Mosquin, with permission.

In their analysis of range disjunctions and speciation of the leafy liverwort ***Leptoscyphus*** (Figure 34), Devos and Vanderpoorten (2009) found that rather than having its evolution triggered by episodic shifts in habitat conditions, diversity in this liverwort genus seems to be the product of morphological and molecular divergence that has accumulated gradually. This contrasts sharply with the rapid diversification known in at least some tropical trees.

Figure 34. ***Leptoscyphus normalis***, in a genus that seems to have accumulated its genetic diversity gradually. Photo by Jeremy Rolfe, through Creative Commons.

Hutsemékers *et al*. (2010b) noted that our traditional way of viewing maintenance, diversity, and evolution of aquatic plants has been:

1. decreasing or erasing patterns of isolation by distance
2. increasing outbreeding
3. resulting in downstream increase of genetic diversity.

In the aquatic moss ***Platyhypnidium riparioides*** (Figure 31), the geographic partitioning of genetic variation at the scale of the river basin and indirect measures of dispersal fail to support these principles. Instead, the results suggest an overall weaker dispersal ability of the moss compared to that of pollen or wind-dispersed seeds. Unlike the flowering plants, dispersal of sperm to the egg is more difficult in aquatic species of flowing water. Instead, dispersal of fragments is the more common means of arriving at new sites, accounting for the lower degree of diversity among sites for ***Platyhypnidium riparioides***. But overall, bryophytes are considered to be more mobile than flowering plants (Preston & Hill 1999).

One of the predictions for island floras is that they would be subject to **Baker's Law**, that colonization by self-compatible organisms is more likely to be successful than colonization by self-incompatible organisms because of the ability for self-compatible organisms to produce offspring without "pollination" agents. By extension, this would mean that monoicous bryophytes would be more successful in colonization that dioicous taxa.

Patiño *et al*. (2013) examined whether loss of dispersal power and bias toward self-compatibility (Baker's Law) were true for island bryophytes. They found that life history traits of oceanic bryophytes differed statistically from those on continents. On the other hand, life history traits between continental bryophytes and those of continental islands were similar. In this regard, monoicous species of bryophytes were in significantly greater

proportion on oceanic islands than on continents. At the same time, oceanic islands had a greater proportion of species that produced specialized asexual propagules, favoring short-distance dispersal. Nevertheless, for the four species examined, the relative frequency of fertile shoots was higher on islands than on continents. They conclude that this evidence indicates a global loss of long-distance dispersal among oceanic island bryophytes, just as seen with the development of flightless birds!

Factors Contributing to Dispersal

Distance from Source

One of the most obvious factors limiting dispersal is distance to be travelled. Sundberg (2005) found that the spore deposition patterns of ***Sphagnum*** fit the inverse power law (deposition per unit area is proportional to the distance ($R^2 > 0.99$). Nevertheless, when the curves were extended to infinity, they failed to account for all the spores dispersed. For example, in ***Sphagnum squarrosum*** (Figure 35), only 11% could be accounted for. Therefore, something else must be occurring. Sundberg suggests that this "something else" is thermal updraft.

Figure 35. ***Sphagnum squarrosum*** with capsules. Photo by Michael Lüth, with permission.

Sundberg (2012) used cotton cloth traps to assess the ***Sphagnum*** spore density in spore rain. He estimated that densities were approximately 6 million per m^2 over the season in a large area, but were only 1000 m^{-2} in Svalbard, northern Norway, indicating that all rains are not equal. Spore rain was strongly related to distance from source, especially relating to sources within 200 km. It is interesting that he found larger spores at isolated island sites, suggesting that they originated from distant, humid areas. In boreal areas, ***Sphagnum*** accounts for immense numbers of spores, a factor that accounts for its ability to colonize quickly in the wetlands there. Most striking to our consideration of long-distance dispersal is his estimate that 1% of the spores were of a trans- or intercontinental origin and that these spores originate from multiple locations.

Hutsemékers *et al*. (2008) used colonization of 52 slag heaps to assess distance and rate of travel of bryophytes. They found that the number of species per slag heap correlates significantly with time elapsed and area size. Of these colonizers, 44% of the species were recruited from within 6 km. Recruitment from 6-86 km accounted for the remaining 56% that were recruited within 50 years. New slag heaps are mostly colonized by fugitive, weedy species. Those colonized for more than 50 years accumulated perennial species with a **stayer life strategy**. Rare species tend to occur at intermediate stages, experiencing a tradeoff between probability of dispersal and limitation by increasing competition.

Dispersal Pathway

Just as wind-pollinated trees are adapted to disperse their pollen in spring before the leaves come out on the trees to avoid that interference, bryophytes are limited in their dispersal by similar obstructions. Fenton and Bergeron (2006) found that ***Sphagnum*** (Figure 35) spore abundance in boreal forests of northwestern Quebec, Canada, was inversely correlated with local tree stand density, and suggested that this was evidence that wind intensity may play a role in limiting dispersal. I would add to that the ability of trees to serve as spore traps.

Renner (2004, 2005) used data on direction, strength, and speed of both sea currents and wind jets to explain dispersal of plants across the tropical Atlantic Ocean. He used data from genera, partly because of data availability and partly, as he argued, because families may have broken up (evolved) before dispersal and species had too much anthropogenic influence. Nevertheless, 110 genera contain species on both sides of the tropical Atlantic. Dispersal patterns and disjunctions can be related to water currents between Africa and South America and to exceptional westerly winds from northeastern Brazil to northwest Africa. Although dispersal by water in both directions seems to be more common for these genera than wind or animal dispersal, bryologists have considered the saltwater to be lethal to bryophyte spores. Furthermore, wind dispersal seems to have facilitated spread from South America to West Africa, but not in the opposite direction.

Air Currents

Van Zanten and Gradstein (1988) summarize the air currents that can facilitate long-distance dispersal:

4. dry air streams at relatively low altitudes (<3000 m)
5. hurricanes, tropical storms, or depressions
6. wet air streams at relatively low altitude (< 3000m)
7. dry air streams at high altitudes, *e.g.* jet streams (ca 10,000-12,000 m asl)

These means of transport vary in their limiting factors: high UV, desiccation, wet freezing, low atmospheric pressure, ozone. The two dry airstreams subject the diaspores to desiccation, with the jet stream causing dry freezing and strong UV radiation, but the low altitude transport has only moderate UV radiation. Likewise, the wet air stream at low altitude has even lower UV radiation due to absorption and reflection by clouds. Hurricanes and storms can have wet-freezing and lower atmospheric pressure, accompanied by different air composition. These storms are likely to be less effective for long-distance dispersal because of the heavy precipitation that can clean the air of the diaspores. The wet air streams at low

altitudes seem to be the safest mode of travel, with only moderate desiccation and low UV intensity.

Molecular Clocks

Molecular clocks have become useful tools to determine not only the pathway, but also the timing of transport of propagules (Renner 2005). Using molecular sequences (gene regions), one can estimate the age of a particular lineage and determine its approximate arrival time. Using fossils, models can analyze the change in substitution rates of a lineage by combining molecular data with known time constraints, particularly with fossils. These fossil/molecular "clocks" are termed **relaxed clocks**. These molecular clocks become effective tools that can be combined with information on prevailing wind and water currents, position of land mass, and size of land mass.

Weather

One might assume that wind dispersal is going to be affected by weather. Fungi might serve as a model for expectations of the effect of weather on bryophyte dispersal. In a study on fungal dispersal, Gregory and Hirst (1957) determined that airborne spore concentrations were dependent on weather and the phenology of the local flora. Lönnell (2011) considered horizontal wind speed and thermal updrafts/turbulence as factors that influence the dispersal distances.

Fungi demonstrate the importance of intermittent and gusty wind in spore dispersal (Aylor 1990). And like wind-pollinated trees, canopy plants with leaves can trap the spores and thus must be avoided unless they are indeed the target. For tropical bryophytes, this may be the case, but in temperate zones, tracheophyte leaves are rarely the target substrate. Hence, like the windborne pollen seeking a stigma, the bryophyte pollen must avoid the canopy traps in order to travel any great distance. Aylor points out the importance of gusts of wind in once again removing trapped spores and putting them back into the air. He assumes that gusts can enhance the air movement by a factor of five in the canopy compared to the average air movements. In the fungi, and likely in the bryophytes, half the spores that have ventured only a few meters from their source can escape the canopy if they are released from mid-canopy or higher. If this premise holds, then epiphytes gain considerable dispersal advantage by their high starting location.

A further simulation shows that fluid motion such as that of smoke can cause an ejection type of flow that enhances spore escape from its source. In fact, Aylor (1990) contends that movement of smoke (and similar cloud-type movements of spores) create features similar to release from the top of the canopy. Aylor suggests that the most difficult aspect to model is the "takeoff" from the source and "integration into the transport process," in the bryophyte case being from the capsule.

Fires

I must wonder if forest fires play any role in distribution. Certainly there are tremendous updrafts (Figure 36), but are there updrafts that are cool enough for diaspores to survive? Based on my observations in Yellowstone after a massive fire, I have to suspect there might be. There were patches of trees burned on one side, but live on the other, suggesting that bryophytes might also survive there but be subjected to the updrafts. But better evidence came from patches of ***Pleurozium schreberi*** (Figure 37) that were burned on part of a clump but green and healthy only millimeters away. Surely those nearby burned portions were creating updrafts, even if only small ones. It took only a glance at the mountainside to understand the patchiness of the burn itself. Surely these patches of fire created considerable turbulence that could thrust diaspores for considerable distances. If the soot can reach a location, so can the diaspores. And the smoke itself might offer protection from UV light. We need to examine temperature and air movement patterns to further assess the feasibility of these updrafts as dispersal agents.

Figure 36. Wildfire in California, USA. Photo through Wikimedia Commons.

Figure 37. 1989 view of ***Pleurozium schreberi*** next to burned soil from a 1988 fire at Dunraven Pass, Yellowstone, Wyoming, USA. Photo by Janice Glime.

Diaspore Characteristics

Not all bryophytes are created equal. Individual characteristics can determine the likelihood of the spores becoming part of the spore rain. Lönnell (2011) lists diaspore size, shape, weight, type of abscission (active or passive), abscission height, and abscission time to contribute to dispersal distances.

Most experiments on bryophyte dispersal have suffered from distance limitations of only a few meters. Lönnell *et al*. (2012) conducted a novel experiment in which they eliminated the possibility of multiple spore sources by isolating a pot of ***Discelium nudum*** (Figure 38) on a raised bog where its normal clay habitat was unavailable. Hence there was little possibility of other colonies contributing to the experiment. Pots of clay, numbering 2000, were placed at various distances between 5 and 600 m from the mother colony. Within 10 m of the mother colony, the mean colonization rate was greater than 50%. In the 10-50 m range, the colonization rate dropped sharply, but for pots between 50 and 600 m the colonization rate was stable, ranging 1-3%. The estimated number of spores (2-6 per m^2) in that most distant segment was commensurate with the spore output of the mother colony. Lönnell considered this to be evidence that the majority of spores of this species escape the parent colony to travel greater distances. Thus, establishment into new locations at distances measurable in kilometers is likely for this and probably a number of other species with similar spore output and dispersal characteristics.

Figure 38. ***Discelium nudum*** with red antheridia. Photo by David T. Holyoak, with permission.

Work by Hutsemékers *et al*. (2008) adds credence to this assertion of kilometers of dispersal. Using 52 slag heaps in Belgium as pristine soil, they tracked the invasion by bryophytes to heaps at various distances and inferred rate of dispersal by the distance and time of arrival. As expected, the number of species per slag heap is significantly correlated with area size of the heap and time since colonization. It is the weedy species that arrive first, exercising a superior dispersal ability and generally large numbers of spores.

Evidence from Geophysics

Diffusion Models

Levin (1992) contends that generalized diffusion models can explain dispersal of seeds, pollen, and even invertebrate larvae, where winds, currents, and gravity play the major roles. Even organisms that are able to use detailed environmental cues may be dispersed primarily according to diffusion models. Adding habitat-dependent movement can improve the model. Nevertheless, an adequate model can be developed on diffusion alone to explain the spread of oaks and muskrats (Skellam 1951)! However, Levin (1992) suggests that the diffusion model does not apply well on broader scales and that more refined models are needed. He lists the percolation model for fragmented habitats (Gardner *et al*. 1987; Durrett 1988), the correlated random walk for the movement of insects (Kareiva & Shigesada 1983), or clonal growth for branching organisms (Cain 1990, 1991).

It is likely that models mentioned by Levin (1992) apply as well to a number of bryophyte species. Certainly clonal growth is common among bryophytes and can account for small-scale distribution patterns. The percolation model or the correlated random walk may account for distribution of **Splachnaceae** (dung mosses; Figure 39-Figure 40), where the fly may follow a random pattern of visiting dung piles, but the moss dispersal would be closely correlated to that pattern. It would seem as if these fly-dependent taxa might disperse in a manner similar to that of host-specific parasites.

Figure 39. ***Splachnum ampullaceum*** capsules on dung in southern Europe. Photo by Michael Lüth, with permission.

Figure 40. Fly visiting capsules of ***Tayloria mirabilis*** near Cape Horn. Photo by Adam Wilson NYBG, through public domain.

Numerous phytogeographic papers have suggested dispersal patterns over broad areas and linked modern distribution patterns to earlier geologic events. Since major air movement patterns are known, and Van Zanten's work (1975, 1976, 1977a, b, 1978a, b, 1983, 1984, 1985, van Zanten & Gradstein 1987, 1988, van Zanten & Pócs 1981)

provides us with data on aerial survivorship of a number of species, it should be possible to test the diffusion model on bryophytes.

Dust Storms

In their discussion of the global transport of dust, Griffin *et al*. (2002) describe the massive movement of bacteria, viruses, and fungi along with suspended dust particles (and soil pollutants). Just as an example, they estimate that about 13 million metric tons of sediment from Africa land in the North Amazon Basin of South America in a year. Just one dust storm can deliver 200 metric tons.

Charles Darwin, in 1846, expressed the situation as follows: "From the several recorded accounts it appears that the quantity of dust which falls on vessels in the open Atlantic is considerable and that the atmosphere is often rendered quite hazy; but nearer to the African coast the quantity is still more considerable. Vessels have several times run on shore owing to the haziness of the air; and Horsburgh recommends all vessels, for this reason, to avoid the passage between the Cape Verd Archipelago and the main-land." (in Griffin *et al.* 2002). Miles Berkeley (in Griffin *et al*. 2002) concluded that the trade winds could carry fungal spores for thousands of kilometers. German scientists, in 1908, found that the most common bacteria were highly pigmented and all were spore-forming (Griffin *et al*. 2002), suggesting adaptations for aerial dispersal. By 1921, the record height for finding viable bacteria was 21 km above the earth. But these collections had been over land. Finally, in the mid 1930's, Fred Meier, a scientist with the U.S. Department of Agriculture, persuaded Charles Lindbergh to contribute to our knowledge by flying a plane with a metal arm holding microscope slides with a sterile coating of oil while he flew over uninhabited ice, water, and mountains from Maine, USA, to Denmark. These collections revealed fungal spores, pollen, algae, diatoms, and insect wings. Meier then planned sampling over the Caribbean Sea and the Pacific Ocean, but he died in a plane crash in 1938 while doing fieldwork. All these data suggest that bryophytes, too, could enter the jet stream and accomplish long-distance travel.

Not All Storms Are Equal

The next important revelation was that storms of tropical origin were far more likely to enter the upper atmosphere than those of polar origin, carrying nearly 100 times as many fungal spores (Griffin *et al*. 2002). Microbes in the dust in the Virgin Islands show a ten-fold increase during African dust storms. Then a new record for height was set – 77 km above the Earth's surface for some pigmented fungal spores. Of more relevance to the bryophytes is the presence of pollen grains, which might be expected to have similar size and structure to that of bryophyte spores, at 17-19 km above the Earth. This understanding of particle movement is important to our understanding of bryophyte distributions, helping to explain why some tropical bryophytes may appear in polar geothermal areas.

Aloina Example

Numerous authors have attested to the long distance travelling capabilities of bryophyte spores. Kimmerer (1991) found that many spores were trapped 2 m from the plants and contended that spores ensured long-distance dispersal. Pettersson (1940) filtered spores from precipitation in Finland, then grew them to identify them. Large numbers of spores from ***Aloina brevirostris*** (Figure 41) were present, as well as those of ***A. rigida*** (Figure 42), but the genus ***Aloina*** was unknown in Finland. Both species prefer calcareous substrata and thus are limited in their distribution. Pettersson suggested that they came from Siberia, citing the absence of ***A. rigida*** in nearby European countries, but Persson (1944) and Bergeron (1944) both rejected that hypothesis.

Persson argued that Pettersson ignored the other species that accompanied the ***Aloina*** (Figure 42). Among these, ***Bryum pallens*** (Figure 43), ***Leptobryum pyriforme*** (Figure 44), and ***Marchantia polymorpha*** (Figure 45) present no problem, all being common in both Europe and Siberia. However, ***Metzgeria*** was not known from Siberia, although ***Echinomitrion furcatum*** (=***Metzgeria furcata***) (Figure 46) is common in Europe. Persson's second argument was that the ***Aloina*** spores were quite common in the rain (est. at least 60,000,000,000 / km^2). That would be an incredible number to come from such a distance as Siberia. The final complication was that an ***Aloina*** from neighboring European countries had been misidentified as ***Aloina ambigua*** when in fact it was ***Aloina rigida*** (Figure 42), making a European origin of ***Aloina rigida*** quite possible; furthermore, he considered identification of ***Aloina rigida*** without capsules to be difficult, if not impossible.

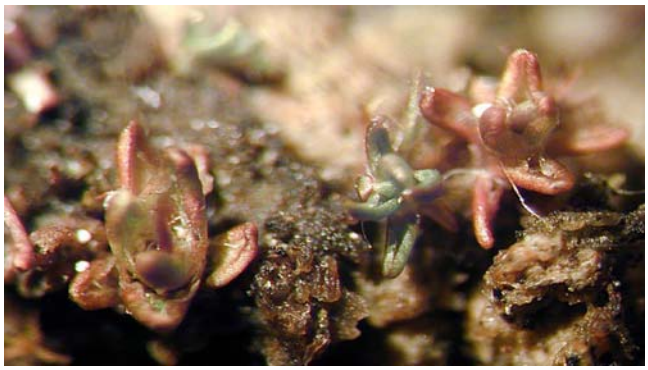

Figure 41. ***Aloina brevirostris*** gametophytes. Photo by Michael Lüth, with permission.

Figure 42. ***Aloina rigida*** gametophytes and sporophytes. Photo by Michael Lüth, with permission.

Figure 43. ***Bryum pallens*** showing red pigmented phase. Photo by David T. Holyoak, with permission.

Figure 44. ***Leptobryum pyriforme*** with capsules. Photo by Michael Lüth, with permission.

Figure 45. ***Marchantia polymorpha*** with gemma cups. Photo by Michael Lüth, with permission.

Bergeron's (1944) arguments against a Siberian origin for the ***Aloina*** (Figure 42) were meteorological rather than biological. First, the weather conditions in Siberia during the preceding week were not likely to have had the force needed to bring the spores into the airstream where they were needed to travel to Finland. Second, rather, the air masses arriving on the day in question originated to the north from other European countries. Third, the air masses leaving the Siberian region did not travel in the direction of Finland. Fourth, the conditions at the collecting site in Finland on the days of sampling did have the right weather conditions to bring down spores, and these were most likely to have come on air currents from the NNW or SSE, either of which would have traversed areas where ***Aloina*** grows and neither of which would have passed over Siberia or joined forces with air from that region. There are lots of factors to consider when attempting to determine the origin of propagules.

Figure 46. ***Echinomitrion furcatum*** (=***Metzgeria furcata***) in Europe. Photo by Michael Lüth, with permission.

Size and Falling Velocity – Distance and Laws of Physics

The first condition of passive dispersal by wind for a diaspore is to get caught by the wind before reaching the ground. For the tiny distances that bryophyte diaspores fall to their substrate, this is a challenge. The laws of physics would predict that atmospheric density of dispersed spores will decrease with increasing distance and increasing height from the colony.

For whatever reason, it appears that when spores exit hanging capsules they can rebound and are elevated (Figure 47) (Cronberg *et al*. (2008). This gives the spores from hanging capsules the same advantage as those from upright capsules. But what causes this upward movement?

Figure 47. ***Bryum argenteum*** spore release, showing upward movement movement of spores. Photo by Nils Cronberg, Hans Berggren, & Rayna Natcheva, with permission.

This can be helped somewhat by animals (I'm guessing especially squirrels and other rodents) that bump them and cause clouds of spores to become airborne. In rangeland, hoofed mammals surely contribute. Once airborne, the falling velocity is important. Small spores like those of bryophytes typically have a falling velocity less than those of larger objects, permitting them to stay airborne longer and have greater opportunity for capture by moving air.

One approach to examining long-distance dispersal is to develop a trajectory model. Trackenberg (2003) developed such a model (PAPPUS) to consider the potential of wind as a dispersal vector. The model included effects of topography, turbulence (including thermal updrafts), and weather conditions. Simulations included initial release height and falling velocity. It improved on most approaches by modelling turbulence. The model was tested against distances measured in the field. Trackenberg considered that sunny weather with thermal turbulence and updrafts would cause a high proportion of long-distance dispersal, even in periods of low horizontal wind speed.

Not only does the model suggest that sunny weather with thermal turbulence and updrafts may be most important, Trackenberg (2003) concluded that stormy weather may have little importance for long-distance dispersal, especially for species with falling velocities less than 1.5 m s^{-1}. Horizontal wind speed seemed to have no effect on diaspores dispersing more than 100 m; frequency of updrafts was positively correlated. I became aware of this importance myself during a blizzard. I'm not suggesting that spores get distributed in blizzards, but the wind patterns can be seen then without equipment. My "aha" moment came as I watched wind and snow swirl around my house and carve a funnel in the snow, raising the snow into the airstream. While this 1 m wide funnel was caused by an L corner of my house, smaller funnels can occur around rocks and other obstructions where bryophytes grow. Snow is a good marker for wind patterns, and it is common for us to see the snow "falling" upward as wind whirls around buildings and other obstructions. Such wind conditions are not restricted to winter. If it is not a rainy day, such conditions would seem ideal for getting the spores away from the ground and putting them into the airways.

Trackenberg (2003) considered the improved predictability of his model to result not only from the addition of turbulence to the model but also to the effect of topography. Those bryophytes that are elevated either by living on trees, rocks, or walls or by living at high elevations have a greater chance of entering the atmosphere. This improvement is in part due to the slow falling velocity of the tiny diaspores of bryophytes. With falling velocities of less than 1.5 m s^{-1}, unstable atmospheric conditions and thermal updrafts under low humidity provide the greatest contributions to dispersal. If diaspore abscission is coupled with these conditions (**xerochasy**), bryophytes can optimize their dispersal capabilities.

In their predictions for immigration into a milled peatland, Campbell *et al.* (2003) assumed that diaspores released from higher altitudes are typically exposed to greater wind velocities (Greene & Johnson 1996) and thus are likely to be carried farther. As discussed above, this probably only matters once they have been lofted into the wind stream by updrafts or other short-distance mechanisms. To determine terminal velocity, Campbell *et al*. (2003) assumed a density of 1 (Gregory 1973) and applied Stoke's law for a sphere with a low Reynolds number. They also assumed that propagules with a slower falling velocity (including bryophytes) and/or with a higher release height from the ground would have a greater probability of dispersing into the mined peatland (Campbell *et al*. 2003; Trackenberg *et al.* 2003). Trackenberg and coworkers warned against using morphology as an indicator of dispersal ability, emphasizing the importance of location of growth and consequent falling distance and upwinds as being of greater importance. For plants in general, Campbell and coworkers found that dispersal distance was most sensitive to falling velocity and weather conditions. Since bryophytes in general have slow falling velocities, we might expect weather to be of greatest importance for them.

Evidence from Restoring Peatlands

Campbell *et al*. (2003) assessed the immigration potential of plants into a mined peatland in southeastern Quebec, Canada. They selected 32 species, including both bryophytes and tracheophytes, as potential colonizers, based on presumed dispersal capabilities. They developed an index of immigration potential based on:

- propagule release height
- falling time (propagule release height/settling velocity)
- propagule wing loading (probably not applicable to bryophyte spores, but possibly to gemmae and bulbils).

Their evidence supported these attributes. Those bryophytes with the higher immigration potentials by wind were usually the more frequent colonizers in the mined peatlands. ***Sphagnum capillifolium*** (Figure 48) and ***Sphagnum fuscum*** (Figure 49), however, were exceptions, with less than a 1% occurrence but relatively high immigration potential. Campbell *et al*. (2003) attributed this to an establishment problem. Rochefort (2000) found that ***Sphagnum*** is particularly vulnerable to drought and the instability of the substrate in the early establishment stages. But Campbell *et al*. found that mosses in general had less of a recolonization constraint than did the herbaceous species in this environment.

Figure 48. ***Sphagnum capillifolium***. Photo by Michael Lüth, with permission.

Figure 49. ***Sphagnum fuscum***. Photo by Michael Lüth, with permission.

Disjunct Distributions

The large number of disjunct taxa in the Andes and Atlantic coastal region of Brazil might lend support to the air current hypothesis (Gradstein & Reiner-Drehwald 2007). Major flyways for birds, especially raptors, often follow mountain ridges because these areas often have air currents that propel the birds forward, saving energy on long migrations. It is reasonable to assume they can similarly provide "flyways" for bryophyte diaspores.

Directional (**anisotropic**) dispersal seems to play a role in Southern Hemisphere distribution. Using data from global winds coverage from the National Aeronautics and Space Administration SeaWinds scatterometer, Muñoz *et al*. (2004) found that the correlation of floristics of bryophytes, lichens, and ferns with wind patterns and wind connectivity is stronger than the correlation with geographic proximity, suggesting that spores travel with the wind.

There seems to be an interesting contrast between the arrival of two species of bryophytes [***Ulota phyllantha*** (Figure 50) and ***Sanionia uncinata*** (Figure 51)] on Macquarie Island in the Antarctic. ***Sanionia uncinata*** has spores only 10-18 µm in diameter, whereas ***Ulota phyllantha*** has cigar-shaped spores 100 µm long. As Rod Seppelt pointed out on Bryonet (6 March 2013), ***U. phyllantha*** occurs abundantly on the coastal rocks along the western side of Macquarie Island (Antarctica) but is rarely seen on the east coast. Its distribution on the island has led to the assumption that it has been distributed by the jet stream from southern South America. On the other hand, ***Sanionia uncinata*** appears to have migrated to Macquarie Island from Australia or New Zealand, matching their genotypes, and differing genetically from other subAntarctic island populations to the east that seem to match the southern South America-Antarctic Peninsula genotypes (Lars Hedenäs, Bryonet 6 March 2013). This migration, contrary to prevailing winds and having a larger dispersal unit, suggests that dispersal by wind will not always follow prevailing winds. Wind directions do change, and Rod Seppelt (Bryonet 6 March 2013) explained that cyclonic low pressure cells can center off the southwest side of Tasmania, pass through the southeast mainland Australia, miss New Zealand and reach to the Ross Sea area of Antarctica. These heavy winds are likely to carry all sorts of propagules from Australia and New Zealand to Antarctica, thousands of kilometers away. Furthermore, during drought periods, huge dust clouds in Australia can reach New Zealand, no doubt carrying spores along with the dust.

Figure 50. ***Ulota phyllantha*** with capsules. Photo by David T. Holyoak, with permission.

Figure 51. ***Sanionia uncinata*** with capsules. Photo by David T. Holyoak, with permission.

Shaw (1982) provides us with more convincing evidence of "everything is everywhere" and the flyway hypothesis. The rare circumboreal ***Plagiobryum zieri*** (Figure 52) has been found in the Huehuetenango Province of Guatemala, far from its nearest neighbor in Colorado, USA. Shaw suggested that the tendency of the spores in this species to remain in tetrads may be a preadaptation to its ability to survive such long-distance travel and become established in its high altitude homes.

Such disjunctions as 28 species of bryophytes common to Central America and the Himalaya Mountains (Sharp 1974) likewise lend credence to long distance dispersal of bryophyte diaspores. They not only support "everything is everywhere," but also emphasize the importance of the "environment selects."

Figure 52. ***Plagiobryum zierii*** from southern Europe. Photo by Michael Lüth, with permission.

Finding a species at both poles of the Earth tends to make one think of long-distance dispersal, and ***Pohlia nutans*** (Figure 53) not only supports the concept that "everything is everywhere," but it clearly supports the "environment selects." Present in Iceland in geothermal areas, common in the Northern Hemisphere, and present on the geothermal areas of the continent of Antarctica, it is the epitome of the environment selects because it is absent in other (non-geothermal) habitats in Antarctica (Skotnicki *et al*. 2002). The Antarctic populations of ***P. nutans*** exhibit low levels of genetic diversity (RAPD & DNA sequences of conserved nuclear ribosomal RNA), supporting the conclusion that they have been derived from a single dispersal event leading to vegetative growth, mutation, and stepping stone dispersal within the continent, a pattern also discernible for the geothermal ***Campylopus pyriformis*** (Figure 21, Figure 54).

Figure 53. ***Pohlia nutans*** with abundant capsules. Photo by Michael Lüth, with permission.

Lewis Smith (1991) considered southern South America to be a continuous source of diaspores for the Antarctic and attributes this to relatively frequent storms that track eastward over the southeast Pacific Ocean. They gain momentum over the southern part of South America where they pick up spores. Sometimes a blocking anticyclone over the South Atlantic Ocean deflects the winds, sending them off to Antarctica.

Figure 54. ***Campylopus pyriformis*** with capsules. Photo by Michael Lüth, with permission.

Perhaps the best explanation is one from Schofield and Crum (1972), that continental drift, long-distance dispersal, and fragmentation of a previously continuous landscape all have been considered meritorious explanations. But "no single hypothesis is sufficient to accommodate all species within any disjunctive pattern." Nevertheless, many of the bryophyte disjunctions are similar to those of tracheophytes, suggesting that similar mechanisms are at play.

Long-range dispersal in bryophytes is supported primarily by their distribution patterns and our knowledge of air movement patterns and the ability of updrafts to carry particles of various sizes. Survival of a number of taxa at atmospheric low temperatures and UV radiation suggests that such long distances may occur, but probably infrequently.

Stepping Stones

It is likely that many species disperse through relatively short distances most of the time, reaching distant locations eventually through a series of dispersal events from location A to location B, then from location B to location C, a means I shall call **stepping stones**, as that term has been used in the literature several times.

At least in some species, we can document evidence of a stepping stone means of species range expansion. For example, Derda and Wyatt (1999b) found that ***Polytrichum commune*** (Figure 55-Figure 56) had a high mean genetic identity between populations (0.867-0998), but that there was significant differentiation among regions that increased with distance. This, coupled with region-specific genotypes, suggested that this species dispersed from location A to location B and then from location B to location C, *i.e.*, the "stepping stone" method. At the same time, some distant populations had multilocus genotypes that were very similar, suggesting that an occasional long-distance dispersal event had occurred.

Figure 55. ***Polytrichum commune*** in its typical abundance, facilitated by new shoots from rhizomes. Photo by Christopher Tracey, through Creative Commons.

Bischler and Boisselier-Dubayle (1997) provide us with an example that supports the concept of stepping stones. They found that in liverworts, there are few differences among the alleles within a population. Rather, intrapopulation differences are more typically an expression of phenotypic plasticity. But over a larger area, a species typically consists of a series of small populations that are reproductively isolated from each other, presumably due to dispersal limitations on the sperm. They considered that these facts are consistent with repeated dispersal and founder events. Further variation can arise from genetic drift. They found a contradiction in the restricted gene flow between populations and the limited genetic differences among geographically disjunct populations.

Figure 56. ***Polytrichum commune*** with abundant capsules that provide spores for long-distance travel. Photo by David T. Holyoak, with permission.

Could it be that rather than stepping stones or multiple dispersal events there could have been a single event that left a number of isolated founder populations that were further divided by genetic drift? Such a proposal is not unreasonable. We know that certain weather events can carry dust for long distances [for example from the Sahara in Africa to Texas in the USA or to California, USA (Reardon 2013) or to southern England (Ken Adams, Bryonet 6 March 2013)] or change the usual direction of weather patterns. Tornadoes can certainly pick up propagules and drop them off in a number of distant locations, sometimes far distant. Hurricanes can make similar deposits, particularly on oceanic islands. Bischler and Boisselier-Dubayle (1997) point out that liverworts have lower levels of genetic variability than do mosses. Rather, they seem to respond to habitat variation by more non-genetic responses through plasticity. Although they consider this to support a history of repeated dispersal and founder events, it does not rule out the possibility of a single dispersal event populating a number of isolated locations, then differing due to genetic drift, founder principle, or subsequent genetic modification. Their success may be due to a genetic complement that permits phenotypic plasticity.

Disjunct distributions always raise questions as to their causes – extinctions, land drift, or incomplete dispersal? Delgadillo (1987) reported that there is evidence of "extensive floristic exchange" in Mexico among the major alpine areas of the Neovolcanic Belt. However, floristic differences and ages among the mountains indicate that dispersal has not been unidirectional nor occurring through a single event. This would seem to indicate that it is not a **flyway** unless air currents change directions, perhaps with seasons. Nevertheless, this range of mountains seems to have provided a **barrier** to the dispersal of some mosses in a north-south direction, but not in the opposite direction. This might be interpreted as an example of "the environment selects," but more ecological information is needed to support that conclusion. In any case, it is likely that mountains present barriers to species that disperse through "stepping stone" pathways and that are unable to survive the climate of the mountain tops.

Dispersal by birds for any instance seems to be discounted by many researchers for a number of regions. Cruden (1966) sums up some of the concerns for transport of seeds:

1. Internal carriage is highly unlikely because it takes at least a month for migration from, for example, California, USA, to Chile, whereas the gut contents are dispelled within a few hours.
2. External carriage is likewise unlikely because the birds frequently preen themselves.
3. The disjunct plant groups do not seem to have any special qualifications for long-distance dispersal. Rather, they live in open, unstable habitats; their seeds can be dispersed by animals; and they are self-compatible.

But some of the objections applied to bird dispersal for tracheophytes do not seem to apply as well to bryophytes. It is unlikely that internal carriage of bryophyte diaspores occurs on long flights, but it could occur in a stepping stone fashion. External carriage is more likely. If a bird in fact walked through a patch of dispersing capsules, numerous spores could adhere. Because of their fine nature and small size, it seems unlikely that preening could remove all of them, and some are also likely able to continue adherence even through the splashing of a bird's bath. Furthermore, like seed plants, only a single spore is needed in the right place to begin a new population, and the birds are likely to

seek out the same kind of habitat as the one where the spore first joined the journey, *i.e.*, a suitable habitat. Cruden (1966) has noticed a correspondence between wintering areas of the birds and plant distributional ranges. He likewise suggests that mountain hopping has been undervalued as a possible migrational route for the plants, in some cases at least following the flyways of the birds. Whereas shorebirds seem to satisfy the long-distance requirements, mountain hopping could account for distribution by a larger number of birds. This latter mechanism could follow the long-distance travel on a shore bird, and at least for bryophytes, seems like a plausible mechanism.

Gene Flow

Gene flow is an indirect measurement of dispersal. While it cannot tell us distance values, it can suggest the magnitude of gene dispersal, hence spore dispersal (assuming that spore dispersal is greater than gamete dispersal). Gene flow results in increased genetic variation within the population and prevents that population from exhibiting genetic differentiation from other populations. For ***Leucodon temperatus*** and ***L. luteus***, both epiphytes, the gene diversity between populations relative to the total diversity was low (Akiyama 1994). Akiyama interpreted this as evidence of extensive gene flow between populations. He considered the low genetic divergence to be a result of their epiphytic habitat, which would suggest that lots of new invasions by spores occurred.

Genetic diversity can be maintained even as a result of small remnant populations in ***Trichocolea tomentella*** (Figure 57). The apparent infrequent gene flow among populations of this species indicates that it suffers dispersal limitations, even on a small spatial scale. On the other hand, new colonization within a population is not affected by its isolation, suggesting that it benefits from random short-range dispersal of fragments. It furthermore appears to have a long life span that permits it to spread through branching. On the other hand these characteristics suggest that it is not a good colonizer because of its limited dispersal.

Figure 57. ***Trichocolea tomentella***, a leafy liverwort. Photo by Michael Lüth, with permission.

Korpelainen *et al*. (2005) evaluated gene flow in bryophytes in a broader context. They found that most bryophyte species (*i.e*., mostly mosses) have a fair amount of gene flow between populations, based on the genetic differentiation that exists among populations. That suggests that there is a fair amount of invasion of populations by spores of other populations.

On the other hand, Derda and Wyatt (1990, 1999a, b) found genetic evidence in ***Polytrichum*** species to indicate that distribution of genetic variation by spores was limited. For ***P. commune*** (Figure 55-Figure 56) the mean genotypic diversity was 0.546. For ***P. piliferum*** (Figure 58) the mean genetic diversity within populations was only 0.037 (Derda & Wyatt 1999a), whereas in ***P. commune*** it was 0.061 (Derda & Wyatt 1999b). Derda and Wyatt (1999b) concluded that long distance dispersal did occasionally occur, based on "region-specific multilocus genotypes" that occasionally occurred distant from the apparent parent population. The fact that this species has a worldwide distribution suggests it is capable of at least some long-distance dispersal. More commonly, it appeared that genotypes moved from location to location in a "stepping-stone" fashion. As one would expect, the genetic similarities between regions generally decreased with the distance between the regions. Evidence from ***Polytrichum juniperinum*** (Figure 59) and ***P. strictum*** (Figure 60) suggests that dispersal distances and gene flow may depend in part on latitude (Derda & Wyatt 2003). For ***P. juniperinum***, Derda and Wyatt found that spore dispersal in the upper Midwest and Pacific Northwest of the USA and Canada was apparently low and relatively less effective south of the Pleistocene glacial margins, whereas colonization from distant **refugia** seems to have been more effective in the northern latitudes. Members of the **Polytrichaceae** are unique in having an **epiphragm** stretched across the peristome teeth, providing only tiny holes from which spores can be dispersed (Figure 61). Van Zanten (1973) considered that long-range dispersal was unlikely in the **Polytrichaceae** genus ***Dawsonia*** (Figure 10), citing horizontal spore ejection by raindrops or other agents that strike the mature capsule. It is likely that other members of the family suffer the same problem.

Figure 58. ***Polytrichum piliferum*** with young capsules. Photo through GNU free documentation license.

Polytrichum strictum (Figure 60), a species that has often been treated as a subspecies of ***P. juniperinum*** (Figure 59), has some of the highest gene diversity levels

known for mosses (HTP = 0.205), with strong regional partitioning of the genetic structure (Derda & Wyatt 2003). This might be explained by the lack of re-invasion of spores into a colony, permitting genetic drift and gene divergence. This lack of re-invasion is consistent with the poor spore dispersal predicted by Van Zanten (1973).

Figure 59. ***Polytrichum juniperinum***. Photo by Li Zhang, with permission.

The story for ***Hylocomium splendens*** (Figure 33) in Scandinavia seems to be quite different from that of ***Polytrichum*** (Figure 58-Figure 61). Cronberg *et al*. (1997) found that among populations from four vegetations zones, eleven out of thirteen loci screened by allozyme electrophoresis demonstrated variation. The relative differentiation among the populations was low (G(ST) = 0.073), indicating a high level of gene flow between populations. Furthermore, although the Subarctic-alpine population was apparently a single widespread clone, it was comprised of many rare genotypes that often occurred together within 10 x 10 cm patches. Cronberg *et al*. concluded that this population had spread by dispersal of vegetative fragments. In the lowland populations, identical genotypes often occurred in multiple patches, which Cronberg *et al*. interpreted to indicate that these had arisen by independent sexual recombinations, not dispersal. Hmmm...Why not by fragments?

Figure 60. ***Polytrichum strictum*** with male splash cups. Photo by Kristian Peters, through GNU free documentation license.

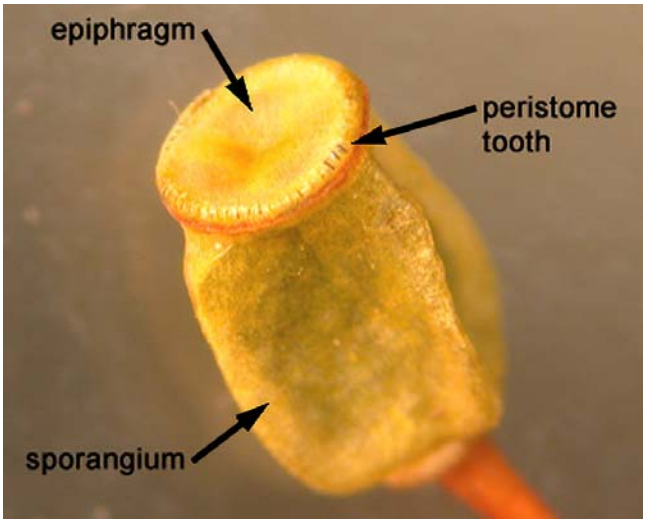

Figure 61. Capsule of ***Polytrichum commune*** showing epiphragm stretched across the 64 short teeth. Photo with permission from Botany Website, UBC.

It appears that even annual shuttle species that would seemingly rely on dispersal of much more than a few meters may have little genetic mixing between populations. Roads and Longton (2003) found no field germination of spores in ***Tortula acaulon*** (=***Phascum cuspidatum***; Figure 4) and spores only inconsistently produced gametophytes in ***Tortula truncata*** (as ***Pottia truncata***; Figure 2). As discussed above for the latter species, 67% of the spores never left the clump and 70% were deposited within 2 m. Nevertheless, that left 30% to be deposited farther away. However, there were no genotypes in common between populations and no variation within populations, suggesting that all members of the population had come from a single spore or clone.

Grundmann *et al*. (2007) obtained what seems like conflicting data for ***Pleurochaete squarrosa*** (Figure 62). Using allozymes, they showed no isolation by distance, but using DNA sequence data instead, there was evidence of isolation based on distance. Shaw (1995) used 15 allozyme loci to assess ***Scopelophila cataractae*** (Figure 63) and concluded that it was native to both America and Asia, having spread by long-distance dispersal.

Figure 62. ***Pleurochaete squarrosa*** wet. Photo by David Holyoak, with permission.

Figure 63. ***Scopelophila cataractae***, a species that seems to have spread by long-distance dispersal. Photo by David T. Holyoak, with permission.

Many bryophytes exhibit little variation within populations and reasonable variation between populations, suggesting that most within-population members are derived from the same clone. Genetic differences between populations suggest that most have arisen by a single invasion of a single propagule.

Spore Size and Number

Size matters. Aerosols – particles suspended in air like those in smoke – disperse easily to great distances, but the particles typically have a diameter less than 5 µm (Lönnell 2011). Size affects the terminal velocity of falling objects, with increasing size causing a greater terminal velocity (Lönnell 2011). But does this have any meaning for a bryophyte propagule? And if so, how is it affected by updrafts, vortices around the substrate, hydration, or surface ornamentation?

There seems to be an assumption that dispersal declines rapidly as diaspore size increases. As Frahm (2009) reminds us, bryophyte spores, typically only one cell, mostly range in size from 7 µm to 100 µm. Schmidt (1918) considered that spores smaller than 20 µm are easily dispersed, a position supported by van Zanten and Pócs (1981) who thought the small spore size permitted them to lift into the air column more easily. Mogensen (1981) tells us that theoretically, wind that would carry a 20 µm spore for 1000 km would only carry a 55 µm spore approximately 40 km. But experimental evidence for this seems to be lacking, and the large spore size of some ephemeral taxa, such as ***Ephemerum*** (Figure 64-Figure 65), would seem to suggest that occasionally these large spores do travel. In fact, van Zanten and Gradstein (1988) found no correlation between spore size and species range for neotropical liverworts. They cited three species with some of the largest spores [***Brachiolejeunea phyllorhiza***, ***Cheilolejeunea unciloba***, and ***Leucolejeunea xanthocarpa*** (Figure 66) as having transoceanic distribution

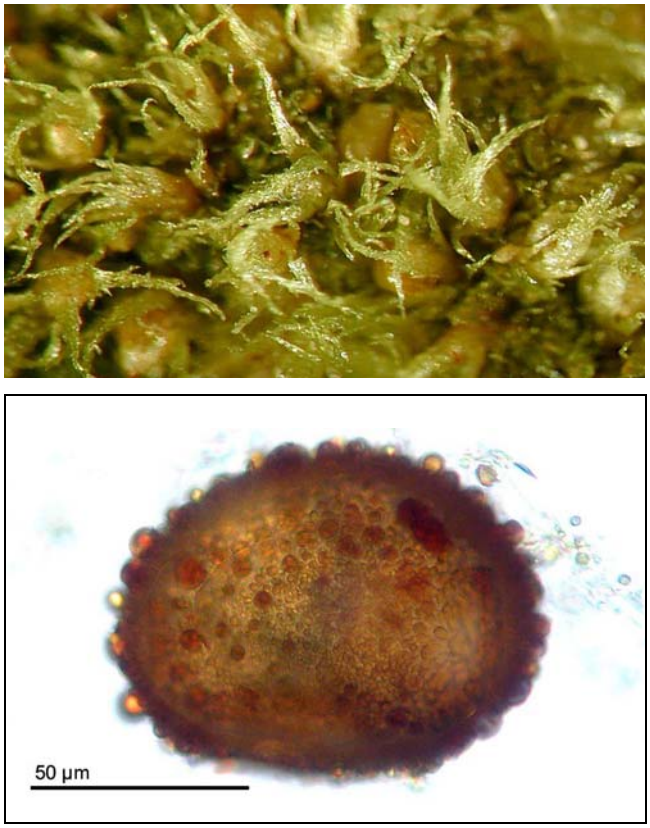

Figure 64. ***Ephemerum serratum***. **Upper:** Leafy gametophytes with capsules. **Lower:** One spore. Photos by Michael Lüth, with permission.

In describing dispersal of testate amoebae in the Arctic and Antarctic, Wilkinson (2001) found that the large species (up to 230 µm) were confined to only one of those areas, whereas the cosmopolitan species had a maximum size of 135 µm. Size matters. The same principle of smaller travels farther should be applicable to bryophyte propagules. But most bryophyte spores have a diameter that is less than 50 µm (Lönnell 2011; Figure 67), with liverworts generally having larger spores than mosses, presenting a greater number of species with spore diameters in the 40-100 µm range than do mosses. Among the species for which I could easily find numbers, the liverworts tended to produce fewer spores than the mosses, a factor one might expect to accompany larger spores (Table 2).

Figure 65. ***Ephemerum serratum*** (formerly ***E. minutissimum***) spores. Photo by David T. Holyoak, with permission.

Figure 66. ***Leucolejeunea xanthocarpa***, a transoceanic species with large spores. Photo by Jia-Dong Yang, through Creative Commons.

Despite the widespread assumption that small spores lift more easily, hence disperse more easily, than large spores (Van Zanten & Pócs 1981), there seems to be no empirical evidence for the assumption (McIntosh 1997). McIntosh points out that producing smaller spores permits production of more spores, and just by that increase, the probability of going farther increases.

In their examination of 24 Asian bryophytes, He and Zhu (2010) concluded that mosses have a higher spore output than liverworts (Table 2). They further observed an inverse relationship between spore size and spore number, a conclusion also supported by Lönnell (2011; Figure 68). This is especially borne out in the genus ***Archidium*** (Figure 22), which may have as few as four spores and these are the largest found among bryophytes (Crum 2001).

Noguchi and Miyata (1957) asserted that mosses that have abundant spores can have wide geographic ranges, but tend to have rather confined habitats. This relationship might relate to spore size, with small spores being more abundant than larger ones. And small spores do not bring with them the nutritional reserve that could give them a good start in their new location. Could this be the explanation for their "confined habitats?"

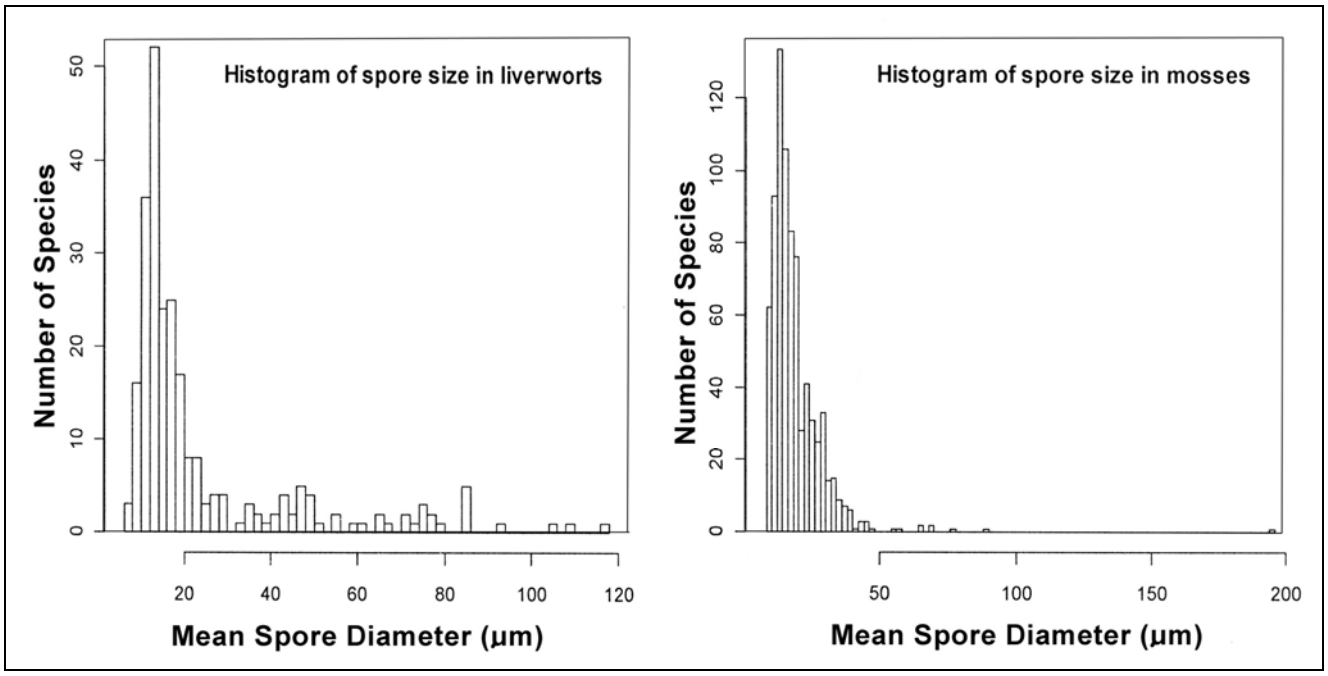

Figure 67. Comparison of spore size distributions in liverworts and mosses. Redrawn from Lönnell 2011.

Table 2. Numbers of spores per capsule in a variety of bryophytes. Liverwort taxa are in bold face.

Archidium	4-28	Ingold 1959
Riccia gougetiana	192	Schuster 1966
Riccia glauca	220	Schuster 1966
Riccia crystallina	246	Schuster 1966
Leptocolea* (=*Cololejeunea*) *magnilobula	257	He & Zhu 2011
Sphaerocarpos michelii	760	Schuster 1966
Acrolejeunea emergens	<1000	He & Zhu 2011
Trocholejeunea sandvicensis	1450	He & Zhu 2010
Fossombronia foveolata* var. *cristula	1660	He & Zhu 2010
Sauteria alpina	2100	Schuster 1966
Reboulia hemisphaerica	2410-2500	Schuster 1966; Patidar *et al*. 1987
Monosolenium tenerum	3160	He & Zhu 2010
Pellia epiphylla	4500	Schuster 1966
Ptychanthus striatus	5038	He & Zhu 2011
Conocephalum conicum	5300	Schuster 1966
Tortula acaulon *Phascum cuspidatum*	5500	Ingold 1959
Preissia quadrata	8000	Schuster 1966
Targionia hypophylla	1196-7385	Patidar *et al*. 1987; He & Zhu 2010
Physcomitrium courtoisii	8760	He & Zhu 2010
Anthoceros agrestis	>17,000	Bisang 2001
Sphagnum tenellum	18,500	Sundberg & Rydin 1998
Pohlia elongata	20,700	He & Zhu 2010
Cephaloziella varians	14,000-23,750	Lewis Smith & Convey 2002
Lophocolea cuspidata	23,900	Schuster 1966
Reboulia hemisphaerica	25,000	Schuster 1966
Ptilidium pulcherrimum	27,400	Jonsson & Söderström 1988
Schistostega pennata	36,000	Ingold 1959
Anastrophyllum hellerianum	42,000	Pohjamo & Laaka-Lindberg 2003
Sphagnum rubellum	54,000	Sundberg 2002
***Riccardia* sp.**	56,400	He & Zhu 2010
Sphagnum papillosum	62,250	He & Zhu 2010
Sphagnum junghuhnianum	68,750-73,300	He & Zhu 2010
Dicranella varia	71,450	He & Zhu 2010
Ditrichum pallidum	79,160	He & Zhu 2010
Jungermannia truncata	84,150	He & Zhu 2010
Trematodon longicollis	85,800	He & Zhu 2010
Lophozia ventricosa* var. *silvicola	86,000	Laaka-Lindberg 2000
Chiloscyphus profundus* =*Lophocolea heterophylla	93,000	Jonsson & Söderström 1988
Orthocaulis* (=*Barbilophozia*) *attenuata	115,000	Jonsson & Söderström 1988
Sphagnum lindbergii	129,545	Sundberg 2002
Sphagnum palustre	130,000	He & Zhu 2010
Ceratodon purpureus	100,000-120,000	Kreulen 1972
Grimmia pulvinata	200,000	Ingold 1959
Sphagnum squarrosum	243,000	Sundberg & Rydin 1998
Tetraplodon angustatus	250,830	He & Zhu 2010
Rhynchostegium serrulatum	280,000-700,000	Ingold 1959
var. *confertum*	250,000-750,000	Ingold 1974
Tetraphis pellucida	348,300	He & Zhu 2010
Scapania* (=*Diplophyllum*) *albicans	400,000	Schuster 1966
Polytrichastrum alpinum	440,000-873,000	Convey 1994
Atrichum undulatum	450,000	Ingold 1959
Funaria hygrometrica	55,800-495,000	Nakosteen & Hughes 1978; He & Zhu 2010
Polytrichastrum sexangulare var. *vulcanicum* (=*Pogonatum sphaerothecium*)	516,200	He & Zhu 2010
Dicranum scoparium	523,500	He & Zhu 2010
Haplocladium microphyllum	675,830	He & Zhu 2010
Pogonatum dentatum	712,000	Ingold 1959
Scapania undulata	1,000,000	Schuster 1966
Tortula muralis	1,000,000	Ingold 1959
Polytrichum juniperinum	1,400,000	Kreulen 1972
Buxbaumia viridis	1,000,000-9,000,000	Wiklund 2002
Polytrichastrum formosum	2,200,000	Ingold 1959
Buxbaumia aphylla	5,500,000	Ingold 1959
Polytrichum commune	8,983,000	He & Zhu 2010
Dawsonia lativaginata	80,000,000	Kreulen 1972

Lönnell (2011) compared spore sizes among spore-producing organisms, considering those of bryophytes to range 10-50(-100) µm, fungi 3-10-(300) µm, and ferns 30-100 µm. Crum (2001) gives a broader range from 5 (***Dawsonia***; Figure 10) to 310 (***Archidium***; Figure 22) µm, but few are greater than 30 µm. The generalization still holds that those taxa that produce small spores produce lots of them and those with large spores produce few (Schuster 1984) (50 million in ***Dawsonia***, 4 in ***Archidium***; (Table 2).

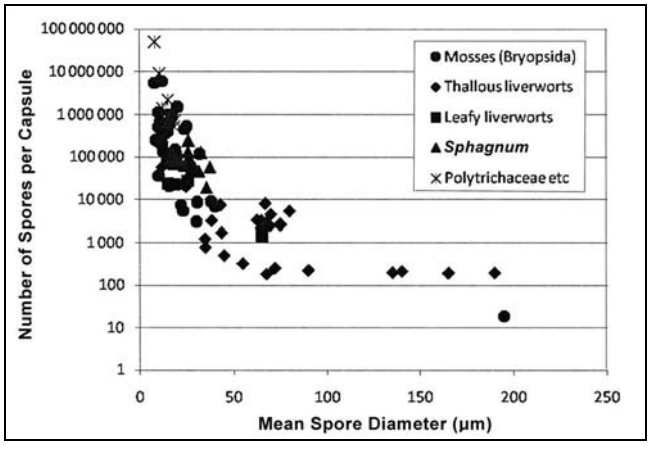

Figure 68. Inverse relationship of number of spores produced per capsule to spore size. Redrawn from Lönnell 2011.

Large Spores

Archidium (Figure 22), as a genus, sets the record for spores size in mosses. This larger size permits it to maintain a large food reserve that becomes available when the moss germinates. In its open habitat, this permits it to develop quickly and complete its life cycle before conditions once again become unfavorable for growth. ***Archidium brevinerve*** has the largest average spore diameter (235 µm); ***A. ohioense*** (Figure 69) has the largest measured spore (310 µm) (Snider 1975). In Europe the most widespread species in the genus is ***A. alternifolium*** (Figure 22) with an average spore size of 162 µm and range of 139-223 µm (Boros *et al*. 1993). Among the liverworts, ***Asterella*** has spores 135-160 µm in diameter (Figure 70). ***Sphaerocarpos*** (Figure 71-Figure 72) sheds its spores in tetrads, making those spore dispersal units quite large. They furthermore are highly decorated, creating air spaces that could increase surface area without adding weight and increasing floatability. Some spores are **precocious** (Figure 75), *i.e.*, germinating within the spore wall and typically before leaving the capsule. Such spores are consequently larger and presumably heavier, as for example those of ***Tuyamaella molischii*** (Lejeuneaceae; Figure 73-Figure 75) that are up to 140 µm long (Rui-Liang Zhu, Bryonet 6 March 2013).

Figure 69. ***Archidium ohioense*** with sporophytes. Photo by Li Zhang, with permission.

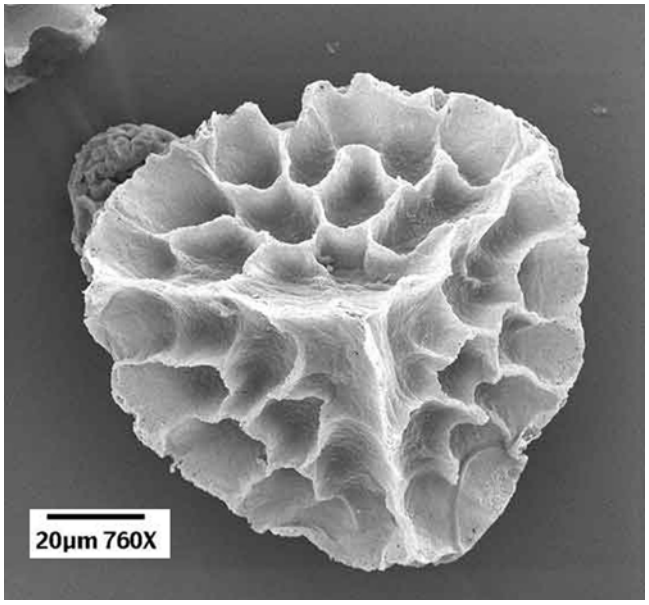

Figure 70. ***Asterella bolanderi*** spore proximal view SEM. Photo by William T. Doyle, with permission.

Figure 71. ***Sphaerocarpos michelii***. Photo by Jan-Peter Frahm, with permission.

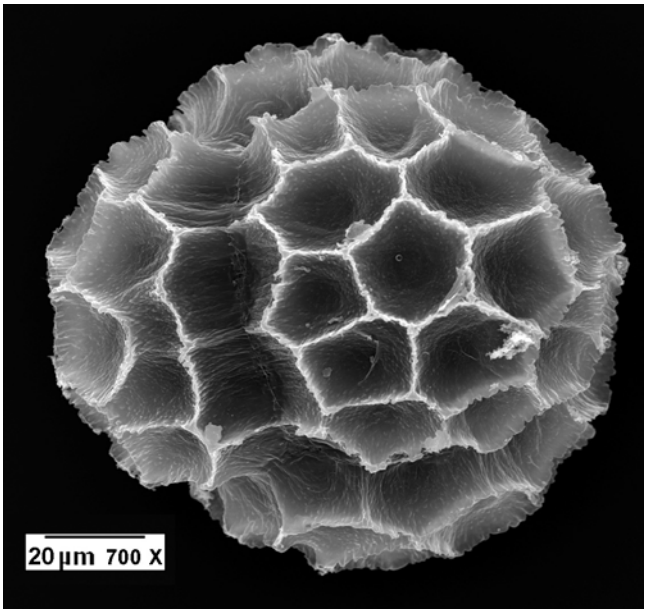

Figure 72. ***Sphaerocarpos texanus*** spore SEM, showing highly decorated wall. Photo courtesy of Karen Renzaglia.

Figure 73. ***Tuyamaella molischii*** var. ***molischii***, an epiphyllous liverwort from Guangxi Pinglongshan, China. Photo by Rui-Liang Zhu, with permission.

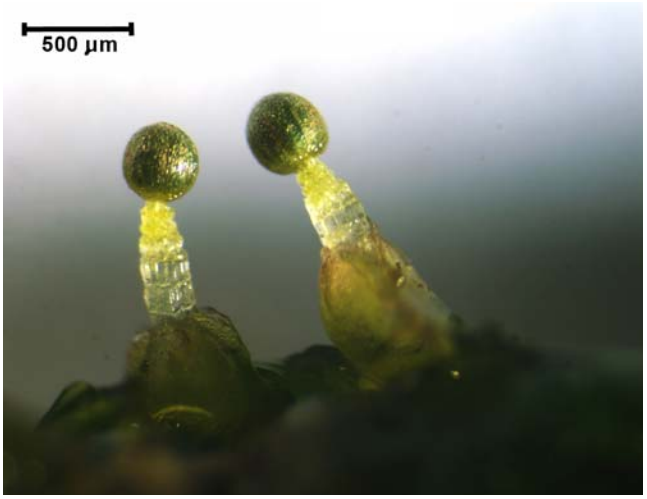

Figure 74. ***Tuyamaella molischii*** var. ***molischii*** capsules from Guangxi Pinglongshan, China. Photo by Rui-Liang Zhu, with permission.

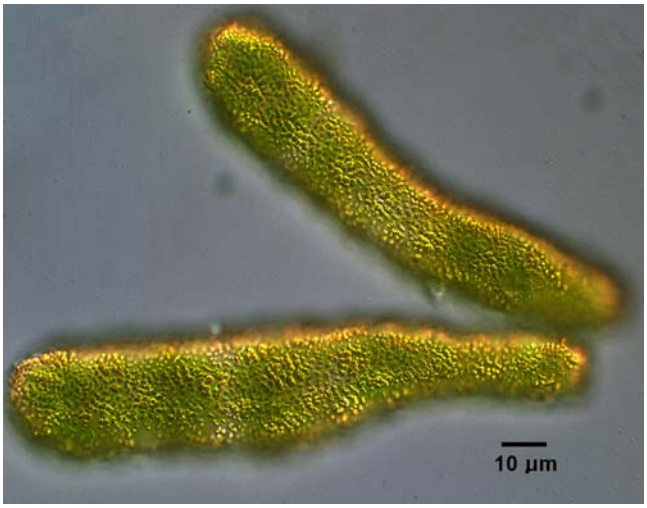

Figure 75. ***Tuyamaella molischii*** var. ***molischii*** precocious spore development, from Guangxi Pinglongshan, China. Photo by Rui-Liang Zhu, with permission.

In ***Archidium alternifolium*** (Figure 22), little or no protonema develops when the spore germinates (Miles & Longton 1992a). Rather, a germling shoot arises from the dehiscing spore(!), or shortly thereafter from a short protonema. This ability most likely arises through the complements of an adequate food supply in the large spore, precluding the need for a protonema to store such energy before a shoot can be formed. But other factors might also be at play. Could it be that necessary hormones to stimulate the shoot growth are carried in this large spore, sacrificed in small spores to make room for the little bit of nutrient matter it can provide? Such hormones, in the case of small spores, might then be provided by the protonema, or in the surrounding environment (see discussion on Delayed Germination in subchapter 4-7).

It appears that the large size of the spore in ***Archidium alternifolium*** (Figure 22) might afford other advantages as well. When Miles and Longton (1992a) cultivated the spores on agar, germination spanned a period of several months. Furthermore, the spores remained viable for up to four years following field collection of fresh material. But it is interesting that in the field these spores seem to lack what it takes for any dispersal. Rather, they remain in the capsule, attached to their parent plants. Despite the spore longevity and size, according to Miles and Longton, it is the fragments that predominate in the diaspore bank and form the recolonizing population following disturbance.

Convey and Lewis Smith (1993) suggested that large spore sizes observed in short-lived species may be important in local colonization in the Antarctic. Those taxa that are annual or short-lived invest more in spore dispersal than those in most perennial taxa. Nevertheless, on Signy Island in the Antarctic, spore size did not seem to influence dispersal potential in the five taxa identified (Marshall & Convey 1997).

For whatever reason, acrocarpous spores of Michigan, USA, mosses are generally smaller (mostly <25 µm in diameter) than those of pleurocarpous taxa (mostly >25 µm), based on sizes provided by Crum (1973). These evolutionary trends may not relate to habitat, but we do know that pleurocarpous mosses are perennial and rely less on spores for their reproduction than do many of the acrocarpous taxa. Having larger spores provides more energy for a better start in life. Liverwort taxa may have a similar division between leafy and thallose taxa, if Schuster's table (Table 3) on spore size is any indication, but the number of taxa represented is far too small to draw any generalizations.

Table 3. Spore size (µm) in liverworts. The first six are leafy. Based on Schuster (1966).

Scapania (=*Diplophyllum*) *albicans*	10-14
Blepharostomaceae	8-16
Chiloscyphus (=*Lophocolea*) *cuspidata*	14-16
Scapania undulata	15-20
Sendtnera (=*Herbertus*) *adunca*	25
Ptilidiinae	15-65
Sphaerocarpos michelii	30-40
Pellia epiphylla	50-60
Sauteria alpina	60-70
Preissia quadrata	60-75
Ricciella (=*Riccia*) *crystallina*	65-80
Reboulia hemisphaerica	60-90
Conocephalum conicum	70-90
Riccia glauca	80-100
Riccia gougetiana	180-200

The number of spores per meter square is a function not only of the number of spores per capsule, but also the density of the capsules present. Some of these numbers are enormous (Table 4).

As already noted, spore number is determined not only by the number per capsule, but also by the number of capsules produced. More capsules can correlate with wider dispersal and wider distribution. Robinson (1990) pointed out this relationship in the **Leucobryaceae**, where ***Octoblepharum albidum*** (Figure 76) typically has many sporophytes and has one of the widest distributions in the family. In many genera in this family, sporophytes are reduced, but propagation by leaves and leaf fragments is common. Robinson suggests that birds and other arboreal animals could facilitate dispersal among the epiphytic members of the family.

Spore size is an integral part of life history strategies. Longton (1988) summarized some of these relationships for arid regions. He found that perennial stayers are typically acrocarpous mosses with small spores, long spores, and "other features promoting dispersal." Annual shuttle species, conversely, produce large spores, often in submersed capsules, promoting rapid germination and establishment *in situ*, but not well adapted for dispersal. Perennial shuttle species are mostly marchantialian liverworts with large spores. Fugitives stay at a given site and are able to do this by having small, easily dispersed spores.

Jenkins *et al.* (2007) attempted to use existing data from many data sets to answer the question of size vs dispersal distance. They divided organisms into active and passive dispersers, defining active dispersers as those that arrived at a new location under self-propulsion. This includes most vertebrates and arthropods, but many other animals depend primarily on passive sources. Plants, including bryophytes, are mostly passive dispersers.

Jenkins and coworkers found that active dispersers, as expected, dispersed significantly farther and were significantly greater in size ($P<0.001$). Passive dispersers, on the other hand, had random dispersal distances compared to mass/size. They concluded that while size is important for active dispersers, it is not for passive dispersers. But could there still be a relationship for dispersal units less than a certain size that permits them to be dispersed by air currents? Jenkins *et al*. consider that dispersal-size relationships for microbes cannot be tested by direct observation. Perhaps that for bryophytes will be somewhat easier. In their analysis for passive dispersers, Jenkins and coworkers used organisms weighing in the range of 10^{-8} to 10^{-9} g, dominated by plant seeds. This hardly seems a good model for bryophytes with single-celled spores as their dispersal agents.

Table 4. Number of bryophyte spores per m^2. Liverwort taxa in bold face.

Anthoceros agrestis	14 mil/m^2	Bisang 2001
Sphagnum	16 mil/m^2	Sundberg 2002
Atrichum undulatum	37 mil/m^2	Longton & Schuster 1983
Pleurozium schreberi	100 mil/m^2	Longton 1976
Ptilidium pulcherrimum	20-300 mil/m^2	Jonsson & Söderström 1988
Grimmia pulvinata	7,400 mil/m^2	Longton & Schuster 1983
Tortula muralis	38,300 mil/m^2	Longton & Schuster 1983

Figure 76. Capsules of the epiphytic ***Octoblepharum albidum***. Photo by Janice Glime.

Spore Weight

Hughes *et al*. (1994) developed a set of provisional conclusions regarding the relationship of dispersal mode and other attributes of plants and their habitats. Although these were developed with seed plants in mind, examining them for bryophytes might be instructive in developing our own hypotheses. They concluded that seeds larger than 100 mg tend to be adapted for dispersal by vertebrates, whereas those less than 0.1 mg tend to be unassisted.

Bryophyte spore weights do not seem to have been a priority for bryologists, so it is necessary to estimate. Most spores range from 20 to 100 µm in diameter (Boros *et al*. 1993). A 20 µm spore has a radius of 10 µm. Knowing that, we can calculate its weight by assuming it is a sphere, starting by determining the volume ($V = 4/3\ \pi\ r^3$). Hence, the volume would be 4.188 x 1000 = 4188 cubic microns. Assuming that a spore is mostly water, and knowing that the weight of water is 1000 g per liter, a cubic micron is 10^{-15} L or 10^{-9} µL. Hence, 1 cubic micron weighs 10^{-12} grams or 10^{-3} nanograms. A 20 µm spore would weigh only 4.2 x 10^{-9} g (0.0042 µg, or 4.2 nanograms) when fully hydrated ($V = 4/3\ \pi\ r^3 = 4188$ cubic µm; 1 cubic µm = 10^{-9} µl; 1 µl = 1 µg of water; 1 µg weighs 1 million picograms). Using a sphere as our model, we can derive the formula:

$$\text{spore weight} = 4/3\ \pi\ r^3\ (10^{-3}) \text{ nanograms}$$
or
$$\text{spore weight} = 4/3\ \pi\ r^3\ (10^{-6})\ \mu g$$

It is rather easy to do this calculation at <http://www.wolframalpha.com> and inserting "weight of sphere of water 20 microns in diameter."

Spores that are 100 µm in diameter would weigh 0.524 µg and often travel only downward by gravity, as in ***Archidium*** (Figure 22). Since bryophyte spores therefore fall in the less than 0.1 mg category, they support the hypothesis of Hughes *et al*. (1994) that diaspores less than 0.1 mg tend to be dispersed unassisted. Nearly all of the spores of bryophytes are apparently unassisted in their dispersal (*i.e.*, unassisted by animals, with only undirected wind and water for assistance).

Even at 300 µm diameter in ***Archidium*** (Figure 22) (Snider 1975), the spores of such bryophytes would weigh only 14.1 µg. Spores are usually dry when they travel, making them even less in weight.

The formula provides an estimate of the maximum weight of a spore with the density of water. Most spores are not fully hydrated and the spores may be slightly flattened into a tetrahedron with one rounded side. Whitaker and Edwards (2010) assumed a spore shape of a tetrahedron with a circular base to calculate the weight of a ***Sphagnum*** spore and determined a weight of 1.7 nanograms for a spore with a base diameter of 28 µm. If we assume that this spore is all water and spherical with a diameter of 28 µm, it would weigh 11.5 nanograms, a rather substantial difference in estimation caused not only by the shape assumption, but also by the water assumption.

Spores vary in weight between species, even at the same spore sizes. These variations depend on food reserves and water content (Jeff Duckett, Bryonet 6 March 2013). Green spores are short-lived, commonly remain hydrated, and typically store their food as starch, giving them a specific gravity greater than 1 and making them heavier than brown spores. Brown spores are generally smaller, long-lived, and use both protein and lipid reserves. They are usually very dehydrated and have a specific gravity considerably less than 1. Hence, green spores usually sink in water; brown ones usually float and, presumably, more easily become airborne.

But Gradstein (Bryonet 11 March 2013) argues that green vs non-green spores from nearly 100 tropical species do not correlate with range sizes or with long-range dispersal, based on an experimental study (van Zanten & Gradstein 1988). No differences correlated with drought or

low temperatures for exposures from a few hours to a year or more.

We can estimate weight by the size of the spore, but as noted, not all spores are created equal. The specific gravity is a more important measure of the transportability than the weight (mass) alone. Peter Poschlod (pers. comm. 6 March 2013), like Duckett, points out that some spores float on water whereas others sink. Among the ones that sink immediately are those of ***Sphagnum***. Using spore traps in peatlands, Poschlod (1995) was unable to find any ***Sphagnum*** spores. Rather, the traps produced vegetative parts, especially those of ***Sphagnum*** (Figure 77). Dry ***Sphagnum*** is especially light weight and easily becomes airborne, as I witnessed one day while watching ants trying to repair their mound during a windstorm. In grasslands, on the other hand, vegetative diaspores tended to be the exception. Nevertheless, in the grasslands it appeared that grazing animals, especially sheep, transported the mosses, particularly ones such as ***Abietinella abietina*** (Figure 78) that in Central Europe does not produce capsules.

Figure 77. ***Sphagnum*** protonemata growing on a ***Sphagnum*** branch in the field. Photo by Andras Keszei, with permission.

Survival and Longevity

Some spores, under the right conditions, can survive extremely long periods (Table 5). Gubin *et al*. (2003) reported viable moss spores from permafrost sediments in northeast Eurasia, citing ages of tens to thousands of years of preservation.

Figure 78. ***Abietinella abietina***, a species that seems to be transported by sheep in grasslands. Photo by Michael Lüth, with permission.

Van Zanten and Pócs (1981) surmised that spores from taxa in dry habitats had a generally greater drought resistance than those from wet habitats. Since liverworts tend to live in wetter habitats, grow where there is less air turbulence, and have larger spores, they further concluded that moss spores should be expected to travel farther.

Most spores that arrive at a given area will not have travelled terribly far. The majority will land within a few cm to a meter of the parent, but some are carried by air currents to far off places. In this longer transport, they will be subjected to high UV radiation and extremes of moisture and temperature.

Table 5. Known longevity for bryophyte spores, based mostly on Crum 2001 and arranged from least to most. Liverworts are in bold face.

Lejeuneoideae	**7-8 d**	**Gradstein 1994**
Cyathodium tuberosum	**9 mos**	**Tiwari 1935**
Conocephalum conicum	**<1 mo**	**Crum 2001**
Plagiochasma intermedium	**<1 yr**	**Crum 2001**
Blepharostoma trichophyllum	1 yr	Crum 2001
Polytrichastrum alpinum	16 mos	Crum 2001
Marchantia polymorpha	**<17 mos**	**O'Hanlon 1926**
Riella americana	**17 mos**	**Studhalter 1931**
Grimmia elatior	17 mos	Crum 2001
Mannia fragrans	<18 mos	Inoue 1960
Targionia hypophylla	**18 mos**	**O'Hanlon**
Grimmia muehlenbeckii	18 mos	Crum 2001
Physcomitrium pyriforme	2 yrs	Meyer 1941
Preissia commutata	**>2 yrs**	**Teodoresco 1929**
Anomodon longifolius	29 mos	Crum 2001
Sphagnum	3 yrs	Chalaud 1932
Riella paulsenii	**3 yrs**	**Porsild 1902**
Brachythecium velutinum	1.5-4 yrs	Herguido & Ron 1990
Blindia acuta	4 yrs	Crum 2001
Microbryum starckeanum	4.75 yrs	Lesage 1918
Bucklandiella (=*Racomitrium sudeticum*)	7 yrs	Crum 2001
Aloina ambigua	9 yrs	Llo Stark, pers. comm.
Dicranoweisia cirrata	9 yrs	Malta 1922
Funaria hygrometrica	11 yrs	Hoffman 1970
Riella capensis	**13 yrs**	**Studhalter 1931**
Riella affinis	**16 yrs**	**Tenge 1959**
Ceratodon purpureus	16 yrs	Chalaud 1932
Anoectangium aestivum	19 yrs	Malta 1922
Oedipodium sp.	20 yrs	Chalaud 1932
Dicranella sp.	50 yrs	Chalaud 1932
Ricciocarpos natans	**50 yrs**	**Conrad 1996**

Sphagnum in experiments suggest that ***Sphagnum*** spores may have a half-life of 1-20 years, but that individual spores may survive for several decades and possibly even centuries (Sundberg & Rydin 2000). Refrigerated spores retained 15-35% viability for 13 years.

Some of the records of spore longevity from herbarium specimens have been suspect due to the possibility for contamination. However, Bristol (1916) reported germination of spores and development of protonemata from spores that had been collected from the top 24 cm of soil in Great Britain 49 years earlier and stored in bottles.

Egunyomi (1979) tested the germination success of tropical moss spores that had been stored at room temperature for various periods of time from 1-3.5 years. Of the 22 species tested, 15 failed to germinate at all. Five species had better than 50% germination. He chose four of

these (***Microcampylopus nanus***, ***Weissia papillosa***, ***Mittenothamnium overlaetii***, ***Weisiopsis nigeriana***) that had been stored at least two years for further experimentation of extreme conditions for 4 weeks: -2°C, 8°C, continuous immersion in water at room temperature, alternate wetting and air drying every 24 hours. None of the species at -2°C survived for 4 weeks. At 8°C, all survived four weeks, with survival percentages ranging 43-81%. Continuous immersion, like the -2°C, resulted in 0% survival after 4 weeks, but alternate wetting and air drying resulted a range of 45-76% survival with the success ranks by species being the same as in the 8°C treatment.

Atmospheric Conditions – UV and Desiccation

It is likely that conditions that favor the dispersal of protozoa and algae also favor the dispersal of bryophyte spores. Hence, we might expect cloudy or overcast skies to help filter UV light (Schlichting 1961). Fires and volcanoes can put particulates in the atmosphere, likewise serving as UV filters. Clouds also can prevent severe desiccation.

Drought Tolerance

Drought tolerance has the greatest correlation with transoceanic distribution (van Zanten & Gradstein 1988). Van Zanten and Gradstein found that only 5% of the transoceanic species had lost the ability to germinate after five days (the minimum time calculated for crossing the Atlantic), whereas 32% of the endemic species exhibited that limitation. Among the transoceanic species, half were able to germinate after 70 days, whereas among the endemic species only half could still germinate after 25 days. Six transoceanic species could still germinate after 100 days of desiccation: ***Anastrophyllum auritum*** (60% germination), ***Andrewsianthus jamesonii*** (50%), ***Gymnocoleopsis multiflora*** (50%), ***Herbertus subdentatus*** (Figure 79) (40%), ***Dumortiera hirsuta*** (Figure 80) (10%), and ***Chiloscyphus*** (as ***Lophocolea***) ***muricata*** (Figure 81) (5%). Some even lasted 150 days. Nevertheless, three endemic species germinated after 100 days of desiccation: ***Cephalozia crassifolia*** (Figure 82) (10%), ***Marchantia chenopoda*** (Figure 83-Figure 84) (80%), and ***Fossombronia*** sp. (Figure 85) (80%), with the latter species even germinating after 150 days. These three endemic taxa have large, dark-colored spores, suggesting they could also survive UV light, but van Zanten and Gradstein suggest that these are probably adaptations for surviving adverse climatic periods, not long-distance dispersal.

Figure 79. ***Herbertus subdentatus***, a species with 40% germination after 100 days desiccation. Photo by Michael Lüth, with permission.

Figure 80. ***Dumortiera hirsuta*** thallus with archegoniophore, a species whose spores had 10% survival of desiccation for 100 days. Photo by George Shepherd, through Creative Commons.

Figure 81. ***Chiloscyphus muricatus***, a species whose spores had 5% survival of desiccation for 100 days. Photo by Andrew Hodgson, with permission.

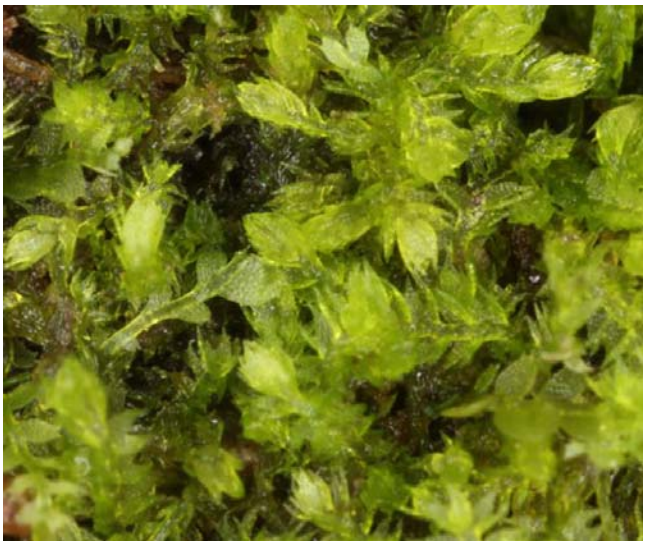

Figure 82. ***Cephalozia crassifolia***, an endemic species whose spores had 10% survival of desiccation for 100 days. Photo by Jan-Peter Frahm, with permission.

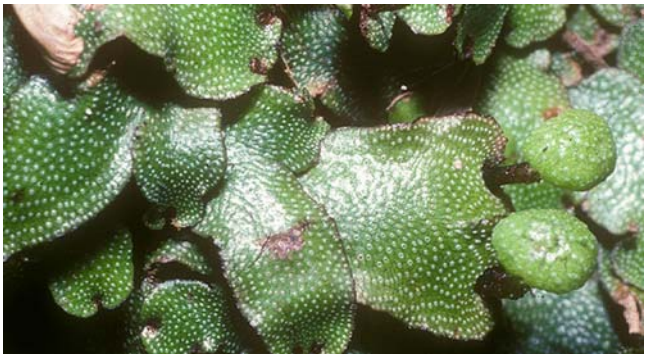

Figure 83. Thallus and antheridiophores of ***Marchantia chenopoda***, an endemic species whose spores had 80% survival of desiccation for 100 days. Photo by Janice Glime.

Figure 84. ***Marchantia chenopoda*** with archegoniophore and gemma cups. Photo by Janice Glime.

Figure 85. ***Fossombronia japonica***, genus with an endemic species whose spores had 80% survival of desiccation for 100 days. Photo by Li Zhang, with permission.

The liverwort ***Gymnocoleopsis multiflora*** has unusual spores that are very durable despite thin spore walls and hygrophytic habit (van Zanten & Gradstein 1988). Both spores and sporelings are fairly resistant to UV radiation, as well as being very durable. These appear to be adapted to the high alpine habitat where it lives. By contrast, ***Riccardia amazonica*** and ***Stictolejeunea balfourii*** live in the understory of wet primary rainforest and their spores have very poor drought resistance. Such examples suggest that the spore adaptations may be more related to the habitats of the parents than to dispersal capabilities. In fact, most of the transoceanic species van Zanten and Gradstein tested came from more open habitats such as forest margins – habitats that would require more of the same habitat adaptations as long-distance space travel, and where getting into the airstream may be easier than in the forest.

Frost Resistance

Van Zanten and Gradstein (1988) found that spores of transoceanic species had significantly better frost tolerance than endemic species, especially among spores that were desiccated for one week before the freezing treatment. Those spores that had been dried had better resistance in small-spored species than in large-spored ones, suggesting again that small-spored species should travel farther.

Nevertheless, wet freezing does not seem to favor the transoceanic species more than the endemic species (van Zanten & Gradstein 1988). Hence, it is not likely to affect the dispersability of liverworts. Interestingly, fresh spores are less likely to survive dry freezing, and this danger is more pronounced in the endemic species.

UV Protection

The greatest danger, considered by van Zanten (1976) and van Zanten and Gradstein (1988), is that of UV radiation damage. This poses a special problem because dry conditions that make them light in weight are also usually sunny conditions. Schlichting (1961) considered the greater success of UV-sensitive organisms (algae and protozoa) under humid and cloudy conditions to be due to the diminished impact of UV radiation, a concept supported by van Zanten and Gradstein. The added moisture also counteracts the severe desiccation often experienced in the upper atmosphere. The fact that algae have been collected by aircraft from 2000 m above the Earth suggests that bryophyte diaspores likewise occur there. Schlichting (1958) even reported viable moss spores from fingerbowls exposed at 2 m above the ground over periods of 45 minutes to 32 hours.

But we also know that UV light is used to kill cells, and bryophyte spores are no exception. Van Zanten and Gradstein (1988) tested the effects of UV radiation on spores in nearly 100 tropical liverwort species by flying them from Amsterdam to Los Angeles on the wings of a commercial 747 jet. Only two species, both from above 3000 m asl in the Andes, survived the journey, suggesting that the jet stream is not an available avenue to most species, at least among liverworts. This greater resistance to UV damage displayed by high altitude species may explain the distribution of species along mountains – perhaps a better explanation than the flyway explanation. But the two aspects could work together. In short, most species seem to be unable to survive the dosage of UV radiation required for long-distance dispersal under most conditions.

Some spores travel with chlorophyll. But van Zanten and Gradstein (1988) found no correlation between chlorophyll presence and species range. Furthermore, they found no relationship between precocious germination and local dispersal or between non-green and long-distance dispersal. There also seemed to be no dormancy effect.

Some spores have dark pigments; others have cuticular ridges or other extrusions, including papillae. It would be interesting to correlate those characters with success of the spores in travelling long distances where they must survive the greater desiccation and UV light of the atmosphere.

We need to understand just what levels of UV are present under dispersal conditions, what levels kill spores and other diaspores, and how long the exposure must last to cause damage. On the other side, we need to understand what characteristics of spores protect them from this damage, how moisture affects that damage potential, and is there a set of conditions and adaptations that would permit long-distance dispersal.

Liverwort Spore Survival

Fulford (1955 in Schuster 1966) considered that spore survival of leafy liverworts was short, but she actually had only one citation (Figure 86; Bernstein 1928) – for one species (***Blepharostoma*** sp; Figure 87) – to back up this assumption; since then we have learned that some have considerable longevity. Inoue (1960) tested spore longevity in six liverwort taxa (Table 6) and found survival up to 18 months in three of them. Malta (1922) failed to obtain germination of spores from ***Plagiochila asplenioides*** (Figure 88) or ***Pellia epiphylla*** (Figure 89-Figure 90) after four years or of ***Preissia quadrata*** (Figure 91) after eight years of storage. Nevertheless, as van Zanten and Gradstein (1988) have demonstrated, those species with transoceanic distributions typically have longer viability.

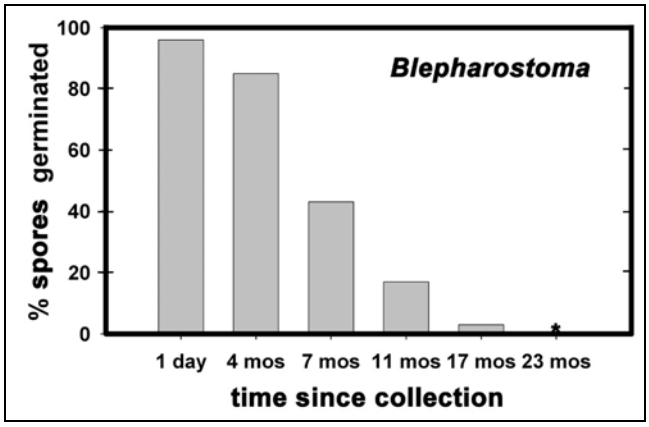

Figure 86. Decline in spore germination in ***Blepharostoma*** from the first day after collection onward. * refers to one spore that germinated out of 512 after 23 months. Based on data from Bernstein 1928.

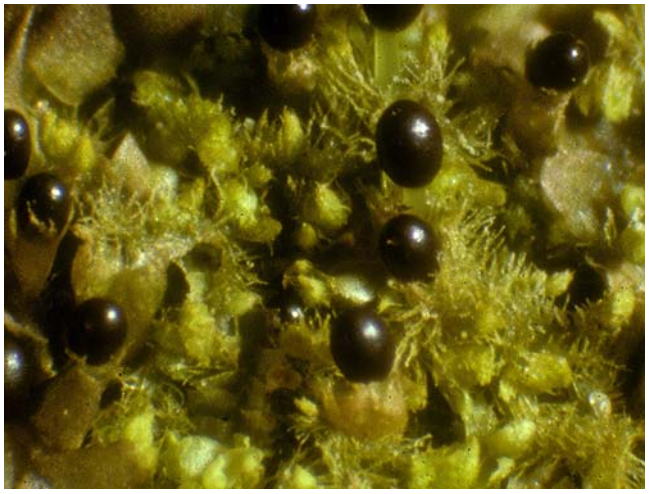

Figure 87. ***Blepharostoma trichophyllum*** with capsules, a species with short spore survival. Photo by Janice Glime.

Table 6. Percentage of spore viability in Marchantiales. From Inoue (1960).

	1 mo	6 mos	12 mos	18 mos
Reboulia hemisphaerica	100	100	95	11.3
Plagiochasma intermedium	-	48	0	0
Mannia fragrans	100	100	76	0.0
Marchantia polymorpha	100	100	87	43
Marchantia paleacea	100	100	72	21
Conocephalum conicum	0	0	0	0

Figure 88. ***Plagiochila asplenioides***; spores failed to germinate after four years of storage. Photo by Dick Haaksma, with permission.

Figure 89. ***Pellia epiphylla*** with sporophytes; spores failed to germinate after four years of storage. Photo by Kristian Peters, with permission.

Figure 90. ***Pellia epiphylla*** spore. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 91. ***Preissia quadrata*** with archegoniophores; spores failed to germinate after eight years of storage. Photo by Janice Glime.

Schuster (1983) has suggested that many liverworts that survive as relict populations are limited in their dispersal success by being dioicous, being unable to withstand desiccation, and lacking asexual reproductive structures. He suggested further that successful dispersal can be enhanced by 1) formation of sexual propagules (***Lophozia-Scapania*** model), 2) production of large numbers of very small spores per sporophyte (numerically overwhelming), 3) dispersal of spores mixed as monads, diads, and tetrads (***Haplomitrium*** model) (see Figure 92), 4) spores permanently united in tetrads (***Cryptothallus-Sphaerocarpos*** model), 5) acquisition of desiccation tolerance coupled with numerical overwhelming (xerothermophyte model), and 6) monoicism (***Calypogeia-Isopaches*** (=*Lophozia*) ***bicrenatus-Cololejeunea*** model).

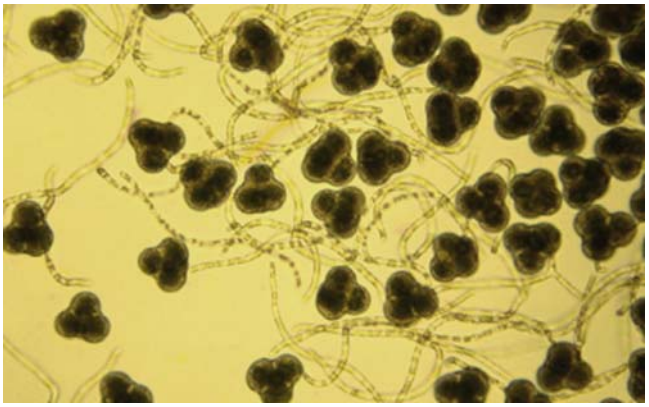

Figure 92. ***Porella navicularis*** spore tetrads as they appear after meiosis and before separation. From botany website, University of British Columbia, with permission.

Adaptations for Survival

Many bryophyte spores seem to be particularly endowed to survive extremes during their travels. The first evidence of this is that they have resisted decay and remain in huge numbers in deposits from the Silurian and Devonian periods. But biochemical evidence tells us more of their survival capabilities. Each spore obtains a **callose** (glucose polymer related to cellulose) deposit before the **exine** (outer layer of spore) completely forms (Crum 2001). Then the exine attains a **polysaccharide** deposit impregnated with **sporopollenin** (that waxy substance similar to cutin that covers pollen). Last, the **intine** develops with cellulose and other polysaccharides. Once the formation of the wall is complete, **Takakiopsida**, **Sphagnopsida**, **Andreaeopsida**, and **Bryopsida** spores deposit a **perine** layer that creates ornamentation. As Crum (2001) describes it, this layer is the "detritus" from the walls of the spore mother cells and remains of the columella. Thus, liverworts and hornworts, lacking a columella, also lack the perine deposit. It is the sporopollenin layer that affords all these spores their resistance to water and decay (Crum 2001).

There is considerable documentation that under the right conditions, some spores can survive for considerable periods. Green spores, typical of species that occur in moist habitats, have a shorter viability due to their higher metabolic rate (Crum 2001). Green spores store starch as their food reserve, but yellow spores, those of longer viability, typically store oils and these species are common in drier habitats. Marin (1981) reported that among 120 species of mosses, green spores were more common (87%) than non-green spores. All epiphytic mosses had green spores, whereas non-green spores occurred in taxa of drier or disturbed soils and rocks. Some taxa use protein for their food reserves [the liverwort ***Blasia*** (Figure 93-Figure 94) and hornworts], but this form seems to be slower to metabolize and cannot be used for quick growth (Crum 2001).

Figure 93. ***Blasia pusilla*** from Europe, a species that stores its food reserves as protein. Photo by Michael Lüth, with permission.

Figure 94. Open capsule of ***Blasia pusilla*** showing spores and elaters. Photo by Walter Obermayer, with permission.

Sundberg and Rydin (2000) found that buried ***Sphagnum*** spores could survive at least three years at various depths in peat. Curiously, light-colored spores of ***S. balticum*** (Figure 95) and ***S. tenellum*** (Figure 96) had higher survivorship than the darker spores of ***S. fuscum*** (Figure 49) and ***S. lindbergii*** (Figure 97), suggesting possible differences in stored food reserves. Spore size did not seem to influence longevity between species, but within a single species (***S. balticum***, ***S. tenellum***) the small spores from small capsules seemed to have a greater longevity than those from medium-sized and larger capsules, something that seems counter-intuitive.

Figure 95. ***Sphagnum balticum*** with capsules in southern Europe. Photo by Michael Lüth, with permission.

Figure 96. ***Sphagnum tenellum*** with capsules, a species where spores from smaller capsules survive longer. Photo by Dick Haaksma, with permission.

Figure 97. ***Sphagnum lindbergii*** with capsules, a species with dark-colored spores that survive shorter periods than light-colored spores of accompanying species. Photo by Michael Lüth, with permission.

Survival in Water

Waterways offer a means of rapid dispersal. In streams they can carry diaspores great distances. In flood plains (Figure 98), diaspores can be buried in mud or travel with a river, germinating at some later point in time when they somehow reach the surface. Spores and gemmae require light to germinate, permitting these diaspores to remain dormant as long as their energy stores permit and their ability to fend off other organisms that might use them for a food source (bacteria, fungi, small animals).

Figure 98. Eroded material transported by water to River Baihe, a tributary of Yellow River Tibet. Such flood plains can house dormant bryophyte diaspores that are ready to grow when the water recedes. Photo by Sven Bjork, with permission.

To test the viability of spores and fragments of bryophytes from various habitats, Dalen and Söderström (1999) stored sets of these from ***Ceratodon purpureus*** (Figure 27), ***Codriophorus*** (=***Racomitrium***) ***aciculare*** (Figure 99), ***Dicranoweisia crispula*** (Figure 100), ***Oligotrichum hercynicum*** (Figure 101), and ***Schistidium rivulare*** (Figure 102), and for six months in water or dry. All species except ***S. rivulare*** exhibited reduced spore germination frequencies at all time intervals when stored in water compared to stored dry. ***Schistidium rivulare***, a species that includes rocks in the splash of rivers and streams, demonstrated longer spore survival than did the other species. This species also had the highest regeneration frequencies from fragments. Nevertheless, diaspores of all these species survived at least some time in the water. In all species, the regeneration frequencies of fragments tended to be lower than those of spores. On the other hand, fragments did not experience any reduction in survival when stored in water compared to stored dry.

Figure 99. ***Codriophorus*** (formerly ***Racomitrium***) ***aciculare*** with capsules, a species whose spores survive a short time in water. Photo by Jan-Peter Frahm, with permission.

Figure 100. ***Dicranoweisia crispula*** with capsules, a species whose spores survive a short time in water. Photo by Jan-Peter Frahm, with permission.

Figure 101. ***Oligotrichum hercynicum*** with capsules from southern Europe, a species whose spores survive a short time in water. Photo by Michael Lüth, with permission.

Figure 102. ***Schistidium rivulare*** with sporophyte, a species whose spores and fragments survive well in water. Photo courtesy of Betsy St. Pierre.

Survival of Spores vs Asexual Diaspores

Egunyomi (1978) compared viability of spores with that of gemmae in ***Octoblepharum albidum*** (Figure 76, Figure 103). He found that spores retain high viability for more than 8 months at temperatures of 22-30°C, 60-75% humidity, whereas gemmae lose viability at about 6 months under those conditions. Germination did not occur in darkness, suggesting that the propagules would not germinate within a diaspore bank. Nevertheless, some germination occurred in as little as 1 lux, suggesting that the species might be able to germinate among a heavy plant cover, but the question remains whether it could grow enough to survive and thrive there. Furthermore, if spores or gemmae were exposed to light, then cultured in dark, a light intensity of 800 lux for 48 & 36 hrs respectively was necessary for them to germinate at all.

Figure 103. ***Octoblepharum albidum*** gemmae. Gemmae of this species survive for a shorter period than do the spores at temperatures of 22-30°C and 60-75%. Photo by Li Zhang, with permission.

Germination of spores from herbarium specimens suggest that weedy species may remain viable longer than other taxa. ***Ceratodon purpureus*** (Figure 27) spores were the oldest to germinate – after 16 years (Malta 1922) – but this species surprisingly does not appear in the diaspore bank (Lönnell 2011). Most of the spores in the study by Malta did not germinate if they were more than 10 years old, and the greatest number were viable for only 5 years. In fact, within only 50 days of dry storage, a 30-40% loss in viability can occur (Löbel 2009). But perhaps it is the unnatural storage conditions of a lab or herbarium that causes such loss of viability. For ***Sphagnum*** spores, 15-35% survived 13 years of storage in humid, refrigerated conditions (Sundberg & Rydin 2000). On the other hand, tubers of ***Anisothecium*** (=***Dicranella***) ***staphylinum*** (Figure 104) remained viable for 50 years of storage (Whitehouse 1984). Keever (1957) found that herbarium specimens of ***Grimmia laevigata*** (Figure 105) still had 20% viability after ten years. Malta (1922) found survival of 19 years in plants of ***Anoectangium aestivum*** (Figure 106) and Maheu

(1922) found protonemal growth from plants of ***Syntrichia ruralis*** (Figure 24) after 14 years of storage.

Figure 104. ***Anisothecium*** (=***Dicranella***) ***staphylina*** in Europe, a species whose tubers remained viable for 50 years of storage. Photo by Michael Lüth, with permission.

Figure 105. ***Grimmia laevigata*** with capsules in southern Europe, a species whose plants retained 20% viability after ten years of storage. Photo by Michael Lüth, with permission.

Figure 106. ***Anoectangium aestivum*** from Europe, a species whose plants survived for 19 years in a herbarium. Photo by Michael Lüth, with permission.

Species from flood plains and other disturbed habitats may have some of the longest dispersal times. They may have considerable distances to traverse to reach a new location, and they may have long periods of unsuitable habitat requiring long survival. ***Riccia*** provides a good example of such a need. Breuil-Sée (1993) found that specimens of ***Riccia macrocarpa*** from Tunisia survived in a dry state in the herbarium for more than 23 years. Within three days of rehydration they exhibited new cells at the apices.

Long-distance Survival

Van Zanten, in his numerous papers on dispersal (1975, 1976, 1977a, b, 1978a, b, 1983, 1984, 1985, van Zanten & Gradstein 1987, 1988, van Zanten & Pócs 1981), has shown the possibilities for long-range dispersal based on experimental evidence of survival. Van Zanten (in Gradstein & Pócs 1989) showed that New Zealand **endemics** (growing only in that area) had less resistant spores than those of wide-ranging taxa and that spores of tropical moss species, especially lowland rainforest taxa, are less resistant to drought than are temperate taxa, but surprisingly, the tropical taxa survive wet-freezing at -30°C! Tropical liverworts had similar relationships, but in general were less viable under extreme conditions than were the mosses (Van Zanten & Gradstein 1987). Trans-oceanic liverworts from Colombia have better resistance to desiccation and wet-freezing than endemic taxa. Nevertheless, only spores of ***Marchantia chenopoda*** (Figure 83), of the 61 species tested, survived travel on the wing-tips of an airplane. But death rates were also very high for the spores transported inside the wing. Van Zanten and Gradstein concluded that jet-stream altitudes were not favorable to long-distance dispersal, but that travel in wet air currents at high altitudes was a possibility for most of these liverworts. Dry air currents were more lethal.

Van Zanten (1977b, 1978b) found one puzzling relationship in longevity. After testing survival of drought, dry freezing, and wet freezing (up to 3 years), he found that spores from Northern Hemisphere bryophyte species tended to have a longer viability than those from the Southern Hemisphere. Not surprisingly, species with restricted distributions tended to have shorter periods of viability than species that occurred on multiple continents.

> It appears that some spores, perhaps even the majority, can survive for many years provided they remain dry and in the dark. A false start in which they become hydrated and begin germination can be fatal if they are not permitted to continue development and produce sugars photosynthetically.

Establishment Success

As Brent Mishler pointed out on Bryonet (6 March 2013), particulate matter from China commonly reaches California. Dust from the Sahara reaches Texas. The opportunities for worldwide dispersal seem sufficiently common that most bryophytes should be everywhere, but "the environment selects." Once the propagules enter the transport stream, they must survive, arrive, germinate, and establish (SAGE).

Greater success of spores as a means of establishment through dispersal seems to be correlated with a lower age of first reproduction and greater phenological flexibility, but suffers a tradeoff, being correlated with decreased longevity (Longton 1997). For the conservation of rare species, the conditions of establishment upon arrival are particularly important (Cleavitt 2005). Hutsemékers *et al*. (2008) determined that rare species not only require specific habitat conditions, but that they typically are unable to compete. Therefore, when new habitats, such as slag heaps, are created, the rare species tend to enter at intermediate stages, after establishment of widespread species, but before the perennial competitors become established.

Buck (1988), in his study of the Tepui of Venezuela, hypothesized that the lack of moss flora on the summit of the Tepui was due to lack of dispersal from great distances and that available spores came from surrounding lowlands. Thus, failure of a diverse moss flora on the summit must be due to lack of adaptation for germination and survival on the summit. He was fortunate enough to be able to test this hypothesis when he discovered a "world within a world" on top of a Tepui. A sinkhole, 352 m wide and just as deep, provides a haven away from wildly fluctuating moisture and temperature conditions of the summit. In this sunken world, a forest similar to that of the lowland exists. He did indeed find that the moss flora in this sunken forest reflected that of lowland and not that of the summit, supporting his hypothesis that it was ecological conditions and not lack of dispersal that created the depauperate flora.

Germination success seems to be a major problem for spores, and much less so for vegetative propagules. Miles and Longton (1990) found no evidence of spore germination for ***Polytrichum strictum*** (Figure 60) in the field, but did find new shoots arising from vegetative fragments. By contrast, in ***Funaria hygrometrica*** (Figure 107-Figure 109), spore germination and establishment occurred frequently. Intermediate results were evident in ***Atrichum undulatum*** (Figure 6) and ***Bryum argenteum*** (Figure 7), with frequent regeneration from shoot fragments, and spores germinating, but sporelings usually failed to develop. Shoots seemed to develop easily in the latter two from protonemata planted in the field.

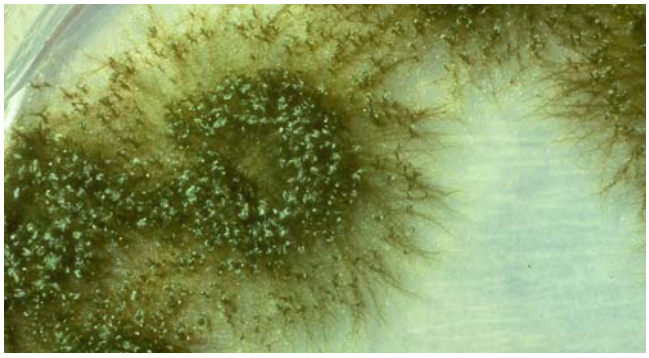

Figure 108. ***Funaria hygrometrica*** cultures. Each donut-shaped colony developed from a single spore, demonstrating how easily this moss can spread upon arrival. Photo by Janice Glime.

Figure 109. ***Funaria hygrometrica*** capsules, demonstrating the prolific production of capsules and spores. Photo by Li Zhang, with permission.

In the Negev Desert, it may be the ants in the genus ***Messor*** (Figure 110) that ensure the success of at least some moss spores (Loria & Herrnstadt 1980). They carry the capsules of ***Crossidium crassinerve*** (Figure 111) away to their nests, thus greatly increasing the likelihood that at least some spores will arrive in a suitable site for protonematal survival.

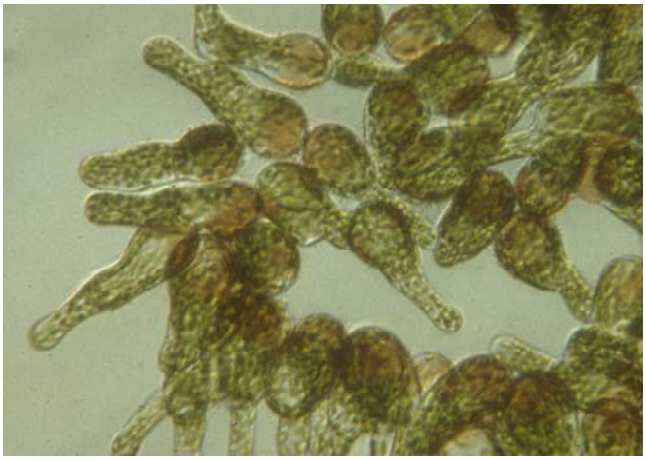

Figure 107. ***Funaria hygrometrica*** germinating spores on agar, demonstrating the ease of germination of many spores. Photo by Janice Glime.

Figure 110. ***Messor barbarus***, an ant that carries moss capsules, hence dispersing spores. Photo by José Miguel León Ruiz, through Creative Commons.

Figure 111. ***Crossidium crassinerve*** with a young sporophyte that might later be used in an ant's nest. Photo by Michael Lüth, with permission.

Figure 113. ***Tortula muralis***, a species that has poor germination in company of its parents. Photo by Kruczy89, through Creative Commons.

Spores can be a means of surviving while competitors make living conditions impossible. Newton and Mishler (1996) found evidence of inhibition by mature plants on the germination of spores. However, if something were to destroy those mature plants, the sporebank could provide a new source of propagules for re-establishment. In fact, it appears that mature plants can have a sneaky way of prolonging time until germination of their spores. Mishler and Newton (1988) found that germination rates of both ***Dicranum*** (Figure 112) and ***Tortula*** (Figure 113) were greatly lowered on substrates of their parents. Although both ***Dicranum*** (Figure 98) and ***Tortula*** were severely affected by the presence of their parents, fragments were less affected than spores. ***Dicranum*** had an even greater inhibitory effect than did ***Tortula***. Mishler and Newton compared this to the inhibitory effect that female ***Dicranum scoparium*** (Figure 112) has on spores that produce dwarf males when they germinate on the female plants. Mishler and Newton (1988) found that spores did better in continuously hydrated conditions, whereas fragments fared better when they had occasional drying.

Figure 112. ***Dicranum scoparium*** on the forest floor where it grows dwarf males on its own leaves. Photo by Janice Glime.

Keever (1957) found that spore germination of ***Grimmia laevigata*** (Figure 105) does occur on granite rock, but even there, fragments were more successful. One factor that influences the success of fragments vs spores is state of hydration, and this may have played a role in the establishment of ***Grimmia laevigata***.

Hedderson (1992) found that rare mosses in the Terra Nova National Park, Newfoundland, Canada, were typically representatives of temperate, Arctic-montane, or montane floras. They are species at the edges of their ranges. He found that dispersal potential was negatively associated with rarity. These species have a narrow range of habitats and therefore are likely to have establishment problems.

Adherence

Arrival on the proper substrate is pretty much the end of the transport part of the story for most substrata, but for epiphytes and bryophytes on other vertical surfaces, or for those in flowing water, the problems don't end there. They must next adhere so that wind and rain don't take them once again on their journey. Van Zanten and Gradstein (1988) found that for Neotropical liverworts, the spore surface of epiphytes typically had finely verrucose spores with rosettes of large papillae (Figure 114). They suggested that these decorations were an adaptation that permitted them to adhere to rough surfaces such as bark. Epiphyllous and desert taxa, on the other hand, typically have spores that lack these rosettes (Figure 115). Both groups may gain further advantage by having precocious spore germination (Figure 75), permitting them to continue growth upon landing and gain a wider surface of adhesion.

Adherence may also be a problem in some aquatic habitats, such as streams and flood plains. But here the relationship is not so clear. Spores of ***Riella*** (Figure 116) are clearly spiny, possibly permitting them to adhere to the substrate more easily, but those of ***Fontinalis*** (Figure 117), a genus that typically adheres to rocks or underwater roots, are nearly smooth, having only small, rounded papillae.

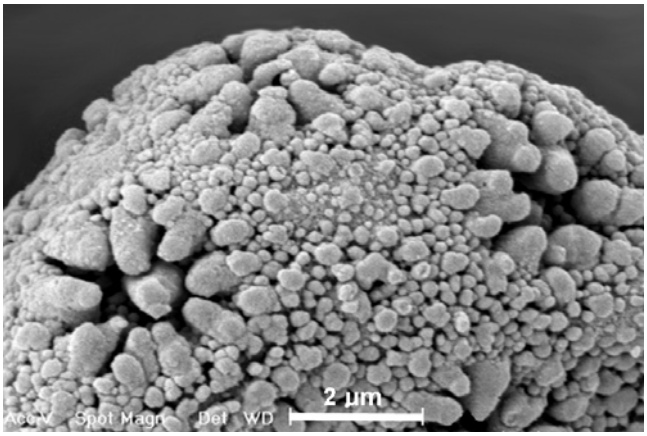

Figure 114. ***Frullania chevalieri*** spore SEM showing the rosettes of papillae. This spore exhibits characteristics that are common among epiphytes. Photo by Matt von Konrat, with permission.

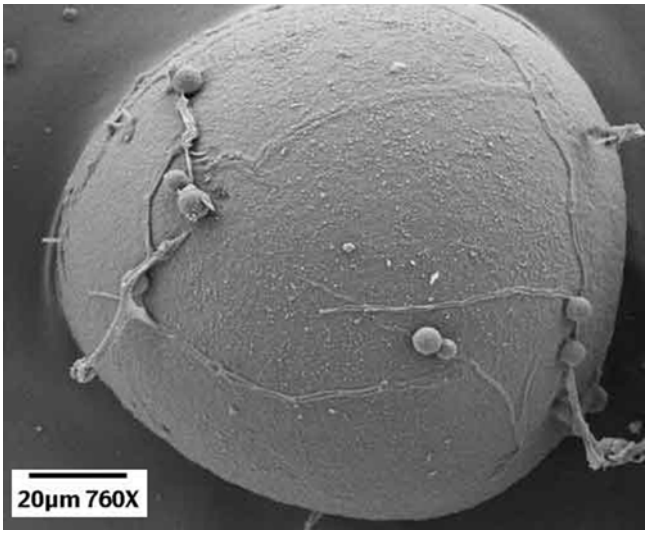

Figure 115. ***Geothallus tuberosus*** (**Sphaerocarpaceae**) spore SEM, a species of hot deserts. The large size and smooth surface are typical of spores that don't travel far and don't have adherence problems on their landing surfaces. Photo by William T. Doyle, with permission.

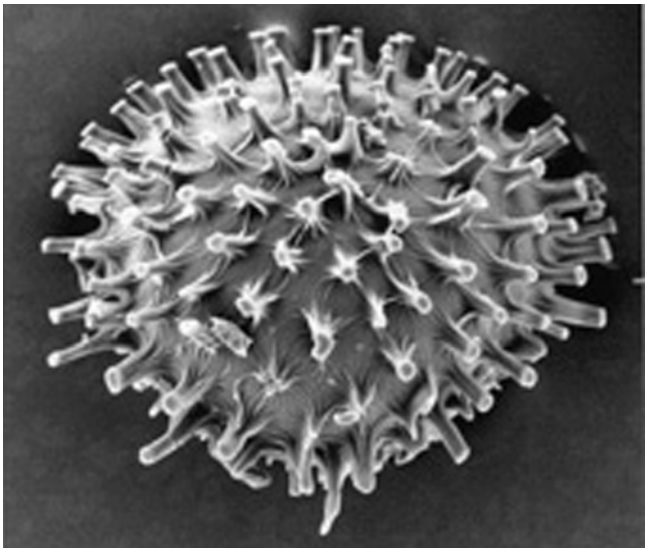

Figure 116. ***Riella americana*** spore SEM. Photo by William T. Doyle, with permission.

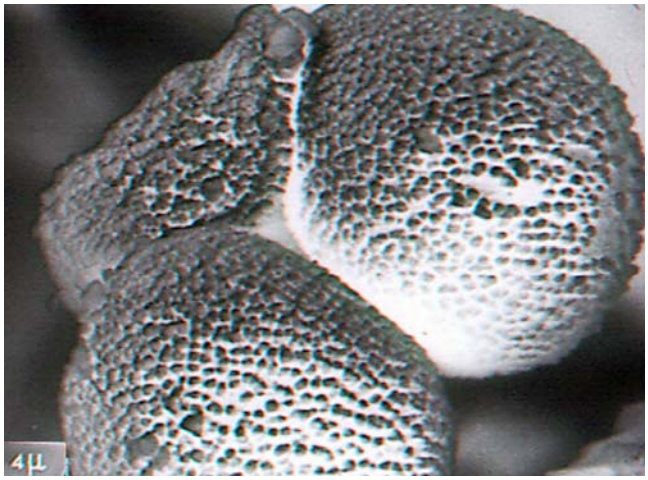

Figure 117. ***Fontinalis squamosa*** spore tetrad SEM. Photo by Janice Glime.

Conditions Matter

It is clear that survival while getting there is only part of the battle. Although the spores may arrive in viable condition, they may not succeed in germinating. Hassel and Söderström (1999) collected spores from ***Pogonatum dentatum*** (Figure 118) and germinated them in the laboratory. They had 96.6% germination within 21 days. They tested success in the field by sewing spores from 0.5, 1, and 2 capsules on 37 replicate quadrats of 10x10 cm. Considering the large estimated number of spores per capsule of 712,000, germination success was abysmal, with means of 11, 10, and 12 shoots produced, respectively, in the first year. They suggested that they had exceeded maximum density for successful protonemata. But it could also mean that some other field condition was not conducive to protonema development.

During (1986) found a similar problem in ***Funaria hygrometrica*** (Figure 107-Figure 109). In the greenhouse, shoots emerged from chalk grassland soil samples, even after two years, but in the field, none emerged. During considered that this failure in the field might be due to insufficient water or nutrients.

Figure 118. ***Pogonatum dentatum*** in Norway. Photo by Michael Lüth, with permission.

Drought tolerance of liverwort sporelings is significantly different between transoceanic and endemic species. This is a critical period for many species, with 30% of transoceanic species germinating after 50 days of desiccation and 30% of endemic species reduced to 30% germination after only 13 days. Both groups have a sporeling longevity of only about half that of spore longevity.

The problem of crowding, as suggested by Hassel and Söderström (1999) for ***Pogonatum dentatum*** (Figure 118), is only one problem faced by germinating spores close to the parent, and is one of little significance for long distance dispersal. The low numbers are more likely due to other problems in the field as well, including perhaps too much UV light, insufficient nutrients or moisture, or unsuitable temperatures. Noguchi and Miyata (1957) pointed out that at least some mosses with wide geographic ranges have abundant spores but are confined in their frequency by having rather specific habitats.

Multiple factors contribute to the success of a species upon its arrival. The conditions required for germination and development of the protonema and gametophore buds may differ, and are all part of the niche of a species, a topic that will be discussed in more detail in another volume. But it is appropriate to consider some examples here as we define limits of establishment.

Wiklund and Rydin (2004) compared spore establishment of two forest bryophytes, one [***Neckera pennata*** (Figure 15-Figure 16)] an epiphyte and the other [***Buxbaumia viridis*** (Figure 119)] an inhabitant of decaying logs. Using *in vitro* experiments, they determined that ***Neckera pennata*** was less successful at germinating at a low *p*H than was ***Buxbaumia viridis***. The tradeoff was that ***N. pennata*** exhibited earlier germination at low water potential and survived longer when desiccated. They suggested that the higher *p*H would speed up germination and enable the spores to exploit short moist periods. This niche separation at the time of establishment is often not apparent by the range of tolerance of mature plants but can be critical to establishment of spores.

Figure 119. ***Buxbaumia viridis*** capsules on log. Photo by Hermann Schachner, through Creative Commons.

Sphagnum spores under wet, anaerobic conditions had much lower survivorship (dying within 2-3 years) than those under wet or periodically desiccated aerobic conditions, suggesting that respiration not only continued but was necessary for their survival (Sundberg & Rydin 2000). Refrigerated spores lasted up to 13 years. This infra-species size difference, coupled with the ability to survive freezing in upper atmosphere conditions, might permit the small spores, already better adapted for long-distance transport, to survive the greater time they are likely to be in transport.

Sphagnum provides a good example of the need for a specific nutrient. Despite the apparently good longevity of spores of ***Sphagnum*** species, few protonemata (Figure 77) have been observed in the field (Sundberg & Rydin 2002). Sundberg and Rydin attribute this absence to the need for phosphorus in greater concentrations than that typically found in natural waters. Various peat substrata were tested and it appeared that the amount of phosphate released was the determining factor in successful germination. Moose dung increased the success rate, as did litter from *Betula pubescens*. *Pinus sylvestris* litter did not help.

It appears that ***Sphagnum*** has other establishment needs as well. ***Sphagnum*** spp. fragments that arrived at a restoration project were unable to succeed unless they joined a ***Polytrichum strictum*** (Figure 120) carpet (Groeneveld *et al*. 2007). Apparently the carpet was important in keeping the developing ***Sphagnum*** moist. Groeneveld *et al*. considered that buffering of the temperature, making it cooler in daytime and warmer at night, may have been important as well.

Figure 120. ***Polytrichum strictum*** with ***Sphagnum*** growing between the stems. Photo by Andrew Hodgson, with permission.

Cleavitt (2002) tested the stress tolerance of fragments of pairs of rare and common species of mosses in view of their asexual dispersal potential. Habitat specificity in the three common species was more likely to correspond to physiological differences. For example, the common ***Mnium spinulosum*** (Figure 121) was intolerant of high light conditions and therefore only became established in the deep shade of conifer stands. The common ***Bryum pseudotriquetrum*** (Figure 122) was intolerant of desiccation and only became established on stream banks and other moist areas. The striking observation was that the rare ***Mielichhoferia macrocarpa*** (Figure 123) was tolerant of both high light and desiccation, but had the slowest rate of recovery, suggesting that some other factor contributed to its rarity, such as competition during its slow recovery, or insufficient time to recover in natural conditions before again suffering desiccation. And other factors in the environment could also be important establishment factors.

Figure 121. ***Mnium spinulosum*** from Europe, a species intolerant of high light conditions during establishment. Photo by Michael Lüth, with permission.

Figure 122. ***Bryum pseudotriquetrum*** with capsules from Europe, showing its typical wet habitat, here along a stream. Photo by Michael Lüth, with permission.

Figure 123. ***Mielichhoferia macrocarpa***, a species tolerant of high light and desiccation, but one that has poor establishment success. Photo © Robin Bovey at PhytoImages website, with permission.

Bryophytes can be slow colonizers compared to some of the other taxa. Nevertheless, on Surtsey, they were among the first arrivals on the solidified lava. The typically early colonizers among the Cyanobacteria were remarkably scarce. Their most common locations were near steam vents, usually near moss clumps, particularly ***Funaria hygrometrica*** (Schwabe 1974; Figure 107-Figure 109) These nitrogen-fixing blue-green bacteria were especially attached to the protonemata. The moss ***Racomitrium*** (Figure 29), however, seemed to inhibit the growth of Cyanobacteria.

Slow Establishment

As we have noted above for ***Mielichhoferia macrocarpa*** (Figure 123), slow recovery may account for the lack of success in some species that arrive by diaspores. Leck and Simpson (1987) noted this problem for species recovered from a wetland diaspore bank. They identified 14 mosses, 2 liverworts, 7 ferns, and 1 horsetail, with ***Bryum*** sp (Figure 122) and the fern *Onoclea sensibilis* having the greatest densities. The highest densities occurred in the surface samples. Germination of spores and/or growth of these diaspores was slow compared to that required for seeds from seedbanks and they considered this slowness to be a factor in the absence of the bryophyte species on the surfaces of the wetlands.

Dispersal Limitation

A number of studies suggest that dispersal limitation is the best explanation for the patterns of abundance and distribution of bryophytes in some fragmented habitats (Pharo & Zartman 2007). But edge effects can also play an important role. Because of their small size, fast colonization-extinction rates, high substrate specificity, and dominant haploid condition, Pharo and Zartman consider them to be ideal model systems for testing the effect of fragmented landscapes on bryophyte community structure.

Nearness of source has been shown repeatedly as an important determinant of colonization, although Hylander (2009) found no relationship between colonization rate and nearness to mature forest stands for boreal forest bryophytes. This nearness component was well illustrated by Zartman and Shaw (2006) in their study of two epiphyllous species [***Radula flaccida*** (Figure 124), ***Cololejeunea surinamensis***] in the Amazon tropical rainforest. While extinction rates were the same for these species in both fragmented and continuous forests, colonization rate was much greater in the continuous forest sites (Figure 125).

Kimmerer (2005) demonstrated the importance of dispersal at a small scale in the colonization of treefall mounds in the Adirondack Mountains, USA. When spores and fragments of ***Polytrichum ohioense*** (Figure 126), ***Dicranella heteromalla*** (Figure 127), ***Atrichum angustatum*** (Figure 5), ***Diphyscium foliosum*** (Figure 128), and ***Pogonatum pensilvanicum*** (Figure 129) were sown on the mounds, these species became established, with the highest success occurring with fragments. Under natural conditions, only 1-2 of a possible 13 species established on any single mound and likewise, in the experiment, sown propagules were far more successful than natural dispersal to mounds with no added propagules.

Kimmerer considered this to be strong evidence of dispersal limitation on treefall mounds.

Figure 124. ***Radula flaccida*** with gemmae, an epiphyllous species that does best in continuous forest. Michaela Sonnleitner, with permission.

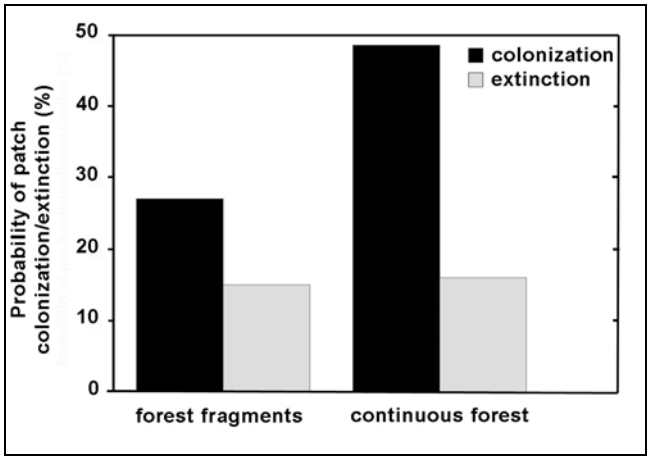

Figure 125. The colonization and extinction rates of ***Radula flaccida*** and ***Cololejeunea surinamensis*** on epiphylls in the Amazon tropical rainforest. Data for the two liverworts were very similar and thus were combined. Redrawn from Zartman & Shaw 2006.

Figure 126. ***Polytrichum ohioense***, a species that seems to be dispersal limited when colonizing treefall mounds. Photo by Janice Glime.

Figure 127. ***Dicranella heteromalla*** on a soil bank. Despite its numerous capsules, its fragments are more successful at establishment on treefall mounds. Photo courtesy of Eric Schneider.

Figure 128. ***Diphyscium foliosum*** male plants (green) and female capsules and perichaetial leaves. Fragments are more successful in establishment than are spores. Photo by David Holyoak, with permission.

Figure 129. ***Pogonatum pensilvanicum*** with capsules on a soil bank. Note the ground cover of protonemata and absence of leafy gametophytes. Photo by Bob Klips, with permission.

Recolonization

In some habitats, bryophytes are among the first organisms to colonize a disturbed site. These are generally fugitives and other species that cannot tolerate the competition of tracheophytes. They take advantage of the sun but must tolerate greater drying than the species living in forested habitats. But they must also have good dispersal capabilities to arrive there and thrive before the competition arrives.

Arrival in disturbed habitats can be extensive, as Greven (1994) observed in an experimental garden. Between 1972 and 1991, 91 species arrived in the garden. The greatest number of taxa occurred on the chalk soils (40 spp), with peat having the fewest (6 spp). Even several rare taxa arrived.

In an urban environment, a community can re-establish itself in 1-2 years (Nehira & Nakagoshi 1987). Thalloid liverworts and pleurocarpous mosses were the first to regenerate, ahead of the acrocarpous mosses. This is somewhat unusual as the acrocarpous mosses typically have more asexual diaspores than do pleurocarpous mosses, but regeneration may have occurred from remnants and fragments, a dispersal mechanism common among pleurocarpous taxa. Regrowth occurred primarily in the spring and autumn, despite little seasonal variation in the number of airborne diaspores, suggesting the importance of rainfall and perhaps cool temperatures.

Forests

The slow rate of recolonization in harvested regrowth forests is illustrated by the smaller number of species present, presumably due to the slow rate of dispersal and establishment of species common in old-growth forests (Cooper-Ellis 1998). In the Central Cordillera of Colombia, Corrales *et al.* (2010) considered the dispersal of propagules among the various forest types to be the primary mechanism driving the regional pattern of bryophyte distribution.

Proximity to other suitable bryophytes seems to be a major factor in what species will become established after a disturbance. Even in the limited microcosm of a leaf, Cobb *et al.* (2001) found that bryophytes colonizing *Acer macrophyllum* leaves (**epiphyllous**) in Olympia, Washington, USA, after experimental removal of the epiphylls, were primarily due to lateral encroachment (75%). Only ~8% of the exposed area had been recolonized one year after removal of bryophytes, reaching 27% after three years. The 25% not colonized by encroachment included incompletely removed plant parts and aerially dispersed diaspores.

On the other hand, in young boreal forest stands, there was no indication of higher colonization by bryophytes close to the mature stands where bryophytes were undisturbed (Hylander 2009). Following a forest fire, bryophytes that recolonize can either arrive anew or survive the fire. Survival of the fire could be the result of migrating to a safe site during the fire (*i.e.*, local dispersal to safety) or by enduring the conditions (Hylander & Johnson 2010). Endurance can be due to wetness, burial, or positioning in the protection of logs, rocks, or other blockades to the fire. Hylander and Johnson (2010) found an average of three refugia per 50 x 50 m reference plot, with a mean of 4.8 bryophytes associated with them. But in the area that had been burned, only a mean of 1.5 species could be found in the refugia. However, other factors seemed to be more important than refugia. There was no correlation between the number of refugia and the number of forest species that colonized the plots. The refugia were mostly on rocky or mesic sites, not wet sites. The importance of these refugia most likely depends on the intensity and nature of the fire. A ground fire will have a very different effect from a crown fire.

Schmalholz and Hylander (2010) examined a similar question regarding the role of forest floor refugia in response from clear-cut logging. They found survival differences based on microtopography. The shelter of boulders and stumps resulted in significantly more survival (~30%) than on level forest floor (10%) for transplanted bryophytes. These boulders and stumps also resulted in less change in species composition.

Evidence from Europe suggests that the same forest can be colonized by a bryophyte species multiple times. Cronberg *et al.* (2002) found repeated recruitment among populations of ***Hylocomium splendens*** (Figure 33) on 10 Baltic islands. He identified 103 haplotypes among 694 shoots with number of clones increasing significantly with increasing age of the islands. He likewise showed that the number of genotypes of ***Plagiomnium affine*** (Figure 130) correlated with the age of the forest stand in Europe (Cronberg 2005). Using 23 allozyme loci and six populations of ***P. affine***, they sampled 602 shoots and found 16 haplotypes. Among these, 12 were unique to single populations. Allelic richness and diversity were significantly correlated with forest age at the ramet level but not quite so at the genet level.

Figure 130. ***Plagiomnium affine***, a species for which the number of genotypes correlates with forest age. Photo by Michael Becker, through Creative Commons.

Patch Fragmentation

Logging has an impact on the distribution of bryophytes. Isolated patches that remain may be invaded by new species and disturbed areas will both lose old species and gain new ones. In the temperate rainforest of British Columbia, Canada, Baldwin and Bradfield (2007) compared bryophytes on the forest floor, downed logs, and tree bases. They found that the dispersal-limited groups

such as perennial stayers and the microclimate-sensitive groups declined in species richness or frequency as patch size decreased. These microclimate-sensitive groups included those from closed canopy, log-dwelling species, and liverworts. Colonists and open canopy species showed little relationship to patch size. In the patch size range of 0.6-63.6 ha, most of the patch size effects disappeared when the three smallest patches (0.6-1.8 ha) were not included in the analysis. Therefore, patch sizes of at least 3.5 ha seem to provide suitable habitat to sustain the diversity of bryophyte functional groups in this temperate rainforest habitat. It is likely that part of this decrease in diversity is due to dispersal limitation.

Summary

Most bryophytes are adapted for wind dispersal, with the occasional updraft or gust permitting somewhat greater distances. Epiphytes gain height through their host. However, the majority of spores seem to land within 2 m of their parents. It follows that spore density in the atmosphere decreases with distance from the source and increases with height of the colony.

Members of the **Polytrichaceae** have a membrane connecting their teeth and disperse spores by disturbance such as rain drops. These are ejected horizontally and apparently do not travel far.

Bryophytes that live on temporary and disturbed substrata, such as logs and arable land, require either good dispersal or the ability to survive in diaspore banks.

Tracheophyte dispersal models have limited applications to bryophyte dispersal. Bryophyte spores are much smaller than seeds and lack multiple layers of tissues to protect them. Vegetative diaspores may mimic some of the elongate shapes, but spores tend to travel farther than vegetative propagules.

Bryophytes seem to support the concept that "everything is everywhere, but the environment selects." Unfavorable light, photoperiod, substrate, temperature, and moisture conditions can prevent establishment of a species once it arrives. This concept is supported by the small size of spores, the distribution patterns, and patterns of establishment on newly formed islands.

Molecular Clocks can be used to estimate time of arrival and help us to trace the dispersal routes.

Weather, dust storms, and fires can play a significant role in creating air currents, protecting from UV, and maintaining moisture.

Even diffusion models can help us understand dispersal, but size, falling velocity, and access to the air stream all have roles in the distance travelled. Long-range dispersal is facilitated by wind, requiring updrafts to get spores into the atmosphere. There the spores must survive UV light, desiccation, and extremes of temperature, especially sub-freezing temperatures. In some areas there is clear evidence of **stepping stone** progression once the first propagule arrives and succeeds in the area.

Small spores travel the farthest; large spores provide more energy for the start of growth. Spores range from 5 µm in ***Dawsonia*** to 310 µm in ***Archidium***, with numbers per capsule ranging from 4 in ***Archidium*** to 50 million in ***Dawsonia***. Most bryophyte spores range about 20-100 µm and hence weigh about 0.004 µg to about 0.52 µg, all falling in the size category where wind dispersal is expected. Few animal dispersers are known for bryophytes. Most spores seem to fall within 2 m of their parents, but only a few need be caught into updrafts in order to accomplish long-distance dispersal. Limited **gene flow** between populations, demonstrated by genetic variation between them, suggests that most populations arise from a single propagule and that there is little mixing. This is further supported by the lack of genetic variation within populations.

Height of origin, such as epiphytes or species on walls and boulders increase dispersal effectiveness. Many dispersal periods are correlated with dry weather, especially for small spores, but at least in some locations, spores can be trapped from the atmosphere year-round. Some capsules require more than a year to develop whereas others mature in a few weeks. Few data exist that identify the species of atmospheric travellers, but certainly ***Funaria hygrometrica*** is one of them. Often the spores that are travelling are different from the species of a particular environment.

Long-distance dispersal is limited by drought tolerance and UV radiation (lethal for most species). For Neotropical liverworts, there is no dispersal advantage based on spore size, bisexuality among small-spored species, presence of chlorophyll, verrucosity of spore wall, and presence of gemmae. Bisexuality seems to have a positive advantage in large-spored (>35 µm) species. Species with greater source distributions and greater area of suitable destination habitats have greater dispersal potential. Dark-colored spore walls may protect against UV radiation. **Callose** deposits on the spore, waxy **sporopollenin** on the surface, and in most mosses a **perine** layer, all may contribute to protection of the spore.

Wet freezing has equal effect on transoceanic and endemic species. Both spores and sporelings survive longer with good drought tolerance. Among large-spored species (>25 µm), xerophytes survive dispersal better than mesophytes or hygrophytes. Dispersal by water is possible in many taxa, with survival times ranging from a few days to many months. **Spore longevity** is known from 7 days to 50 years.

Once arriving, spores and vegetative diaspores must adhere. For spores, verrucose surfaces can facilitate catching on something, such as tree bark.

Because of the limits of dispersal, ability to remain viable in soil banks, and changes in environmental conditions, the bryophytes that become established following a disturbance may differ considerably from the original flora.

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CHAPTER 4-9

ADAPTIVE STRATEGIES: SPORE DISPERSAL VECTORS

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CHAPTER 4-9

ADAPTIVE STRATEGIES: SPORE DISPERSAL VECTORS

Figure 1. Capsules of ***Splachnum ampullaceum***, adapted for fly dispersal by both red colors and their odor. Note the special landing platform (**hypophysis**) below the cylindrical capsule. Photo by Michael Lüth, with permission.

Dispersal Types

Gao *et al*. (2000) examined the Chinese bryophyte flora and concluded that there are five classes of spore dispersal. These are wind dispersal, vapor-wind dispersal, water dispersal, decay dispersal, and insect dispersal. But more digging reveals that additional dispersal agents may be at work among the animals, including earthworms, spiders, molluscs, birds, and even mammals.

Hughes *et al*. (1994) concluded that the availability of specific dispersal vectors seems to have no influence on dispersal mode. I think that one could use flies that visit the **Splachnaceae** on dung to argue against that conclusion, but there do not appear to be any studies that attempt to correlate dispersal mode with availability of the vector.

For spores to gain access into the atmosphere, they must be expelled away from the capsule and join wind currents before they fall to the ground. One can flick a newly opened capsule and see clouds of spores emitted. It is likely that deer, rabbits, squirrels, and various small rodents bump these extended capsules, likewise sending up clouds of spores. To this end, the **peristome teeth** (Figure 2-Figure 4) of many mosses work like a saltshaker and permit only a portion of the spores to escape in one event. This helps to insure that dispersal takes place over an extended period of time and may then encounter more climatic conditions wherein some are suitable for good or even long-distance dispersal.

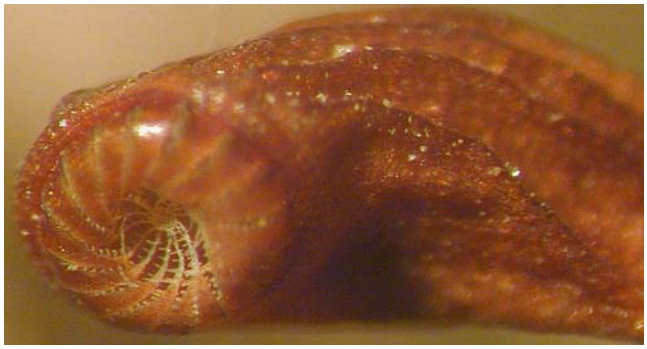

Figure 2. Peristome teeth of ***Funaria hygrometrica***, showing the chambering that helps in the slow dispersal of spores. Photo by Michael Lüth, with permission.

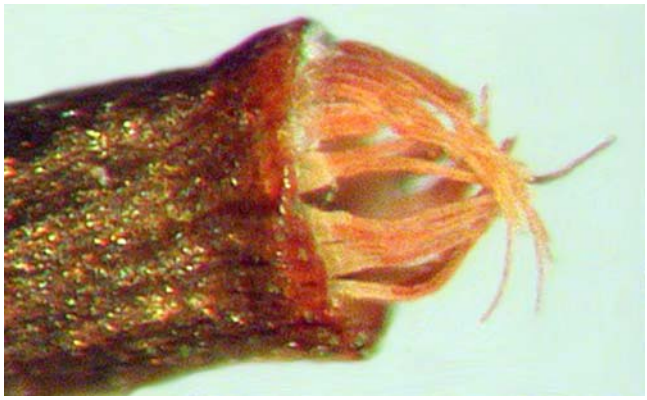

Figure 3. Peristome teeth of ***Aloina aloides*** showing spaces between teeth that create a saltshaker effect to slow dispersal. Photo by Michael Lüth, with permission.

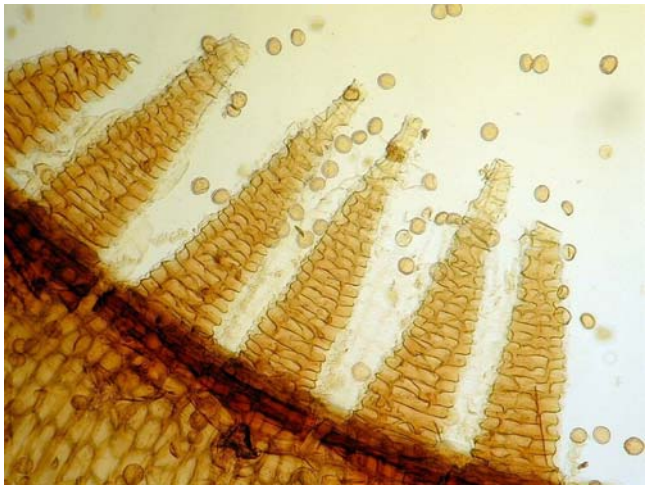

Figure 4. Peristome teeth and spores of ***Ptychostomum pendulum***. Photos by Michael Lüth, with permission.

Wind Dispersal

Wind dispersal is assumed to be the rule among most bryophytes. But few data were available to support that concept for long-distance dispersal.

As we discussed in examining long distance dispersal, any propagule released from a greater height or elevation has a greater probability of being exposed to greater wind velocities (Greene & Johnson 1996). This means that greater heights increase the opportunities for wind dispersal. Campbell *et al.* (2001) contend that mosses have high immigration potential due to the wind-dispersal ability of their spores. This would seem to argue against the conclusions of Hughes *et al.* (1994) that the availability of specific dispersal vectors has no influence on dispersal mode. As already discussed in the previous sub-chapter, successful wind dispersal relates to release height and falling time (slow for spores due to small size). Wing loadings in bryophytes are very low and probably have insignificant effect. Release height can be increased by explosive behavior of some capsules, and location on trees or at higher elevations likewise increases the opportunities to become airborne..

Lönnell (2011) reminds us that according to Stoke's law (Figure 5) spores can travel farther than larger diaspores of the same shape and density, given the same wind speed. [Stoke's Law: If particles are falling in a viscous fluid by their own weight due to gravity, then terminal velocity, also known as settling velocity, is reached when this frictional force combined with the buoyant force exactly balance the gravitational force.] Lönnell compared small seeds to large seeds, stating that, even if larger seeds can increase the buoyancy with features like pappi or wings, small seeds can still travel farther. Bryophyte spores lack such features as wings, but do possess pappi and other surface features. I am unaware of any study that has examined the role of variations in these markings as a means to facilitate wind dispersal. Perhaps they do, however, create buoyancy in water, permitting them to float and thus get dispersed farther.

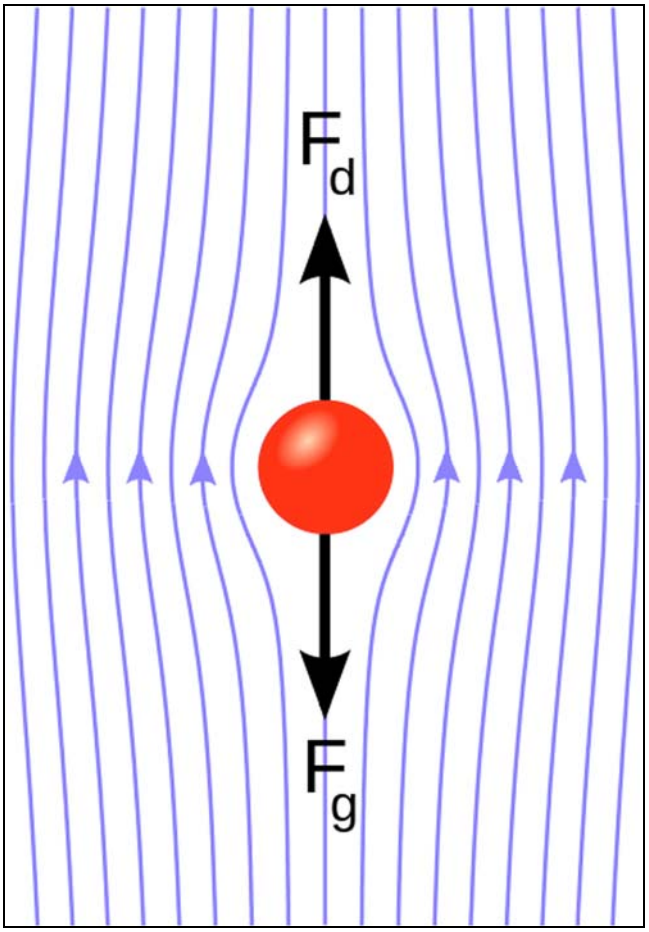

Figure 5. Stokes sphere showing movement of fluid around it. F_d is the frictional force, known as Stokes' drag. F_g is the force by gravity. Image from Wikimedia Commons.

Cronberg *et al*. (2008) were able to capture the effects of wind on the initial dispersal of spores of ***Bryum argenteum*** when they filmed the life cycle. They found that the release was rapid. The peristome opened and closed in response to minor changes in atmospheric moisture conditions. The capsules in this species hang down, with gravity causing the spores to collect over the peristome, but on the inside. When the peristome teeth open, a group of spores fall out and are dispersed in a cloud. Air movements can carry the spores upward (Figure 6).

Figure 6. ***Bryum argenteum*** spore release, showing upward movement. Photo by Nils Cronberg, Hans Berggren, & Rayna Natcheva, with permission.

We lack measures of density of bryophyte spores in the atmosphere, but experience with other organisms and particles are instructive. Schlichting (1978) tells us that there are 0.3-7.5 billion particles greater than 0.2 µm in diameter in one cubic meter of "clean air." And joining these organisms are spores of bryophytes. Puschkarew (1913) found an average of 2.5 protozoan cysts in a cubic meter of air, attesting to the success of somewhat larger structures being transported.

In sampling airborne algae in Michigan, USA, Schlichting (1964) found the greatest numbers of algae and protozoa between noon and midnight on cloudy days, with more during July and August than during September through May, although this may have related more to innate life cycles than to that year's weather conditions. The wind elevation angle (*i.e.*, horizontal vs vertical) seemed important in determining the number of organisms present; wind direction and speed seemed less important. Updrafts were more important than downdrafts or horizontal wind. Rainfall during the preceding 24 hours was detrimental to organism presence, most likely quickly washing them from the atmosphere. Sizes of the most common propagules ranged from the one-celled alga ***Chlorella*** with diameters of ca. 2-8 µm to those of cysts of the protozoan ***Oikomonas***, for which living cells range up to 100 µm or more (without knowing the species, we cannot determine the size of the cysts, but they are likely to be similar). This range encompasses the majority of spore sizes of bryophytes.

But wind is constantly changing, and averages can be misleading. Sudden changes in direction can stir up tiny tornadoes that may dislodge and uplift spores. This might be especially true on glaciers. Bonde (1969) collected plant propagules from wind-blown debris on St. Mary's Glacier at 3350 m. He found 35 species of seed plants, but he also found viable parts of the moss ***Polytrichum piliferum*** (Figure 7), lichens, and *Selaginella*.

Figure 7. ***Polytrichum piliferum***, a moss whose fragments are known from wind-blown debris. Photo by David T. Holyoak, with permission.

In the Southern Hemisphere, it appears that wind has played an important role in geographic distribution of bryophytes. Muñoz *et al*. (2004) found that there was a stronger correlation of floristic patterns with wind patterns than with geographic proximities, supporting wind dispersal for the arrival of many organisms in the Southern Hemisphere. These wind patterns followed "wind highways" that resulted in directional dispersal and distribution.

Felicísimo *et al*. (2008) attempted to understand the role of global wind patterns in dispersal by not only wind data but also the pathway of a tracked seabird, the Cory's Shearwater (***Calonectris diomedea***). Birds are able to locate the pathways that require the least energy to carry them to their destination, going higher or lower, following mountains or other areas where updrafts and wind movement help to carry them where they need to go. The shearwaters followed the pathways predicted by the air pattern model, but when they reached the Atlantic sector of the Intertropical Convergence Zone, they were hindered by the near-surface westerlies. Only after these westerlies ceased were the birds able to cross this zone. Hence, we have evidence for seasonal differences in the most energy-effective pathways.

To understand the diaspore rain, it is necessary to trap the propagules, then culture them. Ross-Davis and Frego (2004) report success with diaspore traps using nutrient agar plates. These trapped diaspores grow well from both spores and vegetative propagules at indoor ambient conditions – so well that they need to be transplanted due to crowding. But patience is required; it takes nine months for them to reach a recognizable stage.

Splachnaceae

This family is best known for its spore dispersal by flies. But Walsh (1951; see also Bryhn 1897) has observed an alternative method – wind dispersal. He observed that in ***Splachnum sphaericum***, when the capsule dried, the

peristome teeth became reflexed, adhering to the outside of the capsule. From the inside, the spores were push out as the capsule dried and shrank. And the **columella** extruded from the capsule – a phenomenon known in only a few mosses. The spores form a ring around the top of the capsule and adhere to each other in clusters. The teeth remain hygroscopic and withdraw when moisture returns. Furthermore, the spores likewise withdraw and the capsule once more becomes turgid and swollen. This extension and intrusion of peristome and spores can continue to occur as moisture changes occur. When the peristome reflexes, it typically carries adhering spores away from the capsule.

Figure 8. Young capsules of ***Splachnum rubrum*** with **operculum** (cap) still intact on all but one capsule. Note that the umbrella-shaped structure is a **hypothesis** that occurs at the base of the capsule. Spores are housed inside the cylindrical structure above it. Photo by Michael Lüth, with permission.

Figure 9. Capsules of ***Splachnum rubrum*** that have shed their opercula. Note the exserted teeth and the ring of spores at the capsule opening. Photo by Michael Lüth, with permission.

When struck by a strong wind, the extruded clusters may extend from the capsules in either clumps or threads. Sometimes the wind causes the threads to bend back upon themselves, in which case the thread more closely resembles a clump. But in some cases the clusters or threads may break loose, effecting dispersal. The stickiness of the spores is important in assuring that both genders arrive on the new substrate, hence making spore production possible in that generation. But Walsh was unable to observe the fate of these escaped spores. The dung substrate necessary for the life cycle to continue is rare relative to all the other possible landing substrates available. I would think that even though wind dispersal is possible, it would be rare that successful landing on a suitable dung substrate would occur.

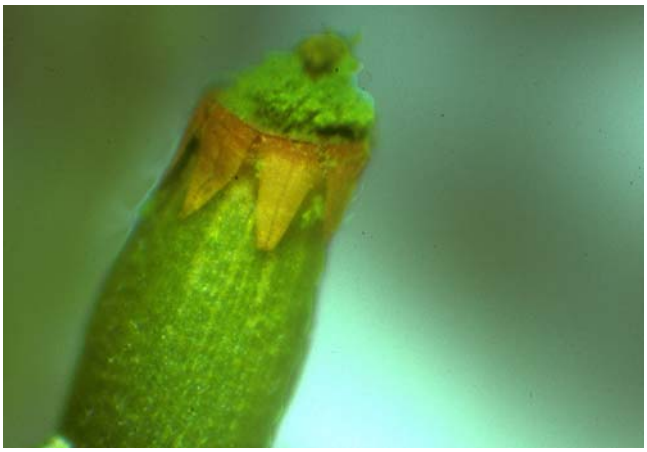

Figure 10. Peristome of ***Splachnum ampullaceum*** with teeth reflexed against capsule and columella extruded at the center of the spore mass. Photo by Janice Glime.

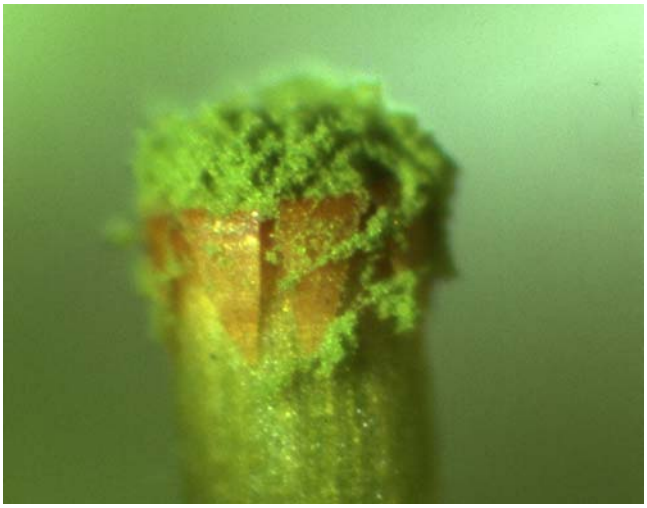

Figure 11. Peristome of ***Splachnum ampullaceum*** showing peristome teeth reflexed against the capsule and spore clusters clinging to them. Photo by Janice Glime.

Liverworts

Schuster (1966) considered liverwort dehiscence and spore dispersal to be timed to occur when there would normally be strong, drying winds to dry the outer layer of the capsule wall, causing the valves to curl backward. Since outer walls would dry first, they would be more contracted than inner walls.

Liverworts are aided in spore dispersal by elongate structures with spiral thickenings called **elaters** (Figure 12). These respond to changes in moisture, causing walls of cells between spirals to contract, thus resulting in twisting of elaters and contortion or bending of cells. When the elater reaches a certain point of tension due to remaining water adhering to walls of drying cells, it

suddenly releases the remaining water and jerks into its original shape, thrusting nearby spores into the air. There are variations on this theme, discussed in the subchapter on Marchantiophyta. Schuster (1966) considers that in liverworts, numerous small spores (6-18 µm in diameter) are an adaptation for wind dispersal.

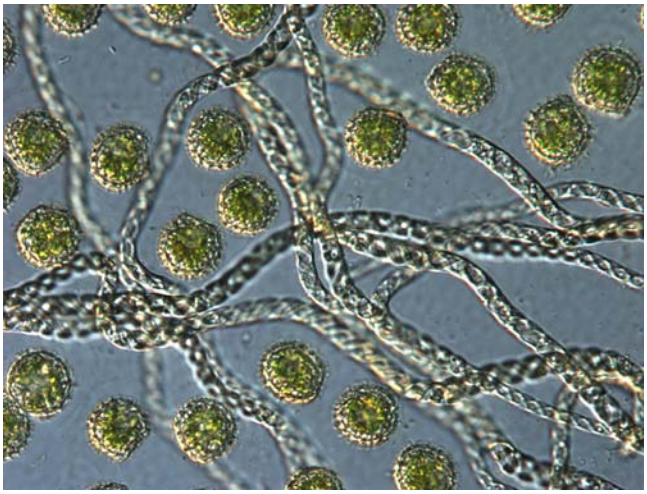

Figure 12. ***Hymenophyton*** sp. spores and elaters. Photo by Karen Renzaglia, with permission.

Invasive Species

The invasive ***Campylopus introflexus*** (Figure 13) has spread rapidly over Europe, apparently by its small spores (Hassel & Söderström (2005). Once there, it spreads rapidly by programmed fragmentation of deciduous leaves. ***Orthodontium lineare*** (Figure 14), another invasive species in Europe, spreads by numerous small spores. It lacks vegetative reproduction, although its ability to grow from fragments remains to be tested. Because it must establish and spread by spores, it requires about thirty years before it is able to produce mature spores; ***Campylopus introflexus*** requires only ten. It appears that the spread of spores in both species is predominantly (or entirely) by wind.

Figure 13. ***Campylopus introflexus***, an invasive weed in Europe. Photo by Michael Lüth, with permission.

Figure 14. ***Orthodontium lineare***, an invasive species in Europe. Photo by Michael Lüth, with permission.

Decay Dispersal

Some capsules lack peristome teeth and do not dehisce (**cleistocarpous capsules**; Figure 15-Figure 18). In these cases, the capsule must decay or be eaten for spores to escape.

Figure 15. ***Goniomitrium enerve*** with cleistocarpous capsules. Photo by David Tng, with permission.

Figure 16. ***Physcomitrella patens*** cleistocarpous capsule. Note neck of archegonium forming a dark projection at the tip of the calyptra. Photo through Wikimedia Commons.

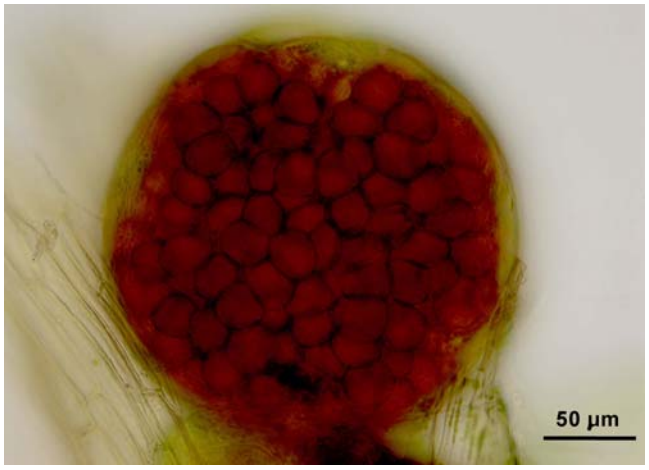

Figure 17. ***Micromitrium synoicum*** cleistogamous capsule. Photo from Duke University Herbarium, through Creative Commons.

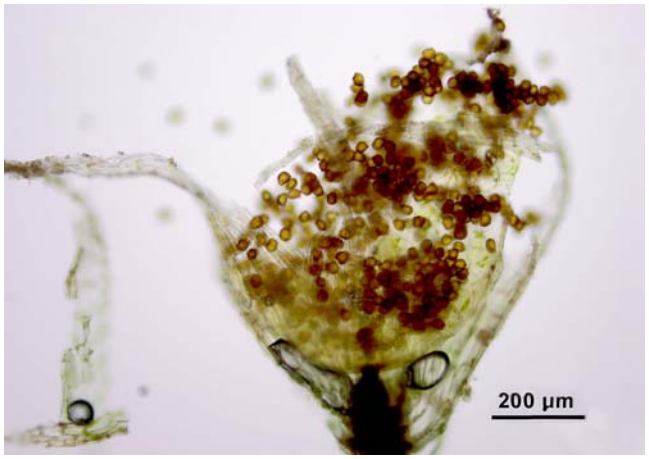

Figure 18. ***Micromitrium synoicum*** cleistogamous capsule breaking apart, showing spores. Photo from Duke University Herbarium, through Creative Commons.

Even some capsules with an operculum and peristome may use decay as a means of releasing spores. In ***Fontinalis novae-angliae*** (Figure 19) and ***F. dalecarlica*** (Figure 20), abrasion by flowing water and debris (in New Hampshire, USA) often erodes the capsule wall away with the operculum still intact. The capsules in this genus tend to be quite thick, perhaps an adaptation against premature erosion. But the question remains, are the spores still viable in these older capsules that seem to be heavily endowed with phenolics, or are these capsules that aborted before reaching the maturity needed for normal dehiscence and dispersal? Since these spores disperse in late winter, observations on the actual dispersal seem to be lacking, my own included.

I have observed capsules in these two species, still submersed, but not yet mature. Korstelius (2003) observed very different behavior in ***Fontinalis antipyretica*** (Figure 21) from the dense capsule walls I observed after spring runoff. He reported that sporophytes in this species are produced under water, but that dry conditions were needed for the capsule to dehisce. Under such conditions, the operculum tears loose, lifted by hygroscopic movements of the exostome teeth. Spores are released by reversible changes in the shape of the capsule! Misha Ignatov (Bryonet 29 March 2013) observed the teeth in the lab and watched them gyrate as they dried (Figure 22).

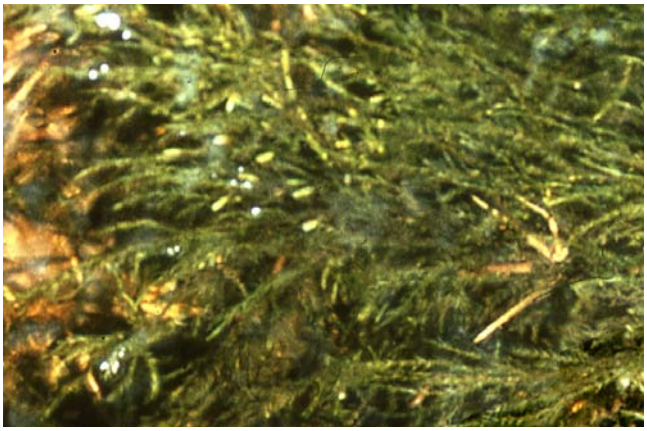

Figure 19. ***Fontinalis novae-angliae*** with capsules. Photo by Janice Glime.

Figure 20. ***Fontinalis dalecarlica*** with capsules. Photo by Janice Glime.

Figure 21. ***Fontinalis antipyretica***. Photo courtesy of Betsy St. Pierre.

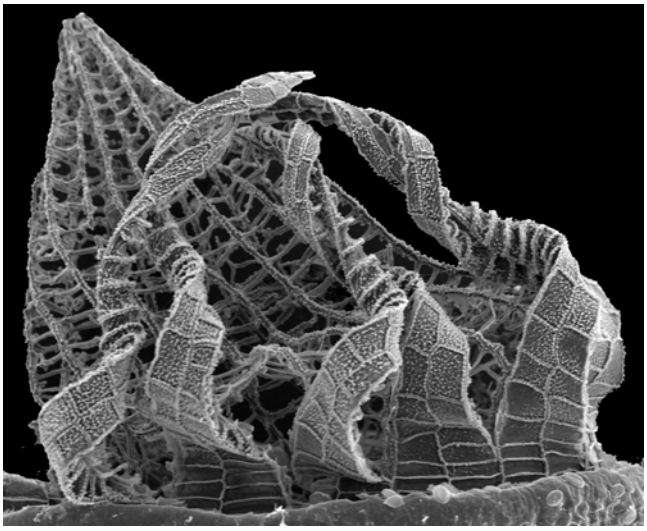

Figure 22. ***Fontinalis*** sp. peristome (SEM) showing the contorted teeth as they dry. Photo by Misha Ignatov, with permission.

Buxbaumia aphylla (Figure 23) seems to disperse its spores more commonly by having the capsule split across the broad, flat upper surface. The capsule wall peels back, exposing the spores (Figure 23). In my observations, this appears to be the typical case – I have not found capsules with intact walls and exposed teeth, the condition one would expect for dispersal through the capsule opening. In fact, my early observations led me to think these capsules were being eaten, but careful periodic observations by my graduate student, Chiang-Liang Liao, proved me wrong. Nevertheless, once the spores are exposed, it appears some insects may indeed feed on them and potentially disperse them. Müller (2012) found that adult fungus gnats (Mycetophilidae; Figure 24) in Germany feed on these spores (Figure 24-Figure 25) and thus might carry spores on their bodies, consequently dispersing them.

Figure 23. ***Buxbaumia aphylla*** showing the peeled back capsule wall that exposes the spores. The lower capsule has lost its operculum and the teeth are showing. Photo by Janice Glime.

Figure 24. ***Buxbaumia aphylla*** with fungus gnats eating spores from the few remaining capsules. Photo by Jörg Müller, with permission.

Figure 25. ***Buxbaumia aphylla*** capsules partially eaten by fungus gnats. Photo by Jörg Müller, with permission.

It may surprise the novice to find that in the fly-dispersed family Splachnaceae exist non-fly-dispersed species that require capsule decay for release of spores from the capsules. In these species, there are no teeth and the capsule does not dehisce. Among these are ***Voitia nivalis*** (see Figure 26) (Goffinet & Shaw 2002) and ***Tayloria callophylla*** on soil (Figure 27); others are epiphytic except for two additional coprophilous but **cleistocarpous** (capsule not opening) species.

Figure 26. ***Voitia hyperborea*** in Svalbard, showing cleistocarpous capsules. Photo by Michael Lüth, with permission.

Figure 27. ***Tayloria callophylla*** with capsules, from New Zealand. This is a species that occurs on soil and lacks the expanded hypophysis typical of ***Splachnum***. Photo by Zen Iwatsuki, with permission.

Carrión *et al*. (1995) cite xerophytic ***Phascum*** spp. (Figure 28), ***Pterygoneurum*** spp. (Figure 29), and ***Acaulon*** (Figure 30) as sharing cleistocarpous capsules, large spore size, and highly sculptured spores. But interesting anomalies exist. ***Pterygoneurum sampaianum*** (Figure 31) has two spore sizes and spore wall thicknesses. Carrión *et al*. suggest this permits most germinations to occur in suitable habitats of parents while allowing for at least some longer transport to new locations. Vitt (1981) surmised that cleistocarpy was important in ephemeral habitats, where large spores have a better chance of surviving until the conditions become favorable again. Having two types of spores would be advantageous in these conditions.

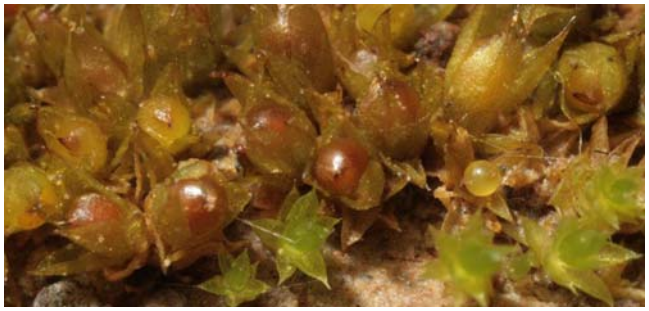

Figure 28. ***Tortula acaulon*** (=***Phascum cuspidatum***) with cleistocarpous capsules. Photo by Jan-Peter Frahm, with permission.

Figure 29. ***Pterygoneurum ovatum*** with ovate capsules. Photo by Kristian Peters, with permission.

Figure 30. ***Acaulon triquetrum*** with cleistocarpous capsules. Photo by Michael Lüth, with permission.

Figure 31. ***Pterygoneurum sampaianum*** in sand, a species with two spore sizes. Photo by Jan-Peter Frahm, with permission.

Surely through such a long period of evolution some of these cleistocarpous capsules must have evolved invertebrate partners that help in the destruction of the capsule wall. Or is it bacteria, or fungi, that do the deed? But certainly some open as a result of torque resulting from drying.

Animal Dispersal

Volk (1984) considered animals to be the most important means of dispersal for the **Marchantiales** in Namibia, suggesting that dispersal was facilitated by the spore ornamentation.

When we think of animal dispersal, we think of "velcro" plants that attach their propagules by small hooks to the fur of their host, or we think of seeds passing through the digestive tract unharmed while the host benefits from the surrounding fruit. But are bryophytes too small to utilize such large animal carriers? Are capsules good substitutes for fruits? We must think on a small scale, and the obvious disperser seems to be insects, those creatures upon which the pollen grain must so often depend. But most people know only about the ability of the **Splachnaceae** to hitch a ride on an unsuspecting insect, the fly, to achieve the dispersal of their spores. It appears we have been missing something.

Earthworms

As earthworms pass soil particles through the gut, they also transport bryophyte diaspores. Van Tooren and During (1988) found that spores were more successful at germination than vegetative diaspores when taken from earthworm castings (Figure 32). Interestingly, During (1986) found that spores from more than 1 cm down were

more likely to germinate than those in the first centimeter. He suggested a higher mortality rate among those in the first centimeter, or that most of the spores were washed down to deeper layers. It is likely that a spore in that first cm would get enough water and light to effect germination, but that they might not remain wet enough, or have enough light, to survive after germination; they might also get water frequently, activating respiration, but having insufficient light to germinate, thus losing considerable energy each time they get wet. Nevertheless, it is also a good hypothesis that many got washed down to lower layers.

Figure 32. Earthworm castings, a potential means of bringing bryophyte diaspores to the surface. Photo by Muhammad Mahdi, through Creative Commons.

Gange (1993), examining primarily fungal spores, found that earthworm castings had higher concentrations of spores than did the surrounding soil. If they likewise concentrate bryophyte spores, this could be an effective dispersal mechanism, perhaps placing diaspores into the diaspore bank, or removing the diaspores from the diaspore bank, despite the high mortality rate seen by Van Tooren and During (1988). A high mortality is not 100%, so those spores that do survive might be effective in later establishment.

Insects and Spiders

It is likely that arthropods such as insects and spiders have a greater role in bryophyte spore dispersal than we had imagined. Such characteristics as hairs on the arthropod or sticky spores facilitate such dispersal.

Ignatov and Ignatova (2001) report that small spiders, mites, and beetles that walk among the cave moss (***Schistostega pennata***) (Figure 87) plants become "more or less dirty" with spores. Smooth-bodied insects seem to be poor carriers, but hairy arthropods such as spiders, especially ***Trochosa*** spp. (Figure 33), and harvestmen (**Opiliones**) are more likely to carry the sticky spores.

Schuster (1966) reports observing lathridiid beetles feeding on spores of the leafy liverwort ***Lophozia porphyroleuca***, but alas, that was in a herbarium. In fact, one of the bits of "evidence" often cited to say that bryophytes are inedible is the lack of dermestid beetles found in bryophyte herbaria, whereas seed plants must be stored with mothballs if we don't want them to disappear into the guts of these beetles. But this one observation of a lathridiid beetle eating liverwort spores does not prove that they ever disperse them in nature, or for that matter, even eat them in nature. On the other hand, this family of beetles is known to eat fungal spores, digest the exine, and disperse them in viable condition from the other end of the gut. So maybe...

Figure 33. ***Trochosa spinipalpis***, a hairy spider that might contribute to dispersal of sticky spores. Photo by Jørgen Lissner, with permission.

Ants

A somewhat more believable story, but one Schuster (1966) considers least credible, is that Szepesfalvy considers ants to disperse spores of the liverwort ***Athalamia hyalina*** (Figure 34) because ants use spores (Figure 35) as food (Loria & Herrnstadt 1980) and these spores are often found injured. Based on this evidence, it is likely that some are also dispersed unharmed.

Figure 34. ***Athalamia hyalina***, a liverwort that serves as food for ants. Photo by Adolf Ceska, with permission.

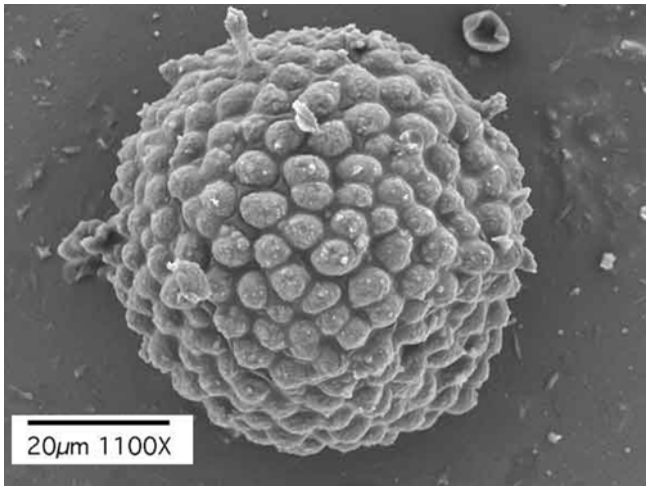

Figure 35. ***Athalamia hyalina*** distal spore wall SEM. Photo by William T. Doyle, with permission.

Rudolphi (2009) considered that the ant ***Lasius platythorax*** might be a passive dispersal agent of the asexual propagules of the moss ***Aulacomnium androgynum***. Both the moss and the ants occur on dead wood in Swedish forests. Experiments showed that 33% of the ants has gemmae adhering to them within less than two minutes of exposure to the mosses. Half of these gemmae continued to adhere to the ants for approximately 4 hours, indicating that the ants could be effective dispersal agents.

Figure 36. ***Lasius platythorax***, dispersal vector for gemmae of ***Aulacomnium androgynum***. Photo by April Nobile, <ww.antweb.org>, through Creative Commons.

Figure 37. ***Aulacomnium androgynum*** showing clusters of gemmae. Photo by Des Callaghan, with permission.

Aquatic Insects

Even aquatic insects may contribute to dispersal. Revill *et al.* (1967) cultured the flora and fauna occupying the surfaces of four aquatic Diptera [***Tipula triplex*** (see Figure 38), ***Bittacomorpha clavipes*** (Figure 39), ***Chaoborus punctipennis*** (see Figure 40), ***Chironomus*** sp. (as *Tendipes*; Figure 41)]. Using 51 cultures from washings, they found algae, protozoa, Cyanobacteria, and moss protonemata. ***Bittacomorpha clavipes*** carried significantly more of these organisms than the other three species.

Figure 38. ***Tipula abdominalis*** larva. Photo through Creative Commons.

Figure 39. ***Bittacomorpha clavipes*** adult. Photo from William Vann at Edupics, free for educational use.

Figure 40. ***Chaoborus flavicans*** larva at water surface. Photo by Malcolm Storey (DiscoverLife), through Creative Commons.

Figure 41. ***Chironomus*** larva. Photo by Gerard Visser <www.microcosmos.nl>, with permission.

Sticky Spores

Ignatov and Ignatova (2001) found that spores of ***Schistostega pennata*** (Figure 42-Figure 43) were covered with a sticky substance, much like spores in the **Splachnaceae** (Figure 44-Figure 47). This substance causes many spores to stick together and prevents effective transport by wind. On the contrary, the spores are better adapted to transport by arthropods and other animals to which they adhere. Although Gaisberg and Finckh (1925) reported their inability to be transported by wind, commenting that they are glued together and are dispersed through animals, it appears that most bryologists have paid little attention to the sticky nature of the spores or their mode of transport until the publication of Ignatov and Ignatova in 2001.

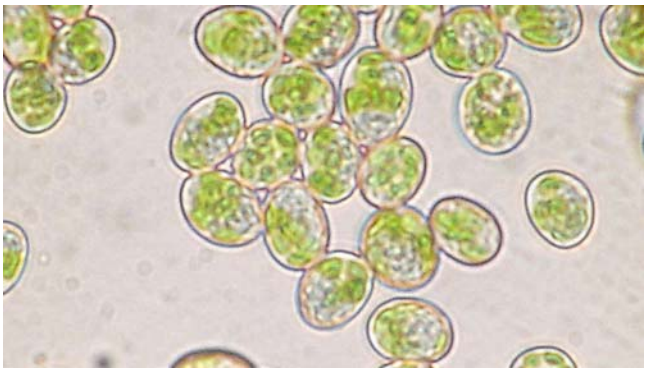

Figure 42. Elliptical spores of ***Schistostega pennata*** demonstrating tendency to stick together. Photo by Misha Ignatov, with permission.

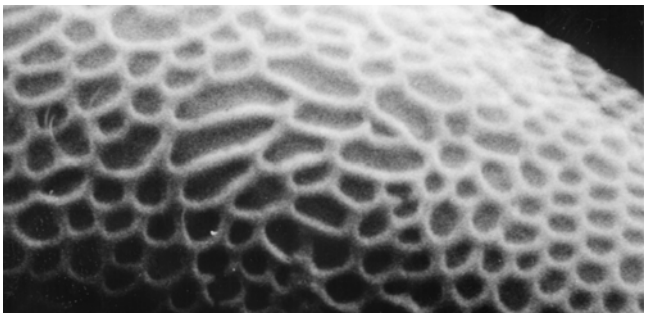

Figure 43. SEM image of spore surface of ***Schistostega pennata*** showing sticky perine. Photo by Misha Ignatov, with permission.

The ***Schistostega pennata*** sporophyte (Figure 87) shares another unique character with Splachnaceae (cf. Koponen 1990); its seta continues growth after the capsule has opened. But it also shares with liverworts the habit of producing its capsule before the seta elongates. In fact, it may even lose its operculum before elongation begins. The seta itself is unique, having long-rectangular, thin-walled cells with round chloroplasts scattered in such a way that the seta appears to have be fluorescent.

Using sticky tape to trap insects near ***Schistostega pennata***, Ignatov and Ignatova (2001) found spores, probably of ***S. pennata***, adhering to adult members of the fly family **Dolichopodidae**. They also found that some ants (***Formica rufa***) and beetles (***Geotrupes stercorarius***; Figure 91) climbed among the ***S. pennata*** and that the beetles carried spores of this species.

Even the elliptical spore shape is unusual, characterizing both ***Schistostega*** (Figure 43) and the **Splachnaceae**. This shape increases the surface area relative to volume, making attachment easier. Demidova and Filin (1994) have suggested that the light green color of the bulk of spores contrast to the deeply colored ones near the top of the capsule in this species and **Splachnaceae**. They suggest that these light-colored spores would also help attract insects. The autoicous sexual condition (but with separate male and female plants originating from the same protonema and thus from one spore) insures that both sexes will be available (Ignatov & Ignatova 2001). [Note that many bryologists consider this a dioicous condition because the male and female shoots are different; whichever interpretation or term is used, this presents a special case.]

Muscidae and Dung Mosses

The same nomenclatural problem of separate sexes arising from one protonema exists for ***Splachnum rubrum*** (Figure 44) and ***S. luteum*** (Figure 45). The family **Splachnaceae**, discussed also in the chapter on nutrients and Terrestrial Diptera, is the only other group of bryophytes considered to be specially adapted for animal dispersal. The oldest report seems to be that of Bryhn (1897), reporting that flies visited ***Splachnum rubrum*** (Figure 44) and carried the spores to fresh dung. Wettstein (1921) expanded on this observation, verifying dispersal by flies in additional species in the family. Since then, A Koponen, T. Koponen, Cameron, and Marino, among others, have studied this fascinating family extensively, demonstrating not only that flies carry the spores, but determining the attractants.

Among the 73 species in this family, approximately half are **entomophilous**, being dispersed by flies (Diptera) (Erlanson 1930; Koponen & Koponen 1978; Goffinet *et al*. 2004; Marino *et al*. 2009). These same species are **coprophilous**, growing on feces or carrion. Their capsules are often brightly colored and are known to attract flies through their scent, which typically mimics that of decaying organic matter. The relationship between the fly and the moss is typically species-specific, with the capsules producing a unique odor as its attractant. Furthermore, it is the sporophytes that produce the odors (Erlanson 1930; Pyysalo *et al*. 1978, 1983; Marino *et al*. 2009), with the gametophytes being nearly odorless. Interestingly, there was an inverse relationship between the size of the **hypophysis** and the strength of the odor (Marino *et al*. 2009), but perhaps this is an energy tradeoff.

In this family, the peculiar odor attracts the flies that subsequently walk about on the capsules and the spreading **hypophysis** (Figure 1), getting sticky spores (Figure 46) on their bodies, as in ***Schistostega***. The flies are usually attracted to both the dung substrate and the odor of the moss capsules. After investigating the capsules, the flies then travel to other dung, attracted to the odor of the wet dung, and deposit some of the spores as they wander about on the dung.

So why should such an elegant moss choose to live on something as unpleasant to humans as dung, and nowhere else? There seems to be no simple answer, so let's examine the facts. This parasol, modified in various ways among

the species, is sterile tissue of the sporophyte. Perched atop the umbrella, like the knob to which the spokes of a wheel would be attached, is the capsule, housing the spores. The teeth differ in structure from those of most mosses (Koponen 1978, 1982) and are reflexed at maturity, exposing an open tiny canister of spores (Figure 46).

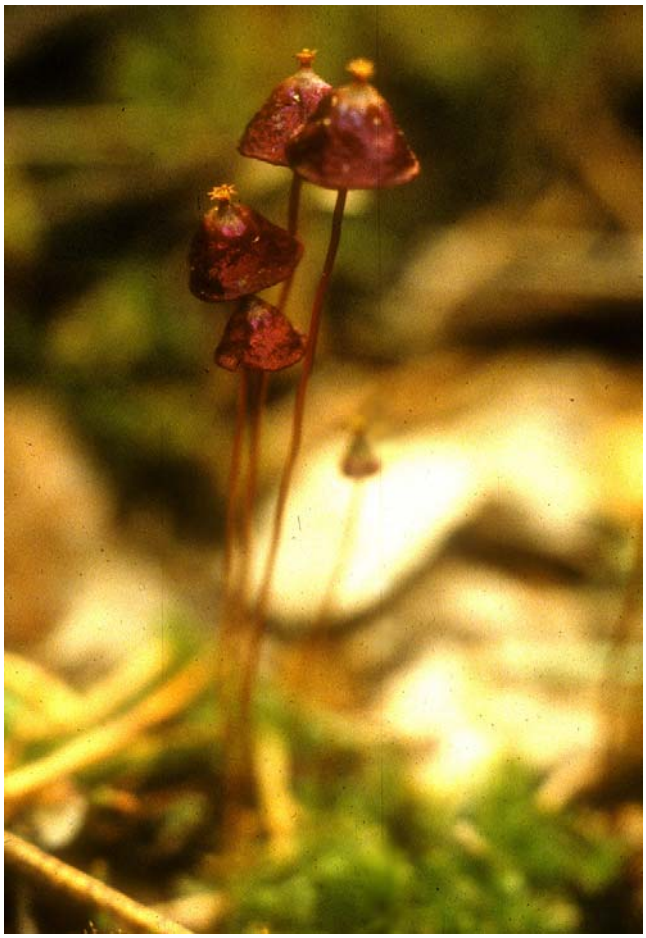

Figure 44. Capsules of ***Splachnum rubrum***, showing the broadly expanded, umbrella-like hypophysis under the capsule. Flies are attracted to the iridescent red color and the odor, with the hypophysis providing a landing platform. Photo by Janice Glime.

Figure 45. ***Splachnum luteum*** with one of its fly dispersers sitting on the hypophysis. Photo from Biopix, through Creative Commons.

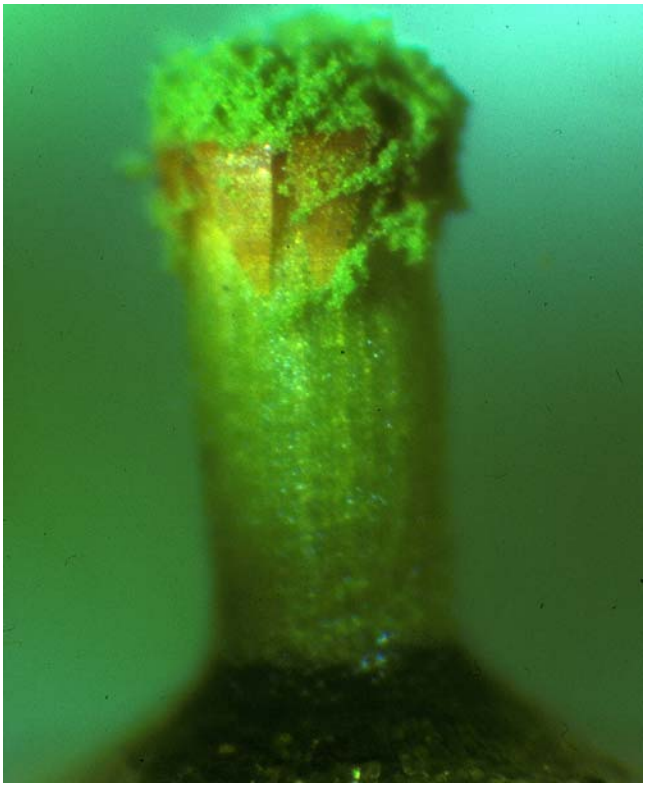

Figure 46. Capsule of ***Splachnum ampullaceum*** showing sticky spores with part of expanded **hypophysis** at base. Photo by Janice Glime.

This greatly expanded sterile tissue is the **hypophysis**, concealing a spongy tissue similar to a maple tree's mesophyll. The hypophysis itself is generally brightly colored in ***Splachnum***, although somewhat more ordinary in other genera, and provides a landing platform for flies. In ***Splachnum ampullaceum*** (Figure 47) it is yellow to deep pink, and the plants are so crowded that if the colors don't attract your attention, the sheer numbers will. This of course also amplifies the odor. In ***Splachnum rubrum*** (Figure 44), the hypophysis is an iridescent purple-red, and I have to wonder if it reflects UV light, visible to some Diptera (Bishop 1974; Gerry *et al*. 2009), but not to us.

By this time, the dung is old and dry, emitting no more odor than the soil beneath, so it is not likely to attract would-be dispersers. However, since the moss has a "perfume" of its own (Erlanson 1930), emitting the unpleasantness of rotting food, sour or musty, from its hypophysis, it attracts the flies. Although these odors are generally faint to our insensitive noses, to a fly they are a virtual invitation. Steere (1958) describes some of the odors. ***Tetraplodon*** (Figure 51) smells of a strong acetic ester, ***Splachnum sphaericum*** (Figure 48) of lactic acid, and ***S. luteum*** (Figure 45) of a butyl compound. These chemicals (Table 2) include volatile octane derivatives and organic acids such as acetic, propionic, and butyric acids that are concentrated in the hypophysis (Koponen 1990).

When the capsule is moist, the columella, with a swollen end, serves as a plug after the operculum is shed. But on a dry day, the capsule contracts and the columella extrudes from the capsule, carrying upward with it clumps of spores exposed to the world. Instead of travelling by wind as individuals, typical of most other mosses, the spores of this moss clump together like the pollen of an

orchid, and apparently to the same advantage. They are picked up inadvertently on the hairs of flies (Koponen 1990; Eriksson 1992) exploring the odor and seeking reward. Once leaving the lure of the capsule, the fly, less discerning than a bee, is likely to be attracted to the odor of fresh dung, and hence carries the clumps of spores to their new home. But the story does not end there. It seems that the fly can even gain an advantage that insures its greater success. Scatophagids, the most frequent and effective of fly visitors, reputedly have greater copulatory success after visiting these mosses (Cameron & Wyatt 1986) – an aphrodisiac for flies!

Figure 47. ***Splachnum ampullaceum*** in southern Europe, showing the high density of sporophytes. Photo by Michael Lüth, with permission.

Figure 48. ***Splachnum sphaericum*** capsules, exhibiting a density that intensifies the lactic acid odor. Photo through Creative Commons.

Diversification of Spore Dispersal Strategy

The fly assemblages differ among individuals and among clumps of the **Splachnaceae** species. Koponen and Koponen (1978) experimented with attraction to **Splachnaceae** in Finland and demonstrated that different combinations of ***Poliaetes lardarius*** (Figure 49) and other dung flies were attracted to sticky traps baited with hidden sporophytes of ***Splachnum ampullaceum*** (Figure 47), ***S. vasculosum*** (Figure 50), and ***Tetraplodon mnioides*** (Figure 51). Marino (1991a) studied **sympatric** (having overlapping distributions) moss assemblages in central Alberta, Canada. Each moss species attracted 10-17 spore-carrying fly species, but visiting fly species assemblages differed by 77-92% among **Splachnaceae** species (Table 1). Furthermore, the Diptera species captured on the dung were less diverse than those captured from the capsules of the mosses (Marino 1988; 1991b). Marino (1991a) concluded that species-specific recruitment of fly guilds appears to result from differences in attraction to sporophytes through distinct odors created by the moss (especially the capsules), visual cues, or combinations of these.

Figure 49. ***Poliaetes lardarius*** side view, a dung fly attracted to ***Splachnum ampullaceum***. Photo by Richard Bartz, through Wikipedia Commons.

Figure 50. ***Splachnum vasculosum*** capsules and male splash platforms. Photo by Dick Haaksma, with permission.

Table 1. Mean (± 1 S.D.) number of spores (x 10^3) carried by fly species trapped on 4 species of mosses in a trapping experiment at Ft. Assiniboine, Alberta. The number of flies carrying spores is shown in parentheses. Fly species in which only a single individual carried spores are not shown (Marino 1991b).

	Moss species			
Fly Species	*Tetraplodon angustatus*	*Tetraplodon mnioides*	*Splachnum ampullaceum*	*Splachnum luteum*
Eudasyphora cyanocolor Zett.	74±100 (13)	29±17 (10)		24±30 (2)
Helina cothurnata Rondani	52±39 (11)			
Phormia terrae-novae R.D.	16±5.3 (2)	20±20 (9)		
Scatophaga furcata Say	26±27 (6)		32±22 (6)	16±24 (9)
Calliphora vomitoria L.		46±50 (11)	29±12 (3)	16±13 (4)
Pegoplata patellans Pand.			23±19 (26)	14±14 (18)
Phormia regina Meigen		42±50 (4)		
Ravinia sp. 1		6.2±1.8 (6)		12±9.1 (16)
Sepsis spp.	5.8±3.8 (3)			
Cynomyopsis cadaverina L.		30±27 (7)		
Hydrotae meteorica L.		17±7.7 (7)		
Muscina assimilis Fallen		20±8.2 (4)		
Lucilia sp. 1		23±13 (4)		
Fannia spathiophora Mall.		24±35 (3)		
Pegohylomyia sp. 1		14±12 (2)		
Mydaea sp. 1			25±23 (5)	
Scatophaga suilla Fab.			29±22 (5)	
Hebecnema nigricolor Fallen			40±48 (5)	
Hydrotae militarus L.			45±65 (3)	
Phaonia curvipes L.			15±14 (2)	
Polietes orichalceoides Huck.			69±19 (2)	
Myospila meditabunda Fab.				3.5±2.2 (5)
Pegoplata nigriscutellata Stein				6.2±1.8 (2)
Hydrotae scambus Zett.				3.7±1.8 (2)
Hylomyza partita Meigen				6.2±1.8 (2)
Total	(37)	(63)	(59)	(60)

Table 2. Volatiles detected in the hypophysis and urn of five members of **Splachnaceae**. From Koponen *et al.* 1990. Indications for ***Aplodon wormskioldii*** based on Pyysalo *et al.* 1983.

	Splachnum luteum	***Splachnum vasculosum***	***Splachnum sphaericum***	***Aplodon wormskioldii***	***Splachnum rubrum***
Octanal	-	-	x	-	x
3-Octanone	x	-	x	-	-
3-Octanol	-	x	x	x	-
Trans-2-octenal	-	x	x	x	-
1-Octen-3-ol	x	x	x	x	x
1-Octenol	x	x	x	x	-
2-Octen-1-ol	-	x	x	-	-
2-Octenol	-	-	x	-	-
2-Ethyl-hexanal	-	-	x	-	-
Phenylacetylene	-	-	x	x	-
Benzyl alcohol	-	-	x	-	-
Phenole	x	-	x	-	x
Cyclohexycarboxylic acid	-	x	-	-	-
Phenethyl alcohol (2-phenyl ethanol)	-	-	-	-	x
Phenylacetic acid	-	x	x	x	x
Acetic acid	-	-	x	x	-
Propionic acid	-	-	x	x	-
Butyric acid	-	-	x	x	-
Valeric acid	-	-	x	x	-
Caproic acid	-	-	x	x	-
Benzoic acid	-	-	x	x	-
Phenylacetic acid	-	-	x	x	-
Palmitic acid	-	-	x	x	x

Cameron and Wyatt (1986) studied dispersal for ***Splachnum ampullaceum*** (Figure 47), ***S. rubrum*** (Figure 44), ***S. sphaericum*** (Figure 48), ***S. vasculosum*** (Figure 50), and ***Tetraplodon mnioides*** (Figure 51) and found that the fly family **Scatophagidae** (***Scatophaga***; Figure 52) was both the most frequent and most effective visitor to the moss colonies. Other visitors included ***Delia*** (**Anthomyiidae**), ***Myospila*** (**Muscidae**; Figure 53), and ***Eudasyphora*** (as *Pyrellia*; **Muscidae**; Figure 54). They further demonstrated that wind is not an effective dispersal agent for these species.

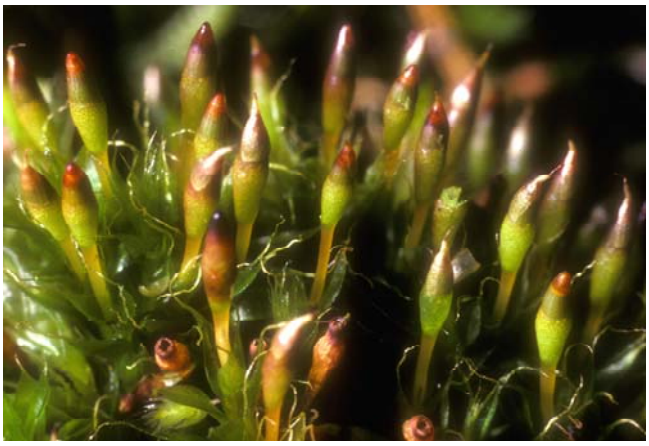

Figure 51. ***Tetraplodon mnioides*** capsules. Photo by Zen Iwatsuki, with permission.

Figure 52. ***Scatophaga stercoraria***, member of a genus that visits **Splachnaceae** capsules. Photo by Luc Viatour <www.Lucnix.be>, through Creative Commons.

Figure 53. ***Myospila meditabunda***, member of a genus that visits **Splachnaceae**. Photo by Valter Jacinto, through Creative Commons.

Troilo and Cameron (1981) consider the transport of spores in the ***Splachnum ampullaceum*** (Figure 47) by flies [***Eudasyphora*** (as *Pyrellia*) ***cyanicolor*** (Figure 54)] to be passive. This fly species oviposits on carrion, but it will use dung when carrion is not available, whereas ***S. ampullaceum*** grows almost exclusively on dung. The moss capsules attract them, and if they are chased away, they quickly return. The capsule is adapted by its bright colors, expanded hypophysis that serves both to attract and as a landing platform, a dung-like odor, teeth that extend outward, and a shrinking capsule that forces the adhesive spores outward. Cameron and Troilo (1982) added to this story by documenting that landing by ***Eudasyphora cyanicolor*** flies demonstrated a 20-fold preference for yellow-colored disks over blue or red disks placed among sporophytes of ***S. ampullaceum*** in Michigan, USA, suggesting the spore dispersal may not be passive after all. In fact, they never visited the red disks. This is an interesting observation and begs further investigation. Flies are typically attracted to red (don't wear red in mosquito or blackfly season!). And ***S. ampullaceum*** typically has a mix of yellow and pinkish red capsules (Figure 1). On the other hand, pink flowers do not usually attract flies.

The most activity of ***Eudasyphora*** (**Muscidae**; Figure 54) on the capsules was on warm days when the odors were strongest (Troilo & Cameron 1981). The moss is a successful odor mimic, as demonstrated by fly visits that equalled those to carrion and exceeded those to a protein source or fly medium (Figure 55). But once there, the visit to the moss capsule was significantly shorter than visits to carrion or protein substitute. Moreover, the flies never exhibited feeding behavior on the capsules, only sampling behavior. Troilo and Cameron consider this to be a **commensal** relationship in which the moss benefits from dispersal but the flies are neither benefitted nor harmed. One could argue that the moss is being a parasite by taking energy from the flies and using it for dispersal while providing nothing in return, but others have argued that the flies may get the benefit of increased mating opportunity.

Figure 54. ***Eudasyphora cyanicolor***, a carrion fly. Photo by Tristram Brelstaff, through Creative Commons.

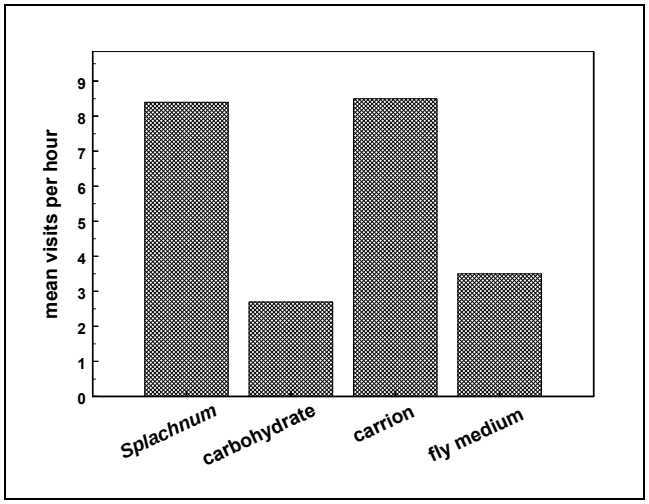

Figure 55. Mean number of visits by the carrion fly ***Eudasyphora cyanicolor*** (Figure 54) on ***Splachnum ampullaceum*** (Figure 47) and three nutritional substrates. Note that there was no evidence of feeding on ***S. ampullaceum***. Graph based on table from Troilo & Cameron 1981.

Many of the fly species associated with the **Splachnaceae** studied by Marino (1991b) are anthomyiids. By mimicking the flower and odor cues typically used by the adult **Anthomyiidae**, a family with seed predators and pollinators, the mosses have achieved what appears to be a very effective means of spore dispersal.

This very targetted means of dispersal may be a tradeoff between energy needed for attraction and that needed for spore production (Marino 1991a). These species have fewer spores **and** smaller spores than most mosses. This high energy requirement may account for the evolution from a specialist such as these entomophilous species to the generalist strategy of the coprophilous species such as ***Tetraplodon paradoxus*** (Figure 56), and the two ***Voitia*** species (**Voitioideae**; Figure 57) that lack sporangial dehiscence. In ***Tayloria*** (Figure 58), both anemophilous and entomophilous species exist.

Figure 56. ***Tetraplodon paradoxus***, a species with indehiscent capsules. Photo by Michael Lüth, with permission.

Figure 57. ***Voitia nivalis*** with capsules. Photo by Michael Lüth, with permission.

It appears that the dung habitat may provide another significant role. One advantage to this dispersal type is that it ensures that both male and female spores will arrive at the same site. In populations of ***Tayloria tenuis*** (Figure 58) on cattle droppings in the Eastern Pyrenees, the protonemata are at first the only conspicuous stage (Lloret 1991). The plants are clustered and despite high mortality, the entire dung substrate is soon covered with protonemata. Within 1-2 years the leafy plants develop and ultimately produce capsules. These capsules are often numerous, as seen in ***Splachnum ampullaceum*** (Figure 47). This is in part due to the female:male ratio of 2:1, at least in the ***Splachnum*** species [***S. ampullaceum*** (Figure 47), ***S. sphaericum*** (Figure 48), ***S. rubrum*** (Figure 44)] of Isle Royale, Michigan, USA (Cameron & Wyatt 1990). But in experiments, environmental conditions can alter this ratio, with low light, *p*H, and nutrients favoring the production of males.

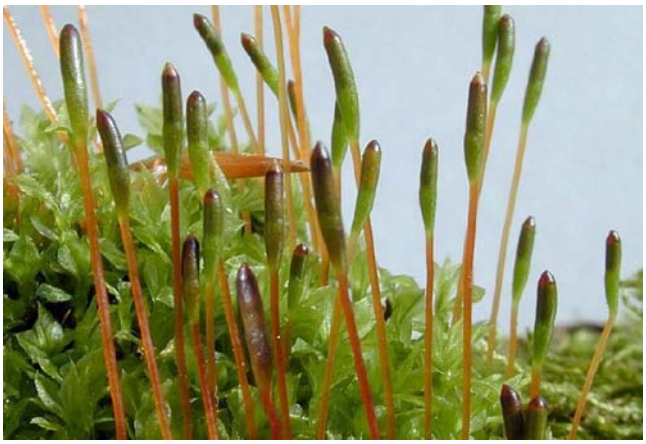

Figure 58. ***Tayloria tenuis*** with capsules, a species that grows on dung. Photo by Michael Lüth, with permission.

In ***Splachnum ampullaceum*** (Figure 47), males and females can arise from the same protonema, ruling out any bias in dispersal of spores. For this high degree of fertilization success, dispersal of the sperm to the female benefits from the density of the plants. Cameron and Wyatt (1990) found that the average sperm dispersal distance is

less than 5 mm. This proliferation of sporophytes is reminiscent of the Asteraceae, acting as a single unit through the clumping of so many capsules. Furthermore, the early period of establishment has served to eliminate weak genotypes among the protonemata, although there is no guarantee that these same weaknesses would occur among the leafy plants.

As the capsules mature, that moist and smelly dung that once attracted the flies becomes dry and looks more like a cardboard Frisbee, or in the case of moose dung, like a clump of well-done toasted marshmallows. Nevertheless, once spores are sent upon their way, the remaining plants are soon covered by larger pleurocarpous mosses that are typical of the forest soil. This is an ephemeral habitat for the **Splachnaceae**.

All of this attraction is costly, requiring energy to produce the hypophysis and make volatile attractants. To maintain this, the mosses are able to access the higher concentrations of N, P, and Ca that occurs in dung (Webster 1987). Meanwhile, most other mosses typically die in areas with such high nitrogen concentrations resulting from manuring (Geissler 1982). There have also been suggestions that the growth of the protonemata may be promoted by substances such as Gibberellic Acid produced by accompanying fungi (Von Maltzahn & MacQuarrie 1958; Vaarama & Tarén 1959).

Cameron and Wyatt (1986) have suggested that the **Splachnaceae** requirements for dung may actually be a requirement for their fly dispersers, and the flies travel from one dung heap to another. There seems to be an interesting correlation between means of dispersal and substrate that supports this hypothesis. As noted earlier, all of the **entomochorous** (*i.e.* requiring insect dispersal) species are also **coprophilous** (living on dung or corpses); the **anemochorous** (wind-dispersed) species are **humicolous** or epiphytic (Goffinet & Shaw 2002). In the subfamily **Voitioideae**, three taxa are coprophilous but cleistocarpous (capsule not opening), lacking a peristome and dispersing spores only after the sporangial wall disintegrates.

Flies are not restricted to landing on dung, to any particular moss species, or to any particular habitat (Marino 1986), so this diverse behavior would seem to limit successful dispersal. Nevertheless, spore success is typically very low among mosses, so even this hit-or-miss mechanism may be better than wind dispersal. And certainly it must be for these sticky spores.

In summary, Koponen (1990) considers three categories of adaptations of bryophytes for entomophily in the **Splachnaceae**:

- adaptations to a substrate of animal origin
- morphological adaptations
- chemical adaptations

In support of this, Koponen cites ***Splachnum*** (Figure 50) and the entomophilous species of ***Tayloria*** (Figure 62-Figure 63) as being restricted to the dung of herbivorous mammals. ***Tetraplodon*** (Figure 59-Figure 60) grows on skeletal remains, antlers, stomach pellets of predatory birds, or on dung. The entomophilous ***Aplodon wormskioldii*** (Figure 61) grows on corpses, on caribou (reindeer) dung, bones and antlers, on owl pellets, or on enriched gravel.

Figure 59. ***Tetraplodon angustatus*** with capsules on caribou antler at Jasper, Canada. Photo by Janice Glime.

Those of us in the Northern Hemisphere are familiar with this fascinating family of mosses largely because of their ability to attract flies, but in the Southern Hemisphere, such attraction does not exist, or does it?! Mighell (2011) investigated ***Tayloria mirabilis*** (Figure 62-Figure 63), a South American endemic, because it had been suspected of having fly dispersal. They trapped 218 flies over the plants on dung and found that 63 of them had spores of ***T. mirabilis***. The flies comprised seven species from Muscidae and Calliphoridae. Furthermore, germination of the transported spores were 46.7% successful; identity of the spores was verified by DNA analysis. This example becomes more interesting when we realize that the plants (and flies) are associated with more than one kind of forest dung and that all the current large forest mammals there are exotic! Rapid evolution or pre-adaptation?

Figure 60. ***Tetraplodon angustatus*** with capsules on caribou skull at Jasper, Canada. Photo by Janice Glime.

Figure 61. ***Aplodon wormskioldii*** with capsules in Svalbard. Photo by Michael Lüth, with permission.

Figure 62. ***Tayloria mirabilis*** capsules, a species that attracts flies in the Southern Hemisphere. Photo by Jan-Peter Frahm, with permission.

Figure 63. ***Tayloria mirabilis*** capsules and fly near Cape Horn, Chile. Note the spores on the front leg and around the eye. Photo by Adam Wilson, through NYBG public domain.

In the same year, Jofré *et al*. (2011) reported a second example of fly-attracting Splachnaceae in the Southern Hemisphere. This time, it was ***Tayloria dubyi*** (Figure 64) growing on bird dung in the subAntarctic region of Cape Horn, Chile. The bird dung appears to be exclusively that of the Snow Goose ***Chloephaga picta*** (Figure 65). When Jofré Acevedo (2008) germinated the spores in the lab, they grew much better on snow goose dung than on horse or cattle dung. ***Tayloria dubyi*** releases its spores in the same months as the highest activity of Diptera (Jofré *et al*. (2010). Based on these findings, Jofré *et al*. (2011) trapped 64 flies, comprised of ***Palpibracus chilensis*** (**Muscidae**), ***Dasyuromyia*** sp. (**Tachinidae**), and an unidentified member of the **Sarcophagidae,** in traps above the sporophytes, but no flies appeared in traps above nearby ***Sphagnum***, suggesting that ***Tayloria dubyi*** also attracts the flies.

Once we understood that flies were indeed attracted to the capsules of the **Splachnaceae**, not just (if at all) to the odors of the dung, work began to elucidate the attracting compounds. Koponen *et al*. (1990) identified 23 compounds in the hypophysis and urn among five Splachnaceae, demonstrating that the individual species were often unique. Data from the setae are not included here. The only volatile compound in the substratum was benzaldehyde, a compound not found in the capsules or setae.

Figure 64. ***Tayloria dubyi*** capsules, a Southern Hemisphere species of **Splachnaceae** that apparently attracts flies. Photo by Jocelyn Jofré., with permission.

Figure 65. ***Chloephaga picta*** (Snow Goose), potential bryophyte dispersal agents through the gut as well as feet and feathers. Photo by Fabien Dany <www.fabiendany.com>, through Creative Commons.

Molluscs

Could it be that slugs that consume capsules (Figure 66) do indeed carry spores to new locations? But alas, a slug by its very nature is slow, and such dispersal would not move the spores very far from home. Nevertheless, consumption can result in movement of spores to a new location, even if not very far away. But can they live?

Figure 66. Slug preying on capsules of ***Leucolepis acanthoneuron***. Photo from Botany website, UBC, with permission.

Boch *et al*. (2013) tested the possibility that slugs could eat bryophyte spores, and that the spores could subsequently germinate. They fed capsules of four bryophyte species to three slug species. Overall, approximately in half (51.3%) all 117 bryophyte samples fed to slugs, representing four bryophyte species [***Bryum pallescens*** (Figure 67), ***Funaria hygrometrica*** (Figure 110, ***Leptobryum pyriforme*** (Figure 68), ***Pellia endiviifolia*** (Figure 69)], spores did germinate from feces. It is interesting that there was no difference between bryophyte species, but there were large differences among the three slug species (Figure 70). Spores from the feces of the slugs ***Arion lusitanicus*** (Figure 71) and ***A. rufus*** (Figure 72) had 76% and 74% success, respectively. Those from ***Limax cinereoniger*** (Figure 73), on the other hand, were only 12.9% successful. This mechanism would enhance the population size by moving spores away from the parent, but at the same time being more likely than wind dispersal to deposit them in places where they can grow successfully. Türke *et al*. (2013) found that slugs could transport seeds in the gut for 5 m, giving us an estimate of potential bryophyte dispersal distance.

Figure 67. ***Bryum pallescens*** with capsules, a species for which spores can be dispersed by slugs. Photo by David Holyoak, with permission.

Figure 68. ***Leptobryum pyriforme*** with capsules, a species for which spores can be dispersed by slugs. Photo by Michael Lüth, with permission.

Figure 69. ***Pellia endiviifolia*** males with reddish antheridial cavities and females in center1 David Holyoak, with permission.

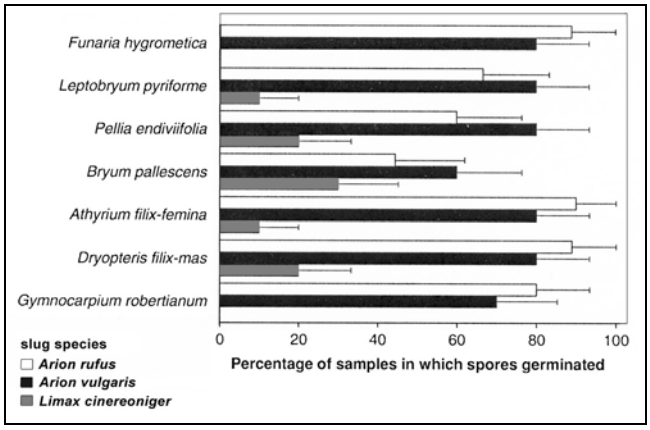

Figure 70. Germination percentages of bryophyte spores from feces of three species of slugs. Redrawn from Boch *et al*. 2013.

Figure 71. ***Arion lusitanicus***, a species than disperse bryophyte spores through its feces. Photo by Håkan Svensson, through Wikimedia Commons.

In an experiment to determine success of spores that travelled through the digestive tract of slugs (***Arion*** spp.; Figure 71), all plates containing eaten spores of ***Mnium hornum*** (Figure 74) and ***Brachythecium rutabulum*** (Figure 75) produced shoots, whereas only 80% of the plates with uneaten mature ***Mnium hornum*** spores and 70% of those with uneaten ***Brachythecium rutabulum*** spores produced shoots (Davidson 1989). Furthermore, the eaten spores showed little infection, suggesting some antibiotic property acquired from the digestive tract. Nitrogen, secreted in mucus and disposed in feces, may have enhanced the success of these spores.

Figure 72. ***Arion rufus***, a species than disperse bryophyte spores through its feces. Photo by Walter Siegmund, through Wikimedia Commons.

Figure 73. ***Limax cinereoniger***, a species in which most bryophyte spores died on the way through the digestive tract. Photo by Teemu Mäki, through Creative Commons.

Figure 74. ***Mnium hornum***, a species whose spores are eaten by slugs in southern Europe. Photo by Michael Lüth, with permission.

Figure 75. ***Brachythecium rutabulum*** with capsules. Spores of this species are eaten by slugs. Photo by David Holyoak, with permission.

Using 11 species of mosses and 1 of liverworts, Boch *et al*. (2014) supported the concept that slugs can increase bryophyte establishment. They demonstrated that through their herbivory, the slugs reduce light competition, permitting a greater diversity of bryophytes to establish. Furthermore, the spores they ingest are able to germinate

after passing through the digestive tract of the slug (**endozoochory**). After 21 days in an experimental setup, bryophyte cover was 2.8 times as high in enclosures with slugs that had previously been fed sporophytes when compared to enclosures with slugs that had not been fed sporophytes or with no slugs.

After 21 days the bryophyte cover was on average 2.8 times higher (3.9% versus 1.4%) and after eight months the bryophyte species richness 2.6 times higher (5.8 versus 2.2) in enclosures containing slugs previously fed with bryophyte sporophytes than in the other treatments. After 8 months, the increased vascular plant cover reduced the bryophyte diversity. Enclosures that had no seed sowing had 1.6 times as many bryophyte species compared to those receiving seeds.

But if we look further, we find that long distance travel by slugs and snails is indeed a possibility. Malone (1965) determined that fresh-water snails were able to attach to the feed of the killdeer (***Charadrius vociferus***) and travel there for sufficient time to accomplish overland dispersal, remaining alive. Adults of the snail ***Lymnaea obrussa*** could survive at least 14 hours. It is likely that other birds, both aquatic and terrestrial, could carry snails as well, providing considerable time for dispersal and making long-distance dispersal possible. And how long might the spores survive in a snail or slug eaten by a bird? Will those spores also be viable?

Fish

The ability of fish to transport bryophytes remains to be demonstrated. My student experimented with rainbow trout, known to strike at almost anything, to see if they would eat mosses in their attempts to remove aquatic insects. The student was unable to get the fish to attack the moving moss or eat it to get at insects. Finally, in desperation, he force fed it ***Fontinalis duriaei*** (Figure 76). Then he waited to collect the feces. The moss did appear in a cylindrical package of feces. It emerged in bright green color and looked healthy. We put it in a jar of stream water from which the moss had been collected, kept it cold, and waited expectantly. Alas, the second day the ***Fontinalis*** was pale and appeared to be dead. No growth ever ensued.

Figure 76. ***Fontinalis duriaei***, a species refused by rainbow trout and that does not survive in feces from force-fed fish. Photo by Michael Lüth, with permission.

Birds

Until recently, birds were barely considered as dispersers of bryophytes. Ducks are dispersers (Proctor 1959), but we have no idea how important they are. Spores of ***Riella*** (Figure 77; Tenge 1959) pass through the digestive tract of Mallards (***Anas platyrhynchos***; Figure 78) and remain viable (Proctor 1961). Assuming a mean residence time similar to that of seeds, which is about 7.5 hours, a migrating Mallard could move spores of this liverwort 20-30 km easily, and at times up to 1,400 km (Mueller & van der Valk 2002). It could, but does it?

Figure 77. ***Riella cossoniana*** showing sporangia (dark spheres) that can be dispersed by ducks. Photo by Jan-Peter Frahm, with permission.

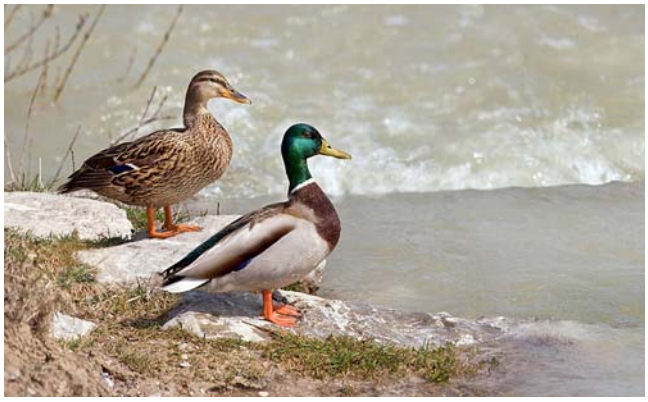

Figure 78. ***Anas platyrhynchos*** (Mallards) female and male, potential dispersal vectors for aquatic bryophyte diaspores. Photo by Richard Bartz, through Wikimedia Commons.

Proctor (1961) suggested that the rarity of ***Riella americana*** may result from very specialized dispersal. Griffin (1961) found a large population of this species in a playa lake in Texas, USA, where its population measured 60 cm in width and approximately 1.7 km long. The production of gemmae may contribute to such large populations (Studhalter 1931). He examined 25 nearby similar lakes within a 25 km radius and could find no trace of the liverwort.

Following these observations, Proctor (1961) experimented with the possibility that this liverwort was dispersed by ducks. He used three Mallard ducks (***Anas platyrhynchos***; Figure 78) that had been used previously for similar experiments with the alga *Chara*. These ducks were provided with approximately 57 liters of the ***Riella americana***, which they readily ate. The plants had abundant sporophytes with what appeared to be mature brown spores. The feces were collected after approximately 1 hour and handled according to treatments in Table 3. The feces contained may spores that had separated from their masses, no intact sporophytes, and thallus fragments that were clearly dead. Feces were collected for three days, and on the third day they were separated by individual duck. It was interesting that one male and one female had numerous spores in their feces, but the second female had none! Germination success ranged from 0 - >30%.

Table 3. Various storage effects on germination of ***Riella americana*** spores collected from Mallard duck feces. Germination follows 60 days of treatment, then 14 days of inoculation at 24°C on sterile tubes of soil and water in light. + = <10% germination; ++ = 10-30% germination; +++ = >30% germination; - = no germination; blank = not enough spores for test. Based on Proctor 1961.

	day 1	**day 2**	**day 3 male**	**day 3 female**
ice (-10°C)	++	+		
water at 1°C	+++	+++	+++	+++
water at 24°C	+++	+++	+	+
water at 37°C	+++	+++	+++	+++
dried, stored at -10°C	-	+	++	++
dried, stored at 24°C	+++	+++		
dried, stored at 37°C	+++	+++		

Proctor (1961) found that the spores of ***Riella americana*** (Figure 79) from feces germinated as well as fresh spores (not eaten). These spores mature at the time ducks and other water birds are migrating through that area of Texas in early autumn, so their transport through water bird guts is quite possible. Proctor (1961) suggests that many spores can be transported in the gut for up to 80 km. Furthermore, as already suggested by Studhalter (1932) and Persson and Imam (1960), external transport of spores and even fragments on feathers, beaks, and feet is a likely possibility. This notion is supported by the presence of spines on the spores (Figure 79) (Studhalter 1933). Furthermore, the spores have sufficient longevity to survive in muds or on birds (3 years for ***R. americana***, 12 years for ***R. capensis***). And it is possible that some remain in tetrads during dispersal, further protecting them from UV light and desiccation. Considering these dispersal potentials, it seems that something else must explain the rarity. Perhaps there is too much herbivory before they can become established? Could timing be important to avoid herbivory during establishment?

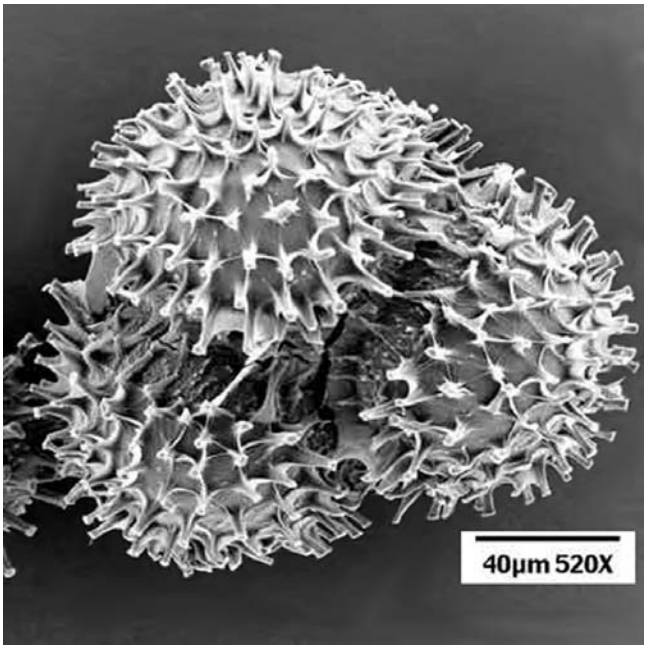

Figure 79. ***Riella americana*** spore tetrad SEM, exhibiting spines that could attach to feathers of ducks. Photo by William T. Doyle, with permission.

Riella is not the only bryophyte to experience dispersal by ducks. Des Callaghan (Bryonet 26 August 2016) reported that his friend had sent him a moss shoot grown from a fragment in a Mallard dropping (***Anas platyrhynchos*** (Figure 78). This turned out to be the moss ***Didymodon insulanus*** (Figure 80).

Recent studies have revealed that other birds may also be dispersers. Using fecal samples from the herbivorous Upland Goose (***Chloephaga picta***; Figure 65) and White-bellied Seedsnipe (***Attagis malouinus***; Figure 81), Behling *et al*. found vegetative diaspores, including various moss fragments. Experiments continue to determine their viability. ***Attagis malouinus*** feeds among the low vegetation, sits among the mosses, and may even spread its wings across the mosses in the tundra, affording numerous opportunities for snagging the local bryophytes.

Figure 80. ***Didymodon insulanus***, a species whose fragments survived the digestive tract of a Mallard. Photo by David T. Holyoak, with permission.

Figure 81. ***Attagis malouinus***,, a species that carries bryophyte propagules among its feathers. Photo by Jacob Wijpkema <jacob.wijpkema@gmail.com> & Tini Dijk <tini.wijpkema@gmail.com>, with permission.

Just imagine how far diaspores might travel by **ectozoochory** (on the outside of an animal) among the bird plumage. We know birds survive airplane travel, so bird travel is not a stretch. And the idea is not so far-fetched when we consider the number of bipolar species of bryophytes and the number of birds that travel those same distances from Arctic to the Antarctic. Lewis *et al*. (2014) developed a method to screen feathers of wild birds that travelled these long distances in their annual migrations. They concluded that the entire flock of migrating birds may leave their northern breeding grounds carrying potentially viable propagules, providing opportunities for dispersal everywhere they land to feed or rest.

Szepesfalvy (1955 in Schuster 1966) found ***Riccia frostii*** (Figure 82) concentrated along goose paths in central Hungary and suggested that the spores of this species were distributed on feet and beaks of these domestic geese. And we cannot, without testing it, eliminate the possibility of distribution of spores in feces (Figure 83), although it would require having the geese eat something that ate the spores or carried them on its surface. Szepesfalvy also suggested that spores and overwintering thallus pieces of ***Riccia bischoffii*** var. ***ciliifera*** (Figure 84) are distributed by pheasants, but both of these suggestions are based on circumstantial evidence and the correlation may be one of habitat rather than dispersal agent. Furthermore, these birds are surely not the only animals to frequent these paths. Szepesfalvy also suggested a relationship between presence of hares and distribution of ***Oxymitra paleacea*** (Figure 85), but this meets the same problem of verification.

Brandon Stone reported to Bryonet (9 April 2003) that he found sporophytes of the moss ***Pyrrhobryum spiniforme*** (Figure 86) in a bird's nest at 1300 m on Moloka'i in Hawai'i. A bird expert told him the bird was most likely not a native bird. Transport of such sporophytes at the right stage could contribute to dispersal over more than the normal range of dispersal from capsules on the ground.

Figure 82. ***Riccia frostii***, a liverwort that can concentrate along goose paths, presumably due to having the geese spread the spores. Photo by Rosemary Taylor, with permission.

Figure 83. Canada Goose (***Branta canadensis***) dung at a wildlife station, Ohio, USA – a potential dispersal mechanism. Photo by Janice Glime.

Figure 84. ***Riccia bischoffii*** var. ***ciliifera***, a species with overwintering fragments that may be dispersed by geese. Photo by Jan-Peter Frahm, with permission.

Several birds frequent upturned roots where ***Schistostega pennata*** (Figure 87) is common in Russia, and there is evidence that these may transmit spores (Ignatov & Ignatova 2001). The tiny Winter Wren (***Troglodytes troglodytes***; Figure 88-Figure 89) visits upturned roots to look for insects and sometimes nests there. Above one nest near a convenient perch, there were protonemata of ***S. pennata***, suggesting they may have arrived as spores on the birds.

Figure 85. ***Oxymitra paleacea***. Photo by EncycloPetey, through Creative Commons.

Figure 86. ***Pyrrhobryum spiniforme*** showing sporophyte that is used in making birds' nests in Hawaii. Photo by Michael Lüth, with permission.

A more convincing case of bird dispersal is that of the cock ***Tetrastes bonasia*** (Hazel Grouse; Figure 90) (Ignatov & Ignatova 2001). These large birds take dust baths near the upturned roots. Feathers collected there did have spores of ***S. pennata*** attached. However, no chloroplasts seemed to be present, so it is unlikely that they were still viable. The birds also help in dispersal of spores by capturing beetles such as ***Geotrupes*** (Figure 91) with adhering spores and distributing their parts to other locations. Mice and frogs also visited tip-up areas, but there was no direct evidence that they transported spores.

Figure 87. Capsule and seta of ***Schistostega pennata***. Note the delicate, white stalk and the sticky spores on the outside of the capsule. Photo with written permission from Misha Ignatov.

Figure 88. ***Troglodytes troglodytes*** (Winter Wren), known to build nests near good locations for ***Schistostega pennata***, possibly transporting spores. Photo by Sonja Kübelbeck, through Wikimedia Commons.

Figure 89. ***Troglodytes troglodytes indigenus*** on a moss-covered tree from Kuwait, a winter wren that might disperse bryophyte spores to a perch above its nest. Photo by Bob McCaffrey, through Creative Commons.

Figure 90. ***Tetrastes bonasia*** (Hazel Grouse) transports bryophyte spores and also eats beetles that carry them, but viability of the spores is unknown. Photo by Kallerna, through Wikimedia Commons.

Figure 91. ***Geotrupes stercorarius*** on moss, a beetle species that can carry spores, then get transported farther when captured by birds. Photo by Thomas Bresson, through Wikimedia Creative Commons.

We have already noted that slugs can carry viable spores in their digestive tracts. Birds eat snails. Could it be that the spores could survive both digestive tracts? Wada *et al*. (2011) addressed this very question. Japanese land snails are preyed upon by birds, including the Japanese White-eye (***Zosterops japonicus***; Figure 92) and the Brown-eared Bulbul (***Hypsipetes amaurotis***; Figure 93). Of the 119 snails (***Tornatellides boeningi***; Figure 94) fed to Japanese White-eyes and 55 snails fed to Brown-eared Bulbuls, 14.3% and 16.4% of the snails, respectively, passed through the gut alive. For us, the logical next question is whether this provides an additional means of dispersal for bryophyte spores, potentially giving them a free ride to greater distances while being protected from the bird's digestive system by the snail. Kawakami *et al*. (1965) suggested that it is.

Figure 92. Japanese White-eye (***Zosterops japonicus***). Photo by Ltshears, through Creative Commons.

Figure 93. Brown-eared Bulbul (***Hypsipetes amaurotis***). Photo by Lip Kee Yap, through Wikimedia Commons.

Figure 94. ***Tornatellides boeningi***, a species that can pass through bird guts and survive. Photo by Shinichiro Wada, through Creative Commons.

Griffin *et al*. (1982) suggested that ***Dendrocryphaea latifolia*** may have reached the high Andes of Colombia by wind or birds, but there is no direct evidence to support this.

As Ken Adams suggested on Bryonet (5 March 2013), birds might occasionally be responsible for long-range bryophyte dispersal. Spores could lodge on or among feathers or feet, especially in mud, protecting them from both desiccation and UV light. Michael Richardson (Bryonet 5 March 2013) suggested that this could occur as short hops (stepping stones), with birds depositing spores at resting or feeding points along the way. When those establish, they provide a new and closer source for dispersal to more distant locations. Richardson suggested that gulls might be good vectors because of their need for fresh-water baths and their puddle-hopping behavior. Terry McIntosh (Bryonet 5 March 2013) suggested that birds may account for some of the wide disjunctions in western North America for species that are restricted to open soil in the grassy edges of saline ponds and depressions. This could explain the distribution of such species as ***Entosthodon rubiginosus*** and ***Tortula nevadensis***.

Fife and de Lange (2009) suggested that shearwaters (*e.g.* ***Puffinus bulleri***, **Procellariidae;** Figure 97) may have been responsible for transporting propagules of the pan-tropical ***Calymperes tenerum*** (Figure 95) to the

Chatham Islands and Kermadecs off the coast of New Zealand. These fantastic birds fly from Alaska to Australia and other parts in the deep Southern Hemisphere, then back to Alaska each year. Buller's Shearwater is endemic to New Zealand and is a regular visitor to the Chathams (Allan Fife, pers. comm. 11 June 2017). It has also been considered to responsible for transporting the fern ***Asplenium pauperequitum*** to the Chathams (Cameron *et al*. 2006).

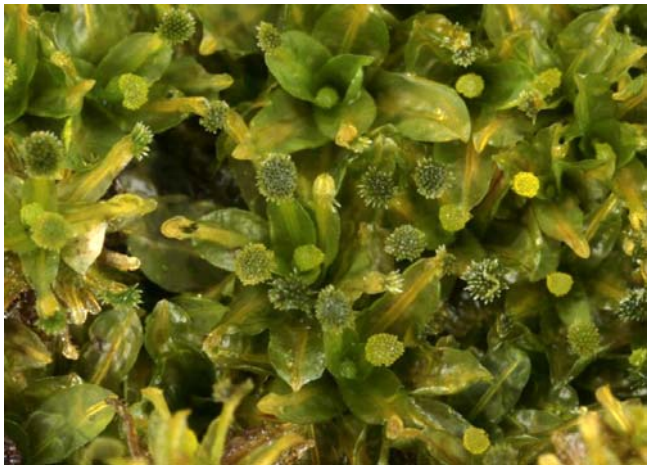

Figure 95. ***Calympperes tenerum*** with gemmae. Photo by Jan-Peter Frahm, with permission.

Jesús Muñoz (Bryonet 15 March 2013) studied the effects of wind on Cory's Shearwater (***Calonectris diomedea***; Figure 96) migration and suggested that it might be worth investigating those same wind patterns for bryophyte dispersal. Earlier in this chapter I suggested that propagules might follow "wind highways." Could this following be in the protection of the feathers and mud of birds? Felicísimo *et al*. (2008) used a model to show that the Cory's Shearwaters closely follow the "wind highways" that require the least energy to reach their breeding and wintering areas. The Manx Shearwaters (*Puffinus puffinus*; Figure 97) chose a route that was 25% longer, avoiding turbulence on the shortest distance (González-Solís *et al*. 2009). The wind patterns (not the shortest route) drive the shearwaters in their movements and could do the same for bryophytes (Felicísimo *et al*. 2008; González-Solís *et al*. 2009).

Figure 96. ***Calonectris diomedea*** (Cory's Shearwaters). Photo by Antlewis, through Creative Commons.

Figure 97. Manx Shearwater (***Puffinus puffinus***) in Iceland, a potential bryophyte dispersal agent. Photo by Chiswick Chap, through Creative Commons.

Brent Mishler (Bryonet 5 March 2013) suggested that vegetative fragments could travel in mud on birds' feet as well, and that molecular testing could be used to track such long-distance dispersal. Rob Gradstein (Bryonet 11 March 2013) suggests a less molecular, more challenging approach: 1) capturing migratory birds to look for bryophyte spores, gemmae, and fragments on their feathers, feet, and beaks; 2) flying spores, gemmae, and fragments on birds across long distances to test for germinability of the diaspores after the long trip.

Even feet of terrestrial birds can carry spores, and probably other propagules. Davison (1976) reported finding spores of bryophytes on the feet of the Song Thrush (***Turdus philomelos***; Figure 98) in beechwood in Great Britain, although he considered that these were transported only a short distance.

Even the tiny hummingbird may contribute to long-distance dispersal of bryophytes. Torres-Dowdall *et al*. (2007) reported the use of bryophytes in the construction of nests of the hummingbird called Picaflor Rubi (***Sephanoides sephaniodes***; Figure 99-Figure 100) in Chile. Osorio-Zúñiga (2012) later examined the nests of the Picaflor Rubi (also known as Picaflor Chico). He identified *Lophosoria quadripinnata* (a tree fern), appearing as the "garment" in 100% of the nests, and three moss species, all pendent species, that frequently comprised the outside of the nests [***Weymouthia cochlearifolia*** (16.6% of nests) (Figure 101), ***W. mollis*** (26.6%) (Figure 102), and ***Ancistrodes genuflexa*** (100%) (Figure 103-Figure 104). These outside mosses all produced sporophytes in both the old and new nests (Figure 107-Figure 109). In addition to these species, old nests also had ***Eriodon conostomus*** (Figure 105), ***Ptychomnion ptychocarpon***, and ***Dicranoloma robustum*** (Figure 106), all producing sporophytes (Figure 109). For species present in 100% of the nests, the growing heights were 10-18 m above ground and were not the most abundant species in the forest.

In continuing this study, Osorio-Zuñiga *et al*. (2014) introduced the concept of **synzoochory** for bryophyte dispersal as an intermediate between endo- and ectozoochory. In **synzoochory**, the propagules are deliberately transported, usually by mouth or beak, but without ingestion. These researchers found seven species of mosses were transported this way by the hummingbird

Sephanoides sephanoides (Figure 99). These likewise were to be used in nests, but the researchers found that the birds were selective, choosing mosses with capsules in greater frequency than their appearance in the habitat. They also preferred the fern *Lophosoria quadripinnata* and the moss ***Ancistrodes genuflexa*** (Figure 103-Figure 104), with the other mosses [***Weymouthia mollis*** (Figure 102), ***Weymouthia cochlearifolia*** (Figure 101), ***Eriodon conostomus*** (Figure 105), ***Ptychomnion ptychocarpon***, ***Dicranoloma robustum*** (Figure 106), ***Rigodium toxarion***] being minor components. This behavior of the birds gave two opportunities for greater dispersal – first from one tree to another in the beak, then for longer distances for the spores from the elevated position of the nest. In some cases the mosses were elevated from the ground to the nest.

Figure 98. Song Thrush (***Turdus philomelos***), a bird known to carry moss spores on its feet. Photo by Taco Meeuwsen, through Wikimedia Commons.

Figure 99. Picaflor Rubi (***Sephanoides sephaniodes***), a hummingbird that selects mosses for her nest. Photo by Suemili, through Wikimedia Commons.

Figure 100. ***Sephanoides sephaniodes*** on moss-constructed nest, looking quite camouflaged. Photo by Diucón, through GNU Free Documentation.

Figure 101. ***Weymouthia cochlearifolia***, a pendent moss used in the nests of the Picaflor Rubi. Photo by Juan Larrain, with permission.

Figure 102. ***Weymouthia mollis***, a pendent moss that is placed on the outside of the nests of the Picaflor Rubi. Photo by Juan Larrain, with permission.

Figure 103. ***Ancistrodes genuflexa***, a pendent moss used in the outside of the nests of the Picaflor Rubi. Photo by Felipe Osorio Zúñiga, with permission.

Figure 104. ***Ancistrodes genuflexa*** with capsules. Photo by Felipe Osorio Zúñiga, with permission.

Figure 105. ***Eriodon conostomus*** with capsules. Photo by Juan Larrain, through Creative Commons.

Figure 106. ***Dicranoloma robustum***. Photo by Juan Larrain, through Creative Commons.

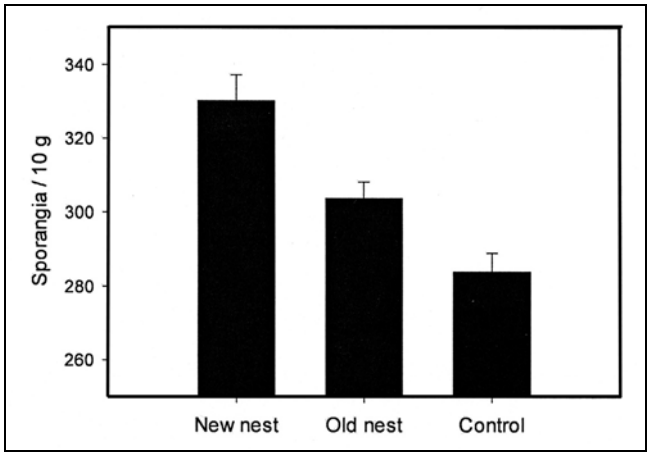

Figure 107. Sporophyte number vs nest age in 10 g of nest mosses for the Picaflor Rubi (***Sephanoides sephaniodes***). Redrawn from Osorio Zúñiga (2012).

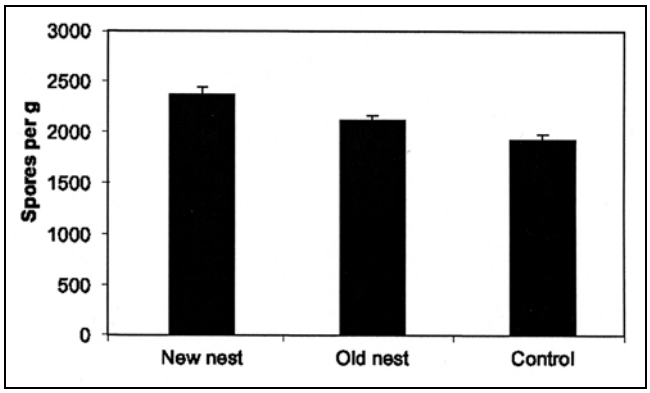

Figure 108. Effect of nest age on spore number per gram of moss in nests of the Picaflor Rubi (***Sephanoides sephaniodes***). Redrawn from Osorio Zúñiga (2012).

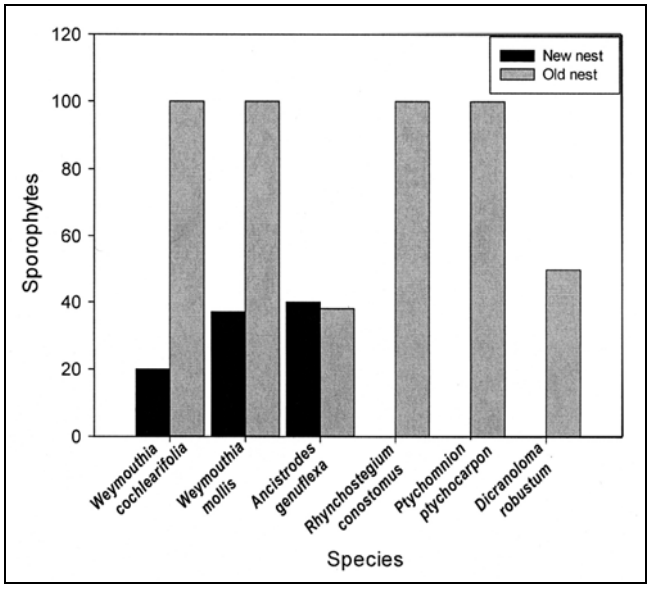

Figure 109. Number of sporophytes compared to nest age for bryophytes in nests of the Picaflor Rubi (***Sephanoides sephaniodes***). Redrawn from Osorio Zúñiga 2012.

As noted above, members of the **Splachnaceae** are known for their ability to attract flies that subsequently disperse their spores. But it appears that this is not always the case. Lewis *et al*. (2014) considered the long-distance dispersal that was evidenced in ***Tetraplodon*** (Figure 56, Figure 59-Figure 60). The amphitropical disjunctions required explanation. The researchers compared stepwise migration along the Andes, direct long-distance dispersal, and ancient vicariance. Using four loci from each of 124 populations throughout the global range, they analyzed genetic evidence for the dispersal pathway. Three clades emerged, indicating three pathways of dispersal. There is no evidence of modern or historical wind connectivity between the polar regions, and these spores are not easily dispersed by wind. The researchers concluded that migratory birds most likely accounted for the long-distance dispersal of ***Tetraplodon***, suggesting that the order Charadriiformes were the most likely dispersers.

Additional information on birds that eat capsules is in Volume 2, Chapter 16-2.

Mammals

Both large and small mammals step on bryophytes. Fur and hooves are likely to carry at least some forms of bryophyte propagules. Pauliuk *et al*. (2011) investigated dry grassland dispersal by sheep. They collected gametophyte fragments from the fleeces and hooves of 12 sheep, including two breeds. They also grew microscopic diaspores collected from soil that adhered to the hooves. Among the species in the pasture, 40% were transported, comprising 16 moss species. Sheep breeds collected different arrays of species, with dense, curly fleece carrying more fragments and larger species than sheep with smooth and fine hair. Pleurocarpous species, small species, and mats were represented more frequently in proportion relative to the vegetation; large species, acrocarpous life forms, wefts, and turfs were underrepresented. Hooves carried mostly acrocarpous colonist species.

In the Arctic, ***Voitia hyperborea*** (sometimes considered a variety of ***V. nivalis***; Figure 26) has a capsule that does not open (Steere 1974). It appears that musk oxen and caribou may help in dispersal by chewing on the capsules as they graze other plants. In any event, it would seem that some animal agent is necessary for the dissemination of spores. During (personal communication, 29 May 2006) suggested that whole capsules may possibly be dispersed, but that the spores in ***Voitia nivalis***, at least, have a structure that suggests they are sticky like those of other genera of the **Splachnaceae** and may adhere to beetles or even larger animals once the capsule begins to decay and expose them. More detail on the dung mosses is in the habitat subchapter on dung mosses.

In the Alps, ***Voitia nivalis*** is apparently dispersed by ruminants. It can be found in shelters or on the trails of sheep, chamois, and ibex, often on dry cliff ledges (Geissler 1982). This dispersal could carry fragments and other diaspores trapped on the feet and among fur or through feces holding spores inadvertently eaten along with forage.

There is some evidence that rodents contribute to the dispersal of fungal spores through ingestion and subsequent

deposit of feces (Trappe & Maser 1976; Cázares & Trappe 1994; Janos *et al*. 1995). It is likely that rodents likewise contribute to bryophyte spore dispersal, not only through ingestion, but also by transporting spores in their fur. Others are likely to hitch a ride in mud on the feet. Nevertheless, it appears that direct data to support this role are lacking for bryophytes. We do know that rodents eat bryophytes, as shown for this mouse dining on ***Funaria hygrometrica*** capsules (Figure 110). Andrew Spink photographed a vole eating mosses (Figure 111).

Figure 110. Mouse eating ***Funaria hygrometrica*** capsules on Isle Royale, Michigan, USA. Photo courtesy of Steve Juntikka.

Matt Dami (Bryonet 26 August 2016) reported providing mice with capsules of the mosses ***Dicranum flagellare*** (Figure 112) and ***Polytrichum commune***. They consumed the capsules and the fecal samples were collected and cultured on nutrient agar. Both species grew from the ingested spores, but ***P. commune*** (Figure 113) had much more germination success and far more vigorous growth.

Figure 111. Bank vole eating mosses in The Netherlands. Such close contact is likely to carry spores from the capsules seen in the picture. Photo by Andrew Spink, with permission.

Figure 112. ***Dicranum flagellare***, a species whose spores survive the digestive tract of a moss. Photo by Bob Klips, with permission.

Figure 113. ***Polytrichum commune*** with capsules. Their spores seem to thrive when passed through the digestive tract of a mouse. Photo by Bob Klips, with permission.

Spores adapted for animal dispersal are sticky and elliptical, as in **Splachnaceae** (dung mosses) or ***Schistostega pennata*** (luminous moss), these being dispersed by flies. Beetles, earthworms, and slugs are likely dispersers, albeit for short distances. Ducks are known to carry spores, and small nesting birds may use setae and capsules in nests, but the effectiveness of these dispersal agents is unknown.

Water Dispersal

Conrad (1996) examined water samples in a *Taxodium* (bald cypress) swamp biweekly for spores. He also cultured both herbarium specimens and propagules from the diaspore bank. Although two other liverwort species regenerated from soil diaspores, ***Ricciocarpos natans*** (Figure 114) grew only from the spores (Figure 115) in the water samples and Conrad concluded that its presence in the swamps is entirely due to water dispersal.

Figure 114. Floating thalli of ***Ricciocarpos natans***. Photo by Janice Glime.

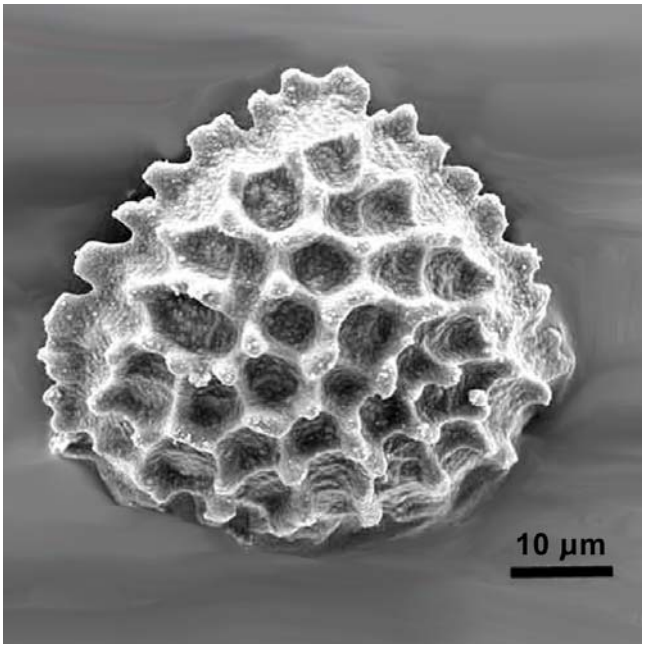

Figure 115. SEM of ***Ricciocarpos natans*** spore, a spore most likely transported by water. Depressions in the surface may aid in flotation. Photo by William T. Doyle, with permission.

Aquatic liverworts often have spines on their spores. Porsild (1903) believed that these served as attachment aids for spore dispersal by aquatic animals. However, other scientists believe that they instead act as anchors to hold the spores onto rough surfaces so that not all are lost during heavy flows of streams (Studhalter 1933). In any case, some aquatic species, *e.g.* ***Ricciocarpos natans*** (Figure 115) and ***Riccia fluitans*** (Figure 116), do not have these spines, suggesting that the surface configuration may have more to do with phylogeny than with environment. On the other hand, they may aid flotation, permitting the water to carry them off.

It is fairly common for rock-dwelling bryophytes of streams and rivers to project their sporophytes above the water level where they can be wind dispersed (Figure 117). This requires timing to produce sporophytes at a time when the water level is down.

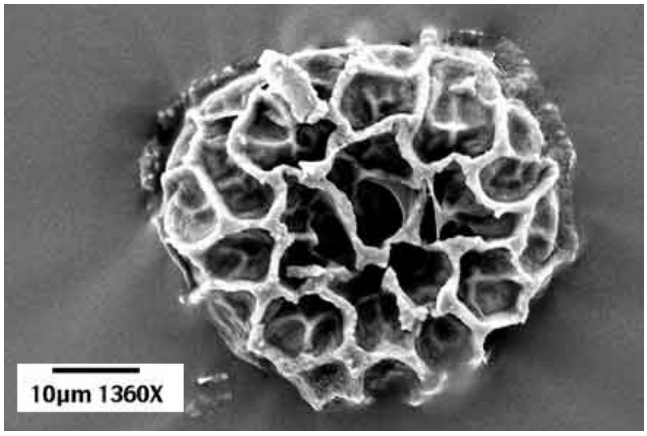

Figure 116. ***Riccia fluitans*** spore distal view SEM. Photo by William T. Doyle, with permission.

Figure 117. ***Hygrohypnum alpinum*** with emergent capsules. Photo by Michael Lüth, with permission.

Common Adaptations

Mahabalé (1968) reviewed the characteristics of spores of aquatic tracheophytes. He found that the spores are short-lived and germinate quickly. These are water-dispersed. Those that are semi-aquatic or are facultatively aquatic have spores with thick outer walls and are dispersed by either insects or wind.

Cox (1983) tested the hypothesis that aquatic spores would have large, long axes and move in planes such as the water surface, rather than in three dimensions. He also predicted a greater incidence of dioicism. He found that data supported these hypotheses for a variety of aquatic spores, including bryophytes. He also found that many spores had flotation devices. Cox considered these traits to provide "an efficient search vehicle." He considered dispersal in the aquatic environment to be a random search and that movement in one plane reduced that search territory.

As Mahabalé suggested, spores of the liverwort ***Riccia gougetiana*** (Figure 118) are over 200 µm in diameter (Schuster 1966); those of ***Riella*** (Figure 79) are 70 µm, nearly four times as large as the diameters of most air-dispersed spores (Mahabalé 1968; Cox 1983). ***Pellia epiphylla*** (Figure 119-Figure 120), a common streamside species, disperses its spores as a single mass (Cox 1983),

but it also has elongate spores (Figure 120). ***Gymnocolea*** (Figure 121) uses deciduous perianths as its floating dispersal unit. Elongate dispersal units are seen in vegetative dispersal units such as fragments of ***Fontinalis*** (Figure 122) (Glime *et al*. 1979).

Figure 118. ***Riccia gougetiana***, a species with 200 µm spores. Photo by Jonathan Sleath, BBS website, with permission.

Figure 119. ***Pellia epiphylla*** capsule dehisced, showing clumps of spores. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

Figure 120. ***Pellia epiphylla*** spore. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

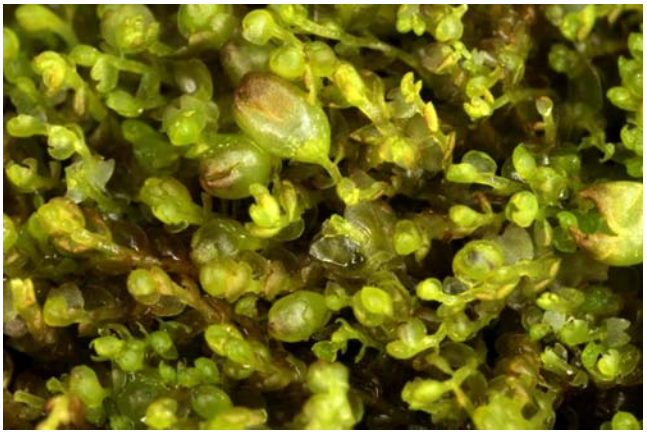

Figure 121. ***Gymnocolea inflata*** showing enlarged, oblong terminal perianths. Photo by Jan-Peter Frahm, with permission.

Figure 122. ***Fontinalis dalecarlica*** fragments imbedded in ice from a stream in New Hampshire, USA. Photo by Janice Glime.

Marine Dispersal?

No species is known to grow in marine waters, but Engel and Schuster (1973) raised the question of marine dispersal. They reasoned that species subject to tidal action or ocean spray were the best candidates. They assumed that bryophytes would not survive long exposures to salt water and presumed that freshwater drainage from adjacent forests above the beach and high rainfall made it possible for species subjected to saltwater to survive. Hence, they concluded that marine dispersal was not possible, but this has not been tested.

Flood Plains and Dry Flats

Volk (1984) suggested that the distribution of spores by animals is most important for genera like ***Riccia*** (Figure 118) that inhabit seasonally dry habitats, particularly in southwest Africa and the Mediterranean. Whereas annual species of **Marchantiales** produce large numbers of spores, in the perennial species spore number is typically reduced and is even more rare among species with bulbils. Those that do support significant spore production can have ornamented spores that facilitate transport by animals, or perhaps aid in flotation. Despite the periodic invasion by water, this may not be an effective means of dispersal to carry the spores to new locations. Large flooding episodes can bury spores and other propagules so much that they may not resurface for decades (Figure 123-Figure 124).

Figure 123. Eroded material transported by water to River Baihe, a tributary of Yellow River, Tibet. Photo by Sven Bjork, with permission.

Figure 124. Floodplain on Isle of Wight. This magnitude of flood is reached once in ten years. Photo through Wikipedia Creative Commons.

Schuster (1966) considered the dispersal of ***Riccia*** (Figure 125) and ***Ricciocarpos*** (Figure 115) spores by mud and water to be very frequent. They typically grow at the margins of rivers and streams in the floodplain, where their spores mature in spring or in late summer or fall when flooding is common. The hornwort genus ***Notothylas*** (Figure 126) is also likely to be dispersed in this way. In ***Riccia*** (Figure 125) and ***Sphaerocarpos*** (Figure 127), the spores are exceptionally large (65-200 µm diameter), are accompanied by elaters, and are dispersed by water.

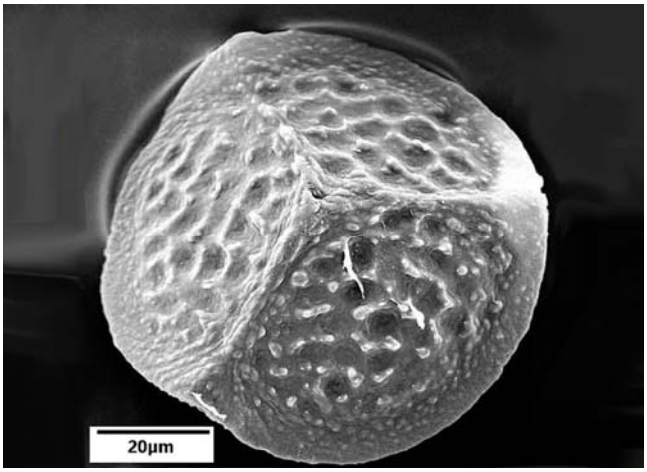

Figure 125. ***Riccia beyrichiana*** spore proximal view SEM, showing its larger size compared to that of ***Notothylas.*** Photo by William T. Doyle, with permission.

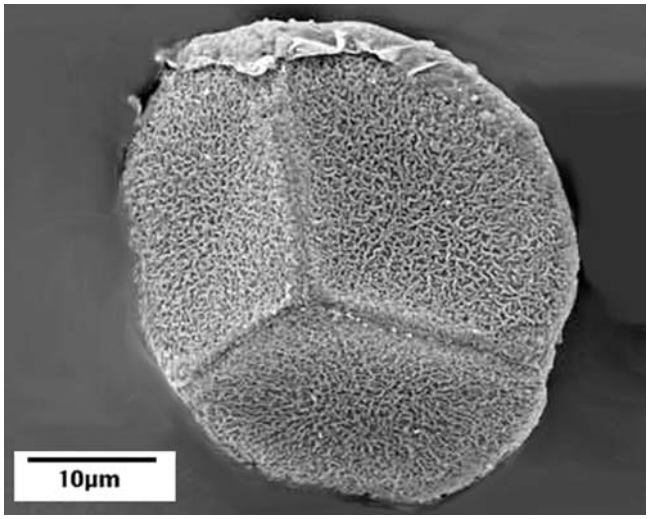

Figure 126. ***Notothylas obicularis*** spore proximal view SEM. Photo by William T. Doyle, with permission.

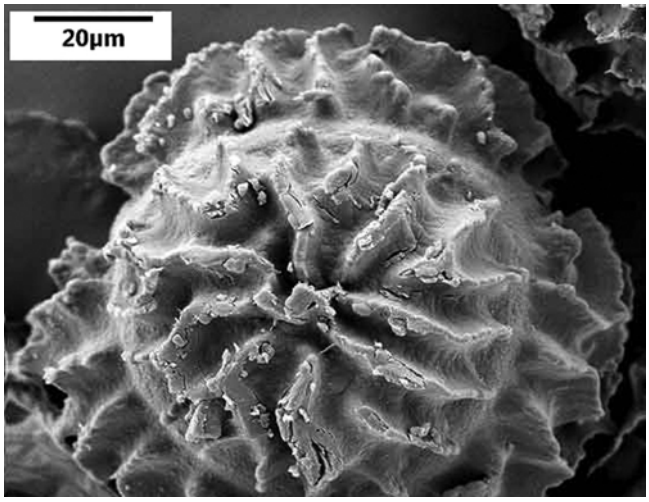

Figure 127. ***Sphaerocarpos stipitatus*** distal spore wall SEM. Photo by William T. Doyle, with permission.

Raindrops

The genus ***Diphyscium*** (Figure 128) has a flat side on its capsule. Crum (1983) reports that raindrops hitting this flat side can cause "little puffs" of spores that are propelled up to 5 cm from the capsule. It could be that the same phenomenon occurs in ***Buxbaumia***.

Figure 128. ***Diphyscium foliosum*** flat-topped capsules where raindrops expel spores. Photo by Hermann Schachner, through Creative Commons.

Exploding Capsules?

Lacking peristome teeth, ***Sphagnum*** has an explosive capsule that behaves much like an air gun. It exerts an internal pressure of 4-6 atmospheres, a pressure equal to that of the "huge tires of heavy trucks" (Crum 1973). If you place mature capsules under a lamp with a tin cup or other "roof" to catch the spores, you can hear the capsules pop as the lids strike the cover, a phenomenon reported by one of the bryologists following a ***Sphagnum*** collecting trip at a ***Sphagnum*** conference in Great Britain. Some bryologists claim to have heard the capsules popping in the field, with the sound being generated entirely by the explosions of the capsules.

Vortex Rings

This explosion is a necessary event for the toothless ***Sphagnum*** to get its spores above the **laminar flow** region near the capsule and into the **turbulent flow** that can carry the spores away from their parent. But it seems that this is more than just a straight shot. Whitaker and Edwards (2010) report what seems to be the first evidence of plants using a **vortex ring** (Figure 130-Figure 129). The vortex ring is a self-sustaining flow field that can carry one fluid (in this case, a mass of spores) through another (in this case, the surrounding atmosphere) without significant drag. The result is that spores go farther.

When the spores explode from a ***Sphagnum*** capsule, this vortex ring, shaped like a mushroom cloud, forms and dissipates very quickly above the capsule (Figure 129-Figure 131). As the spores are ejected from the capsule, they are "entrained by the co-moving vortex bubble that forms at the lip of the capsule and moves upward" (Figure 131). The advantage of this vortex ring is that it moves the spores much farther than an air-gun mechanism could. This is the result of a self-sustaining flow field that moves the donut-shaped mass of spores upward.

Figure 129. ***Sphagnum*** spore vortex taken as a time series every 100 microseconds. Photo by Clara Hard, Joan Edwards, and Dwight Whitaker from Whitaker & Edwards 2010, with permission.

The large number of spores (~100,000) in a single capsule form a bubble with a radius of 5 mm (Whitaker & Edwards 2010). These vortex rings cause a thrust augmentation by acceleration of the additional ambient fluid created at the time of the explosion (Krueger *et al*. 2008). The ring itself is "generated by the transient ejection of a jet from a tube or orifice" such as the opening of the ***Sphagnum*** capsule.

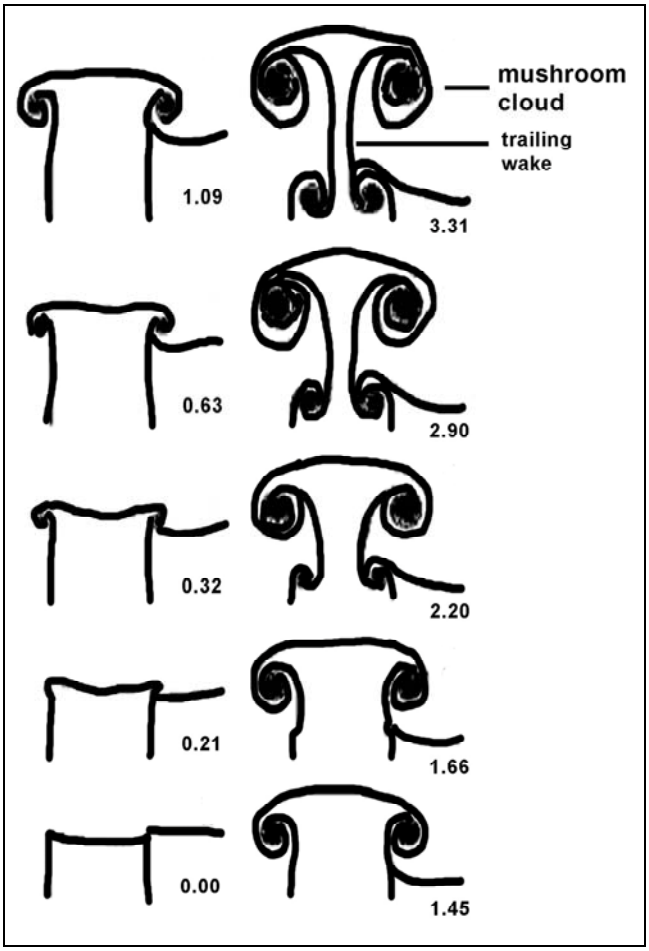

Figure 130. The development of a vortex ring with its mushroom cloud and trailing wake following the expulsion of a ***Sphagnum*** operculum. Redrawn from Whitaker and Edwards at <www.math.lsa.umich.edu>.

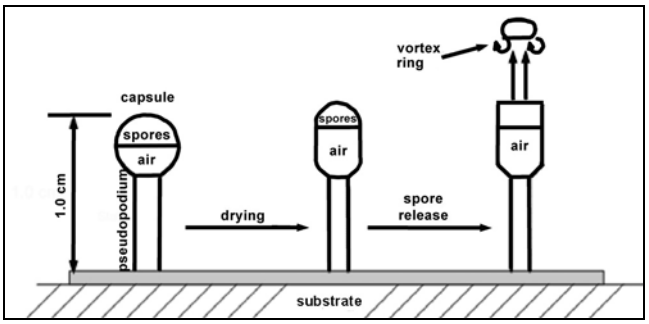

Figure 131. ***Sphagnum*** spore capsule from fresh to drying to release of the operculum. Redrawn from Miller 2010.

As Mustain (2010) points out, it is these vortex rings that help the squid speed through the water and the human heart to push blood from chamber to chamber. They are present in the clouds arising from an erupting volcano and propel jellyfish in the sea (Krueger *et al*. 2008). For ***Sphagnum***, it permits this short plant to place its spores (Figure 132) into the winds that start about 10 cm above the surface (Whitaker & Edwards 2010). The ring keeps the spores together, preventing their useless descent to the ground. They calculated that the vortex ring typically

shoots more than 11 cm into the air, sometimes as high as 17 cm. Furthermore, Johan L. van Leeuwen from the Netherlands' Wageningen University (in Mustain 2010) reports that this shot of spores reaches about 144 kph!

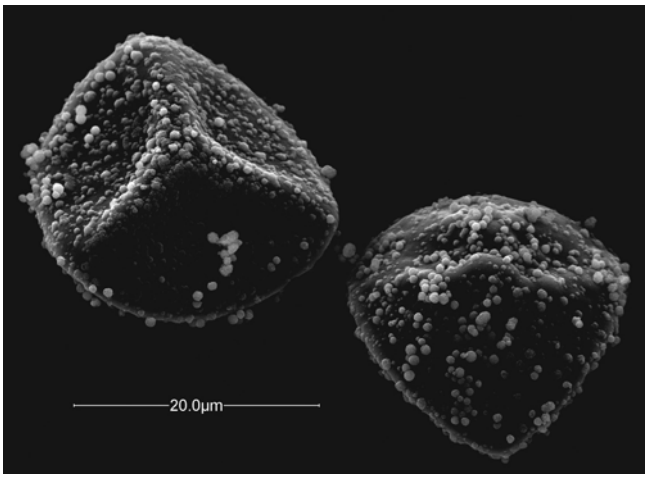

Figure 132. ***Sphagnum*** spores SEM. Photo by Dwight Whitaker and Joan Edwards, with permission.

Role of Stomata

Unlike many of the other bryophytes, ***Sphagnum*** has its stomata located away from the base and top of the capsule, suggesting that their function might be different. Boudier (1988) reported that the stomata of ***Sphagnum*** were not, as assumed, involved in any respiratory function in this genus, but rather that they are "false stomata" that give the capsule hardness and give the capsule wall flexibility. Beerling and Franks (2009) added to this that they were of importance in controlling and facilitating water loss from the capsule. Chater *et al*. (2011) determined that the stomata of bryophytes, like those of tracheophytes, are under the control of ABA and respond to environmental signals in the same way as guard cells of tracheophytes. Duckett *et al*. (2009, 2010a) conducted further experiments by pricking the ***Sphagnum*** capsules and demonstrating that both intact and pricked capsules dried out and dehisced over an 8-12 hour period. During this time the stomatal guard cells gradually collapsed. This seems to be in direct contradiction to the assertion of Ingold (1959), who concluded that the dehiscence mechanism of ***Sphagnum*** capsules depends on a capsule wall that is impermeable to gases. Ingold suggested that cuticularization of the guard cells with age could block the air passage. Duckett *et al*. (2009, 2010a) contend that, rather than an air-gun explosion (as understood by Ingold), the spore discharge results when differential shrinkage of the capsule walls causes the rigid operculum to pop off.

The shrinkage of the ***Sphagnum*** capsule wall has been known for some time. Maier (1974) described the importance of a rigid zone of resistance in the capsule wall that permits the capsule to maintain its diameter even as the remainder of the capsule shrivels as it dries. This rigid wall tissue causes the shape of the capsule to change from spherical to cylindrical. This causes maximum stress in the area of the operculum, causing the wall (line of dehiscence) to break.

Duckett *et al*. (2009, 2010a) concluded, as did Boudier (1988), that the only role for the stomata in ***Sphagnum*** is to aid in capsule drying and thus shrinkage. Duckett *et al*. determined that there is no potassium-regulating mechanism for these guard cells.

The behavior of guard cells in **Anthocerotophyta** (Figure 134-Figure 137) seems to be support for the dispersal role. Lucas and Renzaglia (2002) found that the guard cells in this group do not respond to abscisic acid (ABA). Furthermore, in young tissues K^+ and malate are localized in all epidermal cells, but once the tissues mature, they occur only in the guard cells. This permits them to serve as an osmoticum that causes the guard cells to swell due to water influx. This behavior is coupled with a pattern of function in which the guard cells do not respond to light (Lucas & Renzaglia 2002; Duckett *et al*. 2010b). Rather, they begin closed in young tissues, then open as tissues mature, and remain open. This behavior permits older epidermal tissues to dry out (Figure 137). Duckett *et al*. (2010b) suggest that the same mechanism is at work in mosses. Such drying could contribute to dispersal.

Figure 133. ***Anthoceros agrestis***, showing involucre where stomata are young and closed and capsule where stomata are mostly mature and open. Photo by Jan-Peter Frahm, with permission.

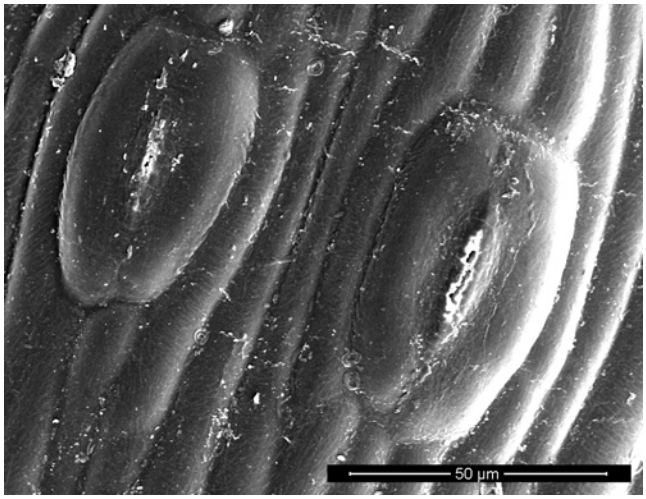

Figure 134. SEM of ***Anthoceros punctatus*** stomata in the sporophyte. Photo courtesy of Jeff Duckett and Silvia Pressel.

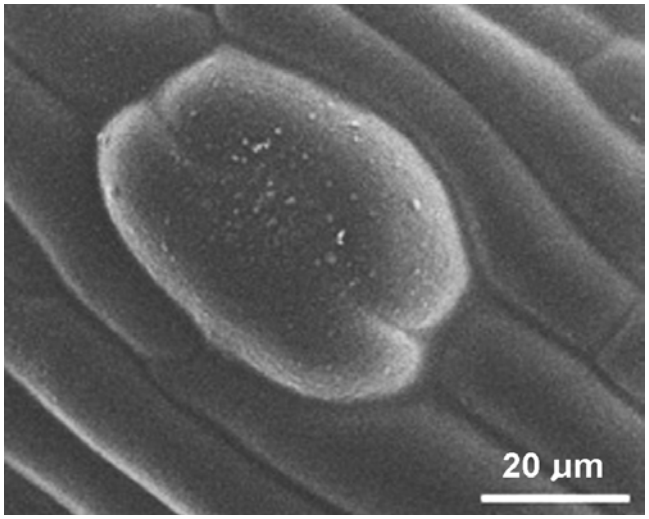

Figure 135. ***Paraphymatoceros minutus*** closed stoma from inside involucre. Photo modified from Jeffrey Duckett, Ken P'ng, Karen Renzaglia, and Silvia Pressel, with permission.

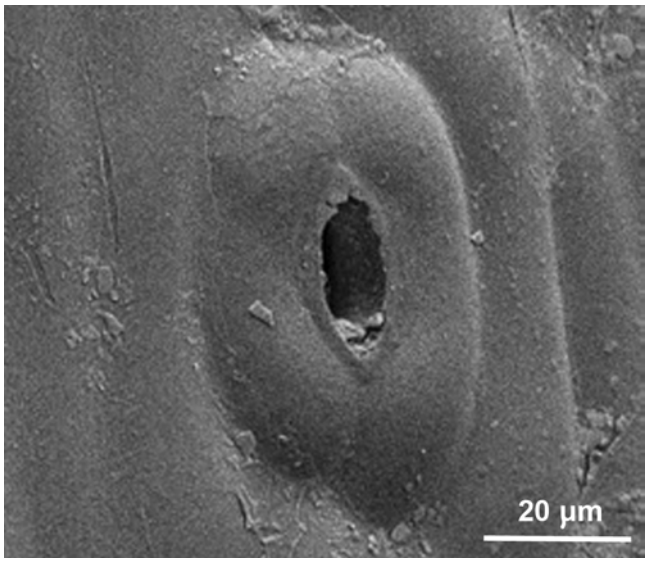

Figure 136. ***Paraphymatoceros minutus*** newly opened stoma from immediately above involucre, *i.e.* older tissue than that within the involucre. Photo modified from Jeffrey Duckett, Ken P'ng, Karen Renzaglia, and Silvia Pressel, with permission.

The functioning of bryophyte guard cells has been largely ignored. Pressel *et al*. (2014) followed their development in hornworts and determined that the guard cells contain giant, starch-filled chloroplasts as they begin to differentiate. These chloroplasts divide, regaining their spherical shape after the aperture opens. After opening of the guard cells, wall material accumulates over them and wax rodlets line the pores. Pressel and coworkers considered it unlikely that the guard cells moved after maturity, based on the widespread presence of open guard cells. This propensity to remain open suggests that the stomata may function in facilitating the desiccation of the sporophyte, ultimately facilitating dehiscence and dispersal.

If guard cells do indeed function to facilitate dispersal by drying the capsule, then those species with few guard cells should have diminished dispersal capacity. Sundberg (2010a) cites some species within the ***Sphagnum*** section ***Subsecunda***, including ***Sphagnum cyclophyllum*** (Figure 138), ***S. microphyllum***, ***S. macrophyllum*** (Figure 139), and ***S. pylaesii*** (Figure 140), as species that have small, thin-walled capsules with short pseudopodia, large opercula, and no or few pseudostomata. Hence, they have no explosive discharge of spores (Andrews 1960, 1961; Shaw *et al*. 2004). These same species have only limited geographic distribution, suggesting that the lack of stomata and explosive discharge may contribute to a limited dispersal. On the other hand, Sundberg (2010a) found that 14 boreal species with circumpolar or amphi-Atlantic distributions, including four species with a distribution also in the southern Hemisphere, (Daniels & Eddy 1990) have the explosive dispersal mechanism.

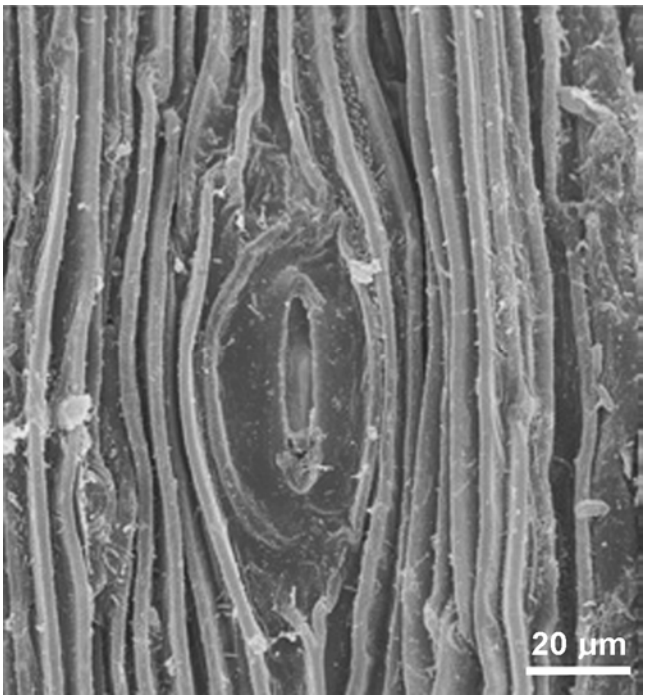

Figure 137. ***Phaeoceros laevis***, open stoma flanked by desiccated and shrunken epidermal cells well above dehiscence point. Photo modified from Jeffrey Duckett, Ken P'ng, Karen Renzaglia, and Silvia Pressel, with permission.

Figure 138. ***Sphagnum cyclophyllum***, a species that lacks explosive discharge of spores. Photo by Blanka Shaw, with permission.

Figure 139. ***Sphagnum macrophyllum***, a species that lacks explosive discharge of spores. Photo by Janice Glime.

Figure 140. ***Sphagnum pylaesii***, a species that lacks explosive dispersal of spores. Photo by Michael Lüth, with permission.

But what about the role of stomata in other bryophytes? Only ***Sphagnum*** has the reputation of an explosive discharge. Stomatal density in non-***Sphagnum*** mosses can depend on the environment, at least in some members of the **Polytrichaceae** (Figure 141-Figure 142). Szymanska (1931) found that even within the same species, plants in moist habitats had more stomata per mm^2. This supports the concept that the stomata are used to help dry the capsules, although not necessarily resulting in any "explosion." Abella *et al.* (1999) found no taxonomical value for the stomata in ten species of **Pottiaceae**, so perhaps these numbers too respond to the environmental humidity or differ with habitat dryness among species within a genus.

Egunyumi (1982) found correlations between stomata number and seta length in tropical African mosses, represented by 29 species in 12 families. These stomata ranged in number from 2 to more than 200 per capsule. This relationship might also reflect humidity of the habitat, but more data are needed to support this idea. Egunyumi found that stoma size correlated significantly with epidermal cell size, a taxonomic character. Stomatal position differed among species, with ***Wijkia trichocoleoides***, ***Trichosteleum microcalyx***, ***Stereophyllum radiculosum*** (Figure 143), and ***Stereophyllum virens*** having stomata raised above the level of epidermis, whereas in ***Brachymenium leptophyllum*** and ***Bryum coronatum*** (Figure 144) they were sunken.

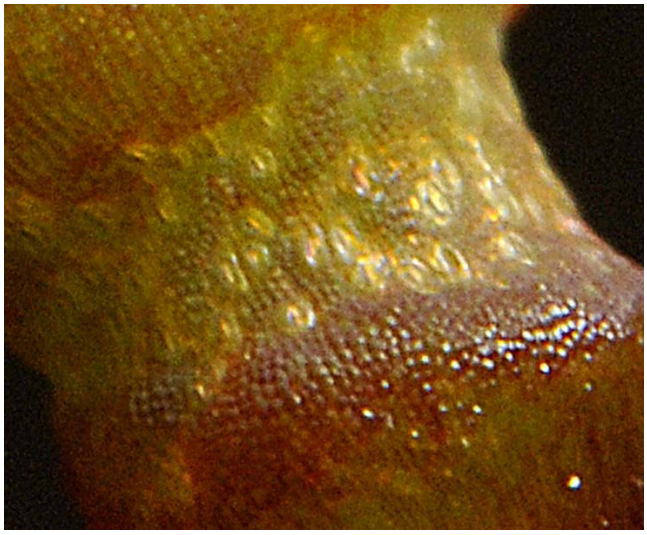

Figure 141. ***Polytrichum*** sp. stomata on capsule. Photo by George Shepherd, through Creative Commons.

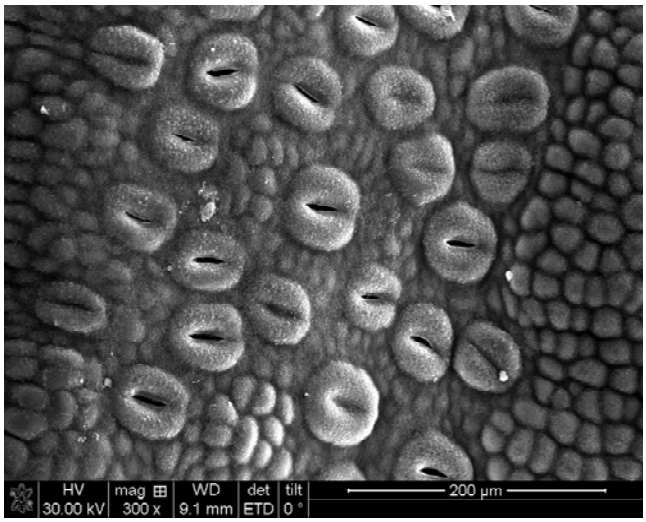

Figure 142. Stomata on neck of ***Polytrichum juniperinum*** capsule. Photo courtesy of Jeff Duckett and Silvia Pressel.

In their work on ***Funaria hygrometrica*** (Figure 145), Sack and Paolillo (1983) found that subsidiary cells in that species actually have thickened walls close to the guard cell at maturity. They reported that the guard cell walls have thin areas that are capable of flexing. The guard cell also has fibrillar layers that are oriented both axially and radially with respect to the pore. It seems that few guard cells in bryophytes have been described in such detail, but the structure is sounding a lot like that of tracheophyte guard cells. The role of stomata in spore release seems to be a promising area for research.

Figure 143. ***Stereophyllum radiculosum***, a moss that has its stomata raised above the capsule epidermis. Photo by Niels Klazenga, with permission.

Figure 144. ***Bryum coronatum*** with capsules that have sunken stomata. Photo by Jan-Peter Frahm, with permission.

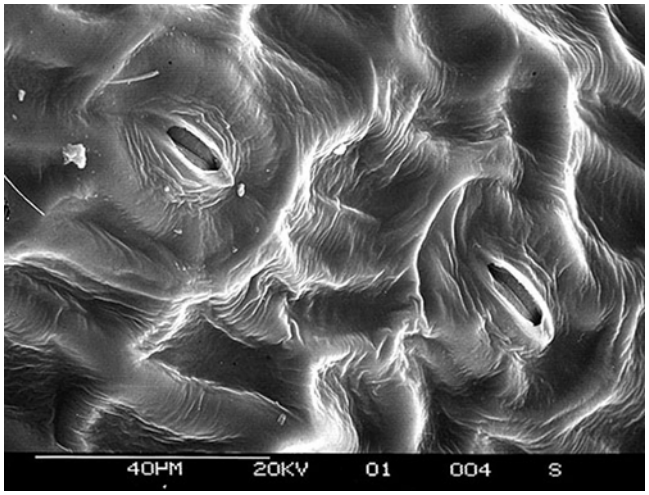

Figure 145. ***Funaria hygrometrica*** stomata. Photo from Botany 321 Website, UBC, with permission.

Is This an Explosion in *Sphagnum*?

Here we may have a semantic problem, with Duckett *et al.* (2009, 2010a) attempting to dispel our long-held interpretation of the method of spore expulsion by declaring it "not an air gun." But is it an explosion? While explosion can be defined as "a release of mechanical, chemical, or nuclear energy in a sudden and often violent manner with the generation of high temperature and usually with the release of gases" – certainly not descriptive of this event – the term has gained much broader meanings. Among these, we might be more comfortable with "a violent blowing apart or bursting caused by energy released from a very fast chemical reaction, a nuclear reaction, or the escape of gases under pressure." The question to be resolved is whether there are gases under pressure. Whereas Duckett *et al*. have demonstrated that the operculum is released by the distortion of the capsule, an internal pressure is necessary to qualify this as an explosion. If indeed Crum (1973) is right and the internal pressure is 4-6 atmospheres, then the release of this pressure upon dehiscence of the capsule fits at least one definition of an explosion. In any case, a vortex ring results, and that seems to be visual proof that pressure has been released.

Sundberg (2010b) disagrees with the interpretation of Duckett *et al.* (2009, 2010a) and contends that it truly is an air-gun ejection of spores. He points out that approximately 35% of the ***Sphagnum*** capsule volume is air. To test the role of the stomata in producing this gun, Sundberg used ***S. centrale*** (Figure 146) and ***S. fuscum*** (Figure 147). Using 16 capsules of each species, he pricked half of them in the lower half into the interior (ca 1 mm deep). Within 12 hours, all but one of the capsules had dehisced, with the ones not pricked presenting audible snaps. Spores from not-pricked capsules were ejected 50-150 mm, leaving the capsules nearly empty. The pricked capsules, on the other hand, also opened their lids, but no snap could be heard and the spores only spilled in clumps in a heap below the capsule opening, discharging only 5 mm or less. He considered this evidence that the normal discharge was explosive.

Figure 146. ***Sphagnum centrale***, a species that disperses its spores explosively. Photo by Janice Glime.

Figure 147. ***Sphagnum fuscum*** with capsules, a species that ejects its spores explosively. Photo by Dale Vitt, with permissions.

Falling Rate

Using a filming technique similar to that of Whitaker and Edwards (2010), Sundberg (2010a) examined the settling speed of spores from 14 species of ***Sphagnum***. They determined a maximum discharge speed of 3.6 m s^{-1} and a maximum height of 20 cm (mean 15 cm). The cloud (vortex ring) size was positively related to capsule size, giving species with larger capsules a dispersal advantage. Half the spores remained in clumps, usually of 2-4 spores. Single spores, with a deltoid shape, settled at 0.84-1.86 cm s^{-1}, a speed about 52% slower than would be expected for spherical spores of the same diameter. Larger spores settled faster, following Stokes' law. Sundberg suggested that the combination of the added height from the explosion and the slow settling speed serve to increase dispersal distance and may account for the wide distribution of boreal ***Sphagnum*** species. On the other hand, Fenton and Bergeron (2006) suggested that ***Sphagnum*** invasion into young dense forests might be dispersal limited, but they allowed for the possibility of unsuitable available substrata. It is likely also that the forest interfered with dispersal, trapping spores on bark and among the leaves.

A *Sphagnum* Spore Mimic

This spore dispersal mechanism is so good that it has been stolen by the fungus ***Bryophytomyces sphagni*** (Ascomycota) (Currah & Davey 2006). This parasite grows in the capsules of ***Sphagnum***, replacing the ***Sphagnum*** spores with its own. This does nothing to interfere with the capsule explosion. Hence, the fungal spores are dispelled in that same manner as would have been for the ***Sphagnum*** spores.

Summary

Spores are the most successful agents of long-distance dispersal in bryophytes, whereas vegetative means help the population to become established and spread once having arrived. **Peristome teeth** in mosses, an **explosive capsule** in ***Sphagnum***, and **elaters** in liverworts help in dislodging spores and dispersing them. Most bryophytes are adapted for wind dispersal, with the occasional updraft or gust permitting somewhat greater distances. However, the majority of spores seem to land within 2 m of their parents. Invasive species seem to benefit from both rapid vegetative dispersal and long-distance travel.

Cleistogamous capsules require capsule decay for dispersal, relying on distribution by animals, especially invertebrates, or becoming established near home. Capsules of taxa like ***Buxbaumia***, on the other hand, often split despite having teeth and may rely on such insects as fungal gnats to disperse spores.

Earthworms can transport spores on their moist surfaces or through the gut, and theme may be transported further if the earthworms are eaten while carrying the spores.

Animal dispersal in **Splachnaceae** and ***Schistostega pennata*** is facilitated by sticky, elliptical spores, and in the case of **Splachnaceae**, also by odors. Other animal dispersal appears to be chancier, with ducks, beetles, ants, slugs, earthworms, and small nesting birds contributing.

Water dispersal is important for water-dwelling species, and in floodplain taxa, a dormancy mechanism is usually necessary. Dormancy also provides spores with the ability to survive in the soil below 1 cm where they do not receive light and therefore will usually not germinate in the presence of water. Dispersal may be facilitated by decorations on the spores that create air pockets, aiding flotation. Others have spines and hooks that may aid in animal attachment and dispersal.

Raindrops on the flat side of a ***Diphyscium*** capsule help to discharge the spores.

Stomata seem to play a role in dispersal by facilitating drying of the capsule. In ***Sphagnum***, the ejection of spores is explosive, forming a **vortex ring** that drives the spores about 10 cm into the air, enough to get them into the air stream. This mechanism is so effective that the fungus ***Bryophytomyces sphagni*** lives in the ***Sphagnum*** capsule and is dispersed by the same mechanism.

Acknowledgments

I thank Joan Edwards for her patience in helping me to understand the vortex ring mechanism. Juan Carlos Villarreal sent me literature that was not available to me. Karen Renzaglia provided images that I requested for specific purposes. Jeff Duckett and Silvia Pressel permitted me to rummage through their images to find ones I needed to illustrate this chapter. Steve Trynoski offered several suggestions after a critical reading of this subchapter.

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CHAPTER 4-10

ADAPTIVE STRATEGIES: VEGETATIVE PROPAGULES

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CHAPTER 4-10

ADAPTIVE STRATEGIES: VEGETATIVE PROPAGULES

Figure 1. Deciduous branch tips of ***Campylopus cryptopodioides***. Photo by Michael Lüth, with permission.

Vegetative Reproduction

Vegetative reproduction comes in many forms. These range from breakage of leaves and stems that have become brittle through desiccation to specialized gemmae that occur on leaves or special stems and are nurtured by the parent plant, ready to go when finding a suitable substrate, to tubers that occur on roots and protonemata.

Such asexual structures seem to have evolved through **heterochrony** (developmental change in the timing of events, leading to changes in size and shape), including **neoteny** (retention of juvenile characteristics in adults of species) Newton & Mishler 1994). Hence, we can see gemmae that look like reduced leaves, as in ***Aulacomnium*** (Figure 2).

We might assume that in disturbed habitats, such as industrial areas, vegetative means to reproduce might offer advantages over more fragile-seeming protonemata necessitated by spore dispersal. But this is not always true. Nordhorn-Richter (1982) found the extent of bryophyte distribution in an industrial area of Germany was not improved by presence of asexual propagules except among members of ***Plagiothecium*** (Figure 3-Figure 4). On the other hand, vegetative reproduction offers the advantage of being ready to start developing an adult plant, reaching maturity much more quickly than a plant from a spore. Furthermore, bryophytes produce asexual propagules at a younger age than that needed for sexual reproduction.

Figure 2. ***Aulacomnium palustre*** gemmae that are modified leaves. Photo by Zen Iwatsuki, with permission.

Figure 3. ***Plagiothecium laetum***. Photo by Christian Peters, with permission.

Figure 4. ***Plagiothecium laetum*** leaves with scattered gemmae. Photo by Kristian Peters, with permission.

Longton and Schuster (1983) listed six basic means of asexual reproduction in bryophytes:

1. multiple gametophores from the protonema of one spore
2. decay of older gametophyte parts with the separation of younger parts
3. development of multiple shoots by rhizomes and stolons
4. development of gametophores from rhizoids
5. regeneration from fragments
6. production of specialized "propagula."

Frey and Kürschner (2011) shortened and summarized this list, identifying three types of asexual reproduction that are recognized today:

1. asexual reproduction *s. str.* by **regeneration** from somewhat specialized caducous organs (leaves, leaf apices, shoots, branches, bulbils) and by production of specialized propagules (gemmae, protonemal brood cells, tubers)
2. **fragmentation** of plants or parts of plants into essentially unspecialized fragments
3. **clonal** reproduction (cloning from branches, stolons, and rhizomes).

Cloning results when a branch of a protonema or a plant becomes separated from its parent. This can occur by decay of the protonema or disintegration of plant modules. In gametophores, cloning requires the formation of **ramets** (individuals, "daughter plants"). Frey and Kürschner (2011) consider cloning to be a "keystone factor for asexual reproduction, habitat colonization, and habitat maintenance." While this cloning mechanism is not dispersal in the usual sense, it does contribute to placing the species in new locations. For example, when we (Zhang, Raeymaekers, and Glime, unpublished) mapped the locations of ***Pleurozium schreberi*** (Figure 5) in m^2 plots and followed them yearly for five years, we found that they appeared to "move" from one location to another within the plot, often changing position by several centimeters, sometimes forming two clumps.

Figure 5. ***Pleurozium schreberi*** in the boreal forest. Photo by Janice Glime.

Although sexual reproduction may provide the opportunity for new gene combinations, a number of bryophytes [*e.g.* ***Cyrtomnium hymenophylloides*** (Figure 6; Miller & Mogensen 1997)] persist without any evidence of sexual reproduction. In reviewing the literature, Rolstad & Gjerde (2003) considered that some bryophytes have poor dispersal capability due to the absence of spore production. In this case, vegetative diaspores and even fragments

maintain the species and carry it to new locations. As in ***C. hymenophylloides***, the absence of sexual reproduction may only occur through part of its range, whereas other species seem never to produce capsules (Miller & Mogensen 1997). Rather, in ***C. hymenophylloides*** of North America and Greenland new growth arises from axillary and apical buds that appear to be the principal means of reproduction. Miller and Mogensen assumed that these were dispersed by wind but considered that water and gravity were also possible. It is interesting that populations may be all male, or more typically, all female.

Figure 6. ***Cyrtomnium hymenophylloides***. Photo by Michael Lüth, with permission.

In general, not counting fragmentation, there seems to be only one type of asexual reproduction within a species (Li Zhang, Bryonet 16 March 2010). Nevertheless, many exceptions occur. Pressel *et al.* (2007) reviewed the propagules in ***Bryum*** (see below) and related genera. In this genus one can find rhizoidal and chloronemal tubers, axillary bulbils, chloronemal brood cells, and foliar and protonemal gemmae. ***Ptychostomum*** (=***Bryum***) ***capillare*** (Figure 7) and ***Bryum dichotomum*** (Figure 8) have three types, but only one type has been found in any individual at a given time (Imura 1994). However, Zhang found two types on the same individual of ***Fissidens*** sp. (Figure 9-Figure 12, Figure 117) – rhizoidal gemmae and tubers. Gemmae (Figure 10-Figure 12) in this species come in a variety of shapes and types. ***Octoblepharum albidum*** (Figure 13) has three modes (Zhang *et al.* 2003). In this species, new plants can grow from the leaf tips where first rhizoids are produced and then buds. These buds grow into plants and may, in turn, produce another "generation" of leaf-tip shoots, much like the walking fern *Asplenium rhizophyllum*. These walking mosses may constitute 5-20% of the population. ***Leucobryum glaucum*** (Figure 14-Figure 15; ***Leucobryum*** Figure 16) has a similar behavior in which the terminal rosette of leaves may produce rhizoids and new plants. But in this case, so far as is known, the new plants drop off and grow if they land on a suitable substrate.

Figure 7. ***Ptychostomum*** (=***Bryum***) ***capillare*** wet, a species that can produce caulonemal, rhizoidal, or leaf gemmae. Photo by David Holyoak, with permission.

Figure 8. ***Bryum dichotomum***, a species with chloronemal, rhizoidal, and leaf gemmae. Photo by Michael Lüth, with permission.

Figure 9. ***Fissidens taxifolius***. Photo by David Holyoak, with permission.

Figure 10. ***Fissidens flaccidus*** axillary gemmae on stem. Photo by Ida Bruggeman, with permission.

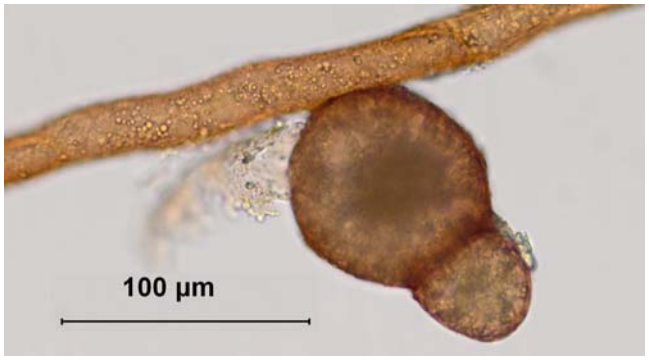

Figure 11. ***Fissidens macaoensis*** rhizoidal tuber. Photo by Li Zhang, with permission.

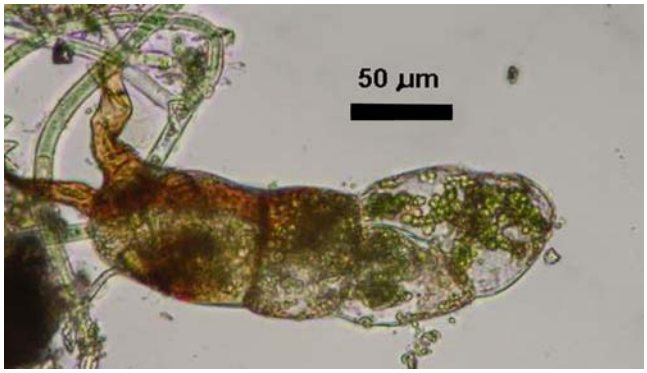

Figure 12. ***Fissidens tenellus*** bud. Photo by Tom Thekathyil, with permission.

Figure 13. ***Octoblepharum albidum***, a moss that can grow new plants at its leaf tips, creating a walking fern type of reproductive strategy. Photo by Michael Lüth, with permission.

Figure 14. ***Leucobryum glaucum*** with young apical rhizoids. Photo by Nancy Ironsides, with permission.

Figure 15. ***Leucobryum glaucum*** with mature apical rhizoids that can serve as propagules. Photo by Sean Edwards, with permission.

Figure 16. ***Leucobryum*** showing rhizoids developing from leaf tips. Photo courtesy of Andi Cairns.

Pfeiffer *et al*. (2006) identified three types of vegetative morpho-types in the pleurocarpous moss ***Rhytidium rugosum*** (Figure 17): **ramet** (individual plant that has grown vegetatively from another individual, *i.e.*, a

branch, becoming part of a clone of that plant) that can become separated when they decay, brood **branch**, and **caducous** (easily detached) shoot apex. They demonstrated successful dispersal of vegetative diaspores through **AFLP** (amplified fragment length polymorphism) fingerprinting, wherein samples from one clone occurred on both studied plots in Germany. Furthermore, the close relationship of the fingerprinting between the two plots suggest clonal rather than sexual (spore) origin for the populations.

Figure 17. ***Rhytidium rugosum*** from Europe, showing what appear to be several ramets. Photo by Michael Lüth, with permission.

Dispersal of vegetative propagules seems to be more of a passive process than that of spores. Few special mechanisms are documented for removal of asexual propagules from the plant. ***Tetraphis pellucida*** (Figure 18-Figure 19), with apical gemmae in splash cups is a notable exception among mosses, with ***Marchantia*** (Figure 20-Figure 21) and ***Lunularia*** (Figure 22) species likewise having gemma splash cups. Others easily "pop" as they become detached by some intruder bumping them, as in ***Dicranum flagellare*** (Figure 23). The extent of transport by animals that brush against them has seldom been documented.

Figure 18. ***Tetraphis pellucida*** with gemma splash cups. Photo by Andrew Spink, with permission.

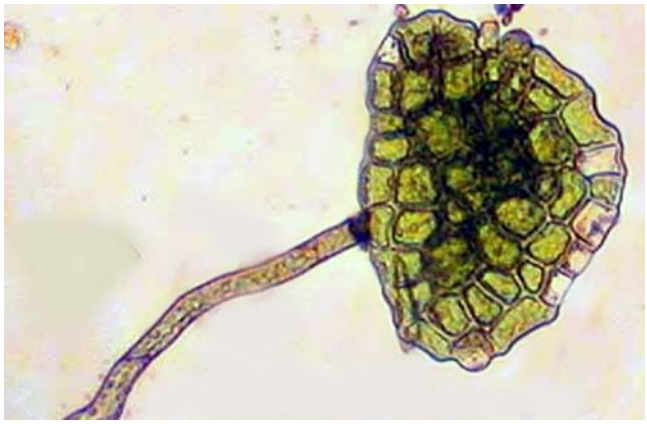

Figure 19. Gemma of ***Tetraphis pellucida*** showing protonema developing from it and lack of an apical cell. Photo from Botany website, UBC, with permission.

Figure 20. ***Marchantia alpina*** with gemma cups in Norway. Photo by Michael Lüth, with permission.

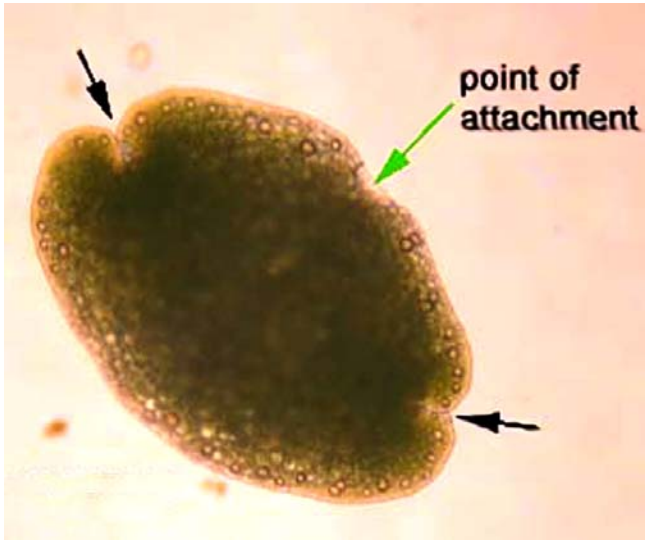

Figure 21. ***Marchantia polymorpha*** gemma showing notch (arrow) where growth begins. Photo by Kavita Uttam UBC, with permission.

Figure 22. ***Lunularia cruciata*** showing gemma splash cup. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 23. ***Dicranum flagellare*** showing flagelliform branches that serve as propagules. It is accompanied by several species of the lichen ***Cladonia***. Photo by Robert Klips, with permission.

Herben (1994) considers habitat to be the important parameter for assessing the role of the reproductive mode of bryophytes, with those in small and unstable habitats showing more frequent formation of propagules. Löbel and Rydin (2009) found that among epiphytes the habitat conditions had no influence on production of asexual propagules, whereas they did influence sporophyte production. Furthermore, sexual colonies had to reach a specific size before they could reproduce sexually, whereas there was no such limit for asexual reproduction. Despite the dispersal limitations of large asexual diaspores, asexual dispersal is still common among epiphytes, with higher growth rates for the asexual diaspores partially compensating for the limited dispersal. Furthermore, habitat turnover most likely favors asexual diaspores that start growth rapidly.

Löbel and Rydin (2009), working in the temperate zone, further considered that competition was not an important character in the epiphytic habitat because of the difficulty of dispersal and ability to spread vegetatively. Yu and Wilson (2001) pointed out the importance of patchiness and arrival times in plants, a concept that seems appropriate for bryophytes, especially epiphytes. They suggest that "trade-offs between different stages of colonization could be far more common in nature than a trade-off between competitive ability and colonization ability."

Botanists have traditionally considered vegetative reproduction (Figure 1) as making only limited contributions to genetic variability and new adaptation. But is this really the case, in particular, of bryophytes? Laaka-Lindberg *et al.* (2003) consider asexual propagules to have a significant role in bryophyte genetic dynamics.

In view of the vegetative propagation sources, Scrosati (2002) has offered a new definition of **genet** to allow for those plants such as bryophytes and algae that routinely propagate from vegetative cells: "For clonal autotrophic macroorganisms, in general, genet may be defined as a free-living individual that develops from one original zygote, parthenogenetic gamete, or spore and that produces ramets vegetatively during growth."

In bryophytes, only a few living cells may start a new plant. And it may be those very cells that are different, different in ways that endowed them, and them alone, to survive whatever killed the remainder of the plant. Through somatic mutations, individual cells may indeed be more adapted than the plant they occupy. And because of their small size, such fragments in bryophytes can be dispersed and serve as propagules. Each individual or part of an individual gametophore in the clone is capable of renewed growth upon relocation. However, while this scenario is theoretically possible, we have no clue how often it occurs.

While spores are the sexual means of reproduction and dispersal of mosses, providing a mechanism for recombination and variation, it is likely that most mosses rely more heavily on various vegetative means for their propagation (Anderson 1963; Steere 1965; Schuster 1966; Longton 1976, 1982; Selkirk 1984; Schofield 1985). For example, in three ***Octoblepharum*** (Figure 13) species in Panama, Korpelainen (1999) found that most populations consisted of a single genet, hence resulting from a single colonization event by one individual.

Clones can be very important in recolonization of minor disturbances. Frego (1996) reported on four boreal bryophytes and their ability to do so. ***Pleurozium schreberi*** (Figure 5) often has pure colonies in black spruce forest (*Picea mariana*). But it also has colonies with minor species as seeming invaders (Figure 24). Frego found that these minor species are able to persist by occupying small disturbance gaps in the ***P. schreberi*** colony. All of the species were able to colonize by encroachment of vegetative shoots. Propagules were important for this encroachment. ***Pleurozium schreberi*** was the most rapid colonizer, probably due to a combination of rapid growth and abundant vegetative propagules.

Figure 24. ***Pleurozium schreberi*** (center) and ***Dicranum polysetum*** (lower left), a common species combination in the boreal forest. Photo by Janice Glime.

Such reliance on asexual reproduction is due in part to the difficulty of completing sexual reproduction in many bryophytes. Since nearly 60% of the bryophytes are dioicous (Wyatt & Anderson 1984), and the monoicous habit usually provides more opportunity for sexual reproduction than the dioicous habit, it is easy to understand the importance of vegetative reproduction (Schofield 1985). Furthermore, some widely distributed species have never been found with sporophytes.

Dispersal potential is a major limiting factor on the distribution of bryophytes (Pohjamo *et al*. 2006). Hence, those species with mixed reproductive strategies have a greater chance of success. Pohjamo *et al*. suggest that such mixed strategies are particularly useful in a heterogeneous landscape where different means of reproduction have different levels of success in each of the microhabitats, and possibly in different years. Traditional thinking suggests that long distance dispersal is generally best by spores, whereas vegetative dispersal places the diaspores close to the parents, generally in the same environment. But what occurs when both are the same size?

Using trapping techniques, Pohjamo *et al*. (2006) tested this propagule size relationship for the leafy liverwort ***Anastrophyllum hellerianum*** (Figure 25-Figure 26), a dioicous inhabitant of **decorticated** (lacking bark) logs in their study area. This species produces gemmae on the branch apices, and these gemmae approximate the size of the spores. In their study, spore dispersal had little dependence on distance in the field or forest. The dispersal of gemmae was more strongly dependent on distance in the open than in forest sites. Rainy periods favored gemmae deposition compared to dry periods, perhaps due to effects of splashing. But weather seemed to have no effect on the dispersal pattern of either spores or gemmae. Gemmae provided the advantage of nearly continuous availability, whereas spore dispersal was seasonal. The striking revelation from this study is that gemmae, at least those of the same size as spores, can contribute to long-distance dispersal.

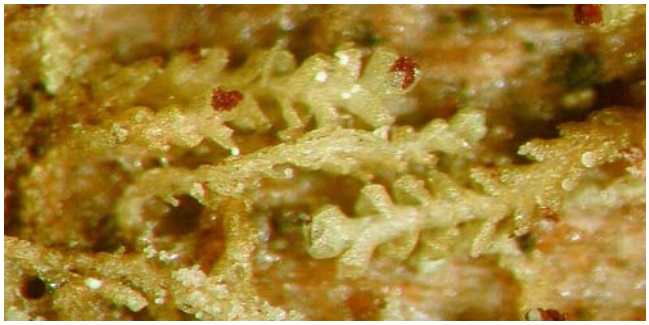

Figure 25. ***Anastrophyllum hellerianum*** with gemmae. Photo by Michael Lüth, with permission.

Figure 26. ***Anastrophyllum hellerianum*** gemmae. Photo by Des Callaghan, with permission.

Adaptations

There seems to be little information on adaptations of asexual propagules for dispersal or establishment. Thiers (1988) examined morphological adaptations of tropical rainforest **Jungermanniales**, including diaspores. She found that these diaspores had a secretion of sticky mucilage with discoid gemmae production. We can guess at some adaptations – projections that help bulbils adhere, dense starch storage in gemmae, thicker cuticles to reduce water loss, physiological ability to withstand desiccation, hormones (ABA) to induce dormancy, but these are guesses and remain to be tested as actual factors.

Fragmentation

Bryophytes have the ability to produce new plants from almost any part, making fragmentation a viable means of reproduction. Such a process requires that at least some cells lose their specificity (**dedifferentiate**), then differentiate into a new plant (Giles 1971). Giles considered that as long as cells remain on the parent plant, they will not dedifferentiate. But there are some indications among the leafy liverworts that such detachment is not always necessary before new plantlets are able to grow, particularly if the leaf is attached to a fragment rather than an attached plant (Fulford 1936; Glime 1970). This might suggest that the cells require a continuing source of an inhibitor to prevent dedifferentiation.

Fragmentation is the simplest form of asexual reproduction, a method used by the Japanese for the development of moss gardens (Ando 1971, 1987). Cells detached from virtually any part of a moss or liverwort are capable of regeneration into a new plant. This is true of leaves in which the tips dehisce to function as propagules (Reese 1997). Some of these devices are highly specialized, as for example, the caducous branchlets of ***Leucodon andrewsianus*** (Figure 27) where sporophytes are unknown (Reese & Anderson 1997).

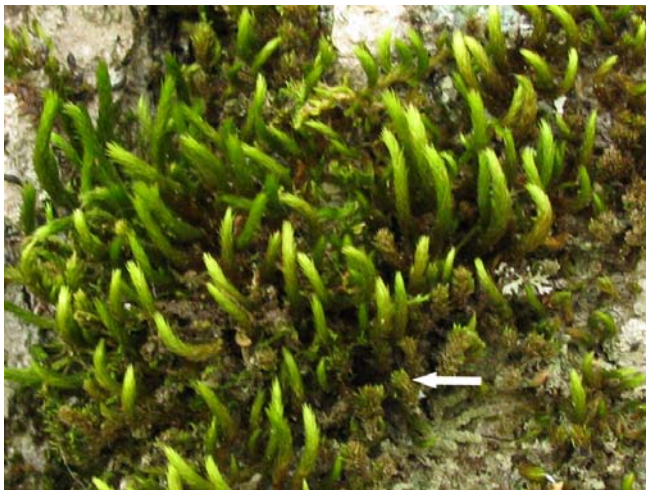

Figure 27. ***Leucodon andrewsianus*** on bark near Twin Lakes, Michigan. Arrow indicates caducous branchlets. Photo by Janice Glime.

Correns (1899) recognized the importance of the regenerative capacity of vegetative parts. They have historic importance in fossils as well. Miller (1985) reported fossil evidence that the dispersal and establishment of mosses had occurred as gametophyte fragments, suggesting that this is an ancient mechanism of reproduction and dispersal. This contention was supported by Lindskog and Eriksen (1995) who found fossil plant fragments in the debris layers of the ice core of a glacier in northern Scandinavia. These fragments compared well with the composition of the surrounding vegetation. Olga Belkina has supplied me with photographs indicating the presence of fragments and the establishment of colonies of ***Hygrohypnella polaris*** (Figure 28-Figure 30) on a glacier at Svalbard (Belkina & Mavlyudov 2011). Mosses are scattered across the glacier, as shown in Figure 31.

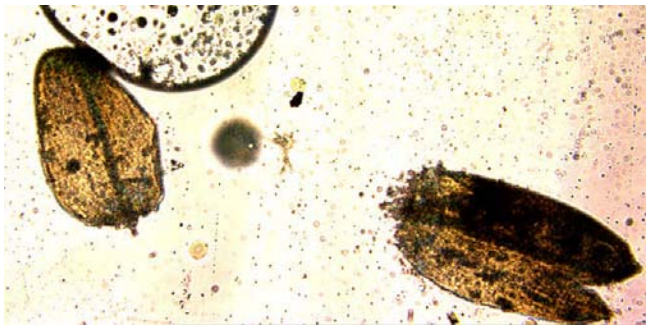

Figure 28. Fragments of ***Hygrohypnella polaris*** from glacier. Photo by Olga Belkina, with permission.

Figure 29. ***Hygrohypnella polaris*** on glacier. Photo by Olga Belkina, with permission.

Figure 30. Lower surface of ***Hygrohypnella polaris*** cushion with green branches and pedestal near it on glacier, indicating that it has been overturned and begun growth on the opposite side. Photo by Olga Belkina, with permission.

Figure 31. Austre Grønfjordbreen glacier with the moss ***Hygrohypnella polare*** in the foreground. Photo by Bulat Mavlyudov, with permission.

Because vegetative reproduction tends to be more successful than that from spores, having fragments or specialized structures can be a safety net. For example, in experimental plantings of ***Polytrichum juniperinum*** (as *P.*

alpestre) (Figure 32), Miles and Longton (1990) could find no evidence that spores germinated in the field. However, new shoots formed readily from shoot fragments. In the same experiment, production of shoots from spores in the short-lived ***Funaria hygrometrica*** (Figure 33-Figure 34) was readily apparent. In ***Atrichum undulatum*** (Figure 43) and ***Bryum argenteum*** (Figure 35), many spores germinated, but often the gametophores failed to develop. Rather, those species, like the ***Polytrichum juniperinum*** (Figure 32), regenerated more easily from fragments.

Figure 32. ***Polytrichum juniperinum*** (= *P. alpestre*), a species that forms new shoots easily from apices. Photo by Des Callaghan, with permission.

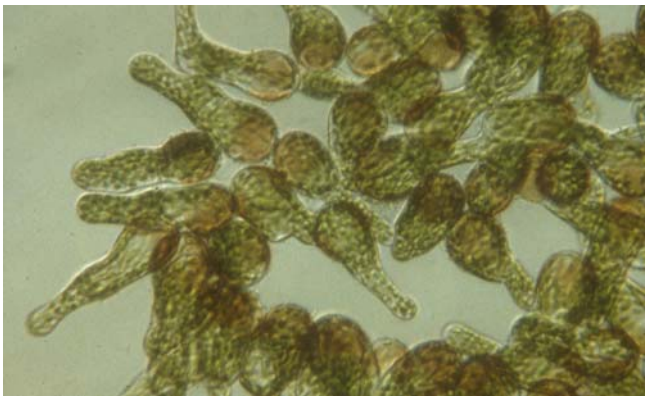

Figure 33. Germination of spores of ***Funaria hygrometrica***. Photo by Janice Glime.

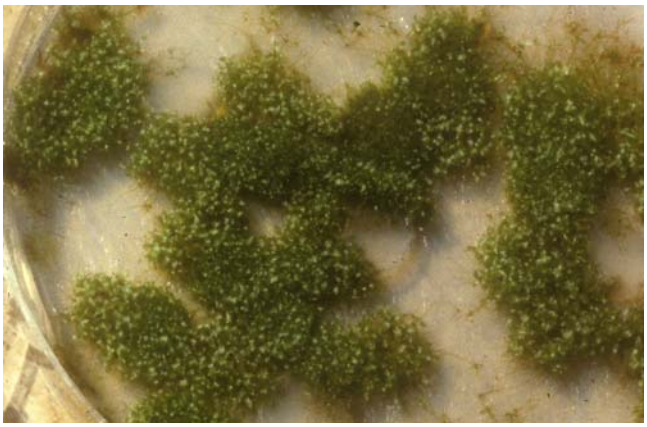

Figure 34. Young plants of ***Funaria hygrometrica*** germinated from spores. Each clump is the result of one spore, demonstrating the large number of vegetative reproduction by buds on the protonemata. Photo by Janice Glime.

Figure 35. ***Bryum argenteum***, a species with caducous tips but spores that often fail to germinate. Photo by George Shepherd, through Flickr Creative Commons.

Leaves and Stems

Peter Poschlod (pers. comm. 6 March 2013) considers fragmentation to be the most important dispersal diaspore in peatlands, citing the absence of ***Sphagnum*** spores in traps, but the frequent presence of vegetative fragments (Poschlod 1995). Furthermore, he has regenerated protonemata and shoots from leaf fragments of both ***Sphagnum*** from peatlands (Poschlod & Pfadenhauer 1989) and brown mosses from fens (Poschlod & Schrag 1990).

In most cases, regeneration from fragments starts with a protonema. Longton and Schuster (1983) reported that even apparently dead or dark, moribund lower shoots of ***Pleurozium schreberi*** (Figure 5) and ***Bryum argenteum*** (Figure 35) are capable of producing protonemata. Clymo and Duckett (1986) likewise reported the development of protonemata and/or shoots from lower shoot tissues that appeared to be dead or moribund. Using cores from at least 30 cm depth of ***Sphagnum papillosum*** (Figure 36), ***S. magellanicum*** (Figure 5), and ***S. recurvum*** (Figure 37) they were able to culture numerous new shoots. They estimated that the fragments in the cores were 25-60 years old. The growths appeared to arise from both fragments and spores, with the latter producing protonemata first. Nevertheless, some protonemata arose directly from old stems, whereas most of the growths from fragments directly produced stems and leaves. Regeneration required both light and air, explaining the lack of growth prior to removal through coring. These cores also gave rise to five species of leafy liverworts, but it is unclear if these came from fragments, gemmae, or spores.

Polytrichum species seemed to be incalcitrant to growth from leaf fragments, but in 1980, Wilmot-Dear succeeded in demonstrating regeneration from leaves in four species of the former ***Polytrichum***, growing them at 20°C in a 12:12 light:dark cycle. ***Polytrichum commune*** (Figure 38), ***P. juniperinum*** (Figure 32), and ***Polytrichastrum formosum*** (Figure 39) developed long, much-branched secondary protonemata that produced buds. ***Pogonatum urnigerum*** (Figure 40) directly developed buds with no initial protonema. ***Polytrichum piliferum*** (Figure 41) produced short, unbranched protonemata, each with a single terminal bud. These regenerants arose

primarily from the large cells at the bases of lamellae, but some arose from the basal cells of the lamellae themselves. In ***Pogonatum urnigerum*** regeneration tended to decrease from the tip to the base of the leaf, whereas in ***Polytrichum*** and ***Polytrichastrum*** it decreased from base to tip. Only ***Pogonatum aloides*** (Figure 42), a species with persistent protonemata, did not regenerate from leaves. Wilmot-Dear advised that more experiments should be conducted on temperature prior to regeneration. ***Atrichum*** seems to regenerate from leaves rather easily. Gemmell (1953) reported leaf regeneration in ***Atrichum undulatum*** (Figure 43). I have seen it in ***Atrichum angustatum*** (Figure 44).

Figure 36. ***Sphagnum papillosum***, a species that can regenerate from 30 cm cores. Photo by Michael Lüth, with permission.

Figure 37. ***Sphagnum recurvum***, a species that can regenerate from 30 cm cores. Photo by Malcolm Storey, <www.discoverlife.com>, through Creative Commons.

Figure 38. ***Polytrichum commune***, a species that can grow from leaf fragments. Photo by James K Lindsey, with permission.

Figure 39. ***Polytrichastrum formosum***, a species that can grow from leaf fragments. Photo by James K. Lindsey, with permission.

Figure 40. ***Pogonatum urnigerum***, a species in which regeneration decreases from apex to base. Photo by David Holyoak, with permission.

Figure 41. ***Polytrichum piliferum***, a species that regenerates protonemata from leaves. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

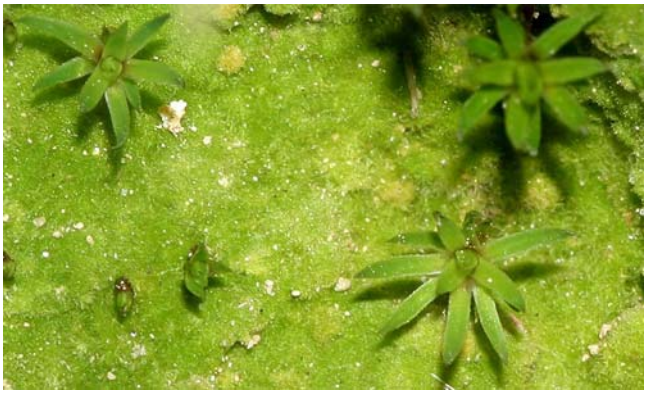

Figure 42. ***Pogonatum aloides*** with persistent protonemata. Photo by Walter Obermayer, with permission.

Figure 43. ***Atrichum undulatum*** from Gratiot River, MI, USA. These leaves can grow new plants from fragments. Photo by Janice Glime.

Figure 44. ***Atrichum angustatum*** with dry plants, protonemata, and buds. Photo by Janice Glime.

Newton (1972) likewise found differences in regeneration from detached leaves in **Mniaceae** species. Those of ***Plagiomnium undulatum*** (Figure 45) experienced more rapid regeneration than did ***Mnium hornum*** (Figure 46). Fragments of both species survived frost before and during regeneration. But males failed to survive desiccation of young gametophyte regenerants from leaves, whereas 77% of the females survived.

Figure 45. ***Plagiomnium undulatum***, a species with relatively rapid regeneration from detached leaves. Photo by Hermann Schachner, through creative Commons.

Figure 46. ***Mnium hornum***, a species with somewhat slower regeneration from detached leaves. Photo by Bob Klips, with permission.

Early reports of regeneration from deciduous leaves or branches of leafy liverworts are provided by Cavers (1903) and Watson (1964, p. 94). I have observed the development of a young plant from a leaf in the stream-dwelling leafy liverwort ***Scapania undulata*** (Figure 47-Figure 48; Glime 1970). In this case, some of the plantlets developed from the center of the leaf while it was still attached to a stem fragment (Figure 48). This was not an isolated incident – several such plantlets or buds were collected in debris in drift nets being used to capture stream insects. It is interesting that this collection occurred on 1 March in Plymouth, NH, USA, before the spring melt. At this time most of the plants would be completely submerged and the stream would typically have a moderate flow from intermittent snow melt. Greatest stream flow usually occurs in this area in early April, providing a dispersal means for the plantlets. The species typically grows submersed or on rocks where it is kept moist most of the year by flowing water that splashes against the rocks. ***Bazzania denudata*** (Figure 49) develops plantlets on normal leaves still adhering to the plant (see Figure 50) (Fulford 1936), as in the case of ***Scapania undulata*** (Figure 47-Figure 48). ***Plagiochila*** (Figure 51), on the

other hand, can form similar growths, but these usually occur on deciduous leaves (Schuster 1960, 1966).

Figure 47. ***Scapania undulata*** in a typical habitat on a rock in a stream where it is nearly always wet. Moving water can easily break off fragments in this location. Photo by Dick Haaksma, with permission.

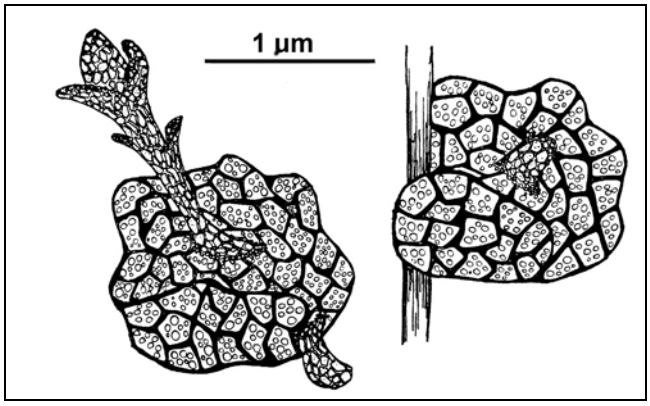

Figure 48. Detached leaf (**left**) with two developing plantlets and attached leaf (**right**) with beginning plantlet on ***Scapania undulata***. Drawing courtesy of Flora Mace.

Figure 49. ***Bazzania denudata***, a leafy liverwort that produces plantlets from normal leaves, but that also has fragile thin branches (shown here) projecting from beneath the stems and looking denuded. Photo from UBC Botany website, with permission.

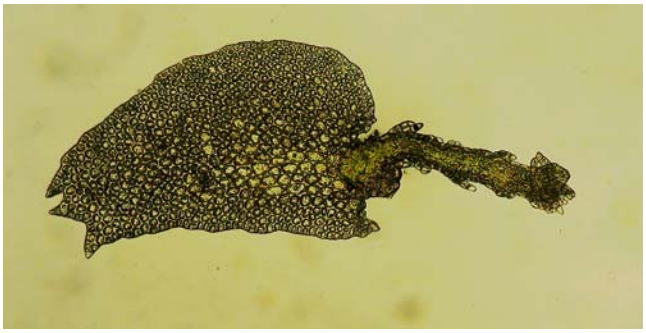

Figure 50. ***Bazzania adnexa*** leaf fragment with germling. Photo by Tom Thekathyil, with permission.

Figure 51. ***Plagiochila asplenioides***, member of a genus that forms growths on its deciduous leaves. Photo by Dick Haaksma, with permission.

Herbarium specimens often are not as dead as they look, and even bryophytes in nature in desert types of habitats can remain desiccated for many years. Maheu (1922) rehydrated ***Syntrichia ruralis*** (Figure 52) after 14 years of continuous desiccation. The shoots of this species regenerated from their leaves.

Figure 52. ***Syntrichia ruralis*** hydrated, a species that regenerated from leaves after 14 years of desiccation. Photo by Misha Ignatov, with permission.

Stark *et al*. (2004) found that dried plants do not regenerate as quickly as fresh material. In the desert moss ***Syntrichia caninervis*** (Figure 53), fresh material

regenerated in 3-14 days (Figure 54). They used juvenile, green, yellow-green, and brown leaves, representing 0, 2, 6, and 12 years old respectively, to determine regeneration. the 0-2-year-old leaves had somewhat greater viability, regenerated more quickly, and extended their protonemal filaments farther in the 58 days of the experiment. They likewise produced shoots more quickly and accumulated a greater biomass. They also found that female leaves were more likely to produce a shot than were male leaves. The sexes did not differ in time required to produce a protonema, linear extension of the protonema, or in rate of biomass accumulation. Nevertheless, protonemata derived from male leaves tended to emerge more quickly and produce greater total biomass, ultimately resulting in predominately protonemata. As a consequence, females had a higher success of shoot production, perhaps explaining rarity of males in ***S. caninervis***.

Figure 53. ***Syntrichia caninervis***, a species that is very desiccation tolerant and regenerates from leaves. Photo by John Game, through Creative Commons.

Figure 54. ***Syntrichia caninervis*** regeneration from leaf. Photo courtesy of Lloyd Stark.

Regenerants

Many leafy liverworts produce **regenerants** (new plants) (Barbara Crandall-Stotler, Bryonet 24 April 2021). In ***Lophocolea*** sp., these are produced along the leaf edges (Figure 55) (Emmet Judziewicz, Bryonet 23 April 2021). These tend to occur as the growing season is ending or the plant is in a less than favorable habitat (Barbara Crandall-Stotler, Bryonet 24 April 2021), such as this ***Lophocolea*** species (Figure 55) growing at a higher, drier, cooler than usual altitude. The regenerants develop like a sporeling (Figure 56), causing the leaves to resemble the juvenile leaves of the species. In ***Lophocolea*** sp., these are bilobed (Figure 56). These regenerants are able to re-establish the population once suitable growing conditions return.

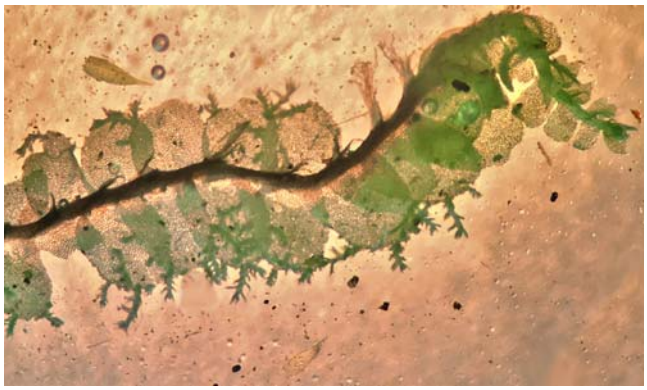

Figure 55. ***Lophocolea*** sp. with regenerants, found at Acacia koa kīpuka at 1700 m on Mauna Loa, Hawaii. Photo by Emmett Judziewicz and Virginia Freire, with permission.

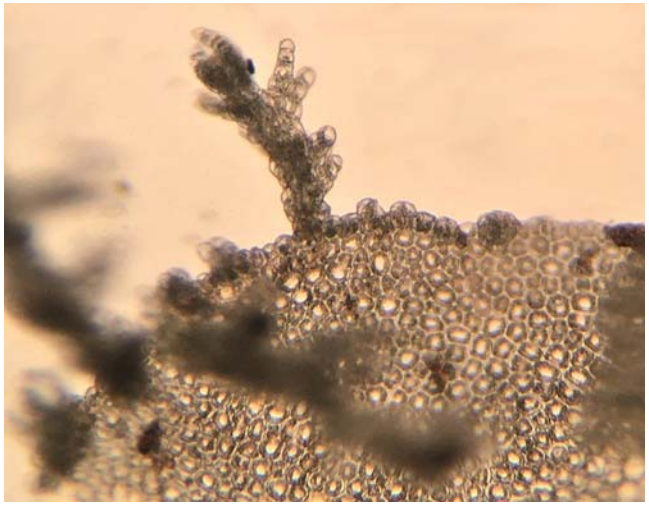

Figure 56. ***Lophocolea*** sp. with regenerant. Photo by Emmett Judziewicz and Virginia Freire, with permission.

Protonemata

Protonemata have been largely ignored in the ecology of bryophytes. This is not surprising due the their inconspicuous nature, difficulty in identification, and often short life. But Pasiché Lisboa (2014) has contributed to our knowledge by studying their dispersal potential in the moss ***Callicostella belangeriana*** and ***Taxiphyllum taxirameum*** (Figure 57). Spores from wild-collected capsules were cultured axenically to get protonemata in the lab. These

protonemata were placed on cardboard and splashed by three sequential drops of dyed water from 1 and 2 m height. This resulted in dispersal up to 80 cm, and it was more likely that a protonema hit by a drop would move than that it would remain stationary. These dispersed protonemata had a high survival rate, and even though most stayed within 10-12 cm, it provides an additional means for a colony to spread. I do wonder if the same dispersal would occur from soil instead of cardboard.

Figure 57. ***Taxiphyllum taxirameum*** with capsule, a species for which raindrop dispersal of spores has been demonstrated up to 80 cm. Photo by Bob Klips, with permission.

Perianths

But leaves and branches are not the only dispersal units through fragmentation. In ***Lophozia*** (=***Gymnocolea***) ***inflata*** (Figure 58), non-fertile **perianths** (leaves surrounding female reproductive structures) become more globose and are shorter than the fertile ones, and they develop a line of dehiscence where they are constricted at the base (Schuster 1966). Almost any disturbance will break them free. On dry days, these may drop to the ground, but more typically, when they are struck by raindrops, the perianths become free, or may already be free, and with their included air bubble they easily float. Such perianths then are carried away by water. But one could argue equally well that this light weight would permit them to be carried by wind should they be broken free on a dry and windy day. However, there is little documentation of regeneration from liverwort parts, so we can only guess that these perianths are able to form new plants. Perianths of ***Chonecolea doellingeri*** likewise are easily dislodged, but these do not become inflated (Schuster 1966).

Calyptrae

Britton (1902) reported that ***Fissidens fontanus*** (as *Octodiceras julianum*) (Figure 59) is able to regenerate from its calyptra, producing protonemata. The capsules of this species fall off just before maturity while they are still green and the calyptra is still attached. Together they are able to float, hence creating a potential dispersal unit of the calyptra. Its vegetative dispersal capabilities may account for its widespread occurrence in many kinds and locations of aquatic habitats.

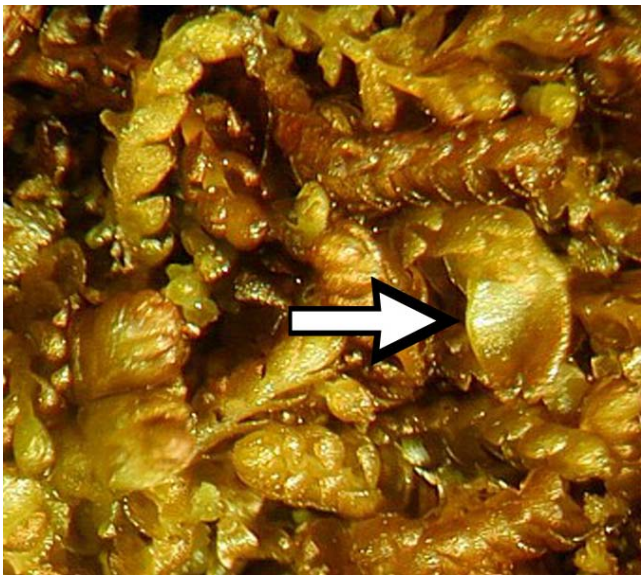

Figure 58. Perianth (**arrow**) of ***Lophozia*** (=***Gymnocolea***) ***inflata***. Photo by Michael Lüth, with permission.

Figure 59. ***Fissidens fontanus***, a species that can regenerate from its calyptra. Photo by Jan-Peter Frahm, with permission.

Kortselius *et al*. (2017) reported that the aquatic moss ***Fissidens fontanus*** is known to achieve asexual reproduction through the calyptra, developing gametophytes.

Wynne and Budke (2012) took the calyptrae one step further in ***Funaria hygrometrica*** (Figure 62). They looked at the ability of the calyptra to produce protonemata as a function of time and discovered several things: 1) The calyptrae remain alive and capable of producing protonemata for at least 28 days after detachment from the capsule; 2) the younger calyptrae produced significantly more protonemata that the oldest of three developmental stages.

Figure 60. ***Fissidens fontanus*** calyptrae with germination. Photo courtesy of Hans Kruijer.

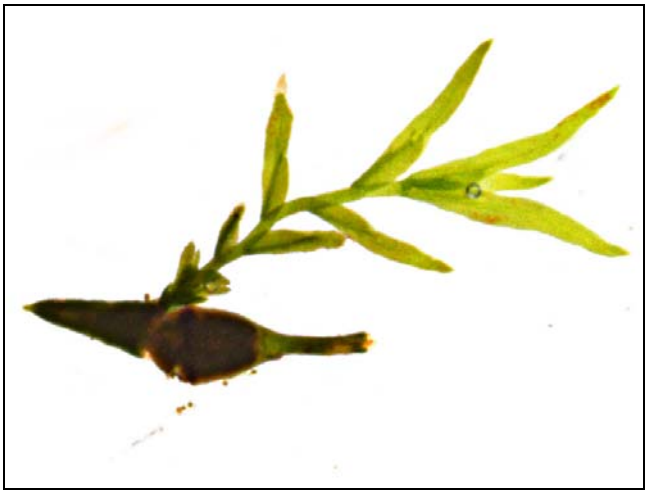

Figure 61. ***Fissidens fontanus*** calyptra with germination. Photo courtesy of Hans Kruijer.

Figure 62. ***Funaria hygrometrica*** young sporophytes with calyptrae. Photo by Michael Lüth, with permission.

Involucres

The **involucre** (protective sheath originating from thallus and surrounding single gametangium or sporophyte) is not a structure one would normally consider as a dispersal unit. Nevertheless, in ***Metzgeria*** (Figure 63), this seems to be the case (Kuwahara 1968, 1973). Eight species in this genus, including ***M. acuminata***, ***M. agnewii***, ***M arborescens***, ***M. filicina***, ***Echinomitrion*** (=***Metzgeria***) ***furcata*** (Figure 64), ***M. grollei***, ***M. imberbis***, and ***M. liebmanniana***, all have demonstrated the ability to grow branches from female involucres into normal vegetative thallus. These liverworts have come from Europe, Africa, South America, and North America, suggesting that the phenomenon might be present in other taxa that produce involucres. Since these are early papers, it is likely that other examples are known. But do these have any significance for fragmentation and dispersal?

Figure 63. ***Metzgeria conjugata*** with sporophyte and basal involucre. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Figure 64. ***Metzgeria furcata***, a species that can regenerate from the involucre. Photo by Des Callaghan, with permission.

Paraphyses

Many mosses produce paraphyses that surround the antheridia and archegonia. These are usually considered to

help maintain more constant moisture conditions than would be possible without them, help to squeeze sperm out of the antheridia, and may also function to protect against frost, solar radiation, and herbivore damage. But the presence of chlorophyll in a structure that would not seem to need it caused Correns (1890) and Hill (1903) to suspect that they might also serve as propagula. Hill even observed protonema-like branching in paraphyses (Figure 65) from ***Rhodobryum roseum*** (Figure 66-Figure 67). But early attempts to actually grow new plants from these paraphyses failed (Heald 1898; LaRue 1930).

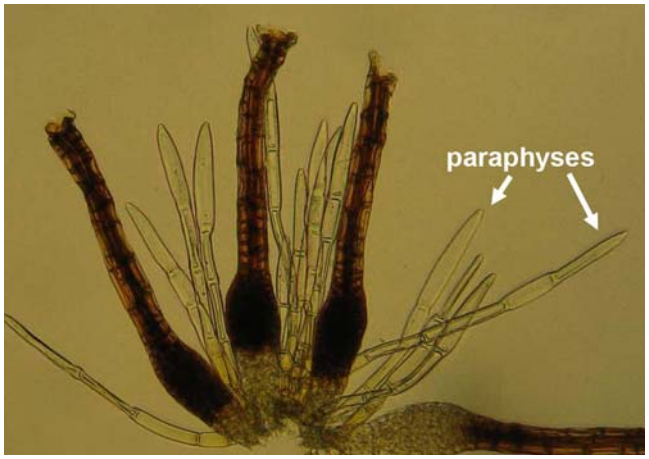

Figure 65. ***Zygodon intermedius*** archegonia among paraphyses. Photo by Tom Thekathyil, with permission.

Figure 66. ***Rhodobryum roseum***, a moss in which paraphyses can develop protonemata. Photo by Hermann Schachner, through GNU Free Documentation.

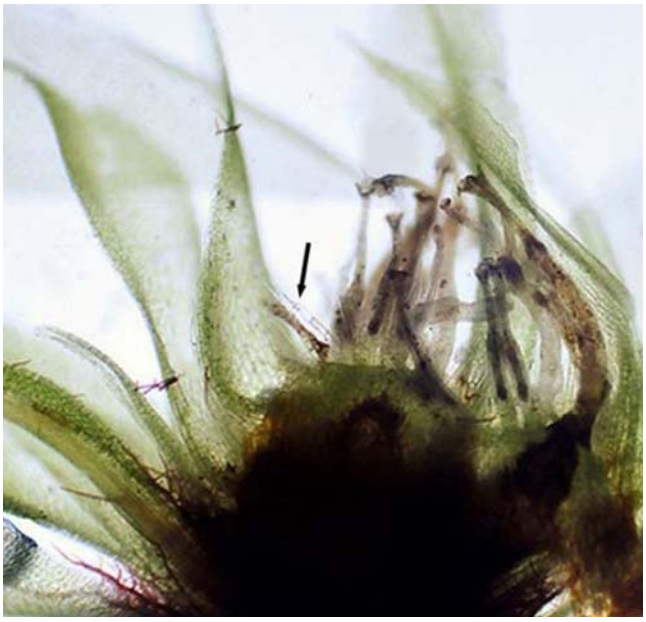

Figure 67. ***Rhodobryum roseum*** perichaetium. Arrow indicates paraphysis. Photo by George J. Shepherd, through Creative Commons.

Finally, Reese (1955), also convinced that a regenerative function was implied by the presence of chlorophyll in the paraphyses, managed to culture paraphyses of three species and successfully produce regeneration: ***Ptychostomum*** (=***Bryum***) ***capillare*** (Figure 7) 10%; ***Aulacomnium palustre*** (Figure 68) 12.5%; ***Funaria hygrometrica*** (Figure 69) 25%. ***Ptychostomum capillare*** and ***Funaria hygrometrica*** required only one month for the first evidence of regeneration, whereas ***Aulacomnium palustre*** required two months. Reese suggested that the ease of obtaining regenerants from these three mosses suggests that other mosses with green paraphyses might also regenerate in this way. But this leaves one question remaining, how are they dispersed?

Figure 68. ***Aulacomnium palustre*** in MI, USA. Photo by Janice Glime.

Figure 69. ***Funaria hygrometrica*** with young sporophytes. Photo by Andrew Spink, with permission.

Falling Epiphytes

In the tropics, where epiphytes abound, bryophytes can fall from the canopy. Within dense canopies, these bryophytes can fall to another branch that is within their tolerance range for light, temperature, and humidity. Others will fall to the ground. Clumps of plants in the Neotropics ranged in size from 90 cm^3 to 36,000 cm^3 with the number of individual plants per clump ranging 2-9 (Matelson *et al*. 1993). Unfortunately for us, data for bryophytes were not separated from the general assessment. Matelson *et al*. found that these falling epiphytes can contribute to the NH_4^+ and K^+ of the forest floor. There were no significant differences in longevity among the eight plant categories (bryophytes being one category), suggesting that perhaps some of the bryophytes could continue to live and possibly be re-dispersed by wind or animals.

Moss Balls

Some fragments get dispersed by snow and ice and may even blow around as moss balls on glaciers. McDaniel and Miller (2000) reported both bryophyte and vascular plant fragments in late-spring snowbeds in the Adirondack Mountains, NY, USA. The alpine fragment diversity far exceeded that from a forested site, and the bryophyte diversity exceeded that of the vascular plants. Among the bryophytes, 82% were sufficiently healthy and complete to permit identification to genus or species. An interesting revelation was the presence of liverworts from the alpine samples, suggesting that their absence from late-glacial sediments may be due to the fossilization process (taphonomy) rather than their absence in the flora or their inability to disperse by fragments. Although rare, some of the fragments in the alpine areas came from lower elevation balsam fir and red spruce-balsam fir forests. Fragments deposited on the snow would be available for immediate establishment when the snow melted, with cool temperatures and plenty of water to get started. The bryophytes will be there when the glaciers melt.

Cushions of mosses from large basalt outcrops can create moss balls when they become detached from their substrate (Pérez 2010), particularly due to activity of the Dark-rumped Petrels (***Pterodroma phaeopygia***) that burrow to make nests under outcrops. Such detachment can be facilitated by rainfall, desiccation, wind, frost, and animal disturbance. These balls can form as the clumps are transported down steep slopes (26-34°) by geomorphic processes such as frost (especially needle ice activity), runoff, and wind. At the Haleakala crater, Maui, Hawaii, USA, these balls contained ***Grimmia trichophylla*** (Figure 71) and ***G. torquata*** (Figure 72). Pérez found that the larger mosses tended to become flattened because they were less disturbed by needle ice, hence remaining immobile for longer periods of time. These potential moss balls generally moved less than 100 cm (83%); only 5% moved 200-839 cm. Trapping of dust grains and small soil particles, combined with water-holding capacity of the mosses, created a greater water storage capacity in these balls (310%) compared to that in the soils of the site (16.8%). Pérez interpreted this as a self-replicating dispersal system on these slopes.

Figure 70. ***Pterodroma phaeopygia*** (Galapagos Petrel, Dark-Rumped Petrel) that burrows and disrupts mosses, causing moss balls to form. Photo by Lip Kee, through Creative Commons.

Figure 71. ***Grimmia trichophylla*** on a boulder. Clumps such as this are easily broken off and can become moss balls. Photo by Michael Lüth, with permission.

Figure 72. ***Grimmia torquata***. Once free, a clump can become a moss ball; lower branches grow toward the center of an upside down plant. Photo by Michael Lüth, with permission.

I have seen moss balls that fell from the talus slopes near the Red River in New Mexico, USA. There were numerous balls on the ground near the base of the slope, some quite rounded and others irregular in shape (Figure 74-Figure 73).

Figure 73. Detached moss ball formed by rolling down the talus slope shown in Figure 74. Photo by Janice Glime.

Animals – Breaking or Ingesting Bryophytes

Some fragments have a little help from the animals in the vicinity. We are finding an increasing number of animals that ingest bryophytes, including insects, earthworms, molluscs, rodents, and occasionally larger mammals. (See next subchapter.)

Extreme Environments

In extreme environments, fragments may be important in dispersal. They can be produced under the most harsh conditions and be blown around in an arrested state until landing in a suitable microhabitat.

Antarctic & Arctic

On the continent of Antarctica, only three bryophytes were known to produce sporophytes: ***Bryum pseudotriquetrum*** (as *Bryum algens*; Figure 75) (Filson & Willis 1975), ***Hennediella heimii*** (as *Bryum antarcticum*; Figure 76) (Kanda 1981), and ***Grimmia trichophylla*** (Figure 71; Selkirk 1984). However, birds and other animals scratching among the plants dislodge numerous fragments (Selkirk 1984). When Selkirk (1984) set out Tauber traps (Tauber 1974) to collect the diaspores on the surface of the snow in the Antarctic, she found that only two species had been dispersed by specialized structures: ***Ulota phyllantha*** (Figure 77) by gemmae (Figure 77-Figure 79) and ***Dicranella cardotii*** by stem tips. Most of the plants, however, had been dispersed by various fragments of leaves and stems. She further verified that many of these moss taxa were actually growing from vegetative fragments at all the types of sites she observed where bare, colonizable areas were available.

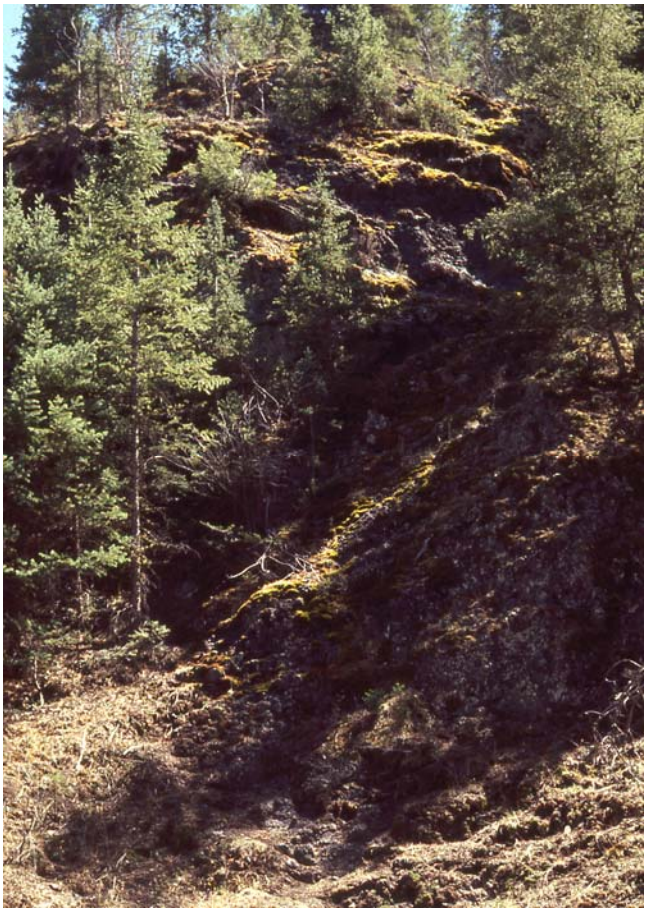

Figure 74. Talus slope near the Red River, New Mexico, USA, a source of mosses that roll down the slopes and across the valley below, breaking off tips and becoming rounded moss balls. Photo by Janice Glime.

Figure 75. ***Bryum pseudotriquetrum***, one of three bryophytes known to produce sporophytes in the Antarctic. Photo by David T. Holyoak, with permission.

Figure 76. ***Hennediella heimii*** with capsules, a species that produces capsules in the Antarctic. Photo by David T. Holyoak, with permission.

Figure 77. Brown gemmae of ***Ulota phyllantha***, a dispersal unit found in Tauber traps in the Antarctic. Photo by Michael Lüth, with permission.

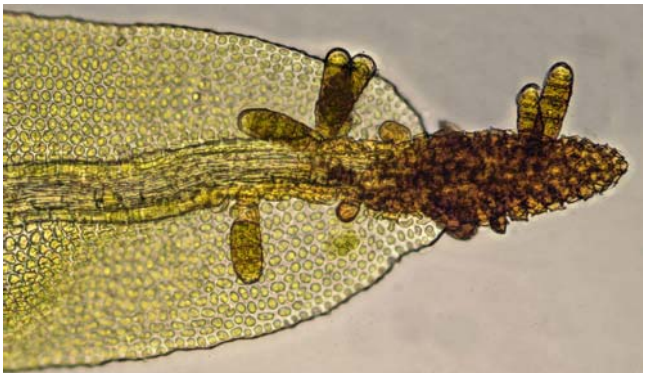

Figure 78. ***Ulota phyllantha*** gemmae at tip of leaf. Photo by Dick Haaksma, with permission.

In Arctic Canada, Miller and Howe Ambrose (1976) estimated a total of 33,820 bryophyte fragments per cubic meter of granular snow! Of these, 97% were less than 2.25 mm, so small that airborne dispersal was likely. They found that almost all the viable fragments were leaf-bearing moss stem tips. Based on their experiments and the number of fragments available, they estimated that over 4000 viable propagules occurred per cubic meter of granular snow. They suggest that the same winds that serve to disperse these fragments serve as the agent to break the fragments from the plants. Cold air and desiccating conditions make the plants more fragile and contribute to the breakage.

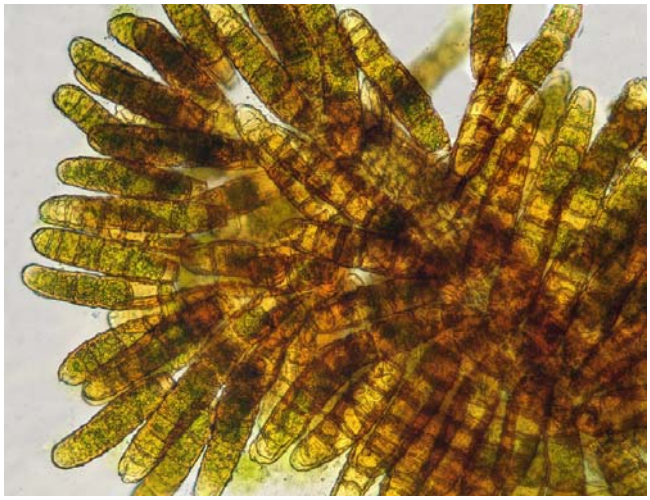

Figure 79. ***Ulota phyllantha*** gemmae at tip of leaf. Photo by Dick Haaksma, with permission.

Alpine

Many bryophytes seldom or never produce sporophytes in harsh environments such as that of alpine summits, requiring them to rely on asexual means for reproduction and dispersal. Robinson and Miller (2010) compared two species of ***Sphagnum*** from the Adirondack Mountains and other high altitude sites in eastern North America. These two species [***S. pylaesii*** (Figure 80), ***S. tenellum*** (Figure 81)] live in similar habitats, but their life strategies differ. Robinson and Miller used 17 microsatellite loci to infer dispersal from the gene flow estimates. Branch fragments of ***S. pylaesii*** were coated with UV-fluorescent dye and released from two alpine summits. Fragments were located after 12 and 24 h and 1 week using UV LED light sources in the evening. Both species exhibited more genetic variation than expected. However, the species differed, with ***S. pylaesii*** having high differentiation and low gene flow between populations throughout its North American distribution. ***Sphagnum tenellum*** was less differentiated and showed higher levels of gene flow. Robinson and Miller concluded that fragments played an important role in transport both on summits and to other alpine summits.

Figure 80. ***Sphagnum pylaesii***, a species that can be dispersed by branch fragments. Photo by Michael Lüth, with permission.

Figure 81. ***Sphagnum tenellum*** with capsules. This is a species that exhibits greater gene flow than ***S. pylaesii***, perhaps due to its capsule production. Photo by Dick Haaksma, with permission.

Vegetative Diaspores

Correns (1899) examined 915 types of mosses with **vegetative diaspores** (specialized propagula of Longton and Schuster). Since then, usage of terminology has diverged among the countries of the world, and even within one country. In the recent *Glossarium Polyglottum Bryologiae* (Magill 1990), bryologists from around the world attempted to standardize terminology. In that edition, Magill used the concept of Goebel (1905) that divided vegetative diaspores into two groups based on their development at germination. He applied the term **propagula** to those diaspores that have an apical cell and can grow directly into a leafy shoot if the apical cell is reactivated (Figure 83, Figure 95). Unfortunately, this definition is clouded by its impracticality and because even these diaspores usually produce protonemata.

Köckinger and Kucera (2007) considered that ***Barbula amplexifolia*** (Figure 82) reached the Austrian Alps by vegetative gemmae across the cold Pleistocene steppes from Central Asia. They support this conclusion by the absence of male plants and sporophytes in the Alps and the low level of morphological and anatomical variability. They suggest that extensive road construction through the forests may be facilitating their recent increase in distribution.

Figure 82. ***Barbula amplexifolia*** with capsules in India. Photo by Michael Lüth, with permission.

Figure 83. Deciduous branches (**propagula**) of the moss ***Campylopus pilifer***, representing a common means for its reproduction. Photo by Michael Lüth, with permission.

Magill (1990) likewise used the concept of Goebel to define **gemmae** as vegetative diaspores with no apical cell and that always must begin growth with a protonemal phase (Figure 19, Figure 95). These units then include caducous leaves and endogenous gemmae, as well as those specialized, oval, round, or irregularly shaped structures we have always called gemmae in the strictest sense.

Among the **propagula**, Imura and Iwatsuki (1990) identified four aboveground types:

1. **Deciduous shoot apices** (Figure 35, Figure 84) result from an area weakened by a cleavage in the cell walls. These often already have rhizoidal initials at their basal parts. Such shoot apices occur in ***Bryum argenteum*** (Figure 35) and ***Campylopus sinensis*** (=***C. japonicus***) (Figure 84).

Figure 84. ***Campylopus sinensis*** (=***C. japonicus***) with broken tips. Photo from Hiroshima University website, with permission.

2. **Caducous branchlets** (caducous = deciduous) seem like deciduous shoot apices, except that they are branchlike structures with minute leaves and are attached to the parent plant by one-celled stalks. A good example of these is in ***Pterigynandrum filiforme*** (Figure 85; Bergamini 2006). Although such branches are not common among pleurocarpous bryophytes, they can also be found in ***Pseudotaxiphyllum*** (=***Isopterygium***) ***elegans*** (Figure 86), ***Leucodon***

sciuroides (Figure 87), ***Platygyrium repens*** (Figure 88-Figure 89), and ***Pseudoleskeella nervosa*** (Figure 90).

Figure 85. ***Pterigynandrum filiforme***. Photo by Dick Haaksma, with permission.

Figure 86. ***Pseudotaxiphyllum*** (=***Isopterygium***) ***elegans*** with caducous filiform branches that serve as propagules. Photo by Jan-Peter Frahm, with permission.

Figure 87. ***Leucodon sciuroides*** var. ***sciuroides***. Photo by David Holyoak, with permission.

Figure 88. ***Platygyrium repens*** with bulbils at tips of branches. Photo by Dick Haaksma, with permission.

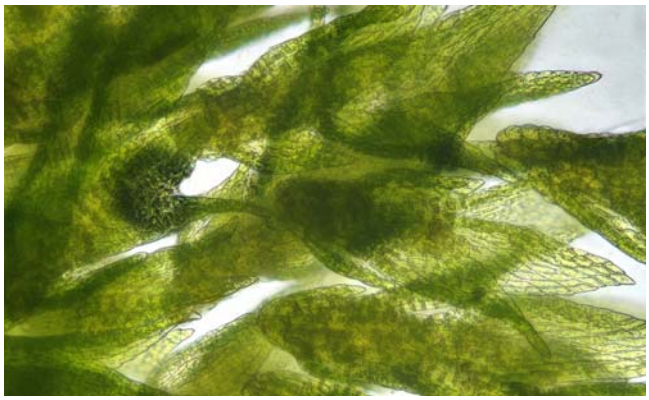

Figure 89. Microscope view of ***Platygyrium repens*** bulbil branches. Photo by Dick Haaksma, with permission.

Figure 90. ***Pseudoleskeella nervosa*** showing bulbils (caducous branchlets) at branch tips. Photo by Hermann Schachner, through Creative Commons.

3. **Flagella** are slender branches with reduced leaves and occur in the axils of upper leaves. The basal portion is multicellular, thus separating them from caducous branchlets. These are common in ***Dicranum flagellare*** (Figure 23).
4. **Bulbils** (Figure 91-Figure 95) usually occur on one-celled, short stalks and have what appear to be partially developed leaves. Some are round and bulb-like, others are thread-like. They are common in ***Pohlia*** (Figure 91-Figure 94).

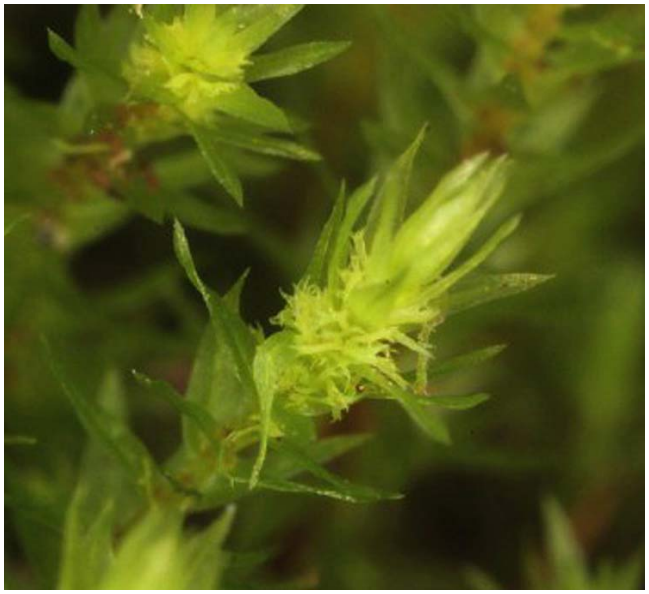

Figure 91. ***Pohlia flexuosa*** with flagelliform bulbils. Photo by Jan-Peter Frahm, with permission.

Figure 92. ***Pohlia bulbifera.*** Photo by David T. Holyoak, with permission.

Figure 93. ***Pohlia bulbifera*** bulbils in leaf axil. Photo by Des Callaghan, with permission.

Figure 94. ***Pohlia filum*** with bulbils in Europe. Photo by Michael Lüth, with permission.

Gemmae can be filamentous, spindle-shaped, globular, discoid, or multi-horned (Figure 95). They occur on various parts of the gametophyte and sometimes have pale, thin-walled cells at the base. Protonemal and rhizoidal "gemmae" are usually labelled **bulbils** on materials from biological supply houses. Two types of gemmae can be identified based on their origin on the plant:

1. **Caducous leaves** are very specialized leaves of reduced size that may or may not differ from normal leaves in basic structure. In ***Aulacomnium***, most of the taxa produce special branches with gemmae (caducous leaves) that are easily detached, reduced leaves (Imura *et al*. 1991). In ***Campylopus fragilis*** (Figure 98-Figure 99) and ***Syntrichia laevipilum*** (as ***Tortula pagorum***; Figure 96-Figure 97), the caducous leaves are on short branches at the axils of upper leaves (Imura & Iwatsuki 1990). ***Thuidium cymbifolium*** (Figure 100) produces caducous flagella (Akiyama 2009).

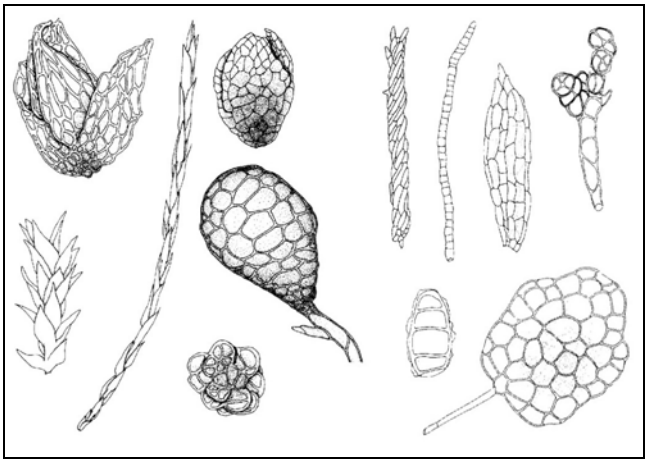

Figure 95. Propagula and gemmae of selected bryophytes. Redrawn from Imura and Iwatsuki (1990).

Figure 96. ***Syntrichia laevipilum*** (=*Tortula pagorum*) with caducous leaves in the axils of upper leaves. Photo by Robert Klips, with permission.

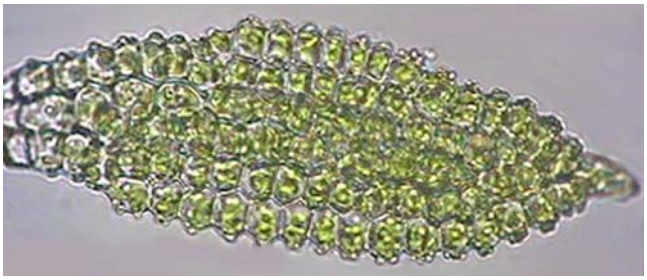

Figure 97. Caducous leaf gemma from axils of upper leaves of ***Syntrichia laevipilum***. Photo by Paul Davison, with permission.

Figure 98. ***Campylopus fragilis*** with short branches having caducous leaves in the axils of upper leaves. Photo by David T. Holyoak, with permission.

Figure 99. ***Campylopus fragilis*** with caducous leaves and branches. Photo by Jan-Peter Frahm, with permission.

Figure 100. ***Thuidium cymbifolium*** with capsules, a species that forms caducous flagella for asexual reproduction. Photo by Li Zhang, with permission.

2. **Endogenous gemmae** (Figure 101-Figure 111) are produced inside a cell initial. Most of the taxa among the mosses with these structures are in the **Grimmiaceae**, but they are common among the **liverworts**, often occurring as patches of non-green color at leaf tips or margins.

Figure 101. ***Heterogemma*** (=***Lophozia***) ***capitata*** leafy plant with sporophyte; this species produces endogenous gemmae (Figure 102). Photo by Jan-Peter Frahm, with permission.

Figure 102. ***Heterogemma*** (=***Lophozia***) ***capitata*** with endogenous gemmae on leaf margin. Photo modified from web site of Paul Davison <www2.una.edu/pdavis/bryophytes.htm>, with permission.

Figure 103. ***Scapania nemorea*** in Europe showing apical gemmae. Photo by Michael Lüth, with permission.

Figure 104. ***Scapania nemorea*** showing mature apical gemmae. Photo by Dick Haaksma, with permission.

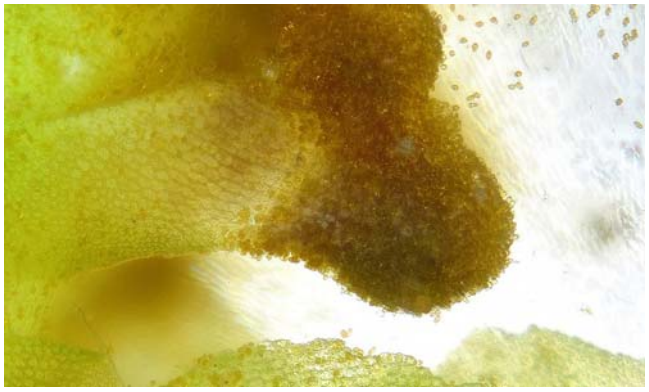

Figure 105. ***Scapania nemorea*** gemmae on leaf. Photo by Dick Haaksma, with permission.

Figure 106. ***Scapania nemorea*** gemmae on leaf margin. Photo by Paul Davison, with permission.

Figure 107. ***Scapania nemorea*** leaf gemmae. Photo by Dick Haaksma, with permission.

Figure 108. ***Lophozia ventricosa*** with leaf gemmae. Photo by Jan-Peter Frahm, with permission.

Figure 109. ***Jubula*** (=***Radula***) ***complanata*** with gemmae on leaf margins. Photo by Walter Obermayer, with permission.

Figure 110. ***Jubula*** (=***Radula***) ***complanata*** gemmae. Photo by Walter Obermayer, with permission.

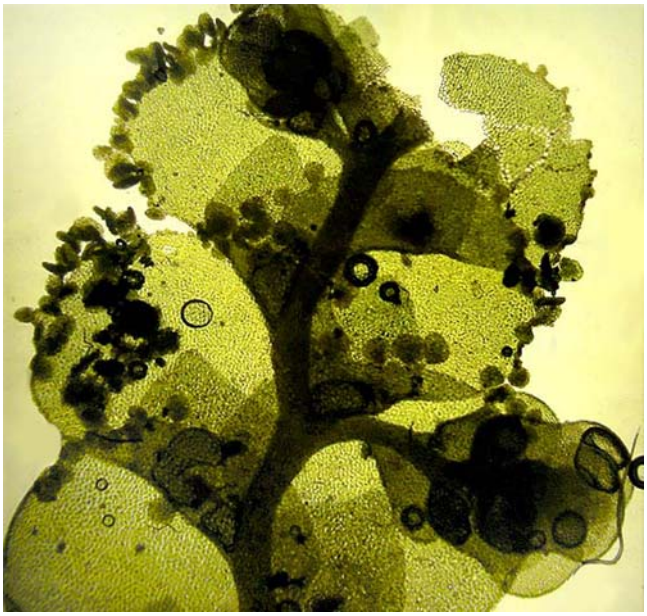

Figure 111. ***Jubula*** (=***Radula***) ***complanata*** leaves with gemmae. Photo by Walter Obermayer, with permission.

Stem and Leaf Gemmae

As one might expect, at least in some cases, the environmental conditions can have a strong effect on forms and numbers of gemmae. For example, the species ***Bryum dichotomum*** has several forms that previously have been named as different species (Dolnik 2006). These species, including the synonym ***B. bicolor*** (Figure 112), have been separated based on the forms and numbers of gemmae. Dolnik germinated the bulbils in culture in the greenhouse under a variety of conditions. In the form of ***B. dichotomum*** identified as its synonym ***B. barnesii*** (Figure 113-Figure 114), environmental conditions had no effect on number of bulbils per leaf axil, but the shape varied with seasonal variability, causing taxonomists to initially consider them to be different species. Both these bulbils and those developing on protonemata can float for several days and remain viable, providing a potential means of long-distance dispersal to locations along streams and shorelines where water levels vary.

Figure 112. ***Bryum dichotomum*** (***B. bicolor*** form). Photo by Michael Lüth, with permission.

Figure 113. ***Bryum dichotomum*** (***B. barnesii*** form) with bulbils in leaf axils. Photo by Kristian Peters, with permission.

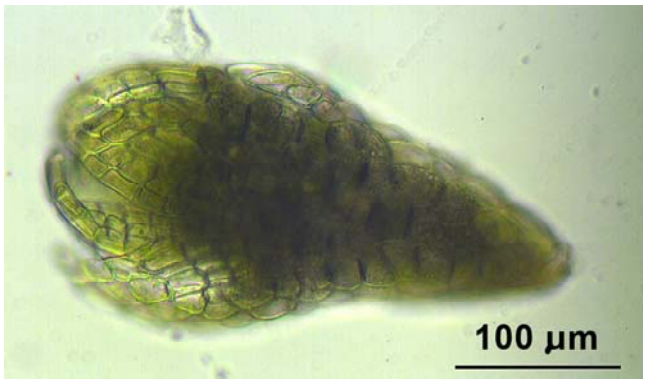

Figure 114. ***Bryum dichotomum*** (***B. barnesii*** form) bulbil from leaf axils. Photo by Kristian Peters, with permission.

In the genus ***Fossombronia***, two species are known to produce budlike vegetative propagules from leaf cells (Zhang *et al*. 2003). In South Africa, ***Fossombronia gemmifera*** has this behavior (Cargill 2000). In Australia, sterile plants of ***Fossombronia cerebriformis*** produce adaxial leaf gemmae at the bases of leaves (Scott & Pike 1984).

Newton (2002) found flagelliform propagules that were ready for dispersal in ***Pilotrichella flexilis*** (Figure 115). These developed from primordia in leaf axils where they had minute juvenile leaves and in some cases rhizoids were present on some branchlets. Although miniature branches often serve as propagules, this is the first time they are known to develop from moss leaves (Schuster 1966). In ***P. flexilis*** these develop directly from the alar cells and do not develop protonemata. The phenomenon of developing miniature shoots from leaf cells is known among the liverworts in the genus ***Plagiochila***.

Figure 115. ***Pilotrichella flexilis***, a species that has flagelliform propagules (miniature branches) developed from primordia in leaf axils. Photo by Claudio Delgadillo Moya, with permission.

Rhizoidal Gemmae

As I began working on this section, I quickly realized I had a nomenclature problem. I had a number of images of rhizoidal tubers – no problem there. But I also had a number labelled **rhizoidal gemmae**, all from bryologists. All but one of these gemma images resembled the tubers. After consulting the *Glossarium Polyglottum Bryologiae*, I was comforted to learn that in mosses, rhizoidal tubers were defined as gemmae born on rhizoids. But one of these images was quite different, that of ***Fissidens macaoensis*** (Figure 116-Figure 118). In this species, the rhizoidal gemmae are elongate filaments that are narrow at the base and expand toward the tips (Figure 117; Zhang & Hong 2011). And it develops **rhizoidal tubers** (Figure 118) at the same time, a seemingly unique character among mosses. Zhang and Hong suggest that these two types of gemmae on the soil surface could be an adaptation that permits easy dispersal up to several hundred m during floods created during the typhoon season in Macao, China.

Figure 116. ***Fissidens macaoensis***, a tiny species with both rhizoidal tubers and rhizoidal gemmae at the same time. Photo by Li Zhang, with permission.

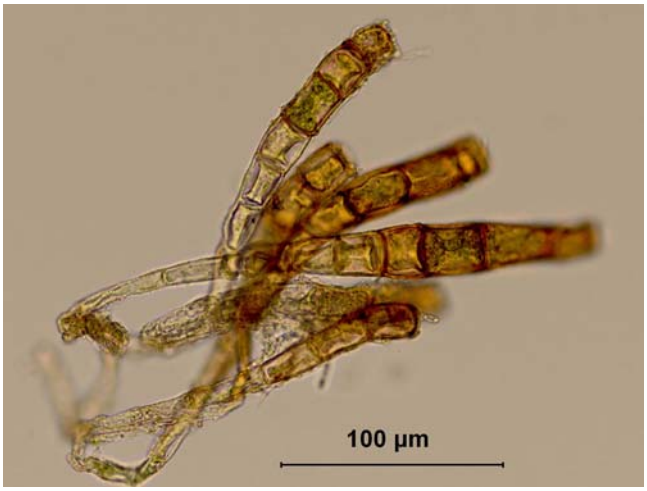

Figure 117. ***Fissidens macaoensis*** rhizoidal gemmae. Photo by Li Zhang, with permission.

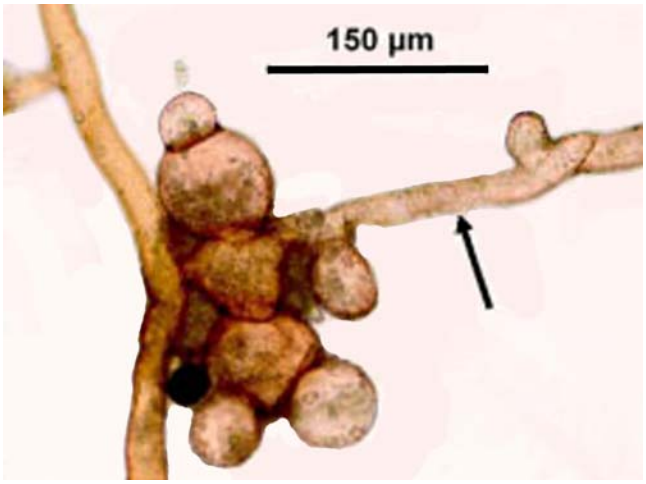

Figure 118. ***Fissidens macaoensis*** rhizoidal tuber. Photo by Li Zhang, with permission.

Risse (1986) observed the development from rhizoidal gemmae of ***Dicranella rufescens*** (Figure 119) and reviewed the rhizoidal gemmae of 82 European moss species and 3 additional ones from outside Europe (Risse 1987). Pressel *et al*. (2007) reviewed the protonemal propagules in ***Bryum*** (Figure 120-Figure 121, Figure 127-Figure 130) and related genera. Lepp (2008) reports over 100 species with rhizoidal gemmae, but most likely there are many more that have not been investigated.

Figure 119. ***Dicranella rufescens*** with rhizoidal gemmae. Photo by David T. Holyoak, with permission.

Figure 120. ***Bryum*** rhizoid with gemma tubers. Photo courtesy of Javier Abaigar Martinez.

Nordhorn-Richter (1984a) discovered that many parts of bryophytes, including asexual propagules, could be distinguished with the fluorescence microscope. She found this to be especially important in finding rhizoidal tubers and other propagules in the genus ***Pohlia*** (Nordhorn-Richter 1984a-d, 1985, 1988).

Figure 121. ***Bryum*** rhizoid gemma tuber. Photo courtesy of Javier Abaigar Martinez.

Whitehouse (1961) reported rhizoidal gemmae from ***Hennediella*** (=***Tortula***) ***stanfordensis*** (Figure 122) in Cornwall, Great Britain, and later Reese (1967) reported them in ***Chenia leptophylla*** (=***Tortula vectensis***; Figure 123-Figure 124) from North America. ***Hennediella stanfordensis*** forms a band nearly 1 km long on the coast near Lizard Point. Male plants seem to be absent, so this species depends on its gemmae, also chloronemal gemmae, and probably fragments. It is a winter annual, surviving the summer primarily through these rhizoidal gemmae.

Figure 122. ***Hennediella stanfordensis***. Photo by Paul Wilson, with permission.

Figure 123. ***Chenia leptophylla***. Photo by Jonathan Sleath, with permission.

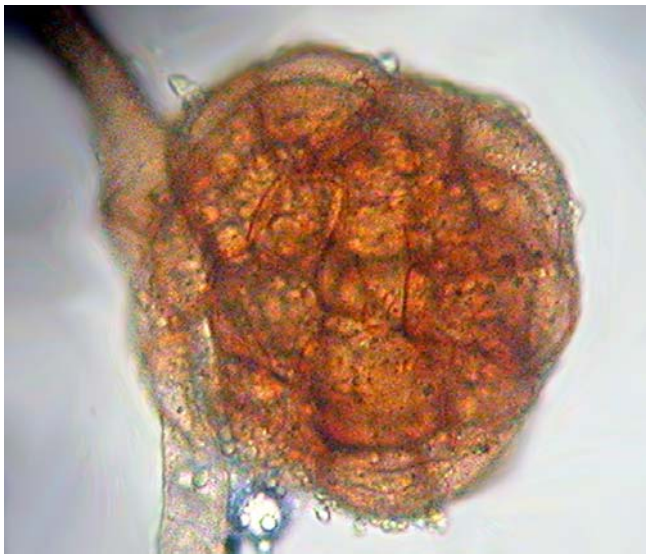

Figure 124. ***Chenia leptophylla*** rhizoidal tuber. Photo by Jonathan Sleath, with permission.

Rhizoidal Tubers

Rhizoidal tubers (Figure 125-Figure 131) occur on the rhizoids and are usually filamentous, branched, or spherical and have diverse origins. Whitehouse (1966) described these for 29 species of European mosses. He considered them to be a means of survival in arable fields and a means of dispersal for taxa living by streams. These often occur on species where sporophytes are unknown. Arts (1994) reported both rhizoidal tubers and protonemal gemmae in nine species of ***Ditrichum*** (Figure 125-Figure 126). They are common in the genus ***Bryum*** (Figure 127-Figure 130), and are likewise known in ***Pohlia*** (Figure 131). Arts (1986a) cultivated tubers of ***Fissidens dubius*** (= ***F. cristatus***; Figure 132) and established that they are drought resistant. The large tubers of ***Campylopus pyriformis*** (Figure 133) are likewise drought resistant and contain large quantities of starch (Arts 1986b). Their dark color may indicate antiherbivore compounds or may serve as a filter against light, decreasing chances of germination under a small amount of soil.

Figure 125. ***Ditrichum cornubicum***, a species with rhizoidal tubers. Photo by David T. Holyoak, with permission.

Figure 126. ***Ditrichum cornubicum*** rhizoidal tuber. Photo by David T. Holyoak, with permission.

Figure 127. ***Bryum canariense*** rhizoidal tubers exposed in the soil. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 128. ***Bryum bornholmense*** rhizoidal tubers. Photo by Dick Haaksma, with permission.

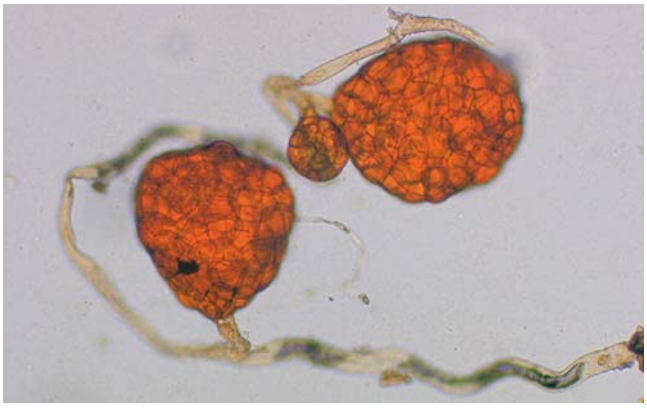

Figure 129. ***Bryum tenuisetum*** rhizoidal tubers. Photo by Chris Hesse, with permission.

Figure 130. ***Bryum torquescens*** rhizoidal tuber. Dick Haaksma, with permission.

Figure 131. ***Pohlia wilsonii*** rhizoidal tuber. Photo by Guillermo M. Suárez.

Figure 132. ***Fissidens dubius***, a species with drought-resistant rhizoidal tubers. Photo by Bernd Haynold, through Creative Commons.

Protonemal Gemmae

Because of identification difficulties, we seldom examine protonemata closely in the field. Hence, to many of us, protonemal gemmae are all but unknown. Nevertheless, Pressel *et al*. (2007) consider them to be relatively common. These protonemal gemmae occur in a variety of families. The moss ***Trematodon brevicalyx*** (**Bruchiaceae**) produces them (Dhingra & Chopra 1983) and they are known in 36 species of ***Bryum*** (Chopra & Rawat 1977; Pressel *et al*. 2007).

It is likely that many species have protonemal gemmae or other reproductive structures that remain to be discovered. For example, these were unknown until recently in the Splachnaceae. Following the discovery of protonemal bulbils in ***Splachnum ampullaceum*** (Figure 134) (Mallón *et al*. 2006), Martinez and Price (2011) studied the development of the protonemata of the epiphytic ***Tayloria rudolphiana*** (Figure 135), likewise a member of the Splachnaceae. In culture, they observed protonemal brood cells for the first time in this species, occurring at the ends of caulonemal filaments where they formed chains of short, somewhat thick-walled spherical cells. These brood cells developed after four months in culture and had abundant chloroplasts and some lipid droplets.

Figure 133. ***Campylopus pyriformis*** with caducous leaves, also producing rhizoidal tubers. Photo by Michael Lüth, with permission.

Figure 134. ***Splachnum ampullaceum*** with capsules. Photo by David Holyoak, with permission.

Figure 135. ***Tayloria rudolphiana***, a species that produces chains of spherical protonemal brood cells at the ends of caulonemal filaments. Photo by Jan-Peter Frahm, with permission.

Zygodon forsteri (Figure 136) is only known from beech bark (***Fagus sylvatica***), often occurring with ***Z. viridissimus*** (, and is rare (Adams & Rumsey 2005). ***Zygodon forsteri*** occurs on rain tracks on trees, on roots in places that collect water, and on callus tissue where squirrels make grooves that aid establishment (Figure 139-Figure 140). The authors suspect that slug herbivory on the capsules of ***Z. forsteri*** is responsible for poor reproduction, but they have documented that the running water disperses its bountiful chloronemal gemmae.

Figure 136. ***Zygodon forsteri*** with capsules that may be eaten by slugs. Photo by César Garcia, with permission.

Figure 137. ***Zygodon viridissimus*** on bark. Photo by J. C. Schou, with permission.

Figure 138. ***Zygodon viridissimus*** leaf with gemmae that may help it to compete with ***Zygodon forsteri***. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 139. Beech knothole callus. Photo from pxfuel, with online permission.

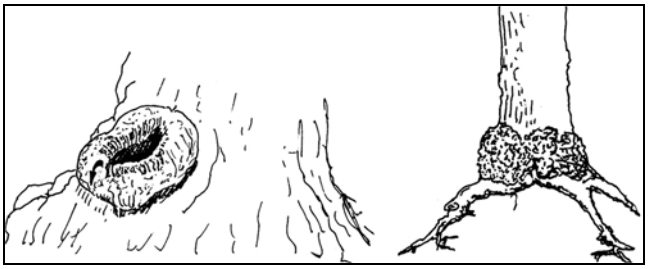

Figure 140. ***Zygodon forsteri*** (**right**) on callus tissue (**left**). Photo modified from Adams *et al.* 2005, with permission.

Even the aquatic moss ***Fontinalis antipyretica*** (Figure 158) produces protonemal gemmae (Ares *et al.* 2014). Thus far, this has only been observed in culture, but few or no observations have been made in the field. These are produced in ageing and desiccating cultures, and the authors suggest that in nature they may be produced in response to diminishing water levels.

Figure 141. ***Fontinalis antipyretica*** chloronemal gemma. Photo modified from Ares *et al*. 2014.

The production of protonemal gemmae seems to be environmentally controlled. Vashistha and Chopra (1984) found that in ***Didymodon recurvus*** the production of protonemal gemmae was favored by low light and high temperature, whereas high light and low temperature resulted in development of gametophore buds. This experimental observation is consistent with the assertion of Whitehouse (1980). He found that the protonemata of ***Barbula trifaria***, ***Gyroweisia tenuis***, and ***Eucladium verticillatum***, as well as those previously reported in ***Schistostega pennata*** (Edwards 1978), seem to be

adaptations for survival and propagation at low light intensities of deep shade. Perhaps this is a mechanism to provide an opportunity for dispersal from an unfavorable location to one with more favorable light?

Pressel and coworkers (2007) found that in culture the protonemal gemma production increased with high nutrient availability and suggested that this may be true in nature as well. They assumed that the protonemal gemmae were both less long lived and less desiccation tolerant than tubers. They suggested that these diaspores helped in initial establishment as well as local spread of the species. The role in the diaspore bank and longevity of these structures remain to be investigated.

It is interesting that development of protonemal gemmae may also be controlled by the hormone **IAA** (Ahmed & Lee 2010). Ahmed and Lee found that both IAA and kinetin controlled the production of gemmae vs gametophore buds in ***Palustriella decipiens*** (=***Cratoneuron decipiens***) cultures from chopped up gametophores, serving as concentration-based external regulators. This does not necessarily imply that the same behavior would occur from protonemata produced by spores because chopped plants could provide hormones that might not be available to a spore germling.

Figure 142. ***Bazzania trilobata*** showing stolons with very reduced leaves. Photo by Dick Haaksma, with permission.

Liberation Mechanisms

Even the mechanisms of liberating the diaspores differ among species. Duckett and Ligrone (1992) identified five liberation mechanisms:

1. random breakage of thin-walled stalk cells
2. formation of new internal walls that separate from old
3. severance along middle lamella of basal cell with or without rounding off of cells
4. formation of highly specialized abscission (**tmema**) cells
5. breakage along intercalary region of thin-walled living cells

In contrast to these specific liberation mechanisms, rhizoidal gemmae lack any separation mechanism, being freed only by decay of the filament that has produced them.

Some bryophytes don't require any special cells or mechanisms to release fragments. For example, the leafy liverwort ***Pycnolejeunea*** will lose a shoot with only a light touch. Others may produce special branches that release with only a touch. This adaptation usually results from reduction in number of cells at the point of attachment. The ease-of-breakage method includes many leafy liverworts. One such species is ***Lejeunea cardotii*** that grows in mats on tree trunks and dead wood. Its stems produce small-leafed branches and these may in turn produce more small-leafed branches. These are fragile and break off easily. Other leafy liverworts, *e.g.* ***Bazzania trilobata*** (Figure 142), likewise get such specialized branches, often originating from under the branch.

Protonemal Gemmae

Most of the protonemal gemmae separate from the parent **chloronema** (part of protonema giving rise to buds) by a **tmema** (abscission) cell (Figure 147-Figure 149). Other taxa with this tmema mechanism include ***Mielichhoferia bryoides*** and ***Rhodobryum roseum*** (Figure 66). Other bryophytes use **schizolysis** to detach their gemmae. This requires the splitting from the parent plant by **lysis** of the cellular connections through rupture of adjoining cell walls. Genera with this strategy include ***Epipterygium*** (Figure 143), ***Plagiomnium*** (Figure 144), ***Rhizomnium*** (Figure 145), and ***Mnium*** (Figure 146).

Figure 143. ***Epipterygium tozeri***, representing a genus that uses lysis to disconnect its gemmae. Photo by David T. Holyoak, with permission.

Figure 144. ***Plagiomnium affine***, representing a genus that uses lysis to disconnect its gemmae. Photo by Michael Lüth, with permission.

Figure 145. ***Rhizomnium punctatum***, representing a genus that uses lysis to disconnect its gemmae. Photo by Li Zhang, with permission.

Figure 146. ***Mnium arizonicum***, representing a genus that uses lysis to disconnect its gemmae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Tmema

A **tmema** (Figure 147-Figure 149) is a specialized abscission cell that permits portions of a protonema to operate independently and create a position of easy breakage (Correns 1899; Duckett & Ligrone 1992). This mechanism seems to be important in the release of protonemal gemmae, with a variety of different developmental patterns (Duckett & Ligrone 1992). Schnepf (1992) reported these from the chloronemata of ***Funaria hygrometrica*** (Figure 150), where they serve to fragment the protonemal filaments. In ***Zygodon*** (Figure 151-Figure 152), ***Bryum pallens*** (=*B. flaccidum*; Figure 153), and ***Dicranoweisia cirrata*** (Figure 154), they occur at the bases of axillary gemmae, and they are characteristic of foliar gemmae in ***Calymperes*** (Figure 155-Figure 156) (Duckett & Ligrone 1992).

Figure 147. Protonema with short tmema cell where protonema can break apart. Photo by Jaime Goode, permission pending.

Figure 148. **Tmema cells** (colorless) and **brachycytes** (short green) of ***Physcomitrella patens*** protonema. Photo courtesy of Anne Genau through Stefan Renfing. Marco Göttig set up the ABA treatment that induced these cell formations.

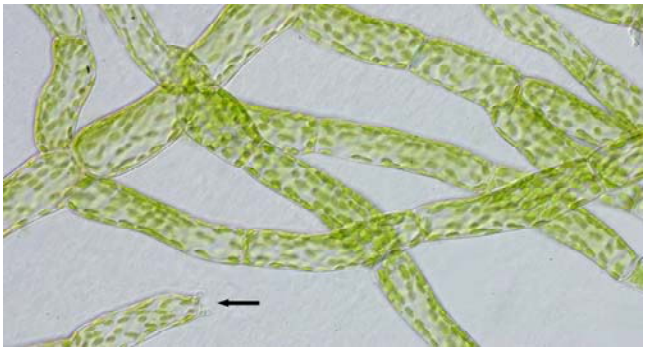

Figure 149. ***Physcomitrella patens*** protonema, showing broken cell that was a **tmema** (**arrow**). Photo by Anja Martin, Labor Ralf Reski <en.wikipedia.org/wiki/Ralf_Reski>, through Creative Commons.

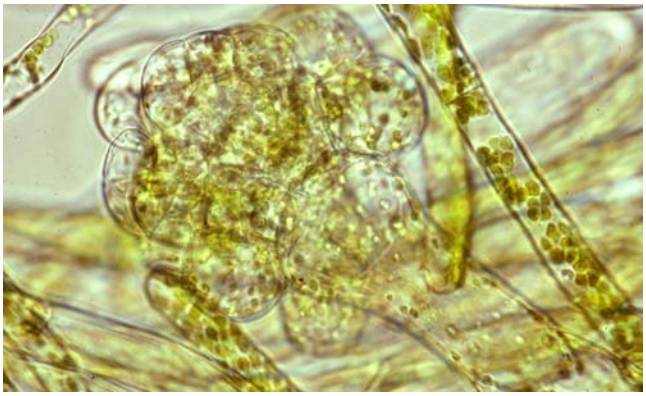

Figure 150. ***Funaria hygrometrica*** protonema with bud. Photo by Martin Bopp, with permission.

Figure 151. ***Zygodon conoideus*** growing on bark. Photo by Michael Lüth, with permission.

Figure 152. ***Zygodon conoideus*** gemmae. Photo by David Holyoak, with permission.

Figure 153. ***Bryum pallens*** (=*Bryum flaccidum*) with axillary filamentous gemmae, each attached by a tmema cell. Photo by Kristian Peters, with permission.

Figure 154. ***Dicranoweisia cirrata*** with capsules, a species that produces axillary gemmae with tmemata. Photo by Michael Lüth, with permission.

Figure 155. ***Calymperes erosum*** with leaf gemmae. Photo by Li Zhang, with permission.

The tmema cell in ***Funaria hygrometrica*** protonemata results from unequal cell division and is followed by the loosening of the old proximal cell wall (Bopp *et al*. 1991). Addition of 10 µM IAA prevents the formation on tmemata, indicating that the formation of this cell results from inadequate IAA. The result of this fragmentation is to create several separate protonemata. In gemmae, the tmemata connect the gemmae to the plant and permit its abscission (Figure 156-Figure 157) (Stapper 2006).

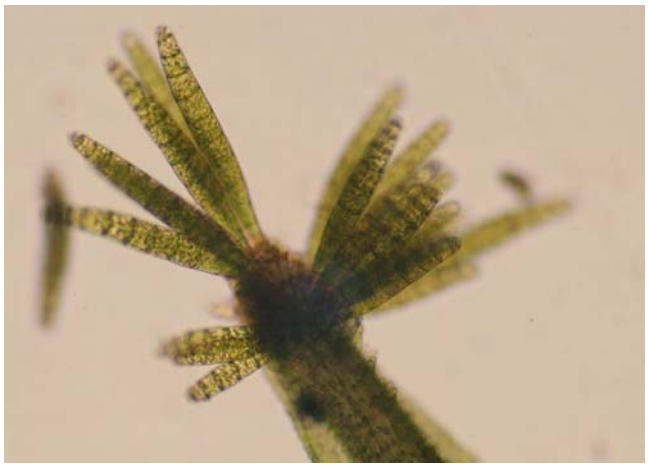

Figure 156. ***Calymperes erosum*** leaf with gemmae attached by tmemata. Photo by Li Zhang, with permission.

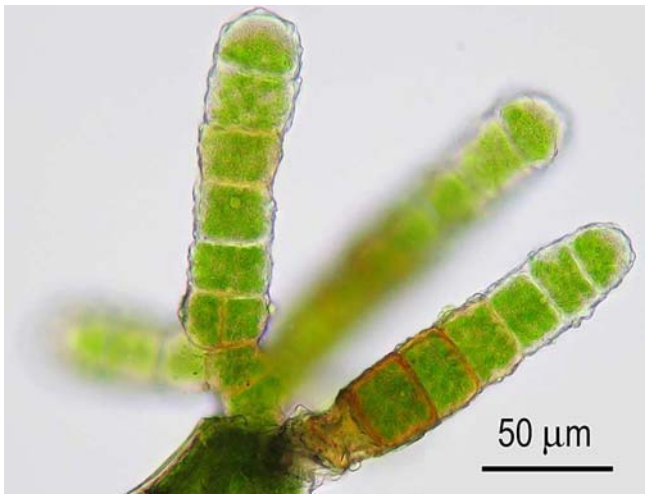

Figure 157. Tmema at base of brood bodies of ***Dicranum tauricum***. Photo by N. J. Stapper, with permission.

Diaspore Bank

Unfortunately, it is difficult to determine whether spores or asexual diaspores contribute to the growth of new plants from the diaspore bank. During (1995) suggested that tubers of some moss species may be very abundant in the diaspore bank, and as seen earlier in the discussion of diaspore banks, these species often are not represented above ground or are sparse there. During contends that such populations seem to rely completely on occasional recruitment. Long rhizoids help to extend the range of some species within a location. He considers population regulation of these species to be a density-dependent mortality of the tubers in the soil.

The forest is often disturbed, whether by fire or by harvesting. Bryophytes are important in maintaining soil moisture and as reservoirs of nutrients that often get released toward the later part of the growing season. Following disturbance, forest floor bryophytes are often recovered from diaspore banks. Caners *et al*. (2009) cultured mineral soil samples from both mixed and coniferous forest stands in northern Alberta, Canada, following harvesting. They found that forest type was not the determinant of the species composition, nor was harvesting intensity. Rather, edaphic variables and geographic space determined the regenerant flora. Nevertheless, light intensity exerted a significant influence on both the species responses and the species assemblages. Low light caused significant reduction in richness and cover of acrocarpous mosses – the fugitive, colonist, and shuttle life-history strategies. Pleurocarpous mosses (perennial stayers), on the other hand, seemed unaffected by light intensity. Higher light intensities supported significantly greater **Shannon diversity** and the frequency of reproduction. Caners *et al*. concluded that diaspore banks were an important repository for forest floor species and provided a source for recovery after harvesting.

Ross-Davis and Frego (2004) found 10 of the 36 species of a forest floor community in both the diaspore bank and the aerial diaspore rain. Of the extant taxa, 36% were not present in either diaspore source. The two dominant mosses, ***Pleurozium schreberi*** and ***Hylocomium splendens***, were present in both the diaspore bank and aerial diaspore rain.

Hence, bryophytes are able to colonize disturbed areas from both the diaspore bank and from the diaspore rain. These two sources contain both spores and vegetative propagules, but not necessarily both from the same species. Distinguishing which type of diaspore germinated is quite difficult and is not usually included in diaspore bank studies.

The Antarctic undoubtedly has many well-preserved bryophyte diaspores buried in the ice and deep in bryophyte mats. Bergstrom and Selkirk (1999) were able to culture propagules from substrate samples 5.5 cm deep on Macquarie Island. They succeeded in germinating 15 bryophyte taxa. They hypothesized that bryophytes that arrived on bare patches in the feldmark, they were able to colonize stable ground but unable to colonize areas subject to surface movement. Instead, some of these propagules became buried. Spherical moss balls, however, were tolerant of the surface movement and disturbance. Of the 15 species that germinated, 10 were not local and came from populations at the warmer lower altitudes. They suggested that such propagules will permit areas respond quickly to climate change by providing species that were tolerant to the new climate.

Propagule Dispersal Distances

It appears that little is known about actual distances that vegetative propagules might travel. Although studies have suggested that the distances are short, *i.e.* measured in centimeters rather than meters (Kimmerer 1991, 1994; Kimmerer & Young 1995), it appears that extensive measurements are lacking. Kimmerer (1991) found that gemmae of ***Tetraphis pellucida*** (Figure 18-Figure 19) travelled to a maximum of 10 cm in her study, and that 50% fell within 1 cm. But surely moss balls (see subchapter on growth forms) can travel great distances. And fragments of bryophytes on glaciers likewise travel hundreds of feet, and potentially much more. In my study on ***Fontinalis*** (Figure 158) vegetative dispersal, one piece had re-established upstream about 20 m from its origin, presumably carried there by some animal (bear or human?).

Figure 158. ***Fontinalis antipyretica***, a moss that spreads vegetatively by rhizomes and disperses by fragments. Photo by Andrew Spink, with permission.

Convincing evidence of long-distance propagule dispersal is that of ***Marchantia polymorpha*** (Figure 159) on the crater of Deception Island, Antarctica. The crater was formed in 1969, exposing new ground following the eruption. In 1971, Young and Kläy reported this species on the new ground approximately 1000 km from the nearest known population in South America. No other colonies on Deception Island of this conspicuous liverwort were known to the scientists. Perhaps more surprising, the thallus had the distinctive dumbbell shape that is typical of a young thallus developed from a gemma! This example supports a conclusion of rapid long-distance dispersal that in this case arrived at a suitable habitat. (Let's hope this wasn't a case of inadvertent human dispersal!)

Figure 159. ***Marchantia polymorpha*** with gemma cups. Photo by Andrew Spink, with permission.

Propagule Survival/Longevity

The first question that comes to mind for long-distance dispersal of vegetative propagules is whether they can survive. These are living, often active fragments, gemmae, bulbils, and other structures that may or may not be dormant. Presumably, living fragments would be the least adapted among these to survive the conditions of the stratosphere. Studlar *et al*. (2007) tested fragment survivability by sending four mosses into the stratosphere on a weather balloon. These were subjected to temperatures as low as -30°C over a period of 4 hours, 2 of which were in the stratosphere. Subsequent culture for 28 days in the lab revealed the ability of these species to survive the stratosphere ride. ***Sphagnum magellanicum*** (Figure 160), ***S. fallax*** (Figure 161), and ***Atrichum angustatum*** (Figure 44) all regenerated with secondary protonemata and juvenile shoots. ***Sphagnum girgensohnii*** (Figure 162), however, did not. These results suggest that at least some vegetative diaspores, including fragments, could travel by wind into the stratosphere.

Figure 160. ***Sphagnum magellanicum*** in Europe, a species that survived travel in a weather balloon. Photo by Michael Lüth, with permission.

Figure 161. ***Sphagnum fallax***, a species that survived travel in a weather balloon. Photo by Michael Lüth, with permission.

Some bryophytes may survive in a dry state for years, providing a larger set of opportunities for the wind or water to distribute them to new locations. Whitehouse (1984) reported that tubers of ***Anisothecium*** (=***Dicranella***) ***staphylinum*** (Figure 163) survived in stored soil for 50 years. Zander (1979) successfully cultured ***Anoectangium*** (Figure 164), ***Barbula*** (Figure 165), ***Desmatodon*** *s.l.* (Figure 166), ***Didymodon*** (Figure 167), ***Gymnostomum*** (Figure 168), ***Hymenostylium*** (Figure 169), ***Leptodontium*** (Figure 170), ***Molendoa*** (Figure 171), ***Oxystegus*** (Figure 172), ***Pleurochaete*** (Figure 173), ***Pseudocrossidium*** (Figure 174), ***Tortella*** (Figure 175), ***Tortula*** (Figure 176), and ***Trichostomum*** (Figure 177) species, all members of **Pottiaceae**, from herbarium plants (not spore) specimens. These were all less than 5 years old.

Figure 162. ***Sphagnum girgensohnii*** at Lake Perrault, MI, USA, a species that did not survive travel in a weather balloon. Photo by Janice Glime.

Figure 163. ***Dicranella staphylina*** on soil, a species that can survive storage in soil for 50 years. Photo by Michael Lüth, with permission.

Figure 164. ***Anoectangium aestivum*** with capsules, a species cultured from herbarium specimens less than 5 years old. Photo by Jan-Peter Frahm, with permission.

Figure 165. ***Barbula unguiculata*** with water on setae and capsules. This species was cultured from herbarium specimens less than 5 years old. Photo by Adnan Erdag, with permission.

Figure 166. ***Tortula hoppeana*** (syn.=***Desmatodon latifolius***) from the mountains in southern Europe. This species was cultured from herbarium specimens less than 5 years old. Photo by Michael Lüth, with permission.

Figure 167. ***Didymodon rigidulus*** in southern Europe, a species cultured from herbarium specimens less than 5 years old. Photo by Michael Lüth, with permission.

Figure 168. ***Gymnostomum aeruginosum*** with capsules in Europe, a species cultured from herbarium specimens less than 5 years old. Photo by Michael Lüth, with permission.

Figure 169. ***Hymenostylium recurvirostrum*** in India, a species cultured from herbarium specimens less than 5 years old. Photo by Michael Lüth, with permission.

Figure 170. ***Leptodontium flexifolium*** in Europe, a species cultured from herbarium specimens less than 5 years old. Photo by Michael Lüth, with permission.

Figure 171. ***Molendoa hornschuchiana*** in southern Europe, a species cultured from herbarium specimens less than 5 years old. Photo by Michael Lüth, with permission.

Figure 172. ***Oxystegus cylindricus*** subsp. ***hibernicus***, a species cultured from herbarium specimens less than 5 years old**s**. Photo by Jan-Peter Frahm, with permission.

Figure 173. ***Pleurochaete squarrosa*** wet, a species cultured from herbarium specimens less than 5 years old. Photo by David T. Holyoak, with permission.

Figure 174. ***Pseudocrossidium revolutum***, a species cultured from herbarium specimens less than 5 years old. Photo by Proyecto Musgo, through Creative Commons.

Figure 175. ***Tortella flavovirens*** in southern Europe. Photo by Michael Lüth, with permission.

Figure 176. ***Tortula muralis*** with water drops in Dunblane, Scotland. This species was cultured from herbarium specimens less than 5 years old. Photo courtesy of Peggy Edwards.

Figure 177. ***Trichostomum brachydontium***, a species cultured from herbarium specimens less than 5 years old. Photo by Barry Stewart, with permission.

Buried propagules must somehow remain dormant in an environment (diaspore bank) that varies both their temperature and their state of hydration. The only factor they lack for germination appears to be light. Risse (1987) reviewed 82 species of European mosses with rhizoidal propagules and demonstrated that tubers and rhizoidal gemmae do not germinate in absence of light. Their germination is dependent upon the intensity of light, not the photoperiod. If the propagules are hydrated for more than ten days without successful germination they do not survive. After fifteen days, their fat reserves are depleted. Furthermore, imbibition of water causes the gemmae to lose their dormancy and become sensitive to dehydration, causing irreversible damage if they are more than 12 hours into their pre-germination phase when they dry out again. This can explain the absence of viable propagules in the first cm of soil where frequent wetting and drying are certain.

Egunyomi (1978) found that spores have longer storage longevity than do gemmae for ***Octoblepharum albidum*** (Figure 13). Even at room temperature and 60-75% humidity, spores were viable after eight months, but gemmae began to lose viability at six months. Light is of utmost importance for germination, with only 8.0% of gemmae germinating at 1 lux, but 90% at 1375 lux.

Imura and coworkers (1992) experimented with the rhizoidal tubers of a moss, ***Leptobryum pyriforme*** (Figure 178-Figure 183), found on the ice surface of a lake near the Syowa Station in the Antarctic. Both protonemata and leafy shoots developed from these tubers after the tubers had been stored for two years in a freezer. This illustrates the tremendous tolerance of these species and the extraordinary survival abilities.

Figure 178. ***Leptobryum pyriforme*** with capsules, a species with tubers that can survive two years in a freezer. Photo by Michael Lüth, with permission.

Figure 179. ***Leptobryum pyriforme*** with tubers from wet meadow and stagnant ditch Minnesota, USA. Photo by Jan Janssens, with permission.

Figure 180. ***Leptobryum pyriforme*** rhizoidal tuber. Photo by Victoria Rozhina.

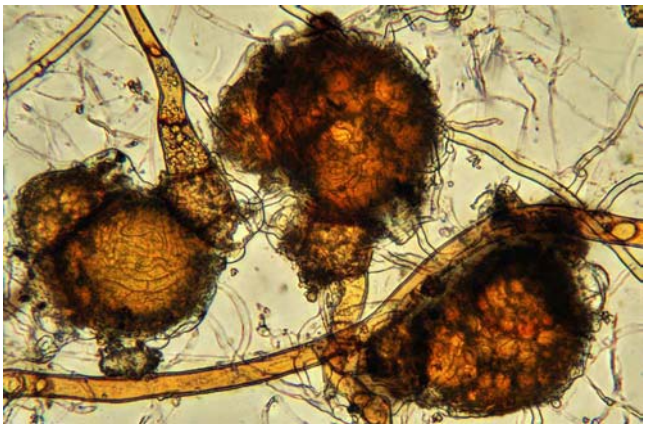

Figure 181. ***Leptobryum pyriforme*** rhizoidal tubers. Photo by Dick Haaksma, with permission.

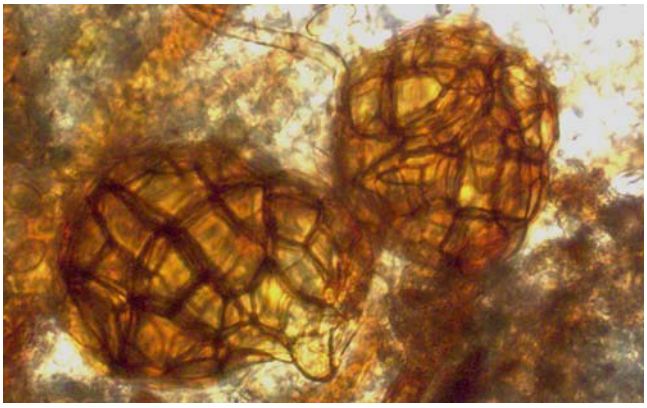

Figure 182. ***Leptobryum pyriforme*** rhizoidal tubers. Photo by Victoria Rozhina.

John Spence (Bryonet 22 November 2010) actually tested long-term viability of tubers in ***Rosulabryum capillare*** (Figure 184) and ***Gemmabryum*** (=***Erythrocarpa*** sp.; Figure 185). Tubers of these species remained viable up to 15 years and germinated in distilled water and normal daylight. Such propagules can remain dormant in soil banks and other locations, germinating after unknown periods of time when they are disturbed and brought to the surface (*e.g.* During 199). Although there are a number of studies on propagules from such situations, the longevity of these propagules is unknown. Herbarium specimens provide a means of checking longevity, but the conditions of a herbarium are quite different from the natural habitat. And even if the propagules could survive the conditions there, they may become dinner for hungry invertebrates.

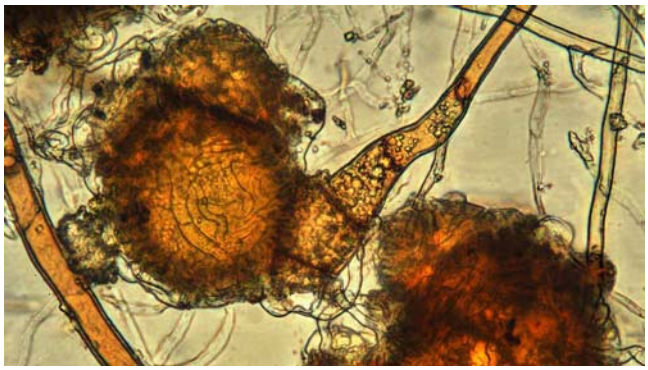

Figure 183. ***Leptobryum pyriforme*** rhizoidal tubers. Photo by Dick Haaksma, with permission.

Figure 184. ***Rosulabryum capillare*** with capsules, a species whose rhizoidal gemmae can survive at least 15 years. Photo by Tom Thekathyil, with permission.

Figure 185. ***Gemmabryum dichotomum*** with bulbils. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Mishler and Newton (1988) experimented with four ***Tortula*** *s.l.* species (Figure 96-Figure 97; Figure 122-Figure 124) and found that fragments, while being less successful at germination than spores, usually developed numerous stems, whereas the spores did not during the 2.5 months of experiments. The protonemata looked different between the spore-derived and the fragment-derived ones. Perhaps they differed physiologically and those derived from spores required a day length or other condition not present in the experiment.

I have observed diatom-covered mosses being eaten by a dipteran larva in the **Rhyphidae** family. These went in "dirty" and came out the other end clean and still bright green. But I have no evidence that these actually survived the digestive tract as viable propagules. Insect guts can have extremely high or extremely low *p*H (Nation 2002) to adapt them to digestion of the few remaining nutrients in detritus, and the particular diet of this larva suggests it might be so-adapted. These extreme *p*H levels are likely to be detrimental to the living cells of the moss.

The potential of a delayed response of the moss to such a detrimental gut environment is exemplified by our experiment on ***Fontinalis duriaei*** (Figure 186). In an experiment to determine if rainbow trout (*Oncorhynchus mykiss*) could be dispersal agents of ***F. duriaei***, we brought in fresh moss with lots of aquatic insects, but the fish did not eat the moss, so we force-fed it. The moss was expelled later through the anus in a neat cylindrical package (Figure 187), still bright green. We isolated it in a cooled jar of its own stream water, but 24 hours later, the moss had lost its green color and appeared to be dead.

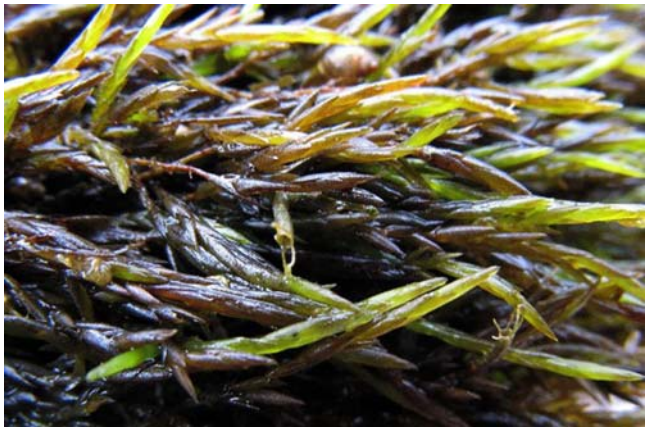

Figure 186. ***Fontinalis duriaei***. Photo by Jan-Peter Frahm, with permission.

Figure 187. Feces packet from rainbow trout, containing ***Fontinalis duriaei*** that has lost its green color 24 hours after its egestion. Photo by Janice Glime.

Vegetative propagula are less likely to survive travel through the gut than spores, and they may be more susceptible to damage when they begin to germinate as well. Hydration without successful germination can kill them. But if they are able to germinate successfully, both fragments and specialized propagula have better chances than spores of producing gametophores, albeit only one per propagule. Propagule banks typically reflect not only the present vegetation, but also past vegetation, providing ready sources following disturbance.

One prerequisite for propagules with long dormancy or lengthy travel is desiccation tolerance. Understanding this is necessary for cryopreservation to maintain species that may become extirpated in the future. Rowntree *et al.* (2007) have used cryopreservation successfully for many species and in doing so have added greatly to our understanding of the mechanisms the bryophytes are able to use to survive. They have found that survival can be enhanced by pretreatment with ABA and sucrose, the latter perhaps providing an energy source upon rehydration. Surprisingly, the pioneer moss ***Ditrichum plumbicola*** had low survival of cryopreservation and likewise responded poorly to pretreatment. With further experimentation, they discovered that the pretreatment with sucrose and ABA caused significant changes in the protonemata. Growth was greatly reduced and propagules had pronounced morphological and cytological changes. Although most cells died, those that survived were markedly different from normal. The surviving cells had thick walls that were darkly pigmented and there were numerous small vacuoles and lipid droplets in the cytoplasm. When there was no ABA-sucrose pretreatment, desiccation and cryopreservation caused minimal cytological changes. These untreated tissues returned to their pre-dehydration state within 2 hours of rehydration. On the other hand, rehydration was normal once ABA and sucrose were removed from the pretreated propagules. Rather, these propagules (from the protonemata) became highly desiccation and cryopreservation tolerant, a behavior similar to that of rhizoids that function as perennating organs in the field. Rowntree and coworkers considered this as evidence that the propagules used ABA to increase their desiccation tolerance.

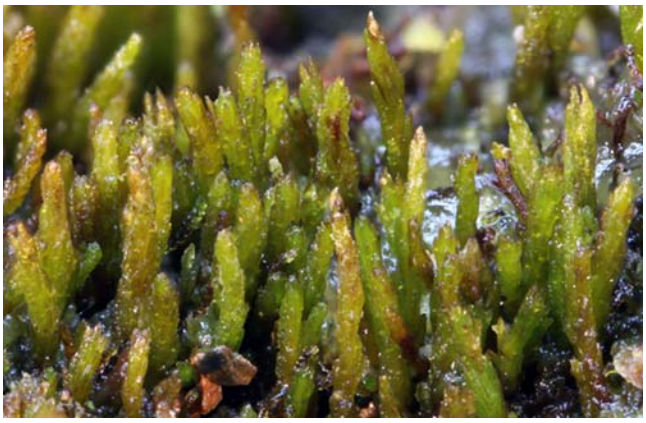

Figure 188. ***Ditrichum plumbicola***, a species with low cryopreservation survival. Photo by Des Callaghan, with permission.

In ***Marchantia inflexa*** (Figure 189) both water and desiccation affect mortality (Chris Stieha, Bryonet 27 February 2016). In his lab, there was less than 10% mortality of gemmae maintained in water for three months, but 20% mortality after only four days of desiccation. In the field they can turn brown within an hour of desiccation. Stieha *et al*. (2014) found that male plants of this species produce the most gemmae and more quickly when compared to females, but the male gemmae have less ability to survive desiccation. Gemmae in this species can move up to 20 cm from the parent plant in a light rain, permitting expansion of the population.

Figure 189. ***Marchantia inflexa***, a species whose gemmae survive well in water but tolerate little desiccation. Photo by Scott Zona, with permission.

Propagule Establishment

Once a propagule reaches its final resting place, it must begin growth and become established (Figure 190). Due to both edaphic and climatic differences, the success of this establishment is less predictable as the distance increases (Karlson & Taylor 1992; Ronsheim 1997; Laaka-Lindberg *et al*. 2003).

Figure 190. Gemmae germinating. Photo by Li Zhang, with permission.

The conditions at germination can be critical. Risse (1987) tested rhizoidal gemmae of mosses, citing their importance in environments that are frequently disturbed by natural or anthropogenic influences. McCrutcheon (1978) reported that light is required for germination, and that if the gemma of ***Bryum rubens*** (Figure 191-Figure 194) becomes imbibed for more than ten days without receiving light, it will die. Its fat storage reserves are depleted in 15 days, so that imbibition can trigger that loss. Furthermore, after imbibition, tubers become sensitive to desiccation and do not regain their pre-germination tolerance if they have entered their pre-germination phase (imbibed) for more than 12 hours.

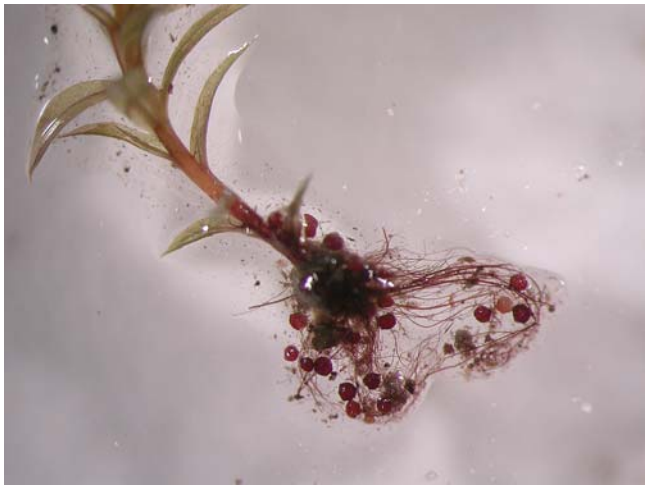

Figure 191. ***Bryum rubens*** rhizoidal gemmae. Photo by Ariel Bergamini, with permission.

Figure 192. ***Bryum rubens*** rhizoidal gemmae along stem rhizoids. Photo by Ariel Bergamini, with permission.

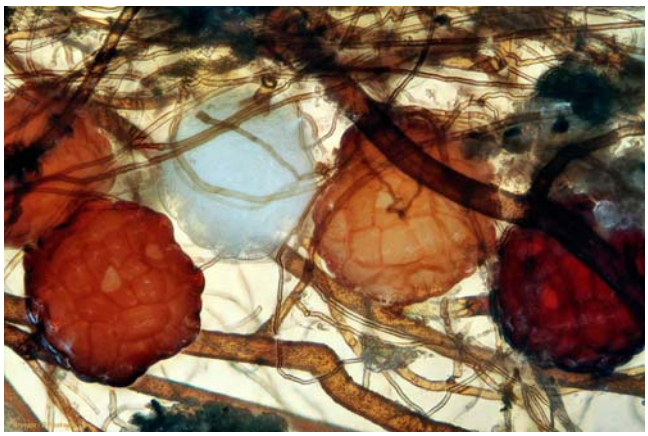

Figure 193. ***Bryum rubens*** rhizoidal tubers in various stages of maturity, showing how prolific they can be. Photo by Dick Haaksma, with permission.

Figure 194. ***Bryum rubens*** rhizoidal tubers. Photo by Dick Haaksma, with permission.

Desiccation

A key factor in establishment is maintenance of sufficient moisture in early stages of development to permit development of a reproductive adult. An interesting example of this is ***Pseudoscleropodium purum*** (Figure 195). One habitat where this species grows is on ant hills of the yellow meadow ant, ***Lasius flavus*** (Figure 196), that is, on the north-facing sides of the ant hills (King 2003). Fragments detached by grazing animals are common on the mounds. After experimentation, King concluded that inability to establish on the south-facing side was most likely due to desiccation and metabolic drain leading to cell death. Transplanted adult mosses, on the other hand, seemed capable of survival.

Figure 195. ***Pseudoscleropodium purum***. Photo by Michael Lüth, with permission.

Figure 196. The yellow meadow ant, ***Lasius flavus***. Photo through Creative Commons.

Inhibitors

Gemmae do have a safeguard against competing with their parents. Most are inhibited by the presence of the parent (Figure 197) and are often even inhibited by related species [*e.g.* ***Bryum rubens*** (Figure 191-Figure 194) by ***Bryum alpinum*** (Figure 198) (McCrutcheon 1978)]. Ashton and Raju (2001) demonstrated inhibition of rhizoidal gemmae in ***Gemmabryum*** (=***Bryum***) ***violaceum*** (Figure 199) by the soil associated with the parents, but gemmae germinated while still attached if placed in fresh soil. This suggests that whatever served as the deterrent may have accumulated in the soil to a greater level than that in the plant. It would be interesting to attempt growing these in the same soil with charcoal as an adsorbant.

Figure 197. ***Lunularia cruciata*** showing ungerminated gemmae on thallus. Both ***Marchantia*** and ***Lunularia*** inhibit the germination of the gemmae on the parent. Photo by Martin Hutten, with permission.

Figure 198. ***Bryum alpinum*** showing competition. Photo by David T. Holyoak, with permission.

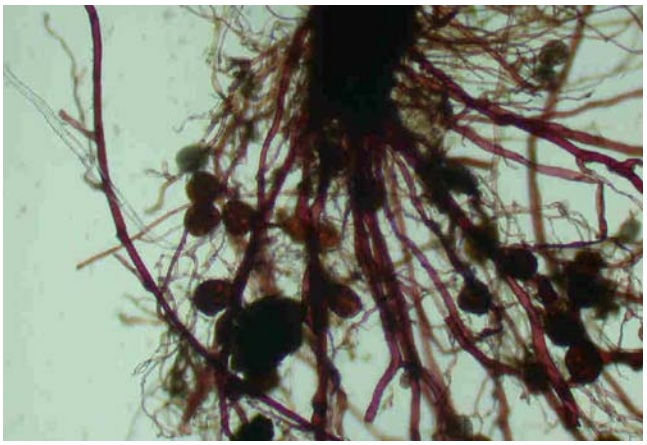

Figure 199. ***Gemmabryum violaceum*** with rhizoidal tubers. Photo by David T. Holyoak, with permission.

Risse (1987) suggested that this inhibition might be caused by sugars, particularly mono- and disaccharides, shown by McCrutcheon (1978) to inhibit tuber germination in ***Bryum rubens*** (Figure 191-Figure 194). Christianson (2000) showed that ABA (abscisic acid) is able to inhibit bud formation in ***Funaria hygrometrica*** (Figure 200), so it could also be the cause of inhibition by parents. This same self-inhibition (inhibition by parents) is known from ***F. hygrometrica*** (Figure 200). On the other hand, the cytokinin hormones leaked from one individual can stimulate bud formation on other nearby individuals of the same or related species (Bopp 1982).

Figure 200. ***Funaria hygrometrica*** showing the distinct margins where colonies contact each other. Photo by Janice Glime.

ABA is a common hormone in tracheophytes, having a variety of functions. It is best known in bryophytes as a responder to desiccation. Mallón *et al*. (2006) examined the effect of various concentrations of ABA on the production and behavior of gemmae in ***Splachnum ampullaceum*** (Figure 134). This species is best known for its ability to attract flies that disperse it among piles of dung, but its ability to produce vegetative propagules was previously unknown. The researchers managed to induce both brood cells and chloronemal bulbils in their protonemal cultures, as well as vegetative propagules, and their results suggest a bet-hedger strategy. The brood cells produced new chloronemal filaments when they were transferred to new media. There was a direct positive relationship between the concentration of ABA and brood cell formation, while at the same time increasingly inhibiting the growth of the protonemata. Furthermore, no buds developed on protonemata grown on media with ABA. Mallón and coworkers suggested that production of the vegetative structures on the protonema might be a desiccation response and would permit the plant to spread rapidly, a behavior that might also help to conserve moisture, if not then, in the future.

Establishment and Rarity

Cleavitt (2002) attempted to determine the factors that contributed to rarity of species [***Mielichhoferia macrocarpa*** (Figure 201), ***Didymodon johansenii***, and ***Mnium arizonicum*** (Figure 146)] and compared three rare and common species pairs in the Front Ranges of Alberta, Canada. She found that propagule viability did not relate to establishment ability. Rather, establishment of rare species may be a function of a complexity of mechanisms that create a narrow realized niche. For example, ***Mielichhoferia macrocarpa***, which occurred in the darkest and wettest sites, was tolerant of high light intensity and desiccation, suggesting that additional factors narrowed its establishment niche. She suggested that the broader apparent physiological tolerance found in these rare species may be due to their greater reliance on asexual reproduction. This suggests that we should look for other physiological factors and dispersal as causes of rarity.

Figure 201. ***Mielichhoferia macrocarpa***, a species that appears to have broad environmental tolerances, but with limiting requirements of some factor(s). Photo by Robin Bovey, with permission through Dale Vitt.

In contrast, Cleavitt (2002) found that the three common species [***Mnium spinulosum*** (Figure 202), ***Bryum pseudotriquetrum*** (Figure 203), ***Didymodon rigidulus*** (Figure 204)] were more likely to occupy habitats that agreed with their physiological requirements. ***Mnium spinulosum*** was limited by high light and thus occurred only in deeply shaded conifer stands; ***Bryum pseudotriquetrum*** was intolerant of desiccation and was thus found in moist areas such as stream banks.

Figure 202. ***Mnium spinulosum***, a common species that is intolerant of high light and lives in conifer forests. Photo by Michael Lüth, with permission.

Figure 203. ***Bryum pseudotriquetrum*** at streamside. Photo by Michael Lüth, with permission.

Figure 204. ***Didymodon rigidulus***, a common species. Photo by Michael Lüth, with permission.

Cleavitt (2002) suggests that rare species may have broader physiological tolerance because they rely on vegetative reproduction largely as fragments. In particular, they have a high tolerance to desiccation in both whole colonies and in fragments. This suggests that they may be rare due to dispersal limitations, slow establishment rates that permit competitors to overpower them, or special environmental factors that were not examined.

Reproductive Problems

But the problems don't end with germination or even successful production of gametophores. These gametophores must likewise be able to reproduce, whether by vegetative means or spores. This is particularly problematic for dioicous species because they must have the successful invasion of both male and female spores for any further reproduction by spores to occur. And if they did arrive at a distant location by spores, it is likely that this is their primary means of dispersal. The same problem exists for vegetative propagules. For dioicous taxa, it is possible that only one gender arrives, whether by specialized structures or by fragments.

Perhaps there are species where the spores travel in tetrads, as is known for ***Haplomitrium gibbsiae*** (Figure 205) (Van Zanten & Pócs 1981). Nevertheless, a tetrad of spores is larger and hence sacrifices ease of transport by air currents. Van Zanten and Pócs suggest that this limitation might also be overcome by having spores remain in relatively compact clouds during transport – a notion that is certainly worthy of consideration. We need to consider if this compact cloud approach might also work for vegetative diaspores.

Figure 205. ***Haplomitrium gibbsiae***, a species where spores travel in tetrads. Photo by Jan-Peter Frahm, with permission.

Epiphytes

It is hard enough to land in the right microhabitat on the ground, but even more challenging to land on a vertical surface. Hence, highly structured bark has more chance of trapping the somewhat large vegetative propagules. But the problems are just beginning at landing. The vertical surface of almost anything is subject to drying, and tree trunks are particularly exposed. Fortunately, the tropical cloud forests manage to maintain a higher moisture content than other types of forest habitats and thus are endowed with dense bryophyte cover on everything (Figure 206).

As one can imagine, establishment of tracheophytes can be more difficult than that of bryophytes. Hence, many depend on bryophyte establishment to provide them with a suitable substrate (Nadkarni *et al*. 2000). Nadkarni and co-workers dropped epiphytic bryophyte fragments 50 cm

above branches of saplings and mature trees of *Ocotea tonduzii*. Only 1% of these fragments were returned for the six months of the experiment. During the same time period, branches in the canopy with intact epiphyte loads retained 24% and branches that had been stripped of their epiphytes retained 5%. They found that a larger surface area and presence of other bryophytes helped in the retention of the fragments.

Figure 206. Mossy forest, Malaysia, where high moisture levels make it easy for epiphytic bryophytes to establish. Photo by Vita Plášek, with permission.

Rosso *et al*. (2001) found that ***Antitrichia curtipendula*** (Figure 207-Figure 209) grows faster in the canopy (60% faster) than in the understory, making it easier for it to become established there than when it falls on lower branches. These researchers considered that its absence in young stands may be due to dispersal limitations compared to that in old growth stands. In old growth stands it has both greater height to launch dispersal and more time to get there.

Figure 207. Habitat of the epiphytic ***Antitrichia curtipendula***. Photo by Michael Lüth, with permission.

Figure 208. ***Antitrichia curtipendula*** growth form. Photo courtesy of Karen Golinski.

Figure 209. ***Antitrichia curtipendula*** on a branch. Photo courtesy of Karen Golinski.

Symbionts Needed

For some bryophytes, a symbiotic relationship is important to survival. ***Blasia pusilla*** (Figure 210) and ***Cavicularia densa*** (Figure 211) have solved this problem by producing gemmae that include their ***Nostoc*** symbiont (Figure 212) (Rikkinen & Virtanen (2008). Others benefit from the presence of soil Cyanobacteria such as ***Anabaena variabilis*** and ***Nostoc muscorum***, as is the case for ***Funaria hygrometrica*** (Rodgers & Henriksson 1976). These Cyanobacteria are able to capture atmospheric nitrogen and make it usable for the bryophytes.

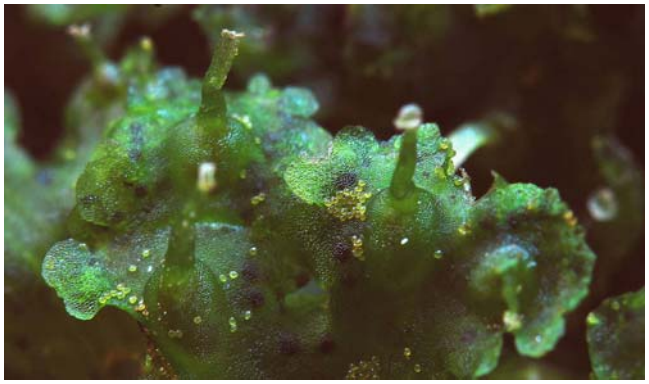

Figure 210. ***Blasia pusilla*** with ***Nostoc*** colonies (dark blue). Photo by Dick Haaksma, with permission.

Figure 211. ***Cavicularia densa*** with gemmae and ***Nostoc*** colonies. Photo from Digital Museum Hiroshima University, with permission.

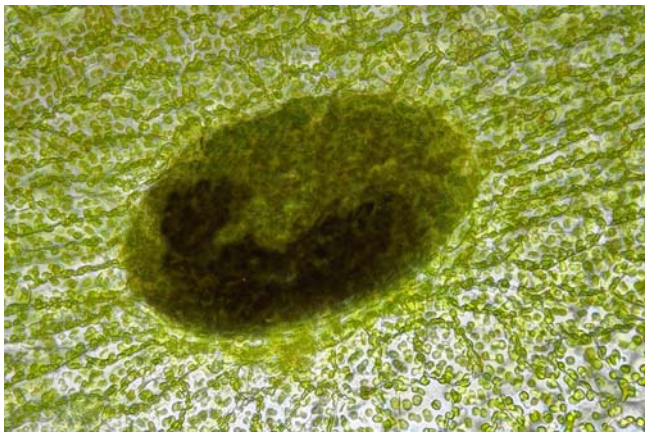

Figure 212. ***Nostoc*** colony on ***Blasia pusilla*** thallus. Photo by Dick Haaksma, with permission.

Other bryophytes need fungal partners (Figure 213) (Bidartondo *et al*. 2003; Martinez-Abaigar 2005; Bidartondo & Duckett 2010; Pressel *et al*. 2010; Bidartondo *et al*. 2011; Desirò *et al*. 2013). Although there have been a number of studies on fungi associated with various bryophytes, these have not dealt with the need for partners at the time of establishment of vegetative diaspores. Are vegetative dispersal structures able to carry their partners with them? Even if so, the conditions must be right for such a partner to flourish along with the bryophyte.

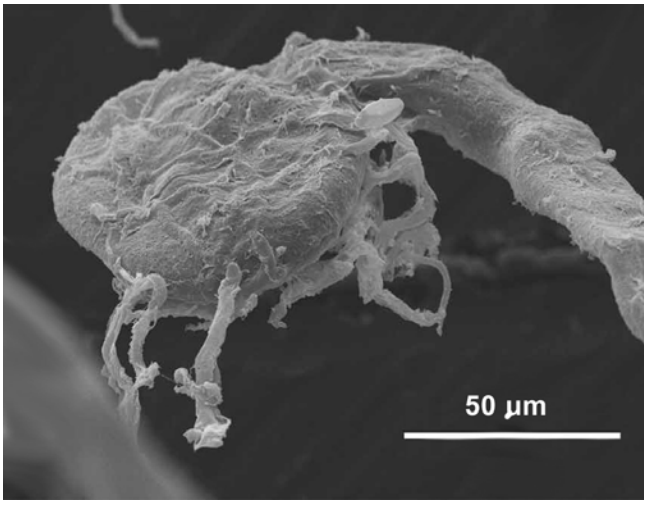

Figure 213. ***Mylia anomala*** rhizoid tip with symbiotic Ascomycete. Photo courtesy of Silvia Pressel, Robert Ligrone, and Jeffrey Duckett.

A somewhat similar problem occurs for ***Dicranum flagellare*** (Figure 23) on logs. It seems to be dispersal limited and can only colonize gaps caused by disturbance when other populations occur nearby (Kimmerer 1994). Therefore, older forests where there are more colonized logs provide a better source of propagules for dispersal. But once it reaches a substrate, it germinates much more rapidly than ***Tetraphis pellucida*** (Figure 18-Figure 19) and persists there longer, perhaps through competition.

Bacteria are important for the development of some bryophytes from spores (Spiess *et al*. 1984), so it is likely that these are also needed for some propagules to complete development, particularly those forming protonemata first.

Tradeoffs

Size matters in dispersal of propagules, but it invokes a tradeoff. Small propagules have the advantage of being produced in large numbers, *e.g.* 500-700 gemmae per leaf in ***Scapania nemorea*** (Figure 103-Figure 107) with 1-celled gemmae or 1000-7000 1-celled gemmae in ***Lophozia ventricosa*** var. ***silvicola*** (Figure 108) compared to only 15-45 in ***Jubula*** (=***Radula***) ***complanata*** (Figure 109-Figure 110) with discoid, multicellular gemmae (Laaka-Lindberg *et al*. 2003). Larger gemmae, on the other hand, have a greater chance for successful establishment where they arrive due to more stored energy.

It is also possible that the vegetative tissues of the vegetative diaspores may provide greater protection against germination in the wrong environment. Spores need only light and water to germinate. Hence, when they are brought to the surface and get a good rain, they germinate. As far as we understand, they do not, as spores, detect whether any other aspect of the environment is suitable. Some vegetative propagules, on the other hand, may be

able to detect inappropriate conditions of *p*H, insufficient nutrients, absence of a fungal partner, absence of hormones from associated bacteria, inappropriate temperature, or toxic metals and other substances. Examining these possible controls on germination of vegetative propagules may help us to understand both longevity of diaspores in the diaspore bank and the comparative success of spores vs vegetative diaspores.

Summary

Vegetative reproduction includes fragments, gemmae, and vegetative diaspores. A genet is therefore those individuals that arise from a single zygote, parthenogenetic gamete, or spore and that produce branches vegetatively. There are six basic means of reproducing vegetatively: 1) multiple gametophores from the protonema of one spore, 2) decay of older gametophyte parts with the separation of younger parts, 3) development of multiple shoots by rhizomes and stolons, 4) development of gametophores from rhizoids, 5) regeneration from fragments, 6) production of specialized propagula. The success of vegetative propagation is due to selection in the face of the difficulty of accomplishing sexual reproduction in a terrestrial environment. Fragmentation is especially common among pleurocarpous, perennial mosses where the dioicous condition and small spore size reduce the success of sexual reproduction. Such fragments can reach densities of 4000 viable propagules per cubic meter of snow. Propagula differ from gemmae in having an apical cell that can grow directly into a leafy shoot without a protonema stage. Propagula include deciduous shoot apices, caducous branchlets, flagella, and bulbils. Rhizoidal tubers can occur underground and many kinds of protonemata produce gemmae.

Splash cups are useful in dispersing gemmae in several liverworts and one family of mosses. Bryophytes getting frozen in ice or caught by flood waters can be carried considerable distances and vegetative dispersal in flowing water environs is essentially guaranteed. But vegetative diaspores have few mechanisms that aid in their liberation and dispersal. Among these are **tmema**, small cells that form a weak link and permit breakage.

Propagules must survive the desiccation, temperatures, and UV light of travel, be able to remain dormant upon arrival until the habitat or weather is suitable for germination, then survive after germination for the dispersal to be successful. Some have inhibitors such as ABA. Some require bacteria or fungi as partners. Some must land and become attached to vertical substrates. The usually larger vegetative structures sacrifice long distance dispersal for the ability to carry more with them and become established more easily. In addition to ABA, sucrose may also help in the survival of desiccation.

Acknowledgments

This chapter has benefitted from several email discussions with Peter Poschlod, especially on *Sphagnum*. Thank you to Bryonetters for interesting discussions on diaspores. A special thanks to Stefan Rensing and his associates Marco Göttig and Anne Genau for inducing and photographing the tmema cells for this chapter.

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CHAPTER 4-11

ADAPTIVE STRATEGIES: VEGETATIVE DISPERSAL VECTORS

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CHAPTER 4-11

ADAPTIVE STRATEGIES: VEGETATIVE DISPERSAL VECTORS

Figure 1. ***Pohlia annotina*** with bulbils in leaf axils. Many species survive on dispersal of vegetative propagules. Photo by Dick Haaksma, with permission.

Dispersal

Laaka-Lindberg *et al*. (2003) stated that dispersal pattern of vegetative propagules (*e.g.* Figure 1) is affected both by the microtopography of the habitat (Kimmerer & Young 1996) and by the type and size of propagule (Söderström & Herben 1997). Kimmerer (1994) further demonstrated that two log-dwelling species [***Orthodicranum flagellare*** (Figure 2) and ***Tetraphis pellucida*** (Figure 35)] differed in the dispersal ability of their propagules.

Conditions upon arrival can play a role in which species can become established following dispersal. Gradstein (2006) demonstrated this with the lowland cloud forest of French Guiana. Vegetative propagules there are protected from desiccation by the daytime fog, permitting good photosynthesis despite high temperatures. Asexual reproduction is significantly more common in the understory than in the canopy despite the greater constraints on dispersability in the understory. The canopy seems to experience better dispersal by spores.

Figure 2. ***Orthodicranum flagellare*** with broken brood branches lying on top of the cushion. Most likely some of these have travelled with an animal that broke them off. Photo by Janice Glime.

Gravity

Whereas spores are light weight and therefore easily lofted away on a slight air current, vegetative structures are often much more bulky and heavy. Shed parts, unless caught in a gust that can even blow heavy maple fruits up into the air, are likely simply to fall to the ground. This seems to be a common means for structures like gemmae, deciduous perianths, and other bulky forms of brood bodies and fragments.

"Galloping mosses" have an intriguing movement, leaving behind a trail of changed rock (Figure 3). The actual method of movement and time required is unknown, but they seem to move rather slowly, staying long enough in one place to chemically change the surface of the rock. Hence, it appears that gravity plays at least a partial role, but water most likely also helps in the movement. Mosquin (2011) reported these slowly moving mosses from the Arctic, where the mosses ***Sphagnum*** and ***Grimmia ovalis*** (Figure 3), and ***Racomitrium ericoides*** (Figure 4) are known for this behavior. When they reach a crack, they may be stopped and remain there (Figure 5).

Figure 3. ***Grimmia ovalis*** "galloping." Photo by Wouter Bleeker, with permission.

Wind Dispersal

Imagine being a small fragment of a leaf or stem being blown by the wind. Lacking the protection of surrounding plants, desiccation is imminent. Bouncing on the ground or off trees or rocks could impose a significant blow to tissues that may be only one cell thick. Exposure to UV radiation is likely to be greater than in their normal niche. Nevertheless, using a weather balloon Studlar *et al*. (2007) showed that at least some species [***Sphagnum fallax*** (Figure 6), ***S. magellanicum*** (Figure 7), ***Atrichum angustatum*** (Figure 8)] can survive these conditions and regenerate from fragments.

Figure 4. ***Racomitrium ericoides***, a moss that contributes to galloping mosses. Photo by Janice Glime

Figure 5. ***Grimmia ovalis*** trapped by cracks, with two clumps that managed to break loose, perhaps because of their larger size. Photo by Wouter Bleeker, with permission.

Figure 6. ***Sphagnum fallax***, a species that seems capable of surviving wind dispersal. Photo by Michael Lüth, with permission.

Figure 7. ***Sphagnum magellanicum***, a species that can regenerate from windborne leaf fragments. Photo by Michael Lüth, with permission.

Figure 8. ***Atrichum angustatum***, a species that regenerates from leaf fragments. Photo by Bob Klips, with permission.

This demonstration gives credence to a number of studies that have inferred vegetative dispersal of bryophytes. And we have already seen viability in 12% of the fragments blown about on the snow in Canada by wind (Miller & Howe Ambrose 1976).

In the Antarctic, Skotnicki *et al*. (2000) found evidence of propagule dispersal from elsewhere, with the RAPD technique indicating short-distance dispersal by both wind and water and long-distance dispersal by wind across the ice caps. The genetic similarities of ***Chorisodontium aciphyllum*** (as ***Sarconeurum glaciale***; Figure 9) from three locations on Ross Island, Antarctica, with those of Arrival Heights, Scott Base, and Crater Hill, a few km away suggest wind dispersal, a concept supported by the prevailing wind direction and absence of the species in areas in between.

Des Callaghan (Bryonet 11 May 2019) demonstrated the wind dispersal of ***Plagiochila exigua*** (Figure 10) in Britain. This rare oceanic plant produces only males, making spore dispersal impossible. But it has **caducous** (deciduous) leaves that are easily dispersed in the wind (Figure 11; see <https://youtu.be/YCHhANT0dUM>).

Figure 9. ***Chorisodontium aciphyllum***, an Antarctic moss that is apparently dispersed by both wind and water. Photo by Jan-Peter Frahm, with permission.

Figure 10. ***Plagiochila exigua*** showing missing caducous leaves at right. Photo by Michael Luth, with permission.

Figure 11. ***Plagiochila exiguua*** dispersing leaves. Photo by Des Callaghan, with permission.

Water Dispersal

Water aids in the dispersal of bryophytes in multiple ways. Aquatic mosses most likely depend primarily on water dispersal. Sexual organs can easily be damaged by abrasives in the water, as for example those in ***Platyhypnidium riparioides*** (Figure 12; Lewis 1973). These same abrasives can free leaves and branches that are possibly able to lodge on a substrate and regenerate. Conboy and Glime (1971) found similar abrasion in stream populations of ***Fontinalis novae-angliae*** (Figure 13).

Figure 12. ***Platyhypnidium riparioides*** in Europe, showing darkened and scoured leaves on lower parts of stems. Photo by Michael Lüth, with permission.

Figure 13. ***Fontinalis novae-angliae*** scoured by stream flow and suspended particles. Photo by Janice Glime.

Fontinalis species in streams are faced first with the problem of producing few sporophytes (Sayre 1945; pers. obs.), then of having spores lodge in a suitable place to stay put and begin new growth, whereas branches can easily get caught against rocks or snagged by submerged branches and roots, giving them an opportunity for new establishment (Figure 14; Sayre 1945; Welch 1948; Glime *et al*. 1979). Once these fragments get lodged against a rock or other suitable substrate, the contact stimulates the growth of rhizoids that eventually attach them to the substrate (Welch 1948; Glime *et al*. 1979; Figure 15-Figure 16). But this takes time, and experiments indicate that it requires at least nine weeks of impingement before the actual attachment (Figure 17; Glime *et al*. 1979). Temperature and flow rate influence the development of these rhizoids in ***Fontinalis duriaei*** (Figure 18) and ***Hygroamblystegium fluviatile*** (Figure 19), with flowing water conditions causing the mosses to produce more rhizoids than pool conditions (Glime 1980).

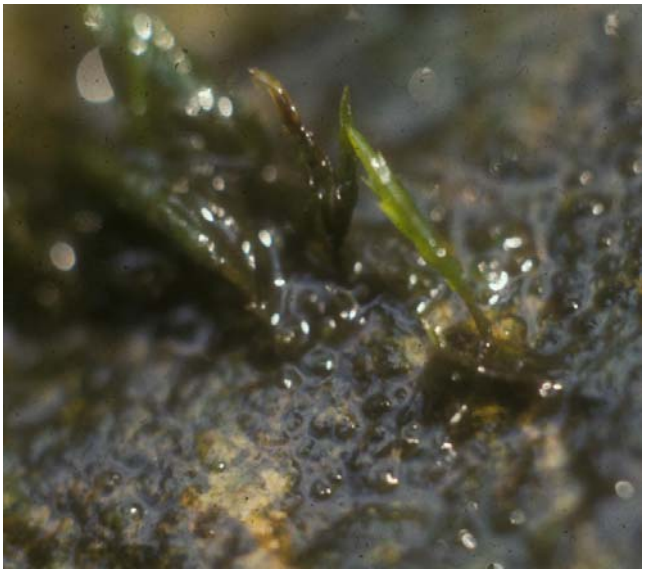

Figure 14. ***Fontinalis novae-angliae*** becoming established from a rhizome fragment in Fox Run, Grafton County, NH, USA. Photo by Janice Glime.

Figure 15. Rhizoids developing from stem wound tissue of ***Fontinalis squamosa***. Note the spiral growth. These have not yet contacted a substrate. Photo by Janice Glime.

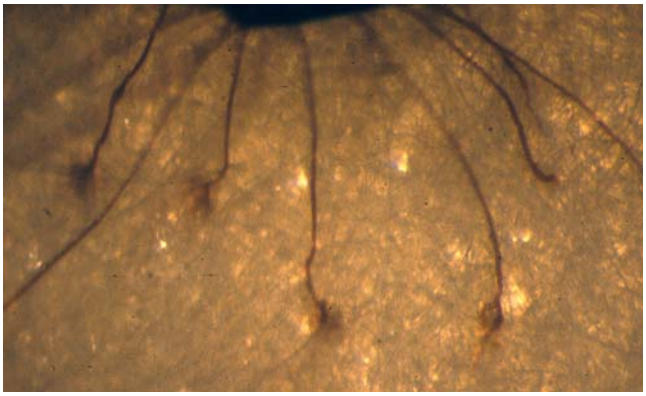

Figure 16. Rhizoids from wounded stem tissue of ***Fontinalis squamosa***, showing the branched growth at their tips where they have contacted a substrate. In this case, the substrate is filter paper in contact with a glass test tube. Photo by Janice Glime.

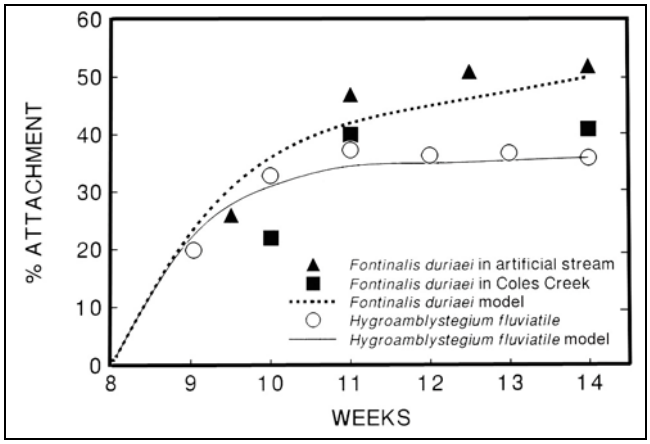

Figure 17. Comparison of times required and percentage of attachment for ***Fontinalis duriaei*** and ***Hygroamblystegium fluviatile*** in contact with rocks in an artificial stream (n=48) compared to rocks placed in Coles Creek, MI, with ***F. duriaei*** held in contact with netting. Based on Glime *et al*. 1979.

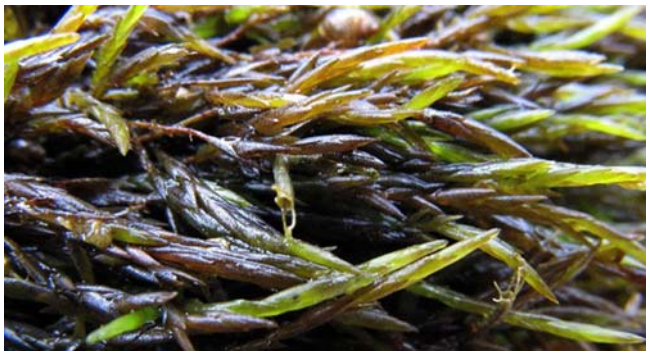

Figure 18. ***Fontinalis duriaei*** in Europe. Photo by Jan-Peter Frahm, with permission.

Figure 19. ***Hygroamblystegium fluviatile*** fragment in culture, showing dense rhizoids that formed, possibly in response to the substrate. Photo by Janice Glime.

In these early experiments, the moss fragments were held against the rocks with netting (Glime *et al*. 1979). But the field application of this concept was then tested by tagging 750 stems of ***Fontinalis duriaei*** (Figure 18) growing in Big Valley Creek, a forested stream in the Keweenaw Peninsula, Michigan, USA (Glime *et al*. 1979). Within the two years following tagging, may mosses could not be found again. But the proof of dispersal lies in two tagged mosses that were found in a different location. One of these was relocated downstream 60 weeks after the tagging date. The second was found nearly 100 m upstream! Possible upstream dispersal agents were fishermen and the black bear (*Ursus americanus*; Figure 20) that chased my graduate student; there was no evidence of beaver activity. And this moss was found attached in its new location only 9 weeks after it was tagged. In both cases, the mosses were attached by rhizoids and were wrapped around fallen tree branches where they most likely were held in place by the flow of water. Several other fragments were found in new locations, but these lacked rhizoid attachments.

Figure 20. ***Ursus americanus*** catching salmon in Alaska stream. Dark patches of mosses can be seen by its feet, suggesting an opportunity for dispersal. Photo by J. Brew, through Creative Commons.

In experiments with ***Fontinalis***, I have observed that stems with broken tips will often produce protonemata or several apical branches (Figure 21-Figure 22).

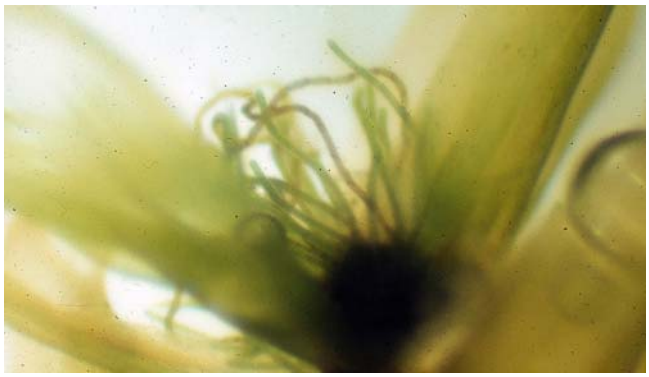

Figure 21. ***Fontinalis hypnoides*** broken shoot apex producing protonemata. Photo by Janice Glime.

Figure 22. ***Fontinalis antipyretica*** apical wound with new growth and rhizoids. Photo by Janice Glime.

In the winter, aquatic mosses can get frozen in the ice (Figure 23). When the ice breaks up, chunks may carry a number of fragments downstream where some may become impinged on suitable substrata.

Figure 23. Fragments of ***Fontinalis dalecarlica*** frozen in ice that has broken up in a New Hampshire, USA, headwater stream. Photo by Janice Glime.

Sayre (1945) demonstrated that connections of waterways could account for the dispersal of ***Fontinalis*** in a series of moraine ponds. Using Polymerase Chain Reaction (PCR) and involved amplification of DNA sequence with several ISSR primers, Korpelainen *et al*. (2004; 2013) found little variation in several bryophytes between lakes and concluded that ***Fontinalis antipyretica*** (Figure 22), ***F. hypnoides*** (Figure 21), and ***Calliergon megalophyllum*** (Figure 24) were dispersed by water between the lakes. This can occur by streams connecting lakes or by flooding that connects them. They did not rule out waterfowl, but found that the direction of flow and genetic patterns indicated that stream flow was a major contributor to the dispersal.

Figure 24. ***Calliergon megalophyllum***, a species that is likely to be dispersed by water. Photo by Julita Kluša <daba.dziedava.lv>, with online permission.

Arts (1982) used circumstantial evidence to show that ***Fissidens fontanus*** (Figure 25-Figure 26) is dispersed by water. All the canals where he found them in Belgium and the Netherlands were fed by water from Maas and this source apparently dispersed them through the Albert Kanaal and the Zuid-Willemsvaart.

Figure 25. Canal with ***Fissidens fontanus*** growing on concrete (arrow). Photo by Michael Lüth, with permission.

Figure 26. ***Fissidens fontanus*** frond. Photo by Michael Lüth, with permission.

Fragments may be the most important means of dispersal in many aquatic bryophytes. For submersed species that produce submersed capsules, capsules are relatively rare and it is likely that most spores never lodge on a suitable substrate. As a result, some of these species are somewhat rare. ***Dichelyma capillaceum*** (Figure 27) is one such rare species in Europe (Hylander 1998). Only two populations are known with sporophytes. In Sweden it occurs along rivers, streams, and lakeshores – only in places that are inundated and then exposed annually. Hylander suggested that it was probably dispersed by fragments and more rarely through long-distance dispersal of spores.

Figure 27. ***Dichelyma capillaceum*** on a tree base in Europe where it gets flooded. Photo by Michael Lüth, with permission.

Antarctic researchers have used the RAPD technique to track populations and determine their genetic relatedness. For example, Dale *et al*. (1999) found ***Hennediella heimii*** (Figure 28) in Miers Valley, Antarctica, along melt streams within the valley, constituting a single large population, whereas it was distinct from populations in nearby valleys. RAPD indicates that ***Chorisodontium aciphyllum*** (Figure 9; as ***Sarconeurum glaciale***) from three locations on Ross Island, Antarctica, appear to all be from one population and differ genetically from populations elsewhere (Skotnicki *et al*. 1999a). Dispersal was apparently in small, meltwater drainage streams. ***Bryum argenteum*** (Figure 29), likewise, has apparently been transported in the Antarctic by water (Skotnicki *et al*. 1999b).

Figure 28. ***Hennediella heimii*** with capsules, a moss that gets transported by melt streams in the Antarctic. Photo by David T. Holyoak, with permission.

Figure 29. ***Bryum argenteum***, a worldwide taxon that seems to be transported by water in the Antarctic. Photo by Dick Haaksma, with permission.

It appears that some species may respond adaptively to being submersed. ***Leptobryum pyriforme*** (Figure 30) produces rhizoidal gemmae (tubers; Figure 31) when the protonema grows in water (Schofield 1981), suggesting a possible secondary dispersal by water movement, or a way of surviving until the water recedes.

Figure 30. ***Leptobryum pyriforme*** with capsules. Michael Lüth, with permission.

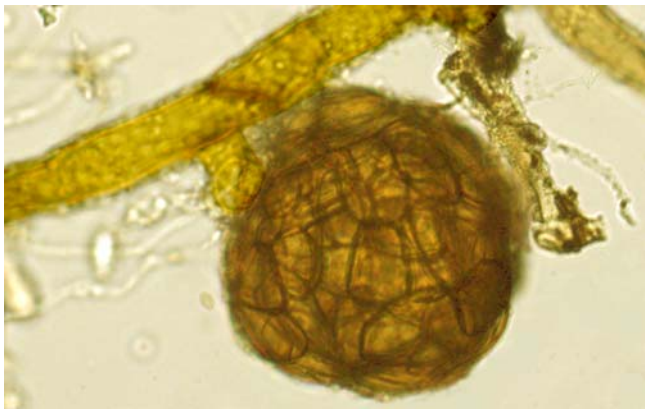

Figure 31. ***Leptobryum pyriforme*** rhizoidal tuber. Photo by Victoria Rozhina.

Water dispersal is a likely avenue for aquatic thallose liverworts. Patidar *et al.* (1986) studied effects of stream velocity on the floating liverwort ***Riccia fluitans*** (Figure 33-Figure 32). They found that a decrease in number of sporophytes was related to increase in water velocity, a likely consequence of reduced fertilization. Nevertheless, increased vegetative dispersal is likely in this species.

Figure 32. ***Riccia fluitans*** showing dead portions that will decay and break the clone apart. Photo by Kristian Peters, with permission.

Figure 33. ***Riccia fluitans*** stranded above water where it is also able to grow. Note the piece dangling from the colony at the bottom of the picture. This ramet can easily break away. Photo by Ralf Wagner at <http://www.dr-ralf-wagner.de/>, with permission.

Splash Cups

Water dispersal is not confined to plants living in or near water. Some bryophytes take advantage of splashing raindrops for their dispersal, providing cups or platforms from which asexual propagules can be splashed. The best-known method of dispersal is that of the **gemma cup** or **splash cup**, commonly taught in introductory botany courses. Although the splash cup and splash platform are somewhat frequent as a means of dispersing sperm, they are relatively rare as mechanisms of propagule dispersal. Several bryophytes have specialized cups where the gemmae are produced and from which they are subsequently dispersed by raindrops (Figure 34, Figure 35). The splash cup mechanism seems to be engineered to maximize the distance its contents can splash, thus forming an effective dispersal mechanism with the help of raindrops. The significance of its size and shape was apparently not recognized until Buller (1942) described its function in the bird's nest fungus, *Cyathus*. Brodie (1951) followed up on the observations of Buller and noted that splash cups commonly form 60-70º angles with the horizontal surface, the cups have a broad basal attachment, and the dispersed objects are lenticular. Gemmae of ***Marchantia polymorpha*** (Figure 34) can travel up to 120 cm when splashed from these cups, and Equihua (1987) suggests that this mechanism partly accounts for the worldwide distribution of this species. This ability to splash with water drops has made the species one of disdain for greenhouse owners who constantly find it invading their pots, spreading farther and farther from the original source through successive generations.

Gemmae in the splash cups of the moss ***Tetraphis pellucida*** (Figure 35) and the liverworts ***Lunularia cruciata*** (Figure 36-Figure 37) and ***Marchantia polymorpha*** (Figure 34) are lenticular. It seems to be a common feature for the splashing to carry the contents about 60 cm in ***L. cruciata*** and ***M. polymorpha*** (Brodie 1951), but in ***T. pellucida***, they seem only to go about 10 cm (Kimmerer 1991). Brodie (1951) considered ***T. pellucida*** too frail to benefit from raindrops striking its apex, finding that the plants bent under the weight.

Figure 34. Lens-shaped gemmae of ***Marchantia polymorpha***. Photo by Michael Lüth, with permission.

Figure 35. Gemma cups of the moss ***Tetraphis pellucida***. Photo by Michael Lüth, with permission.

Figure 36. Gemmae in half-moon-shaped pouches of ***Lunularia cruciata***. Photo by David T. Holyoak, with permission.

Figure 37. Pouch of ***Lunularia cruciata*** showing lenticular gemmae. Photo by Martin Hutten, with permission.

Stieha *et al*. (in prep.) quantified the production and dispersal of gemmae in the clonal thallose liverwort ***Marchantia inflexa*** (Figure 38). They found that these asexual propagules could move great distances during even a light rain, with some most likely leaving the parent clonal population. Further dispersal can occur in a stair-step fashion over time, providing long-distance dispersal. In this species, survival of female gemmae is greater than that of male gemmae.

Figure 38. ***Marchantia inflexa***. Photo by Scott Zona, through Wikimedia Commons.

Animal Dispersal

The dispersal of vegetative parts by animals may be an important mode of travel, at least occasionally. Various insects use fragments of mosses and lichens to build "houses" that they carry on their backs.

Even mammals may eat (perhaps not intentionally) bryophytes, as indicated by ^{14}C studies on animal remains of late Pleistocene large herbivorous mammals (Ukraintseva 1979). But we have no evidence that these bryophyte fragments remain viable after passing through the mammalian digestive tract.

Earthworms

Dispersal in the guts of earthworms (During *et al*. 1987; van Tooren & During 1988) can surely at times beat the 10 cm record for splashing in ***Tetraphis pellucida*** (Figure 35) reported by Kimmerer (1991); these and other invertebrates that eat bryophytes will deposit fragments in new locations. These could be distances of centimeters to hundreds of meters. Not only earthworms, but moles, voles, and ants have underground activities that can bring diaspores from their dormant state below ground to a position of activity above ground. Van Tooren and During (1988) found that eight species of bryophytes from the Netherlands appeared frequently in castings (Figure 39) from the earthworms ***Allolobophora caliginosa***, ***A. chlorotica*** (Figure 40), and ***Lumbricus terrestris*** (Figure 41).

Figure 39. Earthworm castings on moss. Photo by Ken Gergle at Moss and Stone Gardens, with permission.

Figure 40. ***Allolobophora chlorotica***, an earthworm that can transport bryophytes in its feces. Photo by Jacopo Werther, through Wikimedia Commons.

Figure 41. ***Lumbricus terrestris*** on mosses, a species known to ingest mosses and re-deposit them, still viable, in their feces. Photo by Michael Linnenbach, through GNU Free Documentation.

Since the light travels at most only a few centimeters into the soil, these diaspores remain dormant until some disturbance brings them to the surface and light. The species that survived the enzymes, crushing, and scarification of the earthworm guts, then grew to be identified, were ***Bryum klinggraeffii*** (Figure 42), ***Dicranella schreberiana*** (Figure 43), ***Ephemerum recurvifolium*** (Figure 44), ***Pottia*** spp., ***Pottia lanceolata*** (Figure 45), and ***Weissia*** spp. (Figure 46) (van Tooren & During 1988). ***Bryum rubens*** (Figure 47), common in the castings, never produces capsules in the area and presumably survived as rhizoidal tubers. Most of the other taxa probably also survived as vegetative diaspores except for ***Pottia*** sp. and ***Weissia*** sp., which probably originated from spores. Among these, tubers of ***Bryum klinggraeffii*** (Figure 42), ***Bryum rubens*** (Figure 47), and ***Dicranella schreberiana*** (Figure 43) successfully germinated, but in general, there was high mortality among tubers and other vegetative structures. Van Tooren and During suggested that spore survival was higher than vegetative diaspore survival in earthworm guts, but they did not have quantitative measures of this.

Figure 42. ***Bryum klingraefii***, a species that survives earthworm guts. Photo by Des Callaghan, with permission.

Figure 43. ***Dicranella schreberiana***, a species dispersed in earthworm castings in Europe. Photo by Michael Lüth, with permission.

Figure 44. ***Ephemerum recurvifolium***, a species whose vegetative diaspores survive earthworm guts. Photo by Tomas Hallingbäck, with permission.

Figure 45. ***Pottia lanceolata***, a species that survives earthworm gust, probably as vegetative diaspores. Photo by Michael Lüth, with permission.

Figure 46. ***Weissia fallax***, member of a genus known from earthworm castings in Europe. Photo by Michael Lüth, with permission.

Figure 47. ***Bryum rubens*** showing rhizoidal tubers, a possible means of surviving earthworm guts. Photo by Jan-Peter Frahm, with permission.

Arthropods

Isopods

I suspect that isopods (pillbugs, sowbugs, wood lice, rolly pollies) play a greater role in bryophyte dynamics than we understand. They make good experimental animals, and in our experiments, we have learned that both aquatic and terrestrial isopods readily eat some bryophytes (Figure 48-Figure 52), but avoid others, depositing their feces elsewhere. Some fragments can break off during the feeding and others are likely to be broken by their movements. We have not, however, observed any fragments being carried on their bodies and viability of mosses in their feces needs to be tested.

Figure 48. ***Porcellio scaber*** (isopod) eating ***Pleurozium schreberi***. Photo by John Hribljan, with permission.

Figure 49. ***Porcellio scaber*** escaping from ***Rhytidiadelphus triquetrus*** that has been disturbed. Photo by John Hribljan, with permission.

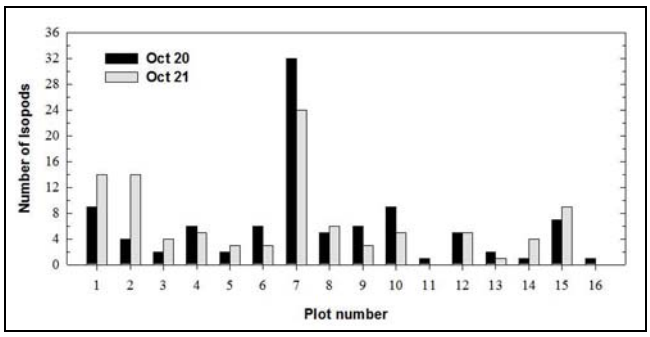

Figure 50. Comparison of abundance of ***Porcellio scaber*** in moss plots in the Keweenaw Peninsula of Michigan, USA, showing variability in numbers both spatially and daily. Graph by John Hribljan, with permission.

Figure 51. Evidence of eaten apical portions of ***Pleurozium schreberi*** by ***Porcellio scaber***. Photo courtesy of John Hribljan.

Figure 52. Evidence that ***Porcellio scaber*** prefers leaves to stems in feeding experiments on ***Rhytidiadelphus triquetrus***. Photo by John Hribljan, with permission.

Mites (Acari)

Edwards (1978) found protonemal gemmae of ***Schistostega pennata*** (Figure 53) attached to the legs of mites. The gemmae, like the spores of this species, are very sticky (Ignatov & Ignatova 2001). While mites themselves most likely do not travel far, they can become passengers on other animals – birds and mammals – that might travel considerable distances. Risse (1986, 1987) suggested that this might also be a possible vector for rhizoid tubers, presumably because the mites move about amid the spaces in the soil.

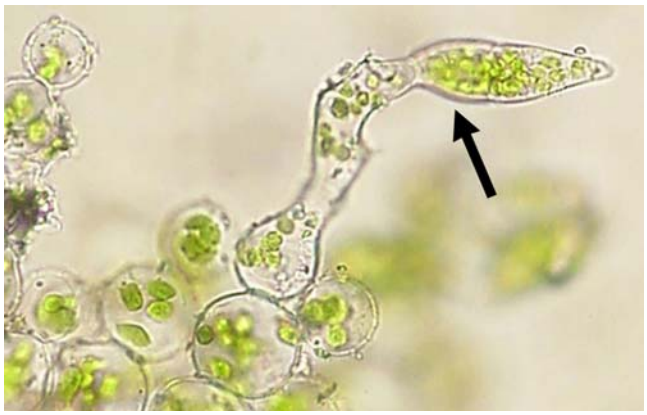

Figure 53. Protonemal gemma (**arrow**) of ***Schistostega pennata***. Photo by Misha Ignatov, with permission.

Zhang *et al*. (2002) observed spider mites (***Halotydeus*** sp.; Figure 54) eating the gemmae of ***Octoblepharum albidum*** (Figure 54) in Hong Kong. It is possible that some of these gemmae will get trapped among the hairs on the legs, thus getting transported by the mite. Others might be knocked off, falling to a new substrate.

Figure 54. ***Halotydeus*** sp. feeding on gemmae of ***Octoblepharum albidum*** in Hong Kong. **Arrow** indicates bases remaining where gemmae have been chewed. Photo by Li Zhang from Zhang *et al*. 2002, with permission.

Harvestmen

Some arthropods have an unusual mode of transporting bryophytes – they grow them on their bodies. These include liverworts on Neotropical harvestmen (Machado & Vital 2001).

Insects

Insects are often responsible for releasing small fragments of bryophytes (Lepp 2008). Larger insects can break dry bryophytes due to the insect weight, and a number of insects actually eat the bryophytes. Some live among the cushions where they often find food and thus move around, potentially transporting the fragments from a cushion to an open space.

Slocum and Lawrey (1976) report that the green lacewing larva (***Nodita pavida***) carries about a "packet" of camouflage constructed of bits of lichen, lichen soredia, pieces of bark, pollen grains, fungal spores, moss gametophyte fragments, and other debris. They demonstrated that the lichen fragments were viable but did not test the mosses. It is likely that they not only were alive, but that some of these fragments also would land somewhere and grow. Larvae of Diptera (flies, especially craneflies) and Trichoptera (caddisflies) construct houses of various shapes and may incorporate bryophyte fragments in them, as will be discussed later in the chapter on aquatic insects.

Aquatic organisms can be dispersed by aquatic insects that carry adhering cells on their bodies (Stewart & Schlichting 1965, 1966; Stewart *et al.* 1970), but their role in bryophyte dispersal is mostly unknown. For example, some caddisfly larvae may construct their homes from mosses, leafy liverworts, or narrow thallose liverworts like ***Riccia fluitans*** (Figure 33; Glime 1978). When these homes (cases) are discarded, the bryophytes can potentially grow in this new location.

Cairns and Wells (2008) reported that the microcaddisfly ***Scelotrichia willcairnsi*** (Figure 55) in Australia fed on the moss ***Platyhypnidium muelleri*** (Figure 56), an activity that could permit transport of fragments that survive travel through the gut. But in addition, and more likely to survive, are fragments that they weave into their case. The case travels with the caddisfly, which may travel considerable distance if it breaks loose from its substrate and becomes part of the drift.

Figure 55. The caddisfly ***Scelotrichia willcairnsi*** with ***Platyhypnidium muelleri*** case. Photo courtesy of Andi Cairns.

Figure 56. The moss ***Platyhypnidium muelleri*** with the caddisfly ***Scelotrichia willcairnsi*** showing numerous cases. Photo courtesy of Andi Cairns.

Weevil Gardens – A few insects disperse mosses in an unusual way. Certain weevils (Curculionidae) have pits on them where mosses are able to grow. This is the case for the moss ***Daltonia angustifolia*** (Figure 57) that attaches in pits on the hardened exoskeletons of weevils, including the weevil ***Gymnopholus reticulatus*** (Figure 57; Gradstein *et al*. 1984).

Gressitt and coworkers (1965, 1968) reported gardens on the backs of several species of weevils, including ***Gymnopholus*** spp. (Figure 57) among others. These weevils live in areas with moss cover on forest ridges and summits in eastern New Guinea (Gressitt *et al*. 1965, 1968). ***Gymnopholus*** species with epizoic bryophytes live more than three years and have hairs or specialized scales not present on species without plants growing on them (Gressitt & Sedlack 1970). In experiments where weevils were kept in cages, older weevils lost their plants, demonstrating the usefulness of these species as dispersal vectors. They are usually sedentary, but they can travel up to 0.25 km in half an hour by walking.

Figure 57. The moss ***Daltonia angustifolia*** living epizootically on the weevil ***Gymnopholus reticulatus***. Photo courtesy of Rob Gradstein.

Ants – Rudolphi (2007) found that ants on stumps served as dispersal vectors, passively carrying the bryophyte dispersal units for a significant time. Rudolphi (2009) used experiments to demonstrate that the ant ***Lasius platythorax*** (Figure 58) may disperse the gemmae of ***Aulacomnium androgynum*** (Figure 59). Both the ants and the ***A. androgynum*** occur on dead wood in Sweden. When the ants were permitted to run over a moss tuft, gemmae adhered to 33% of the ants within only two minutes! Half the gemmae remained attached for about four hours. This is most likely passive dispersal, with no special adaptations by either organism. Since these are active organisms that can travel considerable distances quickly, this could be an important dispersal mechanism.

Figure 58. ***Lasius platythorax***, an ant that disperses gemmae of ***Aulacomnium androgynum***. Photo by April Nobile, through Creative Commons.

Figure 59. ***Aulacomnium androgynum*** gemmae, known to sometimes have dispersal by ants. Photo by Des Callaghan, with permission.

One interesting way that ants (***Formica rufa*** group; Figure 60) contribute to dispersal is in their nest building. Heinken *et al*. (2007) sampled nesting material from 25 ant nest mounds in Germany. They found fragments of 20 bryophyte and 10 lichen species in these mounds. Among the bryophytes, wefts were particularly well represented, whereas tall turfs were poorly represented relative to their abundance. The researchers suggested that fragments lost along the way provided a means of dispersal. Other successful dispersal may occur among fragments in the

mound when the mound decays. Healthy mounds with live ants do not provide a safe site for the bryophytes. The ants are active in maintaining the mound and keep burying the fragments. Any that do manage to remain at the surface are subject to greater drying than those on the surrounding soil. In addition to these problems, disturbance by the ants, birds, and even boars further dislodges them, interrupting growth and detaching the fragments.

Figure 60. ***Formica rufa***, an ant that disperses bryophytes through its nest building. Photo by Richard Bartz, through Creative Commons.

The most common species on these ant mounds were ***Hypnum cupressiforme*** *s.l.* (Figure 145) in 16 of the 25 samples (Heinken *et al*. 2007). These accounted for 67.5% of the fragments. In addition, ***Brachythecium*** spp. (Figure 144) and ***Pleurozium schreberi*** (Figure 61) were often abundant. Species differed by forest type. Five of the 20 bryophyte species rarely produce any spores or vegetative structures, making fragments important in their dispersal. The territory size for this species ranges 200-1500 m^2 and the travelling ranges extend 20-30 (65) m from the nest, making a reasonable dispersal distance.

Figure 61. ***Pleurozium schreberi***, a moss known from ant mounds. Photo by Janice Glime.

Modern genetic techniques permit us to learn even more about insect roles. Korpelainen *et al*. (2011) studied ***Barbilophozia attenuata*** (Figure 62) in an area traversed by ant trails, using spatial genetic structure to unravel the history of the liverwort dispersal. They found significant kinship of colonies along the trails up to 8 m. At distances greater than 25 m, kinship correlation was nearly zero. Gemmae were most important up to 8 m, but spores were important for distances of 25 m or greater. Plants on logs and other raised surfaces can achieve even greater distances by spores. They considered that the large gemmae permitted greater opportunity for establishment than the small sexual spores and gemmae account for the aggregated distribution of the species in the study area. They also concluded that gemmae are favored over spores in areas with frequent disturbance, such as ant trails. Nevertheless, at greater distances, spores become important.

Figure 62. ***Barbilophozia attenuata*** with apical gemmae. Photo by Michael Lüth, with permission.

Lepidoptera – Larvae of ***Aenetus virescens*** (Figure 63) feed on the leaves and rhizoids of both live and dead mosses and liverworts, among other things (Grehan 1984). These bryophytes have the potential of being dispersed in feces, but tests must be made to see if they survive the gut. It is also possible that fragments adhere to these larvae, thus being dispersed.

Figure 63. ***Aenetus virescens*** adult, looking perfectly suited to living among bryophytes, where it might complete its emergence, but it lives only 48 hours as an adult. Its larvae feed on bryophytes, among other things. Photo by Tony Wills, through Wikimedia Commons.

Molluscs

Mollusks such as slugs eat bryophytes, but their sticky surfaces also cause fragments to adhere, effecting their dispersal. The moss ***Orthodicranum flagellare*** (Figure 2) lives on logs and stumps where snails can readily gain

access and contribute to dispersal of the flagelliform branches that serve as propagules (Stolzenburg 1995). Kimmerer and Young (1995) found that this species depends on its asexual brood branches to colonize new logs, with slugs as their primary dispersal vector. In fact, the propagules adhere to the slime trails, with evidence that the slugs (***Philomycus*** sp.; Figure 64) can transport them at least 23 cm. However, the distance is more commonly only about 3.7 cm. The slime helped the propagules adhere to the substrate without interfering with success of germination.

Figure 64. ***Philomycus carolinianus*** on a log, crawling over worms. Photo by Rebekah D. Wallace, through Creative Commons.

Aquatic molluscs also facilitate the dispersal of bryophytes. Both ***Fissidens fontanus*** (Figure 26) and ***Leptodictyum riparium*** (Figure 65) are known from the shells of mussels, a moving substrate that is likely to drop off fragments as it moves (Neumann & Vidrine 1978). Species of ***Fissidens*** are especially vulnerable to grazing by snails and slugs (Figure 66), so it is likely that fragments also get dispersed in the feces of the bodies of these molluscs.

Figure 65. ***Leptodictyum riparium***, a moss that is known to grow on mussel shells. Photo by Michael Lüth, with permission.

Amphibians

Like slugs, most amphibians have moist, sticky skin (Evans & Brodie 1994). Therefore, it is likely that bryophyte fragments and propagules get broken off as they traverse the bryophytes and that many of these same fragments and propagules get transported to new locations. My own pet frog was usually covered by empty seed coats dropped by the finches that shared the room. Evans and Brodie found moss fragments were among the debris they washed from amphibians at the beginning of their sampling. In their experiments, Evans and Brodie found that ***Dyscophus antongilii*** and ***D. guineti*** had the strongest glue among the eleven amphibians tested. D. Bruce Means has captured this adherence to ***Ceuthomantis smaragdinus*** in the image below (Figure 67).

Figure 66. ***Fissidens*** sp. being traversed by a slug. Photo by Janice Glime.

Figure 68 through Figure 73 demonstrate some of the variety of anurans that are able to carry bryophyte fragments. These six images were selected from my collection of 494 anuran images based on discernible adhering debris, giving a very crude estimate of the frequency of such passage. Figure 74-Figure 75 demonstrate that salamanders are also able to carry bryophytes that adhere to the sticky surface.

Figure 67. ***Ceuthomantis smaragdinus*** with several fragments of bryophytes adhering. Photo by D. Bruce Means, through public domain, USFWS.

Figure 68. ***Trachycephalus resinifictrix*** with debris attached to its breast. Photo by John White, with permission.

Figure 69. ***Craugastor bransfordii*** with an adhering bryophyte at the arrow. Photo by Jason Folt.

Figure 70. ***Oophaga pumilio*** on moss, with debris adhering to its skin. Photo by Brian Gratwicke, through Creative Commons.

Figure 71. ***Rana arvalis*** with a bryophyte fragment adhering to its leg. Photo by Petr Balej, with permission.

Figure 72. ***Ascaphus truei*** with an adhering moss fragment on its back. Photo by James Bettaso, USFWS, through public domain.

Figure 73. ***Bufo bufo*** with adhering plant material, demonstrating that even the dry skin of a toad can carry plant fragments. Photo by Karamel, through Wikimedia Commons.

Figure 74. ***Hynobius tokyoensis*** carrying a bryophyte fragment on its head. Photo ©Henk Wallays, through Creative Commons.

Figure 75. ***Nototriton abscondens*** with large bryophyte fragments on its back. Photo by Eduardo Boza Oviedo, with permission.

Turtles

I have experienced this dispersal first-hand by inference. When I (Glime, unpubl) grew ***Conocephalum conicum*** (Figure 76) and ***Fissidens*** (Figure 77) in my garden room in the company of a box turtle (***Terrapene***; Figure 78), both bryophytes spread quickly around the room, something they never did in the absence of the turtle. But eventually the zebra finches discovered the liverwort and each day it grew smaller, with triangles cut from its edges. Alas, the birds seemed to be agents of destruction and not dispersal because ***C. conicum*** soon disappeared completely. The ***Fissidens*** likewise stopped spreading and within some months it too disappeared.

Figure 76. ***Conocephalum conicum***, a liverwort that is eaten by birds and carried by turtles. Photo by Robert Klips, with permission.

Figure 77. ***Fissidens taxifolius***, a moss that seems to be carried by turtles. Photo by David Holyoak, with permission.

Figure 78. ***Terrapene carolina***, a potential bryophyte dispersal vector. Photo through Wikimedia Commons.

McGregor (1961) has a more documented story. He found living thalli of ***Riccia rhenana*** (Figure 79) on the carapace of a snapping turtle (***Chelydra serpentina***; Figure 80) that had ventured nearly 1 km from the nearest pond. This liverwort species grows among cattails, sedges, rushes and grasses of shallow water where it multiplies by growth and division of thalli, mostly in April. The thallus dries up to its growing apex in summer, and McGregor observed it in that dry state for up to 33 days, when it was rehydrated by rains and resumed growth. Its ponds often freeze solid, freezing the thalli in ice. Once again, the thalli die except the growing apex. McGregor reports that these thalli can survive more than five weeks in the ice.

Figure 79. ***Riccia rhenana***, a liverwort known to be carried by a snapping turtle. Photo by Jan-Peter Frahm, with permission.

Figure 80. ***Chelydra serpentina*** (snapping turtle) female searching for a nesting site. Photo by D. Gordon E. Robertson, through Wikimedia Commons.

Birds

Aquatic organisms living in isolated wetlands could have real difficulty being dispersed. But Figuerola and Green (2002) found that widespread distributions of aquatic organisms typically coincide with pathways of migratory waterbirds. They considered that small propagule size would favor dispersal, but we have seen that birds are important dispersers of bryophyte fragments (Lewis *et al*. 2014). Behling *et al*. (2002) have further demonstrated dispersal through **endozoochory** – ingestion of fragments by birds. Birds travel long distances, and rather quickly. Their frequent stops for food makes them ideal dispersal agents because in most cases any adhering bryophyte parts won't be in the atmosphere for very long. (See further details of long migration flights in Chapter 4-8.)

The introduction of the aquatic liverwort ***Ricciocarpos natans*** (Figure 81) into Norway may be the result of transport by waterfowl or some other form of epizoic transport (Skulberg 1978). This has been shown for a number of algae that travel on the feathers and feet of ducks, arriving in viable condition (Schlichting 1958). Both mechanisms seem reasonable for bryophyte spores and leaf fragments, or even small branches.

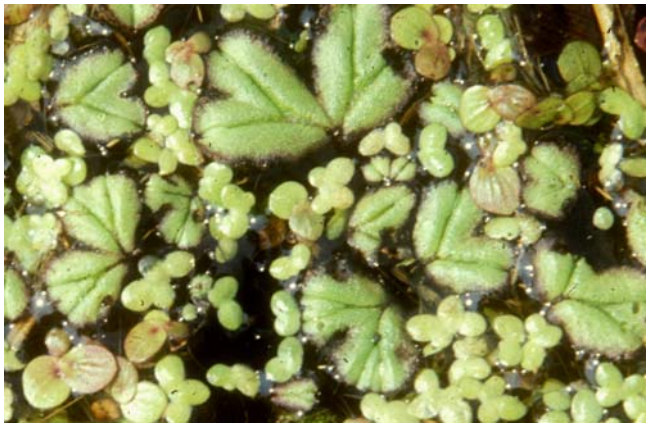

Figure 81. Thalli of ***Ricciocarpos natans*** floating with the duckweeds *Lemna minor*, *Wolffia* sp., and *Spirodela polyrhiza*. Since duckweeds are common foods for waterfowl, it is likely that ***Ricciocarpos*** gets mixed in with the food and stuck to feathers or feet as the birds wade and eat. It may also be eaten, if only inadvertently, and could possibly be dispersed in feces. Photo by Janice Glime.

The **Kelp Gull** (***Larus dominicanus***; Figure 82) in the Argentine Island region of the Antarctic uses bryophytes and other plant material for building its nest (Parnikoza *et al*. 2012). Some of these bryophytes are able to establish in their new locations. If the gull can survive a long flight, most likely the bryophyte can as well.

McGregor (1961) actually found evidence that ducks indeed disperse living bryophytes. A fragment of ***Riccia fluitans*** (Figure 33) was attached to a feather at the back of the neck of a pintail duck (***Anas acuta***; Figure 83) that was soon to become a hunter's dinner. The duck was intercepted just before it descended to land on the Kansas River.

In Hungary, geese (Figure 84) are known to carry such fugitives as ***Riccia frostii*** (Figure 85) on their feathers, feet, or muddy bills, making these liverworts common – you guessed it – along goose trails (Crum 1973). But might they also be transported in the feces? Bryophytes such as ***Riccia fluitans*** (Figure 33-Figure 32) exist among duckweeds (Lemnaceae) and thus will almost certainly be eaten along with them. With 0.7 kg of defecation (French & Parkhurst 2009) occurring every 20 minutes (Bowen & Valiela 2004), there is considerable opportunity for transport, albeit not very far if it has only 20 minutes of residence time. Jasmin *et al*. (2009) found that bryophytes increased in areas of goose foraging in the Arctic, but this may have been due to an increase in available habitat.

Figure 82. ***Larus dominicanus*** (Kelp Gull), a bird that spreads bryophytes by putting them in its nest in the Antarctic. Photo by Steve and Jem Copley, through Creative Commons.

Figure 83. Male and female Northern Pintails (***Anas acuta***). Photo by J. M. Garg, through Wikimedia Commons.

Figure 84. Domestic goose (***Anser***). These are among the known vectors of bryophytes through fragments stuck to feathers or feet. Note bits of mud on lower feathers and feet. Photo through Wikimedia Commons.

Figure 85. ***Riccia frostii***, a liverwort that is a known goose hitchhiker. Photo by Rosemary Taylor, with permission.

Crows seem to be favorites as the villains in moss destruction. Misha Ignatov (Bryonet 23 February 2013) reports seeing the rare (in Moscow) moss ***Dicranum viride*** (Figure 86) scattered over the ground rather than in place on the tree trunks. As he wondered who the destructive villain was, he heard crows overhead, then noticed a number of crow nests. He concluded that the crows were the likely vandals. He hoped that they might be forgiven if in the process the crows succeeded in dispersing the mosses to new locations where they could establish.

Figure 86. ***Dicranum viride*** on tree trunk in Michigan, USA. Photo by Janice Glime.

Erkamo (1976) reported observations of mosses being upturned, especially on flat, open rocks. These were mostly only a few cm in size, but some were 10-15 cm across. He considered the agents of this upheaval to be possible by voles, pheasants, seagulls, or crows, but considers crows (Figure 87) to be the most likely. He has actually seen crows in such activity, and considered that they were probably looking for food such as insects or worms under the moss cover. Erkamo lamented the destruction of beautiful rock scenery that will most likely take years to recover.

Figure 87. ***Corvus brachyrhynchos***, a crow that scatters mosses to find food. Photo by Walter Siegmund, through GNU Free Documentation.

Blackbirds (***Turdus merula***; Figure 88) have found another use for bryophytes that is likely to disperse them. Robin Stevenson (Bryonet 15 April 2010) reported observing **displacement activity** in this species. He observed a male throwing clumps of moss off a rooftop, alternating the activity with altercations with another blackbird. This displacement behavior was most likely part of a fight over territory and the mosses permitted them to take a break that prevented them from killing each other. The battered mosses included ***Grimmia pulvinata*** (Figure 89), ***Hypnum cupressiforme*** (Figure 90), and ***Syntrichia montana*** (Figure 91).

Figure 88. The Blackbird, ***Turdus merula***, resting among lichens. Photo by Mario Modesto Mata, through GNU Free Documentation.

Figure 89. ***Grimmia pulvinata*** (Grey-cushioned Grimmia), a rooftop species that was thrown off by quarrelling blackbirds. Photo by Barry Stewart, with permission.

Figure 90. ***Hypnum cupressiforme*** var ***cupressiforme***, a species tossed from a rooftop by quarrelling blackbirds. Photo by David Holyoak, with permission.

Figure 91. ***Syntrichia montana***, a species tossed about by quarrelling blackbirds. Photo by Barry Stewart, with permission.

Terrestrial bryophytes may get transported, at least for short distances, by bird behavior. For example, blackbirds (***Turdus merula***; Figure 88) forage among mosses to find insects or worms, tossing them aside to gain access (Davison 1976). It is likely that such food items and earthworms are closer to the surface under mosses where the moisture is greater. Davison reports that ***Mnium hornum*** (Figure 92) and ***Polytrichastrum formosum*** (Figure 93) may be tossed 1-2 m in these activities. In an area of 5 sq m, Davison found that 34 clumps with an average diameter of 2 sq cm were displaced in this way over a two-month period in Great Britain. Furthermore, an additional 18 clumps were moved into that same 5 sq m during the same time period (October-November).

Figure 92. ***Mnium hornum***, a moss that can be a victim of crow scavenging. Photo by Janice Glime.

Figure 93. ***Polytrichastrum formosum***, a moss often disturbed by crows seeking food. Photo by Michael Lüth, with permission.

Gathering bryophytes for nests is a likely means of dispersal for nearly every kind of nest in which bryophytes are used, *e.g.*, the Picaflor Rubi (***Sephanoides sephaniodes***; Figure 94-Figure 95) and White-sided Hillstar (***Oreotrochilus leucopleurus***) construct their nests primarily of mosses, especially those with falcate leaves (Calvelo *et al*. 2006). Fragments are likely to be dropped on the way, and many more are broken off or dropped or discarded during the construction of the nest and subsequent usage. For some, the lofty position of a nest in a tree provides the advantage of more opportunity to gain access to air movements that can carry the fragments even further.

Figure 94. Picaflor Rubi (***Sephanoides sephaniodes***), a bird related to the hummingbird that uses bryophytes to build its nest. Photo by Suemili, through Wikimedia Commons.

Figure 95. Picaflor Rubi (***Sephanoides sephaniodes***) on nest that is constructed of mosses, showing how its coloration blends with the moss. Photo by Diucón, through GNU Free Documentation.

When Surtsey was colonized after its ascension from the sea, the moss ***Racomitrium*** (Figure 96) was among the first invaders (Magnússon *et al*. 2009). The Lesser Black-backed Gull (***Larus fuscus***; Figure 97) invaded the island, forming a dense colony. Its primary nesting material was ***Racomitrium***, but it is unclear if it was brought to the island by the birds or it arrived by fragments or spores and spread.

Figure 96. ***Racomitrium lanuginosum***, one of the first mosses to arrive on Surtsey when it arose as a volcanic island. Photo by Juan Larrain, with permission.

Figure 97. ***Larus fuscus*** (Lesser Black-backed Gull) adult and juvenile, probably dispersal agents for ***Racomitrium*** sp. to Surtsey. Photo by Pline, through Wikimedia Commons.

Even when bryophytes are not transported to make nests, the nearness of a nest to bryophytes increases the chances that the bryophytes will become dislodged, and some may adhere to the birds. For example, the Peg-billed Finch (***Acanthidops bairdi***) is a rare bird in Costa Rica and Panama (Elizondo C. 2000). It has rarely been observed, but Mathias Jaschhof was able to photograph four fledglings in the nest (Figure 98). The nest was built in myrtle (*Vaccinium consanguineum*) and consisted of a bulky cup developed from ***Frullania*** sp. (Figure 99) with amendments of ***Leptodontium*** sp. (Figure 100), ***Pilotrichella***, and ***Plagiochila*** sp. (Figure 102) as well as fruticose lichens and a mix of unidentified leafy liverworts and mosses (Elizondo C. 2000). The egg chamber had a layer of fern rhizomes, a thin layer of grass inflorescences, and finally an external layer of ***Thuidium*** sp. (Figure 107).

This latter layer may extend to the outside of the nest and may be surrounded by ***Frullania***.

Figure 98. ***Acanthidops bairdi*** (Peg-billed Finch), a rare bird that builds a cup-shaped nest, sometimes in moss banks, as seen here. Photo by Mathias Jaschhof, with permission.

Figure 99. ***Frullania***, leafy liverwort that is predominant in the nest of the Peg-billed Finch (***Acanthidops bairdi***). Photo by Li Zhang, with permission.

Figure 100. ***Leptodontium***, a secondary moss in the nest of the Peg-billed Finch (***Acanthidops bairdi***). Photo by Felipe Osorio Zúñiga, with permission.

Figure 101. ***Pilotrichella*** sp., a minor component of nests of the Peg-billed Finch (***Acanthidops bairdi***). Photo by Lena Struwe, through Creative Commons.

Figure 102. ***Plagiochila adianthoides***, member of a genus used as a secondary bryophyte in nests of the Peg-billed Finch (***Acanthidops bairdi***). Photo by Michael Lüth, with permission.

Mammals

The role of mammals in dispersal of propagules seems to have gotten less attention than it deserves. Only recently are we seeing documentation that mammals can serve as dispersal vectors through feces, fur, and hooves, and in some habitats these may play a major role. Among these dispersal units are fragments that cling easily to the fur and feathers of some animals. Dispersal of fragments is most likely more important than we have considered (Heinken *et al*. 2001).

Rodents

I have blamed the chipmunks in my moss garden for tearing up my recent moss plantings. They seem to like frolicking across the bryophytes, and more than occasionally the bryophytes end up upside down as the chipmunks (Figure 103-Figure 104) kick them up or drag them with their feet. They seem to especially like ***Leucobryum glaucum*** (Figure 105-Figure 106) and ***Thuidium delicatulum*** (Figure 107). At least those are the most likely to get torn up in my garden, and one chipmunk insisted on making an entrance to a burrow in the middle of the ***T. delicatulum***, destroying the integrity of the mat, hence causing its death. ***Leucobryum*** species have the ability to develop rhizoids on the upturned surface that contacts the soil (Figure 106) and may recover as a moss ball. Mine did not. Gray squirrels (Figure 108), and certainly others, have the same potential to serve as dispersal agents.

Figure 103. ***Tamias sciurus*** (eastern chipmunk) is responsible for kicking up loose mosses and most likely transports fragments. Photo by Oleksii Voronin, through Wikimedia Commons.

Figure 104. ***Tamias sciurus*** (eastern chipmunk) with bark stuck to its fur, showing how easily it could transport bryophyte propagules and fragments. Photo by Janice Glime.

Figure 105. Moss garden showing upturned ***Leucobryum glaucum*** at lower left and mist netting covering clumps to prevent further upheaval. Photo by Janice Glime.

Figure 106. ***Leucobryum glaucum*** with leaf rhizoids (arrow) that develop after the clump has been overturned. Photo by Kristian Peters, through Wikimedia Commons.

Figure 107. ***Thuidium delicatulum***, a moss that a chipmunk used to make an entrance to reach its underground tunnels. Photo by Bob Klips, with permission.

Figure 108. Eastern gray squirrel (***Sciurus carolinensis***) amid mosses. This frisky animal is a likely dispersal agent for gemmae and fragments, especially when scratching to grab seeds, as seen here. Photo by Janice Glime.

In the Arctic, rodents, including moles and lemmings, eat the bryophytes (Ericson 1977), so dispersal of spores and fragments in their whiskers and fur is likely. Hribljan (unpubl) has cultured feces of rodents, collected from Alaska, that had protonemata germinate from them (Figure 109). It is likely that these came from fragments that were present in the feces, but could also have been from spores. Kimmerer and Young (1996) suggested that rodent activity may help ***Orthodicranum flagellare*** (Figure 2) disperse in two ways, by helping to produce gaps among the bryophytes on the logs and possibly by carrying the flagelliform propagules among the locations visited. In this regard, squirrels and chipmunks are likely agents. Could it be that they also inadvertently eat bryophytes as they forage and thus carry them in their guts? At the very least, they probably dislodge epiphytes, aiding their dispersal.

Figure 109. Protonemata and young gametophores germinated from microtine rodent scat collected in Alaska. Photo by John Hribljan, with permission.

Ericson (1977) showed that many of the most abundant forest mosses in northern Sweden are a preferred food for ***Myopus schisticolor*** (wood lemming; Figure 110). ***Ptilidium ciliare*** (Figure 111) and ***Plagiothecium denticulatum*** (Figure 112) are rejected, as are most herbaceous species. When the snow is gone, they feed on green tips of mosses, whereas when they are living under snow the lemmings bite the shoots off at the base. In 1974 and especially in 1975, following heavy grazing in 1973, ***Dicranum scoparium*** (Figure 113) spread to areas where no ***D. scoparium*** occurred in 1973. These rodents appear to have been the agents of both fragmentation and dispersal.

Figure 110. ***Myopus schisticolor*** (wood lemming) by its path amid ***Hylocomium splendens***. Photo by Risto S. Pynnönen, through Wikimedia Commons

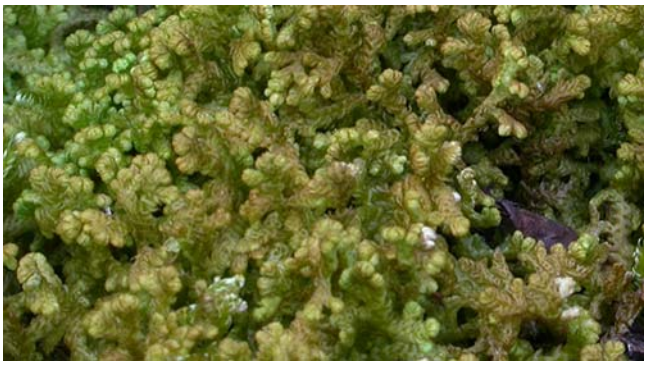

Figure 111. ***Ptilidium ciliare***, a leafy liverwort rejected by the wood lemming (***Myopus schisticolor***). Photo by Li Zhang, with permission.

Figure 112. ***Plagiothecium denticulatum***, a moss rejected by the wood lemming (***Myopus schisticolor***). Photo by Michael Lüth, with permission.

Figure 113. ***Dicranum scoparium***, a moss most likely distributed by rodents in northern Sweden. Photo by Janice Glime.

Eskelinen (2002, 2004) likewise demonstrated that mosses are preferred food of the wood lemming in northern Finland, and that they also are selective. They consume ***Dicranum*** spp. (Figure 113) and ***Polytrichum*** (Figure 114-Figure 115) in greater quantities than would be expected, but avoid ***Hylocomium splendens*** (Figure 110) and ***Pleurozium schreberi*** (Figure 61). Nevertheless, Ericson (1977) found that ***H. splendens*** diminished, presumably due to rodent consumption. Eskelinen (2002, 2004) suggested the preference for ***Polytrichum*** and ***Dicranum*** may relate to their higher N content. If so, preferences may change with habitat and available food choices.

Figure 114. ***Polytrichum commune*** var ***commune***, demonstrating the clone that can result from its branching rhizomes. Photo by David Holyoak, with permission.

Figure 115. ***Polytrichum juniperinum***, a moss that spreads by rhizomes. Photo by Janice Glime.

Ericson (1977) followed the changes in moss cover in Scandinavia for four years and discovered that rodents played a major role in the changes. Only the mosses on windthrows and tree stumps maintained constant cover. The fascinating realization was that different species of bryophytes seemed to suffer declines and increases in different years. In 1974, ***Ptilium crista-castrensis*** (Figure 116) suffered 73% reduction and ***Dicranum scoparium*** (Figure 113) suffered 57%. However, in 1975, the strongest decrease was in ***Hylocomium splendens*** (Figure 110), which suffered 49% reduction, while ***P. crista-castrensis*** increased 43% and ***D. scoparium*** increased 70%! Ericson felt that this might indicate increased growth as a response to fragmentation caused by grazing. However, to increase cover values so significantly, it would seem that at least some dispersal must have been effected.

Figure 116. ***Ptilium crista-castrensis***, a preferred moss for rodent consumption. Photo by Janice Glime.

Ericson (1977) felt that several types of regeneration were common for these species. ***Polytrichum commune*** (Figure 114) and ***P. juniperinum*** (Figure 115), as well as others, can recolonize from protonemata, juvenile plants, and rhizoid fragments (Meusel 1935, Wigglesworth 1947). ***Hylocomium splendens*** (Figure 110; Correns 1899) and species of ***Dicranum*** (Figure 113; Meusel 1935) grow easily from broken parts of stems, and ***Polytrichum commune*** and species of ***Dicranum*** regenerate from isolated leaves (Correns 1899). Callaghan *et al*. (1978) pointed to the need for ***Polytrichum commune*** to reproduce by underground branching into clones because of its finite life expectancy. ***Hylocomium splendens*** solves the problem of life expectancy by producing new shoots in a stair-step fashion, with the oldest part of the plant senescing and decomposing (Callaghan *et al.* 1978), a feature seen also in ***Pseudocalliergon trifarium*** (Figure 117; Bisang *et al*. 2008). However, if the young branch shoot of ***Hylocomium splendens*** is damaged, the entire plant will die (Callaghan *et al*. 1978). On the other hand, it seems to have a low branching rate for the main stem, limiting its clonal growth.

Bank voles (***Clethrionomys glareolus***) include small quantities of mosses in their diets (Watts 1968). Bank voles were caught in the act of eating mosses in The Netherlands. Andrew Spink was able to capture these on film (Figure 118).

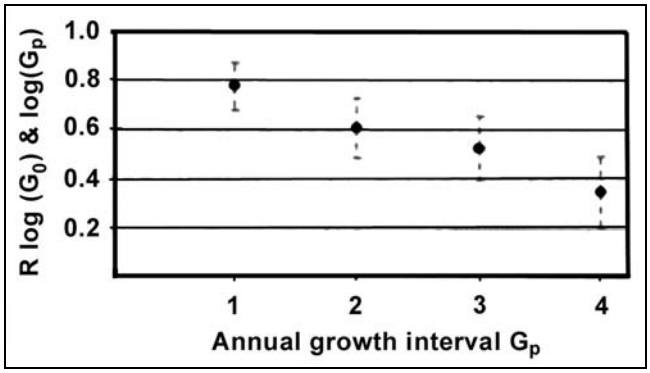

Figure 117. Diminishing growth rates of ***Pseudocalliergon trifarium*** through four years of growth. Redrawn from Bisang *et al*. 2008.

Figure 118. Bank vole eating mosses and most likely carrying fragments from one place to another. Photo by Andrew Spink, with permission.

Flying Fox

The spectacled flying fox (***Pteropus conspicillatus***; Figure 119), a fruit bat, passes bryophyte fragments in its feces (Figure 120-Figure 121), including chloronemata, rhizoids, and shoots (Parsons *et al*. 2007). These are capable of germinating (Figure 122) and may even benefit from nutrients in the adhering feces. Fifteen families of bryophytes were represented in these feces. Among the 48 fragments cultured, 52% germinated, producing rhizoids or shoot extensions. Even rotifers among the bryophytes were still alive. Included among the species were ***Metzgeria*** sp. (Figure 123), ***Acroporium*** sp. (Figure 124), ***Leucobryum juniperoideum*** (Figure 125, and ***Racopilum*** sp. (Figure 126). The germination rate was higher from samples taken during the early part of the season (17 out of 28 fragments) compared to those taken in the later part of the season (7 out of 20). This could represent a shift in diet, change in brittleness of bryophytes (resulting from desiccation) that changes ease of fragmentation, or a change in viability of the bryophytes. It is likely that the bryophytes were eaten unintentionally along with fruit.

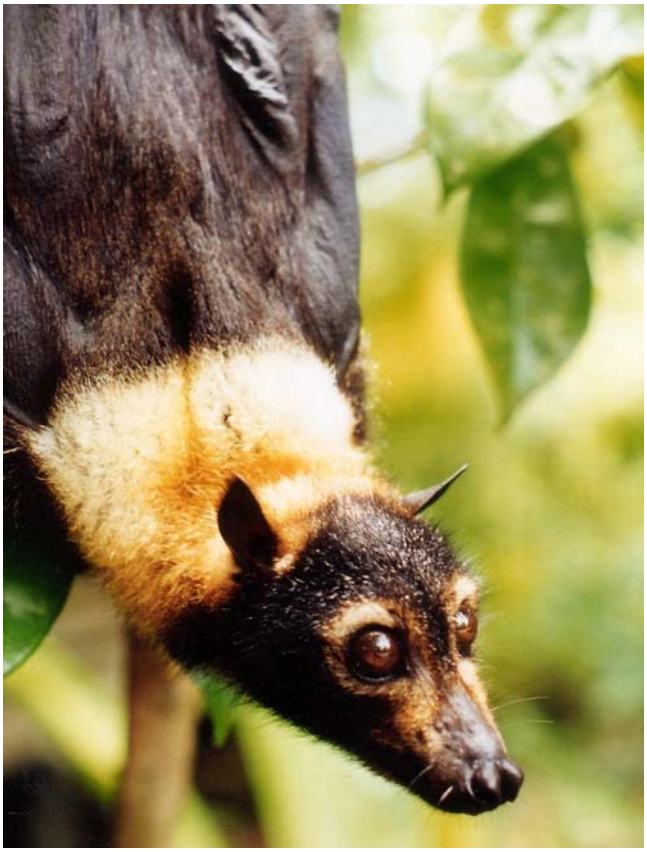

Figure 119. Spectacled flying fox (***Pteropus conspicillatus***). Photo courtesy of Andi Cairns.

Figure 120. Splat (feces) of flying fox on leaf. Photo courtesy of Andi Cairns.

Figure 121. Jennifer Parsons with flying fox splat trap. Photo courtesy of Andi Cairns.

Figure 122. Culture tube with flying fox feces. Photo courtesy of Andi Cairns.

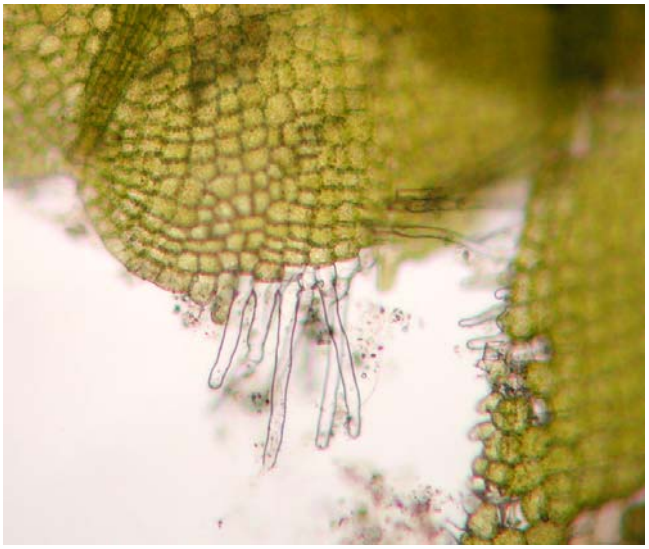

Figure 123. ***Metzgeria*** germinating from flying fox feces. Photo courtesy of Andi Cairns.

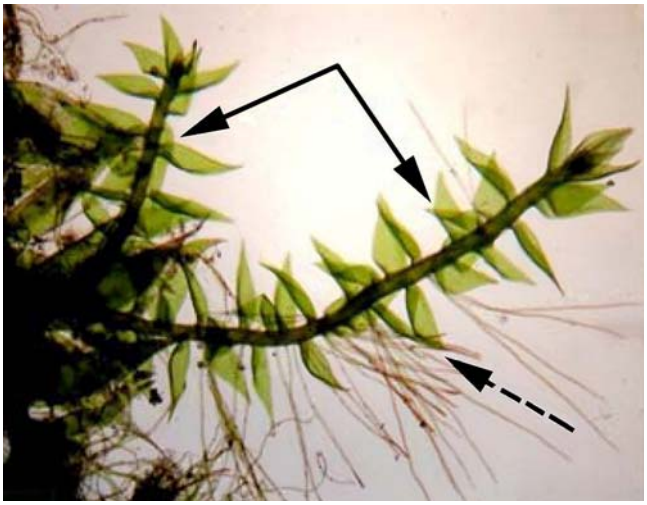

Figure 124. ***Acroporium*** sp. feces from flying fox. Solid arrows indicate new shoots; dashed arrows indicate rhizoids. Photo by Andi Cairns.

Figure 125. ***Leucobryum juniperoideum*** leaf fragment germinating from flying fox feces. Photo courtesy of Andi Cairns.

Figure 126. ***Racopilum*** sp. germinated from flying fox feces (splat). Photo courtesy of Andi Cairns.

Lessons from a Dog

Heinken (2000) conducted an interesting and most instructive study on dispersal of fragments by using a dog. Dogs act as good surrogates to demonstrate the ability of diaspores to adhere to fur, but their habit of wallowing on the ground is unusual among many wild mammals, making some predictions limited. In one year, Heinken walked his dog 49 times in the forest near his home in Germany. He found no seasonal differences in fragment attachments of bryophytes compared to the seasonal pattern observed for seed plant diaspores.

The forest used in the dog study had 20 species of bryophytes occupying 1% of the cover (Heinken 2000). The dog presented 29 bryophyte stem fragments from at least 10 bryophyte species. All the stem fragments had leaves and most had terminal buds. Only 13 of the fragments had branches and these were often numerous. The most frequent species were ***Eurhynchium hians*** (Figure 127) and ***Ceratodon purpureus*** (Figure 128). Other taxa included ***Barbula*** sp, ***Amblystegium varium*** (Figure 129), ***Hypnum cupressiforme*** (Figure 145),

Eurhynchium praelongum (Figure 130), ***Plagiomnium*** sp, ***Rhynchostegium*** cf ***megapolitanum*** (Figure 131), ***R. murale*** (Figure 132), and ***Rhytidiadelphus squarrosus*** (Figure 133). On the other hand, two species [***Atrichum undulatum*** (Figure 134), ***Mnium hornum*** (Figure 92)] that were frequent in the study area were not represented at any time on the dog's fur.

Figure 127. ***Eurhynchium hians***, one of the two most common species on dog fur in a German experiment. Photo by Michael Lüth, with permission.

Figure 128. ***Ceratodon purpureus***, one of the two most common species on dog fur in a German experiment. Photo by Michael Lüth, with permission.

Figure 129. ***Amblystegium varium***, a species found on dog fur in a German experiment. Photo by Jan-Peter Frahm, with permission.

Figure 130. ***Eurhynchium praelongum***, a species found on dog fur in a German experiment. Photo by Michael Lüth, with permission.

Figure 131. ***Rhynchostegium megapolitanum***, a species found on dog fur. Photo by Michael Lüth, with permission

Figure 132. ***Rhynchostegium murale***, a species found on dog fur in a German experiment. Photo by David Holyoak, with permission.

Figure 133. ***Rhytidiadelphus squarrosus***, a species found on dog fur in a German experiment. Photo by Brian Eversham, with permission.

Figure 134. ***Atrichum undulatum***, a moss that did not adhere to dog fur in a German experiment. Photo by Janice Glime.

Sources of the adhering bryophytes were primarily tree trunks, walls, paved places in the city, a grassland plot, and the lawn of the owner (Heinken 2000). The dog would frequently wallow on the ground, then shake and groom himself to remove annoying diaspores, especially seeds. The bryophytes that adhered were primarily wefts or short turfs with acute and often erect or squarrose leaves. Tall turf species with rounded leaves were very under-represented. Mats were likewise rare. Loose wefts, on the other hand, seemed to hitch a ride rather easily. Heinken concluded by saying that for a moss to be transportable it must fragment and that this most probably occurs when the moss is dry, perhaps explaining the seasonal difference found for flying fox feces.

Hoofed Mammals

Larger animals contribute to dispersal in somewhat different ways. Their fur, hair, spaces between toes, feathers, and other parts can trap bryophyte parts and easily transport them for the distance travelled by the animal. Among these are large, hoofed mammals. Cattle and other farm animals are able to transport terrestrial taxa wedged in their hooves, causing certain bryophyte species to frequent cattle trails and ruts made by machinery (Crum 1973). The fur and hairs of hoofed mammals can provide a protective location for diaspores to hitch a ride and may take these diaspores for long distances (de Pablos & Peco 2007). Erika Pénzes-Kónya demonstrated the ability of overturned ***Leucobryum juniperoideum*** to form rhizoids on the overturned clump (Figure 125, Figure 135) after cattle traffic.

Figure 135. ***Leucobryum juniperoideum*** cushion with leaf rhizoids after overturn by cattle. Photo by Erika Pénzes-Kónya, with permission.

When Poschlod (pers. comm. 6 March 2013) applied diaspore traps in grasslands, he found many fewer vegetative parts than in peatlands. Rather, he found grazing animals, especially sheep, serving as long-distance dispersers of vegetative parts, especially from those moss species which do not form capsules (at least not in central Europe where he is familiar with the flora) such as ***Abietinella abietina*** (Figure 136). And this species is astonishingly widespread in all the dry calcareous (and man-made) grasslands there.

Figure 136. ***Abietinella abietina*** in Europe, a moss that is easily broken when dry, as it is here. Photo by Michael Lüth, with permission.

Several researchers have examined sheep and cattle coats (Figure 137) for propagules, primarily seeds, and found that greater seed weight was likely to prevent attachment on vertical surfaces but not on horizontal ones (de Pablos & Peco 2007). The same relationship is not likely to be a problem for the light-weight bryophyte diaspores. Sheep wool held more diaspores than the smoother coats of cattle. Both animals rest by lying down (Figure 138-Figure 139), providing ample opportunity for bryophyte adherence in rocky, mountainous pastures. In addition to clinging to the coats of hoofed mammals, the bryophytes can lodge on the hooves, particularly in the company of mud.

Figure 137. Sheep with full coat of wool before shearing in North Wales. At this stage, bryophyte fragments can easily adhere to the wool. Photo by Janice Glime.

Figure 138. Sheep resting under a tree near Swallow Falls, Wales. In areas where bryophytes are prevalent, this behavior contributes to attaching bryophyte fragments to the wool, facilitating dispersal. Photo courtesy of Kim Barton.

Sheep seem to be particularly good dispersal vectors, particularly those with a dense, curly fleece (Figure 137) (Pauliuk *et al*. 2011). The curly fleece is able to carry more fragments and larger species of bryophytes than those with smooth, fine hair (Figure 139-Figure 140). Twelve sheep representing two breeds were examined and revealed fragments from 16 species of mosses, representing 40% of the species present in the pasture. It is interesting that these were particularly common on the belly and tail! Some species disperse better than others, with pleurocarpous species, small species, and mats being over-represented compared to the pasture vegetation. On the other hand, large species, acrocarpous taxa, wefts, and turfs were under-represented among those cultured. The hooves transported mostly acrocarpous colonists. Short fragments were more likely to occur on the hooves; longer fragments were more common on the wool (Figure 141).

Figure 139. Sheep with closely sheared wool, creating a smooth surface to which bryophyte fragments don't adhere as well as they do to long, curly wool. Photo by Janice Glime.

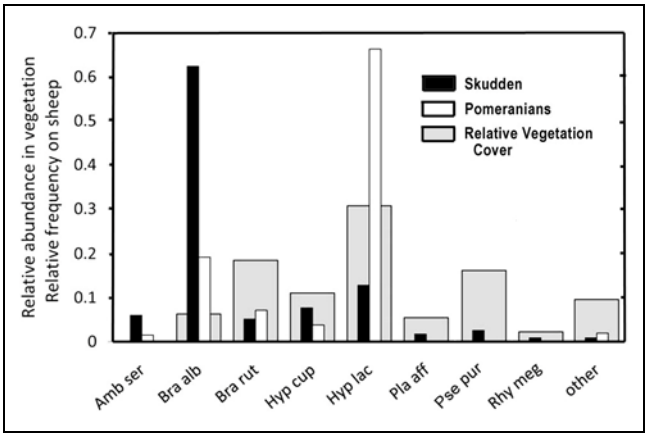

Figure 140. Comparison of proportions of bryophyte species carried by two different breeds of sheep, superimposed on the relative cover of the vegetation where the sheep were grazing. Skudden n = 5,117 fragments, Pomeranians n = 7,2096 fragments. Amb ser ***Amblystegium serpens***, Bra alb ***Brachythecium albicans***, Bra rut ***B. rutabulum***, Hyp cup ***Hypnum cupressiforme*** var. ***cupressiforme***, Hyp lac ***H. cupressiforme*** var. ***lacunosum***, Pla aff ***Plagiomnium affine***, Pse pur ***Pseudoscleropodium purum***, Rhy meg ***Rhynchostegium megapolitanum***. Modified from Pauliuk *et al*. 2011.

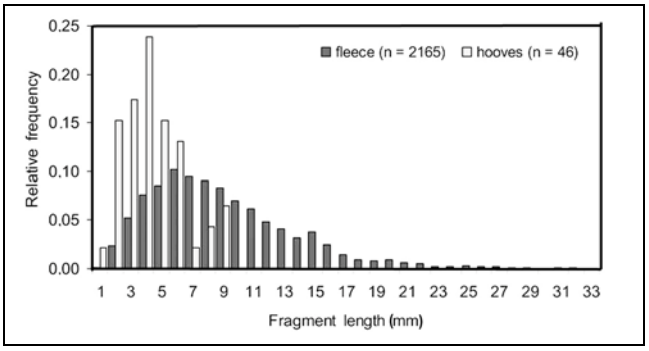

Figure 141. Size distribution of visible bryophyte fragments in fleeces and hooves from 12 sheep grazing on a dry grassland pasture. n = 2206. Modified from Pauliuk *et al*. 2011.

Heinken *et al*. (2001) further elucidated hoofed mammal dispersal by examining 25 shot roe deer (***Capreolus capreolus***; Figure 142) and 9 wild boar (***Sus scrofa***; Figure 143) in deciduous forests in Germany. They located a total of 106 bryophyte fragments (102 stem fragments, 4 leaves), representing 12 species, on the animals in their coats and hooves. This was proportionally somewhat less than the representation of tracheophytes based on percent cover (bryophyte:tracheophyte diaspores 1:30; bryophyte:tracheophyte cover 1:22.5).

Mean fragment length on the animals was 3.6 mm, but ranged 0.5-35 mm (Heinken *et al*. 2001). The fragments came mostly from the **terricolous** (on the soil) species, especially ***Brachythecium velutinum*** (Figure 144), ***Hypnum cupressiforme*** (Figure 145), ***Eurhynchium hians*** (Figure 127), and ***Ceratodon purpureus*** (Figure 128). Robust acrocarpous species in tall turfs were predominantly excluded, whereas the slender pleurocarpous species with erect, acute leaves, growing in wefts, were common. As in the dog study, some species that were frequent in the study area failed to adhere: ***Atrichum undulatum*** (Figure 134), ***Plagiomnium affine*** (Figure 146), ***Pohlia nutans*** (Figure

147), ***Polytrichastrum formosum*** (Figure 93). Others [***Brachythecium rutabulum*** (Figure 148), ***Mnium hornum*** (Figure 92), and ***Plagiomnium*** sp.] only had a few fragments attached. The liverworts in the study area were completely absent on the animals, despite the scattered occurrence of ***Chiloscyphus profundus*** (=***Lophocolea heterophylla***; Figure 149) throughout the study area.

Figure 142. ***Capreolus capreolus*** (roe deer) male and female. Photo through Wikimedia Commons.

Figure 143. ***Sus scrofa*** (wild boar) in forest, lying among mosses. Photo by Rizzo, through Wikimedia Commons.

Figure 144. ***Brachythecium velutinum*** with capsules in southern Europe. Photo by Michael Lüth, with permission.

Figure 145. ***Hypnum cupressiforme***, a species whose fragments commonly appeared on a dog in a German dispersal experiment. Photo by Dick Haaksma, with permission.

Figure 146. ***Plagiomnium affine***, a species that failed to adhere to a dog in a German dispersal experiment. Photo by Michael Lüth, with permission.

Figure 147. ***Pohlia nutans***, a species that failed to adhere to a dog in a German dispersal experiment. Photo by Michael Lüth, with permission.

The bristly coat of the wild boar was more adept at taxi service than the sleek hairs of the deer (Heinken *et al*. 2001). Furthermore, the boars wallow and root in the mud, giving them greater contact for picking up their hitchhikers. In addition to these fur and hair dwellers, they also travelled in the hooves.

Figure 148. ***Brachythecium rutabulum*** (Rough-stalked Feather-moss), a moss that is uncommon among the fragments on a dog in a German dispersal experiment. Photo by Barry Stewart, with permission.

Figure 149. ***Chiloscyphus profundus*** (=***Lophocolea heterophylla***), a liverwort that does not seem able to hitch-hike a ride on roe deer or wild boar. Photo by Michael Lüth, with permission.

Heinken and coworkers (2001) tested the ability to pick up bryophyte fragments by experimenting with a dummy deer. This dummy was placed on its stomach on the forest floor and used to mimic wallowing by giving it a gentle rolling motion. They repeated the experiment 300 times between July and October, cleaning all adhering fragments each time. This "behavior" produced 51 bryophyte fragment hitchhikers. Four of the six terricolous bryophyte species in the sample plots adhered to the ventral hair, with strong differences among bryophyte species. ***Eurhynchium hians*** (slender with erect, acute leaves, forming wefts; Figure 127) had 47 adhering stem fragments, whereas the similarly dominant ***Plagiomnium undulatum*** (robust with rounded leaves, forming tall turfs; Figure 150) had only one adhering fragment.

Figure 150. ***Plagiomnium undulatum***, showing its large, rounded leaves that do not adhere easily to fur. Photo by Des Callaghan, with permission.

Heinken *et al*. (2001) concluded that most of the attachment to fur occurs when the animals lie down or wallow on the ground, or when they rub against rocks, walls, or tree trunks. The hooves can also transport fragments, particularly in adhering mud (Figure 151). The type of fur matters. The boar provides further advantages by its frequent rooting and wallowing, extensive resting periods, and difficulties with grooming. Even their feces (Figure 152) could carry diaspores, but we don't know if they will survive. Since wild boars can travel as much as 5 km per day through the European forests, they could facilitate transport for quite some distance.

Figure 151. ***Sus scrofa*** (wild boar) tracks showing the mud that is a common part of the boar's environment. Mud on the hooves can help to carry bryophyte diaspores. Photo by James K. Lindsey, with permission.

Figure 152. ***Sus scrofa*** (wild boar) scat, a potential but untested means of dispersal. Photo by James K. Lindsey, with permission.

Pérez (2010) considered goats as contributors to dislodging mosses, particularly ***Grimmia trichophylla*** (Figure 153) and ***G. torquata*** (Figure 154) on Haleakala's Crater, Maui, Hawai'i, USA. These were transported downslope to new locations where they could grow, perhaps a combination of fragmentation by goats and gravity.

Figure 153. ***Grimmia trichophylla*** on rock. This moss may be dislodged by goats on Maui, Hawaii, and subsequently roll down the slope, making moss balls. Photo by Michael Lüth, with permission.

Figure 154. ***Grimmia torquata*** on rock. This moss may be dislodged by goats on Maui, Hawaii, and subsequently roll down the slope, making moss balls. Photo by Michael Lüth, with permission.

Bears

When I was searching for images of bears in streams, I found one with a group of bears in a moss-laden tree in the temperate rainforest of Canada (Figure 155). It occurred to me that these bears, and most likely monkeys, big cats, and other climbers, would dislodge some of the bryophytes, hence facilitating their dispersal. Another image of a black bear climbing over a rock with a vascular plant draped around its head suggested that especially for pendent mosses, they could carry them away, perhaps for some distance, and if the bryophyte is lucky, it might even be deposited in another tree.

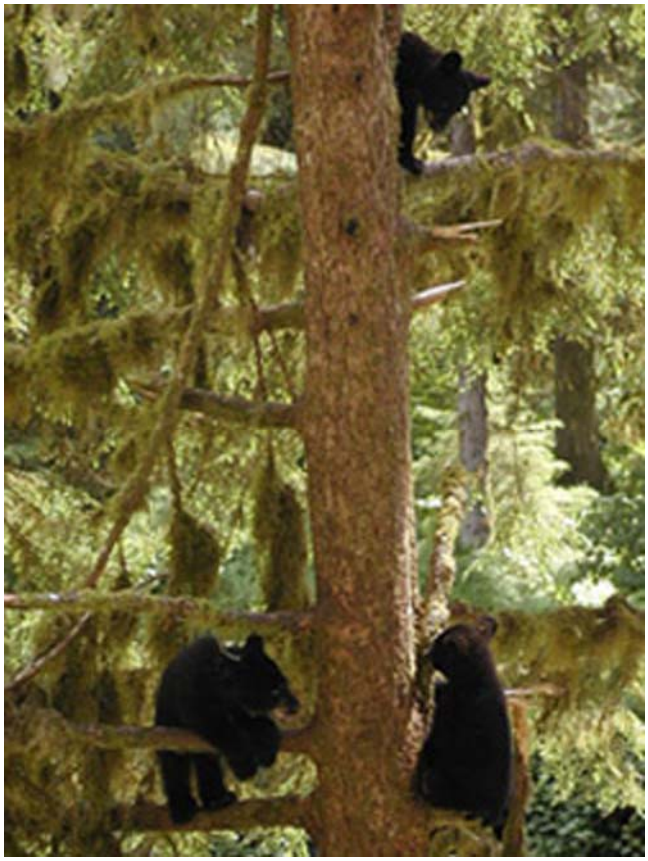

Figure 155. ***Ursus americanus*** among pendent mosses in Tongass National Forest. Photo by Interpretive staff, Tongass National Forest, Alaska, USA, through public domain.

In addition to dispersal of plants on the fur, bears may also disperse them through feces. Wilson and Ruff (1999) report that mosses are included among the food, but we have no information on the viability of mosses that pass through the digestive tract of the bear.

Bryophyte vegetative structures generally are not adapted for animal dispersal. Nevertheless, just by their location they are likely to be carried on amphibian skin, turtle carapaces, slug slime, insect guts and surfaces, hairs of mites and spiders, stuck to feathers and beaks of ducks, and on animal hooves and fur. Nest-building birds that line their nests with mosses often drop pieces, or the moss can even grow while within the nest. It appears that most vegetative parts do not survive the guts of most animals well, but some do and can thus be carried to new locations.

Human Dispersal

Humans are often inadvertent dispersal agents. For example, van Zanten and Pócs (1981) report on fragmentation of mosses by lawn mowers. These are then carried further by the lawn mower or by the human raking up the scraps. Others are torn apart during logging operations, adhering to the equipment, and potentially

being carried many kilometers to another site. And certainly back packs and collecting bags carry small scraps of bryophytes that escape the fate of a herbarium packet. Van Zanten and Pócs (1981) noted that when they walked in a dry meadow in New Zealand, their socks became transport agents of fragments of ***Thuidiopsis furfurosa*** (Figure 156). This suggests that other animals could likewise transport this species on fur or feathers.

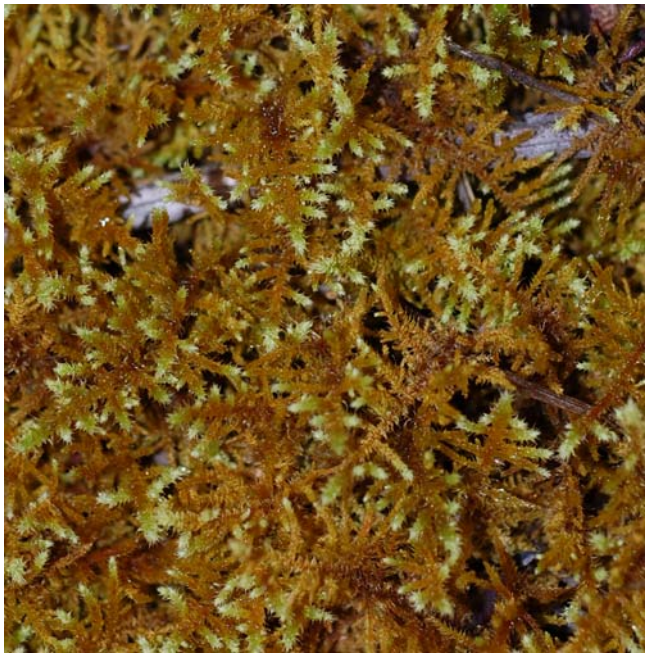

Figure 156. ***Thuidiopsis furfurosa***, a species that is known to cling to socks of bryologists. Photo by David Tng, with permission.

Bryum argenteum (Figure 29) is commonly dispersed by humans. It has deciduous shoot apices that apparently attach to shoes and other clothing as well as to small animals. It is common along paths in cemeteries, around tennis courts, and in golf courses. Clare and Terry (1960) used matchbooks in an elegantly simple experiment to demonstrate dispersal in this species. They "walked" the matchbook across patches of ***B. argenteum***, then across soil. As a control, they walked matchbooks that had not contacted ***B. argenteum*** across other patches of soil. The ***B. argenteum*** became established on the plots where the matchbook had previously visited the mosses, but not on the others, demonstrating how easily it could be dispersed on shoes and feet.

There are several documented cases of bryophytes dispersed by humans. One of the most recent reports is that of Ireland and Shchepanek (1993) for the spread of ***Hyophila involuta*** (Figure 157) in Canada. This species was known only from a few localities in Ontario. However, it is growing abundantly on the sides of most of the locks in the Rideau Canal and the authors suspect that it arrived in both Michigan and Canada from more southern localities by travelling there on boats. The locks are constructed of limestone and sandstone or concrete, and the plants seem to get started along the mortar seams.

Figure 157. Gametophytes of ***Hyophila involuta*** growing on concrete. Photo by Michael Lüth, with permission.

I still recall Iwatsuki commenting in Japan that he didn't need to check what was growing on the concrete retaining walls along the roads – it was all ***Hyophila*** (Figure 157). However, on the locks in Ontario it is nearly devoid on the concrete blocks, occurring predominately on the limestone and sandstone blocks which are more similar to the construct in Japan (Ireland & Shchepanek 1993). In the Ontario locks, it grows only below the water level, sometimes even on the bottom of the locks. Frequent wetting and drying and low light intensity seem to favor its growth, but the plants must also survive seven months out of the water in winter when the locks are drained. These plants never have sporophytes, and with only one report of sporophytes in the United States, it appears that they rely on their numerous multicellular gemmae (Figure 158).

Figure 158. ***Hyophila involuta*** showing numerous gemmae that form at leaf bases. Photo by Michael Lüth, with permission.

Logging vehicles, all-terrain vehicles, and other forest transport have giant tires with the potential to pick up fragments of bryophytes along with soil. Some of these could travel considerable distances to another location before falling off. It appears that hitch hiking is a common mode of travel for ***Riccia*** – in Michigan, USA, ***R. huebeneriana*** (Figure 159) and ***R. cavernosa*** (Figure 160) are often dwellers along disturbed soil of 2-track roads, suggesting a vehicular means of dispersal (Crum 1973).

Horticulture provides several means of introducing species to new locations. ***Marchantia polymorpha*** (Figure 34) is frequently spread throughout a greenhouse by the force of the watering system. This and other bryophytes then travel in the pots with the purchaser. ***Polytrichastrum longisetum*** (Figure 161) is an introduced horticultural weed in West Cornwall, Great Britain (Holyoak 1995).

Figure 159. ***Riccia huebeneriana***, a common liverwort along two-track roads. Photo by Des Callaghan, with permission.

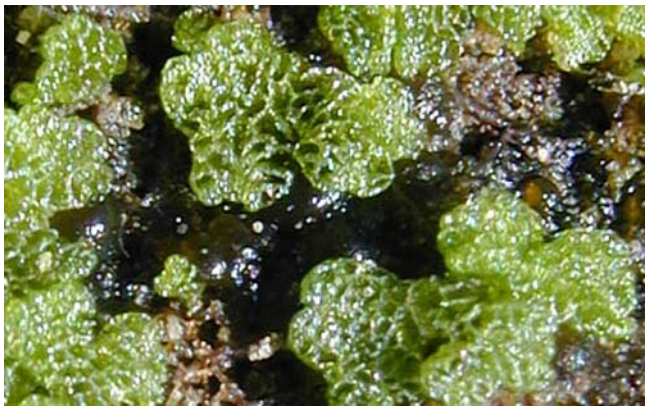

Figure 160. Thalli of ***Riccia cavernosa*** on disturbed soil. Photo by Michael Lüth, with permission.

Figure 161. ***Polytrichastrum longisetum***, an introduced horticultural weed in West Cornwall, Great Britain. Photo by Michael Lüth, with permission.

Bryophytes used as packing material are potential propagules. Degener *et al*. (1969) reported such dispersal to explain the "unnatural distribution" of ***Sphagnum palustre*** (Figure 162). Its appearance in Hawaii seems to be from use of this moss as packing material for tree seedlings. Bryophytes used for packing can escape and become established, as in the case of ***Pseudoscleropodium purum*** (Figure 163), in widely ranging parts of the world (Allen & Crosby 1987).

Figure 162. ***Sphagnum palustre***, a moss that is spread by its use in packing tree seedlings. Photo by Michael Lüth, with permission.

Figure 163. Gametophyte of ***Pseudoscleropodium purum***, a widely transported packing material. Photo by Michael Lüth, with permission.

Golf courses and picnic areas seem to be common sites for invasive species because they get considerable foot traffic from a wide range of locations. The first citing of ***Fissidens taxifolius*** (Figure 77) in Auckland, New Zealand, was reported occurring under a picnic table (Espie 1997). Also ***Rhytidiadelphus squarrosus*** (Figure 133) first appeared in New Zealand on a Dunedin golf course in 1975, presumably arriving with foot traffic, or perhaps a golf bag.

Paths are often bordered by bryophytes (Figure 164-Figure 165). Such is the case in the Tatra Mountains of the Western Carpathians where one can find 15% of the liverwort species of that area (Górski 2009). Górski refers to "walking down" of high mountain species [***Marsupella brevissima*** (Figure 166), ***Pseudolophozia sudetica*** (Figure 169)] to lower sites, "passing" of alpine scree-bed species to habitats associated with humans [***Anthelia juratzkana*** (Figure 170), ***Marsupella brevissima***, ***Pleurocladula albescens*** (Figure 171)], and formation of new combinations of plant communities [with ***Cephalozia bicuspidata*** (Figure 167)] or expansion of communities already associated with human activity [*e.g.* ***Calypogeietum trichomanis***, ***Nardietum scalaris*** (Figure 168)]. Although there is no proof or experimentation to support this, it is likely that at least some of these have arrived in these locations due to human dispersal on foot gear. Others are simply opportunists that are able to

occupy a suitable habitat created by humans, possibly facilitated in their dispersal by the openings created by the paths.

Figure 164. Mosses along forest trail at Clear Creek Park in Ohio, USA. The trail opens new habitats on the slopes and foot traffic can bring propagules to the scene. Photo by Janice Glime.

Figure 165. Mosses at edge of a blacktop path at Three Creeks Park, Ohio, USA. These are easily fragmented by human foot traffic, creating dispersal potential. Photo by Janice Glime.

Figure 166. ***Marsupella brevissima***, a leafy liverwort that gets "walked down" the mountain along paths. Photo by Jan-Peter Frahm, with permission.

Figure 167. ***Cephaloziella bicuspidata***, a species subject to new community combinations due to "walking down" of alpine species. Photo from Botany Website, UBC, with permission.

Figure 168. ***Nardia scalaris***, primary species in the *Nardietum scalaris*. Photo by J. C. Schou, with permission.

Figure 169. ***Pseudolophozia sudetica***, a leafy liverwort that gets "walked down" the mountain along paths. Photo by Jan-Peter Frahm, with permission.

Figure 170. ***Anthelia juratzkana***, a scree-bed species that gets transferred to human habitats. Photo by Michael Lüth, with permission.

Figure 171. ***Pleuroclada albescens***, a scree-bed species that gets transferred to human habitats. Photo by Michael Lüth, with permission.

Bryophytes may even be transported deliberately. My favorite story is one in which ***Fontinalis antipyretica*** (Figure 22) was introduced into South Africa in an attempt to encourage more aquatic insects as food for fish (Richards 1947). The moss spread rapidly and covered the rocks. But at least initially, the attempt to improve the aquatic insect population failed because the native species were adapted to smooth rocks and they in fact lost their habitat.

Despite the role of humans in dispersal, urban areas often exhibit depauperate bryophyte floras. One of the reasons for this is the fragmented nature of the urban landscape, making dispersal difficult (Korpelainen *et al*. 2006), especially for epiphytes. Of course, the inhospitable nature of the urban habitat, especially exposure, makes establishment difficult once a diaspore arrives.

Mystery Dispersal

Most bryophyte dispersal is in fact mystery dispersal. Few species have actually been subjected to experimentation, tagging, or other means to provide scientific data on their dispersal. Dickson *et al*. (pers comm. 23 April 2013) have provided me with one such story for ***Fissidens fontanus*** (Figure 172) in France. This species occurs in many of the abandoned lavoirs that still have flowing clean water; abandoned in the 1960s, the lavoirs were communal wash houses where women did family laundry. They were mainly contracted in the nineteenth century and some villages had more than one. These usually have a roof, but they are open on one or more sides and accessible to birds and insects (and probably an occasional frog). They have become inhabited by algae and bryophytes, the moss ***Fissidens fontanus*** (Figure 173). No capsules are known for this species in Europe. Recent searches of lavoirs have revealed more locations (Piguet *et al*. 2007; Piguet 2009), and it seems to be increasing along rivers in Germany and perhaps in France. Dickson and colleagues raise the question of its dispersal. There are no known connections among the springs that feed them and no ducks have been seen at any of the lavoirs. How does it spread between lavoirs – I'm guessing it was animals.

Figure 172. ***Fissidens fontanus***, a moss that has appeared in lavoirs in France. Photo by Michael Lüth, with permission.

Figure 173. ***Fissidens fontanus*** in lavoir at Vouchoux, France. Photo courtesy of James Dickson.

Invasive Species

Invasive species represent the epitome of dispersal. Often it is the human species that serves as the dispersal vector. But whatever the vector, these species are good at getting there and successful at establishment.

One of the best known of the invasive bryophyte species is ***Campylopus introflexus*** (Figure 174) (Fudali 1992; Schirmel & Buchholz 2013). This species is responsible for altering the invertebrate communities in the acidic coastal dunes of Europe where it is able to form dense carpets. It caused changes in both body size and feeding preference among the arthropods, resulting in changes in hunting mode of spiders. Spiders increased in functional diversity, whereas carabid beetles had a reduction in functional diversity.

Another well-known invasive species is ***Orthodontium lineare*** (Figure 175) (Herben 1994). The key to success for this species is that it seems to be able to grow on whatever substrate is available, being limited only by available space.

Figure 174. ***Campylopus introflexus***, an invasive species in Europe and parts of North America. Photo by Janice Glime.

Figure 175. ***Orthodontium lineare***, an invasive species in Europe. Photo by David T. Holyoak, with permission.

Essl *et al.* (2013) assessed bryophyte invasions and what makes them work, using 82 regions spanning five continents as their data sources. They identified 139 species (106 mosses, 28 liverworts, 5 hornworts) that they considered to be alien in at least one study region. They found that alien numbers were significantly higher on islands than on the studied continental regions. They identified 34 species as accidental hitch-hikers and 27 species as accompanying ornamental plants. These invasive species prefer strongly disturbed habitats [ruderal vegetation (growing on waste ground), roadsides, lawns], whereas forests and rocks are typically avoided. They concluded that the pattern of bryophyte invasions is different from that of tracheophytes.

Summary

Dispersal methods of vegetative diaspores of bryophytes include gravity, wind, water, and animals. Although most bryophytes are suitable for wind dispersal, even for fragments and specialized propagules, gravity accounts for the short distances to which most of these vegetative diaspores travel.

Splash cups are useful in dispersing gemmae in several liverworts and one family of mosses. Bryophytes getting frozen in ice or caught by flood waters can be carried considerable distances and vegetative dispersal in flowing water environs is essentially guaranteed.

Animal dispersal is probably more important than has been presumed, and includes earthworms, arthropods (insects, mites, pillbugs, spiders, harvestmen), slugs, amphibians, turtles, water birds, nest-building birds, and animal feet and fur. Birds and rodents often dislodge bryophytes while searching for food items among them and may carry fragments among their feathers/fur or attached to feet. Humans disperse bryophytes through their own footwear, vehicle tires, horticulture, and packing materials. However, none of the bryophyte vegetative propagules seems to be especially adapted for animal dispersal.

Although most bryophytes are best adapted to wind dispersal, even of fragments and specialized propagules, gravity accounts for the short distances to which most of these vegetative structures travel.

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CHAPTER 4-12

ADAPTIVE STRATEGIES: SPECULATION ON GAMETOPHYTE STRUCTURES

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CHAPTER 4-12

ADAPTIVE STRATEGIES: SPECULATIONS ON GAMETOPHYTE STRUCTURES

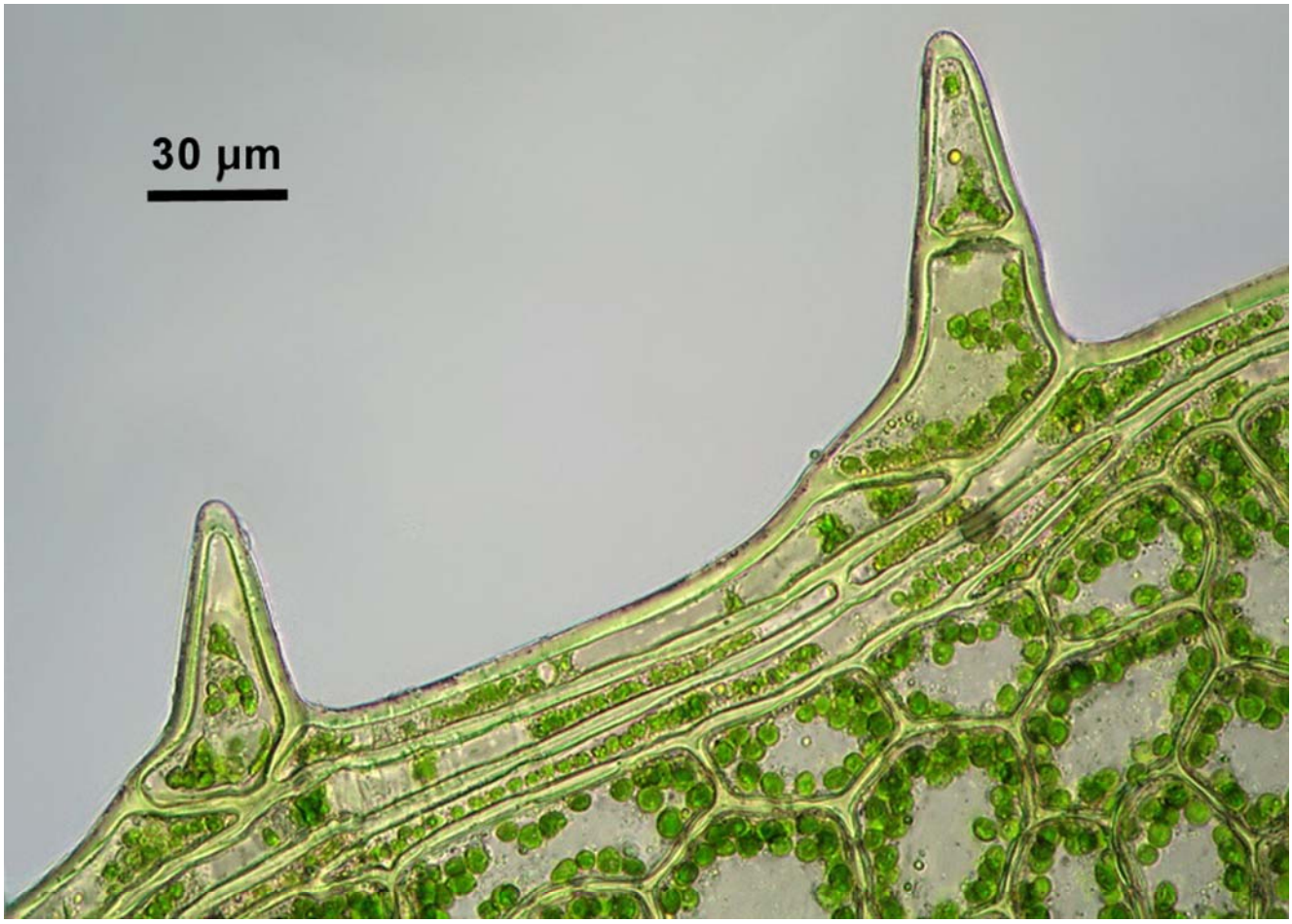

Figure 1. ***Plagiomnium affine*** leaf border with teeth. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Prologue

As I begin this chapter, I am reminded of a conversation I had with Louis Anderson. It was similar to the one relayed by Brent Mishler on Bryonet (8 May 2012) on the position of Lewis Anderson. When asked about the function of something like a hairy surface, he would point out that it had to have some kind of surface. We must keep this admonition in our minds constantly as we question functions of bryophyte parts, forcing us to ask more precise questions and to **test** our hypotheses.

Not all structures have adaptive value. With this caution in mind, we need to be aware if something is really adaptive or it is simply not an encumbrance. If it persists through more than one taxonomic group, is it more likely it has some adaptive significance than if its presence is rare? And if it occurs in all, might it be a necessity? But I dare not go farther in defining adaptive value. Hence, this chapter is necessarily speculative. Do keep that in mind as you read.

The descriptions of structural adaptations are largely the product of the human mind to seek explanations for things. Hence, we seek to learn why a certain structure persists in a bryophyte by trying to find a function for that structure. This teleological approach is not all bad. It can form the basis or our alternative hypotheses, the null hypothesis being that there is no special function.

The next step after identifying a hypothesis is attempting to test it, and this is often quite difficult. It often becomes necessary to ask the question, "What would happen if this structure were absent, as for example the teeth shown in Figure 1?" Modern genetic techniques are permitting us to identify the functions of genes that way, using knock-out genes to disable or remove a gene. Some

structures are suitable for removing or disabling as well and can help us test our hypotheses.

Even with such testing, we must also keep in mind that not all structures have functions, and that structures and genes may not work alone. For selection to work against them, there must be some cost for their presence. If there is no cost, a structure may remain, seemingly with no purpose.

Often this cost is expenditure of energy, whereas when we look for adaptive value we tend to look for things like moisture conservation, herbivory protection, or increased dispersal. All of these relate to survival, so testing of adaptations often is a testing of survival value.

In this regard, we need to consider that Lamarckian evolution suggested that giraffes have long necks so they could reach higher branches where there was less competition for food. But there is no genetic mechanism that can cause a gene to arise due to need. Genes arise randomly through mutations or get lost through deletions. Combinations of genes change due to both mutations and recombinations. The recombinations can occur through mixing in meiosis or through mating with an individual with genotypic differences.

Medina *et al*. (2015) explored phenotypic variation in three Antarctic moss populations as a response to local environments. All three species of mosses studied revealed significant differences among populations for all evaluated morphometric characters. They concluded that in the Antarctic, local variation on a small geographic scale behaved in the same way as variation on a large geographic scale in geographic regions where the climate is more homogeneous. This is an example that may reflect random arrival of propagules, followed by selection by the environmental conditions at the site of arrival. But this is a my hypothesis for which the researchers urged the need for common garden studies and further investigation on many more species.

Linked Genes

A second complicating factor in our search for function is that genes may be kept because of their nearness to another important gene. If gene B resides on a chromosome with gene A, it will go where gene A goes unless it gets moved during a crossover event (a common occurrence during meiosis) or other type of rearrangement. The closer it is to gene A, the lower the chances of gene B becoming separated during a crossover event. If gene A is an important adaptive gene, and gene B does little or no harm, then it will be kept as it travels along with gene A, even if it codes for something that offers no adaptive value. But if gene B is harmful, and gene A is not essential or is unable to provide more benefit than the harm caused by gene B, then gene B will be begin to disappear from the gene pool – and gene A with it. I could explain this further, but you should be able to see my point – not all structures or physiological mechanisms are necessarily advantageous. They may be non-adaptive. They may even remain from a time when they were adaptive to conditions that no longer exist. Thus, we must keep in mind that not all structures or other phenotypic expressions are adaptive. The evolutionary model would, in fact, predict that some are not adaptive. And those that are maladaptive may take hundreds of years or even eons to disappear from the population. In the meantime, they may offer us taxonomic characters that are useful to systematists!

It is not easy to associate a given character with a particular gene. Vanderpoorten and Jacquemart (2004) found that most of the morphological variation in the aquatic moss genus ***Amblystegium*** (***Hygroamblystegium***; Figure 2) result not from genetic differences, but in plasticity of expression. They also found that the evolution of most characters in these aquatic taxa was often independent from phylogeny of the taxon. Rather, the morphological characters in this genus lack independence and stability, making them less useful for distinguishing species.

Figure 2. ***Hygroamblystegium fluviatile***. Photo by Hermann Schachner, through Creative Commons.

Evolutionary Drivers

Kürschner (2004) found common adaptive trends among the bryophytes from the Near and Middle East. These represented independent traits that arose in unrelated taxa evolving under similar habitat conditions. Such convergence suggests relationships of evolution with site ecology and niche differentiation.

Hence, this chapter will present more hypotheses than facts with the challenge to our young (and older) bryologists to test these.

GAMETOPHYTE

Schofield (1981) reviewed the literature and concluded that spore germination patterns, protonemal structure, life span, and methods of vegetative propagation are all related to nature of the habitat. Large, multicellular spores and swollen protonemal cells are more common in habitats that frequently experience desiccation. Protonemata are more specialized in deeply shaded environments. More typical types with strongly elongate cells are more frequent in mesic sites or terrestrial sites with favorable moisture conditions during at least part of the day during most of the growing season. Growth forms may be correlated

genetically, or they may be "molded" by the environment. Energy conservation is often accomplished by having production of gemmae at different times from sexual reproduction.

In **ectohydric** (external) conduction systems, water movement is facilitated by leaf shape, arrangement, orientation (Figure 3), and detailed anatomy; branch arrangement, stem cortical cells; and the presence of rhizoids or paraphyllia (Schofield 1981). Surface ornamentation of leaves, stems, and rhizoids also may contribute. In **endohydric** (internal; Figure 12-Figure 13) conduction, the hydrome and leptome facilitate water movement and may be habitat specific, especially in the **Polytrichidae**. Again, there is little experimental evidence to support the conclusions that currently rest on habitat correlations.

Figure 3. ***Pohlia*** sp. with raindrops large and small, illustrating the way ectohydric water becomes trapped in the leaf axils. Photo by John Game, through Creative Commons.

Wetlands vs Non-wetland Trends

Hedenäs (2001) took compiled data that supports much of the tendencies noted by Schofield (1981) by examining frequencies of 86 character states in 439 species of pleurocarpous mosses on a worldwide scale. These were compared across climatic zones, general habitat, and wetland to non-wetland gradient. He found that 44% of the characters are indeed influenced by climatic zone – the largest sphere of influence in the study. General habitat accounted for 35% and wetland to non-wetland gradient 23%.

In the Hedenäs (2001) study, two complex functions emerged. Water conduction and retention can be measured by differences in stem central strand morphology, leaf orientation, leaf costa type, alar cells, paraphyllia, pseudoparaphyllia, inner perichaetial leaf plications, vaginular paraphyses, capsule stomatal pore, operculum type, and possibly seta length. The second important function is spore dispersal, facilitated by capsule shape and orientation, annulus, exostome and endostome appearance, spore size and maturation time, and possibly seta length. the importance of phylogenetic history cannot be ignored as a limiting factor on adaptive characters, but other drivers include water availability and exposure to wind.

As seen in Chapter 2, bryophytes have a leafy **gametophyte** generation with one set of chromosomes (**haploid**) and a **sporophyte** generation that produces a capsule atop a short or long stalk and having two sets of chromosomes (**diploid**). The morphology of these two generations is strikingly different, so it is expedient to divide our discussion into these two generations.

Proctor (2010), a very astute bryologist who is familiar with both bryophyte physiology and structure, has summarized his perspective, supported by literature, on bryophyte adaptations.

Without considering how traits got that way, or which bryophytes are their ancestors, let us consider the traits themselves and their possible adaptive roles. Proctor (2010) compares the wide diversity of leaf shape, proportions of costa (see below under Costae) and lamina, and cell shape (Figure 4) in the **Dicranaceae** to the essentially uniform structure of the ecologically diverse **Fissidentaceae** (Figure 5; Figure 107). Such comparisons testify to the complexity of such adaptive considerations.

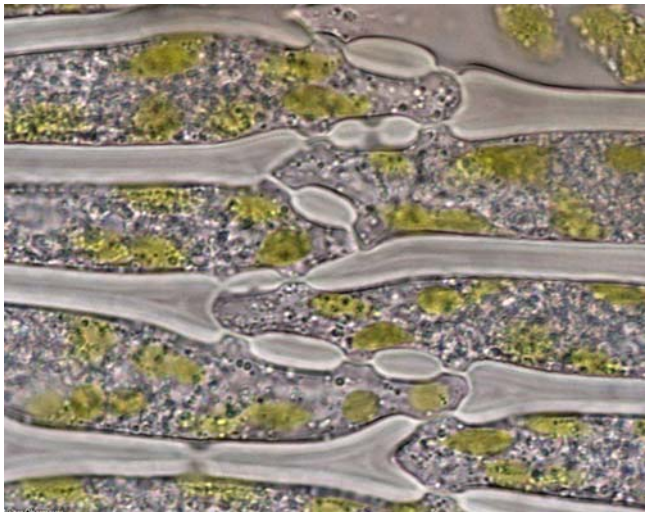

Figure 4. ***Dicranum polysetum*** leaf cells showing porose walls. Photo by Walter Obermayer, with permission.

Figure 5. ***Fissidens rivularis***, showing the costa, 2-ranked leaves, and flattened appearance that are present in all members of the genus. Photo by Des Callaghan, with permission.

Other families seem to have structures that adapt the family to narrower environmental circumstances. For example, the **Orthotrichaceae** live in the xeric locations of rocks and tree bark, supported by desiccation tolerance, cushion growth forms (Figure 6), and small isodiametric leaf cells (Figure 7), all of which help them to survive drying. **Hookeriaceae**, by contrast, have large, thin-walled cells (Figure 8-Figure 9) and survive only in moist, shady locations (Figure 10).

Figure 6. ***Orthotrichum obtusifolium*** forming a cushion on a tree trunk. Photo by Michael Lüth, with permission.

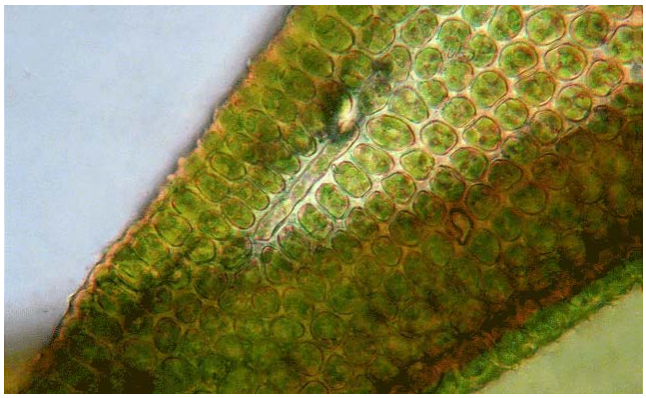

Figure 7. ***Orthotrichum pusillum*** showing isodiametric leaf cells. Photo by Bob Klips, with permission.

Figure 8. ***Hookeria lucens*** leaf showing thin-walled cells. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

Stem

The bryophyte stem offers both support and a way of scavenging into a wider space. Pleurocarpous mosses extend across the ground surface, taking advantage of sunflecks on part of the moss while other parts are in the shade, a phenomenon that has been termed **foraging** (Figure 11). In some mosses, a central strand with specialized elongated **hydroids** and **leptoids** (Figure 12-Figure 13) contribute to transport of water, nutrients, and other substances, whereas in others these must travel from unspecialized cell to cell. Are there habitat conditions when ordinary cells are a better means of providing transport?

Figure 9. ***Hookeria lucens*** thin-walled leaf cells. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

Figure 10. ***Hookeria lucens*** near Swallow Falls, Wales, where this whitish moss is kept moist by other mosses on a damp log in a stream valley. Photo by Janice Glime.

Richard Zander (Bryonet 8 May 2012) suggested that it might help to demonstrate a biophysical principle when one is unable to demonstrate an adaptation experimentally. As an example, he suggests that the cross section of a stem of ***Aloina hamulus*** (Figure 14) shows no central strand or sclerodermis. Rather, only a crowded set of cells is present. Zander compares that crowded set (see *e.g.* Figure 15) to the crowded bubbles of soap froth (Figure

16). And soap films assume the least area or least distance solution to their arrangement. He suggests that a stem with this arrangement therefore uses the least amount of photosynthate to create a plant axis. This would seem to be the simplest unspecialized case.

Figure 11. ***Brachythecium buchananii*** partly in sun and partly in shade. Connected plant parts can transfer photosynthate, and nutrients, from one part to the other through **foraging**. Photo by Michael Lüth, with permission.

Figure 12. ***Bryoxiphium*** stem ls showing long hydroids (green on left) and leptoids (reddish brown) compared to ordinary cortex cells (green or right). Photo courtesy of Izawa Kawai.

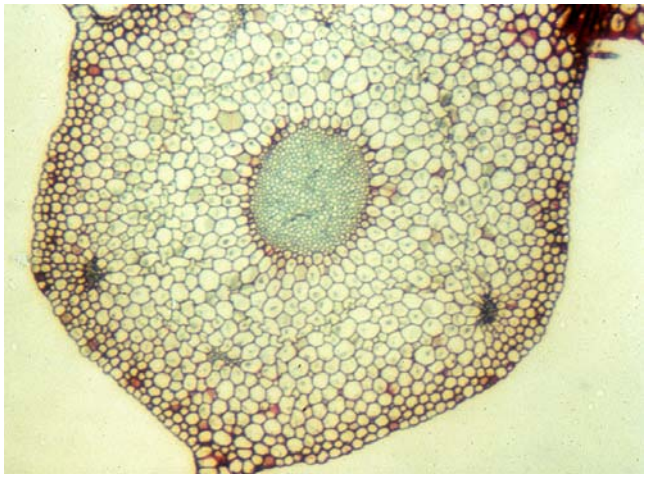

Figure 13. Stem cross section of the moss ***Mnium***. Blue-stained cells in center are **hydroids**; red-stained cells immediately around them are **leptoids**. Photo by Janice Glime.

Figure 14. ***Aloina hamulus***, a xerophytic moss with no central strand in its stem. Photo by Claudio Delgadillo Moya, with permission.

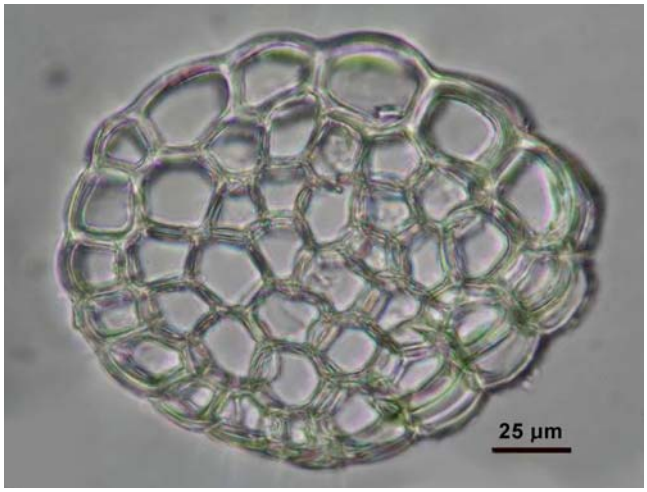

Figure 15. Leafy liverwort ***Telaranea pallescens*** stem cross section showing the "bubble" arrangement of cells described by Richard Zander. Photo by Tom Thekathyil, with permission.

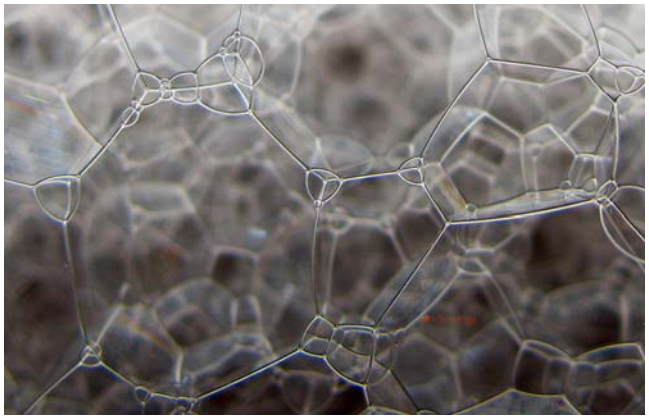

Figure 16. Soap bubble arrangement maximizing contact. Note pyramidal cells at the corners – reminiscent of trigones. Photo by Janice Glime.

Elumeeva *et al*. (2011) screened 22 abundant subarctic bryophytes from diverse habitats. They found that colony water retention did not correlate with individual shoot properties of leaf cell wall properties, water retention capacity, and desiccation rate. Instead, the colony desiccation rate was dependent on the density of water-saturated colonies of bryophytes. Colony desiccation rate was only marginally related to individual shoot desiccation rate, and was negatively correlated with it, suggesting that shoots with higher desiccation rates benefit from the protection of a colony.

Elumeeva and coworkers (2011) identified six distinct species groups based on habitat choice and phylogenetic relationships. ***Sphagnum*** (Figure 20-Figure 21) formed a unique group. **Forest mosses** were characterized by relatively big shoots with rather thick cell walls and loose colonies - tall turfs as well as wefts). **Moist to wet open habitats** had two groups: 1) those growing on stones, open soil patches, and somewhat drier parts of fens and characterized by thick cell walls and smaller amounts of internal and external water; 2) those growing in streams and wet fens and characterized by thinner cell walls but with more internal and external water. **Polytrichaceae** (Figure 17), like **Sphagnaceae**, formed its own group due to the small amount of external water. Similarly, ***Racomitrium lanuginosum*** (Figure 18) stood by itself as a group due in part to its low amount of external water and its unusual cells with thick, sinuose walls (Figure 19) and narrow cell lumen.

Figure 17. ***Polytrichum*** sp.; the ***Polytrichum*** species form a separate structural group due to their poor ability to hold external water. Photo by Annie Martin, with permission.

Figure 18. ***Racomitrium lanuginosum*** showing loose colony that does not hold much external water. Photo by Hermann Schachner, through Creative Commons.

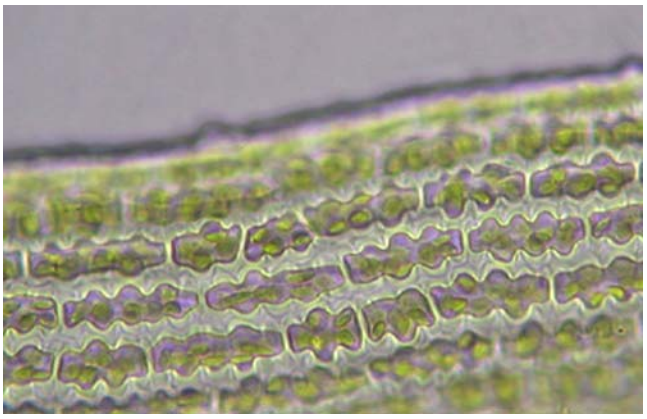

Figure 19. ***Racomitrium lanuginosum*** leaf cells showing sinuose walls and narrow lumen. Photo from Botany Website, UBC, with permission.

They (Elumeeva *et al*. 2011) found the lowest desiccation rate in species of ***Sphagnum*** [varying from 208 ± 15 min in ***S. fuscum*** (Figure 20) to 879 ± 51 min in ***S. lindbergii*** (Figure 21); mean ± SE, w=10]. The highest rates were in species with small shoots: ***Paludella squarrosa*** (Figure 22), ***Codriophorus fascicularis*** (=*Racomitrium fasciculare*; Figure 23), and ***Warnstorfia pseudostraminea*** (Figure 24) (17±2, 15±2, and 20±2 min).

Figure 20. ***Sphagnum fuscum*** hummock, a colony arrangement that holds large amounts of external water. Photo by Peter J. Foss, with permission.

Figure 21. ***Sphagnum lindbergii*** hummock, a colony arrangement that holds large amounts of external water. Photo by Allan Harris, through Creative Commons.

Figure 22. ***Paludella squarrosa***, a species among those with the highest rates of water loss. Photo by Michael Lüth, with permission.

Figure 23. ***Codriophorus fasciculare***, a species among those with the highest rates of water loss. Photo by Janice Glime.

They (Elumeeva *et al*. 2011) suggested that the relationships between the shoot and colony traits could help to predict changes in the hydrological function in bryophyte-dominated peatlands that are experiencing climate-induced shifts in species abundance. These relationships may also be useful in evaluating feedbacks of species shifts as they affect permafrost insulation and carbon sequestration functions.

Figure 24. ***Warnstorfia pseudostraminea***, a species among those with the highest rates of water loss. Photo by Stefan Gey, through Creative Commons.

Stem Structure

Stems are usually circular (Figure 25), but some are triangular in cross section (Figure 26); others are somewhat flattened (Figure 27). They can have layers of cells that differ in wall thickness and coloration. Some of these differences are expressed by cells in the central strand (Figure 25-Figure 26, Figure 30-Figure 31), but not all bryophytes have a central strand (Figure 15, Figure 27-Figure 29). Others are expressed in the outer cells and can contribute to reduction in water loss and strengthening of stems. But little testing has been done to determine how these outer cells really help. Are they hydrophobic? Do any help in the absorption of water? Do the strengthening cells correlate with habitats where stem strength is an advantage? Do the colors and thickness of the outer layer respond to the environment?

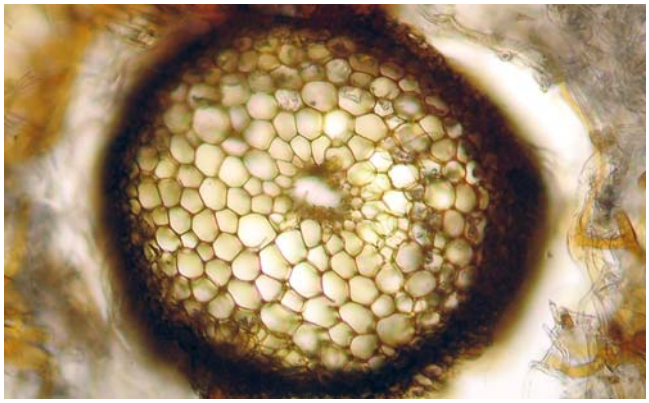

Figure 25. ***Dicranum scoparium*** stem cross section with outer cells having thick, darkly colored walls, thin-walled cortical cells, and rudimentary central strand. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

Figure 26. ***Dendroligotrichum dendroides*** stem cross section showing triangular shape. Image on right shows details of the central strand. Photo by Juan Larrain, with permission.

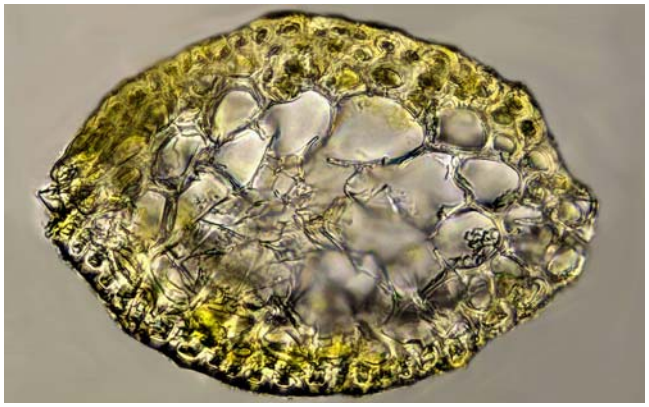

Figure 27. ***Fissidens bryoides*** stem cross section showing thick-walled outer cells and thin-walled central cells with no central strand. Photo by Dick Haaksma, with permission.

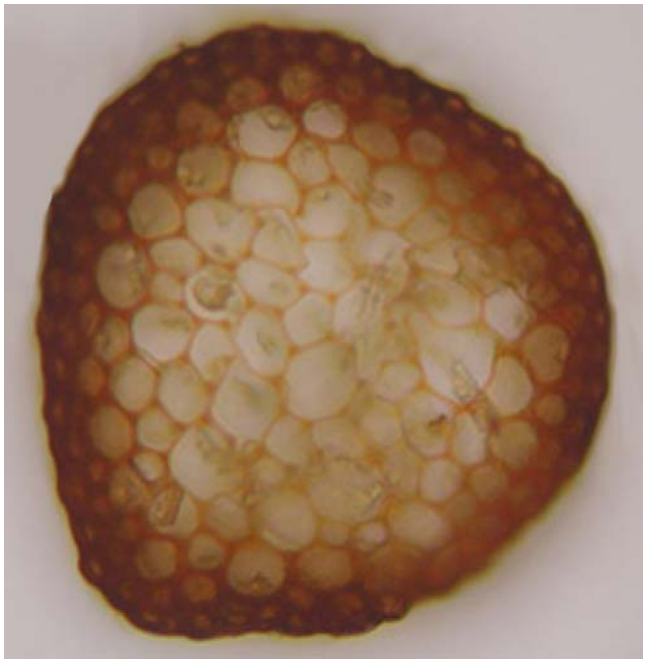

Figure 28. ***Andreaea*** stem with no central strand but with color in all the cell walls, suggesting phenolic pigments. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

Figure 29. ***Hylocomium splendens*** stem cross section showing thick-walled, colored outer cells and thin-walled cortex with no central strand. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

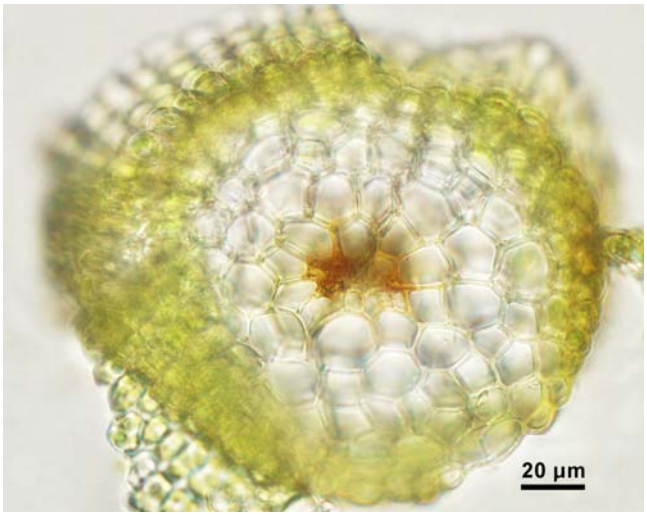

Figure 30. ***Molendoa sendtneriana*** stem cross section showing outer photosynthetic cells, translucent cortex, and central strand. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Several studies have addressed the thickness of the stem and the thickness of the outer layer under different environmental influences. See and Glime (1984) compared the stem thickness and stem wall thickness in ***Fontinalis flaccida*** (quiet water; Figure 32-Figure 33) and ***F. dalecarlica*** (fast water; Figure 34-Figure 35) after growing them in a common garden artificial stream. The new growth on both species retained their distinctness, with ***F. dalecarlica*** having both thicker stems and more thickened outer cells (Figure 36). Furthermore, even the central cortex cells of ***F. dalecarlica*** were thickened, whereas they were not in ***F. flaccida***.

Figure 31. ***Polytrichastrum formosum*** stem cross section showing thick-wall, colored outer cells, colored walls of cortex cells, thin-walled leptoids (food-conducting cells) and thick-walled, colored hydroid cells, the latter two cell groups forming the central strand. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

Figure 32. ***Fontinalis flaccida*** showing thin stems for this quiet-water species. Photo by Lance Biechele, permission pending.

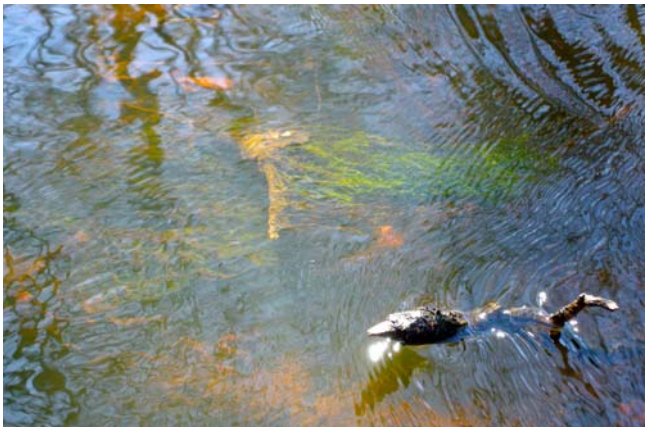

Figure 33. ***Fontinalis flaccida*** in relatively quiet stream water. Photo by Lance Biechele, permission pending.

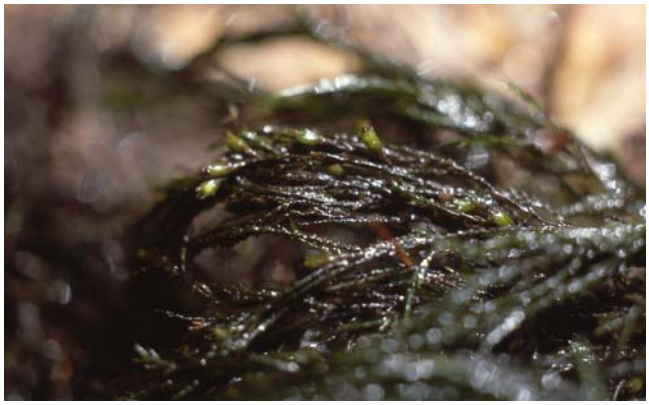

Figure 34. ***Fontinalis dalecarlica*** showing thick, strong stems. Photo by Janice Glime.

Figure 35. ***Fontinalis dalecarlica*** in a fast mountain stream. Photo by Janice Glime.

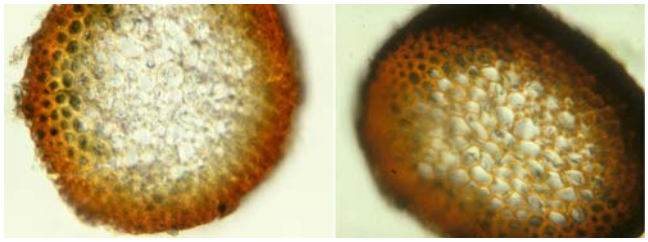

Figure 36. ***Fontinalis flaccida*** (**left**) and ***F. dalecarlica*** (**right**) stem cross sections showing the thickened (and colored) cortex cells and thicker outer layer of ***F. dalecarlica*** (**right**). Photos by Janice Glime.

Li *et al.* (1992) found that stem width in two ***Sphagnum*** species was plastic and differed significantly within species between those grown in water and those grown above water (Figure 37). Those above water developed 1-2 additional rows of hyaline cells in the outer layer of the stem (Figure 38). It is interesting that the less drought-resistant ***S. papillosum*** (Figure 39) had the greater difference in stem width between the two conditions. Despite that difference, ***Sphagnum magellanicum*** (Figure 40) is better at moving water than is ***S. papillosum*** and when grown in mixed clumps or alone it remains wet longer, whereas ***S. papillosum*** dries out quickly when it is in a hummock alone, but retains water as long as ***S. magellanicum*** when it grows mixed with it in about equal numbers (see Chapter 7-3).

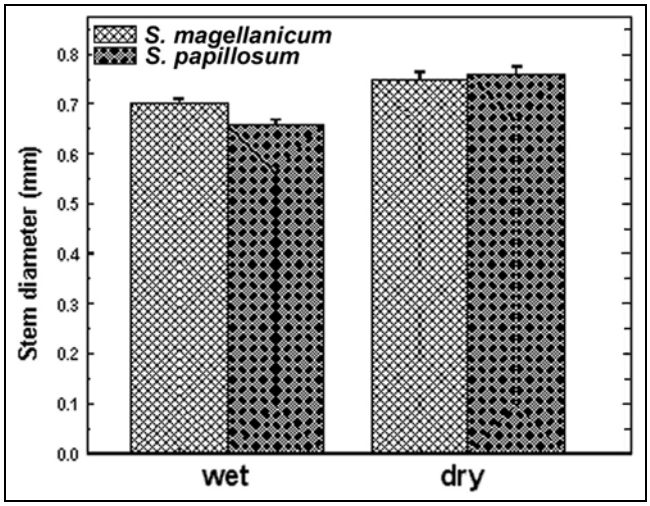

Figure 37. ***Sphagnum magellanicum*** and ***S. papillosum*** stem diameter when grown in wet vs dry (above water level) conditions. Graph by Yenhung Li, with permission.

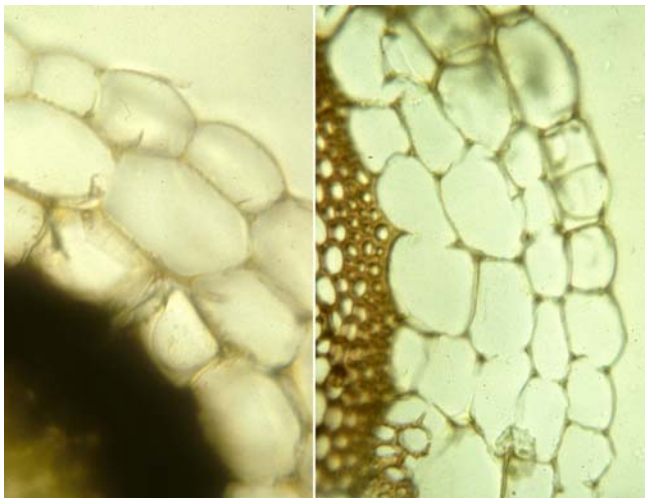

Figure 38. ***Sphagnum magellanicum*** stem cross sections showing outer hyaline layers. **Left:** stem grown in water; **right:** stem grown above water. Photos by Yenhung Li, with permission.

Figure 39. ***Sphagnum papillosum***, a drought-resistant species that develops additional rows of cells when above water. Photo by David T. Holyoak, with permission.

Figure 40. ***Sphagnum magellanicum***, a drought-tolerant species that develops additional rows of cells when above water. Photo by Michael Lüth, with permission.

One of the fascinating aspects of plants is their ability to change their structure in response to their environmental conditions. In at least some mosses, the stem diameter is able to increase in diameter in response to added ABA (Figure 41) (Spirina *et al*. 2020). ABA is known as a stress hormone, and one of its roles is to increase in response to drought, causing dehydration stress tolerance (Takezawa *et al*. 2011). Enlargement of the stem can provide strength, as seen by the response of tracheophytes to physical stress such as high wind (Telewski 2021). Already present in bacteria, ABA was of critical importance in adapting plants to land through added strength and adaptation to drought (Takezawa *et al*. 2011; Telewski 2021).

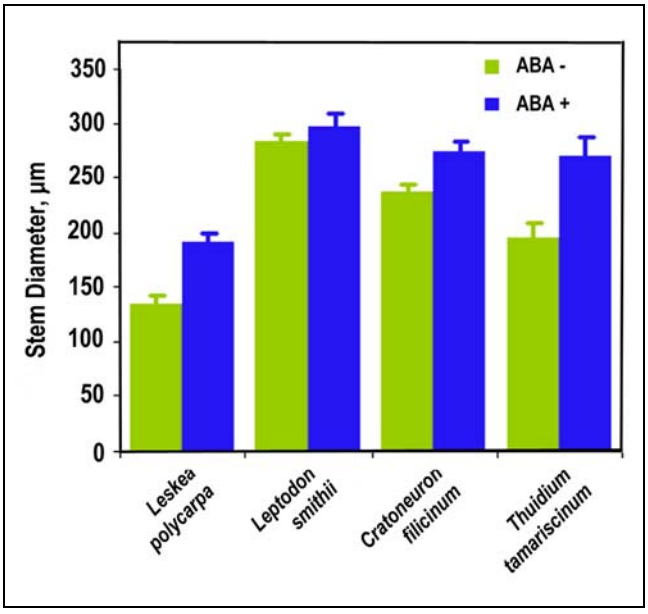

Figure 41. Effects of ABA on moss stem diameter. Modified from Spirina *et al*. 2011, through Creative Commons.

The **thigmomorphogenetic response** is the response to such stresses as mechanical bending or flexing in trees (Jaffe 1973; Telewski 2021). It is caused primarily by wind stress. Typically the trees respond to such bending by a reduction in extension or height growth and an increase in radial growth. A dose-dependent response to ABA contributes to these responses in trees and other plants, and now we know it can happen in bryophytes (Spirina *et al*. 2020).

Paraphyllia

Paraphyllia (Figure 42) are small green outgrowths on stems of some pleurocarpous mosses. They are useful taxonomic characters, permitting us to separate the sometimes look-alikes of ***Pleurozium schreberi*** (lacking paraphyllia; Figure 43) from ***Hylocomium splendens*** (having paraphyllia; Figure 44-Figure 45). But what is their function? The most logical is that of increasing water transport and reducing evaporation. There have been no tests to determine the value of their photosynthetic ability. And how often do they function as propagules, easily broken from the stems when dry? Do they form new plants under those conditions?

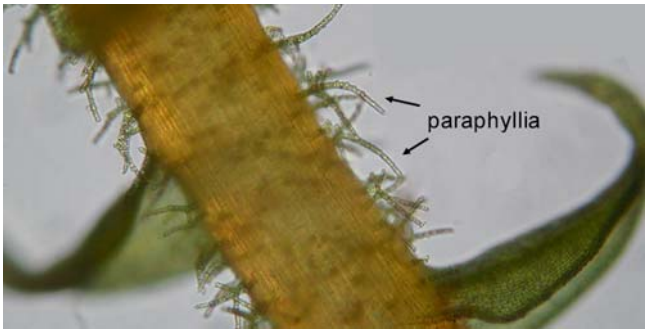

Figure 42. Stem of ***Thuidium*** sp. showing paraphyllia. Photo by Paul Davison, with permission.

Figure 43. ***Pleurozium schreberi***, a moss that lacks paraphyllia. Photo by Janice Glime.

Figure 44. ***Hylocomium splendens***. If you look carefully at the lowest visible part of the red stem in the center, you can see small bits of green paraphyllia. Photo by Rosalina Gabriel, with permission.

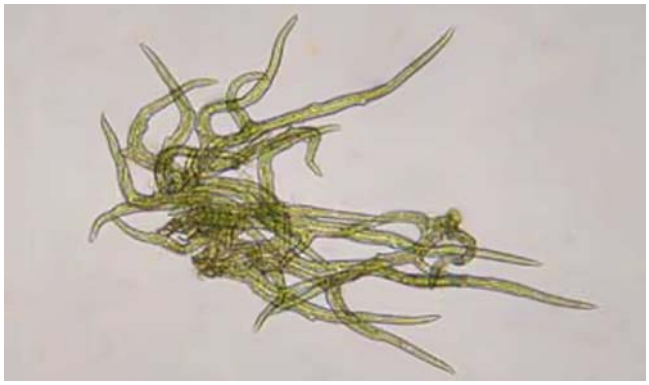

Figure 45. ***Hylocomium splendens*** paraphyllia. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

Spirina *et al*. (2020) compared paraphyllia in various species of mosses. They found that in the **Leskeaceae** (Figure 46-Figure 47), **Neckeraceae** (Figure 48-Figure 49), and **Amblystegiaceae** (Figure 50-Figure 51) these were distributed along the stem near the branch primordia. In these families, abscisic acid (ABA) stimulates increased production of the paraphyllia. On the other hand, they occur all along the stem in **Climaciaceae** (Figure 52-Figure 53), **Hylocomiaceae** (Figure 54-Figure 56), and **Pseudoleskeaceae** (Figure 57-Figure 58). In the **Thuidiaceae** (Figure 42; Figure 59-Figure 61), both types occur.

Figure 46. ***Leskea polycarpa*** (**Leskeaceae**), a species with paraphyllia near the branch buds. Photo by Hugues Tinguy, with permission.

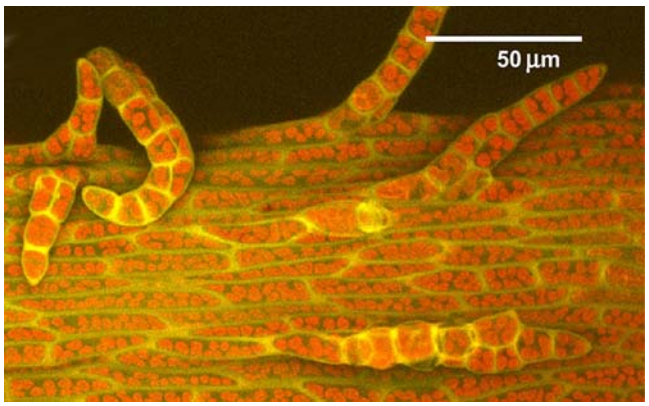

Figure 47. Paraphyllia on stem of ***Leskea polycarpa***. Photo modified from Spirina *et al*., through Creative Commons.

Figure 48. ***Metaneckera menziesii*** (**Neckeraceae**), a species with paraphyllia near branch buds. Photo from Dale A. Zimmerman Herbarium, WNMU, with permission from Russ Kleinman & Karen Blisard.

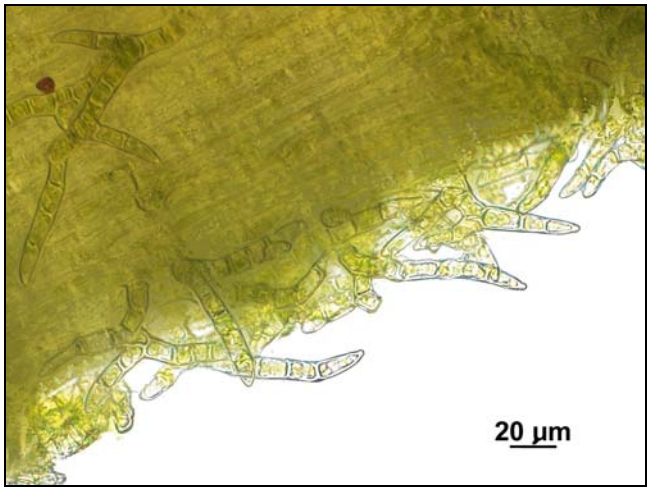

Figure 49. ***Metaneckera menziesii*** paraphyllia on stem near bud. Photo from Dale A. Zimmerman Herbarium, WNMU, with permission from Russ Kleinman & Karen Blisard.

Figure 50. ***Cratoneuron filicinum*** (**Amblystegiaceae**) in water, a species with paraphyllia near branch buds. Photo by Hugues Tinguy, with permission.

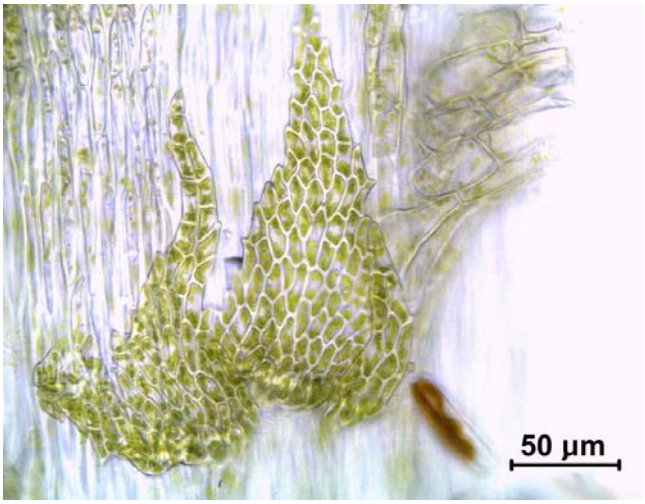

Figure 51. ***Cratoneuron filicinum*** paraphyllia near bud. Photo by Hugues Tinguy, modified, with permission.

Figure 52. ***Climacium dendroides*** (**Climaciaceae**), a species with paraphyllia along the stem. Photo by Vladimir Bryukhov, through Creative Commons.

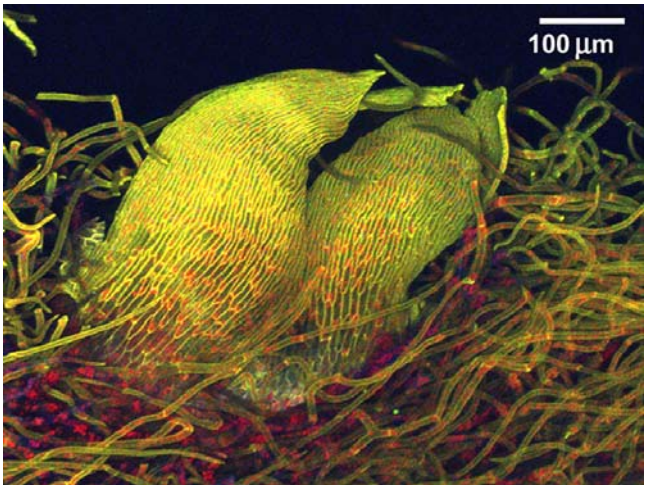

Figure 53. ***Climacium dendroides*** paraphyllia on stem. Photo modified from Spirina *et al*. 2011, through Creative Commons.

Figure 54. ***Hylocomium splendens*** (**Hylocomiaceae**), a species that produces paraphyllia along the stem. Photo by Claire Halpin, with permission.

Figure 55. ***Hylocomium splendens*** showing paraphyllia along stem. Photo from Dale A. Zimmerman Herbarium, WNMU, with permission from Russ Kleinman & Karen Blisard.

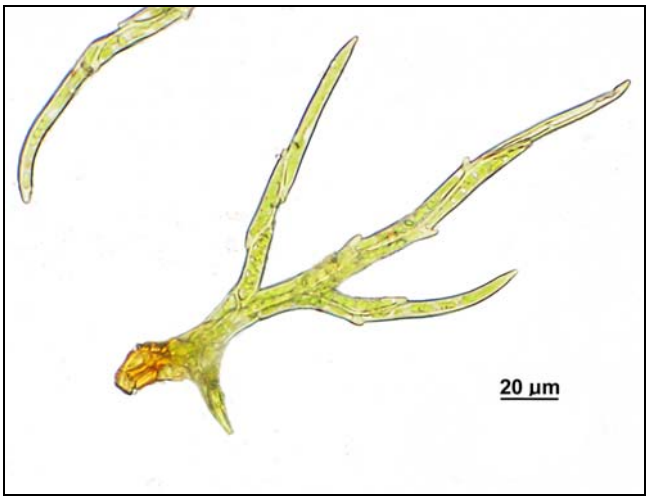

Figure 56. ***Hylocomium splendens*** paraphyllia. Photo from Dale A. Zimmerman Herbarium, WNMU, with permission from Russ Kleinman & Karen Blisard.

Figure 57. ***Pseudoleskea radicosa*** (**Pseudoleskeaceae**), a species with paraphyllia spread along the stem. Photo from Dale A. Zimmerman Herbarium, WNMU, with permission from Russ Kleinman & Karen Blisard.

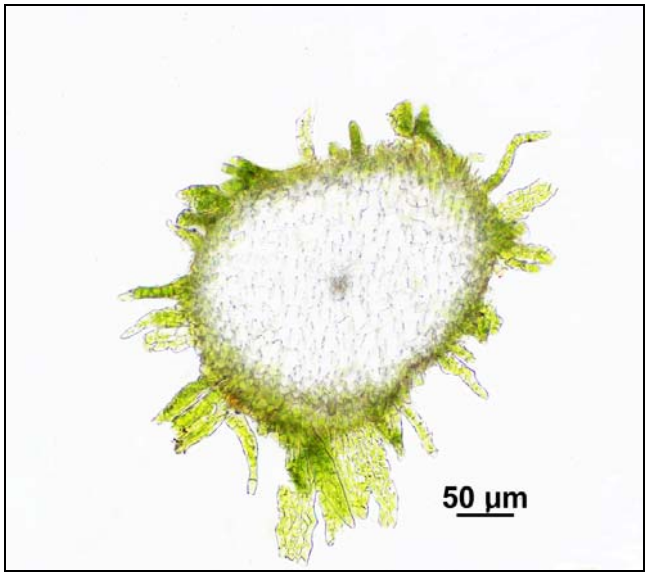

Figure 58. ***Pseudoleskea radicosa*** with paraphyllia on stem cross section. Photo from Dale A. Zimmerman Herbarium, WNMU, with permission from Russ Kleinman & Karen Blisard.

Figure 59. ***Thuidium delicatulum*** (**Thuidiaceae**), a species with paraphyllia along the stem and surrounding the branch buds. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

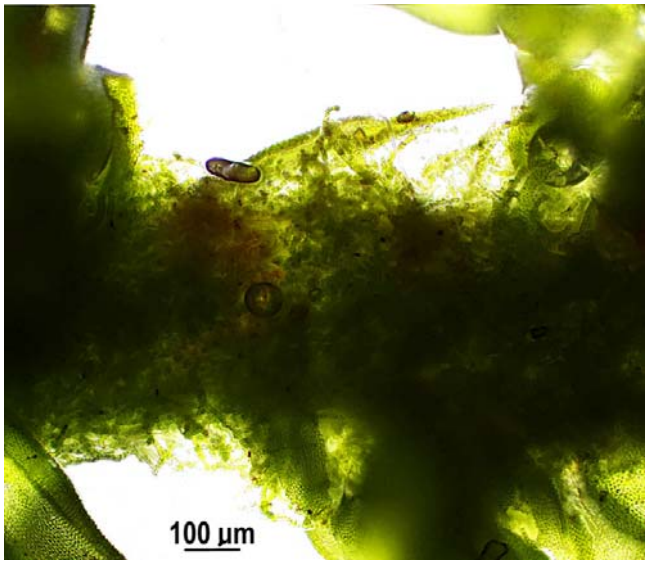

Figure 60. ***Thuidium delicatulum*** paraphyllia showing their density on the stem. Photo from Dale A. Zimmerman Herbarium, WNMU, with permission from Russ Kleinman & Karen Blisard.

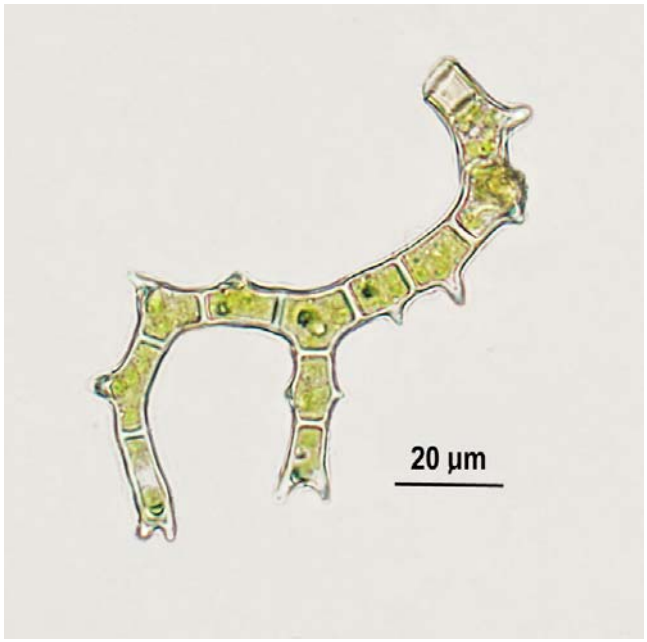

Figure 61. ***Thuidium delicatulum*** paraphyllium. Photo from Dale A. Zimmerman Herbarium, WNMU, with permission from Russ Kleinman & Karen Blisard.

Leaf Margins

Margins of leaves can be flat, **involute** (rolled upward (Figure 62), **revolute** (rolled under; Figure 63-Figure 64), and **bordered** or **unbordered**. The borders can be one cell thick or multiple cells thick. The whole leaf can be **inrolled** (rolled upward; Figure 65-Figure 66), folded (see Keels below), or flattened. And the borders can have teeth or be smooth. Some functions for these will be discussed in the chapter on Water Relations (Chapter 7-4, Vol. 1), but this chapter would not be complete without some consideration of them.

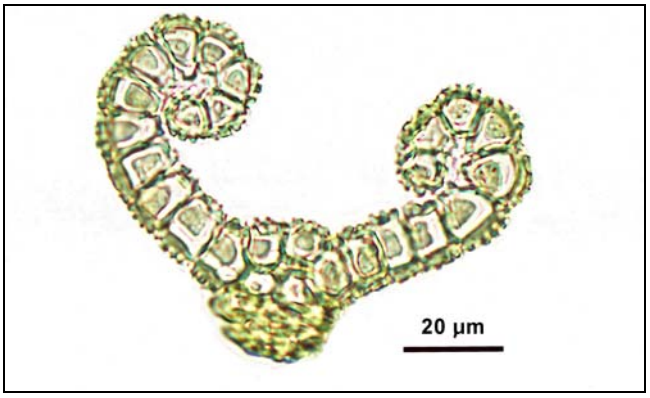

Figure 62. ***Weissia controversa*** leaf cross section showing involute margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

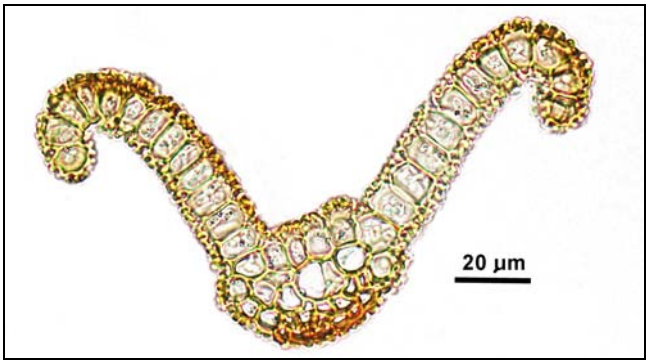

Figure 63. ***Bryoerythrophyllum recurvirostre*** leaf cross section showing revolute leaf margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 64. ***Ceratodon purpureus*** showing revolute leaf margins. Photo by Malcolm Storey, through Creative Commons.

Figure 65. ***Dicranum muehlenbeckii*** showing the curled, inrolled leaves. Photo by Michael Lüth, with permission.

Figure 66. ***Dicranum muehlenbeckii*** leaf cross section showing inrolled leaf. Photo by Michael Lüth, with permission.

Borders or Not

Bryophytes distinguish their leaf borders in a number of ways. While many lack special border cells (Figure 67), they may still have teeth on the border, as discussed below. Others may lack specialized cells but have margins that are more than one cell thick (Figure 74). And those with borders typically have elongate cells (Figure 68-Figure 69) that differ from lamina cells. These specialized border cells may have teeth or lack them.

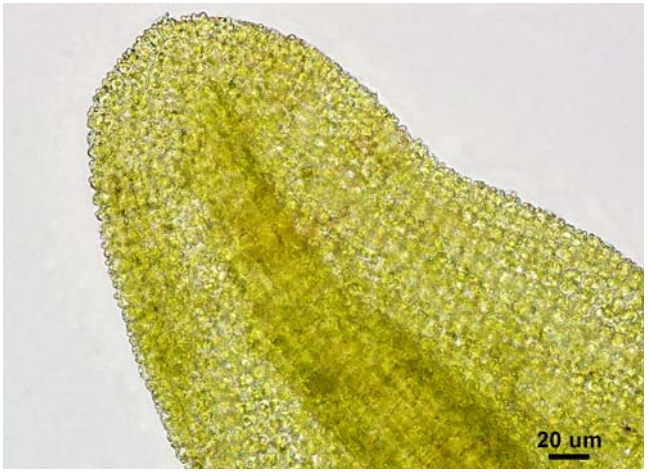

Figure 67. ***Barbula convoluta*** leaf with no border and with papillose cells and a costa. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 68. ***Mnium spinosum*** leaf showing border with colored elongate cells contrasting with nearly isodiametric leaf lamina cells. Photo by Michael Lüth, with permission.

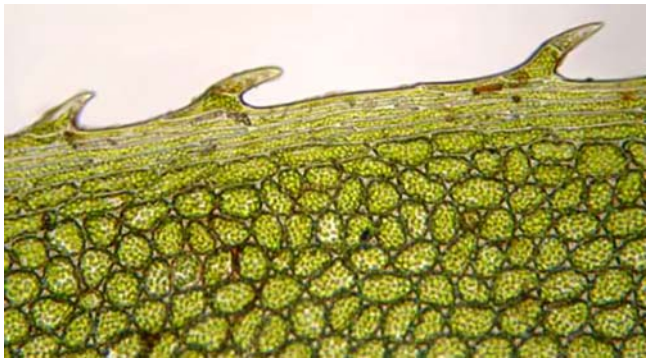

Figure 69. ***Plagiomnium insigne*** showing border that is several cells wide with elongate cells that contrast with the isodiametric lamina cells. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Special border cells are rare among tracheophytes, so this suggests that their presence may indicate a function in bryophytes that is not useful in tracheophytes. In fact, it is likely that this is true. Kürschner (2004) described the contortions and shrinkage of the leaf lamina in **Pottiaceae** (Figure 70-Figure 71) and **Grimmiaceae** (Figure 72-Figure 74). These contortions are typically dependent on the leaf border. As the lamina shrinks while drying, the border remains firm and does not shrink. Hence, the shrinking lamina cells pull and tug on the borders and a twisted leaf results. These leaves wind around the stem helically, benefitting from protection by the stem and reducing further desiccation and protecting against solar radiation. In desert habitats, the adhering sand grains are removed as the twisting leaves respond to water uptake and straighten during a rainfall (Scott 1982).

Figure 70. ***Tortula intermedia*** (**Pottiaceae**) hydrated. Photo by Michael Lüth, with permission.

Figure 71. ***Tortula intermedia*** (**Pottiaceae**) dry with leaves twisted around the stem. Photo by Michael Lüth, with permission.

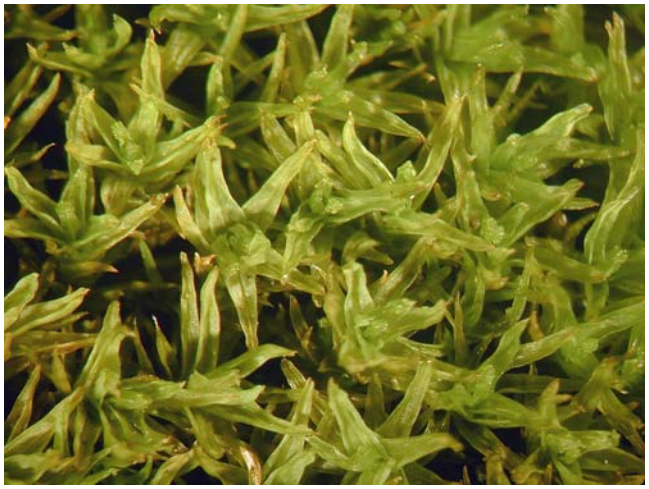

Figure 72. ***Grimmia anomala*** (**Grimmiaceae**) showing hydrated leaves that spread widely around the stem. Photo by Michael Lüth, with permission.

Figure 73. Dry ***Grimmia anomala*** (**Grimmiaceae**) showing leaves twisted around the stem. Photo by Jan-Peter Frahm, with permission.

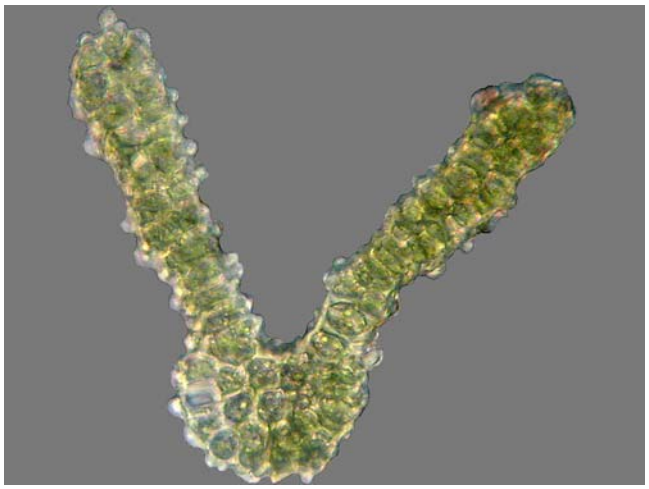

Figure 74. ***Grimmia anomala*** (**Grimmiaceae**) leaf cross section showing areas that are more than one cell thick, especially at the margin. The thickenings may contribute to the way it twists around the stem when dry. Note that the margin consists of a double layer of cells, giving the margin rigidity. Photo by Michael Lüth, with permission.

Marginal Teeth

Marginal teeth in tracheophytes seem to have multiple functions. In tracheophytes, marginal teeth are responsive to temperature (Royer & Wilf 2006; Royer *et al*. 2012). Using 3549 tracheophyte species from six continents, they determined toothed species are more likely to be deciduous, thin leafed, of low leaf mass per area, with ring-porous wood, and have a high leaf nitrogen content. Trees in the canopy are most likely to be sensitive to temperature as a determinant of leaf-margin state compared to shrubs and herbs. Hence, leaf thinness and deciduousness as well as temperature are linked to having teeth. Royer *et al*. argue that by being thin and having thin tissues in teeth along the margins, these deciduous leaves can return their contents to the ecosystem quickly. Perhaps the thin margins permit fungal and bacterial colonies to get established quickly?

Yet another hypothesis was tested by Baker-Brosh and Peet (1997). They observed that teeth were rare in tropical moist forests but frequent in temperate deciduous forests. They hypothesized that in those forests where leaves had to grow anew each year the teeth and lobes served as the site of early season photosynthesis in new leaves. Using $^{14}CO_2$ and autoradiography, they determined that eight species with prominent teeth or lobes did indeed exhibit early season photosynthesis on the margins, whereas in those with entire margins (no teeth; 4 species) there was no early season photosynthesis on the margins. However, seven species that were toothed or lobed likewise lacked early season photosynthesis on the margins. Royer and Wilf (2006) demonstrated that teeth were advantageous for early season photosynthesis in temperate climates. Could there be similar early season photosynthetic behavior to aid growth of new leaves in some mosses, particularly if margins at that stage are predominantly green (Figure 75-Figure 77)?

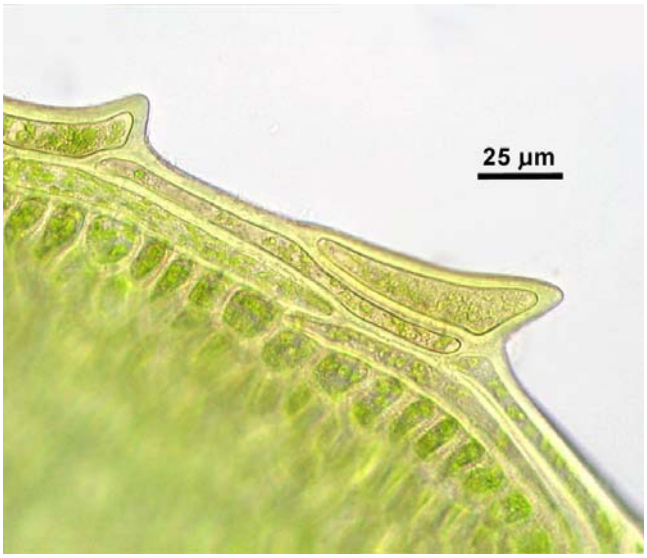

Figure 75. ***Plagiomnium undulatum*** leaf border showing photosynthetic marginal teeth. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 76. ***Plagiomnium undulatum*** showing small leaves at apex where teeth may help in photosynthesis in early development. Photo from <www.aphotofauna.com>, with permission.

Royer *et al*. (2009) further explored the role of teeth in the Australian subtropical rainforest trees. Using 227 sites, they found a correlation between humidity and number of toothed species, with the greatest occurrence of toothed species in the riparian zone and the fewest at the drier ridge tops. They attribute the relationship to the availability of water. Could it be that toothed species of these large leaves lose water more easily due to the increased surface area, negating the early spring advantage in dry sites? Would this incur the same problem in bryophytes, or might the teeth actually confer a water advantage – a site for collecting and absorbing water much like the hair tips discussed below? I am aware of no quantitative study to test this hypothesis in bryophytes.

Applying these tracheophyte principles to bryophytes could bring interesting insights, but I am unaware of any attempt to test the correlations.

In bryophytes, teeth can occur along the margins [singly (Figure 75) or doubly (Figure 77)], but also occasionally projecting from the leaf lamina (Figure 78-Figure 80) or costa (Figure 80-Figure 81).

Figure 77. ***Mnium spinosum*** leaf showing double teeth on leaf margin. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 78. ***Atrichum selwynii*** leaf showing teeth projecting from the dorsal side of the leaf lamina. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 79. ***Atrichum undulatum*** leaf showing teeth in diagonal rows on dorsal side. Photo by Jutta Kapfer, with permission.

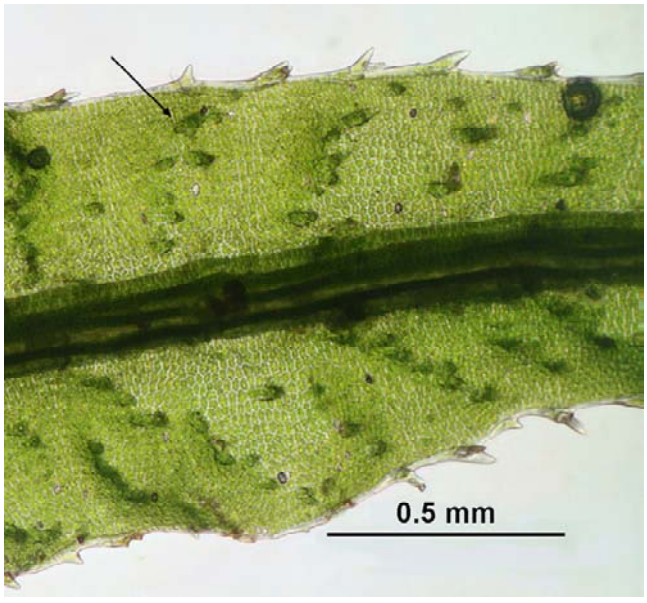

Figure 80. ***Atrichum undulatum*** leaf showing teeth (arrow) on dorsal side on undulations. Photo by Hermann Schachner, through Creative Commons.

Figure 81. ***Mnium spinosum*** back of costa showing tooth on costa. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Among tracheophytes, leaf teeth are postulated to mimic effects of herbivory and thus to discourage additional herbivores on a leaf that has already been eaten. This proposed deterrent may have credence in the fact that antiherbivore compounds often are inducible (Karban & Baldwin 1997; Karban *et al*. 1997; Ceh *et al*. 2005), so a herbivore might recognize that the leaf (or alga) has been eaten and will taste bad without the herbivore having to take a sample. The argument is that the teeth give the appearance that the leaf has been nibbled before.

Could this tracheophyte herbivore deterrent of teeth have a role in bryophytes? Might herbivores consider it a signal that the leaves will taste bad? We don't even know if antiherbivore compounds in bryophytes are inducible. But then, perhaps the insects don't know either and assume the bryophytes behave like tracheophytes. And do these bryophyte teeth really look like evidence of herbivore browsing? Or do they possibly have the deterrent effects that hairs and spines have on browsing by large herbivores? Might they deter such soft-bodied herbivores as snails? It would be easy to see if snails choose to crawl over bryophyte leaves without such teeth in preference to those with them. ***Atrichum undulatum*** would be a good test subject with its teeth on the lamina (Figure 78-Figure 80).

Liverworts

And what about the lobes and teeth of **leafy liverworts** (Figure 82)? Do they have any adaptive value? Could they also have antiherbivore functions? Do they serve to hold water on the leaf surface? Or are they just useful tools for bryophyte taxonomists?

In the leafy liverwort genus ***Plagiochila***, habitats in North America differ from those in the tropics and so do the teeth. In North America, ***P. porelloides*** (Figure 83-Figure 84) lives next to or in water and has small or almost no teeth. In the tropics, where there are many species in the genus, this genus lives on tree trunks and sides of boulders where conditions may be almost xeric. Most of these species have large teeth (Figure 85). When it rains, these liverworts can become quite saturated. Do the teeth help the leaves to hold droplets of water? Could their added surface area provide evaporative cooling? Or is this again an early season adaptation to enhance photosynthesis?

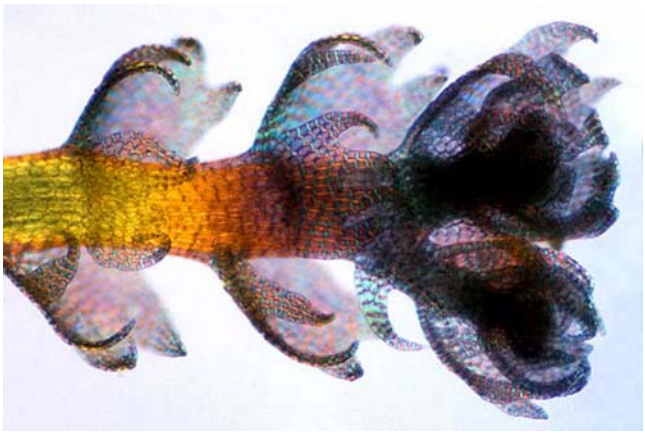

Figure 82. Leafy liverwort showing lobes that curl toward the stem. One can easily imagine these leaves trapping a cohesive drop of water, then slowly bending inward as that dater droplet shrinks. Photo by Bill Malcolm, through Creative Commons.

Figure 83. ***Plagiochila porelloides***, a species that grows in moist areas like stream banks in the Northern Hemisphere. Note that the teeth are much smaller than in most tropical species. Could teeth provide evaporative cooling? Photo by Dick Haaksma, with permission.

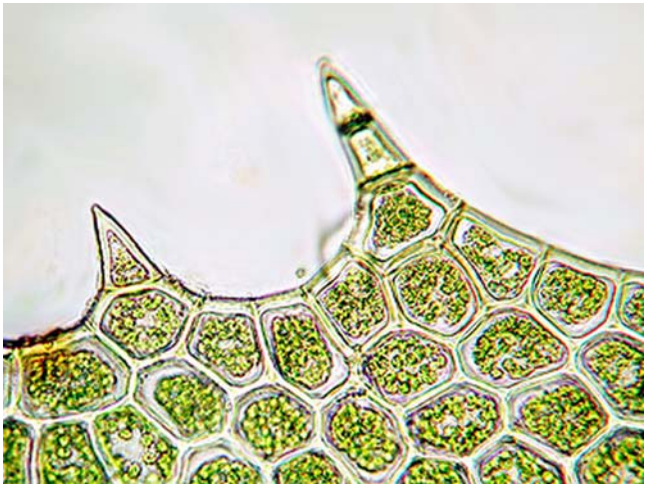

Figure 84. ***Plagiochila porelloides*** leaf teeth showing the smaller size in this streamside and wet habitat species compared to tropical epiphytes and epiliths. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

Figure 85. ***Plagiochila raddiana*** from the Neotropics. How do these teeth function for the tropical epiphytic and epilithic species? Photo by Michael Lüth, with permission.

Some species of liverworts have deep lobes. In some cases these are curved toward the stem (Figure 86) and one can imagine that they help to hold drops of water, clinging to them and curving further inward as the drop decreases in size (Figure 87). Such structure could provide a water reservoir for the leaf, permitting photosynthesis for a longer period of time. If the convex surface faces the light, the water reservoir could permit photosynthesis to continue for a longer period of time without interfering with light capture, while permitting CO_2 to enter from the surface opposing the water drop.

Figure 86. ***Lepidozia reptans***, a relative small species with leaves in a size range where they could trap a cohesive water drop. Teeth may aid in holding that water next to the leaf. Photo by Walter Obermayer, with permission.

Figure 87. Wet ***Ptilidium ciliare*** showing teeth clinging to the leaf beneath, presumably aiding in water retention. Photo by Des Callaghan, with permission.

Presumably, size affects the utility of teeth and lobes. If one compares the large size of the leaf and its lobes in ***Lophocolea*** (Figure 88) with those in ***Cephalozia*** (Figure 89), it appears their functionality should work differently. Small droplets of water are harder to break up than large ones. Does this have any bearing on utility, size, and location of the lobes? Would long, thin lobes on large leaves direct water off the leaf, permitting CO_2 to enter the cells, behaving like the drip tips of some tropical leaves?

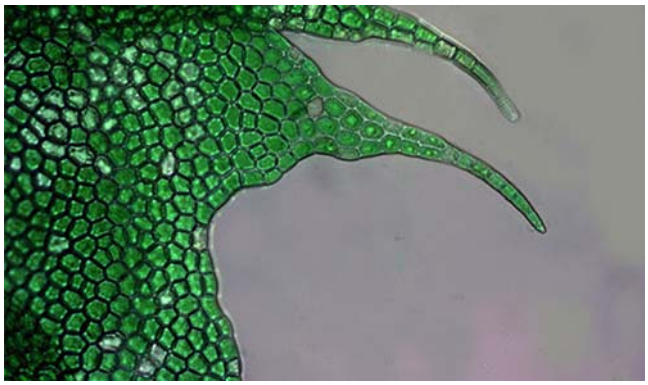

Figure 88. ***Lophocolea bidentata***, a relatively large species showing leaf lobes. Might these aid in holding drops of water? Photo by Aimon Niklasson, with permission.

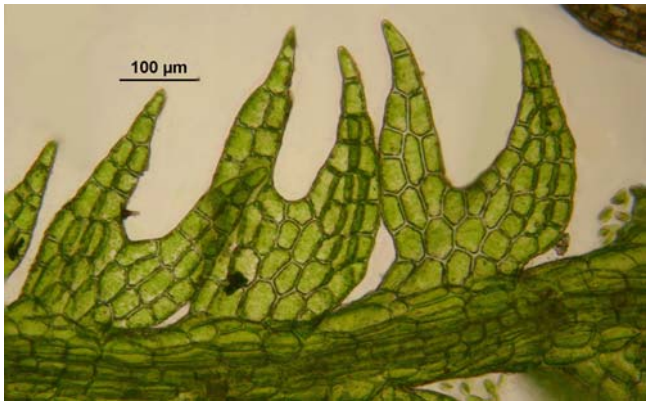

Figure 89. ***Cephalozia bicuspidata***, a much smaller species than ***Lophocolea bidentata***, showing leaf with deep lobes. Could these lobes provide a means of holding onto a drop of water, much as a diving beetle holds onto a bubble of air? Photo by Hermann Schachner through Wikimedia Commons, with permission.

Let's return to the consideration of moisture relationships and number of species with teeth. This might be simplest to demonstrate with epiphytes. In the temperate zone, where epiphytic positions can impose long drought periods, most of the large leafy liverworts have entire leaf margins, *e.g.* ***Frullania*** (Figure 90), ***Porella*** (Figure 91), and ***Radula*** (Figure 92). In the tropics, ***Plagiochila*** (Figure 93) is very common, with many species, and most of these have rather large teeth. Tropical rain forests have long seasons of rainy weather that can maintain the moisture among these liverworts, followed by a long season of drought when the liverworts can remain dormant. Temperate species, on the other hand have the risk of drying before they have repaired the damage from the last drought. Which strategy – teeth or no teeth – permits them to hold water longer? What fun for experimentation!

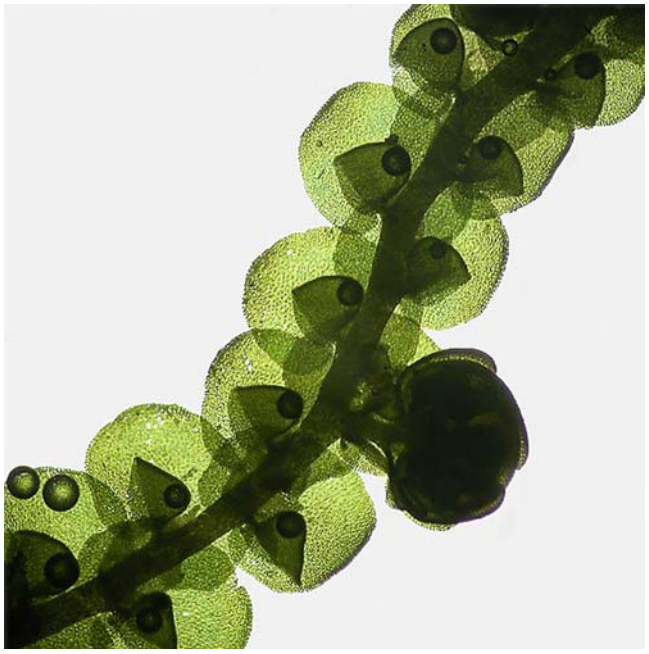

Figure 90. ***Frullania dilatata*** showing lobules and entire margins (no teeth or lobes). Photo by Walter Obermayer, with permission.

Figure 91. ***Porella cordaeana*** showing entire leaf margin. Photo by Jan-Peter Frahm, with permission.

Figure 92. ***Radula*** from the Neotropics showing entire leaf margins. Photo by Michael Lüth, with permission.

Figure 93. ***Plagiochila adianthoides*** from the Neotropics showing toothed leaf margins. Photo by Michael Lüth, with permission.

One might argue that in liverworts like ***Nowellia curvifolia*** (Figure 94), the long lobes provide a stalk for the clusters of gemmae produced at their tips. Such positioning for the gemmae might make it easier for them to escape the plant and travel a greater distance.

Figure 94. ***Nowellia curvifolia*** showing gemmae positioned at the ends of narrow leaf lobes. Photo by Paul G. Davison, with permission.

Hair Tips

Many bryophytes in dry habitats have hair tips on the leaves (Figure 95-Figure 96). One suggestion for their role is that they are able to reflect sunlight (Kürschner 2004). This can protect the underlying cells from sun damage when they are dry and the leaves are compressed against the stem. And in many species, when the plants are dry the leaves twist around the stems so that each hair overlaps the leaf above it (Figure 97).

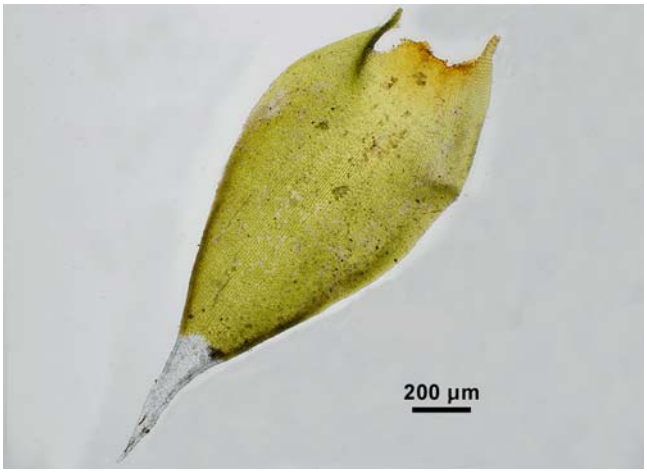

Figure 95. ***Hedwigia ciliata*** leaf showing translucent hair point. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 96. ***Hedwigia ciliata*** with wet plants on the upper left and dry ones on the edge of the colony (lower right). Note how the dry leaves cling to the stem compared to the spreading wet leaves. Photo by Janice Glime.

Figure 97. ***Grimmia decipiens*** showing array of hairs that help fill in spaces between stems. Photo by Des Callaghan, with permission.

A second function has been suggested – that the hair points may help to absorb condensed water vapor from fog and dew (Figure 98-Figure 100) (Kürschner 2004). This phenomenon is well known from physics – small droplets accumulate around thin wires – and on fine hairs. To this role, I would add that the hairs may provide additional capillary spaces that gain water in rain as well and hold it there for longer periods of time, preventing evaporation from the leaves.

Figure 98. ***Grimmia*** cf ***pulvinata***, lightly covered with dew, on churchyard wall. This picture supports the notion that the hairs can act to collect dew that can eventually drip down into the moss mat. In areas with low precipitation and frequent fog, this can be the only source of water for some mosses. Photo by Brian Eversham, with permission.

Figure 99. ***Grimmia horrida*** habitat at edge of fog in northern Portugal. Photo by Michael Lüth, with permission.

Figure 100. ***Campylopus introflexus*** collecting water drops on the fine hairs. Photo by Michael Lüth, with permission.

Figure 101. ***Tortula muralis*** with hair tips trapping water droplets. Photo by Christophe Quintin, through Creative Commons.

If we examine the picture of ***Grimmia*** from Scotland (Figure 102), we can see a third possible function. Note that the frost is held away from the leaves. Frost and ice crystals are very hygroscopic and can draw water out of the leaves as they do from the foods in your freezer. The hairs seem to function, at least in this case, to keep the frost from contacting the leaves, thus avoiding their potential desiccating effect. The same is often seen in leaves of early spring perennial flowers.

Figure 102. ***Grimmia*** capsules and frost at Dunkeld, Scotland. Photo by Allan Water.

As I sorted through images, I was struck by another potential purpose for some hairs. As you will learn in Chapter 7, bryophytes survive desiccation much better than their tracheophyte counterparts. But when they are rehydrated, they must repair damaged membranes, and this seems to take about 24 hours. A short misting or very light rain that evaporates right away may not provide enough hours for repair before the bryophyte is once again desiccated, hence wasting the energy expended in its failed attempt. Hairs can fill in spaces between apices (Figure 103), trapping water droplets and keeping them from entering the moss mat, thus preventing a hydrated period that is too short, or perhaps keeping the water at the tip to be absorbed slowly over time (Figure 104).

Figure 103. ***Grimmia*** at Goudini Spa, South Africa. With hairs in this position, they can capture the cohesive water drops (Figure 104) and prevent them from entering the moss mat during a light shower. When the storm lasts longer, the weight and size of the droplets will finally force them through the hairs. Photo by Janice Glime.

Figure 104. ***Pohlia wahlenbergii*** with cohesive water drops. Note that these drops are mostly too large to penetrate the mat and hence remain at the surface, held together by their own cohesive forces. Photo by J. C. Schou, through Creative Commons.

Finally, I suggest that hair points, at least in some species, can deter some kinds of herbivores. We know that invertebrate herbivores are deterred by hairy leaves of tracheophytes (Karban & Agrawal (2002) and that spiny leaves deter ungulates (Obeso 1997). It is not unreasonable to assume that they can confer similar advantage to bryophytes, particularly when hair points overlap extensively as in ***Grimmia arenaria*** (Figure 105).

Figure 105. ***Grimmia arenaria***, demonstrating long hairs that might protect from bright sun or prevent desiccation. Photo by Des Callaghan, with permission.

Costae

The **costae** are the moss versions of midribs (Figure 106). They are absent in liverworts. Their functions may include movement of water from base to tip of the leaf, or perhaps from tip to base. This can be surmised by the elongate structure of the cells (Figure 107) compared to the shortness of leaf lamina cells in many species. I have referred to base to tip transport because it is the base where water can accumulate in the leaf axil and receive water from the stem through its external movement of water. But in some plants, water might move into the leaf at the tip, possibly absorbed through the apical leaf hair, but empirical data to demonstrate this seems to be lacking.

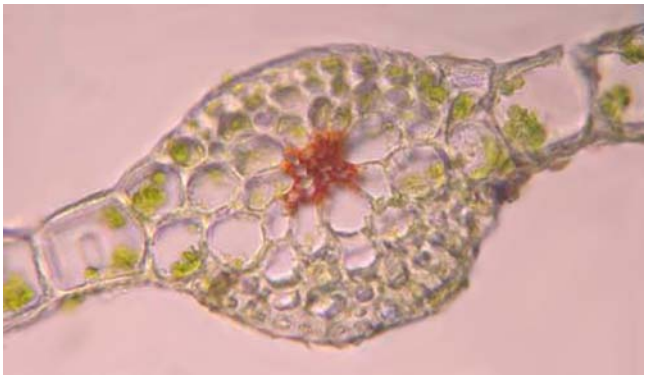

Figure 106. ***Rhizomnium glabrescens*** leaf cross section showing costa. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

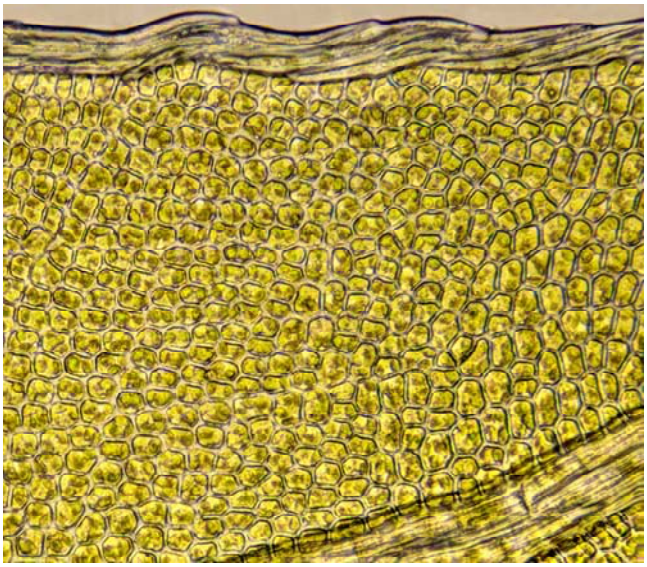

Figure 107. ***Fissidens bryoides*** leaf cells showing elongate cells of costa in lower right. Photo by Dick Haaksma, with permission.

I have constantly been struck by the attempts of ecologists to find a single explanation or advantage for a particular strategy for plants or animals. I am convinced that many of these strategies/structures persist because they provide small advantages for multiple functions. And certainly some are advantageous in some situations or years, but not in others. They may at times even be disadvantageous.

Proctor (2010) points out that in **Sematophyllaceae**, some members have a costa and others do not. The same is true in the **Fontinalaceae**. In the latter family, the costa separates the costate genera ***Dichelyma*** (Figure 108) and ***Brachelyma*** (Figure 109), both occurring in inundated areas but living mostly above water, from the ecostate genus ***Fontinalis*** (Figure 110), a genus that spends most of the year under water. Olsson *et al*. (2009) have shown that in the **Neckeraceae** reduction of the costa has recurred in all three main clades. Proctor (1979) concludes that the presence or absence of a costa, as well as the shape of leaf cells, must have functional consequences, but we are uncertain how important these are for mechanical support vs conduction within the leaf, not to mention simply chance occurrence relating more to ancestry than to (current) function.

Figure 108. ***Dichelyma falcata***, a member of the **Fontinalaceae** with a costa. Photo by Michael Lüth, with permission.

Figure 109. ***Brachelyma subulatum***, a member of the **Fontinalaceae** with a costa and keeled leaves. Photo by Janice Glime.

Figure 110. ***Fontinalis hypnoides*** showing absence of costa. Photo by John Game, with permission.

I was surprised to find that when grown in my artificial stream with considerable air exposure, ***Fontinalis*** produced short costae. Bruce Allen once told me he had also sometimes found ***Fontinalis*** leaves from nature that had short costae. To me this suggests that something suppresses the development of the costa and that under certain conditions that suppression doesn't function. That would imply that the costa came first and that a suppressor developed later. That suppressor is most likely water, which not only affects hydration, but also affects CO_2 uptake, oxygen concentration, and escape of gases such as the developmental hormone **ethylene**.

Costae can provide strength for a leaf. It can represent a tough tissue not eaten by herbivores. It is the structure that remains on leaves of aquatic species such as those of ***Hygroamblystegium*** (Figure 111-Figure 112) when exposed to rapid flow and suspended solids. But is any of these adaptive in any way? Possibly. If the costa is capable of growth into a new plant, it could become a dispersal agent. It could also provide photosynthetic tissue when leaf lamina tissue has been eaten or eroded. But there is no empirical proof that these things occur or if so, are they of any consequence.

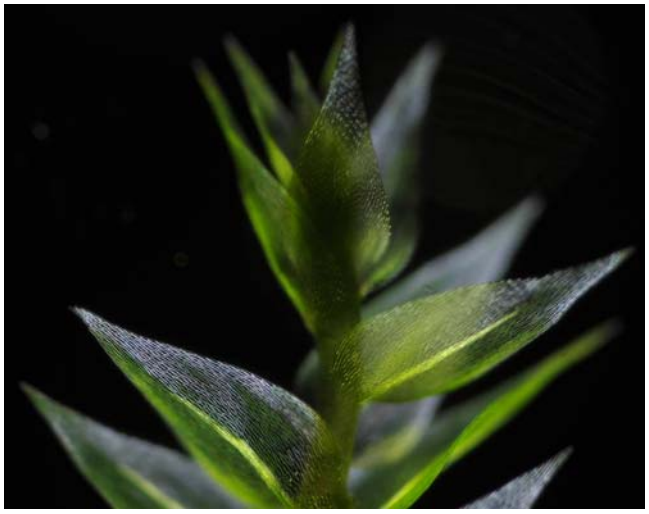

Figure 111. ***Hygroamblystegium tenax*** showing thick costa in leaves. Photo by Martha Cook, with permission.

Figure 112. ***Hygroamblystegium fluviatile*** showing dark costae left from eroded leaves. Photo by Michael Lüth, with permission.

Some amphibious bryophytes actually have reduced or lost costae when they have grown in the water. For example, Rod Seppelt (Bryonet 24 June 2012; Seppelt & Selkirk 1984) observed that the costae of ***Bryum pseudotriquetrum*** (Figure 113-Figure 114) were shorter and weaker on aquatic specimens from lakes in Antarctica compared to those growing out of water. He also reported inducing absence of costae and change in leaf shape in ***Bryum argenteum*** (Figure 115) in culture, with temperature playing a major role in inducing leaf changes; lower temperatures resulted in wider leaves. Furthermore, at 4°C the costa was absent. Clearly in some species the environment can affect how the costa develops. But what does it mean for the plant?

Figure 113. ***Bryum pseudotriquetrum*** showing strong costa of the terrestrial form. Photo by Des Callaghan, with permission.

Figure 114. ***Bryum pseudotriquetrum*** leaf showing costa that becomes shorter and weaker in Antarctic lakes. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

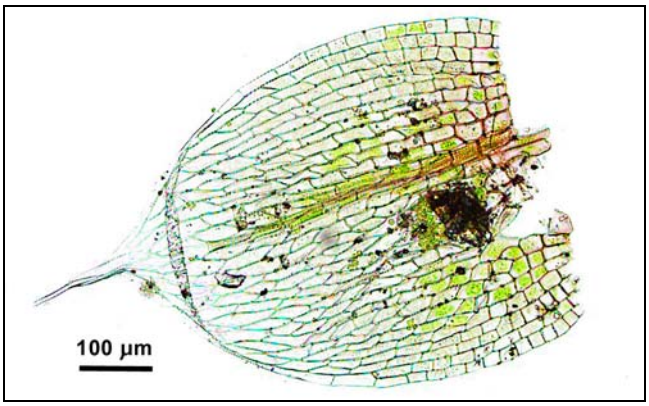

Figure 115. ***Bryum argenteum*** leaf showing well developed costa of a terrestrial form. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

In the genus ***Dicranum*** (Figure 116-Figure 121), the costa varies widely, with almost no differentiation in ***Dicranum rhabdocarpum*** (Figure 116) to phalanges along the costa in ***Dicranum scoparium*** (Figure 121). In other members of the **Dicranaceae**, for example ***Pilopogon peruvianus***, the costa can occupy most of the leaf width (Figure 122).

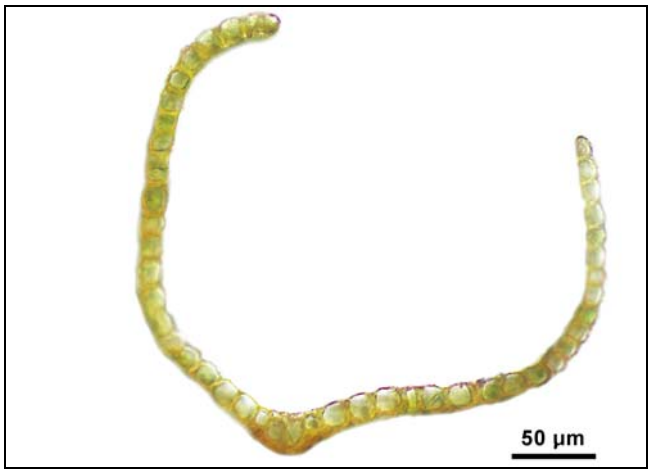

Figure 116. ***Dicranum rhabdocarpum*** leaf cross section showing absence of papillae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 117. ***Dicranum muehlenbeckii*** leaf cross section showing relatively smooth cell surface. Photo by Michael Lüth, with permission.

Figure 118. ***Dicranum brevifolium*** leaf cross section showing costa and mammillate cells. Photo by Michael Lüth, with permission.

Figure 119. ***Dicranum dispersum*** leaf cross section showing costa and thickened margins. Photo by Michael Lüth, with permission.

Figure 120. ***Dicranum fuscescens*** leaf cross sections showing costa and papillose leaf cells. Photo by Michael Lüth, with permission.

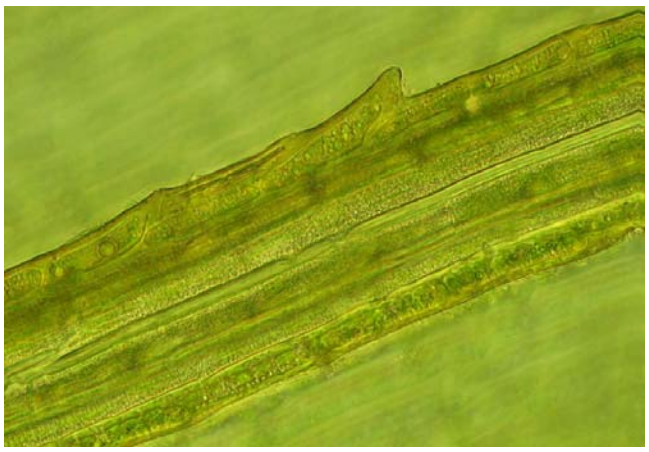

Figure 121. ***Dicranum scoparium*** teeth on back of leaf costa. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 122. ***Pilopogon peruvianus*** showing a costa that occupies most of the leaf. Photo by Michael Lüth, with permission.

Glenn Shelton (Bryonet 15 June 2012) contended that mosses tend to evolve from having multiple costae (Figure 123) to few (single or none). He and colleagues have found a number of tricostate mosses from the Early Cretaceous of Vancouver Island, B.C., Canada, some apparently pleurocarpous, as evidenced by a high degree of branching (including pinnate) and cell morphology. On the other hand, it appears that costa number is quite plastic among major moss lineages – and even within species (see above). And Ben Tan (Bryonet 30 June 2012) enters a word of caution – that folds or plicae at the leaf base can look like short costae, so one must be careful in interpreting fossil costae.

Shelton (Bryonet 15 June 2012) explains that one theory is based on the premise that the costa gives rigidity to the leaf and that multiple costae provide more rigidity. This assumes, then, that the need for this rigidity has been lost in some species. The theory also considers evolution from complex leaf structure to a simpler structure – **reduction**.

Figure 123. ***Vesicularia montagnei*** showing short, double costa. Photo by Tan Sze Wei, Aquamoss website <www.aquamoss.net>, with permission.

Perhaps Kürschner (2004) has the right idea for some species. He notes that the costa is often shiny (Figure 124-Figure 125) in mosses growing in xeric sites. Hence, he suggests that the costa may reflect the solar radiation and thus reduce both evaporation and heat stress. I would need proof to see how a narrow costa could have much impact, and it seems that xeric costae are often darker than the leaf (Figure 124-Figure 125), suggesting they might absorb more heat than the lamina.

Figure 124. ***Syntrichia andicola*** showing shiny costa. Photo by Michael Lüth, with permission.

Figure 125. ***Syntrichia andicola*** showing costa of leaf. Photo by Michael Lüth, with permission.

Zander (Bryonet 25 June 2012) reminded us of the perspective of Gould (2002) that there are minimum constraints on size – a developmental wall to small size for particular organisms. He considers that the elimination of superfluous costal material might depend on size. As leaves get smaller, the costa necessarily gets smaller, and it might no longer serve the same function or advantage it did in larger leaves. Zander points out that acrocarpous mosses usually have costae, but that pleurocarpous mosses may or may not. Is this a size difference, or a difference in phylogenetic history? And perhaps costae persist, or not, because some other linked trait is affected by some selection pressure that has changed over time.

Lamellae

Lamellae (Figure 126-Figure 138) can greatly increase the surface area of a leaf. They provide numerous surfaces, exposed on both sides for absorption of light and especially CO_2 and provide capillary spaces for taking up and holding water.

Members of the family **Polytrichaceae** are defined by the presence of lamellae (Figure 126-Figure 131), but other genera in scattered families have them as well. These include ***Aloina*** (Figure 132), ***Crossidium*** (Figure 133-Figure 134), ***Pterygoneurum*** (Figure 135-Figure 137), and some ***Syntrichia*** (Figure 138).

Figure 126. ***Atrichum undulatum*** leaf lamellae. Photo by Walter Obermayer, with permission.

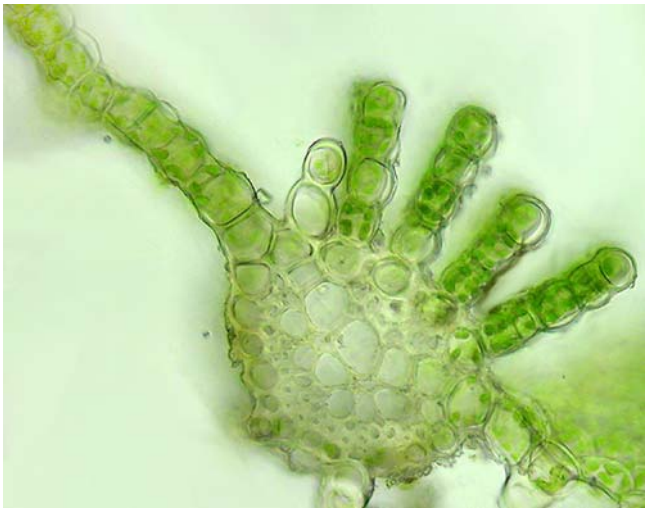

Figure 127. ***Atrichum undulatum*** leaf cross section showing lamellae. Photo by Walter Obermayer, with permission.

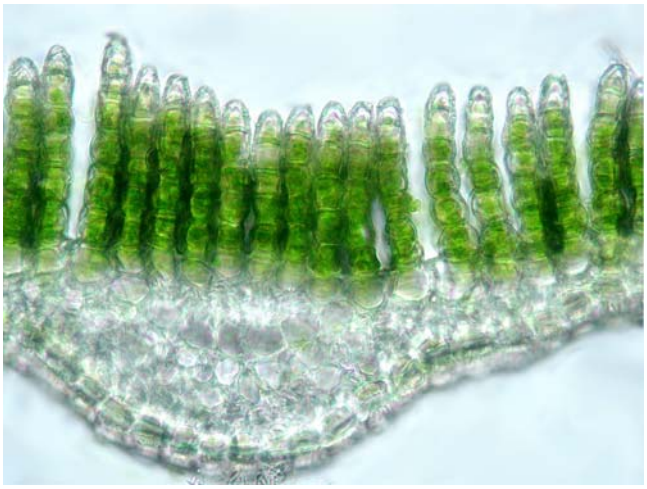

Figure 128. ***Polytrichastrum formosum*** leaf cross section showing lamellae. Photo by Michael Lüth, with permission.

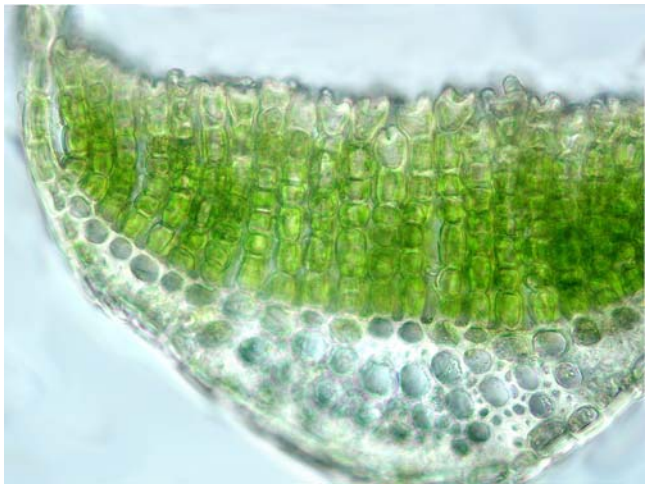

Figure 129. ***Polytrichum commune*** leaf cross section showing lamellae. Photo by Michael Lüth, with permission.

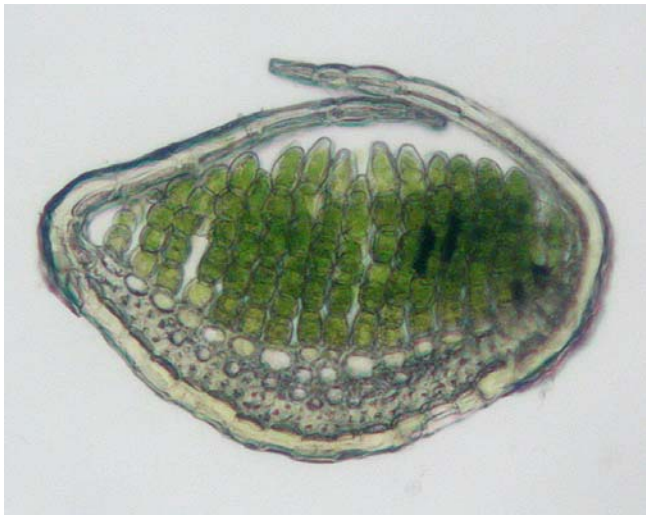

Figure 130. ***Polytrichum hyperboreum*** showing leaf lamina rolled over the lamellae. Photo by Michael Lüth, with permission.

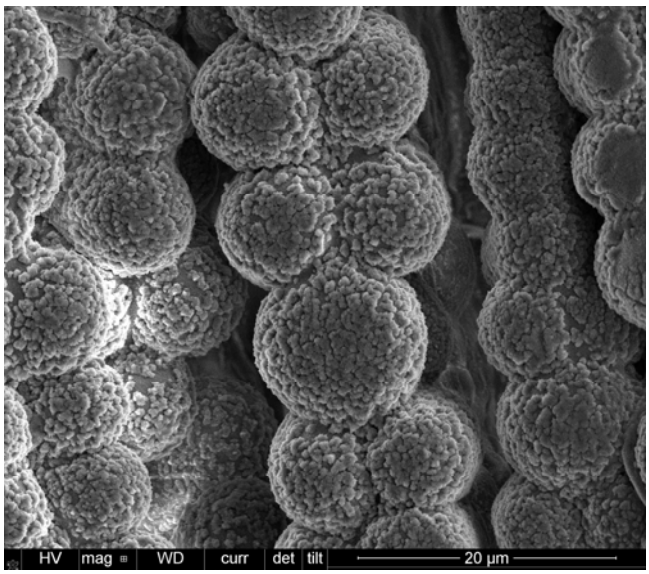

Figure 131. ***Dendroligotrichum squamosum*** SEM showing tops of lamellae. Photo courtesy of Jeff Duckett and Silvia Pressel.

Figure 132. ***Aloina rigida*** with lamellae within the inrolled leaf margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 133. ***Crossidium squamiferum*** showing leaves that appear to be succulent due to lamellae. Note how the leaf curves inward in this species. Photo by Jan-Peter Frahm, with permission.

Figure 134. ***Crossidium aberrans*** leaf showing lamellae along costa. Photo by Michael Lüth, with permission.

Figure 135. ***Pterygoneurum ovatum*** showing fleshy, inrolled leaves that partially cover the lamellae. Photo by Kristian Peters, with permission.

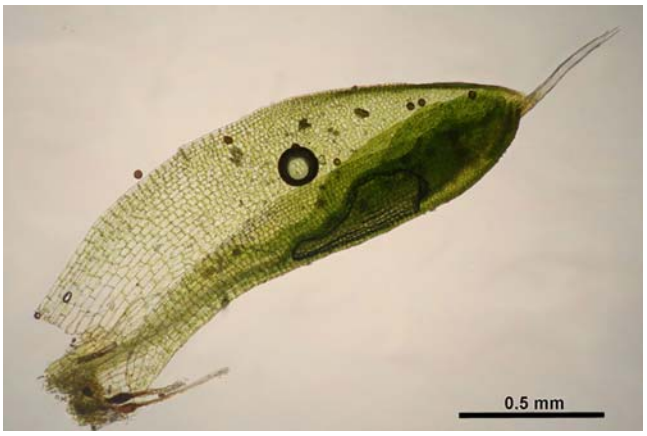

Figure 136. ***Pterygoneurum ovatum*** leaf showing lamellae in upper half. Photo by Hermann Schachner, through Creative Commons.

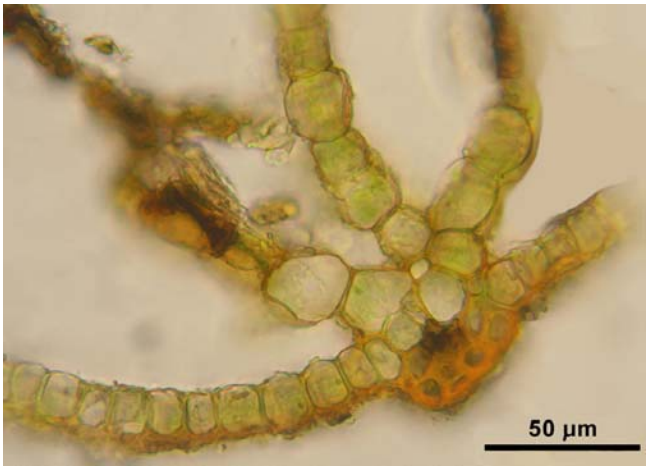

Figure 137. ***Pterygoneurum ovatum*** leaf cross section showing leaf lamellae. Photo by Hermann Schachner, through Creative Commons.

Figure 138. ***Syntrichia papillosa*** leaf showing tips of lamellae. Photo by Des Callaghan, with permission.

Kürschner (2004) suggests that the lamellae facilitate water conduction as well as storing water. These roles are in addition to their photosynthetic role. But this role seems to be incorrect. The surface of cells surrounded by water presents a barrier to CO_2 absorption (Budke 2010). Instead, the waxy cuticle repels the water. The lamellae in ***Polytrichum commune*** (Figure 129) increase the leaf surface area 2.4 fold (Thomas *et al*. 1996). Even the lamellae margins are coated with a waxy cuticle that restricts external capillary water. Thus they serve as photosynthetic tissue rich in chlorophyll.

Proctor (2005) demonstrated that the lamellae in **Polytrichaceae** (Figure 126-Figure 131) are important for the absorption of CO_2, increasing typical uptake by six times that of the projected leaf area, whereas in unistratose leaves of most other bryophytes, CO_2 uptake is limiting. This permits the **Polytrichaceae** to take advantage of high light intensity in open areas by increasing available absorptive surface area. In a number of these species, including some of ***Polytrichum*** (Figure 130), the leaf margins fold over the lamellae, affording protection from excess UV light, preserving moisture, and providing space for CO_2 exchange.

Air Chambers

Air Chambers are present in some of the thallose liverworts, such as species of ***Marchantia*** (Figure 139-Figure 142) (Ishizaki *et al*. 2013) and others (Figure 143-Figure 148). These facilitate the exchange of gasses within the thallus (Ishizaki *et al*. 2013). The small pores at the surface of the thallus in these chambered species permit the exchange of these gasses, providing an entry for CO_2 and exit of O_2.

Figure 139. ***Marchantia polymorpha***, a species with internal air chambers. Photo by Walter Obermayer, with permission.

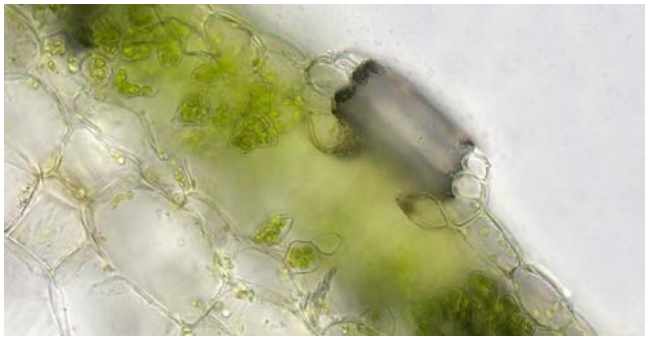

Figure 140. ***Marchantia polymorpha*** pore cs, above air chamber. Photo by Walter Obermayer, with permission.

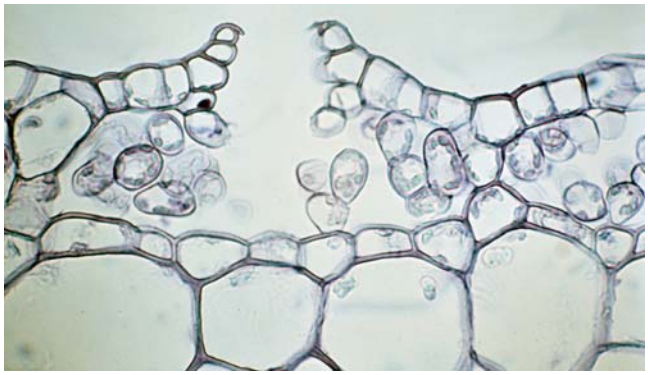

Figure 141. ***Marchantia polymorpha*** thallus cs showing pore and air chamber. Photo ©Wilhelm Barthlott, with permission.

Figure 142. ***Marchantia polymorpha*** pore opening showing surrounding ridge. Photo ©Wilhelm Barthlott, with permission.

Figure 143. ***Mannia androgyna***, in a genus with air chambers in the thallus. Photo by Michael Lüth, with permission.

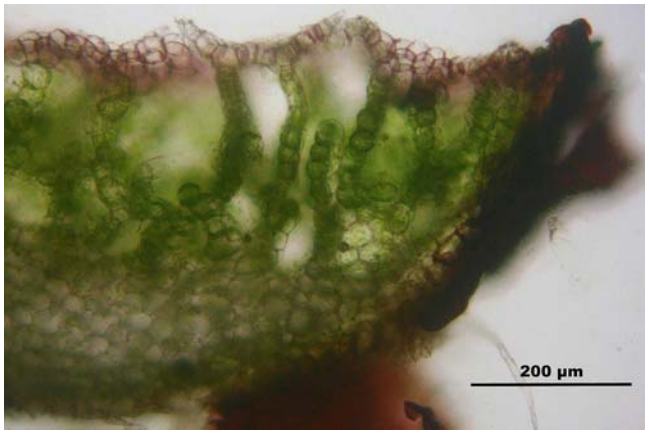

Figure 144. ***Mannia triandra*** thallus section showing air chambers. Photo by Hermann Schachner, through Creative Commons.

Figure 145. ***Conocephalum conicum*** showing pores on the surface and polygonal areas that mark the internal air chambers. Photo by Hermann Schachner, through Creative Commons.

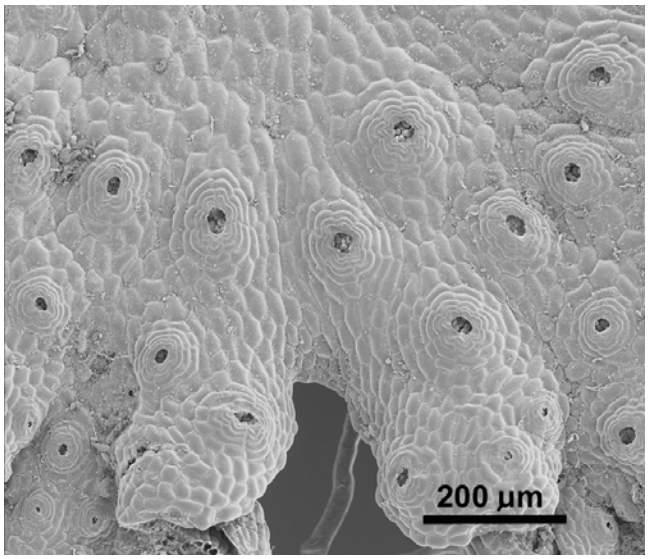

Figure 146. SEM of ***Conocephalum supradecompositum*** thallus with pores. Photo by Jeff Duckett & Silvia Pressel, with permission.

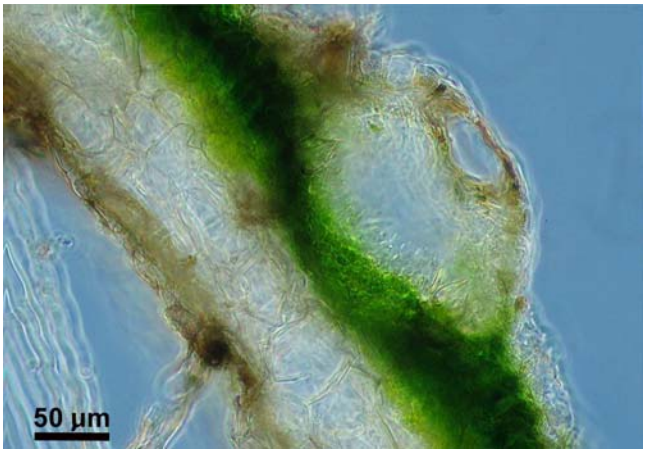

Figure 147. ***Conocephalum conicum*** pore section showing photosynthetic cells in the chamber beneath it. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

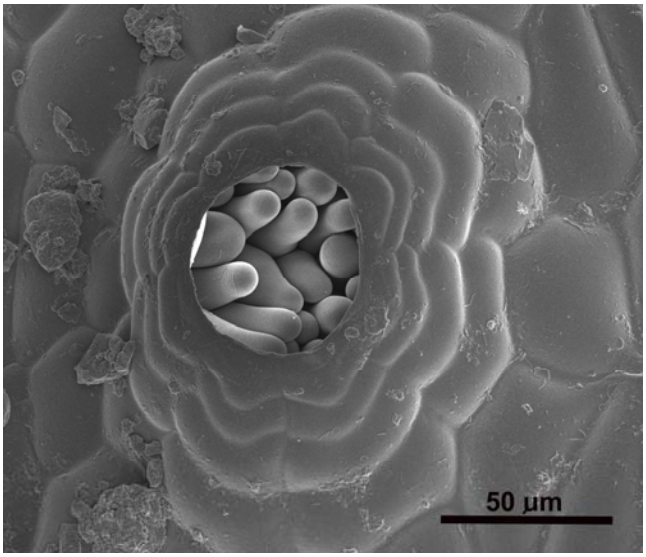

Figure 148. SEM of ***Conocephalum supradecompositum*** pore showing chambers and finger-like photosynthetic cells inside. Photo by Jeff Duckett and Silvia Pressel, with permission.

Keels

Most leaves are slightly concave, some are flat, and some are folded over, forming a **keel** (Figure 149). The most striking of these is the keel in several species of the aquatic moss ***Fontinalis***. The keel appears to give rigidity to the leaf, but when this species occurs in flowing water the keel often is abraded, leaving the leaf in nearly two pieces.

A modification of the keel occurs in the **Fissidentaceae** (Figure 150). This unique structure forms a pocket on the apical edge of the leaf into which the succeeding leaf can partially fit. The double area of each leaf adds rigidity and provides capillary space that presumably holds water for a longer time. When the leaves overlap into the pockets, they can help to make the entire plant more rigid.

Figure 149. ***Fontinalis antipyretica*** showing keeled leaves. Photo by Li Zhang, with permission.

Figure 150. ***Fissidens curvatus*** showing pockets with succeeding leaves fitting into them in some cases. Photo by Tom Thekathyil, with permission.

Leaf Plications

Some genera are characterized by leaf plications (Figure 151-Figure 153). These are typically folded like a Japanese fan. But what is the value of these plications? In tracheophytes, they can add strength. Consider lifting something with a sheet of paper. Then consider lifting the same thing with that same paper after it is fan folded. But is that kind of strength needed by a bryophyte leaf? Does it give a thin leaf a better ability to hold a drop of water?

Figure 151. ***Coscinodon cribrosus*** leaf with plications. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 152. ***Coscinodon cribrosus*** leaf cross section showing plications. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 153. ***Cratoneuron decipiens*** leaf with plications. Photo by Michael Lüth, with permission.

Leaf Cells

Cell shape varies considerably, from small isodiametric cells (Figure 107) to large, nearly hexagonal ones (Figure 154) to elongate ones (Figure 155). Some cells have wall invaginations or wavy walls (Figure 156). Little mention has been made of the advantages of various

cell types. One can imagine that elongate, narrow cells might move water more quickly with fewer walls to cross and formation of capillary space within the cell. I can't even imagine an advantage for the irregular wall shapes in ***Racomitrium*** (Figure 156). Bill Buck once asked me what I thought was the significance of the elongate cells in many pleurocarpous mosses. I couldn't give a good answer then, and now, several decades later, I still can't.

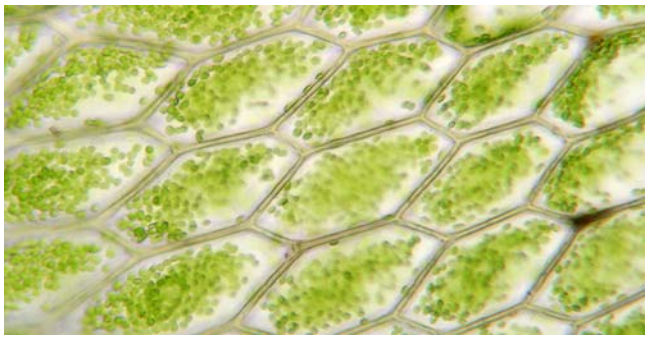

Figure 154. ***Hookeria lucens*** hexagonal leaf cells. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

Figure 155. ***Hygroamblystegium tenax*** showing elongate cells. Photo by Martha Cook, with permission.

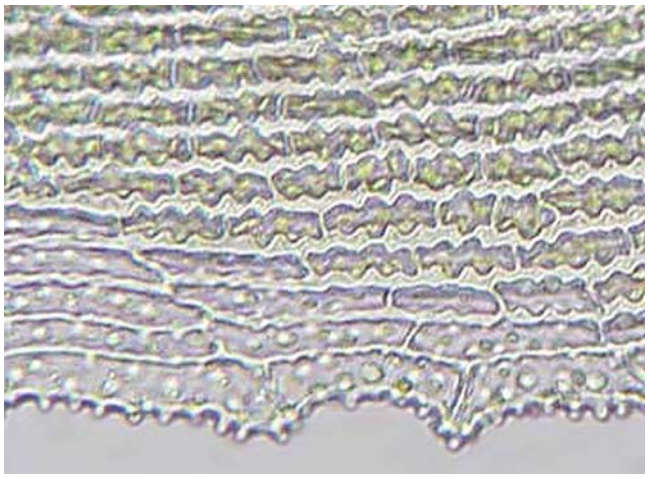

Figure 156. ***Racomitrium canescens*** cells showing wavy walls with invaginations. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

Papillae

Many theories have been proposed for papillae, but little is available as experimental evidence to support them. The papillae have a number of shapes and forms (Figure 157-Figure 159), while varying in size and density. Based on this variability, it seems to me that their functions may not be the same in all species or under all conditions.

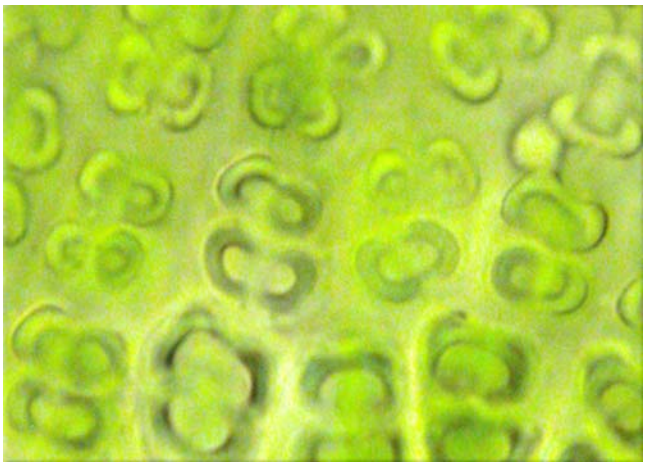

Figure 157. ***Tortula muralis*** leaf cells with C-shaped papillae. Photo by Walter Obermayer, with permission.

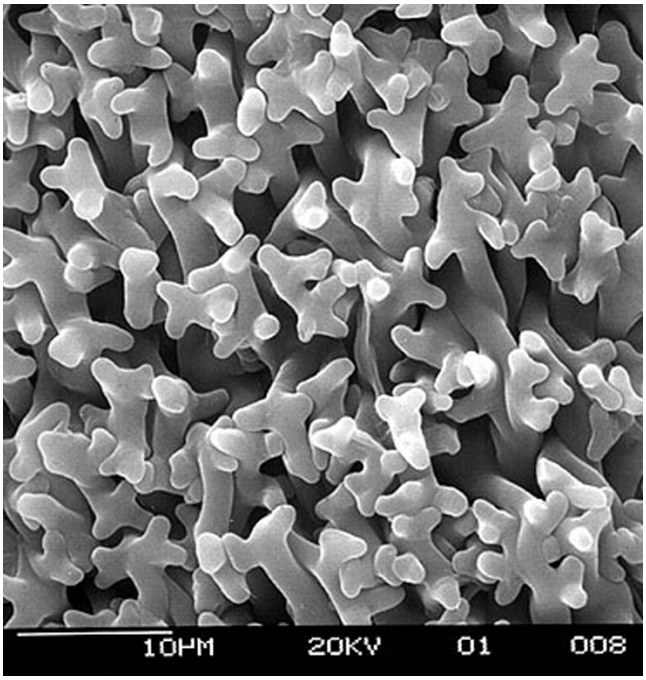

Figure 158. ***Tortula muralis*** SEM of branched papillae. It is easy to see how these papillae could scatter light and protect the chlorophyll during dry periods. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

Figure 159. ***Chrysoblastella chilensis*** leaf cross section showing papillae and capillary spaces between them. Photo by Juan Larrain, with permission.

When lamina papillae are dense, they give the leaf a waxy, often succulent look (Figure 160). The dull surface most likely does the same to the sunlight as it does to our eyes – it bends the light rays, preventing them from making straight entry into the leaf cells and thereby reducing damage to the chlorophyll when the leaf is dry. When the leaf is wet, the capillary spaces fill with water and the leaf surface behaves more like a uniform translucent surface (Figure 161). At least that is how some of us have interpreted the behavior. In experiments in my lab with papillose leaves under the microscope, we found that wet leaves transmitted about twice as much light as dry leaves, supporting that hypothesis.

Figure 160. ***Encalypta streptocarpa*** illustrating the waxy appearance when dry caused by numerous papillae. Photo by Michael Lüth, with permission.

Figure 161. ***Encalypta streptocarpa*** showing translucent appearance of the leaf when wet. Photo by Jan-Peter Frahm, with permission.

In some, perhaps all, the papillae facilitate water uptake by providing capillary spaces (Proctor 1979; Longton 1988; Pressel *et al*. 2010; see Chapter 7-4), but they can also facilitate water loss (Pressel *et al*. 2010). The uptake is usually accomplished by the small channels between the papillae, but in ***Andreaeobryum macrosporum*** (Figure 162), a small capillary channel goes through the papillae toward the cell and facilitates the rapid uptake of water during rehydration (Crandall-Stotler & Bozzola 1990, 1991).

Figure 162. ***Andreaeobryum macrosporum***, a moss for which papillae are known to aid in uptake of water. Photo from Botany website, University of British Columbia, Canada, with permission.

An Alternative to Papillae?

In the moss ***Rhacocarpus purpurascens***, the leaf cell wall has an unusual structure. The wall has three layers that Pressel *et al*. (2010) interpret as "a supreme adaptation to exposed habitats." This moss lives where there are frequent alternations between drought and heavy precipitation. We know that ***Sphagnum*** experiences water logging that prevents photosynthesis, and Pressel *et al*. reasoned that this special wall structure in ***R. purpurascens*** prevents water logging. Its outer cell wall layer is porous, ensuring rapid water uptake and retention. The hydrophobic cuticle-like layer simultaneously prevents water logging. The middle layer serves to extend the period of cell hydration, permitting active metabolism under drying conditions. The ***R. purpurascens*** cell wall

differs in function from cells with papillae in that papillae not only accelerate water uptake, but also accelerate water loss. Pressel *et al*. surmise that unlike the alternating conditions experienced by ***R. purpurascens***, constantly flowing aerated water or underhangs where water logging can depress gas exchange select for mosses that are protected from water logging by surface waxes – a condition seemingly quite different from that seen in tracheophytes.

Stomata

True stomata do not exist in the gametophytes of bryophytes. However, as in tracheophytes, they do occur in many sporophytes. These are well-documented in the sporophytes of hornworts, but are not universal in mosses. They seem to be absent in leafy liverwort capsules, but evidence of potential evolutionary precursors is present in capsules of the genus ***Haplomitrium*** (Figure 163-Figure 164) (Duckett & Pressel 2019).

Figure 163. ***Haplomitrium hookeri***, in a genus that exhibits precursors to stomata in the capsule. Photo by Janice Glime.

Figure 164. ***Haplomitrium hookeri*** with capsules. Photo by Norbert Schnyder, with permission.

Egunyomi (1982) reported sporophyte stomata in 29 tropical African moss species, distributed in 12 families. These mostly have round pores with two guard cells. Capsules he examined ranged in number of stomata from 2 to >200 (***Wijkia trichocoleoides*** - Figure 165). Some stomata are raised above the level of the capsule epidermis [***Wijkia trichocoleoides***, ***Trichosteleum microcalyx*** (Figure 166), ***Stereophyllum radiculosum*** (Figure 167-Figure 168), and ***Stereophyllum reclinatum***]. Others are sunken [***Brachymenium leptophyllum*** (Figure 169) and ***Bryum coronatum*** (Figure 170)]. He found interesting correlations between stomata number and seta length, and between stoma size and epidermal cell size.

Figure 165. ***Wijkia trichocoleoides***, a species with more than 200 stomata in its capsule. Photo by John C. Brinda, through Creative Commons.

Figure 166. ***Trichosteleum*** sp. with capsules, a species with stomata raised above the capsule epidermis. Photo by Jan-Peter Frahm, with permission.

Figure 167. ***Stereophyllum radiculosum*** leaves, a species with stomata raised above the capsule epidermis. Photo by Juan David Parra, through Creative Commons.

Figure 168. ***Stereophyllum radiculosum*** capsule with raised stomata creating visible bumps in the lower part of the capsule. Photo by Juan David Parra, through Creative Commons.

Figure 169. ***Brachymenium leptophyllum*** with capsules that have sunken stomata. Photo from Earth.com, with permission.

Figure 170. ***Bryum coronatum*** with capsules that have sunken stomata. Photo by Aruna Balasubrahmanya , through Creative Commons.

Their function, however, seems to differ from that of tracheophyte stomata, playing a role in dispersal by permitting the capsule to dehydrate and contract. Their function has been the subject of recent research and will be updated soon.

Fluorescence

Fluorescence is seldom mentioned in bryophyte studies. I can remember the excitement of Gisela Nordhorn-Richter when she relayed to me the use of a fluorescent microscope to see propagula in ***Pohlia***. It became a great tool for detecting these often obscure structures with UV light.

Following her enthusiasm, I had the opportunity to examine ***Fontinalis antipyretica*** with a fluorescent microscope and was surprised to find beautiful yellow cell walls and glowing red chloroplasts (Figure 171) – well, the chloroplasts didn't really surprise me, but they certainly made a beautiful image.

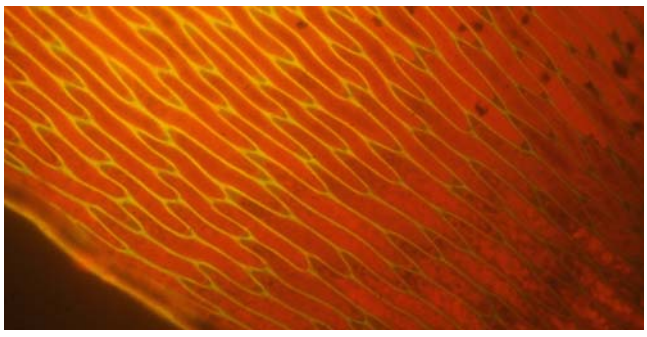

Figure 171. ***Fontinalis antipyretica*** wall fluorescence. Photo by Janice Glime.

Kroken *et al*. (1996) found that both charophytes and bryophytes have fluorescent cell walls. They suggested that the bryophytes inherited this fluorescence ability from the charophytes, citing evidence from time of production and location. A number of charophytes produce these resistant cell walls in response to desiccation stress. Furthermore, ***Coleochaete*** (Figure 172) is the only charophyte known to produce fluorescent tissues at the placental junction in hydrated tissues, induced by sexual reproduction. However, this characteristic is true of all bryophytes tested. Furthermore, in ***Sphagnum***, the maternal tissue in the apical portion of the **pseudopodium** (Figure 173) has fluorescent compounds similar to those in ***Coleochaete*** zygotes. Other known sites of autofluorescence in bryophytes include the sporangial epidermis, spiral thickenings of elaters, rhizoids, and leaves. Kroken and coworkers suggested that this fluorescence represents repeated exaptation. The regulation of deposition has been modified through time, "resulting in a sequence of functions: desiccation resistance and/or microbial resistance in lower charophytes, a role in embryogenesis in ***Coleochaete*** and embryophytes, and finally, decay resistance in innovative structures that characterize bryophytes, such as rhizoids, sporangial epidermis, and elaters.

Fluorescence is discussed in more detail in Chapter 9-5 of this volume.

Figure 172. ***Coleochaete***, the only alga known to produce fluorescent tissues at the placental junction. Photo by Yuuji Tsukii, with permission.

Figure 173. ***Sphagnum*** with capsule, showing the upper portion of the pseudopodium where fluorescent compounds are produced (**arrow**). Photo by Vita Plasek, with permission.

Thallus

Liverworts are of two types – thalloid and leafy. The thallus brings its own set of adaptations, with its thickness making possibilities that are not available to the leafy taxa with their one-cell-thick leaves. Among the **xerophytic** (of dry habitats) adaptations are the ability to roll up, shrivel, or fold the thalli, exposing the normally ventral side where red pigments (**anthocyanin**) or hyaline ventral scales (Figure 174-Figure 175) serve to protect the photosynthetic tissue from damage due to exposure to sunlight while dry (Kürschner 2004). The hyaline scales such as those in many ***Mannia*** (Figure 174-Figure 175), ***Riccia*** (Figure 176), and ***Oxymitra*** (Figure 177) species undoubtedly serve to reduce desiccation and provide capillary spaces to facilitate water uptake upon wetting.

Figure 174. ***Mannia androgyna*** in hydrated condition with reddish edges that characterize the color of anthocyanins on the ventral side. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

Figure 175. ***Mannia fragrans*** showing curling of the drying thallus; hyaline ventral scales and reddish under surface will soon protect the photosynthetic tissue. Photo by Michael Lüth, with permission.

Figure 176. ***Riccia trichocarpa*** showing hairs that can reduce water loss and protect the photosynthetic tissue from damage by UV rays. Photo by Jonathan Sleath, with permission.

Figure 177. ***Oxymitra incrassata*** showing marginal scales. Photo by Chris Cargill, with permission.

The raised cells of the epidermis and the chimney-like hyaline air chambers of some species in ***Exormotheca*** (Figure 178) may likewise serve as protection from solar radiation and protection from desiccation. Thalli of some species have "windows" (**Fensterthallus**), for example the chimney-like, hyaline air-chambers of ***Exormotheca*** (Figure 178-Figure 179), like those in the flowering plant family Aizoaceae (for example *Lithops*). These windows provide a covering that helps to reduce the light intensities that reach the photosynthetic layer (Kürschner 2004). The liverwort thallus is thick and nearly semi-circular in cross section. Internally, it has dense assimilatory columns in its air chambers. The column thickness in the liverworts frequently correlates with the degree of insolation.

Figure 178. ***Exormotheca welwitschii*** in southern Portugal, showing "windows" in the thalli. Photo by Michael Lüth, with permission.

Figure 179. ***Exormotheca*** sp. thallus showing columnar cells that form the windows to the photosynthetic tissue of the thallus. Photo © Wilhelm Barthlott <lotus-salvinia.de>, with permission.

Liverworts such as ***Plagiochasma rupestre*** (Figure 180) have hydrophobic wax globules on the thallus surface, making them unwettable. Such waxes keep xerophytic members of the **Marchantiales** from taking up water through the thallus surface, using their pegged rhizoids instead.

Figure 180. ***Plagiochasma rupestre***, a thallose liverwort with hydrophobic wax on its surface. Photo by Jan-Peter Frahm, with permission.

Thallus pores could serve as a site of water entry, but a ring of wax around the inner margin of the pore in species like ***Marchantia polymorpha*** (Figure 139-Figure 142, Figure 181) serves both to repel water and to make the

opening smaller, making it difficult for cohesive water droplets to enter the air chambers of the thallus. Many thalloid species have hydrophobic cuticular ledges around these pores (Ziegler 1987). These waxes protect the air chambers from becoming water-logged (Schonherr & Ziegler 1975; Kürschner 2004).

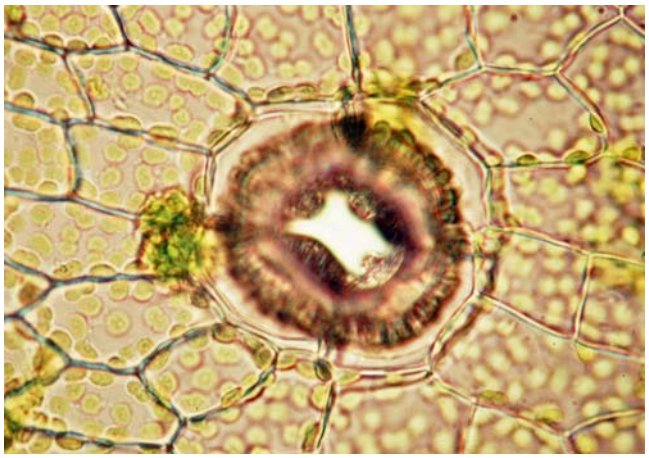

Figure 181. ***Marchantia polymorpha*** thallus pore opening with ridge that is heavily endowed with wax. Photo © Wilhelm Barthlott, with permission.

Once inside the thallus, we must look for adaptations to obtain sufficient CO_2 and to maintain moisture. For the thallose liverworts this problem seems to be solved in a manner similar to that of most flowering plants – a ventilated photosynthetic tissue that has stacks of cells one cell wide interspersed within air chambers (Figure 140-Figure 142) (Proctor 2010). See **Air Chambers** above

Pigmentation

In physiological studies on animals, it is clear that environmentally induced variation is often adaptive. More arachidonic acid makes membranes more pliable. Non-nucleating proteins prevent ice crystallization. Changes from glucose to glycogen prepare an animal for dormancy. Even physical changes, such as color of fur or feathers, can prepare an animal for a change in seasons. Development of red pigment in ***Sphagnum*** (Figure 182) and ***Fontinalis*** (Figure 183-Figure 184) may protect the chlorophyll from high light intensity.

Figure 182. ***Sphagnum*** showing the red colors that develop in some species when they grow in the sun. Photo by Janice Glime.

Figure 183. ***Fontinalis antipyretica*** with red pigments responding to cold spring water and full sun. Photo by Janice Glime.

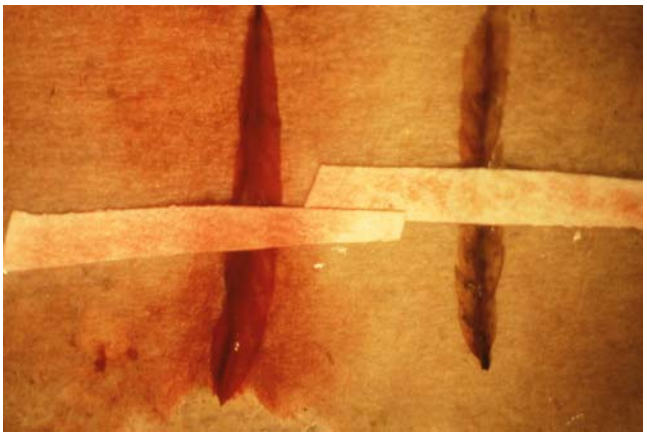

Figure 184. ***Fontinalis antipyretica*** with red pigments, responding to being out of water, but moist, in bright light. Photo by Janice Glime.

Red pigments in high elevations and alpine regions might serve dual purposes. The red color can protect the chlorophyll and DNA from UV damage, but it could also cause the mosses to absorb heat in their cool climate. The images of ***Grimmia elongata*** (Figure 185-Figure 186) illustrate the green and red color expressions in this species.

Figure 185. ***Grimmia elongata*** showing its green form. Photo by Michael Lüth, with permission.

Figure 186. ***Grimmia elongata*** in Norway, exhibiting its red pigments in the high UV light of the high elevation. Photo by Michael Lüth, with permission.

Some pigmentation may just come along for the ride. For example, phenolic compounds are typically colored, but their primary function can be support or antiherbivory. Such support functions are most likely for structures like the costa (Figure 187) or stem rigidity (Figure 188), but they also occur in many leaf borders (Figure 68).

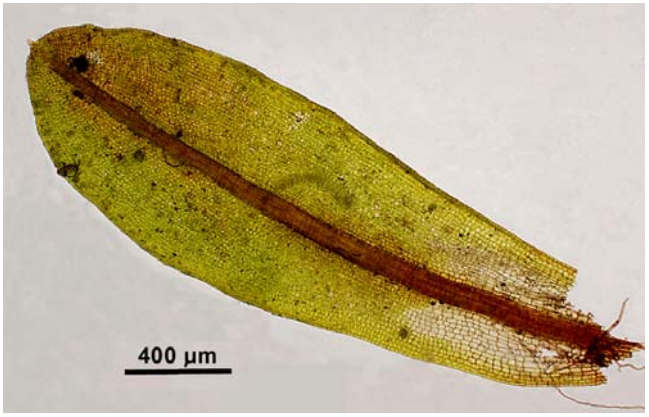

Figure 187. ***Syntrichia inermis*** leaf showing dark color in costa. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

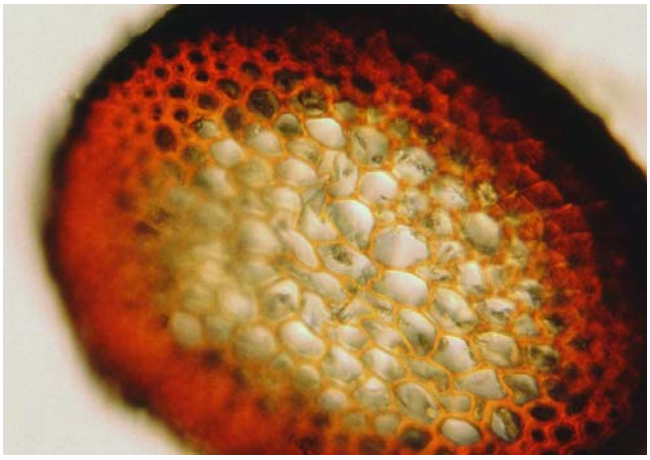

Figure 188. ***Fontinalis dalecarlica*** stem section showing dense coloration in the cell walls. Photo by Janice Glime.

Seta Colors

David Long (Bryonet 24 March 2023) asked why some moss setae are red. Questions like this bring out some of the lurkers because there is no known right answer. In fact, Jack Sharp used to respond to such questions with the admonishment that not al things are adaptive – they simply must not be maladaptive to persist.

This question can be divided into two parts: what biochemistry makes it red, and does it have an adaptive persistence.

Let's first examine possible adaptive significance. Here are my potential hypotheses:

1. In species like *Ceratodon purpureus* where the capsule is likewise red-purple, the pigmentation pathway starts early in development of the sporophyte.
2. Red is a warning color to animals, so the red color could deter herbivory.
3. Red absorbs heat, thus warming the developing sporophyte if that occurs in spring or autumn, possibly speeding up development.
4. Red protects against UV damage and could therefore be helpful in preventing damage to young sporohyte tissues.
5. Lignin-like compounds might provide structural support, and these can be red in color.

Gender

Zander (Bryonet 8 May 2012) suggested that the presence of only males in a population would have the adaptive advantage of conserving photosynthate by the lack of necessity for producing sporophytes. Thus dioicy in dry habitats might be an adaptation to conserve photosynthate. But Stark has reported that in many desert populations the males are absent. Nevertheless, this principle would operate whether the population was male or female. On the other hand, monoicy provides advantages in a moist or otherwise less stressful habitat where there is sufficient energy for producing sporophytes.

Adaptive value of gender expression was discussed in detail in Chapters 3 and will not be discussed further here.

Wound Response

If you are a plant, what you do when you get damaged may have important effects on the future of your species. And if you live in fast-flowing water (Figure 189), that damage is a certainty. Some species are adapted to take advantage of the wounds; others merely protect themselves; some (perhaps most bryophytes) do both. The advantage for bryophytes – a means for dispersing and making new colonies.

We have limited understanding of the means of protection. One study on the biochemical response is that for ***Marchantia polymorpha***. When wounded, ***Marchantia polymorpha*** (Figure 190) produces highly volatile 8-carbon compounds including (R)-1-octen-3-ol and octan-3-one (Kihara *et al*. 2014). These emissions occurred within 40 minutes of the wounding. The importance of arachidonic acid and/or eicosapentaenoic acid was demonstrated by the weak or absent response of the volatiles. In completely disrupted thalli, only minimal amounts of octan-3-one were produced, whereas the greatest amounts were produced in

partially disrupted thalli, compared to undisturbed thalli. This suggests signalling from the disrupted cells that initiates the production of octan-3-one in the undisturbed cells.

Figure 189. ***Cinclidotus danubicus*** habitat, illustrating the power of the water. Damage to leaves can be significant during high-water events. Photo by Michael Lüth, with permission.

Figure 190. ***Marchantia polymorpha*** with an isopod – a potential herbivore. Herbivory and other wounds can stimulate production of highly volatile compounds in this liverwort. Photo by Walter Obermayer, with permission.

Croisier *et al*. (2010) found a variety of responses in the bryophytes they surveyed. Instead of the predominant C8 volatiles, they found a variety of C5, C6, C8, and C9 volatiles in 23 mosses tested. These are **oxylipins** – metabolites derived from oxidative fragmentation of polyunsaturated fatty acids. Both C18 and C20 fatty acids serve as the precursors for the volatile oxylipins that respond to mechanical wounding of mosses. These oxylipins are important hormonal regulators and defense compounds in plants. In liverworts and hornworts, oxylipin production was less pronounced than in the mosses.

This still leaves us with the ecological question of how these volatiles protect the species. Do they deter herbivores, as do many volatiles in tracheophytes? The ***Marchantia*** story suggests they are inducible. Do they protect against fungal and attack? (Fungal attack will be covered later in a chapter on fungal interactions.) Do they play any role in dedifferentiation and regrowth? Do they stimulate the production of rhizoids or protonemata often seen at wound sites? This would seem to be a fertile area of research for understanding hormonal interaction and control of development in bryophytes.

Summary

Bryophytes have a simple structure. That does not mean they have not advanced morphologically. Their stems may have conducting cells, have various phenolic compounds in the cell walls, or be covered with paraphyllia, rhizoids, or tomentum. The leaves may have borders, marginal teeth, lobes, hair tips, costae, lamellae, or keels. The leaf cells may be short and nearly isodiametric (often with thick walls), larger hexagonal cells with thin walls, or elongate narrow cells. These cells may have waxes, papillae, or be swollen. These structures seem to be adaptations to habitats ranging from aquatic to desert.

Aquatic bryophytes that do not spend much time out of water generally lack papillae, have elongate narrow cells, and lack conducting cells in the stems. They may have strong stems with colored cells walls from phenolic compounds, protecting them against moving water and suspended solids. At the other extreme, xerophytic bryophytes are often papillate, have thicker waxes, are reduced in size, and have mechanisms of curling up while dry and expanding when wet. Specialized cell walls, lamellae, and marginal teeth may provide mechanisms to increase photosynthesis while preventing water logging. Hair tips can scatter high light, absorb water, or reduce drying. Pigments can protect bryophytes from high light intensities, especially when low temperatures slow photosynthesis or the plant is dormant due to high temperatures.

Leafy liverworts may be able to hold water droplets with their lobes and teeth. These structures could also serve to deter herbivores. The thallus can have windows to direct light and protect the photosynthetic cells, be protected by waxes and scales, have thallus pores that open and close, permitting gas exchange while preventing internal water logging.

These adaptive value of bryophyte structures are largely speculation, hypotheses waiting to be tested.

Acknowledgments

This chapter is largely the product of discussions with other bryologists, especially on Bryonet. Thank you to Louis Anderson for his constant reminders that things do not always have an adaptive function. My appreciation always goes to the many people who have given me permission to use their images, including those who make them available online through Creative Commons. And thank you to Bryonetters who contributed to the discussion on seta colors.

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CHAPTER 5-1
ECOPHYSIOLOGY OF DEVELOPMENT: HORMONES

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CHAPTER 5-1
ECOPHYSIOLOGY OF DEVELOPMENT: HORMONES

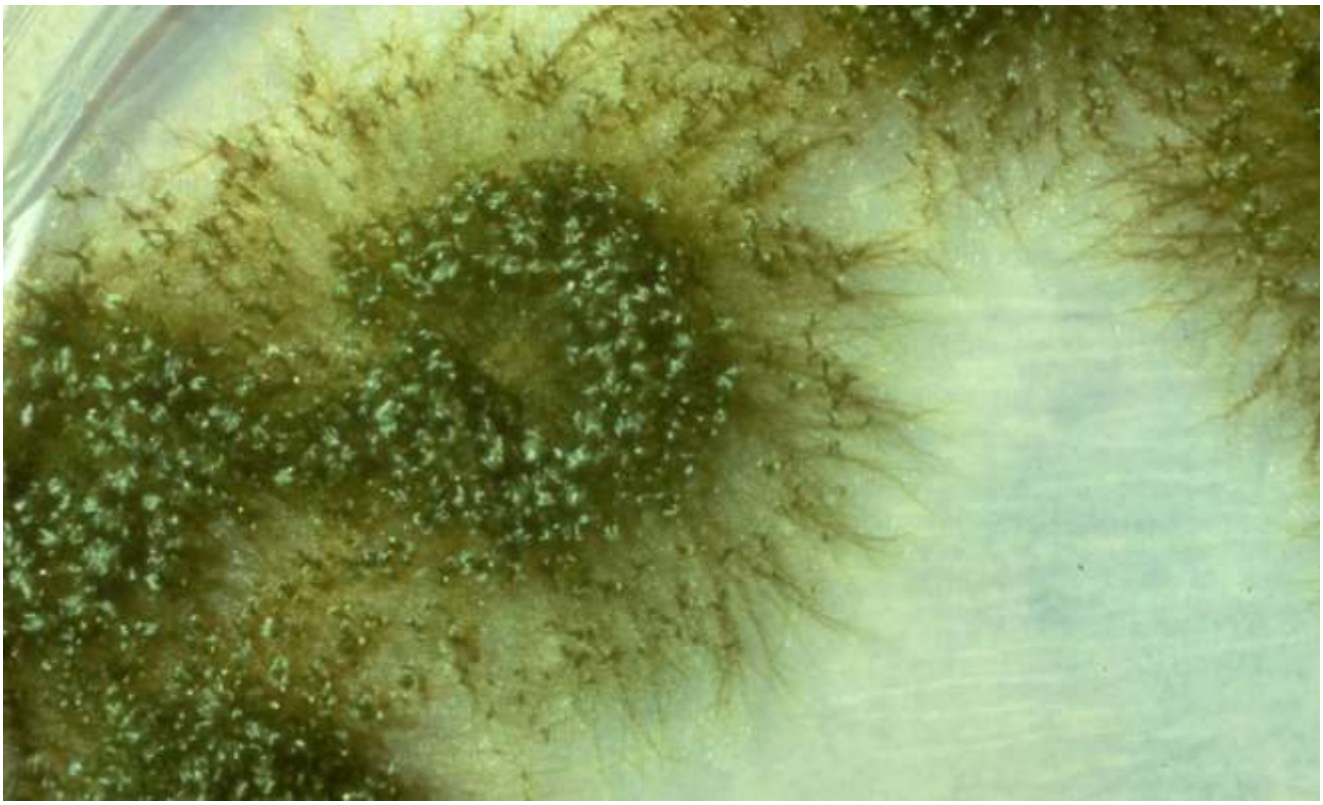

Figure 1. ***Funaria hygrometrica*** demonstrating the doughnut-shaped growth typical of cultures. Photo by Janice Glime.

Introduction

Although the field of development usually attracts scientists with very different interests from those of the ecologist, the two fields nevertheless have important overlaps that define the niche of the organism. It is the development and life cycle that permit the organism to time its life so that it can survive, from having water to grow, to dispersing its sperm and spores, to being dormant when the going is rough. Thus, it is appropriate for the ecologist to have some rudimentary understanding of the environmental controls on the physiological aspects of development and to understand the sorts of responses that might occur.

Bryophytes are limited in their occupancy of the world by a lack of lignin. This compound, providing strength and structure for the mighty sequoia, permits tracheophytes to attain heights unimaginable for the unlignified bryophyte. Height for most mosses standing alone is but a few centimeters, achieving greater heights when supported by their neighbors, the power of the clone! Yet some mosses, like ***Dawsonia*** (Figure 2), achieve heights exceeding 2 dm, with enough strength to maintain it alone.

Figure 2. ***Dawsonia superba***, the tallest stand-alone moss. Photo by Janice Glime.

In some cases, lignin-like compounds may add strength to the cellulose walls of the cells. But perhaps a new discovery may help in understanding how bryophytes maintain their strength. **Extensins**, previously known from tracheophytes, have just been found in mosses for the first time, in what else – ***Physcomitrella patens*** (Figure 3; Schipper *et al*. 2002). These glycoproteins, rich with hydroxyproline, comprise about 5-10% of the dry weight of most primary cell walls and serve to strengthen the walls (Taiz & Zieger 1991). Taiz and Zieger (1991) claim that tracheophyte fibers with a tensile strength similar to that of steel wire may gain their strength from the combination of both lignin and extensin. The importance of extensin to bryophyte strength remains to be demonstrated.

Figure 3. ***Physcomitrella patens*** in its natural habitat. Photo by Michael Lüth, with permission.

Bryophytes, with a very thin cuticle, if any, and leaves only one cell thick, easily lose water. Yet, there are about 15,000 species, more than any other group of plants besides flowering plants. How is it that they are able to survive in such harsh environments where they might completely dry out for months at a time? How do they live in places that **never** get any rainfall?

Then there is the problem of sexual reproduction, of transferring gametes from a male organ to a female organ when the male gamete, the sperm, requires water in order to swim! It seems that one of the best solutions was to produce gametes only when water was available, but that requires developing the gametangia well in advance of the fertilization event in order to be ready on time. Something has to trigger the plants to stop using all their energy for growth and put some of it into making gametangia. A method of receiving and responding to environmental signals was necessary.

Finally, these plants needed ways to get to new homes when theirs were being destroyed, whether by erosion, fire, or other unpredictable events. They needed reproductive structures that could travel in a medium of air and survive without water for a long period of time. Hence, they needed spores that did not swim and these needed a thick cover to prevent total desiccation.

All of these events had to be carefully controlled, timed to take advantage of seasons when water was available for fertilization and when dry air was available for spore dispersal. These "primitive" bryophytes have been successful at organizing their morphology, their biochemistry, and their life cycles in a way best suited to their individual environments.

For these organisms to complete their life cycles, a coordinated set of developmental stages and environmental signals must exist. If this coordination is lacking, the plant may find itself in a life cycle stage that has requirements the environment is unable to supply. Unlike animals, the plant cannot move to a new habitat when the going gets rough. When the spore lands and germinates, a bryophyte must be able to develop its protonema, produce a leafy gametophore, develop archegonia and antheridia, achieve fertilization, develop a sporophyte with a capsule, and disperse its spores without changing its location.

As we have studied the taxonomy of bryophytes during the last two centuries, numerous examples of life cycle adaptations have become apparent through our descriptions of the genera and species that grow in a variety of habitats. It is obvious that many strategies exist, from the **neotenous** (having juvenile traits retained in adults) habit of ***Buxbaumia*** (Figure 4) to produce sporophytes without developing an upright gametophyte, to the highly developed gametophyte of ***Fissidens obscurus***, where sporophytes are generally unknown. Some mosses readily form gametophores on nutrient-poor soil, such as the pioneer ***Funaria hygrometrica*** (Figure 1), whereas others such as ***Pylaisiella*** (Figure 25) seem to benefit from products of associated organisms (Spiess *et al*. 1971, 1972). Some rely predominantly on spores for dispersal, whereas others depend on abundant gemmae. Control of these life cycle differences depends on a complex evolutionary interaction with the environment to select the strategy that bests adapts the bryophyte to its particular set of circumstances.

Figure 4. ***Buxbaumia aphylla***, demonstrating the neotenous development of reproductive structures and ultimately a sporophyte without the development of a leafy gametophyte. Photo by Janice Glime.

While our understanding of development has been progressing since the early descriptive work of Goebel (1930) and Lorch (1931), so has our understanding of moss ecology. During (1979) began to bridge the fields of development and ecology by his presentation of life cycle strategies. He has suggested that the ability to occupy a habitat is dependent upon life span, type of reproduction, time required for maturity, spore size, spore longevity, and growth form. Based on the review presented by Bopp (1981) and knowledge of the importance of growth hormones in regulating development in higher plants, it is

possible now for us to consider the role of hormones during all stages of the life cycle. Reviews on developmental physiology by Bopp (1981), on biochemical constituents by Suire and Asakawa (1981), and recently the review on control of development by Christianson (2000a) begin to make it possible to evaluate environmental signals as they relate to known physiological responses that determine development.

Developmental Adjustments

Like some of the insects that can adjust their life cycle mid course, changing their developmental rates, at least some bryophytes likewise adjust their developmental periods based on seasonal and temperature effects. For example, ***Fontinalis squamosa*** (Figure 5) cultured in early May at 14º and 20°C required 18 days to germinate from tiny (10 µm), early season green spores. Capsules collected at the same time and stored at 10°C until late May provided spores that were larger (25 µm) and germinated under the same conditions in as few as 5 days (Glime & Knoop 1986). Capsules stored at 3°C until late May provided spores that generally failed to germinate, and those that did required a minimum of 15 days, failing to develop further.

In this case, spores shed prematurely apparently developed externally and took longer to germinate. Such adjustments suggest that under natural conditions at different latitudes the moss would have different responses, with the ones at colder temperatures being able to germinate more quickly when the critical temperature was reached, but at very cold temperatures, germination would generally not occur, thus protecting the protonema from potential freezing.

Figure 5. ***Fontinalis squamosa*** spore germinating. Photo by Janice Glime.

In a latitudinal study on ***Meesia triquetra*** (Figure 6), Montagnes and Vitt (1991) found that morphology varied in a linear way with latitude, with variances in characters decreasing with increasing latitude. Among the characters that decreased were annual growth increment, number of leaves produced each year, and leaf length. As leaf length decreased, leaf width increased with increasing latitude, and the tip was less acute, making a shorter, broader, more ovate leaf. However, unlike the insect larvae that are able to adjust their life cycles "on the fly," these morphological changes persisted in a **common garden** (where different populations are grown together with the same conditions), therefore suggesting that they are genetically controlled (Montagnes 1990) and most likely a product of natural selection.

Figure 6. ***Meesia triquetra***. Photo by Michael Lüth, with permission.

Polytrichum strictum (Figure 7) (Longton 1974) likewise had decreased leaf length as it grew farther north, and as expected, less annual growth in length and weight, and fewer leaves per annual growth increment (Figure 8). These factors seemed to be under both external and genetic control.

Figure 7. ***Polytrichum strictum*** from the temperate zone. Photo by Jan-Peter Frahm, with permission.

Figure 8. ***Polytrichum strictum*** from Alaska, USA, showing shorter plants and smaller leaves. Photo by Andres Baron Lopez, with permission.

Hylocomium splendens (Figure 9) varies so much that subspecies and varieties have been named. On the west coast of Canada, it grows in **wefts** (loosely interwoven, often ascending growth form), earning it the subspecies designation ***giganteum***, and has the typical stair-step frond (Figure 10; Montagnes & Vitt 1991). North of the tree line, where it is designated var. ***obtusifolia***, it lacks the stair-step character. The variety ***splendens*** is intermediate to these two taxa.

Figure 9. ***Hylocomium splendens*** in its typical weft form. Photo by Michael Lüth, with permission.

Figure 10. ***Hylocomium splendens*** showing stair-step growth form typical of the north temperate and boreal region. Photo by Janice Glime.

In summary, as demonstrated in ***Meesia***, ***Polytrichum***, and ***Hylocomium***, increasing latitudes can select for mosses with **shorter leaves**, cause **reduced annual growth**, **reduce** the **number of leaves** produced per year, and **change growth form** and **branching patterns**. These differences can be under environmental or genetic control, or both.

Life Cycle Importance

Bryophyte life cycles have stimulated the curiosity of botanists for centuries. Their simple representation of two clearly visible generations makes them choice organisms for introducing the concept of a life cycle to students. Because of their ease of expressing genetic effects, bryophytes have provided the laboratory material for pioneering breakthrough research in several areas of genetics and molecular biology, permitting us to understand not only bryophyte development, but paving the way for understanding tracheophyte development as well (Reski 1998; Schumaker & Dietrich 1998; Christianson 2000b). The first sex (X & Y) chromosomes were found in bryophytes, in ***Sphaerocarpos*** (Figure 11). The continuity of chromosomes during mitosis was elucidated in bryophytes. Discovery of non-Mendelian inheritance was first found in bryophytes. Furthermore, the haploid generation permits us to isolate gene mutations in order to determine their developmental roles.

Figure 11. ***Sphaerocarpos michelii***. Photo by Michael Lüth, with permission.

The moss ***Physcomitrella patens*** (Figure 3) has become the experimental rival of *Arabidopsis*, *Nicotiana*, and *Brassica*. Its most recent advantage is in **reverse genetics** (genotype-driven technique in which genes are either knocked out or added to see the effect on phenotypic expression), enabling geneticists and physiologists to understand gene function by targetting specific genes. Because the moss is haploid, it is much easier to isolate a mutant gene and determine its function. As this new information becomes available, understanding the role of the environment in regulating gene function, and ultimately in influencing development, will become much clearer.

We should expect a variety of geographic differences in the life cycle as well as differences influenced by the weather in a given year in one location. To understand and predict these differences, we must first understand the developmental ecophysiology. This requires that we understand the functions of hormones.

Growth Regulators

Hormones, or growth regulators, were originally defined for animals as substances that are produced in one part of the organism and move to another where they carry out their action, in very small quantities. This definition works less well for plants, wherein ethylene always and others sometimes are produced in their final step at the site of action. But plant hormones differ from those of animals in other major ways as well. They have a much wider array of actions than the limited action ability of most animal hormones (Christianson 2000a). (Or do those animal folks just not understand their hormones as well as the botanists understand theirs?) Rather, in plants the hormones usually act in combinations that present a wide array of possible outcomes. In plants, as in animals, every aspect of development involves hormones.

If hormones are within the organism, why should an ecologist even care to understand their nature and action? Hormones are often leaked into the environment by other

organisms and those external sources may even be necessary to the development of the plants. Plants both excrete hormones and are affected by external hormones (Beutelmann & Bauer 1977). Bryophytes are no exception to these external regulators. This makes the role of the environment of far more importance than for most animal hormone functions (human contributions not withstanding). While the number of hormones known in plants is small (Table 1), the importance of external hormones is poorly known, especially in bryophytes.

Consider for a moment what the bryophytes have been doing for their 400-million-year history. Limited in structure by their lack of lignin, they were not limited in any discernible way regarding their biochemical evolution. This has afforded them three times as long to perfect their development and biochemical adaptations compared to the Magnoliophyta (flowering plants) (Christianson 2000a). In fact, the very absence of large morphological adaptations has increased the selection pressures for cellular level biochemical ones (Christianson 2000a). Here we will examine what we do know about the hormones found in bryophytes.

Auxins

Auxins have long been known as plant growth hormones, and were conclusively demonstrated in bryophytes in 1985 (Law *et al*. 1985), but their mode of action is still not clearly understood. They are amino-acid based hormones, and through studies with Venus flytrap (*Dionaea muscipula*), we have discovered that they have a role in cell extension. This extension seems to be mediated by an efflux of H^+ that accumulates between the cells, breakage of the calcium pectate bonds that glue cell walls together, and appearance of Ca^{++} inside the cells in the area of rapid growth. Concomitant with these events, the auxin **IAA** (indole-3-acetic acid) increases in the region of growth (in this case, the lower side of the midrib). Using the moss ***Funaria hygrometrica*** (Figure 12*)*, Kapoor and Bhatla (1998) suggest that the influx of Ca^{++} to the cells may be induced by the IAA, although in this case it is in callose (complex, branched polysaccharide) synthesis that precedes the differentiation of chloronema (youngest part of protonema) to caulonema (part of protonema giving rise to leafy plants). IAA has a known role in this chloronema to caulonema transformation (Decker *et al*2006).

Table 1. Classes of growth regulators affecting bryophytes, their known presence in mosses and liverworts, and their known functions in that group.

Class	Specific Regulator	Presence	Function
auxins	IAA	mosses, liverworts	membrane transport (esp. Ca), cell elongation, protonema differentiation, stem elongation (promote at low, inhibit at high), rhizoid initiation, seta elongation, tropisms, apical dominance
cytokinins	zeatin	mosses	cell division, aging, bud initiation, archegonium initiation, gametophore production
	isopentenyladenine	mosses	
	Factor H?	mosses	inhibition of caulonema growth, bud initiation, gemma formation
	analogs	mosses, liverworts	promote thallus growth, slow aging, increase Ca in cell
gibberellins	gibberellin-like	?	development, promote growth, enhance antheridial development, decrease archegonial production
dormancy hormones	lunularic acid (LA)	liverworts	growth regulator, dormancy, drought tolerance, antiherbivory?
	abscisic acid (ABA)	mosses hornworts?	drought tolerance, growth form, capsule stomatal closure, gametophore bud inhibition; controls cytokinin response
ethylene	ethylene	mosses liverworts	development, leaf morphology, epinasty, cell elongation, color changes, response to substrate, senescence, suppression of 3rd row of leaves in liverworts, increased number of antheridia, chloronema to caulonema, inhibits seta elongation, may control gametophore bud development
acetylcholine		mosses, liverworts?	light response?; antiherbivory?; cellular regulation?
cryptochromes		mosses, liverworts?	protonema branching, gametophore induction, development, auxin control, photoperiodic responses

While the Venus flytrap provides the advantages of knowing where and when the growth response will occur, the number of responses of a single plant is limited, and the response is extremely rapid, making it difficult to obtain large amounts of data. The moss system provides a slower response that can be controlled by the researcher through externally applied auxin. As a single-cell-thick response system (leaf or protonema, Figure 12), the moss offers strong advantages over leaves or buds of tracheophytes, where any externally applied auxin must slowly penetrate the epidermis or other protective cells and substances. Because of these advantages, we are beginning to understand the role of IAA and calcium through the use of moss models.

Auxin activity seems to be an ancient character present when liverworts first emerged on land (Ishizaki *et al*. 2012). Ishizaki and coworkers demonstrated auxin activity at the bottom of gemma cups and junction of gametophyte and sporophyte in ***Marchantia polymorpha*** (Figure 13), suggesting its importance in actively dividing cells.

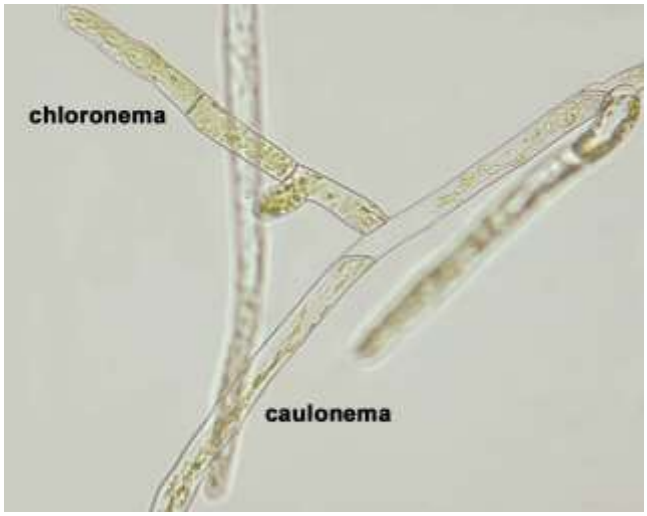

Figure 12. ***Funaria hygrometrica*** protonema with differentiation into chloronema (perpendicular cross walls) and caulonema (diagonal cross walls). Photo by Janice Glime.

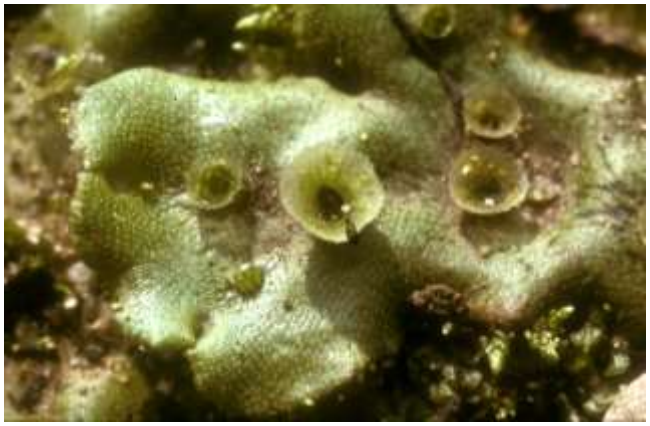

Figure 13. ***Marchantia polymorpha*** vegetative thallus with gemma cups. IAA moves basipetally (away from the tips) in this species. Photo by Janice Glime.

Our knowledge of the role of IAA in moss gametophores is still limited. We do know that the maximum concentrations are at the stem apex and base (Decker *et al.* 2006). The IAA seems to respond to changes in light quality, with red light retarding growth of protonemata but causing elongation of the gametophores, nevertheless making leaves shorter and narrower. Far red light enhances these responses (Bierfreund *et al.* 2003).

Thomas *et al.* (1983) demonstrated that IAA controlled seta elongation in the liverwort ***Pellia epiphylla*** (Figure 14). Although this and other studies provided indications of the presence of IAA in bryophytes, the first definitive HPLC (high-performance liquid chromatography) demonstration of its presence was published in 1985 by Law and coworkers in sterile culture of the liverwort ***Plagiochila asplenioides*** (Figure 15) subsp. ***arctica***. The natural auxin is **indole-3-acetic acid** (IAA), which is produced in the stem and branch tips of higher plants, and among bryophytes the same apical production is indicated in ***Marchantia*** (Maravolo 1976; Gaal *et al.* 1982). Due to its polarity, IAA moves **basipetally** (toward the base), as demonstrated in ***Marchantia polymorpha*** (Figure 13) by Maravolo (1976, 1980), where it travels in the midrib. Its transport is inhibited by aging and ethylene.

Figure 14. ***Pellia epiphylla***, a species in which IAA controls seta elongation. Photo by Malcolm Storey, through Creative Commons.

Figure 15. ***Plagiochila asplenioides***, a liverwort in which the presence of IAA has been demonstrated. Photo by Dick Haaksma, with permission.

In mosses, we know that early development is triggered by the auxin IAA working with **cytokinin** (another hormone) and requiring light that acts through the mediation of **phytochrome** (pigment sensitive to photoperiod) and a blue light receptor (Reski 1998), possibly **cryptochromes**. Auxins respond to light and gravity and thus provide a means for plants to grow in the right direction relative to the Earth. Their mode of action is still controversial, despite extensive research into their movements within plants and plant responses.

IAA seems to be essential for normal stem elongation (Bidwell 1979). When researchers removed the tips of actively growing tracheophytes, growth stopped. If they applied IAA, growth continued. On the other hand, at least in flowering plants, removal of the stem apex can promote growth of the branches, which were heretofore inhibited by the IAA during its downward movement. Similar reactions seem to occur in at least some mosses, as exhibited by the **innovations** (new ascendant branches near the shoot tip; Figure 16) of mosses following **gametangial senescence** (*i.e.* loss of gametangial function with aging), but experimental evidence of the IAA connection in bryophytes seems to be lacking.

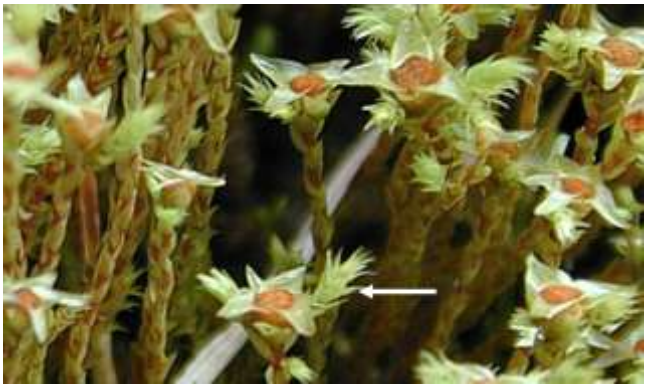

Figure 16. Innovation (arrow) beneath senescing antheridial head of ***Philonotis caespitosa***. Photo by Michael Lüth, with permission.

Auxins play major metabolic roles. IAA, in particular, seems to play a role in membrane transport; Lüttge and coworkers (1972) demonstrated that IAA can enhance leaf uptake of potassium by ***Mnium*** from both KCl and K_2SO_4. Inhibition of IAA by TIBA (2,3,5-triiodobenzoic acid; polar auxin transport inhibitor) reduces starch accumulation at night and disrupts meristem polarity in the thallose liverwort ***Riella helicophylla*** (Figure 17) (Stange 1985). The role of IAA in cell extension is still unclear, but perhaps it again plays a metabolic role in the transport of substances across the cell membrane, particularly calcium, thus increasing the osmotic potential of the cell.

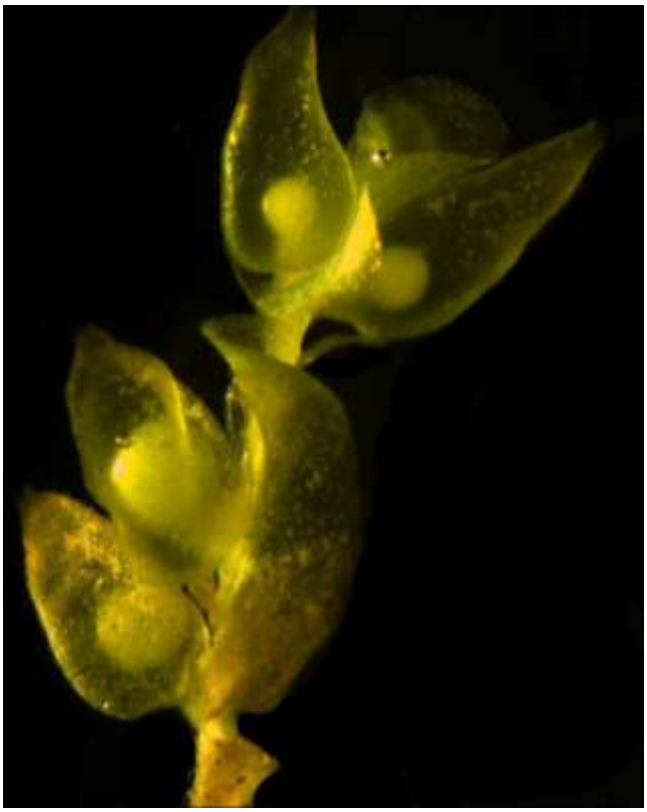

Figure 17. ***Riella helicophylla***, a liverwort where polar auxin transport causes reduction in nighttime starch accumulation and disruption of meristem polarity. Photo from NACICCA, through Creative Commons.

Auxins promote stem elongation at low concentrations and inhibit it at high ones, presumably due to induction of ethylene (Goodwin & Mercer 1983), and concentrations that promote growth in one part of a plant may inhibit it in another. In reviewing the body of literature on auxins in both non-tracheophytes and tracheophytes, Cooke and coworkers (2002) were surprised to find bryophytes exhibited most of the same physiological mechanisms for regulating IAA and for IAA-mediated responses as did the tracheophytes. These responses include **tropisms**, **apical dominance**, and **rhizoid initiation**. Both charophytes (the likely progenitors of bryophytes) and liverworts synthesize IAA via the tryptophan-independent pathway, regulating IAA levels through a balance between the rates of IAA biosynthesis and IAA degradation. All other land plants use the same pathway, but seem to have more precise spatial and temporal control through additional hydrolysis reactions. Although charophyte tips are apparently not sensitive to polar IAA transport inhibitors, both moss and liverwort gametophytes and moss sporophytes carry out polar transport, but sensitivity to the transport inhibitors differs within these groups.

The small quantities in which auxins are present in plants, combined with the small size of bryophytes, have made detection difficult. Their presence was indicated at least as early as 1963 when Cox and Westing demonstrated it in peat extracts. Despite its nanoconcentrations, Bhatla and Dhingra-Babbar (1990) report the presence of IAA in the protonemata of ***Funaria hygrometrica*** (Figure 12), ***Physcomitrella patens*** (Figure 3), and ***Polytrichastrum formosum*** (Figure 18), where it seems to be involved in differentiation. Many researchers (Cove *et al*. 2006; Von Schwartzenberg 2009) consider ***Physcomitrella patens*** to be a potential model system for study of this and other hormones because we now know its genome and can use gene knockout to determine the functions of the genes and ultimately the functions of the hormones.

Figure 18. ***Polytrichastrum formosum***, a moss in which IAA seems to be important in differentiation. Photo by David T. Holyoak, with permission.

Cytokinins

Cytokinins are important in bud formation. Using ***Physcomitrella patens*** (Figure 3) as a model, we can observe that the apical cell of the protonema divides (Reutter *et al*. 1998). When bud development begins, some of the subapical cells produce three-faced apical cells. These are the buds that will develop into the **gametophores**

(leafy shoots). Application of cytokinin enhances bud formation, but the buds often do not develop further. The moss ***P. patens*** produced isopentenyl-type cytokinins, whereas the zeatin-types produced by **tracheophytes** (non-bryophyte plants) were absent.

Cytokinins in bryophytes remained elusive until very recently because of their low concentrations. Cytokinins form another class of hormones that generally cause cell division (mitosis). Higher plants contain various **endogenous** cytokinins (produced within plant), such as zeatin, and scientists have identified many other compounds that act as cytokinins, such as kinetin and benzyl adenine. Unlike IAA, cytokinins travel to the tip of the protonema and accumulate there. Only two cytokinins (zeatin, isopentenyladenine) had been identified in bryophytes by 1979, both from protonemata (Cove *et al*. 1979, Gerhauser unpubl.). By 1990, there were indications that a third exists (Bhatla & Dhingra-Babbar 1990). Now we know that at least 20 of the 40 known cytokinins exist in the moss ***Physcomitrella patens*** (Figure 3), the most abundant of which are cis-Zeatin-riboside-O-glucoside, N6-(Δ2-isopentenyl)adenosine-5′-monophosphate (iPRMP), and trans-zeatin-riboside-O-glucoside as intracellular hormones (von Schwartzenberg *et al*. 2007).

The ability of cytokinins to affect Developmental changes in gametophores has been demonstrated experimentally. Chopra and Sood (1973) have shown that the cytokinin analog **kinetin** promotes growth of thalli in ***Riccia crystallina*** (Figure 27), but it also enhances archegonial formation. Vashistha (1987) likewise found that three different cytokinins applied to the liverwort ***Riccia frostii*** (Figure 19) stimulated vegetative growth and archegonial induction. Besides cell division, this hormone group can prevent or slow aging and cause changes in sex expression in higher plants (Kahn 1971). Cytokinins seem to cause the increase of calcium in the cell and together with calcium may cause an increase in ethylene. Magnesium ions seem to antagonize this calcium transport.

Figure 19. ***Riccia frostii***, a liverwort that responds to cytokinin in the medium. Photo by Rosemary Taylor, with permission.

Mosses respond differently to different concentration levels of cytokinins (Reski & Abel 1985). Among protonemata, only the chloronemata respond to low cytokinin concentrations, At high concentrations, only the caulonemata responded by increased bud formation. Hence, there is a specificity among cells in the concentrations to which they respond.

Reutter *et al*. (1998) were able to connect specific genes with their functions by using transgenic ***Physcomitrella patens*** (Figure 3). Using mutants that were unable to accomplish specific developmental tasks, they showed that cytokinins were able to supply the necessary signals for these events to occur (Figure 20).

In some cases, an outside source is needed to catalyze the production of cytokinins. For example, ***Agrobacterium tumefaciens*** (Figure 21) has the isopentenyl transferase gene that is needed to catalyze the first step in the biosynthesis of cytokinin (Decker *et al*. 2006). For some mosses, this bacterium is needed for development to go from the protonema to gametophore stage. Reutter *et al*. (1998) found that the moss ***Physcomitrella patens*** (Figure 3) responds differently to the same cytokinin when it is internal (**endogenous**) vs external (**exogenous**), and that most of both cytokinin and auxin is outside the moss (Reutter *et al*. 1998; Ralf Reski, pers. comm. 19 September 2013). Reutter *et al*. (1998) suggest that this external presence may permit translocation of the hormones in the bryophytes.

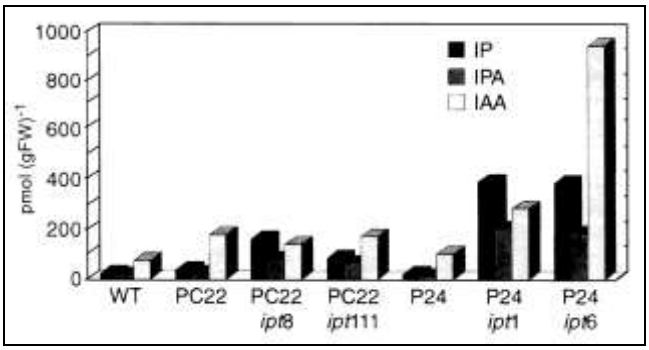

Figure 20. ***Physcomitrella patens*** hormonal contents. WT=wild type, PC22 = mutant defective in gametophore development and plastid division, P24=mutant that does not produce buds, *ipt*=gene of respective transgenic plant. Y axis is the immunoreactive IP, IPA, and IAA equivalent [pmol $(gFW)^{-1}$] in 9-day-old plants in liquid culture. Note that hormone levels are elevated in all the *ipt* transgenics. Redrawn from Reutter *et al*. 1998.

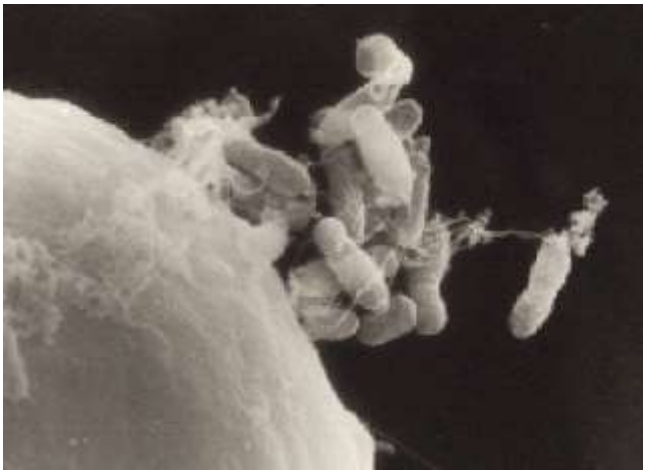

Figure 21. ***Agrobacterium tumefaciens*** on a carrot, a species known to provide hormones to mosses in nature. Photo through Creative Commons.

External application of cytokinins cause ***Physcomitrella patens*** (Figure 3) to develop abnormally, causing bud production without leafy gametophore development and becoming necrotic (Reutter *et al*. 1998). On the other hand, transgenic mutant mosses with the added bacterial ipt gene were able to develop normally with the internal production of cytokinins.

Cytokinins may have important roles in responding to the environment (Lorenz *et al*. 2003). For example, it seems to have a role in the change from juvenile tissue growth to sexual reproduction under high-energy conditions (exogenous carbohydrates or bright light). Thelander *et al*. (2005) found that high-energy conditions resulted in pronounced caulonema formation. Low energy conditions, resulting from low light, short days, or low temperatures, stimulate development of gametangia and subsequent development of sporophytes (Hohe *et al*. 2002).

The limited number of cell types, ability to regenerate from small fragments, and ease of cultivation of the entire life cycle in the laboratory makes bryophytes good experimental organisms for study of the functioning of cytokinins (von Schwartzenberg 2006). And the fully mapped genotype of ***Physcomitrella patens*** (Figure 3) provides us with an ideal study organism. Von Schwartzenberg *et al*. (2007) found that the nucleotide iPRMP is the most abundant extracellular cytokinin in ***Physcomitrella patens***. By using cytokinin oxidase/ dehydrogenase (CKX)-overexpressing plants, von Schwartzenberg and coworkers observed reduced and retarded budding, absence of sexual reproduction, and abnormal protonema cells. Extracellular IP and IPR seem to be the primary cytokinins responsible for inducing buds in ***P. patens***. Control of levels is undoubtedly important.

^{14}C-labelled adenine has also shown up in cytokinin in the culture medium of ***Physcomitrella patens*** (Figure 3), indicating a similar role of adenine in production of cytokinin (Bhatla & Dhingra-Babbar 1990). A similar, perhaps same, substance in ***Bryum klinggraeffii*** (Figure 22) inhibits growth and stimulates gemma formation. Because it leaks into the medium, this substance could have interactive effects on other species of mosses and even control its own population size. More recently, Proust *et al*. (2011) found that **strigolactones** regulate the branching of protonemata in ***Physcomitrella patens*** and act as **quorum sensors** – a way of signalling that no more bryophytes should be added there. Hence, the strigolactones inhibit the growth of both that protonema and that of neighboring colonies.

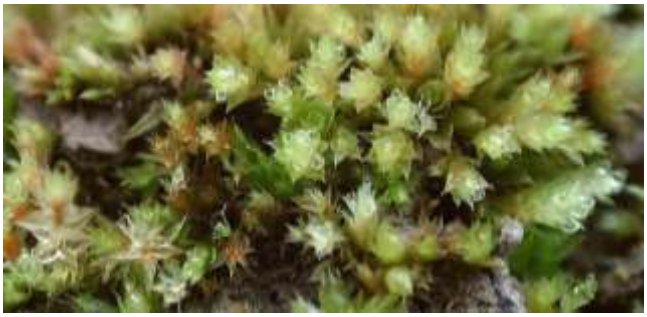

Figure 22. ***Bryum klinggraeffii***, a moss in which a cytokinin-like substance leaks into the environment and inhibits growth while promoting gemma formation. Photo by Michael Lüth, with permission.

Based on the work of Bopp (1963, 1968), Watson (1981) suggested that it could be the inhibitory properties of a hormone (Factor H – see below) that caused differing aggressive patterns among juvenile ***Polytrichum*** *s.l.* (Figure 7-Figure 8; Figure 18) species, thus affecting ultimate community structure. Perhaps more important is the effect of controlling simultaneous production of buds in the population so that they develop together and conserve moisture by creating a smooth surface. This same control would prevent them from over-shadowing one another, avoiding intra-specific light competition.

It seems that the moss need not produce its own cytokinin. Rather, it may serve as host to bacteria that produce this hormone. In ***Funaria hygrometrica*** (Figure 1), the bacterium ***Methylobacterium*** (Figure 23) is epiphytic on the moss, inhabiting leaf surfaces, especially in the grooves between adjacent leaf **lamina** cells (cells of the blade portion of the leaf, exclusive of costa) (Hornschuh *et al.* 2002). In the presence of these bacteria on agar cultures, the protonema produces buds just as it would in the presence of cytokinin, and the exudate also stimulates the growth of the protonemal filaments. Glime and Knoop (1986) suggested a similar relationship in ***Fontinalis squamosa*** (Figure 24), wherein the only protonemata cultures that produced buds on a mineral nutrient medium were the ones that became contaminated with bacteria and fungi.

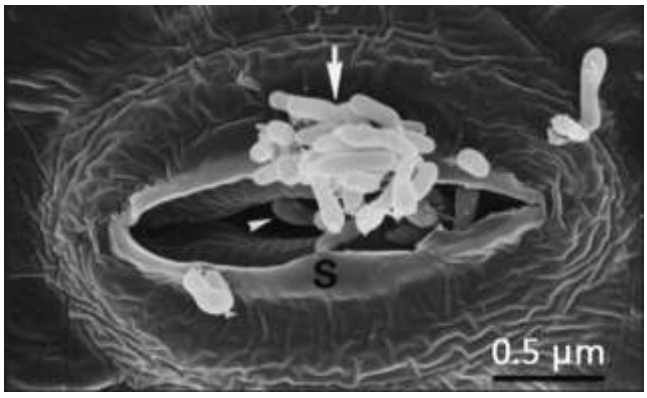

Figure 23. ***Methylobacterium*** sp., a possible source of cytokinins for mosses, on sunflower stoma. Photo by Kutschera U., through Creative Commons.

Figure 24. ***Fontinalis squamosa*** protonema. Photo by Janice Glime.

One aspect of the life cycle that will be discussed in other chapters is the production of asexual structures, a feature that is rare among **tracheophytes** (non-bryophyte plants). One example of this unique phenomenon is the discovery of protonemal gemmae in the aquatic moss ***Fontinalis antipyretica*** (Ares *et al*. 2014). In this species, where capsule production is relatively rare, vegetative shoots are important dispersal units. These dispersal units can come from detached cortical cells, margins and abaxial (away from the stem) surfaces of leaves, leaf laminae, and stems with leaves removed. Likewise, the protonema can continue growth from the filament or its rhizoids. But the discovery by Ares *et al*. is that these protonemata can also produce filamentous gemmae and spherical brood cells. These occur as the cultures age or dry out. Thus in nature they are produced as streams dry and water levels drop, providing a means of surviving these unfavorable periods. It is interesting that bacteria and fungi in the cultures (and in nature) seem to play a role in this development. but at this point in time we do not know what that biochemical interaction may be or how the drying of the environment may trigger the formation of propagules on the protonema.

One of the cytokinins that is effective on bryophytes is produced by the bacterium ***Agrobacterium*** (Figure 21). It appears that flowering plants lack the gene for this cytokinin, but evidence suggests that mosses may in fact possess it, and furthermore, ***Agrobacterium*** in the environment may supply it to some mosses. Addition of ***Agrobacterium tumefaciens*** (Figure 21) to the medium can stimulate the production of gametophores in ***Pylaisiella selwynii*** (Figure 25; Spiess *et al*. 1971), an epiphyte. The presence of this bacterium with the moss on tree bark suggests its possible role in the development of ***Pylaisiella selwynii*** in that habitat.

Figure 25. ***Pylaisiella selwynii*** growing on bark where it encounters the bacterium ***Agrobacterium tumefaciens***, which most likely contributes to its production of gametophores there. Photo by Janice Glime.

Factor H

A possible cytokinin known as **Factor H**, an adenine derivative (Bhatla & Dhingra-Babbar 1990)**,** has been known for much longer as a stimulant for increasing the number of gametophore buds (Klein 1967; Brandes & Kende 1968). **Factor H** has been isolated from the culture medium of ***Funaria hygrometrica*** (Figure 1) and from tissue extracts of several other mosses (Bhatla & Dhingra-Babbar 1990). Its roles in inhibiting caulonema growth and promoting bud formation are clear, thus resembling the behavior of a cytokinin. Christianson (1998b) discovered that not all mosses have the same "Factor H."

Although the experiments mentioned above suggest that mosses respond to this hormone from other species, ***Ceratodon purpureus*** (Figure 26) is not affected by this substance from ***Funaria hygrometrica*** (Figure 1), nor is it able to affect the development of ***Funaria hygrometrica***, but ***Ceratodon*** does exhibit interspecific regulation. Its growth substance does not pass through a dialysis membrane, whereas factor H does.

Figure 26. ***Ceratodon purpureus***, a species that is not affected by "factor H" from neighboring species. Photo by Michael Lüth, with permission.

In 1980, Bopp determined that Factor H not only is not a cytokinin, it is not a cytokinin-like substance. But in 2013, Ralf Reski assured me it is most likely a cytokinin. Its identity seems still to be unknown. It does seem to carry out some of the functions we might attribute to a cytokinin.

The Factor H that has made medical news lately (Büttner-Mainik *et al*. 2011) should not be confused with the natural Factor H produced by bryophytes. The moss ***Physcomitrella patens*** (Figure 3), through recombinant DNA, is able to make the human complement regulatory serum protein Factor H – a substance that can assist in treatment of human diseases, including severe kidney and retinal disorders. It is a cheaper solution that does not involve the need for animals to manufacture the compound.

Gibberellins

Gibberellins (GA) are terpenoid-based hormones (Harborne 1982) that can stimulate stem elongation as well as cell division, depending on the species involved (Bidwell 1979). Gibberellins, unlike auxins, are non-polar and free to move about all over the plant. In studying ***Marchantia polymorpha*** (Figure 13) Melstrom and co-workers (1974) isolated three gibberellin-like substances from the thalli. Chopra and Sood (1973) found that gibberellins could enhance antheridial formation while promoting normal growth in the thallose liverwort ***Riccia crystallina*** (Figure 27). Chopra and Kumra (1986) later found that GA_3 not only enhanced normal growth of ***Riccia gangetica***, but also increased the production of antheridia while causing a decrease in archegonial production.

Figure 27. ***Riccia crystallina***, a species in which gibberellins can enhance antheridial formation while promoting normal thallus growth. Photo by David T. Holyoak, with permission.

However, Bhatla & Dhingra-Babbar (1990) reported that gibberellins still are not confirmed in mosses, although GA-like substances are known in both mosses and liverworts (Chopra & Kumar 1988). Even recent studies have failed to confirm the presence of GA in bryophytes, with the "lab rat" ***Physcomitrella patens*** (Figure 3) failing to respond to gibberellic acid (Hiranoa *et al*. 2007). It appears that GID1/DELLA-mediated GA signaling arose in tracheophytes after they diverged from the bryophyte lineage (Hiranoa *et al*. 2007; Yasamura *et al*. 2007). On the other hand, Ergün *et al*. (2002) demonstrated that at least some bryophytes can produce not only IAA, ABA and zeatin, but also GA_3. Furthermore, the production of GA in mosses should be expected, since its presence is known in algae (Radley 1961; Mowat 1965; Tietz & Kasprik 1986; Tietz *et al*. 1989; Hirch *et al*. 1989).

Gibberellic acid is the hormone responsible for giant growth. I can remember that in my high school years Burpee was experimenting with it on horticultural flowers and encouraged seed buyers to try it and report the results. It didn't do much for my poor flowers in terrible soil. Could the absence of this hormone be part of the reason bryophytes have remained small?

Even if GA is absent in bryophytes, that does not necessarily mean that mosses cannot respond to it. Indeed, the fungi could deliver GA to the mosses and thus facilitate or interfere with development, perhaps accounting for bryophyte specificity to certain habitats. Certainly the presence and use of gibberellins in bryophytes is worthy of further exploration.

Abscisic Acid

Abscisic acid (ABA) is known not only in plants, but also in bacteria, animals, and elsewhere (Hartung 2010; Takezawa *et al*. 2011). It is therefore an important hormone to understand. The moss ***Physcomitrella patens*** (Figure 3) once again provides a suitable organism in which to study its functions. In this, and other bryophytes, it is known to respond to stress, including desiccation (Mayaba *et al*. 2001) and cold tolerance (Minami *et al*. 2003, 2005). In ***Atrichum androgynum*** (Figure 29) this desiccation tolerance seems to be accomplished by increasing the concentration of soluble sugars. In ***Physcomitrella patens*** (Figure 3), 22 genes are activated by ABA, and part of its role appears to be in the period of recovery from desiccation (Khandelwal *et al*. 2010).

The role of ABA in development seems to be ambiguous (Hartung 2010). Nevertheless, high levels of ABA seem to be present in organs of bryophytes that produce sporophytes.

Abscisic acid (**ABA**) is a sesquiterpenoid (15-C compound) that is partially produced via the mevalonic pathway in chloroplasts and other plastids. Therefore, synthesis occurs primarily in the leaves. It appears to be an indirect product in the synthesis of **carotenoids** (yellow to red lipid-soluble pigments). It has a variety of roles in both tracheophytes and bryophytes. In tracheophytes, it is important in regulating transpiration, stress responses, germination of seeds, and embryogenesis. Its most widespread function is in signalling water stress and regulating water loss. Interaction with other hormones gives it a role in most plant developmental processes.

ABA has been confirmed relatively recently in bryophytes, in the protonema of ***Funaria hygrometrica*** (Figure 12) (Bhatla & Dhingra-Babbar 1990; Werner *et al*. 1991). Its presence was unknown in liverworts (Gorham 1990) until 1994 (Hartung *et al.* 1994). However, there are indications that it is present in all bryophytes – at least all that have been tested (Hartung *et al*. 1994). It is known to inhibit the cytokinin-stimulated response of bud induction in the moss ***Funaria hygrometrica*** (Figure 1), making cytokinin a useful bioassay tool for detecting not only the presence but also the concentration of **ABA** (another hormone), since the inhibition is concentration dependent (Christianson 2000b).

The highest concentrations in bryophytes occur in species adapted to dry environments, and conversely, the lowest concentrations in aquatic species, suggesting it had a role in drought tolerance (Hartung *et al*. 1994). For example, in ***Funaria hygrometrica*** (Figure 12) , it makes the protonema drought resistant and in the Marchantiales it induces drought tolerance in the thallus. Burch and Wilkinson (2002) used it to ensure drought tolerance for long-term storage of ***Ditrichum cornubicum*** (Figure 28) protonemata, reducing membrane damage suffered during dehydration and freezing, and providing 100% recovery upon rehydration.

Figure 28. ***Ditrichum cornubicum***, a moss in which ABA has been used to ensure drought tolerance for long-term storage, apparently through accumulation of sugars. Photo by David T. Holyoak, with permission.

The use of ABA for cryopreservation reduces both labor and loss of plant material in ***Ceratodon purpureus*** (Figure 26), ***Funaria hygrometrica*** (Figure 1), ***Physcomitrella patens*** (Figure 3), and ***Sphagnum*** spp. (Christianson 1998a). There are likewise genetic implications for its presence, with 11 expressed sequence tags matching up with tracheophyte stress response genes, "including responses which may involve ABA" (Machuka *et al*. 1999). In ***Atrichum androgynum*** (Figure 29), application of ABA prior to desiccation reduces membrane leakage (Beckett 1999). It appears that this drought tolerance mechanism may be similar to that in higher plants under stress, with ABA reducing membrane damage by reducing the changes in membrane lipids (Guschina *et al*. 2002). On the other hand, ABA does not endow all bryophytes with desiccation tolerance. ***Plagiochila*** (Figure 15) shows no response, and ***Marchantia polymorpha*** (Figure 13) requires both ABA and encapsulation in alginate (sticky gum) beads for successful cryopreservation (Pence 1998). Furthermore, in the desiccation-tolerant ***Syntrichia*** (Figure 30), desiccation tolerance is not under ABA control, despite a large number of desiccation-response genes (Oliver 1996).

But what is the role of ABA in development? Decker *et al*. (2006) found that under the influence of ABA the protonematal subapical cells differentiate into round, short cells (**brachycytes**) or **tmema** cells (short-lived abscission cells), the latter being nearly free of cytoplasm (Figure 31). Thus, ABA has a role in asexual reproduction of the protonema. We know that in ***Funaria hygrometrica*** (Figure 1), when the ABA is removed, these short, round cells (**brachycytes**) germinate and form new protonemata (Schnepf & Reinhard 1997). The role of ABA is at least in part that of restructuring the cell walls of the protonema (Schipper *et al*. 2002; Decker *et al*. 2006).

Figure 29 ***Atrichum androgynum***, a moss in which membrane leakage is reduced by ABA application. Photo by Tom Thekathyil, with permission.

One interesting role of ABA is its ability to convert the aquatic (floating) forms of ***Riccia fluitans*** (Figure 32) and ***Ricciocarpos natans*** (Figure 34) into their terrestrial forms (Figure 33, Figure 35; Hartung *et al*. 1994). In ***Riccia fluitans***, ABA causes changes in the gene expression that cause the nearly filamentous floating form to become the broadly thallose soil form (Hellwege *et al*. 1996). This mechanism may be similar to that seen in the aquatic fern *Marsilea quadrifolia* in which ABA induces changes from aquatic to aerial leaf forms (Hsu *et al*. 2001).

Figure 30. ***Syntrichia ruraliformis*** on sand dunes at Harlech, Wales. This is a desiccation-tolerant moss whose tolerance is not controlled by ABA. Photo by Janice Glime.

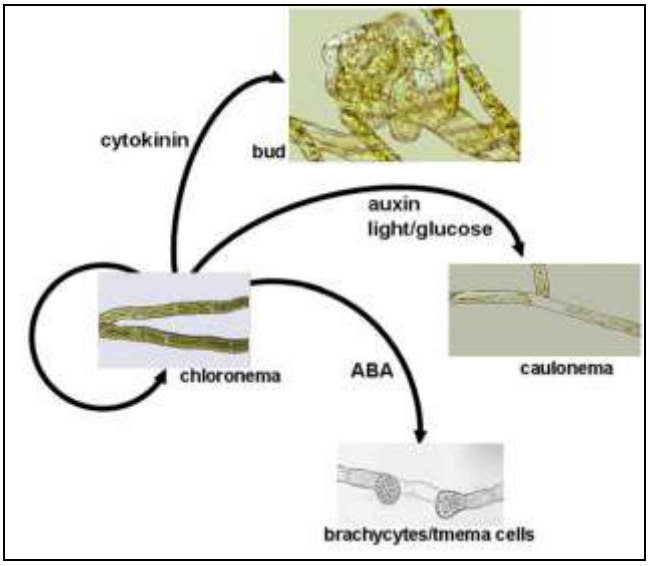

Figure 31. Hormone pathways in the cell cycle for protonemata. Modified from Decker *et al*. 2006.

Figure 32. ***Riccia fluitans*** floating form. Photo by Janice Glime.

Figure 33. ***Riccia fluitans*** soil form. Photo by Michael Lüth, with permission.

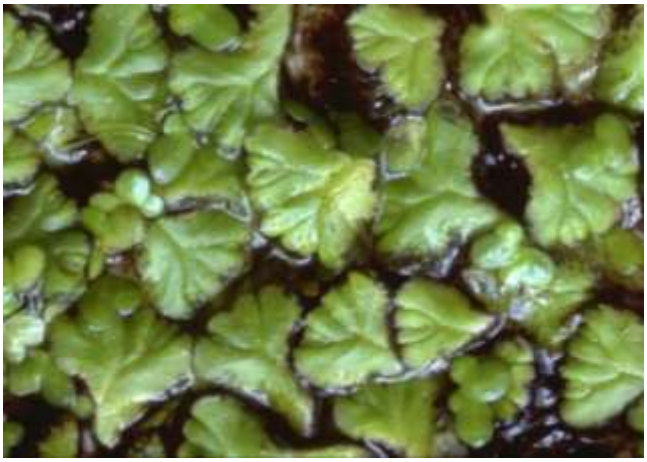

Figure 34. ***Ricciocarpos natans*** floating form. Photo by Jan-Peter Frahm, with permission.

One more important role of ABA in tracheophytes is the movement of K^+ out of guard cells of leaves, causing them to close, and suggesting that it might control membrane permeability. It is interesting that it likewise induces the closure of stomata in capsules of mosses and in Anthocerotophyta (hornwort) sporophytes (Hartung *et al*. 1994). ABA also seems to play a role in regulation of extracellular protein secretion (Decker *et al*. 2006).

Figure 35. ***Ricciocarpos natans*** soil form. Photo by Janice Glime.

It is not unusual for desiccation-tolerant species to also be cold/freezing tolerant. Nagao *et al*. (2005) found that The transformation from starch to sugar in chloroplasts is associated with ABA-induced freezing tolerance in protonemata of ***Physcomitrella patens*** (Figure 36), changing the LT50 from -2°C to -10°C. Compared to untreated cells, ABA-treated cells had more slender chloroplasts and a reduced starch grain content. Instead of one central vacuole, the treated cells often had multiple segmented vacuoles. At -4°C the untreated cells had lesions in the cell membranes; the treated cells did not. Osmotic concentration increased as sugars accumulated.

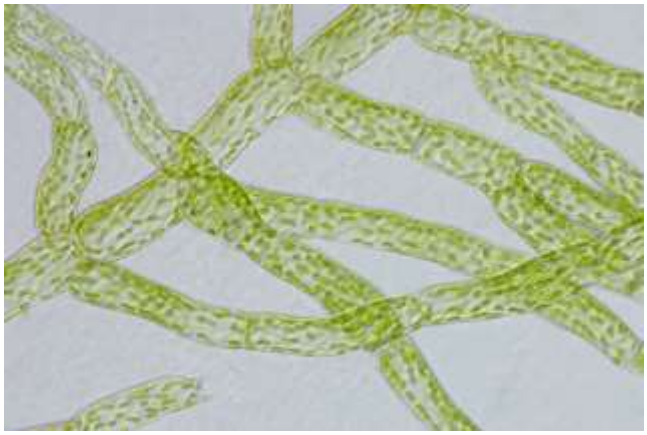

Figure 36. ***Physcomitrella patens*** protonema, a common research organism for hormone studies. Photo from Ralf Reski Lab, through Creative Commons.

Wang *et al*. (2011) found 65 proteins that responded to ABA in ***Physcomitrella patens*** (Figure 3; Figure 36). This involved down regulation of 13 proteins and upregulation of 52 proteins, 4 of which were newly induced. The roles of these proteins included material and energy metabolism, defense, protein destination and storage, transcription, signal transduction, cell growth/division, transport, and cytoskeleton. Most of the up-regulated proteins functioned as molecular chaperones, transcriptional regulators, and defense proteins. Thus the ABA was able to trigger responses that served in defense and protection from oxidative damage. They also learned that ***Physcomitrella patens*** responds to exogenous (applied externally) ABA. This latter response permits them to respond to other organisms in the environment. They found that ABA could inhibit photosynthesis, a phenomenon that suggests we should look at the ability of other organisms to compete with them with this hormone. Such an inhibition may prevent spores from germinating on leaf litter that is leaking ABA. This would seem like an interesting field for ecological research.

Lunularic acid

We know that a hormone similar to ABA, **lunularic acid** (LA), first discovered in ***Lunularia cruciata*** (Figure 37; Schwabe & Nachmony-Bascomb 1963), is present in at least the 47 genera (80 species) of liverworts examined by Gorham (1975, 1990) and is important in dormancy and growth regulation (Schwabe 1990). More recently it has been identified in ***Plagiochila spinulosa*** (Figure 38) (Connolly *et al*. 1999), ***Ricciocarpos natans*** (Figure 34-

Figure 35) (Kunz & Becker 1992), ***Frullania convoluta*** (Flegel *et al*. 1999), and ***Marchantia polymorpha*** (Figure 13) (Friederich *et al*. 1999).

Figure 37. ***Lunularia cruciata*** with gemmae pockets. Photo by Martin Hutten, with permission.

Figure 38. ***Plagiochila spinulosa***, a leafy liverwort known to produce lunularic acid. Photo by Michael Lüth, with permission.

Although reputedly unique to liverworts, this hormone has recently been found in *Hydrangea macrophylla*, a flowering plant (Eckermann *et al*. 2003). In liverworts, the largest amounts of LA occur in dormant and desiccation-resistant thalli (Chopra & Kumar 1988) and its presence confers drought resistance (Schwabe & Nachmony-Bascomb 1963; Schwabe 1972), reminiscent of ABA. Part of this resistance is the initiation of dormancy, an effect that is greater at higher temperatures (Schwabe 1990). Nevertheless, Gorham (1990) found that lunularic acid does not affect stomatal conductance, suggesting that its effect on cells is different from that of abscisic acid.

Lunularic acid is compartmentalized (localized) within cells, hence restricting its function (Gorham 1977), although Imoto and Ohta (1985) found that it is equally distributed between vacuoles and cytoplasm in ***Marchantia polymorpha*** (Figure 13), and that it does not accumulate in chloroplasts, mitochondria, or peroxisomes. Gorham (1977) found it in all organs of ***Marchantia*** and ***Preissia*** (Figure 39), in sporophytes of ***Pellia epiphylla*** (Figure 14), and in the greatest concentration (more than 600 µg/g fresh weight) in young thallus tips of ***Conocephalum conicum*** (Figure 40) grown in continuous light. Higher light intensities increased its concentration; age decreased it. Continuous light caused a greater production of both growth and lunularic acid in thallose liverworts than in any photoperiod interrupted by darkness, creating a condition in which lunularic acid was not inhibitory. Leafy liverworts of the Jungermanniales contained smaller quantities (1-50 µg/g fresh weight) than did the thallose species tested.

Figure 39. ***Preissia quadrata***, a liverwort known to have lunularic acid in all its organs. Photo by Jan-Peter Frahm, with permission.

Figure 40. ***Conocephalum conicum*** showing growing tips where concentration of lunularic acid. Photo by Jan-Peter Frahm, with permission.

Because of its dormancy effect, lunularic acid could act as a growth inhibitor. However, compared to its analogs, this hormone is less effective in inhibiting growth of the liverwort ***Marchantia polymorpha*** (Figure 13) and the flowering plants *Nasturtium officinale* (water cress) and *Phleum pratense* (timothy grass) (Nakayama *et al*. 1996), but is known to inhibit growth in ***Lunularia cruciata*** (Figure 37) (Yoshikawa *et al*. 2002).

Lunularic acid forms a variety of conjugates (Kunz & Becker 1992). Among these are glycosides, suggesting an antiherbivory role as well. This suggestion is supported by Wurzel and coworkers (1990) who found, in ***Ricciocarpos natans*** (Figure 34-Figure 35), molluscicidal behavior against *Biomphalaria glabrata*, a snail that carries schistosomiasis (parasitic disease caused by blood fluke).

Research on lunularic acid in this century is scarce, but we still have much to learn about its role in liverworts.

Ethylene

Ethylene (C_2H_4) is important in every step of the developmental process of higher plants (Abeles 1973), and has been demonstrated in both liverworts (Fredericq *et al*. 1977; Thomas *et al*. 1983) and mosses (Rohwer & Bopp 1985). It is known from the sporophyte of ***Pellia*** (Figure 14), especially during rapid seta elongation (Thomas *et al*. 1983) and from the thallus of ***Marchantia*** (Figure 13) (DeGreef *et al*. 1981). However, Stange and Osborne (1989) found that the liverwort ***Riella*** (Figure 17) appears to have a different pathway for ethylene synthesis from that of higher plants.

Ethylene is an unsaturated hydrocarbon synthesized in tracheophytes via the following pathway:

$$\text{Methionine} \rightarrow \text{SAM} \rightarrow \text{ACC} \rightarrow C_2H_4$$

IAA is possibly the catalyst for the conversion of SAM (S-adenosylmethionine) to ACC (1-aminocyclopropane-1-carboxylic acid) (Bradford & Yang 1980a), as suggested by the 10-fold increase in ethylene obtained when 10^{-6} IAA is supplied in the medium (Bhatla & Dhingra-Babbar 1990). O_2 is required for the conversion of ACC to C_2H_4 (Bradford & Yang 1980b), suggesting that there might be interesting environmental responses for mosses that live part of their lives in water.

Although ethylene is a gaseous substance, it has been termed a growth hormone. It is important in **senescence** (aging) and its presence can cause **epinasty** (leaf and stem curling). In the aquatic moss ***Fontinalis squamosa***, treatment with its precursor ACC causes color changes, wavy leaves, and curled tips (Figure 41), as well as inhibiting growth at high concentrations (Glime & Rohwer 1983). It is likely that these responses are actually to ethylene produced in response to the ACC application.

Figure 41. **Left:** ***Fontinalis squamosa*** grown with ACC, the precursor of ethylene, demonstrating the contorted leaves and curved tips. **Right:** ***Neckera pennata*** exhibiting undulate leaves that could prove to be the result of genetically controlled ethylene behavior. Photos by Janice Glime.

Ethylene production coincides with that of the change from chloronema to caulonema and is probably tied to the increase in auxins (Rohwer & Bopp 1985). We know that ethylene and IAA can work together in both bryophytes and higher plants (Mignone & Basile 2000). In bryophytes, we know that an additive effect exists in at least some, for example ***Riella helicophylla*** (Figure 17), causing "super" cell elongation (Stange & Osborne 1988). Chopra and Sood (1973) demonstrated that ethrel, which produces ethylene in water, causes the production of more antheridia in ***Riccia crystallina*** (Figure 27).

IAA and ethylene often work in tandem, controlling each other's concentrations. For example, in ***Pellia epiphylla*** (Figure 14), IAA results in seta elongation, whereas ethylene inhibits it (Thomas *et al*. 1983). In the leafy liverworts, ethylene works together with auxin and certain arabinogalactan-proteins to suppress the third row of leaves by suppressing development of every third leaf primordium (Basile & Basile 1984; Mignone & Basile 2000). Mignone and Basile considered that ethylene played a suppression role in three processes. It is able to cause reductive development by causing failure in development of primordia to mature organs. It modulates the size and shapes of leaves. And it facilitates the change from diffuse growth to polar/apical growth. Nevertheless, ethylene remains largely a mystery.

The ACC pathway seems to work somewhat differently in bryophytes (Osborne *et al*. 1996). Lower plants seem unable to convert ACC to ethylene, nevertheless producing ethylene continuously. Although the ***Riella helicophylla*** (Figure 17) they studied seemed to take up the ACC easily, no ethylene gas was released. Nevertheless, in ***Fontinalis*** (Figure 41) ACC causes symptoms consistent with those expected from ethylene (Rohwer & Bopp 1985).

Acetylcholine

Acetylcholine – a compound better known for its role in nerve cells, has been conclusively shown in bacteria, protists, and mosses (Hartmann & Kilbinger 1974; Wessler *et al*. 1999), and more recently, in corn (Momonoki 1992). Interestingly, the original report (Hartmann & Kilbinger 1974) found it only in a hybrid of ***Funaria hygrometrica*** (Figure 1) and ***Physcomitrium pyriforme*** (Figure 3), whereas its hydrolyzing enzyme cholinesterase was not found in either (Fluck & Jaffe 1974). Later, however, Gupta *et al*. (2001) found cholinesterase in 30 out of 39 species of bryophytes tested, including five liverworts, with the highest activity in the moss ***Anoectangium bicolor***.

In non-animal organisms, the production of acetylcholine (ACh) is always accompanied by cholinesterase activity, thus preventing it from behaving as a hormone (Wessler *et al*. 1999). Nevertheless, its activity and the activation of acetylcholine receptors can interfere with ion channels and key enzymes – the cellular signalling pathways. In this role, it appears to play a part in regulating such cellular functions as mitosis, cell differentiation, organization of the cytoskeleton, cell-to-cell contact, secretion, and absorption. Furthermore, it appears to contribute to the regulation of immune functions.

But the role of acetylcholine in bryophytes is still unclear (Bhatla & Dhingra-Babbar 1990). Light quality certainly affects its production in at least some bryophytes, with 56 times as much produced in red light as in red/far-red (Bhatla & Dhingra-Babbar 1990). The red/far-red response is indicative of regulation by phytochrome (pigment that measures day length), but researchers disagree on the mechanism. As a growth regulator, it could

have an important role in habitat response and spore germination as a means of interpreting light quality.

In lactic acid bacteria, acetylcholine can be produced in response to osmotic stress (Kets *et al*. 1997). In a moss that is often desiccated by dust and other solutes on the surface, as well as being subjected to frequent desiccation due to weather, perhaps the acetylcholine might respond similarly.

Cryptochromes

Cryptochromes – This almost colorless yellow plant pigment has both enlightened and dumbfounded the plant physiologists since its discovery. Although we know that it responds to light and somehow signals to IAA in a way that affects plant development, its mechanism has remained elusive. Then entered the moss, of course the lab rat of all mosses, ***Physcomitrella patens*** (Figure 3). In 1999, Imaizumi and coworkers posted the identification of a cryptochrome homologue from this moss. ***Physcomitrella patens*** is more than just a convenient, small organism for testing things. It is unique. It is the only plant found thus far in which gene replacement is predictably reliable due to the high frequency of homologous recombination. In plain English, that means that instead of one chance in a million for a transplanted gene entering the genome, it is a predictable certainty.

Hence, to discover how cryptochromes function in plants, researchers (Imaizumi *et al*. 2002) created a moss [a strain of ***Physcomitrella patens*** (Figure 3)] with a defective genome, one that had disruptants for the two known genes for cryptochromes (CRY1 & CRY2). The moss could not make its cryptochromes. The results were rather astounding. They revealed that cryptochrome signals regulate induction of side branching of the protonema, gametophore induction, and development. Furthermore, disruption of these cryptochromes altered the induction of the auxin-inducible genes. Since these modified mosses were more sensitive to external auxin than their unmodified relatives in blue-light responses, it appears that the cryptochromes provide the signal to repress auxin signals that control plant development. This breakthrough in discovering the utility of ***Physcomitrella patens*** in delineating gene function could have astounding contributions to the entire field of plant physiology! In fact, it already does.

Summary

All aspects of development are influenced not only by the internal environment, but also by the external environment. These signals trigger responses in the bryophytes that permit them to survive and take advantage of the ever-changing conditions of their environment, from growth forms to drought resistance to dormancy.

These responses are typically mediated by hormones. Known bryophyte hormones include **auxins** (IAA) that regulate growth and gametangial production, **cytokinins** (**isopentenyladenine**, **zeatin**, and most likely **Factor H**) that regulate protonemal bud formation and branching, **gibberellin**-like compounds that inhibit cytokinin responses, **lunularic acid** and **ABA** (abscisic acid) that regulate dormancy and drought resistance, and **ethylene** that controls antheridial production and triggers **senescence**; **acetylcholine** and **cryptochromes** (photo-receptive pigments) also play a role in controlling bryophyte growth and development. The modes of control of these growth regulators are poorly understood in bryophytes, although in most cases they seem to act similarly to their mode of action in tracheophytes.

Some hormones may be supplied **exogenously**, that is, supplied by other organisms in the environment such as bacteria and fungi. And some of the hormones may be moved from place to place in the bryophyte by external conduction.

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CHAPTER 5-2

ECOPHYSIOLOGY OF DEVELOPMENT: SPORE GERMINATION

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CHAPTER 5-2

ECOPHYSIOLOGY OF DEVELOPMENT: SPORE GERMINATION

Figure 1. Maturing capsules of ***Oligotrichum hercynicum***. Photo by Michael Lüth, with permission.

Spore Maturation

Following meiosis, the spore must mature into the decorated unit that gets dispersed. The spore originally has only one plastid, but this number increases by fission (Mueller 1974). The typical spore wall in bryophytes is composed of three distinct layers: **intine**, **exine** and **perine** (Diego Knop Henriques, Bryonet 28 September 2011). The innermost is the **intine**, basically composed of fibrillar material, mainly pectin, and it plays a pivotal role in spore germination. The **exine** is a thin layer right outside the intine and has **sporopollenin** in its composition. Colpitts *et al*. (2011) demonstrated that spores of ***Physcomitrella patens*** (Figure 2) have the genetic information to produce sporopollenin in their spore walls, a gene that is expressed in the sporophyte generation. Sporopollenin is present in the intine of the spore and confers a great resistance to chemical and environmental factors, as it does in pollen. The **perine** is the outermost layer, also contains sporopollenin, and, in the majority of moss species, is the layer responsible for the spore ornamentation.

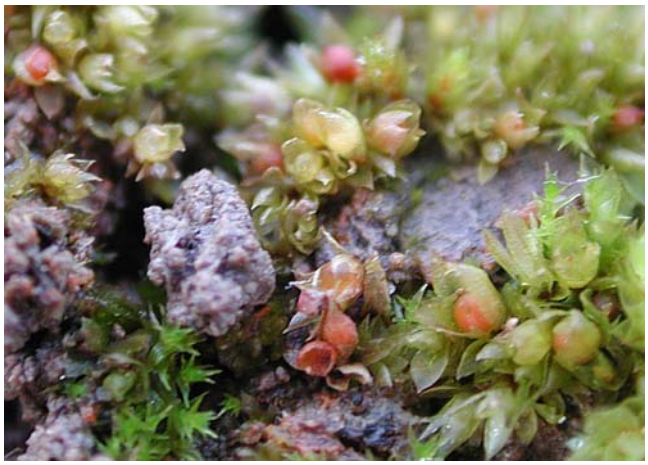

Figure 2. ***Physcomitrella patens*** with capsules. Photo by Michael Lüth, with permission.

Mueller (1974) described the formation of the spore wall in the moss ***Fissidens crispus*** (Figure 3). First the exine forms around the protoplast after meiosis. When the spore is fully enlarged, it is coated by the perine. Then the intine forms. Both the intine and exine originate from within the spore, but the perine comes from material within the capsule, but outside the spore. It is this deposited perine that forms the ornamentation on the spore wall.

Figure 3. ***Fissidens crispus*** capsule that has lost its spores. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Brown and Lemmon (1980) added to this wall description by using ultrastructural analysis of sporogenesis in the moss ***Ditrichum pallidum*** (Figure 4) to describe the internal events of the spore. They found that following meiosis, an extensive system of microtubules is present, underlying the entire distal spore surface where the exine deposition initiates. Following this, the lamellate exine thickens, extending to the proximal surface. The plastid and nucleus migrate to the proximal surface and an elaborate system of microtubules facilitates aperture development. Brown and Lemmon added a fourth layer to the description, a separating layer between the exine and intine. The developed aperture results from a modification of the proximal surface of the spore with a pore that contains fibrillar material surrounded by a thin ring (annulus).

Figure 4. ***Ditrichum pallidum*** with capsules. Photo by Bob Klips, with permission.

Maturation Seasons

Spore maturation tendencies differ with latitudes and climate. They also differ by families, at least in pleurocarpous mosses. Hedenäs (2007) summarized spore maturation seasons for a number of pleurocarpous families:

Winter:
- Brachytheciaceae
- Ctenidiaceae
- Heterocladioideae
- Hylocomiaceae

Summer:
- Plagiotheciaceae
- Amblystegiaceae
- Thuidiaceae

temperate
- Hypnaceae
- Rhytidiaceae

Does Dormancy Exist in Bryophytes?

Heinjo During, on Bryonet 4 March 2016, suggested that we know very little about dormancy in bryophytes. If it exists, it might require a trigger to initiate it. During suggested that low or fluctuating temperatures could be involved. I could also postulate that darkness within the capsule might initiate dormancy before the spores are dispersed. Once dormant, many studies suggest that light and moisture are needed for germination. But During points out that most papers suggest that dormancy of moss spores is rare or absent. Others argue that it may be less rare – lacking investigation.

The behavior of spores in ***Archidium alternifolium*** (Figure 5-Figure 6) suggest that it may experience some sort of dormancy (see Miles & Longton 1992). This species requires an unpredictable but long time to germinate. Could it be that, like some seeds, its spores are immature at the time of shedding and require certain conditions to complete maturation before germinating? This immaturity might be physiological without any morphological indication. Or might there be some inhibitor that must be washed away before it germinates, like some of the desert seeds?

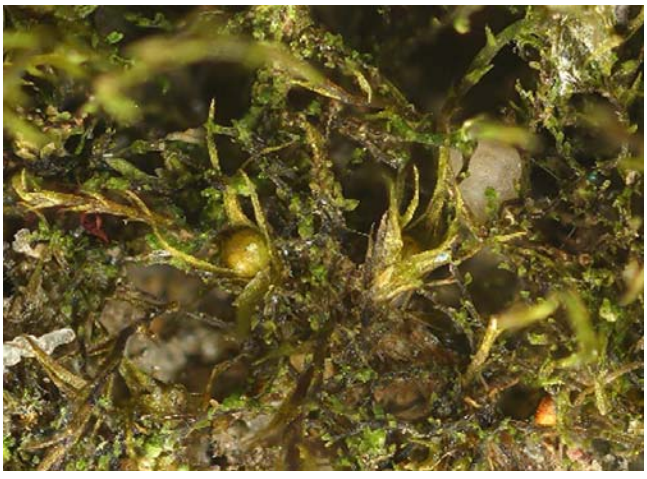

Figure 5. ***Archidium alternifolium*** with capsule. Michael Lüth, with permission.

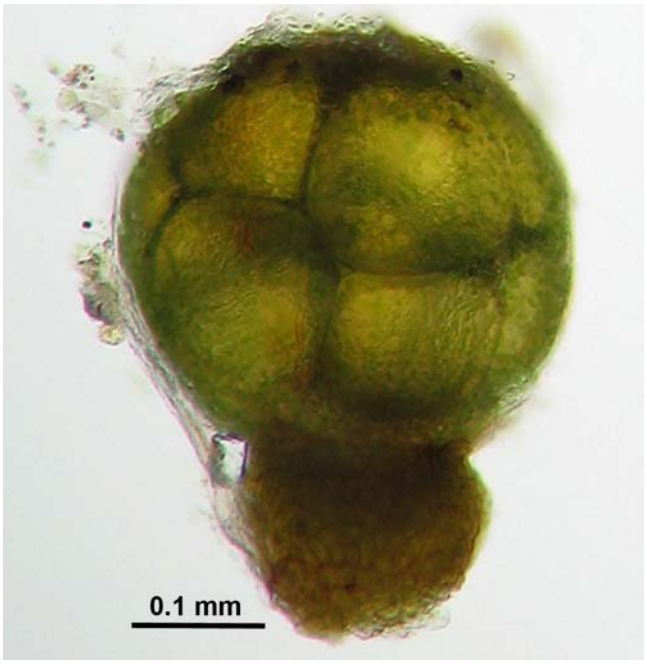

Figure 6. ***Archidium alternifolium*** capsule showing the large spores inside. Photo by Norbert Stapper, with permission.

Some indications of dormancy do exist. McLetchie (1999) examined dormancy/nondormancy cycles in the liverwort ***Sphaerocarpos texanus*** (Figure 39). He found the loss of dormancy increased as the length of time that spores were kept at the various incubation periods from 1-91 weeks. Furthermore, warmer temperatures aided in breaking dormancy. On the other hand, spores held at each of the three thermoperiods germinated best when transferred to 16/10°C and failed to germinate when transferred to the warmer combinations of 35/20 and 30/15°C (see below under Temperature). Thus, warmer temperatures both maintained dormancy and accelerated germination when that temperature dropped. Seasonal changes followed by low temperatures induced these spores to return to a secondary dormancy.

Hock *et al*. (2013) suggested that the spores of ***Phascum cuspidatum*** (Figure 7) in grassland exhibited dormancy. Watson (1983) suggested that chemical inhibition occurs among juvenile members of ***Polytrichum*** *s.l.* (Figure 8).

Figure 7. ***Phascum cuspidatum*** capsules. Photo by Michael Lüth, with permission.

Definition of Spore Germination

Successful germination is prerequisite to establishment in a new location, yet its consideration is lacking in nearly every ecological study. If we are to retain our rare and endangered species, we must understand the germination and establishment requirements that will permit them to become established in our conserved areas.

Bryophyte spores begin their life following meiosis in the capsule (Figure 1). There they wait and develop to maturity before dispersal. Generally, they do not germinate within the capsule.

There is no general agreement on the definition of spore germination. **Swelling** is the result of the uptake of water by the spore; **distension** occurs when the cell wall ruptures and the germ tube is formed. Some authors consider swollen spores as germinated (Bauer & Mohr 1959, Mogensen 1978a). But swelling of the spore is a passive process and therefore it does not fully satisfy a definition of germination. From the physiological standpoint, a spore has germinated when the spore wall has ruptured and when the germ tube has been formed, since these involve active processes. A more precise definition is given by Valanne (1966) who states that the "distension phase is the least ambiguous and most useful practical criterion for spore germination." In some species, among others ***Polytrichum commune*** (Figure 8), there is an intermediate phase between the swelling and the distension in which the germ tube is formed and the spore wall is stretched – the **protrusion phase** (Figure 22) (Karunen 1972).

Figure 8. ***Polytrichum commune*** with capsules. Photo by Kristian Peters, through Creative Commons.

Some species don't wait for environmental conditions become suitable. Rather, they germinate while still in the capsule (D'Rozario & Bera 2006). This is known for ***Marchantia palmata*** as well as a few other liverworts and some mosses. Two forms of germination occur among the bryophytes: **endosporic** and **exosporic**. **Endosporic** development is that development in which the spore cell divides within the cell wall, creating a multicellular structure before a protonemal thread emerges from the spore wall. In these cases, the spore wall stretches as the internal structure expands. This endosporic phase often coincides with **precocious germination**, that is,

development that occurs while the spore is still within the capsule (Nehira 1983). Such a developmental pattern occurs in ***Pellia epiphylla*** (Figure 9-Figure 10) and ***P. neesiana*** (Figure 11) (Bartholomew-Began 1996), distinguishing these taxa from other members of the **Metzgeriales** and from most bryophytes. Such a strategy would be an adaptive device for such taxa as ***Gymnostomum*** (Figure 12; pers. obs.) and others that live in dry habitats where a head start could permit them to reach sufficient size to survive before becoming dry. Nehira (1987) found that the endosporous habit was common among **epiphytic** (tree-dwelling) and **saxicolous** (rock-dwelling) liverworts and mosses. Other taxa, including the mosses ***Andreaea*** (Figure 13), ***Glyphomitrium*** (Figure 14), and ***Pylaisiella*** (Figure 15), and the liverworts ***Cavicularia*** (Figure 16), ***Radula*** (Figure 17), and ***Trichocoleopsis*** (Figure 18), may be endosporous, but do not become multicellular and stretched until after capsule dehiscence (Nehira 1983).

Figure 9. ***Pellia epiphylla***, a liverwort with endosporic development. Photo by David T. Holyoak, with permission.

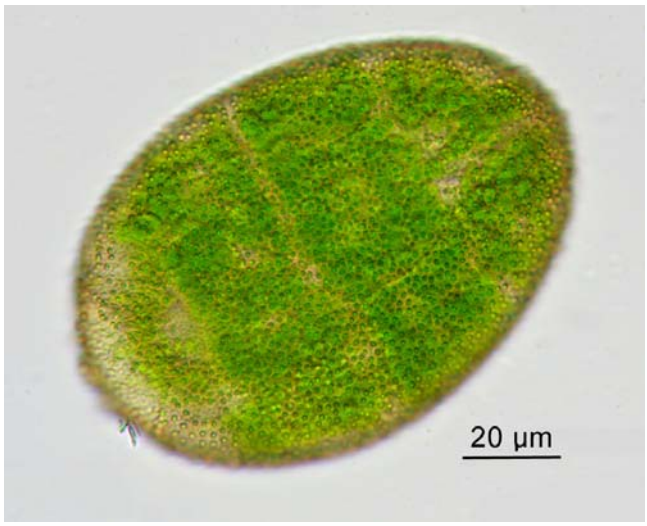

Figure 10. ***Pellia epiphylla*** spore showing endosporous development that occurs within the capsule. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 11. ***Pellia neesiana***, a species with endosporic development. Photo by Jan-Peter Frahm, with permission.

Figure 12. ***Gymnostomum aeruginosum*** with capsule. Photo by Michael Lüth, with permission.

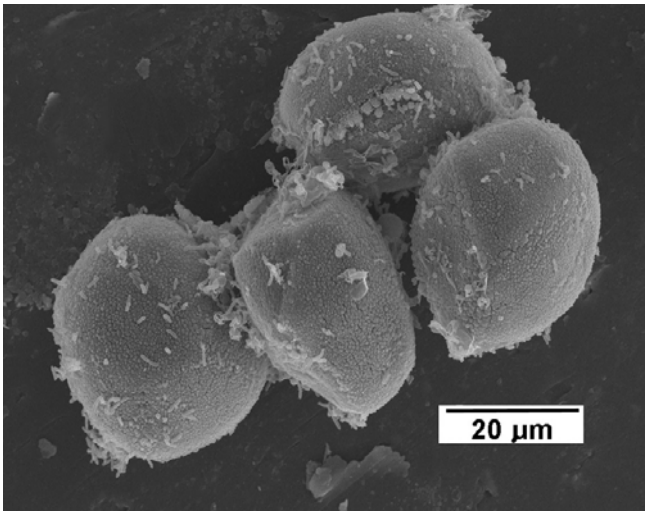

Figure 13. SEM of ***Andreaea rothii*** spores before germination. Photo courtesy of Karen Renzaglia.

Figure 14. ***Glyphomitrium davesii*** with capsules. Photo by Niklas Lönnell, with permission.

Figure 15. ***Pylaisiella polyantha*** with capsules. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 16. ***Cavicularia densa***. Photo by Harum Koh, through Creative Commons.

Exosporic development, occurring in most mosses and liverworts, has its first and only development outside the spore wall (Figure 22), a strategy more appropriate for wetter habitats than those used by species with endosporic development. Many sporeling types are known among the **Bryophyta** (Figure 12-Figure 15), **Marchantiophyta** (Figure 9-Figure 11, Figure 16-Figure 18), and **Anthocerotophyta** (Figure 19-Figure 20); (see Nehira 1983 for illustrations and a review). These are influenced not only genetically, but may also be modified environmentally (Alcalde *et al.* 1996). Even wavelength of light can affect germination patterns, as in ***Anthoceros miyabeanus***, where in red light it is exosporic, but in white light it is endosporic (Wada *et al*. 1984). Could such a difference in wavelength effect precocious development for those receiving mostly red light in the green capsule, but then stimulate exosporic development once the spore has left the capsule and become exposed to white light?

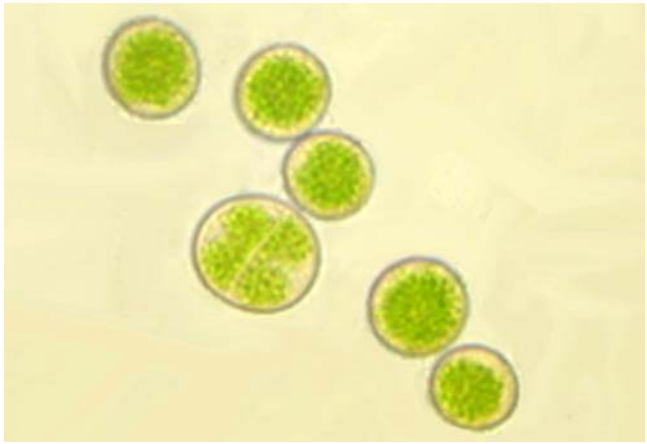

Figure 17. ***Radula recubans*** spores showing one with endosporic development. Photo by Adaíses Simone Maciel da Silva, with permission.

Figure 18. ***Trichocoleopsis sacculata***. Photo by Rui-Liang Zhu, with permission.

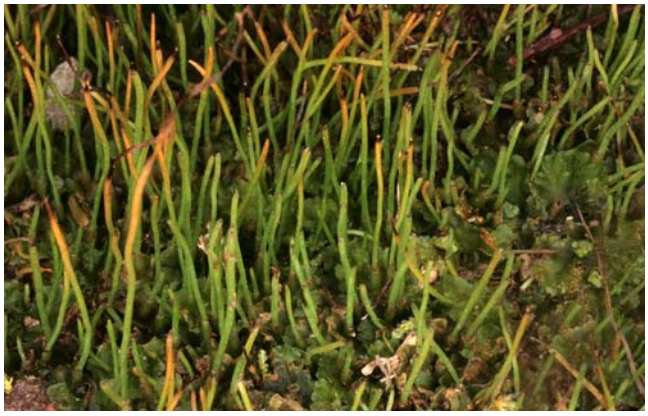

Figure 19. ***Anthoceros fusiformis*** with sporophytes. Photo by Jan-Peter Frahm, with permission.

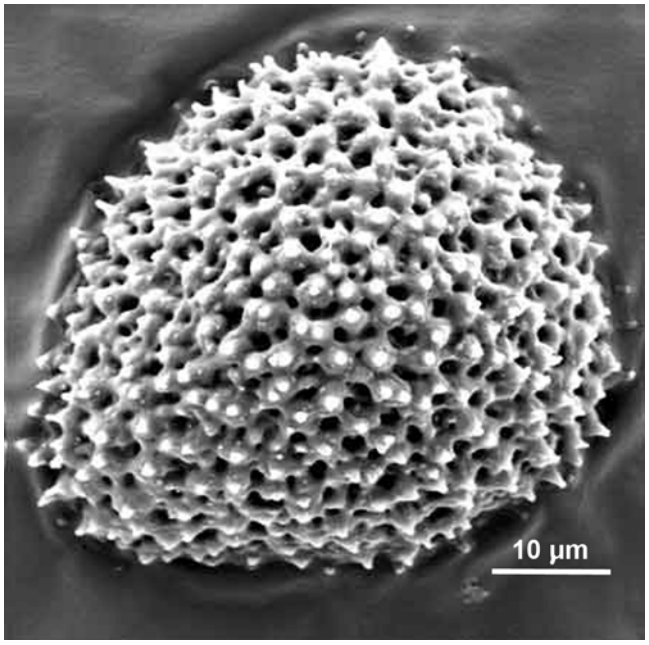

Figure 20. ***Anthoceros fusiformis*** spore distal view, SEM. Photo by Bill Doyle, with permission.

Figure 21. ***Macromitrium sulcatum*** with capsules. Photo by Manju Nair, through Creative Commons.

Figure 22. Exosporic germination of ***Fontinalis squamosa***. Photo by Janice Glime.

Germination Process

The germination process is one in which cell wall thicknesses change (Olesen & Mogensen 1978). For ***Polytrichum commune*** (Figure 8), ***Ceratodon purpureus*** (Figure 112), ***Funaria hygrometrica*** (Figure 23), and ***Macromitrium sulcatum*** (Figure 21), and probably most if not all species, this process involves a thickening of the intine in the region of the aperture, a decrease in the thickness of the exine there, presence of a lamellate structure next to the thin part of the exine, and accumulation of electron-dense material into the thin layer separating the intine and exine. In ***P. commune***, a knob-like structure forms in association with the thickened part of the intine. Water is absorbed through the aperture region, followed by swelling, rupture of the spore wall, protrusion, and recovery followed by spore distension. Spore swelling involves both symmetrical and asymmetrical swelling. The asymmetrical swelling results from swelling of the asymmetrical intine which protrudes beyond the exine and perine of the spore. The symmetrical swelling is not actually a part of the germination, but rather is the result of remoistening.

The swelling stage of spore germination requires water, whereas the distention phase requires light (Bhatla 1994). These requirements exhibit a certain amount of control over the timing of germination and help to prevent the needless loss of resources. These requirements are critical to the maintenance of spores in soil spore banks by preventing germination when the soil is wet but the spore is buried. Additional factors involved in germination are *p*H, calcium ions, and auxins (Bhatla 1994).

Water Needs

Based on studies conducted so far, all bryophytes require water for germination of the spore. The swelling phase of germination seems only to require the physical process of water absorption, resulting in rehydration (Bhatla 1994). Lack of sufficient water may in fact be the means that prevents germination of most spores within the capsule. On the other hand, mechanisms for rapid water uptake to seize upon germination opportunities could be important for some species.

Neidhart (1979) reports that spores of ***Funaria hygrometrica*** (Figure 23) withstand desiccation better in the capsule than when isolated. This seems reasonable since the capsule itself should prevent excessive drying on the interior. However, Neidhart used "young" spores and capsules but did not indicate whether the spores were swollen. Since one problem with desiccation is the leakage of nutrients through damaged membranes upon rewetting, it might be possible that spores in the capsule withstand desiccation better if the capsule can serve as a reservoir of nutrients after rewetting. Little evidence is available to tell us if the moss spores are able to draw upon nutritional sources of the moss as they continue their development in the capsule. Mogensen (1978a, 1981) has indicated that the columella serves as a reservoir of liquid, and that the smallest spores die first as that reservoir dries, permitting the larger spores to continue their growth. A similar series

of abortions of smaller spores occurs in ***Fontinalis squamosa*** (Figure 24; Glime & Knoop 1986). It would be interesting to examine this reservoir to determine if it in fact may be a source of sucrose or other nutritional substances as well.

Figure 23. ***Funaria hygrometrica*** spores. Photo by Eugenia Ron and Tom Sobota, with permission.

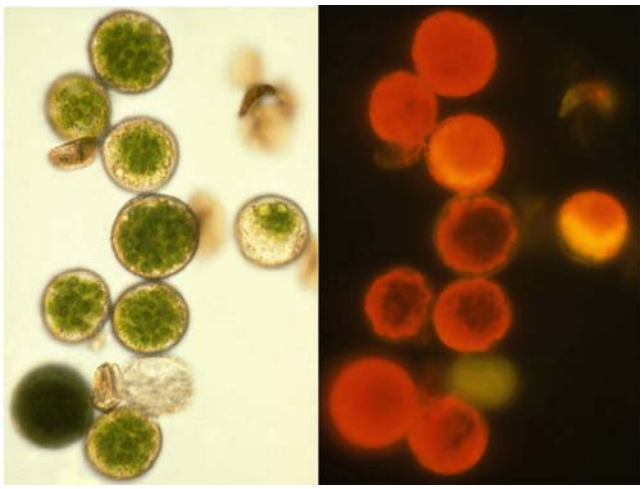

Figure 24. Comparison of chlorophyll in white light (**left**) and chlorophyll fluorescence in UV light (**right**) in large and small spores of ***Fontinalis squamosa***. Note dark gray areas in the photo on right are those areas lacking chlorophyll, and smaller spores tend to disappear in UV light. Photo by Janice Glime.

Once the spores leave the capsule, it is the structure of the spore itself that must serve to prevent desiccation. Bryophyte spores have an innermost layer called the **intine**, consisting of complex polysaccharides such as pectin and callose. The outer wall, the **exine**, is lamellated with plates believed to be **sporopollenin** (phenol-containing polymer known to impart high chemical resistance to exine of pollen), as in higher plants. In some species an opaque zone, termed the **separating layer**, may be seen between the intine and the exine.

Mosses have a further, poorly understood layer, the **perine**, which forms on the outside of the exine in some taxa. The **perine** often forms a pattern characteristic of the species. It is unusual in that it is formed by the sporophyte as an add-on to the outer wall of the spore (Mogensen 1983). It is made from old tissue of the columella and the mother spore wall (Crum 2001). Thus, such a layer is absent in liverworts, which lack a columella. Mogensen (1981) hypothesizes that the perine plays a role in avoiding germination during periods with too little water to survive, such as that provided by dew, and that it is of particular importance as a survival mechanism for the annual shuttle life strategy (living only one or few years in one location). However, we do not know how strongly the perine is bound(?) to the exine layer, or even how. It would be worthwhile to investigate SEM (scanning electron microscope) pictures of the perine of different moss species to see whether certain perine patterns are correlated with habitats liable to desiccation. Furthermore, it is possible that it plays an important role by providing capillary spaces that permit rapid uptake of water during precipitation events, or, as Mogensen suggests, its variation in thickness may provide "significant protection against desiccation of the spore."

Mogensen (1983) hypothesizes that the **exine**, or outer layer of the spore, serves to protect the spore from mechanical damage from the external environment. He bases this hypothesis on its loss of **tensibility** (strength when pulled end-to-end) at maturity, a phenomenon that seems to be common to all bryophytes. On the other hand, a thicker exine might also help to protect the spore from UV, permitting it to take advantage of those long-distance excursions by wind and updrafts.

The **intine** seems also to have a role in rapid uptake of water, through the aperture, facilitating distribution of water to all parts of the cell membrane (Mogensen 1983). The intine might also differ among species in its ability to facilitate this uptake and distribution. Since the thin part of the intine corresponds with the thick part of the exine and vice versa, perhaps water can move from one end of the cell to the other between the layers and thus need only to traverse the thin parts of each layer.

Energy Needs

The presence of water is a necessary prerequisite for the conversion of stored food reserves into glucose for the production of ATP. Any growth following swelling will necessarily require energy, so it is necessary to understand energy storage and requirements for conversion in order to interpret control over successful germination.

The requirement of light for spores to germinate permits them to remain where they have landed until conditions suitable for further development are present. Therefore, energy is not wasted by germination underground, under leaves, or under snow cover. However, even light-requiring moss spores can be induced to germinate by the addition of sucrose in dark conditions, indicating that the need for light is a need for energy. Sood (1975) found that 1.5% sucrose was optimum for germination, but that 4.8% was inhibitory for ***Pogonatum aloides*** (Figure 25), which does not germinate in the dark. Moss spores are green and chloroplast **grana** (stack of chlorophyll packets within the chloroplast where light reactions of photosynthesis take place) are already present before germination. Furthermore, when sufficient starch is present, the spores are able to make chloroplasts in the dark (Bhatla 1994). Therefore, the most obvious hypothesis to explain the need for light is that light causes photosynthesis, which produces glucose and the glucose is converted to sucrose that provides energy and contributes to swelling by causing osmosis.

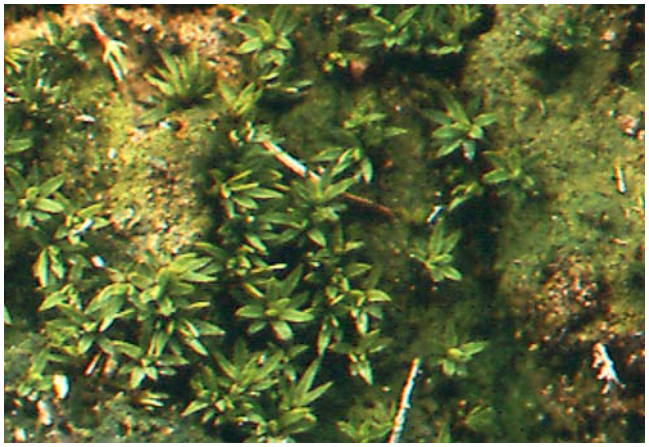

Figure 25. ***Pogonatum aloides*** with persistent protonemata. Photo by Janice Glime.

A second hypothesis is that stored carbohydrates break down into sucrose. We know that α-amylase, the enzyme that breaks starch down to glucose, increases its activity in short days and decreases it in long days in ***Marchantia polymorpha*** (Figure 26). Likewise, **GA_3** (a **gibberellin**) can mimic this photoperiod response (Maravolo 1980). We also know that gibberellin antagonists prevent starch disappearance (*i.e.* prevent metabolism to sugars). Gibberellins, therefore, seem to play a role in starch metabolism leading to germination. However, since gibberellins themselves are not light sensitive, we must look for a photoreceptor. Hahn and Miller (1966) demonstrated that increase in size of chloroplasts in ***Polytrichum commune*** (Figure 8) germinating spores was due to presence of starch. The reaction was red/far-red reversible (*i.e.*, interchanging these two light qualities would reverse the reaction), and only red and white light produced germination and chloroplast replication. Spores of the species would germinate only in light or in darkness + sucrose. The red/far-red reversibility is evidence of **phytochrome** activity, and the coupling of starch degradation with the multiplication of chloroplasts suggests that light is necessary for this starch to sugar conversion, thus supporting the second hypothesis.

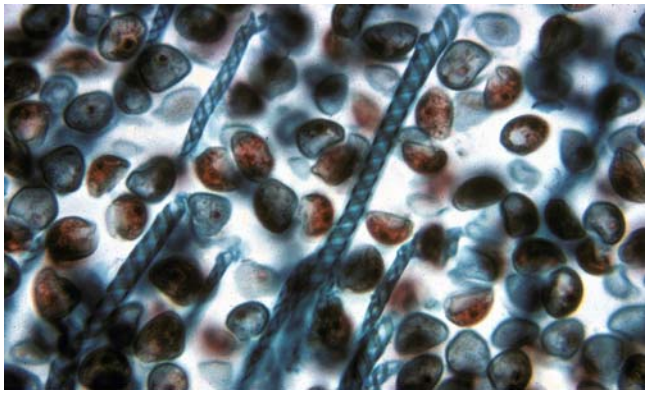

Figure 26. ***Marchantia polymorpha*** spores & elaters (stained) as they would appear in the capsule. Photo from Michigan State University teaching collection, with permission.

The response to short days is likewise consistent with phytochrome activity and would permit the spores to germinate in spring at the beginning of the growing season when most areas in the temperate zone have adequate rain and sufficiently cool temperatures for these C_3 mosses and liverworts to succeed. On the other hand, decreased germination in long days would prevent precocious germination of spring-produced spores that would most likely not succeed in the hotter, drier days of summer.

The decrease in stored carbohydrate (mostly as starch) over time may account for the inability of older spores, especially small ones, to germinate. It would be interesting to correlate stored carbohydrate with spore longevity. Our lack of field data on time of spore germination greatly inhibits our interpretation of the ecological implications of these physiological characteristics.

A third way to obtain sugars is breakdown of fatty acids through the glyoxylic acid cycle. This pathway has been described for germinating seeds, rich in fatty acids. Bryophytes also have fatty acids (Jamieson & Reid 1976; Suire & Asakawa 1981), and these are known in moss spores (Karunen & Liljenberg 1978). They play a role in spore germination of ***Polytrichum commune*** (Figure 8) (Karunen 1972), where, at the end of the protrusion phase, fatty acid degradation gives energy for development of chloroplasts.

It is clear that an energy source is necessary for many (probably all) spores. However, there is no rule that says the method must be the same for all, nor that only one of these could be in effect. Multiple sources of sugars and a variety of options would permit greater success in a wider variety of conditions. Perhaps having multiple possible sources of energy for spore germination is one factor that permits ubiquitous species of bryophytes to be ubiquitous. But what are the relative roles of photosynthesis, glyoxylate cycle, and breakdown of starch in production of sugars and energy during germination of the spore?

In very immature brown spores (lacking chlorophyll) we often see small lipid bodies. Chloroplasts are not yet formed and photosynthesis does not take place. It is reasonable that the first way to obtain sugars in such spores is through breakdown of lipids in the glyoxylate cycle, and lipid catabolism may occur prior to chloroplast formation.

In addition to gibberellins, IAA can have a stimulating effect on germination of spores in light but not in dark (Valanne 1966). How can we explain this? We know light has a stimulating effect on production of sugars. As a result of the change in osmotic potential of the cell, there is uptake of water. IAA makes the cell wall more elastic so that the spore can swell. In the dark there is no sugar production and exogenously supplied IAA has no effect. However, in the same experiment, Valanne noticed a decrease in percent of spores germinated when compared to control cultures with no growth substances. It might be possible that supplied IAA increased the IAA concentration above normal levels. High levels can induce the formation of IAA oxidase, resulting in the catabolism of IAA, and induce the production of ethylene, both of which could explain the lower percent germination of spores in IAA culture media compared with the control medium. This scenario would support hypothesis 1, that light is necessary because photosynthesis is necessary to provide sugars.

IAA probably has its main effect during the swelling of the spore. The inactivation of IAA by IAA oxidase is often correlated with an increase in GA content (Maravolo 1980). We know from tracheophyte studies that GA is sometimes formed in the day and used at night and that it

can cause the same response as a long day in long-day plants (Salisbury & Ross 1978). GA has a stimulating effect on α-amylase, and the resulting breakdown of starch provides material for cell wall formation. GA may thus play a role in the distension phase.

One might propose the following sequence: breakdown of lipid bodies prior to formation of chloroplasts; effect of IAA and photosynthetically derived sugars during the swelling phase; formation of gibberellic acid and breakdown of starch leading to the distension phase. This, however, is the reverse of the process known for tracheophytes. The position of lipid breakdown is the most tenuous, with Karunen's (1972) work showing degradation of fatty acids at the end of the protrusion phase, giving energy for chloroplast development.

It is clear that germination requires **energy**. Three potential pathways could provide that energy: 1) stimulation of **phytochrome** that initiates the **starch** to **sugar** conversion that precedes production of **chlorophyll**, possibly under control of **GA**; 2) conversion of **fatty acids** to sugars, providing energy for production of chlorophyll; 3) photosynthesis of green spores in the light. The requirement for light insures that spores will not germinate under soil or elsewhere where they will never get light. Small spores and older spores have poor germination success, most likely because of diminished energy stores. **IAA** provides the **elasticity** needed, sugar provides **energy** and the **osmotic potential** that brings in water, and **GA** stimulates the **α-amylase** production that precedes **distension**.

Light Needs

Most moss spores have chlorophyll at maturity, and that most likely helps to provide their energy as they germinate, through photosynthesis, as demonstrated in ***Funaria hygrometrica*** (Figure 23) (Krupa 1965).

Light is not required for swelling in most spores (Valanne 1966), but it is for germination. Even in species where swelling (germination) occurs in the dark, some individual spores require light. In ***Ceratodon purpureus*** (Figure 112), starch grains increase at the onset of darkness (Valanne 1971) but disappear from chloroplasts of those that swell in darkness, and the lipid bodies change shape (Valanne 1966). Since these changes do not occur in those species requiring light, it suggests that lack of germination may be due to the inability to mobilize food reserves. We have discussed the ability of **gibberellic acid** to mobilize starch in the presence of light, but what accounts for dark mobilization? Do spores differ in their content of **α-amylase**, with those rich in α-amylase waiting only for sufficient water to carry out their reactions? Is this mechanism purely a random distribution of materials at **sporogenesis** (spore production), or is it a genetically engineered device that conserves resources in some spores while permitting others to germinate early?

The clandestine ***Cryptothallus mirabilis*** (Figure 27), a liverwort that lives **within** a bed of ***Sphagnum***, lacks chlorophyll in the entire plant, including spores (Hill 1969) and has no requirement for light to germinate. It would be helpful to know if it has a ready supply of α-amylase.

Figure 27. ***Cryptothallus mirabilis*** with young sporophytes. Photo by Michael Lüth, with permission.

Although it seems that light intensity is the most important factor in germination of bryophyte spores, Kinugawa and Nakao (1965) found that photoperiod affected the termination of ***Bryum pseudotriquetrum*** (Figure 28). Most spores required more than a 5-hour photoperiod for germination, whereas more than about 12 hours seemed to make little difference, even though only about 75% of the spores were germinating (Figure 29).

Figure 28. ***Bryum pseudotriquetrum*** with capsules. Photo by Michael Lüth, with permission.

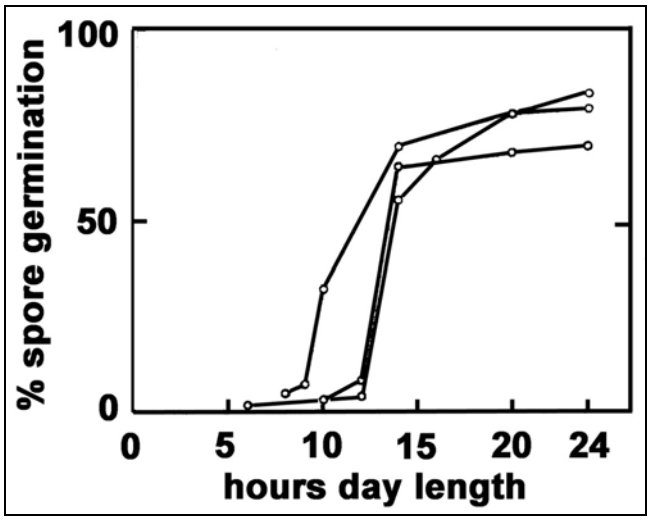

Figure 29. Effect of day length on germination of spores of ***Bryum pseudotriquetrum***. Redrawn from Kinugawa & Nakao 1965.

We know almost nothing about light intensities needed in the field for germination of spores. In the lab, we often add substances that could replace the need for photosynthetic activity. For example, ***Bartramidula bartramioides*** germinated best at 3500-4000 lux of continuous light in the lab, but the addition of a 1% sucrose solution may have had overriding effects to counter the low light and continuous illumination (Chopra & Rahbar 1982).

During (1979) assumes that lack of light and water in the capsule might restrain the germination of spores within the capsule, but it is questionable whether the capsule keeps all the light out. Spores can germinate under very low light intensities, *e.g.*: (1) Spores of ***Schistostega pennata*** (cave moss; Figure 30) germinate in the dark (Nehira 1967). (2) Geissler (1982) found that moss spores germinate under snow, thus under a greater far-red/red light ratio than sunlight (Winchester pers. comm.). (3) Spores of ***Dicranum scoparium*** (Figure 50) and ***Ceratodon purpureus*** (Figure 112) germinate at a light intensity of only 1 lux (Valanne 1966). (4) ***Cryptothallus mirabilis*** (Figure 27), which lives under a thick ***Sphagnum*** layer, is able to germinate in the dark, or under a very low light intensity. These examples show that low light intensity may not be a decisive factor to inhibit the germination of at least some kinds of spores within the capsule, or at least might not be the only factor involved.

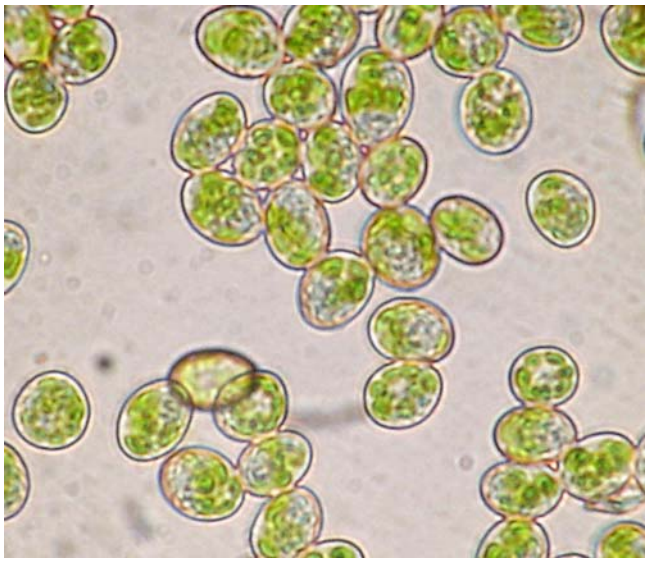

Figure 30. ***Schistostega pennata*** spores, a species where spores germinate in the dark and under snow. Photo by Misha Ignatov, with permission.

On the other hand, the wavelength of light inside the capsule may play a significant role. The capsule wall changes its color during maturation and the color of the capsule at the time of spore maturation could have an effect on the germination of spores. We know that spores of different species germinate under different wavelengths (Valanne 1966). For example, ***Funaria hygrometrica*** spores (Figure 23) will germinate at long wavelengths (580-700 nm) at low light intensities, but require high intensities at short wavelengths (362-500 nm) (Krupa 1967). Since short wavelengths are likely to be filtered out most easily, this could be an effective inhibitory mechanism. Valanne (1966) reported that far red and blue light inhibit swelling of ***F. hygrometrica*** spores and that blue-green light reduces distention in ***Funaria*** and ***Ceratodon*** (Figure 112) to lower than that in the dark. On the other hand, she found that ***Ceratodon*** and ***Dicranum*** (Figure 50) are indifferent to far red light. Bauer and Mohr (1959) showed that the ratio of red to far-red light is important in the germination of ***Funaria***.

In a later study on ***Ceratodon purpureus*** (Figure 112), Valanne (1971) found that illumination with blue light resulted in sporelings with chloroplasts that were richer in starch, had denser stroma, and had more mitochondria than those in red light. The sporelings in red light made more effective use of reserve lipids.

Bauer and Mohr (1959) found that the initiation of germination in ***Funaria*** (Figure 23) depends on phytochrome. The involvement of phytochrome could explain why Krupa (1967) found retarded germination in green light, but after 18 hours at 680 nm (optimum wavelength), followed by 24 hours at 544 nm (green), germination was greater than when 680 nm illumination was followed by dark. In working with ***Octoblepharum albidum*** (Figure 31) spores, Egunyomi (1979) also found that wavelength was important in the onset of germination. Red, cyan, green, mimcro-7, and orange light resulted in germination, but blue, mercury green, deep yellow, and deep red inhibited it. White light resulted in germination and reversed the effects of the inhibitory light, except for the inhibition by mercury green. It might be worthwhile to follow the germination capabilities of the spores of different species during ripening of the capsule, and to relate the spore maturation stages with the changes of color of the capsule. Such color changes in the capsule might be important in preparing the spores for germination at their maturity while preventing it if they are dispersed while still immature.

Figure 31. The epiphytic moss ***Octoblepharum albidum*** with capsules. Photo by Janice Glime.

Not only does the capsule wall change color during the maturation process, but ambient light will change considerably between early spring and summer. As the snow melts and the trees still lack leaves, white light is able to reach the ground. But in a few weeks to months, depending on the latitude, canopy leaves filter out the red light and transmit light high in green and far-red (Bjorkman 1981). These light quality changes could likewise serve as signals to spore germination, and, in combination with

capsule color, could be effective inhibitors for mature spores still inside the capsule.

In some species, such as ***Mnium hornum*** (Figure 32), instead of depending directly on its environment, the spore has an endogenous development cycle that results in the immediate germination of the spore (Newton 1972a, b). Nevertheless, although the germination is independent of both light and temperature, light is still important in maintaining the internal clock; a slight delay of the development caused by short days helps to maintain an annual rhythm in spore maturation (*i.e.*, it resets the clock) and subsequent germination. It is possible that temperature plays a similar role.

Figure 32. ***Mnium hornum*** with capsules. Photo by Jan-Peter Frahm, with permission.

Whereas most bryophytes require light to germinate, a few that live in very low light do not and others require as little as 1 lux. In culture, sugar can substitute for the presence of light and its presence may explain the germination of some species in the dark in nature. Furthermore, the presence of α-amylase could permit spores to convert stored starch to sugar for germination without light. The wave length of light seems to be important for some mosses and could safeguard spores against germinating in the wrong habitat. There are insufficient studies on requirements for spore germination to draw any generalizations about light requirements and habitat, but we can hypothesize that most sun-loving species are more likely to require red light than those that grow in the forest and other low-light habitats. Nevertheless, as mentioned above, ***Ceratodon purpureus***, often found in high light situations, can germinate at only 1 lux. Clearly something more than light intensity and photosynthesis is involved.

Environmental Control over Germination

The three requirements already named – water, energy, and light – obviously will exercise primary control over the germination of spores. However, specific requirements of individual species will further narrow the window of germination. These controls can include *p*H, nutrients, temperature, photoperiod, and exogenous substances, all interacting with internal substances that respond to these environmental cues.

Delay until the right weather (temperature, moisture) occurs is easily perpetuated genetically, but what selects for genes to prevent germination on the wrong substrate? Unless the spore can be re-dispersed, there is no selective advantage that would favor inhibition of germination. Yet there are species where the nature of the substrate does control germination and further development. For example, calcium enhances germination success in the **calciphile** (calcium loving) ***Orthotrichum cupulatum*** (Figure 33), but germination of ***Dicranella cerviculata*** (Figure 34) is depressed by calcium (Vaarama & Tarén 1963). In ***Stereophyllum radiculosum*** (Figure 35), control cultures and those at 22 ppm Ca produced one protonema per spore, whereas those at 50-150 ppm each produced two (Olarinmoye *et al*. 1981). When the leafy liverwort ***Cheilolejeunea clypeata*** was grown on a Ca-free medium, the spores became distended, but the protonema failed to develop during the next five months of culture, whereas in the normal medium young plants had developed (Geldreich 1948).

Are these alternatives in protonemal production adaptive, suggesting that more calcium should be able to support more gametophores? A species loses nothing by germinating in an unsuitable habitat, as opposed to no germination at all. Yet it seems that many spores hang on tenaciously to life for years, awaiting the right set of conditions for germination. And sometimes those needed changes may actually occur.

Figure 33. ***Orthotrichum cupulatum*** capsule that has expelled its spores. Photo by Vita Plasek, with permission.

Figure 34. ***Dicranella cerviculata*** with capsules. Photo by David T. Holyoak, with permission.

Figure 35. ***Stereophyllum radiculosum***. Photo by Scott Zona, with permission.

*p*H

Apinis (1939) contended that most moss spores are almost indifferent to *p*H range. The spores germinate in a wide *p*H range, the protonema range is more restricted, and the *p*H range of the leafy plant in culture corresponds closely to its range in nature. Philippi (1969), on the other hand, found that species from acid or raw humus reacted uniformly, preferring acid, whereas species from wood had a strong divergence of *p*H range. Armentano and Caponetti (1972) felt that *p*H may be the factor that limits the habitat for ***Funaria hygrometrica*** (Figure 23) and ***Tetraplodon mnioides*** (Figure 36), both of which germinate better at a basic *p*H. Vishvakarma and Kaul (1988) found that in culture two liverworts, ***Plagiochasma appendiculatum*** (Figure 37) and ***Reboulia hemisphaerica*** (Figure 38), had an optimum *p*H for germination and thallus growth of 6.0.

Figure 36. Capsules of the dung moss ***Tetraplodon mnioides***. Photo by Zen Iwatsuki, with permission.

But how does *p*H affect spore germination? Does each species have a spore wall requiring a characteristic *p*H, such as that found on tree bark? What is the effect of *p*H on the cation exchange between spores and the substrate? A change in the *p*H can affect enzymatic activities, but it can also affect the solubility and release of certain ions in the substrate and cause, indirectly, a toxic effect. Could it be that *p*H is simply an indicator of needed ions that are associated with the higher or lower *p*H? Vishvakarma and coworkers (1987) found that calcium enhanced spore germination in ***Plagiochasma*** (Figure 37) and magnesium did likewise in ***Reboulia*** (Figure 38); both of these ions are generally associated with high *p*H. Furthermore, as we have seen above, calcium is involved in germination of some species, and its transport may be affected by *p*H.

Figure 37. ***Plagiochasma appendiculatum***. Photo by Michael Lüth, with permission.

Figure 38. ***Reboulia hemisphaerica*** with archegoniophores. Photo by Gideon Pisanty, through Creative Commons.

Nutrients

Although only water and light are generally considered necessary for germination, Arnaudow (1925) was unable to get spores of ***Dicranum scoparium*** (Figure 50) to germinate in water for four weeks, but when particles of earth were added to the water, they germinated in two days.

The cosmopolitan ***Funaria hygrometrica*** (Figure 23) seems to have some precise requirement that is elusive. Its

germination occurs over a wide range of temperature, light intensity, and chemical conditions. According to Hoffman (1966), the soils where it grows have no consistently high or low nutrients and *p*H is neither high nor low. Yet, Hoffman's efforts to grow the moss on soils with various nutrient conditions failed, but soil from burned areas supported growth. In experiments with heated soils, Hoffman found that it grows well on C horizon soils (inorganic parent rock material) heated to 200-300°C, but grows poorly or not at all if the soil has been heated to over 300°C. However, if N and P are added to soils heated to 600°C, it grows well. This suggests that loss of N and P at high temperatures account for its inability to grow. On the other hand, Southorn (1977) relates the presence of ***Funaria hygrometrica*** to the change of source of N and P in the soil. He found that ammonia-N inhibits germination, and that replacement of ***Funaria hygrometrica*** by other bryophytes was correlated with a decrease of phosphate-P. The decrease in abundance may also partly be a result of changing nutrient concentration due to leaching by rain water. Yet Chevallier (1975) demonstrated the requirement of manganese as a **micronutrient** (those required in small quantities) for germination. The restriction of ***F. hygrometrica*** to relatively open areas is consistent with its requirement for light for germination.

But what do other bryophytes require? Most bryophytes have been grown from tissue cultures (see Sargent 1988) using one of several standard media. No comprehensive study in the lab or the field has provided any information on the nutrient requirements, if any, for germination success. Most likely the requirements are few, if any, until after germination and the protonema requires them for growth.

Temperature

One might conjecture that temperature could control when and where species germinate and thus limit distribution. For example, Longton and Greene (1969) found that germination rate steadily increased within a temperature range between 5º and 20ºC in ***Pleurozium schreberi*** (Figure 98), a normal temperature range for spring and autumn. One advantage to this ability to germinate over a wide range of temperatures, with an optimum adjusted to the climate, is that it would permit multiple chances to take advantage of changeable weather in a given season without forfeiting an entire year's crop of spores due to an inopportune germination time. Certainly such strategies exist, as in this ***Pleurozium*** example.

In ***Sphaerocarpos texanus*** (Figure 39), as discussed above, loss of spore dormancy increases as length of time at a suitable temperature increases (McLetchie 1999). Spores kept at 35/20ºC lost dormancy faster than those at 30/15ºC or 25/15ºC. However, the best germination occurred when these spores were subsequently placed at 16/10ºC (typical temperate spring or fall temperatures) and it failed at 35/20ºC and 30/15ºC (late spring and summer temperatures).

At first, McLetchie and Johnson (1997) found that the size of the ***Sphaerocarpos texanus*** (Figure 39) spore tetrad affected the male:female ratio; spores were normally dispersed in tetrads of 2 males and 2 females. However, if the tetrad was less than 90 µm, the sex ratio was female biased. Then McLetchie (2001) found that spores of ***Sphaerocarpos texanus*** behave like eggs of alligators, wherein gender is determined by temperature of the eggs! In this dioicous liverwort the sex ratio is affected by the temperature at which the spore loses its dormancy! At 25/15°C, the population became female biased, whereas at higher temperatures (35/20, 30/15°C) it was not, suggesting a differential survivorship at the spore stage.

The development of physiological races for germination temperature optima in different localities is probably a widespread phenomenon. Dietert (1977) tested ***Funaria hygrometrica*** (Figure 23) and ***Weissia controversa*** spores (see Figure 40) and found optimum temperatures that differed among populations of one species. Populations from colder habitats showed lower germination optima than populations from warmer habitats, thus suggesting that survival of the sporeling did not require the greater temperature. At first, this seems intuitively to be backwards. This temperature relationship is the reverse of McNaughton's (1966) results for *Typha* (cattail) seeds, where a higher temperature requirement for germination of northern seeds protected the seedlings from late freezing that was not a problem for southern populations. On the other hand, this system of cold-adapted species germinating at a lower temperature than those from warm areas provides a longer growing season for individuals in colder climates than would be possible if they had a higher temperature optimum. Since bryophytes are less susceptible to damage by cold and its accompanying desiccation than most tracheophytes, germination early in the season may not be a problem.

Figure 39. The thallose liverwort ***Sphaerocarpos texanus***. Photo by Paul Davison, University of North Alabama, with permission.

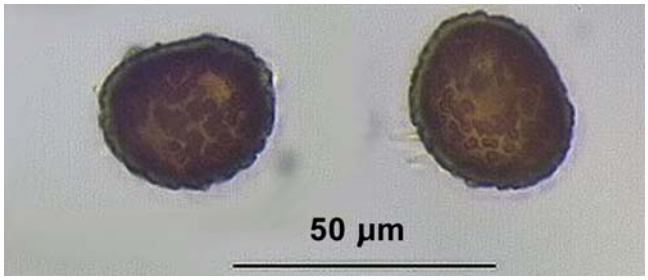

Figure 40. ***Weissia longifolia*** spores, a species that differs among populations in optimum germination temperatures. Photo by Kristian Peters, with permission.

The lack of need for warmer temperatures for sporeling survival is supported by Dietert's later work (1980) that showed optimum germination temperatures for

Funaria hygrometrica (Figure 23) of 30°C, protonema growth at 25°C, and a requirement for cooler temperatures for gametangial formation. In this case, requirements seem to agree with McNaughton's (1966) conclusions that a high germination temperature is necessary to protect the organism from late freezing conditions, but once germination has occurred, sufficiently warm temperatures are assured so there is no selection pressure for the higher temperature optimum. In other words, there is a strong selection pressure against those individuals that germinate at lower temperatures and then experience sub-zero temperatures, but once the temperature has reached 30°C, it is not likely to be sub-zero again, thus permitting those individuals to survive; there is apparently no selection pressure for high or low temperature for development in this case, unless this positions the moss to germinate in the fall and develop over winter.

One problem for spores that germinate and must overwinter as protonemata is desiccation. Frost and ice crystals are hygroscopic and draw the water from the delicate filaments. But if water is available, at least some species can overwinter safely, as can be seen for ***Dicranella heteromalla*** that live through winter in acid mine water (Figure 41).

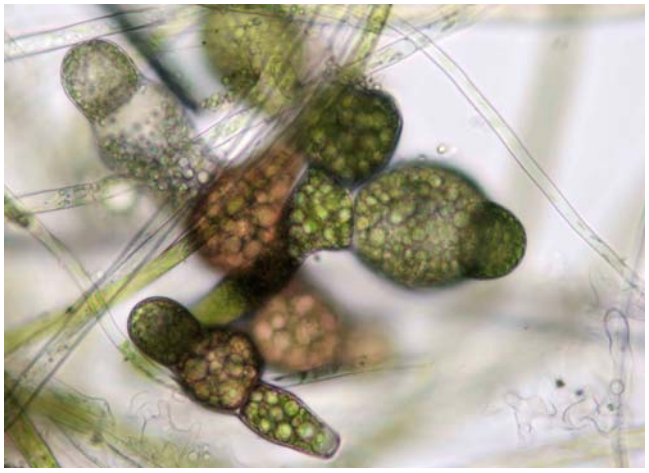

Figure 41. ***Dicranella heteromalla*** protonemata that survived winter in an acid mine lake. Photo by Jan Fott, with permission.

Chopra and Sood (1973) experimented with vernalization and temperature in the thallose liverwort ***Riccia crystallina*** (Figure 42). After 3-4 months only a few spores germinated, and those were in only 4-5% of the cultures. However, a cold treatment of 8-15°C not only increased the percentage of germination but also shortened the dormancy period to 15 days.

In summary, a requirement for a minimum temperature would prevent early germination and the increasing number of spores germinating as the temperature rises protects the population against loss of all germlings at one time in a bad weather event. Populations from colder climates may adapt by having a lower requirement for germination, thus providing them with a longer growing season. In some species, the temperature at which the spores lose their dormancy affects the gender and thus the sex ratio of the colony.

Figure 42. ***Riccia crystallina***, a species that requires a cold period to germinate. Photo by David T. Holyoak, with permission.

Vernalization

We must distinguish between the ability of spores to withstand low temperatures and the necessity for chilling (**vernalization**) for germination. For example, Van Zanten (1976, 1978a, b) froze spores in order to study **freezing tolerance** to demonstrate the possible long-range dispersal of mosses. Some spores kept their ability to germinate after 36 months of freezing.

But withstanding freezing is quite different from the need for cold temperatures for germination. Geissler (1982) illustrated the possible necessity for freezing in some taxa, mentioning that some bryophytes have a hibernation period of two winters, most likely requiring cold, but perhaps merely exhibiting immature spores, as found in seeds of some flowering plants. In ***Orthotrichum anomalum*** (Figure 45) and ***Leucodon sciuroides*** (Figure 43), freezing is favorable for the germination of the spores (During 1979), although it may not be a necessity, whereas ***Splachnum vasculosum*** (Figure 44) does require freezing (-5°C) (During 1979). However, survivorship is greater if spores are frozen in the capsule than if they are fully hydrated (in distilled water). It is likely that water activates the spores before freezing is accomplished and then freezes them in an active rather than a dormant state.

Figure 43. ***Leucodon sciuroides*** with capsules. Photo by Michael Lüth, with permission.

Figure 44. ***Splachnum vasculosum*** with capsules. Photo by Dick Haaksma, with permission.

Membrane damage can occur during freezing of an active cell, causing leakage of necessary nutrients, and a recently activated cell is more likely to have used up the energy resources for repair of membrane damage caused by desiccation (Bewley 1979). Furthermore, leaching of nutrients from a cell with a damaged membrane would be greater in distilled water than in almost any natural medium. This short period of hydration before freezing could leave insufficient nutrients and energy for repair when the cell is reactivated after freezing, and energy could, therefore, be insufficient for normal germination processes.

The achlorophyllous ***Cryptothallus mirabilis*** (Figure 27) actually germinates sooner if exposed to temperatures of -18ºC (Benson-Evans & Hughes 1960 in Schuster 1966). This is perhaps not surprising since it grows among ***Sphagnum*** species, thus being more frequent in northern habitats.

Cold, but not freezing, temperatures could be important for some species to facilitate the conversion of starch to sucrose. Glier and Caruso (1974) found that the activity of starch degradative enzymes of cold-requiring plants increased after a long exposure at 4°C. It is thus possible that cold-requiring bryophyte species use this exposure to metabolize their starch. Species that do freeze and survive could also be cold-requiring, passing through the cold, but above-freezing, temperatures as the temperature warms in spring.

Such aquatic species as ***Fontinalis*** (Figure 22, Figure 24) might require other inhibitory mechanisms to block conversion and subsequent germination in winter since they will seldom experience temperatures below 1°C in the water, or perhaps they are adapted to winter germination, which would coincide with capsule maturation and dispersal.

Germination Inhibitors

Under favorable conditions, most dispersed spores germinate fairly rapidly. Spores of ***Campylopus*** (Figure 46), ***Microdus*** (Figure 47), and ***Hymenostylium*** (Figure 48) germinate in 2, 3, and 4 days respectively (Mehta 1988). ***Funaria hygrometrica*** (Figure 23) spores germinate in 3-5 days. Although some spores have specific temperature requirements, most spores germinate when shed, provided they have suitable light and water, suggesting that they lack dormancy in the form of germination inhibitors and must depend on the sporophyte to permit major dispersal only at a suitable time. Van Zanten (1976, 1978a, b) has demonstrated long-term survivorship for spores of a number of species, suggesting that dryness effectively maintains dormancy. Others survive burial in soil, where darkness maintains dormancy.

Figure 45. ***Orthotrichum anomalum*** with capsules and surrounded by snow, evidence of its benefit for spore germination. Photo by Michael Lüth, with permission.

Figure 46. ***Campylopus flexuosus*** with capsules. Photo by Dick Haaksma, with permission.

Figure 47. ***Microdus brasiliensis***, in a genus with rapid spore germination in the presence of water. Photo by Jan-Peter Frahm, with permission.

Figure 48. ***Hymenostylium recurvirostrum*** with capsules, a genus with rapid spore germination. Photo by Paul Wilson, with permission.

Nevertheless, some spores are shed under what would seem to be suitable germination conditions. What makes them wait? Why don't spores simply germinate on leaves of their parents where most of them land? Certainly avoidance of such a tactic is desirable because they would deprive the parent plant of light, but what is it that prevents such an occurrence? It seems that at least some leafy mosses [*e.g.* ***Syntrichia*** (Figure 49) & ***Dicranum*** (Figure 50)] can provide a diffusible substance, not yet named or characterized, that inhibits the germination of the spores (Mishler & Newton 1988). Such inhibition has been known for a long time in ***Marchantia polymorpha*** (Figure 26), where the gemmae remain dormant on the parent, but begin growing immediately when dispersed from that parent onto a suitable substrate. In fact, it appears that mature plants may inhibit successful germination of both spores and asexual structures in at least some mosses (Newton & Mishler 1996).

Figure 49. ***Syntrichia ruralis*** with capsules & water drops. This genus inhibits germination of its own spores. Photo by Peggy Edwards, with permission.

For desert mosses, brief periods of moisture could cause germination, but subsequent drying would be lethal. Therefore, it would be beneficial for spores to have an inhibitor that prevented germination until sufficient water was present. In some desert seeds, an inhibitor is leached out of the seed by rain water (Fitter & Hay 1981). When rain continues, the concentration of the inhibitor in the seeds decreases below a critical level and germination occurs. When rain stops before this critical level is reached, the inhibitor is resynthesized and germination is postponed until a later rain period.

The same scenario might apply to mosses. We know that mosses can contain high concentrations of phenolic compounds (often serving as inhibitors), especially in some of the capsules that house the spores. These compounds, known to prevent germination in seeds, are likely mechanisms for preventing germination of spores within the capsule. This mechanism may also be important for inhibiting germination of spores that fall onto humic substrata or older moss parts where phenolic compounds are present. Some of the compounds could travel with the spores as they disperse, perhaps inhibiting some individuals more than others, and thus spreading the water requirements and period of dormancy over a wider range that might take advantage of unpredictable conditions.

ABA and ethylene are both known inhibitors of seed germination and could serve as well to inhibit bryophyte germination, with lunularic acid as a possible inhibitor in liverworts. Ethylene could be an effective inhibitor of spores buried in soil, building up in the small spaces there, but is a spore large enough to produce sufficient quantities on a predictable scale to inhibit germination? We don't know if this ever occurs, or even if these substances are present in bryophyte spores. These ideas are conjecture since experimental studies on the effects of either internal or external inhibitors on moss spores are lacking.

Hormonal Regulation

Like phenolic compounds, hormones may intervene in germination of spores. Shukla and Kaul (1991) found that low concentrations of five kinds of auxins, ascorbic acid, benzoic acid, and gibberellic acid all stimulated germination in the liverwort ***Plagiochasma appendiculatum*** (Figure 37), but at concentrations greater than 5 ppm, growth was inhibited. High concentrations could accumulate within the capsule, diminishing after operculum dehiscence. Could hormones from decomposing leaf litter possibly inhibit spore germination? Or could it be that newly dispersed spores have high concentrations that get leached from them by water?

Experiments by Arnaudow (1925) suggest that the gametophyte could exercise control over the germination of spores within the capsule. When embryos of ***Dicranum scoparium*** (Figure 50) were transplanted to ***Atrichum undulatum*** (Figure 53) archegonia (and that was without the help of a computer to guide his hands!), normal development ensued, producing larger capsules than in controls, but remarkably many ***D. scoparium*** spores germinated in the capsules of transplanted sporophytes, producing 3-4-celled protonemata.

Such a phenomenon of germination within the capsule is rare in mosses, occurring for example in ***Dicnemon*** (Figure 51) and ***Eucamptodon*** (Figure 52) (Goebel 1930). Arnaudow found no germinated spores in ***Dicranum scoparium*** (Figure 50) or ***Atrichum undulatum*** (Figure 53) controls, and suggested that nutrition could account for the difference. Could it be absence of an appropriate inhibitor? Or possibly a hormonal stimulant (Table 1)?

Figure 50. ***Dicranum scoparium***, a moss used by Arnaudow (1925) for embryo transplant studies. Photo by Michael Lüth, with permission.

Figure 51. ***Dicnemon calycinum*** with capsules. This is a genus in which spores germinate within the capsule. Photo by Zen Iwatsuki, with permission.

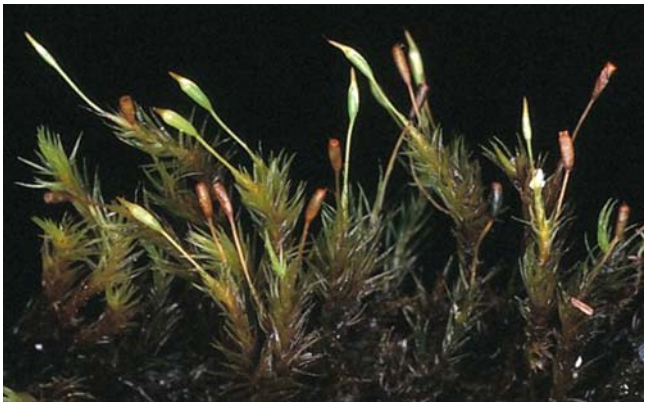

Figure 52. ***Eucamptodon perichaetiale*** with capsules. In this genus, spores germinate within the capsule. Photo by Jan-Peter Frahm, with permission.

There is reason to suppose that gibberellin might be involved; GA stimulates breakdown of starch and causes subsequent swelling of spores. If this is true, under natural conditions one should expect swollen spores in ***Atrichum undulatum*** (Figure 53) and not in ***Dicranum scoparium*** (Figure 50) capsules. Nehira (1963) found ripe spores of ***Dicranum caesium*** (Figure 54) to be 20 µm in diameter and greenish brown. On germination the spores stretched slightly. This suggests that spores of at least this ***Dicranum*** species do not swell in the capsule. On the other hand, Longton and Miles (1982) found 66-81% of ***Atrichum*** spores to be green and round, dependent on habitat. An obvious experiment to test our hypothesis for explaining Arnaudow's observations would be to supply fruiting ***D. scoparium*** plants with GA. Germination of spores within the capsule will support the hypothesis.

Figure 53. ***Atrichum undulatum***, a species of moss used by Arnaudow (1925) for embryo transplant studies. Photo by Michael Lüth, with permission.

Figure 54. ***Dicranum caesium***, a species for which spores do no swell in the capsule. Photo from Digital Museum, University of Hiroshima, with permission.

Table 1. Theorized hormonal control of spore dormancy in ***Dicranum scoparium***, based on experiments of Arnaudow (1925), where embryos of ***D. scoparium*** were transplanted into the archegonium of ***Atrichum undulatum***, causing ***D. scoparium*** spores to germinate within the resulting transplanted capsule. (Z and X are hypothesized substances.)

	Control		**Experimental**
gametophyte	*D. scoparium*	*A. undulatum*	*A undulatum*
	-	Z	X
sporophyte	*D. scoparium*	*A. undulatum*	*D. scoparium*
	-	Z	-
germination	no	no	yes

Suppose, then, that the sporophyte of ***Atrichum*** (Figure 53) might produce abscisic acid, which reduces the

effect of GA (Goodwin & Mercer 1983). In this respect, Oppenheimer (1922) and Buch (1920) mention formation of chemical substances that emanate from the capsule wall and inhibit germination. Such an inhibitor, **lunularic acid**, is known to inhibit germination of gemmae in the liverwort ***Lunularia cruciata*** (Figure 55) while they are retained by the parent thallus (Schwabe 1976). In mosses, where lunularic acid is unknown, abscisic acid could have a similar role (Pryce 1972). This hypothesis is further supported by the fact that operculum dehiscence is usually correlated with spore maturation in mosses (Hancock & Brassard 1974), and abscisic acid could promote this dehiscence, a role similar to that of autumn leaf dehiscence. On the other hand, if abscisic acid does not cause dehiscence of cells, we may find that drying of the capsule is the major factor in determining time of dehiscence, and that the ring of weak cells that facilitates this is under enzymic control or perhaps ethylene control at an earlier stage of development.

Figure 55. ***Lunularia cruciata*** with gemmae in cups and on the thallus. The thallus inhibits their germination. Photo by Martin Hutten, with permission.

In any event, it appears that we should also look closely at the gametophyte as a potential controlling generation for spore dormancy. Hughes (1954) found that control of sporangium production in ***Pogonatum aloides*** (Figure 25) and ***Polytrichum piliferum*** (Figure 56) is photoperiodic, sensed by the gametophyte, and communicated to the sporophyte. Another explanation then is that in transplanted ***Dicranum scoparium*** (Figure 50) sporophytes, communication for spore dormancy was not sent at the proper time by its ***Atrichum undulatum*** (Figure 53) gametophyte.

Another hormonal effect may intervene in dispersal of the entire capsule in such desert mosses as ***Goniomitrium*** (Figure 57) and ***Bryobartramia*** (Scott 1982). Both mosses have a short seta, a **cleistocarpous** (lacking regular mechanism for opening such as operculum or lines of dehiscence), globose capsule, and a calyptra that covers the capsule completely until dispersal (Scott & Stone 1976). Ethylene produced by the sporophyte could accumulate and cause release of capsules. Ethylene inhibits cell elongation, perhaps accounting for the short setae. The autocatalytic ability of ethylene, if captured in enclosed space under the calyptra, may cause **abscission** (breaking away) and **senescence** (aging). In higher plants abscission is the result of synthesis and secretion of a wall-degrading enzyme. Ethylene also softens the cell wall (Salisbury & Ross 1978), and its presence increases production of abscisic acid (ABA).

Figure 56. ***Polytrichum piliferum*** with capsules. Spores in this species respond to photoperiod to germinate. Photo by Michael Lüth, with permission.

Figure 57. ***Goniomitrium enerve*** with capsules. In this genus, the entire capsule disperses. Photo by David Tng, with permission.

Few species experience the germination of spores within the capsule. This inhibition could be caused by insufficient light or by the presence of an inhibitor. Such an inhibitor could be produced by either the gametophyte or sporophyte. We know that high concentrations of auxins, GA, and other hormones can inhibit germination, and the sealed capsule could accumulate such substances to inhibitory levels. Ethylene remains an unexplored possibility in this inhibition and may also play a role in the abscission of the capsule to release the operculum.

The role of hormones in germination of bryophyte spores is poorly understood. It appears that the gibberellins, growth hormones, are involved in at least some cases (Anterola *et al*. 2009). By inhibiting the production of gibberellins in ***Physcomitrella patens*** (Figure 2), Anterola and coworkers demonstrated a reduction in spore germination rate.

Inter- and Intraspecific Interactions

Exogenous inhibitors are those substances produced by other organisms that inhibit spore germination. Some species get downright nasty in their competition. For example, species of the lichen *Cladonia* can produce chemical inhibitors that prevent or reduce moss spore germination (Lawrey 1977). For ***Funaria hygrometrica*** (Figure 23), ***Weissia controversa*** (Figure 58-Figure 59), ***Plagiomnium cuspidatum*** (Figure 60), and ***Physcomitrium pyriforme*** (Figure 111), inhibition by ***Cladonia subcariosa*** (Figure 61), ***C. cristatella*** (Figure 62), and ***Cladonia squamosa*** (Figure 63) in acetone extract was complete, whereas germination was 90% or greater in acetone controls in all except ***Physcomitrium pyriforme***. The ubiquitous pollution-tolerant ***Pohlia nutans*** (Figure 64) exhibited only 34% germination in controls, but maintained from 0.8 to 5.6% germination in the three lichen extracts. The least affected species was ***Amblystegium serpens*** (Figure 64), with 91% germination in controls, and 15-71% germination with lichen extracts. However, such concentrations of lichen extracts may never exist in nature where adhesion onto soil **colloids** (substances having particles that remain dispersed in solution) may render them ineffective, or they may not leave the lichen in sufficient quantity to have any effect (unless bryophytes leach the acids out with acetone!). On the other hand, dead or damaged thalli could indeed leach out lichen acids. Such inhibition can account for some of the moss to lichen successional patterns observed in nature.

Figure 58. ***Weissia controversa*** with capsules. Photo by J. C. Schou, with permission.

Figure 59. ***Weissia controversa*** peristome with spore. Spore germination in this species is inhibited by several species of the lichen ***Cladonia***. Photo by Dick Haaksma, with permission.

Figure 60. ***Plagiomnium cuspidatum*** with capsules. Spore germination in this species is inhibited by several species of the lichen ***Cladonia***. Photo by Bob Klips, with permission.

Figure 61. ***Cladonia subcariosa***, a species that can inhibit germination of some moss spores. Photo through Creative Commons.

Figure 62. *Cladonia cristatella* (British soldier lichen), a species that can inhibit germination of some moss spores. Photo by Janice Glime.

Figure 63. ***Cladonia squamosa***, a lichen species that inhibits germination of spores of some moss species. Photo by Paul Cannon, through Creative Commons.

Figure 64. ***Pohlia nutans*** with capsules, a species in which spore germination is reduced in the presence of lichen extracts. Photo by J. C. Schou from Biopix, with permission.

Figure 65. ***Amblystegium serpens*** with capsules, a species in which spore germination is slightly reduced in the presence of lichen extracts. Photo by Dragiša Savić, with permission.

Gardner and Mueller (1981) found that the effectiveness of lichen acids in inhibiting germination of ***Funaria hygrometrica*** (Figure 66-Figure 67) spores was dependent upon *p*H. At *p*H 7, none of eight lichen acids tested had any effect on germination at concentrations of 2.7×10^{-5} M, but at lower and higher *p*H levels many became increasingly more toxic, whereas others resulted in better germination at *p*H values other than 7. These differences could account for the success or failure of bryophyte species in soils of various *p*H levels where lichens are also growing.

Based on the ease of growing ***Funaria hygrometrica*** (Figure 66-Figure 67) in the laboratory (Bopp 1980), one would expect to find germlings of this species everywhere in nature. Yet this simply is not the case. Longton (pers. comm.) has found he could not grow ***Funaria*** on soil in nature where he had collected it, yet he could grow it there on a Petri plate. If one considers the fact that ***Funaria*** remains only 1-2 years in burned areas (Hoffman 1966), and seldom remains longer than that where it invades other disturbed areas, it appears that the moss must suffer from either self-inhibition, **allelopathy** (influence of plant metabolites on other plants – *i.e.*, chemical warfare), or competition. In fact, Klein (1967) showed that ***F. hygrometrica*** protonemata release Factor H (probably a cytokinin) to the substrate and that it greatly reduces protonemal differentiation. Furthermore, old cultures of ***Funaria*** exhibit senility after about one year (Bopp & Knoop, pers. comm.), suggesting that a diffusable substance might accumulate in the substrate.

To test this theory of inhibition by older protonemata, I (Glime unpubl.) grew spores of ***Funaria hygrometrica*** (Figure 66-Figure 67) on agar that had been previously treated with 1-cm plugs of agar containing old protonemata, plugs with mature plants, and fresh agar. In all treatments, germination occurred within 48 hours, and spores even germinated on some of the plugs. Buds appeared within 10 days, with abundant buds on plates with protonemata, young plants, or mature gametophores. Furthermore, new buds were induced on the protonemata of mature plants. We must therefore conclude that either ***Funaria*** is not inhibited by any chemical that is diffused from existing plants into the agar or that the older cultures were too old and the inhibitor had broken down or become too dilute. These results do not, however, preclude the possibility of an accumulation of products as the plant grows, or the production of a gas (ethylene?) that inhibits encroaching plants.

Figure 66. ***Funaria hygrometrica*** mature plants with capsules. Photo by Michael Lüth, with permission.

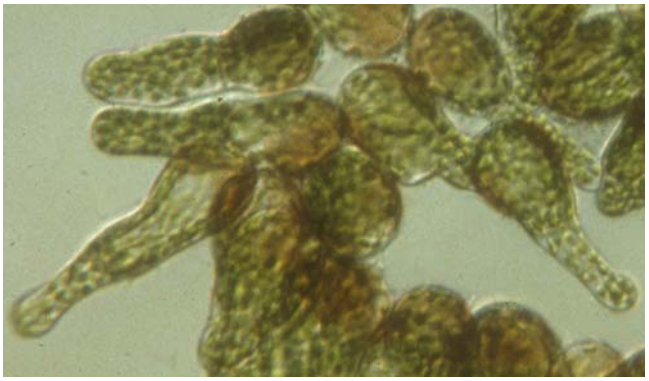

Figure 67. ***Funaria hygrometrica*** germinating spores. Photo by Yenhung Li, with permission.

Since ***Funaria*** (Figure 66-Figure 67) grows in a wide range of habitats, allelopathy seemed unlikely, though not impossible. The toxic source should be a widespread one such as that of humic acid decomposition (Hoffman 1966). Humic acids could lower the *p*H, and Armentano and Caponetti (1972) have shown that a lower *p*H retards its germination. It is significant that ***Funaria*** seldom occurs among other vegetation. Bopp (pers. comm.) has suggested that its growth after fires might be possible because of the ability of charcoal to absorb an inhibitor, although it might relate to nutrient availability as discussed above.

Therefore Raeymaekers and Glime (unpubl.) chose to experiment with humic acid effects on germination, using humic concentrations from 0 to 10%. Mean percent of germinated spores two days after inoculation decreased as the concentration of humic acid increased (Figure 68). At high humic acid concentrations (5% and 10%) the protonemata grew upward (away from the agar) and clustered together with other protonemata. Some protonemata in those concentrations formed swollen cells similar to those found by Sood (1975) in ***Pogonatum aloides*** (Figure 25). Buds were observed 8 days after inoculation in control plants, and 10 days after inoculation on protonemata of the 0.5% and 1% humic acid treatments. No buds were formed after 14 days on protonemata of the 5% and 10% humic acid treatments; however, after three weeks buds were present in 5% and 10% treatments, but in lower quantities than in the other humic acid treatments and the control.

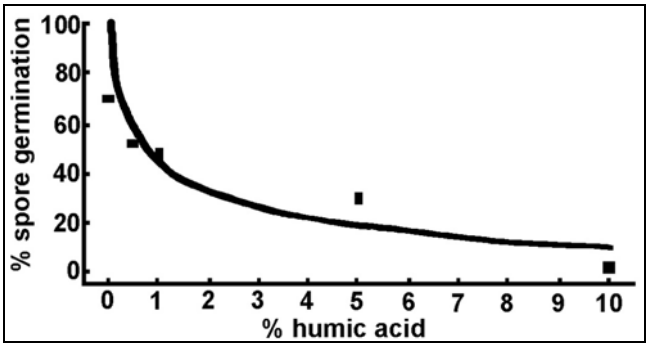

Figure 68. Effects of humic acid concentration on mean percent spore germination in ***Funaria hygrometrica***. From Raeymaekers, unpublished data.

We can conclude that spore germination and bud formation are retarded at high concentrations of humic acids. A concentration of 5% humic acid is not unusual in nature and occurs, at least in the **A horizon** (dark-colored soil layer with organic content and minerals intermixed), of spruce (*Picea*) forest soils (Remezov & Progrebnyak 1965). Fire can remove the humic acids by burning off the organic matter and returning the soil to the mineral layer, or **C horizon**. This may be a factor in permitting such bryophytes as ***Funaria hygrometrica*** (Figure 66-Figure 67) and ***Marchantia polymorpha*** (Figure 26) to colonize rapidly. But how quickly can new growth on a burned area return the lethally high concentrations of humic acids?

Could humic acids alone account for the disappearance of ***Funaria*** (Figure 66-Figure 67) from the areas where it has been a pioneer? It appears that leaf litter may offer more of a deterrent than simply blocking light. That litter is a major source of humic acids. In my moss garden, I discovered that when I left the leaf litter on the mosses all winter, they did poorly the next growing season, even though I removed the litter within days after snowmelt. Even the hardy *Fissidens* that had been doing well for several years showed signs of stress. But this unreplicated anecdotal record hardly is conclusive evidence.

In addition to endogenous inhibitors, spore germination may be affected by its surroundings. The lichen *Cladonia* can be a strong inhibitor, as can humic acids. Such signals would prevent spores from germinating in habitats that would otherwise be unsuitable, on one hand by competition for space from lichens, and on the other by competition for light with trees that drop leaves that release humic acids. A species can even stimulate bud production of its own colony, as in ***Funaria hygrometrica***, by releasing substances that stimulate protonemata to produce buds.

Interspecific Competition

Competition can be a problem of limited physical space, nutrients, or shading (light competition). For a tiny moss, physical space is available between larger plants that invade, and such spaces are usually still available long after ***Funaria*** (Figure 66-Figure 67) has disappeared. Because most nutrients are absorbed through the leaves in **ectohydric** mosses (those conducting water outside the plant) like ***Funaria***, nutrient competition can occur when a canopy intercepts and absorbs or diverts rainwater nutrients before they reach the moss. Since mosses such as ***Funaria hygrometrica*** absorb little or no nutrients from the **rhizosphere**, early invading roots present little nutrient threat.

Light quality alone could account for the restriction of ***Funaria*** (Figure 66-Figure 67) to exposed, barren habitats because the predominant wavelength transmitted through vegetation is green. However, this simple explanation cannot be applied to the distension phase of ***Funaria*** germination, wherein maximum distension occurs in yellow-green and far-red light, with the fewest protonemal cells in blue-green and red light (Valanne 1966). With such a seeming contradiction, I decided to culture ***Funaria*** spores under *Taraxacum* (dandelion) leaves to determine if in fact germination was less successful than in the open.

Few spores germinated on agar under *Taraxacum*, and protonema development was very slow. After 14 days all

control cultures at 29.5 μE m^{-2} s^{-1} (2000 lux) had buds, but those cultures under *Taraxacum* leaves at 9.4 μE m^{-2} s^{-1} (700 lux) failed to produce buds during the next four days, except for a few at the edge of the plate where white light entered. By 23 days, one experimental plate had young plants that were strongly bent toward the light at the edge of the plate. All gametophores under the *Taraxacum* were **etiolated** (abnormally elongated stems, usually in response to low light). While this demonstrates the possible role of other plants in inhibiting germination, it does not indicate whether the difference was caused by light quality or light intensity. As already discussed, the change in ratio of red to far-red light may have been the inhibitory factor (Bauer & Mohr 1959)

External Growth Promoters

It is interesting that bryophytes respond positively to application of herbicides (Balcerkiewicz 1985). On paths sprayed with herbicides, ***Funaria hygrometrica*** (Figure 66-Figure 67), together with ***Marchantia polymorpha*** (Figure 26), stayed a long time and was only slowly replaced by ***Marchantia***, which is a perennial (Raeymaekers pers. obs., Bowers *et al*. 1982). This suggests that herbicides might provide some growth-promoting substance. On the other hand, it might simply be absence of competitors and whatever they do to alter the environment.

Fungi are common growth promoters because of their production of gibberellic acid, which invades their environment. Experiments on ***Dicranum scoparium*** (Figure 50), ***D. undulatum*** (Figure 69), ***Dicranoweisia crispula*** (Figure 70), and ***Pogonatum urnigerum*** (Figure 71), using 0.01% GA, showed that GA can promote both spore germination and protonema growth (Vaarama & Tarén 1959). But most of these experiments with gibberellic acid failed to cause any increase in germination of bryophyte spores, *e.g.* in ***Tetraphis pellucida*** (Figure 72-Figure 73), ***Racomitrium fasciculare*** (Figure 74), and ***Polytrichum strictum*** (Figure 75). Gemmrich (1976) tried to induce germination of ***Marchantia polymorpha*** (Figure 26) in the dark by using GA, but was unsuccessful. However, Vaarama and Tarén discovered that spores stored dry at room temperature lost their viability, but that GA stimulated them to germinate.

Figure 69. ***Dicranum undulatum*** with capsules, a species for which GA promotes both germination and spore growth. Photo by Jan-Peter Frahm, with permission.

Figure 70. ***Dicranoweisia crispula*** with capsules, a species for which GA promotes both germination and spore growth. Photo by Hermann Schachner, through Creative Commons.

Figure 71. ***Pogonatum urnigerum*** capsules, a species in which spore germination is promoted by GA. Photo by Kristian Peters, with permission.

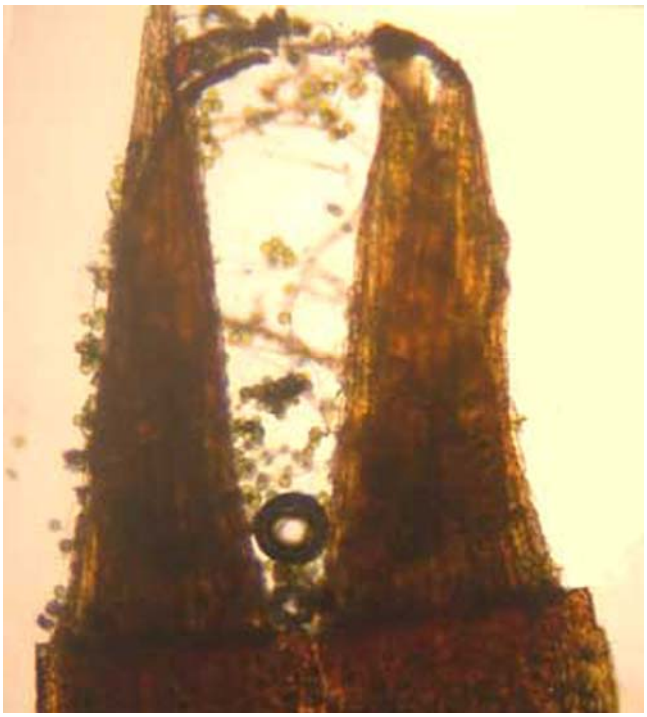

Figure 72. ***Tetraphis pellucida*** teeth and spores. Photo from Botany website, UBC, with permission

Figure 73. ***Tetraphis pellucida*** growing on stumps where wood-decaying fungi can provide GA. Photo by Janice Glime.

Figure 74. ***Racomitrium fasciculare*** with capsules, a species in which GA does not induce germination. Photo by Michael Lüth, with permission.

Figure 75. ***Polytrichum strictum*** with capsules, a species in which GA does not induce germination. Photo by Michael Lüth, with permission.

Merwin (2003) reports that in orchards post-emergence herbicides favor bryophytes. Several studies have noted that long-term use of these herbicides promote the growth of ***Bryum argenteum*** (Figure 76) and ***Marchantia polymorpha*** (Figure 26) under the trees. These actually provide an advantage to the orchard growers because they stabilize the soil, resist trampling, and do not compete with the trees for nutrients. In this case, spores may not be involved because of vegetative propagules, but they cannot be ruled out.

Perhaps the most ecologically relevant evidence in those experiments is that several fungi (*Aspergillus flavus*, *Penicillium martensii*, *Mucor racemosus*, *Fusarium scirpi*, *Rhodotorula mucilaginosa*) promoted germination and growth even more than GA! Fungi isolated from the rotting wood where ***Tetraphis pellucida*** (Figure 73) was growing also stimulated the germination of the spores (Figure 72), but that does not account for its ability to grow on rock faces. It may be interaction with fungal GA that accounts for the production of gametophores of ***Fontinalis squamosa*** (Figure 77, Figure 93) in contaminated laboratory cultures when none of the sterile cultures reached that stage, suggesting that ***F. squamosa*** protonemata might be most likely to succeed on damp rocks that have a fungal mat on them (Glime & Knoop 1986). Vaarama & Tarén obtained similar stimulatory results with fungi and ***Pogonatum urnigerum*** (Figure 71), a soil moss. However, they failed to obtain germination of spores from the rock-dwelling ***Racomitrium fasciculare*** (Figure 74) when culturing it with the mold *Aspergillus flavus*. Although results have varied widely in the GA treatments, one certainly cannot ignore the potential influence of fungi in the development of at least some bryophytes.

Figure 76. ***Bryum argenteum*** with capsules, a species in which herbicides promote growth. Photo by Jan-Peter Frahm, with permission.

Figure 77. ***Fontinalis squamosa*** protonema. Photo by Janice Glime.

Additional evidence for fungal intervention in bryophyte development occurs in ***Funaria hygrometrica*** (Figure 66-Figure 67). Hahn and Bopp (1972) concluded that the addition of fungi hastened bud formation in this species and considered this to be a symbiotic interaction.

Inorganic substances also have an effect on germination and may account for the presence or absence

of species on newly disturbed soil. Gemmrich (1976) found that while gibberellic acid did not induce dark germination of ***Marchantia polymorpha*** (Figure 26), various forms of Fe and Ca did, as well as KNO_3 and $MgSO_4$, with optimum germination on $Ca(NO_3)$.

Pollutants

We seldom consider germination when considering the effects of environmental contaminants. Yet, reductions in numbers of bryophytes from many substrates may indeed be the result of failure to germinate. For example, Francis and Petersen (1989) recommend that spore germination is a good bioassay technique for determining the toxicity of heavy metals. But much work remains to determine the effects of the many contaminants on the many species of bryophytes.

Numerous possibilities of inhibition exist with the presence of pollutants. These can include greater dryness, UV exposure, and a myriad of chemicals. Field studies on effects of such pollutants on spores are lacking. However, laboratory studies can suggest potential problems. One early study on pollutant effects on spores is that by Lewis (1973) on suspended solids from coal. She found that increasing concentrations of coal particles resulted in decreasing germination of spores of ***Platyhypnidium riparioides*** (Figure 78) suspended in Bold's (nutrient culture) medium (Figure 85).

Figure 78. ***Platyhypnidium riparioides*** with capsules, a species in which suspended coal particles caused decreased germination. Photo by Hermann Schachner, through Creative Commons.

Spore Size

Greater spore size may offer an advantage at germination by providing a reservoir of energy that permits long-term storage (see Chapter 3-1, Polyploidy and Spore Size). The trade-off, one would presume, is that large spores do not disperse far, so we should expect taxa with extremely large spores, such as ***Archidium*** (Figure 5-Figure 6) (50-130 µm), to have a small distribution. Surprisingly, ***Archidium*** is relatively widespread in southeastern North America, Eurasia, and New Caledonia (Schofield 1985), and because it is so often overlooked due to its small size, it is likely that it is even more widespread and frequent than that reported. Its large spores seem to permit it to be successful on disturbed soils, but its means of arrival remains a mystery.

Convey and Smith (1993) considered that short-lived species in the Antarctic typically had large spores that could help them in local colonization, whereas small spores characterized more widespread species In assessing the spore sizes of Michigan mosses, as published in Crum (1973), I found that the perennial, pleurocarpous mosses all had relatively small spores, the largest being 24 µm. Acrocarpous mosses, on the other hand, ranged up to 68µm with roughly 40% of the species larger than 24 µm. ***Buxbaumia aphylla*** (Figure 79), a species with one of the largest capsules, has the smallest spores of 6.5-8 µm, perhaps accounting for its ability to colonize disturbed sites. The largest Michigan spores, being multicellular and measuring 60-100 µm, occur on ***Drummondia prorepens*** (Figure 80), an epiphyte. ***Sphagnum*** shows no correlation of spore size with plant size, ranging from a minimum of 17 µm in ***S. squarrosum*** (Figure 82) and ***S. warnstorfii*** (Figure 83) to a maximum of 42 µm in ***S. cuspidatum*** (Figure 84).

Figure 79. ***Buxbaumia aphylla*** capsules with the smallest spores, exposed in upper capsule. Photo by Janice Glime.

Figure 80. ***Drummondia prorepens*** on wood, the species with the largest spores in Michigan. Photo by Dale Vitt, with permission.

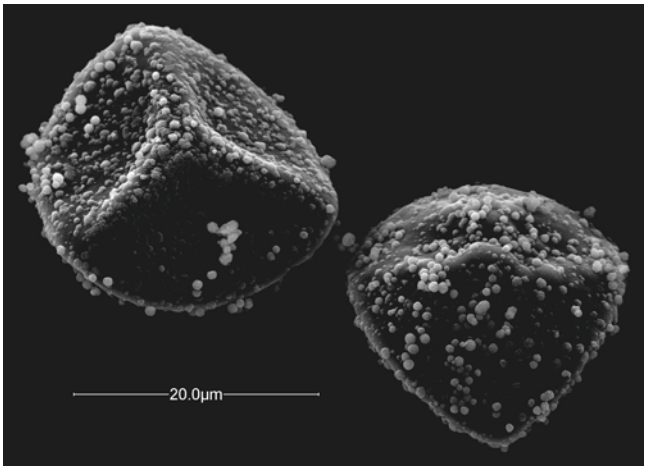

Figure 81. ***Sphagnum*** spore SEM. Photo by Whitaker & Edwards 2010, with permission.

Figure 82. ***Sphagnum squarrosum*** with capsules, a ***Sphagnum*** species among those with the smallest spores. Photo by Michael Lüth, with permission.

Figure 83. ***Sphagnum warnstorfii***, a ***Sphagnum*** species among those with the smallest spores. Photo by Michael Lüth, with permission.

McLetchie and Johnson (1997) found an interesting effect of spore size in the liverwort ***Sphaerocarpos texanus*** (Figure 86). As discussed earlier, this liverwort disperses its spores in tetrads with two male and two female spores, ensuring close neighbors of the opposite sex. However, when the spore size is abnormally small (<90µm), the sex ratio is biased toward females.

Figure 84. ***Sphagnum cuspidatum*** with capsules, a ***Sphagnum*** species with the largest spores. Photo by Bobby Hattaway (DiscoverLife), through Creative Commons.

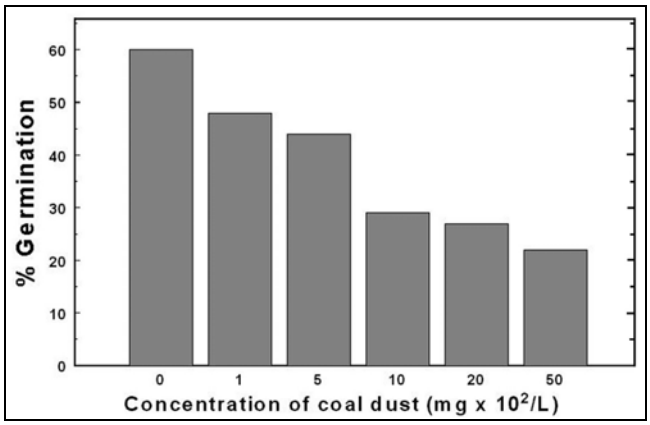

Figure 85. Inhibition of germination of ***Platyhypnidium riparioides*** spores resulting from suspended coal particles. Redrawn from Lewis (1973).

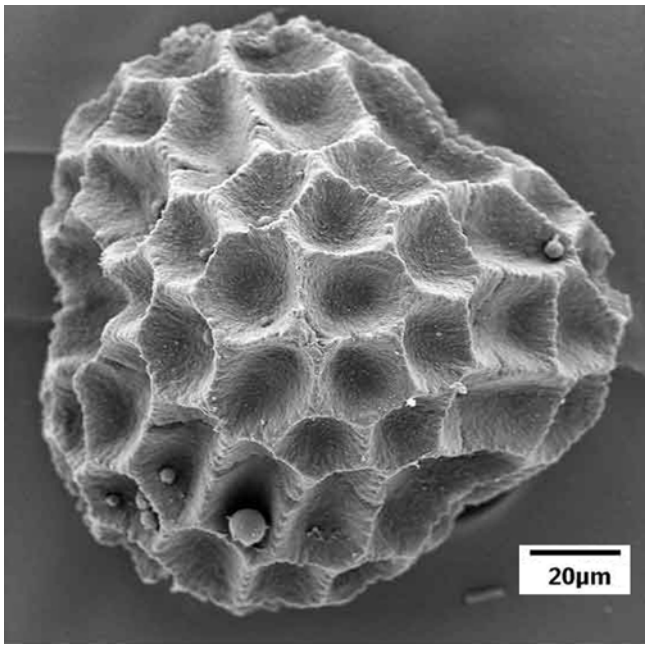

Figure 86. SEM of ***Sphaerocarpos texanus*** distal spore wall. Photo by William T. Doyle, with permission.

Anisospory and False Anisospory

Most mosses and liverworts have only one size of spore, *i.e.*, they have **isospory**. Few have **anisospory**, or two different spore sizes determined genetically. However, **false anisospory** (non-genetic size differences) exists in several genera. Mogensen (1978b) used acetocarmine stain to demonstrate that false anisospory in ***Fissidens dubius*** (Figure 87), ***Macromitrium incurvum***, and ***Rhizomnium magnifolium*** (Figure 88) was due to death of spores; only live ones stain red. In this case, some spores may abort at some point during development, rendering them smaller than those spores that have continued to develop. These arrested spores seem unable to germinate. However, in other cases, there appears to be arrested development of some spores, perhaps due to crowding, that permits other spores to continue their development in the limited space inside the capsule. These aborted spores may or may not be able to germinate, apparently depending on their ensuing conditions. This relationship is much like that of baby birds. The larger (often older) babies get all the food, sometimes leaving the smaller ones to starve, rendering them small or dead. It does not appear that any particular spore has a genetic predisposition to develop or to abort, so the two sizes diverge randomly and there can be multiple sizes due to more than one event of arrested or aborted development.

Figure 87. ***Fissidens dubius*** with capsules, a species in which some spores abort, creating large and small spores. Photo through public domain.

Figure 88. ***Rhizomnium magnifolium***, a species in which some spores abort, creating large and small spores. Photo by Michael Lüth, with permission.

Most reported cases of anisospory seem to be in mosses, not liverworts. However, Pant and Singh (1989) reported the possibility in the liverworts ***Targionia*** (Figure 89-Figure 90) and ***Cyathodium*** (Figure 91). They found a few cases of abnormally shaped spores of unequal size in several species of these two genera. It is more likely, however, that these were again cases of false anisospory due to spore abortion.

Figure 89. ***Targionia hypophylla*** with capsule in the black marsupium. Photo by Des Callaghan, with permission.

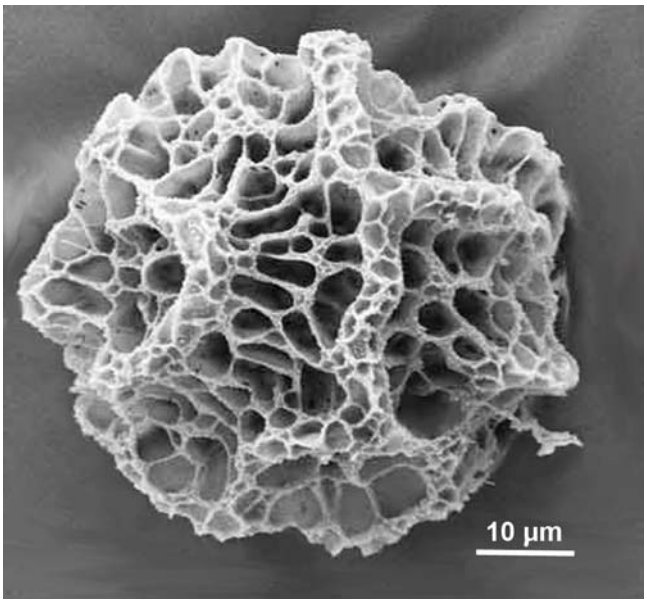

Figure 90. ***Targionia hypophylla*** distal spore wall SEM. This genus sometimes has unequal spore sizes. Photo by William T. Doyle, with permission.

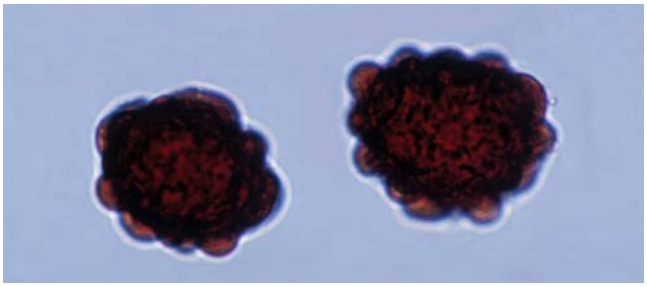

Figure 91. Spores of ***Cyathodium***, where spores are sometimes of unequal size. Photo courtesy of Noris Salazar Allen.

Fontinalis (Figure 93) has false anisospory. At the completion of sporogenesis, tetrads frequently have 1, 2, or occasionally 3 collapsed spores (Figure 92; Glime & Knoop 1986). At any subsequent stage of development of the capsule, one can find two sizes of spores in the same capsule (Figure 93). In early stages, these can both be brown, and only the larger spore becomes swollen and green when cultured on nutrient agar. At later stages, both large and small spores can be green. Large green spores become distended after five days of culturing, whereas small green ones do not. It appears that the smaller ones never germinate, but they do swell in response to the culture medium. These might have insufficient food reserves to succeed.

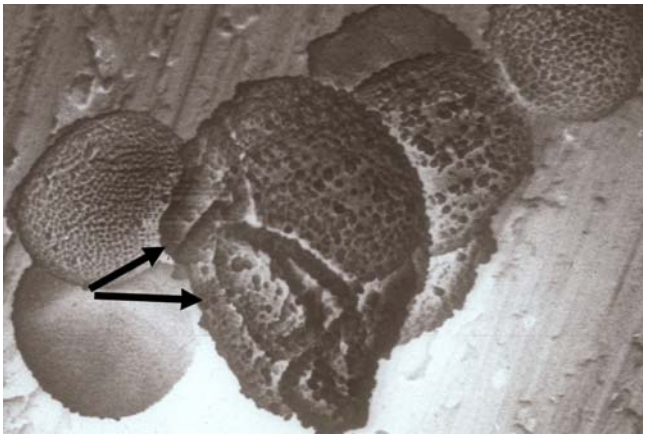

Figure 92. SEM of spore tetrad of ***Fontinalis squamosa*** showing one normal and at least two aborted spores (**arrows**) in the middle tetrad. The remaining visible spore is larger than nearby spores. Photo by Janice Glime.

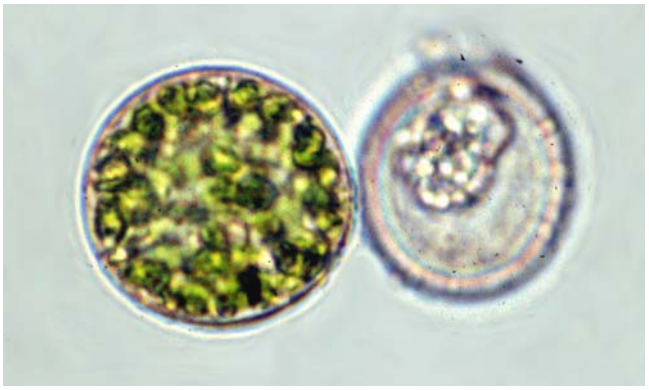

Figure 93. Normal (**left**) and aborted (**right**) spores of ***Fontinalis squamosa***. Photo by Janice Glime.

In the moss ***Bryowijkia ambigua*** (Figure 94), DeLuna (1990) found that anisospory is really a case of aborted small spores and large, multicellular spores. He found that in a tetrad, two spores abort and two remain viable, dividing to become multicellular.

These examples demonstrate the inequality of the spores, but do not provide any genetic clues. The randomness with which collapsed spores of ***Fontinalis*** (Figure 92-Figure 93) occur in the tetrads precludes sex linkage. Furthermore, in a conversation with Gert Mogensen, I was convinced that I could not rule out the continual death of spores, so that there is always a mixture of healthy spores and smaller dead ones. This explanation is further supported by the absence or reduction of chlorophyll fluorescence in the smaller spores, even when they are still green (Figure 24).

Figure 94. ***Bryowijkia ambigua***, a species that has anisospory due to aborted smaller spores. Photo by Li Zhang, with permission.

By using acetocarmine to stain the nucleus, Mogensen (1978a) has demonstrated false anisospory from spore mortality in ***Cinclidium*** (Figure 95). In that genus, mortality predominates in the stationary spore stage, with little occurring later, contrasting with ***Fontinalis squamosa*** (Figure 24, Figure 92), where it occurs at all phases. If Mogensen's model applies, a physiological failure can result from a pair of lethal genes on separate chromosomes, one of which is a sex chromosome. If this results in failure of a developmental process, then we should expect death of the spores to occur at one developmental stage, as Mogensen observed in ***Cinclidium***. Valanne (1966) observed that some spores fail to use their reserves in the dark, even with added GA, IAA, or kinetin, and therefore require light to provide the energy to move to the next life cycle stage, suggesting a potential mechanism for failure.

Figure 95. ***Cinclidium arcticum*** with capsules, a genus in which death of the spores occurs at one developmental stage. Photo by Michael Lüth, with permission.

In ***Fontinalis***, lethality does not seem to be so simple, as it apparently can occur at several spore stages rather than

one. I observed about equal numbers of two spore types in the capsules of ***Fontinalis squamosa*** (Figure 92-Figure 93) at three different stages in spore development. If the early smaller spores were dead, then a new set of dead ones appeared when spores were larger. Without obtaining counts of spores at each of these stages, we cannot eliminate the possibility that two sets of truly anisosporous spores were developing in consort, with no spore death, and that perhaps the two sizes had different germination requirements.

If we assume that spores are dying, one advantage for post-meiotic death would be to reduce competition for resources such as moisture, space, and sugar reserves within the capsule. Furthermore, 50% retarded development could provide a dispersal advantage. Small spores, if still viable, would be adapted for long-distance dispersal, larger ones for germinating close to home. This strategy of functional heterospory is known for the epiphytic moss ***Leptodontium viticulosoides*** (Figure 96) in the Andes (Kürschner & Parolly 1998).

Figure 96. ***Leptodontium viticulosoides***, a species with functional heterospory due to delayed development of some spores. Photo by Claudio Delgadillo Moya, with permission.

If the theory of retarded development is correct, why is non-sex-linked (false) **anisospory** unique to bryophytes? In other groups of plants, **heterospory** is associated with sex, with the female being larger. In bryophytes this is usually not the case, with large females and dwarf males resulting from anisospory known only in ***Macromitrium*** (Figure 97; Ramsay 1979). In flowering plants, retarded development of the seed can permit some seeds to germinate in the fall and others to wait until spring, as in *Melampyrum*. But in that case, it is a result of seed production over an extended period of time, causing different degrees of maturity at fall germination time.

In other groups of plants, heterospory usually occurs in those organisms having endosporous development of the female gametophyte. There is an advantage for the female to be large and provide food for the developing embryo, and it is also an advantage for the male to be small for dispersal (e.g. *Marsilea*, *Selaginella*, seed plants). These are strong selection pressures that would favor sex-linked heterospory in endosporous organisms. In mosses, endosporic development does not occur, although a few taxa do increase to about 4 cells before germination. Hence, this sex-linked advantage is lacking. On the contrary, there is an advantage for heterospory to occur within both sexes to provide for both long distance dispersal of some of the smaller spores and immediate fitness of large spores, in both sexes. Van Zanten and Pocs (1981) feel that green spores are adapted for immediate fitness and short dispersal only, and non-green spores are adapted for long range dispersal. However in ***Macromitrium*** (Figure 97), where dwarf males must sit on females (Ramsay 1979), one might argue for an advantage to short distance dispersal of the annual male so that the perennial female has a supply of sperm each year.

Figure 97. ***Macromitrium*** sp., a genus with true anisospory. Photo by Janice Glime.

However, ***Fontinalis*** (Figure 92-Figure 93) does not have dwarf males. Is it possible that long-range dispersal might occur in the immature brown spores, with germination being a slow process in a suitable habitat, and immaturity delaying germination, allowing an even greater chance for distance dispersal? Certainly their small size would permit them to have wind dispersal, and their roughened surface might serve as protection in the atmosphere.

This leaves us with a developmental question. What determines that non-sex-linked spores in a capsule will be of two sizes? Genetic differences can exist to program different developmental rates. Environmental differences within the capsule could alter the rate of development. If a genetic difference exists, it must separate at meiosis. In this case, we would predict equal numbers of large and small (or fast and slow) spores in all capsules only if the controlling gene is on a sex chromosome. In fact, however, we see varying percentages: 0-14% abortion in *Pleurozium schreberi* (Longton & Greene 1979); 49-61% physiological anisospory in ***Ceratodon purpureus*** (Figure 112) (Valanne 1966); 11-50% in ***Cinclidium*** (Figure 95) (Mogensen 1978a). If the trait is genetic, either it is absent in both gametes, present in only one, or present in both. Following meiosis, three combinations could occur: all small, half small - half large, all large. This pattern is not evident, but Mogensen (1981) has suggested this may be due to the counting technique. On the other hand, if the trait is coupled with differential viability, some capsules of the species should exist with only one kind of spore. This is not the case for ***Fontinalis squamosa*** (Figure 92-Figure 93); however, differential viability might not be 100% effective. If we can demonstrate that both types of spores

germinate, we have proved that Mogensen's explanation for ***Cinclidium*** does not apply to this case.

Whereas Mogensen used acetocarmine, a vital stain, to demonstrate viable DNA in ***Cinclidium*** (Figure 95), we used germination to demonstrate that at least some small spores in ***Fontinalis*** (Figure 92-Figure 93) could germinate. We have not tested both species by the same method, and we do not have evidence that viable DNA in the spore means it is capable of germination. If the spore lacks sufficient stored energy, it still is unlikely to be able to germinate and reach the distention or protonema stage in nature.

The second developmental possibility, internal environmental differences, could result from unequal nutrition or moisture within the capsule. This can easily account for differences in percentages between capsules, as different plants and different positions within the capsule could have different abilities to provide energy. In fact, differentiation could be related to the position of the cells at the time of meiosis. This is supported with the suggestion that the columella serves as a water reservoir, and it could also serve as a nutrient source.

Longton and Greene (1979) found a bisporic composition of spores in ***Pleurozium schreberi*** (Figure 98), similar to the ***Fontinalis squamosa*** (Figure 92-Figure 93) condition. Spores were of two types: green and papillose, or small, brown, and hyaline. Viability of large, green spores was 90-100%, whereas total spore abortion was commonly 0-40%. No "aborted" spores germinated. The observations on ***Fontinalis squamosa*** can likewise be compared with those of Paolillo and Kass (1973) for ***Polytrichum*** (Figure 8). In the two species they studied, they could obtain no germination from "immature" spores. Perhaps they did not wait long enough, or the conditions in the culture did not permit ripening of the ***Polytrichum*** spores, but the spores may have been dead. Some immature spores germinated on agar with sucrose, indicating the importance of nutrition and confirming that not all the small spores were dead, but rather that they lacked sufficient energy.

Fischer (1911) found that non-green fern spores took 4-210 days to germinate. ***Fontinalis squamosa*** (Figure 24) required only five days for ripe spores to germinate in culture, but 18 days for unripened spores, and during that same period spores in capsules at 10ºC in the dark also ripened (Glime & Knoop 1986). This observation on ***F. squamosa*** (Figure 92-Figure 93) suggests that light is not necessary for maturation of spores in the capsule, and that food reserves of the sporophyte or gametophyte suffice for ripening. Those spores cultured in the dark on agar, on the other hand, did not become green and swollen during this time. This indicates these spores are dependent on having either light or a parent plant to provide energy during ripening.

Based on these responses, it appears that maturation of ***F. squamosa*** (Figure 24) spores is dependent on a sugar source. The obvious experiment is to culture immature spores in the dark on agar with sucrose or glucose. However, Paolillo and Kass (1973) used a 2% sucrose solution with ***Polytrichum*** spp. (Figure 8), but spores that lacked fluorescence (suggesting no active chlorophyll) did not germinate in 14 days of culture at 11,800 lux, 28ºC. Possibly the light was too high for maturation, or the temperature too high, but one would expect at least a small percentage to germinate. Spores kept in the capsule for seven days did germinate. This suggests that the mechanism in ***Polytrichum*** (Figure 8) might require more than sugar, or that development outside the capsule was much slower than in the capsule.

Figure 98. Branches of moss ***Pleurozium schreberi*** showing the red stem that distinguishes it. Photo by Michael Lüth, with permission.

Three spore size conditions exist among bryophytes. **Isospory** is the typical condition in which all spores are the same size. **Anisospory** exists in only a few taxa in which there are genetically determined size differences among spores. In some species of ***Macromitrium*** the small spore develops into a **dwarf male**. The remaining species with two spore sizes appear to be cases of **false anisospory** in which some spores abort or mature more slowly, most likely with different causes in different species, some resulting from spore death and some developing more slowly from insufficient nutrition or water. Either of these conditions could be caused environmentally or genetically. If small spores are simply less developed but viable, the two sizes could provide the bryophyte with a bet-hedging strategy in which large spores are ready to germinate and most likely fall close to their parents. Small spores, on the other hand, could require more time for maturity, perhaps outside the capsule, and would be small enough to travel greater distances.

Tradeoffs

As already mentioned, having large spores insures a greater success at germination, but decreases the range of dispersal. Large spores also result in a smaller number of spores, both between species and within a species. But another tradeoff exists that may be more costly. A smaller number or absence of asexual propagules coincides with having large spores in Great Britain (Söderström & During 2005). This may be especially important for many annual shuttle species whose life cycle is too short to accomplish production of both.

Wiklund and Rydin (2004) suggested that spores may have a tradeoff between moisture and suitable *p*H. They interpreted the interaction between *p*H and moisture to indicate that spores can germinate at suboptimal *p*H when abundant water is available, and vice versa. The wood-inhabiting ***Buxbaumia viridis*** (Figure 99) germinated

better than did the epiphytic ***Neckera pennata*** (Figure 100-Figure 101) at low *p*H. ***Neckera pennata***, on the other hand, had earlier spore germination in conditions of low water potential and spores survived longer in a dry state. The researchers considered this represented a trade-off between the ability to colonize substrates with low moisture-holding capacity and low *p*H, favoring ***Buxbaumia viridis***, vs the positive effect that high *p*H has on germination by permitting it to exploit short, moist periods, favoring ***Neckera pennata***.

Figure 99. ***Buxbaumia viridis*** on a log that has lost most of its bark. Photo by Michael Lüth, with permission.

Figure 100. ***Neckera pennata*** showing its tree bark habitat. Photo by Janice Glime.

Figure 101. ***Neckera pennata*** showing capsules. Photo by Michael Lüth, with permission.

Germination Success

Most of what we know about success of germination is based on laboratory results. Field success is likely to be much lower due to decay, herbivory, and inappropriate location. In a study by Hassel and Söderström (1999), it would appear that most spores might be successful if the appropriate conditions are found. They grew spores from ***Pogonatum dentatum*** (Figure 102) on Petri plates and had 96.6% germination after 21 days. However, when they sowed the spores from a half, one, and two capsules in 10x10 cm plots on a newly built forest road in Sweden, only 11, 10, and 12 shoots per block developed, respectively, after one year. However, more appeared the second year, resulting in 17, 20, and 22 shoots. These late appearances could have come from protonemata already established the first year rather than from new germinations. In any case, the success rate from the estimated 712,000 spores per capsule is quite low!

Figure 102. ***Pogonatum dentatum*** with capsules, a species in which not all spores germinate the first year. Photo by Matt Goff <www.sitkanature.org>, with permission.

Germination Time

Germination times vary with type of propagule, size, age, and available water. And light seems to be required for most spores to germinate, although some germinate in the low light of the capsule. ***Aloina*** (Figure 103-Figure 104) and ***Bryum*** (Figure 28, Figure 76) spores germinate in 7-10 days (Llo Stark, pers. comm. 3 February 2015). On the other hand, propagula can germinate in 2-4 days in ***Bryum*** and ***Syntrichia*** (Figure 49). Germination of ***Pogonatum dentatum*** (Figure 102) spores occurred after 21 days (Hassel & Söderström 1999). Bhatla (1994) states that ***Funaria hygrometrica*** (Figure 66-Figure 67) spores germinate in 48 hours, a time period known for a number of mosses, but Krupa (1964) found that some (1%) germinate in as little as 15 hours in continuous light. The epiphytic ***Lindbergia brachyptera*** (Figure 105) spores germinate in 3 days, with 95% germination in 8 days (Zhao *et al*. 2004). ***Brachythecium velutinum*** germinated in 13-39 days from fresh material (Herguido & Ron 1990).

Figure 103. ***Aloina aloides*** capsules, where some spores germinate in the low light within the capsule. Photo by Jan-Peter Frahm, with permission.

Figure 104. ***Aloina aloides*** peristome & spores that sometimes germinate within the capsule. Photo by Kristian Peters, with permission.

Figure 105. ***Lindbergia brachyptera*** with capsules, a species whose spores germinate in 3 days. Photo by Martin Hutten, with permission.

Maciel da Silva *et al*. (2010) found that nutrients affect the time required for germination in ***Bryum argenteum*** (Figure 76). In distilled water, the spores required three days to germinate, whereas when nutrients were added they germinated in two days. Following germination, nutrients were needed for protonema growth to occur.

Heald (1898; Meyer 1948) established the need for light for germination in ***Funaria hygrometrica*** (Figure 66-Figure 67), ***Brachythecium rutabulum*** (Figure 106), ***Bryum algovicum*** (Figure 107-Figure 108), and ***Plagiomnium cuspidatum*** (Figure 109). These species all germinated in three days in the light, but had not germinated after one month in darkness.

Figure 106. ***Brachythecium rutabulum*** with capsules. Photo by J. C. Schou, with permission.

Figure 107. ***Bryum algovicum*** with capsules. Photo by David T. Holyoak, with permission.

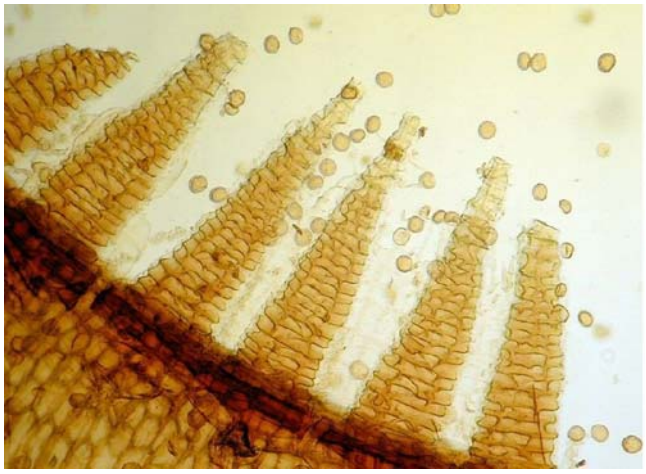

Figure 108. ***Bryum algovicum*** peristome and spores. These spores germinate in the light in three days. Photo by Michael Lüth, with permission.

Figure 109. ***Plagiomnium cuspidatum*** with capsules. Spores of this species germinate in the light in three days. Photo by Bob Klips, with permission.

In summary, germination time depends on the species and the germination conditions.

Spore Resiliency and Longevity

The most remarkable physiological observations I have made are on the capabilities of the spores themselves. I have observed ***Funaria hygrometrica*** (Figure 66-Figure 67) growing from spores that remained in a plate that had been autoclaved at 120ºC, +1 G for 20 minutes. A similar resiliency is demonstrated by the retention of the green color of ***Fontinalis squamosa*** (Figure 92-Figure 93) spores after critical point drying for SEM observation. Becquerel (1932) even reported that moss spores could survive to near absolute zero when dry in a vacuum tube.

Spores of widespread taxa such as ***Funaria hygrometrica*** (Figure 66-Figure 67) are able to survive for more than a year under more natural conditions. During (1986) has found ***Funaria*** gametophytes growing from soil samples that had been stored for two years before sowing them in the greenhouse. However, those sown in the field did not germinate. Kessler (1914) reported germination after four years and Lesage (1918) reported germination after seven years. However, Janzen (1909) was unsuccessful at germinating them after eight and twenty years.

Meyer (1941) collected spores of ***Physcomitrium pyriforme*** (as ***P. turbinatum***; Figure 111) from seven herbaria and attempted to germinate them. Only those collected in the current and previous year germinated. In the same study, spores of ***Funaria hygrometrica*** (Figure 23) germinated for the most recent eight years.

More strikingly, Malta (1921) germinated spores of ***Grimmia pulvinata*** (Figure 110) from specimens that had resided in a herbarium for 70 years, but then he retracted this claim (Malta 1922) when he was unable to repeat the success, assuming that the specimen had been contaminated with fresh spores. In his study of 200 species (Malta 1922), those with the greatest longevity were ***Funaria hygrometrica*** (13 years; Figure 66-Figure 67) and ***Ceratodon purpureus*** (16 years; Figure 112). Mogensen (1983) reports that spores can survive from only an hour to decades. But do we have any clear evidence that bryophyte spores are viable for lengthy periods similar to those of lotus seeds, reputedly of 1000 years? Although Schimper (1848) reported spore viability for fifty years, Wettstein (1925) felt this claim required re-examination. The experience of Malta (1922) supports this caution. When we examine bryophyte specimens, it is not unusual to be looking at another herbarium specimen to verify a new collection. While we are careful not to mix the specimens, spores can easily escape and join the nearby open packets. Such contamination could lead to a misrepresentation of the viability. And herbarium conditions do not represent those found in nature. Quite to the contrary, the dry conditions of the spores may permit them to go into a suspended animation state (Lipman 1936) in which respiration is all but stopped.

Figure 110. ***Grimmia pulvinata*** with capsules. Note the ungerminated spores on the outsides of some capsules. Photo by Michael Lüth, with permission.

Figure 111. ***Physcomitrium pyriforme*** with capsules, a moss that seems to have short-lived spores. Photo by Li Zhang, with permission.

Figure 112. ***Ceratodon purpureus***, with its typically prolific capsules. Photo by Michael Lüth, with permission.

Van Zanten (1976, 1978a, b) has demonstrated the long viability periods of various spores, but even more remarkable is the resiliency of the spores to adverse conditions. Van Zanten (1978a, b) found that even though spores of many species could survive 2-7 months of desiccation, these species did not occur on neighboring land masses that could easily be reached in that time. In his experiments UV radiation was definitely deleterious. Perhaps long exposures to high light intensities and longer day lengths at low temperatures in the atmosphere could result in spore death during dispersal.

Even the aquatic habitat can serve as a sporebank, although we do not have many indications of the longevity. ***Riella americana*** spores (Figure 113) from dried mud germinated after 13 years of storage (Studhalter (1931). In a Delaware River freshwater tidal wetland, Leck and Simpson (1987) found that the greatest densities of spores occurred in the upper 2 cm, and that ***Bryum*** (Figure 28, Figure 76) species were the most common bryophytes, perhaps due to prolific capsule production. Spores of mosses (and ferns) from these muds were much slower to germinate than seeds.

Figure 113. ***Riella americana*** showing spores and decaying thallus. Photo by Jan-Peter Frahm, with permission.

In fact, in flood plains of the Murray River valley of Australia, borders of cypress swamps in Florida, and low areas of southern Illinois, and most likely numerous other places, taxa such as ***Riccia*** (Figure 114-Figure 115) typically appear and survive in these periodically disturbed habitats. Spore longevity in this genus, such as that of ***Riccia albovestita*** reported by Perold (1990) to germinate from six-year-old spores, could favor rapid colonization on such disturbed sites.

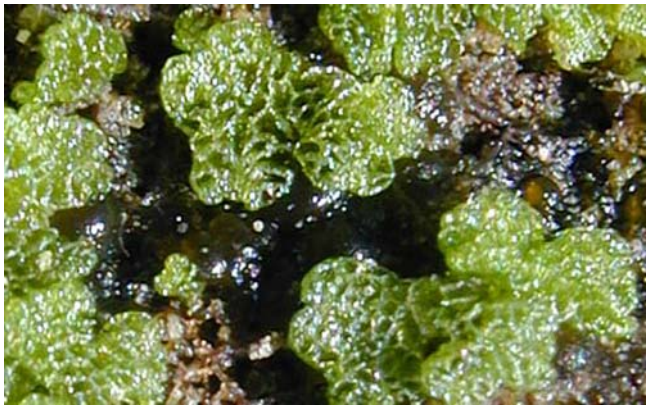

Figure 114. ***Riccia cavernosa*** on mud. Photo by Michael Lüth, with permission.

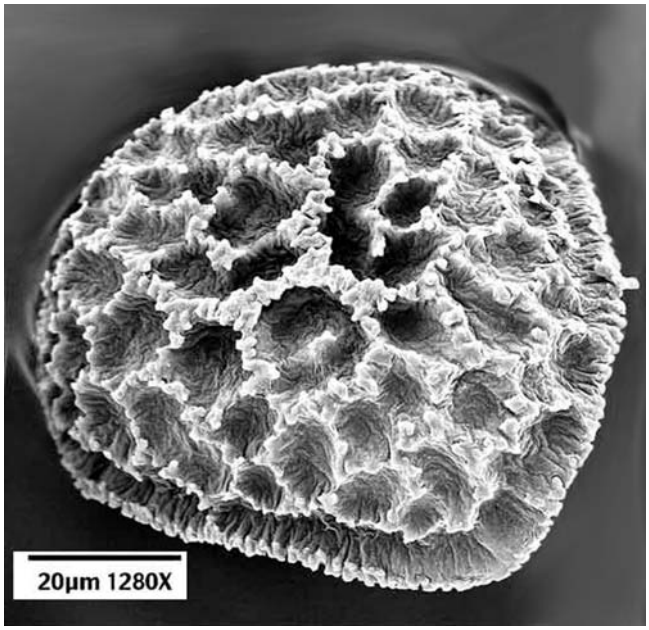

Figure 115. SEM of ***Riccia cavernosa*** spore SEM. Photo by William T. Doyle, with permission.

Even in wet peatlands, ***Sphagnum*** spores persist and germinate after several years. Sundberg and Rydin (2000) found that while viability decreased, spores buried at various depths in peat still germinated after three years. Oddly, the light-colored spores of ***Sphagnum balticum*** (Figure 116) and ***S. tenellum*** **(**Figure 117**)** maintained a higher viability than did the dark-colored spores of ***S. fuscum*** (Figure 118) and ***S. lindbergii*** (Figure 119). Surprisingly, spores that were under wet aerobic conditions survived better than did spores under wet anaerobic conditions, which died in 2-3 years. Another anomaly is that the small spores from small capsules of ***S. balticum*** and ***S. tenellum*** survived better than did the spores from medium and large capsules of the same species. Refrigerated spores maintained 13-15% viability for 13 years. Based on experiments, they estimated that ***Sphagnum*** spores can maintain a half-life in sporebanks for 1-20 years. Sundberg and Rydin attributed the widespread occurrence of ***Sphagnum*** in northern climates to the long viability of their spores in sporebanks and the ability for the spores to germinate whenever favorable conditions become available.

Figure 116. ***Sphagnum balticum*** with capsules. Photo by Michael Lüth, with permission.

Figure 117. ***Sphagnum tenellum*** with capsules. Photo by Dick Haaksma, with permission.

Figure 118. ***Sphagnum fuscum*** with capsules, a species with dark-colored spores. Photo by Dale Vitt, with permission.

But wet habitats are not favorable locations for all spores. Dalen and Söderström (1999) found that survival of spores from five species of mosses was much better when dry than in water. The highest survival rate was for ***Schistidium rivulare*** (Figure 120), perhaps accounting for its common occurrence on emergent rocks in streams. Success was lower in ***Ceratodon purpureus*** (Figure 112), ***Dicranoweisia crispula*** (Figure 70), ***Oligotrichum hercynicum*** (Figure 121), and ***Racomitrium aciculare*** (Figure 122). Nevertheless, survival of some spores for up to six months meant that submerged spore banks and water transport cannot be ruled out. See further discussion of spore longevity in the chapter on dispersal.

Figure 119. ***Sphagnum lindbergii*** with capsules. Photo by Michael Lüth, with permission.

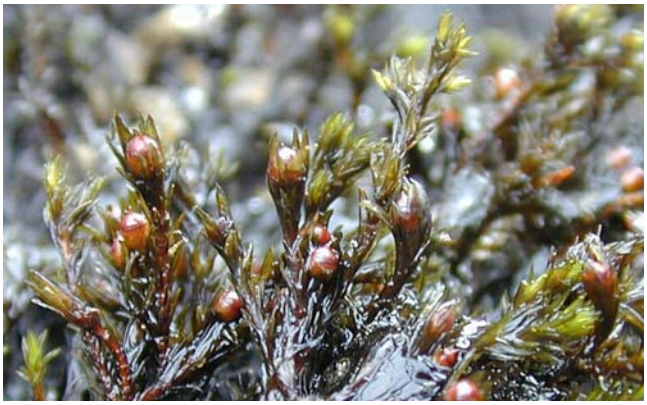

Figure 120. ***Schistidium rivulare*** growing on a wet, emergent rock. Photo by Michael Lüth, with permission.

Figure 121. ***Oligotrichum hercynicum*** with capsules. Photo by Michael Lüth, with permission.

Figure 122. ***Racomitrium aciculare*** with capsules. Photo by Michael Lüth, with permission.

Bryophyte spores are known to survive dormant in mud for up to 13 years, but reports of up to 23 years exist for herbarium specimens. Herbarium specimens can become contaminated with more recent spores; field spores are subject to damage by UV, earthworms, decay, and loss of energy, whereas herbarium specimens are protected from all those factors. Nevertheless, some dormant spores from the sporebank permit bryophytes to colonize newly disturbed sites.

Adaptations to Moisture Extremes

Most spores are adapted to travelling in a dry atmosphere that permits them to be wafted vertically considerable distances. Although spores could be dispersed on damp, cool, cloudy days, they can become clumped and heavy under these conditions, preventing long-distance dispersal. But when it is time to germinate, spores need water. The thickness of the exine layer of the spore may be an adaptation to desiccation. More water needs to be present for distension of the spores when the exine layer is thicker, and this requirement might be a protection against precocious germination.

Certainly the problems of germination of desert mosses differ considerably from those of aquatic mosses. On the one hand, the spore must delay germination until sufficient water is present to permit not only germination but subsequent development of the protonema. On the other hand, spores that are constantly surrounded by water must time their germination with a season during which they can get established and grow, *i.e.*, not too hot, not imbedded in snow or ice, and not subjected to torrential water flow that carries them off to some less suitable place.

Dry Habitats

Although some protonemata may have the ability to withstand desiccation, this ability is more likely to occur in a mature protonema than in one just emerging from the spore, when cell walls are still thin and pliable to permit elongation. Therefore, it appears that timing of spore germination is critical.

Desert bryophytes can be, compared to non-desert bryophytes, very fertile, at least in Australia. Their spore production there is high and asexual production low (Scott 1982). (See Mishler and Oliver, 1991, for contrary evidence in ***Syntrichia ruralis*** (Figure 49) in North American deserts). This high rate of fertility, together with their life strategy (**annual shuttle species**), is an adaptation to the **xeric** (dry) environment. Salt-tolerant, or **halophytic**, species share the same characters with desert bryophytes and are often very productive, *e.g.* ***Schistidium maritimum*** (Figure 123), ***Hennediella heimii*** (Figure 124), ***Ulota phyllantha*** (Figure 125). Some species form polymorphic spores, so that not all spores germinate at once and a false start with too little water will not use up all the spores (Scott 1982), a phenomenon discussed above for some non-desert taxa.

Figure 123. ***Schistidium maritimum*** with capsules. Photo by David T. Holyoak, with permission.

Figure 124. ***Hennediella heimii*** with capsules. Photo by David T. Holyoak, with permission.

Figure 125. ***Ulota phyllantha*** with capsules. Photo by Michael Lüth, with permission.

An interesting adaptation to desiccation is formation of **multicellular spores**. Parihar (1970) gives a complete list of species with multicellular spores. In hepatics these are mainly thallose liverworts and in mosses the species belong to closely related families: Dicnemonaceae, Calymperaceae, and Pottiaceae, all from relatively dry habitats. Mogensen (1981) interprets multicellular spores as an adaptation to desiccation and, at least in mosses, we see that the species that show this characteristic are relatively **xerophytic** (adapted to dry habitats).

Multicellular spores are possible when the **glyoxysomes** [organelle in plant or microorganism cell, containing catalase, where acetate and fatty acids can be used as sole carbon source (glyoxylate cycle)] are not blocked and material for the cell wall can be provided (Neidhart 1979; Mogensen 1981). This is possible through the **glyoxylate cycle** that provides sugars as a source for the carbon skeletons and energy for the synthesis of new cell walls. In unicellular spores the glyoxysomes are blocked prior to germination (Neidhart 1979). This seems to parallel the seeds that are adapted to dry habitats and are rich in fatty acids, using the glyoxylate cycle to germinate.

The environmental signals that cause spores to divide and that prevent germination are not known. From higher plants we know that chilling (5ºC for 6 hours) lowers the **isocitratase** activity. Isocitratase is an enzyme of the glyoxylate cycle and its activity is depressed by an exogenous source of succinic acid (Noggle & Fites 1964). Succinate is a product in the biochemical pathway from fatty acids to carbohydrates. Perhaps the low temperature causes an accumulation of succinate, thus halting germination. A careful study of timing of multicellular development in moss spores and temperature might be an interesting approach to finding mechanisms of control of germination.

Precocious Germination

Precocious germination, like a precocious child, reaches a developmental stager earlier than usual. In the case of germination, the spores germinate within the capsule. This is not a general occurrence among bryophytes.

In ***Brachymenium leptophyllum*** (Figure 127) in South Arabia, spores germinate within the capsule (Kürschner 2004). In this habitat, it permits new plants to establish rapidly near the mother plant, decreasing their risk of extinction in long-range dispersal.

Dendroceros (Figure 126) is a tropical hornwort that differs from other hornworts by growing on tree bark and leaves (Schuette & Renzaglia 2010). It produces green multicellular spores which begin as unicellular **tetrads** (groups of four) following meiosis. These spores expand to 60-75 µ in diameter. These fill the available space around them, resulting in many different shapes and sizes of spores within the capsule. When the spore divides, the resulting cells develop a single large, star-shaped chloroplast with a **pyrenoid** (organelle that facilitates starch formation by concentrating CO_2) in each cell. Individual cells become smaller during this division process. Cell content increases, particularly the protein storage bodies in vacuoles. As in ***Brachymenium leptophyllum*** (Figure 127), this multicellular condition appears to be an adaptation to drying. ***Dendroceros*** is the only desiccation-tolerant hornwort and this same adaptation is also present in a number of other epiphytes among the mosses and leafy liverworts (*e.g.* **Porellaceae,** Figure 128).

Figure 126. ***Dendroceros crispus*** with sporophytes. Photo by Jan-Peter Frahm, with permission.

Figure 127. ***Brachymenium*** cf. ***leptophyllum*** with capsules. Spores in this species germinate within the capsule. Photo by Li Zhang, with permission.

Figure 128. ***Porella cordaeana*** with capsules, in a family with some a desiccation-tolerant species. Photo by Ken-Ichi Ueda through Creative Commons.

Desert mosses have several adaptations within their spores to increase their chances of success. Those in the Mojave Desert contrast sharply with those in Australian deserts, with the latter producing prolific sporophytes. Among these, one strategy is to have a delayed germination in which not all spores germinate at one time, thus providing **multiple chances** to have sufficient water following germination. There seems to be a good correlation between those spores that succeed in xeric conditions and the **absence of an inhibitor** of the **glyoxysomes**. When glyoxysomes are free to operate, they are able to provide a **carbon source** for building **cell walls** through the breakdown of **fatty acids**. Others succeed by having **precocious** germination.

Aquatic

In submerged aquatic mosses such as ***Fontinalis*** (Figure 131), the opposite problem exists. Special adaptations must be present to prevent germination within a continuously wet capsule. One can suppose that the dark-colored capsule might have a high concentration of phenolic compounds that could serve as inhibitors (Figure 129). On the other hand, just by being in a dark-colored capsule, spores may fail to germinate due to lack of light. Furthermore, the glossy, thick capsule wall might effectively prevent water from entering the capsule. However, spores can become swollen and green within the capsule (Glime, pers. obs.; Figure 130). Since these swollen green spores fail to show distension, an inhibitory factor might be implicated. On the other hand, as already discussed, light is most likely necessary for distension, and the level inside the capsule may be too low.

Figure 129. Dark mature capsule of ***Fontinalis squamosa***. Photo by Janice Glime.

Figure 130. Longitudinal section through nearly mature capsule of ***Fontinalis squamosa*** showing green spores and dark capsule wall. Photo by Janice Glime.

Elssmann (1923-1925) has made the interesting observation that at least several species of aquatic bryophytes fail to have operculum dehiscence: ***Platyhypnidium riparioides*** (Figure 78), ***Fissidens fontanus***, (Figure 132), and ***Fontinalis antipyretica*** (Figure 133), as I have in ***F. novae-angliae*** **(**Figure 134**)** and ***F. dalecarlica*** (Figure 131). In most mosses, the annulus forms a circle of cells delineating the separation between operculum and capsule. These cells are often mucilaginous. According to Elssmann, there are small "rifts" in the cuticle due to stresses as the capsule dries, and these provide entry regions where moisture can reach the mucilaginous cells of the annulus. This of course causes the annulus cells to swell and can henceforth separate the operculum from its capsule. For such a process to occur, the capsule must experience drying to create the rifts and permit entry of moisture that swells the annulus. Dihm (in Elssmann 1923-1925) also believed the annulus was important in this context, and indicated "that the ring attains a lower degree of development and mechanical effectiveness in mosses growing on moist earth." Elssmann points out that Loeske likewise referred to a "retrogressive" annulus in ***Fontinalis*** (Figure 129-Figure 135) and ***Fissidens fontanus***. Elssmann sectioned the capsule and determined that annulus cells of ***Fontinalis antipyretica*** were very small and seemed to have no mucilage at all (or perhaps in a very dilute form). In ***Fontinalis***, it appears that abrasion may be a more important factor in exposing the inside of the capsule, and hence the spores.

Figure 131. ***Fontinalis dalecarlica*** capsules, a species which often fails to dehisce its operculum. Photo by Janice Glime.

Once the spores are liberated into the aquatic environment, they face the problem of germinating at the right time. Unless they are under ice and snow, we can assume they have both water and light. Some amphibious mosses appear to solve this problem by producing their capsules only when they are above water. But this requires "planning" – coordinated timing of capsule maturation and spore dispersal. What do they use as signals?

Figure 132. ***Fissidens fontanus***, a species in which capsules do not open. Photo by Michael Lüth, with permission.

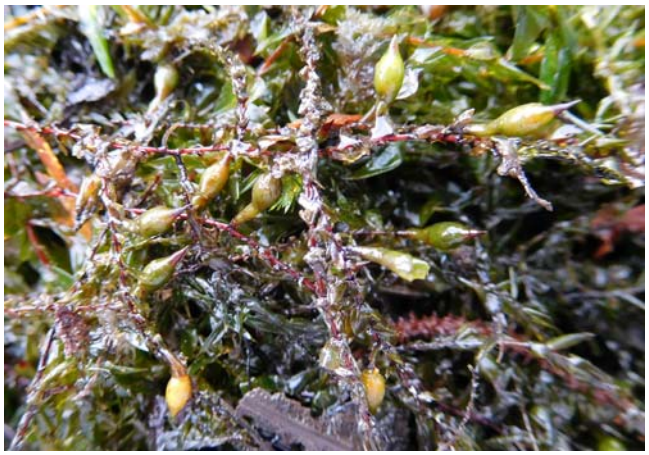

Figure 133. ***Fontinalis antipyretica*** with capsules, a species with very small annulus cells that do not dehisce. Photo courtesy of Rienk-Jan Bijlsma (per Joop Kortselius).

Temperature differences in streams and lakes are moderate compared to those on land, and therefore we might hypothesize that temperature has little influence on time of germination. But in ***Fontinalis squamosa*** (Figure 135), temperature does seem to play a role. At any given time, there are usually two sizes of spores within these capsules: small brown ones, presumably less mature, and larger green ones. It took 18 days before any of the brown ***F. squamosa*** (Figure 24) spores germinated, with many more germinating at 20ºC than at 14ºC (Glime & Knoop 1986).

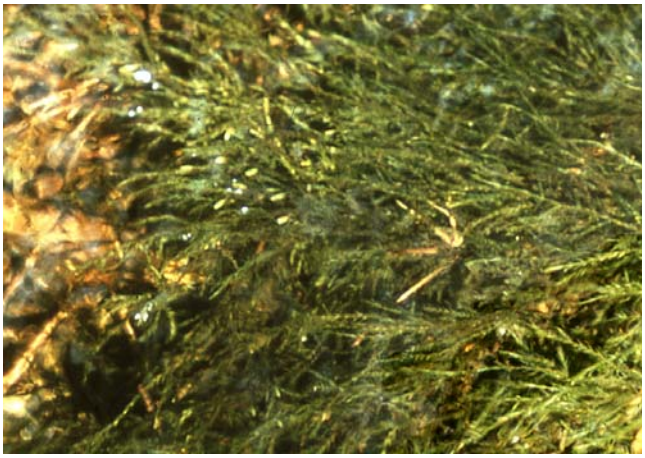

Figure 134. ***Fontinalis novae-angliae*** with capsules, a species that seems to fail in operculum dehiscence. Photo by Janice Glime.

Glime and Knoop (1986) reasoned that ***Fontinalis squamosa*** (Figure 24) is able to take advantage of a long period of spore dispersal, but with different behaviors on the part of the two spore sizes. Since capsules seem to depend on abrasion for dispersal of spores, this is likely to be a somewhat unpredictable event, most likely occurring among the capsules over an extended period of time. Since the greatest abrasion will occur with spring runoff, the cold temperature of the water during runoff could prevent germination, or at least protonema formation, and once warmer temperatures arrived in the spring, the moss could be assured of having continued warm water and no ice to block the light. Once the ice is gone, the temperatures warm rapidly, providing conditions more favorable to the protonemata. But it would seem that germination at 20°C would in most cases be detrimental to ***Fontinalis*** because prolonged exposure of the gametophore to that temperature causes growth to cease in most of its species (Fornwall & Glime 1982, Glime 1982, 1987a, b), and danger of desiccation is imminent due to low stream and lake water levels. Perhaps this higher temperature permits the protonema to become well established over a sizeable area before it produces its temperature-sensitive gametophores, hence permitting development of numerous gametophores that afford each other protection from the drag effect of running water by "safety in numbers."

Figure 135. The brook moss, ***Fontinalis squamosa***. Photo by Michael Lüth, with permission.

Summary

Spores are protected by an inner intine, outer exine, and plates most likely of **sporopollenin**. **Perine** may be deposited by the sporophyte from disintegrating **columella** tissue and the sporocyte wall. Germination of spores begins with **swelling** that results from water intake, followed by **distension** that requires light, resulting in **rupture** of the cell wall and formation of the **germ tube**.

Germination and production of the germ tube require energy that may either be stored in the spore or result from immediate photosynthesis. Various hormones may be involved either in promoting germination or maintaining dormancy, both in the capsule and after dispersal. Evidence of the role of temperature, *p*H, and nutrients, especially in field conditions, is scant. However, some spores require **vernalization** (chilling).

Capsule characteristics may contribute to within capsule **dormancy** through such interventions as light blockage, altered wavelength, lack of water, and dormancy hormones.

Other species, such as the lichen *Cladonia*, may inhibit germination of some species, whereas hormones from some fungi might promote it. Humic acid from litter breakdown may also inhibit germination and contribute to the scarcity of bryophytes on the deciduous forest floor.

Some bryophytes have two sizes of spores, but with the exception of ***Macromitrium***, these appear to be a case of **false anisospory** resulting from one or more abortion events during spore development within the capsule.

Although germination success in the lab is generally high, success of the same species in the field is extremely low. Spore survival, on the other hand, can be extensive, lasting for up to 20 years in some, and probably longer.

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CHAPTER 5-3

ECOPHYSIOLOGY OF DEVELOPMENT: PROTONEMATA

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CHAPTER 5-3

ECOPHYSIOLOGY OF DEVELOPMENT: PROTONEMATA

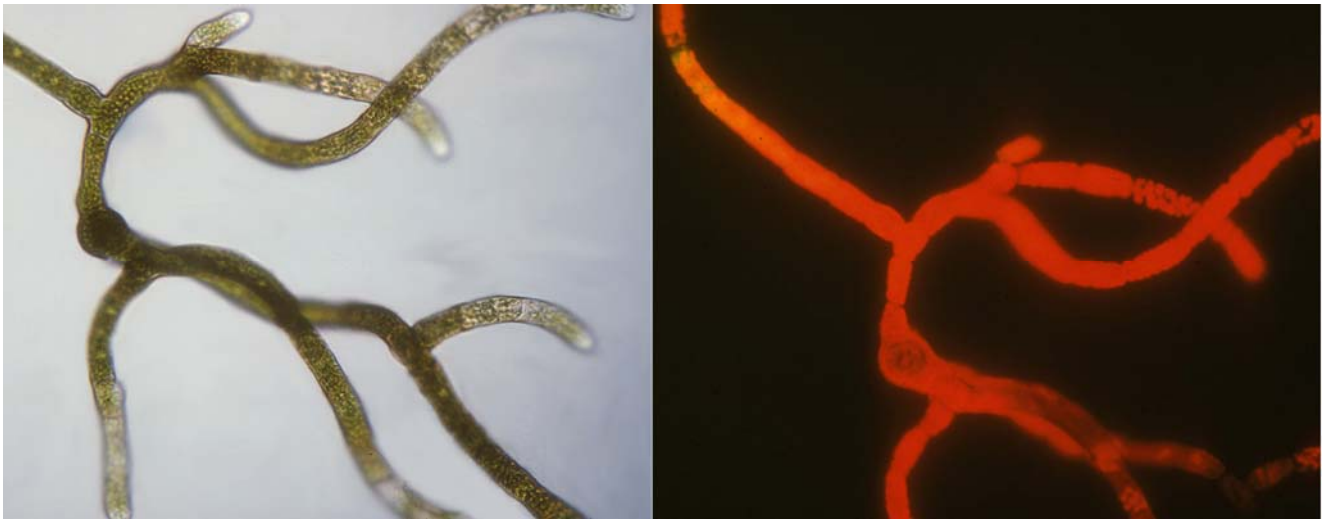

Figure 1. Protonema of ***Fontinalis squamosa***. **Left:** white light. **Right:** UV light showing chlorophyll fluorescence. Photo by Janice Glime.

The Protonema

The **protonema** is an elongate, thread-like structure that develops from the germinated spore of mosses and some liverworts. In most liverworts it is thalloid.

It was Sironval (1947) who defined two clear stages in protonema development. All mosses have the **chloronema** stage (Figure 2), which is the one that develops first from the germinating spore. The **caulonema** (Figure 2) stage is second and in some mosses it is not distinguishable from the chloronema.

The moss protonema typically branches (Figure 1) and can develop into **chloronema**, **caulonema**, or **rhizoids** (Figure 2), depending on the species, conditions, and developmental stage. The **chloronema** is the first thread formed by the germinating spore and is distinguished by its perpendicular crosswalls, short cells, numerous chloroplasts, colorless cell walls, and irregular branching. The **caulonema**, when present, develops later and is the source of gametophore buds in those species with both types of protonemal segments. It is distinguished by its distal position relative to the spore, longer cells with diagonal cross walls, usually brownish cell walls, and fewer, less evenly distributed, smaller, spindle-shaped chloroplasts. The chloronema, at least in culture, is able to grow vertically as well as horizontally, but the caulonema grows only horizontally (Bhatla 1994).

The protonemal stage is the best-studied part of bryophyte development. Due to its relative ease of culture and one-cell-wide structure, it has been the subject of numerous physiological studies to elucidate basic physiological mechanisms in plants.

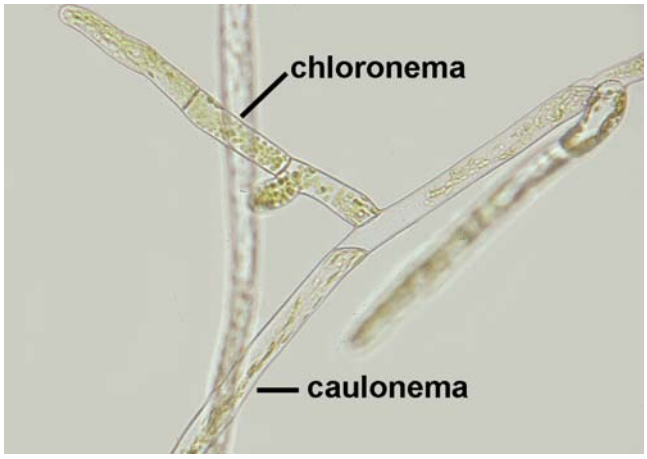

Figure 2. Distinction of chloronema and caulonema on the protonema of ***Funaria hygrometrica***. Photo by Janice Glime.

As discussed earlier with life cycles, spores in most true moss (**Bryopsida**) germinate to form filamentous protonemata, whereas **Sphagnopsida** has a thalloid form, **Andreaeopsida** a massive one, and liverwort protonemata may range from filamentous to thalloid (Mishler & DeLuna 1991). In the **Bryopsida**, non-filamentous protonemata occur in the **Schistostegales**, **Tetraphidales**, and some

genera in the **Grimmiales**, **Dicranales**, **Orthotrichales**, **Hypnobryales**, and **Isobryales** (Nishida 1978, Nehira 1983).

Fulford (1956, in Watson 1974) identified 10 protonemal types in the leafy liverworts, but Nehira (1966) and Schuster (1966) warn us that the protonema form is plastic and can be strongly modified by the environment. Nevertheless, Nehira (1966) identified 24 liverwort sporeling types.

The protonema, simple as it is, has a variety of forms. For example, in ***Lindbergia brachyptera*** (Figure 3), there is no caulonema (Zhao *et al*. 2004). The rhizoids and buds develop from the chloronema. And it takes only three days for the spore to germinate, with 95% of the spores germinated by 8 days.

Figure 3. ***Lindbergia brachyptera***, a species that does not develop a caulonema. Photo by Bob Klips, with permission.

But the environment can likewise cause modifications to the protonema. Such characters as cell shape, growth polarity, rate of mitosis, differentiation of chloronema into caulonema, and branching frequency of filamentous protonemata can change in response to changes in response to light quality and intensity, photoperiod, temperature, hydration, *p*H, hormonal levels, and interaction with microorganisms (Chopra and Kumra 1988; Mishler & DeLuna 1991). Nevertheless, Anderson and Crosby (1965) found that the basic thalloid and massive forms of the Sphagnopsida and Andreaopsida remained unchanged.

Even in mosses such as ***Funaria hygrometrica*** (Figure 2, Figure 8) with well-developed caulonemata, culture in liquid media can inhibit formation of caulonema, resulting in reduced bud formation – suggesting very wet conditions would be detrimental to development of gametophores in these taxa (Johri & Desai 1973). Furthermore, high cell densities cause failure of caulonema differentiation, suggesting some sort of self-inhibition. This might be another adaptive mechanism that prevents gametophores from competing with each other and that permits the protonema time to revert to chloronema, spread to a wider area, or partially die off before putting forth upright plants.

By contrast, ***Tetraphis pellucida*** (Figure 6; **Tetraphidopsida**) produces a bladelike structure from the protonema, described as **protonemal flaps** (Figure 4-Figure 5). Gemmae can develop at the base of the flap. The changes from distended spore to protonema growth to gametophore buds can require increasingly more specialized conditions in this and other species. For example, Forman (1964) found that spore germination in ***Tetraphis pellucida*** (Figure 4-Figure 5) requires a *p*H of 3.0-7.3 whereas growth of the leafy shoot occurs in the much narrower *p*H range of 5.1 to 5.8. This has limiting implications for species that arrive as spores.

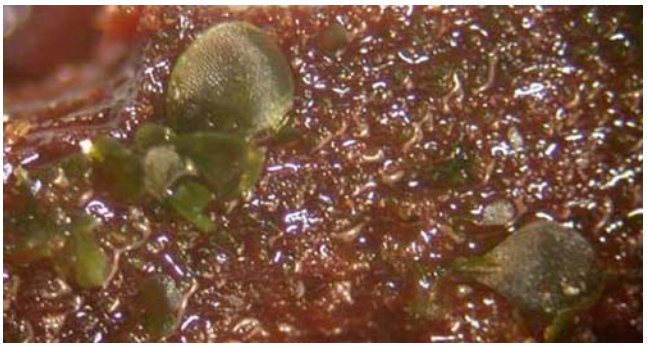

Figure 4. Protonemal flaps of the moss ***Tetraphis pellucida***. Photo from botany website and University of British Columbia, Canada, with permission.

Figure 5. Protonema and protonemal flaps of the moss ***Tetraphis pellucida***. Photo from Botany Website, University of British Columbia, Canada, with permission.

Figure 6. ***Tetraphis pellucida*** with gemmae cups, a species that develops protonemal flaps. Photo by Andrew Spink, with permission.

Temperature requirements, on the other hand, are broader for the leafy shoot, but as the humidity drops, the viable temperature range narrows. Furthermore, the change from chloronema to caulonema can be delayed by inappropriate environmental conditions. Bopp (1961) found that the caulonema stage, and thus the bud stage, can be delayed by low temperature, submersion, or low light.

There seems to be controversy over the degree of difference between chloronema and caulonema, with Bopp (1959) contending that they are distinct stages, and Kofler (1958) and others finding no consistent distinction, even in ***Funaria hygrometrica*** (Figure 2, Figure 7-Figure 8), for which Bopp first made his claim. Several factors appear to lead to these disagreements (Watson 1974). The plasticity of the protonema permits it to respond differently to the varying environmental conditions. The distinction is exhibited more strongly in some species than others, and in some species, apparently no distinction exists. And, Kofler contended that genetic differences are more likely to be expressed in the protonema than in the gametophore or sporophyte because the environment has less time to exert selective pressure on the protonema. Hmmm...

Figure 7. ***Funaria hygrometrica***, a species for which the protonemal physiology has been extensively studied. Photo by Michael Lüth, with permission.

Figure 8. ***Funaria hygrometrica*** spore with branch protonema developing from a chloronema cell. Photo by Janice Glime.

Application of IAA induces the switch from chloronema to caulonema side branches (Johri & Desai 1973; Christianson 2000) and inhibits the further growth and initiation of chloronema branches (Johri & Desai 1973). Application of ABA to chloronema instead results in cell division and the formation of asexual reproductive cells, but not in caulonemata (Christianson 2000). Inadequate calcium causes the chloronema cells to divide unevenly and to form **tmema** (abscission cell that ruptures to release moss gemmae; see below), but not in caulonemata. Cytokinin stimulates the formation of gametophore buds in the caulonema, but not in the chloronema. Perhaps even more surprising, chloronemata exhibit positive phototropism, whereas caulonemata exhibit negative phototropism, much like the differences in response to IAA in stems vs roots of tracheophytes.

But are these applied hormone responses initiated by moss hormone productions? In the well-studied ***Physcomitrella patens*** (Figure 9-Figure 10), we do know that transition from chloronema to caulonema cells is under control of auxin (Gonneau *et al.* 2001). Since IAA concentrations seem to be under environmental influence, variability and inconsistencies may be explained in the near future as we unravel the cryptochrome/IAA complex of reactions in this moss, and plants in general, using gene knockout techniques.

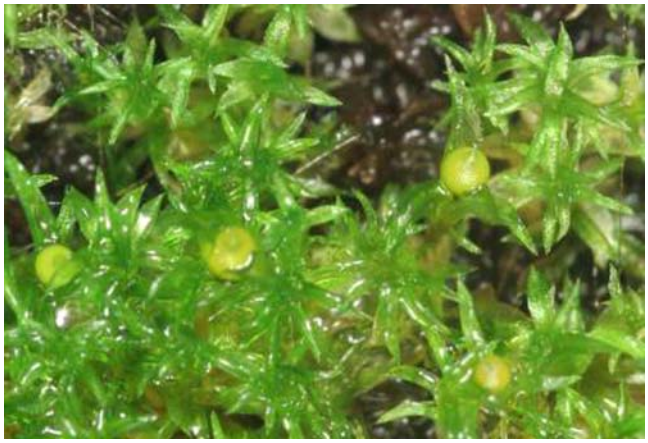

Figure 9. ***Physcomitrella patens*** with capsules, a common research organism because of the ease with which its genes can be manipulated. Photo by David Cove, with online permission.

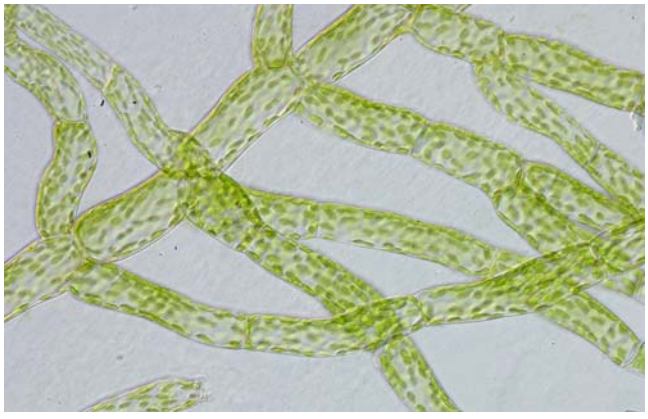

Figure 10. ***Physcomitrella patens*** protonema. Photo from Ralf Reski Lab, through Creative Commons.

Bittisnich and Williamson (1989) identified H^+ efflux at the tips of the chloronema (Figure 2) in ***Funaria hygrometrica*** (Figure 2, Figure 7-Figure 8) and elaborated

the role of acid flux in the extension of the protonema. However, unlike fungal hyphae, pollen tubes, and root hairs, the growth of the moss protonema is slow (Bhatla 1994) and is not confined to the apex. Growth apparently occurs in accordance with the acid growth mechanism, in which H^+ ions, induced by light and IAA, loosen the cell wall. In ***Funaria hygrometrica***, acidification of the medium to *p*H 5.5 increases the extension of the tip cells (Figure 8), whereas buffering to a *p*H of 6.8 prevents it. Calcium seems necessary for the acquisition of new materials to the wall and the ability to extend the wall.

The development of protonemata has not been widely studied, and those studies have concentrated on the changes in morphology resulting from cytoskeletal aspects of tip growth and production of asexual propagules (Pressel *et al*. 2008). Pressel *et al*. set out to remedy the situation by examining the differentiation of the caulonemata and rhizoids. This comprehensive study included more than 200 moss species! They found that the differentiation of caulonemata and rhizoids results in fully differentiated cells that have a remarkable resemblance to the moss food-conducting cells. In both rhizoids and caulonemata, the cytology is dependent on having an intact microtubule cytoskeleton. The vacuole disappears during the differentiation process, a phenomenon that Pressel *et al*. consider to be related to the solute transport functions of the caulonemata and rhizoids.

Figure 11. ***Grimmia orbicularis*** with capsules in its dry rock habitat. Photo by Michael Lüth, with permission.

Figure 12. ***Grimmia orbicularis*** protonema. Photo by Eugenia Ron and Tom Sobota, with permission.

Water Relations

We have often assumed that the protonema stage is the most susceptible to desiccation damage. However, this is not always true. During (pers. comm.) found that unsuccessful cultures of xerophytes such as ***Grimmia*** (Figure 11-Figure 12) produced gametophores only after being put aside and forgotten, *i.e*., after desiccation. But it is surprising that Glime and Knoop (1986) found that after cultures of the aquatic moss ***Fontinalis squamosa*** (Figure 1) had dried out, added water caused the protonemata to swell and again become active. This is further supported by observations on protonemata that dried overnight on a microscope slide. When I added water to observe them for fluorescence, they produced vivid red chlorophyll fluorescence and regained their normal shape. It appears that protonemata may have considerable desiccation tolerance.

Further evidence that the protonema is desiccation tolerant can be gleaned from their dispersal period. As seen in the chapter on phenology, dispersal in spring is commonplace. It would seem, therefore, that the protonema must be growing in summer, when desiccation is most likely. The other period of high spore dispersal is fall, again preceding the dry season of winter in many temperate regions. Although we have insufficient evidence to show that the protonemata are present during these two relatively dry seasons, it appears likely that they are in at least some, if not many, species. Figure 13 shows a hydrated protonema in the field.

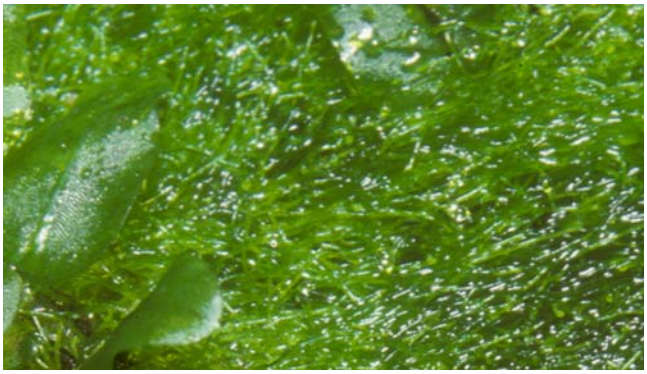

Figure 13. Protonema of ***Plagiomnium*** sp. in the field. Photo by Janice Glime.

Seasonal Light/Temperature Changes

It is hard to talk about light without also considering temperature, since brighter light generally means greater exposure and higher temperatures. Higher temperatures and brighter light are also usually coupled with a longer photoperiod. Knowledge of their effects on protonemal growth and development is based on laboratory cultures.

Light, coupled with temperature, seems to play a role in the pattern of development of protonemata in the aquatic

moss ***Fontinalis***. ***Fontinalis squamosa*** (Figure 15) spores germinated throughout the range of 40 to 3000 lux, and cultures exhibited unipolar, bipolar, tripolar, and one tetrapolar germination (Figure 14, Figure 15) (Glime & Knoop 1986). The number of germ tubes was generally consistent within a single plate, despite having bands of spores from three different capsules. At 3ºC and 120 lux, germination required four weeks, and only distended spores with a single protrusion were present (Figure 16). At 14ºC, 1200 lux, two plates of spores had single threads (Figure 14), one had double threads, and one had short single and double threads. At 20ºC, 2100 lux, two plates had only single germ threads that formed weak spirals and two had many spores with two or three germ threads and no spiral growth (Figure 15); branching was much more extensive than at 14ºC and 1200 lux. Although effects of temperature cannot be separated from those of light intensity, they mimic environmental conditions as they change from winter to summer. Such environmental controls can prevent spores from germinating or protonemata from developing too early in the season. The high degree of branching at higher light and temperatures could afford more self-protection from desiccation by providing overlapping threads (Figure 17). Bipolar and tripolar germination is also likely to be a response to the greater ability to photosynthesize with more light and provide energy for the developing germ tube.

Figure 14. Single-thread protonemata of ***Fontinalis squamosa*** formed at 14ºC and 1200 lux. Photo by Janice Glime.

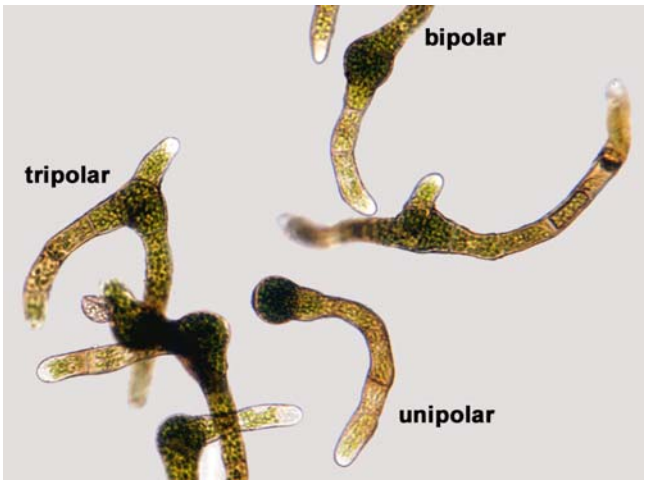

Figure 15. Protonemata of ***Fontinalis squamosa*** showing unipolar, bipolar, and tripolar germination typical at 20ºC and 2100 lux. Photo by Janice Glime.

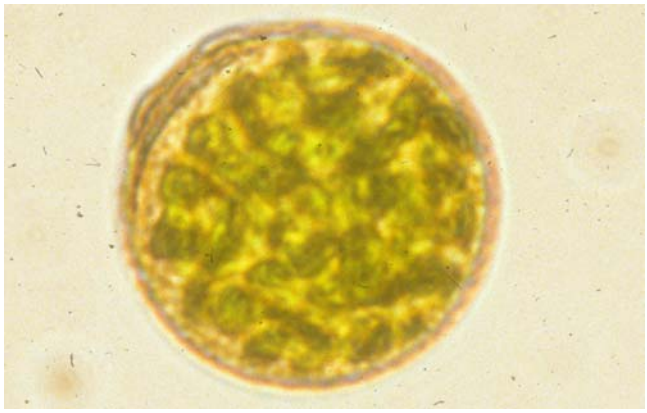

Figure 16. Distended spore of ***Fontinalis squamosa*** as one might find at 3ºC and 120 lux. Photo by Janice Glime.

Figure 17. Dense growth of overlapping protonemata of the moss ***Plagiomnium*** sp., a strategy that can help to conserve water and produce multiple leafy gametophytes. Photo by Janice Glime.

Light

Light Intensity

High light intensity can promote protonemal growth, as in ***Microdus*** (Figure 18), ***Hymenostylium*** (Figure 19), and ***Campylopus*** (Figure 20) (Mehta 1988). In the ephemeral ***Physcomitrella patens*** (Figure 9-Figure 10), high light intensities promote branching of the caulonema, thus proliferating the potential bud sites (Cove *et al*. 1978, 1979). By contrast, ***Bartramia ithyphylla*** (Figure 21) can exhibit branching from the first cell emerging from the spore (Figure 22) (Cove *et al*. 1978, 1979), as can ***Brachythecium velutinum*** (Figure 23) (Herguido & Ron 1990). ***Gymnostomum*** sp. *s.l*. (Figure 24) can branch from multiple caulonemal cells (Figure 25) (Cove *et al*. 1978, 1979). These multiple branches can produce multiple buds, forming a colony or cushion of plants (Figure 26) that help each other to maintain moisture. In species like ***Atrichum altecristatum*** (Figure 27), a large mat of protonemata commonly forms before buds develop, ensuring a colony of plants to protect each other (Figure 28).

Figure 18. ***Microdus brasiliensis***, a species in which high light intensity promotes protonemal growth. Photo by Jan-Peter Frahm, with permission.

Figure 19. ***Hymenostylium recurvirostrum***, a species in which high light intensity promotes protonemal growth. Photo by Michael Lüth, with permission.

Figure 20. ***Campylopus*** sp., a genus in which high light intensity promotes protonemal growth. Photo by Blanka Shaw, with permission.

Figure 21. ***Bartramia ithyphylla*** in a typical habitat. Photo by Michael Lüth, with permission.

Figure 22. ***Bartramia ithyphylla*** protonema showing branching in the cell just outside the spore. Photo courtesy of Eugenia Ron and Tom Sobota at Plant Actions, with permission.

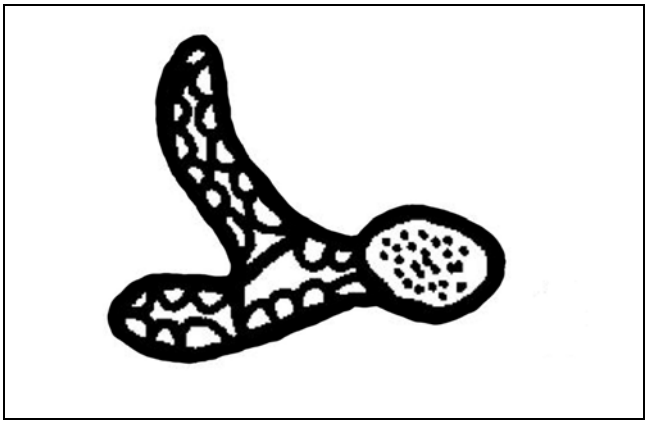

Figure 23. ***Brachythecium velutinum*** protonema branching Redrawn from Herguido & Ron 1990.

Figure 24. ***Gymnostomum aeruginosum*** with capsules, a species that can branch from multiple caulonema cells. Photo by Michael Lüth, with permission.

Figure 25. A species of ***Gymnostomum*** *s.l.* showing multiple branches from caulonema cells. Note the diatom living on it in its rock wall habitat. Photo by Janice Glime.

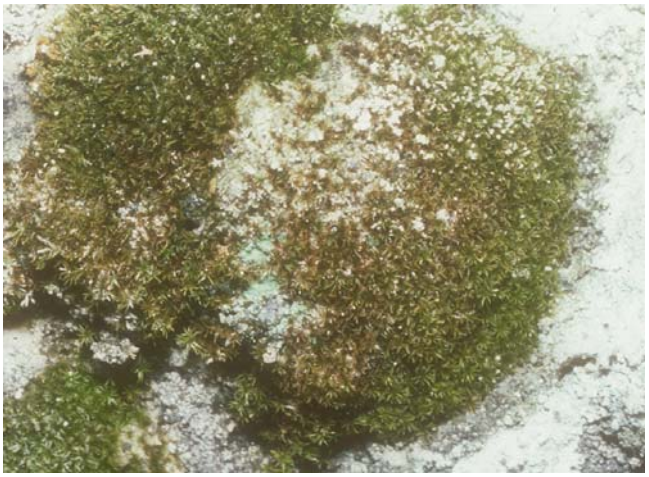

Figure 26. ***Gymnostomum*** forming colony, possibly from multiple buds from one protonema. Photo by Janice Glime.

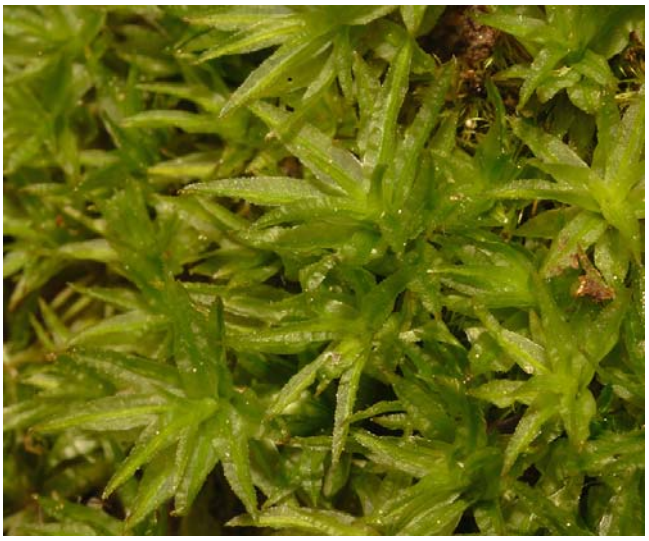

Figure 27. ***Atrichum altecristatum*** drying in an exposed habitat. Photo courtesy of Eric Schneider.

Figure 28. ***Atrichum altecristatum*** mat of protonemata with buds and young gametophores. Photo courtesy of Eric Schneider.

Continued high light promotes secondary caulonemata instead of bud formation. Is this adaptive by extending the plant to a darker location? Or is it merely a way of measuring all the available illuminated space for successful gametophores? Sood (1975) also observed an effect of light intensity on the number of germ tubes arising from the spore in ***Pogonatum aloides*** (Figure 29-Figure 30). At 1000 lux germination was unipolar, increasing at 3000 lux. At 6-8000 lux some spores swelled but failed to germinate. In germinating spores of ***Polytrichum commune*** (Figure 31) and ***P. juniperinum*** (Figure 32), there was a lag in synthesis of chlorophyll, being longer in ***P. commune*** (Karunen 1973). The chlorophyll *a*/*b* ratio at that time in ***P. commune*** was 1.4-1.8, thus providing little antenna effect by chlorophyll *b*. The low concentration of chlorophyll in general and the reduced relative amount of light-gathering chlorophyll *b* would force the gametophyte to require food reserves during early development.

Figure 29. ***Pogonatum aloides*** with protonemata and buds. Photo by Walter Obermayer, with permission.

Figure 30. ***Pogonatum*** protonema. Photo by George Shepherd, through Creative Commons.

Figure 31. ***Polytrichum commune*** showing the extensive turf it can form. Photo by Christopher Tracey, through Creative Commons.

Figure 32. ***Polytrichum juniperinum***, a species that exhibits a lag in chlorophyll production after the spore has germinated. Photo by Janice Glime.

High temperatures required for the protonemata can force a species into a narrow geographic range despite the ability of the spores to germinate at cooler temperatures. For example, ***Anisothecium molliculum*** has an optimum temperature of 25°C, not only for protonemal growth, but also bud formation (Kumra & Chopra 1985), preventing it from living in polar regions.

Although light generally seems to be necessary for spore distension, in some cases the protonema can even grow in the dark. In ***Ceratodon purpureus*** (Figure 33) darkness first induces an increase of starch grains in the chloroplast (Valanne 1971). This is followed by disappearance of starch and an increase in the number of grana lamellae.

Figure 33. ***Ceratodon purpureus*** with capsules, a species in which protonemata can grow in the dark despite its typical exposed habitat. Photo by Michael Lüth, with permission.

At least for ***Fontinalis squamosa***, higher light intensity and temperatures result in more germ tubes arising from the spore, suggesting that more sugars might be available, both for energy and for creating a high osmotic potential. The increased number of protonematal branches at higher light intensities and temperatures could provide a thicker mat to decrease evaporative losses and to increase self-shading against UV light damage.

Protonemata can form numerous branches, leading to numerous buds. When these buds develop into upright gametophores, the presence of many in close proximity permits them to protect each other from desiccation.

Light Quality

It is clear that light quality affects the growth and development of at least some protonemata. Light quality shift from white light to green and far red, as found in the forest, resulted in reduced protonemal growth in ***Pohlia nutans*** (Figure 34), with the least growth occurring in green light (Mitra *et al*. 1959). Giles and von Maltzahn (1967) found that red light stimulates mature leaf cells of ***Plagiomnium affine*** (see Figure 13) to regenerate by protonemata, and they suggested that phytochrome was most likely involved. Although liverworts seem to lack any consistent kind of photoregulation (Hartmann & Weber 1990), mosses respond differently to different wavelengths. Their best chloronema growth seems to be in white light (Bhatla 1994), but we must question whether this is true for all species that grow only under a canopy of green. In ***Funaria hygrometrica*** (Figure 2), the red range stimulates normal growth, whereas the blue range leads to the development of caulonema-like cells. It is possible that these shifts in light quality response could help to signal the time to develop gametophores as the protonemal mat thickens from extensive growth, changing the light quality of underlying strands.

Figure 34. ***Pohlia nutans*** with capsules. This widespread species of open habitats has reduced protonema growth in green light as it might experience in a forest. Photo by Štěpán Koval, with permission.

Imaizumi and coworkers (2002) demonstrated that **cryptochromes** are sensitive to blue light in ***Physcomitrella patens*** (Figure 9-Figure 10). Their reception of blue light permits them to mediate the light response. This moss has two identified cryptochrome genes. Using disruptants of these genes permitted Imaizumi and coworkers to elucidate the method of action of the cryptochromes. Cryptochromes, it turns out, mediate many steps in moss development. These include the induction of side branching of the protonema and induction of the leafy gametophyte. Disrupting cryptochromes caused changes in the auxin responses and revealed that cryptochromes respond to light to repress auxin signals as a means of controlling the development of the bryophyte.

Light quality could also serve to signal that it is time to break dormancy. Both blue and red light will permit maintenance of normal chloroplasts in ***Ceratodon purpureus*** (Figure 33) protonemata, but blue light results in richer starch, denser stromata (colorless matrix of chloroplast in which packets of chlorophyll are embedded), and more mitochondria, whereas red results in a more effective use of lipids (Valanne 1971). Is there any adaptive value in this? Is the moss able to sense the decreasing cover by snow (Figure 35), as voles do, based on light quality and intensity?

Figure 35. ***Atrichum undulatum*** in melting snow. How do mosses sense the coming of snowmelt? Photo by Michael Lüth, with permission.

Photoperiod

In ***Ceratodon purpureus*** (Figure 33), long days stimulate elongation of the protonema, whereas short days result in protonemal branching (Larpent-Gourgaud & Aumaitre 1980). The two systems are antagonists. This relationship suggests that an IAA/cytokinin balance may be the important controlling factor, with long days promoting IAA, probably through phytochrome mediation.

In ***Bryum pseudotriquetrum*** (Figure 36) a day length of ten or more hours is required for germination and protonema growth (Kinugawa & Nakao 1965, Figure 37). However two minutes of light during a 16-hr dark period is sufficient to remove the inhibitory effect developed during the dark period and will likewise stimulate germination and growth. In other words, it is the length of a continuous dark period that is important. This further supports the hypothesis of a phytochrome response and is much like the photoperiodic control of flowering.

Figure 36. ***Bryum pseudotriquetrum***, a species that requires at least 10 hours of daylight for germination and protonema growth. Photo by David T. Holyoak, with permission.

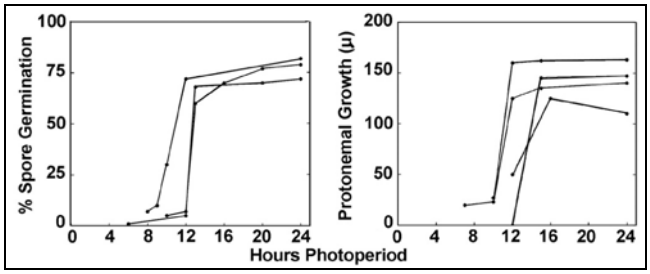

Figure 37. Effect of photoperiod on spore germination after 5 days (**left**) and protonema growth after 3 days (**right**) of ***Bryum pseudotriquetrum***. Redrawn from Kinugawa & Nakao (1965).

Hormonal Response

The complexity of these light responses and the implications of involvement by phytochrome is undoubtedly under the control of hormones. In the ephemeral ***Physcomitrella patens*** (Figure 9-Figure 10), light and hormonal combinations coordinate development (Cove *et al*. 1978, 1979). Bierfreund *et al*. (2003) supported this earlier conclusion by demonstrating that red light retarded the growth of protonemal filaments in ***Physcomitrella patens***. **Gametophores** (upright plants), on the other hand, responded by producing an elongated plant with shorter and narrower leaves. Responses of both protonemata and gametophores were even more pronounced when illuminated with far red light.

Cytokinin in the presence of auxin promotes buds (Gorton & Eakin 1957), and high concentrations inhibit caulonemata (Cove *et al*. 1978, 1979). This combination would therefore promote caulonema growth while the caulonemata are sparse, ensuring sufficient plants for a viable population and providing a sufficiently dense protonematal mat to help maintain moisture at the soil surface. When this mat becomes very dense, self-shading could stimulate the production of auxin and cytokinin and shift the development to bud formation. Once these self-shaded protonemata have shifted to bud development, they are likely to communicate this signal to the surface protonemata and induce buds throughout the mat. Figure 38 shows a developmental scheme modified from Cove *et al*. (1979) to include these environmental stimuli.

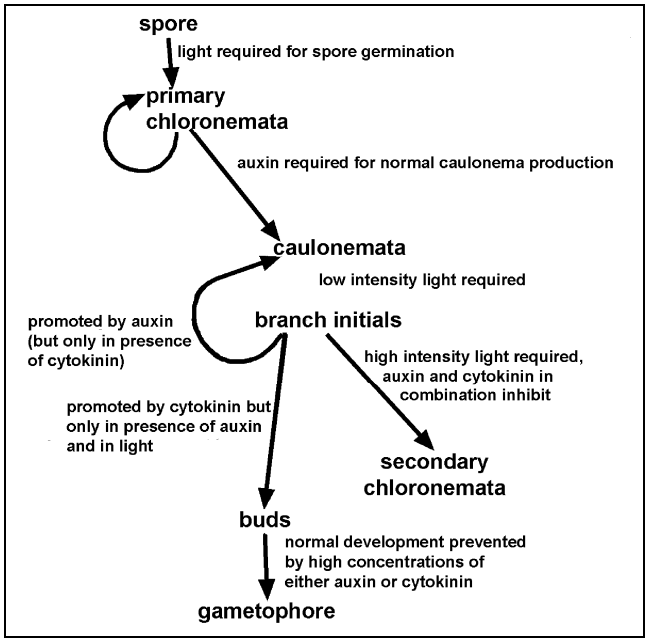

Figure 38. Effects of auxin and cytokinin on ***Physcomitrella patens***. Redrawn from Cove *et al*. (1979).

Bierfreund *et al*. (2003) used ***Physcomitrella patens*** (Figure 9-Figure 10) to determine the distribution of auxin (IAA) in the protonema. As in higher plants, the highest concentrations were in the dividing and young cells. Concentrations declined from the tip cells back to the basal cells of the protonema, supporting earlier work of Bopp and Atzorn (1992).

Auxin is important in the transition of chloronema to caulonema (Johri & Desai 1973; Figure 38) and the appropriate concentration maintains the caulonema state (Bopp 2000). Although we generally think that endogenous hormones from one plant cannot affect another, in ***Funaria hygrometrica*** (Figure 39) the minute quantity of 10^{-16} mol IAA/mg fw seems to be responsible for the change from chloronema to caulonema (Bhatla & Dhingra-Babbar 1990). Such a small quantity could surely leak from other members of the same species or from a different species to help coordinate behavior among individuals. In fact, as the protonema matures, the protonema can excrete most of its auxin to its substrate, as shown in ***Physcomitrella patens*** (Figure 9-Figure 10) (Reutter *et al*. 1998).

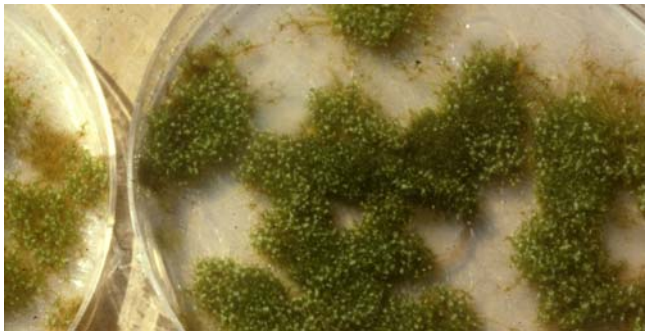

Figure 39. Culture of ***Funaria hygrometrica*** showing distinct colonies resulting most likely from hormonal interaction between clones at the protonemal stage. Each clump is the product of one spore. Photo by Janice Glime.

We already know that uptake of IAA by the protonema occurs; in the lab, uptake of IAA by protonematal cells is both passive and active. The passive component is *p*H-dependent, with the greatest increase in uptake occurring at *p*H 4.5-4.7, indicating a dissociation of the IAA molecule (*p*K = 4.7; ***pK*** is *p*H at which equal concentrations of acidic and basic forms of substance are present). The potential for an exogenous developmental regulator has enormous environmental implications not only for development, but for systematics and ecology as well.

Rose *et al*. (1983) used ***Funaria hygrometrica*** (Figure 7-Figure 8, Figure 39) to show a strong *p*H dependence for the accumulation of auxins. The uptake of the auxin IAA increases when the *p*H is lowered from 7.6 to 4. The IAA appears to have influx and efflux carriers that help to determine the rate of this hormone in and out of the protonema. But these carriers seemed to be present only in low light intensities. At high light intensities (2.0-2.3 W m^{-2}) there was no evidence for them.

Physcomitrella patens (Figure 9-Figure 10) has become a widely used model for plant physiology. It is easy to grow and to standardize the cell culture protocol. Its complete genome is known. These characteristics make it useful to study plant physiological responses. And the protonema is an especially useful tool because it provides an isolated single cell type. ABA causes the subapical cells to form round **brachycytes** (short, thick-walled cells that are drought-tolerant brood cells) or nearly empty **tmema** (abscission cell) (Decker *et al*. 2006). When the cells are subsequently grown free of ABA, the brachycytes serve as propagules and germinate to form new protonema filaments (Schnepf & Reinhard 1997).

These brachycytes also occur in auxin-deficient mutants of ***Funaria hygrometrica*** (Figure 7-Figure 8, Figure 39) (Schnepf & Reinhard 1997). Experiments in this species likewise confirm that ABA induces their production, and that it is concentration dependent. These brachycytes store lipids instead of starch and have altered chloroplast structure. This suggests that they provide a fallback mechanism to maintain the population if it becomes desiccated, a condition known to increase ABA production in mosses (Hajek & Vicherova 2014). Also, in ***Funaria hygrometrica***, application of auxin causes a change in development from the chloronema stage to the caulonema stage (Jayaswal & Johri 1980).

But having the right hormones isn't enough. There must be sufficient energy as well. We have seen that development of the protonema can occur in the dark, and in the early stages that energy is soon exhausted. To this end, the chloronemata are heavily endowed with chloroplasts (Thelander *et al*. 2005). The caulonemata, on the other hand, have more scattered chloroplasts and function to spread the colony by radial growth. The balance between the two protonema types is controlled by light and plant hormones. In ***Physcomitrella patens*** (Figure 9-Figure 10), caulonema formation is induced by high light, thus providing greater photosynthesis. External glucose also stimulates growth. But under low light conditions, the chloronema stage predominates, with chloronemal branching being stimulated by the low light (or perhaps high light suppresses chloronemal branching).

How widespread are these principles when we look at species outside the **Funariaceae**? In ***Hyophila involuta***

(**Pottiaceae**; Figure 40), **nurse protonemata** enhance the growth of other protonemata (Mehta 1990). This is the phenomenon in which substances diffused from an older protonema enhance the growth of the younger, developing protonema. It applies the rule of safety in numbers, in this case helping to protect the protonema and developing buds and gametophytes from desiccation.

Figure 40. ***Hyophila involuta***, a species that benefits from **nurse protonemata**. Photo by Bob Klips, with permission.

Tropisms

Tropisms, the bending, resulting from unequal growth on two sides of a stem, of a plant in response to a stimulus, are adaptive in orienting the plant into its most beneficial position. When the spore germinates, the developing protonema orients to gain the most light. When protonemal buds develop, they orient to obtain light. For the leafy gametophyte, this could mean extending away from gravity, as seen in acrocarpous mosses, or extending outward across the ground, as seen in pleurocarpous mosses. Both strategies of orientation have their advantages and disadvantages in obtaining sufficient light and consequent energy, and both are under control of hormones.

Phototropism

In bryophytes, protonemata are **positively phototropic** (bend toward light), whereas rhizoids are **photonegative** (bend away from light) (Heitz 1942). Although Kofler and coworkers investigated the effects of the environment on bryophyte tropisms as early as 1958 (Kofler 1958, 1971; Kofler *et al.* 1963), bryophyte tropisms have remained largely unstudied until recently. However, because of their simple protonemal structure, much of our current understanding of tropisms in plants has been learned from using bryophytes as model systems.

Yet bryophytes have different **phototropic** responses (directional growth in response to light) from those of tracheophytes. Rather than responding to blue light, as do the tracheophytes, most bryophytes seem to respond to red light, using **phytochromes** instead of **cryptochromes** as their sensory pigments (Wada & Kadota 1989; Esch *et al.* 1999). Jaffe and Etzold (1965) demonstrated that even spores (Figure 41) in ***Funaria*** (Figure 7-Figure 8, Figure 39) respond to red light, resulting in chloronema growth in the opposite direction from that of rhizoids. And even more intriguing is the ability of bryophytes to store a phototropic stimulus (Hartmann & Weber 1988), further suggesting the use of phytochromes. However, the expected dark reversal does not occur, indicating something else is involved (Christianson 2000). Phototropism will be discussed further under gravitropism because of the interaction of these two forces.

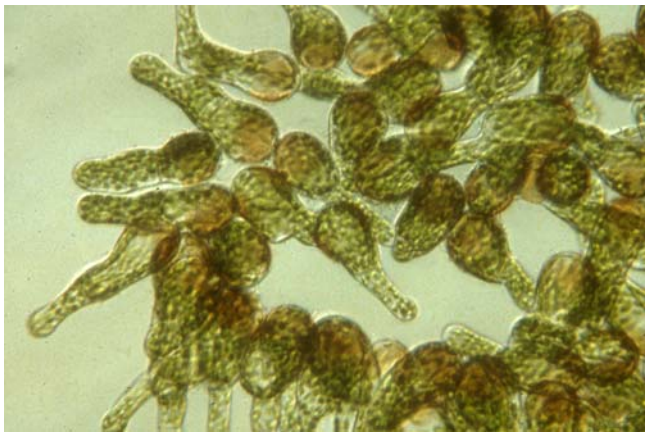

Figure 41. ***Funaria hygrometrica*** spore germination. Photo by Janice Glime.

Gravitropism

Gravitropisms respond to gravity, just as your spoon does when you drop it. But in plants, gravity has a different effect on different bryophyte plant parts and different life stages. In the protonema, it often is masked by the effects of light. Rhizoids are **positively gravitropic**, hence growing toward the earth, but for some species this is not the right position, so other responses have evolved. For acrocarpous mosses, the stems typically grow upward, as do the sporophytes. But like the rhizoids, stems may not always start in the right position. And likewise, the sporophyte might be pointed perpendicular to a vertical rock or tree trunk. For some species, there is a clear tropism in both gametophyte and sporophyte, for some only the sporophyte responds (Figure 42), and for some, both grow straight out from the vertical substrate (Figure 24), perpendicular to it.

Figure 42. ***Oligotrichum hercynicum*** showing a strong tropism in the seta but none in the gametophyte on this vertical surface. Photo by Michael Lüth, with permission.

Gravitropism is well documented in moss protonemata (Sack *et al*. 1998). Barlow (1995) suggested that the more evolutionarily advanced species will posses more systems for sensing gravity, arguing that if a system works, it is not likely to be discarded, thus being kept as new ones evolve. These multiple gravity-sensing systems permit gravity to be involved in a wider range of developmental responses. The sensing of gravity involves a membrane system to sense the gravity.

Schwuchow and Sack (1990) reported for the first time an effect of gravity on **microtubule** (essential protein filament of cell structural skeleton; Figure 43) distribution in plants, based on studies in protonemata of ***Ceratodon purpureus*** (Figure 33). In fact, this moss served as the model organism to demonstrate that microtubules help organelles to maintain their positions within the cell (Schwuchow & Sack 1994). Nevertheless, our understanding of **gravitropism** in protonemata is still in its early stages. We don't even have a very long list yet of mosses with demonstrated protonemal gravitropism, and we seem to know even less about liverworts. Schwuchow *et al.* (2002) have only recently found tropisms in protonemata of ***Barbula unguiculata*** (Figure 44), ***Fissidens adianthoides*** (Figure 45), ***Fissidens cristatus*** (Figure 46), and ***Physcomitrium pyriforme*** (Figure 47-Figure 48), despite the report of positive phototropism in ***Funaria*** protonemata in 1942 by Heitz.

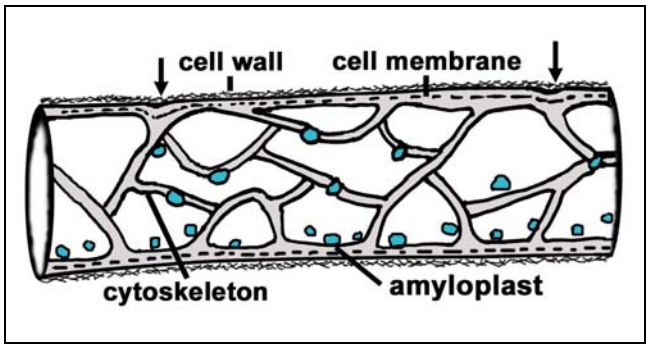

Figure 43. Schematic model of hypothetical relationship of **amyloplasts** (statoliths) of a protonema in response to gravity. Arrows denote pull of **cytoskeleton** on cell membrane. Drawing by Janice Glime.

Figure 44. ***Barbula unguiculata***, a species with tropisms in the protonema. Photo by Michael Lüth, with permission.

Figure 45. ***Fissidens adianthoides***, a species with tropisms in the protonema. Photo by Hermann Schachner, through Creative Commons.

Figure 46. ***Fissidens cristatus***, a species with tropisms in the protonema. Image ©Stuart Dunlop <www.donegal-wildlife.blogspot.com>, with permission.

Figure 47. ***Physcomitrium pyriforme*** with capsules in its soil habitat. Photo by Bob Klips, with permission.

Figure 48. ***Physcomitrium pyriforme*** protonema, a protonema that exhibits tropisms. Photo by Bob Klips, with permission.

The one-cell-thick protonema makes it easy to observe the **amyloplasts** (colorless plastids containing starch, sometimes referred to as statoliths) that respond to gravity. These statoliths are involved in **gravitropism** (directional growth in response to gravity). The ability to knock out or add genes that are easily expressed in the 1*n* plants (having only 1 set of chromosomes) has made the necessary manipulation much easier than in tracheophytes. Walker and Sack (1990) observed that **amyloplast sedimentation** occurred in horizontal protonemata of ***Ceratodon purpureus*** (Figure 33) grown in the dark. Protonemata grew straight up – away from the pull of gravity – at a rate of 20-25 μm h^{-1}, reaching an angle of 84° with the substrate by 24 hours. The tip cells exhibited a cluster of non-sedimenting amyloplasts, a zone free of amyloplasts, and a zone with pronounced amyloplast sedimentation. The sedimentation zone occurs only along lateral walls with some degree toward the horizontal and does not occur toward end walls regardless of their position. The beginnings of this gravitational rearrangement are visible within ~15 minutes of change in the direction of the gravitational pull. At this time Walker and Sack (and also Young and Sack 1992) suggested that the amyloplasts might act like the statoliths that help to orient crayfish and other organisms.

Young and Sack (1992) used time lapse photography to gain further understanding of the gravitropic response in ***Ceratodon purpureus*** (Figure 33). By this method, they observed that a "wrong-way" response occurred first. That is, the protonema initially curved downward in as little as 2 minutes after the protonemata were re-oriented. It required 30-45 minutes for upward curvature to begin. No amyloplast sedimentation occurred before the wrong-way response, but sedimentation seemed necessary for the onset of negative (correct) gravitropism.

But this brings to mind the question of their avoidance of the end walls when those walls are in the position closest to the gravitational pull. In succeeding experiments, Walker and Sack (1991) used centrifugation to displace all the amyloplasts in the apical cell to the end wall. In this position, the amyloplasts acted in the wrong way and the protonema curved downward, likewise in the wrong way. Upward curvature did not occur until sedimentation of amyloplasts occurred toward the lateral wall.

Later Wagner and Sack (1998) reported that the gravitropic response occurs within 1-2 cell divisions in the protonemal tip cells of ***Ceratodon purpureus*** (Figure 33), which grow upward in the dark (Wagner *et al*. 1997). Five mosses and four other species, representing five orders, support the hypothesis that amyloplast sedimentation probably serves in gravity sensing in moss protonemata. It appears that these amyloplasts tug on the **cytoskeleton** (structural support within cell), pulling down on it, much like trapped insects on a spider web. One theory is that this causes the cytoskeleton to pull on the cell membrane, creating larger holes in the membrane that facilitate the entry of Ca^{++}. This creates a higher concentration of Ca^{++} on the upper side of the cell, possibly causing it to inhibit the IAA on that side of the cell.

When auxin transport inhibitors were applied to ***Ceratodon purpureus*** (Figure 33), they strongly inhibited the gravitropic curvature of the apex of the protonema, suggesting the role of IAA in the process (Schwuchow *et al*. 2001). Reducing the concentration of inhibitors reduced the inhibition effect. Applications of high levels of IAA (40 μM) had no effect on the gravitropic response of the protonema apex, suggesting the mechanism differs from that in tracheophytes. But perhaps it is only the effective concentrations that differ. We know that roots respond to different levels from stems in tracheophytes, so we have no reason to expect bryophytes to respond to the same levels.

What little we thought we knew about gravitropisms in moss protonemata was further confused when growing protonemata of the moss ***Ceratodon purpureus*** (Figure 33) took a two-week trip in space on the space shuttle Columbia (Miller & Phillips 2003; Kern *et al*. 2005). On 16 July 2002, plant physiologist Fred Sack carefully opened a Petri dish that had spent the two weeks without gravity and without light. To his surprise, the protonemata had grown in a spiral pattern (Figure 49). This is quite different from the normal tangle of protonemata grown on Earth.

Figure 49. Spiral growth of protonemata of ***Ceratodon purpureus*** aboard space shuttle Columbia. Photo courtesy of Fred Sack.

According to Fred Sack (Miller & Phillips 2003), "These odd spirals mark the first time in space that a plant

normally oriented by gravity has grown in a non-random pattern." The puzzle begins with the **amyloplasts**. These starch bodies experience sedimentation in gravity and seem to tug on the cell skeleton. However, on the shuttle, with no gravity, this should not happen. Rather, they should float at random within the cell. Instead, they bunched together. This indicates a natural propensity for growing in a spiral that is overridden by the gravity of Earth. Perhaps Seifritz was right – all life does have a twist in it.

Another piece of this gravitropic puzzle is that a high-gradient magnetic field can substitute for gravity, causing curvature of tip cells in ***Ceratodon purpureus*** (Figure 33) (Kuznetsov *et al*. 1999). Genetically modified protonemata with larger plastids responded more strongly, supporting the hypothesis that plastids are involved in gravity sensing.

The caulonemata in ***Funaria hygrometrica*** (Figure 7-Figure 8, Figure 39) are negatively gravitropic (Schwuchow *et al*. 1995). So in the dark, they grow upward. Such behavior can increase the opportunity to grow toward more light before there is light for them to sense. As in ***Ceratodon purpureus*** (Figure 33) and ***Physcomitrella patens*** (Figure 9-Figure 10), this upward curvature is temporarily reversed when the cell reaches its final stages of division. Tropism behavior in all three species indicates that subapical amyloplast sedimentation may be a common phenomenon in the protonemata of mosses.

Using ***Physcomitrella*** (Figure 9-Figure 10), Schwuchow *et al*. (1995) provided details of the gravitropic response within the cell. In the dark, a thin strip lacking amyloplasts was visible in the cytoplasm on the upper side of the cell. At this point, they suggested that amyloplast sedimentation might be a common gravitropic response in moss caulonemata. In 2002, Schwuchow *et al*. added ***Barbula unguiculata*** (Figure 44), ***Fissidens adianthoides*** (Figure 45), ***Fissidens cristatus*** (Figure 46), and ***Physcomitrium pyriforme*** (Figure 47-Figure 48) to the list of species with gravitropic protonemata that exhibited amyloplast sedimentation. Ultimately they demonstrated this sedimentation in nine species representing five different orders of mosses. Thus, we can conclude that this phenomenon is widespread among mosses and may be present in all of them.

This scenario is further explained by observations on ***Tortula modica*** (Figure 50-Figure 51) (Chaban *et al*. 1998). Amyloplast sedimentation occurs in the sub-apical zone. These amyloplasts seem to be important in signalling the direction of gravity and sedimentation is present before the tropic response occurs. Although spores require light for germination, the protonema is able to continue development in the dark, but both growth and number of filaments are limited (while resources last). Deprived of light, the protonemata are negatively gravitropic.

Secondary caulonemata, arising from a wound or fragment, likewise are strongly negatively gravitropic in the dark (Chaban *et al*. 1998). These are able to survive and grow well in the dark, most likely gaining resources from the wounded leafy gametophyte. In ***Tortula modica*** (Figure 50), these secondary caulonemata usually arise at the leaf bases. These tropic responses are rapid. When upright caulonemata are moved to make them horizontal or upside-down, the tropism can be seen within an hour and re-orientation to become vertical is completed in 1-2 days.

Figure 50. ***Tortula modica*** with capsules, a species exhibiting amyloplast sedimentation in the sub-apical zone of the protonema. Photo by Kristian Peters, with permission.

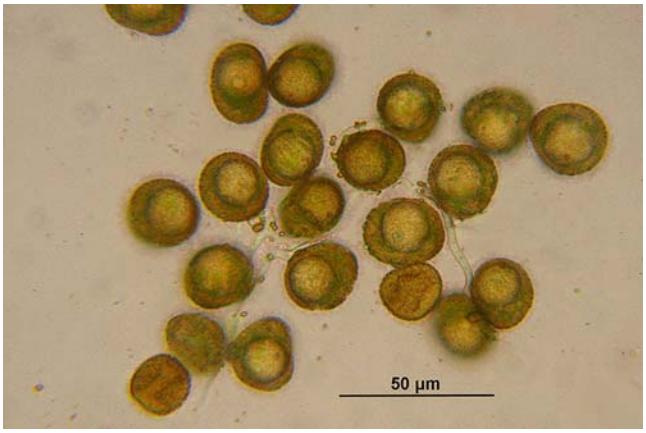

Figure 51. ***Tortula modica*** spores, a species exhibiting amyloplast sedimentation in the sub-apical zone of the protonema. Photo by Hermann Schachner, through Creative Commons.

We know that amyloplasts sediment in response to gravity (Walker & Sack 1992, 1997), just like sand grains dropped into a glass of water. So how do the plant organelles maintain their positions against the pull of gravity? The amyloplasts themselves may help us understand this. Using ***Ceratodon purpureus*** (Figure 33), several groups of researchers demonstrated that only some of the amyloplasts sediment along the length of the protonemal tip cell (Schwuchow & Sack 1993; Kern & Sack 2001; Kern *et al*. 2001). They reasoned that if gravity is the only or the major force determining the position of the amyloplasts, then they should be randomly distributed in space. But instead they are clustered in the subapical region when in **microgravity** (very weak gravity). The same occurs when the cells are rotated in a clinostat. But when controls are inverted and kept stationary, the distribution of the amyloplasts differs considerably due to sedimentation. This indicates that the amyloplast forces and mechanisms are normally masked in stationary cells. Kern and coworkers (2001) hypothesized that a "microtubule-based mechanism normally compensates for the drag of gravity, but at the same time it allows for the regulated amyloplast sedimentation." This basically agrees with the interpretation already put forth by Schwuchow *et al*. (1994) for ***Ceratodon***.

The foregoing research implies that gravity is not alone in controlling direction of growth. Using ***Ceratodon purpureus*** (Figure 33), Wagner *et al*. (1997) showed that in the dark, plastid sedimentation is more pronounced than in the light. In ***Ceratodon purpureus***, the apical protonema cells are negatively gravitropic in the dark, but in unilateral red light they are positively phototropic, thus overriding the gravitropic response (Kern & Sack 1999a, b). At light intensities of $\geq$140 nmol m^{-2} s^{-1}, the phototropism completely overrides the gravitropic response. Partial gravitropic response occurs at lower light intensities. In microgravity, phototropic responses occur. In normal gravity, gravitropism and phototropism compete and "winning" depends on the light intensity. ***Ceratodon purpureus*** demonstrates that phototropism is **phytochrome**-mediated (Lamparter *et al*. 1996, 1998; Kern & Sack 1999b). **Phytochrome** is a blue-green pigment in plants that regulates various developmental responses such as long-day and short-day responses.

Autotropism (tendency of plant organs to grow in a straight line when not influenced by external stimuli) occurs when no external stimuli (gravity, light) are present. Again using ***Ceratodon purpureus*** (Figure 33), Demkiv *et al*. (1997) determined that three stimuli are involved in the direction of protonema growth. In darkness, the protonemata have negative gravitropism. When illumination is uniform from all directions, they grow radially over the substrate, much like those in space or microgravity. In blue or far-red light the gravitropism is blocked, but in red light both gravitropism and autotropism are blocked. Green light (typical light in the forest) allows both gravi- and autotropism (Demkiv *et al*. 1998). Reversal of autotropism inhibition involves the phytochrome system, indicated by the red and far-red effects. Gravitropism occurs simultaneously with starch synthesis and amyloplast formation (Demkiv *et al*. 1997).

Using mutants of ***Physcomitrella patens*** (Figure 9-Figure 10), Jenkins *et al*. (1986) demonstrated that the genes that control gravitropisms of the caulonema do not appear to be involved in the control the tropisms of the leafy gametophyte.

Repp *et al*. (2004) used genetically modified ***Physcomitrella patens*** (Figure 9-Figure 10) to demonstrate the role of **cytokinin** signalling for gravitropism. When a knockout mutant lost its sensitivity to cytokinin, it had greatly reduced ability to respond gravitropically in the dark. Based on several studies, it appears that the cytokinins serve the protonemata primarily to induce gametophore buds (Lehnert & Bopp 1983; Bopp 1984).

Here you are, sitting in the dark, and you need light to continue life for long. What do you do? If you are a young protonema, you grow in the direction where you will most likely encounter light. And to do that, you exercise a **negative gravitropism**. That is, you grow away from gravity and toward the daytime sun. Once you reach sunlight, your **phototropism** takes over and you grow toward light.

Mosses may be "smarter" than seed plants. The moss protonemata apical cells can respond to both gravity and light, unlike most cell types (Kern & Sack 1999b). This permits these tiny structures to advance toward the most advantageous position. Even if they are anchored in a crevice, they can follow the path of light to reach the surface. For example, in ***Ceratodon purpureus*** (Figure 33), a species that is common in such cracks, the tips of the protonemata are negatively gravitropic in the dark and positively phototropic in unilateral red light. Thus, they would grow toward the opening in a crack.

It appears, based on our observations with protonemata, that the statoliths (**amyloplasts**) settle downward within the cell in response to gravity. This pulls on the **cytoskeleton**. The cytoskeleton is attached to the cell membrane, so this downward pull tugs on the membrane in the upper portion of the cell (Figure 43). A plausible theory is that this stretches the membrane, making it more permeable. This in turn permits more Ca^{++} to enter the upper side of the cell, where it inhibits the action of IAA, permitting the lower side of the cell to grow more.

Nutation

Under some circumstances, the protonema will exhibit **nutation** – a spiral or circular growth pattern that is displayed in time-lapse photography by apparent movements of the stem (or protonema) in a circle. In ***Funaria hygrometrica*** (Figure 7-Figure 8, Figure 39), red light causes the protonema to grow into a ring (Simon & Naef 1981). I have observed the same nutation in contaminated cultures of ***Fontinalis squamosa*** (Figure 52) and in air-grown rhizoids of that species. Nutation appears to facilitate a kind of seeking – altering growth directions until a more favorable condition is located. It is beneficial when no directional stimulus is present, such as spiral growth of rhizoids until they contact a substrate, as observed in ***Fontinalis squamosa***. Although nutation is an IAA/ethylene response in higher plants (Morgan & Powell 1970), its occurrence as a response to red light suggests it results from a somewhat different mechanism here since red light is known to inhibit ethylene production. Could this be the same spiraling mechanism seen in the space-travelling ***Ceratodon purpureus*** (Figure 33) protonemata (Figure 49)? The curiosity there is that the entire population of protonemata grew in a spiral.

Figure 52. ***Fontinalis squamosa*** rhizoids showing spiral growth. Photo by Janice Glime.

Interactions

We have already implied that exogenous growth regulators could determine events in the development of the moss protonema. Protonemata in nature grow on substrata that are not sterile. Rather, they are teaming with fungi, bacteria, algae, and exudates of other plants. One might then predict that at least some of the protonemata respond in positive or negative ways to these companions.

One possible outcome of cohabitation is that bacteria, fungi, or other organisms may provide the growth substances needed to stimulate the next phase of development. Fungi commonly produce **gibberellic acid** that escapes into the environment. Vaarama and Tarén (1959) found that not only did 0.01% GA promote both spore germination and protonema growth in several mosses [***Dicranum scoparium*** (Figure 53), ***D. undulatum*** (Figure 54), ***Dicranoweisia crispula*** (Figure 55), and ***Pogonatum urnigerum*** (Figure 56)], but also inoculation with several fungi [***Aspergillus flavus*** (Figure 57), ***Penicillium martensii***, ***Mucor racemosus***, ***Fusarium scirpi***, and ***Rhodotorula mucilaginosa*** (Figure 58)] had even more effect than did the gibberellic acid.

Figure 53. ***Dicranum scoparium*** in a pine forest. In this species, spore germination and protonema growth are promoted by GA and fungi. Photo by Janice Glime.

Figure 54. ***Dicranum undulatum***, a species in which spore germination and protonema growth are promoted by GA and fungi. Photo by Michael Lüth, with permission.

Figure 55. ***Dicranoweisia crispula***, a species in which spore germination and protonema growth are promoted by GA and fungi. Photo by Michael Lüth, with permission.

Figure 56. ***Pogonatum urnigerum***, a species in which spore germination and protonema growth are promoted by GA and fungi. Photo by Michael Lüth, with permission.

Figure 57. ***Aspergillus flavus***, a fungus that interacts with the protonemata of mosses. Photo from Medmyco, through Creative Commons.

Figure 58. ***Rhodotorula mucilaginosa*** colonies, a yeast species that interacts with protonemata through Creative Commons.

In contaminated cultures of ***Fontinalis squamosa*** (Figure 1, Figure 15) most of the protonemata formed mature caulonemata in less than four weeks, whereas in uncontaminated cultures the chloronema state predominated (Glime & Knoop 1986; Glime, unpub data). And only the contaminated cultures ever produced buds. This suggests that at least some microbes might alter the developmental state of the moss.

Spiess *et al*. (1971) found that the bacterium ***Agrobacterium tumefaciens*** (Figure 59) influenced the development of ***Pylaisia selwynii*** (Figure 60). Spiess *et al*. (1986) found 48-68% of six groups of bacterial isolates (283 isolates) from separate samples [***Pylaisia selwynii***, ***Callicladium haldanianum*** (Figure 61)] increased the development of the moss species from which they were isolated but not that of ***Funaria hygrometrica*** (Figure 7-Figure 8, Figure 39). There seemed to be both specificity and fidelity at nearby locations, but species differed between latitudes. Bacterial interaction may be important in bryophyte development.

Figure 59. ***Agrobacterium tumefaciens*** on plant cell. Photo by Martha Hawes, University of Arizona.

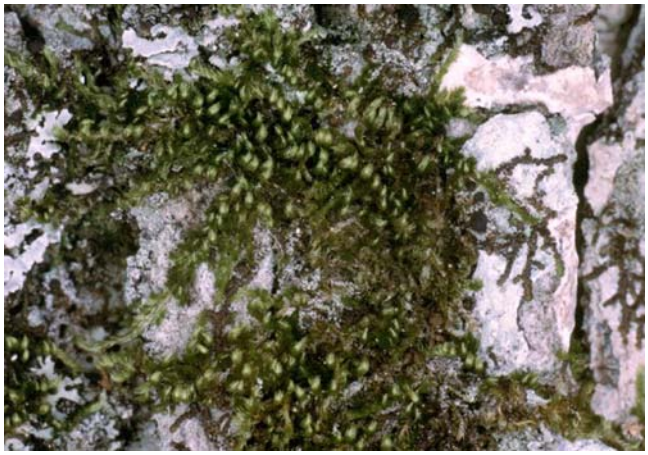

Figure 60. ***Pylaisia selwynii*** on tree bark. Protonema development in this species is enhanced by presence of ***Agrobacterium tumefaciens***. Photo by Jan-Peter Frahm, with permission.

Figure 61. ***Callicladium haldanianum***. Protonema development in this species is enhanced by presence of ***Agrobacterium tumefaciens***. Photo by Misha Ignatov, with permission.

Kutschera (2007) demonstrated a positive interaction between the methanol-using purple bacterium ***Methylobacterium*** [Figure 62; ***M. mesophilicum*** and two other unknown ***Methylobacterium*** species isolated from ***Funaria hygrometrica*** (Figure 7-Figure 8, Figure 39) and sunflower achenes] and the protonemata of bryophytes [moss ***Funaria hygrometrica***; thallose liverworts ***Marchantia polymorpha*** (Figure 63) and ***Lunularia cruciata*** (Figure 64), but there was no benefit observed for the angiosperms studied. The same positive effect occurred for development from gemmae of the two liverworts. Methanol appears to be a waste product of the pectin metabolism of growing plant cell walls. Kutschera postulated that the ***Methylobacterium*** cells accomplished this protonemal developmental stimulation through their secretion of the plant hormones cytokinin and IAA (indole-3-acetic acid). Hence, the sequence seems to be:

1. Uptake and metabolism of plant waste products (methanol, amino acids, *etc*.) by the bacteria
2. Possible release of ammonium ions by bacteria
3. Secretion of cytokinins and IAA by bacterial "waste managers"

4. Bacterial hormonal signals may indicate to the plant that bacterial epiphytes are present and active
5. Hormones stimulate growth of the bryophyte gametophyte
6. Cross signals may help to regulate bryophyte growth.

This hormonal interaction may account for the success of bryophytes in some habitats in nature and the lack of success of at least some protonemata when grown in sterile culture.

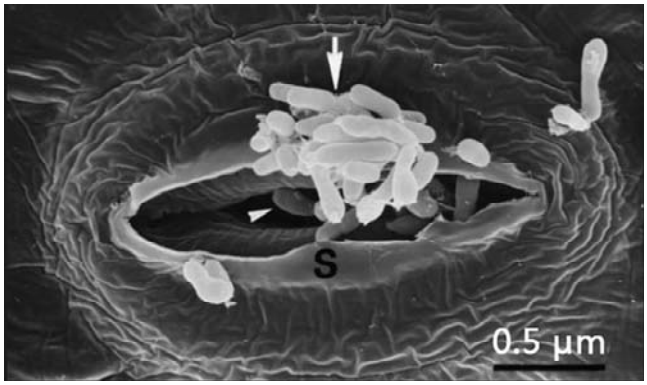

Figure 62. ***Methylobacterium*** in sunflower stoma, a bacterial species that has a positive interaction with protonemata of several bryophyte species. Photo by Kutschera U., through Creative Commons.

Figure 63. ***Marchantia polymorpha***, a species in which there is a positive interaction of the protonema with ***Methylobacterium*** spp. Photo by James K. Lindsey, with permission.

Figure 64. ***Lunularia cruciata***, a species in which there is a positive interaction of the protonema with ***Methylobacterium*** spp. Photo by David Holyoak, with permission.

Fungi have effects on other bryophyte protonemata as well. Hildebrand and coworkers (1978) found that fungal exudates promoted the growth of ***Atrichum*** (Figure 27-Figure 28), ***Funaria*** (Figure 7-Figure 8, Figure 39), and ***Brachythecium*** (Figure 65) protonemata (Figure 66) at low pH. As suggested above for spore germination, ***Splachnum ampullaceum*** (Figure 67) protonematal growth is promoted by several species of fungi (von Maltzahn & MacQuarrie 1958). Certainly growth hormones exuded by the fungi could be of importance here (see Bopp 1980).

Figure 65. ***Brachythecium velutinum*** with capsules, a species that has its protonematal growth promoted by fungi. Photo by Michael Lüth, with permission.

Figure 66. ***Brachythecium velutinum*** germinating spores and young protonemata, a species with fungal stimulation of protonemata. Photo by Eugenia Ron Alvarez & Tomas Sobota, with permission.

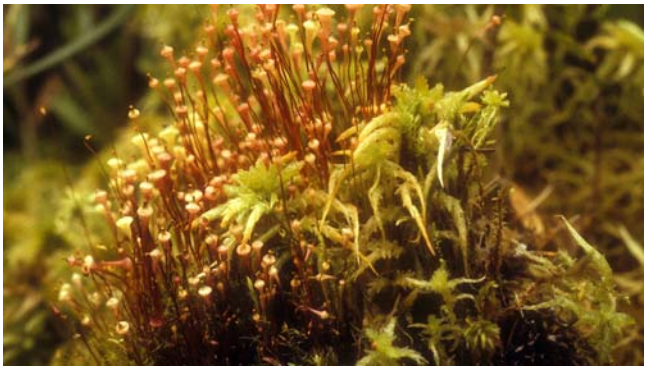

Figure 67. ***Splachnum ampullaceum*** growing among ***Sphagnum*** on dung, where changing dung conditions and fungal exudates influence development. Photo by Janice Glime.

In addition, contributions of vitamins from algae or amino acids or other organic compounds from bacteria might either be essential or promote a growth rate that is compatible with the seasons. Gibberellic acid, produced by many fungi, has a variety of effects, depending on the species of moss. It increases the number and length of protonemal cells in ***Dicranum*** (Figure 53-Figure 54) and ***Dicranoweisia*** (Figure 55), but it has no effect on ***Racomitrium fasciculare*** (Figure 68) (Vaarama & Tarén 1959). Since ***R. fasciculare*** grows on rocks where fungi are less likely to occur, and fungi are a natural source of GA, these differences in responses are consistent with habitat differences.

Figure 68. ***Racomitrium fasciculare***, a rock-dwelling species whose protonemata are not stimulated by GA. Photo by Janice Glime.

We know that the induction **Factor H** (an adenine derivative discussed in subchapter 5-1 on Hormones) is present in ***Funaria*** (Figure 7-Figure 8, Figure 39). It will induce not only other protonemata of ***Funaria***, but it can be induced by other species [*e.g.* ***Leptobryum pyriforme*** (Figure 69)] as well (Klein 1967; Bopp 1976). Such a factor is adaptive in insuring a sufficient breeding population, but perhaps more importantly it insures a community organization that offers resistance against desiccation, where middle plants are protected by outer ones in the population. In submerged mosses such as ***Fontinalis*** (Figure 70-Figure 71) species, on the other hand, moisture conservation is not so critical, and multiple gametophores would only offer competition for the limited substrate available for anchorage.

Figure 69. ***Leptobryum pyriforme***, a species whose protonemata can induce the protonemata of ***Funaria hygrometrica***. Photo by Michael Lüth, with permission.

Figure 70. ***Fontinalis squamosa*** on rock above water near Swallow Falls, Wales. Photo by Janice Glime

Figure 71. ***Fontinalis squamosa*** spore germination. Photo by Janice Glime.

Whereas some interactions can enhance growth of moss protonemata, others inhibit it, preventing the colonization of that substrate. Shrimal (1975) showed that bark extracts of several trees inhibited mitosis in onion root tips and caused non-separation of chromosomes. If these substances have the same effects on mosses, it could explain why some trees lack bryophytic epiphytes.

Inhibition can also occur within a species, as already suggested for ***Funaria*** (Figure 7-Figure 8, Figure 39). In this species, protonemata from several spores in one culture will not intersect (Watson 1981). The mat attains the same density when the protonemata are derived from many spores as when they are derived from only one. Watson also suggests that one species may inhibit another, thus making time an important factor in access to a habitat. And ***Funaria*** is not the only moss where some exudate of the protonema retards development of competing protonemata of the same species. This has been observed in culture in ***Physcomitrella patens*** (Figure 9-Figure 10) as well (Schween *et al*. 2003). It is perhaps a widespread phenomenon.

In ***Funaria*** (Figure 7-Figure 8, Figure 39), this factor of inhibition seems to break down in mature cultures. When I placed disks of agar from a mature culture onto fresh plates and inoculated the plates with spores, some of

the protonemata grew on the disks from the mature cultures. In no case did I find a zone of inhibition around the agar disk. This suggests to me that the substance preventing live protonemata from intersecting might be a gas produced by the growing protonemata. Gases are instrumental in maintaining maximum distance among sporangia of some slime molds, and one gas that could accomplish this in mosses is ethylene. Since ethylene is known to affect ***Funaria*** protonemata (Rohwer & Bopp 1985) and it is a known inhibitor of cell division (Abeles 1973), small concentrations produced by the tips could easily signal their presence to neighbors. Ethylene production is stimulated by the action of IAA on S-adenosylmethionine (SAM), so we might expect the tip (where there is the most IAA) to have the highest ethylene concentration. The longest branches will interact first, and these are the ones most likely to be IAA-rich and apically dominant.

Hormones produced by other organisms in the environment can affect the development of protonemata, and in some cases these may be required to take the bryophyte to its next developmental stage. Among these, GA (gibberellic acid) is a likely candidate. It is produced by many fungi and readily enters the environment. It is known to increase the number and length of protonematal cells in some soil-inhabiting species, but may have no effect on rock-dwelling taxa that normally would have much less contact with soil fungi. Bark exudates may also inhibit growth of some bryophyte protonemata, and some bryophytes may inhibit each other, both of different species and of other clones of their own species.

Nutrients

In some mosses, the form of the protonema is dependent on available nutrients. For example, in nature ***Sphagnum*** (Figure 72-Figure 74) normally has a thalloid protonema (Figure 73-Figure 74). However, in a medium with high potassium, the protonema becomes filamentous (Schofield 1985). Since ***Sphagnum*** normally grows in habitats very low in potassium, this filamentous growth form is not observed in nature.

Figure 72. ***Sphagnum***, a genus with a thalloid protonema. Photo by Janice Glime.

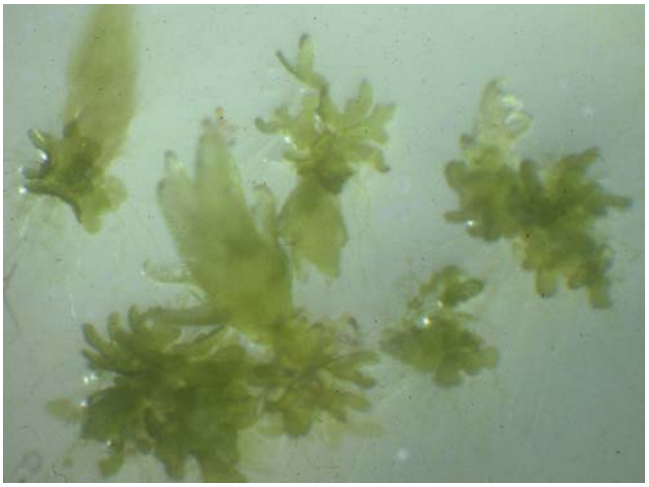

Figure 73. Thalloid protonemata of ***Sphagnum papillosum***. Photo courtesy of Yenhung Li.

Figure 74. ***Sphagnum*** protonemata on the stem of a mature ***Sphagnum*** plant. Photo by Andras Keszei, through Creative Commons on Flickr.

Sucrose may not be a problem in nature, but in culture added sucrose enhances growth, provided the culture does not become contaminated. Yu *et al*. 2008 pointed out that sucrose effects vary among species. The optimal sucrose concentration for the moss ***Microdus brasiliensis*** (Figure 18) was 1-2% (Sarla 1992), whereas both ***Splachnum ampullaceum*** (Figure 75-Figure 76) and ***Atrichum undulatum*** (Figure 35) grew better with no added sucrose (Sabovljević *et al.* 2005; González *et al*. 2006). One problem is that when the concentration of sucrose is too high it causes exosmosis, hence dehydrating the protonema (Fernández & Revilla 2003). Sabovljević *et al*. (2006) demonstrated that a 3% sucrose concentration inhibited the protonemal growth of the moss ***Atrichum undulatum***. Yu *et al*. (2008) tested sucrose:nitrogen effects on protonemata of ***Polytrichum commune*** (Figure 31) at sucrose levels of 0, 10, and 40 g L^{-1} and ammonium nitrate of 0, 0.2, and 0.4 g L^{-1}. The best growth of those protonemata were at ratios of sucrose to nitrogen of 10:0.2, 40:0.2, and 40:0.4.

Figure 75. ***Splachnum ampullaceum*** with capsules, a dung-dwelling species that grows better in culture with no added sucrose. Photo by Michael Lüth, with permission.

Figure 76. ***Splachnum ampullaceum*** peristome and spores that grow best on agar with no sucrose. Photo by Janice Glime.

Nitrogen in the medium can be detrimental to the protonemata at concentrations suitable for tracheophytes (see Chapt 8-1, pp. 1-4). Fangmeier *et al*. (1994) found that high concentrations of ammonium ions in plant cells can cause membrane dysfunction. It appears that established protonemata and plants can harbor sufficient nitrogen that they can be grown in the absence of nitrogen (Duckett *et al*. 2004). Nevertheless, Yu *et al*. (2008) found that when sucrose was added to the medium, growth was better in low concentrations of accompanying nitrogen as ammonium nitrate than with sucrose alone. In fact, the detrimental effects of high concentrations of sucrose can be counteracted by the addition of nitrogen (George 1993; González *et al*. 2006), and for ***Polytrichum commune*** (Figure 31) Yu *et al*. found that even at 4% sucrose there was a positive effect on protonemal growth when sucrose was combined with the appropriate level of ammonium nitrate.

Sundberg and Rydin (2000) showed that ***Sphagnum*** (Figure 73-Figure 74) establishment from spores was limited by the amount of phosphate released by underlying litter. Added moose dung likewise promoted establishment. They concluded that cover of other plants and nutrient release from litter provided safe sites where ***Sphagnum*** spores could germinate and establish new plants.

Calcium seems important to protonema development in some species and may be the actual factor where *p*H affects viability. For ***Funaria hygrometrica*** (Figure 7-Figure 8, Figure 39), Reiss and Herth (1979) suggest that a calcium gradient is responsible for protonemal tip growth. The calcium concentration is highest at the tip where fluorescence is strongest. It is likely that calcium is involved in transport of substances across cell membranes.

Nutrient availability is affected by *p*H. Thus *p*H could affect success of protonemata. In ***Physcomitrella patens*** (Figure 9-Figure 10, Figure 77, Figure 78), changes in pH in the range of 4.5 to 7.0 influenced differentiation of protonemata but did not have any negative impact on growth rate (Hohe *et al*. 2002). In another example, ***Anisothecium molliculum*** has an optimum *p*H of 5.5 for not only protonemal growth, but also for bud formation (Kumra & Chopra 1985). The *p*H may not only alter the ability of bryophyte protonemata to obtain nutrients, but also affect their susceptibility to exudates from other plants and fungi. Following fire, invasion by bryophytes onto the charred substrate seems to be likewise influenced by both *p*H and residual chemicals (Thomas *et al*. 1994). Germination success in the moss ***Campylopus pyriformis*** (Figure 79) is positively influenced by increases in the *p*H in the range of 3.5-6.4.

Figure 77. ***Physcomitrella patens*** in its natural habitat where *p*H and moisture can change considerably as spring flooding recedes. Photo by Michael Lüth, with permission.

Figure 78. ***Physcomitrella patens*** plants with protonemata on the wet soil. Photos by Michael Lüth, with permission.

Figure 79. ***Campylopus pyriformis***, a species whose protonemata grow better as *p*H is increased in the range of 3.5-6.4. Photo by Michael Lüth, with permission.

Various heavy metals seem to alter protonematal form. Kapur and Chopra (1989) found that in the moss ***Timmiella anomala*** (Figure 80), when grown aseptically (conditions free of microorganisms), aluminum causes protonemal cells to become rounded and packed with chloroplasts and starch grains; the filaments themselves form bunches. Zinc and arsenic likewise cause rounded cells, with zinc-damaged cells becoming reddish; most arsenic effects are seen at the terminal and intercalary positions. Mercury causes cells to become broad with dense particles, whereas nickel results in long, thin protonemata with little branching. At 10^{-6} M, nickel increases protonemal growth slightly, but at 10^{-5} M it drastically decreases the number of gametophore buds. Cobalt inhibits protonemal growth but seems to have no effect on bud formation. What do these effects mean to development of the moss, and are they likely to occur in nature where soil chelators (organic compounds that bind metal by forming ring structure around it) may inhibit uptake, or concentrations never reach these levels? Could they actually affect appearance of mature gametophytes resulting from these anomalous forms and hence confound our understanding of the taxonomy?

Landing in the wrong place can inhibit spore germination, but it can also permit germination but inhibit protonema development. In some cases, these unfavorable conditions might cause the protonema to produce dormant cells that can act like gemmae to grow when favorable conditions are forthcoming. Such seems to be the case for protonemata of ***Dicranella heteromalla*** (Figure 81-Figure 82) that spent the winter in a lake with acid mine waste (Jan Fott, pers. comm.).

Figure 80. ***Timmiella anomala***, a species in which heavy metals alter the protonemal form. Photo by Michael Lüth, with permission.

Figure 81. ***Dicranella heteromalla*** with capsules, on a typical soil bank habitat. Photo by Michael Becker, through Creative Commons.

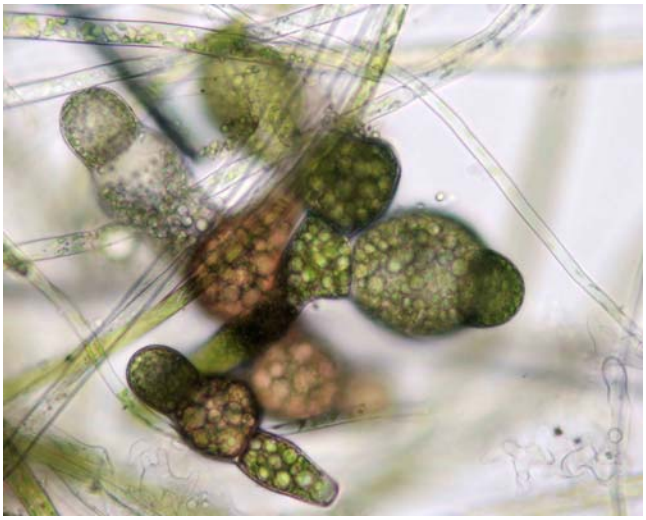

Figure 82. ***Dicranella heteromalla*** protonemata that survived winter in an acid mine lake. Photo courtesy of Jan Fott.

Our knowledge of nutrient requirements is based mostly on cultures of bryophytes and we know little of the generalities that might be important. For example, elevated potassium causes ***Sphagnum*** protonemata to become filamentous instead of thalloid, but in nature we have not observed protonemata in habitats where this condition exists. The level of phosphorus is often limiting and we can assume this plays a role in nature as well. An important observation is that heavy metals such as aluminum, zinc, mercury, and arsenic can cause abnormal protonemata with such symptoms as rounded cells with dense chloroplasts and starch. Elevated nickel, on the other hand, causes the protonemata to be thin. Calcium is undoubtedly important and its function may relate to membrane transport of other ions into the cell. All of these nutrient effects are likely to be affected by the pH because a lower (acidic) pH generally makes most nutrient ions more soluble.

Rhizoids

Botanists have traditionally considered rhizoids to function in anchorage only. In some cases they provide capillary spaces that aid in moving water externally to and even up the stem. But Duckett and Matcham (1995) discovered that the structure of rhizoids in ***Dicranella heteromalla*** (Figure 81-Figure 82) is cytologically similar to the food-conducting cells (**leptoids**) in many leafy mosses and moss sporophytes. This realization suggests that a major role of rhizoids may indeed be uptake, much like the root hairs of tracheophytes.

Rhizoids (Figure 83) form on the protonema at different stages, depending on the species and the growing conditions. On nutrient-free agar and in distilled water the first filaments to emerge from the spore are rhizoidal (Bhatla 1994). They are distinguished by their pigmented (usually brown) cell walls, oblique crosswalls, and discoid or cylindrical plastids. The rhizoids seem to depend on forced calcium entry (active uptake requiring energy) for growth and at least in those tested, respond positively to a calcium gradient (Bhatla 1994).

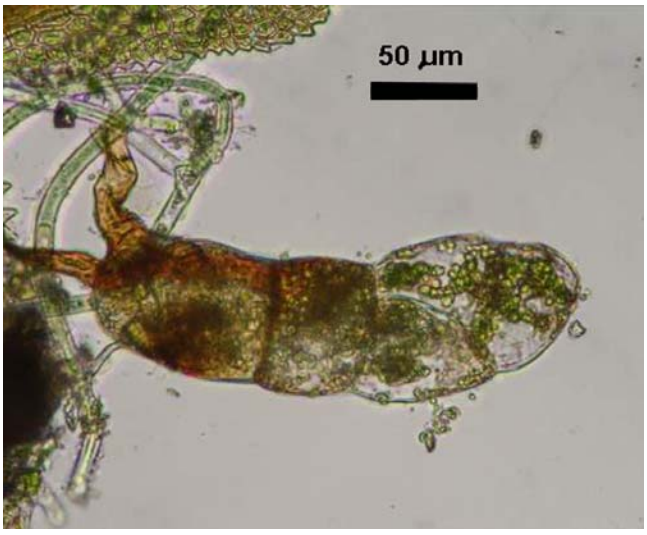

Figure 83. ***Fissidens tenellus*** bud with rhizoids at its base. Photo by Tom Thekathyil, with permission.

Rhizoids usually exhibit strong positive **gravitropism** (grow toward the center of gravity), negative **phototropism** (grow away from light), and **thigmotropism** (alter their growth upon contact), with the latter overriding the effects of the former once a substrate is contacted (Bhatla 1994). When growing in air, they often exhibit a spiral growth (**nutation**) until a substrate is contacted (Glime 1987). Upon contact, they may branch into short, fingerlike tips (Odu 1988), as noted in ***Lophocolea cuspidata*** (Figure 84) (Odu & Richards 1976) and ***Fontinalis squamosa*** (Figure 85) (Glime 1987). Among the liverworts, apical branching seems to be in part phylogenetically constrained, appearing commonly in the **Jungermanniales** (Figure 84) but only in the **Metzgeriineae** (Figure 86) of the **Metzgeriales** and not at all in the **Marchantiopsida** (Figure 87) (Pocock & Duckett 1985). Those liverworts with swollen rhizoids grow exclusively on peat and rotten wood associated with fungal hyphae. Pleurocarpous moss rhizoids become flattened near the tips, but in acrocarpous mosses these flattenings extend well behind the tips of the rhizoids (Odu 1988).

Figure 84. ***Lophocolea cuspidata***, a species in which rhizoids branch upon contact into finger-like tips. Photo from Botany Website, UBC, with permission.

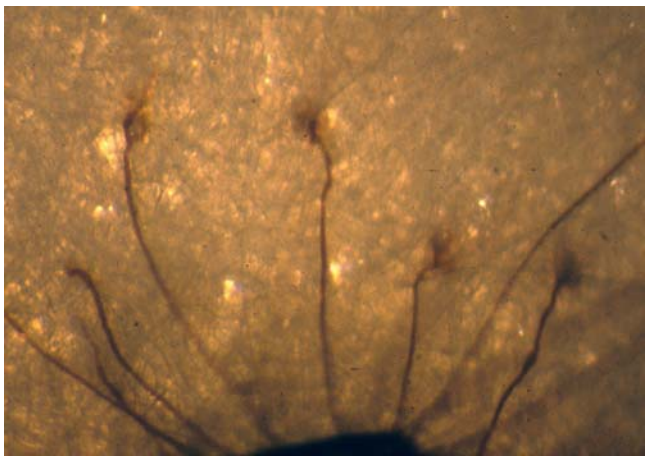

Figure 85. ***Fontinalis squamosa*** rhizoids forming fingerlike tips where they contact the filter paper. Photo by Janice Glime.

Figure 86. ***Metzgeria conjugata***, member of the **Metzgeriineae**, a genus that exhibits branched rhizoids. Photo by David Holyoak, with permission.

Figure 87. ***Cyathodium*** sp., representing the **Marchantiopsida** with the protonema lacking apical branching. Photo courtesy of Noris Salazar Allen.

Adhesion of rhizoids seems to be stimulated by the substrate itself (Odu 1988). Upon contact, rhizoids produce such extra-wall materials as sulfated mucopolysaccharides. These are highly viscous substances that serve as a sticky adhesive, also known in algae and other microorganisms.

But what controls the production of these rhizoids? Goode *et al*. (1992) were unable to get ***Tetraphis pellucida*** (Figure 6) to produce any protonemal rhizoids in culture, yet these occurred routinely in nature. They ascribed this difference to the limited nutrients and different irradiance in the wild. But hormones available from surrounding vegetation, bacteria, and fungi could play a role as well, as they apparently do for the protonemata.

Tmema

Tmema cells (Figure 88) are rounded cells that rupture, setting free a protonemal gemma (Figure 89) (Bopp *et al*. 1991). These cells result from a very unequal division of the cell near the proximal cross wall and divide the chloronema filaments into fragments of only a few cells. The tmema cells have few chloroplasts which soon become reduced in size, but the cell elongates in its proximal direction by expanding its newly formed wall, progressing in the opposite direction from normal cells. The new tmema wall forms inside the old lateral wall and the subsequent loosening of the old wall results in fragmentation of the protonema. This separation also occurs in older, untreated cultures of ***Funaria hygrometrica*** (Figure 7-Figure 8, Figure 39) (>25 days) (Bhatla & Dhingra-Babbar 1990).

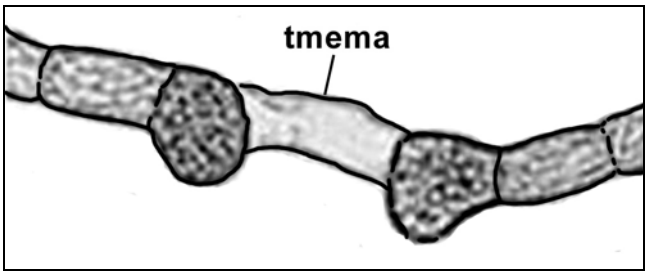

Figure 88. **Tmema** cell in protonema. Redrawn from Decker *et al*. 2006.

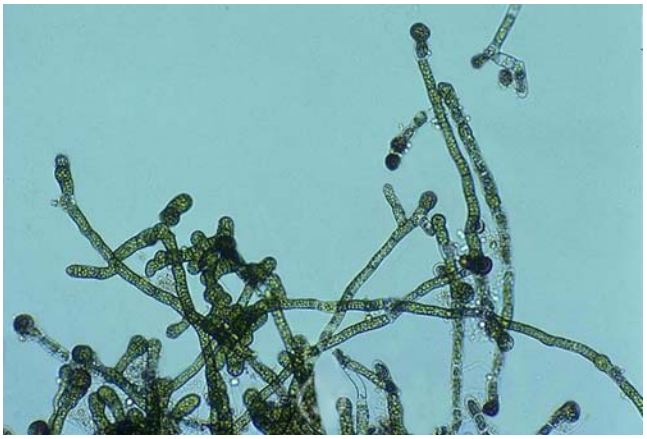

Figure 89. ***Bartramia ithyphylla*** with protonemal gemmae. Photo by Eugenia Ron Alvarez & Tomas Sobota – Plant Actions, with permission

In ***Funaria hygrometrica*** (Figure 7-Figure 8, Figure 39), the ageing protonemata form tmema cells. Formation of these is inhibited by 10 µM IAA, indicating that they form when the protonema is auxin deficient (Bopp *et al*. 1991). Once formed, the cell elongates in the proximal direction by forming a new tmema cell wall, thus reversing its polarity compared to normal cells, which elongate distally. This new wall replaces the old lateral wall and also covers the tip of the tmema cell. The new wall is, however, lacking at the cross wall toward the sister cell of its division. The new wall contains a higher cellulose content and an array of microtubules and microfibrils compared to other cells in the protonema. The old lateral wall loosens and ruptures and the tmema disintegrates as its wall swells and dissipates.

But these are laboratory results. Does the tmema occur in nature? Is it adaptive? Could it permit small fragments of the protonema to have one more chance at dispersal before producing its upright gametophore, hence possibly allowing it to arrive at a place where it could indeed produce enough of its own IAA in a more favorable setting? How remarkable a survival mechanism if indeed it permits another chance at dispersal.

Tmemata seem to have received little attention among bryologists and we seem to have little knowledge of their occurrence in nature. In their cultures of ***Dicranella***

heteromalla (Figure 81-Figure 82), Duckett and Matcham (1995) found that tmemata had formed. These shortened cells were common on chloronemal side branches that produced both terminal and within-filament gemmae. The tmemata serve as abscission cells that permit the detachment of the gemmae. This occurs through the swelling of a new internal wall in the tmema cell, as seen in ***Funaria hygrometrica*** (Figure 7-Figure 8, Figure 39). If this species is grown on nutrient-free agar, the protonemata fail to produce gemmae, but rather produce filaments of different diameters, down to 4-5 μm, that make a spiral path through the medium or form knot-like aggregations if grown on cellophane-covered agar.

Goode *et al*. (1993) observed similar tmemata in cultures of ***Bryum tenuisetum*** (Figure 90). Ligrone *et al*. (1996) described a similar development for tmemata and gemmae in protonemata of ***Aulacomnium palustre*** (Figure 91). Edwards (1978) described tmemata associated with protonemal gemmae in collections of ***Schistostega pennata*** (Figure 92-Figure 93) and noted that this type of gemma with an associated tmema was rare among moss species. Based on my hunt in Google Scholar, I would conclude that they are either rare, or rarely reported.

Figure 90. ***Bryum tenuisetum***, a species that produces tmemata in culture. Photo by Michael Lüth, with permission.

Figure 91. ***Aulacomnium palustre***, a species that forms gemmae and tmemata on its protonemata. Photo by Kristian Peters through Creative Commons.

Figure 92. Protonema of ***Schistostega pennata*** showing filamentous protonema and round refractive cells. Photo by Irene Bisang, with permission.

Figure 93. Protonemal gemma (oblong cell) with short **tmema** at its base on ***Schistostega pennata***. Photo by Misha Ignatov, with permission.

In the copper moss ***Scopelophila cataractae*** (Figure 94-Figure 95), copper concentrations, but not other metals tested, affect the production of protonemal gemmae and associated tmemata (Nomura & Hasezawa 2011). Making the assumption that this moss is able to invade copper-rich substrata because of gemmae, the researchers tested the sensitivity of the protonema. Although the gemmae were suppressed, the copper promoted the growth of the protonema.

Figure 94. ***Scopelophila cataractae*** habitat in India. Photo by Michael Lüth, with permission.

Figure 95. ***Scopelophila cataractae***, a "copper moss" in which copper suppresses production of protonemal gemmae but enhances protonemal growth. Photo by Michael Lüth, with permission.

Tmemata are one means of providing vegetative reproductive structures on the protonema. Various types of protonematal asexual reproductive structures will be discussed in Chapter 5-7 on asexual reproduction. A brief discussion of those associated with protonemata is provided here.

Protonemal Gemmae and Tubers

Production of gemmae on the protonema seems to be affected by a variety of substances and conditions. Chopra and Dhingra-Babbar (1984) found that a variety of substances affect gemma initiation and growth rates of the protonema in ***Trematodon brevicalyx***. These included IAA, GA, ABA, chelates, salicylic acid. In addition, responses were altered by temperature, *p*H, agar, sucrose levels, light levels, and photoperiod.

In ***Hyophila involuta*** (Figure 40), in addition to promoting growth, the protonemal diffusate (from gemma-producing protonemata) + kinetin acted synergistically to enhance gemma formation. ABA (10-5-10-7 M) + protonemal diffusate inhibited gemma production (Mehta 1990).

Sarla and Chopra (1989) found that in ***Bryum capillare*** (Figure 96), kinetin slowed protonemal growth. **Bryokinin** (a type of cytokinin growth hormone found in mosses) inhibited protonemal growth at all levels. Rather, gemmae were produced in response to kinetin and bryokinin.

Figure 96. ***Bryum capillare***, a species in which kinetin and bryokinin slow protonemal growth and induce gemmae. Photo by Andrew Spink, with permission.

More recently, Ahmed and Lee (2010) explored the induction of protonemal gemmae in ***Palustriella decipiens*** (Figure 97). They found that concentration of IAA and kinetin was important in stimulating production of protonemal gemmae. Low concentrations promoted gemmae and bud induction.

Figure 97. ***Palustriella decipiens***, a species in which concentration of IAA and kinetin is important in stimulating protonemal gemmae. Photo by Michael Lüth, with permission.

Liverworts

Little seems to be written about the protonemata of liverworts to explain the details of their development in any ways that may differ from that of mosses. Liverwort protonemata differ fundamentally from those of mosses in that the liverwort protonema is thalloid (Figure 98-Figure 100). As mentioned above, the rhizoids of the liverworts in **Marchantiopsida** do not branch apically, but those of the **Jungermanniales** do (Pocock & Duckett 1985).

Figure 98. ***Sphaerocarpus texanus*** thalloid protonema with rhizoids. Photo from Plant Actions through Eugenia Ron and Tom Sobota, with permission.

Figure 99. Early stage of the liverwort ***Fossombronia caespitiformis*** protonema. Photo from Plant Actions through Eugenia Ron and Tom Sobota, with permission.

Figure 100. ***Fossombronia caespitiformis*** protonema showing rhizoids on a liverwort in the **Metzgeriidae**. Photo from Plant Actions through Eugenia Ron and Tom Sobota, with permission.

Figure 101. Protonemata of ***Schistostega pennata*** holding particles of soil together by building bridges between them. Photo by Misha Ignatov, with permission.

Figure 102. ***Buxbaumia aphylla*** showing persistent protonemata. Photo by Janice Glime.

Ecological Considerations

We have discussed the ability of the protonema to branch, then form many gametophore buds. This permits it to produce many upright gametophores in close enough proximity to create capillary spaces and reduce air movement, thus reducing drying. Furthermore, this mat of protonemata can provide bridges across the tiny soil particles (Ignatov *et al*. 2012), binding the soil and creating more capillary spaces for water retention. In ***Schistostega pennata*** (Figure 92-Figure 93, Figure 101), the sticky surface of the propaguliferous protonema extends across the soil particles, stabilizing the surface in a way that helps to create its own habitat (Ignatov *et al*. 2012).

Because of this binding ability, and the ability to withstand drought and revive upon rewetting, protonemata of a number of species can contribute significantly to soil binding in disturbed areas. To this end, mosses like ***Atrichum*** spp. (Figure 27-Figure 28, Figure 35) can stabilize soil on broad paths and soil banks. Mosses with persistent protonemata, like ***Pogonatum*** spp. (Figure 29-Figure 30, Figure 56) and ***Buxbaumia aphylla*** (Figure 102) are able to stabilize the otherwise bare soil where they live, often on soil banks. Hence, protonemata can play an important role in stabilized disturbed soil in ecosystems.

Summary

The **filamentous protonema** of Bryophyta can differentiate into two types: **chloronema** and **caulonema**, distinguished by short cells with perpendicular crosswalls, numerous chloroplasts, colorless cell walls, and irregular branching in the former and longer cells, diagonal crosswalls, brownish cell walls, and fewer, scattered, small chloroplasts in the latter. IAA induces the switch to caulonema; cytokinins promote branching. Protonemata of **Sphagnopsida**, **Anthocerotophyta**, and most **Marchantiophyta** are thalloid.

Protonemata can produce a variety of **brood cells**, possibly stimulated by **ABA**, and sometimes disarticulated from the protonema by **tmema** cells. Light quantity, quality, photoperiod, and temperature influence both the rate of development and the form of the protonema. Their direction of growth is influenced by both gravity and light, causing **negative gravitropism** in the dark and **positive phototropism** in the light.

Other organisms, especially bacteria and fungi, may supply **IAA**, **cytokinins**, and **GA** that influence

development, and **Factor H** (a likely **cytokinin**) may be supplied both endogenously and exogenously to control population size. Nutrients can affect the development; the ratio of sucrose:nitrogen determines if they are beneficial or detrimental, and heavy metals generally cause abnormalities or arrested development.

Rhizoids exhibit **positive gravitropism** and **negative phototropism**, but also possess **thigmotropism**, typically expanding, branching, or flattening upon contact with a substrate.

Liverworts have thalloid protonemata and in many the rhizoids do not branch at the tips.

Protonemata are important ecologically as early stabilizers of the soil in disturbed areas. By branching and producing many buds, they quickly create cushions and mats that can support each other in maintaining moisture.

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CHAPTER 5-4

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CHAPTER 5-5

ECOPHYSIOLOGY OF DEVELOPMENT: GAMETOPHORES

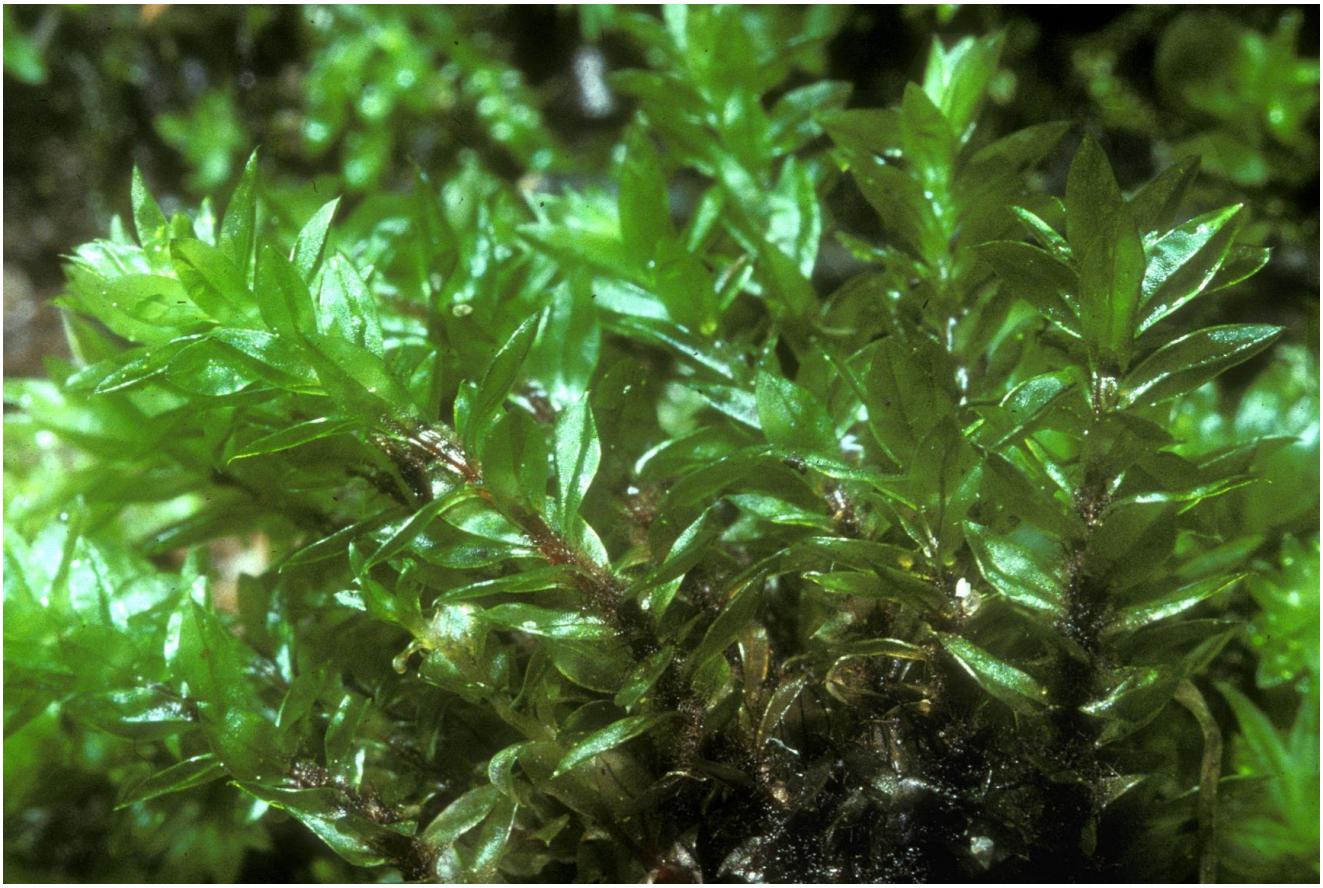

Figure 1. ***Bryum pseudotriquetrum*** gametophores, showing leaves, stems, and rhizoids. Photo by Janice Glime.

Growth

Bryophytes appear to be simple plants, but if one changes perspective, you might agree with Renzaglia *et al*. (2000) that these gametophytes "are the most elaborate of those produced by any land plant." In mosses, it is the apex of branches or stem tips that ultimately develop into reproductive organs. This contrasts with flowering plants that develop their gametophyte without archegonia and antheridia, reducing the male gametophyte to a pollen grain and the female gametophyte to a partitioned embryo sac within the female sporangium (sporophyte tissue).

In mosses and leafy liverworts, gametophore development can be considered a four-part process: stem growth, branch production, leaf development, and rhizoid formation (Figure 1). Since these four processes must compete for energy, it is expected that they are, at least in most cases, distinct events with different environmental stimuli or optima.

Stem Growth

Stem growth in plants occurs primarily as a result of cell elongation, which is sometimes accompanied by cell division (Bidwell 1979). Cell elongation occurs by a loosening of the side walls of the cell to allow expansion. Auxin helps to loosen the wall but exogenous calcium and ethylene inhibit loosening (Ray *et al*. 1983) (probably because Ca forms Ca pectate, which glues cell walls together). Loosening is followed by an uptake of water by the cell, which is an osmotic response to increase of Ca within the cell. The increased turgor then expands the cell. The turgor can be affected by mineral nutrients, photosynthesis, respiration, transpiration, ethylene, water availability, temperature, etc. If **any** of these factors becomes limiting, it can inhibit stem elongation.

When measuring growth, one consideration must be what to measure. When a layperson thinks of growth, it is usually equated with increase in height, but in biological

terms it can include branching and weight gain as well. Measuring extension in height gets complicated by the fact that if light intensity is insufficient, cells will extend with little or no weight gain, and often at a greater than normal rate – the **etiolation** effect (Figure 2). This is especially a problem in laboratory experiments where light intensity is usually considerably below that in nature, even compared to some forested settings. Plants, including bryophytes, become thin, weak, and lose their green color. In this case, false implications of growth occur. This can easily be seen when bryophytes are collected and kept in a sealed plastic bag. Sufficient moisture remains to permit cell extension, and within days (or even hours), one can see thin extensions of the stem with tiny, pale leaves.

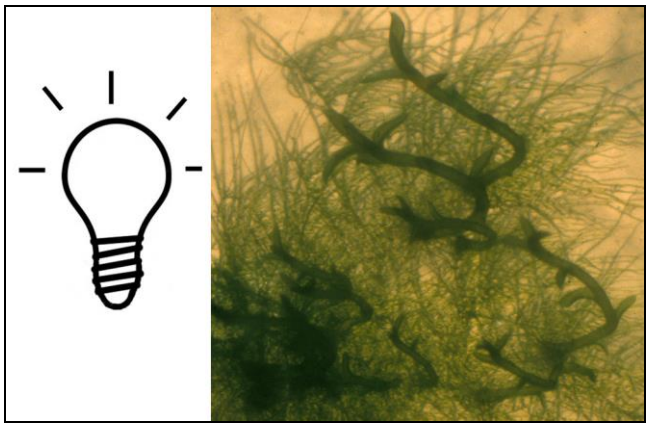

Figure 2. Culture of ***Funaria hygrometrica*** with Petri plate covered on top and the only light source from the side of the plate. Note the etiolated appearance of the shoots in this dim light compared to those in Figure 3. Photo by Janice Glime.

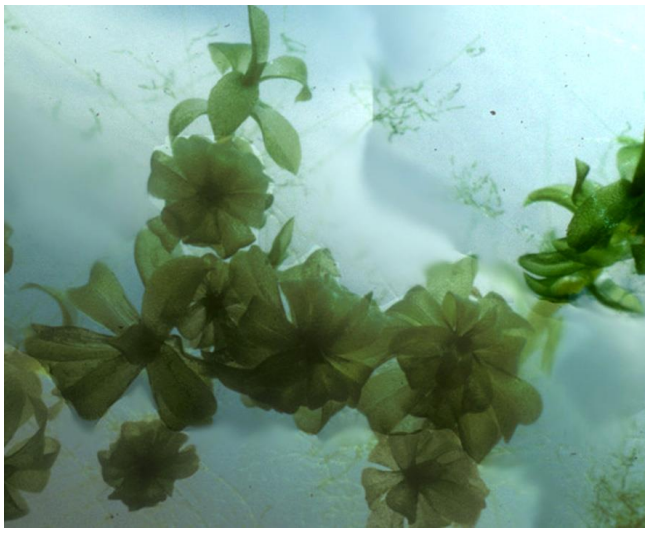

Figure 3. Culture of ***Funaria hygrometrica*** with light from above the plants. Photo by Janice Glime.

Therefore, especially in measuring laboratory growth, one needs to consider weight gain, either alone or in addition to height gain. Furthermore, if the species is pleurocarpous, in particular, and more than a few weeks elapse, length gain of branches and number of branches becomes important. This becomes a non-linear relationship as each branch then starts to grow at a rate similar to that of the main stem.

When growth is promoted, energy is diverted from other events. This diversion can manifest itself as a result of a change in environmental conditions. For example, when grown in red light, ***Ceratodon purpureus*** (Figure 4) exhibited only 20% branching with a weight gain of 16.8 mg per 50 individuals, but when the plants were grown under far-red illumination, there was 100% branching, but only 11.75 mg weight gain per 50 plants (Hoddinott & Bain 1979). This would appear to be counter-intuitive until one recognizes that while the branches were growing, the plants in far-red light were also producing setae, thus diverting energy for another process. Similarly, growth reduction (in length) occurs during archegonia production in ***Fontinalis dalecarlica*** (Figure 5) (Glime 1984). Energy is clearly needed for processes other than branch growth.

Figure 4. ***Ceratodon purpureus*** showing the paucity of branching. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

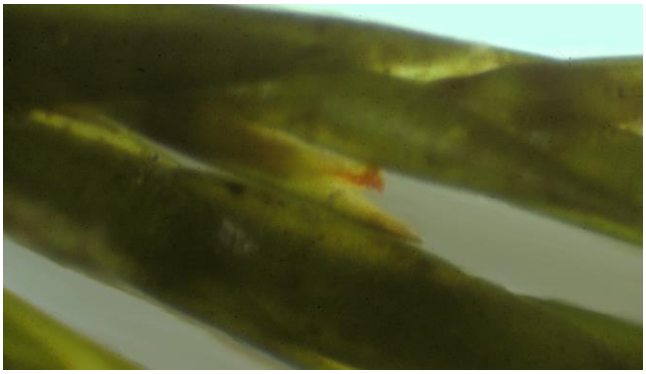

Figure 5. ***Fontinalis dalecarlica*** with archegonium, a phenomenon that coincides with a slowing of vegetative growth. Photo by Janice Glime.

Water

It is certainly nothing new to learn that water is necessary for development of the stem. However, the effect that water availability has on the stem diameter is less well known. In studying ***Sphagnum magellanicum*** (Figure 6) and ***S. papillosum*** (Figure 7), Li *et al*. (1992) found that stem diameter increased in stems with capitula that were farther from the water, and hence drier (Figure 8). This increase in stem diameter resulted from having a greater number of rows of the hyaline cells at the outer part of the stem (Figure 9). This increase in diameter appears to be a tradeoff because at the same time growth rate in stem length decreased.

Figure 6. ***Sphagnum magellanicum***, a species in which stem diameter increases with distance of capitulum from water surface. Photo by Michael Lüth, with permission.

Figure 7. ***Sphagnum papillosum***, a species in which stem diameter increases with distance of the capitulum from the water surface. Photo by David T. Holyoak, with permission.

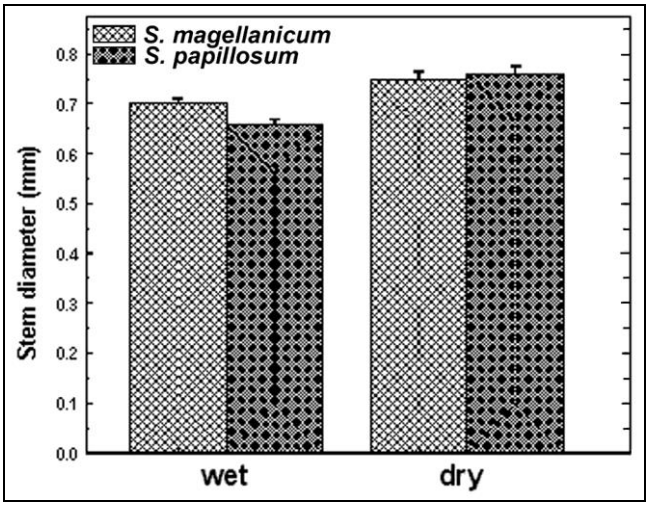

Figure 8. Effect of water level on stem diameter due to number of hyaline cell layers. **Wet** indicates stem tip starting at level 3 (7 cm) above the water; **dry** indicates stem tip starting at level 5 (15 cm) above the water. Based on Li *et al*. 1992.

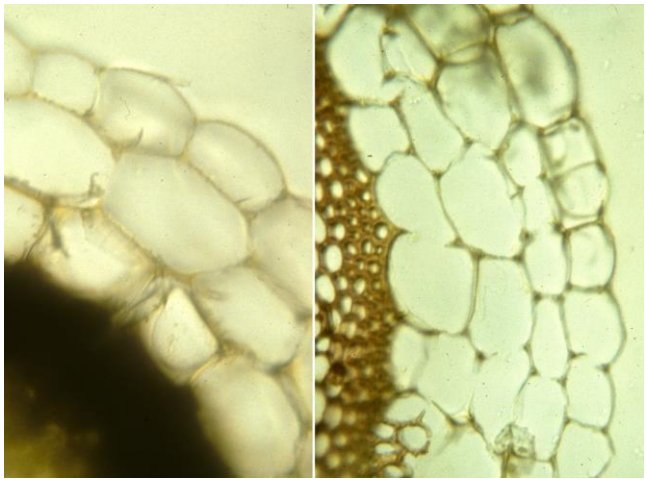

Figure 9. Effect of water level on stem width due to number of hyaline cell layers for ***Sphagnum magellanicum***. **Left:** Stem at level 3 above the water (wet), showing only three rows of hyaline cells. **Right:** Stem at level 5 above the water (dry), showing four rows of hyaline cells. Based on Li *et al*. 1992. Photos courtesy of Yenhung Li.

Light

Too high and too low **light intensity** can control bryophyte growth. At high light intensities, it can be inhibitory, destroying chlorophyll in unprotected leaves, but at suboptimal light intensities, it can cause etiolation, resulting in long, slender stems. For example, the aquatic moss ***Drepanocladus*** (Figure 10) has longer internodes in low light (Lodge 1959), making leaves appear to be sparse.

Figure 10. ***Drepanocladus longifolius***, a species with longer internodes in low light, hence in deep water. Photo by John Game, through Flickr Creative Commons.

Since mosses are shade adapted, optimal light intensity for many is likely to be rather low. ***Riccia frostii*** (Figure 11) females have optimal growth at 3500 lux in continuous light (Vashistha & Chopra 1989), whereas full sunlight is about 70,000 lux. Red light favors their growth (Dagar & Kumra 1988). For ***Marchantia palmata***, optimum intensity for vegetative growth is 4500 lux (Kumra & Chopra 1989), the same intensity needed for maximum number of gametophores in ***Microdus brasiliensis*** (Chopra & Mehta 1987). For ***Fontinalis duriaei*** (Figure 12) photosynthesis attenuated at 5400 lux (Glime & Acton 1979); field intensities where ***Fontinalis duriaei*** grew

ranged up to 6000 lux in spring when leaves were not out yet, diminishing to 4000 lux in summer and 500-1000 lux during much of winter (Glime 1987a).

Figure 11. ***Riccia frostii***, a species in which females have optimal growth in very low light (3500 lux). Photo by Rosemary Taylor, with permission.

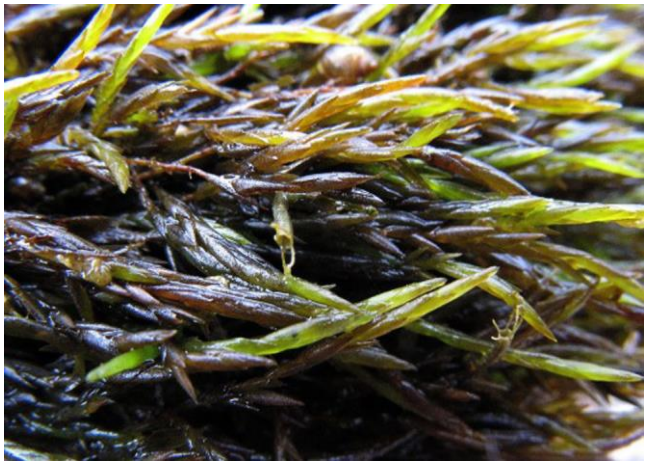

Figure 12. ***Fontinalis duriaei***, an aquatic species where photosynthesis attenuates at low light levels (5400 lux). Photo by Jan-Peter Frahm, with permission.

Stem height can be controlled by light, but some bryophytes respond to different wavelengths from those that affect tracheophytes. In some higher plant species, a five-minute exposure to far-red light at the end of an 8-hour day (with white light) is enough to cause a 400% increase in internode expansion (Morgan & Smith 1981). A flash of red light can stop growth. Stem elongation in etiolated plants can also be stopped by exposing the plant to red light, whereas far-red reverses this effect (Ray *et al*. 1983), suggesting that phytochrome is somehow involved. Incandescent bulbs also cause more stem elongation than fluorescent bulbs because of the higher far-red content of the former (Morgan & Smith 1981, p. 120). On the other hand, moss protonemata bend toward red light. And ***Ceratodon purpureus*** (Figure 4), ***Dicranum polysetum*** (Figure 13), ***Leptobryum pyriforme*** (Figure 14), and ***Polytrichum juniperinum*** (Figure 15) all grew significantly taller in red light than in far-red (Hoddinott & Bain 1979). That may be why these taxa all grow in relatively open areas where full sun is available at least part of the day, providing them with at least some red light.

Figure 13. ***Dicranum polysetum***, a moss that grows taller in red light than in far-red light. Photo by Michael Lüth, with permission.

A comparison of sun and shade forms of these moss species would be interesting. Should we expect moss taxa living under the forest canopy to be more sensitive to far-red light? Or are they necessarily adapted to growing poorly in far-red light in order to prevent growing too tall for their meager support system? Could it be that the chlorophyllous palisade layer of tracheophyte leaves necessitate the response to far-red light in the underlying spongy mesophyll (due to filtering out red light), whereas bryophytes have no such chlorophyllous layer to intervene in the light reaching their primary photosynthetic cells?

Figure 14. ***Leptobryum pyriforme***, a moss that grows taller in red light than in far-red light. Photo by Michael Lüth, with permission.

Branching seems to be under a different set of wave length controls from that of photosynthesis and growth, at least in some bryophytes. The thallose liverwort ***Riccia discolor*** has its maximum apical branching in blue light (Dagar *et al*. 1980). But this type of dichotomous branching is developmentally different from that of mosses and may not be physiologically comparable to the type of side branches produced by mosses.

Figure 15. ***Polytrichum juniperinum***, a moss that grows taller in red light than in far-red light. Photo by Janice Glime.

The chlorophyll *a*/*b* ratios of bryophytes are typical of shade-adapted species (Martin 1980). One must ask how the greater proportion of green light on the forest floor affects development and photosynthesis, and might such shade-adapted plants as most bryophytes be likewise adapted to the wavelengths of light that predominate in the forest. The work of Dagar and coworkers (1980, Dagar & Kumra 1988) on ***Riccia discolor*** may suggest an answer. They found that total chlorophyll content of ***Riccia discolor*** is highest in green light, again attesting to bryophytic adaptation to the low light of shade conditions. But in this species, green light retards growth (Dagar & Kumra 1988), and branches are favored by blue light over yellow or red (Dagar *et al*. 1980). Further discussion on effects of light is in the chapter on light.

Bierfreund *et al*. (2003) found that red light retarded growth of the protonemata in ***Physcomitrella patens*** (Figure 26). On the other hand the leafy gametophytes became elongated, but had shorter and narrower leaves. These effects were more pronounced in far red light.

Bryophytes seem to respond differently to the spectrum than do tracheophytes. Whereas tracheophytes grow best in far-red light, bryophytes seem to respond best to red light. Blue light can cause branching. They experience destruction of chlorophyll at high light intensities and etiolation at low light intensities. Light quality can change the morphology, with red and far red light causing stem elongation and leaf retardation.

Tropisms

It seems that most of the research on tropisms has been done on the protonema. **Phototropism** and **gravitropism** are most likely common for bryophyte stems, but aside from field observations, we know almost nothing about them in mature plants. However, it is clear that stems grow up and rhizoids grow down, just as do stems and roots of tracheophytes. One would expect tropisms in acrocarpous mosses, and surely something is causing their normal upright growth. Yet there seem to be a number of acrocarpous mosses that grow on vertical substrata and do not respond to gravity, and perhaps not to light. Genera such as ***Orthotrichum*** (Figure 16) typically grow outward from their tree trunk habitat and even the sporophyte seems oblivious to gravity. And at least some species of ***Pogonatum*** (Figure 17-Figure 18) and ***Oligotrichum*** (Figure 19) seem to lack a strong gravitropism or phototropism in their gametophytes when growing on a vertical substrate, whereas their sporophytes do bend upward. On the other hand, the stem of the pleurocarpous aquatic moss ***Fontinalis*** exhibits positive phototropism (bends toward light; Figure 20). A strong phototropism is seen for the acrocarpous ***Funaria hygrometrica*** in Figure 3.

Figure 16. ***Orthotrichum sordidum*** growing straight out from its vertical tree trunk substrate. Photo by Janice Glime.

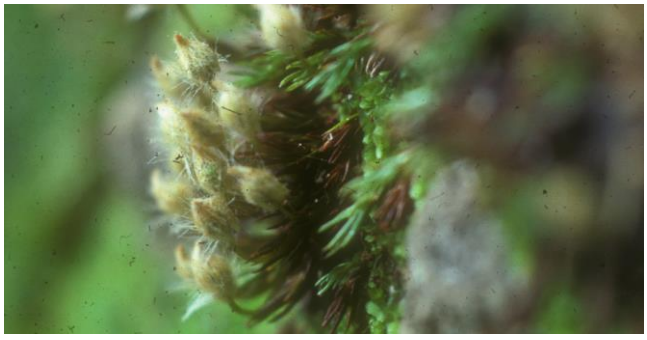

Figure 17. ***Pogonatum sphaerothecium*** showing upward curvature of setae, exhibiting tropisms, while the gametophyte lacks any upward direction. Photo by Janice Glime.

Figure 18. ***Pogonatum tortile*** exhibiting no tropism on stem or seta, but having one at or near seta-capsule junction. Photo by Janice Glime.

Figure 19. ***Oligotrichum hercynicum*** exhibiting a strong geotropism/phototropism in the sporophyte but lacking it in the gametophyte. Photo by Michael Lüth, with permission.

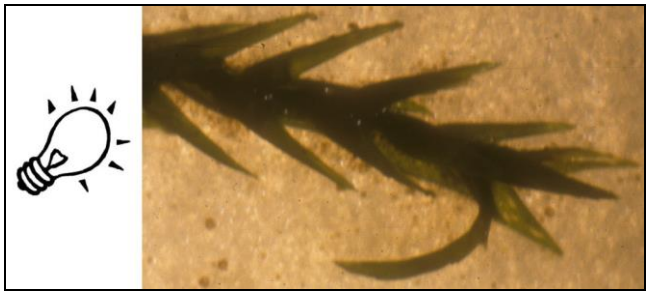

Figure 20. Positive phototropism exhibited by the tip of the moss ***Fontinalis squamosa***. Photo by Janice Glime.

Photoperiod

Not only do light intensity and quality affect bryophytes, but also light duration. Generally, long days result in longer stems along with increased elongation rates in higher plants, but too much light can inhibit elongation. In bryophytes, on the other hand, long days and elevated temperatures often induce dormancy, presumably acting as protection against desiccation during summer (Schwabe 1976). The response in higher plants suggests that increased day length allows more photosynthesis to occur, which in turn increases growth potential. Melstrom *et al*. (1974) suggest that in long days more auxin oxidase inhibitors are produced, allowing auxin levels to increase. Gibberellins also increase in long days. This combination allows growth to continue until hormone levels become too high or building materials are exhausted. Perhaps an inhibitory level may be reached more easily in bryophytes, resulting in earlier dormancy.

On the other hand, in two species of ***Sphagnum*** [***S. magellanicum*** (Figure 6) & ***S. papillosum*** (Figure 7)], there is a high correlation of growth with photoperiod greater than 10 hours; short days induce dormancy (Li & Glime 1991). This perhaps relates to the high light intensity to which these mosses are adapted, and to their higher temperature optimum of 30-35ºC for growth (Li & Glime 1990), compared to an optimum at 25ºC or less in most bryophytes.

But ***Sphagnum*** (Figure 6-Figure 7) is not alone in showing short-day dormancy, and control appears to be unrelated to temperature. In the liverwort ***Reboulia hemisphaerica*** (Figure 21), long days caused archegoniophore elongation at either 15ºC or 25ºC, whereas short days induced no response at any temperature (Koevenig 1973b). Even application of IAA, NAA, VA, and GA_3 could not break the effect of short days. This leaves us to wonder what ultimately controls the response, and is the controlling factor the same in all bryophytes?

Figure 21. Thallus and archegoniophores of ***Reboulia hemisphaerica***. Photo by Michael Lüth, with permission.

In liverworts, it is likely that **lunularic acid**, in response to **phytochrome** activity, plays a role in response to photoperiod (Schwabe 1990). Its ability to induce dormancy would permit it likewise to control growth. Does that mean that ABA controls growth and dormancy in mosses?

Most photoperiod responses in bryophytes have been related to dormancy. While it appears that most bryophytes benefit from cool temperatures of spring and autumn, and are dormant during long, hot days, some taxa such as ***Sphagnum*** are long-day plants and are dormant during short days. Photoperiod plays a role in gametogenesis, with some archegoniophores, like those of ***Reboulia hemisphaerica***, elongating only under long-day conditions.

Temperature

One would expect temperature to play a major role in development of bryophytes, as it does in early spring growth of other plants and a number of **poikilothermic** animals (those, like plants, with their temperatures controlled by the environment). In the aquatic moss ***Leptodictyum riparium*** (Figure 22), elongation increased with temperature until about 23ºC, after which growth declined again (Sanford 1979). This is consistent with the relatively low temperature optimum of most ***Fontinalis*** species, where sustained temperatures above 20ºC are detrimental to growth, and optimal long-term growth is at 10-15ºC (Glime 1987a, b). For the terrestrial ***Microdus brasiliensis***, the optimum is 18ºC (Chopra & Mehta 1987).

Figure 22. ***Leptodictyum riparium***, a species where growth increases with temperature up to about 23°C. Photo by Michael Lüth, with permission.

Schwabe (1976) found that long days and elevated temperatures often induce dormancy in liverworts, putting an end to spring growth. On the other hand, Stevenson *et al*. (1972) found a higher rate of cell division in the moss ***Atrichum undulatum*** (Figure 23) at higher temperatures.

Figure 23. ***Atrichum undulatum***, a moss that has a higher rate of cell division at higher temperatures. Photo by Brian Eversham, with permission.

Growth in ***Tetraphis pellucida*** (Figure 24) seems to be controlled by temperature rather than light (Forman 1964), but in the liverwort ***Reboulia hemisphaerica*** (Figure 25), temperature affected only elongation rate, not length or elongation of the archegoniophore, which was controlled by photoperiod regardless of temperature (Koevenig 1973b). Clearly the growth strategies differ among the bryophytes, but we have little phenological data to demonstrate the periods of growth for most species. We do know that in many spring plants, temperature and photoperiod work together to stimulate growth and elongation. Temperature effects will be discussed more thoroughly in the chapter on temperature.

Growth Regulators

Hormones in plants seem to defy definition (Christianson 1999). In plants, using the terminology of "growth regulators" permits us to define them as substances produced in one place in the organism that acts in small quantities to affect another part. But Christianson contends that this definition does not work well for the "untidy bundle of phenomena in plants." Rather, plant hormones can act locally or be transported and often have numerous roles, interact with other hormones, or are concentration dependent for their functions.

Figure 24. ***Tetraphis pellucida*** with gemmae, a moss in which growth is controlled by temperature rather than light. Photo by Michael Lüth, with permission.

Figure 25. ***Reboulia hemisphaerica*** with archegoniophores, a liverwort that elongates its thallus in response to temperature, but not its archegoniophore. Photo by Michael Lüth, with permission.

Growth and developmental processes are primarily controlled by hormones, particularly the auxin IAA (Sztein *et al*. 1999). In this regard, liverworts differ from mosses and tracheophytes in the way that they regulate their hormone concentrations and activities. Liverworts (and charophytes) regulate free IAA levels by a biosynthesis-degradation strategy, whereas mosses, hornworts, and tracheophytes use conjugation-hydrolysis (Sztein *et al.* 1995, 1999). These lead to differences in total amount of IAA metabolites, proportion of free and conjugated IAA, chemical nature of IAA conjugates, and rates of IAA conjugation. Sztein *et al*. (1999) consider this difference in control mechanisms to have "profound implications for macroevolutionary processes in these plant groups."

Bryophyte hormones operate very much as they do in tracheophytes (Maravolo 1980). In bryophytes, **auxins** are transported directionally, permitting **apical dominance** to occur, and their activity is concentration dependent. The

highest concentrations of auxin occur at the tip and base of the upright gametophore, with distribution throughout the stem, as demonstrated in ***Physcomitrella patens*** (Figure 26) (Bierfreund *et al*. 2003). This species also requires profilin for tip growth (Vidali *et al*. 2007). Profilin is an actin-binding protein and has important regulatory functions, particularly related to the actin cytoskeleton (Wikipedia 2012). Thus it is important in development of organs, wound healing, and identification of "infectious intruders" by the immune system.

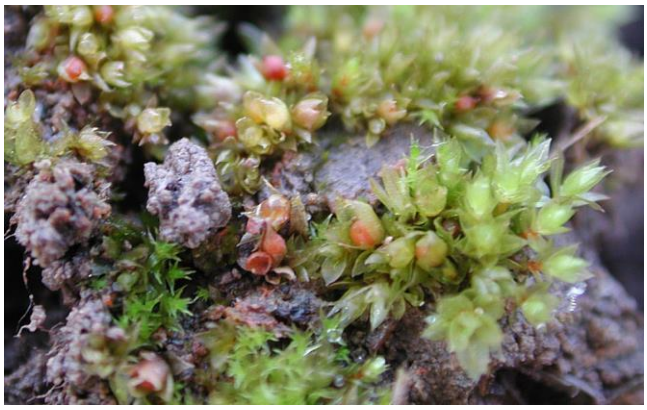

Figure 26. ***Physcomitrella patens*** with capsules, a moss that has demonstrated the concentration of auxin at the tip and base of the upright gametophore, with distribution throughout the stem. Photo by Michael Lüth, with permission.

Chopra and Vashistha (1990) examined the effects of auxins during various stages of the life cycle of ***Bryum atrovirens*** (Figure 27). They found that at lower concentrations of IAA and other auxins the leafy plants developed normally, but at higher levels their forms were not normal.

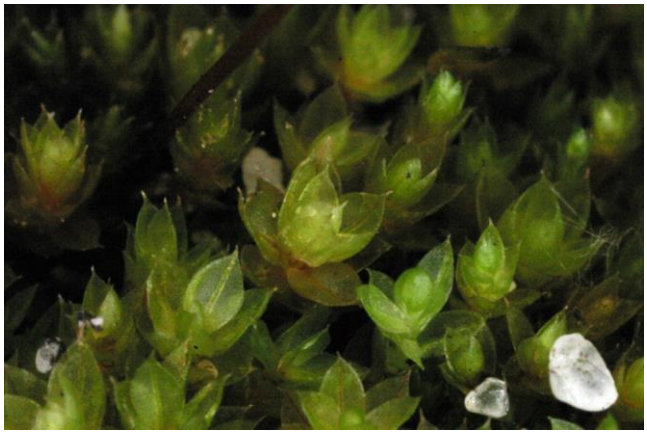

Figure 27. ***Bryum atrovirens***, a species that exhibits abnormal development at higher concentrations of auxins. Photo by Jan-Peter Frahm, with permission.

Gibberellic acid promotes cell enlargement, development of chloroplasts, and degradation of starch, and causes ultrastructural changes in starch granules and **thylakoids** (flattened, membranous vesicle containing chlorophyll; location of photosynthesis), just as in tracheophytes. It influences gravitropic curvature, depending on photoperiod.

While working with *Avena* (wheat) and two liverworts, Kaufman *et al*. (1982) found several basic generalities in hormone-induced cell elongation of plants. During phase one, in which the cellulose fiber matrix of the cell is stretched, rapid growth is due to hormone-induced secretion of H^+, which aids in loosening the cell wall for growth. They discovered that stimulated plants acidified their immediate environment. This rapid response suggests the involvement of H^+ transport (**proton pump**), much like the closing of the Venus flytrap leaf. Ellis and Thomas (1985) demonstrated the same sort of **auxin-stimulated acid efflux** in ***Pellia*** (Figure 28) to create a pH of 4.8 in the medium, in this case as a result of stimulation by light on one side of the seta.

Phase two consists of long-term growth that occurs as new proteins are synthesized. This response occurs much later than phase one, which is basically instantaneous. Hormones and other plant growth regulators can affect both of these steps in a variety of ways.

Bryophytes seem to respond to different concentrations and respond at different rates from those exhibited by tracheophytes. While working with *Avena* (wheat), Kaufman and coworkers (1982) discovered that a tenfold increase in the growth rate of *Avena* internodes appeared about three hours after application of 10^{-5} M **GA_3**, but that 10^{-5} M **IAA** had no effect. On the other hand, when working with the liverworts ***Pellia epiphylla*** (Figure 28) and ***Conocephalum conicum*** (Figure 29), they found that the setae and archegoniophore stalks responded to 10^{-5} M IAA with a two-fold increase in growth rate within 10-15 minutes. Many higher plants also show this rapid response to IAA, but this depends again on the concentration (Osborne 1974; Muir 1974). The rapid response in the liverworts suggested to Kaufman and coworkers (1982) that IAA had a direct effect on the cell membrane, allowing expansion by drawing water into the cell, since growth of the cytoplasm would require slow protein synthesis. We now know that IAA probably works on the cell wall (Goodwin & Mercer 1983), most likely by facilitating the breakdown of **calcium pectate** so the fibers can slide and expand, and this most likely involves an acid efflux via the proton pump from the cells, hence the H^+ observed by Kaufman *et al*. (1982). The freed **Ca^{++}** is then available to enter the cell, most likely accounting for the observed increase in Ca^{++} there.

Figure 28. ***Pellia epiphylla***, a species that responds within 10-15 minutes of an application of 10^{-5} M IAA by rapidly increasing archegoniophore growth. Photo by David Holyoak, with permission.

Figure 29. ***Conocephalum conicum***, a species that responds within 10-15 minutes of an application of 10^{-5} M IAA by rapidly increasing archegoniophore growth. Photo by Jan-Peter Frahm, with permission.

Movement of auxin within the plant is directed and may follow the vascular tissue. In ***Marchantia polymorpha*** (Figure 30), it is transported in the midrib (Maravolo 1976) and movement occurs in both directions at equal velocity. However, the basipetal (away from apical bud) transport is much greater in intensity. Transport can be inhibited by cinnamic acid and ethylene.

Figure 30. ***Marchantia polymorpha*** males with gemmae cups, demonstrating the midribs. Note the notches at the end of each and the dominance of one of them. Photo by Nancy Leonard, with permission.

As is typical with hormone responses, not all bryophytes respond the same way. ***Marchantia palmata*** growth was inhibited by most levels and kinds of auxins (Kumra & Chopra 1989). Furthermore, many chemicals can stop action of IAA (Muir 1974), including other growth hormones. These may actively compete for a binding site on the wall or plasma membrane. Could other plants outcompete bryophytes with a hormonal chemical warfare?

Ethylene is likely to have an early role in gametophore development. We know that seedlings produce ethylene in response to physical contact (Abeles 1973). Thus, if an emerging seedling encounters dense soil or rock, ethylene production inhibits mitosis, thus halting meristematic activity, and the cells respond by less elongation and by growing wider and thicker, giving the stem greater strength. This greater strength, coupled with continuing but reduced cell elongation, can dislodge small obstructions or push through dense soil. If the obstruction is a rock, ethylene production on the side of contact slows elongation on that side, resulting in plant curvature around the rock.

If we apply this principle to a developing or buried moss gametophore, ethylene could respond to particles of dirt and redirect gametophore growth. We have no studies on this aspect of ethylene in mosses, but I have grown ***Funaria hygrometrica*** (Figure 2-Figure 3, Figure 54) cultures where spores were germinated **under** the cellophane sheet on top of agar. An accumulation of ethylene is to be expected in this confined space. Here the normal vertical growth of the moss was prevented and a very etiolated-looking horizontal growth occurred. The leaves were short and the stem was long.

In ***Fontinalis squamosa*** (Figure 31), ethylene causes crumpled branches and stem tips (Figure 32; Glime & Rohwer 1983). G. Mogensen (pers. comm.) has seen similar crumpled branches as a common phenomenon in the Arctic. The crumpling follows a period of late spring or early autumn snow that results in an ice layer on the moss. Because the ice is thin, light is still available, but growth is obstructed. As the moss pushes against the ice, ethylene might be produced as a stress response. If ice surrounds the plant, only a slight space exists between the moss and the ice, permitting an ethylene build up.

Figure 31. ***Fontinalis squamosa*** in alpine water. Photo from <www.aphotofauna.com>, with permission.

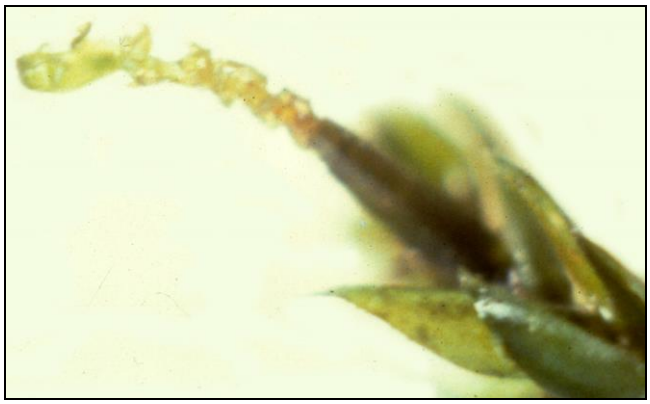

Figure 32. Effects of ACC (and presumably ethylene) on apical leaves of ***Fontinalis squamosa***. Photo by Janice Glime.

Submersed mosses [***Fontinalis*** (Figure 31), ***Drepanocladus*** (Figure 33-Figure 34)] often possess widely spaced leaves and thin stems, whereas the same species in shallow water will have thick stems and overlapping leaves. Fuchsig (1926) observed that this gives the shallow water individuals a greater resistance to desiccation with weight loss during desiccation being greatest in the deep water form. Two factors would implicate ethylene and IAA as the controlling factors here. In deep water, light is dim and no light inhibition of IAA should occur since UV light in particular is filtered out. Therefore an etiolation response is expected. At the surface, two factors known to enhance ethylene production occur: (1) stress due to wave action and alternate wetting and drying; (2) a high ratio of O_2:CO_2 relative to deep water. Endogenous ethylene could easily account for thicker cells and greater stem strength at the water surface.

Bryophytes seem to respond to many of the same hormones as do tracheophytes, but generally they respond at lower concentrations and may be inhibited at the concentrations that are effective for tracheophytes. Little is known of **ethylene** effects, but it may account for the contorted growth of bryophytes that have been encased in ice. **GA** is important in cell elongation and **IAA** is important in growth, most likely being the initiator of the rapid acid growth phase. It appears that IAA may provide the signal that initiates the **proton pump**. The **H^+ flux** into the cell wall spaces causes the **calcium pectate** bonds to break, freeing **Ca^{++}** that then enters the cell, replacing the positive H^+ ions that were just lost. **Anions** that come with the Ca^{++} create a salt within the cell, causing an osmotic gradient. Water follows by **osmosis**.

Figure 33. ***Drepanocladus aduncus*** in an emergent population with leaves close together. Photo by Michael Lüth, with permission.

Figure 34. ***Drepanocladus aduncus*** branch showing leaves close together. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

As with other processes in plants, the production of ethylene requires energy, as demonstrated by De Greef and coworkers (1979) in the thallose liverwort ***Marchantia polymorpha*** (Figure 30). We can therefore assume that when it enters into the development process there will be a tradeoff of energy that might otherwise be used elsewhere in the plant.

As already noted, the thallose liverwort ***Marchantia polymorpha*** (Figure 30) exhibits apical dominance. The thallus produces its own auxin, creating a **basipetal** (toward the base) gradient (Binns & Maravolo 1972). The auxin accumulates in the midribs and the **acropetal** (outward toward shoot apices) regions of excised thallus discs. Binns and Maravolo concluded that maintaining this gradient is essential for normal growth and regeneration. High concentrations of cytokinin in the tissues destroy the polarity by causing an increase in the auxin-synthesizing capacity of the affected tissues.

External application of auxins had no influence on the growth of the thallus, with no growth acceleration or inhibition of regeneration of the thallus (Binns & Maravolo 1972). Transcinnamic acid and dinitrophenol inhibited regeneration, but auxin reversed the inhibition.

Branches and Apical Dominance

Like tracheophytes, bryophytes exhibit a variety of branching types, ranging from total lack of appearance of apical dominance to strong apical dominance (Figure 35). A spruce tree with its strong central trunk and its secondary side branches is the epitome of apical dominance in tracheophytes. Yet, if the tip is broken, one of the side branches becomes a new leader, taking over the dominance that retards development of other secondary branches. In bryophytes, the acrocarpous mosses realize this type of apical dominance. In some cases, the dominance persists even if the tip is lost and the ability for branches to overtake the damaged central stem seems to be absent. But in others, such severance of the controlling tip results in increased growth of side branches, as in ***Fontinalis*** (Figure 36). Nevertheless, the ability of a single side branch to dominate the others after such a decapitation of the apex seems to be absent in the bryophytes. Rather, multiple side branches develop as **innovations**. This is not unlike the response of many herbaceous taxa of tracheophytes. For example, in snapdragons (*Antirrhinum*) the loss of the apex results in the development of a more bushy plant, and for any number of herbaceous garden flowers, pinching off the apex is a common technique for developing a more robust plant with multiple flowering apices.

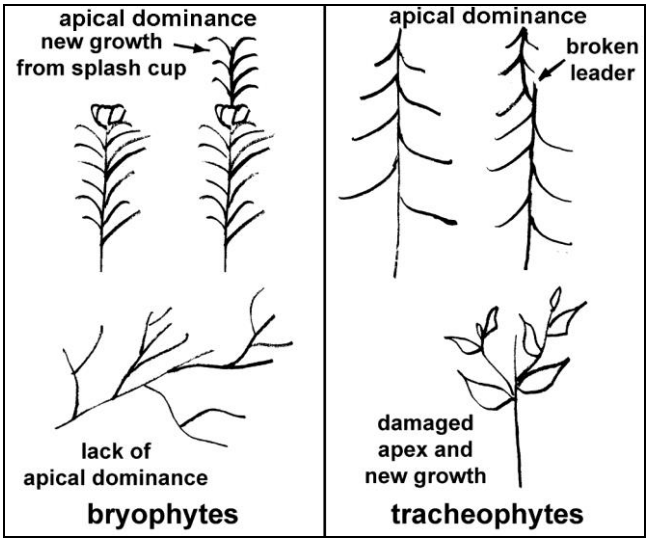

Figure 35. Effects of apical dominance on growth forms of bryophytes and tracheophytes. Drawings by Janice Glime.

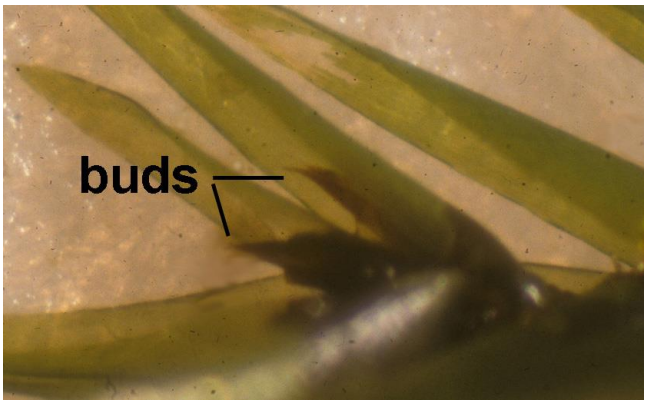

Figure 36. Branch buds developing near the broken tip of ***Fontinalis squamosa***. Photo by Janice Glime.

In acrocarpous mosses, the production of sexual structures terminates the apical growth, particularly the production of antheridial splash cups or capsules. But in some taxa, such as many **Polytrichaceae** (Figure 37), once the splash cup ceases to function in production of sperm, a new stem growth may develop, rendering a series of markers on the stem where remnants of the old splash cups remain (Figure 37). Certainly no flower accomplishes such a strange phenomenon, but cones of the European larch can develop new branches from the ends of the female cones!

Bryophyte branching differs from that of typical tracheophytes in other ways as well. Bryophytes branch below the leaf insertion, whereas tracheophytes produce branch buds in the leaf axil (Figure 38; Schofield 1985). For the tracheophytes, this altered arrangement could provide protection of the developing bud cradled in the leaf base. Furthermore, in tracheophytes, the buds have a meristematic region of dividing cells, whereas in the bryophytes, it is an outer cell of the stem that becomes specialized to form a branch, subsequently forming the apical cell of this branch (Figure 39-Figure 40).

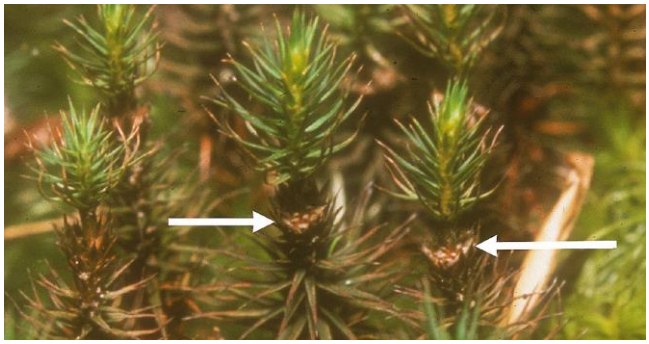

Figure 37. New growth from a senescent antheridial splash cup of ***Polytrichum ohioense***. Photo by Janice Glime.

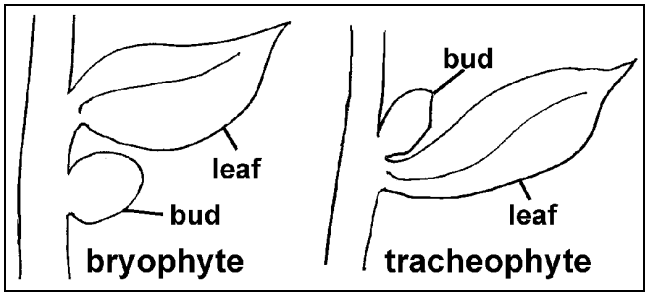

Figure 38. Position of branch buds in bryophytes vs. tracheophytes. Drawing by Janice Glime.

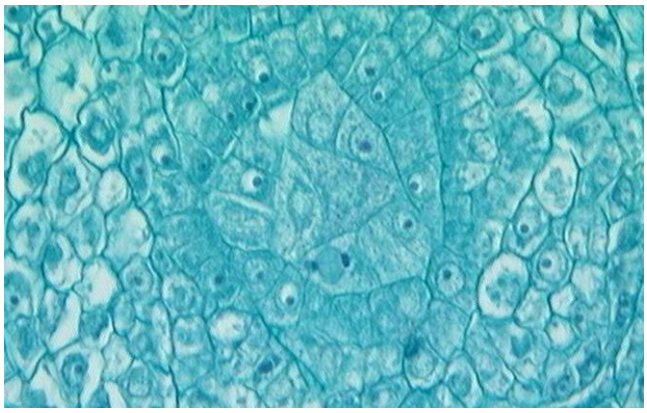

Figure 39. ***Polytrichum*** stem apex cross section showing three cutting faces. Photo by Magda Turzańska, with permission.

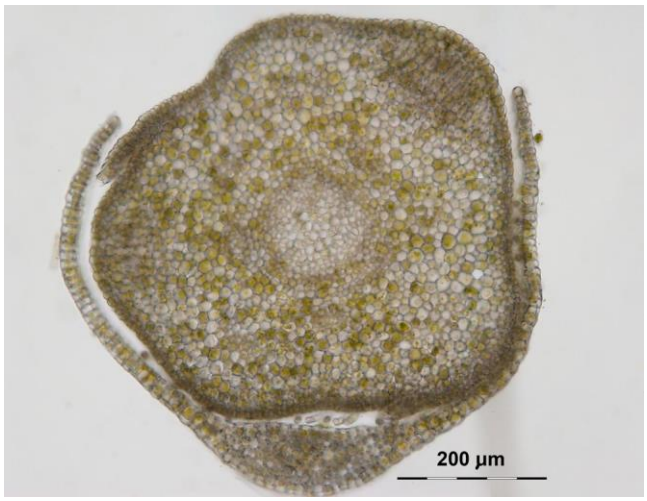

Figure 40. Mature ***Polytrichum*** stem cross section. Photo by Magda Turzańska, with permission.

Despite the differences in their apical development that uses apical cell cutting faces instead of a meristematic region, many bryophytes have apical dominance. In these taxa, removal of the apex promotes the development of branch buds, with those nearest the cut apex developing the most, as one sees in tracheophytes. Once these buds begin development, they re-establish the inhibition of the lateral buds beneath them.

We have already discussed the energy tradeoffs inherent in growth. One thing that is common among the species of mosses studied is the growth of either the main stem or the lateral branches to the exclusion of the other. ***Racomitrium lanuginosum*** (Figure 68) has two periods of main stem growth, one in spring and the other in autumn, whereas the lateral branches are initiated and elongate in the first part of summer (Tallis 1959). ***Hylocomium splendens*** (Figure 41) appears to have one period of elongation during which the bud for the next year of growth is initiated. This bud will not develop further until the present stem section has completed its growth (Busby *et al*. 1978). Sanford (1979), in his studies with the aquatic moss ***Leptodictyum riparium*** (Figure 22), also found that increased branch growth was correlated with decreased main axis growth. With this kind of tradeoff, we should expect an environmental role in determining when the plant elongates shoots and when it elongates branches.

Figure 41. ***Hylocomium splendens*** showing buds for next years growth. Photo from website of the Botany Department, University of British Columbia, Canada, with permission.

Environmental Factors

In his work with ***Racomitrium lanuginosum*** (Figure 68), Tallis (1959) observed that low main stem growth and favorable growth conditions such as temperatures between 12 and 15°C best favored shoot growth. Furthermore, in a cold, humid environment, his plants had few branches and these were small, but in a warm, moist environment, his plants had several long lateral branches. He also found that high humidity and shading may inhibit branching for up to a full year. He suggests that lateral branching might be induced by high light in combination with alternate wetting and drying at a mean temperature that is above the minimum threshold.

Chopra and Rashid (1969) likewise found that increased light intensity promoted lateral bud formation in mosses. This apparent action by light intensity is supported by the fact that in many plant species, bud expansion is initiated in the spring when light intensity increases and tree canopy closure is incomplete. Low light and low temperatures also delay budding in mosses (Bopp 1968).

But when light intensity increases in the spring, the temperature also increases. However, Pitkin (1975) states that the direct effect of temperature on bryophyte growth is small, except at low temperatures, but that temperature has a strong indirect effect through its effect on humidity and **evapotranspiration** (loss of water through evaporation from among plants and from plants themselves). However, temperature may be more direct through control by growth regulators.

Alghamdi (2003) found that the type of available N can greatly influence the production of branches. In solutions containing only amino acids as the N source, the Java moss (***Taxiphyllum barbieri***; Figure 42), an aquatic moss, produced more branches as concentrations increased with four different amino acid sources (but not **methionine** – amino acid that is relatively insoluble in water), while producing many fewer branches in ammonium or nitrate at the same concentrations of N (Figure 43). Could seasonal pulses of leaf litter decomposition, providing pulses of amino acids, play a role in the seasonal timing of branching vs stem elongation for forest bryophytes? What else can play a role?

Figure 42. ***Taxiphyllum barbieri***, an aquatic moss that produces more branches when supplemented with some amino acids than when supplemented with ammonium or nitrate. Photo by Buchling, through Creative Commons.

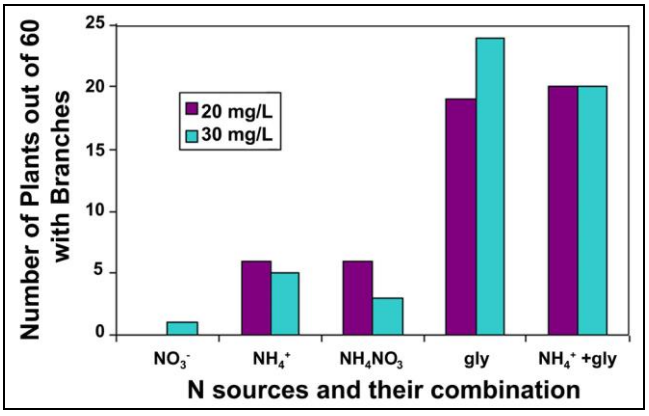

Figure 43. Effects of different types of nitrogen source on branch production in the Java moss, ***Taxiphyllum barbieri***. **gly** = glycine. Graph from Alghamdi 2003.

As discussed in the chapter on Nutrients, deficiencies can alter morphology and color of the bryophytes. Shaw (1991) suggested that for ***Funaria hygrometrica*** (Figure 2-Figure 3, Figure 54) growing on a mine site, differences in morphology might have been caused by heavy metal toxicity. But coupled with these metal-caused malformations, he suggested that **somatic** (cellular level) mutations could also contribute to the extensive **phenotypic** (form) variability.

Growth Regulators

Apical dominance is indicative of hormone actions. In tracheophytes, IAA produced in the tip of the plant and interacting with cytokinins inhibits the development of branches below the tip, permitting the main stem to be the leader. In bryophytes, we have indications that the same sort of action is present.

Bryophyte apical dominance appears to work the same way as in the meristematic tracheophytes. MacQuarrie and von Maltzahn (1959) linked apical dominance with IAA in the acrocarpous moss ***Splachnum ampullaceum*** (Figure 44). Stange (1964) demonstrated apical dominance in another acrocarpous moss, ***Funaria hygrometrica*** (Figure 2-Figure 3, Figure 54).

Figure 44. ***Splachnum ampullaceum***, a moss with known apical dominance due to IAA distribution. Photo by Michael Lüth, with permission.

Many acrocarpous mosses lose apical dominance when sporophytes are produced, resulting in innovations such as those in ***Bryum*** (Figure 45) or when antheridia develop as in ***Philonotis*** (Figure 46). This suggests that the sporophyte or archegonium causes the stem apex to cease producing IAA. We have already seen that in ***Polytrichum***, male plants (Figure 37) retain their apical dominance and resume growth from the center of the male splash cup when the succeeding year's growth begins.

Figure 45. Innovation (**arrow**) in ***Bryum versicolor***. Photo by Michael Lüth, with permission.

Figure 46. ***Philonotis fontana*** showing multiple branches just below the antheridial head. Photo by Janice Glime.

The role of apically supplied IAA is indicated in experiments where the gametophore is decapitated and an agar block containing 1mg/ml IAA is placed on the cut tip (Knoop 1984). In this case, stems without the agar block develop buds and branches, but in those with the agar block, the IAA inhibits lateral development in the same manner as an intact apex. Application of kinetin (a cytokinin) induces bud formation in those stems with an apical IAA source. A theoretical relationship to bud development is shown in Figure 47.

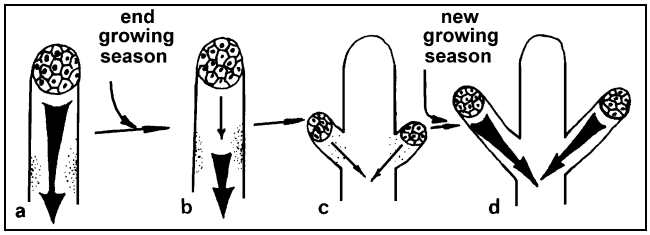

Figure 47. Theoretical relationship of auxin (IAA) and cytokinin in controlling branch production. **a**) Apical region during active growing season shows large production of IAA (**arrow**), inhibiting localized concentrations of cytokinin. **b**) End of growing season slows apical activity and production of IAA. **c**) Increased cytokinin:IAA ratio stimulates bud initiation. **d**) New apices become dominant and begin IAA production with new growing season.

The genus ***Plagiomnium*** exhibits a mix of upright growth that ultimately terminates in gametangia and

horizontal growth (**plagiotropic**). The moss ***Plagiomnium cuspidatum*** (Figure 48) responds to addition of IAA on a decapitated stem by exhibiting varying degrees of lateral bud suppression (Nyman & Cutter 1981). However, for the behavior to mimic that of controls with no decapitation, cytokinin must also be present.

Figure 48. Upright and plagiotropic growth forms of the moss ***Plagiomnium cuspidatum***. Photo by Michael Lüth, with permission.

This relationship of buds with cytokinin does not seem to apply to all mosses. In the moss ***Plagiomnium cuspidatum*** (Figure 48), the cytokinin is synergistic with IAA in inhibiting bud development; IAA alone is unable to inhibit branch buds (Knoop 1984). Because bryophytes have very low concentrations of IAA, they are probably extraordinarily sensitive to it. Thus budding might be inhibited at quite low levels. The apparent synergism may be based on a concentration problem. Furthermore, both cytokinin and IAA can induce production of ethylene, and this could explain the apparent synergism between IAA and cytokinin in ***Plagiomnium***.

Ethylene is known to inhibit development under some circumstances in plants. If ethylene is in fact the effector in branch inhibition, one might look for differences in ethylene production between acrocarpous and pleurocarpous mosses. Inhibition of branches by ethylene suggests that pleurocarpous mosses, or highly branched mosses, must have low endogenous ethylene relative to acrocarpous or unbranched mosses. If this is true, we should expect pleurocarpous mosses to be more sensitive to exogenous ethylene than acrocarpous mosses and that they might be less likely to produce ethylene in response to environmental stimuli; alternatively, they may be highly branched because they are not responsive to it. Whatever the mechanism, we should expect mosses lacking apical dominance to respond differently.

Cytokinins have been shown to enhance IAA-induced ethylene formation (Goodwin & Mercer 1983), which is likely to cause senescence. But in the acrocarpous moss ***Anoectangium thomsonii***, Chopra and Rashid (1969) observed that, at any concentration of added kinetin, there was an increase in the number of buds and the rate of bud initiation. However, further shoot development was inhibited.

We need to further examine the case of ***Plagiomnium cuspidatum*** (Figure 48). Although this moss is acrocarpous, it has lateral (**plagiotropic**) branches in addition to its upright stem (Figure 48). These branches may behave more like branches of pleurocarpous mosses in their response to ethylene, IAA, and cytokinins. Because ethylene is a gas, it is more difficult to work with and quantify.

Pleurocarpous Mosses

Studies on the effects of growth substances on pleurocarpous mosses appear to be rare, probably due to the greater convenience in growing small acrocarpous mosses on agar [*e.g.* ***Physcomitrium*** (Figure 49), ***Funaria*** (Figure 2-Figure 3)]. However, our own studies on ***Fontinalis*** (Figure 50-Figure 51) may offer some insight.

Figure 49. ***Physcomitrium pyriforme*** with capsules, showing its small size. Photo by Jan-Peter Frahm, with permission.

Tremaine and Glime (unpub.) grew ***Fontinalis duriaei*** (Figure 12) in liquid culture with 10^{-6} and 10^{-8} M IAA and found that after two weeks there was significantly more growth at 10^{-8} M than at 10^{-6} M or controls (no IAA), with intermediate growth in the controls (Duncan's New Multiple Range test, $p < 0.05$). This contrasts sharply with the optimum of 10^{-5} M for higher plants (Haney 1978). But effects on branching and apical dominance were inconclusive even after 8 weeks.

In a separate study, Hover and Glime (1983, unpubl) grew ***Fontinalis duriaei*** (Figure 12) with kinetin additions and got rather confusing results. At 0.001 and 0.01 mg L^{-1} added kinetin, the mosses produced fewer branches per stem than did the controls with no kinetin addition, but at 1.0 mg L^{-1} they produced significantly more branches than did controls. They speculated that this may have been due to a competitive action between the exogenous kinetin and the plant's own cytokinin that could have resulted in suppressing production of the natural cytokinin.

Berthier (1966) found that maximum apical dominance in ***Fontinalis*** (Figure 50) occurred at 5% sunlight and that full sunlight caused maximum inhibition of axis growth. Shade inhibited branching. This and the studies mentioned above suggest that shade increases IAA and sun reduces the IAA:cytokinin ratio. This is consistent with events leading

to an etiolation response and the known destruction of IAA by high light intensity, especially UV, in tracheophytes.

Figure 50. ***Fontinalis antipyretica*** with wounded tip that now has grown rhizoids and a new branch. Photo by Janice Glime.

Figure 51. ***Fontinalis antipyretica*** var. ***gigantea***, showing broken branch tip (center) with single new branch that has presumably resulted from loss of apical dominance. Photo by Malcolm Storey, through Creative Commons.

We know that high concentrations of ACC, an ethylene precursor and presumably resulting in ethylene production, inhibit branch development and bud production in ***Fontinalis squamosa*** (Figure 31) and ***F. antipyretica*** (Figure 50) (Glime & Rohwer 1983). Inhibitory effects of high IAA concentrations seem to be due to its effects in increasing ethylene production (Goodwin & Mercer 1983). This relationship implies that it could actually be ethylene that inhibits branch formation. Valadon and Mummery (1971) have shown that abscisic acid (ABA) also has a linear relation to bud reduction in ***Funaria hygrometrica*** (Figure 2-Figure 3, Figure 54). But abscisic acid is also known to promote ethylene production in some tissues (Craker & Abeles 1969), so it is possible that again ethylene was the actual inhibitor.

Although ***Fontinalis*** (Figure 50) does not appear to have a strong apical dominance, Berthier (1966) demonstrated that removal of its apex resulted in branches on each side of the apex. I (Glime) have observed similar phenomena in explants of ***Fontinalis antipyretica* var. *antipyretica*** (Figure 50, see also Figure 36), but when my student and I removed the apices from ***F. antipyretica* var. *gigantea*** (Figure 51), the removal had no observable effect on branching. Since this variety does little branching normally, it may have been an inappropriate taxon to test.

But why does it appear that ***Fontinalis*** can't grow branches and stems simultaneously? Since both produce leaves that are photosynthetic, where is the tradeoff? Perhaps the experiments of Tremaine and Glime (unpub.) on ***Fontinalis duriaei*** (Figure 12) provide some insight into the relationship. They found the mosses in 10^{-6} M IAA to look healthiest (bright green) at the end of the experiment compared to the controls or those at 10^{-8}M, both of which grew more than those at 10^{-6}M. It appears that the tradeoff may be that the energy used for growth reduces the concentration of chlorophyll in the leaves as it distributes its building materials to new cells and tissues. This will reduce the leaf weight and the magnitude of photosynthesis per leaf area. Hence, it is most likely beneficial to hold one growth type constant while the other expands.

Spiess *et al*. (1972), working with the pleurocarpous ***Pylaisiella selwynii*** (Figure 52), also found that cytokinins increased bud formation but not further development, and thus concluded that the auxin:cytokinin ratio was important. They observed also that the number and morphology of the buds were both concentration dependent.

Figure 52. ***Pylaisiella selwynii*** on bark, where bud formation depends on cytokinin, but not further development. Photo by Janice Glime.

Thallose Liverworts

Even thallose liverworts exhibit apical dominance. In ***Marchantia polymorpha*** (Figure 30), hormones may control the fan shape of the thalli. The apical dominance of these plants is expressed as greater growth of one lobe compared to the other one. When the thallus develops, two apical notches are present. The larger lobe that develops is the one nearest to the midrib. If the two notches are cut at an early growth stage, inhibition of the smaller lob ceases and it grows to equal the size of the dominant lobe. But it is not IAA that causes the new growth, but rather IAA inhibits the growth of the smaller lobe. The larger lobe, on the other hand, is not affected by IAA. This suggests that once a branch of the thallus becomes dominant the two lobes have different sensitivity to IAA as an inhibitor.

Branch buds of bryophytes are known to be sensitive to both cytokinin and auxin concentration. Three cytokinins tested stimulated vegetative growth, as well as archegonial production, in ***Riccia frostii*** (Figure 11),

whereas the auxin NAA only enhanced archegonial induction (Vashistha 1987). In studies on mosses, Chopra and Rashid (1969) found that low concentrations of exogenously applied IAA somewhat increases bud formation. At higher concentrations, IAA is inhibitory (Spiess *et al*. 1973).

Both cytokinins (Chopra & Gupta 1992) and IAA (Tremaine & Glime unpub.) appear to be important in controlling bryophyte growth. Chopra and Gupta (1992) found that of the three cytokinins they tested, 10^{-4}M was optimal for vegetative growth in ***Riccia discolor***.

Nutrients

Koevenig (1973a) suggests that the growth hormones IAA, NAA, **BA** (6-benzyladenine, a cytokinin), and GA_3 may only aid in elongation but not actually induce it, implying that other substances are needed, such as the metals. Many compounds influence plant growth. Sharma *et al*. (1960) reported that ***Haplomitrium*** (Figure 53) gametophytes grew better on media containing various amino acids, indicating that organic material must be present in the substrate. Copper can stimulate growth of some bryophytes at elevated concentrations (0.01 ppm), presumably through greater photosynthesis (Sommer 1931; Glime & Keen 1984), wherein it is needed in plastocyanin, a chloroplast protein. Nevertheless, it soon becomes inhibitory at higher concentrations.

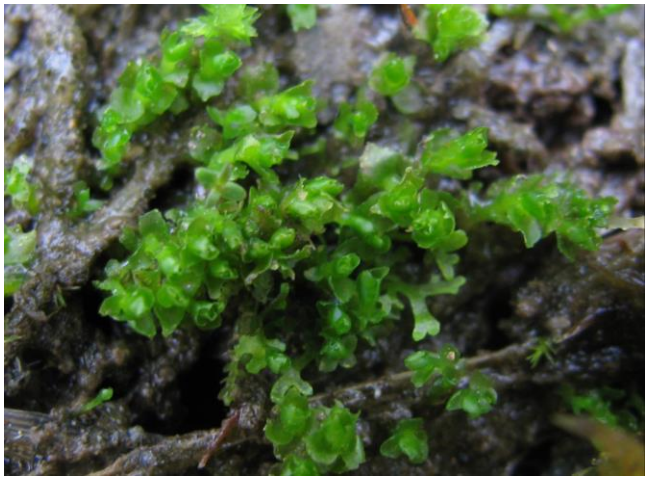

Figure 53. ***Haplomitrium hookeri***, a leafy liverwort that grows best on a medium with amino acids as its nitrogen source. Photo by Janice Glime.

Laboratory cultures are usually much richer in nutrients than are the places where bryophytes normally grow. For example, in ***Funaria hygrometrica*** (Figure 2-Figure 3, Figure 54), field stem length never reaches that observed in the laboratory. One reason for this might be a deficiency of magnesium in its habitat and ample quantity in the culture medium. Hoffman (1966) found that ***Funaria*** remained small but healthy in a magnesium-deficient medium. Tamm (1953) found that rainwater, the major source of nutrients for ectohydric mosses, contained no magnesium in the open, although it did under spruce trees. Since ***Funaria*** does not grow in the shade of trees, it is likely to be suffering from a magnesium deficiency in the open, and this might account for its shorter stature in nature. However, etiolation due to lower light intensity in the laboratory cannot be ruled out.

Figure 54. ***Funaria hygrometrica*** with archegonia and young sporophytes. Photo by Andrew Spink, with permission.

Leaves

Leaf development occurs when sufficient nutrients are available and temperature and light are adequate for growth. Thus leaf expansion can occur in consort with apical growth and branch growth, or the plant may produce numerous branches and leaves, delaying stem expansion until later, as in the capitula of ***Sphagnum*** (Figure 55). However, controls of these phenomena are different, and the reduced leaves on elongated stems in the ***Funaria*** (Figure 2-Figure 3, Figure 54) cultures under cellophane discussed earlier attest to this fact.

Figure 55. Dense branches in capitula of ***Sphagnum wulfianum***. Photo by Jan-Peter Frahm, with permission.

Moss leaves typically are endowed with pigments and antiherbivore compounds that permit them to survive in their habitats. One of the compounds occurring in some moss cell walls appears to be a phenolic compound, as suggested by its ability to fluoresce under UV light (Figure 56).

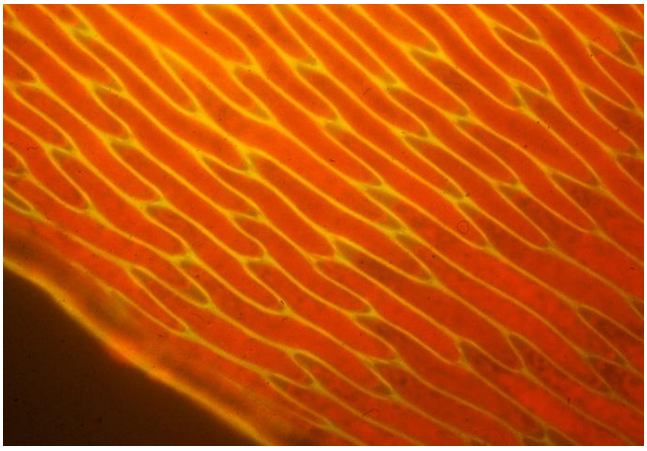

Figure 56. Fluorescence of cell walls under UV light in a leaf of ***Fontinalis antipyretica***. Photo by Janice Glime.

Light

In some species leaf dimensions and leaf shape are highly plastic and dependent on light and moisture conditions. Hoddinott and Bain (1979) found that red vs. far-red light caused significant differences in leaf dimensions. ***Ceratodon purpureus*** (Figure 4) and ***Polytrichum juniperinum*** (Figure 15) had longer leaves in red light, whereas ***Leptobryum pyriforme*** (Figure 14) and ***Pohlia proligera*** (Figure 57) had longer leaves in far-red light. In ***Ceratodon*** and ***Leptobryum***, leaf width was greater in red light, whereas in ***Polytrichum*** it was greater in far-red light. These wave length changes resulted in overall leaf shape changes in ***Leptobryum***, ***Pohlia***, and ***Polytrichum***. ***Dicranum polysetum*** (Figure 13) and ***Funaria hygrometrica*** (Figure 58) leaf shapes were indifferent to red/far-red differences. Hopefully our new molecular techniques will help us sort out some of the environmentally induced differences.

Figure 57. ***Pohlia proligera.*** Some members of this genus has leaves that are longer in far-red light. Photo by Michael Lüth, with permission.

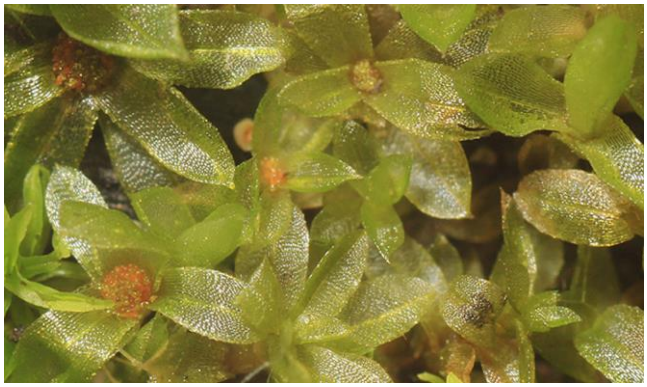

Figure 58. ***Funaria hygrometrica***, a species for which light quality changes did not change leaf shape. Photo by Barry Stewart, with permission.

Water

Water modifies leaf form as well. ***Drepanocladus*** (Figure 59) has longer and proportionally narrower leaves and loses its **falcation** (curved shape; Figure 60-Figure 61) in water (Lodge 1959). Furthermore, the normally straight ***Fontinalis*** leaves (Figure 62) become falcate (Figure 63) when grown in air (pers obs).

Figure 59. ***Drepanocladus fluitans*** growing above water and demonstrating curved leaves. Photo by Michael Lüth, with permission.

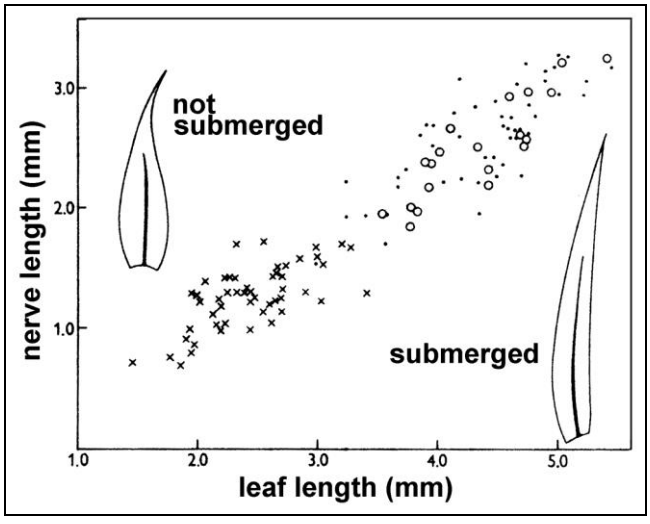

Figure 60. Modifications in leaf morphology of ***Drepanocladus fluitans*** due to submergence, in this case causing elongation. Redrawn from Lodge 1959.

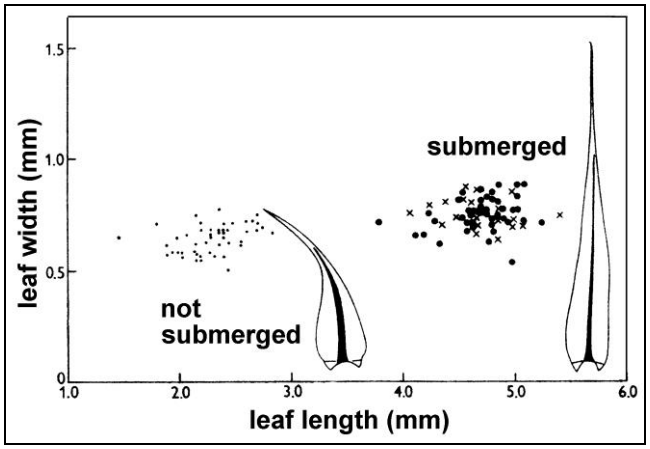

Figure 61. Modifications in leaf morphology of ***Drepanocladus fluitans*** due to submergence, in this case causing loss of falcation. Redrawn from Lodge 1959.

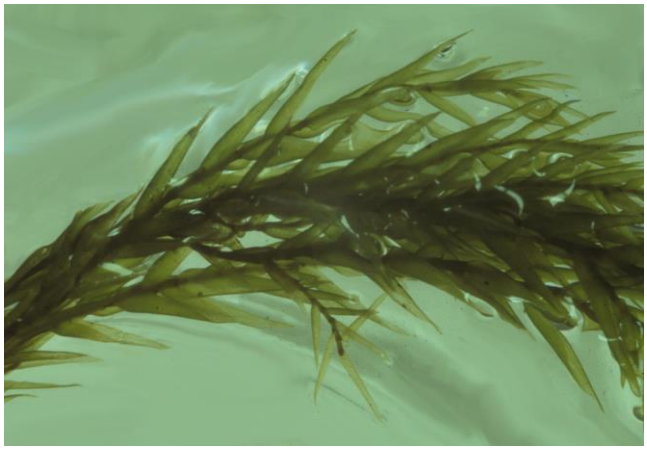

Figure 62. ***Fontinalis novae-angliae*** with normal submerged leaves. Photo by Janice Glime.

Figure 63. Falcate leaves of ***Fontinalis novae-angliae*** grown on moist paper out of water. Compare these to the straight leaves in Figure 62. Photo by Janice Glime.

Salt can cause similar modifications to effects of being above water, suggesting that loss of water from the leaves can trigger these changes. For example, cell length of ***Drepanocladus*** leaves increases as salt concentrations increase (Figure 64; Lodge 1959). On the other hand, Voth (1943) found that ***Marchantia polymorpha*** (Figure 30) had rapid maturity and slightly smaller cells in higher concentrations of salts.

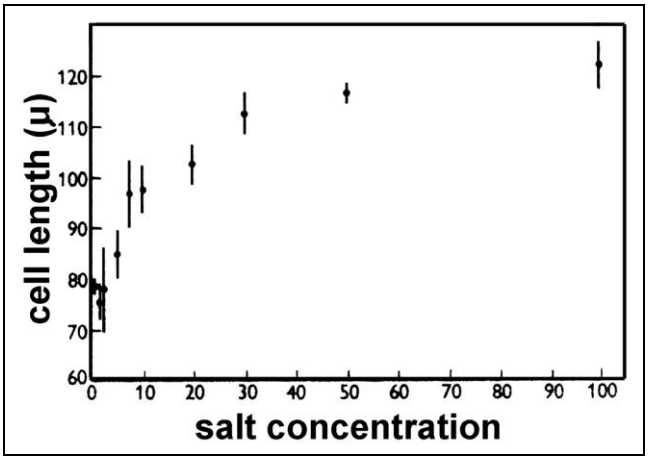

Figure 64. Relationship between leaf cell length and salt concentration in ***Drepanocladus fluitans***. Concentrations are relative percents of highest concentration with individual ions kept in same proportions. Redrawn from Lodge 1959.

In ***Sphagnum***, leaf response differs among species. In ***S. papillosum*** (Figure 7), the leaf becomes significantly longer when the capitulum is farther from water, but in ***S. magellanicum*** (Figure 6), there is little difference (Li *et al.* 1992; Figure 65). ***Sphagnum*** cell dimensions are also altered by water availability, with leaves of these two species grown under drier conditions having longer cells with unaltered width (Figure 66) and more pores per cell (Figure 65 right; Figure 67). Such evidence demonstrates the plasticity of species to respond to the environment and emphasizes the importance for common garden experiments in systematic studies.

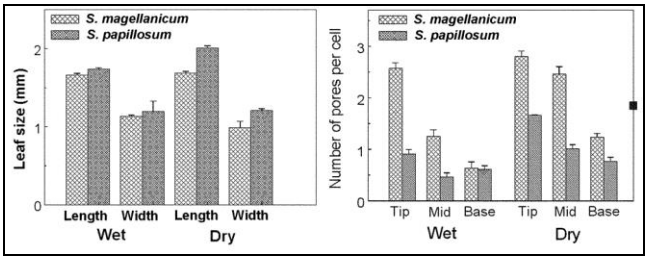

Figure 65. Effect of water level (water availability) on **left:** leaf length and **right:** number of pores per cell in ***Sphagnum magellanicum*** (Figure 6) and ***S. papillosum*** (Figure 7). Wet denotes 0 cm initial distance of capitulum from water; dry denotes 10 cm initial distance. Bars represent standard error. From Li *et al.* 1992.

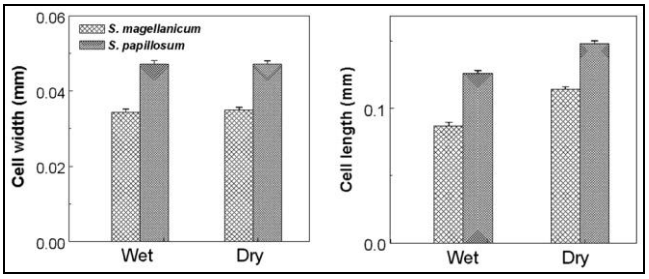

Figure 66. Effect of water level (water availability) on hyaline cell width and length in ***Sphagnum magellanicum*** and ***S. papillosum***. Wet denotes 0 cm initial distance of capitulum from water; dry denotes 10 cm initial distance of capitulum from water. Bars represent standard error. From Li *et al.* 1992.

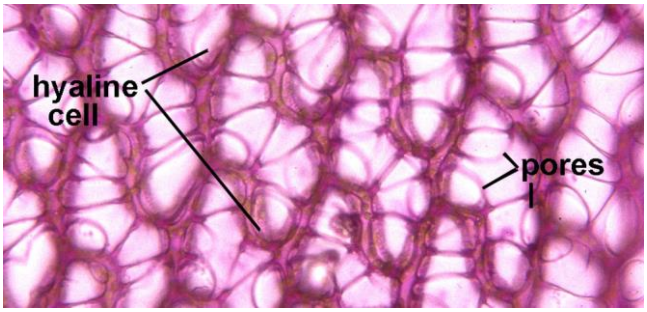

Figure 67. ***Sphagnum papillosum*** leaf showing hyaline cells and pores. Photo courtesy of Yenhung Li.

Hair points (hair-like extensions of leaf tip) in ***Racomitrium lanuginosum*** (Figure 68) are shortened by 50-100% in high humidity or shade (Tallis 1959). Cyclic weather conditions reduce hairs, causing maximal hair length on lateral branch zones but short hairs on in-between zones of the main axis. When the stem apex is removed, leaves have short or no hair points. When branches are produced, hair points arise on their leaves, suggesting that a controlling substance is produced by the stem apex and to a lesser extent by branch apices.

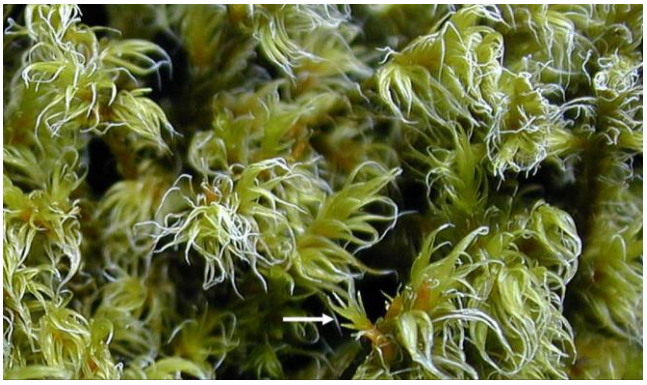

Figure 68. Apical hairs of ***Racomitrium lanuginosum*** showing reduced hairs at arrow. Photo by Michael Lüth, with permission.

The moss ***Schistidium apocarpum*** (Figure 69-Figure 70) varies considerably in the development of hair points, even on the same plant. ***Schistidium rivulare*** (Figure 71), which does not produce hair points, probably differs from ***S. apocarpum*** in its production of some growth-controlling substance.

Figure 69. ***Schistidium apocarpum*** with well-developed hair points. Photo by Michael Lüth, with permission.

Figure 70. ***Schistidium apocarpum*** with no hair points on leaves. Photo by Christophe Quintin, with permission.

Figure 71. ***Schistidium rivulare*** showing the absence of leaf hair points. Photo courtesy of Betsy St. Pierre.

Nutrients

Generally we look at the way nutrients affect whole plants, but they can especially affect development of leaves. For example, the difference between nitrogen as ammonium or organic N rather than nitrates in a low carbohydrate medium caused ***Sphagnum fallax*** (Figure 72) to develop leaves with no hyaline cells (Hintikka 1972). And nutrients can affect color (Glime & Marr unpublished). The role of nutrients on growth and development will be discussed in the chapter on nutrients.

Figure 72. ***Sphagnum fallax***, a species that alters its hyaline cells depending on the form of nitrogen. Photo by David T. Holyoak, with permission.

Growth Regulators

Little seems to be known about the hormonal control of leaf development. Exogenous application of auxin stimulates activity of the GUS-stained GH3 and DR5 genes in leaves of bryophytes, as demonstrated in ***Physcomitrella patens*** (Figure 26), but these genes did not demonstrate activity without the external auxin stimulus (Bierfreund *et al*. 2003).

We do know something about the role of ethylene in creating anomalous effects in leaf development, and these certainly have ecological relevance. As mentioned earlier, when growth of moss leaves and branches in the Arctic is impeded by ice, the result is crumpled leaves and branch ends. Similar crumpling resulted from growing ***Fontinalis squamosa*** (Figure 31-Figure 32) in high concentrations of ACC (resulting in elevated ethylene) and is consistent with effects of ethylene in lignified vascular plants. In some cases, ***F. squamosa*** leaves became wavy, much as the normal form of ***Neckera pennata*** (Figure 74), and in others they were more contorted, like stepping on a wadded up ball of paper (Figure 32; Glime & Rohwer 1983).

In ***Fontinalis antipyretica*** (Figure 73), application of ACC resulted in undulations on both young leaves and old, mature leaves (Figure 74; Glime & Rohwer 1983). Ethylene permits cells that have reached a certain stage to continue elongation, but inhibits it in younger cells. This results in uncoordinated development of the leaf cells and a surface that is not flat. It is very likely that similar hormonal regulation results in the natural waviness of leaves like those of ***Neckera*** (Figure 74). Since ***Fontinalis*** has been considered as closely related to the Neckeraceae, where undulations are characteristic of several species, it suggests that a gene controlling ethylene production or ACC distribution might be responsible for this morphology.

Figure 73. ***Fontinalis antipyretica*** showing normal, smooth leaves. Photo by Kristian Peters, with permission.

In nature, such events are likely to occur in response to leaf litter cover, ice, snow, and other physical barriers. By preventing diffusion of ethylene, unequal concentrations of ethylene result around different parts of plants, and as ethylene buildup occurs, contorted growth can result. An ethylene-induced growth differential between stems and leaves could explain the appearance of reduced leaves on **stolons** (horizontal stems from which upright stems arise) of certain species of ***Fontinalis*** (Glime 1980). If these stolons are a response to burial in a sandy substrate, or even burial among other ***Fontinalis*** branches that impede flow, ethylene production and accumulation could be the biochemical agent.

Figure 74. **Left:** ***Fontinalis antipyretica*** exhibiting undulate leaves induced by 10^{-4}M ACC. **Right:** ***Neckera pennata*** exhibiting genetically undulate leaves. Photos by Janice Glime.

In ***Fontinalis antipyretica*** (Figure 73), the response to ethylene precursor ACC was similar (Glime & Rohwer 1983) to the response of fern gametophytes, where mitosis ceased and cell elongation was enhanced by ethylene (Edwards & Miller 1972). In ***F. antipyretica***, shoot apices appeared truncated because older leaves with yet undeveloped cells had sustained cell elongation, whereas the center of the bud, where cell formation was incomplete, ceased its production of new cells and remained small (Figure 75). In these plants, elongation of outer leaves accounted for all growth of the plant during the 8-week experiment (Glime & Rohwer 1983).

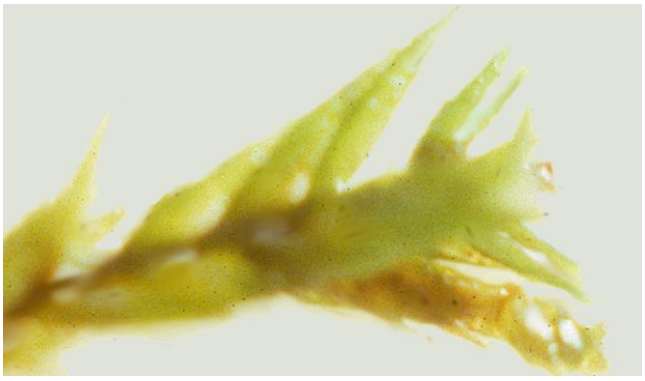

Figure 75. Effects of ACC (and presumably ethylene) on the shoot apex of ***Fontinalis squamosa***. Note truncated tip where leaves did not elongate while nearby leaves continued growth. Photo by Janice Glime.

The modified apex of ***Fontinalis squamosa*** (Figure 31) is usually accompanied by red to brown leaf coloration in elevated ACC (Figure 76). It appears that ethylene (or ACC) stimulates a color change to a reddened color in the cell walls.

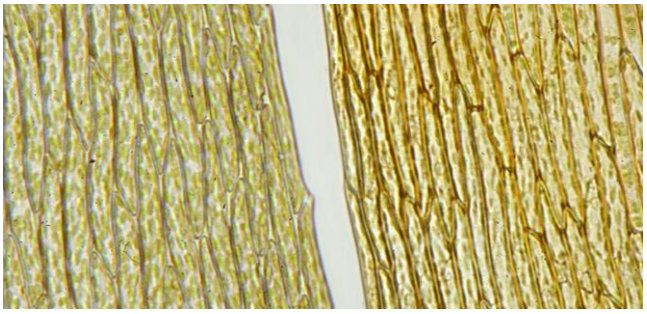

Figure 76. Effect of ACC on leaf cell wall color in ***Fontinalis antipyretica***. **Left:** Normal cells. **Right:** Cells subjected to 10^{-4}M ACC. Photo by Janice Glime.

As noted above, ***Fontinalis*** also can develop a modified leaf shape when grown exposed to air. When it is submersed during growth, leaves are straight, but in our lab cultures where it grew in a thin film of water and continuously received exposure to air while remaining wet, leaves became falcate (curved like a sickle; Figure 63). This may have been another example of ethylene production in the high oxygen, low CO_2 environment of air, as opposed to that in water. It is interesting that the other two genera in the family, ***Brachelyma*** and ***Dichelyma*** (Figure 77), have falcate leaves and grow most of the year out of the water.

Figure 77. ***Dichelyma falcata*** exhibiting falcate leaves. Photo by Michael Lüth, with permission.

Liverwort Leaf Suppression

Something happens as liverwort leaves develop! Something suppresses every third leaf during development. The result is that liverworts have two rows of leaves and a third row that may fail to develop completely or that develops into small leaves called **amphigastria** or **underleaves**.

Ethylene seems to have played a major evolutionary role in these bryophyte leaf arrangements. Basile and Basile (1983a, b, 1984, 1994) have shown that **hydroxyproline** (crystalline amino acid abundant in major glycoprotein of plant primary cell wall) will induce underleaves of liverworts to reach the size of lateral leaves, and in some cases induce development of underleaves when they are unknown in nature. They contend that loss of normal-sized underleaves in bryophytes, such as seen in ***Haplomitrium*** (Figure 78), is an evolutionary result of inhibition by ethylene, because ethylene antagonists such as hydroxyproline can induce these bryophytes to produce normal leaves where small underleaves would normally be. This is consistent with the widespread belief that 3-ranked leafy liverworts (Figure 78) are the primitive form, with 2-ranked ones being derived (and as implied here, derived due to suppression of the third row that results in reduced underleaves typical of many leafy liverworts; Figure 79).

Figure 78. ***Haplomitrium mnioides***, a leafy liverwort with three equal rows of leaves. Photo by Li Zhang, with permission.

Ethylene is known as a **senescence** hormone, *i.e.* it causes aging. In high concentrations it can cause cells to **plasmolyze** (cell membrane & contents pull away from cell wall) and die (Figure 80), as shown by Glime and Rohwer (unpub. data).

Figure 79. Ventral view of ***Calypogeia fissa***, a leafy liverwort with the underneath row of leaves suppressed. Photo by Michael Lüth, with permission.

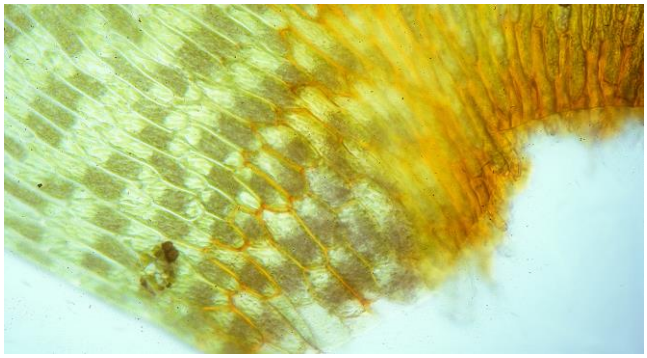

Figure 80. Plasmolyzed basal leaf cells in ***Fontinalis antipyretica*** subjected to 10^{-3}M ACC. Photo by Janice Glime.

Ethylene has a number of potential effects on leaves, but these have rarely been documented. It causes cell walls to become red, makes leaves wavy, and gives stem apices a truncated appearance (due to inability of young cells to elongate while older ones continue to elongate). Its most important role appears to be in the evolution of leafy liverworts with **underleaves** or no underleaves, compared to those with three equal rows.

Cuticle

Bryophytes, for a long time, were considered to lack a cuticle. But in fact, many do have varying degrees of cuticle (Figure 81) (Stránsky *et al*. 1967; Nilsson & Mårtensson 1971; Haas 1982). Cook and Graham (1998) noted the structural similarities between the osmiophilic surface layer on the liverwort ***Monoclea gottschei***, the moss ***Sphagnum fimbriatum***, and the hornwort ***Notothylas orbicularis*** with those of tracheophyte cuticles in that there is an "osmiophilic layer on the outer cell wall that bears some structural resemblance to early developmental stages of vascular plant cuticles." Of 43 moss species tested, Proctor (1979) demonstrated cuticles on 12 that were comparable to those on tracheophyte leaves.

We now know that cuticles in bryophytes can be present in the sporangial epidermis, spiral thickenings of elaters, rhizoids, and leaves (Kroken *et al*. 1996). As time progressed, so did regulation of their deposition. These cuticles initially seemingly had the functions of desiccation resistance and/or microbial resistance, as seen in lower charophytes. They have played a role in embryogenesis in the early land alga/plant ***Coleochaete*** and in embryophytes. Ultimately, they have an important role in decay resistance such as that of rhizoids, sporangial epidermis, and elaters of bryophytes

Salminen *et al.* (2018) noted that as photosynthetic organisms ventured onto land they developed new polymers such as cutin and suberin as a protection against water loss, solar radiation, and other potentially harmful abiotic factors. But we know little about these in bryophytes. Nevertheless, because of the variability of habitats exhibited by bryophytes and their early position in evolution on land, Salminen and coworkers proposed that liverworts and mosses were an attractive model systems for determining the specific functions and activity of lipid transfer proteins (LTPs) associated with cuticle synthesis and evolution of the plant cuticle.

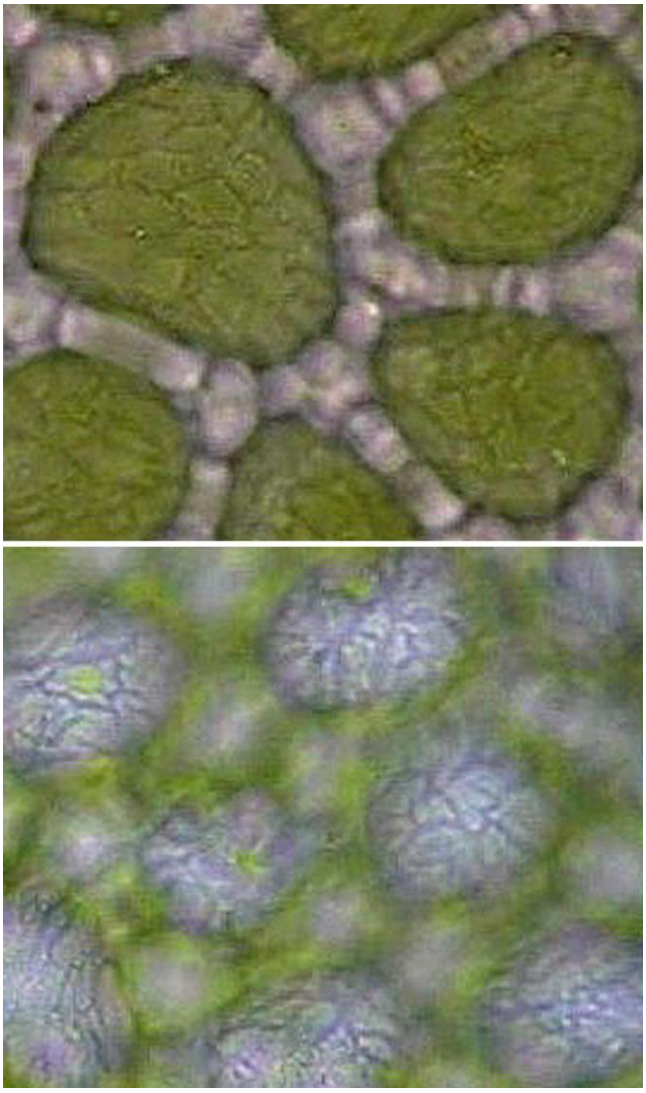

Figure 81. ***Mylia anomala*** showing cuticle. Photo by Paul G. Davison, with permission.

But our ecological knowledge of bryophyte cuticles seems to stop at recognition of their existence. I could find no reports on environmental or physiological control, and thus far there does not even seem to be evidence to support environmental correlation. Nor do we know at what developmental stage the bryophyte leaf or thallus begins production of the cuticle. We know that in tracheophytes, the cuticle can at times serve as a barrier to the entry of fungi and other pathogens (Kolattukudy 1985), but that role seems to be controversial, with many fungi possessing the enzymes needed to gain entry through the cuticle (Köller 1991). Stomata or wounding usually are the points of entry for fungal hyphae.

Do cuticles add to the ability of bryophytes to deter invasion of fungi? Is there any correlation between presence of cuticles similar to those of tracheophytes and the absence of fungal pathogens in bryophytes in nature? Do such pathogens attack the bryophytes only after they have been wounded? And how do the cuticles affect decomposition of dead and dying bryophytes?

Cuticles are **hydrophobic** (repelling water) and thus could facilitate photosynthesis by preventing the water barrier to CO_2 entry in bryophytes. In some cases, this hydrophobia could direct water to the base of the leaf

where there may be no cuticle and water entry is possible, while permitting photosynthesis in the rest of the leaf. This also could facilitate the spreading of the leaf upon hydration by dew or rain. This hydrophobia works on its inner surface as well, reducing water loss through the surface. In trachelphytes, interaction between the plant cell walls and cuticle in the presence of a pathogen on the surface can trigger internal plant chemical defenses (Ziv *et al*. 2018). But do bryophytes benefit from any of these possibilities?

Calyptrae

Since I seem to have neglected the gametophyte role in the protection of the sporophyte, this is perhaps an appropriate place to discuss it because of the role of the cuticle. Further information on the role of the calyptra is discussed in subchapter 5-9 of this volume on the Sporophyte. Budke *et al*. (2011) asked "A hundred-year-old question: Is the moss calyptra covered by a cuticle?"

Using the easily cultured ***Funaria hygrometrica*** as the study object, Budke and coworkers noted the role of the calyptra in protecting the developing sporophyte from desiccation. Using both SEM and TEM, they compared the calyptra, leafy gametophyte, and sporophyte sporangia. These methods revealed a multi-layered cuticle on the calyptra, including layers analogous to the cuticular layer, cell wall projections, electron-lucent, and electron-dense cuticle proper observed in tracheophytes. They hypothesized that the apex of the developing sporophyte in particular would be well protected. They found that the calyptra rostrum has a significantly thicker cuticle than the other tissues examined and differs by specialized thickenings of the cuticular layer (cuticular pegs) at the regions of the anticlinal cell walls – the first report of cuticular pegs in bryophytes.

Budke *et al*. (2013) followed these observations by experiments to verify the role of the cuticle in protecting the developing embryo in ***Funaria hygrometrica***. When the cuticle of the calyptra was removed chemically, they found that under low humidity conditions there is significant negative impact to moss sporophyte fitness, including decreased survival, increased tissue damage, incomplete sporophyte development, more peristome malformations, and decreased reproductive output.

Using four bryophyte species, Budke and Goffinet (2016) subsequently found that shorter sporophytes are associated with smaller calyptrae and thinner calyptra cuticles, whereas taller sporophytes are associated with larger calyptrae and thicker calyptra cuticles. Using sectioning techniques, they found that the cuticle of the sporophyte thickens during later develpment. The calyptrae, on the other hand, have a mature cuticle early in their development, and this persists throughout development. This can become an adaptive strategy in which resources are allocated, or not, to a thickened cuticle. Limited cuticle development can provide resources for other types of development for survival in different developments. Therefore, we should expect differences in cuticle thickness of the calyptra in wet vs dry environments, or at least in the species restricted to each.

Rhizoids

Rhizoids in bryophytes have an important role in anchoring the plants to the substrate and thus helping them adhere under the force of wind, water, or animal activities. It is therefore not surprising that these factors, along with temperature, are influential in the development of rhizoids.

Temperature

Furness and Grime (1982) demonstrated that switching of developmental processes can be due to different temperature optima. In ***Brachythecium rutabulum*** (Figure 82) growth is greatest at 20°C, primary branching at 16°C, and rhizoid production at 12°C. By contrast, in ***Fontinalis hypnoides*** (Figure 83), rhizoids are produced at 15-20°C (Figure 84-Figure 86), whereas the growth optimum is 10-15°C (Glime 1980, 1982; Glime & Raeymaekers 1987), and branching occurs during late winter, spring, and early autumn when the temperature is usually less than 10°C (Figure 86). In ***F. dalecarlica*** rhizoid production is negatively correlated with branch production (Glime 1984). This timing for ***Fontinalis*** permits the rhizoids to grow during warm summer months when the moss is most likely to have a sustained period without disturbance of heavy flow, thus affording it an opportunity to attach.

Figure 82. ***Brachythecium rutabulum***, a moss for which 20°C is optimum for growth. Photo by Michael Lüth, with permission.

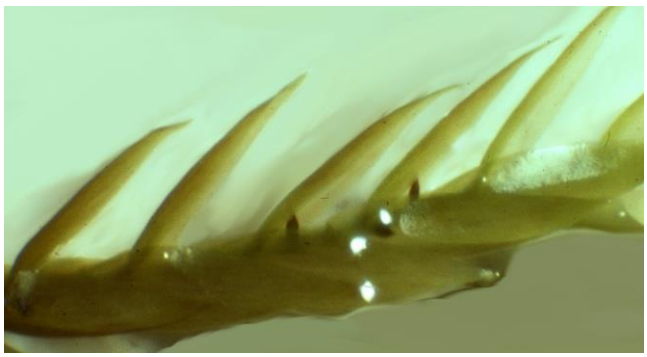

Figure 83. ***Fontinalis hypnoides***, a species that lives in both streams and lakes. Photo by Janice Glime.

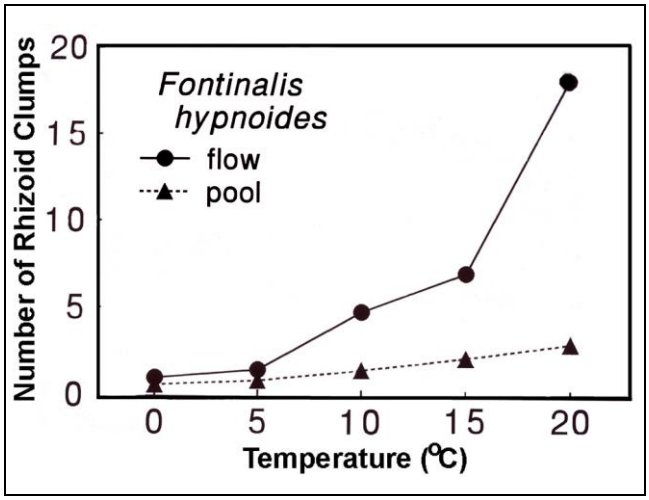

Figure 84. Flow and temperature effects on mean number (n=40 stem tips in each condition) of rhizoid clumps in ***Fontinalis hypnoides*** from the Keweenaw Peninsula of Michigan, USA, after 15 weeks in flowing water and pool conditions in artificial streams. From Glime & Raeymaekers 1987.

Light

Light can influence both form and production of rhizoids in bryophytes. In ***Riccia crystallina*** (Figure 85) red light favors smooth rhizoid production, whereas at high intensities more rhizoids are produced and more are **tuberculate** (having "pegs" or extensions of cell wall protruding into cell; Figure 87) (Chopra & Sood 1973). In 0.5% sucrose, there are 50% more smooth ones than tuberculate ones, but at 2% sucrose there are twice as many tuberculate as smooth ones, suggesting that the role of light in governing morphology may be one of sugar concentration, thus implicating a role for photosynthesis.

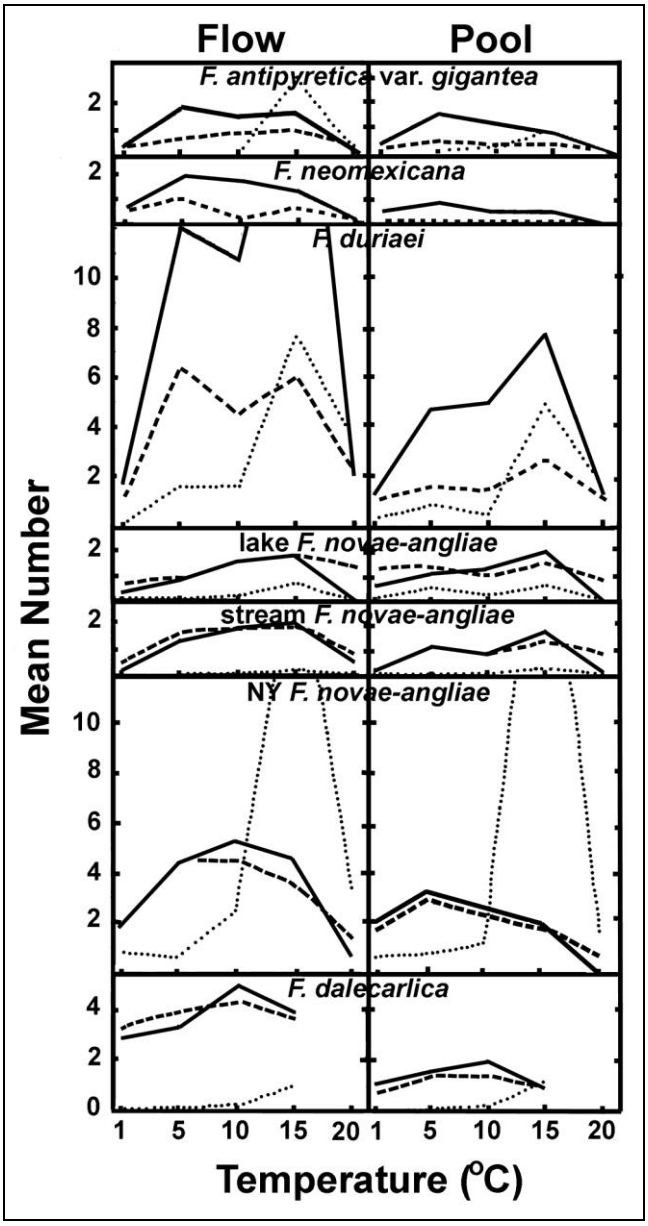

Figure 86. Flow and temperature effects on mean number (40 replicates at each condition) of rhizoid clumps (**dotted line**), branches per cm (**dashed line**), and cm growth of stem + branches (**solid line**) after 15 weeks in flowing water and standing water (pool) conditions in artificial streams. There are no data for ***F. dalecarlica*** at 20ºC. All populations are from the Keweenaw Peninsula of Michigan, USA, except where noted for New York, USA. From Glime & Raeymaekers 1987.

Figure 85. ***Riccia crystallina***, a liverwort in which red light favors production of smooth rhizoids. Photo by Des Callaghan, with permission.

Figure 87. ***Conocephalum conicum*** showing an example of smooth (**upper**) and pegged (**lower**) rhizoids. Photo by Paul Davison, with permission.

On the other hand, **phytochrome** is implicated, not photosynthesis, in controlling rhizoid production, based on research on ***Marchantia polymorpha*** (Figure 88) (Otto & Halbsguth 1976). Production of rhizoids at different wavelengths is subject to the typical red/far-red reversibility that characterizes involvement of phytochrome. Further implication in the role of phytochrome is that application of 10^{-4} M IAA for one hour has the same effect as one hour of red radiation.

Figure 88. ***Marchantia polymorpha*** showing rhizoids. Their production differs depending on wavelength of light and application of IAA. Photo from Botany Website, University of British Columbia, Canada, with permission.

Tropisms

We know a lot about tropisms in protonemata, but that does not seem to be the case for gametophores. As late as 2004, Cove and Quatrano determined that there are no extensive studies on gametophore tropisms. A search in Google Scholar in 2017 confirmed that is still the case, but some genetic studies are helping us to understand tropic responses in bryophytes. We understand that tropisms permit the plant to position its leafy shoot in the best position to obtain the maximum light for photosynthesis (Knight *et al*. 1991).

Early studies by Rawitscher (1932) indicated that ***Marchantia polymorpha*** (Figure 30) exhibits tropic responses to gravity, light and other factors. Miller and Voth (1962) demonstrated negative gravitropism of the thallus of this species. On thalli grown in an inverted position, the gemmae cups curved back toward the thallus. Furthermore, when the thalli were oriented vertically, the gemmae cups curve upward. Position had no effect on rhizoids, internal structure, pores, or position of terminal scales.

Physcomitrella patens (Figure 26) has not escaped tropism studies. Upright stems of this moss exhibit negative gravitropism, with no gravitropic response when the plants are rotated slowly vertically (Jenkins *et al.* 1986). At least three genes appear to be involved in the protonema gravitropism, with mutations in these altering the gravitropic form of the protonema, but none of these mutations affects the gravitropism of the leafy plant.

Genetic knock-out experiments are enabling us to understand many processes in plants, including tropisms in bryophytes. Knight and coworkers (Knight & Cove 1989; Knight *et al*. 1991) used genetic analysis of mutant ***Physcomitrella patens*** (Figure 26) in which the gravitropism was reversed. They found that both protonemata and gametophores respond to re-orientation by growing with negative gravitropism. In the mutant, the protonemata respond, but the gametophores do not, indicating control by mutation of a single gene.

Using ***Physcomitrella patens*** (Figure 26), Bao *et al*. (2015) were able to observe the phototropic response of the gametophore. In this species, the response is slow, taking more than 24 hours after the onset of a directed light source. They attributed the slow response to the slow growth of the moss. They found that red and far-red light were more effective than blue light.

Bennett *et al*. (2014) contributed to the story by experimenting with auxins and auxin transport inhibitors on the gametophytic shoot of ***Physcomitrella patens*** (Figure 26). These disrupt the apical function and leaf development. **PIN-mediated** (a protein) auxin transport regulates apical cell function, leaf initiation, leaf shape, and shoot tropisms in moss gametophytes. PIN mutants sometimes produce sporophytes that are branched, a condition rarely seen among natural moss variants.

In ***Physcomitrella patens*** (Figure 26), we know that cryptochrome signals are important regulators in many stages of moss development (Imaizumi 2002). These include the induction of side branching on protonemata, induction of the leafy gametophyte, and development of the leafy plant. When the cryptochromes are disrupted, auxin responses were altered, including altering the expression of auxin-inducible genes. This study indicates that light signals received by the **cryptochromes** act to repress auxin signals and in that way they control plant development.

In the moss ***Ceratodon purpureus*** (Figure 89), the polarity of the axis from regenerating protoplasts is influenced by the direction of light (Cove & Quatrano 2004). There is a delay in the response when the light direction is changed – a limitation that prevents the stem from tracking the sun as the Earth turns. For example, when protoplasts regenerate in red light at 25°C, there is a delay of about 9 hours before any response is observed. The lag is shorter with far-red light. Their ability to "memorize light direction" indicates use of **phytochrome**. They indicated that the phototropic response "turns off" the gravitropic response in this species and in ***Physcomitrella patens*** (Figure 26).

Figure 89. ***Ceratodon purpureus***, a moss in which polarity is influenced by light. Photo by Michael Lüth, with permission.

Rhizoids locate their substrate by a combination of gravitropism and phototropism, followed by a **thigmotactic** response (contact response) (Glime 1987c). Light can play a strong role in determining the direction of rhizoid growth. In ***Fontinalis squamosa*** (Figure 31), rhizoid growth was strongly photonegative (Figure 90), just as that of roots in tracheophytes. In most cases, this negative phototropism will permit the rhizoids to locate the substrate, which typically occurs in the same direction as the gravitational pull.

Figure 90. Strong negative phototropism of ***Fontinalis squamosa*** rhizoids at broken ends of stems. Photo by Janice Glime.

But in ***Fontinalis squamosa***, direction of light can be overridden by contact. Although the rhizoids were initially negatively phototropic, once they contacted the substrate they continued growing in that direction even when the light was reversed to come through the glass substrate (Glime 1987c).

One might suspect that **gravitropism** (directional growth in response to gravity) could be a cue for direction of growth in ***Fontinalis*** rhizoids, but I have not been able to induce a gravitropic response in ***Fontinalis antipyretica*** or ***F. squamosa*** (Glime 1987c). Instead, a strong negative phototropism occurs, even when it means rhizoids must grow pointed toward the stem apex, as in Figure 90. ***Funaria hygrometrica*** (Figure 2-Figure 3, Figure 54), on the other hand, has positively gravitropic rhizoids (Figure 91) that are indifferent to light (Kofler 1958). ***Funaria*** does not grow on vertical substrata, so gravitropism would be an adaptive feature for ***Funaria***, whereas in ***Fontinalis*** it could be maladaptive for a plant that tends to grow on vertical faces on downstream sides of rocks. On the other hand, light will always be from above in habitats suitable for ***Funaria***, so absence of phototropism may have no selective disadvantage.

Figure 91. ***Funaria hygrometrica*** showing rhizoids growing downward toward gravity. Photo by Jan-Peter Frahm, with permission.

Schofield (1985) has concluded that in general rhizoids are negatively phototropic and positively gravitropic (Schofield 1985). However, this behavior might be different if we look at taxa that typically grow on vertical rocks, as suggested by ***Fontinalis*** (Figure 92) data (Glime 1987c). Despite all the basic physiological work on plant tropisms in protonemata, we know very little about bryophyte tropisms in other parts of the plants.

Figure 92. ***Fontinalis novae-angliae*** becoming established on a rock. Photo by Janice Glime.

Otto (1976) demonstrated several attributes of the rhizoids of gemmae of ***Marchantia polymorpha*** (Figure 30, Figure 93). They always grow from the **ventral** (lower) side – a response that could be either gravity or light driven. However, in alternating gravity in the darkness they form no rhizoids, but when gravity is constant they produce them with or without light. They also respond to contact, producing more rhizoids when contacting the substrate than when growing free in the air.

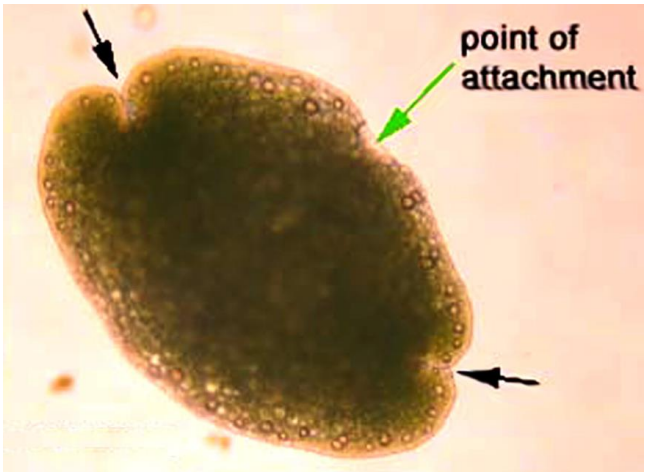

Figure 93. ***Marchantia polymorpha*** gemma. Black arrows indicate apical notches that serve as growing points. Photo by Kavita Uttam, Botany website, UBC, with permission.

Adhesion

Once a bryophyte makes contact with a solid surface, the tips tend to flatten and branch (Figure 94). These branched tips typically produce an adhesive substance that is especially important on vertical surfaces and in streams. Odu (1989) characterized this substance in the leafy liverwort ***Lophocolea cuspidata*** (Figure 95) and determined that it is a sulfated mucopolysaccharide. But attachment to a submersed rock in flowing water is much more challenging. Hence, we might find that this glue is different from that of ***L. cuspidata***.

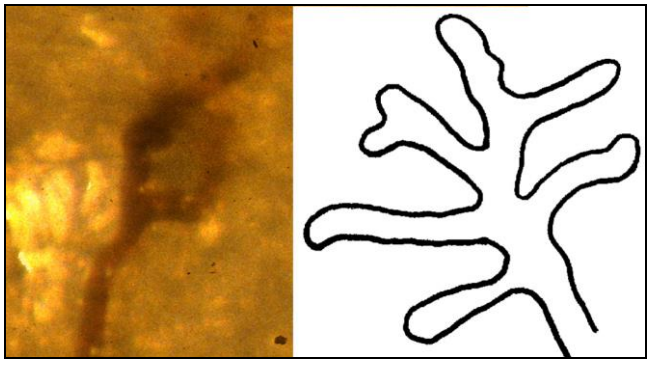

Figure 94. Branched tip of ***Fontinalis squamosa*** rhizoid in response to contact. Photo by Janice Glime; drawing by Margaret Minahan.

It is interesting that the flattened portion of the rhizoid occurs only at the tips in the pleurocarpous mosses, whereas in the acrocarpous mosses it extends far back from the tip (Odu 1989). Yet few acrocarpous mosses occur on vertical surfaces, most likely due to the small area available for adhesion compared to the weight of an outward-growing moss. Pleurocarpous mosses, on the other hand, have abundant surface area in contact with the substrate, and rhizoids typically occur throughout.

Figure 95. ***Lophocolea cuspidata***, a leafy liverwort that produces an adhesive (sulfated mucopolysaccharide). Photo by Jan-Peter Frahm, with permission.

Growth Regulators

Hormones are certainly involved in the differentiation of rhizoids. Maravolo (1980) found that auxins and gibberellic acid both stimulate the formation of rhizoids and cause cell division and elongation. Auxins in tracheophytes are known to stimulate roots and stems differently, so it is not surprising that rhizoids and stems of bryophytes respond differently to the same concentrations. Kumra and Chopra (1987) have shown that in callus cultures, lower concentrations of auxins stimulate differentiation into thalli and rhizoids, but at higher concentrations, only the rhizoids develop. Kaul *et al*. (1962) likewise found that high concentrations of NOA, 2,4−D, TCPA, IBA, and IPA stimulate rhizoid production in ***Marchantia*** (Figure 96). They also found that the responses of rhizoids to growth hormones differed in liquid vs solid culture media. Others have shown that IAA induces rhizoid production in wounded parts of plants (LaRue 1942; Maravolo & Voth 1966).

Figure 96. ***Marchantia polymorpha*** ventral side showing rhizoids. Photo by Botany Website, UBC, with permission.

Contrary to the popular belief that rhizoids function only in anchorage, Rose and Bopp (1983) found that rhizoids actually take up auxins from the environment. They found that the auxins are transported from the tip to the base of the rhizoids, where it accumulates.

Wounding

New growth results in most bryophytes as a result of wounding. In ***Fontinalis*** (Figure 97), this is typically preceded by the production of rhizoids that appear to be highly negatively phototropic. Furthermore, the rhizoids are **thigmotactic**, responding to contact by branching. But to find that surface, they have an interesting growth habit. They grow in a spiral (Figure 97). This spiral permits them to experience a larger area in which to locate a surface to which they need to attach. I am unaware of this behavior in other bryophytes, and it may indeed be peculiar to aquatic bryophytes.

Figure 97. Rhizoids on an explant of ***Fontinalis squamosa***, exhibiting spiral growth from the cut stem. Photo by Janice Glime.

LaRue (1942) has shown that in liverworts wounding induces rhizoids. He also showed that 1% IAA induced rhizoids all over the setae and capsules of ***Amblystegium*** sp. (Figure 98). IAA is produced by the breakdown of tryptophan in dying cells (Sheldrake 1971), and Maravolo and Voth (1966) have shown that IAA stimulates rhizoid production in gametophytes. In ***Fontinalis*** (Figure 100), I have found that my explants always produce rhizoids at or near the broken lower end of a stem piece, as in Figure 97, suggesting a polar substance such as IAA is responsible. However, the ultimate effector could be IAA-induced ethylene. Disintegrating xylem is a major source of IAA, as a result of tryptophan breakdown, so that this may be an important source for some bryophytes that establish primarily on rotting logs.

Numerous experiments show that ethylene levels rise as a result of wounding. In fact, most experiments on plants probably begin with elevated ethylene due to handling by the experimenter. If this is true, what occurs in a moss subjected to continual stress of a fast current? Using artificial streams in the laboratory, Glime and her students (Glime *et al*. 1979) found that rhizoids of several aquatic mosses [***Hygroamblystegium fluviatile*** (Figure 99), ***Fontinalis duriaei*** (Figure 100)] began to adhere to rocks after about 9 weeks and little additional attachment occurred after 14 weeks of contact (Figure 101). In these experiments, pieces of freshly wounded moss were tied to the rocks to insure contact and maintain their location. Odu (1978b) found a much shorter period of rhizoid growth for ***Calliergonella cuspidatum*** (Figure 102), ***Pleurozium schreberi*** (Figure 103), and ***Brachythecium rutabulum*** (Figure 104), species that grow mostly on soil or in standing water. Their rhizoid growth rates leveled off after about 6 weeks, and after 10 weeks there was no further growth.

Figure 98. ***Amblystegium radicale***. Photo by Des Callaghan, with permission.

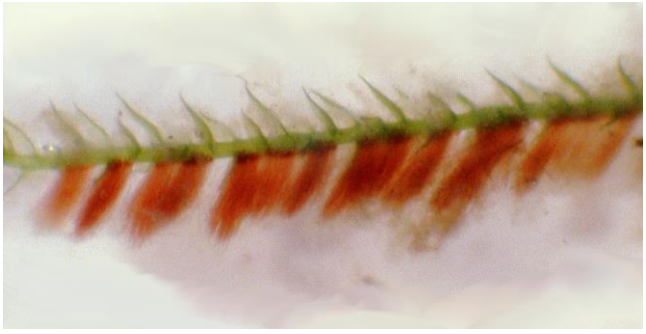

Figure 99. ***Hygroamblystegium fluviatile*** with rhizoids grown in culture. Photo by Janice Glime.

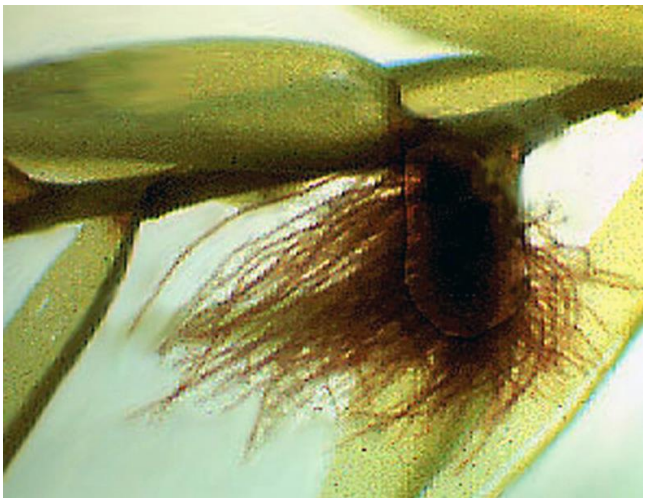

Figure 100. ***Fontinalis hypnoides*** rhizoids produced in culture. Photo by Janice Glime.

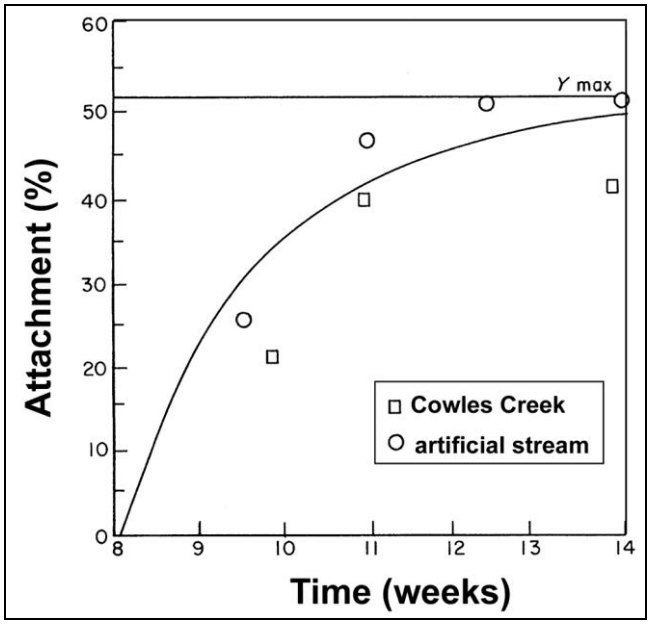

Figure 101. Model for rhizoid attachment to four rock types (shale, granite, basalt, sandstone – data combined) in ***Fontinalis duriaei*** in a natural and an artificial stream. n = 12 for each rock type and each stream. Based on Glime *et al.* 1979.

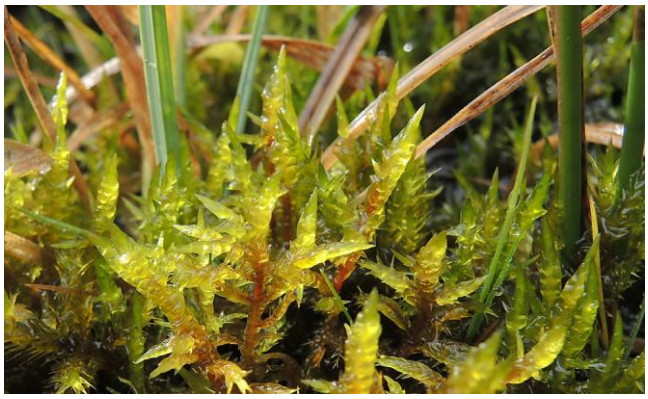

Figure 102. ***Calliergonella cuspidata*** in its typical habitat. Photo by Michael Lüth, with permission.

Figure 103. ***Pleurozium schreberi***, a ground-dwelling species with rapid rhizoid development. Photo by Sture Hermansson, with online permission.

Habitat Conditions

Odu (1978a, 1979) has found that acrocarpous mosses produce rhizoids all the way around the stem, but these are generally restricted to the stem base (Figure 106-Figure 105). These patterns are adaptive to the growth habit since acrocarpous mosses grow outward from a substrate and therefore can utilize only basal attachment. Compare that to the ventral positions in the two pleurocarpous mosses in Figure 99 and Figure 100. But substrate is not the only determining factor in rhizoid form. Acrocarpous moss rhizoids typically are longer, due to longer cells, than those of pleurocarpous mosses, even on vertical substrata (Figure 107; Odu 1978a).

Figure 104. ***Brachythecium rutabulum***, a ground- and rock-dwelling species with rapid rhizoid development. Photo by J. C. Schou, with permission.

Figure 105. ***Bryum*** sp. showing rhizoids that surround the stem at base. Photo by Michael Lüth, with permission.

Figure 106. ***Cyrtomnium hymenophyllum*** demonstrating rhizoids that surround the stem at base. Photo by Michael Lüth, with permission.

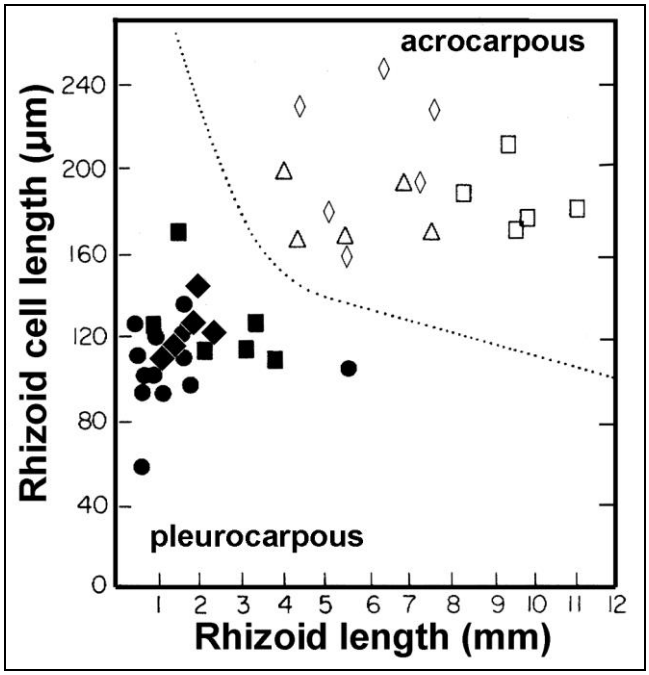

Figure 107. Relationship of cell length to rhizoid length in acrocarpous (◊***Bryum capillare***, Δ***Pohlia nutans***, □***Dicranum scoparium***) and pleurocarpous (●***Hypnum cupressiforme* var. *cupressiforme***, ■***Rhynchostegium confertum***, ♦***Homalothecium sericeum***) mosses, showing the greater length typical of acrocarpous mosses. Means are of 50 cells with 10 rhizoids used per species. Redrawn from Odu 1978a.

Figure 108. ***Hypnum cupressiforme*** on one of its many substrates. Photo by Dick Haaksma, with permission.

Mosses that grow prostrate on hard substrates typically develop rhizoid tufts (Odu 1978a), as seen for ***Fontinalis*** (Figure 100). In some cases these fuse, creating even greater physical strength. Pleurocarpous mosses generally produce rhizoids on only one side of the stem and these can occur throughout the stem (Odu 1979), as they do in most Jungermanniopsida (leafy liverworts; Schuster 1966). They have a **dorsi-ventral** (top-bottom) orientation so that if a pleurocarpous moss is turned upside down, its rhizoids initially grow from its new **dorsal** (upper) surface and then bend downward. However, eventually the stem itself twists so that it once again has the original ventral side next to the ground (Odu 1979). This twisting takes 5-18 days to turn 90º in ***Hypnum cupressiforme*** (Figure 108) and 10-30 days to turn 180º. Rhizoid production increases on the new growth in this twisted position. This twisting indicates that the stem has a top-bottom polarity that controls rhizoid orientation and that the growth of the rhizoids on that side of the stem is not a tropic response. Even in pleurocarpous mosses that initially grow upright, such as ***Pleurozium schreberi*** (Figure 103) and ***Calliergonella cuspidatum*** (Figure 102), rhizoids grow on only one side of that vertical stem. That upright stem eventually becomes the horizontal stem and the rhizoids are on the ventral side. In ***Funaria hygrometrica*** (Figure 2-Figure 3, Figure 54), rhizoids of germinating spores formed toward the positive electrode (Chen & Jaffe 1979), suggesting that this polarity may begin at the spore stage.

Based on Odu's (1978b, 1979) observations, I predicted that the pleurocarpous ***Fontinalis*** (Figure 31) should have rhizoids arising on all sides of the stem, since moving water prevents it from having one side that is always down. That is exactly what I observed in my culture experiments (Figure 109) (Glime 1980). Such an arrangement in stream mosses facilitates attachment in moving water. But how do these rhizoids attach without wasting energy by growing in all the wrong directions? Perhaps the rhizoids release ethylene upon contacting a substrate and the ethylene serves to inhibit further lengthening and instead serves to thicken the cells to provide a more secure attachment. We know, in fact, that once the rhizoids of ***Fontinalis squamosa*** (Figure 94, Figure 97) contact a surface they branch prolifically and attach (Glime 1987c; Figure 94). This is consistent with observations of Odu and Richards (1976) on the leafy liverwort ***Lophocolea cuspidata*** (Figure 95) and the mosses ***Hypnum cupressiforme*** var. ***cupressiforme*** (Figure 108) and ***Platyhypnidium riparioides*** (Figure 110) that respond similarly to contact.

The number of rhizoids produced by gametophores is also related to substrate. Odu (1978a, b) found that mosses that grew on boulders or tree trunks produced more rhizoids than did those on soil. When several species were moved from boulders to soil, they produced fewer rhizoids.

Stream mosses often produce abundant rhizoids (Figure 99-Figure 100), but taxa from other wet habitats often lack them. This absence is typified by such genera as ***Sphagnum*** (Figure 6-Figure 7) and ***Drepanocladus*** *s.l.* (Figure 111). The only species of ***Sphagnum*** known to have rhizoids is an epiphyte. If wet habitat species are grown out of water, will rhizoids develop? I tested this by gathering submersed ***Drepanocladus exannulatus*** (Figure 111) with no rhizoids and placing explants on a Petri plate of inorganic nutrient agar. Rhizoids appeared. Thus rhizoids in ***D. exannulatus*** seem to be under environmental control.

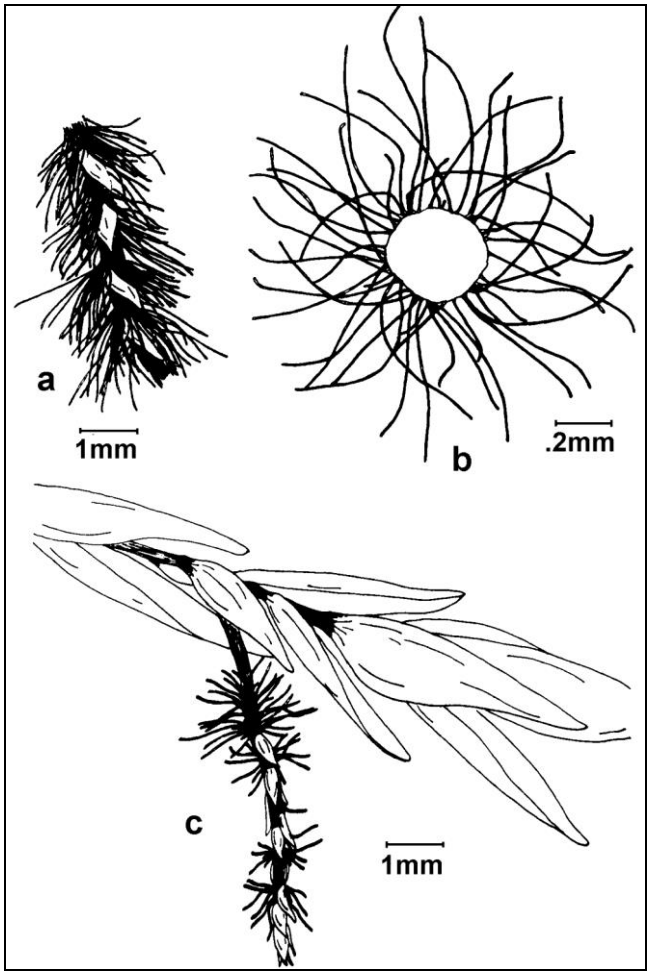

Figure 109. Rhizoids of ***Fontinalis*** on stoloniferous branches. **a**. ***Fontinalis dalecarlica***. **b**. cross section of stoloniferous branch of ***Fontinalis dalecarlica***. **c**. ***Fontinalis novae-angliae***. From Glime 1980.

Figure 110. ***Platyhypnidium riparioides***, a rock-dwelling species that produces rhizoids in response to contact. Photo by Hermann Schachner, through Creative Commons.

My observations on ***Fontinalis hypnoides*** (Figure 100) (Glime 1980) help to explain the control of rhizoid production in the aquatic habitat. The number of rhizoids increased with temperature when cultured at 1, 5, 10, 15, and 20°C. Furthermore, mosses in flowing water produced more rhizoids than those in standing water. The latter observation might be explained by **ethylene** control, since ethylene is known as an inhibitor of rhizoid elongation in ferns (Miller *et al*. 1970). In our experiments on ***F. squamosa*** (Figure 31), **ACC** (ethylene precursor) inhibited rhizoid production with increasing concentrations in cultures on wet filter paper, and the inhibition was more severe in mosses in water (Glime & Rohwer 1983). Since ethylene is not very soluble in water, it could easily accumulate around the moss and be a cause for the retardation of rhizoids in standing water, whereas flowing water would remove the ethylene. On the other hand, this removal action must counteract the increased production of ethylene we might expect to result from the mechanical stress of flowing water. But no one has demonstrated that mechanical stress does indeed induce ethylene production in bryophytes, as it does in tracheophytes. And we can reasonably expect the effective concentrations are different in bryophytes. Just as roots and shoots respond differently in tracheophytes, different parts of bryophytes can respond differently from each other and from parts with similar functions in tracheophytes.

Figure 111. ***Drepanocladus exannulatus***, a species that is devoid of rhizoids under water, but that can produce them when grown on an agar substrate. Photo by Michael Lüth, with permission.

Rhizoids seem to have evolved in adaptive ways to fit the habitats of their owners. Acrocarpous mosses that generally are upright have rhizoids that surround the base of the stem; pleurocarpous mosses that generally grow horizontally produce rhizoids only on their lower sides. The aquatic pleurocarpous moss ***Fontinalis*** produces them all around the stem, enabling it to attach from whatever side makes contact with a substrate. Mosses that grow on vertical substrata produce numerous rhizoids. Many mosses, especially on vertical substrata, have rhizoids that branch upon contact, permitting them to occupy a greater cementing surface. Stream mosses produce many rhizoids, whereas quiet-water species usually lack them, and this can differ within the same species in response to flow. Quiet water species may similarly produce rhizoids when growing out of the water. ACC inhibits the production of rhizoids, suggesting ethylene may be involved in these environmental responses.

Conduction

If ***Dicranella heteromalla*** is in any way typical of mosses, we have been underselling the role of the bryophyte rhizoid. Rather than simply anchoring the mosses, it appears that they may have important roles in nutrient absorption (Duckett & Matcham 1995). Their structure is very similar to that of food-conducting cells in leafy gametophyte stems and sporophytes. From this they suggested that the major role of the rhizoids might be solute uptake.

Bryophyte Senescence

Senescence is the process in which the cell reaches a state wherein it cannot undergo either progressive or regressive development and its only future change will lead toward death of the cell (Giles 1971).

Only in bryophytes can the lower part of the plant be completely dead while the upper part is still very much alive. ***Sphagnum*** is a classic example, exhibiting healthy, reproductive tops and dead bases, decades old (Figure 112). In mosses such as ***Hylocomium splendens*** (Figure 113), one might find 4-7 years of live growth atop several more years of senescent or dead plant.

Figure 113. Living plants of ***Hylocomium splendens*** forming a turf on top of their own senesced branches (**arrow**). Photo by Michael Lüth, with permission.

Figure 112. ***Sphagnum girgensohnii***, showing dying and dead lower parts. Photo by Bernd Haynold through Wikimedia Commons.

Figure 114. Mature capsules that mark the onset of senescence in ***Tetraphis pellucida***. Photo by Janice Glime.

At least in some taxa, the initiation for senescence results from the production of male gametangia or capsules. In many acrocarpous mosses, these structures can effectively prevent further growth of the plant by occupying what would have been the region of apical growth, as shown for ***Tetraphis pellucida*** (Figure 114) (Kimmerer 1991). In this species, high density increases sexual reproduction, which increases capsule production and proportion of males, which in turn initiate senescence for the population. Some mosses overcome this apical growth termination by producing innovations – side branches near the tip that become new tips and continue the growth upward (see chapter on gametophore development).

As in higher plants, it appears that ethylene induces senescence, as shown in ***Marchantia*** (Figure 30) (Stanislaus & Maravalo 1994). Spermine, spermidine, and putrescine can reverse it. If we dare to generalize from this meager example, the story makes sense. As the moss grows and the cushion or mat (or whatever) becomes more dense, there is less and less air movement in the lower part of the growth form (see Figure 115). This permits gases to accumulate, so if ethylene is being produced, this surely is a place for it to reach higher concentrations. Now all we need to do is show that indeed there is ethylene given off here, that it accumulates, that it reaches high enough concentration, and that it indeed induces senescence in most (all?) bryophytes!

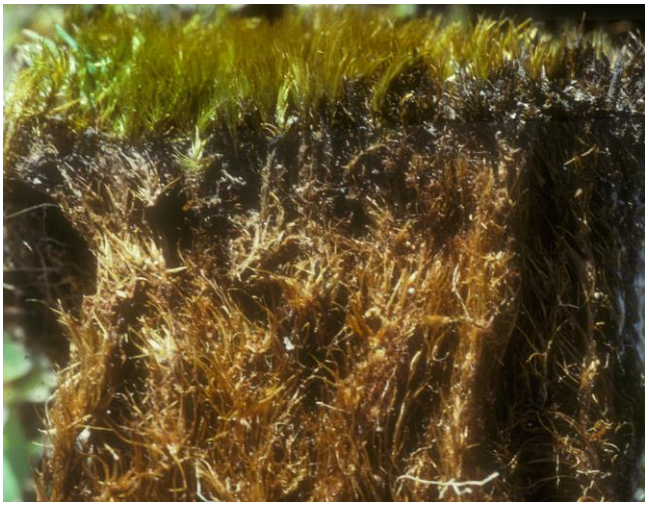

Figure 115. Senescence in lower, brown portion of ***Dicranum scoparium***. Photo by Janice Glime.

Ecological Interaction

External factors may control differentiation and growth of gametophores in bryophytes. The physical effects of accompanying plants are widely recognized. However, with sensitivities at such microlevels as affect bryophytes, exudates from other organisms also have the potential to effect changes in developmental patterns. This might be especially true if dying plants leak substances that collect on the surfaces of the bryophytes, dissolved only in the adhering humidity and readily absorbed by the mosses in what would, under these circumstances, be relatively high concentrations. Nevertheless, although the potential seems relatively high, few studies have addressed these potentials.

The presence of other plants will naturally affect moisture and light availability. In general, other plants help to maintain a more humid environment than would be available if the bryophyte were directly exposed to air. This seems to be accomplished mostly by maintaining a small space in which air movement is reduced, thus reducing the evaporation rate from the bryophyte. In ***Brachythecium*** (Figure 104) populations, litter of the stinging nettle (*Urtica*) stimulates growth (Willis 1978). Willis attributes this added growth to moisture and nutrient release, but we cannot rule out the possibility of hormonal interaction as well.

The reduction in light caused by accompanying plants may provide an advantage by reducing the destructive effect of UV light when the bryophyte is dry. However, when the surrounding plants become too dense, they can effectively block the light and also prevent the bryophyte from occupying the substrate, thus crowding it out. Deciduous trees are very effective at this by losing their leaves and completely covering the bryophytes, thus preventing them from getting any light. They may further inhibit bryophyte growth during decay by releasing humic acids that can inhibit growth (see discussion under spore germination), or possibly even releasing growth regulating substances. Whatever their action, leaves seem to be destructive to my moss garden if I leave them there over winter, even if I remove them as soon as the snow melts. Considerable decay occurs during that snow-covered period.

Leaf litter seems to be the major cause for the paucity of bryophytes on the forest floor in a deciduous forest. Bryophytes there are restricted to elevated areas such as rocks or slopes where leaves do not collect. In one set of experiments to determine what species of plants would grow following a disturbance similar to a tip-up hole (from a tree falling over), researchers dug holes in the forest floor. Bryophytes invaded the holes, but only on the sides. Litter collected on the bottoms of the holes, and although tracheophytes germinated there, no bryophytes succeeded.

Sheldrake (1971) has suggested that natural exogenous hormones could be important in bryophyte distribution. He found **IAA** in many substrates inhabited by bryophytes, and he concluded the IAA was not produced by the bryophyte because the same concentrations occurred without bryophytes. Garjeane (1932) noted that contact with soil and decaying vegetation stimulated rhizoids in liverworts, and Maravolo and Voth (1966) showed that liverwort rhizoid length and rhizoid formation are stimulated by IAA. Therefore, bryophytes might grow better in microhabitats where these hormones collect. Disintegrating xylem is a major source of IAA, so this may be a contributing factor to the luxuriant growths of liverworts on logs in moist woods.

Odu (1978b) found that living tracheophytes had just the opposite effect on moss rhizoids. Mosses transplanted from grassland to bare soil increased their number of rhizoids and those transplanted from boulders to bare soil produced more rhizoids than those transplanted to grasslands. It would seem that IAA was not the inhibitor involved since we have already seen that it stimulates rhizoids, but perhaps concentration is a factor. Furthermore, bare soil may have more available IAA as a result of bacterial breakdown of organic matter (Sheldrake 1973), with a cover of grass depriving the mosses of access (Odu 1978b). On the other hand, an easily diffusible substance such as **ethylene** could account for the ability of living plants to inhibit the rhizoids, since no inhibition occurred on soil with plants removed but with the litter remaining.

Neighboring plants can affect bryophyte growth by altering the available light and level of humidity. They can serve as a filter, protecting the bryophytes from damaging UV rays. The environment experiences a wide range of exudates from the plants that live there, undoubtedly influencing development of some bryophyte taxa. Litter provides humic acids that are known to inhibit bryophyte growth, and decaying xylem releases IAA that can stimulate rhizoid production. Crowding is likely to create patches of elevated ethylene that could be inhibitory to bryophyte development.

Summary

Growth in bryophytes is both stem and branch growth, making it non-linear, but can also be a weight gain without any elongation. Growth in very low light causes etiolation. Water and light are necessary for growth, with a wide range of light being optimal among

the various taxa. A common optimum seems to be around 3500-5500 lux for shade-adapted taxa.

Stems usually exhibit a strong positive phototropism and negative gravitropism, whereas rhizoids exhibit the opposite. Short or long photoperiods may induce dormancy, depending on the habitat and species.

Bryophytes respond to most of the same hormones as tracheophytes but at different, usually lower, concentration levels. Among other things, IAA enhances growth, cytokinins stimulate buds, gibberellins affect rhizoid growth and form, and ethylene causes senescence and in leafy liverworts inhibits dorsal leaf development. These hormones furthermore affect each other's actions. Many bryophytes exhibit apical dominance, facilitated by IAA. In addition, the form in which N is available can alter the growth form, branching, and growth rate.

Apical sexual structures usually terminate growth of that stem, but innovations (new branches near the tip) can cause the plant to continue growth and may facilitate lateral spread.

Humidity, light, salt concentration, and nutrients all influence the leaf shape, hairs, and color, and can cause the species to appear to be a different one in a different habitat.

Rhizoids respond to contact with a substrate by flattening and widening their tips, branching, and halting growth in other directions. Wounding causes the production of rhizoids and/or protonemal growth at the site of the wound.

Leaf litter inhibits the growth of bryophytes, in part by blocking light, but apparently also by depositing humic substances that are inhibitory or even lethal. In other cases, other plants, fungi, or bacteria in association with the bryophytes provide them with needed hormones.

Bryophytes are the only plants where the lower portion of the plant can be senescent or dead and still maintain a healthy upper portion.

Acknowledgments

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CHAPTER 5-6

ECOPHYSIOLOGY OF DEVELOPMENT: FRAGMENTS

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CHAPTER 5-6

ECOPHYSIOLOGY OF DEVELOPMENT: FRAGMENTS

Figure 1. ***Dicranum viride***, a moss that fragments regularly by a row of abscission cells across the upper half of the leaf. Note the broken leaf tips. Photo by Michael Lüth, with permission.

Fragmentation

Fragmentation may be random pieces that break due to abrasion, decay, or animal severance, or they may be programmed genetically by means of an abscission layer such as demonstrated in ***Dicranum viride*** (Figure 1). In certain habitats, fragmentation may be a regular phenomenon, accounting for nearly all the reproduction.

Even fossil evidence supports the importance of fragments in the dispersal and reproduction of bryophytes (Miller 1985). And buried fragments often retain viability, providing the source for the flora when a disturbance returns an area to previous conditions (Wasley 2004).

Yet, when we diagram life cycles, fragmentation is usually ignored, and certainly for many flowering plants it is unimportant. However, in bryophytes it is often the fragments that perpetuate the species. Likewise, Giordana and coworkers (1996) found that regeneration from the detached leaves was the major form of regeneration in moss ***Pleurochaete squarrosa*** (Figure 2). Other bryophytes, such as ***Hyophila crenulata***, share their successful regeneration from fragmentation with other means such as gemmae (Olarinmoye 1981).

Mishler and Newton (1988) contend that in perennial mosses reproduction and spreading is almost entirely by means other than spores. Many populations exist for which capsules are unknown, particularly for dioicous taxa (having males and females on separate plants; unisexual). Even when all individuals in the population can produce both sexes (monoicous; bisexual), water is needed at the right time for sperm and egg to meet, so success rate will vary with habitat and with weather in a given year. Newton and Mishler (1994) suggest that vegetative reproduction, including specialized propagules, can occur

under more stressful conditions. Whereas spores germinate best on previously uncolonized substrates, vegetative reproductive units can do well even in contact with existing colonies. However, they suggest that such vegetative units cannot travel as far as spores – tradeoffs again.

Figure 2. ***Pleurochaete squarrosa***, a moss that relies on detached leaves for regeneration. Photo by Michael Lüth, with permission.

Some mosses even provide special means to accomplish fragmentation. ***Dicranum viride*** (Figure 1), ***D. fragilifolium*** (Figure 3), and ***Tortella fragilis*** (Figure 4) have a weakened area of cells that break easily, releasing the upper portion of the leaf. This is so typical that these species can be identified by their chopped off appearance. Other species have **caducous** leaves (leaves that normally detach).

Figure 3. ***Dicranum fragilifolium*** on rock, showing broken leaves. Photo by Janice Glime.

Figure 4. Broken tips on leaves of ***Tortella fragilis***. Photo by Michael Lüth, with permission.

The success of fragments within short range (Newton & Mishler 1994) is supported by experiments by Nehira and Nakagoshi (1987). They removed a community of bryophytes and found that the community became re-established within 1-2 years. Most of the growth occurred in spring and autumn despite little seasonal variation in propagule dispersal. Thallose liverworts and pleurocarpous mosses were able to regenerate more quickly than the acrocarpous mosses. Yet these same fragments may have been eaten or decayed before ever growing if the researchers had not removed the parent colony. Newton and Mishler (1994) found that at least for the dry habitat mosses they studied, the parent plants seemed to inhibit growth of the fragments, with growth commencing once they were separated.

Fragmentation is likely to determine success of the species in some environments. Miles and Longton (1990) found that ***Funaria hygrometrica*** (Figure 5) reproduced and spread easily by spores, whereas ***Atrichum undulatum*** (Figure 6) and ***Bryum argenteum*** (Figure 7) were likely to experience failure before sporelings produced gametophores. On the other hand, these latter two species freely accomplished regeneration from shoot fragments. This ability of ***Atrichum*** to regenerate easily from leaf fragments permitted it to dominate the ground cover rapidly after the construction of a parking lot on the Michigan Technological University campus (Glime 1982). ***Funaria hygrometrica***, on the other hand, apparently manages to arrive, presumably by spores, and colonize charred ground within a year after a fire, as occurred after the big Yellowstone fire (Glime pers. obs.).

Figure 5. ***Funaria hygrometrica***, demonstrating the prolific production of capsules. Photo by Niels Klazenga, with permission.

Even on rocks, where one might expect a small spore and protonema to have more success than a large fragment, it seems that fragments dominate the reproductive success. Keever (1957) did find that spores germinated on granite, but colonization through fragmentation was more rapid. One such rock-dwelling (and bark-dwelling) species is ***Orthodicranum montanum*** (Figure 8). Chrobak and Sharp (1955) established that this species grew well from leaf fragments. The proximal (basal) half of the broken leaf was more successful than whole leaves or the distal portion of the leaf (Figure 9).

Figure 6. ***Atrichum undulatum*** with drying plants that can break more easily than hydrated plants. Photo by Michael Lüth, with permission.

Figure 7. ***Bryum argenteum***, a moss that easily loses its tips as dispersal units. Photo by Janice Glime.

Figure 8. ***Orthodicranum montanum*** on bark. Photo by Janice Glime.

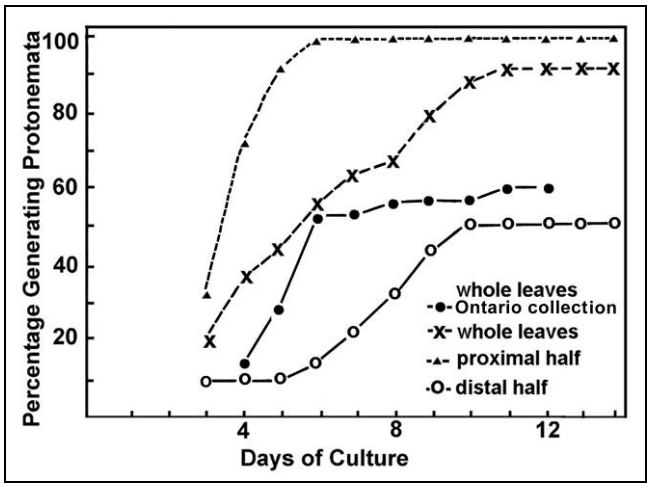

Figure 9. Success of producing protonemata from various leaf parts of ***Orthodicranum montanum*** from Michigan, USA, and Ontario, Canada. Redrawn from Chrobak & Sharp 1955.

Arctic and Alpine

Mogensen (1986) found that ***Platydictya*** (Figure 10) was dispersed in Greenland primarily by vegetative propagules and Bonde (1959) found viable ***Polytrichum piliferum*** (Figure 11) fragments among the wind-blown debris of a Colorado glacier. Lindskog and Eriksen (1995) found that the fragments of mosses, in particular, that were on the glacier reflected accurately the composition of the surrounding vegetation.

Figure 10. ***Platydictya jungermannioides***. Photo by Des Callaghan, with permission.

Figure 11. ***Polytrichum piliferum***, a moss that reproduces by fragments on the Colorado Glacier. Photo by David T. Holyoak, with permission.

McDaniel and Miller (2000) demonstrated the importance of fragments in alpine areas of the Adirondack Mountains of New York, USA, and suggested that fragments dispersed in winter might be a significant means of establishing new populations following spring snowmelt. It would certainly much easier for fragments to glide across a snow pack than to travel amid ground vegetation.

In the Arctic, fragments on the ice are common, and are easily moved around over the smooth surface, permitting rapid transport over considerable distances. Miller and Howe Ambrose (1976) found that fragments of mosses were distributed across the snow by wind on Bathurst Island in the Canadian high Arctic. They were able to grow these fragments in culture, with only 12% of the fragments producing evidence of viability by growth of protonemata, shoots, or rhizoids. The leaf-bearing tips of leafy shoots were the most likely to produce new growth. Nevertheless, this yielded an estimate of more than 4000 viable fragments per cubic meter of snow! Liverworts, however, did not fare as well, with only one fragment producing new growth. They surmised that such moss fragments may be "routine" in Arctic climates.

The importance of fragments may reach its climax in the Antarctic. In colonizing a new Antarctic volcanic island, fragments of ***Campylopus*** (Figure 12), ***Marchantia***, (Figure 13) and ***Bryum*** (Figure 7) species seemed to be the most important means of arrival (Smith 1984).

Figure 12. ***Campylopus pilifer*** showing fragments formed by tips of plants. Photo by Michael Lüth, with permission.

Figure 13. ***Marchantia polymorpha*** with dead portions that can create fragments. Photo by Michael Lüth, with permission.

In Antarctica on Mt. Rittmann, ***Pohlia nutans*** (Figure 14-Figure 17) only establishes on geothermally heated ground (Skotnicki *et al*. 2002). The geothermal heat (17-35°C) permits the moss to survive. It is apparently dispersed only by fragments (Figure 16-Figure 17) from elsewhere in Antarctica.

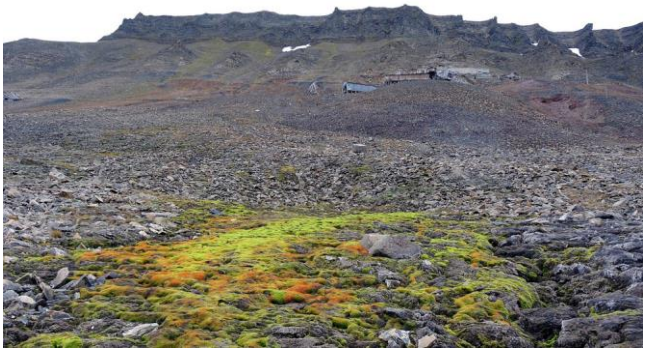

Figure 14. ***Pohlia nutans*** below old mine on Svalbard (Arctic). Photo by Michael Lüth, with permission.

Figure 15. ***Pohlia nutans*** on Svalbard (Arctic), a species often spread by fragments. Photo by Michael Lüth, with permission.

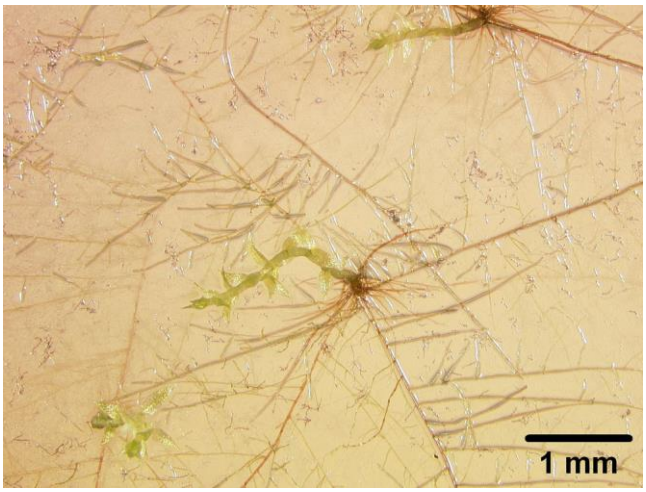

Figure 16. ***Pohlia nutans*** fragment and protonemata with buds and developing gametophores. Photo by Sean Robinson, with permission.

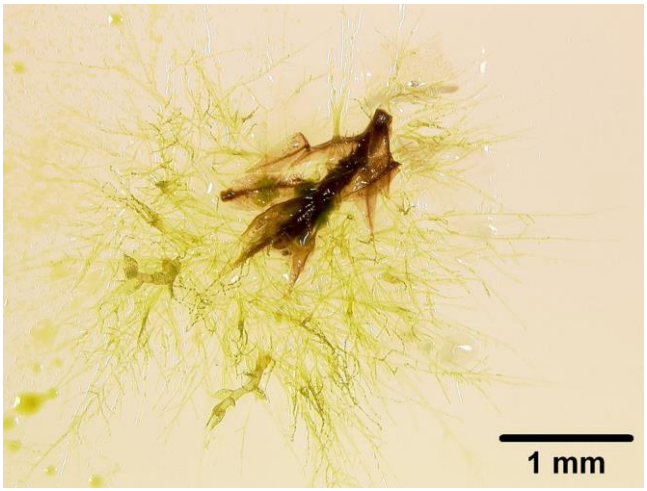

Figure 17. ***Pohlia nutans*** fragment and protonemata with buds and developing gametophores. Photo by Sean Robinson, with permission.

Figure 18. Fragments of ***Fontinalis dalecarlica*** caught in ice of a stream. Fragmentation appears to be its primary form of dispersal and new establishment. Photo by Janice Glime.

Streams and Other Aquatic Habitats

In flowing streams, sporophytes seem rare, and asexual propagules seem to be unimportant. However, significant dispersal can occur from fragments during spring runoff, and entire clumps as well as branches and smaller fragments become impinged on rocks and roots in the stream. The larger surface area of fragments makes it more likely that they will become lodged than will the small spores and asexual propagules. Glime *et al*. (1979) demonstrated that for ***Fontinalis duriaei*** these actually do become established in nature, occasionally even achieving upstream movement (by feet of bears?).

For aquatic mosses and liverworts, fragmentation may be the only means of reproduction for many years before appropriate conditions exist for completing sexual reproduction. In dioicous mosses such as ***Fontinalis***, sexual reproduction seems to be so infrequent as to be totally ineffective as a means of providing dispersal units (spores), whereas fragments are numerous during times of ice melt and high water (Figure 18; Conboy & Glime 1971, Glime *et al.* 1979, Glime & Knoop 1986). Even when spores are produced in this genus, the spore faces numerous challenges in becoming located where its subsequent protonema will neither be washed away nor desiccated, and sufficient light will be available for development. Since there is no documentation of the occurrence of any protonema of any ***Fontinalis*** species in the field, we can only conjecture about the success of reproduction by spores in this genus.

Dedifferentiation

Dedifferentiation is the process involved in the return of a cell to its embryonic state (Figure 19). It is necessary before a mature cell can form into a different kind of cell, or into a protonema, permitting the development of new plants from fragments. In bryophytes, virtually all cells seem to have the ability to undergo dedifferentiation once they have been isolated from the intact plant (Giles 1971). This is not the case for cells such as xylem elements of tracheophytes, which no longer have protoplasm and hence are non-living.

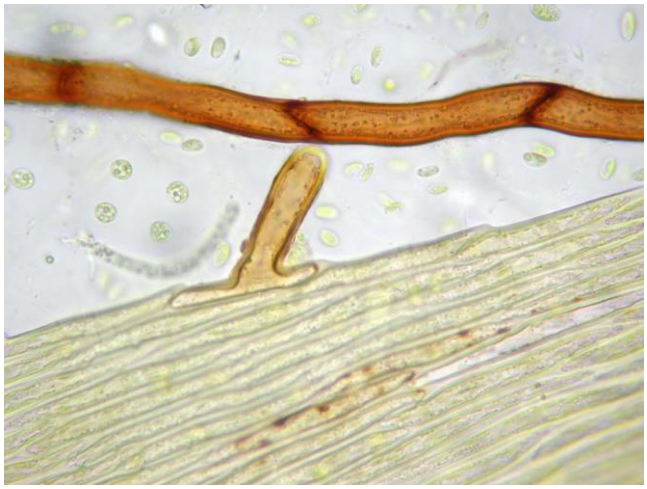

Figure 19. ***Warnstorfia fluitans*** leaf fragment with rhizoid that has dedifferentiated and redifferentiated into a different kind of cell. Photo by Heike Hofmann © swissbryophytes <swissbryophytes.ch>, with permission.

Moss fragments seem to retain their polarity, resulting in protonemata at the apical end and rhizoids at the basal end, but inverting them causes the base to act as the apex and vice versa (Westerdijk 1907), suggesting a gravimetric response by some growth factor. Mosses tend to have more regenerative ability at the base of the gametophyte than at the apex. Their sporophytes, however, are strongly polar in regeneration (von Wettstein 1924). Liverworts, on the other hand, seem to be much more strongly polar, and new growth is nearly restricted to the apical end of the gametophytes, but the sporophyte seems to lack polarity (Giles 1971). This strong polarity of the liverwort gametophyte regeneration, however, decreases with tissue age (Kreh 1909).

Earliest known reports on regeneration from bryophyte fragments come from Necker in 1774 (Giles 1971). Kreh (1909) showed that for liverworts, every part of the plant except the antheridia could regenerate. Nevertheless, few reports of liverwort regeneration from fragments are known. In mosses, even the seta will regenerate into a protonema, forming diploid gametophytes (von Wettstein 1924).

It is common for the nuclei to increase in size in dedifferentiating cells (Giles 1971). The dedifferentiation process involves a sort of "budding" of the chloroplasts and mitochondria, producing more of these organelles. At the same time, nucleolar volume increases only in regenerating cells. We now understand that the nucleolus is not an organelle in its own right, but rather that it is the site of extensive protein synthesis, hence staining more densely. This is an indication of building activity in the regenerating cell.

In ***Campylopus pyriformis*** (Figure 20) fragments, it is the chloronema that gives rise to buds, with no caulonema forming. By contrast, and unlike the growth from a spore, the caulonema of ***Plagiomnium affine*** (Figure 21) grows nearest the plant fragment and the chloronema is the farthest and youngest tissue (Sironval 1947; Bopp 1959a,b; Giles 1971). The ensuing buds develop, therefore, nearest the leaf fragment from the caulonema. Up to 100 secondary protonemata may originate from the dedifferentiated leaf cells of a single leaf in this species.

Figure 20. ***Campylopus pyriformis*** showing fragments of branch tips. Photo by Michael Lüth, with permission.

Figure 21. ***Plagiomnium affine***, a moss that develops protonemata from fragments. Photo by Janice Glime.

Secondary Protonemata from Fragments

Secondary protonemata are those produced from mature tissues that have been damaged or cut. Hence, these protonemata develop on fragments. At first thought, one might expect that these would behave in the same way as primary protonemata (produced from a spore), but further consideration should remind us that fragments provide a large store of nutrients, including energy sources, from the plant fragment.

Like primary protonemata, the secondary protonemata of the moss ***Tortula modica*** is negatively gravitropic in the dark (Ripetskyj *et al*. 1999). When placed in the light, the apical parts of the protonemata begin to branch and apical cells of side branches and main protonemal filaments frequently differentiate as buds. One might consider this event as being possible because of the energy sources available from the fragment. When the fragments were illuminated from below, an intensity of at least 4.5 μmol m-2 s-1 was necessary to induce phototropism and light-directed development of branch buds and directed growth of side branches. In lower light intensities the apical cells grew away from the light (*i.e.*, away from gravity as well).

To further understand the role of spore grown vs secondary protonemata, Wagner and Sack (1998) grew the moss ***Ceratodon purpureus*** from protoplasts. In these protoplasts, the emerging filament was mostly gravimorphic, with more than 66% of the filaments emerging above the horizontal. The tip-growing cells of these filaments began to exhibit a gravitropic response within 1-2 cell divisions. But in these filaments, plastid sedimentation did not occur, contrasting with dark-grown filaments.

Gravity Effects

As we might expect, based on studies on protonemata, secondary protonemata also respond to gravity. In ***Tortula modica***, the secondary protonemata are negatively gravitropic in the dark (Ripetskyj *et al*. 1999). In the light, these protonemata branch near the apical cells and these branch tips typically differentiate as buds. A light intensity of at least 4.5 μmol m^{-2} s^{-1} was required to induce phototropism in apical cells, cause light-directed initiation of branch primordia, and direct development of side branches and bud initiation. At lower light intensities, the apical cells grew away from light (*i.e.* negatively gravitropic).

Callose Formation

Scherp *et al*. (2001) documented the formation of callose in tissue fragments in all groups of multicellular photosynthetic organisms, including bryophytes. They found that in bryophytes and other multicellular green plants, callose is a regular component of the developing septa in juvenile cells during cytokinesis. Wound callose did not occur in cells that already had callose in the newly formed septa.

Establishment

It appears that fragments may survive better in water than spores, thus providing an additional means of long-distance dispersal. Dalen and Söderström (1999) tested

five species of mostly terrestrial mosses and found that in all five taxa, regeneration frequency of fragments was lower than that of spores, but that fragments survived as well in water as they did dry, whereas spores did not.

Light quality and intensity may be influential in success of fragments. Dagar and coworkers (1980) found that for the thallose liverwort ***Riccia discolor*** regeneration is best in diffused light. Red light can induce regeneration; far-red inhibits it (Giles & von Maltzahn 1967, 1968). There is evidence the red/far-red system may affect the "budding" or division of the chloroplasts (Hahn & Miller 1966), and its reversibility suggests that phytochrome may be active during the process. Little else seems to be known about light effects specifically on fragments, so these phenomena may be restricted to certain taxa or habitats.

When dispersal occurs over long distances, it is quite likely that only one gender will arrive, making its survival dependent on asexual means. As discussed elsewhere, fragments seem to provide the easiest means by which bryophytes can be propagated for gardens, so one should expect that nature makes widespread use of this ability as well. When a plant is damaged, the damaged surface will often produce protonemata and/or rhizoids (LaRue 1942) and subsequently develop a new leafy gametophore. In other cases, the new plant may develop directly with no protonemal intermediary, as in the leafy liverwort ***Scapania undulata*** (Figure 22) that developed from a leaf fragment (Figure 23; Glime 1970).

Figure 22. ***Scapania undulata*** growing in its streamside, wet habitat. Photo by Michael Lüth, with permission.

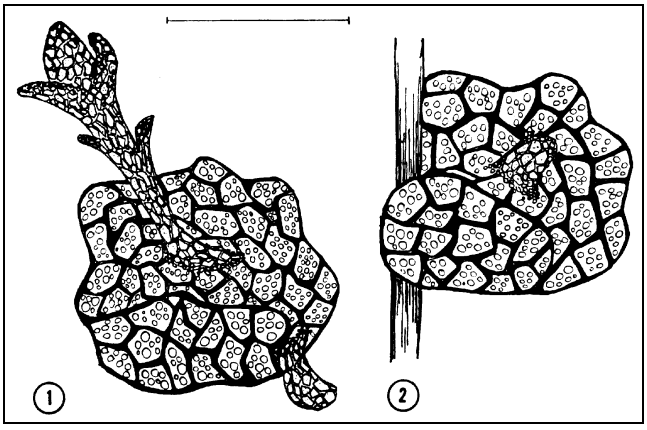

Figure 23. ***Scapania undulata***, leafy liverwort known to reproduce from fragments. **1:** Young plant growing from detached leaf. **2.** Bud of young plant growing on leaf still attached to living stem. Drawings by Flora Mace.

It is the parent plant that determines which of these will develop – chloronema, caulonema, or rhizoids. Knoop (1984) tells us that small explants result in reversion to an early developmental stage wherein single leaf cells behave like spores and form chloronemata. On the other hand, large fragments revert back only to caulonemata, or go directly to buds and gametophore plants. Furthermore, apical leaves regenerate more easily than basal leaves (Gay 1971). It is puzzling that in ***Plagiomnium undulatum*** (Figure 24), basal leaves regenerate only from the lamina, whereas apical ones regenerate only from the costa (Schröder *et al.* 1970).

Figure 24. ***Plagiomnium undulatum***; basal leaves regenerate from the lamina, apical cells from the costa. Photo by Janice Glime.

Mishler and Newton (1988) demonstrated that fragments can require conditions opposite to those required for spores. In their study, ***Syntrichia princeps*** (Figure 25) fragments were slightly more successful when they experienced periodic drying, whereas the spores required continuously hydrated conditions. With such requirements, it is easy to understand why fragments are more successful on rocks and sand than are spores. Mishler and Newton attribute this success to the ability of fragments to produce a protonemal mat and new shoots much more rapidly than could spores. Furthermore, as mentioned earlier, the existing plants exhibited a much stronger inhibitory effect on the spores than on the fragments.

Figure 25. ***Syntrichia princeps***, a moss whose fragments fare better with periodic drying. Photo by Jan-Peter Frahm, with permission.

On the other hand, both spores and fragments can be inhibited by the presence of mature plants (Mishler & Newton 1988). ***Dicranum*** (Figure 1, Figure 3) seemed to be more inhibitory that ***Syntrichia princeps*** (Figure 25), perhaps relating to the dry habitat of the latter. They considered that at least some of this inhibition was due to chemical exudates.

In an aquatic habitat, Florschütz and coworkers (1972) found that fragments of ***Fissidens crassipes*** (Figure 26) produced caulonemata, this time on moist bricks. This ability permitted them to spread rapidly in response to a rise in water temperature.

Figure 26. ***Fissidens crassipes*** growing on rock. Photo by Michael Lüth, with permission.

Regeneration often occurs from small leaf fragments that have begun to decay. This could be an indication that an inhibitor has been lost, or some colonizing microorganism could be providing a hormonal signal that starts the development. When growing ***Leucolejeunea clypeata*** on Ca-free media, Geldreich (1948) discovered that only contaminated leaves of Ca-deficient plants produced regenerants. It was only mature or old and necrotic leaves that regenerated, and these Ca-deficient leaves had oil bodies that were characteristic of old, senescent leaves. Since the contaminating microorganisms were typical of soil flora, and regenerants of this species are known in nature (Fulford 1947), perhaps the microorganisms do indeed play a role in providing the necessary stimulus.

Liverworts rarely regenerate from fragments. Occasionally a leaf may produce a new plant, as for example that of ***Scapania undulata*** (Figure 22-Figure 23), an aquatic leafy liverwort mentioned earlier (Glime 1970). Could it be that liverworts dry out too rapidly and cells lose their viability before new plants can arise? Would this explain the accomplishment of this aquatic species?

Growth Regulators

Like all other developmental processes, hormones and other growth regulators influence the developmental pathway of fragments. Patidar and coworkers (1987) found that 0.03 ppm gibberellin can stimulate regeneration in the thallose liverwort ***Targionia hypophylla*** (Figure 27). Concentration is of course important; at 0.1 ppm gibberellin is inhibitory to ***T. hypophylla***.

Figure 27. ***Targionia hypophylla***. Photo by Michael Lüth, with permission.

Few studies seem to have centered specifically on growth regulators of fragments, yet many in vitro studies are actually studies of fragments, particularly those of pleurocarpous mosses. Presumably, the same growth regulation applies to fragments as to the intact plants covered earlier. Yet, literature on the wound response seems to be lacking, as is literature on the remarkable ability of some fragments to persist under extremely stressful conditions. For example, we have grown ***Fontinalis flaccida*** from specimens dried for three months under herbarium conditions (ca. 30% relative humidity). In another case, ***Fontinalis novae-angliae*** that had been boiled for about 12 hours daily for two weeks developed new leaves on one portion of the remaining stem when it was returned to its native stream (Glime & Carr 1974). And what permits a partially decayed stem to suddenly spring forth a new plant after it has been uncovered from many years of burial (During *et al*. 1987)?

Using the aquatic moss ***Palustriella decipiens*** (Figure 28-Figure 29), Ahmed and Lee (2010) experimented with a wide range of IAA and kinetin concentrations on fragments. They found that protonemal gemma production varied with concentration, but was best at 10^{-8} M IAA and kinetin. Higher concentrations caused the gemmae to become brown. Low concentrations of IAA and kinetin induced bud formation.

Figure 28. ***Palustriella decipiens***, an aquatic moss that regenerates from fragments and protonemata of those fragments respond to applications of IAA + kinetin to produce buds. Photo by Michael Lüth, with permission.

Figure 29. ***Palustriella decipiens*** protonemata with gemmae, produced at 10^{-8} M kinetin. Photo by Ahmed and Lee, with permission.

Animal Dispersal

Dispersal by animals is scarcely known in the bryophytes. Yet, we must suppose that the various activities of animals contribute to bryophyte movement. Various aquatic insects, especially Trichoptera (caddis flies), use mosses or liverworts in their cases, so the insect will carry the bits around wherever it goes. When drift carries the insect downstream, the moss goes too, and if the insect crawls upstream in the quiet interface at the bottom, the moss comes along. Lacewings [***Leucochrysa*** (***Nodita***) ***pavida***] carry viable bryophytes (and lichens) on their backs as camouflage (Slocum & Lawrey 1976).

Bears, beaver, and other animals can get mosses tangled among their toes and carry them for miles. Birds carry them off to build nests. I have even concluded that the turtle in my garden room was responsible for the distribution of ***Conocephalum conicum*** (Figure 30) all over the room from the single spot where it had been planted. When the turtle died, the spread of the liverwort stopped. In a field experiment, I found fragments of tagged ***Fontinalis duriaei*** (Figure 31-Figure 32) upstream from their initial location, a movement that could only have been effected by animals such as bears or humans.

Figure 30. ***Conocephalum conicum*** showing evidence of herbivory (arrows) that could lead to dispersal of fragments. Photo by Janice Glime.

Figure 31. ***Fontinalis duriaei*** held by Janice Glime, demonstrating how easily mosses might be dispersed by flowing water and trapped by branches and roots in the water. Photo by Zen Iwatsuki, with permission.

Figure 32. ***Fontinalis duriaei*** fragment. Photo by Janice Glime.

It is likely that rodents contribute to dispersal, although they may do more harm than good. I have watched chipmunks run across my moss garden and kick up clumps as they ran. Nancy Ironsides (Bryonet 10 June 2011) found rhizoids on the apical leaves of ***Leucobryum glaucum*** (Figure 33) and attributed these to disturbance by animals. Pénzes Kónya (2003) considered "big wild animals" to be major dispersers of ***Leucobryum juniperoideum*** (Figure 34) during dry periods. The caducous leaves function as gemmae by producing rhizoids (Figure 35) and forming new plants, especially during the rainy spring, but the disturbance of dry mosses seems to outpace the regeneration from disturbed plants.

Others may spread bryophytes as they eat them (Slack 1936, Mutch & Pritchard 1984), particularly if they only digest the surface organisms and return the moss fragments with their feces. Suren and Winterbourn (1991) found that 14 aquatic invertebrate taxa had bryophyte fragments in their guts, and two tipulid larvae regularly consumed bryophytes. I tested the hypothesis that rainbow trout, known to strike at anything, could serve as dispersal agents by eating the aquatic ***Fontinalis duriaei*** (Figure 31-Figure 32). However, the fish could not be tempted to strike at or eat the moss, even when it housed numerous aquatic insects. Finally, we force fed the fish. The moss was

delivered back as feces in a neat, cylindrical package with bright green moss (Figure 36). At last it seemed we had demonstrated a potential upstream dispersal mechanism! But, alas, we were surprised the following day to find that the moss had lost all its color, even though it was maintained in a gallon jar of its own stream water at a cool temperature. It does not appear that rainbow trout are likely dispersal vectors after all!

Figure 36. Feces of rainbow trout consisting primarily of ***Fontinalis duriaei*** as a result of force-feeding. Photo by Janice Glime.

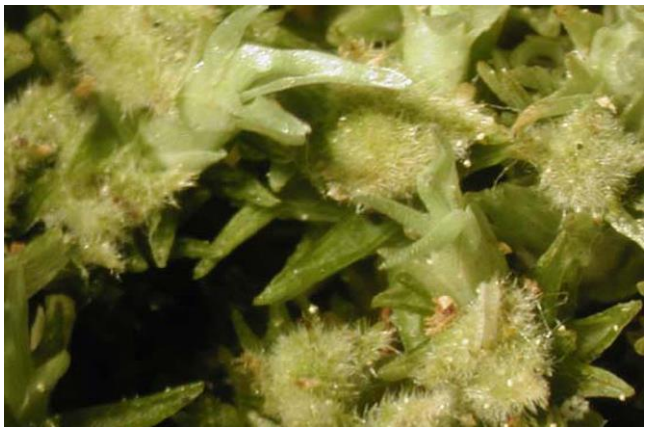

Figure 33. ***Leucobryum glaucum*** with apical rhizoids on leaves. Photo by Nancy Ironsides, with permission.

I have watched larvae of the **Rhyphidae** dipteran eat wet, dirty (most likely with diatoms) mosses and observed fragments of green moss come out the other end, clean. These fragments would be ideal propagules, although not dispersed very far, but I did not culture them to see if they met the same fate as the trout package.

Further discussion of bryophyte fragment dispersal is in the adaptations subchapter on dispersal.

Figure 34. ***Leucobryum juniperoideum*** cushions. Photo by Michael Lüth, with permission.

Figure 35. ***Leucobryum juniperoideum*** with leaf rhizoids after overturn by cattle. Photo courtesy of Erika Pénzes-Kónya.

Summary

Fragmentation results from random breakage or from genetically programmed cleavage areas on leaves, buds, or stems. For perennial mosses, especially pleurocarpous mosses, it is typically the primary means of spreading. Arctic/alpine and aquatic habitats may rely primarily on this type of reproduction. Fragments are more likely to become established than spores and survive better in water than do spores. Their establishment can be inhibited by the presence of mature plants, but they have a greater competitive ability than spores.

Regeneration from mature cells requires **dedifferentiation** and may begin as protonemata, rhizoids, or both. Light quality and intensity may play a role in early development. Little is known about growth regulation, but gibberellin can stimulate regeneration in at least some bryophytes. Dispersal can be accomplished by wind, water, and animals, sometimes because the animal transports the bryophyte for use in a nest or house.

Acknowledgments

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CHAPTER 5-7
ECOPHYSIOLOGY OF DEVELOPMENT: BROOD BODIES

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CHAPTER 5-7

ECOPHYSIOLOGY OF DEVELOPMENT: BROOD BODIES

Figure 1. ***Syntrichia laevipila*** (=*Tortula pagorum*), an acrocarpous moss with terminal gemmae. Photo by Michael Lüth, with permission.

Introduction

Ecology is a field of interconnections. Hence, writing any chapter brings with it many choices about where to include information. This chapter is in part redundant with the chapters on dispersal because an understanding of propagules was necessary to complete the dispersal story. That chapter emphasized travelling about and the environmental factors that influenced the success of that travel. This chapter emphasizes the physiology, but for clarity there is considerable overlap in what one must understand. The chapter is written to be independent so that one can read it without having to read the earlier chapter in order for it to make sense.

Definitions

Imura and Iwatsuki (1990) defined **propagules** as vegetative **diaspores** that have an apical cell and can grow directly into leafy shoots. However, most diaspores produce a protonema. **Gemmae**, by their definition, are vegetative diaspores that lack an apical cell and in which a protonema precedes development of a leafy shoot (Figure 2, Figure 37). While this is a clean separation, it is not always practical to determine the germination pattern, and multicellular gemmae may be construed as propagules. In the multilingual glossary for bryology (Magill 1990), **propagule** (Figure 3-Figure 4) is defined in a more practical way as a reduced bud, branch, or leaf serving in reproduction. This does not imply absence of a protonema, and indeed, there often is one. **Diaspore** is given as a synonym. **Gemmae** (Figure 2) are distinguished as uni- or multicellular, filamentous, globose, ellipsoidal, cylindrical, stellate, or discoid brood bodies, **relatively undifferentiated**, serving in vegetative reproduction. In other words, they are specialized structures. **Brood body** is the more inclusive category, including both propagules and gemmae. These are genetically identical to their parents, thus producing clones (Laaka-Lindberg 2000). Bryophytes are the only group of plants with any sort of gametophytic brood body (Wyatt 1994).

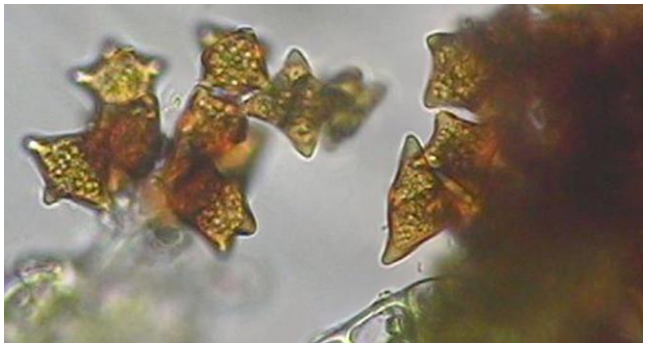
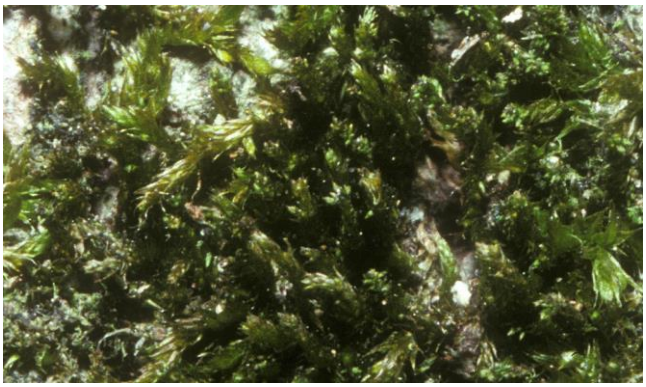


Figure 2. Leaf gemmae of ***Lophozia bicrenata***, a leafy liverwort. Photo by Paul Davison, University of North Alabama, with permission.

Figure 3. ***Leskeella nervosa*** with bulbils at leaf bases. Photo by Michael Lüth, with permission.

Figure 4. ***Bryum gemmilucens*** showing axillary propagules. Photo by Michael Lüth, with permission.

The evolutionary pathway has capitalized on success of fragments by selecting more and more specialized fragments. Mosses such as ***Leskeella nervosa*** (Figure 3), ***Platygyrium repens*** (Figure 5), ***Dicranum flagellare*** (Figure 6), and ***Bryum argenteum*** (Figure 7-Figure 8), to name a few, have special shoots that easily break off and disperse. This explains why ***Bryum argenteum*** is so common along paths in open areas such as cemeteries and roadsides. Each step of a boot carries tiny branches from the parent plants to a new location. To demonstrate its remarkable dispersal success, Clare and Terry (1960) prepared bare soil, then used a matchbook to "walk" on ***Bryum argenteum*** (Figure 7-Figure 8). They then "walked" on the bare soil with the same matchbook. As a control, they "walked" on a different part of the prepared soil with a different matchbook. True to its natural success, the ***Bryum argenteum*** grew well where the matchbook had previously walked on the moss, but did not appear on the control area.



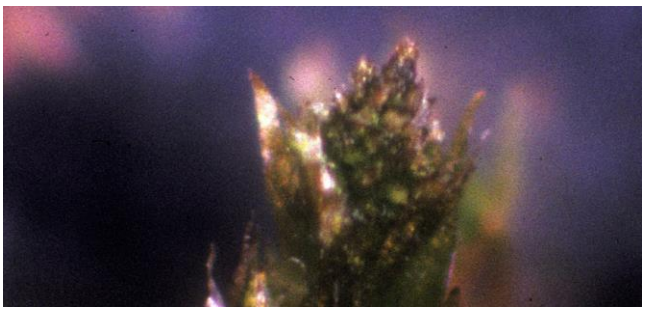


Figure 5. ***Platygyrium repens Platygyrium repens*** with bulbils crowded at branch tips. Photos by Janice Glime.

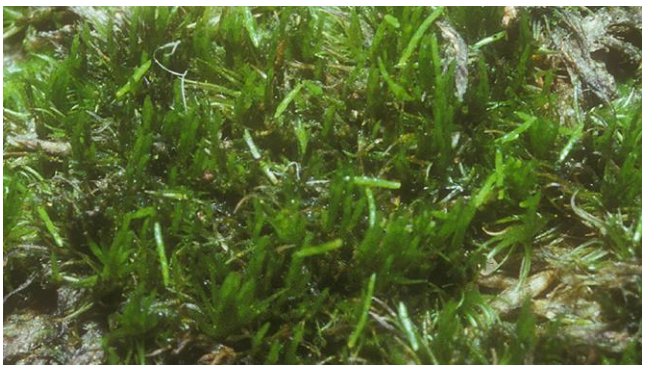


Figure 6. ***Dicranum flagellare*** with deciduous flagelliform branches. Photo by Janice Glime.

Figure 7. ***Bryum argenteum*** showing bulbous tips that break off easily to form new plants. Photo by Michael Lüth.

Figure 8. ***Bryum argenteum*** showing bulbous tips that break off easily to form new plants. Photo by Michael Lüth, with permission.

Imura (1994) recognized specialized vegetative reproductive structures in 186 species (15.7%) of Japanese mosses, including deciduous shoot apices, caducous branchlets, bulbils, flagella, rhizoidal tubers, gemmae, caducous leaves, and endogenous gemmae. He considered these to be adaptations to the dioicous habit (*e.g.* ***Syntrichia laevipila***, Figure 1) and unstable habitat conditions.

Brood Bodies

Brood bodies are a specialized means of asexual reproduction that permit plants to propagate and disperse, often when conditions are unfavorable in the present location. Perhaps this is why, among dioicous mosses, they are more common on upright mosses (Figure 4), where there is some hope of falling away from the parent plant, rather than landing within a mat that keeps them where they started. Herben (1994) claims that reproductive processes, including brood bodies, are crucial for between-habitat dispersal. Those mosses in the British flora that inhabit small patches and unstable habitats are more likely to have vegetative brood bodies. But shoot density also can determine the number of brood bodies. Kimmerer (1991a) found that low-density populations of ***Tetraphis pellucida*** (Figure 9) were more likely to reproduce asexually by gemmae, whereas greater density increased incidence of sexual reproduction and subsequent spores. She (1991b) found that most **gemmae** landed within 10 cm of the colony, whereas spores travelled as far as 2 m. [Brodie (1951) considered that ***T. pellucida*** was too delicate to benefit much from splashing by raindrops, perhaps accounting for the much shorter dispersal distance compared to that of sperm in ***Polytrichum*** of up to 60 cm.] The asexual strategy permits mosses to colonize an area rapidly by gemmae, then move on by spores when space is saturated. Kimmerer (1991a) felt this was of particular importance in unstable environments such as rotting stumps where ***T. pellucida*** commonly occurs. On the other hand, ability to "move" by gemmae provides an opportunity to seek a mate when stranded in a single-sex clone.

Chrobak and Sharp (1955) showed that scales from the deciduous flagelliform branches of ***Dicranum flagellare*** (Figure 6) were more likely to form protonemata than whole leaves or their proximal or distal halves (Figure 10).

Figure 9. ***Tetraphis pellucida*** with terminal gemma cups, the only moss with gemma splash cups. Upper photo by Janice Glime, lower by Paul Davison, University of North Alabama, with permission.

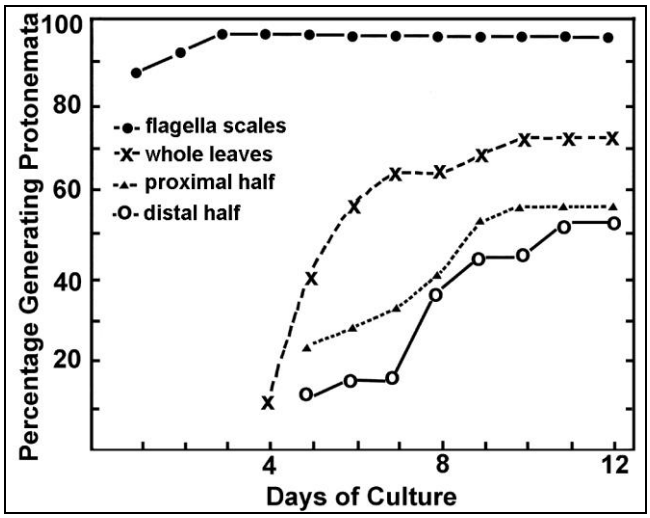


Figure 10. Success of producing protonemata from various leaf parts of ***Dicranum flagellare*** compared to that of the scales on the flagelliform brood branches. Redrawn from Chrobak & Sharp (1955).

Even in the ***Sphagnum***-dominated peatlands, dispersal by gemmae is an advantage in regeneration. While ***Sphagnum*** must wait for recolonization by spores that often have poor success on the acid peatland substrate with its low nutrient quality, ***Aulacomnium palustre*** (Figure 11) can colonize rapidly from gemmae that have survived the disturbance (Li & Vitt 1994). Furthermore, perhaps again due to the more advanced state of the propagula, *A. palustre* had a much wider tolerance range for nutrient concentrations, being the only species not inhibited by N inputs. ***Sphagnum angustifolium*** (Figure 12), ***S.***

magellanicum (Figure 13), and ***Polytrichum strictum*** (Figure 14) all had poor regenerative ability.

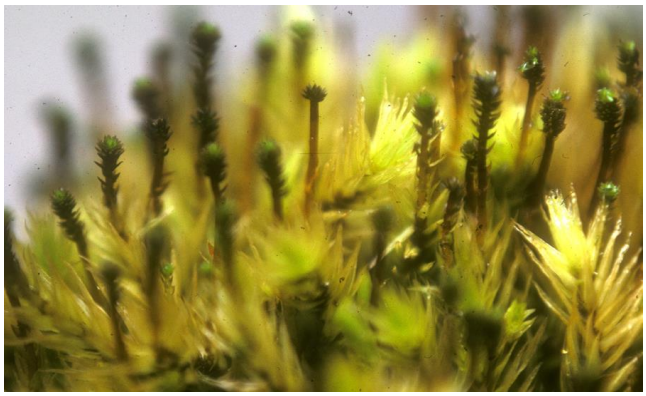


Figure 11. ***Aulacomnium palustre*** showing special extension of the stem with gemmae. Photo by Zen Iwatsuki, with permission.

Figure 12. ***Sphagnum angustifolium***, a species that does not regenerate well. Photo by Michael Lüth, with permission.

Figure 13. ***Sphagnum magellanicum***, a species that has poor regenerative ability. Photo by Michael Lüth, with permission.

Figure 14. ***Polytrichum strictum***, a species with poor regenerative ability. Photo by Des Callaghan, with permission.

It is reasonable then, that certain habitat conditions might favor the **apogamous** (condition of producing sporophytes without union of gametes) or **aposporous** (producing gametophyte from sporophyte tissue without meiosis) reproduction of bryophytes. Chopra (1988) was able to increase apogamy by reducing water or light levels and by raising the sugar concentrations in the growth medium. Likewise, low hormone concentrations favored apogamy. Not surprisingly, this plasticity was correlated with a high chromosome number (suggesting polyploidy) and genetic variation. Apospory, on the other hand, was favored by the opposite conditions: suitable temperature and light, sufficient humidity, and lack of sugar in the medium. It was furthermore stimulated by wounding and the removal of apical dominance.

In the leafy liverwort ***Odontoschisma denudatum*** (Figure 15-Figure 16), gemmae are produced in branched chains on the leaf margins (Duckett & Ligrone 1995). The initial cells of these gemmae are distinguished by forming a protrusion that contains a large central nucleus, small vacuoles, starch-free chloroplasts, and scattered cytoplasmic lipid droplets. Unlike other leaf cells, they lack oil bodies. However, as the gemmiferous filaments develop, oil bodies arise. These are closely associated with the cytoplasmic lipid bodies. These bodies swell rapidly, quickly reaching their final diameter. As the gemmae mature, the walls become dense and may account for their extreme water repellence. This repellant surface could permit them to be dispersed on the surface of a water film or in the air.

Figure 15. ***Odontoschisma denudatum***, a species with apical gemmae. Photo by Michael Lüth, with permission.

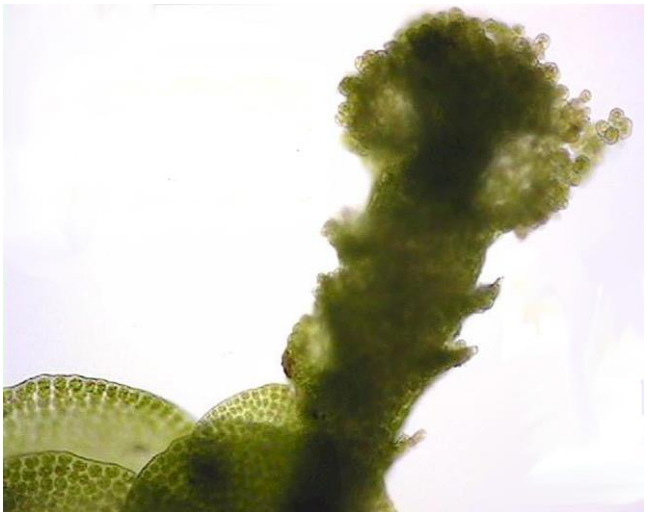


Figure 16. ***Odontoschisma denudatum*** showing apical gemmae. Photo by Paul Davison, with permission.

The germination and development of gemmae in the tropical moss ***Calymperes*** have been described (Egunyomi & Olarinmoye 1983; Duckett & Ligrone 1991).

Tubers

Tubers are defined very differently in mosses and liverworts (Magill 1990). In liverworts, they are extensions from the growing apex, growing downward gravitropically, and serving as perennating structures during conditions unfavorable for growth. In mosses, they are gemmae formed on the rhizoids (Figure 17).

Figure 17. ***Bryum radiculosum*** rhizoids with tubers. Photo by Michael Lüth, with permission.

A number of moss species form tubers on their rhizoids (Arts 1987a; Table 1). Risse (1987) described these rhizoidal gemmae in 82 species of European mosses. They serve as asexual means of reproduction, although one must question just how they get dispersed. Perhaps earthworms and other forms of disturbance accomplish the task. However, in their study of plant diaspores from earthworm guts, van Tooren and During (1988) found few bryophytes that regenerated from tubers so obtained, although bryophytes emerged frequently from some samples by other means. They interpreted this as a low survival rate of vegetative diaspores in the earthworm digestive tract. Risse (1987) reported that mites disperse protonemal gemmae in ***Schistostega pennata*** (Figure 18).

Figure 18. ***Schistostega pennata*** showing pinched off gemmae on the protonema. Photo by Irene Bisang, with permission.

These tubers are densely packed with lipid droplets or starch grains (Duckett & Pressel 2003). In ***Phaeoceros laevis*** (hornwort; Figure 19), tuber cells deposit protein into the cell vacuoles as the cells differentiate, forming abundant starch in their plastids and lipid droplets in the cytoplasm (Ligrone & Lopes 1989). Such rich storage contents suggest that they should germinate rapidly and produce new plants quickly, using their abundant food reserves. Using ***Haplodontium notarisii*** (Figure 20), Arts (1988a) showed that this moss did just that, germinating in two weeks, and several weeks later producing numerous upright gametophores to form a colony.

Figure 19. ***Phaeoceros laevis*** with sporophytes. Photo by Bob Klips, with permission.

Figure 20. ***Haplodontium notarisii***, a moss that stores dense starch in its tubers, permitting them to germinate and grow rapidly. Photo by Jan-Peter Frahm, with permission.

Such tubers provide a diaspore bank that can help to revegetate disturbed ground (During *et al*. 1987) and benefit from extended longevity. Arts (1989) has demonstrated that even in a state of desiccation in a herbarium, such tubers can survive and germinate after 10 years. Such a strategy is common among colonist species (During *et al*. 1987; Arts 1990a; Table 1), and seems to be confined among the mosses to acrocarpous species. This colonist connection suggests that perhaps they do not have to arrive, but are already there, much like buried seeds awaiting the day they once more arrive at the surface and receive light. During (1995) suggests that such colonist populations are maintained completely through occasional recruitment. He suggests that within extant populations there must be a density-dependent tuber mortality to regulate the population.

Development

There are more developmental pathways for propagules than there are kinds of propagules. Even within the same genus, Ligrone and coworkers (1996) found differences in the origins of the gemmae. In ***Tortula latifolia*** (Figure 21), gemmae develop on the upper leaf surface from single initial cells of both the lamina and the costa, whereas in ***Syntrichia*** (=***Tortula***) ***papillosa*** (Figure 22) they develop only on the costa. In both cases the old wall and cuticle of the cell initial rupture and a new, highly extensible wall replaces it. Subsequent divisions of this gemma **primordium** produce a 6-8-celled gemma. Mucilage develops around these gemmae and eventually the plasmodesmatal connections are severed, leaving only the mucilage to connect the gemmae to the leaf. Multiple gemmae may form in this way from the same initial and remain in a chain until the leaf becomes fully hydrated. Despite their disconnection from the parent leaf, these gemmae accumulate lipids, indicating that they are functionally photosynthetic.

Table 1. Examples of bryophytes with tubers reported in the literature.

Species	Reference
Archidium alternifolium	Arts 1990b
Archidium globiferum	Arts 1998
Atrichum crispum	Arts 1987d
Atrichum tenellum	Arts 1987d
Barbula cylindrica	Ellis & Smith 1983
Didymodon tophaceus	Side 1983
Bryum barnesii	Wilczek & Demaret 1980
Bryum bicolor	El-Saadawi & Zanaty 1990
Bryum bicolor	Risse 1993
Bryum cruegeri	Whitehouse 1978
Bryum dunense	Cortini Pedrotti & Aleffi 2001
Bryum veronense	Cortini Pedrotti & Aleffi 2001
Campylopus pyriformis	Arts 1986c
Chrysoblastella chilensis	Matteri 1984
Conocephalum conicum	Paton 1993
Cynodontium bruntonii	Arts 1990a
Didymodon nicholsonii	Arts 1987b
Discelium nudum	Side & Whitehouse 1987
Ditrichum difficile	Arts 1998
Ditrichum heteromallum	Deguchi & Matsui 1986
Ditrichum heteromallum	Risse 1985b
Ditrichum lineare	Matsui *et al*. 1985
Fissidens beckettii	Arts 1998
Fissidens cristatus	Arts 1986a
Funaria hygrometrica	El-Saadawi & Zanaty 1990
Haplodontium notarisii	Arts 1988a
Leptobryum pyriforme	Imura *et al*. 1992
Pleuridium acuminatum	Arts & Risse 1988
Pleuridium ecklonii	Arts 1998
Pleuridium nervosum	Arts 1998
Pohlia lutescens	Hart & Whitehouse 1978
Pohlia molanodon	Arts 1986b
Pottia bryoides	Arts 1987c
Pottia intermedia	Risse 1985a
Pottia lanceolata	Arts 1987c
Pottia truncata	Arts 1987c
Pseudocrossidium revolutum	Arts 1988b
Scopelophila cataractae	Arts 1988b

Figure 21. ***Tortula latifolia*** showing gemmae on costa and lamina. Photo by Michael Lüth, with permission.

Figure 22. ***Syntrichia*** (=***Tortula***) ***papillosa*** showing gemmae restricted to costa. Photos by Michael Lüth, with permission.

Lipids are commonly stored in brood bodies of mosses, including ***Aloina aloides*** var. ***ambigua*** (Figure 23), ***Pohlia annotina*** (Figure 24), ***Ephemerum serratum*** (Figure 25), ***Leptodictyum riparium*** (Figure 26), ***Weissia controversa*** (Figure 27) (Goode *et al*. 1993), and ***Splachnum ampullaceum*** (Figure 28) (Mallón *et al*. 2006). Due to the hydrophobic properties of lipids, large amounts can be stored, permitting these brood bodies to survive when the protonema or plant is damaged by desiccation. Such lipids are most common in long-lived propagules.

Figure 23. ***Aloina aloides***, a species with brood bodies that store lipids that help them survive desiccation. Photo from Proyecto Musgo, through Creative Commons.

Figure 24. ***Pohlia annotina*** with bulbils, a species that stores lipids in its brood bodies, permitting them to survive desiccation. Photo by Dick Haaksma, with permission.

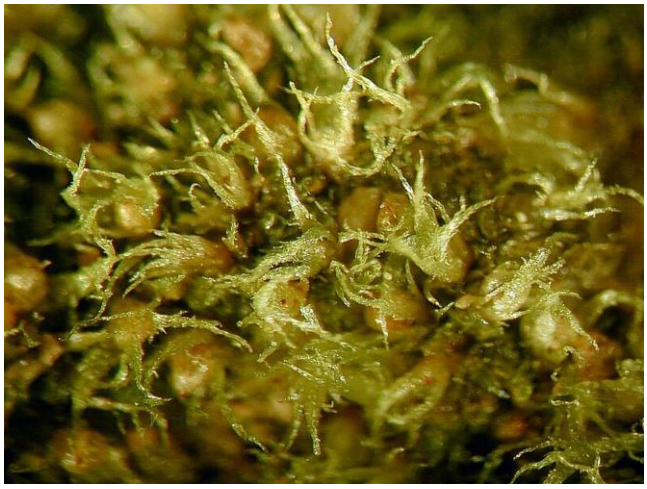


Figure 25. ***Ephemerum serratum*** with capsules. This species produces brood bodies that store lipids, a protection against desiccation. Photo by Michael Lüth, with permission.

Figure 26. ***Leptodictyum riparium***, a species that produces brood bodies that store lipids and survive when the moss dies from disturbance or desiccation. Photo by Tan Sze Wei, Aquamoss website <www.aquamoss.net>, with permission.

Figure 27. ***Weissia controversa*** with capsules. This species stores lipids in its brood bodies, permitting the to survive when the plants die of desiccation or disturbance. Photo by Michael Lüth, with permission.

Figure 28. ***Splachnum ampullaceum*** with capsules. This species stores lipids in its brood bodies, permitting them to survive desiccation. Photo by Michael Lüth, with permission.

Some gemmae can even produce more gemmae. In ***Bryoerythrophyllum campylocarpum*** (=***Hyophila crenulata***), the still-attached gemmae can germinate to produce more gemmae (Olarinmoye 1981).

Hormonal Effects

Hormones control every stage of development, but their role in gemma production and germination is not clear, or at the very least, differs among species.

Rawat and Chopra (1976) found that secondary protonemata of ***Bryum klinggraeffii*** (Figure 29) produce a diffusable substance when gemmae are produced. This induces gemma production on young protonemata that have not yet reached the critical size. Such a mechanism could insure maximum gemma production and greater survival if the initial stimulus for gemma production was indeed an unfavorable environment. The biggest advantage may be that it creates a colony that can reduce water loss.

Figure 29. ***Bryum klingraeffii***, a species in which protonemata produce a diffusable substance that stimulates gemma production on young protonemata. Photo by Des Callaghan, with permission.

Auxins

Stange (1971, 1977, 1983) suggested that gemmae require **auxin** transport from the parent plant, based on disruption of gemma differentiation in ***Riella helicophylla*** (Figure 30) when treated with an auxin antagonist. Contrasting with the auxin requirement suggested by Stange (1983) for ***Riella helicophylla*** gemmae, external auxins inhibit production of gemma cups in ***Marchantia palmata*** (Kumra & Chopra 1989). In ***Lunularia cruciata*** (Figure 31), auxins produced in the apical buds of the thalli inhibit the germination of the gemmae on the thallus (LaRue & Narayanaswami 1957).

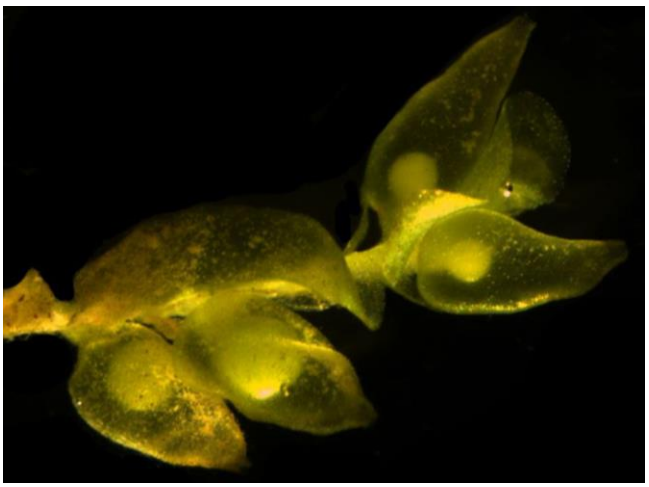


Figure 30. ***Riella helicophylla***, a liverwort that seems to require external auxins for gemma differentiation. Photo from NACICCA, through Creative Commons.

Figure 31. ***Lunularia cruciata*** showing ungerminated gemmae on the thallus. Photo by Martin Hutten, with permission.

However, when ethylene and IAA are applied together in cultures of ***Riella helicophylla*** (Figure 30), the combination has positive, additive effects on cell elongation of gemmae (Stange & Osborne 1988). On the other hand, gemmae generally fail to germinate while still on the parent thallus of ***Marchantia*** (Figure 44-Figure 45) species, suggesting that these two genera might, like roots and stems of tracheophytes, respond differently to the same hormones. Botanists have assumed that the inhibition of gemmae on the parent thallus is due to an inhibitory substance diffused from the parent. That inhibition can carry over to germination in the vicinity of the parent as well. Schneider and Sharp (1962) found that when gemmae of ***Tetraphis pellucida*** (Figure 32) were grown on culture media that previously had had mature plants, the germination was inhibited. This suggests some sort of hormone leakage, but probably not the gaseous ethylene.

Figure 32. ***Tetraphis pellucida*** with gemmae, a species where the gemmae are inhibited by the parents. Photo by Michael Lüth, with permission.

Marchantia polymorpha (Figure 44) exhibits apical dominance, resulting from polarity (Binns & Maravolo 1972). This can be attributed to the behavior of auxins. Binns and Maravolo found evidence that there is an endogenous, basipetal auxin gradient that is vital to normal growth. Interestingly, cytokinins can destroy the polarity by causing the auxin-synthesizing capacity to increase.

Since gemmae are such diverse structures, arising from protonemata, thallus, apical branches, leaf axils, and leaves, one might expect a variety of environmental and hormonal controls over their production. Naming the hormones would be pure speculation, but we know that IAA moves basipetally, hence accumulating downward. We also know that more ethylene is likely to be produced in the older part of the stem, and there is less air movement, resulting in more accumulation. Perhaps it is some interaction of these two hormones that results in the basal propagules, but why in some taxa and not others? Bulbils are apical in some taxa, such as ***Platygyrium repens*** (Figure 3), and gemma cups are apical in ***Tetraphis pellucida*** (Figure 32).

Cytokinins

We know that cytokinins are needed to stimulate bud production on protonemata, so early researchers experimented with cytokinin effects on gemma production on the protonema. Logic would suggest that if cytokinins stimulate buds, they might inhibit protonemal gemma production.

Rahbar and Chopra (1982) found that the usual substances did not induce buds in the moss ***Hyophila involuta*** (Figure 33). In fact, when the protonemata were grown on basal Knop's medium, auxins, gibberellic acid, abscisic acid, chelates, vitamin B_{12}, activated charcoal, coconut milk, and altered hydration, *p*H, temperature, and light intensity and duration all failed to induce buds. Rather, they found that added cytokinins could initiate multicellular protonemal gemmae. Chopra and Dhingra-Babbar (1984) found similar responses in the moss ***Trematodon brevicalyx***. Demonstrating the complexity of the bryophyte developmental system, Rahbar and Chopra (1982) demonstrated that for bud induction ***H. involuta*** required the interaction of IAA with kinetin or DMAAP.

Figure 33. ***Hyophila involuta***, a moss in which cytokinins can induce gemma production. Photo by Niels Klazenga, with permission.

Mehta (1990) further explored the role of kinetin on ***H. involuta*** (Figure 33) and was able to isolate a protonemal diffusate from those protonemata that had gemmae. These protonemata served as "nurse protonemata" by promoting the growth of nearby protonemata. He found that kinetin (10^{-5}-10^{-8} M) plus the protonemal diffusate acted synergistically on gemma formation. ABA (abscisic acid, 10^{-5}-10^{-7} M), on the other hand, was inhibitory, resulting in no gemma formation.

Unlike ***Hyophila involuta*** (Figure 33) in Knop's plus Nitsch's medium, ***Ptychostomum*** (=***Bryum***) ***capillare*** (Figure 34) produced gemmae in both solid and liquid Nitsch's basal medium (Sarla & Chopra 1989). When the medium was supplemented with kinetin or 2iP (bryokinin), the protonemata produced gemmae, whereas the cytokinin 6-benzylaminopurine (BAP) caused the formation of buds instead, while the 2iP inhibited the growth of the protonemata. Gemmae on media with kinetin or BAP regenerated, producing secondary protonemata, but these failed to produce gemmae or buds in response to kinetin. Hence, not all cytokinins are created equal – they may cause opposite responses.

Figure 34. ***Bryum capillare***, a moss that responds differently to different cytokinins, in some cases producing protonemal gemmae whereas in others they are inhibited. Photo by David T. Holyoak, with permission.

More recent work by Ahmed and Lee (2010) demonstrated that production of protonemal gemmae can vary with the concentration of IAA and kinetin in the moss ***Palustriella*** (=***Cratoneuron***) ***decipiens*** (Figure 35-Figure

36). In this species, kinetin influenced both gemma formation and gametophyte regeneration. Only low concentrations of IAA and kinetin (10^{-8}M) caused production of green, oval, mostly intercalary gemmae. Higher concentrations resulted in brown gemmae.

Figure 35. ***Palustriella decipiens***. Photo by Michael Lüth, with permission.

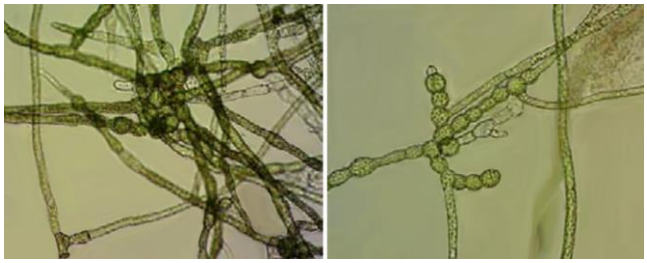


Figure 36. Effects of 10^{-8}M IAA (**left**) and 10^{-8}M kinetin (**right**) on gemma formation on protonemata of ***Palustriella decipiens***. Photos modified from Ahmed & Lee 2010.

But the role of cytokinin not only interacts to control production of gemmae, in ***Marchantia polymorpha*** (Figure 44) it inhibits the germination of the gemmae (Binns & Maravolo 1972). Could production of exogenous cytokinins be the factor that prevents germination of gemmae on the parent thallus?

Environmental Effects

For any plant system to be effective, it must be tuned to its environment. Propagules are no exception, being finely tuned to kick in when conditions favor their growth and development.

Temperature

For plants living outside the tropical regions, cold can inhibit growth and freezing may actually kill the tissues. Therefore, it is reasonable to expect that those species that survive have developed means to sense temperature conditions in both the production and germination of gemmae and to maximize these when conditions are best suited to continued growth.

In Arctic populations of ***Tetraphis pellucida*** (Figure 32), gemmae (Figure 37) have a broad range of germination conditions similar to those of the spores (Forman 1964). The broad 18-30°C range for gemma production sharply contrasts to sporophyte maturation requirements of -0.2 to 7.3°C, or 0-5°C in dark cultures. Such low temperature requirements account for the capsule maturation in spring. Gemmae, as for example gemmae of ***Aulacomnium heterostichum*** (Figure 38), which germinated after two years of storage in a freezer, seem to be able to persist as well as spores in cold conditions, and certainly better than some (Imura *et al*. 1991).

Light

Chopra and Rawat (1977) found that the response to temperature can be light dependent. In ***Bryum klinggraeffii*** (Figure 29) the initiation of secondary protonemata is correlated with protonemal age and growth. Although the gemmae of ***B. klinggraeffii*** are formed at or above 20°C in both light and dark, at 10-15°C in the light this species forms larger, lobed green structures and stunted gametophores. The addition of 1.0 ppm kinetin causes moruloid buds to differentiate on the protonemata, but at lower concentrations of kinetin, these protonemata produce gemma-like structures. This 1ppm concentration even inhibits previously formed gemmae from developing into gametophores, instead resulting in stunted gametophores. But in a sister species, ***Bryum coronatum*** (Figure 39), temperatures of 30°C in both light and dark induce the formation of protonemal gemmae that resemble the rhizoidal gemmae. In ***Leptobryum pyriforme*** (Figure 49), the gemmae develop on both the protonemata and gametophores in the dark. The short story is that for these species low temperatures and sufficient light results in energy being shifted to the development of gametophores. The conditions that favor gemma formation do not favor bud formation.

Figure 37. ***Tetraphis pellucida*** gemma showing germination and development of rhizoid. Photo with permission from Biology 321 Course Website at the University of British Columbia, Canada, with permission.

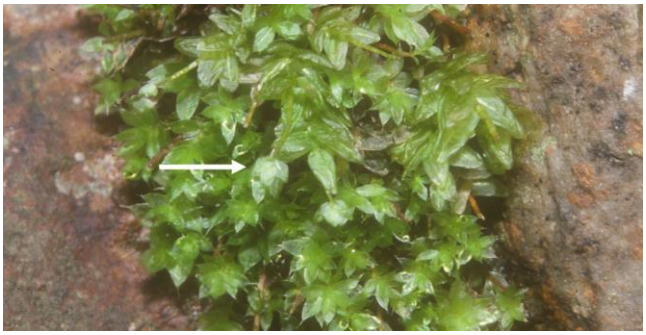


Figure 38. ***Aulacomnium heterostichum*** showing terminal gemmae (arrow). Photo by Janice Glime.

Figure 39. ***Bryum coronatum***, a moss that produces protonemal gemmae when the temperatures reach 30°C. Photo by Michael Lüth, with permission.

Whitehouse (1980) found that ***Schistostega pennata*** (Figure 18), ***Eucladium verticillatum*** (Figure 40), ***Gyroweisia tenuis*** (Figure 41), and ***Saelania glaucescens*** (as ***Didymodon trifarius***; Figure 42) all produce protonemal gemmae at low light intensities, but not at higher ones. These species can all grow in rock crevices, and such a mechanism might permit them to "try again" by dispersing if they germinate in a crevice that is too dark to complete the life cycle. A similar low-light response causes many protonemata to produce aerial shoots that break off and presumably serve as propagules (Whitehouse 1980). Similarly, in ***Marchantia palmata***, maximum production of gemma cups is attained when the plants receive continuous light at 4500 lux (Kumra & Chopra 1989). Full sunlight is about 70,000 lux. In ***Marchantia nepalensis***, having only 50-100 lux inhibits the production of gemma cups (Chopra & Sood 1970).

Figure 40. ***Eucladium verticillatum*** (Whorled Tufa-moss) with mite. This moss responds to low light intensities by producing protonemal gemmae. Photo by Barry Stewart, with permission.

Figure 41. ***Gyroweisia tenuis***, a moss in which the protonemata produce protonemal gemmae in low light. Photo by Michael Lüth, with permission.

Figure 42. ***Saelania glaucescens***, a moss that responds to low light by producing protonemal gemmae. Photo by Michael Lüth, with permission.

Hence, we might surmise that photoperiod plays a role in gemma production. Lockwood (1975), working with the leafy liverwort ***Cephalozia media***, found that the magnitude of the normal reproductive response could be significantly stimulated or inhibited by low concentrations of certain amino acids or kinetin. Certain metabolites (10^{-6}M arginine, cysteine, tryptophan plus kinetin) could overcome photoperiodic control of the reproductive response. Generally, organic compounds which stimulated asexual reproductivity under short photoperiod inhibited sexual reproductivity under long photoperiod.

Germination of gemmae and other propagula is likewise affected by light. In ***Philonotis hastata*** (Figure 43), the greatest germination rate for brood branches was around 750 lux, with percentage germinating decreasing in both directions from that figure (Egunyumi 1981). Such a low optimum would permit these propagula to germinate in the presence of tracheophyte ground flora where light is often minimal. In ***P. hastata***, elongation of the propagules occurs on older, basal parts of the stem, and these are the most mature, becoming partially detached. However, both young and old brood branches will form new plants from any part. These are able to germinate in both low and high light, but in high light they typically fail to complete development of gametophores.

Figure 43. ***Philonotis hastata***. This wet habitat moss has its greatest gemma germination at around 750 lux. Photo by Jan-Peter Frahm, with permission.

Otto and Halbsguth (1976) found that rhizoid induction on gemmae of ***Marchantia polymorpha*** (Figure 44) was dependent on wavelength of light. The most effective wavelength was 350 nm, whereas no rhizoids were produced at less than 550 or more than 670 nm. They attributed this response to phytochrome and showed that an application of 10^{-4}M IAA for one hour had the same effect as the red-far red reversibility known for phytochrome.

Figure 44. ***Marchantia polymorpha*** thallus with gemma cups. Photo by Michael Lüth, with permission.

Water Relations

No growth can occur in the absence of water, but water can also affect the production of gemmae as an adaptive strategy to take advantage of flooding. In ***Bryoerythrophyllum campylocarpum*** (=***Hyophila crenulata***), gemmae occur on the protonema and are sensitive to humidity, with greater humidity causing greater gemmae production (Olarinmoye 1981). Flooding results in abundant basal protonematal gemmae. In its habitats of gutters, drainage areas, and other periodically flooded areas, these abundant gemmae facilitate spreading. The location of gemmae on protonemata provides them with the longest conditions of sufficient humidity compared to those on the stem or leaves.

In ***Marchantia***, which is not typically a flood plain species, Kaul *et al*. (1962) found that gemmae did not produce rhizoids when grown in liquid culture, but did in solid media.

Gender

It appears that gender can also play a role in timing of gemmae production. This is expected, since the energy required by production of antheridia and sperm is considerably less than that needed for the development of the sporophyte following fertilization. Thus, we might expect a delay in gemma production in females of a species, providing a longer span of energy to be diverted to the young sporophyte. Fuselier and McLetchie (2002) addressed this relationship in the dioicous ***Marchantia inflexa*** (Figure 45). In a low-light environment, the onset of gemma production and plant size early in development were under sex-specific selection. Furthermore, females paid a higher price for plasticity in the onset of gemma production under high light. Selection for asexual fitness shifted the offspring toward monomorphism rather than sexual dimorphism. However, there were negative tradeoffs between the asexual and sexual fitness, at least in females, under some light conditions. Fuselier and McLetchie suggest that the opposing selection forces of these two reproductive strategies (sexual and asexual) might explain the persistence of sexual dimorphism of mature plants, while selection favored immature plants in which gender was indistinguishable.

Figure 45. ***Marchantia inflexa***, a species where the sexes respond differently to light intensity. Photo by Scott Zona, through Creative Commons.

Mallón *et al*. (2006) experimented with vegetative propagules in the dung moss ***Splachnum ampullaceum*** (Figure 46) and suggested that ABA might be important in the ability of the protonema to produce brood cells and survive desiccation. This added production of brood cells would also permit the colony to spread, perhaps accounting for the very dense populations that are typical (Figure 46).

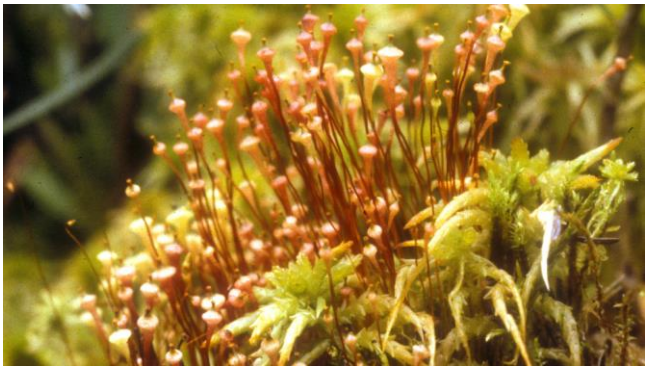


Figure 46. ***Splachnum ampullaceum*** growing on dung in a cow pasture. Photo by Janice Glime.

Nutrients and Inhibitors

We know that sucrose can cause germination of gemmae in ***Marchantia nepalensis***, suggesting that a photosynthetic response is needed to provide a continuous energy supply (Chopra & Sood 1970). This is supported by the increased germination with increased light intensity.

One factor we know to be important in any cell growth is calcium. Grotha (1983) found evidence in ***Riella helicophylla*** (Figure 30) suggesting that the distal lobe of the gemma and the non-dividing cells of the rhizoid initials of the gemma have zones that facilitate Ca^{+2} absorption.

Other plants can have an effect on the success of gemmalings. This is manifest not only in competition for light, but in chemical warfare as well. The epiphytic leafy liverwort ***Radula flaccida*** is affected by leachates and extracts of the supporting tree upon which it grows (Olarinmoye 1982). Although these seem to have no effect on the germination of the gemmae, they are important in the later establishment of the gemmaling, affecting cell length, leaf size, and rhizoid development. These effects seem to be dependent on the species of tree leaf involved and could account for differences in the colonization success on different species of trees.

Dormancy

One control of gemmae survival under conditions of cold or dehydration lies in their ability to maintain dormancy. We know that ***Marchantia*** gemmae (Figure 44) are unable to germinate while remaining on the parent plant, a condition in which we assume the parent to be responsible for inhibiting the germination and thus attaining gemma dormancy. But some dormancy seems to be under environmental control in ways that protect the young gemmalings from unfavorable environmental conditions. For example, the leafy liverwort ***Lophozia ventricosa*** var. ***silvicola*** (Figure 47) produces gemmae that are able to grow and replace dead shoots of the parent colonies. But these gemmae can be deposited throughout the growing season, some of them arriving upon favorable substrata when winter is imminent. Laaka-Lindberg and Heino (2001) propose that some gemmae are destined to become non-germinating gemmae, entering a "season-specific" dormancy. They suggest that only the dormant gemmae are able to survive winter. this is a good "bet hedging" strategy that permits some gemmae to get an early start on the competition while the season is still favorable, but permits some gemmae to safely overwinter while some of the germinated gemmalings might not make it through.

Figure 47. ***Lophozia ventricosa*** with gemmae that can replace dead shoots. Photo by Jan-Peter Frahm, with permission.

Dormancy is an adaptive strategy of utmost importance to organisms inhabiting unpredictable environments. Laaka-Lindberg (2000) considered it a way to spread the risk and enhance survival by making more effective use of resources. By remaining dormant when conditions are less favorable, resources are not lost to competition (Rees 1996; Hyatt & Evans 1998). Dormancy has been viewed by some as an alternative to dispersal, creating a facultative response in patchy environments where some patches are suitable and others are not (Cohen & Levin 1991; McPeek & Kalisz 1998). It is also a way to survive over winter in the leafy liverwort ***Lophozia ventricosa*** var. ***silvicola*** (Figure 47), with summer-produced gemmae germinating immediately and late-season gemmae becoming dormant for the winter (Laaka-Lindberg 2000).

Like spores, gemmae are typically under the control of light for germination, failing to germinate in the dark (Risse 1987). Schwabe (1972) reported that ***Lunularia cruciata*** (Figure 48) could survive dormant for months in total darkness. In ***L. cruciata***, long days induce dormancy. Nevertheless, it is a complex interaction of photoperiod, temperature, and phytochrome response that determines dormancy or germination. Furthermore, lunularic acid within the gemma cup promotes dormancy. The presence of other plants of their own or other species also provides an inhibitory function, as discussed earlier. The ability of lunularic acid to inhibit algal and fungal growth and to delay seed germination in some species suggests it may be allelopathic not only to its own offspring, but to other groups of taxa as well, thus potentially making the environment more friendly toward the success of the gemmalings once conditions are suitable for them.

Figure 48. ***Lunularia cruciata***, a liverwort where dormancy is induced by a variety of environmental conditions. Photo by David Holyoak, with permission.

This dormancy in ***Lunularia cruciata*** (Figure 48) permits gemmae to remain dormant underground in soil banks (Schwabe 1972). However, it is not that simple. If they are wet, they will not survive more than 10 days without germinating, and their fat reserves are depleted in 15 days if they are unable to replace it through photosynthesis. Furthermore, once they have imbibed water and begun to germinate, in as few as 12 hours, they are sensitive to desiccation and will not survive if dried at that stage.

Many have observed the dormancy of gemmae while still in the cups on the thallus of ***Marchantia polymorpha*** (Figure 44). Yet, when these gemmae get splashed onto the soil or the thallus dies around them, they seem able to germinate immediately. Schwabe (1976) has shown that it is lunularic acid from the parent thallus, serving as an inhibitor, that is responsible for this dormancy. Kumra and Chopra (1989) have shown that application of exogenous auxins inhibit growth of both gemma cups and vegetative plants of ***Marchantia palmata***. The auxin IAA is likewise known to inhibit germination of gemmae of ***Lunularia cruciata*** (Figure 48) in the lab (LaRue & Narayanaswamy 1957).

Lunularic acid occurs in the soluble fraction of the cell (as well as in association with the cell wall; Schwabe 1990). Therefore, inhibitors such as lunularic acid can be leached from the plant (Schwabe & Nachmony-Bascomb 1963), especially older parts of the thallus (Schwabe 1990), therefore potentially having an effect on neighbors of the same or even different species. Since leaching is likely to be greater during dry periods or immediately following them, this could cause a seasonal or weather-related response.

Germination Time

Germination times vary with type of propagule, size, age, and available water. And light seems to be required for most (all?). Propagula can germinate in 2-4 days in ***Bryum*** and ***Syntrichia*** (Llo Stark, pers. comm. 3 February 2015).

Tradeoffs

There are tradeoffs in using energy to produce brood bodies instead of spores. Whereas spores require a prior fertilization, which requires abundant water for sperm to swim, spores disperse farther than brood bodies and are able to germinate maximally on previously uncolonized substrates; brood bodies do not require fertilization, hence negating the need for excessive water, but can only disperse locally, yet, at least in some cases, are more successful amid other plants than are spores (Newton & Mishler 1994). Egunyomi (1978) found that the protonemata of gemmae grow faster, a factor likely to be true for most bryophytes, but that spores produce more gametophytes. However, one must be cautious in transferring these laboratory results to field generalizations. In the field, protonemata from spores may be less successful than gemmae just because they take longer to develop and therefore are more likely to encounter unfavorable conditions, including competition. In a later study on ***Bryum coronatum*** (Figure 39) in Nigeria, Egunyomi (1982) found that vegetative propagules may succeed where capsules fail. In that species, 41% of the setae had no capsules and 42% of the capsules did not dehisce. The spore germination was 65-88%, but the protonemal growth was abnormal, suggesting that spreading by spores in nature might be rather limited. On the other hand, this species is likely to succeed in dispersal through its numerous axillary propagules.

But production of gemmae usually comes at a price. Sharing of energy can mean no one does well, so it is not surprising that sporophyte development does not coincide with gemma development. In ***Tetraphis pellucida*** (Figure 32), one cannot find gemma cups and sporophytes on the same plant. Both need to occupy the same location at the shoot apex, making it physically impossible. But typically, even the population tends to have these at different times.

Risse (1987) found that among colonist species, propagation is almost entirely vegetative, giving little chance for new combinations of genes. Tubers are common among mosses of disturbed habitats. In ***Leptobryum pyriforme*** (Figure 49), if the protonema is grown in water, gametophore production ceases while tubers and rhizoidal gemmae develop abundantly.

Figure 49. ***Leptobryum pyriforme***, a prolific moss in disturbed areas. Photo by Michael Lüth, with permission.

Hedderson (1995) demonstrated that in the **Pottiales**, production of sporophytes decreases with increasing life expectancy and is negatively associated with production of asexual brood bodies. Among the **Funariales**, **Polytrichales**, and **Pottiales**, dioicous taxa are more likely to produce asexual brood bodies, as are monoicous taxa for which gametangia are unknown. However, production of these brood bodies is positively associated with a longer life expectancy, suggesting that at least the brood bodies do not deplete the plant of its energy supply.

Competition for resources and energy are likely to account for the suppression of gemma production during the production of sexual structures (Terui 1981). In ***Marchantia polymorpha*** (Figure 44), this response can be counter-acted by the application of high sucrose concentrations, thus inducing development of gemma cups.

Because of competing energy requirements, the two genders are likely to differ in their production of gemmae. Female plants require considerably more energy to produce archegonia and sporophytes than do male plants to simply produce antheridia. For example, Laaka-Lindberg (2001) found that in the leafy liverwort ***Lophozia ventricosa*** var. ***silvicola*** (Figure 47), shoots lacking gametangia produced three times as many gemmae as female shoots, and that males produced twice as many. In ***Marchantia polymorpha*** (Figure 44), the number of gemma cups produced by females was less than 1/6 that produced by their male counterparts (Voth 1941). Interestingly, when phosphate supplies decrease to stress levels, the number of cups on male plants decreases while the number on females increases, making them nearly equal!

Ecological Function

Many types of asexual propagules comprise the propagule bank, available to colonize when disturbance brings them to the surface. In this way, taxa such as ***Leptobryum pyriforme*** (Figure 49) and ***Bryum rubens*** (Figure 50) readily colonize disturbed habitats and tip-up mounds (Risse 1987).

As Ross-Davis and Frego (2004) pointed out, our understanding of the role of bryophyte propagules in structuring communities is meager. To address this question, they examined the propagule rain and buried propagule banks of the mature mixed forests in southeastern New Brunswick, Canada. They found 51 taxa in the diaspore rain and buried propagule banks, but only 36 of these were present in the forest floor community. Differences in phenology were evident in the high seasonal variability within the aerial diaspore sources. Considering the hundreds of species available in the geographic region, these propagule sources are relatively limited, undoubtedly to nearby sources. The extant community was most similar to that of the aerial diaspores, suggesting that the buried diaspore bank was reminiscent of a different ecosystem and was ready if that set of conditions returned. Further discussion of brood bodies is in the adaptations subchapter on dispersal.

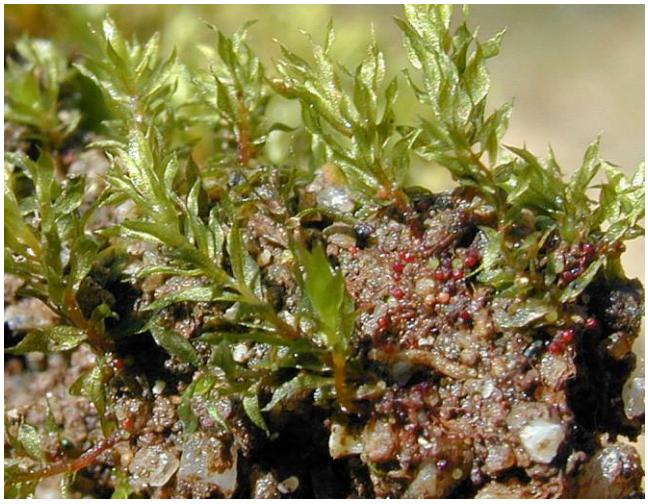


Figure 50. ***Bryum rubens*** showing red rhizoidal tubers in disturbed soil. Photo by Michael Lüth, with permission.

Summary

Brood bodies include both gemmae and propagules (vegetative diaspores). Propagules can be defined as reduced buds, branches, or leaves that serve in reproduction. Gemmae are relatively undifferentiated vegetative reproductive structures and come in a variety of shapes and sizes. Brood bodies provide a safe mode to survive environmental disturbances such as desiccation, physical disturbance, and freezing. Colonist species rely almost entirely on brood bodies to invade newly disturbed habitats. Asexual means are important in colony spread of non-perennial taxa. Brood bodies are most common on dioicous (unisexual) species and compete for energy, thus typically not being present during sporophyte production. As a result, they are often more common on males than on females.

Tubers of mosses occur on the rhizoids, but in liverworts they are extensions of the growing apex and grow toward the ground to serve as a perennating structure. In both cases they provide a diaspore bank that makes the species available when favorable conditions return.

Gemmae seem to require auxin (IAA) to develop and are inhibited from germination by the parent plant, presumably by lunularic acid in liverworts and probably by ABA in mosses. Production is affected by light intensity, wavelength, and moisture availability. These factors plus photoperiod and temperature are known to affect their germination and dormancy as well. Addition of sucrose enhances germination, suggesting the importance of photosynthesis to provide energy.

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CHAPTER 5-8
ECOPHYSIOLOGY OF DEVELOPMENT: GAMETOGENESIS

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CHAPTER 5-8
ECOPHYSIOLOGY OF DEVELOPMENT: GAMETOGENESIS

Figure 1. Antheridial splash cups of ***Polytrichum juniperinum***. Photo by Janice Glime.

Definition

Gametogenesis – the development of gametes (*genesis* means origin) is the essential process leading to sexual reproduction. In bryophytes, gametes are produced by mitotic division of tissue within multicellular structures, the **antheridia** (male) and **archegonia** (female), collectively known as **gametangia**. The location of these structures on the mosses is the basis for dividing the mosses into two large groups, the **acrocarpous** mosses that produce archegonia at the tips of upright stems, and the **pleurocarpous** mosses that produce archegonia on side branches of a generally horizontal stem. The differences in location of these archegonia can present differences in the ease with which the sperm can reach the archegonium, and hence reach the egg.

Developmental Stages

Lal and Bhandari (1968) described the developmental stages of the sex organs of the moss ***Physcomitrium carpathicum***. The archegonium begins its development in a manner similar to that of the antheridium. In these early stages, it produces a stalk, then the two-sided apical cell gains a third cutting face and the archegonium develops from this cell. The antheridial development is similar to that of other mosses. This chapter will examine the interaction of hormones and the environment as they influence this development.

Environmental Factors

The timing of the induction of gametangia is a critical function in the life cycle of bryophytes. For sexual reproduction to be successful, gametangia must form at a time when they can survive and they must mature at a time when it is safe and sufficient water is present for the sperm to reach the egg. This timing is controlled by external signals in the environment, and this is interpreted internally through such controls as hormones and nutrient levels.

Water Availability

Gametogenesis (development of gametes) must be timed in such a way as to take advantage of the most

critical need in fertilization – water. Because sperm in bryophytes must swim to the archegonium, adequate water is critical, but too much water or rapidly flowing water may dilute or carry off the sperm and make directional movement toward the archegonium all but impossible. In fact, timing of moss reproduction, whether a response to day length or temperature or other environmental stimulus, is often related to the season of proper moisture. Since gametangial initiation can occur several (or many) months prior to the actual time of fertilization, environmental cues other than moisture must trigger the process. It is therefore an expected consequence that different species within a genus respond to different environmental cues for gametogenesis, permitting them to live in different habitats. And even within species, populations can differ widely (Clarke & Greene 1970). But for many bryophytes, water is an important signal for gemetangia to develop, perhaps because it permits the gametophyte to be active and produce sugars needed for energy.

Gametangium Developmental Need for Water

Waterfalls can provide continuous moisture sufficient for sperm dispersal and even contribute to dispersal itself. At Churchill Falls, Labrador, Canada, the bryophytes are very fertile within the spray zone, whereas other vegetation expresses retarded phenology (Brassard *et al*. 1971). It could be that the spray itself induces gametangial production. Kumra and Chopra (1983) found that culture in liquid media favors antheridial induction in ***Barbula indica*** var. ***gregaria*** (Figure 2) and ***Bryum coronatum*** (Figure 3) over that in solid gel culture, greatly hastening it in ***Barbula indica*** var. ***gregaria***.

Figure 2. ***Barbula indica*** var. ***gregaria***, a moss where liquid medium favors antheridial production. Photo by Li Zhang, with permission.

Figure 3. ***Bryum coronatum***, a moss where liquid culture favors antheridial induction. Photo by Michael Lüth, with permission.

Sphagnum (Figure 4) provides a good example of effect of water on gametangial maturation. Sundberg (2002) studied nine sites in Sweden for six years, during which the nine most abundant species produced capsules. Capsule production related most to moisture regime of the previous summer, with more precipitation resulting in more capsules. This presumably relates to success of gametangial formation. Capsule success in wetter pits related positively to spring precipitation in the same year as capsule production, suggesting it was also important for fertilization success. Further discussion of timing of reproduction with moisture availability is in the phenology chapter.

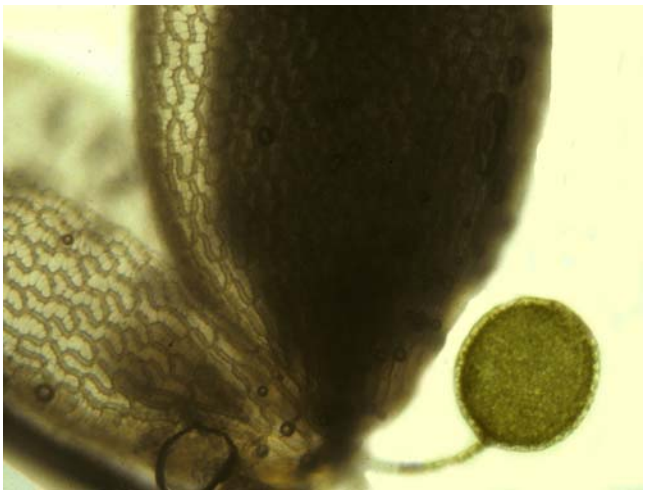

Figure 4. ***Sphagnum papillosum*** antheridium, a species for which moisture is important for gametangial success. Photo courtesy of Yenhung Li.

Swimming Sperm

For sperm to reach the archegonium, they must swim. But a tiny sperm cell (Figure 5) cannot carry that much energy with it, so the distance is limited. Some mosses maximize the effect of rainwater by producing **splash cups** (Figure 1) or **splash platforms** (Figure 6) that house the antheridia.

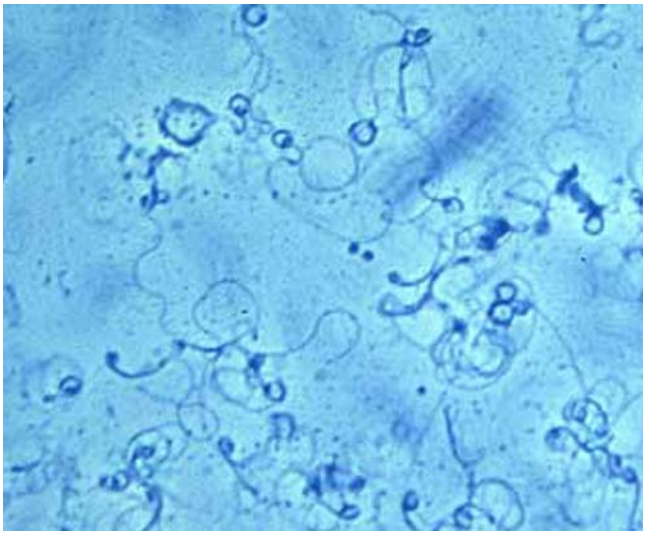

Figure 5. ***Marchantia polymorpha*** stained sperm. Photo from Botany Website, UBC, with permission.

The study by Andersson (2002) on ***Plagiomnium affine*** (Figure 6) provides insight into just how this splash works. He is the only one who has published photographs of the arrival and splash of an actual raindrop, eliminating the problem of laboratory tests where the drops do not reach terminal velocity. The splash is somewhat reminiscent of the expulsion of ***Sphagnum*** Figure 4) spores from a capsule, both demonstrating fluid dynamics. When the raindrop first hits a hard surface (splash cup or platform), it forms a crater many times the diameter of the drop. A jet of water then rises from the center of the crater (Rayleigh's jet). One or more large drops may be pinched off. In a splash cup, this force is typically sufficient to push all the water out of the cup.

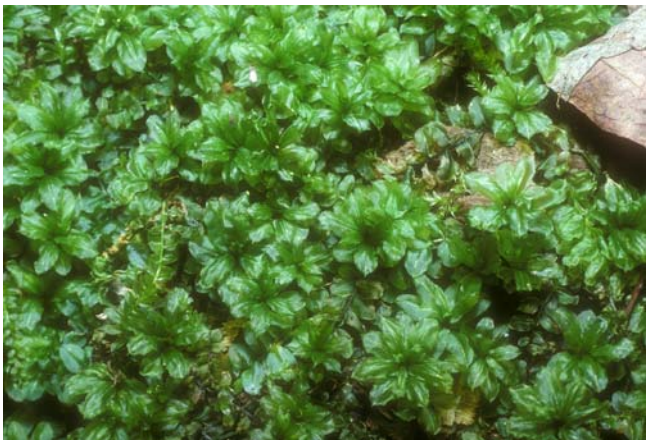

Figure 6. ***Plagiomnium affine*** showing antheridial platforms and runners. Photo by Janice Glime.

Splash cups and platforms are not flat, so the water angles are oblique (Andersson 2002). As the water flows outward from the point of impact, the edge of the water mass bends upward to form a crown. As the drop collapses, the circle of water widens and the crown bends up more. Wave motions travel both vertically and horizontally; a thick cylinder of water forms around the upper rim of the crown and small jets of water extend outward. As these jets become unstable, they break into many tiny droplets that shoot out from the crown with high velocity. The crown collapse occurs after about 8 ms on a wet surface. Most of the droplets are less than 0.5 mm, and many are less than 0.05 mm. The spermatozoids are only about 1 µm (0.001 mm) in diameter and can therefore easily be carried by the droplets of water.

Most experiments with splash cups have not been at distances that mimic terminal velocity. Based on data from Laws (1941), a 3 mm drop would need to be dropped from about 7 m to reach terminal velocity, a height not available in most labs. Reynolds (1980) considered that distances of 30 cm splash from point of impact would not be uncommon.

But does this splash really disperse the sperm? To be dispersed, sperm must be able to exit the antheridium, and this requires that the antheridium must burst. That criterion is satisfied by the first raindrop to strike a mature antheridium (Andersson 2002). But... members of the **Mniaceae** shrivel when dry and do not rewet easily. ***Mnium*** (Figure 7-Figure 8) species may require soaking for an hour before they are ready for making a slide (Koponen 1974), indicating that the leaves in a rainstorm are not ready to make a splash platform in less than an hour. Furthermore, the forest canopy traps many of the raindrops and reduces their velocity (Andersson 2002) or even diverts them so that they run down the trunk instead of striking the forest floor beneath them. Hence, it may take some time before the splash platform is exposed directly to raindrops in a storm, and this might not be achieved at all in a light shower.

Figure 7. ***Mnium spinosum*** wet. Photo by Michael Luth, with permission.

Figure 8. ***Mnium spinosum*** dry. In this condition, it is slow to take in water. Photo by Michael Luth, with permission.

To add further to the complications of reaching a female, the sperm are not released directly as individuals from the antheridium. Rather, they are released in a package, a **vesicle** of fluid. This vesicle must be disturbed by water drops before it will break apart. The vesicles become separated from each other by lipid drops and slowly dissolve, freeing the sperm.

Some seed plants have a chemical delay mechanism to prevent seed germination in a short rain shower, with chemical inhibitors being removed in a more significant rainstorm that is sufficient to sustain the young plant. The intervening factors required for a raindrop to splash the bryophyte sperm successfully seems like a mechanical method to delay sperm dispersal until it is certain there will be sufficient water for the sperm to complete their journey after the splash, with the delay in freeing sperm contributing to this mechanism.

The moss ***Plagiomnium affine*** (Figure 6) is less fortunate than the species with real cups. Its antheridial

platforms succeed only in splashing droplets with sperm about 100 mm (Andersson 2002). Fortunately, most of the females within 80 mm are successfully fertilized, but that does not permit much outcrossing.

In ***Polytrichum ohioense*** (Figure 9), the 2-3 mm cup permits sperm to be splashed 60 cm or more (Brodie 1951). A similar distance is accomplished by the splash platform of ***Marchantia polymorpha*** (Figure 10) (Buller 1942). Even greater distances, up to 230 cm, are achieved by antheridial splash cups of ***Dawsonia longifolia*** (Figure 11-Figure 12) (Clayton-Greene *et al.* 1977; see chapter on sexuality), aided by its greater height (up to 50 cm). These dispersal distances match the observed maximum distances between males and sporophyte-bearing females observed in the field. Very small splashes create an aerosol effect that could permit the sperm to float for considerable distances, and wind can increase the distance downwind.

Figure 9. ***Polytrichum ohioense*** with spent antheridial splash cups producing new growth. Photo by Janice Glime.

Figure 10. ***Marchantia polymorpha*** male splash platforms. Photo by David T. Holyoak, with permission.

Figure 11. ***Dawsonia longifolia*** with perigonia. Photo by Allan Fife, with permission.

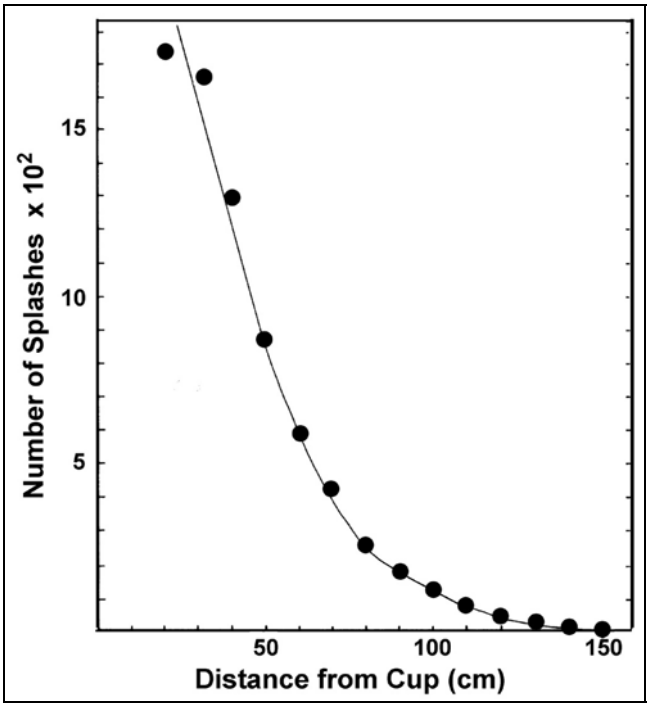

Figure 12. Distance of splashes from 0.055 ml drops dropped from 228 cm and splashed from the splash cup of ***Dawsonia longifolia***. Redrawn from Clayton-Greene *et al.* (1977).

Monoicous species (having male and female organs on the same plant) have a greater chance for fertilization than **dioicous** species because there will always be gametangia of the opposite sex nearby. Rohrer (1982) compared the success of dioicous species with and without splash cups in an aspen forest and a swamp forest of Michigan's northern Lower Peninsula. Those with splash cups had significantly higher sporophyte production (Figure 13). Unfortunately,

splash cups are relatively uncommon, but leaves surrounding antheridia can sometimes act as splash cups or platforms by spreading when hit by a raindrop (reference forgotten ☺).

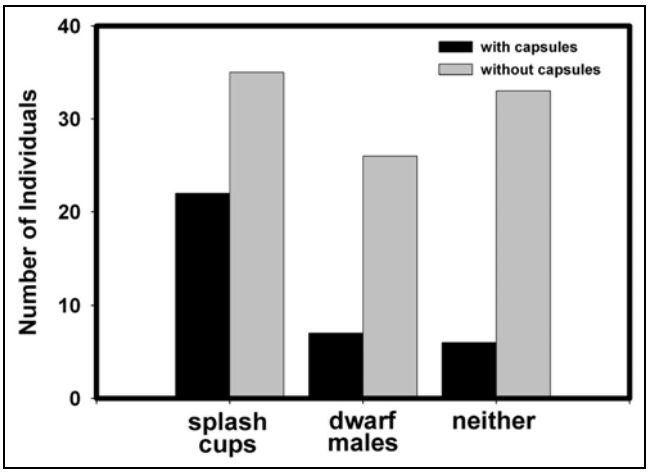

Figure 13. Effect of splash cups and epiphytic dwarf males on number of individuals with sporophytes in dioicous mosses of an aspen forest in the northern lower peninsula of Michigan, USA. Based on data from Rohrer 1982.

Paraphyses

This story is not complete without a discussion of **paraphyses**, those sterile structures, usually filamentous, that accompany most gametangia among the bryophytes. For something to persist this commonly while requiring energy for their development, we usually consider them to have some adaptive function. But little if any testing has been done to show that they make a difference.

Paraphyses usually occur in sufficient density to produce capillary spaces. With this knowledge, we can theorize as to their value. Such spaces would mean that water drops would be drawn between them, providing swimming spaces surrounding the archegonia. For antheridia, these can create water pressure that could aid in the rupture of the antheridium and hence the release of sperm.

But this does not seem to be the only excuse for their continued existence. In the Neckeraceae, structures that can be interpreted as paraphyses develop after fertilization in ***Neckeropsis*** (Figure 14), forming on the perichaetia (Merced-Alejandroa & Sastre-De Jesús 2009). These researchers found that transitions between uniseriate and multiseriate paraphyses occur at different stages in the developing reproductive branch. In early stages they are more typical of paraphyses in most mosses; this stage is the terminal stage in some ***Neckeropsis*** species. In other species, these continue to become multiseriate and ligulate to lanceolate. But what could their function be if they do not develop until after fertilization?

Figure 14. ***Neckeropsis undulata***, a genus in which paraphyses develop after fertilization. Photo by Michael Luth, with permission.

As discussed earlier, Reese (1955) tested a very different function for these paraphyses. He was able to demonstrate their ability to regenerate plants in ***Bryum capillare*** (Figure 15-Figure 16), ***Aulacomnium palustre*** (Figure 17), and ***Funaria hygrometrica*** (Figure 18-Figure 19). Could this be a back-up plan for unsuccessful sexual reproduction? Most likely it is actually a rare occurrence in nature, and thus its most frequent function is most likely that surmised by the early bryologists who considered them to have both a capillary function to draw in water, but also to retain water among the developing gametangia.

Figure 15. ***Bryum capillare*** males with antheridia and paraphyses. Photo by Dick Haaksma, with permission.

Figure 16. ***Bryum capillare*** antheridia, and paraphyses that can regenerate. Photo by Dick Haaksma, with permission.

Figure 17. ***Aulacomnium palustre*** males, a species in which paraphyses can regenerate new plants. Photo by David T. Holyoak, with permission.

Figure 18. ***Funaria hygrometrica*** with antheridia. Photo by Barry Stewart, with permission.

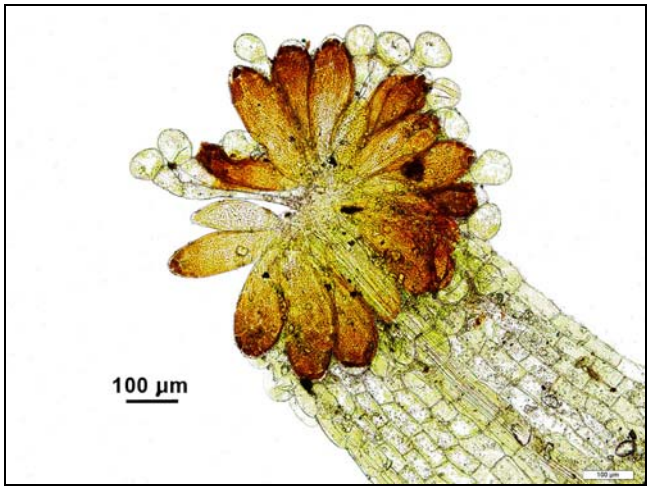

Figure 19. ***Funaria hygrometrica*** antheridia with paraphyses (white) that can regenerate. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Photoperiod and Light Intensity

Bryophytes, like flowering plants, can be classified into a variety of short-day and long-day types (Benson-Evans 1964; Maravolo 1980; Glime 1984; Li & Glime 1991). Tracheophyte species that occupy a wide latitudinal range, such as *Typha latifolia*, show population differences in response to day length (McNaughton 1966), and Longton (1972) has demonstrated this for the mosses ***Polytrichum*** (Figure 1, Figure 9) and ***Psilopilum*** (Figure 20). The physiological response mechanism in these two taxa is unknown, and a large number of substances can induce the same response, depending on the species.

In 1983, Chopra and Bhatla contended that mosses, except for ***Sphagnum plumulosum*** (=***S. subnitens***; Figure 21), appeared to be independent of photoperiod for the induction of gametangia. On the other hand, they found that all liverworts tested to date, except ***Ricciella crystallina*** (=***Riccia crystallina***; Figure 22) (Chopra & Sood 1973a), were either long-day or short-day plants. But they clarified this statement – it appears that even in liverworts, the response seems to be quantitative, with greater light intensities increasing the photoperiod response.

Figure 20. ***Psilopilum cavifolium***, member of a genus where populations can show differences in response to day length. Photo by Niklas Lonnell, with permission.

In mosses, other factors such as light intensity and temperature modify the response. For example, ***Bartramidula bartramioides*** [optimum of 3500-4000 continuous light (Chopra & Rahbar 1982)] and ***Leptobryum pyriforme*** (Figure 23) respond linearly to increasing light intensity for gametangial response (Chopra

& Rawat 1977; Chopra & Bhatla 1983), whereas ***Bryum argenteum*** (Figure 44-Figure 45), ***B. coronatum*** (Figure 3), and ***Barbula indica*** var. ***gregaria*** (Figure 2) respond to a specific light intensity for their optimal response (Chopra & Bhatla 1983). In ***Bryum coronatum*** and ***Barbula indica*** var. ***gregaria***, antheridia develop under "ordinary" cultural conditions (Kumra & Chopra 1983), requiring no specific photoperiod for induction, but having a greater response as the photoperiod increases. ***Philonotis turneriana***, on the other hand, remains sterile under "ordinary" conditions. Temperature likewise plays a role, but its role is primarily to constrain the photoperiodic effect within certain temperature limits. However, in ***Philonotis turneriana*** a temperature of 18°C is needed for induction. In ***Barbula indica*** var. ***gregaria*** and ***Bryum coronatum***, the antheridial induction increases as the temperature increases, up to 24°C.

Figure 21. ***Sphagnum plumulosum***, one of the first mosses known to respond to photoperiod for gametangial induction. Photo by J. C. Schou <http://www.biopix.com/>, with permission.

Figure 22. ***Ricciella*** cf ***crystallina*** (=*Riccia crystallina*) Bareilly India. Photo by Michael Lüth, with permission.

Knoop (1984), like Chopra and Bhatla (1983), contends that most mosses seem to be day-neutral. Nevertheless, Benson-Evans (1964) examined a large number of bryophyte taxa with varying environmental influences on initiation of gametangia; photoperiod seemed to be the overriding influence in most cases. In ten liverworts (4 Marchantiales, 6 Jungermanniales), the plants were long-day plants. ***Riccia glauca*** (Figure 24), ***Phaeoceros laevis*** (Figure 25), and ***Sphagnum plumulosum*** (Figure 21) are short-day plants. The moss ***Pogonatum aloides*** (Figure 26) (Benson-Evans 1964) and liverwort ***Ricciella crystallina*** (Figure 22) (Chopra & Sood 1973b) are day-neutral. ***Phaeoceros*** spp. (hornworts) are predominantly long-day induced, a condition that may be true for most hornworts (Schofield 985). Temperature and other external factors can modify these responses, and surely energy will play a role. But are most mosses really day-neutral?

Figure 23. ***Leptobryum pyriforme*** with capsules, a moss that produces more gametangia as light intensity increases. Photo by David T. Holyoak, with permission.

Figure 24. ***Riccia glauca***, a long-day liverwort. Photo by Jan-Peter Frahm, with permission.

Figure 25. ***Phaeoceros laevis***, a long-day hornwort. Photo by Robert Klips, with permission.

Figure 26. ***Pogonatum aloides*** with male splash cups. Photo by David T. Holyoak, with permission.

Despite the tendency for liverworts to be controlled by photoperiod, ***Lophocolea*** (Figure 27) in southern Illinois, USA, is day neutral (Zehr 1979). And the mosses ***Diphyscium foliosum*** (Figure 28), ***Atrichum angustatum*** (Figure 29), and liverwort ***Trichocolea tomentella*** (Figure 31) are long-day plants for gametangial production. ***Nowellia curvifolia*** (Figure 30) is likewise a long-day liverwort, but only for initiation. They will continue to develop unless the process is halted by desiccation.

Figure 27. ***Lophocolea heterophylla*** on a log, a day-neutral liverwort, at least in southern Illinois, USA. Photo courtesy of Betsy St. Pierre.

Figure 28. ***Diphyscium foliosum*** showing female plants with perichaetial leaves and purplish male plants. Photo by Li Zhang, with permission.

Figure 29. ***Atrichum angustatum*** males, a long-day species for gametangial production. Photo by Bob Klips, with permission.

Figure 30. ***Nowellia curvifolia***, a long-day liverwort for gametangial induction. Photo by Michael Lüth, with permission.

Figure 31. ***Trichocolea tomentella***, a long-day plant for gametangial production. Photo by Michael Luth, with permission.

Voth and Hamner (1940) found that photoperiod controlled the development of gemma cups vs gametangiophores in ***Marchantia polymorpha*** (Figure 10). Short days stimulated gemma cup production, whereas long days stimulated more gametangiophores. Miller and Colaiace (1969) found that this species could be grown from gemmae and induced to produce antheridiophores and

archegoniophores in 3-6 weeks under a 24-hour photoperiod at 23°C.

Perhaps ***Fontinalis*** can again give us insight into these seemingly different results. Members of this genus, like ***Fontinalis novae-angliae*** (Figure 32), that are common in fast water of mountain streams face the problem of losing their tiny sperm rapidly downstream as soon as they are released. Goebel (1930) suggests that ***Fontinalis*** can only reproduce when it is in standing water because the water would otherwise wash the sperm away too easily. Hence, it appears that those mosses that live submersed in streams must time their sperm release to coincide with low water levels when the moss is moist, but not in rushing water.

Figure 32. ***Fontinalis novae-angliae*** in a swift mountain stream in New Hampshire, USA. Photo by Janice Glime.

This need for timing of sperm release suggests that a photoperiod response would be beneficial in those regions where low water level periods are somewhat predictable. Indeed, in ***Fontinalis dalecarlica*** (Figure 33), photoperiod seems to control production of gametangia quantitatively, rather than being an on-off signal, with short days causing the maximum number of archegonia to be mature when the moss is above water, but wet, during late summer and early autumn (Figure 34; Glime 1984). Longer days seem to lengthen the time for archegonia production, but aeration (from being above water) is also an important factor, resulting in more archegonia compared to those on submersed stems. Maturation of gametangia when the antheridia and archegonia are located above water, but moist, provides moisture for fertilization but protects the sperm from being washed away by fast water (Figure 35). Perhaps initiation of archegonia is more complex in mosses, causing the appearance of being day-neutral when the combination of stimulating factors is not present.

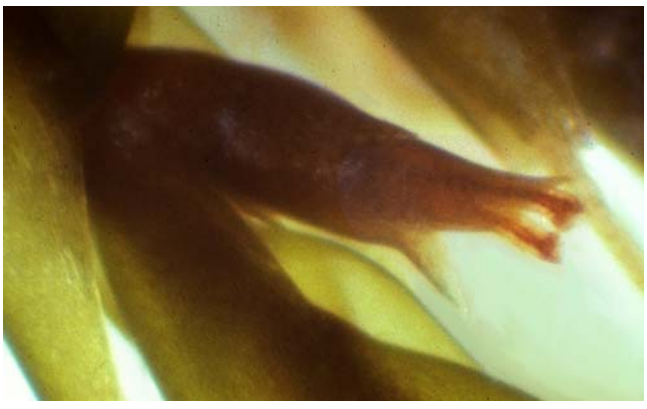

Figure 33. ***Fontinalis dalecarlica*** archegonia, a genus that responds to day length. Photo by Janice Glime

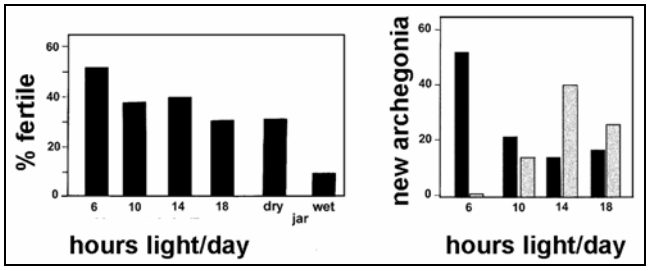

Figure 34. Effects of photoperiod and exposure to air on production of archegonia in ***Fontinalis dalecarlica*** (Figure 33) after 16 weeks of cultivation in artificial streams. **Left:** Day length effect and effect of submersed (wet) vs emergent (dry) at 14-hr photoperiod. Fertility does not differ significantly among the photoperiods, but emergent mosses produced significantly more than wet ones ($p < 0.01$). **Right:** Effect of photoperiod on development time required for archegonia. Black bars ▮ are numbers of archegonia produced during weeks 1-7; gray bars ▒ are numbers produced during weeks 7-16. n = 40 plants in each condition. From Glime 1984.

Leitgeb (1868) found ***Fontinalis antipyretica*** (Figure 35) to produce antheridia from spring until fall, but he did not mention whether the number maturing remained constant. At least for ***Fontinalis dalecarlica*** (Figure 33) from North Carolina, the fact that production is not perfectly responsive to short days, but rather occurs more slowly during longer days, assures the moss of having at least some gametangia ripe whenever water conditions are right (Glime 1984). It is a bet-hedger in the sense of Stearns' (1976) r and K strategies. ***Fontinalis*** can afford to be a bet-hedger because its vegetative parts are both persistent and capable of reproducing by fragmentation. Even a series of years when gametangial maturity does not match the right water level would not cause a serious reproductive problem.

Figure 35. ***Fontinalis antipyretica*** partially above water, providing an opportunity for splashed sperm to locate an archegonium. Photo by Jan-Peter Frahm, with permission.

The suitable photoperiod may be altered by temperature, permitting the plant to be plastic and able to

complete its life cycle in different geographic regions where the photoperiod relationship to temperature is different. For example, ***Fossombronia brasiliensis*** is a short-day plant at 18ºC, requiring 6-12 hours of night, whereas at 10ºC its light requirements are more quantitative (Chin *et al*. 1987). Furthermore, photoperiod affected the sex ratio, with more female gametangia being produced at 10ºC and more male gametangia at 18ºC.

Continuous light can favor some moss gametangial production. For the moss ***Microdus brasiliensis*** (Figure 36), Chopra and Mehta (1987) found that gametangial production increased with increasing photoperiod, with continuous illumination at 18ºC being optimal.

Figure 36. ***Microdus brasiliensis***, a moss in which gametangial production increases with increasing photoperiod. Photo by Jan-Peter Frahm, with permission.

Light intensity can also control fertilization success. ***Phascum cuspidatum*** (Figure 37) has greater fertilization in shade, due to larger antheridia and greater dehiscence, than in sun (Hughes & Wiggin 1969). Since free water is required for fertilization, this mechanism provides a longer period of moisture while the sperm attempts to reach the egg.

Figure 37. ***Phascum cuspidatum*** with capsules, a moss with greater fertilization in shade. Photo by Michael Lüth, with permission.

Little seems to have been done to understand the relationships of photoperiod in gametangial development in the **Anthocerotophyta**. Benson-Evans (1964) reported that this group is comprised of short-day plants, but I haven't found enough references to justify that assertion. She reported that ***Phaeoceros laevis*** (Figure 25) is sterile in 18-hour days, but produces gametangia in 8-12 hour days. Ridgeway (1967) found photoperiod to be the critical factor to induce antheridia and ***Anthoceros*** (Figure 38), ***Phaeoceros***, and ***Notothylas*** (Figure 39), whereas a range of temperatures from 10 to 20°C had almost no effect. However, at 5 and 25°C, the six species studied failed to produce antheridia. At 10°C, none of the species produced antheridia in 18-hour days, whereas all produced them in that photoperiod at 8°C. Most also produced them at 4 and 12°C.

Figure 38. ***Anthoceros agrestis***, a hornwort that produces gametangia in response to photoperiod, shown here with sporophytes. Photo by Jan-Peter Frahm, with permission.

Figure 39. ***Notothylas orbicularis*** with involucres, a species that responds to photoperiod but not temperatures. Photo by Michael Lüth, with permission.

Using single-spore cultures, Lazarenko and Lesniak (1972) found that the long-day (16 hours daylight) ***Desmatodon cernuus*** is sterile in 24 hours of light. Such requirements from the natural environment could eliminate the sexual reproduction in populations that develop in more northern latitudes and may explain the reliance of some species on asexual reproduction. The sibling species ***Desmatodon ucrainicus*** is fully self compatible.

In a more recent study, Lee *et al*. (2010) found that it can actually be the change in photoperiod that induces gametangia. In ***Pohlia nutans*** (Figure 40), changes from long days to short days effected gametangial initiation. It appears we need many more studies before we can assess the importance of photoperiod (and light intensity) on gametangial induction in bryophytes, especially mosses.

Figure 40. ***Pohlia nutans*** with perigonia, a plant that responds to a change in photoperiod to initiate gametangia. Photo by Michael Lüth, with permission.

But it appears that we know little about the effects of light intensity or light quality on the development of gametangia or the success of fertilization. Could it be that in certain wavelengths the sperm are more likely to die, particularly in the UV range?

Photoperiod response is likely to be one of the most frequent differences seen between populations at different latitudes. Wavelength is also likely to be a selection factor, especially at high altitudes. Selection forces would be strong against those individuals that produced gametangia at times when completion of reproduction was unlikely due to low temperatures and possibly strong UV light. Weitz and Heyn (1981) demonstrated that reaction to day length was one of the traits that differed among populations of the ubiquitous moss ***Funaria hygrometrica*** (Figure 41) from various geographic-climatic regions.

Figure 41. ***Funaria hygrometrica*** (Common Cord-moss) male plants with antheridial splash platforms. Photo by Barry Stewart, with permission.

The moss ***Bartramidula bartramioides*** is unusual in having a high nutrient requirement. Chopra and Rhabar (1982) found that it grew best at full strength Knop's medium plus Nitsch's nimor nutrient solution. Gametangial **induction** (initiation of development) occurred at 25±2°C, 3500-4000 lux continuous light.

Nutrients

Nutrient supply as a control of gametogenesis occurs throughout the plant kingdom, although it is probably best developed in the algae. The green algae ***Oedogonium*** (Singh & Chaudhary 1990) and ***Chlamydomonas*** (Figure 42) (Trainor 1959; Matsuda *et al*. 1992) recognize the approach of winter by the diminishing supply of nitrogen in a usable form, developing gametes and creating zygotes (then zygospores) that are able to survive the winter. It is appropriate to ask what role nutrients play in the life cycles for organisms that have quite low nutrient requirements – the bryophytes.

Figure 42. ***Chlamydomonas***, a genus that responds to diminishing N supply by producing gametes. Photo by Janice Glime.

Ramina *et al*. (1979) demonstrated the role of nutrients in *Bougainvillea*, where flower production increased in direct relationship to leaf production but decreased in relation to branch production (which used nutrients without making more). In the aquatic moss ***Fontinalis dalecarlica*** (Figure 33), production of gametangia likewise is inversely related to branch production from 10 August to 14 October (Figure 43), again suggesting an energy limitation (Glime 1984).

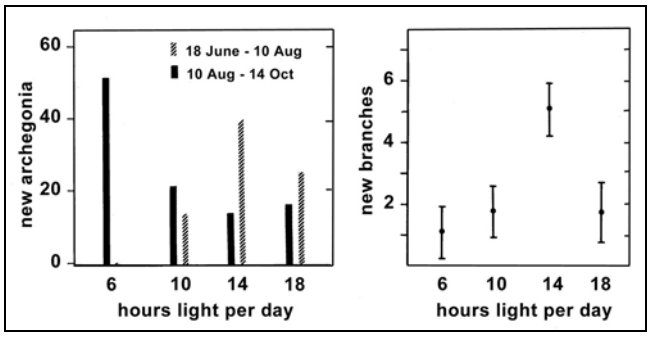

Figure 43. Effect of photoperiod on number of archegonia vs branches in ***Fontinalis dalecarlica***. Redrawn from Glime 1984.

Selkirk (1979) has shown that limited nitrates cause gamete production in several species of the liverwort ***Riccia*** (Figure 24), and Joenje and During (1977) showed that lower nutrients stimulate the production of sex organs

in ***Bryum argenteum*** (Figure 44-Figure 45). A low N:high C ratio in ***Marchantia*** (Figure 10) likewise stimulated production of sexual branches (Lockwood 1975). On the other hand, in ***Fossombronia brasiliensis*** (see Figure 46), N as nitrate caused more gametangial production than when it was supplied as ammonium (Chin *et al*. 1987). Such differences can help to explain differences in habitat preferences among species.

Figure 44. ***Bryum argenteum*** with several plants showing antheridial apices. Photo by Dick Haaksma, with permission.

Figure 45. ***Bryum argenteum*** perigonium showing antheridia. Photo by George J. Shepherd, through Creative Commons.

Figure 46. ***Fossombronia*** sp. ***Fossombronia brasiliensis*** produces gametangia in response to nitrate nitrogen. Photo by Ken-ichi Uedo, through Creative Commons.

Carbohydrates are important for gametangial formation in at least some bryophytes. Whereas ***Bryum argenteum*** (Figure 44-Figure 45), ***B. coronatum*** (Figure 3), and ***Barbula indica*** var. ***gregaria*** (Figure 2) produce gametangia in the absence of carbohydrates in culture, ***Ricciella crystallina*** (Figure 22) and ***Bartramidula bartramioides*** respond to enhanced carbohydrates (Chopra & Bhatla 1983), and addition of sugar in culture seems to be essential for ***Bartramidula bartramioides*** (Chopra & Rahbar 1982). But, as discussed above, Chopra and Bhatla (1983) found that a high carbohydrate:nitrogen ratio was more important than carbohydrates alone in the initiation of gametangia. In particular, bryophytes are likely to respond to depletion of nitrate or ammonium (depending on species), whereas organic nitrogen (amino acids, peptone, urea) affects gametangial formation differently among various species of liverworts.

Amino acids and kinetin, both found in the environment, can alter the photoperiodic response of gametangial induction in the leafy liverwort ***Cephalozia lunulifolia*** (=***C. media***; Figure 56) (Lockwood 1975). Arginine, cysteine, and tryptophan plus kinetin negated photoperiodic control. Those compounds that stimulated asexual reproduction (gemmae) under short photoperiods would also inhibit gametangial activity under long-day conditions. Addition of inorganic nitrogen had no effect on these responses.

Thus, as concluded by Chopra and Bhatla (1983), the importance of the nutrient status varies by species. Generally, however, low nutrient levels seem to be the most important in gametangial induction.

The need for sugar may be an artifact of culture. In their study of the liverwort ***Cryptomitrium himalayense***, Awasthi *et al*. (2013) found that sugar was necessary in the lab for gametangial induction, but when cultured on soil, this species produced gametangia under the same temperature of 21°C and long day (16 hours light) regime with colder nights (8 hours darkness at 15°C), but with no added sugar necessary.

Belkengren (1962) had some rather unusual results in ***Leptodictyum riparium*** (Figure 47). In this species, he was able to induce gametangia by culturing in continuous light, using a CO_2-free period followed by addition of sugar or CO_2. I don't know how this relationship would apply in nature.

Figure 47. ***Leptodictyum riparium***, a species that can produce gametangia in continuous light. Photo by David T. Holyoak, with permission.

I find it interesting that the same nutrient status that favors gametangial production also favors vegetative growth in ***Bartramidula bartramioides*** (Chopra & Rahbar 1982). This was demonstrated using Knop's major nutrients plus Nitsch's minor nutrients at full strength with 1% sucrose. Perhaps the added sucrose gave it the energy it needed to support both.

A low nutrient status in the environment can trigger transport of nutrients from leaves to younger, growing parts in tracheophytes (Salisbury & Ross 1978), and Ogawa and King (1979) have shown that in *Pharbitis nil*, translocation of assimilate is essential for flowering. Perhaps translocation of assimilate accounts for the stimulus to produce gametangia under low nutrient conditions in bryophytes as well, but at present we have no clue that this occurs. By contrast, working with ***Bartramidula bartramioides***, Chopra and Rahbar (1982) showed that optimum conditions for induction of gametangia included full strength nutrient solution.

In ***Ricciella crystallina*** (Figure 22), there was no response in growth of thalli when calcium nitrate concentration was doubled or even quadrupled in Knop's solution (Sood 1974). However, increasing potassium nitrate cause a "considerable" increase in growth. Changing to ammonium nitrate or ammonium sulphate caused the formation of callus tissue. Fe-EDDHA and Fe-EDTA had no effect on thalli, but slightly increased production of archegonia (optimum at 10^{-5} M). Urea as a nitrogen source supported both robust growth and increased archegonial production. Amino acids likewise affected sexuality, with hydroxyproline, serine, threonine, asparagine, glutamic acid, alanine, and leucine causing production of more archegonia. Glycine, tryptophan, aspartic acid, and valine caused production of more antheridia.

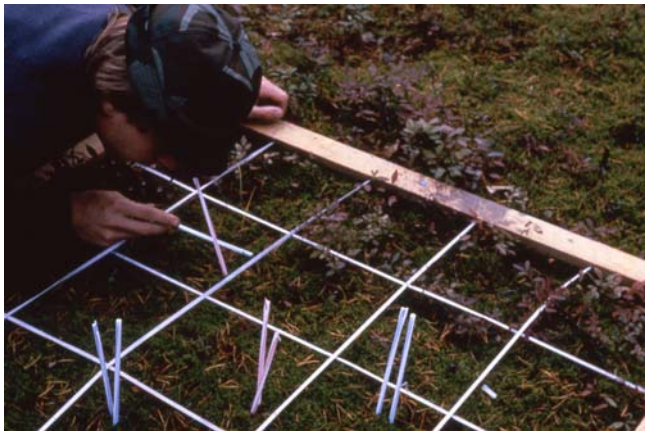

Figure 48. Geert Raeymaekers measuring distances between sporophytes on ***Pleurozium schreberi*** following simulated acid rain treatment. Photo courtesy of Geert Raeymaekers.

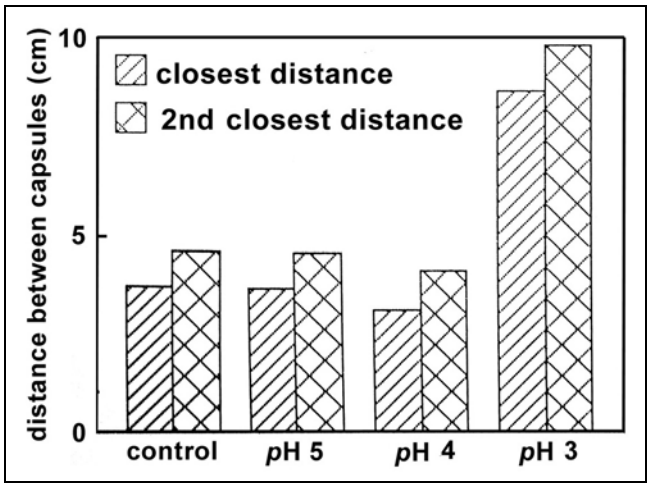

Figure 49. Comparison of distances between sporophytes in ***Pleurozium schreberi*** under simulated acid rain treatments. Redrawn from Raeymaekers 1986.

*p*H

Chopra and Bhatla (1983) concluded that bryophytes exhibit maximal gametangial initiation within a specific *p*H range, and that the *p*H of the medium changes during gametangial production. Bhatla (1981) found that a *p*H of 4.5 inhibited sexual induction in the moss ***Bryum argenteum*** (Figure 44-Figure 45). Raeymaekers (1986) found that a *p*H of 3.5 inhibited formation of capsules (Figure 48-Figure 49) in the acid-loving ***Pleurozium schreberi*** (Figure 50), thus indicating a possible connection with gametangia (Figure 51). Whether pH plays a role in induction of gametangia is unknown, but certainly low pH of acid precipitation can be detrimental to some mosses by interfering with sexual reproduction.

Rhabar and Chopra (1982) found that ***Bartramidula bartramioides*** produced more gametangia in liquid media than on semi-solid media. The two media exhibit different changes in *p*H, but these changes do not affect the time of gametangial induction. However, increasing *p*H, up to *p*H 7.0, increases the percentage of fertile gametophytes.

Figure 50. ***Pleurozium schreberi***, a moss whose sexual reproduction is sensitive to low *p*H. Photo by Bob Klips, with permission.

One interesting correlation in several species of ***Splachnum*** (Figure 66) is that low *p*H, along with low light and nutrient concentration, can favor males over females

(Cameron & Wyatt 1990). This results in clumps of one gender, but the changing *p*H with aging of the dung could favor a change in gender in later populations, ultimately resulting in the presence of both sexes on the same dung. In fact, the ratios on Isle Royale, Michigan, were typically 2:1 females to males.

In the eleven species of bryophytes from a Brazilian Atlantic Rainforest, Maciel-Silva *et al*. (2012) found that monoicous and dioicous species had different responses to *p*H. At sea level, the monoicous taxa were favored by a lower *p*H.

Figure 51. Archegonia of ***Pleurozium schreberi*** showing the loose perichaetial protection they have. Photo by Janice Glime.

Temperature

Temperature induces a variety of responses in flowering plants (Salisbury & Ross 1978), and we might expect even more variety in bryophytes, where some species remain active throughout winter even at high latitudes and altitudes. For example, ***Fontinalis hypnoides*** (Figure 52) produces more gametangia at 15°C than at 1, 5, 10, or 20°C (Glime 1982). Clarke and Greene (1970) showed that the reproductive response of ***Pohlia nutans*** (Figure 40) to day length is dependent upon temperature. In ***Leptobryum*** (Figure 23), low temperature is necessary for induction of antheridia, but once started they are independent of temperature (Chopra & Rawat 1977). On the other hand, for the thallose liverwort ***Ricciella crystallina*** (Figure 22), it appears that temperature is the overriding factor, provided there was a certain minimum photoperiod provided (Chopra & Sood 1973a).

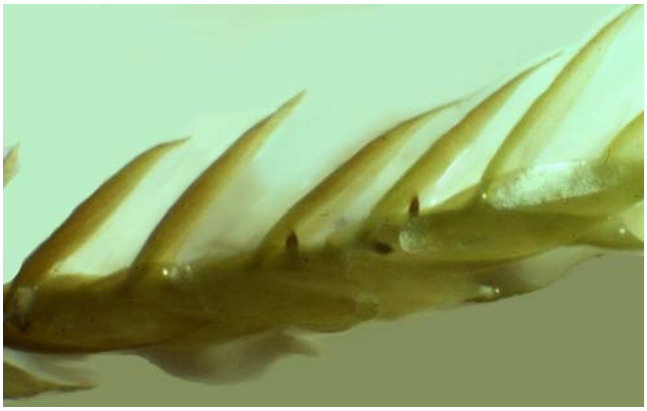

Figure 52. ***Fontinalis hypnoides***, a moss that produces maximum gametangia (seen in early development here) at 15°C. Photo by Janice Glime.

Chopra and Bhatla (1983) suggest that bryophytes operate in a range of temperatures, and that responses to light intensity and photoperiod might only operate within a range of temperatures that are broad in some species and narrow in others. Nevertheless, bryophytes do not seem to require any low temperature pretreatement for the induction of gametangia.

Hohe and coworkers (2002) found that both temperature and day length affect the expression of a MADS-box gene in ***Physcomitrella patens*** (Figure 53). In particular, one gene that was concentrated in the shoot apex and developing sporophytes produced higher RNA under conditions of 15ºC, 8 hours light per day, whereas vegetative growth was predominant at 25ºC, 16 hours light per day, suggesting that lower temperatures and photoperiod were important in sexual reproduction. This interdependence of temperature and photoperiod is an important way to coordinate gametangial production with the appropriate time for sporophyte development.

Figure 53. ***Physcomitrella patens***, a moss that responds to both photoperiod and lower temperatures for gametangial development. Photo by Jan-Peter Frahm, with permission.

Environmental Signalling Interactions

In many cases, perhaps most, the response to photoperiod or temperature or nutrients does not respond to just that one factor. The response is likely to differ in different geographic regions, and this can be the result of selection for a different factor as the trigger, perhaps because one factor cannot be expressed in this

environment. In ***Fossombronia brasiliensis*** (Figure 46), Chin *et al*. (1987) found that at 18°C the plants were short-day plants, requiring a night length of 6-12 hours. (Short-day plants typically are long night plants, measuring number of hours of darkness). When the temperature was only 10°C, this species became a quantitative short-day plant. But temperature also affected the gender expression, with more male gametangia being produced at 18°C and more female gametangia being produced at 10°C. Furthermore, the type of nitrogen available made a difference, with nitrate nitrogen causing production of more gametangia than did nitrogen in the form of ammonia.

In the dioicous moss ***Bryum argenteum*** (Figure 44-Figure 45), temperature, light intensity, and photoperiod all play a role in gametangial formation (Chopra & Bhatla 1981b). Both males and females produce the maximum gametangia at 25±2°C and in the light intensity range of 1800-2000 lux. At higher light intensities, vegetative growth occurs instead. If the temperature is lowered to 10±2°C, the response decreases. Chopra and Bhatla consider this species of ***Bryum*** to be a quantitative day-neutral plant because it is able to produce gametangia in as little as 8 hours of light, increasing production as the day lengthens.

The thallose liverwort ***Asterella tenella*** (Figure 54) requires the right conditions of both temperature and day length (Bostic 1981). For this species, **archegoniophores** (female reproductive branches) were induced under short days (10 hours) with 15°C daytime and 10°C nighttime temperatures.

Figure 54. ***Asterella tenella*** with archegoniophores. Gametangia are induced by short days in this species. Photo by Li Zhang, with permission.

Hormones

These physical cues must somehow be translated into biochemical responses. In the fern *Blechnum spicant*, gibberellic acid is known to illicit production of antheridia (Fernandez *et al*. 1997). In flowering plants, it can cause flowering. Since one known function of GA in flowering plants is increased water uptake (Salisbury & Ross 1978), this role might be important in maintaining an adequate internal water supply during gametogenesis of bryophytes.

Induction of **gametogenesis** by gibberellic acid is consistent with the role of GA_3 in increasing alpha-amylase activity, thus facilitating the metabolism of starch to sugar through hydrolysis. We know from the studies on ***Marchantia*** (Figure 10) (Maravolo 1980) that this starch conversion permits energy-supplying sugars to move to the actively growing regions such as gametangia. This sequel is so consistent with the need for sugar to maintain the sporophyte condition in callus culture (Bauer 1963b) and its requirement for gametophore production (Maravolo 1980), that one is tempted to accept this explanation alone. But how does this relate to photoperiod and temperature? And why do some plants respond to short days and others to long ones? I must conclude, as most flowering plant physiologists have done, that more than one substance is involved. In ***Fontinalis dalecarlica*** (Figure 33), the quantitative response to short days suggests a two-substance response – one present continuously and one that must accumulate as a function of photoperiod/light (Glime 1984).

Salisbury and Ross (1978) state that high auxin concentrations inhibit flowering and Benson-Evans (1961) found that auxins inhibit development of sexual organs in the thallose liverwort ***Conocephalum conicum*** (Figure 55). Growth substances such as 2,4-D and NAA induced receptacle formation but not gametangial production. Application of auxin at 16°C caused cell elongation of the archegoniophore, but not production of new cells. Therefore, it seems that gametogenesis might require the suppression of IAA.

Figure 55. ***Conocephalum conicum*** with antheridia whose development is inhibited by auxins. Photo by Malcolm Storey, through Creative Commons.

IAA seems to have other interesting reproductive functions. For example, in the dioecious hemp, IAA caused predominantly female sex expression (Chailakhyan & Khryanin 1978), but Salisbury and Ross (1978) point out that auxin levels and flowering seldom correlate in any meaningful way. In experiments on the leafy liverwort ***Cephalozia lunulifolia*** (Figure 56), kinetin + IAA inhibited sexual reproduction (Lockwood 1975). Tremaine and Glime (unpub. data) supplied IAA to ***Fontinalis duriaei*** (Figure 57) at concentrations of 10^{-6} and 10^{-8} M on a 12 hr light/12 hr dark cycle and there was no sign of gametangial initiation after 5 weeks. Yet this species usually produces gametangia during short days (personal observations).

Figure 56. ***Cephalozia lunulifolia*** with perianths (light color) enclosing archegonia. Photo by Michael Lüth, with permission.

Figure 57. ***Fontinalis duriaei*** archegonia, a species in which they fail to initiate with added IAA. Photo by Janice Glime.

Cytokinins can also play a role in sexual development. In the liverwort ***Riccia discolor***, 10^{-4} M kinetin proved to be the best concentration for promoting archegonial development as well as enhancing growth (Chopra & Gupta 1992).

Hormones may not affect the antheridial and archegonial inductions equally, possibly explaining how bryophytes manage to begin antheridial development long before archegonial development in most species. Chopra and Bhatla (1983) demonstrated that gibberellins contribute to the stimulation of antheridial formation in the bryophytes they investigated, whereas cytokinins stimulate archegonial induction while inhibiting antheridial induction in ***Ricciella crystallina*** (Figure 22) and ***Bryum argenteum*** (Figure 44-Figure 45). They found that auxins, gibberellins, and cytokinins can interact in controlling the gametangial response – no surprise there.

The hormone **IAA** may likewise have the opposite effects on the two sexes (Chopra & Bhatla 1983). In the thallose liverwort ***Ricciella crystallina*** (Figure 22), IAA increased archegonial induction, but in the mosses tested [***Bryum coronatum*** (Figure 3), ***B. argenteum*** (Figure 44-Figure 45), ***Barbula indica*** var. ***gregaria*** (Figure 2)], it favored antheridial induction.

Bhatla and Chopra (1981; Chopra & Bhatla 1981a) examined hormonal regulation of gametangial induction in ***Bryum argenteum*** (Figure 44-Figure 45) and found that both IAA and gibberellins (GA3) increase the induction of male gametangial branches while inhibiting the female clones in this dioicous moss. Cytokinins (kinetin, DMAAP) increased gametangial induction in the female clone while slightly inhibiting it in the male clone. When IAA and kinetin were both present, they were able to nullify the inhibitory capacity of each other. Cyclic AMP prevented kinetin from inhibiting male gametangial induction but stimulated the kinetin effect on females. ABA served as an inhibitor of both growth and gametangial induction in both sexes. Females proved to be more sensitive to ABA than males.

Cyclic AMP is one factor that may help in the control of hormone action and hence in controlling gametangial formation (Chopra & Bhatla 1983). This compound is a common mediator of hormone action in animals and is now known to increase gametangial induction in the moss ***Bryum argenteum*** (Figure 44-Figure 45). Cyclic AMP also increases antheridial induction in ***Bryum coronatum*** (Figure 3) and ***Barbula indica*** var. ***gregaria*** (Figure 2). To further confuse the investigator, it can overcome the inhibitory effects of ammonium ions and concentrations of sucrose that are too high, hence increasing gametangial formation, as Chopra and Bhatla have shown in ***Bryum argenteum***.

Environmental Hormone Interactions

Interactions with the environment can supply bryophytes with hormones, such as yeast extract and sex hormones from animals (Chopra & Bhatla 1983). These can increase the induction of both antheridia and archegonia.

Basile *et al*. (1969) found that the leafy liverwort ***Scapania nemorea*** (Figure 58) regularly associates with the bacterium ***Pseudomonas estorquens***. This association provides it with stimulation for both larger growth and earlier reproductive maturity than sterile cultures.

Figure 58. ***Scapania nemorea***, a liverwort that associates with ***Pseudomonas estorquens*** that stimulates earlier reproductive maturity. Photo by Li Zhang, with permission.

Sugars

Chopra and Rhabar (1982) found that sugar (1%) was necessary for gametangial induction in ***Bartramidula bartramoides***. On the other hand, ***Bryum argenteum*** (Figure 44-Figure 45) has markedly lower gametangial induction in 4% sucrose (Bhatla & Chopra 1979). Adding cyclic 3',5'-AMP neutralized the effects of the sucrose, but the concentrations are different for male (10^{-7}) and female (10^{-5}).

Overall Physiology

In summary, metabolic changes are needed for the initiation of gametangia (Chopra & Bhatla 1983). Liverworts may have an increase in cellular levels of carbohydrates, auxins, RNA, and proteins as the gametangial development begins. Enzymes and their concentrations change. Phenolic compounds change. And new colors develop. Reynolds and Maravolo (1973) found that two of the phenolic compounds inhibited IAA oxidase activity and two enhanced it in ***Marchantia polymorpha*** (Figure 10). The significance of this interaction in gametangial development seems still to be a mystery.

Both vegetative growth and gametangial development are regulated by and favored by iron and copper chelating agents such as EDTA and EDDHA (Chopra & Bhatla 1983). But it is interesting that in ***Riccia*** (Figure 24) these chelates favor archegonial development more than antheridial formation, whereas the opposite is true in ***Bryum argenteum*** (Figure 44-Figure 45) (Chopra & Bhatla 1983). Salicylic acid (the effective compound in aspirin) inhibits gametangial formation in most bryophytes, probably by chelating iron and copper or other metals involved in needed enzymes. We know that in ***Bryum argenteum*** there are marked changes in iron and copper levels. Iron seems to induce the reproductive phase, but copper inhibits it. In ***Bartramidula bartramioides***, on the other hand, salicylic acid enhances both vegetative growth and gametangial formation.

Cyclic AMP enhances antheridial production in the moss ***Bryum coronatum*** (Figure 3) and ***Barbula indica*** var. ***gregaria*** (Figure 2) and overcomes the inhibitory effects of ammonium ions and high levels of sucrose on gametangial development in ***Bryum argenteum*** (Figure 44-Figure 45) (Chopra & Bhatla 1983).

In an attempt to understand the physiological changes leading to development of gametangia in liverworts, Rao and Das (1968) studied ***Exormotheca tuberifera***, ***Plagiochasma articulatum***, ***Reboulia hemisphaerica*** (Figure 59), ***Fimbriaria angustata***, and ***Pallavicinia canara***. In ***Fimbriaria angustata***, a sharp rise in respiration and a doubling of the C:N ratio accompanied the transition from vegetative to reproductive state in females. Formation of archegoniophores occurred with an increase in the plant's own IAA, RNA, and protein. Carbohydrates accumulated in the archegoniophore at the expense of the gametophyte as the sporangia developed. By contrast, the antheridial production was correlated with a decrease in levels of IAA, RNA, and protein, and unlike the females, there was no notable increase in the C:N ratio.

Color Changes

Both antheridia and archegonia are often recognizable first by the addition of red coloration as they develop. In archegonia, this is often present in the neck canal cells (Figure 33, Figure 57). In antheridia, the color can be so intense that it is visible through the surrounding leaves, making branch tips red in some species of ***Sphagnum*** (Figure 60). In ***Marchantia berteroana*** (Figure 61), production of the flavone acacetin stops and instead 8-hydroxyapigenin and 8-hydroxyluteolin glycosiduronic acids (previously absent) become the predominant flavonoids (Markham *et al*. 1978). Acacetin seems instead to be important during the asexual phase.

Figure 59. ***Reboulia hemisphaerica*** male & female gametangiophores. Photo by Bob Klips, with permission.

Figure 60. ***Sphagnum*** with red antheridial branches. Photo by Janice Glime.

Figure 61. ***Marchantia berteroana*** antheridial heads showing red color. Photo by Clive Shirley, Hidden Forest, with permission.

Delay of Gametogenesis

But suppose that gametogenesis is **not** a process to be **initiated**, but rather it is a natural process that **must be stopped**. Sexual reproduction is ancient. It no doubt began with like cells bumping into each other and managing to stay together long enough to fuse. No special

male and female existed; no special inducers were needed. Perhaps something was needed to cause the two membranes to lose their integrity at the region of contact. Then the process became more sophisticated. Attracting substances drew cells together; different strains arose, some repelling and others attracting. Ultimately, special structures housed these one-celled gametes, and then some control was possible. As this scenario continued, the process became more complex and more controlled. The joining and dividing cycle of primitive cells was then subject to controlled delays. Whole sequences of differentiation were interjected to delay the sexual process. These sequences are the ramifications by which we identify species, genera, even phyla of plants. Therefore, it is reasonable that gametogenesis is controlled by inhibitors, factors of the surrounding tissues that retard gamete production and allow productivity of the organism to increase.

It follows that the multitudinous environments for the many species have caused this problem to be solved in multitudinous ways (see Stebbins & Hill 1980). Thus in one species a high concentration of IAA prevents gametogenesis, whereas in another the lack of alpha-amylase or GA deprives the prospective gametangia of the necessary energy source. As long as the raw ingredients (*e.g*. energy, nitrates, amino acids) are being diverted to other sources, gametogenesis is retarded. Such a multitude of ways can accomplish this that surely no consistent pattern could be recognized or even expected. The possibilities of combinations of concentrations and mobilities necessary to override the limits caused by the parent plant are almost limitless.

Male vs. Female

It is often considered a paradox that bryophytes tend to have female-biased sex ratios, whereas flowering plants usually have male biased sex ratios (Rydgren *et al*. 2010). Early control over gender was most likely simple. Internal environment may have been important. For example, Bhandari and Lal (1968) observed abnormal archegonia in ***Physcomitrium immersum*** that behaved as antheridia. Each had an egg, ventral canal cell, and neck canal cells as would be found in a normal archegonium, but in some these divided repeatedly, forming instead a mass of antheridial cells. They suggested that this is evidence of common origin of the two sexual organs.

Such behavior is somewhat suggestive of sex determination in maple (*Acer*) flowers. In these plants, the concentration of plants affects the ethylene concentration as the flower develops and determines the sex ratio by abortion of one of the parts. Factors related to sex ratio in bryophytes have been discussed in the chapter on sexuality. Therefore, they will be covered only briefly here.

We have noted that bryophytes, or at least many of them, do have sex chromosomes, a phenomenon known for plants first in the liverwort genus ***Sphaerocarpos*** (Figure 62) (Allen 1930; Anderson 2000). The gender is expressed only in the gametophyte generation by having either a small Y chromosome (male) or an X chromosome (female). This determination is made at meiosis, providing two male and two female spores. The monoicous (bisexual) taxa seem to have been derived mostly from polyploidy in which the chromosome number is duplicated and both X and Y chromosomes are present.

Figure 62. ***Sphaerocarpos michelii***, member of the genus where X and Y sex chromosomes were first discovered. Photo by Jan-Peter Frahm, with permission.

When the sexes are separate, *i.e*. dioicous/unisexual taxa, it is not unusual to find all male or all female populations, derived from a single spore carrying genes for only one gender. In other cases, one gender may outcompete and overgrow the other. Such is the case with ***Marchantia papillata*** subsp. ***inflexa*** (Figure 63), a dioicous thallose liverwort that lives on rock and bark surfaces (McLetchie *et al*. 2001). In this case, the females seemed to benefit from light to moderate disturbance and gradually eliminated the males. However, at high disturbance levels, the males dominated. This change in dominance seemed to result from dispersal of gemmae within the patch. We have seen in the brood body chapter that females typically produce fewer gemmae, instead spending energy to support the female reproductive organs and developing sporophyte.

Figure 63. ***Marchantia papillata*** subsp. ***inflexa***, a species in which females can outcompete males in disturbed areas. Photo by Scott Zona, with permission.

McLetchie *et al*. (2001) found that in ***Marchantia papillata*** subsp. ***inflexa*** (Figure 63) spores were needed to colonize large areas following disturbance, and that sexual reproduction predominated. However, as the population grew and the space became fully occupied, reproductive effort shifted to less sexual and more asexual means. Does this strategy predominate? It would seem more advantageous to reproduce asexually to fill the area, then reproduce by more widely dispersed spores when it gets crowded.

Maintaining the sexual specificity can get complicated in regenerants. Bauer (1963a) explained that sex determination in regenerated tissue can take two forms:

1. Sex determination is restored following de-differentiation, as in ***Funaria hygrometrica*** (Figure 18-Figure 19).
2. Sex determination is disturbed, causing the sexual balance to remain permanent or to slowly return to normal, as seen in members of **Splachnaceae** (Figure 64).

In the **Splachnaceae**, as the tendency toward femaleness is weakened, the male expression becomes more common until eventually only male plants can arise (Bauer 1963a). Surprisingly, this can occur even in species such as ***Splachnum rubrum*** (Figure 64) wherein sex determination is genetic. This species produces dwarf males, but these are usually sterile. The change in gender from vegetative offspring could be from cytoplasmic or genetic changes. However, Bauer reasoned that the constant changes among intermediate kinds of sex determination provides evidence against gene mutation.

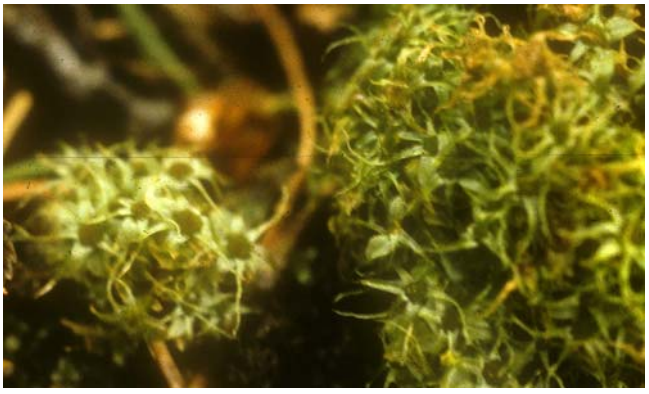

Figure 64. ***Splachnum rubrum*** with antheridial splash platforms, a species where gender is genetically determined. Photo by Janice Glime.

Rydgren *et al*. (2010) explored the ability of maintaining a female-biased sex ratio by testing it in ***Hylocomium splendens*** (Figure 68), a dioicous pleurocarpous moss that is common on the boreal forest floor. They found that males had a slightly lower production and survival of vegetative offspring than did the non-sporophytic females. This bias is important in a species such as this where sporophytes are uncommon. The slightly better success of males permitted them to expand into female clones, thus facilitating reproduction.

Differential Survival

Not all sex ratio differences are the result of adult competition. Shaw and Gaughan (1993) studied eleven populations of the moss ***Ceratodon purpureus*** (Figure 65) and found that at the time of germination female gametophytes outnumbered males 3:2, suggesting differential survival rates of spores or germlings. Furthermore, female clones formed much more biomass than did male clones, further increasing the bias. Nevertheless, male clones produced more stems, permitting them to provide additional gametangia and sperm.

Figure 65. Prolific production of capsules exhibited by ***Ceratodon purpureus***, suggesting a predominance of females. Photo by Michael Lüth, with permission.

Sex ratio can often change dependent upon growing conditions, even in species where gender of an individual is genetically predetermined. Shaw and Beer (1999) observed that despite chromosomal sex determination in ***Ceratodon purpureus*** (Figure 65) that would produce equal numbers of male and female cells at meiosis, the sex ratio varied considerably among families of offspring. Some genetically identical individuals (*i.e.*, grown from a single spore) that maintained a nearly 1:1 gender ratio had progeny that produced either predominately male or predominately female offspring.

This discrepancy between offspring sex ratios of two families of siblings suggests that there is a differential germination of spores, most likely related to environmental factors. Additional factors that may be relevant are the differences in size, maturation rates, and reproductive output of the male and female gametophytes in this species.

One factor that can account for highly biased sex ratios is simply the gender of the spore that lands there. Generally, one spore will produce multiple gametophores of one gender. However, Cameron and Wyatt (1990) rejected this as an explanation of the highly biased sex ratio in ***Splachnum***. They concluded that the unbiased and abundant dispersal by flies precluded such a bias by ensuring that both genders would arrive on the substrate. But even more interesting is the fact that in ***Splachnum ampullaceum*** (Figure 66), a single spore can give rise to both male and female gametophores. Instead, it is low light, *p*H, and nutrients that favor production of males over females.

Figure 66. Massive number of capsules of the dung moss ***Splachnum ampullaceum*** resulting from the guaranteed close proximity of males. Photo by Michael Lüth, with permission.

There is some evidence that at least in some bryophytes gender may be determined like that of crocodile eggs – by temperature. For the liverwort ***Sphaerocarpos texanus*** (Figure 67), sex ratios showed female bias among spores that broke dormancy after treatment at 25/15°C for 1-8 weeks (McLetchie 2001), despite a 1:1 ratio of male:female among spores produced (McLetchie 1992). In both field and laboratory-grown cultures, pure female clones were most common, followed by mixed sex, and least frequently, pure male (McLetchie 1992). It appears that the male spore has a lower survival and germination rate that continues into the gametophyte stage.

There seems also to be a physiological gender bias that depends in part on ecological conditions. In ***Mnium hornum*** (Figure 77) and ***Plagiomnium undulatum*** (Figure 76), only female regenerants from fragments survived desiccation (77%) (Newton 1972b). Such a strategy could soon create a population of predominantly females.

McLetchie and coworkers (2001) demonstrated that competitive interactions between genders could account for some sex differences at gametophyte maturity in the dioicous thallose liverwort ***Marchantia papillata*** subsp. ***inflexa*** (Figure 63) in Trinidad. Using differential equations, they modelled interactions of the two genders under various disturbance regimes. They found no way to stabilize the sex ratio, but rather, under conditions of low to moderate disturbance, females would gradually eliminate males. Under high disturbance conditions, males would eliminate females. Successful germination of gemmae dispersed within the patch played an important role. Since females of this species have only a narrow window in which to produce gemmae without interfering with energy needed for sexual reproduction, they would have less opportunity for successful gemma dispersal and establishment under large disturbance, but under conditions of small disturbance, already established female thalli might be able to outgrow male thalli. Although gemmae appear to be the most important means of maintaining replacement due to disturbances within patches, spores are the primary means for colonizing areas of major disturbances. Production of spores among initial colonizers when the patch becomes fully occupied is maximal, but that production subsequently declines as the sex ratio drifts toward one or the other gender.

Additional information on the costs and tradeoffs of producing archegonia vs antheridia is covered in Chapter 3 of this volume.

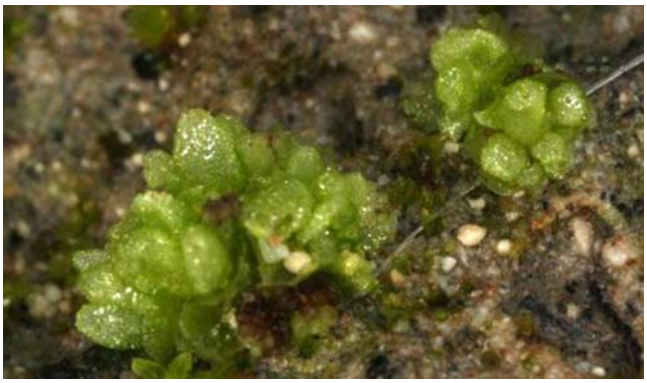

Figure 67. ***Sphaerocarpos texanus***, a species in which females seem to outcompete males. Photo by Jan-Peter Frahm, with permission.

Bisexual Gametangial Differentiation

Differentiation of a single cell such as a spore ultimately into an organism with cells of many functional types is always intriguing. Differentiation of parts of an organism into male and other parts into female is no less intriguing. What determines which branch, which gametangial cluster, will become male and which female? If we can understand these processes in plants, perhaps we can begin to understand the complexities that contribute to cross-gender behavior in humans.

Using the dioicous ***Hylocomium splendens*** (Figure 68) as a model, Rydgren and Økland (2002) examined a Norwegian population for five years. During that time, the tissue devoted to gametangia differed. That population had a 4:1 ratio of male to female branches. Of those females, ~30% produced sporophytes. Production of sporophytes varied three-fold during the five years, relating to weather favorability for growth and development. Large segments with high relative growth rates were more likely to produce sporophytes, with a distinct lower size threshold. Although the size limit increased in years with low sporophyte production, the lowest limit was ~2 mg segment dry weight. Furthermore, production of sporophytes was much greater in upper parts of plants, regardless of size differences, suggesting a role for light in initiation of sexual branches.

Figure 68. ***Hylocomium splendens*** bearing sporophytes. Photo by Janice Glime.

Hormonal Regulation of Gender

In some trees, such as *Acer*, ethylene concentration affects the male:female ratio. But in the small space of a bryophyte mat, could such a high concentration accumulate? There seems to be no evidence that packing of gametophytes, hence higher ethylene production, is a sex determinant. Nevertheless, lab evidence demonstrates that ethylene control is a possibility. Location of sexual structures on the bryophyte could result from a balance among IAA, ethylene, and GA_3. Chopra and Sood (1973b) showed that GA_3 plus ethrel (which produces ethylene in water) enhanced antheridia production, whereas IAA + cyclocel (CCC) enhanced archegonia production in ***Ricciella crystallina*** (Figure 22). This is consistent with the role of IAA in favoring femaleness in flowers (Salisbury & Ross 1978). If this relationship holds true, a strong apical dominance, concomitant with apical production of IAA, should produce archegonia at the apex. This is exactly the correlation seen in acrocarpous mosses. Conversely, lack of apical dominance should result in archegonia on side branches, as we see in pleurocarpous mosses. However, Schofield (1985) reminds us that IAA is not involved in sex determination in the same way in all taxa, inducing female sex organs in the liverwort ***Riccia*** (Figure 24) and male organs in the mosses ***Barbula*** (Figure 2) and ***Bryum*** (Figure 45). Because it is common in the environment, IAA could serve as an environmental control, interfering with sexual coordination and hence sporophyte production for some taxa in some habitats. It is likely that hormones interact and that concentrations or relative concentrations are important in gender determination.

Dwarf Males

Dwarf males present an interesting modification to sexual differentiation. In theory, the presence of dwarf males should increase the success of fertilization for a species, particularly among dioicous taxa. However, in two habitats in Michigan, USA, the presence of dwarf males had no significant impact on sporophyte production of dioicous mosses (Rohrer 1982). Dwarf males have been discussed in detail in Chapter 3; this chapter will concentrate on physiological relationships.

In the moss ***Trachybryum megaptilum*** (=***Homalothecium megaptilum***; Figure 69), males are typically dwarf, but this is a function of being on a female plant (Wallace 1970). Occasional full-sized males are found growing alone, but dwarf males never occur on these full-size males. Despite differences in gametophore appearance, there is no morphological difference between male and female spores. Wallace suggested that some substance released from the female plant might inhibit growth of the male plant.

In ***Dicranum*** (Figure 70), it appears that female plants present a growth-inhibiting substance that keeps their epiphytic males small (Loveland 1956). On the other hand, in ***Macromitrium*** (Figure 71) it is genetically determined in those taxa that are truly **anisosporous** (having a bimodal distribution of spore sizes with smaller spores generally producing males), whereas isosporous taxa again seem to be affected by hormones from females (Une 1985). Auxin, applied as 2,4-d, results in dwarf males, suggesting again a role for IAA.

Figure 69. ***Trachybryum megaptilum***, where dwarf males form on female plants. Photo through Creative Commons.

Another puzzle that has physiological implications suggesting hormonal concentration gradients is development of morphs among gametangia of a single reproductive head. In ***Plagiomnium medium*** (Figure 72), antheridia typically surround archegonia. In the border zone between the two sexes, Bryan (1927) always found at least one abnormal gametangium in each of the 100's of heads examined, from nearly perfect to possessing a combination of antheridial and archegonial cells. This likewise suggests some sort of hormonal control that involves concentrations or interaction – or both.

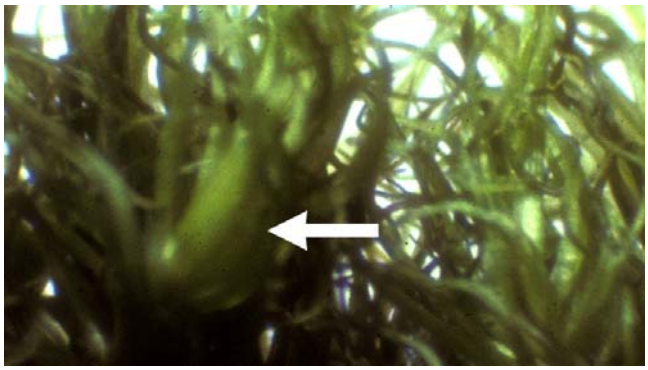

Figure 70. Dwarf male (**arrow**) of ***Dicranum polysetum*** growing on a female plant. Photo by Janice Glime.

Figure 71. ***Macromitrium piliferum*** with capsule, an autoicous moss in a genus where isosporous spores may form dwarf males in the presence of auxin. Photo by Jan-Peter Frahm, with permission.

Figure 72. ***Plagiomnium medium***, a moss in which antheridia usually surround the archegonia. Photo by Jan-Peter Frahm, with permission.

Different Controls

One consequence of sexual differences is that antheridia and archegonia can be under different controls. This can result in maturation of males and females at different times, perhaps accounting for sterility in many populations. Allsopp (1964) suggested that nutritional factors cause male and female production at different times on monoicous species. Lockwood (1975) found that amino acid additives promoted maleness and inhibited femaleness in ***Cephalozia lunulifolia*** (Figure 56); ammonium nitrate plus citrate also inhibited female gametangia. Machlis (1962) found that males of ***Sphaerocarpos donnellii*** (Figure 73) dropped the *p*H of their media from 5.3 and 7.1 to 4.1 in 15 days, whereas females raised the *p*H, suggesting physiological and possibly nutritional differences. Riemann (1972) suggested that mild, humid winters may result in maturation of the male and female of ***Rhytidiadelphus triquetrus*** (Figure 74) at different times, whereas harsh winters regulate their timing. Berthier (1966) has shown that antheridial production in ***Fontinalis*** (Figure 75) is greater under conditions of minimal growth and greater dominance by the main axis; fewer antheridia occurred in high light at 15ºC, whereas 8ºC and 90% light produced the most antheridia. It is likely that a wide variety of these mechanisms play a role in **protandry** (male gametangia mature first) and **protogynandry** (female gametangia mature first) among bryophyte species.

Figure 73. ***Sphaerocarpos*** sp. ***Sphaerocarpos donnellii*** can lower the *p*H of its medium to 4.1. Photo by Belinda, through Creative Commons.

Figure 74. ***Rhytidiadelphus triquetrus***, a moss that may have males and females mature at different times when winters are mild but mature together when they are harsh. Photo by Janice Glime.

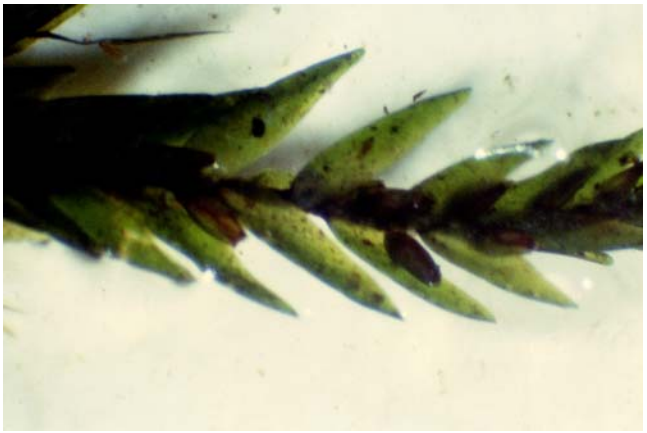

Figure 75. ***Fontinalis antipyretica*** var ***gigantea*** with perigonia (male). Antheridia are produced during times of minimal growth. Photo by Janice Glime.

One selective factor at work is that antheridia generally require a longer time to mature than do archegonia, as discussed earlier regarding phenology. Therefore, they must begin development sooner to mature when the population of female structures is receptive. ***Plagiomnium undulatum*** (Figure 76) has met this challenge with very different signals to initiate gametangia. Males require long days and diurnal temperature fluctuations to produce gametangia, whereas females require a short 7.25- to 12-hour day at 10ºC or warmer (Newton 1972a). We have already seen that more male gametangia are produced by the liverwort ***Fossombronia brasiliensis*** at 18ºC and more female gametangia at 10ºC. These differences in temperature and/or photoperiod can permit male gametangia to start development sooner and be ready when female gametangia are ready. But such timing differences meet new challenges when spores are dispersed to new locations where timing of day length and temperature can be different from that of the parent location, so that males and females are no longer synchronized. If only vegetative reproduction follows after introduction by a single spore, no opportunity arises for selection of synchronized variants; instead the species may persist sterile for centuries.

Figure 76. Vegetative branches of ***Plagiomnium undulatum***. Photo by Michael Lüth, with permission.

Newton (1972a, b) found that male and female plants themselves differed in photoperiod response in ***Mnium hornum*** (Figure 77). In short days, the number of males and females was about equal, but in intermediate and long days significantly more female plants arose from buds and produced mature plants. Even regeneration favored females. Thus, in northern areas where sufficiently warm temperatures may occur only during long days, a disproportionate number of females can result. This shifts the population toward dependence on regeneration, due to insufficient fertilization, further promoting females. Similarly, Longton and Greene (1969a,b) found that ***Pleurozium schreberi*** (Figure 50-Figure 51) produced capsules predominantly in coniferous forests due to lack of males elsewhere.

Figure 77. Male plants of ***Mnium hornum***, exhibiting a splash platform. Photo by Michael Lüth, with permission.

The problem of separate stimuli for the two sexes is further complicated by non-sex-related selection pressures after dispersal. Van Zanten and Pocs (1981) concluded that monoicous species of Jungermannidae have better dispersal than dioicous species because the percentage of monoicous species with a bipolar distribution is greater than that of dioicous species. This is reasonable since production of spores is more likely to occur in monoicous taxa, and these are dispersed more easily than asexual propagules due to the smaller size of spores. Since selection pressures related to sporophyte development are absent in isolated dioicous individuals, selection pressures would revert to gametophyte benefits. These could easily be different in male and female plants because of different amounts of time required for development of male and female gametangia.

Day length and **temperature** influence the onset of gametogenesis, and we have good evidence that responses to these variables vary within a species throughout the world (Monroe 1965, Clarke & Greene 1970). In dioicous species, vegetative reproduction is the only mechanism for reproduction until a second spore arrives. By that time environmental selection pressures and genetic drift in these small populations have had ample time to make the two sexes uncoordinated. If the signal for gametogenesis is different in the two sexes, there might never be an opportunity for the two gametes to meet. I would predict what van Zanten and Pocs (1981) have already illustrated, that long range dispersal of dioicous species would result in a large number of physiological species with low or no sexual reproduction.

All of these controlling factors suggest that Dan Norris may have been right in his comments to Bryonet on 2 May 2003 – the conditions of monoicy and dioicy and all their subsets may not be as distinct as we present them. The expression of gender may be under control of the environment and not any predetermined genetic distinction.

Numbers of Gametangia

Although each female branch typically produces only one sporophyte, archegonia occur in clusters within **perigonia**. One might ask why all this wasted energy to produce multiple archegonia if only one is successful. Even if all get fertilized, only one embryo succeeds in emerging from its archegonium. Could it be that multiple archegonia are needed to produce sufficient attractant for the sperm to find the location? Or might there be dangers lurking as sperm enter the archegonia, making backups necessary? Have we examined them closely enough to know that all eggs are simultaneously receptive, or might it be that this is a way to insure that one of the eggs is ready at the time of successful sperm dispersal?

The male gametangia generally outnumber female gametangia, but not always (Table 1). Since males must disperse the sperm, with nearly all of them being unsuccessful in fertilizing an egg, large numbers are necessary to provide enough chances for a few to succeed. Note in Table 1 that the ratio of male to female gametangia is considerably higher in the dioicous taxa.

Table 1. Mean number of gametangia per inflorescence, based on data for inflorescences that had gametangia in immature to dehisced stages. From Une & Tateishi (1996).

Physcomitrella patens subsp. *californica*	♀	2.0	Paroicous	Une & Tateishi 1996
	♂	7.2		
Astomum crispum	♀	3.3	Autoicous	Deguchi & Hidaka 1987
	♂	14.1		
Aulacopilum japonicum	♀	2.2	Autoicous	Deguchi & Hidaka 1987
	♂	3.3		
Venturiella sinensis	♀	3.6	Autoicous	Deguchi & Hidaka 1987
	♂	5.1		
Fabronia matsumurae	♀	2.7	Autoicous	Deguchi & Hidaka 1987
	♂	5.8		
Entodon challengeri	♀	5.5	Autoicous	Deguchi & Hidaka 1987
	♂	8.0		
Pogonatum inflexum	♀	3.4	Dioicous	Imura 1994
	♂	64.4		
Atrichum rhystophyllum	♀	4.6	Dioicous	Imura 1994
	♂	76.4		
Trachycystis microphylla	♀	9.8	Dioicous	Imura & Iwatsuki 1989
	♂	43.1		
Bryum argenteum	♀	5.5	Dioicous	Miles *et al*. 1989
	♂	10.6		
Pleurozium schreberi	♀	8.2	Dioicous	Longton & Greene 1969a
	♂	6.1		

In the survey of literature presented by Une and Tateishi (1996), ***Pleurozium schreberi*** (Figure 50-Figure 51) had more female than male gametangia per inflorescence, and ***Bryum argenteum*** (Figure 44-Figure 45) had little difference between them. Perhaps this is possible because these species are so successful at vegetative reproduction. In Canada, large geographic areas have only one gender of ***Pleurozium schreberi***, yet the species is still quite successful. ***Bryum argenteum*** is easily spread by broken tips.

Gender Recognition

Recognizing the gender of a bryophyte is often difficult if reproductive structures are absent. For mosses like ***Polytrichum***, old splash cups may be present, with new growth proceeding from the center (Figure 78). But even these can eventually change sex and thus determination of the sex of the moment may be less convincing. Size often plays a role, but this is affected by growing conditions as well, so one must assess it for each population. In ***Marchantia polymorpha*** (Figure 10), the male plants are narrow compared to females if one examines the thallus ~1 cm back from the tip, but then one needs both genders at hand to make the assessment (Voth 1941). Voth has observed another difference that I have not confirmed – the female plants have a smoother upper surface and reflect more light than male plants, at least in culture, but again, one really needs the male plants for comparison.

Figure 78. ***Polytrichum juniperinum*** with new growth from the antheridial splash cups. Photo by Janice Glime.

Yet, somehow, through biochemical means, a sperm is able to recognize a female of its own species, be it on a separate plant or the same one, and travel in that direction. As discussed in the chapters on life cycles of bryophytes, this recognition is facilitated by a concentration gradient from the disintegrated neck canal cells of the archegonium. But the nature of that exudate, and particularly what makes it specific for that species, remains a mystery.

Fertilization

Success of fertilization varies widely from very successful monoicous annual taxa to poorly successful dioicous perennials (Rohrer 1982). Rohrer found that success varied by habitat, with only 19.3% of the populations of the dioicous, vs 75.9% of monoicous taxa producing sporophytes in a dry aspen (*Populus*) forest. In a wet coniferous forest, the success of monoicous taxa increased to 84.1%, whereas that of dioicous taxa decreased to 12.3%. Surprisingly, having dwarf males epiphytic on female plants did not significantly increase the production of sporophytes in dioicous taxa.

Although several archegonia are typically present on a branch or stem tip, in most species only one sporophyte develops. Stark and Castetter examined the archegonia of ***Trichostomum planifolium*** (= ***T. perligulatum***) at the end of the fertilization season and found that 8% of the archegonia and 7% of the antheridia were abortive. In 13 of the 47 fertilized perichaetia they examined, there was at least one aborted embryo in addition to the developing embryo. Only two had more than two fertilized archegonia. There were no cases where more than one embryo developed. The abortions were all in early developmental stages. Hughes (1979) found that in ***Phascum cuspidatum*** (Figure 37) archegonial initiation ceases when one of the archegonia has been fertilized. The archegonial abortion raises the question of causes of this abortion. Is there an inhibitory substance produced by the first developing embryo that stops the others? Is there insufficient energy for more than one to continue? Could the hybrid status enter into the success or failure?

A more in depth discussion of fertilization is in Chapter 3.

Self-incompatibility

Fertilization is the termination of the gametogenesis development phase. Successful fertilization must be followed by successful development of the embryo to the mature sporophyte. We know that seed plants have a variety of mechanisms that prevent self-fertilization, either as prezygotic mechanisms that prevent the sperm from reaching and penetrating the egg or from postzygotic mechanisms that interfere with development of the embryo or mature sporophyte. This self-incompatibility has barely been explored in bryophytes.

We have suggestive evidence that self-compatibility exists among bryophytes. Boisselier-Dubayle *et al*. (1996) found the monoicous leafy liverwort ***Plagiochasma rupestre*** (Figure 79) to be self-compatible based isozyme markers of progeny. Lazarenko and Lesniak (1972) cultured two species of ***Desmatodon*** to determine their self-compatibility. ***Desmatodon cernuus*** was sterile in 24 hours of light, being a long-day plant at 16 hours of illuination and requiring low temperatures in the dark for normal sporophyte development. On the other hand, ***Desmatodon ucrainicus*** was completely self compatible in 24 hours of light, successfully producing sporophytes in single-spore cultures. However, this study raises a caution. One must reproduce the conditions of gametangial development, fertilization, and sporophyte development to test self-compatibility or other conditions involving reproduction.

When a spore travels to a new geographic area, it can encounter changes to the environmental signals needed for its normal development. Failing these signals, the reproductive state might never be initiated. Absence of such developmental signals seems to interfere with sexual reproduction in ***Desmatodon cernuus*** (Lazarenko & Lesniak 1972).

Jesson *et al*. (2011) considered that both polyploidy and monoicism could strongly depress inbreeding. They tested this in 21 populations of ***Atrichum undulatum*** (Figure 80). In one population, using allozyme markers, they found that the rates of selfing were greater than zero, despite the population having only one-third monoicous individuals. Lazarenko (1974) found that an inbred clone of ***Tortula cernua*** (=***Desmatodon randii***; Figure 81) was able to persist through 15 generations. This clone also gave rise to a sterile line that thus forth reproduced vegetatively, but also by producing apogamous capsules through 14 generations because the few spores, despite lacking an exosporium, were able to germinate. These studies suggest that self-incompatibility is not strong among bryophytes and that self-fertilization is possible.

Figure 79. ***Plagiochasma rupestre***, a self-compatible monoicous liverwort. Photo by Michael Lüth, with permission.

Figure 80. ***Atrichum undulatum*** males with splash cups and antheridia. This is a long-day plant. Photo by Janice Glime.

Figure 81. ***Tortula cernuua*** with capsules, a species that can survive 15 generations of inbreeding. Photo by Lars Hedenäs, with permission.

Stark (1983) reported that the autoicous ***Entodon cladorrhizans*** (Figure 82) was self-fertile and protandrous on a given stem. He found that approximately 90% of the perichaetia developed sporophytes and that this was independent of the number of perichaetia per stem, attesting to a high success rate for fertilization. Since only one archegonium typically develops a mature sporophyte in any given perichaetium, this is a good percentage. Self-fertilization is evidenced by significantly higher frequency of fertilization on bisexual stems than on those with only perichaetia, by the tendency for unfertilized perichaetia to be near the end of the stem away from perigonia, and by the highest fertilizations occurring on stems with perigonia.

Figure 82. ***Entodon cladorrhizans***, an autoicous moss with abundant sporophytes. Photo by Bob Klips, with permission.

Trichostomum planifolium is a protogynous monoicous desert moss, but it has a period of gametangial overlap, ending with a period of only ripe male gametangia

(Stark & Castetter 1995). Based on their observations of the population in southern New Mexico, USA, Stark and Castetter concluded that this moss is self-compatible, with common occurrences of fertilization from gametangia on the same stem. They supported this conclusion by the fact that stems that lacked a sporophyte had fewer antheridia and had no perigonia (n=3) and that all stems that produced sporophytes had at least one perigonium. The evidence is circumstantial and not definitive, but does suggest self-compatibility.

Zieliński (1986) used two peroxidase alleles to indicate presence of self-fertilization. He found that 38 of the 40 progeny examined in ***Pellia epiphylla*** (Figure 83) subsp. ***borealis*** were monomorphic for one of the two alleles involved and interpreted this to mean that self-fertilization had occurred. But we really need to know more than just the constancy of two alleles. Logic would suggest that in many cases the heterozygosity resulting from cross-fertilization would make those individuals more fit, consequently selecting against those individuals lacking a mechanism to prevent self-fertilization. But does this exist among bryophytes?

Figure 83. ***Pellia epiphylla***, a species wherein identity of alleles suggests selfing. Photo by Li Zhang, with permission.

We know that seed plants often (usually?) are self-sterile. They have several mechanisms during and following pollination/fertilization to prevent success of self-fertilization, and these can provide suggestions for possible mechanisms in bryophytes:

- different maturation times of male and female parts
- dispersal vector behavior – moving from mature females to mature males (several animal vectors are now known)
- sperm unable to swim in neck of archegonium
- failure of self-fertilized embryo to develop
- rejection of self-fertilized embryos by plant
- better competition by hybrid embryos
- failure of next generation to reproduce

But do we know that any of these mechanisms occur in bryophytes? Gemmell (1950) suggested that all monoicous species were obligate inbreeders. This seems unlikely since evolution from dioicous to monoicous is a common direction in bryophytes. Lazarenko and Lesnyak (1972) disproved the suggestion of Gemmell by demonstrating cross breeding in ***Desmatodon*** (Figure 84), including cross breeding between two different species in the genus. Now we are raising the question whether monoicous bryophytes actually have mechanisms to ensure outbreeding in at least a portion of the population.

Figure 84. ***Desmatodon latifolius*** with abundant capsules, a species in which hybrids among species in the genus are known. Photo by Michael Lüth, with permission.

Just in time for this writing, Stark and Brinda (2013) published their study on ***Aloina bifrons*** (Figure 85), a dioicous moss living in the dry Mojave Desert, USA. Despite being dioicous in an environment unfriendly toward fertilization by water, this moss had frequent sporophyte production, leading the researchers to question its dioicous status (Stark & Delgadillo M. 2001). They found that it could, at least occasionally, be **rhizautoicous**. They found **ramets** (individuals in clone of genetically identical individuals that have grown in given location, originating vegetatively from single plant), connected by single rhizoids, that produced both **perichaetia** (archegonial groupings) and **perigonia** (antheridial groupings).

Figure 85. ***Aloina bifrons***, a moss that is apparently facultatively autoicous. Photo from Proyecto Musgo, through Creative Commons.

But all is not well for self-fertilization because it leads to all those dangers of inbreeding that make the offspring less fit. Rather, Stark and Brinda (2013) found that ***Aloina bifrons*** (Figure 85) actually practices self-incompatibility. First, it practices **protandry** – a condition wherein the male reproductive structures mature before the female structures. There was some overlap in maturity times between archegonia and antheridia, and self-fertilization did occur within single clones. However, sporophytes aborted during the embryonic development. Stark and Brinda did allow for the possibility that these cultures might require a resting phase to continue their sporophyte development, so we are still left wondering.

It appears that we know little about incompatibility mechanisms in bryophytes. Let's recall that the monoicous condition in bryophytes is aparently derived from the dioicous condition. Hence, the mechanisms had to arise anew after the monoicous taxa arose. We should perhaps expect that self incompatibility is an imperfect condition that is still evolving. But for now, there are no studies to determine if more embryos abort from self-fertilizations than from outbreeding. There is no evidence to determine the effect of self-fertilization on future generations. There is no study that has examined the success of sperm from the same plant vs different plants in reaching and penetrating the egg. Hence, we have no idea how extensive or important self-incompatibility is in bryophytes.

Geographic and Habitat Relationships

Certainly physiological evolution has occurred as species have broadened their ranges to more and more distant locations. ***Pleurozium schreberi*** (Figure 50-Figure 51) often is without capsules because no male plants are present. Longton and Greene (1969a,b) found that females are more abundant worldwide, causing us to ponder on the cause. Could it be that male expression requires a temperature and photoperiod combination that is not available in their more cosmopolitan distribution?

Working with ***Macromitrium*** (Figure 71), Une (1985) found a possible explanation for the absence of mature males in some species. In isosporous ***Macromitrium***, female protonemata developed buds at 10ºC, but after 160 days the males had failed to produce buds, making it impossible for them to complete a life cycle in a short growing season.

Two ***Pohlia*** (Figure 86) species provide evidence to suggest that changes in the reproductive response are possible mechanisms for survival in widespread locations, and this plasticity may explain the abundant capsules seen on some ***Pohlia*** species. Clarke and Greene (1970) found that gametangial maturation was faster in the Arctic and sub-Arctic than in Britain, permitting these species to complete their maturation in the shorter Arctic summer. Lewis Smith and Convey (2002) indicated that in the Antarctic sexual reproduction likewise was highly successful, suggesting that the severe climate with its low temperatures and short growing season is not a severe detriment to successful gametangial production. They consider that microhabitats make this reproduction possible. Most of the fertile species are monoicous, short acrocarpous species on rather calcareous soils. Could it be that calcium is an important part of the reproduction story?

Figure 86. ***Pohlia filum*** growing in an alpine area and producing abundant sporophytes. Photo by Michael Lüth, with permission.

In the Brazilian Atlantic Rainforest, an altitudinal cline permits us to compare reproductive performance. Maciel-Silva *et al*. (2012) monitored eleven species for fifteen months at sea level and a montane site to compare reproductive performance. The highest level of reproduction was among monoicous taxa, especially for sexual branches and fertilized gametangia. At sea level, there were more females and more sexual branches than at the montane site. But these differences seemed only to compensate for other factors because the sporophyte frequency was similar in both sites. Microhabitats like decaying wood were important in maintaining sufficient water levels for good gametangial production. Water availability and maintenance may have been the major factor influencing the success of sporophyte production.

Another geographic problem is that timing that is ideal in one locality may be all wrong in another. Signals for production of gametangia may come from photoperiod, signalling an upcoming rainy season, but in another, the rainy season may be during a different part of the year. For example, ***Octoblepharum albidum*** (Figure 87) in Brazil times its reproductive maturity to coincide with the rainy season (Pôrto & Oliveira 2002). The capsules begin their development during the rainy season, but complete it during the subsequent dry season when they disperse their spores. In this case, the rainfall seems actually to enhance development of gametangia, hence ensuring the correct timing. The behavior of ***Sematophyllum subpinnatum*** (Figure 88) in these tropical lowland forests is similar (Oliveira & Pôrto 2001). Although both antheridia and archegonia develop and mature throughout the year, they increase in number during the rainy season. Subsequent appearance of sporophytes primarily from June to September indicates that most fertilization events occur during the rainy season.

Odu (1981) found similar timing in tropical Africa. The perennial ***Racopilum africanum*** (Figure 89), ***Fissidens weirii***, and ***Thuidium gratum***, and an annual ***Stereophyllum*** sp. (Figure 90) all develop their gametangia at the onset of the rainy season, complete fertilization during that season, and produce mature capsules ready for spore dispersal at the onset of the dry season.

Figure 87. ***Octoblepharum albidum***, a moss in which rainfall seems to enhance gametangial production. Photo by Niels Klazenga, with permission.

Figure 88. ***Sematophyllum subpinnatum***, a species in which antheridia and archegonia are produced throughout the year, but increase in the rainy season. Photo by Michael Lüth, with permission.

Figure 89. ***Racopilum africanum*** with young sporophytes that are initiated near the beginning of the rainy season and mature at the beginning of the dry season. Photo by Jan-Peter Frahm, with permission.

Figure 90. ***Stereophyllum radiculosum***, a moss that develops its gametangia at the beginning of the rainy season. Photo by Scott Zona, with permission.

For the mosses ***Bryum coronatum*** (Figure 3), ***Hyophila involuta*** (Figure 91), and ***Barbula indica*** (Figure 2) in southwestern Nigeria, gametangia development starts at the onset of the rainy season (March), providing them sufficient water to mature (Fatoba 1998). But their maturation requires 8-10 months (ending November – January), whereas the rainy season ends in mid October. The southwestern Nigerian rainy season has a "little dry season" (mid-July to mid-September, but mostly in August) (Adejuwon & Odekunle 2006), although the length decreases away from the coast. This little dry season might influence the persistence of the long developmental period for these gametangia. Temperatures typically range 26-28°C annually, so they have little influence on the bryophyte timing. This 8-10 months for maturation of gametangia places time of fertilization so that it permits the capsules to mature and spores to be dispersed in October – November, early in the regular dry season.

Figure 91. ***Hyophila involuta***, a moss that begins gametangial development at the beginning of the rainy season in Nigeria. Photo by Niels Klazenga, with permission.

In desert habitats, even timing can fail to provide an opportunity for gametangial production. The desert moss ***Syntrichia caninervis*** (Figure 92) had 85% non-sexual ramets in a 10-hectare study area in the southern Mojave

Desert of Nevada, USA (Bowker *et al.* 2000). Those that had sexual expression were associated mostly with shaded microsites, higher soil moisture content, and taller ramets. The taller ramet may have been a result of the greater moisture available, but it also may have been the size that had reached the required threshold for available energy as discussed earlier in this chapter.

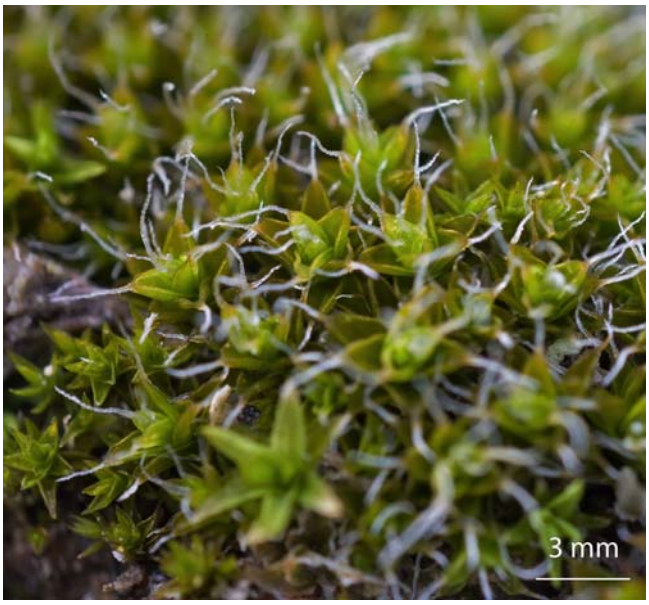

Figure 92. ***Syntrichia caninervis***, a moss with 85% non-sexual ramets in the Mojave Desert. Photo from Proyecto Musgo, through Creative Commons.

In another desert moss, ***Syntrichia inermis*** (Figure 93), also from the Mojave Desert, more than 90% of the plants are monoicous (Stark 1997). In this species archegonia are initiated and receptive in the same winter, whereas antheridia require 1-3 years to reach maturity. Abortion is only 3-4% for both gametangia, but only 50% of the current cycle of perichaetia become fertilized. The slowest growth rates known, an 18-month dormancy period during sporophyte maturation, and the longest known period for antheridial maturation attest to limitations placed on reproduction in this moss by its desert habitat.

Figure 93. ***Syntrichia inermis*** with capsules, showing high sporophyte production of this monoicous moss. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Tradeoffs – Cost of Reproduction

Reproduction of any type comes at a price. Sexual reproduction requires considerable energy, and it benefits a plant to maximize success of its gametes in achieving fertilization. Actual measures of energy costs for any process in bryophytes are rare. The cost of reproduction can be indicated indirectly by its apparent effect on production of other structures and growth. For example, in ***Marchantia polymorpha*** (Figure 10), gemmae cups are generally not produced on the same portions of a colony as are the sexual structures (Figure 94) (Une 1984). But Une suggested that this might actually be due to age of the thallus, or to available nutrients, assuming that the interior of the colony where the gametangial branches occurred was the older and hence may have used up more of the available nutrients.

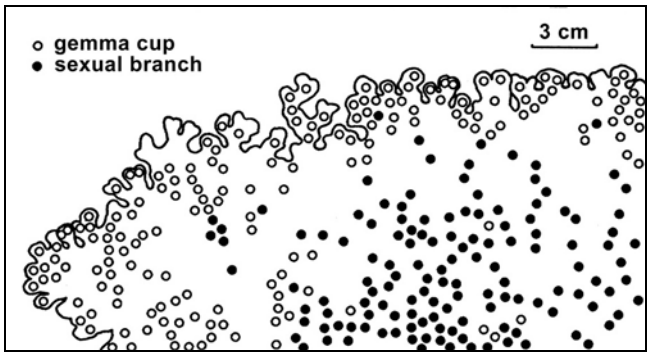

Figure 94. Location of gemma cups and archegoniophores in a colony of female ***Marchantia polymorpha***. Modified from Une 1984.

The example of the leafy liverwort ***Lophozia ventricosa*** (Figure 95) var. ***silvicola*** demonstrates the high cost of being female (Laaka-Lindberg 2001). Female plants allocated 24% of their biomass to sexual reproduction whereas their male counterparts expended only 2.3%. The cost to the female was reduced stem length and both genders exhibited modified branching of gametangial shoots. When compared with asexual shoots, both genders had reduced stem length. Predictably, asexual plants produced the most gemmae (mean 2100), males next (1360), and females least (800).

Figure 95. ***Lophozia ventricosa*** with gemmae, a species with a high cost for gametangia. Photo by Michael Lüth, with permission.

The desert moss ***Syntrichia inermis*** (Figure 93) seems to tell a different story. In that species, it is more costly, by an order of magnitude, to produce male sexual organs than female ones (Stark *et al*. 2000). Stark *et al*. attributed this extra cost to the longer time required for development, greater number of male gametangia per perigonium than for archegonia per perichaetium, and presence of paraphyses among antheridia in that species. It would be interesting to see if this sex ratio could be modified by providing the limiting resources, presumably sugar.

Stark and coworkers (1998, 2001) found other indications of tradeoffs resulting from sexual reproduction in ***Syntrichia caninervis*** (Figure 92). Interestingly, non-sex-expressing individuals exhibited lower biomass, shorter total stem length, fewer branches, and shorter ramets than sex-expressing individuals; all individuals weighing more than 2 mg dry weight were sexually expressing, suggesting a threshold size needed for reproduction in order to provide sufficient energy. Furthermore, when inflorescence number was considered, the biomass of males and females did not differ.

McLetchie (1996) found that distance between male and female plants, as expected, decreased sexual success of the plants, but he also found that smaller males were less successful in accomplishing successful fertilization in the dioicous, thallose ***Sphaerocarpos texanus*** (Figure 67). From this he concluded that successful fertilization is sperm-limited. One might also argue that these could represent maturity differences.

For the epiphyte ***Neckera pennata*** (Figure 96), Wiklund and Rydin (2004) found a similar indication of minimum size. The first reproduction occurred at a colony size of 12-79 cm^2, requiring an estimated 19-29 years until the plants were sexually active! These apparent thresholds suggest that a critical size is important for sex expression. This implies that an energy threshold is required, and thus there must be a tradeoff between stored energy and sexual productivity.

Not only is production of gametangia expensive, but the ensuing production of sporophytes likewise is costly. It is therefore not surprising that Stark and coworkers (2001) found that 63% of the fertilized perichaetia of ***Syntrichia caninervis*** (Figure 92) had abortive sporophytes. This need for energy to produce the sporophyte seems to be subject to high selection pressure, as most bryophytes produce only one sporophyte per apex despite having multiple archegonia.

Relative fitness of sexual and asexual individuals can depend on the environmental conditions. In ***Marchantia papillata*** subsp. ***inflexa*** (Figure 63), Fuselier and McLetchie (2002) found that light intensities can shift sexual fitness and alter the timing of asexual reproduction. There were negative tradeoffs between the asexual and sexual fitness of females at some light intensities. In high light intensities, female plants suffer a sex-specific cost for their plasticity in timing, and asexual fitness shifts the population toward monomorphism of sexes. Fuselier and McLetchie concluded that opposing selective forces on sexual vs asexual expression could explain persistence of sexual dimorphism despite selection against dimorphism in the pre-adult phase.

Bisang and Ehrlén (2002) clearly demonstrated costs of sexual reproduction in female plants of the polysetous ***Dicranum polysetum*** (Figure 97). They used a retrospective method to estimate photosynthetically active gametophyte biomass present at the onset of the sporophyte cycle and determined that reproductive effort, that is the proportional investment into reproductive structures, was 16% when sporophytes were successfully produced and only 1.3% when no fertilization occurred. The reproductive output of capsule number and dry weight were positively correlated with vegetative apical growth, whereas the reproductive effort was inversely related to dry mass of the annual segment preceding sporophyte initiation, indicating that energy was evidently shunted from that apical gametophyte tissue into the sporophyte. But even the next growth cycle paid the price of that reproduction; the probability of initiation of subsequent perichaetia was reduced as a result of sporophyte development, and when new perichaetia did develop, they were reduced in mass. In plants with sporophytes, investments in innovations were negatively correlated with reproductive structures. And, more sporophytes per plant resulted in reduced mass per sporophyte.

Figure 96. ***Neckera pennata***, a moss that requires 19-29 years before plants are sexually active. Photo by Jan-Peter Frahm, with permission.

Figure 97. ***Dicranum polysetum*** showing multiple sporophytes from a single stem. Photo by Janice Glime.

Summary

Gametes in bryophytes are produced in **antheridia** (sperm) and **archegonia** (eggs). The location of these structures divides mosses into **acrocarpous** mosses with terminal gametangia and **pleurocarpous** with side- branch gametangia. Water is needed for dispersal of sperm and in some cases this is aided by the presence of splash cups or splash platforms. Once released the sperm swims to the archegonium, attracted by some factor released when the neck canal cells of the archegonium disintegrate.

Both **monoicous** and **dioicous** taxa of bryophytes exist, and chromosome numbers suggest that monoicous taxa are derived through **polyploidy**. Sex determination is under genetic control in at least some bryophytes, with either an X or a small Y chromosome programming females vs males, respectively. There are implications that expression of these genetic differences is manifest in **IAA** differences, but it appears that **ethylene** could interact with IAA or that concentrations or relative concentrations may be important.

Some ***Macromitrium*** taxa have two spore sizes that translate into dwarf males from small spores, but generally dwarf males seem to be determined by some factor from the female upon which they land. Gender survival ratios, already discussed in the chapter on sexuality, are altered by spore survival, protonemal survival, competition, and survival of the gametophores. It may furthermore be altered by the environment to express one or the other sex.

Initiation of gametangia may be an ancient event that must be controlled by inhibition rather than initiation. The apparent initiation could instead be a set of conditions that override or immobilize inhibitors. Initiation of gametangia can be triggered by light intensity, photoperiod, temperature, and water availability, but it appears that many bryophytes, especially mosses, may respond to some combination of these. Liverworts seem to be more dependent on photoperiod. Other factors that influence gametangial development and gender expression include *p*H and form and availability of N. There may be a minimum size, at least for some taxa, before gametangia will develop, implying need for sufficient energy supply. Antheridia typically initiate before archegonia and take longer to develop. Because these two gametangia are initiated at different times, they are often under different controls that can cause a mismatch in maturity times. This can be particularly problematic when they disperse to a new geographic region and may account for absence of sporophytes on particular species in some geographic regions.

Acknowledgments

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CHAPTER 6-1
LIMITING FACTORS AND LIMITS OF TOLERANCE

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CHAPTER 6-1
LIMITING FACTORS AND LIMITS OF TOLERANCE

Figure 1. Janice Glime overlooking geothermal vents that stretch the limits of tolerance of bryophytes. Photo by Zen Iwatsuki, with permission.

Sad, faint, and weary, on the sand
Our traveller sat him down; his hand
Cover'd his burning head.
Above, beneath, behind, around.
No resting for the eye he found;
All nature see'd as dead.

One tiny tuft of Moss alone
Mantling with freshest green a stone
Fix'd his delighted gaze;
Through bursting tears of joy he smiled.
And while he raised the tendril wild.
His lips o'flow'd with praise.

O! shall not He who keeps thee green,
Here in the waste, unknown, unseen.
Thy fellow-exile save?
He who commands the dew to feed
Thy gentle flower, can surely lead
Me from a scorching grave.

Pushing the Limits

Crum (2004) quotes from Stark (1860, Popular History of British Mosses) concerning the tiny tuft of ***Fissidens*** that Mungo Park found in the African interior. Park wrote "I considered my fate as certain, and that I had no alternative but to lie down and perish." Just as Park was giving up, he spied the tiny moss.

So many have failed to see the tenacity with which the bryophytes hold on to life. Their limits of tolerance seem to outrange any other group in the Kingdom Plantae. But the mechanisms by which they do this have remained obscure to the average biologist, and even to most physiologists. Yet they have much to teach us about basic principles of physics and chemistry applied to living organisms to create their physiological processes.

When I began my studies of bryophytes, I did so because no one could answer my questions. It seemed as if we knew almost nothing about them. There was in fact a wonderful literature, mostly from other countries, that I discovered later and that none of my professors (not

bryologists) had ever read. Nevertheless, the mysteries of how bryophytes survived where they did continued to intrigue me, and most answers seemed nowhere to be found in the published literature. Then I became interested in ***Fontinalis*** and began to question just what determined which streams would have it and which did not. Soon I was testing it to its limits, trying to ascertain why it seemed unable to occur in certain parts of the world and only in certain streams in other parts. In fact, my friends soon began asking, if I liked ***Fontinalis*** so much, why was I always trying to kill it!? I was testing its limits of tolerance.

Bryophytes have unique physiologies that are often envied by the horticulturalists and agriculturists. Their ability as a group to survive cold and desiccation is unparalleled by any other major group of plants. It is these physiological abilities that permit them to occupy bizarre habitats like iron stoves (Figure 2) and darkened caves, geothermal vents and meltwaters (from snow and ice), and only a liverwort was able to survive on the first samples of moon rock.

Figure 2. Old iron stove with bryophytes growing on it. Photo by Janice Glime.

The tolerance of bryophytes for conditions that would impose severe stress on other members of the kingdom led a group of astrophysicists at a special session on space colonization at the 40th American Institute of Aeronautics and Astronautics (AIAA) Aerospace Sciences Meeting, held in Reno, Nevada, 14-17 January 2002, to suggest that these organisms should be introduced to the moon for **terraforming** (making desert planet etc. habitable; Davis 2002). (Never mind the arguments as to which celestial body should be colonized first.) Indeed, based on their importance in Earth's polar and alpine **ecosystems** (communities & habitat) where most flowering plants are unable to survive, it was suggested that following preparation by the microbial stage, it is the bryophytes that would be able to transform the planet/moon into a habitable body. But, the scientists advised, further research is needed to improve our understanding of the physiological and ecological roles these organisms might play in such a system. Do they realize how little we know of their role on Earth?

Our understanding of bryophyte physiology is at best poor. Compared to tracheophytes, bryophytes have enjoyed few physiological studies, and many assumptions have been made about their physiology. Perhaps the most widespread and erroneous assumption was that all bryophytes have the same sort of basic physiological mechanisms for obtaining water and nutrients, and for retaining them or losing them. Implicit in this was the assumption that all gained water and nutrients from leaf surfaces. However, recent studies on bryophyte physiology suggest that physiological mechanisms may be the most variable character among different populations and species of bryophytes. While tracheophytes were spending their genetic evolution on morphological adaptations to environmental conditions, it seems that bryophytes may have been spending theirs perfecting a multitude of physiological and biochemical strategies. Before we delve into the physiology itself, we will begin with a discussion of our understanding of stress factors and plants as they might apply to bryophytes.

C-S-R Triangle

In 1976, Stearns reviewed the concepts of life strategy or life history tactic to help explain a system of co-evolved adaptive traits that permit species to survive in a range of habitats, and these concepts have subsequently become known as **life cycle strategies** or **life history strategies**. Numerous papers exist arguing pros and cons of using the term *strategy* for a non-thinking, non-planning plant, but the term conjures up the appropriate concepts in our thinking and I can think of no other that does quite as satisfactory a job, so the term strategy has become part of my own ecological jargon as it has likewise in ecological literature.

While Stearns (1976) was developing the life strategy concepts, Grime (1977) took a slightly different approach and suggested that external factors that limit plant **biomass** (living & dead plants or plant parts) may be classified as either stress or disturbance. Following this concept, **stress** refers to those conditions that restrict production, such as low light, insufficient water or nutrients, or suboptimal temperature. **Disturbance** is the partial or total destruction of the plant biomass arising from herbivores, pathogens, humans, wind damage, frost, desiccation, erosion, or fire. (It seems that pollution belongs there too!) Plants respond to these limiting factors with three types of strategies: **stress-tolerant**, **ruderal**, and **competitive** (Table 1), reminiscent of Ramensky's (1938) **patients** (stress-tolerant), **explerents** (ruderal – growing in wastes or among rubbish), and **violents** (competitive), which will be discussed in more detail with growth forms (During 1992). Using Grime's (1977) scheme, individual species of plants, therefore, represent compromises between the conflicting selection pressures of competition, stress, and disturbance. These relationships can be arranged in a triangle known as the **C-S-R model** (Figure 3). Grime (1979) considers it highly unlikely that plants can tolerate extremes of both stress and disturbance. Some, however, might be able to tolerate each independently.

Table 1. Grime's (1977) suggested basis for the evolution of three strategies in tracheophytes.

Intensity of Disturbance	Intensity of Stress	
	Low	High
Low	competitive strategy	stress-tolerant strategy
High	ruderal strategy	no viable strategy

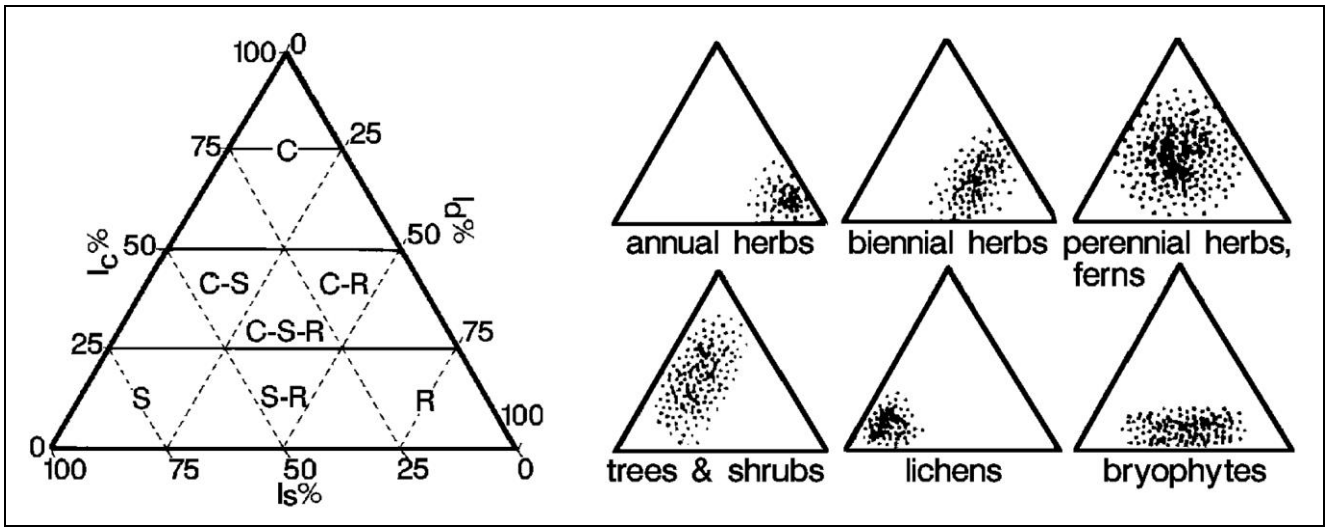

Figure 3. **Left:** Model of equilibria between competition, stress, and disturbance in plants, showing relative importance (I_c, I_s, I_d). Strategies include competitors (**C**), stress-tolerators (**S**), and ruderals (**R**). **Right:** Diagrams of the strategy ranges of various groups of plants compared to the distribution of competitors, stress-tolerators, and ruderals. Redrawn from Grime 1977.

Grime (1974) proceeds to define **competition** as "the tendency of neighboring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space." **Stress**, in Grime's usage, encompasses "the external constraints which limit the rate of dry matter production of all or part of the vegetation."

Competitors tend to have moderate to long life spans, relatively low reproductive efforts, high potential relative growth rates, high dense canopies of leaves, abundant litter, and high morphological plasticity. The plant forms are diverse, including perennial herbs, shrubs, and trees. This strategy generally does not fit the bryophytes due to their relatively slow growth rate. In fact, Grime and coworkers (1990) concluded that none of the bryophytes in their study have a competitive strategy. Rather, they are stress tolerators. Their lack of a "sophisticated" transport system renders them unable to monopolize resources and dominate the vegetation of an undisturbed ecosystem. It is only in aquatic habitats, particularly streams and bogs/poor fens, where they may be able to compete with tracheophytes due to their perennial above-substrate persistence. Nevertheless, competition with such life cycle stages as seedlings is real, with deep mats of bryophytes suspending the young plants where they either are unable to reach the earth to anchor their roots or are unable to reach the light to obtain energy. And competition among bryophytes occurs, although on such a slow, yet dynamic scale that it has seldom been documented. Competition as a strategy will be discussed later.

Stress tolerators similarly have a long life span and low reproductive effort, but they have low potential relative growth rates, little but persistent litter, and little morphological plasticity. The plant forms are most diverse, including such distant ones as lichens, bryophytes, and trees. Among the bryophytes, one advantage is that they are able to reproduce asexually by fragmentation when stress may be too severe for gametes, embryos, or sporogenous tissues to survive.

Ruderals are more like competitors, but they have very short life spans and high reproductive rates. They are mostly ephemerals that tend to have relatively homogeneous life histories and habitats. Flood plain bryophytes can be considered here (Figure 4).

Figure 4. The floating liverwort *Riccia fluitans* stranded above water as it would be following a flood. It will form a broader thallus on land. Photo by Jan-Peter Frahm, with permission.

Severe Stress

With their inability to move when living conditions become stressful, plants must have plasticity to survive. For most plants, diversity is maintained through the second set of genetic information, available when conditions change, and permitting the next generation to benefit from whatever combination is appropriate. Although self-fertility is usually prevented within flowers, fern gametophytes, and moss branches, it often is not prevented between flowers of the same plant and certainly not among flowers of the same clone; the same seems to be true in bryophytes, although much less evidence supports this contention.

Such genetic diversity, the product of outcrossing (breeding with a different population or genetically different individual), would seem only to benefit plants when they must cope with long-term changes, those that last over the course of several years, decades, or millennia. A different method of coping must be available for those

stresses that are encountered within the course of a single growing year as a result of seasonal changes. Low-level stress is undoubtedly present in all habitats and functions merely as a modifier of growth rates and competition, whereas severe stress, such as coping with winter, has an immediate impact on the survival of the organism (Grime 1977). Not only can severe stress eliminate a species from a habitat directly, but it can also eliminate a species indirectly by reducing its competitive ability, making it vulnerable to replacement by more stress-tolerant species. Strategies of growth thus must respond to seasonal variation in temperature, nutrient, and moisture supplies, a concept consistent with the life-form definition of Mägdefrau (1982). Grime and coworkers (1990) found a functional specialization in the life cycle of bryophytes, with a different set of strategies for the established (adult) phase than those being used in the regenerative (juvenile) phase, thus providing one means for coping with seasonal changes.

The **relative growth rate** (**RGR**) of a species is generally considered the best measure of the success of the species relative to other individuals or species in a given environment. Furness and Grime (1982) found that RGR for bryophyte species could be correlated with stress conditions in laboratory experiments. For the short-lived ruderal ***Funaria hygrometrica*** (Figure 5), RGR = ca. 50 mg g^{-1} day^{-1}, and for the competitive ***Brachythecium rutabulum*** (Figure 6), RGR = 70 mg g^{-1} d^{-1}. By contrast, stressed bryophytes such as **epilithic** (living on rock) species had much lower productivity (RGR = 5-20 mg g^{-1} d^{-1}). Since tracheophyte RGR ranges from 4 to 400 mg g^{-1} d^{-1} (Poorter & Remkes 1990), it seems that bryophytes are on the low end of the scale, and if Furness and Grime are right in their conclusion that low RGR relates to stress tolerance, bryophytes in general should be particularly good at it.

Figure 5. The short-lived ruderal species, ***Funaria hygrometrica***, illustrating its high reproductive rate. Photo by Michael Lüth, with permission.

Grime (1977) considered four types of environments that impose severe stress. He regarded the arctic-alpine and arid habitats to have low production, with stress being imposed primarily by the environment. In shaded habitats, stress is plant induced, and for bryophytes, this causes a release of competition from less tolerant tracheophytes, giving bryophytes an advantage. In nutrient-deficient habitats, bryophytes can often again dominate due to lack of tracheophyte competition. To these stressful habitats, I would add the habitats with extremes of high mineral loading, very high or very low *p*H, or high temperatures. Polluted environments can present any or all of these conditions, as can geothermal fields (Figure 1).

Figure 6. The competitive species ***Brachythecium rutabulum***. Photo by Janice Glime.

Bryophytes, as a group, tend to be wide-ranging in this scheme, with their center of distribution being in the stress-tolerant ruderals (During 1992). Økland (1990) considered even the mosses in a Norwegian mire to be stress tolerators. He made this judgment because they occurred in dry, shaded sites, relative to those of ***Sphagnum***, and by their narrow habitat niches within the mire. These were generally bryophytes with wide niches in other vegetation types. It seems that bryophytes in general are stress tolerators, relegated to living where other taxa are unable to survive.

Genetic Adaptations

The ability of a plant to tolerate a condition is dependent upon three factors: genetic components, currently interacting factors, and past history. Shaw (1987) used ***Funaria hygrometrica*** (Figure 5) to illustrate the effect of pretreatment (past history) versus genetics on tolerance to zinc and copper for protonema growth and stem production. For that species, the protonema growth responded to past history, but for the stem production, genetic differences were more important. Furthermore, genetic differences between populations were more important than pretreatment. Such results suggest the possibility of selection as a result of past history in the genetically different populations.

Genetic drift (random changes in gene frequencies due to isolation of a small population) can also account for differences between populations in widely separated areas. I (Glime 1987) found vastly different growth rates between the populations of Fontinalis novae-angliae (Figure 7) from New Hampshire and Michigan when they were grown in a common garden. Vitt *et al*. (1993) found that ***Scorpidium scorpioides*** (Figure 8) from Canada grew best in extreme-rich fen waters, whereas plants from The Netherlands grew best in water from moderate-rich fens and in nutrient-enhanced conditions. Either of these cases could represent genetic drift, but both could also represent past history (*e.g.* physiological acclimation) or natural selection. For the ***S. scorpioides***, past history may well play a role because both

populations grew best in water of the type from which they had been collected, suggesting that at least it is possible that osmotic relationships of the existing cells may have been affected by the change in water chemistry.

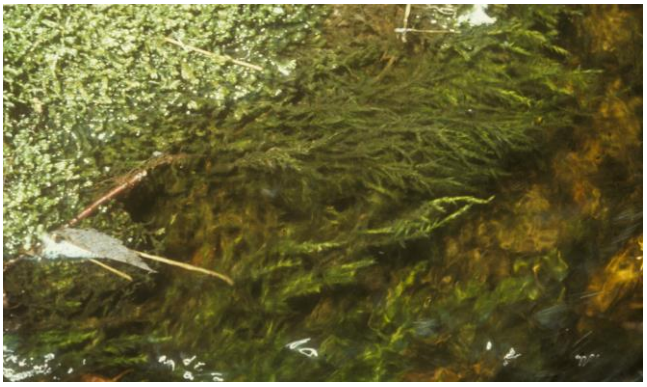

Figure 7. *Fontinalis novae-angliae* growing on rock at edge of stream. Photo by Janice Glime.

Figure 8. ***Scorpidium scorpioides*** growing in a fen. Photo by Michael Lüth, with permission.

One significant mechanism that permits plants to respond to stresses in a short period of time is by production of **inducible proteins** (proteins produced only when certain conditions are present) (Wray 1992), a genetically controlled phenomenon, but also potentially a result of past history. Such production is mitigated by inducible enzymes that respond to environmental cues such as toxic metals, salts, anaerobic conditions, temperature extremes, pathogens, and nutrient availability. Others respond secondarily to internal hormonal cues such as ABA (abscisic acid), ethylene, and GA (gibberellic acid). These hormonal mechanisms would appear to be available to the bryophytes, since all of these hormones are known in bryophytes. Inducible proteins are less well known among the bryophytes, but may some day prove to be important in their success. We are already gathering considerable information on stress proteins that respond to dehydrating conditions and high temperatures, as will be discussed when we examine water relations. Furthermore, Grime and coworkers (1990) contend that morphological plasticity is of reduced importance for bryophytes in exploiting disturbed habitats. Rather, their dispersal and regeneration abilities permit them to occupy inaccessible and disturbed habitats such as cliffs, walls, and forest clearings.

We can conclude that genetic components, currently interacting factors, and past history can work together or alone to elicit the responses we see in many bryophytes as they respond to stress.

Crystals – Adaptive?

Many new things appear due to mutations and developmental errors, but most of these fail to persist into a second generation. Some do persist, to the consternation of humans, with no apparent function. One such genetic invention may have been that of crystals formed by some mosses.

Jean Faubert (Bryonet 24 August 2010) reported a whitish substance under mosses in their fern greenhouse. Joselito Arocena (Bryonet 24 August 2010) suggested that this layer might be an accumulation of crystals of calcium oxalate, perhaps associated with mycorrhizal fungi, although Faubert did not find direct evidence of fungal presence. Such formations occur around roots of tree throws. Arocena *et al*. (2001) suggested that these crystals may protect fungal hyphae (*Piloderma fallax*) from desiccation and decrease the build up of calcium and oxalate in fungal cells. When associated with mosses, the formation of calcium oxalate may help them maintain their phosphorus supply and protect them from predators. The oxalate form could provide a reservoir during times of low calcium (Tuason & Arocena 2009). There is also an association between calcium oxalate and phosphorus, with more calcium oxalate crystals being formed under high levels of phosphorus.

Neil Bell (Bryonet 25 August 2010) reported that ***Mniodendron colensoi*** (=***Hypnodendron colensoi***; Figure 9), a moss in the preserved patches of Kauri forest on the North Island of New Zealand, has prominent crystals in the costae of leaves. Bryologists have assumed these to be calcium oxalate, but verification is needed.

Figure 9. ***Mniodendron colensoi***, Bill Malcolm, with permission.

Jeffrey Duckett and Silvia Pressel (Bryonet 25 August 2010) used X-ray analysis to test fresh material from New Zealand and found abundant calcium but no other cations or anions. They therefore presumed that the substance was indeed calcium oxalate.

Do Nutrients Limit Bryophytes?

Those who culture bryophytes know what nutrients to manipulate and what nutrient levels may be too much. But we seem to know much less about the effects of nutrients in nature.

Wang *et al*. (2014) addressed this question in the cushion moss ***Leucobryum juniperoideum*** (Figure 10-Figure 12). In eastern China, this moss occurs only in certain habitats. The **epigeic** (ground-dwelling) populations (Figure 10) occur only in areas that have a moso bamboo (*Phyllostachys edulis*) forest. The **epixylous** (on logs lacking bark) (Figure 11) are restricted to areas with Chinese fir (*Cunninghamia lanceolata*) forest. **Epilithic** (rock-dwelling) populations (Figure 12), on the other hand, live in both of these habitats. N and P concentrations differred markedly between the epigeic and epixylous habitats, with soil concentrations of these nutrients being much higher in the latter. So why is this species restricted to logs in the *Cunninghamia* forests? In experiments, growth of ***L. juniperoideum*** was reduced by N additions of 0.1 mol L^{-1} over six months. On the other hand, addition of up to 0.1 mol L^{-1} P caused growth increase. Furthermore, high concentrations of N (200 mg L^{-1}) significantly reduce germination rates and delay early development from spores. P, on the other hand, has no such negative effects. Thus, high soil concentrations of N are limiting in the distribution of this species.

Figure 10. ***Leucobryum juniperoideum*** on soil. PHoto by David T. Holyoak, with permission.

Figure 11. ***Leucobryum juniperoideum*** on log. Photo by Jan-Peter Frahm, with permission.

Figure 12. ***Leucobryum juniperoideum*** on a rocky substrate. Photo by Li Zhang, with permission.

Summary

Some bryophytes are able to live in bizarre habitats like iron stoves, deep caves, and glacial surfaces. These habitats test the limits of tolerance of the species. The high tolerances of some bryophytes led a group of aerospace scientists to suggest that bryophytes should be used for **terraforming** on the moon.

Bryophytes have evolved a variety of life cycle strategies for coping with the wide diversity and seasonal changes in their earthly habitats. Grime categorized plants by their limiting factors into **stress-tolerant**, **ruderal**, and **competitive** (**C-S-R model**), similar to Ramensky's **patients**, **explerents**, and **violents**, respectively. Compared to other plants, bryophytes fall along the bottom of the C-S-R triangle as non-competitors but with many stress tolerants and ruderals.

The **relative growth rate** (**RGR**) serves as a good measure of the success of a species. The ability of the species to tolerate its conditions and have a healthy growth rate is dependent upon genetic components, currently interacting factors, and past history. Genetic drift and physiological responses to the environment help to make populations look different.

Inducible proteins are able to respond to changes in the environment, thus permitting the plant to behave differently under different environmental circumstances.

Many adaptive mechanisms elude us, while others may have no modern function at all. Incorporation of calcium oxalate is one of those factors that thus far has escaped our understanding.

Acknowledgments

In this, and many other chapters, Jean Faubert has been helpful in reporting errors to me, a service I greatly appreciate. Bryonetters have contributed to the discussion on calcium oxalate.

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CHAPTER 7-1

WATER RELATIONS: CONDUCTING STRUCTURES

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CHAPTER 7-1

WATER RELATIONS: CONDUCTING STRUCTURES

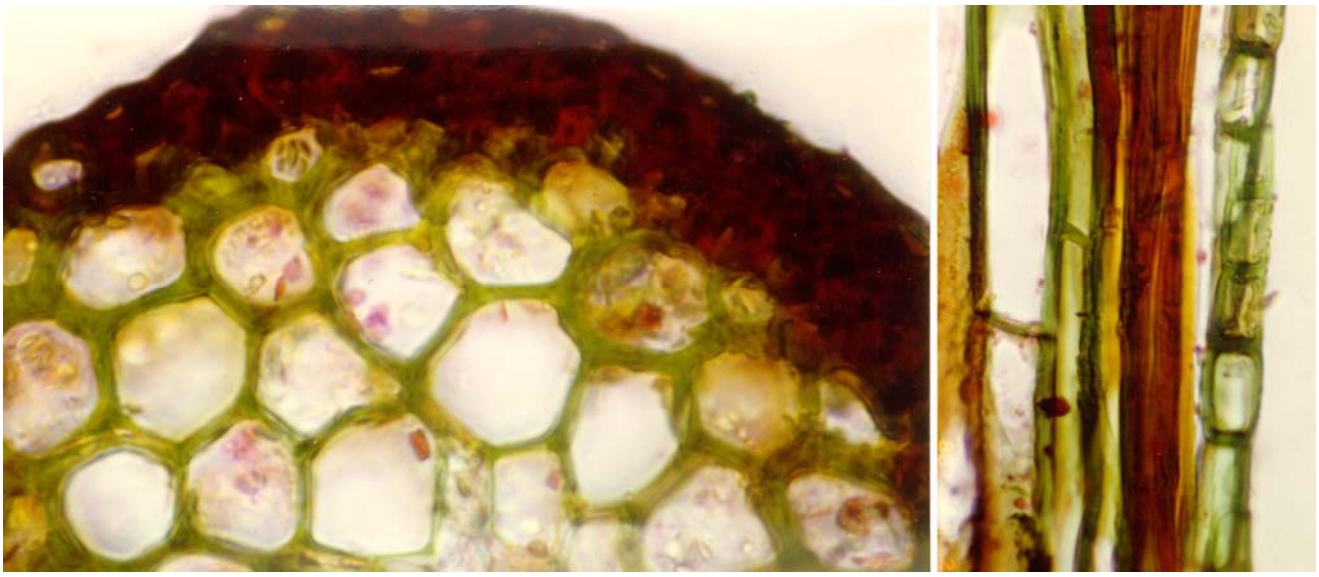

Figure 1. Cross section (**left**) and longitudinal section (**right**) of the moss ***Bryoxiphium***, showing in vertical section how cells that appear in cross section to be only parenchyma cells may in fact be elongate cells suitable for conduction. Photo courtesy of Isawo Kawai.

Movement to Land

The most obvious need for photosynthetic organisms in their move from water to land was the continued need for water. At this time, most photosynthetic organisms still had a dominant gametophyte, and all indications are that the movement onto land carried with it that gametophytic dominance. As life on land progressed through evolution, plants with sophisticated vascular tissue ultimately developed. At the same time, the gametophyte in these highly vascularized tracheophytes (lignified vascular plants) solved its water problems by ultimately being contained within the protection of sporophytic tissues in the seed plants.

This reduction of the gametophyte might necessarily have forced a reduction in conducting tissues because the surrounding sporophytic tissue on the one hand reduced available space and on the other made vascularization much less necessary in the gametophyte. But in gametophyte-dominant bryophytes, survival on land required a means for getting water, and the nutrients carried with it, from one part of the plant to another. Despite their being the first land plants, as Raven (2002) has put it, plant biologists have taken a "top-down" view of land plants, seemingly expecting the bryophytes to have a simpler version of the same system as tracheophytes.

But bryophytes have been around much longer than tracheophytes, and their gametophytes have remained dominant. Hence, should we not expect them to have evolved means of water movement in the gametophyte generation during all these millennia? First of all, consider the desiccation-tolerant tracheophytes. These are almost all small plants (Raven 2002). Many bryophytes are likewise desiccation tolerant, and they too are small.

Bryophytes as Sponges

Sponges, both animal and synthetic, gain and retain water through small chambers and capillary spaces. Bryophytes, due to their small size and tiny leaves, are natural arrays of chambers and capillary spaces. As this story unfolds, you will soon see that bryophytes are indeed sponges, aiding their own water needs and in some cases massively affecting the **ecosystem** (interacting community & habitat).

All life needs water, and the most severe stress for organisms venturing onto land was undoubtedly just that. But already, algae had developed means of becoming dormant through zygospores when they faced unfavorable circumstances. However, those first land organisms had to find ways to get water to all their internal parts, and often this water was in very limited amounts. For bryophytes, surviving water loss and prolonged periods of drought was a necessity for survival, so it is not surprising that during their 450 million years of evolutionary history (Proctor 2000a) they have perfected physiological mechanisms that

outdistance those of their tracheophyte counterparts (Oliver *et al*. 2000a). This ability has led plant physiologists to use bryophytes as model systems for the study of desiccation tolerance physiology, even to the extent of attempting to introduce those genes to crop plants (Comis 1992; Oliver *et al*. 2000b). And this use has made it into the agricultural literature with articles such as "Miracle Moss" (Comis 1992).

It appears that despite the typical relegation of bryophytes to the category of "non-vascular," conduction has played a major role in the phylogenetic history of bryophytes. Hedenäs (1999) examined the importance of various character states on the phylogenetic history of **pleurocarpous** mosses (typically the ones that grow horizontally) and determined that, based on redundancy analysis, gametophyte variance relates to characters associated with water conduction. Furthermore, one of the most important environmental variables in this phylogeny was the non-wetland to wetland gradient. On the other hand, Proctor (2000b), in "The bryophyte paradox: Tolerance of desiccation, evasion of drought," points out that a desiccation-tolerant tree is hardly conceivable. Height necessitates highly developed conducting systems that are unnecessary in short plants, and even among the bryophytes, it is the tall ***Dawsonia*** (Figure 2) and ***Polytrichum*** (Figure 3-Figure 4) that have conducting systems that almost mimic those of **tracheophytes** (plants having tracheids, *i.e.* the lignified vascular plants).

Figure 2. ***Dawsonia***, one of the tallest and most highly structured of all mosses. Photo by Janice Glime.

Ecosystem processes cannot be understood without understanding the role of bryophytes and their water relations. A lack of understanding of bryophyte water relations has led ecologists to conduct inappropriate experiments or draw erroneous conclusions about such topics as nutrient cycling and effects of air-borne pollutants on mosses in general in the ecosystem. Mosses such as ***Polytrichum*** (Figure 3-Figure 4), among the most conductive bryophytes in the northern hemisphere, have been used to generalize about the behavior of soil and airborne minerals in mosses during ecosystem processes. But this moss can behave very differently from most of the other genera that carpet forest floors. Puckett (1988) warns that mosses with internal conduction (as in ***Polytrichum***) do not make good monitors. Anderson and Bourdeau (1955) concluded that dew and rain were the main sources of water for bryophytes, excluding the groundwater source so vital for tracheophytes. It is therefore important that ecosystem ecologists, especially those studying water relations and nutrient cycling, have a basic understanding of the variety of ways that bryophytes move water and nutrients.

Figure 3. ***Polytrichum commune*** with capsules 1 Kristian Peters, through Creative Commons.

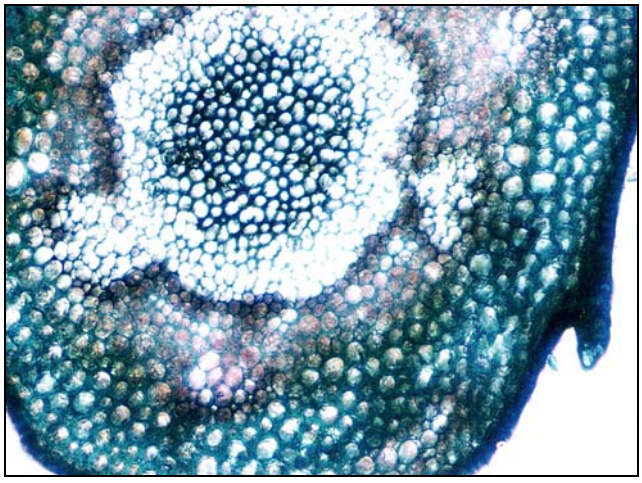

Figure 4. ***Polytrichum*** stem cross section showing central hydrome and surrounding leptome – the essence of its vascular system. Photo courtesy of Isawo Kawai.

Nearly every botany book on the market defines bryophytes as non-vascular plants, distinguishing them in this way from all other embryophytes. In fact, **many bryophytes are vascular**, but **lacking lignin** [associated with cellulose in cell walls of **sclerenchyma** (thick-walled supporting cells), xylem vessels, and tracheids; Hébant 1977] and the variety of perforated and spirally thickened cells typical of xylem. [Note that **lignin-like** compounds bind to cell walls in bryophytes, especially in spores and

elaters (Ligrone *et al*. 2008).] Rather, many bryophytes have unique cells that perform conduction in rather different ways from the "true vascular plants." Kawai has published a series of colored photographs (*e.g.* Figure 1), using specific stains, that illustrate the wide presence and variety of such tissues among many families of mosses (Kawai 1971a, b, c, 1976, 1977a, b, 1978, 1979, 1980a, b, 1981, 1982, 1989, 1991a, b; Kawai & Ikeda 1970; Kawai & Ochi 1987; Kawai *et al*. 1985, 1986; Ron & Kawai 1990). Hence, it is safer to distinguish the bryophytes as non-lignified plants (still waiting to be disproved) or **non-tracheophytes**, and the lignified vascular plants as **tracheophytes**. This puts a slightly new perspective on the way we look at their roles in ecosystems.

When we consider bryophytes, we are tempted to think about wet habitats where mosses grow close to water, basking in the sun of a bog, or cooling off in the spray of a waterfall. Certainly these are habitats where bryophytes are common, but keep thinking. What about those rocks on the cliff or the sand of the dunes (Figure 5)? In fact, can you think of any habitat that has plants but where it is impossible to find mosses? There are not many, and if you visualize some of the rocky habitats in your mind, you realize that these organisms undergo tremendous changes in moisture and temperature, even within a single day, occupying habitats where no vascular plants can survive.

Figure 5. ***Aloina ambigua*** growing in sand. Photo by Michael Lüth, with permission.

If we try to speculate about those first organisms to survive on land, we would probably consider them to be simple organisms with no organized vascular systems. There was no selection pressure for any wasteful vascular tissue while these organisms were living in the water. Water may have been the primary force limiting plants from vast colonization of land. Gray (1985) suggests that it was the ecophysiological tolerance to desiccation, appropriate life cycle strategies, and short vegetative life cycle that permitted widespread colonization during the mid **Ordovician** (~441-504 million years ago) to the mid Early Silurian (~400-440 million years ago) – strategies that describe bryophytes.

Even with so many diverse habitats occupied by plants today, we still consider the move from water to land to have been a major one. Imagine the changes that were necessary. Consider that the greatest overriding challenge was to keep their cells wet. Land plants responded to this challenge in two ways. Some, the ones we traditionally called **vascular plants** (the **tracheophytes**), acquired **lignin**, developed a complex water transport system, and encased themselves in a waxy, waterproof **cuticle**. Others, the **bryophytes**, developed strategies that we are only beginning to understand, including external transport, cell-to-cell transport, and the ability to survive desiccation. In the words of Proctor (2000a), "Bryophytes... evolved desiccation tolerance and represent an alternative strategy of adaptation to life on land, photosynthesizing and growing when water is available, and suspending metabolism when it is not. Limited by mode of life, but also liberated: prominent on hard substrates such as rock and bark, which are impenetrable to roots and untenable to vascular plants. Bryophytes (in species numbers the second biggest group of green land plants) may be seen as mobile phones, notebook computers and diverse other rechargeable battery-powered devices of the plant world – not direct competitors for main-based equivalents, but a lively and sophisticated complement to them."

Bryophytes are adapted to land but restricted in their morphology by a biochemical impasse, *i.e.* the inability to synthesize lignin (Niklas 1976). Because they lack lignin, they lack the tracheids and vessels of other plants, but have produced instead vascular strands with similar elongate shapes. Nevertheless, they are unable to support a large structure or great mass because they lack the strengthening ability of lignin. Because of their importance in both structure and physiology, water relations seem an appropriate place to start in our consideration of the limits imposed on bryophytes, for without that understanding, we cannot understand their other limitations, nor can we fully evaluate their ecological relationships.

Conducting Structures

Conducting structures are not new expressions in bryophytes. Edwards *et al*. (2003) found at least fourteen types of such structures in mesofossils from a Lochkovian (Lower Devonian) locality in the Welsh Borderland, Shropshire. These are distinguished by variation in the combination of cells in the central strand and the cell wall architecture. The elongate cells may have smooth, uniformly thick or thin walls, walls with smooth projections pointed inward, or bilayered walls. The innermost walls are perforated by pores with the dimensions of plasmodesmata. These perforations are not well organized and some resemble the secondary thickenings most similar to the S-type tracheids of the **Rhyniopsida** (Figure 6-Figure 7), a primitive tracheophyte with lignified vascular tissue. Edwards and coworkers suggest that the imperforate bilayered examples may have been used in water conduction, cells that exhibited globular residues may have facilitated metabolite movement, and smooth-walled elongate cells seemed to be involved in support. Edwards and coworkers were unable to identify these mesofossils to genus, but concluded that there was widespread anatomical diversity among these early bryophytes.

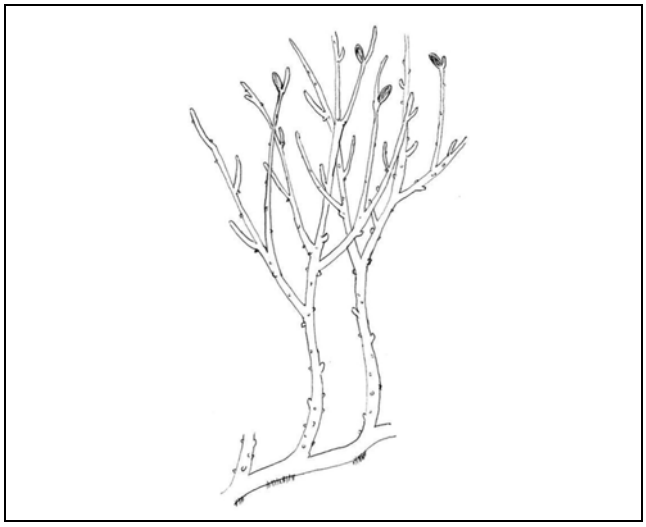

Figure 6. ***Rhynia gwynne-vaughanii*** reconstruction, member of **Rhyniophyta** – an early vascular plant. Photo by Griensteidl, through Creative Commons.

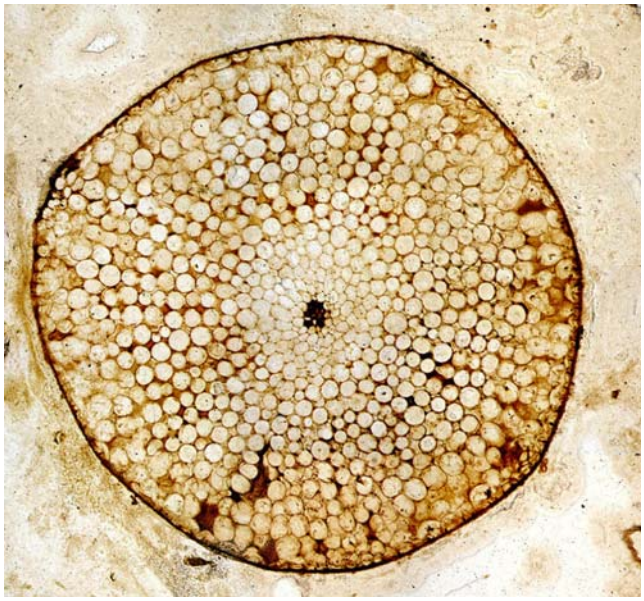

Figure 7. ***Rhynia gwynne-vaughanii*** stem cs fossil. Photo by Plantsurfer, through Creative Commons.

Bryophytes have two paths of water movement, often both in the same plant: internal through a **central cylinder** (**endohydric**) and external along the surface of the leafy or thallose plant (**ectohydric**) (Buch *et al*. 1938). Some thallose liverworts, **Polytrichaceae**, and **Mniaceae** represent the endohydric groups (Buch 1945, 1947; Proctor 2000b), but there are many others with at least some internal conduction. ***Metzgeria furcata*** (Figure 12), a "thallose" liverwort in the **Jungermanniopsida**, and others in the **Marchantiopsida**, have midribs (Figure 13) with enlarged internal cells (Figure 14), but the relative importance of these midrib cells for conduction is largely unknown.

In ***Asterella wilmsii*** (see Figure 8), numerous lipid bodies are present in the thallus cells. Ligrone and Duckett (1994a) suggested that these were associated with the perennation in winter. In the same species, vacuolar microtubule associations resemble the microtubule-based translocation system of many animals, but they differ greatly from the bulk flow known in sieve elements and actin-based cytoplasmic streaming of tracheophytes.

Figure 8. ***Asterella*** sp.; ***Asterella wilmsii*** produces numerous lipid bodies in the thallus cells. Photo by Brian du Preez, through Creative Commons.

Ligrone and Duckett (1994b) also found that food conducting cells in both gametophytes and sporophytes of bryoid mosses have a polarized organization and an axial system of endoplasmic microtubules. The polarity corresponds with a source to sink gradient with distal cellular ends (toward the sink) containing denser cytoplasm than that at the proximal ends. The cytoplasmic polarity and endoplasmic microtubules are unique in the plant kingdom, but are reminiscent of arrangements seen in animal neurons and in fungi.

The arrangement of the microtubules seems to aid in rapid rehydration, at least in ***Polytrichastrum formosum*** (Figure 9) (Pressel *et al*. 2006). It is this arrangement that permits rapid re-establishment of the cytoplasmic architecture of the leptoids (Figure 58). This reassembly of the endoplasmic microtubule systems establishes the time frame for recovery.

Figure 9. ***Polytrichastrum formosum***, a species that experiences rapid rehydration due to its arrangement of microtubules. Photo by Daniel Cahen, through Creative Commons.

But even in conduction structures, mosses once again exhibit diversity. In both ***Polytrichum juniperinum*** (Figure 10) and ***Mnium hornum*** (Figure 11) decapitation greatly reduces cellular polarity (Ligrone & Duckett 1996a). But only in ***Mnium*** was there a disappearance of endoplasmic microtubules, loss of longitudinal alignment of organelles, and accumulation of abundant starch when subjected to decapitation. And in ***Polytrichum*** starch accumulated in the cortical parenchyma cells.

Figure 10. ***Polytrichum juniperinum***, a species that loses much of its polarity when decapitated. Photo by Bob Klips, with permission.

Figure 11. ***Mnium hornum***, a species that experiences rapid rehydration due to its arrangement of microtubules. Photo by Hermann Schachner, through Creative Commons.

Sphagnum seems to have found yet another way to accomplish formation of conducting cells. The cytology is very similar to that in bryoid mosses, but the development of the central strand (Figure 37-Figure 40, Figure 42-Figure 45) of the stem in ***Sphagnum*** is not homologous with that known in other mosses (Ligrone & Duckett 1998b).

Furthermore, mosses differ from liverworts in location of their conduction elements (Ligrone *et al*. 2000). In mosses, these occur in both the gametophyte and sporophyte. In liverworts, however, they occur only in the gametophyte. In the liverworts, the **Calobryales** and **Pallaviciniaceae** have water-conducting cells with walls that are perforated by pores derived from plasmodesmata. In the mosses, this type of water-conducting cell is known only from ***Takakia*** (Figure 25-Figure 27), a moss initially considered to be a liverwort until its sporophyte was discovered.

In the liverwort ***Symphogyna africana***, conducting cells have a different path or origin (Ligrone & Duckett 1996b). The cortical microtubules, wall microfibrils, and secondarily modified plasmodesmata are consistently aligned to form helices of about 45º, reminiscent of flowering plant vessels. Ultimately, the cytoplasm dissolution causes lysis of all cellular membranes, with membrane-bounded fibrillar material becoming deposited onto the walls. When the plugs of amorphous electron-transport material dissolves, open pits form. This formation of conducting elements resembles, in some aspects, the formation of vessels in flowering plants.

Conduction to other parts of the bryophytes has a similar polarized transport, facilitating long-distance movement of nutrients (Ligrone *et al*. 2000). This occurs in rhizoids and caulonemata and in the thallus parenchyma cells of at least some liverworts.

Diversity presents again when we compare cell wall components, equalling the diversity found in "higher" plants (Ligrone *et al*. 2002). Not only were there differences among the orders, diversity occurred within the order **Polytrichales**. Furthermore, the water-conducting cells of ***Takakia*** (Figure 25-Figure 27) are not homologous with those of other mosses, nor are they homologous with the ***Haplomitrium*** (Figure 28) or metzgerialean liverworts.

Broadly speaking, imperforate bilayered examples may have been involved in water conduction, cells with globular residues with or without pitting involved in metabolite movement, and smooth-walled examples with or without projections involved in support.

In liverworts, conducting tissues are restricted to the gametophyte, whereas in mosses, they are sometimes also in the sporophyte (Ligrone *et al*. 2000). Among the liverworts, the **Calobryales** and **Pallaviciniaceae** in the **Metzgeriales** have water-conducting cells with walls perforated by pores derived from plasmodesmata. The **hydroids** (water-conducting cells) of bryoid mosses are imperforate. In the **Polytrichaceae**, there is an axial system of microtubules in the **leptoids** (food-conducting cells) and in the parenchyma cells of the stems and setae of other mosses such as ***Sphagnum***, representing the variety of expression of conducting cells in the bryophytes..

Figure 12. ***Metzgeria furcata*** thallus with midrib. Photo by Des Callaghan, with permission.

Figure 13. ***Metzgeria furcata*** thallus showing distinct midrib with elongated cells and one layer of parenchyma cells in the thallus. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

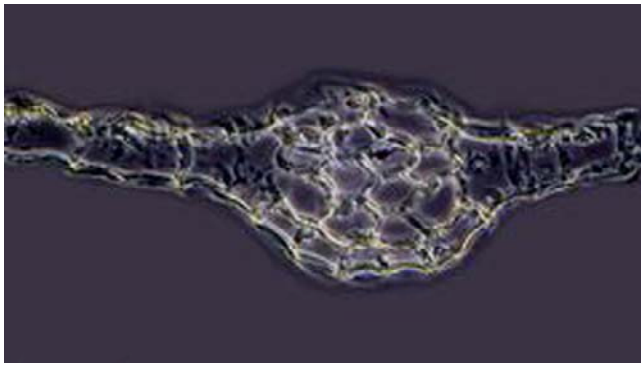

Figure 14. ***Metzgeria furcata*** thallus cross section at midrib. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Ectohydric mosses typically maintain a constant internal water content by absorbing water from the external capillary spaces as needed (Proctor 2000b). The ectohydric and endohydric modes each require their own structural adaptations. Lacking lignin, xylem is not possible. Furthermore, in the lignified vascular plants, it is the sporophyte generation that carries out organized internal conduction, and the gametophyte, with rare exception, does not. By contrast, in bryophytes it is the leafy gametophyte that must obtain and conduct water and nutrients about the plant, although conduction also occurs in the moss sporophyte (Ligrone *et al*. 2000; see Chapter 5-9).

Although the hornworts (**Anthocerotophyta**) have been considered by some to be reduced from more advanced plants, water-conducting tissue is unknown in this phylum (Ligrone *et al.* 2000), although Hébant (1977) reported the presence of cells resembling phloem sieve cells (leptoids?) in ***Dendroceros*** (Figure 15). Likewise, few liverworts (**Marchantiophyta**) have specialized conducting tissues in their gametophytes (Figure 16-Figure 22), and none have them in the sporophyte. Nonetheless, conducting strands have been known since 1901 in the thallose liverwort ***Pallavicinia lyellii*** (Figure 23; Tansley & Chick 1901). As in mosses, ***Pallavicinia*** conducting strands (Figure 24) closely resemble tracheids, with long cells, tapering ends, and obliquely oriented pits, and they, like xylem cells, are dead at maturity (Richardson 1981).

Figure 15. ***Dendroceros borbonensis***, a hornwort (**Anthocerotophyta**). Photo by Jan-Peter Frahm, with permission.

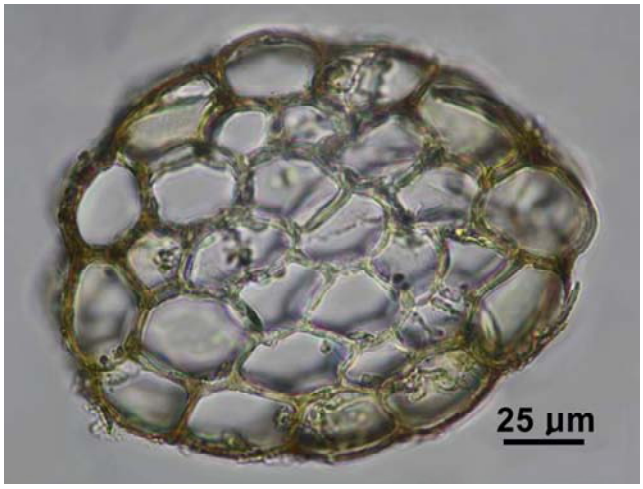

Figure 16. ***Kurzia*** sp. (leafy liverwort, **Jungermanniopsida**) stem cross section. Photo by Tom Thekathyil, with permission.

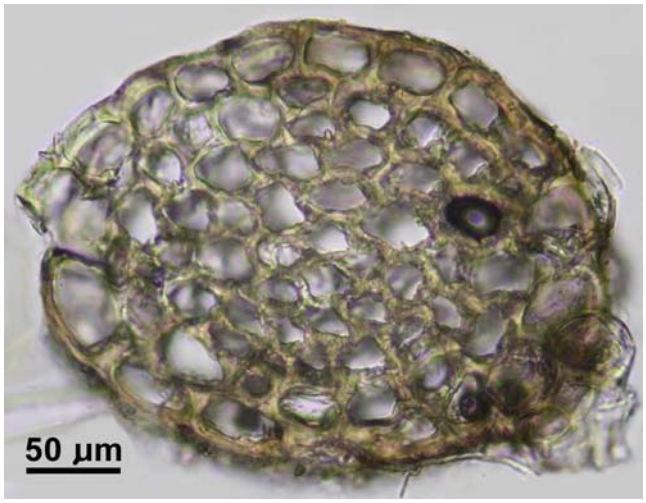

Figure 17. ***Lepidozia*** sp. (leafy liverwort, **Jungermanniopsida**) stem cross section. Photo by Tom Thekathyil, with permission.

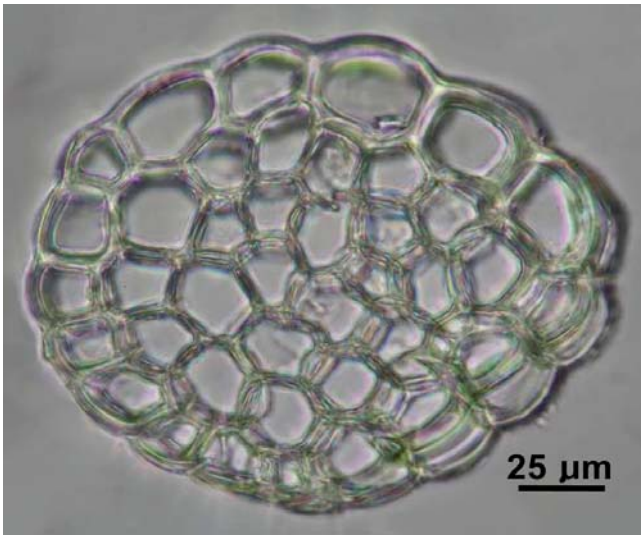

Figure 18. ***Telaranea pallescens***, a leafy liverwort in the **Lepidoziaceae** (**Jungermanniopsida**), stem cross section. Photo by Tom Thekathyil, with permission.

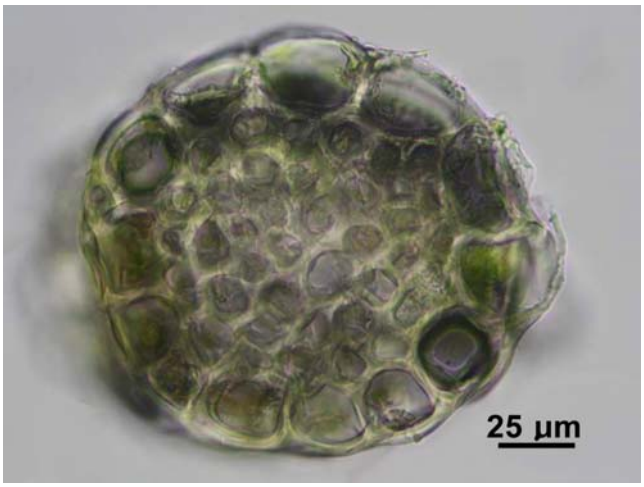

Figure 19. ***Telaranea tridactylis***, a leafy liverwort in the **Lepidoziaceae** (**Jungermanniopsida**), stem cross section. Photo by Tom Thekathyil, with permission.

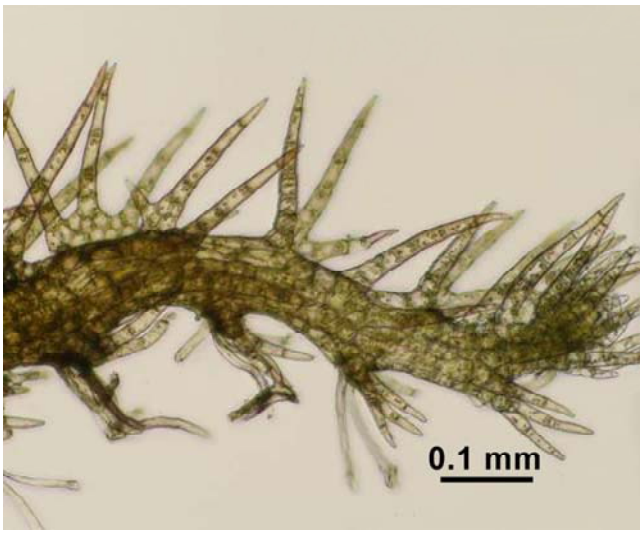

Figure 20. ***Temnoma palmata***, a leafy liverwort (**Pseudolepicoleaceae**, **Jungermanniopsida**). Photo by Tom Thekathyil, with permission.

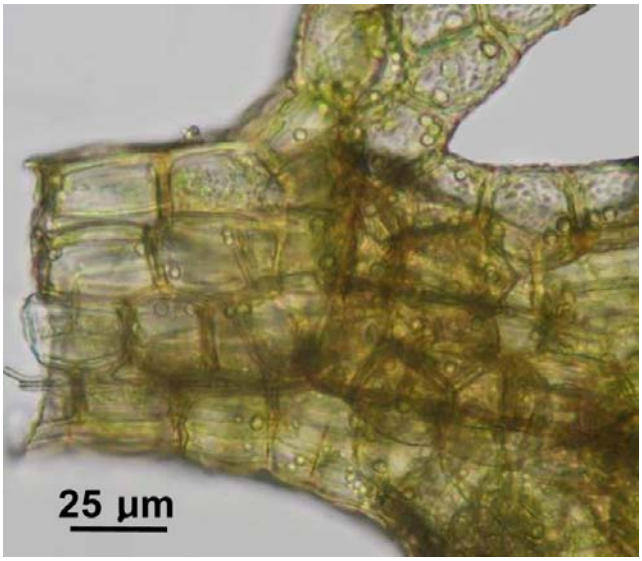

Figure 21. ***Temnoma palmata*** stem showing parenchyma cells and leaf base. Photo by Tom Thekathyil, with permission.

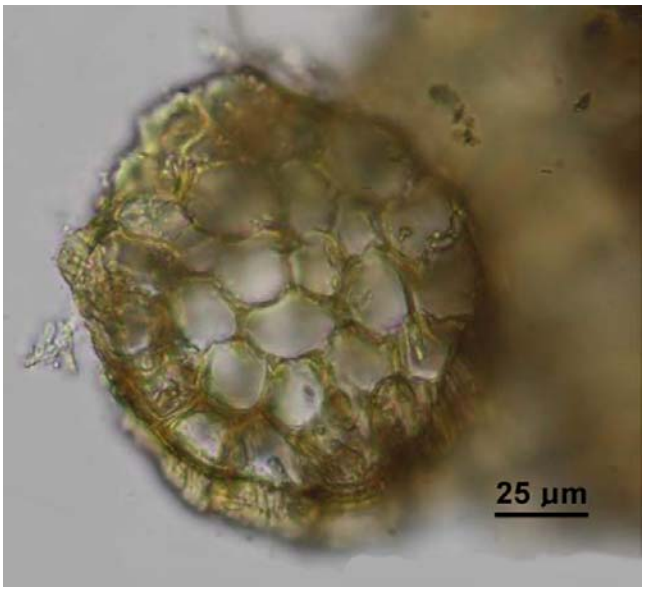

Figure 22. ***Temnoma palmata*** stem cross section. Photo by Tom Thekathyil, with permission.

Figure 23. ***Pallavicinia lyellii*** thallus. Photo by Jan-Peter Frahm, with permission.

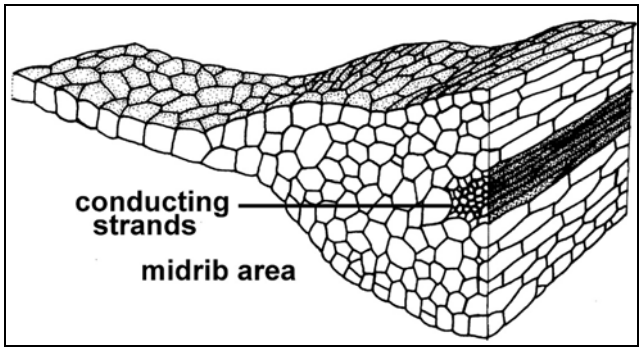

Figure 24. ***Pallavicinia lyellii*** cross section of thallus. Drawing from Hébant (1977).

Unlike the liverworts, as already noted mosses can have conducting cells in both generations (Ligrone *et al.* 2000). In some liverworts of **Calobryales** and in **Pallaviciniaceae** of the **Metzgeriales** (Figure 23-Figure 24) and the moss ***Takakia*** (a primitive moss once thought to be a liverwort; Figure 26), there exist water-conducting cells with perforated walls derived from **plasmodesmatal pores** (Ligrone *et al*. 2000), but these do not seem to be organized into a distinctive **central strand** (group of elongate cells forming central axis of stems and thalli of some bryophytes, usually thin-walled and often colored; Figure 58). Furthermore, the water conducting cells of ***Takakia*** (Figure 25-Figure 27) do not seem to be homologous with either the hydroids of other mosses or with those of the **Metzgeriales** or the leafy liverwort ***Haplomitrium*** (Figure 28), lending support to its basal lineage (Ligrone *et al*. 2000).

Figure 26. ***Takakia lepidozioides*** showing rhizomes and stems. Photo from the Herbarium of Hiroshima University, with permission.

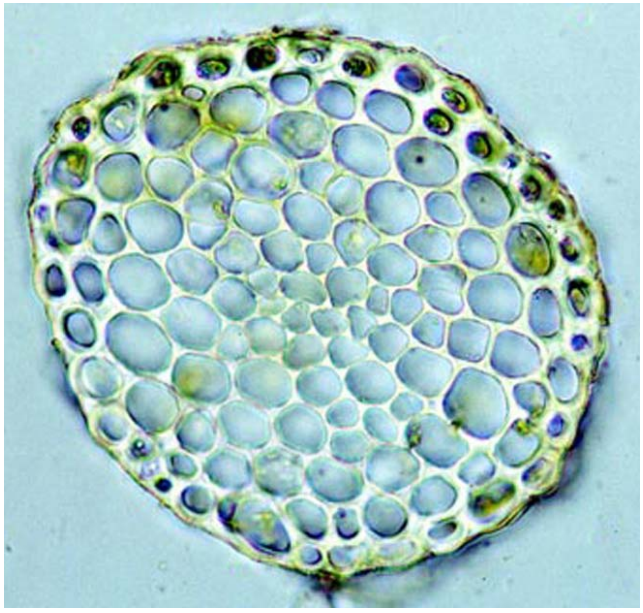

Figure 25. ***Takakia lepidozioides*** stem cross section. Photo from the Herbarium of Hiroshima University, with permission.

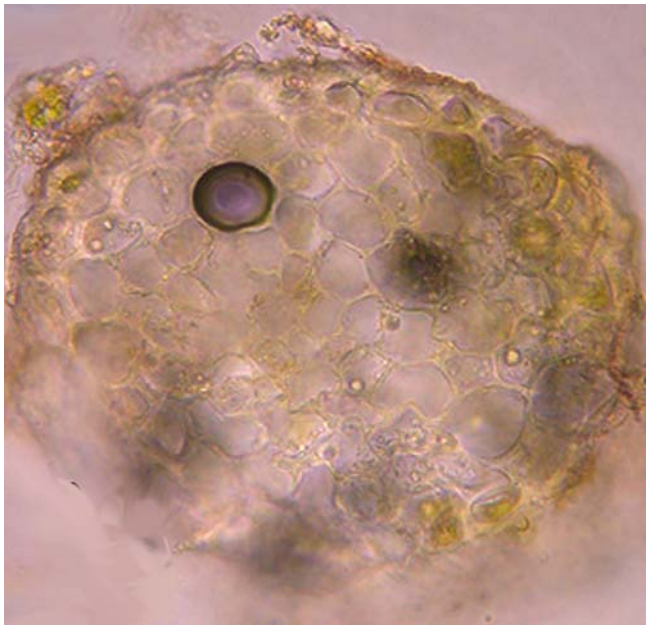

Figure 27. Cross section of stem of ***Takakia lepidozioides*** showing no evidence of a central strand. Photo with permission from Botany website, UBC.

Figure 28. ***Haplomitrium gibbsiae*** showing stems that lack a central strand. Photo by Jan-Peter Frahm, with permission.

Dendroligotrichum dendroides (Figure 29, Figure 49, Figure 73) can reach 60 cm height and transports water **endohydrically** (internally) (Atala & Alfaro 2012). Its water-conducting **hydrome** follows Murray's law, *i.e.* the sum of the radii of the conduits to the third power (Σr3) is maintained across branching of these conduits. This means that the conduction system is optimized for maximal water transport per unit of 'vascular' tissue biomass. As the vascular tissue ascends toward the apex, there is **acropetal** (base to apex) tapering and an increase in conduit number at ascending levels. Since this architecture is similar to that of tracheophytes, Atala and Alfaro reasoned that it had undergone the same selection pressures in its evolution.

Figure 29. ***Dendroligotrichum dendroides***, a moss with non-lignified vascular tissue. Photo by Felipe Osorio-Zúñiga, with permission.

Leptomes and Hydromes

Kawai (1991a) describes the moss stem as having a basic structure much like that of tracheophytes with an **epidermis** surrounding the **cortex** (Figure 30-Figure 31). This basic structure describes most of the **pleurocarpous** mosses that move internal substances mostly horizontally.

Among the **acrocarpous** mosses (those mostly upright mosses with the sporophyte at the stem apex), more complex stems can have a conducting cylinder in the center of the stem. This cylinder connects the base of the stem to the apex, but in most cases it is not connected to the leaves by any sort of leaf trace. The center of this conducting cylinder is comprised of **hydroids** and **stereids**, making up the **central strand** (Figure 32) (Zamski & Trachtenberg 1976). As you can guess from the name, **hydroids** are water-conducting cells. They are somewhat similar to tracheids but lack any horizontal connections (*i.e.* no pits) and are not lignified. And as you will see later, their chemistry and development are different from that of tracheids. Hydroids collectively make up the **hydrome** (also known as **hadram** or **hydrom)** (Scheirer 1980).

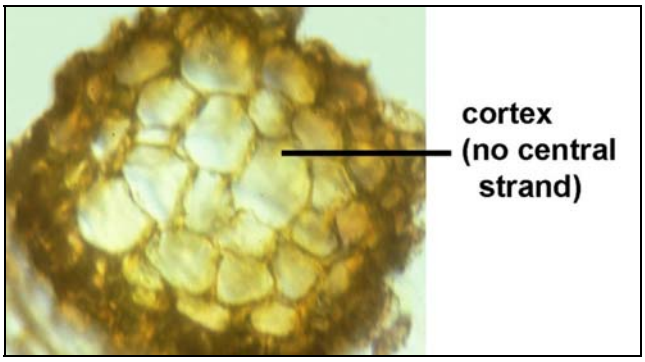

Figure 30. ***Trichodon cylindricus*** stem cs showing lack of central strand. Photo by Janice Glime.

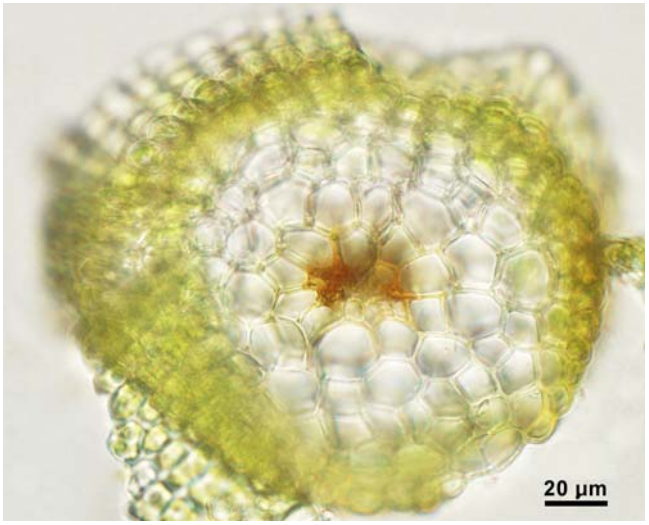

Figure 31. ***Molendoa sendtneriana*** (acrocarpous; **Pottiaceae**) stem cross section showing a central tissue that is differentiated. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Stereids are elongate, thick-walled, slender, and fiber-like cells that add support to the stem, typically arranged in a cylinder around the hydrome. The stereids are collectively known as the **sterome** (Hébant 1977) (also known as sterom; Zamski & Trachtenberg 1976). They can also occur in the leaf **costa** (midrib-like strand; Figure 61), as will be discussed below, where they also serve as support.

Hébant (1977) describes the living parenchyma cells around the central strand in the **Polytrichaceae** to be a **hydrom sheath**, a term originated by Tansley and Chick (1901). This seems like an unnecessary term with only limited usage. However, Hébant reports that both starch grains and oil droplets are frequent in these cells. In ***Polytrichum commune*** (Figure 3), these cells have accelerated enzyme activity at the same time the protoplasts of the hydroids degenerate. Furthermore, some members of the **Polytrichaceae** have stereids among the

central strand cells. These have acid phosphatase activity in ***Dawsonia longifolia*** (Figure 2), suggesting they may have a role in the maturation of the hydroids.

Whereas the hydrome is relatively common, the **leptome** (also known as leptom; Figure 32) is less well known. The simple structure of its cells (**leptoids**) makes them difficult to distinguish from cortex parenchyma cells in cross section, but in vertical section they can be seen as longer cells surrounding the central strand and somewhat resembling phloem sieve cells (Figure 1, Figure 56). Their function, like that of phloem cells, is for photosynthate conduction, but they may also transport hormones or other substances. These cells in the **Polytrichales** (Figure 35) have oblique sieve plates, organized marginal endoplasmic reticulum, and partial nuclear degeneration (Scheirer 1975; Crandall-Stotler 1980).

In mosses like the **Mniaceae** (Figure 32-Figure 34) and **Polytrichaceae** (Figure 35), distinguishing the hydroids is fairly easy. However, not all distinctive cells in the center of the stem are hydroids. In other mosses, small to large cells comprise a distinctive central tissue (Figure 31), but we have no experiments to demonstrate their functions in conduction. It was not until 2002 (Ligrone *et al*. 2002) that immunocytological testing revealed the nature of the central tissue cell walls of 8 mosses and 4 liverworts. Little follow-up work has occurred, hence much of our understanding is still conjecture.

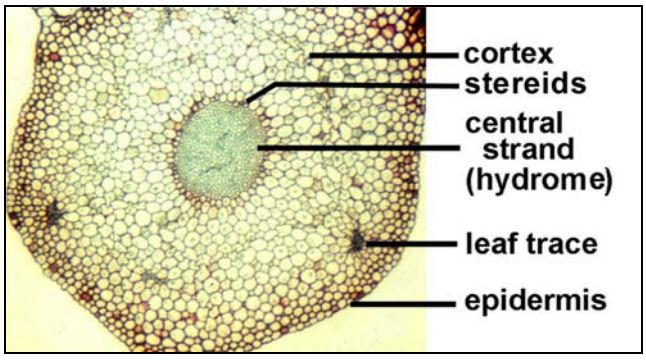

Figure 32. ***Plagiomnium*** (**Mniaceae)** stem cross section illustrating well-developed central strand. Photo by Janice Glime.

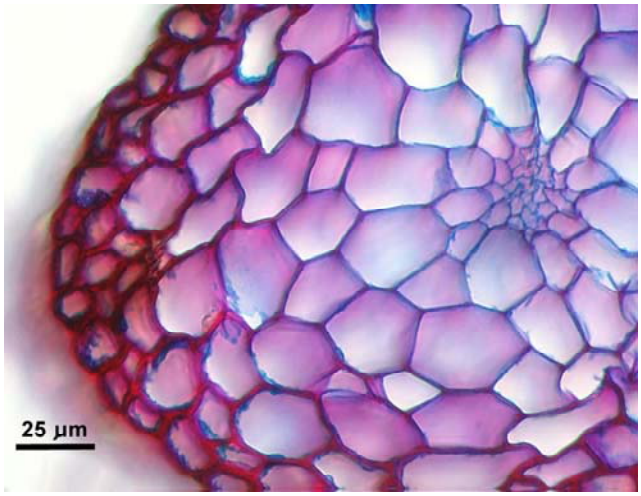

Figure 33. ***Plagiomnium ellipticum*** stem cross section showing central strand with **hydroids**. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

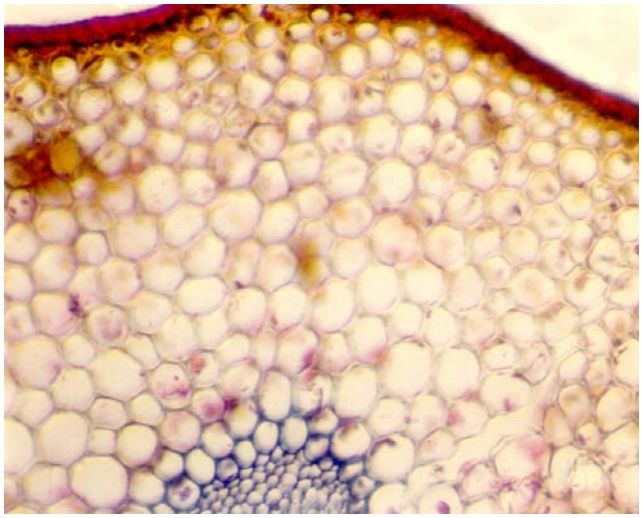

Figure 34. ***Rhizogonium*** (**Mniaceae**) stem cross section showing **hydroids** (stained blue in center). Photo courtesy of Isawo Kawai.

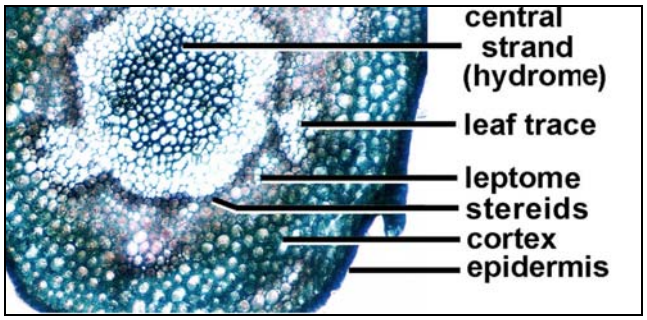

Figure 35. ***Polytrichum*** stem cross section illustrating well-developed central strand. Photo courtesy of Isawo Kawai.

Consider, for example, the genus ***Sphagnum*** (Figure 36). Central cells can vary considerably among species (Figure 37-Figure 42) and can be much smaller than the outer layer that comprises the epidermis (Figure 43). Yet these small cells of the central core are not conducting cells (Hébant 1977). Instead, ***Sphagnum*** typically uses its descending branches as wicks because they form capillary spaces around the stem (Figure 36).

Figure 36. ***Sphagnum obtusum*** showing descending branches that help to create capillary spaces and the wicking activity for upward movement of water. Photo by Michael Luth, with permission.

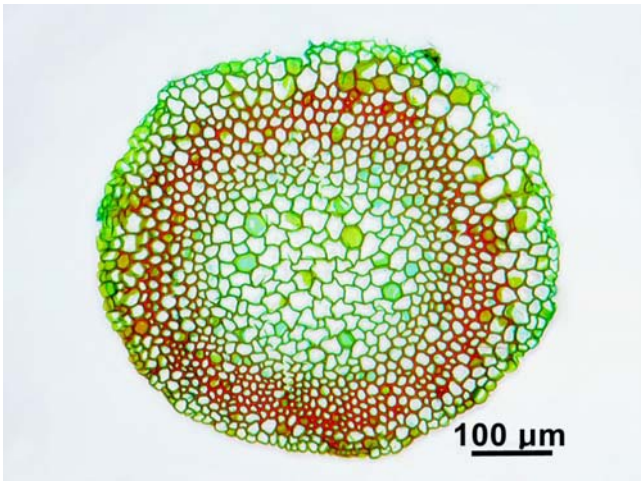

Figure 37. ***Sphagnum obtusum*** stem cross section with larger parenchyma cells in the center, surrounded by smaller thick-walled cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

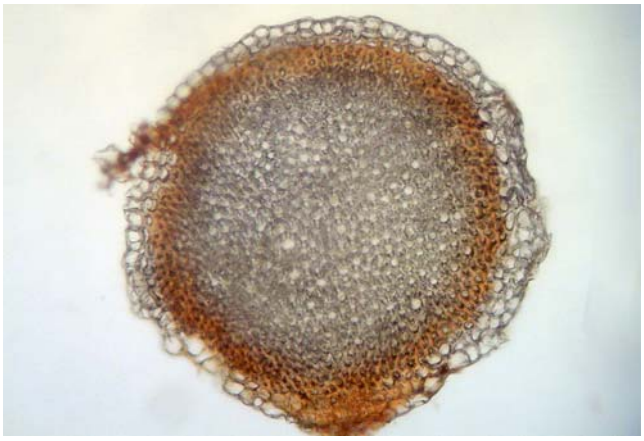

Figure 38. Stem cross section of ***Sphagnum contortum*** with three distinct cell types but no hydroids. Photo by Michael Lüth, with permission.

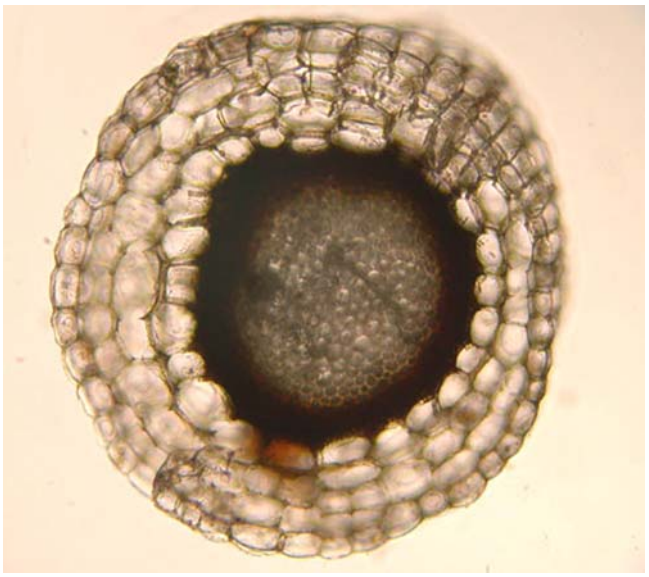

Figure 39. ***Sphagnum*** stem cross section with small-celled central core, dark band of cells, and 3-4 layers of outer hyaline cells. Photo from Botany website, University of British Columbia, Canada, with permission.

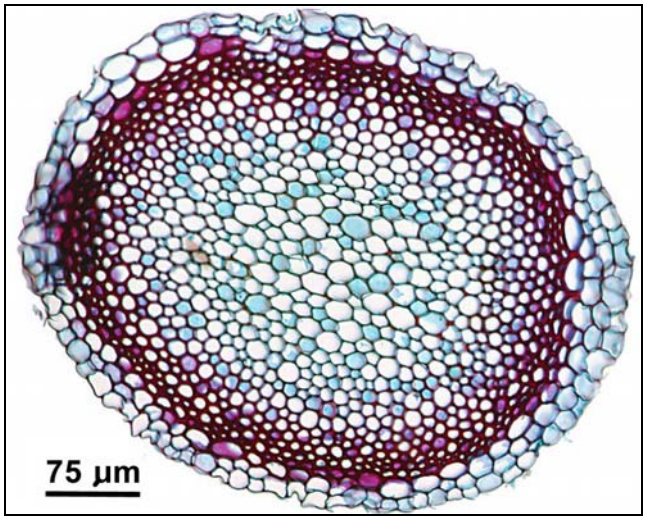

Figure 40. ***Sphagnum squarrosum*** stem cross section with central parenchyma cells, a strengthening layer, and two distinct layers of hyalocysts. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

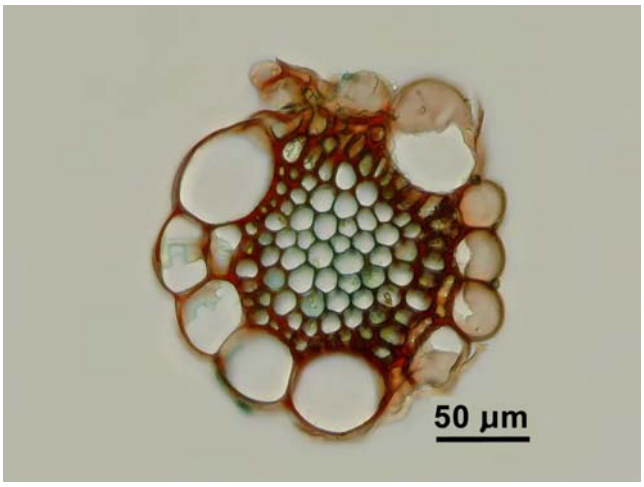

Figure 41. ***Sphagnum squarrosum*** branch cross section showing very different outer hyaline cells and overall appearance from that of the stem in Figure 40. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

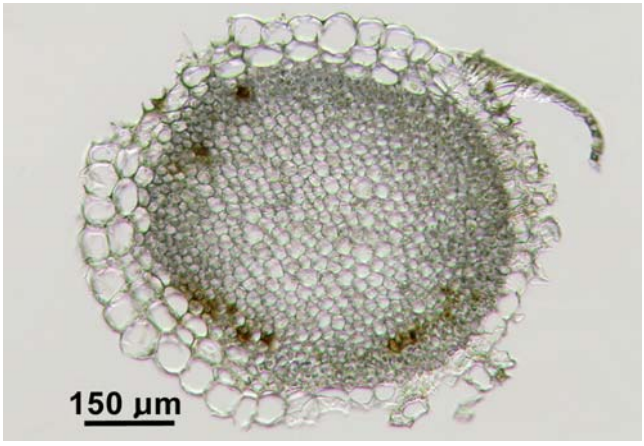

Figure 42. ***Sphagnum fimbriatum*** stem cross section showing only two kinds of cells: central core and outer hyaline cells (**hyalodermis**). Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

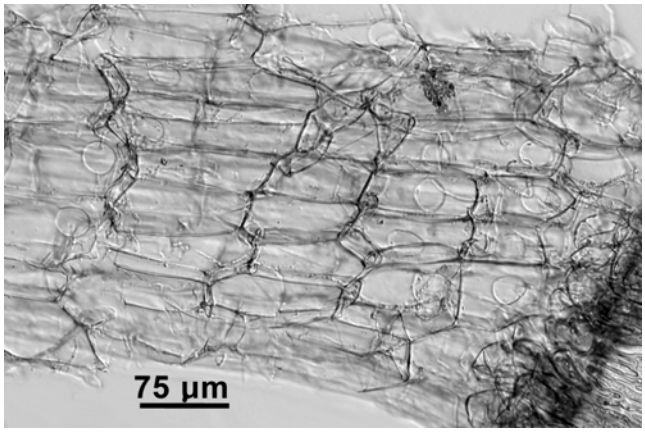

Figure 43. Longitudinal view of ***Sphagnum fimbriatum*** stem hyalodermis showing pores. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Schimper (1857) determined that the hyaline outer cells of stems and the hyaline cells of leaves in ***Sphagnum*** were dead at maturity (Figure 44). Furthermore, they have true perforations strengthened by spiral fibers (Figure 45). Branches are smaller than the stem and typically have a single outer hyaline layer and smaller, often thick-walled cells in the central core (Figure 46-Figure 47).

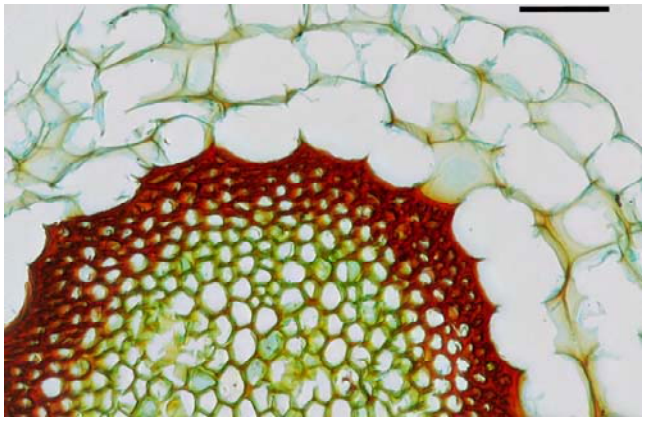

Figure 44. ***Sphagnum papillosum*** stem cross section with central core and dead outer layers of hyalocysts. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

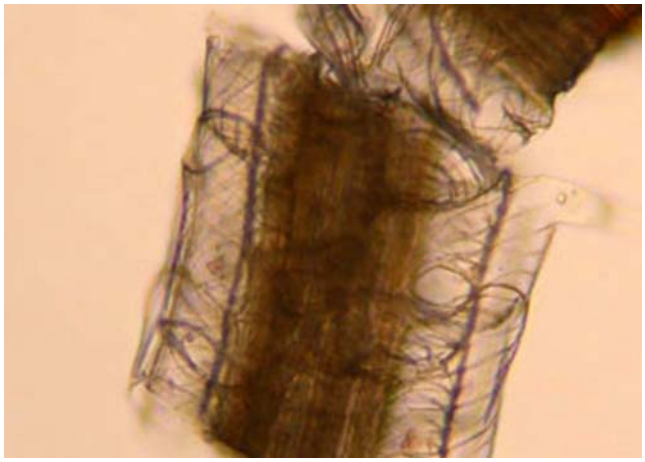

Figure 45. Longitudinal view of ***Sphagnum papillosum*** stem showing **central core** and outer hyaline cells (**hyalocysts**) with **fibrils** and **pores**. Photo from Botany website, University of British Columbia, Canada, with permission.

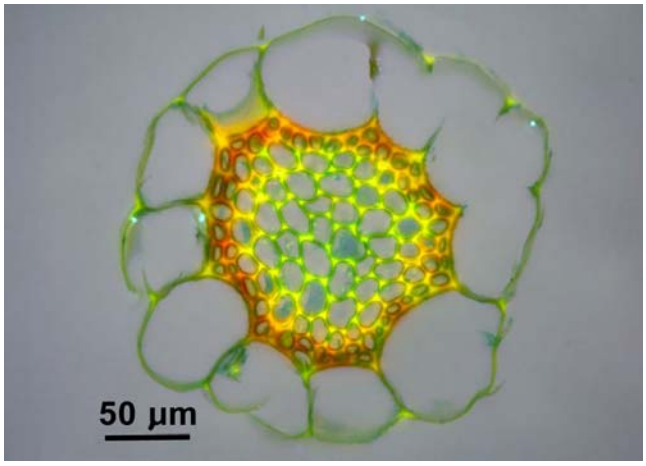

Figure 46. ***Sphagnum papillosum*** branch cross section demonstrating its differences from the stem in Figure 44. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

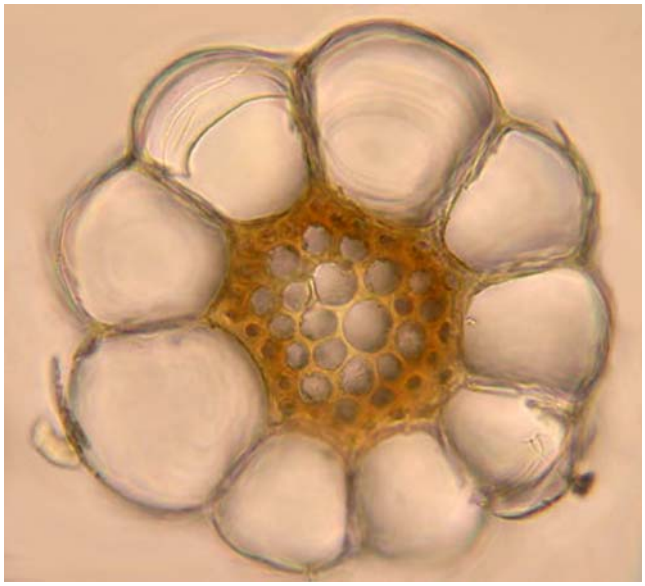

Figure 47. ***Sphagnum papillosum*** branch cross section. Photo from Botany website, University of British Columbia, Canada, with permission.

Schnepf (1973) later found that microtubules are fundamental in the development of the spiral thickenings of ***Sphagnum*** by lifting the plasmalemma off the wall to form an extraplasmatic space in which wall material is accumulated. The wall area where the pore will form becomes progressively thinner until only the cuticle remains. The cuticle eventually ruptures, making a pore. The protoplasts likewise eventually disappear.

The **Marchantiophyta** lack water-conducting cells except for two families of leafy and two of thallose liverworts (Ligrone *et al*. 2000, 2002). These conducting cells are formed by protoplasmic degeneration due to acid phosphatases, as in the mosses, but their wall development is different from that of the mosses (Crandall-Stotler 1980). They lack wall hydrolysis but possess numerous plasmodesmata-derived pores on all walls and never develop polyphenolic compounds (Hébant 1978). No food-conducting cells are known among the **Marchantiophyta** (Figure 48).

Figure 48. ***Porella navicularis*** (**Marchantiophyta**, **Jungermanniopsida** – a leafy liverwort) stem cross section showing absence of central strand. Photo from Botany website, University of British Columbia, Canada, with permission.

Hydroids

The elongated, water-conducting **hydroids** typically occur in groups of 2-3 in bryophyte stems (Hébant 1970); they are similar to tracheids, but lack lignin and secondary wall thickenings (Taylor 1988). Consequently, hydroids are usually thin-walled (Zamski & Trachtenberg 1976) and lack the helices and other thickenings typical of tracheids. Vanderpoorten and Goffinet (2009) sum up three major differences between hydroids of bryophytes and the tracheids and vessels of tracheophytes: hydroids lack secondary wall patterns; bryophyte lignin-like polymers are not cell-specific as they are in tracheophytes and are more likely to offer protection against microbes; hydroids collapse during water stress, making them highly resistant to cavitation (drop in vascular pressure due to vapor pockets resulting from desiccation) (Ligrone *et al.* 2000). This combination creates a fundamental difference in response to drying, with bryophytes being desiccation tolerant and tracheophytes preventing desiccation by pumping water from the soil, closing stomata, and reducing water loss with a waxy cuticle (Vanderpoorten & Goffinet 2009).

Table 1. Comparison of percentage of structural components of tree leaves and of plants of the moss ***Polytrichastrum*** (=*Polytrichum*) ***ohioense***. From Lawrey 1977.

Litter type	soluble carb	hemi-cellulose	cellulose	"lignin"	ash
Pinus resinosa leaves	35.41	13.44	19.37	23.56	3.68
angiosperm tree leaves	43.89	11.59	20.43	11.04	6.97
Polytrichastrum ohioense	16.51	14.07	24.37	12.90*	4.24

*Not a true lignin in mosses.

Hydroids senesce at maturity and become dead, empty cells, like those of xylem, with slanted end walls that abut on the end wall of the next cell, as in tracheids (Richardson 1981). This change from living cells to empty dead cells is a result of acid phosphatase activity that degenerates the protoplasm (Crandall-Stotler 1980). Hydroids of **Bryophyta** typically lack perforations but sometimes have secondary polyphenolic thickenings on the lateral walls of cells (Scheirer 1975). Scheirer (1973) used ***Dendroligotrichum*** (Figure 49) (**Polytrichopsida**) to demonstrate that hydrolysis leaves behind only cellulose remains of the primary walls of end walls of hydroids. Subsequent examination by electron-dense crystals of Prussian blue on the end walls in ***Polytrichum commune*** (Figure 50) suggests that these end walls are highly permeable (see Figure 51), but that substances are unable to move through the lateral walls (Scheirer & Goldklang 1977).

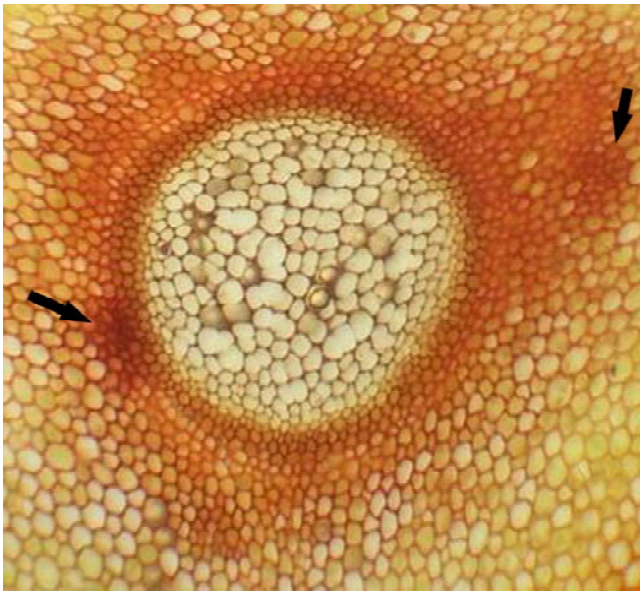

Figure 49. ***Dendroligotrichum dendroides*** stem cross section showing hydroids in center (**brown walls and mostly empty**), surrounded by stereids (**brown walls and interior brown**) and leptoids (**rusty-colored walls and contents**). Note vascular branches (**arrows**) that go into the cortex. The central strand has a few sclereids (thick walls) and these are living cells. Photo by Juan Larrain, with permission.

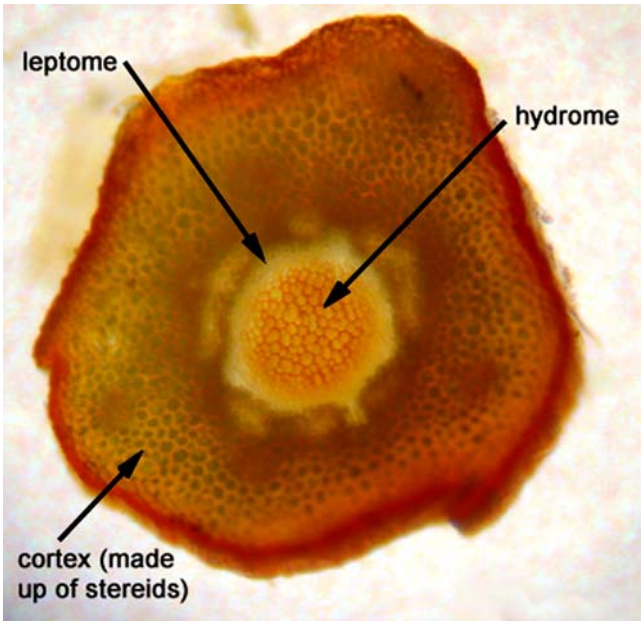

Figure 50. ***Polytrichum commune*** stem cross section. Photo by Julie Chou from Botany website, University of British Columbia, Canada, with permission.

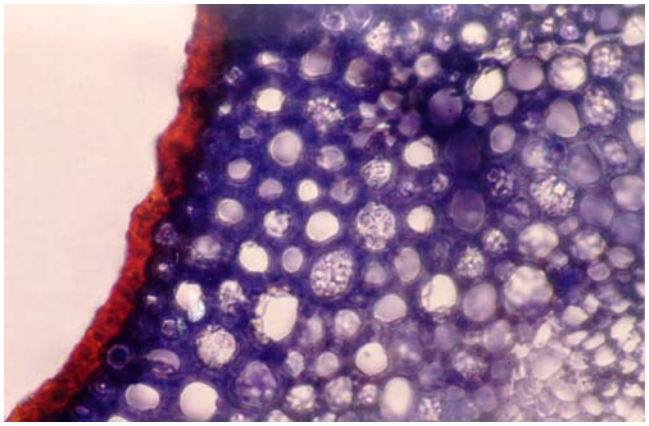

Figure 51. Cross section of ***Polytrichum*** stem stained with aniline blue to show thin areas in end walls of cortical cells. Photo courtesy of Isawo Kawai.

To understand any relationship between hydroids of bryophytes and tracheids or vessels of tracheophytes, we must understand their structure. We can consider that part of their structural development is similar to that of tracheophytes because they, like xylem cells, are dead at maturity (Richardson 1981). But is their chemical nature similar? It appears that the bryophytes have derived their water conducting cells in a variety of ways.

Hébant (1973a) found that strong activity of acid phosphomonoesterases occurs in the differentiating water-conducting cells of various mosses and at least one liverwort. But a lesser activity is also present in leptome cells and certain parenchyma cells of some **Polytrichales**.

Some chemical labelling tests gave similar results in as divergent taxa as ***Takakia*** (Figure 25-Figure 27) and ***Polytrichum*** (Figure 50-Figure 51), but different results in ***Mnium*** (Figure 74) (Ligrone *et al*. 2002). And Ligrone and coworkers found labelling of both water-conducting cells and parenchyma cells in ***Haplomitrium*** (Figure 107), but only of water-conducting cells in ***Polytrichum***. Ligrone *et al*. found that the arabinogalactan protein (AGP) antibody labelled the water-conducting cells in all Bryophyta tested (8 species) except the large polytrichaceous moss ***Dawsonia*** (Figure 52). No labelling occurred in the liverworts (4 species). Hence, it appears that the chemicals present are similar, but that they occur at different places within the plants.

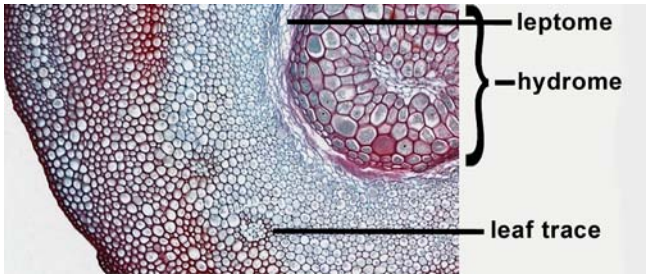

Figure 52. ***Dawsonia*** stem cross section to show hydrome, leptome, and leaf traces. Photo from Wikimedia Creative Commons.

Differences in labelling between the water-conducting cells and the cortical cells appeared to be mostly quantitative in these few species (Ligrone *et al*. 2002). On the other hand, electron microscopy revealed clearly distinct differences in the location of the antibodies within the cell walls of these two cell types, suggesting that their presence in a particular location was tissue specific in its regulation. Even within the **Polytrichaceae** (Figure 49-Figure 52) there is considerable diversity in the immunocytochemistry. In short, the bryophytes have a widely diverse chemistry in their conducting cells, but as such, they differ strongly from those of tracheophytes. Ligrone *et al*. (2002) consider the presence of several carbohydrate antigens in the cell walls of hydroids to indicate that hydrolysis of non-cellulosic polysaccharides is not part of the maturation process, a strong contrast to that in tracheophytes (see Hébant 1977).

Accompanying these chemical differences are differences in structure. True **perforation plates** (end walls of vessels) have not been found in **Polytrichaceae** (Figure 49-Figure 52) (Frey & Richter 1982) or most other mosses (Hébant 1973b). Consequently, Frey and Richter (1982) set out to discover them in mosses. In the dendroid moss ***Canalohypopterygium tamariscinum*** (Figure 53), they found structures resembling perforation plates of *Ephedra* (Gnetophyta), although they were not numerous and were restricted in location to branching areas. Perhaps this type of vascular structure permits them to be dendroid, lacking the close structure of leaves along the stem needed for capillary action. Smith (1964) had already demonstrated perforations in the conducting elements of the liverwort ***Symphyogyna circinata*** (Figure 54). Furthermore, pits are known, particularly in end walls, from ***Haplomitrium*** (Figure 107) [considered to be basal to leafy liverworts (Crandall-Stotler & Stotler 2000)] and ***Takakia*** (Figure 25-Figure 27) (now classified as a primitive moss in the **Takakiopsida**), as confirmed by electron microscope.

Figure 53. ***Canalohypopterygium tamariscinum***. Photo by Pieter Pelser, with online permission for educational use.

Although hydroids do not seem to contain true lignin, as do tracheophyte xylem cells, they do contain a polyphenolic cell wall component that functions similarly to lignin (Pressel *et al*. 2010). This compound protects the wall from hydrolytic attack and aids in internal transport of water. In ***Rhacocarpus purpurascens*** (Figure 55), Edelman *et al*. (1998) found walls composed of "mainly

lignin, **hemicellulose** (H-bonded to cellulose in plant cell walls), and cellulose in a ratio of ca. 9:8:5." Although the resonance spectrum indicated various characteristics typical of lignin, some specific peaks associated with known lignin compounds were missing. Thus the question remains, is this true lignin?

Figure 54. ***Symphyogyna circinata***. Photo by Filipe Osorio, with permission.

Figure 55. ***Rhacocarpus purpurascens***, a moss that produces a cell wall substance similar to lignin. Photo by Michael Lüth, with permission.

Leptoids

Leptoids (Figure 56) are very similar to phloem sieve cells, and in fact, Behnke (1975) calls them just that. Taylor (1988) considers that in some cases they are nearly identical to protophloem cells of certain tracheophytes. They, along with parenchyma cells, comprise the **leptome** (=leptom) (Hébant 1970, 1974; Behnke 1975; Figure 32). We know that they are typical in the **Polytrichaceae**, but have also been found in ***Sphagnum***, **Hookeriaceae**, **Neckeraceae**, and **Orthotrichaceae** (Ligrone & Duckett 1994b, 1998a; Duckett & Ligrone 2003). Except in the setae of a few species (Hébant 1974), leptoids have not been found in the arthrodontous mosses (considered more advanced) and are unknown in liverworts. It is likely that they are much more common than we realize because in cross section without stain they appear no different from the unspecialized parenchyma cells.

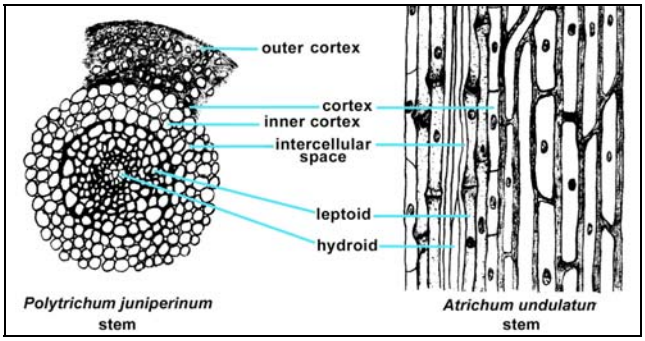

Figure 56. Cross section of ***Polytrichum juniperinum*** and longitudinal section of ***Atrichum undulatum*** stem to illustrate parts of central strand (leptoids and hydroids) and stem structures. Drawings by Margaret Minahan, modified from Hébant (1977).

In the moss family **Polytrichaceae** (Figure 56, Figure 58), leptoids have an axial system of microtubules with polarized cytoplasmic organization (Ligrone *et al*. 2000). In other mosses, including ***Sphagnum*** (Figure 36-Figure 47), such organization may also occur in stem and seta parenchyma cells. Even rhizoids and caulonemata of mosses and liverworts and thallus parenchyma cells of liverworts may have a similar organization for transporting nutrients **symplastically** (through cells, inside the membrane) for longer distances. But, as will be seen later in this chapter, these food and water conducting cells are fundamentally different from the phloem sieve cells and tracheids of tracheophytes. Nevertheless, Ligrone *et al*. (2002) found that the cell wall and tissue complexity of bryophytes are "on a par with higher plants."

The **leptoids** are distinct in vertical section by their elongate shape and slightly oblique end walls (Figure 59) (Behnke 1975). At maturity, the nucleus degenerates, as in phloem sieve cells (Richardson 1981), but protoplasm remains. In ***Polytrichum*** (Figure 56), the leptoids are not connected end-to-end by sieve plates or pores as in tracheophytes, but by numerous **plasmodesmata**. However, Cortella and coworkers (1994) considered the thin areas of central strand parenchyma cells to be primary pit fields in ***Hookeria lucens*** (Figure 57) stems and suggest that these cells have a conducting function.

Figure 57. ***Hookeria lucens***. Photo by Jiří Kameníček, with permission.

Even the development of leptoids seems similar to that of phloem sieve cells. During leptoid maturation in **Polytrichaceae**, **ribosomes** (centers of protein synthesis) disintegrate and nuclei become smaller and inactive, although they do not dissolve completely as in tracheophytes; mitochondria persist. The parenchyma cells contain starch-storing chloroplasts. As in their tracheophyte counterparts, leptoids move carbohydrates and other substances away from the apex.

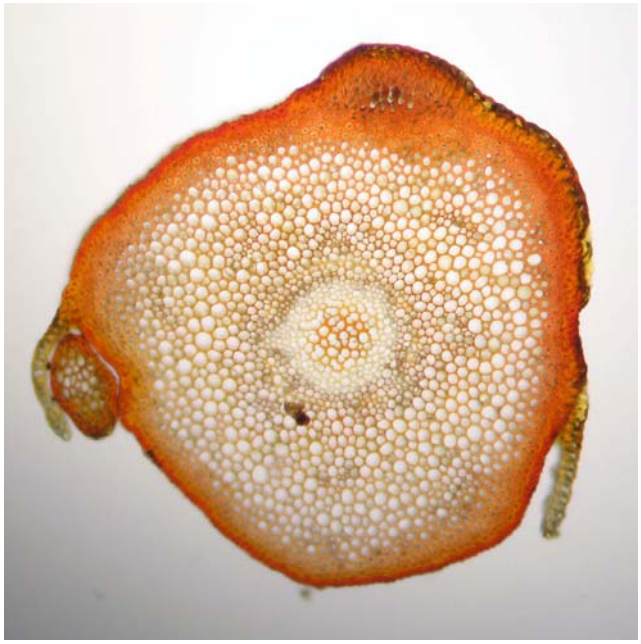

Figure 58. ***Polytrichastrum formosum*** stem cross section showing central **hydroids** (**with orange walls in center**) and considerable differentiation in the cells of the **central strand**. **Leptoids** are present outside the central strand and are not discernible in cross sectional view. Photo from Botany website, University of British Columbia, Canada, with permission.

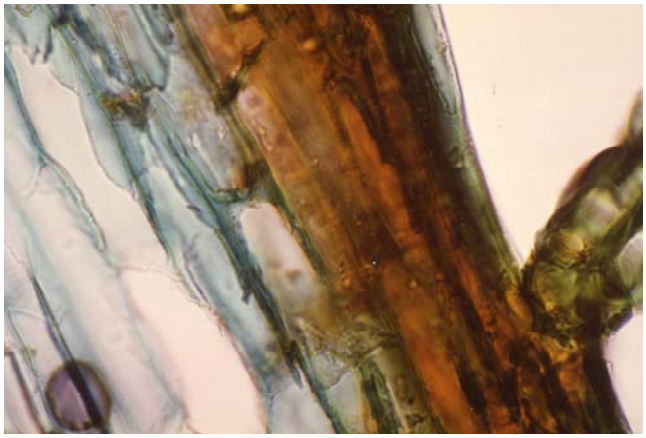

Figure 59. ***Hypnum*** sp., a pleurocarpous moss, stem longitudinal section. Note the long cell with what appear to be broken side walls, a disintegrating diagonal cross wall, and a partially missing protoplast. This appears to be a **leptoid**, but we need conduction tests to verify it. Photo courtesy of Isawo Kawai.

Rhizome

The **rhizome** (underground, horizontal stem connecting upright plants), on the other hand, has **hypodermal** and **radial strands** but lacks connecting traces and a sterome. The **hypodermis** (Figure 60), also present in some stems, consists of one to several layers of distinct cells just beneath the epidermis and may be thick-walled or colored.

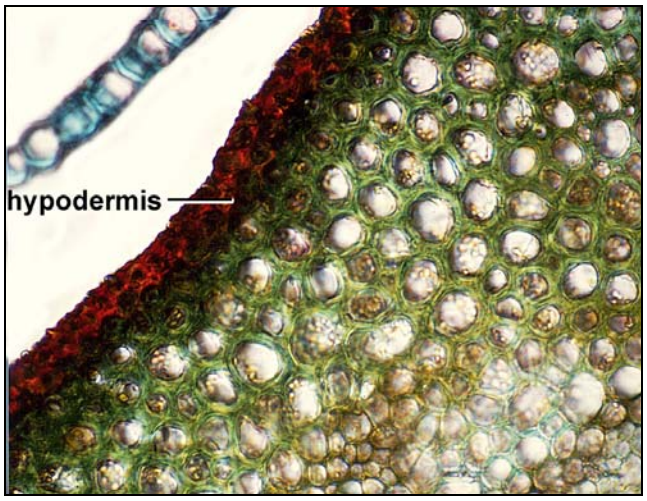

Figure 60. ***Polytrichum*** stem cross section showing **hypodermis**. Photo courtesy of Isawo Kawai.

Long-distance transport brings its own set of problems. These plants can undergo transpiration, causing them to lose water (Raven 2003). In some liverworts and many mosses, but not hornworts, there are dead cells in the tissues. These may function in long-distance **apoplastic** (outside cell membranes) water transport. Symplastic transport, on the other hand, seems to have a high resistance to flow, emphasizing the importance of apoplastic movement.

Leaves

In most tracheophytes, the leaf is a critical structure in creating the movement of water from the roots to the tops of tall plants. This movement, known as the **transpiration stream**, requires the loss of water from the leaf, creating a vapor pressure deficit that brings water upward like someone sucking on a straw. But bryophytes typically do things quite differently, as we shall see in a later sub-chapter. They typically take in water from above, not below, hence requiring a new look at the role of leaves in water movement. It appears that the greatest need is not to move water to the leaves, but rather to move substances made in the leaves to other parts of the plants.

Costa

Within the leaf, water may move cell to cell among the **lamina** cells (Figure 61), but many leaves have a **costa** (Figure 61-Figure 62) that is often accompanied by supporting **stereid** cells (Figure 63). Unlike the midrib of ferns and seed plants, the costa does not branch and rebranch to deliver water or other substances to or from cells of the leaf lamina (Figure 62), although in some taxa, for example ***Hygrohypnum*** (Figure 64), it may have one or more branches. Nevertheless, the costa has elongate cells

that we might expect to facilitate a more rapid movement of water within the leaf (Figure 62), but does it?

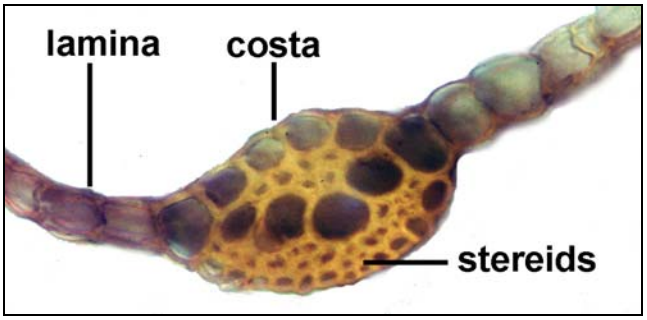

Figure 61. Cross section of moss leaf blade showing arrangement of broad portion (lamina), costa, and supporting stereids. Large cells in costa serve for conduction. Photo by Janice Glime.

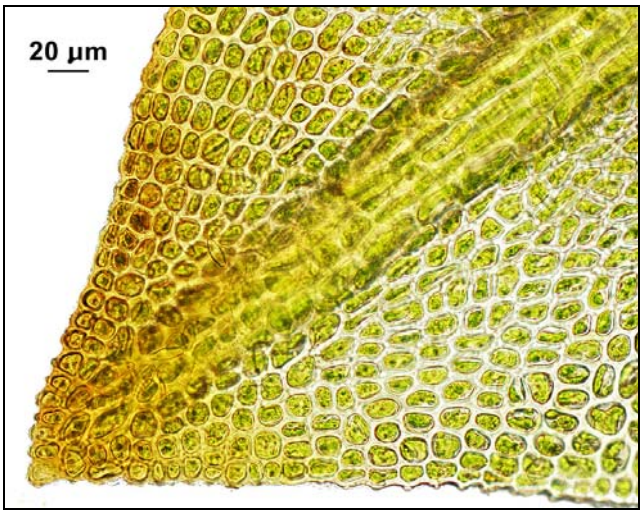

Figure 62. ***Crumia latifolia*** leaf showing elongate costa cells and nearly isodiametric lamina cells. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

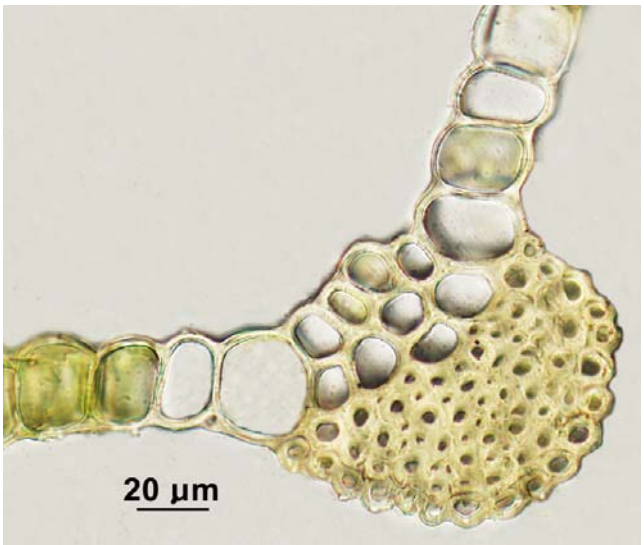

Figure 63. ***Crumia latifolia*** leaf cross section showing enlarged costa with many stereids supporting the conducting cells. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

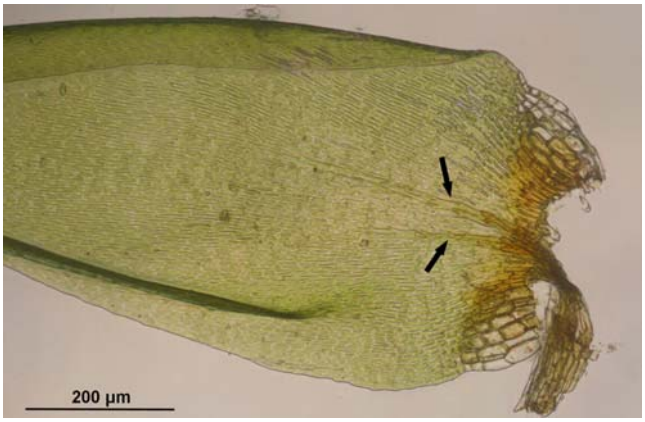

Figure 64. ***Hygrohypnum eugyrium*** leaf showing two branches of the costa (**arrows**). Photo by Hermann Schachner, through creative Commons.

On closer examination of the costa, we find that those elongate cells are living cells with oblique end walls, thin cell walls, and living protoplasm (Hébant 1977)! These are not hydroids, but are **leptoids**. Hence, it appears that in addition to its supporting role, the costa can have the role of conducting substances from the leaf toward the stem. (We will see shortly how this system connects to the leaf traces in the stem.) It appears that the costa should not have a role in conduction of water.

Sphagnum

Sphagnum (Figure 65) has the most unusual water system in its leaves of any bryophyte. Its leaves have two types of cells, and rarely a border in addition. These two types are the water-holding, colorless, dead **hyaline** cells and the green **chlorophyllose** (**photosynthetic**) cells (Figure 66-Figure 67). The hyaline cells serve as water reservoirs for the photosynthetic cells. Their walls have true perforations and are strengthened by spiral thickenings, suggesting the structure of tracheophyte vessels (Figure 66-Figure 67) (Hébant 1977). The pores (perforations) begin with a thinning of an area of the cell wall and presence of a thin membrane. Eventually these rupture to create the pore, using the process already described above for the hyaline cells of ***Sphagnum*** stems.

Figure 65. ***Sphagnum*** leaves showing the patterning caused by the network of chlorophyllose cells and hyaline cells. Photo by Michael Lüth, with permission.

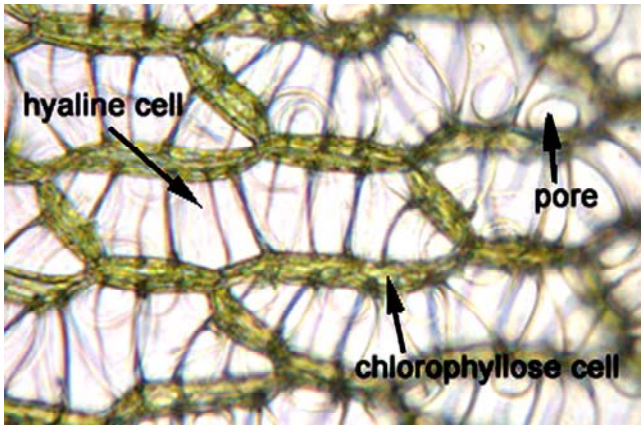

Figure 66. ***Sphagnum*** cells showing hyaline cells with spiral thickenings and pores, intermixed with chlorophyllose cells. Photo from Botany website, University of British Columbia, Canada, with permission.

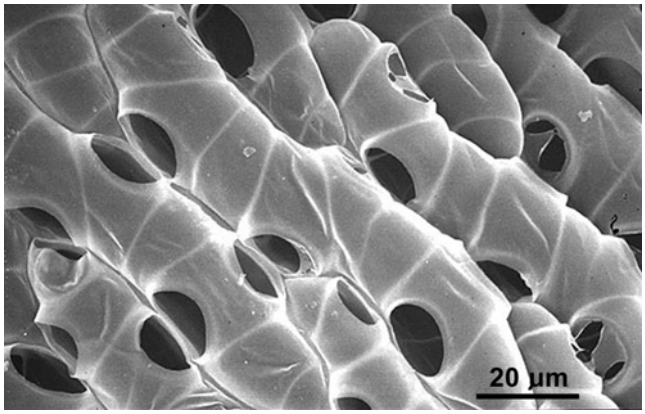

Figure 67. ***Sphagnum*** hyaline cells with spiral fibrils and pores. The photosynthetic cells are hidden by the hyaline cells in this leaf. Photo from Botany website, University of British Columbia, Canada, with permission.

Leafy Liverworts

Leafy liverwort leaves never have a costa (Figure 68), leaving us to assume that transport of water and other substances in the leaves, if needed, is cell-to-cell transport through ordinary leaf parenchyma cells. But in this group (**Jungermanniopsida**), leaves are never more than one cell thick, giving all cells direct exposure to water from the atmosphere or other surroundings.

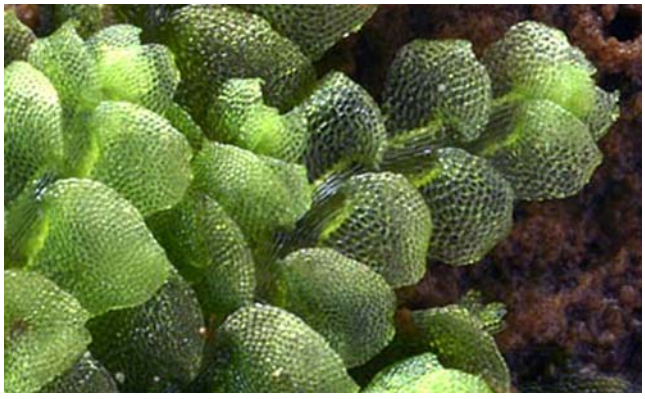

Figure 68. ***Calypogeia fissa*** (**Jungermanniopsida**) showing absence of costa in leaves and one-cell-layer leaf thickness. Photo by Des Callaghan, with permission.

We might also ask the role of **underleaves** (Figure 69) in this group. These may be non-existent (*e.g.* ***Jamesoniella***, Figure 70) to quite large (*e.g.* ***Porella***, Figure 71). Underleaves may be an evolutionary left over with no function, but their persistence suggests they may offer some advantages in water retention. They create capillary spaces on the under side of the stem and thus may aid in water retention. This space may also aid water uptake by holding water, but in many cases this would require that the stem (Figure 72) absorb the water. It would be interesting to experiment with different types of underleaves to see how they affect water uptake, especially by the stem, and how long they are able to hold a water reservoir.

Figure 69. ***Calypogeia integristipula*** demonstration of underleaves. Photo by Michael Lüth, with permission.

Figure 70. ***Jamesoniella undulifolia*** showing absence of underleaves (**arrow**). Photo by David T. Holyoak, with permission.

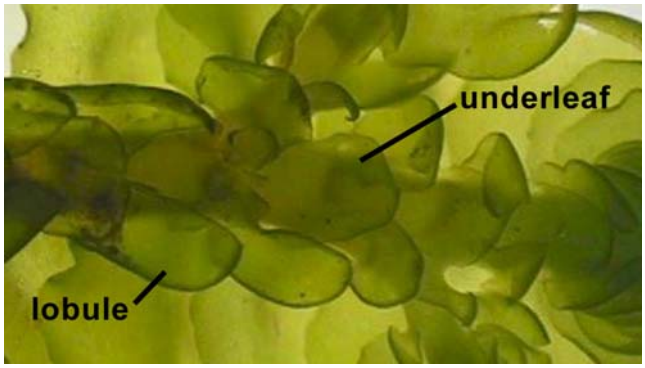

Figure 71. ***Porella platyphylla*** showing its large underleaf and lobule. Photo by Paul Davison, with permission.

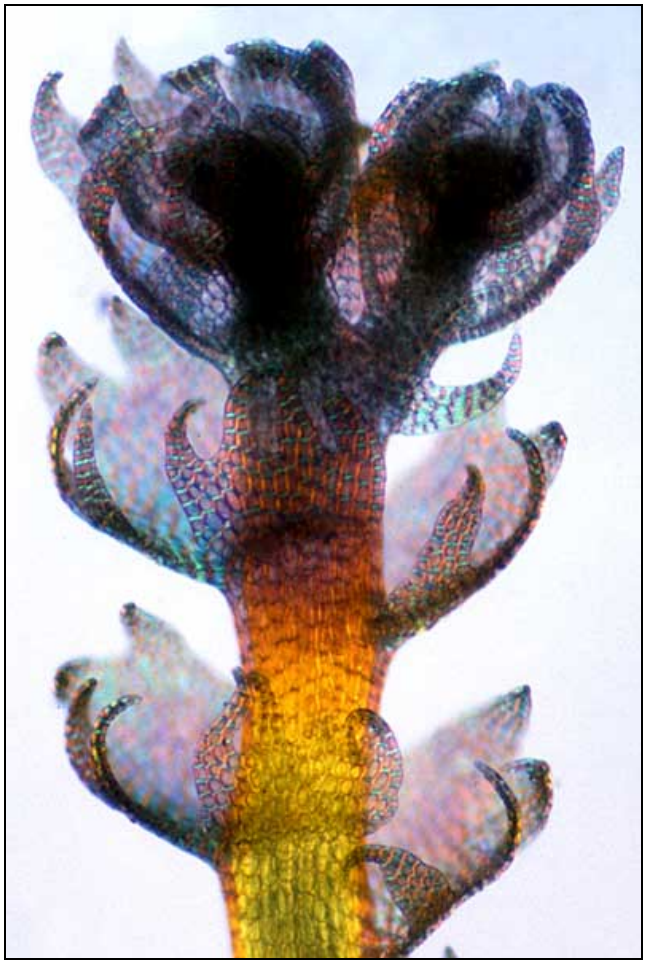

Figure 72. Leafy liverwort showing parenchymatous cells of stem. Photo by Bill Malcolm, with permission.

Another water reservoir in a number of leafy liverworts is the **lobule** (Figure 71). This structure, present in ***Frullania***, ***Porella***, **Lejeuneaceae**, and others can create a small reservoir of water suitable for small aquatic invertebrates such as rotifers and Protozoa to carry out their entire life cycle. These are discussed further in Chapter 7-4.

Leaf Traces

Conduction from stems into leaves is typically through the parenchyma cells of the stem cortex, as will be described in a later sub-chapter. True **leaf traces** (conducting cells connecting the leaf costa to the hydrome; Figure 73) exist in some **Polytrichales**, but in other cases they do not quite reach that far. In the **Mniaceae** and **Splachnaceae** there are **false leaf traces** (Figure 74) that extend into the cortex from the leaf but do not connect with the central strand of the stem (Figure 75) (Hébant 1977). In ***Funaria hygrometrica***, some specimens have true leaf traces that reach the central strand, and others do not.

Hébant (1969) found that in ***Polytrichum*** (Figure 4), the true leaf traces extend from the leaf costa toward the central strand, but they become reduced near the central strand. Nevertheless, Hébant (1969) found that 7-8 hydroids of each leaf trace could connect to the central strand in grassland ***Polytrichum commune*** (Figure 50). This connection, however, seems to be related to water availability. In bog populations, only three hydroids form the connection. For specimens grown under water, no leaf traces connected to the central strand.

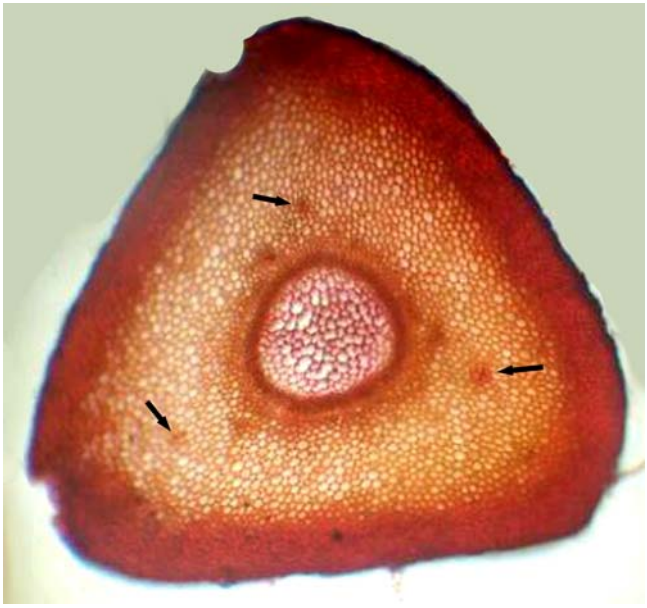

Figure 73. ***Dendroligotrichum dendroides*** stem cross section showing leaf traces in the cortex (**arrows**). Photo by Juan Larrain, with permission.

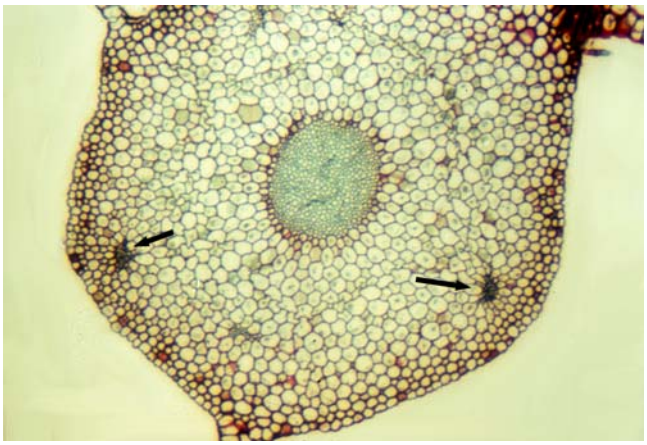

Figure 74. ***Mnium*** stem cross section showing distinct central strand and false leaf traces (**arrow**) that do not connect directly to the leaves. Photo by Janice Glime.

Figure 75. ***Rhizomnium glabrescens*** leaf cross section showing hydroids in center and stereids near the outer margins. In this family (**Mniaceae**), the central strand produces false leaf traces that do not connect to the costa of the leaf. Photo from Botany website, UBC, with permission.

But wait! Many kinds of leaves have a **costa**, the rib that extends part way or all the way down the center of the leaf. But the costa cells are fairly wide cells, albeit elongated, and contain a living protoplast (Hébant 1977). The end walls are oblique and have numerous plasmodesmata. They are in fact **leptoids**, not hydroids, and do not seem to have an important water conducting function in many mosses, if any. Rather, they conduct **photosynthate** and other substances from the leaf to the stem. These materials are thus deposited in the stem tissue. Could these actually connect with leptoids in the stem, permitting transport to stem tips or to rhizomes? In fact, in ***Polytrichum commune*** they do connect to the leptoids of the stem axis. Why then are there hydroids in the leaf traces? What do they connect? Is there any correlation between having a costa with leptoids and a stem with a central strand? Do all leaf leptoids connect with stem leptoids? So little we know...

Rhizoids

Rhizoids have generally been assumed to function in attachment and little else. However, depending on the species and habitat, they may have important roles in water movement as well.

All liverworts except ***Haplomitrium*** (Figure 28) produce smooth, unicellular rhizoids. Duckett *et al*. (2013) reviewed the **pegged** and **smooth rhizoids** (Figure 76-Figure 78) of the complex thallose liverworts and noted that their roles differ. The mature smooth rhizoids of all liverworts remain alive. This permits them to function in nutrition, anchorage, and as conduits for mycobiont entry (Figure 77). They also collapse when dehydrated, a condition that is irreversible. Pegged rhizoids, on the other hand, are dead at maturity, permitting them to function in a "highly effective internalized external water-conducting system." This works especially well in the archegoniophores (Figure 79-Figure 80) of such liverworts as ***Marchantia***. They are cavitation-resistant with elastic walls that permit them to retain functional integrity during desiccation.

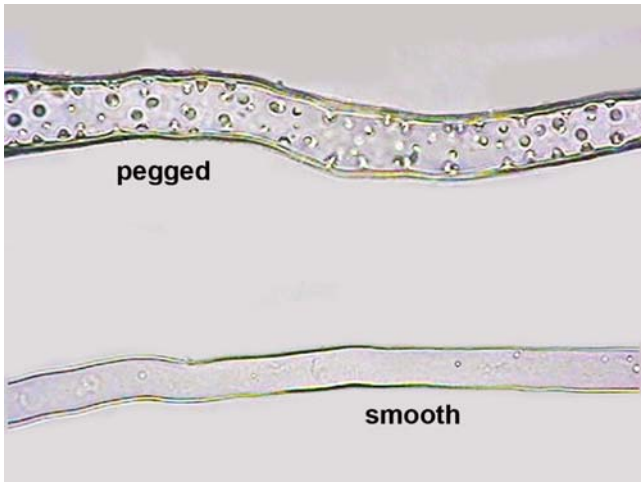

Figure 76. ***Conocephalum conicum*** pegged and smooth rhizoids. Photo by Paul G. Davison, with permission.

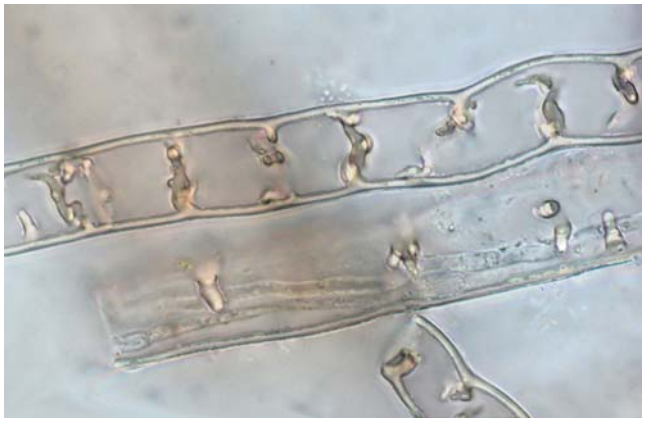

Figure 77. ***Marchantia polymorpha*** pegged rhizoid with fungus. Photo by Walter Obermayer, with permission.

Figure 78. ***Marchantia polymorpha*** ventral surface showing rhizoids. Photo from Botany Website, UBC, with permission.

Figure 79. ***Marchantia polymorpha*** with rhizoids whowing on the stalk where they are not included within the inrolled thallus. Photo by George Shepherd through Creative Commons.

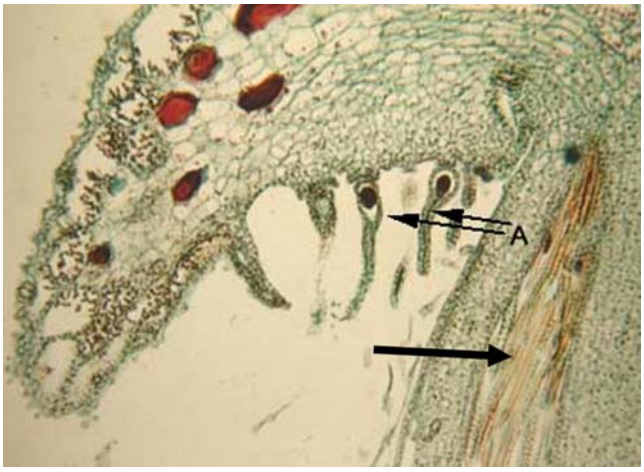

Figure 80. ***Marchantia polymorpha*** archegoniophore, with A indicating archegonia. The large arrow indicates the rhizoids rolled inside the stalk. Photo from Botany Website, UBC, with permission.

But to what degree do rhizoids in bryophytes facilitate the uptake of water and nutrients? Jones and Dolan, as recently as 2012, concluded that there was little direct evidence on nutrient uptake by bryophyte rhizoids. Nevertheless, they suggested that their functions include water transport in some mosses and liverworts. As far as I know, we lack experimental studies to tell us the magnitude of uptake.

Rhizoids can also serve as perennating organs (Frey & Kürschner 2011), often producing propagules.

Sporophyte Conduction

In tracheophytes, it is the sporophyte that has the vascular tissue, and in the setae of mosses, one might find conducting tissues (a central strand) even when it is absent in the gametophyte. This should not be too surprising since the gametophyte is much better adapted to absorbing water from the atmosphere than the cuticle-endowed sporophyte. It is most likely necessary for a number of substances to be transported from the gametophyte into the sporophyte as it develops. And as we might expect, these conducting strands in setae are best developed in the **Polytrichaceae** (Hébant 1977), a family in which the peristome exhibits the more primitive character of nematodontous teeth.

Is perhaps no coincidence that a species with a vascularized stem also has a vascular seta. This seems to be the case in ***Plagiomnium undulatum*** (Figure 81).

On the other hand, leptoids can occur in the setae of some arthrodontous mosses even when they are absent in the gametophytes. Nevertheless, leptoids of setae, unlike those of tracheophytes, show less differentiation than in their gametophytic counterparts. In the setae of the **Polytrichaceae**, leptoids are not intermixed with specialized parenchyma cells and apparently lack enlarged plasmodesmata in their end walls, as seen in gametophytes of some taxa (Hébant 1974). To add interest to the picture, the leptoids are present in forms that are transitional between the parenchyma cells and the fully differentiated leptoid cells (Hébant 1974).

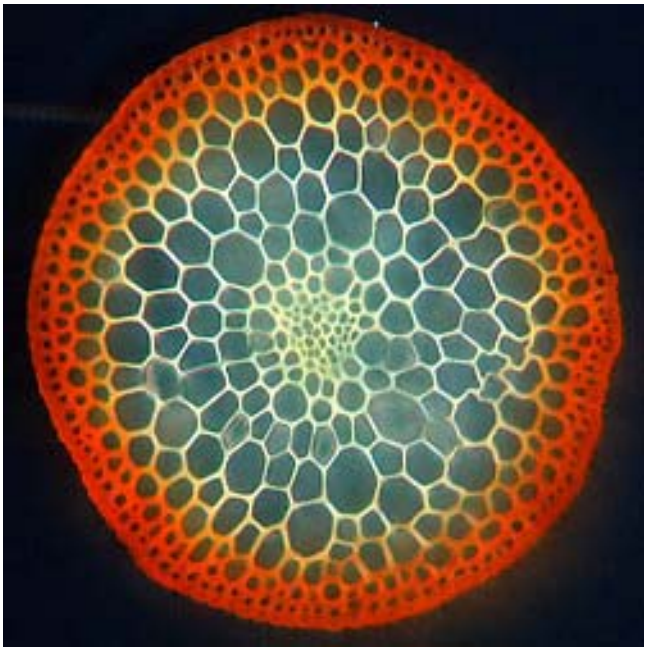

Figure 81. ***Plagiomnium undulatum*** seta cs showing central conducting strand. Photo by Norbert J. Stapper, with permission.

Meager evidence exists for the presence of **leptoids** in setae of other genera. Among these are ***Funaria***, ***Meesia***, and ***Splachnum*** (Hébant 1977). In ***Tortula muralis*** (Figure 82), Favali and Gianni (1973) have claimed that the leptoids are intermixed with the parenchyma cells in the seta and a similar claim was put forth by Bassi and Favali (1973) for ***Mnium orthorrhynchum***, but Hébant (1977) was unable to find any convincing evidence that this was true in either case.

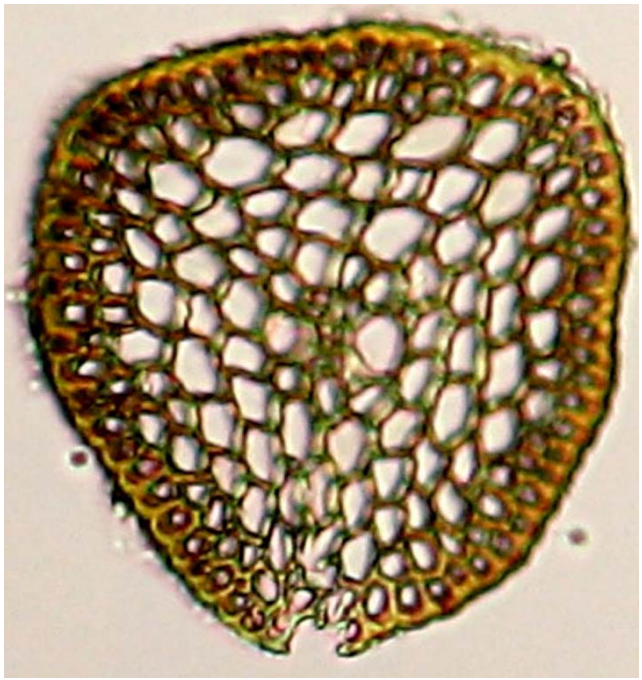

Figure 82. ***Tortula muralis*** seta cross section showing modified cells in center of seta. Photo from Botany website, University of British Columbia, Canada, with permission.

Figure 83. ***Tortula muralis*** or ***plinthobia*** stem cs. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Stem sections indicate that at least a central strand is present in the acrocarpous mosses ***Dicranum scoparium*** (an **arthrodontous** moss; Figure 84-Figure 85) and ***Tetraphis pellucida*** (a **nematodontous** moss; Figure 86-Figure 87). The presence of leptoids cannot be determined from these views, nor can the function of the central strand. Cross sections of these setae can be compared with stems of the same species in Figure 82-Figure 87.

Figure 85. ***Dicranum scoparium*** stem cross section showing differentiated central tissue with hydroids, but representing a genus where leptoids are often absent. There appear to be hydroids that are breaking up, possibly surrounded by a narrow band of leptoids. Photo from Botany website, University of British Columbia, Canada, with permission.

Figure 84. ***Dicranum scoparium*** seta cross section showing broken center with modified cells similar to those of stem (Figure 85). Leptoids do not seem to be visible. Photo from Botany website, UBC, with permission.

Figure 86. ***Tetraphis pellucida*** seta cross section. In this case, most of the cortex is occupied with thick-walled supporting cells. Hydroids occur in the middle. Photo from Botany website, University of British Columbia, Canada, with permission.

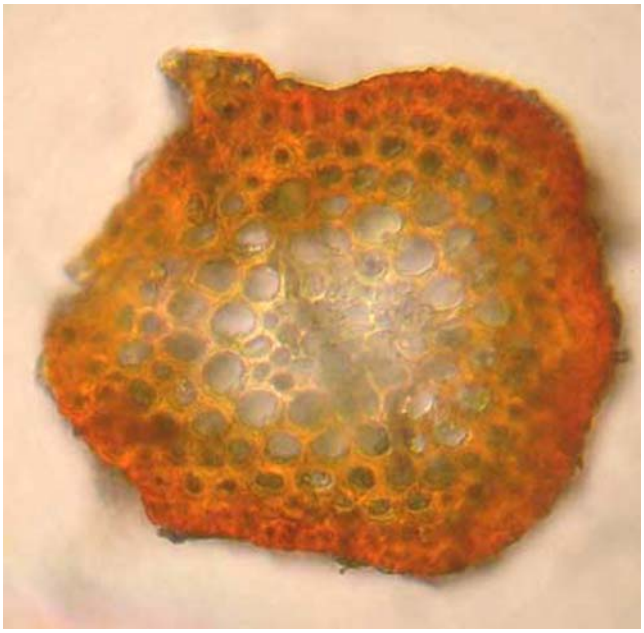

Figure 87. ***Tetraphis pellucida*** stem cross section. As in the seta (Figure 86), most of the cortex is occupied with thick-walled supporting cells. Hydroids occur in the middle but occupy a larger area than in the seta. Photo from Botany website, University of British Columbia, Canada, with permission.

Hébant (1977) pointed out that no electron microscope study existed on the histology of the conducting tissue of the capsule. He could offer little on its organization, stating that the conducting strand terminates shortly after it enters the capsule. In ***Funaria hygrometrica*** and ***Polytrichum commune*** the hydroids terminate within the capsule as a small ampulla, but such an ampulla is absent in ***Dawsonia***, ***Dendroligotrichum***, and ***Fissidens***.

Adaptation and Evolution

The hydroids and leptoids present interesting evolutionary implications, since it appears that they are primitive characters that are lost in more advanced bryophyte taxa (Hébant 1970; Behnke 1975). Unlike most tracheophytes, the mosses retain conducting cells in both generations, but the haploid generation is the first to lose leptoids evolutionarily, as in ***Funaria*** (Behnke 1975), a moss that still has a central strand in the stem (Malcolm & Malcolm 2006) and leptoids in its setae (Hébant 1977).

Being Acrocarpous

Some acrocarpous mosses may lack a central strand. For example, ***Leptodontium flexifolium*** (Figure 88-Figure 89) grows on acid substrata but lacks the central strand (Figure 89), but it has a leaf costa (Figure 88). Even the ubiquitous ***Ceratodon purpureus*** (Figure 90), a moss that occurs on substrata from roadsides and exposed rocks to pools in the Antarctic, lacks a central strand (Figure 91), and likewise has a costa (Figure 92-Figure 93). Other taxa that frequently become dry, like ***Grimmia*** species (Figure 94) also often lack specialized cells in the center of the stem (Hébant 1977).

Figure 88. ***Leptodontium flexifolium***, an acrocarpous moss. Photo by Des Callaghan, with permission.

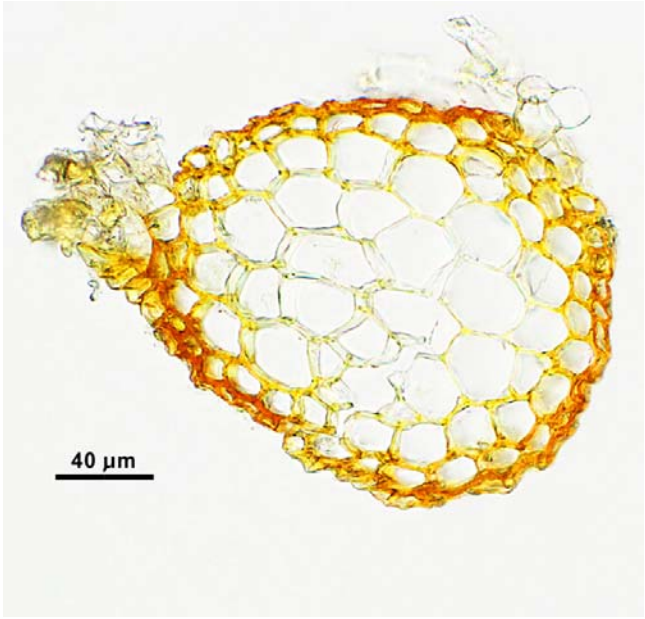

Figure 89. ***Leptodontium flexifolium*** stem cross section showing absence of hydroids. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

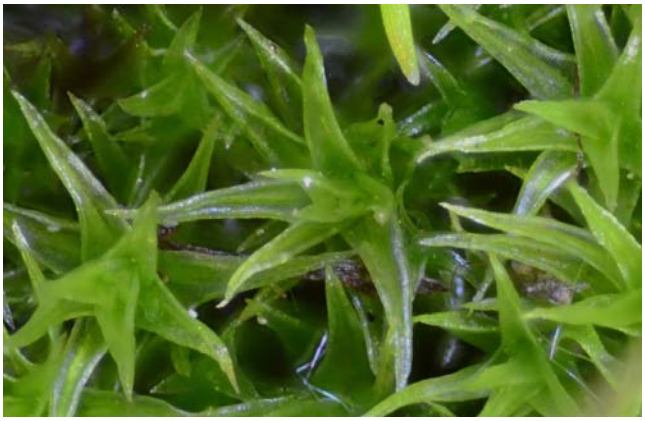

Figure 90. ***Ceratodon purpureus*** leaves. Photo by Don Loarie, through creative Commons.

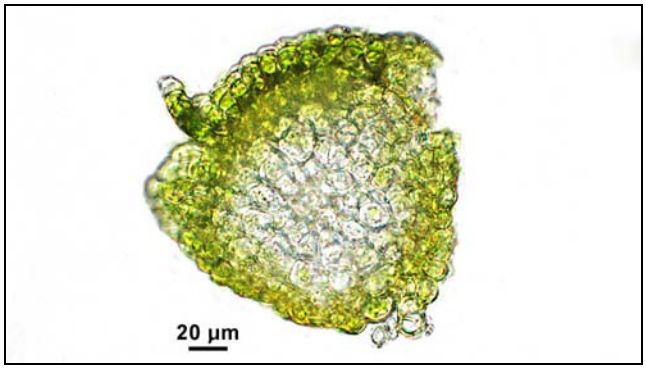

Figure 91. ***Ceratodon purpureus*** stem, a moss with a wide range of habitats from dry fields to Antarctic pools, yet it lacks hydroids. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 92. ***Ceratodon purpureus*** showing distinct costa. Photo by Malcolm Storey, through Creative Commons.

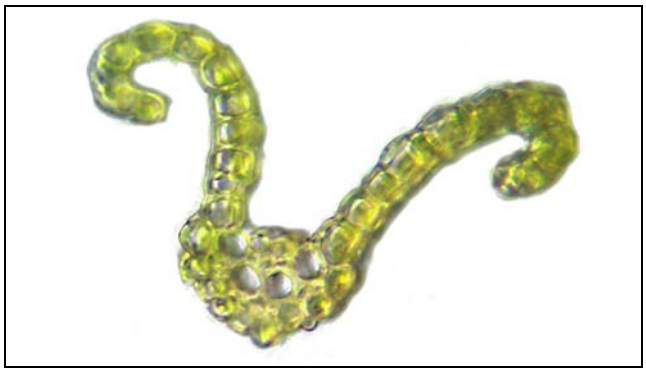

Figure 93. ***Ceratodon purpureus*** leaf cross section showing costa and involute margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Being Pleurocarpous

Pleurocarpous taxa that grow close to the ground may have less need for hydroids when all their leaves are more or less equally placed to gain water, as can be seen in ***Calliergonella lindbergii*** (=*Hypnum lindbergii*; Figure 95). Pleurocarpous mosses (Figure 95-Figure 98) have fewer problems in getting wet and sharing water among cells because they grow horizontally, compared to the need for upright mosses to distribute water, especially tall ones that grow alone, like ***Dawsonia*** spp. (Figure 2). On the other hand, these mosses may have evolved the loss of hydroids before our extant species existed and have not regained their hydroids, as might be the case for ***Hylocomium splendens*** (Figure 97-Figure 98), a moss that grows in fairly open wefts, but lacks a central strand. Nevertheless, it would seem that the pleurocarpous mosses still need to transport photosynthate and hormones, among other things. Hence, we should expect leptoids in many, if not all, pleurocarpous mosses. Unfortunately, it is hard to find information on leptoids in these taxa. The same need, and lack of information, could be said for leafy liverworts.

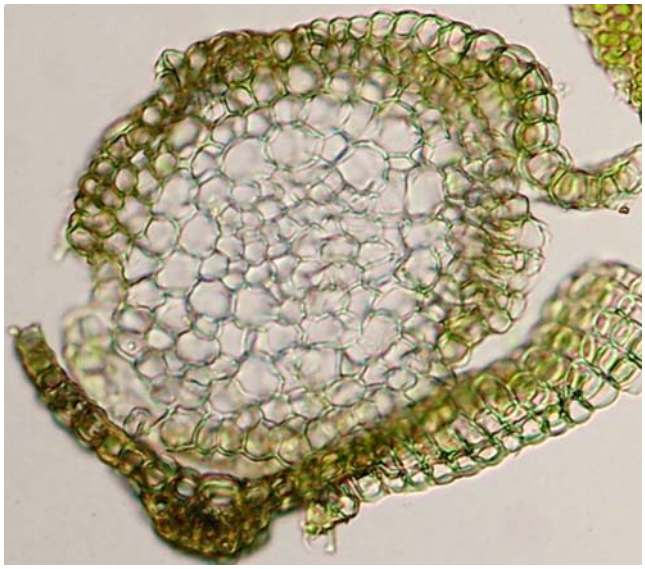

Figure 94. ***Grimmia pulvinata*** stem cross section showing little differentiation in the central cells of the cortex. Are these hydroids? This genus can have hydroids or lack them. The tissues flaking away from the stem are leaf cross sections. Photo from Botany website, UBC, with permission.

Figure 95. ***Calliergonella lindbergii*** forming a thick mat. Photo by Michael Lüth, with permission.

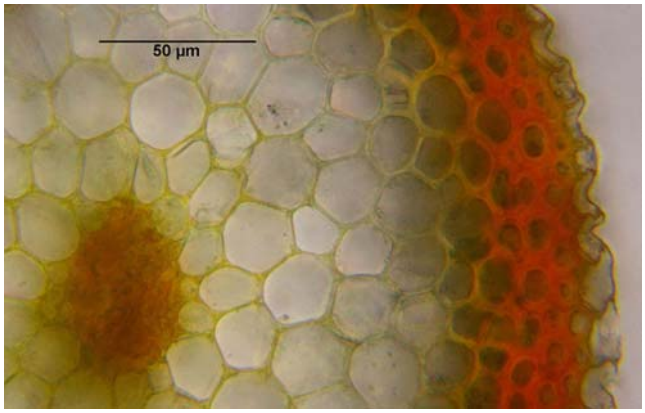

Figure 96. ***Calliergonella lindbergii***, a pleurocarpous moss, stem cross section showing a small area of differentiated central tissue. Photo by Hermann Schachner, through Creative Commons.

Figure 97. ***Hylocomium splendens***, showing its open growth habit that will permit easy escape of water. This moss grows in an almost dendroid pattern, but together with many stems that form wefts. Photo by Dale Vitt, with permission.

Figure 98. ***Hylocomium splendens***, a pleurocarpous moss, stem cross section showing absence of any hydroids or central strand. Photo from Botany website, University of British Columbia, Canada, with permission.

In ***Climacium*** (Figure 99), the stem has very reduced strands of conducting tissue (Hébant 1977). This moss stands upright like a small tree. The stem is nearly naked, making external upward transport limited. Hence this moss must rely on water that lands on the leaves. Instead of specialized water conducting cells, ***Climacium*** species have good supporting tissues in their stems, permitting the stem to support the leafy tree-like portion.

Figure 99. ***Climacium dendroides*** showing the nearly naked supporting stem. Photo by Keith Bowman, with permission.

Aquatic

It should be no surprise that aquatic taxa like ***Fontinalis*** (Figure 100-Figure 102) lack hydroids. Likewise, in ***Touwia*** (Figure 103), a pleurocarpous moss in the **Neckeraceae**, there is no cross-sectional evidence of a central strand (Figure 104). Rather, like ***Fontinalis***, this streambed moss has many thick-walled cortex cells that help to protect the stem from breakage in stream flow. Its leaves likewise have a thick **costa** (Figure 105) that can resist the ravages of flow. But even in such epiphytic taxa as ***Neckera crispa*** conducting cells are lacking, suggesting an evolutionary loss early in this branch. Taxa like ***Touwia*** with a strong costa but no conducting cells in the stem suggest that the costa cells that are elongate in a leaf where other cells are shorter may serve a function more important than conduction – that of supporting tissue, and may sometimes serve both functions. It is likely that they also have regenerative ability.

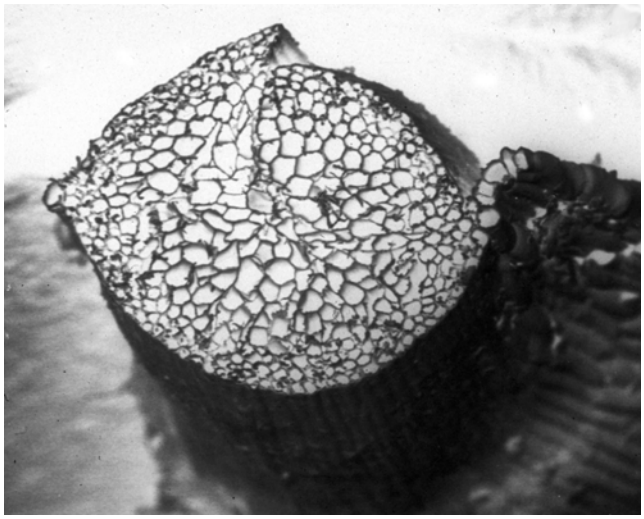

Figure 100. ***Fontinalis squamosa*** SEM image of stem cross section, showing the absence of specialized cells in the center of the stem. Photo by Janice Glime.

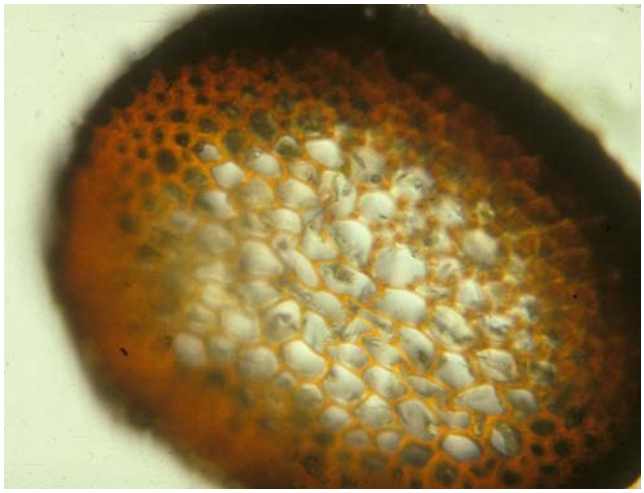

Figure 101. ***Fontinalis dalecarlica*** stem cross section showing absence of hydroids. Note the thick-walled outer cortical cells that give this stem the strength needed to survive in the rapidly flowing water of mountain streams. Photo by Janice Glime.

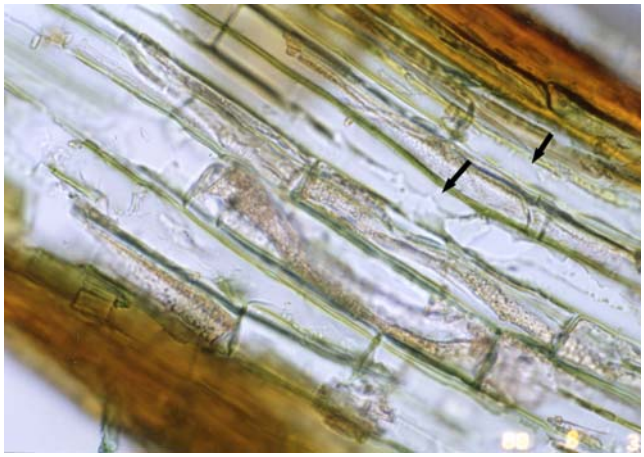

Figure 102. Longitudinal section of stem of ***Fontinalis gracilis*** showing elongated, thin-walled cells of the cortex. The cells at the arrows appear to be particularly long. Could they be leptoids? Photo by Isawo Kawai, with permission.

Figure 103. ***Touwia laticostata*** (?) branches showing leaves with thick costae. Note the remaining costae on the lower branch after it suffered abrasion. Photo courtesy of Andi Cairns.

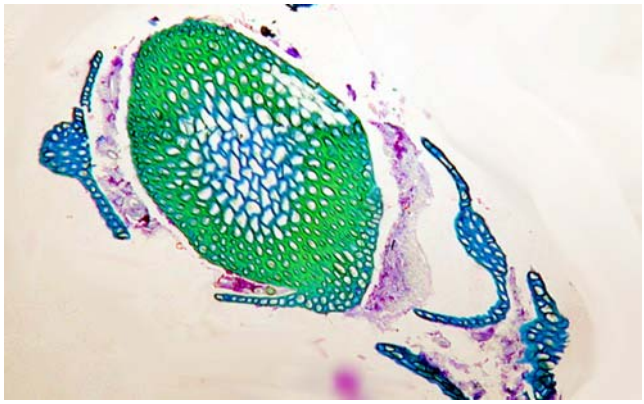

Figure 104. The moss ***Touwia laticostata*** (?) stem (lacking discernible hydroids) and leaves with thick costa. Photo courtesy of Andi Cairns.

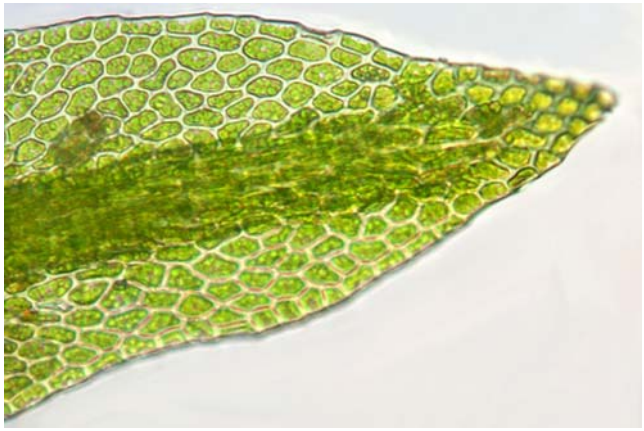

Figure 105. ***Touwia laticostata*** (?) leaf showing thick costa. Photo courtesy of Andi Cairns.

Using a Partner

Epiphyllous bryophytes have an unusual habitat on their host leaves. Water usually does not stay and is even repelled by the host leaf surface. ***Radula flaccida*** (Figure 106) has at least partially solved the problem by producing rhizoids that penetrate the host leaf cuticle and epidermal cells, extending into the tissues of the host (Berrie & Eze

1975). Berrie and Eze found that both water and dissolved phosphorus salts can be obtained from the host leaf. Hence, it appears that the liverwort is at least partially a parasite (Hébant 1977).

Figure 106. ***Radula flaccida*** habit with gemmae, growing on a leaf. Photo by Michaela Sonnleitner, with permission.

Throughout the kingdoms we see examples where two organisms share responsibilities in their mutual survival. Among these partners, the fungi seem to have perfected the strategy, making it possible for plants to greatly increase their available surface area without expending the effort to build the needed tissues. Such is the case for some bryophytes, a partnership for which we have limited understanding. Among those with such a relationship is the genus ***Haplomitrium*** (Figure 107) (Carafa *et al*. 2003). ***Haplomitrium*** secretes mucilage (Figure 108) from its underground rhizomes, forming an environment that harbors fungal hyphae. In ***H. gibbsiae*** (Figure 107), the fungus is restricted to the epidermal cells where it forms lumps, but in ***H. ovalifolium*** it also infects the adjacent cortical cells, forming lumps. Through such partnerships, these species can gain access to both deeper and wider sources of nutrients in the sol substrate.

In tracheophytes, this partnership strategy has been used by a number of **hemiparasites** that partner with a fungus that partners with a tree or shrub. This arrangement permits them to gain carbohydrate energy from the photosynthesizing canopy while living in the darker environment under its protective cover. Our knowledge of bryophyte partnerships is still too primitive to ascertain how important this relationship is in permitting many bryophytes to subsist in such low light conditions.

Figure 107. ***Haplomitrium gibbsiae*** leafy plant showing slimy rhizomes. Photo courtesy of Jeff Duckett and Silvia Pressel.

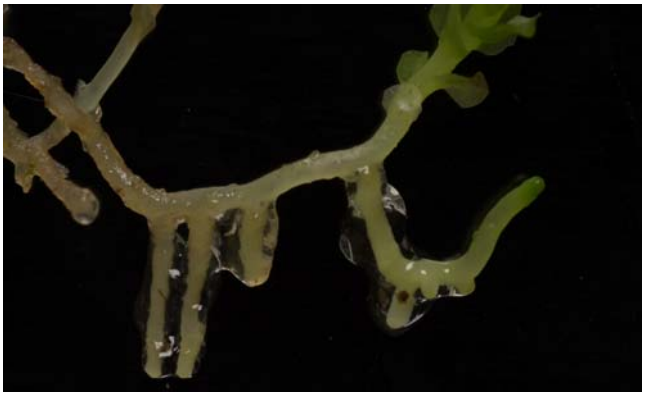

Figure 108. ***Haplomitrium gibbsiae*** rhizomes covered with thick mucous. Photo courtesy of Jeff Duckett and Silvia Pressel.

Summary

Movement onto land required means of obtaining and retaining water. Bryophytes, reputedly the first colonizers, often are not the nonvascular plants we once thought them to be. They often possess **hydroids**, surrounded by **stereids**, that conduct water and together comprise the **hydrome**. Hydroids lack lignin and spiral thickenings, distinguishing them from tracheids and vessels of tracheophytes. **Leptoids** that conduct sugars, arranged as in tracheophytes, with the water-conducting cells surrounded by the sugar-conducting cells, are less well known because they are distinguishable in longitudinal section. In a few mosses, these stem conducting tissues connect by leaf traces to the leaves. Bryophytes usually have a thin **cuticle**, but it seems to lack wax in most cases. **Rhizoids**, although anchoring the plants as do roots, typically do not serve in obtaining water, but exceptions exist. **Acrocarpous** species more commonly have a central conducting strand, whereas **pleurocarpous** mosses remain close to the substrate and a central strand may not be useful.

Bryophytes function like sponges in the ecosystem by holding water and maintaining moisture in the soil below. But they also absorb water like a sponge, using capillary spaces. At times when water is limiting, the bryophytes are able to survive through their exceptional desiccation tolerance.

Mosses may have a **costa** (rib similar to a midrib) in the leaf, but it does not branch to reach all the cells (as in most tracheophytes) and may not always serve a conduction role. This is connected to the stem vascular strands only in the **Polytrichaceae**. Thallose liverworts may have a midrib to transport water and other substances, but leafy liverworts have no evidence of water-conducting cells in the stem and no **costa** in the leaf.

Even sporophytes have elongated cells in the seta. In younger sporophytes these may be important in conduction of nutrients to the developing capsule.

Aquatic species presumably do not need conduction since they are bathed in water. But they still need to move solutes and especially sugars from leaves to other locations. Some bryophytes have mycorrhizal associates that help take in water and

minerals. Others are connected by rhizomes that permit them to "scavenge" by obtaining photosynthate from connected stems that are in more favorable positions.

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CHAPTER 7-2

WATER RELATIONS: MOVEMENT

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CHAPTER 7-2
WATER RELATIONS: MOVEMENT

Figure 1. *Grimmia nutans* supporting drops of water that will eventually be absorbed into the moss through the leaf surface. Photo by Michael Lüth, with permission.

Water Movement

Early experiments with dyes demonstrated that in mosses water is able to move in conducting tissue of the central cylinder, leaf traces, and the costa (Zacherl 1956), depending on capillary spaces, as it does in tracheophytes (Table 1). Bopp and Stehle (1957) confirmed not only these internal pathways, but that movement also occurs from cell to cell (**symplastic**) in the cortex of the lower part of the stem, as well as on the outer surfaces of leaves and stems (Figure 1). But it is more likely that most of the movement across the cortex and internal leaf is through the free space of the cell walls where it does not have to cross cell membranes until it reaches its destination (Proctor 1984). Such **apoplastic** (outside cell membrane or in free space) movement across the cortex is known even in ***Polytrichum juniperinum*** (Figure 2) (Trachtenberg & Zamski 1979), where a central strand and leaf traces are available to facilitate movement of water.

Table 1. Relationship of bryophyte structures, size of space, and capillary rise. From Proctor (1982), based on Slatyer (1967).

Radius of meniscus	Ht of capillary rise	Bryophyte structures in similar size range
1 mm	1.5 cm	Large, concave leaves; spaces among shoots
100 µm	15 cm	Spaces between leaves, paraphyllia
10 µm	1.5 m	Space within sheathing leaf base, tomentum, hyalocyst of ***Sphagnum*** & ***Leucobryum***
1 µm	15 m	Interstices between leaf-surface papillae
100 nm	150 m	Spaces between cell-walls?
10 nm	1.5 km	Spaces between cell-wall microfibrils
1 nm	15 km	Glucose molecule

As in tracheophytes, water movement in both endohydric and ectohydric mosses is facilitated by tension forces (Zamski & Trachtenberg 1976), but unlike the case in tracheophytes, water moves in both directions in a source-sink fashion dependent upon availability (Bowen

1933a). This bi-directional movement applies not only to external movement, but to the hydrome as well. For bryophytes, the first water availability most commonly does not start with the soil, but with the tips of stems and leaves by way of rain, fog, or dew.

Figure 2. ***Polytrichum juniperinum***, a moss with good **symplastic** conduction, but that can also use apoplastic movement. Photo by Des Callaghan, with permission.

Early observations showed that in general external conduction is much more rapid than internal conduction (Bowen 1933a, b, c; Clee 1939). This most likely relates to frictional resistance in the small internal routes. On the other hand, we should expect water to rise higher in small internal capillary spaces (Table 1). What seems strange, however, is that the utility of internal conduction in at least some bryophytes can change with age toward greater use of external conduction. Mizushima (1980) found that in older stems of ***Entodon rubicundus*** no internal conduction could be detected at 75% atmospheric humidity, but in younger stems, a slow internal conduction could be detected in the **central strand**. Both young and old stems exhibited external conduction, travelling up to 1 cm in 12 hours. This loss of internal conduction in older plants may support the contention of Kawai (1991), among others, that mosses may have been derived from vascular plants by reduction.

One item of curiosity is that not all bryophytes have **vacuoles** (Oliver & Bewley 1984). Surely this plays some role in their ability to hold water, and most likely affects nutrient placement and protection from toxic substances as well, but no one seems to have looked at this role in bryophyte physiology (Bates 2000).

Ectohydric

Ectohydric mosses (almost all mosses) rely primarily on external transport of water and can absorb water over the entire plant surface (Figure 3). These taxa generally have no water repellent layers, or these are restricted to such locations as the apices of papillae, and they are easily wetted (Proctor 1982, 1984). Movement is due to capillarity and the relationships are complex. As the moss becomes hydrated, its capillarity changes due to expansion of leaves, untwisting, and other forms of movement and gyration (Deloire *et al*. 1979). They benefit from a large surface area relative to their volume (Proctor 1984) due to numerous leaves and often such structures as **paraphyllia** (reduced leaflike structures on the stem or branches of some pleurocarpous mosses) and **tomentum** (felt-like covering of abundant rhizoids on stem).

Figure 3. Capillary water (**arrow**) held among the leaves of ***Bryum***. Photo courtesy of John Hribljan.

Castaldo Cobianchi and Giordano (1984) concluded that in the ectohydric ***Zygodon viridissimus*** (var. *rupestris*) (Figure 4-Figure 5), having an apical cell with no surface wax or papillae might provide a "starting-point" for rehydration since the dry leaves are appressed to the stem. When water repellent layers are lacking, plants generally reach full hydration within minutes (During 1992). Thus, virtually all pleurocarpous mosses, many of acrocarpous mosses, and most of leafy liverworts are readily wet by the first few minutes of rain. You will soon know which ones are resistant to uptake by leaves because they will stubbornly refuse to rehydrate for you when you want to make a leaf slide. Only dousing in boiling water seems to coax the water inside the plant to restore its normal hydrated shape.

Figure 4. ***Zygodon viridissimus*** dry showing leaves appressed to stem. Photo by Michael Lüth, with permission.

Figure 5. ***Zygodon viridissimus***, a moss in which the apical cell of the leaf lacks wax, permitting water entry. Photo by David Holyoak, with permission.

The **ectohydric** habit depends on entry of water through the moss surface and permits a moss to respond to dew and fog by absorbing water directly, even though rooted plants may never receive a drop of it. Such bryophytes can live in high elevations and on deserts that receive less than 25 cm rainfall per year, obtaining water that cannot be measured by conventional precipitation methods. Most tuft-forming (acrocarpous) mosses are (partially) endohydric, whereas most mat and carpet formers (pleurocarpous mosses) are ectohydric (Richardson 1981). In addition, some upright mosses such as ***Sphagnum*** (Figure 6) and ***Andreaea*** (Figure 7) are ectohydric. Schipperges and Rydin (1998) clearly showed this by clipping the capitula from the stem; these clipped capitula were unable to recover from desiccation, whereas unclipped capitula became rehydrated. But Even ***Sphagnum*** has highly specialized cells in the stem that have all the traits of a bryophyte type of conducting cell (Ligrone & Duckett 1998).

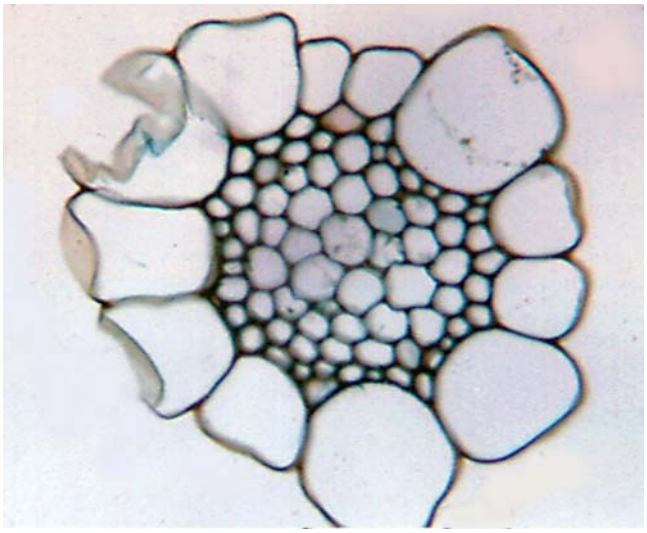

Figure 6. Cross section of ***Sphagnum*** stem with large, hyaline epidermal cells and small cortex cells. Photo by Janice Glime.

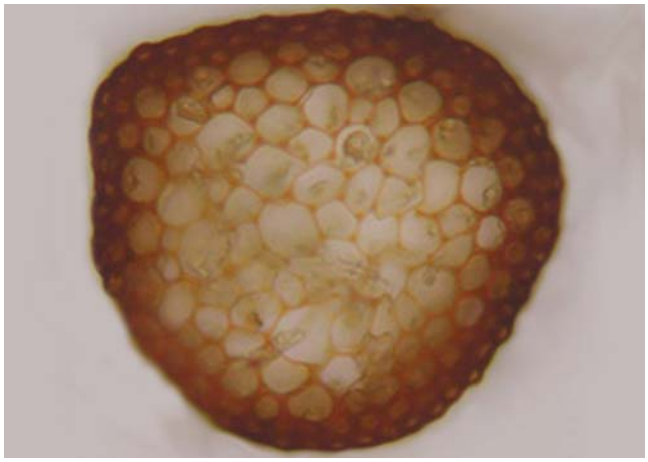

Figure 7. Cross section of ***Andreaea*** stem with no central strand. Photo from Biology 321 Course Website, University of British Columbia, with permission.

In **ectohydric** bryophytes, the uppermost leaves and shoot apices have the most rapid conduction of water, so that lower leaves are often supplied last (Zacherl 1956). Zacherl believed that no internal conduction was possible in the absence of a central strand. This apical movement may be beneficial in conserving water when water is scarce and only the leaves at the tips of the stems are receiving enough light for photosynthesis. These also are the leaves most exposed to fog and dew.

Using dyes and ***Dicranum scoparium*** (Figure 8) as a model subject, Bowen (1933c) demonstrated that external conduction was "exceptionally rapid" and internal conduction slow. Mägdefrau (1935), using the same species, determined internal conduction to be only about 1/3 the total conduction – not bad for a bryophyte. Klepper (1963) found that under conditions of desiccation, the protoplasts of this species become dense and evacuolate, undoubtedly developing considerable **imbibitional pressure** (due to adsorption of water by colloidal particles, much as seeds do). This would cause them to readily take in water when it becomes available.

Figure 8. ***Dicranum scoparium***. Photo by Michael Lüth, with permission.

Once the water enters the plant the distinction between endohydric and ectohydric no longer matters. Although the initial movement of water is clearly ectohydric in most dry mosses, once it has entered the moss it has the opportunity to move apoplastically to reach places where it is needed

for cellular metabolism. It is interesting that endohydric bryophytes can be facultatively ectohydric. Bayfield (1973) found that ***Polytrichum commune*** (Figure 9) was ectohydric under moderate moisture flux, but under high evaporative flux (*i.e.* dry air) it was predominantly endohydric.

Figure 9. ***Polytrichum commune***, a moss that is ectohydric under moderate moisture flux but endohydric under dry air. Photo by George Shepherd, through Creative Commons.

Despite all the laboratory experiments on conduction, we still have little concept of the relative importance of the two pathways over a large time scale in nature. Certainly, as demonstrated in ***Polytrichum*** (Figure 9), the relationship changes as the moss dries. Is it not likely that internal movement of water from older to younger parts then predominates, keeping the photosynthetic and growing apical tissue wet as long as possible? Surely the same apoplastic routes available to ***Polytrichum*** are available to all mosses. The natural transpirational stream that carries water from the shoot apices to the atmosphere could be expected to play a similar role to that found in tracheophytes and maintain upward movement (or outward in pleurocarpous mosses) through capillary spaces as long as water was available and internal tension did not exceed that resulting from transpirational loss.

What quantities do the various mosses move from moss mat to atmosphere and how much is moved from the soil to the moss mat? Do the mosses provide an overall net gain to the soil by preventing rapid loss to the atmosphere following rainfall? Do they retain water that would otherwise be lost as runoff, contributing it slowly to the soil and plant roots beneath? Or is their major contribution that of depriving the soil of water during showers of short duration? There is no mass balance equation that includes the role of bryophytes in the overall water budget in any ecosystem.

Endohydric

Endohydric mosses, including ***Polytrichum*** (Figure 2, Figure 9, Figure 13), ***Mnium*** *s.l.* (Figure 10,Figure 17), and ***Bryum*** (Figure 3), generally have surfaces that contain a water-resistant cuticle (Lorch 1931; Buch 1945; Bayfield 1973; Proctor 1979a), thus reducing their ability to take in water through their leaves. In some of these, that cuticle is endowed with a wax similar to that found in tracheophytes (Proctor 1979b; Haas 1982). However, this waxy coating of a moss leaf offers only a low water diffusion resistance similar to that of tracheophyte mesophyll (Nobel 1977; Proctor 1980) and may be more important in repelling water to permit a higher CO_2 diffusion into the leaf (Proctor 1984). Among ectohydric mosses, waxy cuticles seem to be either generally lacking or very thin. Mosses like ***Polytrichum*** and many members of the Marchantiales are actually water repellent, thus requiring half an hour or more to take up water (Proctor 1984). These **endohydric** bryophytes utilize, in the case of mosses, the system of non-lignified **hydroids** and **leptoids** to conduct water and sugars, respectively.

Figure 10. ***Mnium spinosum*** with water droplets on its leaves. This moss is very slow to absorb water due to its water-resistant cuticle. Photo by Michael Lüth, with permission.

But it appears that even these endohydric mosses rely on ectohydric transport. Instead of moving water inside the moss at the first opportunity during its external vertical rise, it is the tips of the plants that exhibit primary water absorption (Brown 1982). Water travels upward through the capillary spaces created by the leaves. Mosses like ***Polytrichum*** may facilitate this apical absorption by preventing any significant absorption by the cuticularized lower and more mature leaves.

In these predominantly endohydric mosses, rhizoids may serve functions of conduction much as do roots and root hairs. It appears that endohydric mosses such as ***Polytrichum*** (Figure 2, Figure 9, Figure 13), ***Dawsonia*** (Figure 11), and ***Climacium*** (Figure 12) transport water from the substrate beneath to their tips before moving it through an internal conducting system, sometimes called the **central strand**. Although ***Polytrichum commune*** (Figure 9) has demonstrated the ability to transport water externally along its stems, Mägdefrau (1938) contended that the major conduction is internal through the central strand. However, Trachtenberg and Zamski (1979) determined that despite the ability of rhizoids to absorb and transmit water, the major absorption is still through the aerial gametophyte, due to its greater efficiency. Because of the extensive development of conduction cells in ***Polytrichum*** (Figure 13), where central **hydroids** are surrounded by a cylinder of **leptoids**, Hébant (1970) considers this and other mosses to have similarities to the xylem and phloem of primitive vascular plants.

Figure 11. ***Dawsonia polytrichoides***, a moss with good internal conduction. Photo by Niels Klazenga, with permission.

Figure 12. ***Climacium dendroides***, a moss with external conduction from base to tip. Photo by Jan-Peter Frahm, with permission.

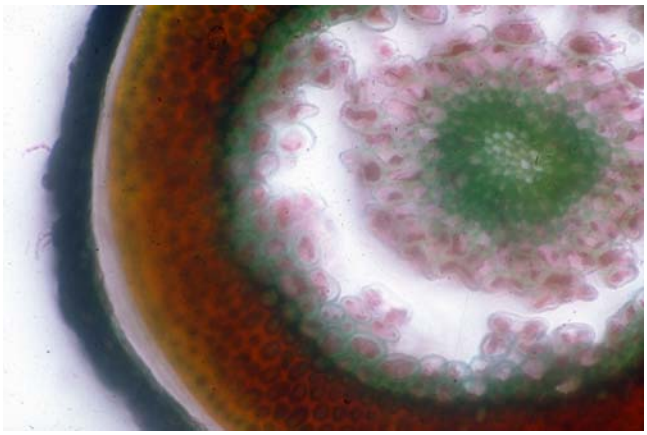

Figure 13. Cross section of a ***Polytrichum*** stem showing green **hydroids** of the **central strand** in center and larger **leptoids** surrounding them. Photo by Isawo Kawai, with permission.

But how does the water reach the leaves in the **endohydric** mosses? Zacherl (1956) used fluorescent dyes to show that in ***Polytrichum*** (Figure 2, Figure 9, Figure 13), the **costa** (midrib-like structure) links with the central strand, forming true leaf traces. In many taxa, however, there is no connection between the central strand and the costa, and in some cases there is no costa at all. Furthermore, Colbert (1979) showed that there is no connection between the central strand of the stem and that of the branches in ***Climacium americanum*** (Figure 14), ***C. dendroides*** (Figure 12), ***Rhytidiadelphus triquetrus*** (Figure 15), and ***Rhytidium rugosum*** (Figure 16).

Figure 14. ***Climacium americanum***, a moss with a central strand with no connection to the leaf. Photo by Bob Klips, with permission.

Figure 15. ***Rhytidiadelphus triquetrus***, a moss with a central strand that does not connect to the leaves. Photo by Janice Glime.

Figure 16. ***Rhytidium rugosum***, a moss with a central strand that does not connect to the leaves. Photo by Michael Lüth, with permission.

Nevertheless, in the absence of those connections the extension of the costa into the stem cortex still can function to complete internal transport across normal cortical cells (Zacherl 1956). For example, in ***Mnium*** (Figure 10) the costa does not link directly with the central strand of the stem, but ends blindly in the ground tissue, forming **false leaf traces** (Figure 17). The ends of the costae (Figure 18) act as wicks, transferring liquids across the ground tissue from the central strand and into the leaf costa, most likely using a diffusion gradient across the cortex.

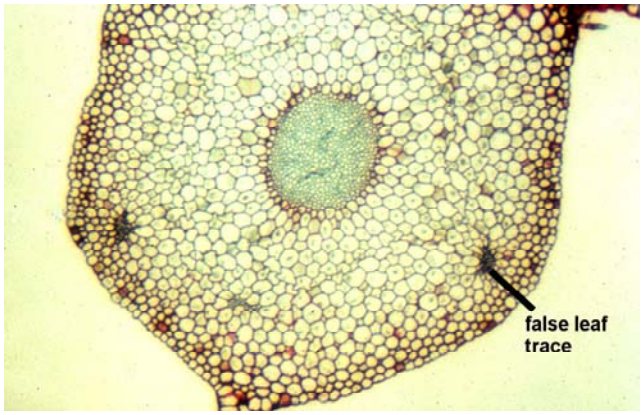

Figure 17. Cross section of ***Mnium*** stem showing false leaf traces. Photo by Janice Glime.

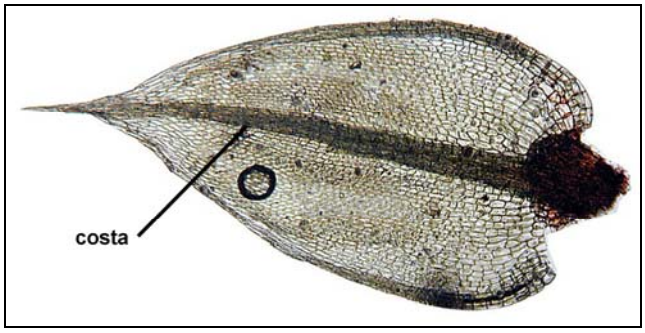

Figure 18. Leaf of ***Bryum pallescens***, showing costa of conducting cells. Photo by Michael Lüth, with permission.

The cortex behaves as capillary tubes and draws the water across the stem parenchyma to the leaf, much as water traversing the roots of tracheophytes. Trachtenberg and Zamski (1979) demonstrated, using PbS and Pb-EDTA (which accumulates Pb ions in tissues in proportion to the amount of water passing through), that the water actually moves in the capillary spaces of the cell walls – **apoplastic conduction**. Beckett (1997), using pressure volume isotherms, determined that cryptogams, including bryophytes, contain significant amounts of intercellular water when fully hydrated, whereas flowering plants do not. It is this extracellular pathway that permits water to move from leaf surfaces inward and into stems, where it can be conducted in the hydrome as well as apoplastically. It is interesting that the uppermost leaves are the first ones to receive water internally (Zacherl 1956), just as in the ectohydric mosses.

Trachtenberg and Zamski (1979) further learned that the **sterome**, assumed to be supporting tissue, can provide an alternative pathway for water conduction. That its mass was much greater than needed for support had already been noted by Lorch (1931). Furthermore, xerophytic mosses have a very large sterome (Goebel 1915) that is used for conducting and holding water. In mosses such as Fabroniaceae and Orthotrichaceae that lack a hydrome, the sterome is large (Van der Wijk 1932) and seems to supply this function. In fact, Trachtenberg and Zamski (1979) suggest that the transport from hydrome to leaves in ***Mnium*** (Figure 17) may take place through stereids. They support their hypothesis by demonstrating that the lead chelate solution applied to the leaves penetrates the sterome. They suggest that the most probable means of translocation of water from leaves into the stem is through the dense mass of stereids in leaves and leaf bases to the central cells of leaves and leaf traces to the hydrome. But only in the Polytrichaceae does there seem to be a connection between the leaf traces and both the leaf and hydrome. Rather, the apoplastic route through cell walls in the stem cortex is a more likely route in most cases.

Mixohydric bryophytes are those in which both endohydric and ectohydric methods are important. Many of the species in this group are small, acrocarpous mosses of loams or clays. These soils dry out frequently, but their fine texture permits them to maintain a moist top layer for a period of time after rain. Hébant (1977) contends that truly mixohydric mosses are not very abundant, implying that the ectohydric pathway is far more important in most. However, in reality, most (perhaps all) mosses are mixohydric in that they have both internal and external means of conduction to at least some degree.

Nocturnal

For many mosses, nighttime is the only period of rehydration. This is especially true for desert mosses such as ***Syntrichia ruralis*** (Figure 19). Csintalan *et al*. (2000) found that this moss obtained sufficient water through nighttime dew to accomplish 1.5 hours of net photosynthetic gain immediately after dawn. They suggested that such early morning periods might permit regular molecular repair due to desiccation damage during prolonged dry periods.

Figure 19. ***Syntrichia ruralis***. Photo by Michael Lüth, with permission.

But it appears that desert habitats are not the only places where nighttime moisture benefits the bryophytes. Carleton and Dunham (2003) contended that the uppermost growing tips of mosses could not be hydrated by simple capillary movement of water from the forest floor in the boreal forest. Rather, even in this mossy habitat, they

showed a nocturnal gain in mass due to vapor from the forest floor. As the forest floor cooled at night, distillation occurred with moisture condensing on the moss surface. The cooling temperatures and moisture provided by the forest floor was sufficient to cause the moss tips to reach dew point. This seems to be most evident in late summer when the lower organic layers have warmed the most and the surface temperature is thus relatively lower at night, causing the condensation. When a vapor barrier was used to prevent ground water from rising, no mass gain was in evidence.

Mechanisms of Water Movement

Bopp and Stehle (1957) found that a mechanism similar to the diffusion pressure deficit seen in higher plants worked in moving water up the moss. By using fluorescent dyes, Bopp and Stehle showed that water moved up the leafy gametophyte both internally and externally, but that dye went quickly to the foot of the sporophyte imbedded in the gametophyte, then moved up the seta through the central strand. In mosses with the calyptra removed, the flow rate increased, suggesting that transpiration loss may perform a function of pulling water, similar to that found in tracheophytes. Maier-Maercker (1982b) found an accumulation of radio-labelled and heavy metal ions in the annulus of the moss ***Plagiomnium cuspidatum*** (Figure 20), similar to that found in tracheophyte guard cells, suggesting that this area may be one of transpirational water loss.

Figure 20. ***Plagiomnium cuspidatum*** capsules showing annulus **arrows**) where labelled metal ions accumulated, suggesting a site of transpiration loss. Photo by Robert Klips, with permission.

Although bryophytes lack leaf stomata, they do lose water through their wax-free leaves. For example, the transpirational loss rates of the moss cover in the lichen tundra (16-20% of total precipitation) is not unlike that from the ericaceous shrubs of the tundra heath (24-26%) or the alpine dwarf shrub heath (16-20%), whereas tracheophytes in a wet meadow can have 135% loss (Larcher 1983 – data from many authors).

Using mosses from five different habitats ranging from wet to dry, Bowen (1933a,b,c) determined that the water ascends the mosses as capillary films between the leaves and stem, being absorbed at the stem and branch apices by the younger cells with unthickened walls. From there it diffuses through internal tissues laterally, then downward, not upward as in tracheophytes. Conduction from the base through the central strand is slow in cut stems but much slower when the stem base is still intact (Bowen 1933a,b,c). In the latter case, water must penetrate the thick walls of the rhizoids and stem/rhizome. And at least some of the species have cuticles on the rhizoids!

Once water reaches the central strand, it travels there preferentially (Hébant 1977). Internal ascending water travels through the narrow, elongated, thin-walled cells (presumably hydroids). In addition to apical absorption, leaves and stem epidermis absorb some of the water, albeit less readily due to cell-wall thickening and cuticles.

The capacity of both internal and external water conduction seems to diminish as the moisture of the habitat increases (Bowen 1933a, b, c). Mägdefrau (1935) contends that at 90% humidity, ***Polytrichum*** (Figure 2, Figure 9, Figure 13) can maintain its turgor with internal conduction only, but at 70% both internal and external conduction are necessary. For all other families of mosses, with the possible exception of the Mniaceae, a significant amount of external conduction seems necessary.

Vitt (1990) suggests that those mosses that must endure a greater range of fluctuations in water availability may be more plastic in their responses. At least among the boreal mosses, the ectohydric, drought-tolerant ***Hylocomium splendens*** exhibits highly variable growth over its North American range, but the endohydric, less drought-tolerant ***Polytrichum strictum*** (Figure 21) exhibits more constant growth throughout its range (Vitt 1990).

Figure 21. ***Polytrichum strictum*** with sporophytes. Photo by Michael Lüth, with permission.

It is possible that there is some relationship between the absence of conducting cells and the horizontal growth habit of many mosses. However, Blaikley (1932) and Bowen (1933a) disagree as to the mechanisms for external conduction, arguing about the importance of soil water, presumably more available to the pleurocarpous habit. Blaikley feels that water contributed by the soil surfaces is necessary, whereas Bowen found leaf bases had drops of water when the soil surface was dry. The methodology of tracking the water is important here, and one is encouraged to read the arguments presented by Bowen (1933a) against broad interpretations based on the use of dyes. In most cases, she argues, they would be impossible to distinguish from naturally colored tissues, and the faint stain of cortical cells may be overlooked, whereas the presence of dyes in

the central strand may be more concentrated and thus more easily discerned. Rather, Bowen argues that water, and hence dye, accumulate in the central strand, whereas their movement across the cortex is transitory only. Thus, when water appears to have reached a certain height in the stem from internal movement through the hydrom, it may in fact have arrived there from the aerial surfaces across the cortex. Using 12 plants of ***Polytrichum commune*** (Figure 9) and blocking the entry of water into the hydrome from the cut surface with wax, she was able to demonstrate rapid movement externally, up to 42 cm in one hour, reaching a maximum of 96 cm in 24 hours (Bowen 1931). When basal leaves were removed (and the wounds sealed) and the cut stems were not blocked, she demonstrated considerably less movement internally through the hydrome. Using only three plants, the greatest rise internally was only 12 cm.

It is interesting that the dependence on endohydric gametophytic conduction seems to have diminished in the evolution of bryophytes, with the creeping (pleurocarpous) taxa exhibiting less developed conducting systems. Instead, the ectohydric habit is well-developed. Yet, no pattern exists (Hébant 1977). Even the xerophytic ***Orthotrichum*** (Figure 22) lacks a central strand, although despite its acrocarpous appearance it is technically pleurocarpous and thus related to taxa that have apparently lost the central strand.

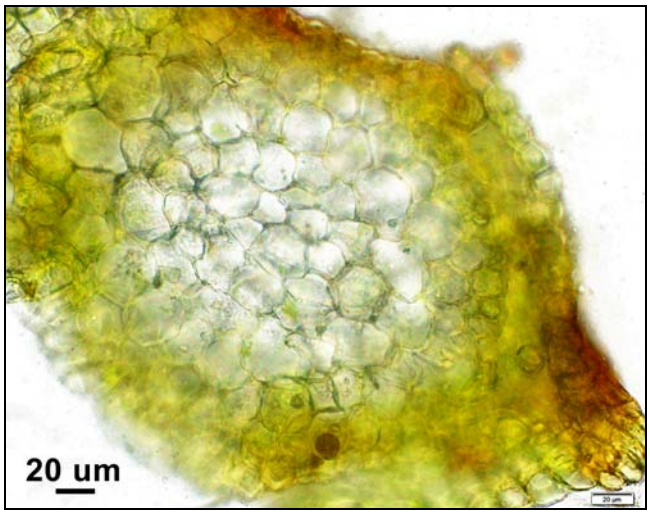

Figure 22. ***Orthotrichum pumilum*** stem cross section showing absence of central strand. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

It seems that for bryophytes, ectohydric conduction may be adaptive. Mägdefrau (1935) contends that the humidity would need to be at least 90% for the plant to succeed with internal conduction only. Gametophyte conduction is slow. Bopp and Stehle (1957) found that it required 40 hours for water to travel 10 cells in the rhizoids of ***Funaria hygrometrica*** (Figure 28)! The external pathway is much more rapid. The slowness of internal transport relative to external transport (Table 2) can easily account for the success of the external mechanisms. Furthermore, Bowen (1933a) demonstrated that the time required for movement can be more accurately measured by sensitive chemical tests that measure very small amounts of water which advance most rapidly up (or down) the plant, suggesting that external conduction is even more rapid than supposed.

Mosses such as ***Pleurozium schreberi*** and ***Hylocomium splendens*** form important intermediaries between the soil and atmosphere in the boreal forest (Sokołowska *et al*. 2017). Hence, understanding how water movement functions in these keystone species is important. These researchers examined the conduction of both food and water in these species. Both species exhibit symplasmic transport for short distances by using food-conducting cells. ***Pleurozium schreberi*** is furthermore able to transport substances apoplastically over long distances through the central strand of hydroids. ***Hylocomium splendens*** lacks hydroids (Figure 27). Both species have increased internal transport when air humidity is reduced significantly, but this increase is somewhat greater in ***H. splendens***. These differences affect the desiccation tolerance. ***Hylocomium splendens*** typically dries faster than ***P. schreberi*** (Hiejmans *et al*. 2004; Elumeeva *et al*. 2011), perhaps explaining why ***H. splendens*** prefers wetter habitats (Busby *et al* 1978).

Figure 23. ***Pleurozium schreberi***, a species with both apoplastic and symplastic internal conduction. Photo by Bob Klips, with permission.

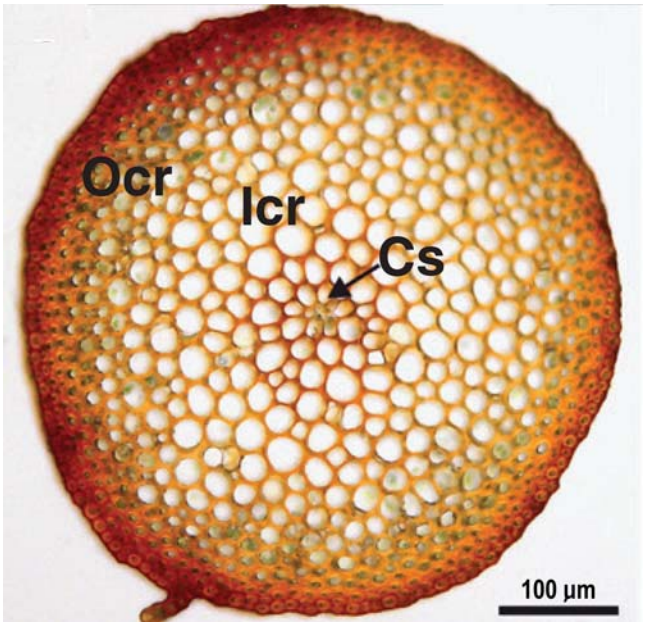

Figure 24. ***Pleurozium schreberi*** stem cs showing hydroids. **Cs** = central strand with hydroids; **Icr** = inner cortex; **Ocr** = outer cortex. Photo by Katarzyna Sokolowska.

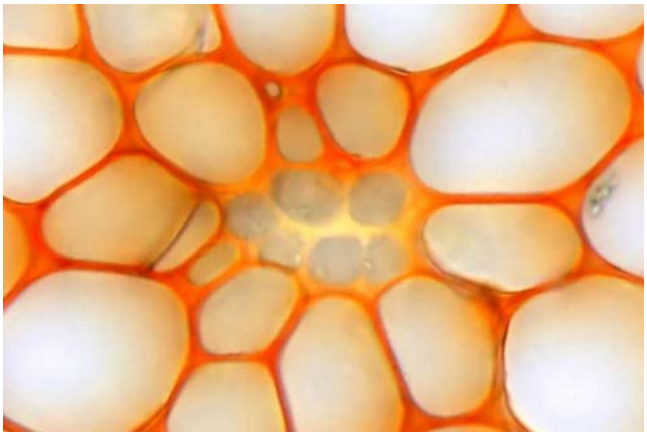

Figure 25. ***Pleurozium schreberi*** stem cs showing hydroids with yellow walls in center. Photo by Katarzyna Sokolowska.

Figure 26. ***Hylocomium splendens***, a species with no central strand and slow internal conduction. Photo by Paul Slichter, with permission.

Figure 27. ***Hylocomium splendens*** stem cross section showing absence of hydroids. Photo from Botany Website, UBC, with permission.

To summarize, water is known to move from one bryophyte part to another by four pathways: hydroids, free spaces in cell walls, cell to cell, and externally.

Figure 28. ***Funaria hygrometrica***. Photo by Michael Lüth, with permission.

Table 2. Effectiveness of internal conduction compared to total in mosses after 24 hours in 70% relative humidity. Conduction measurements are grams water/0.2 grams dry mass; % is percent of internal compared to total rate. From Mägdefrau (1938).

	Internal Conduction	Total Conduction	%
Sphagnum recurvum	0.07	6.54	1
Drepanocladus vernicosus	0.79	22.73	3.5
Rhytidiadelphus triquetrus	0.11	1.67	6.5
Thamnobryum alopecurum	0.007	0.019	37
Plagiomnium undulatum	1.13	2.22	51
Polytrichum commune	2.24	3.32	67

Transport to Sporophyte

The seta, lacking leaves, must necessarily conduct water internally. Conduction from the gametophyte to the **sporophyte** tissue seems to be governed by several factors, as observed in ***Funaria hygrometrica*** (Figure 28) (Bopp & Stehle 1957). The sporophyte receives its water from the **haustorial foot** that is imbedded deeply into the central strand of the gametophyte.

In ***Dicranum undulatum*** (Figure 29), it appears that the embryo has a role in development of the conducting strand in the gametophyte stem, as no conducting strands were present below archegonia that had not been fertilized (Roth 1969). Hébant and Berthier (1972) made similar observations on ***Polytrichastrum alpinum*** (Figure 30). This underscores the apparent importance of the transfer of water from the gametophyte central strand to the sporophyte. There are no plasmodesmatal connections between the gametophyte and the foot of the seta (Hébant 1977). However, the **transfer cells** have extensive wall ingrowths (**labyrinth,** Figure 31) that greatly increase the surface area of the plasma membrane, thus increasing transport (Hébant 1977). In ***Funaria hygrometrica*** (Figure 28) fluorescent dyes showed that the jacket around this foot was separated by a narrow intercellular space which became colored before the central strand (Bopp & Stehle 1957). This capillary space moved the liquid quickly to the

central strand of the sporophyte. When comparing species that had no transfer cells, Bopp and Weniger (1971) found that uptake by the sporophyte was greatly reduced.

Figure 29. ***Dicranum undulatum***, a moss where conducting strands seem to develop only in stems under archegonia with embryos. Photo by Jan-Peter Frahm, with permission.

Figure 30. ***Polytrichastrum alpinum***, a moss where conducting strands seem to develop only in stems under archegonia with embryos. Photo by Michael Lüth, with permission.

Hébant (1977) describes detailed studies of a variety of mosses in which the very tip of the sporophyte foot directly penetrates the central strand of the gametophyte. At the end of the foot, an appendage of mostly necrotic cells is the only separation of the conducting cells between the two generations. Conduction in the sporophyte was increased when the calyptra was removed; the apparently non-closing stomata of the capsule may contribute to transpirational water loss.

As can be observed in ***Physcomitrium immersum*** (=*Physcomitrium cyathicarpum*), both generations have **transfer cells** at the junction, and the foot epidermal cells are rich in organelles (Lal & Chauhan 1981), especially mitochondria (Hébant 1977), suggesting there might be considerable active transport between the two generations.

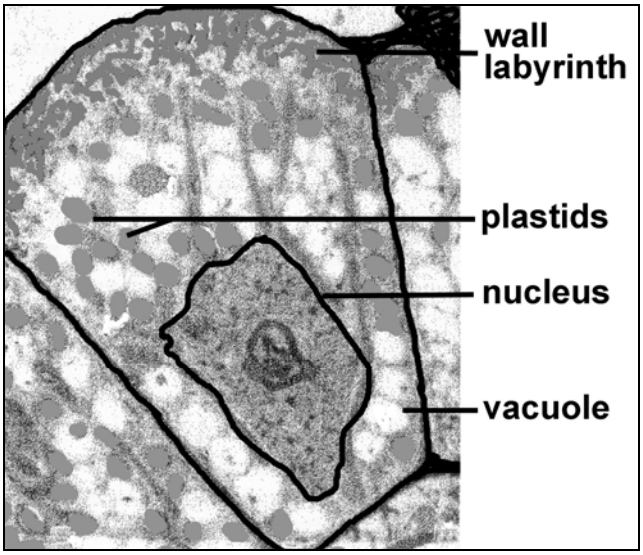

Figure 31. Transfer cell between gametophyte and sporophyte showing wall labyrinth. Computer-drawn from photo in Lal and Chauhan (1981).

Summary

We have seen that bryophytes have remarkable abilities to gain, retain, and recover from loss of water. They gain it in their cells both through external (**ectohydric**) capillary movement and internal (**endohydric**) transport. Endohydric movement is accomplished either cell-by-cell or through designated elongate cells (**hydroids**). Some mosses survive on moisture in clouds and nighttime dew. Nutrients and water are transferred to the sporophyte through the **foot**, using special **transfer cells** with **labyrinth** walls.

Acknowledgments

This chapter has benefitted from the help of Beth Scafone and Medora Burke-Scoll, who helped me tow the line in explaining things without leaving too much to one's imagination, but at the same time not repeating myself.

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CHAPTER 7-3

WATER RELATIONS: PLANT STRATEGIES

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CHAPTER 7-3

WATER RELATIONS: PLANT STRATEGIES

Figure 1. ***Tortula muralis*** with water drops collected on the leaf awns and setae. Note their collection around the young capsules. Such collection can occur in fog and mist and may serve as the only source of water in some habitats. Photo courtesy of Peggy Edwards.

Water Strategies

Water strategies in bryophytes have been approached in a variety of ways, from splashing gemmae (Brodie 1951) to uptake (Proctor 1981; Rice & Schneider 2004; Rice 2012; Jonas & Dolan 2012; Sand-Jensen & Hammer 2012) to transport (Hébant 1977; Mulder *et al*. 2001; Proctor & Tuba 2002; Pressel 2006; Rice 2012) to moving nutrients (Buch 1945, 1947; Proctor 1981) to retention (Kennedy 1993; Mulder *et al*. 2001; Rixen & Mulder 2005).

Mosses often appear to be completely dead, only to be revived by water. Angela Newton (pers. comm., Bryonet) reported that epiphytic mosses in the lowland tropical rainforests, where mosses may appear dead after severe desiccation, recover quickly with actively growing apical and axillary buds on completely dried out plants and even on plants scorched by fire (see Figure 2)! Leaf and stem tissues from xerophytic mosses can regenerate after as many as 19 years of desiccation (Table 1); some spores remain viable after 70 years (Malta 1921). As surmised by Oliver *et al*. (2005), **desiccation tolerance** appears to be a primitive trait that permitted plants to invade land. **Desiccation tolerance** (**DT**) is the ability of an organism or structure to tolerate and survive after equilibrating to a relative humidity (RH) of ≤50% (Alpert & Oliver 2002; Koster *et al*. 2010). An understanding of this tolerance in modern bryophytes is fundamental to a general understanding of desiccation tolerance.

Figure 2. ***Polytrichum*** showing fresh, green growth one week after a forest fire that scorched adjacent plants in Baraga, Michigan, USA. Photo by Janice Glime.

Table 1. Records of revival after extended periods in a herbarium (Alpert 1982, *Volk 1984, +Glime pers. obs.).

Anoectangium compactum	19 years
Dicranoweisia cirrata	9 years
Riccia canescens	*7 years
Grimmia elatior	5 years
Oxymitra	*4 years
Anomodon longifolius	2 years
Bryum argenteum	2 years
Orthotrichum rupestre	2 years
Grimmia muehlenbeckii	18 months
Andreaea rothii	13 months
Racomitrium lanuginosum	11 months
Syntrichia ruralis	8 months
Fontinalis flaccida	+3 months

Most people who are not very familiar with bryophyte physiology consider them to be plants that require damp or wet habitats. But compared to **tracheophytes** (non-bryophytes; plants with lignified vascular tissue), bryophytes are the ones adapted to drying conditions (Vitt *et al*. 2014). Even in bryophytes that seem to lack physiological desiccation tolerance, morphological or life history adaptations permit them to survive periodic drought.

Although of the known 21,000 species of bryophytes, only 210 have been documented as desiccation tolerant (Wood 2007), but most have never been tested. In fact, Vitt *et al*. (2014) argue that "many members of both moss and liverwort lineages are desiccation tolerant, allowing them to survive in periodically dry habitats, and that in many of the moss lineages this physiological desiccation tolerance is remarkably high." But among seed plants, fewer than 1% of those tested are desiccation tolerant (Proctor & Pence 2002). Among bryophytes, even the aquatic moss ***Fontinalis*** has at least some desiccation-tolerant species (Glime 1971). For example, ***Fontinalis flaccida*** survived and grew after three months of drying on a herbarium sheet (pers. obs.). If one considers the types of microhabitats bryophytes occupy, and lack in most species of any kind of water storage organ, we should expect that most have at least some degree of desiccation tolerance. This notion is further supported by the high survival rate of bryophytes despite a high surface-to-volume ratio that facilitates rapid drying (Proctor *et al.* 2007).

Poikilohydry vs Homoiohydry

The strategy of maintaining internal moisture levels that agree closely with the ambient atmospheric levels is a risky physiological strategy and used mostly by lower plants such as bryophytes. Proctor and Tuba (2002) considered there to be two contrasting strategies for land plants to deal with the irregular supply of water they faced on land and that these relate closely to the matter of scale. Tracheophytes use internal transport to carry water from the soil to the distant canopy (**homoiohydry**). **Poikilohydric** bryophytes (and some tracheophytes), on the other hand, depend on desiccation tolerance, becoming dormant when desiccated. Hence, their cells are either **turgid** (swollen) or desiccated. But **desiccation tolerance** (DT) requires a whole series of adaptations to permit the cell to regain its original state. Essential cell components and their functional relationships must be preserved through the drying-rewetting cycles presented by their environment. In some cases, this tolerance is induced by water stress. This strategy is particularly beneficial on hard substrates such as rocks and on dry soils in seasonally dry climates where lacking roots that would prevent them from obtaining deeper water in soils. Thus, among tracheophytes, this strategy is most common in warm, semiarid climates, whereas in bryophytes the strategy occurs from polar to tropical regions (Proctor & Tuba 2002; Lakatos 2011). The time scale also differs, with tracheophytes requiring one to several days to resume activity whereas bryophytes (and lichens) typically can become dry and rehydrated within an hour or less (Proctor & Tuba 2002).

In bryophytes, external water conduction seems to be present in all species, but is often supplemented by internal conduction. External conduction is typically diffuse (Proctor & Tuba 2002). The plants can survive drying to the point where there is no liquid phase remaining in the cells and water content may be reduced to only 5-10% dry weight (equilibrium water potential of -100 MPa or less). But when these bryophytes are remoistened, mostly normal metabolism returns within minutes to hours. Those capillary spaces between leaves and branches are able to maintain an external water reservoir that is available to the photosynthesizing cells without blocking the free exchange of gasses (Dilks & Proctor 1979; Proctor & Smith 1995; Zotz *et al*. 2000). This relationship seems to be essential to the functioning of the bryophytes. At the same time, cell water content seems to affect photosynthesis in the same way as that in tracheophytes (Dilks & Proctor 1979; Tuba *et al.* 1996; Proctor 2000).

Some mosses, as for example ***Barbula convoluta*** (Figure 3), can maintain their turgor for some time after rain ceases, an ability that is made possible by contact or proximity to the moist ground surface (Proctor & Tuba 2002). Typically, water is able to reach distant cells either by travelling externally through capillary spaces or internally through free spaces of the cell walls (Figure 4). To permit photosynthesis by making gas exchange possible, many mosses exhibit a water-repellent cuticle on the younger cell surface, preventing them from trapping water droplets there (Kershaw 1972, 1985; Dilks & Proctor 1979; Proctor 1979b; Nash 1996; Tuba *et al*. 1996; Zotz *et al*. 2000) and thus permitting gas exchange.

Figure 3. ***Barbula convoluta***, a moss that maintains turgor for a longer time than most mosses following rain. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

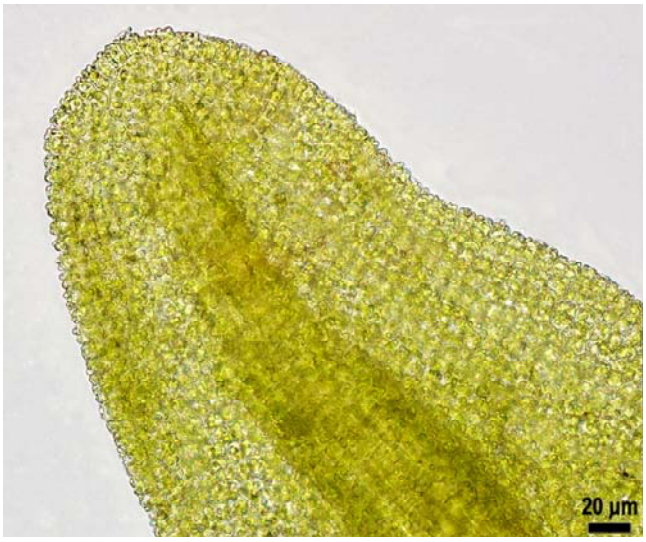


Figure 4. ***Barbula convoluta*** leaf cells showing small size and papillose surface that hold water longer than large cells. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

In some cases, the physiological desiccation tolerance is induced by water stress (Proctor & Tuba 2002). Both **constitutive** (always present; fully desiccation tolerant) and **inducible** [produced when drying conditions occur; previously known as modified desiccation-tolerant (Oliver *et al.* 1998)] desiccation tolerance exist among plants (Stark *et al*. 2013) and these will be discussed in Chapter 7-6 of this volume.

Cellular structure remains intact in desiccation, but upon rapid uptake of water it can be disrupted. However, in bryophytes the cellular integrity returns rapidly. Photosynthetic activity recovers quickly, perhaps due to protection of the chlorophyll (Tuba 1984; 1985). During desiccation, there seems to be no gene activity, but gene expression occurs rapidly following rehydration. Among these activities is the production of a number of proteins called **rehydrins**. These seem to be involved in stabilizing and reconstituting membranes that have been damaged by dehydration. Oliver *et al*. (2005) suggest that vegetative desiccation tolerance, at least in bryophytes, has changed little from early land invaders and may be using a mechanism that was first used in spores.

Even though many bryophytes tolerate high degrees of desiccation (Dilks & Proctor 1974; Nörr 1974; Dhindsa & Bewley 1976), **water content** and availability are important for potential accumulation of photosynthates (Alpert 1979). Patidar (1988) found that in ***Asterella angusta*** the moisture content is the most important determinant of **thallus** (flattened, nonvascular plant body) size. In ***Plagiochasma appendiculatum*** (Figure 5), optimum growth occurs at 60% moisture, whereas branching and growth are able to occur from 10-100% moisture (Vishvakarma & Kaul 1988)! ***Reboulia hemisphaerica*** (Figure 6), on the other hand, requires 70-80% moisture for optimum growth, with growth and branching occurring from 40 to 90%. In other words, no matter how desiccation tolerant a plant might be, it requires water to grow. Representative water contents of bryophyte plants from a wide range of field habitats in the temperate zone, Great Britain, are given in Table 2.

Figure 5. ***Plagiochasma appendiculatum***, a liverwort with both branching and growth throughout the range of 10-100% moisture. Photo by Michael Lüth, with permission.

Figure 6. ***Reboulia hemisphaerica***, a liverwort in which growth and branching occur in the range of 40-90% moisture. Photo by Jan-Peter Frahm, with permission.

Mosses grown in fully hydrated conditions afforded by saturated air enjoy optimal growth and development (Davy 1927). They exhibit more rapid development, more stem branching, more numerous rhizoids, smaller leaves, and smaller and fewer cells with larger chloroplasts than mosses existing at less than full saturation. Even at the scale of a single boulder, bryophytes distribute themselves according to their ability to achieve photosynthetic gain. When examining bryophytes that occupied various microsites on exposed granitic boulders, Alpert and Oechel (1987) found that those species that occurred in microsites with lower water availability were able to attain maximum net photosynthetic gain at a lower water content and to recover better from prolonged desiccation than those taxa in less **xeric** (dry) microsites. Alpert (1985, 2000) supports the hypothesis that the reason even **xerophytic** mosses (those adapted to dry habitats) are limited in their ecological distribution is that they often are unable to maintain positive carbon balance during repeated cycles of wetting and drying. Alpert and Oechel (1985) demonstrated this with ***Grimmia laevigata*** (Figure 7-Figure 8), a desiccation-tolerant plant that was unable to maintain this balance under a natural, highly xeric regime of wetting

and drying in certain microhabitats on exposed granitic boulders in California chaparral. Thus, there is an "inherent trade-off between desiccation tolerance and growth rate."

Table 2. Percent water content (compared to dry mass) of bryophytes at full turgor, not including free external water. Values represent means of two measurements. Table based on Dilks and Proctor (1979); those marked with * from Skre *et al*. (1983) include new growth and 1-year-old growth; those with + from Proctor (2000).

species	water content, % dry mass
Mosses	
*Sphagnum subsecundum**	1225
Pilotrichella ampullacea+	>1200
Hookeria lucens	516
*Pleurozium schreberi**	485-625
*Hylocomium splendens**	485-545
Brachythecium rutabulum	249
Syntrichia intermedia	233
Homalothecium sericeum	223
Pseudoscleropodium purum	207
Thuidium tamariscinum	203
Dicranum majus	202
Leptodon smithii	187
Rhytidiadelphus loreus	165
Pleurochaete squarrosa	165
Neckera complanata	162
Racomitrium lanuginosum	142
Anomodon viticulosus	141
*Polytrichum commune**	95-125
Liverworts	
Pellia epiphylla	1180
Conocephalum conicum	871
Porella platyphylla	230
Plagiochila spinulosa	222
Bazzania trilobata	210

Figure 8. ***Grimmia laevigata***, a poikilohydric moss, in its wet state. Photo by Michael Lüth, with permission.

Rod Seppelt (Bryonet 27 June 2022) summarized some of the Antarctic studies on the role of cushions in maintaining water content. Microbial associates within the cushion provide the CO_2 (~2000 ppm) needed for photosynthesis while ambient concentrations are only 350-400 ppm. When temperatures drop to below 0ºC at night, the cushion likewise drops until the water in the cushion begins to freeze. Then latent heat is able to elevate the cushion temperature to ~2ºC. This provides time before partial denaturing of proteins begins.

Water content in a bryophyte ranges widely throughout the year. For example, Klepper (1963) measured 23.8-258% in ***Dicranum scoparium*** (Figure 9), Romose (1940) 10-950% in ***Homalothecium sericeum*** (Figure 10), Morton (1977) 19-214% in ***Pseudoscleropodium purum*** (Figure 11), and 58-307% in ***Dicranum bonjeanii*** (Figure 12). Whereas many mosses benefit from high water content, too much water is not good for photosynthesis. Water on the surface blocks CO_2, and most likely high internal water content also interferes with physiological processes (Proctor 2000). Dilks and Proctor (1979) found optima as low as 200% water content and as high as 1500% among the same bryophytes shown in Table 2. Respiration seems to peak around 200% for most of these taxa.

Figure 7. ***Grimmia laevigata***, a poikilohydric moss, in its dry state. Photo by Michael Lüth, with permission.

Figure 9. ***Dicranum scoparium***, a moss with measured water content ranging 23.8-258%. Photo by Janice Glime.

Figure 10. ***Homalothecium sericeum***, a moss with measured water content ranging 19-214%. Photo by David Holyoak, with permission.

Figure 11. ***Pseudoscleropodium purum***, a moss with measured water content ranging 19-214%. Photo by Michael Lüth, with permission.

Figure 12. ***Dicranum bonjeanii***, a moss with measured water content ranging 58-307%. Photo by Michael Lüth, with permission.

Richardson (1981) divides mosses into three water strategies by habitat: **aquatic**, **mesophytic** (living in continually moist habitats), and **poikilohydric** (organism dries as its habitat dries and resumes normal metabolic activity after rehydration; Figure 8). Unlike most other plants, water content of predominantly poikilohydric bryophyte species is highly related to environmental conditions and weakly regulated by their internal and morphological structures. This strategy permits them to colonize such xeric environments as boulders and tree trunks. In these environments, mosses enjoy release from competition by higher plants, but must still survive the low light intensity created by the trees above.

Some bryophytes do appear to be able to survive in absence of precipitation. In caves in Poland, only 18.1% of the species occurred in very wet places or where there was dripping water, whereas in places that were continuously dry(!), 25% occurred (Jedrzejko & Ziober 1992). Certainly in those dry places atmospheric humidity must have provided the needed water for these very **hygroscopic** (readily absorbing water from air), **ectohydric** (relying mainly on water transport along external surface of plant by capillarity) bryophytes. Shaun Russell (pers. comm.) found that in montane areas of Africa with virtually no rainfall, fog collected on bryophyte surfaces, providing sufficient water for them to survive. A similar phenomenon occurs in geothermal areas (Figure 13).

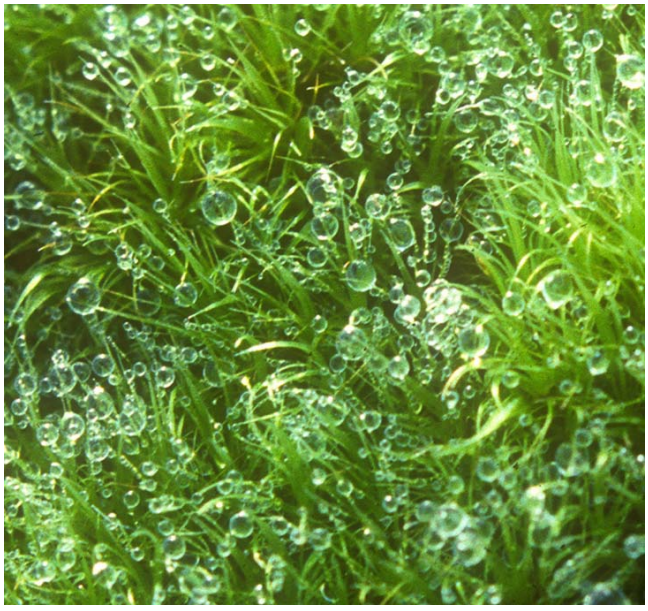


Figure 13. ***Campylopus holomitrius*** with water droplets captured from the "steam" emitted by geothermal vents in New Zealand. Photo by Janice Glime.

The drought-tolerant ***Pseudocrossidium crinitum*** (=*Barbula aurea*; Figure 14) seems to have compensated for its low water availability by having relatively low levels of light compensation and saturation responses for photosynthesis (Rundel & Lange 1980). Such low levels would permit the moss to carry out photosynthesis early in the morning when dew is available and before high evaporation stress occurs. These aerial sources of water are of little use to tracheophytes that must take water in by their roots, not their leaves.

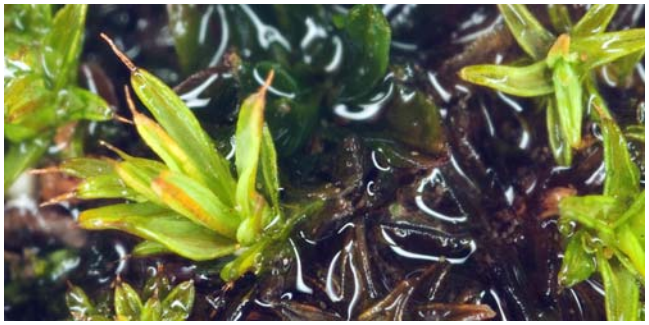


Figure 14. ***Pseudocrossidium crinitum***, a xerophyte with low light compensation and saturation levels. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

As one would expect, degree of drought tolerance is generally greatest in plants from dry habitats (Clausen 1952, 1964; Johnson & Kokila 1970; Dilks & Proctor 1974). Seki and Yamaguchi (1985) suggest that on some islands with strong summer winds, Shannon diversity decreases as saturation deficits increase. Richardson (1981) claims that aquatic mosses and those that grow in humid forests are damaged quickly by drought. But even such high humidity plants as ***Hookeria lucens*** (Figure 15) are able to survive desiccation for days (Horst Tremp, Bryonet).

Figure 15. ***Hookeria lucens***, a drought-intolerant moss. Photo by Michael Lüth, with permission.

Glime (1971) found that two aquatic mosses (***Fontinalis*** spp.; Figure 16) were able to survive on the stream bank out of water (Figure 17) for up to one year and still grow when rehydrated. However, those dried in the laboratory were apparently dead after only 55 hours, perhaps due to rapid drying. Steere (1976) found that ***F. squamosa*** (Figure 18) from Alaska could not survive a week of air drying. One reason for apparent differences here is that it is difficult to determine when a moss is dead, and even though all leaves may be dead, the stem may still harbor life. ***Fontinalis*** is subject to annual emergence when stream level drops (Figure 16), and perhaps slow drying on the stream bank permitted it to become dormant and to preserve sufficient energy to repair its membranes upon rehydration. The rapid drying of a laboratory, with unnaturally low humidity and no acclimation period, may have prevented the necessary physiological changes that could permit it to survive. Oliver and Bewley (1984) have demonstrated that it takes longer for the cellular physiology to return to normal in a rapidly dried bryophyte than in a slowly dried one.

Figure 16. ***Fontinalis dalecarlica*** and ***F. novae-angliae*** above water, in Fox Run, New Hampshire, USA. When these mosses were placed away from the stream bed for up to one year, at least some of them survived from all re-submersion dates (Glime & Carr 1974). Photo by Janice Glime.

Figure 17. ***Fontinalis antipyretica*** in dry stream. Photo by Janice Glime.

Figure 18. ***Fontinalis squamosa*** on rock above water near Swallow Falls, Wales. Photo by Janice Glime.

A similar pattern of submersion and desiccation is endured by ***Hydropogon fontinaloides*** in the Amazon basin (Mägdefrau 1973). It hangs from trees during the dry season, but during the wet season it floats in water. The behavior of ***Cratoneuron filicinum*** (mistakenly published as *Hygrohypnum luridum*; Figure 19), typically a stream margin species, may explain the lab results. This moss was unable to synthesize protein when rehydrated after it was dried quickly over silica gel for one hour (Bewley 1974). However, it was able to tolerate drying down to 33% of its fresh mass when dried slowly, and slow drying for 5 hours to 66% of its fresh mass had no detrimental effects on protein synthesis.

Figure 19. ***Cratoneuron filicinum***, a moss that is unable to synthesize protein when rehydrated if it dries too quickly. Photo by Teplov through Arctoa, with permission.

Just what endows bryophytes with the ability to inhabit arid microsites that are totally inhospitable for tracheophytes? As you can see from the foregoing examples, we can divide these adaptations into anatomical/structural, growth/life form, and physiological adaptations.

Life cycle adaptations, a major means for an immobile organism to cope with changing weather and seasons, have been addressed in Chapter 4-6. Schofield (1981) points out that spore germination patterns, protonemal structure, life span, and methods of propagation are all related to the habitat characteristics. Water availability is important to all of these aspects. Multicellular spores are more common in habitats where the spores are subject to desiccation. Protonematal specialization is common in deeply shaded habitats, whereas in mesic habitats the protonemal cells are elongate, *i.e.*, having typical protonematal structure. In the leafy **gametophore** (upright leafy plant), characters such as leaf shape, leaf arrangement and orientation, leaf anatomy, stem cortical cells, hydroids, leptoids, branch arrangement, presence of rhizoids, and presence of paraphyllia all affect water movement. Such small features as surface ornamentation of leaves, stems, and rhizoids affect water absorption and retention and influence habitat specificity.

Role in Ecosystem Water Cycle

In areas where bryophytes dominate the forest floor, their role in the water cycle can be extraordinary. This is especially true where permafrost prevails (Henry Santeford, pers. comm.). Bryophytes hold melt water until they become saturated. At that point in time, all new melt water is suddenly released and can cause flooding. It is important in some areas to be able to predict this flooding regime for the safety of both animals and humans. Hence, we need to understand both holding capacity and evaporation rates of water from the bryophytes.

Penman (1948) helps us to understand evaporation as it might apply to bryophytes. Although he compared evaporation from bare soil, grass, and open water, the principles apply. He suggests that we need to combine two theoretical approaches to evaporation, an aerodynamic basin in which evaporation is due to turbulent transport of vapor by eddy diffusion, and an energy basis in which evaporation is a way of degrading incoming radiation. This approach eliminates the problem of measuring surface temperature and overcomes the problem of estimating effects as if one is measuring evaporation from a lake surface. Using this method, supported by empirical data, indicates that evaporation from grass follows a seasonal cycle relative to that evaporating from open water, a phenomenon Penman attributes to the change in photoperiod.

In other circumstances, bryophytes may prevent the underlying roots from getting water (Beth Scafone, unpubl. data). If there is a quick rain shower, bryophytes act as sponges, trapping the water before it reaches the soil. On the other hand, bryophytes can reduce evaporation of water from the soil following heavy rain, thus permitting the roots to grow for longer periods of time.

Structural Adaptations

When I moved to the Upper Peninsula of Michigan, I was struck by the fact that only red oaks were able to live here. A simple difference in one structure made their survival possible in a cold region with long winters – narrow vessels. Large vessels in other North American species cavitate and the water is unable to reconnect on an appropriate time schedule that permits the oaks to complete their life cycle and gain sufficient energy to continue the establishment of the species.

Watson (1919) warned of the difficulty in dealing with bryophyte identification because of the entirely different appearance they can present in the wet vs dry state. The bryologist must know them in both conditions. I once spent half an hour in an unfamiliar locality trying to identify ***Hedwigia ciliata*** because I had only seen it dry (Figure 20-Figure 22) and these plants were fully hydrated (Figure 23-Figure 24). The plant may even appear to be dead during drought, only to revive quickly when moistened, resuming its normal functions.

Figure 20. ***Hedwigia ciliata*** dry at Canyon Falls, Michigan, USA, a state that was very familiar to me. Photo by Janice Glime.

Figure 21. ***Hedwigia ciliata*** dry, 21 August 2018, Esrey Park, Michigan, USA. Photo by Janice Glime.

Figure 22. ***Hedwigia ciliata*** dry, showing julaceous leaf arrangement and white leaf tips. Photo by Larry Jensen, with permission.

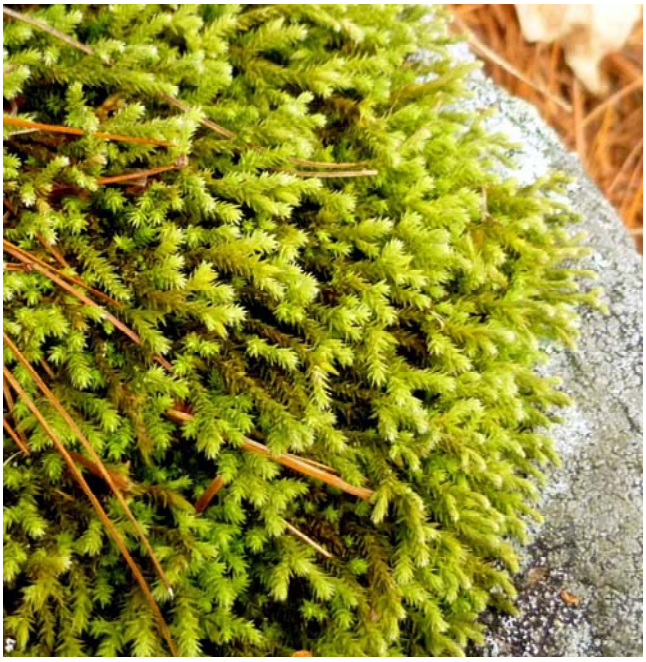


Figure 23. ***Hedwigia ciliata*** wet, totally changing color and leaf angles from those of the dry form. Photo by Allen Norcross, with permission.

Figure 24. ***Hedwigia ciliata*** wet, contrasting with the grey-green of the dry form. Photo by Bob Klips, with permission.

Many studies have demonstrated the importance of anatomy in determining the mechanical properties of plant tissues, including bryophytes (Hébant 1977; Rossi *et al.* 1998; Niklas *et al*. 2006; Frenzke *et al*. 2011; Atala & Alfaro 2012; Vincent 2012). Getting water and nutrients into and out of a plant is size dependent. Adaptations vary even within a species due to its plasticity in responding to the environment (Sarafis 1971; Buryová & Shaw 2005). As discussed by Raven and Handley (1987), for plankton organisms, any size above ~50 µm diameter restricts the growth rate because of the greater restriction of uptake by the boundary layer. Thus, for macroscopic aquatic photosynthetic organisms, even favorable velocity of water and plant morphology cannot reduce the boundary layer restrictions on nutrient uptake enough to compensate for the decrease in uptake rate. Movement of nutrients within the plant involves **cyclosis** (cytoplasmic streaming) in algae, phloem and xylem in tracheophytes, and in bryophytes it often involves both cyclosis and transport through leptoids and hydroids.

Raven and Handley (1987) consider that the energy cost for transporting nutrients would be higher for those organisms using cyclosis than for those using vascular tissue. They also consider that there is a penalty for height in tracheophytes, causing reduced specific growth rate under both resource-saturated and resource-limited conditions. Coupled with this penalty is reduced resource use efficiency with increased plant height. The reason for these penalties is the need for greater supporting tissue and a greater percentage of the tissue dedicated to vascular tissue. But there is also some compensation. Taller plants can capture more light energy and reach more nutrients and water in the soil. Smaller plants, on the other hand, have a potentially higher specific growth rate under these same resource-limited or resource-saturated conditions. The lack of need for supporting structures, requiring breadth, permits smaller plants such as bryophytes to have all or nearly all of their tissues as photosynthetic tissues. Raven and Handley left us with the challenge to discover the differences in transport needs and solutions resulting from these different morphologies.

In the desert moss ***Syntrichia caninervis*** (Figure 25), conservation of moisture is paramount, surpassed only by the need for rapid uptake. It can therefore serve as a model for adaptations against desiccation. Its growth form is tufted and its leaves are folded upward and twisted around the stem when dry (Figure 26 (Zheng *et al*. 2010). The leaf cells are endowed on both the upper and lower surfaces with C-shaped papillae that may have a role in deflecting sunlight to protect the DNA and chlorophyll during dry periods or to reduce the temperature. The leaf costa extends beyond the leaf to form an awn that has forked teeth and is able to capture moisture from the atmosphere. The protonemal cells are small and have thick walls; their cytoplasm is highly concentrated with only a small vacuole.

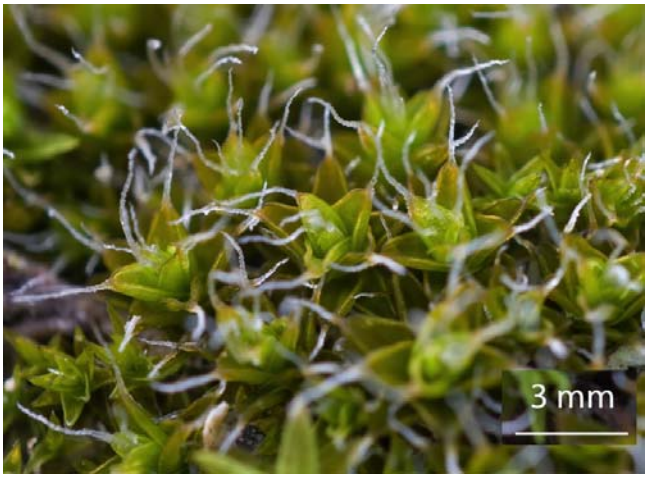


Figure 25. ***Syntrichia caninervis*** hydrated, a desert moss that increases its wax content as it ages. Note the awns that can trap atmospheric moisture from fog. Photo from Proyecto Musgo, through Creative Commons.

Figure 26. ***Syntrichia caninervis*** dry with leaves held close against the stems. Photo by Shari Hagwood, through public domain.

Thallose Liverworts

The structure of most thallose liverworts is so different from that of mosses or leafy liverworts that their water relations warrant separate consideration. They are adapted for predominantly ventral uptake. Thallose liverworts like ***Conocephalum conicum*** (Figure 27) and ***Cyathodium cavernarum*** (Figure 28) use ventral appendages (**scales**; Figure 27) to provide capillary spaces that conduct water externally on the underside of the thallus. Marchantialian species use specialized capillary systems on the ventral surface of the thallus to conduct water in either direction. Cell walls of the scales contain **tannins** (McConaha 1939), perhaps acting as an antibiotic.

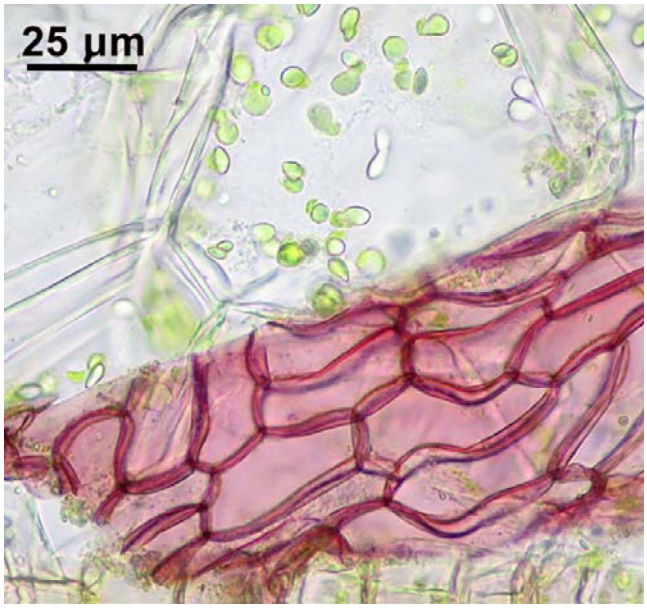


Figure 27. ***Conocephalum conicum*** ventral scale (purple) that provides capillary spaces for external water movement. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

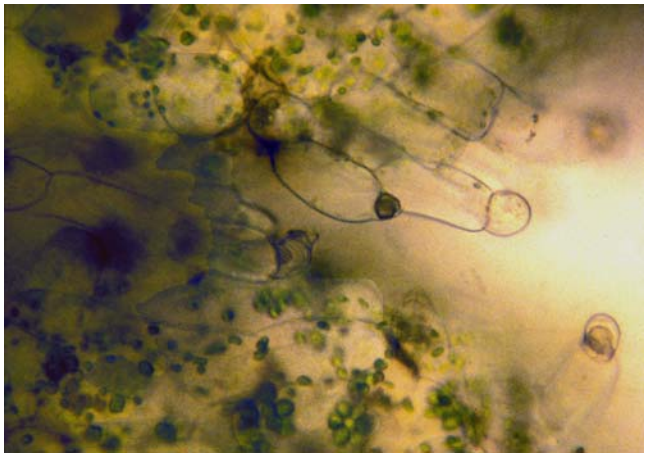


Figure 28. Scales of ***Cyathodium cavernarum***. Photo courtesy of Noris Salazar Allen.

Scales

Exposed surfaces of scales and thallus are often reddish-purple due to the flavonoid pigment **phlobaphene**, formed by oxidation of tannic compounds (McConaha 1939), but the role of phlobaphene is not clear. It is possibly a defense against would-be toxins from tannic compounds that contact the ventral surface. (There is evidence that tannins are toxic to bryophytes, not within their cell walls, but when they are able to act on cell constituents.) Since all these ventral surfaces are wettable, these cells are more susceptible to damage by such toxins.

Kürschner (2004) surmised that the anthocyanin pigments in ventral scales (Figure 27) protected the ventral surface from the sun when the thallus was rolled up, as it typically does in many species of ***Riccia*** (Figure 29-Figure 31). Furthermore, even hyaline scales (Figure 32) of ***Riccia*** and ***Oxymitra*** (Figure 33) can reduce desiccation. Some species, especially of ***Riccia***, sink into the soil surface as the soil dries, reappearing only after precipitation or heavy dew.

Figure 29. ***Riccia beyrichiana*** well hydrated and looking succulent. Photo by Michael Lüth, with permission.

Figure 30. ***Riccia beyrichiana*** drying. Note the loss of succulence in the now thin thallus; the thallus edges are beginning to curl. Photo by David Holyoak, with permission.

Figure 31. ***Riccia beyrichiana*** dry, showing curling of the thallus. Photo by Andrew Spink, with permission.

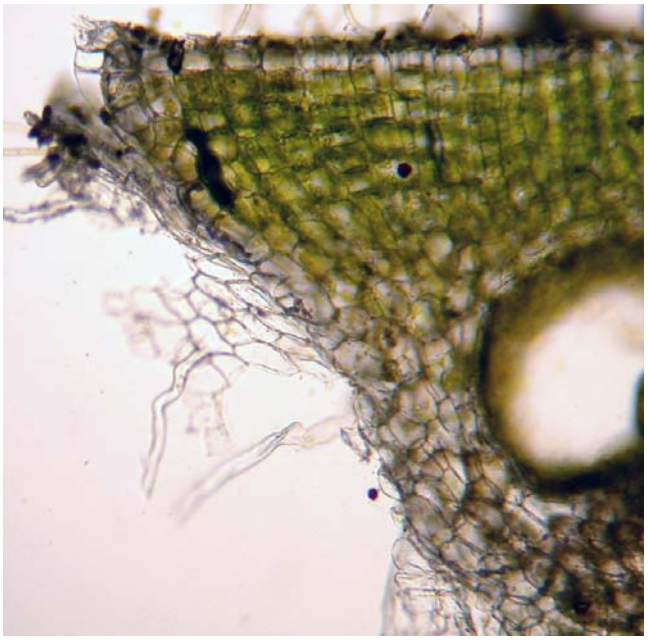


Figure 32. ***Riccia sorocarpa*** showing scales. Photo from Botany website, UBC, with permission.

Figure 33. ***Oxymitra incrassata*** showing ventral hyaline scales at the margins. Photo by Michael Lüth, with permission.

This high degree of wettability provides a greater possibility for water entry in thallose forms. For example, in ***Marchantia*** (Figure 34-Figure 35), water is conducted along the midrib as well as in interstitial spaces between the blade and scales, distributing water throughout the surface of the thallus. Water movement in ***Marchantia*** is relatively slow, at 0.4 mm per sec, improving slightly in ***Lunularia*** (Figure 53-Figure 54) and ***Reboulia*** (Figure 6), to approximately 0.5 mm per sec, despite their less highly developed capillary systems. However, McConaha (1939) found that movement from base to apex in ***Conocephalum conicum*** *s.l.* (probably ***C. salebrosum***; Figure 36) generally takes only about 20-30 seconds, roughly 1 mm per sec. Despite its slowness, McConaha found this external movement to be much faster than would be possible by internal conduction.

Figure 34. ***Marchantia polymorpha*** with gemmae cups located on the midrib. Photo by Walter Obermayer, with permission.

Figure 35. ***Marchantia polymorpha*** ventral surface showing blackish midrib (**arrow**) and white scales and rhizoids. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Figure 36. ***Conocephalum salebrosum***, where water travels from base to apex in about 20-30 seconds. Photo by Janice Glime.

Rhizoids

Ventral structures seem to be important in this group. In marchantialian liverworts, two types of rhizoids (Figure 37-Figure 38) provide somewhat different functions. The smooth-walled rhizoids (Figure 37-Figure 38) are alive (Duckett & Ligrone 2003) and emerge from beneath the ventral scales (Figure 39), providing contact with the substrate, whereas the **tuberculate** (pegged) rhizoids (Figure 38) are dead (Duckett & Ligrone 2003) and form a capillary system parallel to the thallus beneath each scale (McConaha 1941). The pegged rhizoids begin growth at

right angles to the thallus but change their orientation to follow that of the scales. The pegs, extending into the pegged rhizoid cell, prevent the collapse of the cell when dehydrated, thus maintaining its capillary role (Duckett & Ligrone 2003). When the **archegoniophore** (stalk supporting female reproductive organs) forms, the pegged rhizoids are wrapped within the archegoniophore by the folded thallus (Figure 40) and function in internal water conduction (Duckett & Ligrone 2003). The presence of the pegs also prevents the collapse of this stalk when the thalli dehydrate (Duckett & Ligrone 2003). These rhizoids have an outer layer of pectic material (like that of apples).

Figure 37. ***Riccia*** sp. with rhizoids on ventral side. Photo by Bernd Haynold, through Creative Commons.

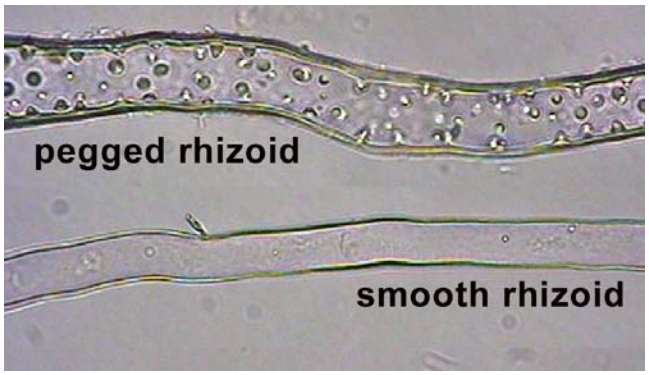


Figure 38. Pegged and smooth rhizoids of ***Conocephalum conicum*** *s.l.* Photo by Paul Davison, with permission.

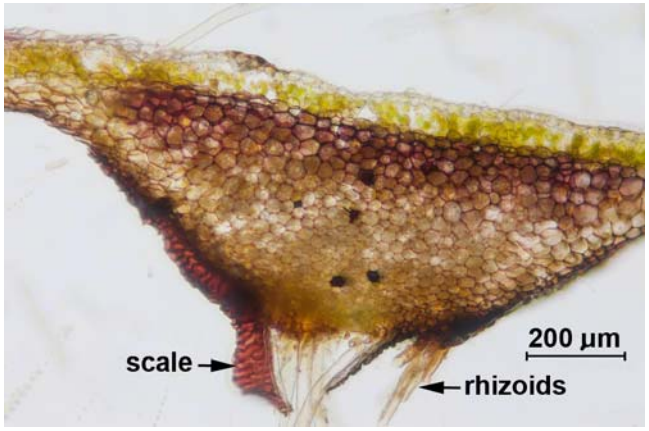


Figure 39. ***Preissia quadrata*** thallus cross section showing position of scale and rhizoids. Photo by Kristian Peters, with permission.

Figure 40. ***Marchantia polymorpha*** archegoniophore showing white rhizoids that are incompletely enclosed by the stalk of the archegoniophore. Photo by George Shepherd, through Creative Commons.

Previously treated mostly as a taxonomic anomaly, it appears that these two types of rhizoids have distinctly different functions (Duckett *et al*. 2013). The smooth rhizoids are alive, functioning in nutrition, anchorage, and as entry locations and conduits for fungal symbionts. Their role for fungal entry does indeed require that these rhizoids be alive. The pegged rhizoids, on the other hand, are dead at maturity, a condition first noted by Kamerling (1897), and function as water conduits through these empty tubes. Kny (1890) was the first to suggest that pegs prevent the rhizoid walls from collapse with water loss. Duckett *et al*. (2013), however, were the first to test this hypothesis. The pegs, along with elasticity, seem to provide the ability of the rhizoids to maintain their functional integrity by preventing their collapse when they are dry. This ability is essential to their function in conduction, a role demonstrated by Bowen (1935) and others (McConaha 1939, 1941), who used dyes to show conduction by capillarity and transpiration. The famous German morphologist Goebel (1905) observed that it is the liverworts with high transpiration rates that also have the most highly developed pegged rhizoids. This is in contrast with those of **hygrophilous** (water-loving) taxa such as ***Dumortiera*** (Figure 41-Figure 42) and ***Cyathodium*** (Figure 43).

Figure 41. ***Dumortiera hirsuta***, a hygrophilous species showing fringe of hairs on thallus and archegonial heads, but lacking the pegged rhizoids and scales of the dry habitat species. Photo by Jan-Peter Frahm, with permission.

Figure 42. ***Dumortiera hirsuta*** thallus showing smooth rhizoids on the ventral surface. Photo by Chris Lobban, with permission.

Figure 43. ***Cyathodium tuberosum***, a simple thallus lacking the complex scales and two types of rhizoids. Photo by Jan-Peter Frahm, with permission.

Among the leafy liverworts, thallose liverworts, and ferns, living rhizoids die and collapse upon dehydration, an irreversible response (Pressel 2007). Duckett *et al*. (2013) concluded that smooth rhizoids of liverworts grow at the apex, a character they share with root hairs, fungal hyphae, and moss protonemata. Furthermore, the smooth rhizoids exhibit considerable endoreduplication of Golgi bodies similar to that in moss caulonemata. They reach lengths that commonly are greater than 20 mm, sometimes reaching 30 mm in ***Marchantia polymorpha*** (Figure 35), making them the longest cells in liverworts. Duckett and coworkers suggest that this combination of characters may explain their inability to regenerate when damaged (Pressel *et al*. 2008a; Duckett *et al*. 2013).

On the other hand, rhizoids of mosses (and protonemata) can recover from desiccation except at the apical cell (Pressel 2007; Rowntree *et al.* 2007; Pressel *et al.* 2008b). The pegged rhizoids furthermore are devoid of air bubbles when desiccated, a further indication that they are highly resistant to **cavitation** (formation of a space; air blockage, as when water column in xylem becomes separated by air; collapse of cells), as are the hydroids of mosses (Ligrone *et al*. 2000).

Duckett *et al*. (2013) identified pegged rhizoids in 26 species of thallose liverworts and absence in 5. They compared the diameters of the smooth and pegged rhizoids and measured the time required for dyes to reach the archegonial heads in the taxa compared to time required in several mosses. The rates ranged 30-150 mm h^{-1} in the thallose liverworts, 28-14 mm h^{-1} in mosses, and 127-141 mm h^{-1} in ferns.

Duckett *et al*. (2013) point out that these pegged rhizoids fulfill the three criteria for conduction defined by Raven (1993): dead at maturity, specialized walls, preferential conduction of water. Duckett and coworkers added a fourth criterion, the ability to maintain functional integrity through periods of dehydration, as in moss hydroids (Ligrone *et al*. 2000). This maintenance of functional integrity becomes a problem, because unlike trees and stems, there is no adjacent cell to help in rehydration.

Xerophytic liverworts such as ***Riccia*** (Figure 44), ***Reboulia*** (Figure 6), ***Targionia*** (Figure 45), ***Asterella*** (Figure 46), and ***Lunularia*** (Figure 53-Figure 54) have both **tuberculate** (pegged) and smooth rhizoids, scale leaves, and well-defined assimilatory and storage zones, whereas moisture-loving ***Dumortiera*** (Figure 41), ***Cyathodium*** (Figure 43), ***Pallavicinia*** (Figure 47) (Daniels 1998), ***Monoclea*** (Figure 48), ***Neohodgsonia*** (Figure 49), and some aquatic ***Riccia*** species (Figure 50-Figure 51) (Duckett & Ligrone 2003) lack these complex structures. Even in ***Marchantia*** (Figure 34-Figure 35), with its strong midrib, water moves externally along the midrib and in the spaces between the scales, providing a film of water throughout the thallus (McConaha 1941).

Figure 44. ***Riccia sorocarpa*** thallus section showing ventral rhizoids, dorsal midribs, and internal photosynthetic layer. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 45. ***Targionia hypophylla***, a thallose liverwort with pegged and smooth rhizoids and scales. Photo by Des Callaghan, with permission.

Figure 46. ***Asterella saccata*** showing scales around the thallus margin. Photo by Jan-Peter Frahm, with permission.

Figure 47. ***Pallavicinia lyellii***, a simple thallus lacking the complex scales and two types of rhizoids. Photo by Des Callaghan, with permission.

Figure 48. ***Monoclea*** cf. ***gottschei*** with the salamander ***Oedipina gracilis***. This liverwort is a simple thallus lacking the complex scales and two types of rhizoids, but clearly having a waxy surface. Photo by William Leonard, with permission.

Figure 49. ***Neohodgsonia mirabilis*** with archegonial heads in New Zealand, a simple thallus lacking the complex scales and two types of rhizoids. Photo by Odontites, through Creative Commons.

Figure 50. ***Riccia fluitans***, an aquatic species with no rhizoids or scales. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

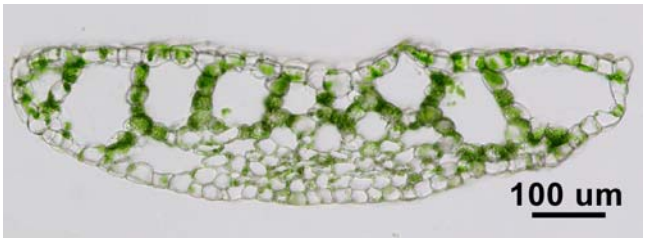


Figure 51. Cross section of thallus of ***Riccia fluitans***, an aquatic species with no rhizoids or scales; note the large air spaces for gas exchange and flotation. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

In ***Preissia*** (Figure 39), it appears that the numerous rhizoids compensate for a less compact arrangement of the capillary system. Volk (1984) found that ***Riccia*** (Figure 52), a common inhabitant of ephemeral habitats such as flood plains, absorbs water by capillary action among the rhizoids and the lower surface of the thallus. The thallus rolls or folds when it is dry, thus exposing the rhizoids, scales, and/or cilia. These serve both to absorb water and to provide a reflective surface that protects the **chlorophyllous** (photosynthetic) cells of the thallus. In others, a crystalloid crust serves a similar function of reflectance.

Fungal Partners

Despite their roles in anchorage (smooth rhizoids) and conduction (pegged rhizoids), it seems that smooth rhizoids have a major role in the **endosymbiosis** (internal partnership) of fungi (Pressel *et al*. 2010, 2012; Duckett *et al*. 2013). Our understanding of the value of this partnership is meager. In other plants, fungi serve to increase absorptive surface area and often tap into the roots of a tracheophyte, transferring carbohydrates from plants that reach the canopy to plants that are in the low light beneath them. Such a role remains unknown in the bryophytes, but I am confident that we shall discover that at least some species have this advantage. After all, these partners have been around much longer than the flowering plants, known as **hemiparasites**, that have succeeded in developing this life style. In the leafy liverworts, infections occur exclusively through rhizoids with the Ascomycete ***Rhizoscyphus ericae*** as partner (Read *et al.* 2000; Pressel *et al*. 2008a, c). This is a widespread fungus that lacks host specificity. Fungal partnerships are discussed in more detail below under "Mosses and Leafy Liverworts."

Main Thallus Structure

Midribs: Seeing the midribs in valleys (Figure 44, Figure 52) makes me think that water is directed from the thallus surface to the midrib in some species. I have to wonder if water is absorbed more easily there. Once the water enters the midrib cells, it can be carried to more distant parts of the thallus more quickly than by travelling through other, shorter thallus cells. It has fewer cell walls to cross.

Figure 52. ***Riccia nigrella*** showing valleys with midribs that could be used to direct water into the thallus. These valleys facilitate folding when dry. Photo by Des Callaghan, with permission.

The rib of ***Lunularia cruciata*** (Figure 53-Figure 54) has parenchymatous cells in which plasmodesmata-derived pores are grouped in small, sparse fields, particularly on transverse oblique walls (Giordano *et al*. 1989). This suggests that the rib cells may be able to transport water and other substances through the ends of cells. These longer cells should, then, move water faster than crossing the many walls of the hyaline parenchyma (Figure 55). Giordano and coworkers suggested that the reticulate cells may serve a water-holding role and facilitate lateral distribution by both **symplastic** (within protoplasm) and **apoplastic** (outside the protoplasm, in intercellular spaces) conduction of substances arriving by way of the rib. They suggest this mechanism may be present in all members of **Marchantiales** with this thallus construction.

Figure 53. ***Lunularia cruciata*** indicating rib area (**arrows**). Photo by Luis Nunes Alberto, through Creative Commons.

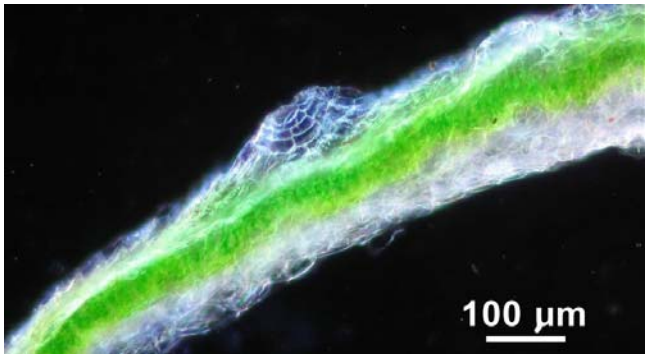


Figure 54. ***Lunularia cruciata*** thallus showing pore and hyaline parenchyma cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

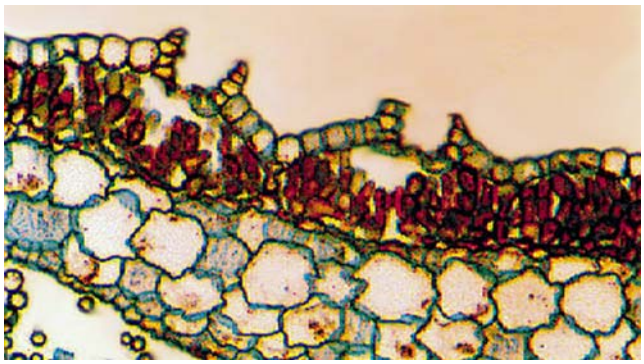


Figure 55. Cross section of ***Marchantia*** thallus, showing hyaline parenchyma and two pores. Photo from Department of Botany Teaching Collection, Michigan State University, East Lansing, MI, USA.

Rolling Thallus: Midribs may also facilitate rolling of the thallus by creating a crease through the middle of the plant (compare Figure 52 to Figure 56). Rolling conserves water, but at the same time it exposes the ventral surface where scales help to conserve water (Figure 56). Such rolling is common in species of ***Riccia*** (Figure 56, Figure 84-Figure 85), often supplemented with hairs that cover the thallus.

Figure 56. ***Riccia nigrella*** with dry thallus folded at the midrib. Compare this to Figure 52. Photo by Michael Lüth, with permission.

Internal Conduction: The liverwort ***Lunularia cruciata*** (Figure 53-Figure 54) may exemplify a means for water movement between cells in thallose liverworts (Giordano *et al*. 1989). The thallus has **reticulate** (like network) **hyaline** (colorless) **parenchyma** (thin-walled) cells (Figure 54) with between wall thickenings, large **primary pit fields** (thin area in walls of many cells in which one or more pits usually develop) with numerous pores derived from **plasmodesmata** (narrow threads of cytoplasm that pass through cell walls of adjacent cells and allow communication between cells) on unthickened areas of walls.

Spongy Thallus

The spongy thallus of ***Riccia cavernosa*** (Figure 57) looks like it should have an important adaptive value. The basal layer gives rise to a layer of irregular vertical column of chlorophyllose cells overtopped by colorless epidermal cells (*Riccia cavernosa* 2012). While these might seem to have functions similar to those of ***Exormotheca*** (Figure 59-Figure 61), instead some of these epidermal and chlorophyllose cells collapse, creating large air spaces at several levels in the tissue of the thallus. The light that reflects from these cavities has a glistening appearance. But does this sequence of events provide any advantage to the plant? At first glance, it looks very much like a sponge, but at a much smaller scale.

Figure 57. ***Riccia cavernosa*** showing spongy thallus. Photo by Richard Orr, with permission.

The basal pad of isodiametric cells gives rise to a layer of irregular vertical columns of chloroplast-containing cells, topped by colorless oval epidermal cells (*Riccia cavernosa* 2012). But early in development, large air spaces develop at several levels in this tissue due to the collapse of some of the epidermal and chlorenchyma cells. The light reflecting inside these cavities gives the thallus its characteristic glistening appearance.

Ballooning of Epidermis

In some species of ***Riccia*** (Figure 29-Figure 32) the epidermal cells are balloon-like (Figure 58) and may contribute to protection from desiccation (Kürschner 2004). However, I wonder if those cells don't provide a greater role in focussing the light into the thallus to the chlorophyllous cells when the thallus is hydrated. Kürschner suggested that the chimney-like, hyaline air chambers of ***Exormotheca*** (Figure 59-Figure 61) may also have a function in protecting the underlying tissue during dehydration.

Figure 58. ***Riccia atromarginata*** showing balloon epidermal cells. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 59. ***Exormotheca pustulosa*** showing ballooning of epidermal cells. Photo by Jonathan Sleath, with permission.

Figure 60. ***Exormotheca welwitschii*** showing ballooning of epidermal cells. Photo by Michael Lüth, with permission.

Figure 61. ***Exormotheca*** thallus section showing columns of photosynthetic tissue and ballooning surface. Photo by Wilhelm Barthlott, with permission.

Cuticle

For many years we considered the cuticle to be absent in bryophytes, with scattered references referring to them, but with no definitive data on their surface chemistry. However, not only are waxy cuticles present, but waxes are present on the leaves and thalli, albeit in less noticeable quantity than in tracheophytes. In fact, Brockington *et al*. (2013) considered the cuticle in the thallose liverwort ***Marchantia polymorpha*** (Figure 34) to be "an overlooked innovation in land plants."

Knowing that ***Marchantia polymorpha*** (Figure 34-Figure 35) has a cuticle, one should not be surprised that the shiny thallose liverwort ***Monoclea gottschei*** (Figure 48) and the hornwort ***Notothylas orbicularis*** (Figure 62) have an **osmiophilic layer** (refers to lipid-containing bodies; a cuticle) with structural resemblance to that of early developmental stage tracheophyte cuticles (Cook & Graham 1998).

Figure 62. ***Notothylas orbicularis***, a species with a demonstrated osmiophilic layer, *i.e.* cuticle. Photo by Michael Lüth, with permission.

What emerged as more interesting in this study is that not all of these bryophyte versions are created equal. In the liverwort ***Monoclea gottschei*** (Figure 48) the layer is nodular, in the hornwort ***Notothylas orbicularis*** (Figure 62) it can be either nodular or sheetlike, and in ***Sphagnum fimbriatum*** (Figure 63) it is sheetlike with regular ridges that run parallel to the edges of the "thalli" (Cook & Graham 1998). It appears that cuticle is ancient, and Cook and Graham suggest that it may have arisen before the charophycean algae and bryophytes diverged from their common ancestor.

Figure 63. ***Sphagnum fimbriatum***, a species with a cuticle. Photo by Michael Lüth, with permission.

The thallose liverwort ***Plagiochasma rupestre*** (Figure 64) has a non-wettable thallus endowed with hydrophobic wax globules, preventing it from absorbing water through its surface (Kürschner 2004). Instead, it uses the pegged rhizoids for water uptake, a phenomenon that may be common to all members of **Marchiantiales**. This dorsal surface wax may have an important role in preventing water logging in the underlying air chambers.

Figure 64. ***Plagiochasma rupestre*** thallus showing smooth rhizoids on edges and waxy surface. Photo by Hugues Tinguy, with permission.

The presence of a cuticle on the upper surface of a thallose liverwort raises the question of water absorption in these species. But based on the foregoing discussions of scales and rhizoids, we know that it occurs predominantly through the ventral surface, facilitated by the scales and rhizoids. Presumably there is no cuticle on that surface, but that does not yet seem to have been demonstrated.

In the **Polytrichaceae**, waxes may serve a different function. Rather than keeping water in, the leaves of these species must keep water out to permit maximum photosynthesis (Figure 65) (Clayton-Greene *et al*. 1985). Their lamellae provide extra photosynthetic tissue, but water can become trapped there due to the capillary spaces. This protection from water is further enhanced by the rolled margins (Figure 66) of species like ***Polytrichum juniperinum*** (Figure 67).

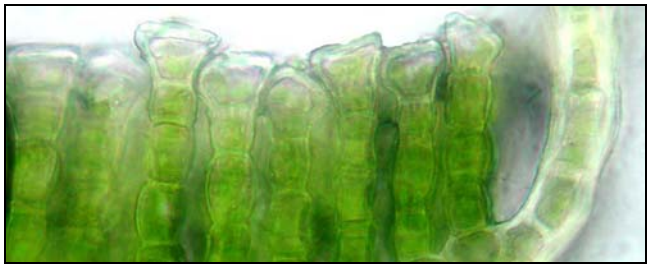


Figure 65. ***Polytrichastrum pallidisetum*** showing leaf lamellae where photosynthesis occurs. Note thickened end cells that help keep water from entering capillary spaces between lamellae. Photo by Michael Lüth.

Figure 66. ***Polytrichum hyperboreum*** showing inrolled leaf margins that cover the lamellae and protect them from water logging in the capillary spaces. Photo by Michael Lüth, with permission.

Figure 67. ***Polytrichum juniperinum*** showing lamellae and leaf edge that is rolled over them to help keep water out of the capillary spaces. Photo by John Hribljan, with permission.

Pores

The wonderful ventral efficiency of rhizoids and scales is often challenged by a dorsal (upper) surface that does little to conserve water. In fact, this dorsal surface water loss may facilitate the movement of water and nutrients through the plant, as it does in leafy tracheophytes. The pores on the dorsal surface function much as do the stomata of tracheophyte leaves in losing water (Figure 55, Figure 73). Maier-Maercker (1982) found that ***Conocephalum conicum*** (Figure 36) loses water through transpiration from these dorsal thallus pores (Figure 68), accumulating radioactively labelled ions in the cells surrounding the air pores.

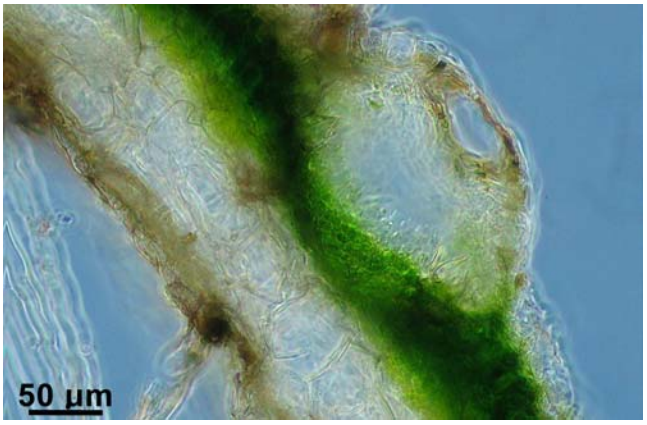


Figure 68. ***Conocephalum conicum*** pore section. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

The single-layered leaves of leafy liverworts and most mosses preclude the presence of stomata there as they would provide only a hole through the leaf, hardly a useful character. Even multicellular layers of moss leaves have no use for stomata because there is no chamber where the gases may gather. But thallose liverworts meet those two requisites – multiple cell layers (Figure 69) and chambers internally (Figure 70). Furthermore, as mentioned above for ***Marchantia polymorpha*** (Figure 34), the thallus has a cuticle that can at least to some degree repel water. Hence we might presume that it likewise is somewhat resistant to gas exchange, creating a problem for photosynthesis.

Raven (2002) provided evidence that stomata evolved from pores of an epidermis over plant organs at least three cell layers thick, with intercellular gas chambers, and with a cuticle. In this anatomical arrangement, the presence of pores most likely confers an adaptive advantage for photosynthesis.

Figure 69. ***Conocephalum conicum*** photosynthetic cells under epidermis, showing thallus that is more than three cell layers thick. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

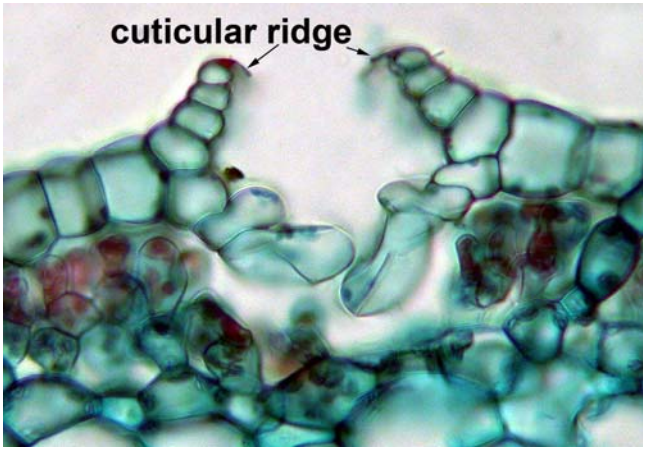


Figure 70. ***Marchantia polymorpha*** thallus pore in longitudinal section, showing cuticular ridge. Cells stained with purple are photosynthetic cells. Note the chamber beneath the pore. Photo by George Shepherd, through Creative Commons.

In some cases, thalloid liverworts seem to lose great quantities of water, 2-3 times that of leaves of the weeping birch tree *Betula pendula* (McConaha 1941). Under extreme conditions, they transpire equivalent to their total content of water in an hour. One reason for this rapid transpiration rate is the areolation of the thallus that creates a large surface area where water can be lost. The pores in these thalli (Figure 71), permitting contact between outside air and internal moisture, have only limited ability to close, thus being a major source of water loss. McConaha (1941) claims that the ventral specializations compensate for the losses from dorsal areolation and pores. Proctor (1980) found that these areolate thalli have internal resistances similar to those of mesophytic leaves of flowering plants (Proctor 1980). As in the flowering plants, the water loss is correlated with pore size and density.

Figure 71. ***Marchantia chenopoda*** pores showing rim of cuticle projecting into the pore opening. The polygons outline the internal chambers that create the areolation. Photo by George Shepherd, through Creative Commons.

But the photosynthetic cells project into these chambers beneath the pores (Figure 70), and flooded cells cannot exchange gases freely. It should be no surprise then that the openings themselves prevent the entrance of water into the chamber. Their small size (Figure 71) contributes to this. In the absence of a wetting agent, the cohesive forces of water make the aggregation of water molecules too large to enter the holes. This smallness of the hole is further enhanced by the presence of a **cuticular ridge** (Figure 71-Figure 74) that not only narrows the entrance, but that also repels the water, *i.e.* is **hydrophobic**.

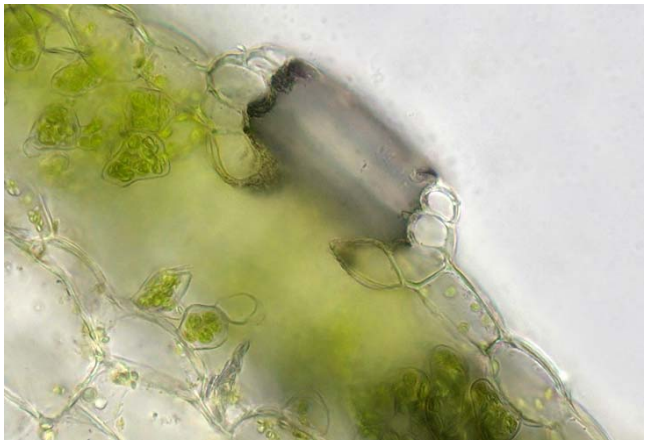


Figure 72. ***Marchantia polymorpha*** pore in longitudinal section. Photo by Walter Obermayer, with permission.

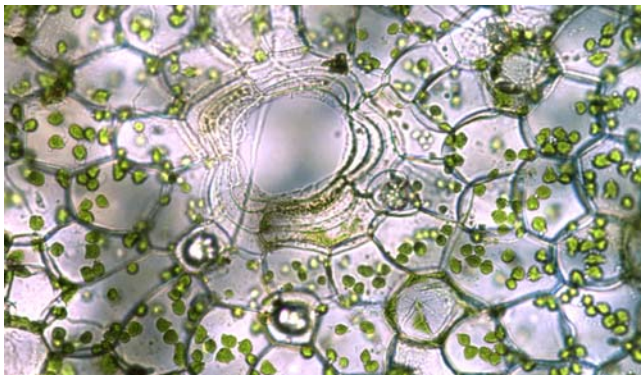


Figure 73. Pore opening in thallus of ***Cyathodium cavernarum***, showing cuticular ridge. Photo courtesy of Noris Salazar Allen.

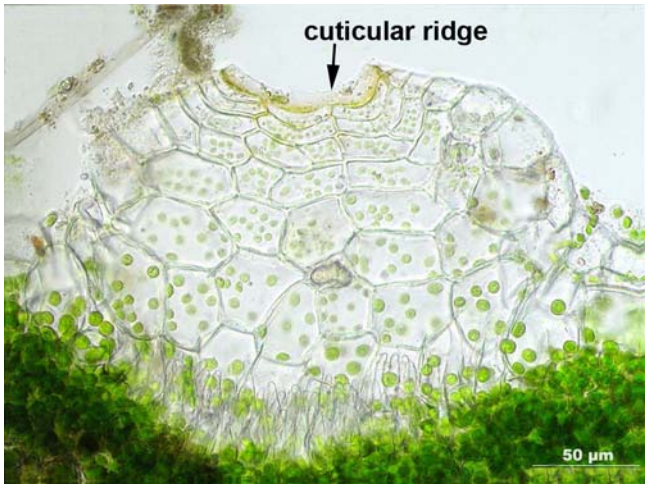


Figure 74. ***Conocephalum conicum*** pore longitudinal section showing the cuticular ridge. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

Schönherr and Ziegler (1975) found that of the fourteen thallose liverwort species they studied, twelve of them have such **hydrophobic** (repelling water) ridges, and that **cutin** is present in these ridges. Furthermore, the researchers considered the pores in these species to be "perfect" in keeping water out of the thallus. ***Plagiochasma rupestre*** (Figure 75) and ***P. peruvianum***, on the other hand, lack such ridges and liquids are able to enter the thallus through the pores. While the waxes and small size of the holes keep water out, the water in vapor form within the thallus is able to escape through the pores, along with oxygen, while CO_2 enters. Therefore, the openings must maximize carbon gain per unit water loss (Raven 2002).

Figure 75. ***Plagiochasma rupestre***, a thallose liverwort with no cuticular ridge on its pores, but with a waxy cuticle on the thallus. Photo by Michael Lüth, with permission.

While these pores are an advantage for a hydrated, photosynthesizing thallus, they are a liability for a drying thallus due to the loss of water vapor. But at least some of the liverworts seem to be able to partially control the opening. This is accomplished by curving of the stack of cells surrounding the opening, creating partial closure. In ***Preissia*** (Figure 76-Figure 77, Figure 39), the barrel-shaped pores (Figure 77) change shape to accomplish control of water loss (Lepp 2008). When turgid with water, the cells at the bottom of the barrel keep the pore open, but when the conditions are dry, the cells lose their turgor and collapse, narrowing the opening at the bottom of this barrel. Those in ***Marchantia*** (Figure 70-Figure 72) behave similarly (Raven *et al*. 2005). A further aid, presumably, is the ability to fold the upper side of the thallus inward, as discussed above, creating a less exposed surface and slowing the rate of water loss.

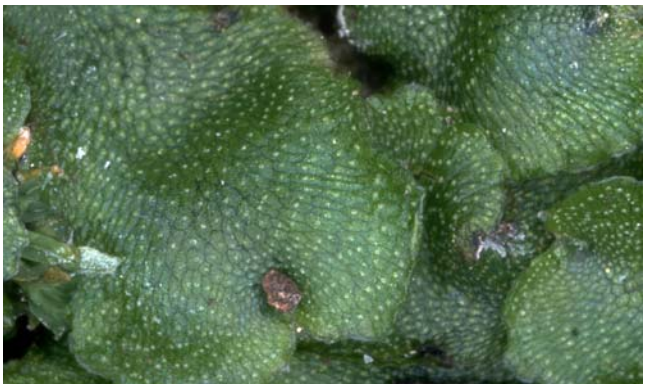


Figure 76. ***Preissia quadrata*** thallus showing pores (light-colored dots). Photo by Jan-Peter Frahm, with permission.

Figure 77. ***Preissia quadrata*** thallus showing pores with cuticular ridges. Photo by Kristian Peters, with permission.

Archegoniophores and Antheridiophores

In thallose liverworts, the horizontal orientation cannot serve as a model for water movement in the vertical **archegoniophore**. As determined by Duckett *et al*. (2013), the archegoniophore has more efficient water movement than the stems of mosses. They attribute this to the efficiency of movement through the rhizoids and capillary spaces among them, as well as the hydrophobic nature of the thallus surface surrounding these rhizoids (Figure 78).

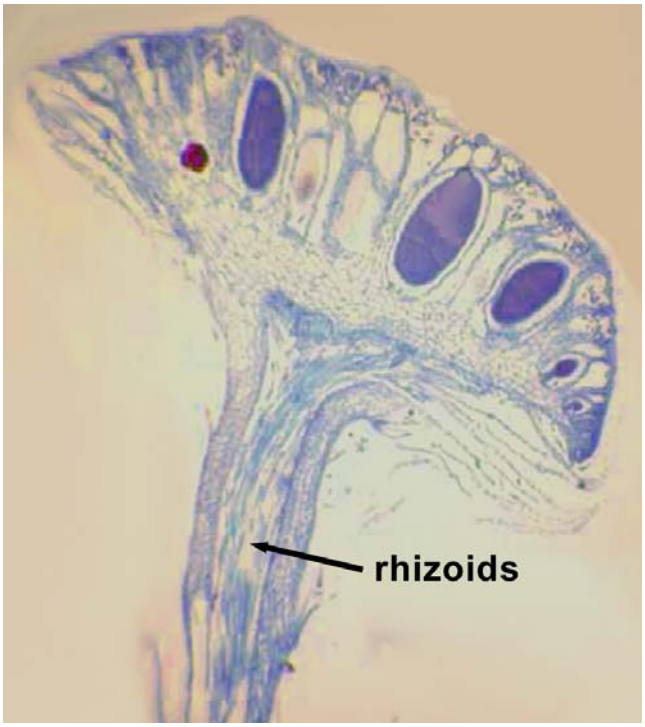


Figure 78. ***Marchantia polymorpha*** antheridial head showing location of rhizoids within the antheridiophore. Photo from Botany website of the University of British Columbia, BC, Canada, with permission.

The importance of this rhizoid-thallus combination for the archegoniophore is suggested by comparing its response to drought with that in mosses. For example, ***Marchantia*** (Figure 79) archegoniophores and heads can remain fully hydrated for several hours in full sunlight at 20-30°C while the shoots of neighboring ***Polytrichum commune*** (Figure 80) with their bases in standing water become wilted and must have added rainwater to recover (Duckett *et al.* 2013), suggesting an efficient system of transport in the archegoniophore.

Figure 79. ***Marchantia polymorpha*** archegoniophore and archegonial head. Note rhizoids along stalk (archegoniophore) where they emerge from the folded thallus that makes the stalk. Photo by George Shepherd, through Creative Commons.

Figure 80. ***Polytrichum commune***, a moss that wilts in full sun despite its wet substrate and colonial habit. Photo by Michael Lüth, with permission.

Duckett *et al*. (2013) suggest that the length of the archegoniophore is limited to a maximum of 7-10 cm (in ***Conocephalum***; Figure 81) because of the problems of air bubbles in the mucilaginous matrix surrounding the pegged rhizoids in the grooves of the archegoniophore, a condition analogous to an embolism in the vessels of tracheophytes (see Canny 2001 a, b).

Figure 81. ***Conocephalum conicum*** with tall archegoniophore. Photo by Adolf Ceska, with permission.

Antheridiophores provide yet a different mechanism (Duckett & Pressel 2009). Present only in the genus ***Marchantia***, they present an antheridial head (Figure 82) on a stalk that is much shorter than that of the mature archegoniophore, rarely exceeding 30 mm. Rather than being hydrophobic, the heads are highly hydrophilic and absorb raindrops much like a sponge. Whereas upward flow occurs in the stalk during dry periods, downward flow carries the motile sperm toward the archegonia on immature (shorter) archegoniophores (Figure 83) during rainfall.

Figure 82. ***Marchantia polymorpha*** with antheridial heads where water is absorbed like a sponge. Photo by Rudolf Macek, with permission.

Figure 83. ***Marchantia polymorpha*** young archegoniophores that receive sperm from temporarily taller antheridiophores. Photo by Rudolf Macek, with permission.

Dormancy

Volk (1984) found that when ***Riccia*** (Figure 84-Figure 85) has less than 150 mm of rainfall per year, it requires other means to survive, and it seems that dehydration/dormancy is the solution (Figure 84-Figure 85). Some thallose ***Riccia*** species are able to survive up to 7 years in this dehydrated state, enduring temperatures up to 80°C. The annual species compensate for this water loss by producing huge numbers of spores, taking advantage of their ornamentation for distribution by animals.

Figure 84. ***Riccia sorocarpa*** in a fresh, active state. <www.aphotofauna.com>, with permission.

Figure 85. ***Riccia sorocarpa*** in a dry, dormant state. Photo by Michael Lüth, with permission.

Mosses and Leafy Liverworts

We typically think first about structural adaptations for water retention, so we will start there. Sarafis (1971) considered that ***Polytrichum commune*** (Figure 80) had four ways of controlling water loss:

1. Community level – gregariousness
2. Plant level – leaf density & size, plant height
3. Organ level – leaf movement and inrolling
4. Molecular level – wax on leaf surface

These all relate to structure, but internal structure and cellular level physiology are additionally important.

Vitt *et al*. (2014) consider the avoidance strategies of mosses to differ somewhat from those of liverworts and hornworts. Leaf arrangement has greater variation in mosses. Xerophytic leaves and stems often possess large **trigones** (thickenings in corners of cell walls; Figure 86) and nodular intermediate thickenings on interior walls, forming branched **vittae** (like costa, but 1 cell thick) in the lamina of leaves such as those of ***Herbertus aduncus*** (Figure 87-Figure 88) that enhance water uptake and storage, often with protruding **papillae** on their dorsally exposed, superficial walls. Xerophytic stem cells are thick-walled. These wall adaptations consist mostly of hemicelluloses, pectins, and cellulose, substances that would facilitate apoplastic water uptake, movement, and retention (Proctor 1979a). Water spreads over the leaves that have papillae, filling the spaces next to the leaf surface, but leaving the tips of the papillae dry to facilitate gas exchange. In taxa from moist but intermittently dry habitats, the outer cell walls are typically exposed but water-repellent. In ***Nowellia*** (Figure 89), ***Marsupella*** (Figure 90), and ***Solenostoma*** (Figure 91) with concave, overlapping leaves, surface tension may account for this repellent property (Proctor, 2009), but in other cases, thin coats of epicuticular waxes are hydrophobic (Duckett & Soni 1972; Heinrichs *et al*. 2000). And what is the function of the pore-like connections between cells (Figure 92) in more mesic mosses like ***Dicranum scoparium***?

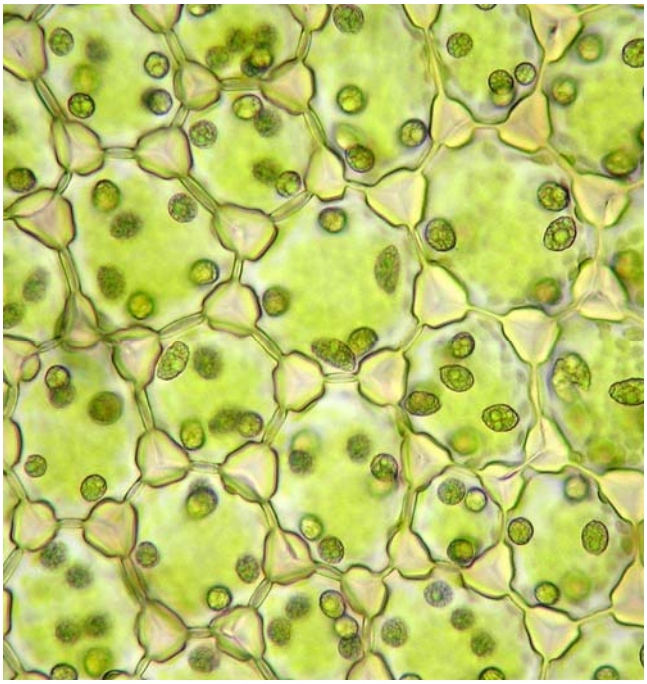


Figure 86. ***Heteroscyphus conjugatus*** leaf cells showing trigones. Photo by David Tng, with permission.

Figure 87. ***Herbertus aduncus*** in a temperate rain forest. Photo by Ian Cruickshank, through Creative Commons.

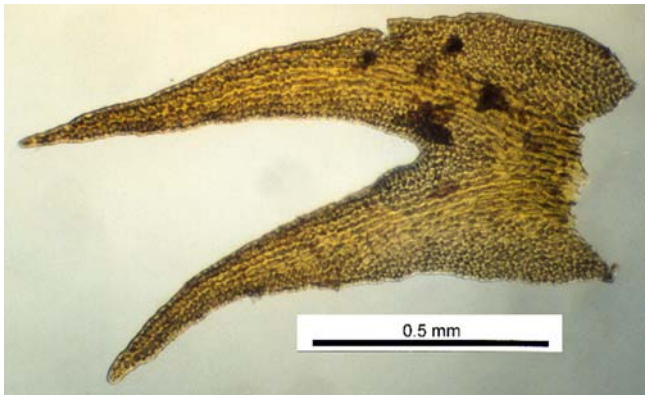


Figure 88. ***Herbertus aduncus*** leaf showing vitta in each leaf lobe. Photo by David H. Wagner, with permission.

Figure 89. ***Nowellia curvifolia*** showing deeply concave, overlapping leaves where water becomes trapped. Photo by Štěpán Koval, with permission.

Figure 90. ***Marsupella emarginata*** showing concave leaves that can trap a drop of water. Photo by Hermann Schachner, through Creative Commons.

Figure 91. ***Solenostoma hyalinum*** showing overlapping, concave leaves that can trap water. Photo by David T. Holyoak, with permission.

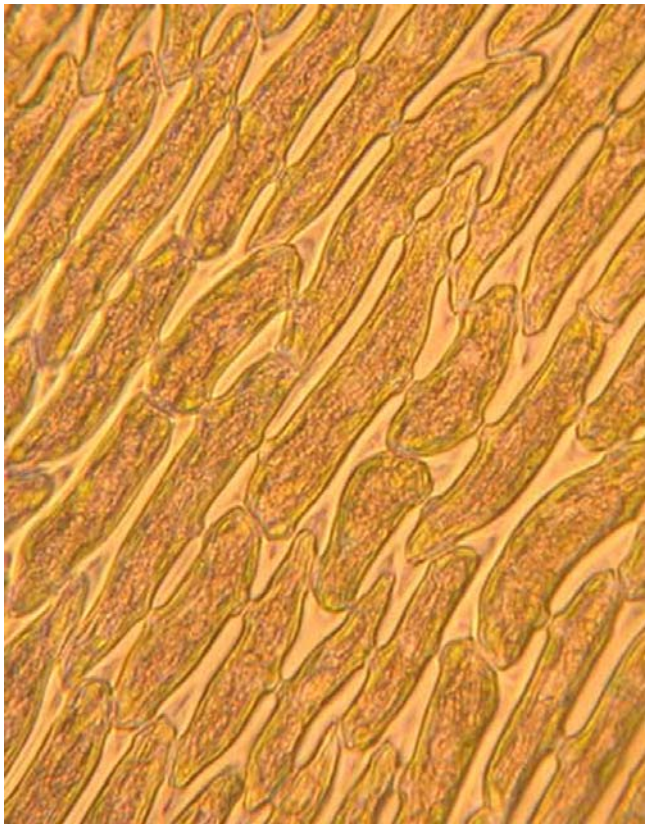


Figure 92. ***Dicranum scoparium*** cells showing pore-like connections between cells. Photo from Botany website, UBC, with permission.

Bayfield (1973) considered that water loss in endohydric ***Polytrichum commune*** (Figure 80) to be controlled by its leaf arrangement changes. This was accompanied by changes in water potential deficit of the shoots, with conduction being primarily internal under high evaporative flux and external under moderate flux. The ectohydric ***Racomitrium lanuginosum*** (Figure 93), by contrast, has little control over its water loss.

Figure 93. ***Racomitrium lanuginosum***, an ectohydric moss with little control over water loss. Photo by Hermann Schachner, through Creative Commons.

After examining 439 taxa of pleurocarpous mosses, Hedenäs (2001) reported that most differences in taxonomic character states between environments relate to two functions: 1) water conduction and retention; 2) dispersal. Those morphological characters that seem important for water relations relate to **stem central strand** (Figure 94-Figure 95), **leaf costa type** (Figure 96-Figure 97), **paraphyllia** (Figure 98), **pseudoparaphyllia** (Figure 99), **alar cells** (Figure 96), and **leaf orientation** (Figure 20-Figure 24, Figure 100-Figure 102). The latter two also relate to the **ability to change leaf orientation during drying** (Figure 103-Figure 105). But if acrocarpous mosses (upright mosses with terminal sporophytes) had been included, surely many more characters might be added, as it is mostly acrocarpous mosses that occupy the most xeric of habitats.

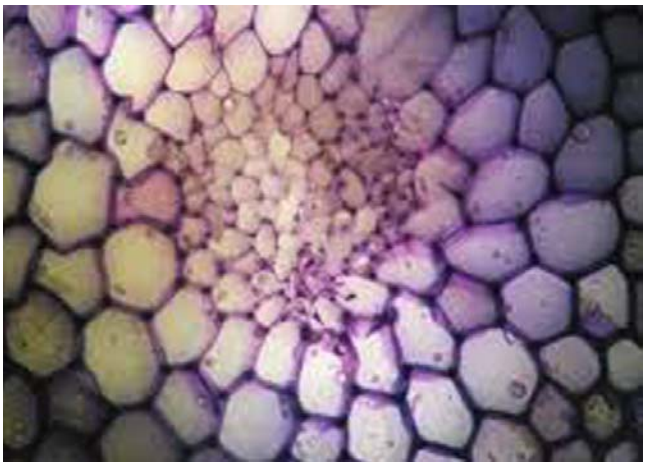


Figure 94. ***Haplomitrium*** sp. stem cross section with central strand that disappears in wet habitats. Photo by Rachel Murray and Barbara Crandall-Stotler, with permission.

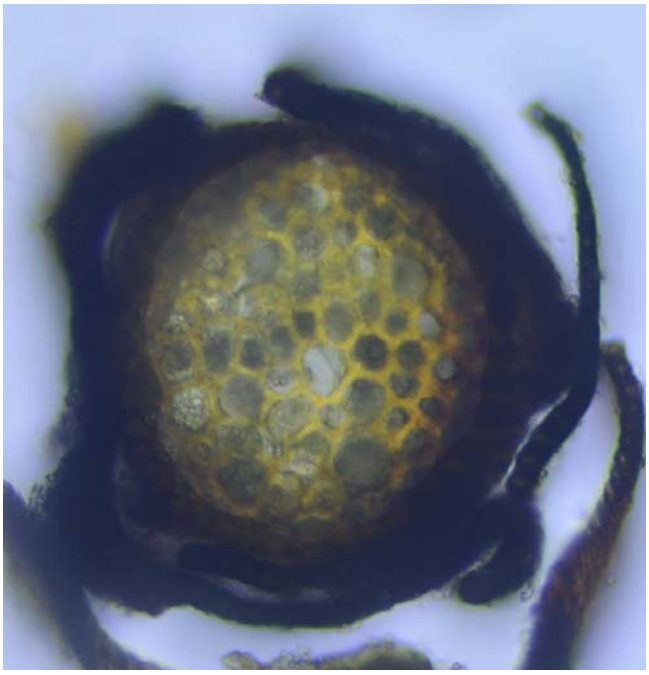


Figure 95. ***Andreaea rothii*** stem cs showing absence of central strand of conducting cells. Photo by Randal, through Creative Commons.

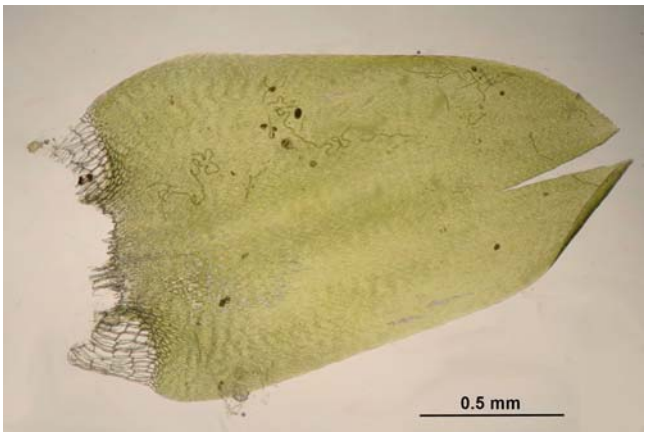


Figure 96. ***Calliergonella cuspidata*** leaf showing alar cells and absence of costa. Swelling of alar cells upon hydration can physically push the leaf away from the stem. Photo by Hermann Schachner through Creative Commons.

Figure 97. ***Bryhnia-graminicolor*** leaf showing costa and prorate cells. Photo by Bob Klips, with permission.

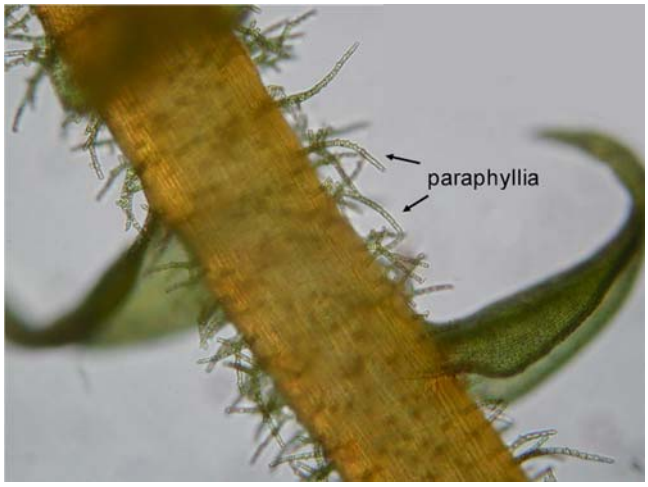


Figure 98. ***Thuidium paraphyllia*** on stem. Photo by Paul Davison, with permission.

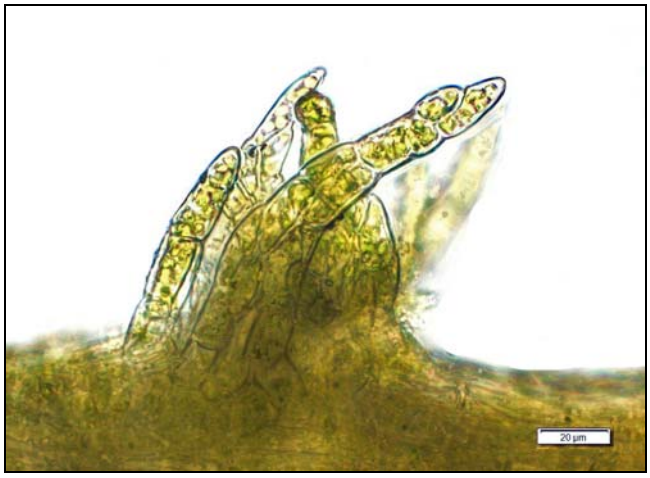


Figure 99. ***Homomallium mexicanum*** pseudoparaphyllia surrounding a branch bud. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 100. ***Calypogeia muelleriana*** showing overlapping leaves in two rows, making the branches flattened. Photo from Botany Website, UBC, with permission.

Figure 101. ***Thelia asprella*** showing leaves adhering tightly to stems and branches (**julaceous**). Photo by Bob Klips, with permission.

Figure 102. ***Polytrichum formosum*** male showing spreading leaves in wet condition. Photo by Andrew Spink, with permission.

Figure 103. ***Polytrichum formosum*** dry, showing leaves tightly wrapped around the stem. Photo by Sharon Pilkington, with permission.

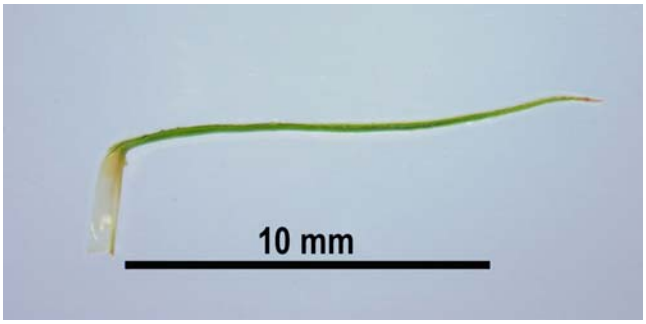


Figure 104. ***Polytrichastrum formosum*** leaf showing the hyaline basal cells that facilitate the spreading of the leaf when hydrated. Photo courtesy of Norbert Ethan.

Figure 105. ***Polytrichastrum formosum*** leaves with lowest leaf holding water at its base.. Photo courtesy of Norbert Ethan.

One feature of structural adaptations is that many are **plastic**, *i.e.* they can change depending on their growing conditions (Buryová & Shaw 2005). For example, **conducting strands** are absent in the liverworts ***Moerckia flotoviana*** (Figure 106) and ***Haplomitrium hookeri*** (Figure 94, Figure 107) under high humidity or liquid culture (Hébant 1977). **Hair points** (colorless, hair-like extensions at leaf tip) of ***Schistidium apocarpum*** (Figure 108) likewise are absent in humid conditions (Figure 109).

Figure 106. ***Moerckia blyttii***, a thallose liverwort that doesn't develop conducting cells in wet habitats. Photo by Michael Lüth, with permission.

Figure 107. ***Haplomitrium hookeri***, a liverwort that doesn't develop its central strand in wet habitats. Photo by Des Callaghan, with permission.

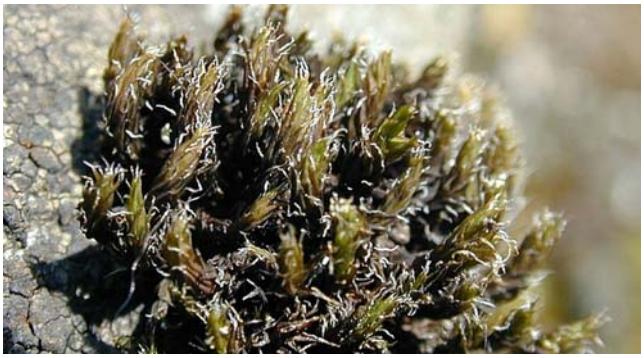


Figure 108. ***Schistidium apocarpum*** with hyaline hair points, on an exposed rock. Photo by Michel Lüth, with permission.

Figure 109. ***Schistidium apocarpum*** without hyaline hair points, growing in a more shaded or moist environment. Photo by Jan-Peter Frahm, with permission.

Rhizoids are less well developed or absent in wet conditions (Smith 1988), even in the same species. In ***Andreaea blyttii*** (Figure 110), increased moisture results in longer, wider leaves that are more curved with longer cells in the basal margin, wider **costae** (midrib of leaf), and longer stems, but with a decrease in number of leaves per stem (Heegaard 1997). Even in typically aquatic taxa such as ***Drepanocladus*** (*sensu lato*), leaves become longer, and falcation (leaf curvature) is lost in submersed leaves (Figure 111) compared to those grown out of water (Figure 112), and the reduced light in submersed conditions results in greater **internode** distances (distances between leaf insertions) (Lodge 1959). A similar response is seen in ***Fontinalis*** (Figure 113). It is interesting that increases in salt concentration increase cell length in this genus. Plasticity itself is an important adaptation.

Figure 110. ***Andreaea blyttii***, a moss that changes its leaf morphology in response to moisture changes. Photo by Michael Lüth, with permission.

Figure 111. ***Drepanocladus aduncus*** with straight leaves resulting from growing under water. Photo by Michael Lüth, with permission.

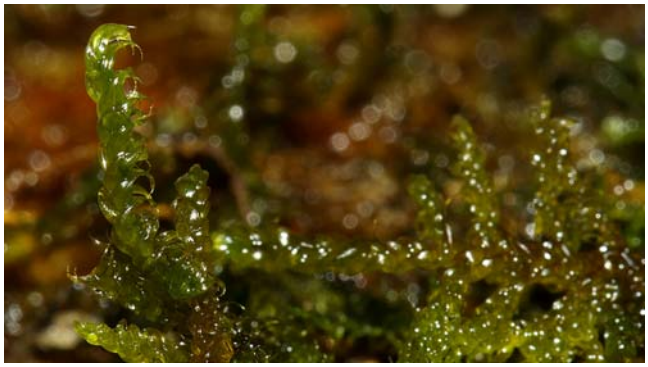


Figure 112. ***Drepanocladus aduncus*** with falcate leaves resulting from growing above water. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

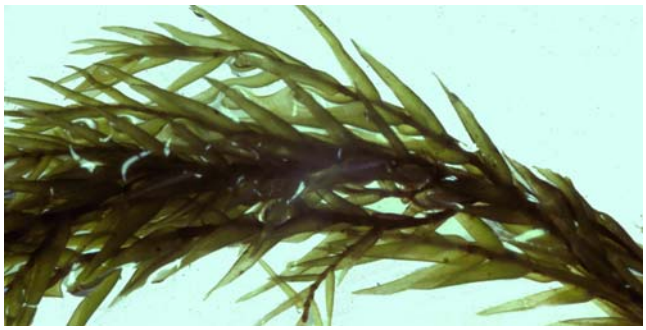


Figure 113. ***Fontinalis novae-angliae*** with normal submersed leaves. Photo by Janice Glime.

Figure 114. ***Fontinalis novae-angliae*** with leaves grown out of water, but wet, exhibiting an atypical falcate habit. Photo by Janice Glime.

Proctor (2010) reminds us that adaptations are subject to phylogenetic constraints and that entire clades may represent adaptations to desiccation. All plants must obtain water and CO_2, but there are multiple ways that this can be achieved.

Growth Form

Growth form is important both for obtaining and retaining water. For example, ***Grimmia pulvinata*** (Figure 115) forms cushions. In this moss, and most likely others with this growth form, size matters. As the clump grows larger, the surface to volume ratio decreases as the larger cushion is accompanied by greater height in the center. This reduces exposed area for gas exchange, but it also reduces the portion exposed to the atmosphere for water loss. In ***Grimmia pulvinata*** the larger cushions have lower area-based evapotranspiration rates due to a higher boundary-layer resistance, but the relative water storage capacity per dry weight does not change (Zotz *et al*. 2000). Consequently, the hydrated period is considerably longer in larger cushions. And as predicted, the CO_2 exchange rate decreases with increasing size of the cushion, with both net photosynthesis and dark respiration decreasing.

Figure 115. ***Grimmia pulvinata*** showing cushion form that conserves water. Photo by Michael Lüth, with permission.

Living in **clumps** affects the ability to gain and to retain moisture. The cushion growth form decreases the surface to volume ratio, thus reducing surface water loss. Clump shape is important in this relationship, particularly in ameliorating wind effects (Proctor 1981; Zotz *et al.* 2000; Rice *et al*. 2001; Rice & Schneider 2004; Rice 2012). But for this system to work, the surface must be as smooth as possible. Greater roughness, resulting from protruding shoots, increases the turbulent air flow, thus increasing evaporation (Proctor 1981; Rice & Schneider 2004). A consequent advantage to the cushion growth form and its retention of water is the slowing of the drying rate (Sand-Jensen & Hammer 2012).

Fortunately, this is a self-regulating condition. As a shoot emerges from the surface, the greater exposure and greater evaporation cause its growth to attenuate. Even herbivores might contribute to this evening, choosing the protruding branch because it is easier to munch on. Hence, the surrounding mosses are able to catch up in length, returning the clump to its smooth structure. Thus, moisture limitations create a more matted clump with a smoother surface, limiting turbulent flow and wind penetration into the clump (Longton 1979; Guerra *et al*. 1992; Nakatsubo 1994).

Nakatsubo (1994) examined the importance of the growth form of sub-alpine mosses in controlling their evaporative water loss. The xerophytic species were comprised of large cushions and compact mats. Mesophytic species from the coniferous forest floor were represented by smooth mats, wefts, and tall turfs. The evaporation rate per dry weight was much less in the xerophytic species than in the mesophytic species. However, when compared on a basal area, the evaporation rates were similar. One advantage of the xerophytic species was their ability to increase weight per basal area without increasing roughness.

The density of the clumps seems to be a plastic character that can be modified by the environment (Gimingham & Birse 1957; LaFarge-England 1996; Bates 1998; Rossi *et al*. 2001). For example, the endohydric ***Polytrichum juniperinum*** var. ***alpestre*** (Figure 116), when in humid habitats, forms a looser clump structure with greater roughness than when in drier habitats (Birse 1957).

Figure 116. ***Polytrichum juniperinum*** var. ***alpestre*** showing contacting leaves of adjoining shoots in moist habitat. Photo by Des Callaghan, with permission.

Elumeeva *et al*. (2011) set out to determine the important characters that maintained moisture in sub-Arctic bryophytes. They found that individual shoot properties seemed to have little effect on colony water retention capacity. That is, leaf cell wall properties, water retention capacity, and desiccation rate of shoots made little difference in the water relations of the colony. Rather, the colony desiccation rate was determined by the density of the water-saturated colony. The desiccation rate of the individual shoot had a marginally significant negative effect on the colony rate.

In ***Polytrichastrum formosum*** (Figure 102), the plants are relatively tall and arranged in loose clumps. Nevertheless, the leaves of adjoining shoots touch, permitting water drops to be trapped by the resulting web. Drop size is an important consideration in conducting experiments using artificial rain. Raindrops usually range 0.5 mm (light rain) to 5 mm (heavy rain) (Best 1950; Brandt 1989; Yakubu *et al*. 2016). Using this size range, Zajączkowska *et al*. (2016) determined that clumps of ***P. formosum*** were able to retain almost 60% of the applied water. When water was applied to the tips, water ran down the shoots and continued to run down until about 2 minutes after the water application ceased. When a drop lands on a leaf, it is more likely to be trapped by the leaf axil or by a leaf. Thus these clumps are benefitted by the catchment web formed by the overlapping leaves.

With these clump advantages, we might ask why so many mosses use other growth forms that are less compact. But moisture is not the only need for the mosses. A compact nature reduces light penetration, reduces CO_2 diffusion into the clump, and increases shoot-to-shoot competition for nutrients (Bates 1989; Rice 2012).

Mulder *et al*. (2001) explored the role of species richness on biomass, then compared it when these communities were exposed to experimental drought. They found that under drought conditions biomass increased with greater species richness. They determined that the interaction was facilitative rather than niche complementarity or the result of sampling effects. Survivorship increased for almost all species as richness increased, with the least drought-resistant species receiving the most benefit in biomass. Rixen and Mulder (2005) found similar results in the Arctic tundra.

Stems and Branches

Most stem and branch arrangements relate to growth form or life form (see Chapter 4-5 of this volume). However, in some cases there is internal or structural modification, exemplifying the plasticity of some bryophytes. For example, ***Philonotis fontana*** (Figure 117-Figure 118) exhibits variation among populations in leaf dimensions, whereas their cell dimensions show little response to differences in water regime or light level (Buryová & Shaw 2005).

Figure 117. ***Philonotis fontana***, a species whose leaf dimensions vary with habitat. Photo by Des Callaghan, with permission.

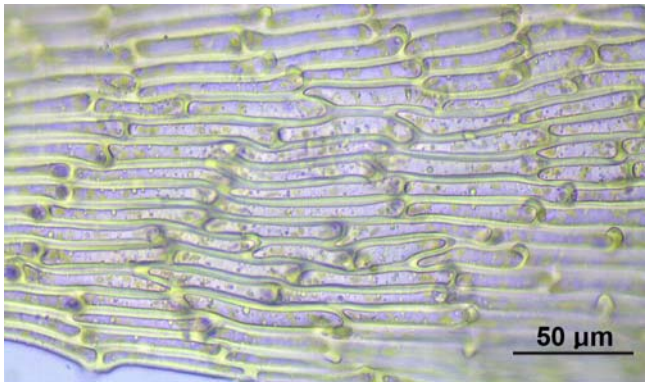


Figure 118. ***Philonotis fontana*** leaf lamina showing cells. These cells vary little in dimensions in different water or light regimes. Photo by Kristian Peters, through Creative Commons.

Overlapping leaves from neighboring shoots help in the support of the mosses in a clump. In stems, the alternating layers of stiff and soft structures, such as those of the **Polytrichaceae**, the strength benefits from the **periodic component materials** (Vincent 2012) that occur in many biological structures and provide stronger mechanical features (Dunlop *et al*. 2011; Fratzl *et al*. 2016). This layering provides the stem with both supportive strength and flexibility that prevents breakage. In ***Polytrichastrum*** (Figure 102) and other members of the **Polytrichaceae**, the thicker cell walls surrounding the stem provide a higher bending strength (Niklas 1992), much like a paper straw compared with a paper lollipop stick (the former bends; the latter breaks). We also know that a lollipop stick made with twisted paper threads is stronger than a solid, non-twisted one, and that many trees likewise gain strength this way. This possibility needs to be explored in bryophytes.

Schröder (1886) considered the ability of moss stems to resprout from a dormant stem to be one method for withstanding prolonged drought. I had a similar experience with the aquatic moss ***Fontinalis dalecarlica*** (Figure 119). In this case, the moss was boiled for 14 hours a day for two

weeks in the lab, then returned to the stream. One year later, new growth was present on this moss that was still attached to the numbered rock used in the boiling treatment. Such ability of stem tips to recover from environmental stresses have been largely overlooked.

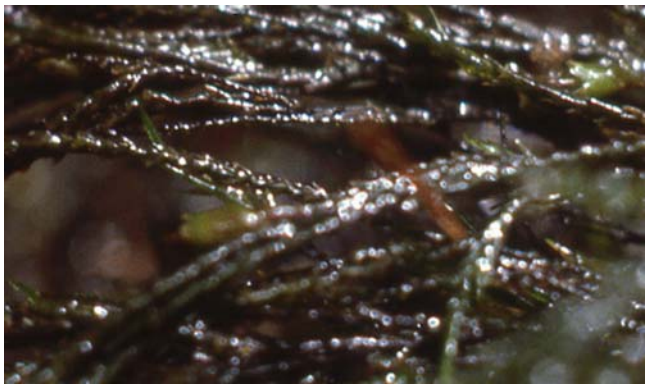


Figure 119. ***Fontinalis dalecarlica*** with from Fox Run, New Hampshire, USA, where a plant similar to this produced a green leaf one year after being boiled for 14 hours a day for two weeks. Photo by Janice Glime.

Sphagnum*:** Li and coworkers (1992) examined the responses of two closely related ***Sphagnum hummock species, ***S. magellanicum*** (Figure 120) and ***S. papillosum*** (Figure 121), to distance from water surface and related these responses to structural and physiological adaptations of the two species. They found that both species increase growth in length as water becomes more available, *i.e.* as the distance from water level decreases. Likewise, dry mass is maximal under wet conditions, with new branches being a major mass contributor, especially in ***S. papillosum***. Furthermore, while experimenting with effects of distance from water on ***S. magellanicum*** and ***S. papillosum***, Li and coworkers found that dry conditions result in wider stems (Figure 122), with thicker hyaline layers (Figure 123-Figure 124), than stems with apical capitula near the water surface (Figure 132), presumably increasing both absorption and water-holding ability.

Figure 120. ***Sphagnum magellanicum***, a hummock species with efficient water movement. Photo by Michael Lüth, with permission.

Figure 121. ***Sphagnum papillosum***, a species with inefficient water movement. Photo by David Holyoak, with permission.

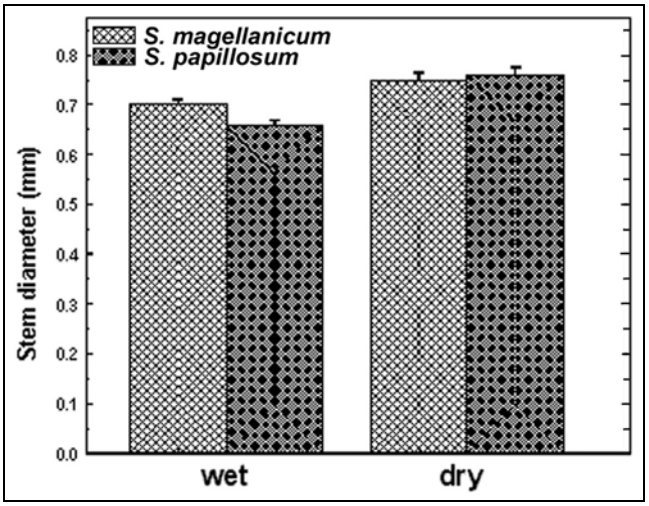


Figure 122. Effect of water level (water availability) on stem diameter in ***Sphagnum magellanicum***, a more desiccation-resistant species, and ***S. papillosum***, a more desiccation-tolerant species. Wet denotes 0 cm initial distance of capitulum from water; dry denotes 10 cm initial distance. Bars represent standard errors; stem diameter in dry treatment is significantly greater (Figure 123) in both species. From Li *et al.* 1992.

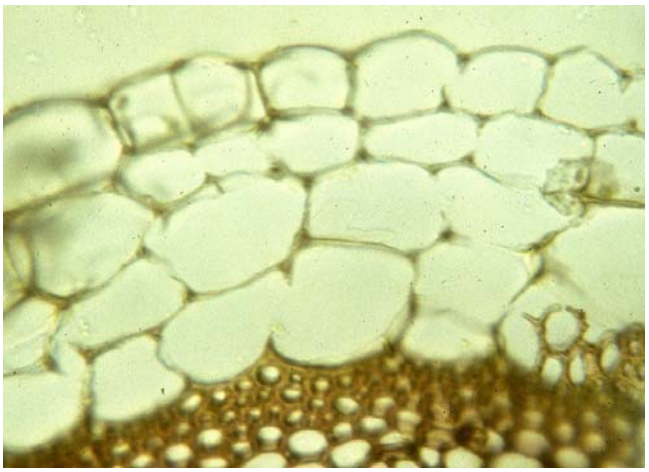


Figure 123. ***Sphagnum magellanicum*** stem at highest level (5) above water surface. Photo courtesy of Yenhung Li.

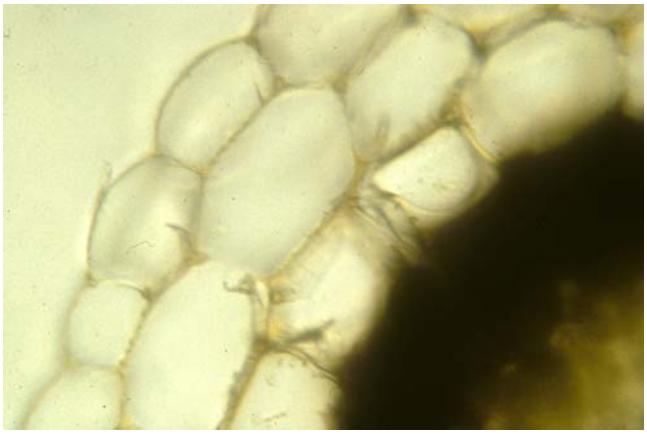


Figure 124. ***Sphagnum magellanicum*** stem at level 3 above water surface. Photo courtesy of Yenhung Li.

Sphagnum has pores in its stem (Figure 125), in most species, and has very rapid movement of water externally up the stem by capillary action, adapting it for its annual cycle of being stranded well above water level in many species. Some species of ***Sphagnum*** have special **retort cells** (Figure 126) on the stems for absorbing water.

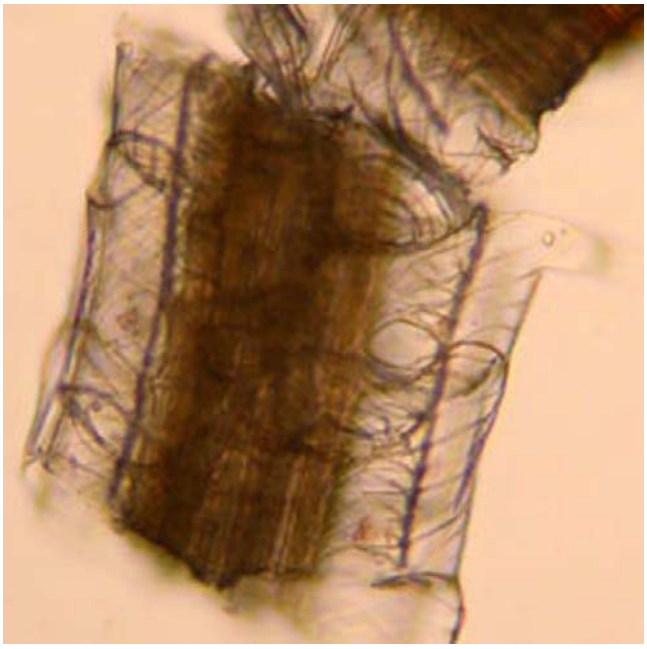


Figure 125. ***Sphagnum papillosum*** stem showing pores. The spiral thickenings of stem cells are unique in this moss. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Daniels (1989) found that while there is little differentiation between **spreading** and **pendant** branches (Figure 127-Figure 128) among ***Sphagnum*** plants growing in pools, hummock plants have more closely spaced **fascicles** (groups of branches), comparatively short spreading branches, and thin, closely appressed pendant branches (Figure 128). Pendant branches help to preserve stem water and maintain the wick effect as water level drops. Daniels determined that leaves of pendant branches on submerged plants photosynthesize actively, while those of hummock plants do not. He found that the two species growing in wet hollows (***Sphagnum cuspidatum***; Figure 129) or as wet carpets (***Sphagnum recurvum***; Figure 130) had the highest percentage of unbranched stems. The low hummock species ***Sphagnum papillosum***, on the other hand, had up to six **capitula** (terminal clump of branches; Figure 131) per stem; the two species growing in the high-humidity, shaded wet woodland exhibited intermediate degrees of branching.

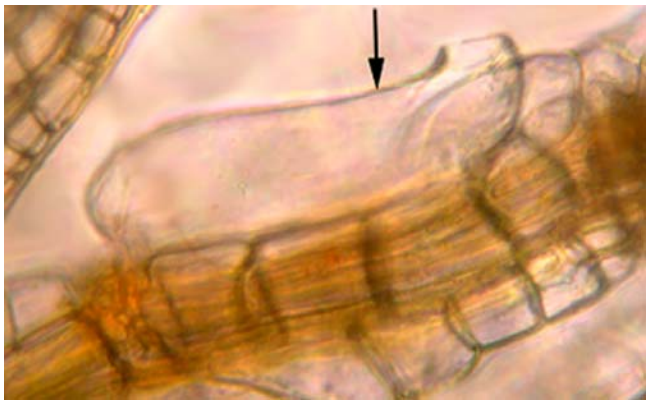


Figure 126. Retort cell (**arrow**) of ***Sphagnum***, showing pore. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

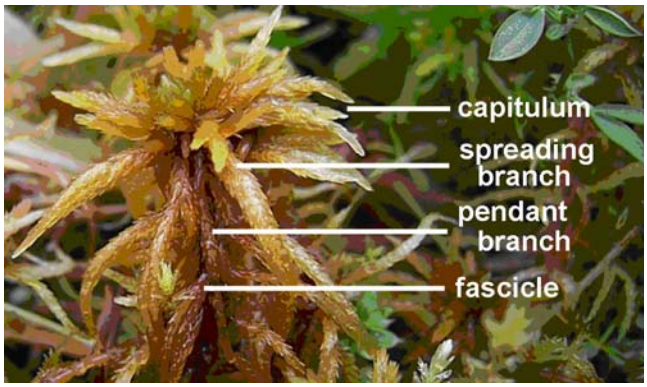


Figure 127. ***Sphagnum teres*** indicating two major branch types, compact capitulum, and joining of branches into fascicles. Photo by Michael Lüth, with permission.

Figure 128. Spreading branches and pendant branches on two hummock ***Sphagnum*** species. **Left: *S. magellanicum***. **Right: *S. papillosum***. Photos courtesy of Yenhung Li.

Figure 129. ***Sphagnum cuspidatum***, a species from hollows with a high percentage of unbranched stems as seen in the single capitula. Photo by J. C. Schou, with permission.

Figure 130. ***Sphagnum recurvum***, a species of wet carpet with a high percentage of unbranched stems, as seen in the single capitula. Photo by J. C. Schou, with permission.

Figure 131. ***Sphagnum papillosum*** with branched capitula. Photo by J. C. Schou, with permission.

Sphagnum magellanicum (Figure 120) has greater ability to move and hold water than does ***S. papillosum*** (Figure 121) (Li *et al*. 1992). Therefore, when they grow together in the same hummock, ***S. magellanicum*** will not only stay wet longer, but if it is dominant it will keep ***S. papillosum*** wet (Figure 132). However, it will fail to do so if ***S. papillosum*** is dominant (Figure 132). This is further supported by lab experiments in which ***S. magellanicum*** moved water farther externally in 20 hours than did ***S. papillosum*** (Figure 133; Figure 134).

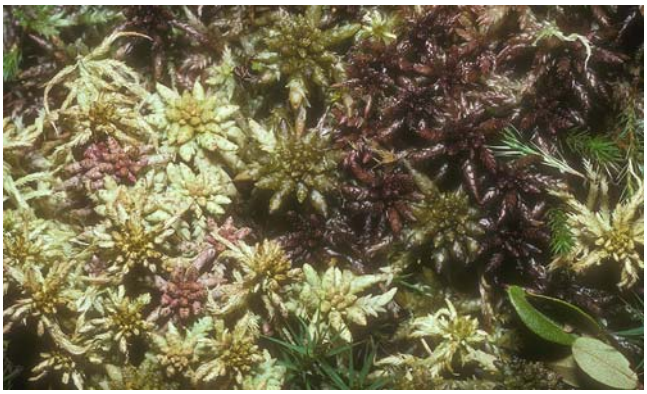


Figure 132. Predominately ***Sphagnum papillosum*** (**olive colored**) lower on the hummock (**left side of picture**) causes both species to be dry, whereas predominately ***S. magellanicum*** (**red**) higher on the hummock (**upper right side of picture**) keeps both species wet. Photo by Janice Glime.

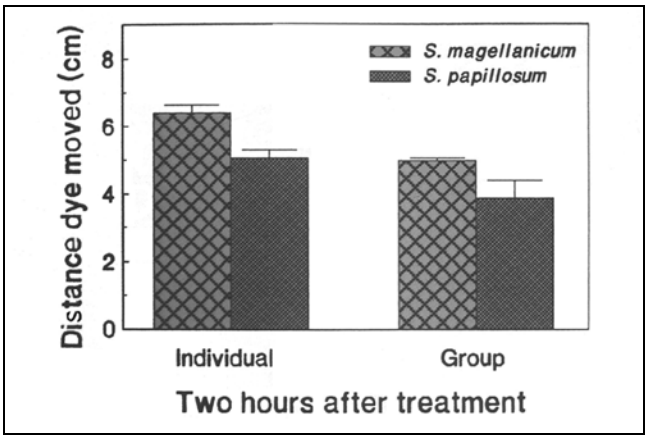


Figure 133. Comparison of distance travelled by dye after 20 hours in two ***Sphagnum*** species from lower (***S. papillosum***) and higher (***S. magellanicum***) positions in the hummock. Group refers to those kept together at field density with half of each species. From Li *et al*. 1992.

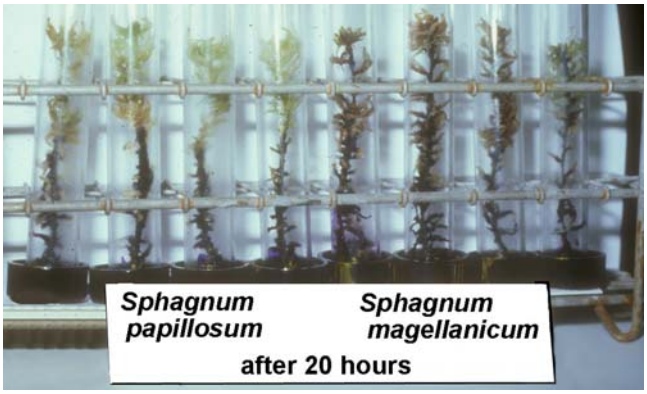


Figure 134. Comparison of upward transport in a low (**left**) and high (**right**) hummock species of ***Sphagnum***. Movement of water is indicated by purple dye. Photo courtesy of Yenhung Li.

Central Strand

In addition to the structural adaptations of stems and branches already described, the vascular system itself may be modified. The **central strand** (Figure 135) is typically composed of hydroids that are elongated and impose fewer cell end walls through which water must travel. Hébant (1973) found that variation occurred in the vascular elements, particularly in length and diameter, degree of inclination of end walls, and structure of the walls themselves. For example, whereas walls of hydroids are usually thin, they can be very thick, as in the swollen walls of hydroids in the setae of ***Dicranum scoparium*** (Figure 136) or the lateral walls of hydroids in the gametophyte central strand of the **Polytrichales** (Figure 137). But insufficient data exist to relate these variations to adaptive function.

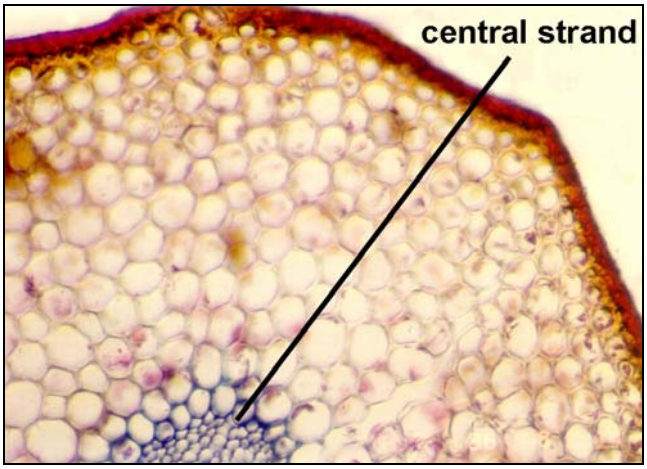


Figure 135. Stem cross section of ***Rhizogonium*** showing narrow cells of central strand. Photo courtesy of Isawo Kawai.

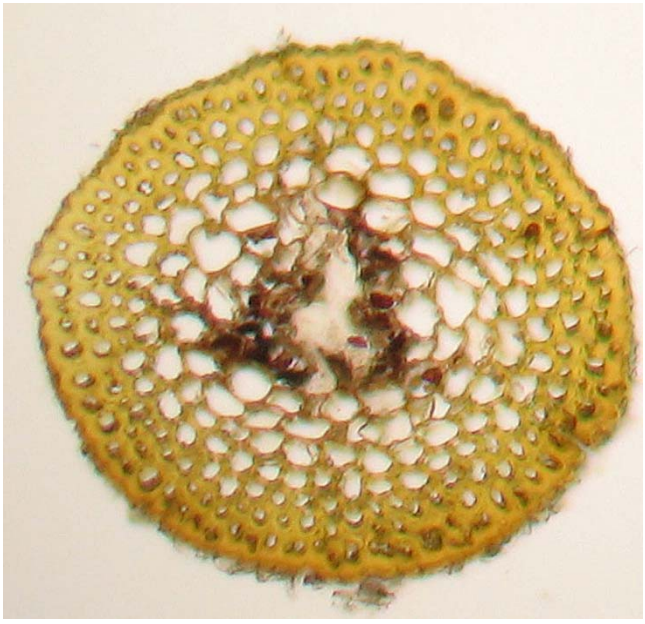


Figure 136. ***Dicranum scoparium*** seta cross section showing hydroids. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

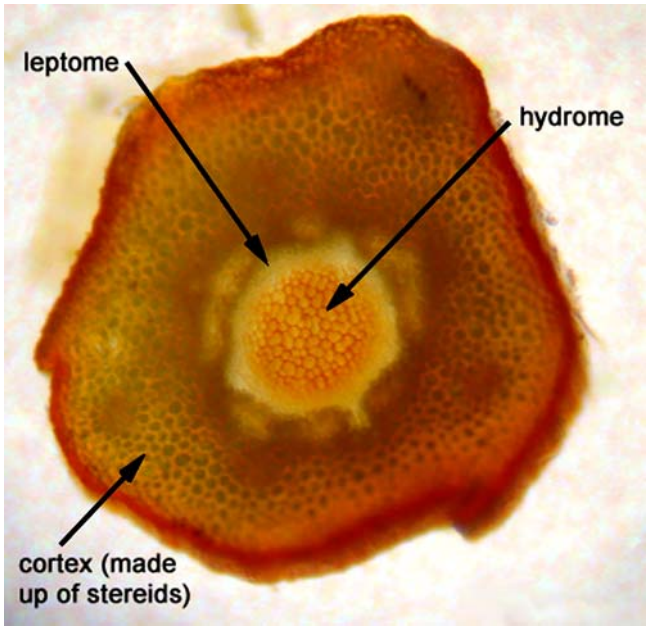


Figure 137. ***Polytrichum commune*** stem cross section showing central strand. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Using several references for comparison, Hébant (1977) showed that the number of hydroids within the ***Polytrichum commune*** (Figure 80) central strand (Figure 137) can vary with habitat, following an apparent moisture gradient. In a pseudo-alpine grassland he reports 900 hydroids in the central strand, peat bog 400, cultivated in artificial peat 280, and cultivated under water 70. There is no clear indication as to how these numbers affect the rate of conduction, but one would presume that more hydroids conduct more water.

Although in general, leafy liverworts lack conducting tissues in both leaves and stems (Crandall-Stotler 2014), ***Haplomitrium*** seems to be an exception. At least it possesses a differentiated central strand (Figure 94). But there seem to be no experiments to demonstrate how well this actually serves as conducting tissue.

Rhizoids and Tomentum

Rhizoids and **tomentum** (layer of matted woolly down on surface of plant; Figure 138) are adapted for water uptake. Pressel and Duckett (2011) found that rhizoids of all representatives they tested in **Polytrichales**, **Dicranales**, and **Bryales** (Figure 139) were **hydrophilic** (tendency to be wetted by water). For example, there is a sharp contrast between the leaves with a waxy cuticle in **Bartramiaceae** (Figure 140) and the highly hydrophilic tomentum-forming rhizoids (Figure 140) with papillae.

Figure 138. ***Rhizomnium magnifolium*** showing dense brown rhizoidal tomentum on lower half of stem. Photo by Michael Lüth, with permission.

Figure 139. ***Bryum pseudotriquetrum*** (**Bryales**) showing dense rhizoidal tomentum along stem. Photo by Misha Ignatov, with permission.

Figure 140. ***Breutelia chrysocoma*** (**Bartramiaceae**) showing rhizoidal tomentum. Photo by Michael Lüth, with permission.

Mosses with dense rhizoids or **tomentum** (Figure 138-Figure 140) seem to be well equipped to retain and conduct water by capillary action. Smith (1988) found that ***Bryum pseudotriquetrum*** (=*Bryum algens*; Figure 139), with a dense rhizoidal tomentum (Figure 139), held significantly more water than colonies with sparse rhizoids. But the tomentose form lost water more rapidly per unit dry mass than did the ones with sparse rhizoids. Could this be attributed mostly to loss of water from the tomentum? In ***Schistidium antarctici*** (Figure 141), the xeric form has less densely packed shoots and thicker cell walls that maintain lower water content than the high-water-holding-capacity hydric turf form. Mosses in Smith's study took several times longer to drop to minimal water contents than did lichens in the same conditions.

Figure 141. ***Schistidium antarctici***, a moss that becomes morphologically modified by moisture conditions. Photo courtesy of Rod Seppelt.

In acrocarpous mosses, rhizoids are produced all the way around the base of the stem, serving on the lower parts for anchorage, and in mosses like the **Polytrichaceae**, for limited conduction (Odu 1978). Rhizoids further up the stem provide capillary spaces that can both store water and facilitate movement. In pleurocarpous mosses, rhizoids appear only on the side of the stem (Figure 142) toward the substrate (Odu 1978), except in the case of those in flowing water (Glime 1987). In ***Fontinalis*** (Figure 143), where rhizoids have a critical function in anchorage and this aquatic moss may encounter its substrate in any direction from the stem, the individual rhizoids grow in a spiral (Figure 144) until they encounter the substrate, then form multiple branches (Figure 145) in a small space and cement themselves to the substrate, presumably offering no function of water movement (Glime 1987).

Figure 142. ***Hygroamblystegium fluviatile*** rhizoids on one side of stem. Photo by Janice Glime.

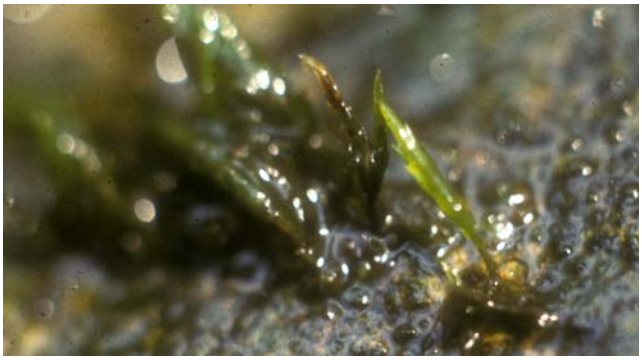


Figure 143. ***Fontinalis novae-angliae*** cemented to the rock by its rhizoids. Photo by Janice Glime.

Figure 144. ***Fontinalis squamosa*** rhizoids growing in a spiral where they are suspended above the substrate. Photo by Janice Glime.

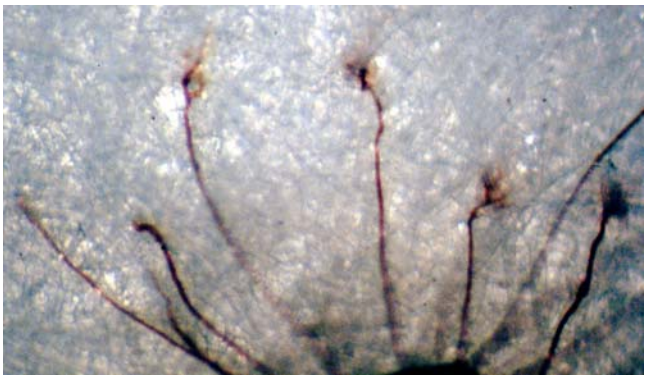


Figure 145. ***Fontinalis squamosa*** rhizoid tips branching when they encounter a paper towel substrate. Photo by Janice Glime.

Higuchi and Imura (1987) cultured three moss species to determine the effects of submersion on the rhizoid characters. The thickness, surface decorations, and positions where the rhizoids arise appear to be stable in altered moisture conditions, but in ***Macromitrium gymnostomum*** the mucilage that is present in terrestrial cultures is lost in water culture. Rhizoids generally are not produced on submersed mosses in standing water (Odu 1978). Could it be that ethylene, which inhibits their development, cannot escape easily? This conserves energy, because it would seem that they are needed neither for anchorage nor absorption and conduction. In flowing water they need anchorage and the flow would prevent ethylene from accumulating, if that is the mechanism.

Surprisingly, Trachtenberg and Zamski (1979) found a cuticle on the rhizoids of ***Polytrichum juniperinum*** (Figure 146), sharply contrasting with roots and root hairs of tracheophytes, which serve as absorbing organs and have no waxy cuticle. This suggests that they may play little role in water uptake, but rather prevent water loss to the substratum. This raises questions about how widespread this cuticle is on rhizoids of other taxa and how it affects the capillary action they might otherwise afford. Perhaps they play only a role in conservation of water and not in its uptake. Or are these cuticles designed to provide capillary spaces that hold water around the rhizoids and facilitate uptake?

Figure 146. ***Polytrichum juniperinum*** males, a moss that has a cuticle on its rhizoids. Photo by Jan-Peter Frahm, with permission.

It is noteworthy that the leafy liverwort ***Haplomitrium*** (Figure 94, Figure 107, Figure 153) lacks rhizoids (Duckett *et al*. 2013). On the other hand, ***Treubia*** (Figure 147-Figure 148) appears to possess rhizoids that facilitate nutrient uptake (Field *et al.* 2014). These unusual liverworts have leaves in three equal ranks and use underground stems (**rhizomes**) for anchorage and for fungal associations. All other liverworts produce **unicellular** (having only one cell) rhizoids (Figure 149). But only the thallose liverworts produce two types. Mosses, on the other hand, have multicellular rhizoids that can branch (Figure 150).

Figure 147. ***Treubia lacunosa*** dorsal view. Photo by Jan-Peter Frahm, with permission.

Figure 148. ***Treubia lacunosa*** with sporophyte, a species with underground stems. Photo courtesy of Jeff Duckett & Silvia Pressel.

Figure 149. ***Cephalozia*** sp. rhizoids showing that they are one-celled. Photo by Jan Fott, with permission.

Figure 150. ***Bryum stirtonii*** rhizoid showing multiple cells, papillae, and branching. Photo by Michael Lüth, with permission.

Mucilage

Stem apices are protected by mucilage secreted by specialized hairs (Berthier *et al*. 1974). This mucilage seems to play a strong role in protecting the actively dividing tissue, permitting fragments to survive long periods of desiccation until they are able to grow again, and most likely playing a role in water retention, especially for the critical apical cells.

In liverworts and the moss ***Takakia*** (Figure 151) there are **slime papillae** (Figure 152) that may serve a water absorption/retention function as well. The leafy liverwort ***Haplomitrium*** (Figure 153) produces extensive mucilage on its rhizomes (Figure 153-Figure 154). It is interesting that these slime papillae appear in the green alga ***Coleochaete*** (Figure 155), the genus that seems most closely related to embryophytes, causing one to wonder if slime papillae may have been a prerequisite for land adaptation in early plants.

Figure 151. ***Takakia lepidozioides***, a moss with slime papillae. From the Herbarium of Hiroshima University, Hiroshima, Japan, with permission.

Figure 152. Stem of ***Takakia lepidozioides*** showing slime papillae that might serve in water absorption and retention. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Figure 153. ***Haplomitrium gibbsiae*** leafy plant with mucous on its rhizomes. Photo courtesy of Jeff Duckett and Silvia Pressel.

Figure 154. ***Haplomitrium gibbsiae*** rhizome with mucous. Photo courtesy of Jeff Duckett and Silvia Pressel.

Figure 155. ***Coleochaete*** thallus, an extant green alga that has the most characters in common with bryophytes. Photo by Yuuji Tsukii, with permission.

The thallose liverwort ***Conocephalum conicum*** (Figure 27, Figure 36, Figure 68) has mucilage ducts in its thallus. Clee (1943) suggests that these may aid in water retention.

Cuticles and Waxes

Bryophyte leaves have frequently been described as lacking a cuticle. However, this ancient concept has proven to be false. Even leafy liverworts can have a cuticle. The details of the leaf cuticle will be discussed in the next subchapter, but we need to consider how such a cuticle might affect the whole plant water movement. Loss of water from leaves can create a transpiration stream that draws water upward, but in most bryophytes the greater movement of water is external. Hence, it is not surprising that little is known of the effects of a transpiration stream on water movement in bryophytes. It would be interesting to know if stems have a cuticle, but I am aware of no studies that isolated the stems to look for it. For now, we will concentrate on other aspects of water movement.

Capillary Spaces

Although several adaptations to holding water seem to exist [porose leaf cells, ridges, folds, sheathing leaf bases (Figure 156), rhizoids, tomentum], Proctor (1979a) contends that most of the water is held in the larger capillary spaces between the moss shoots. Small amounts of dew that accumulate at the moss tip (Figure 157), *i.e.* the growing region, may be critical to survival (Lange 1969; Kappen *et al.* 1979). Hair points that wrap around the succeeding leaves above (Figure 158) help to deflect light and reduce evaporative loss by creating a diversion for air currents. Proctor (1980) experimented by removing hair points and found that when present they reduced water loss by 35% in ***Grimmia pulvinata*** (Figure 115) and ***Syntrichia montana*** (=*S. intermedia*; Figure 159). Thus far, it has been difficult to demonstrate that papillae afford any such advantage (Frey & Kürschner 1991). Nevertheless, in leaves they can act as a rapid capillary water movement system (Proctor 1979a; Longton 1988; Pressel & Duckett 2011).

Figure 156. ***Bartramia ithyphylla*** illustrating the sheathing leaf base that provides capillary spaces that can hold water. Photo by Michael Lüth, with permission.

Figure 157. ***Campylopus introflexus*** showing water droplets at tips of plants. Hair points, like fine wires and spider webs, provide locations where the cohesive, adhesive water droplets can cling. Photo by Jan-Peter Frahm, with permission.

Figure 158. ***Polytrichum piliferum*** illustrating leaf hairs that overlap the next leaf and help shield it from light, at the same time creating capillary spaces. Photo by Michael Lüth, with permission.

Figure 159. ***Syntrichia montana*** showing long hair points that can reduce evapotranspiration by up to 35%. Photo by Michael Lüth, with permission.

The leafy liverwort ***Trichocolea*** (Figure 160-Figure 162) is highly adapted to take advantage of capillary action. Its leaves are highly dissected and **paraphyllia** (leaflike appendages between the leaves; see Figure 163) are abundant, permitting this species to act like a sponge. Zehr (1979) observed that it experienced only short-term vapor deficits in its moist habitat and thus was able to grow anytime temperatures were above freezing. Paraphyllia such as those in ***Hylocomium splendens*** (Figure 164-Figure 165) and ***Thuidium tamariscinum*** (Figure 166) create capillary spaces much like a tomentum. Other mosses such as **Mniaceae** utilize **paraphyses** (Figure 167) among the archegonia and antheridia to conserve water, using the same capillary principle.

Figure 160. ***Trichocolea tomentella*** dry, a leafy liverwort with finely divided leaves and paraphyllia. Photo by Hermann Schachner, through Creative Commons.

Figure 161. ***Trichocolea tomentella*** wet, a leafy liverwort with finely divided leaves and paraphyllia. Note the numerous capillary spaces afforded by the filamentous divided leaves. Photo by Jan-Peter Frahm, with permission.

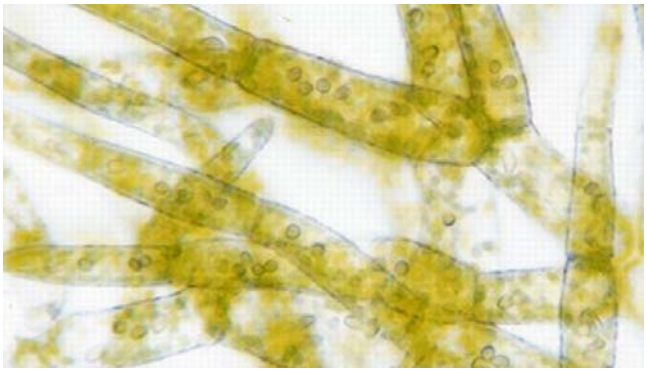
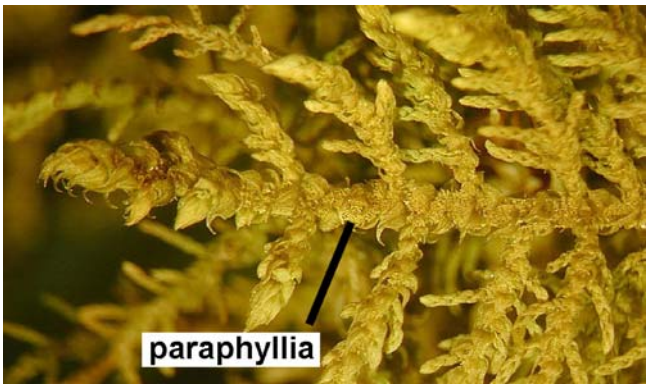


Figure 162. ***Trichocolea tomentella*** cells of divided leaves. Photo by Malcolm Storey from Discover Life <www.discoverlife.org>, through Creative Commons.



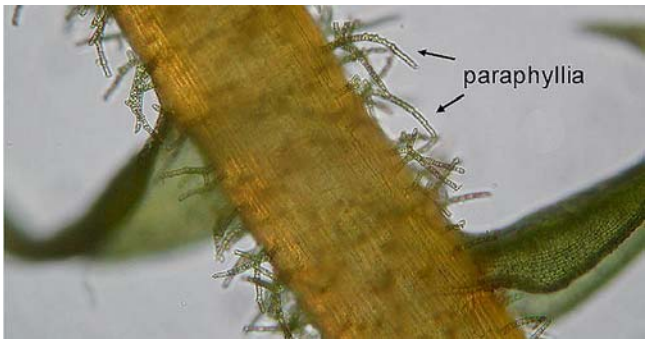


Figure 163. ***Thuidium recognitum*** showing branched paraphyllia on the stem and branches. Photos by Michael Lüth (**upper**) and Paul Davison (**lower**), with permission.

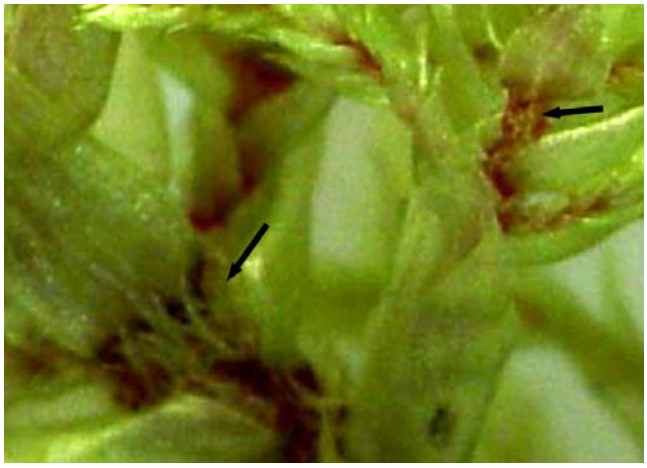


Figure 164. ***Hylocomium splendens*** showing paraphyllia on stem. Photo by Rosalina Gabriel, with permission.

Figure 165. ***Hylocomium splendens*** paraphyllia. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Figure 166. ***Thuidium tamariscinum***, showing paraphyllia on stem (**arrows**). Photo by Brian Eversham, with permission.

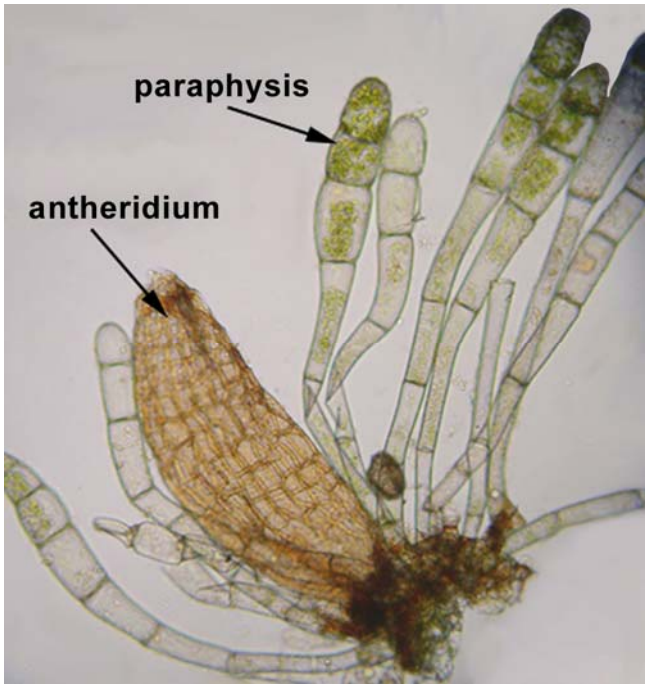


Figure 167. ***Plagiomnium insigne*** antheridia and paraphyses that create capillary spaces. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Cellular Structure

Sun-exposed rock surfaces and similar habitats require the greatest degree of desiccation tolerance. One such desiccation-tolerant species is ***Andreaea rothii*** (Figure 168-Figure 170), a small, blackish cushion moss that grows on hard, acidic mountain rocks. It is able to recover and photosynthesize after 12 months of desiccation at 32% relative humidity at 20ºC (Proctor & Tuba 2002). Similar tolerance is exhibited by the small cushions of ***Grimmia pulvinata*** (Figure 171-Figure 172) on dry wall tops, ***Racomitrium lanuginosum*** (Figure 93; Figure 173-Figure 175) of mountain and subarctic fellfields (Figure 173), and ***Syntrichia ruralis*** (Figure 176-Figure 177) of dry sand dunes and steppe grasslands. A common characteristic among these and other tolerant mosses is their small or narrow cells with dense contents and small vacuoles. Their leaf surfaces are readily wetted and the leaves quickly expand within minutes of rewetting.

Figure 168. ***Andreaea rothii*** in cushions on rocks, a habitat that frequently presents desiccating conditions. Photo by Claire Halpin, with permission.

Figure 169. ***Andreaea rothii*** showing tightness of the stems in the cushion. Photo by Štěpán Koval, with permission.

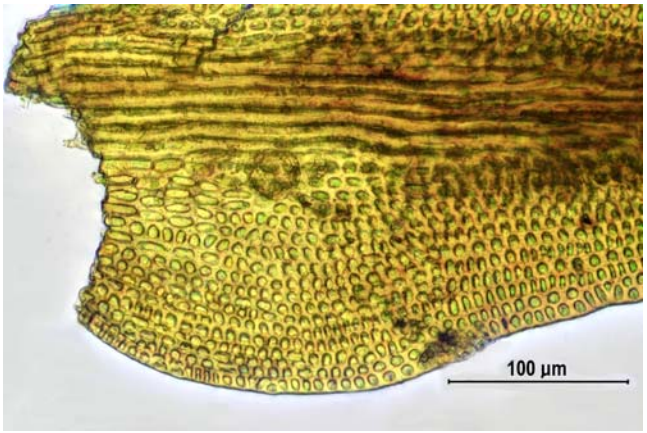


Figure 170. ***Andreaea rothii*** leaf cells showing small size and isodiametric shape. Photo by Claire Halpin, with permission.

Figure 171. ***Grimmia pulvinata*** with capsules, forming a cushion on the top of a wall. Photo by Michael Becker, through Creative Commons.

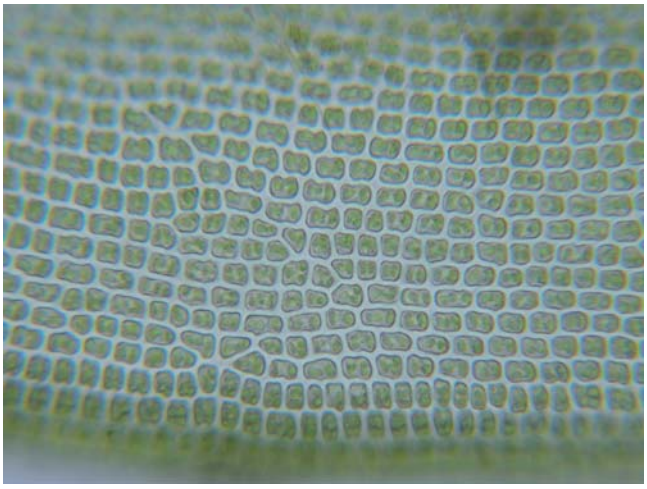


Figure 172. ***Grimmia pulvinata*** showing small, isodiametric leaf cells. Photo by Claire Halpin, with permission.

Figure 173. ***Racomitrium lanuginosum*** on rocky field. Photo by Brucedc, through Creative Commons.

Figure 174. ***Racomitrium lanuginosum*** cushion on rock. Photo by Hugues Tinguy, with permission.

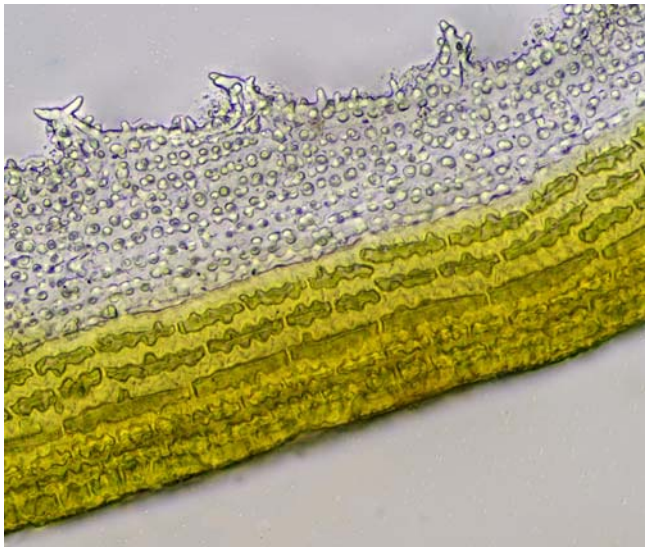


Figure 175. ***Racomitrium lanuginosum*** leaf cells showing wavy margins, thick walls, and cell elongation. Photo by Claire Halpin, with permission.

Figure 176. ***Syntrichia ruralis*** in their usually dry habitat of a rock crevice. Photo by Darkone, through Creative Commons.

Figure 177. ***Syntrichia ruralis*** isodiametric leaf cells with papillae (creating darker spots on the cells). Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

Liverworts in general are less desiccation tolerant than mosses, but some are able to survive frequently dry habitats (Clausen 1952). The leafy liverwort ***Porella platyphylla*** (Figure 178-Figure 182) grows in dry but shaded habitats on dry calcareous rock or base-rich bark. It recovers completely after 60 days of desiccation at 50% relative humidity (Hinshiri & Proctor 1971). Other leafy liverworts such as ***Frullania dilatata*** (Figure 183-Figure 185) and ***Gymnomitrion*** spp. (Figure 186-Figure 187) grow on sun-exposed rocks. But the leafy liverwort ***Porella platyphylla*** has moderate cell size and large vacuoles, contrasting with what seems to be typical in DT mosses (Marschall *et al*. 1998).

Figure 178. ***Porella platyphylla*** in crevice. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

Figure 179. ***Porella platyphylla*** on vertical rock, an infrequently wet habitat. Photo by Joanne Denyer, with permission.

Figure 180. ***Porella platyphylla*** showing rolled leaf edges of a drying plant. Photo by Hermann Schachner, through Creative Commons.

Figure 181. ***Porella platyphylla*** ventral view showing lobules that hold water droplets and keep the photosynthetic tissue hydrated. Photo by Hermann Schachner, through Creative Commons.

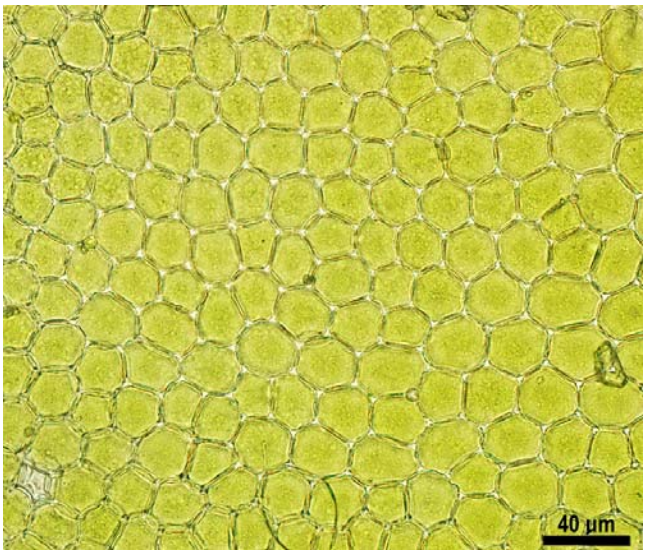


Figure 182. ***Porella platyphylla*** leaf cells showing larger but still isodiametric size. Note **trigones** at the corners, places where capillary water can be held. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

Figure 183. ***Frullania dilatata*** on tree trunk, a frequently dry habitat. Photo by Bernd Haynold, through Creative Commons.

Figure 184. ***Frullania dilatata*** showing the closely overlapping leaves that trap capillary water in this xerophyte. Photo by Bernd Haynold, through Creative Commons.

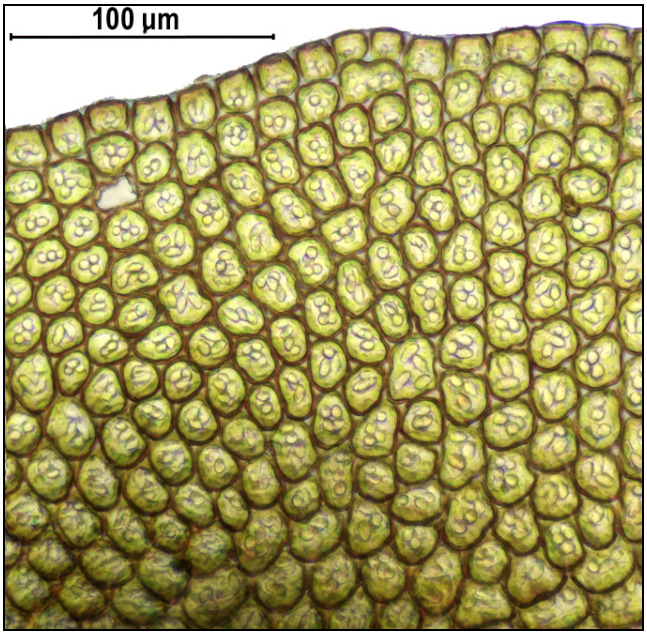


Figure 185. ***Frullania dilatata***, a xerophytic liverwort, showing isodiametric leaf cells with oil bodies and **trigones**. Photo by Claire Halpin, with permission.

Figure 186. ***Gymnomitrion*** sp. on tree trunk, a xeric habitat. Photo by Claire Halpin, with permission.

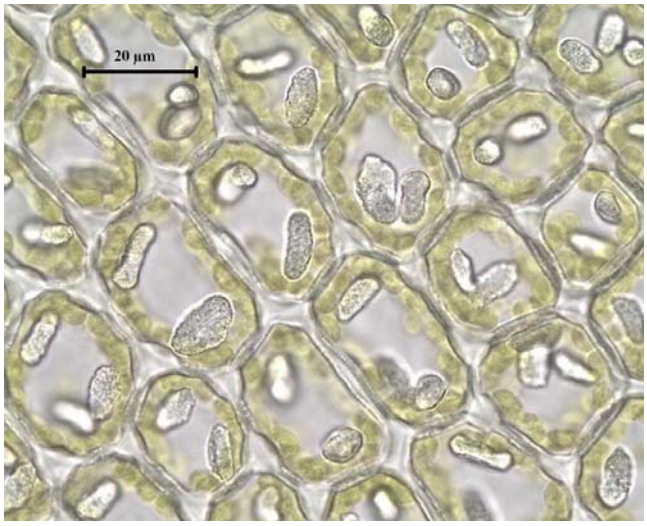


Figure 187. ***Gymnomitrion concinnatum*** leaf cells with oil bodies. The cell walls have adequate spaces and **trigones** for water storage. Photo by Hugues Tinguy, with permission.

Although 50% relative humidity seems to be the level commonly used for determining desiccation tolerance, some structures, and possibly some species, can tolerate even lower levels.

Fungal Partners

Fungal partners associated with roots have been termed **mycorrhizae**, and the same term is applied to fungi that serve as fungal partners to bryophytes. The existence

of these relationships has been mostly overlooked until recently, although we have recognized for quite some time that many bryophytes had fungi associated with them. Hence, our knowledge of their importance to the bryophyte is meager. It is likely that they serve a similar role to that in tree roots in scavenging a wide area for water, minerals, and perhaps organic nutrients. But I would also consider it likely that at least some of them play a role similar to that in the **hemiparasites** such as Indian pipe (*Monotropa uniflora*). That is, for those bryophytes living in dense shade, they could find a third partner that has more access to light – a leafy tracheophyte – that provides photosynthate that can be transferred from the tracheophyte, by way of the fungus, to the bryophyte. I am afraid I can see no substance that is likely to be produced by the bryophyte that is useful to the tracheophyte, making the bryophyte also a hemiparasite. Nevertheless, such a 3-way linkage remains to be demonstrated.

In an attempt to unravel the evolution of the fungal symbioses of bryophytes, Pressel *et al*. (2010) examined the ancient basal bryophytes ***Treubia*** (Figure 147-Figure 148) and ***Haplomitrium*** (Figure 153-Figure 154). In these liverworts they found intracellular fungal lumps, inter cellular hyphae, and thick-walled spores. Unlike the well known glomerophytes found as symbionts in thallose liverworts and lower tracheophytes, these were more ancient fungi (Figure 188-Figure 189).

In leafy liverwort families sister to the **Schistochilaceae**, the Ascomycete fungus ***Rhizoscyphus ericae*** occurs in the rhizoids (Pressel *et al*. 2010). This fungus has a wide range of hosts, including flowering plants in the Ericales (includes blueberries and heath plants) and an Antarctic species of the leafy liverwort ***Cephaloziella*** (Figure 190). Figure 191 shows a member of the **Ascomycota** inhabiting the leafy liverwort ***Mylia anomala***. In the **Basidiomycota**, the genus ***Sebacina*** (Figure 192) is associated with leafy liverworts, but this fungus is host specific. Neither of these liverwort fungi seems to digest its host, whereas the **Basidiomycota** in the thallose liverworts of **Aneuraceae** have regular colonization and digestion cycles. The hornworts also demonstrate mycorrhizal relationships with fungi, but thus far there is no evidence that such a mycorrhizal relationship exists in mosses. It might be worth looking for it in **Polytrichaceae** and **Sphagnaceae**.

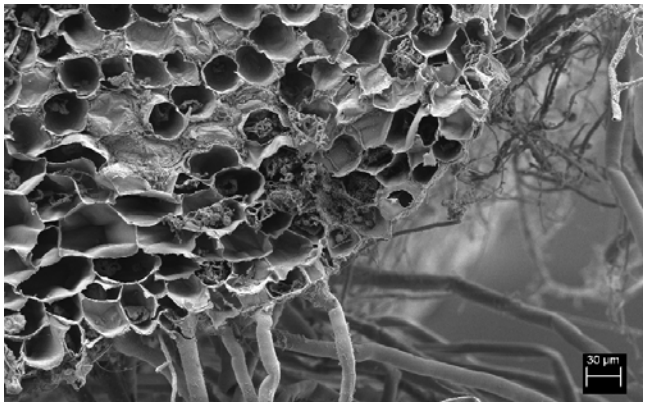


Figure 188. SEM of ***Treubia*** cross section showing the number of cells with resident fungi. Photo courtesy of Jeff Duckett and Silvia Pressel.

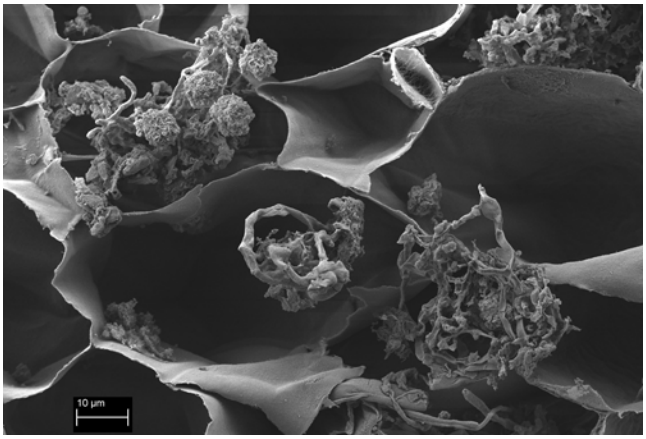


Figure 189. SEM of ***Treubia*** cross section with fungi in cells. Photo courtesy of Jeff Duckett and Silvia Pressel.

Figure 190. ***Cephaloziella elachista***; an Antarctic species in this genus serves as one of the hosts of the fungus ***Rhizoscyphus ericae***. Photo from Earth.com, with permission.

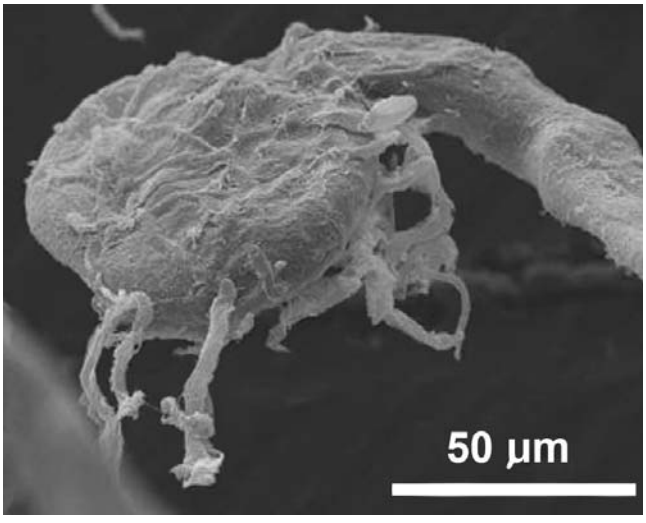


Figure 191. Swollen rhizoid tip with **Ascomycota** in leafy liverwort ***Mylia anomala***. Photo courtesy of Silvia Pressel and Jeff Duckett.

Figure 192. ***Sebacina incrustans***, member of a genus of basidiomycete fungi that is associated with leafy liverworts. Photo by James K. Lindsey, with permission.

We are at a very early stage in our understanding of mycorrhizae in bryophytes. In tracheophytes these associations permit the host plant to gain water and nutrients from a much wider area by accepting these from a fungus that has grown over a wide area, as much as 15 hectares, weighing 10,000 kg (Smith *et al*. 1992). Their role in bryophytes is less clear, but the ancient origin of this association suggests that by now it could be quite sophisticated and beneficial.

Protonema

The protonema stage of mosses is a delicate threadlike stage in which every cell is surrounded by air with the potential for creating desiccation. But is it really so delicate?

In experiments, Pressel and Duckett (2010) demonstrated that protonemata can survive slow drying but not fast drying. This suggests that during slow drying there is time to manufacture something that protects the cells from the effects of desiccation. Indeed, pre-treatment with abscisic acid permits the protonemata to survive fast drying as well. During slow dehydration the cells undergo profound changes, including vacuolar fragmentation, reorganization of endomembrane domains, changes in cell wall thickness, changes in plastid morphology, changes in mitochondria morphology, and a controlled dismantling of the cytoskeleton. During fast drying, these events do not occur or are incomplete. The abscisic acid permits the rapidly drying cells to partially mimic their behavior during slow drying, permitting them to survive.

Leafy Liverwort Gemmae

Liverworts have leaf gemmae that are usually small structures along the leaf margins. Germination on the leaf is not desirable, so it is no surprise that they have a means of preventing it. This prevention may relate to their hydrophobic surface (Duckett & Ligrone 1995). In ***Odontoschisma denudatum*** (Figure 193), the wall chemistry changes during maturation, with an increase in electron-opacity.

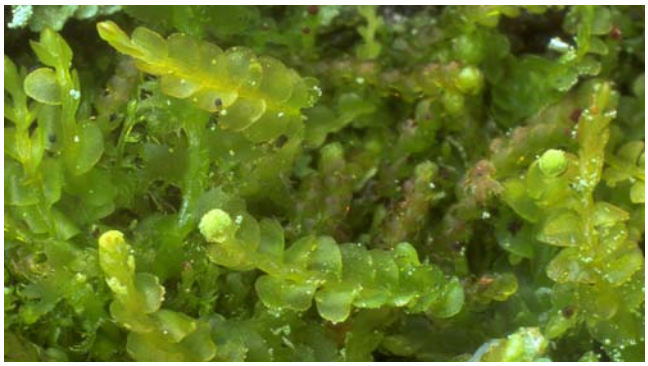


Figure 193. ***Odontoschisma denudatum*** with gemmae on apical leaves (yellowish). Photo by Jan-Peter Frahm, with permission.

Sporophyte

When we examine mature sporophytes with their capsules and spores, we don't give a second thought to the dangers of drying out. But we are misled by this resistant mature sporophyte. Rather, based on studies of field-collected gametophytes of ***Microbryum starckeanum*** (Figure 194) and ***Tortula inermis*** (Figure 195) (both species of dry habitats) with immature sporophytes, McLetchie and coworkers found that the sporophyte generation is more sensitive to desiccation and thermal stress than is the leafy gametophyte (McLetchie & Stark 2006; Stark *et al*. 2007). This may of course differ in species with a different phenology in different environmental conditions, but it bears questioning our perception of the importance of desiccation during sporophyte development. This need for desiccation tolerance of the sporophyte may be especially important for species like those of ***Polytrichum*** (Figure 80) that require as much as 20 months for sporophyte development and span an entire year of weather conditions (Arnell 1905; Longton 1972).

Figure 194. ***Microbryum starckeanum***, a species in which the sporophyte is more sensitive to desiccation than is the gametophyte. Photo from BBS website, with permission.

Figure 195. ***Tortula inermis*** dry leaves and immature capsules, a species in which the young capsules are more sensitive to desiccation than are the gametophytes. Photo by Michael Lüth, with permission.

It appears that the embryonic sporophytes are the stage most susceptible to desiccation stress (Stark 2002, 2005). Nevertheless, some desert mosses have embryonic sporophytes that can tolerate desiccation for long periods, most likely benefitting from **desiccation hardening** (development of resistance to desiccation) (Stark *et al*. 2014). Several examples exist from non-desert mosses, although the tie to desiccation is unclear. In the boreal forest moss ***Hylocomium splendens*** (Figure 164-Figure 165) (Callaghan *et al*. 1978) and desert moss ***Syntrichia caninervis*** (Figure 25) (Stark *et al*. 2000), the number of aborted sporophytes outnumbers that of mature sporophytes. Similarly, in the boreal forest moss ***Pleurozium schreberi*** (Figure 196) 38% of the sporophytes aborted (Longton & Greene 1969).

Figure 196. ***Pleurozium schreberi***, a boreal forest moss with a high percent of abortions. Photo by Michael Lüth, with permission.

Calyptra Protection

If we imagine the hairy calyptrae of such mosses as ***Polytrichum*** (Figure 197), we must ask ourselves how the calyptra avoids absorbing water and holding it against the capsule, creating water logging, or contrarily, draws water from the capsule due to capillary spaces created by the hairs. In other words, why doesn't it behave like a bath towel? To answer this question, we will look at calyptra development, timing, structure, and its ultimate role.

Figure 197. Hairy calyptra on capsule of ***Polytrichum juniperinum***. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

The **calyptra** develops from the archegonium, which expands as the embryo develops. In some cases, the calyptra falls early in capsule expansion, but in others, such as ***Polytrichum*** (Figure 197), it may remain until the spores are ready for dispersal. One might then question the role of the calyptra in protecting the embryo through to development of spores. Budke *et al.* (2012) demonstrated that the maternal calyptra provides protection of early post-embryonic sporophytes against desiccation, but that later development of the capsule may incur cuticle development that protects as the capsule emerges from the calyptra. This demonstrates that the calyptra cannot be considered a vestigial structure, but rather that it is essential in preventing desiccation. Haig (2013) agrees that the presence of the calyptra delays the onset of transpiration. Hence, it is prudent to examine the calyptra characters that may provide this desiccation protection.

Cuticle: In ***Funaria hygrometrica*** there is a 4-layered cuticle on the calyptra for its duration (Figure 198) (Budke *et al*. 2012). Budke *et al*. (2011, 2012, 2013) demonstrated that the cuticle on this calyptra conferred significant protection to the developing sporophyte.

Figure 198. ***Funaria hygrometrica*** showing calyptra that has a 4-layered cuticle. Photo by Fred Essig, with permission.

Hairs: There appear to be two kinds of hairs on calyptrae, "true" hairs (Figure 197) and undeveloped archegonia. In ***Fontinalis***, the calyptral hairs develop from aborted archegonia whose eggs (Figure 199) were presumably not fertilized (Glime unpubl.). This results in a small number of "hairs" near the base of the calyptra.

Figure 199. ***Fontinalis squamosa*** calyptra with young archegonium SEM. Photo by Janice Glime.

The hairs on the calyptrae in taxa such as ***Polytrichum*** (Figure 197) and ***Orthotrichum*** (Figure 200) could function to prevent desiccation during early development or to deter herbivory both early and late in development, but earlier in development they could also serve important functions for the archegonium, helping to conserve moisture to protect the egg or other uses we haven't considered. I haven't followed the development in taxa other than ***Fontinalis*** (Figure 199), but the hairs seem too large and numerous in most taxa to be just a lingering of the archegonia or associated paraphyses. If they continue to elongate as the calyptra develops, then there may be some advantage that would favor that prolonged use of energy for their development.

Figure 200. ***Orthotrichum stramineum*** with calyptra showing long hairs. Photo by Des Callaghan, with permission.

Cuticle

It is likely that many bryophyte sporophytes have a **cuticle**. For example, the large, waxy-looking capsule of ***Buxbaumia viridis*** (Figure 201), and most likely the other members of the genus, has a layered cuticle (Koch *et al*. 2009). And in ***B. viridis*** this cuticle is waxy with massive wax layers having small embedded and superimposed platelets and granules on top of this complex. Although until recently the only documented sporophyte cuticles had been those of the **Polytrichales**, this complex of cuticle components is common in various groups of tracheophytes.

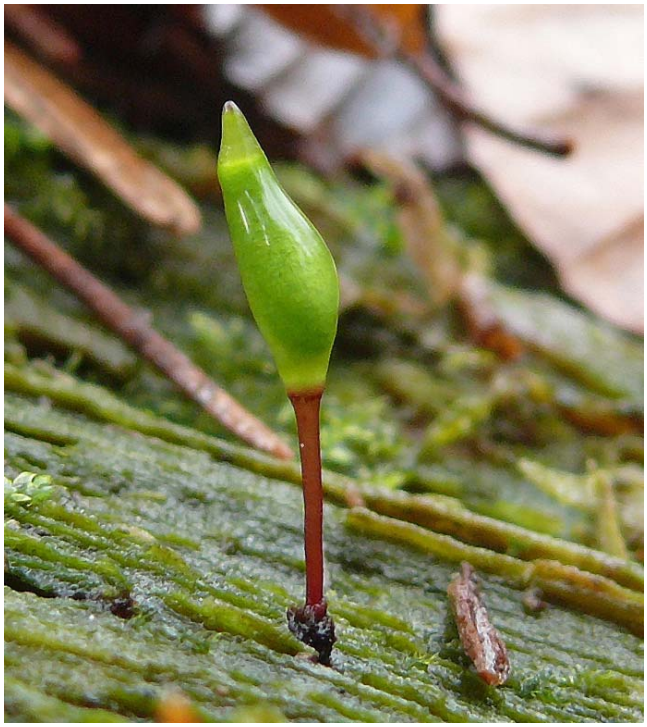


Figure 201. ***Buxbaumia viridis*** capsule showing shiny, waxy cuticle. Photo by Bernd Haynold, through Wikimedia Commons.

Pressel and Duckett (2011), suspecting that capsule waxes were more common than those of these two groups, examined a wider array of taxa, particularly those with shiny surfaces. They demonstrated that ***Bartramia*** (Figure 202), ***Plagiopus*** (Figure 203-Figure 204), and ***Mnium*** (Figure 205-Figure 207) invested as much in surface waxes of the capsule as did ***Polytrichum*** (Figure 197). They interpreted these waxes as having a role in preventing accumulated water from depressing gas exchange in the capsules, that is, prevention of water logging.

Figure 202. ***Bartramia pomiformis*** capsule showing waxy surface. Photo by Walter Obermayer, with permission.

Figure 203. ***Plagiopus oederiana*** with capsules showing waxy surface. Photo by Michael Lüth, with permission.

Figure 204. ***Plagiopus oederiana*** waxy capsule with calyptra at near maturity. In this case, the calyptra does little to protect the nearly mature capsule, most likely making the cuticle more important. Photo by Janice Glime.

Figure 205. ***Mnium*** sp. with water on young capsules, illustrating the potential for water logging. Photo by Alan S. Heilman, through Creative Commons.

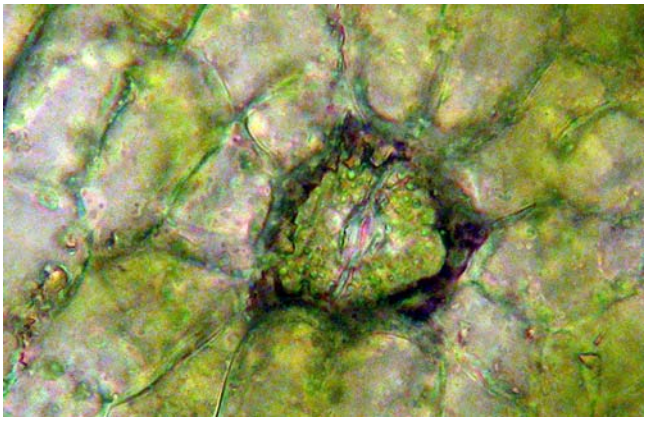


Figure 206. ***Orthotrichum pusillum*** immersed stoma on calyptra. Photo by Bob Klips, with permission.

Figure 207. ***Mnium hornum*** with capsule showing waxy surface. Photo by J. C. Schou, with permission.

In the moss genus ***Orthotrichum*** (Figure 200) many species have immersed stomata (Figure 206). These openings are surrounded by protruding cells that maintain an air space between the capsules and the calyptra (which remains attached and covers most of the capsule until the spores are ripe; Figure 200) (Pressel & Duckett 2011). The waxes repel the water on the capsule and prevent it from being drawn under the calyptra by capillary action. That is, a primary role for these surface waxes may be to prevent water logging in this and other species.

But this cuticle story apparently does not begin with the capsule. The young sporophyte is covered by a calyptra. And as noted earlier, in ***Funaria hygrometrica*** (Figure 198, Figure 208-Figure 211) this calyptra is covered by a waxy cuticle four layers thick at all stages, hence providing protection long before the developing sporophyte develops its own cuticle that ultimately arises on the sporangium (Budke *et al*. 2012). When the calyptra cuticle is removed during periods of low moisture, the sporophyte suffers significant damage, including decreased survival, increased tissue damage, incomplete sporophyte development, more peristome malformations, and decreased reproductive output (Budke *et al*. 2013). This is in contrast to the conclusion of Pressel and Duckett (2011) that the cuticles function primarily to prevent water logging. I have for my entire career as an ecologist failed to understand why ecologists get into so many arguments over two or more different explanations for the same thing, in this case the presence of stomata. There seems to me to be no evolutionary argument against multiple functions for the same thing, at the same or at different times. Just consider the many functions of our brains, or the many uses for fingernails.

Budke *et al*. (2012) examined the development of the cuticle on both the calyptra and the capsule, using ***Funaria hygrometrica*** (Figure 198, Figure 208-Figure 211) as a model organism. These researchers found that the sporophyte cuticle does not mature until the formation of the capsule.

Figure 208. ***Funaria hygrometrica*** with expanding archegonia (now calyptrae) with young sporophytes still mostly protected within the perichaetial leaves. Photo by Andrew Spink, with permission.

Figure 209. ***Funaria hygrometrica*** young sporophytes and calyptrae emerging from the protection of the perichaetial leaves. Photo by Michael Lüth, with permission.

Figure 210. ***Funaria hygrometrica*** mature capsules that have lost the calyptrae. Photo by Robert Klips, with permission.

Figure 211. ***Funaria hygrometrica*** mature capsule showing waxy surface. Photo by Sarah Gregg, with permission.

As among leaves, the capsule waxes vary in structure. In ***Tetradontium brownianum*** (Figure 212), there are fine rods around the stomata, whereas in ***Pylaisia polyantha*** (Figure 213) there are both rods and fine whorls (Pressel & Duckett 2011).

Figure 212. ***Tetradontium brownianum***, a species with fine rods in the cuticle around the stomata of the capsules. Photo by Michael Lüth, with permission.

Figure 213. ***Pylaisia polyantha*** capsule, a species with both rods and fine whorls in the cuticle around the stomata. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Peristome: Peristome teeth likewise have cuticles, with differences related to habitat conditions at the time of spore discharge (Pressel & Duckett 2011). In **Polytrichales**, the spores are dispersed when raindrops pounce on the diaphragm (**epiphragm**; Figure 214) that connects the teeth (Watson 1971). For this mechanism to work, the teeth must not only remain dry, but must repel water so that it does not block the small openings between the teeth where spores must exit (Pressel & Duckett 2011).

Figure 214. Top view of ***Polytrichum*** epiphragm showing the 64 adherent teeth. Water splashing on the membranous epiphragm (like a child on a trampoline) disperses the spores. Photo by George Shepherd, through Creative Commons.

On the other hand, most mosses disperse their spores when it is dry. Water is taken up and lost rapidly from between the ornamentation on these peristomes (Pressel & Duckett 2011). These include all **Bryopsida** they tested: ***Amblystegium*** (Figure 215), ***Bryum*** (Figure 139), ***Coscinodon*** (Figure 216), ***Dicranella*** (Figure 217), ***Didymodon*** (Figure 218), ***Fissidens*** (Figure 219), ***Funaria*** (Figure 220), ***Grimmia*** (Figure 115), ***Hypnum*** (Figure 221), ***Mnium*** (Figure 205-Figure 207), ***Rhynchostegium*** (Figure 222), ***Schistidium*** (Figure 109), ***Syntrichia*** (Figure 25), ***Tortula*** (Figure 1, Figure 195). These water gains and losses permit rapid closure in wet conditions and accelerate opening under dry conditions.

Figure 215. ***Amblystegium serpens*** capsules. Photo by Michael Lüth, with permission.

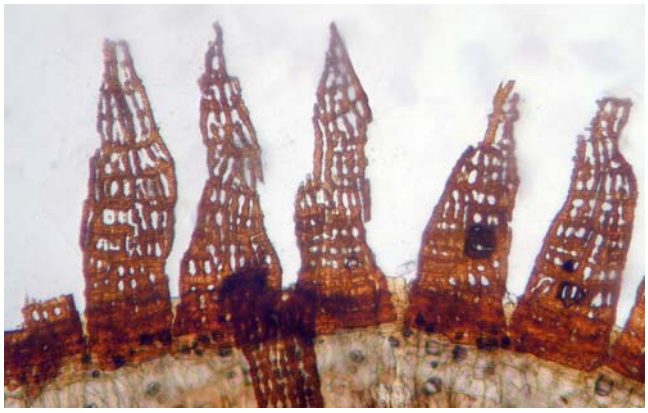


Figure 216. ***Coscinodon cribrosus*** peristome. Photo by Michael Lüth, with permission.

Figure 217. ***Dicranella varia*** capsule showing peristome. Photo by Kristian Peters, through Wikimedia Commons.

Figure 218. ***Didymodon rigidulus*** with capsules. Photo by Hermann Schachner, through Creative Commons.

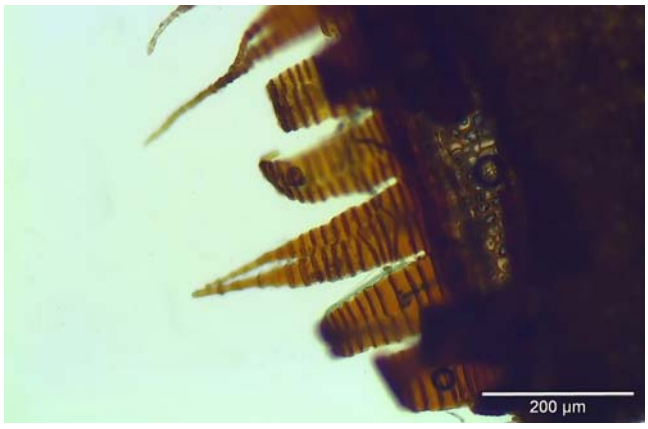


Figure 219. ***Fissidens adianthoides*** peristome. Photo by Kristian Peters, with permission.

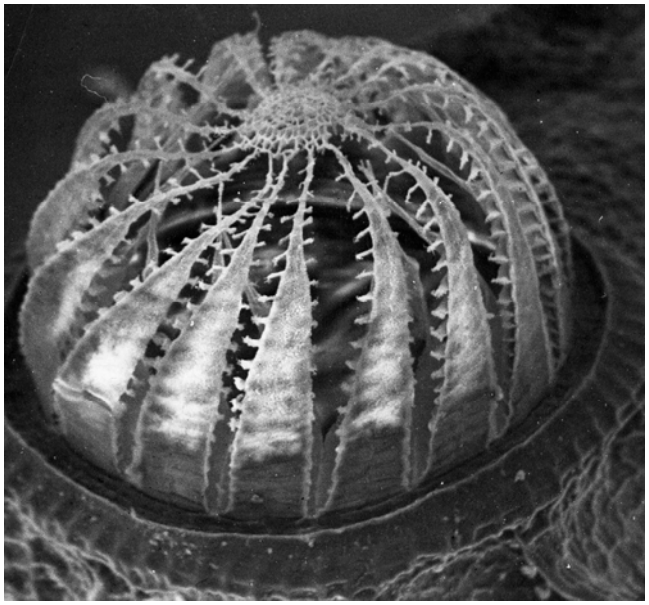


Figure 220. Peristome teeth of ***Funaria hygrometrica***, a species in which teeth move in response to drying conditions and spores escape from the spaces between the teeth. Photo by George Shepherd, through Creative Commons.

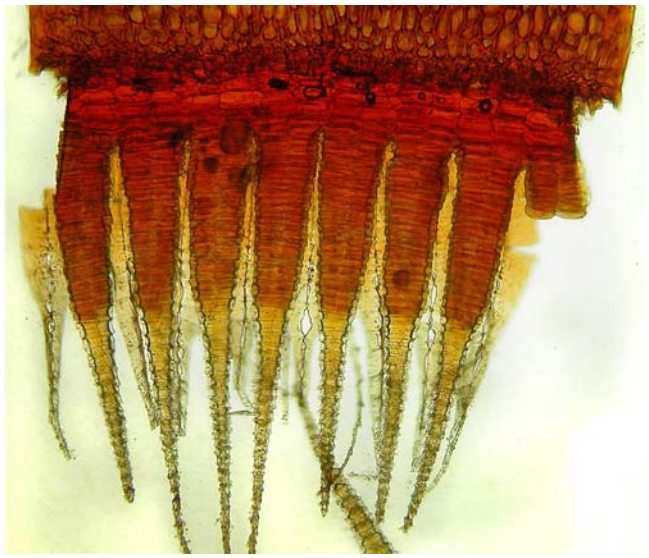


Figure 221. ***Hypnum cupressiforme*** peristome. Photo by Walter Obermayer, with permission.

Figure 222. ***Rhynchostegium confertum*** with capsules. Photo by Michael Lüth, with permission.

But what happens in capsules with no teeth or only rudimentary peristomes? As an example, in ***Weissia*** (Figure 223) water is prevented from entering the capsule by a highly water-repellent capsule rim (Figure 223). If water entered the capsule, it could cause premature germination or interfere with ultimate dispersal.

Figure 223. ***Weissia fallax*** capsule showing rudimentary peristome. Note the waxy appearance of the reddish annulus around the teeth. Photo by Michael Lüth, with permission.

Guard Cells and Stomata

Capsules of many (most?) mosses have guard cells and stomata. The guard cells usually resemble those of tracheophytes, having a doughnut shape, and surrounding the **stoma** (opening; Figure 206, Figure 224). These are mostly located at the base of the capsule. In addition to the cuticle, we might expect the **guard cells** to play a role in water relations of the capsule. After all, the stomata and guard cells have existed through 400 million years of land plant evolution (Chater *et al*. 2011).

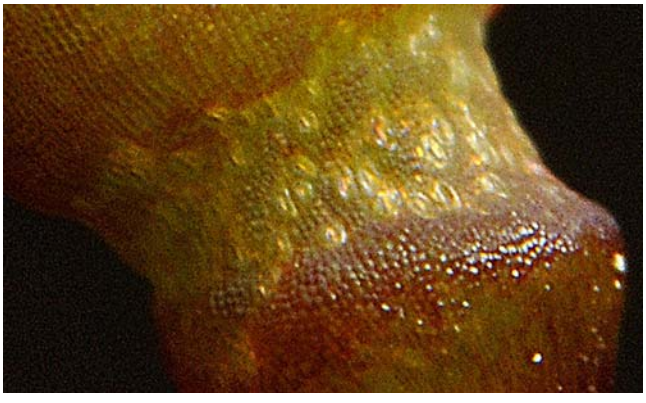


Figure 224. ***Polytrichum*** stomata on capsule base. Photo by George J. Shepherd, through Creative Commons.

Like the cuticle, the role of the pores and stomata has been overlooked in bryophytes. Although we have known about the stomata in moss capsules for a long time, and used them as taxonomic characters in genera such as ***Orthotrichum***, we have largely ignored their function, failing even to ask what it might be.

When thinking about adaptations to drought, we usually think of the survival of the gametophyte. What danger could there be to a dry capsule full of spores, right? But before that capsule is full of spores, it is a photosynthetic body in need of water. Perhaps the young seta with no capsule has little problem, but once the capsule starts to differentiate, water needs most likely increase dramatically. And once meiosis begins, water needs are critical. An interruption during meiosis could lead to a variety of anomalies, many of which could cause spore death.

Paton and Pearce (1957) reviewed the early literature on stomata in bryophytes, pointing out that in ***Sphagnum*** they do not mature. In fact, the capsule pores of ***Sphagnum*** are considered **pseudostomata** (Figure 225-Figure 227). Their function seems to be limited, facilitating capsule dehydration, shape change, and dehiscence (Duckett *et al*. 2009; Merced 2015). This is not surprising, because in ***Sphagnum***, the seta is only a few cells high (Figure 228). Instead, the capsule is elevated on a **pseudopodium** (Figure 228-Figure 229) that is developed from the gametophyte. This pseudopodium does not extend until the capsule is mature. Hence, the role of the pseudostomata to create a transpiration stream for nutrient transport would seem futile. Rather, Duckett and coworkers (2009) provide evidence that the pseudostomata remain open when the capsule is mature, causing the capsule to dry and shrink, forcing the spores out.

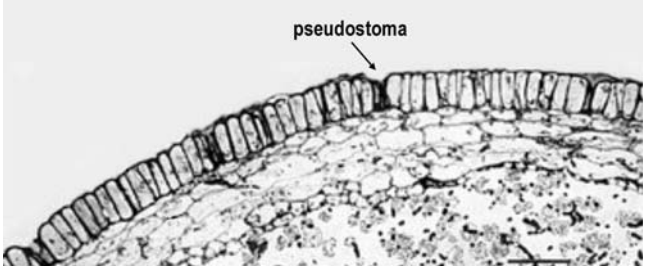


Figure 225. ***Sphagnum*** pseudostomata in capsule. Modified from photo by Amelia Merced, with permission.

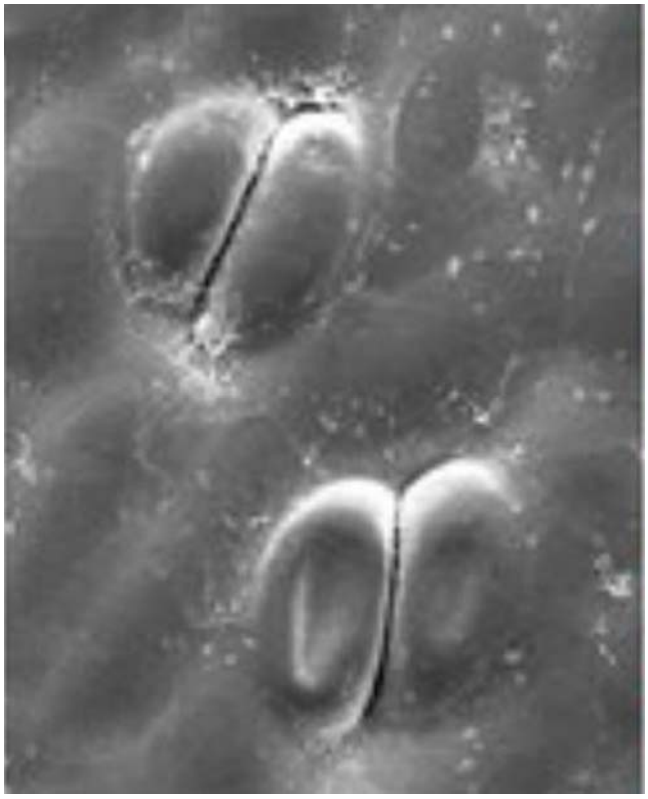


Figure 226. ***Sphagnum*** pseudostomata (SEM) in capsule. Photo by Amelia Merced, with permission.

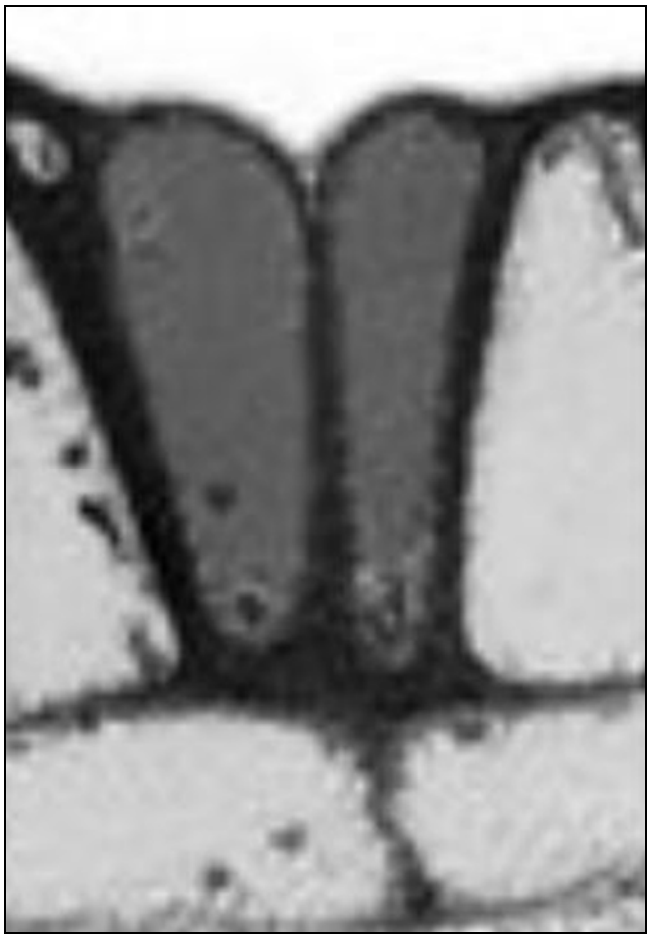


Figure 227. ***Sphagnum*** pseudostomata in capsule section. Photo by Amelia Merced, with permission.

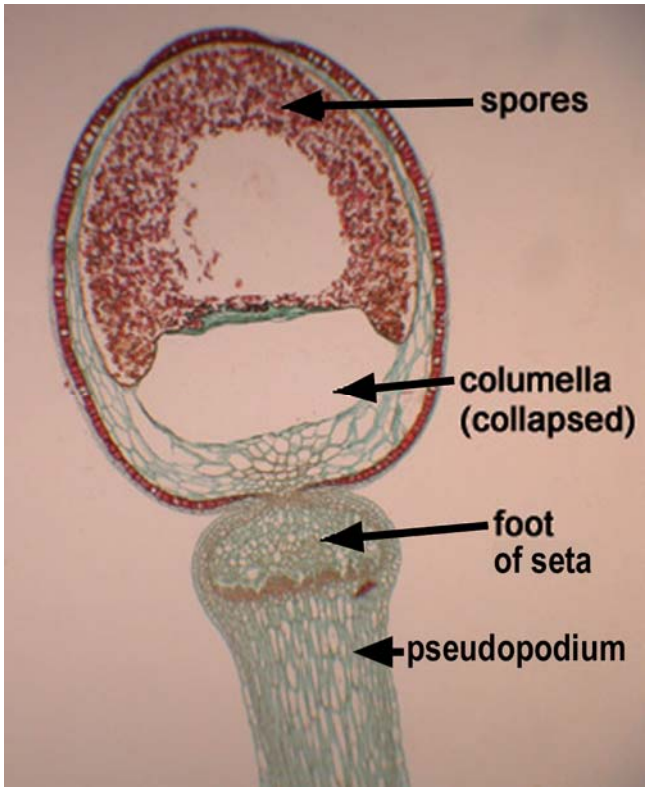


Figure 228. ***Sphagnum*** sporangium on pseudopodium. Photo from Botany website, UBC, with permission.

Figure 229. ***Sphagnum*** with pseudopodium and capsule. Photo from Botany Website, UBC, with permission.

Stomata also are absent in the liverworts (but can have thallus pores), present in at least some hornworts (Figure 238-Figure 241), and absent in the moss order **Andreaeales** (Figure 230-Figure 231) (Paton & Pearce 1957). As in the tracheophytes, the number of guard cells associated with a stoma is usually two (Figure 224-**Error! Reference source not found.**). Known exceptions (single circular guard cells) occur in **Funariaceae** (Figure 198, Figure 208-Figure 211, Figure 232) and ***Buxbaumia aphylla*** (Figure 233). Larger numbers of guard cells (3-4) occur but do not seem to be consistent in any single taxon and are thus considered an anomaly.

Figure 230. ***Andreaea rothii*** with capsules that have no stomata. Photo by Jan-Peter Frahm, with permission.

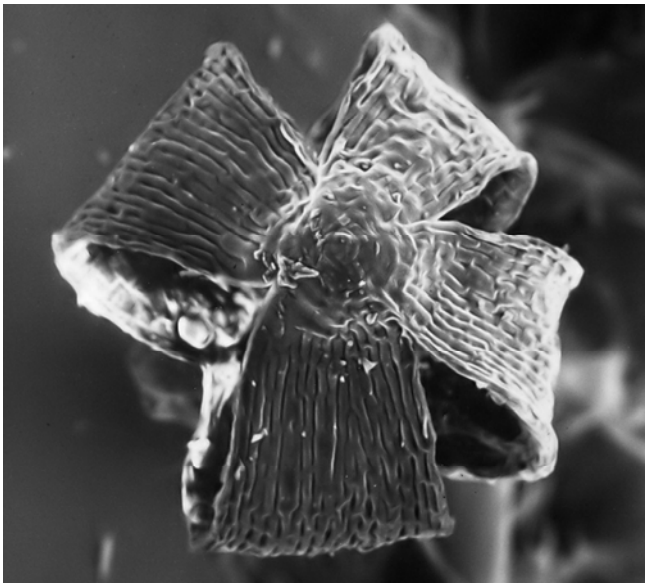


Figure 231. ***Andreaea*** capsule SEM, a capsule that lacks stomata. Photo by George Shepherd, through Creative Commons.

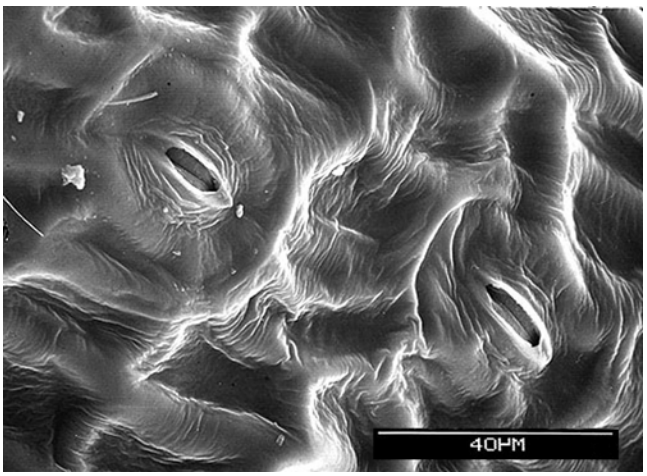


Figure 232. ***Funaria hygrometrica*** stomata showing circular guard cells. Photo courtesy of Jeff Duckett and Silvia Pressel.

Figure 233. ***Buxbaumia aphylla*** capsules, a species with single circular guard cells. Photo by Štěpán Koval, with permission.

The walls of the guard cells are strongly cuticularized (Paton & Pearce 1957). The number of stomata in capsules that have been examined varies from 4 to over 200. Species with a long seta generally have more stomata than species with a short seta or immersed capsules. This supports the hypothesis that they are needed to provide an adequate transpiration stream to transport nutrients from the leafy gametophyte to the sporophyte capsule (Haig 2013), but both are adaptations that would support wind dispersal.

Guard cells are usually located at the base of the capsule. In reality, they tend to be located below the area covered by the calyptra, where gas exchange and water loss are possible. This is consistent with a role to permit water loss, but could they also serve in gas exchange? It appeared that the capsule guard cells did not respond to changes in humidity (Copeland 1902). Rather, they are only able to close when the sporophyte is dehydrated or reopen when it is remoistened. This is consistent with their potential role in bringing nutrients upward.

In the moss ***Physcomitrella patens*** (Figure 234-Figure 236), the stomata of the sporophytes do indeed respond to environmental signals with the hormone abscisic acid (ABA) serving as a signalling component. In fact, the genes controlling ABA in ***P. patens*** can be moved to mutant ***Arabidopsis thaliana*** (flowering plant) that has lost its ABA-regulatory gene and cause stomata in that plant to behave normally. When ***P. patens*** mutants lack the ABA regulatory gene, the response to ABA is greatly reduced.

But wait! While ABA may affect guard cell closure in ***Physcomitrella patens*** (Figure 234-Figure 236), it appears that the guard cells in mosses have a somewhat different mechanism to function. First of all, there seems to be no potassium-regulating mechanism (Duckett *et al*. 2010a). Instead, their primary role seems to be to permit water to escape when the capsule is mature (Boudier 1988; Beerling & Franks 2009; Duckett *et al*. 2009, 2010b). This loss of water causes the capsule to become distorted enough to force the rather stiff circular cap (**operculum**) to pop off, exposing the spores (Figure 237).

Figure 234. ***Physcomitrella patens*** with sporophyte. Photo by Ralf Reski Lab through Wikipedia Commons.

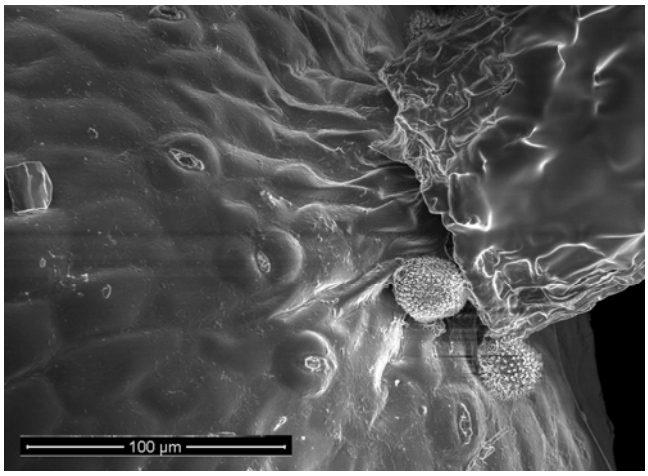


Figure 235. ***Physcomitrella patens*** capsule stomata SEM. Photo courtesy of Jeff Duckett and Silvia Pressel.

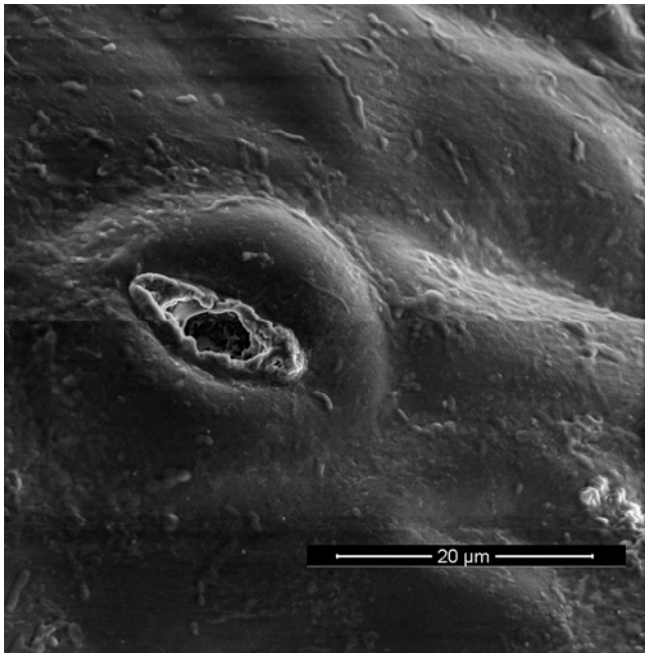


Figure 236. SEM of ***Physcomitrella patens*** stoma. Photo courtesy of Jeff Duckett and Silvia Pressel.

Figure 237. ***Physcomitrella patens*** with open capsules. Photo by Hermann Schachner, through Creative Commons.

It appears that the stomata endow the capsule with multiple advantages. Loss of water during development could be important to create a transpiration stream that moves nutrients upward from the gametophyte to the capsule of the sporophyte, especially in mosses (Haig 2013). If this interpretation is correct, the water loss is essential to maintain continuous movement of water and associated nutrients upward. In fact, Haig interprets the elevation of the capsule on an elongated seta to be an adaptation that increases the movement of water by placing the capsule into the zone of turbulent air above the quiet boundary layer. The placement of the stomata at the base of the capsule gives them exposure while the calyptra reduces water loss from the part of the capsule where spores are developing.

Ziegler (1987) pointed out that in some mosses the sporophyte guard cells have thick walls and do not open and close. This type of guard cell occurs in species that have reduced photosynthetic tissue in the capsule and have been considered evolutionarily reduced. Bryophyte guard cells also differ from those of tracheophytes in that they are larger than the surrounding cells, whereas in tracheophytes they are smaller.

Paton and Pearce (1957) found that the stomata become functionless at a relatively early stage in capsule development, suggesting that this loss in function protects the developing spores against desiccation. They were able to demonstrate this early loss of function in the hornwort ***Anthoceros*** (Figure 238-Figure 239) and in mosses in the **Bryales**. Based on their studies on the hornwort ***Phaeoceros*** (Figure 240), Duckett and Ligrone (2003) say no to the function of capsule guard cells in gas exchange, at least in hornworts; they could find no response to moisture changes or to ABA in the hornwort ***Phaeoceros*** stomata (Figure 241). But if providing a nutrient stream through water transport is to be ruled out, we need experiments that block the stomata to compare with development in capsules that have not had them blocked.

Figure 238. ***Anthoceros agrestis*** with capsules. Photo by Michael Lüth, with permission.

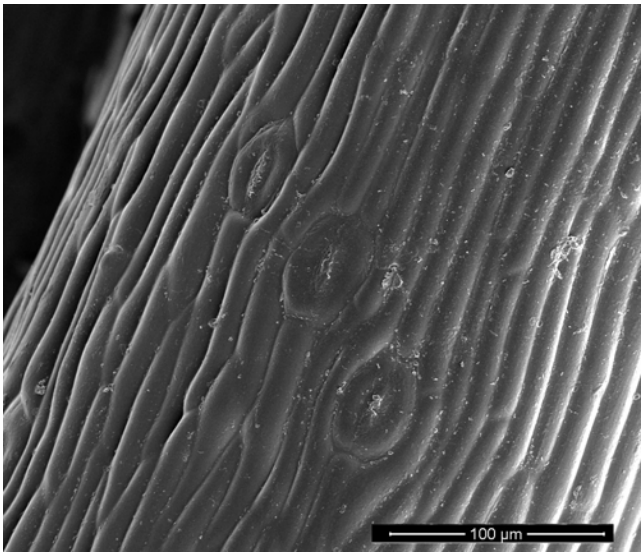


Figure 239. ***Anthoceros punctatus*** SEM image of sporophyte showing stomata. Photo courtesy of Jeff Duckett and Silvia Pressel.

Figure 240. ***Phaeoceros laevis*** with sporophytes dehiscing. Photo by Bob Klips, with permission.

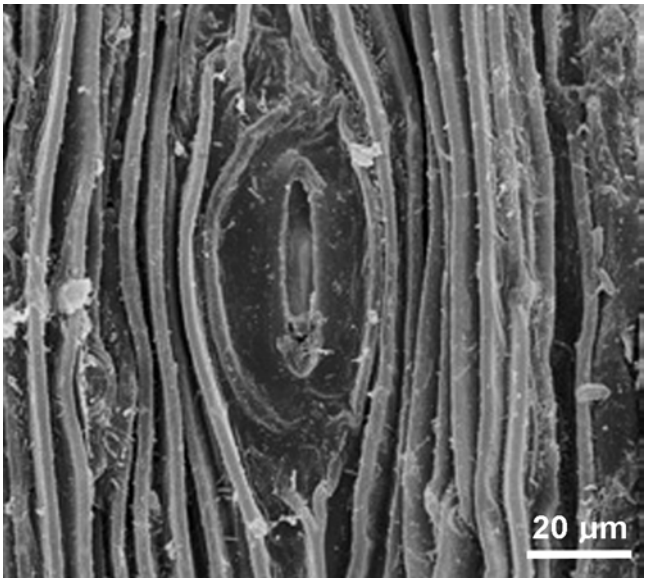


Figure 241. ***Phaeoceros laevis***, open stoma flanked by desiccated and shrunken epidermal cells well above dehiscence point. Photo courtesy of Jeff Duckett, Ken P'ng, Karen Renzaglia, and Silvia Pressel.

On the other hand, in greenhouse-grown ***Funaria hygrometrica*** (Figure 242) the stomata (Figure 232) open on the fourth day of capsule expansion (Garner & Paolillo 1973). By the fifth day, continuing through the tenth day, they close in darkness and reopen in light. They also can be closed by the application of abscisic acid (ABA) (Garner & Paolillo 1973; Chater *et al*. 2011). Thus far we have no evidence to demonstrate the usefulness of this opening and closing. It could enhance gas exchange; it could control water loss during the critical stages of meiosis; and it could serve as a transpiration stream to bring nutrients from the gametophyte. And the function could change or disappear at maturity.

Figure 242. ***Funaria hygrometrica*** capsules. Photo by Li Zhang, with permission.

Indeed it appears that the function changes as the ***Funaria hygrometrica*** (Figure 232, Figure 242) capsule ripens. As maturity approaches, the stomatal responsiveness declines and about half the stomata remain open day and night (Garner & Paolillo 1973)! Furthermore, more stomata become exposed when the calyptra is shed (Duckett *et al*. 2009, 2010a). The stomata no longer provide a mechanism to conserve water.

Further complicating our interpretation of stomatal function during capsule development is the apparent lack of relationship between the presence of stomata and habitat. In the liverworts, stomata are totally absent. But liverworts produce mature capsules before elongation of the stalk occurs, negating the necessity for long distance translocation of nutrients and being consistent with the observations of Paton and Pearce (1957) that fewer stomata occurred on moss capsules with short or absent setae than on those with emergent, longer setae. The widespread absence of stomata in at least some species among so many moss taxa [*e.g.* ***Atrichum*** (Figure 243), ***Pogonatum*** (Figure 244), ***Acaulon*** (Figure 245), ***Campylopus*** (Figure 246), ***Leucobryum*** (Figure 247), ***Cinclidotus*** (Figure 248), ***Discelium*** (Figure 249), ***Nanomitrium***, ***Fontinalis*** (Figure 250), ***Tetraphis*** (Figure 251), ***Catoscopium*** (Figure 252), ***Cyclodictyon*** (Figure 253), ***Leucodon*** (Figure 254) (Paton & Pearce 1957)] suggests they are not essential for gas exchange. Furthermore, since most of these genera have long setae, one could argue against their function in creating a transpiration stream for nutrient transport. One might also argue that the well developed vascular tissue in both gametophytes and sporophyte setae of the **Polytrichaceae** makes the presence of stomata to create a transpiration stream unnecessary for nutrient transport, yet some members of the family have stomata and guard cells. And the stomata in tracheophytes are certainly necessary to maintain function of the xylem tissue in these larger plants. But there is no rule that says they can't serve different functions at different times or in different species.

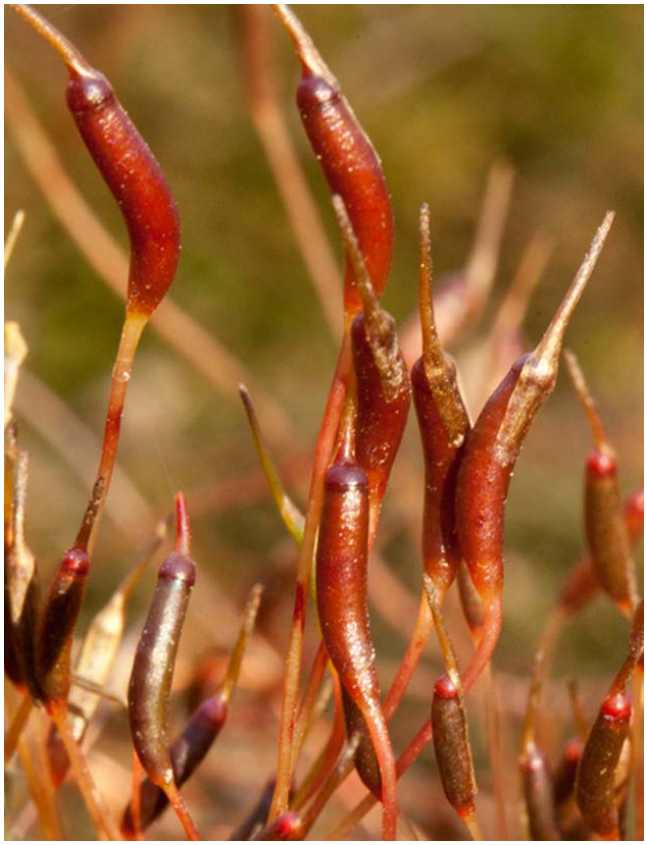


Figure 243. ***Atrichum crispulum*** capsules – in a genus in which at least some species lack stomata. Photo by Bob Klips, with permission.

Figure 244. ***Pogonatum urnigerum*** capsules, member of a genus in which some species lack stomata. Photo by Kristian Peters, with permission.

Figure 245. ***Acaulon muticum*** with capsules, a genus in which species lack stomata. Photo by Michael Lüth, with permission.

Figure 246. ***Campylopus nivalis*** capsules, a species that lacks stomata. Photo by Michael Lüth, with permission.

Figure 247. ***Leucobryum glaucum*** with mature capsules, member of a genus in which capsules often lack stomata. Photo by Janice Glime.

Figure 248. ***Cinclidotus fontinaloides***, a species that lacks stomata. Photo by Michael Lüth, with permission.

Figure 249. ***Discelium nudum*** capsule, a genus in which at least some members lack stomata. Photo by Des Callaghan, with permission.

Figure 250. ***Fontinalis squamosa*** var ***curnowii*** with capsules, in a genus that lacks capsule stomata. Photo by David Holyoak, with permission.

Figure 251. ***Tetraphis pellucida*** capsule, in a genus that lacks stomata. Photo by Walter Obermayer, with permission.

Figure 252. ***Catoscopium nigritum*** with capsules, in a genus that lacks capsule stomata. Photo by Hermann Schachner, through Creative Commons.

Figure 253. ***Cyclodictyon bicolor*** with capsules, in a genus that lacks capsule stomata. Photo by Amelia Merced, with permission.

Figure 254. ***Leucodon sciuroides*** with capsules, in a genus that lacks capsule stomata. Photo by Hermann Schachner, through Creative Commons.

Merced and Renzaglia (2013) demonstrated the remarkable similarity between stomata in the highly developed ***Oedipodium*** (Figure 255) and the very reduced ***Ephemerum*** (Figure 256) capsules. The capsule structure differs, with ***Oedipodium*** having extensive spongy tissue along the capsule apophysis where stomata are concentrated and ***Ephemerum*** lacks such tissue but has minimal substomatal cavities. Although ***Oedipodium*** (Figure 255) has numerous long-pored stomata and ***Ephemerum*** has few round-pored stomata, the stomatal ultrastructure and wall thickenings of these two taxa are quite similar. Both have sporophytes with a cuticle that is thicker on the guard cells and extends on the walls surrounding the stomata. When the capsules are older, epicuticular waxes and pectin clog the pores, closing them much like the stomata of fir trees in winter. Merced and Renzaglia argue that the cuticle, water-conducting cells, and spongy tissues of ***Oedipodium*** all support the role of stomata in facilitating gas exchange and water transport as the sporophyte develops. They also contend that the existence of stomata exclusively on capsules may indicate a function in drying and dispersal of spores.

Figure 255. ***Oedipodium griffithianum*** with young capsules, a species with a well developed spongy apophysis and many stomata. Photo by Des Callaghan, with permission.

Figure 256. ***Ephemerum recurvifolium*** with capsules, a moss that lacks a spongy apophysis and has few stomata. Photo by Tomas Hallingback, with permission.

Hence, we have four potential functions for the stomata of capsules. These include a role in creating a transpiration stream to aid in nutrient transport, prevention of water logging that inhibits gas exchange, regulation of gas exchange, and drying that contracts the capsule and aids in spore expulsion.

Spores

Spore physiological adaptations are seldom discussed. Fan *et al*. (2023) have just published a study that compares spore germination of six peatland bryophytes under various water regimes. They found that frequent dry-wet cycling reduced spore germination more than less frequent cycling. And habitat mattered. Hummock species such as ***Sphagnum capillifolium*** (Figure 257) and ***S. fuscum*** (Figure 258) had a greater spore germination percentage after continuous dry treatment, whereas the hollow species [***S. angustifolium*** (Figure 259), ***S. squarrosum*** (Figure 260), ***S. subsecundum*** (Figure 261)], had the opposite response, with highest germination following the wet treatment. Both hummock and hollow species exhibited the greatest spore viability after the dry treatment, and viability gradually decreased with the increased frequency of dry-wet cycling. Hummock species had greater %germination than did hollow species (Figure 262.

Figure 257. ***Sphagnum capillifolium***, a hummock species. Photo by Bernd Haynold, through Creative Commons.

Figure 258. ***Sphagnum fuscum***, a hummock species. Photo by Jutta Kapfer, with permission.

Figure 259. ***Sphagnum angustifolium***, a species of hollows. Photo by Mark Rahill, with permission.

Figure 260. ***Sphagnum squarrosum***, a species of hollows. Photo by Keto Gyekis, with online permission.

Figure 261. ***Sphagnum subsecundum***, a species of hollows. Photo by Mark Rahill, with permission.

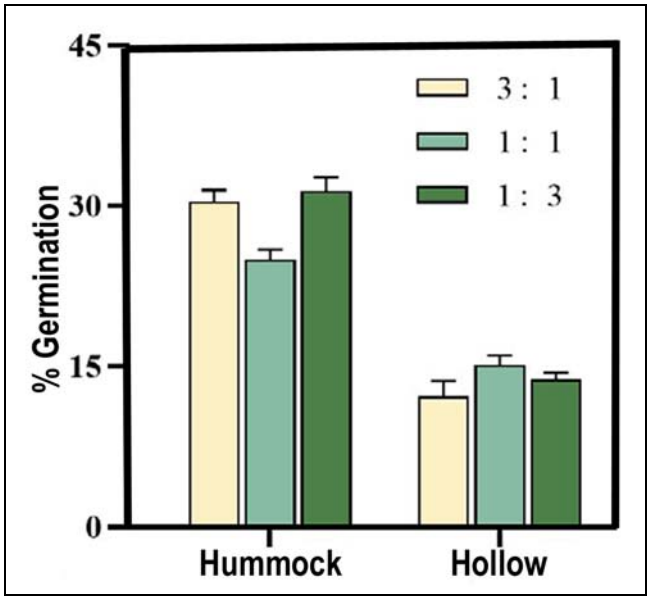


Figure 262. Mean spore viability + standard error following different wet-dry cycle regimes of six peatland ***Sphagnum*** species. 3:1, 1:1, and 1:3 respectively represent the ratio of days of dry and wet treatment in dry-wet cycling. n=5. Image modified from Fan *et al*. 2023.

Hummock vs hollow species seem to have evolved different responses to wetting. Hummocks that have sufficient oxygen and intermittent flooding are more suitable for high spore germination percentage of ***Sphagnum*** spores than the continuously waterlogged hollows (Sunberg & Rydin 2000). But Feng *et al*. (2017) found that in ***S. fallax***, (Figure 263) more wet-dry cycling promoted higher spore germination rates. Furthermore, Feng and coworkers suggested that the strong microbial activity of the intermittently flooded environments could facilitate spore germination by breaking down the spore wall.

Figure 263. ***Sphagnum fallax***, a species in which spore germination rates benefit by frequent wet-dry cycles. Photo by Hermann Schachner, through Creative Commons.

It appears that the **Gaia hypothesis** may be operating at many levels in the ecosystem, and that the bryophytes are no exception. Their behavior with such companion

species as bacteria permits the combination to act as a super organism.

Summary

Poikilohydric bryophytes depend on desiccation tolerance (**DT**), becoming dormant when desiccated. Bryophytes gain water in their cells both through external (**ectohydric**) capillary movement and internal (**endohydric**) transport. When fully hydrated, their water content is typically high, up to more than 1200% of their dry mass. When dry, they can survive months to many years. Structural adaptations of stems and whole plants such as **growth form**, **branch** and **leaf arrangements**, **rhizoidal tomentum**, **mucilage**, **central strand**, **hydroids**, **paraphyllia**, **ventral scales, cuticles**, and **stomata** aid in moving water, facilitating entry, or reducing loss.

In xerophytic bryophytes, leaves and stems often possess large **trigones** and **nodular intermediate thickenings** on interior walls. Some liverworts have branched **vittae** such as those of ***Herbertus aduncus*** that enhance water uptake and storage. **Papillae** create capillary spaces to hold water on leaf surfaces. Leaf cells are usually small and basal **alar cells** help the leaf change positions to be near the stem upon drying. Xerophytic stem cells are thick-walled. These wall adaptations consist mostly of hemicelluloses, pectins, and cellulose, substances that would facilitate apoplastic water uptake, movement, and retention.

Thallose liverworts benefit from ventral transport by **rhizoids** and **scales**. The dorsal surface is covered by a **cuticle** but gas exchange may occur through pores overlying photosynthetic chambers. The pores are ringed by cells with cuticular ridges that prevent water drops from entering but that allow water vapor to escape, as well as admitting CO_2 and expelling O_2. Midribs may help to gather and direct water both externally and internally. Some have **ballooning cells** on the epidermis. For many taxa, dormancy is a "last resort" to avoid the effects of desiccation.

Fungal partners occur in both thallose and leafy liverworts, but their role is not known. Smooth rhizoids facilitate fungal entry; pegged rhizoids transport water and the pegs prevent collapse upon drying.

In mosses and leafy liverworts, **growth form** can help in both movement and conservation of water. Clumps reduce transpiration and provide additional capillary spaces. **Mixed species** can help each other, especially if one is good at moving water and one is good at retaining it. Mosses may have a **central strand** where water moves, but this is apparently absent in all liverworts except the **Haplomitriopsida**. **Leaf cuticles** occur in both mosses and liverworts and may repel water to avoid water logging or reduce loss by transpiration. **Rhizoids** and **tomentum** help in the movement of water upward. **Mucilage** in some liverworts, especially **Haplomitriopsida**, can be of great value in holding water about the plants.

The **protonema** can usually withstand slow drying. Like the guard cells in some stomata, it is responsive to **ABA**. ABA may be linked to **inducible desiccation tolerance** in the gametophores. **Constitutive desiccation tolerance** is the most common form of desiccation tolerance in bryophytes, but as the plants age they may switch to inducible desiccation tolerance. **Hardening** can occur following slow drying and may last more than a few days.

The sporophyte and calyptra both have **cuticles**, and at least in ***Funaria hygrometrica***, the cuticle in the calyptra matures first, helping the calyptra to protect the young embryo. Calyptra hairs, thallus hairs, paraphyllia, and paraphyses all function to help in movement of water and reduce rate of drying. Capillary spaces provided by these can further facilitate absorbing and holding water, bathing the tissues in water and reducing water loss.

The sporophytes of most(?) mosses and hornworts have **guard cells** and **stomata** that cease to open and close at sporophyte maturity. Their function(s) are ambiguous, but they may contribute to creating a transpiration stream to move nutrients upward, regulating capsule hydration during development, and drying the capsule prior to dehiscence and dispersal.

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CHAPTER 7-4a

WATER RELATIONS: LEAF STRATEGIES – STRUCTURAL

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CHAPTER 7-4a

WATER RELATIONS: LEAF STRATEGIES – STRUCTURAL

Figure 1. ***Campylopus introflexus*** demonstrating the ability of water to cling and collect on the thin, wiry leaves. Photo by Michael Lüth, with permission.

Much of what we know about water uptake by bryophytes has been through observation. While the observations are probably valid, broad generalizations have emerged and these have been applied to all mosses, especially by non-bryologists, and can lead to inappropriate experiments and conclusions.

Larson (1981) experimented with three species of bryophytes (and 8 lichens) using a "raining" wind tunnel environment to determine the effects of various structures on water uptake and storage. Larson found that the time required to reach saturation did not differ between lichens and mosses, varying from three minutes in the moss ***Polytrichum juniperinum*** (Figure 2) to over 300 minutes in the lichen ***Stereocaulon saxatile***. The rate of absorption increases with the ratio of surface area to weight, making it extremely rapid in finely divided plants. Hence, comparison of leaf structure and plant form become important in considering the role of bryophytes in the water cycling of an ecosystem (Proctor *et al*. 1998; Wu *et al*. 2007).

Schofield (1981) considered leaf shape, arrangement, orientation, surface ornamentation, and detailed anatomy to be important in influencing water movement. These adaptations are complemented by branch arrangement, stem cortical cells, rhizoid structure, and presence of paraphyllia.

Figure 2. ***Polytrichum juniperinum*** hydrated (**left**) and dry (**right**) showing change in leaf position to wrap around stem. Photo by Michael Lüth, with permission.

Bryophytes hold their water in three ways (Proctor *et al*. 1998): **apoplastic** water in cell-wall capillary spaces and held by matric forces; **symplastic** (internal osmotic) water; external capillary water. For many bryophytes, the external capillary water is a highly important, albeit variable, component. This external water complicates any measurements of relative water content (RWC) because it makes measurement of the bryophyte at full turgor a difficult endeavor. Proctor *et al*. found that full-turgor water ranged from 110% dry weight (dw) in ***Syntrichia ruralis*** (Figure 3) and ***Andreaea alpina*** (Figure 4) to 1400% dw or more in ***Dumortiera hirsuta*** (Figure 5) and ***Conocephalum conicum*** (Figure 6-Figure 7). Most species had an osmotic potential ($\Psi\pi$) at full turgor of -1.0 to -2.0 MPa, but thallose liverworts had values that were much less negative (-0.35 to -0.64 MPa).

Figure 3. ***Syntrichia ruralis*** with raindrops, a moss with low water content. Photo by Peggy Edwards, with permission.

Figure 4. ***Andreaea alpina***, a moss with low water content. Photo by Andrew Hodgson, with permission.

Figure 5. ***Dumortiera hirsuta***, a thallose liverwort that holds a high water content. Photo by Li Zhang, with permission.

Figure 6. ***Conocephalum conicum***, a thallose liverwort that holds a high water content. Photo by Robert Klips, with permission.

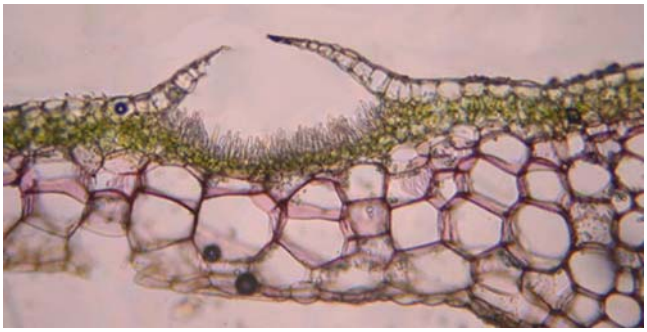

Figure 7. ***Conocephalum conicum*** thallus section with pore From website of the Botany Department, University of British Columbia, with permission.

Pressel *et al*. (2009) pointed out that despite the ancient history of liverworts, we know little about the physiology of their desiccation tolerance. Desiccation causes a number of cytological changes in liverworts, including fragmentation of the vacuole, rounding of the chloroplasts and mitochondria with thylakoids, and cristae becoming rearranged but remaining undamaged, all responses that are similar to those of mosses and **tracheophytes** (non-bryophyte plants; plants with lignified vascular tissue). Furthermore, chlorophyll fluorescence shows half–recovery within minutes to 2 hours, but requires 24-48 hours to reach normal, unstressed values. And like desiccation tolerance in mosses, the de- and repolymerization of the cortical microtubule cytoskeleton

are associated with de- and rehydration. But liverworts have oil bodies, and these play a role unknown in mosses, as will be seen below.

Guerra *et al*. (1992) described the adaptations of xeric mosses in the gypsiferous zones of the southeast Iberian Peninsula, listing 15 modifications for conserving water. I have included these and some of my own observations here.

Overlapping Leaves

Most bryophytes have their leaves inserted at angles on the stem. In some cases, especially leafy liverworts (Figure 8), these are **incubous** in arrangement [leaves overlapping from base to tip like shingles on a roof, with the part of the leaf closer to the stem base being nearer the substrate (ventral) and the more apical side emerging on the upper (dorsal) side of the stem], whereas others are **succubous** [basal edge dorsal, apical edge ventral – the leaf succumbs to the leaf above it].

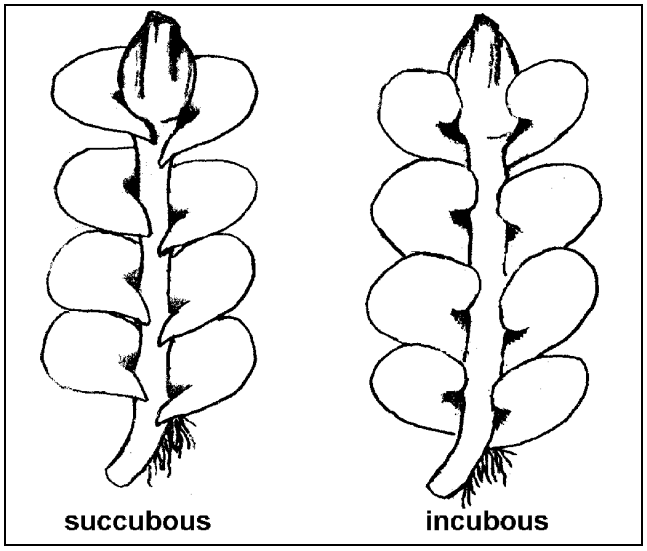

Figure 8. Succubous leaf arrangement of liverworts such as ***Jungermannia*** (**left**) and incubous arrangement of those such as ***Calypogeja*** (**right**). Note the decurrent leaf bases in the liverwort on the left. Redrawn by Margaret Minahan from Iwatsuki.

Clee (1937) found that in the succubous ***Plagiochila asplenioides*** var. ***major*** (Figure 9), water could move up to 3.7 cm in one minute. However, with the incubous arrangement, water moved less than 1 cm per minute. On the other hand, Basile and Basile (1987) questioned the role of the incubous vs. succubous leaf orientation in water conduction. They found that conduction proceeds equally in both orientations and that there is no correlation between the direction of leaf overlap and the angle of the substrate slope where they commonly grow. This seems reasonable since water coming from the top in rainfall would be presented with the opposite direction from water coming from beneath the branch. Hence, we could consider the branches in Figure 8 to be the above and below presentations of the same plant. Certainly if water is available from both above and below, it should make little difference if the plant is succubous or incubous. We need experiments to compare the effect on liverworts that form protruding shelves, those that are growing upright from a substrate, those that are adnate to a vertical surface, and those that grow horizontally adnate to a substrate. Then we need to compare the direction of the water source – base or tip of plant, dorsal or ventral surface.

Figure 9. ***Plagiochila asplenioides*** with overlapping, succubous leaves. Photo by Michael Lüth, with permission.

Among mosses, Bowen (1933) considered the erect habit of leaves to hold and conduct more water than spreading leaves. This effect is enhanced if the leaves have **decurrent** bases (extensions of the leaf base down the stem; Figure 8).

Bayfield (1973) found that as water content declined in ***Polytrichum commune*** (Figure 10), the leaf arrangement changed (see also changes in ***Polytrichum juniperinum*** Figure 2). As the moisture decreased, the leaves wrapped closer around the stem, seemingly increasing moisture retention, a phenomenon that makes ***Hedwigia ciliata*** (Figure 11) almost unrecognizable when wet if one is only familiar with the dry state. Bayfield also found that external conduction is possible in the capillary spaces between the stem and the overlapping leaf bases. In the endohydric ***Polytrichum*** species, the loss of water is controlled by a complex series of changes in the leaf arrangement, whereas in the ectohydric ***Racomitrium lanuginosum*** (Figure 12-Figure 13), little or no mechanical control is exercised over water loss. It is likely that all ***Polytrichum*** (Figure 2, Figure 10) species benefit from this movement of the leaves upon drying.

Figure 10. ***Polytrichum commune*** showing the dry lower leaves that are beginning to wrap around the stem compared to the wide-spreading upper leaves that are well hydrated. Photo by Michael Lüth, with permission.

Figure 11. ***Hedwigia ciliata*** showing wet leaves (**upper left**) and dry leaves (**diagonally across lower right**) as a result of drying from the edge of the mat inward. The plants were growing on exposed boulders at the base of a cliff. Photo by Janice Glime.

Figure 12. ***Racomitrium lanuginosum*** dry showing twisted leaves and prominence of awns at the leaf tips, but little mechanical control over water loss. Photo by Michael Lüth, with permission.

Figure 13. ***Racomitrium lanuginosum*** wet showing transparent awns that are much less conspicuous than in dry plants. Photo by Des Callaghan, with permission.

Leaves Curving or Twisting upon Drying

Many species have leaves that curve or twist when they dry, particularly those in xeric habitats. These leaves curve toward the stem and thus reduce the exposed surface area. Among these are ***Campylostelium pitardii*** (Figure 14), ***Phascum cuynetii***, and ***Pterygoneurum sampaianum***.

Figure 14. ***Campylostelium pitardii*** with capsules, a species whose leaves curve or twist when dry. Photo by Proyecto Musgos, through Creative Commons.

Thickened Leaf

Many leaves partially protect themselves from water loss by having all or part of the leaf more than one cell thick. This is a common character for the borders and costa, where it most likely serves for support and possibly water movement, but in the leaf **lamina**, this reduces the exposed surface area (Figure 17).

Some leaves are **bistratose** in the upper part of the leaf, *i.e.* the part most exposed when the plant is dry. Among these are the xerophytic species ***Syntrichia caninervis*** (Figure 115) subsp. ***spuria***, ***Dicranella varia*** (Figure 15), and ***Didymodon australasiae*** (Figure 16) (Guerra *et al*. 1992).

Figure 15. ***Dicranella varia***. Note the twisted leaves on the dry mosses in the foreground. Photo by J. C. Schou, with permission.

Figure 16. ***Didymodon australasiae*** showing leaves curved around the stem in this dry state. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Some species protect the photosynthetic cells with hyaline cells, as in ***Leucobryum*** (Figure 18) and ***Octoblepharum*** (Figure 19). ***Fissidens grandifrons*** (Figure 20) differs from most other members of the genus ***Fissidens*** by having leaves that are multiple cell layers thick, most likely an adaptation to its habitat in fast-flowing water of streams and waterfalls. ***Fissidens*** accomplishes a degree of protection and provides capillary water-holding spaces by creating a pocket (Figure 21-Figure 24), giving this region a thickness of two layers of cells; the next leaf toward the apex often fits into this pocket. But this flattened moss nevertheless moves water slowly through its external surface (Table 1).

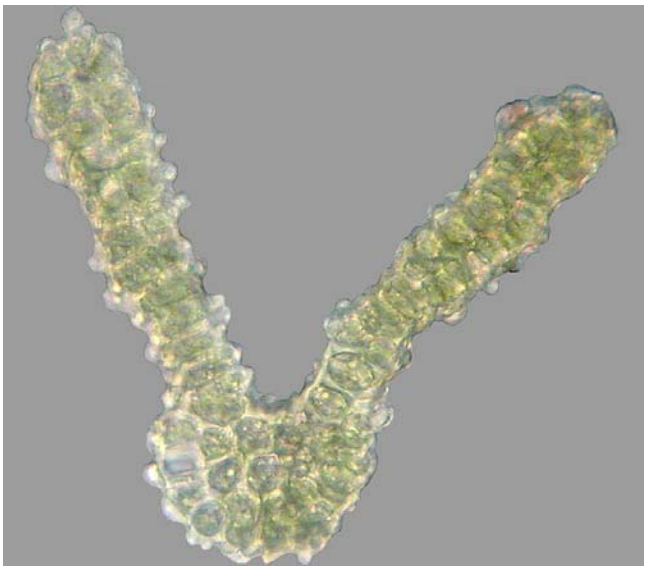

Figure 17. ***Grimmia anomala*** leaf section showing double layer of cells in parts of the lamina and papillae on the cells. Photo by Michael Lüth, with permission.

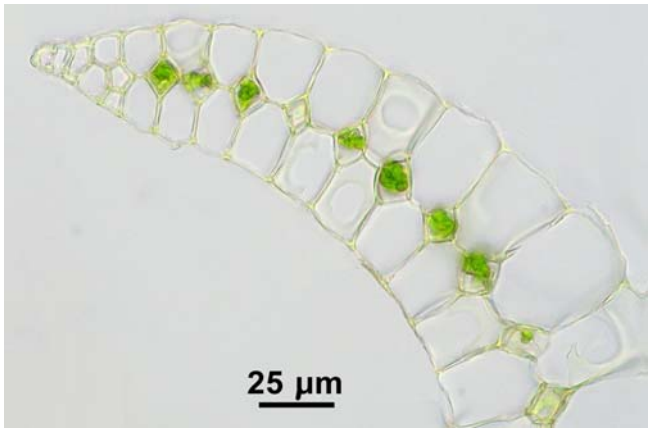

Figure 18. ***Leucobryum glaucum*** leaf cross section showing multiple layers with outer hyaline cells and central photosynthetic cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

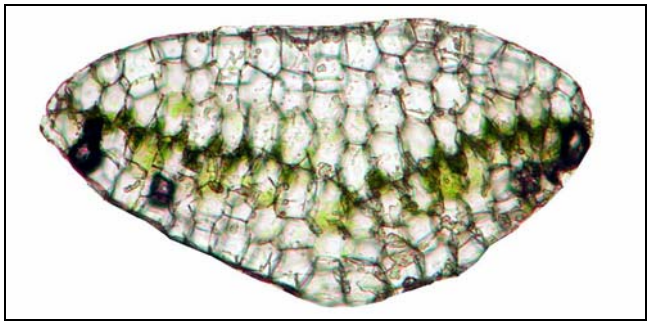

Figure 19. ***Octoblepharum albidum*** leaf cross section showing multiple layers of hyaline cells. Photo by Michael Lüth, with permission.

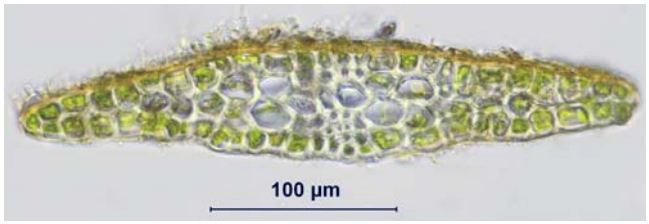

Figure 20. ***Fissidens grandifrons*** leaf cross section showing multiple layers that help this species to survive in torrents of water in waterfalls and snowmelt streams. These layers may also aid its survival when the water recedes, stranding it out of the water. Photo by Li Zhang, with permission.

Figure 21. ***Fissidens asplenioides*** showing flattened branch with each leaf fitting into the pocket of the one below it. Photo by Michael Lüth, with permission.

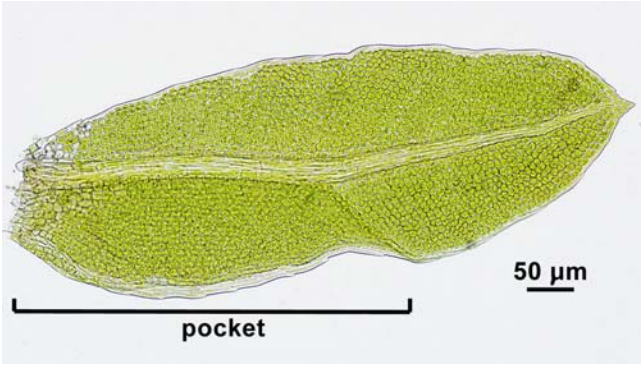

Figure 22. ***Fissidens crispus*** leaf showing pocket. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 23. ***Fissidens taxifolius*** leaves showing one leaf fitting into pocket of the next. Photo by Walter Obermayer, with permission.

Figure 24. ***Fissidens taxifolius*** leaf cross section through pocket. Note that the costa forms the region where the two halves join. Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Concave Leaves

Proctor (1979a) found that many taxa of ectohydric mosses have concave leaves (*e.g.* Figure 25-Figure 26). When examined in moist weather, the concavities on the upper sides of the leaves will generally be full of water. This helps to solve the problem of gas exchange by exposing one surface to the atmosphere while keeping the other surface bathed in water. And most of the CO_2 needed for photosynthesis comes from respiration in the soil and litter. Gas diffusion in air is about 10^4 times faster than in water (Proctor 1982). Other mosses, like ***Campylopus*** (Figure 1) and ***Polytrichum*** (Figure 2, Figure 10), are able to roll their leaves, like some grasses, when they are dry. In this mode, mosses like ***Syntrichia ruralis*** (Figure 28) can look much darker and expose less surface area to the atmosphere, whereas the wet cells change the optical properties, making the cell walls more translucent (Glime & Church, unpubl.).

Figure 25. The moss ***Scleropodium touretii*** illustrating deeply concave leaves. Photo by Michael Lüth.

Figure 26. ***Pseudoscleropodium purum*** showing concave leaves. Photo by Aimon Niklasson, with permission.

Figure 27. ***Syntrichia ruralis*** dry. Photo by Janice Glime.

Figure 28. ***Syntrichia ruralis*** wet. Photo by Janice Glime.

Leaf spreading upon re-moistening is rapid in most bryophytes. Yenhung Li (unpublished data) found that in ***Sphagnum*** sp., ***Ptilium crista-castrensis*** (Figure 29), ***Pleurozium schreberi*** (Figure 30), and ***Dicranum polysetum*** (Figure 32), the first leaves spread within 1.5 to 2 seconds of receiving water (Table 1). To wet all the leaves in pieces 0.7 cm long required less than 2 minutes for most taxa, but required 24 minutes in ***Rhodobryum ontariense*** (Figure 31). The highest rate of conduction among the 15 taxa was in ***Pleurozium schreberi*** (140 mm min^{-1}).

Figure 29. ***Ptilium crista-castrensis***, a moss that rewets quickly. Photo by Michael Lüth, with permission.

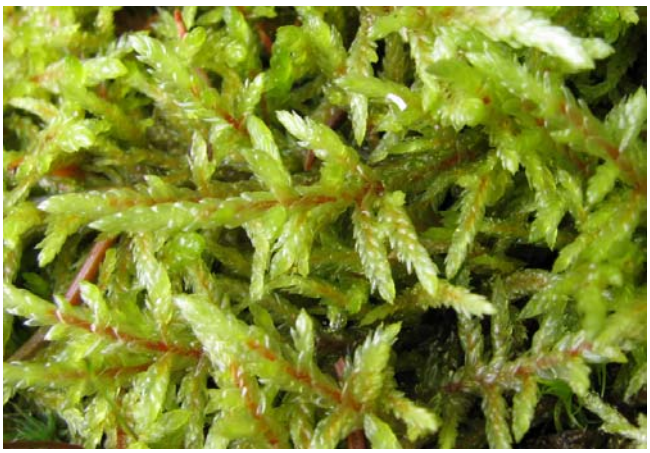

Figure 30. ***Pleurozium schreberi***, a feather moss that rewets quickly. Photo by Janice Glime.

Figure 31. ***Rhodobryum ontariense***, a moss that rewets very slowly. The dense cluster of leaves are all at the top of the stem. Photo by Janice Glime.

Figure 32. ***Dicranum polysetum***, a boreal forest moss that rewets quickly. Photo by O. V. Ivanov, with permission.

Table 1. Mean time required for leaf spreading and conduction rate after rewetting along 0.7 cm branches in 15 species of bryophytes (n = 30 & 10 respectively). Based on Yenhung Li, unpublished data.

Species	sec for spreading	conduction mm/min
Ptilium crista-castrensis	2	0.93
Dicranum polysetum	2	70.00
Pleurozium schreberi	5	140.00
Hedwigia ciliata	5	11.48
Climacium dendroides	8	21.00
Fontinalis duriaei	9	2.60
Dicranella heteromalla	10	11.48
Lophozia barbata	10	24.1
Anomodon attenuatus	14	0.06
Fontinalis antipyretica var. *gigantea*	26	27.5
Porella platyphylla	34	0.75
Sphagnum sp.	90	6.0
Bryum pseudotriquetrum	149	0.82
Fissidens adianthoides	284	0.08
Rhodobryum ontariense	1421	0.06

Li found some indication that small leaves can spread more quickly than large ones, at least in ***Fontinalis***. ***Fontinalis duriaei*** (Figure 33) has smaller and thinner leaves than does ***F. antipyretica*** var. ***gigantea*** (Figure 34-Figure 35), and ***F. duriaei*** can spread its leaves in 1/3 the time required for ***F. antipyretica*** var. ***gigantea***. However, the difference may be due to the stiffness of the **keel** (leaf fold; Figure 35) in ***F. antipyretica*** var. ***gigantea***, whereas ***F. duriaei*** has flat leaves.

Figure 33. ***Fontinalis duriaei***, a species with flat, relatively narrow leaves that spread more quickly than larger leaves with a keel in ***Fontinalis antipyretica*** var. **gigantea**. Photo by Janice Glime.

Among the slowest species to re-wet in Li's study were ***Fissidens adianthoides*** (Figure 36) and ***Rhodobryum ontariense*** (Figure 31), both for rate of conduction and leaf wetting. ***Fissidens adianthoides*** has leaves that are large and partly two-layered. There is little overlap between the leaves in this genus except at the two-layered pocket (Figure 37), and Church and Nelson (unpubl data) noted that when the leaves of ***F. adianthoides*** are dry there is little or no overlap even at the pocket. Therefore, lack of capillary space may account for its slow response. The slowness of ***Rhodobryum ontariense***, which has all its leaves crowded at the top of the stem like a palm tree (Figure 31), may likewise be explained by lack of capillary spaces (Figure 38). Below the crowded rosette of leaves at the apex are very reduced scale-like leaves along the stem, providing little capillary space and rendering it the slowest among the 15 species observed by Li. It required 123 minutes for the water to travel 0.7 cm up the stem! Although Li's data indicate a slight trend for rapid conduction to be coupled with rapid leaf spreading, there are enough exceptions to indicate that the relationship is not so simple.

Figure 34. ***Fontinalis antipyretica*** showing keeled leaves that spread slowly but that conduct water externally relatively rapidly. Photo by Jan-Peter Frahm, with permission.

Figure 35. ***Fontinalis antipyretica*** leaf showing keel (**lower side of image**). Photo by Malcolm Storey, through Creative Commons.

Figure 36. ***Fissidens adianthoides***, a moss providing little capillary space, hence slow external conduction. Photo by Niels Klazenga, with permission.

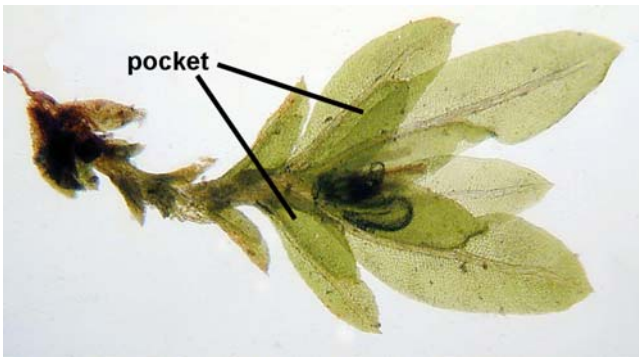

Figure 37. ***Fissidens arnoldii*** showing the overlap created by leaf pockets where the leaf blade has two, but separated, layers. Photo by Michael Lüth, with permission.

Figure 38. ***Rhodobryum ontariense*** dry, with its leaves twisted upward. Note the bare stem that seemingly provides no capillary spaces for external conduction. Photo by Michael Lüth, with permission.

Cucullate Leaves

Cucullate is hooded or boat-shaped, referring to the apex of leaves in this case. The cavity created by this leaf form is able to hold water, in part due to surface tension. An example of this is the moss ***Phascum cuynetii***; some ***Sphagnum*** (Figure 39) species also have cucullate leaves.

Figure 39. ***Sphagnum*** sp. from the Neotropics showing cucullate leaves. Photo by Michael Lüth, with permission.

Plications

Plications, or Japanese fanfolds, in the leaf may reduce evaporation by reducing the exposed area and creating nearly dead space between the folds. On the other hand, it might simply be a means of neatly folding the leaf as it dries and loses the turgidity that kept it concave. These plications are present in ***Brachythecium*** (Figure 40), ***Coscinodon*** (Figure 41-Figure 43), and ***Hamatocaulis vernicosus*** (=*Drepanocladus vernicosus*; Figure 44), among others. Some taxa exhibit these only as they are drying or dry, so the system is responsive to water loss. When it is rehydrated, the plications permit the leaf to expand.

Figure 40. ***Brachythecium*** leaves showing plications. Photo by Bob Klips, with permission.

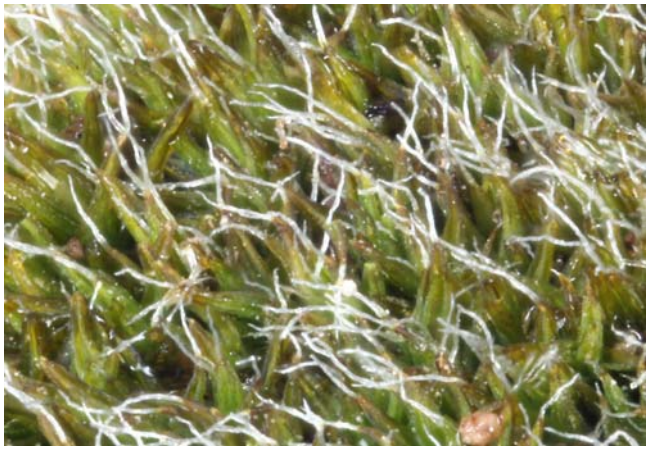

Figure 41. ***Coscinodon cribrosus***. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

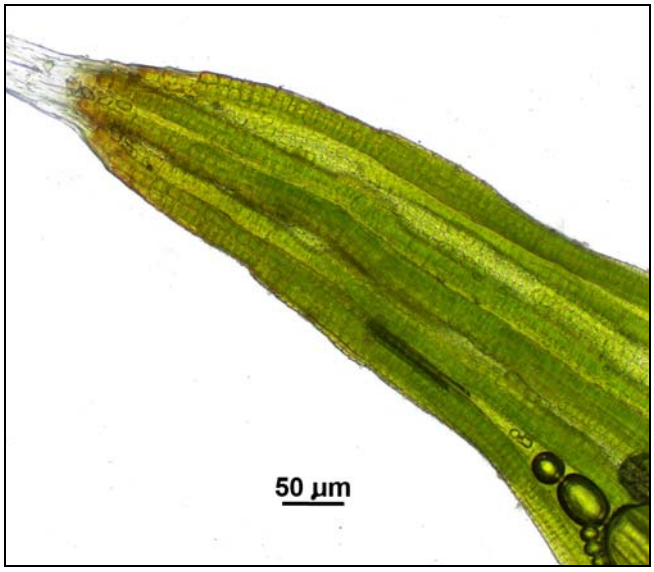

Figure 42. ***Coscinodon cribrosus*** leaf with plications. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 43. ***Coscinodon cribrosus*** leaf cross section showing plications. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 44. ***Hamatocaulis vernicosus*** showing plications at arrow. Photo by Des Callaghan, with permission.

Revolute and Involute Margins

Just as elongate cells of the border permit leaves to become contorted as they dry, the involute (Figure 45-Figure 48) and revolute (Figure 49-Figure 50) margins add structural support to the margin that causes contortions when the leaf dries (Figure 50). This contorted condition is known as **crispate**.

Figure 45. ***Weissia controversa*** that has recently been wet, showing **involute** leaf margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 46. ***Weissia controversa*** dry, showing **crispate** leaf arrangements. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

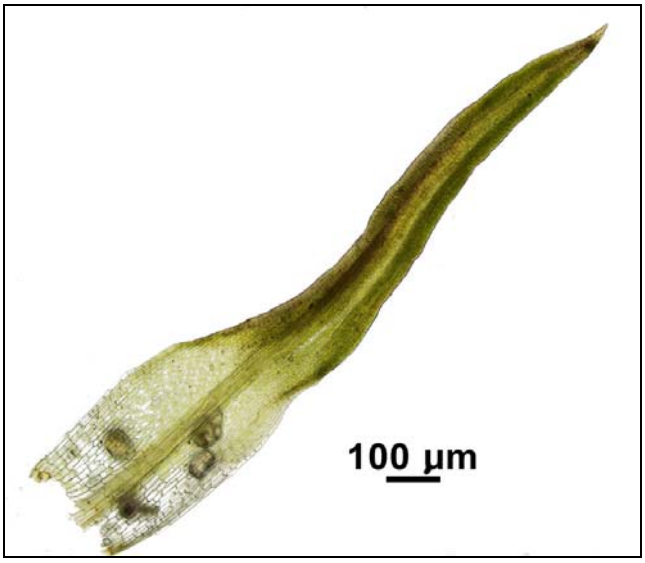

Figure 47. ***Weissia controversa*** leaf showing **involute** margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

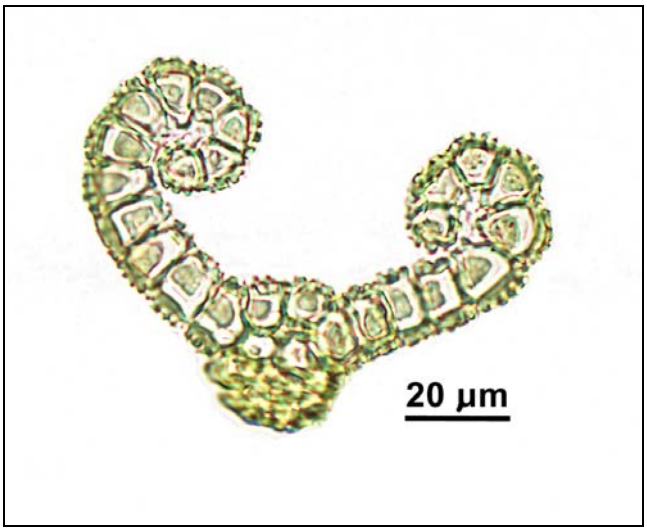

Figure 48. ***Weissia controversa*** leaf cross section showing **involute** leaf margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

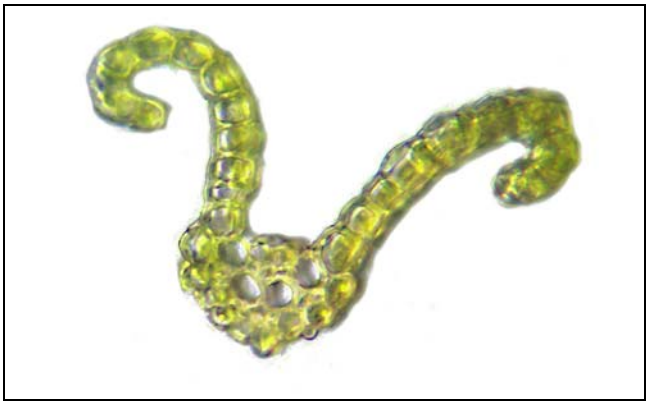

Figure 49. ***Ceratodon purpureus*** leaf cross section showing **revolute** leaf margin. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

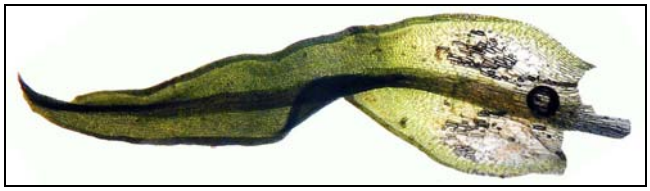

Figure 50. ***Bryoerythrophyllum recurvirostrum*** leaf showing strong costa and **revolute** leaf margin that cause its **crispate** appearance when dry. Photo by Michael Lüth, with permission.

Both **Pottiaceae** and **Grimmiaceae** exhibit crisp, contorted leaves where the lamina is able to shrink and the leaf can roll with marginal rolling increasing as the plants dry (Kürschner 2004). The leaves wind spirally around the stem as they dry, reducing water loss and protecting the chlorophyll and DNA from excessive sunlight. The untwisting of the leaves provides another service – removal of trapped sand particles and other particles held by the leaves. When the lamina folds inward, it reduces desiccation. Kürschner suggests that the shiny costa may increase reflection of sunlight, further reducing desiccation. In these two families that occupy dry, open habitats, parallel evolution has adapted them to their similarly dry niches.

Borders

Borders are usually elongate cells that may be light in color or heavily pigmented. But in some species, the leaf margin may be heavily pigmented with chlorophyll in multiple cell layers. Such is the case in species of ***Pseudocrossidium*** (Figure 51-Figure 54) (Kürschner 2004). These species have marginal cells that form a well developed chlorophyllous region (Figure 52). They are protected by the **revolute** (rolled under; Figure 52-Figure 53) leaf margin that helps to maintain their hydration (Herzog 1926; Kürschner 2004).

So if the costa conducting cells all have protoplasm (**leptoids**), this leaves us with the question of water transport within the leaf. **Leaf borders** with elongate cells such as those in ***Atrichum*** (Figure 55) and the **Mniaceae** (Figure 56) provide benefits similar to those of the costa and seem to speed the movement of water from the base of the leaf to more distal parts, or in some cases from the tip toward the middle, but unfortunately, I have been unable to find any published study to verify this memory. Other roles are discussed in Chapter 7-4.

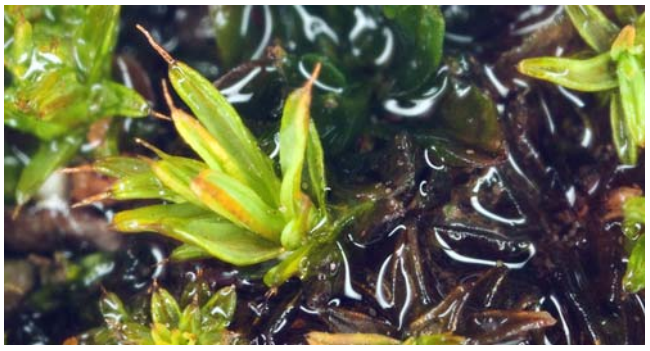

Figure 51. ***Pseudocrossidium crinitum*** hydrated. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

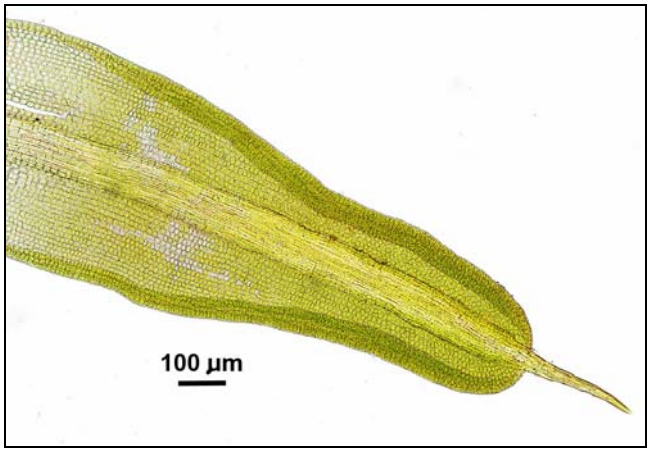

Figure 52. ***Pseudocrossidium crinitum*** underside of leaf showing thickened, revolute, chlorophyllose margin. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

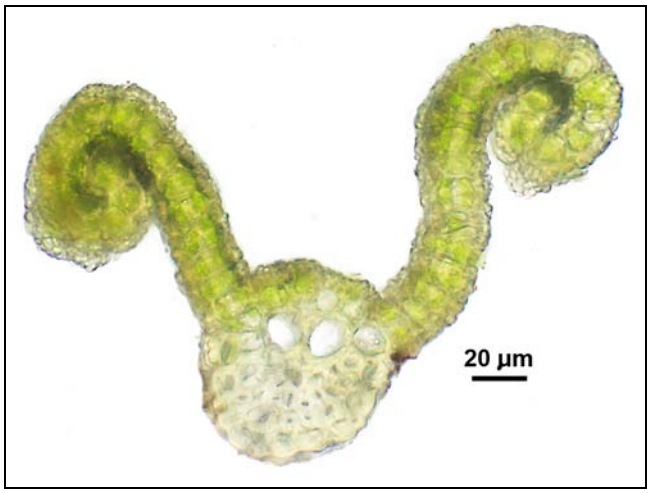

Figure 53. ***Pseudocrossidium crinitum*** leaf cross section showing revolute margin. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 54. ***Pseudocrossidium revolutum*** showing curled leaves and revolute margins in dry condition. Photo from Proyecto Musgo, through Creative Commons.

Figure 55. ***Atrichum selwynii*** leaf showing border with elongated cells and double border teeth. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

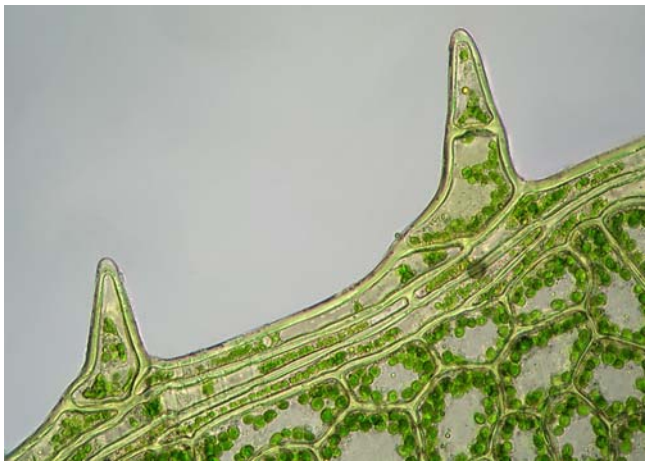

Figure 56. ***Plagiomnium affine*** leaf border showing elongate cells compared to wider but shorter leaf lamina cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

It appears that long border cells (Figure 56) are able to move water and facilitate uptake. But they may provide an additional role in the wet to dry state transition of the leaf in at least some taxa (Lowell 1998). When the leaf of ***Atrichum undulatum*** (Figure 57) is wet, the elongate cells of the border are turgid and extend the leaf lamina out into a nearly straight surface. But as the leaf dries, the opposing forces of the drying leaf cells and the border result in the contorted leaf shape that is exhibited by the dry ***Atrichum undulatum*** leaf (Figure 57). The margins roll toward each other and the tip rolls toward the base, creating a "boat" shape. The border acts much like a wire sewn into the edges of a cloth ribbon, but somewhat more flexible.

In ***Atrichum*** (Figure 57) the leaf is **prestressed**; that is, it has a natural dry state that is highly convoluted, but when wet the turgor forces it to become straight (Lowell 1998). Thus, when the leaf dries, the leaf itself contorts into a form that is able to trap and hold water next to the leaf and stem surface. As Lowell describes it, the border is like the party toy that you blow into and it extends straight out, but when it is relaxed, it forms a coil. Species of **Mniaceae** (Figure 58) with borders seem to have similar responses, with the borders causing the leaf margins to curl toward each other, the leaf to become somewhat concave, and the leaf to become contorted.

Figure 57. ***Atrichum altecristatum*** drying (**lower plants**) and moist (**upper plants**). Photo courtesy of Eric Schneider.

Figure 58. ***Plagiomnium*** branch with contorted leaves due to drying. Although this moss has been rewet, it is slow to hydrate and regain its shape. Photo source unknown.

A similar adaptation appears in **Lejeuneaceae** and ***Porella***, where a hyaline row of marginal leaf cells function in water storage (Daniels 1998). Perhaps the same function occurs in some of the mosses such as some ***Fissidens*** (Figure 59-Figure 60) or ***Plagiomnium*** (Figure 56) with well-developed borders. Because of their elongate structure, water can be expected to move more quickly along the border because of fewer end walls to traverse. Yet there seems to be little experimentation to demonstrate that these cells are of any advantage in gaining or moving water to vital parts, or holding water.

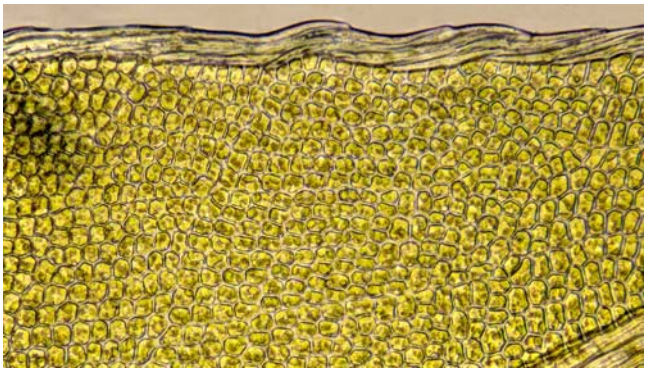

Figure 59. ***Fissidens bryoides*** leaf cells and border, showing elongate border cells. Photo by Dick Haaksma, with permission.

Figure 60. ***Fissidens bryoides*** showing leaves being constricted by their borders. Photo by Michael Lüth, with permission.

Leaf Teeth

Lots of ideas have been presented to suggest the evolutionary significance of teeth in tracheophytes, from deterrents to insects (making the leaf look like something has eaten it, stimulating production of antiherbivore compounds or being spiny) to dripping points for water to help reduce growth of fungi and epiphytes. But what might their value be to bryophytes (Figure 61-Figure 62)?

One interesting observation is that teeth and lobed leaves of deciduous trees are more common in deciduous forests, but they are rare in tropical forests (Baker-Brosh & Peet 1997). Baker-Brosh and Peet hypothesized that they might provide sites for early season photosynthesis. They found that eight species with prominent teeth or lobes did indeed have early season photosynthesis on the margins of the leaves, but not in seven others and none in the four entire-leafed species in the experiments.

Figure 61. ***Mnium spinosum*** leaf showing small, nearly rounded lamina cells compared to the elongate border cells and prominent paired teeth. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Royer and Wilf (2006) noted that toothed leaves of tracheophytes were common in cold climates and that the percentage of toothed leaves correlated negatively with temperature in **mesic** (containing a moderate amount of moisture) environments. They conducted experiments in Pennsylvania and North Carolina, USA, to determine the advantages of the teeth. They found that the physiological activity at the leaf margins was greatest early in the first 30 days of the growing season. And toothed margins were more active in photosynthesis and transpiration than were those of untoothed leaves. They supported the observations of Baker-Brosh and Peet 1997, showing that the leaf margins were more active in leaves from Pennsylvania, which was colder, than those of the California leaves. This strategy maximizes carbon gain during the season when the temperature is limiting but moisture and nutrients are not limiting.

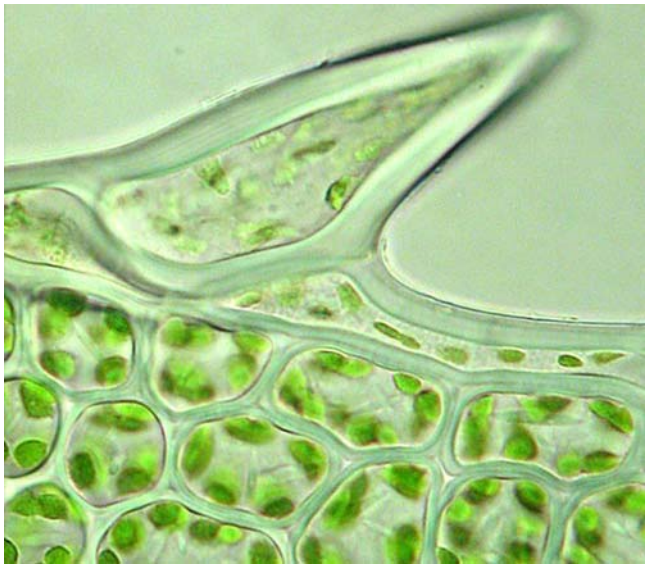

Figure 62. ***Atrichum undulatum*** leaf cells and border showing enlarged tooth with chlorophyll. Photo by Walter Obermayer, with permission.

Obeso (1997) found that spines on the European holly (*Ilex aquifolium*) deterred browsing by ungulates, and that the spines were inducible, decreasing significantly when browsing was prevented for one year.

Another possibility for the adaptive value of teeth is their bearing on water relations. Royer *et al*. (2009) found that among the 227 sites they studied in the Australian subtropical rainforest, both the percentage of species and abundance of toothed species declined from **riparian** (wetlands adjacent to rivers or streams) habitats to ridge-top habitats. Hence, we can rule out any protective value that teeth might have against desiccation. On the contrary, this correlation suggests that teeth could have a role in reducing water in saturated leaves.

Do these tracheophyte models help us to suggest roles for teeth in bryophytes, or are they simply not a detriment to the mosses and liverworts that have them? Do leaf teeth suggest that something has eaten the leaves? We don't know if antiherbivore compounds are inducible in bryophytes, so there may be no disadvantage to having teeth as a warning unless most of the leaves with teeth do have antiherbivore compounds, inducible or not. It seems unlikely that the teeth have any painful effect to deter browsers. And we don't even understand how deciduous tree leaves benefit from teeth in more moist climates.

It is possible that the bryophyte teeth do have a photosynthetic role in spring when new leaves are forming. The apex, especially of acrocarpous mosses, has the most exposure to light, and the marginal parts of the leaves will have the most exposure, so it is possible that they have such a role. But experiments to demonstrate such a benefit are lacking.

Teniolae

The **teniola** is a border-like row of differentiated cells (Figure 63), differing from a true border by being intramarginal (*i.e.* not at the margin). They are more than one cell thick and this condition may extend also throughout the blade portion. These are found in ***Calymperes*** (Figure 64) and function for support, but may also provide water transport (Reese 1993).

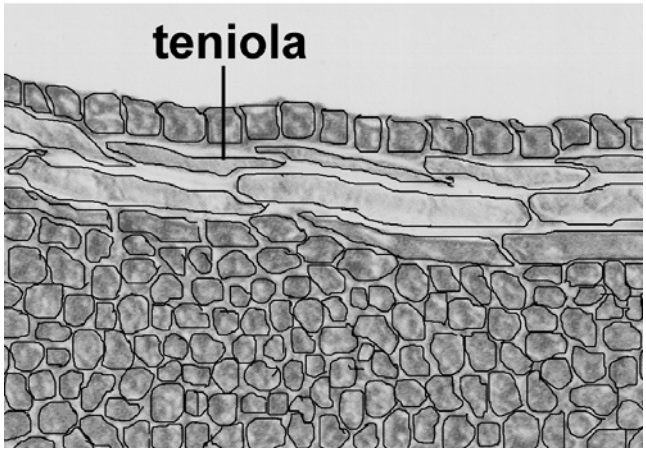

Figure 63. Portion of leaf showing the intramarginal border, the **teniola**. Drawing by Janice Glime.

Figure 64. ***Calymperes motleyi***, member of a genus that has **teniolae**. Photo by Jan-Peter Frahm, with permission.

Costa

The **costa** is the supporting structure for many moss leaves, often also providing an avenue of water transport (Frahm 1985) (Figure 65-Figure 66). It resembles a midrib both in appearance and function (Figure 67). Habitat seems to play some role in its development, although its predisposition to presence or absence is usually genetically determined.

Figure 65. ***Mnium hornum*** showing distinct costa and teeth. Photo by Bob Klips, with permission.

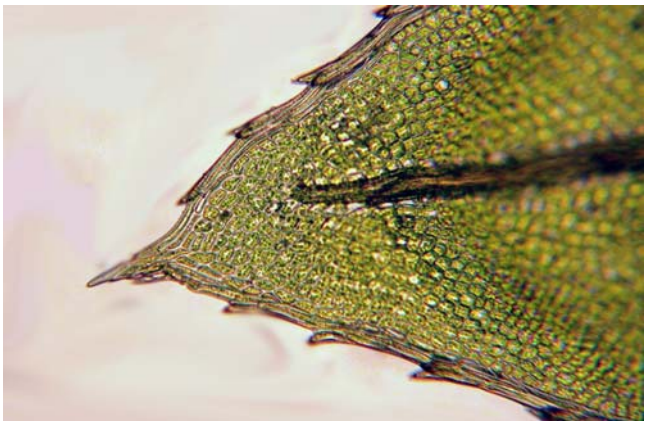

Figure 66. ***Mnium hornum*** leaf showing elongate cells of costa and border. Photo by Bob Klips, with permission.

Figure 67. Cross section of ***Trichodon cylindricus*** showing costa. Photo by Janice Glime.

The costa of some species may be shorter, thinner, and even disappear when it develops in water (Zastrow 1934). For example, the submerged forms of ***Warnstorfia exannulata*** (=*Drepanocladus exannulatus*) (Figure 68-Figure 69) have a costa that only reaches midleaf, whereas the terrestrial forms have a strong costa; similarly, ***Cinclidium stygium*** (Figure 70) normally has a strong costa above water, but when grown submerged it becomes thin and small (Zastrow 1934). When cultured in artificial streams where the leaves were exposed to air, ***Fontinalis novae-angliae*** developed short double costae, although

these are normally absent when it grows submersed (Glime, unpubl.). The broad costa in ***Campylopus*** (Figure 71-Figure 72) not only serves as the photosynthetic organ, but as a water reservoir as well, adding to the possible advantages of growing a costa above water.

Figure 68. ***Warnstorfia exannulata*** branch. Photo from Proyecto Musgo, through Creative Commons.

Figure 69. ***Warnstorfia exannulata*** leaf showing costa typical of emergent leaves. Photo by Kristian Peters, with permission.

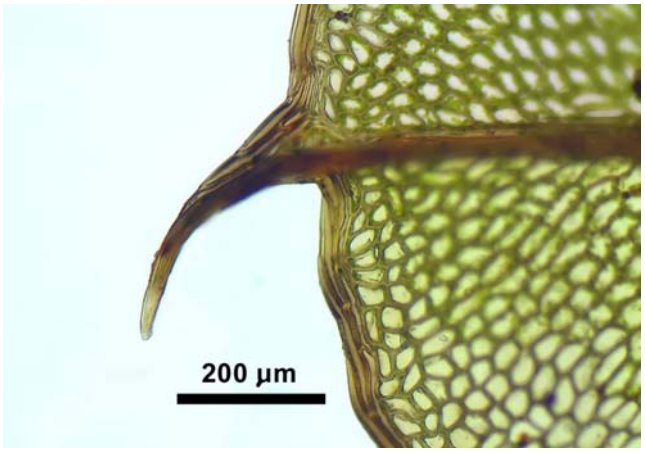

Figure 70. ***Cinclidium stygium*** with leaf tip, costa, and border. Its strong costa indicates that it was grown above water. Photo by Kristian Peters, through Wikimedia Commons.

Figure 71. ***Campylopus lamellinervis*** showing the broad, thickened costa and a tomentum on the stem that absorbs moisture. Photo by Michael Lüth, with permission.

Figure 72. Leaf cross section of ***Campylopus flexuosus*** showing broad costa with cells that have water-holding capacity as well as photosynthetic capacity. Photo by Michael Lüth, with permission.

Guerra *et al.* (1992) considered **nerve enlargement** to be an adaptation to the xeric environment, providing stiffening that supports the leaf during desiccation. Bell (1982) suggested that it also might retain water.

Stereids

In the stem, **stereids** are thick-walled cells that contain living protoplasm and have been compared to xylem parenchyma cells (Hébant 1970). In leaves, they form ribs on one or both sides of the costa (Figure 73) and may function as protection against desiccation (Frahm 1985). They occur in a variety of families, including **Dicranaceae** (Figure 74) and **Pottiaceae** (Figure 75-Figure 76).

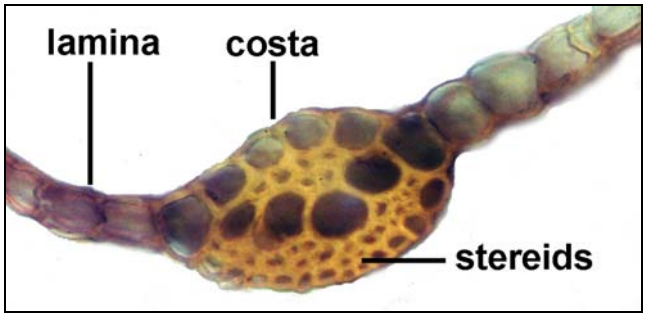

Figure 73. ***Trichostomum tenuirostre*** (moss) leaf cross section showing stereids. Photo by Janice Glime.

Figure 74. ***Dicranum scoparium*** (**Dicranaceae**) leaf cross section. This leaf has few sclereids but has relatively large conducting cells, in this case smaller than the leaf lamina cells. Photo from Botany website, University of British Columbia, Canada.

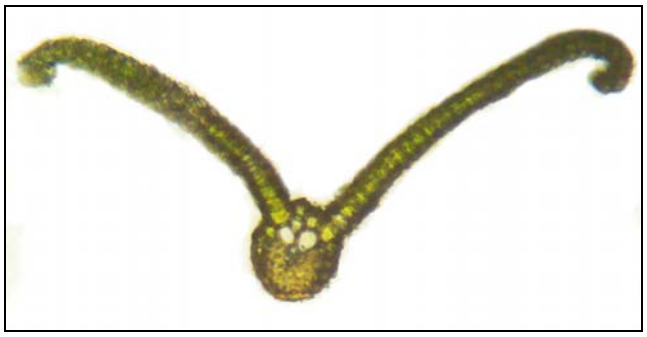

Figure 75. ***Syntrichia inermis*** (**Pottiaceae**) leaf cross section. Note the enlarged costa with stereid cells on the bottom and conducting cells near the top. In this case, the lamina cells are covered with papillae that may help in water intake, a function thus far demonstrated for only one species. More likely they channel the water. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 76. ***Syntrichia princeps*** (**Pottiaceae**) leaf cross section showing costa with stereids (pinkish color on lower portion) and large leptoids. Photo by Paul S. Wilson.

It appears that the structure of the costa can have adaptive value relating to moisture conditions. Those ***Campylopus*** taxa surviving habitats with changeable conditions have well-developed costal stereids (Frahm 1985). Frahm found that dorsal costal **lamellae** (Figure 95) aid in water uptake, whereas the ventral costal stereids (Figure 77) common among ***Campylopus*** species help to reduce desiccation. ***Campylopus savannarum*** survives its savannah habitat with the aid of such stereids, whereas ***Campylopus*** taxa occurring on wet cliffs, dripping rocks, and swamps lack stereids (Figure 78).

Figure 77. ***Campylopus flexuosus*** leaf cross section showing ventral (lower) stereids. Photo by Amelia Merced, Duke Herbarium.

Figure 78. ***Campylopus tallulensis*** leaf cross section showing thin-walled ventral costal cells typical of the more humid mountainous regions. Photo by Amelia Merced, with permission.

Lamellae

The term **lamella** shares the same root word as laminate and refers to layers, in this case vertical stacks of cells that form rows, often reaching the length of the leaf (Figure 82, Figure 83). They may cover the costa, the blade, or a liverwort thallus. These rows are arranged in such a way that they somewhat resemble a book that has just been opened and laid to rest, with its pages still parting and standing upward from the middle. Some of the most **xerophytic** (referring to plants of dry habitats) mosses, such as ***Aloina*** (Figure 79), have branched filaments over the costa, giving it a **succulent** (fleshy) appearance; ***Crossidium*** (Figure 80-Figure 81) achieves a similar effect with dense filamentous outgrowths from the costa in the upper half of the leaf.

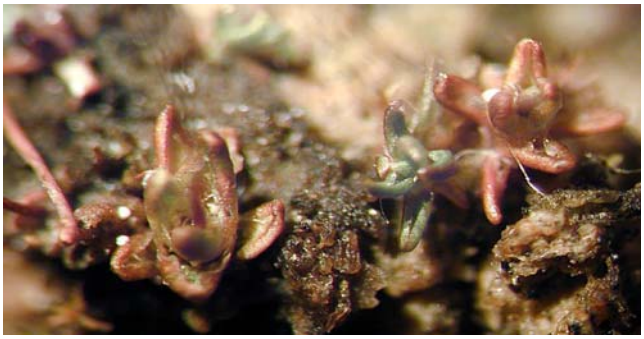

Figure 79. ***Aloina brevirostris***, illustrating the succulent appearance caused by the numerous filaments on the costa. Photo by Michael Lüth, with permission.

Figure 80. ***Crossidium crassinerve*** with filaments on leaf costae. Photo by Michael Lüth, with permission.

Figure 81. ***Crossidium aberrans*** leaf showing filaments on costa. Photo by Michael Lüth, with permission.

Members of the **Polytrichaceae**, such as ***Polytrichum*** and ***Dawsonia***, which are all **endohydric** (having internal water transport), have vertical lamellae (Figure 82, on their leaves that provide capillary spaces and create dead air spaces that can reduce water loss across the broad surface of these atypically large moss leaves (Figure 82-Figure 85). In addition, some species [***Polytrichum hyperboreum*** (Figure 86-Figure 87), ***P. piliferum*** (Figure 88-Figure 89), ***P. juniperinum*** (Figure 90-Figure 91)] have the edge of the leaf **lamina** (flattened part of leaf not including costa or border) rolled over the lamellae, creating an internal structure somewhat like the **palisade mesophyll** (columnar cells of inner leaf tissue) of a flowering plant, with the lamina behaving in some ways like an epidermis. The leaves have the additional ability to flex like a hinge when water fills the thin-walled leaf base cells (van Zanten 1975), causing the leaves to be spread lengthwise away from the stem under moist conditions but be straight or curved around the stem when dry (Figure 2). Such behavior retards water loss and protects the chlorophyll during dry periods, while permitting maximum use of light during wet periods.

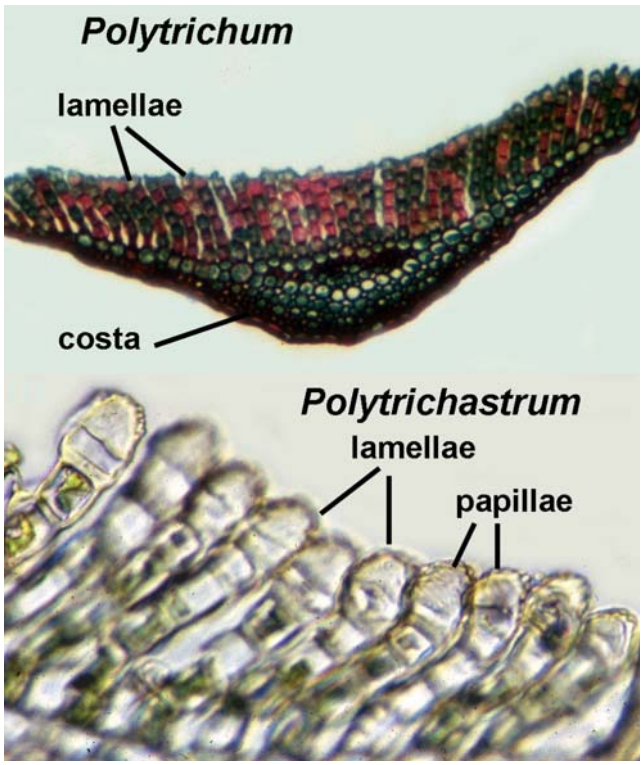

Figure 82. Cross sections of lamellae of **Polytrichaceae**. **Top:** stained section of ***Polytrichum***. **Bottom:** ***Polytrichastrum alpinum*** with papillose terminal cells on the lamellae. Photos by Janice Glime.

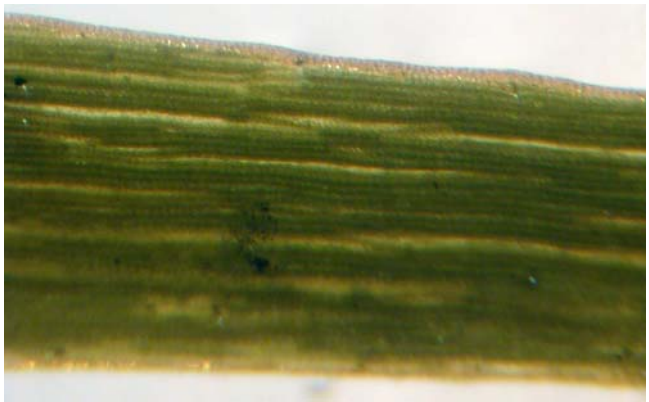

Figure 83. Lamellae on leaf of ***Polytrichum ohioense***, viewed down onto leaf surface at 100X. Photo courtesy of John Hribljan.

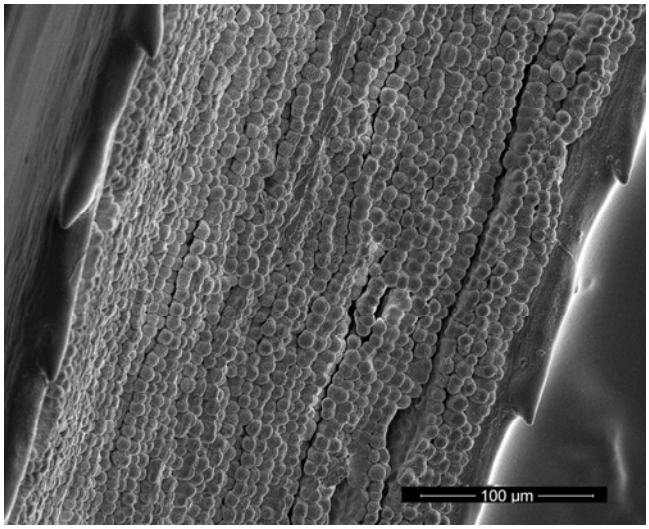

Figure 84. SEM of ***Dendroligotrichum squamosum*** (**Polytrichaceae**) showing tops of lamellae. Photo courtesy of Jeff Duckett and Silvia Pressel.

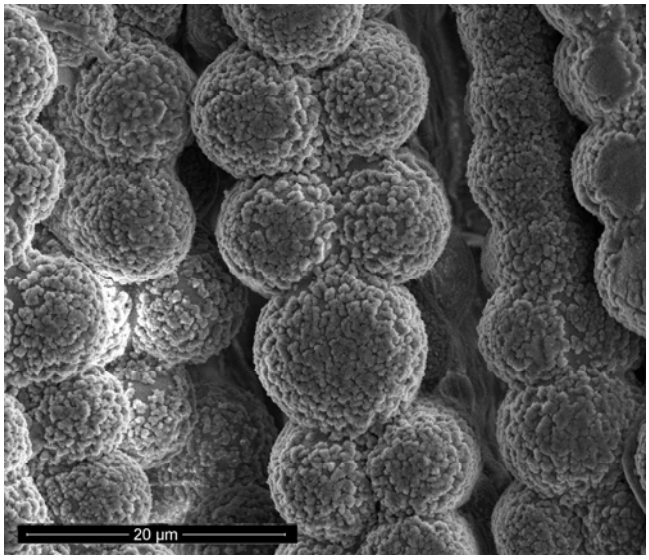

Figure 85. SEM of ***Dendroligotrichum squamosum*** leaf showing terminal cells of lamellae. Photo courtesy of Jeff Duckett and Silvia Pressel.

Figure 86. ***Polytrichum hyperboreum*** showing leaf lamina rolled over the lamellae. Photo by Michael Lüth, with permission.

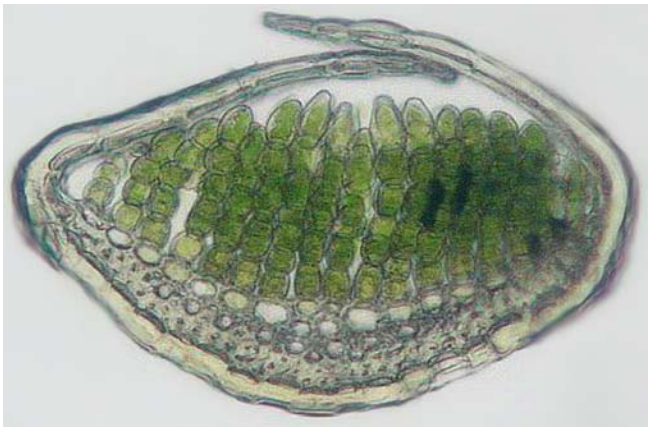

Figure 87. ***Polytrichum hyperboreum*** leaf cross section showing lamina folded over lamellae. Photo by Michael Lüth, with permission.

Figure 88. ***Polytrichum piliferum*** showing leaf lamina rolled over the lamellae. Photo from Botany Department website, University of British Columbia, Canada, with permission.

Figure 89. ***Polytrichum piliferum*** leaf cross section showing leaf lamina rolled over the lamellae. Photo from Botany website, University of British Columbia, Canada, with permission.

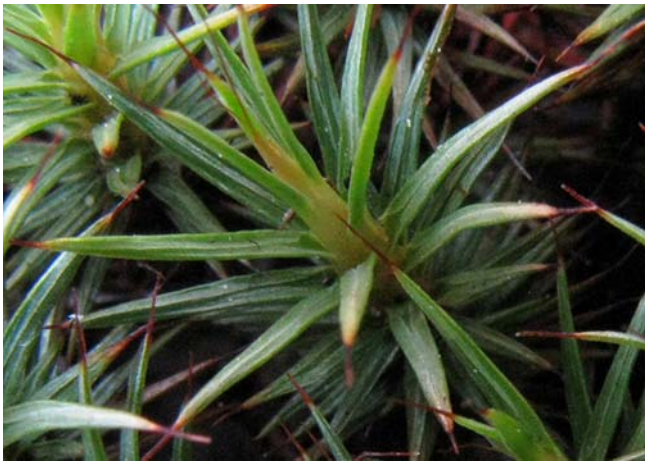

Figure 90. ***Polytrichum juniperinum*** showing leaf lamina rolled over leaf lamellae. Overlap can be seen easily near leaf bases where the overlap is incomplete, permitting water to enter the basal cells. Photo by Janice Glime.

Figure 91. ***Polytrichum juniperinum*** leaf cross section showing leaf lamina rolled over leaf lamellae. Photo by John Hribljan, with permission.

In ***Pilopogon laevis*** (Figure 92) the costa is ribbed on the back of the leaf; in ***P. peruvianus*** (Figure 93-Figure 94) it has 3-4-cell-high lamellae on the back of the leaf, adapting this species to its dry coastal desert habitat. Likewise, ***Campylopus pilifer*** (Figure 95) has similar lamellae and prefers such dry habitats as rocks, soil-covered boulders, and gravel. On the other hand, ***C. introflexus*** (Figure 96) has only 1-2-cell-high lamellae and lives on humus, wet sand, and peat.

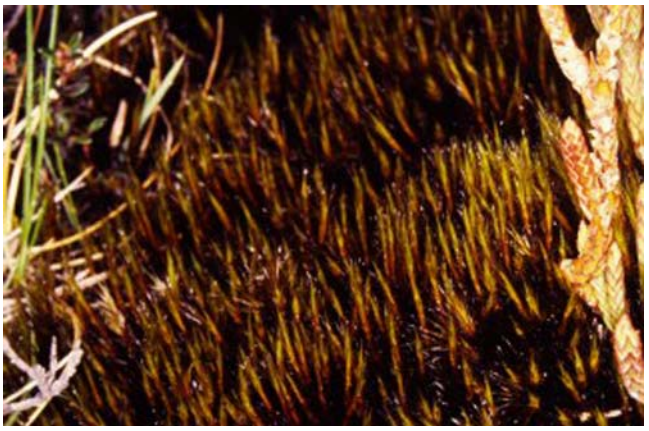

Figure 92. ***Pilopogon laevis***, a species with a ribbed costa. Photo by Jan-Peter Frahm, with permission.

Figure 93. ***Pilopogon peruvianus*** in its desert habitat. Photo by Michael Lüth, with permission.

Figure 94. ***Pilopogon peruvianus*** leaf cross section showing 3-4 cell high lamellae. Photo by Michael Lüth, with permission.

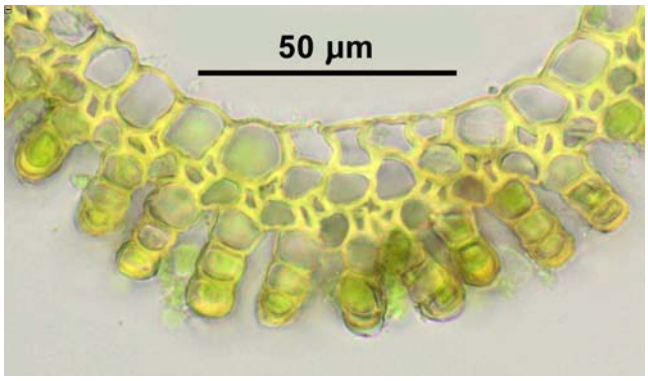

Figure 95. ***Campylopus pilifer***, a plant of rocks and gravel, leaf cross section showing deep lamellae. Photo by Amelia Merced, Duke Herbarium, with permission.

Figure 96. ***Campylopus introflexus***, a plant of humus, wet sand, and peat, leaf cross section showing shallow lamellae. Photo by Gilles Bailly, through Creative Commons.

Although Frey and Kürschner (1991) found a correlation between costal lamellae and increasing aridity, the lamellae of ***Polytrichum*** seem not to be so much an adaptation to prevent water loss as to provide for additional surface area [2.4-fold in ***Polytrichum commune*** (Figure 97-Figure 98)] and gas exchange during photosynthesis (Thomas *et al.* 1996). Proctor (1979a, b) and Thomas *et al.* (1996) described wax on the terminal cells of the lamellae of ***Polytrichum*** and attributed to this wax the repulsion of water, preventing it from entering between the lamellae. Perhaps lamellae are adapted to increasing gas exchange and are more important in water retention or repulsion than in absorption, at least in some species.

Figure 97. ***Polytrichum commune*** leaves with waxy surface that keeps water out of the lamellae. Photo by James K. Lindsey, with permission.

The genus ***Atrichum*** (**Polytrichaceae**) also has shallow to deep lamellae, and these have been used to justify separation into different species. The lamellae shown in Figure 99-Figure 101 fall within ***Atrichum undulatum*** var. ***undulatum***, but any lamellae more than 4 cells high would indicate a different variety (Crum 1983), or species (The Plant List 2010).

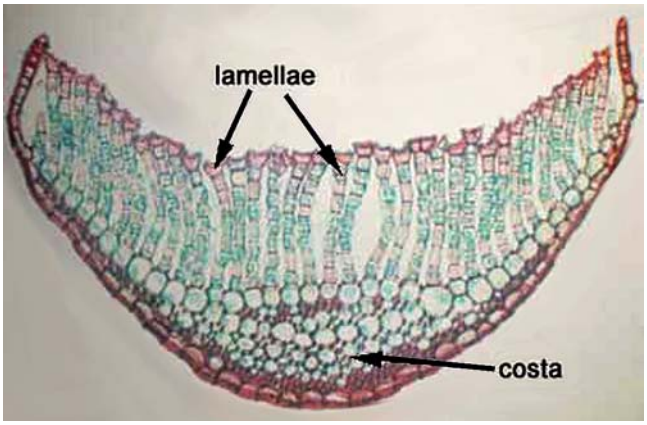

Figure 98. ***Polytrichum commune*** leaf cross section with lamellae showing terminal cell with different stain from other lamellae cells, perhaps due to the presence of wax. Photo from Botany website, UBC, with permission.

Figure 99. ***Atrichum undulatum*** leaf showing leaf lamellae and border with teeth. Photo by Walter Obermayer, with permission.

Figure 100. ***Atrichum undulatum*** leaf (costa) cross section showing small, thick-walled stereids, large transparent conducting cells, and lamellae 3-4 cells high. Photo by Walter Obermayer, with permission.

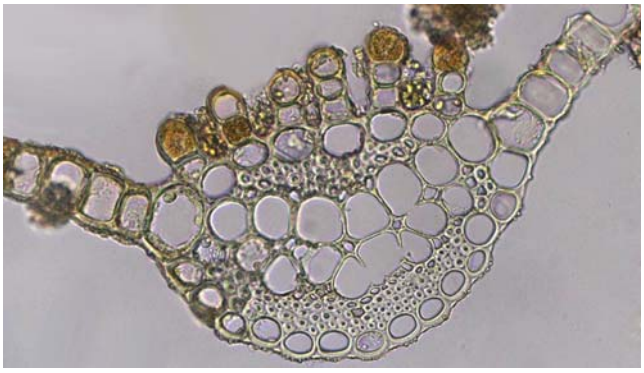

Figure 101. ***Atrichum undulatum*** leaf (costa) cross section showing small, thick-walled stereids above and below the large, transparent conducting cells. Lamellae are on top of the costa and are only 2-3 cells high. Photo by Walter Obermayer, with permission.

Lobules and Storage Organs

Liverworts have an evolutionary history that separates some of the major groups by their water relations (Heinrichs *et al*. 2005). In the **Jungermanniidae**, two clades split. The **Porellales** are predominantly epiphytes that have specialized **lobules** (Figure 102) or water sacs and **endosporous** protonemata. The **Jungermanniales** (Figure 103) are frequently terrestrial, lack water sacs, and normally develop **exosporous** protonemata.

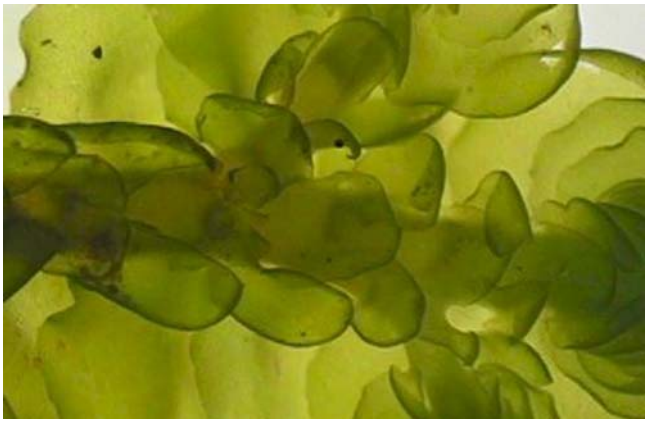

Figure 102. Ventral side of ***Porella platyphylla*** showing underleaves along stem and lobules on each side of them. Photo by Paul Davison, with permission.

Figure 103. ***Lophozia wenzelii***, a member of the **Jungermanniales,** showing the absence of lobules. Photo by Des Callaghan, with permission.

Daniels (1998) has compared leafy liverworts growing in a variety of habitats. **Xerophytic** (dry habitat adapted) taxa such as ***Frullania*** (Figure 104) have helmet-shaped leaf **lobules** and ***Radula*** (Figure 105) has a saccate lobule, both functioning for water storage. ***Porella*** (Figure 102), capable of both an **epiphytic** (living on plants) and a **saxicolous** (living on rock) habit, has leaf folds underneath (lobules) and large underleaves. Liverwort plants in the humid rainforests such as those in the **Lejeuneaceae** (Figure 106-Figure 108) have smaller lobules than those growing in drier, more exposed habitats (Cornelissen & ter Steege 1989; Gradstein 1995). Such structures help to hold water in capillary spaces in the absence of multiple rows of leaves. Some aquatic invertebrates, especially rotifers, live in these watery lobules (see Volume 2, Chapter 4-5 on Rotifers). It is likely that the pockets of ***Fissidens*** (Figure 21-Figure 24, Figure 37) may have similar water-holding functions.

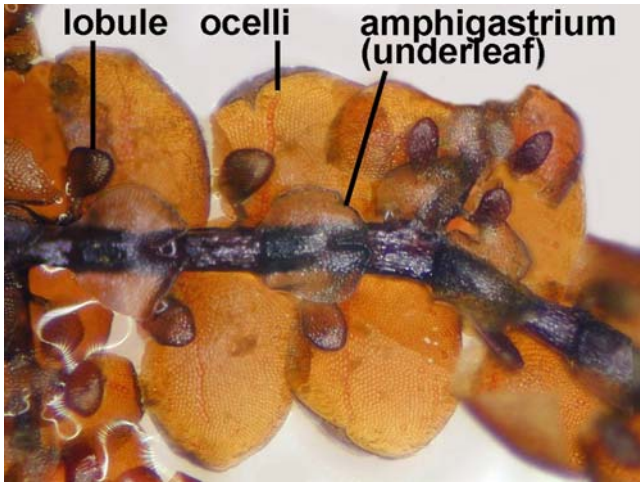

Figure 104. ***Frullania tamarisci*** showing lobules. Photo by Michael Lüth, with permission.

Figure 105. ***Radula*** from the tropics with saccate lobules (**arrows**). Photo by Michael Lüth, with permission.

Figure 106. **Lejeuneaceae** epiphylls from Panama. Photo by Janice Glime.

Figure 107. ***Lejeunea patens*** showing small lobules. The upper three have air bubbles trapped in them. Photo by Jan-Peter Frahm, with permission.

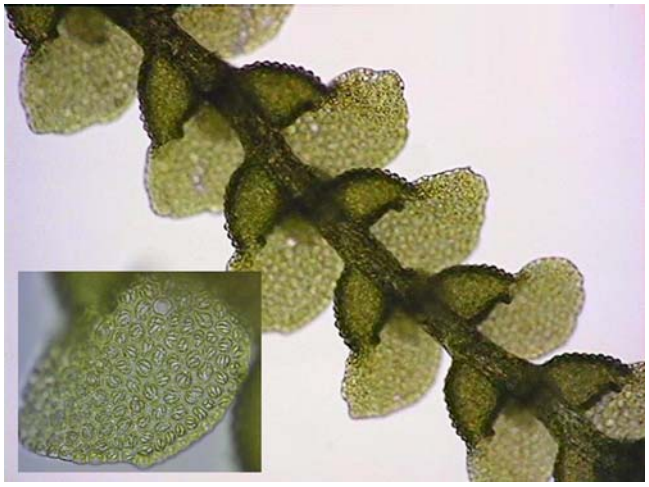

Figure 108. ***Cheilolejeunea evansii*** branch showing ventral lobules. Photo by Paul Davison, with permission.

Hair Points

Hair points are common on leaves of xerophytic mosses, including species of ***Campylopus*** (Figure 109-Figure 110), ***Grimmia*** (Figure 111), ***Schistidium*** (Figure 112-Figure 113), ***Hedwigia*** (Figure 134), and ***Syntrichia*** (Figure 114). As discussed earlier, Loeske, in 1930, demonstrated that in ***Schistidium apocarpum*** (Figure 112-Figure 113) hair points are actually lost when the mosses are kept in damp air or deep shade. Proctor (1979a) and Kürschner (2004) consider these hairs to be organs that reflect some of the solar radiation, thus reducing energy absorption, temperature, and evaporation. But they reduce water loss more directly as well; hair points on ***Syntrichia intermedia*** (Figure 114) and ***Grimmia pulvinata*** (Figure 111) reduce the boundary layer conductance by about 20-35% in experiments (Proctor 1980). Not only does this thicker boundary layer trap stagnant air, thus reducing evaporation loss, but it increases the distance from the leaf surface to the surrounding air, thus decreasing the diffusion gradient (Proctor 1982).

Figure 109. ***Campylopus introflexus*** showing dry hair tips. Compare to Figure 110. Photo by Michael Lüth, with permission.

Figure 110. ***Campylopus introflexus*** showing hair tips that have collected moisture from the atmosphere. Photo by Michael Lüth, with permission.

Figure 111. ***Grimmia pulvinata*** showing the long hairs that reduce the boundary layer conductance and trap atmospheric moisture. Photo by Michael Lüth, with permission.

Figure 112. ***Schistidium apocarpum*** exhibiting the lack of hair points typical of this species when it is grown in wet or shaded habitats. Photo by Christophe Quintin, through Creative Commons.

Figure 113. ***Schistidium apocarpum*** exhibiting the leaf hair points that develop when the plants are in dry areas. Photo by Christophe Quintin, through Creative Commons.

Hair points may also help in trapping and absorption of water vapor from fog and dew (Figure 109-Figure 110). Dry tips can reflect sunlight (Figure 109), reducing water loss (Kürschner 2004).

Figure 114. ***Syntrichia intermedia*** demonstrating prominent hair points. Photo by Jan-Peter Frahm, with permission.

As suggested by the example of ***Campylopus introflexus*** (Figure 109-Figure 110), hair points can help in collecting moisture from the air as well (Figure 110). Shaun Russell has described to me that in African highlands the mosses act as tiny collectors that trap moisture from the fog. This is often their only source of water for an entire year. Chang and coworkers (2002) have measured the water available to epiphytes in fog (Table 2) and in precipitation in a subtropical montane forest in Taiwan. In a one-year study, they found that the fog endured for a mean of 4.7 hours per day at its low in the summer to 11 hours per day the rest of the year, reaching nearly 15 hours per day in November. Furthermore, it contributed more than 50% of the nutrient ions reaching the bryophytes.

Table 2. Absorption rate of fog in dominant epiphytes during a single dense fog event on 24 February 2001 at Yuanyang Lake, Taiwan. From Chang *et al*. (2002).

Species	absorption rate g H_2O gdw^{-1} h^{-1}
Bazzania fauriana	1.28
Bazzania sp. 2	0.90
Pleurozia acinosa	0.67
Mastigophora diclados	0.59
Schistochila acuminata	0.58
Dicranoloma blumii	0.42
Scapania sp. 1	0.38
Bazzania sp. 1	0.23

Zhang *et al*. (2009) considered the effect of dew as an important moisture source in the Gurbantunggut Desert, Northwestern China. They measured dew quantities with micro-lysimeters and demonstrated the increase in dew deposition as the crust grew larger. Mosses had the highest deposition compared to that of lichen crusts, cyanobacterial crusts, and bare sand ($p < 0.05$). Interestingly, the retention time for the moisture gained from dew did not follow this pattern. Instead, it was held longest by sand, followed by the cyanobacterial crust, moss crust, and lichen crust, in that order.

Tao and Zhang (2012) further examined the function of hair points in the desert moss ***Syntrichia caninervis*** (Figure 115). The hair points in this case comprised only about 4.8% of the shoot weight, but they were able to increase the absolute water content by 24.9%. And, during dehydration, those moss samples with hair points always

had a higher water content than did those without. Furthermore, the shoots with hair points took 20 minutes longer to become completely dehydrated. And of course there was greater dew accumulation on the shoots with leaf hair points, increasing the dew on the crusts by 10.3%. Following short simulated rainfall events, the evaporation of water from the crusts was always slower when the leaves had hair points in contrast to the rapid loss of water trapped from dew (Zhang *et al*. 2009).

Yuan Ming Zhang's research team filmed the events following application of a drop of water on the hair points of ***Syntrichia caninervis*** (Figure 115). The water moved quickly down the hair point and was absorbed by the leaves within seconds. Like a fine wire, the hair tips serve as a conduit for the water. This mechanism permits these mosses to extract water from dew or fog, and to benefit from rapid absorption of the first few drops of rain, maximizing its period of hydration. Zhang *et al*. (2011) supported the significance of this rapid rewetting. In lab experiments they showed that within the first minute the photosynthetic yield (F_v/F_m) recovered to 90% of its rate after 30 minutes. Cytological changes occurred rapidly, indicating no damage to membranes or organelles. This rapid recovery makes it possible for it to use the water collected by the hair points from fog, dew, rain, and melting snow for immediate recovery, making it possible to attain positive photosynthetic gain in its desert ecosystem.

Figure 115. ***Syntrichia caninervis***, a desert crust moss with hair points that are important to the hydration of the crust. Photo by John Game, through Creative Commons.

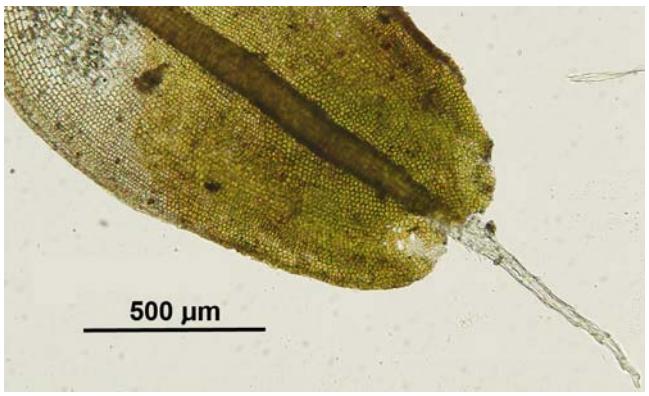

Figure 116. ***Syntrichia caninervis*** leaf showing awn. Photo by Yuan Ming Zhang.

Duration of the rainfall or dew fall event is important. Proctor (2004) found that in ***Grimmia pulvinata*** (Figure 111), dew fall did not enter the moss sufficiently to rehydrate it. Could these hair points prevent wetting and drying cycles that are too frequent for adequate repair of dehydration damage in mosses regularly subjected to hot, dry days? Is this a mechanism to prevent the leaf from becoming hydrated at a time when it will dehydrate again within hours? This is reminiscent of the dormancy mechanism in desert seeds wherein a chemical must be washed off before the seed will germinate. This keeps the seed from germinating unless there is enough rainfall to sustain the young seedling until it reaches a size where it can survive. In these mosses, it requires a rainfall that will hydrate the moss long enough for it to repair the damage of desiccation and make a positive photosynthetic gain before becoming dehydrated again.

Nucleation

It appears that bryophytes are good nucleators. This is a phenomenon in which a small object, known best from bacteria and proteins, causes the formation of ice around itself. Moffett *et al*. (2009) suggest that this phenomenon is widespread among bryophytes. Nucleation occurs when the difference in vapor pressure over ice and water is at or close to the maximum. At these temperatures, typically -8 to -18°C, ice grows at the expense of supercooled water. Moffett *et al*. suggest that the nucleation ability permits the bryophytes to collect water from fog, dew, and cloud water. It is interesting to note that airborne bryophytes may use this nucleation to initiate precipitation.

Papillae

Papillae in bryophytes are small projections from cells, especially common in the **Pottiaceae** (Figure 117-Figure 118). Kou *et al*. (2014) attempted to limit the confusion of many terms in their descriptions by providing four terms to describe them: simple, forked, branched, and pedicellate.

Papillae can both facilitate rapid water uptake (Proctor 1979a; Longton 1988; Kürschner 2004) and accelerate water loss (Pressel *et al*. 2010). Species that benefit from these papillae must, as a consequence, shut down under drying conditions. This is consistent with the role of surface waxes (discussed in Chapter 7-4b of this volume). The thick surface waxes of tracheophytes are usually associated with conditions of drying. In bryophytes, however, they are often characteristic of species from constantly flowing aerated water or other places where water logging depresses gas exchange (Pressel *et al*. 2010). In other words, often they are important for their **hydrophobic** (water-repelling) nature.

The role of papillae, those little bumps and extensions on cell walls (Figure 118), has been controversial for a long time, but their common appearance on bryophytes of dry habitats cannot be ignored. Nevertheless, Loeske (1926) points out that papillae are also found in a number of wetland and aquatic taxa, including ***Dichodontium pellucidum*** (Figure 119-Figure 120), ***Philonotis*** (actually **prorate** cells – end walls overlap and protrude; Figure 121-Figure 122), ***Aulacomnium palustre*** (Figure 123-Figure 124), ***Helodium blandowii*** (Figure 125-Figure 126), and ***Paludella*** (Figure 127). Loeske observed that the papillae

are maintained in a number of species through a wide range of wet to dry habitats. On the other hand, these taxa are common in wet meadows, lake shores, and other wet habitats where they may periodically be dry while being exposed to high sunlight, suggesting that the papillae may be of value under those exposed conditions.

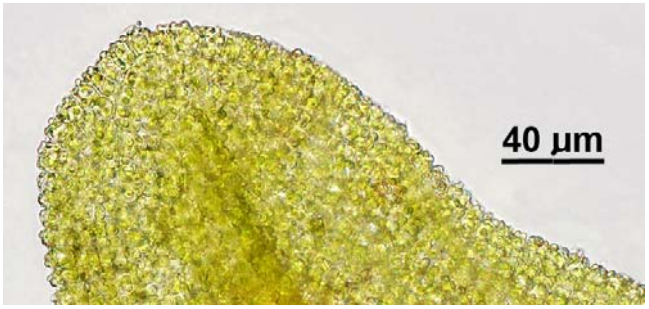

Figure 117. ***Barbula convoluta*** leaf cells showing papillae (especially visible as tiny projections along the margins). Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 118. ***Chrysoblastella chilensis*** leaf cross section showing papillae. This leaf is well endowed with stereids in the costa. Photo by Juan Larrain, with permission.

Figure 119. ***Dichodontium pellucidum*** showing dull, waxy look that results from surface papillae. Photo by Jan-Peter Frahm, with permission.

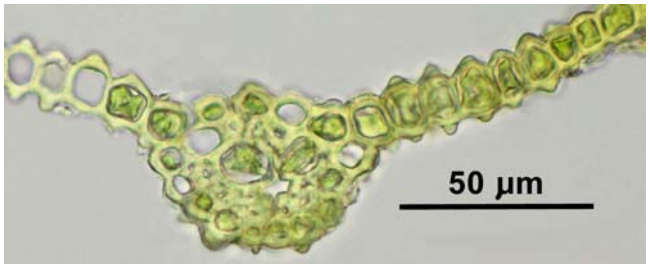

Figure 120. ***Dichodontium pellucidum*** leaf cells in cross section showing papillae. Photo by Amelia Merced through Duke University Plant Biology website, with permission.

Figure 121. ***Philonotis fontana*** exhibiting dull appearance resulting from **prorate** cells. Photo by Malcolm Storey, through Creative Commons.

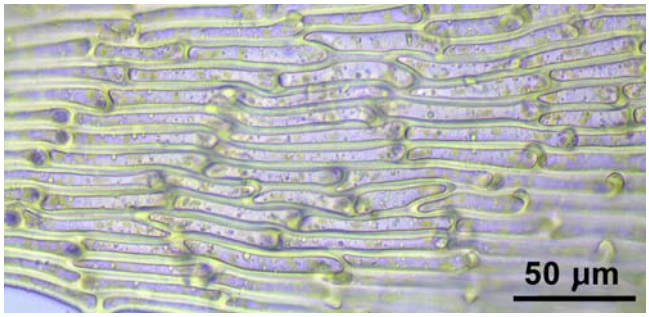

Figure 122. ***Philonotis fontana*** leaf lamina showing **prorate** cells that have an appearance similar to papillae. Photo by Kristian Peters, through Creative Commons.

Figure 123. ***Aulacomnium palustre***, wetland moss with papillae. Photo by David T. Holyoak, with permission.

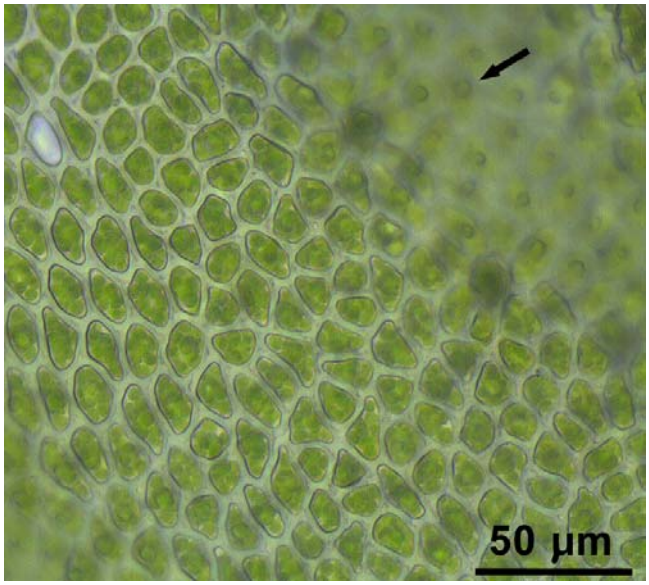

Figure 124. ***Aulacomnium palustre*** leaf lamina showing papillae, best seen in the upper right corner at arrow. Photo by Kristian Peters, through Creative Commons.

Figure 125. ***Helodium blandowii***, a moss that feels "crunchy" due to papillae. Photo by J. C. Schou, through Creative Commons.

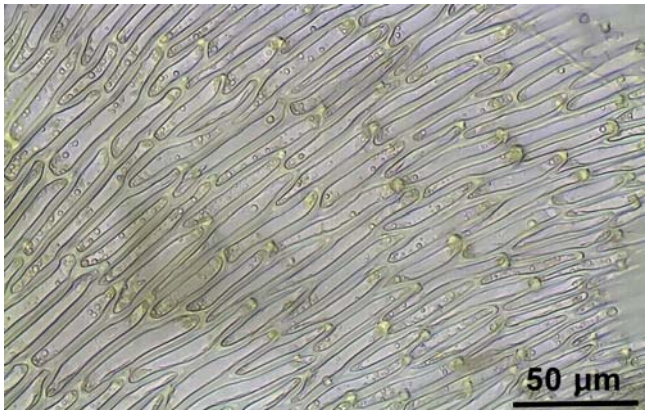

Figure 126. ***Helodium blandowii*** leaf with **prorate** cells. Photo by Kristian Peters, with permission.

Figure 127. ***Paludella squarrosa***, emergent in full sun. Photo by Michael Lüth, with permission.

Some papillae are quite decorative, adorning species that typically live on limestone rocks or other highly desiccating habitats. ***Encalypta ciliata*** (Figure 128-Figure 130) has branched papillae and lives on limestone rocks and other dry locations.

Figure 128. ***Encalypta ciliata*** in a hydrated state, showing the nearly translucent appearance of the leaves. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 129. ***Encalypta ciliata*** in a dry state, showing the dull surface of the contorted leaves. Photo by Li Zhang, with permission.

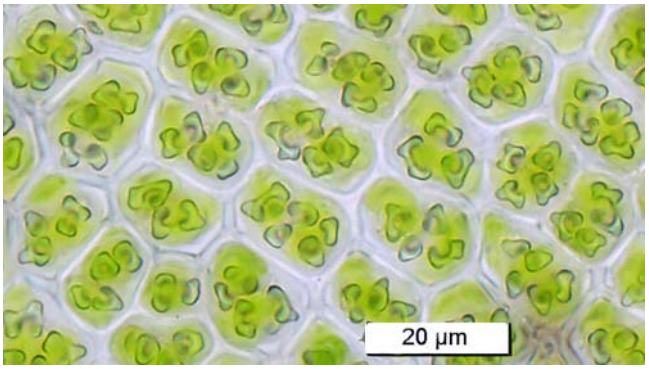

Figure 130. ***Encalypta ciliata*** leaf cells with multiple papillae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Proctor (1979a, 1984, also Longton 1988) described the interstitial spaces between papillae as forming a capillary conducting system that is capable of rapid water movement, as we might expect in ***Tortula muralis*** (Figure 131-Figure 132). (See also the chapter on Leaf Strategies – Cuticles and Waxes in this volume.) But papillae may be most important in altering the boundary layer and creating a dead space that reduces water loss. Both of these ideas, as well as their role in deflecting UV light, remain to be tested.

Figure 131. ***Tortula muralis*** leaf cross section showing the multiple papillae on each cell. Photo from Botany Department website, University of British Columbia, with permission.

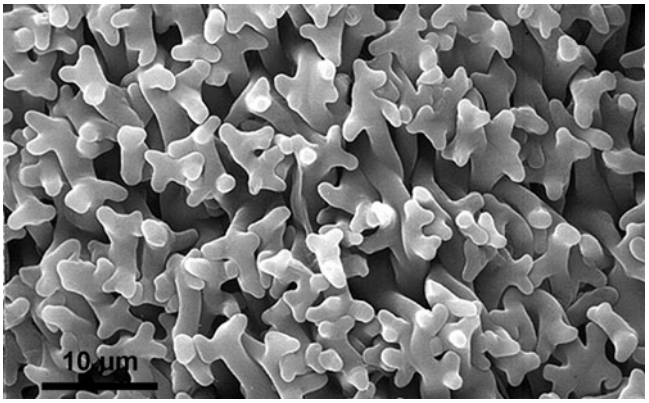

Figure 132. SEM of papillae on ***Tortula muralis***, illustrating the type of channelling described by Proctor (1984). Photo with permission from Botany 321 website, <www.botany.ubc.ca/bryophyte/LAB8.htm>, with permission.

Hedwigia ciliata (Figure 133-Figure 134) is a moss that has white tips on its leaves, presumably protecting the underlying leaves from sun damage. But we need to examine the role of these tips in water uptake as well. The leaf and awn cells are heavily endowed with papillae that give the leaves a waxy appearance despite the absence of waxes.

Figure 133. ***Hedwigia ciliata*** with hyaline tips and awns on leaves. Photo by Michael Lüth, with permission.

Figure 134. Hyaline hair tip on the leaf of ***Hedwigia ciliata***. Note the numerous papillae on these **awn** (hair tip) cells as well as on the **lamina** cells. Photo by Janice Glime.

At least some leaf papillae (***Andreaeobryum macrosporum***, Figure 135) are constructed in such a way that they provide a channel for the uptake of water (Crandall-Stotler & Bozzola 1990, 1991). This channel is within each papilla and is different from the channels formed between the papillae (*cf.* Proctor 1984). SEM observations indicate the channel within the papilla facilitates the rapid uptake of water during rehydration (Crandall-Stotler & Bozzola 1990, 1991). So far, this channel has not been demonstrated in any other species.

So how can papillae function both for water absorption and water loss, and why would evolution tolerate such a seeming contradiction? Pressel *et al*. (2010) may have answered this question. They found that in ***Rhacocarpus purpurascens*** (Figure 136), the **trilamellate** (having 3 layers) walls have a porous outer layer that permits rapid uptake of water, whereas its cuticle-like layer is highly hydrophobic and prevents water-logging. Could it be that the papillae of bryophytes create that space needed to prevent water-logging? But Pressel and coworkers contend that papillae in ***R. purpurascens*** accelerate water loss,

resulting in a metabolic shutdown when the plants are water-stressed. With the wide variety of shapes, sizes, and density of papillae among the bryophytes, it is still possible that some have the ability to prevent water-logging during the critical periods when the plants are wet in normally dry habitats. If this ability exists, it may be of considerable importance in at least some cases.

Figure 135. ***Andreaeobryum macrosporum***, a moss for which papillae are known to aid in uptake of water through a channel in the papilla. Photo from Botany website, University of British Columbia, Canada, with permission.

Figure 136. ***Rhacocarpus purpurascens*** showing shiny leaves. Photo by Michael Lüth, with permission.

One such species is the desert moss, ***Syntrichia caninervis*** (Figure 115, Figure 137-Figure 139). When Wu *et al*. (2014) compared absorption of rhizoids to that of leaves, the leaves were clearly the greater absorptive organs. They tested absorption by dropping water onto the upper and lower leaf surfaces, both of which have C–shaped papillae (Figure 137) (Zheng *et al*. 2010). Wu and coworkers found that the adsorption by the papillae is so rapid that they could not determine the leaf angles. They concluded that in this case the papillae are **superhydrophilic** (having a highly efficient water absorption mechanism). The spaces between the papillae form microcapillary spaces that serve as an efficient conducting system (see also Koch *et al*. 2008).

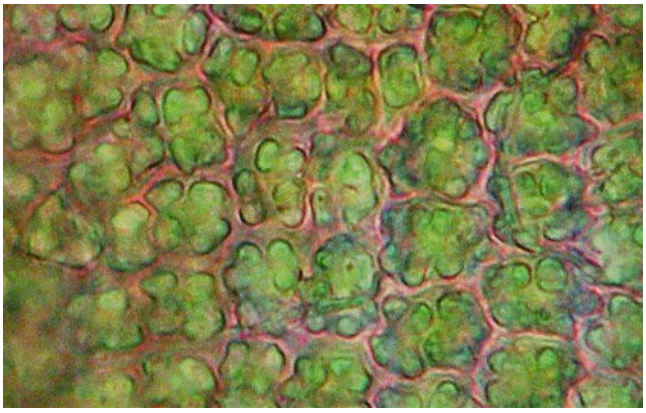

Figure 137. ***Syntrichia caninervis*** leaf papillae. Photo by Michael Lüth, with permission.

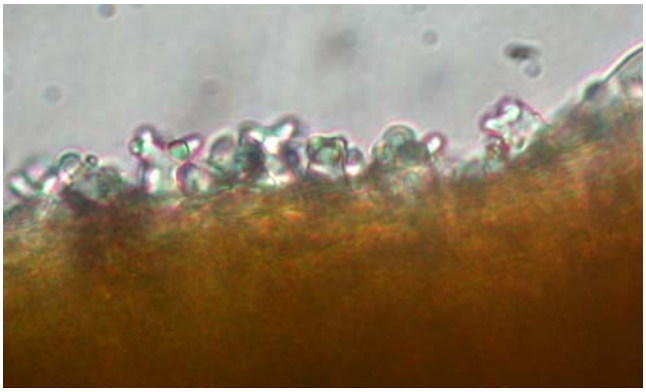

Figure 138. ***Syntrichia caninervis*** side view of leaf papillae that appear C-shaped from above. Photo by Terry McIntosh, with permission.

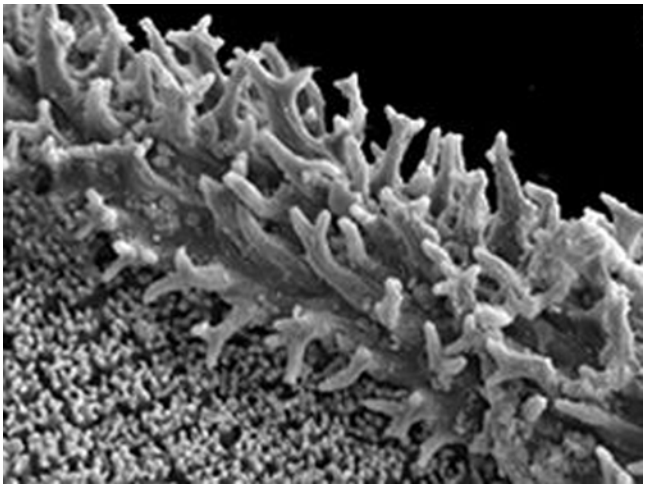

Figure 139. ***Syntrichia caninervis*** var. ***caninervis*** showing long papillae on costa and smaller ones on cells. Photo by M. T. Gallego.

The only thing that seems clear about papillae is that our understanding of them is not clear. It is likely that papillae cannot be lumped into one function, but that shapes, structure, and arrangement may create different capabilities, and these must coordinate in various ways with surface waxes, cell wall components, and other leaf surface features to optimize their role in the climates where the bryophytes live.

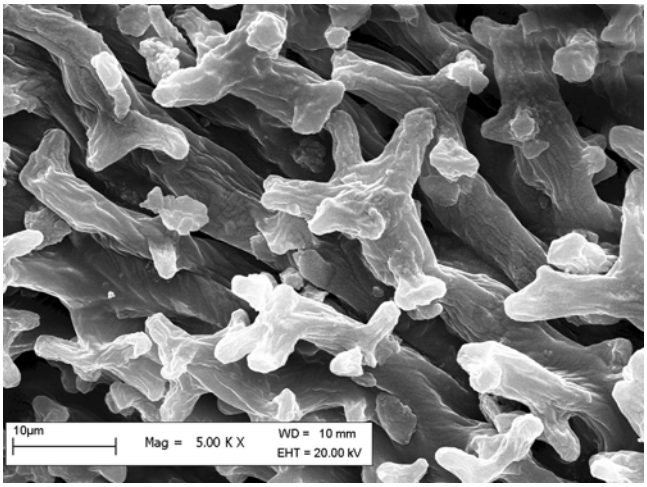

Figure 140. ***Syntrichia caninervis*** SEM of papillae on abaxial leaf surface. Photo by Zhang Yuan Ming.

Leaf Bases and Alar Cells

Many mosses have the advantage of enlarged, thin-walled cells at the base of the leaf (**alar cells**) (Figure 141-Figure 142). These serve as entry points for water into the leaf and stem, but in many species their enlargement when fully hydrated also forces the leaf away from the stem, exposing greater surface area for photosynthesis, and perhaps even for water capture.

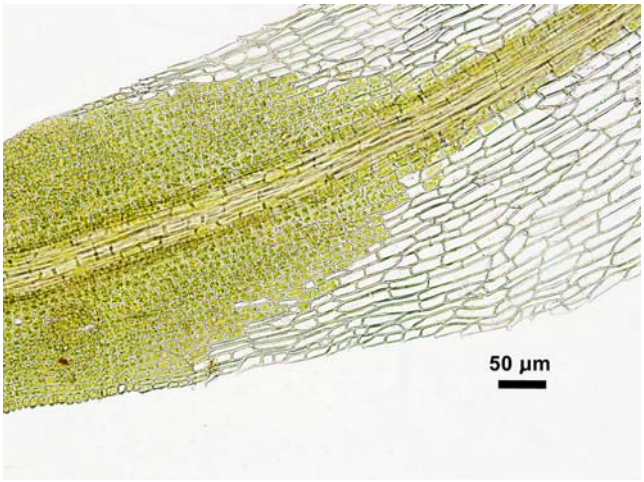

Figure 141. ***Tortella tortuosa*** leaf base showing enlarged hyaline cells where water can enter and cells can swell. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Those alar cells that are thin-walled shrink upon drying and readily gain water as it moves along external capillary spaces. Tucker and coworkers (1975) describe shrinkage of the basal cell cytoplasm during dehydration, creating gas pockets. Upon rehydration, the pockets of gas shrink and disappear within 10-30 seconds and the cytoplasm expands to fill the entire cell. This can explain the rapid unfolding of leaves upon rewetting in many taxa of bryophytes, with alar cells acting like the bulliform (expansion) cells of grasses.

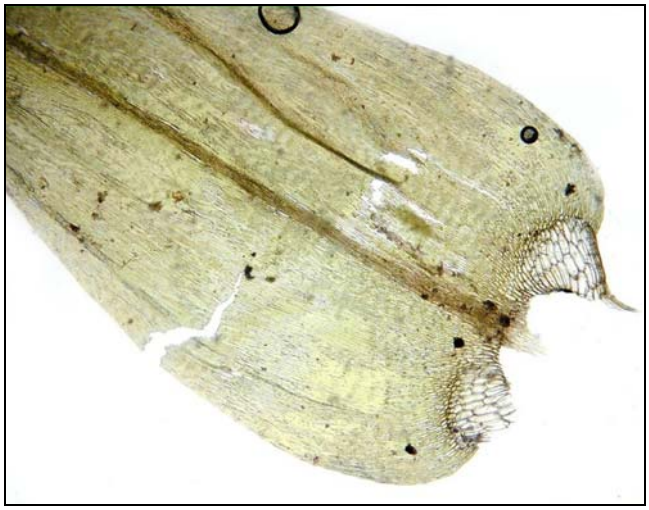

Figure 142. Leaf of ***Calliergon giganteum*** showing costa and enlarged **alar cells** at leaf base. Photo by Michael Lüth, with permission.

Wu *et al*. (2014) demonstrated the importance of adjusting the leaf angle in the desert moss ***Syntrichia caninervis*** (Figure 115, Figure 144). Although this moss is extremely desiccation tolerant, it must balance the need for water conservation with the need for light for photosynthesis when it is hydrated. This is accomplished by the movement of the leaves in response to moisture changes. As leaves become hydrated, they can move from a steep angle of 69-84° with the horizontal axis (Figure 144) to one of only 30° (Figure 115) within 7 seconds of becoming hydrated, with the first leaves moving within 1 second. They are able to obtain maximum net photosynthetic gain at a shoot relative water content of only 60%. The hyaline cells at the leaf base facilitate the rapid absorption of water, but they also swell and force the leaf away from the stem mechanically. It is interesting that the loss of leaf hair retards the leaf angle adjustment. When water was added to the soil instead of being added as an aerial source of water, the absorption rate was reduced, indicating that most water absorption is through the leaves.

Figure 143. ***Syntrichia caninervis*** leaf showing hyaline cells at the base that force the leaf away from the stem when it is hydrated. Photo by Dorothy Allard.

Figure 144. ***Syntrichia caninervis*** dry showing leaves twisted about the stem. Photo by Misha Ignatov, with permission.

Leaf Cell Shape

Bill Buck once asked me what I thought about the elongate cells in mosses such as ***Fontinalis*** and what the significance of such elongate cells might be, predominant in pleurocarpous mosses but rare in acrocarpous ones. I don't know that either of us has a better answer than we did then, but long, narrow cells should have an advantage in water movement. Elongate cells mean that fewer end walls must be crossed for water and other substances to traverse the interior of the leaf from tip to base or vice versa. The split between acrocarpous and pleurocarpous mosses suggests to me that the innovation of elongate cells, perhaps unnecessary in aquatic ancestors, occurred early in the evolution of pleurocarpous mosses and was rarely achieved among the acrocarpous species.

In the acrocarpous moss ***Bryum pseudotriquetrum***, this elongation is partially achieved (Figure 145). This is a moss of wet habitats that dry out. The leaves are usually out of the water, and having somewhat elongated cells should improve transport.

Figure 145. ***Bryum pseudotriquetrum*** leaf showing somewhat elongate cells, bordered by longer cells. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

It is interesting that many acrocarpous mosses have short leaf cells and tend to be more endohydric, whereas the pleurocarpous mosses, largely lacking a central strand and endohydric conduction, have mostly elongate leaf cells. Although these elongate cells would seemingly facilitate conduction between cells and from the leaf surface to the stem, we lack experimental evidence to support this.

Porose Cells

Porose cells provide more cause for speculation. These cells, uncommon among bryophytes, would seem to provide linkages to adjoining cells while permitting the cells to have otherwise thick walls. Such porosity is easily seen in ***Dicranum polysetum*** (Figure 146). I am unaware of any experiments to demonstrate that this is actually true or to compare the rate of transport in leaves with such cells to those in leaves with non-porose cell walls.

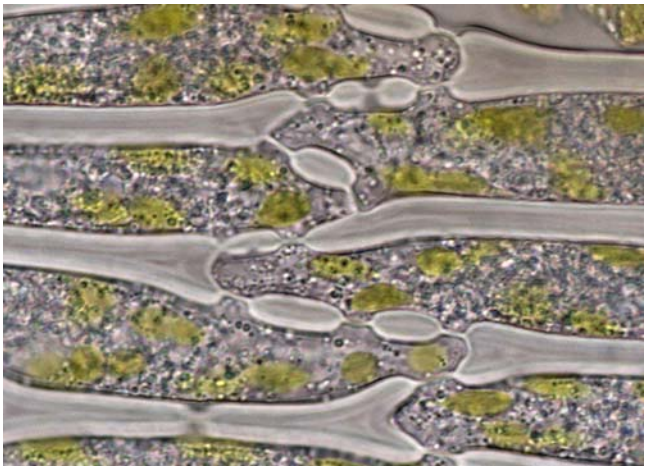

Figure 146. ***Dicranum polysetum*** leaf cell wall structure. Photo by Walter Obermayer, with permission.

Hyalocysts

Colorless or **hyaline** cells (Figure 147) are typical of leaves of ***Sphagnum*** (Figure 148) and ***Hedwigia*** (Figure 134), and the awns of numerous xerophytes. Frahm (1985) examined the correlation between **hyalocysts** and habitat in ***Campylopus*** (Figure 149). ***Campylopus shawii*** occurs in wet swamps where it can obtain and store water easily; it has large ventral hyalocysts. ***Campylopus setifolius***, on the other hand, grows on wet, dripping rocks that dry out occasionally; it has smaller hyalocysts, presumably to reduce the water loss to evaporation from these cells. The presence of ventral hyalocysts in ***C. flagelliferus*** (Figure 149) seem to adapt it to its life restricted to the bark of living trees where it needs a means of rapid water uptake.

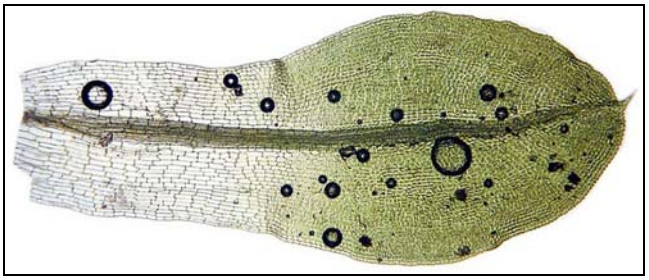

Figure 147. Leaf of ***Tortula vahliana*** showing hyalocysts in basal half of leaf. Photo by Michael Lüth, with permission.

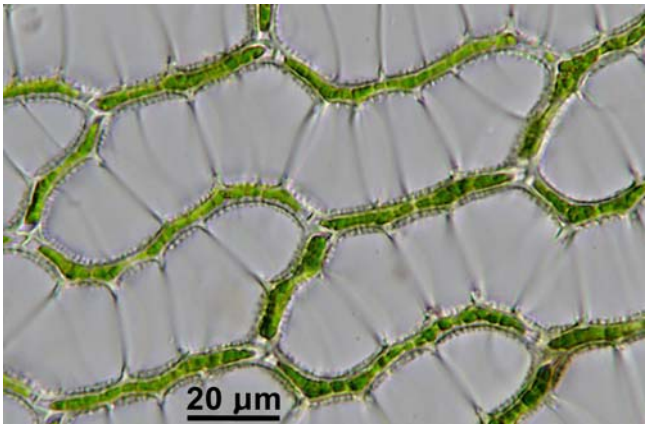

Figure 148. ***Sphagnum papillosum*** leaf cells showing large hyaline cells with fibrils and green photosynthetic cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 149. ***Campylopus flagelliferus***, an epiphyte with ventral hyalocysts. Photo by Jan-Peter Frahm, with permission.

Species of the cushion moss, ***Leucobryum*** (Figure 18, Figure 150), appear very succulent because of the hyalocysts among the photosynthetic cells. In this case, the leaf is several cells thick and the hyalocysts give them a whitish appearance. ***Leucophanes*** (Figure 151-Figure 152) has two different types of hyalocysts. The base of the leaf has a V-shaped arrangement of hyaline cells and the leaf lamina has an upper and lower layer of hyaline cells surrounding the photosynthetic cells.

Figure 150. ***Leucobryum juniperoideum***, showing the thick, whitish leaves. Photo by Michael Lüth, with permission.

Figure 151. ***Leucophanes molleri*** leaf showing v-shaped hyaline base. Photo courtesy of Noris Salazar Allen.

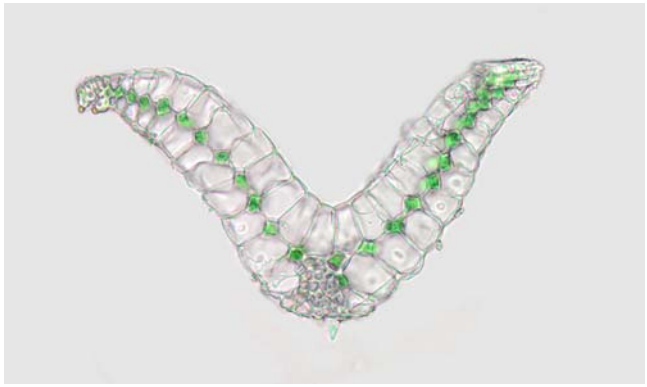

Figure 152. Cross section of ***Leucophanes molleri*** leaf showing hyaline cells surrounding the photosynthetic cells. Photo courtesy of Noris Salazar Allen.

Sphagnum species are considered xerophytic hydrophytes with many adaptations to deal with periodic drought (Andrus 1986). Living in a watery mire for most of the year, this genus has no internal conducting system and must face a severe threat of drying in the full sun of the summer when the water table is low. The ectohydric ***Sphagnum*** is a poor drought tolerator, but a relatively good drought avoider (Li *et al.* 1992). It has two types of leaf cells, small photosynthetic cells and large hyaline cells (Figure 153).

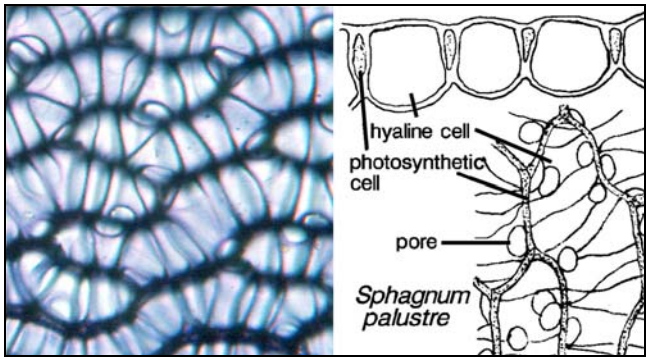

Figure 153. ***Sphagnum*** leaf cell types and pores. **Left:** ***Sphagnum*** leaf cells stained with crystal violet. Photo by Janice . Glime. **Right:** ***Sphagnum palustre*** photosynthetic and hyaline cells as seen in cross section (**upper**) and flat (**lower**). Drawings by Margaret Minahan.

Hyaline cells bathe the photosynthetic cells in water by providing a reservoir. Since the hyaline cell is a dead cell, its sole purpose seems to be to supply water to the photosynthetic portion of the leaf. These cells give some species of ***Sphagnum*** (Figure 153-Figure 154) the ability to hold up to 25 times their own mass in water (Andrus 1986).

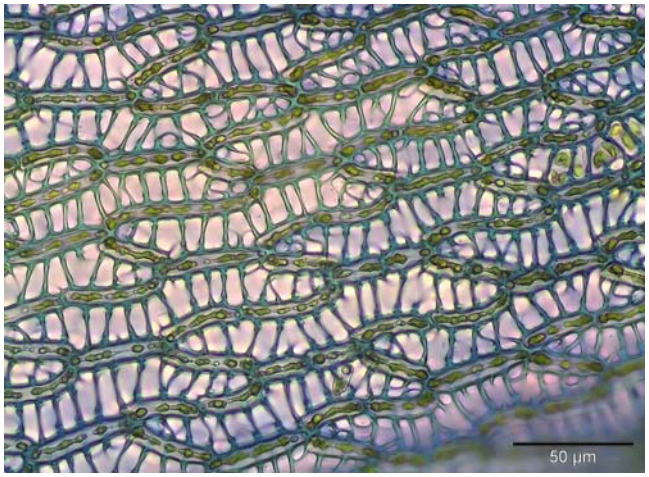

Figure 154. ***Sphagnum fallax*** leaf cells under normal nutrient conditions. Hyaline cells disappear under certain high N or low carbohydrate conditions in culture. Photo by Kristian Peters, with permission.

Transplant studies indicate that species of ***Sphagnum*** differ in abilities to inhabit different heights above the water level, and these differences seem to correlate with the positions they occupy in the field (See Li *et al.* 1992, Rydin 1993, and discussion in competition chapter). Studies by Hintikka (1972) hint that the mechanism for some of these adaptive differences may not relate to water, but to other factors associated with submersion. When grown in sterile culture, ***S. fallax*** (Figure 154) produced no hyaline cells in the presence of high ammonium, high organic nitrogen, or low carbohydrates. In nature, ammonia from decomposing plant matter would be greater under water than around emergent plants, quickly diffusing away in the atmosphere. Likewise, amino acids from organic decomposition would be present only in submersion water, not in rainfall. Response to low carbohydrates may be a limit in carbon available for making additional cell wall tissue, a need for an energy source, or it could relate to CO_2 from decomposing plant material in interstitial bog or fen waters.

Sphagnum seems to require a tremendous water content to achieve its maximal net photosynthesis, probably supplied by the large reservoir of water in its non-photosynthetic hyaline cells. In ***S. fuscum*** (Figure 155), a hummock top species, 600-1000% saturation was optimal, whereas in ***S. angustifolium*** (Figure 156), which tends to occur somewhat closer to the water surface, 900-1300% was optimal (Silvola & Aaltonen 1984), indicating the greater need for water in species that live closer to the water level. The photosynthetic decrease with water reduction was steeper for ***S. fuscum***, and plants in the field generally occurred where their water content was within this 600-1000% range. In ***S. angustifolium***, however, plants often occurred where their water content was outside their optimum range, thus defining narrow and broad relative niches.

Sphagnum is well known for its morphological plasticity in response to water availability (Miller 1991). For example, ***Sphagnum magellanicum*** (Figure 157) and ***S. papillosum*** (Figure 158) in dry conditions produce leaves that are longer (Figure 159) with more pores per cell (Figure 160). Li and coworkers (1992) suggest that these modifications may promote water-holding and absorbing properties.

Figure 155. ***Sphagnum fuscum*** in its typical position atop a hummock. Photo by Michael Lüth, with permission.

Figure 156. ***Sphagnum angustifolium***, a species that lives low on a hummock. Photo by Michael Lüth, with permission.

Figure 157. ***Sphagnum magellanicum***, a species that makes longer leaves under dry conditions. Photo by Janice Glime.

Figure 158. ***Sphagnum papillosum***, a species that makes longer leaves under dry conditions. Photo by Michael Lüth, with permission.

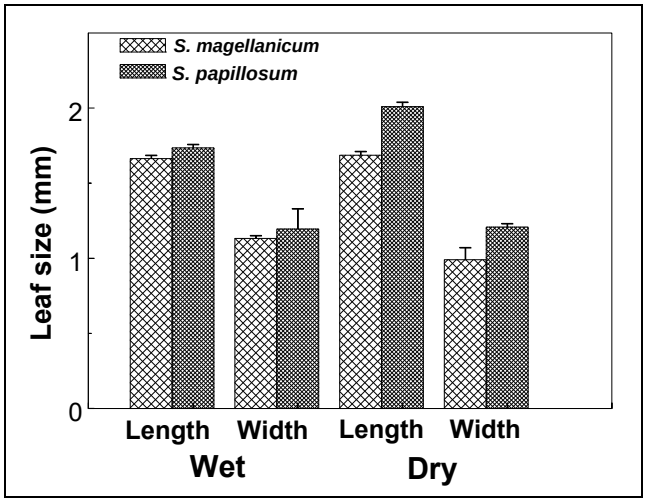

Figure 159. Comparison of leaf dimensions in ***Sphagnum magellanicum***, a drought-resistant species, and *S. papillosum*, a more drought-tolerant species. Based on Li *et al*. (1992).

Yet, these two species also differ in their water relations (Li *et al*. 1992). ***Sphagnum magellanicum*** (Figure 157) seems to be a better competitor for water than is ***S. papillosum*** (Figure 158) under dry conditions. This is exhibited by its better water transport ability and greater water content under the same atmospheric moisture conditions (Figure 161). This greater ability may be facilitated by its greater stem diameter due to larger hyaline cells, greater pore number, and smaller leaf size. On the other hand, ***S. papillosum*** (Figure 158) seems to be a better drought tolerator, having a higher survivorship following severe drought conditions.

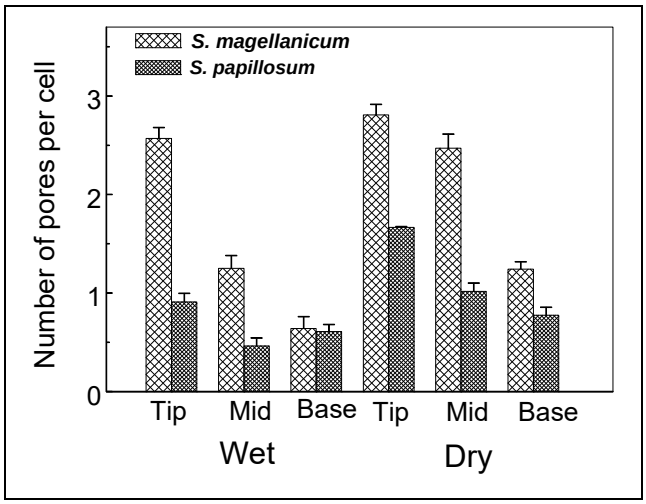

Figure 160. Comparison of number of pores per leaf cell in ***Sphagnum magellanicum***, a more drought-resistant species, and ***S. papillosum***, a more drought-tolerant species. Based on Li *et al*. 1992.

Superiority in water transport permits ***S. magellanicum*** (Figure 157) to occupy a higher position in the hummock than does ***S. papillosum*** (Figure 158). Li and coworkers (1992) found that when the two species grow intermixed in the higher hummock positions, both species grow better than if either is alone, provided at least half the plants are ***S. magellanicum***. They suggest that lateral transport among stems may occur to facilitate this, with ***S. magellanicum*** providing water for both species. If ***S. papillosum*** is dominant, even at somewhat lower positions in the hummock, both dry out more quickly.

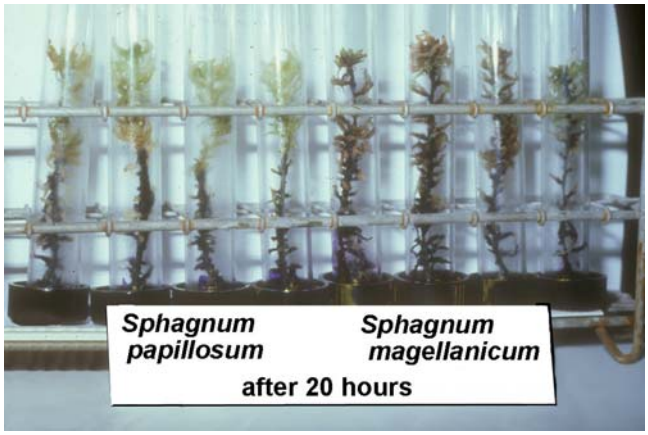

Figure 161. Comparison of distance a water-soluble dye has moved in 20 hours in ***Sphagnum papillosum*** and ***Sphagnum magellanicum***. Photo courtesy of Yenhung Li.

Cancellinae

The **cancellinae** (sing. cancellina) occur in few bryophytes, but especially in the **Calymperaceae**, **Pottiaceae**, ***Encalypta*** (Figure 163-Figure 164), and some species of ***Leptodontium*** (Figure 162). They are large, empty basal leaf cells, usually hyaline, that form a lattice. In the **Calymperaceae**, these are porate (having pores), and may serve as water storage cells.

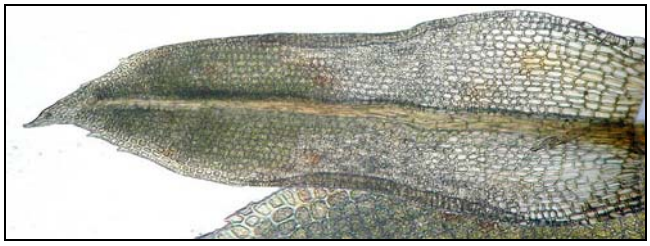

Figure 162. ***Leptodontium*** from the Neotropics showing cancellinae in the upper leaf. Photo by Michael Lüth, with permission.

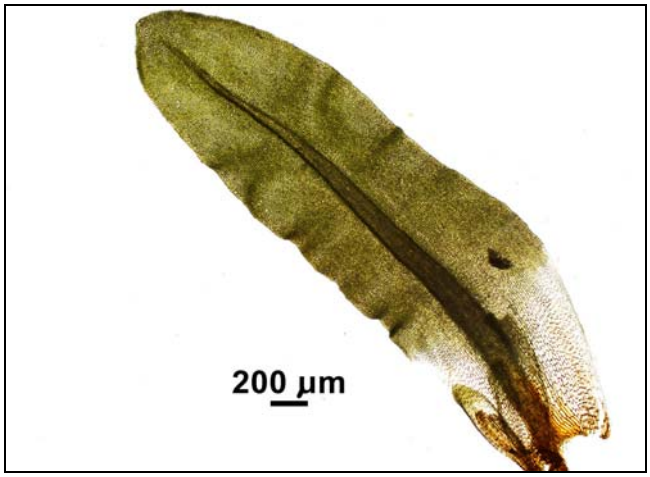

Figure 163. ***Encalypta vulgaris*** leaf showing lattice of cancellinae (gold walls) at base of leaf. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

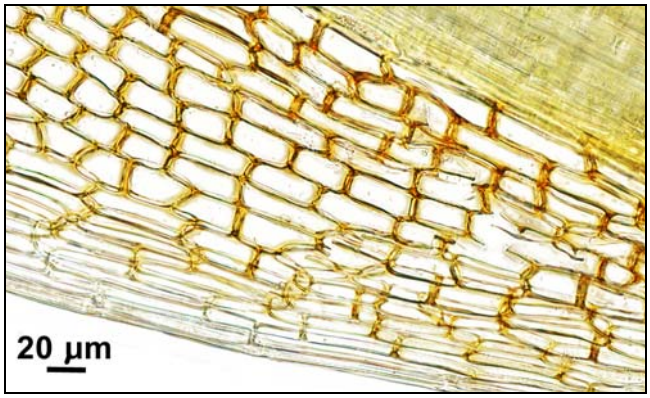

Figure 164. ***Encalypta vulgaris*** leaf showing lattice of cancellinae (cells with gold walls). Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Cell Structure

Cells structures can differ in a variety of ways that can affect water uptake, movement, and conservation. These differences include cell wall thickness, cell wall components, pores in the walls, internal papillae, presence of oil bodies, and vacuole size. These differences have the potential to alter the water relations of the leaves.

Cell Walls

Guerra *et al.* (1992) included **incrassate** cell walls among the adaptations of xerophytic mosses. Examples of these include ***Aloina aloides*** (Figure 165-Figure 166) and ***Didymodon fallax***. (Figure 167-Figure 168).

Figure 165. ***Aloina aloides***, a dry habitat moss with incrassate leaf cell walls. Photo by Michael Lüth, with permission.

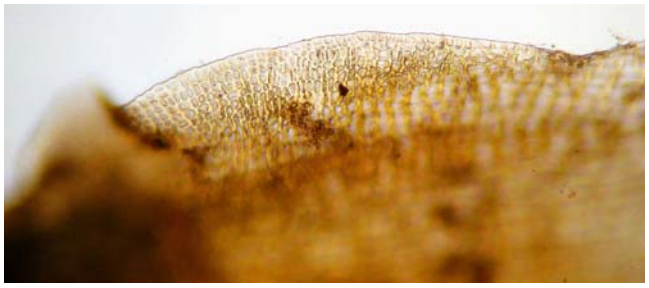

Figure 166. ***Aloina aloides*** leaf cells showing incrassate cell walls. Photo by Heike Hofmann © swissbryophytes <www.swissbryophytes.ch>, with permission.

Figure 167. ***Didymodon fallax***, a dry habitat species. Photo by David T. Holyoak, with permission.

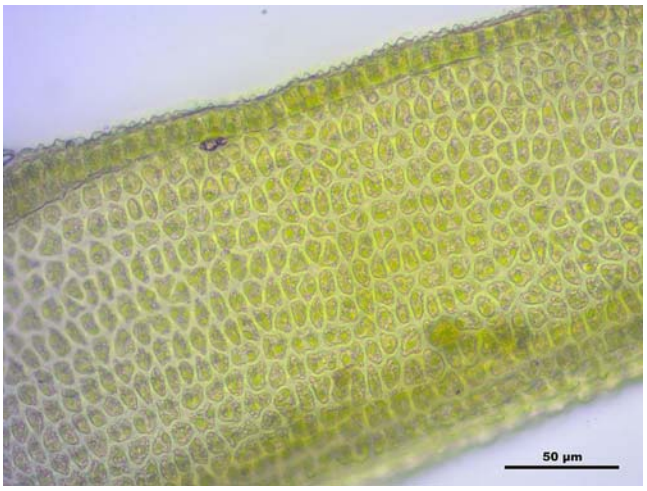

Figure 168. ***Didymodon fallax*** with incrassate leaf cell walls. Photo by Hermann Schachner, through Creative Commons.

Proctor (1979a) contends that coarse leaf cell walls (Figure 169) seem to aid water movement, possibly creating more internal capillary spaces among the fibrils of the cell wall (Proctor 1982). Proctor (1984) noted that mosses of dry habitats tend to have thick cell walls that can occupy more than half the cross section of the leaf. Fajuke (2010) further found that six mosses from Nigeria had thick cell walls that helped them survive desiccation.

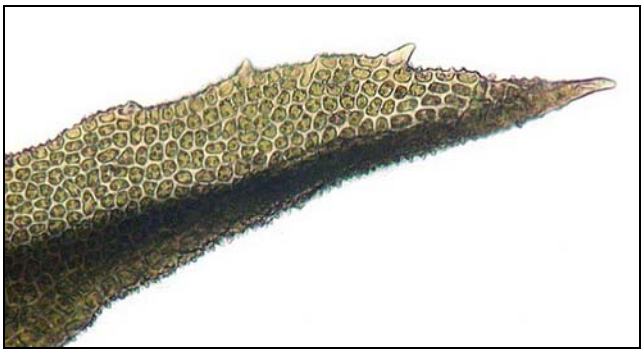

Figure 169. Leaf of ***Zygodon dentatus*** showing thick cell walls and papillae. Photo by Michael Lüth, with permission.

On the other hand, Frey and Kürschner (1991) could find no correlation between thickened cell walls and increasing aridity. Proctor (1982) also pointed out that such xerophytic mosses as ***Syntrichia*** (Figure 170-Figure 171), ***Encalypta*** (Figure 172-Figure 173), and ***Anomodon viticulosus*** (Figure 174-Figure 175) have quite thin walls and external conduction, suggesting that the thick walls are associated with species having internal conduction.

Figure 170. ***Syntrichia ruralis***, a moss of xeric habitats. Photo by Michael Lüth, with permission.

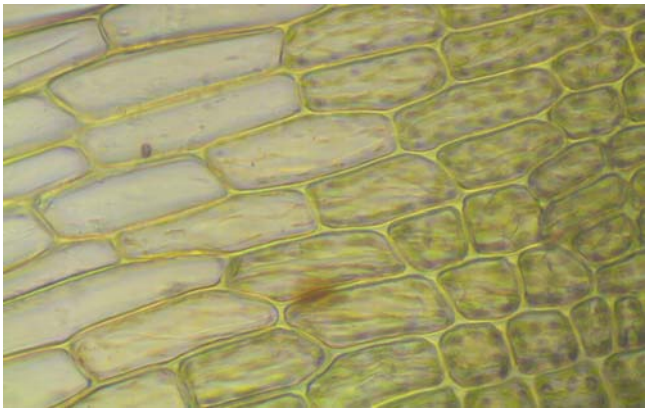

Figure 171. ***Syntrichia ruralis*** leaf lamina cells showing thin walls. Photo by Kristian Peters, with permission.

Figure 172. ***Encalypta rhabdocarpa*** showing xeric habitat in Europe. Photo by Michael Lüth, with permission.

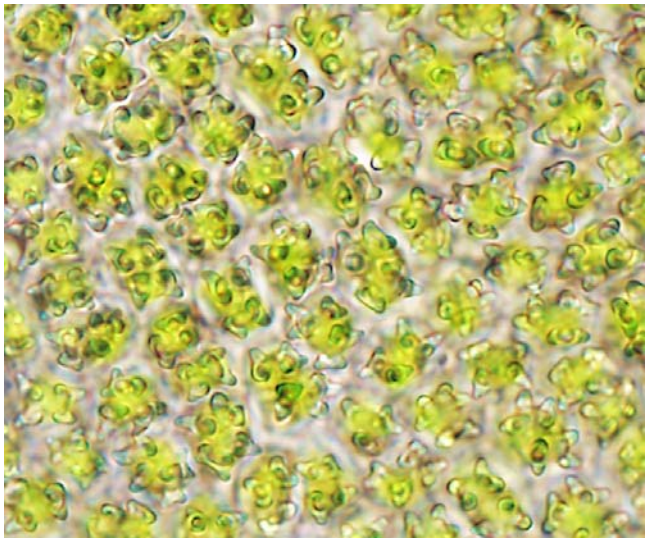

Figure 173. ***Encalypta vulgaris*** leaf cells with branched papillae and thin cell walls. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 174. ***Anomodon viticulosus***, a xerophytic moss with thin cell walls and papillae. Photo by Janice Glime.

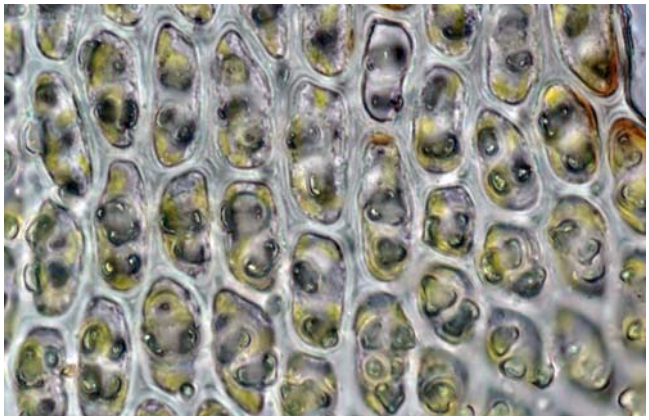

Figure 175. ***Anomodon viticulosus*** leaf cells and papillae. Proctor (1982) considered this species to have thin cell walls, but that does not appear to be the case in this example. Photo by Walter Obermayer, with permission.

The moss ***Rhacocarpus purpurascens*** (Figure 136) appears to have a unique means of facilitating rapid absorption of fog, dew, and rain (Barthlott & Schultze-Motel 1981; Edelmann *et al*. 1998). It has four layers of cell wall with a "peculiar architecture," forming cavities within the wall.

Flexibility of the cell wall is undoubtedly an aid to cell survival. This permits the cells to shrink upon dehydration, up to 50-70% in ***Syntrichia ruralis*** (Figure 176), without allowing for air to enter the drying cells (Moore *et al*. 1982).

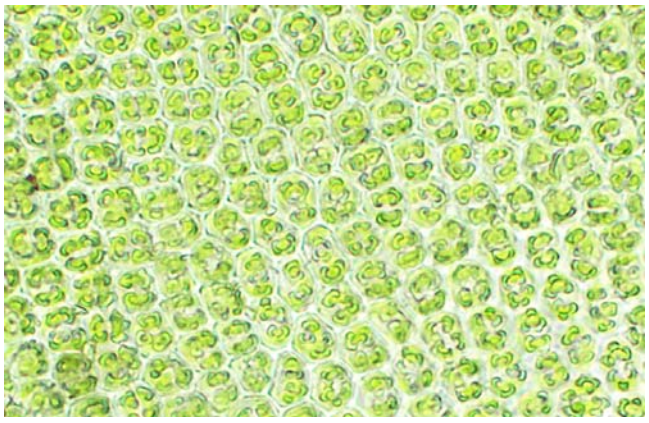

Figure 176. ***Syntrichia ruralis*** leaf cells with c-shaped papillae and thin walls. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Popper and Fry (2003) suggest that the addition of **xyloglucans** to the cell wall components may have been an important contribution to the ability of bryophytes to invade land. The presence of high concentrations of uronic acids would have permitted these plants to hold nutrient ions until such time as water was available for transport.

Cell walls seem like the first line of defense against desiccation. Autofluorescing compounds that can strengthen these walls are present in sporangial epidermis, spiral thickenings of elaters, and rhizoids, and leaf cells in the special case of ***Sphagnum*** (Figure 177) Kroken *et al*. (1996). In charophytes, these resistant compounds have multiple functions that include desiccation resistance and microbial resistance in lower charophytes, a role in embryogenesis in ***Coleochaete*** (Figure 178) and embryophytes, and decay resistance in structures that characterize bryophytes, such as rhizoids, sporangial epidermis, and elaters.

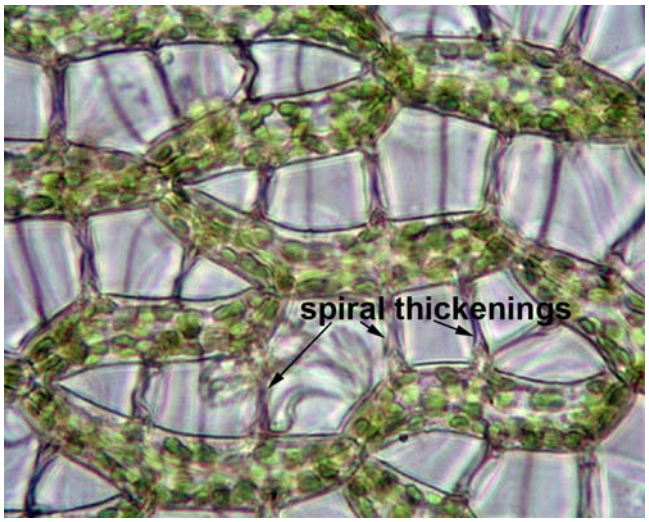

Figure 177. ***Sphagnum palustre*** cells showing the spiral thickenings on the hyaline cells. Photo by Malcolm Storey, through Creative Commons.

Figure 178. ***Coleochaete***, an alga with slime papillae and other characters that are more common among bryophytes. Photo by Yuuji Tsukii <http://protist.i.hosei.ac.jp/>, with permission.

It appears that the resistance of cell walls to desiccation is an ancient trait, already present in the green alga ***Coleochaete*** (Figure 178) (Kroken *et al*. 1996). In fact, it seems to be unique to ***Coleochaete*** among the charophytes and the resistance is produced in response to desiccation stress.

But bryophytes also have this ability – sexual reproduction induces autofluorescence in the cell walls of well-hydrated tissues at the placental junction, suggesting that these cell walls are endowed with compounds (phenols?) that endow them with desiccation resistance (Kroken *et al*. 1996). A similar phenomenon occurs in the gametophyte tissue at the apical end of the **pseudopodium** (gametophyte stalk that suspends the ***Sphagnum*** capsule away from the plant; Figure 179), suggesting a similar role to that of other bryophytes and even ***Coleochaete*** (Figure 178).

Figure 179. ***Sphagnum*** **pseudopodia** supporting capsules. The swollen upper end is desiccation tolerant and houses the foot of the sporophyte. Photo by Joan Edwards, with permission.

Lignin: The presence of lignin in bryophytes has been a controversial topic for ages. Lignins are present in xylem and sclerenchyma cells of tracheophytes. To demonstrate whether these substances might be present in bryophyte and charophyte cell walls, Ligrone *et al*. (2008) examined the charophyte *Nitella* and a number of bryophytes. Using polyclonal antibodies that labelled lignified walls in tracheophytes, they found that these also bound to the cell walls of bryophytes. But rather than the specific locations found in tracheophytes, the locations in mosses and liverworts were not tissue-specific. Hornworts (***Megaceros flagellaris*** and ***M. fuegiensis***; Figure 180) differed somewhat in that labelling was stronger in pseudoelaters and spores than in other cell types. Cell walls were likewise labelled in the charophyte *Nitella*, but a lack of binding suggested that lignins or lignin-like substances were absent in ***Coleochaete***.

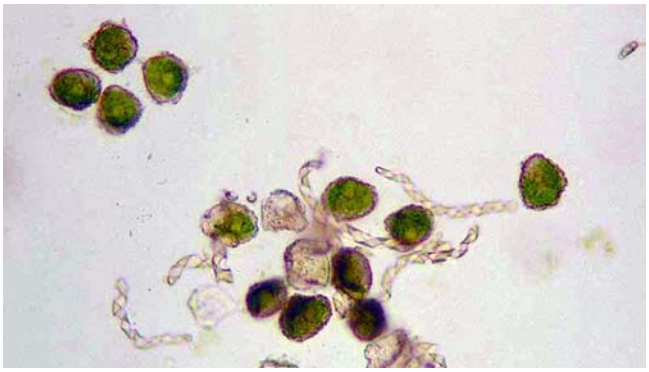

Figure 180. ***Megaceros*** spores and elaters, a genus in which lignin labelling is stronger in spores and elaters than in other cell types. Photo by Christine Cargill, with permission.

Oil Bodies

Oil bodies are common in the leaf cells of leafy liverworts (Pfeffer 1874; Garjeanne 1903; Müller 1905, 1939; Schuster & Hattori 1954; Pihakaski 1972a, b; Stewart 1978; Schuster 1992; Asakawa 2004), but similar structures are generally absent in mosses. Kronestedt (1983) found that they had seasonal variability in the nature of the matrix and the amount of lipophilic material in the floating liverwort ***Ricciocarpos natans*** (Figure 181). The globules can coalesce to form larger units. Their role has remained a mystery (He *et al*. 2013), but recently several researchers have provided evidence that they may have a crucial role in desiccation tolerance.

Oil bodies seem to have different developmental pathways in different species. Pihakaski (1966, 1968, 1972a) compared their development in two leafy liverworts – ***Bazzania trilobata*** (Figure 182-Figure 183) and ***Lophozia ventricosa*** (see Figure 184). The component parts are the same in both species: an outer membrane that envelops the whole oil body, a granular stroma layer that varies in size and thickness, specific globules enveloped by the stroma layer, and a thin inner membrane that surrounds the specific globules. But the oil bodies in these two species develop in different ways. In ***B. trilobata***, they develop from vacuole-like formations in the shoot apex or in leaf primordia where certain substances segregate. In this species, granular dense bodies are visible in the cells of the shoot apex, but these shrink in size as oil bodies develop and are absent in the mature leaf cells. In ***L. ventricosa*** they originate by aggregation and fusion of lipid bodies.

Figure 181. ***Ricciocarpos natans***. Photo by Štěpán Koval, with permission.

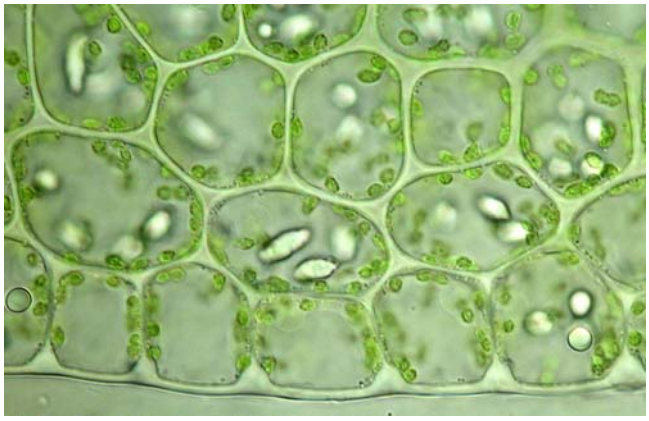

Figure 182. Oil bodies (transparent) in leaf cells of ***Bazzania trilobata***. Photo by Walter Obermayer, with permission.

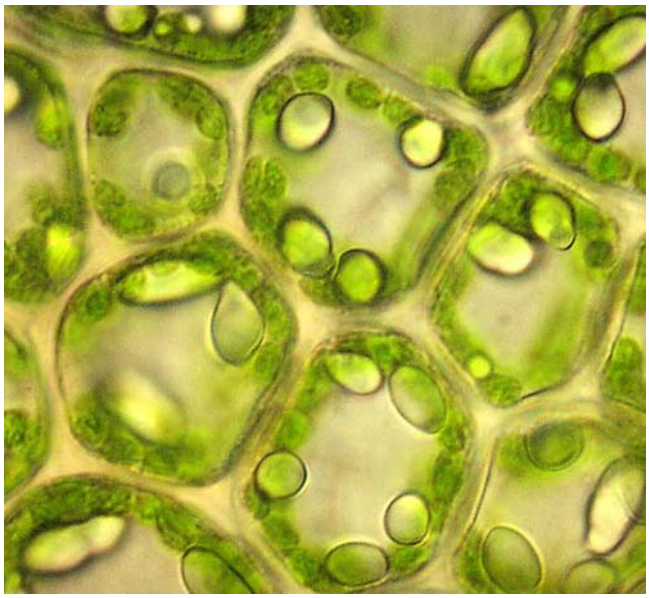

Figure 183. Oil bodies (transparent) in leaf cells of ***Bazzania trilobata***. Photo by Walter Obermayer, with permission.

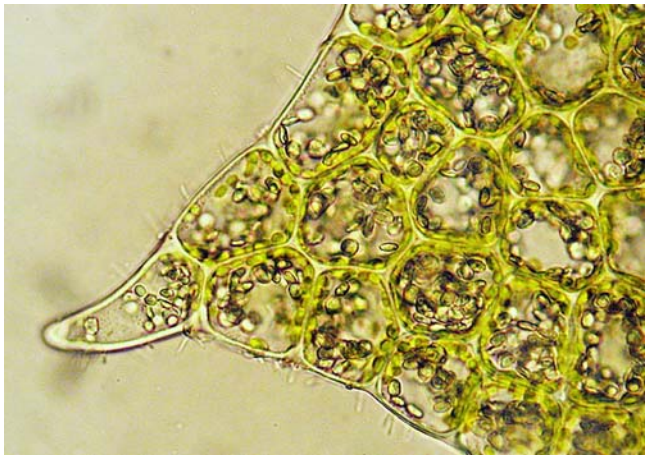

Figure 184. ***Lophozia incisa*** leaf cells with oil bodies. Photo by Walter Obermayer, with permission.

Duckett and Ligrone (1995) followed the development of oil bodies in gemmae of ***Odontoschisma denudatum*** (Figure 185). They appear suddenly early in development, forming flat structures associated with the endoplasmic reticulum. Suire (2000) provided evidence that liverwort oil bodies are secretory cell compartments that originate from the endoplasmic reticulum. The oil bodies remain closely associated with the cytoplasmic lipid bodies throughout development but do not fuse with them. Finally they take on their ultimate shape and become suspended by fine cytoplasmic bridges within the vacuoles.

Oil bodies are notorious for disappearing in herbarium specimens. Pressel *et al*. (2009) described this behavior for desiccation-tolerant liverworts. They found that while they are dry, they remain substantially unchanged, but when they are rewet, they initially change drastically, becoming flattened. It requires up to 48 hours for them to regain their normal shapes. However, if the liverworts are dried faster than would typically happen in nature, they, and other organelles, disintegrate when the liverwort is rewet. Pressel *et al*. suggested that loss of shape upon normal rewetting could be evidence of a shift in soluble carbohydrates or other substances into the cytosol, indicating that the oil bodies may be critical to the desiccation tolerance of liverworts.

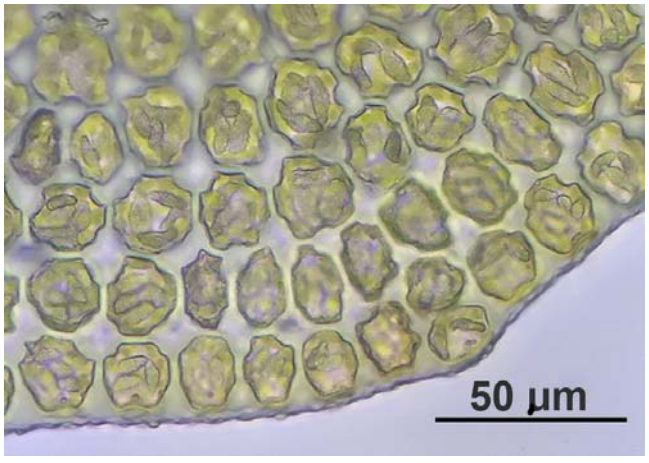

Figure 185. ***Odontoschisma denudatum*** "cuticular" papillae (see leaf edge), leaf cells, and oil bodies. Photo by Kristian Peters, with permission.

Galatis *et al*. (1978) found phenolic and "polysaccharidic" compounds but no protein in the oil bodies of ***Marchantia palacea*** (Figure 186). On the other hand, He *et al*. (2013) reported that in ***Marchantia polymorpha*** (Figure 187) the oil bodies (Figure 188) contain a protein complex that is immunologically related to plastid and cytoplasm enzymes of the **isoprenoid** synthesis (isoprenoids belong to a class of organic compounds composed of two or more units of hydrocarbons, with each unit consisting of five carbon atoms in a specific pattern; they have a wide range of roles in physiological processes of plants and animals). Suire *et al*. (2000) similarly found isoprenoid biosynthetic enzymes similar to those found in plastids and the cytosol of ***Marchantia polymorpha***. The suggested paucity of protein in the oil droplets of liverworts (Galatis *et al*. 1978) is likewise in sharp contrast with that found in the green alga ***Chlamydomonas reinhardtii*** (Moellering & Benning 2010). In this alga, 259 proteins were associated with lipid droplets.

Figure 186. ***Marchantia paleacea*** thallus with archegoniophores, a species with phenolic and "polysaccharidic" compounds but no protein in the oil bodies. Photo from Briofitas de Mexico, through Creative Commons.

Figure 187. ***Marchantia polymorpha*** with ice crystals. This species has oil bodies that contain a protein complex. Photo by David Taylor, with permission.

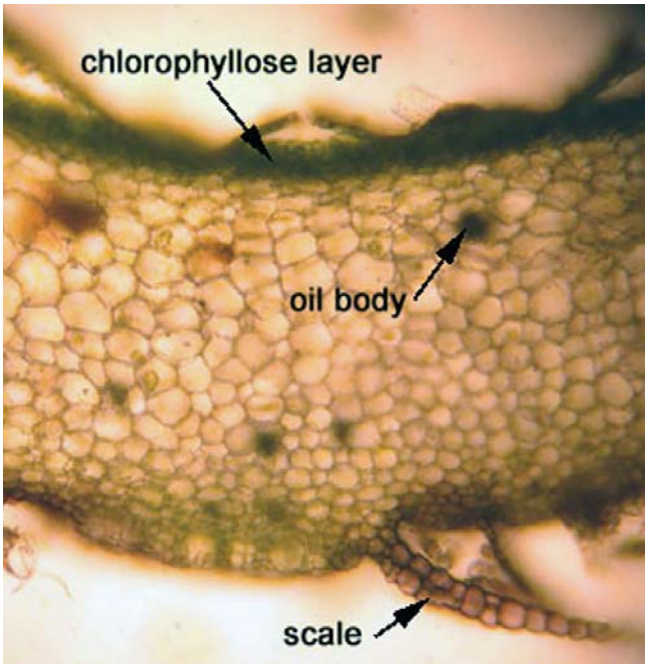

Figure 188. ***Marchantia polymorpha*** thallus vertical section showing oil bodies. Photo from Botany Department, University of British Columbia, with permission.

Oil bodies of liverworts produce mono-, sesqui-, and diterpenoids, aromatic compounds such as bibenzyl, bis-bibenzyls, and acetogenins (Asakawa 2008; Asakawa *et al*. 2013). These often aromatic compounds have such activities as causing allergenic contact dermatitis, antimicrobial action, antifungal and antiviral action, cytotoxicity, insecticidal action, insect antifeedant, superoxide anion radical release, 5-lipoxygenase, calmodulin, hyaluronidase, cyclooxygenase, DNA polymerase β, and α-glucosidase and NO production inhibition, antioxidant, piscicidal, neurotrophic, and muscle relaxation. But these are mostly uses of interest to humans and do little to tell us how the liverwort benefits from them.

It appears that mosses do have their own version of oil bodies. Huang *et al*. (2009) reported abundant oil bodies in the photosynthetic gametophyte and the spores of ***Physcomitrella patens*** (Figure 189-Figure 190). These researchers found that neutral lipids in these oil bodies in the gametophyte were largely steryl esters and triacylglycerols, and unlike some reports on the liverwort oil bodies, they had proteins. These proteins were programmed by three oleosin genes. The expression of these oleosin genes were tissue specific. Structural proteins cover the surfaces of the lipid droplets and prevent them from coalescing during desiccation (Huang *et al*. 2009; He *et al*. 2013).

The number of oil bodies in apical gametophyte tissue decreases during the production of sex organs in ***Physcomitrella patens*** (Figure 189-Figure 190) (Huang *et al*. 2009). In spores, the oil bodies serve as food reserves for **gluconeogenesis** (formation of glucose from smaller molecules) and are equivalent to those of seed oil bodies. It appears that these oil bodies have an energy function for reproduction, but could they be important in providing the energy needed during rehydration as well?

Figure 189. ***Physcomitrella patens***, a species produces abundant oil bodies in its leafy gametophyte and spores, but the oil bodies decrease during sex organ production. Photo by Michael Lüth, with permission.

Figure 190. ***Physcomitrella patens*** sporophyte with spores that contain oil bodies. Photo by Ralf Reski Lab through Wikipedia Commons, with permission.

It seems surprising to me that we know so little about the functioning of oil bodies, especially in liverwort leaf cells. We cannot discount them as a non-functioning structure that happened and wasn't eliminated because they are so widespread. And they have tremendous variability, both in morphology and in chemical constituents. More than 1600 lipophilic compounds have been extracted from liverworts (Ludwiczuk & Asakawa 2019)!

Hieronymus (1892) suggested that oil bodies protected against UV light stress. Schuster (1966) suggested that they help maintain the liverworts through cold, drought, and osmotic stress.

Early experiments demonstrate a role in antiherbivory, with snails preferring species with fewer oil bodies (Stahl 1888). And when oil bodies were leached from some of the liverworts, those were preferred over the non-leached ones. Further support of the antiherbivory hypothesis was demonstrated by genetic manipulation of ***Marchantia*** (Figure 187-Figure 188). Those plants defective in oil bodies were more likely to beaten than were the normal populations (Kanazawa *et al*. 2020; Romani *et al*. 2020). Likewise in ***Marchantia***, Peñuelas *et al*. (2019) demonstrated that mutant plants with reduced sesquiterpenes experienced greater foraging by ***Spodoptera littoralis*** caterpillars (Figure 191).

Figure 191. ***Spodoptera littoralis*** larva, a species that responds to reduced sesquiterpenes in ***Marchantia*** by eating more of it. Photo by Ishbb, through Creative Commons.

We know that essential oils extracted from liverworts serve as antibiotics against a wide range of organisms (Asakawa & Ludwiczuk 2018). Furthermore, we know that extracts from plants that have reduced oil bodies also have reduced antibiotic activity against bacteria and fungi (Romani *et al*. 2020).

One of the functions of oil bodies is that they enclose vast quantities of sesquiterpenoids and other compounds, meanwhile protecting the cells from the toxicity of these chemicals (Tanaka *et al*. 2016; Romani *et al*. 2022). Mapping of oil body types suggests that they were present in the most recent common ancestor of liverworts and were probably the first secretory structure in land plants.

Tanaka *et al*. (2016) found that nutrient starvation and non-axenic growth in ***Marchantia*** greatly increases the number of oil bodies, suggesting a possible role in maintaining nutrient reserves. This notion is supported by the chemical properties of the carbohydrates present and the maintenance of turgidity after dehydration (Pressel *et al* 2009).

To protect the cells from the toxic nature of the specialized compounds, the oil bodies not only compartmentalize the compounds, but also the enzymes needed to make them (Tissier 2018; Suire *et al*. 2000). Hence, the cells are completely protected from these toxic substances. Furthermore, the substances are typically volatile and the oil bodies prevent them from evaporating too quickly. This explains the various aromas one can smell when the tissues are crushed.

Vacuoles

Bryophytes, for some reason, were long thought to lack vacuoles. However, this is not the case, as demonstrated in the liverwort ***Lunularia cruciata*** (Figure 192) (Carginale *et al*. 2004), the mosses ***Physcomitrella patens*** (Figure 189) (Nagao *et al*. 2005), ***Ephemerum cohaerens*** (Figure 193) (Kwok & Rushing 1999), and ***Fontinalis antipyretica*** (Figure 194) (Bruns 1998). In fact, the vacuoles can be quite large, as witnessed by the chloroplasts crowded around the periphery of the cell in many species. But there has been no systematic study to indicate which bryophytes have vacuoles and which do not. We might ask if there is some correlation between the ability to withstand drought or to take up water, or even to hold on to cellular water as the environment dries and the presence of one or more vacuoles.

Vacuoles are known in plants to contain solutes that control the water uptake by the vacuole (Taiz & Zeiger 1991). In bryophytes, Nagao *et al*. (2005) have demonstrated that ABA affected the appearance of vacuoles during treatment with freezing. Since ABA is also involved in drought tolerance and has resulted in the increased osmotic concentration of protonemal cells, this mechanism of vacuolar preparation should be explored for possible relationships to drought tolerance in various bryophytes. Could presence of a vacuole help the cell take in water more quickly by storing solutes that create an osmotic gradient, yet are safely out of the way of cellular metabolism? Could it also have a role in the ability of the cells to shrink as they dry and expand when wet?

Figure 192. ***Lunularia cruciata*** thallus section through gemmae cup. This is a species of thallose liverwort with demonstrated vacuoles. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 193. ***Ephemerum cohaerens*** leaf, a species with demonstrated cell vacuoles in the leaves. Photo by Dick Haaksma, with permission.

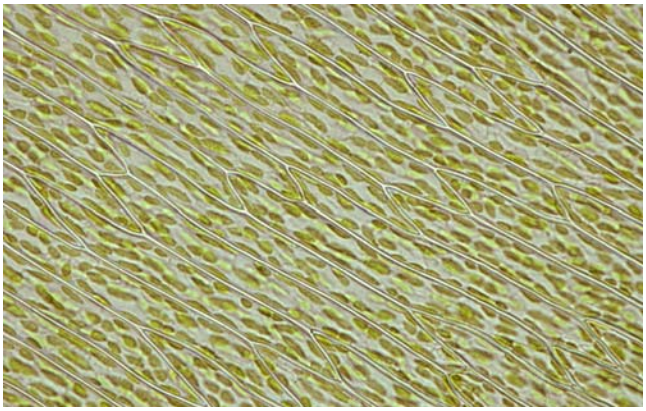

Figure 194. ***Fontinalis antipyretica*** leaf cells, a species with demonstrated cell vacuoles in the leaves. Photo by Janice Glime.

Slime Papillae

In leafy liverworts, **slime papillae** on marginal leaf cells can help to absorb and hold water, as in the leaf margins of ***Porella*** (Figure 195) and ***Heteroscyphus*** (Figure 196) (Daniels 1998). The presence of slime papillae in ***Takakia*** (Figure 197) was among the reasons why several bryologists originally considered that genus to be a liverwort, but capsule structure confirmed its similarity to mosses.

Figure 195. ***Porella pinnata***, a species with slime papillae on the leaf margins. Note white margins at arrows on right. Photo by Des Callaghan, with permission.

Figure 196. ***Heteroscyphus coalitus***, a leafy liverwort with slime papillae. Photo by Tom Thekathyil, with permission.

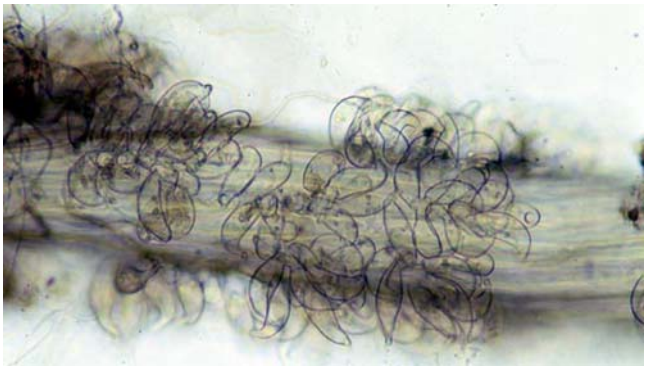

Figure 197. ***Takakia lepidozioides*** slime papillae. Photo from the Herbarium of Hiroshima University, with permission.

Summary

Bryophytes gain water in their cells both through external (**ectohydric**) capillary movement and internal (**endohydric**) transport. Structural adaptations such as **overlapping leaves**, **concave leaves**, **crispate leaves**, **plications**, **revolute** or **involute margins**, **lamellae**, **multi-layered leaves**, **lobules, hair points**, **papillae**, **costae**, **stereids**, **borders**, **leaf teeth**, **teniolae**, **alar cells**, **hyaline cells**, **cancellinae**, **resistant cell walls**, **oil bodies**, and **vacuoles**, aid in moving water, facilitating entry, or reducing loss. In areas with high fog occurrence and little or no rainfall, fog can be a major contributor to the bryophyte water budget.

Overlapping leaves, **concave leaves**, **revolute margins**, and **involute margins** help to hold water in capillary spaces. **Alar cells** provide a point of entry through thin walls that balloon up and mechanically spread the leaves. The **costa** and **border** cells may move water more quickly because the cells are long and have fewer end walls to be crossed. **Plications** permit leaf expansion in hydrated leaves and conserve moisture in drying conditions, as do **twisting** and **contorted** leaves. **Hair points** collect water from fog and dew and slow down drying by reducing exposed surface area of the leaf above. In leafy liverworts, **lobules** retain water for species of dry habitats. **Lamellae** may repel water and prevent water logging in some species, but hold water in capillary spaces in others.

Cell walls may contain **phenols** and other fluorescing materials similar to lignin to resist water loss. **Oil bodies** may provide rehydration energy, but their role in water relations is still poorly understood. **Vacuoles** hold water within the cell and permit expansion and contraction of the cell. **Slime Papillae** may contribute to absorption and holding of water.

Acknowledgments

An earlier version of this chapter benefitted from the help of Beth Scafone and Medora Burke-Scoll, who helped me tow the line in explaining things without leaving too much to one's imagination, but at the same time not repeating myself. Ron Gratz translated part of the work by Loeske. Linda Luster checked the literature citations, proofread, and made glossary suggestions from a layperson's perspective. I was fortunate to have Ken Kellman ask on Bryonet for examples of bryophytes with a demonstrated cuticle; he was kind enough to share his collected references with me. Thank you to Noris Salazar Allen for sending me the leaf images of *Leucophanes*.

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CHAPTER 7-4b

WATER RELATIONS: LEAF STRATEGIES – CUTICLES AND WAXES

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CHAPTER 7-4b

WATER RELATIONS: LEAF STRATEGIES – CUTICLES AND WAXES

Figure 1. ***Pohlia wahlenbergii*** var. ***glacialis*** in Norway. The drops of water on the surface are being repelled by hydrophobic surface waxes, preventing water logging. Photo by Michael Lüth, with permission.

Bryophytes Do Have Cuticles

Anyone who has observed the speed with which many mosses and leafy liverworts absorb water would assume that they lack waxes. But as we examine these bryophytes with chemical and SEM methods, we find that this assumption is not reliable (Buda *et al*. 2013). For example, the simple moss ***Physcomitrella patens*** (Figure 2) has a cuticle with a chemical composition and structure similar to that of flowering plants. It is likely that the cuticle was a necessary factor in the evolution to land, regulating water status and providing protection from biotic and abiotic stresses. Using knockout genes to create mutant plants that were "severely deficient in cuticular wax accumulation" Buda *et al*. found that these plants also had reduced desiccation tolerance. The gene responsible for the cuticle wax formation in ***Physcomitrella patens*** is the same one as that in *Arabidopsis thaliana*, indicating its evolution early in the invasion of land.

Figure 2. ***Physcomitrella patens***, a moss from which the cuticular wax gene has been isolated. Photo by Janice Glime.

Although thickened waxy cuticles seem to be rare in moss gametophytes, various mosses have some sort of cuticular covering. In some mosses, this is expressed as granules, platelets, or ribbons that are soluble in chloroform (Proctor 1982), satisfying the test for cuticular wax in tracheophytes. This type of cuticle endows ***Pohlia cruda*** (Figure 3), ***P. wahlenbergii*** (=*P. albicans*; Figure 4), ***Saelania glaucescens*** (Figure 55), ***Schistostega pennata*** (Figure 5), ***Pogonatum urnigerum*** (Figure 6), and many **Bartramiaceae** with their **glaucous** (whitish) appearance (Proctor 1982). We shouldn't be surprised that ***Pogonatum urnigerum*** has surface waxes similar to those of tracheophytes, but even primitive mosses such as ***Andreaea rupestris*** (Figure 7) have surface waxes that are similar to the epicuticular waxes of tracheophytes (Haas 1982).

Figure 3. ***Pohlia cruda***, a whitish moss due to cuticular waxes. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 4. ***Pohlia wahlenbergii*** with drops of water, presumably repelled by the surface waxes. Photo by J. C. Schou, with permission.

Figure 5. ***Schistostega pennata*** showing whitish cast of the cuticle. Photo courtesy of Martine Lapointe.

Figure 6. ***Pogonatum urnigerum*** wet, showing the waxy (**glaucous**) appearance of the leaves. Photo by Janice Glime.

Figure 7. ***Andreaea rupestris*** showing slightly glaucous appearance. Photo by Janice Glime.

In addition to most of the species already named, Stránsky *et al*. 1967) found n-alkanes (19-33 carbon atom chains) in ***Leucobryum glaucum*** (Figure 8)**,** ***Rhytidiadelphus triquetrus*** (Figure 9), ***Conocephalum conicum*** (Figure 10), ***Porella platyphylla*** (Figure 11), ***Pellia fabbroniana*** (Figure 12), and ***Pellia epiphylla*** (Figure 13). Even ***Sphagnum*** is known to have waxes (lignoceryl alcohol) in ***S. capillaceum*** (*S. nemoreum*; Figure 59), ***S. fuscum*** (Figure 60), and ***S. magellanicum*** (Figure 61) (Ives & Neill 1958).

Figure 8. ***Leucobryum glaucum*** showing appearance of waxes on a moss with hyaline cells. Photo by Janice Glime.

Figure 9. ***Rhytidiadelphus triquetrus***, a moss expressing waxes that are n-alkanes. Photo by Michael Lüth, with permission.

Figure 10. ***Conocephalum conicum*** showing a waxy surface. Photo by Jan-Peter Frahm, with permission.

Figure 11. ***Porella platyphylla*** on bark, showing slightly glaucous appearance due to wax. Photo by Michael Lüth, with permission.

Figure 12. ***Pellia fabbroniana*** with waxy epidermis and propagules. Photo by Eugenia Ron Alvarez and Tomas Sobota at Plant Actions, with permission.

Figure 13. ***Pellia epiphylla*** showing slightly waxy appearance due to wax on its surface. Photo by Kristian Peters, through Creative Commons.

The documentation of cuticle in bryophyte leaves is somewhat scant. Nevertheless, Proctor (1979b) examined 43 species of mosses and determined that 12 of these have a well developed surface wax on the leaves that is comparable to that of flowering plants. Eight more have traces of wax. Not surprisingly, all of these species are **endohydric** (have internal conduction). If a moss has a waxy or glaucous look, it most likely has surface wax. A good example of this is the leaves of ***Polytrichum*** (Figure 14-Figure 18) On the other hand, ***Atrichum undulatum*** (Figure 19-Figure 21), in the same family (**Polytrichaceae**), has no discernable wax and lacks the waxy appearance. Instead of having leaves that curl inward and wrap around the stem upon drying, members of ***Atrichum*** have wavy leaf surfaces and become contorted when they dry (Figure 22-Figure 23).

Figure 14. ***Polytrichum commune*** leaves showing waxy surface. Photo by James K. Lindsey, with permission.

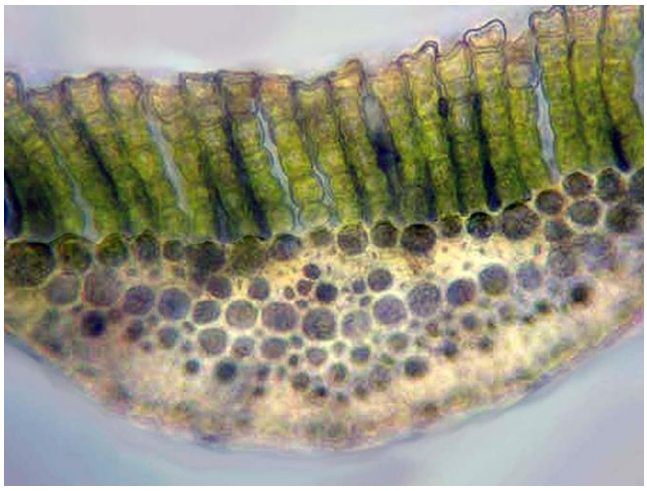

Figure 15. ***Polytrichum commune*** leaf lamellae where waxes are present on the terminal cells. Photo from Botany Department, University of British Columbia, with permission.

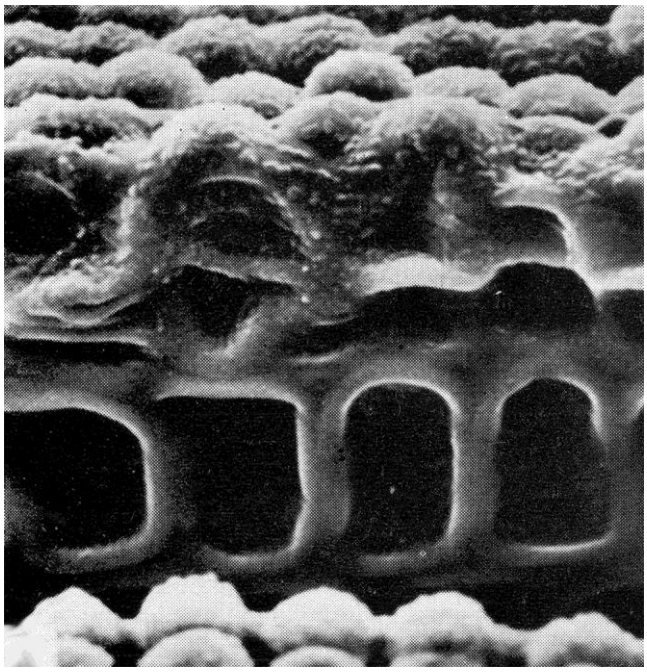

Figure 16. SEM of ***Polytrichum commune*** leaf cuticle. Photo by Michael Proctor, with permission.

Figure 17. ***Polytrichum juniperinum*** showing leaves with lamina rolled over lamellae and waxy appearance. Photo by Michael Lüth, with permission.

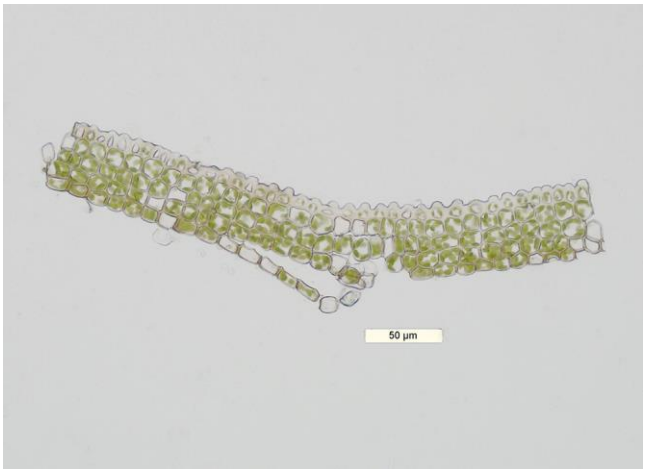

Figure 18. ***Polytrichum juniperinum*** side view of lamella with thick waxy layer on top. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

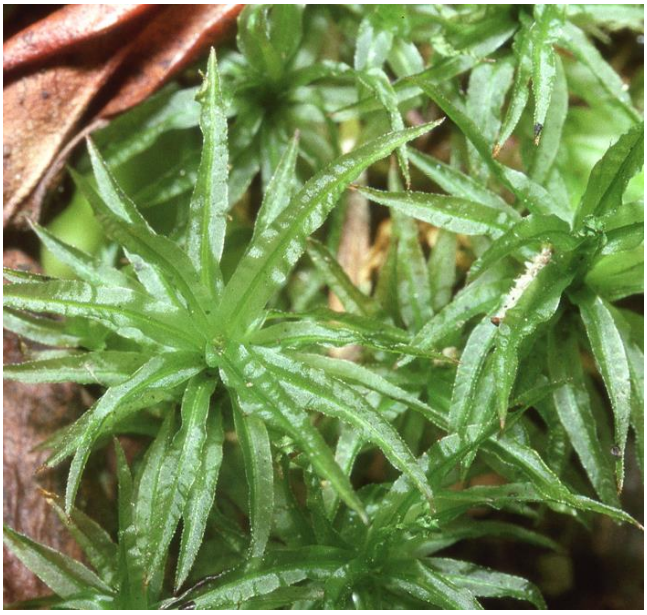

Figure 19. ***Atrichum undulatum*** showing lack of glaucous coloring and presence of wavy leaves that curl and twist when drying. Photo by Janice Glime.

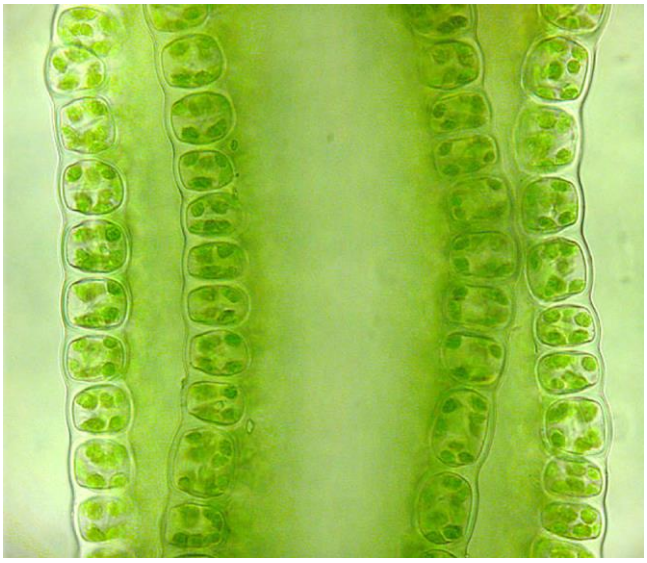

Figure 20. ***Atrichum undulatum*** leaf showing tips of lamellae. Photo by Walter Obermayer, with permission.

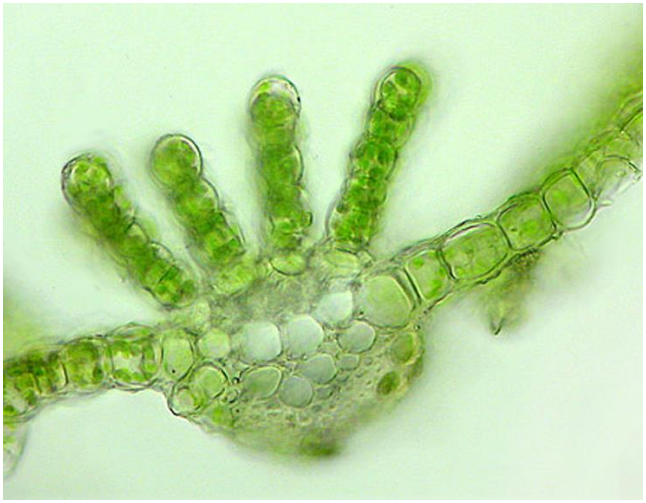

Figure 21. ***Atrichum undulatum*** leaf cross section showing lamellae. This moss has little or no wax on its leaves. Photo by Walter Obermayer, with permission.

Figure 22. ***Atrichum altecristatum*** drying (**lower part of image**). Photo by Eric Schneider, with permission.

Figure 23. ***Atrichum undulatum*** leaf lamellae and out of focus areas that indicate undulations. Photo by Walter Obermayer, with permission.

The array of species with demonstrated waxes is a mixed group of xerophytes and hydrophytes (Proctor 1979b, 1982). ***Pohlia wahlenbergii*** (Figure 24-Figure 26), a glaucous moss of wet habitats, has a high content of wax, whereas ***Pohlia nutans*** (Figure 27-Figure 28), a ubiquitous moss often found in dry habitats, has little wax. ***Pohlia cruda*** (Figure 29-Figure 31), a species of moist places, has a high content like that of ***P. wahlenbergii***. It appears that the wax in these species is important to prevent water logging, allowing for gas exchange for photosynthesis.

Figure 24. ***Pohlia wahlenbergii*** showing a wet habitat that is typical for it. Photo by Michael Lüth, with permission.

Figure 25. ***Pohlia wahlenbergii*** showing water droplets that are repelled by the waxy surface. Photo by Michael Lüth, with permission.

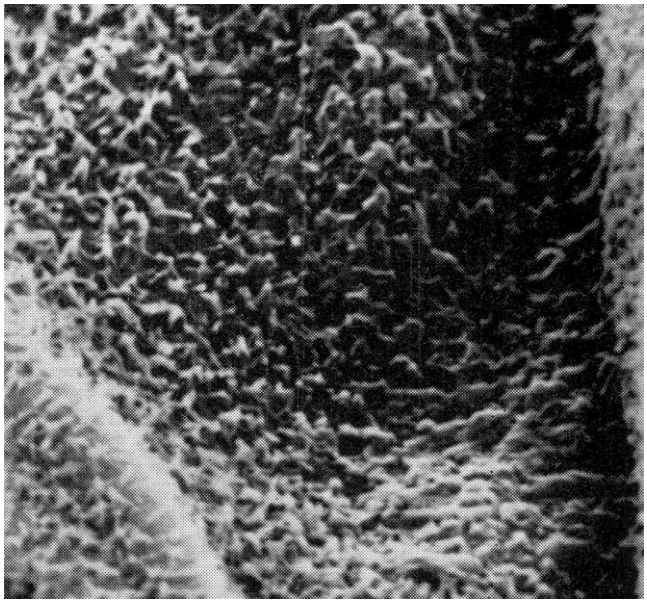

Figure 26. SEM of ***Pohlia wahlenbergii*** cuticle. Photo by Michael Proctor, with permission.

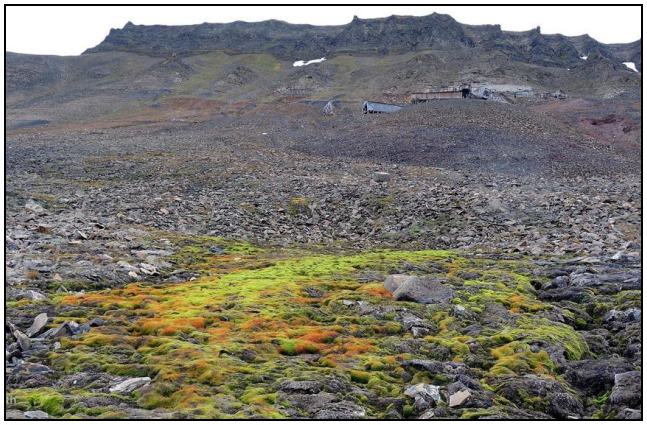

Figure 27. ***Pohlia nutans*** showing a typical dry, exposed habitat for the species. Photo by Michael Lüth, with permission.

Figure 28. ***Pohlia nutans*** showing the lack of a glaucous or waxy appearance. Photo by Michael Lüth, with permission.

Figure 29. ***Pohlia cruda*** in a crevice where moisture can be maintained, showing a waxy appearance. Photo by Michael Lüth, with permission.

Figure 30. ***Pohlia cruda***, a glaucous moss with a high leaf wax content. Photo by Michael Lüth, with permission.

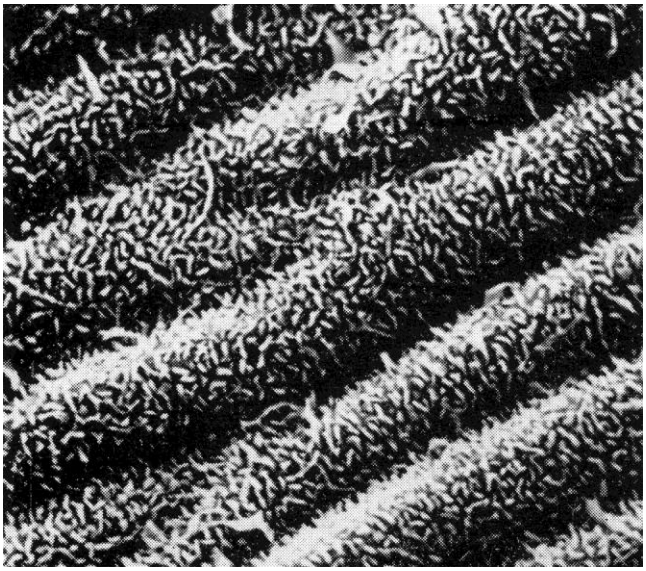

Figure 31. SEM of ***Pohlia cruda*** cuticle. Photo by Michael Proctor, with permission.

Bartramia pomiformis (Figure 32-Figure 34) has a whitish appearance and has a high degree of wax covering (Figure 34) (Proctor 1979b). In the same family, ***Conostomum tetragonum*** (Figure 35) has an intriguing 3-d mesh of wax (Figure 36).

Figure 32. ***Bartramia pomiformis*** in its typical rock crag habitat. Photo by Janice Glime.

Figure 33. ***Bartramia pomiformis*** showing glaucous leaves. Photo by Michael Lüth, with permission.

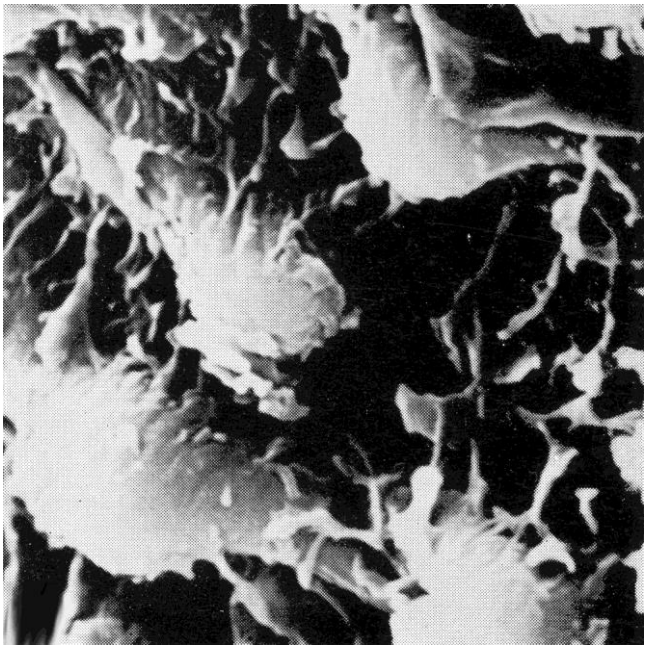

Figure 34. SEM of ***Bartramia pomiformis*** leaf cuticle. Photo by Michael Proctor, with permission.

Figure 35. ***Conostomum tetragonum*** showing the glaucous appearance of the leaves. Photo by Des Callaghan, with permission.

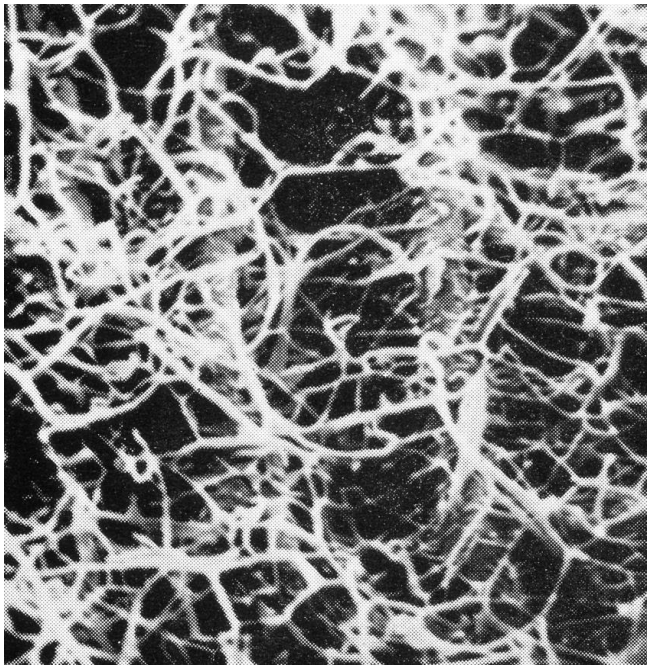

Figure 36. SEM of ***Conostomum tetragonum*** leaf cuticle. Photo by Michael Proctor, with permission.

Xu *et al*. (2009) found surface wax on the leaves of the desert moss ***Syntrichia caninervis*** (Figure 37). These waxes were comprised of fatty acids, alcohols and alkanes. In this species, the wax crystals shift as the leaf ages, increasing the percentage and weight (13.6%; 1150 μg g^{-1} DW) of very long-chain components in young leaves to 37.2% and 2640 μg g^{-1} in older leaves. Furthermore, when juvenile leaves experienced dehydration followed by rehydration the wax content of juvenile leaves increased by 35.17%. In lab-cultivated leaves subjected to three wet/dry cycles, the wax content increased by 1900%.

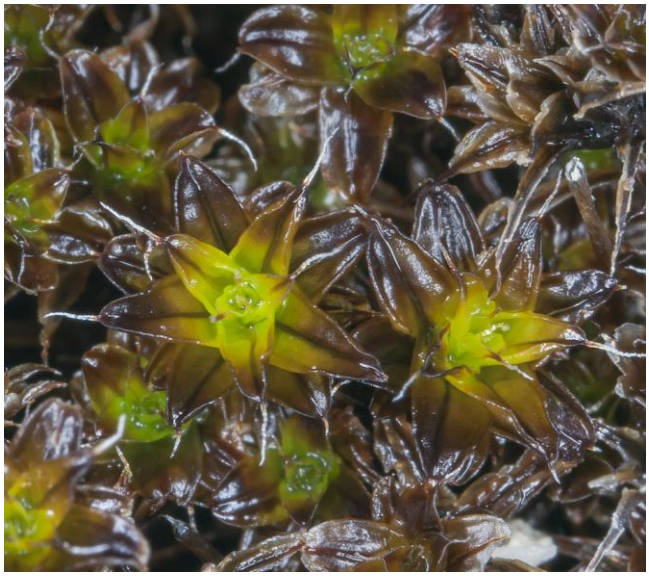

Figure 37. ***Syntrichia caninervis***, a desert moss with a cuticle comprised of fatty acids, alcohols, and alkanes. Photo by John Game, with permission.

Some bryophytes are puzzling at first glance. For example, ***Hedwigia*** (Figure 38-Figure 40) species appear to be waxy, yet absorb water rapidly. But members of the **Hedwigiales** lack waxes (Pressel & Duckett 2011). This puzzle unravels when we understand the role of the papillae (which typically make leaves look whitish) on the leaves of **Andreaeales**, **Grimmiales** (Figure 41-Figure 42), **Pottiales** (Figure 43-Figure 46), **Hedwigiales**, and **Orthotrichales**. Based on experiments by Proctor (1979a) and confirmed by Pressel and Duckett (2011), the water enters these leaves by flowing within channels in the **striated** (having linear marks, slight ridges, or grooves on surface, often one of number of similar parallel features) cell walls and between the papillae, causing rapid uptake of water through the leaf surface between the papillae. These taxa lack waxes.

Figure 38. ***Hedwigia ciliata ciliata*** dry, showing whitish leaves resulting from numerous papillae. Photo by Des Callaghan, with permission.

Figure 39. ***Hedwigia ciliata*** wet, showing ability to spread when hydrated. Photo by Hermann Schachner, through Creative Commons.

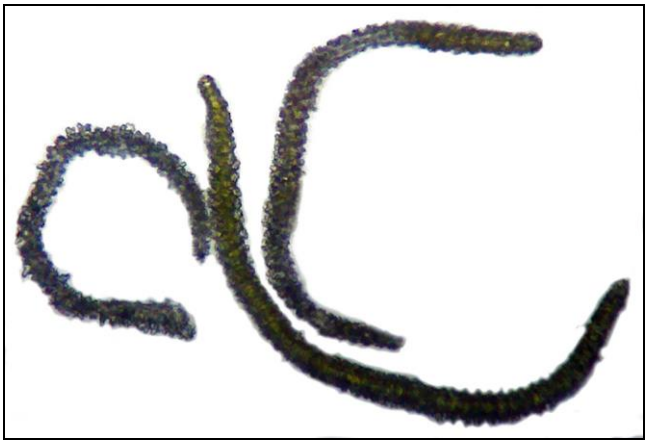

Figure 40. ***Hedwigia ciliata*** leaf cross sections showing dense papillae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 41. ***Racomitrium lanuginosum*** (**Grimmiales**) showing awns on leaves. These leaves lack waxes. Photo from Botany Department website, University of British Columbia, with permission.

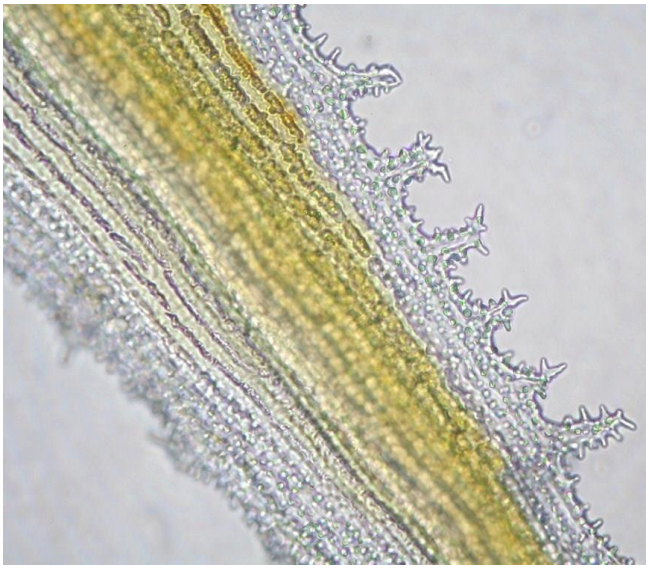

Figure 42. ***Racomitrium lanuginosum*** (**Grimmiales**) leaf awn and cell papillae. Photo from Botany Department website, University of British Columbia, with permission.

Figure 43. ***Tortula muralis*** in its dry state. Photo by Christophe Quintin, through Creative Commons.

Figure 44. ***Tortula muralis*** in its wet state. Note the water collected on the awns. Photo by Christophe, Quintin through Creative Commons.

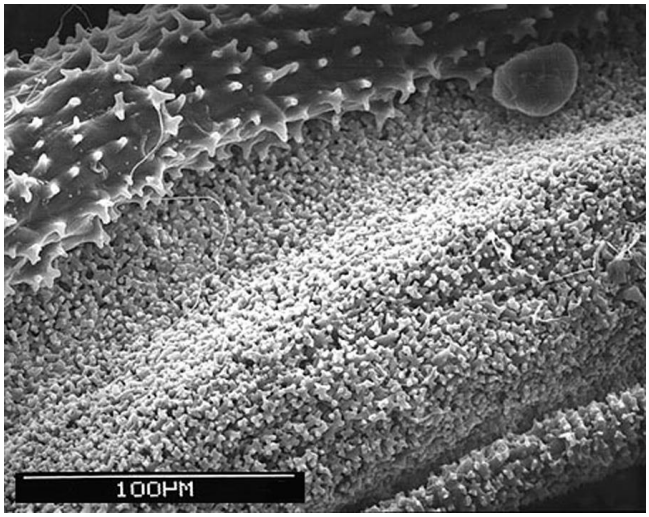

Figure 45. SEM of ***Tortula muralis*** (**Pottiales**) papillae showing their density and channels where water moves and enters the leaf. Photo from Botany Department website, University of British Columbia, with permission.

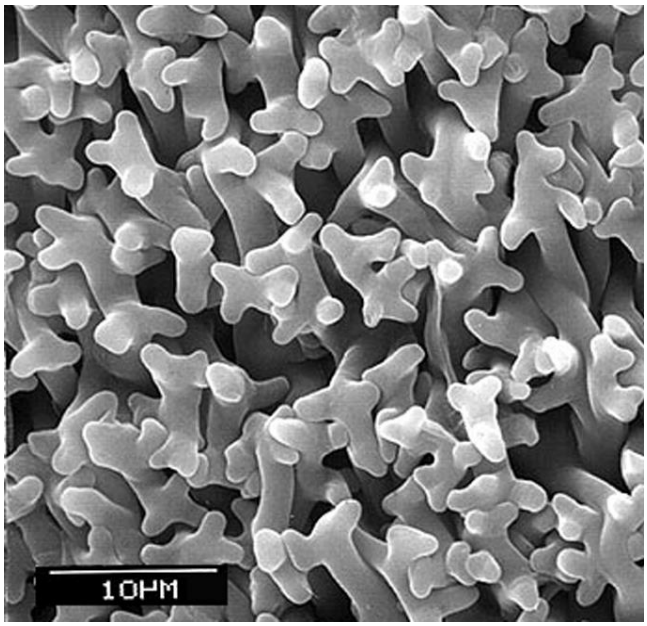

Figure 46. SEM of ***Tortula muralis*** (**Pottiales**) papillae showing the spaces between them where channels are provided for water transport and entry to the leaf cells. Photo from Botany Department website, University of British Columbia, with permission.

In genera such as ***Aloina*** (Figure 47), ***Crossidium*** (Figure 48-Figure 49), and ***Pterygoneurum***, (Figure 50-Figure 52) the water enters between the leaf lamellae (Figure 51-Figure 52) (Proctor 1979a; Pressel & Duckett 2011). All these taxa grow in habitats where intermittent dehydration/rehydration, often in rapid sequence, is common. However, in the **Polytrichaceae** (Figure 14-Figure 18), water logging between the lamellae is an issue, depressing gas exchange needed for photosynthesis (Proctor 1979a, 1982, 1984). These leaves are protected by abundant waxes that prevent water from entering the spaces between the leaf lamellae. Instead, air bubbles are trapped in these spaces.

Figure 47. ***Aloina rigida*** showing waxy leaves. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 48. ***Crossidium aberrans*** leaves with lamellae. Photo by Michael Lüth, with permission.

Figure 49. ***Crossidium aberrans*** leaf cells showing lamellae in center where water is easily absorbed. Photo by Michael Lüth, with permission.

Figure 50. ***Pterygoneurum papillosum*** showing succulent appearance of leaves due to lamellae. Photo by Michael Lüth, with permission.

Figure 51. ***Pterygoneurum ovatum*** leaf showing lamellae where water enters the leaf. Photo by Hermann Schachner, through Creative Commons.

Figure 52. ***Pterygoneurum ovatum*** leaf cross section showing lamellae where water enters leaf. Photo by Hermann Schachner,through Creative Commons.

One of the problems that bryophytes must face is having ice or ice crystals on their surfaces (Figure 53-Figure 54). These crystals are very hygroscopic, potentially causing the kind of dehydration that can occur to your meat in the freezer. A waxy cuticle could serve like a plastic freezer bag, in this case preventing the water from being drawn from the cells. This role for the wax, if present, remains to be tested.

Figure 53. ***Polytrichum*** sp. with frost, a condition that could draw water out of unprotected cells. Photo by Allan Water.

Figure 54. ***Hedwigia ciliata*** in ice, a frequent condition for this rock dweller. The ice, like freezer ice, draws water out of plant cells. Photo by Michael Lüth, with pernission.

The presence of a white flocculent material on the moss ***Saelania glaucescens*** (Figure 55-Figure 57) is widely known. ***Saelania glaucescens*** has been a puzzle to bryologists and biochemists. Its whitish covering is predominantly on the backs of the leaves and takes the form of a hoary appearance, not a smooth or shiny surface. Although this material has been identified as kauranol plus several minor waxes (Nilsson & Mårtensson 1971), the reason for the peculiar arrangement that looks like a thin layer of minute angel hair remains a mystery. Bryologists have suggested that it might be caused by parasitic fungi or bacteria, but there is no evidence to support these ideas (Mårtensson & Nilsson 1974). Likewise, it does not seem to be the result of any normal metabolic product. Proctor's (1979b) analysis demonstrates that this is a heavy coating of waxes with weblike ridges covered by a fine, cobwebby matrix of wax.

Figure 55. ***Saelania glaucescens*** showing waxy appearance. Photo by Michael Lüth, with permission.

Figure 56. ***Saelania glaucescens***, a moss in which the waxy extrusions are so large that they are visible to the naked eye. Photo by Jan-Peter Frahm, with pernission.

Figure 57. SEM of ***Saelania glaucescens*** cuticle. Photo by Michael Proctor, with pernission.

Sphagnum

Sphagnum fimbriatum (Figure 58-Figure 62), a peatmoss of wet habitats, has an osmiophilic layer (one that stains with osmium tetroxide, indicating wax) that resembles the early developmental stage of tracheophyte cuticle (Cook & Graham 1998). One might think that a wet habitat moss would not need such protection, but in summer these peatmosses can become quite dry, so such a layer may help to reduce desiccation. On the other hand, this layer may prevent water logging at times when this moss is submersed (*cf*. Pressel & Duckett 2011). The cuticle in ***S. fimbriatum*** is sheetlike with regular ridges that run parallel to the edges of the "thalli." Our next question is how can a leaf with a cuticle use it for protection from desiccation and yet be able to absorb water. In ***Sphagnum***, this may be facilitated by the pores, but might the structure of the cuticle play a role?

Figure 58. Dry ***Sphagnum fimbriatum***, a moss with a known osmiophilic layer resembling an early developmental cuticle of tracheophytes. Photo by Michael Lüth, with pernission.

Figure 59. ***Sphagnum capillaceum*** (= *S. nemoreum*), a ***Sphagnum*** species known to have waxes (lignoceryl alcohol). Photo by Michael Lüth, with pernission.

Figure 60. ***Sphagnum fuscum***, a ***Sphagnum*** species known to have waxes (lignoceryl alcohol). Photo by Michael Lüth, with pernission.

Figure 61. ***Sphagnum magellanicum***, a species known to have waxes. Photo by Michael Lüth, with pernission.

Figure 62. ***Sphagnum fimbriatum*** leaf cross section, a moss that has an osmiophilic (waxy) layer on the outside of the leaf cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with pernission.

Leafy Liverworts

Even the leafy liverworts can have waxes. Heinrichs *et al*. (2000) support the contention of Cook and Graham (1998) that this innovation occurred prior to the evolution of bryophytes from their algal ancestor. Although only six (5 of ***Plagiochila*** plus ***Plagiochilion mayebarae***) of the 81 species of **Plagiochilaceae** in the study had surface waxes on their leaves (Heinrichs *et al*. 2000), this is a family with

many members in damp or wet, even submersed, habitats. They found that ***P. tabinensis*** contains 1.4% of its dry weight as surface waxes. These are comprised of steryl esters, triacylglycerols, and free fatty acids.

By using the electron microscope, Heinrichs and Reiner-Drehwald (2012) found surface wax in the leafy liverworts ***Lejeunea flava*** (Figure 63), ***Mytilopsis albifrons***, ***Dinckleria pleurata***, and ***D. fruticella***, representing the families **Lejeuneaceae**, **Lepidoziaceae**, and **Plagiochilaceae**, respectively.

Figure 63. ***Lejeunea flava***, a leafy liverwort known to have a cuticle with surface wax. Photo by Jonathan Sleath, with pernission.

Admissibility of Water

If leaves of bryophytes are covered with waxes, how does water enter these largely ectohydric plants? One suggestion is that the bases of the leaves may lack a cuticle, but that would seem to slow down water entry and be maladaptive for gathering dew or taking advantage of short desert rainfall events. But the structure of the wax itself may solve this problem. Shepherd and Wynne Griffiths (2006) describe the layered sheets of wax as probably discontinuous and surrounded by further solid amorphous regions. The crystalline regions are considered impermeable, but water and solutes are able to diffuse through the cuticular wax by way of the amorphous zones. This requires a greater travel distance than a straight path through the surface, but it seems a better route than travelling to the leaf base, then travelling internally through cell contents and cell walls to reach the tip of the leaf.

Multiple Forms – Multiple Roles

The cuticle, like many plant features, can serve multiple advantages for plants. In tracheophytes it is able to reduce water loss, prevent water logging, protect against high light intensity, reduce the temperature, reduce osmotic stress, prevent physical damage, protect against altitudinal stresses (light, extreme temperatures, wind), and protect against pollution (Shepherd & Wynne Griffiths 2006).

In tracheophytes, waxes exist in several forms, including rods, ribbons, filaments, tubes, and plates (Shepherd & Wynne Griffiths 2006). Among the bryophytes, for five ***Plagiochila*** (leafy liverwort) species studied, two exhibited wax platelets and three exhibited wax rodlets (Heinrichs *et al*. 2000). Proctor (1979b) demonstrated several forms among mosses (Figure 31, Figure 34, Figure 36, Figure 57).

Among the tracheophyte forms, wax tubes are associated with mid-chain oxy-substituents, such as β-diketones, hydroxy-β-diketones, diols, and secondary alcohols (Shepherd & Wynne Griffiths 2006). Platelets are associated with primary alcohols with a terminal oxy-substituent. Are these same factors influential in bryophyte wax morphology? If so, is there any adaptive significance for these differences?

Temperature

We know that in tracheophytes temperature, light intensity, and humidity influence the wax morphology, but since these three factors typically act together, it is often difficult to tease out cause and effect (Shepherd & Wynne Griffiths 2006). For example, in *Citrus aurantium*, a higher daytime temperature during leaf development reduces the quantities of alkanes, primary alcohols, fatty acids, and alkyl esters per unit area (Riederer & Schneider 1990). But except for the esters, the amounts of these same compounds increase with higher night-time temperatures.

At higher temperatures, the waxes are more likely to form plates and flakes, whereas at lower temperatures they are more likely to form vertical structures such as rods and tubes (Shepherd & Wynne Griffiths 2006). But waxes at higher temperatures also often form complex dendritic shapes. Tubular forms of waxes are thermodynamically unstable due to their high surface area to volume ratio, so an input of energy, typically heat, can transform them into compact planar forms that are thermodynamically more stable. And tubes can turn into dendrites when the temperature is raised. On the other hand, rapid cooling can also favor dendrite formation. Furthermore, more waxes are produced at lower temperatures.

Light

Shorter, less elaborate wax structures are often associated with greater illumination (Shepherd & Wynne Griffiths 2006). Thick waxes such as those in *Eucalyptus* leaves increase reflectance and reduce photosynthesis, but in "non-waxy" leaves (*i.e.* not appearing waxy or glaucous), there is no effect. In wheat, reflectance is proportional to the amount of wax present, with higher reflectance reducing light transmission to underlying mesophyll cells (Johnson *et al*. 1983). Higher radiation levels can cause an increase in wax thickness in many plants, suggesting an inducible mechanism to protect the cells (Baker 1974; Giese 1975; Reed & Tukey 1982; Shepherd *et al*. 1995).

But it seems unlikely that the thin cuticle of bryophytes has much of an effect on reflectance or photosynthesis. Nevertheless, as will be seen in the chapter on light relations, many bryophyte leaves transmit more light when wet than when dry, suggesting that papillae or other surface features may screen light, thus protecting the DNA and chlorophyll, but that when water fills in the spaces, light is transmitted rather than scattered. Are these waxes protective agents against UV radiation when the

bryophytes are dry? But UV reflectance is an uncommon adaptation among tracheophytes. It can range from <10% in most plant species, to 70% in only a few others (Caldwell *et al*. 1983; Barnes *et al.* 1996).

Waxes may play yet another role for the light-limited bryophytes. Droplets held on wettable tracheophyte leaves can focus solar radiation up to 20 times (Brewer *et al*. 1991). We might imagine that bryophyte leaves or multiple plant tips might trap water droplets that likewise focus the light in some low-light habitats. This focussing would occur at the actively growing tips in most acrocarpous mosses.

Salt Stress

Waxes also protect leaf cells from salt stress (Shepherd & Wynne Griffiths 2006). Examples from tracheophytes suggest that an increase in wax production may be an inducible response to increased salt exposure. Fujiwara *et al*. (2002) found that pre-treating cabbage seedlings with NaCl induced hardening, improving drought resistance. It would be interesting to compare wax content among bryophytes that grow within areas affected by salt spray to the same species grown away from its influence.

Contact Angles and Entry

Contact angles are important for water entry. Brewer *et al*. (1991) found that changes in the contact angle and wettability are also associated with changes in wax composition and morphology in tracheophytes. These observations present interesting questions for bryophytes. If leaves have waxes over the leaf lamina, but lack waxes at the base, water will roll to the leaf base where uptake is easy. This movement to the leaf base would further facilitate the solution of deposited nutrients and carry them to the base for absorption (Cape 1996 for tracheophytes). Because of the mode of water uptake in bryophytes, this feature is likely to be more important than it is in tracheophytes. Hence, we should expect the angle of the leaf to be important in this nutrient and water gathering. At the same time, it presents dangers for collecting deposited pollutants.

Combined Role and Water Relations

Let's continue under the assumption that at least in some cases the waxes on bryophytes may play a role in reflectance and scattering of light to a degree that can lower the temperature of the bryophyte cells they cover. This will, in turn, reduce the vapor pressure difference between the leaf tissue and the air, reducing the loss of water through transpiration. But all these assumptions remain to be tested in bryophytes.

Altitude Protection

High altitude imposes stresses that include weathering, dehydration, low temperatures, and greater UV light intensity. In conifers, a thicker wax coverage is characteristic of high altitude growth (Günthardt 1984; Riolo 1999). We need to look for a similar relationship in bryophytes.

Pollution Protection

Ozone

In tracheophytes, ozone causes a severe reduction in the formation of new wax, but it does not seem to affect existing wax (Carlsson *et al*. 1994; Hellgren *et al*. 1995). Its effect on bryophyte cuticles remains unknown, but failure to replace cuticle could have severe consequences in prevention of water logging and protection from UV radiation.

CO_2

The effects of CO_2 on tracheophytes are varied, in some cases causing an increase in waxes and in others a decrease (Shepherd & Wynne Griffiths 2006). The effect on bryophyte cuticles remains to be demonstrated.

Repelling Water

Despite all of these reports on waxes on the cuticle of bryophytes, we know little of their role. Mårtensson and Nilsson (1974) comment that not all of the aforementioned waxy species are shiny, including ***Rhytidiadelphus triquetrus*** (Figure 9), although I would consider it to be shiny. Others, such as ***Sphagnum subnitens*** (Figure 64-Figure 65) and ***S. subfulvum*** (Figure 66) are shiny when dry, but lose their shine when moist, suggesting that the relationship is complex and is not a matter of simple reflection. It would be interesting to determine their role in repelling water to avoid water logging vs retaining water in times of drought.

Figure 64. ***Sphagnum subnitens*** dry with a waxy shine. Photo by Michael Lüth, with pernission.

Figure 65. ***Sphagnum subnitens*** wet with a less waxy look than dry plants. Photo by Barry Stewart, with pernission.

Figure 66. ***Sphagnum subfulvum***, a species that is shiny when dry due to waxes. Photo by Michael Lüth, with pernission.

The role of repelling water may be more important than that of retaining water. I have mentioned a potential role of repelling water, as seen in Figure 1. Gas exchange works poorly through a wet surface. Waxy or oily surfaces help to repel the water, yet allow a higher rate of gas exchange than does water. Hence it is not uncommon to find such surfaces among aquatic bryophyte taxa (Proctor 1984).

Proctor (1984) contends that the ability to shed surface water is important to bryophytes in their low-light habitats of crevices and caves or in waterside habitats of waterfalls. He cites the waxy surfaces of the tops of photosynthetic lamellae of the **Polytrichaceae** (Figure 6, Figure 14-Figure 18) as support for this contention. This might also be supported by the waxy surface of ***Pohlia cruda*** (Figure 29-Figure 31), a common species in crevices.

As discussed in Chapter 7-3 of this volume, the pores of ***Marchantia*** (Figure 67), as in the stomata of tracheophytes, have strongly water-repellent ledges (Schönherr & Ziegler 1975; Figure 68), like the waxy ridges of tracheophytes, preventing water from entering and interfering with the photosynthetic interior.

Figure 67. ***Marchantia polymorpha*** with gemmae cups and tiny white dots that indicate pores. Photo by Jan-Peter Frahm, with pernission.

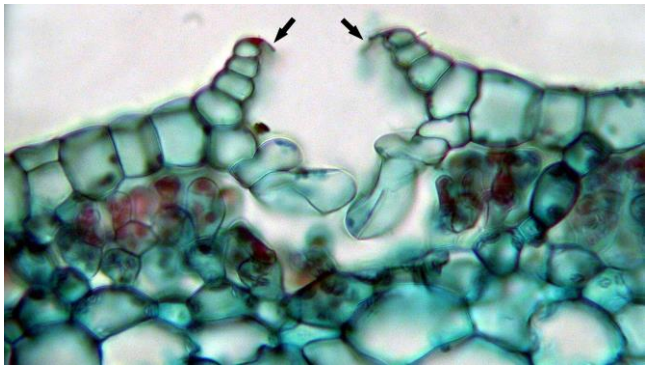

Figure 68. Section through pore of ***Marchantia polymorpha***, with waxy ledge indicated by arrows. Photo by George Shepherd, through Creative Commons.

Mosses like ***Plagiomnium*** (Figure 69) have both upright and horizontal stems. But this genus has a different problem from most mosses in obtaining water. Its leaves repel water, as known by anyone who has tried to wet them to make a slide. It has perhaps solved this problem by its well-developed hydroids and leptoids, and even false leaf traces (Figure 70).

Figure 69. ***Plagiomnium ellipticum*** with drops of water on its water-repellent (waxy) surface. Photo by Des Callaghan, with pernission.

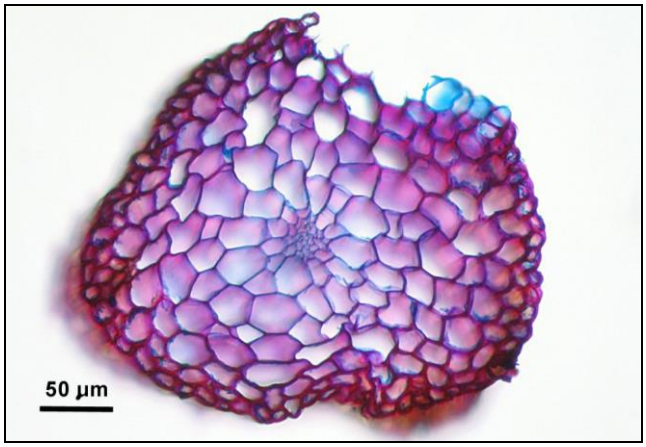

Figure 70. ***Plagiomnium ellipticum*** stem cross section. This is a moss with both upright and horizontal (plagiotropic) stems. It most likely benefits from having both hydroids and leptoids to transport substances because its leaves are very resistant to getting wet and typically repel water. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with pernission.

In some cases, there are special adaptations for bringing water into the leaves while at the same time being able to prevent water loss. In ***Rhacocarpus purpurascens*** (Figure 71), a moss of exposed habitats that experience frequent alternation of drought and heavy precipitation, the cell walls are trilamellate (Pressel *et al*. 2010). The outer layer is porous and ensures rapid uptake of water and retention. At the same time its very hydrophobic cuticle-like layer prevents waterlogging. The middle lamellar stratum permits extension of protoplast hydration, allowing the metabolism to remain active under drying conditions. ***Sphagnum***, on the other hand, can become waterlogged and experience depressed metabolism as a result.

Figure 71. ***Rhacocarpus purpurascens***, a moss that repels water. Photo by Michael Lüth, with pernission.

Summary

Bryophytes gain water in their cells both through external (**ectohydric**) capillary movement and internal (**endohydric**) transport. Structural adaptations such as **overlapping leaves**, **concave leaves**, **crispate leaves**, **plications**, **revolute** or **involute margins**, **lamellae**, **multi-layered leaves**, **lobules, cuticles**, **hair points**, **papillae**, **costae**, **stereids**, **borders**, **cancellinae**, **teniolae**, **alar cells**, **hyaline cells**, **pores**, **oil bodies**, **vacuoles** aid in moving water, facilitating entry, or reducing loss. In areas with high fog occurrence and little or no rainfall, fog can be a major contributor to the bryophyte water budget.

Waxes are known from all the major groups of bryophytes, including such aquatic taxa as ***Sphagnum***, and occur in a wide range of habitat moisture, but many species seem to lack them. Glaucous species may be so because of waxes or because of dense papillae. The water repellant nature of waxes keeps water from entering pores of a thallus and prevents water from remaining on plants in a way that blocks gas exchange. The presence of waxes may relate to endohydry or to living in places where water lingers on the plants. The role may be more to keep water away than to hold water in.

Waxes need to be arranged on a leaf to admit water, at least at the base, but they may have an amorphous layer that transmits water. Multiple forms of waxes seem to be correlated with various environmental parameters such as UV light, temperature, salt stress, contact angle, and altitude, but these correlations have not been explored in bryophytes. Cuticles can offer protection from such pollutants as ozone and CO_2 and may play a role in preventing absorption of airborne pollutants that land on the surfaces of the leaves.

Acknowledgments

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CHAPTER 7-5

WATER RELATIONS: PHYSIOLOGICAL ADAPTATIONS

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CHAPTER 7-5

WATER RELATIONS: PHYSIOLOGICAL ADAPTATIONS

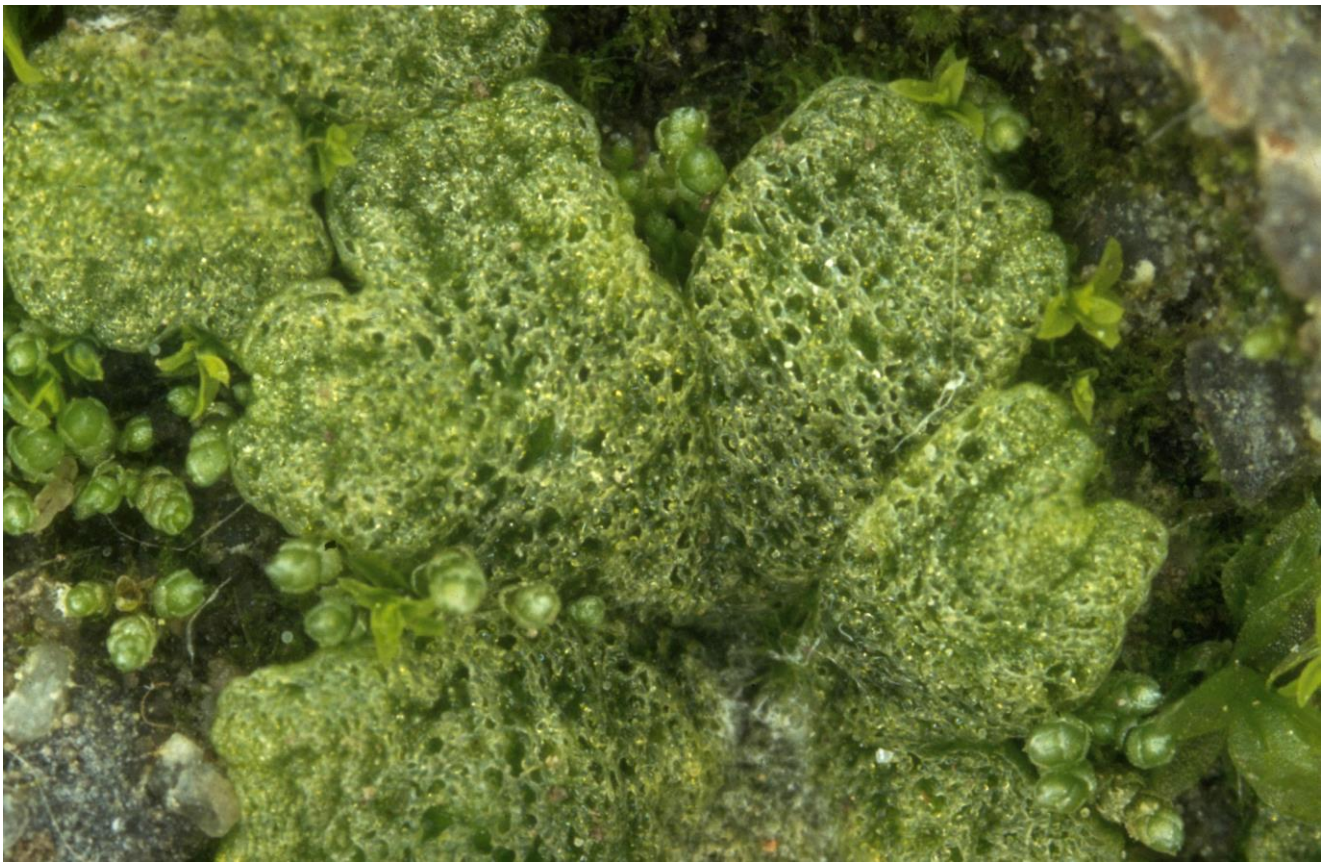

Figure 1. ***Riccia cavernosa***, a thallose liverwort that dries out during drought and recovers in the fall when rain returns. Photo by Jan-Peter Frahm, with permission.

Water Relations on Land

Proctor (2014) points out that one of the basic needs of bryophytes is that of coping with the intermittent availability of water. To this end, poikilohydry is efficient at the small scale of a bryophyte, whereas endohydry is more beneficial for the large tracheophytes.

Physiological adaptations relate on one end to the morphology and on the other to the biochemistry. Although we have recognized morphological characters for a very long time, few have actually been tested experimentally on a large scale for their adaptive value in altering physiology. The biochemical adaptations, on the other hand, constitute a new and emerging field of bryology, one that coincides closely with physiology of tracheophytes. By using the more easily studied bryophytes, we have gained the possibility of better understanding of the physiology of tracheophytes. This unusual interest in bryophytes is largely because of the relative ease with which genes can be moved into them or knocked out of them and their expressions be observed. And both bryophyte and fern gametophytes exhibit desiccation tolerance, whereas this ability is rare among sporophytic seed plants (Watkins *et al*. 2007). Long live the gametophytes! Even the lichens seem to have less desiccation tolerance than the bryophytes (Green *et al*. 2011).

Oliver *et al*. (2000) hypothesized that for photosynthetic plants to move onto land, desiccation tolerance was crucial. Using species of "resurrection plants" from both bryophytes and tracheophytes, Fisher (2008) concluded that desiccation tolerance arose among propagules as a means of survival. In bryophytes, nearly every part is a potential propagule in most species. For example, Maheu (1902) found that the moss ***Tortula muralis*** (Figure 2) would regenerate protonemata after

being stored dry for 14 years. Physiological adaptations may permit the bryophyte to retain water or to recover from loss of water, and to change its strategies with the seasons or the climate.

Figure 2. ***Tortula muralis***, a moss species that can survive drought as protonemata. Photo by Christophe Quintin, through Creative Commons.

Alpert (2000) presented two main puzzles from the observed habitat patterns of desiccation-tolerant plants. "What are the mechanisms by which plants tolerate desiccation?" and "Why are desiccation-tolerant plants not more ecologically widespread?" There appear to be multiple mechanisms of tolerance, including protection from oxidants and loss of normal configuration of macromolecules during dehydration. Alpert suggests that their inability to occupy a wide ecological range is due to their inability to maintain a cumulative positive carbon balance during their repeated wet/dry cycles and the tradeoffs between desiccation tolerance and growth rate.

Drought Tolerance vs Avoidance

As clear as the two words **tolerance** and **avoidance** may seem, they can lead to confusion because of differences in perspective. During (1979) tells us that **drought tolerance** is the ability to survive and maintain activity despite a lack of water in the environment. Proctor (2000) gives a more physiological definition that considers drought-tolerant plants to be those that are able to maintain a more or less normal metabolism at lowered cell volume and water potential, while tolerating elevated ionic concentrations in the cytoplasm and external environment. This physiological type of maintenance may be in evidence for the drought-tolerant ***Hedwigia ciliata*** (living on exposed boulders; Figure 82) and ***Grimmia pulvinata*** (often living on concrete; Figure 3). During a 5-day sequence of natural field drying, they showed no sign of plants drying and both maintained their photochemical efficiency, exhibiting normal day-night patterns (Schroeter *et al*. 1999).

Plants that show **tolerance** have vegetative parts that endure the stress period as best as possible (During 1979). But where is that lack of water, in the environment, or in the plant? I prefer to clarify this and say that **drought tolerance** is the ability of the plant to survive in a **habitat** that becomes dry. **Desiccation tolerance** is the ability of the **plant** to survive periods during which the **cells** are water-stressed and the plant itself has become dry; it suffers dehydration of all its metabolic systems. Such vegetative desiccation tolerance is rare among tracheophytes, with few species withstanding vegetative desiccation: 60-70 species of fern and fern allies and 60 species of angiosperms (Oliver *et al*. 2000). Instead, most tracheophytes survive through reproductive structures. Bryophytes (and lichens), on the other hand, exhibit vegetative desiccation tolerance as well as through reproductive structures (Kappen & Valladares 1999; Proctor et al. 2007).

Figure 3. ***Grimmia pulvinata***, a drought tolerator growing on concrete. Photo with permission from Botany Department website, University of British Columbia, Canada, with permission.

For sake of clarity, let us consider **drought** to be a condition of the environment and **desiccation** to be a condition of the plant, in this case the bryophyte. For tracheophytes, drought in the environment nearly always causes desiccation in the plant, but for bryophytes, this may not so often be the case.

Using that terminology, **drought tolerance** can be accomplished in two ways: **desiccation tolerance** and **desiccation avoidance**. **Desiccation avoidance** is the ability to prevent desiccation from occurring within the plant or the ability to go into a **dormant stage** during periods of low water availability; it is often characterized by plants that die and leave stress-tolerant **diaspores** (any structures that become detached from parent plant and gives rise to new individuals) that will grow the next season. Note the use of the word **stage** here, not **state**. For bryophytes, spores and gemmae provide dormant **stages**, although the entire **mature** sporophyte might be considered a stage that does not require water. On the other hand, a desiccation-tolerant vegetative plant can go into a dormant **state**, where metabolic activity slows to an imperceptible level, but where this same plant stage will regain its ability to gain carbon and grow.

Using these concepts, Smith (1986) considers that true desiccation tolerance among plants is rare or non-existent. The tracheophytes may in fact never be desiccation tolerators (Larcher 1983), generally relying on avoidance by storing water or by going into a dormant life cycle stage until the return of sufficient water (Smith 1986). Bryophytes, on the other hand, can be true desiccation tolerators, and suffer relatively little damage at relative humidity levels far below those tolerated by tracheophytes (Table 1). They do this in a vegetative stage through mechanisms that avoid desiccation damage.

Desiccation resistance, the ability to maintain an adequate water supply under drought conditions, is actually **drought avoidance**. Drought avoidance also includes the

ability to revert to a dormant stage that requires no water, such as spores and tubers. Water is essential to all life, and the ability to obtain it under limiting conditions or to store it until more is available permits some organisms to live in conditions that are intolerable for others. Most perennial bryophytes do not have the option of disappearing into the soil for the winter, and in fact the period of greatest drought for many of them is in the summer. However, bryophyte growth generally ceases during this hot and often dry time and metabolic activity is slowed considerably, if not completely.

Table 1. Comparison of desiccating percent relative humidity levels tolerated by various groups of plants. Table modified from Larcher (1983).

Plant	%RH Tolerated without injury	%RH Moderate injury
Marine algae		
Deep water algae	99-97	14-41
Algae of the ebb line	95-86	69-204
Intertidal algae	86-83	204-252
Liverworts		
Hygrophytes	**usually 95-90**	**92-90**
Mesophytes	**usually 92-50**	**90-36**
Xerophytes	**usually (36)-0**	**0**
Mosses		
Water mosses and hygrophytes	**95-90**	**69-141**
Mesophytes	**usually 90-50 extreme 10**	
Xerophytes	**usually 5**	**0**
Fern gametophytes		
Forest ferns	>90	50-90
Rock ferns	40-60	20-30
Tracheophytes (tissue sections)		
Leaf epidermis		96-92
Mesophyll	96	95-90
Root cortex		97-95

Both desiccation avoidance and desiccation tolerance strategies are available to bryophytes (Figure 4-Figure 5). You will soon see that whereas desiccation tolerance may be unavailable to tracheophytes, it is of considerable importance for bryophytes.

Desiccation Tolerance

In 1702 Anthony von Leeuwenhoek examined dry sediment from a gutter after hydrating it for an hour, and found tiny animals swimming about (Alpert 1982, 2000). These animals, rotifers, seemingly had arisen from the dead. Leeuwenhoek followed with experiments that showed these animals could remain in this dry state for months. But he did not imagine that they had lost all moisture because they retained their normal oval shape. During the next century, experiments demonstrated that rotifers, nematodes, and tardigrades all could undergo a dry, dormant state. In fact, some organisms can survive for over ten years without water, reaching immeasurably low water potentials (Alpert 2000). In this desiccated state they can endure temperature extremes from 0272 to 100°C.

But what was this dormant state? Words such as **anabiosis** (temporary state of suspended animation or greatly reduced metabolism), **abiosis** (absence of life), **revivification (**restoring life), and **resuscitation** (action of making something active or vigorous again), arose to describe the dry state and ability to return from it (Alpert 1982). The term **cryptobiosis**, however, seems most appropriate, avoiding the question of whether or not the organism is still alive. Instead, it refers to the state of an organism when it shows no visible sign of life, when its metabolic activity is immeasurable (hidden life).

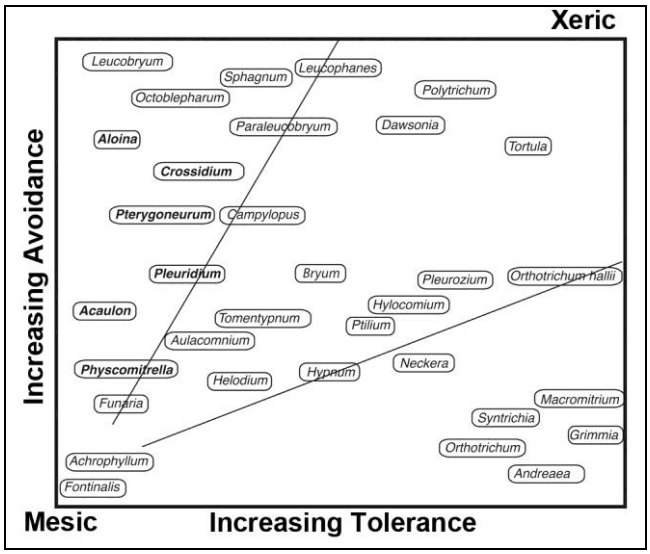

Figure 4. Distribution of a number of genera of mosses relative to mesic and xeric conditions and their strategies of avoidance vs tolerance. Modified from Vitt *et al.* 2014.

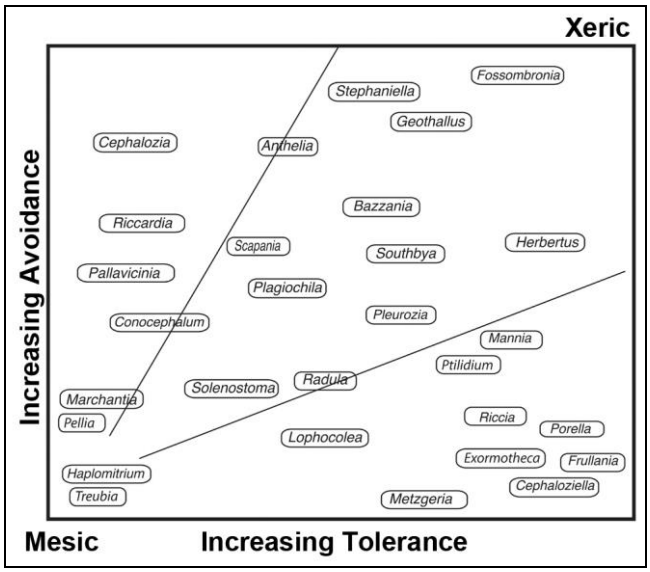

Figure 5. Distribution of a number of genera of mosses relative to mesic and xeric conditions and their strategies of avoidance vs tolerance. Modified from Vitt *et al.* 2014.

Low temperature physics helped to clarify the issue. Recognizing absolute zero as -273ºC, the temperature at which everything freezes and all molecular movement stops, Becquerel (1950a, b, c, 1951) subjected tardigrades, rotifers, algae, seeds, bacterial and fungal spores, fragments of the lichen *Xanthoria parietina*, and leaves of the mosses ***Grimmia*** (Figure 79-Figure 80) and ***Barbula*** (Figure 6) to two-hour treatments at temperatures very close to 0.0°K

(0.05-0.008ºK). These organisms returned to their active state and bacteria even reproduced. ***Syntrichia ruralis*** (Figure 77-Figure 93) survived after 24 hours at -198°C (Bewley 1973). Based on typical reduction in metabolism of ½ for every 10ºC drop in temperature, Becquerel calculated that at absolute zero metabolism would be 7.13 trillion times as slow as the normal rate at 15ºC (see Alpert 2000).

Figure 6. ***Barbula convoluta*** var. ***commutata***, a species that survives at temperatures close to 0°K. Photo by Michael Lüth, with permission.

This did not support the hypothesis that life ceased and then was reactivated. In fact, three arguments can be made against that hypothesis, some of which have been demonstrated for desiccated mosses. First, Dilks and Proctor (1976b) have demonstrated that mosses recover more slowly as duration of desiccation increases, ultimately reaching a duration from which they are unable to recover. Second, for most organisms in this cryptobiotic state, there is still a minute uptake of oxygen (Pigòn & Weglarska 1955a,b), indicating retention of metabolism. Third, there is a point at which all these organisms die.

Such desiccation tolerance, a common phenomenon among bryophytes, seems to have been lost in the evolution of tracheophytes. Rather, tracheophytes have experienced increased growth rates, more structural and morphological complexity, and mechanisms for conserving water rather than recovering from its loss (Oliver *et al*. 2000). Only in their reproductive structures, particularly seeds and underground storage organs, have tracheophytes retained and diversified the strategy of desiccation tolerance.

Norris (1990) contends that four dimensions of water relations must be understood to understand the problems of bryophytes compared to tracheophytes. To this I have added the fifth as a result of more recent experiments:

1. hydration/dehydration frequency
2. hydration duration
3. dehydration duration
4. degree of water loss
5. rate of water loss.

With the need for repair whenever moss cells become dry, it is not surprising that the frequency of the wet-dry cycle and the duration of the hydration period are important in determining survival. Even in such xerophytic bryophytes as ***Grimmia pulvinata*** (Figure 3), living on rock walls in Britain, the median length of wet and dry periods is generally between 5 and 15 hours (Proctor 2004). The longest dry periods in early summer are typically 15-17 days, with the longest continuously wet period lasting nearly 28 days. The moss cushions typically remain wet about 1.7 times the duration of rain. It appears that dew fall is insufficient to cause hydration in this species, perhaps because water drops are trapped by the long hairs instead of reaching the leaf lamina. Such a mechanism could protect the species against frequent (daily) wet-dry cycles in which the nightly wet period is insufficient for damage repair before the moss becomes dry again. Growth occurred primarily in autumn when the moss was wet for long periods, despite relatively low levels of irradiation.

Like others, Stark *et al*. (2013) argued that desiccation tolerance is the most important evolutionary innovation permitting plants to colonize land. They used the desert moss ***Pterygoneurum lamellatum*** (Figure 7) and chlorophyll fluorescence to test recovery from drying of 30 minutes to 53 hours. As in other studies, rate of drying is a major factor in recovery, with only the shoot apex escaping the severe damage of very rapid drying. Rapidly desiccated shoots have slower growth rates, fewer regenerative shoots, and a compromised photosynthetic system. The responses to differences in rate of drying indicate that this xerophytic moss has inducible desiccation tolerance, in contrast to the assumption that xerophytic bryophytes have only constitutive desiccation tolerance.

Figure 7. ***Pterygoneurum lamellatum***, a desert moss with inducible desiccation tolerance. Photo by Michael Lüth, with permission.

Although ***Sphagnum*** (Figure 63) may not be a good model for other kinds of bryophytes, it gives us an idea of the evaporative relationships of these non-tracheophytes. ***Sphagnum*** in a foggy coastal blanket bog in Newfoundland demonstrated that the bog surface loses little water during foggy periods, due, in part, to absence of a vapor pressure deficit. On the other hand, during dry, clear periods the surface of the bog dries, increasing the surface resistance to evaporation (Price 1991); at the same time, higher available energy from the sun causes the rate of evaporation to be higher than on foggy days. This results in a daily evaporation rate of 1.5 mm per day on clear days, contrasting to 0.7-1.1 mm per day for foggy or rainy days.

If we put the two strategies, avoidance and tolerance, into a different perspective, we find that some species tend to avoid drought by holding water more effectively while some survive better at a lower water content. Table 2 lists the survival time of a number of bryophytes. Mechanisms

to accomplish survival vary. As we have seen already (in Chapter 7-4a & b of this volume; Li *et al*. 1992) ***Sphagnum magellanicum*** (Figure 8) is superior to ***S. papillosum*** (Figure 9) at retaining water and transporting it from lower parts of its environment, but ***S. papillosum*** has a greater rate of survival (95%) after laboratory drying (80% for ***S. magellanicum***). Thus, ***S. magellanicum*** is more of a drought avoider whereas ***S. papillosum*** is more of a short-term drought tolerator. On the other hand, ***S. papillosum*** death (65%) surpasses that of ***S. magellanicum*** (50%) when both are dried for 30 days.

Figure 8. ***Sphagnum magellanicum***, a moss with good water retention and transport but inferior desiccation survival. Photo by Michael Lüth, with permission.

Figure 9. ***Sphagnum papillosum***, a moss with poor transport and water holding ability, but good desiccation survival. Photo by Michael Lüth, with permission.

Table 2. Known durations of desiccation survival in bryophyte gametophyte plants.

Sphagnum fuscum	2-4 d	Schipperges & Rydin 1998
Sphagnum papillosum	2-4 d	Schipperges & Rydin 1998
Sphagnum balticum	2-4 d	Schipperges & Rydin 1998
Sphagnum cuspidatum	2-4 d	Schipperges & Rydin 1998
Sphagnum magellanicum	2-4 d	Schipperges & Rydin 1998
Sphagnum magellanicum	14 d	Sagot & Rochefort 1996
Sphagnum fallax	14 d	Sagot & Rochefort 1996
Fontinalis flaccida	3 mos	Glime unpubl
Barbula torquata	18 mos	Moore *et al*. 1982
Oxymitra	4 yrs	Volk 1984
Riccia canescens	7 yrs	Volk 1984
Grimmia laevigata	10 yrs	Breuil-Sée 1993
Syntrichia ruralis	14 yrs	Breuil-Sée1993
Tortula muralis protonema	14 yrs	Maheu 1902
Anoectangium compactum	19 yrs	Malta 1921
Riccia macrocarpa	23 yrs	Breuil-Sée1993

Lloyd Stark (pers. comm. 18 July 2015) found conflicting results among the publications on the duration of the dry period of ***Sphagnum***. Desiccation tolerance alone did not explain the conflicting results. Sagot and Rochefort (1996) dried fragments three species of ***Sphagnum*** [***S. fallax*** (Figure 14-Figure 16), ***S. fuscum*** (Figure 10), ***S. magellanicum*** (Figure 8)] and dried them at 60% relative humidity. These species were able to tolerate up to 14 days of desiccation under these conditions. On the other hand, when Schipperges and Rydin (1998) completely dried ***S. fuscum*** and ***S. magellanicum***, and three other species, none of the five species survived. On the other hand, if the water content was maintained above 100% (normal hydration of ***Sphagnum*** is much greater than that), all the species survived 3-12 days in this "dry" condition. But with the standard water content considered to be near 10% dry weight (~equilibration with 50% relative humidity), This hardly qualifies as dry.

Hájek and Beckett (2008) likewise found that hummock species ***Sphagnum magellanicum*** (Figure 8) and ***S. fuscum*** (Figure 10) under desiccation conditions lose more water before turgor starts dropping than do other ***Sphagna*** from less exposed habitats (73% vs 56% on average). Nevertheless, the **osmotic potentials** [potentials of water molecules to move from hypotonic solution (more water, less dissolved solutes) to hypertonic solution (less water, more dissolved solutes)] across semi-permeable membrane at full turgor are similar in all species (-1.1 MPa). Unlike the desiccation-tolerant ***Racomitrium lanuginosum*** (Figure 78) and ***Syntrichia ruralis*** var. ***arenicola*** (Figure 77), the hummock ***Sphagnum*** species have more rigid cell walls than those of wet habitats. Thus, the leaves of hummock species lose turgor at higher relative water contents (0.61) than species lower in the hummock-hollow complex (0.46). Hummock species also begin a photosynthetic decline sooner during drying. On the other hand, the hummock species recover more completely after rehydration.

Hajek and Vicherova (2014) were able to harden 13 species of ***Sphagnum*** (Figure 8-Figure 9) to desiccation. Hardening agents included drought, slow drying, ABA application, and chilling or frost. They measured tolerance by recovery of chlorophyll fluorescence parameters after severe desiccation. The hardening was accomplished by subjecting the shoot apices to a very high relative humidity (98-99%) for seven days prior to exposing them to desiccating conditions. With that preparation, the bryophytes were able to tolerate 56% relative humidity. This indicates that in ***Sphagnum*** desiccation tolerance is inducible.

Despite its ability to induce desiccation tolerance, one important role of ***Sphagnum*** (Figure 8-Figure 9) as an ecosystem engineer is its ability to retain water (Hajek & Vicherova 2014). Its ability to survive desiccation is seasonal. Following initial dehardening in the lab, untreated shoots of ***Sphagnum*** lack desiccation tolerance. Nevertheless, desiccation tolerance was induced by all hardening treatments except chilling, and especially by slow drying, even in the aquatic section *Cuspidata*. Under field conditions, ***Sphagnum*** species in hollows and lawns developed desiccation tolerance several times during the growing season as the precipitation and lowered water table created changing conditions. On the other hand, hummock

and aquatic species responded only to frost in late autumn, becoming desiccation tolerant. The protonemata did not develop desiccation tolerance, suggesting that this may be a limiting stage in the life cycle. The desiccation avoiders do not develop desiccation tolerance and must live in compact hummocks or submerged. Thus, there seems to be a tradeoff between desiccation tolerance in species lower on the hummocks and submerged vs resources spent on water retention and desiccation avoidance at higher positions.

Figure 10. ***Sphagnum fuscum***, a hummock species. Photo by Michael Lüth, with permission.

Hájek and Beckett (2008) suggest that the higher water-holding capacity of hummock ***Sphagna*** (Figure 8-Figure 10) would allow them to continue their metabolism longer during desiccation, *i.e.*, they have greater desiccation avoidance. On the other hand, their faster recovery makes them desiccation tolerators. Species in lower positions suffer fewer wet-dry cycles but have more elastic cell walls, permitting them to maintain turgor through a wider range of conditions and thus continue metabolism.

Hájek and Beckett (2008) found that ***Atrichum androgynum*** (Figure 11), a moss of the New Zealand forest floor, behaved in a manner similar to hummock ***Sphagnum*** (Figure 8-Figure 10) species. Proctor (2000) suggests that it is the ability to use external water conduction that permits bryophyte leaf cells to maintain full turgor most of the time. Their carbohydrate content is similar to that of embryos in desiccation-tolerant seeds. They are furthermore able to recover rapidly without protein synthesis. As larger plants evolved, vegetative desiccation tolerance was lost; growth rates increased, structural and morphological complexity evolved (Oliver *et al*. 2000), and water conservation mechanisms were selected over rapid intake and recovery.

Oliver *et al*. (1993) noted that carbon balance, damage limitation, and cellular repair are necessary components of desiccation tolerance. Using desiccation tolerance of three desiccation-tolerant species of ***Syntrichia*** (Figure 12-Figure 13, Figure 77), they learned that electrolyte leakage is not an important measure of tolerance, but that differences in protein synthesis could be used to assess damage limitation. Using this assessment, they found the order of tolerance in descending order to be ***Syntrichia caninervis*** (Figure 12), ***S. ruralis*** (Figure 77), and ***S. norvegica*** (Figure 13). This basis of classification and ranking correlates well with the water stress considered to be present in their natural habitat.

Figure 11. ***Atrichum androgynum***, a species that retains turgor at lower water concentrations, much like a hummock ***Sphagnum*** species. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Figure 12. ***Syntrichia caninervis***, the most desiccation-tolerant of three ***Syntrichia*** species on the basis of protein synthesis. Photo by Michael Lüth, with permission.

Wagner and Titus (1984) compared two ***Sphagnum*** species – ***S. fallax*** (Figure 14-Figure 16), a hollow species that lives close to the water table, and ***S. capillifolium*** (Figure 17-Figure 18) (=***Sphagnum nemoreum***), a hummock species. Here, the relationship is somewhat surprising. The hollow species ***S. fallax*** is more desiccation tolerant than the hummock dweller ***S. capillifolium***. ***Sphagnum fallax*** not only recovers a greater proportion of its predesiccation photosynthetic rate, but it also has a higher survival rate after 5-10 days of desiccation. This relationship can be explained by events in its habitat. ***Sphagnum fallax*** dries more frequently and for longer periods of time than does the hummock-dwelling ***S. capillifolium***. ***Sphagnum capillifolium*** is able to retain moisture longer in the field. Growth habit may explain this ability, with ***S. fallax*** being larger and having a wide-spreading head, whereas ***S. capillifolium*** has a compact **capitulum** (head) (Figure 18) and lives in tightly packed clumps (Figure 17).

Figure 13. ***Syntrichia norvegica***, the least desiccation-tolerant of three ***Syntrichia*** species on the basis of protein synthesis. Photo by Michael Lüth, with permission.

Figure 14. Habitat of ***Sphagnum fallax*** on hummocks in the pool where they undergo water level fluctuations. Photo by Michael Lüth, with permission.

Figure 15. ***Sphagnum fallax*** showing spreading branches in capitula and large spaces between plants. Photo by Michael Lüth, with permission.

Figure 16. Close-up view of a hummock of ***Sphagnum fallax***. Photo by Michael Lüth, with permission.

Figure 17. ***Sphagnum capillifolium capillifolium*** hummock showing the tight relationship between plants. Photo by Barry Stewart, with permission.

Figure 18. ***Sphagnum capillifolium*** capitulum showing the tightness of the branches. Photo by Bernd Haynold through Creative Commons, with permission.

Bu *et al*. (2013) consider that peatlands have hummocks with drought-tolerant species and hollows with drought-intolerant species. They found that drought reduces the biomass production, height increment, and side shoot production of both hummock species [***Sphagnum palustre*** (Figure 19) and ***S. capillifolium*** (Figure 17-Figure

18)] and hollow species [***S. fallax*** (Figure 14-Figure 15). Bu and coworkers found that the leaf hyaline cell percentage increases in the hummock species but not in the hollow species. Furthermore, the nitrogen and carbon contents of the hummock species respond more to drought than they do in the hollow species. Instead, it is the presence of neighboring species of ***Sphagnum*** that causes the decrease in carbon in all three species. Despite this effect, there is no change in the competition under wet or dry treatment for any of the six species combinations. Contrary to expectations, ***Sphagnum fallax*** exhibits a change from facilitation in wet conditions to competition under dry conditions. This suggests that hummock species can facilitate the hollow species in wet environments but can outcompete them for water under drying conditions. The inability of hollow species to grow on hummocks could be the combination of superior competitors and the greater drought.

Figure 19. ***Sphagnum palustre***, a drought-tolerant hummock species. Photo by Michael Lüth, with permission.

Wood (2007) summarized vegetative desiccation tolerance of bryophytes. Defining it as the "unique ability to revive from the air-dried state," he considered desiccation-tolerant species to be those that can survive equilibration with either modestly dry air (*i.e.*, 70-80% RH) or extremely dry air (*i.e.*, 0-30% RH). He considered these desiccation-tolerant species to comprise seven bryological classes: **Andreaeopsida**, **Bryopsida**, **Polytrichopsida**, and **Tetraphidopsida** (mosses), **Jungermanniopsida** and **Marchantiopsida** (liverworts), and the **Anthocerotopsida**. This omits the **Andreaeobryopsida** and the **Sphagnopsida**. The **Andreaeobryopsida** may be omitted simply due to lack of data. The **Sphagnopsida**, on the other hand, do indeed have desiccation tolerance in at least some species. In defense of the omissions, only 210 out of ~21,000 bryophyte species (*ca.* 1.0%) have been experimentally determined to possess vegetative desiccation tolerance – 158 species of mosses, 51 species of liverworts, and 1 species of hornwort.

Desiccation Avoidance

Many options of desiccation avoidance are available to tracheophytes that are not available to bryophytes. Bryophytes cannot make use of deep roots or increase the length of their roots (or in bryophytes - rhizoids), as do many tracheophytes, because this would have little effect at the scale of a bryophyte. Nor do they have large underground storage organs to permit dormancy. But many do have underground **tubers** (see Chapter 4-10 of this volume) that store significant quantities of lipids or starches (Duckett & Pressel 2003) and that seem to be an adaptation to drought avoidance (El-Saadawi & Zanaty 1990).

Bryophytes cannot conserve water by using an alternate photosynthetic pathway to store CO_2 (Rundel *et al*. 1979, James 1981) because it would provide no water conservation advantage due to their lack of leaf stomata. Their developmental structure does not permit the loss of leaves because no buds occur at the base of each leaf, and one must wonder if such a small stem could store sufficient energy to support the growth of new leaves prior to any new input from photosynthesis.

The plants protect each other from desiccation and may hide buds of younger shoots within the clump. In ***Bazzania trilobata*** (Figure 20), field plants are able to tolerate drying, whereas lab drying is lethal (Sollows *et al.* 2001). Field conditions do not provide the desiccation level one might suppose by measuring air moisture. But it is also likely that the drying rate is different, and the integrity of the clump may have been altered in the lab.

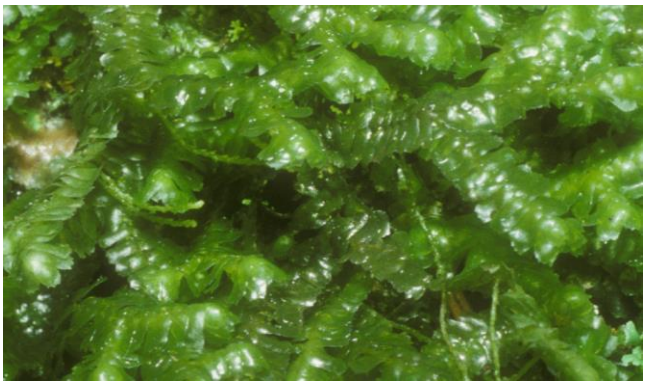

Figure 20. ***Bazzania trilobata*** illustrating overlapping leaves and layering of branches. Photo by Janice Glime.

Many bryophytes can roll their leaves, as do some vascular plants, and they have several other related options to reduce the exposed surface area. These include curling and contorting the leaves (see Chapter 7-4 in this volume), a mechanism that creates small air spaces and presumably decreases air movement across the leaf surface. Others appress their leaves closely to the stem, protecting the upper surface from exposure and overlapping leaves sufficiently to protect even portions of the back surface of the leaf from exposure. And, despite their lack of specialized energy-storing organs (with some exceptions), they do have life cycle options. Perhaps the most important of these adaptations is the ability to withdraw water from the cell and form extracellular ice, with desiccation tolerance being an important adaptation (Dilks & Proctor 1975). (See Chapter 7-9 and 7-10 for further information on effects of freezing.)

Life Cycle and Life Strategy Adaptations

Hedderson and Longton (1996) evaluated the relationship between life history traits and taxonomic group, relating these to water relationships. They found

that 40-50% of the life history variation was related to water relations. The capacity for water uptake and retention arranges species from short-lived **monoicous** (having both sexes on same plant) taxa that produce few, large spores to those **dioicous** (having separate sexes) taxa with the opposite traits. The **endo-ectohydric** (internal vs external water control) gradient similarly relates to the investment in spores as a function of life expectancy.

One way to survive dry periods is to avoid them by leaving your spores behind to carry on the species. In the Murray River Valley, Australia, where flooding occurs every spring, long dry periods ensue and many taxa such as the ephemeral mosses persist there as spores (Peintinger 1988). In such genera as ***Riccia*** (Figure 1), which typically inhabit seasonally dry areas, dispersal of spores by animals, aided by the ornamentation of the spore, is important (Volk 1984; see Chapter 4-8 in this volume). Survival is facilitated by the ability to endure temperatures as high as 80ºC when dry, whereas temperatures higher than 50ºC when wet will injure them.

Alternatively, ephemeral bryophytes such as ***Riccia cavernosa*** (Figure 1), ***Physcomitrella patens*** (Figure 21), and ***Physcomitrium eurystomum*** (Figure 22) are able to grow on the muddy floodplain soil (Peintinger 1988), then become dormant in the fall until water returns again.

Figure 21. ***Physcomitrella patens*** on wet soil after flooding recedes. Photo by Michael Lüth, with permission.

Figure 22. ***Physcomitrium eurystomum***, an ephemeral bryophyte that grows on floodplains. Photo by Michael Lüth, with permission.

For some bryophytes, altering their phenology according to available water is an adaptive strategy to take advantage of water when it is available. ***Octoblepharum albidum*** (Figure 23) in Nigeria produces antheridia and archegonia two months earlier when watered regularly (Egunyomi 1979). In nature, they produce archegonia during the rainy season, then produce capsules and take advantage of the dry season for dispersal of spores. This moss furthermore has leaves that can regenerate after as much as 29 weeks of dry storage, permitting an alternate means of propagation in those years when weather is not favorable for sexual fertilization.

In the very hot and dry summers of Kuwait, El-Saadawi and Zanaty (1990) found that a different avoidance strategy can be used. ***Bryum bicolor*** (Figure 24) forms subterranean rhizoidal **tubers** (see Figure 25) (Risse 1993) and stem tubers that permit it to be dormant as an avoidance mechanism, but it also exhibits tolerance in its protonemata, main stems, and stem apices (El-Saadawi & Zanaty 1990). ***Funaria hygrometrica*** (Figure 26) survives only by avoidance in the same conditions, using subterranean corm-like or bulbiform bases and bulbils to span the drought period.

Figure 23. ***Octoblepharum albidum*** growing epiphytically in India. This moss modifies its **phenology** (timing of life cycle events) when more water becomes available. Photo by Michael Lüth, with permission.

Figure 24. ***Bryum bicolor***, a moss that survives drought through stem apices and rhizoidal tubers. Photo by Michael Lüth, with permission.

Figure 25. ***Bryum sauteri*** rhizoidal tubers, a means of surviving drought. Photo by David T. Holyoak, with permission.

Figure 26. ***Funaria hygrometrica*** with young sporophytes, growing abundantly on charcoal, where it will continue growth for several years until competition moves in. Note the bulbiform basal leaves that can protect the plant and young sporophyte during drought. Photo by Janice Glime.

Even in less xeric conditions, drought-resistant **tubers** (Figure 25) are present in such taxa as ***Atrichum tenellum*** (Figure 27), ***A. crispum*** (Figure 28) (Arts 1987), and ***Fissidens cristatus*** (Figure 29) (Arts 1986). In ***Haplodontium notarisii*** (Figure 31), tubers are viable for up to 10 years (Arts 1988).

Figure 27. ***Atrichum tenellum***, a moss that can survive drought as tubers. Photo by Michael Lüth, with permission.

Figure 28. ***Atrichum crispum***, a moss that can survive drought as tubers. Photo by Jan-Peter Frahm, with permission.

Figure 29. ***Fissidens cristatus***, a moss that is able to survive drought and freezing as tubers. Photo by Jan-Peter Frahm, with permission.

Some bryophytes actually require a dry season. In ***Orthotrichum anomalum*** (Figure 30), this dry period is necessary for the **operculum** (capsule lid) to dehisce (Johnsen 1969). The leafy gametophyte grows only when it is cool and moist, but watering during the dry period is detrimental.

Figure 30. ***Orthotrichum anomalum*** with dehisced capsules. Photo by Michael Lüth, with permission.

Seasonal Changes

As we have just seen, the physiological state of the bryophyte, and hence **desiccation tolerance**, varies with the **season**. Many bryophytes [*e.g.*, ***Plagiochila spinulosa***

(Figure 32), ***Hylocomium splendens*** (Figure 61-Figure 62), ***Scorpiurium circinatum*** (Figure 33), ***Syntrichia ruralis*** (Figure 93), ***Racomitrium aquaticum*** (Figure 34)] seem to be most sensitive during autumn and early winter, the times when most bryophytes resume growth after a hot summer (Dilks & Proctor 1976a). Desiccation tolerance increases from spring to a maximum in early summer, the season when many species become dormant. Some degree of acclimation may be occurring, resulting in increased tolerance as summer approaches (Richardson 1981).

Figure 31. ***Haplodontium notarisii*** with capsules, a moss that can survive for ten years as tubers. Photo by Jan-Peter Frahm, with permission.

Figure 32. ***Plagiochila spinulosa***, a leafy liverwort species that is most sensitive to desiccation during autumn and early winter. Photo by Michael Lüth, with permission.

Figure 33. ***Scorpiurium circinatum***, a species that is most sensitive to desiccation during autumn and early winter. Photo by Michael Lüth, with permission.

Figure 34. ***Racomitrium aquaticum***, a species that is most sensitive to desiccation during autumn and early winter. Photo by Michael Lüth, with permission.

Bryophytes apparently adjust their desiccation tolerance and resistance according to their experiences with the environment (Dilks & Proctor 1976a), as will be discussed in greater detail later with regard to rehydration. That is at least part of the reason for different studies showing different results, even from the same researchers. It is interesting that not all bryophytes adjust in the same way, with one group of bryophytes having their least desiccation tolerance time in autumn and winter and others in late summer in Britain (Figure 35), in this case coinciding with differences among their habitats. ***Andreaea rothii*** (Figure 36) seems to have no response to season.

Ochi (1952) examined the effects of season on drought tolerance and concluded that mosses with active buds at the beginning of the growing season are generally more drought resistant then than in other seasons. Seemingly in contrast to this statement, Ochi showed that in Japan ***Dicranum japonicum*** (Figure 37) survives drought longer (28 weeks) if the plant has active buds in early January rather than in early September or April (~4 weeks),

whereas ***Polytrichastrum formosum*** (=*Polytrichum attenuatum*; Figure 38), when dried on the same dates, survives longest when buds become active in September (>56 weeks compared to 28 in January and 11 in April). He concluded that these seasonal strategies represent three types of seasonal fluctuations in osmotic value: higher values in summer (dry season), lower in winter (wet season); higher in winter, lower in summer; no seasonal fluctuations (those from wet habitats).

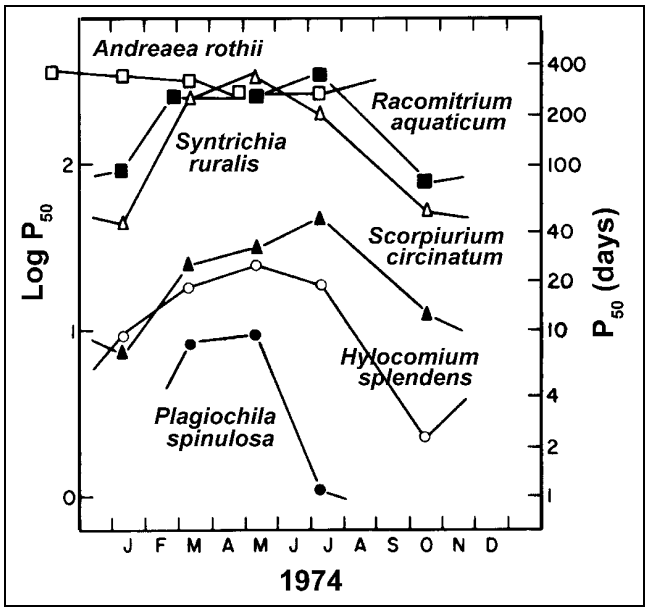

Figure 35. Relationship between season and maintenance of photosynthesis during desiccation of British bryophytes. P_{50} is the number of days (in this case) of desiccation at which photosynthesis upon rehydration is reduced to 50% its initial value. Redrawn from Dilks and Proctor (1976a).

Figure 36. ***Andreaea rothii***, a season-neutral moss with respect to its desiccation tolerance. Photo by Michael Lüth, with permission.

Davey (1997) found that in Antarctic bryophytes, the photosynthetic rate following a desiccation/rehydration cycle decreased from spring to summer to autumn. The pattern was clearest in the hydric taxa, with less effect in the xeric species.

Figure 37. ***Dicranum japonicum***, a moss where early January buds result in ability to survive drought longer. Photo by Li Zhang, with permission.

Figure 38. ***Polytrichastrum formosum***, a moss that survived longest when buds became active in September. Photo by David T. Holyoak, with permission.

Akande (1984, 1985) likewise attributed seasonal differences in desiccation tolerance of four **epiphytic** (growing on other plants, especially trees) bryophytes to changes in osmotic values, with osmotic values increasing from wet to dry season. He found that the mosses ***Entodontopsis nitens*** (=*Stereophyllum nitens*) and ***Calymperes palisotii*** (Figure 39) had a greater osmotic potential and greater desiccation tolerance than the leafy liverworts ***Mastigolejeunea florea*** and ***Frullania spongiosa***.

Figure 39. ***Calymperes palisotii***, a moss in which good osmotic potential increases desiccation tolerance. Photo by Scott Zona, with permission.

Figure 40. ***Cratoneuron filicinum***, a moss species intolerant of rapid drying. Photo by Ivanov, with permission.

Physiological Adaptations

All of us have observed that bryophyte assemblages differ with habitats (*e.g.* Šinžar-Sekulić *et al*. 2005). Oliver *et al*. (2000) note that most of the desiccation-tolerant plants are bryophytes, in addition to algae and lichens. They agree that desiccation tolerance was an important step in the evolution of land plants. They suggested that such tolerance requires constitutive cellular protection coupled with active cellular repair. But as evolution progressed, plants gained structural and morphological complexity. Plants developed mechanisms that conserve water within the plant, and vegetative desiccation like that seen in bryophytes was no longer necessary.

But Alpert and Oechel (1985) contend that desiccation-tolerant plants are rarely present in the most xeric microhabitats, suggesting that in these locations they are unable to maintain a positive cumulative carbon balance. They demonstrated this in ***Grimmia laevigata*** (Figure 83), the dominant green plant on exposed granitic boulders in the California, USA, chaparral by measuring the response of net CO_2 flux to light, temperature, plant water content, and previous desiccation.

Among desiccation-tolerant bryophytes, rehydration is rapid, with leaves returning to normal form in as little as 2 minutes and chloroplasts returning to normal conformation in 2-5 minutes in such desiccation-tolerant mosses as ***Syntrichia ruralis*** (Figure 77) (Tucker *et al.* 1975; Oliver & Bewley 1984). On the other hand, following rapid drying such intolerant species as ***Cratoneuron filicinum*** (Figure 40) still have misshapen organelles after 24 hours, and about half the cells of slow-dried plants still contain misshapen organelles (Oliver & Bewley 1984). In slow-dried plants respiration recovers, but it does not in rapid drying of desiccation-intolerant plants.

Charron and Quatrano (2009) considered two general mechanisms for survival in the xeric aerial environment. The descendants of the early land plants evolved specialized transport tissues while the bryophytes retained and perfected their co-equilibrium of their water content with that of their surroundings, relying on cellular processes to recover from damages due to water stress.

Bates (1997) examined the effects of wet/dry cycles on the nutrient economy of two pleurocarpous mosses of different habitats – ***Brachythecium rutabulum*** (Figure 56-Figure 57; wet ground, among grasses, logs; shade or open) and ***Pseudoscleropodium purum*** (Figure 41; grasslands and heaths). When provided with weekly drying periods of 24 hours every week, these plants had noticeably less biomass production than those plants that were continuously hydrated. ***Brachythecium rutabulum*** experienced bleaching of green tissues, unlike ***Pseudoscleropodium purum***. When NPK (mix of nitrogen, phosphorus, and potassium salts) was added to the growing solutions once a week, ***Pseudoscleropodium purum*** exhibited growth stimulation even among the weekly desiccated plants. Uptake of N was similar in both hydrated and desiccated plants of both species. P and K^+ were considerable in ***B. rutabulum***, but in desiccated plants they was greatly reduced. As with phosphorus, uptake of P and K^+ differed little between hydrated and intermittently desiccated ***Pseudoscleropodium purum***. In both species, P and K^+ were leaked from cells during desiccation, were retained on the cells by cation exchange, and taken up again during rehydration. But even this maintenance has a cost. K^+ and Mg^{+2} intracellular levels in new growth are maintained at the expense of exchangeable cations. Uptake is greatest during the early stages of recovery, most likely due to damaged membranes, and that is when the NPK application has the greatest effect on growth. These experiments suggest that ***P. purum*** has a lower nutrient requirement than ***B. rutabulum*** and they explain why ***B. rutabulum*** requires a more continuous hydration to maintain its greater production. An interesting revelation is the ability of these species to initiate new growth without additional nutrient absorption.

Bohnert (2000) asked what makes desiccation tolerable. He considered that bryophytes tolerated rapid desiccation, using protective mechanisms. Most research has focussed on repair mechanisms. The photosynthetic apparatus and cell integrity are maintained during desiccation, but rehydration leads to cellular damage. Despite this damage, recovery is rapid. **mRNA** (messenger RNA, the molecule that carries information from DNA to the ribosome) exists in **RNPs** (nucleoproteins that contain RNA) before the stress conditions arise. During recovery,

non-reducing sugars, **dehydrins** (group of proteins produced in response to cold and drought stress), and **rehydrins** (transcripts used during rehydration) appear. Hoekstra (2005) reported on the importance of fatty acid saturation in membranes in imparting survival of desiccation.

Figure 41. ***Pseudoscleropodium purum***, a species in which intermittent desiccation seems to have little effect on K and P uptake. Photo from Proyecto Musgo, through Creative Commons.

Yang *et al*. (2012) sought the genetic determinant(s) for stress tolerance. Using ***Syntrichia caninervis*** (Figure 12) they identified ScALDH21, a gene that responds to **ABA** (abscisic acid, a stress hormone; see Chapter 7-7 Water Relations – Biochemistry) and desiccation and that plays an important role in response to desiccation and salinity stresses.

When the desiccation-tolerant ***Syntrichia ruralis*** (Figure 77) is desiccated, it retains all its pigments, chlorophyll included, and is able to recover physiological function rapidly upon rehydration (Hamerlynck *et al*. 2002). But all is not equal among these plants of both sun and shade habitats. ***Syntrichia ruralis*** has lower plant mass, as well as lower tissue N, C, total photosynthetic pigment concentrations, and carbon isotope discrimination (Δ) values compared to shade plants. The ratio of carotenoid to chlorophyll in sun plants is typical of high light plants, but the ratio of chlorophyll *a* to chlorophyll *b* in these plants is lower than expected, resembling those of plants adapted to shade. As a consequence, the levels of optimal quantum efficiency of **PS II** ($\mathbf{F_v/F_m}$) (= variable fluorescence / maximum fluorescence; PS II is photosystem II of photosynthesis, where oxygen is liberated from water) are lower in the sun plants. Reciprocal transplants reveal that ***Syntrichia ruralis*** is able to adjust to altered light levels. This is evidenced by increases in F_v/F_m, **NPQ** (non-photochemical quenching), light-adapted PSII yield (φPS II) in transplanted sun plants, and concurrent decreases in sun-transplanted shade plants. Nevertheless, the transplanted sun plants did not adjust sufficiently to reach performance levels exhibited by the undisturbed shade plants. These plants demonstrate at least some ability to adjust to the loss of shade canopy or other disturbance in the light regime.

Sphagnum (Figure 8, Figure 9, Figure 14-Figure 18) has a unique cell structure (Figure 42) providing a water reservoir. We might expect that this reservoir increases the drying time, sparing the moss from the detrimental effects of rapid drying. But differences do exist among ***Sphagnum*** species.

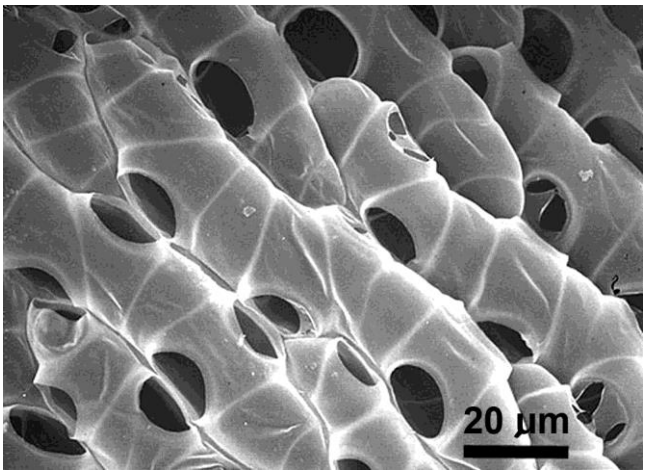

Figure 42. ***Sphagnum*** **hyaline leaf cells** and pores. Photo from Botany Department website, University of British Columbia, Canada, with permission.

In the hummock-forming ***Sphagnum fuscum*** (Figure 10) and ***S. magellanicum*** (Figure 8), desiccation results in a greater water loss before turgor sets in, compared to other non-hummock species (mean of 73% water loss vs 56%, respectively) (Hájek & Beckett 2008). The hummock species have more rigid cell walls than those of wet habitat species (epsilon = 3.55 vs 1.93 MPa, respectively). This rigidity results in loss of turgor in chlorophyllous cells at a higher relative water content in hummock species compared with species of wet habitats (0.61 vs 0.46) and at less negative osmotic potentials (-2.28 vs -3.00 MPa, respectively). Compared with other species, hummock ***Sphagnum*** (Figure 8, Figure 9) species that have been desiccated to -20 or -40 MPa recover more completely after rehydration. The **mesophytic** (intermediate habitat based on moisture) ***Atrichum androgynum*** (Figure 43) responds similarly to the hummock ***Sphagnum*** species.

Figure 43. ***Atrichum androgynum***, a moss that behaves similarly to hummock ***Sphagnum*** species when it loses water. Photo by Jan-Peter Frahm, with permission.

Under a given rate of desiccation, the hummock species of ***Sphagnum*** (Figure 8-Figure 10), with their higher water content, continue their metabolism longer than species with lower water-holding capacities (Hájek & Beckett 2008). And these species recover faster, indicating a higher drought tolerance. These behaviors permit them to survive in the drought-exposed hummocks. The species growing in wet habitats have smaller water-holding capacities but are able to maintain turgor and have more elastic cell walls that permit them to metabolize longer during drying.

Most ***Sphagnum*** (Figure 8-Figure 10) species live where intermittent desiccation is inevitable. Hence, this genus appears to have inducible desiccation tolerance (Hájek & Vicherová 2013). In experiments to **harden** (process by which a plant becomes tolerant to the effects of such stresses as frost and drought) the species, Hájek and Vicherová subjected them to slow drying, ABA application, and chilling or frost. In the laboratory, ***Sphagnum*** species that were de-hardened and remained untreated lacked desiccation tolerance. Slow drying, ABA application, and frost induced hardening and desiccation tolerance. The section ***Cuspidata*** (Figure 44) – aquatic species – did not exhibit hardening. Similar hardening occurs multiple times each year among hollow and lawn species in the field. Hummock and aquatic species, on the other hand, develop their tolerance only in late autumn, a phenomenon that Hájek and Vicherová attributed to frost. Protonemata, however, did not develop desiccation tolerance under any of the hardening treatments. The hummock species exhibit a tradeoff, having greater water-holding capacity to the detriment of their physiological desiccation tolerance.

Figure 44. ***Sphagnum cuspidatum***, an aquatic species that does not seem to experience hardening. Photo by Bernd Haynold, through Creative Commons.

Cratoneuron filicinum (Figure 40) demonstrates the effects of slow vs rapid drying on a semi-aquatic species (Krochko *et al*. 1978). In rapid drying, the cell contents are very disrupted and become increasingly disorganized over the next 24 hours. In slow drying, only some cells have this appearance while others maintain their cellular integrity. The greater the rate of drying, the more protein synthesis is reduced on rehydration, but it will resume following rapid water loss down to 50% of the fresh weight. On the other hand, respiration does not resume following rapid drying and rewetting.

Mode of Conduction

Can the mode of conduction provide a beneficial edge that permits success when faced with limited water? Raven (1999) claims there is a "mechanistically mysterious size limit" for poikilohydric, desiccation-tolerant plants, suggesting an upper limit of 1 m. Anderson and Bourdeau (1955) demonstrated that external water can travel only to a "certain level." Bowen (1933c) and Mankiewicz (1983, 1984a,b, 1987a,b) remind us that this upper limit is imposed by the height to which water can rise by capillarity alone, a distance Hébant (1977) considers to be only a few centimeters without the addition of other forces. As stated by Mankiewicz, "geometry of bryophytes may be constrained by the cohesive and adhesive forces of water," a statement he was able to confirm by empirical measures of flow rates through bryophyte colonies. However, we are reminded that most bryophytes receive their water from above, hence that capillary limit is of little importance for most of them. Therefore, we might ask, is the endohydric system important for the slow-growing, short bryophyte?

Bowen (1933a,b,c) compared conduction of bryophytes in wet, moist, and dry habitats. External water movement was faster than internal movement in all but two cases [***Thamnobryum alopecurum*** (Figure 50) and ***Plagiomnium undulatum*** (Figure 52)]. ***Plagiomnium undulatum*** has a well-developed internal conducting system and lacks significant capillary channels externally. ***Thamnobryum alopecurum***, on the other hand, typically lives where it is constantly wet from splashing or dripping water and seems to lack external conduction, perhaps due to external saturation. However, as the moisture of the habitat increases, the ability of the bryophyte plant to conduct decreases both externally and internally.

All of the taxa Bowen (1933a,b,c) studied had a **central strand** (Figure 45), varying considerably in relative size. But just how important is that strand in moving water from substrate to plant tissues? If the central strand is important in water movement, should we expect it to be most important in those mosses that suffer frequent drought conditions? In the epiphytic (but pleurocarpous) ***Hypnum cupressiforme*** var. ***filiforme*** (Figure 46-Figure 47), the central strand appears only occasionally and is absent in branches. In the boreal forest floor ***Rhytidiadelphus triquetrus*** (Figure 48), the cells are short with numerous transverse walls, suggesting inefficient water movement through walls. Nevertheless, in ***Aulacomnium palustre*** (Figure 49), internal conduction seems not to exist, despite a "relatively large central strand;" external conduction is rapid, suggesting that other factors, not the central strand, are more important in determining importance of internal versus external conduction.

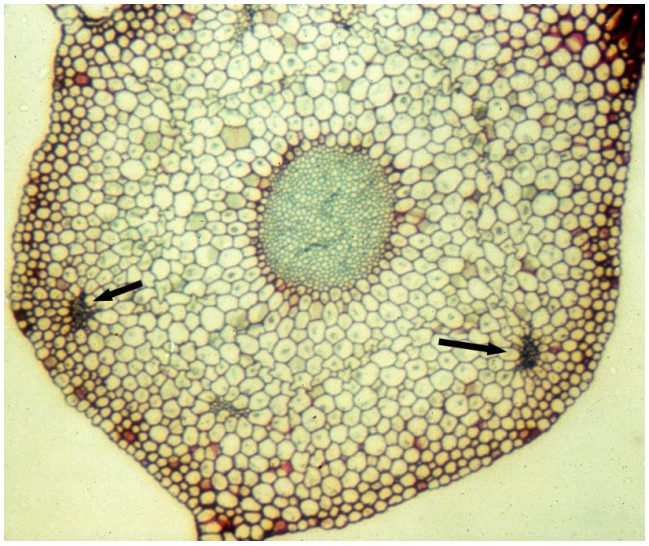

Figure 45. ***Mnium*** stem cross section showing central strand. Arrows indicate leaf traces. Photo by Janice Glime.

Figure 46. ***Hypnum cupressiforme*** in its epiphytic habitat. This moss usually lacks a central strand. Photo by Dick Haaksma, with permission.

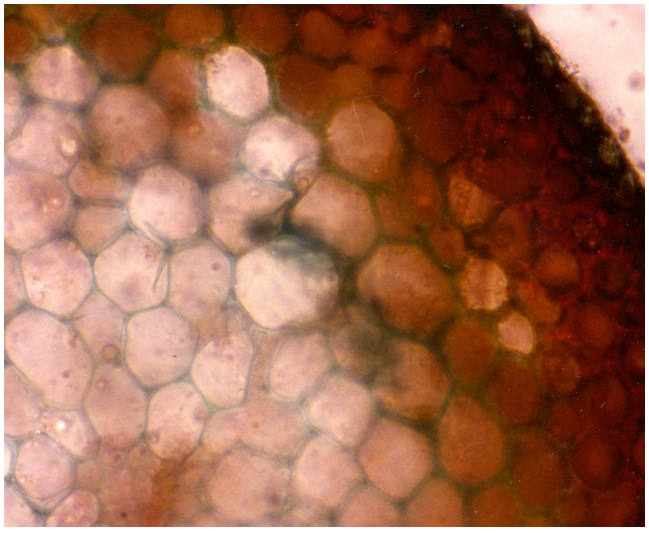

Figure 47. Cross section of stem of ***Hypnum*** sp. showing indistinct central strand. Photo by Isawo Kawai, with permission.

Figure 48. ***Rhytidiadelphus triquetrus*** on the forest floor. This moss has short stem cells with numerous transverse walls, making internal transport slow. Photo by Michael Lüth, with permission.

Figure 49. ***Aulacomnium palustre***, a moss with predominately external conduction despite its central strand. Photo by Janice Glime.

When Bowen (1933b) compared nine species of moist habitat bryophytes (Figure 53), she found that external conduction likewise predominated in all but ***Rhizomnium magnifolium*** (Figure 52; as ***Mnium punctatum***, but based on her description most likely what is now called ***Rhizomnium magnifolium***). ***Thamnobryum alopecurum*** (Figure 50), apparently erroneously reported in cm instead of mm in her table, has almost no water movement internally or externally (Mägdefrau 1935), but relies instead on the constant humidity of waterfalls and streamsides. Among the dry habitat mosses in the study, only ***Plagiomnium undulatum*** (Figure 52) exhibits more rapid internal conduction than external conduction.

Figure 50. ***Thamnobryum alopecurum***, a moss of dripping habitats that seems to have little water movement internally or externally. Photo by Michael Lüth, with permission.

Based on Bowen's (1931, 1933a,b,c) comparisons, we can derive little satisfaction about the relationship between the central strand and habitat. None of the species lacking a central strand were examined, nor were any extremely xerophytic or aquatic mosses or any liverworts examined. However, external adaptations to movement of water do seem to correlate with habitat, with those mosses from wet habitats having poor conduction capability both internally and externally, relative to taxa from drier habitats (Figure 53). The central strand appears to have only a minor role in conduction, being most useful in those taxa with a well-developed central strand, such as the **Mniaceae** (Bowen 1933c), and providing almost no value in those taxa with a small strand (Mägdefrau 1935; Zacherl 1956).

Despite Bowen's (1931, 1933a,b,c) small sample size and the presentation of "representative" data rather than means, one can still infer several patterns that indicate water pathway adaptations. The **Mniaceae** are a good example (Figure 52). There is good external conduction in ***Mnium hornum*** (Figure 52), where the leaf insertion is relatively small, but the leaves are strongly overlapping, as are the plants. In the very tomentose ***Rhizomnium magnifolium*** (Figure 52), with somewhat overlapping and encircling leaves, external conduction is relatively good, but internal conduction is much better than in ***Mnium hornum***. However, in ***Plagiomnium undulatum*** (Figure 52), where the leaves are non-overlapping and the leaf tapers to the equivalent of a petiole at insertion, external conduction is almost non-existent. It is noteworthy that members of this family are particularly difficult to rehydrate for slide preparation, presumably due to thickened cell walls and cuticular substances on the leaves. It is reasonable to expect rapid internal conduction in the **Mniaceae** because these mosses have well developed central strands of conducting tissue. In ***Plagiomnium undulatum*** the central strand occupies up to 2/3 of the stem diameter. Members of the family **Mniaceae** and ***Polytrichum commune*** (Figure 54-Figure 55) are also the only ones examined that have hydroids in the leaves (Bowen 1931, 1933a,b,c). As noted in ***Aulacomnium palustre*** (Figure 49), factors other than the size and construction of the central strand are important in determining relative conductance.

In ***Brachythecium rutabulum*** (or ***B. rivulare***?) (Figure 56-Figure 57), the slightly decurrent leaf bases form channels that retain capillary films of water. In ***Entodon rubicundus*** and ***Calliergonella cuspidata*** (Figure 58), internal conduction is appreciable in young tissues, becoming negligible in older stems (Mizushima 1980). Bowen (1933b) attributes this to the changes in **hypodermal tissues**, which are thin-walled in young stems, becoming thick-walled in older ones. Rather, the epidermis absorbs water and sends it cell-to-cell to the tip of the plant where the young hypodermal cells permit the water to penetrate to the center of the plant where a very thin central strand occupying about 10% of the stem exists. Entry of water into the apex is rapid, as is the external movement to the tip. ***Campylopus brevipilus*** (Figure 59) has a central strand of 5-15 cells in diameter. As might be expected in a genus so well adapted to dry habitats, even this more wetland species has little absorption through its stem epidermis and movement of water through the hypodermis is slow, entering primarily at the stem apex. Likewise, little conduction occurs from the base through the central strand.

Figure 51. ***Entodon rubicundus*** with capsules & dew drops, a species with internal conduction in young tissues. Photo by Shu Suehiro, permission pending.

Figure 52. Comparison of external morphology of three members of the Mniaceae. **Left:** ***Rhizomnium magnifolium***. **Middle:** ***Mnium hornum***. **Right:** ***Plagiomnium undulatum***. Photos by Michael Lüth, with permission.

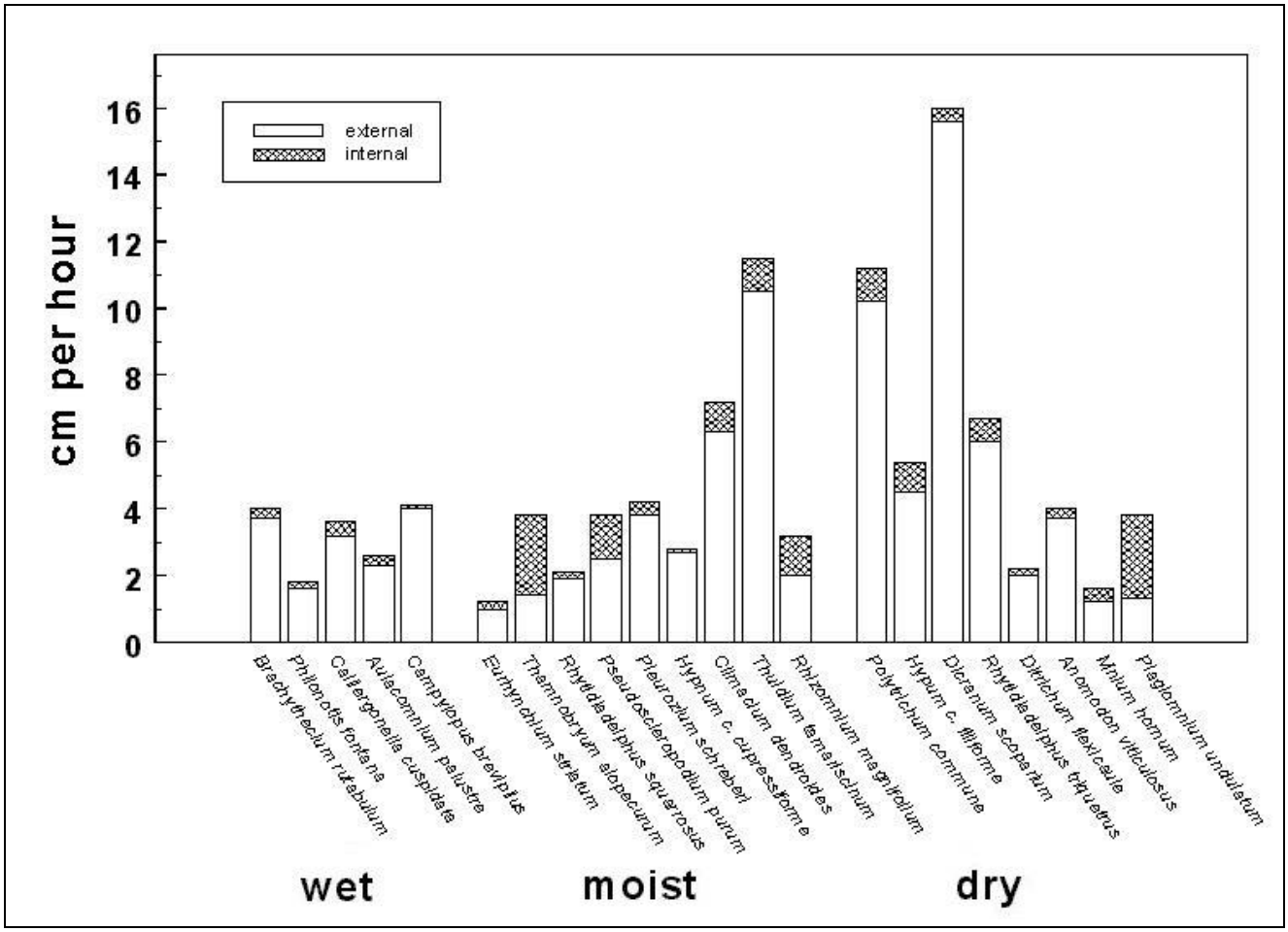

Figure 53. Comparison of movement of water up the stems in wet, moist, and dry habitat mosses. Note that for ***Brachythecium rutabulum***, ***Hypnum cupressiforme*** var. ***filiforme***, and ***Rhytidiadelphus triquetrus*** the internal movement is for 18 hours. (Based on the description of decurrent leaf bases and habitat, ***Brachythecium rutabulum*** may actually have been ***B. rivulare***.) For ***Thuidium tamariscinum***, ***Hypnum cupressiforme*** var. ***filiforme***, and ***Dicranum scoparium***, the external water reached the tip before one hour. In ***Ditrichum flexicaule*** and ***Anomodon viticulosus*** the water reached the tip in 15 minutes. Based on Bowen (1931, 1933a,b,c).

Figure 54. ***Polytrichum commune***, a moss with good internal conduction in stem and leaves. Photo by Michael Lüth, with permission.

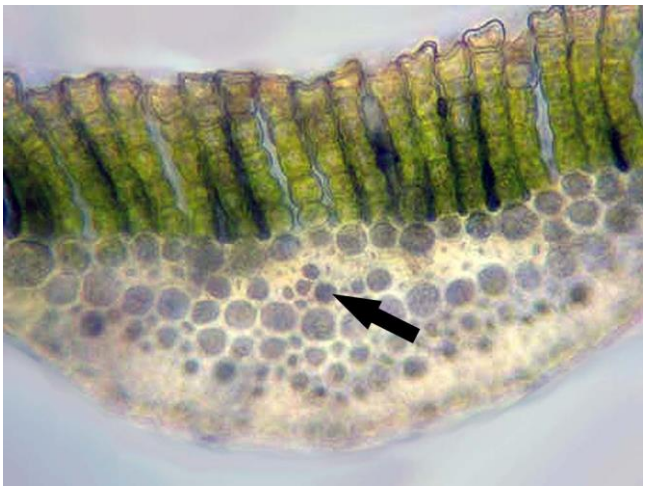

Figure 55. ***Polytrichum commune*** leaf cross section showing hydroids (**arrow**). Photo from Botany website, University of British Columbia, with permission.

Figure 56. ***Brachythecium rutabulum***, a moss whose leaf bases create capillary channels. Photo by Janice Glime.

Figure 57. ***Brachythecium rutabulum*** leaf showing slight decurrency that aids in holding capillary water. Photo by Tom Thekathyil, with permission.

Figure 58. ***Calliergonella cuspidata*** has mostly internal conduction in young stems but lose it in older stems. Photo by Des Callaghan, with permission.

Figure 59. ***Campylopus brevipilus***, a moss in which water enters through the stem apex. Photo by Michael Lüth, with permission.

Could it be that the central strand serves a different function? In an Alaskan black spruce forest, Skré *et al.* (1983) found that endohydric ***Polytrichum commune*** (Figure 54-Figure 55), which has a well-developed central strand (Figure 60) and considerable internal conduction, suffers less moisture stress than the three ectohydric mosses studied [***Hylocomium splendens*** (Figure 61-Figure 62), ***Pleurozium schreberi*** (Figure 64), and ***Sphagnum subsecundum*** (Figure 63)] during the summer dry period. ***Hylocomium splendens*** remained below its water compensation point for nearly 50% of the July measurement period. The rates of water loss and moisture level required to reach field capacity correlate well with the moisture status observed for mosses in the field. This water retention in the endohydric ***Polytrichum*** supports the suggestion of Skré and coworkers that a major function of the central strand may be water storage.

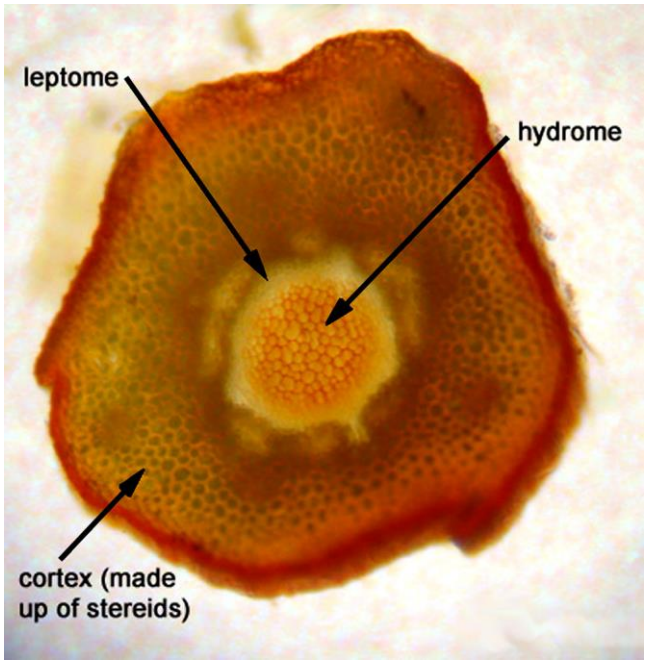

Figure 60. ***Polytrichum commune*** stem cross section showing hydrome. Photo from Botany website, University of British Columbia, Canada, with permission.

Figure 61. ***Hylocomium splendens***, an ectohydric, on black spruce forest floor. Photo by Janice Glime.

Figure 62. ***Hylocomium splendens*** stem cross section showing absence of central strand. Conduction is external. Photo from Botany website, University of British Columbia, Canada, with permission.

Figure 63. ***Sphagnum subsecundum***, an ectohydric moss. Photo by Michael Lüth, with permission.

Osmotic Potential and Turgor

Unlike tracheophytes, whose net photosynthesis decreases when the water potential drops below -1 to -3 bars (Busby & Whitfield 1978), drought-tolerant mosses can resume normal photosynthesis after a drop in water potential to about -1000 bars, a condition found during the dry, hot days of summer in the open (Dilks & Proctor 1979). Even in the shaded forest, the water potential of a moss can drop to -200 to -400 bars. While flowering plants and ferns may have negative photosynthesis at water potentials of -12 to -15 bars, mosses such as the woodland to semi-shaded species ***Hylocomium splendens*** (Figure 61-Figure 62), ***Pleurozium schreberi*** (Figure 64), and ***Tomenthypnum nitens*** (Figure 65) can continue net photosynthesis until the water potential falls below -55 to -100 bars (Busby & Whitfield 1978), and ***Camptothecium lutescens*** (Figure 66) from the United Kingdom can maintain a net positive photosynthesis down to -150 bars (Dilks & Proctor 1979). The drought-intolerant moss ***Hookeria lucens*** (Figure 67), on the other hand, must maintain 100% humidity and cannot maintain positive photosynthetic gain when the water potential drops below 80 bars (Dilks & Proctor 1979). Yet this highly drought-intolerant moss, relatively speaking, has primary cell walls with **pit fields** in its stem parenchyma, structures common to tracheids and vessels and permitting lateral transport, suggesting that ***Hookeria lucens*** may use these cells in internal conduction (Cortella *et al*. 1994).

Figure 64. ***Pleurozium schreberi***, an ectohydric moss with leaves completely covering the stem. Photo by Janice Glime.

Figure 65. ***Tomentypnum nitens***, an ectohydric moss. Note dense tomentum covering stems. Photo by Michael Lüth, with permission.

One adaptation to maintaining water is to increase the osmotic value of the cells. Ochi (1952) compared a number mosses and showed that the highest osmotic values were generally in mosses adapted to xeric conditions. He obtained high values (0.90-0.62) in such tree-trunk and sunny rock dwellers as ***Hedwigia ciliata*** (Figure 82), ***Thamnobryum subseriatum*** (=*Thamnobryum sandei* var. *cymbifolium*?) (Figure 68), ***Myuroclada maximowiczii*** (Figure 69), ***Thuidium cymbifolium*** (Figure 70), ***Neckera yezoana***, and ***Anomodon giraldii*** (Figure 71). Intermediate values characterized those on soil (0.70-0.30), including ***Dicranum japonicum*** (Figure 37), ***Pogonatum inflexum*** (Figure 72), ***Plagiomnium maximoviczii*** (Figure 73), and ***Plagiomnium cuspidatum*** var. ***trichomanes*** (Figure 74). In shady, wet, forested areas, Ochi obtained the lowest value (0.26), exemplified by ***Plagiomnium vesicatum*** (Figure 75) and ***Hookeria acutifolia*** (Figure 76). Surprisingly, values were highest in older plants and mature portions, not the vital young buds.

Figure 66. ***Camptothecium lutescens***, a moss that can maintain photosynthesis at very low water potential. Photo by Michael Lüth, with permission.

Figure 67. ***Hookeria lucens***, showing thin leaves that are very drought-intolerant. Photo by Michael Lüth, with permission.

Figure 68. ***Thamnobryum subseriatum***, a moss from emergent rocks of streams. Photo by Michael Lüth, with permission.

Figure 69. ***Myuroclada maximoviczii***, a rock dweller with high osmotic values. Photo by Janice Glime.

Figure 70. ***Thuidium cymbifolium***, a sunny rock dweller with high osmotic values, with capsules. Photo by Li Zhang, with permission.

Figure 71. ***Anomodon giraldii***, a xerophyte. Photo by Misha Ignatov, with permission.

Figure 72. ***Pogonatum inflexum***, an endohydric soil moss. Photo from Digital Museum, Hiroshima University, with permission.

Figure 73. ***Plagiomnium maximoviczii***, an endohydric species. Photo from Hiroshima University Digital Museum of Natural History, with permission.

Figure 74. ***Plagiomnium cuspidatum***, a soil moss with endohydric water transport. Photo by Hermann Schachner, through Creative Commons.

Figure 75. ***Plagiomnium vesicatum***, an endohydric moist forest soil moss. Note the wide spacing of the leaves – a morphology that is unsuitable for good ectohydric transport. Photo from Digital Museum, Hiroshima University, with permission.

Figure 76. ***Hookeria acutifolia***, a moist forest species with poor desiccation tolerance. Photo by Steve Joya, permission pending.

Proctor (1999) likewise examined a number of bryophytes to determine their osmotic potential. He found that the leafy ones (mosses and leafy liverworts) have a full turgor osmotic potential of -1.0 to -1.5 MPa, whereas the multistratose thallose liverworts have -0.5 to -1.0 MPa.

The full turgor content of water varies with season, ranging 100-300% in bryophytes from well-drained habitats. But Proctor found that the highest turgor occurs in the new growth. The cell walls are highly extensible in most of the thallose liverworts and such drought-tolerant mosses as ***Syntrichia ruralis*** var. ***arenicola*** (Figure 77) and ***Racomitrium lanuginosum*** (Figure 78), but it is quite low in certain leafy liverworts with very rigid cell walls. Unlike Ochi (1952), Proctor found that variations in water relation parameters seem to bear little relationship to habitat for most bryophytes. He attributed this lack of relationship to the consideration that they are usually only metabolically active when they are fully hydrated.

Some bryophytes can tolerate turgor up to 1400% of their dry mass [***Dumortiera hirsuta*** (Figure 79) & ***Conocephalum conicum*** (Figure 80)] (Proctor *et al*. 1998). On the other hand, xerophytic mosses such as ***Syntrichia ruralis*** (Figure 77) and ***Andreaea alpina*** (Figure 81) reach full turgor at only 110%.

Figure 77. ***Syntrichia ruralis*** var. ***arenicola***, a drought-resistant moss with very extensible cell walls. Photo by Michael Lüth, with permission.

Figure 78. ***Racomitrium lanuginosum***, a drought-resistant moss with very extensible cell walls. Photo by Janice Glime.

Water Content

Given sufficient water, water content is related to the cell's osmotic potential. Low water content seems to be related to a xeric habitat (Hernández-Garcia *et al.* 1999), suggesting tolerance rather than the avoidance that might be obtained by maintaining high osmotic potential. In the xeric and mesic pine forests of Tenerife, water content of all mosses tested was <140% of dry mass. ***Hedwigia ciliata*** (Figure 82), ***Grimmia laevigata*** (Figure 83), ***G. trichophylla*** (Figure 84), and ***Pterogonium gracile*** (Figure 85), the rock dwellers, have the lowest field water content and fastest absorption and water loss rates among the species. ***Polytrichum juniperinum*** (Figure 86), ***Bartramia stricta*** (Figure 87), and ***Anacolia webbii*** (Figure 88) have the highest field water content and slowest water absorption and loss rates. The highest drought tolerance occurs in ***H. ciliata***, ***B. stricta***, ***G. laevigata***, and ***G. trichophylla***.

Figure 79. ***Dumortiera hirsuta*** showing hairs on edges of thalli and a turgid condition. Photo by Li Zhang, with permission.

Figure 80. ***Conocephalum conicum***, a liverwort that can tolerate turgor up to 1400% of its dry mass. Photo by Dick Haaksma, with permission.

Figure 81. ***Andreaea alpina***, a xerophytic moss that can only tolerate turgor up to 110% of dry weight. Photo by Andrew Hodgson, with permission.

Figure 82. ***Hedwigia ciliata***, a very drought-tolerant species. Photo by Michael Lüth, with permission.

Figure 83. ***Grimmia laevigata***, a rock-dweller with low water content and rapid water uptake. Photo by Jonathan Sleath, with permission.

Figure 84. ***Grimmia trichophylla***, a rock-dweller with low water content and rapid water uptake. Photo by Michael Lüth, with permission.

Figure 85. ***Pterogonium gracile***, a rock-dweller with low water content and rapid water uptake. Photo by David Holyoak, with permission.

Figure 86. ***Polytrichum juniperinum***, an endohydric moss with high water content and slow water absorption. Photo by Keith Bowman, with permission.

Figure 87. ***Bartramia stricta***, a moss with high water content and slow water absorption. Photo by Michael Lüth, with permission.

Figure 88. ***Anacolia webbii***, a rock-dweller with low water content and rapid water uptake. Photo by Jan-Peter Frahm, with permission.

Nevertheless, most bryophytes apparently do not exhibit the low **water capacity** (50-250%) that permits some seed plants and lichens to survive areas with very low rainfall (During 1992). Known **water capacities** (percent of wet mass relative to dry mass) in bryophytes mostly fall into the high water capacity range of 650-1700% (During 1992), except for endohydric taxa, ranging 190-577% (Coufalová 1951). For example, the damp forest leafy liverwort ***Bazzania trilobata*** (Figure 89) at saturation had a moisture content of 1300% of its dry mass (Sollows *et al*. 2001).

Figure 89. ***Bazzania trilobata***, a damp forest species with a saturation moisture content of ~1300% dry weight. Photo by Jan-Peter Frahm, with permission.

Nichols (1918) reported that ***Sphagnum*** (Figure 63) pads, used for bandages in World War I, could absorb up to 22 times their mass (water capacity = 2200%), making them 5-6 times as absorptive as cotton pads. Other bryophytes, as in some South African montane areas, survive on the water they collect from early morning mist in low-lying clouds (Russell 1982), suggesting that these bryophytes may indeed have low water capacities. Furthermore, many bryophyte taxa are tolerant of very low water contents (5-10% of dry mass), resuming photosynthesis upon remoistening (Proctor 1990).

It appears that at least for some bryophytes, it is best to be wet or be very dry. Water pressure in the range of –100 to –200 MPa is best for survival in a dry state (Proctor 2001). Akande (1984, 1985) has examined the effects of the degree of dehydration on Nigerian bryophytes and found that those maintained at 0% humidity for one week and for one month both resumed respiration more quickly than those maintained for the same time period at 32% and 54% (Akande 1984). He found that the leafy liverwort ***Mastigolejeunea florea*** is less desiccation-tolerant than the two mosses studied, but all three taxa did have individuals that survived at 0%, 32%, and 54% relative humidity at ambient temperature (Akande 1985).

Water-logging

Despite their needs for high water content, bryophytes cannot afford to be too wet or they are unable to carry out photosynthesis. Acquiring CO_2 must occur through the leaf surface, and a continuous layer of water interferes with that transfer. Silvola (1991) found that in all the boreal forest mosses he tested except ***Polytrichum commune*** (Figure 54-Figure 55), photosynthesis decreased when the water content exceeded a certain optimal level (see also Williams & Flanagan 1991). It is likely that the leaf lamellae provided air spaces for CO_2 transfer in ***P. commune***. Many ***Sphagnum*** species suffer similarly from water-logging.

Inducible vs Constitutive Desiccation Tolerance

As recently as 2011, Green *et al*. reviewed the literature and reported that bryophytes appear to all be constitutive. To support this they cite that no protein synthesis is required upon rehydration before metabolism can commence. Bryophytes furthermore appear to always be protected from desiccation mortality. Further support is the constant presence of high sucrose levels. And the cellular structure is usually maintained during desiccation.

Both **constitutive** (always present; fully desiccation tolerant) and **inducible** [produced when drying conditions occur; previously known as modified desiccation-tolerant (Oliver *et al.* 1998)] **desiccation tolerance** exist among bryophytes (Stark *et al*. 2013). Those with **constitutive desiccation tolerance** (**CDT**) are not dependent on the rate of drying to determine their recovery, whereas those that depend on **inducible desiccation tolerance** (**IDT**) are. Reduced or no desiccation tolerance following rapid drying is generally an indicator that the plants are IDT plants. Tracheophytes, with the exception of some ferns (Watkins *et al*. 2007), are IDT plants (Oliver *et al*. 1998, 2000), whereas bryophytes are mostly CDT plants (Toldi *et al*. 2009), hence their high ability to survive drying.

Those bryophytes with **constitutive desiccation tolerance** (**CDT**) are not dependent on the rate of drying, whereas those with only **inducible desiccation tolerance** (**IDT**) are. Therefore, the IDT plants, including IDT bryophytes, are likely to die when exposed to rapid drying.

But bryophytes can use both strategies. Stark and coworkers have investigated the inducible protections that permit bryophytes to survive desiccation. Those bryophytes that survive slow drying but not rapid drying provide us with evidence that something happens during that slow drying process, and that happening provides the inducible desiccation tolerance (Stark *et al*. 2013). Bryophytes also possess constitutive desiccation tolerance, a tolerance that is common among terrestrial bryophytes. For example, the desert moss ***Pterygoneurum lamellatum*** (**Pottiaceae;** Figure 7) exhibits both a constitutive and an inducible response. The bryophyte tolerance strategy couples **constitutive** cellular protection during dehydration with the **induction** of a recovery/repair mechanism upon rewetting (Oliver *et al*. 2005; Toldi *et al*. 2009; Stark & Brinda 2015).

More recently, Stark and Brinda (2015) have found that not only can a desert moss have both inducible and constitutive desiccation tolerance, but it can have each in different parts of the same shoot at the same time or in different stages in the life cycle. Stark and Brinda propose that as the sporophyte grows older, the presence of sugars in the sporophyte facilitates desiccation tolerance. This would help to explain the greater danger of death by desiccation in the early embryonic stage before significant sugar accumulation occurs. At the same time, the early embryo exhibits inducible desiccation tolerance (IDT) and requires slow desiccation, usually not a problem within the protection of the apical gametophyte leaves. As the embryo develops and the seta emerges from these protective leaves, the sporophyte changes from IDT to partially CDT. Stark and Brinda suggest that this evolutionary change resulted from selection pressures of intermittent drying in this exposed sporophyte. This exposed sporophyte tissue is most likely subject to faster rates of desiccation, making an inducible system inadequate to meet the time demands and selecting for the constitutive desiccation tolerance. The presence of a waxy cuticle in the capsules of ***Funaria hygrometrica*** (Figure 26) provide an example of this CDT (Budke *et al*. 2011, 2012, 2013).

Stark and Brinda (2015) concluded that once the seta elongation phase reaches the stage of capsule expansion, sucrose imported from the gametophyte (Renault *et al.* 1992) should be present in the sporophyte, endowing the sporophyte with the raw materials needed to tolerate rapid drying (Stark & Brinda 2015). In ***Acaulon muticum*** (Figure 92), small vacuoles are present in the placental region of the sporophyte-gametophyte junction (Rushing & Anderson 1996). These abundant vacuoles may be present in the embryonic sporophyte as well, where they could provide protection from water stress in the rapidly growing sporophyte.

Wolkers *et al.* (2001) had already suggested that a slower rate of drying may permit the proteins and sucrose to interact in a more protective manner. For example, in ***Physcomitrella patens*** (Figure 21, Figure 90) and ***Syntrichia ruralis*** (Figure 93), a slow drying treatment induces the production of either ABA (see below) or dehydrin, or both (Werner *et al.* 1991; Hellwege *et al.* 1994; Cuming *et al*. 2007). When ABA is applied to the outside of ***Exormotheca holstii*** (Hellwege *et al.* 1994), it elevates sucrose levels and increases protection against rapid drying (see also Pence 1998; Oldenhof *et al.* 2006). Koster *et al*. (2010) demonstrated the genetic connection between ABA and the expression of several homologs to stress proteins, including two dehydrin-like proteins. The only problem with this logic is that the natural presence of ABA is still unknown in ***Physcomitrella patens*** and ***Syntrichia ruralis*** (Stark & Brinda 2015).

Figure 90. ***Physcomitrella patens*** sporophyte, a species in which a slow drying treatment induces the production of either ABA or dehydrin. Photo from Ralf Reski Lab, through Wikipedia Commons.

In ***Aloina ambigua*** (Figure 91), Stark and Brinda (2015) considered that the seta may elongate too fast for the inducible desiccation tolerance system to respond. This exposed tissue may therefore rely on the constitutive system to provide desiccation tolerance for the developing capsules.

Figure 91. ***Aloina ambigua*** with capsules. The seta may grow too rapidly in this species for inducible desiccation tolerance to protect it. Photo by Michael Lüth, with permission.

Hardening

Hardening is a phenomenon known for flowering plants, but the concept is usually associated with preparation for winter. Beckett *et al*. (2005) induced desiccation hardening in the moss ***Atrichum androgynum*** (Figure 11) by reducing the relative water content of apical portions for 1/2 to 3 days, followed by storage fully hydrated for another day. Plants were then desiccated for 16 hours over silica gel, and the recovery of PSII during rehydration was monitored. Hardening affected photosystem II (PSII) before desiccation, decreasing its efficiency, especially at saturating light intensities. Upon rehydration, however, hardened plants recovered their PSII activity more quickly and greatly increased the non-photochemical quenching in the first few hours compared to those plants not subjected to hardening. Beckett *et al*. concluded that hardening shifts the photosynthetic apparatus from a state of high efficiency to one of less efficiency but having a photoprotected state.

Hardening can confound physiological experiments when comparing desiccation tolerance. Once hardened, the plant is likely to receive the benefits in desiccation resistance for a prolonged period of time, such that a rehydration period of 24-72 hours may not remove that benefit (Bopp & Werner 1993; Stark *et al*. 2014). Instead, regenerates from fragments (regenerated more than once to eliminate prior hardening) or plants grown from spores may be necessary to create plants that have no prior desiccation experience, hence no hardening (Stark & Brinda 2015).

Figure 92. ***Acaulon muticum***, a species with small vacuoles in the placental region that may protect the sporophyte from water stress. Photo by Michael Lüth, with permission.

Desiccation-induced Changes

Iljin (1953, 1957) considered that mechanical injury to the protoplast membranes during the drying and rewetting processes is the primary cause of desiccation sensitivity. He considered the tensions that develop in cells during dehydration, pulling protoplasm inward as the vacuoles shrink and cell walls pulling membranes outward, are the primary causes of lethal injuries in drought-sensitive species. Drought-tolerant plants mitigate these tensions by such cellular aspects as reduced cell size, small or absent vacuoles, lack of plasmodesmata, easily deformed cell walls, and reduced osmotic pressure. For example, small cytoplasmic vesicles (vacuoles) are present in such desiccation-tolerant species as ***Syntrichia ruralis*** (Figure 93), ***Neckera crispa*** (Figure 94), ***Pleurozium schreberi*** (Figure 64), and ***Triquetrella papillata*** (Figure 95) (Oliver & Bewley 1984). But this does not hold true for all species – in the desiccation-tolerant ***Ceratodon purpureus*** (Figure 96-Figure 98) and ***Didymodon vinealis*** (Figure 99), the vacuoles are quite large. And the desiccation-intolerant ***Cratoneuron filicinum*** (Figure 40) does not have large vacuoles. **Plasmodesmata** (microscopic channels that traverse cell walls of plant and some algal cells, enabling transport and communication between them) likewise do not seem to be related to desiccation-tolerance, but these are difficult to see and often require electron microscopy for viewing.

Figure 93. ***Syntrichia ruralis***, a species in which slow drying induces the production of ABA. Photo by John Game, with permission.

Figure 94. ***Neckera crispa***, a species with small cytoplasmic vesicles (vacuoles). Photo by David Holyoak, with permission.

Figure 95. ***Triquetrella papillata*** from New Zealand, a species with small cytoplasmic vesicles (vacuoles). Photo by Jan-Peter Frahm, with permission.

Figure 96. ***Ceratodon purpureus***, a desiccation-tolerant species dry on a rock. Photo by Michael Lüth, with permission.

Figure 97. ***Ceratodon purpureus*** hydrated on a rock. Photo by Michael Lüth, with permission.

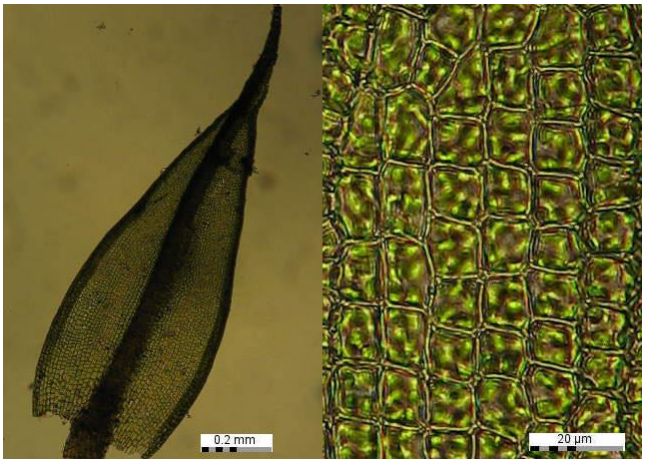

Figure 98. ***Ceratodon purpureus*** leaf and leaf cells, a desiccation-tolerant species with large vacuoles. Photo by Tom Thekathyil, with permission.

Figure 99. ***Didymodon vinealis***, a desiccation-tolerant species with large vacuoles. Photo by Michael Lüth, with permission.

Henckel and Pronina (1968, 1969, 1973) suggest that those plants that are drought-tolerant are continuously prepared for desiccation, *i.e.*, have constitutive desiccation tolerance. However, this theory likewise did not fit the evidence presented by slow vs rapid drying in bryophytes. Bewley (1979) suggested that instead, three factors are critical to desiccation tolerance:

1. limiting damage during desiccation to a reparable level
2. maintaining physiological integrity in the dry state so that metabolism can be reactivated quickly upon rehydration
3. putting repair mechanisms into effect upon rehydration, in particular to retain or regain integrity of membrane and membrane-bound organelles.

As bryophytes desiccate, a series of changes occurs. In ***Physcomitrella patens*** (Figure 21, Figure 90), these changes include plasmolysis, chloroplast remodelling, and microtubule depolymerization, as demonstrated by desiccation for more than one month to 10% of fresh weight (Wang *et al*. 2009). Nevertheless, Wang and coworkers found that the membranes retain their integrity. These changes involved 71 responsive proteins. Most of these were involved in metabolism, cytoskeleton, defense, and signaling. But not all changes seem to be that of repair

or stability. Cytoskeletal protein degradation might cause cytoskeletal disassembly and resulting changes in cell structure. **Late embryogenesis abundant proteins (LEA proteins)** and reactive oxygen species-scavenging enzymes are among those prominently induced, possibly helping to reduce the damage caused by desiccation. Oliver *et al*. (2004) likewise found that the LEA proteins were the most abundant transcripts associated with drying tissues. They suggest that the LEA proteins might play a role in recovery from desiccation.

Oliver *et al*. (2004) took a genetic approach to understanding desiccation tolerance, using the desiccation-tolerant ***Syntrichia ruralis*** (Figure 93). They found that the **transcriptome** (set of all RNA molecules, including mRNA, rRNA, tRNA, and other non-coding RNA transcribed in a cell) has a diverse population of transcripts that reflects a period of metabolic upheaval in the gametophyte cells. Much of the emphasis in this transcriptome is on the protein synthesis machinery, ion and metabolite transport, and the biosynthesis and repair of membranes. When gametophytes are rehydrated, there is a large number of transcripts that code for enzymes involved in oxidative stress metabolism and phosphorylating activities.

When ***Pterygoneurum lamellatum*** (Figure 7) is subjected to very rapid drying, it is severely damaged throughout the entire shoot except the shoot apex (Stark *et al*. 2013). This damage results in slower growth rates, fewer regenerative shoots, and a damaged photosynthetic system as demonstrated by alterations in fluorescence.

Cell Contents

As one might expect, cell contents respond to desiccation stress. In the mosses ***Bryum argenteum*** (Figure 100) and ***Didymodon vinealis*** (Figure 101) from cryptogamic crusts, the free proline content was significantly greater than in those from a typical (wetter) grassland (Xu *et al*. 2005).

Figure 100. ***Bryum argenteum*** in crack in parking lot, a species that manufactures proline in dry habitats. Photo by Paul Davison, with permission.

In the moss ***Plagiomnium acutum*** (Figure 103), concentrations of proline, soluble sugar, and reducing sugar all increase noticeably during dehydration, reaching maximum concentration after 12 hours (Li *et al*. 2009). As the membrane permeability increases, activities of protective enzymes likewise increase, including SOD, CAT, and POD. DNA degrades gradually, with only some of the low molecular weight fragments remaining. Upon rehydration, all of these changes reverse. ***Physcomitrella patens***, like ***Plagiomnium acutum***, accumulates the osmoprotectants altrose, malitol, ascorbic acid, and proline when subjected to drought stress (Erxleben *et al*. 2012).

Figure 101. ***Didymodon vinealis***, a cryptogamic crust species that maintains high concentrations of proline in dry conditions. Photo by Michael Lüth, with permission.

Figure 102. ***Physcomitrella patens***, a species that accumulates altrose, malitol, ascorbic acid, and proline in response to drought stress. Photo by Michael Lüth, with permission.

Figure 103. ***Plagiomnium acutum***, a moss that demonstrates increases in proline, soluble sugar, and reducing sugar during desiccation. Photo by Liu; permission pending.

Cruz de Carvalho *et al*. (2015) found that the low water potentials in dehydrating cells of the aquatic moss ***Fontinalis antipyretica*** (Figure 104) is coupled with osmoregulation due to increase of such soluble materials a soluble sugars and compatible inorganic ions. These increase turgor pressure. In addition to its role as an osmolyte, sucrose stabilizes membranes and proteins through **vitrification**, *i.e.*, by creating glasslike substances. When the moss was dehydrated slowly, the cell walls became more elastic, permitting cell shrinkage that maintained turgor and helped to preserve metabolic functions. However, in rapid drying, there was a loss of turgor and osmotic potential. Although the sucrose content increased, rehydration of the fast-dried samples resulted in 50% loss of sucrose through cell leakage as a result of cell membrane rupture. Slowly dehydrated leaves, on the other hand maintained their sucrose content upon rehydration. The thick mats of long dangling ***Fontinalis antipyretica*** facilitates slow drying of this species in nature.

Sucrose acts as an osmotic "spacer" in membranes (Werner *et al*. 1991; Oldenhof *et al*. 2006; Cruz de Carbalho *et al*. 2014). This is accompanied by ABA mediation of protein synthesis, strengthening the cellular glasses typical of inducible desiccation tolerance in mosses, as shown in ***Physcomitrella patens*** (Oldenhof *et al*. 2006).

Chloroplast Responses

Bryophyte chloroplasts undergo ultrastructural changes when undergoing desiccation. Chloroplasts become smaller and more spherical with a less-well defined internal structure (Noailles 1978). The general lamellar structure collapses, with the **thylakoids** (chlorophyll vesicles) becoming dispersed; starch granules are lost. This response is similar to that induced by ABA in experiments related to freezing tolerance (Nagao *et al*. 2005).

Bryophyte chloroplasts contain **plastoglobuli** (Tucker *et al*. 1975; Oliver & Bewley 1984) in groups within the stroma. These increase in size and number during dehydration in ***Syntrichia ruralis*** (Figure 93) (Tucker *et al*. 1975).

It appears that the chloroplasts may be altered by desiccation in other ways we do not fully understand. I found that I could not extract chlorophyll effectively from dry ***Fontinalis*** spp. (Figure 104) using acetone unless I rewet them for about 15 seconds first. Tuba (1984) reported a possible decoupling of the chlorophyll from its protein, but later (Tuba 1985) attributed that apparent phenomenon to the separation of upper and lower shoots and the extraction process. In fact, he stated that the chlorophyll *a* and *b* remained unchanged during daily desiccation and early rehydration of ***Syntrichia ruralis*** (Figure 93). He concluded that the **neoxanthin** (a carotenoid pigment), due to its hydrophilous nature, may be adaptive in binding the **LHCP** (light-harvesting chlorophyll protein) to the **PS II** chlorophyll core, thus stabilizing the LHCP.

One factor in the protection of chlorophyll against light damage during desiccation is that the pigment **zeaxanthin** can bind to the chlorophyll-containing thylakoid protein (Deltoro *et al*. 1998; Heber *et al*. 2001). On the other hand, loss of chlorophyll fluorescence during drying of pre-darkened mosses suggests that energy dissipation in the desiccated mosses is unrelated to zeaxanthin availability.

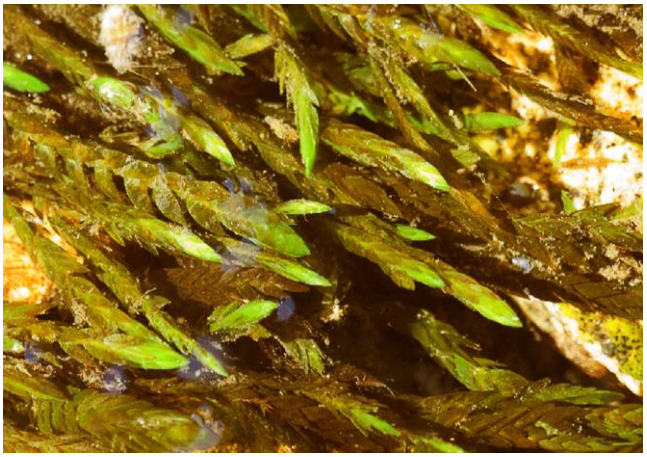

Figure 104. ***Fontinalis antipyretica***, a moss that, when dry, has a delay before its chlorophyll dissolves in alcohol, suggesting that the chlorophyll may be complexed during dehydration. Projecto Musgo, through Creative Commons.

Even among the desiccation-tolerant bryophytes, the rate of recovery of chlorophyll fluorescence varies widely upon rehydration (Proctor 2010). For example, some species have high values of F_v/F_m in the early minutes of recovery, accompanied by low absolute values of F_m. But most recovery curves are logistic (S-shaped curve that starts slow, goes up exponentially, than approaches horizontal) for photosynthetic CO_2 fixation in the light.

Photosynthesis

Lee and Stewart (1971), using ***Calliergonella cuspidata*** (Figure 58), ***Climacium dendroides*** (Figure 105), and ***Hypnum cupressiforme*** (Figure 46-Figure 47), found that the degree of desiccation tolerance correlates with the degree of moisture stress experienced in the habitat. This tolerance is expressed as a rapid recovery of photosynthetic rate in taxa from habitats with severe moisture deficits, whereas those from habitats with no appreciable moisture deficits lose photosynthetic capability more quickly and are slower to recover.

Seel *et al*. (1992) made similar comparisons using ***Syntrichia ruralis*** (Figure 93), ***Bryum pseudotriquetrum*** (Figure 106), and ***Dicranella palustris*** (Figure 107) from a range of habitats with different water availabilities. All three species become photosynthetically inactive when dried to a water content of 100-200%. But recovery differs. The xeric ***Syntrichia ruralis*** from sand dunes recovers to its pre-desiccation photosynthetic rates, but its rate of recovery is affected by irradiance during its desiccation. Those mosses from hydric habitats, when rehydrated, have partial resumption of their photosynthetic electron transport if they are dried in the dark, but if they are dried in even low light they did not resume their photosynthetic activity. Their symptoms indicate a lasting photoinhibition of photosynthesis following rehydration. On the other hand, the desiccation-tolerant ***Syntrichia ruralis*** (Figure 93) experiences significant photoinhibition only when receiving continuous high irradiance (1200 $\mu mol\ m^{-2}\ s^{-1}$) while hydrated. But if it is dehydrated while receiving high irradiance it shows less evidence of photoinhibition after rehydrations. Desiccation at low irradiance has no effect following rehydration. Leaf curling reduces photon flux absorption by 50-60% in dry mosses compared to hydrated mosses, although it is

possible that changes in optical properties of papillae may contribute to that reduction.

Figure 105. ***Climacium dendroides***, a species that shows acclimation to its habitat adjusting its tolerance to the moisture stress experienced in the habitat. Photo by Michael Lüth, with permission.

Figure 106. ***Bryum pseudotriquetrum***, a species that becomes photosynthetically inactive when its water content is decreased to 100-200%. Photo by Michael Lüth, with permission.

Figure 107. ***Dicranella palustris***, a species that becomes photosynthetically inactive when its water content is decreased to 100-200%. Photo by Michael Lüth, with permission.

Both thylakoid lipids and chlorophyll reduction coincide with the loss of photosynthesis in dehydrating ***Atrichum androgynum*** (Figure 11) (Guschina *et al*. 2002).

The desert moss ***Syntrichia caninervis*** (Figure 12) recovers quickly when shoots are remoistened in the dark (Zhang *et al*. 2011). This is an advantage for this moss that receives much of its moisture from dew, a night-time phenomenon. Its leaf hairs are able to trap the dew (and also fog and raindrops) and direct them to the base of the leaf where it rapidly is absorbed. The chlorophyll fluorescence has a narrow optimum range. The moss seems to experience no damage to its membranes or organelles and reaches 90% of its 30-minute photosynthetic yield within the first minute of rehydration. This permits it to take rapid advantage of small amounts of moisture from fog, dew, snow, and short rainfall events.

Mitochondria

The mitochondria [cell organelle that generates most of the cell's supply of **ATP** (adenosine triphosphate), used as a source of chemical energy] become deformed as they dehydrate, becoming small and rounded (Noailles 1978). Internal cristae may be greatly reduced in size or lost completely.

Nuclei

The nuclei seem to suffer little from the effects of desiccation, retaining their normal size (Noailles 1978).

Vacuoles and Vesicles

Normal bryophyte cells have one to several large vacuoles (Noailles 1978). During dehydration, these break down to form numerous small vesicles (Oliver & Bewley 1984). It appears that ABA may be involved in this transformation, since the response is similar to that induced by ABA during freezing (Nagao *et al*. 2005). ABA-treated cells have slender chloroplasts, and the quantity of starch grains is reduced in comparison with those of non-treated cells.

Membranes

Membranes in general suffer from dehydration, including thylakoids, cristae, and cytoplasmic membranes like endoplasmic reticulum and dictyosomes, resulting in the shrinkage of organelles (Noailles 1978). The chloroplast membrane itself may exhibit clefts (Tucker *et al*. 1975). It is the ability to repair this damage that makes many bryophytes desiccation tolerant (Li *et al*. 2009).

Both desiccation-tolerant and intolerant bryophytes leak electrolytes when rehydrated (Gupta 1976, 1977, 1979), as do dry viable seeds, lichens, pollen grains, fungi, and their spores (Simon 1974, 1978). This leakage lasts only a few minutes except in cases of permanent damage (Oliver & Bewley 1984). Oliver and Bewley (1984) listed amino acids, mono-, di-, and tri-saccharides, sugar alcohols, organic acids, hormones, phenolics, phosphates, and various electrolytes as leaked substances during rehydration, although the leakage often lasts only minutes.

The desert moss ***Syntrichia caninervis*** (Figure 12) is the dominant species in the Gurbantunggut Desert, a cold desert in Central Asia. Wu *et al*. (2012) investigated the

membrane changes during desiccation of this species. There are no significant changes in electrical conductivity of the rehydration water during dehydration or rehydration. There also appears to be no ultrastructural damage to the membrane during dehydration or rehydration, but there are major changes in cellular ultrastructure. Wu and coworkers suggest three possible explanations for the apparent disruption of the membranes in desiccated state:

1. Adaptive morphological features of the leaf that remain intact permit the leaves to regain membrane integrity rapidly upon rehydration.
2. The moss becomes dormant rapidly, maintaining some level of membrane integrity.
3. Soluble sugars and free **proline** (constitutive substances) increase rapidly during desiccation, contributing to membrane stabilization.

Plasmolysis

One of the consequences of desiccation can be **plasmolysis** of the cells (shrinkage of protoplast away from cell wall) (Oliver & Bewley 1984). In some cases, very narrow elongate cells seem to resist plasmolysis, perhaps due to the small cell volume and strong adhesion to the cell walls. But plasmolysis can occur in bryophytes and can result in cell damage to both the plasma membrane and the cell wall.

In ***Didymodon vinealis*** (Figure 99) and ***Triquetrella papillata*** (Figure 95), the dehydrated cells contract to 50-70% of the original volume (Moore *et al*. 1982). The cell walls contract, permitting the protoplasm to fill the cell and preventing entry of air into the drying cells.

It appears that at least the liverwort ***Sphaerocarpos donnellii*** (Figure 108) is able to partially compensate for this plasmolysis damage (Grusak *et al*. 1980), where both normal and plasmolyzed tissues are composed primarily of hemicellulose and cellulose. But in plasmolyzed cells, labelled C^{14} is considerably lower than in normal cells. Rather, these cells have higher radioactivity in pectin and hemicellulose and less in cellulose, suggesting a possible mechanism for enhancing wall stability. This transformation would provide numerous sites for cross-linkage between the cellulose microfibrils as walls regenerate.

Figure 108. ***Sphaerocarpos donnellii***, a species that has the ability to partially compensate for plasmolyzed cells. Photo by Belinda Lo, through Creative Commons.

Liverworts

Liverworts have received surprisingly little attention relative to their drought tolerance strategies. Granted, these plants seem to require higher moisture conditions in general, but their presence as epiphytes in many areas attests to the ability of at least some liverworts to survive long periods of drought, and certainly the thallose liverworts of flood plains and other seasonal habitats provide another set of highly desiccation tolerant or desiccation avoider species.

Pressel *et al*. (2009) found that liverworts undergo "profound" cytological changes during dehydration. As in tracheophytes and mosses, these include fragmentation of the vacuole, rounding of chloroplasts and mitochondria with thylakoids, and cristae becoming rearranged but remaining undamaged. Furthermore, chlorophyll fluorescence returns to normal within 24-48 hours during rehydration. And like the mosses, their dehydration and rehydration are associated with the depolymerization and repolymerization of the cortical microtubule cytoskeleton. But unique among the bryophytes is the presence of **oil bodies** in liverworts, membrane-bound organelles that take on many shapes among the species (Kozlowski 1921; Kis & Pócs 1997). And these cellular inclusions, long considered only for their taxonomic value, seem to have an important role in liverwort recovery from dehydration (Pressel *et al*. 2009).

Taxonomists have been aware that these oil bodies usually disappear in herbarium specimens, and that they do not reappear upon re-wetting and microscopic observation. But it appears that to see these in herbarium specimens, one must treat the liverworts as nature does – dry them slowly and give them time to recover upon rehydration. It turns out that they remain largely unchanged while they are dry (Pressel *et al.* 2009), but who observes dry specimens under the microscope? Rather, they become flattened when rehydrated and in the six liverworts tested, they require 48 hours to regain their normal shapes, long after the taxonomist has cleaned the microscope slide. Fast drying causes them to disintegrate upon redrying, along with other liverwort organelles. Pressel *et al.* interpreted this initial loss of shape upon rewetting to indicate a shift in soluble carbohydrates or other components into the cytosol, suggesting that these may be crucial energy reserves needed for recovery and desiccation tolerance.

Kronestedt (1983) found that there was seasonal variability in the oil bodies of the floating liverwort ***Ricciocarpos natans*** (Figure 109). But as He *et al*. (2013) made clear, the function of oil bodies in most liverworts still remains unclear.

Figure 109. ***Ricciocarpos natans***, a species with seasonal variability of oil bodies. Photo by Norbert Stapper, with permission.

Habitat Relations

In their review of lichen and bryophyte desiccation and rehydration, Green *et al*. (2011) considered that the rate of recovery may relate to the length of the hydrated activity period. They reported that species that hydrate and then dry rapidly (*e.g.* rock surfaces) recover rapidly. By contrast, those species from habitats that remain wet for a long time recover from dryness more slowly when rehydrated.

Cruz de Carvalho *et al*. (2014) found that even the aquatic moss ***Fontinalis antipyretica*** (Figure 104) can survive slow dehydration, during which both dehydration and rehydration proteins are induced. These protein profiles are similar to those of the terrestrial moss ***Physcomitrella patens*** and ***Syntrichia ruralis***. The proteins associated with photosynthesis and the cytoskeleton were reduced during dehydration. In their place, the cells accumulated proteins involved in sugar metabolism and plant defenses. Upon rehydration the protein accumulation patterns for photosynthesis and the cytoskeleton return to normal levels. However those for sugar accumulation and defense remain high. During fast dehydration, on the other hand, this moss exhibited little change in proteins. Upon rehydration, proteins were leaked. The researchers suggested that bryophytes from contrasting habitats may share common desiccation tolerance mechanisms.

Summary

Bryophytes may be **desiccation tolerant**, surviving dry tissues and beginning photosynthesis upon rehydration, or they may be **drought avoiders**, using structural adaptations and life cycle stages to escape having a dry vegetative plant. The presence of a **central strand** does not seem to correlate with the degree of internal conduction, but habitat does.

Life cycles are a major protector against dry seasons, permitting bryophytes to survive as tubers, gemmae, spores, fragments, and buds. These stages are typically timed to coincide with drought seasons. They are likely to be combined with physiological changes, including dormancy, in the plants as they respond to changes in the environment.

Xeric bryophytes are more likely to have greater internal conduction and faster external conduction than mesic and hydric taxa. It is possible that the central strand may serve as a water reservoir in some taxa. Physiologically, some bryophytes can increase the osmotic value of the cells, and they typically have a high water capacity compared to drought-tolerant seed plants. Desiccation tolerance permits some bryophytes to remain dormant in a vegetative state for as many as 23 years.

During drying, chloroplasts undergo ultrastructural changes, **mitochondria** become **deformed**, and **vacuoles break down** to form smaller vesicles. Nuclei seem to remain intact. At least some taxa apparently protect their cell membranes from oxidative destruction. **ABA** seems to induce the production of H_2O_2 in light, reduce the loss of K^+, and may facilitate the reduction of oxygen release from photosystem II. Despite these adaptations, plasmolysis can occur and membranes can become damaged, requiring repair upon rehydration.

Liverworts may have one more trick in their cells – **oil bodies** that disappear rapidly upon rehydration, apparently converting oils into more usable forms of stored energy that could contribute to repair.

Acknowledgments

This chapter has benefitted from the help of Beth Scafone and Medora Burke-Scoll, who helped me tow the line in explaining things without leaving too much to one's imagination, but at the same time not repeating myself. I appreciate Lloyd Stark's generosity in sharing the information he found in reviewing papers and in summarizing the seeming conflicts in the literature regarding ***Sphagnum***.

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CHAPTER 7-6

WATER RELATIONS: REHYDRATION AND REPAIR

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CHAPTER 7-6

WATER RELATIONS: REHYDRATION AND REPAIR

Figure 1. ***Palustriella commutata*** rehydrating in the spring runoff. Photo by Michael Lüth, with permission.

Uniqueness of Bryophytes

As Vitt *et al*. (2014) stated, desiccation tolerance is the ability to survive complete loss of free water, a trait found in many bryophytes. One striking difference between bryophytes and tracheophytes is that if you put a dry bryophyte into water, in most cases you will see an immediate change in turgor, and leaves will spread and take their normal hydrated position – one that presents the greatest surface area to the light and atmospheric CO_2. This is particularly striking in mosses from frequently dry habitats, such as ***Hedwigia ciliata*** (Figure 2) from rocks or ***Syntrichia ruralis*** (Figure 3, Figure 21) from open sand. In many mosses, such as ***Polytrichum*** s.l. (Figure 8, Figure 10) and ***Syntrichia***, this ability to spread the leaves when moist and appress them to the stem when dry is the result of enlarged or hyaline leaf base cells (Figure 4) that absorb water easily and swell, forcing the leaf away from the stem.

Figure 2. ***Hedwigia ciliata*** growing on rock. Photo by Janice Glime.

Figure 3. ***Syntrichia ruralis*** on sand dunes at Harlech, Wales. Photo by Janice Glime.

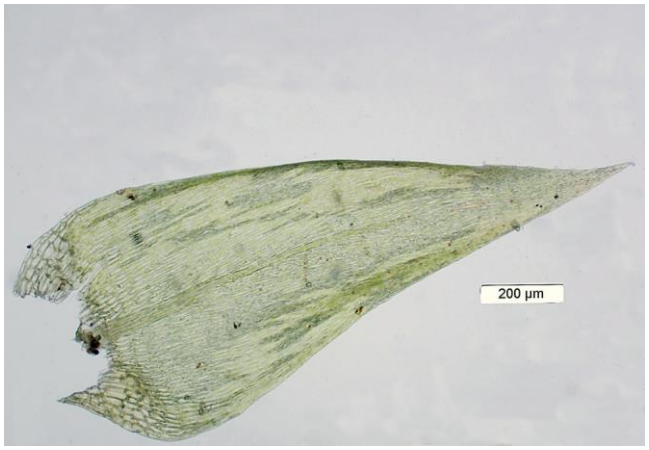

Figure 4. ***Brachythecium rivulare*** decurrent leaf base with enlarged hyaline cells at leaf base. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Bryophytes can look dead, but come back to life when rehydrated. For example, Longton and Schuster (1983) noted that both ***Pleurozium schreberi*** (Figure 5) and ***Bryum argenteum*** (Figure 6) can have dark or moribund lower shoot tissues, but new shoots and protonemata can regenerate from them. Clymo and Duckett (1986) made similar observations on ***Sphagnum***.

Figure 5. ***Pleurozium schreberi*** with moribund lower shoot tissues exposed. Photo by Janice Glime.

Figure 6. ***Bryum argenteum*** showing the moribund lower leaves. Photo from Botany Website, UBC, with permission.

Figure 7. ***Sphagnum girgensohnii***. Note the change in color in lower branches, indicating senescing conditions. Photo by Bernd Haynold through Wikimedia Commons.

Rehydration in mosses is generally very rapid, but some taxa are rather recalcitrant about getting wet inside. ***Polytrichum piliferum*** (Figure 8), common on sand in dry, exposed habitats, and ***Schistidium apocarpum*** (Figure 9), a rock-dweller, can require two hours to become saturated, whereas ***Polytrichum juniperinum*** (Figure 10), a soil moss with wider ecological amplitude than ***P. piliferum***, can become saturated within three minutes (Larson 1981). Larson points out that the surface area to mass ratio is very important in determining the speed of rewetting (Figure 11). The **cuticle** seems to be another contributing factor in mosses like **Polytrichaceae** and **Mniaceae**.

Figure 8. ***Polytrichum piliferum*** in hydrated state. Photo by Janice Glime.

Figure 9. ***Schistidium apocarpum*** in its dry state with leaves wrapped around stem. Photo by Michael Lüth, with permission.

Figure 10. ***Polytrichum juniperinum*** in hydrated state. Photo by Janice Glime.

Duration Survival

Determining the length of time that bryophytes can survive desiccation can be tricky. Although use of herbarium specimens can provide starting dates, these are stored in the dark, which may differ considerably from survival in the light where chlorophyll can be damaged. And one can never be sure how often the moss was wet for examination, often using up resources for repair without having an opportunity to replace them before being put in the dark again and once again desiccated.

Studies to test viability directly after an assortment of desiccation times are rare, requiring careful record keeping and assurance the conditions remain relatively constant over a lengthy period of time. Specimens must then be rehydrated at intervals, requiring multiple specimens and replication, all collected at the same time from one location.

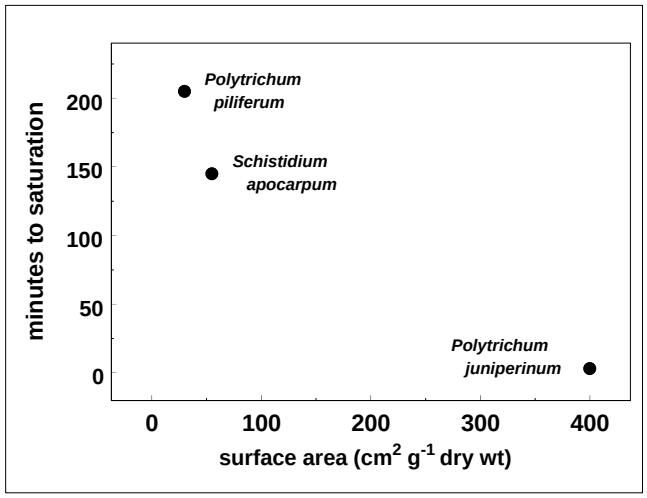

Figure 11. Relationship between surface area and time to saturation upon rewetting of three drought-tolerant mosses. Based on Larson (1981).

Ochi (1952) reminds us that even season of collection will affect the degree to which bryophytes can survive desiccation and the length of time they can remain dry and survive, an interpretation reiterated by Kosokawa and Kubota (1957). For example, Dilks and Proctor (1976b) commented that British species of bryophytes tend to have an increased tolerance to drought in spring and summer.

Hoekstra (2005) concluded that small size was not a limiting factor in desiccation survival longevity. Factors such as membrane deterioration during desiccation affect the length of time an organism can survive the desiccation (Koster *et al*. 2010). Hoekstra (2005) likewise attributed survival to a high level of fatty acid saturation in membranes.

Longevities vary considerably among plants, ranging from a few days in some pollen to decades in some moss spores and even green moss tissue (Hoekstra 2005). In 2000, Alpert (2000) asserted that "some desiccation-tolerant species can survive without water for over ten years." Alpert cited duration periods of adult organisms as 34 years for fungi, 23 years for liverworts, 19 years for mosses, 5 years for ferns and angiosperms, and 1 year for lichens. Hornwort spores can tolerate 21 years of desiccation (Vanderpoorten & Goffinet 2009). Some bryophytes exceed these duration records (Table 1).

Even within a fen, desiccation tolerance can vary widely. When eight fen species were compared, it was the hummock moss species ***Climacium dendroides*** (Figure 12), ***Aulacomnium palustre*** (Figure 13), and ***Tomentypnum nitens*** (Figure 14) that had the highest desiccation survival (>10% of stems after 20 weeks of desiccation). ***Hamatocaulis vernicosus*** (Figure 15), ***Calliergonella cuspidata*** (Figure 16), and ***Bryum pseudotriquetrum*** (Figure 17) had moderate resilience (<10% stem survival after 12 weeks). The lowest survival rates occurred in ***Campylium stellatum*** (Figure 18) and ***Plagiomnium elatum*** (Figure 19) (~0% survival after 6 weeks).

Figure 12. ***Climacium dendroides***, a hummock species with high desiccation survival. Photo by Michael Lüth, with permission.

Figure 13. ***Aulacomnium palustre***, a species that has high desiccation tolerance on hummock tops. Photo by Michael Lüth, with permission.

Figure 14. ***Tomentypnum nitens***, a species with high desiccation tolerance on hummocks. Photo by Michael Lüth, with permission.

Figure 15. ***Hamatocaulis vernicosus***, a species with moderate resilience to desiccation. Photo by Michael Lüth, with permission.

Figure 16. ***Calliergonella cuspidata***, a species with moderate resilience to desiccation. Photo by Michael Lüth, with permission.

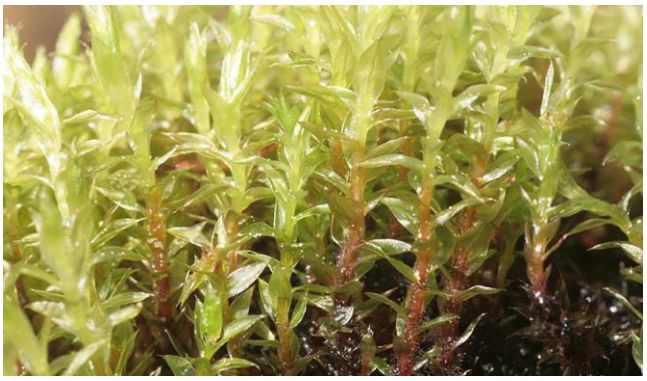

Figure 17. ***Bryum pseudotriquetrum***, a species with moderate resilience to desiccation. Photo by Hermann Schachner, through Creative Commons.

Figure 18. ***Campylium stellatum***, a species with poor survival of desiccation. Photo by Michael Lüth, with permission.

Figure 19. ***Plagiomnium elatum***, a species with poor survival of desiccation. Photo by Michael Lüth, with permission.

Table 1. Bryophytes and known desiccation survival times. Based mostly on Stark *et al*. 2016.

Species	Duration Dry	Reference
Mosses		
Andreaea rothii	13 mos	Proctor 1981
Anisothecium staphylinum	45-48 yr (spores, tubers, or rhizoids in dry soil)	Whitehead 1984
Anoectangium compactum	19 yr	Malta 1921
Anomodon longifolius	2 yr	Richardson 1981
Anomodon viticulosus	45 d	Hinshiri & Proctor 1971
Archidium ohioense	20 yr [4]	Makinde & Fajuke 2009
Barbula torquata	18 mos	Moore *et al*., 1982
Bryum argenteum	2 yr	Richardson 1981
Bryum coronatum	20 yr [4]	Makinde & Fajuke 2009
Dicranella heteromalla	0 d [1]	Streusand & Ikuma 1986
Dicranoweisia cirrata	9 yr	Richardson 1981
Fissidens minutifolius	6 yr [4]	Makinde 1993
Fissidens subglaucissimus	20 yr [4]	Makinde & Fajuke 2009
Fissidens taxifolius	0 d [1]	Streusand & Ikuma 1986
Fontinalis flaccida	3 mos	Glime 2015
Grimmia apocarpa	8 mos	Alpert & Oechel 1987
Grimmia laevigata	10 mos; 10 yr (shoots), 1 mo (protonema)	Alpert & Oechel 1985; Breuil-Sée 1994; Keever, 1957
Grimmia muehlenbeckii	1.5 yr	Richardson 1981
Grimmia pulvinata	<7 yr	Segreto *et al*. 2010
Grimmia elatior	5 yr	Richardson 1981
Grimmia torquata	<7 yr	Segreto *et al*. 2010
Hookeria lucens	~15 d	Dilks & Proctor 1974
Hylocomium splendens	~160 d	Dilks & Proctor 1974
Neckera crispa	~160 d	Dilks & Proctor 1974
Octoblepharum albidum	29 wk (leaves); 20 yr [4]	Egunyomi 1979; Makinde & Fajuke 2009
Orthotrichum rupestre	9 mos; ~2 yr	Alpert & Oechel 1987; Richardson 1981
Plagiothecium undulatum	100 d	Dilks & Proctor 1974
Racomitrium lanuginosum	>239 d	Dilks & Proctor 1974
Rhytidiadelphus loreus	>100 d	Dilks & Proctor 1974
Scorpiurium circinatum	~120 d	Dilks & Proctor 1974
Sphagnum fallax	14 d	Sagot & Rochefort 1996
Sphagnum fuscum	14 d; 0 d [2]	Sagot & Rochefort 1996; Schipperges & Rydin 1998
Sphagnum magellanicum	14 d; 0 d [2]	Sagot & Rochefort 1996; Schipperges & Rydin 1998
Sphagnum [3 spp.]	0 d [2]	Schipperges & Rydin 1998
Syntrichia caninervis	3 yr; 6 yr	Oliver *et al*. 1993; Oliver *et al*. 2005
Syntrichia norvegica	3 yr	Oliver *et al*. 1993
Syntrichia ruralis	3 yr; 14 yr	Oliver *et al*. 1993; Maheu 1922; Stark *et al*. 2016
Tortula muralis	3 yr; 14 yr	Kosnar & Kolar 2009; Glime 2015
Triquetrella papillata	8 wk	Moore *et al*. 1982
13 Antarctic species	<1 yr	Davey 1997
8 fen spp.	8–20 wk	Manukjanová *et al*. 2014
protonemal resting cells	49 yr	Bristol 1916
Liverworts		
Bazzania trilobata	0 d	Sollows *et al*., 2001
Marchantia berteroana	<1 yr	Davey 1997
Oxymitra paleacea	4 yr	Volk 1984
Plagiochila spinulosa	~30 d	Dilks & Proctor 1974
Reboulia hemisphaerica	4 yr	Volk 1984
Riccia canescens	7 yr	Volk 1984
Riccia macrocarpa	23 yr	Breuil-Sée 1993
Riccia macrospora	2 yr	Volk 1984
Riccia marginata	2 yr	Volk 1984
Saccogyna viticulosa	~200 d	Dilks & Proctor 1974
13 species of hepatics [3]	≤20 mos	Volk 1984

[1] shoots allowed to regenerate only 10–14 d

[2] 13 species of *Sphagnum* were shown capable of hardening to DT when partially desiccated at high RHs (Hájek & Vicherová, 2014)

[3] in the genera *Corsinia*, *Mannia*, *Plagiochasma*, and *Riccia*

[4] based on visible presence of neutral red stain in vacuoles upon rehydration

The duration of desiccation that plants can survive is dependent on the antioxidant pool present at the time of desiccation (Kranner *et al*. 2002; Moore *et al*. 2009). This is because longer periods of desiccation result in greater oxidative damage.

Certain events must occur upon rehydration for the bryophyte to survive (Pressel & Duckett 2010). Using moss protonemata, they determined that cell death will occur if these events do not occur. Slow drying will usually prevent these cell death threats.

This raises the question of desiccation survival under desert conditions, where drying can be quite rapid. For leaves, development will be interrupted, but they seem able to resume (Stark 2005). On the other hand, when sporophyte development is interrupted frequently, the sporophyte seems to fail, with only 9 out of 248 surviving during the 4-year study period. Embryonic abortion accounted for 69% of these, whereas 30% was attributable to herbivory. In the Mojave Desert moss ***Crossidium crassinerve*** (Figure 20) required a rain event of at least 2 mm to fully rehydrate. In most cases, the only useful hydration periods occurred in the cooler months of October to April, with a mean hydroperiod of 3.7-4.9 days. Although most dry periods were less than 25 days, Stark recorded them as long as 191 days. In a late winter rain event, the moss patches dried slowly over a period of several days, but during a summer event, the patches were dry in as few as 3 hours.

Figure 20. ***Crossidium crassinerve***, a species in the Mojave Desert where it requires at least 2 mm of rain to fully rehydrate. Photo by Jan-Peter Frahm, with permission.

Resumption of Activity

Upon rehydration, desiccation-tolerant bryophytes generally resume normal activity quickly (Csintalan *et al*. 1999), whereas the resurrection plants among the tracheophytes in the same habitat take much longer (Peterson *et al*. 1994; Marschall & Proctor 1999).

Using the moss ***Anomodon viticulosus*** (Figure 37) and leafy liverwort ***Porella platyphylla*** (Figure 23), both from habitats that dry out frequently, Hinshiri and Proctor (1971) found a consistent pattern of net assimilation upon rehydration. When desiccated up to 22 days at 50% relative humidity in ***Anomodon viticulosus*** (Figure 37) and 60 days in ***Porella platyphylla*** (Figure 23), the plants recovered in 3-4 hours. However, after longer periods, the initial net assimilation was negative, progressively becoming positive during the next several days. After 70 days, respiration in ***Anomodon viticulosus*** is very high in the first 24 hours of rehydration, then drops to normal levels. However, even then recovery is not assured. This negative initial net assimilation explains why frequent desiccation with short periods in which to recover before the next one is usually lethal to the bryophytes. In ***Polytrichastrum formosum*** (Figure 28), full recovery requires 24 hours (Duckett *et al*. 2007).

There are two general strategies that permit drought-tolerant plants to survive periods of desiccation: cellular protection and cellular repair. Those bryophytes that are tolerant of desiccation seem to succeed primarily because of their rapid cellular repair (Oliver *et al*. 1993). According to Oliver (1991), no novel **mRNA**s (messenger RNA; molecule that carries portion of DNA code to other parts of the cell processing) are recruited or favored for translation during desiccation. Rather, in ***Syntrichia ruralis*** (Figure 21), there is a loss of 25 **hydration** proteins (those present in a normal hydrated state), whereas 74 **rehydration proteins** are synthesized upon rehydration. This system, rather than protecting the moss from desiccation as in most tracheophytes, prepares bryophytes for repair. This is probably essential because their one-cell-thick leaves remain at full turgor, carrying out photosynthesis, then become desiccated very rapidly before going into a state of water stress and suspended metabolism (Proctor 2000b).

Figure 21. ***Syntrichia ruralis***, a moss that loses hydration proteins upon drying and synthesizes rehydration proteins upon rewetting. Photo by Michael Lüth, with permission.

Antarctic mosses can suffer severe desiccation for prolonged periods. Rod Seppelt (Bryonet 2007) relates a story of an Antarctic ***Grimmia*** (Figure 22). A student had made a number of attempts at sectioning the dried moss without success. Seppelt suggested wetting the moss first and was amazed to discover, upon examination, that the cells were perfectly intact. When he re-examined the mosses that had been sitting on the lab bench for 15 months, but had been rewet for the sectioning, they had sprouted new shoots!

Figure 22. ***Schistidium chrysoneurum*** (formerly *Grimmia antarctici*) in Antarctica. Photo by Sharon Robinson, through Creative Commons.

Deltoro *et al*. (1998a) compared recovery in seven desiccation-tolerant bryophytes [Figure 23: ***Hedwigia ciliata***, ***Hypnum cupressiforme***, ***Leucodon sciuroides***, ***Orthotrichum cupulatum***, ***Pleurochaete squarrosa***, ***Porella platyphylla*** (Figure 23), and ***Syntrichia ruralis*** (Figure 21)] with that of seven desiccation-intolerant bryophytes [Figure 24: ***Cinclidotus aquaticus***, ***Philonotis calcarea***, ***Lunularia cruciata***, ***Conocephalum conicum***, ***Platyhypnidium riparioides***; ***Barbula bolleana*** (Figure 25-Figure 26), ***Palustriella commutata*** (Figure 1, Figure 27),]. All seven desiccation-tolerant bryophytes experienced full recovery, with many cellular activities back to normal rates within two hours (Deltoro *et al*. 1998a; Marschall & Proctor 1999). However, those species from the hydric and mesic habitats, the desiccation-intolerant ones, were unable to restore their photochemical activity.

Figure 23. Examples of drought-tolerant bryophytes. **Left, top:** ***Hedwigia ciliata***, **Left, Middle:** ***Leucodon sciuroides***, **Left, bottom:** ***Pleurochaete squarrosa***, **Right, top:** ***Orthotrichum cupulatum***, **Right, middle:** ***Hypnum cupressiforme***, **Right bottom:** ***Porella platyphylla***. Photos by Michael Lüth, with permission.

Figure 24. Examples of desiccation-intolerant bryophytes. **Left, top:** ***Cinclidotus aquaticus***, **Left, middle:** ***Philonotis calcarea***, **Left, bottom:** ***Lunularia cruciata***, **Right, top:** ***Conocephalum conicum***, **Right, bottom:** ***Platyhypnidium riparioides***. Photos by Michael Lüth; ***Conocephalum conicum*** photo by Janice Glime.

Figure 25. ***Barbula bolleana*** in a seepage waterfall. Photo by Michael Lüth, with permission.

Figure 26. ***Barbula bolleana***, a desiccation-intolerant moss. Photo by Michael Lüth, with permission.

Figure 27. ***Palustriella commutata***, a desiccation-intolerant species. Photo by J. C. Schou, with permission.

Proctor *et al*. (2007) used ***Polytrichastrum formosum*** (Figure 28) to assess recovery from desiccation. In this endohydric moss, the relative water content (RWC) dropped to 40% before it reduced the net CO_2 uptake to zero. It took only 10-30% RWC upon rewetting for the CO_2 uptake to become positive after 9-18 days of desiccation. Net carbon balance returned after 0.3-1 hours. The F_v/F_m (= variable fluorescence / maximum fluorescence) recovery was inhibited in the light by protein-synthesis inhibitors, but had normal recovery in the dark. Without the inhibitors, the F_v/F_m reached ~80% of pre-desiccation levels within ~10 minutes of re-wetting, but it took 24 hours for full recovery.

Figure 28. ***Polytrichastrum formosum***, a moss that can drop to 40% relative water content before the net CO_2 uptake ceases. Photo by Des Callaghan, with permission.

Even aquatic bryophytes may not die following total desiccation. My experience with boiling ***Fontinalis*** (Figure 29) and with dead-looking mosses following snow-melt is that seemingly dead bryophytes may have living cells that initiate new growth. The desiccated tissues may not recover, but a few cells may be all that are needed to continue the population.

The seemingly drought-intolerant ***Fontinalis antipyretica*** (Figure 29) is actually drought tolerant, provided it is dried slowly (de Carvalho *et al*. 2011). This is consistent with its ability to survive late summer drought in the slow streams and vernal pools where it is common because the recession of water is slow and remaining water will permit the slow drying needed.

Figure 29. ***Fontinalis antipyretica*** in dry stream. This dead-looking moss will recover when water returns to the stream. Photo by Janice Glime.

Leakage and Membrane Repair

Dry mosses are essentially inactive. During this time, membranes often become distorted and leaky (Gupta 1977a. Viable tissues may become leaky due to the shock of sudden immersion, whereas injured or dead cells leak due to membrane disruption. Cruz de Carvalho *et al*. (2015) note that the rupture of membranes results in loss of electrolytes, and that this loss is greatest during rehydration following a rapid drying event. The ability to repair this damage may be an important factor that sets bryophytes apart from tracheophytes.

Upon rehydration, the less tolerant bryophytes initially spend time in repairing membrane damage caused by the dehydration. This is exemplified by the period of 4 to 24 hours that elapse prior to normal photosynthesis and respiration (Peterson & Mayo 1975; Dilks & Proctor 1976b; Proctor 1981). But before that repair occurs, leakage of both photosynthate and mineral ions can be severe, especially during the first two minutes following addition of water (Bewley 1974; Gupta 1977a. As in tracheophytes, the highly soluble K^+ is readily leaked during desiccation (Minibayeva & Beckett 2001; Table 2), but in the bryophytes, much of it is retained by cation exchange sites on the cell walls (Bates 1997). Fortunately, these retained ions can be re-absorbed by the cells during early rehydration. Material leaked into a culture medium is taken back into the cell within one hour (Bewley & Krochko 1982). Furthermore, at least in some liverworts, some of the lost photosynthate is resorbed (Noailles 1978).

In ***Syntrichia ruralis*** (Figure 21), slowly dried plants and undried controls lose only about half as much of electrolytes as do rapidly dried plants (Bewley & Krochko 1982). However, ***Cratoneuron filicinum*** (Figure 30) suffers more extensive loss under both slow and fast drying regimes and the loss is not reversible. Oliver and Bewley (1984b) interpreted these studies to mean that ***Syntrichia ruralis*** has membranes that undergo reversible changes during desiccation, but that these changes are incomplete when they are dried quickly. Upon rehydration it requires several minutes for the membranes to revert to their normal integrity. This mechanism to regain membrane integrity apparently is not working in the desiccation-intolerant ***Cratoneuron filicinum***.

Table 2. Loss of K^+ ions during rehydration following desiccation in bryophytes. **H** = hornwort; **LL** = leafy liverwort; **M** = moss; **TL** = thallose liverwort. Data from Minibayeva and Beckett (2001).

Anthoceros natalensis (H)	89%
Pellia epiphylla (TL)	83%
Hookeria lucens (M)	77%
Dumortiera hirsuta (TL)	55%
Atrichum androgynum (M)	45%
Sphagnum auriculatum (M)	38%
Plagiochila natalensis (LL)	21%
Rhodobryum roseum (M)	0%

Figure 30. ***Cratoneuron filicinum*** in hydrated state. Photo by Michael Lüth, with permission.

The leakage problem causes bryophytes to be vulnerable during frequent wetting/drying events. During each rehydration event, the plant must repair its cell membranes, and that requires energy. Frequent events with insufficient recovery time will eventually exhaust the resources within the cells. Because much repair is needed upon rehydration, it is critical that dry mosses retain the ability to synthesize ATP upon rewetting (Krochko *et al*. 1979). In ***Syntrichia ruralis*** (Figure 21), normal levels of ATP are regained in as little as 30 minutes. On the other hand, the hydrophytic ***Cratoneuron filicinum*** (Figure 30) slowly loses ATP after rewetting if the moss has been dried rapidly. Such behavior would prevent this moss from living in the desert, but poses no problem in its streamside habitat. However, Dhindsa (1985) suggested that it may be NADPH that is available immediately upon rehydration, produced by transhydrogenation from NADH during dark CO_2 fixation. Thus NADPH could be the important factor in repairing cellular damage by reductive biosynthesis of membrane components and other cellular constituents.

When the membrane first begins repair, there is a period of enhanced respiration during which the cell organelles regain normal appearance (Noailles 1978). Membrane repair occurs during this period of enhanced respiration, stopping the leakage (Farrar & Smith 1976; Richardson & Nieboer 1980). This is possible because, unlike the case in tracheophytes, protein synthesis begins immediately (Dhindsa & Bewley 1978), undoubtedly because of the conservation of **polyribosomes** (cluster of ribosomes connected with messenger RNA; play a role in peptide synthesis) in desiccation-tolerant bryophytes. Nothing is known about the role of action potentials in bryophytes and their possible role in membrane repair (Bates 2000), although Trebacz *et al.* (1994) have shown that Ca^{+2} influx and Cl^- efflux in the thallose liverwort ***Conocephalum conicum*** (Figure 24) result in depolarization of the cell membranes.

Mechanical damage is probably the primary cause of desiccation damage in cells. Membranes necessarily become contorted and folded during drying and cell shrinkage. In ***Syntrichia ruralis*** (Figure 21) pockets or **vesicles** (membranous spheres involved in transport or storage within cell) form on the **endoplasmic reticulum** (complex system of membranous stacks involved in membrane production in cell). Oliver and Bewley (1984b) suggested that these vesicles provide membrane material to be used for immediate repair upon rehydration. Other features that can help protect a cell from mechanical damage during dehydration include small cell size, small or no vacuoles, lack of **plasmodesmata** (tiny, membrane-line channels between adjacent cells), flexible cell walls, and reduced osmotic pressure (Iljin 1953, 1957). However, there is not a strong correlation of these attributes with desiccation-tolerant bryophytes. Bryophytes do have plasmodesmata, but electron microscopy is needed to discern them and few have been thus described; thus we cannot evaluate their correlation.

In support of Iljin's (1953, 1957) suggestion, some of the largest cells among bryophytes are those of the **Hookeriaceae**, a family of desiccation-sensitive mosses. And the **Pottiaceae** (including ***Syntrichia ruralis***) generally have small cells and live in dry places. But the vacuole correlation brings Iljin's suggested adaptations into question (Table 3), and even the cells of ***Syntrichia ruralis*** (Figure 21) shrink but are too rigid to collapse when they dry. One problem in attempting to determine just what happens as the cells dry is that in order to "fix" them for examination, we must partially rehydrate the cells (Oliver & Bewley 1984b). Until another method is forthcoming, we cannot observe what a dry cell looks like.

Table 3. Relative cell and vacuole sizes among bryophytes as listed by Oliver & Bewley (1984b).

	cell size	vacuoles
Desiccation tolerant		
Ceratodon purpureus	small	large
Syntrichia ruralis	small	small
Neckera crispa		small
Pleurozium schreberi	long & narrow	small
Barbula torquata	small	large
Triquetrella papillata	small	small
Desiccation sensitive		
Cratoneuron filicinum	long & narrow	small

Melick and Seppelt (1992, 1994) considered that the membrane integrity is restored rapidly and that intracellular carbohydrates likewise are replenished rapidly in the xerophytic ***Syntrichia caninervis*** (Figure 31**).** In an interesting contrast to the membrane repair scenario, Singh *et al*. (1984) concluded that membranes of ***Syntrichia ruralis*** (Figure 21) remain intact during desiccation, at least down to 75% relative humidity (-400 bars). The cellular membranes retain their phospholipid bilayers, and during dehydration the cytoplasmic vesicles form layers of membranes under the **plasmalemma** (cell membrane), appearing to fuse with the surface membrane. They

concluded that the cellular membranes are conserved and ready to expand upon rehydration. Wu *et al*. (2013) found a similar conservation of cell membranes in the desert moss ***Syntrichia caninervis***.

Figure 31. ***Syntrichia caninervis***, a desiccation-tolerant desert moss. Photo by Michael Lüth, with permission.

Based on these various responses of the cell membranes, it is not surprising that Oliver *et al*. (1993) found that electrolyte leakage alone was not a reliable measure of desiccation tolerance in ***Syntrichia ruralis*** (Figure 21). Instead, Stewart and Lee (1972) reported that NADP-linked glyceraldehyde phosphate dehydrogenase is affected by desiccation, and Bewley and his coworkers (Bewley 1972, 1973a, b, 1974, 1979, Bewley & Gwozdz 1975) have carefully documented the loss of polyribosomes and their effect on the ability of the cells to synthesize proteins. Oliver *et al*. (1993) found that comparison of ability to synthesize protein in hydrated and desiccated-rehydrated mosses was the best measure of the capabilities of three ***Syntrichia*** species to repair damage and thus to exhibit tolerance to desiccation.

Pulse release occurs in ***Hylocomium splendens*** (Figure 32) during rehydration, returning carbon and other nutrients, especially potassium, to the soil (Wilson & Coxson 1999). These mosses are able to concentrate carbon and nutrients from atmospheric sources and return them in concentrated form during these pulse releases caused by rainfall striking damaged membranes.

Figure 32. ***Hylocomium splendens*** on forest floor, a species that grows as well with 6 or 7 days of hydration a week, but not with other hydration regimens. Photo by Amadej Trnkoczy, through Creative Commons.

Protein Degradation and Ubiquitin

O'Mahony and Oliver (1999) compared the role of **ubiquitin** in the grass *Sporobolus stapfianus* and the desiccation-tolerant moss ***Syntrichia ruralis*** (Figure 21Figure 31) as a mediator of protein degradation. They found that in *S. stapfianus* the ubiquitin exhibited greater accumulation during drying and rehydration, but that it was hardly detectable in the desiccated tissue. A depletion of ubiquitin monomer levels indicates an increase in protein degradation. In ***Syntrichia ruralis***, the ubiquitin transcripts were stable in the dried tissue. The moss contrasted to the grass in that conjugated ubiquitin, indicative of proteins targeted for removal, was detectable in the moss only during slow drying, whereas it was present in all samples of the grass. O'Mahony and Oliver concluded that ***S. ruralis*** has stable ubiquitin transcripts that rapidly translate during rehydration to permit rapid initiation of cellular repair by degrading targeted proteins, whereas *Sporobolus stapfianus* requires several hours to replace its depleted ubiquitin supply.

Respiration

Respiration during recovery can vary considerably among species. Gupta (1977b) found that after 48 hours of desiccation at 0 and 50% relative humidity, rewetting for 32 hours varied in O_2 uptake from 2X in ***Mnium hornum*** (Figure 33) and ***Porella platyphylla*** (Figure 34) to 6X in ***Scapania undulata*** (Figure 35). This may in part be due to the presence of many respiring microorganisms that benefit from the leaked cellular contents (Gupta 1977a, b). Methods for measuring recovery processes need to take this microorganism respiration into account.

Figure 33. ***Mnium hornum***, a species that doubles its oxygen uptake upon rehydration. Photo by Michael Lüth, with permission.

Reactive Oxygen Species

The greatest damage to cells is caused by reactive oxygen species (Kranner *et al*. 2002; Beckett *et al*. 2004). Among the bryophytes, Beckett *et al*. (2004) demonstrated this in desiccated thalli of the liverwort ***Dumortiera hirsuta*** (Figure 36). In fact, this species produces extracellular superoxide at high rates under normal conditions, but that following mild desiccation stress, it produces considerably

more during rehydration. They postulated that it might have a role in defense against pathogens.

Figure 34. ***Porella platyphylla***, a species that doubles its oxygen uptake upon rehydration. Photo by Janice Glime.

Figure 35. ***Scapania undulata***, a species that has 6X as much oxygen uptake when recovering from desiccation. Photo by David Holyoak, with permission.

Figure 36. ***Dumortiera hirsuta***, a species that produces extracellular superoxide at a high rate, increasing production following mild desiccation stress. Photo by Paul Davison, with permission,

Even aquatic mosses like ***Fontinalis antipyretica*** (Figure 29) has protection from reactive oxygen species. de Carvalho *et al*. (2012) found that when this species was dried slowly and rehydrated, it had a lower production of reactive oxygen species (ROS). This reduced the cellular damage. As it rehydrated, it had an initial high oxygen consumption burst; de Carvalho and coworkers suggested that this may have been due to the burst of ROS production.

Photosynthesis

The desert moss ***Syntrichia caninervis*** (Figure 31) is a dominant soil crust bryophyte in deserts. As such, it has often served as a model for desiccation tolerance. Its photosynthesis recovers quickly following a dehydration-rehydration cycle (Li *et al*. 2010). The recovery occurs in two phases. The initial phase occurs in only three minutes, with a quick increase in maximal quantum efficiency of **PS II** (F_v/F_m) (photosystem II variable vs maximum fluorescence). In only 0.5 minutes from the onset of rehydration, over 50% of the PS II activities resume, including excitation energy transfer, oxygen evolution, charge separation, and electron transport. The second phase is slower and is dominated by an increase of **plastoquinone** (PQ; molecule involved in the electron transport chain in the light-dependent reactions of photosynthesis) reduction and accomplishing equilibrium of the energy transport from the inner chlorophyll antenna system to the reaction center of PS II. No *de novo* chloroplast protein synthesis is needed for this initial recovery of the PS II photochemical activity. The rapid recovery depends on chlorophyll synthesis, quick structural reorganization of PS II, and fast restoration of PS II activity without chloroplast protein synthesis.

Zhang *et al*. (2011) found that in ***Syntrichia caninervis*** (Figure 31), an ectohydric desert moss, minimum and maximum fluorescence and photosynthetic yield recovered quickly when the shoots were rehydrated in the dark. In fact, this species reached 90% of its 30-minute yield rate within the first minute, a phenomenon that was possible because of the lack of damage to membranes.

In ***Syntrichia caninervis*** (Figure 31) remoistening elicited rapid recovery of both fluorescence and photosynthetic yield (F_v/F_m) in the dark, reaching within 1 minute 90% of the value attained in 30 minutes (Zhang *et al*. 2011). The optimum moisture level falls in a narrow range, with chlorophyll fluorescence decreasing both above and below that moisture range. In its desert habitat, it is able to use dew, fog, rain, and melting snow as sources of moisture to permit photosynthesis.

At least in some species, rehydration results in an initial period of rapid respiration (Dilks & Proctor 1976b). In several temperate/boreal bryophytes, this rapid period of respiration is followed by a progressive recovery of photosynthesis generally lasting 1-6 hours. ***Anomodon viticulosus*** (Figure 37), a xerophytic species of well-drained, lightly shaded, base-rich or calcareous rocks and dry stone walls, reached its **compensation point** (photosynthesis = respiration) within a few minutes of hydration, whereas it required about 4 hours for ***Rhytidiadelphus loreus*** (Figure 38), a mesophytic forest floor species. For desiccation-tolerant bryophytes such as ***Anomodon viticulosus***, ***Racomitrium lanuginosum***

(Figure 39), and ***Rhytidiadelphus loreus***, recovery of photosynthesis upon rehydration is rapid (Proctor & Smirnoff 2000). This rapid recovery necessarily requires pre-existing proteins; *de novo* protein synthesis is generally very limited (Proctor 2001).

Dhindsa (1985) determined that desiccation-tolerant mosses such as ***Syntrichia ruralis*** (Figure 21) remain active and fix CO_2 (dark fixation) at an undiminished rate until tissue losses are about 60% of the initial fresh mass, whereas in the intolerant ***Cratoneuron filicinum*** (Figure 30) dark fixation of CO_2 slowly declines as the moss dehydrates. After that, water stress occurs, the moss rapidly proceeds to suspended metabolism, and CO_2 fixation rapidly ceases. Following rehydration, ***S. ruralis*** immediately begins CO_2 fixation, but ***C. filicinum*** does not. For tracheophytes, this recovery system has been perfected primarily in seeds that return from their suspended metabolism by metabolizing starches to sugars for the rapid supply of energy needed to grow and attain photosynthesis. Even in the desert ephemerals, the return process is slow and the frequency of wetting and drying suffered and survived by some desert bryophytes is unattainable by any tracheophyte (Proctor 2000b, 2001).

Figure 37. ***Anomodon viticulosus***, a moss that rapidly rehydrates and is ready for photosynthesis. Photo by Michael Lüth, with permission.

Figure 38. ***Rhytidiadelphus loreus*** on the forest floor, a species that is rapid to regain photosynthetic activity after rehydration, but slower than ***Anomodon viticulosus***. Photo by Michael Lüth, with permission.

Figure 39. ***Racomitrium lanuginosum*** on rock, a species that rapidly regains photosynthetic activity after rehydration. Photo by Michael Lüth, with permission.

Guschina *et al*. (2002) related the rapid recovery to the stress hormone **ABA** in the mesophytic moss ***Atrichum androgynum*** (Figure 40). Changes in phosphoglyceride composition due to water stress indicate an activation of phospholipase D and of phosphatidylinositol metabolism. During rehydration, phosphoglyceride composition recovers close to the original levels. Thylakoid lipids and chlorophyll decline during dehydration, accounting for the loss of photosynthesis. Treatment with ABA reduces the overall extent of changes, probably by reducing lipid changes, thus protecting against membrane damage. But can the moss produce its own ABA? And is it inducible?

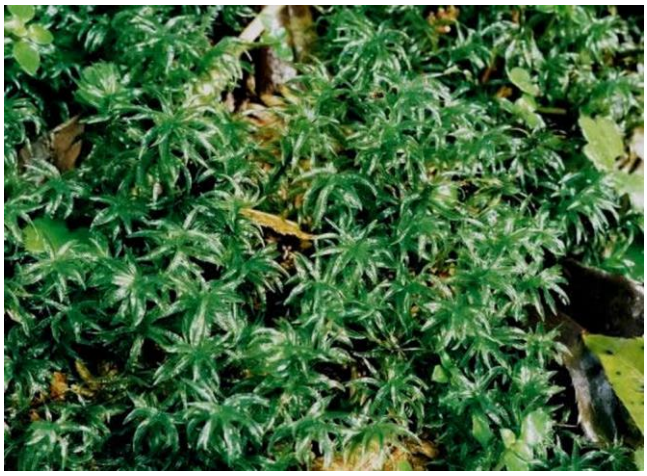

Figure 40. ***Atrichum androgynum***, a moss that uses ABA to aid in rapid recovery from desiccation. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Architectural Changes

We know that many bryophytes, including ***Syntrichia ruralis*** (Figure 21), undergo multiple architectural changes as they dry (Hamerlynck *et al*. 2000). This results in changes to the surface reflectance. Hamerlynck *et al*. found a sigmoidal (logistic) relationship between the relative humidity and the deviation of the moss mat temperature from its dew point, indicating a slow, then rapid, then slow change in the temperature of the mat, and a concomitant change in its water loss. The conditions of drying affect the ability of this species to use thermal

dissipation of excess light energy, thus affecting potential damage to the chlorophyll.

Breuil-Sée (1994) examined the cell interior upon rehydration of the thallose liverwort ***Riccia macrocarpa*** (Figure 41) after 25 years of dehydration in a herbarium. Whereas most bryophytes revive to normal metabolism in a few hours, this 25-year-dry bryophyte required nine days. Cytological evidence of its revival included enlargement of **nucleoli** (sites of ribosome synthesis and assembly in nucleus), evidence for protein synthesis. The dehydrated liverworts had few **mitochondria** (site in cell that generates most of the ATP) and the chloroplasts lacked starch. Its preparation for desiccation was evidenced in granular cytoplasm with many **osmiophilic globules** (lipid-containing bodies in chloroplast), especially along the cell wall. Features already known for dry spores and seeds, such as presence of **plasmodesmata** (microscopic channels which traverse cell walls of plant cells, enabling transport and communication between cells), but absence of **dictyosomes** [stacks of flat, membrane-bound cavities (cisternae) where proteins are stored and that comprise the Golgi apparatus] and **endoplasmic reticulum** (**ER**; interconnected network of flattened, membrane-enclosed sacs or tubes known as cisternae; inner core of cytoplasm and membranes of ER are continuous with outer membrane of nuclear envelope), were evident. The transition of ***R. macrocarpa*** toward active metabolism upon rewetting was marked by 1) enlargement of nucleolus; 2) important modification of nucleus; 3) amplification of endoplasmic reticulum, Golgi, chloroplasts, mitochondria, and vacuoles; 4) disappearance of lipid reserves; 5) synthesis of starch in chloroplasts; 6) cytoplasm densification.

Figure 41. ***Riccia macrocarpa***, a species that resumed normal metabolism upon rehydration after 25 years in a dry state. Photo by Michael Lüth, with permission.

The protonemata are important survival structures in some habitats and for some species. Pressel and Duckett (2010) found that in their experiments the protonemata could survive slow, but not fast drying. During dehydration, the cell experiences vacuolar fragmentation, reorganization of the endomembranes, changes in cell wall thickness, changes in the morphology of plastids and mitochondria, and a controlled dismantling of the cytoskeleton. These events cannot occur during fast drying. Externally applied abscisic acid mimicked the effects of slow drying, permitting the protonemata to survive.

Cellular Changes

Oliver *et al*. (2005) indicated that desiccated cells appear to be intact. Cellular disruption occurs upon rehydration as water is taken up rapidly. Nevertheless, the cellular integrity returns rapidly.

Desert mosses can have remarkable durability to desiccation. Moore *et al*. (1982) found that ***Didymodon torquatus*** (Figure 42) can survive 18 months of desiccation at a water content of only 5% or less. Nevertheless, after only 24 weeks of desiccation, the photosynthetic and respiratory rate upon rehydration were less than that of fresh (hydrated) materials. What is interesting is that in shorter time periods this species returned to control levels within one hour of rewetting. ***Triquetrella papillata*** (Figure 43), however, had a shorter survival time. In both species, the integrity of the organelles was maintained during short periods of desiccation, but that integrity diminished progressively with time. Net photosynthesis was delayed, apparently due to the disappearance of chloroplast and mitochondrial membranes and loss of internal structure.

Figure 42. ***Didymodon torquatus*** dry, a species that can survive extreme desiccation for 18 months. Photo from Canberra Nature Map, through Creative Commons.

Figure 43. ***Triquetrella papillata*** dry, a species that survives a short period of drought. Photo by David Tng, with permission.

Despite this degradation with time, Breuil-Sée (1994) found that the thallose liverwort ***Riccia macrocarpa*** revived after 23 years of drying. Upon rehydration, the endoplasmic reticulum became extended and the nucleolar volume increased, but these events were not observed until day 9.

Leptoid Recovery

Pressel (2006) pointed out the lack of study on the behavior of leptoid cells following rehydration. Using the endohydric moss ***Polytrichastrum formosum***, she documented that desiccation cause dramatic changes in leptoid tissues. The endoplasmic microtubules disappear; the nucleus, mitochondria, and plastids become rounded and longitudinal alignment of the organelles disappears. Cytoplasmic polarity is at least partly retained. Instead of the prominent stacks of endoplasmic reticulum that characterize the hydrated state, the membranous tubules are arranged at right angles to the main cellular axis. The cytoplasm of the leptoids is filled with small vacuoles. The plasmalemma deposits ingrowths of cell wall material, forming labyrinthine extensions. The plasmodesmata of apical meristematic and stem parenchyma cells seem unaffected by dehydration, but in the leptoids they become plugged with electron-opaque material. Starch is depleted in the parenchyma cells adjoining the leptoids. In control plants, the cellular structure is completely re-established in 12-24 hours, but this is not the case in cells treated with oryzalin, a microtubule-disrupting drug. Pressel concluded that the microtubular cytoskeleton is key in the rapid re-establishment of the cytoplasmic architecture of leptoids during rehydration.

Chloroplast Recovery

Proctor *et al*. (2007) found that thylakoids, grana, and mitochondrial cristae of ***Polytrichastrum formosum*** (Figure 28) remain intact during drying and re-wetting. Nevertheless, the form of organelles changes quite noticeably. Chloroplasts lose their prominent lobes, becoming rounded when desiccated. They require ~24 hours to return to their normal shape. Photosynthesis likewise requires 24 hours for full recovery, but is independent of protein synthesis. It appears that the physical structure of the chloroplast remains the same, but that the spatial relationships among the components is altered during dehydration. Proctor *et al*. concluded that the cytoskeleton has a significant role in the bryophyte desiccation response.

Wood and coworkers may have a partial answer to the recovery of the chloroplasts following desiccation (Wood & Oliver 1999; Wood *et al*. 1999; Zeng & Wood 2000; Zeng *et al.* 2002). There is a change in gene expression during rehydration of ***Syntrichia ruralis*** (Figure 21), suggesting that new proteins are being made. It appears that some of these proteins may account for the rapid chlorophyll recovery. We now understand that the moss prepares for its desiccation and rehydration events by altering gene expression in response to desiccation, then altering translational controls as it rehydrates. When the drying rate has been slow, **mRNPs** (messenger ribonucleoprotein particles) are formed in the drying plants, and within these particles they sequester **rehydrin** mRNA (mRNA transcripts used during rehydration). It appears that one of these rehydrins may be responsible for the production of antioxidants during rehydration (Oliver *et al*. 1997). It is the production of these mRNPs that makes slow dehydration so important to the recovery (Oliver 1996). If the moss is dried rapidly, it must make these when it rehydrates.

Wood and coworkers (1999) supported this discovery that ***Syntrichia ruralis*** (Figure 21) has an active recovery mechanism that is induced by rehydration. It makes a set of polypeptides that are not present at any time except during rehydration. These polypeptides were products of a large number of as yet unidentified plant genes and 71% of these are unknown in other plant phyla.

Among these are most likely the cDNA *Rp115* identified by Zeng and Wood in 2000 and which is conserved as mRNA in desiccated gametophytes, and two additional cDNA units (***Elipa* & *Elipb***), both of which have significant similarity to Early Light-Inducible Proteins (ELIP; Zeng *et al.* 2002). The **ELIP** group (coded by *ELIP* genes) includes over 100 stress-inducible proteins (Heddad & Adamska 2002). They are produced in response to light stress and accumulate in photosynthetic membranes where they have a photoprotective function. They are closely related to the light-harvesting chlorophyll *a*/*b*-binding antenna proteins of photosystems I and II. Because of the response of *Elipa* genes to slow desiccation, rapid desiccation/rehydration, salinity, ABA, and rehydration in high light, and the response of *Elipb* genes to ABA or rehydration in high light, Zeng *et al*. (2002) suggested that ELIPa and ELIPb provide an adaptive response to the photodamage that is likely to occur within a moss chloroplast during desiccation, most likely playing an important role in protecting and/or repairing the photosynthetic apparatus.

In support of this hypothesis, Hutin and coworkers (2003) found that when they suppressed this rapid accumulation of ELIPs during high-light stress in a mutant of the flowering plant *Arabidopsis thaliana*, the leaves became bleached and cells suffered extensive photooxidative damage, but when the plant was permitted to accumulate ELIPs before the stress, they exhibited normal phototolerance. Hence, it appears that they do indeed perform a photoprotective function, either by binding the chlorophylls that are released during turnover of the pigment-binding proteins or by stabilizing the proper assembly of those proteins when they are being subjected to high-light stress.

Lüttge *et al*. (2008) found that the three poikilohydric species ***Campylopus savannarum***, ***Rhacocarpus fontinaloides***, and ***Ptychomitrium vaginatum*** achieved photo-oxidative protection in their light-adapted state. This was accomplished by a reduction of chlorophyll fluorescence to near zero. When rewet, they have a very fast recovery in the first 5 minutes, but require more than 80 minutes to reach an equilibrium. Even though they occupy different niches on their rock outcrop habitat, they had similar recovery kinetics, with only their photosynthetic capacity differing slightly.

Photodamage

For the most desiccation-tolerant mosses, those from **xeric** (dry) habitats, **fluorescence** (emission of light of longer wavelength due to absorbance of light from outside source) levels upon rehydration indicate that the

photosynthetic apparatus is fully functional, unlike that of mosses from **hydric** (wet) and **mesic** (moderate) habitats (Deltoro *et al*. 1998a; Marschall & Proctor 1999). **Photoinhibition** (inhibition of photosynthesis by light) is a well-known consequence of desiccation because the **light quenching** is greatly diminished or absent. Only the desiccation-tolerant bryophytes exhibited photo-quenching at low water content in these experiments. Deltoro and coworkers (1998a, b) suggest that this loss of photosynthetic capability in **mesophytic** bryophytes might be not only a consequence of photoinhibition, but also a result of membrane damage, as indicated by the large K^+ leakage. In desiccation-tolerant taxa, they suggest, the ability to enhance the dissipation of thermal energy during dehydration might permit them to take advantage of the erratic water supply in places like the desert and decrease the problems of photodamage during the dehydration stage, thus permitting them to recover quickly.

Measuring Damage

Records of survivability may sometimes be misleading. For example, Makinde and Fajuke (2009) reported survival based on microscopic views of vacuoles as soon as the cells were hydrated without any verification by regeneration, a true test for survival.

Not only do different species respond differently, but leaves and cells vary on the same plant. Streusand and Ikuma (1986) suggested a protocol that requires a large number of cells counted in a given leaf, a large number of leaves, and a large number of shoots. They considered 10 cells in 6 areas of each of 6 leaves per shoot on 10 shoots to be adequate and it provided a near perfect correlation with shoot survival in experiments with different desiccation protocols.

Factors Affecting Recovery

Temperature

In the dry state, plants are much more resilient at temperature extremes than are hydrated plants. As Alpert (2000) pointed out, some can survive as low as -272°C or as high as 100°C. He raises two questions regarding survival of desiccation: What are the mechanisms by which plants tolerate desiccation? and Why are desiccation-tolerant plants not more ecologically widespread? In general, they seem to require protection from oxidants and from loss of configuration of the macromolecules during their dehydration period.

Drying Speed

Many studies have indicated that drying speed is important to successful recovery from desiccation (Krochko *et al*. 1978; Schonbeck & Bewley 1981a; Greenwood & Stark 2014). This varies, based on **inducible** vs **constitutive** desiccation tolerance responses. Those that are harmed by rapid drying, but that recover after slow drying, are able to use an **inducible** system (one that develops in response to desiccation) to protect them against desiccation effects. The slower timing is required for that inducible system to prepare. This system is more likely to be effective in aquatic or wet-habitat species, as demonstrated by the semi-aquatic ***Cratoneuron filicinum*** (Figure 30). In this species, rapid drying results in considerable disruption of the cell contents, whereas following slow drying some cells are able to maintain their cellular organization and integrity. Protein synthesis is reduced upon rehydration under both very slow and rapid drying, but these effects are reversible down to a water loss of 50% of fresh weight. Unlike the observations of Dilks and Proctor (1976b) on several terrestrial boreal/temperate bryophytes, respiration does not occur when the moss is rewet after rapid drying.

Even in such xerophytic taxa as ***Syntrichia ruralis*** (Figure 21), rapid drying causes visible injury, reduced total chlorophyll, reduction in chlorophyll *a:b* ratio, greatly enhanced electrolyte loss, and consequent inhibition of gross photosynthesis (Schonbeck & Bewley 1981a). Partial desiccation for 1-3 hours before rapid drying will eliminate this injury, suggesting that the moss requires time to prepare for its recovery. When ***Syntrichia ruralis*** and hydrophytic ***Cratoneuron filicinum*** (Figure 30) are dried rapidly, the chloroplasts and mitochondria swell and lose their integrity upon rewetting (Krochko *et al.* 1978, 1979), but ***S. ruralis*** regains normal appearance within 24 hours, whereas ***C. filicinum*** loses its cell contents and shows considerable cell degradation. However, if the cells are dried more slowly (*e.g.* 12 hours at 75% RH), both species recover within 24 hours. Dhindsa and Bewley (1978) attribute the ability of ***Syntrichia ruralis*** to survive this swelling of organelles to their ability to synthesize or retain sufficiently the enzymes needed for repair.

Hamerlynck *et al*. (2002) later found that ***Syntrichia ruralis*** (Figure 21) grown in high light intensity has greater desiccation tolerance than plants grown in the shade, but that those plants growing in the shade may benefit from their longer periods of metabolic activity and greater acquisition of resources, permitting them to adjust sufficiently to canopy openings and other disturbances.

Proctor (2003) subjected both desiccation-tolerant and moderately desiccation-tolerant species to drying for various periods up to 240 days. The more desiccation tolerant species (***Grimmia pulvinata***, ***Syntrichia ruralis***, ***Andreaea rothii***, ***Racomitrium lanuginosum***, ***R. aquaticum***, ***Leucodon sciuroides***, ***Pleurochaete squarrosa***, ***Ulota crispa***) had their best long-term survival (>30-120 days) at ~-100 to -200 MPa (20-45% r.h.). The moderately desiccation-tolerant ***Anomodon viticulosus***, ***Porella platyphylla***, and ***P. obtusata*** survived best at the highest humidity used, -41 MPa (74% r.h.). The lower humidities would speed desiccation and only the most tolerant could survive.

Greenwood and Stark (2014) determined that when $\mathbf{F_v/F_m}$ are less than 0.1, ***Physcomitrella patens*** fails to regenerate. The Fv/Fm fluorescence is the standard measurement for stress in plants, testing whether or not plant stress affects photosystem II in a dark adapted state. Fv refers to fluorescence in its variable state; Fm is maximum fluorescence. They used a process of drying that permitted as long as 284 hours for drying and found a significant increase over results obtained using salt solutions to create desired moisture conditions. Survival rates and chlorophyll fluorescence both improved and tissue regeneration time was shortened, demonstrating a much greater desiccation tolerance than was previously known for this species.

Frequency of Dehydration/Rehydration

Upon rehydration, it requires time to repair membranes and regain the energy lost. Oliver and Bewley (1984a) have demonstrated that in some mosses the first 24 hours are spent in repair, and it is only after that period that there is a net photosynthetic gain. For this reason, frequent short sequences of desiccation can be devastating to many species, whereas the same moss can endure long periods of desiccation. For example, ***Didymodon vinealis*** (Figure 44) (Moore *et al*. 1982) recovered completely within one hour of rewetting after 18 months of desiccation at less than 5% relative water content. However, following short periods of desiccation, the integrity of the organelles was progressively lost, including membrane loss from chloroplasts and mitochondria. Repairing this damage resulted in delays in net photosynthetic gain.

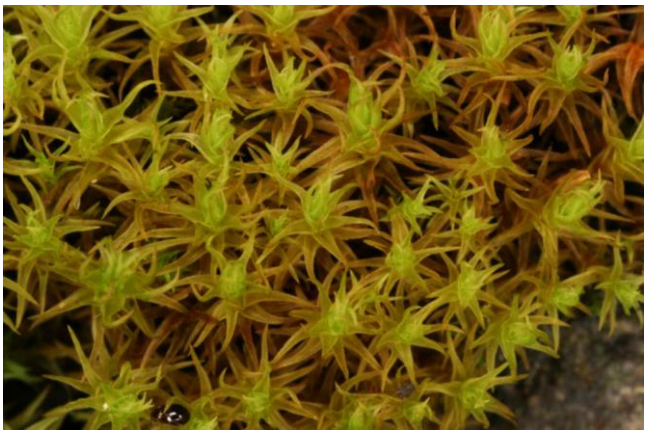

Figure 44. ***Didymodon vinealis***, a moss that is able to recover within one hour of hydration after 18 months of desiccation. Photo by Jan-Peter Frahm, with permission.

Dilks and Proctor (1976b) likewise promoted the understanding that frequency of desiccation can be more important than duration. Using 6 days wet – 1 day dry conditions compared to 1 day wet – 6 days dry, 1 day wet – 1 day dry, and 7 days wet – 7 days dry for a period of 18 weeks, they showed that ***Hylocomium splendens*** (Figure 32) grew equally well in continuous moist conditions and in 6 days wet – 1 day dry (32% relative humidity). However, there was little or no growth among the other treatments. In ***Rhytidiadelphus loreus*** (Figure 45), growth was best in continuously hydrated mosses, then 6 wet – 1 dry day mosses, then 7 wet – 7dry day mosses. There was essentially no growth in the other treatments. Responses by ***Syntrichia ruralis*** (syn.=*Tortula ruraliformis*; Figure 21) were so variable that they could not be interpreted. However, Dilks and Proctor were able to conclude that 63 wet-dry cycles were not harmful, but that constant moist conditions were harmful in this highly desiccation-tolerant moss. ***Rhytidiadelphus loreus***, unlike the other mosses, showed a **hardening** effect (process of increasing resistance to stress factor), indicating less effect from drought as more droughts occurred. ***Syntrichia ruralis*** is always drought-ready so hardening is not discernible.

To test the impact of intermittent desiccation on reproductive success of xerophytic mosses, Mishler and Newton (1988) measured the success of germination of both fragments and spores of four ***Syntrichia*** species [***S. ruralis*** (Figure 21), ***S. princeps*** (Figure 46), ***S. norvegica*** (Figure 47), ***S. laevipila*** (Figure 48)] in continuous versus intermittent moisture. Only ***S. princeps*** fragments did slightly better under the intermittent moisture conditions, as did its spore germination. In all other species, the continuous hydration seemed beneficial to the spores. Establishment success was quite different. None of the spore-derived protonemata gave rise to stems (Mishler & Newton 1988). Fragments, however, produced numerous stems both from protonemata and directly from the fragments, independent of the hydration conditions. Most likely some other physiological or environmental cue was missing for the spore-derived protonemata.

Figure 45. ***Rhytidiadelphus loreus***, a moss that undergoes drought hardening. Photo by Michael Lüth, with permission.

Figure 46. ***Syntrichia princeps***, a moss that has better germination of spores and fragments under intermittent moisture than under continuous moisture. Photo by Jan-Peter Frahm, with permission.

Figure 47. ***Syntrichia norvegica***, a species in which fragments and spores germinate better in continuous moisture than in other moisture regimes. Photo by Michael Lüth, with permission.

Figure 48. ***Syntrichia laevipila***, a species in which fragments and spores germinate better in continuous moisture than in discontinuous regimes. Photo by Jonathan Sleath, with permission.

In other species, high resistance is attained after several short exposures to drought (Clausen 1952; Abel 1956; Patterson 1964; Dilks & Proctor 1976a, b). We know that ***Syntrichia ruralis*** (Figure 21) is capable of drought hardening (Schonbeck & Bewley 1981b). When subjected to daily episodes of desiccation and rehydration, it develops a greater desiccation tolerance. However, the wet-dry cycle may be of less importance for boreal forest mosses. Hanslin and coworkers (2001) exposed ***Dicranum majus*** (Figure 49) and ***Rhytidiadelphus loreus*** (Figure 38) to various watering regimes and found that responses, while differing greatly, lacked any consistent pattern. However, the relative growth rate increased with the length of the wet-dry cycle, provided the total number of wet and dry days remained equal, suggesting that these taxa probably would be unable to take advantage of night-time dew accompanied by day-time drought, but they are adapted to the more weekly or monthly wet-dry cycles typical of the boreal forest.

Davey (1997) showed that Antarctic hydric mosses are susceptible to damage by frequent wetting and drying, but that was not the case for the mesic and xeric mosses, which seemingly were adapted to frequent wet/dry cycles. All the mosses suffered a greater loss of photosynthetic rate as the duration of the dehydration periods increased. Davey suggested that mosses from the drier habitats were adapted to use short periods of rehydration. This is consistent with the use of late night/early morning moisture from clouds in xeric African montane sites and other habitats where nighttime dew is the major source of water. Csintalan and coworkers (2000) supported this concept with their work on ***Syntrichia ruralis*** (Figure 21) in dry grasslands. They found that the moss absorbed progressive amounts of water through the night, permitting it to obtain about 1.5 hours of net photosynthetic gain immediately after dawn. Although this gain on many days may not be enough to offset the carbon loss during the remainder of the day, it does contribute to the overall carbon gain and may permit the moss to gain on a yearly scale when added to those occasions when more dew or moisture is available.

Figure 49. ***Dicranum majus***, a moss that seems to do best when the number of wet and dry days are about equal. Photo by Michael Lüth, with permission.

Carbon Balance

The bottom line in the dehydration/rehydration cycle over the course of the lifetime of the bryophyte is carbon gain (Alpert 2000). Short-term rehydration events can use more carbon in repair processes than can be gained from photosynthesis once everything is working properly. For those species that can regain photosynthetic activity within the first minute, an array of water sources becomes available, including dew and fog in addition to rain and snow. These may be the same species that experience rapid drying because of a desert-like habitat. For these, constitutive desiccation tolerance is important. This strategy may include structural adaptations that slow drying and cellular mechanisms that preserve the integrity of the cellular organelles. But as demonstrated in the desert moss ***Pterygoneurum lamellatum*** (Figure 50), tolerance to slow drying can be inducible (Stark *et al*. 2013).

Oliver *et al*. (1993) proposed a three-part strategy of tolerance that is based on carbon balance, damage limitation, and cellular repair. To support this they used protein synthesis following desiccation/rehydration in three desiccation-tolerant moss species: ***Syntrichia caninervis*** (Figure 31), ***S. ruralis*** (Figure 21), and ***S. norvegica*** (Figure 47). Using this as a measure of repair, they ranked the tolerance of these species as ***S. caninervis > S. ruralis > S. norvegic***a.

Figure 50. ***Pterygoneurum lamellatum***, a desert moss with inducible desiccation tolerance when dried slowly. Photo by Michael Lüth, with permission.

Implications

It appears that characteristics suggested for tracheophytes to permit them to survive desiccation (Iljin 1953, 1957) do not apply well to bryophytes. Rather, Oliver and Bewley (1984b) suggested that tolerant species must do three things to survive drying: (1) limit damage to a level that can be repaired; (2) maintain physiological integrity of the cell so metabolism can quickly reactivate during rehydration; (3) put repair mechanisms into effect upon rehydration, especially to regain integrity of membranes.

Many questions remain to be answered in understanding the recovery process in bryophytes. When studying the grass *Sporobolus stapfianus*, Neale *et al*. (2000) found that *Elip* genes were expressed differently in tissues that were desiccation tolerant than in those that were desiccation sensitive and suggested that there are unique gene regulatory processes occurring as desiccation ensues, permitting different drought-responsive genes to be expressed at different stages during water loss. Since these genes have been identified in bryophytes, it is likely that Zeng *et al*. (2002) are correct in their suggestion of a photoprotective role during the dehydration state of bryophytes.

As summarized by Oliver *et al*. (2005), desiccation tolerance is a primitive trait, a necessary trait for invasion of land. In bryophytes, two aspects permit their survival: constitutive cellular protection and effective recovery/repair mechanism. (To this we must add inducible tolerance in at least some bryophytes.) But upon recovery, the cells behave like any container of light-weight objects that suddenly gets an influx of water, being disrupted initially. Nevertheless, the cell soon regains its integrity. Photosynthetic activity seems little affected and recovers quickly. LEA proteins proliferate, but their role is unknown, perhaps functioning to restructure the membranes and stabilize the cell. More questions!

Summary

Desiccation tolerance most likely originated in the early land bryophytes in their colonization of land. Yet, they remain almost unique in their ability to tolerate desiccation in the vegetative state. Bryophyte gametophytes recover from desiccation by the actions of numerous **rehydration proteins**, including **rehydrins**, and **rapid membrane repair**. The rapidity is dependent upon slow dehydration that gives the bryophyte time to make mRNPs and is provided by a rehydration-inducible recovery mechanism in which new proteins are synthesized rapidly (Oliver 1996). The rapid recovery is complemented by enlargement of the nucleolus, amplification of the endoplasmic reticulum, Golgi, chloroplasts, mitochondria, and vacuoles, disappearance of lipid reserves, and synthesis of starch in chloroplasts during rewetting.

Photosynthesis resumes almost immediately, reaching normal levels within 24 hours, indicating the readiness of the chloroplasts. Because of the resources needed for recovery, short periods of rehydration between frequent drying periods deplete resources and are more harmful than long dry periods, issuing foreboding for moss gardeners.

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CHAPTER 7-7

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CHAPTER 7-7

WATER RELATIONS: BIOCHEMICAL ADAPTATIONS TO DRYING

Figure 1. ***Grimmia affinis*** drying on a rock. Photo by Michael Lüth, with permission.

The biochemistry of bryophytes is still a relatively young field. This is true of the biochemical level of response of bryophytes to desiccation stress. This chapter will attempt to portray what we know and how that biochemistry relates to the habitats of the bryophytes. But at this early stage in our studies, few species have been studied in detail, leaving much of the discussion incomplete or even somewhat ambiguous.

Membrane Chemistry

Since membrane damage is a common response to desiccation stress, Guschina *et al*. (2002) examined lipid composition of membranes in ***Atrichum androgynum*** (Figure 19) during desiccation in an effort to understand the role of the stress hormone **ABA**. Drought stress causes changes in the phosphoglyceride composition of the membranes. Reduction of thylakoid lipids, resulting in chlorophyll damage, causes a loss in photosynthesis as a result of desiccation, as already demonstrated in tracheophytes. Guschina *et al*. found that application of ABA reduced the extent of these membrane lipid changes.

Some plants may take advantage of the leakage through damaged membranes to rid cells of protectants used during dehydration. Working with canopy liverworts in the tropical rainforest of Guadeloupe, Coxson and coworkers (1992) found that for ***Frullania atrata***, exposure to simulated wetting/drying resulted in production of substantial glucose, erythritol, glycerol, and sucrose. They suggest that whereas these sugars may help this liverwort survive severe desiccation, the liverwort subsequently releases them into throughfall upon rewetting.

Robinson *et al*. (2000) suggest that sugars may indeed help some mosses survive desiccation. They found stachyose, an oligosaccharide known for its role in desiccation tolerance of seeds, in ***Bryum pseudotriquetrum*** (Figure 2), but not in ***Ceratodon purpureus*** (Figure 3; most tolerant) or ***Schistidium antarctici*** (Figure 4; least tolerant). This is another example showing that not all bryophytes have the same adaptations to desiccation.

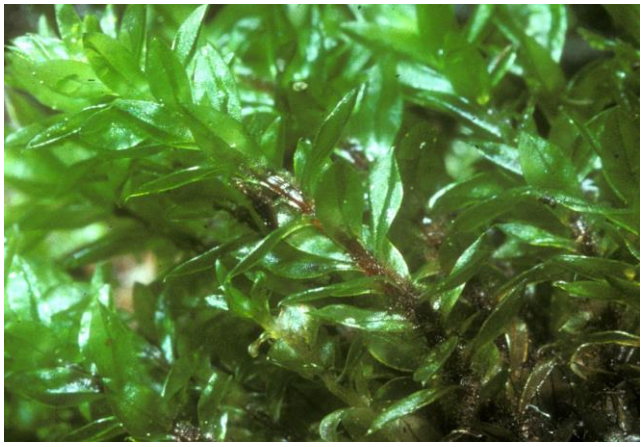

Figure 2. ***Bryum pseudotriquetrum***, a moss in which the sugar stachyose aids in desiccation tolerance. Photo by Janice Glime

Figure 3. ***Ceratodon purpureus***, a moss that does not use stachyose to aid in desiccation tolerance. Photo by Janice Glime.

Figure 4. Drought-intolerant ***Schistidium antarctici*** on Macquarie Island. Photo by Rod Seppelt, with permission.

ABA Role

The stress hormone **ABA** (abscisic acid) is present in many groups of organisms, including animals and bacteria as well as plants (Hartung 2010; Takezawa *et al*. 2011). This ability to protect against abiotic stress may have been one of the most critical attributes permitting plants to move to land.

Using immunoassay, Hartung and coworkers (1987, 1994) demonstrated the presence of ABA in all **Bryopsida**, **Anthocerotophyta**, and **Marchantiopsida** tested. They were able to extract more ABA from the hornwort ***Phaeoceros*** grown under slightly drier areas than from those in wetter areas. Furthermore, they have shown that the sporophyte of ***Phaeoceros laevis*** (Figure 5) produces ABA in response to stress and that the sporophyte guard cells close in response to ABA, much as in tracheophytes. This is in sharp contrast to the findings of Duckett and Ligrone (2004). They were unable to find any response to ABA or to moisture changes in the stomata of ***Phaeoceros***.

Figure 5. ***Phaeoceros laevis*** sporophytes, a hornwort with stomata in the capsule. Photo by Robert Klips, with permission.

In bryophytes, this hormone occurs in ***Physcomitrella patens*** (Figure 6) where it has a major role in dehydration stress tolerance (Takezawa *et al*. 2011). To determine the genetic response of bryophytes to water stress, Cuming *et al*. (2007) used the lab moss ***Physcomitrella patens***. These plants were subjected to ABA as well as osmotic, salt, and drought stress. The response of the protonema differed from that of the gametophore, with 130 genes in the protonema responding to dehydration. Of these, 56 were induced by ABA, but only 10 genes by osmotic stress and 8 by salt stress. Another 51 genes were induced by more than one of these treatments. Many of the ABA and drought-responsive genes were homologues of those expressed during seed development, supporting the assertions of Fisher (2008) discussed in Chapter 7-5. As seen by Wang *et al*. (2009) during dehydration, many of the ABA- and drought-responsive genes include genes for **LEA proteins**.

Figure 6. ***Physcomitrella patens***, a moss in which ABA increases stress tolerance. Photo by Michael Lüth, with permission.

Werner *et al*. (1991) found that even protonemata produce ABA in response to slow drying, as shown in ***Funaria hygrometrica***, and as in mature plants, it imparts drought tolerance. But it does not inhibit water loss. Rather, it appears to induce synthesis of new proteins that impart drought tolerance.

In Cyanobacteria and algae, the few studies on stress-induced ABA production indicate that the excess is released to the external medium (Hartung 2010). Taking an evolutionary approach, Hartung demonstrated that organisms that start to colonize terrestrial habitats increase their ABA production in response to even mild drought stress. Such signals seem to initiate the production of terrestrial organs, perhaps explaining the change from aquatic to terrestrial forms of ***Riccia fluitans*** (Figure 7; see below). In bryophytes, stomata respond to ABA. The levels of ABA in sporophytes of hornworts and mosses that have stomata is especially high, although the regulatory role of the ABA seems ambiguous. Fungi release ABA, and these hormones may interact with the bryophytes through mycorrhizal associations or just through their presence in the environment.

Figure 7. ***Riccia fluitans***, exposed here to air drying. ABA can facilitate conversion to the wider terrestrial form. Photo by Jan-Peter Frahm, with permission.

One of the unusual abilities of ABA is to cause the conversion of the aquatic forms of the thallose liverworts ***Riccia fluitans*** (Figure 7) and ***Ricciocarpos natans*** (Figure 8) into their terrestrial forms (Hellwege *et al*. 1992; Hartung *et al*. 1994). This conversion results in plants with greater volume, hence a smaller surface area to volume ratio, making them somewhat less vulnerable to desiccation.

Liverworts use **lunularic acid** where other plants use ABA as a dormancy hormone and, apparently, to help prepare them for drying, as shown in ***Lunularia cruciata*** (Figure 9) (Schwabe 1990). When subjected to long days, their drought resistance increases (Figure 10), as does their lunularic acid content.

Figure 8. ***Ricciocarpos natans***, stranded here out of water. ABA can facilitate conversion to the terrestrial form. Photo by Janice Glime.

Figure 9. ***Lunularia cruciata***, a thallose liverwort that produces the ABA-like lunularic acid as a dormancy hormone. Photo by Michael Lüth, with permission.

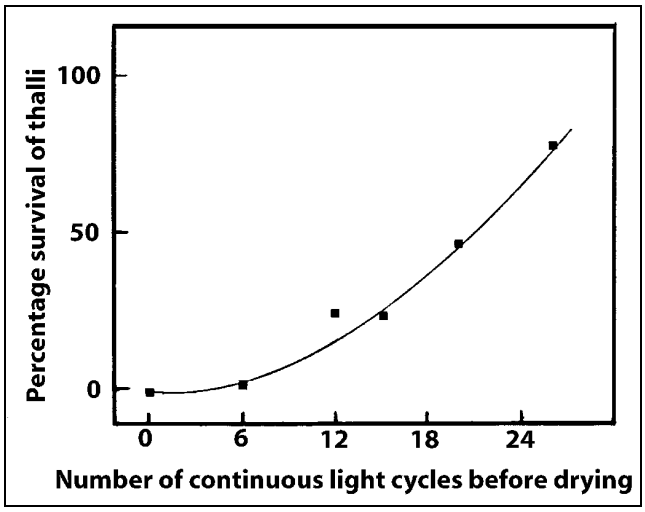

Figure 10. Effect of long-day (continuous) light on induction of drought resistance, resulting in drought survival in the thallose liverwort ***Lunularia cruciata***. Based on Schwabe (1990).

Although the presence of lunularic acid seems to be universal in liverworts, and has functions like those of

ABA, liverworts seem to be fully responsive to ABA. Pence (1998) found that ABA was necessary for the cryopreservation of some liverworts such as ***Riccia fluitans*** (Figure 7) and ***Marchantia polymorpha*** (Figure 21), preventing desiccation damage, but it had little effect on the leafy liverwort ***Plagiochila*** (Figure 11).

Burch and Wilkinson (2002) used ABA and sucrose to increase the success of cryopreservation of the moss ***Ditrichum cornubicum*** (Figure 12) protonemata. We also know that application of ABA increases the desiccation tolerance of the mesophytic moss ***Atrichum undulatum*** (Figure 13) (Beckett *et al*. 2000). Using ***Atrichum androgynum*** (Figure 19), Guschina *et al*. (2002) demonstrated phosphoglyceride composition changes during water stress. ABA treatment reduces the overall extent of these changes, possibly by reducing membrane damage by reducing the lipid changes.

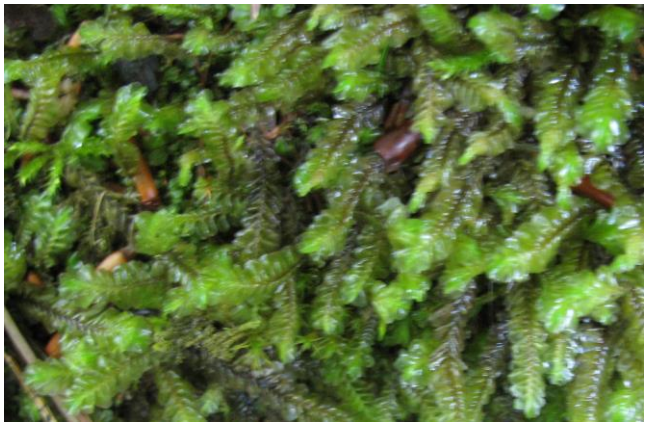

Figure 11. ***Plagiochila asplenioides*** near a stream in Wales. Photo by Janice Glime.

Figure 12. ***Ditrichum cornubicum***, a moss that survives cryopreservation with the help of ABA and sucrose. Photo by David T. Holyoak, with permission.

The Afromontane understory moss ***Atrichum androgynum*** (Figure 19) recovers its CO_2 fixation more slowly than recovery of photosystem II activity following 16 hours of desiccation, then rehydration (Mayaba *et al*. 2001). Pretreatment with ABA increases the recovery rate of both of these activities and doubles the non-photochemical quenching, hence reducing reactive oxygen species. Mayaba and coworkers suggest that this may partly explain the desiccation hardening process in this species. Plants pretreated with ABA, unlike untreated plants, experience a significant increase in soluble sugars that could promote the vitrification (transformation into a glassy substance) of the cytoplasm. This could, in turn, protect the membranes during desiccation. ABA has only a slight effect on the starch concentrations during desiccation. ABA furthermore has no effect on chlorophyll breakdown.

Figure 13. ***Atrichum undulatum*** showing some plants drying and curling. This moss changes its phosphoglyceride composition during drought stress. Photo by Janice Glime.

But how does this relate to preventing the oxidative damage? Beckett and coworkers (2000) suggested that ABA pretreatment may act by reducing the energy transfer between light-harvesting chlorophyll II and photosystem II. This could harden the moss to desiccation stress by reducing the production of reactive oxygen at the site of photosystem II. Experiments indicated that photosystem II photosynthesis recovers faster in the pre-treated plants.

ABA may play another role as well. One of the most serious consequences of desiccation is loss of membrane integrity, causing membranes to become leaky (Bewley 1979). Beckett (1999) found that application of ABA could reduce the loss of K^+ from ***Atrichum androgynum*** (Figure 19) in much the same manner as partial dehydration treatment prior to desiccation. The response is similar to that obtained by reducing the relative water content to 0.6 for three days, which reduces the K^+ loss by 15-20%. This seems to be the ideal combination because using less humid air or more time does not decrease the K^+ loss further. This species, and probably most, experiences **drought hardening** (process of increasing resistance to drought; see Chapter 7-5) as the dry season progresses, as indicated by the loss of 80% of its intracellular K^+ at the beginning of the dry season, but less than 25% by the end of that season (Beckett & Hoddinott 1997).

Abscisic acid (ABA) has already been noted to have an important role in desiccation tolerance. Werner *et al*. (1991) found that slowly dried protonemata of ***Funaria hygrometrica*** survived desiccation, but rapidly ones did not. The slowly dried mosses experienced a six-fold increase in abscisic acid during drying. If ABA is added to the protonemata at an appropriate concentration, the ABA mediates drought tolerance, apparently by inducing the synthesis of new proteins.

Sucrose

De Cruz *et al*. (2014, 2015) found that desiccated cells of the aquatic moss ***Fontinalis antipyretica*** lose 50% of their sucrose through leakage when the cells are rehydrated. Fast dehydration results in higher sucrose accumulation, but it is not enough to induce desiccation tolerance. The increase in soluble sugars helps in osmoregulation during the decreasing turgor pressure of the cells. In addition to serving as an osmolyte, sucrose in bryophytes helps to stabilize membranes and proteins through **vitrification** (process of forming glasslike substances). In ***Fontinalis antipyretica*** desiccation tolerance requires slow dehydration, suggesting that high sucrose content does not act alone to create desiccation tolerance.

Protection from Oxidation

Just what is it that varies among the bryophytes that dry out, become metabolically inactive, and then revive? What physiological mechanism protects, or fails to protect them? How can photosynthesis achieve its maximum rate within 30 seconds upon receiving rain or dew in some desiccated species (Anderson 1980)? Proctor (1990) and Alpert (2000) suggest that in drought-hardening the cell must protect itself from oxidative damage, as well as loss of configuration of macromolecules, and this protection depends on the intensity and duration of desiccation.

Minibayeva and Beckett (2001) noted that drought-sensitive bryophytes can release an **oxidative burst** (respiratory burst; rapid release of reactive oxygen species – superoxide radical and hydrogen peroxide) in response to rehydration. These bursts developed best in the hornwort and two thalloid liverworts tested (Minibayeva & Beckett 2001). A similar oxygen burst is, however, almost absent in all the mosses tested as well as a leafy liverwort and desiccation-tolerant lichens.

Oxidative Damage

Kramer *et al*. (2002) examined the "resurrection plants" – those plants that can survive desiccation – to determine what permits them to survive. They found that in a woody plant desiccation can trigger increases in zeaxanthin and redox shifts of the antioxidants glutathione and ascorbate to their oxidized forms. New ascorbate and glutathione were produced upon rehydration and the oxidized forms from the dehydration event changed back to reduced forms. Using lichens, Kramer *et al*. (2008) further demonstrated that reactive oxygen species can damage nearly every molecule in living cells. These included nucleic acids, proteins, and lipids.

The absence of oxidative bursts in mosses lends support to the hypothesis that mosses protect themselves from the damage such highly reactive oxidative bursts can cause during rehydration. Shiono *et al*. (2000) found that in testing the liverwort ***Marchantia paleacea*** subsp. ***diptera*** (Figure 15), the moss ***Barbula unguiculata*** (Figure 16), and the hornwort ***Anthoceros punctatus*** (Figure 17), the liverwort differed from the other two in its isozyme patterns for **superoxide dismutase**. This enzyme is known for its ability to maintain safe levels of the highly reactive oxides that are produced during cell stress, including effects of desiccation.

Figure 14. ***Physcomitrella patens***, a species that exhibits oxidative bursts in response to a fungal presence. Photo by Michael Lüth, with permission.

Minibayeva and Beckett (2001) conclude that patterns of oxide production are correlated with the moisture status of the habitat. Those species with high basal rates of oxide production grow in moist microhabitats, have a moderately high thallus water content, have high K^+ contents, and have well developed oxidative bursts. Species with such oxidative bursts also lose a high proportion of their intracellular K^+ (55-98% in liverworts and hornworts) upon rehydration. Mosses and the one leafy liverwort were all collected from wet habitats and all produced oxides at low rates compared to the thallose liverworts and hornworts.

Figure 15. ***Marchantia palacea*** subsp. ***diptera*** from Japan. Photo by Janice Glime.

The aquatic moss ***Fontinalis antipyretica*** (Figure 18) exhibits the potential danger of high oxygen levels. De Carvalho *et al*. (2012) demonstrated that under slow dehydration, this species exhibits low production of reactive oxygen species upon rehydration, a phenomenon that reduces the cellular damage and increases cell survival. The slow drying apparently reduces the oxidative burst by limiting production of reactive oxygen species.

Figure 16. ***Barbula unguiculata*** dry, retaining its green color that permits it to respond quickly to rehydration. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 17. ***Anthoceros punctatus***, a hornwort having similar isozyme patterns to those of the moss ***Barbula unguiculata***. Photo by Jonathan Sleath, with permission.

Figure 18. ***Fontinalis antipyretica*** in dry stream. Photo by Janice Glime.

But some bryophytes produce high quantities of oxides even when they are not stressed, and some bryophytes produce them at extremely high rates. For example, ***Anthoceros natalensis*** exceeds 1000 µmol g^{-1} dry mass h^{-1}, whereas excised tracheophyte roots produce only about 1% of that amount (Minibayeva *et al*. 1998). These data do not present a consistent pattern that permits us to interpret the role of oxidative bursts or superoxide dismutase in protecting bryophyte cells that undergo desiccation. Instead, the high oxidative responses in some species may be one to the presence of invading pathogens (see below).

Mayaba *et al*. (2002) later found that ***Atrichum androgynum*** (Figure 19) from the Afromontane understory displays an oxidative burst of hydrogen peroxide (H_2O_2), not superoxides, during rehydration, with maximum rates during the first 15 minutes (Figure 20). The moss even produces peroxide during times when dehydration is insufficient to cause K^+ leakage. Using polyethylene glycol to induce desiccation causes the moss to produce significant amounts of H_2O_2. Mayaba and coworkers suggest that peroxidases might be responsible for the production of H_2O_2. They determined that ABA and light influenced the rate of production of peroxide.

Figure 19. ***Atrichum androgynum***, a moss with an oxidative burst, especially during the first 15 minutes of rehydration. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

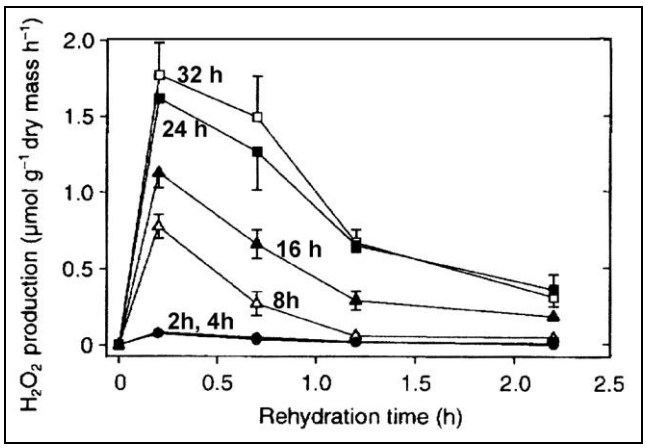

Figure 20. Peroxide (H_2O_2) production during rehydration following various dehydration periods (indicated on each line) in ***Atrichum androgynum*** from KwaZulu-Natal Province, Republic of South Africa, during summer. Vertical bars indicate standard deviation; n=5. Redrawn from Mayaba *et al*. (2002).

This peroxidase system would have several advantages. Peroxidases oxidize phenolics to quinones and generate peroxide (H_2O_2). Peroxide, a well-known antibacterial agent for cleaning cuts and wounds, can itself help to kill invading organisms. Furthermore, peroxide releases free radicals that increase polymerization of phenolics into lignin-like substances. In tracheophytes,

these substances are known to reinforce the cell wall and contain the pathogens. They may have similar roles in bryophytes.

The thallose liverwort ***Marchantia polymorpha*** (Figure 21) contains a peroxidase that has been characterized as a glycoprotein that is different from any known tracheophyte peroxidase (Hirata *et al*. 2000). Hirata and coworkers demonstrated that this peroxidase is able to perform oxidative polymerization of **lunularin**, the liverwort counterpart of ABA.

Figure 21. ***Marchantia polymorpha***, a thallose liverwort that produces a peroxidase with a glycoprotein that differs from those in tracheophytes. Photo by David T. Holyoak, with permission.

Other known constituents also influence the activity of peroxidases. Seel *et al*. (1992a) examined the effects of desiccation on **superoxide dismutase** (enzyme that destroys highly reactive superoxides by converting them into peroxide and O_2) activity in ***Syntrichia ruralis*** var. ***arenicola*** (=*Tortula ruraliformis*; Figure 22), a desiccation-tolerant moss, and ***Dicranella palustris*** (Figure 23), a flush moss with limited desiccation tolerance. Activity of this enzyme is known to enhance membrane integrity (Dhindsa & Matowe 1981; Dhindsa *et al*. 1981; Gong *et al*. 1997). ***Syntrichia ruralis*** var. ***arenicola*** has higher superoxide dismutase activity in both the hydrated and desiccated states than does ***D. palustris*** (Seel *et al*. 1992a). But effects on the activities of peroxidase or ascorbic peroxidase do not seem to be related to hydration state. Nevertheless, both species become depleted of the anti-oxidant ascorbic acid when desiccated. From these experiments, Seel and coworkers deduced that anti-oxidants may be more important than removal of chloroplastic peroxide in endowing desiccation tolerance. Using different methods, Seel and coworkers (1992b) found a greater lipid peroxidation in ***D. palustris*** than in ***S. ruralis*** var. ***arenicola*** following desiccation. Calcium also seems to play a role by increasing superoxide dismutase activity, thus enhancing membrane integrity (Gong *et al*. 1997).

Proctor *et al*. (2007) used the endohydric moss ***Polytrichastrum formosum*** (Figure 30) to try to resolve conflicting implications between physiological and cytological evidence regarding desiccation recovery in bryophytes. They found that protein synthesis inhibitors cause rapid decline of photosynthetic recovery in the light, but not in the dark. Rapid recovery of respiration and photosynthesis indicates that systems are conserved intact during the dehydration and rehydration, an indication that is consistent with the physical evidence that thylakoids and cristae do remain intact during the dehydration-rehydration process. Microbodies that are closely associated with chloroplasts remain unchanged during the dehydration-rehydration process and play an important role in removal of the superoxide radicals (Duckett & Renzaglia 1988; Smirnoff 1993; Minibayeva & Beckett 2001; Mayaba *et al*. 2002). The prominence of these microbodies in leaves of ***Syntrichia ruralis*** (Figure 23) (Robertson 1991) and ***Polytrichastrum formosum*** may be associated with the desiccation tolerance of these two species (Proctor *et al*. 2007).

Figure 22. ***Syntrichia ruralis*** var. ***arenicola***, a desiccation-tolerant moss. Photo by Michael Lüth, with permission.

Figure 23. ***Dicranella palustris*** in flush near Swallow Falls, Wales. This moss has limited desiccation tolerance. Photo by Janice Glime.

Glutathione

Glutathione (GSH) is important in protecting plants from environmental stresses like oxidative stress and pathogens (Bruns *et al*. 2001; Burritt 2008). More recent studies have used glutathione to measure drought stress. Activities of the enzymes glutathione reductase, glutathione peroxidase, and glutathione S-transferase increase during slow drying and likewise during rehydration following rapid drying of the drought-tolerant moss ***Syntrichia ruralis*** (Figure 22) (Dhindsa 1991).

On the other hand, the activity of the enzymes malate dehydrogenase exhibit little change during either dehydration or rehydration. Treatment of the moss tissues with cycloheximide, actinomycin D, or cordycepin suppresses the increased activities of glutathione reductase and glutathione S-transferase, but has a much lower effect on glutathione peroxidase. At the same time, the percentage of total glutathione as oxidized glutathione increases. This increase is correlated positively with levels of lipid peroxidation and solute leakage, but is correlated negatively with the rate of protein synthesis. The oxidized glutathione level serves as a good indicator of oxidation stress and suggests that oxidized glutathione may mediate the drought-stress-induced inhibition of protein synthesis.

In addition to protection from oxidative damage, glutathione may help to protect the bryophyte cells from heavy metal damage following rehydration (Saxena & Saxena 2012). Although it is likely that this benefit has not had any evolutionary selection advantage for very long, current pollution conditions often deposit heavy metals that accumulate while the bryophytes are dry. These could gain entry into the cells along with the resorption of needed cell electrolytes during rehydration and before membrane repair is completed. Bruns *et al*. (2001) have demonstrated a protective detoxification role of glutathione against heavy metals in the aquatic moss ***Fontinalis antipyretica*** (Figure 18), Leinenweber *et al*. (2009) in the terrestrial moss ***Thuidium*** sp. (Figure 24), and Saxena and Saxena (2012) in the moist forest moss ***Sphagnum squarrosum*** (Figure 25).

Figure 24. ***Thuidium tamariscinum***, a species that is able to use glutathione as protection against heavy metals. Photo by Michael Lüth, with permission.

Pathogen Danger

The damaging effects of oxides in the cells leads us to question the advantages that may have kept the oxidative burst in the bryophytes for eons. This may be explained by their role in limiting pathogen invasion and damage.

Cells with damaged membranes resulting from desiccation would be vulnerable to invasion by pathogenic microorganisms. Such oxidative bursts as seen upon rehydration can help to limit the spread of invading pathogens because of oxidation toxicity, as well as inducing expression of defense-related genes. Low and Merida (1996) considered the oxidative bursts in plants to facilitate cross-linking of cell wall proteins, induction of defense-related genes, stimulation of **phytoalexin** (substance produced by plant tissues in response to contact with a parasite and that specifically inhibits growth of that parasite) biosynthesis, and promotion of **hypersensitive response** (HR; mechanism to prevent spread of infection by microbial pathogens, causing rapid death of cells in local region surrounding infection).

Figure 25. ***Sphagnum squarrosum***, a species that is able to use glutathione as protection against heavy metals. Photo by J. C. Schou, with permission.

Gupta (1977) reported the oxidative burst in bryophytes as an "artifact." He found that ***Dicranella palustris*** (Figure 23; a wet-habitat moss) and ***Scapania undulata*** (Figure 26; an aquatic leafy liverwort) had a large number of microorganisms present following dehydration and rehydration. This is a reasonable expectation when membranes are damaged and both electrolytes and organic compounds are able to leak from the cells, especially upon rewetting. Furthermore, the respiratory oxygen uptake increased to about 6X that of controls of ***S. undulata***, 2.5X for ***Dicranella palustris***, and 2X for ***Porella platyphylla*** (Figure 27) and ***Mnium hornum*** (Figure 28). Little increase occurred in ***Syntrichia ruralis*** (Figure 22), the most desiccation-tolerant species. But it appears that the respiratory increases were due to the adhering microorganisms, not to the bryophytes. Such respiratory increase could indicate injury to the bryophytes, but it cannot be a useful tool to measure survivorship or metabolic recovery of the bryophytes. These microorganism growths indicate the potential importance of oxidative bursts that can help to protect the bryophyte cells from invasion from these potentially harmful organisms.

Beckett *et al*. (2004) demonstrated that the liverwort ***Dumortiera hirsuta*** (Figure 29) produced extracellular superoxide at high rates even under normal, unstressed circumstances. Nevertheless, production increased extensively during rehydration, but not during desiccation. It appears that peroxides produce the superoxide, but little H_2O_2 seems to be present in the cell. However, indications are that the concentrations of peroxides are rapidly reduced by the liverwort. Beckett and coworkers likewise suggested a role in protection against bacteria and fungi. Lehtonen *et al*. (2012) verified the importance of such

oxidative bursts in response to a fungal elicitor (chiton) in the moss ***Physcomitrella patens*** (Figure 14).

Figure 26. ***Scapania undulata***, a species in which microbial respiration/oxygen uptake increases by a factor of 6 following rehydration. Photo by Hermann Schachner, through Creative Commons.

Figure 27. ***Porella platyphylla***, a desiccation-tolerant leafy liverwort on tree bark; a species in which microbial respiration/oxygen uptake increases by a factor of 2 following rehydration. Photo by Michael Lüth, with permission.

Figure 28. ***Mnium hornum***, a species in which microbial respiration/oxygen uptake increases by a factor of 2 following rehydration. Photo by Des Callaghan, with permission.

Figure 29. ***Dumortiera hirsuta***, a thallose liverwort that produces extracellular superoxide at high rates even under normal circumstances. Photo by Michael Lüth, with permission.

White and Torres (2010) suggested that endophytes in plants may protect the plants from oxidative damage by the production of antioxidants, thus possibly protecting them against other forms of stress, including desiccation. It appears that this protective role of endophytes (fungi) has not been explored in bryophytes.

Shoot Tips – Variable Tolerance within Plants

Some moss shoot tips may have a rehydration potential not afforded the rest of the plant. In ***Polytrichastrum formosum*** (Figure 30), desiccation in the shoot tips induces the rapid resorption of starch grains in plastids of the meristematic cells without any major **thylakoid** disorganization (Hallet *et al*. 1987). In the adult leaves, however, the starch grains are preserved. Upon rehydration, the plastid ultrastructure of the apex is entirely restored and new starch inclusions appear in less than 4 hours. Little work has been done to relate the resistance of various parts of the bryophyte plants to differences in biochemistry.

Figure 30. ***Polytrichastrum formosum***, a moss where desiccation of the apices causes rapid resorption of starch grains in plastids of the apical meristematic cells. Photo by Des Callaghan, with permission.

The Genes

While the physiologists are attempting to find substances that affect desiccation tolerance and recovery rates, the geneticists are attempting to identify genes and

the biochemical pathways they affect. Chen and coworkers (2002), working with the desiccation-tolerant model system in ***Syntrichia ruralis*** (Figure 22), found a new polypeptide, known as ALDH21A1, that is less than 30% identical to known ALDH proteins. Data suggest that this new aldehyde dehydrogenase plays an important role in the detoxification of aldehydes generated in response to desiccation and may represent a unique stress tolerance mechanism among eukaryotes. Could it be this aldehyde dehydrogenase, perhaps coupled with ABA, that explains why Hamerlynck and coworkers (2002) found ***Syntrichia ruralis*** to be **homoiochlorous** (maintaining constant chlorophyll concentration) in its response to desiccation? Growing in the sun endows these plants with a greater desiccation tolerance than that experienced by shade-grown plants of the same species.

To fit these pieces together requires a great deal of speculation because our knowledge is still too meager. However, let s look at what we know about these pieces and see if we can develop a hypothetical story (Figure 31).

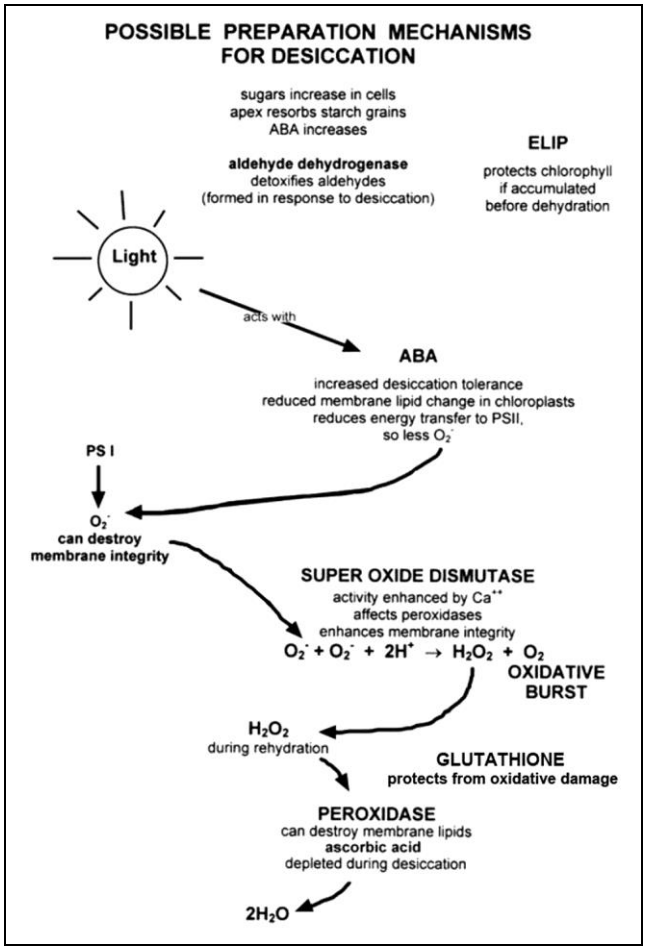

Figure 31. Speculation on possible relationships of the observations that have been made on pre-desiccation events and related rehydration events in desiccation-tolerant bryophytes.

Summary

Membranes become leaky during desiccation. Some mosses protect their membranes with sugars such as stachyose, glucose, erythritol, glycerol, and sucrose.

ABA increases the stress tolerance of bryophytes and is known to turn on the promoters of **stress tolerance genes**. Hence, it is important in controlling transcription. That is consistent with the conclusions of several authors who have determined that drought tolerance in bryophytes evokes control of gene transcription. We also know that **peroxidases** destroy H_2O_2 (**peroxide**), which is harmful to plants. We know that H_2O_2 is responsible for lipid damage of membranes and that lipid peroxidation and increased membrane permeability correlate with the decrease of **superoxide dismutase** (Dhindsa *et al.* 1981). And we know that superoxide dismutase controls **oxygen toxicity** by converting the superoxide radical to less dangerous forms (Michael Potter of Andrew McCammon's group at the University of California, San Diego). Since ***Syntrichia ruralis*** var. ***arenicola*** has a higher concentration of superoxide dismutase than the less desiccation-tolerant ***Dicranella palustris***, we can then hypothesize that the superoxide dismutase is an important contributor to drought tolerance in bryophytes. Perhaps it is one of the 74 proteins produced in response to desiccation stress. Glutathione may help to protect the cells from excessive oxides, but it may have a more important role in protecting against pathogenic microorganisms while they are vulnerable with damaged membranes.

Shoot tips seem able to survive better than other parts of some mosses, but we know nothing about any differences in their biochemistry. New genetic studies are making it possible to learn more about the functions of various compounds in the cells.

Acknowledgments

This chapter, in an early version, has benefitted from the help of Beth Scafone and Medora Burke-Scoll, who helped me tow the line in explaining things without leaving too much to one's imagination, but at the same time not repeating myself.

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CHAPTER 7-8

WATER RELATIONS: HABITATS

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CHAPTER 7-8

WATER RELATIONS: HABITATS

Figure 1. ***Bryum caespiticium*** at a high elevation where winds and ice crystals contribute to desiccation, but where at other times fog can maintain moisture without rain. Photo by Michael Lüth, with permission.

Habitat Relations

Proctor (2014) summarized the importance of water relations for bryophytes in their invasion of land. He pointed out that the poikilohydric strategy is optimal at smaller scales, *i.e.*, bryophytes. Microhabitat and habitat structure are important in conferring the hydration state of bryophytes, and drought sensitivity varies according to species (Irmscher 1912). Norris (1990) found that ***Braunfelsia*** disappeared from some areas of tropical rain forests in Papua New Guinea following disturbance to the forest because of the increased dehydration frequency and the admission of greater wind movement. In the Mediterranean area in the southern and southeastern Iberian Peninsula, Varo and coworkers (1992) found that as the climate has become drier and warmer the bryophyte taxa have changed, with leafy liverworts and pleurocarpous mosses diminishing and ***Sphaerocarpos*** (Figure 2) and acrocarpous mosses becoming more prominent. In central Sweden, greater numbers of bryophytes occur in spruce forests on more moist north-facing slopes, whereas vascular plants are more abundant on the exposed south-facing slopes (Söderström 1981).

Figure 2. ***Sphaerocarpos michelii***, member of a genus that becomes more prominent as the climate dries. Photo by Michael Lüth, with permission.

Bryologists learn inductively through field experience that certain bryophytes are characteristic of dry habitats and others of wet habitats. Actual studies that correlate these conditions with species are less common than descriptive observations, with a number of these being relative to water level in peatlands. Bates *et al*. (2004) used canonical correspondence analysis (CCA) to develop a more rigorous approach to these relationships by sampling epiphytes along a transect across southern Britain from southwest to northeast. With climate, presence of water courses, and forest cover contributing to the analysis, they determined that ***Frullania tamarisci*** (Figure 3), ***Metzgeria temperata*** (Figure 4), ***Microlejeunea ulicina*** (Figure 5), ***Neckera pumila*** (Figure 6), and ***Hypnum andoi*** (Figure 7) were restricted to habitats with high moisture availability. On the other hand, ***Syntrichia ruralis*** (Figure 39), ***Grimmia pulvinata*** (Figure 8), ***Tortula muralis*** (Figure 9), and ***Aulacomnium androgynum*** (Figure 10) only occurred as epiphytes in locations with low moisture. They did not sample these species in other habitats.

Figure 5. ***Microlejeunea ulicina***, a leafy liverwort that is restricted to areas with high moisture levels. Photo by Michael Lüth, with permission.

Figure 3. ***Frullania tamarisci***, a leafy liverwort that is restricted to areas of high moisture content. Photo by Jan-Peter Frahm, with permission.

Figure 6. ***Neckera pumila***, a moss that is restricted to areas of high moisture content. Photo by Jan-Peter Frahm, with permission.

Figure 4. ***Metzgeria temperata***, a leafy liverwort that is restricted to areas of high moisture levels. Photo by Michael Lüth, with permission.

Figure 7. ***Hypnum andoi*** near Swallow Falls in Wales, a moss that is restricted to areas with high moisture content. Photo by Janice Glime.

Figure 8. ***Grimmia pulvinata***, a cushion moss that can only survive as an epiphyte in areas that have high moisture. Photo by Barry Stewart, with permission.

Figure 9. ***Tortula muralis*** habitat on a wall. This moss is unable to live as an epiphyte unless the habitat has low moisture levels. Photo by Janice Glime.

Figure 10. ***Aulacomnium androgynum***, a moss that can only survive as an epiphyte in areas that have high moisture. Photo by Jan-Peter Frahm, with permission.

In mature black spruce forests of central Alaska, the endohydric ***Polytrichum commune*** (Figure 11) is able to avoid moisture stress more so than such ectohydric taxa as ***Hylocomium splendens*** (Figure 12; Skré *et al.* 1983). The latter species remains below its compensation point for water for nearly 50% of the July growing season.

Figure 11. ***Polytrichum commune***, an endohydric moss that is able to avoid moisture stress in black spruce forests more readily than ectohydric taxa. Photo by Michael Lüth, with permission.

Figure 12. ***Hylocomium splendens***, an ectohydric moss. Photo by Janice Glime.

Open expanses of urban areas are notoriously devoid of extensive bryophyte cover, even on trees where taxa are already xerophytically adapted. Hébrard and Rolando (1985) found that when comparing four holm-oak thickets in France, species composition correlated more with plot exposure than with thicket age, suggesting that desiccation, light, and temperature may be most influential. Sheard (1968) likewise found a correlation between the prevailing north wind and the pattern of moss-lichen heath on Jan Mayen Island.

Among the most significant climatic stress inducers for mosses are high temperatures, frost, and drought (Longton 1979). Dry mosses are typically much more heat resistant than wet mosses. For example, Nörr (1974) found that eight European mosses reach lethal limits at 42-51ºC when turgid, but survive to 85-110ºC when dry. Lange (1955) found similar dry survival of mosses from 70-110ºC. Temperature relationships will be discussed more thoroughly in the chapter on temperature.

These relationships also exemplify that, although bryophytes are able to survive on rocky and shallow substrates with little water, they are unable to compete with the tracheophytes in areas where there is sufficient soil, light, and moisture for the tracheophytes to root. But at the extremes, bryophytes may have an advantage. Therefore, it is fitting to conclude our attempt to understand the water stresses of bryophytes by comparing them at the two extremes, the aquatic and the arid habitats.

Using electrolyte leakage as an indication of desiccation stress, Šinžar-Sekulić*et al*. (2005) compared the desiccation tolerance of three mosses from different moisture regimes. ***Thamnobryum alopecurum*** (Figure 13), a moss of open, vertical limestone cliffs, has the highest degree of desiccation tolerance among these three. ***Anomodon viticulosus*** (Figure 14), a moss of limestone rocks in the forest, releases electrolytes under desiccation, causing pronounced changes in the cells. The aquatic moss ***Platyhypnidium riparioides*** (Figure 15) suffers irreversible change following desiccation. It is likely that speed of drying plays a role for the latter species because its frequency on emergent rock habitats suggests that it should be adapted to slow drying. Nevertheless, it seems to live where it stays moist even during periods of low water levels.

Figure 13. ***Thamnobryum alopecurum***, a moss that has high desiccation tolerance on limestone cliffs. Photo by Michael Lüth, with permission.

Figure 14. ***Anomodon viticulosus***, a moss of limestone rocks that releases electrolytes when desiccated. Photo by Michael Lüth, with permission.

Among the hornworts (**Anthocerotophyta**) little information exists on desiccation tolerance. Some are drought avoiders, producing special structures that survive periods of desiccation (Vitt *et al*. 2014). These, occurring on hornworts of seasonally dry localities, include abundant swollen, marginal or apical tubers on the thalli (***Phaeoceros*** spp.; Figure 16-Figure 17) or long-stalked, subterranean ventral tubers (***Phymatoceros***; Figure 18). Both of these special tubers form as the sporophytes mature and persist in the soil crust or soil bank after the vegetative thallus has deteriorated. Rainfall causes these tubers to germinate and form new plants (Crandall-Stotler *et al*. 2006). Hartung *et al*. (1994) found that these tubers contain large amounts of ABA, a hormone known to induce desiccation tolerance in bryophytes (Pence *et al*. 2005). These tubers can survive at least nine months of dryness and still germinate (Vitt *et al*. 2014).

Figure 15. ***Platyhypnidium riparioides***, an aquatic moss that can suffer irreversible damage from desiccation. Photo by Des Callaghan, with permission.

Figure 16. ***Phaeoceros*** sp. showing abundance of light green tubers in the center of the thallus. Photo by Juan Larrain, with permission.

Figure 17. ***Phaeoceros pearsonii*** with thickened tubers. Photo by Li Zhang, with permission.

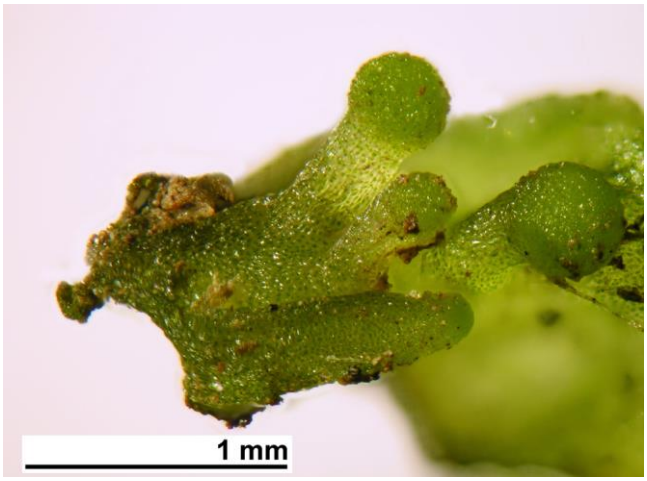

Figure 18. ***Phymatoceros bulbosus*** ventral side with tubers. Photo by David Wagner, with permission.

Other hornworts take advantage of short life cycles. For example, rapid spore release in ***Notothylas*** (Figure 19), coupled with the ability to survive many years dry (Renzaglia *et al*. 2009) permit this genus to avoid drought conditions.

Figure 19. ***Notothylas orbicularis*** showing numerous young horizontal sporophytes. Photo by Michael Lüth, with permission.

Liverworts are known for loving damp habitats, but they contain their xerophytic members as well. Seppelt (pers. comm. 1999) relayed to me that these include species surviving in as little as 150 mm of rainfall per year [***Fossombronia*** (Figure 20), ***Asterella*** (Figure 21), ***Plagiochasma*** (Figure 22)]. At somewhat higher levels (200 mm), such taxa as ***Lethocolea*** (Figure 23), ***Cephaloziella*** (Figure 24), ***Riella*** (Figure 66), ***Enigmella***, and ***Gongylanthus*** (Figure 25) appear. ***Enigmella*** is ephemeral in its vegetative phase, but its reproductive structures are well suited to their environment. Some taxa survive drought by having a shortened life cycle, *e.g.* ***Riccia cavernosa*** in the Arctic (Seppelt & Laursen 1999).

Figure 20. ***Fossombronia angulosa*** with capsule, member of a genus in which some species survive in as little as 150 mm annual rainfall. Photo by Des Callaghan, with permission.

Figure 21. ***Asterella lindenbergiana*** with archegoniophores, a member of a genus in which some species survive in as little as 150 mm annual rainfall. Photo by Martin Hutten, with permission.

Figure 22. ***Plagiochasma appendiculatum***, member of a genus in which some species survive in as little as 150 mm annual rainfall. Photo by Michael Lüth, with permission.

Figure 23. ***Lethocolea glossophylla***, member of a genus in which some species survive in 200 mm annual rainfall. Photo by Jan-Peter Frahm, with permission.

Figure 24. ***Cephaloziella*** cf ***hampeana***, member of a genus in which some species survive in 200 mm annual rainfall. Photo by Barry Stewart, with permission.

Figure 25. ***Gongylanthus ericetorum***, member of a genus in which some species survive in 200 mm annual rainfall. Photo by Michael Lüth, with permission.

Peatlands

Peatlands provide a good ecosystem for comparing adaptations for differences in moisture regimes by habitat. But the dominant moss, ***Sphagnum***, has unusual structural adaptations that can complicate this analysis.

Wagner and Titus (1984) compared desiccation tolerance of the hummock species ***Sphagnum nemoreum*** (Figure 26) to that of the hollow species ***S. fallax*** (Figure 27). The hollow species is more desiccation tolerant than the hummock species. It has both a higher number of plants surviving and a better recovery of its photosynthetic rate. However, its ability to recover decreases as the desiccation periods are lengthened or the water content is decreased. Despite being close to the water, ***S. fallax*** apparently dries more frequently and for longer periods of time than does ***S. nemoreum***. The latter species, instead, is able to remain moist in the field by holding more water when the habitat dries.

Figure 26. ***Sphagnum nemoreum***, a compact hummock moss. Photo by Michael Lüth, with permission.

Figure 27. ***Sphagnum fallax***, a loose moss of hollows. Photo by David Holyoak, with permission.

Schipperges and Rydin (1998) compared the responses of photosynthetic CO_2 exchange in five species of ***Sphagnum*** in response to tissue water content. These species ranged in microhabitat from hummock top (***S. fuscum***; Figure 28), hummock mid to top [***S. papillosum*** (Figure 29) & ***S. magellanicum*** (Figure 30)], wet areas of ombrotrophic bogs and ditches (***S. balticum***; Figure 31), to submerged (***S. cuspidatum***; Figure 32). Laboratory experiments using infrared gas analysis (IRGA) measured recovery of net photosynthesis after several long-lasting desiccation/rehydration events. One important structural adaptation that emerged is the importance of contact between capitula and basal parts of the mosses; if the

capitula were isolated from the water table, they were unable to recover from complete desiccation (<10-20% of compensation point water content; 15°C for 2-4 days). It is interesting that they found no relationship between recovery of net photosynthesis and wetness of the natural habitat. Rather, those species that live under regularly drying conditions are able to avoid death by themselves avoiding drying out, using high capillarity or a dense growth form such as that of ***S. fuscum*** (Figure 28).

Figure 28. ***Sphagnum fuscum***, a hummock top species. Photo by Michael Lüth, with permission.

Figure 29. ***Sphagnum papillosum***, a species of mid to top of hummocks. Photo by Michael Lüth, with permission.

Figure 30. ***Sphagnum magellanicum***, a species of mid to top of hummocks. Photo by Michael Lüth, with permission.

Figure 31. ***Sphagnum balticum***, a species of wet areas of bogs and ditches. Photo by Michael Lüth, with permission.

Figure 32. ***Sphagnum cuspidatum***, a submerged species. Photo by Jan-Peter Frahm, with permission.

Hájek and Vicherová (2013) concluded that ***Sphagnum*** species have inducible desiccation tolerance. These species are generally desiccation intolerant, instead using mechanisms to avoid internal desiccation, as noted by Schipperges and Rydin (1998). Hájek and Vicherová tested the inducible nature of their tolerance by using various bryophyte species, including ***Sphagnum***. They hardened the bryophytes by slow drying, ABA application, and chilling or frost. Both chilling and frost can create desiccating conditions by drawing water from the cells through the hygroscopic nature of ice crystals, much like the effects of freezer burn in your freezer. Presuming that the tolerance was inducible, they monitored the seasonal changes in desiccation tolerance of bog bryophytes. Among these, ***Sphagnum*** species in hollows and lawns developed desiccation tolerance several times during the year as a response to reduced precipitation and lowered water table. The hummock and aquatic species developed this tolerance only in the autumn, possibly responding to frost. Following initial de-hardening in the lab, untreated ***Sphagnum*** shoots lacked desiccation tolerance. On the other hand, all hardening treatments except chilling induced desiccation tolerance in all groups except those in section ***Cuspidata*** (Figure 32), a submersed species. They suggest that lack of adequate desiccation tolerance may prevent ***Sphagnum*** establishment in the drier habitats that are otherwise suitable. Those species that avoid desiccation typically do so by forming compact hummocks – or living submersed. Thus, hummock species invest their

resources in water retention, avoiding desiccation, but have a lower ability to develop desiccation tolerance.

Peatlands typically have moisture gradients, and Hettenbergerova *et al*. (2013) took advantage of this gradient to compare species richness relative to water availability. They were fortunate to have a system that graded from a spring fen to a semi-dry grassland in the Czech and Slovak Republics. They found that the number of species of tracheophytes tended to increase toward the lower moisture values. The species richness had a negative correlation with the N:P biomass ratio, whereas the percentage of endangered species had a positive correlation. These relationships for bryophytes differed markedly from those of the tracheophytes. Instead, bryophyte species richness decreased linearly toward the dry end of the transects, and there was no correlation with any of the nutrient measurements (N, P, K, C, Ca). Furthermore, the bryophytes exhibited a very high percentage of specialists in fen plots.

Sagot and Rochefort (1996) were concerned about the effects of desiccation on regeneration. They found that fragments of ***Sphagnum fallax*** (Figure 27), ***S. fuscum*** (Figure 28), and ***S. magellanicum*** (Figure 30) could survive 14 days without water when air dried at 20°C, relative humidity ~60%, but regeneration was delayed. ***Sphagnum fallax*** and ***S. magellanicum*** survived better than did ***S. fuscum***.

Aquatic Habitats

The aquatic bryophytes are distributed worldwide, but they seem to be more common in temperate than in tropical areas. Aquatic species are classified as **obligate aquatics**, having little or no tolerance to drought conditions, **facultative aquatics**, having some degree of tolerance to desiccation and xerophytic conditions, and **semi-aquatic emergents** (Vitt & Glime 1984), being in locations where they are partly in the water and partly out of it, but usually moist (Figure 33).

Figure 33. ***Fontinalis novae-angliae*** submerged and ***Plagiochila porelloides*** on the rock above the water in a New Hampshire stream. The ***P. porelloides*** is subject to intermittent flooding but can become dry when the stream level is low in mid and late summer. Photo by Janice Glime.

Rehydration in aquatic mosses is much like that of tracheophytes. Whereas many mosses are able to protect their ribosomes during dehydration (Bewley 1974), permitting rapid recovery of protein synthesis and respiration upon rehydration, aquatic bryophytes are not. Instead, irreversible ribosome damage occurs (Krupa 1977). For example, ***Cratoneuron*** (Figure 34), a semi-aquatic moss, loses ATP during rapid drying, and with its damaged ribosomes it is unable to replace it upon rehydration (Bewley & Gwozdz 1975). Aquatic mosses typically suffer membrane damage during desiccation, but **xeric** (dry habitat) mosses often do not (Brown & Buck 1979). Thus, in aquatic mosses, rehydration results in loss of nutrients.

Figure 34. ***Cratoneuron filicinum***, a moss known to lose ATP during rapid drying. Photo by Ivanov, with permission.

Even such obligate aquatic mosses as ***Fontinalis*** are subject to periods low water when they are exposed above water. Carvalho *et al*. (2011) found that the aquatic moss ***Fontinalis antipyretica*** (Figure 65) demonstrates desiccation tolerance. Laboratory experiments can be misleading because this species requires slow drying in order to survive, supporting the hypothesis of induced desiccation tolerance. In fact, Cruz de Carvalho *et al*. (2011) concluded that the protein profiles following rehydration were similar to those of the terrestrial mosses ***Physcomitrella patens*** and ***Syntrichia ruralis*** (Figure 39). They concluded that desiccation tolerance mechanisms were similar regardless of habitat.

Arid Habitats

Contrary to the popular concept that mosses must grow in wet places, a number of species are **xerophytic**, that is, adapted to places like the dry, hot desert. In such habitats, some mosses are able to absorb water from dew and night air, permitting brief photosynthesis during the early hours of morning. They dry again each day, cycling on a 24-hour wet-dry cycle (Kappen *et al*. 1979). Where the sun reaches the mosses directly, as on the south-facing slopes in North American deserts, the temperature can increase by as much as 20ºC in the first 30 minutes of daylight, thus providing too short a period for the moss to gain photosynthetic energy before drying out (Nash *et al.* 1977). In such locations the mosses are restricted to the north-facing slopes. The biomass is quite small, less than 2 g m^{-2}, but at least 18 different species are able to survive, the most common being tuft-forming taxa such as ***Syntrichia ruralis*** (Figure 39), ***Grimmia laevigata*** (Figure 36), and ***Bryum caespiticium*** (Figure 1).

One advantage of having sufficient moisture in the desert habitat is that it can provide evaporative cooling. But that does not seem to be the case in all situations. In the Mojave Desert, Nevada, USA, ***Crossidium***

crossinervium (Figure 62) experienced temperatures above ambient, independent of the state of hydration (Stark 2005). During cooler months, the moss patch exhibited a temperature lower than ambient, again with state of hydration failing to play a role. The periods of hydration were essentially restricted to the cooler months of October to April with hydration lasting 3.7-4.9 days. The longest dry period was 191 days during the measurement period. In late winter, drying was slow, lasting several days, but in the summer the mosses were dry in as little as three hours.

Peatland bryophytes are not the only ones that practice avoidance and tolerance. These practices are also common among bryophytes that live in some of the most harsh moisture conditions on the planet. One mechanism is to go dormant during the dry periods, surviving as spores, gemmae, and probably in some cases protonemata (Vitt *et al*. 2014). Such an **escape strategy** is advantageous to bryophytes that lack a physiological tolerance to desiccation in the leafy gametophore (Figure 35). Liverworts have fewer genera with an escape strategy, but many thallose liverworts have tubers or other means, especially ***Riccia***, to survive (see Figure 69); many leafy liverworts have gemmae.

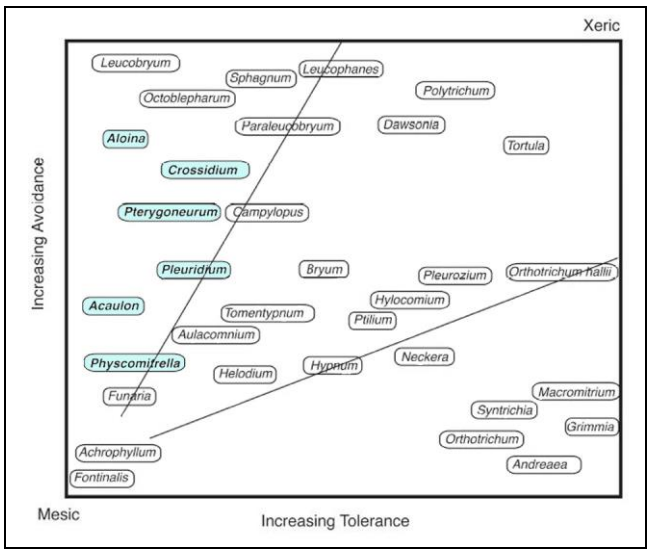

Figure 35. Comparison of representative moss genera that are able to use desiccation avoidance compared to desiccation tolerance. Those genera in blue frames are able to use escape strategies. Modified from Vitt *et al*. 2014.

Figure 36. ***Grimmia laevigata***, a desert survivor. Photo by Michael Lüth, with permission.

In the Sonoran Desert of North America, Alpert (1979) found that an overnight storm provided 85% of the saturated water contents, available at 6 a.m., for ***Bryum capillare*** (Figure 37), ***Grimmia*** spp. (Figure 36), ***Syntrichia*** spp. (Figure 39), and ***Weissia controversa*** (Figure 38). By 9 a.m., eleven of the twelve species investigated had only 2 g water per g of plant dry mass, and by 3 p.m., only 0.5 g remained. By 5 p.m., less than 0.1 g per gram of plant remained, resulting in only about 9 hours of water available from that rare storm. Richardson (1981) points out that it is not damage by drought that eliminates many species from the desert, but the very short time available for photosynthesis.

Figure 37. ***Bryum capillare*** on a tombstone, a moss that benefits from short moisture episodes, but that holds water for only about 9 hours after a desert storm. Photo by Andrew Fogg, through Creative Commons.

Figure 38. ***Weissia controversa*** dry, a moss that may have only 9 hours of hydration following a desert storm. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

One adaptation that permits some mosses to tolerate frequent dehydration/rehydration cycles is that those xeric mosses with undamaged membranes are able to retain ions by binding them to the cell wall (Brown & Buck 1979). Another adaptation in the desert moss is that rapid water loss, typical of the desert, can result in a retention of 50% of the polysomes, whereas slow drying can completely deplete them. Fortunately, in drought-tolerant mosses like ***Syntrichia ruralis*** (Figure 39), the polysomes can be strongly rebuilt after two hours of rehydration (Oliver & Bewley 1984b), but the process continues for a longer

period of time in those that were dried rapidly. RNA synthesis likewise requires six hours after rapid drying and only two hours after slow drying to reach the level of that in non-dried control mosses (Oliver & Bewley 1984a).

Figure 39. ***Syntrichia ruralis***, a drought-tolerant moss. Photo by Michael Lüth, with permission.

One unclear factor in this story is the role of nitrite. Nitrite accumulates during slow dehydration of ***Syntrichia ruralis*** (Figure 39), but not when desiccation is rapid (Mahan *et al.* 1998). Upon rehydration, the nitrite in the slowly-dried moss declines and reaches normal levels within one hour. Mahan and coworkers considered that the nitrite might provide a nitrogen source for the nitrogen metabolism needed during rehydration. On the other hand, Brown and Mahmood (1996) determined that nitrite apparently causes considerable membrane damage in the mesophytic ***Mnium hornum*** (Figure 40); thus we need further research to understand the conditions under which it is detrimental vs adaptive.

Figure 40. ***Mnium hornum***, a moss in which cell membranes suffer damage from elevated nitrite concentrations during dehydration. Photo by David T. Holyoak, with permission.

Marschall (1998) examined the activity of nitrate reductase during desiccation and rehydration of nine bryophytes and concluded that there was no difference in the proportional decrease in nitrogen reductase activity between desiccation-tolerant and non-tolerant bryophyte taxa. Eight of these bryophytes did exhibit detectable nitrate reductase (NR) activity. Pretreatment with KNO_3 did affect the increase in NR activity between these two types, with the desiccation-tolerant ***Syntrichia ruralis*** var. ***arenicola*** (Figure 39) increasing activity by a factor of 3 while the desiccation-intolerant ***Dicranum majus*** (Figure 41) and ***Hookeria lucens*** (Figure 42) had a 6-fold increase in nitrate reductase activity. Following rehydration, ***Syntrichia ruralis*** (Figure 39) exhibited a marked decline in NR activity during the first hour, whereas the epiphytic/saxicolous ***Porella platyphylla*** (Figure 43) maintained a relatively constant low level in the light but increasing NR activity in the dark. While we might assume that these physiological differences relate to survival, it is too early to explain just how this is accomplished.

Proctor (1982) considers such structures as papillae to be adaptive in ensuring that the moss does not spend a long period of time in a semi-dry state, during which it is likely to lose more carbon by respiration than it gains by photosynthesis. He notes that the papilla systems, so common on xerophytic leaves, are often separated by regions where the capillary continuity is broken at high water potentials, causing the leaf to have either an abundant water supply, or none. Such discontinuities could be amplified if the leaf rolls as it dries and bends away from the discontinuity. Vanderpoorten and Engels (2002) considered papillae so important as to be one of only four life history traits contributing to predictability of species occurrence in a particular environment on a regional scale. Nevertheless, experiments on the role of papillae in conserving water have mostly failed (Frey & Kürschner 1991).

Figure 41. ***Dicranum majus*** near Swallow Falls, Wales, a moss that is desiccation-intolerant. Photo by Janice Glime.

Figure 42. ***Hookeria lucens***, a desiccation-intolerant species. Photo by David T. Holyoak, with permission.

Figure 43. ***Porella platyphylla***, an epiphytic/saxicolous liverwort. Photo by Michael Lüth, with permission.

Few bryophytes approach the succulent or sclerophyll strategies known in tracheophytes (Grime 1977), although one might argue for succulence in the Marchantiales. Plants with numerous or large papillae take on the appearance of sclerophylls, and for many years we assumed that papillae functioned to prevent the loss of water. However, as Frey and Kürschner (1991) pointed out, tests to validate that theory have failed. Nevertheless, while it appears that the papillose mosses do not slow down water loss, the papillae may have a function in water uptake (Crandall-Stotler & Bozzola 1991). As discussed earlier with leaf strategies (see Chapter 7-4a of this volume), papillae in ***Andreaeobryum macrosporum*** (Figure 44) are constructed in such a way that they provide a channel for the uptake of water.

Figure 44. ***Andreaeobryum macrosporum***, a moss with papillae that provide a pathway for uptake of water. Botany website, University of British Columbia, Canada, with permission.

I have suggested that papillae on some mosses might also function to scatter light during dry periods, thus aiding in the protection of the chlorophyll from the UV light during the lengthy time the leaf is exposed, with no chance for repair between rainfall events.

Alpert (1979, 1982, 1985, 1988) investigated five species of **poikilohydric** mosses (those that depend on external conditions to regulate their water content): ***Schistidium apocarpum*** (Figure 45), ***Grimmia laevigata*** (Figure 36), ***Hedwigia ciliata*** (Figure 46), ***Orthotrichum rupestre*** (Figure 47), and ***Syntrichia ruralis*** var. ***crinata*** (see Figure 39). These bryophytes are characterized by short cushions of tufted growth, except for ***Hedwigia ciliata***. The latter moss has a whitened appearance due to numerous papillae, and its leaves are closely appressed to the stem when dry. When wet, the leaves spread broadly, causing it to look sufficiently different from its dry state that it causes many bryologists to stop and puzzle over its identity.

Alpert (1979, 1982, 1985, 1988) found that these five mosses were able to colonize unoccupied, stressful boulder habitats, but that they were intolerant of competition or of disturbance beyond their normal desiccation regime. They grew in particular microclimatic niches on the rock substrata and were unable to occupy the most xeric conditions within the same macroclimate, although laboratory studies indicated that they can tolerate both temperatures and droughts that exceed those of the habitats they occupy. Alpert showed through transplant experiments that they could indeed occupy additional locations, suggesting that dispersal and establishment impose limits on their distribution.

Figure 45. ***Schistidium apocarpum*** with capsules, an ectohydric moss. Photo by Michael Lüth, with permission.

Figure 46. ***Hedwigia ciliata***, an ectohydric moss shown here on rock. Photo by Janice Glime.

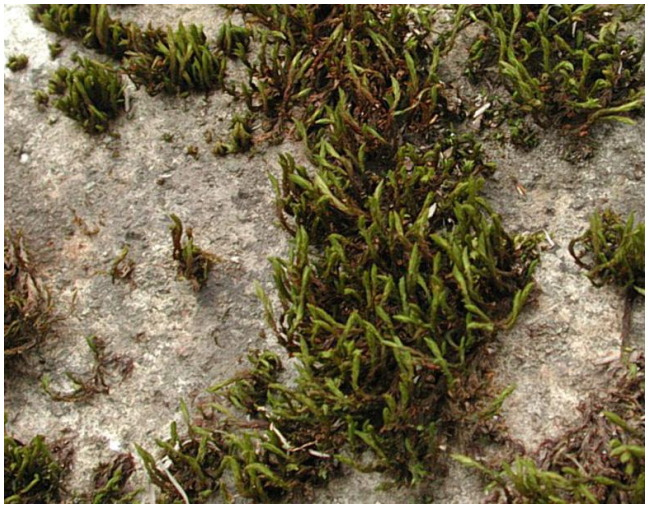

Figure 47. ***Orthotrichum rupestre***, a xerophytic moss on rock. Photo by Michael Lüth, with permission.

The aspect and angle of slope had strong influences on the evaporation stress experienced by these mosses (Alpert 1979, 1982, 1985, 1988). Mosses growing under rock overhangs should experience the least water stress by late day, but do not regain as much moisture as those at 15° and 75° slopes (Figure 48). As expected, mosses at the tops of boulders had the greatest peaks of evaporation stress. Alpert's work illustrates the importance of 24-hour measurements in comparing potential evaporative stresses of different microsites.

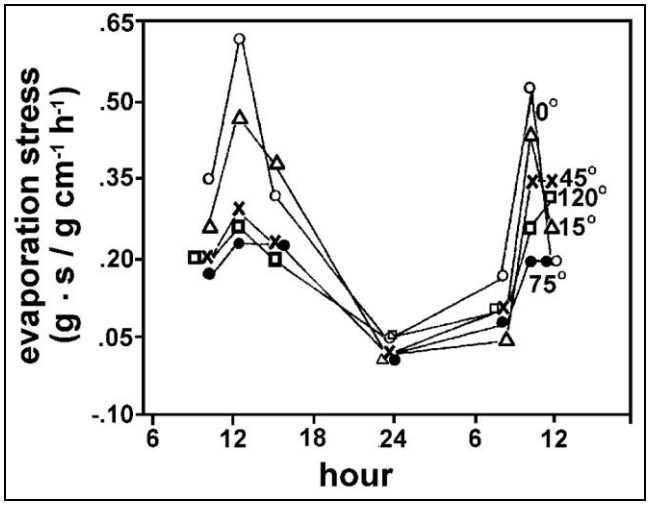

Figure 48. Effects of degree of slope on potential evaporation on 21-22 February 1980 for mosses (based on uniform paper samples) on arid north sides of rocks in five slope microsites. (n=4) Modified from Alpert (1982).

Aspect separated the evaporation stresses even more clearly (Figure 49), with evaporation stress on the east side peaking at about 10:00 hours and at most other aspects peaking at about 12:00 hours (Alpert 1982). Stress on the west side peaked last, at 14:00 hours, but with a lower peak than at the other aspects. The north, as might be expected, had the least daily variation. Although daily evaporation potential was high, a brief nighttime rainfall of no more than 5 mm was sufficient to rewet the moss for several days (Figure 50, Alpert 1982).

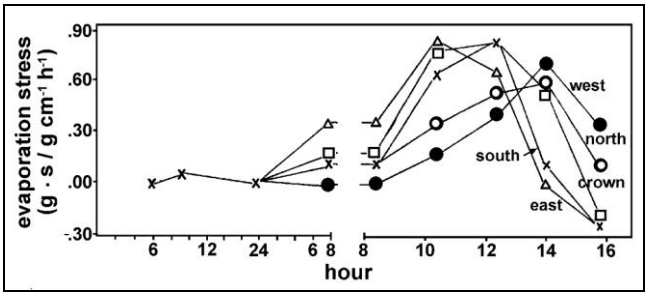

Figure 49. Effect of aspect on potential evaporation on 7-8 March 1980 for mosses (based on uniform paper samples) on arid 45° slope in five aspect microsites. (n=4) Modified from Alpert (1982).

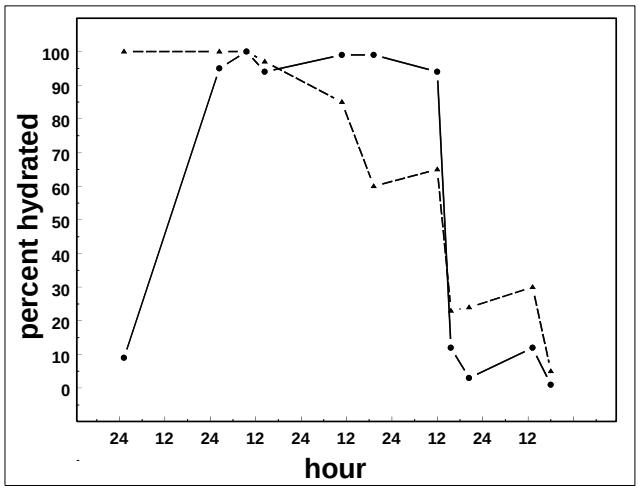

Figure 50. Percent hydration of natural moss cover on boulders following nighttime rainfalls of ~5 mm in spring and winter. Redrawn from Alpert (1982).

Open, exposed soils in temperate climates are arid for bryophytes because of their insignificant soil penetration by which to obtain water. In these habitats, the mosses ***Barbula*** (Figure 51), ***Syntrichia*** (Figure 39), and the thallose liverwort ***Riccia*** (Figure 52) are able to survive (Schofield 1985). The two mosses are both papillose and able to roll their leaves and contort them as they dry. The ***Riccia*** thallus usually has inrolled margins and a thick cuticle; Frey and Kürschner (1991) have demonstrated that thallus and leaf inrolling correlate with increasing aridity, suggesting a protective role. ***Ceratodon*** (Figure 53), ***Funaria*** (Figure 54), and ***Cephaloziella*** (Figure 55) seem to lack any structural adaptations to their sometimes dry habitats, although ***Ceratodon*** does have crispate leaves and rolled margins.

In cryptogamic crusts of arid regions, bryophytes are important in holding water, retaining several times their volume after rainfall (Mücher *et al*. 1988; Rivera-Aquilar *et al*. 2005). This leads to higher germination rates of seed plants compared to areas with no crust (Mücher *et al*. 1988; Rivera-Aquilar *et al*. 2005; Serpe *et al*. 2006)

Figure 51. ***Barbula convoluta*** var. ***commutata***, an ectohydric moss growing on rock over little or no soil. Michael Lüth, with permission.

Figure 52. ***Riccia nigrella***, a thallose liverwort surviving on dry soil. Photo by Michael Lüth, with permission.

Figure 53. ***Ceratodon purpureus*** on rocky soil, a moss that has few structural adaptations to such a dry habitat. Photo by Janice Glime.

A comparison of mosses from a variety of habitats in Israel revealed varying degrees of drought tolerance that related well to their habitats (Di Nola *et al*. 1983). The desert mosses ***Tortula brevissima*** (Figure 56) and ***Trichostomopsis aaronis*** exhibited rapid return of metabolic activity after prolonged drying and were able to resume photosynthesis without new chlorophyll synthesis. The Mediterranean moss ***Barbula fallax*** (Figure 57) behaved similarly to the desert mosses, but ***Homalothecium aureum*** (Figure 58) and ***Didymodon tophaceus*** (Figure 59), more mesic mosses, had slow recovery after desiccation. ***Mniobryum*** sp. (Figure 60) had almost no drought tolerance and was killed by the prolonged drying.

Figure 54. ***Funaria hygrometrica***, a moss with no noticeable xerophytic adaptations, living on sand and rocks. Photo by Michael Lüth, with permission.

Figure 55. ***Cephaloziella stellulifera***, a leafy liverwort that seems to lack structural adaptations to this rock habitat. Photo by David T. Holyoak, with permission.

Figure 56. ***Tortula brevissima***, a desert moss that rapidly returns its metabolic activity upon rehydration. Photo by Michael Lüth, with permission.

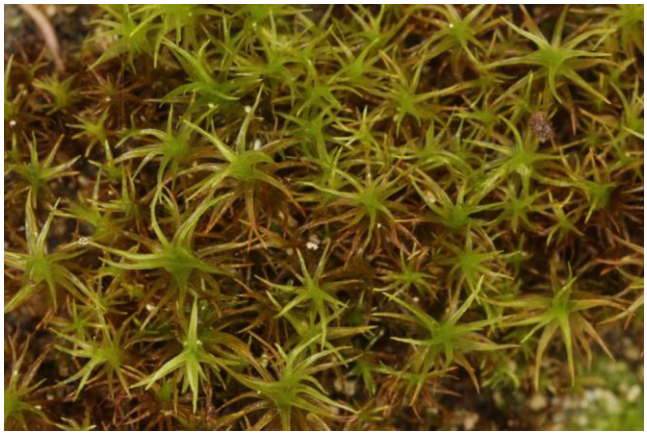

Figure 57. ***Barbula fallax***, a Mediterranean moss that resumes metabolic activity rapidly upon rehydration. Photo by Jan-Peter Frahm, with permission.

Figure 58. ***Homalothecium aureum***, a mesic moss. Photo by Michael Lüth, with permission.

Figure 59. ***Didymodon tophaceus***, a mesic moss. Photo by Michael Lüth, with permission.

Longton (1988b) pointed out the importance of dispersal among desert bryophytes, since many of them are drought avoiders. Since sexual reproduction will occur infrequently, he contends that desert mosses should be acrocarpous **perennial stayers** with long-lived, desiccation-tolerant gametophytes, small spores, and long setae. The **annual** taxa are **ephemeral** (short-lived) mosses and liverworts that can develop rapidly after a rain because their dormancy is accomplished by large spores; their capsules are often immersed, presumably shortening the time required to mature and preserving moisture. The **perennial shuttle** species are mostly thallose liverworts that have both desiccation-tolerant gametophytes and large spores. **Fugitives** generally stay only one to two years while the habitat remains suitable at a site and produce small spores that permit them to be dispersed easily.

Figure 60. ***Mniobryum wahlenbergii***, a moss that has little or no drought tolerance. Photo by Jan-Peter Frahm, with permission.

The short duration of the life cycle is one of the advantages provided to many desert bryophytes. In the southwestern desert habitat (USA), the desiccation-tolerant ***Syntrichia ruralis*** (Figure 39) requires a year to reach maturity, producing new innovations in midwinter and growing slowly through spring (Mishler & Oliver 1991). In late summer, it lengthens rapidly, completing its growth by midwinter. Female gametangia are initiated in midwinter and terminate the growth of these innovations. However, the female gametangia are present during the next 6 to 9 months on these innovations, ultimately disappearing some time between June and August. In the New Mexico populations observed by Mishler and Oliver, there were no male gametangia, and thus no sporophytes produced. Consequently, this plant must propagate entirely by vegetative means.

In the Negev Desert, southern Israel, the dioicous moss ***Bryum dunense*** takes advantage of fog and dew prior to the first winter rain to initiate its reproductive organs (Herrnstadt & Kidron 2005). The sporophytes are most common in partially shaded habitats and appear following the winter rains. This reproduction is supplemented by the typically more reliable reproduction through bulbils in the partially shaded and exposed habitats, whereas secondary protonemata are most abundant in the shaded habitats.

Alpert and Oechel (1985) hypothesized that even the xerophytic mosses cannot live in the most xeric habitats due to their inability to maintain a positive carbon balance. ***Grimmia laevigata*** lives under the xeric conditions of rocks and boulders. When subjected to such extreme conditions of long, severe drought and extreme temperatures, this moss supported the hypothesis.

Sporophyte Damage

The leafy gametophyte is not the only generation affected by desiccation. For desert mosses, too little rainfall in early sporophyte development can also be a problem. In the Mojave Desert, Nevada, USA, the moss ***Syntrichia inermis*** (Figure 61) experienced 66% abortion of sporophytes due to a reduced winter-spring rainfall

(Stark 2002). But unusually heavy rains in the summer likewise resulted in an increase in sporophyte abortion from 9 to 43%. Stark suggested that the summer abortions may have been the result of membrane damage resulting from rapid drying as well as from high temperatures while hydrated. ***Crossidium crassinervium*** (Figure 62) experienced similar sporophyte abortions in the same desert (Stark 2005).

Figure 61. ***Syntrichia inermis*** dry, a moss whose sporophytes experience considerable abortion due to desiccation. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 62. ***Crossidium crassinervium*** with one young sporophyte, a moss whose sporophytes experience considerable abortion due to desiccation. Photo by Michael Lüth, with permission.

Grimmia orbicularis (Figure 63) can suffer sporophyte abortion as a result of poor timing. It was summer rainstorms in the Mojave Desert that led to the demise of ~50% of the sporophytes, mostly in the seta elongation phase (Stark 2001). As in ***Syntrichia inermis*** (Figure 61), Stark suggests that the abortion resulted from stresses caused by wet-dry cycles during summer heat, a time when the moss would normally be dry and have arrested metabolism. This may have been complicated by the premature seta elongation that resulted in more exposure during the remainder of the summer or that set in motion the physiology for capsule maturation at a time when insufficient nutrients were available.

The arid and semi-arid lands occupy approximately 40% of the land on planet Earth (Reed *et al*. 2012). Climate change that changes annual rainfall could result in profound mortality of bryophytes growing there. An increase of rainfall frequency, resulting in only a 1.2 mm increase in summer rainfall, reduced the moss cover of ***Syntrichia caninervis*** (Figure 64) from approximately 25% cover to less than 2% in just one growing season. The addition of small precipitation events resulted in a negative carbon balance; larger events are able to maintain carbon balance. The loss of moss cover changed the nitrogen cycling, reducing soil fertility. On the other hand, increased temperature had no effect.

Figure 63. ***Grimmia orbicularis***, a moss that suffers sporophyte abortion if the wet/dry cycles have the wrong timing during sporophyte development. Photo by Michael Lüth, with permission.

Figure 64. ***Syntrichia caninervis***, a desert moss. Photo by Michael Lüth, with permission.

Syntrichia caninervis has served as a model for successful desert living by bryophytes. Wu *et al*. (2015) demonstrated that when only 2 mm of precipitation wets the leaves of ***Syntrichia caninervis*** (Figure 64), the moss loses carbon. It requires 5 mm of precipitation for a carbon gain. Hence, short storms can be detrimental to the moss, explaining the loss of moss cover with the increase in frequency of rainfall and gain of 1.2 mm rain in the Colorado Plateau, USA (Reed *et al*. 2012).

This loss of carbon is despite the rapid recovery of ***Syntrichia caninervis*** (Figure 64). Within only one minute, it recovers 90% of its photosynthetic yield (Zhang *et al*. 2011). In fact, this species can use moisture from dew and fog, collected and directed into the leaf by its hair points (Tao & Zhang 2012). In addition to the collection effect of the hair tips, mosses from dry habitats have high osmotic values that enable them to absorb water vapor from the air. These attributes seem almost contradictory to the

loss of cover due to a minor increase in rainfall events in the desert, but a short daytime rainfall is quite different from the prolonged moisture available from fog or dew at night. Daytime moisture from a short rainfall lasts for a very short time, apparently insufficient to recover the lost energy before high temperatures and evaporation shut it down. Yet this leaves the question of rebuilding energy at night. It suggests that it is the cellular changes that use up one readily available form of energy but do not permit rebuilding it, whereas the hydrated cells from dew are fully functional and ready for photosynthesis with the first light of day – there should be no delay at all. At this time the moss is still cool from the night and evaporation should be slower.

Desiccation from Salt

Salt pans and regions of salt spray, when not under water, can be the most arid conditions of all. Few bryophytes are adapted to this regime, although some species of ***Fontinalis*** (Figure 65) can tolerate **brackish** (somewhat salty, often from a mix of fresh and salt water) waters. The liverworts ***Riella helicophylla*** (Figure 66), ***R. numidica***, and ***Carrpos*** (?) are among the few (Schofield 1985).

Figure 65. ***Fontinalis antipyretica***, member of a genus where some species tolerate brackish water. Photo by Bernd Haynold, through Wikimedia Commons.

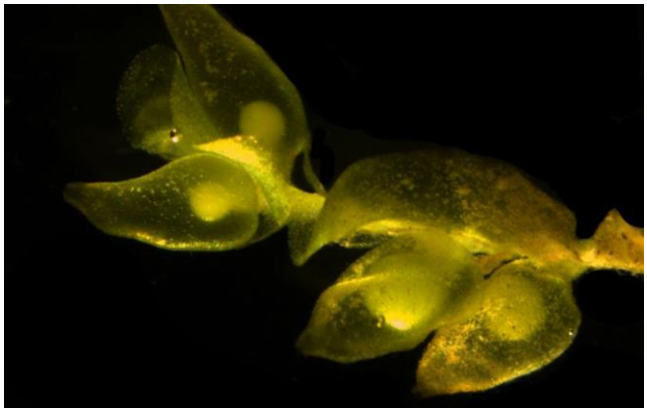

Figure 66. ***Riella helicophylla***, a thallose liverwort that is able to tolerate brackish water. Photo by NACICCA, through Creative Commons.

Flood Plains

The flood plain habitat is one of extremes. For part of the year the inhabitants are under water, but once the water recedes the habitat can become extremely dry. This regime requires different adaptations from other kinds of dry habitats.

A number of thallose liverworts exhibit drought or desiccation tolerance (Figure 69) and are able to live in these alternating habitats (Bischler 1998; Wood 2007). Such genera include fairly small liverworts with thick thalli and short life cycles: ***Corsinia*** (Figure 67), ***Cronisia***, ***Exormotheca*** (Figure 68), ***Monocarpus***, ***Riccia*** (Figure 52), and ***Targionia*** (Figure 70). But larger thalli in the **Aytoniaceae** [***Asterella*** (Figure 71), ***Mannia*** (Figure 72), ***Reboulia*** (Figure 73)] also exhibit desiccation tolerance (Vitt *et al*. 2014). Much of this tolerance may be structural. For example, these genera typically roll their edges to avoid desiccation. Their pegged rhizoids serve as water conduits and help them to resist desiccation in periodically dry habitats by providing capillary spaces [*e.g.* ***Mannia***, ***Plagiochasma*** (Figure 74), ***Targionia***] (Duckett *et al.* 2014). On the other hand, liverworts from moist habitats tend to be drought intolerant (Figure 69). These include genera with thin thalli such as ***Pellia*** (Figure 75), ***Fossombronia*** (Figure 76), ***Moerckia*** (Figure 77), ***Pallavicinia*** (Figure 78), and ***Symphyogyna*** (Figure 79). Likewise, the primitive genera of ***Haplomitrium*** (**Haplomitriidae;** Figure 80), ***Treubia*** (**Treubiidae;** Figure 81), and ***Apotreubia*** (**Treubiidae**) all grow on constantly moist soil and are drought intolerant (Wood 2007).

Figure 67. ***Corsinia coriandrina***, member of a genus with thick thalli and short life cycles. Photo by Michael Lüth, with permission.

Figure 68. ***Exormotheca pustulosa***, member of a genus with thick thalli and short life cycles. Photo by Michael Lüth, with permission.

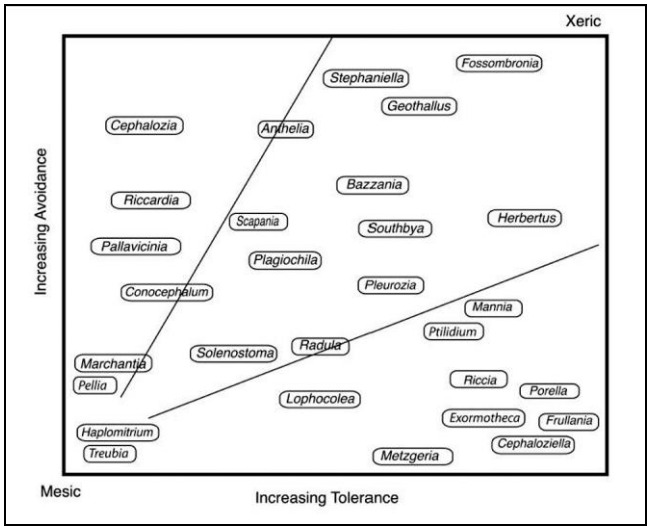

Figure 69. Comparison of liverwort genera with desiccation tolerance vs those with avoidance. Many species of ***Riccia*** are able to use the escape strategy by going dormant to avoid desiccation. From Vitt *et al*. 2014.

Figure 70. ***Targionia lorbeeriana***, member of a genus with thick thalli and short life cycles. Note the black marsupia visible from the ventral side of the thalli. Photo by Michael Lüth, with permission.

Figure 71. ***Asterella saccata***, a large thallus with desiccation tolerance. Photo by Jan-Peter Frahm, with permission.

Figure 72. ***Mannia fragrans***, a large thallus with desiccation tolerance. Note how it rolls as it dries. Photo by Michael Lüth, with permission.

Figure 73. ***Reboulia hemisphaerica***, a large thallus with desiccation tolerance. Photo by Michael Lüth, with permission.

Figure 74. ***Plagiochasma appendiculatum***, a large thallus with desiccation tolerance. Photo by Michael Lüth, with permission.

Figure 75. ***Pellia epiphylla***, member of a genus with thin thalli that are desiccation intolerant. Photo by David T. Holyoak, with permission.

Figure 76. ***Fossombronia caespitiformis***, member of a genus with thin thalli that are desiccation intolerant. Photo by Des Callaghan, with permission.

Figure 77. ***Moerckia blyttii***, member of a genus with thin thalli that are desiccation intolerant. Photo by Michael Lüth, with permission.

Figure 78. ***Pallavicinia lyellii***, member of a genus with thin thalli that are desiccation intolerant. Photo by Jan-Peter Frahm, with permission.

Figure 79. ***Symphyogyna brasiliensis*** female plant, member of a genus with thin thalli that are desiccation intolerant. Photo by George J. Shepherd, through Creative Commons.

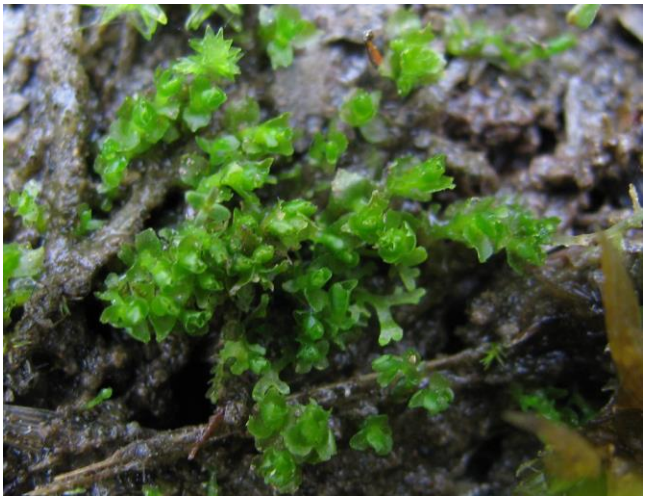

Figure 80. ***Haplomitrium hookeri***, a desiccation-intolerant bryophyte of damp or wet habitats. Photo by Janice Glime.

Figure 81. ***Treubia*** sp, a desiccation-intolerant bryophyte of damp or wet habitats. Photo by Jan-Peter Frahm, with permission.

Volk (1984) elucidated the behavior of the genus ***Riccia*** in these flood plain circumstances in Namibia. These are seasonally very dry habitats and members of the genus ***Riccia*** are very common. In this genus, the dorsal (upper) surface is unable to take in water. The ventral surface can absorb water through capillary action among rhizoids and scales, and in some cases hairs. During the dry period, they roll their thalli, exposing these rhizoids and scales from the ventral surface. This rolling thus facilitates the uptake of water from rainfall when it first occurs. These perennial species are very drought resistant and can survive up to seven years with no new water input. They are able to endure heat to greater than 80°C when dry, whereas temperatures above 50°C injure wet plants. They are unable to compete with other plants, but annual species survive by producing large numbers of spores. Perennial species produce fewer spores and survive primarily by going dormant.

Arctic and Antarctic

Kennedy (1993) asked "What limits the presence, distribution, and abundance of life in Antarctica?" To this question he answered that isolation restricts arrival and the paradigm has been that the extreme cold limits survival. But he challenges the latter tenet, suggesting that instead it is moisture that limits the organisms on vertical, horizontal, and temporal scales. Gradients in meltwater, seepage, and upwelling create moisture differences on a continental scale.

Antarctic communities, in particular, experience physiological extremes in water availability and bryophytes must survive both desiccation and submergence (Wasley *et al*. 2006). Growth rate is slow (mean for 17 yrs was 3.7 g dw m^{-2} y^{-1}) (Kanda 1986), providing limited opportunity to compensate for losses during drying. Exposure accounts for the loss of bryophyte flora in many circumstances. This can be particularly true in Arctic climates. Flock (1978) found that acrocarpous mosses dominated in areas with only light snow cover, but in areas with deep snow the pleurocarpous mosses were more abundant. The reason for this is unclear, but one might hypothesize that pleurocarpous mosses are less likely to suffer apical damage from the heavy snow, and even if they do, they usually have numerous growing points to permit their continuation. In this seasonally arid climate, primarily soil moisture and slope account for the distribution of moss communities (LaFarge-England 1989).

At Wilkes Land, Antarctica, colonies of ***Bryum algens*** with a dense tomentum of rhizoids held significantly more water than those with sparse rhizoids (Lewis Smith 1988). In ***Schistidium antarcticum***, the dense shoot arrangement facilitates its high water-holding capacity in the turf form, whereas when this species has less densely packed shoots and thicker cell walls in xeric cushions it maintains a lower water content. On the other hand, the loss of water was much faster in the turf form and the tomentose form of ***Bryum algens***, but this relationship was reversed when it was expressed as a percentage of the initial water content. The mosses take several times longer to reach minimal water conditions when compared to the lichens.

Some mosses form large mounds on the Antarctic terrain. Robinson *et al*. (2000) were able to demonstrate the relationship of desiccation tolerance to habitat in three of these moss species. ***Schistidium antarcticum*** (Figure 82), limited to relatively wet sites, had the least ability to sustain photosynthesis during desiccation. The worldwide ***Ceratodon purpureus*** (Figure 83) had the most and inhabited the driest sites. Intermediate in tolerance was ***Bryum pseudotriquetrum*** (Figure 84), which occupied intermediate habitats and exhibited the greatest plasticity of the three. These responses fit their typical habitat distribution, with ***Ceratodon purpureus*** being common in the driest sites and ***Schistidium. antarcticum*** living in relatively wet sites. Following desiccation, ***Bryum pseudotriquetrum*** contains **stachyose**, a soluble carbohydrate known to provide desiccation tolerance to seeds.

Figure 82. ***Schistidium antarcticum***, a moss limited to relatively wet sites. Photo by Rod Seppelt, with permission.

By contrast, ***Ceratodon purpureus*** has poor survival when it is submerged (Wasley *et al*. 2006). The wet habitat ***Schistidium antarcticum***, on the other hand, has high submersion tolerance. ***Bryum pseudotriquetrum*** (Figure 84) is an intermediate species that is able to co-exist with both of these species and has flexible responses.

Davey (1999) summed up the Antarctic situation by stating that mosses from hydric habitats had lower carbohydrate and higher protein, nitrogen, and phosphorus content than species from drier habitats, suggesting that the

constant flushing provided nutrients. This emphasizes another aspect of the importance of both water and physical factors in the success of Antarctic mosses.

Figure 83. ***Ceratodon purpureus***, the moss with the greatest ability to sustain photosynthesis during desiccation in the Antarctic study of Robinson *et al*. (2000). Photo Rod Seppelt, with permission.

Figure 84. ***Bryum pseudotriquetrum***, the moss with intermediate ability to sustain photosynthesis during desiccation in the Antarctic study of Robinson *et al*. (2000). Photo by Rod Seppelt, with permission.

Are the responses of Antarctic species different from those of other habitats? Apparently not very. Davey (1997) examined effects of various desiccation regimes on photosynthesis of 14 bryophyte species. Using testing intervals of 6 months and 12 months of desiccation, Davey found that the photosynthetic rate decreased as the length of dehydration period increased in all these species. The xeric species had greater retention of photosynthetic rate than did the hydric species, but even the hydric species retained some photosynthesis. Repeated cycles of wet/dry do more harm than continuous dehydration to the hydrophytic species, but the mesophytic and xerophytic species show the opposite response, suggesting that the mesophytic and xerophytic species were able to recover better during short periods of hydration. As the season progresses from spring to autumn, the percentage loss of photosynthetic rate following dehydration/rehydration increases, and this change is most evident in the hydrophytic species. At the same time, it appears that the long winters with concomitant water stress have driven these species to similar adaptations to those of some desert species.

Longton (1988a) concluded that phenotypic plasticity, opportunistic responses in CO_2 exchange, and a poikilohydric water strategy endowed the polar bryophytes with their considerable frost and desiccation tolerance. But he was quick to point out that this plasticity was not unique to polar bryophytes, but rather was common among bryophytes in general. To really understand polar adaptations we need to do physiological studies on the **endemic** (restricted to a certain area) species.

Bryophytes and water level are intimately related in the Arctic. Where the water table is maintained above the bryophyte surface, marshes develop. Where the water table is high above the permafrost, but remains below the bryophyte surface, fens develop. These moss tundras normally have no standing water and water courses are able to move through them from below the surface, maintaining the fen status. The standing water level is thus the primary factor determining the species alliances in that area. Some species complexes, such as that of the ***Catoscopium nigritum*** community (Figure 85), require a temporary period of desiccation to subsist (Vanderpuye *et al*. 2002).

Figure 85. ***Catoscopium nigritum*** exhibiting its fen community where temporary desiccation is required. Photo by Michael Lüth, with permission.

The role of bryophytes in mediating water in the sub-Arctic is crucial for making climate models that adequately predict the effects of climate change. Using ***Sphagnum fuscum*** and ***Polytrichum piliferum***, Street *et al*. (2012) demonstrated that the model does not adequately predict the effect of turf water content on their primary productivity fluxes.

In subarctic mires, water balance often determines which species will dominate (Sonesson *et al*. 2002). When the codominant mosses ***Sphagnum fuscum*** and ***Dicranum elongatum*** were subjected to increased precipitation, both species increased their growth rate, up to 5 mm per day. ***Sphagnum fuscum*** had a 50% higher response in growth compared to ***Dicranum elongatum***, a species of drier habitats than those of ***S. fuscum***. In winter, the responses were affected by the neighboring plants. ***Sphagnum fuscum*** grew better when it was next to ***Dicranum elongatum***, but ***D. elongatum*** also did better when next more ***D. elongatum***.

In the Arctic tundra, Rixen and Mulder (2005) found that high moss species diversity increased productivity, especially in low-density plots, when the plots were

watered regularly. Furthermore, moisture retention was greater in plots with high species richness. Furthermore, plant height was greater in mixed cultures than in single-species cultures. Likewise, 10 out of 12 species grew better in mixture than in monoculture when the density was high and droughts were short. It is interesting that this is the opposite of the relationships found in temperate moss communities.

As suggested by the Antarctic species discussed above, growth form is important in these cold environments that are frequently subjected to water stress. In the subalpine habitat, Nakatsubo (1994) found that large cushions and compact mats were the most common among the xerophytic species. The mesophytic species of the coniferous forest, by contrast, were smooth mats, wefts, and tall turfs. The relation between evaporation rate per basal area of the moss and dry weight per basal area of the colony correlated closely with the growth form. Nakatsubo concluded that the difference in the evaporation rate per weight between the xerophytic and mesophytic species was largely due to the difference in dry weight per basal area of the colony, and that the growth forms of the xerophytic species were suitable for increasing dry weight per basal area of the colony without increasing surface roughness. Increasing surface roughness would lead to an increase in evaporation rate due to increased exposed surface area and increased air turbulence.

Forest Floor

The forest floor would seem to be the most straight-forward and familiar habitat for most of us who have lived our lives in the temperate zone and who hunt mosses. But water relations in this habitat are not so simple. Bryophytes may actually deprive the trees of water in several ways.

In her collections of water samples under moss mats and without moss mats in a Jack pine forest (*Pinus banksiana*), Scafone (unpublished data) found that there were many occasions when 1-2 cm of water accumulated in the collectors with no moss, but the collectors under the moss mats were dry. This means the soil does not receive any of the throughfall during short or light rainfall events where there is a substantial moss mat on the surface. Such a cover is common in boreal and pine forests, depriving upper fine roots of much needed moisture.

But it appears that mosses can even derive their moisture at night from the soil. Carleton and Dunham (2003) accounted for moisture available to mosses during dry summer weather by explaining nocturnal cooling on the forest floor. Cooling of the soil surface at night was sufficient to bring the moss to dew point, reversing the daytime temperature gradient in the forest floor organic profile. By using a vapor barrier for comparison, they determined that the soil provides an upward movement of water at night that permits moss shoots to survive summer "dry-downs." This happens most noticeably in late summer when organic layers have accumulated the most warmth.

Temperate Epiphytes

Epiphytes are subjected to feast or famine for their water needs. In the growing season, they can get flooded by stem flow and may grow best on the side of the tree that gets better stem flow. In the winter they often remain exposed, unprotected by snow, and subject to the harsh, dry winds.

Trynoski and Glime (1982) demonstrated the apparent role of winter when they mapped the locations of epiphytic bryophytes in a northern deciduous forest in the Keweenaw Peninsula of Michigan, USA. The highest cover at the base was on the north side of the tree, but contrary to popular belief, midway between the base and breast height it was greatest on the south side. They attributed this southern location to the drying winds from the north and a safe haven in the space between the tree trunk and the snow that provided a moist microcosm where sufficient sun could penetrate through the snow to permit photosynthesis in winter.

Where winters are not in a constant state of snow cover, they may afford a better growing season for epiphytes due to cooler temperatures and fewer dry days. In British woods, Pitkin (1975) found that most of the growth of the epiphytes ***Hypnum cupressiforme*** (Figure 86) and ***Platygyrium repens*** (Figure 87) occurred in autumn and winter. A similar pattern of growth was found for epiphytes at a second location, and growth periods in both locations corresponded with greater moisture. When summers were wet, the winter growth did not increase proportionally to the summer increase. In wetter climates, temperature and day length have greater importance in determining growth rates.

Figure 86. ***Hypnum cupressiforme***, a species that grows mostly in winter in British woods. Photo by Michael Lüth, with permission.

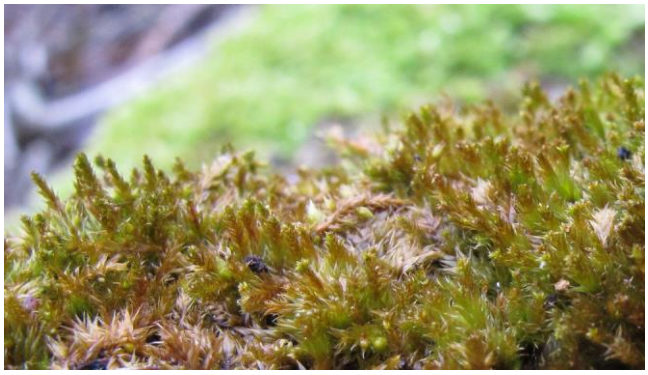

Figure 87. ***Platygyrium repens*** with bulbils, a species that grows most in autumn and winter in British woods. Photo by Michael Lüth, with permission.

Wu *et al*. (1987) found that epiphyllous liverworts in southeast China required about two hours of direct light and ten hours of diffuse light in winter, with light, temperature, and humidity being the primary factors to control their distribution.

Tropics, Rainforests, and Cloud Forests

Cloud forest (Figure 88) and rainforest bryophytes can experience a wide range of water status in a single 24-hour period (Zotz *et al*. 1997). In a submontane tropical rain forest in Panama, both low and high water content limited carbon gain significantly on a daily basis for bryophytes exhibiting a variety of life forms. More than half of the daily carbon gain (mean 2.9 mg C per g plant) is lost through respiration at night.

Figure 88. ***Macromitrium*** habitat on a tree in a New Zealand cloud forest. Photo by Vita Plasek, with permission.

Although we are beginning to understand the broad aspects of tropical bryophyte ecology, understanding of their physiology has been hampered by taxonomic difficulties and remoteness of the study site from most of the research labs. Hence, only a few studies exist on their desiccation tolerance (*e.g.* Renner 1933; Biebl 1964a, b).

Johnson and Kokila (1970) reviewed desiccation responses in primitive photosynthetic organisms and surmised that in the algae, accumulation of fat in cells, thickening of the cell walls, and accumulation of mucilage can facilitate desiccation resistance. Other characters that correlate with resistance in some algae include resistance to plasmolysis in a hypertonic solution, rigid and viscous protoplasm, and more abundant granules. But in the mosses ***Bryum*** (Figure 1) and ***Mnium*** (Figure 40) the viscosity decreased during drying. Hence, Johnson and Kokila considered how applicable these attributes might be to the desiccation tolerance of tropical bryophytes. They examined ten species that represented a wide range of habitats and exhibited a number of structural adaptations that might contribute to survival of drought.

Some species exhibit damage near the tips, with damage spreading slowly to the lower leaves, and others experience more apparent damage near the base (Johnson & Kokila 1970). The species they studied fell into two groups that mostly coincided with this pattern of damage progression:

Low resistance to desiccation:
(those with * have damage near the tips):
- ***Calymperes moluccense****
- ***Fissidens crassinervis***
- ***Leucobryum sanctum****
- ***Semibarbula orientalis****
- ***Syrrhopodon loreus****

High resistance to desiccation:
- ***Bryum coronatum*** (Figure 89)
- ***Leucophanes octoblepharioides*** (Figure 93)
- ***Neckeropsis lepineana*** (Figure 94)
- ***Paraleucobryum longifolium*** (Figure 95)
- ***Pelekium velatum***

Figure 89. ***Bryum coronatum*** surviving on an exposed rock. Photo by Michael Lüth, with permission.

In the tropics, epiphytes can experience long periods of drought during the dry season. Salazar Allen (1985) found that the genus ***Leucophanes*** (Figure 90) survives the drought by an unusual life form strategy. ***Leucophanes*** is an acrocarpous moss that may be branched or unbranched and that forms turfs. The unusual feature is that leaf-tip gemmae germinate on the parent plant to form a new layer of gametophores (Figure 91). In many bryophytes, there seems to be an inhibitory substance that prevents such occurrences (see interaction chapter). However, in ***Leucophanes***, this seems to be an important adaptation for water retention. Lacking subterminal innovations, ***Leucophanes*** benefits from the thicker turf where the numerous stems can protect each other from drying out. It is my guess that if the tips were to become so dry that they would die in an unusually dry year, there would be at least some lower (older) stems with enough life remaining to re-establish the colony. If not, surely some of the gemmae would survive. In any event, this habit of germination of gemmae within the parent colony provides ***Leucophanes*** with a dense turf that could resist drying.

Figure 90. ***Leucophanes molleri*** on tree bark. **Left:** showing plants with leaves tipped with gemmae and **Right:** gemmae on leaf tip. Bar = 20 µm. Photos courtesy of Noris Salazar Allen.

Figure 91. Protonemata forming at the tip of a gemma of ***Leucophanes molleri*** while the gemma is still attached to the parent leaf. Photo courtesy of Noris Salazar Allen.

Among those adapted for drying, with little damage down to 10% humidity, ***Leucophanes octoblepharioides*** (Figure 93) has abundant leucocysts that serve as a water reservoir (Johnson & Kokila 1970). The costa is thickened and prevents the leaf from collapsing. ***Paraleucobryum longifolium*** (Figure 95), a species of exposed situations in the hill forest, has a thickened costa and thick-walled lamina cells. ***Pelekium velatum*** (Figure 92) uses a different strategy with very small leaves pressed against the stem and with papillose cells. ***Neckeropsis lepineana*** (Figure 94) holds its secondary branches at an angle to the tree trunk in a way that subjects it to drying.

Those species with low desiccation resistance are damaged at humidity of 63% and are likely to die at 10% (71-94% of cells damaged) (Johnson & Kokila 1970). These species live in habitats that have near saturation humidity levels. Three of these species live on the ground where the humidity is constantly and exceedingly high. Two are **corticolous** (growing on bark) species [***Calympere moluccense*** (Figure 96) and ***Syrrhopodon loreus***) that live on the wettest side of the tree in areas that are constantly wet due to runoff.

Figure 92. ***Pelekium velatum***, a species with very small leaves and papillae. Photo © <www.NatureLoveYou.sg>, with online permission.

Figure 93. ***Leucophanes*** sp. ***Leucophanes octoblepharioides*** has low resistance to plasmolysis and is shown here surviving on bark. Photo by Niels Klazenga, with permission.

Figure 94. ***Neckeropsis lepineana*** surviving on bark with its branches extended – a common growth form in the tropics. Photo by Li Zhang, with permission.

Figure 95. ***Paraleucobryum longifolium*** on rock, a species adapted for drying by a thickened costa and thick-walled lamina cells. Photo by Janice Glime.

Figure 96. Saturated ***Calymperes*** sp. ***Calymperes moluccense*** lives on the wettest sides of trees in humid areas and is desiccation intolerant. Photo by Niels Klazenga, with permission.

Pardow and Lakatos (2013) explored the desiccation tolerance of epiphytic bryophytes from contrasting microsites in tropical lowland forests of French Guiana. Canopy species are well adapted, as indicated by the recovery of chlorophyll fluorescence, with 13 of the 18 species maintaining more than 75% of their photosynthetic capacity after 9 days at 43% relative humidity. On the other hand, understory species were sensitive to desiccation and were only able to withstand a reduction to 75% relative humidity. The bryophytes were able to reactivate by reaching equilibration with water vapor as their only moisture source.

Pardow *et al*. (2012) noted the importance of lowland cloud forests in the Guianas as a site for high epiphytic bryophyte diversity. This area is subject to frequent early morning fog events that provide moisture for the bryophytes. The growth forms were those that could take greatest advantage of this cloud moisture: tail, weft, and pendent (Figure 97).

Figure 97. ***Papillaria***, a pendent moss in the cloud forest at Mt. Budawang, Australia. Photo by Peter Woodard, through Public Domain

Romanski *et al*. (2011) likewise studied epiphytes, in this case in the lower montane (2400 m) rainforest of Peru. A single tree of *Weinmannia* supported 110 bryophyte species (77 hepatics, 1 hornwort, 32 mosses). They divided the tree into **Johansson zones** (lower trunk, upper trunk, mid-crown, mid-outer crown, outer crown) and found the greatest species richness and abundance on the upper trunk and large branches of the mid-crown. Exposure to light and desiccation appeared to account for the bryophyte distribution, but more research is necessary to tease out these relationships.

Atala *et al*. (2013) expressed concern that dendroid mosses with conducting tissues likewise lacked study. They examined desiccation tolerance in the ***Dendroligotrichum dendroides*** (Figure 98) from Chile, where it grows in the understory of temperate forests. They tested plants from two contrasting moisture conditions and found that both populations exhibited desiccation tolerance. But the responses were not equal. Those from the northern population lost water more slowly and recovered the PSII Fv/Fm to higher values when compared to the southern population. They suggested that exposure to summer droughts in the northern population could contribute to differences in their response.

Figure 98. ***Dendroligotrichum dendroides***, a Chilean species with desiccation tolerance. Photo by Felipe Osorio-Zúñiga, with permission.

Epiphytes

Epiphytes in most habitats have sharply contrasting moisture conditions. When it rains, they can be in a river of water rolling down the tree trunks. But when the rain stops, they are elevated where there is more access to wind and drying can be rapid.

These conditions are not so severe in a cloud forest due to the moisture in the clouds. Bryophytes are able to use such moisture and some are even adapted to collect it by providing fine wirelike structures, expressed as such structures as thin awns or pendent growth forms.

In two Venezuelan cloud forests, León-Vargas *et al.* (2006) the rainfall averages only 20 mm or less in January and February, 200 mm or more in August to October, and variable year-round. Continuous 100% relative humidity occurred 8.5% to 52.2% of the time. Humidity increased at night. Although these cloud forests are among the most ideal for epiphytic bryophytes, even they can have short periods droughts at any time of year. They noted that the pendent life form was probably important in harvesting the moisture from the air in these forests. All of the six pendent bryophyte species survived at least a few days of desiccation.

Pendent Mosses

Pendent mosses (those that hang down; Figure 99-Figure 100) often suffer desiccation, with little surrounding them to help hold in the water. ***Floribundaria floribunda*** (Figure 99) and ***Pilotrichella ampullacea*** (Figure 100) from Uganda humid tropical forests survive partly by avoidance, holding large quantities of external capillary water, with ***Pilotrichella ampullacea*** holding approximately twice as much as ***Floribundaria floribunda*** (Proctor 2002). Both species were able to recover from 11 months of dry storage at 5°C, although they required several days to recover, with ***F. floribunda*** recovering more slowly and less completely. Following 20 hours of air drying, ***P. ampullacea*** achieved a positive carbon balance within 30-60 minutes after rewetting.

Figure 99. ***Floribundaria floribunda***, a species from humid forests in Uganda that survives partly by avoidance, holding large quantities of external capillary water. Photo by Jan-Peter Frahm, with permission.

León-Vargas *et al.* (2006) studied the epiphytes in the Venezuelan cloud forests. The rainfall there drops to an average of 20 mm or less in January and February and increases to 200 mm or more from August to October. Nevertheless, the longest recorded dry period was only 143 hours. Nighttime humidities of 90% relative humidity were common, with 100% for significant periods, creating cloud water deposition in about 50% of the nights. Although these cloud forests are among the most ideal for epiphytic bryophytes, even they can have short periods droughts at any time of year. They noted that the pendent life form was probably important in harvesting the moisture from the air in these forests. All six species of pendent bryophytes survived for at least a few days of desiccation; these recovered better from high than from low humidities.

Altitude Differences in the Tropics

In the tropics, altitude can have a strong effect on both biomass and diversity among bryophytes (Bader *et al.* 2013). The lowlands are characterized by low abundance and low species richness. These could be a consequence of short daily periods of suitable light, temperature, and moisture and nighttime high respiration due to high temperatures. Moisture regimes are quite different, with lowland forests having more concentrated but less frequent precipitation than montane cloud forests. they furthermore have sunny mornings that cause rapid drying. The high levels of moisture in high altitude cloud forests is manifest in a high diversity and cover by bryophytes (Figure 101). But both lowland and montane species are able to survive more than 80 days of dry periods, far exceeding the duration of lowland tropical dry periods.

Figure 100. ***Pilotrichella ampullacea***, a species from humid forests in Uganda that survives partly by avoidance, holding large quantities of external capillary water. Photo by Jan-Peter Frahm, with permission.

Figure 101. Elfin cloud forest in the Luquillo Mountains of Puerto Rico. Photo by Janice Glime.

Summary

Because of their small size, bryophytes are able to occupy microsites in otherwise unfavorable habitats. Their ability to recover from dehydration typically correlates with habitat, with aquatic bryophytes having little ability to tolerate dehydration and resume photosynthesis, whereas dry habitat bryophytes can withstand extended periods of desiccation. In aquatic bryophytes, ribosomes can be damaged irreversibly and membranes are more likely to be damaged than in dry habitat taxa. On the other hand, there is no difference in nitrogen reductase activity between dry and wet habitat bryophytes.

Peatland bryophytes (***Sphagnum***) of lawns and hollows are typically desiccation tolerant, benefitting from inducible tolerance. Those of hummocks generally are intolerant but are desiccation resistant. Submersed species rely on the water of their habitat and have little tolerance for desiccation.

Aquatic bryophytes have poor desiccation tolerance, especially with rapid drying, but usually benefit from slow drying and sometimes can survive considerable dry periods.

A number of bryophytes are xerophytic. Their life cycle is typically short and the strategy is adapted to the short periods of rainfall. But in some arid habitats, nighttime dew is the only source of water for bryophytes. Hair points gather the dew and facilitate its uptake. In others, cooling of soil can bring bryophytes to dew point and draw water upward from the soil. The real limiting factor is carbon balance. If the bryophyte loses too much carbon by respiration and experiences a hydrated state for which the duration is too short to recover it, the bryophyte will perish. Rapid repair and recovery of photosynthesis permit these bryophytes to take advantage of short periods of hydration. The rapid daytime drying makes constitutive desiccation tolerance essential for survival where short daytime storms are common. But at least some of these bryophytes also have inducible desiccation tolerance. Some use an **escape strategy** of desiccation-tolerant gemmae, spores, and protonemata that help these bryophytes succeed in habitats with extensive dry periods. Nitrite and nitrate reductase both seem to be involved in recovery, but more research is need to determine the mechanisms involved. Leaf rolling and papillae seem to provide a protective role, perhaps by reducing light damage of dry cells and facilitating water uptake, but their role in water retention remains to be demonstrated. Compact growth form is also important.

Flood plains have extremes of habitat and require special strategies to weather these. Many of the bryophytes adapted to these extremes are species of the thallose liverwort ***Riccia***. This genus is able to go dormant when it is dry with a variety of strategies, including rolling the thallus, surviving as tubers, having hairs on the surface. Some have small thalli with short life cycles; others have thick thalli that survive the desiccation.

In the Arctic and Antarctic, frost can be a desiccant. Water height above permafrost determines existence of fens, where bryophytes are emergent, and marshes exist where the water table is high above the bryophyte surface. Arctic bryophytes suffer from exposure that creates desiccating conditions. Aspect and angle of slope play important roles in speed and frequency of drying. Acrocarpous mosses do better in areas of light snow cover, whereas pleurocarpous mosses suffer less apical damage from heavy snow. In the Antarctic, the longer the dry period, the lower the subsequent photosynthetic rate, especially among hydrophytic species.

On the forest floor, bryophytes may sequester all the water from a brief rainfall (1-2 cm). In the dry summer, bryophytes may derive moisture from the soil during the cooling temperatures.

Temperate epiphytes may take advantage of cooler temperatures of winter for maximum growth.

In the tropics, carbon balance can, as in the desert, be a problem. When the mosses are hydrated at higher temperatures, respiration loss exceeds photosynthetic gain. This is generally not a problem at higher altitudes in the cloud forests; bryophytes are abundant on nearly every substrate there. Physiology is poorly known for tropical bryophytes, but it appears that they have similar adaptations to those of other locales with similar moisture conditions such as thick costa and thick cell walls. Some (***Leucophanes***) have leaf-tip gemmae that germinate and layer the colony, making a thick turf.

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CHAPTER 7-9
WATER RELATIONS: WINTER PHYSIOLOGY

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CHAPTER 7-9
WATER RELATIONS: WINTER PHYSIOLOGY

Figure 1. ***Racomitrium heterostichum*** encased in ice. Photo by Michael Lüth, with permission.

Freezing tolerance must necessarily be coupled with drought tolerance and therefore this chapter would be incomplete without a discussion of winter effects. While other plants are dormant and have either lost their leaves, died back to ground level, or adapted in other ways to prevent damage from heavy snow and loss of water due to ice crystals, many bryophytes remain exposed, ready to have photosynthesis whenever light, water, and temperatures permit (Figure 1). Here we will examine the conditions related to their winter water relations. Temperature relations will be covered in a different chapter.

Problems in Winter

Bryophytes do have problems to deal with in winter. These include damage to their DNA and photosynthetic tissue (chlorophyll) from the UV light, temperature stress, cellular freezing and structural damage, and desiccation damage due to ice crystals. Alberdi *et al*. (2002) consider that adaptations to cold include high resistance to light stress, high freezing resistance, and high photosynthetic capacity at low temperatures. To this list I must add the ability to regain hydration quickly upon thawing. Most of these topics will be discussed elsewhere in chapters that deal with that particular physiological parameter. This chapter will examine the winter water relations.

The all-important water, whether as fog or rain or dew, is suddenly no longer liquid, but solid. Not only does this present problems for obtaining water, but it also means that hygroscopic ice crystals can draw water from the bryophyte cells.

But not all bryophytes suffer from the problem of ice damage. The thallose liverwort ***Ricciocarpos natans*** (Figure 2-Figure 4) can spend the winter encased in ice and can tolerate temperatures to -30°C (Frahm 2006). Frahm suggested that it was able to survive this frozen condition because it has no water vacuoles, thus providing no free internal water to form crystals that could destroy its

membranes. Rod Seppelt (Bryonet discussion 14 November 1997) also noted an absence of vacuoles in Antarctic mosses. Both ***Ricciocarpos natans*** and ***Riccia fluitans*** (Figure 5-Figure 6) are common in Arctic streams, so we might expect them to have this absence of vacuoles. I find it interesting that no one seems to have reported either presence or absence of vacuoles in ***R. natans*** (based on literature search and question posed on Bryonet in April 2015). Rather, lipids and starch bodies may help in their winter tolerance (Rod Seppelt, Bryonet discussion 14 November 1997).

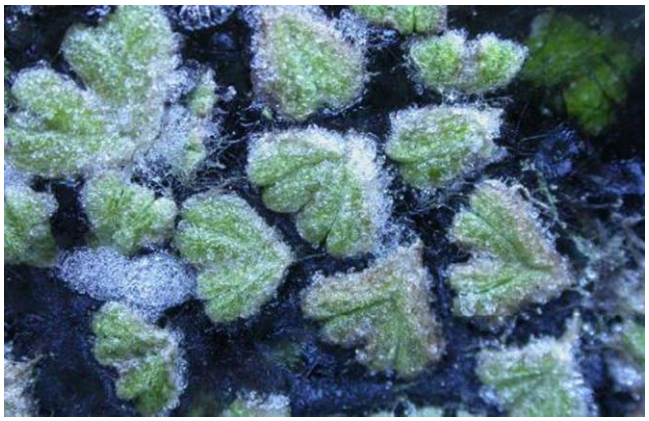

Figure 2. ***Ricciocarpos natans*** in ice. Photo by Jan-Peter Frahm, with permission.

Figure 3. ***Ricciocarpos natans*** thallus, a species with lipids and starch bodies that may help it survive winter. Photo by Norbert Stapper, with permission.

Figure 4. ***Ricciocarpos natans*** section showing the many chambers packed with small chlorophyllose cells. Photo by Norbert Stapper, with permission.

Figure 5. ***Riccia fluitans*** with pearling, a species that survives freezing. Photo by Christian Fischer, with permission.

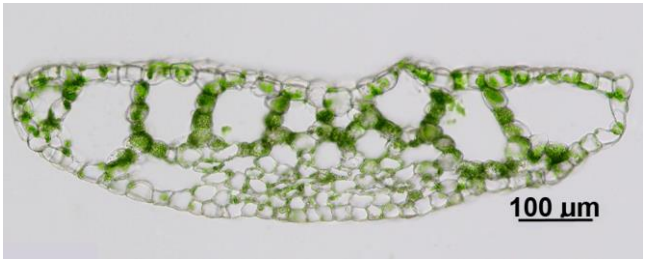

Figure 6. ***Riccia fluitans*** cross section showing large air chambers that help it to float. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Frost Damage

Those venues of green in the spring attest to the survival of bryophytes through the winter, subjected to frost before snow cover arrives and subsisting at near 0°C under the snow. But few studies give us specifics on what species survive and which ones are damaged.

Fletcher (1982) had the opportunity to document the frost responses of a number of species in cultivation. Among the winter survivors, reaching temperatures as low as -3°C, are species from New Zealand [***Papillaria crocea*** (Figure 7), ***Hypopterygium*** spp. (Figure 8), ***Rhizogonium bifarium*** (see Figure 9), ***Cyathophorum bulbosum*** (Figure 10), ***Eriopus brownii***], South Africa [***Hypopterygium*** sp.], Australia [***Gigaspermum repens*** (Figure 11), ***Goniomitrium acuminatum*** subsp. ***enerve*** (=***Goniobryum enerve***; Figure 12)], and Florida, USA [***Rhizogonium spiniforme*** (Figure 13)]. Even the delicate-looking ***Takakia lepidozioides*** (Figure 14-Figure 15) remains healthy. As we might expect, the widespread mosses ***Sphagnum*** spp. (Figure 16) and ***Mnium*** spp. [probably ***Plagiomnium*** since no ***Mnium*** species are present in New Zealand (NZOR 2015); Figure 17] survive the frost. On the other hand, ***Haplomitrium hookeri*** (Figure 18) from New Zealand and ***H. mnioides*** (Figure 19) from Japan had no healthy plants remaining after an exposure to -3°C, despite their ability to survive and grow in the winters in their native habitats.

Figure 7. ***Papillaria crocea***, a winter survivor in NZ. Photo by Janice Glime.

Figure 8. ***Hypopterygium didictyon***, a genus that can withstand temperatures to -3°C. Photo by Juan Larrain, with permission.

Figure 9. ***Rhizogonium novae-hollandiae***. ***Rhizogonium bifarium*** survives temperatures as low as -3°C in New Zealand. Photo by Niels Klazenga, with permission.

Figure 10. ***Cyathophorum bulbosum*** from Tasmania, a moss that survives freezing. Photo by Vita Plasek, with permission.

Figure 11. ***Gigaspermum repens*** with capsules, a moss that tolerates freezing in Australia. Photo by David Tng, with permission.

Figure 12. ***Goniomitrium acuminatum*** subsp. ***enerve*** with capsules, a moss that tolerates freezing in Australia. Photo by David Tng, with permission.

Figure 13. ***Rhizogonium spiniforme*** with capsule, a moss that tolerates frost. Photo by Janice Glime.

Figure 14. ***Takakia lepidozioides*** in its native habitat in Japan. This moss species remains healthy through the Hokkaido winters. Photo from the Digital Herbarium of the University of Hiroshima, with permission.

Figure 15. ***Takakia lepidozioides***, a winter survivor. Photo from the Digital Herbarium of University of Hiroshima, with permission.

Figure 16. ***Sphagnum cristatum***, a New Zealand species that survives in winter there. Photo by Janice Glime.

Figure 17. ***Plagiomnium novae-zealandiae*** from New Zealand. Photo by Jan-Peter Frahm, with permission.

Figure 18. ***Haplomitrium hookeri***, a liverwort that is sensitive to freezing in the lab but survives it in the field. Photo by Des Callaghan, with permission.

Figure 19. ***Haplomitrium mnioides***, a liverwort that is sensitive to freezing in the lab but survives it in the field. Photo by Li Zhang, with permission.

Experiences with freezing in ***Plagiomnium undulatum*** (Figure 20) may help us to understand some of these differential responses (Hudson & Brustkern 1965). If this moss is cooled slowly, it experiences extracellular freezing; this prevents the intracellular freezing that could be fatal. Following that experience, the leaves can be cooled down to -30°C without injury. The slow freezing prevents the formation of extensive extracellular ice. Young shoots, however, cannot withstand temperatures below -12°C.

Figure 20. ***Plagiomnium undulatum***, a moss that uses extracellular freezing to prevent intracellular crystal formation. Photo by Michael Lüth, with permission.

Among the thallose liverworts, ***Lunularia*** (Figure 21), ***Pellia*** (Figure 22), ***Preissia*** (Figure 23-Figure 24), ***Riccardia*** (Figure 25), ***Riccia*** (Figure 26), and ***Marchantia polymorpha*** (Figure 27), all survive frost (Fletcher 1982) and remain healthy. On the other hand, the thallose liverworts ***Moerckia blyttii*** (Figure 28-Figure 29), ***Symphogyna*** sp. (Figure 30), ***Corsinia coreandra*** (Figure 31-Figure 32), and ***Asterella*** (Figure 33) all can become severely bleached when subjected to frost. ***Dumortiera hirsuta*** (Figure 34-Figure 35) doesn't die, but it becomes blackened. Similarly, ***Fossombronia*** (Figure 36) and **Anthocerotophyta** experience decay, but for them the decay is a normal winter occurrence; growth resumes in the spring. In the greenhouse, which reaches -5.5°C, ***Asterella*** and ***Monoclea forsteri*** (Figure 37) are blackened by frost, whereas ***Marchantia*** spp, ***Dumortiera hirsuta***, ***Anthoceros punctatus*** (Figure 38), and ***Phaeoceros laevis*** (Figure 39) remain healthy in the same greenhouse.

Figure 21. ***Lunularia cruciata***, a frost-tolerant thallose liverwort. Photo from <www.aphotofauna.com>, with permission.

Figure 22. ***Pellia endiviifolia*** males with reddish antheridial cavities & females in center, a species that survives freezing. Photo by David Holyoak, with permission.

Figure 23. ***Preissia quadrata*** with archegoniophore, member of a genus that survives freezing. Photo by Michael Lüth, with permission.

Figure 24. ***Preissia quadrata*** thallus section showing several globose oil bodies that may help it to survive desiccation and freezing. Photo by Kristian Peters, with permission.

Figure 25. ***Riccardia*** sp, a thallus that survives freezing. Photo by Niels Klazenga, with permission.

Figure 26. ***Riccia beyrichiana***, a genus that is able to survive frost – and desiccation. Photo by Jan-Peter Frahm, with permission.

Figure 27. ***Marchantia polymorpha*** with gemmae cups, a species that survives frost. Photo by Michael Lüth, with permission.

Figure 28. ***Moerckia blyttii***, a liverwort that is sensitive to frost, becoming bleached. Photo by Michael Lüth, with permission.

Figure 29. ***Moerckia blyttii*** habitat. Photo by Michael Lüth, with permission.

Figure 30. ***Symphyogyna podophylla***, a liverwort genus in which one species is sensitive to frost and becomes bleached. Photo by Andras Keszei, with permission.

Figure 31. ***Corsinia coriandrina***, a thallose liverwort that is sensitive to frost under some conditions. Note bleached tissues, especially in the bottom center. Photo by Michael Lüth, with permission.

Figure 32. ***Corsinia coriandrina*** in its habitat on a ledge, a thallose liverwort that is sensitive to frost under some conditions. Photo by Michael Lüth, with permission.

Figure 33. ***Asterella lindenbergiana***, a thallose liverwort that is sensitive to frost. Photo by Michael Lüth, with permission.

Figure 34. ***Dumortiera hirsuta***, a thallose liverwort that is sensitive to frost and becomes blackened, but doesn't die. Photo by Michael Lüth, with permission.

Figure 35. ***Dumortiera hirsuta*** habitat. Photo by Michael Lüth, with permission.

Figure 36. ***Fossombronia angustata***, a species in which frost causes decay, a normal winter occurrence. Note the patches of colorless plants. Photo by Michael Lüth, with permission.

Figure 37. ***Monoclea forsteri***, a species that is blackened by frost. Photo by Jan-Peter Frahm, with permission.

Figure 38. ***Anthoceros punctatus***, a species that survives to -5.5°C. Photo by Jonathan Sleath, with permission.

Figure 39. ***Phaeoceros laevis*** with capsules, a species that remains healthy to -5.5°C. Photo by Michael Lüth, with permission.

Corsinia coreandra (Figure 31-Figure 32) is a puzzle. It is a xerophyte, but in cultivation frost causes it to become bleached (Fletcher 1982). At the same time in the same garden as the cultivation containers, it remains healthy on an exposed wall top and likewise remains healthy in the greenhouse that goes down to -5.5°C.

Much of what we know about cold tolerance has come from Antarctic studies. The Antarctic continent has only

2% of its land free from ice (Seppelt & Ochyra 2008). These areas are dominated by bryophytes (24 species of mosses; 1 liverwort), lichens, and algae.

We have learned that macromolecular substances (ice-active substances or IASs) can modify the shape of the growing ice crystals (Raymond & Fritsen 2001). These semipurified substances from ***Bryum*** sp. (Figure 40) from the Antarctic contain both protein and carbohydrate. The substances lose most of their recrystallization ability by heat treatment. Raymond and Fritsen suggest that these substances might increase freezing tolerance by preventing ice recrystallization.

Figure 40. ***Bryum pseudotriquetrum*** in Antarctica, a species in which protein and carbohydrate might increase freezing tolerance by preventing ice recrystallization. Photo by Catherine Beard, with permission.

Some bryophytes thrive in habitats where they regularly get exposed to sub-zero temperatures. ***Bryoxiphium norvegicum*** (Figure 41) is such a species (Shirasaki 1984). In Japan, ***B. norvegicum*** subsp. ***japonicum*** lives in an altitudinal range of 80-2350 m, being most abundant in districts where deep snow covers the ground for a long period. But it does not grow where the snow is, but rather grows on the vertical sides of overhanging rocks in ravines. Hence, it survives winter without the protection of snow, but it is sheltered by the rocks from the cold, desiccating winds.

Figure 41. ***Bryoxiphium norvegicum***, a species that grows on vertical surfaces where it is exposed to sub-zero temperatures without snow cover in winter. Photo by Bob Klips, with permission.

Ice Crystals

Ice crystals can cause plant tissues to dry out. Ice crystals are very hygroscopic and thus their presence can result in water being drawn out of tissues. But they also gather water from the atmosphere. Moffett *et al*. (2009) suggest that these ice crystals can sequester water that becomes available when they melt. Because bryophytes are able to absorb water through their leaves, this water can be immediately available and provide rapid rehydration.

Rod Seppelt (pers. comm. 7 April 2015) does not consider it to be unusual that ***Ricciocarpos natans*** (Figure 2-Figure 4) and ***Riccia fluitans*** (Figure 5) can be encased in ice or survive under a layer of snow. As he points out, temperatures within the ice are not typically very cold. As an example, he cites putting a pot of water 80 cm under the Alaskan snow overnight. The air temperature that night dipped to -22°C, but the pot of water remained unfrozen.

Of course dehydration caused by freezing can have other consequences. Dependence on the symbiont ***Nostoc*** is interrupted and nitrogen fixation is significantly reduced in winter due to dehydration resulting from freezing in the epiphytic leafy liverwort ***Porella*** (Figure 42-Figure 43) in Oregon, USA (De Gezelle 2003).

Figure 42. ***Porella cordeana*** in one of its vertical habitats where the symbiotic Cyanobacterium ***Nostoc*** provides it with needed nitrogen. Photo by Michael Lüth, with permission.

Figure 43. ***Porella cordeana*** on a vertical substrate, a species that suffers in winter from diminished nitrogen fixation by its symbiont. Photo by Michael Lüth, with permission.

Desiccating Conditions

If you have ever gone out in early spring in areas where there is snow cover all winter, bryophytes provide a refreshing green cover on the newly emergent ground. This fresh green color requires the presence of water to rehydrate the tissues. But where does it come from?

In many temperate regions, spring brings rain, hence making rehydration an easy task. But in some regions, my own home in the Keweenaw Peninsula of Michigan included, snowmelt is followed by drought, and this is exacerbated along roads by the sand and salt that was used to provide traction for vehicles during winter ice and snow.

Nevertheless, in northern habitats, snowmelt can provide water for a considerable time. In the Cairngorm Mountains, Scotland, ***Kiaeria starkei*** (Figure 44) is immediately ready for photosynthetic activity when its own snow cover disappears (Woolgrove & Woodin 1996). It has just spent its winter at temperatures of 0°C to slightly above, but with no light penetration while the snow depth is greater than 50 cm. When the snow disappears from it, its tissue chlorophyll recovers rapidly to 250% of its winter low and within two weeks its carbohydrate concentrations increase by 60%. This moss has nitrate reductase activity and is able to take advantage of pollutant nitrate, accumulated by the snow, that becomes available as the snow melts.

Figure 44. ***Kiaeria starkei***, a species that is ready to photosynthesize as it emerges from the snow. Photo by Michael Lüth, with permission.

One advantage for bryophytes is that they have a low temperature compensation point. Hence, snowbed bryophytes such as ***Anthelia juratzkana*** (Figure 45-Figure 47) and ***Polytrichastrum sexangulare*** (Figure 48-Figure 49) can maintain photosynthesis at low temperatures with a lower temperature compensation point of about -4 to -5°C. Furthermore, ***A. juratzkana*** can survive in the dark under cold, wet conditions for nine months with no effect on its photosynthetic capability. This makes ***A. juratzkana*** well adapted to grow in the border zone along permanent snow patches. However, the net photosynthesis is reduced due to an increase in respiration rate. ***Polytrichastrum sexangulare***, on the other hand, does not tolerate this border regime as well as does ***A. juratzkana***.

Figure 45. ***Anthelia juratzkana*** growing in a late snowbed area. Photo by Michael Lüth.

Figure 46. ***Anthelia juratzkana*** showing dense alpine growth. Photo by Michael Lüth, with permission.

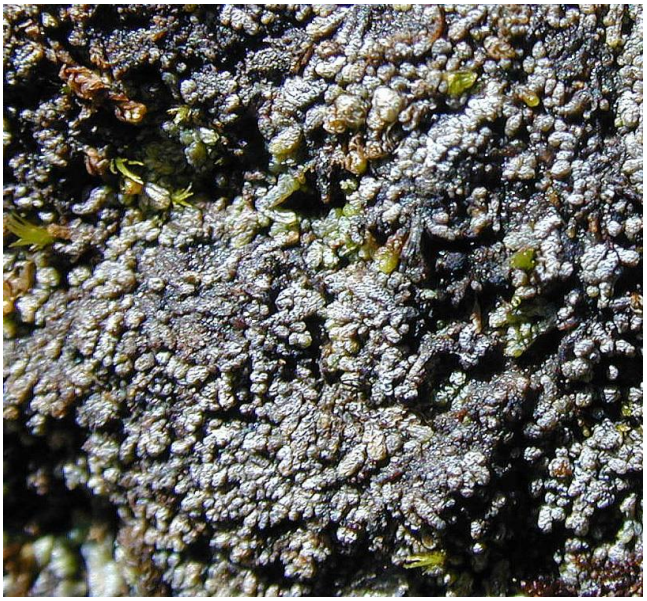

Figure 47. Close view of the leafy liverwort ***Anthelia juratzkana***. Photo by Michael Lüth, with permission.

Figure 48. ***Polytrichastrum sexangulare*** at alpine lake in Europe. Photo by Michael Lüth, with permission.

Figure 49. ***Polytrichastrum sexangulare*** with water drops. This species does not tolerate cold, dark storage in wet conditions as well as ***Anthelia juratzkana*** is able to do. Photo by Michael Lüth, with permission.

In tracheophytes, freezing can cause ice to form within cells, potentially causing membrane damage and subsequent loss of cell constituents. Lenne *et al*. (2010) write "A dehydrating moss gathers no ice." Using the widespread moss ***Ceratodon purpureus*** (Figure 50-Figure 51), they demonstrated that no ice accumulates in the cells during freezing. But external ice does induce desiccation. The effects of this desiccation depend on the cell type. Water-filled hydroid cells **cavitate** like tracheophyte xylem cells, becoming **embolized** (blocked, in this case by ice) at -4°C. Parenchyma cells of the inner cortex of the stem exhibit **cytorrhysis** (complete and irreversible collapse of a plant cell wall due to loss of water through osmosis), losing 20% of their original volume at -20°C **nadir temperature** (lowest temperature of a cycle). It is puzzling that chlorophyll fluorescence shows no evidence of damage after thawing from a -20°C event, especially since the sugar concentrations are insufficient to confer freeze tolerance in these conditions (see below). Furthermore, ice nucleation occurs in hydrated tissues at ~-12°C. The answer to this puzzle seems to lie in the desiccation itself. No damage occurs to those desiccated mosses at -20°C. The very desiccating nature of ice crystals appears to be the mechanism that prepares the moss for the low temperatures.

Figure 50. ***Ceratodon purpureus*** in Antarctica, a species with small leaf cells that do not accumulate ice crystals in winter. Photo courtesy of Rod Seppelt.

Figure 51. ***Ceratodon purpureus*** with capsules, a species that gathers no internal ice. Photo by Ivanov, with permission.

This desiccation relationship is supported in the Antarctic moss ***Polytrichum juniperinum*** (Figure 52) wherein repeated freeze-thaw cycles cause a greater reduction in photosynthesis than constant freezing for the same time period (Kennedy 1993). This is much like the effect of repeated dehydration/rehydration that causes a net carbon loss. This is supported by the observation that freeze-thaw cycles every 12 hours cause more damage than those every 24 or 48 hours. Most of the damage occurs during the first cycle with little occurring during subsequent cycles. Kennedy found that at 10°C the gross CO_2 flux is directly proportional to moss water content between 0.3 and 3.5 g g^{-1} dry mass. Mosses with a low water content withstand freeze-thaw cycles to sub-zero temperatures better than do samples with a high water content. Kennedy suggests that on Signy Island in the Antarctic the populations of ***Polytrichum juniperinum*** may be limited in distribution by sub-zero temperatures and freeze-thaw cycles at times when snow cover is insufficient to provide insulation.

Figure 52. ***Polytrichum juniperinum***, a moss that is damaged by freeze-thaw cycles when snow cover does not provide insulation. Photo by Jan-Peter Frahm, with permission.

Davey (1997) examined Antarctic bryophytes and demonstrated the importance of water. The photosynthetic rate decreased as the length of the dehydration period increased in all bryophytes examined. The photosynthetic capacity is affected by stress, and Davey found that both desiccation and winter freezing caused a loss of photosynthetic capacity. But the base level of photosynthetic capacity is able to survive both. Furthermore, frequent dehydration and rehydration cycles cause a loss of photosynthetic rate that is greater than that in continuous dehydration. Davey hypothesized that water availability is an important contributor to the distribution of bryophytes in the Antarctic, where winter-like weather can occur on almost any day of the year.

Barker *et al*. (2005) found bleaching in ***Syntrichia caninervis*** (Figure 53) during winter in the Mojave Desert, USA. They attributed this loss of green color to frequent rain events during warmer months that year, citing appearance of chlorosis just after that. This is consistent with the effects of frequent dehydration-rehydration events seen by Davey (1997). Under this regime, particularly for short, light rainfall events, the plants do not have enough time to repair membranes before they become dehydrated again, thus losing energy with each mild rainfall event. This leaves them with diminished color for the winter, a condition hopefully to be repaired in the spring.

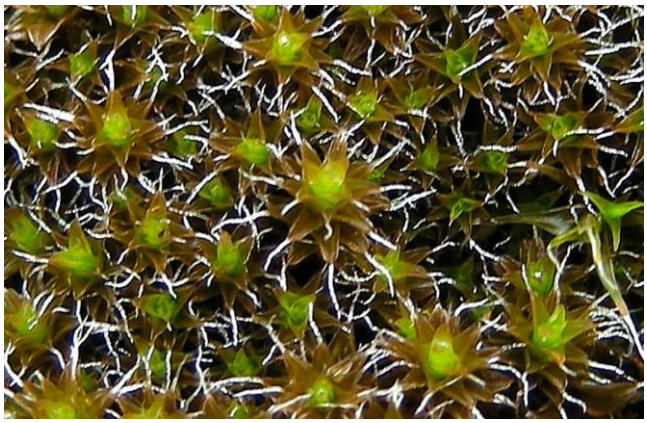

Figure 53. ***Syntrichia caninervis***, a desert species that suffers from too much rain in winter by losing its green color. Photo by Michael Lüth, with permission.

Crossidium crassinervium (Figure 54), from the Mojave Desert, benefits from late winter rain because it permits the moss to dry slowly (several days), whereas in summer the moss dries in as little as 3 hours (Stark 2005). The winter months of October to April constitute the hydrated period for this species, with hydration periods lasting 3.7-4.9 days.

Figure 54. ***Crossidium crassinervium***, a moss that benefits from late winter rains in the desert. Photo by Michael Lüth, with permission.

Desiccation Tolerance

Desiccation tolerance is seasonal, probably in most bryophytes. Only the moss ***Andreaea rothii*** (Figure 55-Figure 56) failed to show seasonal variation in net assimilation following 24 hours of remoistening, compared to clear seasonal differences in the leafy liverwort ***Plagiochila spinulosa*** (Figure 57-Figure 58) and mosses ***Hylocomium splendens*** (Figure 59), ***Scorpiurium circinatum*** (Figure 60), ***Syntrichia ruralis*** (Figure 61-Figure 62), and ***Racomitrium aquaticum*** (Figure 63-Figure 64) (Dilks & Proctor 1976). Those with seasonal variation usually had low desiccation tolerance in autumn and winter and greater tolerance in spring and summer. ***Hylocomium splendens*** differed in having relatively high tolerance in January (winter), with little change from then until July.

Figure 55. ***Andreaea rothii***, a species that shows no seasonal variation in its net assimilation following 24 hours of hydration. Photo by Michael Lüth, with permission.

Figure 56. ***Andreaea rothii*** in a typical vertical rock habitat where snow does not accumulate. Photo by Michael Lüth, with permission.

Figure 57. ***Plagiochila spinulosa*** in a soil bank habitat where it exhibits seasonal differences in photosynthesis. Photo by Michael Lüth, with permission.

Figure 58. ***Plagiochila spinulosa***, a leafy liverwort that has seasonal differences in its hydrated photosynthetic rate. Photo by Michael Lüth, with permission.

Figure 59. ***Hylocomium splendens*** with clinging snow, a moss that exhibits seasonal differences in photosynthesis. Photo by Michael Lüth, with permission.

Figure 60. ***Scorpiurium cirrcinatum***, a moss that exhibits seasonal differences in photosynthesis. Photo by Michael Lüth, with permission.

Figure 61. ***Syntrichia ruralis*** habitat in a cliff splash zone. Photo courtesy of Betsy St Pierre.

Figure 62. ***Syntrichia ruralis***, a species that shows seasonal differences in photosynthetic rates. Photo by Michael Lüth, with permission.

Figure 63. ***Racomitrium aquaticum***, a species that has more desiccation tolerance in spring and summer than in other seasons and has seasonal photosynthetic differences. Photo by Aimon Niklasson, with permission.

Figure 64. ***Racomitrium aquaticum*** in one of its habitats. Photo by Michael Lüth, with permission.

Burch (2003) noted that some mosses are able to survive **cryopreservation** (preservation at low temperatures) with no prior treatment. She suggested that their natural desiccation tolerance already gave them adequate protection during cryopreservation. What is it about freezing that actually kills or damages the bryophytes? Crystals can damage the membranes, but isn't the real damage ultimately desiccation damage? For example, 90-100% of the protonemata of the desiccation-tolerant ***Bryum rubens*** (Figure 65) survived freezing, whereas only 30% of those encapsulated and 20% non-encapsulated ***Ditrichum cornubicum*** (Figure 66) protonemata, with limited desiccation tolerance, survived freezing. These two species each had slightly better survival numbers after 18 days of desiccation with no freezing. ***Cyclodictyon laete-virens*** (Figure 67), a desiccation-intolerant species, did not survive desiccation or freezing. In ***D. cornubicum***, pretreatment with sucrose or ABA in the medium caused a reduction in growth rate of the protonemata, but these compounds resulted in a high level of protection against tissue damage in both dehydration and freezing – 100% regeneration of pretreated plants after thawing compared to 53% of controls (Burch & Wilkinson 2002). Sucrose plus ABA gave the best results.

Figure 65. ***Bryum rubens***, a moss whose protonemata are desiccation-tolerant and survive freezing. Photo by Des Callaghan, with permission.

Figure 66. ***Ditrichum cornubicum***, a moss whose protonemata have limited desiccation tolerance and low freezing survival. Photo by David T. Holyoak, with permission.

Figure 67. ***Cyclodictyon laete-virens***, a moss that does not survive desiccation or freezing. Photo by Des Callaghan, with permission.

Syntrichia ruralis (Figure 62) is one of the model organisms for studying desiccation tolerance. When subject to slow freezing at 3°C decrease in temperature per hour to -30°C, hydrated ***Syntrichia ruralis*** suffers only temporary metabolic changes, and these are reversible (Malek & Bewley 1978). Malek and Bewley attributed the changes to desiccation tolerance resulting from extracellular ice formation. When this same moss is subject to rapid freezing in liquid nitrogen and rapid thawing in 20°C water, all aspects of its metabolism deteriorate. Ribosomes, proteins, and ATP levels decrease and protein synthesis activity is rapidly lost. Malek and Bewley suggest that these problems are the result of intracellular ice crystals. Changing the freezing rate to 60°C per hour – a slower rate than in liquid N, but still a rapid rate – only reduces the levels of ATP and protein synthesis. The **polyribosomes** (protein-synthesizing apparatus) remain intact and active 24 hours after the freeze-thaw cycle. Segreto *et al*. (2010) reported that all species cryopreserved *in situ* regenerated mostly through budding; the number of regenerating samples correlates positively to desiccation tolerance and show higher frost tolerance than previously thought. Herbarium samples up to 7 years old of the most desiccation-tolerant species regenerate by protonemata; shoot tips regenerate better than small plant fragments.

Desiccation tolerance can be an **antagonistic** (one species benefits at the expense of another) interaction. ***Sphagnum fuscum*** (Figure 68) and ***Dicranum elongatum*** (Figure 69) dominate a subarctic mire (Sonesson *et al*. 2002). In winter, ***Sphagnum fuscum*** growth increased when ***Dicranum elongatum*** was its immediate neighbor, but ***D. elongatum*** grew better when it grew with other members of its own species. Neither increased temperature nor UV-B radiation affected these relationships, implying that moisture relations were probably important.

Ice-nucleating Proteins

Ice-nucleating proteins can help to create desiccating conditions and prevent cell freezing. These proteins are small structures that become surrounded by ice, but the water does not crystallize. The principle has been used by orange growers to prevent desiccation of the fruits during winter freezing events. Small nucleating bacteria are able to accomplish desiccation protection by out-competing the larger nucleating bacteria. These small species are sprayed on oranges to protect them. Such proteins or bacteria form centers for ice formation on the outsides of cells, providing a protective covering (Zachariassen & Kristiansen 2000).

Figure 68. ***Sphagnum fuscum***, a species that benefits from having ***Dicranum elongatum*** as its neighbors. Photo by Michael Lüth, with permission.

Figure 69. ***Dicranum elongatum***, a mire species that benefits from association with its own species more than by associating with ***Sphagnum fuscum***. Photo by Michael Lüth, with permission.

Clouds use nucleation centers to create their precipitation (Ahern *et al*. 2007). Bacteria have been known from clouds for a long time. Clouds may be an ideal habitat for these bacteria to live and thrive. Ahern and coworkers found 100 **OTUs** (operational taxonomic units – used when species cannot be named) among 256 clones from clouds. Half of these were identified as bacteria from **psychrophilic** terrestrial habitats (habitats where low-temperature-tolerant organisms can live). Among these bacteria, a mix of fluorescent *Pseudomonas* species dominate and some are known ice nucleators. But none of the cultures demonstrated the ice-nucleation gene. Rather, 55% of the isolates from cloud and rain samples had significant biosurfactant activity. **Surfactants** influence droplet size and are important in lowering the critical supersaturations necessary for activating aerosols into cloud condensation nuclei. Such bacteria facilitate water scavenging and counteract desiccation. Could they perform such functions in some bryophytes?

In ***Sphagnum capillifolium*** (Figure 70-Figure 71) the **chlorophyllous** (containing chlorophyll) cells exhibit extended freezing **cytorrhysis** immediately after ice nucleation at -1.1°C in water (Buchner & Neuner 2010). This cytorrhysis is exhibited as cell shrinkage that appears within only 2 seconds. And the shrinkage is significant – 82%, with chloroplast diameter reduction from 8.9 to 3.8 µm. This is accompanied by a sudden rise in chlorophyll fluorescence. On the other hand, frost damage occurs at a much lower temperature (LT50 at -16.1°C) (LT50 = median time until death after exposure of organism to toxic substance or stressful condition). The ice-nucleation temperature of -1.1°C is likewise the temperature threshold of PS II. Surprisingly, the LT50 for freezing in ***S. capillifolium*** is higher than that in most tracheophytes in the European Alps in the summer.

Atmospheric Source

One big question in this story is the source of the nucleating proteins. Until recently, bacteria seemed to be the only organic source of nucleating proteins (Möhler *et al*. 2008). But only a few bacteria, the pseudomonads, seem capable of this role (Lindow 1983; Ahern *et al*. 2007). This notion has been challenged by the research of Kieft and coworkers (Kieft 1988; Kieft & Ahmadjian 1989; Kieft & Ruscetti 1990) and more recently by Moffett *et al*. (2009).

Bauer *et al*. (2002) supported their challenge and reported that both bacteria and fungal spores contribute to the organic content of cloud water. In fact, the fungal spores in clouds of the Austrian Alps contribute 1.5% of the organic content, whereas the bacteria contribute only 0.01%. Although Pouleur and coworkers did not discuss the roles of these groups in nucleation, their study (Pouleur *et al*. 1992) suggests that slime molds might also provide nucleating proteins.

Hyphomycetous fungi (***Fusarium*** spp.; Figure 72) were also added to the list of organisms providing nucleating proteins to clouds (Pouleur *et al*. 1992). We also know that the fungal partner of at least some lichens contribute nucleating proteins (Kieft 1988; Kieft & Ahmadjian 1989; Kieft & Ruscetti 1990) and that the ***Fusarium*** proteins are more similar to those of lichens than to those of bacteria (Pouleur *et al*. 1992).

Figure 70. ***Sphagnum capillifolium***, a species that loses chlorophyll in response to chilling. Photo by Michael Lüth, with permission.

Figure 71. ***Sphagnum capillifolium*** in Chile, showing plants with diminished chlorophyll. Photo by Juan Larrain, with permission.

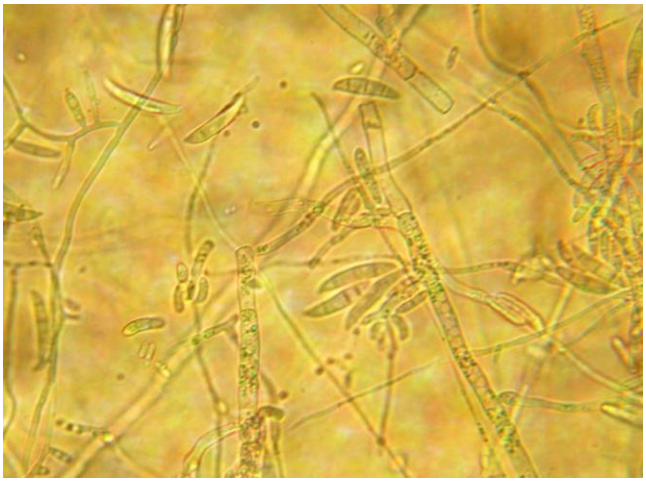

Figure 72. ***Fusarium*** with macroconidia, a filamentous fungal genus that serves as an ice-nucleating center. Photo by Ninjatacoshell, through Creative Commons.

Despres *et al*. (2007) determined aerosol particles in the air by using DNA sequencing. They found that most of the bacteria were **Proteobacteria**, with some **Actinobacteria** and **Firmicutes**. Fungal DNA came from **Ascomycota** and **Basidiomycota**, most likely from spores. Two different DNA sequences came from moss spores.

Christner *et al*. (2008) reported that ice nucleators are widespread in snowfall and the most active ones are biological. Most of these are bacteria. Many of these nucleators, therefore, are likely to be added to the mosses during snowfall and may contribute their survival of low temperatures and winter desiccation.

Fukuta (1966) found that more than 20 organic compounds out of 329 were able to nucleate ice at temperatures >-5°C. Hence, it is possible that even pollutants may contribute to nucleation of water on bryophytes.

Nucleating Proteins in Lichens

Our knowledge of lichens may help us to understand the nucleation relationship in bryophytes. Like bryophytes, lichens are able to survive year round and renew their photosynthetic activity when suitable temperatures and hydration resume. Perhaps the response of lichens can give us some insight into moss behavior relative to nucleation. Most of the **epilithic** (rock-dwelling) lichens (*Rhizoplaca*, *Xanthoparmelia*, and *Xanthoria*) tested by Kieft (1988) had ice nucleation at temperatures above -8°C, whereas their substrates showed negligible nucleation above that temperature. The nucleation activity in the lichen appears to be non-biological. No nucleation-active bacteria could be isolated, and the activity did not cease when the lichen was heated to 70°C or subjected to sonication. An axenic culture of the fungal part of the lichen *Rhizoplaca chrysoleuca* showed nucleation activity at -1.9°C. Kieft hypothesized that these frost-tolerant lichens benefit from increased moisture deposition that results from ice nucleation.

Henderson-Begg *et al*. (2009) remind us that for water to freeze above -36.5°C requires the activity of an ice nucleator. Bacteria are the best known of these, inducing freezing at temperatures up to -1.8°C, but seem to be of little importance in the lichens. The nucleators are common in lichens and can become airborne. Many of these are non-bacterial, but are biological, probably fungal and lichen.

There are several studies that support the presence of lichen fragments in the atmosphere (Tormo *et al.* 2001; Ahern *et al*. 2007). Marshall (1996) demonstrated that lichen **soredia** (asexual reproductive structures) were the most abundant of the airborne propagules of lichens, with peaks occurring after the winter snowmelt while subzero temperatures continued.

Kieft and Ahmadjian (1989) found that of 14 species of **mycobionts** (fungal partners) in lichens, five have nuclei active at -5°C. However none of the 13 photobionts (algae & Cyanobacteria) have ice-nucleating activity at -5°C or warmer. Hence, the ice-nucleating nuclei are produced by the fungal partner of the lichen. Kieft and Ahmadjian suggested that these ice-nucleating proteins are involved in moisture uptake and frost protection.

Kieft and Ruscetti (1990) found that biological ice nuclei in the lichen *Rhizoplaca chrysoleuca* were active at ~-4°C. Their sensitivity to various substances indicated that they were proteinaceous, and they were relatively heat stable and active without lipids, demonstrating that they were significantly different from bacterial ice nuclei.

Nucleating Proteins as a Source of Water

Lindow (1983) found that ice-nucleation activity occurs primarily in the outer membrane of the cells of *Pseudomonas syringae* and *Escherichia coli* into which it has been inserted.. It does not occur in soluble components of these cells. The ability of the ice-nucleating bacteria to operate depends on incubation temperature, growth medium composition, culture age, and genotype (Lindow *et al.* 1982). Their optimum conditions for nucleation in culture occur on nutrient agar containing glycerol at 20-24°C. Their ability to mitigate ice injury on corn seedlings depends on the bacterial population size and the number of ice nuclei active at that temperature.

Compounds for Winter?

Bryophytes produce record numbers of secondary compounds. These are best known for their antibiotic effects, but they can also play a role in both drought tolerance and freezing survival (Xie & Lou 2009). Among these, **bibenzyls** and **bis(bibenzyls)** have desiccation tolerance activity; **phenylpropanoids** have freeze tolerance activity. But the nature of these activities is unknown.

We know from several studies that the proportions of various fatty acids change with temperature (Saruwatari *et al*. 1999). Among these, linolenic acid and eicosapentaenoic acid might increase freezing-tolerance, as suggested by ***Marchantia polymorpha*** (Figure 27). Xie and Lou (2009) likewise reported the freeze tolerance activity of fatty acid derivatives in bryophytes.

Sugars

Sugar concentrations have a role in frost tolerance. **Sucrose** can increase the ability of bryophytes to tolerate rapid drying (Stark & Brinda 2015). Among the bryophytes tested by Rütten and Santarius (1992), only ***Mnium hornum*** (Figure 73-Figure 74) among seven **Bryidae** and one of **Marchantiidae** lack an increase in sucrose concentration concomitant with an increase in frost hardiness. Insignificant changes in **glucose** and **fructose** contents accompany these frost hardiness events.

Figure 73. ***Mnium hornum*** forest floor habitat. Photo by Michael Lüth, with permission.

Brachythecium rutabulum (Figure 75-Figure 76) and ***Hypnum cupressiforme*** (Figure 77-Figure 78) have high sucrose concentrations in summer, similar to those of other species in winter, and thus are frost tolerant even in summer (Stark & Brinda 2015). Those mosses that are highly frost-resistant have a total sugar concentration of ~90-140 mM. Of this sugar, 80-90% is sucrose. Artificial degradation of the sucrose during higher temperatures causes a decline in cold hardiness, supporting the hypothesis that it is important in frost hardiness in these species.

Figure 74. ***Mnium hornum***, a moss that does not contain more sugar with its frost hardiness. Photo by Michael Lüth, with permission.

Figure 75. ***Brachythecium rutabulum*** forest floor habitat in England. Photo by Janice Glime.

Figure 76. ***Brachythecium rutabulum***, a species with high sucrose content and high frost tolerance, even in summer. Photo by Michael Lüth, with permission.

Figure 77. ***Hypnum cupressiforme*** in one of its many habitats. Photo by Dick Haaksma, with permission.

Figure 78. ***Hypnum cupressiforme***, a species with high sucrose content and high frost tolerance, even in summer. Photo by Michael Lüth, with permission.

Some species [***Polytrichastrum formosum*** (Figure 79-Figure 81), ***Atrichum undulatum*** (Figure 82), ***Plagiomnium affine*** (Figure 83-Figure 84), ***Mnium hornum*** (Figure 73-Figure 74), ***Pellia epiphylla*** (Figure 85-Figure 86)] exhibit a distinct increase in cold tolerance from summer to winter (Rütten & Santarius 1992). Mosses have significant differences in frost resistance between summer and winter (15->25°C), but the thallose liverwort ***Pellia epiphylla*** experiences relatively little winter hardening capacity.

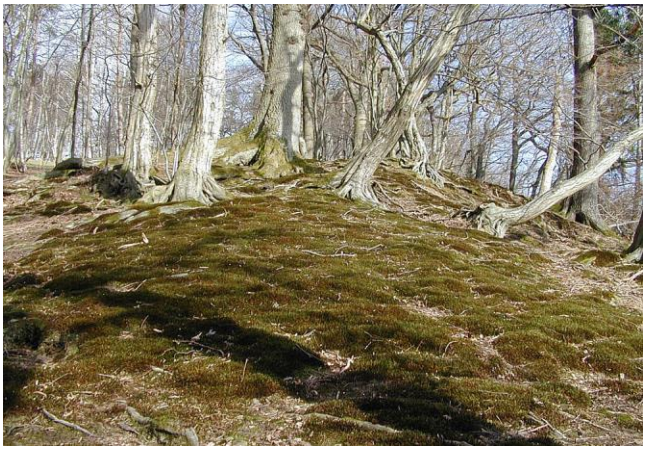

Figure 79. ***Polytrichastrum formosum*** on the forest floor in Europe. Photo by Michael Lüth, with permission.

Figure 80. ***Polytrichastrum formosum*** with frost, a species that has a distinct increase in cold tolerance from summer to winter. Photo by Aimon Niklasson, with permission.

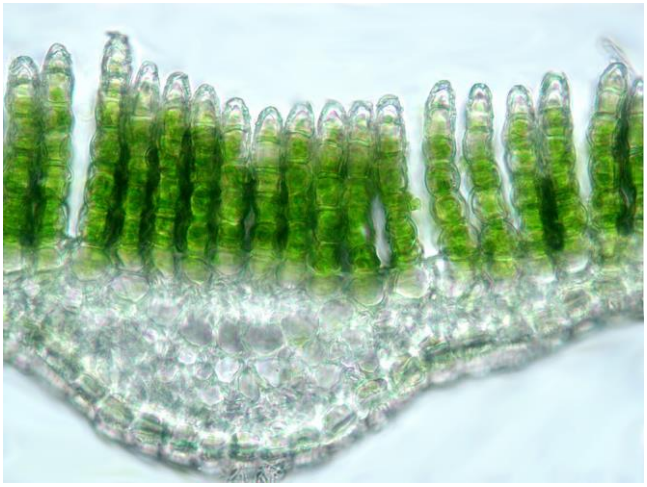

Figure 81. ***Polytrichastrum formosum*** leaf lamellae. The role of lamellae in frost protection is unknown. Photo by Michael Lüth, with permission.

Figure 82. ***Atrichum undulatum***, a species that has a distinct increase in cold tolerance from summer to winter. Photo by David T. Holyoak, with permission.

Figure 83. ***Plagiomnium affine*** forest floor habitat. Photo by Michael Lüth, with permission.

Figure 84. ***Plagiomnium affine***, a species that has a distinct increase in cold tolerance from summer to winter. Photo by Janice Glime.

Figure 85. ***Pellia epiphylla*** protected habitat under grass bank of flush in Wales. Photo by Janice Glime.

Figure 86. ***Pellia epiphylla***, a species that has a distinct increase in cold tolerance from summer to winter. Photo by David T. Holyoak, with permission.

Melick and Seppelt (1994) suggest that the lack of significant changes in soluble carbohydrates in Antarctic bryophytes may result from the extreme climate and the rapid temperature fluctuations during the growing season. On the other hand, maximum water content is present in the summer. Chlorophyll levels decrease in winter in both total chlorophyll and the chlorophyll *a*:*b* ratio, as do the total carotenoids. This decrease may be a response to low light levels that are insufficient for making more pigment.

Using the ***Physcomitrella patens*** (Figure 87) protonema as a model organism, Nagao *et al*. (2003, 2005) concluded that ABA-induced soluble sugars play a role in freezing tolerance. The accumulation of the sugars, at the expense of starches, is associated with morphological changes in the organelles and reduce freezing-induced structural damage to the plasma membrane, while the freezing tolerance of the protonemal cells increases. Nagao *et al*. (2006) identified the sugar as **theanderose**, a sucrose that occurs in close association with ABA treatment that enhances freezing tolerance. **Cycloheximide** inhibits the accumulation of theanderose, resulting in a marked decrease in freezing tolerance. The accumulation of theanderose is promoted during cold acclimation and treatment with hyperosmotic solutes, both of which increase cellular freezing tolerance.

Figure 87. ***Physcomitrella patens***, a moss that stores the sugar **theanderose** in preparation for winter. Photo by Michael Lüth, with permission.

Using the bryological lab rat ***Physcomitrella patens*** (Figure 87), Oldenhof *et al*. (2006) demonstrated that sucrose helps to protect cells during freezing and drying, but accumulation of sucrose alone is not sufficient for survival. ABA serves to cause this sucrose accumulation, up to 22% of dry weight, but only 3.7% occurs in non-ABA-treated tissues. A combination of ABA treatment and the cryoprotectant DMSO permit the tissues to survive a freeze-thaw cycle down to -80°C. DMSO-mediated changes involved in the membranes are important and may be relevant to the essential desiccation tolerance.

Polyols may contribute to cold hardiness as well. Tearle (1987) found that Antarctic lichens contained up to three times the amount of polyols when compared to temperate lichens, endowing them with extra freezing protection. The soluble sugars and polyols from mosses and lichens leach into the fellfield soils in the spring.

ABA

ABA is the stress hormone, and it plays a role in freezing tolerance of plants as well (Minami *et al*. 2003; Takezawa *et al*. 2011). Nevertheless, slow freezing of the protonemata of ***Physcomitrella patens*** to -4°C under normal growth conditions kills more than 90% of the cells. Application of ABA for 24 hours causes a marked increase in the freezing tolerance (see also Nagao *et al*. 2001, 2005, 2006). Cold treatment only slightly increases the freezing tolerance within the same period. Treatment with ABA causes a marked increase in expression of all the PPAR genes within 24 hours. Several of these genes also respond to cold, but much more slowly than they respond to ABA. Treatment with hyper-osmotic concentrations of NaCl and mannitol also increases the expression levels of eleven PPAR genes and the freezing tolerance of the protonemata. Minami and coworkers (2003) suggest that these relationships indicate that stresses increase the expression of genes that result in protection of the protonemata, but the nature of that relationship is unclear.

Nevertheless, in ***Physcomitrella patens*** (Figure 87) protonemata, as in tracheophytes, freezing tolerance increases following incubation at low temperatures in the range of 0-10°C, indicating the importance of acclimation (Minami *et al.* 2005). This tolerance is accompanied by an accumulation of several transcripts for **late-embryogenesis-abundant (LEA)** proteins and boiling-soluble proteins. De-acclimation causes reduction in expression of these proteins and loss of freezing tolerance. But surprisingly, unlike events in tracheophytes, in ***P. patens*** low-temperature-induced freezing tolerance does not coincide with an increase in endogenous ABA, despite increases in expression of stress-related genes. In short, the acclimation is somewhat different from that of tracheophytes.

These observations are further confounded by the experiments of Minami *et al*. (2003) on ***Physcomitrella patens*** (Figure 87). They found that treatment with ABA for 24 hours greatly increases the freezing tolerance of the protonemata; cold treatment alone has only a slight effect on freezing tolerance. Even slow freezing to -4°C kills more than 90% of the cells. On the other hand, hyperosmotic concentrations of NaCl and mannitol increase freezing tolerance of protonemata.

At the same time, research by Takezawa and Minami (2004) identified genes coding for membrane transporter-like proteins. These newly identified proteins increase considerably following treatment with low temperatures, hyperosmotic solutes, or ABA. These genes are regulated by calmodulin.

Arachidonic Acid

Prins (1982) suggested that one reason small mammals eat mosses in winter is the content of **arachidonic acids**. These fatty acids make membranes more pliable and may make it easier for these rodents to run around on frozen ground and snow. But what do these do for bryophytes in winter? Does this extra flexibility also make it easier for them to survive? One protection against freezing is the ability to lose water, avoiding crystal formation that could damage membranes and organelles. With flexible membranes and withdrawal of water, the cells could shrink within the walls during the cold (and dry) period.

In ***Physcomitrella patens*** (Figure 87), production of arachidonic acid increases with higher concentrations of sugar (Chodok *et al*. 2010). Al-Hasan (1989) found that in ***Bryum bicolor*** (Figure 88) more arachidonic acid is produced at 5°C than at 25°C. Both of these studies support the production of arachidonic acid as winter approaches.

Figure 88. ***Bryum bicolor***, a species that produces more arachidonic acid at low temperatures than in warm ones. Photo by Michael Lüth, with permission.

Polyribosomes

Polyribosomes (cluster of ribosomes connected by a strand of messenger RNA and active in protein synthesis) respond to cooling temperatures. In the xerophytic moss ***Syntrichia ruralis*** (Figure 61-Figure 62), when temperatures descend to 2°C an accumulation of polyribosomes occurs while the single ribosomes decrease (Malek & Bewley 1978). This change in numbers reflects rearrangement, but does not involve a change in the number of ribosomal units. Slowly dried ***S. ruralis*** does not contain any polyribosomes when rehydrated, but these reform at 2, 8, and 20°C. Leucine rapidly incorporates into the protein when the plants are rehydrated at 20°C, but its incorporation is less dramatic at 2°C. Cold-hardened ***S. ruralis*** has no changes in the rate of protein synthesis at low temperatures (2°C). In fact, even in summer this species can carry out protein synthesis at low temperatures.

Summary

One of the dangers of frost damage is desiccation. Ice crystals on the inside of cells damage membranes and those on the outside pull water from the cells. Some bryophytes are protected by being encased in ice, preventing the formation of crystals and insulating against severe cold. Absence of vacuoles or having only small vacuoles can help to protect the interior of cells.

Many species survive winter and are ready for photosynthesis when the snow disappears, using the snowmelt water to rehydrate their tissues. Slow cooling, like slow drying may be important in survival. Extracellular freezing can protect against intracellular freezing. Some macromolecular substances can modify the shape of ice crystals in ways that do not damage the cells. Some ice-nucleating structures, made by the plants or available from the atmosphere, including proteins, create a small crystalline structure likewise protecting against damage from larger crystals. On the other hand, some ice crystals on the outsides of the cells can sequester water that is available at suitable temperatures. Desiccation can protect the cells by preventing crystal formation. Cell shrinkage helps to prevent crystal formation. Frequent freeze-thaw cycles, like dehydration-rehydration cycles, can damage the cells if the hydration and photosynthetic period is insufficient to repair membranes and accomplish a carbon gain.

Polyribosomes are active immediately following the freeze-thaw cycle. Lipids, starch bodies, sucrose, ABA, bibenzyls, bis(bibenzyls), and phenylpropanoids help to increase freezing and desiccation tolerance. Arachidonic acid helps to make membranes more pliable. These compounds permit some bryophytes to have seasonal tolerance. In desert habitats winter is often the best growing season because mosses remain hydrated for several days following rainfall events.

Some species become bleached from frost damage, but shoot tips and other parts may remain healthy and provide new growth in spring.

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CHAPTER 7-10
WATER RELATIONS: SNOW ECOLOGY

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CHAPTER 7-10
WATER RELATIONS: SNOW ECOLOGY

Figure 1. Late snowbeds in an alpine habitat in the Khibiny Mountains, Russia. ***Bucklandiella microcarpum*** is in the foreground. Photo by Michael Lüth, with permission.

Snow Effects

Snow can contribute in multiple ways to enhance the productivity. We know little about productivity of bryophytes under snow. What we do know is that light can penetrate snow, but that the light quality is altered. We know that snowmelt provides moisture, and that this melt can occur while the snow pack is still present, even in the middle of winter. We know that the snow can buffer the temperature, maintaining it close to 0°C. Dorrepall *et al*. (2004) demonstrated that ***Sphagnum fuscum*** (Figure 2) experienced an enhancement of 33% in productivity as a result of winter snow addition, while, nevertheless, not increasing growth in length.

Even in areas with considerable snow, bare areas exist, often as a result of winds that clear the snow. Some of these surfaces are rock surfaces that protrude, making them vulnerable to those wind movements of the snow (John 1990). One moss species capable of living in such exposed areas is ***Grimmia longirostris*** (Figure 3) in the Canadian Rocky Mountains.

Figure 2. ***Sphagnum fuscum***, a moss that experiences greater productivity as a result of winter snow. Photo by Julita Kluša <daba.dziedava.lv>, with online permission.

Figure 3. ***Grimmia longirostris***, a species of exposed areas. Photo by Michael Lüth, with permission.

I have long suspected that at least some bryophytes are able to carry out photosynthesis under snow as long as it is not too deep for sufficient light penetration. Pannewitz *et al*. (2003) demonstrate that photosynthesis under the snow occurs in lichens. The snow cover provides effective insulation against the bitter cold of the Antarctic atmosphere, protecting both the mosses and the lichens. But in spring, this insulation proves to be detrimental. It retains the severe cold of winter and prevents the bryophytes from benefitting from the early warming of the air. This delay can last 10-14 days. Furthermore, the hydration provided to the lichens by the snow lasts only briefly once the snow disappears, providing only a brief period for photosynthetic activity. Is this same shortening of the photosynthetic period in effect for bryophytes, or are they able to retain the water longer?

In our study of the bryophytes on trees in the Keweenaw Peninsula of Michigan, USA, we found that those about 1 m above the ground were most common on the south sides of the trees (Trynoski & Glime 1982). We attributed this to a combination of winds from the north and sufficient light and moisture for these bryophytes to have photosynthesis in winter. Trees always have a narrow funnel of space between them and the snow (Figure 4). In this area where snow on the ground reaches a meter or move depth, the snow is an insulator. Dark-colored bark is able to absorb heat and the funnel remains somewhat humid. Light is able to penetrate. I have no measurements of growth or photosynthetic activity for these epiphytes – that needs to be done.

Figure 4. Snow-covered forest showing space between snow and tree trunk. Photo by Janice Glime.

Snow can affect the distribution of species. For example, in Japan ***Bazzania trilobata*** (Figure 5-Figure 7) grows on ground that is well drained all year and is typically sunny (Shirasaki 1987). ***Bazzania yoshinagana*** (Figure 8), on the other hand, grows on the forest floor in densely shaded coniferous forests. It spends its winter covered with deep snow that insulates it from freezing and provides it with moisture.

Figure 5. ***Bazzania trilobata*** habitat where it lives in well-drained locations. Photo by Dick Haaksma, with permission.

Figure 6. ***Bazzania trilobata***, a species of well-drained locations. Photo by Michael Lüth, with permission.

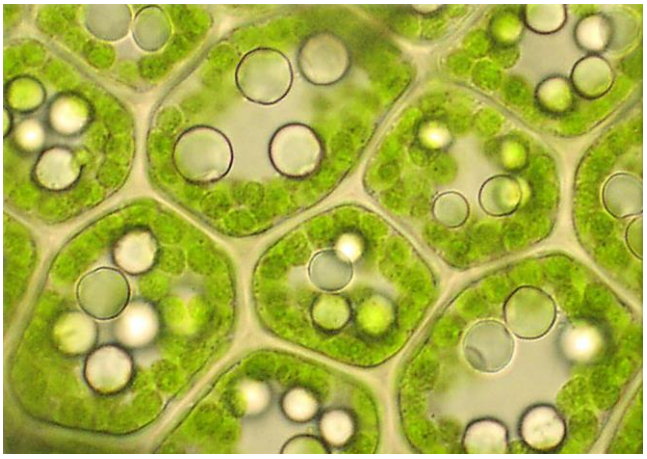

Figure 7. ***Bazzania trilobata*** leaf cells showing spherical oil bodies that may help in surviving desiccation. Photo by Walter Obermayer, with permission.

Figure 8. ***Bazzania yoshinagana***, a species of dense forest shade where it spends its winter under steep snow. Photo by Li Zhang, with permission.

Snowbed Communities

"Areas which experience prolonged snowlie and possess a distinctive bryophyte-dominated vegetation are termed snowbeds" (Woolgrave & Woodin 1996). Snowbeds (Figure 9) create their own unique characters. They shorten the growing season but can extend the period of hydration. Some bryophytes are dependent on these sources of hydration. On the Antarctic peninsulas the snow cover and site exposure seem to define the plant distribution (Melick *et al*. 1994).

Figure 9. Late snowbed at Bjoerndalen, Spitzbergen. Photo by Michael Lüth, with permission.

Snowbeds form in crevices and depressions in alpine regions (Figure 9). These are among the last areas to lose their snow, often near the end of the growing season. Nevertheless, some species grow only in these areas (Björk & Molau 2007). One such species that indicates a location with late snowbeds is the liverwort ***Anthelia*** (Figure 10), a genus whose fossils also indicate areas of late-lying snow in the late-Pleistocene landscape (Miller 1989). These snowbeds provide both a steady water supply and a steady nutrient supply to the adjacent plant communities. Because of this dependence, these communities are particularly vulnerable to climate warming.

Figure 10. ***Anthelia juratzkana***, an indicator of late snowbeds. Photo by Hermann Schachner, through Creative Commons.

Many of the alpine bryophytes display adaptations that make their snowbed habitats tenable. ***Andreaea nivalis*** (Figure 11-Figure 12) is a reddish moss that hangs where snow water glides over the rocks and cliffs (Bailey 1933). Even its name (*nivalis*) means snow-covered. ***Brachymenium erectum*** (Figure 13) grows in snow water in alpine areas and disintegrates so rapidly after maturity that it is easy to miss it altogether. ***Pohlia ludwigii*** (Figure 14-Figure 15) lives in or near snow water. ***Pohlia filum*** (Figure 16) grows in snow water on the south side of Mount Rainier, Washington, USA, and produces brood bodies (Figure 17) in the snow water. ***Polytrichastrum sexangulare*** (Figure 18-Figure 20) likewise lives near the snow. Its setae begin to elongate before the snow is completely gone and as a result they become trailing and twisted (Figure 20). ***Bryum muehlenbeckii*** (Figure 21) has deep red leaves and stems, probably protecting it from UV radiation, and possibly increasing its temperature in its cold habitat near the snowbeds. ***Pohlia wahlenbergii*** var. ***glacialis*** (Figure 22-Figure 23), by contrast, has whitish leaves. On Mt. Rainier it covers large expanses that are wet with snow water. ***Meiotrichum lyallii*** (Figure 24) becomes visible at high elevations as soon as the snow disappears and is common on the higher slopes of Mt. Rainier. All of these bryophytes are acrocarpous mosses. Only ***Isopterygiopsis pulchella*** (Figure 25) is a pleurocarpous snow lover associated with these snowbeds. In all cases, it is likely that these bryophytes are non-competitors with tracheophytes and that take advantage of their C_3 photosynthesis to grow in the cold temperatures when adequate moisture is available.

Figure 11. ***Andreaea nivalis*** in its alpine habitat. Photo by Michael Lüth, with permission.

Figure 12. ***Andreaea nivalis*** in a location where it receives water that glides over rocks and cliffs. Photo by Michael Lüth, with permission.

Figure 13. ***Brachymenium*** in India. ***Brachymenium erectum*** is short-lived in alpine snowbed runoff. Photo by Michael Lüth, with permission.

Figure 14. ***Pohlia ludwigii*** in its late snowmelt water habitat. Photo by Michael Lüth, with permission.

Figure 15. ***Pohlia ludwigii***, a moss that thrives in snowmelt water. Photo by Michael Lüth, with permission.

Figure 16. ***Pohlia filum*** growing in wet soil from snowmelt. Photo by Michael Lüth, with permission.

Figure 17. ***Pohlia filum*** showing the bulbils that are produced while it grows in snowmelt water. Photo by Michael Lüth, with permission.

Figure 18. ***Polytrichum sexangulare*** at alpine lake in Europe. Photo by Michael Lüth, with permission.

Figure 19. ***Polytrichastrum sexangulare***, a late snowbed bryophyte. Photo by Martin Hutten, with permission.

Figure 20. ***Polytrichastrum sexangulare*** showing crooked and twisted setae from developing under snow. Photo by Michael Lüth, with permission.

Figure 21. ***Bryum muehlenbeckii*** in snowmelt water on rock. Note the red color, a common character of alpine bryophytes. Photo by Michael Lüth, with permission.

Figure 22. ***Pohlia wahlenbergii*** var ***glacialis*** in its snowmelt habitat. Photo by Michael Lüth, with permission.

Figure 23. ***Pohlia wahlenbergii*** var ***glacialis***, a species that thrives in snow water. Photo by Michael Lüth, with permission.

Figure 24. ***Meiotrichum lyallii*** with capsules, looking somewhat flattened after snowmelt. Photo by Paul Wilson, with permission.

Figure 25, ***Isopterygiopsis pulchella***, the only pleurocarpous moss living in late snowbeds on Mt. Rainier, USA. Photo by Jan-Peter Frahm, with permission.

In Scotland, some of these same species are dependent on the snowbeds (Rothero 2007). These include ***Andreaea nivalis*** (Figure 11-Figure 12), ***Polytrichum sexangulare*** (Figure 18-Figure 20), ***Kiaeria falcata*** (Figure 26-Figure 27), ***Anthelia juratzkana*** (Figure 10), and ***Pohlia ludwigii*** (Figure 14-Figure 15). Additionally, snowbeds in the UK are habitats for ***Racomitrium heterostichum*** (Figure 28), ***Marsupella brevissima*** (Figure 29-Figure 30), ***Kiaeria starkei*** (Figure 31), ***Moerckia blyttii*** (Figure 32), ***Pleurocladula albescens*** (Figure 33-Figure 34), ***Marsupella arctica***, and ***Marsupella condensata*** (Figure 35). The flushes and mires resulting from melting snowbeds also support growths of ***Pohlia wahlenbergii*** var. ***glacialis*** (Figure 22-Figure 23), ***Scapania paludosa*** (Figure 36), and occasionally ***Sphagnum riparium*** (Figure 37) and ***S. lindbergii*** (Figure 38-Figure 39).

Figure 26. ***Kiaeria falcata*** habitat where snowbeds are important to this species. Photo by Michael Lüth, with permission.

Figure 27. ***Kiaeria falcata***, a moss dependent on snowbeds. Photo by Michael Lüth, with permission.

Figure 28. ***Racomitrium heterostichum***, a snowbed species. Photo by J. C. Schou, through Creative Commons.

Figure 29. ***Marsupella brevissima*** habitat. Photo by Michael Lüth, with permission.

Figure 30. ***Marsupella brevissima***, a snowbed liverwort. Photo by Jan-Peter Frahm, with permission.

Figure 31. ***Kiaeria starkei*** with capsules, a late snowbed moss. Photo by Rosemary Taylor, with permission.

Figure 32. ***Moerckia blyttii***, a snowbed bryophyte. Photo by Michael Lüth, with permission.

Figure 33. ***Pleuroclada albescens*** in a snowmelt bed in Norway. Photo by Michael Lüth, with permission.

Figure 34. ***Pleuroclada albescens***, a snowbed liverwort. Photo by Michael Lüth, with permission.

Figure 35. ***Marsupella condensata***, a species that lives in snowbeds in the UK. Photo by Andrew Hodgson, with permission.

Figure 36. ***Scapania paludosa***, a species that benefits fro snowmelt flushes. Photo by Michael Lüth, with permission.

Figure 37. ***Sphagnum riparium***, a species sometimes found in late snowbeds. Photo by Jan-Peter Frahm, with permission.

Figure 38. ***Sphagnum lindbergii*** where it gains water from spring flushes. Photo by Michael Lüth, with permission.

Figure 39. ***Sphagnum lindbergii***, a species that sometimes benefits from snowbed water. Photo by Michael Lüth, with permission.

In snowbeds, more than 40% of the cover is often comprised of bryophytes (Jägerbrand 2011). This may be as little as 3% of the exposed area during early melt to 80% in the late-melting areas. Björk (2007) found 26 species that grow mostly in snowbeds, 13 of which are found only in those areas. In a late snowbed in western Newfoundland, Canada, Belland (1983) found some of the same species associations as named above for the UK. In particular, ***Andreaea nivalis*** (Figure 11-Figure 12) was common in late snowbeds. Belland found 49 bryophyte species in the eight late snowbeds he investigated. Other dominant species included ***Kiaeria falcata*** (Figure 26-Figure 27), ***Moerckia blyttii*** (Figure 32), and a species of ***Trematodon*** (Figure 40). The uniqueness of this habitat is demonstrated by the disjunct distribution for 13 of these species between western and eastern North America. Eleven of the species are characteristic of snowbed habitats throughout most of the world.

Figure 40. ***Trematodon longicollis***, in a genus represented in snowbeds in Newfoundland, Canada. Photo by Michael Lüth, with permission.

The unique combination of temperature regime and moisture support some of the rare species of the world. On Mt. Washington, New Hampshire, USA, Slack *et al*. (2013) found ***Haplomitrium hookeri*** (Figure 41), ***Aulacomnium turgidum*** (Figure 42-Figure 44), ***Dicranum elongatum*** (Figure 43), and ***Pseudocalliergon trifarium*** (Figure 45) – all rare species in the northeastern USA.

Figure 41. ***Haplomitrium hookeri*** in a late snowbed in Wales. Photo by Janice Glime.

Figure 42. ***Aulacomnium turgidum*** in an alpine area of Norway. Photo by Michael Lüth, with permission.

Figure 43. ***Dicranum elongatum***, a rare species on Mt. Washington, NH, USA. Photo by Hermann Schachner, through Creative Commons.

Figure 44. ***Aulacomnium turgidum***, a rare species that survives on Mt. Washington, New Hampshire, USA. Photo by Michael Lüth, with permission.

Figure 45. ***Pseudocalliergon trifarium***, a rare species that survives the harsh climate on Mt. Washington, NH, USA. Photo by Andrew Hodgson, with permission.

Growth Form Variability

Snowbeds can create unusual growth forms. For example, in the high Arctic of Spitsbergen, the fellfield type of ***Sanionia uncinata*** (Figure 46-Figure 48) had few branchless shoots and formed dense colonies, leading to better desiccation avoidance (Ueno *et al*. 2001). The snowbed type had many branchless shoots and more sparse colonies. Furthermore, there were fewer branches in the upper part of the shoot than in the lower part in the snowbeds. Was this a response to the snow, possibly damaging branch buds, or was the more dense branching in the fellfield an adaptation selected to permit survival in the drier climate there?

Figure 46. ***Sanionia uncinata*** alpine habitat in Europe. Photo by Michael Lüth, with permission.

Figure 47. ***Sanionia uncinata*** with capsules in runoff area. Photo by Michael Lüth, with permission.

Figure 48. ***Sanionia uncinata*** with capsules and showing pinnate growth form. Photo by Michael Lüth, with permission.

The multiple growth forms of some species in the Antarctic seem to be a response to submersion (Seppelt & Selkirk 1984). For example, ***Bryum pseudotriquetrum*** (Figure 49-Figure 50) was originally named as ***Bryum algens*** there due to its different growth form. ***Calliergon sarmentosum*** (Figure 51-Figure 52) assumes a different morphology when shoots develop under water or in damp conditions (Priddle 1979). ***Bryum argenteum*** (Figure 53-Figure 54) in the Antarctic assumes longer and narrower leaves with increased cell size in etiolated shoots (Longton 1981; Seppelt & Selkirk 1984), perhaps due to submersion, or possibly due to growth in the reduced light under snow. ***Ceratodon purpureus*** (Figure 55-Figure 60) lives in shallow lakes in the Antarctic and was originally known as ***Ceratodon minutifolius*** there, differing in leaf shape and leaf apex (Horikawa & Ando 1963; Seppelt & Selkirk 1984).

Figure 49. ***Bryum pseudotriquetrum*** in the Antarctic, a moss with many growth forms. Photo courtesy of Catherine Beard.

Figure 50. ***Bryum pseudotriquetrum*** beside a stream, showing a typical growth form in the North Temperate Zone. Photo by Michael Lüth, with permission.

Figure 51. ***Calliergon sarmentosum*** mountain habitat in Europe. Photo by Michael Lüth, with permission.

Figure 52. ***Calliergon sarmentosum*** aquatic growth form. Photo by Michael Lüth, with permission.

Figure 53. ***Bryum argenteum*** from the Neotropics, exhibiting the broader leaves typical there. Photo by Michael Lüth, with permission.

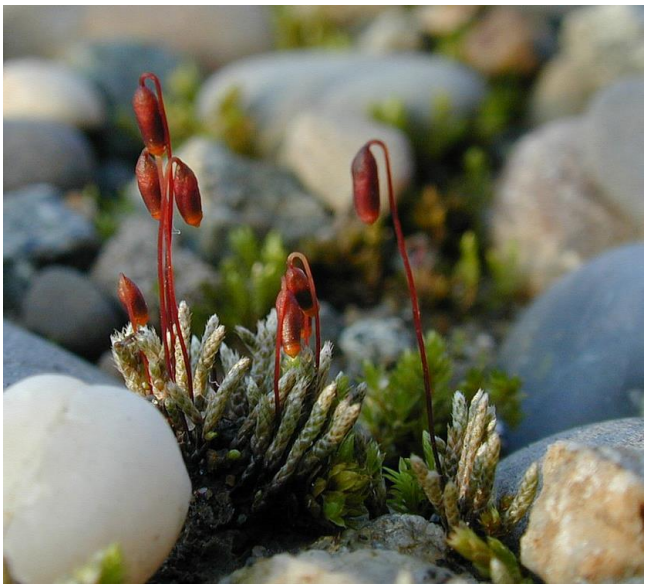

Figure 54. ***Bryum argenteum*** from alpine area in Europe where it exhibits longer, narrower leaves than plants from the tropics. Photo by Michael Lüth, with permission.

Figure 55. ***Ceratodon purpureus*** in Antarctica. Photo by Rod Seppelt, with permission.

Figure 56. ***Ceratodon purpureus*** in Antarctica. (Blackish mosses at right are ***Bryum pseudotriquetrum***.) Photo by Rod Seppelt, with permission.

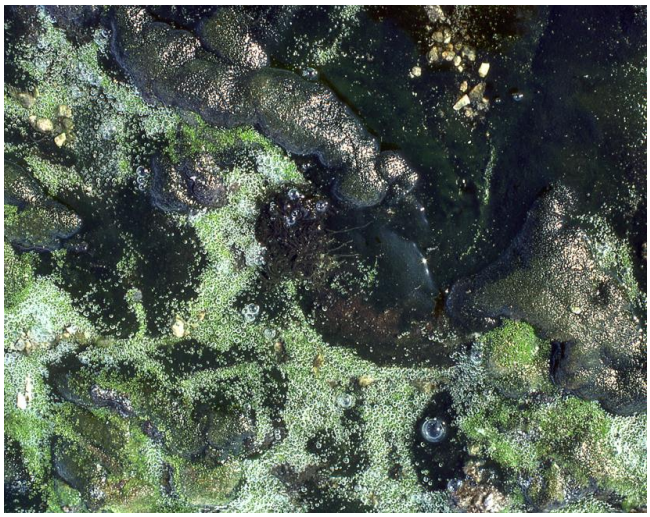

Figure 57. Submerged ***Ceratodon purpureus*** in the Antarctic. Bubbles from photosynthesis here create a condition known as **pearling**. Photo courtesy of Rod Seppelt.

Figure 58. Open growth of well-hydrated ***Ceratodon purpureus***. Photo by Michael Lüth, with permission.

Figure 59. Cushions of ***Ceratodon purpureus*** in the mountains of Norway. Photo by Michael Lüth, with permission.

Figure 60. ***Ceratodon purpureus*** dry among rocks in Michigan, USA. Photo by Janice Glime.

Duration of Snowbeds

The duration of the snowbeds separates communities in Scotland (Woolgrove & Woodin 1994). Prolonged snowlie has negative effects on the ***Marsupella-Anthelia*** community (Figure 29-Figure 30, Figure 35; Figure 10). On the other hand, the ***Polytrichum-Kiaeria*** (Figure 18-Figure 20; Figure 26-Figure 27) community is positively affected by its prolongation. ***Pohlia*** (Figure 14-Figure 16, Figure 22-Figure 23) seems less affected by the duration, but the substrate moisture content is important for it.

Snowmelt

Kaiser (1921) describes his "journey into mossland" during a February thaw in Pennsylvania, USA. So many mosses appeared, bright green, and ready to grow. These winter survivors, especially along streambanks, included ***Plagiomnium cuspidatum*** (Figure 61-Figure 62), ***Leucobryum glaucum*** (Figure 63-Figure 67), ***Bryoandersonia illecebra*** (Figure 68-Figure 69), ***Dicranum scoparium*** (Figure 70-Figure 71), ***Plagiomnium ciliare*** (Figure 72), ***Rhizomnium punctatum*** (Figure 73), ***Conocephalum conicum*** (Figure 74), ***Marchantia polymorpha*** (Figure 75), ***Pellia epiphylla*** (Figure 76), ***Atrichum*** (Figure 77), ***Dicranella*** (Figure 78), ***Pohlia nutans*** (Figure 79-Figure 80), and ***Bartramia pomiformis*** (Figure 81-Figure 82), among others, all benefitting from the snowmelt moisture.

Figure 61. ***Plagiomnium cuspidatum*** hydrated, a moss that survives snow cover to regain photosynthesis in spring. Photo by Hermann Schachner, through Creative Commons.

Figure 62. ***Plagiomnium cuspidatum*** dry. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 63. ***Leucobryum glaucum*** on edge of crevice where it escapes the leaf litter. This site benefits from runoff, but can also suffer exposure. Photo by Janice Glime.

Figure 64. ***Leucobryum glaucum***, one of the mosses that is ready to photosynthesize when the snow melts. Photo courtesy of Eileen Dumire.

Figure 65. ***Leucobryum glaucum*** showing the whitish color due to hyaline cells that help to keep the photosynthetic cells hydrated. Photo by Janice Glime.

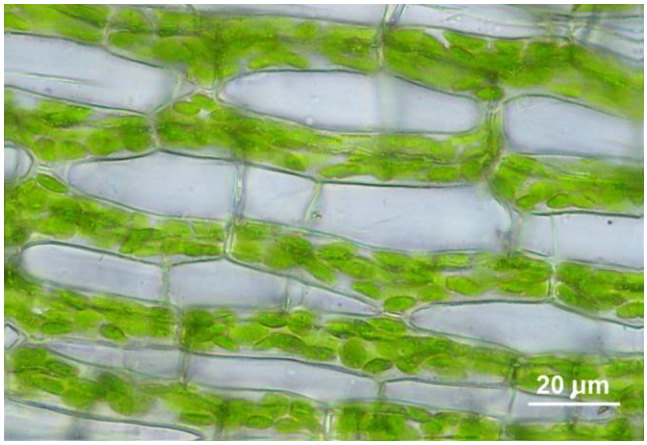

Figure 66. ***Leucobryum glaucum*** showing photosynthetic and hyaline leaf cells. Photo by David Wagner, with permission.

Figure 67. ***Leucobryum glaucum*** leaf cross section showing photosynthetic and hyaline cells. Photo by Walter Obermayer, with permission.

Figure 68. ***Bryoandersonia illecebra***, a moss that one can find when the snow melts in Ohio, USA. Photo by Bob Klips, with permission.

Figure 69. ***Bryoandersonia illecebra*** on tree, a species of vertical surfaces. Photo by Bob Klips, with permission.

Figure 70. ***Dicranum scoparium*** in early autumn, a moss that overwinters and looks bright when the snow melts. Photo by Janice Glime.

Figure 71. ***Dicranum scoparium*** with capsules. Photo by Michael Lüth, with permission.

Figure 72. ***Plagiomnium ciliare*** with antheridia, a moss that overwinters and is ready to grow when the snow leaves. Photo by Robert Klips, with permission.

Figure 73. ***Rhizomnium punctatum*** looking etiolated after its winter snow cover. Photo by Michael Lüth, with permission.

Figure 74. ***Conocephalum conicum***, a liverwort that is active in early spring. Photo by Janice Glime.

Figure 75. ***Marchantia polymorpha*** with gemmae cups, a liverwort that is active when the snow melts. Photo by David T. Holyoak, with permission.

Figure 76. ***Pellia epiphylla*** in the mountains of Wales. Photo by Janice Glime.

Figure 77. ***Atrichum undulatum*** in snow, a species that has a distinct increase in cold tolerance from summer to winter and is ready for photosynthesis when the snow melts. Photo by Michael Lüth, with permission.

Figure 78. ***Dicranella heteromalla***, a soil bank moss that is ready to grow when the snow melts. Photo by Michael Lüth, with permission.

Figure 79. ***Pohlia nutans*** at snowmelt time in the Khibiny Mountains, Russia. Photo by Michael Lüth, with permission.

Figure 80. ***Pohlia nutans***, one of the first plants to be seen in spring. Photo by Michael Lüth, with permission.

Figure 81. ***Bartramia pomiformis*** in its typical cliff-hanger habitat. Photo by Janice Glime.

Figure 82. ***Bartramia pomiformis***, a moss that is green in early spring. Photo by Michael Lüth, with permission.

Gaberščik and Martinčič (1987) demonstrated seasonal changes in growth of ***Sphagnum papillosum*** (Figure 83-Figure 85) in a raised bog in Slovenia, Yugoslavia. They found the greatest growth at the beginning of the growing season, a time when water is usually plentiful. During winter months, the photosynthetic activity declines and ceases completely in February.

Figure 83. ***Sphagnum papillosum*** on exposed rock where it can benefit from spring snowmelt runoff. Photo by Michael Lüth, with permission.

Figure 84. ***Sphagnum papillosum*** in a flush created by melting snow. This one is still wet in late July in the mountains of Wales. Photo by Janice Glime.

Figure 85. ***Sphagnum papillosum***, shown here with sundews. This ***Sphagnum*** species has seasonal changes in growth, with photosynthetic activity declining in winter in Yugoslavia. Photo by Michael Lüth, with permission.

One restoration technique in peat-mined bogs in Canada has been an attempt to enhance the moisture content (Rochefort *et al*. 2002). To do this, ***Sphagnum*** (Figure 83-Figure 85) is reintroduced in the restoration areas and may be covered by extended periods of flooding, especially following snowmelt or heavy rainfall. These flooding events can cause production of **innovations** in which the buds and shoots grow. Some species grow **capitula** (compact apical branches of ***Sphagnum***) from fragments under a variety of conditions. The most species in their study grew from whole plants under long-term conditions of shallow flooding. However, many of the species under long-term flooding suffered from **etiolation** (condition of plants grown in partial or complete absence of light, characterized by long, weak stems and smaller, sparser leaves).

In the Niigata Prefecture of Japan, the floating liverwort ***Ricciocarpos natans*** (Figure 86) is common in cultivated rice fields (Shirasaki 1996). It grows best where there are warmer temperatures and a snow depth of 0.5-3.0 m.

Figure 86. ***Ricciocarpos natans*** with duckweed. Photo by Martin Hutten, with permission.

In western Norway, ***Andreaea rupestris*** (Figure 87-Figure 89) occurs along the flushing gradients created by snowmelt or is associated with snow cover (Hedger 2001). Species in the alpine areas of Norway are sensitive to the timing of snowmelt. In 43 sampled transects, 22 of the 41 taxa show a significant relationship to the time of snowmelt as the altitude increases. But these relationships are not necessarily direct responses to the temperature or water. Rather, at least some of them avoid locations of earlier snowmelt because of competition from other plants, especially tracheophytes.

Figure 87. ***Andreaea rupestris*** in the Khibiny Mountains of Russia in an area with snowmelt water and late snowbeds. Photo by Michael Lüth, with permission.

Figure 88. ***Andreaea rupestris*** with capsules, a species that grows in areas of late snowmelt. Photo by Des Callaghan, with permission.

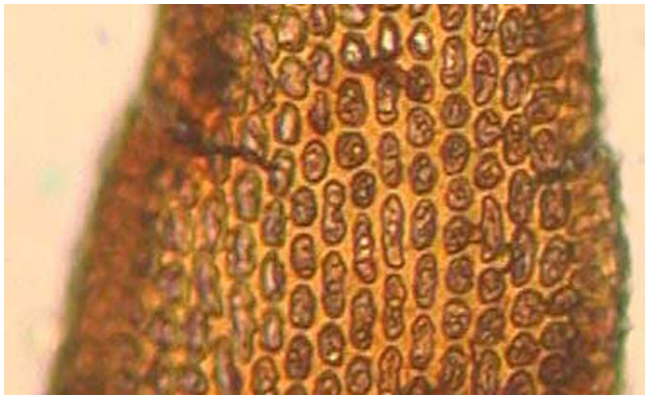

Figure 89. ***Andreaea rupestris*** leaf showing thick, pigmented cell walls that may help to protect the cell contents from cold temperatures and high UV light. Photo from Botany Department Website, University of British Columbia, Canada, with permission.

Snowbed bryophytes must utilize low light and short growing seasons with low temperatures to attain sufficient photosynthesis for carbon gain. ***Anthelia*** (Figure 10) does especially well in the border zone of snowbeds because of its resistance to long-lasting cold, wet, and dark conditions (Lösch *et al*. 1983). ***Polytrichastrum sexangulare*** (Figure 18-Figure 20), on the other hand, is more productive and is therefore able to compete with the tracheophytes at less extreme sites.

Mechanical Effects

Snow has its down side for plants. The sheer weight can crush or break the plants. So how do tiny plants like bryophytes fare under this weight? Kennedy (1993) commented on how few studies have included the biomechanics of bryophytes, reminding us of their need for snow cover resistance.

Among the mosses receiving the greatest mechanical stress due to height is ***Dendroligotrichum dendroides*** s.l. This moss stands alone, supporting a height up to 40 cm where it lives in the forests of Chile and New Zealand. For this species, the dense hypodermal sterome provides considerable stiffness comparable to that of woody stems of tracheophytes. But for many smaller mosses, such support is usually not needed. Rather, the mosses of various habitats have a wide range of mechanical conformations. By contrast, size, development, and phylogenetic position seem to be less important than the habitat in determining growth form and mechanical adaptations.

Freeze-thaw Cycles

Free-thaw cycles can have some of the same damaging effects as dehydration-rehydration. And like many other epiphytes that tolerate the wet-dry cycles, the rock face and tree-trunk-dwelling ***Leucodon sciuroides*** (Figure 90) in the Mediterranean tolerates freezing and thawing with its photosynthetic apparatus fully operational after freezing (Deltoro *et al*. 1999). Both CO_2 fixation and chlorophyll fluorescence return to pre-freezing values during thawing. And like many desert mosses, it recovers its photosynthesis rapidly during thawing. Deltoro and coworkers suggest that this rapid recovery is possible through dissipative pathways that absorb excess light energy in frozen plants.

Figure 90. ***Leucodon sciuroides*** on tree bark, a species that tolerates freezing and is ready for photosynthesis as soon as it thaws. Photo by Michael Lüth, with permission.

Melick and Seppelt (1992) experimented with up to 16 freeze-thaw cycles in Antarctic bryophytes. After 16 days of immersion in water, there is a relatively low loss of glucose and fructose [10-29% of the total sugar pool in healthy mosses, but 69% from the dead ***Schistidium chrysoneurum*** (=***Grimmia antarctici***; Figure 91-Figure 92)]. Freeze-thaw cycles increase this leakage up to 2-3 times except in the dead mosses. ***Bryum pseudotriquetrum*** (Figure 49-Figure 50) lost 65% of its total sugar when subjected to 16 freeze-thaw cycles. The other species [***Ceratodon purpureus*** (Figure 55-Figure 60, Figure 92), ***Schistidium chrysoneurum***, ***Cephaloziella exiliflora*** (Figure 93)] lost less than 28%. This loss does not seem to be related to the freezing temperature.

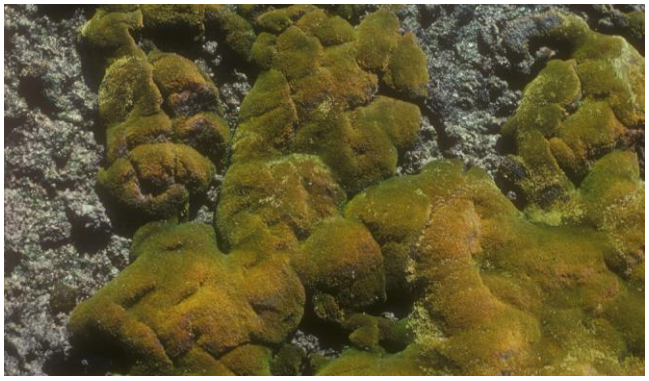

Figure 91. ***Schistidium chrysoneurum*** in the Antarctic. Photo by Rod Seppelt, with permission.

Figure 92. ***Schistidium chrysoneurum*** hummock with ***Ceratodon purpureus*** in the hollows. Photo by Rod Seppelt, with permission.

Figure 93. ***Cephaloziella*** sp. ***Cephaloziella exiliflora*** loses some of its stored sugar during freeze-thaw cycles. Photo by Kristian Peters, with permission.

Schlensog *et al*. (2004) compared the recovery of lichens and mosses after winter in the continental Antarctic. Whereas the lichens recover **photosystem II** (PS II, first protein complex in light-dependent reactions of oxygenic photosynthesis; it captures photons of light to energize electrons) almost fully within a few minutes of hydration, the mosses take much longer to recover. The moss ***Bryum subrotundifolium*** (Figure 94-Figure 96) maintains highly elevated respiration rates for several days following activation. Like the response to desiccation, it appears that this moss must repair damages before it can make a positive photosynthetic gain.

Figure 94. Bed of ***Bryum subrotundifolium*** in meltwater on Antarctica. Photo by Rod Seppelt, with permission.

Figure 95. ***Bryum subrotundifolium***, a moss that maintains high respiration rates for several days following rehydration. Photo by Rod Seppelt, with permission.

Figure 96. ***Bryum subrotundifolium*** in the Antarctic infected with a fungus that is taking advantage of suitable moisture conditions. Photo by Catherine Beard, with permission.

Freeze-thaw protection can be conferred on bryophytes by various compounds present prior to freezing (Rütten & Santarius 1993). In ***Plagiomnium affine*** (Figure 97) the uptake and release of sucrose does little to change the permeability of the leaf cell plasma membranes to sugars, **proline** (amino acid), or polyethylene glycols. However, pretreatment with these compounds sufficient to induce plasmolysis does protect the moss cell membranes from freeze-thaw damage. On the other hand, pretreatment with **glycerol** (compound that is soluble in water and is hygroscopic) causes **plasmolysis** (shrinking of cell membrane away from cell wall) without endowing the cells with protection against freeze-thaw damage.

Figure 97. ***Plagiomnium affine***, a moss protected from freeze-thaw damage by various compounds and plasmolysis. Photo by Michael Lüth, with permission.

Winter Short-term Warming Events

Noting that climate change in northern high latitudes is likely to be greater in winter than in summer, Bjerke *et al*. (2011) examined the potential effects of more frequent short-term warming events. Whereas these warming event effects are known to be damaging to tracheophytes, their effect on bryophytes could be quite different. And the bryophytes and lichens are of major importance in these high-latitude ecosystems. By simulating winter warming events with infrared lamps and soil warming cables in a sub-Arctic heath, Bjerke *et al*. were able to monitor the responses of the feather moss ***Hylocomium splendens*** (Figure 142). In the three winters of simulated warming events, this moss experienced significant reductions in net photosynthetic rates and growth rates (of up to 48% and 52%, respectively), starting in the first summer after these events began. In this species, growth begins early in the spring season, exposing young, vulnerable shoots to the effects of cold. The researchers suggest that the damage under winter warming events may be due to breaking dormancy and experiencing premature growth during the winter warming events that causes damage to those sensitive young shoot tissues. Subsequent drying following these events may cause desiccation damage to the tender shoots.

These winter warming events could change the distribution of acrocarpous vs pleurocarpous mosses in areas with winter snow cover. In the Front Range of the Rocky Mountains, USA, Flock (1978) found that acrocarpous mosses are more abundant in areas that are dry and maintain light snow cover. Pleurocarpous mosses, on the other hand, are more abundant in wet sites with deep snow cover.

As Longton (1988) has pointed out, bryophytes in general have phenotypic plasticity, opportunistic responses in CO_2 exchange, and a poikilohydrous water relationship that endows them with considerable tolerance for desiccation and frost. These make it possible for them to occupy snowbeds where few tracheophytes can succeed.

Protection from Light Damage

A potentially serious problem for desiccated mosses at low temperatures is that they are still able to absorb light energy. This can be a special problem for forest epiphyte species that experience more light exposure in winter, compared to summer, when the tree canopy has lost its leaves. Particularly on those cold days that lack snow cover, over excitation of chlorophyll electrons can be damaging. However, Heber *et al*. (2006) report that some mosses have seasonal differences in their ability to dissipate that excess light energy into heat.

Freezing and thawing can result in photoinhibition, as demonstrated by the endemic moss ***Schistidium chrysoneurum*** (Figure 91) from the Antarctic (Lovelock *et al*. 1995a). Jägerbrand (2011) considered the time immediately following snowmelt to be the most dangerous time for UV damage to bryophytes. Rehydration, lingering low temperatures, and rising UV levels coincide with a time when bryophytes must repair the damage due to absence of light and desiccation from winter. This is especially problematic in the Antarctic where the ozone layer is thinning. Fortunately, this highly variable photoinhibition is reversible during periods of warmer temperatures (Lovelock *et al*. 1995a). The inhibition that occurs between freezing and thawing events recovers best under low light conditions. After four cycles, recovery of hydrated mosses occurred within 12 hours of transfer to 5°C at 15 μmol quanta m^{-2} s^{-1}.

During the dry summers, some desiccation-tolerant mosses are more protected against photo-oxidative damage when they are dry than they are in the humid winters (Heber *et al*. 2006). In mosses such as the **poikilohydric** (having no mechanism to prevent desiccation) ***Rhytidiadelphus squarrosus*** (Figure 98), desiccation reduction of chlorophyll fluorescence does not occur under even strong illumination in the desiccated state once the moss has achieved phototolerance. One protectant is **zeaxanthin** (one of the most common carotenoid alcohols and a powerful antioxidant), which requires drying in light. If the water is lost slowly, fluorescence is quenched. Quenchers accumulate during desiccation and remain stable until hydration occurs. Hydration results in their reversion to non-quenching molecules.

Figure 98. ***Rhytidiadelphus squarrosus***, a moss that requires drying to induce protection (zeaxanthin) against photoquenching. Photo by Michael Lüth, with permission.

Lovelock and Robinson (2002) found that surface reflective properties of leaves also plays a role in dissipating the light, hence protecting the plants from light damage. They suggested that the water content, but not pigments, of the mosses are important in altering the red-edge and photochemical reflectance index. The water content may account for the differences in reflectance among the species. All the mosses maintain high levels of xanthophyll pigments that serve as photoprotectants. Interestingly, their abilities to reflect UV light differs little. ***Bryum pseudotriquetrum*** (Figure 49-Figure 50) has greater reflective values than the other mosses studied and also has higher levels of UV-absorbing pigments, but its carotenoid levels are lower than the other species tested. ***Ceratodon purpureus*** (Figure 55-Figure 60) has higher levels of anthocyanins but lower total chlorophyll concentrations. ***Bryum pseudotriquetrum*** has higher levels of the specific UV-screening pigments; ***Ceratodon purpureus*** and ***Schistidium chrysoneurum*** (Figure 91) have higher levels of pigments that protect against excess visible light.

For ***Schistidium chrysoneurum*** (Figure 91), freezing in darkness reduced the **F_v/F_m ratio** (ratio of variable:maximum fluorescence) and the initial fluorescence (Lovelock *et al*. 1995b). These were reversible when the mosses thawed. The reduction of F_v/F_m may be the result of conformational changes in the pigment-protein complexes due to the desiccation that occurs during freezing. The photoinhibition during freezing is reversible and indicates that processes that protect the moss from photoinhibitory damage during freezing temperatures occur in consort with high solar radiation levels. These protections therefore limit the repair needed when favorable temperatures return.

Winter Growth

Proctor (2000) points out that bryophytes have a desiccation tolerance strategy that differs from that of tracheophytes. Bryophytes are able to survive because they can photosynthesize and grow when water is freely available, then suspend their metabolism when it is not. By being **ectohydric** (conducting water externally), many species can have wide variability in their external capillary water without affecting the water content of the cells. This external source permits the cells to function most of the time with full turgor. When they do desiccate, the period of water stress is brief. They have a carbohydrate content that is similar to that of the maturing embryos of desiccation-tolerant seeds. It is likely that these carbohydrates contribute to their rapid recovery upon rehydration. In short, they mimic temperate winter annuals or mesic desert ephemerals. For example, in the maritime climate of Britain, the wall top moss ***Grimmia pulvinata*** (Figure 99) takes advantage of the mild climate of autumn and early winter for most of its growth (Proctor 2004). During that period the moss is able to maintain hydration for long periods of time to carry out photosynthesis. Like many mosses, it is adapted to frequent and often short wet-dry cycles.

Figure 99. ***Grimmia pulvinata*** on rock where it grows mostly in autumn an dearly linter when it is well hydrated frequently. Photo by Michael Lüth, with permission.

Even growth rates seem to adjust to differences in temperature, perhaps because of differences in available moisture, perhaps just to acclimation (see Fornwall & Glime 1982). For example, ***Brachythecium rutabulum*** (Figure 100) has superior growth in winter compared to summer when grown at temperatures below 18°C (Furness & Grime 1982). Most species of temperate regions seem to have their optimum growth temperature at 15-25°C, but growth can be extensive at temperatures even below 10°C. Gaberščik and Martinčič (1987) demonstrated seasonal changes in growth of ***Sphagnum papillosum*** (Figure 83-Figure 85) in a raised bog in Slovenia, Yugoslavia. They found the greatest growth at the beginning of the growing

season, a time when water is usually plentiful. During winter months, the photosynthetic activity declined and ceased completely in February.

Figure 100. ***Brachythecium rutabulum*** on Populus x canadensis log, emerging from the snow. Photo by Pim Rijkee, through Wikimedia Commons.

Asada *et al.* (2003) found that winter growth of a number of bryophyte species [***Racomitrium lanuginosum*** (Figure 101-Figure 103), ***Pleurozium schreberi*** (Figure 104), ***Sphagnum austinii*** (Figure 105-Figure 106), ***S. fuscum*** (Figure 2), ***S. rubellum*** (Figure 107-Figure 108), ***S. papillosum*** (Figure 83-Figure 85), ***S. lindbergii*** (Figure 38-Figure 39), ***S. tenellum*** (Figure 109-Figure 110), ***S. pacificum*** (Figure 111)] in a coastal peatland in British Columbia, Canada, is an important contribution to the productivity of the system. But for this productivity to occur, water must be available during those times when the temperature permits photosynthesis to occur. Asada further supported the importance of water by demonstrating that productivity in these species correlated more strongly with precipitation than with temperature.

Figure 101. ***Racomitrium lanuginosum*** forming massive hummocks in Iceland. Photo by Janice Glime.

Figure 102. ***Racomitrium lanuginosum*** forming hummocks that benefit from late season snowmelt water. Photo by Michael Lüth, with permission.

Figure 103. ***Racomitrium lanuginosum***, a species that has winter growth in coastal wetlands. Photo by Juan Larrain, with permission.

Figure 104. ***Pleurozium schreberi***, a moss that can tolerate frequent wet-dry cycles and grows best in the seasons with the best hydration. Photo by Janice Glime.

Figure 105. ***Sphagnum austinii*** wetland habitat. Photo by Michael Lüth, with permission.

Figure 106. ***Sphagnum austinii*** with a sundew that shares its habitat. Photo by Michael Lüth, with permission.

Figure 107. ***Sphagnum rubellum*** wetland habitat. Photo by Michael Lüth, with permission.

Figure 108. ***Sphagnum rubellum***, a species that benefits fro winter growth in coastal peatlands. Photo by Michael Lüth, with permission.

Figure 109. ***Sphagnum tenellum*** showing its very wet habitat that permits it to take advantage of late season photosynthesis. Photo by Michael Lüth, with permission.

Figure 110. ***Sphagnum tenellum***, a moss that can benefit from winter photosynthesis. Photo by Michael Lüth, with permission.

Figure 111. ***Sphagnum pacificum***, a moss that takes advantage of late season photosynthesis. Photo by Vita Plasek, with permission.

Growth can actually occur at sub-zero temperatures. ***Brachythecium geheebii*** (Figure 112) and ***Homalothecium philippeanum*** (Figure 113-Figure 114) in Romania montane areas are able to assimilate CO_2 down to -9°C (Atanasiu 1971). ***Isothecium alopecuroides*** (Figure 115-Figure 116) had net gain down to about -8°C. Both of these temperatures are lower than those for evergreen trees tested in winter. But not all bryophytes are created equal. Davey and Rothery (1996) found that in ***Brachythecium austrosalebrosum*** from the Antarctic, respiration rates were highest in summer and lowest in winter regardless of temperature within the natural range, but that in ***Chorisodontium aciphyllum*** (Figure 117-Figure 118) and ***Andreaea depressinervis*** (Figure 119), there was little change with season.

Figure 112. ***Brachythecium geheebii***, a species that can have net photosynthetic gain down to -9°C. Photo by Michael Lüth, with permission.

Figure 113. ***Homalothecium philippeanum*** in a habitat where it can be exposed to sub-zero temperatures. Photo by Michael Lüth, with permission.

Figure 114. ***Homalothecium philippeanum*** on a boulder where it can photosynthesize when the air temperature is as low as -9°C. Photo by Michael Lüth, with permission.

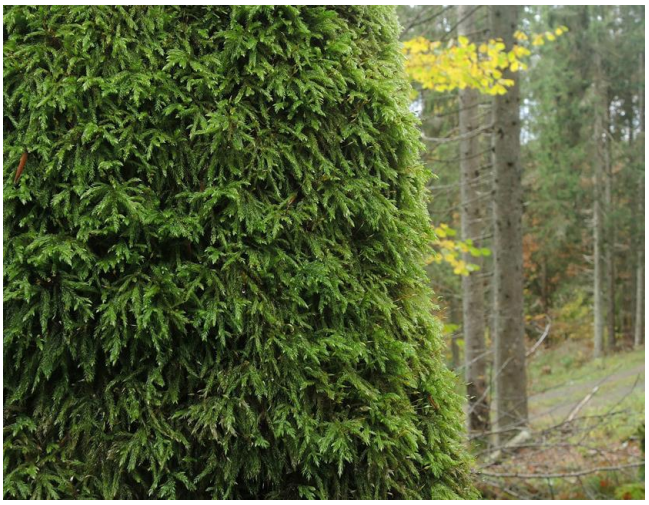

Figure 115. ***Isothecium alopecuroides*** growing epiphytically where it is exposed to sub-zero temperatures. Photo by Michael Lüth, with permission.

Figure 116. ***Isothecium alopecuroides***, a species that has photosynthesis down to -8°C. Photo by David Holyoak, with permission.

Figure 117. ***Chorisodontium aciphyllum*** in Antarctica where its respiration differs little with seasons. Photo from Polar Institute, through Creative Commons.

Figure 118. ***Chorisodontium aciphyllum***, a moss whose respiration differs little with season. Photo by Juan Larrain, with permission.

Figure 119. ***Andreaea depressinervis***, an Antarctic species whose respiration differs little with season. Photo from Wikimedia Commons.

A recent addition to the known flora of the British Isles, the thallose liverwort ***Athalamia hyalina*** (Figure 120) is a Northern Hemisphere montane species (Long *et al*. 2003). In Scotland it has its active growth in the winter and produces its spores in spring. This permits it to live on the thin soil of eroding limestone ledges where it can take advantage of the moisture in fog of winter and intermittent thaws.

Figure 120. ***Athalamia hyalina***, a liverwort that grows in winter in Scotland. Photo by Michael Lüth, with permission.

Winter warming (and possibly summer drought?) in the UK seems to account for the increases in ***Campyliadelphus chrysophyllus*** (Figure 121) and ***Fissidens dubius*** (Figure 122) in a limestone grassland, as demonstrated with experiments in winter warming and increased supplemental rainfall in summer (Bates 2006). Spread of the epiphytes ***Cololejeunea minutissima*** (Figure 123) and ***Colura calyptrifolia*** (Figure 124) seems likewise to be the result of rising temperatures in winter, and possibly a change in the summer moisture. On the other hand, winter warming coincides with decreases in ***Rhytidiadelphus squarrosus*** (Figure 98) and ***Lophocolea bidentata*** (Figure 125).

Figure 121. ***Campyliadelphus chrysophyllus***, a species that is increasing in abundance in the UK as a result of winter warming. Photo by David Holyoak, with permission.

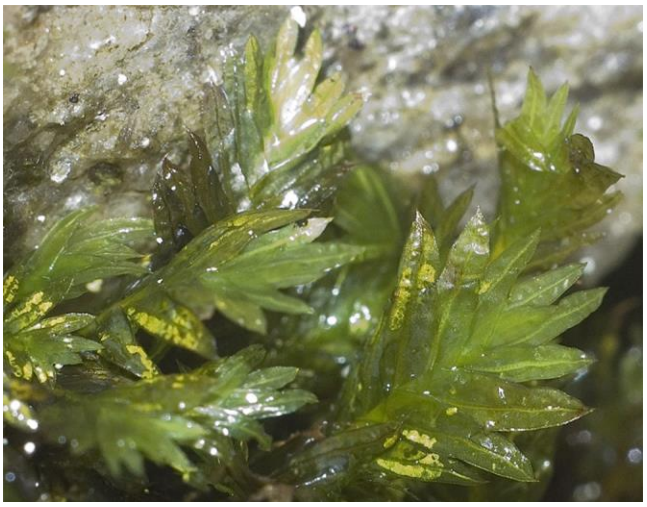

Figure 122. ***Fissidens dubius***, a species that is increasing in abundance in the UK as a result of winter warming. Photo by Aimon Niklasson, with permission.

Figure 123. ***Cololejeunea minutissima*** on bark, a species that seems to be spreading in the UK concomitant with rising mean winter temperatures. Photo by David T. Holyoak, with permission.

Figure 124. ***Colura calyptrifolia*** on bark, a species that seems to be spreading in the UK concomitant with rising mean winter temperatures. Photo by Michael Lüth, with permission.

Figure 125. ***Lophocolea bidentata***, a species that seems to be disappearing from the UK due to winter warming. Photo by Michael Lüth, with permission.

Winter and Reproduction

Since winter is often the season with moisture in some habitats like deserts, we can expect this to be the season of gamete transfer and fertilization. In the Negev Desert of southern Israel, Herrnstadt and Kidron (2005) found that ***Bryum dunense*** initiates its reproductive organs prior to the first winter rain, using atmospheric humidity from dew and fog as the source of water. The most sporophytes form in the partially shaded microhabitats following winter rains, interestingly exceeding those in the shaded microhabitats. When the first rain arrives, ***B. dunense*** is ready to disperse its bulbils and to complete fertilization. The shrubs seem to be essential to provide the partial shade in which this species is most successful at reproducing.

Too little rainfall in winter can be detrimental to desert mosses. ***Syntrichia inermis*** (Figure 126) in the Mojave Desert, Nevada, USA, failed to initiate sporophytes in 1996 and 1997 when the winter-spring rainfall was reduced (Stark 2001). In ***Crossidium crassinerve*** (Figure 127), the appropriate hydration periods occurred in the cooler months of October to April (Stark 2005). Hydration in the summer was detrimental because the patches dried too quickly (as few as 3 hours) following the rainfall, prohibiting sufficient repair and carbon gain. During the four years of the study, the five patches monitored initiated 248 sporophytes; only 9 survived. Embryonic abortion (69%) and capsule herbivory (30%) accounted for most of the deaths.

Acaulon triquetrum (Figure 128) in southwest Germany initiates most of its gametangia in October to December (Ahrens 2003). These develop rapidly, permitting fertilization to occur during the same time period. Sporophytes grow in October-November to January-February, with dispersal in April or May. The **chloronemal** (branches of protonemata that give rise to gametophore buds) filaments are persistent through summer but die off during winter (December – February). The rhizoid system, however, persists throughout the winter, once again giving rise to new chloronemata and gametophores in the spring. Having rhizoids that persist through the winter permits this moss to rapidly occupy bare surfaces, especially the loess created by small, burrowing mammals.

Figure 126. ***Syntrichia inermis*** dry, a species that frequently fails to produce sporophytes due to insufficient rainfall in winter and spring in the Mojave Desert, USA. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 127. ***Crossidium crassinerve***, a species that is hydrated mostly in winter and early spring in the Mojave Desert. Photo by Michael Lüth, with permission.

Figure 128. ***Acaulon triquetrum***, a species that initiates its gametangia October-December in Germany. Photo by Michael Lüth, with permission.

Laaka-Lindberg and Heino (2001) found that the leafy liverwort ***Lophozia ventricosa*** (var. ***silvicola***; Figure 129) in southern Finland has two types of gemmae. One of these becomes dormant and the other is non-dormant. Only the dormant gemmae are able to survive the winter. She provided the evolutionary argument that if the winter mortality (of non-dormant gemmae) increases compared to the mortality during the growing season, then evolution would favor an increase in the percentage of dormant gemmae, especially among those produced at the end of the growing season.

Figure 129. ***Lophozia ventricosa*** with gemmae. This species produces two types of gemmae, one of which survives winter. Photo by Jan-Peter Frahm, with permission.

Spore dormancy is also subject to temperature. Spores require water to germinate, but dormancy loss also occurs in response to temperature. For ***Sphaerocarpos texanus*** (Figure 130) at 35/20°C, loss of spore dormancy increases faster than that in even modestly lower temperatures of 30/15°C or 25/15°C (McLetchie 1999). The best spore germination occurs at 16/10°C and spores fail to germinate at 35/20 or 30/15°C. But low temperatures induce the spores to return to dormancy. McLetchie considered this behavior to be similar to that of seeds of obligate winter annuals.

Figure 130. ***Sphaerocarpos texanus***, a species that loses its spore dormancy at higher temperatures. Photo by Martin Hutten, with permission.

Longton and Greene (1969) demonstrated that in Britain the boreal forest moss ***Pleurozium schreberi*** (Figure 104) sustains survival of its antheridia through winter. The antheridia begin development in August but remain immature through winter. The archegonia likewise overwinter in an immature stage. When spring arrives, both undergo rapid development, preparing them for fertilization in April and May. The sporophyte matures in autumn and spores are dispersed between January and April.

It is likely that the moss ***Dichelyma japonicum*** is excluded from high altitudes and latitudes because its sporophytes have a late sporophyte maturation (Shirasaki 1997). This species grows on the woody plants beside ponds and streams and is covered by deep snow in winter. In the aquatic family **Fontinalaceae**, this species requires deep snow in winter and high precipitation in summer.

Riccia cavernosa (Figure 131) avoids most of the problems of cold, dark, dry winters by having an extremely short life cycle on the banks and sandy flats of the Kobuk River in Alaska (Seppelt & Laursen 1999). Its spore to spore cycle is only three to four weeks of late summer and autumn! Hence, it is able to overwinter as spores and avoid all the problems. On the other hand, this same species (perhaps a different race?) has a life cycle of two - three months of winter and early spring in Australia.

Figure 131. ***Riccia cavernosa***, a species with a 3-4-week life cycle in Alaska and one of 2-3 months in Australia. Photo from <www.aphotofauna.com>, with permission.

Hennediella heimii (Figure 132) holds the record for the most polar sporophytes. Seppelt *et al*. (1992) reported this species with young sporophytes from the Lower Taylor Valley, Victoria Land, Antarctica (77°55'S).

Figure 132. ***Hennediella heimii*** with capsules; this species has the record for capsules at the highest latitude in the Antarctic. Photo by Michael Lüth, with permission.

Asexual Survival

We have learned much about preparation for winter conditions through studies in cryopreservation. The pioneer moss ***Ditrichum plumbicola*** (Figure 133) survives winters and desiccation in the field, but has poor survival of cryopreservation, even with pretreatment (Rowntree *et al*. 2007). Using a series of treatments and observations, Rowntree and co-workers attempted to determine the effects of ABA, sucrose, and desiccation on various stages of the protonemata. What they found was that most of the protonemal cells pretreated with ABA and sucrose died, but the ones that survived had thick cell walls with deep pigmentation, numerous small vacuoles, and cytoplasmic lipid droplets. Those with only desiccation and cryopreservation exhibited little cytological change. Removal of the ABA-sucrose pretreatment permitted normal development and activity of the protonemata, whereas the pretreatment induced propagules from the protonemata, and these propagules were highly desiccation tolerant and easily survived the cryopreservation. In nature, this species forms highly desiccation-tolerant rhizoids that serve the same perennating function.

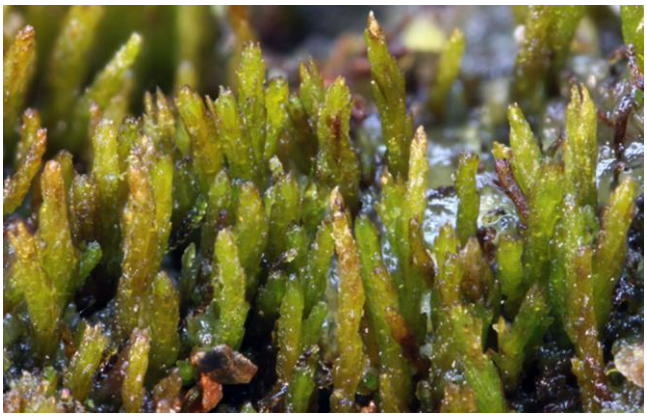

Figure 133. ***Ditrichum plumbicola***, a species that survives winter and desiccation in the field, but it has little ability to survive cryopreservation except as propagules. Photo by Des Callaghan, with permission.

Sympatric Differences

Seasonal differences in reproduction often separate **sympatric** (existing in same or overlapping geographic area) species and keep them separated reproductively. Such is the case for three species of ***Dicranoloma*** in Australia (Milne 2001). In ***D. menziesii*** (Figure 134) and ***D. platycaulon*** (Figure 135), the antheridia are initiated during winter and archegonia in the following spring, whereas in ***D. billardierei*** (Figure 136) the antheridia initiate during late spring to summer whereas archegonia originate in autumn. Differences in development time place the times of fertilization in three different time periods, late summer for ***D. menziesii***, mid autumn for ***D. platycaulon***, and early winter for ***D. billardierei***. For all three species, the winter season is an important period for this process, providing sufficient moisture and avoiding these activities during the high summer temperatures that can cause excessive respiration.

Figure 134. ***Dicranoloma menziesii***, a species separated from its congeners by its reproductive times. Photo by Andrew Hodgson, with permission.

Figure 135. ***Dicranoloma platycaulon***, a species separated from its congeners by its reproductive time. Photo by David Tng, with permission.

Figure 136. ***Dicranoloma billardierei***, a species separated from its congeners by its reproductive times. Photo by Michael Lüth, with permission.

In Japan, ***Trachycystis flagellaris*** (Figure 137) has developing sporophytes that do well in the lower temperatures and deep snow at higher altitudes (Shirasaki 1998). ***Trachycystis microphylla*** (Figure 138), on the other hand, has its sporophyte maturation in early spring; it seems to be restricted to coastal areas with only thin snow cover in winter.

Figure 137. ***Trachycystis flagellaris***, a species whose developing sporophytes survive well under deep snow. Photo by Ivanov, with permission.

Figure 138. ***Trachycystis microphylla***, a species that can survive only a thin snow cover. Photo by Li Zhang, with permission.

Effects of Bryophytes on their Communities in Winter

We cannot ignore the importance of the perennial nature of most bryophytes. Many remain active in winter, but even more importantly they are present and active within hours of snowmelt on their leaves.

The ability of the mosses to remain green and moist throughout winter in some areas is important for their invertebrate inhabitants. For example, in the Black Forest of Germany, ***Rhytidiadelphus squarrosus*** (Figure 98) is home to several species of tardigrades (water bears) (Schuster & Greven 2007). These tiny animals are well attuned to the seasonal changes in moss habitats. Their diversity is greatest in winter, although numbers decline then. (See Volume 2, Chapter 5).

Mosses are able to modify the effects of frost on the soil community. In a feather moss community in northwestern Alberta, Canada, dominated by ***Pleurozium schreberi*** (Figure 104), removal of the moss layer increased soil temperatures in summer and lengthened the frost-free period (Startsev *et al*. 2007). But rather than causing the soil to be warmer, the bare soil had temperatures as low as -13°C during the frost-free times.

In China, mosses are a critical part of the gall nut industry, a valuable source of medicines and chemicals. The gall aphid, ***Kaburagia rhusicola*** spends its winters on mosses, including ***Brachythecium*** spp., ***Entodon***, and ***Oxyrrhynchium*** (Lai & Zhang 1994). The mosses are able to provide both cover and a moist location. The gall aphid ***Kaburagia ovogallis*** uses eight species of the **Brachytheciaceae** for its winter hosts (Li 1990). In fact, as of 1990, 24 species of mosses were identified as winter hosts of various species of gall aphids. By providing more of these mosses, those in the gall nut industry were able to sustain higher yields.

Lichens (especially reindeer "moss") are well known as food for caribou and other large herbivores in winter. But bryophytes are less well known for this role. Oloffson *et al*. (2002) demonstrated the importance of bryophytes and other food sources by using exclosures around parts of snowbeds in Arctic-alpine tundra communities. Following eleven years of exclosure, the snowbed developed significant increase in both tracheophytes and bryophytes. The same response did not occur in the tall herb meadow. The primary herbivores in the study were rodents – grey-sided voles (***Clethrionomys rufocanus***), red voles (***C. rutilus***), field voles (***Microtus agrestis***), root voles (***M. oeconomus***), and lemmings (***Lemmus lemmus***). Bryophytes accounted for most of the cryptogamic changes in biomass. Predominant among those increasing in biomass were ***Sanionia uncinata*** (Figure 46-Figure 48) (584% increase) and ***Polytrichum juniperinum*** (Figure 139) (113,584% increase). ***Pleurozium schreberi*** (Figure 104) was absent in the controls and increased by 2.7g m^{-2} in the exclosures. The researchers concluded that the low competition of the unproductive snowbeds was caused by these mammalian herbivores that depressed the plant biomass. The presence of food under the snow, including the bryophytes, permits these animals to remain hidden from aerial predators.

Figure 140. ***Polytrichum juniperinum***, a species that increases in biomass following grazing by rodents in the Arctic. Photo by Michael Lüth, with permission.

Prins (1982) asked why mosses are eaten in cold climates only. Could it be that they like the sweet taste of sucrose that is stored in some species in preparation for winter?

Winter Dispersal

Winter can be a time for dispersal. Dry, brittle mosses easily break, presenting fragments that can travel long distances across the smooth snow or caught up in winds unimpeded by canopy leaves. McDaniel and Miller (2000) demonstrated this by collecting bryophyte fragments from late-spring snowbeds in the Adirondack Mountains, New York, USA. The diversity of fragments from the higher elevations of alpine and krummholz vegetation was much greater than that in the forested site. (The diversity also surpassed that of the tracheophytes.)

Miller and Howe Ambrose (1976) were able to collect bryophyte fragments from late snowbeds on Bathurst Island in the Canadian high Arctic. These collections contained large numbers of both mosses and liverworts. Most of the species represented those on the nearby ridges and slopes and Miller and Howe Ambrose presumed that these had been dispersed during the previous winter, resulting from surface winds. In lab cultures, 12% of these fragments exhibited viability, producing protonemata, new shoots, rhizoids, or renewed growth. But parts were not equally viable. Detached moss leaves did not grow and only one leafy liverwort fragment was viable. Rather, the leafy gametophore tips were the most successful. Nevertheless, the researchers estimated that a cubic meter of granular snow contained more than 4000 viable propagules!

Pollution Effects – Vital Water or Deadly Poisons?

Kennedy (1993) reminded us that traditional wisdom tells us that life in the Antarctic is restricted by the arrival of new species and the extreme cold. But recently biogeographical evidence indicates that water may be the primary limiting factor. But it can also bring danger.

Winter can be a particularly dangerous time for bryophytes that are subject to air pollution. The snow collects the pollutants over the extended period of snow cover (Thomas 1981). When melting occurs, the bryophytes are subjected to that long-term collection of pollutants, *i.e.*, concentrated pollutants, in what is known as **acid flush** (Woolgrove & Woodin 1996). Woolgrove and Woodin documented that these concentrated pollutants in the snowbed moss ***Kiaeria starkei*** are causing damage to the underlying bryophytes. This damage is greatest when the snow cover is gone and meltwater is delivered to the active plants. This exposure can last for a sufficient period of time that no recovery is measured after 4 weeks. This, combined with the short growing season of these mosses in snowbeds, can have serious impacts on their survival.

Markert and Weckert (1993) found that plants of ***Polytrichastrum formosum*** (Figure 141) had the maximum concentrations of pollutants in winter and the lowest in summer, attributing this to the higher biomass productivity of this species in the spring. But I suspect that part of this effect was due to the accumulation effect by the snow. Hynninen (1986) attributed the greater winter accumulation of heavy metals by ***Sphagnum*** (Figure 83-Figure 85) in moss bags in Finland to the summer holiday breaks. Could these winter highs be due to the absence of rain to wash the pollutants away and the long time for continuous collection?

In the boreal forest ***Hylocomium splendens*** (Figure 142) uses both organic and inorganic nitrogen deposited in the snow (Forsum *et al*. 2008). Snowmelt N is dominated by nitrates (86%), followed by ammonia (11%) and amino acids (3%). The ***H. splendens*** is able to take up 24% of the nitrogen from the snow nitrogen. On the other hand, Björk (2007) showed that 1.0 g m^{-2} yr^{-1} N added to the snow water had little effect on the bryophyte community over a three-year period. Other nutrients become available in the snowmelt water as well (Björk & Molau 2007; Jägerbrand 2011).

Figure 141. ***Polytrichastrum formosum*** with capsules, a species that accumulates the most pollutants in winter. Photo by David T. Holyoak, with permission.

Like growth, uptake of pollutants depends on the availability of water, and it may or may not be significantly affected by temperature. As concluded by Hébrard *et al*. (1974) for ***Grimmia orbicularis*** (Figure 143), the activities of ^{90}Sr transfer to the mosses coincide with those times of maximum rainfall in autumn, winter, and spring. The accumulations of the pollutant in dust on the moss is unavailable to the moss until water enters the cells.

Figure 142. ***Hylocomium splendens***, a species that takes a great deal of its nitrogen from snowmelt. Photo by Chmee, through Creative Commons.

Figure 143. ***Grimmia orbicularis***, a species that collects pollutants that are detrimental to it when it rains. Photo by Michael Lüth, with permission.

Summary

Late snowbeds provide a refuge for bryophytes where there is sufficient water in "spring" and reduced competition from tracheophytes. Species living there have life cycles that take advantage of snowmelt water and that have life cycle stages that can live through winter. The growth forms may be altered and duration of the snow is a determining factor in species composition. Prominent among the snowbed bryophytes are species of ***Anthelia*** and ***Kiaeria***. Snowmelt waters create flushes that have their own species, including several ***Sphagnum*** species.

Freeze-thaw cycles can be beneficial to some and detrimental to other bryophytes. Short thaw periods may be insufficient to repair damage from desiccation and freezing. These can become lethal for some bryophytes that are unable to realize any carbon gain. In some locations, especially the Antarctic, exposure in winter subjects the bryophytes to higher UV light intensities, coupled with low temperatures. Some live in exposed sites where wind clears the snow or on vertical surfaces that do not hold the snow, exposing the bryophytes to drying, intense light, and extreme low temperatures.

On the other hand, some bryophytes grow best in winter when more moisture is available. Others survive winter through asexual propagules. The life cycle adaptations to winter microclimate are effective means for maintaining species differences among sympatric members of the same genus.

Bryophytes occupy habitats where tracheophytes cannot complete their life cycles in the short growing seasons. These bryophytes provide a refuge and food for invertebrates, rodents, and even some large free-range mammals. They modulate the ground temperature, preventing extremes, hold water longer than bare ground, and prevent destructive runoff during spring flushes.

The dry air of winter facilitates breakage of bryophyte fragments. These easily blow across the snow, taking advantage of the absence of leaves on the trees in deciduous forests, making winter dispersal significant.

Pollutants accumulate in the snow and rapid melt may expose the bryophytes to heavy concentrations in a short time frame. In some cases, the bryophytes gain important nutrients from the collected pollutants, but some are detrimental.

Acknowledgments

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CHAPTER 8-1
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CHAPTER 8-1
NUTRIENT RELATIONS: REQUIREMENTS

Figure 1. Mosses growing on an old iron stove, demonstrating their rather low nutrient requirements. Photo by Janice Glime.

What Do Bryophytes Require?

Bowen (1933) claimed that bryophytes are necessarily limited in nutrient supply by their **poikilohydric** (state of hydration controlled by environment) method of water regulation. Their method of receipt of water – predominantly from rainfall and, for most bryophytes, almost nothing from ground water – relegates them to receive nutrients that are dissolved in rainwater or that accumulate as dust. After the first few minutes of rainfall, those nutrient concentrations are extremely small compared to soil nutrients and are biased in their relative concentrations in very different ways. Therefore, it is not surprising that culture conditions designed for tracheophytes are often unsuitable for bryophytes. But is this what the bryophytes "prefer"? Or are these conditions they tolerate and that provide them relatively less competition from tracheophytes? And do they gain any nutrients from the soil?

Nutrient Requirements

Even in the slow-growing bryophytes, nutrients can be a major determinant of both species composition and diversity (Raabe *et al*. 2010; Stevens *et al*. 2010; Schrijver *et al*. 2011). For tracheophytes, we know that the **trace elements** (micronutrients) (Fe, Zn, Mn, Cu, Ni, B, Mo, and Cl) are essential (Welch 1995). These seem to be important for bryophytes as well, but in lower concentrations. Nevertheless, the levels of requirements and tolerance can vary widely not only among species, but also within species (Shaw 1988).

Most knowledge about nutrient requirements of bryophytes comes from culturing them (Voth 1943; Brown 1982), although more recently we have learned much through the effects of atmospheric pollution. We soon learned that concentrations that favored the growth of tracheophytes in the laboratory were too strong for the poikilohydric bryophytes, and dilutions of 10:1 seemed more satisfactory.

Hoffman (1966) performed a complex set of experiments on the moss ***Funaria hygrometrica*** (Figure 2) in which he determined anion (N:P:S) and cation (K:Ca:Mg) combination effects. In his anion experiments, the absence of any of the three nutrients caused poor protonemal growth and no gametophores. On the other hand, the protonemata responded quite differently from the responses of the gametophores to the various cation combinations. This suggests that our usual descriptions of

conditions based on leafy plants may not provide us with any useful information on requirements needed for establishment. Even spores and gemmae may have different requirements (Brown 1982).

Figure 2. ***Funaria hygrometrica***, a species of disturbed habitats that requires N, P, and S among its nutrients. Photo by Michael Lüth, with permission.

Bryophytes seem to require the same nutrients, mostly for the same purposes, as do the tracheophytes. An easy way to remember the **macronutrients** (those needed in large quantities) is with the acronym **CHOPKNS Mg CaFe**, read as See Hopkin's mighty good cafe. These essential metabolic nutrients are maintained **within** the cell in relatively consistent high concentrations. The inconsistencies often found in measurements generally result when the bound portion on the cell surface is included. Table 1 lists the concentrations of macro- and micronutrients typical of various tracheophyte groups.

One factor that plays a major role in bryophyte nutrient needs and toxicity is the osmotic effect. Lacking an epidermis (except some thallose taxa) and having little wax on their surfaces, most bryophytes are especially susceptible to osmotic shock. Voth (1943) used ***Marchantia polymorpha*** (Figure 3) to show that a concentrated nutrient solution could kill the tips and wings of a growing thallus while reducing dry biomass and production of gemmae cups. At intermediate concentrations that retained the same nutrient ratio, the liverwort increased in size, produced a darker color, had more ascending tips, and developed more rhizoids, especially at the lower end of that concentration range. At the lowest set of concentrations, the rhizoids, scales, and lower epidermis had a more intense red-purple color, rhizoids were quite numerous, and gemmae cups diminished in number. Cell walls were especially thin in the strongest solutions and many cells collapsed, whereas in the most dilute solutions the cell walls were thickest.

Figure 3. ***Marchantia polymorpha***, a species that is sensitive to high nutrient concentrations. Photo by David T. Holyoak, with permission.

Table 1. Average mineral element content among plants of several habits. (All data are in parts per thousand). Based on published compilations included in Larcher 1983 and Epstein 1965 for agricultural plants.

Element	Land Plants ($g \cdot kg^{-1}$ dry matter)		Stored in Soil ($g \cdot kg^{-1}$ DM)	Marine Organisms ($g \cdot kg^{-1}$ DM)	Sea Water ($g \cdot L^{-1}$)	Agricultural Plants ($g \cdot kg^{-1}$ DM)
	Range	Mean	Mean	Mean		
N	10-50	20	1	50	0.0003	15
P	1-8	2	0.7	6	0.00003	2
S	0.5-8	1	0.7	10	0.9	1
K	5-50	10	14	10	0.4	10
Ca	5-50	10	14	5	0.4	5
Mg	1-10	2	5	4	1.3	2
Fe	0.05-1	0.1	38	0.4	0.00005	0.1
Mn	0.02-0.3	0.05	0.9	0.02	0.000005	0.05
Zn	0.01-0.1	0.02	0.05	0.2	0.000005	0.02
Cu	0.002-0.02	0.006	0.02	0.05	0.00001	0.006
Mo	0.0001-0.001	0.0002	0.002			0.0001
B	0.005-0.1	0.02	0.01	0.02	0.005	0.02
Cl	0.2-10	0.1	0.1	40	19.3	0.1

Considering these osmotic responses, it is not surprising to find that the same species of bryophytes from different habitats can respond quite differently to various concentrations of nutrients and heavy metals (Brown & Beckett 1985). If a plant has grown from spores at a certain nutrient/ion level, then its osmotic potential is more likely to be adjusted to that of its environment. The same is likely to be true for plants grown from fragments and other propagules. Moving a plant to another location can strongly affect that balance. Hence, monitoring studies that move bryophytes from one location to another need to account for normal ambient ion differences. Taxonomists likewise need to account for ionic differences in the environment because these can alter the morphology of the plants (Brown & Beckett 1985; Glime unpub. data).

The needs of young shoots are typically greater than those of older shoots; thus N, P, and K are found in young shoots in their highest concentrations (Tamm 1953). Nitrogen and phosphorus are essential in making proteins and DNA, and phosphorus is needed in ATP to maintain energy. A relatively high content of potassium is believed to be needed for the normal folding of cytoplasmic enzymes (Bates 2000). Magnesium is needed in chlorophyll and as an activator of several enzymes. Calcium acts as a messenger and is rarely present in the cytoplasm; it is, however, needed to maintain integrity of the plant by being part of the "glue" that cements the cell walls together. Calcium is not easily translocated and accumulates in older segments. However, its increasing concentration in older tissues is partly due to the recalcitrance of the cell wall, where Ca is concentrated, and the loss of dry biomass from older cells, increasing the ratio of Ca to leaf biomass (Bates 1979).

Macronutrients

Some macronutrients often are bound in rocks, unavailable to most plants. Nevertheless, bryophytes and lichens can affect biogeochemical cycles by surface weathering (Porada *et al*. 2014). Porada and coworkers calculated the degree of obtaining N and P from the rock substrate by quantifying the amounts needed by the organisms to account for their biomass increase. Using this indirect method, they estimated that these cryptogams contributed to chemical weathering of 0.058 to 1.1 $Km^3\ yr^{-1}$ of rock.

Nitrogen

Nitrogen (N) relationships for bryophytes are complex. For that reason, most of the discussion of this important nutrient are treated in a separate subchapter on nitrogen.

Nitrogen is essential for amino acids, proteins, DNA, and RNA. For bryophytes, slow growth means that requirements are low. Bryophytes are able to use both nitrate and ammonium, with differences among species. Nevertheless, some can use both (Schuler *et al*. 1955; Burkholder 1959). Others may have abnormalities in development in media with ammonium (Killian 1923; Southorn 1977).

On the other hand, the aquatic moss ***Fontinalis antipyretica*** preferentially assimilates ammonium ions (Schwoerbel & Tillmanns 1974). Others have shown that nitrate reductase only forms in the light (Fries 1945; Schwoerbel & Tillmanns 1974). This might explain why nitrate is the best source of N for ***Funaria*** and ***Weissia controversa*** protonemata in the light (Dietert 1979). Nevertheless, growth on a nitrate medium requires the bryophytes to convert it to ammonium ions before they can assimilate it (Brown 1982). In some habitats, at least some species are able to use amino acids for their N source (Simola 1975). (See Chapter on nitrogen in this volume.)

When bryophytes are co-existing with tracheophytes, the tracheophytes can benefit from added nitrogen, growing faster and out-competing the bryophytes (Berendse *et al*. 2001; Malmer & Wallén 2005). On the other hand, high levels of N in the environment can cause the decrease of both tracheophytes and bryophytes (Dupré *et al*. 2010). In this case, low soil *p*H seems to contribute to the loss of species, but high N levels seem to be more important in the decline of diversity. These results are similar to those of Ferris *et al*. (2000) in coniferous plantations in Britain. In their study, both bryophyte and tracheophyte diversity decreased as available nitrogen increased, but in this case, the *p*H, calcium, and nitrate increased, whereas ammonia decreased.

Schrijver *et al*. (2011) stated that "elevated inputs of biologically reactive nitrogen (N) are considered to be one of the most substantial threats to biodiversity in terrestrial ecosystems." We know that high N levels can be detrimental to bryophytes. This has been demonstrated for ***Leucobryum juniperoideum*** (Figure 4) (Wang *et al*. 2014) and ***Sphagnum*** spp. (Figure 10, Figure 24-Figure 25) (Bragazza *et al*. 2004). Arróniz-Crespo *et al*. (2008) reported decline in bryophyte biomass production and cover in grasslands. Armitage *et al*. (2010) likewise noted that alpine bryophytes have reduced biomass production and reduced cover under high N concentrations. Using transplants of ***Racomitrium lanuginosum*** (Figure 5) they determined that at least this moss has the ability to recover when the high loading of N is gone.

Figure 4. ***Leucobryum juniperoideum***, a species sensitive to high N levels. Photo by Michael Lüth, with permission.

In the Arctic, Gordon *et al*. (2001) found that added nitrogen caused a decrease in lichen cover but did not affect other functional types of plants. Rather, 10 $kg\ ha^{-1}\ yr^{-1}$ increased the proportion of active bryophyte shoots while decreasing their nitrate assimilation capacity, suggesting that the critical load is less than 10 $kg\ ha^{-1}\ yr^{-1}$. It is important to note that not all species responded the same way.

Figure 5. ***Racomitrium lanuginosum***, a species that is able to recover from high N loadings. Photo by Michael Lüth, with permission.

To complicate our understanding of suitable levels of N, we find that when N is no longer limiting, P and K can become limiting, as shown for ***Sphagnum*** (Figure 10, Figure 24-Figure 25) (Bragazza *et al*. 2004). Furthermore, the increased atmospheric N deposition can cause a reduction in the retention of Ca and Mg, a condition that was accompanied by a decrease in stem volumetric density in ***Sphagnum*** hummocks. Weber and Wiersma (1998) found that in two forested watersheds, the leafy liverwort ***Bazzania trilobata*** (Figure 6) and moss ***Dicranum fulvum*** (Figure 7) had elevated N concentrations in the watershed treated with $(NH_4)_2SO_4$ while simultaneously expressing a depression of other nutrients (Al, B, Ca, Cu, Fe, K, Mg, Mn, N, P, Zn).

Figure 6. ***Bazzania trilobata***, a species that is able to accumulate elevated N. Photo by Robert Klips, with permission.

Figure 7. ***Dicranum fulvum***, a rock-dwelling species that is able to accumulate elevated N. Photo by Michael Lüth, with permission.

Phosphorus

Like nitrogen, phosphorus (P) is essential for amino acids, proteins, DNA, and RNA. As in the algae, luxury uptake of P occurs, at least in some mosses, *e.g.* ***Pseudoscleropodium purum*** (Figure 8) (Bates 1987), but in these experiments there was significant **luxury uptake**, followed by storage, in excess of that is needed) only when plots were fertilized to 50% above the control.

We have seen that P can interact with nitrogen. Ellwood and Whitton (2007) found that the aquatic moss ***Warnstorfia fluitans*** (Figure 9) uses only organic phosphate, including P from DNA. Cellular P content is important in influencing phosphatase activities.

Figure 8. ***Pseudoscleropodium purum*** with capsules, a species that is able to take in luxury P when it is increased by at least 50%. Photo by Des Callaghan, with permission.

Figure 9. ***Warnstorfia fluitans***, a species that is able to take in luxury P. Photo by Misha Ignatov, with permission.

Gordon *et al*. (2001) found that not only N, but also P changed both the composition and cover of individual species of bryophytes in a high Arctic heath. They pointed out that the species differed in their response to fertilization, warning that the bryophytes should not be

considered as a single functional group, a concept likewise warned by Turetsky (2003) in her review of the role of bryophytes in carbon and nitrogen cycling.

Benner and Vitousek (2007) found that increasing P on the epiphytic community had a strong effect on N-fixing lichens in Hawaii, but mosses and non-N-fixing lichens also increased somewhat in both abundance and diversity. Increased N, however, had no effect on the epiphytic communities.

N:P Ratios

One of the interesting aspects of nitrogen deficiency is that it can be offset by phosphorus (Gordon *et al*. 2001). That is, these two nutrients are **colimiting**, so the critical load of nitrogen is lower when available phosphorus is greater. On the other hand, Riis *et al*. (2010) found that the growth rate of ***Warnstorfia fluitans*** (Figure 9) increased when the moss had increased P content, but did not with increased N content.

Jirousek *et al*. (2011) used a nitrogen deposition gradient in ***Sphagnum*** (Figure 10, Figure 24-Figure 25) in a highly polluted region of Central-East Europe to assess the N:P ratio. A higher P concentration in the capitula resulted in a lower N:P ratio for these mosses in most of the bogs, despite their N saturation, causing N to still be limiting. Conversely where there was higher atmospheric N deposition, the N:P ratio increased significantly. Species in the ***Cuspidata*** section (Figure 10) of ***Sphagnum*** demonstrated significantly lower N:P ratios in locations with low N deposition.

Figure 10. ***Sphagnum cuspidatum***, a species with low N:P ratios when N deposition is low. Photo by Michael Lüth, with permission.

Arróniz-Crespo *et al*. (2008) assessed the effects of enhanced N deposition on ***Pseudoscleropodium purum*** (Figure 8) and ***Rhytidiadelphus squarrosus*** (Figure 11) in an acidic grassland. The enhanced N deposition caused up to 90% loss of bryophyte cover, with no recovery after 22 months of no further deposition. The N:P ratios increased up to 3X under the enhanced N loading. Activity of the enzyme phosphomonoesterase showed good recovery, especially in ***P. purum***. P limitation appears to be the key factor in bryophyte loss in these grasslands.

Calcium and Magnesium

Calcium (Ca) is an essential nutrient for plants and is used in various structural and regulatory roles in cell walls and membranes (White & Broadley 2003). In this role, it is important in maintaining membrane integrity and cellular adhesion (Brown 1982). In ***Leucolejeunea*** (Figure 12), when Ca was omitted in the growth medium, cells in new growth were not glued together (Fulford *et al* 1947). There are implications that Ca may be associated with nutrient absorption (Odu 1978), especially at the rhizoid base where it accumulates in ***Marchantia*** (Figure 3). In ***Funaria*** (Figure 2), rhizoids developed at the point of maximum Ca entry on the protonema. Iwasa (1965) presented data that implicated its role in promoting bud formation in ***Funaria***. This is consistent with its role as a regulator of growth and development in tracheophytes (White & Broadley 2003; Hepler 2005).

Figure 11. ***Rhytidiadelphus squarrosus***, a species that is sensitive to excess N deposition. Photo by Michael Lüth, with permission.

Figure 12. ***Leucolejeunea***, a leafy liverwort that requires Ca to glue its cells together. Photo by Paul G. Davison, with permission.

Uptake of Ca in plants is passive, requiring no energy. Since Ca is insoluble, once it resides in a cell it will normally stay there and not move to other parts of the plant. In tracheophytes, it is carried to its destination by the xylem. In bryophytes, it is probably carried primarily externally and may accumulate at the tips of stems and branches where it occupies all available exchange sites and makes a visible crunchy, off-white deposit (pers. obs.).

Calcium can be effective in keeping other ions off the exchange sites. In this role, it can cause nutrient deficiencies. This is particularly noticeable in many species of ***Sphagnum*** (Figure 10, Figure 24-Figure 26).

Magnesium (Mg) is essential as the center of the chlorophyll molecule as well as other plant processes. Sources for this nutrient include bedrock and soil, with alkaline and humus-rich soils containing more than acidic soils. Its dynamics are often intertwined with those of calcium. Because both are cations, they compete for binding sites in cation exchange (CEC). In other cases (Canadian mires), however, they may be taken up in proportion to their concentrations in the environment (Malmer *et al*. 1992). In rich fens, both of these nutrients are supplemented from ions dissolved in surface water. Based on their field data, Malmer and coworkers suggested that Ca could give the brown mosses, typical of rich fens, a competitive advantage over ***Sphagnum*** (Figure 10, Figure 24-Figure 26).

Iron

Iron (Fe) can be a micronutrient, but in other species it is a macronutrient. It seems premature to make any generalizations about this in bryophytes.

Iron is important in plants in many enzymes and in the production of chlorophyll. Bryophytes can collect iron in dustfall (Gorham & Tilton 1978), but may also obtain it in water that carries it to and around the plant. It is likely that some can also obtain it from rock substrata.

In low oxygen of deep water, iron forms soluble ferric compounds that can be absorbed by bryophytes. In oxygenated streams, this form quickly oxidizes. Instead of being absorbed, it forms plates on the plants, soon covering them sufficiently to block photosynthesis (pers. obs.).

Micronutrients

Tracheophytes require significant quantities of macronutrients and considerably less of those called **micronutrients** (Mn, Cu, Zn, Mo, Ni, Cl, B). Although comprehensive studies of nutrient deficiency for bryophytes are lacking, we have no reason to believe they would have different requirements than these, but nutrients may be required in different proportions, and certainly in different concentrations.

Most micronutrients will not be limiting in most habitats in nature, but must be included for long-term growth in artificial media. For short periods, bryophytes can generally call upon their stored nutrients and those in surface dust until returned to a natural medium.

Rühling and Tyler (1970) found the sorption and retention relationship of the moss ***Hylocomium splendens*** (Figure 41) to be Cu, Pb>Ni>Co>Zn, Mn. This series has likewise been observed in other bryophyte studies (Brown 1982).

There are many questions about micronutrients for which we have no answers, or have them for very few species. Can they substitute one micronutrient for another? What processes and structures use these micronutrients? Can the presence, absence, or deficiency of a nutrient change the form of the bryophyte? Can such differences make them look like different species in different habitats? What are their deficiency symptoms?

Boron

Boron (B) is used in plant cell walls and affects nucleic acid and carbohydrate metabolism (Pilbeam & Kirby 1983). Boron is important in maintaining membrane structural integrity. As in monocots, bryophytes do not have a strong requirement for boron. Known symptoms of boron deficiency are usually secondary effects of changes in permeability of the membranes.

Boron is essential in the plant process of making lignin, which is, in turn, essential for tracheophyte vascular tissue (Lewis 1980). Thus, before tracheophytes could evolve, a means for uptake and incorporation of boron was necessary. But we know that uptake of boron is present in bryophytes. Sameka-Cymerman *et al*. (1991) found that boron, among other minerals, was taken up from the water by ***Scapania uliginosa*** (Figure 13). On the other hand, the amount incorporated into bryophyte cell walls is considerably less than that in tracheophytes (Matsunaga *et al*. 2004). To date, it is not clear that bryophytes actually require boron.

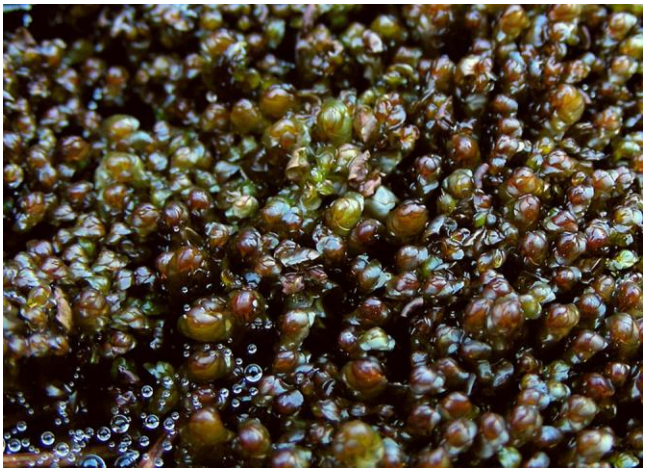

Figure 13. ***Scapania uliginosa***, a species that extracts minerals from the water, including boron. Photo by Michael Lüth, with permission.

As for iron, bryophytes can collect boron from dustfall (Sabovljević *et al*. 2005). However, at least some, including ***Sphagnum*** (Figure 10, Figure 24-Figure 25) species, may not accumulate it to the same degree as do trees (Gorham & Tilton 1978). Obviously, trees have a much greater need for boron because they must make lignin, and they do not generally rely on dust for their nutrients.

Copper

Copper (Cu), like iron, is important in enzymes in plants. As such, it facilitates many plant processes (Yruela 2005). But copper is needed only in small quantities and becomes toxic in larger quantities. This heavy metal is available in soil and can be carried with water that moves up the bryophyte.

Copper can be limiting in some aquatic habitats, and probably some terrestrial ones as well. In their studies on ***Fontinalis dalecarlica*** (Figure 14), Glime and Keen (1984) found that natural Lake Superior water had less than ideal copper concentrations for maximum chlorophyll concentration, with 0.01 mg per liter providing the best chlorophyll (Figure 15). At higher concentrations, chloroplasts lost their green color and at 10 mg / L the cells became brown (Figure 16). With increasing concentrations, the tips of ***F. antipyretica*** became yellow (Figure 19).

Figure 14. ***Fontinalis dalecarlica***, a species that can, in some environments, be copper deficient. Photo by Janice Glime.

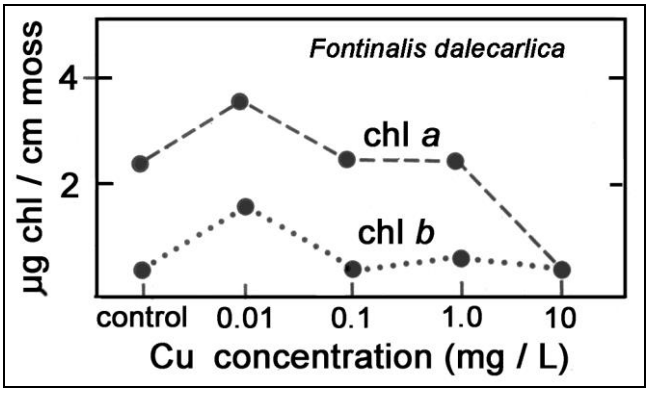

Figure 15. Effect of copper concentration on chlorophyll *a* and *b* concentrations in the aquatic moss ***Fontinalis dalecarlica***. Redrawn from Glime & Keen 1984.

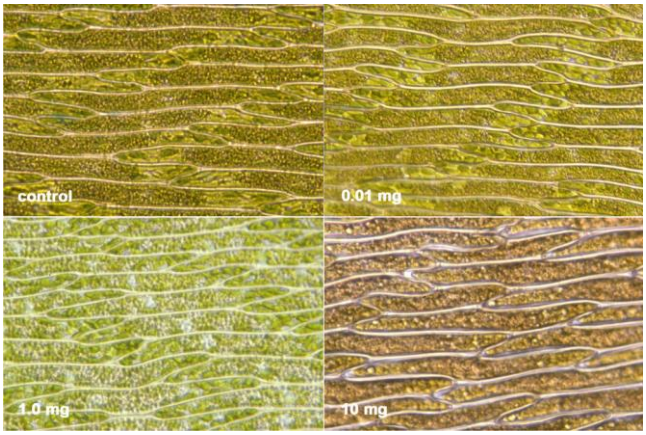

Figure 16. Comparison of cell contents and colors in leaves of ***Fontinalis dalecarlica*** subjected to concentrations 0.01 mg/L, 1.0 mg/L, 10 mg/L) of **copper** as copper foil, Lake Superior water as control,. Photos by Janice Glime.

Claveri and Mouvet (1995) found that the aquatic moss ***Platyhypnidium riparioides*** (Figure 17) suffered from denaturation of chlorophyll pigments after spending 12 days in a copper concentration of 80 µg L^{-1}. They found that uptake of copper was not related to photosynthesis, permitting it to continue uptake even when the chlorophyll was damaged. Furthermore, its uptake does not appear to be influenced by temperature, whereas its damage to chlorophyll increases with temperature. Similar damage to chlorophyll occurs in the aquatic moss ***Fontinalis*** (Figure 50) (Glime & Keen 1984). But this is not just an aquatic phenomenon. It is known also in ***Thuidium*** spp. (Figure 18) (Shakya *et al*. 2008) and is likely to be the case in all except perhaps the copper mosses.

Figure 17. ***Platyhypnidium riparioides***, a species that loses its chlorophyll in excess copper. Photo by Michael Lüth, with permission.

Figure 18. ***Thuidium delicatulum***, member of a genus that is known to be sensitive to copper. Photo by Janice Glime.

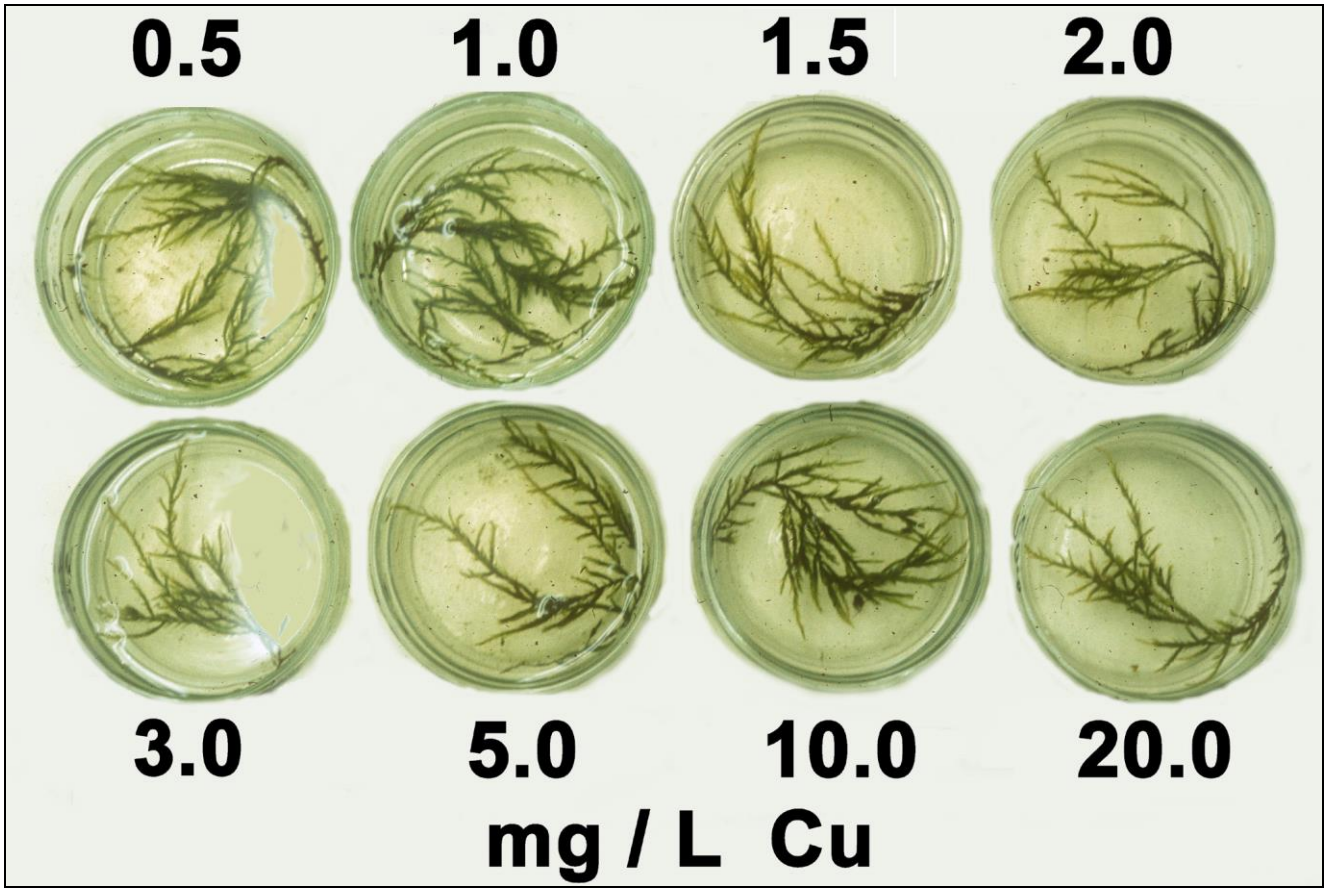

Figure 19. Effects of various concentrations of copper (as copper foil) on the general appearance of ***Fontinalis antipyretica*** (see also Figure 50). Note the yellowed tips at 1.5 mg/L and above. Photo by Janice Glime.

Heavy Metals

It is perhaps more likely that micronutrients, particularly the heavy metals, will be toxic at greater than trace amounts. Many bryophytes have means of sequestering these in ways that are not toxic. The moss that seems to have the greatest tolerance in many polluted and otherwise heavy metal situations is ***Pohlia nutans*** (Figure 20-Figure 21), a species with known tolerance to copper, zinc, and nickel (Shaw 1989).

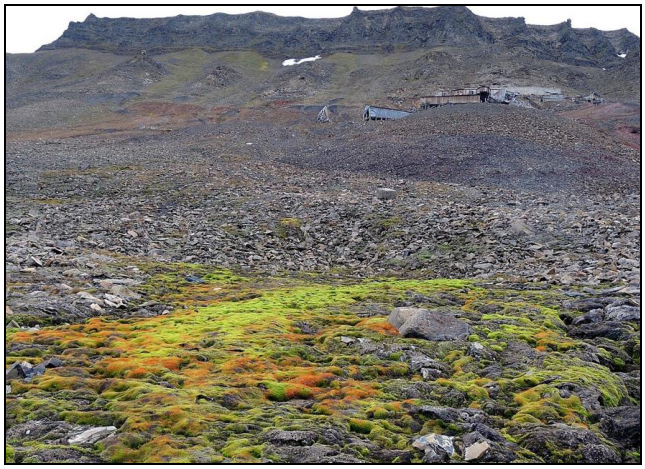

Figure 20. ***Pohlia nutans*** below old mine. Photo by Michael Lüth, with permission.

Figure 21. ***Pohlia nutans***, a heavy metal tolerator. Photo by J. C. Schou, with permission.

Some heavy metals in the environment have no known use by plants, including bryophytes. One such heavy metal is **cadmium**, a toxic by-product of mining and smelting, among other things. In our experiments with ***Fontinalis duriaei***, cells became plasmolyzed at 100 µg Cd per liter (Figure 22) (Glime & Keen 1984). At 1000 µg, the cells deplasmolyzed in a way that suggested membranes were damaged.

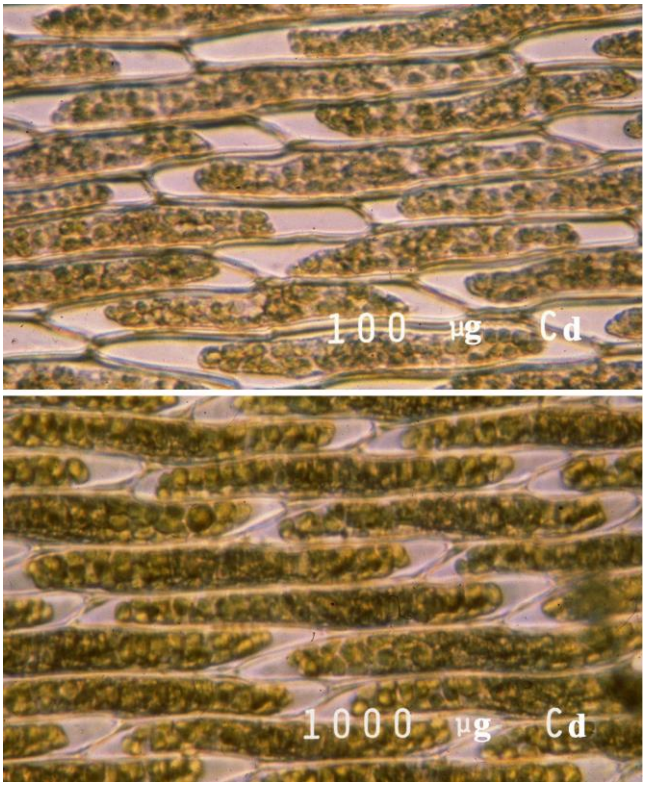

Figure 22. Effects of cadmium on cell contents in ***Fontinalis duriaei***. At 100 µg per liter, cells become plasmolyzed. At 1000 µg per liter, the cells deplasmolyze, demonstrating membrane damage. Photos by Janice Glime, based on Glime & Keen 1984.

Nutrient Content

What is normal nutrient content for bryophytes? Or is there one? In the scattered literature that addresses nutrients outside the laboratory, we find that content can depend on habitat, season, uptake ability, and source. But our understanding of bryophyte mechanisms for regulating their nutrient content is meager at best.

Habitat Differences

Habitats can range widely in nutrient availability. These differences can serve as limiting factors for bryophytes, but for most species we do not understand these limitations. In his discussion of ***Sphagnum*** (Figure 10, Figure 24-Figure 25), Malmer (1988) considered that the concentration differences among the species are mainly caused by differences in growth pattern and site conditions. The concentrations in the living moss and those in the underlying dead peat are not related.

Streams

In streams, phosphorus is typically a limiting nutrient, not to mention CO_2 limitations. On the other hand, pollution, including phosphate from such sources as agricultural fertilizers, can often cause bryophytes to disappear or begin to look unhealthy. One problem for stream bryophytes in high nutrient conditions, whether natural or from pollution, is that the high nutrient level may promote the growth of the periphyton living on their surfaces (Glime, unpublished), causing them to suffer from CO_2 and light competition.

Phosphorus often occurs as agricultural pollution or sewage waste. Frequently it arrives in streams, changing the N:P ratio of those streams. Steinman (1994) examined the effect of phosphorus enrichment on the leafy liverwort ***Porella pinnata*** (Figure 23) in two woodland streams of eastern Tennessee, USA. Not surprisingly, the N:P ratio decreased significantly, and the P:C ratio increased significantly in the liverworts. In this case, the expected epiphyte structure and abundance in the liverworts were not significantly affected, perhaps due to greater grazing by snails.

Figure 23. ***Porella pinnata***, a species that can incorporate added phosphate into its cells. Photo by Des Callaghan, with permission.

Christmas and Whitton (1998) compared the phosphorus content of the stream mosses ***Fontinalis antipyretica*** (Figure 50) and ***Platyhypnidium riparioides*** (Figure 17) to that in the River Swale-Ouse in NE England. They found that both P and N concentrations increased with downstream distance. The mosses likewise showed their lowest concentrations at the headwater site, with increasing levels of both elements with distance downstream. More interesting was the change in N:P ratio with distance downstream, decreasing from 14.9:1 to 6.8:1 in ***F. antipyretica*** and from 12.5:1 to 5.5:1 for ***P. riparioides***, suggesting luxury uptake of P. The PMEase (phosphomonoesterase) was greatest at the lower *p*H (5.5) compared to the higher *p*H values. The enzyme decreased at all three *p*H values with distance downstream. Nevertheless, mean primary production increased by only 15% following enrichment, a difference that was not statistically significant.

Bogs and Fens

We know that by definition, **bogs** and **poor fens** have low nutrient content, **intermediate fens** are characterized by intermediate nutrient levels, and **rich fens** have the highest nutrient levels among these habitats. The bogs and poor fens have similar nutrient concentrations and similar bryophyte species, but differ in their nutrient sources, whereas the species of bryophytes in the intermediate and rich fens differ from each other and from those of the bogs and poor fens. Wojtuń (1994) found that N, P, K, Ca, Mg, and Na were in significantly higher concentrations in ***Sphagnum*** (Figure 10, Figure 24-Figure 25) from the **minerotrophic** (nutrient-rich) fens than from the **ombrotrophic** (low-nutrient) bogs and fens, with K and P

having the greatest differences. As already noted, in the aquatic moss ***Warnstorfia fluitans*** (Figure 9) from an Arctic lake, increased P content caused increased growth, but increased N content did not (Riis *et al*. 2010). Hence we can conclude that at least some nutrients do make a difference to the bryophyte species. This indicates differences in physiology for which we have only minimal understanding.

For ***Sphagnum*** (Figure 10, Figure 24-Figure 25) species, cation exchange (see Chapter 8-4, Uptake) plays a major role in the ability to take up nutrients in low-nutrient situations, but can make a species intolerant of divalent cations such as Ca^{++}. Cation exchange causes calcium to adhere to cells, replacing H^{+} ions along the cell walls. Since the Ca^{++} ion has two positive charges, it occupies two exchange sites. In this way it competes preferentially with other needed nutrients with only one positive charge, especially potassium (Koedam & Büscher 1982).

Hájek and Adamec (2009) found that nutrient content of ***Sphagnum*** (Figure 10, Figure 24-Figure 25) species varied between contrasting microhabitats. The greatest difference was shown between ***S. angustifolium*** (Figure 24) and ***S. magellanicum*** (Figure 25), with the latter having a 40% lower intracellular N content, even when it grew alone. This lower uptake ability by ***S. magellanicum*** can permit ***S. angustifolium*** to outcompete ***S. magellanicum*** when the two are mixed.

Figure 24. ***Sphagnum angustifolium***, a species that outcompetes ***S. magellanicum*** for N. Photo by Jan-Peter Frahm, with permission.

Figure 25. ***Sphagnum magellanicum***, a species that is a poor competitor for N. Photo by Michael Lüth, with permission.

In ***Sphagnum fallax*** (Figure 26) from a fen woodland, its annual accumulation of N, P, and K differed little between a dry and a wet year (Brock & Bregman 1989). How can we account for this ability to maintain the same level of these three essential and often limiting nutrients, despite different opportunities for uptake in different precipitation regimes? On the other hand, Lembrechts and Vanderborght (1985) examined the mineral content (Na, K, Ca, Mg, Al, Fe, P, Cu, Mn, Pb, Zn) of nine species of ***Sphagnum*** (Figure 10, Figure 24-Figure 25) in Belgian bogs and found that the concentrations of all elements except Ca, Zn, and Mn were related to the moisture of the habitat. The concentrations of Ca and Cu were lower in one site due to trophic status and air pollution, respectively.

Figure 26. ***Sphagnum fallax***, a fen species for which N, P, and K accumulation differences between years seems not to be affected by annual precipitation differences. Photo by Michael Lüth, with permission.

The *p*H plays an important role in determining how Ca affects bryophytes, best known in bog and fen systems. Clymo (1973) found that most ***Sphagnum*** (Figure 10, Figure 24-Figure 25) plants grew well in low Ca^{++} at a low *p*H, at high *p*H, or at high Ca^{++}, but not when both *p*H and Ca^{++} concentration were high.

Turetsky *et al*. (2008) found that ***Sphagnum*** species exhibit resource partitioning, with a tradeoff between metabolic and structural carbohydrates. The way that bryophytes use their nutrients has interesting implications for their decomposition and their roles as ecosystem engineers through sequestration of certain nutrients. And these differences must be examined at the species level, not at the bryophyte level, due to species differences.

Forests

In forests, a primary source of nutrients derives from decomposition of leaf litter. But in industrialized areas, air pollution becomes a major source of N, as well as a number of trace elements. P is often limiting. Species diversity is fostered by habitat diversity that provides nutrient levels differing from those of the forest floor. We can observe considerable species differences on soil, rocks, trees trunks and leaves, and logs, which we usually attribute to differences in moisture, but we lack an understanding of the role that nutrients may play in these species differences.

Substrate can make a difference in nutrients available. As already noted, the moss ***Leucobryum juniperoideum*** (Figure 4) is sensitive to high concentrations of nitrogen,

preferring the lower N levels on rocks and logs in some locations with high N in the soil, whereas in others the soil has a low enough concentration to be suitable (Wang *et al*. 2014).

In the highly polluted region of Central-East Europe, Jirousek *et al*. (2011) found that local forestry practice affected the N-limitation experienced in areas with high P and N saturation.

Arctic and Alpine

Bryophytes can be very important in sequestering P in Arctic soils. Chapin *et al.* (1987) found that 75% of the above ground annual P accumulation was in the mosses of an Alaskan black spruce (*Picea mariana*; Figure 27) forest. The mosses ***Sphagnum subsecundum*** (Figure 28), ***Hylocomium splendens*** (Figure 41), and ***Pleurozium schreberi*** (Figure 31) have higher absorption capacity for phosphate than do the fine roots of the spruce. The uptake comparison demonstrated that absorption capacity increases with age in green tissues while decreasing with age in brown tissues in three of the four studied mosses. In the fourth moss species, the endohydric ***Polytrichum commune*** (Figure 44), phosphate is absorbed most rapidly from stems in mineral soil. When mycorrhizal fungi were killed in the plots, phosphate retention by mosses increased and transfer out of the plots decreased, suggesting that P is transferred from the moss carpet to the tree roots by fungi.

Figure 27. Arctic black spruce (***Picea mariana***) forest. Photo by Michael Lüth, with permission.

Figure 28. ***Sphagnum subsecundum***, a black spruce forest moss in the Arctic. Photo by Michael Lüth, with permission.

Species Differences

Nutrient content, as we might expect, can differ widely among species. For example, copper mosses such as ***Scopelophila cataractae*** (Figure 29) can be expected to have high concentrations of copper, although in some cases it is iron rather than copper that is accumulated (Shaw 1987b).

Figure 29. ***Scopelophila cataractae***, a moss with high tolerance of, and possibly dependence on, copper. Photo by David T. Holyoak, with permission.

We have already noted the importance of cation exchange sites in determining the habitat of ***Sphagnum*** (Figure 10, Figure 24-Figure 25) species. Malmer (1988) found that in three hummock ***Sphagnum*** species the cation concentrations of Na, Mg, and Ca depended on the exchange capacity of the species. The sum of the divalent ions Ca^{++} and Mg^{++} was the same throughout the plant. Hájek and Adamec (2009) compared locations of various ions in six species of ***Sphagnum***, demonstrating differences in locations and concentrations (Figure 30).

To understand the ability of mosses to sequester nutrients differentially, Berg and Steinnes (1997) compared wet deposition data to the concentrations of 48 elements in the feather mosses ***Hylocomium splendens*** (Figure 41) and ***Pleurozium schreberi*** (Figure 31). Their results suggest that for some elements, moss content reflects environmental content. This was true for V, Fe, Co, As, Y, Mo, Cd, Sb, Ce, Sm, Er, Tl, and Pb in ***Hylocomium splendens***, and for Mg, V, Fe, Co, As, Se, Y, Mo, Cd, Sb, Tl, and Pb in ***Pleurozium schreberi***. Among these results, I find the difference in Mg as the most interesting. Mg is the element in the center of a chlorophyll molecule and thus is essential for all photosynthetic plants and algae. ***Hylocomium splendens*** had the highest concentrations of Cr, Fe, Co, Ni, Cu, Ga, Nb, Mo, Sb, Eu, Gd, Tb, Dy, Er, Tm, Lu, W, Tl, Pb, and Th, whereas V, Mn, Rb and Cd were highest in ***Pleurozium schreberi***. These differences are interesting because these two species frequently occur in the same habitats, especially in boreal forests.

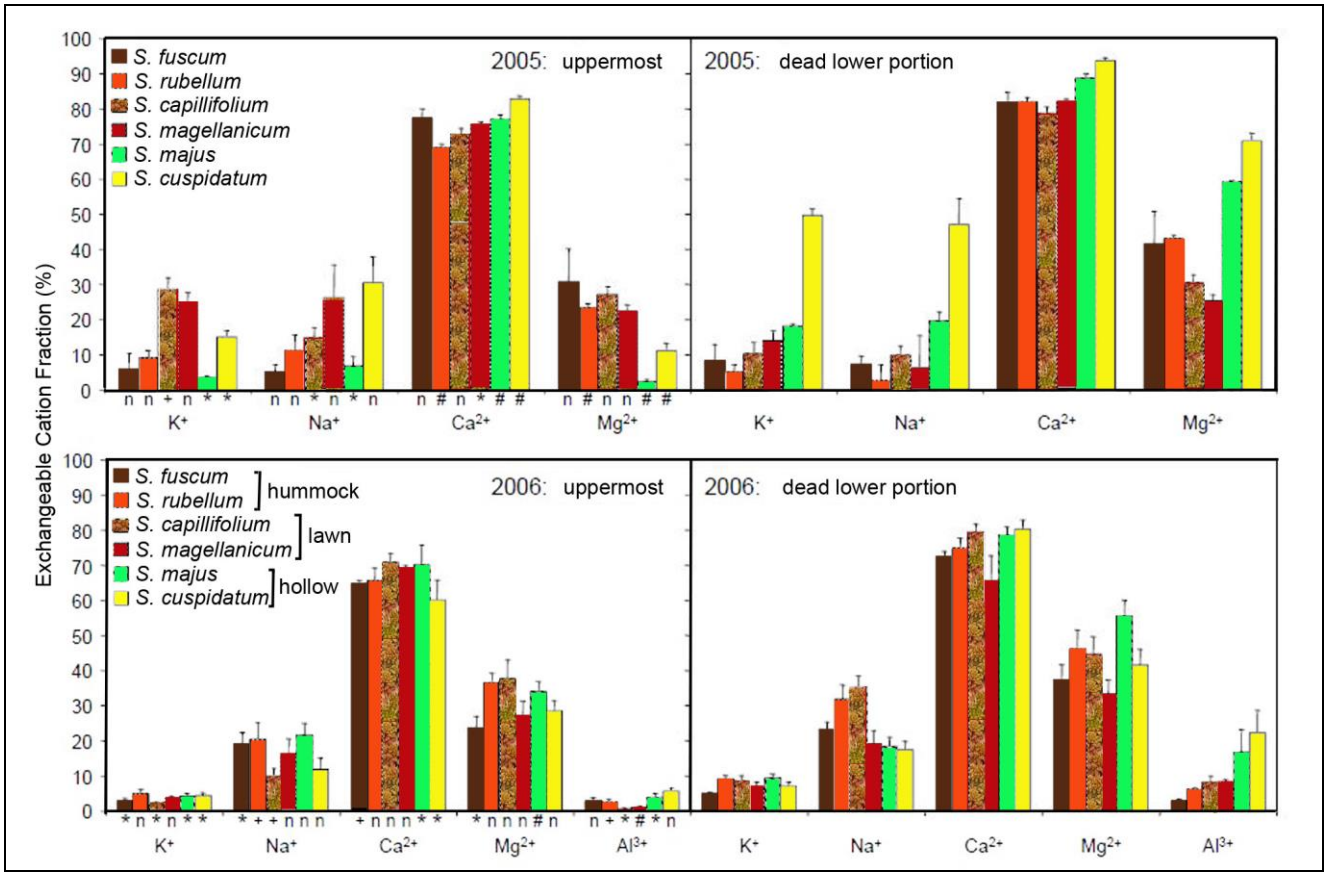

Figure 30. Exchangeable cation fraction from the total cation pool in apical (uppermost) and dead shoot segments of six ***Sphagnum***. species Symbols below the columns are *p* values of the t-test for dependent samples testing the differences between shoot segments: # $p < 0.001$; + $0.01 < p < 0.001$; * $0.05 < p < 0.01$; n $p > 0.05$. Redrawn from Hájek & Adamec 2009.

Figure 31. ***Pleurozium schreberi***, a species for which cell contents reflect the Mg levels in the environment. Photo by Janice Glime.

Figure 32. ***Sphagnum capillifolium***, a hummock species in which N content is proportional to that added. Photo by J. C. Schou, with permission.

Williams *et al*. (1999) found differences in labelled N in waters from two species of ***Sphagnum*** in a bog in northeast Scotland. In the hummock species ***Sphagnum capillifolium*** (Figure 32), labelled dissolved organic nitrogen in moss water was proportional to that added as inorganic N, but in the hollow species ***S. recurvum*** (Figure 33), it was not.

Adaptability and Acclimation

One question that has received little attention is the ability of bryophytes to acclimate or adapt to high concentrations of any given nutrient or pollutant. With the wide range of minerals and other nutrients in the environment, how does an **ectohydric** (moving water on the outside of plant) bryophyte respond to these differences? There is some evidence that they do change

their tolerance. Shaw (1987a) showed that protonemata responded to pretreatment with copper and zinc more than did the stems of ***Funaria hygrometrica*** (Figure 2). But overall, genetic differences had a greater role than acclimation through pretreatment, with some individuals showing a significant response and others showing little or none.

Figure 33. ***Sphagnum recurvum***, a hollow species in which N concentrations do not reflect those of the atmosphere. Photo by Malcolm Storey, <www.discoverlife.com>, through Creative Commons.

In culture conditions, Shaw (1988) demonstrated that populations exhibited a wide range of tolerances in the protonemal and stem stages. To confound the story, Shaw found that in experiments with copper and zinc the populations of ***Funaria hygrometrica*** expressed a greater similarity among environmental correlations than among genotypic correlations, suggesting some sort of acclimation.

A genetic ability to survive and even require some heavy metals such as copper is exhibited by ***Scopelophila cataractae*** (Figure 29) (Shaw 1987b). Out of six populations in eastern USA, five were associated with high copper concentrations. The sixth was associated with high iron concentrations. When cultivated, these populations grew best on soil contaminated with copper, lead, and zinc. It is interesting that this species lacks sexual reproduction in North America. Could that be related?

Plant Nutrient Locations

Nutrients not only have different purposes, but also are located in different positions within the plant and within the cells they occupy. Some are needed structurally and some are used **constitutively** (always present, such as defense compounds). For example, potassium, a highly soluble and mobile nutrient, is present in ***Grimmia donniana*** (Figure 34) and ***Calliergonella cuspidata*** (Figure 35) in a soluble form within the cell, whereas the calcium is primarily in extracellular locations in exchangeable form (Brown & Buck 1985; see also Brehm 1968; Bates 1992; Bates & Brown 1974; Brown & Buck 1979, 1985). Magnesium and zinc, on the other hand, were intermediate, with their locations depending on the species and concentrations. Turetsky *et al*. (2008) demonstrated that a tradeoff between structural and constitutive use of nutrients, especially C and N, in ***Sphagnum*** species gave hummock species the ability to maintain their hummocks by putting more nutrients in recalcitrant structural forms that did not decompose easily.

Figure 34. ***Grimmia donniana***, a species with soluble K in its cells. Photo by Henk Greven, with permission.

Figure 35. ***Calliergonella cuspidata*** growing among sedges. Photos by Michael Lüth, with permission.

Wojtuń (1994) determined that N, P, and K accumulate in the upper parts of ***Sphagnum*** (Figure 10, Figure 24-Figure 25) through active uptake; all three are typically found within the cell, being used in cell metabolism rather than cell wall metabolism (Brown & Wells 1990b). On the other hand, Ca, Mg, and Na are obtained through passive cation exchange. These and other elements acquired through cation exchange tend to accumulate in the lower parts of the plants. The concentration of iron either does not correlate or correlates negatively with the other

elements (Wojtuń 1994). Contents of N, P, K, Ca, Mg, and Na were significantly higher in mosses from **minerotrophic** (high nutrient) habitats than in those from **ombrotrophic** (low nutrient) habitats. The greatest difference among species were for K and P.

Brown and Wells (1990a) showed that heavy metals could alter ion locations, for example by causing potassium leakage due to membrane damage. It is interesting that in the liverwort ***Dumortiera hirsuta*** (Figure 36), pretreatment with 80 mM KNO_3 actually stimulated cadmium uptake, presumably because the potassium removed potentially competing cations from the exchange sites, thus permitting more Cd to bind and be taken up by the cells (Mautsoe & Beckett 1996). This suggests that potassium ions are able to occupy environmentally exposed exchange sites as well as their interior sites. Such locations could make these ions readily available when needed by the cells.

Figure 36. ***Dumortiera hirsuta***, a species in which K^+ removes competing cations from exchange sites, permitting Cd^{++} to bind and then enter cells. Photo by Michael Lüth, with permission.

Ron *et al*. (1999) used ***Hookeria lucens*** (Figure 37) to observe the cause of reddish-brown deposits of minerals in the cells. They identified the minerals bohemite, calcite, diaspore, feldspar, ferrihydrite, gibbsite, jarosite, lepidocrocite, opal, pirolusite, and quartz inside the **hydrom** (unit of water-conducting cells), cortex, and leaf cells. Since not all of these minerals were present in the soil substrate, they hypothesized that the additional ones were derived from a biomineralization process inside the moss cells from such elements as Mn and S, and from those in the soil on which the mosses were growing.

Bates (1987) found that in ***Pseudoscleropodium purum*** (Figure 8) fertilization caused a small net increase in Mg, but shoot N had no significant change in the plant. Ions held on exchange sites did not increase much with fertilizer addition in the field, but in the laboratory, a 30-minute exposure to these caused Ca^{++} and Mg^{++} concentrations to rise notably, whereas exchangeable K^+ fell. But the disappearance of these exchange site nutrients when the mosses were returned to the field caused Bates to question the utility of the exchange sites. Could they serve to keep a ready supply while at the same time preventing excess within the cells? Weekly watering with fertilizer caused maximum net uptake of P, Mg, and Ca. Pulse watering with more concentrated solutions at greater intervals had the least uptake.

Figure 37. ***Hookeria lucens***, a species that can be discolored by minerals in the hydrom, cortex, and leaf cells. Photo by Michael Lüth, with permission.

Determination of the interior location of plant elements has been complicated by damage to the cell membranes during the measurement technique (Brown & Wells 1990b). When this damage happens, ions are released and may become bound to newly exposed cell walls on the insides of the cells.

Cell Wall Sites

The cell walls of tracheophyte roots have exchange sites that permit binding of nutrient ions and facilitate uptake. Similar, and very active, exchange sites are well known on ***Sphagnum*** (Figure 10, Figure 24-Figure 25) leaves (Clymo 1963; Spearing 1972; Schwarzmaier & Brehm 1975). But other bryophytes can have exchange sites as well (Brown & Buck 1979; Glime *et al*. 1982). Unfortunately, this capacity has scarcely been examined for non-***Sphagnum*** bryophytes. Nevertheless, as described above, it appears that such sites exist to varying degrees among the bryophytes in general.

Brown and Buck (1979) reported that in bryophytes Ca^{++} is bound to exchange sites in the cell wall and is insoluble within the cell. The quantity of an element bound to such sites depends on the concentration of that element. The ability of a **cation** (positive ion) to reach a stable equilibrium is relatively rapid, whereas its departure rate when the external supply is removed and replaced with a solution free of the element is often slower, the former taking only about 4.5 minutes to reach half maximum extracellular uptake for 100 µM L^{-1} Cd in ***Rhytidiadelphus squarrosus*** (Figure 11) (Brown & Beckett 1985), but taking days at lower concentrations of <0.13 µM L^{-1} Cd in some aquatic species (Mouvet 1987).

Vázquez Castro *et al*. (1999) examined the location of heavy metals in three aquatic mosses. They found that most of the metal uptake was to the extracellular compartment compared to the intracellular fraction. ***Scapania undulata*** (Figure 48) in particular has a high exchange site affinity for the heavy metals, whereas ***Fissidens polyphyllus*** (Figure 38) has a relatively low attraction. On the other hand, ***F. polyphyllus*** has the highest intracellular contents.

Figure 38. ***Fissidens polyphyllus*** in limestone cave, a species with low affinity for heavy metals. Photo by Janice Glime.

The mechanism of cation exchange is discussed in the subchapter on Uptake (Chapter 8-4 of this volume). Binding preferences vary with concentrations and can be determined based on availability of the ions, previous filling of the exchange sites, type of ligand in the exchange site, and type of ions (Brown & Wells 1990b). For example, potassium, calcium, and magnesium prefer oxygen-rich **ligands** (ion or molecule that binds to a central metal atom to form a complex) such as carboxylic groups (Nieboer & Richardson 1980). Others such as mercury, lead, and gold prefer sulfur- and nitrogen-rich ligands. Some are borderline and have intermediate preferences with heavier elements tending to prefer the sulfur- and nitrogen-rich ligands.

Intracellular Sites

Brown and Wells (1990b) reminded us of the need to separate the locations of the elements within the cells. They furthermore pointed out that many of the elements became bound into compounds, onto membranes, or onto the interior of the cell walls. Others could be stored in vacuoles. Not only potassium, aluminium, and nitrogen occurred inside cells of ***Sphagnum*** (Figure 10, Figure 24-Figure 25), but also magnesium and sodium (Hájek & Adamec 2009). Magnesium is stored in the chlorophyll molecule, where it is essential for that molecule to function in photosynthesis (Brown and Wells 1990b). Sodium has no known use in bryophytes.

Brown and Buck (1979) found that potassium is mainly dissolved within the bryophyte cells. Magnesium is found not only in the cells but also adhering to exchange sites and cell membranes. Hájek and Adamec (2009) looked at nutrient locations in ***Sphagnum*** (Figure 10, Figure 24-Figure 25) and reported that K, Mg, N, Al, and Na occurred within cells, although Mg and Na also could be found on exchange sites. (Note, Al and Na are generally not considered to be plant nutrients.)

Microhabitats and species differences seem to account for nutrient content in ***Sphagnum*** (Figure 10, Figure 24-Figure 25) (Hájek & Adamec 2009). For example, ***Sphagnum magellanicum*** (Figure 25), a hummock species, had an intracellular nitrogen content that was about 40% lower than that in associated species. Such unequal competition for N, even when compared to ***S. magellanicum*** grown alone, suggests its inability to compete for N in mixed patches.

Vertical Distribution

The base of the plant has different concentrations of most elements compared to the apex (Brown & Wells 1990b; Hajek & Adamec 2009). For example, potassium, a soluble and translocatable nutrient, is most concentrated in the actively growing apex of the plant and is intracellular (Figure 39) (Brown & Wells 1990b). Other cellular metabolic components such as nitrogen and phosphorus are likewise concentrated in the growing apex (Brown & Wells 1990b; Hájek & Adamec 2009 – see Figure 30).

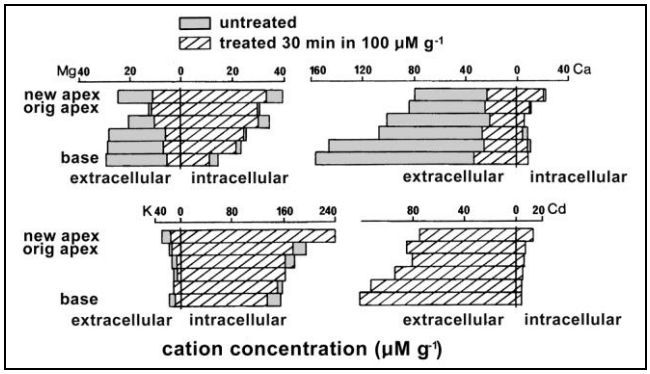

Figure 39. Location of four elements in 2-cm sections from new apical segment to base along the stems of laboratory-grown ***Rhytidiadelphus squarrosus*** (Figure 11). Redrawn from Brown & Wells 1990b.

As in tracheophytes, bryophytes are able to move at least some of their nutrients to actively growing tissue. In ***Hylocomium splendens*** (Figure 41) less new growth occurred when branches of mature segments were removed (Brümelis & Brown 1997). The metals K, Mg, Ca, and Zn in new growth correlated with the initial contents in the juvenile plus mature segments but not with the levels in the pre-experimental segments, suggesting the importance of moving nutrients to growing tissues.

Those elements that are predominantly bound to extracellular sites tend to accumulate in the basal regions of the plant (Brown & Wells 1990b). These include the heavy metals. Their accumulation at the base may be the result of cell death in that region, exposing exchange sites on the cell interiors. Those elements such as manganese that are poorly bound to exchange sites may move upward through evaporative water movement and accumulate at the apex (Lötschert & Wandtner 1982; Malmer 1988), a phenomenon sometimes referred to as transpiration transport.

Malmer (1988) divided three hummock ***Sphagnum*** (Figure 24-Figure 25) species into four segments for nutrient and growth analysis. As one might expect, weight increases mostly in the capitulum, but length increases further down. To facilitate this growth, N, P, and K accumulate in the upper parts of the mosses. The trace elements Al, Fe, Zn, Cd, and Pb increase with the age of the plants. Both Ca^{++} and Mg^{++} are at first bound to exchange sites on the outside the plant and the sum of these two minerals is consistent throughout the ***Sphagnum*** plant.

Nutrient Sources

Mineral nutrients result from weathering and atmospheric deposition (Bates & Farmer 1992). Bryophytes can use five major sources of nutrients: soil, stream water, atmospheric dust, precipitation (including throughfall), and litter (Babb & Whitefield 1977; Parker 1983; Frego & Carleton 1995). For **saxicolous** (rock-dwelling) bryophytes, the only feasible sources are dust and precipitation (Rieley *et al*. 1979), especially for potassium (Bates 1976), although Hébrard *et al*. (1974) demonstrated the ability of ***Grimmia orbicularis*** (Figure 40) to obtain radiolabelled ^{90}Sr from an artificial rock. For pleurocarpous taxa and taxa living in the forest, the atmosphere (dust and precipitation) is generally considered to be the major nutrient source (Brown 1982), but as we shall see, this may not be the whole story. More to the point, what can we expect in uptake of the macronutrients such as phosphorus, nitrogen, and potassium, and are these values controlled, or are they determined by the concentrations in the ecosystem?

Figure 40. ***Grimmia orbicularis***, a species with the ability to take up minerals from its rock substrate. Michael Lüth, with permission.

In a study of bog mosses, Malmer (1988) found that variations in S, Cu, Zn, Cd, and Pb are the results of varying man-made emissions. Na and Mg variations can be traced to oceanic influence. P, Na, Mg, and Ca also seem to vary with moss productivity. Al and Fe are greatest near agricultural and industrialized regions. Unlike the other elements, Mn concentrations are related primarily to the soil and bedrock.

Precipitation

Clearly rainwater has a very different chemical makeup than soil. Some elements are more abundant, whereas others, like Mg, are virtually absent in the open. Hence, mosses that grow in the open and do not get any leachates from canopy trees are likely to be very deficient in some elements. Could the lack of Mg in ***Funaria hygrometrica*** (Figure 2), a species of open sites, explain why it is so short, or might being short be an adaptation to living there?

Larsen (1980) describes the mosses in the boreal forest as growing vigorously, using nutrients that they receive in throughfall, and Weetman (1968) likewise found that feather mosses in a black spruce (*Picea mariana*; Figure 27) forest relied on dust and precipitation for both nutrients and moisture. Tamm (1953, 1964) found that rainwater was sufficient to account for all the nutrients needed by the feather moss ***Hylocomium splendens*** (Figure 41). Weetman and Timmer (1967) concluded the same thing for ***Pleurozium schreberi*** (Figure 31) in the black spruce forest, where N, K, Ca, and Mg were leached from the canopy. This canopy throughfall source annually supplied 9 kg of N per hectare to the moss. In fact, the spruce trees are known to be N-deficient and root prolifically at the base of the green layer of mosses. Since feather mosses such as ***Pleurozium schreberi*** and ***Hylocomium splendens*** are known to mineralize nitrogen, they interpreted this to mean that the moss layer provided the major source of nitrogen for the trees. It is likely that mosses also held a portion of rainfall N in interstitial spaces among leaves in this layer, retaining it where tree roots could absorb it during the time that there was sufficient moisture for them to grow. It is also likely that in late summer when nutrients in the soil are depleted, rehydrating mosses could release nutrients collected as dust, but also from cells with membranes damaged by the drought (Leary & Glime 2005).

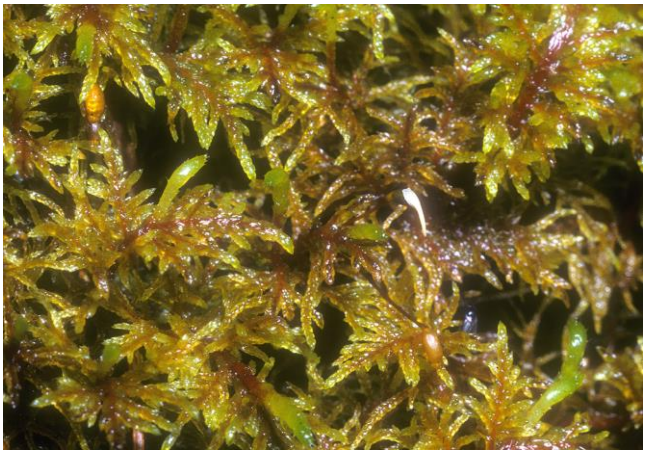

Figure 41. ***Hylocomium splendens*** gametophytes. Photo by Janice Glime.

Nutrient availability from precipitation can vary widely, depending on the canopy, with the lowest nutrient concentrations occurring in the open. Tamm (1953) showed that ***Hylocomium splendens*** (Figure 41) grew more under the canopy than in the open, and that its annual dry biomass increments under the canopy increased with distance from the tree trunk. He attributed these differences to light intensity increases outward from the trunk, whereas in the open he considered there to be insufficient nutrients due to lack of canopy trapping and leaching. However, despite the differences in precipitation nutrient concentrations, tissues of those ***Hylocomium splendens*** plants located in the open had the same nutrient concentrations as did the ones under the canopy, suggesting that they must have obtained their nutrients from something other than rainfall (Brown 1982), but also grew more slowly, thus requiring lower concentrations from the environment.

Forsum *et al*. (2006) not only compared the forms of nitrogen use by ***Hylocomium splendens*** (Figure 41), but also analyzed the nitrogen components of rain. Typically, amino acids in the rainfall are ignored, but Forsum and coworkers found that rain in their boreal forest study site had 78% of its nitrogen in ammonia (NH_4^+), 17% in amino acids, and 5% in nitrates (NO_3^-). Furthermore, they found

that ***H. splendens*** absorbed more N from ammonia than from nitrate or the amino acid glycine when they were applied in solutions similar to those of the local rainfall. See the subchapter on Nitrogen in this volume for a further discussion of amino acids as a nitrogen source.

But certainly the water regime is different in the open as well (Tamm 1953). Trees in the forest redirect the rainfall, with much of it flowing down the trunk, or never reaching the forest floor at all. Trees can have either **centripetal water movement** (toward the bole, *i.e.* main trunk), for example *Acer*, *Fagus*, and *Fraxinus*, or **centrifugal** (toward the outer branch tips), for example *Betula*, *Picea*, and *Tilia*, depending on tree morphology. These patterns affect the source of nutrients and degree to which they reach the ground.

Tamm (1953) and Abolin (1974) both found that water volumes increased at the canopy margin. Barkman (1958) found that the percentage of rainfall reaching the tree bole of spruce (*Picea*) was only 1%. Nihlgård (1970) found that beech retained 19% of the rainfall, permitting 70% to go through the canopy as throughfall and 11% as stemflow. For spruce it was 39%, 58%, and 3%, respectively. In the open, all rainfall will reach the mosses. In her study of nutrient cycling through ***Sphagnum russowii*** (Figure 42) in a Jack pine (*Pinus banksiana*) forest and an open mat, Scafone (unpublished data) often found that moss throughfall collectors in the open had abundant water when those under the canopy were empty. Therefore, since more water reaches the mosses in the open, the total nutrients reaching those mosses could be relatively greater than that estimated by concentration levels, because more water reaches them.

On the other hand, forest trees serve as collectors of minerals in dust, releasing these as they are washed off by rainfall. In the forest, short rainfall events, which are likely to contain high nutrient levels, may not reach the mosses at all, whereas in the open field, they will. Both field and forest mosses will receive nutrients as dustfall, but open field mosses could receive more because there will be no trees to serve as filters or to block the wind.

Figure 42. ***Sphagnum russowii***, a species that grows in both the sun and forest where nutrient inputs are very different. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Bates (1992) suggests that growth rate plays a role in the source of nutrients used by the forest bryophytes. The slow-growing moss ***Pseudoscleropodium purum*** (Figure 8) obtains its minerals largely from "wet deposition," but phosphate is in low concentration in precipitation. Instead, it typically gets this mineral from the substrate.

Bogs

Bogs are defined by their source of nutrients. These come entirely from precipitation (Malmer *et al*. 1992); ground water does not move through the mat. This may be a bit too exclusive for a definition because dust from the atmosphere will also collect on the mosses, and when rainfall occurs the collected dust can go into solution and subsequently into the mosses. This is in contrast to nutrients in fens, particularly rich fens where Ca and Mg are available in surface water.

Atmospheric Dust

In some habitats, atmospheric dust can provide most or all of the mineral nutrients. In many ***Sphagnum*** (Figure 10, Figure 24-Figure 25) bog species, the mosses seem to depend exclusively on aerial deposition for their mineral nutrients (Hájek & Adamec 2009).

The composition of rainfall changes during a single rainfall event as it cleanses the atmosphere of its load of dust. Early rainfall in polluted areas is more acidic than later in the storm because it is washing the pollutants such as sulfates and nitrates out of the atmosphere. This lower *p*H causes more nutrients from the collected dust to go into solution. In the forest, this early rainfall will most likely not reach the mosses on the forest floor, being trapped by the canopy leaves. Meanwhile, the low *p*H of initial rainfall can leach nutrients from the canopy leaves, making them available in the throughfall that later reaches the mosses on the forest floor and on the tree bole. In the field, this low *p*H can be an effective way to dissolve the nutrients in the collected dust on the moss surfaces. A heavy rainfall might wash away a considerable portion, but a light rainfall may simply serve as a solvent while being insufficient to drip through the moss to carry the nutrients away.

By these mechanisms, throughfall alters the composition of rainfall considerably. The canopy enriches the rainfall by collecting dust that subsequently releases nutrients into solution in the rainfall. Schlesinger and Reiners (1974) demonstrated, by using artificial, plastic conifer needles, that the particulate matter of throughfall could increase by 4.5X. But living tree leaves can remove nutrients as well, and may hold more than artificial leaves due to hairs, snail trails, glands, and other features that trap dust particles. N can be removed almost completely from the rainfall by the canopy leaves, whereas K and P are typically enriched by the canopy (Brown 1982). Caterpillars in the canopy can contribute substantial amounts of both N and P through their excreta and feces (Szabó & Csortos 1975), presumably recycling that which is stored in leaves and thus including nutrients that originated in the soil. Mn is rich in litter, but apparently not in the soil, and may also possibly be leached from the canopy (Brown 1982).

In a lab study of ***Mnium hornum*** (Figure 43), Thomas (1970) found that the moss could obtain an adequate supply of Ca and Mg from the substrate below, but that K and P concentrations were less than those found in the soil, suggesting that these nutrients required additional input from precipitation, dustfall, or throughfall. Longton and

Greene (1979) showed similar relationships with ***Pleurozium schreberi*** (Figure 31). The plants had nutrient deficiency symptoms unless additional nutrients were supplied to the leaves. Precipitation and litterfall in the boreal forest were unable to supply sufficient Ca, Mg, and K for ***P. schreberi*** (Brown 1982) so we must consider that precipitation, dustfall, and substrate are all needed to meet the nutrient demands of at least some bryophytes.

Figure 43. ***Mnium hornum*** with capsules, a species that obtains Ca and Mg from the substrate below, but requires additional sources for K and P. Photo by Michael Lüth, with permission.

For the **endohydric** (moving water internally) ***Polytrichum*** (Figure 44) species, inorganic bulk precipitation of N and dust does not account for the entire N input (Bowden 1991). Even when biological nitrogen fixation by associated organisms is included, 35% of the N that has been accumulated by the plant is unaccounted for. Bowden attributed these missing sources to bulk precipitation of organic nitrogen, dry deposition, and dew. Most likely some soil input was also involved, whether directly through rhizoids or by upward movement through external capillary action. Furthermore, we cannot ignore the possibility of transfer from litter and other sources through **mycorrhizae** ("root"-fungal associations), as we will discuss later in this subchapter. Nevertheless, at least 58% of the N in the plant came from bulk precipitation.

Figure 44. ***Polytrichum commune***, an endohydric moss that obtains its N from multiple sources. Photo by Michael Lüth, with permission.

Soil

Several studies cited above have shown that nutrients in rainfall are insufficient to account for the concentrations found in the mosses. Binkley and Graham (1981) found that precipitation could account for only 75% of the nitrogen in ***Eurhynchium oreganum*** (Figure 45) and ***Hylocomium splendens*** (Figure 41) in an old-growth Douglas fir (*Pseudotsuga menziesii*; Figure 46) forest, and they suggested these mosses might obtain some of their N from the underlying soil. Tamm (1953, 1964) felt that ***Hylocomium splendens*** was most likely to obtain its nutrients from accumulations on overlying shoots rather than from the soil by capillary action. But in the tundra ***Hylocomium splendens***, ***Aulacomnium palustre*** (Figure 47), and ***Sphagnum*** (Figure 10, Figure 24-Figure 25) can obtain nitrogen (as ammonium, nitrate, and the amino acid glycine) from 3-8 cm soil depths (McKane *et al.* 1993). Perhaps the translocation of water upward by capillary action brings the nutrients up from lower soil depths. Or is there a fungal connection? In any event, soil seems to contribute to the moss nutrient supply. This concept of soil contributions is further supported by a study on ***Pleurozium schreberi*** (Figure 31), another pleurocarpous feather moss with a growth form similar to that of ***Hylocomium splendens***, that can obtain calcium from $CaCO_3$ in soil as well as from dilute solutions on its leaves (Bates & Farmer 1990).

Figure 45. ***Eurhynchium oreganum***, a moss that seems to obtain some of its N from the soil, but the rest from precipitation. Photo by Adolf Ceska, with permission.

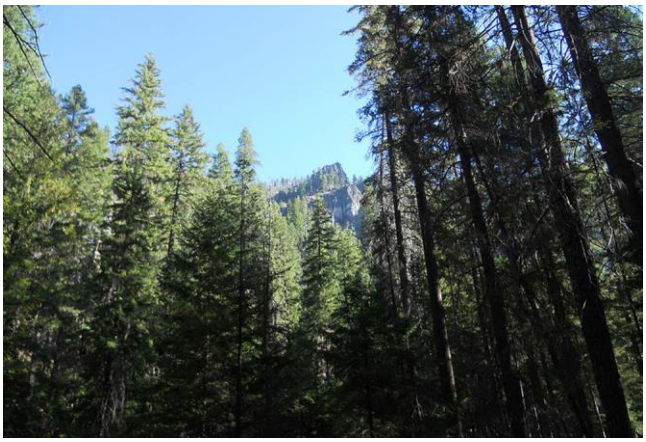

Figure 46. ***Pseudotsuga menziesii*** and ***Pinus ponderosa*** forest. Photo by Jsayre64, through Creative Commons.

Figure 47. ***Aulacomnium palustre*** gametophytes. Photo by Janice Glime.

Van Tooren *et al.* (1990) further supported the concept that ***Hylocomium splendens*** (Figure 41) as well as ***Pleurozium schreberi*** (Figure 31) can obtain micronutrients from the soil. They observed that mosses often have bits of soil and detrital matter nestled among the leaf bases. They tested the hypothesis that these could be derived from the soil substrate and found that indeed nutrients did arrive on the plants from the soil. De Caritat *et al*. (2001) found that geological aspects, sea spray, and human activity all influence the nutrients stored in ***Hylocomium splendens*** and ***Pleurozium schreberi*** in northern Europe. These two moss species had considerable composition of the elements of the underlying bedrock, including B, Ca, K, Mg, Mn, and P. Part of this substrate input is due to redistribution of the soil as dust from open areas. It is in this arena that human activity is most likely to be a contributor by making open, disturbed areas through mining, construction, agriculture, lumbering, and other surface disturbances.

Bryophytes of many habitats seem to have the ability to obtain nutrients both from the soil and from rainwater. Van Tooren and coworkers (1990) explored the relative importance of soil vs precipitation as a source of nutrients for pleurocarpous ***Calliergonella cuspidata*** (Figure 35) on sand and chalk grassland soil. They found that the concentrations of N, P, and K in the plants were higher on chalk soil than on sand, and that these were enhanced by fertilization. However, the plants on the chalk soil did not increase growth when fertilized, whereas those on sand did. They concluded that the soil was providing sufficient nutrients on the chalk grasslands and that some other factor must be limiting their growth.

Our first clue that bryophytes are affected by soil nutrients should have come to us with the realization that some prefer acidic soils and some prefer calcareous soils (Nagano 1972; Bates 1978; Büscher & Koedam 1979; Nakanishi & Hiraoka 1981). ***Grimmia orbicularis*** (Figure 40) demonstrated the ability to absorb ^{54}Mn and ^{90}Sr from the soil (Hébrard *et al.* 1972). Even more impressive, however, is the ability, already noted, of this species to obtain labelled ^{90}Sr from an artificial rock substrate (Hébrard *et al.* 1974). We need to stop thinking of bryophytes as passive collectors and recognize their ability to move substances from one place to another both internally and externally.

Micronutrients

Bryophytes are known for their ability to take up nutrients and accumulate them. This ability has made them useful in geological prospecting and in measuring accumulation of pollutants. Samecka-Cymerman and Kempers (1993) used aquatic bryophytes [***Scapania undulata*** (Figure 48), ***Pellia epiphylla*** (Figure 49), ***Fontinalis antipyretica*** (Figure 50), ***Platyhypnidium riparioides*** (Figure 17)] to indicate mineralization in Poland, confirming the presence of geologically documented polymetallic deposits and indicating their presence in areas that had not yet been explored. The interesting story here is that bryophytes are sometimes able to meet these very minor amounts needed by getting them from the rock substrate.

Figure 48. ***Scapania undulata***, a species that accumulates minerals from the substrate. Photo by Michael Lüth, with permission.

Figure 49. ***Pellia epiphylla***, a species that indicates mineral composition of the substrate. Photo by David Holyoak, with permission.

Figure 50. ***Fontinalis antipyretica***, a species that has been used to indicate metal deposits. Photo by Michael Lüth, with permission.

Litter and the Role of Trees

Parker (1983) suggested that atmospheric nutrients include both dry and wet deposition that not only can provide nutrients to the mosses directly but that also can enrich the litter (and leaves on the trees), permitting the leaves to provide nutrients to the mosses secondarily (see Table 2). ***Brachythecium rutabulum*** (Figure 51) achieved its greatest biomass gain when it was in contact with the stem litter of *Urtica dioica*, apparently intercepting the nutrients in decay products. In a different study, Bates (1992) has related nutrient source to growth rate, concluding that in the rapid-growing species ***Brachythecium rutabulum***, mineral inputs from seasonally deposited tracheophyte litter are especially important.

Figure 51. ***Brachythecium rutabulum***, a species that obtains nutrients from tracheophyte litter. Photo by Michael Lüth, with permission.

Table 2. Nutrient inputs and moss accumulation in an oakwood in Wales. Based on Rieley *et al*. (1979).

	mg m^{-2} yr^{-1}			
	K	**Ca**	**Mg**	**Na**
throughfall	1900	1000	1390	10380
litterfall	1920	2100	420	310
bryophyte accumulation	1430	410	390	160

Dicranum polysetum (Figure 52), ***Ptilidium ciliare*** (Figure 53), and ***Ptilium crista-castrensis*** (Figure 54) intermixed in a mat of ***Pleurozium schreberi*** (Figure 31) all experienced enhanced growth from an application of thick needle litter (Frego & Carleton 1995). But we must again question if fungi have a role here, taking from the litter and supplying to the moss. Nevertheless, litter seems to play an important role in providing a nutrient supply.

Figure 52. ***Dicranum polysetum*** with capsules and litter that serves as a source of its nutrients. Photo by Janice Glime.

Figure 53. ***Ptilidium ciliare***, a species that benefits from nutrients in needle litter. Photo by Janice Glime.

Figure 54. ***Ptilium crista-castrensis***, a species that benefits from nutrients in conifer needles. Photo by Adolf Ceska, with permission.

Although epiphytic bryophytes (those living on other plants) do not penetrate their substrate to obtain nutrients, they can benefit from nutrients flowing down the bole (main trunk) of a tree, some of which are derived from internal metabolites of that tree. Hoffman (1972) found that bryophytes and lichens at the bases of *Liriodendron tulipifera* (tulip tree) recovered 9% of labelled cesium that had been injected into the tree trunk. This illustrates the cycling of nutrients from the tree, probably through **leachates** (solution that percolates through canopy), to the bryophyte layer. The tree base likewise is the recipient of considerable stemflow that carries with it nutrients washed off the leaves and branches. Hence, the bryophytes at the tree base benefit from both leachates from the leaves and from accumulated dust that may contain important nutrients (Figure 55). Fluctuations in K, Ca, and Mg in nature suggested that appreciable quantities are absorbed by bryophytes during autumn from leaf leachates (Bates 1989). Of course, this also makes epiphytes vulnerable to concentrated pollutants in areas where the tree leaves are able to collect these.

Figure 55. ***Dicranum scoparium*** growing at tree base where it collects stemflow nutrients and escapes burial by leaf litter. Photo by Janice Glime.

Even in bogs, the critical nutrient potassium, as well as manganese, becomes available to ***Sphagnum*** (Figure 10, Figure 24-Figure 25) in ombrotrophic bogs through litter decomposition (Malmer 1988).

The more we learn about bryophyte nutrient relationships, the more we realize that they are no simpler than are those of the tracheophytes. Each nutrient and each species must be examined for its own uniqueness, and thus far, we lack sufficient evidence to correlate **functional groupings** (those having similar roles in the ecosystem) with taxonomic or morphological groupings.

Decomposition

The phenomenon that keeps the Earth from running out of nutrients is decomposition. Through a series of breakdowns, organisms return their nutrients to the soil or other substrate. Even bryophytes participate in this process, albeit usually slowly. Rather than losing leaves annually like trees, or dying back and regrowing from underground parts, most bryophytes die from the base while still growing at the tips.

In the taiga, bryophytes form the dominant cover and provide considerable primary productivity in the scheme of things (Oechel & Van Cleve 1986). With this dominance in the ground cover, they play a major role in rapid nutrient absorption, thereby having a large role in controlling ecosystem function. They are able to collect nutrients from dust, incorporate it, and release it slowly. In this way, bryophytes act as **nutrient sinks**.

In a study to understand the effect of climate change on Arctic ecosystems, Lang *et al*. (2009) measured decomposition rates of bryophytes, lichens, and tracheophytes over a 2-year period. Mass loss (decomposition) in tracheophytes was 56%, lichens 44%, and bryophytes a paltry 11%. Nevertheless, percentage loss in **cryptogams** (bryophytes and lichens) varied considerably among species. In particular, ***Sphagnum*** (Figure 10, Figure 24-Figure 25) loss was much slower than that of other mosses and liverworts. Mass loss of non-***Sphagnum*** mosses correlated with the initial N in the plants, a phenomenon that may relate to their nutritive value to the decomposers.

Brock and Bregman (1989) likewise found that organic weight loss during decomposition of the fen moss ***Sphagnum fallax*** (Figure 26) was low. However, the release of N, P, and K (especially) was in greater proportion than that of organic matter loss. These soluble nutrients could easily leak out from damaged membranes of dead or desiccated cells. But despite this, N and P remained as a large proportion of remaining tissues even 12 months after decay initiated. Instead, they found that after a year of death, the cells demonstrated little damage and were poorly colonized by microorganisms.

The same sequestration seen in the Arctic is also present in the tropics. Tropical epiphytic bryophytes are known to sequester N collected from dust and the atmosphere, putting it into recalcitrant forms that remain in the canopy (Clark *et al*. 1998a, b).

What seems to be a common theme in bryophyte decomposition is that it is slow: Russell 1990 – tundra; Verhoeven & Toth 1995 – ***Sphagnum*** (Figure 10, Figure 24-Figure 25); Hobbie 1996 – tundra; Sand-Jenson *et al*. 1999 – Arctic lakes; Liu *et al*. 2000 – montane moist evergreen broad-leaved forest; Moore *et al*. 2007 – temperate peatlands; Turetsky *et al*. 2008 – ***Sphagnum*** in boreal peatlands; Lang *et al*. 2009 – subArctic. This makes the bryophytes a nutrient sink compared to other plant species in most ecosystems. This implies that they get most of their decomposition nutrients from litter decomposition of tracheophytes, not from recycled nutrients from their own tissues.

Snow

We know that snow forms around dust particles in the atmosphere and thus brings nutrients to the soil, efficiently removing them from the atmosphere (Woolgrove & Woodin 1996). As snow partially melts throughout the winter, melt water supplies nutrients to the soil below. When the weather warms in the spring and the snow melts quickly, it typically melts in a flush.

But what role does it have in supplying nutrients to the bryophytes? Are they able to take up nutrients at these near-freezing temperatures? Can they store nutrients to prepare for their spring flush of growth? And what role

does spring melt play in providing a flush of nutrients to be grabbed by mosses before they can reach the soil? Do mosses then serve as sinks, releasing nutrients later as the summer warms and the mosses become desiccated and leak their precious nutrient supply? Or are the mosses damaged and leaking themselves, unable to take advantage of this flush until they have accomplished their own new growth?

If the mosses are able to trap cations on exchange sites, even though they cannot yet absorb and use them, this could later provide a nutrient supply to the roots of tracheophytes at a time when their resources are dwindling, but when they are still actively growing and needing them. Or, bryophytes could deprive them of these atmospheric nutrients by trapping and holding them for an extended period of time – or indefinitely. And how are the important anions held, like NO_3^- and PO_4^{-3}? Certainly nitrogen compounds arrive in this way, suggesting that mosses may take them in immediately if they are removing them from the system.

Woolgrove and Woodin (1996) examined the effect of snowmelt and nitrate uptake in the moss ***Kiaeria starkei*** (Figure 56) at a snowbed in the Cairngorm Mountains of Scotland. They found that although the conditions under the snow are unsuitable for photosynthetic activity due to the low light intensity, this moss is capable of photosynthesis as soon as the snow cover is removed. Tissue chlorophyll increases by 250% and carbohydrate concentrations increase 60% within only two weeks. This moss is also capable of nitrate reductase activity at temperatures as low as 2ºC and is thus able to assimilate more than 90% of the high levels of pollutant nitrate released during the melting season.

Figure 56. ***Kiaeria starkei***, a moss capable of nitrate reductase activity at 2°C. Photo by Michael Lüth, with permission.

On the other hand, in my moss garden in Houghton, Michigan, USA, in an area characterized by northern deciduous forest, the mosses and even the liverwort ***Marchantia polymorpha*** (Figure 3) are brown and appear dead when the snow recedes. Obviously there are still living tissues there because the mosses and the liverwort both produce new growth within a few weeks, dependent on adequate rainfall and temperature. But under these conditions, it would appear that the mosses should be more poised to lose nutrients from these brown tissues than to gain them. Certainly more research is needed on the role of individual bryophyte species in sequestering and later releasing nutrients collected during a season of heavy snow. And what effect does a loading of heavy metals, sulfates, and nitrates have on the survival of the bryophyte layer following a sudden snowmelt release?

A further problem occurs once the snow melts in my moss garden. The snow melt water can be gone in a week, and instead of spring rains, this is typically followed by an extended dry period. In some years, it appears that this wet period is insufficient for them to recover before the drought and they can remain largely brown the entire growing season.

The Salmon Story and Other Animals

The salmon (***Oncorhynchus*** spp.) are fish, so when I read the title of an article on uptake of salmon-derived nitrogen by mosses and liverworts, I was expecting a story about aquatic mosses (Wilkinson *et al*. 2005). However, instead I was soon reminded of the massive midge outbreaks in Iceland that bring the rich geothermal nutrient source of Icelandic lakes to the terrestrial scene, because these salmon are brought to land by their predators and the remains of the carcasses provide a nitrogen source. In both cases, an aquatic nutrient source is brought to land.

It appears that in at least one forested watershed in coastal British Columbia, Canada, the percent N in moss tissues, especially the common moss ***Rhytidiadelphus loreus*** (Figure 57), is higher in forest mosses below the falls where the salmon are than above the falls, where they are not. N content was higher in mosses near bony remains from previous years and near wildlife trails (Wilkinson *et al*. 2005). Seven of the eight bryophyte species examined exhibited decreasing N uptake with distance from the spawning region; the exception was ***Rhizomnium glabrescens*** (Figure 58), an epiphytic species that showed no relationship. Below the falls, the thallose liverworts ***Conocephalum conicum*** (Figure 59) and ***Pellia neesiana*** (Figure 60), both indicators of soil rich in nitrogen and calcium, had the greatest cover. Even species richness was higher in forest areas near the salmon stream than elsewhere.

Figure 57. ***Rhytidiadelphus loreus***, a species that gets some of its nutrients from salmon dropped on land by predators. Photo by Michael Lüth, with permission.

Figure 58. ***Rhizomnium glabrescens***, an epiphytic species that does not benefit from salmon prey dropped on land. Photo by Matt Goff <www.sitkanature.org>, with permission.

Figure 59. ***Conocephalum conicum***, a species that indicates soil rich in N. Photo by Janice Glime.

Figure 60. ***Pellia neesiana***, a species that indicates soil rich in N. Photo by Jan-Peter Frahm, with permission.

Hilderbrand *et al*. (1999) determined that adult female brown bears (Figure 61) excrete as urine 97% of the N consumed from salmon. This most likely is distributed primarily along the wildlife trails. Thus, wolves, bears, and river otters contribute to the success of the bryophytes by bringing their dinner into the forest and leaving the scraps, but also as they venture through the forest by distributing the N as urine and possibly feces.

Figure 61. Brown bear catching salmon that will be carried ashore to be eaten. Photo by Brian W. Schaller, through Creative Commons.

Fungal Partners

A long-neglected aspect of bryophyte nutrient uptake is that of **mycorrhizal** (fungal-"root" symbiosis) associations. This has gotten somewhat recent attention and needs to be considered in understanding bryophyte nutrient relations. Details of studies will be covered in Volume 2 on Interactions – Fungi.

We know that conifers and orchids depend on fungal partners to obtain nutrients, and indeed it may be the case for all forest trees. Now we know that it is a part of some bryophyte relationships, but we lack sufficient data to determine how widespread it is.

In the boreal forest, mycorrhizae are therefore of critical importance. And that forest floor is dominated by feather mosses. Mosses can release significant quantities of N and P from their shoots, especially after drying (Carleton & Read 1991). More of this is released from dead and **senescent** (growing old) parts than from the green parts. Leakage of the sugars glucose, fructose, and sucrose from dry moss shoots is sufficient to support growth of three mycorrhizal fungi in pure culture, so we might hypothesize that the bryophytes at least are capable of enhancing the growth of the tree mycorrhizal fungi. When moss shoots were added to the cultures, the fungi readily colonized them, especially in the senescent regions. Labelled phosphate and carbon previously "fed" to the moss shoots were absorbed by the mycorrhizae and transferred across centimeters to roots infected with these fungi. The extent to which the bryophytes are important in this relationship remains to be investigated.

This raises the question of the value of mycorrhizae to bryophytes. The **achlorophyllous** (lacking chlorophyll) liverwort ***Cryptothallus mirabilis*** (Figure 62) is unable to fix its own carbon through photosynthesis. Both this species and its photosynthetic sister species ***Aneura pinguis*** (Figure 63) interact with **endophytic** (living within a plant) **Basidiomycetes** – the group of fungi responsible for producing all the mushrooms (Ligrone *et al*. 1993). In ***Cryptothallus***, the young fungal hyphae contain abundant **glycogen** (carbohydrate – polysaccharide that forms glucose on hydrolysis) and sometimes **amyloid** (starch-like protein) deposits within the ***Cryptothallus***. The fungi associated with both genera very closely match those of orchids – a group with obligate mycorrhizal associates.

Figure 62. ***Cryptothallus mirabilis***, a species that obtains its carbon and most likely other nutrients through a fungal partner. Photo by David Holyoak, with permission.

Figure 63. ***Aneura pinguis***, a photosynthetic close relative of ***Cryptothallus mirabilis***, that has similar mycorrhizal fungi. Photo by Michael Lüth, with permission.

*p*H Relationships

It is not unusual to find bryophytes in habitats with low *p*H. Merunkova and Chytry (2012) reported that bryophytes in upland grasslands of the southern Czech Republic were mostly on the low-*p*H soils that were low in Ca and P, as well as on organic soils. Underwater bryophytes are relatively rare in limestone streams where the carbon is present as carbonate and not as free CO_2 (pers. obs.). This is discussed further in the subchapter on CO_2 in this volume.

The *p*H not only affects the nutrient uptake ability of the bryophytes, but also can affect the toxicity of such minerals as aluminium (Al) (Bates 1992). Low *p*H makes many minerals, including Al, more soluble. In most cases, this increases the ability of the minerals to enter the bryophyte along with water. Bates found that in woodland soil and on rock substrates, the bryophyte cation exchange capacity (CEC) decreased with decreased Ca and the *p*H in the substrate.

On the margins of forested stream channels, Hylander and Dynesius (2006) found that mosses were more influenced by the *p*H than were liverworts. They furthermore found that having pockets with higher *p*H increased the bryophyte richness. Corrales *et al*. (2010) found that *p*H was one of three factors in determining bryophyte distribution in secondary and planted montane forests in the Central Cordillera of Colombia. Low *p*H is a major factor in making nutrients available.

Protective Devices

As already seen, not all minerals are good minerals. At low *p*H levels, aluminium becomes soluble – and toxic. For some heavy metals the cation exchange sites serve as protection, binding the metals and thus immobilizing them.

The toxic heavy metal lead is accumulated in large quantities in cell walls, but also can occur in the cytoplasm (Basile *et al*. 1994). In bryophytes it accumulates preferentially in gametophyte **hydroids** (water-conducting cells in mosses), sporophyte hydroids at the foot, and transfer cells adjoining the sporophyte. It also occurs in the cytoplasm, chloroplasts, mitochondria, vacuoles, and cytoplasmic reticulum. In ***Funaria hygrometrica*** (Figure 2), the lead is sequestered in tissues, preventing it from reaching the seta and capsules where it could damage developing spores. The **placenta** that joins the gametophyte and sporophyte blocks the transfer of lead to the sporophyte.

Seasonal Nutrient Behavior

Seasonal differences in available nutrients result from litter fall, snow melt, flooding, runoff, available moisture, and seasonal deposition from some kinds of pollution. Nutrient availability may be further mediated by changes in biological needs during the changing life cycle stages of the bryophytes and the tracheophytes that surround them.

Bryophytes, like tracheophytes, have different needs for nutrients in different seasons, and their uptake and movement of those nutrients likewise differs with the seasons. For example, in the boreal feather moss ***Hylocomium splendens*** (Figure 41), airborne nutrients dominate uptake to the growing tissues during winter in a pine forest in Latvia; Ca and Mg are held in green tissues (Brümelis *et al*. 2000). During the relatively dry autumn, Mg is transferred from older brown and decaying tissues upward to the young tissues, but Ca is not.

Snow concentrates nutrients and releases them in a spring pulse (Brümelis *et al*. 2000). Yet, despite the fluctuations of availability of nutrients in the surrounding environment, there is no evidence that bryophytes suffer leaching as a means of maintaining chemical equilibrium with their environment. The cell membranes must therefore control the entry and exit of ions.

The forest floor moss ***Brachythecium rutabulum*** (Figure 51) exploits seasonally deposited vascular plant litter (Bates 1992). ***Pseudoscleropodium purum*** (Figure 8) seems to depend largely on wet deposition for minerals, making its greatest nutrient availability during the season(s) with the most rainfall. But in their study of ***Hylocomium splendens*** (Figure 41) and ***Pleurozium schreberi*** (Figure 31), Berg and Steinnes (1997) found no variations in the element concentrations on different dates in the sampling season. This again raises the question of whether bryophytes are able to regulate their nutrient concentrations, and if so, how?

Markert and Weckert (1989) examined minor elements in ***Polytrichastrum formosum*** (Figure 64), a weedy species in Europe but somewhat rare in North America. They

found considerable variation between stands as well as between seasons. K had little seasonal variation; Al, Fe, Cr, Mg, Pb, and Ti had roughly 80% variation, with their highest concentrations in winter and lowest in summer.

Figure 64. ***Polytrichastrum formosum*** with capsules, a species that has considerable variation in nutrient content among locations. Photo by David T. Holyoak, with permission.

Because of their ability to take up large quantities of heavy metals, bryophytes have been used for monitoring heavy metal pollution, as has been discussed already in several books. These bryophytes often exhibit symptoms of excess, including **chlorosis** (loss of chlorophyll), brown tips (Figure 19), and **plasmolysis** (shrinkage of protoplast of plant cell resulting from loss of water from cell; results in space between cell membrane and cell wall) (Figure 22). In other cases, the damage is so great that membrane integrity is lost and the cells exhibit **deplasmolysis** (swelling of the cytoplasm of a previously plasmolyzed cell; reversal of plasmolysis) (Figure 22).

Richardson (1981) suggested that there are greater seasonal fluctuations in ectohydric mosses like ***Aulacomnium*** sp. (Figure 47) than in endohydric ones like ***Polytrichum*** (Figure 44) due to the ability of ectohydric mosses to absorb nutrients throughout the plant. In the black spruce forests (Figure 27) of Alaska, ***Polytrichum*** (***Polytrichastrum***?) had its highest phosphate uptake rates in below-ground portions. But we must also consider that this moss has ectohydric movement of water that carries water and nutrients to the apex where they are absorbed. The leaves rehydrate slowly, suggesting that they are more water repellant than absorptive.

Williams *et al*. (1999) compared the seasonal nitrogen dynamics in two ***Sphagnum*** species: ***S. capillifolium*** (Figure 32) occupying hummocks and ***S. recurvum*** (Figure 33) in hollows. Rather than rely on natural sources, the researchers added labelled NH_4NO_3 at the levels in the ecosystem where the mosses lived. The proportion of labelled N in the mosses ranged from 11 to 100% during the 14-month study. The lowest measurements occurred in October when the water table reached the surface of the mosses. This was particularly true for ***S. recurvum***. A very small amount of the labelled N was detected as dissolved organic nitrogen in the moss water. There were also times when they could not account for a large proportion of the added N.

In ***Sphagnum*** (Figure 10, Figure 24-Figure 25) in the southern Alps, Na, Mg, and to a lesser extent Ca, became progressively more concentrated in the tissues as the growing season progressed; N, and to a lesser extent, P, were enriched in the photosynthetic cells during this period of intense growth, but were leaked from the cells when the growth rate slowed (Gerdol 1990). Likewise, during cold months, Na, Mg, and Ca were leached from the cell walls.

Bryophyte growth periodicity can differ between years, being influenced by precipitation (Brock & Bregman 1989). And surprisingly, capsules of ***Sphagnum fallax*** (Figure 26) in a fen woodland were formed only during the dry year, somewhat reminiscent of flowering plants that bloom in response to drying conditions or algae that reproduce sexually when nutrients begin to diminish in the water.

Streams have seasonal pulses in nutrients, with the largest usually corresponding to snowmelt and spring runoff. In an acidic stream in Northeast England, Ellwood and Whitton (2007) found that organic phosphate, the form used by those bryophytes, reaches a high peak in late spring. In the moss ***Warnstorfia fluitans*** (Figure 9) this peak coincided with higher concentrations of organic P.

On the other hand, in their study of the aquatic mosses ***Fontinalis antipyretica*** (Figure 50) and ***F. squamosa*** (Figure 65) in a mountain stream in Spain, Mártínez Abaigar and coworkers (2002) found that concentrations of K, Fe, P, and N increased in every portion of the plant through summer and autumn and decreased through winter and spring. Since these concentrations did not track the concentrations of the stream water, they presumed that the concentrations of the mobile elements depended on the growth cycle. Na increased in the plants in winter, presumably as a result of winter deicing salts. Ca and Mg seemed to fluctuate randomly throughout the plant.

Figure 65. ***Fontinalis squamosa***, a species that increases its concentrations of K, Fe, P, and N throughout the plant in summer and autumn. Photo by Janice Glime.

It is hard to generalize from the few studies presented here (see Table 3), but it appears that minor elements may be high in the plants in winter when they are not being used and that the three major elements (N, P, K) are relatively conserved throughout the year. Translocation can provide mobile nutrients from older parts to younger parts prior to and during early stages of growth, thus maintaining sufficient nutrient supply to support the relatively slow growth rate of a bryophyte.

Table 3. Seasons of uptake and loss of nutrients in bryophytes from different habitats. + indicates uptake for that group; - indicates loss for group; no symbol indicates season of highest concentration. These positions should not be interpreted as representative as so few bryophytes have been evaluated seasonally.

Species	Spring	Summer	Autumn	Winter	Reference
Hylocomium splendens				+Ca,Mg	Brümelis *et al*. 2000
Fontinalis antipyretica	+K,Fe,P,N	+K,Fe,P,N	+K,Fe,P,N	Na	Mártínez Abaigar *et al.* 2002
Sphagnum		+N,Na,Mg,Ca	+P,Na,Mg,Ca	-N,P,Ca,Mg,Na	Gerdol 1990
Polytrichastrum formosum		K		Ba,Ca,Cd,Cu,Sr,Mg,Zn Al,Fe,Cr,Mg,Pb,Ti,	Markert & Weckert 1989

Effects on Species Composition

When nutrients increase, it is not unusual for bryophyte cover to decline and even disappear (Arróniz-Crespo *et al.* 2008). In an acidic grassland, Arróniz-Crespo and coworkers found that up to 90% of the bryophyte cover was lost due to enhanced nitrogen deposition. The tissue N:P ratio increased up to three times the original levels. They concluded that it was the limitation by phosphorus that caused damage to photosystem II and consequently caused loss of bryophyte biomass. Pigment concentrations and chlorophyll fluorescence were also affected.

We have seen that bryophytes often do not benefit from added N. Armitage *et al.* (2010) found that high N concentrations in alpine mosses can lead to a decline in production of biomass, reducing the cover of bryophytes. In ***Sphagnum*** (Figure 10, Figure 24-Figure 25) bogs, higher N can increase productivity of tracheophytes and consequently reduce the competitiveness of the bryophytes (Berendse *et al*. 2001). On the other hand, ***Sphagnum*** is a major sink for the sequestration of carbon in the Northern Hemisphere. Elevated CO_2 has little effect on ***Sphagnum*** biomass and N depresses it due to increased competitive growth of tracheophytes and the moss ***Polytrichum strictum*** (Figure 66). Loss of ***Sphagnum*** can reduce the sequestration of carbon.

Figure 66. ***Polytrichum strictum***, a species that can outcompete ***Sphagnum*** when given an enhanced N source. Photo by Michael Lüth, with permission.

When Armitage *et al.* (2010) did transplant experiments with alpine ***Racomitrium lanuginosum*** (Figure 5), they found that after 2 years, tissue N in transplants from high N sites to a lower site only partially equilibrated to its new N availability. On the other hand, reciprocal transplants to the higher N regions almost matched the N concentrations of the native plants. The surprise was that mosses experienced greater shoot growth when stimulated by higher N deposition. In the lower N site, moss depth and biomass increased in transplants, apparently due to a lower C:N ratio that slowed decomposition.

Summary

Although there seems to be little in the way of a comprehensive summary of bryophyte nutrient processes in nature, there are many pieces from which a somewhat clear picture emerges. First off, bryophytes can receive their nutrients from the substrate as well as from precipitation and dust. Those forming thick but horizontal mats are more likely to depend predominantly on precipitation, whereas acrocarpous mosses may receive considerable input from the substrate through upward movement externally and subsequent internal movement.

Bryophytes can suffer osmotic shock when transferred to substrates with high nutrients and most lack sufficient wax in the cuticle to help slow the process. They require the same nutrients as tracheophytes (CHOPKNS Mg CaFe), but in lower concentrations. Needs of young shoots are greater than those of older shoots and nutrients may be moved from old to young tissues. Bryophytes trap nutrients leached from the canopy and may provide it to roots of trees, especially spruce trees, possibly through **mycorrhizae**. Ca and Mg can be obtained from the soil, but K and P require additional sources. Litter of herbaceous and woody plants may supply some of the needed nutrients, provided they don't bury the plants or damage them with tannic acid. Snow collects dust particles and these go into solution as the snow melts, dripping down on the bryophytes. Fungal partners may transfer nutrients into the bryophytes or from the bryophyte mat to tree roots. Even salmon, dragged ashore by bears and other predators, contribute to bryophyte nutrients.

Nutrients tend to increase in bryophyte tissues in late summer and fall, then decrease in winter and spring

when the plants are growing, but this varies with the species, the nutrient, and of course with geographic region. The three major elements (N, P, K) are relatively constant throughout the year. *p*H affects solubility and toxicity of nutrients and heavy metals.

Protective devices include sequestration of heavy metals on cation exchange sites and blocking transport from gametophyte to sporophyte in the placenta.

Elevated nutrients, especially N, can favor tracheophytes, at the expense of bryophytes, through competition. They can also alter the bryophyte species composition.

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CHAPTER 8-2

NUTRIENT RELATIONS: CO_2

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CHAPTER 8-2
NUTRIENT RELATIONS: CO_2

Figure 1. Peat moss, ***Sphagnum fimbriatum***, covering the largest area of carbon sink in the world. Photo by Michael Lüth, with permission.

CO_2 Sources and Limitations

Early Carbon Relations

Colonization of life on the land of Earth began billions of years ago (Graham *et al*. 2014). Evidence suggests that bacteria, then **eukaryotic** (having a nucleus) algae, then bryophytes ventured to endure those early conditions. These early forms made possible the development of the first organic soils. To understand this progression and continuation of life, it is prudent to understand carbon cycling. For most terrestrial plants and algae, the source of this carbon is carbon dioxide (CO_2). Both green algae and bryophytes produce a degradation-resistant form of carbon from that CO_2 that is consequently sequestered. This, in turn, reduces the CO_2 in the atmosphere, having an important impact on the Earth's carbon cycle for 40-100 million years.

This early atmosphere was high in CO_2 compared to levels today (Raven & Edwards 2014). Isotope comparisons using liverwort fossils indicate that in the mid-Cretaceous in the Antarctic, CO_2 concentrations ranged 1000-1400 ppm, agreeing generally with independent proxy data and long-term carbon cycle models (Fletcher *et al*. 2005). Furthermore, the concentration gradient from the atmosphere to the carboxylase in the plant would further drive CO_2 into the plant (Raven & Edwards 2014). This additional CO_2 would permit higher photosynthetic rates per surface area of plant. Later adaptations included increasing the surface area of photosynthetic tissue through development of complex structures and air spaces to permit greater harvesting of light.

Proctor (2010) suggested that in the early atmosphere of plant evolution in the mid-Palaeozoic, the atmosphere had 10X its present concentration of CO_2. It is thus unlikely that these early plants were CO_2 limited. Rather they may have increased their cuticularization, then increased their air spaces to permit them to take up more CO_2 and compensate for the blockage by the cuticle.

Rod Seppelt (Bryonet 27 June 2022) described the interior of the cushions. Due to their tightly packed shoots, they maintain humidity better than do the tracheophytes. This added humidity promotes a high CO_2 concentration

(ca. 2000 ppm compared to 350-400 ppm ambient), largely due to the microbial associates.

Relationships Today

In 1958, the CO_2 in the atmosphere had a concentration of 315 ppm (Scripps CO_2 Program 2016). In December 2016 it had grown to 404 ppm. Elbert *et al*. (2012) estimated that cryptogams (including Cyanobacteria, algae, fungi, lichens, and bryophytes) extract ~3.9 Pg carbon per year, or around 7% of the net production of terrestrial vegetation. Thus, the CO_2 uptake by bryophytes is an important component of global carbon cycling and a necessary contributor to climate modelling.

Normally we don't think of carbon as a limiting resource, although experiments on higher plants have shown that increased carbon dioxide usually increases productivity. Mosses are typically **C_3 plants** with high **CO_2 compensation points** (CO_2 concentration at which net CO_2 fixation is zero) (Raven *et al*. 1998). In other words, they require high levels of CO_2 to balance the CO_2 lost to respiration. **C_3 plants** are those plants that have no special mechanism for storing carbon from CO_2 temporarily in a compound such as **malate** or **oxalate**. Instead, they put all their CO_2 directly into the photosynthetic pathway in a 3-carbon compound, hence the term C_3. This pathway is less efficient because the enzyme **Rubisco** (Ribulose bisphosphate carboxylase/oxidase) is much less effective at binding the atmospheric CO_2 into a 3-C compound within the cell than is **PEP carboxylase**, the enzyme used in the C_4 and CAM pathways to put the carbon in temporary storage C_4 compounds for later use in photosynthesis. However, mosses are not limited by guard cell closure in obtaining CO_2 and thus should be able to obtain CO_2 any time of the day.

In examining 32 terrestrial C_3 plants, Bauer and Martha (1981) found an average CO_2 compensation point of 36.2 µl L^{-1} (=71 mg m^{-3}). However, among these, two mosses showed a somewhat higher CO_2 compensation point of ~43 µl L^{-1}. The compensation point for tracheophytes ranged 31-40 µl L^{-1}. Bain and Proctor (1980) found that the CO_2 compensation point of the aquatic bryophytes they studied were over 100 times higher than those of the C_3 aquatic tracheophyte ***Elodea*** (Figure 2) and the alga ***Chara*** (Figure 3). They were likewise somewhat higher than those of terrestrial bryophytes reported by Dilks (1976).

Figure 2. ***Elodea canadensis***, an aquatic plant with a very low CO_2 compensation point compared to that of mosses. Photo by Sean Blaney, through Creative Commons.

Figure 3. ***Chara*** in Keweenaw Peninsula, Michigan, USA, an aquatic alga with very low CO_2 compensation point compared to that of mosses. Photo by Jason Oyadomari, with permission.

Among tracheophytes, CAM plants, convert CO_2 to malate at night and store it to be used in the daytime, permitting the plants to conserve water by keeping stomata closed in the daytime. In C_4 plants a bundle sheath permits plants to convert CO_2 to a 4-carbon compound for use later. This likewise permits the plants to conserve water by closing stomata when the air is dry but to continue using CO_2 derived from the stored 4-C compounds for photosynthesis.

Bryophytes must live in a delicate balance between sufficient moisture and sufficient CO_2. When leaves are wet on the outside, that water offers significant resistance to CO_2 diffusion. Surprisingly, a thin cuticle permits greater diffusion than even a thin film of water, so mosses living in very wet habitats often are protected from waterlogging by well-developed waxes or other cuticular material (Proctor 1984). ***Polytrichum commune*** (Figure 4) and ***P. strictum*** (Figure 5) are good examples of this, but less obvious examples are ***P. wahlenbergii*** (Figure 6), ***Pohlia cruda*** (Figure 7), ***Philonotis*** (Figure 8), ***Schistostega pennata*** (Figure 9), ***Saelania glaucescens*** (Figure 10), and ***Bartramia pomiformis*** (Figure 11), all with a whitish appearance to the naked eye (Proctor 1984).

Figure 4. ***Polytrichum commune*** showing its somewhat waxy leaves. Photo by Michael Lüth, with permission.

Figure 5. ***Polytrichum strictum*** showing waxy leaves. Photo by Janice Glime.

Figure 6. ***Pohlia wahlenbergii*** var ***glacialis*** showing its whitish color due to a thin cuticle. Photo by Michael Lüth, with permission.

Figure 7. ***Pohlia cruda*** showing its whitish color due to a thin cuticle. Photo by Michael Lüth, with permission.

Figure 8. ***Philonotis fontana*** showing its waxy leaves. Photo by Michael Lüth, with permission.

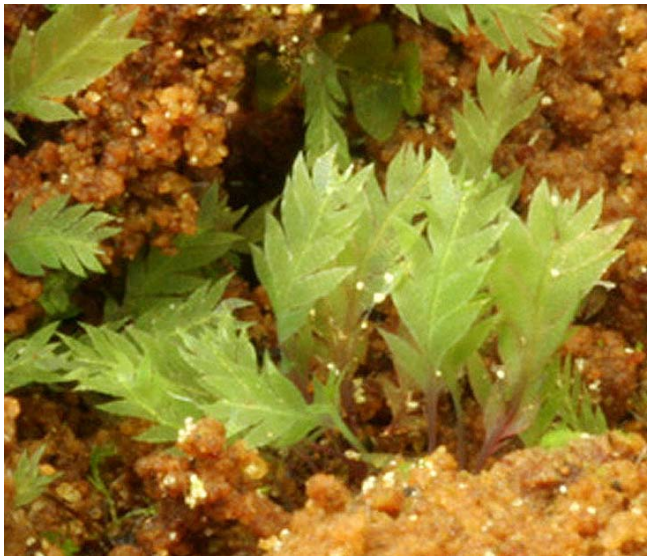

Figure 9. ***Schistostega pennata*** showing waxy leaf surface. Photo courtesy of Martine Lapointe.

Figure 10. Waxy-looking leaves of ***Saelania glaucescens***. Photo by Ivanov, with permission.

Figure 11. ***Bartramia pomiformis*** showing waxy leaves. Photo by Jan-Peter Frahm, with permission.

Sphagnum (Figure 1) partially solves this balance by having water-holding cells (**hyaline cells**) that bathe the photosynthetic cells (Figure 12), while exposing at least one surface (in most) of the photosynthetic cell to the atmosphere. Furthermore, air bubbles become trapped among the leaves and between the leaves and the stem, thus providing an additional source of CO_2. Robinson (1985) considered that no CO_2 was obtained from the **hyaline** (water-holding) cells because all the chloroplasts of the cells were positioned along the wall most exposed to light. On the other hand, members of ***Leucobryum*** (Figure 13-Figure 16) do indeed trap air bubbles in their colorless cells (Robinson 1985), providing an internal source of CO_2 for the chlorophyllous cells residing there and causing these plants to somewhat mimic the internal structure of a seed plant. This same character seems to be present throughout the **Leucobryaceae** family, permitting their multi-layered leaves to function photosynthetically.

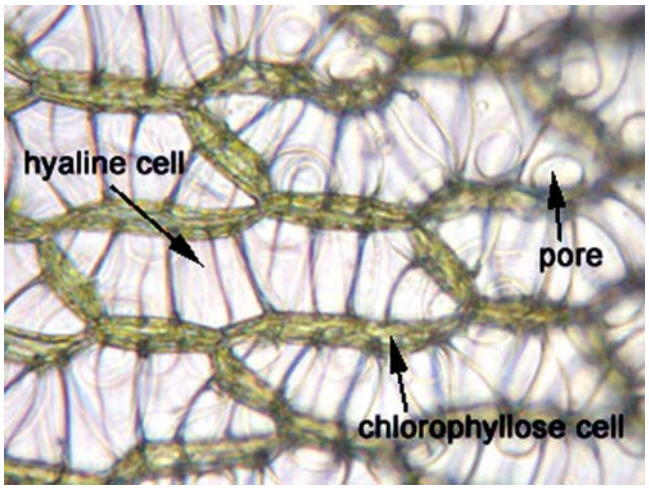

Figure 12. ***Sphagnum*** cells indicating the hyaline cells with pores, holding water, and chlorophyllose (photosynthetic) cells exposed to atmosphere. Photo with from Botany Website, UBC, with permission.

Figure 13. ***Leucobryum glaucum*** showing whitish color caused by hyaline cells that surround the photosynthetic cells. Photo by David T. Holyoak.

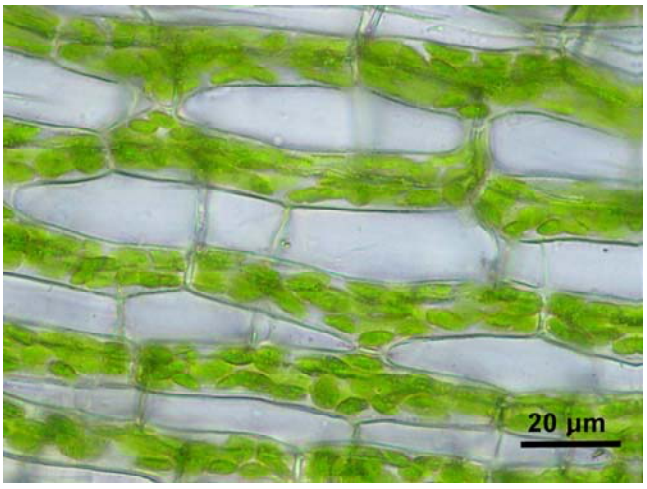

Figure 14. ***Leucobryum glaucum*** leaf cells in lamina view, showing hyaline and photosynthetic cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.

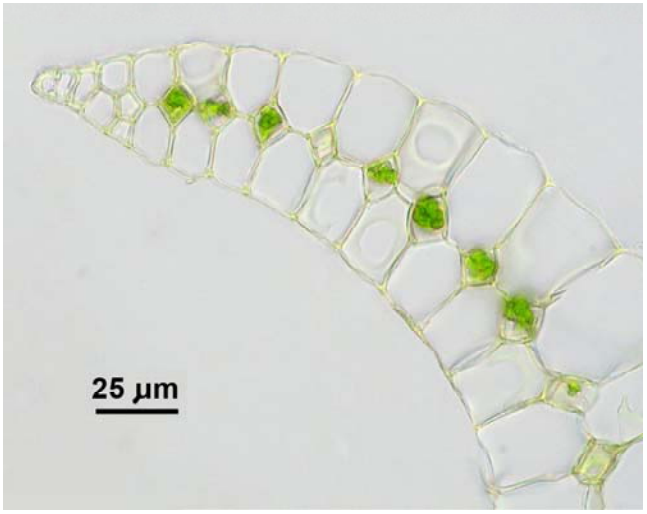

Figure 15. ***Leucobryum glaucum*** leaf cross section showing the photosynthetic cells surrounded by hyaline cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.

Figure 16. Whitish leaves due to hyaline cells of ***Leucobryum juniperoideum***. Photo by Michael Lüth.

Shinde *et al*. (2015) determined that the moss ***Physcomitrella patens*** (Figure 17) has 814 genes that are affected by elevated CO_2 (1500 ppmV). These affect transcriptional reprogramming, photosynthetic regulation, carbon metabolism, and stress responses. CO_2 relationships are not simple!

Figure 17. ***Physcomitrella patens***, demonstrating its whitish appearance due to a thin cuticle. Photo by Michael Lüth, with permission.

Structural Adaptations

Proctor (2010) explains that the maximum rate of CO_2 diffusion is limited by the difference between the external CO_2 concentration and the CO_2 **compensation point** (level of O_2 at which respiration = photosynthesis), as well as the resistance of the moist external bryophyte cell wall to the liquid-phase diffusion of the CO_2. This is limited by the thickness of the external cell walls. Structural differences can increase the plant uptake. A large, simple thallose liverwort provides a single flat photosynthetic surface. This is improved in an epiphyte such as ***Metzgeria*** (Figure 18) that exposes both surfaces. ***Marchantia*** (Figure 19) further increases the uptake surface by its system of internal chambers with photosynthetic cells arranged like tissues of a sponge (Figure 20).

Figure 18. ***Metzgeria furcata*** showing thalli exposed on both sides, thus doubling its CO_2-absorbing surfaces. Photo by Michael Lüth, with permission.

Figure 19. ***Marchantia polymorpha*** pores and gemmae cups. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

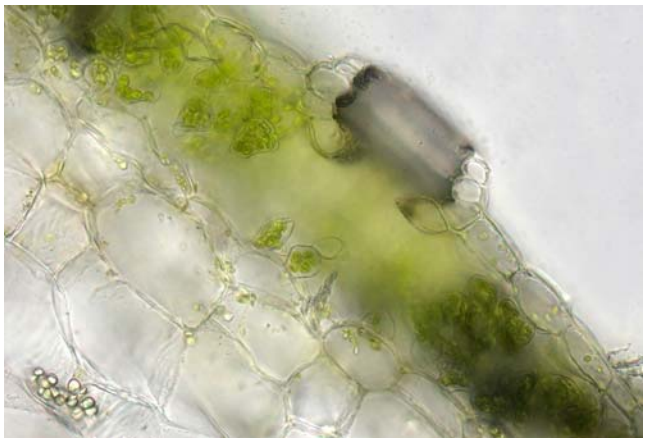

Figure 20. ***Marchantia polymorpha*** cs showing pore and underlying spongy chlorophyllose cells. Photo by Walter Obermayer, with permission.

Perhaps the most obvious adaptation of plants to intake of CO_2 is having stomata in leaves. This apparatus permits tracheophyte leaves to regulate moisture concentration in the leaves. However, when they are closed to conserve water, they are also closed to atmospheric CO_2 that is vitally needed for photosynthesis. Mosses and leafy liverworts lack stomata in their leaves, but generally have leaves that are only one cell thick, thus exposing two sides of the cell for absorption of CO_2. Some thallose liverworts, on the other hand, have a plant body that consists of multiple layers. These typically have a chambered interior with sponge-like tissues that provide lots of surface area. For these to obtain atmospheric CO_2, the chambers connect to the exterior atmosphere through pores that permit its diffusion into the chamber. Raven (2002) suggested that "stomata evolved from pores in the epidermis of plant organs which were at least three cell layers thick and had intercellular gas spaces and a cuticle."

But does this sponge-like interior make a difference? Meyer *et al*. (2008) demonstrated that both external and internal conductances, as well as water use efficiency, were higher in the ventilated (spongy) liverworts and hornworts. Within these two taxonomic groups, however, the values were similar, suggesting that various factors must serve to optimize the involved species for that life form.

Soil CO_2

Šimůnek and Suarez (1993) modelled the CO_2 transport and production in soil. CO_2 can be transported in the unsaturated zone in both the liquid and gas form. Both root and microbial respiration contribute to soil CO_2. The rate of this respiration is affected by water content, temperature, growth, salinity, and plant and soil characteristics.

In a temperate rainforest of New Zealand, bryophytes form a nearly continuous cover (62%) on the forest floor, with a depth less than 30 mm (DeLucia *et al*. 2003). The CO_2 was elevated relative to the atmosphere, presumably due to bacterial and fungal respiration. The net CO_2 exchange was very dependent on water content. Although the CO_2 uptake was quite variable, the annual net carbon uptake by the forest floor bryophytes was 103 g m^{-2}, compared to annual loss of carbon from the forest floor (bryophyte and soil respiration) of -1010 g m^{-2}. This accounted for a reclamation of ~10% of the forest floor CO_2 emitted by respiration.

Tarnawski *et al*. (1994) measured 24-hour changes in atmospheric CO_2 concentrations within and above cryptogam stands in a New Zealand temperate rainforest. They found that CO_2 levels within the forest exceeded those in the open by 30 ppm and had a more variable **diel** (denoting a period of 24 hours) pattern (up to 70 ppm). The mean CO_2 level at a depth of 25 mm in the moss layer was 50% higher than those in the clearing and were higher than in the air of the rainforest.

In the Arctic tundra, there are definite differences in soil respiration rates related to microscale topography, mainly due to differences of soil water table and soil temperatures (Sommerkorn *et al*. 1999). The moss layer serves as a high impact modifier of the CO_2 emission, assimilating 51% to 98% of the daily amount CO_2 released from wet tundra soils.

For most forest floor mosses, the CO_2 should be ample to supply the slow-growing mosses due to production of CO_2 from litter decay. In the tropics, the CO_2 concentrations on the forest floor are greater than those above the canopy (Holtum & Winter 2001), but that enriched supply is still limiting. At 10 cm above the soil the CO_2 level is somewhat higher.

Because CO_2 is often limiting, even in the terrestrial system, increasing levels of CO_2 on the Earth could positively affect the bryophytes. Strain and Cure (1985) reported that the rate of photosynthesis in tracheophytes increases with a rise of atmospheric CO_2. Because bryophytes are C_3 plants, they are able to take advantage of high CO_2 levels. The increased temperatures that accompany the higher CO_2 through the greenhouse effect will cause greater below ground respiratory processes of roots, bacteria, and other organisms (Heal 1979; Silvola 1985). Bryophytes on the soil surface are the first photosynthetic organisms to have an opportunity to use this increased CO_2. Csintalan *et al*. (1997) found a small, but significant increase in CO_2 uptake in the drought-tolerant moss ***Syntrichia ruralis*** (Figure 21) when grown in a concentration of 700 ppm compared to that at the ambient level at that time of 350 ppm.

Figure 21. ***Syntrichia ruralis*** hydrated, a species that benefits from higher levels of CO_2. Photo by Misha Ignatov, with permission.

Sonesson *et al*. (1992) were able to show that the boreal forest moss ***Hylocomium splendens*** (Figure 22-Figure 23) can adapt to higher ambient CO_2 concentrations and utilize higher CO_2. Increasing CO_2 levels to 600 ppm (compared to 350 ppm), resulted in a significant increase in its photosynthesis and growth (Sonneson *et al*. 1996). Botting and Fredeen (2006) similarly showed that CO_2 (430 ppm) was limiting to moss productivity on the sub-boreal forest floor in central British Columbia, Canada.

Figure 22. ***Hylocomium splendens*** showing its extensive cover in the boreal forest. Photo by Andrew Spink, with permission.

Figure 23. ***Hylocomium splendens***, a species that can benefit from a higher CO_2. Photo by Chmee through Creative Commons.

Role of Water in CO_2 Uptake

Both high and low water content are limiting to carbon uptake (Titus *et al*. 1983; Silvola 1991; Zotz *et al*. 1997; Schipperges & Rydin 1998; Jauhiainen & Silvola 1999; Turetsky 2003). This appears to be due to the inability of the bryophytes to use the CO_2 under these conditions. Insufficient water inhibits the enzymes in photosynthesis. When the plants are water saturated, CO_2 diffusion is slowed (Williams & Flanagan 1996; Tuittila 2000). This limitation works differently in ***Sphagnum*** from its behavior in tracheophytes (Rice 2000). In tracheophytes, water limitation lowers chloroplastic demand and increases the resistance to carbon uptake. By contrast, in ***Sphagnum*** water limitation actually decreases the resistance to carbon uptake.

CO_2-Concentrating Mechanisms

CO_2-concentrating mechanisms are familiar in tracheophytes. In tracheophytes, allowing CO_2 into the leaf through stomata means allowing water vapor out (Hanson *et al*. 2014). Even chloroplasts leak water as they allow CO_2 in because both require the same pore size.

Bryophytes have neither of these carbon-storing mechanisms and it seems that all bryophytes are C_3 plants. But it appears that at least some do have a means to concentrate CO_2 (Meyer *et al*. 2008). Like members of the green algae, many hornworts (**Anthocerotophyta**; Figure 24-Figure 25) have **pyrenoids** (protein bodies in chloroplasts of some algae and hornworts; Figure 25) associated with the chloroplasts (Hanson *et al*. 2002, 2014). These pyrenoids are able to maintain a pool of dissolved inorganic carbon (DIC) of 19-108 nmol mg^{-1} chlorophyll (Hanson *et al*. 2002).

Figure 24. ***Anthoceros agrestis*** (**Anthocerotophyta**), representing a phylum in which many members have pyrenoids. Photo by Michael Lüth, with permission.

Figure 25. Hornwort (**Anthocerotophyta**) pyrenoids – the dark circles in the cells. Photo by Chris Lobban, with permission.

Villareal and Renner (2012) remind us of the important role of enzyme Rubisco (Ribulose-1,5-Biphosphate-carboxylase-oxygenase) in carbon fixation. But Rubisco is slow compared to PEP carboxylase, which they lack. These researchers noted that many scientists have hypothesized that carbon-concentration mechanisms evolved during periods of low CO_2 to concentrate CO_2 around the enzyme. But the cladistic analyses of Villareal and Renner do not support this hypothesis; pyrenoids have come and gone in the **Anthocerotophyta** (Figure 24-Figure 25) clades multiple times and do not always coincide with low CO_2.

Raven and coworkers (1998) have suggested that some aquatic mosses might have a "CO_2 concentrating mechanism" that differs from a typical C_3 pathway. The

Anthocerotophyta use pyrenoids to accomplish CO_2 concentration, with the exception of ***Megaceros*** (Figure 26), in which there is no pyrenoid, but the mechanism in aquatic mosses is unknown. In evaluating a number of taxa, Raven's group found no evidence of C_4 or CAM pathways in bryophytes, but Salvucci and Bowes (1981) found that two aquatic taxa, ***Fontinalis antipyretica*** (Figure 27) and ***Fissidens cf. mahatonensis***, seem to be able to concentrate CO_2. What is even more interesting, it appears that it might be facultative. When they measured the CO_2 compensation point of ***F. cf mahatonensis*** in the cool Florida winter (12°C, 10 h day length), the compensation point was consistent with that expected for a C_3 pathway. However, when they measured it for the hot Florida summer (30°C, 14 h day length), the CO_2 compensation point was much lower, although not as low as in a C_4 pathway. They found similar summer/winter CO_2 compensation point relationships in all the aquatic bryophytes tested from Florida. This would be a very beneficial adaptive feature since the CO_2 is easily lost from water at high temperatures. The Section below on Aquatic CO_2 will detail what we know about obtaining CO_2 in water.

Figure 26. ***Megaceros*** (**Anthocerotophyta**), a genus that lacks pyrenoids. Photo by Juan Larrain, with permission.

Figure 27. ***Fontinalis antipyretica***, an aquatic moss that must get its CO_2 from that dissolved in water. Photo by Andrew Spink, with permission.

Bryophytes may be able to use fixed carbon compounds that are different from those used by tracheophytes. Simola (1969) experimented with ***Sphagnum nemoreum*** (syn of ***S. capillifolium***; Figure 28) in sterile culture and found that whereas **mannose** [hexose monosaccharide (6-carbon sugar) with a structure very similar to glucose] and its 6-carbon derivative, **rhamnose**, are toxic to many flowering plants, mannose promotes the growth of ***Sphagnum nemoreum***. On the other hand, other common sugars such as **arabinose**, **galactose**, **ribose**, and **xylose** are toxic to ***Sphagnum***. While the literature is not as complete as that on tracheophytes, we know that at least ***Funaria hygrometrica*** (Figure 29) can use the sugars fructose, glucose, maltose, and sucrose as internal carbon compounds (Simola 1969).

Figure 28. ***Sphagnum capillifolium*** (***nemoreum***), a species for which **mannose** promotes growth. Photo by Bernd Haynold, through Creative Commons.

Figure 29. ***Funaria hygrometrica*** with young sporophytes, a species that can use the sugars fructose, glucose, maltose, and sucrose internally. Photo by Andrew Spink, with permission.

Further evidence of differences in carbon usage by ***Sphagnum*** come from studies on carbon isotope discrimination. In three species that occupy hollows (***S. recurvum*** – Figure 30), carpets (***S. palustre*** – Figure 31), and hummocks (***S. tenerum*** – Figure 32), the delta ^{13}C values (indicating their ability to discriminate CO_2 on the basis of the ^{12}C or ^{13}C isotope) ranged from 19.0 to 27.1, but were unrelated to species (Rice 2000). Rather, they differed significantly (p<0.001) with season. In the spring, discrimination was lower (mean 22.5), with the highest

discrimination in winter (24.7). This difference was mainly due to low photosynthetic rates in winter that reduce the effects of diffusional resistance on carbon isotope discrimination. Microhabitat differences that were present in the field disappeared in the common garden and eliminated any doubt about species differences in ability to discriminate. The observed seasonal differences in carbon isotope discrimination appear to be different from those of tracheophytes, where water limitation lowers chloroplastic demand and increases resistance to C uptake. In ***Sphagnum***, water limitation lowers the chloroplastic demand but also decreases the resistance to C uptake, suggesting that the moss continues to incorporate carbon as it dries.

Figure 30. ***Sphagnum recurvum***, a species of hollows. Photo by Blanka Aguero, with permission.

Figure 31. ***Sphagnum palustre***, a species of carpets. Photo by Bernd Haynold, through Wikimedia Commons.

Carbon isotope ratios have been used for dating all sorts of biological materials, including the age of peatlands. Using carbon isotope technology, MacDonald *et al*. (1987) found that peatland mosses consistently registered carbon ages that were considerably older than those of the macrofossils of the same layer. They found ages that ranged 1400 to 6400 years older than that of their contemporary tracheophytes, and even the live ***Drepanocladus longifolius*** (Figure 33) had a ^{14}C content that was only 85% that of other present-day taxa. They explained this moss phenomenon as an isotope exchange with older sediments, the formation of CO_2 from bicarbonate by chemical processes, and the metabolic production of CO_2, presumably including bacterial decomposition, especially by mycobacteria.

Figure 32. ***Sphagnum tenerum***, a hummock species. Photo by Blanka Aguero, with permission.

Figure 33. ***Drepanocladus longifolius***, an aquatic moss that apparently derives CO_2 from old sediments. Photo by John Game, through Creative Commons.

Aquatic CO_2

In aquatic systems, CO_2 is not very soluble, is easily lost to the atmosphere at warm temperatures, and availability is *p*H-dependent, so it can indeed be limiting. The diffusion coefficient for CO_2 in water is only 10^{-4} times that found in air. The boundary layer between the moss and the flowing water reduces that availability even more. Aquatic bryophytes have high CO_2 compensation points (> 50 µl L^{-1}), higher than that of typical of C_3 tracheophytes (Bain & Proctor 1980).

Raven *et al*. (1998) indicate that stream mosses such as ***Fontinalis antipyretica*** (Figure 27) have very little CO_2 limitation because of the constantly flowing water that renews CO_2 and the reduced boundary layer resulting from water flow. On the other hand, in deep, quiet water, this species has much more difficulty getting CO_2, despite

higher concentrations, due to the increased boundary layer surrounding the moss.

Unlike many aquatic tracheophytes, mosses are apparently unable to use bicarbonates as a source of CO_2 (Bain & Proctor 1980; Allen & Spence 1981). Ruttner (1947) first demonstrated this limitation quantitatively in the mosses ***Calliergon giganteum*** (Figure 34), ***Cratoneuron filicinum*** (Figure 35), ***Eucladium verticillatum*** (Figure 36-Figure 37), ***Fissidens rufulus*** (Figure 38-Figure 39), ***Hylocomium splendens*** (Figure 22-Figure 23), and ***Neckera crispa*** (Figure 40) and the thallose liverwort ***Marchantia polymorpha*** (Figure 19), and Steeman Nielsen (1947) found the same in ***Fontinalis antipyretica*** (Figure 27), even though ***F. antipyretica*** has the enzyme carbonic anhydrase needed for the conversion of bicarbonate to CO_2. Bain and Proctor (1980) further examined mosses from alkaline habitats, yet were unable to demonstrate any use at all of bicarbonates; Allen and Spence (1981) independently determined this once more for ***Fontinalis antipyretica***.

Figure 36. ***Eucladium verticillatum*** in its wet habitat. Photo by Proyecto Musgo, through Creative Commons.

Figure 34. ***Calliergon giganteum***, a species that cannot use bicarbonate as a carbon source. Photo by Misha Ignatov, with permission.

Figure 37. ***Eucladium verticillatum***, a species that is unable to use bicarbonates as a carbon source. Photo by Barry Stewart, with permission.

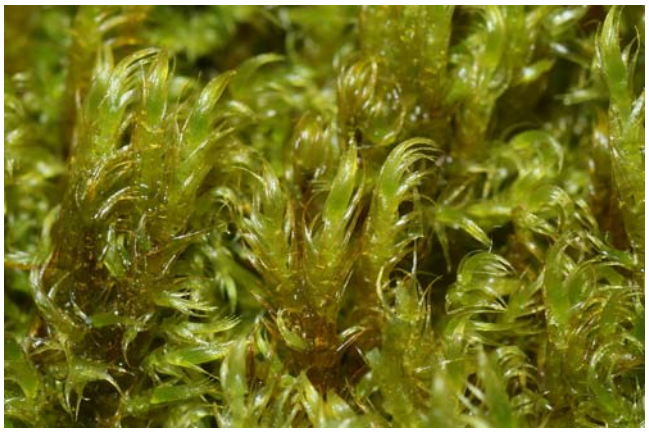

Figure 35. ***Cratoneuron filicinum***, a species that is unable to use bicarbonate as a carbon source. Photo by Barry Stewart, with permission.

Figure 38. ***Fissidens rufulus*** habitat. Photo by Michael Lüth, with permission.

Figure 39. ***Fissidens rufulus***, a species that is unable to use bicarbonate as a carbon source. Photo by Michael Lüth, with permission.

Figure 40. ***Neckera crispa***, a species that is unable to use bicarbonate as a carbon source. Photo by Barry Stewart, with permission.

Therefore, in aquatic systems at higher levels of *p*H, when the CO_2 equilibrium shifts toward bicarbonate or carbonate, CO_2 becomes unavailable. In these conditions, perhaps the CO_2 is transformed from bicarbonates in some taxa by lower *p*H values at the moss-water interface, but no experimental evidence has verified this hypothesis. Thus, the number of mosses growing in alkaline waters is limited, and it seems that many of the ones that do occur in alkaline waters are adapted to growing in the highly aerated water of waterfalls and rapids, as, for example, ***Fissidens grandifrons*** (Figure 41) (pers. obs.). Some grow in very cold glacial meltwater in which more CO_2 is soluble (Vitt *et al.* 1986). Others are restricted to the splash zone at the edge of the water, where CO_2 is trapped as the water moves through the air, as in ***Cratoneuron*** (Figure 42) species (Vitt *et al*. 1986; Glime & Vitt 1987).

When mosses live at great depths, light and temperature can be low. The ability of mosses to grow slowly reduces their need for CO_2 and light. In great depths of Lake Grane Langos, Denmark, ***Sphagnum subsecundum*** (Figure 43) and ***Drepanocladus exannulatus*** (Figure 44) grew faster in deep water than in shallow water! (Riis & Sand-Jensen 1997). Riis and Sand-Jensen concluded that this more rapid growth at greater depths was possible due to lower temperatures that permitted more CO_2 to remain dissolved, CO_2 supersaturation, and nutrient enrichment from the sediments below the thermocline.

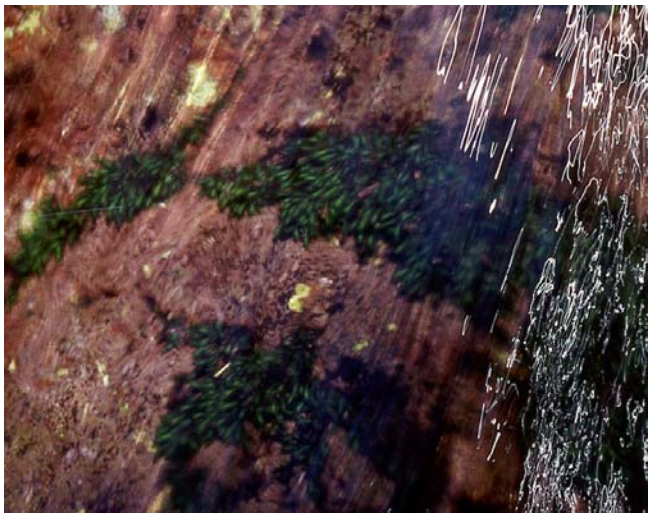

Figure 41. ***Fissidens grandifrons***, in fast-flowing water where there is more CO_2 than in quiet water. Photo by Janice Glime.

Figure 42. ***Cratoneuron commutatum*** var ***fluctuans*** at the edge of water. Photo by Michael Lüth, with permission.

Figure 43. ***Sphagnum subsecundum***, a species that takes advantage of CO_2 supersaturation in deep water. Photo by Michael Lüth, with permission.

Figure 44. ***Drepanocladus exannulatus***, a species that takes advantage of CO_2 supersaturation in deep water. Photo by Michael Lüth, with permission.

Role of *p*H

In the aquatic system, *p*H is important in determining the chemical fate of the CO_2. Under acidic conditions, it remains dissolved as CO_2. But if the water is warm, the CO_2 gas is easily lost to the atmosphere.

At circum-neutral *p*H levels, the CO_2 in water is converted to bicarbonate. At least some tracheophytes are able to use bicarbonates, but studies on use by bryophytes are ambiguous. In basic waters, carbonates are formed and cannot be used by any of the plants.

In situations of higher *p*H, CO_2 can be present for a short time as it is released from sediments or trapped in turbulent water (Lovalvo *et al*. 2010). Bryophytes could take advantage of these ephemeral concentrations before they are converted to unusable forms.

Within the cell, the enzyme **carbonic anhydrase** converts bicarbonates to CO_2 in both bryophytes and tracheophytes (Steeman Nielsen & Kristiansen 1949; Arancibia & Graham 2003). Some tracheophytes use extracellular carbonic anhydrase to convert bicarbonates to free CO_2 (Allen & Spence 1981). There is no direct evidence that bryophytes can use bicarbonates (James 1928; Ruttner 1947; Steeman Nielsen 1947; Bain & Proctor 1980; Allen & Spence 1981; Osmond *et al.* 1981; Glime & Vitt 1984; Prins & Elzenga 1989; Madsen *et al.* 1993; Ballesteros *et al*. 1998; Raven *et al.* 1998); nevertheless, some bryophytes are able to live in the *p*H range of bicarbonates. I have an unconfirmed suspicion that bryophytes may convert limited amounts of bicarbonate to CO_2 at the leaf surface, perhaps by the presence of H^+ released from exchange sites.

To further complicate the story, Farmer *et al.* (1986) found that the aquatic moss ***Fontinalis antipyretica*** (Figure 27) has no **PEP carboxylase** and uses only Rubisco for its fixation of CO_2 in photosynthesis, supporting the earlier conclusion of Steeman Nielsen (1947) that ***F. antipyretica*** cannot use bicarbonates from the water for its photosynthesis. Nevertheless, Harder (1921) had already shown that ***F. antipyretica*** increased its net assimilation from 0.01 to 0.64% when bicarbonate concentration was raised from 0.66 to 3.14 as HCO_3^-. Later, Burr (1941) likewise demonstrated greater productivity in this species in water with more bicarbonate than in that with CO_2. Steeman Nielsen and Kristiansen (1949) offered a possible explanation – that CO_2 might enter photosynthetic reactions in its hydrated form, *i.e*. as bicarbonate.

Bain and Proctor (1980) found that of the 20 aquatic species tested from a variety of habitats, all but the hornwort ***Anthoceros husnotii*** (Figure 45) with pyrenoids had *p*H compensation points in the range expected for CO_2-dependent C_3 plants. Nevertheless, many studies support the concept that all aquatic mosses are C_3 plants (Ruttner 1947; Allen & Spence 1981; Osmond *et al*. 1981; Salvucci & Bowes 1981; Raven 1991; Raven *et al*. 1987, 1994, 1998), despite some living in conditions that have CO_2 concentrations below the expected CO_2 compensation point.

Figure 45. ***Anthoceros husnotii***, a species with pyrenoids, giving it a different *p*H compensation point from that of non-hornworts. Photo from Earth.com, with permission.

Peñuelas (1985) demonstrated what appeared to be use of $NaHCO_3$ (sodium bicarbonate) by ***Fontinalis antipyretica*** (Figure 27) as a carbon source. During photosynthesis by this species, the *p*H increased to 9.6, indicating a CO_2 compensation point of 1.1 mM m^{-3} CO_2. This photosynthetic rate was higher than could be explained by CO_2 alone and when HCO_3^- levels were increased, the photosynthetic rate likewise increased, even though CO_2 levels in the water were held constant. In fact, photosynthesis continued until the *p*H reached 11.8-12.0 for ***F. antipyretica*** and 10.10 for the alkaline-tolerant ***Fissidens grandifrons*** (Figure 41). But to further confuse the issue, in a different stream, Peñuelas found that ***F. antipyretica*** could not use HCO_3^- to photosynthesize, suggesting either different physiological races or different acclimation to conditions. We know that there are genetic differences among populations of this highly variable species (Shaw & Allen 2000). Even if these genetic differences are expressed as a physiological mechanism to use bicarbonate, we still do not understand what that mechanism might be!

Bogs

Hummocks present unique habitats, and their CO_2 relations are no exception. Rydin and Clymo (1989)

described their upper parts as obtaining CO_2 from air rather than water between the ***Sphagnum*** (Figure 28) plants, depending on high CO_2 concentrations in the **acrotelm** (living layer of peat) water. In fact, they found that the CO_2 concentration in that layer was twice that in the outside atmosphere (Rydin & Clymo 1989; Smolders *et al*. 2001).

As the atmospheric levels of CO_2 rise and N deposition provides critical and often limiting nutrients, the composition of plant communities changes. This is particularly true in ***Sphagnum*** (Figure 46-Figure 51) bogs (Berendse *et al*. 2001). In this case, we expect productivity of tracheophytes to increase as they benefit from greater CO_2, often decreasing the competitiveness of the bryophytes and causing tracheophyte expansion. ***Sphagnum*** is one of the most important groups of plants to serve as a carbon sink in the Northern Hemisphere, facilitated by its slow decomposition. But when Berendse and coworkers studied the effects of raised CO_2 and N on ***Sphagnum*** and other plants in four locations in Western Europe, the elevated CO_2 had no effect on ***Sphagnum*** biomass increase. N, on the other hand, caused a decrease in ***Sphagnum*** growth due to competition.

In a bog in the Netherlands, ***Sphagnum divinum*** (previously in ***S. magellanicum***; Figure 46) benefitted from elevated CO_2 by exhibiting increased growth in height in the second and third growing seasons (Heijmans *et al*. 2001). Tracheophytes that grew close to the more rapidly growing ***S. divinum*** were affected negatively by the increased ***Sphagnum*** height. Mitchell *et al*. (2002) found that on one harvested peatland the initial colonizer was ***Polytrichum strictum*** (Figure 5). Under a treatment of added CO_2 (560 ppm), the later colonizer ***Sphagnum fallax*** (Figure 47) was able to successfully compete with the ***P. strictum***.

Figure 46. ***Sphagnum divinum***, a species that increases in height growth when living in higher CO_2 levels. Photo by David Holyoak, with permission.

Van der Heijden *et al*. (2000a) found that not all ***Sphagnum*** had the same response to elevated CO_2. ***Sphagnum papillosum*** (Figure 48), an oligo-mesotrophic species, benefitted in growth from elevated CO_2 (720 ppm). On the other hand, the ombrotrophic ***S. balticum*** (Figure 49) received no growth benefit, despite elevated sugar in stems and capitula in both species. Unlike many of the studies discussed in subchapter 8-1, in this case additional N along with elevated CO_2 benefitted ***S. papillosum***, but it had no effect on ***S. balticum***. Doubling CO_2 without N addition cause lower N levels in both species.

Figure 47. ***Sphagnum fallax***, a species that competes better in an atmosphere with higher CO_2. Photo by Michael Lüth, with permission.

Figure 48. ***Sphagnum papillosum*** with sundew. Photo by Michael Lüth.

Figure 49. ***Sphagnum balticum***, a species that does not benefit when additional N accompanies elevated CO_2. Photo by Michael Lüth, with permission.

The response of ***Sphagnum fallax*** (Figure 50) may explain the elevated sugars (van der Heijden *et al*. 2000b).

Initially, elevated CO_2 stimulated photosynthesis, but after 3 days of exposure it was down-regulated to pre-elevation values. However, the elevated CO_2 continued to cause reduced dark respiration. At the same time there was a continuous increase in soluble sugar in the capitula. Doubling the CO_2 caused a decrease of N in the capitula, but not in the stems. This N reduction was coupled with a decrease in amino acids but did not affect soluble protein levels, causing a shift in N partitioning.

Figure 50. ***Sphagnum fallax***, a species that stores elevated sugars when the CO_2 is elevated. Photo by Jan-Peter Frahm, with permission.

Not all ***Sphagnum*** grows in hummocks. ***Sphagnum cuspidatum*** (Figure 51) grows primarily submerged. When it was subjected to added CO_2 for 12 weeks, only the highest CO_2 concentration in the water caused increased growth in length and biomass (Paffen & Roelefs 1991).

Figure 51. ***Sphagnum cuspidatum***, a submerged moss that is indifferent to added CO_2 until the levels are quite high. Photo by Michael Lüth, with permission.

In addition, some bryophytes may be able to tap into a source of carbon we usually don't consider in bryophytes. Rydin and Clymo (1989) have demonstrated that at least in ***Sphagnum*** the fixed carbon can be transported within the stem. Using ^{14}C labelling on ***Sphagnum papillosum*** (Figure 48), they found almost the entire alcohol-soluble fraction moved from older parts to the apex, with little transfer of the insoluble fraction.

Methane

Methane (CH_4) is the product of **anaerobic** (no oxygen) bacterial breakdown. In several bogs of Canada, the highest emissions occurred in raised-bog and patterned-poor-fen pools where the peat is degrading (Bubier 1995). Methane is much more effective as a greenhouse gas compared to CO_2. And wetlands are the largest natural source for methane. Submerged ***Sphagnum*** (Figure 51) uses methane that is converted through symbiosis with partly endophytic **methanotrophic** (able to gain carbon from methane) bacteria, leading to highly effective *in situ* methane recycling (Raghoebarsing *et al*. 2005). These bacteria live in the hyaline cells and on leaves where they convert the methane to CO_2. This conversion provides 10-15% of the carbon source for these ***Sphagnum*** species.

CO_2 and Desiccation Tolerance

Syntrichia ruralis (Figure 21) is a common desiccation-tolerant moss. When subjected to elevated CO_2 it showed increased net CO_2 uptake in high CO_2 conditions by more than 30% (Tuba *et al* 1998). Both desiccation-tolerant and non-tolerant plants, bryophytes included, show initial positive responses of photosynthesis to elevated CO_2, but both groups exhibit reduced or even reversed photosynthetic rates in the longer term (Tuba *et al*. 1999). This slightly later study implies that increased CO_2 levels will have little advantage for either group of bryophytes.

Translocation

Rydin and Clymo (1989) found that carbon is transported within ***Sphagnum*** (Figure 50) plants. This could provide a physiological mechanism that moves older carbon compounds from deeper parts of the peatlands upward. This could dilute the ^{14}C pool within the living plant and change both the location and the proportions of ^{12}C, ^{13}C, and ^{14}C. If ***Sphagnum*** is able to take in carbon from deep sediments and move it upward in the water column, this would result in false readings for carbon dating. Might the moss be preferentially moving ^{12}C upward from older peat and thus reducing its proportion of ^{14}C? If so, we need to re-evaluate our methods for dating peat.

By contrast, it appears that mosses like ***Grimmia*** (Figure 52) that receive their water from above can actually move carbon as photosynthate from the tip of the plant to the base and even to underground parts, much as we would find in a tree (Alpert 1989). Lacking any specialized conducting cells, this moss presents a puzzle as to its mechanism of movement, although as we shall see later in this chapter, it uses the source-sink principle used by tracheophytes.

Figure 52. ***Grimmia caespiticia***, a moss that moves photosynthetic carbon from the tip to the base. Photo by Michael Lüth, with permission.

Importance of Bryophytes in C Cycling

Porada *et al*. (2013) estimated that the terrestrial net uptake of carbon by bryophytes and lichens is 0.34 to 3.3 Gt yr^{-1} (gigatons). This appears to be small until you consider bogs and polar habitats where bryophytes dominate the vegetation. In those locations, the bryophytes are significant carbon sinks.

Turetsky (2003) noted that bryophyte growth and metabolism have a direct influence on the carbon flux into the ecosystem. She found that annual accumulations of C in the bryophytes are a better measure for understanding the carbon cycle. Growth of such species as those of ***Sphagnum*** (Figure 46-Figure 52) can range from ~19-1,656 g m^{-2} yr^{-1}, with carbon comprising about 48% of this biomass. Feather mosses in the boreal forest have a net primary productivity ranging 24-80 g C m^{-2} yr^{-1}. In the Antarctic, ***Polytrichum juniperinum*** (Figure 53) has a net primary productivity of 213-350 g m^{-2} yr^{-1}, whereas ***Chorisodontium aciphyllum*** (Figure 54) living there has 162 g m^{-2} yr^{-1} (Fenton 1980). Nevertheless, Turetsky noted with surprise that the bryophyte net primary productivity (NPP) of polar, boreal, and temperate regions were comparable.

Figure 53. ***Polytrichum juniperinum***, a species that has a net primary productivity of 213-350 g m^{-2} yr^{-1} in the Antarctic. Photo by Bob Klips, with permission.

Figure 54. ***Chorisodontium aciphyllum***, a species that has a net primary productivity of 162 g m^{-2} yr^{-1} in the Antarctic. Photo by Matt Amesbury, through Creative Commons.

Flushing contributes loss of carbon from plant and litter layers, particularly following desiccation (Turetsky 2003). Soluble organic compounds are lost as membranes become distended and cannot continue to retain the soluble contents. During rewetting, these leaked compounds can become leached to the environment (Proctor 1982; Wilson & Coxson 1999). Mats of the boreal/alpine moss ***Hylocomium splendens*** (Figure 22-Figure 23) released a pulse of organic carbon equivalent to -15 kg ha^{-1} following rain events (Wilson & Coxson 1999). The soluble C from living ***H. splendens*** was 23-75% of that released. Tropical epiphytes can release equivalent to 122 kg ha^{-1} yr^{-1} of soluble sugars (Coxson *et al*. 1992).

The carbohydrate leachates from the boreal forest moss ***Pleurozium schreberi*** (Figure 55) can support the growth of mycorrhizal fungi and can even reach ***Pinus contorta*** (Figure 56) through this pathway (Carleton & Read 1991). Similarly, soluble carbohydrates can penetrate to deeper layers of peatlands and wetlands where they are taken up by microbes (Charman *et al*. 1999; Chasar *et al*. 2000). They further influence this activity by providing suitable habitat for invertebrates (Gersen 1982; Merrifield & Ingham 1998) that break up the bryophytes into smaller pieces that provide more surface area for the microbes to colonize. Microfungi associated with the bryophytes can decompose organic carbon (Tsuneda *et al*. 2001; Thormann *et al*. 2002). Any of this released carbon can also be exported to streams and lakes (Schindler *et al*. 1997; Carpenter *et al*. 1998; Elder *et al*. 2000).

Figure 55. ***Pleurozium schreberi***, a moss species in which carbon leachates support the mycorrhizal fungi of ***Pinus contorta***. Photo by Rob Routledge, through Creative Commons.

Figure 56. ***Pinus contorta***, a species that can benefit from mycorrhizae that use carbon leachates from mosses. Photo by Walter Siegmund, through Creative Commons.

The bryophytes have physical effects on the return of carbon from other plants. They can reduce soil temperature and increase soil moisture, thus affecting the rate of decay and carbon cycling (Van Cleve *et al*. 1983; Sveinbjornsson & Oechel 1992; Eckstein 2000). Their external capillary action enhances the possibilities for decomposition (Turetsky 2003).

Climate Change – an Antarctic Problem

Bryophytes in the Antarctic must contend with large temperature fluctuations within a single day. Pannewitz *et al*. (2005) note the importance of understanding the effects of climate change on the bryophyte component in order to predict the effects of climate change on vegetation there. Their results from variations in temperature, light, moisture content, and CO_2 suggested that it would be very difficult to predict the effects of climate change on these communities. Increases in temperature are likely to cause increases in CO_2 as long-standing dead portions begin to decay. They found that there was a large response to increases in CO_2 by two of the three bryophytes they tested [***Bryum pseudotriquetrum*** (Figure 57), ***B. subrotundifolium*** (Figure 58)], with increasing temperatures causing a greater response. CO_2 saturation wasn't reached at the 20ºC temperature tested. ***Bryum pseudotriquetrum*** exhibited no saturation up to 2000 ppm CO_2 at 20ºC. ***Bryum subrotundifolium***, however, became saturated above 1000 ppm. Thus CO_2 was limiting for both species at the ambient CO_2 of 360 ppm.

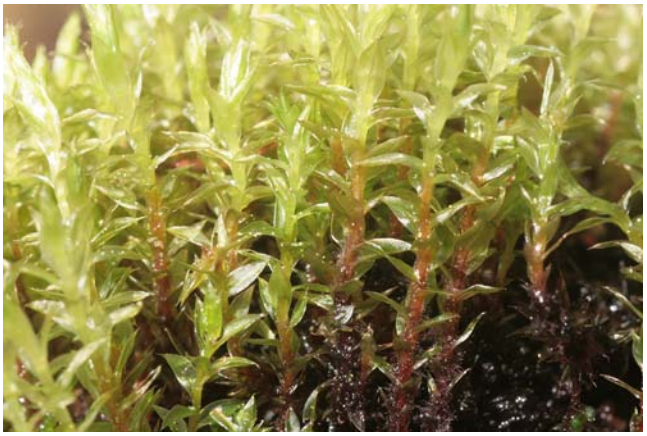

Figure 57. ***Bryum pseudotriquetrum***, a species whose CO_2 saturation is above 2000 ppm. Photo by Hermann Schachner, through Creative Commons.

Figure 58. ***Bryum subrotundifolium***, an Antarctic bryophyte in which CO_2 saturation is reached when CO_2 exceeds 1000 ppm. Photo by Rod Seppelt, with permission.

On the other hand, ***Hylocomium splendens*** (Figure 22-Figure 23) (Sonesson *et al*. 1996) and Arctic tracheophytes (Oechel et al. 1997) demonstrated that such enhancement of photosynthesis could be short-lived. This short-term enhancement could be the result of rapidly reaching nutrient limitation (Oechel & Billings 1992). However, in the Antarctic nutrients are rarely limiting (Kappen & Schroeter 2002), at least in part due to the rich guana deposits (Green *et al*. 2000a, b). Nevertheless, Pannewitz and coworkers (2000) concluded that increased CO_2 in the atmosphere would probably not have long-term effects because the ambient levels might already be high in the Antarctic. On the other hand, I would expect that increased temperatures there would increase the very slow rate of decomposition, thus potentially causing great increases of CO_2 for the bryophytes at the ground level where they live.

Bryophytes and tracheophytes might respond differently to CO_2 and climate change. Green *et al*. (1998) found that the relationships between the electron transfer rate (ETR) and CO_2 in photosynthesis of bryophytes differs from that found in tracheophytes. Dark respiration responds strongly to cause substantial changes in CO_2 exchange rates. In Antarctic populations of ***Bryum argenteum***, there is a strong linear relationship between gross photosynthesis and the electron transfer rate, an unusual response exhibited by the C_3 bryophytes compared to that of C_3 tracheophytes. This relationship varied with temperature; Green and coworkers suggested that light suppression of dark respiration might be involved.

Summary

The early atmosphere had considerably more CO_2 than the current one. However, in the last 60 years, CO_2 concentrations have risen from 315 to 404 ppm in the atmosphere.

Soils release CO_2 through respiration by bacteria, fungi, and other soil organisms. Bryophytes are able to trap much of this CO_2 before it reaches the atmosphere.

Thallose liverworts may have a spongy interior with pores to facilitate exposure of internal photosynthetic cells to CO_2. Mosses are C_3 plants that benefit from high CO_2 concentrations and cool to moderate temperatures (up to 25ºC). They have difficulty obtaining CO_2 when they are wet and the presence of cuticular waxes in species such as ***Polytrichum*** spp. and ***Saelania glaucescens*** facilitates the absorption of CO_2 by repelling water. ***Sphagnum*** keeps its photosynthetic cells moist on 2-3 sides while permitting 1-2 sides to be exposed to the atmosphere.

Hornworts may have pyrenoids that concentrate CO_2 around the enzyme Rubisco, facilitating photosynthesis. Some aquatic mosses may be able to concentrate CO_2 and this may be facultative, being enhanced on hot days. In acid conditions they use CO_2 dissolved in the water, but some evidence suggests that in the mid-*p*H range some species may be able to use bicarbonates.

Some bryophytes can use amino acids. At least some ***Sphagnum*** species use methane as a carbon source. And some species can move C up or down within the plant.

Bryophytes, especially in wet habitats, may be able to move water up from sediments, taking advantage of decompositional carbon. Others may move photosynthate from actively growing apical parts to lower parts for storage.

Bryophytes may serve as carbon sinks, especially in peatlands.

Acknowledgments

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NUTRIENT RELATIONS: NITROGEN

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Figure 1. ***Physcomitrella patens*** growing on previously flooded soil. Note the nitrogen-fixing blue-green bacterium, ***Nostoc***, at the **arrow**. Photo by Michael Lüth, with permission.

N Forms

Nitrogen is available in many forms. The most abundant of these, N_2 gas, cannot be used by plants or animals and must be converted by **Cyanobacteria** or bacteria before plants can use it. Animals can only obtain it by eating other organisms that have already placed the N into amino acids. Other forms of N that plants can absorb include **ammonium** (NH_4^+), **nitrite** (NO_2^-), **nitrate** (NO_3^-), and organic forms such as **amino acids** and **urea**. As we shall soon see, not all bryophytes have the same ability to use these forms and some are toxic to most taxa.

Nitrate and Ammonium

Plants, including bryophytes, can take in and use both NO_3^- (nitrate) and NH_4^+ (ammonium). The form of nitrogen needed by bryophytes varies with species and habitat. Aquatic higher plants use nitrogen in three inorganic forms: NO_2^- (nitrite) (Schwoerbel & Tillmanns 1964, 1977), NO_3^-, NH_4^+ (Schwoerbel & Tillmanns 1972; Rudolph & Voigt 1986). Bryophytes usually absorb NH_4^+ more easily than they absorb NO_3^- (Schwoerbel & Tillmanns 1974; Simola 1975; Miyazaki & Satake 1985; Schuurkes *et al*. 1986). Cation vs anion exchange sites may determine the use of nitrate (anion) vs ammonium (cation), causing ***Sphagnum*** to have a strong preference for ammonium because of its extensive cation exchange sites (Wanek & Pörtl 2008).

Vanderpoorten (2000) reported that NH_4^+ N is one of the best factors to explain differences in aquatic ***Amblystegium*** (Figure 2) distributions in river systems. Frahm (1975) found that the brook moss ***Fontinalis antipyretica*** var. ***gigantea*** (Figure 3) had a low tolerance for NH_4^+, but Schwoerbel and Tillmanns (1974, 1977) found conflicting evidence showing that this species uses NO_3^- and NH_4^+, with NH_4^+ being taken up first if provided together with NO_3^-. In fact, it is unable to uptake NO_3^- in the dark (Schwoerbel & Tillmanns 1974). To show the complexity of the N relationships, growth on a nitrate medium requires the bryophytes to convert it to ammonium ions before they can assimilate it (Brown 1982). It is possible that various strains have developed within species that have different tolerance levels for some of their nutrients.

Figure 2. ***Amblystegium fluviatile***, an aquatic moss sensitive to ammonium levels. Photo by Michael Lüth, with permission.

Figure 3. ***Fontinalis antipyretica*** var. ***gigantea*** dry, a moss with mixed responses to ammonium as its nitrogen source. Photo by Janice Glime.

Physiology of Nitrate and Ammonium

Assuming that bryophytes operate as do **tracheophytes** (lignified vascular plants), NO_3^-, once in the plant, is converted to NH_4^+. In leaves, the intermediate product, NO_2^-, is reduced by **nitrite reductase** (enzyme that facilitates addition of hydrogen and loss of oxygen from NO_2^- during photosynthetic electron transport process). No intermediate product is released and the final product is NH_4^+. Since photosynthesis provides the **NADH** (nicotinamide adenine dinucleotide + H, the active coenzyme form of vitamin B_3) and **ferredoxin** needed for conversion of nitrogen oxides to NH_4^+, the conversion process is enhanced by the same things that enhance photosynthesis – high light and warm temperatures (Salisbury & Ross 1978). Thus, more ammonium is produced.

		nitrite reductase		
NO_3^-	→	**NO_2^-**	→	**NH_4^+**
nitrate		nitrite		ammonium

Morphological Anomalies

Brown (1982) suggested that the *p*H or alkalinity affects availability of N for plants, with NO_3^- being more available in neutral or alkaline soils and NH_4^+ in acidic soils and water. But NH_4^+ is usually toxic to plants in any appreciable quantity. Sironval (1947) found that NH_4^+ ions caused degeneration of the **caulonema** (part of protonema from which buds arise) of ***Funaria hygrometrica*** (Figure 4) and Southorn (1977) found they caused morphological abnormalities in the same species. Killian (1923) likewise found morphological abnormalities in the leafy liverwort ***Scapania*** (Figure 5). On the other hand, Burkholder (1959) found that cultured bryophytes did equally well on both NO_3^- and NH_4^+ salts.

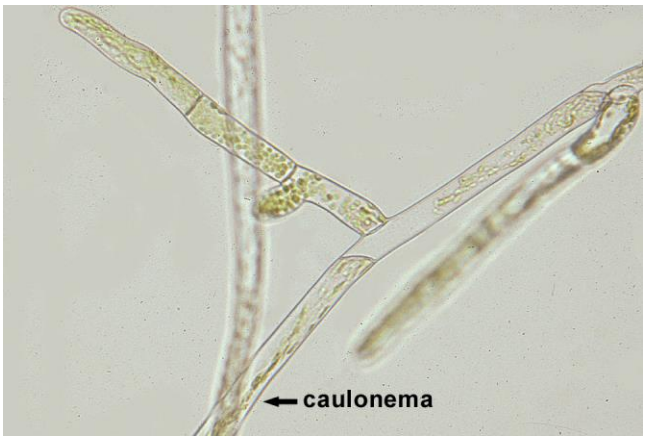

Figure 4. ***Funaria hygrometrica*** protonema showing caulonema, a stage that seems to degenerate when ammonium ions are added. Photo by Janice Glime.

Figure 5. ***Scapania undulata***, an aquatic leafy liverwort that exhibits morphological abnormalities when ammonium concentrations are too high. Photo by David T. Holyoak, with permission.

An interesting consequence of *p*H differences was suggested by Machlis (1962). In ***Sphaerocarpos texanus*** (Figure 6), male plants are smaller than females in the field. Machlis attributed this to the ability of male plants to absorb NH_4^+ ions more readily than females, causing them to have a lower *p*H, which could suppress growth. He supported this suggestion by growing the plants on potassium, which caused no *p*H change, and likewise no reduction in the size of male plants.

Figure 6. ***Sphaerocarpos texanus***, a thallose liverwort in which male plants absorb NH_4^+ ions more readily than do females, causing males to have a lower *p*H, possibly accounting for growth suppression and smaller males. Photo by Martin Hutten, with permission.

Benefit or Detriment?

In a study designed to determine the effects of various forms of N on bryophyte function, Alghamdi (2003) studied the popular, fast-growing aquarium moss ***Taxiphyllum barbieri*** (Java moss, Figure 7). He found that the benefit to the moss depends on what parameter you measure (Figure 8). For example, dry biomass increase was greatest in high NO_3^- concentrations (30 mg L^{-1} N), whereas the greatest increase in length occurred in high NH_4^+ concentrations (30 mg L^{-1} N). This difference resulted in the least biomass increase per stem length in high NH_4^+ concentrations, despite the relatively high increase in length in that treatment. The overall appearance of the mosses in high NH_4^+, then, was to appear long and thin compared to those in other treatments, but not dissimilar to the plants in the control (standard nutrient solution but with no N source). Based on the lower growth in the NH_4NO_3 media, Alghamdi reasoned that in the presence of NH_4^+, the NO_3^- became unusable because of the inhibition of nitrate reductase by NH_4^+ (see Syrett & Morris 1963; Orebamjo & Stewart 1975). At the same time, the lower concentration of NH_4^+ (15 mg L^{-1} N) in combination compared to NH_4^+ alone (30 mg L^{-1} N) reduced the growth. This relationship was consistent with much greater growth at 30 mg L^{-1} N than at 10 mg L^{-1} N as NH_4^+ (Figure 8).

Figure 7. ***Taxiphyllum barbieri***, an aquarium moss subjected to high ammonia concentrations from fish waste products. Photo by Tan Sze Wei, Aquamoss website <www.aquamoss.net>, with permission.

NO_2^- caused only modest improvements in biomass and length over N-free controls (Figure 8), but caused considerable increase in chlorophyll *a* (Alghamdi 2003; Figure 10). The chlorophyll *a*:*b* ratio was highest in the high NO_3^- treatment, due to mosses in that treatment having the least chlorophyll *b* per biomass of moss, a concentration even lower than that of controls (Figure 10). In fact, effects of inorganic N form on chlorophyll *b* resulted in either no improvement over N-free controls, or depressed levels of chlorophyll *b*. However, chlorophyll *a* was higher in nearly all nitrogen treatments than in controls. Baxter *et al*. (1992) found a similar but slight decrease in total chlorophyll concentration in ***Sphagnum cuspidatum*** (Figure 9), typically a submersed species, with increasing levels of NH_4^+, but in Alghamdi's experiments, ***Taxiphyllum barbieri*** (Figure 7) actually had total chlorophyll increase, although not statistically significant, with increase from 1 to 30 mg L^{-1} N as NH_4^+ (Figure 10).

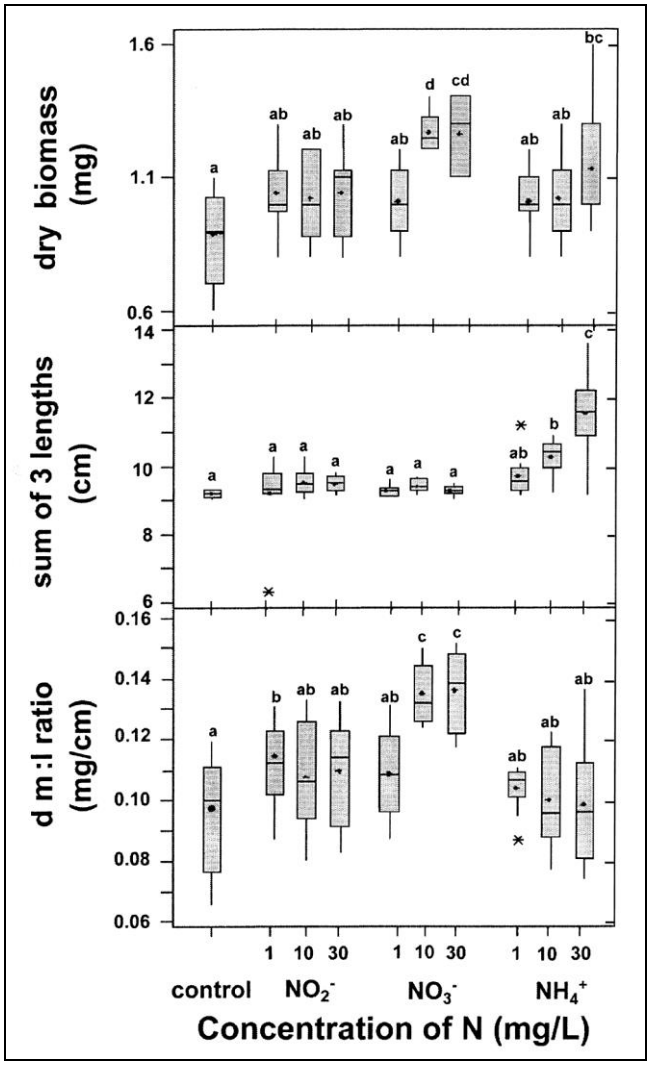

Figure 8. Effects of various forms of inorganic N (control = no N) on growth in length (l) and biomass (d m) of ***Taxiphyllum barbieri***. Box mean (dot) and median (horizontal line); bottom of box is first quartile and top is third quartile. Whiskers represent lowest and highest observations still inside region defined by lower limit Q1-1.5 (Q3-Q1) and upper limit Q3+1.5 (Q3-Q1); *represents outliers that extend beyond whiskers; n=15 sets of 3 stems. Means with same letters are not significantly different from each other (DNMRT, $\alpha = 0.05$). Based on Alghamdi 2003.

Figure 9. ***Sphagnum cuspidatum***, an aquatic species that has a decrease in chlorophyll with an increase in ammonium ions. Photo by Jonathan Sleath, with permission.

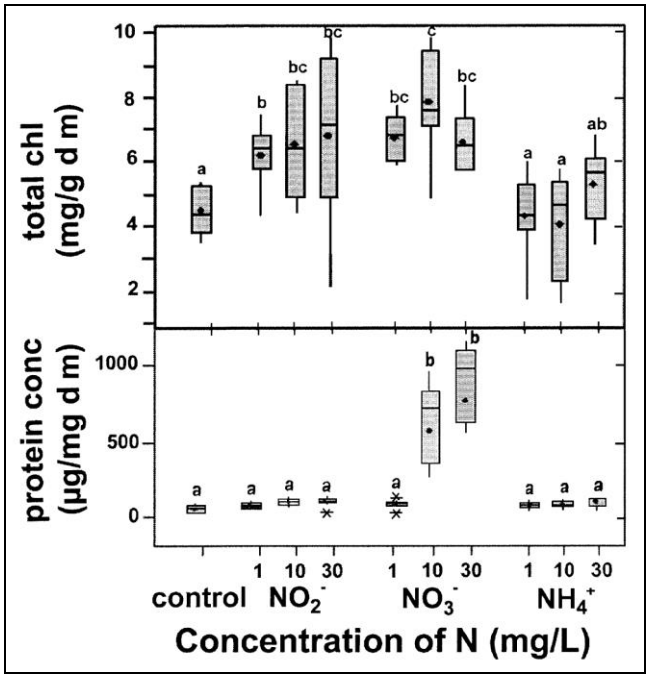

Figure 10. Effects of various forms of inorganic N (control = no N, NO_2^- = nitrite, NO_3^- = nitrate, NH_4^+ = ammonium) on chlorophyll *a* and protein concentrations of ***Taxiphyllum barbieri***. Notation as in Figure 8; n = 15 sets of 3 stems. Based on Alghamdi 2003.

Protein concentrations in ***Taxiphyllum barbieri*** (Figure 7) showed a very different picture from other measurements, with little difference among treatments except at 10 and 30 mg L^{-1} NO_3^- (Figure 10; Alghamdi 2003). In ***Sphagnum cuspidatum*** (Figure 9) Baxter *et al*. (1992) found the addition of NH_4^+ (as NH_4Cl) generally caused an increase in amino acids, at least within the first 15 days, in both locations studied, with arginine increasing the most at the unpolluted site and actually decreasing at the NH_4^+-polluted site. The latter study suggests that ***Sphagnum cuspidatum*** may acclimate to a higher level of NH_4^+ in a way that it eventually requires higher levels than populations not continuously exposed to such high levels. Clearly the uses of the various forms of N in bryophytes are complex and one cannot give a simple answer as to which form is best.

Species Differences

In ***Sphagnum*** (Figure 18, Figure 33-Figure 23), differences exist among the species. ***S. flexuosum*** (Figure 11) is apparently unable to utilize NO_3^- (Schuurkes *et al*. 1986), and Touffet (1971) found that NO_3^- actually reduced the growth of ***Sphagnum*** and was less effectively utilized than NH_4^+ when it was the only N resource. Nevertheless, in many ***Sphagnum*** species nitrate reductase, an inducible enzyme (Deising 1987), permits use of NO_3^-. High levels of NH_4^+ inhibit nitrate reductase, and hence reduce growth, by inhibiting NO_3^- uptake (Rudolph *et al*. 1987). Rudolph and Voigt (1986) demonstrated that 322 µM was a favorable concentration of NO_3^- in ***S. magellanicum*** (Figure 12), whereas at 225 µM NH_4^+ the chlorophyll content decreased. At 600 µM NH_4^+, nitrate reductase activity was reduced by as much as 20%. These factors most likely limit mosses in particular habitats.

Figure 11. ***Sphagnum flexuosum***, a species that is unable to use nitrate. Photo by Michael Lüth, with permission.

Figure 12. ***Sphagnum magellanicum***, a species that benefits from added nitrate. Photo by Janice Glime.

Growth is promoted by added nitrate and ammonium in ***Sphagnum fallax*** (Figure 13), a species of hollows and lawns (Twenhöven 1992). ***Sphagnum magellanicum*** (Figure 12), typically a hummock species, exhibits no benefit with the same treatments. In fact, both species on hummocks exhibit reduced growth in added nitrate and

ammonium. On the other hand, growth is reduced in levels that are lower than the levels resulting from the present atmospheric inputs, suggesting that these bogs were originally N limited. This changes the competitive status of these two species. ***Sphagnum fallax*** is typically competitive, whereas ***S. magellanicum*** is stress tolerant. When N deposition is elevated in previously N-limited conditions, ***S. fallax*** is able to outcompete ***S. magellanicum***.

In the sub-Antarctic on Marion Island, increased NH_4^+ caused an increase in CO_2 assimilation for four moss species, but NO_3^- had a greater effect. Cl^- added with the NH_4^+ may have caused the lesser increase with NH_4^+ additions (Smith 1993). These increases are significant in this habitat with such low soil nutrient levels.

Figure 13. ***Sphagnum fallax***, a competitive species, with capsules. Photo by David T. Holyoak, with permission.

Long Term Effects

The negative effects of elevated nitrate and ammonia in fens are demonstrated in Dutch fens (Paulissen *et al*. 2004). These researchers found that ***Scorpidium scorpioides*** (Figure 14) and other brown mosses declined, whereas ***Sphagnum squarrosum*** (Figure 15) and ***Polytrichum commune*** (Figure 16-Figure 17) increased, lowering the *p*H. ***Scorpidium scorpioides*** did best on nitrate; ammonium nitrate decreased its growth somewhat, and ammonium itself was very toxic. ***Sphagnum squarrosum*** and ***Polytrichum commune*** experienced little affect from the N treatment.

Figure 14. ***Scorpidium scorpioides***, a species that declines when nitrates and ammonia are supplemented. Photo by Jan-Peter Frahm, with permission.

Figure 15. ***Sphagnum squarrosum***, a species that declines when nitrates and ammonia are supplemented. Photo by Janice Glime.

Figure 16. ***Polytrichum commune***, a species that increases when fertilized with nitrate and ammonium. Photo by Michael Lüth, with permission.

Figure 17. ***Polytrichum commune***, with capsules. This is a bog competitor that benefits from added nitrate and ammonium. Photo by Michael Lüth, with permission.

Organic Nitrogen

Most agricultural plants seem to absorb their nitrogen in the form of NH_4^+ or NO_3^-, but it seems that bryophytes have more options. ***Sphagnum*** (Figure 18, Figure 23, Figure 33) is able to use urea (along with phosphate) in the

Alaskan wetlands, resulting in an increase in biomass compared to controls (Sanville 1988). In nature, amino acids likewise can be abundant, present as breakdown products of plant and animal wastes, litter, and corpses. Yet few culture studies or field tracer studies have included these organic forms until recently. Is it possible that bryophytes can use this organic N as their primary source? If so, they may benefit from organic leachates in early stages of litter decomposition of a soil environment.

In bogs and poor fens, NH_4^+ seems to be the predominant form of available N (Rosswall & Granhall 1980). NO_3^- is often lost through denitrification (Hemond 1983). Not surprisingly, some studies show that ***Sphagnum*** seems to require most of its inorganic N as NH_4^+ (Schuurkes *et al*. 1986). But Simola (1975, 1979) showed that ***Sphagnum nemoreum*** (=***S. capillifolium***; Figure 18) and ***S. fimbriatum*** (Figure 19-Figure 20) both could use amino acids. Simola (1975) examined the effects of common peat amino acids – those most likely to be available to the ***Sphagnum***. For ***Sphagnum nemoreum*** NH_4NO_3 proved to be the best N source, with the ammonium ion being used more effectively than nitrate. The amino acids arginine and alanine as the only N source proved to provide satisfactory growth. On the other hand, this species made no use of the amino acids leucine, lysine, isoleucine, or methionine. Lysine actually inhibited growth. This species is more tolerant to organic nitrogen than are tracheophytes, especially of the non-proteinogenic amino acid hydroxyproline. More recently, McKane (1993), using tracer studies, found that for ***Sphagnum***, ***Aulacomnium palustre*** (Figure 21), and ***Hylocomium splendens*** (Figure 22), the amino acid **glycine** was actually the preferred form of nitrogen over NH_4^+ and NO_3^-.

Figure 18. ***Sphagnum nemoreum***, a species that can use amino acids as a nitrogen source. Photo by Michael Lüth, with permission.

It appears that in Arctic ecosystems, organic nitrogen (amino acids, especially glycine) may actually be the preferred source of N for some bryophytes, including ***Sphagnum rubellum*** (Figure 23) (Kielland 1997). Even amino acids with higher molecular weights, such as **aspartate** and **glutamate**, can be absorbed at higher rates than inorganic N. Kielland suggested that the high capacity for absorbing amino acids might be an adaptation to the low inorganic N availability in the Arctic.

Figure 19. ***Sphagnum fimbriatum*** habitat, a species that can use amino acids, most likely available from decomposing leaf litter in its habitat. Photo by Dick Haaksma, with permission.

Figure 20. ***Sphagnum fimbriatum***, a species that can use amino acids as a nitrogen source. Photo by Michael Lüth, with permission.

Figure 21. ***Aulacomnium palustre***, a species that "prefers" glycine over ammonium and nitrate. Photo by Janice Glime.

Figure 22. ***Hylocomium splendens***, a species that "prefers" glycine over ammonium and nitrate. Photo by Michael Lüth, with permission.

Figure 23. ***Sphagnum rubellum***, a species that exhibited decreased growth when receiving elevated ammonium nitrate. Photo by Michael Lüth, with permission.

The Arctic is not the only place where amino acids can provide N for bryophytes. ***Hylocomium splendens*** (Figure 22) in the boreal forest can utilize glycine (Forsum *et al*. 2006). When ammonium, nitrate, and glycine were applied in spray solutions similar to the concentrations in precipitation, this moss took up the greatest labelled N compared to other concentrations. This included a 17% contribution from amino acid N.

Even floodplain bryophytes can use amino acids. Schuler *et al*. (1955) found that in culture the thallose liverwort ***Sphaerocarpos texanus*** (Figure 6) grew more typically on a mix of amino acids than it did on NH_4NO_3 alone.

Burkholder (1959) examined the effects of 20 amino acids (0.0001 M AA to 0.0016 M AA) with and without the addition of NH_4NO_3 on the color and growth of ***Atrichum undulatum*** (Figure 24). **Glycine**, **L-cystine**, **L-cysteine**, and **L-tyrosine** were the only treatments with amino acids alone in which the moss retained its green color. Others were yellow-green, brown-green, or brown (in DL-serine and DL-tryptophan). When grown in combination of each of these 20 amino acids with NH_4NO_3, plants in all treatments grew more than in any of the amino acids alone except in the highest concentration (0.0016 M) of **DL-tryptophan**. Growth was generally greatest in the lower concentration of amino acid (0.0001 M) plus NH_4NO_3.

Figure 24. ***Atrichum undulatum*** with capsules, a species that is able to use some amino acids, but not others. Photo by Andrew Hodgson, with permission.

The report of amino acid utilization by the aquatic Java moss (***Taxiphyllum barbieri***, Figure 7) (Alghamdi 2003), seems unusual among the aquatic mosses and may somehow relate to its ability to live in aquaria and tropical streams where most other bryophytes seem unable to survive. Could this in some way relate to the higher annual temperatures of its tropical habitat? Or is the lack of evidence for amino acid usage in many other species simply a lack of testing?

Alghamdi (2003) chose common soil water-soluble amino acids (**glycine**, **methionine**, **serine**, **arginine**, and **alanine**) to compare their effects on growth, branching, chlorophyll, and protein on the aquatic moss ***Taxiphyllum barbieri*** (Figure 7). He found that four of these amino acids induced branching, relative to the controls, but no branching appeared in any of the **methionine** treatments (Figure 25).

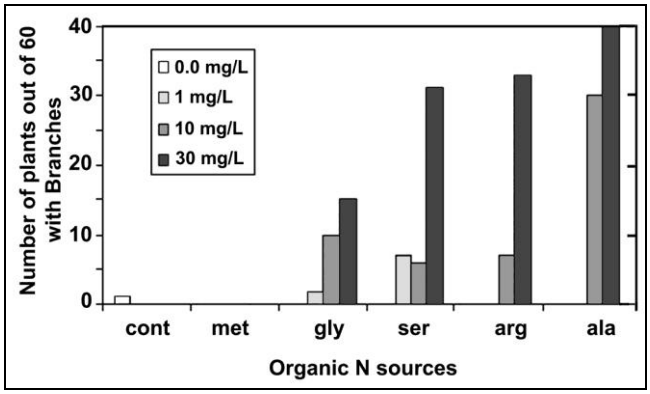

Figure 25. Effects of water soluble amino acids on number of branches in the Java moss, ***Taxiphyllum barbieri***. **cont** = control, **gly** = glycine, **meth** = methionine, **ser** = serine, **arg** = arginine, **ala** = alanine. From Alghamdi 2003.

Methionine proved to be inhibitory to growth in length whereas **serine** caused an increase in both dry biomass and length relative to controls (Figure 26;

Alghamdi 2003). **Arginine** as the only N source at 1, 10, and 30 mg L^{-1} caused a striking increase in the biomass and ratio of dry biomass to length, but maintained a length somewhat less than that of the N-free controls (Figure 26). This resulted in unusually short, wide plants, combined with high protein concentrations but below normal chlorophyll concentrations at the lowest level applied (1 mg L^{-1}; Figure 27).

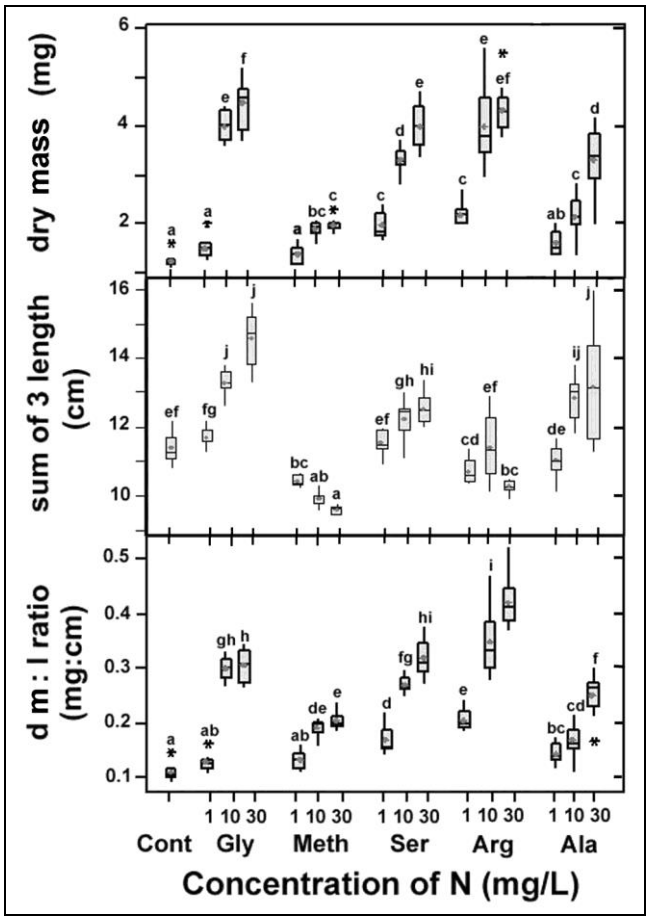

Figure 26. Effect of water soluble amino acids on the biomass, length, and robustness (wt:length) of the Java moss, ***Taxiphyllum barbieri***. Cont = control, Gly = glycine, Meth = methionine, Ser = serine, Arg = arginine, Ala = alanine. Length and biomass represent sum of 3 stems; n = 10 sets of 3 stems. Notation as in Figure 8. Based on Alghamdi 2003.

Methionine likewise caused an increase in biomass and decrease in length growth with concentration increase (1, 10, 30 mg L^{-1}). **Alanine** caused an increase in both length and biomass with concentration, with the overall effect being one of a more robust plant at higher concentrations, having a higher biomass to length ratio than that of the controls. The mosses responded to 1 mg L^{-1} **glycine** much as they did to the N-free medium, but at higher concentrations (20 and 30 mg L^{-1}) their length and biomass both increased considerably over that of controls.

Alghamdi (2003) then compared the effects of glycine, which seemed to produce the "healthiest" plants, to those of the inorganic forms of N. This aquatic moss did less well on the inorganic forms NH_4NO_3 or NO_3^- than on NH_4^+ alone or NH_4^+ + the amino acid **glycine** and did best on glycine alone, producing more biomass, longer stems, and more branches (Figure 28, Figure 29). In fact, glycine seemed to induce branching (Table 1).

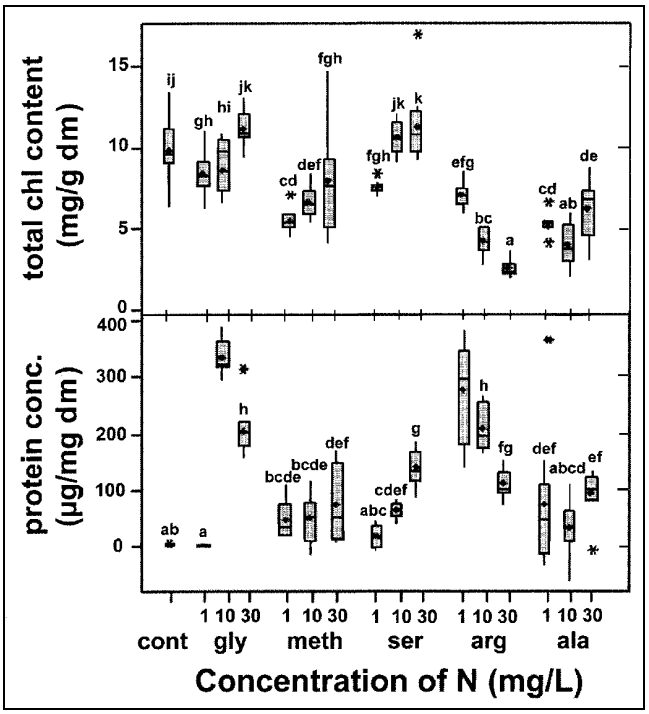

Figure 27. Effect of water soluble amino acids on the protein content and total chlorophyll concentration of the Java moss, ***Taxiphyllum barbieri***. cont = control, gly = glycine, meth = methionine, ser = serine, arg = arginine, ala = alanine. n = 10 sets of 3 stems. Notation as in Figure 8. From Alghamdi 2003.

In the same series of experiments, Alghamdi (2003) examined the effects of inorganic N and glycine on the chlorophyll and protein content of ***Taxiphyllum barbieri***. Glycine, both alone and in combination with NH_4^+, resulted in the highest protein concentrations (Figure 30). The effects on chlorophyll were less clear, but the highest total chlorophyll occurred in the highest glycine concentration (Figure 30). NH_4^+ at 20 mg L^{-1}, however, produced similar chlorophyll concentrations, but at 30 mg L^{-1} the chlorophyll content decreased.

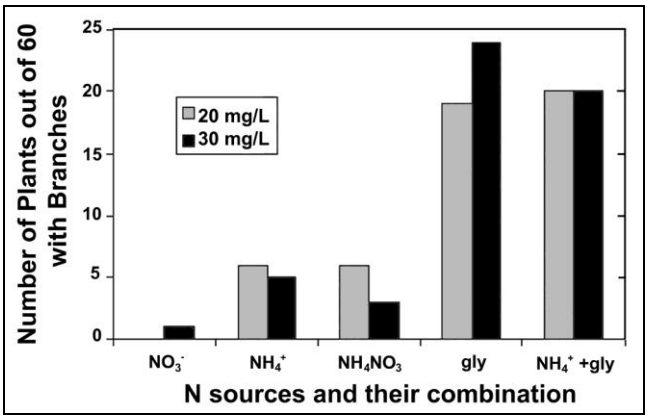

Figure 28. Effect of N source as nitrate (NO_3^+), ammonium (NH_4^+), glycine (gly), and combinations at two concentrations on number of branches in ***Taxiphyllum barbieri***. The combinations have half the total N from each source. From Alghamdi 2003.

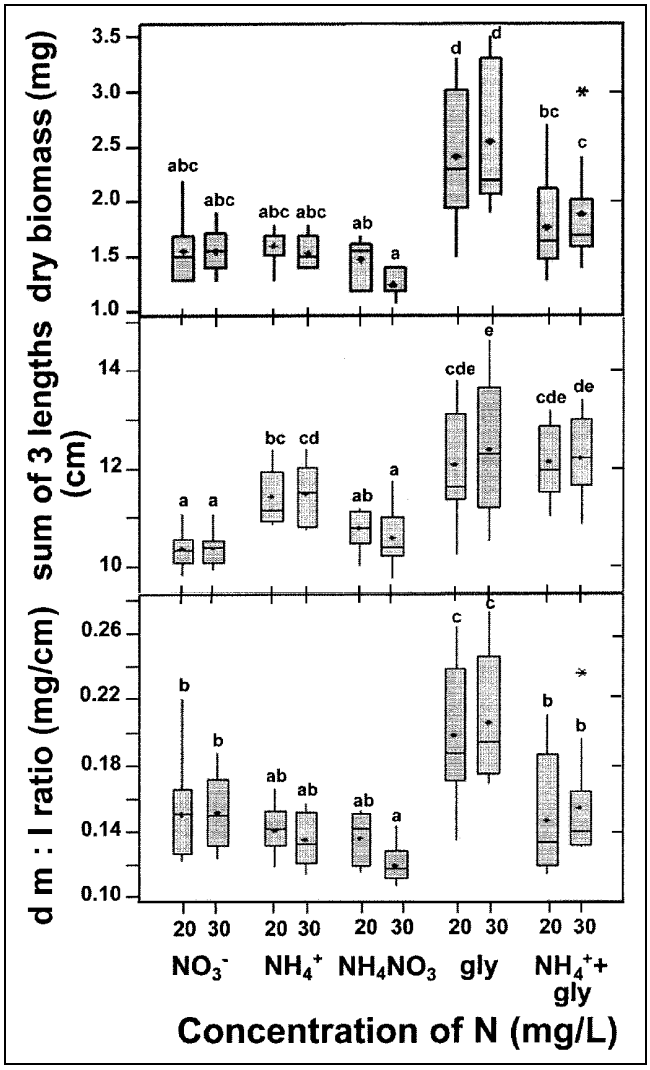

Figure 29. Effect of nitrate (NO_3^+), ammonium (NH_4^+), glycine (gly), and combinations on the increase in biomass (d m) and length (l) and robustness (wt:length) of the Java moss, ***Taxiphyllum barbieri***. Notation as in Figure 8; n = 10 sets of 3 stems. From Alghamdi 2003.

Table 1. Effect of various N forms on moss branching in ***Taxiphyllum barbieri***. From Alghamdi 2003.

Treatment	Moss Branching
glycine	long with many short branches
NO_3^-	short and no branches
NH_4^+	long and few short branches
glycine + NH_4^+	long with many short branches and slightly thin
NH_4NO_3	short, thin and few short branches

Other organic compounds, such as nucleic acids, are also released from organism tissues as they decay. Based on his data showing that ***Atrichum undulatum*** (Figure 24) had good growth in a medium with yeast nucleic acids as its N source, Burkholder (1959) tested growth of this species on the nucleic acid bases. Growth of leafy shoots was good in **adenine** and **guanine**, but there was no growth in uracil or thymine. Growth in xanthine, uric acid, and cytosine was less than that in NH_4NO_3.

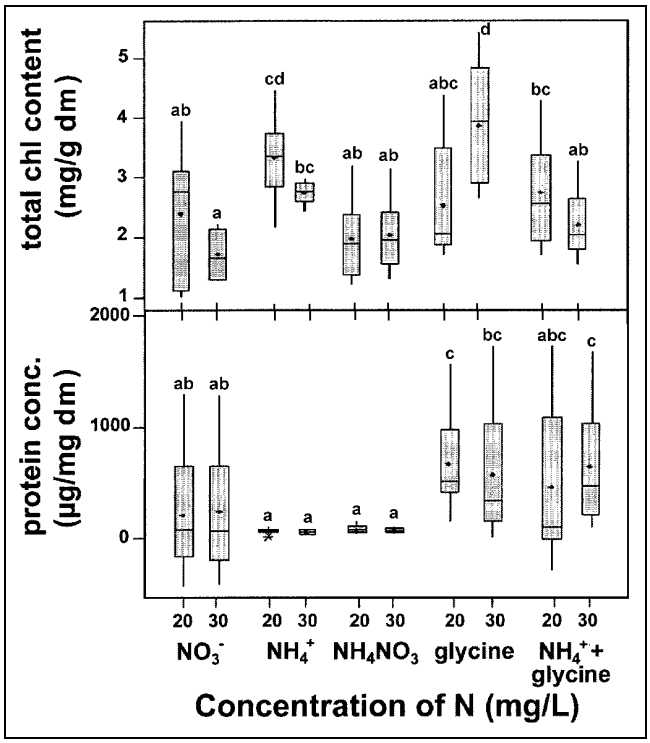

Figure 30. Effects of inorganic N compared to glycine on the protein and chlorophyll content of Java moss (***Taxiphyllum barbieri***). Notation as in Figure 8; n = 10 sets of 3 stems. From Alghamdi 2003.

Both uracil (in the presence of NH_4NO_3) and aspartic acid caused ***Sphagnum squarrosum*** (Figure 15) to become thalloid (resembling its protonema), as did hydroxyproline + glycine, occasionally (Burkholder 1959). Not all mosses responded in the same way. Growth of ***Leptobryum pyriforme*** (Figure 31) and ***Splachnum sphaericum*** (Figure 32) and others was "excellent" on a medium with **NH_4NO_3** plus **uracil**, but was poor in ***Sphagnum squarrosum***. On the other hand, while growth of ***Leptobryum pyriforme*** was good with **uric acid** and **cytosine**, ***Splachnum sphaericum*** had poor growth. The ability to use nucleic acids, amino acids, and other organic N compounds could permit bryophytes to take advantage of partially decomposed litter in which these nitrogen sources leak from the dead tissues.

Figure 31. ***Leptobryum pyriforme***, a species that grows well with uric acid and cytosine. Photo by Michael Lüth, with permission.

Figure 32. ***Splachnum sphaericum*** with capsules, a species with good growth on NH_4NO_3 plus uracil, but poor growth with uric acid and cytosine. Photo by Michael Lüth, with permission.

When N (as NH_4NO_3) was added to a mire in central Sweden, ***Sphagnum fuscum*** (Figure 33), ***S. magellanicum*** (Figure 12), and ***S. rubellum*** (Figure 23) exhibited increased concentrations of amino acids in the capitulum (Nordin & Gunnarsson 2000). But the growth in length decreased at the same time. The researchers demonstrated that when the amino acid N concentrations exceeded 2.0 mg N g^{-1} dry mass, growth was negatively affected. The amino acid N concentrations did not serve as a good measure of N deposition rates when the deposition rates were less than 1.0 g m^{-2} yr^{-1}.

Brown (1982) suggested that in low N environments the mosses may be able to move organic molecules containing N from dying and dead cells to the growing apex. It is very likely that these molecules would be amino acids, as well as dipeptides and other organic compounds.

Some amino acids, leaking into the environment from decaying vegetation, could cause developmental anomalies leading to abnormal growth forms in bryophytes. For example, amino acids, such as **hydroxyproline**, can cause desuppression in the development of underleaves in liverworts (Basile & Basile 1980; Basile *et al*. 1988), causing them to look like normal leaves. In the moss ***Atrichum*** (Figure 24), amino acids inhibited leafy shoot development (Burkholder 1959). This might be another example of the **Gaia hypothesis** (Lovelock, 1988), wherein the ecosystem behaves like a superorganism and species depend on other species for their biochemical needs during development. The N relationships of bryophytes are proving to be more complex than we previously thought.

Figure 33. ***Sphagnum fuscum***, a species that exhibited decreased growth when receiving elevated ammonium nitrate. Photo by Jutta Kapfer, with permission.

Nitrogen Uptake

With the variety in forms of N used by various species, we might expect sites and mechanisms of uptake to vary as well. Atmospheric deposition of N serves as the major source of N for many bryophytes (Soares & Pearson 1997). These researchers raised concerns about the ability of increased levels of these N sources in pollution to inhibit nitrate reductase and affect cation, total N, and organic acid concentrations.

Using ***Racomitrium lanuginosum*** (Figure 34), ***Rhytidiadelphus loreus*** (Figure 35), and ***Philonotis fontana*** (Figure 36) and a single field misting with 3 mol m^{-3} NH_4^+ and NO_3^- Soares and Pearson (1997) found a 20% increase in tissue N after 48 hours. Labelled N experiments on ***R. lanuginosum*** revealed N partitioning, with the highest N uptake in the upper stem and leaves. High concentrations of N resulted in reduced N uptake efficiency. The ammonium decreased nitrogen reductase activity and caused organic acids and cations to decline. However, nitrate treatments cause the opposite response.

Figure 34. ***Racomitrium lanuginosum***, a species has elevated N in the upper stems and leaves following added ammonium and nitrate. Photo by Michael Lüth, with permission.

Figure 35. ***Rhytidiadelphus loreus***, a species that rapidly takes up added N in the first 48 hours. Photo by Michael Lüth, with permission.

Figure 36. ***Philonotis fontana***, a species that rapidly takes up added N in the first 48 hours. Photo by Michael Lüth, with permission.

What controls the rate of uptake in various species? Jauhiainen *et al*. (1998) found that among seven ***Sphagnum*** species, the greatest uptake rate was by individuals (not species) that had the largest capitula and a high number of ion exchange sites. These species were the lawn species ***S. pulchrum*** (Figure 37), ***S. fallax*** (Figure 13), ***S. papillosum*** (Figure 38), and ***S. magellanicum*** (Figure 12). However, when compared on the basis of dry mass, the most effective species were the hummock species ***S. fuscum*** (Figure 33) and ***S. rubellum*** (Figure 23). These species were also the most effective ones in retaining available nitrogen.

Figure 37. ***Sphagnum pulchrum***, a lawn species with a large capitulum and high nitrogen uptake. Photo by Michael Lüth, with permission.

Kopáček and Blažzka (1994) examined ammonium uptake in alpine streams of the High Tatra Mountains, Slovakia. Maximum uptake rates of ammonium N by bryophytes ranged 6-11 mg m^{-2} h^{-1}. The uptake rate did not seem to relate to *p*H during 3- to 5-hour testing periods. Nevertheless, nitrification of ~50% of the NH_4^+-N added occurred in non-acidified streams, but was negligible in acidified streams.

In the aquatic liverworts ***Jungermannia vulcanicola*** (Figure 39-Figure 40) and ***Scapania undulata*** (Figure 5, Figure 41), uptake activities were similar (Miyazaki & Satake 1985). Uptake was greatest at the plant tips and decreased toward the base. Uptake of ammonium at the tip was between 1.9 X 10^{-5} and 5.8 X 10^{-5} g N g dry wt^{-1} h^{-1}. Nitrate uptake was less than that of ammonium.

Figure 38. ***Sphagnum papillosum***, a lawn species with a large capitulum and high nitrogen uptake. Photo by Michael Lüth, with permission.

Figure 39. ***Jungermannia vulcanicola***, a Japanese species with a high tolerance for acid. Photo by Angela Ares, with permission.

Figure 40. ***Jungermannia vulcanicola***, a species in which N uptake is greatest at the plant tips and decreases toward the base. Photo by Angela Ares, with permission.

Figure 41. ***Scapania undulata***, showing a typical habitat. Photo by Michael Lüth, with permission.

Bryophytes have a variety of options for obtaining N. In the Antarctic, ***Bryum pseudotriquetrum*** (Figure 42-Figure 43) and ***Sarconeurum glaciale*** (Figure 44) are able to retain more of the N from precipitation than does the dry soil of the fellfields where they live (Greenfield 1992). The N forms are retained by ion exchange and chelation, enabling them to supplement the low nutrient levels in the rocks and poor-nutrient soils.

Figure 42. ***Bryum pseudotriquetrum*** in the Antarctic, a species that retains N from precipitation. Photo courtesy of Catherine Beard.

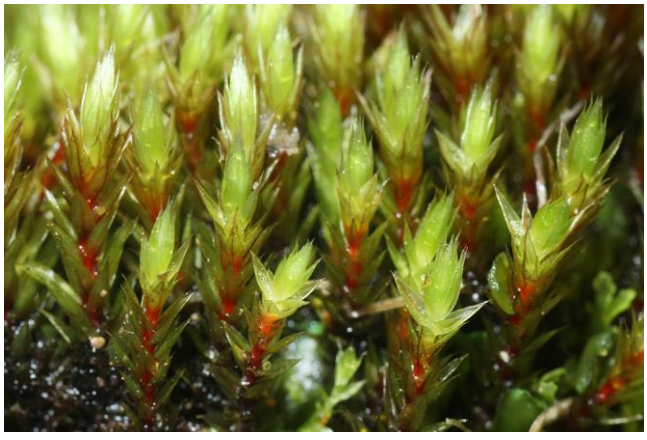

Figure 43. ***Bryum pseudotriquetrum***, a moss that retains N from precipitation. Photo by Barry Stewart, with permission.

Figure 44. ***Sarconeurum glaciale*** with the lichen ***Xanthoria mawsonii*** on it. ***Sarconeurum glaciale*** retains N from precipitation. Photo from Australian Antarctic Data Centre, through Creative Commons.

Bryophytes are diverse in their abilities and physiologies. We have often assumed that they are unable to take N from the soil. However, Ayres *et al*. (2006) demonstrated clearly that mosses are able to derive N from the soil. In fact, they suggested that uptake from soil might be common among mosses, but this prediction needs to be tested.

Nitrogen Fixation

With 78% of our atmosphere being composed of nitrogen and only about 5% of biomass being nitrogen, one would expect this element to be no problem for living systems to obtain. But unlike phosphorus, it cannot normally be obtained from bedrock. And just as you and I can make no use of the free, gaseous nitrogen we breathe, most plants can't either. Instead, plants require their nitrogen fixed into ammonium (NH_4^+) or nitrate (NO_3^-) salts (or converted to amino acids) before they can obtain and convert it to specific amino acids and proteins they need.

Nitrogen fixation is the process of trapping atmospheric nitrogen and converting it to NH_4^+ and in some cases, converting it to NO_3^-. Elbert *et al*. (2012) estimated that cryptogamic covers, including **Cyanobacteria**, algae, fungi, lichens, and bryophytes, account for nearly half of biological N fixation in terrestrial communities. Bryophytes play a crucial contributor in many communities by providing suitable habitat for the N-fixers.

N fixation by **Cyanobacteria** associations with bryophytes may be important in many ecosystems where it has hardly been recognized (Cullimore & McCann 1972; Madhusoodanan & Dominic 1996). Nitrogen fixation is a major source of usable nitrogen for bryophytes, particularly in bogs and fens. Like many tracheophytes, bryophytes can use N released by N fixation from associated bacteria and **Cyanobacteria**. The **heterocysts** (large, transparent, thick-walled cell in filaments of some **Cyanobacteria**; site of nitrogen fixation; Figure 45) of **Cyanobacteria** make them a rich source of amino acids as a result of their **nitrogen-fixing** activity. That is, they are able to convert atmospheric N to a form usable by other living organisms.

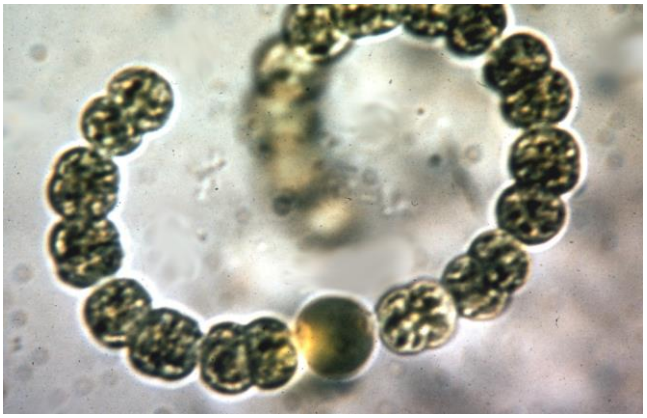

Figure 45. ***Anabaena*** (**Cyanobacteria**) showing heterocyst in middle lower part of picture. Photo by Janice Glime.

In the process of nitrogen fixation in **Cyanobacteria**, the simple CH_2O group from sugars, fixed by cells adjacent to the heterocyst, is moved into the heterocyst (Figure 46). Atmospheric nitrogen (N_2) enters adjacent cells and is passed to the heterocyst. In the heterocyst **nitrogen reductase** (enzyme that catalyzes addition of H^+ to N to form NH_4^+) catalyzes the transformation of N_2 to the reduced NH_4^+ with H^+ obtained from the CH_2O group.

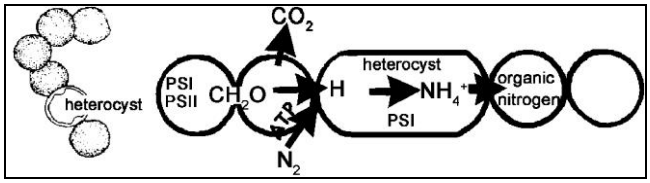

Figure 46. Nitrogen fixation in **Cyanobacteria**, with atmospheric nitrogen entering an adjacent cell and being transferred to the **heterocyst**, where it is converted to ammonium (NH_4^+). The ammonium is then moved to the adjacent cell where it is converted into organic compounds, typically amino acids. Diagram by Janice Glime.

Many studies have shown that some bryophytes, especially peatland bryophytes, obtain N through N fixation processes of surface-dwelling **Cyanobacteria** (Figure 47) as well as other bacteria (Cullimore & McCann 1972; Granhall & Selander 1973; Alexander *et al*. 1974; Basilier *et al*. 1978; Smith & Ashton 1981; Smith 1984; Nakatsubo & Ino 1986, 1987; Bentley 1987; Given 1987; Bergman *et al.* 1993; Madhusoodanan & Dominic 1996). In the **Cyanobacteria**, the most significant contributions come from taxa such as ***Nostoc*** (Figure 1, Figure 48), ***Anabaena*** (Figure 49), and ***Calothrix*** (Figure 50) that have the special cells called **heterocysts**. These cells provide a "safe" environment for nitrogen fixation because they lack the oxygen-generating reactions of photosystem II. The enzyme **nitrogen reductase** is unable to make the conversion in an aerobic environment, hence requiring a location where photosynthetic oxygen is not available. Since only the **Cyanobacteria** and some true bacteria are able to use the abundant atmospheric nitrogen, this conversion makes a significant contribution to usable nitrogen in the ecosystem.

Figure 47. **Cyanobacteria** on ***Campylopus*** at geothermal vent in New Zealand. Photo by Janice Glime.

Figure 48. ***Nostoc***, a typical N-fixing **Cyanobacterium** that can be found associated with bryophytes. Note the enlarged heterocysts. Photo by Janice Glime.

Figure 49. ***Anabaena***, a common N-fixing symbiont that lives among bryophyte leaves. Photo by Yuuji Tsukii, with permission.

The **Cyanobacteria** fix more nitrogen than is essential for their own needs and release the excess to their environment. Significant contributions of N through N fixation by **Cyanobacteria** occur in grasslands (Vlassak *et al*. 1973), boulder communities (Snyder & Wullstein 1973a, Jones & Wilson 1978), tropical forests, especially in

epiphyllous communities (those growing on a leaf) (Bentley 1987), poor ***Sphagnum*** (Figure 18, Figure 23, Figure 33) mires (Basilier 1979), boreal forests (DeLuca *et al*. 2002; Gundale *et al*. 2011), and polar turfs (Alexander 1975; Alexander *et al*. 1978).

Figure 50. ***Calothrix***, a nitrogen-fixing **Cyanobacterium** that can live in association with ***Phaeoceros***. Note the heterocyst at the base of each filament. Photo by Yuuji Tsukii, with permission.

In the terrestrial moss ***Hymenostylium recurvirostre*** (Figure 51), association with ***Nostoc*** (Figure 48) is common. Labelled ^{15}N from N gas, converted by ***Nostoc***, resulted in the highest concentrations in the new rhizoids, then new shoots, then old shoots and old rhizoids (Jones & Wilson 1978). Jones and Wilson suggest that these locations indicate the nitrogen is being translocated from old to young tissues. Not only is free NH_4^+ available, but also large quantities of extracellular amino acid leakage is associated with this ***Nostoc***. In view of the discussion above on bryophyte use of amino acids, it is likely that the moss and its neighbors might be using these amino acids as part of their N source.

Figure 51. ***Hymenostylium recurvirostrum*** with capsules, a species that commonly has ***Nostoc*** associates. Photo by Michael Lüth, with permission.

In some of the liverworts and hornworts, **Cyanobacteria** seem to behave symbiotically (Saxena 1981), but more frequently it seems to be only a matter of suitable habitat. For example, in the moist Pacific northwest, approximately 85% of the sampled epiphytic leafy liverwort ***Porella navicularis*** (Figure 52-Figure 53) harbors ***Nostoc*** (**Cyanobacteria;** Figure 48) in distinct colonies under the leaf curled margins and in other plant crevices (Dalton & Chatfield 1985). Nitrogen fixation is measured by the acetylene reduction method, and the product C_2H_2 is used as the measure of fixation. The production of fixed N on ***P. navicularis*** resulted in a mean of 53.5 nmol C_2H_2 g^{-1} d m h^{-1} and reached up to 316 nmol C_2H_2 g^{-1} d m h^{-1}. Dalton and Chatfield (1985) at first thought the ***Porella*** association was symbiotic, but the low number of heterocysts (3-7%) is typical of free-living ***Nostoc***; symbiotic ones typically have a frequency of 30-40%. In either case, the effect is the same; by providing a suitable habitat for **Cyanobacteria**, the mosses facilitate an increase of available N in the system.

Figure 52. ***Porella navicularis*** on tree. Photo from Botany website, UBC, with permission.

Figure 53. ***Porella navicularis***, a suitable substrate for ***Nostoc*** and N fixation. Photo from Botany website, UBC, with permission.

Temperate bryophytes often have associated **Cyanobacteria**, especially ***Nostoc***. Soil associations with bryophytes can benefit the ecosystem in several ways. Not only do they provide additional usable N to the ecosystem, as in the ***Hymenostylium recurvirostre*** (Figure 51) association in Upper Teesdale (Wilson 1975), but they also provide a buffer against erosion and leaching of nutrients already in the upper soil layers.

Few studies have quantitatively addressed the role of micro-organisms in bryophyte communities, particularly in peatlands where their role is significant (Gilbert *et al*. 1999). Nevertheless, these micro-organisms are undoubtedly key players in nutrient cycling through the microbial loop.

Table 2. Comparison of N fixation rates by **Cyanobacteria** associated with bryophytes in various habitats. Rates converted to nmol N using the 3:1 ratio of reduced acetylene to fixed N given by Nakatsubo and Ino (1987) and Vlassak *et al*. (1973). gfm = grams fresh mass; gdm = grams dry mass. Table compiled by Medora Burke-Scoll.

Location	Habitat	Bryophyte and Cyanobacteria partner	Rate	Reference
Tropical	Lava and on volcanic island	*Funaria hygrometrica* + *Nostoc* & *Anabaena*	0.42 nmol N cm^{-2} hr^{-1}	Rodgers & Henriksson 1976
Tropical	Undisturbed forest floor	*Chiloscyphus coalitus* + *Anabaena* &/or *Nostoc*	1.87 nmol N gdm^{-1} hr^{-1}	Brasell *et al.* 1986
Tropical	Undisturbed forest floor	*Chiloscyphus fissistipus* + *Anabaena* &/or *Nostoc*	8.2 nmol N gdm^{-1} hr^{-1}	Brasell *et al.* 1986
Tropical	Undisturbed forest floor	*Bazzania adnexa* + *Anabaena* &/or *Nostoc*	1.23 nmol N gdm^{-1} hr^{-1}	Brasell *et al.* 1986
Tropical	Undisturbed forest floor	*Hypnum chrysogaster* + *Anabaena* &/or *Nostoc*	3.1 nmol N gdm^{-1} hr^{-1}	Brasell *et al.* 1986
Tropical	Undisturbed forest floor	*Pohlia nutans* + *Anabaena* &/or *Nostoc*	3.27 nmol N gdm^{-1} hr^{-1}	Brasell *et al.* 1986
Tropical	Undisturbed forest floor	*Tortella calycina* + *Anabaena* &/or *Nostoc*	2.57 nmol N gdm^{-1} hr^{-1}	Brasell *et al.* 1986
Tropical	Undisturbed forest floor	*Pohlia nutans* + *Anabaena* &/or *Nostoc*	3.27 nmol N gdm^{-1} hr^{-1}	Brasell *et al.* 1986
Temperate	Grassland	*Ceratodon purpureus* + *Nostoc*	10.4 nmol N gdm^{-1} hr^{-1}	Vlassak *et al.* 1973
Temperate Japan	Aquatic	*Sphagnum capillaceum* + *Stigonema, Hapalosiphon, Scytonema,* & *Nodularia*	0.13 nmol N gfm^{-1} hr^{-1}	Morimoto & Maruyama 1982
Temperate	Peatland	*Sphagnum* + *Stigonema, Hapalosiphon, Scytonema,* & *Nodularia*	0.13 nmol N gfm^{-1} hr^{-1}	Morimoto & Maruyama 1982
Temperate	Coniferous forest floor (Bilberry-spruce forest)	*Sphagnum girgensohnii* + *Anabaenopsis*	None detected *included only plant apex.	Basilier 1979
Temperate	Forest margin	*Sphagnum papillosum* + endophytic *Nostoc*	0.033 nmol N gdm^{-1} hr^{-1} (only plant apex)	Basilier 1979
Temperate	Fen	*Sphagnum angustifolium* + endophytic *Nostoc*	43.3 nmol N gdm^{-1} hr^{-1} (only plant apex)	Basilier 1979
Temperate	Fen	*Drepanocladus aduncus* + unidentified epiphytic Cyanobacteria	25.67 nmol N gdm^{-1} hr^{-1} (only plant apex)	Basilier 1979
Temperate	Fen	*Sphagnum riparium* + epiphytic *Hapalosiphon*	26.67 nmol N gdm^{-1} hr^{-1} (only plant apex)	Basilier 1979
Temperate	Lakeside	*Sphagnum annulatum* + *Nostoc*	15.3 nmol N gdm^{-1} hr^{-1} (only plant apex)	Basilier 1979
Temperate	Desert	*Grimmia* + *Azotobacter*	0.065 nmol N gdm^{-1} hr^{-1}	Snyder & Wullstein 1973b
Temperate	Desert	*Syntrichia ruralis* + *Azotobacter*	0.061 nmol N gdm^{-1} hr^{-1}	Snyder & Wullstein 1973b
Boreal Iceland	Iceland Lava field	*Grimmia* + *Anabaena* & *Nostoc*	0.13 nmol N/20 cm plant · hr^{-1}	Englund 1976
Boreal	Iceland Lava field	*Racomitrium* + *Anabaena* & *Nostoc*	0.1 nmol N/20 cm plant · hr^{-1}	Englund 1976
Subalpine	Forest floor	*Sphagnum* + Cyanobacteria	0.743 nmol N gdm^{-1} hr^{-1}	Lambert & Reiners 1979
Subalpine	Peatland	*Sphagnum lindbergii* + *Nostoc* & *Scytonema*	1.3 nmol N gdm^{-1} hr^{-1}	Granhall & Selander 1973
Subalpine	Peatland	*Sphagnum* + Cyanobacteria	0.29 nmol N gdm^{-1} hr^{-1}	Lambert & Reiners 1979
Subalpine	Aquatic	*Sphagnum* + Cyanobacteria	0.13 nmol N gdm^{-1} hr^{-1}	Lambert & Reiners 1979
Subalpine	Forest floor	*Atrichum* + Cyanobacteria	0.053 nmol N gdm^{-1} hr^{-1}	Lambert & Reiners 1979
Subalpine	Forest floor	*Dicranum* + Cyanobacteria	0.023 nmol N gdm^{-1} hr^{-1}	Lambert & Reiners 1979
Subalpine	Forest floor	*Pleurozium schreberi* + Cyanobacteria	0.026 nmol N gdm^{-1} hr^{-1}	Lambert & Reiners 1979
Subalpine	Forest floor	*Plagiomnium cuspidatum* + Cyanobacteria	0.15 nmol N gdm^{-1} hr^{-1}	Lambert & Reiners 1979

Subalpine	Forest floor	*Polytrichum* + Cyanobacteria	0.011 nmol N gdm^{-1} hr^{-1}	Lambert & Reiners 1979
Subalpine	Forest floor	*Bazzania trilobata* + Cyanobacteria	0.033 nmol N gdm^{-1} hr^{-1}	Lambert & Reiners 1979
Subalpine	Coniferous forest floor	Feather mosses	0.23 nmol N gdm^{-1} hr^{-1}	Granhall & Lindberg 1978
Subalpine	Coniferous forest floor	*Sphagnum*	7.47 nmol N gdm^{-1} hr^{-1}	Granhall & Lindberg 1978
Alpine zone of Mt. Fuji	Mountain summit	*Aongstroemia fuji-alpina, Ceratodon purpureus,* & *Bryum + Nostoc*	3.4 nmol N cm^{-2} hr^{-1}	Nakatsubo & Ohtani 1991
Antarctic	East Ongul Island, Antarctica. Sand near a rocky peak.	*Ceratodon purpureus* & *Bryum pseudotriquetrum + Nostoc*	2.37 nmol N cm^{-2} hr^{-1}	Nakatsubo & Ino 1987
Antarctic	Marion Island (highly minerotrophic receiving nutrient-rich mire runoff)	*Brachythecium subplicatum + Anabaena, Calothrix, Hapalosiphon, Nostoc, Sphaerocystis, Stigonema,* & *Tolypothrix*	103.5 nmol N gdm^{-1} hr^{-1}	Smith & Russell 1982
Antarctic	Marion Island (exposed wind-swept rocky ridges)	*Ditrichum strictum* (balls) + *Anabaena, Calothrix, Hapalosiphon, Nostoc, Sphaerocystis, Stigonema,* & *Tolypothrix*	0.12 nmol N gdm^{-1} hr^{-1}	Smith & Russell 1982
Antarctic	Marion Island (submerged)	*Grimmia falcate + Anabaena, Calothrix, Hapalosiphon, Nostoc, Sphaerocystis, Stigonema,* & *Tolypothrix*	5.15 nmol N gdm^{-1} hr^{-1}	Smith & Russell 1982
Antarctic	Fumaroles near summit of Mt. Melbourne	*Campylopus pyriformis* & *Cephaloziella exiliflora + Mastigocladus laminosus*	11 nmol N gdm^{-1} d^{-1}	Broady *et al*. 1987

Arctic, Antarctic, and Alpine

In bryophyte-**Cyanobacteria** associations in the Antarctic (Smith & Russell 1982; Smith 1984; Nakatsubo & Ino 1987; Line 1992; Pandey *et al*. 1992), Arctic (Alexander *et al*. 1978), and alpine/subalpine zones (Lambert & Reiners 1979), N fixation may be a very important contribution of this limiting nutrient to the nutrient-poor ecosystems (Smith & Ashton 1981). Although Smith and Ashton failed to show much acetylene reduction to indicate fixation activity in the field on sub-Antarctic Marion Island at ~0°C, they considered that during the warm summer, fixation by **Cyanobacteria**l flora of bryophytes could approach that exhibited in the lab at ~20°C, thus contributing significantly to the available N in the ecosystem. In a 48-hour field incubation with an air temperature of -1.7°C and moss moisture of 300-1500%, only the moss ***Ditrichum strictum*** associations had any positive acetylene reduction (1.17 & 1.21 µg g^{-1} $48h^{-1}$). The more protected, but nevertheless very cold, ***Clasmatocolea humilis*** and ***Cryptochila grandiflora*** (=***Jamesoniella grandiflora***; Figure 54) associations failed to demonstrate any fixation.

Figure 54. ***Cryptochila grandiflora***, an Arctic species that apparently has no cyanbacterial N fixation. Photo by Juan Larrain, through Creative Commons.

Arctic and Subarctic

In the Arctic soils of Svalbard, Norway, N fixation by both Free-living and bryophyte associations of **Cyanobacteria** is the only significant source of N input to the soil ecosystem (Solheim *et al*. 1996). The most important bryophytes for harboring such associations were ***Calliergon richardsonii*** (Figure 55) and ***Sanionia uncinata*** (Figure 56). An interesting factor in the fixation was grazing by geese (Figure 57). Grazed areas had a 10-fold maximum fixation (693.6±1.5 nmol C_2H_4 h^{-1} gdm^{-1}) compared to ungrazed areas (65.3±16.6 nmol C_2H_4 h^{-1} gdm^{-1}), perhaps because in these areas the **Cyanobacteria** also occurred on the grass. The transfer of fixed N to the plants supported high plant productivity. On the other hand, where birds harbored under cliffs, the concentration of bird droppings inhibited N fixation.

Figure 55. ***Calliergon richardsonii***, an important substrate for **Cyanobacteria** in the Arctic. Photo by Michael Lüth, with permission.

Figure 56. ***Sanionia uncinata***, an important substrate for **Cyanobacteria** in the Arctic. Photo by Hermann Schachner, through Creative Commons.

Figure 57. Barnacle Goose foraging, creating conditions for a higher N fixation rate. Photo by Arthur Chapman, through Creative Commons.

Increased levels of UV-B radiation in the sub-Arctic could have an effect on the rate of nitrogen fixation in bryophyte-**Cyanobacteria** associations (Solheim *et al*. 2002). These researchers found that it causes a 50% decrease in N-fixation potential in the dominant lichen ***Peltigera aphthosa*** (Figure 58), a species with ***Nostoc*** as its N-fixing symbiont. Furthermore, the moss ***Sanionia uncinata*** (Figure 56) in vegetation exposed to experimentally enhanced levels of UV-B for 3 and 4 years in the high Arctic in Svalbard exhibited a 50% reduction in N-fixation potential compared to controls after 3 years. ***Hylocomium splendens*** (Figure 22) failed to show a reduction in N fixation potential after seven years of exposure to increased UV-B. In that same experiment, a 50% increase in precipitation caused a 6-fold increase in N fixation potential.

Nitrogen fixation by **Cyanobacteria** seems to have been important in the colonization of Surtsey, a subArctic island south of Iceland, formed by volcanic eruptions from 1963-1967 (Henriksson *et al*. 1987). By 1987 it had extensive colonies of mosses [***Bryum argenteum*** (Figure 59-Figure 60), ***Ceratodon*** (Figure 61), ***Racomitrium*** **spp.** (Figure 62)] that had **Cyanobacteria** associates capable of N-fixation, primarily ***Nostoc calcicola***. ***Racomitrium canescens*** (Figure 62) exhibited an unidentified N-fixing ***Nostoc*** species living **inside** its cells.

Figure 58. ***Peltigera aphthosa***, a species with Cyanobacteria symbionts. This lichen declines in the presence of elevated UV-B radiation. Photo by Steven K. Sullivan, through Creative Commons.

Figure 59. ***Bryum argenteum***, a pioneer on Surtsey. Photo by Paul Davison, with permission.

Figure 60. ***Bryum argenteum*** capsules – a species that reproduces mostly by fragments. Photo by Dick Haaksma, with permission.

Figure 61. ***Ceratodon purpureus*** with capsules, a colonizer on Surtsey. Photo by Michael Lüth, with permission.

Figure 62. ***Racomitrium canescens***, a species known to sometimes have ***Nostoc*** inside its cells. Photo by Marko Vainu, through Creative Commons.

Antarctic and SubAntarctic

Like Surtsey, the Antarctic lacks litter, so bryophytes have little litter source for N. Without litter, making soil is a slow process. Hence, having an N-fixing partner is often an essential part of life (Smith & Ashton 1981; Smith & Russell 1982).

In support of the suggestion that contributions to N in the summer may be significant, Nakatsubo and Ino (1987) found that approximately 330 mg N m^{-2} was fixed per growing season in some areas of the Antarctic. Fogg and Stewart (1968) found that most N fixation occurs at temperatures above 10°C, thus explaining the lack of activity in the Smith and Ashton (1981) study. Temperatures in the moss-**Cyanobacteria**l associations in summer in the maritime Antarctic typically are in excess of 10°C, often reaching 20°C during midday (Huntley 1971). Smith (1984) found that the fixation rate increased at temperatures from -5°C to a maximum at 25-27°C, decreasing sharply after that. Saturation occurred at ~1000 µmol m^{-2} s^{-1} photon flux density, decreasing at higher levels. Once suitable temperatures were available, moisture seemed to be the most important criterion, causing an increase in fixation up to the highest water content measured: 3,405%! The chemical conditions suitable for fixation seem to be restrictive, with an optimum *p*H in this system of 5.9-6.2 and a negative response to the addition of P, Co, or Mo (Smith 1984). Hence, under warmer conditions, fourteen out of nineteen bryophyte associations did indeed exhibit fixation, with values increasing as moisture content increased (Smith & Russell 1982). Rates ranged from 0.36 to 310.57 nmol C_2H_2 g^{-1} dw h^{-1} (acetylene reduction as indirect measurement of N fixation) among the fourteen with measurable fixation. Surprisingly, in their study, temperature and radiation seemed to have no effect on the rate.

Alpine and Subalpine

The alpine zone likewise is nitrogen limited due to the slow decay rate and limited organic layer. **Cyanobacteria** are important in binding the soil and in providing reduced N. In the subalpine zone of the White Mountains of New Hampshire, USA, the moss ***Plagiomnium cuspidatum*** (Figure 63) provides a suitable habitat for **Cyanobacteria** (Lambert & Reiners 1979). Nevertheless, in an association under the subalpine forest, the ***Sphagnum*** (Figure 15) association was the only one with significant N fixation activity. Lambert and Reiners attributed the activity, in the capitulum, to bacteria, although they considered **Cyanobacteria** to be a possibility.

Figure 63. ***Plagiomnium cuspidatum***, a species that hosts **Cyanobacteria** in the White Mountains, northeastern USA. Photo by Hermann Schachner, through Creative Commons.

On Mt. Fuji, the moss communities of the dry SW slope are nearly devoid of N-fixing activity, but on the moist NE-facing cliffs they exhibit high activity, especially with ***Nostoc*** colonies (Nakatsubo & Ohtani 1991), again demonstrating the importance of moisture. In the somewhat less severe climate of the Alaskan blue spruce taiga system, feather mosses such as ***Pleurozium schreberi*** (Figure 64) and ***Hylocomium splendens*** (Figure 22) are important substrates for N-fixing aerobic and facultative anaerobic bacteria (Billington & Alexander 1983). Here the mosses were quite important, exhibiting daily June and July rates of 74, 119 and 109 µg C_2H_4 m^{-2} d^{-1} of N fixation, respectively, for 3 years of study.

Figure 64. ***Pleurozium schreberi***, a common substrate for N-fixing **Cyanobacteria** in the boreal forest. Photo by Janice Glime.

Peatland Associations

Sphagnum (Figure 18, Figure 23, Figure 33) is highly colonized by a variety of **Cyanobacteria**, both on its surface (Hooper 1982), and in its hyaline cells (Figure 65-Figure 66; Granhall & Hofsten 1976; Granhall & Lindberg 1978), especially by ***Nostoc*** (Figure 48) and ***Hapalosiphon*** (Figure 67) (Sheridan 1991). In bogs and fens, **Cyanobacteria** on bryophyte surfaces can contribute considerable usable N to the ecosystem (Alexander *et al*. 1974; Basilier *et al*. 1978, Basilier 1979; Lambert & Reiners 1979; Rosswall & Granhall 1980, Hooper 1982). Chapman and Hemond (1982) determined that the contribution was greater than that from the only other known input, bulk precipitation (as NO_3^-). Three types of ***Sphagnum*** (Figure 18, Figure 23, Figure 33) N-fixing associations fix N: epiphytic **Cyanobacteria**, intracellular **Cyanobacteria**, and N-fixing bacteria (Granhall & Selander 1973, Granhall & Hofsten 1976).

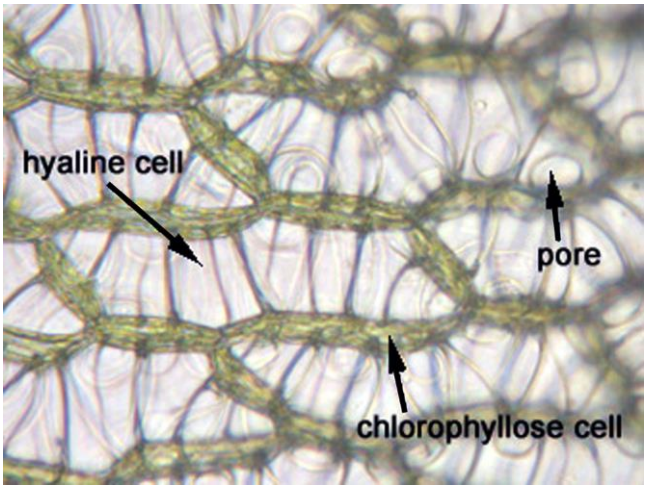

Figure 65. ***Sphagnum*** cells showing the hyaline cell. Photo from Botany website, UBC, with permission.

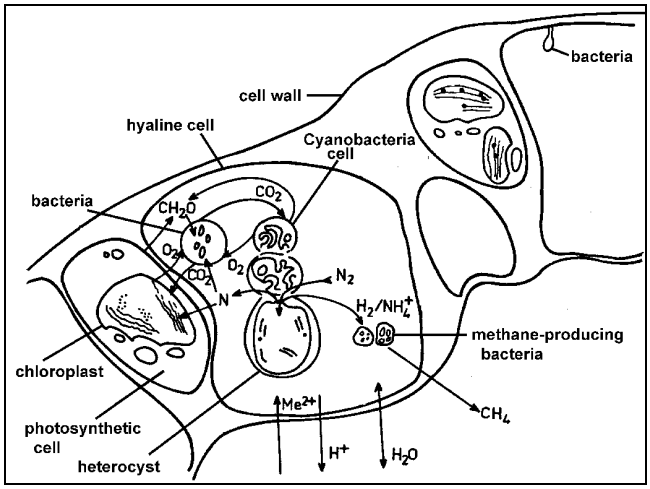

Figure 66. Potential interactions of micro-organisms within the hyaline cell of ***Sphagnum***. Redrawn from Granhall & Hofsten 1976.

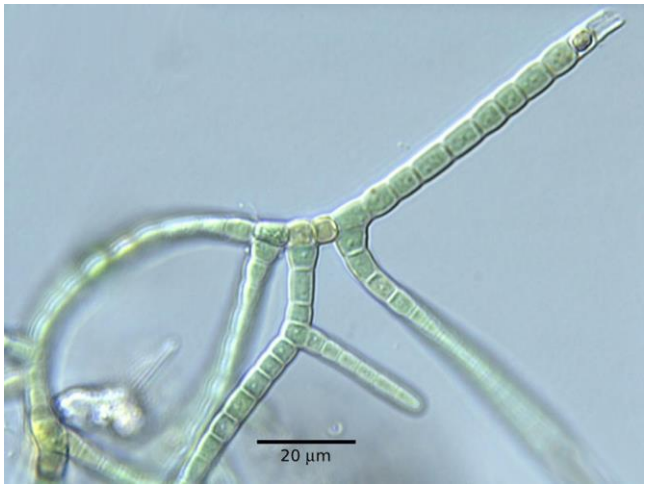

Figure 67. ***Hapalosiphon***, a common member of **Cyanobacteria** that occurs on bryophytes. Photo by Jason Oyadomari, with permission.

Basilier (1979) reported N-fixation activity by **Cyanobacteria** on ***Sphagnum*** (Figure 18, Figure 23, Figure 33), ***Drepanocladus*** (Figure 68), and ***Calliergon*** (Figure 55) in phosphorus-rich environments. Basilier and coworkers (1978), as well as Granhall and Selander (1973), found that the highest N fixation rates in their studies occurred on species of the mosses ***Sphagnum*** and ***Drepanocladus*** (*s.l.*), with a mean value of 9.4 g m^{-2} yr^{-1}. In fact, **Cyanobacteria** associated with ***Sphagnum*** can have higher N fixation per heterocyst than do free-living **Cyanobacteria** in the same condition (Basilier 1980). Granhall and Lindberg (1978) reported a total rate of 0.8-3.8 g fixed N m^{-2} yr^{-1} in wet ***Sphagnum*** communities in a mixed pine and spruce forest in central Sweden. Zimicki (1976) and Basilier *et al*. (1978) have estimated N fixation in various sites for ***Sphagnum riparium*** (Figure 69) to be 0.5-6.4 g m^{-2} yr^{-1}.

Basilier *et al*. (1978) found that the fixation rate in the ***Sphagnum riparium*** (Figure 69) association was strongly light dependent, but that *p*H in the range of 4.3 to 6.8 had little effect. Maximum fixation occurred around noon with the middle of the growing season exhibiting the highest rates. Interestingly, they found that rates on the apical

portions and non-green portions of the ***Sphagnum*** were lower than other green parts, and that the highest rates occurred on the periphery of the moss community. On the other hand, using ^{15}N as a tracer, Basilier (1980) later found that enrichment of N from **Cyanobacteria** fixation appeared within two hours in the apex of ***Sphagnum***. It appears that habitat comparisons need to be made to determine where the highest rates might occur – and why.

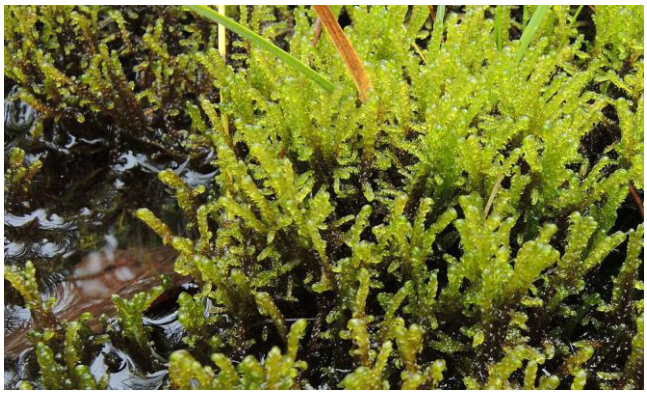

Figure 68. ***Drepanocladus cossonii***, a species that houses N-fixing **Cyanobacteria** in P-rich environments. Photo by Michael Lüth, with permission.

Figure 69. ***Sphagnum riparium***, a substrate for N-fixing **Cyanobacteria**. Photo by Michael Lüth, with permission.

Once the **Cyanobacteria** convert the N to NH_4^+ and amino acids, these are available not only for the bryophytes they occupy, but also for the tracheophytes rooted among them. In Thoreau's Bog in Massachusetts, N fixation exceeded atmospheric N deposition (Hemond 1983), and Hemond concluded that microbial N fixation provides sufficient quantity of N that N may never be limiting to primary productivity in a bog (or poor fen) ecosystem.

Boreal Forests

The boreal forest productivity is limited primarily by available soil N. Bryophytes on the forest floor serve as C and N pools. Recently, researchers have realized the role of N-fixation by **Cyanobacteria** in association with bryophytes in the boreal forest. DeLuca *et al*. (2002) reported that N-fixation reached only 0.5 kg N ha^{-1} yr^{-1}. On the other hand, they found that ***Nostoc*** (Figure 48) living in association with ***Pleurozium schreberi*** (Figure 64) fixes 1.5-2.0 kg N ha^{-1} yr^{-1} in Scandinavian and Finnish boreal forests. They suggest that previous estimates of N-fixation in boreal forests may be too low.

Pleurozium schreberi (Figure 64) is able to modulate its N content based on the amount of N input. With N addition, the N-fixation per unit moss mass and per unit area decreases sharply (Gundale *et al*. 2011). This causes the N pool in the moss to remain stable except at very high additions. This effect on the bryophytes provides at least part of the explanation for the constancy of N acquisition by woody plants up to 12 kg ha^{-1} yr^{-1} additional N. The researchers suggested that bryophytes limit the acquisition of anthropogenic N by woody plants in the boreal forest.

Egorov (2007) found that the nitrogen regime of most of the moss species in the Khibiny Mountains of Eurasia was self-supporting. He attributed this to nitrogen fixation by the epiphytic **Cyanobacteria** on the mosses, accounting for 28% of the total N in the mosses during the growing period.

Hylocomium splendens (Figure 22) is another important feather moss in the boreal forest. And like ***Pleurozium schreberi*** (Figure 64) it is a major contributor to the conversion of N to a usable form by providing a suitable substrate for **Cyanobacteria** (Zackrisson 2009). It is interesting that both of these feather mosses contribute greater N-fixation rates at northern latitudes (64-69° N) than at the more southern latitudes. This is mostly accomplished by species of ***Nostoc*** (Figure 48) and ***Stigonema*** (Figure 70) as the **Cyanobacteria** N fixers. Of further interest is the greater tolerance to N pollution in ***Hylocomium splendens*** when compared to ***P. schreberi***. Consistent with its tolerance to N pollution, ***H. splendens*** exhibited a somewhat higher N-fixation rate at high fertility sites. But ***Hylocomium splendens*** contributed about 50% less to the total N than did ***P. schreberi***. Together, these two species contribute 1.6 kg fixed N ha^{-1} yr^{-1}.

Figure 70. ***Stigonema turfacea***, member of a genus that is common on bryophytes as a nitrogen fixer. Photo by Jason Oyadomari, with permission.

Temperate Forests

Lindo and Whitely (2011) pointed out that we know about the symbiotic Cyanobacteria-bryophyte associations that contribute significantly to the nitrogen levels on the florest floor through nitrogen fixation. But contributions of this process in the canopy are poorly understood. Older trees can contribute bio-available nitrogen to the ecosystem through the **Cyanobacteria**-bryophyte associations where

atmospheric nirogen is fixed in the canopy, potentially making a major contribution to the nitrogen dynamics of the forest. This seems to be especially true in the temperate rainforest. Lindo and Whitely (2011) found that **Cyanobacteria** density was significantly greater in epiphytic bryophytes compared to mosses on the forest floor, with the highest rates (0.76 kg N ha^{-1} yr^{-1}) at 30 m in the canopy compared to the forest floor (0.26 kg N ha^{-1} yr^{-1}). Thus this relationship is important in the canopy of large, old trees in a coastal temperate rain forest with high epiphytic bryophyte biomass.

Tropics

Although associated **Cyanobacteria** are best known from bryophytes in northern habitats, they also exist in the tropics. In the cloud forest on a volcano in the French West Indies, ***Sphagnum erythrocalyx*** is substrate for the N-fixing **Cyanobacterium *Hapalosiphon flexuosus*** (see Figure 67) (Sheridan 1991). The mean rate of methane production caused by N reduction was 19.1 nmol C_2H_4 gdw^{-1} h^{-1} with an annual contribution of N by N fixation of 4.02 kg N ha^{-1} yr^{-1}. The production in the uppermost green capitula was 4.5X that in the basal portions.

Epiphylls

Epiphylls are those organisms that live on leaves. These are common in warmer climates where the leaves remain on the plant for more than one year. In rainforests, epiphyllous liverworts provide the moist microhabitat needed for high rates of nitrogen fixation by associated bacteria and **Cyanobacteria** (Bentley & Carpenter 1980; Bentley 1987; Carpenter 1992), which may be transferred to the host leaves (Bentley & Carpenter 1984).

At least some micro-organisms living in association with epiphyllous liverworts are able to transfer this fixed nitrogen directly to their host plants (Figure 71; Bentley & Carpenter 1984), thus constituting a loose arrangement that benefits the tracheophyte as well as the bryophyte. In the palm ***Welfia georgii***, 10-25% of the N in the leaf was derived from the micro-organisms harbored there among the leafy liverwort cover.

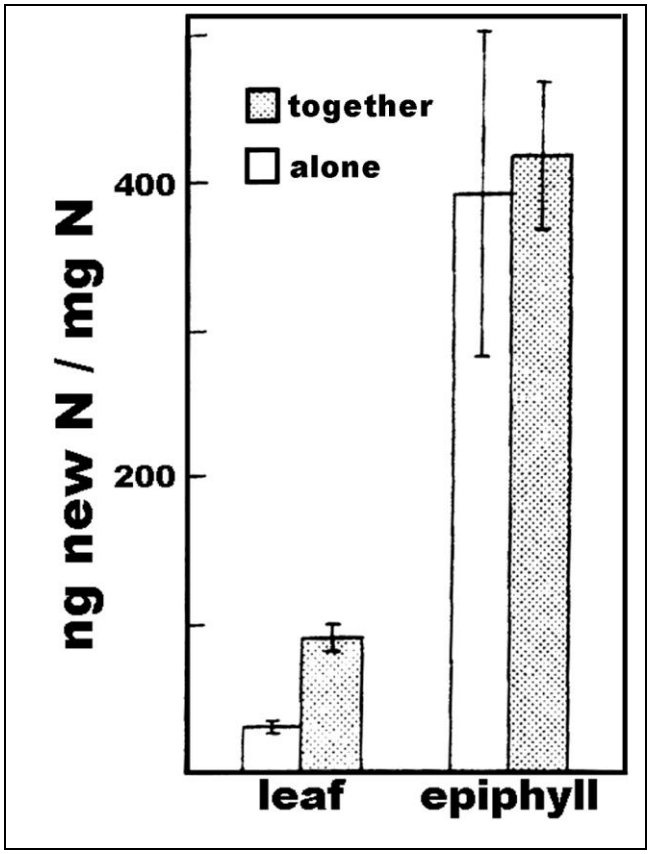

Figure 71. Means and standard errors of 5 hrs of production of fixed nitrogen in leaves of the palm *Welfia georgii* incubated alone (with epiphylls removed) and leaves with intact epiphylls, indicating a much greater transfer of new N to the leaf when epiphylls are present. Redrawn from Bentley & Carpenter 1984.

Liverwort Symbiosis

Several attempts have been made to explain the high degree of N fixation in liverwort associations. In an early attempt, Griggs (1937) grew liverworts from Katmai volcanic ash on N-free sand for three years to determine their success compared to that of liverworts on the same medium, but with the addition of 4 mg L^{-1} NH_4NO_3. During that three-year period, the ones with the additive grew no better, but toward the end of the three years, the N-free cultures became pale and unhealthy. When 4 mg L^{-1} NH_4NO_3 was added to the N-free cultures, they promptly revived. Griggs took this as evidence that no N fixation had occurred.

Nevertheless, at least the thallus of the liverwort ***Blasia pusilla*** (Figure 72) has symbiotic **Cyanobacteria** that do perform N fixation (Rodgers 1978; Peters 1991). In fact, there are many genetic strains of ***Nostoc*** (Figure 48) associated with ***Blasia*** (West & Adams 1997; Costa *et al*. 2001). The presence of ***Nostoc*** induces both structural and metabolic changes within the ***Blasia*** thallus (Kimura & Nakano 1990; Meeks 1990).

Figure 72. ***Blasia pusilla***. **Arrow** indicates ***Nostoc*** colony. Photo by Walter Obermayer, with permission.

Nostoc (Figure 48) is only capable of invading the liverwort when the ***Nostoc*** is in its mobile stage (Kimura & Nakano 1990). That is, when the segments (called **hormogonia**) of a filament separate, they are mobile by a gelatinous sol-gel transformation that permits them to

slither and glide. In this stage they are able to invade the thallus of ***Blasia pusilla*** (Figure 72) and induce the morphological changes that permit the partnership to work. At the same time, the ***B. pusilla*** signals the ***Nostoc*** by producing two **auricles** (earlike lobes), each with an enclosed chamber housing a slime papilla that fills the chamber with mucilage (Renzaglia 1982a). The mucilage attracts the ***Nostoc***, which then takes up residence in the chamber (Figure 73). Once the ***Nostoc*** arrives, the auricle increases in size and closes its opening. Following the invasion, the surrounding cells of the ***Blasia*** thallus have attenuated growth and produce branched filaments from hyaline cells that penetrate the ***Nostoc*** colonies (Kimura & Nakano 1990). These filaments form a labyrinth of wall ingrowths into the ***Nostoc*** cells, suggesting that they may have the role of transfer cells for exchanging metabolites (Ridgway 1967; Duckett *et al*. 1977). Once it has settled into its thallus home, the ***Nostoc*** produces numerous heterocysts, which are essential for the N fixation.

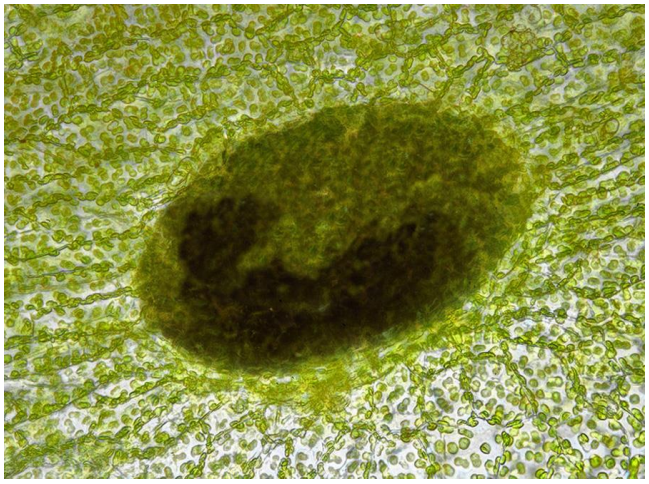

Figure 73. ***Blasia pusilla Nostoc*** colony, the site of N fixation. Photo by Dick Haaksma, with permission.

When the ***Nostoc*** (Figure 48) grows deeply embedded within the liverwort thallus, it no longer has access to dissolved CO_2. Stewart and Rodgers (1977; 1978) determined that the ***Nostoc*** obtains its carbon through transfer from the ***Blasia*** (Figure 72) thallus to ***Nostoc***, suggesting that this is really a **mutualistic** relationship (one in which both partners benefit). Within the thallus the ***Nostoc*** requires a higher light intensity and higher temperature (above 17ºC) for maximal activity compared to those living alone (max activity above 12ºC) (Rodgers 1978). Hence, the liverwort provides a safe compartment that will remain moist much longer than the external environment, and even provides the needed carbon source for its symbiont.

The ability to colonize rapidly, symbiont intact, is facilitated in ***Blasia pusilla*** (Figure 72) by the production of two types of gemmae (Figure 74-Figure 75). These gemmae permit the symbiont to travel with the gemma and easily renew the partnership arrangement upon germination (Renzaglia 1982b; Duckett & Renzaglia 1993). Taxa that depend on spores for their dispersal would not benefit from this convenience.

Figure 74. ***Blasia pusilla*** showing gemmae on stalk. Photo by Des Callaghan, with permission.

Figure 75. ***Blasia pusilla*** gemmae "star" gemmae. Photo by Dick Haaksma, with permission.

As already noted, the epiphytic leafy liverwort ***Porella navicularis*** (Figure 52-Figure 53) provides a suitable substrate for ***Nostoc*** (Figure 48) in western North America (Dalton & Chatfield 1985). This association is present in a broad geographic range. The presence of these ***Nostoc*** (Figure 48) symbionts in liverworts seems to be restricted to taxa that are pioneers (Schuster 1992a, b), living in temporary or poorly colonized habitats that are likely to be low in usable N.

Hornwort Associations

Hornworts (**Anthocerotophyta**) are well known for their symbiotic associations with **Cyanobacteria**, especially ***Nostoc*** (Figure 48) in association with ***Phaeoceros*** (Figure 76) and ***Anthoceros*** (Figure 77) (Peirce 1906; Ridgway 1967; Enderlin & Meeks 1983; Steinberg & Meeks 1987). A wide diversity of ***Nostoc*** strains infect these hornworts (West & Adams 1997), and it appears that ***Anthoceros*** harbors a ***Nostoc*** that is unique from that of ***Blasia*** (Figure 72) (Leizerovich *et al.* 1990). But ***Phaeoceros*** also hosts the filamentous ***Calothrix*** (**Cyanobacteria**; Figure 50) (West & Adams 1997). This multiplicity of symbiotic genera is apparently unusual; Rai

et al. (2000) indicate that typically only one genus will infect a particular taxonomic group of plants.

Figure 76. ***Phaeoceros carolinianus*** showing bluish green color typical of plants with *Nostoc* inhabitants. Photo by Michael Lüth, with permission.

For the association to begin, the ***Nostoc*** (Figure 48) must form **hormogonia** (portions of filament in **Cyanobacteria** that become detached and reproduce by cell division) that can break away and move through the environment to reach the hornwort (Wong & Meeks 2002), just as in ***Blasia*** (Figure 72). But it seems that the hornwort makes certain that this occurs, if there is ***Nostoc*** in the vicinity. Free-living ***Nostoc*** rapidly forms hormogonia when in the presence of ***Anthoceros punctatus*** (Figure 77), or even in the presence of agar preconditioned with ***A. punctatus*** (Campbell & Meeks 1989), indicating a diffusable substance from ***A. punctatus*** that stimulates this response.

Figure 77. ***Anthoceros punctatus***, a species that stimulates formation of hormogonia in ***Nostoc***. Photo by Jonathan Sleath, with permission.

Both ***Nostoc*** (Figure 48) and the hornwort seem to be modified physiologically once joining in symbiosis (Joseph & Meeks 1987; Campbell & Meeks 1992). Before the partnership can work, the ***Nostoc*** must form heterocysts (large, transparent, thick-walled cells found in filaments of certain **Cyanobacteria**; sites of N fixation) (Wong & Meeks 2002). This is where the enzyme **nitrogenase**, needed for the N fixation, is located in both free-living and symbiotic strains (Rai *et al*. 1989). When mutants of ***Nostoc punctiforme*** (Figure 78), unable to form **heterocysts**, were introduced to ***Anthoceros punctatus*** (Figure 77), the partnership formed, but no N fixation occurred; the mutants did not produce any nitrogenase.

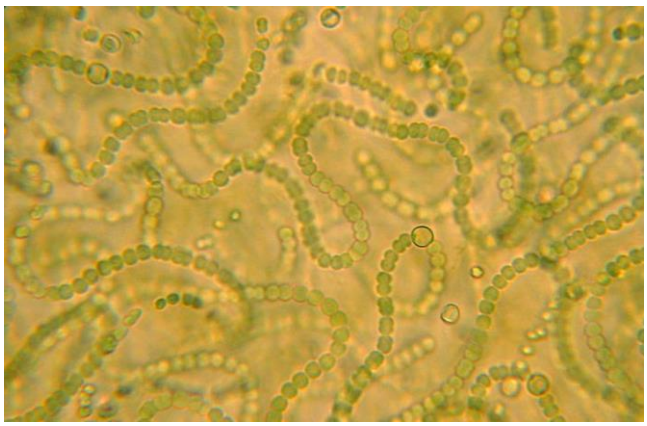

Figure 78. ***Nostoc punctiforme***, a species that does not fix N when it cannot form heterocysts. Photo by Thibul, through Creative Commons.

As in the ***Blasia*** (Figure 72) symbionts, the nitrogenase of the ***Nostoc*** (Figure 48) must have an anaerobic environment in which to fix nitrogen. Campbell and Meeks (1992) demonstrated this by showing that the symbiont could produce fixed N only under anaerobic conditions when grown outside its host. However, when it grew in its ***Anthoceros punctatus*** (Figure 77) host, it could be grown anaerobically; the special cavities where it grew on the host provided the anaerobic conditions needed.

Perhaps one explanation for the success of N fixation within the host lies in the structure of the symbiont heterocyst, contrasting with that of the free-living ***Nostoc*** (Figure 48) strains. When growing inside the host, the ***Nostoc*** heterocyst lacks the outer polysaccharide layer typical that in of free-living ***Nostoc*** (Campbell & Meeks 1992). Rather, it appears that when the ***Nostoc*** grows in the cavities of ***Anthoceros punctatus*** (Figure 77), the cavities replace that wall function. ***Anthoceros*** also mediates the nitrogenase activity, supressing it in the presence of NO_3^- (Campbell & Meeks 1992) and NH_4^+ (Steinberg & Meeks 1991). The end product of the ***Nostoc*** fixation is NH_4^+, accounting for 75% of the introduced radioactive N after 0.5 min, but only 14% after 10 minutes of incubation (Meeks *et al*. 1985), indicating a rapid transformation to something else. Glutamine and glutamate are quickly synthesized via the glutamine synthetase-glutamate synthase pathway, preventing the toxic buildup of NH_4^+. Thus one end result of the symbiosis is that the intracellular levels of NH_4^+ are low compared to those of symbiont-free ***Anthoceros***.

Only 10% of the NH_4^+ is assimilated into the ***Nostoc*** (Figure 48); 1% is lost to the medium; ***Anthoceros*** (Figure 77) incorporates the remainder (Meeks *et al*. 1985). Prakasham and Rai (1991) demonstrated that there is a specific methylammonium transport system in the symbiotic ***Nostoc***, which may account for the reduced NH_4^+ levels and rapid transfer to the host. In symbiont-free ***Anthoceros*** supplied with high levels of NH_4^+, the glutamate dehydrogenase system is functional, permitting

an NH_4^+ buildup (Meeks *et al*. 1983). Therefore, it appears that the ***Nostoc*** partner provides a very effective and safe source of NH_4^+ for the ***Anthoceros*** host (Meeks *et al*. 1985).

As in the ***Blasia*** (Figure 72) partnership, ***Nostoc*** (Figure 48) living within the hornwort gets its carbon primarily from its host plant (Stewart & Rodgers 1977). In fact, ***Nostoc*** isolated from ***Anthoceros punctatus*** (Figure 77) had only 12% of the Rubisco activity of free-living strains, with an equal reduction in CO_2 fixation (Steinberg & Meeks 1989; Rai *et al*. 1989). However, the distribution and levels of Rubisco were similar in the two strains (Rai *et al*. 1989), with 4.3% and 5.2% of the protein as Rubisco in symbionts and free-living ***Nostoc***, respectively (Steinberg & Meeks 1989), suggesting that there is regulation of the Rubisco activity and not an alteration at the gene transcription level. This could be related to the fact that the structure of the chlorophyll complex differs somewhat; the ***Nostoc*** contains the typical cyanophycean granules, but it lacks **phycobilisomes**, the cellular organelle located on the surface of the thylakoids of the chlorophyll complex and in which the biliprotein pigments (**phycocyanin**, **phycoerythrin**) are present (Honegger 1980).

Because the ***Nostoc*** (Figure 48) has reduced ability to fix its own carbon, this transfer of fixed carbon from ***Anthoceros punctatus*** (Figure 77) to ***Nostoc*** is necessary for the fixation of N_2. When the ***Nostoc***-hornwort association was deprived of light for 28 hours, the rate of acetylene reduction (as a measure of N fixation) declined by 99%, but resumed up to 64% of its illuminated activity when supplied with glucose in the dark (Steinberg & Meeks 1991), indicating the need for light and photosynthetic activity for the partnership to work. These researchers found that photosynthates produced immediately by the **Cyanobacterium** can supply at least one-third of the reductant needed for nitrogenase activity in the short-term for the symbiosis to work. When gametophytes were deprived of light, but sporophytes were provided with light, nitrogenase activity continued (Stewart & Rodgers 1977), suggesting a transfer of sugar from the sporophyte to the gametophyte, then to the ***Nostoc***. These factors suggest that the ***Nostoc***, living in the reduced light of the interior of the hornwort thallus, may be dependent upon the hornwort for glucose or similar carbohydrate as an energy source in order to continue its N fixation, thus completing a true mutualistic relationship with its host.

The local sites of the host plants act as islands that effectively keep the ***Nostoc*** (Figure 48) strains in isolation. Even within a single host plant there may be a great diversity of cyanobacterial strains, and these strains seem to be restricted to one site (Costa *et al*. 2001). Nevertheless, some host plants shared strains of ***Nostoc*** that could be found growing 2000 m away. Furthermore, strains found in ***Blasia*** (Figure 72) could also be found in the lichen *Peltigera neopolydactyla* (Figure 79). Although different cavities can easily host different strains in both ***Blasia*** and the **Anthocerotophyta**, a single cavity seems only to host one strain.

Lunar Rocks

Liverworts were among the few organisms to grow successfully on lunar rocks. But why? The thallose liverwort ***Marchantia polymorpha*** (Figure 80) exhibited a tremendous increase in growth following being sprinkled with Apollo 11 or 12 lunar rock material. Hoffman (1974) followed up on this observation by testing the effects of basalt from Minnesota and C-horizon substrate from the Valley of Ten Thousand Smokes, Alaska. In both cases, the growth of ***M. polymorpha*** was significantly increased. But what caused this surge of growth? Nitrogen was absent in any form in both the lunar material and the basalt, and neither P nor K was abundant, so the three typical fertilizer nutrients seem not to be the cause. The macronutrients Ca, Mg, and S were all more abundant in basalt than in the C-horizon soil, but the C-horizon soil caused the greater stimulation. Iron remains a possibility, being abundant in all three substrata. We already know that it stimulates the growth of ***Funaria hygrometrica*** (Figure 4) (Hoffman 1966). And it is also known to stimulate N fixation in Cyanobacteria (Mills *et al*. 2004; Moore *et al*. 2009). On the other hand, no data were gathered on the *p*H, which could affect the solubility, and therefore availability, of all the nutrients. Some have speculated that survival of the liverwort was possible due to partnering **Cyanobacteria** that could trap and convert the atmospheric nitrogen. Perhaps we need to look for soil and rock components that foster the N fixation reaction.

Figure 79. ***Peltigera neopolydactyla***, a lichen with the same strains of ***Nostoc*** as those found in ***Blasia***. Photo by Jason Hollinger, through Creative Commons.

Figure 80. ***Marchantia polymorpha*** with **gemmae**, a species that can grow on lunar rocks. Here it shows red-violet coloration similar to that which develops on the ventral part of the thallus in response to N and P deficiency. Photo by Dick Haaksma, with permission.

Other Stressful Habitats

In **cryptogamic crusts** (*i.e.* soil crusts of algae, lichens, bryophytes, fungi, and micro-organisms; Figure 81) of prairies, deserts, and grasslands, **Cyanobacteria** are able to maintain an active state longer when water is held by the bryophytes. This increases their contribution to the usable N in the soil (Vlassak *et al*. 1973; Giddens 1982; Belknap *et al*. 2001). The crust itself is vital to maintaining both water and nutrients in the soil during and following heavy storms.

In geothermal fields and following fires, bryophytes again provide the moist environment needed to maintain N-fixing micro-organisms (Brasell *et al*. 1986). Hence, we must ask if the bryophytes are net users of nitrogen, or do they facilitate a net gain to the system. At least in some habitats they definitely facilitate a gain by providing the right habitat for fixation to occur, accompanied by leakage of the new N products.

Figure 81. Cryptogamic crust with the moss ***Syntrichia inermis***. Photocourtesy of Lloyd Stark.

Likewise, bryophyte-**Cyanobacteria** associations are important in the colonization of volcanic lava. **Cyanobacteria** are common on bryophytes of dry lava fields (Englund 1976) as well as on the moist, warm bryophyte surfaces near steam vents (Broady *et al* 1987). Both ***Anabaena variabilis*** (=***Tricormus variabilis***; Figure 82) and ***Nostoc muscorum*** were associated with ***Funaria hygrometrica*** (Figure 4) on the newly formed volcano Surtsey off the Icelandic coast (Rodgers & Henriksson 1976). Although the ***Funaria*** did not directly affect the fixation rate, growth of both the ***Funaria*** and the **Cyanobacteria** benefitted by the association, and the N content of ***Funaria*** also increased as a result of the cyanobacterial N fixation.

Although moss associates are responsible for most N fixation in Arctic and subarctic ecosystems, legume associations are considered the predominant N fixers in temperate ecosystems (Stewart 1967). Nevertheless, in some temperate habitats bryophytes are the only plants able to occupy the habitat. For example, on granite outcrops, bryophytes, especially ***Grimmia*/*Schistidium*** (Figure 83), are well known for their role in accumulating soil and nutrients and holding the moisture needed for tracheophyte establishment. Microbial nitrogen fixation on these bryophytes is part of this successional story (Snyder & Wullstein 1973a; Jones & Wilson 1978).

Figure 82. ***Anabaena variabilis***, a species associated with ***Funaria hygrometrica***. Photo from Cyanosite, through public domain.

Figure 83. ***Schistidium apocarpum*** with capsules on granite rock where they accumulate nutrients and prepare the substrate for tracheophytes. Photo by Michael Lüth, with permission.

Nitrogen Translocation

We know that N is needed in amino acids, proteins, nucleic acids, and ribonucleic acids. But where do they go in the plants? Eckstein and Karlsson (1999) compared their locations in the boreal forest moss ***Hylocomium splendens*** (Figure 22) and the wet habitat moss ***Polytrichum commune*** (Figure 16-Figure 17). They demonstrated that both **endohydric** (having internal conduction) and **ectohydric** (using external conduction) species were able to move N compounds from one **ramet** (attached branch serving like a separate organism) to another. Current-year segments of both species appeared to be strong **sinks** for nitrogen, as demonstrated by their considerable increase in the labelled N pool during the season. **Sinks** are locations where something, such as plant nutrients, organic pollutants, or metal ions, is stored and immobilized through natural processes.

In the period of June to September, ***Polytrichum commune*** (Figure 16-Figure 17) lost labelled N from all segments (Eckstein & Karlsson 1999). The researchers attributed this to transfer of N to underground structures (sinks). However, in ***Hylocomium splendens*** (Figure 22), the one-year-old segments had increased labelled N, whereas the older segments lost 50% of the labelled N they had absorbed. This ability to transfer nutrients from one

part to another is especially beneficial in nutrient-poor environments.

N Sequestering

Sinks can be seasonal, with actively used nutrients moving from locations such as leaves to storage locations as winter approaches or simply be storage of excess. Once incorporated into the bryophytes, nutrients, including N compounds, can either be sequestered or recycled. In some cases they are moved to young, growing tissues. In the tropics, epiphytic bryophytes can sequester inorganic nitrogen from atmospheric deposition. Clark *et al*. (2005) estimated that the epiphytic bryophytes and epiphytic assemblages retained 33-67% of the inorganic N deposition from cloud water and precipitation, retaining 3.4 kg N ha^{-1} yr^{-1}, accounting for 50% of the inorganic N in atmospheric deposition. This effectively removes 50% of the suitable N sources and sequesters them in the bryophyte tissues.

In the boreal species ***Hylocomium splendens*** (Figure 22) in a subarctic birch woodland, retention of labelled N varied from three to ten years, depending on the method used (Eckstein 2000). The ability to transport the N compounds to other locations in the plant and a relatively long life span for the growth segments could explain the long residence time of the labelled N. This species uses **acropetal** (from base upward) transport, thus minimizing losses from by the environment by storage in older segments.

Some nutrients are lost to grazing, and in the Arctic, Snow Geese (*Chen caerulescens*; Figure 84) contribute to this herbivory (Kotanen 2002). But mosses can play a role in this goose scenario. Tissues of grasses and sedges that are eaten by the geese are not compensated for their losses, with tissue N responding poorly to N additions. Kotanen suggests that the abundant mosses in these freshwater wetlands sequester the added N, preventing it from reaching forage plants and returning to the ecosystem through feces. But in tracer studies, Kotanen found that mosses did not prevent the grasses and sedges from likewise taking up ammonium and nitrate at or below the moss surface. Nevertheless, most of the added N was absorbed by the mosses before it reached the soil, diverting N away from the forage plants and sequestering it in the moss peat.

Figure 84. ***Chen caerulescens*** grazing on grass that competes with mosses. Mosses, however, take up added N. Photo by Walter Siegmund, through Creative Commons.

N Deficiency Effects

For agricultural plants we know all the symptoms of deficiency. Even the house plant owners are often aware of deficiency symptoms. But for bryophytes, we know little.

One of the symptoms of nutrient deficiency in crop plants is presence of red coloration in the leaves. When the thallose liverwort ***Marchantia polymorpha*** (Figure 80) was grown without nitrate and phosphate, the ventral cell layers developed a red-violet color in the cell walls (Voth & Hamner 1940).

We know that some algae use diminishing N availability in their medium as a signal to go into a sexual phase and produce resting zygotes (Trainor 1959; Singh & Chaudhary 1990; Matsuda *et al*. 1992). Do any bryophytes also use any nutrient signal to become sexual?

In the thallose liverwort ***Marchantia*** (Figure 80), a low ratio of N to C stimulates production of sexual branches (Lockwood 1975). In seeming contrast, the liverwort ***Fossombronia brasiliensis*** produces more gametangia when N is supplied as nitrate than when it is supplied as ammonium (Chin *et al*. 1987). In ***Bryum argenteum*** (Figure 59-Figure 60), reduced nutrient levels stimulate the production of sex organs (Joenje & During 1977), but it wasn't clear which nutrient(s) deficiency might be critical for the reproduction.

Several species of the thallose liverwort ***Riccia*** (Figure 85) produce archegonia and antheridia in response to limiting nitrates (Selkirk 1979). On the other hand, urea not only increased archegonial production significantly in ***Riccia crystallina*** (Figure 85) but also increased growth (Sood 1974). It is more interesting that in this species the amino acids hydroxyproline, serine, threonine, asparagine, glutamic acid, alanine, and leucine increased archegonia production, whereas glycine, tryptophan, aspartic acid, and valine increased production of antheridia.

Figure 85. ***Riccia crystallina***, a species that produces more archegonia and grows more when given urea. Photo by David T. Holyoak, with permission.

In other cases, organic N compounds alter the photoperiodic induction of gametangia. In the leafy liverwort ***Cephalozia lunulifolia*** (=***C. media***; Figure 86), the amino acids arginine, cysteine, and tryptophan plus kinetin can override photoperiodic control (Lockwood 1975). And these amino acids had similar negating effects over the photoperiodic short-day initiation of gemmae.

Furthermore, adding inorganic N as nitrate or ammonium did not override the effects of the amino acids.

Low levels of N can also reduce gemma production in the thallose liverwort ***Marchantia polymorpha*** (Figure 80) (Wann 1925; Duckett & Pressel 2009). This seems also to explain the loss of gemma production in this species two years following a fire (Duckett & Pressel 2009). On the other hand, ***Ceratodon purpureus*** (Figure 61) and ***Funaria hygrometrica*** (Figure 4) on bonfire sites have early gemma production, as do ***Bryum*** (Figure 59-Figure 60) species in arable fields (Duckett *et al*. 2004; Pressel *et al*. 2007). Ball (2010) reported that nitrate levels go up following a fire, and that these results are persistent. The charcoal resulting from the fire stimulates the conversion of ammonia to nitrates through the action of bacteria. This suggests that some of these bryophytes may benefit differently from different forms of nitrogen.

Figure 86. ***Cephalozia lunulifolia***, a liverwort in which the amino acids arginine, cysteine, and tryptophan plus kinetin can override photoperiodic control of gametangia and gemmae initiation. Photo by Hermann Schachner, through Creative Commons.

N Enrichment

The unusual way in which bryophytes respond to nitrogen addition has interesting effects in the ecosystem. As already noted, increases in nitrogen often result in a reduction of bryophyte cover and diversity or replacement of one species by another. But even though the bryophyte productivity decreases as N deposition increases, the stored N can increase within the bryophyte (Gundale *et al*. 2011).

This has interesting implications for the ecosystem, because it buffers the N reaching the tree roots, at least in boreal forests (Gundale *et al*. 2011). Predictably, N fixation by associated **Cyanobacteria** decreases as N fertilization increases. In the boreal feather moss ***Pleurozium schreberi*** (Figure 64), the tissue concentrations of nitrogen increased but the biomass decreased with increasing nitrogen addition. Because feather mosses provide considerable biomass on the boreal forest floor, they can have considerable impact on the nitrogen that is able to reach the trees, trapping nitrogen from precipitation, providing niches for **Cyanobacteria**, and sequestering nitrogen from airborne dust.

Many studies in peatlands have included enrichment of N to determine effects on bryophyte productivity. In an Arctic heath community, where N and P are colimiting, Gordon *et al*. (2001) found that applications of N (0, 10, & 50 kg ha^{-1} yr^{-1}) and P (0 & 5 kg ha^{-1} yr^{-1}) caused a decrease in lichen cover; applications of 10 kg ha^{-1} yr^{-1} resulted in a higher proportion of physiologically active bryophyte shoots. Nevertheless, individual bryophyte species responded differently, suggesting that we cannot draw generalizations from limited fertilization experiments.

Added N can affect different life stages differently. In Wales populations of ***Racomitrium lanuginosum*** (Figure 34), growth was stimulated initially with the highest N addition level (60 kg N ha^{-1} yr^{-1}) (Jones *et al*. 2002). However, after 6 months, all concentrations (20, 40, & 60 kg N ha^{-1} yr^{-1}) caused decreased growth compared to the control with no N addition. By contrast, optimum regeneration from fragments occurred at 20-40 kg on bare soil, but under a canopy of the grass *Festuca ovina* (Figure 87) it was best at 0-20 kg N.

Figure 87. *Festuca ovina*, a grass that benefits the growth of ***Racomitrium lanuginosum*** fragments on the soil at its base. Photo by J. C. Schou (BioPix), with permission.

Thus we have seen that N enrichment, including that from atmospheric pollution, can be detrimental to bryophytes, especially in some conditions. This has resulted in the disappearance of some species (Strengbom *et al*. 2001). Strengbom and coworkers found that in a boreal forest after fertilization had been stopped for nine years, there were no signs of bryophyte recovery. Mycorrhizal fungi produced more sporocarps on the formerly fertilized plots than on those still receiving N, but the species composition was very different from that of never-fertilized controls. After 47 years of no fertilization, the mosses ***Brachythecium reflexum*** (Figure 88) and ***Plagiothecium denticulatum*** (Figure 89) showed enhancement from the previous N fertilization. On the other hand, the common moss ***Hylocomium splendens*** (Figure 22) was still less abundant than in the controls that were never treated with N. These changes were in contrast to the constancy of tracheophyte composition during and after cessation of N treatments.

Figure 88. ***Brachythecium reflexum***, a species that showed enhancement of coverage 47 years after N fertilization ceased. Photo by Michael Lüth, with permission.

Figure 89. ***Plagiothecium denticulatum***, a species that showed enhancement of coverage 47 years after N fertilization ceased. Photo by Hermann Schachner, through Creative Commons.

In a boreal forest of northern Sweden, simulated N deposition had no short-term effects on the above- or below-ground biomass of the understory (Nordin *et al*. 1998). The recovery increased with the N dose. In the plots with 0.5 kg N ha^{-1} the highest concentrations of labelled N occurred in the bryophytes [***Dicranum majus*** (Figure 90) and ***Pleurozium schreberi*** (Figure 64)], whereas in higher applications the grass *Deschampsia flexuosa* (Figure 91) exhibited the highest levels. The elevated N also resulted in greater herbivory on the blueberry *Vaccinium myrtillus* (Figure 92). This raises the as-yet unanswered question of how increased N affects herbivory on bryophytes.

The reduction of bryophyte productivity with increased N deposition is a recurring theme (Koranda *et al*. 2007). Koranda and coworkers sought an explanation for this reduced productivity. Using fragments of ***Thuidium tamariscinum*** (Figure 93) and ***Hylocomium splendens*** (Figure 22), they assessed the effects of ammonium nitrate (30 kg ha^{-1} yr^{-1}) for 80 days. In this experiment, there was no growth change in ***T. tamariscinum***, whereas ***H. splendens*** showed growth reduction. The latter also exhibited a significant increase in N concentration, whereas only ***T. tamariscinum*** had a significant increase in amino acid N. Both species exhibited a reduction in lipid concentration, accompanied by strikingly enhanced turnover rates of carbon storage pools in the fertilized plants. Koranda and coworkers interpreted these results to indicate that the depressed growth of ***H. splendens*** may be caused by enhanced synthesis of N-containing organic compounds, most probably of cell wall proteins. Disturbance of the cellular carbon metabolism may also contribute.

Figure 90. ***Dicranum majus*** with capsules. This species exhibits among the highest concentrations of labelled N when given 0.5 kg N ha-1. Photo by Michael Lüth, with permission.

Figure 91. *Deschampsia cespitosa*, a species that exhibits the highest concentrations of labelled N at N applications higher than 0.5 kg N ha^{-1}. Photo by Rasbak, through Creative Commons.

Figure 92. *Vaccinium myrtillus*, a species that experiences greater herbivory when treated with elevated N. Photo by Anneli Salo, through Creative Commons.

Figure 93. ***Thuidium tamariscinum***, a species that exhibited no change in growth rate under elevated ammonium nitrate. Photo by Hermann Schachner, through Creative Commons.

In a nutrient-deficiency condition, with 10 weeks of watering with distilled water daily, ***Pseudoscleropodium purum*** (Figure 94) grew faster than did ***Brachythecium rutabulum*** (Figure 95) (Bates 1994). When those populations were subjected to a nutrient pulse of 8 daily additions of KH_2PO_4 and NH_4NO_3, followed by 10 weeks of no nutrient additions, growth of ***P. purum*** was significantly stimulated, whereas that of ***B. rutabulum*** was not. ***Pseudoscleropodium purum*** increased its uptake of P, less so of N, and conserved these more effectively in nutrient-deficient conditions than did ***B. rutabulum***. Cation exchange appears to be important in sequestering nutrient cations. These results can explain differences in habitat – ***P. purum*** lives where nutrient inputs are unpredictable, coming as wet deposition; ***B. rutabulum*** lives in a more continuous nutrient supply, apparently coming from the soil.

Figure 94. ***Pseudoscleropodium purum***, a species that conserves N and P in nutrient-deficient conditions. Photo by Phil Bendle, with permission.

Sphagnum magellanicum (Figure 12) has a different set of habitat conditions and illustrates differences in ammonium and nitrate enrichment effects. As noted earlier, this species was favored by nitrate concentrations up to 322 µM, whereas ammonium concentrations ≧ 255 µM caused decreases in chlorophyll content and growth (Rudolph & Voigt 1986). At 600 µM of added ammonium there was a 20% reduction in nitrate reductase activity and net photosynthesis.

Figure 95. ***Brachythecium rutabulum*** with water droplets, a species that is not stimulated by N and P additions. Photo by Christophe Quintin, through Creative Commons.

Calliergonella cuspidata (Figure 96) in a calcareous fen in the mountains of Switzerland showed no observable morphological changes due to increased N levels, whereas the same species showed a number of morphological changes in higher light intensities created by cutting of the tracheophyte vegetation (Bergamini & Peintinger 2002).

Figure 96. ***Calliergonella cuspidata***, a species that does not change morphology in response to increased N levels. Photo by Michael Lüth, with permission.

In a different set of experiments, Heijmans *et al*. (2001) elevated the nitrogen levels (5 g N m^{-2} $year^{-1}$ as ammonium nitrate) in a bog in The Netherlands for three years, added at 3-week intervals during the growing seasons. As one might expect, the tracheophyte biomass increased. But for the ***Sphagnum*** (Figure 18, Figure 23, Figure 33), growth was significantly reduced in the third growing season. It is likely that this was the result of encroaching tracheophyte cover.

Can we expect a different response from a submersed species of ***Sphagnum***, such as ***S. cuspidatum*** (Figure 9)? In a culture experiment lasting 12 weeks, this species was grown at various levels of ammonium (Paffen & Roelefs 1991). In highly enhanced CO_2, this species had increased growth in length and biomass, both with and without ammonium enrichment, but with only ammonium enrichment there was no increase in biomass.

Bryophytes have often been used as monitors. In terrestrial habitats, the moss bag became popular. In aquatic habitats, bryophytes can be used *in situ* or as transplants. The aquatic moss ***Fontinalis antipyretica*** (Figure 97) has been used to assess a variety of pollutants. Mosses such as this have the advantage of accumulating pollutants rather than representing the momentary levels found in chemical assays. For understanding its indications as a biomonitor for NH_4^+, it was necessary to understand the pattern of uptake and the way in which high concentrations could alter physiological performance (Vieira *et al*. 2009). These researchers learned that the concentrations that had significant impact on membrane permeability were the same as those that caused a significant lowering of photosynthetic capacity. As time passes in those higher concentrations, the damage threshold is lowered.

Figure 97. ***Fontinalis antipyretica***, a species that sequesters a variety of pollutants. Photo by Štěpán Koval, with permission.

Habitat Relations

Surprisingly, some of our best studies on canopy bryophytes are from the tropics. Clark *et al*. (1998) estimated the N accumulation of epiphytic bryophytes in a tropical montane forest in Costa Rica to be 1.8-3.0 g N m^{-2} yr^{-1}. N release from bryophyte litter in the canopy and on the ground was initially rapid, with ~30% released. Release from green shoots on the forest floor was greater, with ~47% of the initial N released in the first 3 months. The researchers found no evidence for net N immobilization by either litter or green shoots, but the remaining N in the litter, as already seen above in other species, was **recalcitrant** (substance that degrades at extremely slow rate if at all when released into environment). The epiphytic bryophytes retained 0.8-1.3 g N m^{-2} yr^{-1}. The ability of these epiphytes to retain inorganic N from atmospheric deposition gives them a major role in converting mobile forms of N to highly recalcitrant forms.

Previous research at this site indicated that epiphytic bryophytes retain inorganic N from atmospheric deposition to the canopy (Clark *et al*. 1998). Therefore, they play a major role in transforming N from mobile to highly recalcitrant forms in this ecosystem.

In a study of layer differences in a wooded meadow, Kull *et al*. (1995) found that upper layers have the best access to light and the lower layers have higher N-use efficiency and/or better ability to acquire N. The herbaceous layer has the highest level of foliar nitrogen compared to the tree and moss layers. However, the herbaceous layer is co-limited by light and nitrogen, whereas the moss layer is limited only by light.

On Signy Island in the Antarctic, the dry turf had lower total N concentrations per dry weight (0.79%) than did the wet carpet (2.17%) (Christie 1987). In December, the meltwater and pools of the dry turf had 230 μg N L^{-1} while 165 μg N L^{-1} was present in the wet carpet. ***Nostoc muscorum*** was present at both sites and exhibited high levels of nitrogen fixation. Biological N fixation accounted for 45.9 mg m^{-2} yr^{-1} in the dry turf and 192.4 mg m^{-2} yr^{-1} in the wet carpet. Christie attributed additional inputs to penguin activity.

Throughout this chapter we have seen differences both among species and among habitats. We have barely scratched the surface in understanding these differences and why they occur.

Nitrogen Cycling

In those habitats where bryophytes form a major component of the ecosystem, their role in N cycling can be important. This is particularly true in cold biomes and tropical rainforests (Cornelissen *et al*. 2007). As we have seen, bryophytes host N-fixing bacteria and **Cyanobacteria** that contribute significant usable N to the soil. They furthermore modify the soil climate through control of hydrology and temperatures. They provide safe sites to soil organisms that contribute to litter breakdown.

Temperature plays an important control on the rate of breakdown in the Alaskan tundra. Warming from 4° to 10° significantly increases the rates of nitrogen mineralization, causing a significant effect on the rate of N cycling in litter and tundra soils (Hobbie 1996). Among the growth forms, graminoid litter had the fast rate, whereas moss and deciduous shrub litter had the slowest decomposition rates. This is largely due to the placement of bryophyte nutrients into recalcitrant forms (Hobbie 1996; Cornelissen *et al*. 2007). Decomposition will be discussed further in a separate chapter of this volume.

Summary

Nitrogen is available to bryophytes as **ammonium** (NH_4^+), **nitrite** (NO_2^-), **nitrate** (NO_3^-), and organic forms such as **amino acids** and **urea**. Nitrite, however, is generally toxic. Ammonium can lower internal *p*H and suppress growth. Nitrite can cause an increase in chlorophyll *a*, whereas nitrate can cause a decrease in chlorophyll *b*, both causing an increase in the *a*/*b* ratio. But effects on amino acid and protein concentration vary among species and among habitats. In the Arctic, amino acids and urea are utilized by both bryophytes and tracheophytes. ***Sphagnum*** species often seem to benefit more from amino acids than from ammonium.

Much of the nitrogen uptake is from precipitation; some is from the soil. But our knowledge of nitrogen uptake mechanisms is meager, and the mechanisms

differ among species. These include ion exchange sites and chelation and can be affected by *p*H, iron and phosphorus concentrations, and temperature.

Some, perhaps many, bryophytes solve the nitrogen problem through symbiotic partners, especially **Cyanobacteria**, that carry out **nitrogen fixation**. This process seems to be especially important in the polar and alpine regions under warmer summer conditions up to ~25ºC. But more xeric conditions such as among **epiphyllous** tropical bryophytes and associated with prairie and grassland cryptogamic crusts also benefit from N fixation. In all of these habitats, bryophytes have an **important role** in maintaining the moisture necessary for the fixation to occur.

Peatlands have a high N fixation rate, and **Cyanobacteria** are common in association with ***Sphagnum***. They have a wider *p*H tolerance range (4.3-6.8) than the **Cyanobacteria** in the cold habitats (5.9-6.2).

The liverwort ***Blasia pusilla*** provides a special chamber in each **auricle** where it is moist with mucilage and the **Cyanobacteria** enter and grow. It then seals the chamber and produces filaments that penetrate the ***Nostoc*** colonies. Finally the ***Nostoc*** produces numerous heterocysts. The ***Nostoc*** even travels with the gemmae.

Anthoceros punctatus forms a similar partnership, as do most of the hornworts, but it even stimulates the *Nostoc* to form hormogonia, permitting it to slither toward the hornwort. In both liverwort and hornwort partnerships, the ammonium produced by the cyanobacterial heterocyst is quickly converted to glutamine and glutamate to avoid the buildup of toxic ammonium. The ***Anthoceros*** gets almost 90% of the fixed N and provides fixed C to its **Cyanobacteria** partner.

Moon rock, and rock taken from volcanic areas on Earth, stimulate the growth of bryophytes, but we don't know why. One possibility is the high concentration of iron; another is that symbionts thrived on these rocks, providing N fixation.

It appears that bryophytes play a major role as a substrate for N fixation in many nutrient-poor habitats, making than essential component of those ecosystems.

Nitrogen content varies with species, habitat, season, type of N available, and concentration of N in the ecosystem. It can be sequestered in slowly decaying tissues or translocated to growing regions.

N deficiency, or the wrong form of N (*e.g.* NH_4^+), can cause bryophytes to become long and thin, appearing etiolated. **Glycine**, **serine**, **arginine**, and **alanine** can induce branching. **Methionine** not only did not induce branching, but it also inhibited growth. Glycine caused the greatest weight and length gain of these amino acids in Java moss. Even nucleic acids are usable N sources, with good leafy shoot growth in **adenine** and **guanine**, but no growth in **uracil** or **thymine** in some species and good growth in others. In ***Sphagnum squarrosum*** **uric acid** and **cytosine** caused the plant to be come thalloid.

N enrichment can have initial stimulating effects followed by long-term negative effects, in some case because of competition from other kinds of plants. These differences vary by species and habitat.

Nitrogen cycling among bryophytes is not well understood. We do know that they can release it when dry tissues are rehydrated, but they can also sequester it, serving as sinks, or expose it in recalcitrant forms as tissues decay.

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CHAPTER 8-4
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Figure 1. Drops of "steam" from geothermal vents resting on the wire-like leaves of ***Campylopus holomitrius*** and providing a source of nutrients and a means of trapping airborne nutrients. Photo by Janice Glime.

Uptake

The **role** of bryophytes in nutrient uptake within ecosystems is generally ignored because of their small stature. Weetman and Timmer (1967) showed that the common feather moss ***Pleurozium schreberi*** (Figure 2) in a black spruce (*Picea mariana*; Figure 3) forest took up only 23-53% of N, P, K, and Mg taken up by trees. Nevertheless, that is a non-trivial figure. But bryophyte contributions to sequestering nutrients can be substantial. Yet we have little concept of whether their net contribution is beneficial or detrimental in those ecosystems where they abound.

Figure 2. ***Pleurozium schreberi***, a common feather moss in black spruce forests. Photo by Michael Lüth, with permission.

Figure 3. ***Picea mariana*** forest in Northern Alberta, Canada, with ***Pleurozium schreberi*** and ***Hylocomium splendens***. Photo by Richard Caners, with permission.

General Considerations

Sources

First we need to recall that the sources of nutrients for bryophytes include precipitation, dust, and to a limited extent, substrate. Brown (1982) explains that bryophytes absorb mineral nutrients over their entire surface (Figure 1). This ability is promoted by two characteristics of bryophytes: a large surface area to volume ratio, and a low surface resistance, relative to **tracheophytes** (lignified

vascular plants), due to the limited development of cuticle. This is further enhanced within the bryophyte by typically having leaves of only one cell layer in thickness, hence exposing every leaf cell directly to the nutrient supply immediately. Based on what we know thus far, actual entry into the cell is most likely similar to that of tracheophytes.

Site of Uptake

Their typical differences in site of uptake would seemingly remove the bryophytes from competition with tracheophytes for soil nutrients. Due to lack of vessels and tracheids, we have assumed that uptake of nutrients by bryophytes is primarily through their leaves. Even in the endohydric ***Polytrichum*** (Figure 4), water entry is gained primarily at the tips of the plants by water that has travelled upward through external capillary spaces (Trachtenberg & Zamski 1979). Hence, we can expect that most nutrient entry is not through rhizoids, but through leaves, and at least in some mosses may be greater at the tips than in lower parts of the plant. Brown and Wells (1990) remind us that despite their small size, the bryophytes have intricate surface areas that are effective at trapping both dust and moisture that can subsequently enter the bryophyte (Figure 1). The ratio of surface area to volume in bryophytes is enormous compared to that of trees and other tracheophytes.

Figure 4. ***Polytrichum commune***, a moss with internal conduction, but that transports nutrients externally through capillary spaces. Photo by Michael Lüth, with permission.

Rhizoids

Even if bryophytes were to use their rhizoids to gather some nutrients, the soil penetration by these structures is generally shallow and well above the zone occupied by most fine roots of tracheophytes, especially trees. Instead, we have assumed that bryophytes typically rely largely on dust on their surfaces and on nutrients dissolved in rainfall. In forests, these arrive primarily through leachates acquired in canopy throughfall. This is a quite different strategy from that of tracheophytes, although in ***Polytrichum commune*** (Figure 4) it does appear that some nutrients might enter through the rhizoids (Chapin *et al*. 1987). On the other hand, ***P. commune*** and other forest floor mosses in the black spruce forest (Figure 3) lose nutrients to the black spruce fine roots through **mycorrhizae** (fungal associates).

Growth Form

Growth form affects nutrient trapping and subsequent uptake. Taylor and Witherspoon (1972) found that ***Dicranum*** (Figure 5), which grows in a relatively tight clump, retains more particles than do open lichens such as *Cladonia*/*Cladina* (Figure 6), even though these lichens display considerable surface area. Hence, we should expect such tight cushions to be more effective at trapping than more open bryophytes like ***Brachythecium*** (Figure 7) or ***Mnium*** (Figure 8). On the other hand, Shacklette (1965) found that bryophytes were significantly contaminated with soil particles, including insoluble ones such as Al, Be, Fe, Si, and Zr. But, it would appear that even deeper soil is not immune to moss nutrient scavenging, perhaps through a combination of capillary action and concentration gradient.

Figure 5. ***Dicranum*** in its dry state, showing tight growth form that traps dust particles easily. Photo courtesy of Herschel Horton.

Figure 6. ***Cladina portentosa***, a highly branched lichen. Photo by Taka, through Creative Commons.

Figure 7. ***Brachythecium rutabulum***, showing open growth form that traps less dust than the more cushiony forms like ***Dicranum***. Photo by Janice Glime.

Figure 8. ***Mnium hornum***, an open bryophyte that may trap less dust than cushion forms. Photo by Tim Waters, through Creative Commons.

Age

Bryophyte uptake can relate to **age**. In studying the Alaskan black spruce (*Picea mariana*) forest (Figure 3), Chapin *et al*. (1987) found that in three of the moss taxa studied, the phosphate absorption capacity increases with age of green tissue, but decreases with age of brown tissue.

In the aquatic moss ***Warnstorfia fluitans*** (Figure 9), an **acidophile** (preferring acid habitats), iron (Fe) **accumulates** in the cell wall (Satake 2000). The highest concentrations are in the base, increasing toward the tip. In addition to the biological accumulation within the walls, iron is held on the mosses in crystal form.

Figure 9. ***Warnstorfia fluitans***, a species that can accumulate iron in its cell walls. Photo by Michael Luth,with permission.

Nutrient Concentration

Lou *et al*. (2013) found that the content of the heavy metals Pb, Cr, and Cu in the moss ***Haplocladium microphyllum*** (Figure 10) correlated with the concentrations in the medium. Iron (Fe), on the other hand, increased in a similar manner until the concentration in the medium reached 400 mg L^{-1} as Fe^{++}. Below that level the iron facilitated uptake of other nutrient ions. The absorption capacity for these metals follows the order Fe>Cr>Cu>Pb. Like most things in nutrient relationships, the amount matters. At low concentrations, both lead and copper ions, as with iron, promote the absorptive capacity of other nutrient elements. At high concentrations the same metals decrease uptake of other nutrient elements. Chromium is an exception, inhibiting absorption capacity of the nutrients P, K, Ca, S, Fe, and Cu even when the Cr concentrations are low. Lou and coworkers found that Pb and Cr are stored primarily in the peripheral cortex of the moss stem in ***Haplocladium microphyllum***. It is not clear how this affects uptake of other ions.

Figure 10. ***Haplocladium microphyllum***, a species in which uptake is dependent on concentration. Photo by Robin Bovey, with permission through Dale Vitt.

Water Source

The standing or flowing water habitat of ***Sphagnum*** fen (Figure 11) species contrasts sharply with the rainfall source of many other bryophytes. Although species occupying raised bogs with no ground water input may rely almost entirely on rainfall, those mosses in fen situations undoubtedly get nutrients from the ground water as well. In a study of 21 species of ***Sphagnum*** (Figure 21-Figure 29) in Poland, this genus demonstrated its ability to accumulate N, P, and K in the upper parts of the plant through active uptake, whereas Ca, Mg, and Na accumulated through passive **cation exchange** (Wojtun 1994; see below), suggesting an arrangement of nutrients within the plant similar to that of the tracheophytes.

Figure 11. Rich fen showing marl deposits (Ca^{++}) on plants. Photo by Janice Glime.

A number of researchers have concluded that **cryptogamic crusts** (soil crusts of algae, Cyanobacteria, fungi, lichens, and bryophytes) that live on the soil in areas with low rainfall increase the availability of essential elements, such as N, Cu, K, Mg, and Zn, thus benefitting seeds, seedlings, and mature tracheophyte plants (Harper & Pendleton 1993; Belnap & Harper 1995; Harper & Belnap 2001). This is most likely due to a combination of trapping airborne nutrients and preventing loss due to erosion and leaching from the soil. We are only beginning to understand the extent and role of bryophytes in nutrient trapping, sequestration, and release in various habitats.

Cation Exchange

Once we understand external transport, we must examine how the nutrients actually enter the moss. Are all nutrients equally capable of entry? Most likely not, but how is that controlled? And can these bryophyte leaves function as well as roots of tracheophytes in the absorption of nutrients?

Brown and Buck (1985) considered the **cation exchange capacities** (**CEC**; see below) of bryophyte cell walls to be important in their uptake and sequestering ability. Potassium (K) can be held on exchange sites, then remain in solution once it enters the plant. These researchers warned that it was important to know the locations of minerals within and on the bryophytes because ions such as those of Ca and Pb can remain on exterior exchange sites whereas Mg and Zn can be both internal and external.

Dainty and Richter (1993) identified two classes of weak-acid binding sites. One had a low *p*K (2-4) and the other a high one (>5). ***p*K** is the *p*H at which equal concentrations of acidic and basic forms of a substance are present; it is the negative $\log_{10}$ of the dissociation constant of the electrolyte. The binding sites are related to the uronic, amino, and phenolic acid contents of the cell walls. Dainty and Richter concluded that "valence-dependent reductions in cation activities in the wall phase are an important contributor to the differences in the *p*K estimates."

The ability of bryophytes to take up nutrients from weak solutions (Babb & Whitfield 1977) permits them to grow in situations that may be limiting to tracheophytes. We know that many (perhaps all) bryophytes sequester nutrients on exchange sites (Clymo 1964; Craigie & Maass 1966; Wells & Brown 1990; Bates 1997), but that the exchange capacity varies among species (Büscher *et al.* 1983).

Polyuronic Acids and CEC

In bryophytes, **cation exchange** is the process in which positively charged ions in the environment are able to replace H^+ ions at the surface of the cell walls, particularly those of leaves. **Cation exchange capacity** (CEC) is due to high concentrations of non-esterified **pectates**, mostly **polyuronic acids**, within the cell walls (Clymo, 1963; Craigie & Maass, 1966) and seems to be the first step in uptake of nutrient cations (Koedam & Büscher 1983). Fine roots of tracheophytes use this method as the first step in obtaining cationic nutrients from their surroundings. Koedam and Büscher (1983) demonstrated that CEC in mosses, typically much higher than in tracheophyte roots (Table 1; Knight *et al.* 1961), was related to soil preference and carbonate content of the bryophytes.

Table 1. Mean cation exchange capacity of cell walls of tracheophyte roots compared to that of bryophyte gametophores. Tracheophytes from Klein & Horst 2005; bryophytes from Bates 1982b.

	μg g^{-1} dry mass	
Calcicolous bryophytes		
Ctenidium molluscum	15,510	
Tortella tortuosa	15,160	
Schistidium apocarpum	12,940	
Homalothecium sericeum	12,460	
Orthotrichum cupulatum	12,250	
Syntrichia ruralis	10,160	
Calcifugous bryophytes		
Ptychomitrium polyphyllum	6,690	
Racomitrium fasciculare	3,330	
Dicranoweisia cirrata	3,200	
Andreaea rothii	2,660	
Grimmia donniana	2,610	
Racomitrium lanuginosum	2,330	
Tracheophytes	**0-5 mm**	**5-20 mm**
field bean	491.0	543.7
yellow lupine	422.0	527.4
barley	106.8	59.1
rye	63.1	65.5

The **uronic acids** are important in creating cation exchange sites. Popper and Fry (2003) have demonstrated that bryophytes (including hornworts, thalloid and leafy liverworts, and basal mosses) have higher concentrations of **glucuronic acid** in their primary cell walls than any of the other land plants. Basal mosses have higher concentrations than more advanced mosses, and the highest occurs in ***Sphagnum*** (Figure 21-Figure 29). ***Anthoceros*** (Figure 102-Figure 103) was unique in having a repeat-unit of glucuronic acid-α(1→3)-galactose, a substance nearly lacking in other kinds of plants in the study. **Galacturonic acid** is known as a subunit in some **xyloglucans**, a group of hemicellulose cell wall compounds (Peña *et al.* 2012). In particular, Peña *et al.* (2008) found that mosses and liverworts have **xyloglucans** that contain galacturonic acid, making them distinctly different from those xyloglucans demonstrated in both hornworts and tracheophytes. Popper and Fry (2003) considered that the cell wall xyloglucans may have been pre-adaptive substances that permitted early colonization of land, permitting rapid acquisition of nutrients during periods of short-lived surface water availability.

The role of cation exchange in nutrient uptake in poor nutrient habitats is further supported by the greater ability of ***Sphagnum*** (Figure 21-Figure 29) to exchange Ca^{++} and Mg^{++} ions for H^+ ions, providing them with a mechanism to obtain the very limited nutrients in their habitats. For example, Temple *et al.* (1981) reported the exchange capacity of ***Sphagnum*** to range 0.9 to 1.5 meq per gram dry biomass, whereas that of other mosses generally ranges 0.6-1.1. Figures in meq on tracheophytes were hard to

find; I was able to find that wheat (*Triticum vulgare*) has a low CEC of 0.02 meq per gram dry biomass of roots, with the highest in that study of 0.2 meq in cress (*Lepidium sativum*) (Wiersum & Bakuma 1959).

On the other hand, if the Ca^{++} content of the habitat is too high, ***Sphagnum*** will bind so much Ca^{++} to its leaf surfaces that it will eventually kill the moss (personal observation). Although this cation exchange process is beneficial in obtaining nutrients, it can also result in accumulation of high levels of heavy metal pollutants (Brown 1984) such as Cd because the moss lacks sufficient selectivity in either binding or uptake of these non-nutrients (Brown & Bates 1990).

The Mechanism

As early as 1961, Knight *et al*. found a correlation between **uronic acid** contents and cation exchange capacity. ***Sphagnum*** (Figure 21-Figure 29), in particular, has extensive binding sites through its use of the **polyuronic acid** known as **galacturonic acid** (Clymo 1963). Through this capability, ***Sphagnum*** is able to outcompete tracheophytes. By creating an "intense nutrient impoverishment" for other plants, ***Sphagnum*** gains a competitive edge (Van Breemen 1995). It can impede growth of peatland shrubs such as leatherleaf (*Chamaedaphne calyculata*; Figure 12) (Bartsch 1994) by sequestering nutrients the shrubs need for growth.

Figure 12. ***Chamaedaphne calyculata***, a species that must compete with ***Sphagnum*** for nutrients. Photo by Uleli, through Creative Commons.

Polyuronic acids such as galacturonic acid have a **carboxyl group** ($COOH^+$) protruding on the outer surface of the cell wall. This carboxyl group freely exchanges its H^+ for other cations in its surroundings (Figure 13). Hence, when cations such as K^+, Mg^{++}, and Ca^{++} filter through the bryophyte layer, these ions are often bound on these bryophyte cell wall exchange sites.

Seemingly all bryophytes have a large number of exposed exchange sites, compared to those even of roots of tracheophytes (Knight *et al*. 1961). These exchange sites are essential to the uptake of nutrients in non-***Sphagnum*** bryophyte taxa as well. For example, ***Pseudoscleropodium purum*** (Figure 14) ceased absorbing Mg^{++} and lost intracellular Mg when the exchange sites were saturated with $CaCl_2$, suggesting adherence to exchange sites may be a necessary prerequisite to Mg^{++} uptake (Bates 1989). Addition of both K^+ and Ca^{++} greatly increased their concentrations in the exchangeable fraction of the cell but significantly reduced the concentration of Mg^{++}. Malmer *et al*. (1992) found that the concentrations of Mg^{++} and Ca^{++} in Canadian mire species [three ***Sphagnum*** species and ***Tomentypnum nitens*** (Figure 15), all from hummocks] correlated with the surface water concentrations. It is interesting that when Ca^{++} is increased, the brown mosses are more competitive than are ***Sphagnum*** species. And there is evidence that brown mosses as well as ***Sphagnum*** can lower the *p*H, but that they typically do it at a higher level of *p*H (Figure 16) (Glime *et al*. 1982).

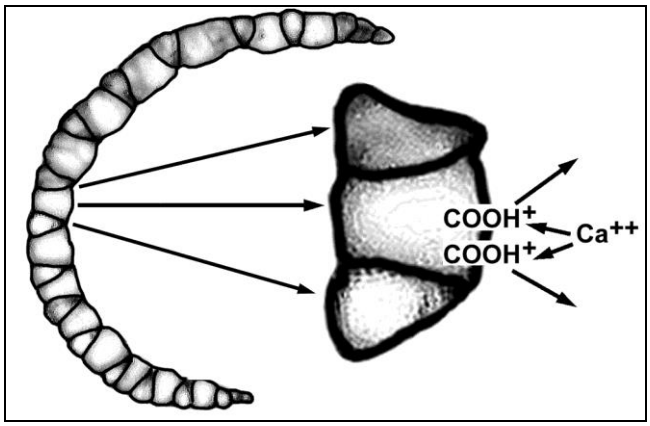


Figure 13. View of leaf cross section of ***Sphagnum*** (**left**) with two enlarged chlorophyllous cells and hyaline cell on **right**. Enlargement shows **carboxyl groups** ($COOH^+$) of the **polyuronic acid** and one Ca^{++} that will exchange for two H^+ ions in cation exchange. Drawing by Janice Glime.

Figure 14. ***Pseudoscleropodium purum***. Photo by Michael Lüth, with permission.

Figure 15. ***Tomentypnum nitens***, a species in which the Mg^{++} and Ca^{++} correlate with surface water concentrations. Photo by Michael Lüth, with permission.

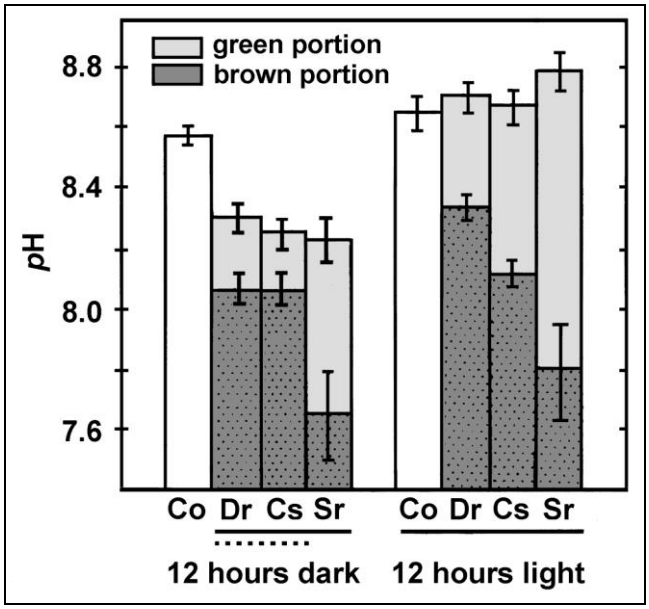


Figure 16. Comparison of *p*H-lowering ability of three mosses from an alkaline fen, Lawrence Lake, Barry County, Michigan, USA, following 48-hour incubation. Co = control lake water, Dr = ***Drepanocladus revolvens*** (=***Scorpidium revolvens***; Figure 17), Cs = ***Campylium stellatum*** (Figure 18), Sr = ***Sphagnum russowii*** (Figure 41). 12 hours dark and light indicate last cycle completed. Vertical lines represent 95% confidence intervals. Horizontal lines indicate no significant differences among green (active) (——) and brown (senescent) (• • •) moss species (distribution-free multiple comparisons test, $\alpha = 0.05$; n = 10). Starting *p*H = 8.25. From Glime *et al*. 1982.

Figure 17. ***Drepanocladus revolvens***, an alkaline fen moss that lowers the *p*H of its medium. Photo by Michael Lüth, with permission.

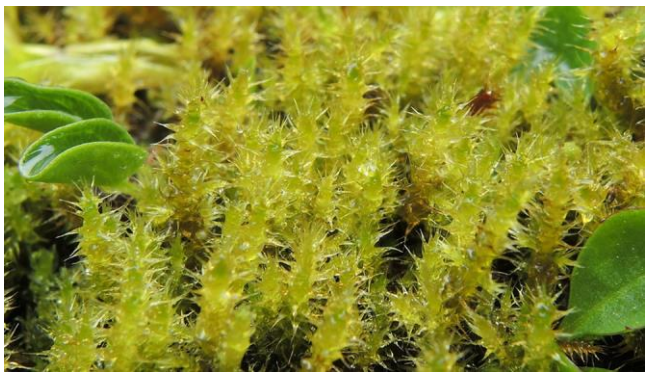


Figure 18. ***Campylium stellatum***, alkaline fen moss that lowers *p*H of surroundings. Photo by Michael Lüth, with permission.

Cation Competition

So how does competition between cations happen? Divalent cations such as Ca^{++} and Mg^{++} require two binding sites. When there are many of these ions in the environment, they compete for binding sites, occupying two of them in paired sites. Other ions that require two sites then have more difficulty finding the pair of sites they need to bind.

Because plants have a finite number of exchange sites, ions must compete with each other for those locations. Thus, if one cation is in excess, it can cause cellular deficiency of other cations that are unable to gain access to these exchange sites. Based on their experiments with ***Hylocomium splendens*** (Figure 19) and ***Sphagnum***, using artificial precipitation, Gjengedal and Steinnes (1990) considered that cations such as Na^{+} and Mg^{++} in the precipitation may occupy exchange sites and affect the uptake of other ions by this competition. They found that uptake of Zn and Cd were *p*H dependent and that increasing temperatures increased the uptake for all four of the metals tested (Ca, Cu, Pb, Zn).

Figure 19. ***Hylocomium splendens***, a species in which cations such as Na^{+} and Mg^{++} in the precipitation may occupy exchange sites and affect uptake of nutrient cations. Photo by Michael Lüth, with permission.

Figure 20. ***Calliergonella cuspidata***, a species whose growth is inhibited at high Ca concentrations. Photo by Michael Lüth, with permission.

Complexing reactions with anions such as Cl^{-} may also interfere with uptake. When Bates and Farmer (1990) applied $CaCl_2$ to three bryophytes, their responses varied by habitat. ***Pseudoscleropodium purum*** (Figure 14) and

Calliergonella cuspidatum (Figure 20) from chalk soil exhibited significantly reduced growth at high Ca concentrations (5 mol $CaCl_2$ m^{-3}), whereas ***P. purum*** and ***Pleurozium schreberi*** (Figure 2) from acidic clay were unaffected by the additions. The mosses from the chalk soil had lower initial tissue levels of K and Mg, suggesting that the additional $CaCl_2$ caused deficiencies in these nutrients through exchange site competition.

Ions in the external solution will first establish equilibrium with the exchange sites (Brown 1982). This physical process is completed very rapidly in the lab, but may require days in the field (Brown & Bates 1990). Once that is established, the remaining ions are available for uptake to the interior of cells (Pickering & Puia 1969). Hence, high concentrations of minerals will ultimately increase the uptake.

The number of exchange sites seems to be adaptive, at least in ***Sphagnum***. ***Sphagnum*** section ***Acutifolia*** (Figure 21), which inhabits drier locations, has more exchange sites per unit of biomass than do members of section ***Cuspidatum*** (Figure 22), which are wet hollow species (Brown 1982). Both Clymo (1963) and Spearing (1972) showed that the number of exchange sites correlated positively with height above water of the optimum habitat for ***Sphagnum*** species. This permits hummock species to hold nutrients on their cell surfaces until they are needed without having to wait for rainfall to provide a new source.

Figure 21. ***Sphagnum fuscum*** (Section **Acutifolia**) hummock, a ***Sphagnum*** species with a high number of cation exchange sites. Photo by Jutta Kapfer, with permission.

Figure 22. ***Sphagnum cuspidatum*** (Section **Cuspidatum**), a wet hollow species with a relatively low number of cation exchange sites. Photo by Jutta Kapfer, with permission.

Monovalent ions have little effect on CEC for divalent ions (Brehm 1968). But CEC of monovalent cations drops to 0.025 - 0.14 times capacity when in company of divalent cations, presumably due to double binding of divalent ions, much like doubling the strength of a magnet.

Brehm found that dead and living material have the same CEC on a dry weight basis. Nevertheless, living ***Sphagnum*** (Figure 21-Figure 29) cells contain most of the K^+ and Na^+, Ca^{++} is mostly on the external exchange sites, and Mg^{++} is on both locations. On the other hand, branches and stems of ***Sphagnum*** have very different CEC. The living ***Sphagnum*** is able to maintain a relatively constant cellular content of cations, even when the concentrations of the medium varies widely.

The ability of an exchange site to hold a given positively charged ion depends not only on the valence (charge) of the ion, but also on concentration. When there is a flood of H^+ ions, these will replace the other, more rare and higher mass cations. Again, this is like a magnet; it is harder for a magnet to hold something heavy than something light (like H^+). Hence, basic cations from the bryophyte surface are released into the soil (Foth & Ellis 1997). A striking example of this phenomenon is the case of acid rain making a ***Sphagnum*** (Figure 21-Figure 29) peatland alkaline and causing the ***Sphagnum*** to die! (Kilham 1982). The acid rain caused the release of alkaline positive ions from the surrounding hillside, which ultimately washed into the peatland. Although ***Sphagnum*** is equipped to bind such ions and make its surroundings more acid, it was not equipped to handle the large concentration that resulted from the uphill release. Instead, cations such as Mg^{++} and Ca^{++} accumulated on the surface of ***Sphagnum*** and eventually killed it. In forested ecosystems, cations released from soil exchange sites become available to roots, may be leached from the organic layer into deeper layers, or may be lost through runoff.

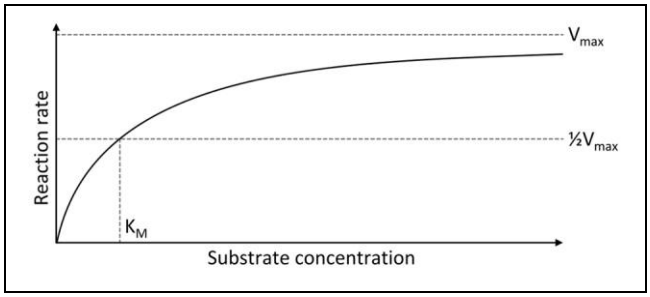
Heavy Metal Relationships

Several bits of information suggest that heavy metals like cadmium use cation exchange of low valence ions to aid their uptake. For example, in the thallose liverwort ***Dumortiera hirsuta*** (Figure 23), pretreatment with 80 mM KNO_3 causes higher Cd^{++} uptake, suggesting that potassium is able to strip exchange sites of competing cations, allowing higher valence cadmium to then strip some of those sites and enter cells (Mautsoe & Beckett 1996).

Figure 23. ***Dumortiera hirsuta***, a liverwort that uses cation exchange to take up heavy metals. Photo by Li Zhang, with permission.

The heavy metals, in turn, influence uptake of potassium and magnesium – two essential nutrients (Carballeira *et al*. 1999). The researchers suggested that loss of K, a very soluble nutrient, from the cells might be due to the effect of the heavy metals on the cell membranes, changing their permeability. The cation Mg^{++} was most likely displaced from the cation binding sites by the heavy metals.

In one experiment, three aquatic bryophytes were exposed for 60 minutes to solutions of 0, 1, 10, 50, 100, and 200 ppm each of Cd, Co, Cu, Ni, Pb, and Zn (Carballeira *et al*. 1999). Locations of these metals plus K and Mg were determined. Most metals remained on extracellular locations, rather than intracellular. On the other hand, only negligible amounts appeared in the particulate fraction. The relationship between water concentration and extracellular concentration could be modelled with a **Michaelis-Menten** equation:



$$v = \frac{d[P]}{dt} = \frac{V_{max}[S]}{K_M + [S]}$$

v = reaction rate
[S] = concentration of substrate S
P = product
t = time
V_{max} = max rate achieved at saturating substrate concentration
K_M = substrate concentration at which reaction rate is half of V_{max}
d [P]/dt = change in product per change in time

But the three aquatic species in this study by Carballeira *et al*. (1999) differed markedly. In ***Scapania undulata*** (Figure 24-Figure 25), the extracellular cation-binding sites demonstrated high metal affinity. On the other hand, ***Fissidens polyphyllus*** (Figure 26) has relatively low affinity. Nevertheless, ***F. polyphyllus*** had the highest internal concentrations of these metals at the end of the experiment. The uptake priorities were the same for all three species.

In these aquatic bryophytes, ***Fontinalis antipyretica*** (Figure 27), ***Scapania undulata*** (Figure 24-Figure 25), and ***Fissidens polyphyllus*** (Figure 26), the extracellular compartment held more metals than did the intracellular compartment (Vázquez Castro *et al*. 1999). The extracellular cation-binding sites of ***S. undulata*** had a high metal affinity, whereas it was relatively low in ***F. polyphyllus***. On the other hand, ***F. polyphyllus*** after the incubation in the metal solutions had the highest intracellular metal contents. All three species had the same ranking of metal uptake.

Uptake of heavy metals in these aquatic bryophytes led to considerable losses of intracellular K (probably due to effects on plasma membrane properties) (Carballeira *et al*. 1999). Similarly, Mg^{++} cellular contents decreased, but it was apparently due to competition by the metals on the binding sites, limiting uptake. Species differences were again interesting. ***Scapania undulata*** (Figure 24-Figure 25) exhibited the highest losses of K from internal cell sites, followed by ***Fontinalis antipyretica*** (Figure 27). On the other hand, ***S. undulata*** had the lowest losses of Mg from its extracellular exchange sites. These experiments help to explain competition among nutrients and locations in the short term, but long-term effects could be different, as seen in Chapter 8-3 on nitrogen.

Figure 24. ***Scapania undulata*** in its stream edge habitat. Photo by Michael Lüth, with permission.

Figure 25. ***Scapania undulata***, a species with high metal affinity on its cation exchange sites. Photo by Hermann Schachner, through Creative Commons.

Figure 26. ***Fissidens polyphyllus***, a species with low affinity for heavy metals. Photo by Janice Glime.

Figure 27. ***Fontinalis antipyretica***, a species that loses potassium and magnesium when exposed to heavy metals. Photo by Bernd Haynold, through Wikimedia Commons.

Much of what we know about uptake of minerals into plants comes from studies on these heavy metal pollutants. Cadmium, a common pollutant in areas with agricultural fertilizers and other human uses, moves from extracellular sites of the bryophytes to intracellular sites. In ***Rhytidiadelphus squarrosus*** (Figure 28) cadmium altered photosynthetic rates (Wells & Brown 1987). Its activity at the **plasmalemma** (cell membrane) may exercise control over other ions, affecting their accumulation within the cell, and *vice versa*.

Figure 28. ***Rhytidiadelphus squarrosus***, a species that has an altered photosynthetic rate in the presence of cadmium. Photo by Michael Lüth, with permission.

Differing Affinities

Breuer and Melzer (1990a) contributed to the explanation of ion competition using ***Sphagnum*** (Figure 21-Figure 29) from a high moor. They found that when two or more ions are present, there is an order to the binding success: $Pb^{++}>Cd^{++}\geq Ca^{++}>Mg^{++}>K^{+}>Na^{+}\geq NH_4^{+}$. Hence, those with higher binding affinities were able to suppress the binding of the lower affinity ions.

Breuer and Melzer (1990b) commented that ***Sphagnum*** (Figure 21-Figure 29) "shows behaviour of a relatively ideal ion exchanger." And, while species differ in their capacity, the coefficients of selectivity are independent of species. These bound cations can readily be displaced if another cation is present at a higher concentration, has a larger hydrated atomic radius, or has a higher valency (Bates 2000).

In ***Sphagnum*** (Figure 21-Figure 29) Hájek and Adamec (2009) found the exchangeable cation content decreased in the order of $Ca^{++} \geq K^{+}$, Na^{+}, $Mg^{++} > Al^{+++} > NH_4^{+}$, whereas the intracellular element content demonstrated the order of N > K > Na, Mg, P, Ca, Al. While Ca occurred primarily on exchange sites, Mg, Na, and especially K, Al, and N occurred inside the cells. Vertical position in the bog influenced the nutrient uptake and location. Hummock species have a higher cation exchange capacity (CEC) and accumulate more exchangeable Ca^{++}. By contrast, the hollow species have a lower CEC and accumulate more exchangeable Na^{+}, especially among the lower dead shoot segments. Intracellular N and P were consistently lower in the dead portions, indicating their translocation to growing upper portions. ***Sphagnum magellanicum*** (Figure 29) has about 40% lower N content in its cells compared to other species, suggesting its inability to compete for N. This can cause it to lose competition to other species (Hájek & Adamec 2009), but its drought tolerance aids it in occupying tops of hummocks (Li *et al*. 1992). This leaves us wondering why it has such a low N content.

Figure 29. ***Sphagnum magellanicum***, a species with low N content. Photo by Michael Lüth, with permission.

Rühling and Tyler (1970) demonstrated the order of binding affinity of several heavy metal cations using ***Hylocomium splendens*** (Figure 19): Cu ≅ Pb > Ni > Co > Zn ≅ Mn. In a two-hour experiment, these heavier cations preferentially bound to the exchange sites even when lighter cations of Ca^{++}, K^{+}, Mg^{++}, and Na^{+} were present in high concentrations. However, this sequence changed when the elements were supplied individually. Other researchers also demonstrated differences from this sequence in ***Rhytidiadelphus squarrosus*** (Figure 28) (Brown & Beckett 1985), ***Brachythecium rutabulum*** (Figure 7) (Brown & Buck 1978), and ***Pohlia nutans*** (Figure 30) (Webster 1985). These differences may relate to damage by some of the elements, such as cell membrane damage by mercury in some of the experiments,

concentration differences, and possible contamination from soil particles (Brown & Wells 1990).

Figure 30. ***Pohlia nutans***, a species of exposed, low-nutrient habitats. Photo by Michael Lüth, with permission.

In the moss ***Rhytidiadelphus squarrosus*** (Figure 28), competition occurs in the order of Cd ≅ H > Ca > Mg ≫ K on the extracellular sites (Wells & Brown 1990), suggesting that the low weight of H compensates for the higher valency of Cd. However, affinity of the intracellular Cd transport site occurred in the order of Ca > Cd > Mg ≫ K. Thus, internally calcium was a competitor for cadmium, but magnesium was not. Cadmium experienced maximum uptake at *p*H 5.6 and was very sensitive to *p*H. Potassium had no competitive ability against these ions. This presents another interesting question. How do internal differences in *p*H affect uptake, transport, and storage of ions? And what are the extent and locations of those *p*H differences?

Nieboer and Richardson (1980) found a divalent metal ion selectivity binding order of Pb > Cu > Cd > Co ≅ Fe > Ni > Zn > Mn, although Rühling and Tyler (1970) found a slightly different order for ***Hylocomium splendens*** (Figure 19): Cu ≅ Pb > Ni > Co > Zn ≅ Mn, an order that seems to be widespread in bryophytes (Bates 2000). However, once the sites are nearly fully occupied, this preferential binding is no longer the strongest force, possibly accounting for differences illustrated here. Isolated binding sites are only able to bind one position on the cation, hence eliminating the advantage for higher valency ions. In fact, at this stage, the isolated sites are more likely to bind univalent ions than divalent ones and more likely to bind divalent ones than trivalent ones (Richter & Dainty 1990). This is because divalent and trivalent ions require adjacent binding sites, whereas monovalent ions can utilize isolated sites. It is also likely that in systems with lower *p*H, more sites are occupied by H^+ ions, creating more isolated sites. This would favor the binding of lower valency ions such as K^+ and account for the high selectivity at a low *p*H.

Habitat Differences

Cation exchange sites can serve two conflicting purposes: bind the cations against further uptake, or concentrate them for absorption sites (Büscher *et al*. 1990). These roles have rarely been discussed for terrestrial bryophytes. This affects the bryophyte tolerance of various substrates. Using the **acidicline** (preferring soils with *p*H <5) species ***Atrichum undulatum*** (Figure 31), ***Leucobryum glaucum*** (Figure 32, ***Mnium hornum*** (Figure 33), and ***Polytrichum formosum*** (Figure 34, and the **neutrocline** (preferring *p*H close to neutral, *i.e.* >5) species ***Homalothecium sericeum*** (Figure 35) and ***Plagiomnium undulatum*** (Figure 36), Büscher *et al*. found that a**cidophilous** and **acidicline** taxa generally have lower CEC and are more able to tolerate the toxic aluminium (Al) levels, but not high levels of Ca. **Neutrocline** taxa instead avoid habitats with aluminium in the substrate and thrive on high calcium levels. (But what is the mechanism causing the avoidance?) They concluded that cation exchange properties do not protect mosses against potentially toxic ions, including aluminium, by sequestering them. But they did conclude that the exchange sites could increase the availability of cations. High CEC favored fixation of Al ions over Ca ions, indication that a low CEC is needed for taxa to tolerate acid soils.

Figure 31. ***Atrichum undulatum***, an **acidicline** species that has relatively low cation exchange capacity. Photo by Michael Lüth, with permission.

Figure 32. ***Leucobryum glaucum***, an **acidiphile** with lower numbers of cation exchange sites. Photo by James K Lindsey, with permission.

Figure 33. ***Mnium hornum***, an **acidiphile** with lower numbers of cation exchange sites. Photo by Tim Waters, through Creative Commons.

Figure 34. ***Polytrichum formosum***, an **acidiphile** with lower numbers of cation exchange sites. Photo by Michael Lüth, with permission.

Figure 35. ***Homalothecium sericeum***, a **neutricline** species with higher numbers of cation exchange sites. Photo by Michael Lüth, with permission.

Bates (1992) found that in epilithic and woodland soils the cation exchange capacity decreases with decreasing Ca content, and likewise with decreasing *p*H of the substrate. This change might help to protect the bryophytes against the toxic aluminium that increases in concentration in acidic solutions, *e.g.* soils polluted by acid rain.

Figure 36. ***Plagiomnium undulatum***, a **neutricline** species with higher numbers of cation exchange sites. Photo by Michael Lüth, with permission.

Calcareous rocks, inhabited by **calcicoles** (Ca-preferring species), typically have Ca^{++} concentrations 16-17 times that found in species from non-calcareous rocks (**calcifuges –** species avoiding Ca) (Bates 1982a). The calcicoles exhibit 3-4 times as many cation exchange sites as the calcifuges. Bates suggested that the calcicole mosses may require greater Ca^{++} concentrations to maintain cell membrane integrity.

Uptake Rate

Uptake of these nutrients is very rapid when concentrations are high. Half the maximum extracellular uptake can be achieved in 4.45±1.03 minutes in 100 µmol L^{-1} Cd (Brown & Beckett 1985). This rate is concentration dependent and at lower (more natural) concentration levels it can take several days to reach equilibrium (Mouvet 1987). Release of the cations from the exchange sites when the element is removed from the medium takes even longer, as shown in the aquatic liverwort ***Chiloscyphus polyanthos*** (Figure 37-Figure 38) (Maurel-Kermarrec *et al*. 1985). The uptake ability varies between clones that grow within meters of each other (Wells & Brown 1987; Wells 1988). This can result from differences in light/moisture availability in the open vs under shrubs, as demonstrated in ***Rhytidiadelphus squarrosus*** (Figure 28) (Wells & Brown 1987). This difference could have been caused by thicker cell walls in the higher light population of ***R. squarrosus***.

Figure 37. ***Chiloscyphus polyanthos*** in a typical habitat. Photo from <www.aphotofauna.com>, with permission.

Figure 38. ***Chiloscyphus polyanthos***, a leafy liverwort with cation exchange. Photo by Michael Lüth, with permission.

In summary, nutrient uptake into the moss is initially dependent on available exchange sites, but then it depends on affinity of a particular nutrient for appropriate transport sites of cell membranes, presence of competing elements, and turnover rate of the uptake site (Brown & Bates 1990), and perhaps cell wall thickness (Wells & Brown 1987).

Desiccation and Loss

Brown and Brumelis (1996) found that desiccation and duration of drought affected cellular location of elements in ***Hylocomium splendens*** (Figure 19), a boreal forest floor species. Rehydration partially reversed these effects.

When bryophytes become desiccated, nutrients leave the cells through leaky membranes (Bewley 1979). But Bates (1997) has shown that in ***Brachythecium rutabulum*** (Figure 7) and ***Pseudoscleropodium purum*** (Figure 14), leaked K^+ ions are able to remain on leaf surfaces (Figure 14), held there on exchange sites, and are re-absorbed upon hydration. Like tracheophyte roots, bryophytes utilize cation exchange sites to hold nutrients at their surfaces until those nutrients are moved into the plant.

Anion Uptake

Bryophytes also have exchange sites for **anions** (negatively charged ions), but these are far less abundant and likewise their role is less well understood (Clymo 1963). Even now, little is known about anion uptake. Wells and Richardson (1985) found that only living shoots of ***Hylocomium splendens*** (Figure 19) were able to accumulate arsenate and selenite, both **anions**. Arsenate uptake is inhibited by phosphate (anion) competition when both are supplied at the same time. On the other hand, if plants were incubated in phosphate before providing arsenate and selenite, it had no effect on their uptake. It appears that arsenate and selenite are accumulated by separate transport systems in this species and that these systems may be the ones responsible for phosphate uptake. *p*H was important, with arsenate uptake optima occurring between 3 and 5, whereas selenate was optimal at *p*H 3.

Polytrichum commune (Figure 4) has a well-developed conducting system and was the only bryophyte one study that had more uptake in brown portions than in green ones (Chapin *et al*. 1987). ***Sphagnum*** species were the only ones with significant P uptake in the current growth. But in seeming contradiction, the anionic form of N (nitrate) was preferred by ***Sphagnum*** over the cationic ammonium source of N (Rudolph *et al*. 1982). This preference likewise contradicts the results of Wanek and Pörtl (2008) who concluded that ***Sphagnum*** (Figure 21-Figure 29) prefers ammonium because of its numerous cation exchange sites. But it does coincide with the inhibition of nitrogen reductase by ammonium (Syrett & Morris 1963; Orebamjo & Stewart 1975). Furthermore, Wanek and Pörtl (2008) found that amino acids contributed a significant fraction of the N used by ***Sphagnum*** from the lowland rainforest in Puerto Rico

Brown (1982) suggested that anion adsorption is probably especially low in mosses because they have low iron and aluminium content and high cation exchange capacity Clymo 1963; Chapin *et al*. 1987). Phosphorus, as the phosphate anion, is taken up primarily from the mineral substrate (Bates 1992). Chapin *et al*. (1987) concluded that accumulation of the phosphate anion, as they observed in mosses of the Alaskan black spruce (*Picea mariana*, Figure 3) forest, was therefore by active absorption similar to that of higher plants. In these forests, mosses hold 17% of the phosphorus pool, despite accounting for 75% of the annual P accumulation. The mosses have a greater ability to absorb phosphate than do fine roots of the black spruce.

Proton Pumps

After ions have reached the surface of the cell, they require energy to enter the cell. In tracheophytes, the **proton pump** is well known in such activities as bringing nutrients into root hairs, opening and closing guard cells, closure of the Venus flytrap, and growth, to name only a few. In bryophytes, the proton pump has likewise been demonstrated, and like that of tracheophytes, it uses ATP to "pump" H^+ ions out of a cell (Figure 39). This leaves the cell with a negative charge that attracts cations into the cell (Raven *et al*. 1998). The resulting negative charge provides the force needed to bring in K^+, NH_4^+, Mg^{++}, Ca^{++}, sugars, and amino acids, and probably other cations that have not yet been confirmed experimentally.

Cotransport

As a positively charged ion enters the cell, it typically brings along an associated anion by **cotransport**. The pump, at the same time, regulates the *p*H within the cell to about 7.3-7.6. In bryophytes, the leaf cell surface and interstitial spaces between the cells provide sites where adhering cations are able to enter the cell through the proton pump mechanism.

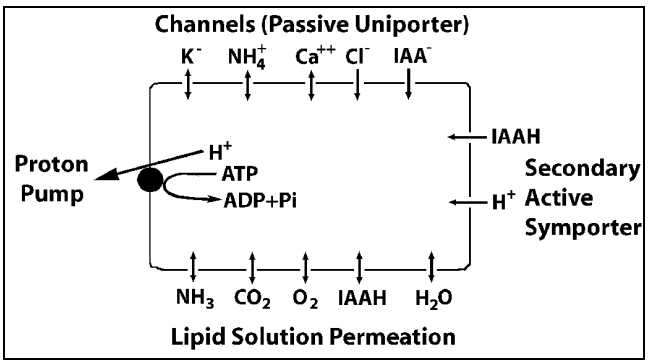


Figure 39. Known transport processes through the plasmalemma of a bryophyte cell. Diagram based on Raven *et al*. 1998.

As a result of ion movement through CEC and the proton pump, the bryophyte most likely has an influence on the **rhizoidosphere** (soil space immediately surrounding rhizoids) similar to that of tracheophytes on the rhizosphere (Raven *et al* 1998), although in the case of bryophytes, leaves may contribute to the alteration of conditions even more than the rhizoids. The rhizoidosphere is acidified in the process of cation exchange and proton pumping to bring nutrient cations into the cells, creating positive charges within the cells and accumulating organic anions in the cell vacuoles.

Pinocytosis

Pinocytosis results when a cell ingests a liquid by budding small vesicles inward from the cell membrane, thus containing the droplet. The droplet of liquid then is incorporated into the cell cytoplasm. Gullvåg *et al*. (1974) observed this mechanism in ***Rhytidiadelphus squarrosus*** (Figure 28) when it was treated with lead-rich particles in the lab. When they tested mosses that were exposed to lead pollution in the field, they found that the lead was bound within the nucleus. The importance of pinocytosis for incorporating nutrients into the cells of bryophytes seems to lack study.

Nanoparticles

The concept of nanoparticles is a relatively new idea in bryophyte ecology. Canivet *et al*. (2014) found, for the first time, that nanoparticles of iron in a mineral water suspension could penetrate the leaves of the moss ***Physcomitrella patens*** (Figure 40). In follow-up experiments Canivet *et al*. (2015) further demonstrated the penetration of iron nanoparticles into the moss ***Physcomitrella patens***. Using concentrations of 5 ng, 50 ng, 500 ng, 5 µg, and 50 µg per plant, they found no effect on ATP concentrations, reactive oxygen species, malondialdehyde, or glutathione, suggesting that the plants had not been physiologically harmed at any of these concentrations. The role of nanoparticles in providing essential nutrients or harming the plants seems to thus far lack exploration.

Figure 40. ***Physcomitrella patens***, a moss that can take up nanoparticles of iron. Photo by Michael Lüth, with permission.

Influence of Cellular Structures

Many studies have treated cellular influences as if the cells were homogeneous (Brown & Wells 1990). First, the nutrient must cross the cell membrane But in fact, once inside the cell, the nutrient may be held in solution, like K, or bound into amino acids and proteins, like some of the N and P. The chlorophyll molecule can take Mg out of play. When these binding compounds take the nutrient out of solution, they affect the concentration gradient from outside to inside the cell, affecting the concentration gradient used for the nutrient to cross the cell membrane and enter the cell. Others are bound to intracellular binding sites, again altering uptake rate.

Pickering and Puia (1969) described three phases of element uptake against time, an "unusual" process compared to that in algae and tracheophytes (Brown & Wells 1990). The first phase is the initial rapid uptake as the ions diffuse into interstitial spaces in the tissues (Pickering & Puia 1969). Then the uptake is controlled by equilibration with cell wall exchange sites. The final phase is a slow, linear increase of intracellular uptake. This third phase does not occur in dead material. As demonstrated in ***Rhytidiadelphus squarrosus*** (Figure 28), carriers can be used to transport the element across the membrane (Brown & Beckett 1985; Wells & Brown 1987). Specificity of these carriers determines how much inter-element competition there is for the intracellular uptake. This in turn affects the rate of uptake.

Location Is Important

As already noted, location of nutrients on and in the bryophytes is important (Brown and Buck (1985). The method used can present a bias that is misleading regarding normal nutrient concentrations. A nutrient adhering to the cell wall is not immediately available to the cells and may not be representative of the needs of the cells. Others may be held in the spaces within the walls. To fully understand the nutrient physiology, we must understand where these nutrients are located on and in the bryophyte plants (see Table 2).

Table 2. Element locations in bryophytes. Based on Brown 1982.

- in particles trapped by leaves
- in solution on exterior & in matrix of cell wall
- as ions bound to external exchange or chelating sites & on plasma membranes
- in solution in cytoplasm & vacuoles
- as insoluble substances in cytoplasm & vacuoles
- in leptome (especially Polytrichaceae)

New Growth

When new branches are formed and expand in the absence of additional nutrients, these nutrients must be obtained from existing tissues. In some cases, this is through **acropetal** (base to tip) transfer, as seen in ***Rhytidiadelphus squarrosus*** (Figure 28) (Wells 1988). Potassium, a very soluble nutrient, declines in lower portions as the apex grows. Calcium, on the other hand, is

not soluble and is taken from the initial apical segment, not transported from older tissues. Magnesium exhibited a somewhat similar response, but all segments lost Mg from intracellular sites as the apex grew.

Specificity

Some nutrients are taken up more easily than others. Leblond (2004) examined the uptake of heavy metals in the moss ***Pseudoscleropodium purum*** (Figure 14). The nutrient elements manganese and potassium had the highest retention. Non-nutrient ions of sodium, aluminium, and silica had the least retention. Youngest tissues accumulated the most nutrients, but internal redistribution occurred. Leblond found that soluble materials were taken in more easily than those deposited as particulates.

We know that cation exchange sites selectively bind higher valency cations (Richter & Dainty 1990). But at least in ***Sphagnum russowii*** (Figure 41-Figure 43) there are two classes of exchange sites. The well-known one is associated with polygalacturonic acids and accounts for more than 50% of the cation exchange capacity (Richter & Dainty 1989). In addition to that, **phenolic acids** account for about 25%, whereas **amino acid, sulfate ester,** and **silicate deposits** in the cell wall contribute to a lesser degree.

Figure 41. ***Sphagnum russowii***, a species with both polygalacturonic acid and phenolic acid exchange sites. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

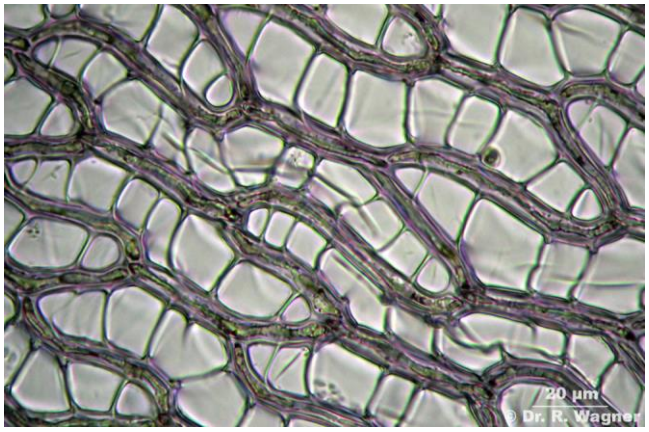


Figure 42. ***Sphagnum russowii*** leaf cells showing the exposed surface area of the hyaline cells (longer, wider cells with cross bars here). Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 43. ***Sphagnum russowii*** leaf cells in cross section showing the exposed surface area of the much larger hyaline cells where cation exchange can occur on both inside and outside of the cell. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

When studying aquatic bryophytes, Burton and Peterson (1979) found that 33% of the cell-wall-bound Zn could be removed by the enzyme **pronase** (mix of enzymes that break down proteins), suggesting that a considerable portion of its binding might be due to protein binding. Richter and Dainty (1989) found a small number of binding sites that are more specific to small valency cations such as potassium. If these sites include phenolic compounds, one can presume that such binding sites might be widespread in bryophytes, wherein phenolic compounds are common (Mues & Zinmeister 1988; Liao 1993; Basile *et al*. 1999). Is this yet another use for these presumed "secondary" compounds? If so, what does it mean for cycling of potassium if it can be bound to the cell walls? Does this help the plant to retain its valuable potassium when cell membranes, damaged by desiccation, permit potassium to leak from the cell? Such a mechanism could contribute to the survival of bryophytes after desiccation and permit them to become a long-term sink for this and other ions.

We know that cation exchange is a somewhat selective process. Higher valency ions are bound preferentially over lower ones because they occupy more than one exchange site. Cations have binding preferences (Nieboer & Richardson 1980, 1981). **Class A** includes K, Ca, Mg, and S. These elements prefer oxygen-rich ligands, such as carboxylic groups. **Class B** elements such as Ag, Cu, H, Hg, Pb, and Au are toxic and prefer ligands that are rich in sulfur and nitrogen. The third group is a borderline class that includes Cu^{++}, Ni^{++}, Pb^{++}, and Zn^{++}. Hence, the quantity of any element bound to the cell wall will depend on concentration in the medium (precipitation, water, soil), its affinity for type of exchange site, and the total number of suitable exchange sites.

Dead cells may actually have more exchange sites than live ones due to shrinkage of cell membranes that cover them on the inside. On the other hand, Wells (1988) found that when the cells are killed by a strong acid, the exchange capacity decreases, a phenomenon he attributed to loss of cytoplasm.

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Fortunately, bryophytes seem to have uptake specificity for things they need over things they do not. For example, the thallose liverwort ***Dumortiera hirsuta*** (Figure 23) preferentially took up Ca, Mg, and Zn over Cd (Mautsoe & Beckett 1996). When KNO_3 was used to pretreat the plants, Cd uptake occurred, suggesting that the high concentration of K^+ removed the competing ions from the exchange sites and they were subsequently replaced by Cd. Light and increased temperatures also stimulated Cd uptake. Even ***Sphagnum*** (Figure 21-Figure 29, Figure 41-Figure 44), the champion of cation exchangers, distinguishes among ions in ways that do not seem to depend strictly on valence. It accumulates Al and Mn, but excludes Cu and Zn, accumulating much less of these than the concentrations in the surrounding fen water (Li & Glime 1990).

Shimwell and Laurie (1972) found that ectohydric and mixohydric mosses differ in their absorption, retention, and excretion of heavy metals. During droughts, **ectohydric** (having external conduction) mosses excrete such heavy metals as Zn and Pb, forming surface crusts containing up to 6% Pb and 1-5% Zn. In **mixohydric** (having both external and internal conduction) mosses, on the other hand, the metals generally are located at the base of the moss carpet in the older growth, suggesting their accumulation in older tissues and lack of internal transport.

Seasons

Since most bryophytes gain most of their nutrients from precipitation, we might assume that most nutrient uptake therefore occurs when it rains. Yet the relationship is most likely not so simple. Francez and Loiseau (1999) found that ***Sphagnum fallax*** (Figure 44) was more efficient at intercepting applied N (as NH_4NO_3) in August than in June, even though August had the lowest rainfall. Dust accumulation can benefit bryophytes that are able to absorb nutrients in early morning dew and even on humid nights when there is no benefit for tracheophytes.

Figure 44. ***Sphagnum fallax***, a species that takes up more N in August than in June. Photo by Michael Lüth, with permission.

Bates (1992) considered that in rapidly growing species such as ***Brachythecium rutabulum*** (Figure 7) the seasonal deposition of tracheophyte litter is especially important. In the slower-growing species such as ***Pseudoscleropodium purum*** (Figure 14), wet deposition may be the most important.

Turner and coworkers (2003) found that rates of acid phosphatase activity in moss apices differed markedly among species, but most taxa had the most activity in winter and least in summer. Nevertheless, tissues maintained relatively constant N and P concentrations throughout the year. A negative correlation between phosphatase activity and P concentration in the tissues suggests that the enzyme may become active in response to phosphorus needs and serves to indicate nutrient stress.

Núñez-Olivera *et al*. (2001) found that seasonal differences in several aquatic bryophytes [***Fontinalis antipyretica*** (Figure 27), ***F. squamosa*** (Figure 45, ***Jungermannia eucordifolia*** (Figure 46), and ***Pellia endiviifolia*** (Figure 47)] did not mimic the seasonal differences in their native streams. Rather, the concentrations depended on the interactions of internal and external factors. The elements that had the most persistent annual cycle were mostly essential nutrients: N, P, and Fe, plus the non-essential Na. The lowest concentrations occurred in spring and the highest in autumn. Concentrations were lowest during periods of growth.

Figure 45. ***Fontinalis squamosa*** in alpine water. Photo from <www.aphotofauna.com>, with permission.

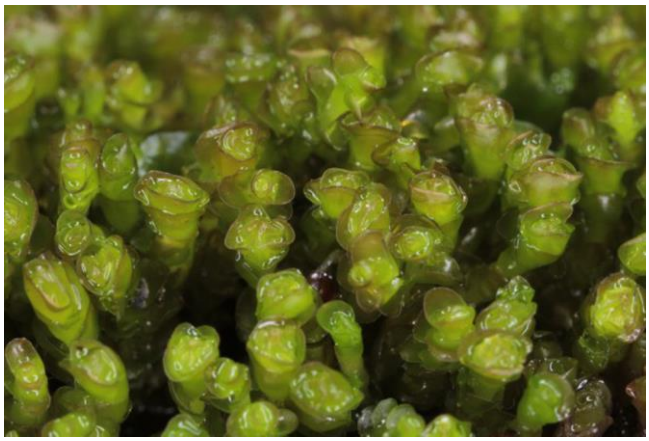

Figure 46. ***Jungermannia eucordifolia***, a species for which internal nutrient concentrations do not mimic those of its stream habitat. Photo by Jan-Peter Frahm, with permission.

Figure 47. ***Pellia endiviifolia***, a species for which internal nutrient concentrations do not mimic the seasonal changes of its habitat. Photo by Janice Glime.

Glucose Uptake

External glucose can enhance growth of at least some bryophytes (Jennings 1918). ***Ceratodon purpureus*** (Figure 48) grew 4-5 times as much when provided with glucose on nutrient agar compared to nutrient agar without glucose. This implies that organic sources of carbon that may be available in the substrate are suitable carbon sources for at least some mosses. Vujičić *et al*. (2009) found that the best conditions for axenic culture of the moss ***Dicranum scoparium*** (Figure 49) was in MS medium enriched with sucrose at 1.5% at 18-20°C.

Figure 48. ***Ceratodon purpureus***, a species that grows faster when external glucose is supplied. Photo by Michael Lüth, with permission.

Bryophytes can store their carbohydrates as sucrose and fructan, as exhibited in ***Porella platyphylla*** (Figure 50) and ***Sphagnum flexuosum*** (Figure 51-Figure 52) (Marschall 2010). Galloway and Black (1989) demonstrated that the bryophytes they tested have the necessary enzymes for sucrose to enter cellular metabolism by the sucrose synthase pathway. Adding glucose, fructose, and sucrose to the medium causes these bryophytes to down-regulate photosynthesis when the bryophytes are kept either in the dark or in the light (Marschall 2010). On the other hand, when no carbohydrates were added, darkness had little influence on total carbohydrates, suggesting that they maintain a well-regulated carbohydrate pool.

Figure 49. ***Dicranum scoparium*** on forest floor, a species that seems to benefit from added sucrose in culture. Photo by Janice Glime.

Figure 50. ***Porella platyphylla***, a species that stores carbohydrates as sucrose and fructan, growing better when these and other sugars are added to the growth medium. Photo by Janice Glime.

Figure 51. ***Sphagnum flexuosum*** in its habitat on the forest floor. Photo by Michael Lüth, with permission.

Figure 52. ***Sphagnum flexuosum***, a species that stores sucrose and fructan and down-regulates photosynthesis when sugars are available in the medium. Photo by Michael Lüth, with permission.

Sugars differ in their effects on bryophyte development (Sabovljevic *et al*. 2005). In ***Bryum argenteum*** (Figure 53), added sugars have a positive effect on development of the protonema and multiplication of the shoot. On the other hand, all tested sugars had a negative effect on both of these developmental stages in ***Atrichum undulatum*** (Figure 31).

Figure 53. ***Bryum argenteum***, a species for which added sugars have a positive effect on development. Photo from India Biodiversity Images, through Creative Commons.

Not only do bryophytes store sugars, but as we might expect as a consequence, they also release them (Coxson *et al*. 1992). In the tropical montane rainforest of Guadeloupe, frequent wet-dry cycles cause the epiphytic bryophytes to accumulate 950 kg ha^{-1} of sugars and polyols. These are released during rewetting, contributing to sugars available to other organisms in the canopy. The canopy leafy liverwort ***Frullania atrata*** (Figure 54) stored 17% of its dry biomass as sugar and polyol reserves, whereas the lower canopy species ***Phyllogonium fulgens*** (Figure 55) stored less than 6%. On the other hand, it was the lower canopy bryophytes that released the most sugars and polyols (0.9 g m^{-2}) during rewetting, compared to 0.3 g m^{-2} for the upper canopy. This release yielded an estimated 122 kg ha^{-1} from the upper canopy. These sugars contribute significantly to nutrient cycling by providing an energy source for the decomposer organisms.

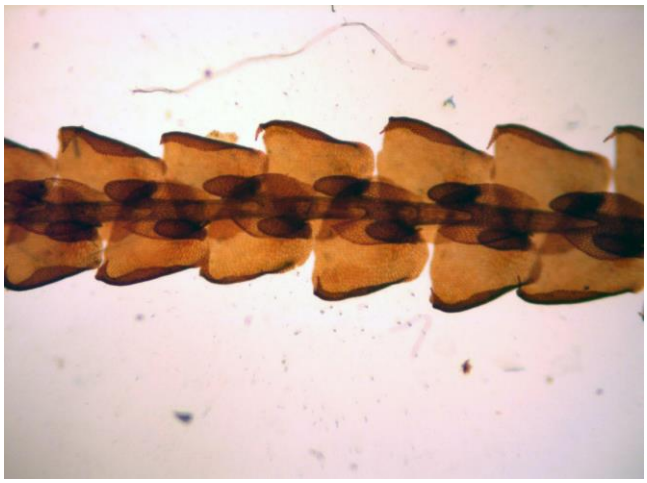

Figure 54. ***Frullania atrata***, a species that has 17% of its dry biomass as sugars in the canopy of a tropical cloud forest. Photo by Juan Larrain, with permission.

Figure 55. ***Phyllogonium fulgens***, a Neotropical species that lives in the lower canopy and stores less than 6% of its dry biomass as sugars. Photo by Michael Lüth, with permission.

Fungal Connections – Mycorrhizae?

One mode of uptake by bryophytes has largely been ignored by ecologists until recently, potentially causing researchers to be looking in the wrong places or not all important places for bryophyte effects on ecosystem nutrient budgets. That mode is by means of **mycorrhizae** (fungal associations that function in transfer of nutrients to roots or rhizoids) or similar partnerships with **fungi**.

In 1976, Kottke and coworkers recognized that the ability of mosses to compete was affected by differential growth stimulation of the mosses by fungi. Still, little attention was paid to moss-fungal interactions from an ecosystem perspective, but bryologists began noticing that many mosses seemed to have fungal hyphae associated with their underground parts. Meanwhile, the tree physiologists were recognizing that fungal partners were critical to the nutrient and water uptake of trees. And orchid growers recognized that the native fungi must be kept with the orchids for successful growth. Now, fungi are recognized as essential to the nutrient uptake of tree

roots, and stories about their partnerships with roots are replacing the traditional teaching emphasis on root hair mechanisms of uptake.

Ecologists estimate that 95% of all plant species are in genera that form mycorrhizal associations (Sylvia *et al*. 2004). In temperate and boreal forests, up to 95% of the short roots of trees form **ectomycorrhizae** [form of symbiotic relationship that occurs between a fungal symbiont and the roots (or rhizoids) of various plant species]. Mycorrhizae are critically important to most forest trees, which depend on them to increase surface area and contact nutrients in a much greater volume of soil than the tree is able to reach. Bryophytes, likewise, are able to take advantage of this partnership to reach sources otherwise unavailable to them. Even in the Antarctic, such fungal relationships can be important, as in the leafy liverwort ***Cephaloziella exiliflora*** (Figure 56) (Williams *et al*. 1994; Chambers *et al*. 1999). There are also indications that nutrients are transferred from the moss mat to the tree roots through mycorrhizae (Chapin *et al*. 1987). But we know little of the extent of these relationships.

Figure 56. ***Cephaloziella exiliflora***, a leafy liverwort with fungal associations in the Antarctic. Photo by Tom Thekathyil, with permission.

Although Boros reported a unique parasitic fungus on mosses in 1926, most botanists considered the bryophytes to be almost immune from fungal attack; even less attention was paid to the possibility of any sort of fungal partnership. In 1970, Kamal and Singh reported on the **rhizoidosphere** fungal flora of bryophytes. In 1975, Pirozynski and Malloch offered the theory that mycorrhizae were an essential part of the invasion of land by the original bryophyte-like plants, helping them to survive in an environment that was poor in nutrients and sustained frequent periods of desiccation. But actual proof of a mycorrhizal partnership, extant or extinct, was not forthcoming.

Finally, in the 1980's, reports of bryophyte mycorrhizal (shouldn't it be mycorrhizoidal?) associations began to appear in the literature (Parke & Linderman 1980; Rabatin 1980; Pocock & Duckett 1985a; Iqbal *et al*. 1988a, b; Ligrone 1988). These have included associations with ***Funaria hygrometrica*** (Figure 57) (Parke & Linderman 1980; Iqbal *et al*. 1988a), ***Sphagnum palustre*** (***cymbifolium***) (Figure 58-Figure 59), ***Polytrichum commune*** (Figure 4) (Iqbal *et al*. 1988a), and in ***Marchantia emarginata*** (=***M. palmata***, Figure 60) both rhizoids and the ventral thallus (Iqbal *et al*. 1988b).

Figure 57. ***Funaria hygrometrica*** protonemata and buds, as well mature plants with capsules – a mycorrhizal species. Photo by Janice Glime.

Figure 58. ***Sphagnum palustre*** habitat. Photo by Michael Lüth, with permission.

Figure 59. ***Sphagnum palustre***, a species with mycorrhizal associations. Photo by Michael Lüth, with permission.

Figure 60. ***Marchantia emarginata***, a species with mycorrhizal associations. Photo from Taiwan Mosses, through Creative Commons.

Ligrone and Lopes (1989) demonstrated **vesicles** and **arbuscules** ("little trees"; branched structures formed by fungi within plant cells; Figure 61) in both rhizoids and parenchyma cells of the thallose liverwort ***Conocephalum conicum*** (Figure 62), suggesting a true mycorrhizal association. The arbuscules are thought to be the site of nutrient exchange (Harrison 1999), at least in roots. Even ***Phaeoceros laevis*** (Figure 63), a member of the **Anthocerotophyta** and host of a ***Nostoc*** (**Cyanobacteria**; Figure 64-Figure 65) symbiont, has a fungal associate that appears to be mycorrhizal (Ligrone 1988). When ***P. laevis*** is infected, the plastid forms a networking structure, the vacuole mass decreases, and the organelle density increases, all modifications suggestive of a partnership.

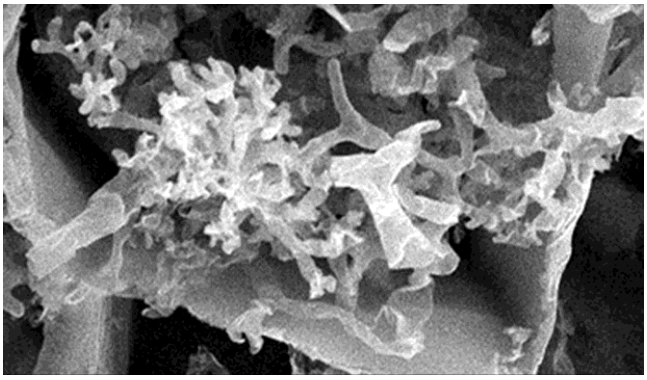

Figure 61. Arbuscules typical of those formed in roots by VAM fungi, but in this case within the thallus of the liverwort ***Marchantia foliacea***. Photo by Julia Russell, with permission.

Figure 62. Thallus of ***Conocephalum conicum***. Photo by Janice Glime.

Figure 63. ***Phaeoceros laevis*** sporophytes, a species with both **Cyanobacteria** (***Nostoc***) and a fungal associate. Photo by Robert Klips, with permission.

Figure 64. Colonies of **Cyanobacteria** (***Nostoc*** or ***Aphanothece***) with mosses. Photo by Janice Glime.

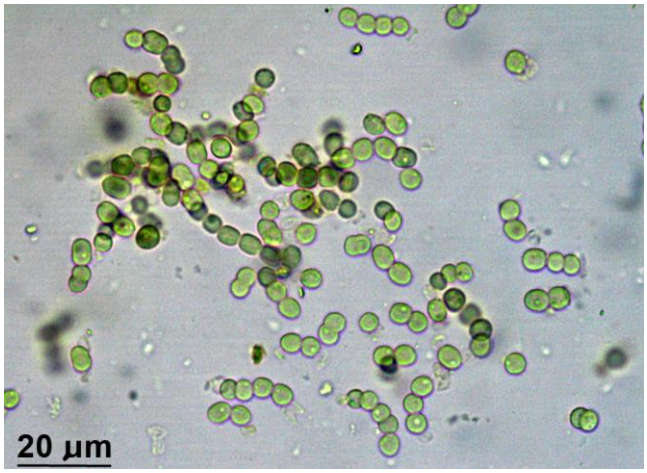

Figure 65. ***Nostoc*** colonies from the hornwort ***Anthoceros agrestis***. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

In 1985, Pocock and Duckett (1985b) investigated the rhizoids of 206 of the 284 British liverworts. They found that swollen rhizoids occurred in 33 species of the Jungermanniales and were always associated with fungal hyphae. Swollen and branched rhizoids were particularly well developed in the **Lepidoziineae** (Figure 66) and **Cephaloziineae** (Figure 94) and often occurred on flagelliform shoots, but were better developed on the

underground axes. Duckett *et al*. (1991) later described the highly specialized associations between ascomycetous fungi, known for their ectomycorrhizal partnerships, and 46 species of British liverworts. They found the majority of these ascomycetous fungi to occur with the leafy liverwort suborders **Lepidoziineae** and **Cephaloziineae**. [Ascomycetous associations are found in a relatively small number of families of leafy liverworts (Read *et al*. 2000)]. Strikingly, 33 of these 46 British liverwort taxa form flagelliform axes (Duckett *et al*. 1991). These axes have elongate parenchyma cells with abundant plasmodesmata in their transverse end walls. Their apices are mucilaginous and the subapical amyloplasts appear to act in detecting gravity, much as they do in protonemata. In addition to serving as perennating structures, these axes appear to be major organs of assimilation. Is this facilitated through a mycorrhizoidal partnership?

In all these leafy liverwort cases, the fungi infect the individual rhizoids independently, but most of these 46 taxa nevertheless have abundant fungi-infected rhizoids that extend 20-30 cm into the peaty substrate (Duckett *et al*. 1991). What an extension for a tiny bryophyte! In the liverworts ***Lepidozia*** (Figure 66), ***Kurzia*** (Figure 67), and ***Telaranea*** (Figure 68), but known in no others, the rhizoids swell prior to fungal infection. In ***Cladopodiella*** (Figure 69), the fungi form a pseudoparenchymatous sheath around the swollen rhizoidal tips.

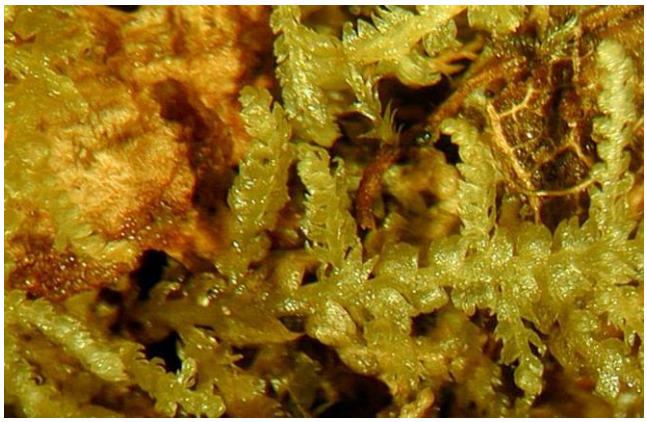

Figure 66. ***Lepidozia reptans***, a species in which rhizoid tips swell prior to fungal association. Photo by Michael Lüth, with permission.

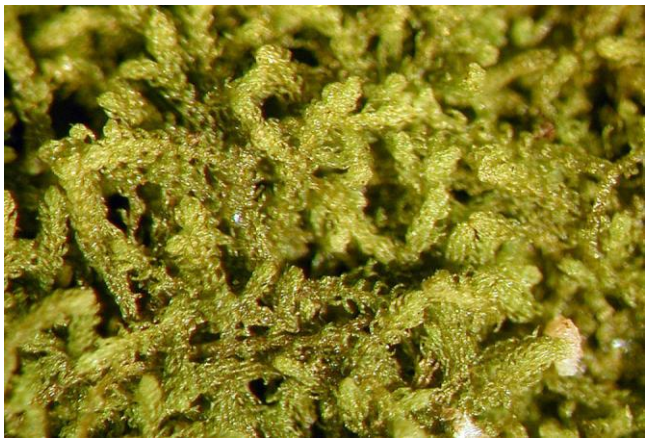

Figure 67. ***Kurzia cf trichoclados***, a species in which rhizoid tips swell prior to fungal association. Photo by Michael Lüth, with permission.

Figure 68. ***Telaranea nematodes***, a species in which rhizoid tips swell prior to fungal association. Photo by Michael Lüth, with permission.

Figure 69. ***Cladopodiella fluitans***, a species in which fungi form a sheath around rhizoid tips. Photo by Kristian Peters, with permission.

By 1988, Boullard had presented evidence that the fungal symbiotic relationship with the liverworts was evolutionarily very old. Yet, in 1990, During and van Tooren pointed out that "in only very few cases have these interactions been analysed functionally."

Other associations have been documented in the field. Although not truly mycorrhizoidal because they lack the composite structure definitive of this relationship, bryophytes now are known to enter into partnerships. Even buried wood, inoculated with ^{32}P, was able to provide P for the living tips of ***Hypnum cupressiforme*** (Figure 70-Figure 71) through a saprotrophic fungus, ***Phanerochaete velutina*** (Figure 72), that connected to the older parts of the moss (Wells & Boddy 1995).

Figure 70. ***Hypnum cupressiforme*** growing on a log. Photo by Michael Lüth, with permission.

Figure 71. ***Hypnum cupressiforme***, a species that is able to derive phosphorus from buried wood. Photo by David Holyoak, with permission.

Figure 72. ***Phanerochaete velutina***, a fungal associate of ***Hypnum cupressiforme*** on wood. Photo by James K. Lindsey, with permission.

The fungal association may in some small way benefit the neighboring plants, and they in turn the bryophyte (Duckett & Read 1995). As noted earlier, Chapin *et al*. (1987) have found an association that may indeed benefit the trees. In an Alaskan forest they found that the mycorrhizal fungi of the black spruce (*Picea mariana*, Figure 3) stimulated the moss carpet above to release phosphorus to the tree roots! When the mycorrhizae were inhibited, more P remained with the mosses and less escaped from the plots, where it presumably went to tree roots.

Rhizoids of at least some leafy liverworts in the **Lepidoziaceae** (Figure 66), **Calypogeiaceae** (Figure 73), **Cephaloziaceae** (Figure 94), and **Cephaloziellaceae** (Figure 56) can be infected by the same fungus, ***Hymenoscyphus ericae*** (Figure 74), an ascomycetous fungus, that infects members of the Ericaceae such as *Calluna* (Figure 75), *Erica* (Figure 76), *Rhododendron* (Figure 77), and *Vaccinium* (Figure 78-Figure 79) (Duckett & Read 1995). So far, there appears to be no evidence of a transport pathway from moss to fungus to ericaceous plant or vice versa, but the presence of one of these host plants would enhance the opportunities for the fungus to grow there and thus provide greater opportunities for the fungus to join with the other host. This is similar to the partnership between *Monotropastrum humile* (an achlorophyllous flowering plant; Figure 80), a fungus, and a beech tree (*Fagus crenata*, Figure 81) (Kasuya *et al*. 1995). The fungus in the *F. crenata* appears to be the same as that in the *M. humile*, and evidence implies that the fungus joins the two tracheophytes. In this way, the *M. humile* could take advantage of the sunlight reaching the canopy of *Fagus crenata* by receiving carbohydrates from the canopy transferred through the fungus to the *M. humile*. The fungus appears to be a member of the Russulaceae (Figure 82) (Yamada *et al*. 2008; Matsuda *et al*. 2011).

Figure 73. ***Calypogeia azurea***, a leafy liverwort that can be infected with ***Hymenoscyphus ericae***. Photo by Hermann Schachner, through Creative Commons.

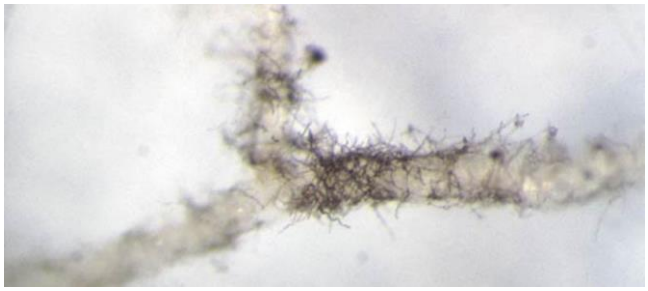

Figure 74. ***Hymenoscyphus ericae*** on ***Rhododendron*** root, a species that can infect leafy liverworts in **Lepidoziaceae** (Figure 66), **Calypogeiaceae** (Figure 73), **Cephaloziaceae** (Figure 94), and **Cephaloziellaceae** (Figure 56). Photo by Mark C. Starrett, David A. Heleba, and Adam R. Wheeler, through Creative Commons.

Figure 75. ***Calluna vulgaris***, a host for the fungus ***Hymenoscyphus ericae***. Photo by Janice Glime.

Figure 76. ***Erica*** sp., a host for the fungus ***Hymenoscyphus ericae***. Photo by Janice Glime.

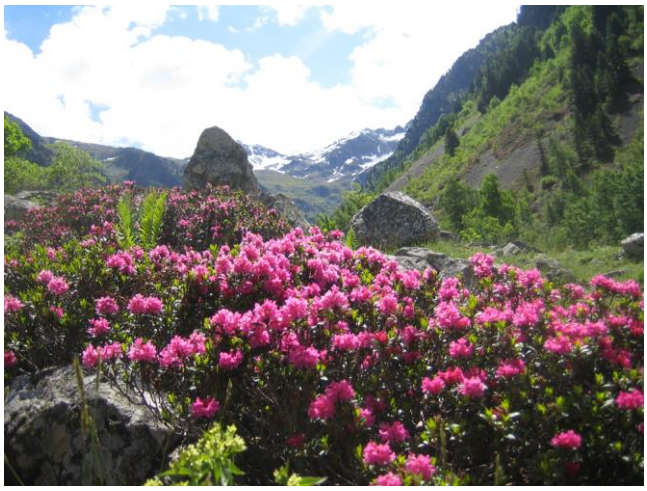

Figure 77. ***Rhododendron ferrugineum***, a host for the fungus ***Hymenoscyphus ericae***. Photo by Albert Kok, through Creative Commons.

Figure 78. ***Vaccinium angustifolium*** in ***Pinus banksiana*** forest. ***Vaccinium*** is a host for the fungus ***Hymenoscyphus ericae***. Photo by Photo by Mricon, through Creative Commons.

Figure 79. ***Vaccinium angustifolium***, a host for the fungus ***Hymenoscyphus ericae***. Photo by Mricon, through Creative Commons.

Figure 80. ***Monotropastrum humile***, an achlorophyllous flowering plant that partners with a beech tree through a fungal partner. Photo by Qwert, through Creative Commons.

Figure 81. ***Fagus crenata***, host tree for ***Monotropastrum humile*** and its fungal partner. Photo by Alpsdake, through Creative Commons.

Figure 82. *Russula.cavipes* with mosses, an ectomycorrhizal fungus in the family Russulaceae that is associated with *Monotropastrum humile* and *Fagus crenata*. Photo by James K. Lindsey, with permission.

Cryptothallus mirabilis

It appears that the fungi may be to some liverworts what the mycorrhizae are to the grape fern *Botrychium* and to many of the saprophytic forest floor flowering plants – a means of getting sufficient energy when the canopy is blocking an extensive portion of the light. Such a relationship is essential to the thallose liverwort ***Cryptothallus mirabilis*** (Figure 83), a European species known as ghostwort. It occurs nestled in mires and lacks chlorophyll. Certainly for it, a partnership is essential. But this liverwort has a **Basidiomycota** fungus as its ectomycorrhizal partner (Ligrone *et al*. 1993). They concluded that this liverwort is a **parasite**! It was thought that its fungal partner joined it to a species of *Betula* (birch), from which it ultimately obtained its carbohydrate energy source (Wiehle 1988; Pocock & Duckett 1984; Frey & Kürschner 1991; Read *et al*. 2000), much like the parasitic flowering plant *Monotropa uniflora* (Figure 84), the Indian pipe. However, Ligrone *et al*. (1993) disagree. They found that the fungi in *Betula* roots had a different morphology from those in the associated ***C. mirabilis***. It appears that the association of ***C. mirabilis*** is more like that of the goblin fern *Botrychium mormo*, wherein the fungus derives carbon from decomposing litter and transfers some of it to the fern, permitting it to live in low light (Gundale 2002). But could it also be that the form of the fungus depends on the host, thus differing between that of the ***C. mirabilis*** and that of the *Betula*?

Bidartondo *et al*. (2003) determined that ***Cryptothallus mirabilis*** (**Basidiomycota**; Figure 83-Figure 86) is an **epiparasite**, depending on a species of the fungus ***Tulasnella*** (Figure 85-Figure 86). This fungus forms **ectomycorrhizal** (symbiotic relationship between fungal symbiont and roots of plant species) associations with surrounding trees. It is able to transfer labelled ^{14}C from birch (*Betula*) seedlings in the lab, and presumably from tree roots in the field. Species of this same genus are also associated with ***Aneura pinguis*** (Figure 87) (Kottke *et al*. 2003) and some orchids (Clements & Ellyard 1979; Roche *et al*. 2010).

Figure 83. ***Cryptothallus mirabilis***, an achlorophyllous thallose liverwort in the **Aneuraceae**. This parasitic liverwort depends on a basidiomycete fungus to provide it with nutrients and energy. Photo by Michael Lüth, with permission.

Figure 84. ***Monotropa uniflora***, an achlorophyllous flowering plant that gets its carbon through its fungal partner. Photo by Magellan, through Creative Commons.

Figure 85. ***Tulasnella*** sp. ectomycorrhizae from a ***Betula pendula*** association. Photo courtesy of Martin Bidartondo.

Figure 86. ***Cryptothallus mirabilis*** and its symbiotic partner ***Tulasnella*** sp. Photo courtesy of Martin Bidartondo.

Figure 87. ***Aneura pinguis***, a species with chlorophyll and that is closely related to ***Cryptothallus mirabilis***. Photo by Michael Lüth, with permission.

When it develops, the ***Cryptothallus mirabilis*** (Figure 83) fungus (Figure 88-Figure 91) forms large, intracellular coils in the liverwort (Ligrone *et al* 1993). Then the liverwort cytoplasm proliferates and the starch content of its plastids decreases. As the hyphae die back and aggregate into large masses, the liverwort cells senesce. In ***C. mirabilis***, the fungal hyphae contain abundant glycogen and occasionally amyloid deposits. It is interesting that the fungal partner in ***C. mirabilis*** is identical to the one in ***Aneura pinguis*** (closely related but photosynthetic; Figure 87) from alpine sites but different from the fungus in ***A. pinguis*** from a chalk pit and sand dunes. In ***C. mirabilis***, net carbon transfer is to the liverwort, and it is likely that there is transfer from the fungus to the liverwort in ***A. pinguis*** as well. In addition to the morphological similarities, further support for this hypothesis in ***A. pinguis*** is that spores of both liverwort species fail to develop beyond a few cells in **axenic** (sterile) culture.

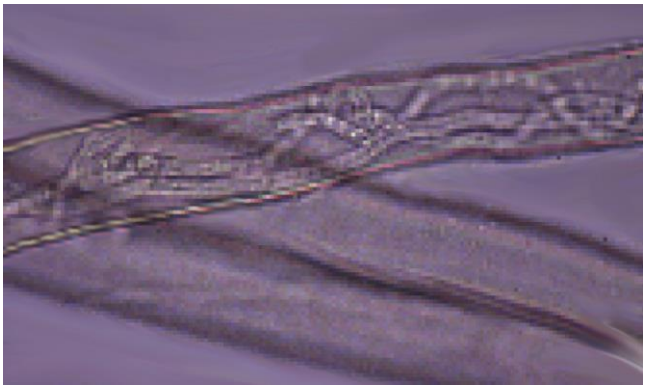

Figure 88. ***Cryptothallus mirabilis*** rhizoid with ***Tulasnella*** sp. Photo by Martin Bidartondo, with permission.

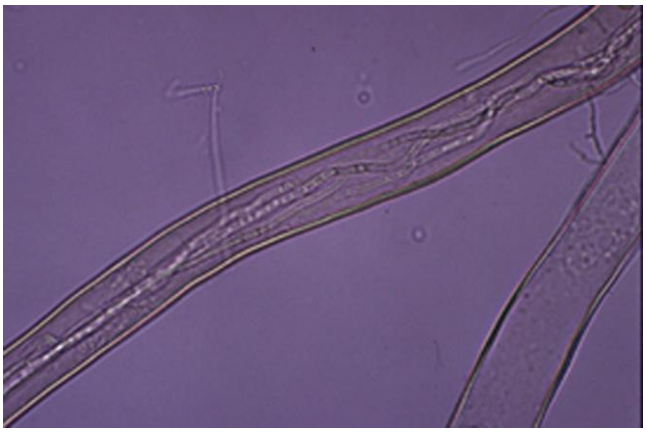

Figure 89. ***Cryptothallus mirabilis*** rhizoid with its fungal partner ***Tulasnella*** sp. Photo courtesy of Martin Bidartondo.

Figure 90. ***Cryptothallus mirabilis*** with ***Tulasnella*** sp. Photo by Martin Bidartondo, with permission.

Figure 91. ***Cryptothallus mirabilis*** with fungal partner ***Tulasnella.*** Photo courtesy of Martin Bidartondo.

Bidartondo and Duckett (2010) concluded that most of the thalloid liverworts contain **Glomeromycota** (Figure 92) that form arbuscular mycorrhizae with them. Many leafy liverwort species and members of the thallose **Aneuraceae** have a relationship with **Basidiomycota**. Whereas the **Aneuraceae** associate almost exclusively with species of ***Tulasnella***, eight leafy liverwort genera predominately associate with members of ***Sebacina vermifera*** (**Basidiomycota**; see Figure 93). ***Sebacina*** species have a habit of surrounding plants, so some of them may envelop the plants and prevent photosynthesis. It is interesting to note that when multiple species of bryophytes occur together, they rarely share the same fungal species. Furthermore, the bryophyte symbioses are not like those of the tracheophytes.

Figure 92. ***Claroideoglomus claroideum***, a member of **Glomeromycota**, common on bryophytes. Photo from Biomesfirst09, through Creative Commons.

Figure 93. ***Sebacina incrustans***, a jelly fungus, on moss, surrounding it an ultimately able to kill it. Photo © Slavko Serod, with online permission for non-commercial use.

Underground and Other Partnerships

It appears that ***Cryptothallus*** (Figure 83) is not the only liverwort capable of living below ground with an **Ascomycota** fungal partner (Duckett *et al*. 1989). In bog communities, the leafy liverworts (**Jungermanniales**) ***Cephalozia*** (Figure 94), ***Cladopodiella*** (Figure 69), ***Kurzia*** (Figure 67), ***Lepidozia*** (Figure 95), ***Odontoschisma*** (Figure 96), and ***Telaranea nematodes*** (Figure 68) can all develop extensive underground stem systems with numerous rhizoids that have swollen, fungus-containing tips. These liverworts can produce new shoots down to 24-30 cm in peat and to 10 cm in rotten logs (***Lepidozia reptans***, Figure 95).

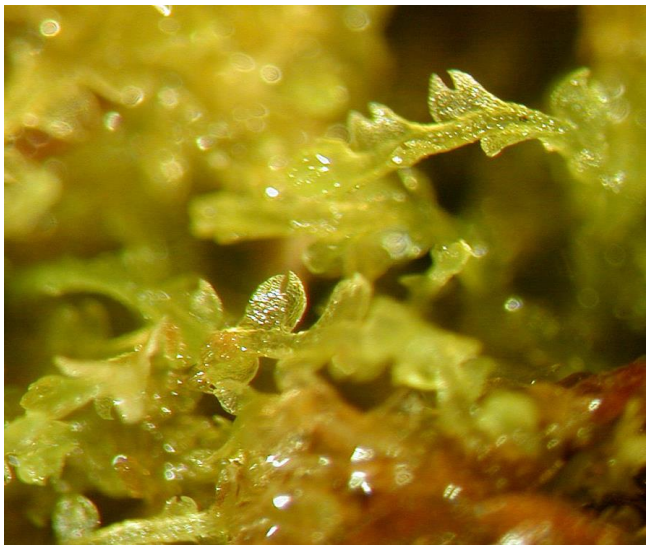

Figure 94. ***Cephalozia macrostachya***, member of a genus that houses fungi in swollen rhizoid tips in bogs. Photo by Michael Lüth, with permission.

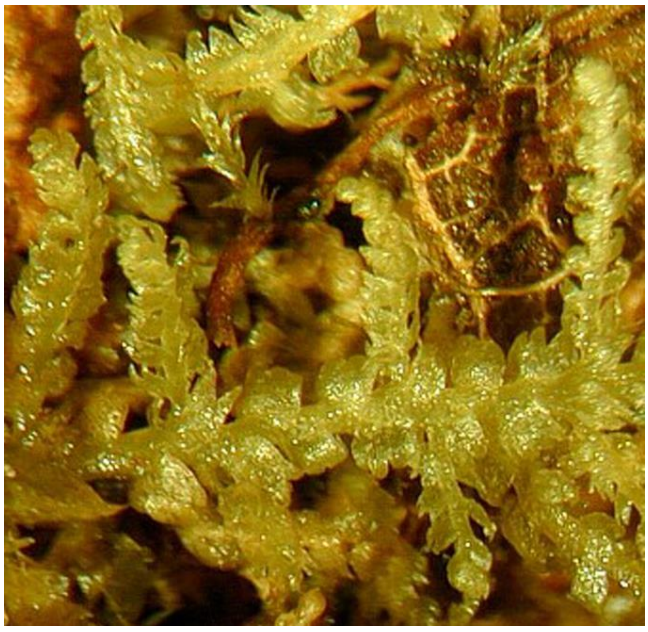

Figure 95. ***Lepidozia reptans*** growing on rotten wood that its rhizoids can penetrate down to 10 cm. Photo by Michael Lüth, with permission.

Figure 96. ***Odontoschisma macounii***, a species that houses fungi in swollen rhizoid tips in bogs. Photo by Michael Lüth, with permission.

In Malaysia, members of the leafy liverwort family **Lepidoziaceae** (Figure 95) can produce such axes down to 1.5 m in the peaty soil of the upper montane rainforest (Duckett *et al*. 1989). When these develop in the dark, they retain their partnership morphology, but when the shoots are exposed to light they regenerate into leafy shoots and lose their gravitropic response. This loss of fungal partnership morphology appears to be related to the disappearance of subapical amyloplasts, known to have a gravimetric response. Duckett and coworkers suggest that these liverworts may be acting as alternative hosts to ericaceous mycorrhizae, particularly in places like Malaysia. In Great Britain, less than 20% of the **Jungermanniales** (Figure 94-Figure 95) have rhizoidal fungi, whereas in the montane forests of Malaysia, where ericaceous shrubs are extensive, the percentage may be as high as 80-90%.

As the search continues, more and more fungal taxa are being described in bryophyte associations, but not all are mycorrhizal (Khan *et al*. 1997; Döbbeler 1997; Brouwer 1999). In fact, a number appear to be parasitic; others are just coexisting, perhaps benefitting from the modulated temperature and moisture. Nevertheless, approximately 300 species of **Ascomycota** appear to grow obligately on bryophytes (Döbbeler 1997). More than 40 species of **Ascomycota** in six orders occur on the **Polytrichaceae** alone, primarily on ***Polytrichum*** *s.l.* (Figure 4, Figure 34) and ***Dawsonia*** (Figure 97) (Felix 1988). Some fungi, for example ***Lemprospora*** (Figure 98) and ***Octospora*** (Figure 99), are known only from bryophytes (Döbbeler 1997; Brouwer 1999); in other cases, the bryophyte has never been found without its fungal associate (Döbbeler 1997). ***Octospora*** and other genera infect the subterranean rhizoids of **Polytrichaceae** (Figure 4, Figure 34, Figure 97), while others occupy the spaces between the vertical leaf lamellae (Felix 1988). In fact, 20 different **Ascomycota** species are known to occupy that unusual habitat without apparently having any effect on the moss.

Figure 97. ***Dawsonia superba***, a genus that has **Ascomycota** associates. Photo by Jan-Peter Frahm, with permission.

Figure 98. ***Lamprospora seaveri***, a fungus that only occurs on bryophytes. Photo by G. Moyne, through Creative Commons.

Figure 99. ***Octospora excipulata***, a fungus that lives exclusively on bryophytes. Photo by Malcolm Storey, through Creative Commons.

Raspe and De Sloover (1998) suggested that the discomycetous fungus ***Mniaecia jungermanniae*** (Figure 100-Figure 101), which lives exclusively on leafy liverworts in the **Jungermanniales** (Figure 100), might have achieved the first step toward mutualism. This destructive parasite grows inside the bryophyte rhizoids but

does not seem to afford any direct benefit to the liverwort. It appears it has a long way to go to reach mutualism.

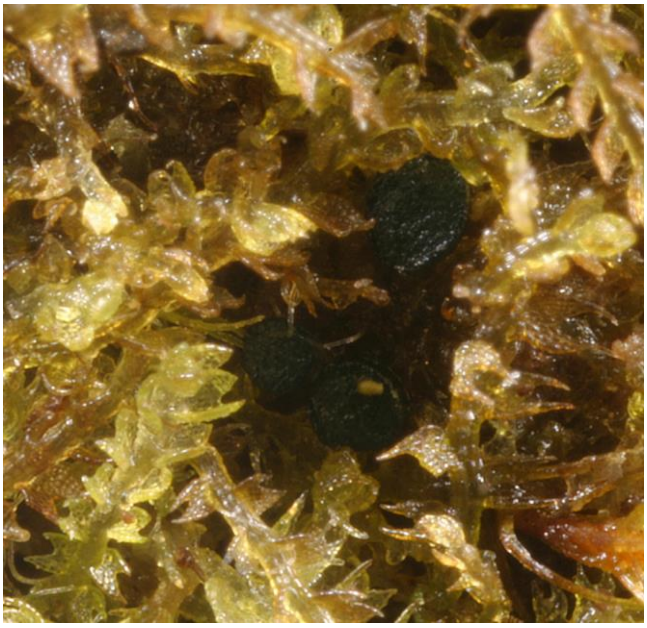

Figure 100. ***Mniaecia jungermanniae*** (fungus in center) on leafy liverworts. Photo by Malcolm Storey (DiscoverLife), with online permission.

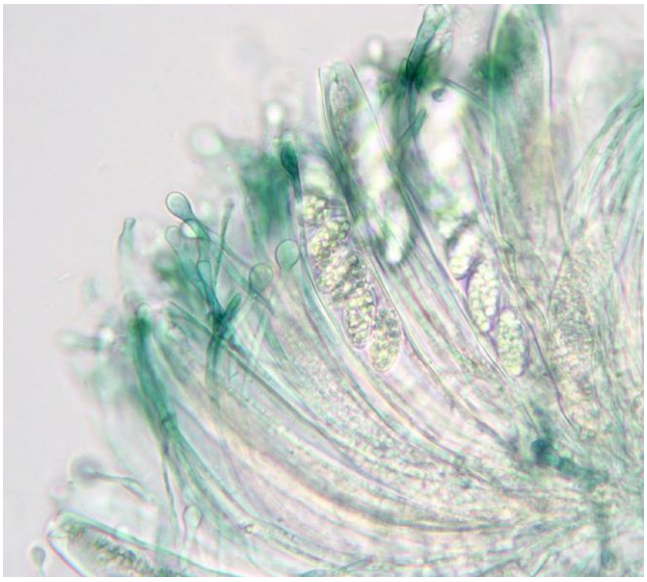

Figure 101. ***Mniaecia jungermanniae*** asci and ascospores. Photo by Malcolm Storey (DiscoverLife), with online permission.

We have noted several times that bryophytes obtain phosphate, and possibly other nutrients, from the bedrock. It is likely that at least in some cases fungi contribute to this nutrient source. Calling them "**rock-eating mycorrhizae**," Schöll *et al*. (2008) demonstrated that tunnels occur in mineral grains. They attributed these to hyphae from ectomycorrhizae that can dissolve mineral grains. Whether these fungi are directly associated with bryophytes, or they use litter or other plants for their carbon source, these fungi permit phosphates and other nutrients to enter nutrient cycling, potentially making some of them available to the bryophytes.

Arbuscular Mycorrhizae

Harrison (1999) reported that arbuscular mycorrhizae, restricted to the fungal order **Glomales** (**Zygomycota**, more recently named **Glomeromycota**; Figure 92), infected some bryophytes. Schüßler (2000) reported that a member of this order, ***Claroideoglomus claroideum*** (Figure 92), formed a mycorrhiza-like symbiosis with the hornwort ***Anthoceros punctatus*** (Figure 102-Figure 103). Following inoculation with spores, Schüßler found branched hyphae within the thallus within 20 days. This was the first definite experimental establishment of an arbuscular mycorrhiza-like association between a member of the **Glomales** and a bryophyte, although Felix (1988) had reported mycorrhiza-like associations in a number of taxa (Table 3). In 2003, Jakucs *et al*. found vesicles of a glomalean fungus in the moss ***Hypopterygium*** (Figure 104), suggesting that there might indeed be a mutualistic relationship in which the fungus also benefits, but that hypothesis still awaits verification.

Figure 102. ***Anthoceros punctatus*** with young sporophytes; ***Claroideoglomus claroideum*** forms a mycorrhizal association with this species. Photo by Des Callaghan, with permission.

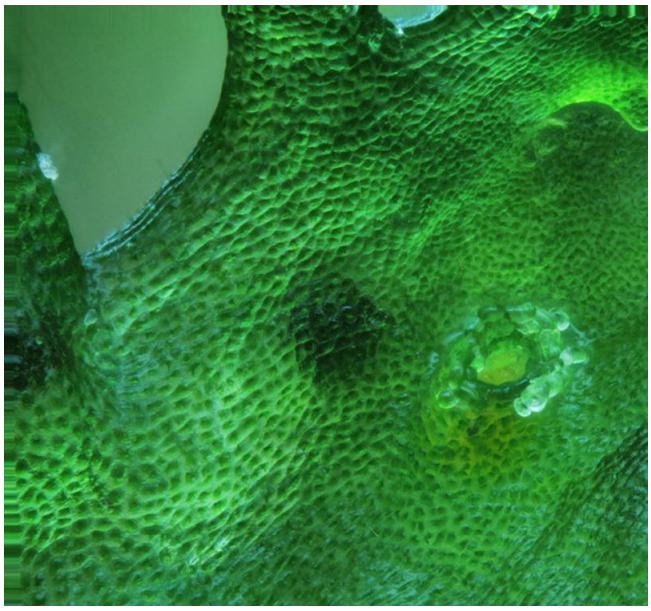

Figure 103. ***Anthoceros punctatus*** antheridial pit and ***Nostoc*** colony (dark area). Photo by Des Callaghan, with permission.

Figure 104. ***Hypopterygium didictyon***, a species that associates with a glomalean fungus (Figure 92). Photo by Juan Larrain, through Creative Commons.

Table 3. Mycorrhiza-like fungus-bryophyte associations. From Felix (1988) and Russell & Bulman (2004).

Fungus	Bryophyte	Reference
various spp	*Anthoceros*	Kamal & Singh 1970, Singh 1974
	Riccia	"
	Funaria	"
	Polytrichum commune	Grasso & Scheirer 1983
	Haplomitrium	Carafa *et al*. 2003
phycomycetous mycorrhizae	*Marchantia berteroana*	Baylis 1970
swollen rhizoids	liverworts	Pocock & Duckett 1985b
Endogone	bryophytes	Gerdemann 1968
Glomus tenuis	*Pogonatum*	Rabatin 1980
Glomus mosseae group	*Marchantia foliacea*	Russell & Bulman 2004
Claroideoglomus claroideum	*Anthoceros punctatus*	Schüßler 2000
Mycena cinerella	*Atrichum undulatum*	Hildebrand *et al*. 1978
	Brachythecium rutabulum	"
	Funaria hygrometrica	"

Figure 105. ***Mycena*** sp.; ***M. cinerella*** forms mycorrhizae with ***Atrichum undulatum***, ***Brachythecium rutabulum***, and ***Funaria hygrometrica***. Photo by James K. Lindsey, with permission.

Figure 106. ***Endogone pisiformis***, a genus known to form mycorrhizae with bryophytes. Photo by Adolf and O. Ceska, with permission.

There is a certain degree of specificity among the bryophyte species that have fungal associations. Russell and Bulman (2004) found that ***Marchantia foliacea*** (Figure 107-Figure 109) from two locations in New Zealand supported ***Glomus*** (Figure 109) (*n.b.*, many species of ***Glomus*** are now placed in ***Claroideoglomus***; Figure 92) arbuscular fungi internally (Figure 109), but that ***M. polymorpha*** (Figure 110) did not. Every ***M. foliacea*** thallus they examined contained this ***Glomus*** species in the parenchyma tissue around the midrib. The fungus invaded the thallus through the smooth rhizoids and grew upward through the thallus, forming arbuscules only in the upper portion of the thallus. The hyphae crossed directly through the cell walls of the liverwort. This same fungus forms mycorrhizal associations with the conifer, *Podocarpus* (Figure 111), and it may be that this fungus is shared by both plants. Unfortunately, we still have no evidence if this relationship between the fungus and the liverwort is truly symbiotic.

Figure 107. ***Marchantia foliacea*** thallus, a species that houses arbuscular growth of the mycorrhizal fungus ***Glomus*** (Figure 92) around the midrib. Photo courtesy of Julia Russell.

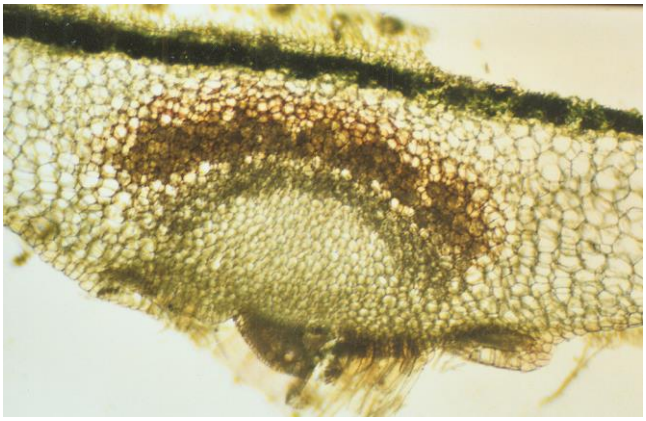

Figure 108. ***Marchantia foliacea*** thallus with arbuscular growth of the mycorrhizal fungus ***Glomus*** (Figure 92) around the midrib. Photo courtesy of Julia Russell.

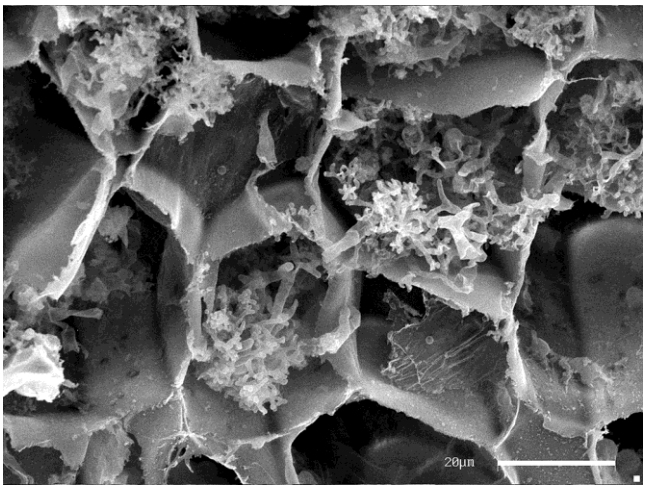

Figure 109. SEM ***Marchantia foliacea*** thallus with arbuscular growth of the mycorrhizal fungus ***Glomus*** in cells around the midrib. Photo courtesy of Julia Russell.

Figure 110. ***Marchantia polymorpha*** developing archegoniophores, a species that does not form an association with the fungus ***Glomus*** (Figure 92). Photo by Bob Klips, with permission.

The specificity of some of the groups for specific plant phyla is fascinating. For example, **Zygomycota** (Figure 112) colonize members of **Anthocerotophyta** (Figure 102) and **Marchantiophyta** (Figure 110, Figure 113), but not **Bryophyta** (Figure 104) (Read *et al*. 2000). On the other hand, members of the **Glomales** (Figure 92) isolated from the flowering plant *Plantago lanceolata* were able to colonize the thallose liverwort ***Pellia epiphylla*** (Figure 113) and produce arbuscules and vesicles.

Figure 111. ***Podocarpus***, a genus whose roots serve as host for ***Glomus*** (Figure 92) and may share it with bryophytes. Photo by Koppchen, through Creative Commons.

Figure 112. **Zygomycota** sporangia, a phylum that colonizes hornworts and liverworts, but not mosses. Photo by Kristi Yim, through Creative Commons.

Figure 113. ***Pellia epiphylla***, a species that can be colonized by the same member of **Glomales** as those found on the flowering plant *Plantago lanceolata*. Photo by Michael Lüth, with permission.

Figure 114. ***Plantago lanceolata***, a species that has the same fungal partner as ***Pellia epiphylla***. Photo by Forest & Kim Starr, through Creative Commons.

These fungal-bryophyte associations form structural associations similar to those of vesicular-arbuscular mycorrhizae of tracheophytes. Despite the large number of associations recognized between bryophytes and fungi, Read and coworkers (2000) still stressed the "need for analysis of the functional attributes of these symbioses." They presented further evidence that these fungal associations were ancient, being important to the first plants to colonize land. This contention is supported by fossil evidence of glomalean fungal structures associated with early bryophytes in Ordovician sediments that are 460 and 400 million years old (Remy *et al*. 1994; Redecker *et al*. 2000).

Beneficial or Harmful?

The fungal associates are not always beneficial to the bryophytes. Zobel *et al*. (1999) treated a sub-Arctic forest community with fungicide and found that the bryophytes and dwarf shrubs increased in biomass relative to the control. Could it be that the fungi are frequently stealing from the bryophytes and making nutrients available to trees?

Summary

Unlike tracheophytes, bryophytes take up nutrients over their entire surface. With leaves only one cell thick in most taxa every leaf cell is thus exposed to environmental sources of nutrients. The three most limiting nutrients (N, P, K) accumulate in the upper parts of the plants through active uptake, whereas Ca, Mg, and Na accumulate through passive **cation exchange**. Bryophytes have high **cation exchange capacity** (CEC) due to **polyuronic acids** in their cell walls. Once ions are bound on exchange sites, a **proton pump** removes H^+ ions from the cell, creating a **charge gradient** that brings in positive ions. These bring along negative ions by **cotransport**. It appears that bryophytes have two, perhaps more, types of exchange sites, permitting differential binding of ions. They also seem to have specificity for things they need over things they do not. Anion exchange sites can contribute to phosphate uptake. Abundance of cation sites compared to anion sites can account for the preference of ammonium (cation) over nitrate (anion).

Further active processes are able to distinguish ions formed by N, P, and K from more exchangeable cations such as those of Ca^{++} or Mg^{++}, and they are generally able to maintain relatively constant levels of these essential nutrients despite changes in environmental concentrations. Increasing temperatures increase the uptake, which is also pH-dependent. Some uptake occurs through **pinocytosis** and entry of **nanoparticles**.

Fungi are often associated with the rhizoids of bryophytes. It may be that a large number of bryophytes are afforded the advantages of fungal partner relationships, providing them with considerably more surface area for acquiring nutrients. The thallose liverwort ***Cryptothallus mirabilis*** has a fungal partner (***Tulasnella***) that provides carbohydrates for this non-chlorophyllous plant.

Many bryophyte-fungal associations have been discovered, but the types of interaction lack our understanding. We know that glomalean fungi are frequently associated with bryophytes, but the association has not been clearly described. This could be a very fruitful area for further research.

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CHAPTER 8-5

NUTRIENT RELATIONS: TRANSLOCATION AND TRANSPORT

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CHAPTER 8-5

NUTRIENT RELATIONS: TRANSLOCATION AND TRANSPORT

Figure 1. ***Bazzania trilobata*** and other bryophytes growing together. Note the dead tissue in the lower right part of the clump, where nutrient sinks can be mobilized to supply growing apical tissues. Such clumps can play a significant role in the distribution of forest nutrients. Photo by Michael Lüth, with permission.

Translocation and Transport

One of the most poorly understood abilities of bryophytes by "vascular" botanists is the ability of bryophytes to transport nutrients within the plant. Understanding that transport of nutrients occurs through specialized vascular tissue (xylem and phloem), they have sometimes assumed that the "non-vascular" bryophytes are unable to move substances from one part of the plant to another. Hence, the assumption has been that as bryophytes die (Figure 1), decomposition will return the component nutrients. But while bryophytes lack tracheids, vessels, and sieve cells, they do not lack the ability to transport substances from one part of the plant to another, *i.e.* **translocation**. In some cases, such as ***Polytrichum*** (Figure 17), they actually transport substances through their **leptoids** (phloem-like cells; Figure 2) and **hydroids** (xylem-like cells; Figure 2). Those mosses such as ***Polytrichum*** with well-developed leptoids form a **leptome**, similar to the cylinder of phloem in a tree trunk. The collective hydroids in the center of the stem form the **hydrome**, also known as the **hydrom**. But it is clear that lack of even these special conducting cells is no deterrent to transport or to translocation in bryophytes. Hence, we can find nutrient elements in a number of locations within and upon the plant (see subchapter 8-4).

One aid to the transport of substances from cell to cell is the presence of **plasmodesmata** in the cell walls (Mahmoud 1965; Oliver & Bewley 1984). These connecting threads permit substances to move from cell to cell without traversing cell membranes, although the movement is undoubtedly slower than that of the movement of water in the interstitial capillary spaces of cell walls.

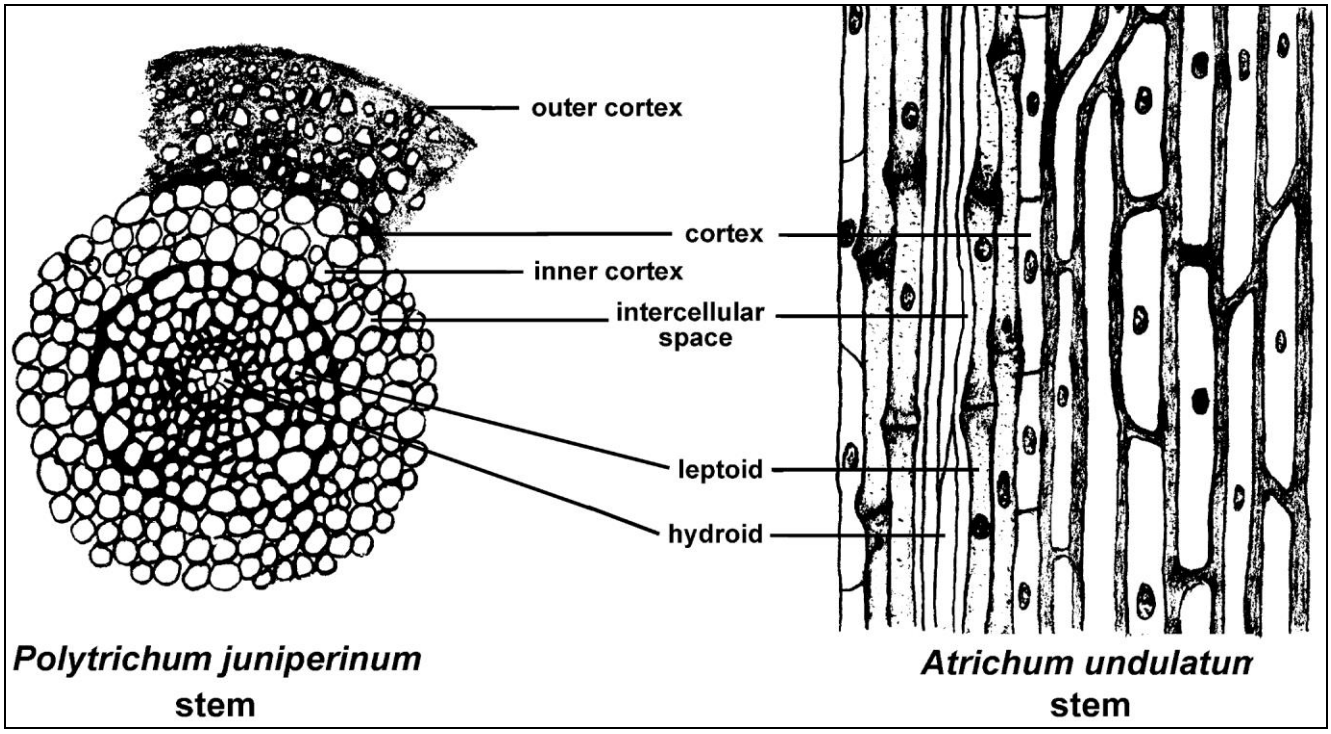

Figure 2. Cross section of ***Polytrichum juniperinum*** and longitudinal section of ***Atrichum undulatum*** stem to illustrate parts of central strand (leptoids and hydroids) and stem structures. Drawings by Margaret Minahan, based on Hébant (1977).

Duckett and Ligrone (2003) list several specific examples in their note "What we couldn't have done if we'd stayed in Europe: Selection and serendipity in the Southern Hemisphere." They demonstrated the presence of "food-conducting cytology" (*i.e.* food conducting cells) in the widespread groups of **Hookeriaceae** (Figure 3), **Neckeraceae** (Figure 4), **Orthotrichaceae** (Figure 5-Figure 6), and ***Sphagnum*** (Figure 7-Figure 11), as well as in most caulonemata and rhizoids. Furthermore, this food conducting organization is present in the axes of the primitive moss ***Takakia*** (Figure 12-Figure 13) and the moss-like leafy liverwort ***Haplomitrium*** (Figure 14-Figure 15), as well as being widespread in Marchantialian thalli.

Figure 3. ***Hookeria lucens*** (**Hookeriaceae**), a family with food-conducting parenchyma cells. Photo by Jonathan Sleath, with permission.

Figure 4. ***Neckera pennata*** (**Neckeraceae**) , a family with parenchyma food-conducting cells. Photo by Michael Lüth, with permission.

Figure 5. ***Orthotrichum pumilum*** (**Orthotrichaceae**), a family with food-conducting parenchyma cells. Photo by Michael Lüth, with permission.

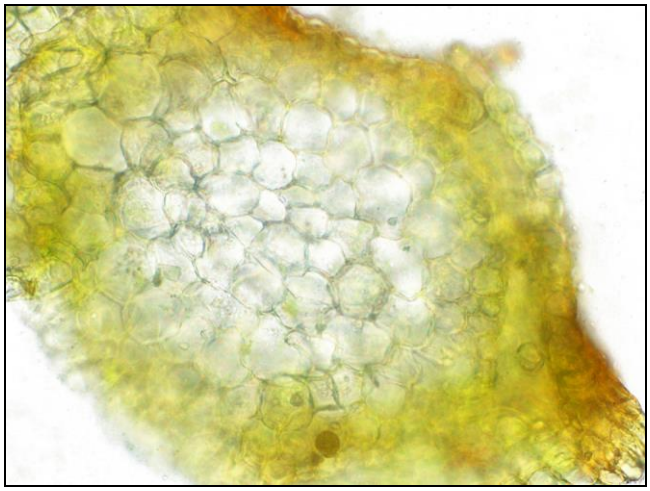

Figure 6. ***Orthotrichum pumilum*** (**Orthotrichaceae**) stem cs showing parenchyma cells in center of stem where nutrients can move from cell to cell. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 7. ***Sphagnum contortum***, a species with non-specialized food conducting cells. Photo by Michael Lüth, with permission.

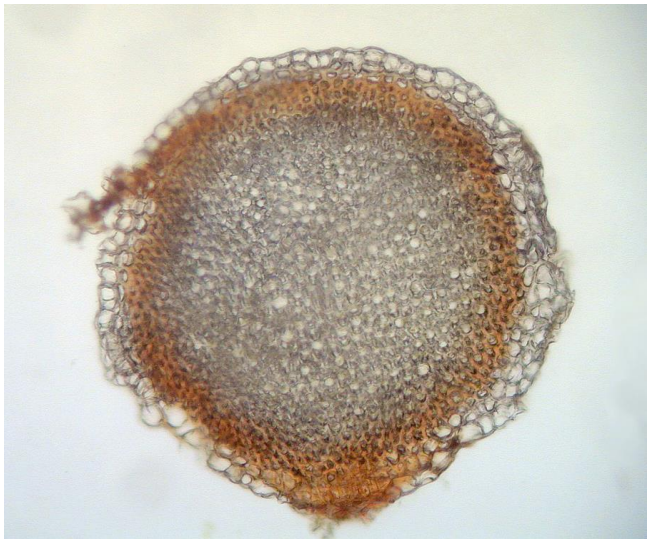

Figure 8. ***Sphagnum contortum*** stem cs showing lack of specialization in central food-conducting cells. Photo by Michael Lüth, with permission.

Figure 9. ***Sphagnum papillosum***, a species with non-specialized food-conducting cells. Photo by David Holyoak, with permission.

Figure 10. ***Sphagnum papillosum*** stem cs showing differentiation of stem cells with little differentiation in conducting cells in the center. Photo by Ralf Wagner <www.drralf-wagner.de>, with permission.

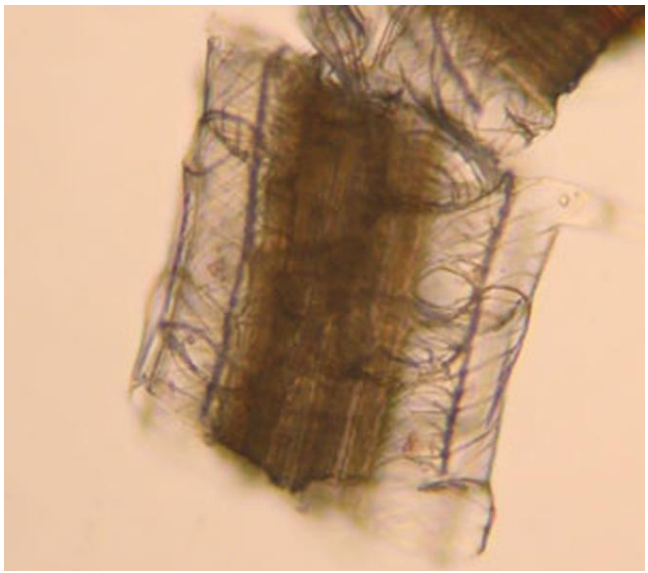

Figure 11. ***Sphagnum papillosum*** stem, vertical view, showing outer thin-walled cells and dense central core. Photo from Botany Website, UBC, with permission.

Figure 12. ***Takakia lepidozioides***, a primitive moss that conducts internally through cells that appear to be unspecialized. Photo by Rafael Medina, through Creative Commons.

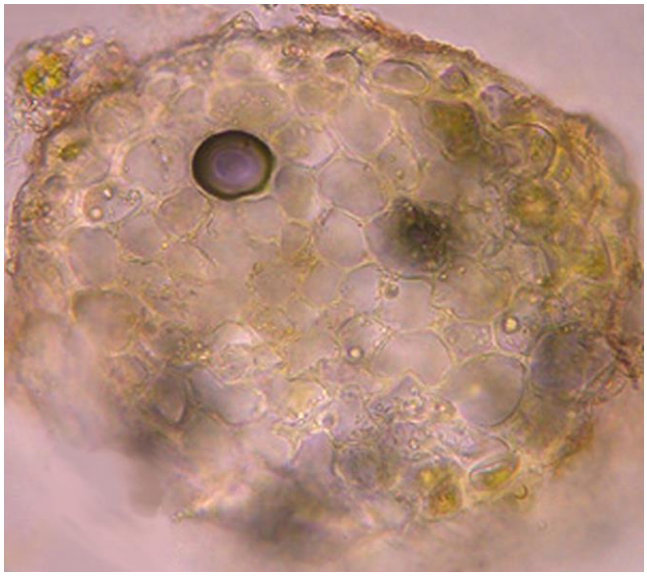

Figure 13. ***Takakia lepidozioides*** stem cs showing unspecialized conducting cells. Photo from Botany Website, UBC, with permission.

Figure 14. ***Haplomitrium hookeri***, a primitive liverwort that has some internal conduction. Photo by Des Callaghan, with permission.

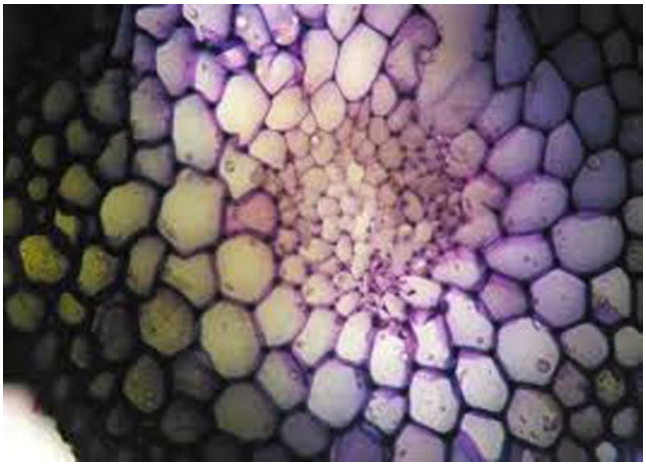

Figure 15. ***Haplomitrium*** stem cs showing differentiated cells in the center of the stem. Photo by Rachel Murray and Barbara Crandall-Stotler, with permission.

We have seen that bryophytes move water about internally as well as externally. There is ample evidence that they likewise move nutrients, hormones, and photosynthate within the plant, and of course, nutrients get moved externally with capillary water as well. Within stems, leptoids may serve to enhance nutrient movement; Hébant (1974) demonstrated that "sieve elements" (**leptome**) of ***Polytrichum commune*** (Figure 16-Figure 17) exude liquid. **Polytrichaceae** have highly specialized leptoids with polarized cytoplasmic organization within the axis. In the endohydric moss ***Polytrichastrum alpinum*** (Figure 18), labeled ^{14}C supplied as CO_2 travelled at the rate of 7.5 cm h^{-1} within the stems of a population in Point Barrow, Alaska, whereas in some tracheophytes, the rate may be little more than 1 cm per hour for water movement. In other mosses, including ***Sphagnum*** (Figure 7-Figure 11), less specialized parenchyma cells of the stem and seta carry out similar functions.

Figure 16. ***Polytrichum commune***, a moss with extensive internal conduction. Photo by Michael Lüth, with permission.

It does not require the sophisticated structures of ***Polytrichum*** (Figure 16-Figure 17) to move substances within mosses. Alpert (1989) demonstrated that photoassimilate moved from the leaves to the stem bases and even underground stems in ***Grimmia laevigata*** (Figure 19), a predominantly ectohydric moss, but he was unable to demonstrate any movement of mineral nutrients in this way (see stem of a related species, Figure 20).

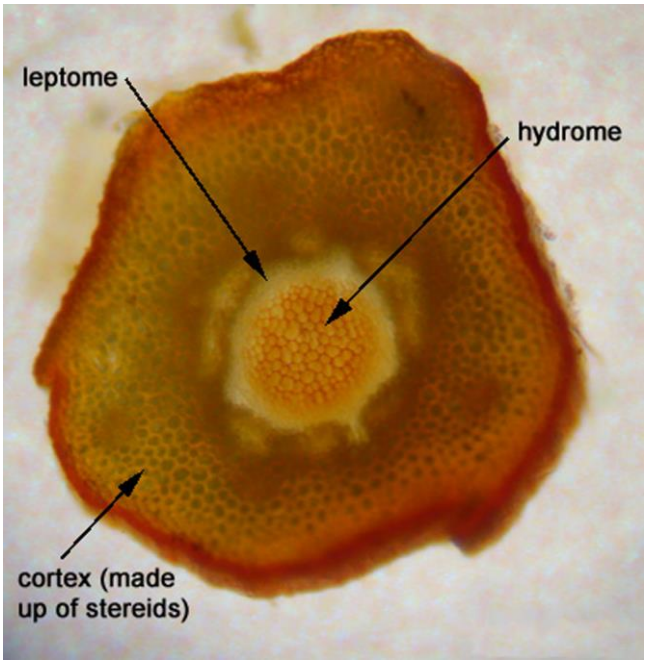

Figure 17. ***Polytrichum commune*** stem cs showing highly specialized conducting system with a leptome and hydrome. Photo from Botany Website, UBC, with permission.

Figure 18. ***Polytrichastrum alpinum*** with capsules, an endohydric moss. Photo by Michael Lüth, with permission.

Figure 19. ***Grimmia laevigata***, an ectohydric moss. Photo by Michael Lüth, with permission.

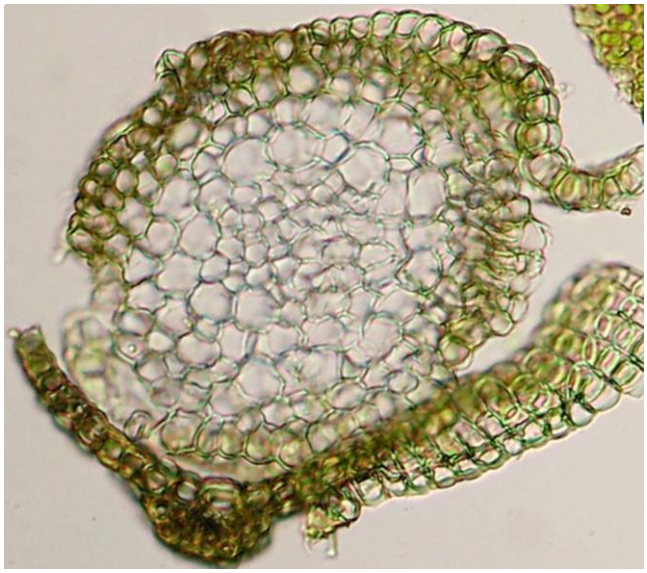

Figure 20. ***Grimmia pulvinata*** stem cs showing smaller cells in the central parenchyma cells of the stem. Photo from Botany Website, UBC, with permission.

Movement from Older to Younger Tissues

Consider the impact on our thinking when we discovered that even ***Sphagnum*** (Figure 7-Figure 11) moves nutrients from older, dead portions to younger tissues. Among these, it appears that in ***Sphagnum*** cellular N and P move to shoot segments, but that metallic elements do not (Hájek & Adamec 2009). Such ability permits it to live in extremely low nutrient habitats, yet have sufficient nutrients to sustain life and growth for centuries. Particularly in habitats such as true bogs, where all nutrients arrive through precipitation, the ***Sphagnum*** is able to trap and hold 50-90% of the deposited N (Li & Vitt 1997). This leaves little for tracheophytes, and Aldous (2002) found that the tracheophytes received less than 1% of that N supply.

Rydin and Clymo (1989) had already demonstrated that ***Sphagnum*** (Figure 7-Figure 11) is able to move both P and C upward through 7 cm of stem length. If the ***Sphagnum*** holds and relocates its N within its own tissues, the tracheophytes have little ability to compete for the limited supply of N they so greatly need. For example, Aldous (2002) demonstrated that ***Sphagnum capillifolium*** (Figure 21) translocates its N supply to growing tissues within the capitulum. In a relatively clean site in Maine, it moved 11-32% of its N and in an N-polluted site, it moved 64-83% within the 2-cm segments examined. Gerdol (1990) found that N, P, and K in ***Sphagnum*** of ombrotrophic bogs in the Alps were directly absorbed in the chlorophyllose cells (Figure 22), but also partly recycled from ageing tissues to the growing capitulum.

Figure 21. ***Sphagnum capillifolium*** (***nemoreum***), a species that moves its N to growing tissues in the capitulum. Photo by Aimon Niklasson, with permission.

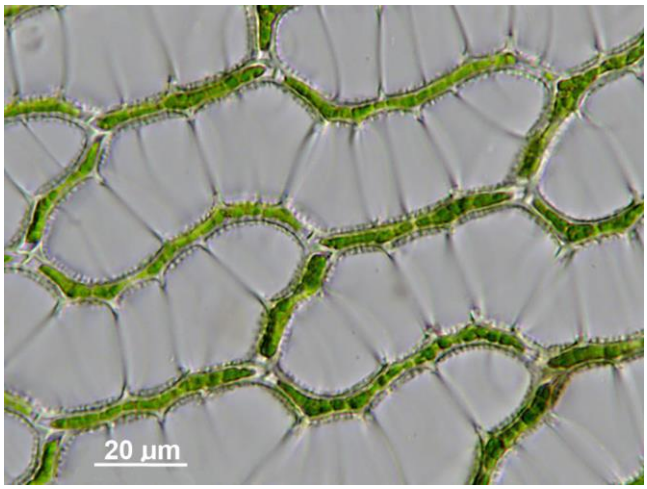

Figure 22. ***Sphagnum papillosum*** leaf cells showing network of green chlorophyllose cells and transparent hyaline cells. Note that the hyaline cells are long with spiral wall thickenings. These cells have pores what expose the inside cation exchange sites. Photo by Ralf Wagner <www.drralf-wagner.de>, with permission.

Potassium is a highly soluble nutrient. Garciadeblas *et al*. (2007) demonstrated that ***Physcomitrella patens*** (Figure 23) expresses the same potassium and sodium transport systems as that found in flowering plants. Hence, we find that potassium is able to move from older to young tissues.

Bakken (1995) suggested that the reason the acrocarpous moss ***Dicranum majus*** (Figure 24) has a low N demand and persistence of N in young tissues at sites with high N is that it moves N from older to younger tissues. ***Pleurozium schreberi*** (Figure 25), a large, pleurocarpous, feather moss with no central strand or special conducting cells, is even able to move its nutrient supply about. And it is selective about it. It is able to move the soluble K^+ and Mg^{++} from plant base to apex, but, as in tracheophytes, the insoluble Ca^{++} is non-translocatable (Bates 1979). In fact, the concentration of Ca^{++} increases with distance from apex, assumedly reflecting its longer time to accumulate there. As a component of the cell wall, the concentration of Ca^{++} would increase as the cell sap was lost after death. But that is not the full explanation of its increasing concentration there. Ca^{++} supplied below the ***Pleurozium*** mats moves up the stems externally, taking advantage of the exchange sites and capillary movement of water (Bates & Farmer 1990). If it behaves like ***Sphagnum*** (Figure 21-Figure 22), broken cells will expose more exchange sites on the insides of cells, permitting Ca^{++} to be bound there.

Figure 23. ***Physcomitrella patens***, a species that transports K in the same manner as flowering plants. Photo by Jan-Peter Frahm, with permission.

Figure 24. ***Dicranum majus*** with sporophytes. Photo by Michael Lüth, with permission.

Figure 25. ***Pleurozium schreberi***. Photo by Michael Lüth, with permission.

Directional Differences

Wells and Brown (1996) demonstrated internal movement in the moss ***Rhytidiadelphus squarrosus*** (Figure 26). By collecting the moss and depriving it of any external nutrient supply, they were able to determine that apical growth continued, facilitated by **acropetal** (base to tip) transfer of cations (K^+, Mg^{++}, and Ca^{++}) from basal segments in proportion to that cation pool. When the mosses were pretreated with these three cations, the status of the shoots did not influence the elements that arrived in the newly grown shoots. Rather, acropetal transfer of externally bound cations occurred.

Figure 26. ***Rhytidiadelphus squarrosus***, a species with internal nutrient transport that seems to depend on living cells. Photo by Michael Lüth, with permission.

Surprisingly, even the heavy metals travel. Rühling and Tyler (1970) found that in ***Hylocomium splendens*** (Figure 27-Figure 28) metals such as Cu, Fe, and Mn are taken in by the young tissues and moved to the older ones. Could this be a means of sequestering them where they are less dangerous to the moss?

Figure 27. ***Hylocomium splendens*** on spruce forest floor. Photo by Janice Glime.

Species Differences

It seems that bryophytes differ among species in their nutrient mobilities, and in which nutrients go where. Eckstein and Karlsson (1999) compared the movement of N in the pleurocarpous moss ***Hylocomium splendens*** (Figure 27-Figure 28) and the acrocarpous ***Polytrichum commune*** (Figure 16-Figure 17), both common in boreal forests. In both species, the current year of growth served as a sink for N. In ***P. commune*** the older segments showed a net loss of N from June to September, a loss the authors interpreted as resorption of N to the subterranean rhizome.

Figure 28. ***Hylocomium splendens*** stem cs, showing central parenchyma cells. Photo by Botany Website, UBC, with permission.

By contrast, in ***Hylocomium splendens*** (Figure 27-Figure 28), the one-year-old segments, like the youngest segments, increased in N, whereas the older segments lost 50% of the N initially measured there (Eckstein & Karlsson 1999). All the N lost from the older segments could be identified in the two youngest segments. Thus, as the three-year-old segments of ***H. splendens*** died and became brown, N moved upward in the plant to younger segments. It is interesting that one species (***P. commune***, Figure 16-Figure 17) behaved as trees do in the fall, moving the N downward, whereas the other (***H. splendens***) behaved as trees or crop plants do in spring, moving it to the new growth.

Even the aquatic mosses behave like tracheophytes in their transfer of nutrients from older to younger segments. The soluble N, P, and K are concentrated in the apical regions of ***Fontinalis squamosa*** (Figure 29) and ***F. antipyretica*** (Figure 30-Figure 31), whereas the less soluble Ca, Mg, and Fe increase toward the base (Mártínez Abaigar *et al*. 2002). However, there are two possible explanations for this: N, P, and K are moved from older to younger tissues, just as they are in tracheophytes, or younger, more active tissues actively uptake these three nutrients. Mártínez Abaigar and coworkers considered both factors to be contributing.

Figure 29. ***Fontinalis squamosa*** in Wales, an aquatic species that concentrates its N, P, and K in apical portions. Photo by Janice Glime.

Figure 30. ***Fontinalis antipyretica***, an aquatic species that concentrates its N, P, and K in apical portions. Photo by Dick Haaksma, with permission.

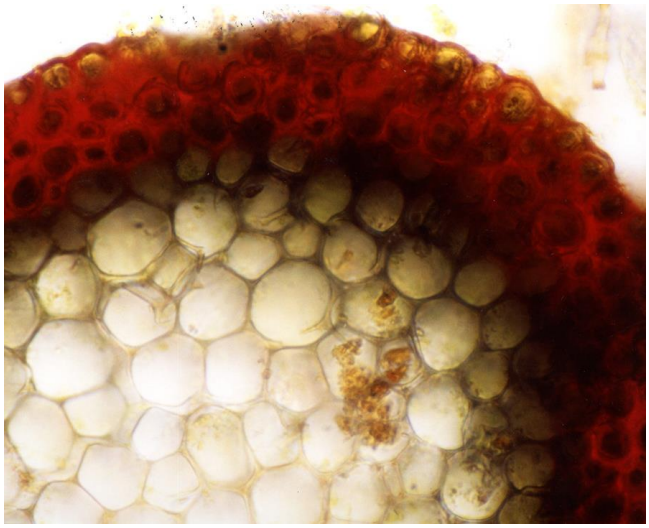

Figure 31. ***Fontinalis antipyretica*** stem cs stained with Aniline blue + eosin, showing differentiation of the cells. Photo courtesy of Isawo Kawai.

Mechanisms of Transport

Source to Sink?

This evidence of movement leads us to the question of how movement occurs. One possible mechanism is the **source to sink** phenomenon. In this case, a substance moves from an area of higher concentration (**source**) to one of lower concentration (eventual **sink**). But for this movement to continue, the final destination (**sink –** site of accumulation) must metabolize or store the substance in an insoluble form so that the recipient tissues become a sink and concentration gradients can continue from the source. For example, carbon moved as sucrose can be converted to starch or cellulose, or other constituent, causing the concentration of sucrose to continue to be higher at the source (see discussion under Sporophyte Conduction below).

In ***Rhytidiadelphus squarrosus*** (Figure 26) the rate of movement from old to young tissues is inversely related to the pool size, so that small segments move proportionally more nutrients to the developing tissues (Wells & Brown 1996), following a source-to-sink principle. When side branches were removed from ***Hylocomium splendens*** (Figure 27-Figure 28) to adjust the nutrient pool, loss of those branches led to lower concentrations of K^+, Mg^{++}, Ca^{++}, and Zn^{++} in the young shoots, indicating the importance of movement from older to younger tissues in this boreal forest feather moss (Brümelis & Brown 1997). These young segments did, however, produce more branches when branches on mature segments were removed. It seems that nothing is ever simple.

It appears that ***Pleurozium schreberi*** (Figure 25) could be a nitrogen **sink**. ***Pleurozium schreberi*** absorbs N in quantities apparently beyond its needs (Raeymaekers 1987; Raeymaekers & Glime 1990). And as might be expected, K^+ is easily leached out of the moss under stress of simulated acid rain and desiccation (Raeymaekers & Glime 1990). Thus, it appears that this moss that can provide 100% cover in Jack pine (*Pinus banksiana*; Figure 32) and other northern and boreal forests could have a major impact on nutrient flux. As an accumulator of N, it could become a sink, or it could release its excess load slowly over time. With its propensity for losing K^+ when suffering membrane damage from desiccation, ***P. schreberi*** and other bryophytes could be a means of sequestering K^+ from throughfall and dust, then releasing it later, perhaps hoarding it until rain comes, releasing it to tracheophyte roots at a time when the K^+ is most vulnerable to loss from the roots by leaching and runoff. This seemed to be the case for loss from ***Sphagnum*** when it was released near the end of the growing season, a result of rainfall that ended summer drought in a forested fen (Leary & Glime unpublished data). On the other hand, doe ***P. schreberi*** the very presence of its thick mat could prevent or diminish runoff loss, slowly releasing the K^+ to the soil as the rainfall event progresses. Our understanding of this process of bryophyte storage and later release to roots is as yet too limited to know the net impact.

Figure 32. ***Pinus banksiana*** forest where ***Pleurozium schreberi*** can form 100% ground cover. Photo from Minnesota Department of Natural Resources, through Creative Commons.

Enrichment Effects

When the moss is enriched with a nutrient, the translocated load can likewise be enriched. When input of N as $^{15}NH_4{}^{15}NO_3$ was compared at low and high levels, ***Sphagnum capillifolium*** (Figure 21) increased its annual N translocation from 11% to 80% (Aldous 2002). Aldous (2002) estimated that translocation contributes 0.5-11% of the annual N budget of the moss. This observation is consistent with the observation that N translocation is higher in the high N deposition Adirondack sites than in the low deposition Maine sites in the northeastern USA. However, the Maine sites had a low water table and severe drought during the year of measurement and thus we cannot assume that the greater movement in the Adirondacks was due to the greater concentration of N.

Internal Transport

Internal conducting cells are present in some members of both liverworts and mosses, but are unknown in hornworts (Ligrone *et al*. 2000). In mosses, they can be present in both generations, whereas in liverworts they are present only in the gametophyte. This is predictable in that liverworts form their setae after the capsule matures and is ready for dispersal. Thus, any conducting tissue would be of little value, and furthermore have little time to develop.

Structural Facilitation

Mosses also have the ability to conduct nutrients through **symplastic** transport in rhizoids and caulonemata, and similarly in the thallus parenchyma of liverworts (Ligrone *et al.* 2000). The **symplast** is the living protoplasm of the cells that is interconnected between cells, and substances can move through it following a concentration gradient.

In ***Takakia*** species (mosses), **Calobryales** (liverworts) and **Pallaviciniaceae** (liverworts) the water-conducting cells have perforated walls with pores derived from plasmodesmata. In the bryoid mosses, the water conducting cells (**hydroids**) are imperforate. In the **Polytrichaceae** (Figure 2, Figure 16- Figure 18) the **leptoids** (in this family they are highly specialized food-conducting cells) the cytoplasmic organization is polarized and has a distinct axial system of microtubules. In ***Sphagnum*** (Figure 7-Figure 11) and other mosses there are less specialized parenchyma cells in the leafy stem and seta.

Rydin and Clymo (1989) considered that the dominant understanding of ***Sphagnum*** (Figure 33) was that the lack of any anatomical specialization in the stem (Figure 34-Figure 35) caused those mosses to rely instead on external conduction in the capillary spaces. However, in their experiments they demonstrated that this thinking was wrong. Instead, internal transport is both "rapid and quantitatively important." In fact, when labelled ^{32}P and ^{14}C were supplied below the tips of ***S. recurvum*** (Figure 33), both moved to the top of the plant regardless of the direction of external mass flow. High concentrations of the labelled P and C were in the stem. Furthermore, if the stems were steamed above and below the point of application, the labelled P and C failed to move, suggesting that live cells were needed for the transport. ***Sphagnum recurvum*** has a central mass of parenchyma that is 20-50 cells across. These cells have end walls with perforations of about 100 nm and a density of 7-13 μm^{-2}, providing a single cell wall with ~1500 perforations.

Figure 33. ***Sphagnum recurvum***, a species that transports P and C internally. Photo by Malcolm Storey, <www.discoverlife.com>, through Creative Commons.

It is likely that most bryophytes have some sort of conduction specialization within the stem. ***Sphagnum*** (Figure 33-Figure 35) has revealed its internal system within the central portion of the stem (Ligrone & Duckett 1998). This system is manifest by the absence of large central vacuoles, presence of a spindle-shaped nucleus with prominent axial system of endoplasmic microtubules, membrane-bound tubules and vesicles, and a high frequency of plasmodesmata in the crosswalls, all characteristics that are common to food-conducting cells. These same characters are also known in the food-

conducting cells of **Bryopsida** and suggest an organization specialized for symplastic transport. They are also known in rhizoids and caulonemata of mosses and in thallus parenchyma cells of liverworts (Ligrone *et al.* 2000).

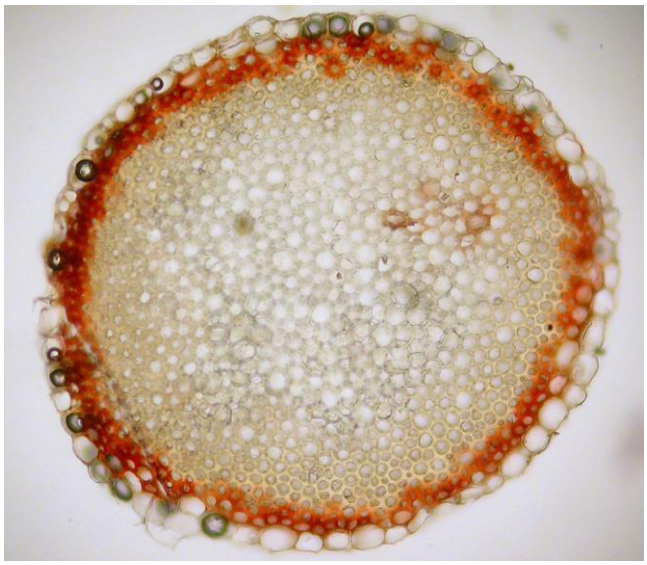

Figure 34. ***Sphagnum*** stem cross section with parenchyma cells in center. Photo by David Tng, with permission.

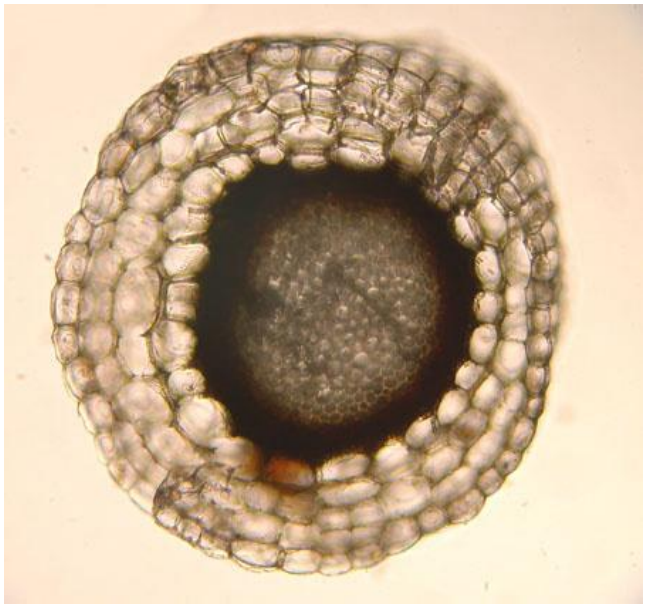

Figure 35. ***Sphagnum*** stem cs showing large outer cortex cells and small cells in central strand. Photo from Botany Website, UBC, with permission.

Leptome Transport

In tracheophytes, we tend to think of the phloem as transporting sugars downward, but other substances are transported there as well, and the direction of flow may at times be reversed. In bryophytes, the same is true.

Trachtenberg and Zamski (1978) determined that in addition to photosynthate, the **leptome** of ***Polytrichum juniperinum*** (Figure 36-Figure 37) moves ionic solutes such as sulfate and lead, whereas the chelated forms of iron and lead move in the **hydroids**. Ions from the moss surface are able to move across the cortex through the free space between the cells (**apoplastically** – see below). The leptome actually acts much like the endodermis of a root in serving as a barrier between the hydrome and the cortex. Thus, it becomes a site where toxic ions accumulate and are not transported to the rest of the plant. In their experiments, Trachtenberg and Zamski found that lead (Pb) moved in this way, accumulating in the leptome, but no Pb was found within the cytoplasm of any cortex cells. The leptoids, on the other hand, had heavy deposits. Hence, it appears that an active **symplastic** mechanism controls the movement of solutes and heavy metals in much the same way as the endodermis of a root. It is interesting that the stem of a moss has developed this same safeguard.

Figure 36. ***Polytrichum juniperinum***, a species that moves ionic solutes such as sulfate and lead in the **leptome**, but moves the chelated forms of iron and lead in the **hydroids**. Photo by Janice Glime.

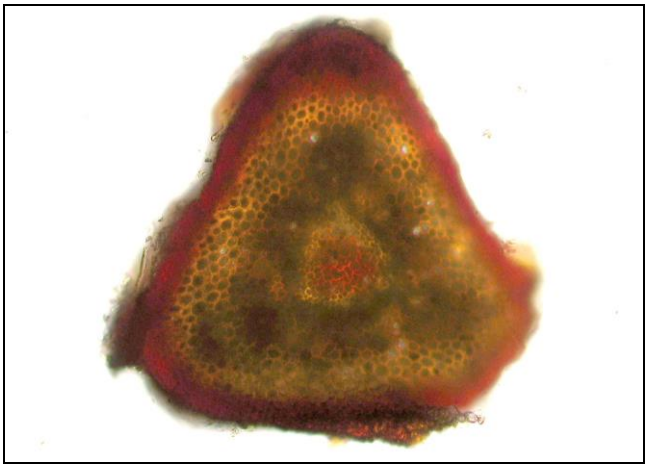

Figure 37. ***Polytrichum juniperinum*** stem cs with central hydroids and surrounding leptoids. Photo from Botany Website, UBC, with permission.

To obtain the same toxicity with the EDTA (chelated) Cu and Zn requires 500X more concentrated solution than with the ionic form. The chelation changes the mode of translocation within the bryophyte, with bound (chelated) ions moving in the free space to the leptome. These observations are consistent with the structure of the leptoid cells, which have large nuclei and an abundance of endoplasmic reticula (Eschrich & Steiner 1967; Hébant 1976), both permitting the cells to exercise high metabolic activity.

A similar phenomenon for copper and zinc has been seen in gemmae of ***Marchantia polymorpha*** (Figure 38) and protonemata of ***Funaria hygrometrica*** (Figure 39-Figure 40) (Coombes & Lepp 1974). Copper was more toxic than zinc to both species at levels above 8 mg L^{-1}. Protonemata did not grow and spores did not germinate in ***Funaria hygrometrica***. Even at 1 mg L^{-1}, few buds formed in ***Funaria***. In zinc, it produced rounded protonemal cells that could be interpreted as brood cells, known to occur as a response to unfavorable conditions (Van Andel 1952). In ***Marchantia***, rhizoid formation on gemmalings was inhibited at 1 ppm copper. Zinc did not cause any noticeable changes. In these bryophytes, there was a delicate line between essential levels and toxic levels of copper, with levels above 0.5 mg L^{-1} being deleterious to development.

Figure 38. ***Marchantia polymorpha*** gemmae cups showing gemmae. Copper and zinc are toxic to these gemmae. Photo by Walter Obermayer, with permission.

Figure 39. ***Funaria hygrometrica***. Photo by Michael Lüth, with permission.

Carbon Transport

We know that the **leptome** (that part of the stem of some mosses composed of **leptoids**, Figure 41) conducts assimilates, and that sucrose applied to the outside of the plant ends up in the leptoids (Trachtenberg & Zamski 1978). In tracheophytes, many other substances can travel in the phloem, the tracheophyte counterpart of the leptome. But, in a bryophyte, how does one examine what is travelling in a tube so small it cannot be seen without a microscope, for which preparation is likely to disrupt the whole process?

Figure 40. ***Funaria hygrometrica*** spore with developing protonema. Zinc and copper are toxic to both the spore and the protonema. Photo by Janice Glime.

One of the most fascinating techniques (to me at least) in all biology is the use of aphids to determine what travels in conducting tissues. Well, even bryophytes can have aphids! And Thomas and Lombard (1991) have taken advantage of this fascinating tool to determine just what travels in the leptoids of ***Polytrichum commune*** (Figure 16-Figure 17). The aphid, ***Myzodium modestum*** (Figure 42), a moss aphid and thus quite small, inserts a needlelike stylet into the moss conducting tissue (leptoids) to get nutrients. Thomas and Lombard found that when ***P. commune*** leaves are treated with ^{14}C-sucrose, 17-34% of the labelled carbon can be detected in 2-15 aphids within four hours. In fact, these aphids are so efficient at removal that the movement of sucrose to other parts of the plant and to shared underground rhizomes is reduced from its normal 4% to 1% or less.

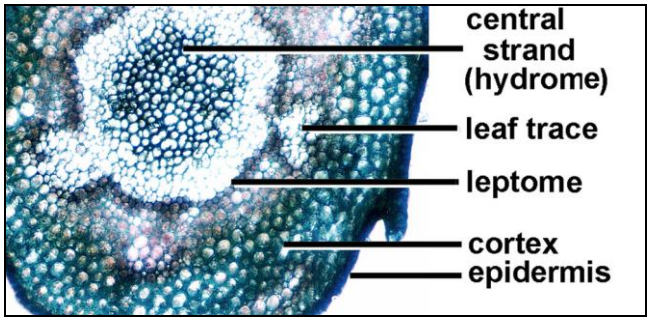

Figure 41. Cross section of ***Polytrichum*** stem. Photo courtesy of Isawa Kawai.

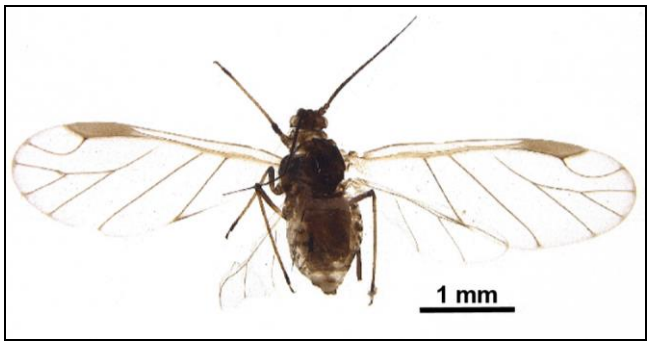

Figure 42. ***Myzodium modestum*** adult, a species that taps into the "sap" in leptoids of ***Polytrichum***. Photo from CBG Photography Group, through Creative Commons.

In ***Polytrichum commune*** (Figure 16-Figure 17), labelled ^{14}C from sucrose applied externally quickly appeared in the growing stem apex, young leaves, bud initials, and underground axes, all sinks for this C source (Reinhart & Thomas 1981). It appears that the C is more likely to move **acropetally** (toward the tip) than **basipetally** (toward the base). Nevertheless, labelled C travels from the leaves both acropetally (Eschrich & Steiner 1967) to the growing shoot apex and basipetally to underground rhizomes (Collins & Oechel 1974). The movement of externally applied sucrose requires ATP as an energy source for uptake, followed by movement from the **apoplastic** free space (see below) into the leptome, similar to **phloem loading** in tracheophytes (Reinhart & Thomas 1981).

The movement of externally applied labelled ^{14}C in ***Polytrichum commune*** (Figure 16-Figure 17), and by implication also the plant's own photosynthate, reaches several other leaves within two hours and reaches the rhizome within 72 hours or less (Reinhart & Thomas 1981). Experiments using radioactively labelled ^{14}C demonstrate that C moves in mosses in a **source-to-sink** fashion, as it does in tracheophytes. Furthermore, movement to the underground axis in this and other mosses allows translocation to neighboring members of a clone (Thomas *et al*. 1988, 1990), either directly through rhizomatal connections or indirectly through carbohydrates that escape into the soil/moss medium and can be absorbed. The carbon is both used and stored, with labelled carbon appearing in starches and cell wall polysaccharides one week and six weeks later, respectively (Thomas *et al*. 1988).

As you might expect, the patterns of translocation will vary between species of bryophytes, even in the same ecosystem. For example, near Fairbanks, Alaska, in a *Picea mariana* forest (Figure 43), ***Polytrichum commune*** (Figure 16-Figure 17) retained the most of labelled ^{14}C after 2 hours, while ***Sphagnum subsecundum*** (Figure 44) retained the least (Skré *et al*. 1983). However, after 35 days, it was ***Sphagnum subsecundum*** that had the highest fraction of radiolabelled ^{14}C in the brown tissues, with ***Polytrichum commune*** coming in second. The two pleurocarpous feather mosses, ***Hylocomium splendens*** (Figure 27-Figure 28) and ***Pleurozium schreberi*** (Figure 25), had no consistent pattern of translocation after 2 hours or 35 days. All four species exhibited high loss of labelled ^{14}C to respiration (presumably photorespiration) during the first 2 hours, which coincided with the peak of the growth season.

Sphagnum papillosum (Figure 9-Figure 11) translocated ^{14}C in the soluble fraction from older parts of the moss to the apex, with very little transfer into the insoluble fraction, to neighbors, or into the gas phase (Rydin & Clymo 1989). In fact, the transfer of ^{14}C to the capitulum from lower portions of the plant was about equal to that lost from the capitulum through respiration. The capitulum also transferred about twice as much ^{14}C to the insoluble fraction and about half as much to its neighbors. After 22 weeks, about 25% of the remaining labelled carbon was incorporated into new tissues.

Figure 43. Black spruce (***Picea mariana***) in Alaska taiga, home of ***Polytrichum commune***, ***Sphagnum subsecundum***, and feather mosses ***Pleurozium schreberi*** and ***Hylocomium splendens***. Photo from NOAA, through public domain.

Figure 44. ***Sphagnum subsecundum***, a species that stores carbon in its lower brown tissues. Photo by Michael Lüth, with permission.

Apoplastic Transport

Cell walls and extracellular spaces form the **apoplast** of a plant, including any bryophyte. Because the apoplast provides capillary spaces, it facilitates the movement of water and solutes across the plant tissues (Figure 45). Even the cell wall is composed of cellulose fibers that provide minute capillary spaces (Figure 46). But little seems to be published about apoplastic transport in bryophytes. (See above under Leptome Transport and under Carbon Transport; below under Sporophyte Conduction).

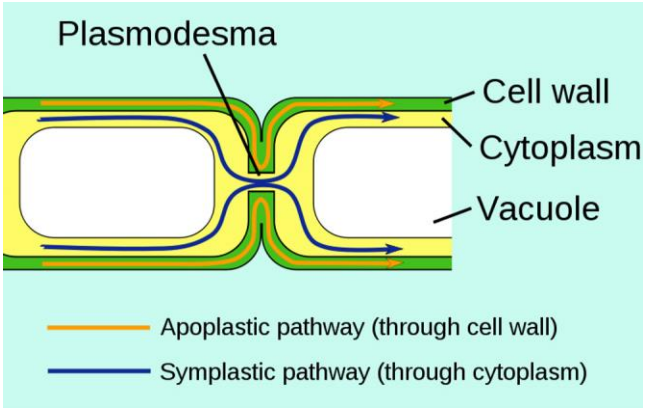

Figure 45. Apoplastic and symplastic pathways through cells. Note that such large vacuoles are not common in healthy bryophytes. Image by Jackacon, through public domain.

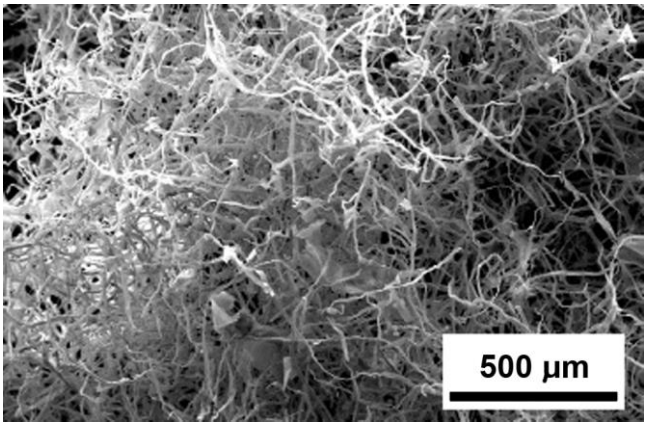

Figure 46. Cellulose SEM showing spaces among the fibers. Photo by Guiotoku *et al.* 2012, through Creative Commons.

David Hanson (Bryonet) has raised the interesting question about apoplastic movement of sugars in bryophytes. Would this sugar excretion that is beneficial to bacteria and fungi be less favorable in flowing water? I might add, would it instead facilitate the proliferation of the microbial community in the water, providing a nearby source of CO_2 for the CO_2-limited aquatic species? There is much to learn about nutrient relationships of bryophytes.

Desiccation Effects

Few studies have addressed the effects of desiccation on internal transport in bryophytes. In particular, the specialized food conduction cells (**leptoids**) of desiccation-tolerant mosses like ***Polytrichastrum formosum*** (Figure 47-Figure 48) undergo numerous changes during dehydration (Pressel *et al*. 2006). The endoplasmic microtubules disappear; the plastids, nucleus, and mitochondria become rounded and lose their longitudinal alignment of organelles. Instead of the typical stacks of endoplasmic reticulum of hydrated tissues, membranous tubules arranged at right angles to the main cellular axis appear. Small vacuoles fill the internal cytoplasm. The plasmalemma forms labyrinthine tubular extensions that outline newly deposited cell wall ingrowths. Leptoids become plugged with electron-opaque material while nearby parenchyma cells are depleted of their starch deposits. However, upon rehydration the leptoids return to their normal cytology within 12-24 hours. When the toxic oryzalin is provided to the plants, it prevents this recovery, indicating the importance of processes of living cells. Pressel and coworkers interpreted this to indicate a key role of the microtubular cytoskeleton in the recovery of the leptoids.

External Translocation

It is well known that water moves externally in mosses (and also internally to varying degrees). Nutrients in the solution move with the water, and nutrients adhering to the leaves can be carried with the water as well. Even soil nutrients can be moved upward this way.

As mosses die, especially those with an upright habit, ions can be moved externally from basal portions to upper portions rather easily (Brehm 1971; Brown 1982). Dead and dying lower tissues release ions that go into solution in the external surface film. Evaporative loss of water (**transpiration**) from the capitulum of ***Sphagnum*** (Figure 7-Figure 11) and from apices of **Bryopsida** causes water to move upward through the external capillary spaces. As it does, it carries with it the ions leaked from dead and dying cells. These can then be absorbed on the exchange sites of the apex. Brown (1982) considered that the higher concentrations of Ca^{++}, K^{+}, and Mg^{++} in ***Mnium hornum*** (Figure 49) in higher light intensities (Thomas 1970, in Brown 1982) could be the result of increased transpiration. But is it moved internally or externally? It has a well-developed internal conduction system (Figure 50).

Figure 47. ***Polytrichastrum formosum*** capsules, a moss with internal conduction. Photo by Michael Lüth, with permission.

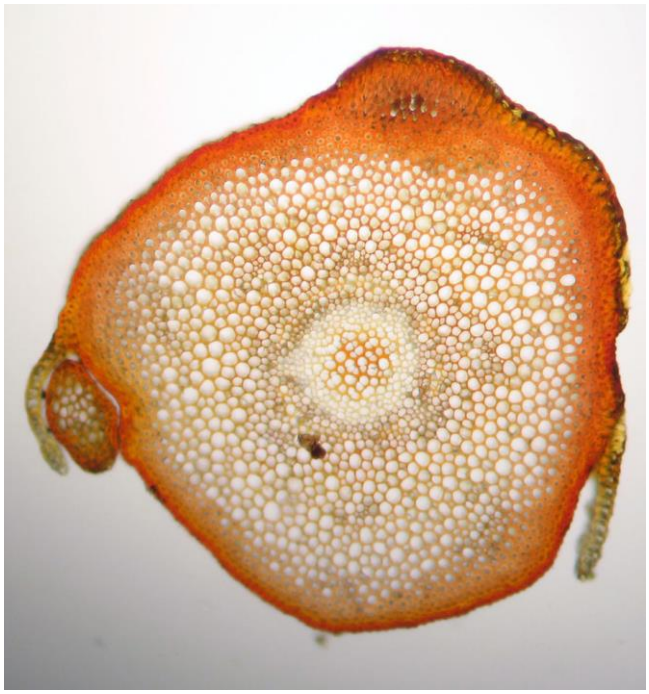

Figure 48. ***Polytrichastrum formosum*** stem cs showing leptoids and hydroids. The leptoids undergo structural changes when dehydrated and regain normal structure when rehydrated. Photo by Botany Website, UBC, with permission.

Figure 49. ***Mnium hornum***, a species that may transport nutrients through a transpiration stream. Photo by Michael Lüth, with permission.

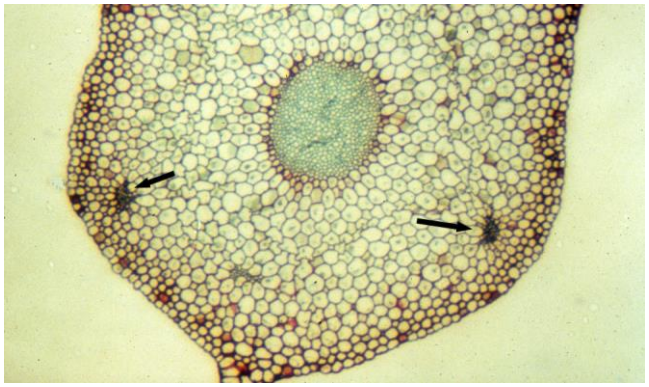

Figure 50. ***Mnium*** stem showing central strand where hydroids occur and leaf traces (arrows) connect to leaf bases. Photo by Janice Glime.

Sporophyte Conduction

As we have already seen for water, the sporophyte gets nutrients, hormones, and an energy supply from the gametophyte through the sporophyte **foot** (Figure 51-Figure 53) (Courtice *et al*. 1978). Some of the evidence for this transfer is indirect. For example, in ***Polytrichastrum formosum*** (Figure 47-Figure 48), a decrease in the amino acid arginine in the gametophyte is coincidental with an increase in the sporophyte (Whel 1975). Whel suggested that this parallels the tracheophyte movement of N from a mature to young organ.

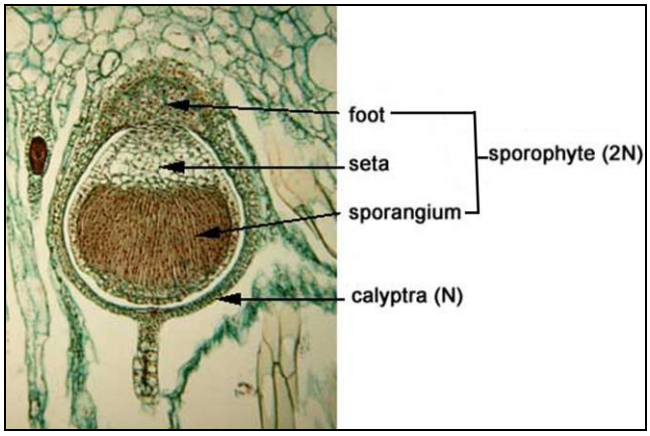

Figure 51. ***Marchantia polymorpha*** (thallose liverwort) capsule ls showing location of the foot next to gametophyte tissues. Photo from Botany Website, UBC, with permission.

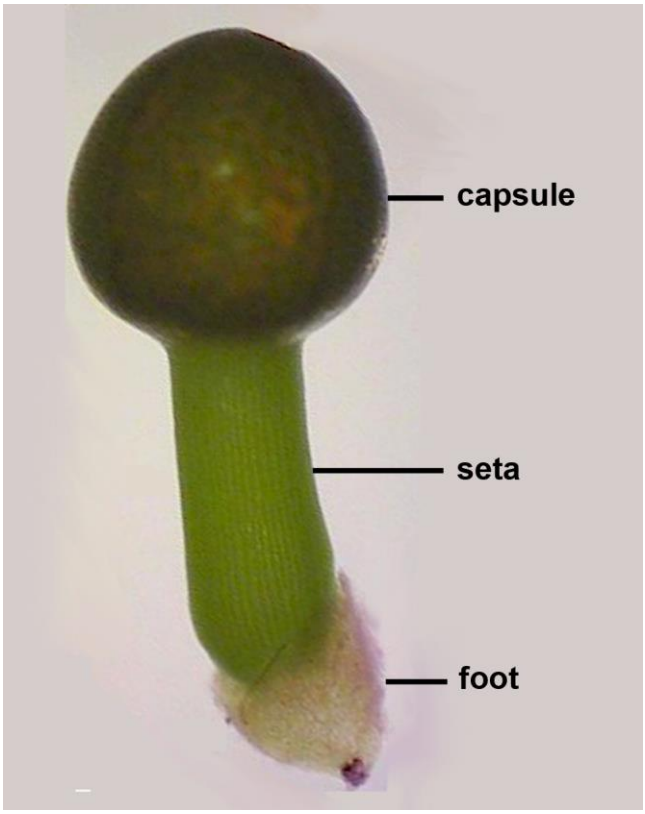

Figure 52. Liverwort (***Pellia***) young sporophyte. Photo by Paul Davison, with permission.

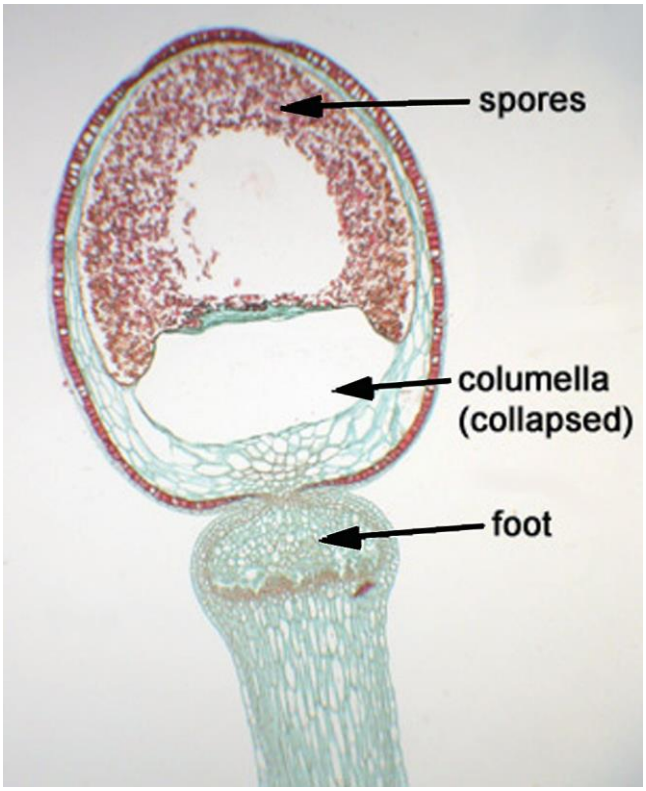

Figure 53. ***Sphagnum*** capsule ls showing foot imbedded in pseudopodium (gametophyte) tissue. Photo from Botany Website, UBC, with permission.

The internal structure reveals **transfer cells** at the gametophyte-sporophyte junction (Figure 54; Lal &

Chauhan 1981). The transfer cells are found in the foot of the sporophyte and in the adjacent gametophyte tissue and are endowed with an extensive and complex wall labyrinth. Ligrone and Renzaglia (1990) demonstrated that the hornwort ***Dendroceros tuberculatis***, as in other hornworts, is endowed with dense protein deposits in the vacuoles of both gametophyte transfer cells and the sporophyte foot. The structure of the transfer cells suggests a function in the movement of metabolites from the gametophyte to the sporophyte by their numerous mitochondria and intense enzyme activity, especially of phosphatases and some respiratory enzymes (Lal & Chauhan 1981).

The junction cells are the first to differentiate in the young sporophyte (Kwok & Rushing 1999). The transfer cells on both sides of the junction have plastids and starch content, with numerous small vacuoles and lipid deposits in the junction cells, further supporting the role of this region in transfer of nutrients to the sporophyte.

Caussin *et al*. (1983) demonstrated that sporophytes of ***Polytrichastrum formosum*** (Figure 47-Figure 48) absorb the amino acids glycine, threonine, and α-aminoisobutyric acid through the **haustorial** (absorptive) foot, using the transfer cells. Removal of the haustorial foot significantly reduced the absorption of these amino acids into the sporophyte.

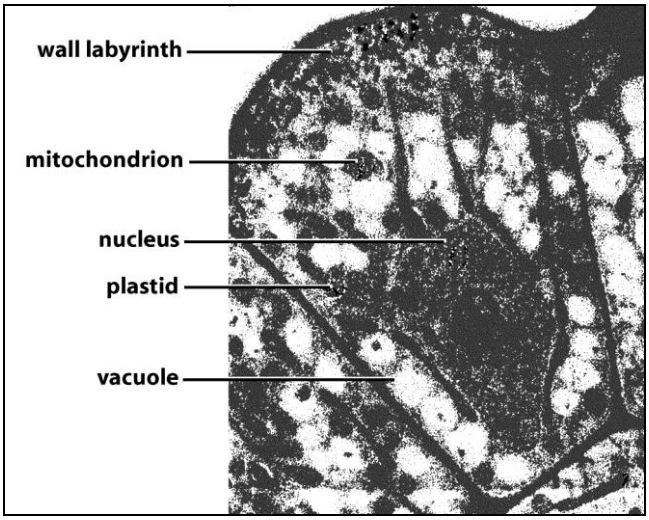

Figure 54. Transfer cell showing wall labyrinth. Computer-drawn from photo in Lal and Chauhan (1981).

Chevallier *et al*. (1977) demonstrated that radioactive orthophosphate moved from the gametophyte to the capsule and eventually to the spores in ***Funaria hygrometrica*** (Figure 55). However, once the capsule turned from green to brown, indicating maturity, the original 18% transfer rate turned to zero. But this is not the only potential means for the sporophyte to get its nutrients. It is, at least in ***Funaria hygrometrica***, able to absorb nutrients directly through its capsule, hence opening the possibility that it gets some sporophyte nutrients from dust and rainwater.

It appears that K^+ moves into the developing sporophyte rapidly, whereas Ca^{++}, which is generally immobile, moves more slowly (Brown 1982). In Brown's study, as the gametophyte senesced, its K^+ diminished and the concentrations of Ca^{++} and Mg^{++} increased, presumably due to movement of K^+ from the senescing gametophyte to the young sporophyte, followed by Ca^{++} and Mg^{++} occupying the vacated exchange sites on the gametophyte.

Figure 55. Capsules of ***Funaria hygrometrica***. Photo by Janice Glime.

Marsh and Doyle (1981) demonstrated that sugars are transported actively by the transfer cells. A more startling discovery is that the sporophyte of ***Anthoceros punctatus*** (Figure 56) transfers sugars from the photosynthetic sporophyte to the thallose gametophyte, where it is used by its ***Nostoc*** (Figure 57) partner (Stewart & Rodgers 1977)!

Figure 56. Thallus of ***Anthoceros punctatus*** with young sporophytes. Photo by Des Callaghan, with permission.

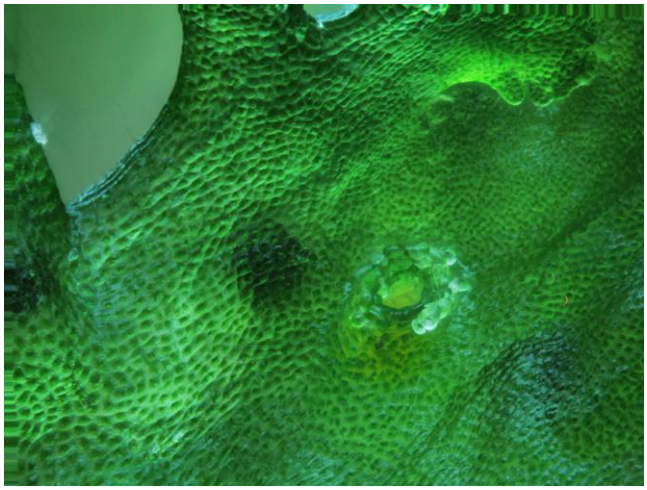

Figure 57. ***Anthoceros punctatus Nostoc*** colonies (dark area). Photo by Des Callaghan, with permission.

As nutrients cross the **placenta** (gametophyte-sporophyte interface) into the sporophyte, there is another opportunity for nutrient discrimination. Basile *et al.* (2001) found that the gametophyte accumulated much greater quantities of Pb and Zn than did the sporophyte in ***Funaria hygrometrica*** (Figure 55). These two elements accumulated in the placental **transfer cells** on both gametophytic and sporophytic sides. When the two metals were applied in the lab, Basile and coworkers found that the two generations had different accumulation quotients.

The size of the sporophyte seems to play a role in determining the rate of transfer of carbon in the photosynthate from the gametophyte to the sporophyte (Browning & Gunning 1979). In ***Funaria hygrometrica*** (Figure 55), labelled gametophyte photosynthetic products were transported to the sporophyte at a linear rate for up to 12 hours after treatment with $^{14}CO_2$. Movement from the **haustorium** (nutrient exchange area in foot of sporophyte) to the capsule, through the seta, occurs at the slow rate of 1-3 mm h^{-1}. And larger sporophytes received the photosynthate at a faster rate than did smaller ones. Does this mean that there is a source-sink movement, with larger capsules forming a larger sink? Or is there a transpiration stream involved in which larger capsules lose water faster, hence drawing water up from the gametophyte much like a tracheophyte water stream? Both water stress and lack of light inhibited transport, but if only the sporophyte was darkened, it had no effect. This again suggests the possibility of a source-sink movement, with the source (gametophyte) becoming depleted of photosynthate in the dark. But it is also possible that a transpiration stream could be involved, as suggested by the loss of movement under drought stress. Both could contribute.

In members of ***Polytrichum*** *s.l.* (Figure 58-Figure 59), transport of carbon from the gametophyte to the sporophyte is especially important (Renault *et al*. 1992). The calyptra completely covers the capsule and is fortified with dense hairs, limiting photosynthesis by the capsule. In ***Polytrichastrum formosum*** (Figure 47-Figure 48) sucrose serves as the primary soluble sugar for both the sporophyte and gametophyte. However, in the **apoplast** (capillary spaces in cell wall) of the **vaginula** (bottom part of archegonium when calyptra separates; foot of sporophyte is imbedded in vaginula – Figure 60) the sugars are primarily hexoses, with the conversion from sucrose to hexose facilitated by a cell wall **invertase** at *p*H of 4.5. The highest concentration (~230 mM) of soluble invertase occurs in both the haustorium and the vaginula, where a soluble invertase has its highest activity (*p*H 7.0). Glucose uptake is carrier-mediated, with little dependence on external *p*H. Once glucose is absorbed into the haustorium, it is converted to sucrose. Hence, sucrose is converted at the gametophyte-sporophyte interface to fructose and glucose, then converted back to sucrose after the haustorium cells absorb hexose. These changes may permit the sugar accumulation in the haustorium.

A more detailed anatomy of the gametophyte-sporophyte junction in the moss ***Acaulon muticum*** (Figure 61) may clarify some of the nutrient transfer (Rushing & Anderson 1996). This junction has the sporophyte foot imbedded in the gametophyte vaginula, with intervening placental space. The basal cell of the foot develops extensive wall ingrowths. Sporophyte cells that contact that basal cell likewise develop ingrowths on their outer tangential and radial walls that contact the basal cell. These young sporophyte cells have numerous mitochondria, strands of endoplasmic reticulum, and dictyosomes, especially adjacent to areas of extensive wall development. The plastids contain abundant reserves of starch. The wall ingrowths continue to become more extensive on all walls of the sporophyte foot, but never occur on the upper wall of the basal cell where it contacts the remainder of the sporophyte. As the sporophyte develops, the plastids of the foot contain fewer starch reserves. The gametophyte vaginula does not exhibit wall ingrowths until the sporophyte foot is well developed. Rushing and Anderson suggested that the early development of the wall ingrowths in the sporophyte foot and especially the basal cell may facilitate the rapid movement of both water and nutrients from gametophyte to sporophyte.

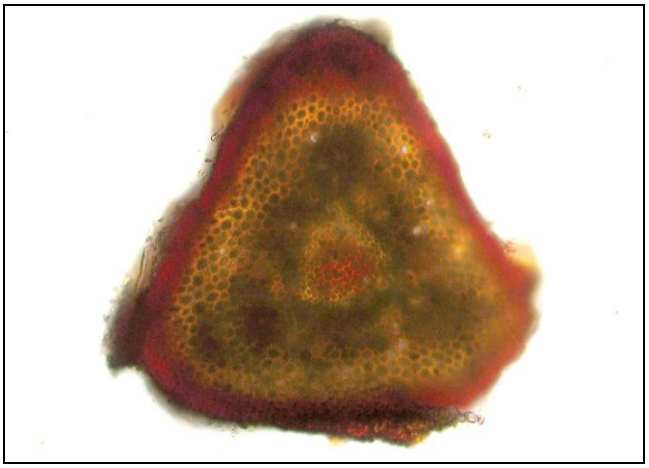

Figure 58. ***Polytrichum juniperinum*** stem CS showing conducting hydrome and leptome that continue into the seta. Photo from Botany Website, UBC, with permission.

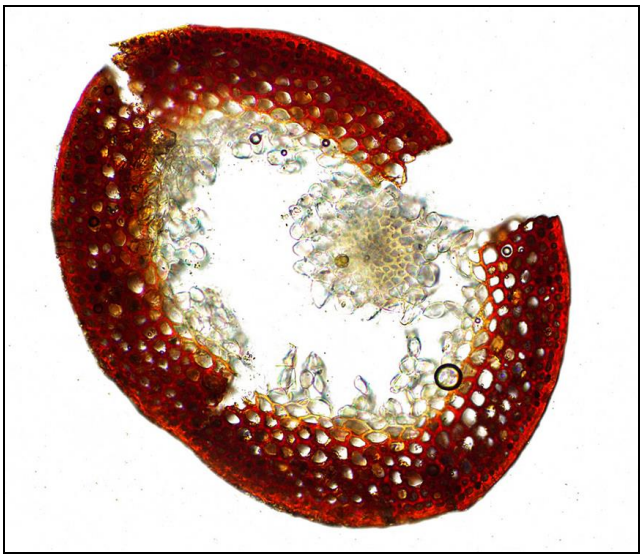

Figure 59. ***Polytrichum juniperinum*** seta cross section showing cells in the center where conduction occurs. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

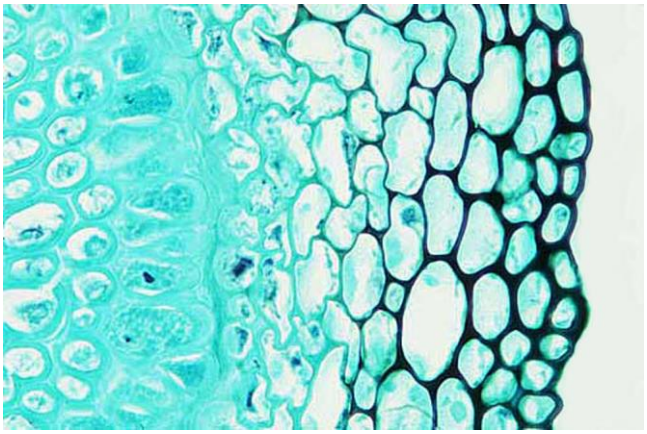

Figure 60. **Vaginula** cross section showing turquoise-stained cells on left that contact the sporophyte foot. Source unknown.

Figure 61. ***Acaulon muticum***, a species with a very short seta that helped us understand the structure of the vaginula and foot. Photo by Michael Lüth, with permission.

There has been much recent speculation into the role of the stomata in the sporophyte of bryophytes. Haig (2013) suggests an important function in conduction. Once the calyptra has been "outgrown" by the capsule, leaving the lower part of the capsule exposed, the stomata may provide a transpiration stream that helps to draw resources from the gametophyte up to the sporophyte, much as the open stomata of tree leaves facilitate the transpiration stream of water and nutrients upward in trees. Haig contends that the seta serves to raise the capsule above the boundary layer, facilitating the movement of moisture from the moss to the air and coincidentally moving the nutrients upward from the gametophyte. Haig further suggests that the calyptra serves to protect the gametophyte from excessive transfer to the developing sporophyte.

Summary

While most bryophytes obtain their nutrients primarily from atmospheric dust and precipitation, acrocarpous mosses may also receive considerable input from the substrate through upward movement externally and subsequent internal movement. Cation exchange sites hold nutrients on leafy surfaces and facilitate uptake and discrimination between ions. Further active processes are able to distinguish ions formed by N, P, and K from more exchangeable cations such as those of Ca^{++} or Mg^{++}, and they are generally able to maintain relatively constant levels of these essential nutrients despite changes in environmental concentrations. Bryophytes use pathways both through cells (**symplastic**) and between cells (**apoplastic**) to move internal substances, just as do the tracheophytes. And they may even have a filter similar to the endodermis, in the form of a **leptome**, at least in the **Polytrichaceae**. Leptome cells may become disfigured during desiccation, but they return rapidly to normal configuration following rehydration.

Many bryophytes also behave like tracheophytes in moving essential ions such as those formed by N, P, and K from older to younger parts, whereas less soluble ions like Ca^{++} remain in older tissues. Their ability to acquire ions from rainwater and hold them in their tissues makes them a sink for forest nutrients, but some, especially K^{+}, may be released in heavy rainfall following a dry period, returning the nutrients to the forest floor as a pulse. Heavy metals may be sequestered in older tissues or on external exchange sites. Movement may additionally occur through **source to sink** mechanisms or a transpiration stream.

Sucrose is transported in the **leptome**, as well as through stem parenchyma cells. Radiolabelled carbon quickly appears in the stem apex, young leaves, bud initials, and underground axes. Most of the movement is toward the apex (**acropetal**), but some also moves to the base (**basipetally**). Some reaches other stems in the clone. The **leptome** also moves ionic solutes, whereas the chelated forms move in the **hydroids**.

Sugars and nutrients move from the gametophyte to the sporophyte through the **transfer cells** in the sporophyte foot. But members of the **Anthocerotophyta** may transfer photosynthate from the green sporophyte to the gametophyte to nourish the ***Nostoc*** colonies. Stomata at the base of the capsule may create a transpiration stream that helps to move resources from the gametophyte to the sporophyte once the capsule is partially free of the calyptra.

Their ability to move nutrients from old to young tissues and to store them both externally and internally raises serious questions about their role in the nutrient cycling in the habitats where they are abundant. On the other hand, they may release potassium when roots need it the most.

Acknowledgments

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CHAPTER 8-6

NUTRIENT RELATIONS: DEFICIENCY

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CHAPTER 8-6

NUTRIENT RELATIONS: DEFICIENCY

Figure 1. ***Dicranum spadiceum*** in an alpine habitat where nutrients are typically deficient. Photo by Michael Lüth, with permission.

Nutrient-deficient Habitats

Tracheophytes have well-known adaptations to low nutrients. Among the herbaceous seed plants adapted for low nutrient habitats, a small growth form with narrow leaves or basal rosettes seems to predominate (Grime 1977). Evergreenness is common in both dry and wet habitats (bogs and fens), presumably affording the plant the opportunity of using their leaves for several years without having to provide the nutrients to grow a new supply. Like the shade plants, these plants possess an inherently slow growth rate.

Bryophytes in general seem to grow best in low-nutrient habitats (Figure 1). It is interesting that their productivity is no greater in extreme rich fens than in bogs and poor fens (Vitt 1990). Furthermore, the addition of nutrients to bryophytes in intermediate fens does not result in an increase in productivity. If we compare the bryophytes to the low-nutrient-adapted plants described by Grime (1977), the bryophytes are likewise small, have narrow leaves, and are mostly evergreen (but not leathery). As discussed earlier, they are able to move soluble nutrients from older tissues to growing apices. Furthermore, bryophytes are able to survive in low-nutrient habitats despite their small size and slow growth rate. In nutrient-rich habitats, they have no chance of competing with the fast-growing tracheophytes.

In bogs and fens, ***Sphagnum*** seems to have its own way of "competing" for the limited supply of nutrients. In experiments where both ***Sphagnum fuscum*** (Figure 2) and *Drosera rotundifolia* (sundew, Figure 2) were fertilized with N, the ***Sphagnum*** was able to advance its growth (Svensson 1995), seemingly ready to outcompete the tiny *Drosera* plants for light. However, the *Drosera* tapped into the nutrients at a different depth in the system, elongated its vertical stem that connected two successive years of

growth, and hence kept up with the vertical growth of the ***Sphagnum***. Interestingly, the *Drosera* made more but smaller leaves and increased its leaf thickness, thus not increasing its shading effect on the moss. Svensson concluded that the moss relocates the nutrients within itself, thus preventing their potential spread to tracheophytes.

Figure 2. Sundew (*Drosera rotundifolia*) (three round leaves) growing with ***Sphagnum fuscum***. Photo by Michael Lüth, with permission.

Bryophytes can be deprived of nutrients in habitats that are rich in nutrients. This paradox results from nutrient competition for the binding sights. Calcium compounds such as $CaCl_2$ can raise both exchangeable and intracellular Ca^{++} concentrations and displace other exchangeable essential nutrients such as K^+ and Mg^{++} (Bates & Farmer 1990), both of which are often in limiting supply. But the interesting response to addition of $CaCl_2$ that Bates and Farmer found is that the low-nutrient mosses ***Pleurozium schreberi*** (Figure 3) and ***Pseudoscleropodium purum*** (Figure 4) from acidic clay were unaffected, whereas ***Calliergon cuspidatum*** (Figure 5) and ***Pseudoscleropodium purum*** from chalk ($CaCO_3$) soil suffered reduced growth, apparently due to the resulting K^+ and Mg^{++} deficiencies.

Figure 3. ***Pleurozium schreberi***, a low-nutrient species that was unaffected by $CaCl_2$. Photo by Janice Glime.

Ion concentrations in the substrate or in water can be misleading relative to nutrient availability. A low-nutrient substrate such as a rock in a forest might actually place the bryophyte in a position to obtain considerable nutrients from throughfall that has collected nutrients from the canopy trees. And bryophytes dwelling in a stream with reasonably fast flow will have a continuous supply of new nutrients that can compensate for low concentrations (Birks & Dransfield 1970).

Figure 4. ***Pseudoscleropodium purum***, a low-nutrient species that was unaffected by $CaCl_2$ on acidic soil but suffered on chalk soil. Photo by Michael Lüth, with permission.

Figure 5. ***Calliergonella cuspidata***, a species that suffers from addition of $CaCl_2$ on chalk soil. Photo by Michael Lüth, with permission.

Nutrient Deficiency Symptoms

It takes nerve to title a section Nutrient Deficiency Symptoms when you are writing about bryophytes. This has apparently never been systematically studied for bryophytes in general! A search in Cambridge Abstracts brought one reference, a field study following fire: "Germination of ***Ceratodon purpureus*** (Figure 6) on all the burnt surfaces, and of ***Funaria hygrometrica*** (Figure 7) on the charred surfaces appeared to be nutrient or *p*H-limited. Growth of ***C. purpureus*** and ***Dicranella heteromalla*** (Figure 8) appeared to be nutrient- or *p*H-limited on some or all of the burnt surfaces." This 1994 study by Thomas *et al.* appears to be the only field study in recent years even to allude to nutrient deficiency symptoms in any context. And that one is merely a guess.

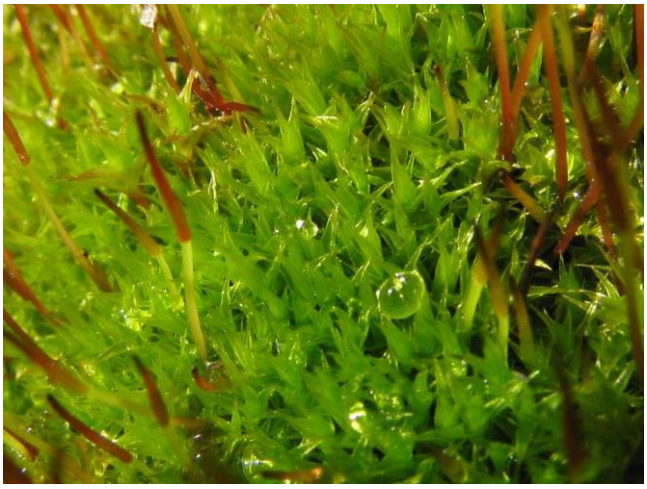

Figure 6. Healthy ***Ceratodon purpureus*** with young sporophytes. Photo by Jiří Kameníček, with permission.

Figure 7. ***Funaria hygrometrica*** growing among charcoal. Photo by Janice Glime.

Figure 8. ***Dicranella heteromalla***, a species that appears to be *p*H- or nutrient-limited when growing on burned substrata.

Culture studies for the purpose of keeping bryophytes alive are the most productive avenue for locating possible clues as to the response of bryophytes to limiting nutrients. But, since bryophytes tend to have much lower nutrient requirements than do tracheophytes (Griggs & Ready 1934; Voth 1943; Burkholder 1959; Southorn 1977; Dietert 1979), most of the trial and error in culture experiments revolves around getting nutrient concentrations low enough that algae, fungi, and bacteria don't predominate. For whatever reason, the total nutrient content of bryophytes, indicated by what is left in dry matter ash content, is lower than that of any other group of plants, algae, bacteria, or fungi, except for the woody parts of trees and shrubs (Table 1; Larcher 1983, 1995).

Table 1. Comparison of mean dry matter ash content for various groups of organisms. From compilation of Larcher (1983, 1995).

Bacteria	8-10%
Fungi	7-8%
Planktonic algae without skeletal material	~5%
Diatoms	up to 50%
Seaweed	10-20%
Mosses	**2-4%**
Ferns	6-10%
Grasses	6-10%
Dicotyledonous herbs	6-18%
Geophytes	5-10%
Succulents	10-20%
Halophytes	10-55%
Cacti	10-16%
Tundra herbs	~5%
Swamp plants	5-15%
Ericaceous dwarf shrubs	
Leaves	3-6%
Shoots	1-2%
Broad-leaved trees	
Leaves	3-4%
Wood	~0.5%
Bark	3-8%
Conifers	
Needles	~4%
Wood	~0.4%
Bark	3-4%

In addition to ions that compete for exchange sites, another problem with nutrient solutions is that they may have higher osmotic values than those internal ones of the bryophytes, causing osmotic shock (Brown 1982). Furthermore, the slow growth of bryophytes permits them to call upon nutrient reserves for a considerable time before deficiency symptoms appear. If multiple nutrients are limiting, the result is likely to be simply retarded growth rate, at least in the short term.

In a study on the epiphyllous leafy liverwort ***Radula flaccida*** (Figure 9), Olarinmoye (1975) found that when grown in distilled water, these liverworts became chlorotic and brittle, but still demonstrated considerable growth extension, indicating they most likely were using nutrient reserves. They did best in a nutrient medium diluted to 10-20% of the normal strength bryophyte medium, a solution already dilute compared to that used for most tracheophytes.

Figure 9. ***Radula flaccida***, a species that becomes chlorotic and brittle when grown in distilled water. Photo by Michaela Sonnleitner, with permission.

N and P Deficiency

Nutrient deficiency, especially N and P, can reduce plant growth by hindering physiological and biochemical processes. Deficiency can reduce protein synthesis and photosynthetic rates, while increasing carbohydrate content. But are bryophytes typically nutrient deficient? There are numerous examples that suggest they typically are not. It appears that they require much lower concentrations of nutrients than do other plants, obtaining most of their nutrients from precipitation. For example, when the nutrients of rainwater near Fairbanks, Alaska, were amplified to 2-5 times their normal concentration, bryophytes showed no growth increase, and some responded negatively (Skré & Oechel 1979). Even the large moss ***Pseudoscleropodium purum*** (Figure 4) showed no response to increased nutrients in a field experiment (Bates 1987). Rather, although ***P. purum*** may exhibit a temporary increase in internal nutrient concentrations, those relatively quickly return to the concentrations typical under normal rainfall (Bates 1989).

Despite the lack of direct field evidence, Richardson (1981) recognized that inadequate nutrient supply can cause stress and reduce photosynthetic performance of mosses. On the other hand, some bryophytes such as ***Ceratodon purpureus*** (Figure 12) may alter their growth form under low nutrient conditions. In this moss, greater shoot initiation occurs on media deficient in N (Seppelt & Hancock 1991). Hmmm... Wouldn't that be maladaptive?

Figure 10. ***Ceratodon purpureus*** showing young capsules and early spring color. Photo by Michael Lüth, with permission

Figure 11. ***Ceratodon purpureus*** showing color phase that can reflect nutrient differences or hydration differences – or age. Photo by Janice Glime.

Figure 12. ***Ceratodon purpureus*** with mature capsules, showing dry color phase of leaves. Photo by Michael Lüth, with permission.

Few visible deficiency symptoms seem to have been documented for bryophytes, contrasting with the symptoms that are highly documented for tracheophytes. In tracheophytes, N deficiency causes plants to be light green with lower leaves yellow due to transport of N to growing tissues; stems are short and slender, and the root-to-shoot ratio is high (Salisbury & Ross 1992). Growth is directly related to N availability in feather mosses (Sveinbjörnsson 2002). P deficiency causes plants to become dark green, often with red-purple on the undersides of leaves. As in N deficiency, the stems are short and slender. For those bryophytes that have been studied, similarities in nitrogen and phosphorus deficiency symptoms exist, but bryophyte responses in general for these two deficiencies seem to be more distinct from each other than in tracheophytes. Development of chlorosis is a typical N deficiency symptom in both tracheophytes and bryophytes. ***Funaria hygrometrica*** (Figure 7, Figure 13) responded to absence of either N or P at the protonemal stage by producing few protonemata on the deficient agar, and those soon became chlorotic in the N-free medium (Hoffman 1966), failing to produce gametophores (Dietert 1979). ***Atrichum undulatum*** (Figure 14) had a similar response of gametophores becoming yellow (Burkholder 1959). Likewise, no new gametophores were produced in the P-free medium (Hoffman 1966). ***Weissia*** (Figure 15) also became chlorotic in the absence of N (Dietert 1979), the gametophore tissue soon became tough and fibrous, and the leaves were scalelike. In P-free media, the entire culture became dark brown.

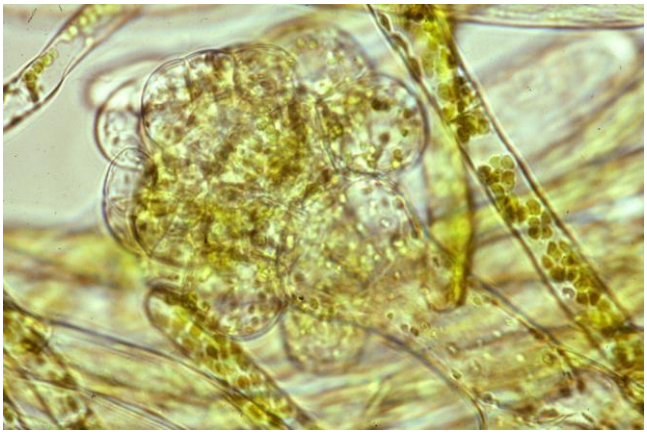

Figure 13. ***Funaria hygrometrica*** protonema with bud; protonemata development is greatly reduced when P or N is deficient. Photo by Janice Glime.

Figure 14. ***Atrichum undulatum***, a species whose leaves turn yellow when N or P is deficient. Photo by Janice Glime.

Figure 15. ***Weissia controversa*** var. ***densifolia*** with capsules; some members of the genus become chlorotic in the absence of N. Photo by Barry Stewart, with permission.

When mature ***Fontinalis antipyretica*** (Figure 16) was cultured in a P-free medium for four weeks, all plants had dark green leaves, as in tracheophytes, although some had scattered chlorotic leaf tips (R. Marr & Glime unpub). In the N-free medium, all had pale green leaves, again being similar to symptoms of tracheophytes. By contrast, in experiments with excess N, ***Fontinalis dalecarlica*** (Figure 17) and ***F. novae-angliae*** became deep green (Glime unpub., Figure 18-Figure 19).

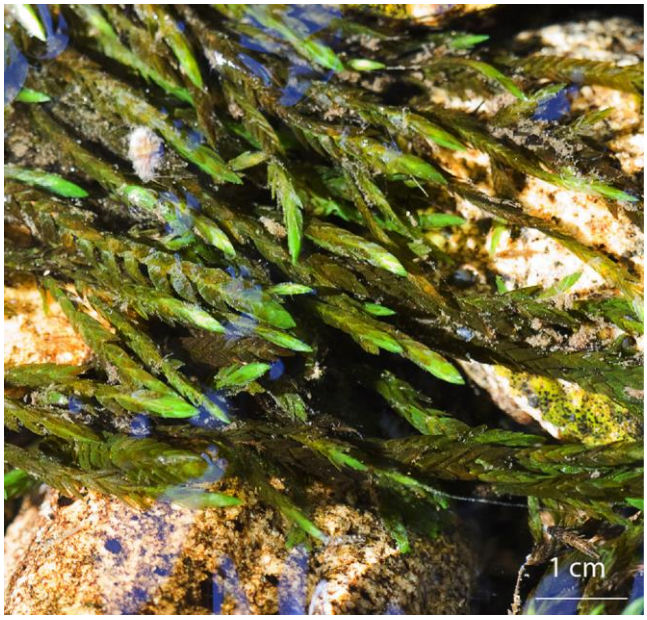

Figure 16. ***Fontinalis antipyretica***, a species of streams and lakes. Photo from Proyecto Musgo through Creative Commons.

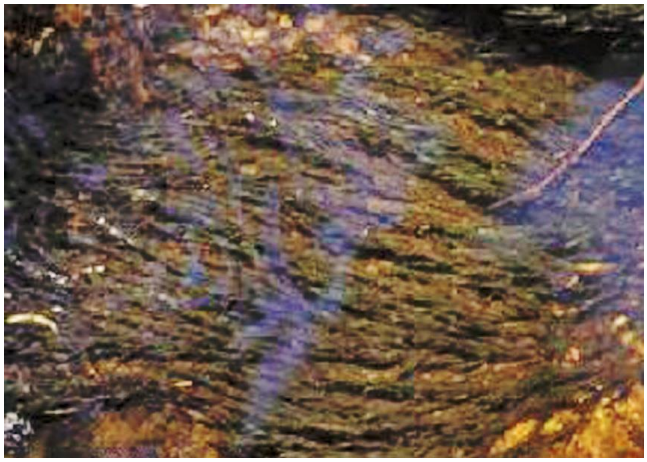

Figure 17. ***Fontinalis dalecarlica*** in its stream habitat. Photo by Kristoffer Hylander, with permission.

Figure 18. ***Fontinalis novae-angliae*** habitat. Streams typically are N-limited. Photo by Janice Glime.

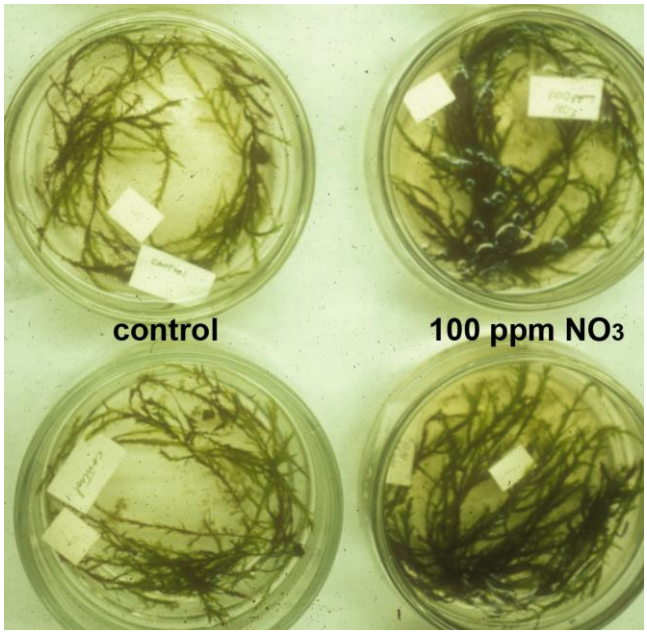

Figure 19. ***Fontinalis novae-angliae*** in control stream water and 100 ppm NO_3, showing much darker green in the high N medium. Photo and research by Janice Glime.

Although roots of tracheophytes are affected by nutrient deficiencies, there seem to be no studies that examine the effects on bryophyte rhizoids.

Phosphorus has been considered a major limiting factor for mire plant growth (Watt 1966; Small 1972; Moore & Bellamy 1974; Li & Glime 1990). On the other hand, mosses may be more competitive against tracheophytes under low P conditions; Richards (1959) reported that mosses can uptake most of the phosphate fertilizer when mosses and grasses are growing together. Apparently the phosphorus can be stored and used later in other locations; Rydin and Clymo (1989) reported the transport of phosphorus in ***Sphagnum*** (Figure 20-Figure 29), suggesting that it was being stored for use later.

Figure 20. ***Sphagnum magellanicum***, a species for which growth is typically limited by inadequate P. Photo by Michael Lüth, with permission.

The greatest number of field studies on nutrient additions have been done on the genus *Sphagnum*, but deficiency information is again based primarily on lab studies. Sanville (1988) and Aerts and coworkers (1992) found that ***Sphagnum*** production in the field increases in response to nutrient addition, suggesting that it has been growing under deficiency conditions. In support of this, Li and Glime (1990) used lab studies to demonstrate that low nutrient concentration is a major factor causing low productivity or death of parts of ***Sphagnum***. Limiting P can limit the growth of mature ***Sphagnum magellanicum*** (Figure 20-Figure 21) and ***S. papillosum*** (Figure 22-Figure 23). Boatman and Lark (1971) found that P was likewise limiting for the protonema growth of ***Sphagnum magellanicum*** (Figure 21, ***S. papillosum*** (Figure 23), and ***S. cuspidatum*** (Figure 24).

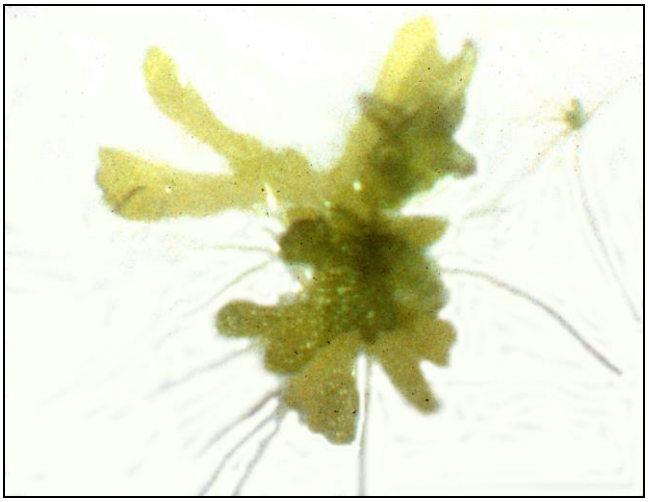

Figure 21. ***Sphagnum magellanicum*** protonema, a stage harmed by limiting P in the environment. Photo courtesy of Yenhung Li.

Figure 22. ***Sphagnum papillosum*** supporting the moisture needs of the sundew ***Drosera rotundifolia***. ***Sphagnum papillosum*** is limited in its growth by inadequate P. Photo by Michael Lüth, with permission.

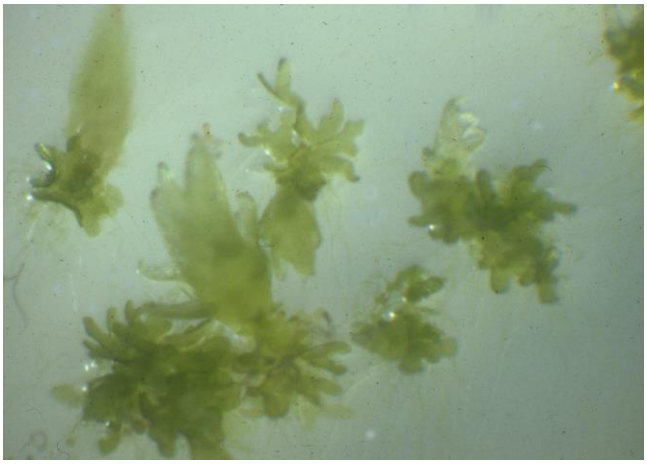

Figure 23. ***Sphagnum papillosum*** protonema buds, a stage that is limited by low P in its environment. Photo courtesy of Yenhung Li.

Figure 24. ***Sphagnum cuspidatum***, a species of peatland valleys and pools that has reduced protonema growth in media with low P. Photo by Michael Lüth, with permission.

Li and coworkers (1993) demonstrated that both high and low concentrations of P can cause ***Sphagnum magellanicum*** (Figure 25) to produce red pigments, a character common for this moss when it is in strong sunlight in nature (Rudolph 1963, 1964; Rudolph & Vowinkel 1969). What are the implications of this? Does absence of red color mean anything relative to P availability, or only that light is inadequate for pigment development?

Figure 25. ***Sphagnum magellanicum*** showing red pigments that are typical of bright light or low P. Photo by Jan-Peter Frahm, with permission.

Sphagnum (Figure 20-Figure 25) cell structure (Figure 26) and general morphology change in response to nutrient concentrations (Figure 30). Baker and Boatman (1989) found that the stem length between branch fascicles in ***Sphagnum cuspidatum*** (Figure 24) was positively related to the N content of the capitula, whereas the capitulum dry biomass was negatively related, suggesting that branches continued to develop somewhat normally, but expansion of the stem between these branches was reduced under N deficiency. Yet, there was no correlation between interfascicular length and capitulum dry biomass. Hintikka (1972) found that ***Sphagnum fallax*** (Figure 27) failed to develop hyaline cells in a medium high in NH_4^+ or organic N, but low in carbohydrates (Figure 28-Figure 29). Furthermore, Baker and Boatman (1992) found that hyaline cell length of branch leaves in ***Sphagnum*** is directly correlated with the CO_2 concentration, whereas it is inversely correlated with the N and P concentrations (Figure 30). As might be expected, the lengths of the hyaline and chlorophyllose cells were closely correlated with each other, but also correlated with leaf length. On the other hand, short leaves had few and poorly differentiated hyaline cells.

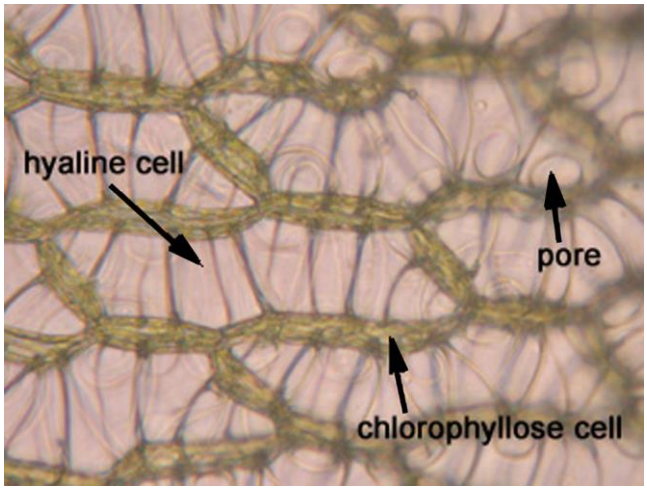

Figure 26. ***Sphagnum*** cells. Photo from Botany Website, UBC, with permission.

Figure 27. ***Sphagnum fallax***, a species that experiences morphological when it is nutrient deficient. Photo by Michael Lüth, with permission.

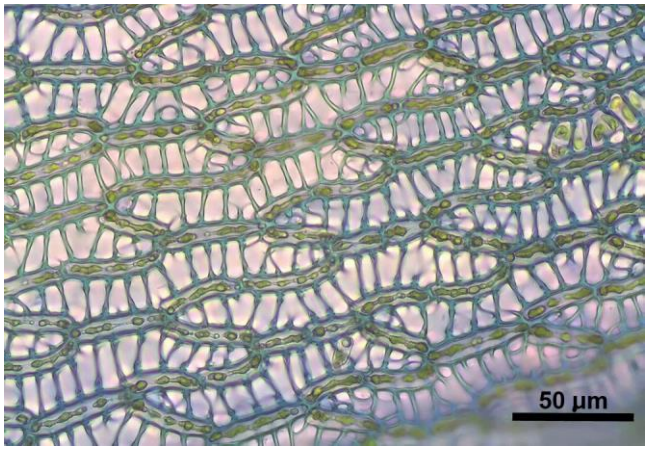

Figure 28. ***Sphagnum fallax*** leaf cells showing normal hyaline cells with fibrils. Photo by Kristian Peters, with permission.

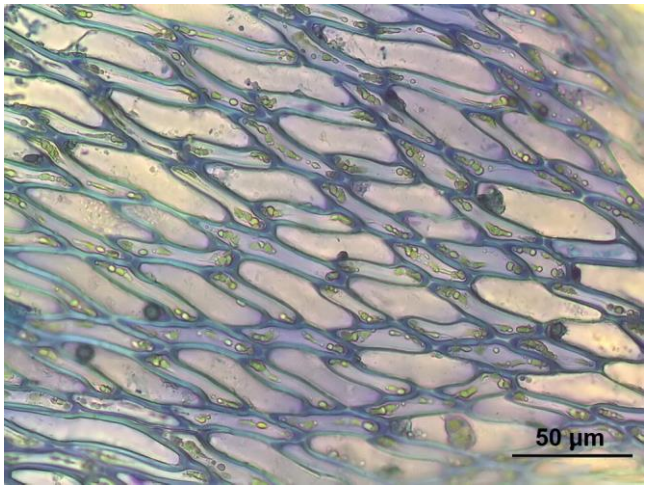

Figure 29. ***Sphagnum fallax*** with diminished leaf cells, suggesting a nutrient imbalance. Photo by Kristian Peters, with permission.

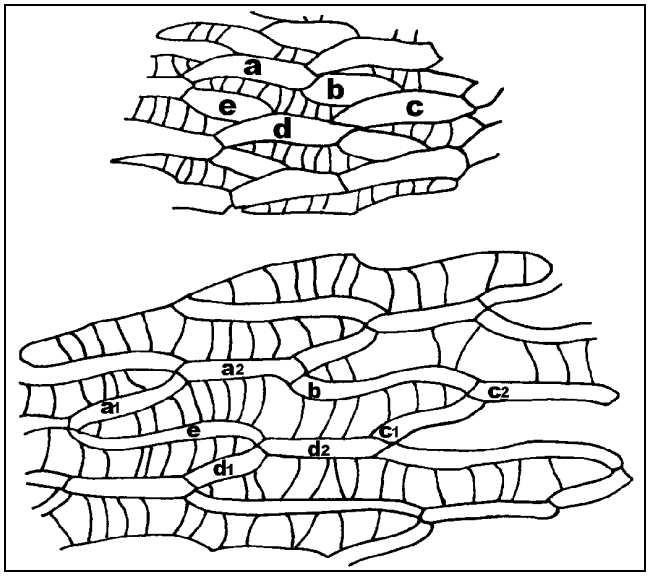

Figure 30. Arrangement of photosynthetic and hyaline cells in ***Sphagnum capillifolium*** leaves grown in high N & P/low CO_2 (ambient) treatment (**upper**) compared to those in low N & P/high CO_2 (5%) treatment (**lower**). Based on Baker & Boatman (1992).

Baker and Boatman (1992) suggested that the presence of well-differentiated hyaline cells in ***Sphagnum*** (Figure 26, Figure 28) provided a "scavenging system" for inorganic nutrient ions when they were in low concentration. The additional surface area on the interior of the cells, highly endowed with polyuronic acids, provides a large surface for binding and facilitating uptake. While this suggestion may be true, the notion of cause and effect is questionable. The plant can hardly make a decision that it needs more or longer of these cells in order to get nutrients.

How does this change in hyaline cells affect the desiccation tolerance of the moss? Perhaps one explanation is that bogs and fens are never N limited due to their Cyanobacteria flora, but that if the system is getting dry, little of the N is reaching the new leaves at the top because of the loss of capillary water. This would result in longer leaves and more hyaline cells, providing the hyaline cells needed to hold a water reservoir. But would the timing work? Would these young leaves get the signal soon enough to have the hyaline cells ready when they need them for maintaining hydration?

Liverwort deficiency studies are even more limited than those of mosses. Voth and Hamner (1940) reported that N deficiency caused a reduction in growth of ***Marchantia polymorpha*** (Figure 31) and the plants were stunted. Symptoms in ***Marchantia polymorpha*** more closely resembled those of tracheophytes. In cultures lacking N, P, or both, the midrib was darker (Figure 32) and scales, rhizoids, and the lower epidermis became red in about 10 days (Voth 1941). After 2 weeks, the N-free plants ceased growing and produced no gemmae cups; they produced few dichotomies and thalli remained narrow. Eventually the upper surface became chlorotic. Those plants lacking P likewise had a very dark midrib (Figure 32) and red underside, but contrasted sharply with the N-free plants in having frequent dichotomies with broad thalli, giving the thalli a rosette appearance, and producing numerous gemmae cups (Figure 33). As in the mosses, ***Leucolejeunea clypeata*** (see Figure 34) plants were light yellow to white in the absence of P (Fulford *et al*. 1947).

Figure 31. ***Marchantia polymorpha*** showing normal thallus and midrib. Photo from Botany Webpage, UBC, with permission.

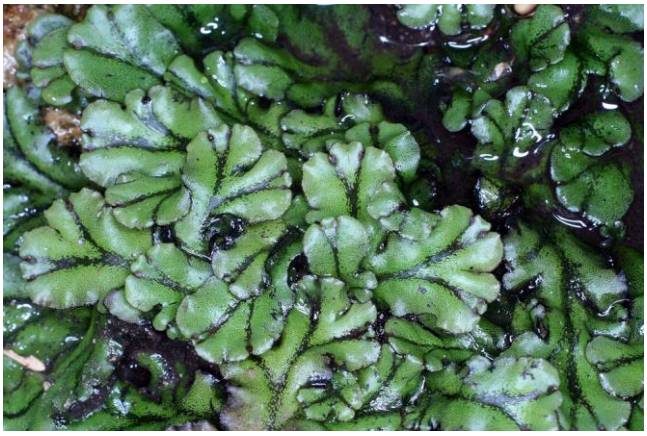

Figure 32. ***Marchantia polymorpha*** showing darkened midrib typical of severe N or P deficiency. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

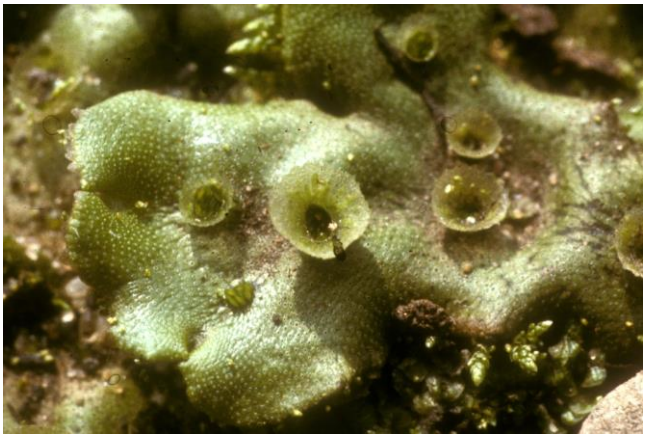

Figure 33. Thallus of ***Marchantia polymorpha*** with gemmae cups that are more abundant when P is deficient. Photo by Janice Glime.

Figure 34. ***Leucolejeunea*** sp., a species that becomes white or yellow when it is deprived of P. Photo by Jan-Peter Frahm, with permission.

K Deficiency

Potassium is also a translocatable nutrient, the most easily moved – and lost – of all the nutrients in both tracheophytes and bryophytes due to its high solubility and low ionic mass. When deficient in K^+, tracheophytes exhibit mottled or chlorotic leaves with small spots of dead tissue, usually at the tips and between veins, and especially at the margins; stems are slender. In bryophytes older parts may exhibit leaf margin chlorosis somewhat similar to effects seen on tracheophytes.

When cultured in a liquid medium with no potassium for four weeks, all samples of ***Fontinalis antipyretica*** (Figure 16) remained bright grass-green in color, although some were slightly pale (R. Marr & Glime unpub). By contrast, ***Marchantia polymorpha*** (Figure 33) *(*on solid agar) exhibited tan coloration in its older thallus parts, especially along the wing margins near the tip (Voth 1941). In tracheophytes, K^+ is important in the regulation of guard cells. No connection has been made between K^+ and the cells surrounding ***Marchantia*** pores (Figure 35-Figure 36), but it is possible that K^+ is likewise involved in their tendency to close under dry conditions.

Figure 35. ***Marchantia polymorpha*** gemmae cup with thallus showing numerous pores. Photo by Bernard de Cuyper, with permission.

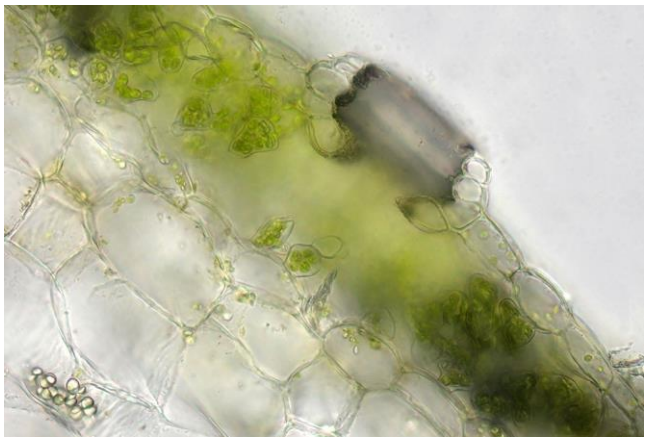

Figure 36. ***Marchantia polymorpha*** pore cs showing a stack of cells that can bend to decrease the pore diameter. Photo by Walter Obermayer, with permission.

Ca Deficiency

Calcium is important in maintaining membrane integrity (Brown 1982) and in binding cells together. Brown suggests that Ca^{++} may be required in greater concentrations by mosses that grow in Ca^{++}-rich sites. These mosses can have 16-17X as much Ca^{++} as species from Ca^{++}-poor habitats (Bates 1982). Mosses in calcareous habitats have 3-4X as much Ca-exchange

capacity as mosses from Ca^{++}-poor habitats (Bates 1978). Brown (1982) reasons that the Ca^{++} may be used to maintain membrane integrity. He suggests that these **calciphilic** (Ca^{++} loving) bryophytes may have inherently leakier membranes at low Ca^{++} concentrations and that it is also more difficult for them to uptake ions such as K^+. Jefferies (1969) reported that ***Cephalozia connivens*** (Figure 37) (a **calcifuge** – avoiding Ca) had maximal K^+ uptake at 0.1 mM Ca^{++} and *p*H 4, whereas ***Mesoptychia turbinata*** (calcicole – of Ca-rich habitats) did best at 3.0 mM Ca^{++} and *p*H 4-8. Nevertheless, K^+ efflux was unaffected by the Ca^{++} concentration in these two liverworts. Patterson (1946) suggested using a K:Ca ratio of 49:1 to maintain membrane integrity when using KCl to test osmotic potential. Osmotic tests that lack Ca^{++} should be suspect because they do not provide the Ca^{++} needed to keep the membrane intact.

Figure 37. ***Cephalozia connivens***, a **calcifuge**. Photo by Michael Lüth, with permission.

Calcium deficiency is known to interfere with growth because the cell walls cannot cement together properly, lacking the Ca needed for the calcium pectate bonds. In algae, new crosswalls fail to form between newly divided nuclei (Reed 1907). This element has low solubility and is generally not translocatable, so it cannot be taken from older leaves to supply the growing tips. Thus, necrosis of leaf tips and margins and death of the stem apex are common in Ca-deficient tracheophytes, often preceded by chlorosis (Voth 1941). Bryophytes seem to be no exception. In ***Marchantia polymorpha*** (Figure 31), the Ca^{++}-deficient plants had less growth and biomass increase than controls (Voth 1941). Nehira (1973) also showed that Ca^{++} was required for rhizoid differentiation in ***Marchantia***, with Ca^{++} accumulating at the rhizoid base.

In the leafy liverwort ***Leucolejeunea clypeata***, the response is somewhat unusual, although perhaps only visible because of the one-cell-thick leaves. Growth in a medium with no calcium causes normally flat cells to become swollen (Figure 38; Geldreich 1948a), although it has no effect on already mature cells, suggesting weak or easily extended cell walls, consistent with insufficient Ca pectate. However, these leaves still test positive for pectic substances, but negative for presence of calcium, indicating that some other element such as Mg or K has been used in place of Ca. Geldreich suggests that the rounding is the result of this substitution because magnesium and potassium do not have the hardening property of calcium pectate, thus permitting elasticity to the cell wall. This is an interesting result because some species of ***Fissidens*** [***F. cristatus*** (Figure 39-Figure 40) vs ***F. adianthoides*** (Figure 41)] are separated based on this rounded cell character difference. Might this simply be an environmental expression of calcium deficiency? On the other hand, Geldreich did not find the cell difference witnessed by Fulford *et al*. (1947) on ***L. clypeata*** with this same treatment.

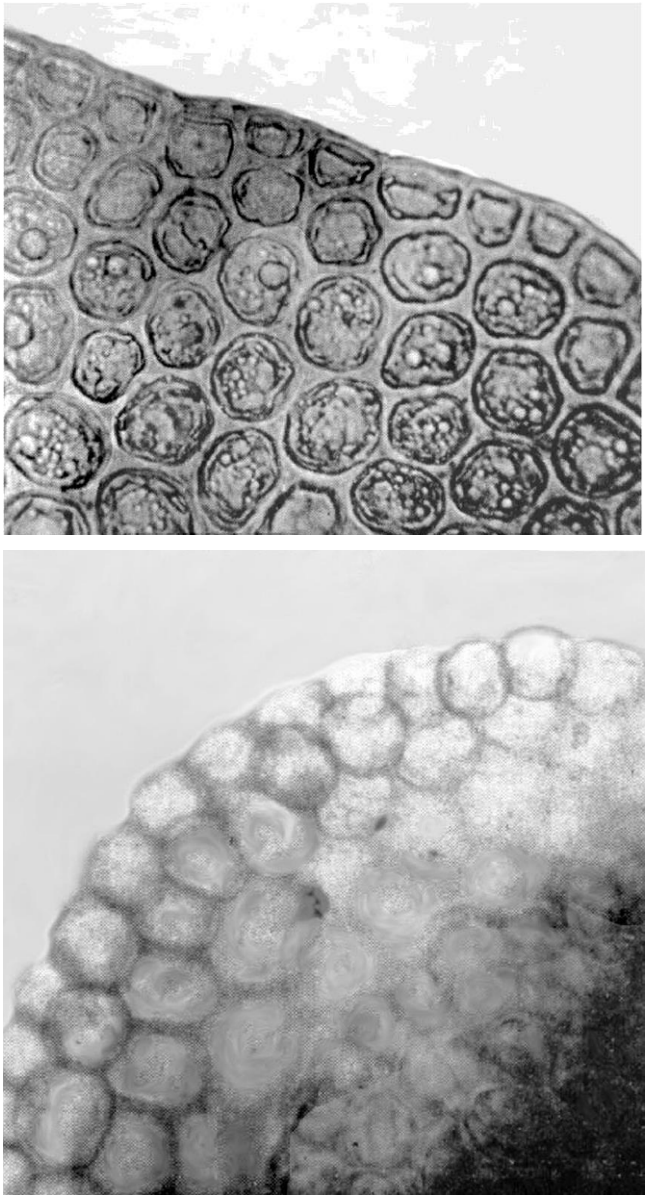

Figure 38. Effects of a Ca-deficient environment on leaf cells of ***Leucolejeunea clypeata***. **Upper:** leaf grown on normal nutrient agar, showing distinct cell walls and flat surfaces. **Lower:** leaf grown on Ca-deficient agar, showing bulging cells. Photos retouched from Geldreich 1948a.

Figure 39. ***Fissidens cristatus***, a species that has rounded leaf cells. Photo by Stuart Dunlop <www.donegal-wildlife.blogspot.com>, with permission.

Figure 40. ***Fissidens cristatus*** leaf, showing rounded cells. Photo by Malcolm Storey (DiscoverLife), with online permission.

Figure 41. ***Fissidens adiantoides*** with capsules, a species with hexagonal leaf cells. Photo by Bob Klips, with permission.

A second symptom of Ca^{++} deficiency in ***Leucolejeunea clypeata*** (Figure 38) is the configuration change in the oil bodies (Geldreich 1948a). In normal cells, the oil bodies are ovoid and typically one per cell. In the Ca^{++}-deficient leaves, the shape varied from globose to ovoid and they numbered up to seven per cell. This is another trait change that could confound identification in some taxa.

Unlike the response of ***Leucolejeunea clypeata*** (Figure 38), wherein the protonema failed to develop on a Ca^{++}-free medium (Geldreich 1948b), ***Funaria hygrometrica*** protonemata (Figure 7, Figure 13) grew rapidly on Ca^{++}-free agar, but these were from already established transplanted cultures (Hoffman 1966). The gametophores that developed were small, a response typical of Ca^{++}-deficient tracheophyte sporophytes, with soft tissues that were easily torn; the entire culture turned black. In the chelated form, Ca^{++} becomes unavailable, at least for ***Funaria hygrometrica*** (Iwasa 1965), unlike the chelated form of iron, which is the more usable form, suggesting that on organic substrates this moss might suffer from a Ca^{++} deficiency. This should be explored as a possible cause of its preference for inorganic soil and ash and its disappearance when other plants arrive.

Marchantia polymorpha (Figure 31-Figure 33) likewise responded to reduced Ca^{++} supply (12 mg/L) by developing black tips (Voth 1941). The wings of the apical notches became black first, followed by the meristematic region. Then a V-shaped zone developed progressively back from the tip. Many of these blackened tips became watery, but by the end of the 32-day experiment many of the blackened tips were curled upward, dry, and brittle. This is similar to the response of the alga *Spirogyra*, in which the apical cell eventually contains a dark lecithin-like substance (Reed 1907). Voth (1941) showed that in ***Marchantia***, early symptoms were internal, with maturing cells having larger vacuoles and fewer chloroplasts. One interesting response is that while dorsal cells are breaking down, the ventral cells surrounding the smooth rhizoids are persistent and become a source of regenerated thalli – tenacity to the end!

Mature ***Fontinalis antipyretica*** (Figure 16, Figure 43), on the other hand, responded to Ca^{++} deprivation by becoming pale yellow-green with a hint of brown (R. Marr & Glime, unpub).

Mg Deficiency

Deficiency of magnesium in tracheophytes results in lower leaves becoming mottled or chlorotic due to translocation of the Mg^{++} to developing apical tissues; leaves often become reddish; tips and margins turn up, causing the leaves to become cupped. Symptoms such as cupped leaves are more difficult to detect, if they exist, in bryophytes. The absence of veins might even make this trait unlikely. In some cases, lacking definitive studies among the bryophytes, deficiency symptoms can be inferred from the symptoms of excess from a competing nutrient. Most mosses need very little calcium, and calcium from limestone rock is more often detrimental than helpful to mosses. Clymo (1973) demonstrated that Ca^{++} coupled with high *p*H, at which it is most soluble, actually killed most ***Sphagnum*** species, with ***Sphagnum squarrosum*** (Figure 42) being the most tolerant in the study. ***Sphagnum*** is particularly sensitive to $CaCO_3$, forming crusts on its branch tips and soon losing vigor. Hence, these crusts of $CaCO_3$ are symptomatic that the moss is likely to be deficient in the Mg^{++} and K^{+} that must compete for binding sites.

Figure 42. ***Sphagnum squarrosum***, a species tolerant of high *p*H and Ca levels. Photo by Janice Glime.

The effects of Mg^{++} absence seem to be similar to those of Ca^{++} deficiency for ***Funaria hygrometrica*** (Figure 7, Figure 13) (Hoffman 1966). Protonemata grew well and new gametophytes formed, but like the Ca^{++}-deficient plants, these were smaller than those receiving the nutrient. In the culture study, the stems turned brown and eventually many entire gametophores turned brown. But other than the color changes, the leafy plants appeared to be quite healthy. When mature ***Fontinalis antipyretica*** (Figure 43) was cultured in a Mg^{++}-free medium for four weeks, all plants seemed to remain normal in appearance (R. Marr & Glime unpub). ***Marchantia polymorpha*** (Figure 31-Figure 33) likewise seemed to remain a healthy color, but had less area growth and dry biomass compared to controls (Voth 1941). This differs from tracheophyte symptoms in which the plants become chlorotic. Long-term absence or deficiency of Mg^{++} would undoubtedly cause chlorosis, and eventually death, because Mg^{++} is needed to form the chlorophyll molecule.

S Deficiency

Sulfur is rarely a limiting nutrient, even for tracheophytes, but soils in parts of Australia, Scandinavia, southwestern grain-producing parts of Canada, and northwestern U. S. A. can be sulfur deficient. Sulfur is used in the amino acids cysteine and methionine, thus is needed for building proteins. Sulfur is not readily translocated in plants, so deficiencies are exhibited by young tissues. In tracheophytes, the terminal bud remains alive, but young leaves and veins of older leaves become chlorotic (Salisbury & Ross 1992).

As with Ca^{++} deficiencies, ***Funaria hygrometrica*** protonemata (Figure 7, Figure 13) grew on S-free agar, developing gametophores (Hoffman 1966). But these gametophores were likewise small and they later became slightly chlorotic. Depriving mature ***Fontinalis antipyretica*** (Figure 43) of S for four weeks seemed to have no effect on its appearance (R. Marr & Glime unpub). Likewise, ***Marchantia polymorpha*** (Figure 31-Figure 33) growing on S-free agar showed no visible symptoms (Voth 1941). However, S in the atmosphere during the experiments may be sufficient to provide the needs for these low-nutrient, slow-growing plants.

Fe Deficiency

In the soil, high *p*H contributes to iron deficiency in plants, and in acidic soils Al can interfere with Fe uptake. Furthermore, Fe needs to be in a chelated form for cells to absorb it across the membrane. Once delivered to the tissues, Fe is also immobile and cannot be moved easily from older to younger tissues. In tracheophytes its deficiency causes interveinal chlorosis similar to that for Mg^{++} deficiency, but in the case of Fe it is the younger leaves that become chlorotic. Although it is not required in chlorophyll, it is apparently needed by the enzymes used to synthesize chlorophyll and it is needed especially in the electron transport system.

In bryophytes, symptoms of Fe deficiency are poorly known and vary with species. When transplanted to agar with no iron, ***Funaria hygrometrica*** protonemata (Figure 7, Figure 13) grew rapidly, but produced very few new upright gametophores (Hoffman 1966). Those that were produced became chlorotic and the plants eventually turned brown. When mature ***Fontinalis antipyretica*** (Figure 43) was cultured without Fe for four weeks, the stems became bright red, especially near the base, and some leaves were likewise red at the base (R. Marr & Glime unpub). When unchelated iron was provided as $FeCl_3$, all ***F. antipyretica*** plants had yellow-brown leaves with bright green stems. Normally the stems of this species are brown. One must ask why the symptoms differed when unchelated iron was supplied. Did something in the medium or in the plant chelate it to a limited extent? What could account for the red coloration with no Fe?

Comparisons of the macronutrient deficiency symptoms in the mosses ***Fontinalis antipyretica*** (Figure 43) and ***Funaria hygrometrica*** (Figure 7, Figure 13) and thallose liverwort ***Marchantia polymorpha*** (Figure 31-Figure 33) are presented in Table 2.

Table 2. Deficiency symptoms in ***Fontinalis antipyretica*** (Figure 43) based on unpublished data of Robert Marr and Janice Glime, ***Funaria hygrometrica*** (Figure 7, Figure 13) based on Hoffman (1966), and ***Marchantia polymorpha*** (Figure 31-Figure 33) based on Voth (1941).

	Fontinalis	***Funaria***	***Marchantia***
N	pale green	few protonemata, chlorotic	midrib dark, scales & rhizoids red
P	dark green	few protonemata, no gametophores	midrib dark, scales & rhizoids red
K	no visible effect		tan coloration of older parts
S	no visible effect	small, chlorotic	no visible effect
Mg	no visible effect	small, stems brown many leaves brown	less growth
Ca	pale yellow-green	small, soft tissues	less growth black tips
Fe	stems bright red	few gametophores, chlorotic, brown	

Micronutrient Deficiency

It is difficult to deprive plants of micronutrients because the minute quantities needed can occur as contaminants. Any bryophytes brought from the field are likely to have sufficient quantities on their surfaces to last them for a long time. Even when grown on nutrient-

deficient agar (missing B, Cl, Cu, Mn, Mo, and Zn), ***Funaria hygrometrica*** (Figure 7, Figure 13) continued to produce protonemata (Hoffman 1966). Although gametophores developed, they remained stunted and their stems turned dark. The tissues were tough and difficult to tear, much like in the N-deficient cultures. When Marr and Glime (unpub) deprived mature ***Fontinalis antipyretica*** (Figure 43) of micronutrients for four weeks, most plants exhibited no symptoms, except that 8 apical pieces developed brown tips (in 4/5 replicate containers). On the other hand, when Cu was added to ***Fontinalis dalecarlica*** (Figure 44) in Lake Superior water, greener cells resulted.

Figure 43. ***Fontinalis antipyretica*** with brown tips (**arrow**) such as might be seen with a nutrient deficiency.

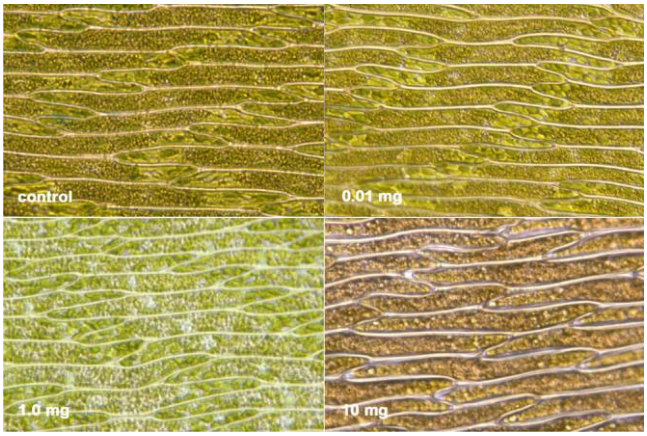

Figure 44. ***Fontinalis dalecarlica*** showing the greenest leaf cells at 1.0 mg copper per liter. Photo by Janice Glime.

Biochemical changes that affect the ability of the plant to tolerate stress may also occur. For example, in ***Marchantia palacea*** var. ***diptera*** (Figure 45) grown in copper-deficient media, the enzyme Cu/Zn-superoxide dismutase was inactivated (Tanaka *et al*. 1995). This enzyme group is important in maintaining membrane integrity (Dhindsa & Matowe 1981; Dhindsa *et al*. 1981; Gong *et al*. 1997). Therefore, its destruction or inactivation may result in greater membrane damage during desiccation, resulting in a loss of nutrients from the cell. Such losses can result in a multiplicity of symptoms because other nutrients have become deficient as well.

Figure 45. ***Marchantia palacea*** var. ***diptera***, a species that disables the enzyme Cu/Zn-superoxide dismutase when grown in a copper-free medium. Photo by Janice Glime.

Oxygen Deficiency

One rarely considers plants in the context of oxygen deficiency, but apparently even some members of this oxygen-producing group can suffer from insufficient oxygen. When the aquatic leafy liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 46) was cultured in a non-aerated solution, it accumulated considerably less phosphorus in the first three days, probably due to blockage of mitochondrial respiration, followed by a net loss of P, indicating probable membrane damage (Mártínez Abaigar 2002).

Figure 46. ***Jungermannia exsertifolia*** subsp. ***cordifolia***, a species that seems to require oxygen to take in P. Photo by Michael Lüth, with permission.

Community Effects of Deficiencies

Although nutrient concentration often may not cause evident deficiency or excess symptoms in bryophytes, it can have a strong effect on community composition. Bryophyte-dominated peatlands provide a good example. Following an extensive literature survey, Bedford *et al*. (1999) suggest several generalizations regarding peatlands: "(1) plant community type changes across broad nutrient gradients; (2) species richness declines as various indicators of nutrient availability increase beyond some

threshold; and (3) rare and uncommon species are almost always associated with species-rich communities." Perhaps it is safer to agree with Bedford *et al*. (1999) in their conclusions that our "generalizations do not always hold within community types; for many community types, the threshold beyond which richness declines has not been established, and high or low diversity may occur below that threshold; and (4) the failure of many studies to include bryophytes precludes drawing strong conclusions about nutrient availability and diversity in peatlands."

Brunkman (1936) found that moss cover in other habitats seemed to have little to do with nutrients. Cover on clays and clay loams in Alberta, Canada, ranged from 7 to 92%, on sandy loams from 59 to 92%, and on Jack pine (*Pinus banksiana*) sand to sandy loams, from 3 to 71%. Brunkman found these data to be "confounding," and interpreted them to mean that the moss does not correlate with soil type, and by inference, probably does not correlate well with nutrients. He had to conclude that mosses were of little or no value as indicators of possible timber values and volumes because "the moss cover wanders all over the site values without any sequence . . ."

On the other hand, Epstein and Yeatman (2003) found that bryophytes increase when tracheophytes such as *Betula nana* resorb higher percentages of N, depriving other shrubs of the nutrient and thus favoring bryophytes. Thus, even if the bryophytes do not directly respond to the nutrients, they may respond because of the resulting change in competition from tracheophytes for space and light.

Nevertheless, Marczonek (1984) showed that ***Conocephalum conicum*** (Figure 47) population density is dependent on the soil levels of Ca^{++} and Mg^{++}. ***Pellia epiphylla*** (Figure 48) likewise has increased densities with increases of these two elements as well as N and K. ***Meesia triquetra*** (Figure 49) occurs where there is both a high *p*H and high concentration of Ca^{++} (Montagnes 1990). These are but few examples of the many *p*H and nutrient relationships that exist among the bryophytes. Many more will be discussed as we examine individual habitats later in this book. This surely is evidence that mosses and liverworts can and do get nutrients from the soil and that bryophytes do have minimal nutrient requirements, which they satisfy with either precipitation or substrate or both. The availability of these nutrients determines their growth and distribution, but not in isolation from other factors such as water availability and competition.

Figure 47. ***Conocephalum conicum***, a species in which population density is dependent on soil levels of Ca^{++} and Mg^{++}. Photo by Michael Lüth, with permission.

Figure 48. ***Pellia epiphylla***, a species that has increased densities with increases of $Ca^{++,}$ Mg^{++}, N, and K. Photo by Robert Klips, with permission.

Figure 49. ***Meesia triquetra***, a species that prefers high *p*H and a high concentration of Ca^{++}. Photo by Michael Lüth, with permission.

Summary

Bryophytes have low nutrient demands compared to tracheophytes, and this may permit them to thrive in habitats such as rock surfaces where they collect dust and throughfall, or in streams where a new supply of nutrients constantly flows by.

N and P deficiency can reduce protein synthesis and photosynthetic rates, while increasing carbohydrate content. N deficiency in bryophytes causes chlorosis and may result in tough, fibrous gametophores with scalelike leaves. In liverworts, at least, it causes a reduction in growth and gemmae cups. Liverworts also may develop red pigments in the absence of N, P, or both. In phosphorus-free media, mosses may become dark brown or may be dark green with only the tips exhibiting chlorosis. Low P limits growth. However, in the liverwort *Marchantia*, absence of P resulted in frequent dichotomies and broad thalli with numerous gemmae cups.

Carbohydrate deficiency, coupled with a high concentration of NH_4^+ or organic N can cause *Sphagnum* to fail to develop hyaline cells. These hyaline cells may provide a "scavenging system" for inorganic nutrient ions when they are in low concentration.

With **potassium** deficiency, older parts may exhibit leaf margin chlorosis somewhat similar to effects seen on tracheophytes. *Marchantia* likewise develops pale thallus margins.

Mosses growing in Ca^{++}-rich habitats may develop 3-4X as much Ca-exchange capacity as those from Ca^{++}-poor habitats. The Ca^{++} may be necessary to maintain membrane integrity and therefore would be important in retaining K^+. Ca^{++} deficiency can result in reduced growth, lack of rhizoid differentiation, failure of protonemata to develop, black thallus tips, change in shape and increase in number of oil bodies in liverwort leaf cells, small gametophores, and soft tissues. If Ca^{++} is absent during cell development, the cell walls can become more elastic and appear rounded. Internal changes may include larger vacuoles and fewer chloroplasts.

Deficiency of Mg^{++} can result in smaller gametophytes with stems and leaves turning brown. Otherwise, Mg^{++}-deficient bryophytes seem to be healthy.

Sulfur deficiency symptoms are similar to those of Ca^{++} and Mg^{++}, with reduced gametophore growth and chlorosis, but few other symptoms. However, there is often sufficient S in the atmosphere to sustain the bryophytes.

Iron deficiency symptoms seem to vary among species. They include reduction in number of upright gametophores, chlorosis, red stems, red leaf bases, and bright green stems (with unchelated iron).

Micronutrient deficiency can result in stunted growth and dark-colored stems with tough tissues. Enzymes needed to maintain membrane integrity may fail, perhaps due to absence of the metal part of the enzyme.

In aquatic habitats, even oxygen can become limiting, resulting in inability to accumulate P.

Nutrient balance affects competition, and bryophytes often gain an advantage when tracheophytes are nutrient-deficient.

Acknowledgments

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CHAPTER 8-7

NUTRIENT RELATIONS: FERTILIZATION

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CHAPTER 8-7

NUTRIENT RELATIONS: FERTILIZATION

Figure 1. ***Gymnostomum aeruginosum*** growing on calcareous rock. Photo by Michael Lüth, with permission.

Fertilization Effects

We often learn about things in science by serendipity. And when it comes to learning about bryophytes in ecosystems, we often learn by what we do to their neighboring tracheophytes. Hence, when we fertilize our gardens or add fertilizers to restore impoverished land, the bryophytes respond, in their own way, along with the intended tracheophytic plants.

In general, fertilizers are detrimental to bryophytes. This is often because added fertilizers benefit tracheophytes that were unable to grow well in their absence and once being fertilized are able to overgrow the slow-growing bryophytes (Virtanen 2000), depriving them of light. One effect of fertilizers is that they frequently change the *p*H, often making it more alkaline; this is especially true for lime fertilizers. Few bryophytes are favored by high *p*H levels (Figure 1), and at the very least, the species composition is likely to change (Miles 1968; Miles 1973). Moreover, lime often has a desiccating effect, like that of chalk dust on your hands. However, some specific nutrients may be limiting and certain fertilizers may actually benefit the bryophytes.

Surprisingly, bryophytes in a polar semi-desert at Svalbard Arctic archipelago increased their cover as a benefit from applications of N, P, and K (with little effect by increased temperature), while there was a significant decrease in the cover of the flowering plants *Dryas octopetala* (Figure 2) and *Saxifraga oppositifolia* (Figure 3) (Robinson *et al*. 1998). A strong winter injury seemed to account for the ultimate decrease in *Dryas octopetala*. On the other hand, ***Hylocomium splendens*** (Figure 4) and ***Rhytidium rugosum*** (Figure 5) exhibited significant reductions in growth in a combined temperature and fertilizer enhancement experiment in a subArctic-alpine community in Sweden (Jägerbrand *et al*. 2003).

Figure 2. ***Dryas octopetala***, an Arctic species that decreases cover when fertilized with N, P, and K. Photo by Jörg Hempel, through Creative Commons.

Figure 3. ***Saxifraga oppositifolia***, an Arctic species that decreases cover when fertilized with N, P, and K. Photo by Smiley.toerist, through Creative Commons.

Figure 4. ***Hylocomium splendens***, a species that experienced significant reductions in growth in a combined temperature and fertilizer enhancement experiment in a Swedish sub-alpine zone. Photo by Michael Lüth, with permission.

Figure 5. ***Rhytidium rugosum***, a northern species adapted to low nutrients. Photo by Michael Lüth, with permission.

Changes in nutrient concentrations can affect the lipid content of bryophytes, thus affecting their ability to tolerate cold and desiccation. In the Arctic, growing shoots contain more lipids than carbohydrates (Rastorfer 1972). The lipid content of ***Sphagnum fuscum*** (Figure 6-Figure 7) increases during spring in the actively growing parts while decreasing in the senescent parts (Karunen & Salin 1981). ***Dicranum elongatum*** (Figure 8) uses lipids as storage material in its senescent parts (Karunen & Mikola 1980; Karunen & Liljenberg 1981). The conversion to carbohydrates may lower the freezing point, but I have not seen evidence to support this suggestion.

Figure 6. ***Sphagnum fuscum*** showing its typical hummock growth. Photo by Michael Lüth, with permission.

Figure 7. ***Sphagnum fuscum*** showing older (lower) parts where lipids decrease in spring, while increasing in the upper, growing parts. Photo by J. C. Schou, with permission.

Figure 8. ***Dicranum elongatum***, a moss that stores lipids in its senescent parts (**lower**). Photos by Michael Lüth, with permission.

Al-Hasan *et al*. (1991) found that the addition of $Ca(NO_3)_2$ caused a shift in lipid content in the mosses ***Ctenidium molluscum*** (Figure 12), ***Dichodontium pellucidum*** (Figure 10), ***Pogonatum urnigerum*** (Figure 11), and ***Tortella tortuosa*** (Figure 12), with total lipids decreasing steadily with increasing concentrations of $Ca(NO_3)_2$ in the culture medium. At the same time, the proportion of the predominant polyunsaturated fatty acids also decreased [arachidonic acid (20:4) in ***C. molluscum***, eicosatrienic acid (20:3) in ***P. urnigerum***, and linoleic (18:2) and linolenic (18:3) acids in ***D. pellucidum*** and ***T. tortuosa***].

Figure 9. ***Ctenidium molluscum***, a moss that shifts its lipid content with the addition of $Ca(NO_3)_2$. Photo by Michael Lüth, with permission.

Figure 10. ***Dichodontium pellucidum***, a moss that shifts its lipid content with the addition of $Ca(NO_3)_2$. Photo by Michael Lüth, with permission.

Figure 11. ***Pogonatum urnigerum***, a moss that shifts its lipid content with the addition of $Ca(NO_3)_2$. Photo by Michael Lüth, with permission.

Figure 12. ***Tortella tortuosa***, a moss that shifts its lipid content with the addition of $Ca(NO_3)_2$. Photo by Michael Lüth, with permission. Photo by Michael Lüth, with permission.

Temperature also plays an important role in the storage of certain lipids and fatty acids. The content of triglycerides increases in ***Dicranum elongatum*** (Figure 8) plants photosynthesizing at low temperatures of 1-6ºC (Karunen 1981).

N Additions

Because bryophytes receive much of their nutrient input directly from the atmosphere, their responses to added atmospheric inputs of such pollutants as NO_3^- and NH_4^+ can be rapid. If mosses are nutrient deficient, they should respond immediately and positively to these additions.

It appears that at least some bryophytes can use more N than they normally get. As noted in Chapter 8-6, ***Fontinalis novae-angliae*** (Figure 13) and ***F. dalecarlica*** (Figure 14) both became considerably darker green in response to higher N concentrations (Glime, unpubl.); ***Dicranum majus*** (Figure 15) likewise had its highest chlorophyll content from the highest N location (Bakken 1995).

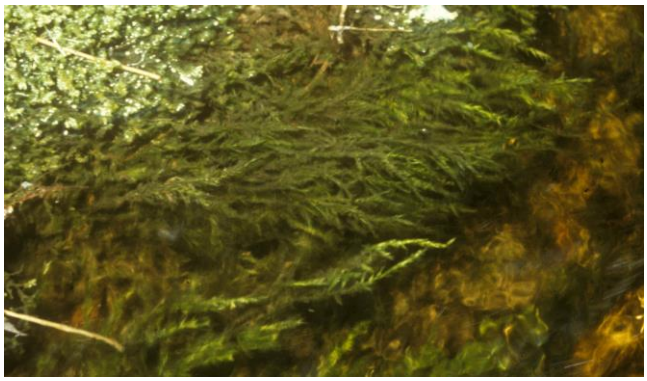


Figure 13. ***Fontinalis novae-angliae***, a species that attains a darker color in N concentrations much higher than their native streams. Photo by Janice Glime.

Figure 14. ***Fontinalis dalecarlica***, a species that attains a darker color in N concentrations much higher than their native streams. Photo by J. C. Schou, with permission.

Figure 15. ***Dicranum majus***, a species that increases its chlorophyll content in higher concentrations of N. Photo by Michael Lüth, with permission.

Muller (1997) compared N content of plants from a plot receiving low doses of NH_4N0_3 diluted in rainwater (30 kg N ha^{-1} $year^{-1}$) to plants from a control plot that received the same amount of rainwater without added N. The treatment simulated a tripling of the natural N deposition, while the added water represented only 7% of its annual precipitation. Although the N found in tracheophytes (0.7 mg N g^{-1}) in this study provided inconsistent results (Schleppi *et al*. 1999), the moss ***Thuidium tamariscinum*** (Figure 16) had a dry matter increase in N of 1.3 mg g^{-1} (7%) (Muller 1997). At the same time, treated ***Hylocomium splendens*** (Figure 4) tended to become brown (Muller 1997), while ***Sphagnum nemoreum*** (= *S. capillifolium*; Figure 17) seemed to have a reduction in photosynthetic pigments as a result of the added N (Schleppi *et al*. 1999). It appears that the mosses were harmed by the added N in this form, except for the greater storage of N in ***Thuidium tamariscinum***. On the other hand, Heeschen and coworkers (1996) contended that N is a "critical nutrient" for bryophytes in raised bogs. But the form matters.

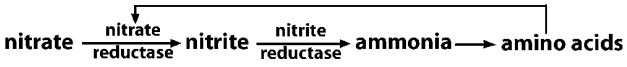
Figure 16. ***Thuidium tamariscinum***, a moss that benefits from increased N input. Photo by Michael Lüth, with permission.

Figure 17. ***Sphagnum nemoreum*** (= *S. capillifolium*), a species that loses chlorophyll when N is added to its growing medium. Photo by Michael Lüth, with permission.

Li and Vitt (1997) in their experiments on nutrient applications in peatlands in Alberta, Canada, found that the added N increased the productivities of two dominant mosses, ***Sphagnum fuscum*** (Figure 6-Figure 7) in a bog and ***Tomenthypnum nitens*** (Figure 18) in a rich fen,

whereas the productivity of two dominant shrubs, *Rhododendron groenlandicum* (=*Ledum palustre* subsp. *groenlandicum*; Figure 19) in the bog and *Betula pumila* (Figure 20) in the rich fen, was unaffected. Furthermore, Nordin and Gunnarsson (2000), working with ***Sphagnum fuscum***, ***S. magellanicum*** (Figure 21), and ***S. rubellum*** (Figure 22) from two mires in Sweden, found that addition of NH_4NO_3 actually caused decreased growth, but resulted in higher concentrations of amino acids in the tissues. When tissue amino acid concentrations exceeded 2 mg, growth in length decreased, suggesting the amino acids may have reached a toxicity level or that the feedback mechanism caused a toxic buildup of NH_4NO_3.

Woodin *et al*. (1985) found that precipitation high in NO_3^- (as often found in acid rain) induces the nitrate reductase in ***Sphagnum fuscum*** (Figure 6-Figure 7). Eventually this causes a rise in ammonia, which in turn inhibits the nitrate reductase activity. Nitrate reductase is typically the limiting component in the conversion to amino acids, so it provides a control mechanism that attempts to moderate the concentration of NH_4^- and amino acids in the plant:



But it is important to keep in mind several intervening factors. Bryophytes in bogs and poor fens typically have **Cyanobacteria** associated with them, and ammonium inhibits nitrate reductase, reducing the symbiotic N fixation by the **Cyanobacteria**. Furthermore, ammonium is more available in acid soils. (See Subchapter 8-3 for further discussion of these intervening factors.)

Figure 18. ***Tomentypnum nitens***, a moss with increased productivity when N is added. Photo by Michael Lüth, with permission.

Figure 19. ***Rhododendron groenlandicum***, a species that does not seem to respond to added N in a bog. Photo through Creative Commons.

Figure 20. ***Betula pumila***, a species that does not seem to respond to added N in a bog. Photo through Creative Commons.

Figure 21. ***Sphagnum magellanicum***, a species in which addition of NH_4NO_3 caused decreased growth but increased amino acids. Photo by Michael Lüth, with permission.

Figure 22. ***Sphagnum rubellum***, a species in which addition of NH_4NO_3 caused decreased growth but increased amino acids. Photo by Michael Lüth, with permission.

As one might expect, what is good for one bryophyte may destroy another. Dirkse and Martakis (1992) found that in Swedish forests, fertilization with NH_4NO_3 elicited a positive response from ***Lophocolea heterophylla*** (Figure 24) while causing a "distinctly negative" response from ***Ptilidium ciliare*** (Figure 24). In another experiment with the aquatic ***Sphagnum cuspidatum*** (Figure 37), Paffen and Roelofs (1991) were unable to demonstrate any response to added NH_4^+ unless the CO_2 concentration was increased simultaneously. This suggests that it is the usable C source (CO_2) that is limiting in that habitat, not the N source.

Figure 23. ***Lophocolea heterophylla***, a liverwort that responds positively to NH_4NO_3. Photo by Michael Lüth, with permission.

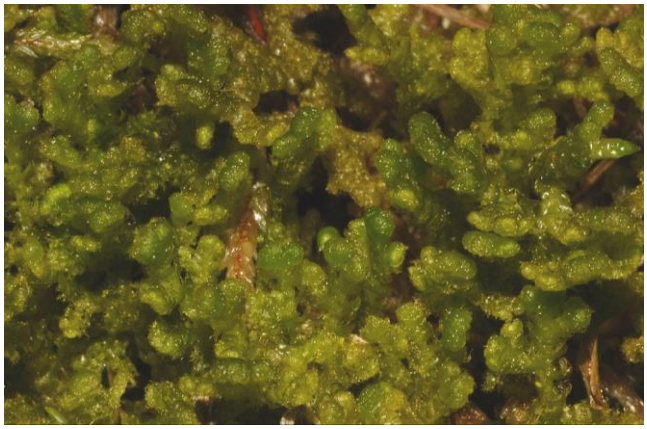


Figure 24. ***Ptilidium ciliare***, a liverwort that responds negatively to the addition of NH_4NO_3. Photo courtesy of Eric Schneider.

Nitrate reductase is formed only in the light in ***Fontinalis antipyretica*** (Figure 28) (Schwoerbel & Tillmanns 1974). If this is true in other bryophytes, it might explain why Fries (1945) was able to obtain only slight growth of ***Leptobryum pyriforme*** (Figure 25) and none in ***Funaria hygrometrica*** (Figure 26) when he cultured them on NO_3^- in the dark. In the light, on the other hand, ***Funaria hygrometrica*** and ***Weissia controversa*** (Figure 27) grew best on the NO_3^- source (Dietert 1979), but poorly even on a buffered NH_4^+ medium. And ***Fontinalis antipyretica*** grew best on NH_4^+ ions because of the suppression of nitrate reductase by NH_4^+ (Schwoerbel & Tillmanns 1974). Many bryophytes can reduce NO_3^- to NO_2^- in the dark, but light is required to stimulate conversion of NO_2^- to NH_4^+ (Brown 1982).

Figure 25. ***Leptobryum pyriforme***. Photo by Michael Lüth, with permission.

Figure 26. ***Funaria hygrometrica*** with its prolific capsules, a species that grows best on nitrate and not on ammonium. Photo by Michael Lüth, with permission.

Figure 27. ***Weissia controversa***, a species that grows best on nitrate and not on ammonium. Photo by Michael Lüth, with permission.

The aquatic moss ***Fontinalis antipyretica*** (Figure 28) responded to high levels of KNO_3 with a toxicity response that interfered with its physiological gas exchange (Stolz & Weise 1976). Its maximum sensitivity was in late spring, with minimal sensitivity in mid summer. High N levels can cause complete O_2 depletion in ***Fontinalis***-colonized waters, interfering with P uptake. Total gas exchange of ***F. antipyretica*** increased 10-12 fold when air turbulence in the culture system increased from 25 to 45 L h^{-1}; P uptake increased accordingly.

Figure 28. ***Fontinalis antipyretica*** in flowing water with lots of oxygen. Photo by Michael Lüth, with permission.

P Additions

Phosphorus typically comes from the mineral substrate, animal dung, and decomposition. The presence of ***Funaria hygrometrica*** (Figure 26) seems to correlate with the addition of phosphate fertilizer (O'Toole & Synnott 1971). Could this simply be tolerance, or is it a requirement? After all, this moss grows on charcoal, which typically binds ions, providing a low-nutrient habitat. In ***Polytrichum formosum*** (Figure 29), there seems to be a clear benefit; Vagts and Kinder (1999) reported an "exceptional stimulatory effect of NPK on this moss in a heathland."

Figure 29. ***Polytrichum formosum***. Photo by Michael Lüth, with permission.

In an Alaskan study, addition of P in a stream resulted in an increase in cover of the mosses ***Hygrohypnum alpestre*** (Figure 30) and ***H. ochraceum*** (Figure 31-Figure 32), suggesting that these mosses had been P limited (Figure 33; Bowden *et al*. 1994). P concentrations are typically low in stream ecosystems and limit algal productivity as well.

Figure 30. ***Hygrohypnum alpestre***, a species that increases in cover in the Arctic when P is added to the streams. Photo by Michael Lüth, with permission.

Figure 31. ***Hygrohypnum ochraceum*** showing its abundance in the splash of a stream. Photo by Michael Lüth, with permission.

Figure 32. ***Hygrohypnum ochraceum***, a species that increases in cover in the Arctic when P is added to the streams. Photo by Michael Lüth, with permission.

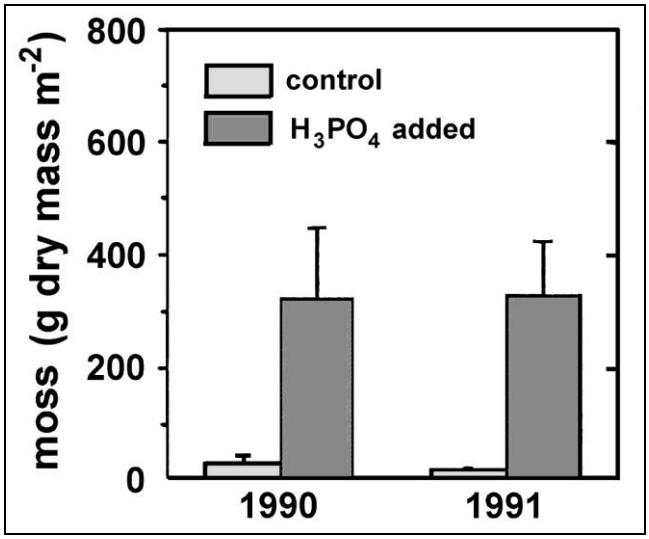


Figure 33. Comparison of moss growth and biomass in unfertilized control reaches (0.05µM) and reaches fertilized by H_3PO_4 to a concentration of 0.3µM in the Kuparuk River, Alaska, USA. From Bowden *et al.* (1994).

In their study on a stream population of ***Fontinalis antipyretica*** (Figure 28), Stolz and Weise (1976) found that the incorporation of P is an active process and is temperature dependent. The RNA fraction was the cell fraction most sensitive to these concentrations.

N and P seem to act together in strange ways. In ***Schistidium*** (Figure 34) in Alaska, the addition of either N or P caused the cover to increase, but when both were added together the cover decreased (Gordon *et al.* 2001). In bogs and fens, the nutrient relationship can be quite complex. Thormann and Bayley (1997) found that when N or P was added to the water, net primary productivity of ***Sphagnum fuscum*** (Figure 6-Figure 7) decreased significantly and that water level was the primary limiting factor.

Figure 34. ***Schistidium apocarpum*** with capsules; members of ***Schistidium*** in Alaska respond positively to addition of either N or P, but not when they were added together. Photo by Christophe Quintin, through Creative Commons.

Ca and Mg Additions

Liming ($CaCO_3$) is a common practice for eliminating bryophytes from lawns and other areas where they are unwanted. ☹ One of the problems created by liming is desiccation. But Ca^{++} from $CaCO_3$ can also harm bryophytes by competing with other nutrient ions by occupying too many exchange sites. This makes it difficult for other ions to bind to the cell walls and enter the bryophyte. But added Ca^{++} is not always harmful to bryophytes. Helsper *et al*. (1983) found that repeated Ca^{++} applications to a *Calluna*-dominated heathland in the Netherlands resulted in an increase in bryophytes.

The entry of Ca^{++} and Mg^{++} seem to interfere with each other, most likely through competition for exchange sites. The rich fen moss ***Scorpidium revolvens*** (Figure 35) responded to applications of $MgCO_3$ and $CaCO_3$ in relation to hardness (Tahvanainen 2004). At high Mg:Ca ratios and low hardness or at low Mg:Ca and high hardness, growth was suppressed, causing a bell-shaped response curve. In other words, growth increased, then decreased as Ca^{++} increased (0-18 mg L^{-1}), but increased with the Mg level (0-12 mg L^{-1}).

Figure 35. ***Scorpidium revolvens***. Photo by Michael Lüth, with permission.

Fe Additions

Iron can be a micronutrient or a macronutrient in plants and is needed in various enzymes. In oxygenated

water, iron forms iron oxides that are insoluble and precipitate out. However, in an aquatic system, deep water becomes **anaerobic** (lacking oxygen) and the iron then changes to its ferrous state and forms ferrous hydroxide, which is soluble. An interesting consequence of this relationship occurred in our study of a reservoir dam system (Glime & Keen 1984). The dam had the capability of providing outflow from four different depths. When the bottom depth was used, anaerobic water exited the reservoir and joined the shallow river below. The ***Fontinalis duriaei*** (Figure 36) in that river soon became covered with iron "pebbles." As the ferrous iron reached the photosynthesizing mosses, it changed to its ferric state and formed iron oxides with the photosynthetic oxygen. These ferric oxides adhered to the mosses as chunks or pebbles.

Figure 36. ***Fontinalis duriaei***, a species that can become plated with iron when reduced iron meets oxygenated water and plants producing oxygen. Photo by Michael Lüth, with permission.

CO_2 Additions

When plants are submersed, CO_2 can easily be limiting. This seems to be especially true for ***Sphagnum*** as it enjoys the warmer temperatures of summer when CO_2 is quickly lost from the warm water. Addition of CO_2 to water in which ***S. cuspidatum*** (wet kitten moss; Figure 37) was growing caused strong increases in both biomass and length (Paffen & Roelofs 1991). Addition of NH_4^+ without additional CO_2 had no effect on growth.

Figure 37. ***Sphagnum cuspidatum*** growing in water. Photo by Michael Lüth, with permission.

But once again, relationships are not so simple. When atmospheric CO_2 was increased to 700 ppm in combination with low levels of N deposition (6 g m^{-2} yr^{-1}), ***Sphagnum recurvum* var. *mucronatum*** (Figure 38) responded with increased productivity, exhibiting a 17% increase in dry biomass (Heijden *et al*. 2000). But when N increased with the CO_2, no growth differences occurred. In fact, even at the highest N level coupled with the high CO_2 level there was a reduction of total N in the capitulum but not in the stems. This reduction in the capitulum coincided with reduced amino acids, but the soluble protein levels remained the same.

Figure 38. ***Sphagnum recurvum*** var. ***mucronatum***, a species that benefits from added CO_2, but not when receiving added N at the same time. Photo by Jan-Peter Frahm, with permission.

Excess Nutrients

Some bryophytes require low nutrient conditions, and many simply cannot survive fertilization or high nutrient situations. The effect of high mineral concentrations has been a source of consternation for many bryologists who have attempted terrariums or culture of bryophytes. Standard nutrient concentrations usually need to be diluted to about 10% that used for tracheophytes and algae (Jeff Duckett, pers. comm. 23 February 2017), but as you will see in this chapter, that varies widely.

This problem of excess came to the attention of Bryonetters. Formation of a white crust on the tips of plants has attracted attention in a number of species. The discussion began when Caitlin Maraist (Bryonet 18 July 2016) cultured ***Ceratodon purpureus*** (Figure 39) on Turface (a clay that has been heated to improve absorption) moistened with DI water. The plants developed a white precipitate on their leaf tips. Timea Deakova (Bryonet 19 July 2016) reported having the same problem when culturing ***Dicranum*** species (Figure 8, Figure 15).

Figure 39. ***Ceratodon purpureus*** with capsules, a species that accumulates a white precipitate when grown on Turface. Photo by Michael Lüth, with permission.

Lars Hedenäs (Bryonet 19 July 2016) reported ***Syntrichia ruralis*** *s.l.* (Figure 40) as commonly having such a crust when growing in "strongly calcareous and periodically dry habitats... When dry, the upper leaf portions (hair-points and uppermost lamina) become brittle" with what appears to be a precipitated calcium compound.

Figure 40. ***Syntrichia ruralis***, a species that precipitates a white crust at the leaf tips when it dries in strongly calcareous habitats. Photo by Michael Lüth, with permission.

When ***Syrrhopodon texanus*** (Figure 41) grows on mineral-rich sandstones, groups of plants can become white with salts accumulated on leaf tips, but adjoining species do not seem to have these accumulations (David Taylor, Bryonet 18 July 2016). This raises interesting questions about the various abilities of bryophytes to tolerate these salts. Why do some deposit them at their tips and others do not? How does this relate to internal vs external conduction? And what physiological adaptations permit some bryophytes to tolerate these salts without suffering from **exosmosis** (loss of water through the cell membranes due to the higher salt concentration on the outside of the cell)?

Figure 41. ***Syrrhopodon texanus***, a species of mineral-rich sandstone where it can accumulate salts on the leaf tips. Photo by Janice Glime.

Fertilization and Community Structure

It is easy to see that, rather than benefit, mosses may suffer from increased fertilization both from acid rain inputs and from airborne farm fertilizers, as shown in many field experiments (Mickiewicz 1976; Brown 1982; Jäppinen & Hotanen 1990; Kellner & Mårshagen 1991). In industrialized areas, heavy metals, needed by the bryophytes in minute quantities, can further result in the decline of bryophytes when the industrial sources greatly increase the quantities of these pollutants. In some cases, this pollution fertilization may be beneficial to the bryophytes, as in the pine-heath system where nutrient levels are especially low. Under such circumstances, mosses including ***Pohlia*** (Figure 42-Figure 43) and ***Pleurozium schreberi*** (Figure 44) can replace lichens, including *Cladonia* spp., particularly if irrigation is supplied (Persson 1981). Skré and Oechel (1979) found that ***Sphagnum nemoreum*** (= *S. capillifolium*; Figure 17) also increased its productivity in fertilizer experiments, as did the litter-inhabiting species ***Brachythecium oedipodium*** (Figure 45) and ***Plagiothecium laetum*** (Figure 46) with higher N, P, or Mg (van Dobben *et al*. 1992). Increases in productivity and growth of bryophyte species can lead to changes in community structure.

Figure 42. ***Pohlia nutans***, demonstrating its ability to form extensive mats. Photo by Michael Lüth, with permission.

Figure 43. ***Pohlia nutans*** with capsules, a species that can replace lichens when nutrients are added to nutrient-poor habitats through pollution. Photo by Jan-Peter Frahm, with permission.

Figure 44. ***Pleurozium schreberi***, a species that can replace lichens in heathlands when fertilized by pollution. Photo by Sture Hermansson, with online permission.

Figure 45. ***Brachythecium oedipodium*** increased its productivity in fertilizer experiments with N, P, and Mg. Photo by Michael Lüth, with permission.

By contrast, Skré and Oechel (1979) found that ***Hylocomium splendens*** (Figure 4) and ***Pleurozium schreberi*** (Figure 44) in the black spruce (*Picea mariana*; Figure 47) forest near Fairbanks, Alaska, did not increase in cover with fertilizer additions, suggesting that nutrients were already more available than in the pine-heath system studied by Persson (1981) or that these populations were adapted to lower nutrient levels. Jäppinen and Hotanen (1990) found that these common boreal species, also including ***Dicranum*** (Figure 48) and ***Sphagnum*** (Figure 52) species, were killed by fertilizer applications designed to improve timber yield, but that ***Polytrichum commune*** (Figure 49) seemed unaffected. The overall effect, then, of the addition of nutrients is that species that are typical of poor sites (lichens, Ericaceae, feather mosses) shift toward associations of species typical of rich sites (Poaceae and litter-inhabiting mosses).

Figure 46. ***Plagiothecium laetum*** increased its productivity in fertilizer experiments with N, P, and Mg. Photo by Kristian Peters, with permission.

Figure 47. Black spruce (***Picea mariana***) forest. Photo by Herbert Pöhnl, through Creative Commons.

Figure 48. ***Dicranum polysetum***, a boreal forest species that is killed by forest fertilization designed to improve timber productions. Photo by Janice Glime.

Figure 49. ***Polytrichum commune***, a boreal forest species that unaffected by forest fertilization designed to improve timber productions. Photo by Michael Lüth, with permission.

On the other hand, disappearance of ***Rhytidiadelphus squarrosus*** (Figure 50) was not coupled with an increase in tracheophyte cover in either acidic or calcareous grassland (Morecroft *et al*. 1994). Rather, it appears to have responded to additions of NH_4NO_3 or $(NH_4)_2SO_4$ (ammonium sulfate) additions through disruption of its N metabolism (Bates 2000).

Figure 50. ***Rhytidiadelphus squarrosus*** with competing vascular plants. Photo by Michael Lüth, with permission.

Peatlands can respond differently in different geographic regions. Aerts and coworkers (1992) attributed the lower productivity of northern Swedish peatlands compared to those in southern Sweden to the 10X greater input of atmospheric N in the southern location. They supported this hypothesis by adding N and P at both sites. At the northern site, added N increased productivity 4-fold, but added P had no effect. Conversely, at the southern site, added N (4 g m^{-2} y^{-1}) had no effect on productivity, whereas adding P (0.4 g m^{-2} y^{-1}) increased productivity 3-fold. This trend is likewise supported by comparing a low and high deposition site in the Netherlands. Atmospheric N deposition there has been increasing, causing peatlands to increase in available N (Limpens *et al*. 2003). This increase in N seems to have coincided with an increase in ***Sphagnum fallax*** (Figure 52). However, Limpens *et al*. could find no evidence that ***S. fallax*** outcompeted any of the other five ***Sphagnum*** species in the area. Nevertheless, when N was added at a low deposition site, this species did expand its coverage. They determined that at the high deposition site ***S. fallax*** was limited by P. They concluded that when the capitulum N concentration is raised to 7 mg L^{-1} or higher and the P concentration is 0.7 mg L^{-1} or higher, this species can increase and dominate.

Li and Vitt (1997) found that while moss productivity increased 4-300% with N enrichment (3 g m^{-2} yr^{-1} as NH_4Cl), the productivity of the peatland shrubs *Betula pumila* (Figure 20) and *Rhododendron* (=*Ledum*) *groenlandicum* (Figure 19) did not. In fact, they concluded that the moss layer immediately retained nearly all of the added N. Likewise, Bayley *et al*. (1987) found that when N was added to a boreal peat system in the form of NO_3^-, 90% was taken up by the ***Sphagnum*** lawn (Figure 51) within 24 hours, resulting in a growth increase by the ***Sphagnum***. No growth increase occurred in the tracheophytes, even after five years of experimentation (Vitt 1991). Sanville (1988) likewise found that ***Sphagnum*** production increased in response to nutrient addition.

Figure 51. ***Sphagnum*** lawn. Photo through Creative Commons.

Figure 52. ***Sphagnum fallax***. Photo by Michael Lüth, with permission.

In the high Arctic heath, bryophytes are a major ecosystem component. When N and P were added to that system for eight years, there was no change in bryophyte cover, but physiological processes shifted in the bryophyte layer (Gordon *et al*. 2001). Only 10 kg ha^{-1} yr^{-1} of N increased the proportion of physiologically active bryophyte shoots while decreasing their capacity to assimilate NO_3^-. Effects of added P were even greater. When both nutrients were added, the species composition changed, with some bryophytes increasing in abundance

and others decreasing. Since N and P are both limiting in this Arctic system, increasing either will have an effect on the ecosystem. Thus, if mineralization increases as a result of global warming, we can expect shifts in the community structure of the Arctic ecosystems.

Predicting the behavior of tundra and peatland communities is not simple. Chapin and Shaver (1989) found that in Alaska the mosses (and lichens) had the greatest N and P use efficiency, but, unlike deciduous leaves, declined in N use efficiency with the addition of N plus P. Nevertheless, they can be efficient scavengers of available N, competing effectively with tracheophytes. In the Arctic tundra, Marion and coworkers (1987) found that litter recovered 1.3-16.3% and mosses 5.4-16.4% of labelled N, whereas above ground tracheophytes recovered only 2.6-5.0%. Although we tend to think of the tundra as being nutrient limited, it appears that it may not be nutrient limited for the mosses. Oechel and Sveinbjörnsson (1978) found that the addition of a dilute nutrient solution to the mosses there did not increase photosynthetic productivity or growth. One reason for this lack of response, or even decline in productivity, upon the addition of nutrients is that NO_3^- causes the induction of nitrate reductase activity, as shown for ***Sphagnum fuscum*** (Figure 6-Figure 7) by Woodin and coworkers (1985). Thus it appears that the feedback system controls the N levels in the mosses (see above under N Additions). Skré and Oechel (1979) likewise found that ***Hylocomium splendens*** (Figure 4) and ***Pleurozium schreberi*** (Figure 44) did not increase productivity after fertilizer additions, but surprisingly, ***Sphagnum capillifolium*** (Figure 17) did. Perhaps its position high in the hummock is less suitable than other locations for the N-fixing Cyanobacteria that maintain N levels in bogs and fens.

In some habitats, increasing the nutrient content can shift dominance from cryptogams, including mosses, to tracheophytes (van Dobben *et al*. 1992). When N (as NH_4NO_3) was added to a forest ecosystem in Sweden in an 18-year experiment, cryptogams, including the soil mosses ***Pleurozium schreberi*** (Figure 44) and ***Hylocomium splendens*** (Figure 4), and the heath family Ericaceae lost dominance to the grass *Deschampsia flexuosa* and **ruderal** (disturbed habitat) species. Both bryophytes were strongly "disfavored" by the addition of N at all levels. The other additions (P, K, Mg, S, and micronutrients) had similar effects but to a much smaller degree. ***Pleurozium schreberi*** was disfavored by S and micronutrients. Added P and N significantly stimulated the growth of ***Pseudoscleropodium purum*** (Figure 54), whereas ***Brachythecium rutabulum*** (Figure 53) did not respond (Bates 1994). The ***P. purum*** plants showed a greater uptake of P and to a lesser extent N than did the ***B. rutabulum*** while also conserving them more efficiently. Bates explained this difference in that ***P. purum*** depends on an unpredictable supply of nutrients from precipitation, whereas ***B. rutabulum*** probably obtains more of its nutrients from its substrate. Some nutrients are sequestered onto cell wall exchange sites of ***P. purum*** and taken up later as needed.

Figure 53. ***Brachythecium rutabulum***. Photo by Michael Lüth, with permission.

Figure 54. ***Pseudoscleropodium purum***, a species for which added P and N significantly stimulated the growth. Photo by Janice Glime.

Natural fertilizers have their effects too. Vanderpuye and coworkers (2002) suggest that fertilization by vertebrates may account for the type of moss tundra seen in Svalbard. Manuring of very cold ecosystems by seabirds (Figure 55) produces moss carpets characterized by a thin active layer over a thick accumulation of peat with no standing water. They suggest that in Sassendalen the role of the seabirds is replaced by reindeer (Figure 56) that create intense manuring in these favorable grazing areas.

Figure 55. Little Auks (***Alle alle***) on Svalbard, a source of manuring that provides nutrients for mosses. Photo by Alastair Rae, through Creative Commons.

Figure 56. Reindeer, large numbers that can contribute to manuring that provides nutrients for bryophytes. Photo by Roger S. Key, with permission.

In the boreal forest, it appears that effects of added nutrients on bryophyte community structure can be long lasting. Even 47 years after N fertilization ceased, the community structure had not returned to pre-fertilization composition (Strengbom *et al.* 2001). ***Brachythecium reflexum*** (Figure 57) and ***Plagiothecium denticulatum*** (Figure 58) had increased. On the other hand, the typically abundant ***Hylocomium splendens*** (Figure 4) had decreased relative to controls. At the same time, there seemed to be no difference in species composition of tracheophytes, but the sporocarp production of the N-sensitive mycorrhizal fungi had decreased.

Figure 57. ***Brachythecium reflexum***, a species that increased following N fertilization. Photo by Michael Lüth, with permission.

Figure 58. ***Plagiothecium denticulatum***, a species that increased following N fertilization. Photo by Michael Lüth, with permission.

Summary

Fertilizers typically harm bryophytes by benefitting their tracheophyte competitors. They can also raise the *p*H, creating conditions unfavorable for bryophytes. Only in the Arctic do fertilizers sometimes seem to benefit bryophytes, where nutrients are low and cool temperatures favor bryophyte growth. Fertilizers such as $Ca(NO_3)_2$ cause a decrease in the lipids that are needed for tolerance of cold and desiccation, whereas cold temperatures increase them.

Increases in N, especially as nitrate, increases the chlorophyll content in some species, such as ***Thuidium tamariscinum***, while causing others, such as ***Hylocomium splendens***, to turn brown. Peatland mosses often respond positively to N addition (as NH_4NO_3) while shrubs decrease. Ammonium is toxic, and the amino acid and nitrate balance must be such that it does not inhibit the conversion of NH_4^+ to amino acids. Light is needed for nitrate reductase to work, converting the nitrate to nitrite, which is then converted by nitrite reductase to ammonia and placed into amino acids. CO_2 is often limiting, making the addition of nutrients of little value. High N levels can also deplete the oxygen, preventing P uptake.

Added P seems to benefit aquatic mosses, at least in Alaska, causing an increase in bryophytic cover. Nevertheless, when N and P are added together, they can cause a decrease in productivity, even though each of these benefits when added alone.

Although Ca^{++} is an essential nutrient, it is usually harmful to bryophytes, interfering with uptake of other cations. Ca^{++} and Mg^{++} compete with each other for exchange sites and can reduce the uptake of K^+.

CO_2 is especially limiting in aquatic environments, especially in warm weather. Under good photosynthetic conditions, iron can form iron oxide on the surface of bryophytes due to the high oxygen concentration resulting from photosynthesis.

Heavy metals, typically added from industrial air pollution, are usually detrimental to bryophytes, often causing loss of chlorophyll and brown tips.

Natural fertilization by seabirds and mammal dung favors the development of some species, especially in the tundra. On the other hand, added fertilizers in the boreal forest can depress bryophyte productivity for many decades.

Acknowledgments

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CHAPTER 8-8

NUTRIENT RELATIONSHIPS: CYCLING

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CHAPTER 8-8

NUTRIENT RELATIONSHIPS: CYCLING

Figure 1. Nutrients may be tied up in bryophytes for decades, or recycle within months, in forests with abundant bryophytes, as in this forest with ***Isothecium myosuroides***. Photo by Michael Lüth, with permission.

Storage and Release

Bryophytes are of particular importance in cold biomes and tropical forests (Cornelissen *et al*. 2007). In these ecosystems, they offer a number of important contributions:

1. They are substantial members of the above-ground biomass, often along with lichens.
2. They host N-fixing bacteria, thus providing a major soil N input.
3. They control soil chemistry and nutrient availability through their leakage of recalcitrant polyphenols, control of soil hydrology, and temperature modification.
4. They erode rocks but prevent soil erosion.
5. They provide food for animals.
6. They both protect and compete with tracheophytes.

In all of these roles, they influence the nutrient cycling of these ecosystems.

Few quantitative studies have addressed the role of bryophytes in ecosystem nutrient cycling (Brown & Bates 1990). Nevertheless, bryophytes may play a significant role in the retention and release of important limiting nutrients like nitrogen in many types of ecosystems (Figure 1). Nutrients collected from aerial dust and throughfall are returned to the ecosystem from bryophytes through leaching and decomposition. Bowden (1991) found that in primary succession on exposed **New Hampshire sands**, the rate of nitrogen accumulation in ***Polytrichum*** (Figure 2) was 10.1 kg ha^{-1} y^{-1}. Even for this endohydric moss, he found that 58% of the annual input of nitrogen is from bulk precipitation. As suggested by this study, the bryological component of the ecosystem often plays a significant role in nutrient cycling (During 1990; Bates 1992; Nakatsubo 1997). When the ***Polytrichum*** was removed from the soil, nitrogen losses from the ecosystem temporarily exceeded

inputs, underlining the importance of the mosses in sequestering and holding nitrogen at the site. Lamontagne (1998) found that nitrification increased 13-fold under lichen and moss patches. In this case, the lichens did not fix atmospheric nitrogen and thus did not contribute directly to the nitrogen supply. Without the mosses (and lichens), the nitrogen from precipitation and throughfall can be lost to surface water that ultimately ends up in waterways and is carried from the local system. Furthermore, the mosses and lichens can contribute organic acids that leach nitrogen from the underlying bedrock, thus making it available to plants.

Figure 2. ***Polytrichum commune***, a species that accumulates carbon in growing shoots and brown portions. Photo by Andrew Spink, with permission.

Only in **peatlands and the polar latitudes** have most ecosystem ecologists traditionally acknowledged the role of the bryophytes in storing or releasing nutrients. Nevertheless, bryophytes play several roles in the nutrient status of their native ecosystems. Whereas tracheophytes obtain nutrients only after mediation by the soil, most bryophytes obtain nutrients before they reach the soil.

The **boreal** feather moss ***Hylocomium splendens*** (Figure 3) in a subarctic birch woodland has a retention time of 3-10 years for N, transporting the N within the plant to the growing tips (Eckstein 2000). Such a retention can have a strong impact on the nutrient dynamics of a forest with 100% bryophyte cover on the forest floor.

Figure 3. ***Hylocomium splendens***, a feather moss. Photo by Michael Lüth, with permission.

In the **Alaskan black spruce forest** (Figure 4), the bryophyte layer intercepts and accumulates more of every nutrient element but Ca^{++} than it receives from throughfall and litter (Oechel & van Cleve 1986), again suggesting that soil nutrients are also contributed. In the boreal forest, bryophytes are limited in biomass, but they nevertheless are major contributors to cover and primary productivity (Oechel & van Cleve 1986). They furthermore act much like a sponge in their ability to take up nutrients rapidly. Their further ability to modify the soil temperature and prevent permafrost makes them major ecosystem engineers for the nutrient regime.

Figure 4. Black spruce (*Picea mariana*) forest at Arctic Chalet, Inuvik, NT. Photo through Creative Commons.

Even in **tropical forests**, where trees can create up to five levels of canopy, the "insignificant" bryophytes can be significant in altering the nutrient regime. The bryophytes serve as filters for nutrients in rainfall, throughfall, and stemflow. This role is a complex one, differing among species of bryophytes, seasons, state of hydration, and types of nutrients (Glime 2001).

Working in **chalk grasslands**, During (1990) suggested that even when bryophytes are patchy they have a major impact on nutrients and tracheophytes associated with them, particularly during partial dieback and decomposition in the summer months. In chalk grasslands, bryophytes grow and absorb nutrients during autumn and winter, thus not competing with the inactive tracheophytes. They release nutrients by decomposition in spring and summer, hence serving to sequester nutrients in the ecosystem and provide them to the tracheophytes when nutrients are needed most for growth. It is clear that we cannot afford to ignore their potential role in ecosystem-level nutrient cycling.

Storage Locations

Many factors determine where nutrients are stored in bryophytes. External storage on exchange sites provides a ready supply as nutrients are used within the cells. Storage in underground stems can provide nutrients for new growth in spring. And many compounds are stored structurally, making them unavailable until the slow process of decomposition once again releases them.

Methodology Matters

Because of their tremendous surface area, bryophytes are typically "contaminated" with surface dust. This presents serious problems when trying to assess their nutrient content. While it seems obvious that washing would reduce the problem, it brings problems of its own. The success of washing mosses has rarely been quantified. Hence, degree of removal can vary widely between samples and researchers. And some species, with retentive sites such as boat-shaped leaves or clasping bases, will retain more soil particles than others. Furthermore, particulate matter may partially solubilize in the wash and could increase uptake. On the other hand, if the adhering dust contains sulfur or nitrogen oxides, the resulting acids could cause the loss of ions by leaching. The sudden change in ionic balance can have unpredictable influence on the adhering portion (*i.e.* those on exchange sites), causing a shift in the nutrient component of the bryophyte.

Published studies on the nutrient content of bryophytes have used a variety of methods, and one must assess the method to determine if the values given are appropriate for the interpretation needed. Lack of attention to bound ions on the moss surface can give misleading values.

Studies indicating locations of nutrient concentrations of bryophytes often do not provide a true picture of those constituents within the cells. Rather, they include the numerous ions located on exchange sites on the surfaces of the plant. Hence, in reviewing nutrient concentrations we must pay particular attention to the methods in separating the external from the internal components. Nevertheless, both internal and external storage have an impact on the nutrient cycling of the ecosystem.

Determining the positions of ions on and in bryophytes is largely a chemical process. Two different methods have revealed similar locations. Brehm (1968, 1970) found those located on the extracellular exchange sites by displacing the cations with 0.01N mineral acids. He followed this with formaldehyde to rupture the cells, releasing the internal soluble ions. The remaining cations were displaced with normal acid. Brown and coworkers used 1000 mg L^{-1} Sr (Bates & Brown 1974) or Ni (Brown & Buck 1978a, b, 1979) to displace the bound extracellular cations, followed by boiling to release soluble ions, and then recovering residual material by a total digestion in concentrated HNO_3. Both groups found that Na^+ and K^+ occurred in the cytosol, while Ca^{++} remained largely as an extracellular exchangeable form on plant external and intercellular surfaces. This makes sense because a major role of Ca^{++} is in forming calcium pectate bonds to cement cell walls together. Mg^{++} and Zn^{++} showed intermediate patterns of location. Nevertheless, a complete understanding of affinities is necessary to interpret the concentrations. Brown and Bates (1972) used Ni to replace Pb, but later Brown (1982) pointed out that they had failed to release all the Pb from exchange sites and that a concentration greater than 1000 mg L^{-1} would be needed to remove elements like Pb that have a very high affinity for exchange sites.

Mineral Nutrients

Several studies have identified the locations where bryophytes store mineral nutrients. Brown (1982) states that in general the monovalent cations, *e.g.* K^+, are concentrated near the apex and the divalent elements toward the base. We also know that in tracheophytes N, P, K, Mg, and Cl move easily due to greater solubility, whereas B, Ca, and Fe are relatively insoluble and immobile. One of the factors contributing to high concentrations of ions of such elements as Al, Ca, Fe, and Mn in older segments is that as cells die or other ions move to the apex, new binding sites are exposed, permitting more of these ions to accumulate there.

Brown and Buck (1985) likewise found that K^+ resided in the cytosol of ***Grimmia donniana*** (Figure 5) and ***Calliergonella cuspidata*** (Figure 6), whereas Ca^{++} and Pb^{++} were in extracellular exchangeable forms. Mg^{++} and Zn^{++} seemed to be intermediate in behavior, with locations depending on the species and total element concentration.

Figure 5. ***Grimmia donniana***, a species in which K^+ resides in the cytosol and Ca^{++} and Pb^{++} in an extracellular locations. Photo by Hermann Schachner, through Creative Commons.

Figure 6. ***Calliergonella cuspidata***, a species in which K^+ resides in the cytosol and Ca^{++} and Pb^{++} in extracellular locations. Photo by Michael Lüth, with permission.

What We Learned from Heavy Metals

Much of our knowledge of ion storage locations is derived from storage of heavy metal contaminants in the environment. For example, ***Rhytidiadelphus squarrosus*** (Figure 7) stores Pb in electron-dense regions of the plasma membrane, in vesicles, vacuoles, chloroplasts, and nuclei, and in the cell wall (Gullvåg *et al.* 1974; Ophus & Gullvåg 1974; Skaar *et al*. 1973). But ***Hylocomium splendens*** (Figure 3) in the same study only contained electron dense regions in the cell wall (Gullvåg *et al*. 1974). The researchers reasoned that the thicker cell wall of ***H. splendens*** might prevent entry.

Figure 7. ***Rhytidiadelphus squarrosus***, a species that stores lead in its plasma membranes. Photo by Michael Lüth, with permission.

In the aquatic moss ***Platyhypnidium riparioides*** (Figure 8), Cu accumulates in three locations: intercellular in the cell wall free space, exchange sites on the cell wall, and residual within the cell (Mouvet & Claveri 1998). These three locations are those we should expect to hold most of the cations of a bryophyte, suggestion that heavy metals like Cu could compete with nutrients needed in greater quantity.

Figure 8. ***Platyhypnidium riparioides***, a species that is able to store copper in the cell wall free space, on exchange sites on the cell wall, and residual within the cell. Photo by Michael Lüth, with permission.

Oil and Lipid Bodies

Oil bodies (isoprenoid essential oils; Figure 9-Figure 13) are well known in leafy liverworts, providing distinct diagnostic characters and provide distinctive odors, yet their function seems to remain unknown (He *et al*. 2013). Speculation includes protection from herbivores (Stahl 1888), pathogens, cold temperatures, excessive light (Hieronymus 1892), and UV radiation and desiccation (Gavaudan 1927; Chalaud 1931). These oil bodies are often associated with bryophytes that live in high light, but no physiological studies have demonstrated that they in fact make a difference. Perhaps the best argument for considering them to be food reserves is that most seeds store lipid droplets as a food reserve that is used for germination and subsequent growth (Huang *et al*. 2009).

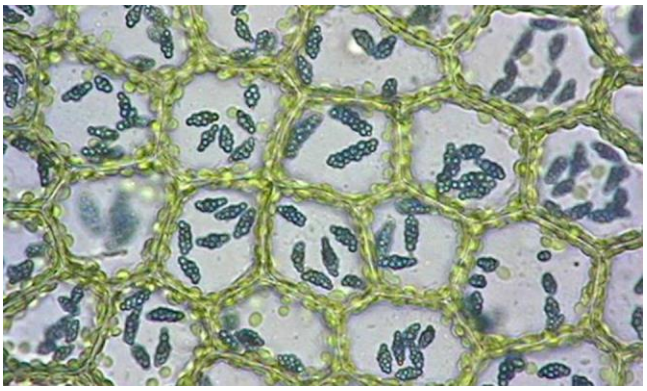

Figure 9. ***Calypogeia peruviana*** cells with botryoid oil bodies stained blue. Photo by Paul Davison, with permission.

Figure 10. ***Nardia scalaris*** leaf cells with oil bodies. Photo by Hermann Schachner, through Creative Commons.

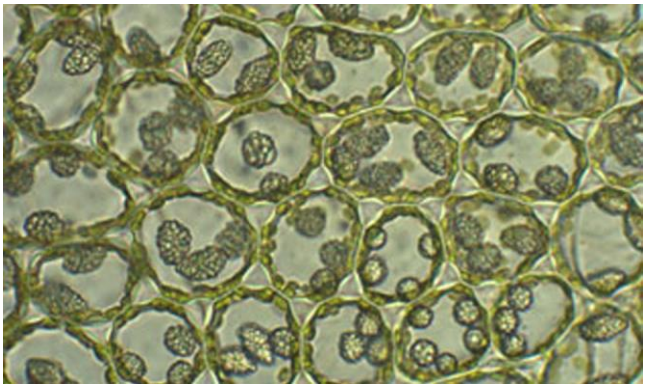

Figure 11. ***Nardia lescurii*** oil bodies and trigones. Photo by Blanka Shaw, with permission.

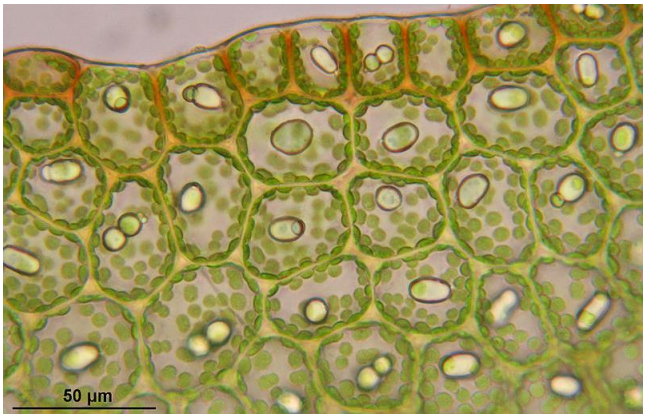

Figure 12. ***Nardia compressa*** leaf cells. Photo by Hermann Schachner, through Creative Commons

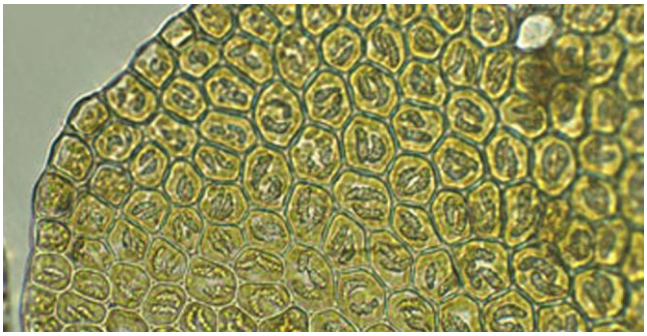

Figure 13. ***Rectolejeunea maxonii*** oil bodies 1 Blanka Shaw, with permission.

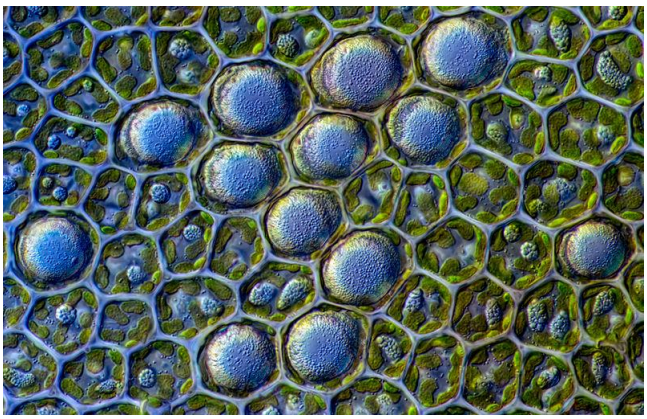

Figure 14. ***Frullania fragilifolia*** ocelli (blue bulges filling cells) and smaller oil bodies, also stained blue. Photo by Des Callaghan, with permission.

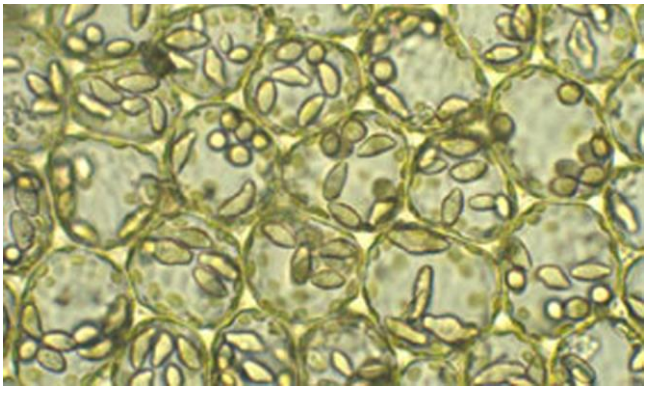

Figure 15. ***Jungermannia*** sp. oil bodies. Photo by Blanka Shaw, with permission.

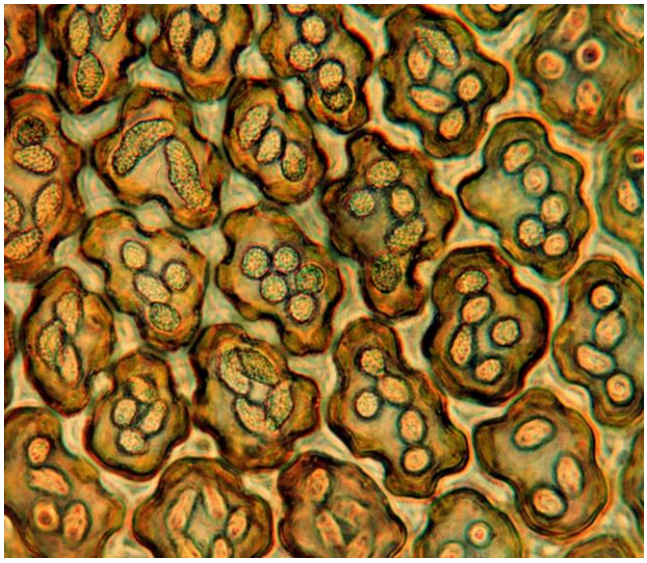

Figure 16. ***Frullania pycnantha*** oil bodies. Photo by Matt von Konrat, with permission

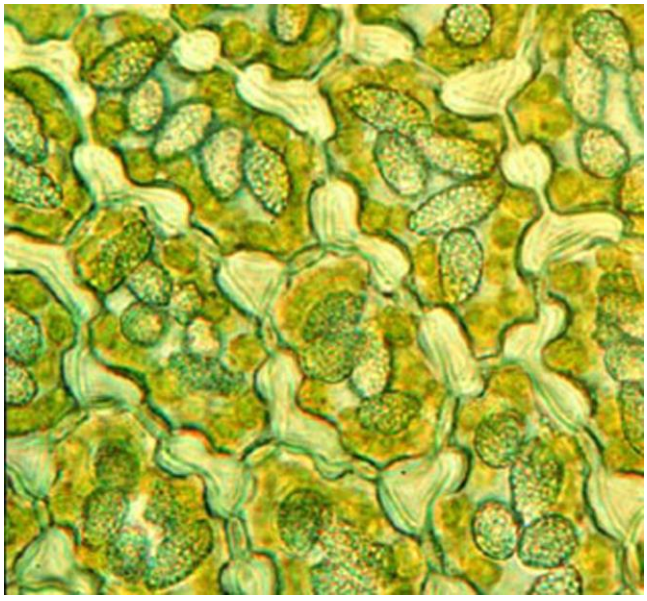

Figure 17. ***Frullania squarrosula*** oil bodies (granular greenish ovals). Photo by Matt von Konrat, with permission.

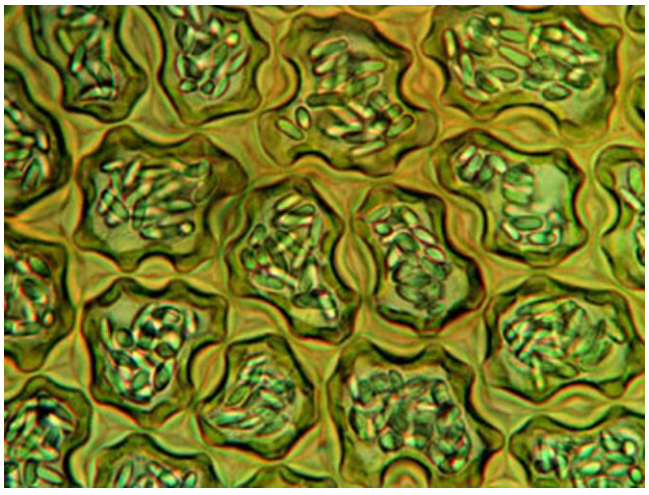

Figure 18. ***Jubulopsis novae-zelandiae*** oil bodies and cell wall trigones. Photo by Matt von Konrat, with permission.

Nevertheless, the oil bodies of liverworts seem to have an important function in cell metabolism (He *et al*. 2013). Understanding it may help us to understand how these plants tolerate their environment. But is that tolerance to light, desiccation, low temperatures, periods of low nutrients, herbivores, or something else?

More recently, Pressel *et al*. (2009) described the role of liverwort oil bodies in desiccation tolerance. These are well known to "disappear" when the liverworts are dried, thus disappearing in herbarium specimens. However, in their study, Pressel and coworkers found that instead they become unchanged in the dry state, but become flattened upon rewetting. Then, after 48 hours, they regain their normal morphology. Nevertheless, if they are dried too quickly, the oil bodies do indeed vanish upon rewetting and do not reappear. The abilities of these oil bodies to recover as flattened bodies under natural conditions, then regain their shape after 48 hours of recovery suggests that they may shift soluble carbohydrates or other important substances into the cytoplasm, permitting rapid recovery of the cell from drought.

Some mosses may also develop similar structures. Huneck (1984) reported that in mosses these are comprised of lipids, not oil drops. Jönsson and Olin (1898) reported that these lipids occurred only in certain taxonomic groups and exhibited seasonal variation. Among 50 species in Sweden, the contents varied widely, but they generally produced maximum concentrations in spring and autumn during their growth periods. These mosses furthermore lack the distinctive odors exhibited by many liverworts (Lorch 1931).

In mosses, the lipid drops occur in such varied locations as alar cells, basal laminal cells, upper laminal cells, and costa, sometimes occurring in all of these in the same leaf (Frahm 1994). But when present in the **Dicranaceae** (Figure 19), they consistently occur in basal laminal cells, but may also occur elsewhere. Frahm made one interesting discovery in the herbarium specimens he assessed – the lipid bodies tended to be most frequent in specimens collected in the cold season, at high elevations and Arctic regions. If you want to explore these further, they become more visible with a Fuelgen reaction using wet mosses treated with Schiff's reagent; this gives the lipid bodies a deep violet color.

Figure 19. ***Dicranum scoparium*** leaf base cells showing fat droplets. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Des Callaghan (Bryonet 30 July 2013) reported large oil droplets in the cells of the perichaetial leaf of ***Diphyscium foliosum*** (Figure 20-Figure 22). Ida Bruggeman (Bryonet 31 July 2013) reported that members of ***Fissidens*** will often produce several small, shiny droplets, a common occurrence in the ***Fissidens*** subgenus ***Aloma*** (Figure 23-Figure 24). Frahm (1994) reported that oil drops in laminal cells of **Dicranaceae** (Figure 19) were taxonomically important and considered these to serve as a means of storage in the species that had them. It is likely that all of these apparent "oil droplets" are in reality fat droplets.

Figure 20. ***Diphyscium foliosum*** showing perichaetial leaves around capsule. Photo from Botany 321 Website, UBC, with permission.

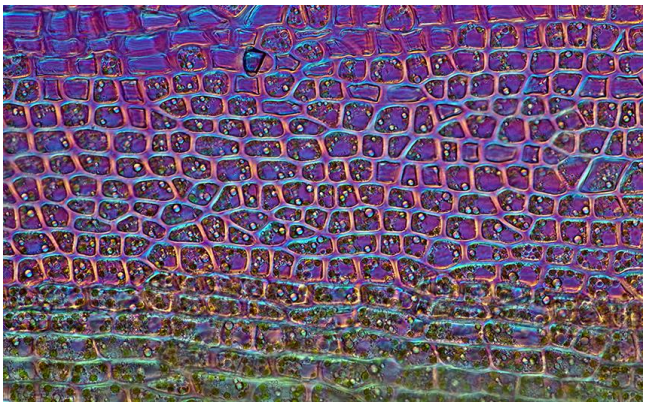

Figure 21. ***Diphyscium foliosum*** perichaetial leaf with lipid droplets under polarized light. Photo by Des Callaghan, with permission.

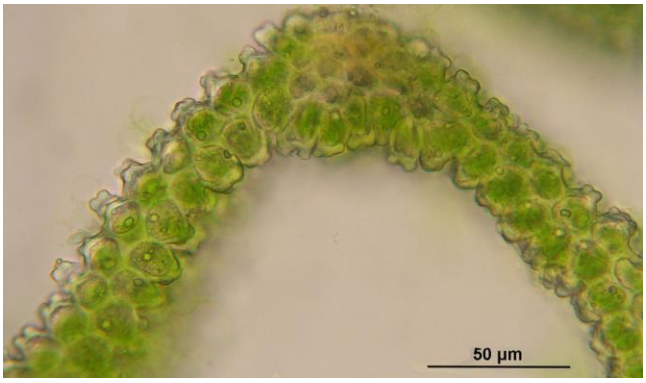

Figure 22. ***Diphyscium foliosum*** leaf cs showing fat droplets. Photo by Hermann Schachner, through Wikimedia Commons.

Figure 23. ***Fissidens exilis*** with capsules, a member of the subgenus ***Aloma***, that exhibits oil/fat droplets. Photo by Malcolm Storey, through Discover Life, with online permission.

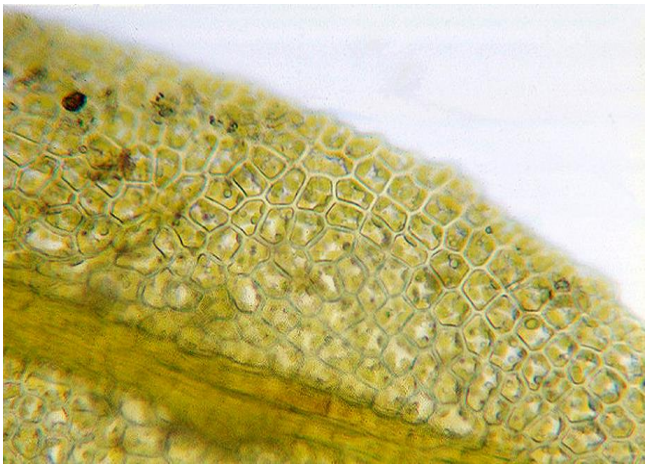

Figure 24. ***Fissidens exilis*** leaf cells showing fat/oil droplets. Photo by Malcolm Storey, through Discover Life, with online permission.

Silvana B. Vilas Bôas-Bastos (Bryonet 31 July 2013) reported observing oil/fat droplets in the basal cells of the ***Dicranella hilariana*** (Figure 25). Rut Caparrós (Bryonet 8 August 2013) reported seeing large oil droplets in the vaginula of ***Ulota*** when the sample is crushed under the cover glass. Alison Downing (Bryonet 1 August 2013) saw what appeared to be oil bodies in ***Chrysoblastella chilensis*** (Figure 26-Figure 27), but was discouraged by colleagues who said mosses didn't have oil bodies. However, Matteri (1984) reported starch grains and what appeared to be oil drops in ***C. chilensis*** in the central tissue of tubers and postulated that they might serve as a means of perennation. She noted that these tubers do not readily separate from the stems and thus considered it unlikely that the tubers served in dispersal. Allan Fife (Bryonet 4 August 2013) described these tubers in New Zealand as common in axils of lower stems in this species.

As the bryophytes remain dry for longer periods of time, these oil/fat droplets gradually become smaller (Frahm 1994), disappearing rapidly in liverworts. In the **Dicranaceae** (Figure 19, Figure 35), however, they make take 8 years to completely disappear, slowly becoming smaller. In the leafy liverworts, the species that live in dry habitats manage to keep their oil bodies longer, making it possible to see them even in herbarium specimens.

Figure 25. ***Dicranella hilariana***, a species that has oil/fat droplets. Photo by Piers Majestyk, with online permission.

Figure 26. ***Chrysoblastella chilensis***, a species that produces oil/fat droplets. Photo by Tom Thekathyil, with permission.

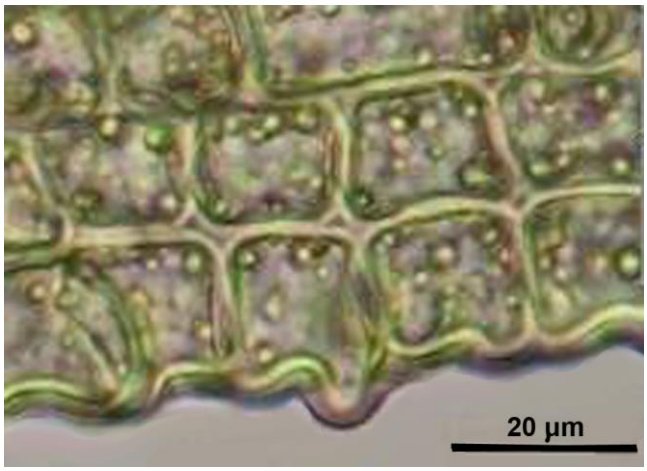

Figure 27. ***Chrysoblastella chilensis*** leaf margin cells showing oil/fat droplets. Photo by Tom Thekathyil, with permission.

Rod Seppelt (Bryonet 31 August 2013) observed that when cutting stems of some species of ***Bryum*** (Figure 28), vast quantities of lipids were released – perhaps the same

as those substances being interpreted as oil droplets in moss leaves. It appears that we need help from the biochemists to determine what these substances are. Then we need ecophysiologists to determine their use to the bryophytes and ultimate role in nutrient cycling.

Figure 28. ***Bryum*** stem cs, a genus in which lipid droplets may be released by the stem when it is cut. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

External Storage

Bryophytes do not need to store nutrients internally to have an impact on the ecosystem. Their ability to simply trap dust and retain it within the mat can be useful to some taxa while depriving others. Trapped soil and retained nutrients are apparently essential for some epiphytic taxa, especially in the tropics (Pocs 1982). This role has already been reported for orchids in Madagascar, where the moss ***Leucoloma*** (Figure 29) provides both the substrate and the nutrient source for epiphytic orchids (La Farge 2002).

Figure 29. ***Leucoloma triforme*** on bark, a moss genus that helps to support epiphytic orchids. Photo by Michael Lüth, with permission.

Rooting in epiphytic mosses is now known for trees! The koa tree (*Acacia koa*) in Hawaii produces nodules containing the N-fixing ***Bradyrhizobium*** (Figure 30) on adventitious roots (those arising above ground), but much larger and more abundantly, in the mosses growing in lofty places on the same tree (Figure 33-Figure 33; Leary *et al.* 2004)! These mossy habitats trap organic soils largely derived from decomposing heartwood and leaf litter of the host tree and contain significantly higher concentrations of exchangeable cations, total N, and significantly lower Al than the terrestrial soils. Is it the nutrients, the reduced Al, the moisture-holding capacity of the moss, or some moss exudate that stimulates these large nodules? Most likely it is the combination.

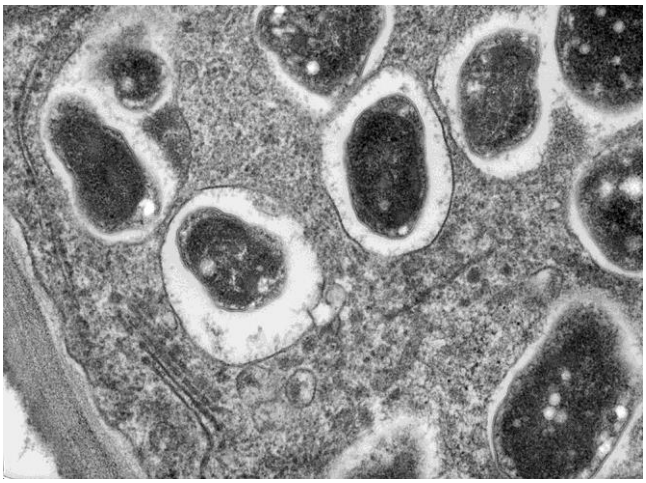

Figure 30. ***Bradyrhizobium*** nodule showing bacteria imbedded in the nodule tissue. Photo by Louisa Howard, through public domain.

Figure 31. Koa tree (*Acacia koa*) showing location of moss and nodules (**arrow**). Photo courtesy of James Leary.

Figure 32. Koa tree (*Acacia koa*) showing location of nodules with moss. Photo courtesy of James Leary.

Figure 33. Koa tree (*Acacia koa*) nodules among mosses. Photo courtesy of James Leary.

Bryophytes as Nutrient Sinks

Storage of nutrients in older parts or placing them in structural compounds can result in **nutrient sinks**. These serve as reservoirs that accumulate and store a nutrient; these sinks may result from continually transporting nutrients to new tissues, storing them in older tissues (Figure 34), or binding them in incalcitrant compounds. In any case, the sink makes the nutrient unavailable to other components of the ecosystem.

Figure 34. ***Dicranum elongatum*** showing brown senescent tissues where insoluble nutrients may remain for many years. Photo by Michael Lüth, with permission.

By trapping nutrients from the throughfall before they ever reach the soil, bryophytes serve as nutrient filters. This leads us to ask their role in parcelling out nutrients to the soil. Do bryophytes serve as nutrient sinks, and if so, do they eventually return their nutrient store to the forest soil? It may be too early to make generalizations, but let us consider some examples.

First of all, we know that bryophytes store their nutrients in structural compounds as well as within localized positions within the leaf cells. For example, Bakken (1995) pointed out that in ***Dicranum majus*** (Figure 35) N is stored in proteins and in chlorophyll. These organic components may be maintained within the moss for a long time, particularly while it is still alive. We have already seen that bryophytes move nutrients from old to young tissues, thus depriving the soil of these nutrients through the pathway of decay.

Figure 35. ***Dicranum majus***, a species that stores nitrogen in proteins and chlorophyll. Photo by Michael Lüth, with permission.

In an old-growth Douglas fir forest (*Pseudotsuga menziesii*; Figure 36), where bryophytes occupied only 0.13% of the total forest biomass, they contributed 20% to the biomass and 95% to photosynthetic tissue of the forest floor (Binkley & Graham 1981). Their biomass contribution of 1075 kg ha^{-1} was composed of 92% ***Eurhynchium oreganum*** (Figure 37) and 7% ***Hylocomium splendens*** (Figure 3). The canopy throughfall contributed 3 kg ha^{-1} yr^{-1} N. By adding the moss component, Binkley and Graham added 10% to the estimates of understory N uptake.

Figure 36. ***Pseudotsuga menziesii*** forest. photo by Dave Powell, through Creative Commons.

Figure 37. ***Eurhynchium oreganum*** . Photo by Matt Goff <www.sitkanature.org>, with permission.

In an Alaskan black spruce (*Picea mariana*; Figure 4) forest, ***Sphagnum*** (Figure 64-Figure 66), ***Hylocomium splendens*** (Figure 3), and ***Pleurozium schreberi*** (Figure 38) have a higher capacity to absorb phosphate than do the fine roots of *Picea mariana* beneath them (Chapin *et al.* 1987). In boreal ecosystems, mosses can take up to three times as much N, P, and Mg as can *Picea mariana* (black spruce) (Figure 40; Oechel & van Cleve 1986) and add 5% to Ca^{++} and K^{+} uptake (Binkley & Graham 1981). Oechel and van Cleve (1986) contend that mosses have a major impact on both nutrient availability and soil temperature, competing with the trees and shrubs for available nutrients. But the question that remains is whether the mosses ultimately return them to the forest soil, thus serving as temporary sinks that release the nutrients when the mosses are dry and dormant. Since many bryophytes are dormant in the summer when the trees are growing, they may serve as reservoirs, providing nutrients at the most crucial time in the fall when the soil is depleted and rains return to leach the nutrients from the bryophytes. On the other hand, it appears that ***Polytrichum***, perhaps through use of rhizoids for nutrient uptake, must compete with the fine roots near the surface and thus had the lowest P absorption rate of the four mosses studied in the spruce forest (Chapin *et al.* 1987). ***Polytrichum commune*** (Figure 39) exhibits translocation of nutrients to younger segments and ramets.

Figure 38. ***Pleurozium schreberi***, a feather moss. Photo by Michael Lüth, with permission.

Figure 39. ***Polytrichum commune*** clone. Photo by Michael Lüth, with permission.

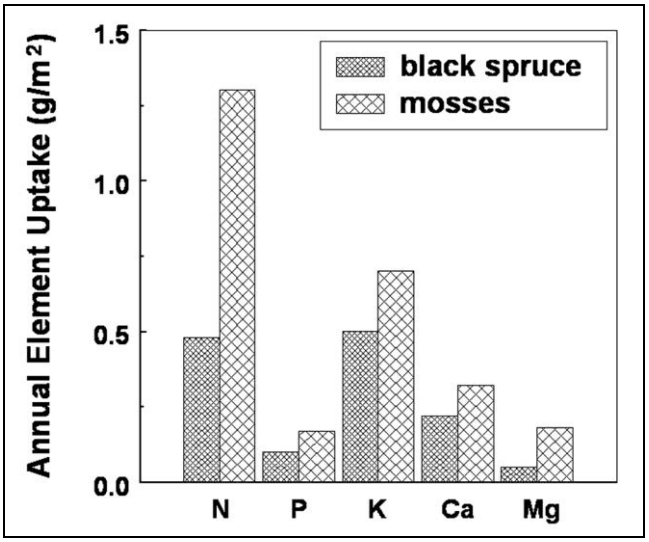

Figure 40. Comparison of annual nutrient uptake by mosses and black spruce trees (*Picea mariana*). Figure based on Oechel & van Cleve 1986, in Glime 2001.

In a different northern black spruce forest in Canada, feather mosses, primarily ***Pleurozium schreberi*** (Figure 38), sequestered 23-53% of the nutrient uptake estimated for their associated trees (Weetman & Timmer 1967). They prevented nutrient return to the tree roots by retaining those nutrients that reached the mosses as throughfall from canopy leachates. However, despite their sequestering of throughfall nutrients, Weetman and Timmer considered that the mosses were the major source of N for the trees because the mosses were able to accumulate nutrients on the shallow soils of these rocky sites. Weetman (1968) supported this hypothesis by demonstrating that there is a greater concentration of black spruce roots under the moss patches than elsewhere.

Weber and van Cleve (1984) demonstrated that feather mosses, primarily ***Hylocomium splendens*** (Figure 3) and ***Pleurozium schreberi*** (Figure 38), in the **Alaskan black spruce** (*Picea mariana*, Figure 4) **forest** can retain much of the N that enters the system and release it very slowly to the underlying organic layers, *i.e.* the root zone. But the return is very slow indeed. They found that the deeper layers of soil had incorporated little of the labelled N even three years later. It appears that N storage may work differently from that of other nutrients. In the two most common feather mosses, ***Pleurozium schreberi*** and ***Hylocomium splendens***, 90% of the labelled N could still be recovered in the mosses 28 months after application (Weber & van Cleve 1981). One reason for such a high retention is that these species are able to move their N from older, senescing branches, to young ones (Eckstein & Karlsson 1999); 50% of the labelled N was missing from older branches, all of which could be accounted for in the younger branches.

Behaving in a manner similar to tracheophytes, ***Hylocomium splendens*** (Figure 3) in a **dry pine forest** in Latvia was able to move Mg^{++}, but not Ca^{++}, from brown and decaying segments toward the tips in autumn when it was dry (Brümelis *et al.* 2000). However, both elements were tightly held in green portions with no evidence of return to the environment through leaching. Such sequestering of N, Mg, and Ca would create a sink where

throughfall nutrients might not reach the forest floor for years or even decades, rather than days or weeks. Oechel and van Cleve (1986) suggest that in Alaska bryophytes have such great ability to immobilize nutrients that they can reduce tracheophyte productivity as succession proceeds from deciduous to coniferous woodland.

After 13 years of primary succession in a New Hampshire, USA, **sand pit** that had previously been a mature hemlock-maple-yellow birch forest (*Tsuga canadensis-Acer saccharum-Betula alleghaniensis*), there was a 10.1±1.9 kg ha^{-1} yr^{-1} N accumulation in 50-60 cm of soil beneath ***Polytrichum*** spp. (Figure 39) (Bowden 1991). The N content in the 50 cm of soil beneath the ***Polytrichum*** had increased from 98±7 kg ha^{-1} in 1969 to 229±26 kg ha^{-1} in 1982. Bowden reasoned that since the accumulation rate of N was probably much lower during early years in succession, it is likely that the accumulation rate later in succession was even higher than this. Surprisingly, the N content of living biomass of moss below ground was higher than that of above ground portions, with the soil portion accounting for ~55%. Presence of the moss seems to have accounted for a significant trapping and retention of N in the ecosystem, perhaps preparing the environment for success of larger and more N-demanding plants.

In the **chalk grassland**, bryophytes are able to absorb nutrients from the senescing autumn leaves. These nutrients would probably otherwise be leached from the system while the tracheophytes are inactive for the duration of winter (van Tooren *et al.* 1988). These leachates, incorporated into the bryophytes, are then released in the spring and summer from the decomposing bryophytes and used by the high-demand tracheophytes. Furthermore, bryophytes can act as sponges for the N in acid rain during winter when tracheophytes are unable to absorb it. We should expect that bryophytes in many temperate forests likewise are able to act as nutrient reservoirs, storing nutrients and releasing them in the hot, dry summer when availability is low due to tracheophyte demands.

In the **temperate forest**, bryophytes may be rare or abundant. In those forests where they are abundant, they could likewise play the role of a nutrient reservoir. However, the ***Pseudoscleropodium purum*** (Figure 41) in European **oak forests** demonstrates a different dynamic from that of the bryophytes in the boreal forest. Bates (1989b) found that the levels of cations within the moss component under an oak (*Quercus*; Figure 42) canopy were in dynamic equilibrium with the precipitation and/or throughfall (Bates 1989b; Brown & Bates 1990).

Figure 41. ***Pseudoscleropodium purum***. Photo by Michael Lüth, with permission.

Figure 42. European oak (***Quercus***) forest understory habitat. Photo through Creative Commons.

The dominant and invasive moss ***Pseudoscleropodium purum*** (Figure 41) readily absorbed the natural leachates of K^+, Ca^{++}, and Mg^{++}, particularly as the tree leaves were senescing in autumn (Bates 1989a, b). When sprayed with dilute solutions containing Ca^{++}, K^+, and Mg^{++}, this moss absorbed most of the cations, but those that were not absorbed were released back to the ecosystem through the remaining growing season (Bates 1989a). The bulk of these were released during the next 10-15 days. Bates tracked P and K in ***P. purum*** for 74 days after application and found that only 6.3% of the P and 12.1% of the K were recovered in the moss throughfall, reaching the soil. But only 31% and 23%, respectively, remained in the moss tissues. Bates (1989a) suggested that the missing nutrients may have been incorporated by microorganisms or retained in litter. A likely consequence of this is rapid recycling of nutrients within the ecosystem.

Ecologists have theorized that bryophytes may behave like a slow-release fertilizer. They remove nutrients from the precipitation as it passes through them, then slowly release it during the succeeding weeks. This may be facilitated by the damage caused to membranes during drying. In other cases, cations bound to exchange sites may be released back to the ecosystem instead of being absorbed. This slow release mechanism can be beneficial to the ecosystem by reducing loss through leaching and providing a steady supply of nutrients as they are being removed by the roots. But there seem to be no data thus far to support or refute this hypothesis on a broad scale.

Just as in tracheophytes, we cannot generalize about bryophyte nutrient behavior because bryophytes exhibit differences as vast as those of tracheophytes, perhaps even more so. ***Hylocomium splendens*** (Figure 3), likewise a large moss, growing on a lime-contaminated site, did not release its excess Ca^{++} and Mg^{++} when moved to an uncontaminated site (Brümelis *et al*. 2000). Hence, bryophytes can serve as sinks, depriving the soil of nutrients returned by throughfall and stemflow. Since bryophytes tend to grow best, at least in deciduous forests, at the bases of trees where stemflow provides a concentrated pool of nutrients from leaves, branches, and atmosphere, this bryophytic filter could have considerable impact on both the nutrients supplied to the trees and on the herbaceous ground cover in the vicinity. Their presence at tree bases seems to be due to the slight rise in topography that reduces leaf litter accumulation, but could it also be due to the added nutrients?

In a North Wales **oak** (*Quercus petraea*; Figure 43) **woodland**, the dominant bryophytes were ***Dicranum majus*** (Figure 35), ***Rhytidiadelphus loreus*** (Figure 44), ***Plagiothecium undulatum*** (Figure 45), ***Polytrichastrum formosum*** (Figure 46), and ***Thuidium tamariscinum*** (Figure 47), occupying 90% of the ground vegetation standing crop (Rieley *et al.* 1979). These species were investigated to determine the effects of moss harvesting on the ecosystem. This moss layer readily absorbed the Ca^{++}, K^{+}, and N leached from the canopy (Table 1). It is interesting that ***Rhytidiadelphus*** removed NO_3^- whereas ***P. formosum*** removed NH_4^+. However, Mg^{++} suffered a net loss from the bryophyte layer to the soil. ***Rhytidiadelphus loreus*** actually returned more Mg^{++} to the soil than it intercepted, but removed Ca^{++} and K^{+}, perhaps exchanging some of these for Mg^{++} on exchange sites.

Figure 43. ***Quercus petraea*** forest. Photo by Rosser, through Creative Commons.

Figure 44. ***Rhytidiadelphus loreus***, a species that easily absorbs Ca^{++}, K^{+}, and N leached from the forest canopy leaves. Photo by Michael Lüth, with permission.

Polytrichastrum formosum (Figure 46) seemed to have little effect on nutrient concentrations, with leachates from the moss equalling those in the canopy throughfall for Ca^{++}, K^{+}, Mg^{++}, and Na^{+} (Rieley *et al.* 1979). In any case, a large portion of these nutrients were returned to a pathway that would make them available to the root zone. This suggests once more the role of bryophytes as a reservoir for at least some nutrients, providing a slower release than that of episodic throughfall, a role also supported in the Black Forest (Weetman 1968). Clearly, we need to understand the differences in nutrient retention among species and what causes those differences to be there.

Figure 45. ***Plagiothecium undulatum***, a species that easily absorbs Ca^{++}, K^{+}, and N leached from the forest canopy leaves. Photo by Michael Lüth, with permission.

Figure 46. ***Polytrichastrum formosum*** with capsules, a species that easily absorbs Ca^{++}, K^{+}, and N leached from the canopy. Photo by Michael Lüth, with permission.

Figure 47. ***Thuidium tamariscinum***, a species that easily absorbs Ca^{++}, K^{+}, and N leached from the canopy. Photo by Brian Eversham, with permission.

Table 1. Bryophyte-related behavior of essential nutrients in a Welsh oakwood, in mg m^{-2} yr^{-1}, based on data from Rieley *et al.* 1979 in Longton 1984.

	Ca^{++}	Mg^{++}	K^{+}
Total input to bryophyte layer	3100	1810	2920
Bryophyte accumulation	410	390	1430
Excess input over bryophyte accumulation	2690	1420	1490

Weetman (1968) suggests that mosses may actually supply tree roots more directly. When he found that roots in a **black spruce forest** (Figure 4) were concentrated in decomposing mosses, he considered that mosses might serve as a collecting point for elements, especially N, absorbed by mosses from throughfall. Whether N was obtained from throughfall, soil, or airborne dust for ***Hylocomium splendens*** (Figure 3), a reservoir that is not easily leached and carried away by rainfall could be an asset to these N-poor forests (Tamm 1953). However, Berg (1984) provides conflicting information that suggests that N may be bound in phenolic compounds in the cell wall and essentially unavailable, even in dead tissue.

Chapin and coworkers (1987) found that mosses account for 75% of the P accumulated annually above ground in an **Alaskan *Picea mariana*** (Figure 4) forest, while they account for only 17% of the P pool in aboveground vegetation. In fact, ***Sphagnum subsecundum*** (Figure 48-Figure 49), ***Hylocomium splendens*** (Figure 3), and ***Pleurozium schreberi*** (Figure 38) have a higher capacity to absorb phosphate than do the fine roots of the black spruce beneath them. Again we beg the question, do they serve as a reservoir for slow release of P, or do they keep recycling it within their own tissues, moving it to growing parts, and depriving the roots?

Even those mosses that release some of their nutrients during senescence may hold them for many years. ***Hylocomium splendens*** (Figure 3) is an abundant feather moss in the **boreal forests and northern taiga**. In a subarctic birch woods, this species retained N for 3-10 years, depending on which measure was used (Eckstein 2000). Using ^{15}N labelling, Eckstein found that the mean residence time (MRT) and annual nutrient production (ANP) for N were similar to values found in woody evergreen tracheophytes. These dominant feather mosses may retard the nutrient turnover in these forests first through their **acropetal** (base to apex) movement of nutrients and second by making unfavorable conditions in the forest floor. Eckstein suggested that such dominant taxa of bryophytes could act as ecosystem engineers to retard the nutrient turnover on the forest floor through production of acidic, nutrient-poor litter and depression of summer soil temperatures. These influences help to maintain a system more favorable for the mosses.

Longton (1992) contends that the humus contributed by moss may maintain soil fertility through chemical associations that retain the mineral ions and prevent loss through drainage. Some of these associations are of extraordinary duration. Dowding *et al*. (1981) determined that on Devon Island, Northwest Territories, Canada, 50% of the Ca in the **mesic tundra meadows** was bound in bryophytes with a decomposition time of 22 years.

Figure 48. ***Sphagnum subsecundum***, a species that accumulates carbon in growing shoots and brown portions. Photo by Michael Lüth, with permission.

Figure 49. ***Sphagnum subsecundum***. Photo by Michael Lüth, with permission.

One mechanism by which bryophytes can create long-term nutrient sinks is through incorporation into less soluble organic compounds. N can be bound to phenolic compounds in the cell wall or retained in proteins bound by tannic acid compounds in the cell (Berg 1984). Furthermore, cation exchange sites can strongly bind divalent positive ions, rendering these ions unavailable to other ecosystem components, thus making the bryophytes effective competitors, much as they are in bogs and fens.

Soil and rock type also play a role in nutrient retention by bryophytes. For example, Simon and Szerényi (1985) demonstrated that the level of NH_4^+ and NO_2^--N in soil under mosses increases from xerophytic to mesophytic species. $CaCO_3$ and *p*H seem to play a role in these differences, but nothing mechanistic can be inferred yet.

Even the **epiphytes** can make perceptible differences in nutrient cycling by intercepting and absorbing throughfall and stemflow nutrients, as demonstrated for Amazonian epiphytes (Herrera *et al*. 1978). But it appears they can also acquire nutrients that are in the vascular tissue of the main trunk! When ^{137}Cs was introduced into the stems of *Liriodendron*, 60% appeared in those bryophytes and lichens on the tree trunk and only 27% in soil bryophytes, with another 9% in bryophytes at the base of the tree (Hoffman 1972).

Luxury Nutrients

Most plants have the ability to store nutrients and use them later, at least to some degree. Tracheophytes transport the soluble nutrients from older, lower leaves to upper, growing ones, often leaving the older leaves chlorotic and eventually dying. Algae store luxury nutrients, using them later as supplies in the ecosystem dwindle, perhaps permitting them to accomplish a sexual phase that permits them to become dormant until better nutrient conditions prevail. Brown and Bates (1990), in investigating the moss ***Pseudoscleropodium purum*** (Figure 41), found luxury consumption and accumulation of some nutrient elements (K, Ca, and P) throughout the year, but other nutrients were retained poorly (Bates 1989b). However, they (Bates 1987; Brown & Bates 1990) found that ***P. purum*** had poor retention of these luxury nutrients, except for orthophosphate, with rapid transfer of the luxury elements to other parts of the nutrient cycle. Brown and Bates (1990) could find no evidence that these additional nutrient supplies could permanently enhance growth. It would seem that mosses are able to discriminate to a certain extent, maintaining required metabolic levels of N, P, and K, while excluding or excessively storing the ones that normally occur as trace amounts.

Brown (1982) also interpreted the work of Thomas (1970) on light intensity and nutrient concentrations in the moss plant to indicate luxury consumption of N and P. Thomas had found that concentrations of N and P in ***Mnium hornum*** (Figure 50) were negatively correlated with light intensity, whereas growth was positively correlated with intensity. This suggested to Brown that the faster-growing mosses in the light had sufficient nutrients and that therefore the higher concentrations in the slower-growing plants in lower light were luxury nutrients. Earlier work by Weetman and Timmer (1967) on ***Pleurozium schreberi*** (Figure 38) tends to support Brown's interpretation. They found that as the light intensity under the forest canopy decreased from 38% to 17% of full sunlight the nutrient concentration increased in the moss without any significant changes in total nutrient uptake. But one could also interpret the decreased concentrations in high light intensity to mean that the moss was using up its nutrient supply and moving nutrients from older tissues to actively dividing cells, consequently lowering the overall concentrations.

Figure 50. ***Mnium hornum***, a species in which concentrations of N and P are negatively correlated with light intensity. Photo by Michael Lüth, with permission.

These additional nutrient supplies are not permanently retained within the new growth, but rather stored throughout the plant, as in tracheophytes. Li and Vitt (1997) reported preliminary results using ^{15}N that indicate mosses may be a major sink for applied N in peatlands, implicating luxury storage.

Mártínez Abaigar and coworkers (2002) found that increased levels of KH_2PO_4 caused the leafy aquatic liverwort ***Jungermannia exsertifolia*** **subsp.** ***cordifolia*** (Figure 51) to accumulate significantly more P and K in its tissues. However, as exposure continued, the K concentrations fluctuated whereas P concentrations continued to increase. Concentrations of 20 mg L^{-1} PO_4^{-3} seemed to saturate the liverwort at 0.53% dry biomass (DM). When tissue P concentration exceeded 0.45% DM, the net photosynthesis declined, suggesting toxicity. P enrichment did not affect the chlorophyll concentration, but the chlorophyll *a*:*b* ratio did decline, as did the ratio of chlorophyll to **phaeopigments** (non-photosynthetic pigments which are degradation products of chlorophyll pigments), likewise suggesting P toxicity.

Figure 51. ***Jungermannia exsertifolia*** subsp. ***cordifolia***, a species that accumulates more P and K when treated with KH_2PO_4. Photo by Des Callaghan, with permission.

Although bryophytes need only minute quantities of heavy metals, the ability to store metals in vesicles or bind them to the cell walls (abilities seemingly missing in tracheophyte leaves) permits bryophytes to store excessive amounts. Under the insult of atmospheric trace metal deposition, ***Hylocomium splendens*** (Figure 3) accumulated 14-24% more Cu, Fe, Pb, Ni, and V than did ***Pleurozium schreberi*** (Figure 38), but both mosses maintained similar concentrations of Cd, Mn, Zn, and Cr (Ross 1990), showing an inability to regulate those non-limiting ions. Nevertheless, it appears that bryophytes would accumulate most heavy metals, bound in vesicles or other locations, and release them to the cell if needed. At the very least, they could accumulate a heavy load in the cell walls. Burton (1979) found that ***Fontinalis antipyretica*** (Figure 52-Figure 53) maintained 80-90% of its accumulated Zn in the cell walls.

Figure 52. ***Fontinalis antipyretica*** showing its growth habit in a stream. Photo by Janice Glime.

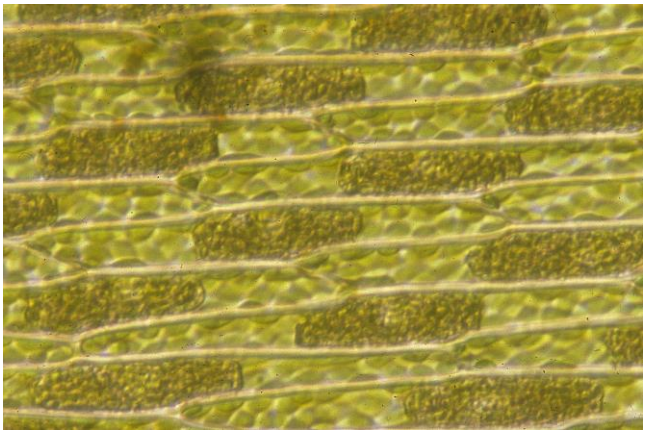

Figure 53. ***Fontinalis antipyretica*** showing cell walls, where 80-90% of its uptake of zinc is stored. Photo by Janice Glime.

Carbon Sinks

In addition to the storage of mineral nutrients, bryophytes form carbon sinks. Storage of C as photosynthate, predictably, can be found in leaves, but labelled C soon accumulates in other places as well (Skré *et al*. 1983). In particular, in four boreal forest mosses [***Polytrichum commune*** (Figure 2), ***Hylocomium splendens*** (Figure 3), ***Pleurozium schreberi*** (Figure 38), and ***Sphagnum subsecundum*** (Figure 48-Figure 49)] carbon accumulated in the growing shoot tips and in the senescent brown tissues. Large amounts were lost to respiration during the peak summer growing season.

The Vernal Dam

The **vernal dam hypothesis** predicts that spring herbs sequester nutrients during the spring when they have maximum growth, thus serving as sinks that retain nutrients that might otherwise be lost during runoff (Tessier & Raynal 2003). In their original hypothesis, Muller and Bormann (1976) considered the forest floor herbs to be sinks that would store nutrients in the spring when the trees were still dormant, then release these in the summer when the herbs were dormant and the trees were active (Rothstein 2000). Although this theory has been widely accepted, its basic assumptions have never been tested: 1. nutrients would otherwise be lost from the system in the spring; 2. forest floor herbs release nutrients to the system in the spring. In their study of a northern hardwood forest in the Catskill Mountains, New York, USA, Tessier and Raynal (2003) found that evergreen, wintergreen, and deciduous plant species do indeed sequester nutrients during the spring. Soil microbes, on the other hand, seem to remain the same or decrease in their nutrient content during that same period. In forests, a burst of growth occurs in the spring, and nutrient sequestering can occur among spring herbs near the surface while trees are tapping nutrients at lower depths. The high sunlight available while the trees are still barren of leaves permits numerous spring herbs to grow and bloom, slowly resorbing their nutrients to underground organs during the remainder of the year. But do these nutrients ever get released? And would they have been lost otherwise?

Eickmeier and Schussler (1993) have traced the parameters affecting the activity of the spring herb, *Claytonia virginica* (Figure 54), in the forest. They found that shading reduced its biomass, while enhancing its tissue nutrient concentration. This resulted in both reduced specific leaf weight and RUBISCO activity. Fertilization with 192 kg ha^{-1} total N, P_2O_5, and K_2O caused an increase in above ground vegetative biomass and increased tissue concentrations of N and P, but K concentrations were not affected. In conditions of high irradiance, RUBISCO activity increased, but it was unaffected under shaded conditions. Eickmeier and Schussler have interpreted these results to mean that *Claytonia virginica* is unable to acclimate to low irradiance and therefore depends on the brief period before leaf out to achieve its growth. Thus, it does indeed sequester nutrients that it could not obtain if it did not have this brief period of growth before leaf out. But does this support the vernal dam? It seems that it does. Under low light of summer, *C. virginica* lacks the capacity to store significant quantities of nutrients (Anderson & Eickmeier 1998). However, in brighter light, such as might be found before canopy leaf out, Anderson and Eickmeier (2000) found that *C. virginica* is able to increase the amount of N and P stored in its tissues when fertilized, and it lacks large storage organs such as those found in some spring ephemerals. Rather, it retains many nutrients in its above ground tissues and does indeed release them later in the summer rather than storing them.

Figure 54. *Claytonia virginica*, a species that takes advantage of the brief period before leaf out in spring to bloom, only releasing its nutrients later in summer and therefore creating a **vernal dam**. Photo by Janice Glime.

In sharp contrast, Rothstein (2000) found that the clonal forest herb *Allium tricoccum* (Figure 55) and other forest floor species in one northern hardwood forest did not

take up significant quantities of NO_3^- and that removal of the spring ephemerals did not affect the leaching rate of NO_3^-. In fact, many spring ephemerals resorb their nutrients and store them in underground parts (Anderson & Eickmeier 2000). Rather, Rothstein found that microorganisms took up eight times as much N as did the spring herbs. Furthermore, there was no decrease in summertime N mineralization when spring ephemerals had been removed, supporting the earlier study by Zak *et al*. (1990). Thus, in his study, Rothstein (2000) found that it was the microbes and forest floor litter that dominated the spring sink and created the vernal dam.

Figure 55. ***Allium tricoccum***, a spring ephemeral that does not take up NO_3^-. Photo by Hardyplants, through public domain.

But what would occur if this litter were predominantly conifer litter supporting a forest floor that was covered with bryophytes? What is the behavior of bryophytes as the leaves fill the canopy and reduce their light? Certainly in northern ecosystems where the bryophytes are the dominant forest floor vegetation, this question is worthy of consideration. Patterson and Baber (1961) have found that many temperate mosses are dormant in late summer and autumn. Schwabe (1976) found that long days and elevated temperatures often induce dormancy, a phenomenon that can protect them against effects of desiccation during the summer.

Might shade-adapted bryophytes also experience a vernal dam? Light is most available in early spring, and with their C_3 photosynthesis, the bryophytes are well adapted to the low temperatures following snow melt. The melting snow has provided a continuous supply of moisture, and at least some light penetrates the thin layer of lingering snow. Spring would also seem to be a season of nutrient pulse for the bryophytes with nutrients provided by the melting snow as well as through aerial cleansing by the spring rains. Summer, with few showers, may be a nutrient-poor period, although the rains that occur will surely bring a good nutrient supply from the leachates and dust accumulations of the forest canopy leaves. Summer light availability, coupled with the high temperatures, would logically seem like a period appropriate for dormancy of most bryophytes. But few studies have considered the role of sunflecks in enhancing bryophyte photosynthesis. With no stomata to open and direct contact with the atmosphere, bryophytes would seem to be even better suited than C_3 tracheophytes at taking advantages of these brief pulses of light and processing the captured energy while awaiting the next pulse. Such activity has been reported for tracheophytes and is discussed in the chapter on light.

This leaves us with the questions of when do the bryophytes need the most nutrients, when do they retain them best, and when might they release them, making them available to the soil below, and hence to the tracheophytes rooted beneath them. We can hypothesize that they would be most likely to release them when they are first wet after a period of drought, losing them before their membranes are repaired. But how long does that last, and how much is lost? Do their numerous exchange sites retain most ions, awaiting the time when the cell can once again bring them in through active transport? Is potassium preferentially lost because other ions compete for the exchange sites, making this very soluble low valence ion the most easily leached away from the plants? It appears that at least in some ecosystems bryophytes might indeed be vernal dams. The role of bryophytes in nutrient cycling is one of which we know very little.

Release during Desiccation/Rehydration

Seasonal events are very much the product of the types of seasons of a given area and what differs among them. Temperature, which folks in the temperate zone seem to consider almost exclusively as a seasonal indicator, may not be the factor most important to the bryophyte nutrient regime. Rather, seasonal differences in precipitation and moisture availability may be the primary controlling factors. This seems to be the case with nutrient release in the feather moss ***Hylocomium splendens*** (Figure 3) in a subalpine spruce-fir forest (Wilson & Coxson 1999), a phenomenon known as **pulse release** because it accumulates (some) nutrients over time, then releases them suddenly. During rehydration, nutrients and C leaked from the desiccated cells is released from the cell surfaces in a pulse release to the throughfall from the mosses. Organic C release to the forest soil can reach up to 1544 mg m^{-2} under these conditions. Experiments comparing this release to that of an inert mulch layer indicated that 23-75% of that pulse release originated in the moss mats. Release of both C and K is increased when drying is rapid. Wilson and Coxson compared the mosses to capacitors, storing low concentrations of nutrients from dust and minor rainfall events, then releasing them in higher concentrations during high rainfall events. Such a release would put the nutrients into the soil when it was most usable to the tracheophyte plants through uptake of the abundant water.

Buck and Brown (1979) likewise found that seasonal releases were tied to dehydration-rehydration processes in ***Fontinalis antipyretica*** (Figure 53) and ***Plagiomnium undulatum*** (Figure 45). Both K^+ and Mg^{++} were lost from dry cells, but clung to the extracellular exchange sites. Although K^+ in these plants had much higher concentrations in the intercellular spaces than on the exchange sites, the quantities on the extracellular sites also rose during desiccation, accounting for the losses suffered following desiccation and the pulse release to the soil during rehydration. Scafone (unpubl data) found that a pulse of K^+ is released from ***Sphagnum russowii*** (Figure 56) in the autumn at the time it is most beneficial for the tree roots in preparation for winter. In ecosystems where the bryophyte cover is typically significant it could play a

crucial role in the preparation of forest conifers for winter. This relationship might be of considerable importance for management of these forests to survive the occasional extreme winter.

Figure 56. ***Sphagnum russowii***, a species that releases a nitrogen pulse in the autumn. Photo by Michael Lüth, with permission.

Bryophytes affect the decomposition rates on the forest floor. Decomposition rates under mosses were more rapid than those under lichens (Sedia & Ehrenfeld 2006), presumably due to higher moisture content.

Canopy Releases

In the **montane forest of the tropics**, and probably elsewhere, epiphytic bryophytes accumulate considerable N, much of which is fixed from atmospheric N by microbes (Clark *et al*. 2005). The epiphytic bryophytes, along with the full epiphyte assemblage, retained 33-67% of the nitrogen that was deposited by cloud water and precipitation, with the equivalent of a 50% annual accumulation of the nitrogen in the atmosphere. The bryophytes convert the soluble, highly mobile inorganic forms to organic forms that are retained in the canopy community, potentially being released during dehydration/rehydration cycles.

Even the **cloud forest** canopy experiences pulse release of nutrients from the canopy bryophytic epiphytes (Coxson 1991). During episodes of drying and rewetting, nutrients are leached from the newly rehydrated bryophytes. This leaching is greatest for the ions that normally reside in the intracellular pools. Coxson found that effluxes from stem segments of bryophytes from the Guadeloupe tropical montane rainforest could reach 80.1 kg ha^{-1} yr^{-1} for K, 1.4 kg ha^{-1} yr^{-1} for P, and 11.8 kg ha^{-1} yr^{-1} for N, although efflux rates from intact bryophyte mats were considerably smaller: 28.7 kg ha^{-1} yr^{-1} for K and 0.2 kg ha^{-1} yr^{-1} for P. Coxson surmised that the lower rate in the field reflected recycling of the leached nutrients within the moss mat. Nevertheless, the through flow loss provides a significant input to the forest floor below and to epiphylls on the leaves below them.

Coxson *et al*. (1992) estimated that more than 30% of the days cause these epiphytes to experience severe desiccation. These wet-dry cycles cause the canopy bryophytes to accumulate 950 kg ha^{-1} of sugars and polyols. These sugars are then released in pulse form during rewetting episodes and subsequently translocated by through flow precipitation within the canopy. But the upper canopy leafy liverwort ***Frullania atrata*** accumulates sugars and polyols equivalent to 17% of its dry weight, whereas the lower canopy moss ***Phyllogonium fulgens*** (Figure 57) accumulates less than 6%. Wet-dry cycles cause the release of fructose, mannitol, glucose, erythritol, glycerol, and sucrose into the throughfall. Despite the smaller storage levels of the lower canopy moss, bryophytes at that level released more (0.9 g m^{-2}) compared to the upper canopy bryophytes (0.3 g m^{-2}). Coxson and coworkers concluded that this release of carbon sources has a significant impact on nutrient cycling by providing suitable carbon for the microbes that carry out decomposition and non-symbiotic nitrogen fixation in these forests.

Figure 57. ***Phyllogonium fulgens***, a lower canopy species in the Neotropics that accumulates less sugars and polyols than bryophytes in the upper canopy. Photo by Michael Lüth, with permission.

Hölscher *et al*. (2003) compared nutrient fluxes in three successional stages in an **upper montane rainforest** of Costa Rica. All three sites had *Quercus copeyensis* (Figure 58) as a dominant species, with various other species mixed in. The epiphyte litterfall of bryophytes and lichens differed greatly, with the highest values in the old-growth forest, which likewise had the greatest epiphyte abundance. Nevertheless, total nutrient throughfall and stemflow differed little among the three successional stages. Potassium in stemflow was only 5% in the old-growth forest, whereas it was 17% in the early successional forest and 26% in the secondary forest. Hence, in old-growth canopies the bryophytes retained the most potassium, releasing it almost entirely in throughfall.

In a **montane moist evergreen broad-leaved forest** in Yunnan, China, moss litter (including ***Homaliodendron scalpellifolium*** (Figure 59), ***Symphyodon perrottetii***, ***Herberta longifolissa*** **sic** (=*Herbertus longifolius* or *H. longifissus*?), and ***Bazzania tridens*** (Figure 60) had the slowest decay rate (0.22) compared to canopy tree leaf litter and bamboo (Liu *et al*. 2000). Bryophyte decomposition rates were less correlated with nutrient composition and lignin concentration in their initial mass

than were the tracheophyte rates (trees 0.55, bamboo 0.4). Whereas the turnover time for tree leaves was 1.5-2.50 years, it was 4.55 for the bryophytes.

Figure 58. ***Quercus copeyensis***, where old-growth forests experience the highest levels of bryophytic epiphyte litterfall. Photo by Helicongus, through Creative Commons.

Figure 59. ***Homaliodendron scalpellifolium***, one of the species that have the slowest decay rates (0.22) compared to canopy tree leaf litter and bamboo. Photo from Taiwan Liverworts color illustrations, through Creative Commons.

Figure 60. ***Bazzania tridens***, one of the species that have the slowest decay rates (0.22) compared to canopy tree leaf litter and bamboo. Photo by Li Zhang, with permission.

Bogs and Fens

In **black spruce** (*Picea mariana*; Figure 4) stands, bryophytes are the major source of N for the trees (Weetman & Timmer 1967). But the cation exchange ability of ***Sphagnum*** (Figure 64-Figure 66) continues even after ***Sphagnum*** dies, making nutrient release by dead plants slow, at least in forested peatlands (Brock & Bregman 1989), while competition for nutrients continues by means of exchange on the newly exposed walls of dead cells. Exacerbating this problem is the slow rate of organic mass loss during decomposition, as is known for ***Sphagnum recurvum*** (Figure 61), although the release of N, P, and K was larger than that of organic matter (Brock & Bregman 1989). But even after 12 months of decay, a large proportion of the original N and P remained associated with the peat. This slow decomposition process is supported by the poor colonization by organisms and almost total absence of damage to the dead cells.

Figure 61. ***Sphagnum recurvum***, a species with slow decomposition. Photo from Biopix, through Creative Commons

The same cation exchange ability that permits ***Sphagnum*** (Figure 64-Figure 66) to compete with trees for nutrients can also aid competition by facilitating toxicity to the root zone (Klinger 1988). The peat mosses can trap heavy metals in the root zone, making them more toxic due to the acid conditions; they can create anaerobic conditions in the rooting zone; and their chelation of cations can accelerate iron hardpan formation.

Despite our many studies on nutrients in peatlands, Bedford and coworkers, in a 1999 publication, state that the high variances in plant and soil N:P ratios of wetlands suggest it may be necessary to understand nutrient limitations at both the species and the community level before we can predict the effects of nutrient enrichment. If this need still exists for wetlands, it exists a hundred-fold for non-wetland bryophyte systems.

Bogs and fens are rapidly diminishing on our planet as development fills them in and at best puts a water hole somewhere else for wetland replacement. It is unlikely that any new wetland will become a bog or ***Sphagnum*** fen, and even if it does, it will be decades to centuries before there is even any evidence it will ever happen. Yet we continue to create conditions unfavorable for these diminishing habitats. Bergamini and Pauli (2001) have shown that fertilization of any sort is likely to destroy these fragile

systems that are not adapted for high nutrient input. In their study, after only 1.5 years, fertilized peatland plots contained 39% less bryophyte biomass on the N-fertilized plots and 53% less on the NPK-fertilized plots than the unfertilized controls. Likewise, bryophyte species diversity diminished. Competition for light by tracheophytes accounted for only part of the decline. Yet, in this ecosystem bryophytes play a crucial role in nutrient cycling and availability, both directly (Rieley *et al.* 1979) and indirectly, through their water-holding capacity (Mägdefrau & Wurtz 1951) and their ability to control water content of the uppermost soil layers (van Tooren *et al.* 1985).

Scheffer *et al*. (2001) compared decomposition rates in a ***Sphagnum***-dominated (Figure 62) and a non-***Sphagnum*** (Figure 63) fen. In both habitats, the sedge (*Carex*) litter had the highest decomposition rate compared to that of ***Sphagnum papillosum*** (Figure 64) and ***S. squarrosum*** (Figure 65-Figure 66). But in the ***Sphagnum*** site, all litter types exhibited net mineralization, whereas in the sedge-dominated site, there was net immobilization. The researchers postulated that nutrient availability and adaptation of the microbial communities might account for the decompositional differences in the two sites.

Figure 62. Boreal forest fen with ***Sphagnum fuscum***. Photo by Richard Caners, with permission.

Figure 63. Intermediate non-***Sphagnum*** fen. Photo by Janice Glime.

Figure 64. ***Sphagnum papillosum***, a species with a much lower decomposition rate than that of sedges (***Carex***). Photo by Janice Glime.

Figure 65. ***Sphagnum squarrosum*** habitat. Photo by Janice Glime.

Figure 66. ***Sphagnum squarrosum***, a species with a much lower decomposition rate than that of sedges (***Carex***) in a fen. Photo by Janice Glime.

Turetsky *et al*. (2008) found that moss species were more important than micro-environmental conditions in determining the early stages of decomposition in four peatland types in boreal Alberta, Canada. ***Sphagnum*** (Figure 64-Figure 66) species partitioned resources into metabolic and structural carbohydrates. Hummock species decomposed slowly, but the hummock microhabitat itself corresponded to a rapid decomposition rate. This is at least

partly due to the pore structure created by the mosses. The mosses form tissues that resist decomposition, suggesting that they may stabilize losses of carbon from peatlands as the climate warms.

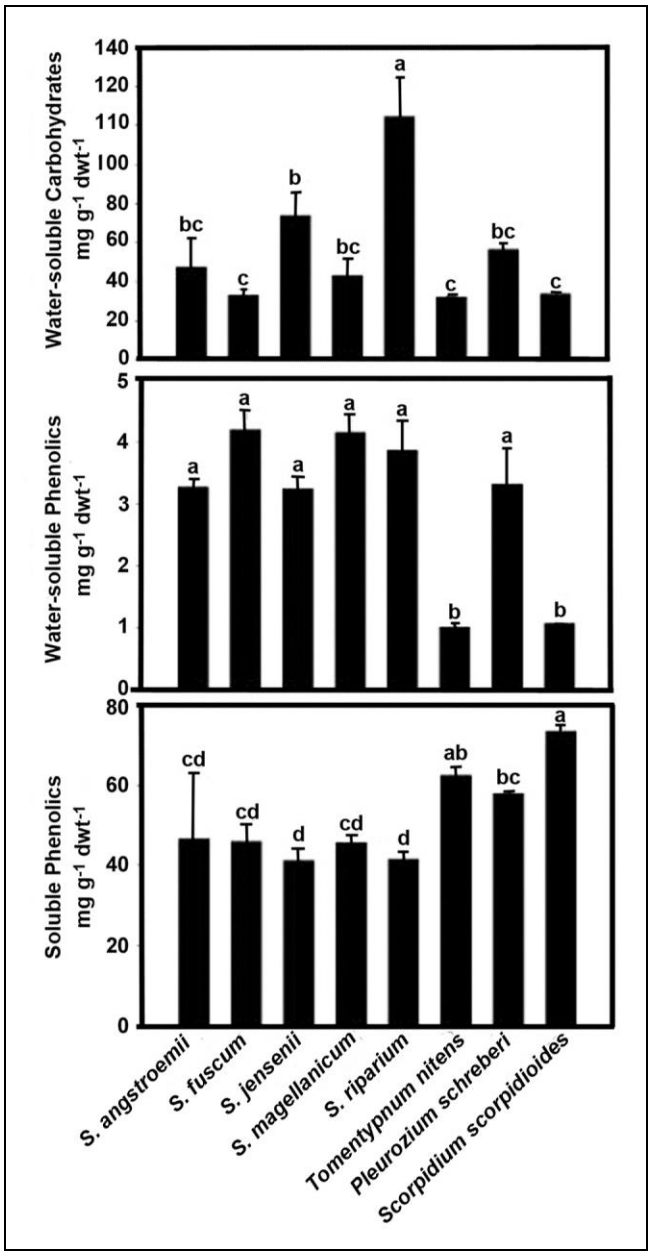

Figure 67. Concentrations of soluble components of moss litter (5 ***Sphagnum*** and 3 non-***Sphagnum***) collected from Canadian peatlands, including hot water-soluble carbohydrates, hot water-soluble phenolics, and soluble nonpolars (lipids). Data are means ± one standard error. Same letter superscripts denote non-significant comparison of means (one-way ANOVA; species $p < 0.05$). Redrawn from Turetsky 2003.

*p*H Effects

Nutrient availability is limited by the ability of that nutrient to dissolve in water, reach the plant, then enter the plant. Most nutrients become more soluble at low *p*H and may be totally unavailable at higher *p*H levels. At the same time, toxic metals such as Al become more soluble at low *p*H and can harm the plants.

Riccia discolor has better growth in the range of *p*H 3-5 than at any other *p*H (Patidar & Kaul 1984). The restriction of various taxa of ***Sphagnum*** (Figure 64-Figure 66) to specific somewhat narrow *p*H ranges accounts in part for the successional pattern of bogs and fens. ***Sphagnum*** taxa that require lower *p*H ranges tend to occur higher on the hummock where the water level is unable to dilute the effects of cation exchange and its release of H^+ ions.

The species that always surprises me is ***Calliergonella cuspidata*** (Figure 6**).** This species grows in the contrasting-moisture habitats of **chalk grasslands and fens**. There it grows best at a *p*H of 7.5 and 5 ppm Ca^{++}, whereas at *p*H of 6.0 growth stops even with 5 ppm or more of Ca^{++} (Streeter 1970). These *p*H differences most likely reflect the differences in uptake ability of Ca^{++} and other nutrients.

In **rivers**, taxa seem likewise to be limited by *p*H. The availability of free CO_2 only at lower *p*H (Figure 68) levels severely limits productivity for mosses, whereas many, perhaps all, aquatic tracheophytes can utilize bicarbonates. Several attempts to demonstrate use of bicarbonates by aquatic bryophytes have failed, presenting a clear picture of CO_2 limitation (Bain & Proctor 1980, Allen & Spence 1981). Field studies in streams have revealed that the leafy liverworts ***Scapania undulata*** (Figure 69) and ***Nardia compressa*** (Figure 70) occur mostly in the *p*H range of 5.2-5.8, whereas the moss ***Fontinalis squamosa*** (Figure 71) occurs mostly at 5.6-6.2 (Ormerod *et al*. 1987), suggesting that these bryophytes have somewhat different abilities to acquire CO_2. ***Jungermannia vulcanicola*** (Figure 72-Figure 73) survives the low *p*H of acid streams (1.9-4.7) in Japan (Satake & Miyasaka 1984; Yokouchi *et al*. 1984; Satake *et al*. 1990). ***Leptodictyum*** (Figure 74) can grow at a *p*H of 3.4 in organic lakes of Japan (Satake 1980). ***Warnstorfia fluitans*** (Figure 75) can live in acidic lakes with the low *p*H range of 3.4-3.8 (Satake 2000). In aquatic habitats, these *p*H differences affect the uptake of N forms and the ability to obtain CO_2 for photosynthesis, as well as affecting toxicity of pollutants.

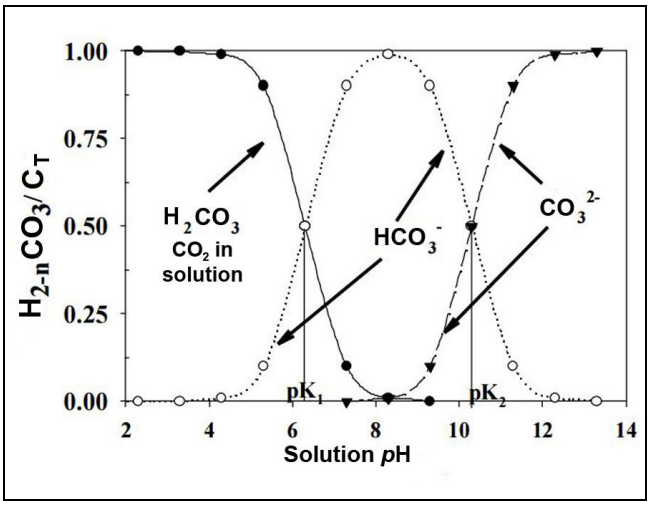

Figure 68. Distribution of carbonate species as a fraction of total dissolved carbonate in relation to solution *p*H. Note that H_2CO_3 represents CO_2 dissolved in water; HCO_3^- is bicarbonate, and CO_3^{2-} is carbonate. Modified from Soil Chemistry 5-1 < http://lawr.ucdavis.edu/classes/ssc102/Section5.pdf >.

Figure 69. ***Scapania undulata***, a species with a preferred *p*H range of 5.2-5.8. Photo by Michael Lüth, with permission.

Figure 70. ***Nardia compressa***, a species with a preferred *p*H range of 5.2-5.8. Photo byMichael Lüth, with permission.

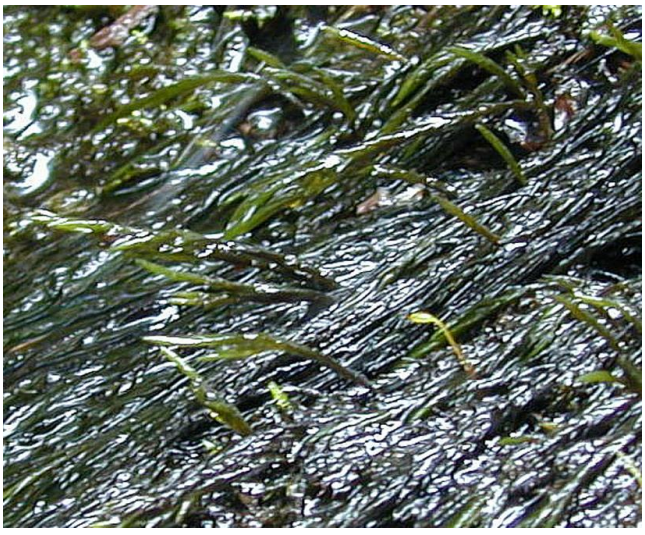

Figure 71. ***Fontinalis squamosa***, a species with a preferred *p*H range of 5.6-6.2. Photo by Michael Lüth, with permission.

Figure 72. ***Jungermannia vulcanicola*** acid stream habitat. Photo courtesy of Angela Ares.

Figure 73. ***Jungermannia vulcanicola***, an acidophile that prefers a *p*H range of 1.9-4.7. Photo courtesy of Angela Ares.

Figure 74. ***Leptodictyum riparium***, a species that can grow at a *p*H of 3.4 in organic lakes. Photo by Michael Lüth, with permission.

Figure 75. ***Warnstorfia fluitans***, a species of acidic lakes with the low *p*H range of 3.4-3.8. Photo by Michael Lüth, with permission.

In an 18-year study of a **pine forest** stand in central Sweden, van Dobben and coworkers (1992) found that ***Pohlia nutans*** (Figure 76) experienced a 10-fold increase when acidified, whereas ***Pleurozium schreberi*** (Figure 38) almost disappeared.

Figure 76. ***Pohlia nutans***. Photo by Michael Lüth, with permission.

In **geothermal** areas, as we will discuss later, distribution by *p*H is pronounced, whether by competition leading to more narrow realized niches, or by real limitations imposed by the acidity, and perhaps the accompanying sulfur. The low *p*H, and in some cases high *p*H, can affect nutrient solubility and may make certain ions toxic or, in high *p*H, make them unavailable.

Although many mosses seem to survive at low *p*H levels, competition from tracheophytes and limited nutrients can severely limit their abundance. In a **grassland** experiment, Virtanen *et al*. (2000) found that virtually no mosses were present on plots with a soil *p*H of 3.3-4.5. Rather, bryophyte biomass and diversity increased with soil *p*H.

Indicator Species

Despite the limited ability of bryophytes to use soil nutrients, soil characters can still limit their distribution, making some of them suitable indicators. Some of this may be that they have greater ability to take up soil nutrients than we have imagined, perhaps through mycorrhizae, and some may result from airborne dust derived from the soil. For example, ***Ceratodon purpureus*** (Figure 77) is able to tolerate high N content (Dierssen 1973), although this widespread moss seems to be able to tolerate roadside gravel and rock ledges where one would expect N content to be low. On the other hand, ***Aulacomnium palustre*** (Figure 78), ***Pleurozium schreberi*** (Figure 38), ***Pogonatum urnigerum*** (Figure 79), and ***Polytrichastrum alpinum*** (Figure 80) indicate low N. Such mosses as ***Funaria hygrometrica*** (Figure 81), ***Pohlia cruda*** (Figure 82), and ***Leptobryum pyriforme*** (Figure 83) indicate good base saturation, whereas poor base saturation is indicated by good growths of ***Psilopilum laevigatum*** (Figure 84).

Figure 77. ***Ceratodon purpureus*** with capsules, a species with wide habitat tolerance that can tolerate high N levels. Photo by J. C. Schou, with permission.

Figure 78. ***Aulacomnium palustre*** with gemmae, a species that indicates low N. Photo by Janice Glime.

Figure 79. ***Pogonatum urnigerum***, a species that indicates low N levels. Photo by Janice Glime.

Figure 80. ***Polytrichastrum alpinum***, a species that indicates low N levels. Photo by Michael Lüth, with permission.

Figure 81. ***Funaria hygrometrica***, a species that indicates good base saturation. Photo by Michael Lüth, with permission.

Figure 82. ***Pohlia cruda*** with capsules, a species that indicates good base saturation. Photo by Michael Lüth, with permission.

Figure 83. ***Leptobryum pyriforme*** with capsules, a species that indicates good base saturation. Photo by Michael Lüth, with permission.

Figure 84. ***Psilopilum laevigatum*** with capsules, an indicator of poor base saturation. Photo by Michael Lüth, with permission.

Use of mosses for prospecting was popular for a time during mining exploration, but their short penetration into the soil made them of limited value. Copper mosses – ***Mielichhoferia*** (Figure 85-Figure 86), ***Dryptodon*** (see Figure 87), ***Scopelophila*** (Figure 88-Figure 89) to be discussed in the Habitats volume – seem to be reliable indicators of the presence of copper (Persson 1948; Shacklette 1967), although it may actually be the sulfur

associated with the copper that encourages their growth (Hartman 1969). They are unknown in the copper-rich area of the Keweenaw Peninsula of Michigan, where the copper occurs as pure copper with no associated sulfur (pers. obs.). Nevertheless, their tolerance for the ore is higher than that of other mosses.

Figure 85. Habitat of ***Mielichhoferia mielichhoferiana***, a copper moss. Photo by Michael Lüth, with permission.

Figure 86. ***Mielichhoferia mielichhoferi***, a copper moss with calcium deposits on it. Photo by Michael Lüth, with permission.

Figure 87. ***Dryptodon patens***; ***Dryptodon atrata*** is a copper moss. Photo by Michael Lüth, with permission.

Figure 88. ***Scopelophila ligulata***, a copper moss in its habitat. Photo by Michael Lüth, with permission.

Figure 89. ***Scopelophila ligulata***, a copper moss. Photo by Michael Lüth, with permission.

Needed Research

In 1992, Bates summarized our needs for understanding the physiology of nutrient uptake, translocation, and loss in bryophytes. We have made considerable progress since that time, but we still are unable to make sweeping generalizations. To understand clearly the ecosystems in which bryophytes form a significant ground cover or a significant epiphytic element, we must understand the role of the bryophytes in nutrient uptake and sequestering. We still have little understanding of what makes the various species differ in their ability to subsist on low nutrients. We likewise lack understanding of the effects nutrient deficiencies or excess may have on the morphology of the species. And we are only beginning to understand how long nutrients might remain within the bryophyte before being returned to the ecosystem. We have learned that, contrary to the perception of tracheophyte ecologists, the bryophytes move essential nutrients from older tissues to younger ones, often being recalcitrant toward returning anything to the soil unless the whole plant dies. But we don't know how widespread this phenomenon is in the many ecosystems where bryophytes form a significant ecosystem component. We have barely realized that bryophytes obtain their nutrients from the soil as well as the rain, but we can add little to the hypothesis

put forth by Bates (1992) that rapidly growing species may depend on the substrate and slower growing species mostly on precipitation. The nutrient role of bryophytes in ecosystems has come of age – we know that it is significant, and now it demands our attention.

Summary

Bryophytes can play a significant role in nutrient cycling in many kinds of ecosystems. Their ability to bind nutrients on their cell walls permits them to take these in when they become hydrated. They intercept atmospheric input and often hold it, preventing it from reaching the forest floor. In some locations, under conditions of wetting and drying, they can release nutrients during the first few minutes of rehydration when adhering inorganic and organic molecules dissolve in the throughfall. However, once their membranes are repaired, they tend to hold the nutrients on their surface exchange sites or within cells, or even between cells.

Nutrient concentration studies must be interpreted with caution due to the ability of bryophytes to hold dust readily on their surfaces. But even so, this is a role in the ecosystem that prevents this dust from reaching other plants or that releases it at some later point in time.

Mosses may have a limited capacity to retain **luxury nutrients** such as K, Ca, and P, but most of the essential macronutrients seem to be regulated to a relatively constant level. Heavy metals, on the other hand, tend to accumulate to high levels.

In boreal forests, feather mosses retain nutrients and move the soluble ones to young, growing tissues. Hence, nutrients may be bound within the mosses for decades. Nevertheless, spruce roots seem to flourish under the mosses, suggesting that mosses may accumulate nutrients that become available to the roots. ***Polytrichum*** seems to compete with the fine roots and therefore has a low absorption rate for P. For some reason, perhaps because the N is moved to underground portions, N is able to accumulate under ***Polytrichum***.

In chalk grasslands, bryophytes trap and retain leachates from the autumn leaves, then release them in the summer when demand is highest for tracheophytes. Other nutrients, such as N, are retained in bryophytes as organic compounds that are bound in cell walls or retained in proteins. And the level of NH_4^+-N and of NO_2^--N in soil under mosses increases from xerophytic to mesophytic species, but we don't know why.

At least some epiphytic mosses even seem to obtain nutrients from the vascular tissue of tree trunks. Epiphytic mosses in the tropics can provide a suitable habitat for legume nodule formation, for example ***Bradyrhizobium*** in the *Acacia koa* tree in Hawaii, providing a significant contribution to the overall N budget.

Seasonal behavior can, as in the case of ***Sphagnum russowii***, release nutrients such as K^+ in the autumn when the trees need it in preparation for winter. But some bryophytes hold to their nutrients tenaciously at exchange sites, again depriving the soil. ***Sphagnum*** in bogs and fens can be destroyed by nutrient enrichment, but even dead plants can retain the nutrients already stored. These mosses can also trap heavy metals and retain them in the soils, making the root zone toxic for trees. Because of their movement of nutrients to young tissues and incorporation into incalcitrant compounds, bryophytes can serve as nutrient **sinks**.

Low *p*H makes nutrients more soluble, but some bryophytes cannot survive, in some cases due to competition from tracheophytes, but in others most likely because the *p*H change disrupts the normal balance of nutrient uptake. High *p*H levels, especially accompanied by high concentrations of Ca^{++}, can result in competition for exchange sites that are needed for nutrient uptake. In aquatic systems, high *p*H reduces the available CO_2, thus limiting photosynthesis. Some bryophytes serve as indicator species because of their ability to tolerate or not tolerate such conditions as high Ca^{++} or low *p*H.

Having learned how mosses gain, use, and lose nutrients, we must ask ourselves how these plants are able to subsist on such low concentrations of nutrients. In addition to their efficient absorption of nutrients in low concentrations, they benefit from their generally slow growth habit, thus greatly reducing their requirements per units of time and space.

Their ability to move nutrients from old to young tissues and to store them both externally and internally raises serious questions about their role in the nutrient cycling in the habitats where they are abundant.

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CHAPTER 9-1

LIGHT: THE SHADE PLANTS

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CHAPTER 9-1
LIGHT: THE SHADE PLANTS

Figure 1. Bryophytes growing in deep shade, with ***Frullania tamarisci*** hanging in the foreground. Photo by Michael Lüth, with permission.

Bryophytes Are Shade Plants

As in tracheophytes, bryophytes become light limited at low light intensities (Tixier 1979). For example, epiphyllous bryophyte cover increased fourfold in a clearing in Costa Rica compared to that in the dark understory (Monge-Nájera 1989). Nevertheless, bryophytes exist in places with very low light intensities (Figure 1). The atmosphere, canopy, and surrounding ground cover all contribute to diminishing the light reaching the moss surface (Figure 2), and latitude reduces the radiation reaching bryophytes near the poles.

It is their ability to make a net gain from photosynthesis at very low light intensities that permits bryophytes to live in places inhospitable to other plants. For example, herbaceous plants of a rich forest floor can retain 43-72% of the light that manages to penetrate the canopy, thus making the potential bryophyte substrate below very low in light indeed (Bodziarczyk 1992). Such total coverage becomes a competitive inhibitor for young seedlings, and even few bryophytes can tolerate such low light. But forests create an even greater toll on the light available to the soil substrate. They drop leaf litter that totally obscures the soil, making it uninhabitable for any bryophyte, and, most bryophytes seem unable to occupy the surface of this constantly changing leaf substrate. Thus, they are excluded from most of the deciduous forest floor by this inevitable litter-caused light limitation.

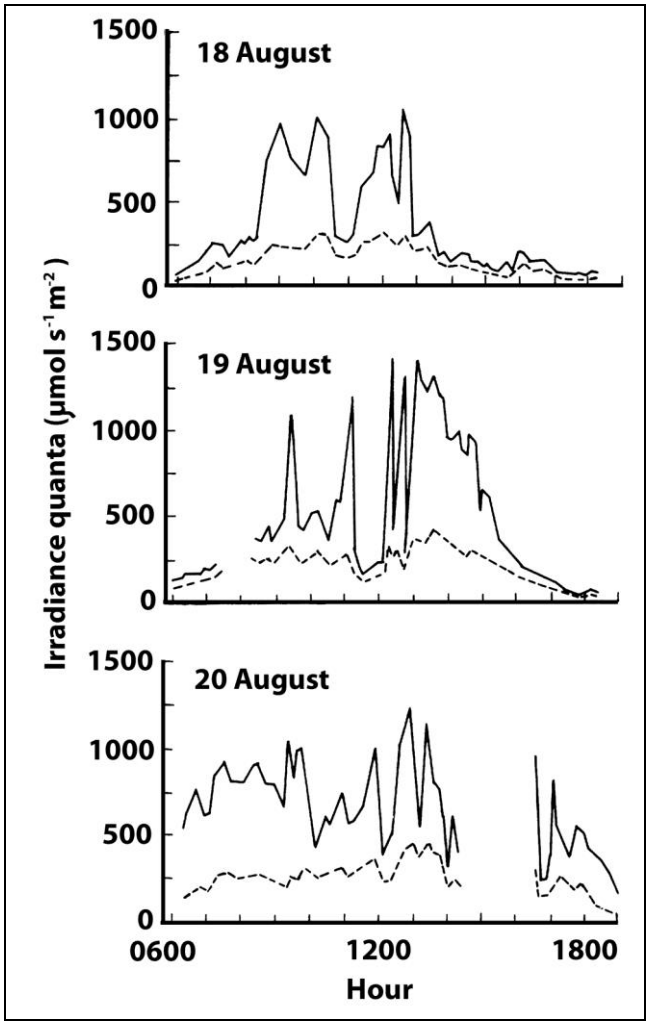

Figure 2. Irradiance at the moss surface - - - and total solar irradiance —— in PAR units for three consecutive days in central Alaska in a black spruce forest. Figure redrawn from Skré *et al*. 1983.

Compensation Point

Net photosynthetic gain is that net carbon which is stored; it reflects net loss of carbon as CO_2 in respiration and photorespiration. Think of it like your paycheck. Your gross income is much greater than that on your paycheck because you have taxes subtracted from it. Think of respiration as the tax and the paycheck as net photosynthesis. The level of light at which CO_2 gain by photosynthesis just equals that lost by respiration is referred to as the **light compensation point**, *i.e.*, the light level at which net photosynthesis is zero. The mean annual light input must be above that level for the plant to maintain positive carbon gain. The highest intensity at which net photosynthesis increases is referred to as the **light saturation point**. And some bryophytes, especially some aquatic taxa, have very low light compensation and light saturation points.

In the bamboo forests (2200-3200 m asl) of Central Africa the bryophytes dry out in the daytime and regain moisture from the vapor-saturated atmosphere at night (Lösch *et al*. 1994). The mountain sites (2200-3200 m asl) had six times higher daily sums of PAR, temperatures 10-25°C, and relative humidities 60-100 %. Nevertheless, photosynthetic optima of lowland (rainforest) species were somewhat higher than that found for bryophytes at the mountain sites. The light compensation points were smaller (3-12 µmol photons m^{-2} s^{-1}) in the lowland than in the highland species (8-20 µmol photons m^{-2} s^{-1}). On the other hand, the slopes of the curves in the low light range of the lowland species were distinctly steeper than in the high light range. Bryophytes in the rainforest (800 m asl) receive extremely high ambient CO_2 due high decomposition. This CO_2 advantage, coupled with their low light requirements and optimal temperature and humidity conditions provide sufficient photosynthetic conditions for them in this dark environment. Those from the higher elevation bamboo forests and tree-heath environments can take advantage of the higher light conditions despite variable temperatures and humidities.

Light Quality

Light quality differs among habitats. In the open, plants experience the full spectrum of sunlight in what we call white light. However, in the forest, the green canopy absorbs much of the red light, reflecting and transmitting green light. These differences in wave lengths and their respective differences in energy are important in a number of plant functions, with photosynthesis being among those affected.

Federer and Tanner (1966) demonstrated these differences in various habitats. The light quality differs even between hardwoods (most deciduous trees) and softwoods (conifers). Furthermore, light quality differs between clear and cloudy days. Light among all species groups tested had an energy maximum at 550 nm, a minimum at 670-680 nm, and a very high maximum in the near infrared. The light within the canopy is both beam solar radiation and diffuse sky radiation and these are both reflected and scattered.

But how do these differences in light quality affect the bryophytes? In ***Physcomitrella patens*** (Figure 3), no inhibition was present under high light illumination (Cerff & Posten 2012). These researchers found that a combination of red and blue light is most effective in reaching high growth rates and chlorophyll formation rates.

Figure 3. ***Physcomitrella patens***, a species that has good photosynthetic output in a combination of red and blue light. Photo by Janice Glime.

Light Measurement

Light has been measured in a variety of units, and unfortunately, most of them are not directly interconvertible because they measure different things. These different aspects of light also play different roles in physiology of bryophytes. Light wavelengths that stimulate photosynthesis are restricted to those that activate chlorophyll, whereas short wavelengths of ultraviolet light can bleach and damage chlorophyll. Other wavelengths stimulate red and yellow accessory pigments. Yellow pigments (**cryptochromes)** help plants measure the duration of light and respond to different wavelengths.

Traditionally, light was measured in **foot candles** – the intensity of light from one candle on a square foot of surface one foot from the candle. This English unit is, fortunately, easily convertible to metric units of **lux** (**lumens per sq meter**) **–** the intensity of light from one candle on one square meter of surface that is one meter from the candle. Thus, one lux is less bright than one foot candle, and to convert from foot candles to lux, one must multiply by 10.764.

PAR (= PhAR) units measure only **photosynthetically active radiation** and are based on measurements in sunlight. In general, about 45% of incoming sunlight lies within the spectral range of 380-710 nm (Larcher 1995), the range used by photosynthesis, thus the range of PAR. Ultraviolet light waves are shorter (UV-A at 315-380 nm; UV-B at 280-315 nm) and have no role in photosynthesis; they do, however, cause chlorophyll and DNA damage. Light available for photosynthesis (PAR) has been reported as photosynthetic photon flux density (**PPFD**), expressed as µmol m^{-2} s^{-1}, or as **watts** per meter square (W m^{-2}). The light reaching the Earth's outer atmospheric limits is 1360 W m^{-2} (the solar constant). By the time it reaches Earth's surface, only 47% remains, thus making full sunlight ~640 W m^{-2}. This varies considerably across the face of the Earth due to reflectance, scattering, cloud cover, and global position.

At sea level, maximum intensity can reach ~1 kW m^{-2}, with PAR intensities of ~400 W m^{-2}. Full sunlight ranges ~70,000-100,000 lux (or 7,000-10,000 foot candles), with the higher number when there is a highly reflective white sand near the equator at midday or a complete snow cover on a sunny day. The generally-accepted value of maximum light is 680 lumens per watt of radiant power (Commission Internationale de l'Eclairage, Paris 1970). Fortunately, it is possible to provide a rough equivalent of PPFD at full sunlight of 1800 µmol photons m^{-2} s^{-1} because we know the spectral quality of sunlight. However, when light is measured in shade, where leaves filter out red light and transmit green, or under water, or other places where the full spectrum of sunlight is not represented in the same proportions, such a conversion is not directly possible.

Table 1 gives approximate conversions under several more predictable conditions.

Having said all this, we have only looked at one end of the spectral effect – the light source (McCree 1973). Once light strikes the leaf, it encounters not only chlorophyll pigments (actually two chlorophylls in the plant kingdom, *a* and *b*), but it also encounters accessory pigments of various mixes of yellow, orange, and red (Figure 4) occurring in cell walls, cytoplasm, and plastids. Furthermore, cell shape can bend and focus or scatter light, depending on cell wall structure.

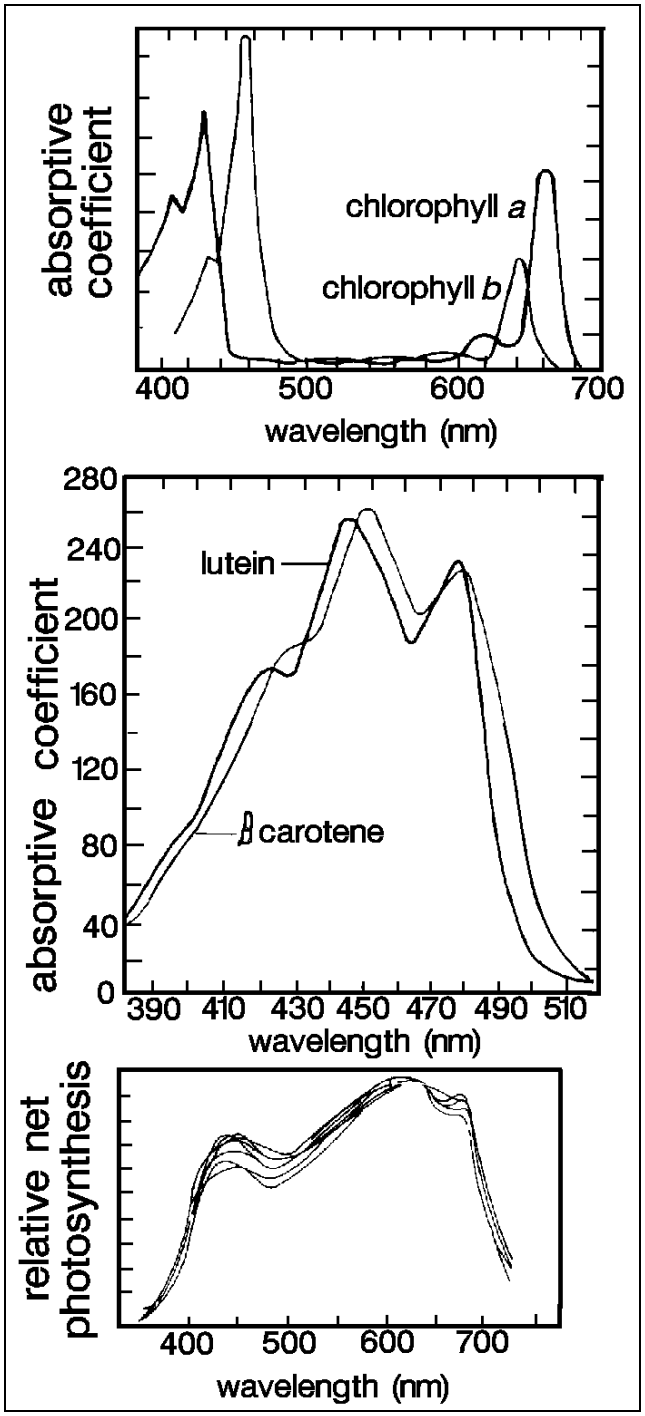

Figure 4. Top: Absorption spectra of chlorophylls *a* and *b*, dissolved in diethyl ether. Middle: Absorbance spectra of lutein and ß carotene in ethanol. Bottom: Action spectra of 22 species of crop plants. From Salisbury & Ross 1978.

Thus, our measurements of light are biased representations of light from the perspective of humans and not that of a plant leaf that must use that energy to activate the photosynthetic pathway. But, alas, it is the best we can do at present. This is not all bad, because the differences in response of various plants to the same measured light output give us indirect indications of differences in adaptations to light capture and cause us to probe further

for causes. Unfortunately, lumens and lux tell us even less because we have no measure of the wavelengths being received by the plant and thus know less about what sorts of adaptations to examine. It is like a human looking at a flower that reflects UV. We don't see what the bee sees.

Table 1. Conversions between PAR (PhAR) units or Klux (400-700 nm) units to µM photons m^{-2} s^{-1} for light under ~predictable spectral conditions. (From McCree 1981; Larcher 1995).

To convert from: Multiply by factor in column to obtain µM m^{-2} s^{-1}	W m^{-2} (PAR)	Klux
daylight (sunny)	4.6	18
daylight (diffuse)	4.2	19
metal halide lamp	4.6	14
fluorescent tube (white)	4.6	12
incandescent lamp	5.0	20

Adaptations to Shade

Just what is it that permits bryophytes to succeed where light levels are so low, particularly when compared to tracheophytes? Certainly simple structure is one factor. Tracheophytes are actually adapted to protect themselves from high light intensity by having a thick, waxy cuticle and an epidermis. And the palisade layer in many taxa protects spongy mesophyll from light by using chlorophyll and other pigments to absorb much of it before it reaches the photosynthetically adapted spongy tissue. Bryophytes, on the other hand, have none of these adaptations and expose their photosynthetic cells directly to the light by having only one leaf cell layer in most cases (Figure 5. Only thallose liverworts like ***Marchantia*** (Figure 6) have an arrangement somewhat similar to spongy mesophyll (Figure 7), and a few mosses like the **Polytrichaceae** have a folded-over leaf margin surrounding leaf lamellae (Figure 8, lower), somewhat resembling palisade tissue of a tracheophyte. In fact, knowing the structure of a bryophyte, we must ask ourselves instead how they survive in the sun.

Figure 5. **Upper:** Leaves of ***Mylia anomala***. **Lower:** Cells showing chloroplasts in one-cell-thick leaf of the leafy liverwort ***Mylia anomala***. Photos by Michael Lüth, with permission.

Figure 6. ***Marchantia polymorpha ruderalis*** showing pores on surface. Photo by David Holyoak, with permission.

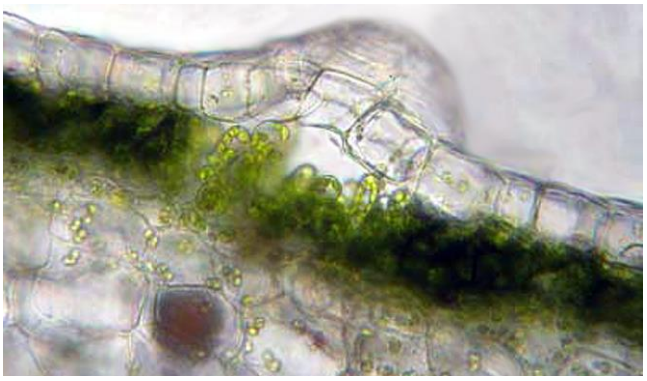

Figure 7. Cross section of thallus, through pore, of ***Marchantia polymorpha***. Note the spongy nature of the photosynthetic layer where it is visible below the pore. Photo by Jennifer Steele, Botany Website, UBC, with permission.

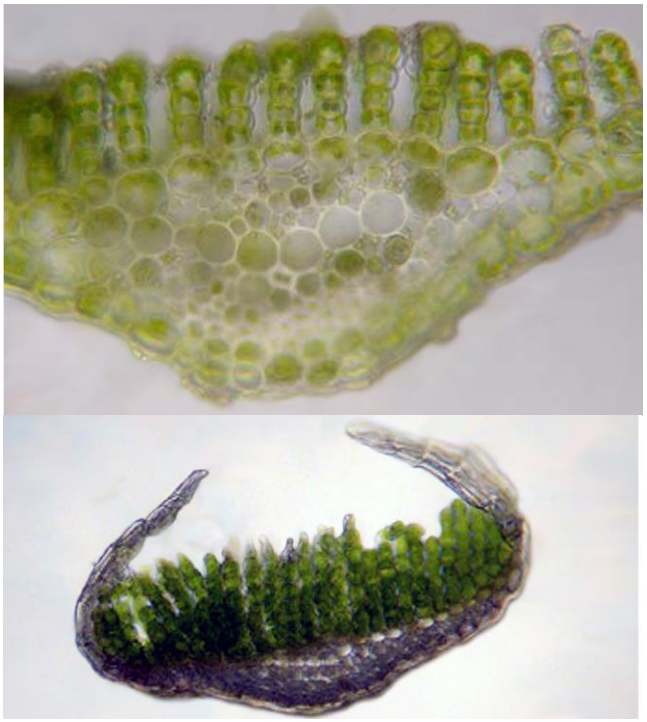

Figure 8. **Upper:** Leaf lamellae of ***Pogonatum contortum***, typical of those found in all members of the Polytrichaceae. **Lower:** Leaf lamellae with leaf lamina rolled over them in ***Polytrichum piliferum***. Photos with permission from Botany Website, UBC, with permission.

Most bryophytes are physiologically adapted to low light intensities and therefore have low chlorophyll *a*:*b* ratios (1.0-2.5:1, Mishler & Oliver 1991) compared to tracheophyte sun plants (C_3 = 3:1, C_4 = 4:1, Larcher 1983). Marschall and Proctor (2004) examined 39 moss and 16 liverwort species and determined that despite considerable variability, chlorophyll values were typical of shade plants. Median values of total chlorophyll were 1.64 mg g^{-1} for mosses and 3.76 mg g^{-1} for liverworts. Mosses had a chlorophyll *a*:*b* ratio of 2.29 and liverworts of 1.99, suggesting that liverworts are more shade-adapted than mosses. The reduced chlorophyll *a*:*b* ratio is due to increased levels of chlorophyll *b*, a typical shade adaptation that permits more trapping of photons that are then transferred to chlorophyll *a*. Even in those bryophytes that are sun species, the ratio tends to be low and the optimum light level likewise low. For example, ***Plagiochasma intermedium*** (Figure 9) has its optimum light intensity at 3500 lux with a day length of 10 hours (Patidar & Jain 1988); ***Riccia discolor*** has the same intensity optimum (Gupta *et al*. 1991). But full sunlight can be 70,000-100,000 lux.

Figure 9. ***Plagiochasma intermedium***, a species with an optimum light intensity of only 3500 lux and 20-hour days. Jan-Peter Frahm, with permission.

Marschall and Proctor (2004) found that the **PPFD** (photosynthetic photon flux density) at 95% saturation had a median of 583 µmol m^{-2} s^{-1} for mosses and 214 µmol m^{-2} s^{-1} for liverworts, again suggesting that liverworts are adapted to a lower light regime. Not surprisingly, two ***Polytrichum*** (Figure 10) species had the highest values. Their system of lamellae (Figure 8) provides them with considerable surface area to exchange gas and enhance their photosynthetic capability. Other bryophytes appear to be limited by their lack of sufficient surface area for CO_2 uptake. Green and Snelgar (1982) report that in the thallose liverwort ***Marchantia foliacea*** (Figure 11) the internal air chambers do little to facilitate photosynthesis compared to ***Monoclea forsteri*** (Figure 12) which has a solid thallus. Rather, the spaces facilitate water retention and the authors suggest that ***Marchantia foliacea*** would fare better photosynthetically if it had a solid thallus in very moist environments. Presumably this would afford it more photosynthetic tissue for light capture.

Figure 10. ***Polytrichum commune***. Two ***Polytrichum*** species have the highest photosynthetic values. Photo by A. J. Silverside, with permission.

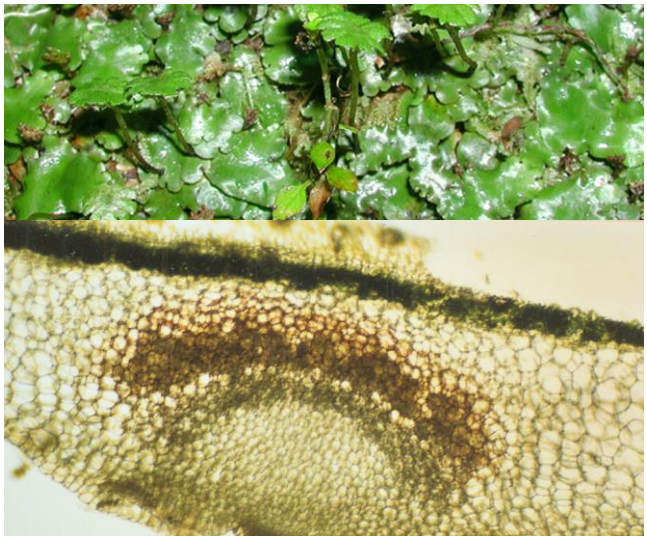

Figure 11. **Upper:** ***Marchantia foliacea*** thallus. **Lower:** Cross section of thallus of ***Marchantia foliacea*** showing the nearly solid nature of the thallus. Air chambers occur within the green layer near the upper surface. The brown layer is a layer of arbuscular mycorrhizal fungi. Photos by Julia Russell, with permission.

Figure 12. Thallus of ***Monoclea forsteri***. Photo by Jan-Peter Frahm, with permission.

Tuba (1987) explains that because poikilohydric plants must depend on atmospheric moisture to regulate their internal water content, they are most likely to photosynthesize during early morning hours when there is dew, and during rainstorms, since those are the only times

their cells are hydrated sufficiently. These plants are most likely to be desiccated during periods of high light levels. Thus, it is logical that their chlorophyll is adjusted to low light levels and that their light compensation (Table 4) and light saturation points are low when compared to those of most flowering plants (Table 2). Nevertheless, the light compensation points seem to be slightly higher than those of shade-adapted flowering plants (Table 2), suggesting that bryophytes may benefit from occasional **sunflecks** (patches of light due to movement or gaps among the canopy leaves), or that we have insufficient data thus far to be making these generalities!

Table 2. Comparison of light compensation and saturation points for photosynthetic organisms from various habitats. From Larcher 1983, compiled from various authors.

Plant group	Compensation light intensity I_k in Klux	Light saturation I_S in Klux
Land plants		
Herbaceous plants		
C_4 plants	1-3	>80
Agricultural C_3 plants	1-2	30-80
Herbaceous sun plants	1-2	50-80
Herbaceous shade plants	0.2-0.5	5-10
Woody plants		
Winter-deciduous foliage trees and shrubs		
Sun leaves	1-1.5	25-50
Shade leaves	0.3-0.6	10-15
Evergreen foliage trees and conifers		
Sun leaves	0.5-1.5	20-50
Shade leaves	0.1-0.3	5-10
Understory ferns	0.1-0.5	2-10
Mosses and lichens	**0.4-2**	**10-20**
Water plants		
Planktonic algae		(7) 15-20
Tidal-zone seaweeds	1-2	10-20
Deep-water algae		1-2
Seed plants	<1-2	(5) 10-30

We do know that bryophytes are able to adjust to low light levels by increasing their number of chloroplasts, as demonstrated for ***Funaria hygrometrica*** in Figure 13.

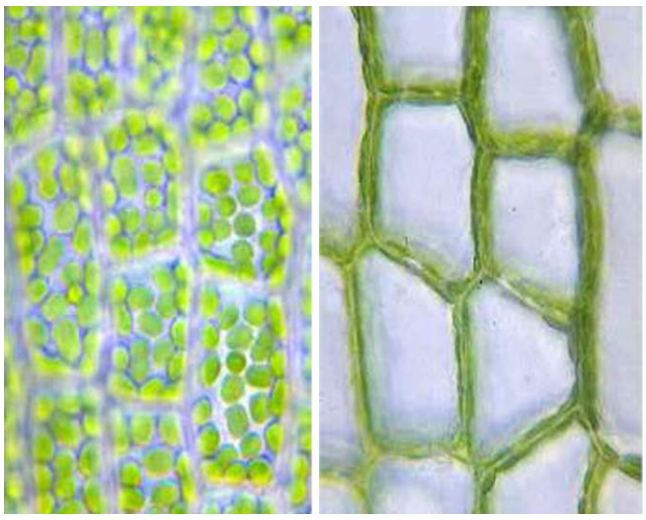

Figure 13. ***Funaria hygrometrica*** cells from dim light (**left**) and strong light (**right**). Photos by Winfried Kasprik.

Compensation Points

Certainly some bryophytes are able to grow over a relatively wide range of light intensities, increasing their growth rate as the intensity increases. For example, in ***Marchantia palacea*** var. ***diptera*** (Figure 9), this growth increase occurs from 5.4 to 60 W m^{-2} (Taya *et al*. 1995). However, above that level, there is a significant and rapid decrease in growth.

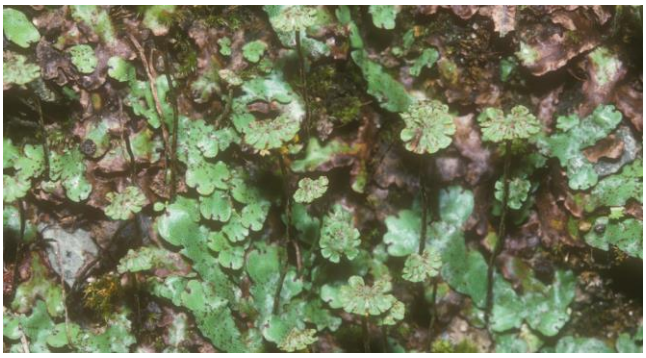

Figure 14. Thalli and archegoniophores of ***Marchantia palacea*** var. ***diptera*** from Japan. Photo by Janice Glime.

Compensation points suggest that there is indeed adaptation within the bryophytes to both low and high light levels (Table 3-Table 4). For example, in Antarctic lakes, ***Drepanocladus*** (*sensu lato*) (Figure 15) has a light compensation point similar to that of algal communities (0.11 W m^{-2}, ~ 0.5 µM m^{-2} s^{-1}), whereas ***Calliergon*** (Figure 16), which occurs in shallower water, has a compensation point of 0.64 W m^{-2}, ~ 2.9 µM m^{-2} s^{-1} (Priddle 1980). ***Fissidens serrulatus*** (Figure 17) could maintain a positive net photosynthesis down to 7 µmol m^{-2} s^{-1} (Gabriel & Bates 2003). This is not surprising for a species that occupies caves and the deep shade of forest ravines. ***Hylocomium splendens*** (Figure 18), typical of conifer forests, required 30 µM m^{-2} s^{-1} to reach its compensation point at natural concentrations of CO_2 of 400-450 ppm (ppm = mg L^{-1}) (Sonesson *et al*. 1992).

Table 3. Published light compensation and saturation points for bryophytes.

	Condition	Comp lux	Sat lux	Reference
Fontinalis	5ºC	15		Burr 1941
	20ºC	40		
Atrichum undulatum	spring	3000	5000	Baló 1987
	summer	1000	10,000	
Polytrichum formosum	spring	4000	10,000	Baló 1987
	summer	1000	25,000	
Plagiomnium affine	spring	4000	15,000	Baló 1987
	summer	1000	25,000	
Chiloscyphus rivularis		1750		Farmer *et al.* 1988

	Condition	Comp µM m^2 s^{-1}	Sat µM m^2 s^{-1}	Reference
Pellia borealis		4.6-	81	Szewczyk 1978
Fissidens serrulatus	21ºC	7	24	Gabriel & Bates 2003
Andoa berthelotiana	21ºC	8	20	Gabriel & Bates 2003
Echinodium prolixum	21ºC	9	27	Gabriel & Bates 2003
Bazzania azorica	21ºC	9	29	Gabriel & Bates 2003

Plagiomnium spp.	25ºC	10	400	Liu *et al*. 1999
Frullania tamarsci	21ºC	10	36	Gabriel & Bates 2003
Lepidozia cupressina	21ºC	12	30	Gabriel & Bates 2003
Myurium hochstetteri	21ºC	31	68	Gabriel & Bates 2003
Pilotrichella ampullacea	tropics		100	Proctor 2002
Floribundaria floribunda	tropics		100	Proctor 2002
Hylocomium splendens	summer	30	100	Sonesson *et al*. 1992
Brachythecium rutabulum	8 May 6 July	65 4	200 30	Kershaw & Webber 1986

Table 4. Published light compensation points, relative to natural (full sun) irradiance, for bryophytes.

Drepanocladus	0.03%		Priddle 1980
Calliergon	0.16%		Priddle 1980
Fissidens serrulatus	~0.4%		Gabriel & Bates 2003
Thuidium cymbifolium	0.57%[+]		Hosokawa & Odani 1957
Hylocomium cavifolium	0.57%[+]		Hosokawa & Odani 1957
Thamnium sandei	0.57%[+]		Hosokawa & Odani 1957
Homaliodendron scalpellifolium	0.57%[+]		Hosokawa & Odani 1957
Calliergonella cuspidata	1%		Kooijman unpubl
Hylocomium splendens	1.7%	summer	Sonesson *et al*. 1992
	~2%	Sept	Skré & Oechel 1981
Racomitrium lanuginosum	~2%	5ºC	Kallio & Heinonen 1975
Pleurozium schreberi	~2.5-5%	Sept	Skré & Oechel 1981
Racomitrium lanuginosum	~7.5%	15ºC	Kallio & Heinonen 1975
Sphagnum angustifolium	2.1%[*]	10ºC	Harley *et al*. 1989
Sphagnum angustifolium	7.1%[*]	20ºC	Harley *et al*. 1989

[*]Converted from μM m^{-2} s^{-1} assuming 1800 μM m^{-2} s^{-1} at full sunlight.
[+]Converted from lux, assuming full sun of 70,000 lux.

Figure 15. ***Drepanocladus aduncus***, a genus that in Antarctic lakes has a light compensation point similar to that of algae. Photo by Michael Lüth, with permission.

Figure 16. ***Calliergon richardsonii***, a genus of shallow water and with a much higher light compensation point than that of the submersed ***Drepanocladus***. Photo by Michael Lüth, with permission.

Figure 17. Gametophyte with sporophyte of ***Fissidens serrulatus***. Photo by Michael Lüth, with permission.

Figure 18. Side view of the feather moss ***Hylocomium splendens***. Photo from Botany Website, UBC, with permission.

A low compensation point and a low light saturation value are typical for C_3 plants, and thus for bryophytes (Table 2). The low light compensation point in tracheophytes is in part due to the ability of C_3 plants to open their stomata quickly to take advantage of CO_2 exchange whenever sufficient light is available. However, lacking stomata, bryophytes are not limited by stomatal opening speed, so response time to take in CO_2 should not impose the same kinds of limits it does in tracheophytes. On the other hand, higher levels of CO_2 permit photosynthetic gain at high light intensities by increasing

the light saturation point. For light energy to be used in photosynthesis, there must be sufficient CO_2 for the fixation of photosynthetic product. Otherwise, excess excitation energy can damage the photosynthetic apparatus. Therefore, we should expect to find a higher light saturation point when the CO_2 concentration is higher, as already seen for ***Hylocomium splendens*** (Figure 18) (100 µmol m^{-2} s^{-1} at a CO_2 concentration of 400-450 mg L^{-1}) (Sonesson *et al*. 1992). This is a relatively high level of CO_2 (but a reasonable level at the soil interface) and likewise a high level of light saturation. We will see shortly that such a high light saturation level in this CO_2-enriched environment will permit the plants to take advantage of bursts of light (**sunflecks**; Figure 19) reaching the forest floor. Again, it would appear that lacking stomata, bryophytes are positioned to be able to make immediate use of these short bursts and have the physiological apparatus to accommodate them.

Figure 20. ***Hypnum cupressiforme*** in an open habitat on rock. Photo by Michael Lüth, with permission.

Figure 19. ***Leucobryum glaucum*** with sunflecks. Photo by Janice Glime.

Figure 21. ***Hypnum cupressiforme*** in a shaded habitat on a lob. Photo by Michael Lüth, with permission.

Sunflecks

Importance of sunflecks (patches of bright light due to movement or gaps among the canopy leaves; Figure 19) for forest floor tracheophytes is well known. However, bryophyte usage of these bursts of light has been largely ignored (Kubásek *et al*. 2014). These researchers suggest that the anatomy of bryophyte gametophytes would allow a more rapid induction of photosynthesis due to the one-cell thickness, lack of stomata that must be opened, and only thin cuticle. They compared 10 moss species from sun and shade sites. By providing light after dark acclimation, they found that the moss photosynthesis did indeed induce much faster than observed in tracheophytes, reaching 50% of maximum gross photosynthesis in only 90 seconds. Maximum photosynthesis occurred in only 220 seconds, compared to 500-2000 s for most tracheophytes. Shade-grown mosses had a photosynthetic capacity comparable to that of sun grown plants. ***Hypnum cupressiforme*** (Figure 20-Figure 21) from shade induced photosynthesis slightly faster than did those from sunnier forest gaps (Figure 22). This high photosynthetic capacity permits these forest mosses to make efficient use of sunflecks.

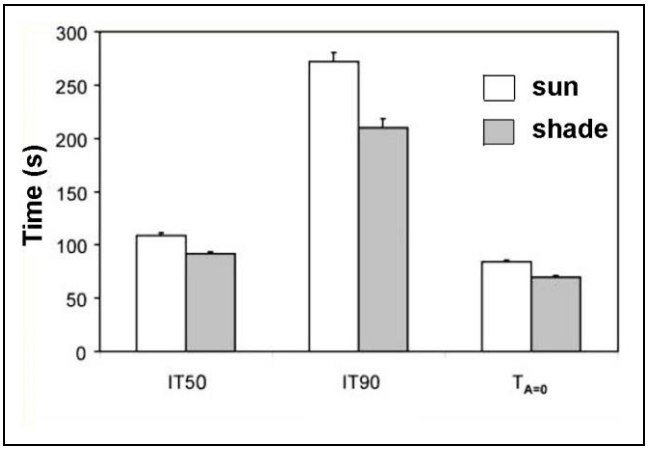

Figure 22. Comparison of induction rates (IT50 and IT90) and time needed to reach net carbon uptake ($T_{A=0}$) of four gap and four shade samples of the forest moss ***Hypnum cupressiforme***. One hour of dark acclimation with ambient CO_2 (400 µmol mol^{-1}) was followed by saturating irradiance of 1200 µmol m^{-2} s^{-1}. Means are ± SEM, n=4. All means comparing gap and shade groups differ at $P<0.025$. Modified from Kubásek *et al*. 2014.

Bryophyte photosynthetic capacity may be higher than is usually understood (Kubásek *et al*. 2014). For example, the sun species ***Bryum argenteum*** (Figure 23) under saturating light had 9 µmol m^{-2} of projected area s^{-1} under ambient CO_2 and 20 µmol m^{-2} of projected s^{-1} under 2000

ppmV of CO_2. This is similar to the photosynthetic capacities of many understory tracheophytes.

Figure 23. ***Bryum argenteum***, a sun-tolerant moss made whitish by hyaline tips of overlapping leaves. Photo by George Shepherd, through Creative Commons.

Some tracheophyte physiologists have expressed surprise that shade-grown mosses do not have significantly lower photosynthetic capacity than gap-grown mosses (Jiri Kubásek, pers. comm. 5 April 2007). But consider the adaptations that cause tracheophytes to have less ability to take advantage of sunflecks. First they must open stomata, the slowest process in the induction of photosynthesis. Then, they have layers of cells to protect them from the high light intensity. And often they have a thick cuticle that reflects the sun, whereas it is thin in bryophytes. Bryophytes have none of these constraints and therefore can respond quickly to the short duration of sunfleck light.

Typically, however, light saturation points for bryophytes are low compared to those of tracheophytes. Gabriel and Bates (2003) found that most of the species they examined from an evergreen laurel forest had a saturation point less than 30 µmol m^{-2} s^{-1}, although the lowest among the seven species they studied was 20 µmol m^{-2} s^{-1}. The highest was for ***Myurium hochstetteri*** (Figure 24-Figure 25), which was saturated at 68 µmol m^{-2} s^{-1}. See also Chapter 9-2 for further discussion of Sunflecks.

Figure 24. ***Myurium hochstetteri*** habitat. Photo by Michael Lüth, with permission.

Figure 25. ***Myurium hochstedteri***, the bryophyte species with the highest light saturation point among those tested in the laurel forest. Photo by Michael Lüth, with permission.

Light Effects on Morphology

Sometimes added light can give unexpected results. Such is the case with ***Calliergonella cuspidata*** (Figure 26). In experiments where tracheophytes were cut, creating more exposure in a calcareous fen in the Swiss mountains, the moss ***Calliergonella cuspidata*** exhibited a number of morphological differences (Bergamini & Peintinger 2002). It had smaller increments in length on the main axis, shorter offshoots, greater branching density, higher number of offshoots, and greater biomass per unit length. On the other hand, there were no observable effects of increased N supply.

Figure 26. ***Calliergonella cuspidata***, a species that has longer leaf intervals when shaded by tracheophytes. Photo by Michael Lüth, with permission.

Summary

In general, bryophytes are adapted to low light, relative to other land plants. They do well in forests as long as they are not buried by leaf litter. Most taxa have a low **light compensation point** and a low **light saturation point**. Light is usually measured as **photosynthetically active radiation** (**PAR**), but this ignores the ability of accessory pigments to trap other wavelengths and transfer the energy to chlorophyll *a*.

Most bryophytes are adapted to capture of low light intensities due to their one-cell-thick leaves and lack of well-developed cuticle. Responses of bryophytes to low light are similar to those of tracheophytes, with increased chlorophylls and antenna pigments, depressed light saturation and compensation points, and deeper green color. However, some bryophytes at least do not have a lower chlorophyll *a*:*b* ratio in low light compared to high light, as would the typical tracheophyte. Rather, bryophytes in general have a lower chlorophyll *a*:*b* ratio in all light conditions than do tracheophytes. This suggests that the bryophyte, with its chlorophyll *a* concentrations maintaining proportionality to chlorophyll *b* concentrations, would be ready for brief opportunities when bright light becomes available. Liverworts seem to be better adapted to shade than mosses, with a lower chlorophyll *a*:*b* ratio, higher concentration of total chlorophyll, and lower **PPFD**.

Such a strategy would adapt these plants well to the forest habitat where so many reside, permitting them to take advantage of changing positions of the sun as it filters through trees and brief bursts of light as **sunflecks** when the wind changes the arrangement of the overarching canopy.

There is a broad range of **light compensation points** among bryophytes, ranging from 0.03% of full sunlight in deep water species to 7.5% in sun species. **Light saturation points** are likewise low, although some bryophytes seem able to use bursts of high light intensity and can increase their saturation points when higher levels of CO_2 are available.

Acknowledgments

I thank Jiri Kubásek for many email discussions about bryophytes and sunflecks.

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CHAPTER 9-2

LIGHT: ADAPTATIONS FOR SHADE

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CHAPTER 9-2

LIGHT: ADAPTATIONS FOR SHADE

Figure 1. Hemlock hardwood forest in West Virginia, showing the absence of bryophytes among the leaf litter on the forest floor but growing on exposed rocks. Photo by Janice Glime.

Structural Adaptations for Light Capture

Among my favorite posters at the meetings of the Ecological Society of America, 1993, were the several posters on light focussing by seed plants (DeLucia *et al*. 1996). These illustrated principles I have considered for bryophytes but been unable to test. They found that epidermal cells (**lens cells**) that are rounded at the surface can focus the light in the leaf. In shade leaves, these lens cells are spherical; in the sun they are elliptical. In bryophytes, some leaves have **mammillose** (swollen) cells that are similar to the lens cells they describe (Figure 5). The ability of these cell surfaces to focus light on the chloroplasts has not been explored, except in the case of the protonemata of ***Schistostega pennata*** (Figure 2-Figure 4), as will be discussed in Chapter 9-5 of this volume.

Figure 2. ***Schistostega pennata*** with mature plants in upper left and luminescent protonemata in lower center. Photo courtesy of Martine Lapointe.

Figure 3. ***Schistostega pennata*** protonema with light-focussing cells. Photo courtesy of Irene Bisang.

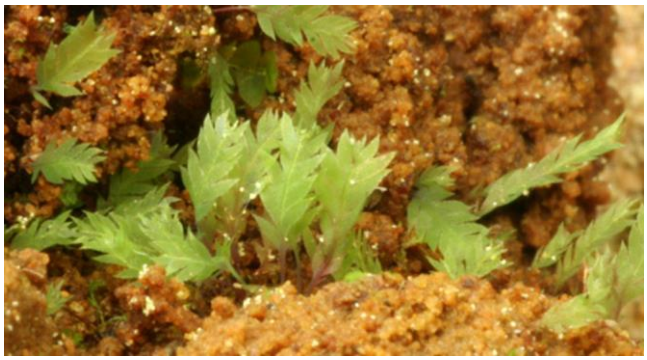

Figure 4. ***Schistostega pennata*** leafy gametophytes. Photo courtesy of Martine Lapointe.

Tracheophytes can move their leaves instead of their chloroplasts. In their study, DeLucia *et al*. (1996) found that further adjustments to the light reaching the chloroplasts of tracheophyte leaves were facilitated by leaf angles. In mesic woods, fewer than 10% of the leaves were angled more than 60º, whereas in xeric sites with high light intensity more than 75% of the leaves were angled. Leaf thickness also related to moisture, with 75% of taxa at the three most open sites having leaves more than 0.4 mm thick, while at more mesic sites less than 12% of the taxa reached such a thickness. High sunlight resulted in palisade tissue on both sides of the leaf.

In a different poster, DeLucia *et al*. (1996) noted attenuation of green light by 2.7 times and red light by 8 times in the air space at the palisade/mesophyll interface. By applying oil to fill the air spaces, they reduced reflectance and caused a decrease in fluorescence by 50%. They interpreted this to mean that reflectance in the air space caused more light to be available for absorbance by the chloroplasts. A thick palisade reduces the reflectance and therefore reduces the light reaching the spongy mesophyll. At light intensities of less than 30 μM m^{-2} s^{-1}, the air space reflectance increased the photosynthetic rate by 30-50%, with lesser increases at higher light intensities.

If we consider the bryophyte branch to act like a leaf, these principles could be tested in bryophytes. Lens-shaped leaf cells (Figure 5) could focus light on cells of overlapped leaves that are more moist because of their internal position. Such a focussing would be facilitated by the tendency for moss chloroplasts to arrange themselves around the periphery of the cell, thus leaving the center of the cell available for focussing without increasing absorption. Can we find any correlation between the leaf or branch position of bryophytes and the light regimes under which they grow?

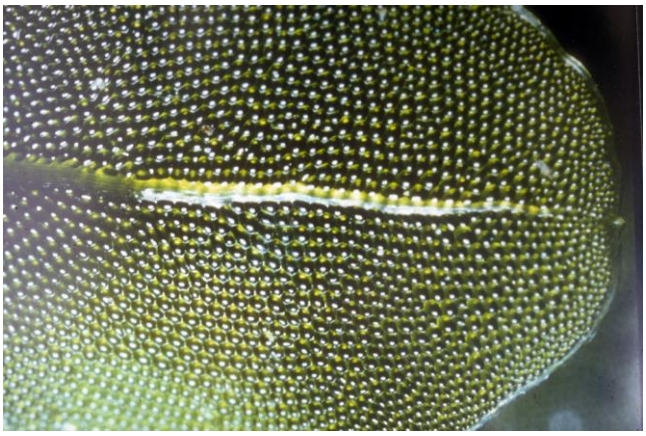

Figure 5. Leaf of ***Plagiomnium tuomikoski*** showing bulging (**mammillose**) cells that could focus light within the cell. Photo by Zen Iwatsuki, with permission.

Lamellae

Mosses like ***Polytrichum*** (Figure 6-Figure 7) and ***Atrichum*** (Figure 8-Figure 9) have a leaf structure with **lamellae** (Figure 7, Figure 9) similar to the structure of palisade tissue in seed plants, while the internal structure of a branch in most other bryophytes in many ways resembles the air spaces and spongy mesophyll of seed plants.

Figure 6. ***Polytrichum juniperinum*** showing leaf edges rolled over the lamellae. Photo by Janice Glime.

Figure 7. ***Polytrichum juniperinum*** leaf lamellae and rolled over edge of leaf. Photo courtesy of John Hribljan.

Figure 8. ***Atrichum altecristatum*** leaves with lamellae. Photo courtesy of Eric Schneider.

Figure 9. Cross section of leaf showing the **lamellae** of ***Atrichum selwynii***. Photo from Botany Website, UBC, with permission.

Surface Reflectance

Lovelock and Robinson (2002) have found that various mosses differ in their surface reflectance properties and that the differences do not correlate with pigment concentrations, suggesting that surface shape and water content may play a role in surface reflectance. In studying the Antarctic mosses ***Bryum pseudotriquetrum*** (Figure 10), ***Ceratodon purpureus*** (Figure 11), and ***Schistidium antarcticum*** (Figure 11), Lovelock and Robinson (2002) found that the reflectance spectra were similar to those of angiosperm leaves with chlorophyll having the major influence. The mosses likewise did not differ from angiosperms in their UV reflectance, but they did differ significantly at 526, 550, and 850 nm light wavelength and seemed to have a different **cold hard band** – that portion of the absorbance that correlates with the formation of the chlorophyll-protein complex that protects against freezing damage. It is no surprise that ***Ceratodon purpureus*** had higher concentrations of **anthocyanins** (Figure 12), since it is frequently red-tinged, whereas it had lower chlorophyll concentrations than the other two species. ***Bryum pseudotriquetrum*** (Figure 10) had higher levels of UV-absorbing pigments but lower carotenoid levels than the other two taxa, but the other two taxa had higher levels of pigments associated with photoprotection from visible light. The correlation between surface reflectance and plant pigment concentration was low, suggesting that surface structure may have played a major role in reflectance. Rehydration of dry ***Schistidium antarcticum*** resulted in a significant increase in the photosynthetic reflectance (Figure 11), but it is unclear as to the mechanism. The surface reflectance is highly influenced by the environmental conditions under which the mosses are growing and seems to be linked to water content and morphology of the individual plants and their clone.

Figure 10. ***Bryum pseudotriquetrum*** growing in Antarctica. Photo courtesy of Jan Beard.

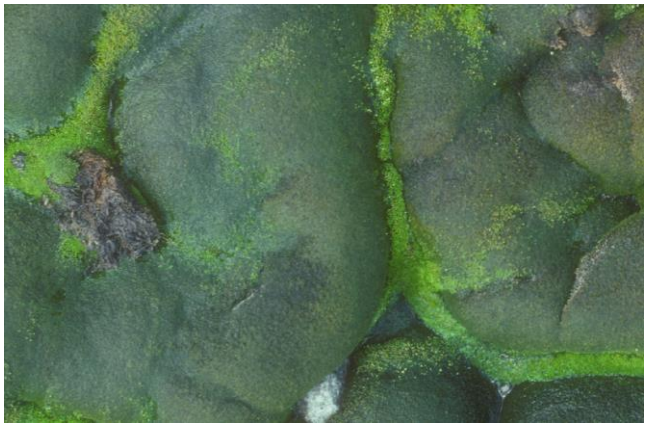

Figure 11. Wet ***Schistidium antarcticum*** hummocks illustrating the high reflectance. ***Ceratodon purpureus*** is in the hollows. Photo courtesy of Rod Seppelt.

Figure 12. ***Ceratodon purpureus*** with anthocyanins protecting it from the high levels of UV light in the Antarctic. Photo courtesy of Rod Seppelt.

Altering Wavelengths

Light is modified as it travels through the atmosphere, losing energy and lengthening the wave lengths, thus

changing the quality of the light. This of course doesn't mean good or bad, but rather means the color composition of the light changes.

The mosses themselves also alter the light quality. They reflect the colors we see, absorb others, and transmit still others. They typically absorb blue and red light, as do tracheophytes, but they differ from tracheophytes in having a green peak that responds to the red, brown, or green coloration of various species (Bubier *et al*. 1997). In their study, Bubier and coworkers examined boreal forest and peatland mosses, including feather mosses (forests; Figure 13), brown mosses (rich fens; Figure 20), and ***Sphagnum*** (bogs and poor fens; Figure 14-Figure 19). They found that the mosses are typically less reflective than are tracheophytes, resulting from strong water absorption features in the range of 1.00-1.20 μm. This absorption results in reflectance peaks at ~0.85, 1.10, and 1.3 μm (NIR 1, 2, & 3). ***Sphagnum*** species have a minor absorption at 0.85 μm that is absent in all brown and feather mosses and in all tracheophytes. Furthermore, the red absorption is narrow in ***Sphagnum***. Bubier and coworkers concluded that the overall moss reflectance in the 1.50-2.50 region is lower than that for tracheophytes because of the higher water content of moss tissue. This is further supported by the high reflectance of lichens, which typically have dry tissues.

Figure 13. ***Pleurozium schreberi***, a feather moss from the forest floor. Photo by Sture Hermansson, with online permission.

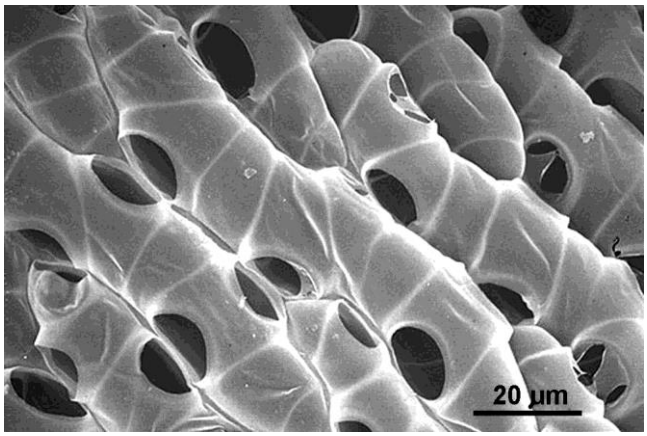

Figure 14. ***Sphagnum*** hyaline cells & pores (SEM), a structure that may alter the light quality that is reflected and that enters the photosynthetic cells. Photo from Botany Website, UBC, with permission.

Figure 15. ***Sphagnum austinii***, exhibiting one of the many colors in the genus ***Sphagnum***. Photo by Des Callaghan, with permission.

Figure 16. ***Sphagnum balticum*** (brownish red) and ***S. cuspidatum*** (light green) showing two contrasting colors in the genus ***Sphagnum***). Photo by Jan-Peter Frahm, with permission.

Figure 17. ***Sphagnum capillifolium***, one of the red species of ***Sphagnum***. Photo by Blanka Shaw, with permission

Figure 18. ***Sphagnum fuscum***, one of the brown species of ***Sphagnum***. Photo by Andres Baron Lopez, with permission.

Figure 19. ***Sphagnum magellanicum***, one of the species that becomes red in bright light. Photo by Michael Lüth, with permission.

Figure 20. ***Warnstorfia exannulata***, one of the brown mosses. Photo from Biopix, through Creative Commons.

Papillae

I wonder how papillae (Figure 21-Figure 28) might fit the reflectance model. I have long thought that papillae might serve to scatter the light on a dry moss while permitting transmission on a wet one. It would seem like a relatively easy thing to test with a microscope and photometer. And does the shape of the papillae make a difference (Figure 21-Figure 28)?

Figure 21. ***Tortula muralis***, a papillose moss of open habitats. Photo from Botany Website, UBC, with permission.

Figure 22. ***Tortula muralis*** showing leaves that look waxy due to papillae. Photo by Christophe Quintin, through Creative Commons.

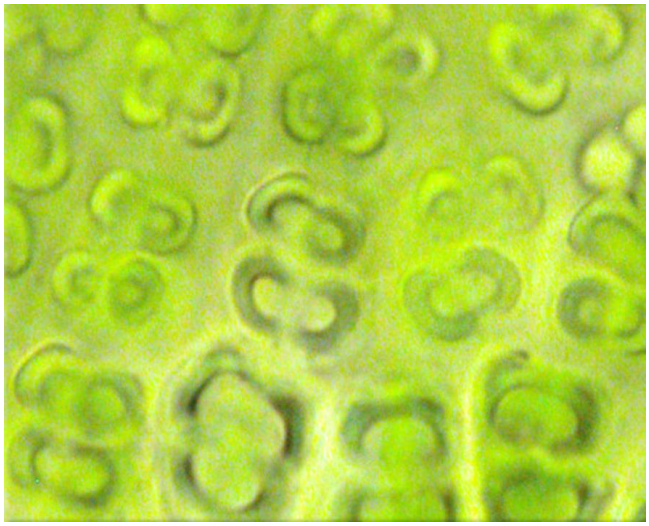

Figure 23. ***Tortula muralis*** leaf cell papillae. Photo by Walter Obermayer, with permission.

Figure 24. ***Tortula muralis*** leaf CS showing papillae on both sides of the leaf. Photo from Botany Website, UBC, with permission.

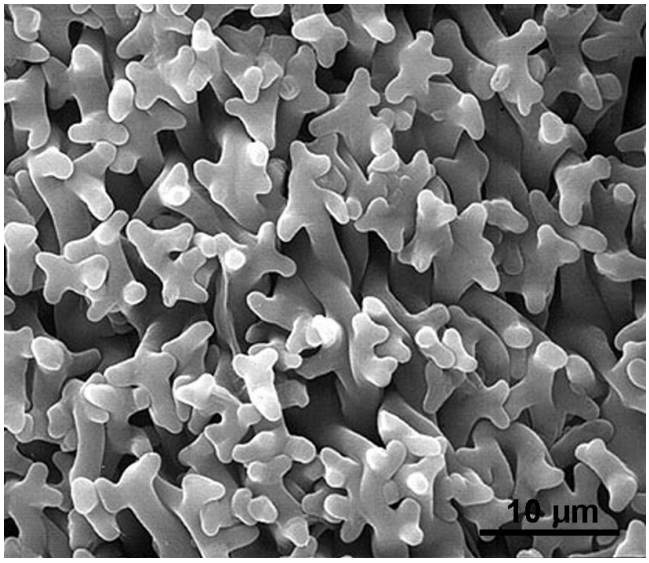

Figure 25. ***Tortula muralis*** papillae (SEM). Photo from Botany Website, UBC, with permission.

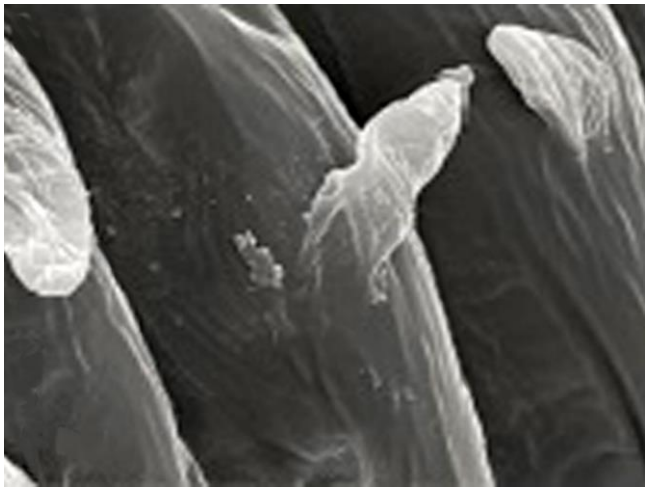

Figure 26. ***Callicostellopsis meridensis*** leaf papillae (SEM). Photo by Duarte-Silva *et al*. 2013, through Creative Commons .

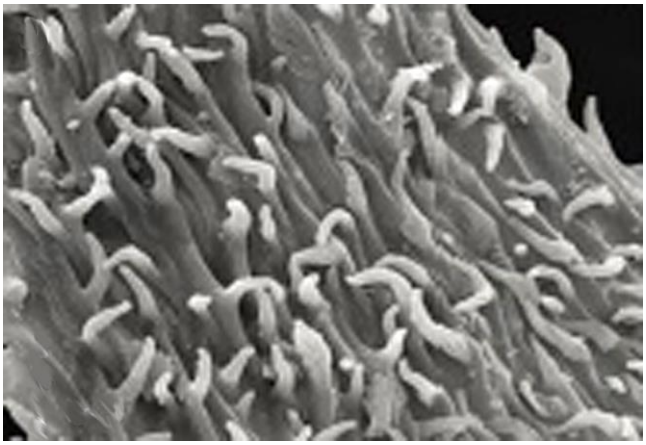

Figure 27. ***Hypnella pilifera*** leaf papillae (SEM). Photo by Duarte-Silva *et al*. 2013, through Creative Commons.

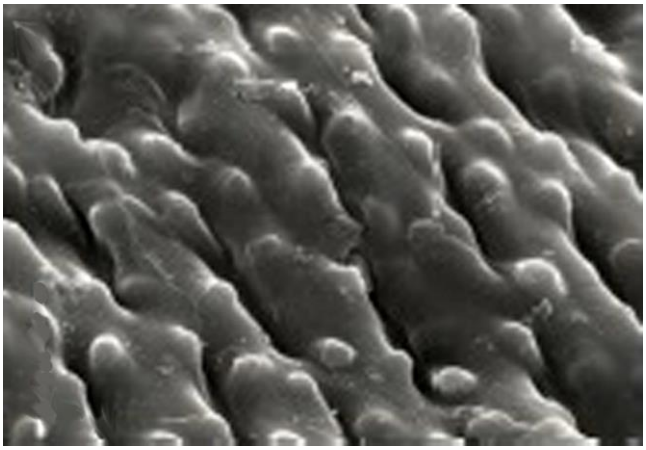

Figure 28. ***Pilotrichidium*** leaf papillae (SEM). Photo from Duarte-Silva *et al*. 2013, through Creative Commons.

The role of papillae has been controversial at best. Crandall-Stotler and Bozzola (1991) have shown that at least ***Andreaeobryum macrosporum*** (Figure 29) leaf papillae have narrow channels through which water can enter upon rehydration. It has occurred to me that these channels might also behave as fiber optics – a notion that remains to be tested.

Figure 29. ***Andreaeobryum macrosporum***, a moss with channelled papillae. Photo from Botany Website, UBC, with permission.

Proctor (1982) explains that in concave leaves, water is held in the concavity while the convex surface remains dry.

It is this convex surface that often is exposed to light. In papillose mosses such as ***Thuidium*** (Figure 30-Figure 31) and ***Hedwigia*** (Figure 32-Figure 35), the tops of papillae tend to remain dry, even when the leaf surface is wet, giving them that waxy or dull appearance. The tiny channels, when present, could function as fiber optics, much as the fur of a polar bear, but on a much smaller scale. Hence, the light could be focussed through the papillae onto the chloroplasts while water is obstructing and altering the light entering other parts of the cell. As can be seen in Table 1, there are lots of potential light adaptations in bryophytes that remain to be tested.

Figure 30. ***Thuidium delicatulum***, a moss of light shade. Photo by Janice Glime.

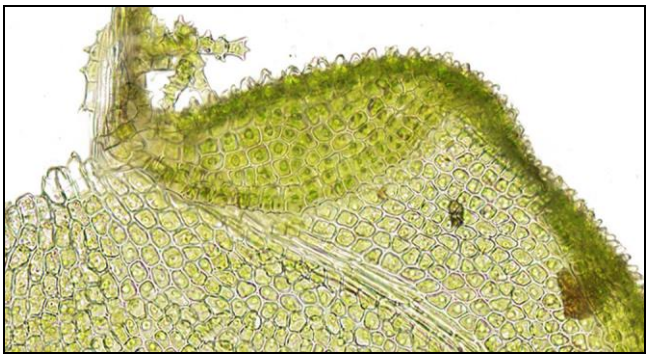

Figure 31. ***Thuidium delicatulum*** leaf showing papillae (see edges). Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 32. ***Hedwigia ciliata*** wet on upper left and dry at the edges of the clump on the right. Photo by Janice Glime.

Figure 33. ***Hedwigia ciliata*** showing overlapping leaves with white tips. Photo by Des Callaghan, with permission.

Figure 34. Leaf tip of ***Hedwigia ciliata*** showing papillae on cells. Photo by Janice Glime.

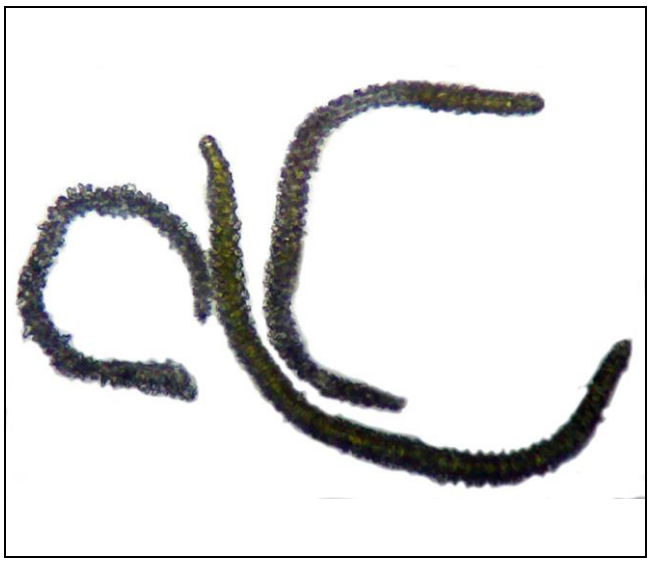

Figure 35. ***Hedwigia ciliata*** leaf cs showing papillae on both surfaces. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Table 1. Comparison of sun and shade leaves of bryophytes and seed plants. + = high rates or large amounts, - = low rates or small amounts, ? = unknown. [Data for seed plants (**tra**) from Larcher 1983, compiled from many authors, with characteristics applying to structures that don't exist in bryophytes omitted; bryophyte (**bry**) data based on literature presented in this volume.]

Characteristic	Sun Leaves		Shade Leaves	
	bry	tra	bry	tra
Structural features				
Area of leaf blade	+	-	+	+
Cell number	?	+	?	-
Chloroplast number per unit area	?	+	?	-
Density of packing of the membrane systems in the chloroplasts	?	-	?	+
Chemical features				
Dry matter	+	+	-	-
Energy content of dry matter	?	+	?	-
Water content of fresh tissue	-	-	+	+
Cell-sap concentration	?	+	?	-
Starch	?	+	?	-
Cellulose	?	-	?	+
Lignin	?	+	?	-
Lipids	?	+	?	-
Acids	?	+	?	-
Anthocyanin, flavonoids	+	+	-	-
Ash	?	+	?	-
Ca/K	?	+	?	-
Chlorophyll *a*/*b*	$\frac{+}{-}$	+	$\frac{+}{-}$	-
Chlorophyll *a* (P-700)	-?	+	+?	-
Photosystem II pigment complex	-	-	+	+
Chlorophyll/xanthophylls	?	-	?	+
Lutein/violaxanthin	+	+	-?	-
Functional features				
Photosynthetic capacity	-	+	+	-
Respiratory intensity	?	+	?	-

Leaf Area Index

The **leaf area index** (**LAI**) has been used to show structural responses of tracheophyte leaves to high vs low light conditions. This value represents the percentage of ground area covered by leaves, hence **(total leaf area) / (area of ground)**. Likewise, bryophytes can exhibit a leaf area index that is directly proportional to the light intensity (Sluka 1983). Unfortunately, few measurements have been taken on bryophytes. Simon (1987) compared two desiccation-tolerant mosses with one more mesic species and found what she considered to be high LAI values. For ***Syntrichia ruralis*** (Figure 36), the LAI was 44, for ***Ceratodon purpureus*** (Figure 37) 129, and for the more mesic ***Hypnum cupressiforme*** (Figure 38) 103. These indeed seem to be enormous. By contrast, forest floor tracheophyte species in a montane forest had an LAI of only 3.8 (Schleppi *et al*. 1999); in a tropical cloud forest the LAI was only 1.6 in a gap less than 8 months old, increasing to the pre-gap level of 5.1 in three years (Lawton & Putz 1988). Larcher (1995) considered 4-6 to be optimal for herbaceous plants with horizontal leaves and 8-10 optimal for grasses. Asner *et al*. (2003) reviewed more than 1000 LAI studies from around the world and found that the maximum for an ecosystem was 18 with a mean of 5.2±4.1. The macroalga *Fucus serratus* (Figure 39) achieved its maximum productivity for an individual at LAI 8-10, while the community did best at 6-8 (Binzer & Sand-Jensen 2002). At the biome level, the LAI seems to range from 0.5 to 16, hardly making a showing against the high values measured by Simon (1987) for bryophytes.

Figure 36. ***Syntrichia ruralis***, a species with a high leaf area index (LAI) compared to most tracheophytes, but not as high as forest bryophytes like ***Hypnum cupressiforme***. Photo by Michael Lüth, with permission.

Figure 37. ***Ceratodon purpureus***, a moss with a very high LAI. Photo by Jiří Kameníček (BioLib, Obázek), with permission.

Figure 38. ***Hypnum cupressiforme***, exhibiting a high leaf area index. Photo by Michael Lüth, with permission.

Figure 39. ***Fucus serratus***, a brown alga with a leaf area index (LAI) closer to that of tracheophytes than to bryophytes. Photo by Stemonitis, through Creative Commons.

Just why should bryophytes have such enormous LAI values? As we know from tracheophytes, leaves arranged with minimal overlap vertically will have maximal exposure to sunlight, whereas crowded leaves that overlap (having a high LAI) will cause the plant to exhibit self-shading. Furthermore, leaves that have a strong vertical orientation will have minimal direct exposure to light, thus requiring more leaves. This latter condition would seem to describe some mosses, but not the thallose or two-ranked leafy liverworts. Simon (1987) suggested that the high leaf area found in bryophytes might facilitate uptake of the high levels of CO_2 found near the soil surface. Other advantages might result from the vertical growth and close packing with neighbors, with clustered apical leaves taking maximal advantage of the light. On the other hand, the entire moss branch might behave much like a single leaf of a tracheophyte, with overlapping leaves protecting the chlorophyll from UV damage and maintaining moist internal spaces. New techniques for tracheophytes using models that incorporate both LAI and a foliage clumping index indicate that both measures are needed to separate sun from shade leaves (Chen *et al*. 2003), and it seems that this technique might permit us to explain the high leaf area index of bryophytes, where many leaves are shaded by the upper leaves of the same plant or by overlying branches of prostrate plants.

Self-shading

Because of their three-dimensional nature, plants typically shade themselves. As a result of the high leaf area index, a moss cushion is a source of rapid light extinction due to self-shading. Using Antarctic mosses, Davey and Ellis-Evans (1996) demonstrated that irradiance decreases with increasing depth within the moss – no surprise there. Furthermore, the greatest loss of light was at wavelengths around 675 nm and less than 450 nm, in the neighborhood of those portions of the spectrum causing the greatest chlorophyll activity. Of course species differed in light attenuation, with stem orientation being the most important factor, along with stem density, leaf size, orientation, and pigment content. Light penetration increased upon drying – seemingly a maladaptive trait that would permit light to damage chlorophyll, but an expected result for mosses that curl or fold their leaves upon drying. On the other hand, Davey and Ellis-Evans suggested that this deeper light penetration of dry mosses might permit photosynthesis to occur in the deeper layers (these most likely also being more moist) and thus make up for some of the photosynthetic loss in the drier apical parts.

Bryophyte Canopy

As we have just seen, not only do trees and other tracheophytes provide a canopy over the bryophytes, but the bryophytes themselves provide a canopy that alters the light reaching the lower parts of the plants. This canopy is structured differently and functions differently, relating to issues of scale and external transport of water and nutrients (Rice & Cornelissen 2014). Hence bryophytes demand different methodologies to truly understand their use of light and ultimate photosynthetic product.

Habitats vary in their light quality and intensity and the bryophytes further alter this light in the bryophyte canopy (Figure 40) (Tobias & Niinemets 2010). These authors set out to document bryophyte differences in chlorophyll, carotenoids, nitrogen concentrations, and photosynthetic electron transport capacity as they varied with the light profiles above and within populations of the moss ***Pleurozium schreberi*** (Figure 41). Light differences between habitats resulted in increases in chlorophyll, chlorophyll:N, and chlorophyll:carotenoids as light decreased, thus increasing the light harvesting in low light and increasing light protection in higher light. N levels in the plants were independent of light intensity. In the upper moss canopy (Figure 41) where light was at least 50-60% of the above-canopy light, changes in moss chemistry and photosynthetic output were similar to those observed in the between-habitat light gradient. However, deeper canopy layers mimicked the effects of senescence (Figure 40), with pigment and nitrogen concentrations and photosynthetic capacity decreasing with light availability. They considered the chemical and physiological variation in the moss canopy to be a balance between acclimation and senescence.

Figure 40. ***Pleurozium schreberi*** showing a canopy with an active green layer and a senescent lower layer. Photo by Janice Glime.

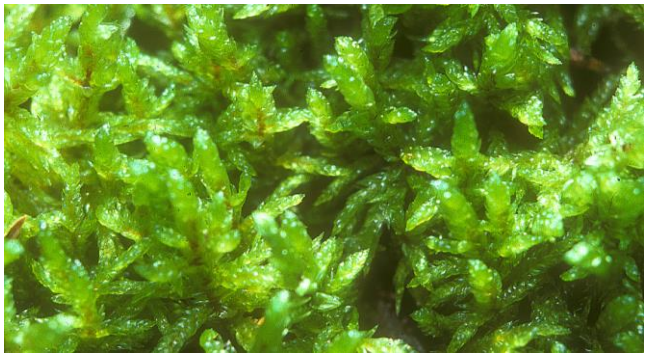

Figure 41. ***Pleurozium schreberi*** as seen at the top of the moss canopy, a typical species in boreal forests. Photo by Janice Glime.

In low light, the foliage is less densely aggregated and plant density is lower, permitting greater light penetration and greater light interception per unit of leaf area (Niinemets & Tobias 2014). In healthy tissues, chlorophyll increases as light levels diminish. But one of the consequences of aging in mosses is that the tissues senesce. This senescent zone is likewise deeper in the moss mat and consequently gets less light. This senescent moss zone has reduced chlorophyll content.

Canopy architecture differs among species. Species, especially of pleurocarpous mosses, that are able to branch and from new leaves from lateral buds are able to extend into areas with greater light as well as providing more opportunities for catching sunflecks (Niinemets & Tobias 2014). One advantage is that plants in high light intensity tend to have cushion growth forms that protect them from the accompanying desiccation. Those in shaded habitats often also experience the greater moisture that permits them to spread horizontally and capture more light.

Rice *et al*. (2014) examined the effects of drying on light relations in ten species of ***Sphagnum*** (Figure 15-Figure 19). They found that spatial variation in the rate of photosynthetic electron transport increased during drying and in high light intensities. There was a positive relationship between that rate and light intensity, but the relationship with drying was negative, and the light and moisture interacted to create the spatial variation. Within the canopy of the moss ***Pleurozium schreberi*** (Figure 41-Figure 41), the mat temperature reached a 9°C span. In the leafy liverwort ***Bazzania trilobata*** (Figure 42), the Lambert-Beer Law predicted the attenuation of light within the liverwort canopy.

Figure 42. ***Bazzania trilobata***, illustrating overlapping branches. Photo by Jan-Peter Frahm, with permission.

Growth and Branching

Low light in plants often results in **etiolation**, elongated growth that often lacks accompanying weight gain, creating thin and often chlorotic plants with long internodes and small, rudimentary leaves. Such growth is seen in grass when a board or rug rests on it for a period of weeks. Bryophytes are no exception to this phenomenon, and increased elongation in incubators should not be mistaken for healthy plants if the plants become long and thin. For example, in one study ***Dicranum majus*** (Figure 43) had its greatest elongation at the lowest irradiance (20 μm m^{-2} s^{-1}) (Bakken 1995).

Figure 43. ***Dicranum majus*** with capsules, a species that has the greatest elongation in low light. Photo by Michael Lüth, with permission.

Bates (1988) examined the effect of shoot spacing on growth and branch development in ***Rhytidiadelphus triquetrus*** (Figure 44). Using intermittent moisture supply and spacings of 5, 10, 20, and 50 mm between shoots, he found that main axis growth was promoted by decreased spacings. Although etiolation occurred when shoots were close together, there was no self-thinning and overall growth seemed to be optimal at or near the closest spacing tested. As a result, productivity was greatest in the most dense colonies (1000 shoots dm^{-2}). Since growth occurs at the tip, there probably is very little effective light loss at these 5 mm spacings between plants, and water is conserved.

Figure 44. ***Rhytidiadelphus triquetrus***. Photo by Janice Glime.

In fact, van der Hoeven and During (1997) found that when plots of three pleurocarpous mosses (***Calliergonella cuspidata*** (Figure 45), ***Ctenidium molluscum*** (Figure 46), and ***Rhytidiadelphus squarrosus*** (Figure 47) were thinned by 50%, the original density returned rapidly, suggesting that density might be regulated by an intrinsic mechanism. Bates (1988) concluded that this dense packing is an indication of the advantage of reduced water loss in the more densely packed shoots and that this advantage outweighs the reduction in light. However, for ***Ctenidium molluscum***, thinning to 50% caused increased growth, presumably due to increased photosynthesis, while its neighbors, ***Rhytidiadelphus squarrosus*** and ***Calliergonella cuspidata*** gained no advantage from the same thinning (van der Hoeven 1999). The differences in morphology may account for the success of ***C. molluscum*** following thinning, for it has dense, overlapping leaves, compared to the spreading leaves of ***R. squarrosus*** and large, slightly overlapping leaves of ***C. cuspidata***. These mosses, after thinning, returned rather quickly to their original density. Like Bates (1988), Van der Hoeven and During (1997) suggested that they have an intrinsic control over their density.

Figure 45. ***Calliergonella cuspidata***, demonstrating overlapping leaves on exposed, ascending shoots. Photo by Michael Lüth, with permission.

Figure 46. ***Ctenidium molluscum***, demonstrating strongly overlapping leaves and branches. Photo by Michael Lüth, with permission.

Figure 47. ***Rhytidiadelphus squarrosus***, demonstrating spreading leaves on ascending shoots. Photos by Michael Lüth, with permission.

Pedersen and coworkers (2001) tested this moisture/light trade-off using one acrocarpous (***Dicranum majus***, Figure 43) and two pleurocarpous (***Ptilium crista-castrensis*** (Figure 48), ***Rhytidiadelphus loreus***, Figure 49) mosses and a leafy liverwort (***Plagiochila asplenioides***, Figure 50). Using several controlled moisture and light levels, they determined that ***Dicranum majus*** and ***Rhytidiadelphus loreus*** had peak growth rates at intermediate densities where light and moisture were balanced, a relationship noted by Bergamini *et al*. (2001) as well. On the other hand, when the environment was either dark or humid, the effect of increased density was negative. ***Ptilium crista-castrensis*** exhibited decreased growth rates under most experimental combinations and ***Plagiochila asplenioides*** seemed to be unaffected. In all cases, it required light levels that were higher than in their natural spruce forest (Figure 53) habitat before the advantages of greater density were manifest, indicating that it is competition for light that limits optimal density, not low water availability. In a similar experiment, Scandrett and Gimingham (1989) found that ***Pleurozium schreberi*** (Figure 40-Figure 41), ***Hylocomium splendens*** (Figure 51), and ***Hypnum jutlandicum*** (Figure 52) likewise exhibited more intraspecific inhibition from crowding in low light than in high light, but yields were higher among sown fragments in low light.

Figure 48. ***Ptilium crista-castrensis***, a species that seems to exhibit no growth rate change with changes in light and moisture levels. Photo by Janice Glime.

Figure 49. ***Rhytidiadelphus loreus*** with capsules, a species that has peak growth rates at intermediate densities where light and moisture are balanced. Photo by David Holyoak, with permission.

Figure 50. ***Plagiochila asplenioides***, a species for which growth seems unaffected by light and moisture levels. Photo by Michael Lüth, with permission.

Figure 51. ***Hylocomium splendens***, a species in which thinning increases branching. Photo by Michael Lüth, with permission.

One consequence of thinning seems to be increased branching (Rydgren *et al*. 1998; Pedersen *et al*. 2001). And it seems that in ***H. splendens*** (Figure 51), the increased light increases production of gametangia and subsequent sporophytes (Rydgren *et al*. 1998). This species had ten times as many sporophytes two years after half the bryophyte cover had been removed, compared to non-thinned plots.

Figure 52. ***Hypnum jutlandicum***, a common gap species. Photo by Michael Lüth, with permission.

Figure 53. ***Picea mariana*** forest showing reduced light on the forest floor. Photo through Creative Commons.

We know that light is necessary to make new chlorophyll, and thus we might predict that there is a depth within a moss cushion at which the light attenuates beyond that needed for chlorophyll manufacture. Van der Hoeven, *et al*. (1993) found that chlorophyll concentration decreased down the shoot as light intensity decreased, but they considered that where only 50% of the shoot was green, the light intensity was too high to attribute the mortality of leaves to low light values. Skré and coworkers (1983), however, found that self-shading coincided with the transition from green to brown parts in ***Hylocomium splendens*** (Figure 51) and felt that light attenuation helped to explain the death of the green moss tissue.

Skré *et al*. (1983) showed (Figure 54) that in ***Hylocomium splendens***, PAR (photosynthetically active radiation) at a depth of 3 cm in natural moss canopies is reduced to ~17%; to ~8% in ***Pleurozium schreberi*** (Figure 40-Figure 41); to ~12% in a mixed canopy of ***Pleurozium schreberi*** and ***Polytrichum commune*** (Figure 55); and to only 1% in ***Sphagnum subsecundum*** (Figure 56). Visnadi and Vital (1989) found that there were more species entangled among themselves in the indirect sunlight of the riverbank than in the river bed, where direct light was available, indicating that self-shading, and neighbor-shading, might not always be a bad thing.

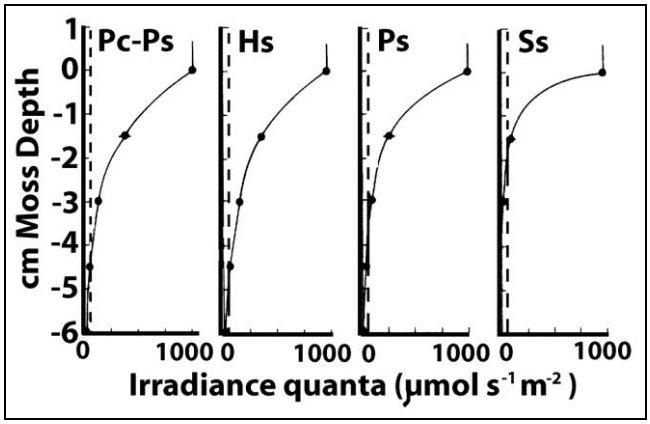

Figure 54. Diminishing PAR in the moss clump. PcPs = ***Polytrichum commune*** and ***Pleurozium schreberi***. Hs = ***Hylocomium splendens***. Ps = ***Pleurozium schreberi***. *Ss* = ***Sphagnum subsecundum***. Figure redrawn from Skré *et al*. 1983.

Figure 55. ***Polytrichum commune***, a species that is able to reduce the light available to ***Pleurozium schreberi***. Photo by Christopher Tracey through Creative Commons, with permission.

Figure 56. ***Sphagnum subsecundum***, a species that can reduce PAR to only 1% in 3 cm. Photo by Michael Lüth, with permission.

Chlorophyll Fluorescence

Chlorophyll fluorescence (light re-emitted by chlorophyll molecules during return from excited to non-excited states; Figure 57) is one measure of stress in leaves. This is expressed as the ratio of variable fluorescence ($\mathbf{F_v}$ = difference between the maximum and minimum fluorescence) to maximum fluorescence ($\mathbf{F_m}$ = fluorescence resulting from flashing a leaf in the dark with bright light), known as $\mathbf{F_v/F_m}$. The ratio is usually about 80% efficiency; lower measures indicate stress.

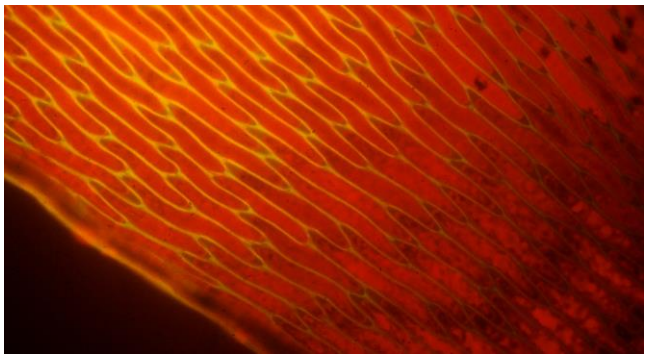

Figure 57. ***Fontinalis antipyretica*** leaf showing red chlorophyll fluorescence. Photo by Janice Glime.

Rice *et al*. (2005) demonstrated that the $\mathbf{F_v/F_m}$ ratio decreased when three bryophytes [***Bazzania trilobata*** (Figure 42), ***Sphagnum girgensohnii*** (Figure 60), ***Pleurozium schreberi*** (Figure 40-Figure 41)] were exposed to high light intensity, indicating stress. But in many bryophytes, while some leaves may be at stress levels, others may be at ideal levels. Using laser technology, Rice *et al*. developed a method to measure surface roughness and depth to first vertical canopy contact, thus permitting a more accurate measurement of light penetration and turbulence and providing a tool that may permit a better understanding of CO_2 exchange.

Morphological Responses

It appears that, like tree leaves, bryophytes might respond structurally to differences in light levels. Dalby (1966b) compared the leaves of the tufa-forming moss ***Eucladium verticillatum*** (Figure 58-Figure 59) from deep shade with those from the open and found that those grown in deep shade had much broader leaves, not unlike the response seen in some tree species (Figure 61).

Figure 58. ***Eucladium verticillatum***, a tufa-forming moss. Photo by Michael Lüth, with permission.

Figure 59. ***Eucladium verticillatum***, a species that when grown in deep shade has much broader leaves. Photo by Michael Lüth, with permission.

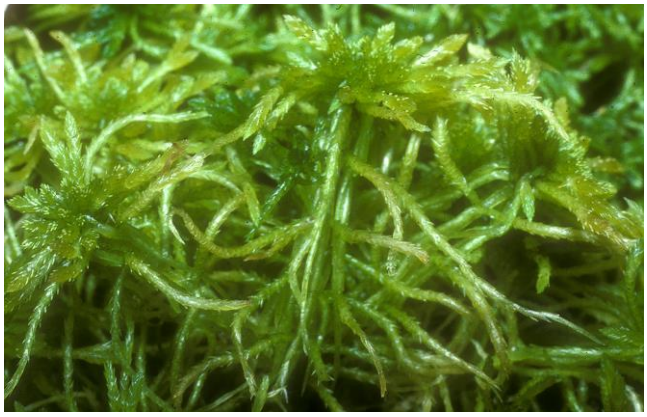

Figure 60. ***Sphagnum girgensohnii***, a species of peatland forests and *Thuja* swamps. Photo by Janice Glime.

At least some species exhibit a seasonal change in their light extinction curves that can be due to a change in leaf weight similar to that seen when tree leaves respond to high light. ***Calliergonella cuspidata*** (Figure 45), ***Ctenidium molluscum*** (Figure 46), and ***Rhytidiadelphus squarrosus*** (Figure 47) all exhibit a higher extinction coefficient in September than in December. In fact, the shoots are 1.5-2.1 times as heavy in September as in December, being so dense that the light intensity at the bottom of the plant approaches zero (van der Hoeven *et al*. 1993; Figure 62).

In culture, the thallose liverwort ***Marchantia paleacea*** var. ***diptera*** (Figure 63) exhibited an increase in growth rate with increasing light intensity over the range of 5.4 to 60 W m^{-2}, whereas a significant decrease occurred at light intensities >60 W m^{-2}. Many ***Sphagnum*** (Figure 15-Figure 19) species are high-light plants. In a growth study, weight increase of the species was greatest in unshaded conditions when the water table was low, but in shaded conditions, there was little difference with water table (Clymo 1973). However, when length was considered, plants of all ***Sphagnum*** species grew less in low water conditions, especially if they were also shaded – hardly an etiolation response.

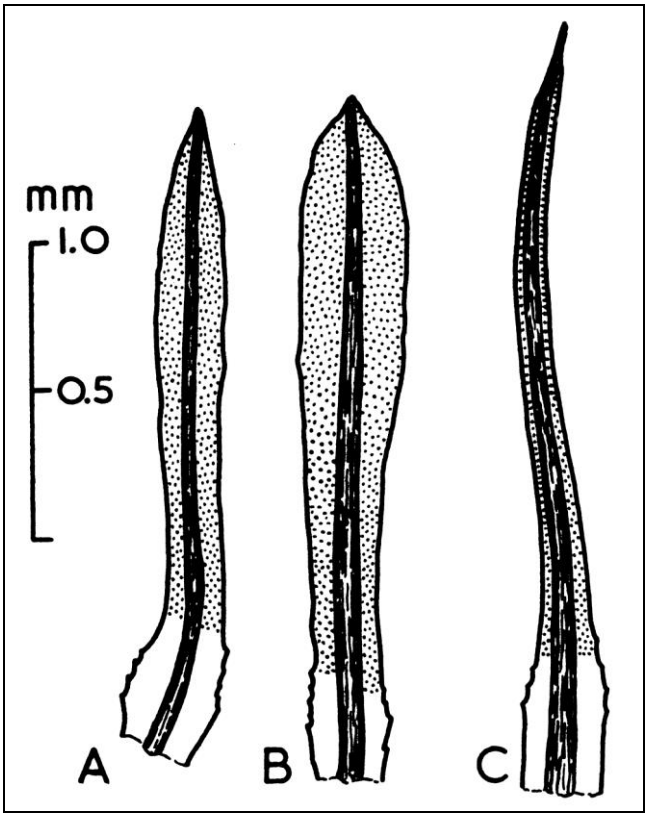

Figure 61. Effect of light intensity on ***Eucladium verticillatum*** leaves. **A** and **B** from deep shade in Kimeridge, Dorset, England; **C** from open at Lyme Regis, Devon. Redrawn from Dalby 1966a.

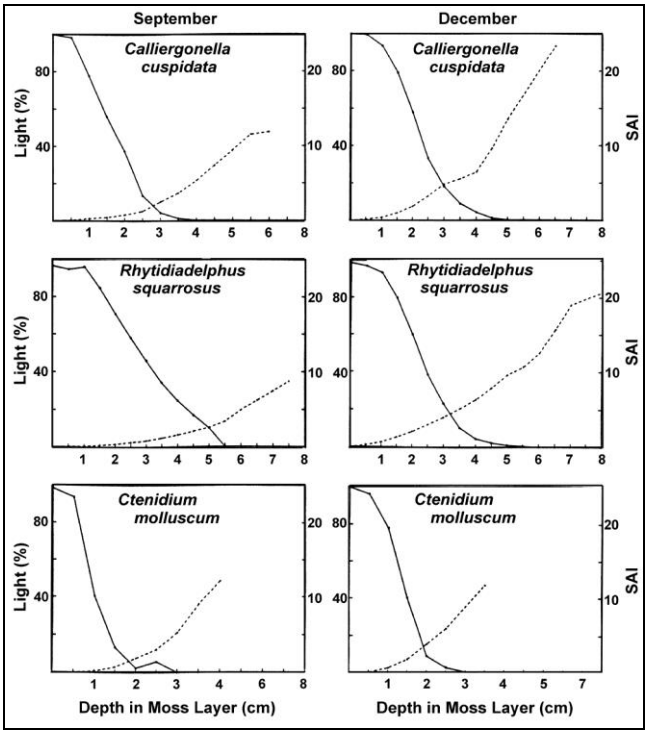

Figure 62. Vertical profiles of light extinction (% of surface; solid line) and shoot area index (SAI, cm^2/cm^2; dashed line) of three mosses in September (n=3) and December (n=5). Redrawn from van der Hoeven *et al*. 1993.

Figure 63. ***Marchantia palacea*** var. ***diptera***, a species that increases its growth rate with increasing light intensity. Photo by Janice Glime.

Physiological Adaptations to Low Light

Although bryophytes in general seem to be shade adapted, at least in their chlorophyll ratios, there are still differences among the species that adapt them to different habitats or give them a competitive edge. For example, ***Plagiomnium acutum*** (Figure 64) has greater capacity to absorb and use low light, giving it a greater photosynthetic assimilation efficiency than its associate ***Herpetineuron toccoae*** (Figure 65) in shady and wet habitats (Li *et al* 1999).

Figure 64. ***Plagiomnium acutum***. Photo by Yingdi Liu, with permission.

Figure 65. ***Herpetineuron toccoae*** leafy plants with sporophytes. Photo with permission by Li Zhang at <www.hkflora.com>, with permission.

Buryová and Shaw (2005) affirmed that light treatments had a greater effect of growth and other characters of ***Philonotis fontana*** (Figure 66) than did water. Different populations, representing different genetic variants, exhibited different patterns of plasticity of form. Variation of leaf dimensions had a strong genetic component (20-30% of total variation), but cell dimensions (Figure 67) seemed to have little genetic variation.

Figure 66. ***Philonotis fontana***, a species in which growth rate is affected by light intensity more than by water. Photo by Des Callaghan, with permission.

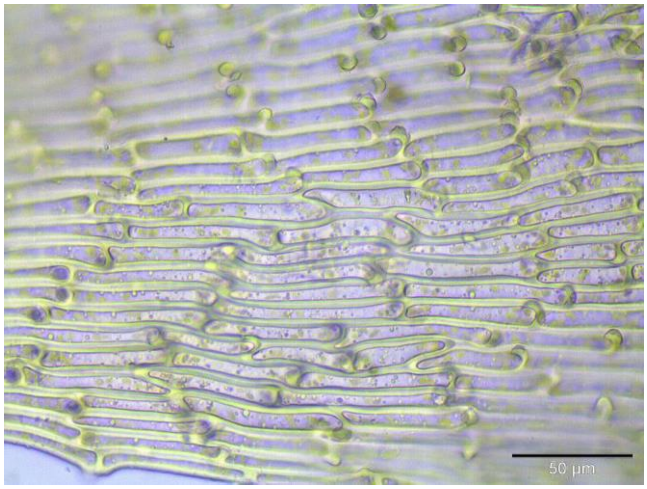

Figure 67. ***Philonotis fontana*** leaf lamina showing prorate cells. These cells have little genetic variation. Photo by Kristian Peters through Creative Commons.

But what are the characteristics that enhance photosynthesis in bryophytes? Waite and Sack (2010) examined ten Hawaiian bryophyte species and quantified 35 physiological and morphological traits. The moss species, typical of shade species, exhibited low leaf mass per area and low gas exchange rate. But their light-saturated photosynthetic rate per mass did not correlate with habitat light intensity. Instead, using canopy mass, not leaf mass, other photosynthetic parameters and morphological traits did correlate with microhabitat light characters. This relationship resulted in an inter-correlation of leaf area, cell size, cell wall thickness, and canopy density. Furthermore, structural allocations such as costa size, canopy height, and mass were linked with these modifications.

Chlorophyll

Bryophytes are C_3 plants. As such, they are adapted to light capture at low light intensities. In tracheophytes, the primary adaptation to low light is to increase the antenna pigment chlorophyll *b*. This provides more opportunities to trap light energy reaching the leaf and to transmit it to the action site of chlorophyll *a*. Sluka (1983) supported the concept of increased chlorophyll concentrations at low light intensities in bryophytes by showing that total chlorophyll content of mosses is inversely proportional to light intensity. As in tracheophytes, it is chlorophyll *b* that increases in response to low light. Szarek (1994), working in the High Tatra Mountains of southern Poland, found that higher light intensities in the middle reaches of the stream did not have any effect on chlorophyll *a* concentrations of mosses compared to areas with less light.

In tracheophytes, this increase in chlorophyll *b* results in a lower *a*:*b* ratio. Thus, it is not surprising that bryophytes, as predominantly shade plants, typically have a low *a*:*b* ratio compared to tracheophytes. Mishler and Oliver (1991) reported *a*:*b* ratios of 1.00-2.5 for the xerophytic moss ***Syntrichia ruralis*** (Figure 36), a desiccation-tolerant moss that likewise has a higher chlorophyll concentration at low light intensities (Hamerlynck *et al*. 2002). Nevertheless, these *a*:*b* ratios, even for sun-grown plants, were typical of shade-adapted tracheophytes, whereas the carotenoid:chlorophyll ratio of sun plants was typical of sun-adapted tracheophytes. These acclimation responses reversed in a reciprocal transplant experiment, indicating that this species is capable of making short-term adjustments. Nevertheless, transplanted sun plants of ***S. ruralis*** did not perform as well in shade as did previously shade-grown plants. Hamerlynck *et al*. (2002) considered this to indicate that the sun-acclimated plants were able to maintain their photoprotective mechanisms, losing them only slowly, whereas the shaded plants were able to maintain activity longer, due to greater moisture, allowing them to adjust to changes rapidly following disturbance that exposed them to greater sunlight. This ability to adjust permits them to persist in their semi-arid grassland home.

Tuba (1987), as already discussed, has a different explanation. He suggests that these low *a*:*b* ratios are important because poikilohydric plants must depend on atmospheric moisture to regulate their internal water content and that such moisture is most typically available during periods of low light – during a storm or early morning. Since these plants are often desiccated during periods of high light levels, Tuba suggests that it is logical that their chlorophyll is adjusted to low light levels, but that having light compensation points slightly higher than those of shade-adapted tracheophytes permits bryophytes to benefit from occasional sunflecks.

It therefore comes as a surprise to find that the chlorophyll *a*:*b* ratio in many bryophytes does not decrease in response to low light, while the total chlorophyll increases. For example, in experiments on three species of the thallose liverwort ***Riccia***, the highest chlorophyll concentrations occurred in the shade-grown ***Riccia discolor***, and the lowest occurred in the floating aquatic species, ***Riccia fluitans*** (Figure 68), as one would expect. But surprisingly, the chlorophyll *a*:*b* ratios did not differ among the species (Patidar *et al*. 1986). In ***Sphagnum fimbriatum*** (Figure 69), both chlorophyll *a* and chlorophyll *b* increased in dim light; in dim light at 25ºC, the *a*:*b* ratio increased only slightly, while at 15ºC, no such increase was observed (Koskimies-Soininen & Nyberg 1991). Similarly, Rincòn (1993) compared six species of bryophytes under seven different light conditions and found, as expected, that the total chlorophyll was highest at the lowest level of light, but that the chlorophyll *a*:*b* ratio did not differ significantly among the treatments.

Figure 68. Terrestrial form of ***Riccia fluitans***. Photo by Michael Lüth, with permission.

Figure 69. ***Sphagnum fimbriatum***, a species that increases both chlorophylls *a* and *b* in low light. Photo by J. K. Lindsey, with permission.

Yang and coworkers (1994) found that seventeen species of bryophytes at Yuan-Yang Lake in China had lower chlorophyll *a*:*b* ratios (mean 2.41) than the two aquatic tracheophytes sampled (mean 3.08), but that these bryophyte ratios were considerably higher than values for bryophytes reported in the literature. They considered this to be a demonstration of the ability of bryophytes to adjust their chlorophyll *a*:*b* ratio within a limited range to a higher light intensity (250 µmol m^{-2} s^{-1}).

As discussed earlier in the study by Marschall and Proctor (2004), chlorophyll content seems to account for liverworts being more common in shade, with more mosses able to survive in bright, open areas. Pande and Singh 1987) found higher concentrations of both carotenoids and chlorophyll in liverworts, with the exception of ***Stephensoniella brevipedunculata***, compared to mosses, but in this study liverworts all came from shade and mosses from open areas. Doera and Chaudhary (1991) examined

chlorophyll content of several bryophytes and found that chlorophyll *a* ranged 0.402 ± 0.052 to 2.002 ± 0.700 mg g^{-1} dry mass, with chlorophyll *b* ranging 0.265 ± 0.067 to 1.634 ± 0.070 mg g^{-1}. Lowest chlorophyll concentrations were found in the moss ***Entodon prorepens*** (Figure 70) (0.667 mg g^{-1} dry mass) and highest in the liverwort ***Cyathodium tuberosum*** (Figure 71) (3.636 mg g^{-1} dry mass), consistent with the observations of Marschall and Proctor (2004). In these bryophytes, low light intensity resulted in increase in total chlorophyll content and lower chlorophyll *a*:*b* ratio. On the other hand, Antarctic populations of ***Ceratodon purpureus*** (Figure 12) can decrease chlorophyll *a*:*b* ratios in high light (Post 1990). Is it any surprise that these responses are not always the same, that they differ with species, temperature, moisture content, and light level?

Figure 70. ***Entodon prorepens***, a species with low chlorophyll concentrations. Photo by Li Zhang, with permission.

Figure 71. ***Cyathodium cavernarum***, a species with a high concentration of chlorophyll. Photo by M. C. Nair, through Creative Commons.

Mártínez Abaigar *et al*. (1993) have compared the chlorophyll concentrations on a per unit area basis. Their results, compared to light and water availability, appear in Table 2. Examination of the table does not reveal any relationship among these species with either light availability or water availability and chlorophyll concentration. However, there seems to be a good correlation between chlorophyll concentration and submersion. Only ***Schistidium rivulare*** (Figure 72-Figure 73) among the emergent taxa has a high chlorophyll concentration. This might be explained by the dark coloration of the cell walls that would filter the high light intensity before it reaches the chlorophyll.

Figure 72. ***Schistidium rivularis*** exposed on rock and illustrating its black coloration. Photo by Janice Glime.

Figure 73. ***Schistidium rivularis*** with sporophyte, showing blackish coloration. Photo courtesy of Betsy St. Pierre.

Table 2. Chlorophyll concentrations as mg m^{-2} for bryophyte species occurring in full sun, sun, shade, and deep shade and five water availabilities (I = immersed, E = emerged, D = dry; LSA = Leaf Specific Area, LSW = Leaf Specific Weight). Species are arranged from highest to lowest chlorophyll concentrations. From Mártínez Abaigar *et al*. 1993.

	chl mg m^{-2}	light availability	water availability	LSA cm^2 g^{-1}	LSW mg cm^{-2}
Schistidium rivulare	351±17	full sun	I-E-D	133±7	7.51±.4
Fontinalis squamosa	341±14	sun	I	271±13	3.7±.18
Fontinalis antipyretica	290±14	full sun	I	226±16	4.42±.31
Fissidens grandifrons	289±13	full sun	I	222±4	4.5±.08
Rhynchostegium riparioides	257±4	deep shade	I-E	224±9	4.47±.18
Cinclidotus fontinaloides	250±13	full sun	I-E-D	164±15	6.11±.56
Cratoneuron filicinum	246±4	full sun	I-E-D	274±15	3.65±.2
Fissidens grandifrons	244±11	deep shade	I	211±8	4.73±.18
Jungermannia cordifolia	173±6	full sun	I	351±15	2.85±.12
Hygrohypnum duriusculum	157±8	full sun	I-E-D	313±25	3.2±.26
Scapania undulata	150±7	shade	I-E-D	262±10	3.81±.15
Cratoneuron commutatum	121±10	full sun	E	187±25	5.36±.72
Brachythecium rivulare	116±5	full sun	I	456±41	2.19±.2
Pellia endiviifolia	97±7	shade	E	446±15	2.24±.08

Figure 74. ***Schistidium rivulare***, exhibiting dark pigmentation. Photo by Michael Lüth, with permission.

Other Pigments

Other pigments also change in response to light intensity, as shown for ***Rhytidiadelphus triquetrus*** (Figure 44), ***R. squarrosus*** (Figure 47), and ***Mnium hornum*** (Figure 75-Figure 76) (Brinkmeier *et al*. 1999). In these mosses biflavonoid concentration was correlated with periods of active growth and varied with light intensity. The shade-adapted liverworts in Nainital, Kumaun Himalaya, exhibited higher carotenoid concentrations than did the mosses growing in the open (Pande & Singh 1987). However, the chlorophyll:carotenoid ratio seemed not to differ, at least during the rainy season, which is the period of maximum growth. It is reasonable that carotenoid content would be adaptive to shade plants because it can serve as an antenna pigment, much like chlorophyll *b*, providing additional light capture capability and transferring that energy to the chlorophyll *a* reaction center. Such an adaptation is known not only in bryophytes, but also in tracheophytes, where total carotenoid content and β-carotene increase simultaneously with chlorophyll in the shade (Czeczuga 1987). On the other hand, **lutein** (deep yellow pigment) increases in the sunlight.

Figure 75. ***Mnium hornum***, a species in which pigments change in response to light. Photo by Bob Klips, with permission.

Figure 76. ***Mnium hornum***, illustrating a lighter color that could be a response to different light conditions. Photo by Michael Lüth, with permission.

It is interesting that many of the pigments seem to vary together in concentration, at least in the Antarctic mosses tested (Lovelock & Robinson 2002). Total chlorophyll was correlated highly with total carotenoids (0.91), which in turn were highly correlated with each other (lutein and xanthophyll cycle pigments). **Anthocyanins** also correlated but somewhat less highly with chlorophyll. However, the photoprotective **zeaxanthin** and **antheraxanthin** were negatively correlated with total chlorophyll, as one would expect if chlorophyll *b* increases in response to low light.

Several researchers have found that hydrated mosses, unlike tracheophytes, require only a few molecules of zeaxanthin per reaction center to dissipate light energy (Bukhov *et al*. 2001; Heber *et al*. 2005). Desiccation-dependent fluorescence quenching, however, is independent of zeaxanthin and appears to be a property of the reaction center complex of photosystem II rather than the antenna system.

Chloroplast Movement

In at least some mosses, the chloroplasts move in response to light direction. This ability of chloroplasts to orient themselves in response to direction of light, thus maximizing absorption of light energy, is known elsewhere in the plant kingdom. The green alga *Mougeotia* (Figure 77) has an axial chloroplast that can rotate on its axis to face the sun. Often the two ends seem to rotate independently so the chloroplast becomes twisted in the middle. The ferns *Adiantum capillus-veneris* (Figure 78), *A. caudatum* (Figure 79), *A. diaphanum* (Figure 80), and *Pteris cretica* (Figure 81) all exhibit chloroplast movement in their leaves, responding to blue light; *A. capillus-veneris* chloroplasts also responded to red light (Augustynowlcz & Gabrys 1999). The prothallus of the fern *Dennstaedtia punctiloba* (Figure 82-Figure 83), growing in lava caves, exhibits a luminescence similar to that seen in the moss ***Schistostega pennata*** (Figure 2-Figure 4) (Glime & Iwatsuki, pers. obs.). In ***Schistostega pennata***, chloroplasts of the protonemata orient themselves to attain maximum light, as discussed in the light subchapter on cave mosses.

Figure 77. ***Mougeotia*** sp, a genus with a flat chloroplast that rotates on its axis to respond to position of incoming light. Photo by Yuuji Tsukii, with permission.

Figure 78. ***Adiantum capillus-veneris***, a species in which leaf chloroplasts move in response to the direction and intensity of light. Photo by Tigerente, through Creative Commons.

Figure 79. ***Adiantum caudatum***, a species in which leaf chloroplasts move in response to the direction and intensity of light. Photo by Guz Hengman, through Creative Commons.

Figure 80. ***Adiantum diaphanum***, a species in which leaf chloroplasts move in response to the direction and intensity of light. Photo by Phil Bendle, with permission.

Figure 81. ***Pteris cretica***, a species in which leaf chloroplasts move in response to the direction and intensity of light. Photo by Forest and Kim Starr, through Creative Commons.

Figure 82. ***Dennstaedtia punctilobula***, a species in which the gametophyte prothallus chloroplasts move in response to the direction and intensity of light, giving them a luminescence similar to that of ***Schistostega pennata***. Photo by John Knouse, through Creative Commons.

Figure 83. ***Dennstaedtia punctilobula*** luminescent prothalli from a lava cave in Iceland. Photo by Janice Glime.

In protonemata of the moss ***Physcomitrella patens*** (Figure 84), the direction of light, intensity, and wavelength are all important to chloroplast arrangement. When the light is perpendicular to the protonema axis the chloroplasts accumulate next to the crosswalls, but when it is parallel to the protonema axis, *i.e.* perpendicular to the crosswalls, there is no accumulation of chloroplasts there (Kadota *et al*. 2000). The response depends on the intensity, with lower intensities (red light 0.118 W m^{-2} or blue light 0.01-85.5 W m^{-2}) inducing accumulation, whereas higher ones (red light $\geq$ 60 W m^{-2} or blue light 285 W m^{-2}) do not. These responses are mediated by phytochrome. But the protonemata of ***Physcomitrella patens*** respond not only to the direction of light (Kadota *et al*. 2000), but also to mechanical stimuli (Sato *et al*. 2003). This causes the chloroplasts to accumulate on the side of the cell where contact is made – in as little as 30 minutes! Could this be an adaptation to high light by placing the chloroplasts on the side next to the substrate and therefore on the side farthest from the light source? Such a position would provide more cytoplasm to serve as a filter from UV light and high light intensity. On the other hand, it would also permit the side toward the sun to act as a focussing lens. There is so much we don't know!

Figure 84. ***Physcomitrella patens*** plants with their protonemata on the left. Photo by Michael Lüth, with permission.

Movement of chloroplasts is a response to blue light intensity (Königer 2014). In low light, they spread out, maximizing light interception. In high light, they move to the sides of the cells in an avoidance reaction, minimizing light interception. But most mosses may be slower to react or not react at all. ***Physcomitrella patens*** (Figure 84) had no net change in light transmission under increasing blue light intensities up to one hour at 100 µmol photons m^{-2} s^{-1}. The fern *Adiantum capillus-veneris* (Figure 78) likewise showed no accumulation response and only a slow avoidance response. The tracheophyte *Arabidopsis thaliana* (Figure 85), on the other hand, exhibited both strong accumulation and avoidance responses.

Figure 85. ***Arabidopsis thaliana***, a species that exhibits both strong accumulation and avoidance responses to increasing levels of blue light. Photo by Nicole Hanley, through Creative Commons.

Light and Storage

The ultimate consequence of changing chlorophyll concentrations and chloroplast position is an altered ability to store photosynthate. Kobe and Silander (1993) have shown that in four trees adapted to low light intensities, survivorship of juveniles in low light conditions is positively related to carbohydrate reserves and inversely related to high-light growth. This demonstrates the importance of storing carbohydrates as opposed to using all of them for growth during periods of high light. Such correlations have not been tested for bryophytes, but may relate to storage of carbohydrates in the spring before the canopy foliage appears for use of the developing sporophyte during the summer and autumn. Kobe and Silander contend that the trade-off between storage and growth relates to survivorship in low-light habitats. Rincòn and Grime (1989) have shown that production of biomass is not correlated with shoot extension in five grassland bryophytes, and that it in fact can be an inverse relationship, with shoot extension occurring later, again indicating the importance of storage. Could this be related to the ability to store carbohydrates for use later in low light when IAA may facilitate more elongation? (IAA is inhibited by light in tracheophytes.)

In ***Sphagnum fimbriatum*** (Figure 87) low light caused increased storage of total lipids (Koskimies-Soininen & Nyberg 1991). However, in darkness, as one might expect, lipid content decreased. When low light was accompanied by a decrease in temperature, the moss stored more palmitic, stearic, linoleic, and arachidonic acids in the galactolipids monogalactosyl diglyceride (MGDG), *i.e.* the chloroplast lipids. At the same time, oleic and α-linolenic acids decreased. The MGDG lipids are important in cold hardening and adjustment of plant metabolism to low temperatures. For example, arachidonic acid has a freezing point of -49.5^{o}C (Gellerman *et al.* 1972), thus maintaining membrane fluidity at any temperature these mosses are likely to experience in nature. Karunen (1982) suggested that the presence both of high quantities of angiospermous type galactolipid fatty acids and the lowest quantities of algal type in the aquatic moss ***Fontinalis*** (Figure 86) had evolutionary significance in placing this as an advanced genus, at least biochemically.

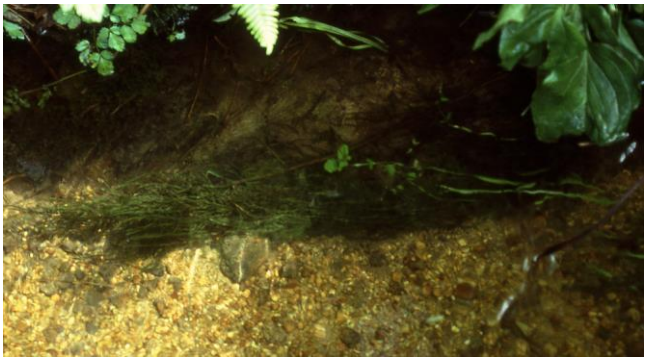

Figure 86. ***Fontinalis duriaei***, a species with high quantities of flowering plant type galactolipid fatty acids and very low quantities of the algal type. Photo by Janice Glime.

Figure 87. ***Sphagnum fimbriatum***. Photo by Michael Lüth, with permission.

One cannot generalize from these results, however. When Koskimies-Soininen and Nyberg (1991) compared their results for the shade plant ***Sphagnum fimbriatum*** (Figure 87) with similar experiments on the high light species ***Sphagnum magellanicum*** (Figure 19), the responses to light and temperature were different. At low temperatures, ***S. fimbriatum*** does not increase its unsaturated glycolipids, reaching its lowest level at 10ºC, whereas ***S. magellanicum*** reaches its lowest level at 0ºC. In fact, we should expect differences among species, as these are the very things that make many species become species. For example, Li and coworkers (1999) compared photosynthesis of ***Plagiomnium acutum*** (Figure 64) and of ***Herpetineuron toccoae*** (Figure 65) under different weather conditions. Photosynthesis of ***P. acutum*** was lower on sunny days than that of ***H. toccoae***, but on cloudy and rainy days it was higher. They determined that ***P. acutum*** has a higher CO_2 assimilation efficiency in shady and wet habitats. Working with mosses on semi-arid granitic boulders, Alpert and Oechel (1987) also found that species occurring in microhabitats with lower light availability had a higher rate of net photosynthesis at low photon flux densities than did other mosses from that site, suggesting a higher chlorophyll concentration.

Based on the literature, it appears that photosynthetic rates of mosses are considerably less than those of tracheophytes. This is consistent with their slow growth rates. For example, in comparing the shade liverwort ***Marchantia polymorpha*** (Figure 88) with the sun moss ***Ceratodon purpureus*** (Figure 37), Aro and coworkers (1981) found that the plastid ultrastructures of these two bryophytes were characteristic of shade and sun plants respectively, but both exhibited the photosynthetic rates typical of shade plants. But Martin and Adamson (2001) disagree with the method of representing these determinations of photosynthetic rates in bryophytes. They found that indeed the CO_2 uptake rate (*i.e.* photosynthetic rate) is much lower than that of tracheophytes when expressed per unit of biomass, but when they used the rate per chlorophyll concentration to compare maximum photosynthetic rates of bryophytes vs tracheophytes under the same conditions of light saturation and ambient CO_2, the photosynthetic rates between bryophytes and tracheophytes did not differ (Shouldn't we expect that?)

The chlorophyll seems to behave the same way in both; it is the concentrations of chlorophyll that differ.

Figure 88. ***Marchantia polymorpha*** with archegoniophores, a shade plant with plastids characteristic of shade plants. Photo by Rudolf Macek, with permission.

Forest Gaps

Forest gaps are well known to foresters as sites where trees experience release growth, expressed in larger tree rings and greater annual production. Wayne and Bazzaz (1993) explored the relative effects of forest gaps compared to shadehouses on two species of birch [*Betula populifolia* (Figure 89) and *B. alleghaniensis* (Figure 90)] and found that leaf structure (specific leaf mass, leaf mass ratio) in shadehouses more closely resembled that of sun plants than did that of the gap-grown plants, but that gap-grown plants behaved more like sun plants in chlorophyll *a*:*b* ratios and maximum net photosynthesis.

Figure 90. ***Betula alleghaniensis***, a forest gap species that exhibits chlorophyll *a*:*b* ratios and max net photosynthesis of sun plants when living in gaps. Photo by Keith Kanoti, through Creative Commons.

Despite their adaptations to low light, many bryophytes also benefit from the brighter spots in the forest. Even in the relatively open forest types like spruce (Figure 53), light attenuation between canopy and forest floor can be considerable (Figure 93) (Tuba & Nyilas 1980). In stands of *Pseudotsuga menziesii* (Figure 91) and *Tsuga heterophylla* (Figure 92) in Oregon, USA, bryophyte abundance increases in canopy gaps and other places with a higher irradiance within the forest (Rambo & Muir 1998).

Figure 89. ***Betula populifolia*** leaves, a forest gap species that exhibits chlorophyll *a*:*b* ratios and max net photosynthesis of sun plants when living in gaps. Photo by Richtid, through Creative Commons.

Figure 91. ***Pseudotsuga menziesii*** & Pinus ponderosa forest showing difference in light at the top of the canopy and in lower parts of the canopy. Photo by Jsayre64, through Creative Commons.

Figure 92. ***Tsuga heterophylla*** forest in Alaska showing the reduced light reaching the forest floor. Photo by Willow and Monk, through Creative Commons.

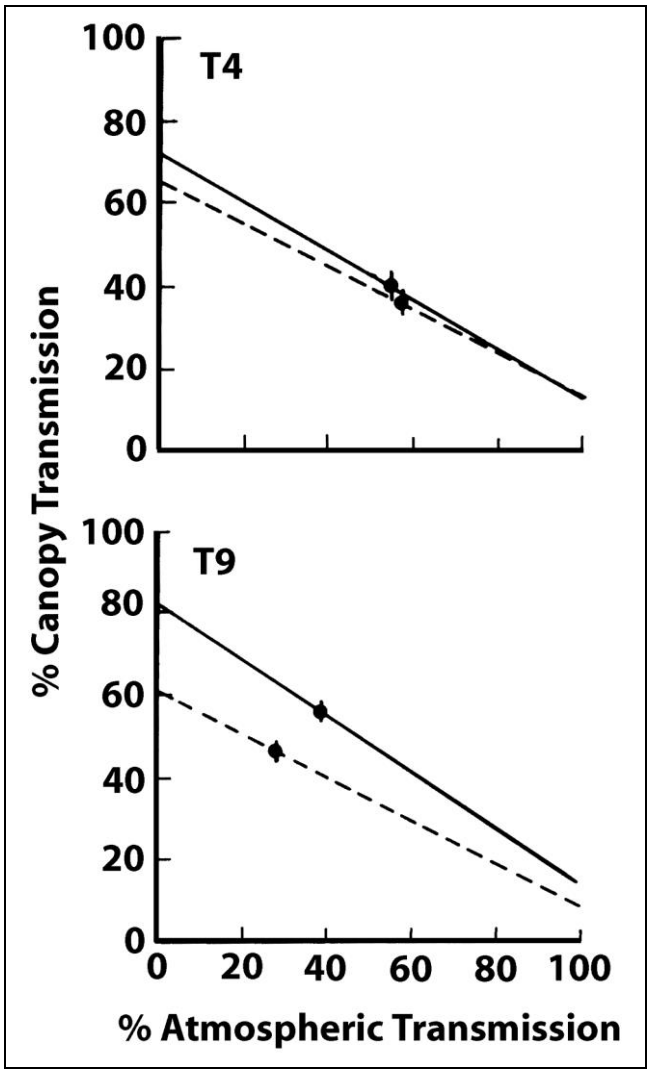

Figure 93. Linear regression of transmission of canopy light to forest floor as a % of atmospheric radiation, expressed as a % of radiation incident on the atmosphere. T4 and T9 are two sites in a mature black spruce forest in central Alaska. In transect 4 ── represents 68% canopy closure; - - - represents 36% canopy closure. In transect 9 ── represents 49% canopy closure; - - - represents 33% canopy closure. Figure redrawn from Skré *et al*. 1983.

For bryophytes, forest gaps provide periods of high intensity light that for some species can enhance growth, while for others the additional desiccation and high temperatures can mean cessation of growth. However, in the margins of the gaps, where sunlight is intermittent during the day, bursts of sun, or sunflecks, can be significant contributors to the productivity. Studies on vascular plants suggest that responses to light gaps having intermittent light can be significantly different from continuous low or high light (Wayne & Bazzaz 1993). There are few studies on bryophytes to explore the importance of sunflecks within the forest or the effect of intermittent light in gaps. Yet, in many temperate forests, such intermittent light may be more the rule than the exception. Wayne and Bazzaz (1993) suggest that the plasticity of response by some species to intermittent light may have potential for niche differences and coexistence. Such studies should not be difficult to do on bryophytes using either laboratory conditions or strobe lighting in the field, and with modern electronic recording equipment, even natural sunflecks can be recorded and productivity monitored..

But not all gaps are beneficial to bryophytes. Brunkman (1936) puzzled over the presence of ***Hylocomium splendens*** (Figure 51) in some of the *Myrtillus* associations but not others. After careful quadrat study, he learned that the ***Hylocomium splendens*** all but disappeared within four years of cutting the forest. He attributed this disappearance to light, since the soil was "decidedly wet," allowing for the indirect effect of sunlight on the available moisture. Since he found the uncut forest to be just as wet as the cut forest, he concluded that light was the factor resulting in the loss of ***H. splendens*** in the open. He likewise cited differences in moss cover between north and south slopes (71% and 3%, respectively) as evidence that light was the critical factor. He reasoned that the south slope would have a much longer light day and light season than the north slope. On the other hand, ***Hylocomium splendens***, ***Pleurozium schreberi*** (Figure 41), and ***Hypnum jutlandicum*** (Figure 52) commonly occur in the gaps formed by degenerate *Calluna vulgaris* (Figure 94) bushes in the dry heathland (Scandrett & Gimingham 1989), so it appears that they can benefit from more light under the right conditions.

Figure 94. ***Calluna vulgaris*** showing reduced cover in areas with shorter or dying plants. Photo by Willow, through Creative Commons.

In one North American forest, where a storm had uprooted nearly half the trees, moss cover disappeared rapidly, whereas in the part where trees remained upright, the moss cover was nearly normal (Brunkman 1936). Brunkman (1936) further cited evidence from two adjacent plots, one of spruce (Figure 53) with 85% mean cover of moss on 16 quadrats and another of poplar (*Populus*, Figure 95) with 6% mean cover on 16 quadrats. Then he compared the densities of the trees on these and other plots in an attempt to correlate the light availability with decrease in moss cover. To his surprise, no correlation existed. To explain this anomaly, he considered the fact that poplar is lacking leaves for eight months of the year, whereas spruce is never without leaves. While Brunkman seemed uncomfortable with the lack of correlation, he still considered that tree density was important above 0.5, and he concluded that densities above 0.8 have high moss cover, the lowest being 59%. He noted that in light gaps, the moss cover would be moderate to high, and the flora of flowering plants would include a "decidedly larger number of individuals."

Larsen (1980) contends that if a gap occurs in a boreal spruce forest (Figure 53), the spaces are occupied to a greater extent by herbaceous species and moss cover will diminish. It appears that the relationship of moss cover to light availability may be complicated by the availability of suitable species and the length of time since the light became available. In any event, the species occupying the lighted gap will be different from those occupying the forest before the opening was created (Larsen 1980).

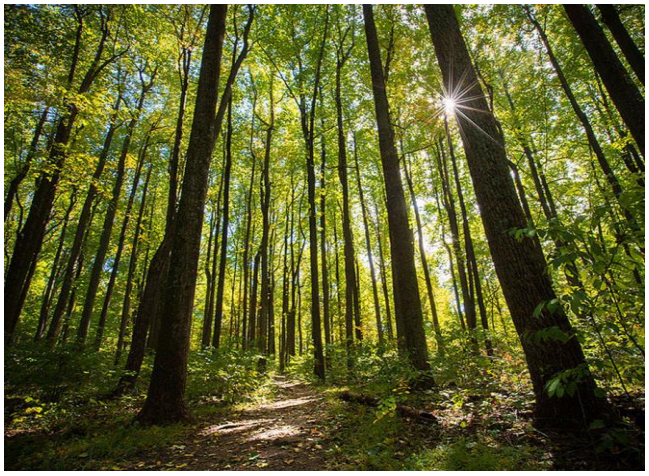

Figure 95. ***Populus*** forest showing sunflecks on the forest floor. Photo from Shenandoah National Park, through Creative Commons.

In an attempt to determine the importance of "reserve trees" to forest management, Shields (2006) examined not only the woody and herbaceous plants in openings with a single central tree (reserve tree) to those of the forest matrix in uneven-aged northern hardwood forests (Figure 96) in the Upper Peninsula of Michigan, but also the bryophytes. He found that bryophyte cover in the opening was only one-third that of the forest matrix, with four species [***Marchantia polymorpha*** (Figure 88), ***Pleurozium schreberi*** (Figure 13), ***Ptilidium pulcherrimum*** (Figure 97), ***Sphagnum*** sp. (Figure 98)] disappearing completely. ***Brachythecium*** spp. (Figure 99) and ***Atrichum undulatum*** (Figure 100) both decreased in importance as the opening size increased. These disappearances most likely involved several factors. Not only did the light increase in the opening, but temperature increased and moisture decreased. Furthermore, substrate availability changed, with coarse woody debris being less available in the cutover openings than in the forest matrix.

Figure 96. Northern hardwood forest in northern Michigan. Photo by Janice Glime.

Figure 97. ***Ptilidium pulcherrimum***, a species sensitive to sun exposure, on a log. Photo by Michael Lüth, with permission.

Figure 98. ***Sphagnum girgensohnii*** in spruce forest, a species that disappears in forest openings. Photo by Michael Lüth, with permission.

Figure 99. ***Brachythecium salebrosum***, a species that decreases in importance in forest gaps. Photo by Michael Lüth, with permission.

Figure 100. ***Atrichum undulatum***, a species that decreases in importance in forest gaps. Photo by Michael Lüth, with permission.

Sunflecks

Sunflecks (Figure 95; Figure 101), those tiny patches of bright light that dance about on the forest floor, have reached a new level of importance in our understanding of forest floor dynamics. Skré *et al*. (1983) found that up to 35% of the forest floor in a black spruce (*Picea mariana*, Figure 53) forest in central Alaska could experience sunflecks at the midday soil surface. These flecks usually had an intensity ~76% that of the light reaching the forest canopy and were the major source of light for bryophytes there. Such sunflecks are known to provide for photosynthesis in exposed parts of clones with the resultant photosynthate translocated to shaded parts of the connected clone internally.

For bryophytes, sunflecks have an advantage over full sunlight because of that intermittence (remember how we measure Vmax? The least disturbance of the canopy changes their position, thus striking different branches or patches of bryophytes. For a photosynthetic bryophyte leaf, this means relief from the constant bombardment of light energy on the chlorophyll molecules and prevents these low-light adapted plants from suffering from excitation damage. The light dances about from ramet to ramet as it does from leaf to leaf on the trees. Rincòn and Grime (1989) found sunflecks to be very important for six bryophytes from a variety of habitats and referred to the ability of bryophytes to be plastic in rate and direction of shoot proliferation as a "foraging" mechanism that permitted them to exploit resources where they became available, in this case, sunflecks. Bergamini and Peintinger (2002) found a similar foraging behavior in ***Calliergonella cuspidata*** (Figure 102) and contended that pleurocarpous mosses have a morphological strategy comparable to the "spacer and branching" strategy of some stoloniferous tracheophytes. Even such upright mosses as ***Polytrichum*** are known to have interconnected ramets that translocate photosynthate to one another.

Figure 101. ***Hylocomium splendens*** in a sunfleck. Photo courtesy of Carrie Andrew.

In the heavily shaded sites of New Zealand, the hornwort ***Megaceros pellucidus*** (Figure 103) experiences a maximum photon flux density of less than 10 μmol m^{-2} s^{-1} (Watkins *et al*. 2011). Daylight sees only weak variation in intensity. The dense canopy provides little opportunity for sunflecks. Interestingly, hornworts from low light conditions (0.2 μmol m^{-2} s^{-1}) had the same carotenoid concentrations as those from higher light conditions (6.9 μmol m^{-2} s^{-1}), but the chlorophyll content of high light plants was approximately 2X that of low light plants, whereas the chlorophyll *a*/*b* ratio was the same in both low and higher light conditions. A significant difference is that in low light the hornworts exhibited an absorbance band at 340 nm that was not present in the higher light conditions.

Figure 102. ***Calliergonella cuspidata*** with lateral branching pattern that permits foraging of the sunlight. Photo by Michael Lüth, with permission.

Figure 103. ***Megaceros pellucidus***, a species that lives in very low light levels in New Zealand forests. Photo by Scott Zona, through Creative Commons.

Figure 104. ***Cryptothallus mirabilis*** with sporophytes protruding from its peat substrate. This liverwort completely lacks chlorophyll and depends on a fungus to obtain its energy. Photo by Michael Lüth, with permission.

Litter Burial

Of course the most drastic effect of the forest canopy on the bryophytes of the forest floor is the virtually total loss of light caused by leaf litter (Figure 1). Although there may be allelopathic effects from the decomposition of leaves that leads to the release of tannins, loss of light is ultimate death to nearly every plant. Johnsen (1959) demonstrated the severity of litter on bryophytes by showing that raking away litter can greatly increase both number of species and cover of bryophytes on the forest floor. It is the leaf litter that relegates the bryophytes to the steep slopes, tip-up mounds, and other places where leaf litter cannot easily accumulate.

The Partnership Choice

While many bryophytes suffer from self-shading that prevents the lower leaves from photosynthesizing, one species actually lives in that shaded habitat, receiving little or no light due to the surrounding moss vegetation. This species is the thallose liverwort ***Cryptothallus mirabilis*** (Figure 104). Its name tells much of its story, for it is indeed a hidden thallus, growing beneath the surface in peat, raw humus, or moss carpets (Schofield 1985), yet miraculously surviving in the darkness there. It is totally lacking in chlorophyll (Potemkin 1992); even its spores lack chlorophyll (Hill 1969). It obtains its carbon through a fungal partnership (Malmborg 1933; Airy Shaw 1949; Ligrone *et al*. 1993; Bidartondo *et al*. 2003), although it may not contribute anything to the relationship. It appears that it subsists much like the flowering Indian pipe (*Monotropa uniflora*, Figure 105), actually being a third member in a parasitic relationship with trees, including *Betula* (Figure 89-Figure 90), that reach the canopy to convert light energy into stored energy in the photosynthate (Bidartondo *et al*. 2003). The photosynthate is transferred from the tree to the fungus to the liverwort.

Figure 105. ***Monotropa uniflora***, a hemiparasitic flowering plant that uses a fungus to connect to carbon sources. Photo by Magellan, through Creative Commons.

Summary

In general, bryophytes are adapted to low light, relative to other land plants. Bryophyte cells may act as lens cells, at least in some cases, focussing light on the chloroplasts or even on leaves beneath them. Branches may behave like leaves in scattering, focussing, and reflecting light while providing air spaces that give access to CO_2. Papillae may serve to scatter light when the leaves are dry or to channel it like a fiber optic when wet. But these are all speculations.

The **leaf area index** (**LAI**) of bryophytes appears to be enormous compared to that of tracheophytes (44-129 compared to 3.8 for the forest floor taxa). Perhaps

the branch should be considered instead of the leaves of bryophytes. This same density of leaves results in considerable self-shading, with rapid light extinction within a moss cushion. Light often penetrates deeper in dry mosses, in some cases reaching a level where sufficient hydration exists for photosynthetic activity. Chlorophyll likewise diminishes with depth in a cushion, but this may be a function of age rather than light intensity, at least in some species. Dense packing of stems does not usually seem to deter vertical growth and may actually enhance it through greater conservation of water, despite the attenuation of light. On the other hand, densely overlying mosses seem to benefit from thinning that exposes underlying branches to more light. It appears that light is more important than hydration at determining optimal density.

As in tracheophytes, leaf morphology may respond to shade by such changes as broader leaves. Even leaf weight may decrease as less light becomes available. Other responses to low light are similar to those of tracheophytes, with increased chlorophyll *b* and antenna pigments, depressed light saturation and compensation points, and deeper green color. However, some bryophytes at least do not have a lower chlorophyll *a*:*b* ratio in low light compared to high light, as would the typical tracheophyte. Rather, bryophytes in general have a lower chlorophyll *a*:*b* ratio in all light conditions than do tracheophytes. This suggests that the bryophyte, with its chlorophyll *a* concentrations maintaining proportionality to chlorophyll *b* concentrations, would be ready for brief opportunities when bright light becomes available. Such a strategy would adapt these plants well to the forest habitat where so many are residing, permitting them to take advantage of changing positions of the sun as it filters through trees and brief bursts of light as **sunflecks** when angle of the sun changes or the wind changes the arrangement of the overarching canopy. These same adaptations would likewise permit mosses intertwined with grasses to one day be covered by a stem, but a few weeks later have grown past it to receive full light. Accessory antenna pigments such as carotenoids increase with chlorophyll *b*.

Some species have chloroplasts that move in response to direction of light, maximizing light absorption. In ***Physcomitrella patens***, chloroplasts accumulate on the side of the protonema where contact is made, presumably giving them maximum protection from light.

Reduction in photosynthesis in low light has its price in reduced storage of photosynthate. In bryophytes, storage can occur without growth, with growth occurring later based on stored reserves. Low light can also increase storage of lipids and temperature can alter the types of lipids being stored. Such adaptations differ among species, especially between sun and shade species.

Sunflecks provide bryophytes with bursts of bright light without the damaging effects of continuous bombardment of UV light and high light intensity on shade-adapted plants. Particularly in pleurocarpous mosses, the many branches provide "**foraging**" opportunities that permit production of photosynthate that can be translocated to other parts of the clone. Even the upright ***Polytrichum*** is able to translocate photosynthate from one stem to another in ramets of one connected clone.

Litterfall can completely bury bryophytes and put them in nearly total darkness. However, some bryophytes may benefit from litter in low-light conditions by forming fungal partnerships that acquire photosynthate from the surrounding leaf litter through this the fungus.

Acknowledgments

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CHAPTER 9-3

LIGHT: EFFECTS OF HIGH INTENSITY

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CHAPTER 9-3
LIGHT: EFFECTS OF HIGH INTENSITY

Figure 1. ***Encalypta rhabdocarpa*** in the alpine region where high-intensity UV light can damage chlorophyll and DNA. Photo by Michael Lüth, with permission.

Effects of High Light Intensity

Exposure to UV light has been hypothesized as a major deterrent of evolution to land. Both chlorophyll and DNA are easily damaged by high intensities of direct sunlight (Figure 1). In fact, it has been suggested that a major role of lignin, absent in bryophytes, is to protect cells against UV light. But it appears that the crafty bryophytes have a number of tools at their disposal.

Light and Moisture Relations

One danger of high light intensity in bryophytes is damage it can do to chlorophyll when the moss is dry. In experiments with a number of species, Churchill and Nelson (unpubl. report 1994; pers obs.) have found that the light intensity transmitted through a wet moss leaf is about twice that transmitted through a dry leaf. Takács *et al*. (2000) found that the non-chlorophyll blue-green fluorescence of ***Syntrichia ruralis*** (Figure 2) and two lichens increased by an order of magnitude upon drying. They attributed these changes in blue-green fluorescence to altered optical properties, not to any change in pigment or phenolic concentration. Lovelock and Robinson (2002) likewise found that the state of hydration affects the ability of the moss to absorb or reflect light. This increased reflection and decreased absorption by the dry leaf should provide at least some protection from damaging effects of UV radiation that could destroy chlorophyll and damage DNA. It suggests that there may be internal and/or external scattering of light by dry moss, whereas wet moss has a

more homogeneous surface and interior, permitting light to travel with less scattering.

Figure 2. ***Syntrichia ruralis*** showing hyaline hair points that are drawn close to the stem when the moss is dry and leaves are twisted around the stem. Photo by Michael Lüth, with permission.

Hamerlynck and coworkers (2002) hypothesized that because of its strong desiccation tolerance characters, the moss ***Syntrichia ruralis*** (Figure 2) would be unable to acclimate to different light intensity regimes. However, they found that in this species sun plants had lower biomass, and lower tissue N, C, and chlorophyll concentrations than shade plants of the species (Figure 3). Interestingly, while the carotenoid:chlorophyll ratios of sun plants were typical of sun plants, they found that as in most bryophytes the chlorophyll *a*:*b* ratios were typical of shade plants. When transplanted to shade, sun plants were able to adjust to the lower light level by increasing their photosystem II yields; these yields decreased in shade plants transplanted to the sun. Conversely, sun plants transplanted to shade continued to be out-performed there by non-transplanted shade plants. They suggest that in this species, shade plants may be able to adjust relatively quickly to disturbance that exposes them to greater light and desiccation.

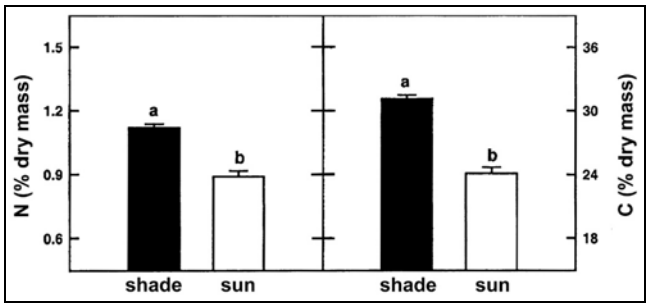

Figure 3. Comparison of N and C content of ***Syntrichia ruralis*** grown in shade and sun in Kiskunság National Park near Budapest, Hungary. Vertical bars indicate 1 SE; letters indicate significant differences ($p<0.05$). Redrawn from Hamerlynck *et al*. 2002.

Photoinhibition

Because high light intensities can damage chlorophyll, they can cause photoinhibition. Even sun plants like ***Sphagnum*** (Figure 49) are vulnerable. Shaded ***Sphagnum*** plants from temperate and Alaskan populations were given more light following removal of tracheophytes, and plants from full sun were shaded (Murray *et al*. 1993). Previously shaded mosses from both locations in the high-light treatment (800 μM m^{-2} s^{-1}) lost significant photosynthetic capacity in just two days and did not recover in the next 14 days. Increased variation in chlorophyll fluorescence relative to maximum fluorescence suggested this was a result of photoinhibition. By contrast, mosses that were moved from full sun to shade grew at a rate 2-3 times as great as that of those in control plots. Murray and coworkers suggested that the inability to acclimate might relate to low tissue N content of these mosses from low-nutrient habitats.

Bryophytes are limited on both ends of the light scale. At low intensities, they have insufficient energy to replace that lost by dark respiration and photorespiration, but on the other end they suffer chlorophyll damage and photoinhibition. Cleavitt (2002) demonstrated that this photoinhibition in ***Mnium spinulosum*** (Figure 4) restricted its occurrence to deeply shaded conifer stands, whereas ***Bryum pseudotriquetrum*** (Figure 5) was limited by its lack of desiccation tolerance. ***Mielichhoferia macrocarpa*** (Figure 6), on the other hand, occurred in the darkest and wettest sites, yet was tolerant of both high light intensities and desiccation. She showed that what we perceive to be narrow physiological limits that we would expect to limit rare species may not tell the whole story. It appears that our knowledge of light limits and adaptations, coupled with physiological responses of bryophyte tissues, needs additional study.

Figure 4. ***Mnium spinulosum***, a species restricted to deep shade. Photo by Jan-Peter Frahm, with permission.

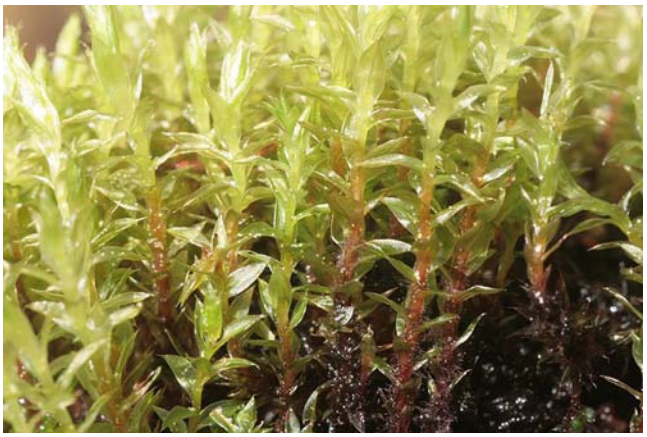

Figure 5. ***Bryum pseudotriquetrum***, a species limited by moisture. Photo by Hermann Schachner, through Creative Commons.

Figure 6. ***Mielichhoferia macrocarpa***, Robin Bovey, with permission from Dale Vitt.

In Antarctica, the bryophytes experience full exposure to sunlight in summer, but are at least partially protected by ice in winter (Post *et al*. 1990). This high summer exposure causes photoinhibition to be a major factor limiting productivity in these ecosystems. Post and co-workers have documented the damaging effects of low temperatures and high light on the bryophytes in this exposed polar environment. ***Schistidium antarctici*** (Figure 7) experiences daily changes in photosynthetic capacity, resulting from the changing environmental variables of light and temperature. (See also Chapter 11-2 of this volume.

Figure 7. ***Schistidium antarctici***, a species that changes its photosynthetic capacity daily in response to the variable Antarctic weather. Photo courtesy of Rod Seppelt.

Adaptations to High Light

When working with ***Pohlia wahlenbergii*** (Figure 8) from a subalpine area, Coxson and Mackey (1990) were surprised to find that it had a peak of photosynthesis at 8 mg CO_2 g^{-1} h^{-1} in the morning, declined to 5 mg CO_2 g^{-1} h^{-1} by late afternoon, then fully recovered by late evening. They considered that it might have full recovery from photodestruction of pigment complexes, but such a degree of photosensitivity would be unusual for plants living in high light environments. However, this would seem to be consistent with observations on ***Ceratodon purpureus*** (Figure 9) (Rintamaki *et al*. 1994). One of its mechanisms to tolerate high light is its rapid turnover of the D1 reaction center protein in photosystem II. In mosses such as ***Ceratodon purpureus***, this permits rapid replacement of light-damaged protein, thus serving as protection against photoinhibition. Once again, it seems the bryophytes have outdone the tracheophytes.

Figure 8. ***Pohlia wahlenbergii***, a species tolerant of high light. Photo by Michael Lüth, with permission.

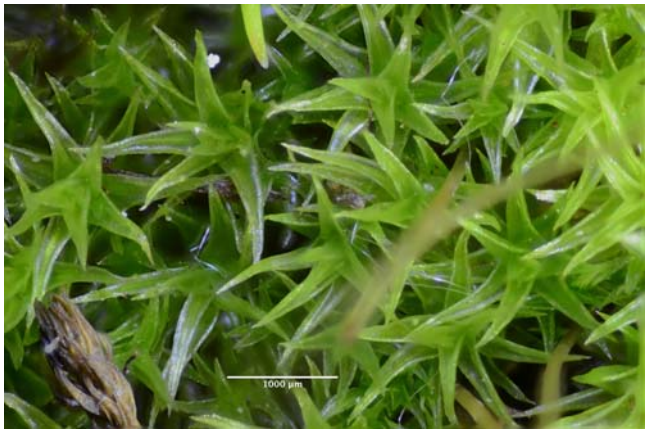

Figure 9. ***Ceratodon purpureus*** leaves, a species tolerant of high light. Photo by Don Loarie, through Creative Commons.

Plants adapt to high light either by structural adaptations or by protective pigments. Tracheophytes have protective epidermal layers, and in most groups there is a palisade layer beneath that epidermis that further serves to absorb light before it reaches the photosynthetic tissue of the spongy mesophyll. Bryophytes lack this structure. Hence, bryophytes must invest more in cellular level

protection to mitigate the damaging effects of high light intensity (Robinson & Waterman 2014). In some cases, the bryophytes use mechanisms already known in algae, such as thermal energy dissipation that is associated with the LHCSR protein, a mechanism no longer present in tracheophytes.

Structural Adaptations

Waite and Sack (2010) found that ten Hawaiian mosses did not demonstrate a correlation between habitat irradiance and light-saturated photosynthetic rate per biomass. However, they found that other photosynthetic parameters and structural traits (leaf area, cell size, cell wall thickness, and canopy density) were aligned with microhabitat irradiance. Furthermore, internally, high light can cause a decrease in thylakoid stacking (Post 1990).

Bryophytes often have filters that help to protect them from high light intensity. For example, several ***Polytrichum*** (Figure 10) species have **lamellae** (Figure 11) that are enclosed by the inrolled **lamina** (Figure 11) of the leaf, thus rendering the leaf a structure that is not very different from that of a deciduous tree. Others have leaves with **filaments** [***Crossidium*** (Figure 12-Figure 13)], **hyaline tips** [***Hedwigia ciliata*** (Figure 14-Figure 16), ***Bryum argenteum*** (Figure 17-Figure 18)], and **awns** [***Tortula*** (Figure 19-Figure 22), ***Syntrichia*** (Figure 2)] that overlap the next leaf and help to deflect light before it reaches the cell interior. Hyaline hair tips, partially covering adjoining leaves when dry (Figure 14, Figure 20), are spread out of the way of the photosynthetic tissue upon hydration (Figure 15, Figure 21).

Figure 10. ***Polytrichum juniperinum***, a species with lamellae and rolled over leaf edges. Photo by Janice Glime.

Figure 11. Leaf cross section of ***Polytrichum juniperinum*** showing leaf edge rolled over lamellae. Photo from Botany Website, UBC, with permission.

Figure 12. ***Crossidium aberrans***, a species with filaments on the leaves. Photo by Michael Lüth, with permission.

Figure 13. ***Crossidium aberrans*** leaves showing filaments on costa. Photo by Michael Lüth, with permission.

Figure 14. ***Hedwigia ciliata*** dry. Photo by Janice Glime.

Figure 15. ***Hedwigia ciliata*** wet. Photo by Robert Klips, with permission.

Figure 16. ***Hedwigia ciliata*** leaf showing transparent awn. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 17. ***Bryum argenteum*** showing tight leaves that overlap and protect each other from light damage. Note the white tips of each leaf. Photo by Michael Lüth, with permission.

Figure 18. ***Bryum argenteum*** leaves showing the hyaline upper half. Photo by Heike Hofmann © swissbryophytes <swissbryophytes.ch>, with permission.

Figure 19. ***Tortula brevissima*** showing partially appressed leaves in its dry habitat. Photo by Michael Lüth, with permission.

Figure 20. ***Tortula brevissima*** dry with twisted leaves and appressed. Photo by Michael Lüth, with permission.

Figure 21. ***Tortula brevissima*** wet, with spreading leaves. Photo by Michael Lüth, with permission.

Figure 22. ***Tortula brevissima*** leaf tip and awn. Photo by Heike Hofmann ©swissbryophytes <swissbryophytes.ch>, with permission.

Frey and Kürschner (1991) have demonstrated a correlation between "glass hairs" (Figure 13, Figure 18, Figure 16, Figure 22) and increasing aridity, suggesting that they could be useful as UV shields as aridity, and correlated light exposure, increase. Many taxa curl their leaves (Figure 23), wrap their leaves around the stem (Figure 20), or appress leaves (Figure 20) when dry, causing each leaf to help protect at least part of the next leaf. Structures such as papillae become more transparent when wet, typically doubling their ability to transmit light (Glime, unpubl. data). Short turfs likewise help to protect mosses from high light intensity through self-shading (Schofield 1985).

Epiphytes like ***Octoblepharum*** (Figure 24-Figure 25) and ***Leucobryum*** (Figure 26-Figure 27) have numerous hyaline cells that might help to filter the light before it reaches the photosynthetic cells. But I have seen no experiments that demonstrate if this really alters the light intensity. They could, instead, focus the light on the interior photosynthetic cells while serving as a water reservoir to maintain photosynthesis in a dry atmosphere.

Figure 23. ***Atrichum altecristatum*** drying, showing curling leaves compared to more moist expanded leaves in the background. Photo by courtesy of Eric Schneider.

Figure 24. ***Octoblepharum albidum***, a moss that shields its photosynthetic cells with hyaline cells. Photo by Janice Glime.

Figure 25. Cross section of ***Octoblepharum albidum*** leaf. Photo courtesy of Noris Salazar Allen.

Figure 26. ***Leucobryum glaucum*** with its typical whitish color due to hyaline cells in an upper and lower layer. Photo by James K Lindsey, with permission.

Figure 27. ***Leucobryum glaucum*** leaf cs showing hyaline cells surrounding the photosynthetic cells. Photo by Ralf Wagner <www.drralf-waner.de>, with permission.

In boreal wetlands, bryophytes have distinct spectral characteristics compared to those of tracheophytes in the visible, near-infrared (NIR), and short-wave infrared (SWIR, 1.50-2.50 µm) regions (Bubier *et al*. 1997). In the visible portion of the spectrum, these mosses exhibit typical absorption in the blue and red regions but differ from the tracheophytes in having a "green" peak reflective of the color (red, brown, or green) of individual species. The reflectance in the NIR region of mosses is usually less than in the tracheophytes, with strong water absorption features at ~1.00 and 1.20 µm, causing distinct reflectance peaks at ~0.85, 1.10, and 1.30 µm. These are diagnostic of the three groups of mosses – ***Sphagnum*** (Figure 48-Figure 49), feather mosses (Figure 28), and brown mosses (Figure 29). Bubier and coworkers suggested that these may indicate different cellular characteristics. The high water content causes the overall reflectance of the mosses in the SWIR region to be lower than that found in tracheophytes.

Figure 28. ***Pleurozium schreberi***, a common feather moss in boreal forests. Photo by Janice Glime.

Figure 29. ***Scorpidium revolvens***, one of the rich fen brown mosses. Photo by Michael Lüth, with permission.

For aquatic bryophytes, water depth affects light intensity and quality. Mártínez Abaigar *et al*. (1993) found that ***Scapania undulata*** (Figure 30-Figure 31) had a Leaf Specific Area (LSA) of 317 cm^2 g^{-1}DW at 5 cm depth, but at 45 cm depth, the LSA increased to 399 cm^2 g^{-1}DW. Concomitantly, Leaf Specific Weight was reduced from 3.16 mg cm^{-2} to 2.50 mg cm^{-2}. These differences can be interpreted as a response to lower light availability at 45 cm and parallel the kinds of changes that occur in tracheophyte leaves. Canopy leaf fall likewise causes an increase in accessory pigments relative to chlorophyll *a* in this liverwort by increasing the light coming through the canopy.

Figure 30. ***Scapania undulata*** with just a hint of red color, suggesting sun exposure (or nutrient deficiency?). Photo by David T. Holyoak, with permission.

Figure 31. ***Scapania undulata*** showing red coloration that can be stimulated by high light intensity. Photo by Michael Lüth, with permission.

Some structural timing changes are likely to help in protecting developing tissues from high light damage. In tracheophytes, bud scales and leaf primordia can prevent desiccation and most likely prevent light damage to developing tissues when the canopy is free of leaves in the spring (Budke *et al*. 2012). But mosses have no such mechanism. Nevertheless, in the moss ***Funaria hygrometrica*** (Figure 32-Figure 35), there are indications that the **calyptra** plays this role for the developing sporophyte. Not only does the calyptra remain on the developing tip of the young sporophyte until the capsule begins to form, but as the calyptra develops, it produces its cuticle before any cuticle develops on the young capsule. In fact, the calyptrae are covered by four layers of cuticle at all stages. Although Budke and co-workers emphasized the importance of the cuticularized calyptra in preventing desiccation, I would consider it likely that this structure also serves as a filter to protect the developing apical cells from UV-B.

Figure 32. ***Funaria hygrometrica*** archegonia (developing calyptrae) and young sporophytes. At this stage, the cuticle has already formed on the calyptra. Photo by Andrew Spink, with permission.

Figure 33. ***Funaria hygrometrica*** with developing capsules covered by calyptrae. Photo courtesy of Steve Juntika.

Figure 34. ***Funaria hygrometrica*** with nearly mature capsules, showing calyptrae split on lower side of capsule. Photo by Li Zhang, with permission.

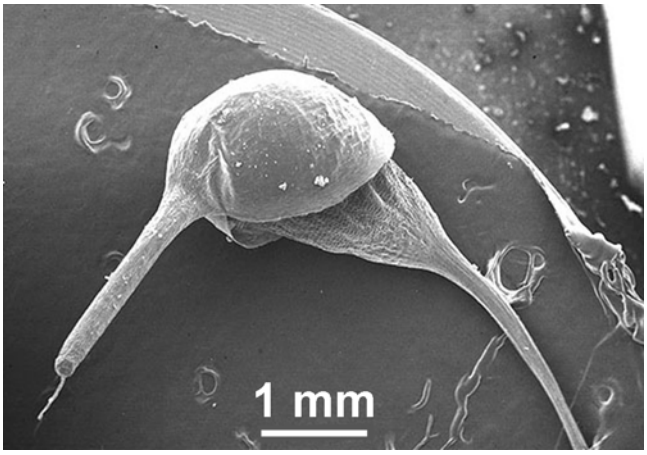

Figure 35. ***Funaria hygrometrica*** capsule SEM showing calyptra that is split on one side, possibly influencing the curved shape of the capsule. The upper side of the capsule is covered as it completes development. Photo from Botany Website, UBC, with permission

Pigmentation

Plant leaves and plant cells are much like a system of filters and lenses. We have already discussed the use of cell structure (lenses) to focus light on a particular location or to alter its intensity. Another way to protect chlorophyll and DNA from high light intensity is through colored pigments (filters) that absorb light.

Increased levels of chlorophyll *b* and xanthophylls, both antenna pigments, are consistent with the suggestion that it is the antenna pigments that dissipate light energy in ***Rhytidiadelphus squarrosus*** (Figure 36); specifically, **zeaxanthin** strongly enhances **light quenching** (dissipation of light energy) in an atmosphere of 20% CO_2 (Bukhov *et al*. 2001a). This appears to be fundamentally different from mechanisms in tracheophytes, as represented by spinach and *Arabidopsis* (Figure 37), where the reaction center appears to be important in quenching. In ***R. squarrosus***, it requires only a few short light pulses, separated by a prolonged dark period, to stimulate the production of additional zeaxanthin (Bukhov *et al*. 2001b). But that was in 20% CO_2! What can it do in the more normal 0.04% CO_2? The interaction of zeaxanthin with thylakoid protonation permits the effective thermal dissipation of light energy in the chlorophyll antenna system of photosystem II in this bryophyte, but not in the two tracheophytes.

It appears that there is a physiological mechanism that facilitates pigment production in response to high light. The gaseous hormone **ethylene** inhibits the synthesis of carotenoids and chlorophyll (Kang & Burg 1972), but stimulates the production of red pigments. Ultimately, its production is inhibited by red light, a convenient feedback mechanism to stop production when the cells have enough red pigment. Ethylene is inhibited by CO_2 and requires O_2 for its formation.

Red pigments become more common in mosses at low temperatures. In our experiments with ***Fontinalis squamosa*** (Figure 38-Figure 40) (Glime & Rohwer 1983), a water-soluble red pigment (anthocyanin derivative?) was produced as a wall pigment in aborted apical buds (Figure 41) and some of the older leaves under treatment with ACC, an ethylene precursor.

Figure 36. ***Rhytidiadelphus squarrosus***, a species that produces zeaxanthin to dissipate strong light. Photo by Michael Lüth, with permission.

Figure 37. ***Arabidopsis thaliana***, a tracheophyte that uses the reaction center of photosynthesis to quench excessive light. Photo by Nicole Hanley, through Creative Commons.

Figure 38. ***Fontinalis squamosa*** in alpine water, showing a healthy green color. Photo from <www.aphotofauna.com>, with permission.

Figure 39. ***Fontinalis squamosa*** stranded above water in the low water levels of summer. Photo by Janice Glime.

Figure 40. ***Fontinalis squamosa*** showing dark pigmentation out of water. Photo by Michael Lüth, with permission.

Figure 41. ***Fontinalis squamosa*** broken-branch buds showing dark pigmentation. Photo by Janice Glime.

In ***Fontinalis antipyretica*** (Figure 42), red leaves were present in a population growing in cold mountain water in full sun (Figure 43-Figure 44) (Glime & Rohwer 1983). A similar response occurred when shoots were kept out of the water under fluorescent light (Figure 45). A similar response is present in ***Ceratodon purpureus*** (Figure 46) in the Antarctic (Post 1990). In high light, the leaves become ginger-colored, a color caused largely by an increase in anthocyanin and decrease in chlorophyll concentrations (Figure 60).

Figure 42. ***Fontinalis antipyretica*** var ***antipyretica*** with reddening that can be caused by exposure to high light. Photo by David Holyoak, with permission.

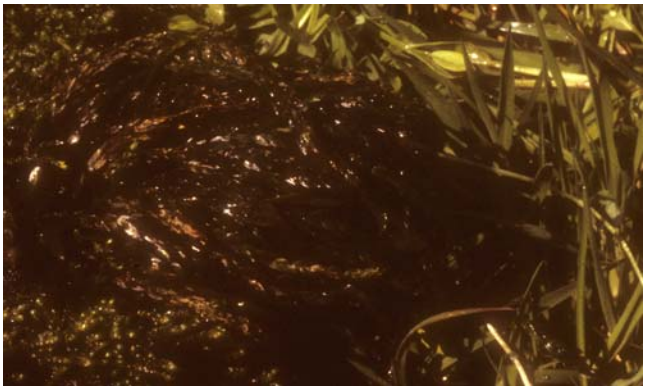

Figure 43. Red ***Fontinalis antipyretica*** in response to bright light of full sun in shallow, cold water emerging from an underground stream in Germany. Photo by Janice Glime.

Figure 44. ***Fontinalis antipyretica*** cells of red plants that were exposed to bright light in cold water (see Figure 43). Photos by Janice Glime.

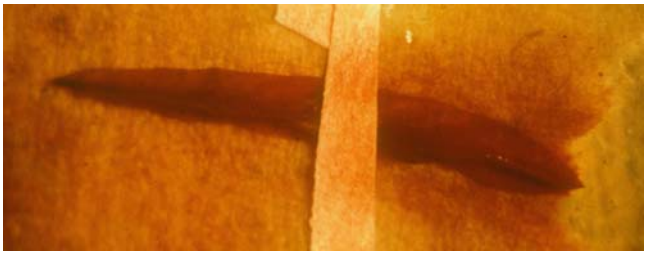

Figure 45. Red ***Fontinalis antipyretica*** in response to bright lights on stem kept out of water under fluorescent light in an experiment. Photo by Janice Glime.

Figure 46. ***Ceratodon purpureus*** on Antarctica, showing red pigmentation in this exposed site. Photo courtesy of Rod Seppelt

In intense light and cold these C_3 bryophytes would have a high photosynthesis/photorespiration ratio due to the fact that photorespiration is low at low temperatures, whereas photosynthesis, while lowered at these temperatures, will not be lowered as much as photorespiration (Zelitch 1971). This high ratio will result in a high O_2/CO_2 ratio that will favor an increase in ethylene production; ethylene will then inhibit production of carotenoids and chlorophyll while stimulating anthocyanin production. The resulting pigmentation will then reflect, scatter, and transmit red light. Since red light should inhibit ethylene production (Kang & Burg 1972), it appears that this system should be self-limiting, with intense red pigment reducing or turning off ethylene production and protecting chlorophyll from overexcitation in intense light (Figure 47). However, this assumes that the red pigment behaves like anthocyanin.

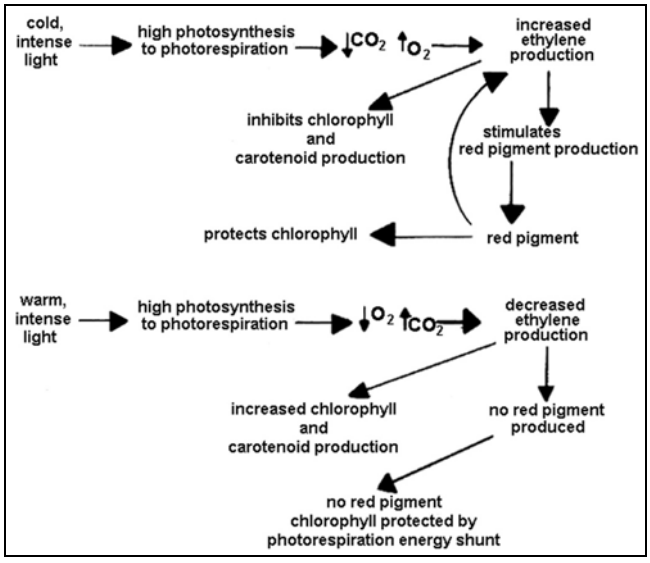

Figure 47. Proposed role of intense light in the production of ethylene and red pigment under cold and warm conditions.

Maseyk *et al*. (1999) compared New Zealand samples of ***Sphagnum cristatum*** (Figure 48) of different colors to determine the effects of pigmentation on photosynthetic response. Brown mosses required higher light intensities (photon flux densities, PFD) than did green samples, had lower quantum efficiencies, and had higher light compensation points, all suggesting that the pigments played a role in filtering out light. An interesting correlation to this was that brown moss samples had a wider range of optimum water content (1400-3000%) than did green mosses (1200-2000%).

Figure 48. Multi-colored capitula of ***Sphagnum cristatum***. Photo by Janice Glime.

Gerdol (1996) found that ***Sphagnum magellanicum*** (Figure 49) had its greatest growth rates in the shade in plants with the highest chlorophyll *b* concentrations and that a high ratio of chlorophyll to carotenoids was also beneficial in the shade. In the open, growth rates were negatively correlated with the chlorophyll *a*:*b* ratio. Gerdol suggested that this negative relationship is due to the greater ease with which chlorophyll *a* is degraded under environmental stress.

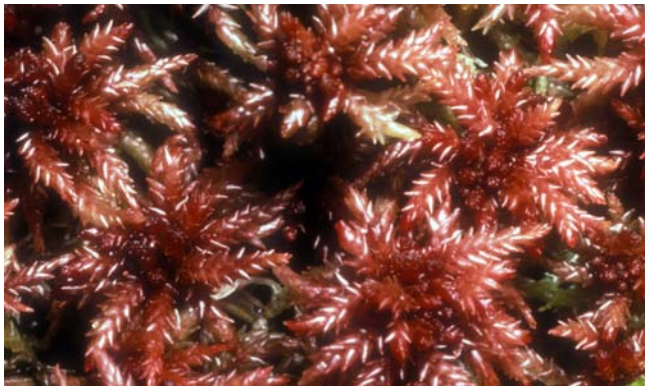

Figure 49. Red ***Sphagnum magellanicum*** resulting from **sphagnorubin** produced when nights are cold and days are bright in the autumn. Photo by Janice Glime.

Light quality matters. In the thallose liverwort ***Marchantia polymorpha*** (Figure 50-Figure 51) the red/far-red ratio matters. De Greef and Fredericq (1969) tested this liverwort in a series of R/FR ratios in 10-minute exposures at the end of the day. In a decreased R/FR ratio, there was a decrease in chlorophyll content. The growth of this liverwort was similar to that shown for seedlings of tracheophytes. The researchers concluded that high levels of the Pfr form of phytochrome were necessary to maintain optimal chlorophyll content in these thalli.

Figure 50. ***Marchantia polymorpha*** demonstrating the pale color of sun plants. Photo by James K. Lindsey, with permission.

Figure 51. ***Marchantia polymorpha*** demonstrating the dark color of shade plants. Photo by Walter Obermayer, with permission.

Sphagnorubin

As with anthocyanin, concentration of **sphagnorubin**, a red wall pigment in some species of ***Sphagnum*** (Figure 49), was also highest in the open (Gerdol 1996). However, the sphagnorubin concentration was not correlated with chlorophyll concentration and growth rate.

Sphagnorubin is a flavonoid related to anthocyanin (Rudolph *et al.* 1977). Schmidt-Stohn (1977) found that in ***Sphagnum magellanicum*** (Figure 49), its synthesis is related to rapid changes in chlorophyll concentration. When Gerdol (1996) did not find the expected negative correlation with chlorophyll concentration, he assumed that the timing of the chlorophyll and sphagnorubin metabolic pathways were different. Sphagnorubin is produced when nights are cold (5°C) and daytime light is intense, but not when both nights and days are warm (18°C) (Rudolph *et al*. 1977; Gerdol *et al* 1998).

Chlorophyll Ratios in Aquatic Bryophytes

Whereas the brook moss ***Fontinalis antipyretica*** (Figure 42-Figure 45) likewise can be brilliant red in nature in intense light and cold water (Glime 1984), on the other end of the scale, aquatic bryophytes alter pigment concentrations as light attenuation occurs with increasing depth. In ***Scapania undulata*** (Figure 30-Figure 31) populations, plants growing at 5 cm depth gained chlorophyll *a* in summer (from 3.43 to 3.69 mg g^{-1} dw) while losing chlorophyll *b* (from 1.17 to 0.87 mg g^{-1} dw), suggesting that they had a much higher light availability in summer (Mártínez Abaigar *et al*. 1993). At 45 cm depth, they lost chlorophyll *a* in summer (from 4.08 to 3.41 mg g^{-1} dw) and likewise lost chlorophyll *b* (from 1.47 to 1.15 mg g^{-1} dw). The increase in chlorophyll *b* with depth was significant ($p<0.01$) in both spring and summer, whereas chlorophyll *a* had a significant increase with depth in spring ($p<0.01$) but not in summer ($p>0.05$). The resulting chlorophyll *a*:*b* ratio was significantly less at 45 cm in both seasons. Variance in carotenoid ratios was extremely small, causing differences of less than 5% between the two depths to be significant for spring samples.

Martínez-Abaigar *et al*. (2003) subjected the aquatic moss ***Fontinalis antipyretica*** (Figure 42) and aquatic leafy liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 52) to 3 different radiation regimes for 36 days in the laboratory. In ***F. antipyretica***, UV-A had little biological effect. UV-B caused decreases in both chlorophyll and carotenoid concentrations, chlorophyll *a*/*b* ratios, chlorophyll/phaeopigment ratios, net photosynthetic rates, light saturation point, maximum quantum yield of photosystem II, and apparent electron transport rate, along with increases in their **sclerophyll index** and dark respiration rates. Most of these changes were indicative of plant stress. In the liverworts, however, UV-B caused only an increase in the concentration of UV-absorbing compounds and a decrease in F_v/F_m. The researchers concluded that these differences would permit the liverwort to tolerate higher levels of UV-B radiation. But in my observations of ***Fontinalis antipyretica*** growing near the surface in cold water in full sun, the mosses were a deep red-green, protected by red pigments (Figure 42-Figure 44).

Figure 52. ***Jungermannia exsertifolia*** subsp. ***cordifolia***, a species that produces more UV-absorbing compounds in response to high light. Photo by Michael Lüth, with permission.

The **sclerophyll index** has rarely been applied to bryophytes. It was developed to compare features of Australian sclerophyllous plants (literally, hard-leaved plants) and included broad, leathery leaves; reduced leaf size; needle leaves; winged stems; spiny stems; sunken stomata; cutinization and lignification of leaves; development of tannins and resinous substances; strong

development of palisade mesophyll and weak development of spongy mesophyll; and presence of hairs, scales, or waxy bloom on leaf surface (Grieve 1955). Few of these can be applied to bryophytes, but instead **sclerophyll index in bryophytes** is defined as ratio of dry mass to shoot area (Monteforte López 2014), including reduced leaf size, cutinization of leaves, development of tannins (phenolic compounds), thicker leaves, presence of awns or papillae, and waxy bloom might be instructive.

Using 17 species of bryophytes from low light habitats of Yuan-Yang Lake at 1760 m elevation in northern Taiwan, Yang *et al*. (1994) found that the mean chlorophyll *a*/*b* ratio was 2.41, with all mean ratios equalling or exceeding 2.17. Two hydrophytes used for comparison had a mean of 3.08. Nevertheless, these 17 bryophytes had a higher chlorophyll *a*/*b* ratio than most mosses reported in the literature, suggesting that they were adapted (or acclimated) to the intense illumination of that elevation (250 μmol m^{-2} s^{-1}).

UV Absorption

Bryophytes are able to produce pigments that absorb UV-A and UV-B while permitting most of the photosynthetically active radiation to penetrate (Jorgensen 1994). These pigments are primarily **phenylpropanoids** and **flavonoids**. Jorgensen suggests that these pigments may have evolved along with the high biosynthetic activity that is needed for UV protection. One of the necessary components of this evolution was to provide a means of sequestering these protective compounds that would otherwise be toxic. Clarke and Robinson (2008) demonstrated that the Antarctic moss ***Ceratodon purpureus*** (Figure 46) produced cell wall-bound UV protective compounds, an effective place to sequester them to protect their own cells. These UV-B protective compounds not only protect against damaging radiation, but at least some are also important in antiherbivory and antimicrobial activity (Davidson *et al*. 1989; Graham *et al*. 2004).

Unlike the popular perception, some mosses are able to grow in large numbers in full sun. How do these mosses cope with high light and UV-B radiation? ***Physcomitrella patens*** (Figure 53) is one of these sun-dwelling mosses. This remarkable tiny moss actually has greater ability to survive UV-B stress than the flowering sun plant *Arabidopsis thaliana* (Figure 37) (Wolf *et al*. 2010). This moss has ~400 genes that are expressed in response to UV-B radiation! Its response pathways are also distinct.

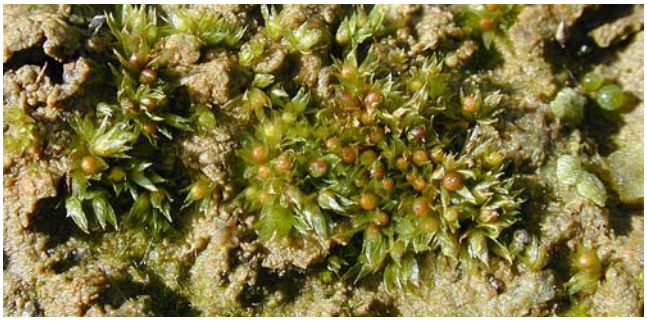

Figure 53. ***Physcomitrella patens***, a tiny sun-dwelling moss that survives high light better than the weedy tracheophyte *Arabidopsis thaliana* (Figure 37). Photo by Michael Lüth, with permission.

In Norway, Wilson *et al*. (1998) found that the growth of ***Hylocomium splendens*** (Figure 54-Figure 55) was strongly stimulated by UV-B when provided with extra water, but under its natural water conditions, UV-B displayed no effect on growth or appearance. On the other hand, leaves of the shrub *Vaccinium vitis-idaea* (Figure 56) became thicker, whereas those of deciduous dwarf shrubs became thinner.

Figure 54. ***Hylocomium splendens*** with its typical forest floor color. Photo by James K. Lindsey, with permission.

Figure 55. ***Hylocomium splendens*** showing the yellowish color typical when the tree canopy is cut. Photo by John Game, through Creative Commons.

Figure 56. ***Vaccinium vitis-idaea***, a species that develops thicker leaves in high light intensity. Photo by Jonas Bergsten, through public domain.

Frey and Kürschner (1991) found a correlation between black pigmentation and increasing aridity in mosses. This most likely is an adaptation to protect the moss from UV light during periods of drought. Normally, water helps to protect chlorophyll from UV light, but during periods of drought, this is not possible. The dark color could serve as a filter against the UV, becoming more transparent to light when water returns. Certainly the color should not be needed for warmth by absorbing heat rays since it is during the warmest periods that high light intensity and desiccation provide the greatest problems.

Many members of the leafy liverwort genus ***Frullania*** (Figure 57) possesses red coloration, grading into nearly black. This genus typically lives on trees and boulders, often at high elevations or high in the canopy. Deeply pigmented species can actually require high light, and account for the presence of this species at high elevations above timberline or high in the canopy of the tropics. On Barro Colorado Island, Panama, epiphyllous liverworts grow more quickly in high light intensities than in the shade, attesting to their adaptations to high light intensity (Coley *et al*. 1993). But these locations also often have higher UV-B light, so the pigmentation may serve as an in important filter against UV damage.

Figure 57. Red coloration of ***Frullania tamarisci***. Photo by Michael Lüth, with permission.

Searles *et al*. (2002) examined the responses of peatland mosses in southern South America to near-ambient (90%) and reduced (20%) UV-B radiation for three growing seasons. The reduction of UV-B cause an increased height growth in ***Sphagnum magellanicum*** (Figure 49), but the plant density decreased. Hence, there was no net influence on biomass production. ***S. magellanicum*** experienced a 10-20% decrease in UV-B-absorbing compounds under the low UV-B regime, but there were no effects on chlorophyll or carotenoid concentrations.

UV radiation is much more intense in terrestrial habitats because in aquatic habitats water quickly absorbs it. It appears that aquatic mosses and liverworts may differ from each other in their UV-absorbing spectra. In ten mosses and four liverworts from a mountain stream at 2,000 m elevation, only the liverworts had high levels of methanol-extractable UV-absorbing compounds, with the exception of ***Polytrichum commune*** (Figure 58) (Arróniz-Crespo *et al*. 2004). Accumulations of such compounds could protect liverworts against the high UV-B light on stream rocks above and near the surface.

Figure 58. ***Polytrichum commune***, a species that produces high levels of methanol-extractable UV-absorbing compounds in high light. Photo by Michael Lüth, with permission.

In their study of aquatic bryophytes, Mártínez Abaigar *et al*. (1993) found very little seasonal or species-specific differences in carotenoid ratios, suggesting that the carotenoids responded little to changes in light intensity in these bryophytes. We know that UV-B quickly loses energy in water, converting to longer wavelengths, and perhaps reducing the danger of UV-B damage in aquatic bryophytes.

UV-B penetration changes throughout the day as the Earth turns and the sunlight travels through less atmosphere as time approaches 12:00 hours, then decreases as the rays strike at a greater angle, once again having to penetrate more atmosphere. The aquatic leafy liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 52) exhibited significant **diel** (within 24 hours) changes, responding within a few hours to changes in radiation levels (Fabón *et al*. 2012). The strongest response was to UV-B. High levels of photosynthetically active radiation (PAR), UV-A, and UV-B radiation elicited significant and rapid diel changes in the components of the **xanthophyll cycle** (process of enzymatic removal of epoxy groups from xanthophylls, *e.g.* violaxanthin, antheraxanthin, diadinoxanthin) to create so-called de-epoxidised xanthophylls). Furthermore, the F_v/F_m, phi PSII (absolute quantum yield of CO_2 fixation in photosystem II), and non-photochemical quenching likewise responded quickly to the changes in radiation levels. These changes provided dynamic photoinhibition and protection of PSII, with the xanthophyll cycle providing protection from the excess radiation.

Accessory pigments such as carotenoids can serve to protect chlorophyll from damage by high intensity UV light (Siefermann-Harms 1987) such as that in the Antarctic. The three mosses examined by Siefermann-Harms all had sustained high levels of xanthophyll pigments, especially at exposed sites (Lovelock & Robinson 2002). Among these was an increase in **violaxanthin** (Post 1990). These pigments are photoprotective and indicate that the moss most likely is subjected to continual high levels of photochemical stress (Lovelock & Robinson 2002). ***Ceratodon purpureus*** (Figure 59-Figure 60) had a higher carotenoid:chlorophyll ratio in high light intensities (0.55) than in low ones (0.35).

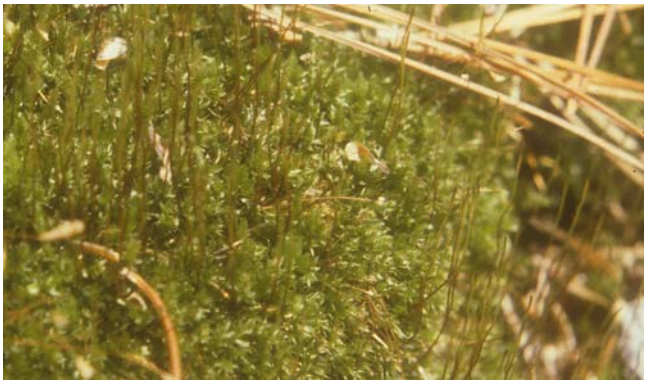

Figure 59. ***Ceratodon purpureus*** green form as it appears when the snow melts. Photo by Janice Glime.

Figure 60. ***Ceratodon purpureus*** in its golden form that has been subjected to high light intensity. Photos by Janice Glime.

Since the Antarctic has received much publicity due to the ozone hole and resulting increase in UV-B penetration through the atmosphere, many of our studies on bryophyte responses to increased UV-B radiation have involved Antarctic bryophytes. Responses are seasonal, resulting in an increase in photoprotective pigments as the ice melts and the mosses become exposed (Dunn & Robinson 2006). One interesting result of these studies is finding that the two cosmopolitan mosses ***Bryum pseudotriquetrum*** (Figure 5) and ***Ceratodon purpureus*** (Figure 46, Figure 59-Figure 60) appear to be better protected against UV-B radiation than is the Antarctic endemic ***Schistidium antarctici*** (Figure 7). Of these three mosses, ***B. pseudotriquetrum*** accumulates the highest concentration of UV-B protective pigments, exhibiting a positive correlation between UV-B radiation and both UV-B-absorbing and anthocyanin pigments. Under desiccating conditions, this species has greater concentrations of these protective pigments than in well-hydrated conditions. This combination would mean that at low temperatures and low moisture, the moss would have limited physiological activity and thus be protected from potential UV-B damage.

Ceratodon purpureus (Figure 59-Figure 60) is the most exposed species of the three studied (Dunn & Robinson 2006). It uses a different strategy of protection, with concentrations of UV-B absorbing pigments being stable through varying light and moisture conditions (Dunn & Robinson 2006). Dunn and Robinson suggested that this is evidence that the protective pigments are constitutive in this species. On the other hand, the anthocyanin pigments were responsive, providing increased antioxidant protection during exposure to high levels of UV-B radiation.

The endemic ***Schistidium antarctici*** (Figure 7), unlike these two cosmopolitan species, is poorly protected, showing no evidence of pigment production in response to UV-B stimulation (Dunn & Robinson 2006). This raises an interesting question of survival, since this species grows along side ***Ceratodon purpureus*** (Figure 59-Figure 60). Are there physiological mechanisms that permit its survival, or is it indeed more vulnerable to a diminished ozone layer, as suggested Dunn and Robinson?

A study by Proctor and Smirnoff (2011) may explain the survival of ***Schistidium antarctici*** (Figure 7). Mosses typically saturate at moderate light levels. Light intensities above those levels can therefore be harmful because of more excited electrons than the photosynthetic apparatus can handle. These saturating levels are similar to those of shade species, demonstrated by the moss ***Plagiomnium undulatum*** (Figure 61) and leafy liverwort ***Trichocolea tomentella*** (Figure 62). But what about bryophytes that live in exposed sites with no shade to protect them? ***Andreaea rothii*** (Figure 63-Figure 64), ***Schistidium apocarpum*** (Figure 65), many ***Sphagnum*** species (Figure 48-Figure 49), and ***Frullania dilatata*** (Figure 66) show a non-saturating electron transfer rate at high light levels, accompanied by high non-photochemical quenching (protection from the adverse effects of high light intensity by dissipating excess excitation energy). ***Plagiomnium undulatum*** and ***Schistidium apocarpum*** can use oxygen and carbon dioxide interchangeably as **electron sinks** (in this case, binding the electrons so they cannot do damage). These two moss species have a high capacity for oxygen photoreduction when CO_2 assimilation is limited. But when the atmosphere is reduced to 1% O_2 with normal levels of CO_2, non-saturating electron flow is not suppressed. Nitrogen + saturating CO_2 causes a higher relative electron transport rate while depressing the non-photochemical quenching. These high abilities of supporting the electron transport by oxygen photoreduction may be a mechanism to permit such mosses as the Antarctic ***Schistidium antarctici*** to survive the high UV-B levels in the Antarctic.

Figure 61. ***Plagiomnium undulatum***, a shade species. Photo by Janice Glime.

Figure 62. ***Trichocolea tomentella***, a shade species. Photo by Michael Lüth, with permission.

Figure 63. ***Andreaea rothii*** wet, from the Black Forest Germany, a sun species. Photo by Michael Lüth, with permission.

Figure 64. ***Andreaea rothii*** dry, living in an exposed site. Photo by Michael Lüth, with permission.

The moss ***Hennediella heimii*** (Figure 67) from Southern Victoria Land, Antarctica, is provided with glacial melt water during the summer. When Pannewitz *et al*. (2003) monitored this moss for 18 days in summer, they found that it had a constant potential photosynthetic activity during that entire period. It grew in the predicament of high light and low temperatures. Nevertheless, it showed no sign of photoinhibition or light saturation, and its electron transport rate response to photosynthetic photon flux densities remained linear at all temperatures. The researchers speculated that it must have a highly effective non-photochemical quenching system.

Figure 65. ***Schistidium apocarpum***, a species that physiological adaptations in addition to its color, awns, and ability to wrap leaves around its stem, all of which aid it in living in exposed sites. Photo by Michael Lüth, with permission.

Figure 66. ***Frullania dilatata***, a desiccation-tolerant leafy liverwort. Photo by Michael Lüth, with permission.

Figure 67. ***Hennediella heimii***, a species that shows no sign of photoinhibition even in the high UV-B light of the Antarctic continent. Photo by Michael Lüth, with permission.

When the snow melts on the Antarctic Peninsula, bryophytes are suddenly exposed to high UV-B levels while still at near-freezing temperatures. Post and Vesk (1992) studied the only continental Antarctic liverwort,

Cephaloziella varians (Figure 68-Figure 69). It occurs in full sun once its ice cover melts. The researchers compared plants from sun-exposed and shaded sites. Those from full sun exhibited dark purple leaves with an anthocyanin-like pigment in thick cell walls. These purple plants grew in dense turfs, were larger, had more closely spaced leaves, and had a higher carotenoid to chlorophyll ratio than did the shaded green plants. The shaded green plants, on the other hand, contained more chlorophyll per unit weight. Like a number of other bryophyte studies, this one showed no variation in the chlorophyll *a*/*b* ratio with differences in light intensity. In low light levels the green plants exhibited higher photosynthetic oxygen evolution rates. The two colors of leaves in similar positions on the plants had more appressed thylakoids in green leaves than did the purple leaves. These differences are the same as expected under varying light exposure.

Figure 68. ***Cephaloziella varians*** amid **Polytrichaceae**. This Antarctic endemic produces red pigments in high light. Photo by Kristian Peters, with permission.

Figure 69. ***Cephaloziella varians*** showing red coloration typical in high light. Photo by Kristian Peters, with permission.

Snell *et al*. (2007) experimented with the same leafy liverwort species, ***Cephaloziella varians*** (Figure 68-Figure 69), by covering it with screens containing Mylar polyester for 44 days. This treatment resulted in changes in thalli, which are normally black, to exhibit a green color. This was the result of reduced concentrations of the anthocyanidin **riccionidin A** in the plant tips. These plants were then exposed to an abrupt increase in their UV-B radiation when the screens were removed. Within only 48 hours the plants were visibly darker. This color change was due to *de novo* synthesis of riccionidin A that reached the same concentrations as that in plants that had not been covered during those 44 days. This synthesis required an equivalent of 1.85% of the carbon fixed during those 48 hours. The F_v/F_m and photochemical quenching were likewise the same in both groups of plants. Nevertheless, the level of chlorophyll fluorescence indicated that non-photochemical quenching was higher in the plants that had just experienced the sudden increase in UV-B.

Otero *et al*. (2008) examined five liverworts and ten mosses from open aquatic habitats of Tierra del Fuego on the southern tip of Argentina, where the atmosphere is thinner than in temperate regions, to determine their responses to UV radiation. They found that the species differed in spectra form and area under the absorbance curve (AUC). The spectra had one, two, or no defined peaks. They suggested that phenolic derivatives might be responsible for the differences in peaks among the species. These phenolic derivatives could serve not only as screening compounds, but also as antioxidants. The AUC values for most of the liverworts were higher than those for most of the mosses. The liverworts ***Noteroclada confluens*** (Figure 70) and ***Triandrophyllum subtrifidum*** (Figure 71) had much higher bulk UV-absorption capacity of the methanolic extracts (BUVACME) than did any other bryophyte in the study. The researchers concluded that "accumulation of UV-absorbing compounds might often increase protection against UV radiation in liverworts, but rarely in mosses." Could this difference be related to their location in southern Argentina? But Otero and coworkers did not find the BUVACME of these aquatic bryophytes to differ significantly from that found elsewhere on the planet.

Figure 70. ***Noteroclada confluens***, a species with an unusually high bulk UV-absorption capacity. Photo by Michael Lüth, with permission.

Figure 71. ***Triandrophyllum subtrifidum***, a species with an unusually high bulk UV-absorption capacity. Photo by Shirley Kerr, with permission.

Huttunen *et al*. (2005) compared the UV-absorbing compounds in herbarium specimens of terrestrial and peatland mosses collected from 1926 to 1996 from the sub-Arctic to see if it had changed as fluorines in the atmosphere increased the ozone hole, permitting greater penetration of UV light. They found that the average amount of total compounds (sum of A280-320 nm absorption) per mass from the lowest to the highest was ***Polytrichum commune*** (Figure 58), ***Pleurozium schreberi*** (Figure 28), ***Hylocomium splendens*** (Figure 54-Figure 55), ***Sphagnum angustifolium*** (Figure 72), ***Dicranum scoparium*** (Figure 73), ***Funaria hygrometrica*** (Figure 32-Figure 35), ***Sphagnum fuscum*** (Figure 74), ***Sphagnum warnstorfii*** (Figure 75), ***Sphagnum capillifolium*** (Figure 76), and ***Polytrichastrum alpinum*** (Figure 77). The amount of UV-B-absorbing compounds per specific surface area correlated with the summertime daily global radiation and latitude, but they found no trend in concentration of UV-B-absorbing compounds from 1920 to 1990 except in ***Sphagnum capillifolium***, which showed a significant decreasing trend in concentrations. Huttunen and coworkers suggested that this lack of correlation with the increasing size of the ozone hole could be the result of degradation of the protective compounds or the difficulty in extracting the wall-bound pigments p-coumaric acid and ferulic acid (Davidson *et al*. 1989) and the sphagnorubins (Geiger *et al*. 1997).

Figure 72. ***Sphagnum angustifolium***. Photo by Kristian Peters, through Creative Commons.

Figure 73. ***Dicranum scoparium*** on forest floor. Photo by Janice Glime.

Figure 74. ***Sphagnum fuscum***, sun-dwelling sun species. Photo by Michael Lüth, with permission.

Figure 75. ***Sphagnum warnstorfii***, exhibiting its sun-exposed red pigments. Photo by Michael Lüth, with permission.

Figure 76. ***Sphagnum capillifolium***. Photo by Li Zhang, with permission.

Figure 77. ***Polytrichastrum alpinum*** with capsules, a species of exposed, usually cold, habitats. Photo by David T. Holyoak, with permission.

Caldwell *et al.* (1998) concluded that some of the most important consequences of elevated UV-B might be indirect effects. In tracheophytes, these include changes in susceptibility of plants to attack by pathogens (fungi & bacteria) and insects, changes in the competitive balance among plants, and altered nutrient cycling. More direct effects seem to occur through altered gene activity rather than direct damage. These changes may be exacerbated or diminished by other changes that are coupled with increased UV-B, such as temperature and CO_2 level changes. Although these indirect effects would seem to be critical, if forest trees and other tracheophyte examples are indicative, we should look for these effects in bryophytes.

Early land plants faced high levels of UV light and at the same time water scarcity from their beginnings on land (Martínez-Abaigar & Núñez-Olivera 2022). Through time, they have developed various physiological and structural adaptations to minimize the effects of UV light on the cell contents. These adaptations vary among the species, with mosses being more UV-tolerant that liverworts.

Desiccation Effects and Light

High light intensities are often coupled with desiccating conditions. Yet, it appears that the mosses that live in such desiccating conditions seldom suffer light damage during their dehydrated periods, and photosynthesis is able to resume immediately upon rehydration, not requiring synthesis of new chlorophyll to resume (Di Nola *et al*. 1983). For example, the desiccation-tolerant moss ***Syntrichia ruralis*** (Figure 2) retains all its pigments upon drying, thus rapidly recovering its photosynthetic functions upon rehydration (Hamerlynck *et al*. 2002). This species permits recovery on a daily basis by a thermal dissipation of the excess light energy as the moss dehydrates in the morning, and recovery upon rehydration depends on light conditions and the rapidity of drying.

Tracheophytes do not enjoy this pigment conservation (Heber *et al*. 2001) and rapidly lose their photosystem II capability under desiccation conditions (Hamerlynck *et al*. 2002). In desiccation-tolerant bryophytes, protein protonation, coupled with the presence of high levels of zeaxanthin, seems fully capable of dissipating excess light energy (Heber *et al*. 2001). A similar rise in zeaxanthin with dehydration occurs in the desiccation-tolerant tracheophyte *Selaginella lepidophylla* (Figure 78Figure 79) (Casper *et al*. 1993). This rise occurs during the dehydration process, and Casper *et al*. hypothesized that zeaxanthin-related protection is engaged in response to the dehydrating conditions, even in low light levels. Nevertheless, chlorophyll fluorescence is lost during drying of predarkened desiccation-tolerant mosses, suggesting that energy dissipation in the dry state is not related to protonation and high levels of zeaxanthin.

Deltoro *et al*. (1998a) found that desiccation-tolerant bryophytes [***Hedwigia ciliata*** (Figure 14-Figure 16), ***Hypnum cupressiforme*** (Figure 80), ***Leucodon sciuroides*** (Figure 81-Figure 82), ***Orthotrichum cupulatum*** (Figure 83), ***Pleurochaete squarrosa*** (Figure 84), ***Porella platyphylla*** (Figure 85), and ***Syntrichia ruralis*** (Figure 2)] were able to resume photosynthesis rapidly upon rehydration, whereas desiccation-intolerant bryophytes [***Barbula ehrenbergii*** (Figure 86-Figure 87), ***Cinclidotus aquaticus*** (Figure 88), ***Conocephalum conicum*** (Figure 89), ***Lunularia cruciata*** (Figure 90), ***Palustriella commutata*** (Figure 91-Figure 92), ***Philonotis calcarea*** (Figure 93), and ***Platyhypnidium riparioides*** (Figure 94)] from mesic and hydric habitats were unable to resume their photosynthetic activity.

Figure 78. *Selaginella lepidophylla* showing the edges curling up as it dries and exposing the white ventral surface that helps to reflect high light. Photo through Creative Commons.

Figure 79. *Selaginella lepidophylla* dry, illustrating its mechanical response to drying. Photo by Nicole Koehler, through public domain.

Figure 80. ***Hypnum cupressiforme***, a widespread, desiccation-tolerant species. Photo by J. C. Schou, with permission.

Figure 81. ***Leucodon sciuroides*** wet, a desiccation-tolerant epiphyte. Photo by Michael Lüth, with permission.

Figure 82. ***Leucodon sciuroides*** dry, showing appressed leaves and decreased surface area. Photo by Michael Lüth, with permission.

Figure 83. ***Orthotrichum cupulatum***, a xerophytic epiphyte. Photo by Michael Lüth, with permission.

Figure 84. ***Pleurochaete squarrosa***, a desiccation-tolerant moss. Photo by Michael Lüth, with permission.

Figure 85. ***Porella platyphylla***, a desiccation-tolerant leafy liverwort epiphyte. Photo by Michael Lüth, with permission.

Figure 86. ***Barbula ehrenbergii***, a desiccation-intolerant moss. Photo by Michael Lüth, with permission.

Figure 87. ***Barbula ehrenbergii***, a species that is unable to resume photosynthesis after desiccation. Photo by Michael Lüth, with permission.

Figure 88. ***Cinclidotus aquaticus***, a species of wet habitats that is unable to resume photosynthesis after desiccation. Photo by Michael Lüth, with permission.

Figure 89. ***Conocephalum conicum***, a species of damp, usually shaded, habitats that is unable to resume photosynthesis after desiccation. Photo by Janice Glime.

Figure 90. ***Lunularia cruciata***, a species that is unable to resume photosynthesis after desiccation. Photo by David Holyoak, with permission.

Figure 91. ***Palustriella commutata***, a species of wet habitats. Photo by J. C. Schou, through Creative Commons.

Figure 92. ***Palustriella commutata***, a species of wet habitats that is unable to resume photosynthesis after desiccation. Photo by David T. Holyoak, with permission.

Figure 93. ***Philonotis calcarea***, a species of wet habitats that is unable to recover photosynthesis after desiccation. Photo by Michael Lüth, with permission.

In examining the xanthophyll content of a desiccation-tolerant leafy liverwort, ***Frullania dilatata*** (Figure 66), they found an increase in de-epoxidized xanthophylls in response to dehydration (Deltoro *et al*. 1998b), whereas this did not occur in the desiccation-intolerant ***Pellia endiviifolia*** (=***Apopellia endiviifolia***; Figure 95), and the latter species had less ability to dissipate the light while dry. Upon rehydration, ***Frullania dilatata*** resumed full photosynthetic capability rapidly, whereas ***P. endiviifolia*** suffered irreversible damage to photosystem II. They suggested that ***F. dilatata*** likewise possesses a desiccation-induced production of zeaxanthin, but they were unable to rule out the loss of K^+ from damaged membranes in ***P. endiviifolia*** as a causal factor for its demise.

Figure 94. ***Platyhypnidium riparioides***, a species of submersed and wet habitats that is unable to recover photosynthesis after desiccation. Photo by Hermann Schachner, through Creative Commons.

Figure 95. ***Pellia endiviifolia***, a species with weak ability to dissipate light when dry. Photo by Michael Lüth, with permission.

Bartoskova *et al*. (1999) offer a somewhat different explanation for observed changes in chlorophyll fluorescence during drying. Working with leaves of ***Rhizomnium punctatum*** (Figure 96), they found a 50% decrease in the F685/F735 ratio in the chlorophyll fluorescence spectrum during drying. No changes occurred in the E475/E436 bands of fluorescence. They could find no functional changes resulting from desiccation at the energy transfer level and suggested that the change in fluorescence ratio is the result of a rearrangement of chloroplasts into groups that enhance the effect of chlorophyll reabsorption. My own experience in extracting chlorophyll from dry mosses is that they extract better if they are rehydrated first. This would be consistent with the grouping of chloroplasts, hence preventing the solvent from reaching the interior of the clump. In a conversation with Zoltan Tuba, I learned that he had experienced a similar response.

Figure 96. ***Rhizomnium punctatum***, a species that may rearrange its chloroplasts upon drying. Photo by Michael Lüth, with permission.

At least in alpine areas, where UV light may be more intense, desiccation can affect moss (and lichen) fluorescence differently from its effects on tracheophytes. In its dehydrated state, the moss ***Grimmia alpestris*** (Figure 97) had very low chlorophyll fluorescence, whereas it was high in the alpine tracheophytes tested (Heber *et al*. 2000). Conversely, upon rehydration, the mosses and lichens experienced increased chlorophyll fluorescence, whereas the tracheophytes experienced a decrease. This is because, unlike their tracheophyte counterparts, the mosses and lichens do not experience photodamage in their dry state. Both groups of plants form potential chlorophyll fluorescence quenchers as a response to desiccation, but only the dehydrated mosses and lichens responded to the energy transfer from light by exhibiting a decrease in fluorescence. It appears that among these alpine taxa, only the poikilohydric ***Grimmia alpestris*** has a deactivation pathway that enables it to avoid photodamage both in its hydrated and dehydrated states.

Figure 97. ***Grimmia alpestris***, a species that has a deactivation pathway that permits it to live in high light conditions. Photo by Jan-Peter Frahm, with permission.

Beckett *et al.* (2005) found that **hardening** (process of increasing resistance) of the moss ***Atrichum androgynum*** (Figure 98) during drying permitted it to recover fully from dehydration, whereas lack of time for this preparation did not (Figure 99). That is to say, mosses that hardened by slow drying before the silica gel desiccation treatment had a better recovery than mosses that were placed immediately into the desiccation treatment from full hydration. More importantly, hardening greatly increased the photochemical quenching during the first few hours of rehydration. In these early stages photophosphorylation occurs, but not carbon fixation. Thus, it is in these early stages that photoprotection is most important, and the moss experiences reduced efficiency during drying in order to accomplish photoprotection during rehydration.

Figure 98. ***Atrichum androgynum***, a species that recovers fully from dehydration if it is able to undergo hardening during drying. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

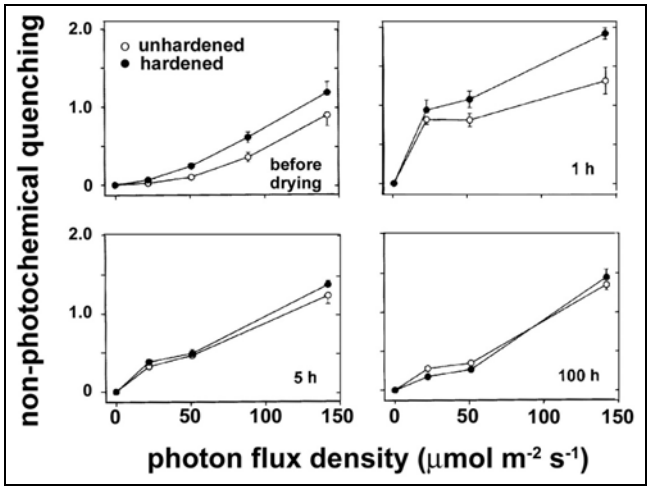

Figure 99. The effect of hardening on the non-photochemical quenching upon rehydration of 1, 5, and 100 hours compared to quenching prior to desiccation in ***Atrichum androgynum***. Redrawn from Beckett *et al*. 2005.

Mosses, as in the tracheophyte resurrection plant *Selaginella lepidophylla* (Figure 78-Figure 79), often have mechanical responses that help to protect them from the damaging effects of light. Lebkuecher and Eickmeier (1991, 1993) have shown that the rolling of the fronds of *S. lepidophylla* serves to protect the plant from light and thermal damage that could be expected in the dry state. In that species, some damage occurs during the drying phase before the curling is complete. It is likely that mosses like ***Hedwigia ciliata*** (Figure 14-Figure 16) and ***Syntrichia ruralis*** (Figure 100) might accomplish the same thing. Might the smaller bryophytes curl quickly enough to avoid that early damage? In ***Hedwigia ciliata***, an appression of

leaves against the stem is realized, and the tips of the branches tend to curve upward, reducing exposure. In ***S. ruralis***, the drying leaves twist (Figure 100) and become more vertically oriented. Hamerlynck *et al*. (2000) suggested that ***S. ruralis*** has a "coordinated suite of architectural and physiological characteristics maintaining the photosynthetic integrity of these plants." These include not only their ability to change the positions of their leaves, but also to alter the surface reflectance as water leaves the leaf cells. This alteration causes more reflectance from a dry surface than from a wet one.

Figure 100. Dry ***Syntrichia ruralis*** exhibiting dark color and twisted leaves that protect it from high light intensity. Photo by Janice Glime.

In the Antarctic, where desiccation is frequent, Lovelock and Robinson (2002) also found significant differences among species and the sites they occupied based on their surface reflectance properties, especially at ~700 nm, whereas pigment concentration did not seem to be important.

Avoidance – Hiding under Rocks

Imagine a light so intense that you must hide under a rock to avoid damaging your pigments. The only light you ever see is that which comes through the rock, or occasionally reflects off the ground around that rock. There are some mosses that take just such a refuge. Using the rock as a filter, ***Syntrichia inermis*** (Figure 101) survives the intense light (and dryness) of the Californian desert by living beneath a piece of translucent rock (Werger & During 1989).

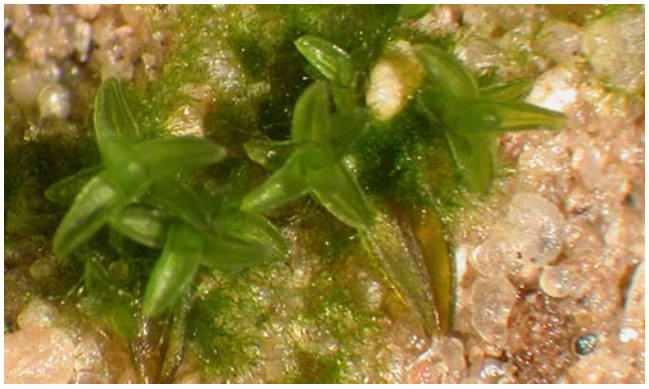

Figure 101. ***Syntrichia inermis***, a moss capable of living under quartz pebbles in the desert. Photo courtesy of Lloyd Stark.

As we have seen, polar deserts are unfriendly habitats due to the damaging effects of UV radiation. For **Cyanobacteria** (Figure 102) and algae, living under translucent rocks is a way to escape that damaging radiation (Thomas 2005). These assemblages can be as productive as their neighbors that are not protected by rocks. Is seems likely to me that some members of these microbial communities might enhance the habitat for the few species of bryophytes that live there. For example, **Cyanobacteria** can convert atmospheric nitrogen to a form usable by the bryophytes. Non-photosynthetic bacteria can provide CO_2. This remains another microecosystem begging for ecological study.

Figure 102. **Cyanobacteria** under quartz rock. Photo by Michael Wing, public domain through NSF funds.

Williams (1943) described a "moss peat" under translucent pebbles in the American Great Plains, but there seems to be no publication of the actual species. The rare moss ***Aschisma kansanum*** is known only from this unique habitat, where it occurs at the base of nearly clear quartz pebbles (Cridland 1959). The thick, leathery protonema, which is persistent, covers the buried part of the pebbles overlying sandy Pleistocene gravels. And in the Antarctic, where mosses must "worry" about the effects of UV light – what better place to hide than behind glass, in the form of quartz. And there one might also find the tiny ***Hennediella heimii*** (Figure 103) beneath the rock (Fife 2005).

Figure 103. ***Hennediella heimii***, a moss that lives under quartz rocks in the Antarctic. Photo by Michael Lüth, with permission.

Marchand (1998) determined that about 1.5% of the full sunlight hitting a milky quartz rock penetrated through about 2.5 cm of rock, comparing this to the light reaching a potted plant in a well-lit office. In some cases, visible light can reach a depth of 5 cm. The rock offers the added advantage of reflecting much of the heat and registering temperatures ~7ºC less than under a dark-colored volcanic rock.

Terry Hedderson (Bryonet 22 February 2005) tells of quartz-field bryophyte communities beneath stones in the Knersvlakte area of Namaqualand and from the inselbergs of Bosmansland, both in South Africa. He provides this anecdotal account: "The bryophyte assemblages seem to come in two forms: In some areas where there are extensive and relatively deep patches of translucent small quartz pebbles, one can find entire communities comprising ***Bryum argenteum*** (Figure 17-Figure 18), ***Riccia*** spp. (Figure 104), ***Hennediella longipedunculata***, other small **Pottiaceae**, ***Chamaebryum***, ***Gigaspermum*** (Figure 105) and others, buried to a depth of a few centimetres (3-10 say). These often occur with various Aizoaceae seedlings, as mentioned by a previous contributor. Some of the best examples that I've seen of these are on the summits of Ghamsberg and Pellaberg in Bosmansland. In areas where the pebble cover is less continuous (like in the Knersvlakte), I have found communities under flattish single stones that are imbedded in a clay matrix. Here they often occur with lots of blue-greens, with the main bryophyte component comprising ***Archidium dinteri***, ***Bryum argenteum***, various ***Riccias*** and small ***Fissidens*** spp (Figure 106). The vast majority of stones have only blue-greens and it is not at all clear what determines whether bryophytes are present or not. In both cases the plants are often quite vigorous and healthy looking, and not the least bit etiolated, so I imagine that they receive sufficient light."

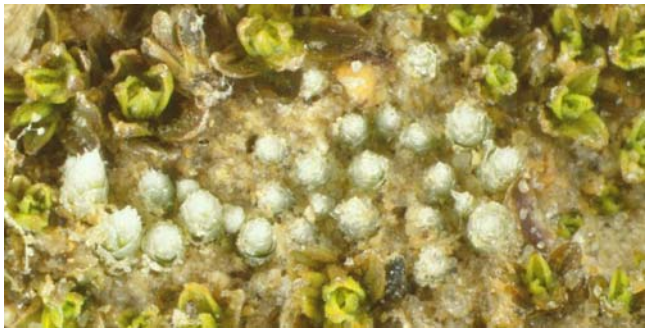

Figure 105. ***Gigaspermum*** sp, a genus that can occur under translucent quartz rocks in bright sun. Photo by Jan-Peter Frahm, with permission.

Figure 106. ***Fissidens bryoides*** with capsules, a tiny species such as those that might occur under flat stones in high light. Photo by Janice Glime.

But records of these sequestered mosses are far more rare than those of algae. This intriguing habitat has led a number of bryologists to overturn numerous rocks in places like the Namib Desert, so far only to find more algae.

In the Antarctic, bryophytes (and algae) occur beneath rocks, stones, and sand (Lewis-Smith 2000). Seppelt (2005) finds buried mosses there occupying ephemeral riverbeds and other places where they have been buried by sand carried by wind or water. ***Bryum pseudotriquetrum*** (Figure 5) and ***B. subrotundifolium*** (Figure 107) can be uncovered by sweeping away the sand. In these habitats, as in sand dunes and volcanic tephra, the acrocarpous mosses are able to grow upward and eventually emerge into the light. For those buried by sand, refracted and reflected light may help to sustain them through photosynthesis as they wend their way to the top.

Figure 104. ***Riccia sorocarpa***. Members of this genus are known from under quartz rocks. Photo by Michael Lüth, with permission.

Figure 107. ***Bryum subrotundifolium*** with Collembola among sand grains on Antarctica. Photo courtesy of Catherine Beard.

Lava fields often provide cracks through which rays of light may penetrate. Yojiro Iwatsuki (the finder), Zen Iwatsuki, and I were surprised in Iceland to uncover a miniature moss garden, predominately ***Saelania glaucescens***, hidden under a fissure in the lava rock (Figure 108). Juana María González-Mancebo related an experience in the Canary Islands (Bryonet, 22 February 2005) where the researchers found 69 species of bryophytes living among the second layer of rock, under the rocks of the first layer of lava, in lava tubes, and in volcanic pits. Even the epiphyte ***Neckera intermedia*** (Figure 109) can grow in the more humid lava flows of Tenerife.

Figure 108. ***Saelania glaucescens*** exposed by our removal of several pieces of the broken volcanic rock above it. Photo by Janice Glime.

Figure 109. ***Neckera intermedia***, an epiphyte that can grow in lava flows. Photo by Jan-Peter Frahm, with permission.

If you are a moss in the Mojave Desert, you can have a rough life. The sunlight is intense and hot. Moisture is all but non existent most of the time. But ***Syntrichia caninervis*** has found an unusual way of coping. It lives under white, translucent quartz rocks (ScienceFriday.com 2020). On those rare occasions when it does rain, the moss begins rehydrating immediately and remains moist long enough to replenish its energy supply. Undoubtedly the rock helps to maintain a longer hydration period, but it also filters the intense light.

Figure 110. ***Syntrichia caninervis*** growing under white quartz rock, Mojave Desert, California, USA. Photo by Kirsten Fisher, with permission.

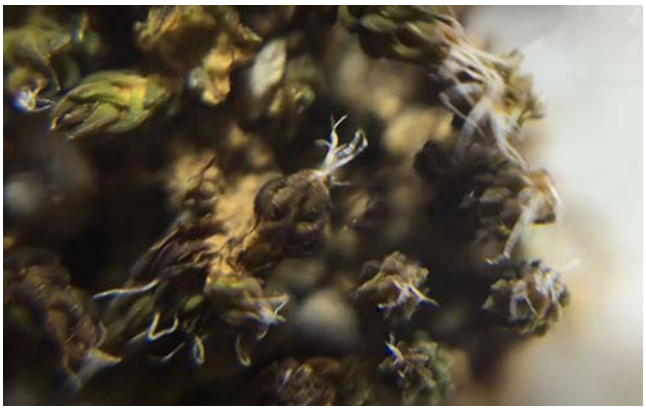

Figure 111. ***Syntrichia caninervis*** dry, from under quartz rock, Mojave Desert, California, USA. Photo by Kirsten Fisher, with permission.

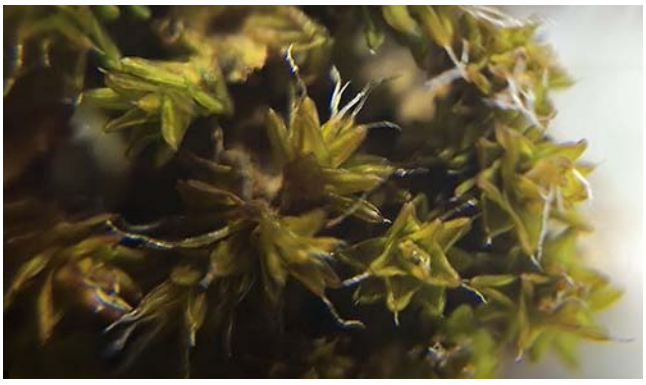

Figure 112. ***Syntrichia caninervis*** from under quartz rock, 50 seconds after wetting. Photo by Kirsten Fisher, with permission.

Summary

Due to their one-cell-thick leaves, bryophytes are especially susceptible to damage by UV light. Dry plants are especially vulnerable to chlorophyll and DNA damage due to the lack of protective water. Some have altered optical properties that reduce the light penetration into cells. Bryophytes can suffer photoinhibition due to overstimulation of chlorophyll in high light, which can result in a decrease in thylakoid stacking.

Some mosses have **lamellae**, **inrolled leaf lamina**, **filaments**, **hyaline tips**, and **awns** that partially cover the leaf and protect it from light. Others curl the leaves or wrap them around the stem. Aquatic mosses are protected by their water medium.

In response to high light intensities, bryophytes experience a decrease in chlorophyll. By having a relatively high amount of chlorophyll *a* compared to chlorophyll *b* in their shade plants, they are ready for sunflecks and other short periods of light availability, thus making up for the low productivity that is possible in the shade.

Pigments can filter light and reduce its energy, thus protecting the chlorophyll and DNA. Ethylene stimulates the production of red pigments, which are particularly common at low temperatures and in bright light. In ***Sphagnum***, this red pigment is a cell wall pigment, **sphagnorubin**. **Violaxanthin** is known to increase in response to high light. **Zeaxanthin** responds by disabling the chlorophyll antenna pigments (**quenching**), thus reducing the energy reaching the chlorophyll *a*.

Bryophytes are superior to tracheophytes in preserving their chlorophyll during desiccation and are thus ready for photosynthesis upon rehydration. This may be due to a rearrangement of the chloroplasts into protective groups. **Hardening** is important in this preparation.

Some bryophytes avoid the intense radiation by growing under translucent rocks. These locations are especially important in deserts where light is intense and desiccation is a major problem, As see in ***Syntrichia caninervis***..

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CHAPTER 9-4

LIGHT: SEASONAL EFFECTS

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CHAPTER 9-4
LIGHT: SEASONAL EFFECTS

Figure 1. Winter condition of *Thuidium tamariscinum*, when the canopy is gone and the temperature is cold. Photo by Michael Lüth, with permission.

Bryophyte View of Light

Light is a constantly changing parameter in the world of the bryophytes. They experience long and short periods (**photoperiod**) as the seasons change. They experience high intensity and low intensity as the leaves grow on the trees. They experience changes from white light to green light as the canopy closes. And each of these changes is coupled with changes in temperature and available moisture. Each of these requires its own set of adaptations to permit the bryophyte to survive. But bryophytes can also take advantage of these changes as signals to them of the upcoming series of climatic events.

High Light and Low Temperatures

When plants are metabolically slowed by low temperatures (ca. 1ºC) and light intensity is high (Figure 1), photo-oxidation damage can occur in cells (Kuiper 1978). This can result in such responses as rupture of the chloroplast envelope, formation of vesicles in thylakoids, and rapid degradation of linolenic acid. Adamson and coworkers (1988) suggest that such photoinhibition may be the major factor in limiting production of Antarctic bryophytes.

Blue light seems to be especially effective in the photo-oxidation of unsaturated fatty acids, indicating that carotenoids (yellow pigments absorb blue light) contribute to the process. One of the causes of the breakdown of chlorophyll can be attributed to the degradation of its complexing lipid, monogalactose diglyceride (Kuiper 1978). Ironically, it is the unsaturated fatty acids that are susceptible to this oxidation, causing a risky condition for plants preparing for the cold of winter while sustaining the bright light of autumn. However, presence of tocopherol, an anti-oxidant, can nullify this photo-oxidation process (Kuiper 1978) and may play a key role in protection of chlorophyll during autumn and spring when such low temperature and bright light conditions prevail.

When days are bright and nights are cold, ***Sphagnum magellanicum*** (Figure 2) produces **sphagnorubin** and becomes a deep wine red (Gerdol 1996). When the plants occur in the open, where higher light intensities are expected, the concentration of sphagnorubin is greater.

However, in intense light and warm temperatures ***Sphagnum magellanicum*** does not produce much red pigmentation (Rudolph *et al*. 1977). In this case the photorespiration/ photosynthesis ratio would be high due to the fact that photorespiration has a $Q_{10} = 3$ with very little damping at higher temperatures. Photosynthesis, however, is observed to reach an optimum and then decrease its rate rapidly (Zelitch 1971). This would result in a high CO_2/O_2 ratio that would decrease ethylene production and stimulate chlorophyll and carotenoid synthesis. Anthocyanin (and sphagnorubin?) production would not be enhanced and so no red pigmentation would be found. In the case of warm temperatures, the red pigment would convey no adaptive advantage since the greatly increased photorespiration would serve as an energy shunt to protect the chlorophyll from overexcitation by the intense light (Bidwell 1979).

Figure 2. ***Sphagnum magellanicum*** colored by sphagnorubin. Photo by Michael Lüth, with permission.

A second function of red pigment at low temperatures could be the heat absorption and warming of the moss, a mechanism already known to warm flowers, such as those enclosed in a red spathe in ***Symplocarpus foetidus*** (Figure 3), and to increase respiration in cold-adapted copepods (Byron 1982). Zehr (1979) has suggested that the red color of the leafy liverwort ***Nowellia curvifolia*** (Figure 4), induced by exposure to light when leaves fall, increases the temperature of the liverwort to allow greater photosynthesis and respiration in winter.

Figure 3. ***Symplocarpus foetidus*** showing red spathe that creates a warm space, attracting flies that pollinate the flowers inside. Photo by Sue Sweeney, through Creative Commons.

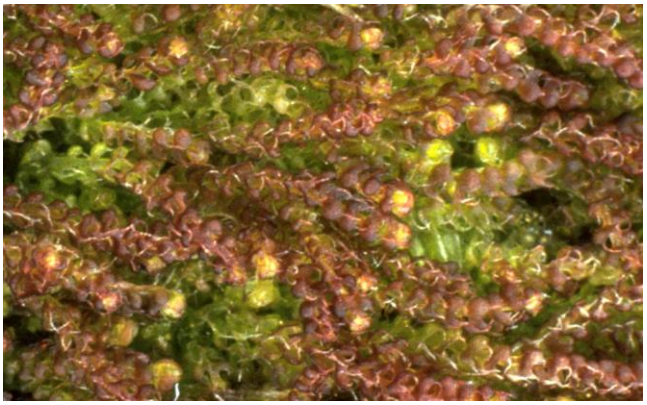

Figure 4. ***Nowellia curvifolia*** demonstrating its red leaves of fall. Photo by Jan-Peter Frahm, with permission.

Light Effects on Reproduction

Humans don't think in terms of high light intensities for reproduction, but it appears that at least some mosses do. ***Hylocomium splendens*** (Figure 26) had poor reproduction in all populations except those that had received extra light as the result of removal of stems (Rydgren & Økland 2001). Those that were merely clipped to remove all growing tips and provide extra light did no better than the controls, suggesting that it was not the stimulus of the wounding or the extra energy diverted away from growing buds that caused the greater reproduction. In the second year of the experiment, the removal group had ten times as many sporophytes as the other treatment groups. But is this an indication of good or of bad conditions? Many algae and even flowering plants go into a sexual stage when growing conditions are poor, providing a means for the species to survive through its offspring.

To confound the issue further, Hughes and Wiggin (1969) found that in ***Phascum cuspidatum*** (Figure 5), light had just the opposite effect. Plants grown in culture in the shade had significantly more antheridia, more antheridial dehiscence, and larger antheridia than plants grown with light from the north sky. They did find more archegonial heads on plants grown in the light, but the success of fertilization was greater for plants grown in the shade (11%) than in the light (6%). However, they suggested that some of these differences could be accounted for by differences in population sizes.

Figure 5. ***Phascum cuspidatum*** with capsules. Photo by Michael Lüth, with permission.

In the Antarctic, bryophytes are frozen in winter, but in summer they are fully exposed to the polar sun. In fact, Post *et al*. (1990) found that the major limiting factor to

Antarctic bryophyte productivity is photoinhibition. This would not be unusual for C_3 plants such as bryophytes growing at low temperatures in high light. Nevertheless, this topic has rarely been studied in bryophytes.

Seasonal Effects on Pigments

Light intensity changes with the seasons, and at least some plants are adapted to respond to those changes. Tracheophytes change their chlorophyll concentration based on the amount of light reaching the leaf. Plants grown in low light will increase their chlorophyll *b* concentration, and thus their chlorophyll *a*:*b* ratio decreases. Those plants kept indoors in low light will suddenly turn red or become bleached if they are put out in bright sunlight, and the photosynthetic apparatus will become permanently damaged. Leaves growing on the shady side of a tree will be thinner and darker, while those in the sun put on extra layers of palisade tissue. Bryophytes cannot change their leaf thickness in response to light changes, but it is possible for them to change the chlorophyll concentration and the ratio of shoot area to biomass. A bryophyte branch can effectively operate like a leaf of a seed plant and thus some of the same size ratio responses are possible.

Hicklenton and Oechel (1977) found that ***Dicranum fuscescens*** (Figure 6) from northern Canada exhibited an increase in the light required to saturate photosynthesis from early season until mid summer, with the trend reversing later in the season. They suggest that ability to photosynthesize at low light levels is an advantage to mosses that are still under the snow in early spring. Mosses exposed to high light when they are acclimated to low light actually experience damage, and it appears that the continuous light of summer in the Arctic may likewise be deleterious (Kallio & Valanne 1975). However, the continuous light damage occurred in laboratory experiments and it may be that plants living in the Arctic may acclimate to the seasonal change in photoperiod (Richardson 1981).

Figure 6. ***Dicranum fuscescens***, a species that changes its light saturation point as the season changes. Photo by Michael Lüth, with permission.

Van der Hoeven *et al*. (1993) found that shoot area to dry weight ratio increased from September to December in three pleurocarpous bryophytes, but they could offer no explanation for the shift (Table 1). They assumed chlorophyll per gram dry weight would not change seasonally, based on a study of ***Pleurozium schreberi*** (Figure 7) (Raeymaekers & Glime 1986). But if these species are more active in summer, a decrease in chlorophyll might be expected in December. On the other hand, if they store photosynthate in the summer and have maximum growth during the cooler autumn and early winter, the loss of weight per shoot length might be expected.

Figure 7. ***Pleurozium schreberi***, a species that does not have seasonal changes in chlorophyll content. Photo by Janice Glime.

Table 1. Shoot area to dry weight ratio of mosses in September (n=20) and December (n=25). From van der Hoeven *et al*. (1993).

	September	**December**
Calliergonella cuspidata	143±12	302±45
Rhytidiadelphus squarrosus	140±10	230±30
Ctenidium molluscum	147±11	226±43

There is sufficient indirect evidence that we might expect chlorophyll differences with seasons. For example, we know that photosynthetic capacity changes between summer and winter in at least some mosses. In ***Plagiomnium acutum*** (Figure 8) and ***P. maximoviczii*** (Figure 9), photosynthetic capacity diminishes from 126 and 95 µM CO_2 kg^{-1} dw s^{-1} in summer to 58 and 62 in winter, respectively (Liu *et al.* 2001). On the other hand, the light compensation point of 40 µmol m^{-2} s^{-1} in summer drops to 20 µmol m^{-2} s^{-1} in winter while the light saturation point drops similarly from 400 µmol m^{-2} s^{-1} in summer to 200 µmol m^{-2} s^{-1} in winter. This can most likely be attributed to the lower respiration rate in winter.

Figure 8. ***Plagiomnium acutum***, a moss that changes chlorophyll concentrations and light compensation points between summer and winter. Photo by Yingdi Liu, with permission.

Figure 9. ***Plagiomnium maximoviczii***, a species that changes chlorophyll concentrations and light compensation points between summer and winter. Photo from Hiroshima University Digital Museum of Natural History, with permission.

Although Raeymaekers and Glime (1986) found similar chlorophyll content in the 2 cm terminal parts of ***Pleurozium schreberi*** (Figure 7) in August (2.1 mg/g dw), end of September (2.1), and end of October (2.2) in Baraga County, Michigan, I have observed that ***Fontinalis*** becomes pale by the end of summer (Figure 10) and bright to dark green by February (Figure 11), remaining deep green until June, in New Hampshire and the Upper Peninsula of Michigan. Mártínez Abaigar *et al*. (1993) found distinct differences in chlorophyll *a* with season in two species of ***Fontinalis*** (Figure 15). There is no reason to expect all species to behave the same way, nor to expect the same species to behave the same way in all parts of its distribution.

Figure 10. ***Fontinalis antipyretica*** exhibiting typical late summer and autumn colors. Photo by Malcolm Storey, through Creative Commons, with online permission.

Figure 11. ***Fontinalis antipyretica*** exhibiting typical late winter to early spring colors. Photo by Malcolm Storey, through DiscoverLife, with online permission.

In their study of 13 aquatic bryophytes, Mártínez Abaigar *et al*. (1993) found considerable differences among species in the chlorophyll concentration changes with seasons (Figure 15). For example, ***Fontinalis antipyretica*** (Figure 11) had its highest content in summer, whereas ***F. squamosa*** (Figure 12) had its highest in spring with summer exhibiting the second lowest (Figure 13), the lowest being in autumn. They reported that the greatest chlorophyll content occurred in the immersed species [***Fontinalis antipyretica***, ***F. squamosa***, ***Fissidens grandifrons*** (Figure 14) from San Pedro, ***Jungermannia cordifolia*** (Figure 16), and ***Platyhypnidium riparioides*** (Figure 17-Figure 18)]. The emergent ***Cratoneuron commutatum*** (Figure 19) had the least. This relationship to water is very likely correlated with light availability; the submerged taxa should produce more chlorophyll.

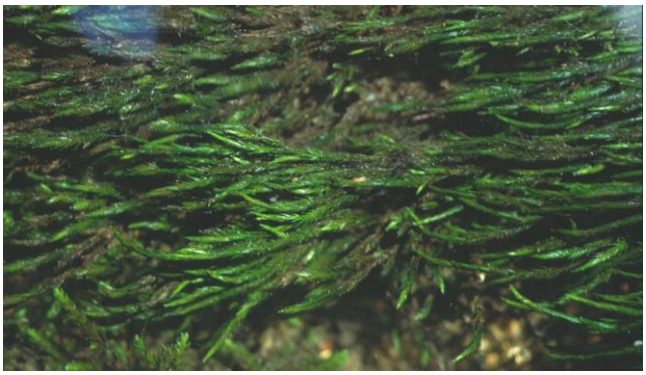

Figure 12. ***Fontinalis squamosa*** with a healthy spring color. Photo by Jan-Peter Frahm, with permission.

Figure 13. ***Fontinalis squamosa*** on rock above water near Swallow Falls Wales in mid-summer. Photo by Janice Glime.

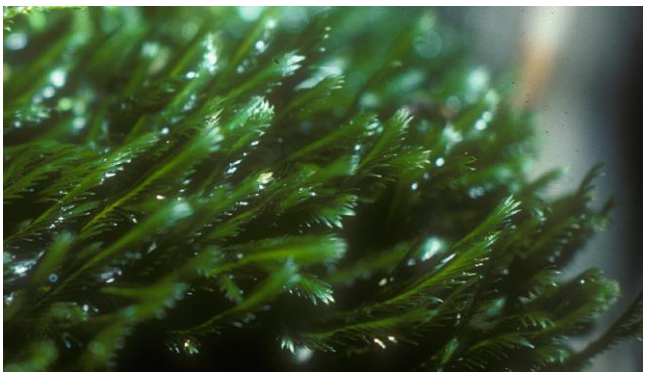

Figure 14. ***Fissidens grandifrons*** exhibiting dark coloration due to high chlorophyll concentrations. Photo by Janice Glime.

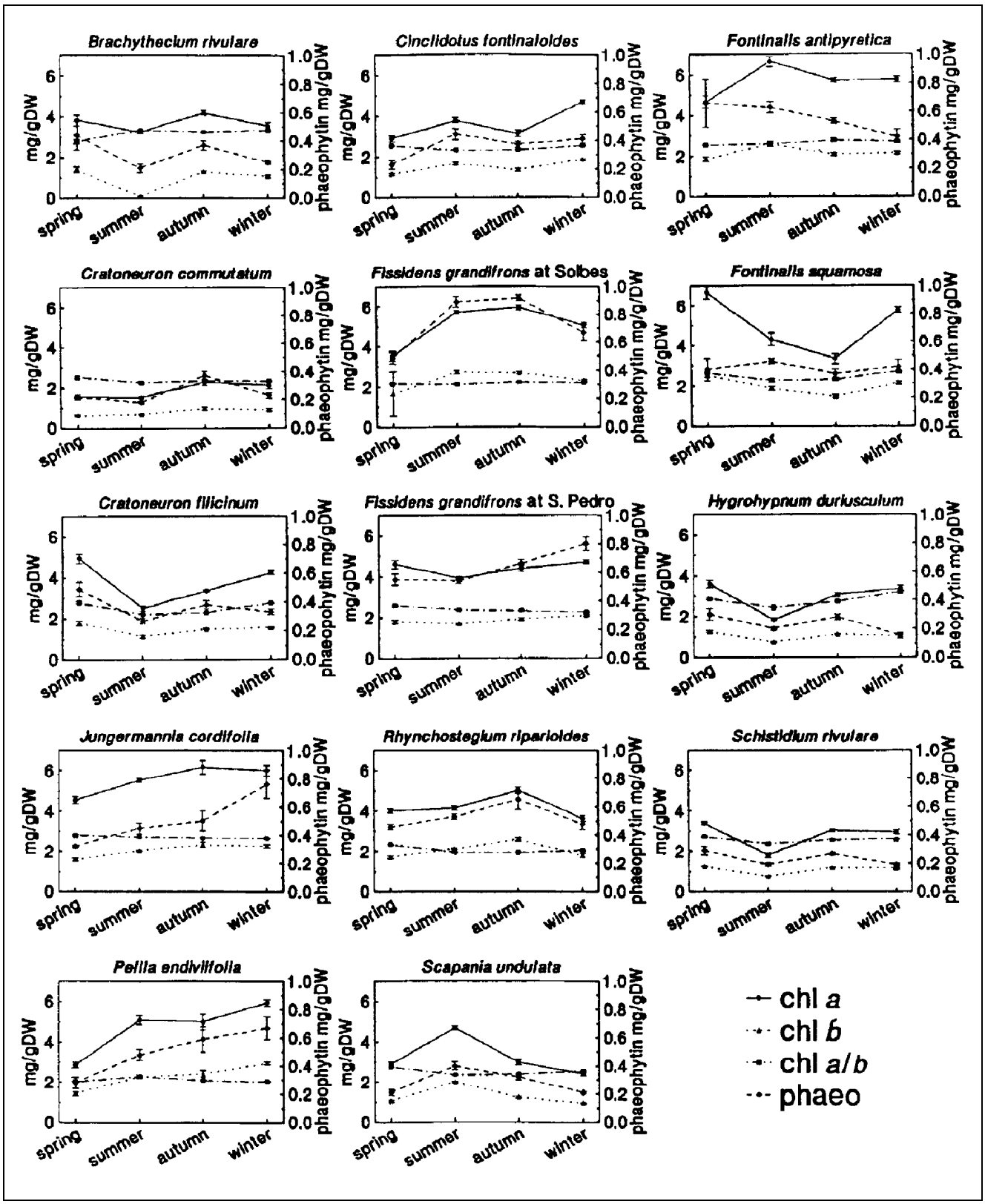

Figure 15. Seasonal changes in chlorophyll (left axis) and phaeophytin (right axis) concentrations (mg/gDW) in 13 species of aquatic bryophytes. Based on Mártínez Abaigar *et al*. 1993.

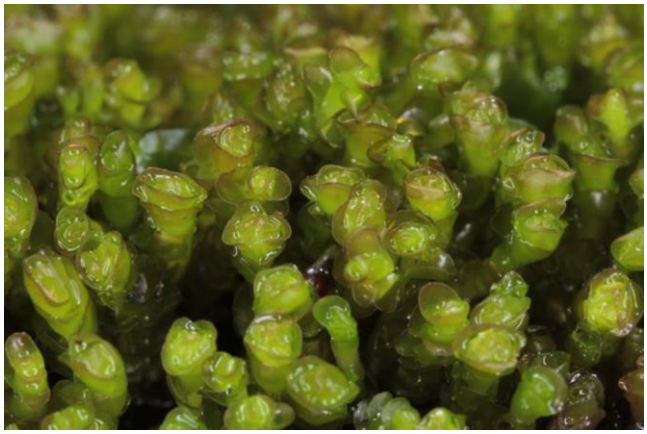

Figure 16. ***Jungermannia cordifolia***, one of the species with the highest chlorophyll content among aquatic species. Photo by Jan-Peter Frahm, with permission.

Figure 17. ***Platyhypnidium riparioides*** showing its habitat and green color. Photo by Hermann Schachner, through Creative Commons.

Figure 18. ***Platyhypnidium riparioides*** showing its bright green color. Des Callaghan, with permission.

Chlorophyll is not the only pigment to respond to seasons. In ***Rhytidiadelphus squarrosus*** (Figure 20), ***R. triquetrus*** (Figure 21), and ***Mnium hornum*** (Figure 22), the biflavonoid and coumestane concentrations likewise showed seasonal variation, with concentrations increasing with periods of active growth (Brinkmeier *et al*. 1999). These concentrations were also affected by light intensity, independent of season.

Figure 19. ***Cratoneuron commutatum*** exhibiting a low concentration of chlorophyll. Photo by Michael Lüth, with permission.

Figure 20. ***Rhytidiadelphus squarrosus***, a species in which biflavonoid and coumestane concentrations increase with periods of active growth. Photo by Michael Lüth, with permission.

Figure 21. ***Rhytidiadelphus triquetris***, a species in which biflavonoid and coumestane concentrations increase with periods of active growth. Photo courtesy of Carrie Andrew.

We cannot rule out light intensity as the cause for these observed seasonal differences. In their study on ***Brachythecium rutabulum*** (Figure 23), Kershaw and Webber (1986) found that total chlorophyll increased from 1.70 mg chl g^{-1} on 8 May to 11.1 mg chl g^{-1} on 11 October, corresponding with full canopy conditions that reduced the light intensity reaching the moss. Concomitantly, light saturation declined from 200 µmol m^{-2} s^{-1} to 30 µmol m^{-2} s^{-1} and the light compensation point declined from 65 µmol m^{-2} s^{-1} to 4 µmol m^{-2} s^{-1}.

Figure 22. ***Mnium hornum***, a species in which biflavonoid and coumestane concentrations increase with periods of active growth. Photo by Michael Lüth, with permission.

Figure 23. ***Brachythecium rutabulum***, a species that increases its chlorophyll content as the tree canopy reduces its available light. Photo by Michael Lüth, with permission.

Mishler and Oliver (1991) found that the amount of green tissue and concentration of chlorophyll per dry weight were higher in summer than in winter or early summer in the xerophytic moss ***Syntrichia ruralis*** (Figure 24). The chlorophyll *a:b* ratios, however, did not follow any seasonal pattern.

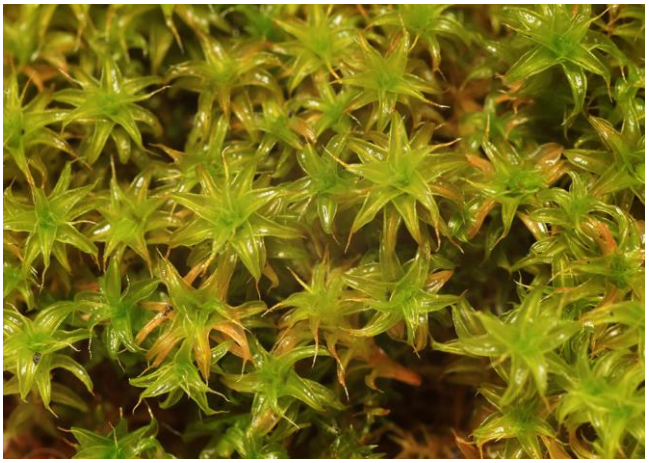

Figure 24. ***Syntrichia ruralis***, a species in which chlorophyll content in summer in the Organ Mountains of southern New Mexico, USA. Photo by Barry Stewart, with permission.

But what do bryophytes do in total darkness, as found under deep snow in winter? Only 3-4 mm of older crystalline snow is required for snow to become opaque (Gates 1962), rendering photosynthesis impossible. It appears that at least some of them should have no problem. When grown in total darkness for four months, the leafy liverwort ***Plagiochila asplenioides*** (Figure 25) rapidly lost starch, but exhibited little loss of chlorophyll (Suleiman & Lewis 1980). Once revived, the tissues were photosynthetically viable immediately. Thus, we should expect that many bryophytes might become photosynthetically active as soon as the snow recedes. Furthermore, low light levels penetrating the snow prior to total melt are sufficient to initiate photosynthesis.

Figure 25. ***Plagiochila asplenioides***, a species that loses almost no chlorophyll in the dark, but does lose starch. Photo by Michael Lüth, with permission.

Colors of Light

Those bryophytes living on the forest floor receive quite a different light quality from those in the open. The canopy, with its massive quantity of green leaves, serves as an effective filter against red light, the part of the spectrum creating the greatest photosynthetic activity. Thus, bryophytes on the forest floor must succeed in light that is weighted toward green and diminished in red wavelengths.

But the color of light is a seasonal attribute. When the canopy is gone from a deciduous forest in winter, light quality is nearly that of full sunlight, whereas in summer it is highly displaced toward the green end of the spectrum when red light is filtered out by the canopy. And the quality of light changes at the two ends of the photoperiod as well as light penetrates a greater distance through the atmosphere when it arrives nearly parallel to the Earth's surface.

Lakes present a similar problem, but for different reasons. Water, both liquid and as snow, is an effective filter against both UV light and the low-energy red wave lengths. Hence, the deeper into the water, or snow, the less of these wavelengths available to the moss. Older, crystalline snow is almost completely opaque to infra-red light. While this water medium is good as protection against UV light, it is detrimental in providing appropriate wavelengths for maximal photosynthesis. Nevertheless, bryophytes, with their single layer of cells, are well adapted, compared to tracheophytes, to capture what little light is able to penetrate, and they benefit from the blue and

green wavelengths that have greater penetration through water and ice. One adaptation to this blue and green light environment is that green light can cause major increases in content of chlorophylls and carotenoids in aquatic bryophytes (Czeczuga 1987). The yellow carotenoids are able to capture the blues and greens that penetrate to the greatest depths. Carotenoids, like chlorophyll *b*, serve as antenna pigments, creating additional surfaces for trapping light and transferring it to the active site of chlorophyll *a*. Might a similar change occur in terrestrial bryophytes, adapting them to life beneath the green filter created by the canopy?

Turbidity of water can have other effects on the light quality. Algae will act much like the canopy and absorb red light with their chlorophyll pigments. Detrital and suspended matter also block and filter the light, altering the quality and the intensity. These can have physiological effects on the bryophytes.

Few studies have examined the effects of the wavelength of light, *i.e.* its color, on the growth or physiology of bryophytes. Most of these have been laboratory studies on tropisms, germination, or growth (see chapter on development). However, Jägerbrand and During (2006) experimented with Icelandic ***Hylocomium splendens*** (Figure 26) and ***Racomitrium lanuginosum*** (Figure 27) in the greenhouse using shade cloth (black netting; green plastic film) compared to colorless plastic film to alter the light quality and intensity in a manner consistent with forest shade. The reduced light of both shade types caused greater elongation, reduced biomass growth, and a lower biomass:length ratio in new growth for both species, but the number of branches, branch density, and biomass:length ratio were higher for ***H. splendens*** (Figure 28). Both shade treatments caused similar increases in length (etiolation) and decreases in the biomass:length ratio. Branch density was significantly decreased by the reduction in red:far red ratio in ***Racomitrium lanuginosum***, typically a sun species. Such a response to shade would permit greater light penetration and reduce self-shading. Similar behavior is seen in the needles of balsam fir (*Abies balsamea*), in which the arrangement of needles on branches is relatively flat on shade branches but go all the way around the upper half of the branch on sun branches.

Figure 26. ***Hylocomium splendens***, a species in which a reduction in the red:far red ratio cause a decrease in branch density. Photo by Sheila, through Creative Commons.

Figure 27. ***Racomitrium lanuginosum***, a species in which a reduction in the red:far red ratio cause a decrease in branch density. Photo by Michael Lüth, with permission.

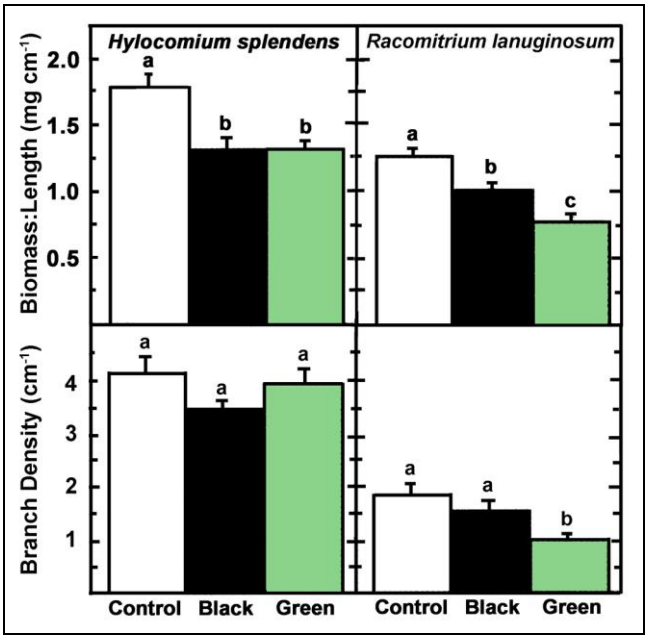

Figure 28. Effects of simulated shade on branch density and biomass to length ratio in two bryophytes. Bars indicate ± SE. Bars with different letters within treatment indicate significant differences (Tukey-Kramer post-hoc-tests, $p<0.05$ except ***Racomitrium lanuginosum*** branch density at $p<0.10$). Redrawn from Jägerbrand & During 2006.

Photoperiod Effects

An alternation of day and night has been with plants since their inception. Thus, we should expect that most species have taken advantage of this alternation in various ways. Continuous light over a long period of time can cause mosses to lose their chlorophyll (Kallio & Valanne 1975). The stroma thylakoids are destroyed, much like the destruction seen in continuous dark in the cave experiments of Rajczy (1982). However, many moss taxa flourish in the continuous light of summer in the Arctic, so destruction in this way must not be universal. Or does it depend on the wavelengths?

Continuous darkness will cause bryophytes to use up their reserves. For example, ethanol-soluble sugars and lipids decrease in green portions of ***Racomitrium***

barbuloides (Figure 29) maintained in continuous darkness, whereas senescent brown portions of the moss do not lose these substances (Sakai *et al*. 2001). Starch, on the other hand, is maintained within the cells under continuous dark treatments. When this same moss was subjected to continuous light, the ethanol-soluble sugars and lipids initially increased in the green portions, but then decreased, concomitant with a significant decline in photosynthetic capacity. The maximum sugar and lipid concentrations stored under 12 hours light/12 hours dark were similar to those in continuous light, but this day/night treatment did not result in diminished photosynthetic capacity.

Figure 29. ***Racomitrium barbuloides***, a species in which continuous darkness results a decrease in ethanol-soluble sugars and lipids. Photo from Digital Museum, Hiroshima University, with permission.

This marked diurnal periodicity under a normal light regime is manifest in peak times for photosynthetic activity. Early morning hours provide the best moisture conditions, so it is not surprising that subalpine populations of ***Pohlia wahlenbergii*** (Figure 30) exhibited their highest photosynthetic activity in the early hours of morning. This high rate repeated itself in the early evening, suggesting photosensitivity and repair (Coxson & Mackey 1990), or could it be only a moisture relationship? Another possible explanation for the peak twice a day is an endogenous rhythm (Coxson & Mackey 1990). In any case, this would appear to be an adaptive behavior for bryophytes that must contend with drying in the afternoon sun, particularly in their most active photosynthetic tissues near the tips.

Figure 30. ***Pohlia wahlenbergii*** var. ***glaciale***, whose peaks in photosynthetic activity are early morning and evening. Photo by Michael Lüth, with permission.

In ***Marchantia polymorpha*** (Figure 31-Figure 32), short photoperiod, and not nutrient supply, cause the plants to produce more gemmae cups (Figure 31), whereas on a long photoperiod more gametangiophores (Figure 32) are produced than on plants in a short photoperiod (Voth & Hamner 1940).

Figure 31. ***Marchantia polymorpha*** gemmae cups, a stage that is promoted by a short photoperiod. Photo by Michael Lüth, with permission.

Figure 32. ***Marchantia polymorpha*** archegoniophores, a stage that is promoted by long photoperiods. Photo by Janice Glime.

Photoperiod can play a role in development, productivity, acclimation, and other aspects of the bryophyte life (Kallio & Saarnio 1986). These topics will be discussed in other chapters related to these topics.

Summary

Changes in light quality, duration, and intensity can signal changing seasons and cause physiological changes that prepare bryophytes for winter or summer conditions. But high light intensities can damage chlorophyll and DNA, especially at low temperatures.

When photooxidation occurs under high light intensities, bryophytes can experience photoinhibition in the form of rupture of the chloroplast envelope, formation of vesicles in thylakoids, and rapid degradation of linolenic acid. Some bryophytes respond to the damaging effects of high light intensity

and low temperatures by producing **light-quenching pigments** such as **sphagnorubin**. At warm temperatures, photorespiration provides an energy shunt to protect chlorophyll from overexcitation. Red pigments may also warm the bryophytes by absorbing heat.

Increased light intensity may stimulate the production in gametangia, but in others it inhibits them. Chlorophyll concentrations may change with seasons, with some bryophytes having high concentrations in early spring, enabling them to take advantage of low light under diminishing snow. Shoot area to dry weight increases in some bryophytes during autumn, perhaps likewise permitting the plants to take advantage of diminishing light. Some mosses have diminished capacity for photosynthesis in winter, but their compensation point and saturation points are also depressed. The changes vary with species and are part of what makes them different species. Nevertheless, generally the chlorophyll *b* concentration increases as light diminishes. Bryophytes that have been under the snow for months are generally ready to begin photosynthesis immediately upon receiving enough light.

Forest canopy leaves filter out a large portion of red light and transmit green light to the bryophytes below. Water accomplishes a similar filtering function, but the green light can cause chlorophylls and carotenoids to increase in aquatic taxa.

Reduced light can cause greater elongation, reduced biomass growth, and a lower biomass:length ratio in new growth, while the number of branches, branch density, and biomass:length ratio can be higher. However, greatly reduced light can cause etiolation, thus reducing self-shading. A reduced ratio of red:far red can decrease branch density.

Continuous light is detrimental to some taxa, but bryophytes in polar regions thrive on the added summer light. Continuous dark can cause some mosses to use up their energy reserves, but low polar temperatures minimize this effect. Many, perhaps most, bryophytes have their peak photosynthetic activity in early morning and late evening when the most moisture is available. Moss gardeners, take note!

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CHAPTER 9-5

LIGHT: REFLECTION AND FLUORESCENCE

JANICE M. GLIME AND MAGDALENA TURZAŃSKA

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CHAPTER 9-5

LIGHT: REFLECTION AND FLUORESCENCE

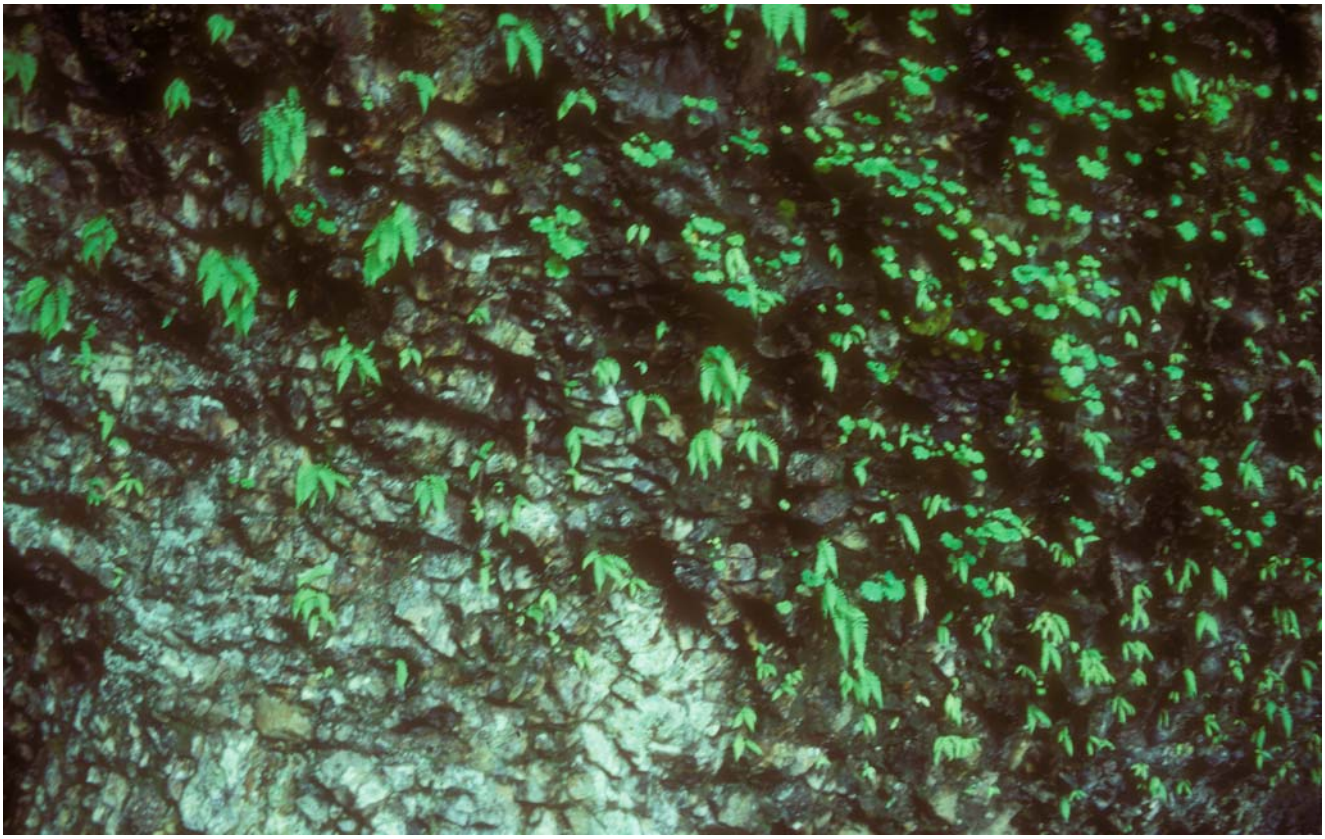

Figure 1. ***Schistostega pennata***, the luminous moss, growing on the roof of a cave in Rausu, Japan. Photo by Janice Glime.

Cave Mosses - Reflectance

Caves provide a classical example of gradients, with diminishing light and temperatures gradually descending or ascending from the mouth to an interior temperature near 10°C. As light diminishes, so does ability of the plant to meet its light compensation point. Thus, through this gradient, we see that flowering plants are the least tolerant, then ferns, followed by bryophytes, and last algae as the most tolerant (Dalby 1966b).

In non-commercial caves where light diminishes rapidly, or in buried lava caves, finding these bryophytes can be difficult and time consuming. Hanley (1982) used an echo sounder to locate bryophytes in caves and other dark areas such as deep lakes. However, in many caves, artificial lights provide sufficient illumination for algae, bryophytes, and ferns to succeed deep within the cave (Boros 1964). In fact, in many commercial caves, bryophytes have been considered to be a nuisance and measures have been taken to remove them, often using sodium hypochlorite. However, to avoid release of chlorine and other dangerous gases into caves, researchers tested hydrogen peroxide. But even the dilute 15% hydrogen peroxide necessary to remove bryophytes is destructive to fragile limestone formations, and the solution must be buffered with bits of limestone rock for at least 10 hours before its application (Faimon *et al*. 2003). I fail to understand why the bryophytes are considered offensive!

Schistostega pennata – Luminous Moss

No moss seems to be revered more than the clandestine cave moss ***Schistostega pennata*** (Figure 1-Figure 3), also known as dragon's gold (Berqvist 1991). Always a delight to find, its protonemata shine like emerald jewels from the darkness of a rock crevice or cave. So intriguing is this moss that the Japanese have a monument to it in Hokkaido (Iwatsuki 1977, Kanda 1988; Figure 2), where it grows in profusion in a cave barely large enough for a child to stand. At just the right position, you can see its marvelous reflections, but move the wrong way and they

are lost. The frond-like gametophyte and terminal sporophyte have none of that ethereal luminescent quality (Figure 3). Ignatov *et al*. (2012) examined the developmental pattern of this species and determined that it has sexual reproduction in September.

Figure 2. Monument to ***Schistostega*** in Hokkaido, Japan. Photo by Janice Glime.

Figure 3. ***Schistostega pennata*** plants showing their frond-like appearance and capsules at the end of the stem. Photo by Martin Hutten, with permission.

This unusual jewel-like property (Figure 4) is the result of the protonema (Gistl 1926). The cells are lens-shaped (Figure 7) and their upper surface is curved in such a way as to focus the light on the interior of the cell (Figure 6; Figure 5). This "normal" form is reached only when they grow in light that comes at all times from the same oblique direction. The chloroplasts orient themselves so that they are always at the most intensely lighted spot on the inner wall of the cell (Figure 7). If a change in the light direction occurs, as may happen seasonally, the chloroplasts can reposition themselves within one to three hours.

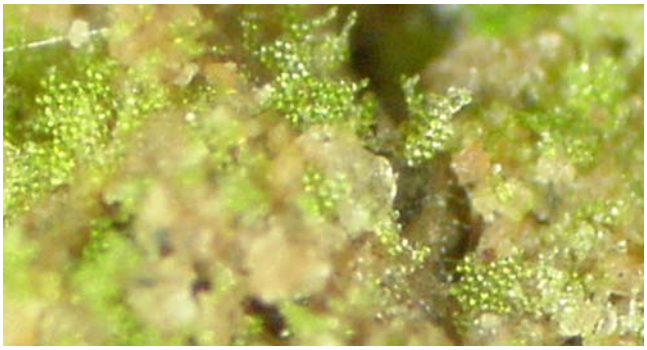

Figure 4. Protonemata of ***Schistostega pennata*** showing upright clumps. Photo courtesy of Misha Ignatov.

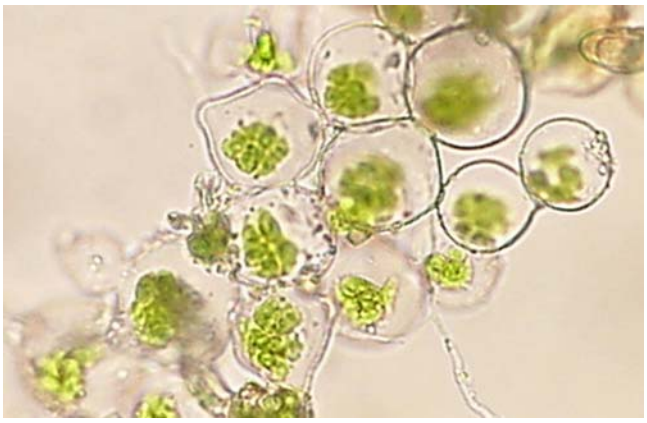

Figure 5. Protonema of ***Schistostega pennata*** showing lens-shaped cells. Photo courtesy of Misha Ignatov.

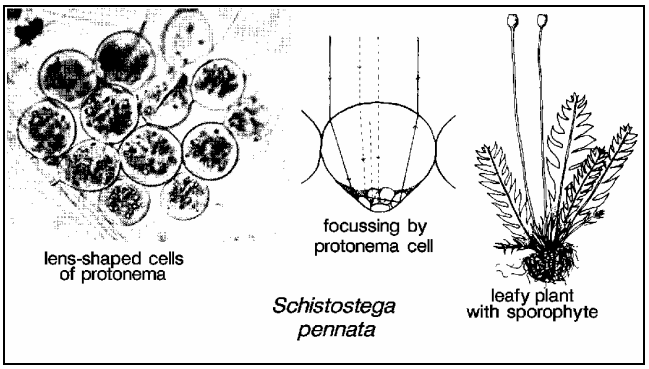

Figure 6. The cave moss, ***Schistostega pennata***, reprinted with permission from Zen Iwatsuki.

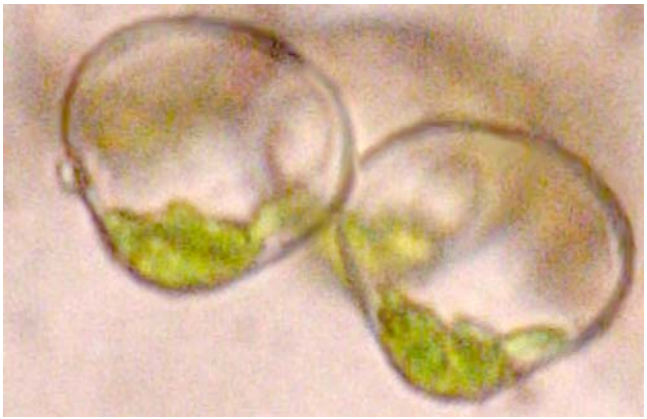

Figure 7. Lens-shaped cells of protonema of ***Schistostega pennata*** with chloroplasts arranged on one side of cell to focus light. Photo courtesy of Misha Ignatov.

Like Crum (1973), we find appeal in retelling the account by Kerner von Marilaun in *Pflanzenleben*, as translated by F. W. Oliver in *The Natural History of Plants*:

> "On looking into the interior of the cave, the background appears quite dark, and an ill-defined twilight only appears to fall from the center on to the side walls; but on the level floor of the cave innumerable golden-green points of light sparkle and gleam, so that it might be imagined that small emeralds had been scattered over the ground. If we reach curiously into the depth of the grotto to snatch a specimen of the shining objects, and examine the prize in our hand under a bright light, we can scarcely believe our eyes, for there is nothing else but dull lusterless earth and damp, mouldering bits of stone of yellowish-grey color! Only on looking closer will it be noticed that the soil and stones are studded and spun over with dull green dots and delicate threads, and that, moreover, there appears a delicate filigree of tiny moss-plants, resembling a small arched feather stuck in the ground [Figure 10]. This phenomenon, that an object should only shine in dark rocky clefts, and immediately lose its brilliance when it is brought into the bright daylight, is so surprising that one can easily understand how the legends have arisen of fantastic gnomes and cave-inhabiting goblins who allow the covetous sons of earth to gaze on the gold and precious stones, but prepare a bitter disappointment for the seeker of the enchanted treasure; that, when he empties out the treasure which he hastily raked together in the cave, he sees roll out of the sacks, not glittering jewels, but only common earth. . . . On the floor of rocky caves one may discern by careful examination two kinds of insignificant-looking plant-structures, one a web of threads studded with small crumbling bodies, and the other bluish-green moss-plants resembling tiny feathers. The threads form the so-called protonema, and the green moss-plants grow up as a second generation from this protonema ... the gleams do not issue from the green moss-plants, but only from their protonema."
>
> "From the much branched threads ... numerous twigs rise up vertically, bearing groups of spherical cells arranged like bunches of grapes. All the cells of a group lie in one plane, and each of these plants is at right angles to the rays of light entering through the aperture of the rocky cleft. Each of the spherical cells contains chlorophyll-granules, but in small number ... and they are always collected together on those sides of the cells which are turned towards the dark background of the cave.... Taken together, these chlorophyll-granules form a layer which under low power of the microscope appears as a round green spot ... the light which falls on such cells through the opening of a rocky cleft behaves like the light which reaches a glass globe at the further end of a dark room. The parallel incident rays which arrive at the globe are so refracted that they form a cone of light, and since the hinder surface of the globe is within this cone, a bright disc appears on it. If this disc, in which the refracted rays of light fall, is furnished with a lining, this also will be comparatively strongly illuminated by the light concentrated on it and will stand out from the darker surroundings as a bright, circular patch.... It is well worthy of notice that the patch of green chlorophyll-granules on the hinder side of the spherical cell extends exactly so far as it is illumined by the refractive rays, while beyond this region, where there is no illumination, no chlorophyll granules are to be seen. The refracted rays which fan on the round green spot are, moreover, only partially absorbed; in part they are reflected back as from a concave mirror, and these reflected rays give a luminous appearance. This phenomenon, therefore, has the greatest resemblance to the appearance of light which the eyes of cats and other animals display in half-dark places, only illumined from one side, and so does not depend upon a chemical process, an oxidation, as perhaps does the light from a glow-worm or of the mycelium of fungi which grow on decaying wood. Since the reflected light-rays take the same path as the incident rays had taken, it is clear that the gleams of the ***Schistostega*** can only be seen when the eye is in the line of the incident rays of light. In consequence of the small extent of the aperture through which the light penetrates into the rock cleft, it is not always easy to get a good view.... If we hold the head close to the opening, we thereby prevent the entrance of the light, and obviously in that case no light can be reflected. It is, therefore, better when looking into the cave to place one's self so that some light at any rate may reach its depth. Then the spectacle has indeed an indescribable charm."

The result of these very reflective chloroplasts in ***Schistostega pennata*** is that the protonema takes on the appearance of "goblin gold" and can create quite eerie effects (Figure 4-Figure 5; Figure 8-Figure 9).

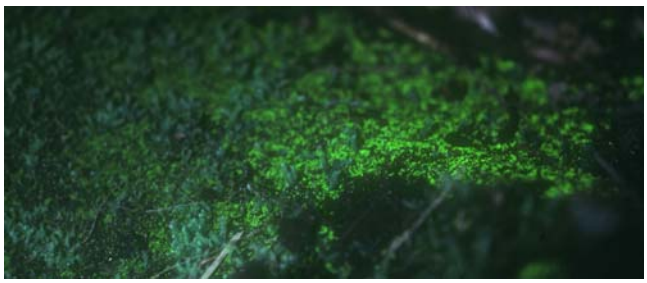

Figure 8. Luminous appearance of ***Schistostega pennata*** protonemata. Photo by Janice Glime.

Figure 9. Luminous protonemata of ***Schistostega pennata*** in natural light. Photo by Martin Hutten, with permission.

Figure 10. A single plant of ***Schistostega pennata*** among its protonemata, the "small arched feather." Photo by Des Callaghan, with permission.

In Japan, there is an opera written about this moss! The opera, written by Ikuma Dan, is based on a book of the same title, "Luminous Moss," by Taijun Takeda (Glime & Iwatsuki 1987). The story relates the tragedy of several sailors who were stranded by a blizzard on the northern island of Hokkaido. With no hope of escaping that remote northern tip of the island before spring to find food and shelter elsewhere, they hid in a cave. As their rations ran out and their fellow sailors died of starvation, they did the only thing they could to survive – they became cannibals. Finally, the captain alone remains. When he is brought to trial for his unthinkable acts, he reflects on the halo of green (the luminous moss) about the heads of each who has been a cannibal, but he tells the courtroom that the halo is visible only to those who have not been cannibals. He alludes to the cannibal in each of us as we struggle to survive among the millions of the world. Today a cave in Hokkaido is set aside as a memorial to protect this unusual moss (Kanda 1971, 1988; Figure 2).

Schistostega pennata (Figure 8-Figure 10) is widespread in the North Temperate Zone. Bowers (1968) and Conard (1938) have reported it from the Upper Peninsula of Michigan, where I have seen it growing on the roof of a cave behind a waterfall. Outside that same cave, I have observed the leafy gametophore, which resembles a tiny fern frond (Figure 11), growing on a small ledge of the rock wall, but protonemata there, if present, did not exhibit their highly reflective property. Bowley (1973) found the moss in several localities in Vermont, Champlin (1969) reported it from Rhode Island, Christy and Meyer (1991) from Wisconsin, Case (1975) found it in Alberta, Canada. Matsuda (1963) reported it in artificial caves in Japan. Perhaps the most unusual report is that of Koike (1989) who reported its culture in empty bottles in urban areas of Japan. Reinoso Franco *et al*. (1994) considered it to be an acidophile, at least on the Iberian Peninsula.

When I went to Germany, I was delighted to find ***Schistostega pennata*** (Figure 8-Figure 11) growing at the base of a boulder where it probably did not get direct sunlight except at sunset and most likely did not get direct rainfall very often either. Perhaps one reason for its success in such habitats is the presence of protonemal gemmae (Edwards 1978). In the Europe, ***Schistostega pennata*** also grows in rabbit holes (Glenny 2020).

Figure 11. ***Schistostega pennata*** showing frond-like branches of leafy gametophyte. Photo with permission from Botany Website, UBC, with permission.

Cyathodium

In the thallose liverwort genus ***Cyathodium*** (Figure 12), some species that grow in caves and similar low-light environments also emit a yellowish luminescence from their thalli (Crum 1973). These liverworts are tropical and subtropical and in China grow in karst caves (Zhang *et al*. 2004).

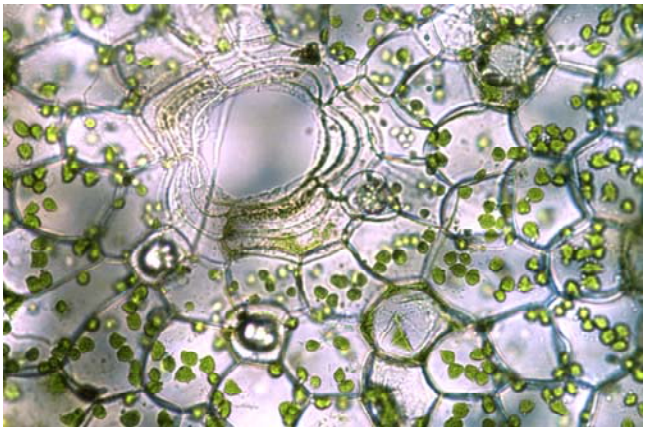

Figure 12. View through pore of ***Cyathodium cavernarum***, a thallose cave liverwort that emits a yellowish luminescence in caves. Photo by Noris Salazar Allen.

Mittenia plumula

In Australia, a similar moss, ***Mittenia plumula*** (Figure 13), lives on dimly lit, clay-covered rock ledges, at the entrances to wombat holes (Figure 14-Figure 15), and on tip-up mounds of fallen trees (Figure 16-Figure 17). The latter habitat makes the moss rather common after cyclone damage that causes trees to topple. In these locations, the moss lives on soil. Stone (1961, 1986) concluded that ***Mittenia*** belongs in the order **Schistostegales** with ***Schistostega*** (Figure 1-Figure 11). Both have a pinnate leaf arrangement, protonemata with similar luminescent properties, similar pale color of the leafy plant, and similar habitats.

Figure 13. ***Mittenia plumula*** showing leaves with bluish tint. Photo courtesy of David Glenny.

Figure 14. ***Mittenia plumula*** in wombat hole in Australia. Photo by Tony Markham, with permission. See <https://www.youtube.com/watch?v=PaXJTcaz1RE>.

Figure 15. ***Mittenia plumula*** growing in a wombat hole in Australia. Photos by Janice Glime.

Figure 16. ***Mittenia plumula*** habitat on tip-up mound. Photo courtesy of David Glenny.

Figure 17. ***Mittenia plumula*** protonemata on tip-up mound. Photo courtesy of David Glenny.

Mittenia plumula differs from ***Schistostega pennata*** by having protonemata with cylindrical filaments instead of spherical cells that act as a lens. Unlike ***Schistostega pennata*** (Figure 1-Figure 11), where the protonemal cells are spherical and are obviously acting as a lens, the

protonema of ***Mittenia plumula*** (Figure 18-Figure 20) is composed of cylindrical filaments and the chloroplasts are not on one side of each cell to take advantage of focused light. Nevertheless, under the compound microscope there is a faintly visible blue luminescence from the filament walls. This luminescence resembles the iridescence seen in some tropical plants of dark forest floors, for instance in ***Selaginella willdenowii*** (Figure 21).

Figure 18. ***Mittenia plumula*** protonemata in rabbit hole. Photo from Wildlife in the Marches at <www.youtube.com> .

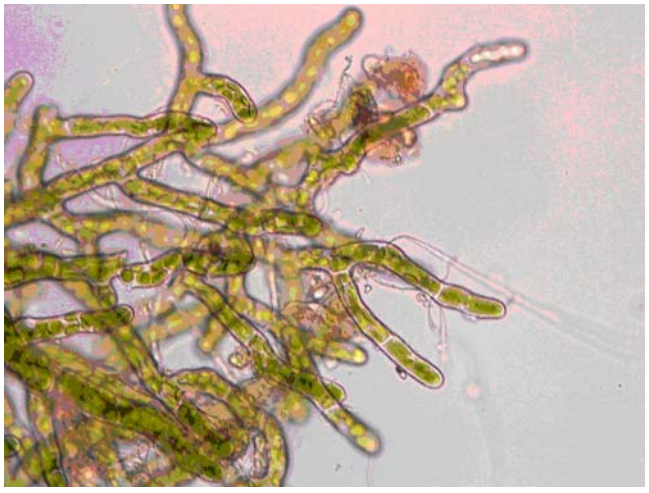

Figure 19. ***Mittenia plumula*** protonemata. Photo courtesy of David Glenny.

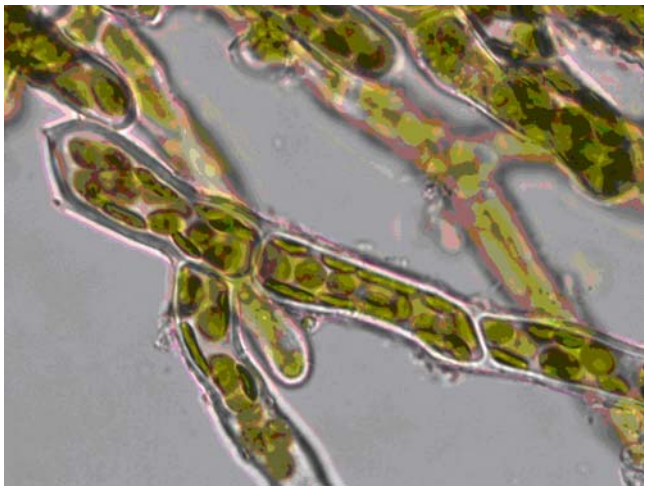

Figure 20. ***Mittenia plumula*** protonemata. Photo courtesy of David Glenny.

Figure 21. ***Selaginella willdenowii*** exhibiting **iridescence**. Photo courtesy of David Glenny.

Cave Communities

Growth of other bryophytes in caves far from a natural light source has been a source of fascination for both bryologists and non-bryologists all over the world, and these bryophytes often form zones around electric lights (Haring 1930). So fascinating are these plants of low light that their descriptions have appeared in non-botanical journals. Boros (1964) was able to publish a paper in the first volume of the *International Journal of Speleology* (**speleology** is the study of caves), reporting on mosses growing around electric light sources deep within a cave. Dalby (1966b) later published a similar article on their growth under reduced light in caves, this time in the first volume of *Studies in Speleology*. Numerous communities have been described from caves around the world: Shiomi (1973) in Japan; Maheu and Guerin (1935) in France; Rajczy (1979) in Greece; Ziober (1981), Komáromy *et al*. (1985), Rajczy *et al*. (1986), and Buczkó and Rajczy (1989) in Hungary; Lo Giudice & Privitera (1984) in Italian grottos; Stefureac (1985) in Romanian grottos; Weber (1989) for both animals and flora, including bryophytes, in two German caves and artificial caverns; Kubešová (2009) in the Czech Republic. Even *Science* has accepted articles on mosses in Virginia (USA) caverns, including the famous Luray Cavern (Lang 1941, 1943), and Prior (1961) again studied Luray Cavern mosses, publishing in *The Bryologist*.

Most cave bryophytes are not specific to these habitats. Reinoso Franco *et al*. (1994) have found ***Schistostega pennata*** with ***Isopterygium elegans*** (Figure 22; low-light species of canyons and crevices), ***Diplophyllum albicans*** (Figure 23; forest epiphyte), ***Calypogeia arguta*** (Figure 24), ***C. azurea*** (Figure 25; also an epiphyte), ***Pogonatum nanum*** (Figure 26), and ***Fissidens curnovii*** at a *p*H of 5.7 in caves.

Figure 22. ***Isopterygium elegans***, a species that is able to grow in low light. Photo by Michael Lüth, with permission.

Figure 23. ***Diplophyllum albicans***, a species that is able to grow in low light. Photo by Michael Lüth, with permission.

Figure 24. ***Calypogeia arguta***, a species that is able to grow in low light. Photo by Des Callaghan, with permission.

Figure 25. ***Calypogeia azurea***, a species that is able to grow in low light. Photo by Hermann Schachner through Creative Commons.

Figure 26. ***Pogonatum nanum***, a species that is able to grow in low light. Photo by J. C. Schou, with permission.

The widespread ***Fissidens taxifolius*** (Figure 27) grew in Crystal Caverns in Virginia, USA, and aroused the curiosity of a visitor who delivered it to Conard (1932). This moss grew on the damp ceiling, forming circles about 8" from several electric light bulbs, having appeared only a few years earlier. The moss looked normal, but the leaves were further apart than in typical specimens, not an unusual trait for a moss of low light.

Figure 27. ***Fissidens taxifolius***, a common moss that can grow on the ceiling of caves. Photo by Jan-Peter Frahm, with permission.

A variety of species seem to be capable of growing in caves. Buczkó & Rajczy (1989) reported nineteen bryophyte taxa from three caves in Hungary. Dalby (1966a) reported the occurrence of the **tufa**-former (rock former resulting in carbonates built upon bryophytes and other plants due to addition of photosynthetic oxygen to dissolved minerals), ***Eucladium verticillatum*** (Figure 39), in a poorly lit cave, also occurring in caves in Hungary (Buczkó & Rajczy 1989). In Crystal Cave, Wisconsin, Thatcher (1949) found ***Barbula unguiculata*** (Figure 28), ***Brachythecium populeum*** (Figure 29), ***Brachythecium salebrosum*** (Figure 30), ***Bryoerythrophyllum recurvirostrum*** (Figure 31), ***Bryum caespiticium*** (Figure 32), ***Bryum capillare*** (Figure 33), ***Ceratodon purpureus*** (Figure 34), ***Fissidens taxifolius*** (Figure 27), ***Leptodictyum riparium*** (Figure 35), ***Marchantia polymorpha*** (Figure 36), ***Plagiomnium cuspidatum*** (Figure 37), and ***Warnstorfia fluitans*** (Figure 38). Like Conard, Thatcher observed the leaves to be more distant than is typical.

Figure 28. ***Barbula unguiculata***, a species that is able to grow in caves. Photo by Michael Lüth, with permission.

Figure 29. ***Brachythecium populeum*** with capsules, a species that is able to grow in caves. Photo by Janice Glime.

Figure 30. ***Brachythecium salebrosum***, a species that is able to grow in caves. Photo by Michael Lüth, with permission.

Figure 31. ***Bryoerythrophyllum recurvirostrum***, a species that is able to grow in caves. Photo by Michael Lüth, with permission.

Figure 32. ***Bryum caespiticium*** with capsules, a species that is able to grow in caves. Photo by Bob Klips, with permission.

Figure 33. ***Bryum capillare***, a species that is able to grow in caves. Photo by Andrew Spink, with permission.

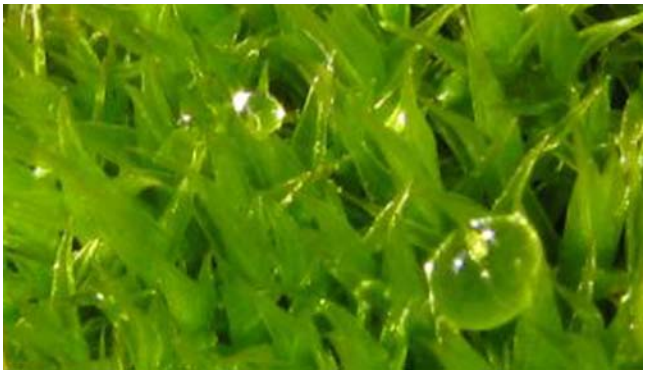

Figure 34. ***Ceratodon purpureus***, a species that is able to grow in caves. Photo by Jiří Kameníček, with permission.

Figure 35. ***Leptodictyum riparium***, a species that is able to grow in caves. Photo by Michael Lüth, with permission.

Figure 36. ***Marchantia polymorpha***, a species able to grow in caves. Photo from Botany Website, UBC, with permission.

Figure 37. ***Plagiomnium cuspidatum***, a species that is able to grow in caves. Photo by Michael Lüth, with permission.

Figure 38. ***Warnstorfia fluitans***, a species that is able to grow in caves. Photo by Michael Lüth, with permission.

Komáromy *et al*. (1985) likewise found ***Eucladium verticillatum*** (Figure 39), a ***Brachythecium*** (***B. velutinum***), and two species of ***Fissidens*** [***F. dubius*** (Figure 40), ***F. pusillus*** (Figure 41)] in a cave. Within only one year from its first illumination, Howe Cavern in New York, USA, already was adorned with ***Amblystegium serpens*** (var. ***juratzkanum***; Figure 42), ***Amphidium mougeotii*** (Figure 43), ***Brachythecium rutabulum*** (Figure 44), ***Bryum caespiticium*** (Figure 32), ***Bryum capillare*** (Figure 33), ***Leptobryum pyriforme*** (Figure 45), and ***Marchantia polymorpha*** (Figure 36) encircling its new lights (Haring 1930). Buczkó and Rajczy (1989) found that ***Amblystegium serpens*** (=*A. juratzkanum* var. *juratzkanum*; Figure 42) was the most characteristic moss in several Hungarian caves, extending furthest from the cave entrance that provided the only light, surviving at only 232 lux. Niklas Lönnell reported to Bryonet (3 March 2010) that ***Eucladium verticillatum*** (Figure 39) introduced at an underground station in Stockholm, Sweden, thrives decades later on moist areas of the walls where artificial light is available.

Figure 39. ***Eucladium verticillatum***, a tufa-forming moss. Photo by Michael Lüth, with permission.

Figure 40. ***Fissidens dubius***, a known cave dweller. Photo by Bernd Haynold, through Creative Commons.

Figure 41. ***Fissidens pusillus***, a species known to live in caves. Photo by Michael Lüth, with permission.

Figure 42. ***Amblystegium serpens***, a common cave moss in Hungary. Photo by Michael Lüth.

Figure 43. ***Amphidium mougeotii***, a species that colonized within one year around lights in a cave. Photo by Michael Lüth, with permission.

Figure 44. ***Brachythecium rutabulum*** with capsules, a species that colonized around lights in a cave within one year. Photo by Tim Waters, through Creative Commons.

Figure 45. ***Leptobryum pyriforme***, an invader of bare soil in caves. Photo by Michael Lüth.

Tufa formers such as ***Eucladium*** (Figure 39) (von der Dunk & von der Dunk 1980), ***Barbula*** (Figure 28), and ***Didymodon*** (Figure 46) are found in many of these caves, since the caves are usually limestone, and tufa formers must be adapted to relatively dim light to survive the calcium carbonate covering they must endure.

Figure 46. Tufa-forming ***Didymodon tophaceus***, a former of didymodontoliths. Note carbonates at base encrusted on older stems. Photo by Michael Lüth, with permission.

With all these reports, it is not unexpected then that Koponen (1977) reported mosses at a depth of 176 m in a mine at Vihanti, Finland. The surprising fact is that the mosses he found are the very light-tolerant ***Ceratodon purpureus*** (Figure 34) and ***Pohlia nutans*** (Figure 47). But then, these two mosses seem to do well in extremes, as long as it is not too hot.

Jedrzejko and Ziober (1992) illustrated the effects of light on the species composition of moss communities and the ability of mosses to survive at low light intensities with their study of bryophytes in seven Polish caves. More than 50% of the bryophyte flora occurred where they had full access to daylight. As the investigators went deeper into the caves, the number of species decreased, but with 1.3% of the species occurring only in the darkest zone.

Figure 47. ***Pohlia nutans***, a widespread moss that frequents caves and mines. Photo by Michael Lüth.

Rockhouses

Rockhouses are really just small caves created by deep recesses in bedrock cliffs. But despite their smaller size, they can create conditions much different from those of their surroundings outside the cavity. They tend to be buffered from extremes in both temperature and moisture, with cold blasts emanating in the summer and protection from severely cold winds in the winter. Nevertheless, despite their moderate climate, their low light levels greatly restrict the potential flora. It is therefore interesting that the greatest affinities of these floras are with the tropics (Farrar 1998). While the species in the rockhouses tend to be endemic to the eastern United States, the conditions created for them mimic the low light intensities of the dense rainforests. It is possible that the climatic moderation of the rockhouses might have permitted adapted plant groups to persist here since the time when a tropical/subtropical climate existed in the eastern US during the Pre-Pleistocene. It is in these secluded habitats that a number of endemic ferns reside, but the most numerous plants are the bryophytes. Farrar considered both groups to be preadapted to this habitat by their vegetative reproduction and their ability to have net photosynthetic gain in very low light.

Responses to Low Light in Caves

If you have ever picked up a board from your lawn, you know how thin and long the grass stems can be. This elongation response by plants in low light is termed **etiolation**. Dunham and Lowe (1927) described etiolation of bryophytes in caves and among boulders in New England, USA. But at least some light should be present, right? Nevertheless, Fries (1945) succeeded in growing the mosses ***Funaria hygrometrica*** (Figure 48) and ***Leptobryum pyriforme*** (Figure 45) from protonemata on inorganic media in total darkness. Thus, it would appear that some growth can occur, using the plant's reserves, even in the absence of light.

Rajczy (1978-1979) chose to experiment with growing mosses in total darkness of a cave. He used two common Hungarian species, ***Atrichum undulatum*** (Figure 50) and ***Plagiomnium ellipticum*** (Figure 51), which he planted in flowerpots along with their original soil. These were placed in a cave where the climate is very constant, having a temperature of 9.5 ±1ºC and 95-100% relative humidity. ***Plagiomnium ellipticum*** rapidly became brown and within three months had produced long, fine, vertical, leafless stems of 4-6 cm length. ***Atrichum undulatum***, on the other hand, remained green for two years. Its chloroplasts increased from a mean of 8.8 to 10.3 per cell from May to October. In the cave both species had a much higher ratio of dark CO_2 fixation that did the control samples from normal light (Table 1). One interesting event in Rajczy's experiment was that isopods (***Mesoniscus graniger***; Figure 49) consumed all the dead material of the plants. The mosses soon grew pale, then partly brown.

Figure 48. ***Funaria hygrometrica***, a species that is able to grow without a media carbon source in the dark. Photo by Michael Lüth, with permission.

Table 1. Incorporation of CO_2 into moss biomass in caves compared to controls. From Rajczy 1978-1979.

$^{14}CO_2$ Incorporation				
	Net Activity (cmp/leaf)			Contrib dk
	total fix	dark fix	light fix	fix to total fix
Atrichum undulatum				
control	898	85	813	9%
cave sample	174	81	93	47%
Plagiomnium ellipticum				
control	3790	340	3450	9%
cave sample	550	220	330	40%

Figure 49. ***Mesoniscus graniger***, an isopod consumer of dead mosses. Photo by Richard Kovács, through Creative Commons.

When ***Atrichum undulatum*** (Figure 50) cells were examined with the electron microscope after four months of experiment (September), the chloroplasts differed considerably from those of the control plants. The size of the grana had increased but their number decreased and they were arranged mostly at the periphery of the chloroplast. There were no starch grains. Then, in March, there was a most unexpected change. The chloroplasts contained starch once more and the grains appeared to be identical to those of the control plants. Thylakoids (Figure 52) were even thinner than in September, and only 1-2 stroma thylakoids were present. From 3 to 10 broad, low grana were present.

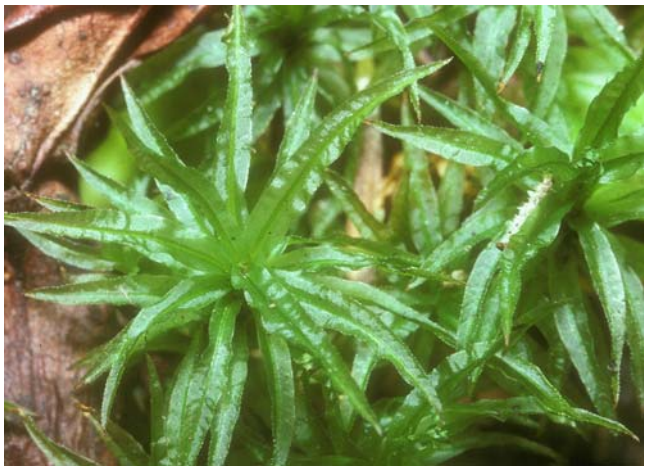

Figure 50. ***Atrichum undulatum***, a species that acclimates to living in caves. Photo by Janice Glime.

Figure 51. ***Plagiomnium ellipticum***, a species that seems unable to live in the low light of caves. Photo by Michael Lüth, with permission.

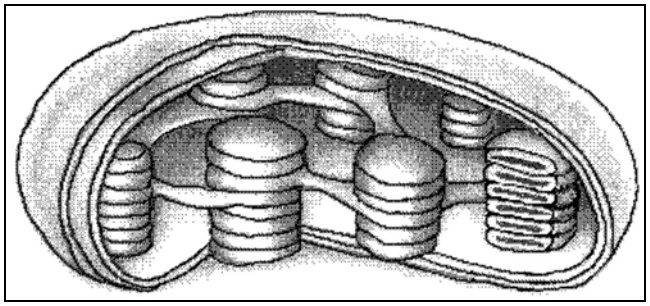

Figure 52. Chloroplast with cutaway view to show inner and outer membrane, stacks of thylakoids that form grana, and connecting stroma. Drawing by Janice Glime

Surprisingly, ***Plagiomnium ellipticum*** (Figure 51) also had starch grains in March. However, these were not like those of their control plants. Some were far larger, and most chloroplasts lacked them. Most of the chloroplast envelopes were torn up.

In April, samples taken from the cave to the lab had measurable photosynthesis, although they had no exposure to light prior to the time of measurement. For ***Atrichum undulatum*** (Figure 50), photosynthesis reached 15-20% of that in the controls. Both species retained some photosynthetic activity for the two years of the experiment, but that of ***Atrichum undulatum*** was greater.

Rajczy (1978-1979) interpreted these results to mean that the mosses were subsisting on heterotrophic energy sources. He could find no other explanation for the sudden appearance of starch after 10 months in the cave. Furthermore, he cited the dark-culturing experiments of Servettaz (1913), Pringsheim and Pringsheim (1935), and Fries (1945) to support his position. Could the mosses be using electromagnetic rays? symbiosis? chemosynthesis? Cave algae are known to subsist using these unusual methods of obtaining energy (Kol 1966; Hadju 1979). And why did both species [***Atrichum undulatum*** (Figure 50) and ***Plagiomnium ellipticum*** (Figure 51)] have starch grains in March when the grains had disappeared earlier? Did some endogenous rhythm, lacking stimulus by photoperiod or temperature, trigger a change in metabolic activity?

Reflectance in the Desert

In desiccation-tolerant species, surface properties often change. This can result in a change in surface reflectance, as exemplified in the xerophytic moss ***Syntrichia ruralis*** (Figure 53) (Hamerlynck *et al*. 2000). In this species, distinct differences occur in the ability to establish thermal dissipation of excess light energy throughout a range of light levels, helping to protect the sensitive chlorophyll and DNA.

Figure 53. ***Syntrichia ruralis***, a species that changes its optical properties when dry vs wet. Photo by Jan-Peter Frahm, with permission.

In the Antarctic, surface reflectance properties differed over a range of water content, but did not correlate with pigment content (Lovelock and Robinson 2002). Nevertheless, the photochemical reflectance was correlated with the concentrations of active xanthophyll-cycle pigments and the photosynthetic light use efficiency as

measured by chlorophyll fluorescence. The water content had a strong influence on both the amplitude and position of the red-edge and may itself cause the differences in reflectance. Continuous high levels of xanthophyll pigments indicate the continual high light levels.

Fluorescence and Other Light Emissions

(coauthored with Magdalena Turzańska)

Definitions

Wikipedia defines **fluorescence** as "emission of light by a substance that has absorbed light or other electromagnetic radiation of a different wavelength." One little-known property of at least some bryophytes is their ability to fluoresce various colors in UV light. Lichenologists are familiar with this property in lichens (Figure 54-Figure 55), using it as an identification tool (Hale 1956). Bees know it in flowers (we call them nectar guides), being attracted to fine lines of marsh marigold (*Caltha palustris* – Figure 56-Figure 57) and black patches of oriental poppy (*Papaver orientale* – Figure 58) petals and by their emission of fluorescence in the UV light of the sun. In fact, Talamond *et al*. (2015) consider **autofluorescence** to be abundant in plant cells. But bryologists seem rarely to use it

Figure 54. The lichen *Xanthoria polycarpa* in natural light. Photo through Creative Commons.

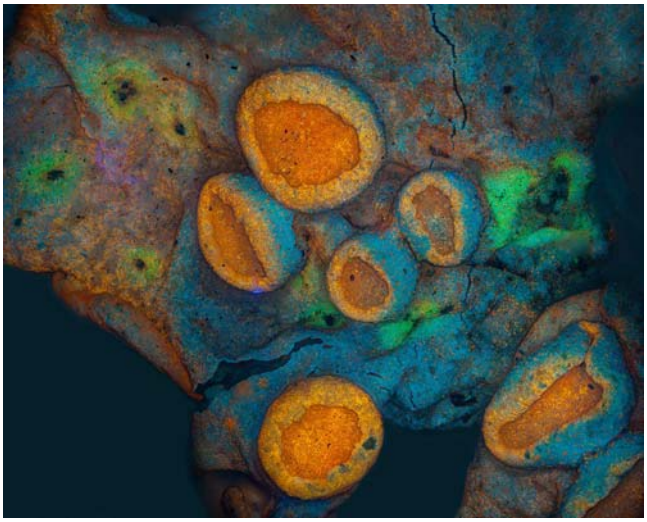

Figure 55. *Xanthoria polycarpa* showing fluorescence in UV light. Photo by Walter Machielsen, with permission.

Figure 56. *Caltha palustris*, a species whose flowers appear yellow to us, but that reflect UV rays seen by bees. Photo by H. Zell, through Creative Commons.

Figure 57. *Caltha palustris* in UV light, showing UV-reflecting lines. Photo courtesy of Dave Kofranek.

Figure 58. The oriental poppy (*Papaver orientale*) has patches that appear black to us, but that reflect UV light that is visible to bees, guiding them to the center of the flower where the pollen and stigma reside. Photo by Janice Glime.

Fluorescence should not be confused with **bioluminescence**. Fireflies have bioluminescence. Some dinoflagellates (think red tides) have bioluminescence. This is a form of chemiluminescence produced by living organisms. It requires a light-emitting molecule (**luciferin**)

and an enzyme (**luciferase**), wherein the enzyme catalyzes the oxidation of the luciferin. The luciferin and its associated enzyme differ among species. The reaction may also require **ATP** (energy-carrying molecule, adenosine triphosphate). In **luminescence**, something adds energy, causing an electron to get bounced from one orbital to another, emitting light, then decaying back down (Jerry Jenkins, Bryonet 23 April 2022). Bioluminescence is not known in land plants, but since it is present in some bacteria, it is possible that we have not discovered it in some bacteria-bryophyte associations. **Triboluminescence** results from mechanical energy such as crushing sugar cubes or rubbing quartz crystals. Heat produces **incandescence** (emitted from hot body as result of high temperature, *e.g.* incandescent light bulb).

Phosphorescence (microsecond decay that changes spin state, causing prolonged emission of light even in darkness) is a form of luminescence that results from the absorption of radiation (such as light or electrons) and continues for a noticeable time after these radiations have stopped. We have seen these in various items that glow in the dark after being exposed to light. I have seen them on cards with a cross or on ceilings to look like stars.

Fluorescence is not seen by the human eye during the day because our eyes are less sensitive to those short wave lengths and the longer "visible" light waves keep us from seeing it. However, with the right equipment, *i.e.* a UV light source, we can detect it. The discovery of a liverwort that was fluorescing precipitated one of the longest running threads on Bryonet.

Jerry Jenkins (Bryonet 23 April 2022) provided us with a detailed description of the light emissions from organisms. For example, he noted that the light emitted by ***Zygodon rupestris*** (=***Zygodon viridissimus* var. *rupestris***; Figure 59), shared by Ken Kellman (Bryonet 21 April 2022), could be **fluorescence** or **phosphorescence**. These cannot be distinguished just by using a UV flashlight.

Figure 59. ***Zygodon rupestris***, a species known for blue fluorescence. Photo by Jonathan Sleath, with permission.

It is intriguing that the ***Zygodon rupestris*** (Figure 59) does not emit this light when dry (Ken Kellman, Bryonet 21 April 2022). Kellman suggested that perhaps in the dry state the UV light is blocked from entering the cells and thus there is no stimulation. This could be possible due to structural changes that make the dry cells less transparent. A second possibility is that UV light is able to enter the cell, but that the change in structure due to drying makes it impossible for the emitted visible light to get out for us to see. Jenkins (Bryonet 23 April 2022) suggested that it is also possible that it is fluorescence that is quenched or red-shifted out of the visible range in the dry moss. This could be caused by neighboring molecules or by binding to membranes [or cell walls?]. Those neighbors can affect the energy levels and frequency of light emission of the excited electrons. (See Wilson & Hastings 2013 for more detail on the mechanism of fluorescence.)

Jerry Jenkins (Bryonet 23 April 2022) ultimately concluded that it was **photoluminescence** (which includes fluorescence) that emitted light from ***Zygodon rupestris*** (Figure 59) when irradiated with UV. The incoming UV photon interacts with an orbiting electron, causing it to achieve an excited state. Some of the photon energy is transferred to the electron. The remainder is used in vibrations and rotation. As the electron decays, it emits a photon, but with less energy than that of the incoming photon. Thus, the light has a longer wavelength and is shifted toward the red end of the spectrum into the visible spectrum.

Compounds That Fluoresce

The specific compounds in bryophytes that fluoresce have not been studied extensively. However, we know more about those in tracheophytes. Wolfbeis (1985) listed the following compounds from leaves that emit blue-green fluorescence: alkaloids (berberine, quinine, lysergic acid), aurones, chalcones, chromones, coumarins (umbelliferone, esculetin, scopoletin), flavones (except 5-hydroxyflavones), flavins (FMN, FAD, riboflavin), flavonols, furocumarins (psoralen), hydroxycinnamic acids (caffeic, ferulic, sinapic), isoflavones, nicotinamides (NADH, NADPH), phenolic acids (salicylic, gentisic, ellagic), polyenes (phytofluen), pterines (folic acid, dihydrofolate), quinones (phyllohydroquinone), stilbenes (resveratrol), other coenzymes (pyridoxal-5'-phosphate), and degradation products (kynurenine, polyadenylic acid).

The internal environment can modify the fluorescent response, including such factors as temperature, viscosity, spatial constraints, *p*H, polarity, and presence of quenchers, such as heavy metals and oxygen, influencing the spectral characteristics and yield (Cerovic *et al*. 1999).

Parts That Fluoresce

Chlorophyll fluorescence is well known in algae and plants, including bryophytes (Shi *et al*. 1992; Proctor & Smirnoff 2011), giving an indication of the health of the plant by its ability to emit light from its active chloroplasts (*e.g.* Csintalan *et al*. 1999; Deltoro *et al*. 1999; Arróniz-Crespo 2008). As in tracheophytes and algae, the chlorophyll of bryophytes fluoresces red in UV light. In the hornwort ***Anthoceros*** sp., the chlorophyll fluoresces a brilliant red whereas the cell walls fluoresce blue (Figure 60-Figure 64). In ***Fontinalis antipyretica***, the cell wall fluoresces yellow, contrasting with the red chloroplasts (Figure 65). A similar contrast is present in ***Sphagnum***, with photosynthetic cells showing red chlorophyll fluorescence and cell walls showing a blue-green fluorescence in UV light (Figure 66-Figure 68). In ***Funaria hygrometrica***, there is a strong chlorophyll fluorescence, but the cell walls seem to lack any

fluorescence visible in the UV light of a microscope (Figure 69).

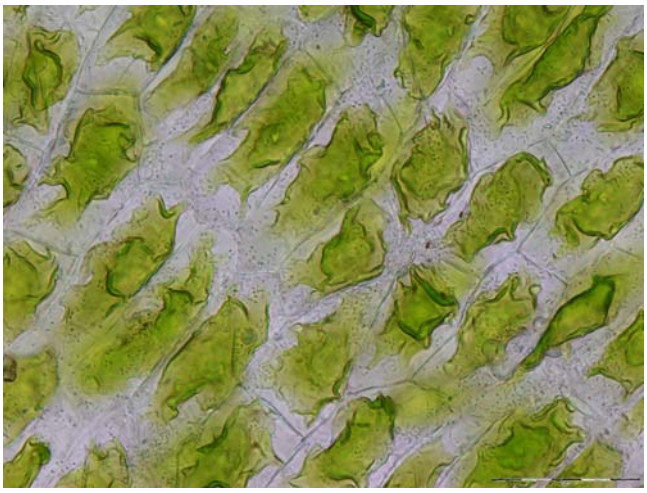

Figure 60. ***Anthoceros*** sp. gametophyte cells in white light. Photo by Magdalena Turzańska.

Figure 61. ***Anthoceros*** sp. gametophyte red chlorophyll fluorescence and cell walls fluorescing blue. Photo by Magdalena Turzańska.

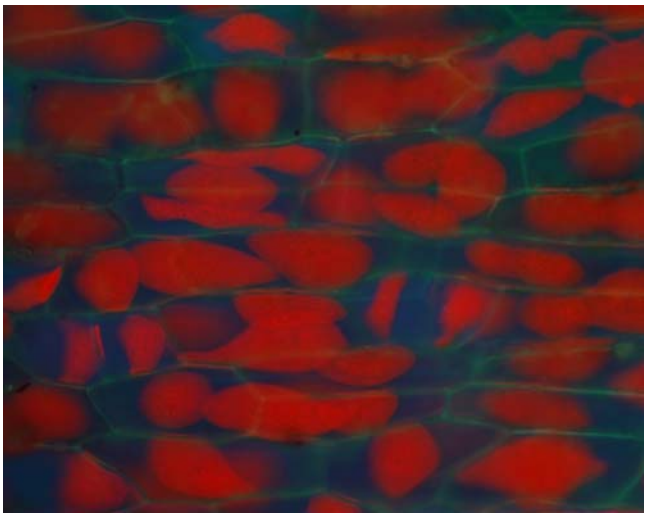

Figure 62. ***Anthoceros*** sp. gametophyte red chlorophyll fluorescence and cell walls fluorescing blue. Photo by Magdalena Turzańska.

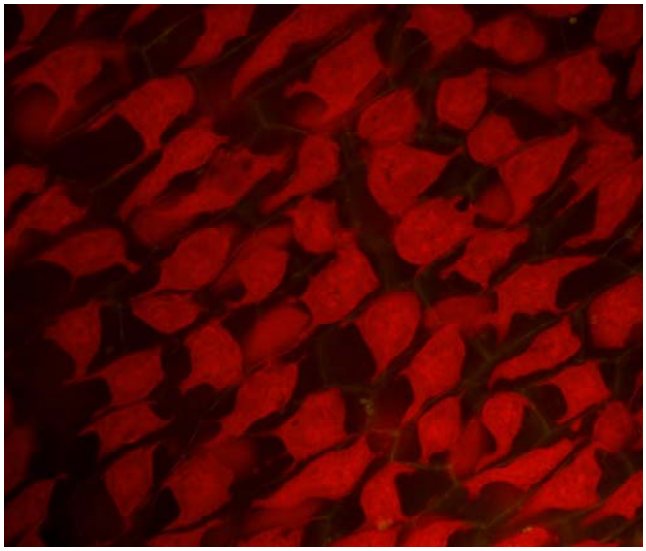

Figure 63. ***Anthoceros*** sp. gametophyte red chlorophyll fluorescence and cell walls fluorescing blue. Photo by Magdalena Turzańska.

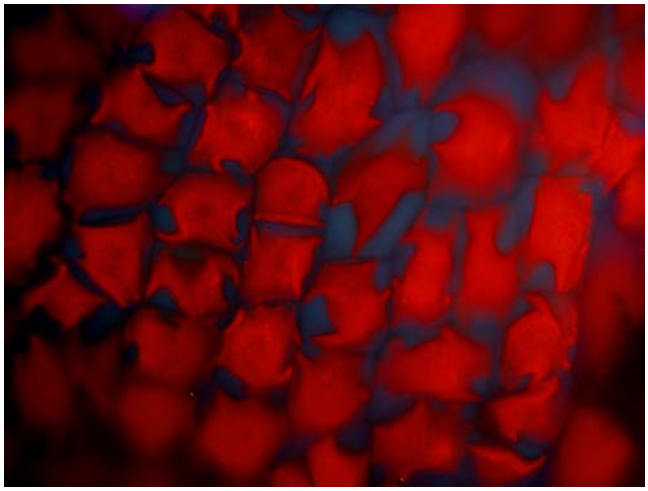

Figure 64. ***Anthoceros*** sp. gametophyte red chlorophyll fluorescence and cell walls fluorescing blue. Photo by Magdalena Turzańska.

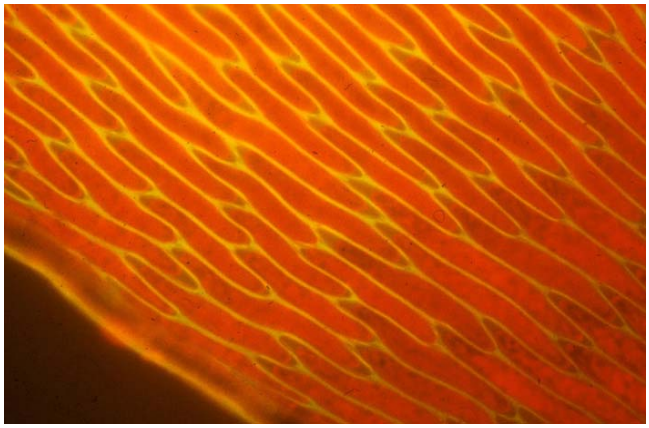

Figure 65. ***Fontinalis antipyretica*** cell wall showing yellow fluorescence, contrasting with the red of the chlorophyll fluorescence. Photo by Janice Glime.

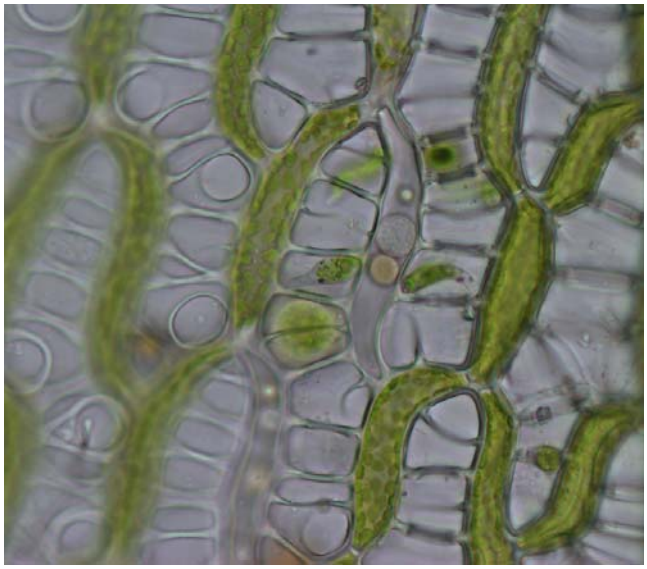

Figure 66. ***Sphagnum*** sp. leaf with algae in hyaline cells. Photo by Magdalena Turzańska.

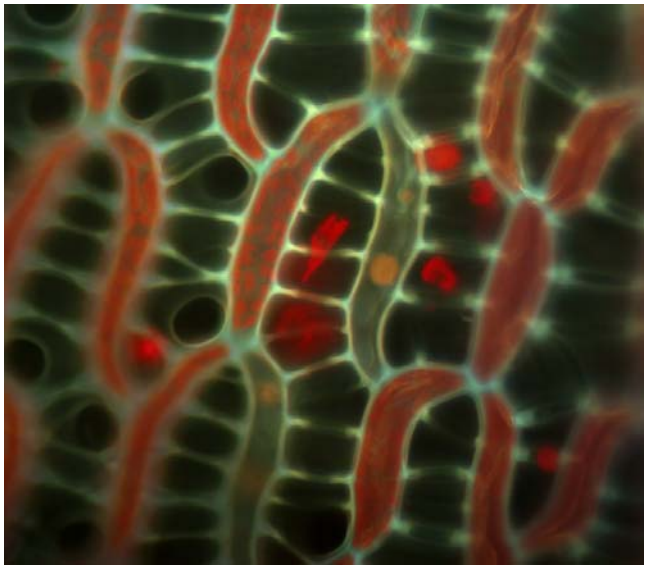

Figure 67. ***Sphagnum*** sp. leaf fluorescence of the leaf in Figure 66 with algae fluorescing red in hyaline cells and cell walls fluorescing greenish. Photo by Magdalena Turzańska.

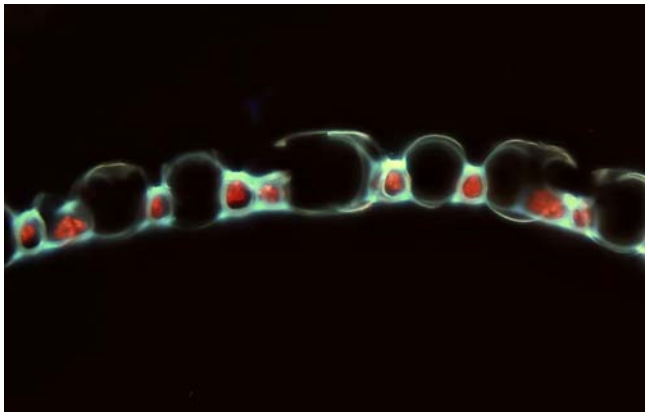

Figure 68. ***Sphagnum*** sp. leaf fluorescence in cross section with chlorophyll fluorescing red and cell walls fluorescing green in UV light. Photo by Magdalena Turzańska.

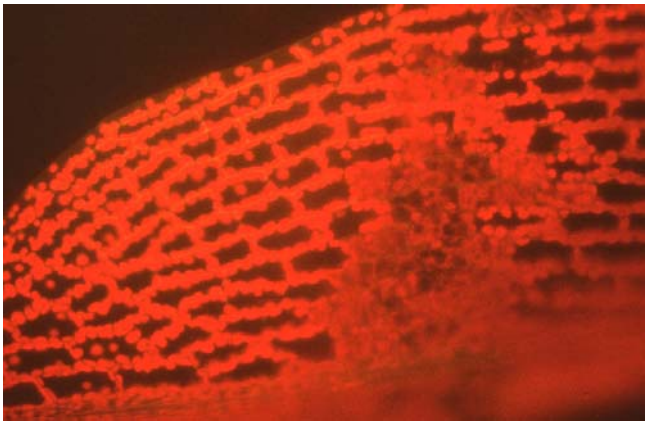

Figure 69. ***Funaria hygrometrica*** leaf chlorophyll fluorescence, showing the typical red fluorescence of that molecule. Note that the cell walls lack fluorescence under the UV light of a microscope. Photo by Janice Glime.

The use of fluorescence to detect the damage to chlorophyll has been established for some time (Proctor 2003). These uses include indication of effects of various intensities of desiccation (Proctor 2003) and of metal contaminant locations within the cell, as shown in ***Fontinalis antipyretica*** (Figure 70-Figure 71) (Chorvatova *et al*. 2021).

Figure 70. ***Fontinalis antipyretica***, an aquatic moss with cell wall fluorescence under UV light and a species where one can trace metals using fluorescence. Photo by Hermann Schachner, through Creative Commons.

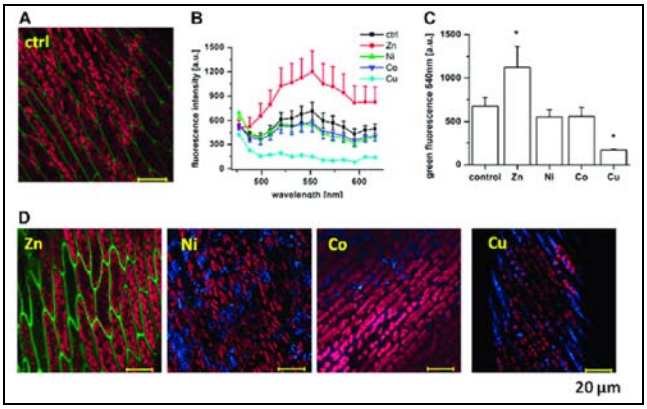

Figure 71. Fluorescence of various metals in ***Fontinalis antipyretica*** located by UV light. From Chorvatova *et al*. 2021.

Various parts of bryophytes are known to fluoresce. Ridgway and Larson (1966) reported on the usefulness of the fluorescence technique to follow sporogenesis in the hornwort ***Anthoceros*** sp. (Figure 72-Figure 76). Similar changes in color seem to occur in ***Riccia*** sp. (Figure 77-Figure 80). Using a UV microscope enables us to examine the development and greening of spores (Figure 78-Figure 79), protonemal bud initiation, callose distribution to find phloem-like elements, callose in cross walls of leptoids, events leading to egg formation, events following fertilization (Sarafis 1971; Brandes 1967), and locating elusive propagules (Nordhorn-Richter 1984 a,b,c, 1985 a,b, 1988).

Figure 72. ***Anthoceros punctatus***, member of a genus in which fluorescence permits us to follow development of spores, at least in some species. Photo by Jonathan Sleath, with permission.

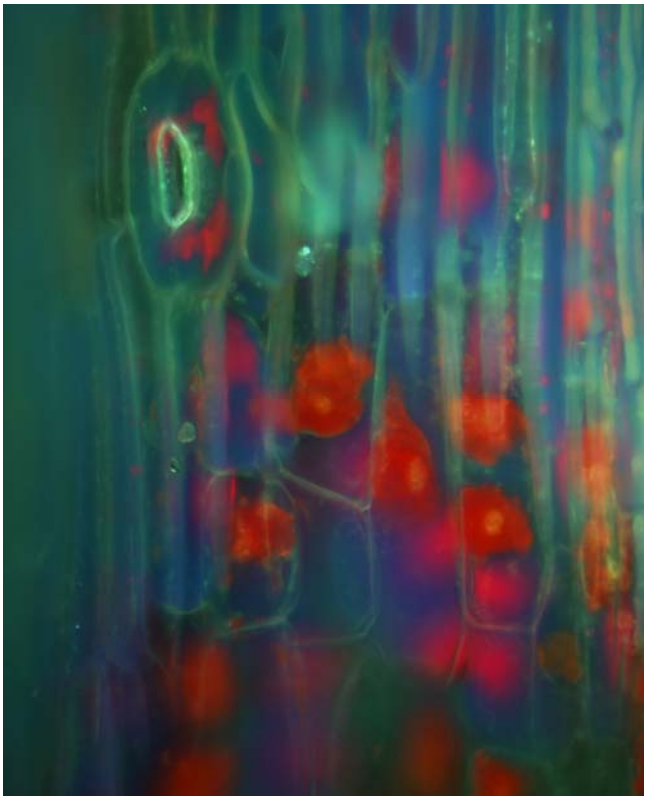

Figure 73. ***Anthoceros*** sp. sporophyte fluorescence showing greenish cell walls and red of chlorophyll in developing spores. Photo by Magdalena Turzańska.

Figure 74. ***Anthoceros*** sp. sporophyte fluorescence. Note the clarity of the stomatal openings. Photo by Magdalena Turzańska.

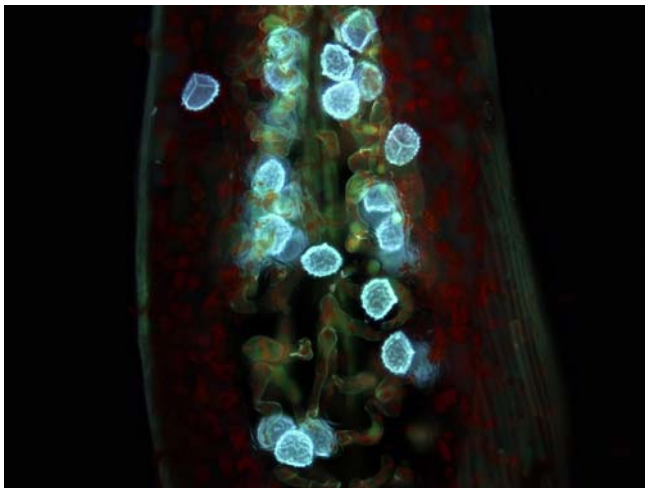

Figure 75. ***Anthoceros*** sp. sporophyte showing blue spore fluorescence. Photo by Magdalena Turzańska.

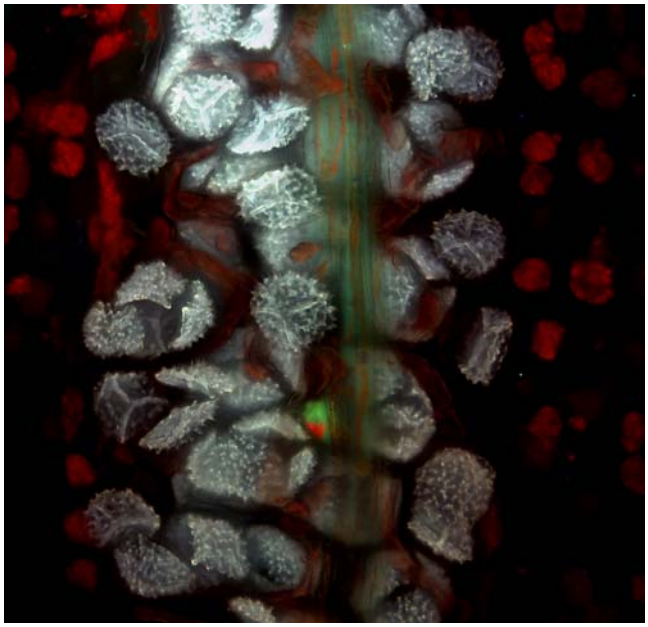

Figure 76. ***Anthoceros*** sp. sporophyte showing pale fluorescence. Photo by Magdalena Turzańska.

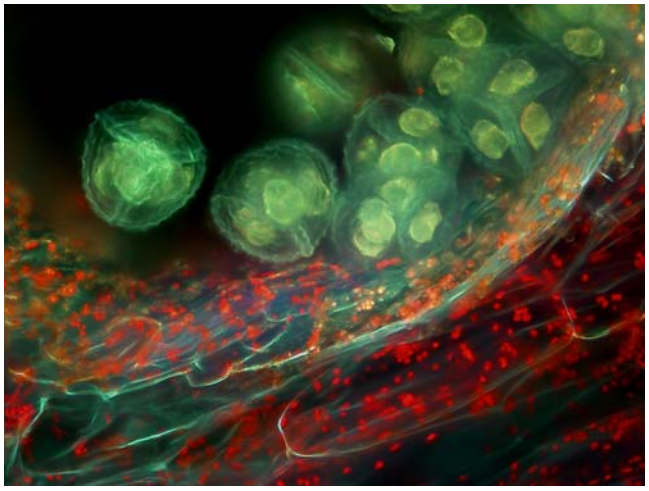

Figure 77. ***Riccia cavernosa*** young sporangium with green fluorescence of young spores. Photo by Magdalena Turzańska.

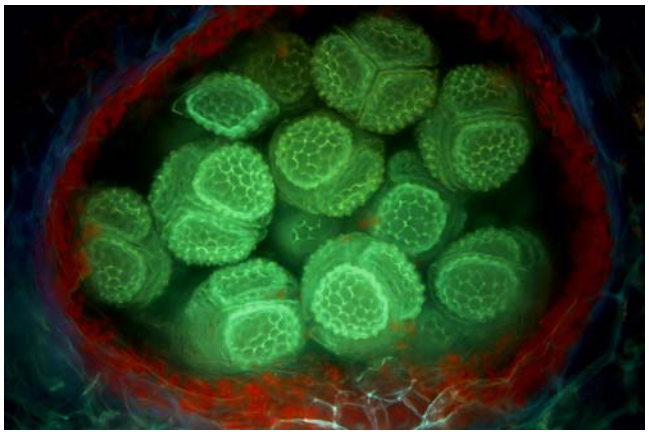

Figure 78. ***Riccia*** sorocarpa sporangium with spore tetrads showing green fluorescence and decoration on the spores and nuclei no longer visible through the spore wall. Photo by Magdalena Turzańska, with permission.

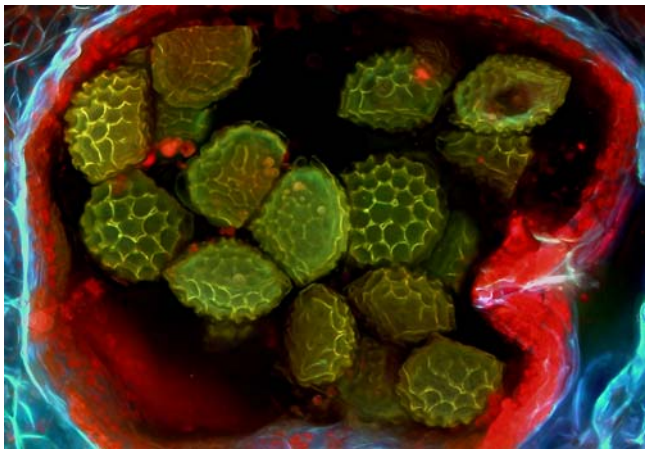

Figure 79. ***Riccia*** sp. mature spores fluorescing differently from younger spores in Figure 78. Photo by Magdalena Turzańska, with permission.

The change in color of the cell walls in spore tetrads to those of the mature spores in ***Riccia*** sp. suggests that the compounds present change with maturity. The sporangia stand out from the coloring of the thallus internal cell walls in ***Riccia*** (Figure 80).

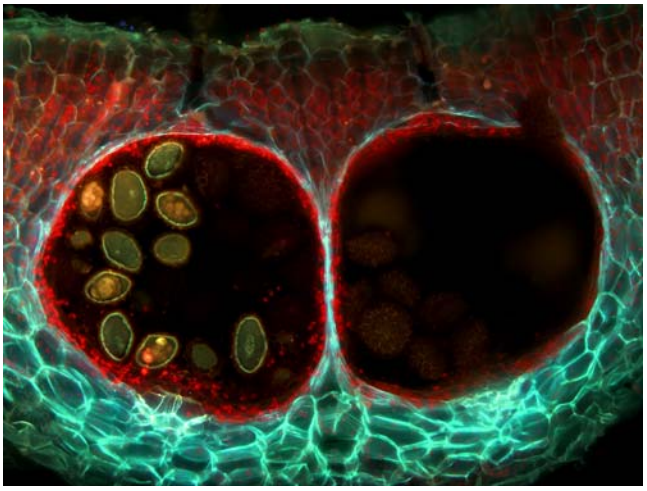

Figure 80. ***Riccia*** sporangia with red chlorophyll fluorescence and blue-green thallus cell wall fluorescence. Spore walls are fluorescing gold. Photo by Magdalena Turzańska.

My first encounter with the phenomenon of **fluorescence** in bryophytes was on a field trip in Europe where I entered in conversation with Gisela Nordhorn-Richter. She had stopped at a display of microscopes at her university just because the poor guys didn't have many visitors. She took her research organisms, members of the genus ***Pohlia*** (Figure 81-Figure 82), to test the quality of the microscopes, one of which had UV light capabilities. To her amazement, gemmae lit up all over the place, displaying far more than she had been able to see without the UV aid. She then looked at other species and found that this was a good tool to help in determining number and shape, enabling her to delineate species more easily (Nordhorn-Richter 1984 a,b,c, 1985 a,b, 1988).

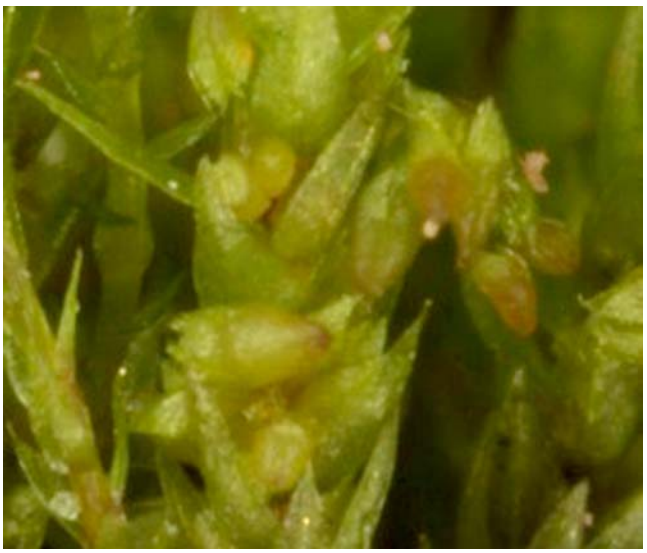

Figure 81. ***Pohlia bulbifera*** showing location of bulbils – structures that can be located in UV light by their fluorescence. Photo by Jan-Peter Frahm, with permission.

Figure 82. ***Pohlia bulbifera*** bulbils that fluoresce, making them easier to locate. Photo by Des Callaghan, with permission.

An image of a gemma of ***Lunularia cruciata*** (Figure 83-Figure 84) from Robin Young indicates that this structure fluoresces blue in UV light. Furthermore, the gemmae of ***Zygodon rupestris*** fluoresce blue (Figure 147). Gemmae can provide multiple colors, including a golden shade in liverworts ***Calypogeia*** sp. (Figure 85), ***Metzgeria*** sp. (Figure 86), and ***Radula complanata*** (Figure 87), and mosses ***Aulacomnium androgynum*** (Figure 88) and ***Tetraphis pellucida*** (Figure 89-Figure 90). The gemmae of ***Tetraphis pellucida*** suggest that the fluorescence color changes with age.

Figure 83. ***Lunularia cruciata***, a species with fluorescing gemmae. Photo by David Holyoak, with permission.

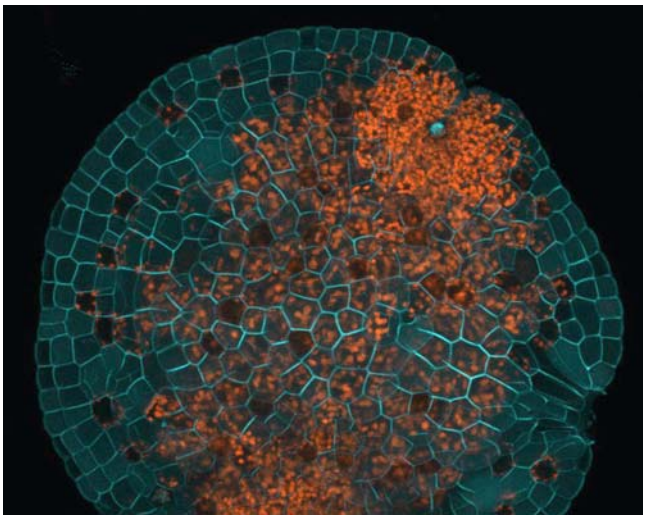

Figure 84. ***Lunularia cruciata*** gemma fluorescing. Photo by Robin Young, with permission.

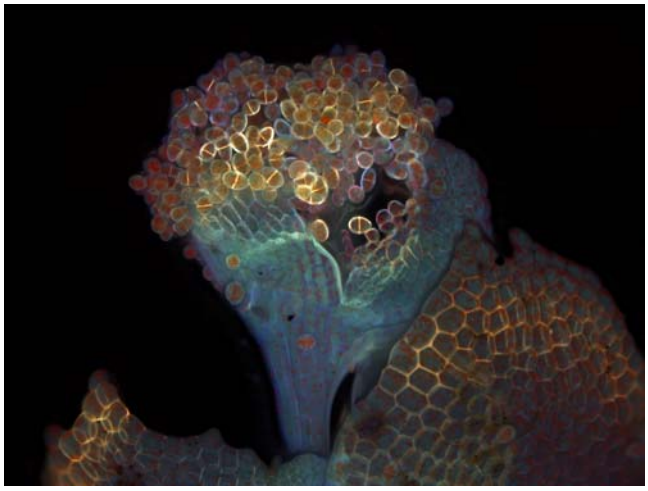

Figure 85. ***Calypogeia*** sp. gemmae with wall fluorescence. Photo by Magdalena Turzańska.

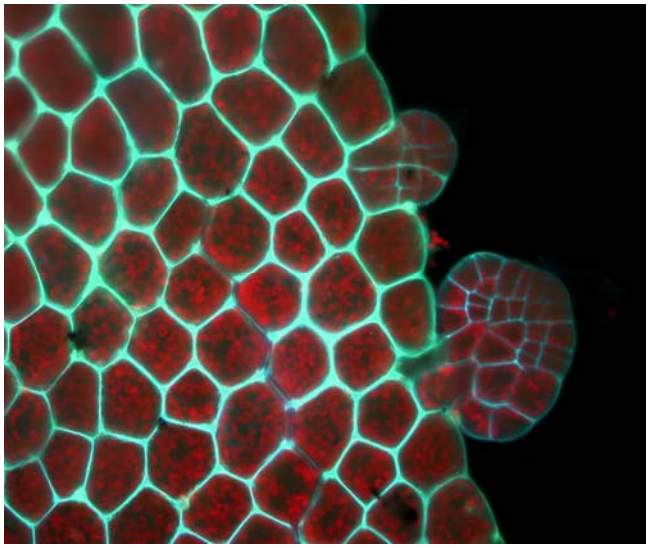

Figure 86. ***Metzgeria*** sp. showing fluorescence of cell walls, including that of marginal gemmae. It appears that the conspicuousness of the gemmae depends on the concentration of the fluorescing substance. Photo by Magdalena Turzańska.

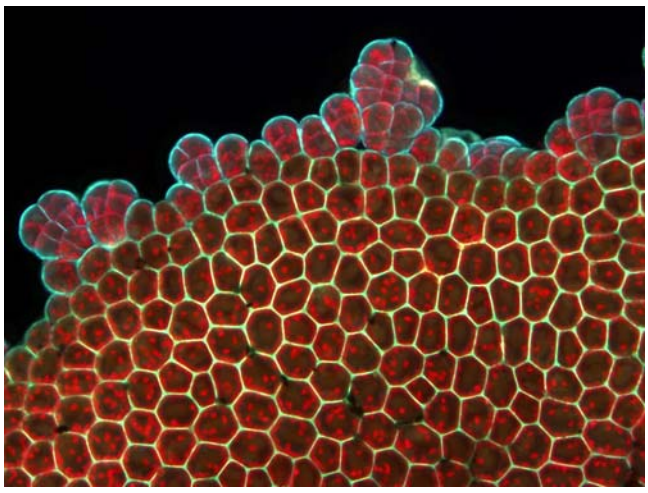

Figure 87. ***Radula complanata*** yellow leaf cell wall fluorescence with blue-green gemma cell wall fluorescence. Photo by Magdalena Turzańska.

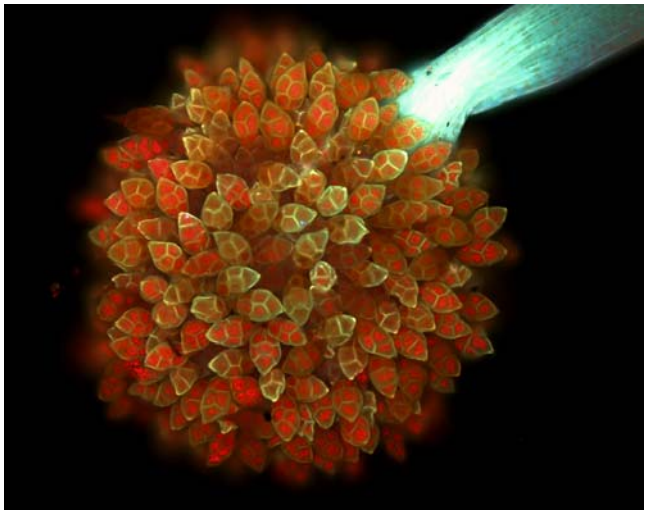

Figure 88. ***Aulacomnium androgynum*** gemmae with wall and chlorophyll fluorescence. Photo by Magdalena Turzańska.

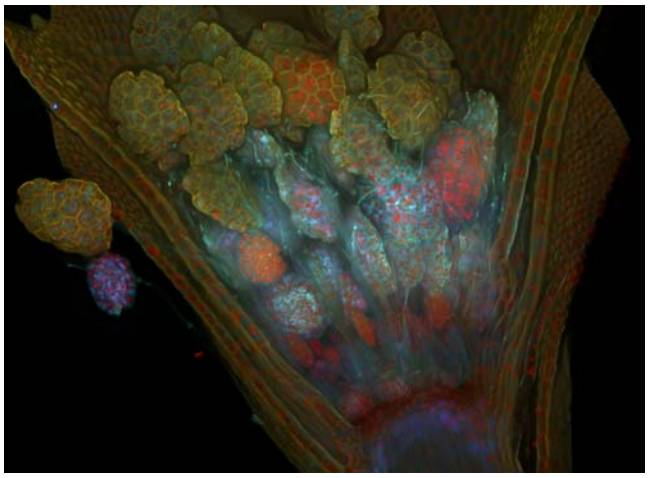

Figure 89. ***Tetraphis pellucida*** gemmae cup fluorescence showing golden cell walls of cup and multiple colors of gemmae, presumably indicating different ages. Photo by Magdalena Turzańska.

Figure 90. ***Tetraphis pellucida*** gemma fluorescence showing golden cell walls, red chloroplasts, and something blue. Photo by Magdalena Turzańska

Even branch buds can become more obvious because of a deep chlorophyll fluorescence. This is illustrated in ***Physcomitrella patens*** (Figure 91).

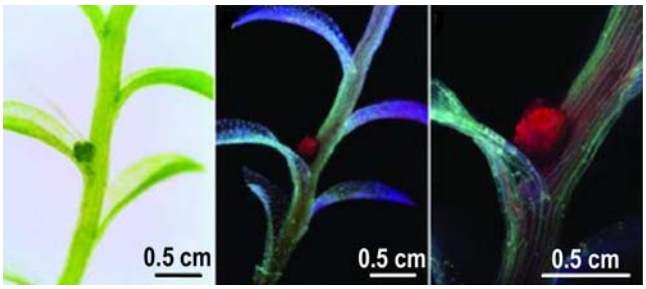

Figure 91. ***Physcomitrella patens*** normallight and fluorescence showing greenish leaf cell walls and bright red of bud due to dense chlorophyll. Photo modified from Beata Zagórska-Marek, with permission; published in American Journal of Botany with Creative Commons attribution <https://creativecommons.org/licenses/by/4.0/#>.

Merced and Renzaglia (2017) used fluorescence as a tool in viewing the stomata of a variety of bryophytes. In a species of ***Bartramia*** (Figure 92-Figure 93) the guard cells fluoresce red due to chloroplasts, but the rest of the capsule has a blue-green color in UV light. They also showed the coloration in UV light for ***Orthotrichum*** sp. (Figure 94-Figure 95), ***Physcomitrium*** sp. (Figure 96-Figure 97), and ***Polytrichum*** sp. (Figure 98).

Figure 92. ***Bartramia pomiformis*** with capsules. Photo by Northern Forest Atlas, with permission through Jerry Jenkins.

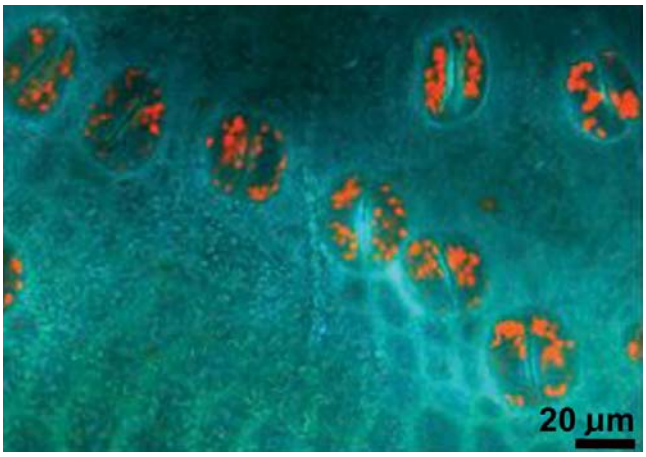

Figure 93. ***Bartramia*** guard cells with chloroplasts and cell walls fluorescing. Photo from Merced & Renzaglia 2017, with permission.

Figure 94. ***Orthotrichum alpestre***, in a genus where guard cells are of taxonomic importance. Photo by Michael Lüth, with permission.

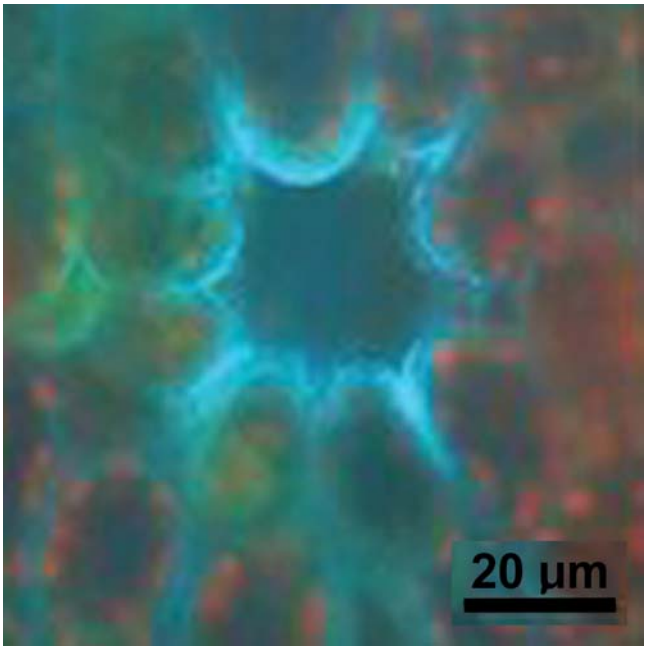

Figure 95. ***Orthotrichum*** guard cells with chloroplasts and cell walls fluorescing in UV light. Photo modified from Merced & Renzaglia 2017, with permission.

Figure 96. ***Physcomitrium patens*** showing capsules Photo by Hugues Tinguy, with permission.

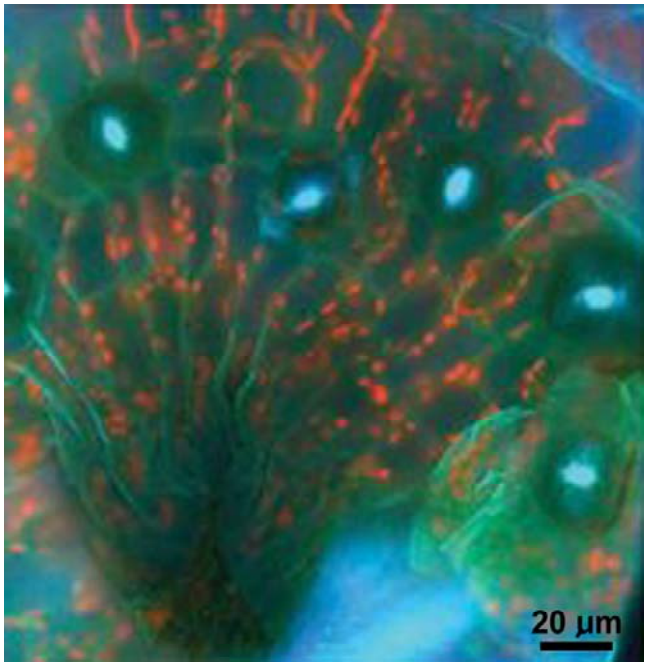

Figure 97. ***Physcomitrium*** guard cells and chloroplasts (**orange**) in fluorescence microscopy. Photo from Merced & Renzaglia 2017, with permission.

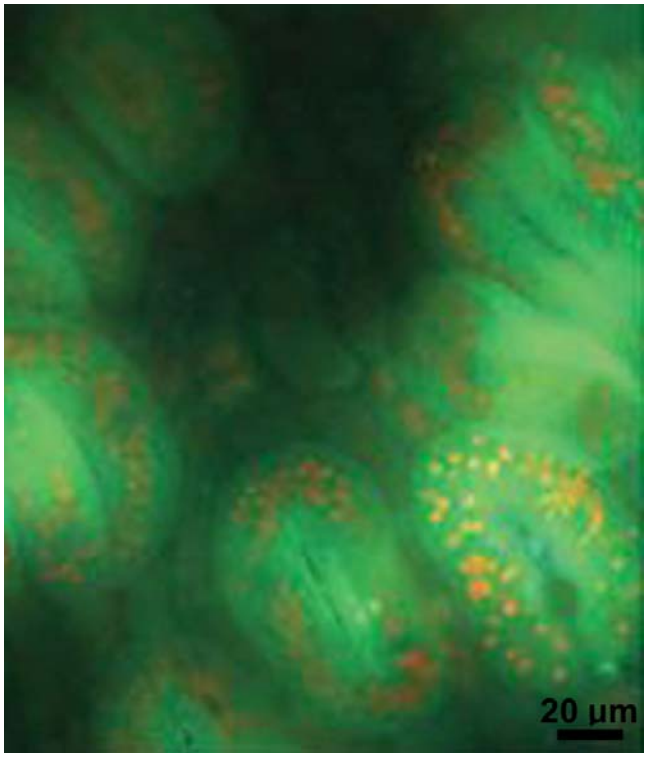

Figure 98. ***Polytrichum*** guard cells with chloroplasts (orange) using fluorescence microscopy. Photo from Merced & Renzaglia 2017, with permission.

In addition to the fluorescence of stomata in the sporophyte, it appears that the gametophyte thallus and the cells surrounding the pores of ***Conocephalum conicum*** (Figure 99-Figure 101) and ***Marchantia polymorpha*** (Figure 102) also exhibit fluorescence.

Figure 99. ***Conocephalum conicum*** showing raised pores. Photo by Dick Haaksma, with permission.

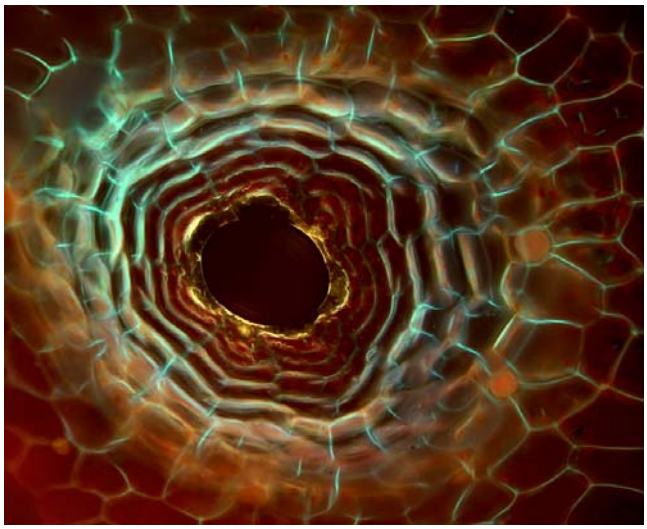

Figure 100. ***Conocephalum conicum*** pore fluorescence. This image has been enhanced by increasing the color contrast using Photoshop. Photo by Magdalena Turzańska, with permission.

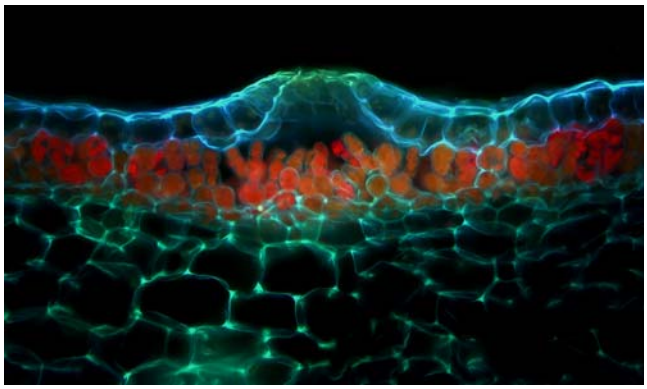

Figure 101. ***Conocephalum conicum*** thallus section showing pore and fluorescence. Note the bright red chlorophyll in photosynthetic cells under the epidermis. Photo by Magdalena Turzańska.

Little has been published about fluorescence of sexual structures. Nevertheless, in her photographic images Magdalena Turzańska illustrates that the antheridia (Figure 103-Figure 108) and archegonia (Figure 109-Figure 110) and associated paraphyses can exhibit a colorful display.

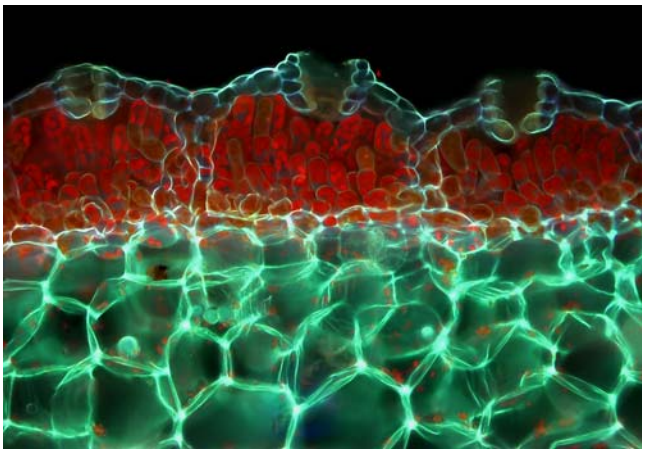

Figure 102. ***Marchantia polymorpha*** thallus section showing fluorescing pore, chlorophyll fluorescence, and fluorescing thallus tissue. Photo by Magdalena Turzańska.

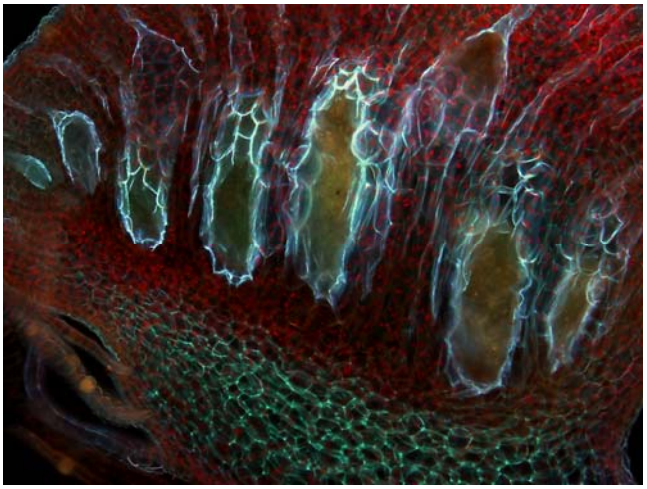

Figure 103. ***Conocephalum conicum*** antheridia showing fluorescence of their walls, chlorophyll in surrounding cells, and green walls of non-photosynthetic thallus cells. Photo by Magdalena Turzańska.

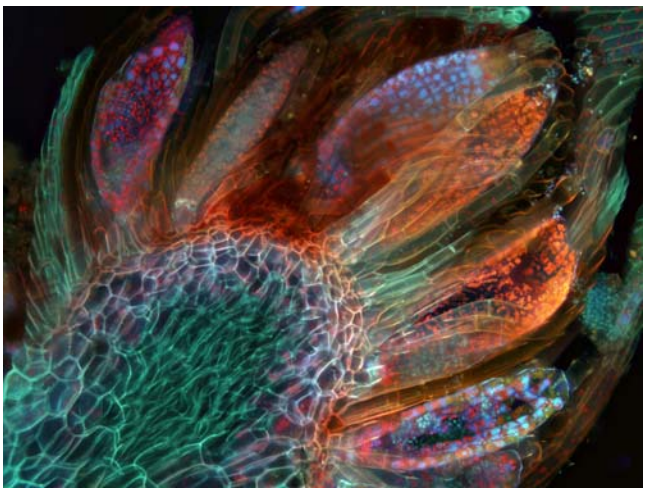

Figure 104. Moss antheridia fluorescence providing a colorful contrast to that of the stem. Photo by Magdalena Turzańska, with permission.

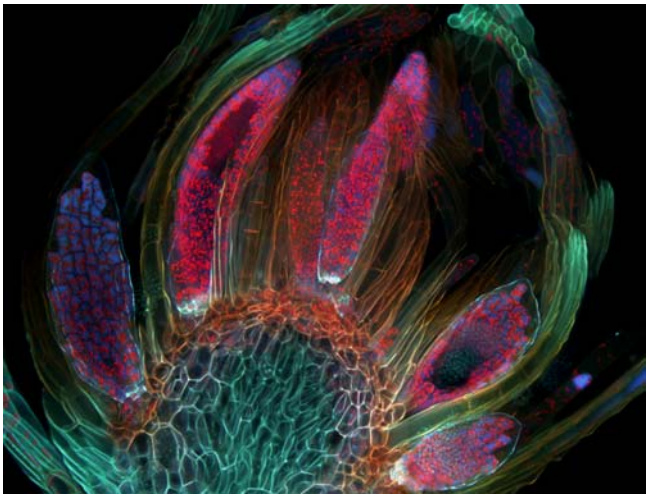

Figure 105. Moss antheridia fluorescence with intense coloration. Photo by Magdalena Turzańska.

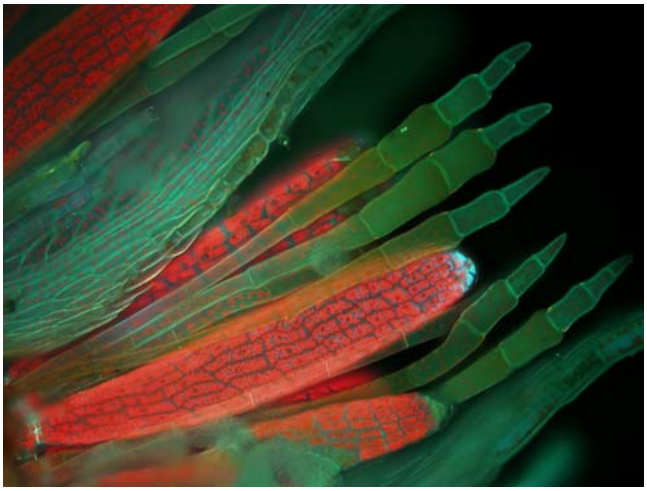

Figure 106. ***Mnium hornum*** antheridia fluorescence barely visible at tips due to chlorophyll fluorescence; paraphyses have strong green fluorescence. Photo by Magdalena Turzańska.

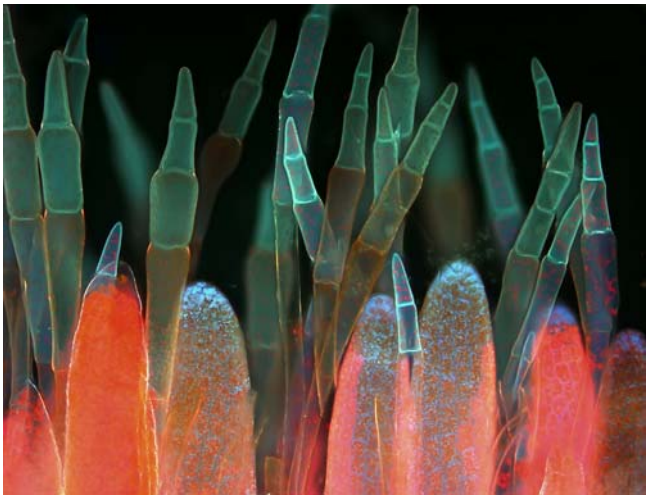

Figure 107. ***Mnium hornum*** antheridia and paraphyses fluorescing. Photo by Magdalena Turzańska, with permission.

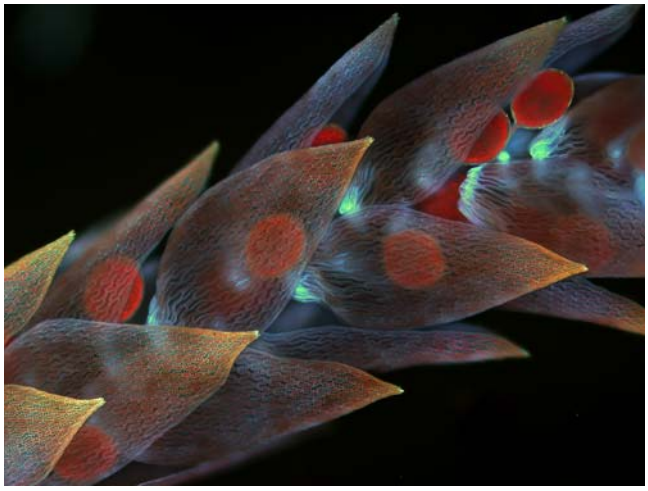

Figure 108. ***Sphagnum*** sp. antheridia showing fluorescence in UV light. Photo by Magdalena Turzańska.

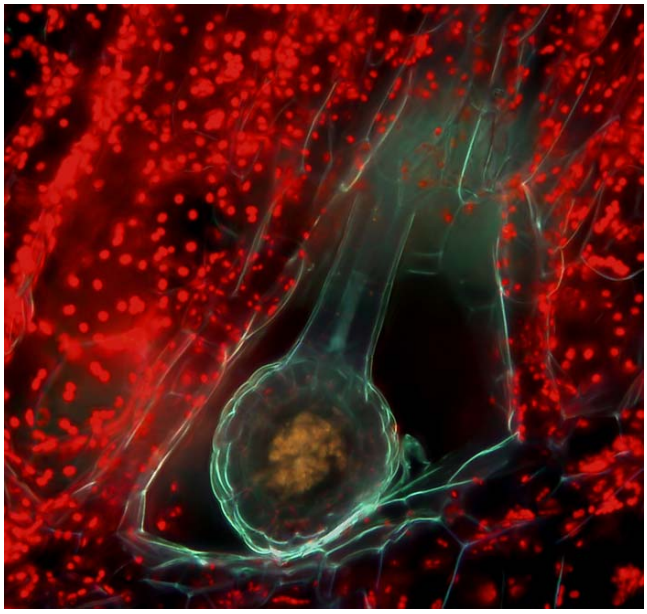

Figure 109. ***Riccia*** sp. archegonium fluorescence, surrounded by chlorophyll fluorescence of the thallus. Photo by Magdalena Turzańska.

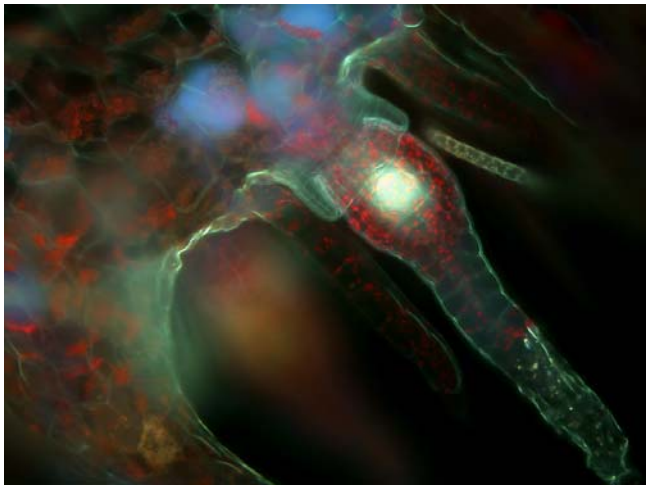

Figure 110. ***Marchantia polymorpha*** archegonium green fluorescence with red chlorophyll fluorescence at base and bright egg. Photo by Magdalena Turzańska.

The fluorescence of sporophytes seems to be largely unknown. The only images I have seen are those of Magdalena Turzańska for ***Phascum*** sp. (Figure 111) and ***Sphagnum*** sp. (Figure 112) The latter appears to lack capsule fluorescence, but exhibits it in the pseudopodium. It would be interesting to see if the fluorescence of spores and capsule are more common in species lacking a peristome, perhaps serving to attract arthropod dispersal vectors.

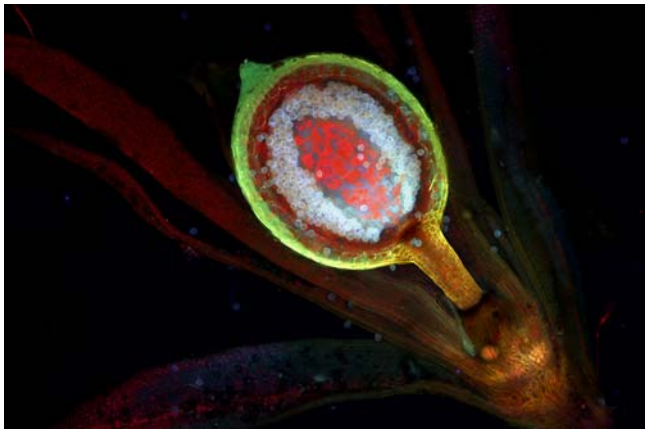

Figure 111. ***Phascum*** sp. fluorescence of capsule and spores in capsule with no peristome. Photo by Magdalena Turzańska.

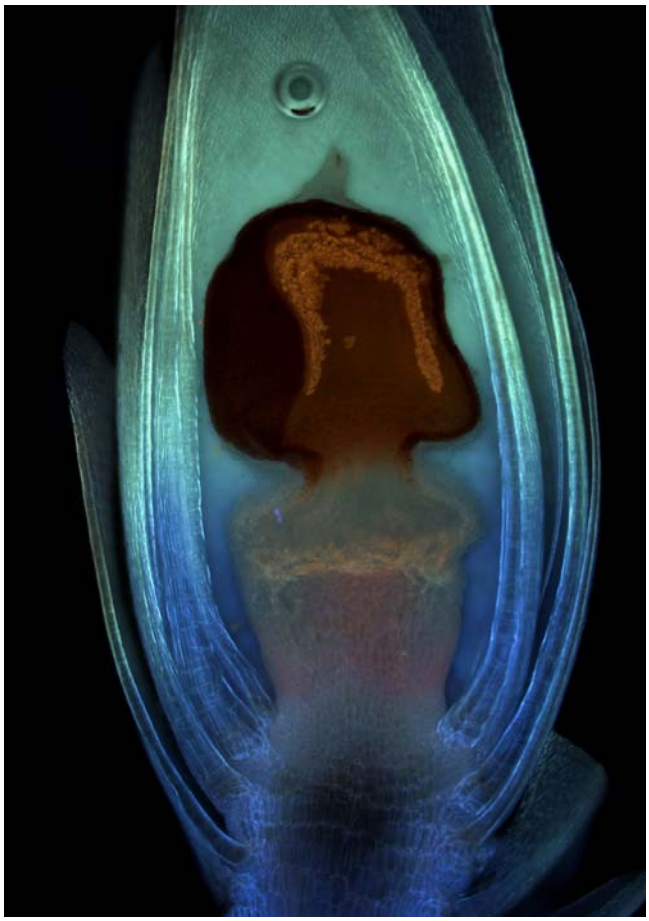

Figure 112. ***Sphagnum*** sp. fluorescence with capsule apparently not fluorescing, but the developing pseudopodium has some pink, green, and greenish fluorescence. Photo by Magdalena Turzańska.

In liverworts, the spores are nestled among elaters that may help to loosten and expel the spores from the capsules. These, too, can fluoresce (Figure 113-Figure 114). Since I have few records, it is too early to determine if this is a common character in liverwort elaters. I have even fewer examples of fluorescence in peristomes (Figure 115).

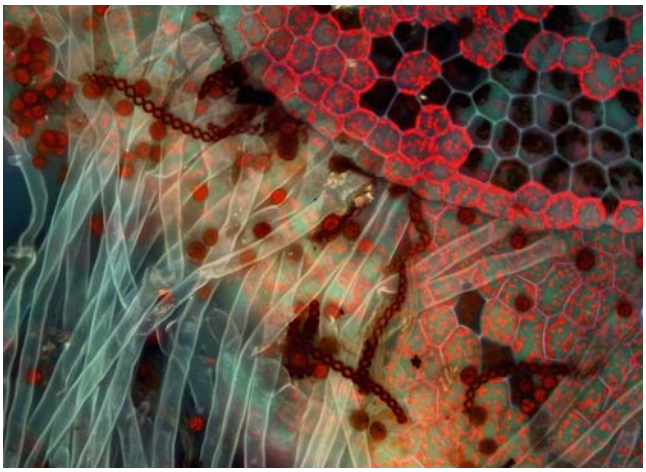

Figure 113. ***Marchantia*** elater dark red fluorescence in UV light. Photo by Magdalena Turzańska.

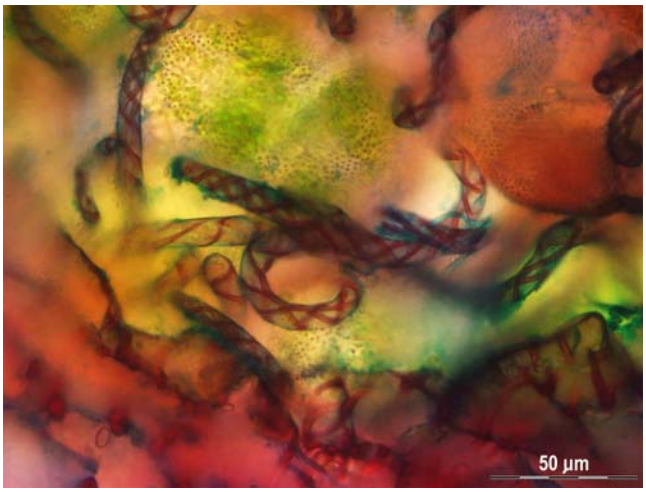

Figure 114. ***Pellia*** elater dark red fluorescence in UV light. Photo by Magdalena Turzańska.

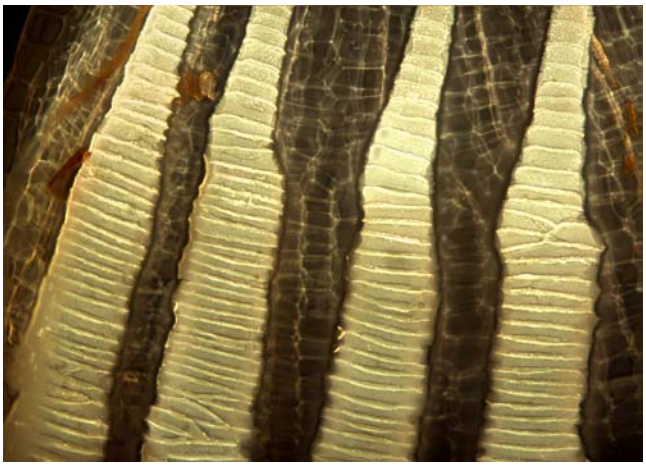

Figure 115. Moss peristome golden fluorescencein UV light. Photo by Magdalena Turzańska.

In addition to the fluorescence of the plant parts, it is often possible to distinguish the presence of epiphytes more easily using UV light. This can be seen in Figure 66-Figure 67 for algae on ***Sphagnum***, in Figure 116-Figure 117 for **Cyanobacteria** on ***Hylocomium splendens***, and ***Blasia pusilla*** (Figure 118-Figure 121). Can it be used as well to detect and help identify bacteria on the bryophytes?

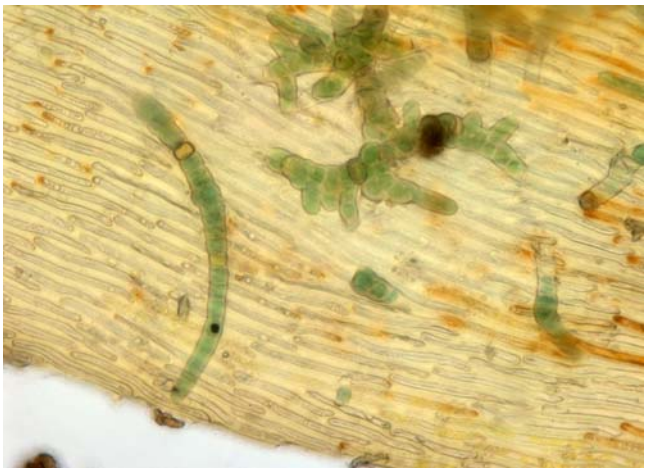

Figure 116. ***Hylocomium splendens*** with ***Stigonema*** (**Cyanobacteria**). Photo by Magdalena Turzańska.

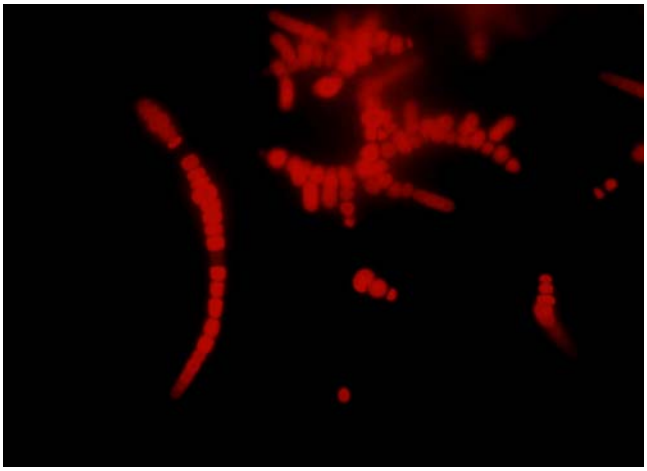

Figure 117. ***Stigonema*** (**Cyanobacteria**) on ***Hylocomium splendens*** fluorescence. Photo by Magdalena Turzańska.

Figure 118. ***Blasia pusilla Nostoc*** colonies. Photo by Magdalena Turzańska.

Figure 119. ***Blasia pusilla*** with ***Nostoc*** (**Cyanobacteria**). Photo by Magdalena Turzańska.

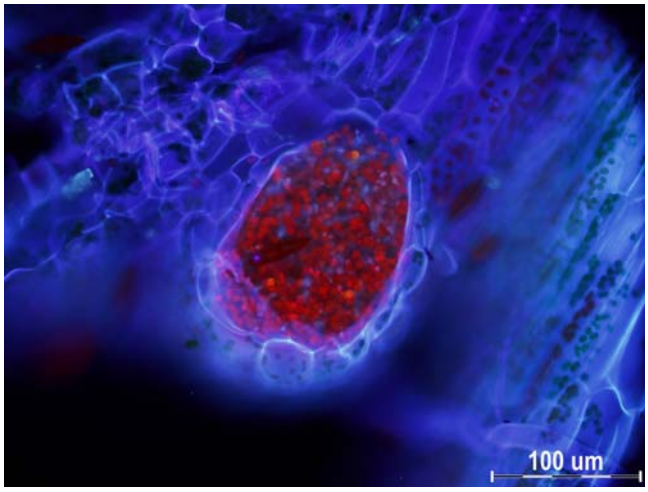

Figure 120. ***Blasia pusilla*** blue fluorescence of thallus and red **Cyanobacteria** fluorescence. Photo by Magdalena Turzańska.

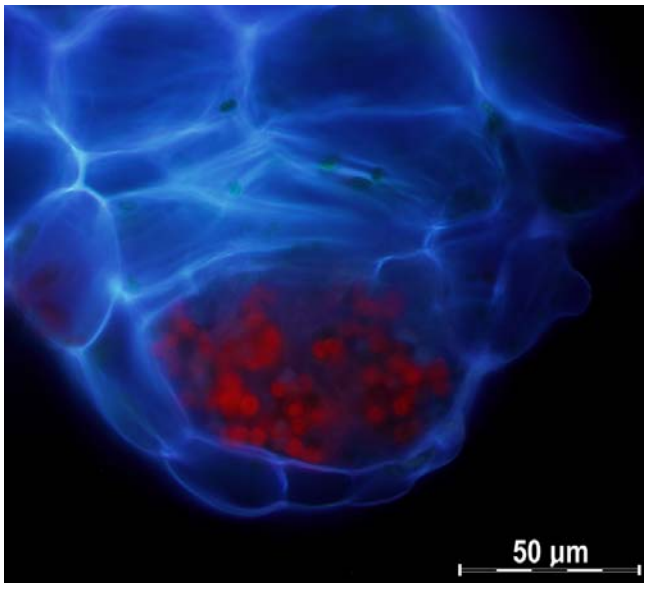

Figure 121. ***Blasia pusilla*** with red fluorescence of **Cyanobacteria** and blue thallus fluorescence. Photo by Magdalena Turzańska.

Which Species Fluoresce?

For some reason, the method of viewing bryophytes with UV light has been neglected. It was not until Dale Kruse inquired about bryophyte fluorescence on Bryonet (25 March 2011) that the subject again surfaced: "I just returned from a trip to Puerto Rico where I visited the rainforests of the Caribbean (El Yunque) National Forest. A 'non-bryological' employee there suggested there were fluorescent mosses in the forests of El Yunque. I did a quick search on the web and found very little information. I have seen fluorescent lichens but not mosses." Bryologists responded with skepticism, suggesting it was a fungus or bacterium (or possibly a lichen). Then Michael Lüth responded (Bryonet 26 March 2011): "We saw a fluorescent ***Frullania dilatata*** (Figure 122-Figure 124) on an excursion, when someone held a fluorescent lamp to a tree searching for some lichens." And Michael was able to show us proof (Figure 123).

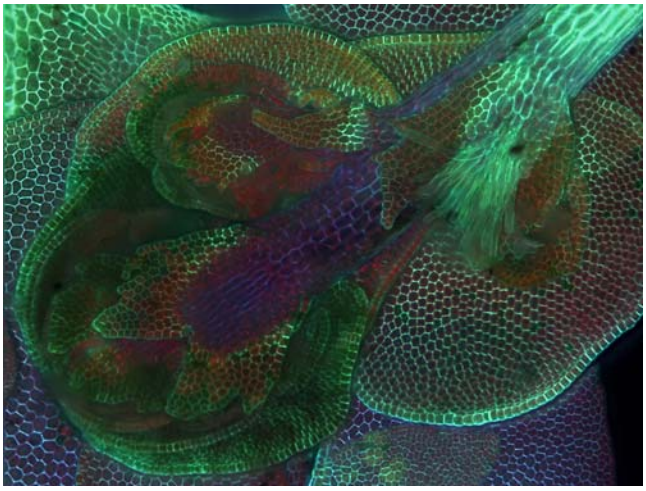

Figure 124. ***Frullania dilatata*** green cell wall fluorescence. Photo by Magdalena Turzańska.

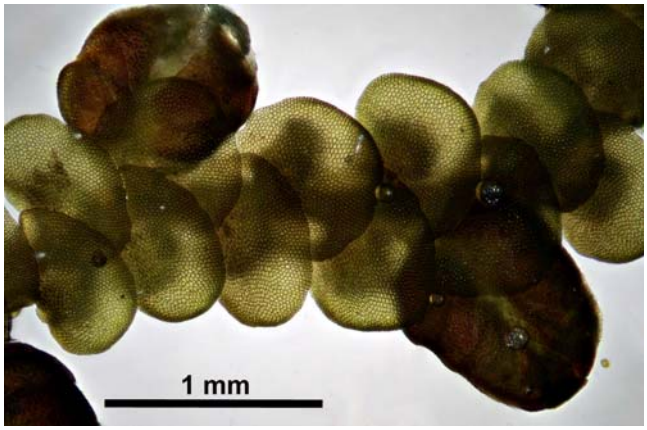

Figure 122. ***Frullania dilatata***, a species that exhibits purple fluorescence. Photo by Claire Halpin, with permission.

In 2022, the topic of fluorescence erupted on Bryonet again. Emmet Judziewicz and Virginia (Bryonet 13 March 2022) reported that on a casual one-hour walk in the Hawaiian rainforest, their UV flashlight revealed a "striking bright red fluorescence" in several leafy liverworts. These included **Cephaloziaceae**: ***Fuscocephaloziopsis connivens*** (Figure 125-Figure 126) **subsp.** ***sandvicensis***, ***Odontoschisma denudatum*** (Figure 127), and **Lepidoziaceae**: ***Lepidozia australis*** (Figure 128), ***Telaranea nematodes*** (Figure 129), but the common ***Bazzania praerupta*** (=***Bazzania cordistipula***; Figure 130-Figure 131) did not exhibit red florescence, nor did the other common leafy liverworts they examined.

Figure 123. ***Frullania dilatata*** demonstrating purple fluorescence under UV light from a special UV-emitting hand lens. Photo by Michael Lüth, with permission.

Figure 125. ***Fuscocephaloziopsis connivens***, a species that exhibits a bright red fluorescence in UV light. Photo by Hermann Schachner, through Creative Commons.

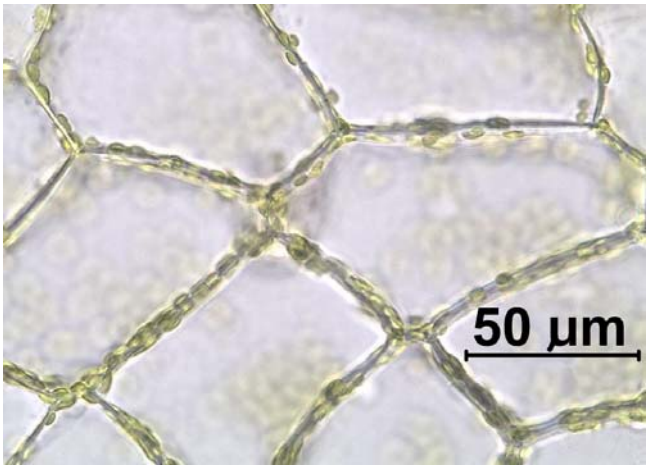

Figure 126. ***Fuscocephaloziopsis connivens*** cells showing chloroplasts clinging to cell walls. Photo by Hugues Tinguy, with permission.

Figure 127. ***Odontoschisma denudatum***, a species that exhibits a bright red fluorescence in UV light. Photo by Hermann Schachner, through Creative Commons.

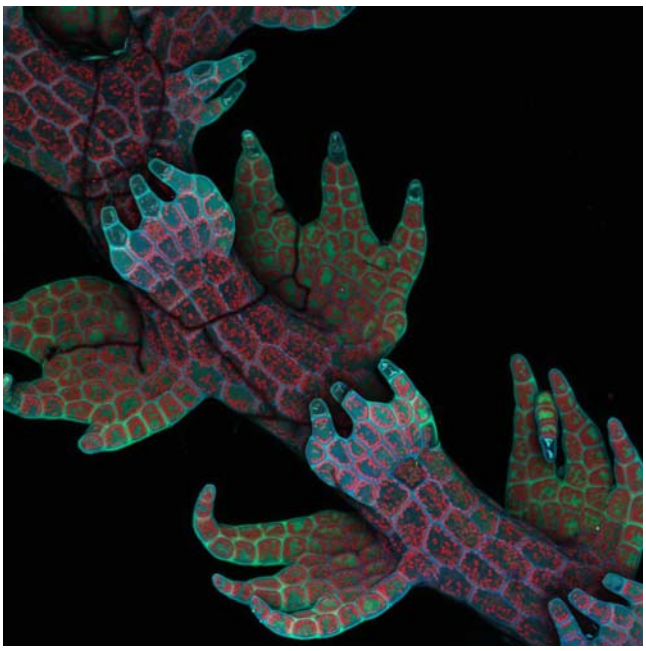

Figure 128. ***Lepidozia australis*** showing fluorescence. Photo by Robin Young, with permission through CC-BY-NC 4.0.

Figure 129. ***Telaranea nematodes***, a member of the **Lepidoziaceae** that exhibits fluorescence in UV light. Photo by Michael Lüth, with permission.

Figure 130. ***Bazzania praerupta***, a species in the **Lepidoziaceae** that does not fluoresce in UV light when viewed macroscopically. Photo by Lin Shanxiong, through Creative Commons.

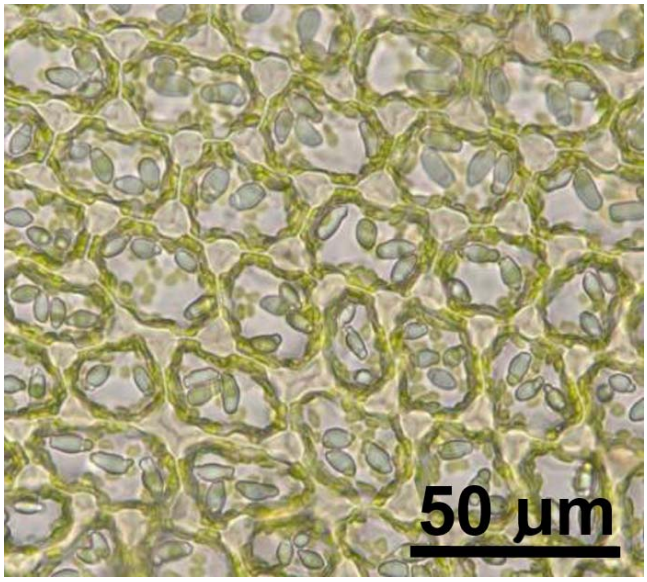

Figure 131. ***Bazzania praerupta*** leaf cells showing large trigones, but lacking papillae. Photo by Lin Shanxiong, through Creative Commons.

Andi Cairns (pers. comm. 27 March 2022) reported ***Bazzania vittata*** (Figure 132-Figure 134, Figure 174) fluorescing blue beside a ***Bazzania corbieri*** (Figure 132-Figure 134, Figure 135) that was not fluorescing. The adjacent mosses ***Leucobryum aduncum* var. *aduncum*** (Figure 132-Figure 133, Figure 136) and ***Pyrrhobryum paramattense*** (Figure 132-Figure 133, Figure 137) were likewise not fluorescing. Herbarium specimens of ***Bazzania vittata*** from Thornton Peak in North Queensland, Australia, also fluoresced blue even when **dry** (Andi Cairns, pers. comm. 29 March 2022). She explored an additional ~20 specimens of dried leafy liverworts from the Australian Wet Tropics and the only one that fluoresced blue under UV light was ***Bazzania vittata*** (Andi Cairns, pers. comm. 30 March 2022).

Figure 132. ***Bazzania vittata*** fluorescing blue in UV light with non-fluorescing ***Bazzania corbieri***, ***Leucobryum aduncum* var. *aduncum***, and ***Pyrrhobryum paramattense***. Photo by Will Cairns, courtesy of Andi Cairns.

Figure 133. ***Bazzania vittata*** fluorescing blue in UV light with non-fluorescing ***Leucobryum aduncum* var. *aduncum***, and ***Pyrrhobryum paramattense***. ***Bazzania corbieri*** appears to be fluorescing purple in some branches – perhaps dead ones with cells or structures no longer hiding the fluorescence? Photo by Will Cairns, courtesy of Andi Cairns.

Figure 134. ***Bazzania vittata*** fluorescing blue in UV light with non-fluorescing ***Bazzania corbieri***, ***Leucobryum aduncum* var. *aduncum***, and ***Pyrrhobryum paramattense***. Photo by Will Cairns, courtesy of Andi Cairns.

Figure 135. ***Bazzania corbieri***, a non-fluorescing species. Photo by Andrew Franks, with permission.

Figure 136. ***Leucobryum aduncum* var. *aduncum***, a species that lacks fluorescence. Photo by Niels Klazenga, with permission.

Figure 137. ***Pyrrhobryum paramattense*** with capsules, a species that lacks fluorescence. Photo by Peter Woodard, through Creative Commons.

David Glenny found fluorescence of ***Bazzania tayloriana*** (Figure 138) in New Zealand, reported again by John Braggins (Bryonet 18 April 2022) (Figure 139). This is true for specimens from both North and South Islands of New Zealand.

Figure 138. ***Bazzania tayloriana***, a species that exhibits blue fluorescence in UV light. Photo courtesy of John Braggins.

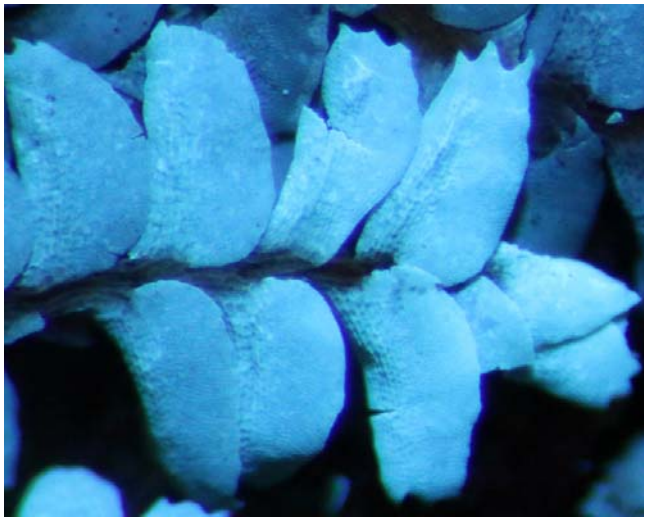

Figure 139. ***Bazzania tayloriana*** showing blue fluorescence. Photo courtesy of John Braggins.

In California, USA, when Ken Kellman (Bryonet 21 April 2022) discovered that the bark of the valley oak (***Quercus lobata***; Figure 140) was fluorescing dark red under the light of a uvBeast V3 MINI, he found that the fluorescence was coming from a tiny moss that proved to be ***Zygodon rupestris*** (Figure 59, Figure 141-Figure 142). But when he used UV light on the dry specimens, there was no fluorescence. Fluorescence appeared again when the moss was rewet. Both the leaves and the gemmae (Figure 143-Figure 144) were glowing red. The nearby mosses ***Antitrichia californica*** (Figure 145) and ***Homalothecium nuttallii*** (Figure 146) did not fluoresce, wet or dry.

Figure 140. ***Quercus lobata***, a species that can serve as substrate for fluorescent ***Zygodon rupestris***. Photo by JKehoe Photos, through Creative Commons.

Figure 141. ***Zygodon rupestris*** on a tree in the UK. Photo by Claire Halpin, with permission.

Figure 142. ***Zygodon rupestris***, a species known to exhibit fluorescence when hydrated but not when dry. Photo by Jonathan Sleath, with permission.

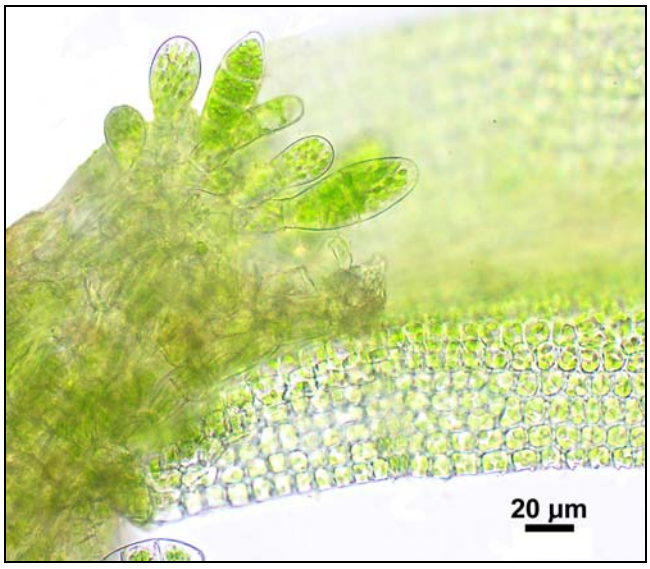

Figure 143. ***Zygodon rupestris*** leaf with gemmae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 144. ***Zygodon rupestris*** gemmae, a plant part that is able to fluoresce. Photo by Claire Halpin, with permission.

Figure 145. ***Antitrichia californica***, a pleurocarpous moss species that seems to lack macroscopic fluorescence capability. Photo by John Game, through Creative Commons.

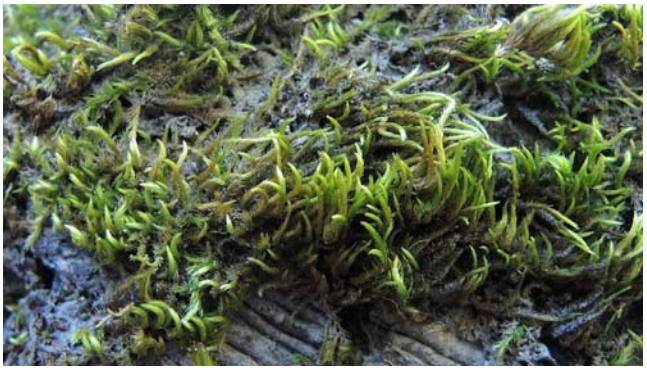

Figure 146. ***Homalothecium nuttallii***, a pleurocarpous species that seems to lack fluorescence capability. Photo by Michael Lüth, with permission.

Tom Ottley (Bryonet 23 April 2022) followed up on these observations with different collections of ***Zygodon rupestris*** (Figure 141-Figure 144). Although it seemed to be that the gemmae were fluorescing, after some difficulty he was able to determine with high power of the microscope that it was an alga that was fluorescing dark red. With the help of a UV microscope, Ottley (Bryonet 5 May 2022) was able to see two sorts of fluorescence in ***Z. rupestris*** (Figure 147). One was the bright whitish-blue from the contents of the gemmae (Figure 147) and the other was red from the chloroplasts of the associated algae (Figure 147). He found no detectable fluorescence in the laminal cells of the moss leaves.

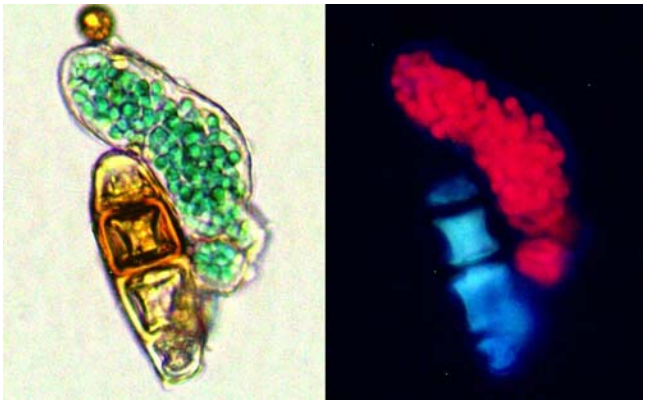

Figure 147. ***Zygodon rupestris*** fluorescence. **Left**: gemma and alga in LED white light. **Right**: gemma and alga fluorescing in UV light. Photo courtesy of Tom Ottley.

Eric Whiting (Bryonet 26 March 2022) was inspired by the Bryonet discussion to re-examine some of his ***Fossombronia*** (Figure 148) samples from semi-arid regions of Australia. Using a hand-held battery unit, he was able to see what appeared to be fluorescence in these, but not in other soil-crust bryophytes from New South Wales, Australia. However, with a stronger UV light he discovered that it was **reflectance** and not fluorescence (Eric Shiting, Bryonet 6 May 2022). He raised the question of whether reflectance could reduce the incoming light energy sufficiently to lower it to a tolerable level. He questioned whether UV light might be equally well reflected.

Figure 148. ***Fossombronia cf wondraczekii*** in Australia, in a genus that seems to lack macroscopic fluorescence. Photo by Bernd Haynold, through Creative Commons.

Magdalena Turzańska has documented the fluorescence of additional species with her photography. These include the liverworts ***Blasia pusilla*** (Figure 149-Figure 150), ***Barbilophozia*** (Figure 151), ***Cephalozia bicuspidata*** (Figure 152), ***Calypogeia*** sp. (Figure 153), ***Gymnocolea inflata*** (Figure 154), ***Lepidozia reptans*** (Figure 155), ***Lophocolea heterophylla*** (Figure 156-Figure 157), ***Marsupella sp***. (Figure 158), ***Metzgeria*** sp. (Figure 160), ***Plagiochila asplenioides*** (Figure 161), ***Radula complanata*** (Figure 162-Figure 163), and ***Trichocolea tomentella*** (Figure 164), and mosses ***Brachythecium*** sp. (Figure 165), ***Mnium hornum*** (Figure 166), ***Polytrichum piliferum*** (Figure 167-Figure 168), ***Tetraphis pellucida*** (), and ***Thuidium tamariscinum*** (Figure 169-Figure 171).

Figure 149. ***Blasia pusilla*** thallus section with **Cyanobacteria**. Photo by Magdalena Turzańska.

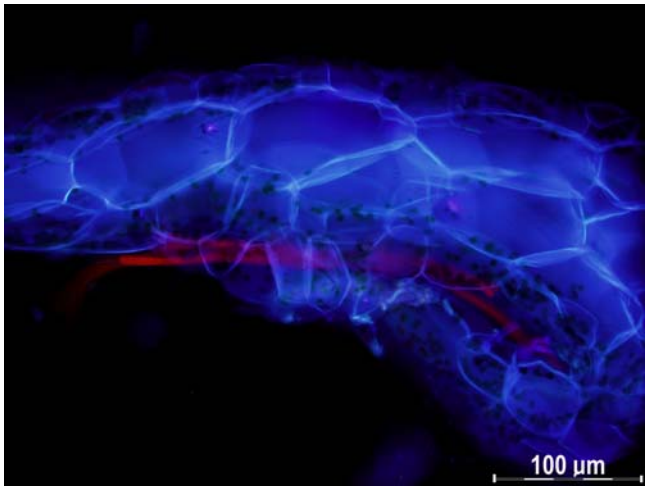

Figure 150. ***Blasia pusilla*** thallus section showing brilliant blue fluorescence. **Cyanobacteria** are fluorescing red. Photo by Magdalena Turzańska.

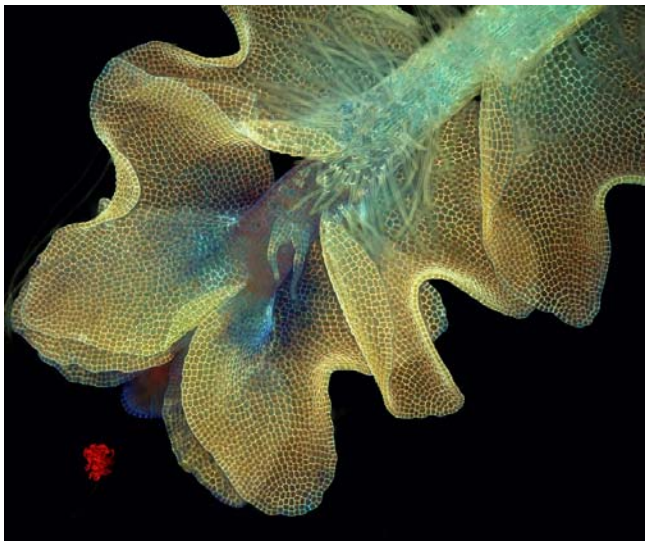

Figure 151. ***Barbilophozia*** sp. showing fluorescence in the leaf cell walls with the base of the leaf glowing blue. The stem has yet another shade of blue. The hair-like filaments are rhizoids. **Cyanobacteria** are fluorescing red in the lower left. Photo by Magdalena Turzańska.

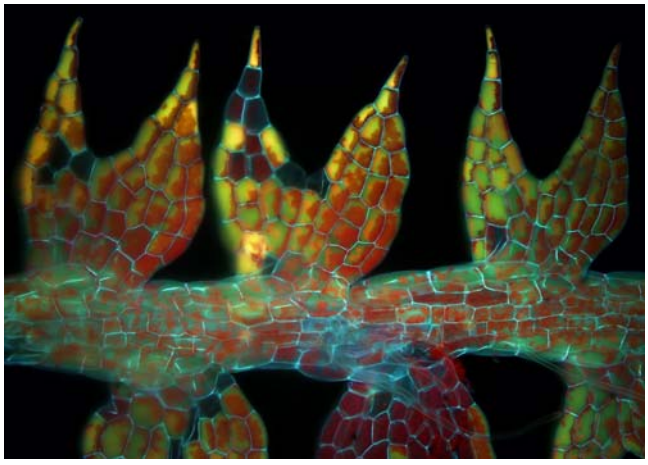

Figure 152. ***Cephalozia bicuspidata*** fluorescence, a tiny species that might be more easily located at night with a UV source. Photo by Magdalena Turzańska.

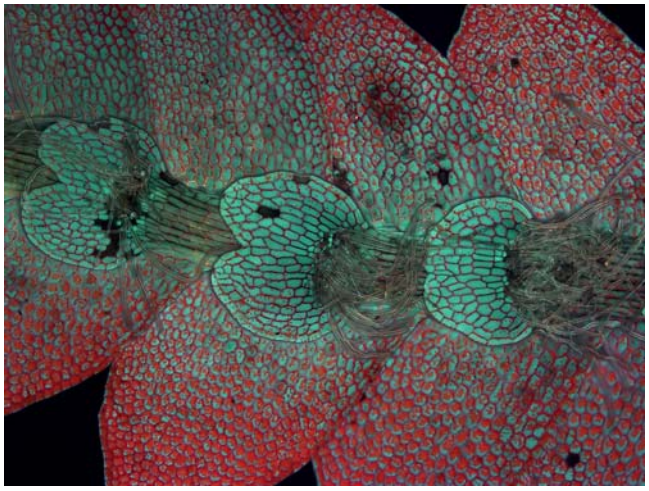

Figure 153. ***Calypogeia*** sp. with cell wall fluorescence; the fluorescence makes it easier to see the underleaves. Photo by Magdalena Turzańska.

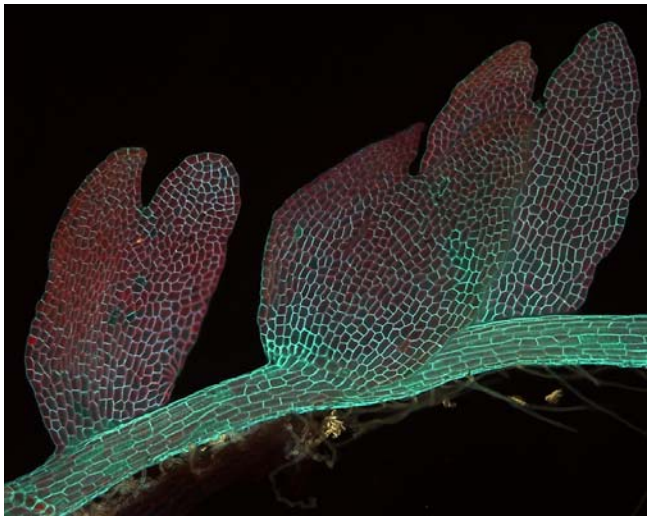

Figure 154. ***Gymnocolea inflata*** with green fluorescence of cell walls. Photo by Magdalena Turzańska.

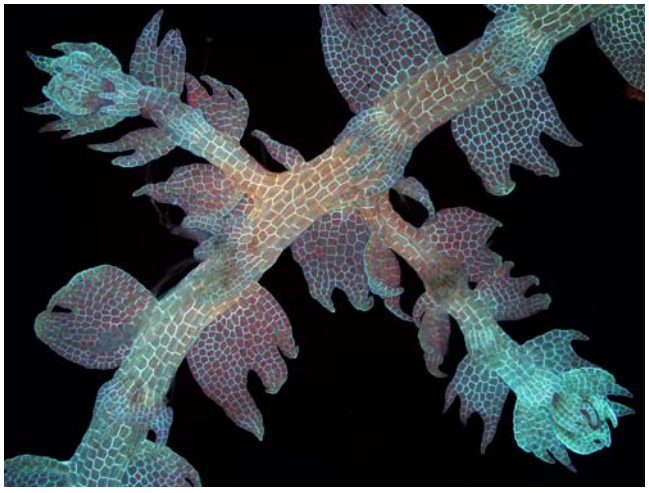

Figure 155. ***Lepidozia reptans*** ventral view showing blue cell wall fluorescence. Photo by Magdalena Turzańska.

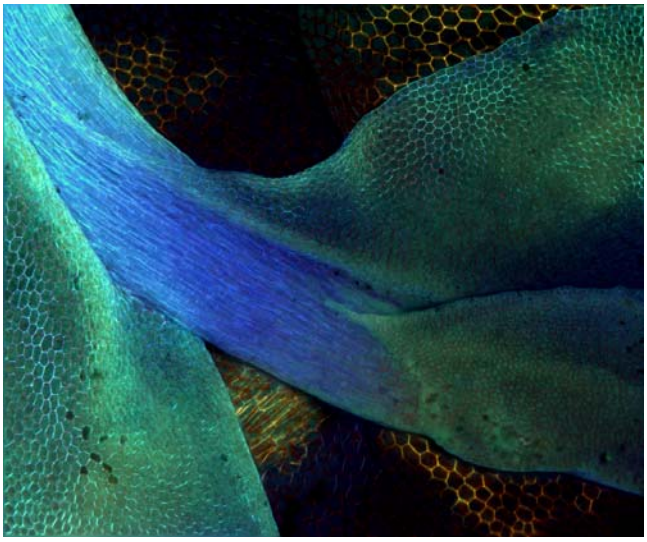

Figure 156. ***Lophocolea heterophylla*** fluorescence showing blue stem cells and greenish leaf cell walls. Photo by Magdalena Turzańska.

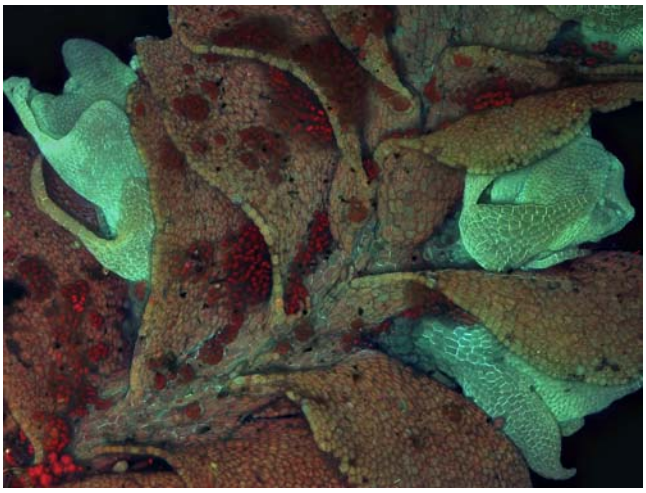

Figure 157. ***Lophocolea heterophylla*** with red patches of **Chlorophyta** fluorescing on leaves that are apparently dead or at a different stage of maturity from the branches with greenish cell wall fluorescence. Photo by Magdalena Turzańska.

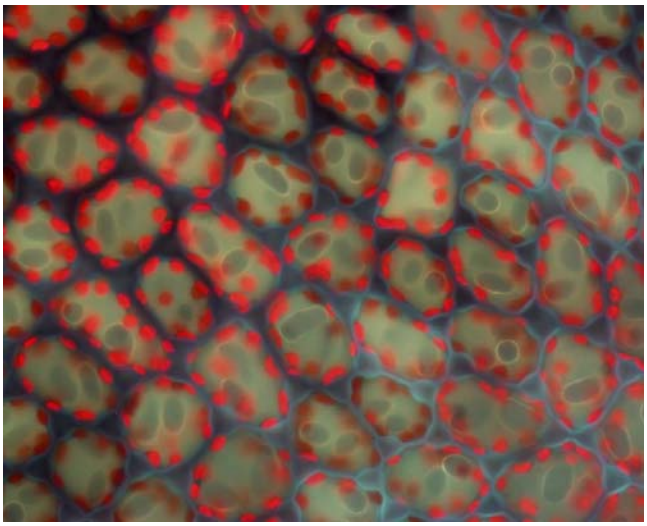

Figure 158. ***Marsupella*** sp. leaf cells fluorescing blue. Photo by Magdalena Turzańska.

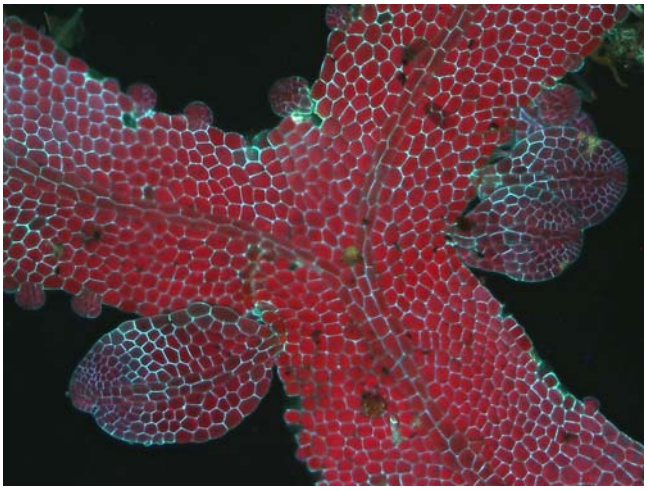

Figure 159. ***Metzgeria*** sp. blue-green fluorescence of cell walls. Photo by Magdalena Turzańska.

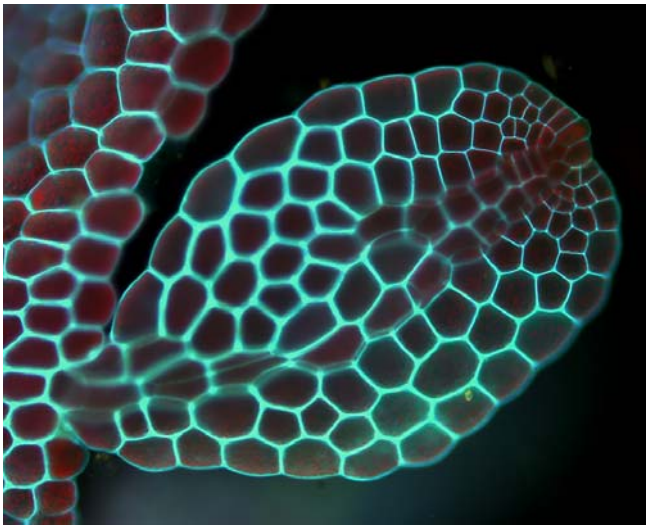

Figure 160. ***Metzgeria*** sp. showing blue-green cell wall fluorescence. Photo by Magdalena Turzańska.

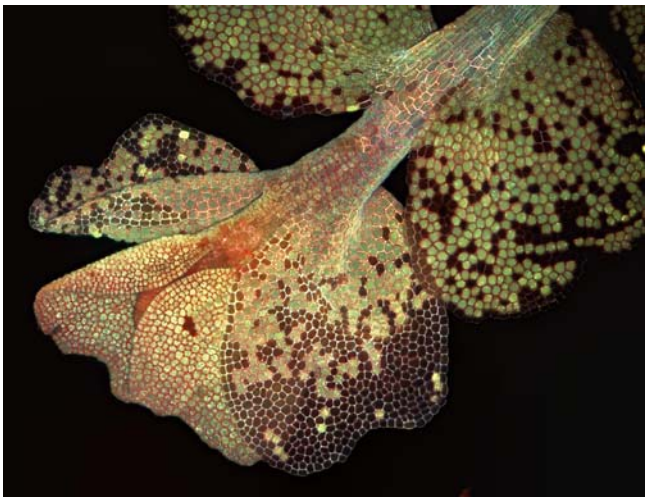

Figure 161. ***Plagiochila asplenioides*** exhibiting golden leaf cell wall fluorescence. Stem cell walls have a more pinkish cast. Photo by Magdalena Turzańska.

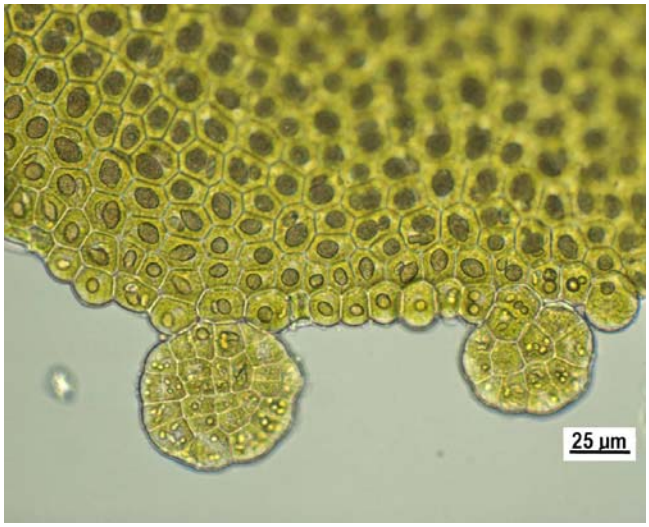

Figure 162. ***Radula complanata*** with gemmae, shown in white light. Photo by Blanka Aguero, with permission.

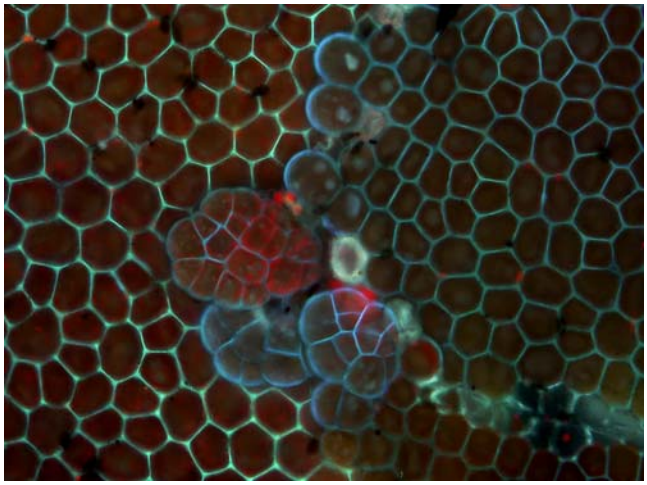

Figure 163. ***Radula complanata*** leaf cell wall and gemmae cell wall fluorescence. Note the difference in color between the blue gemmae cell walls and greenish walls of lamina cells. Photo by Magdalena Turzańska.

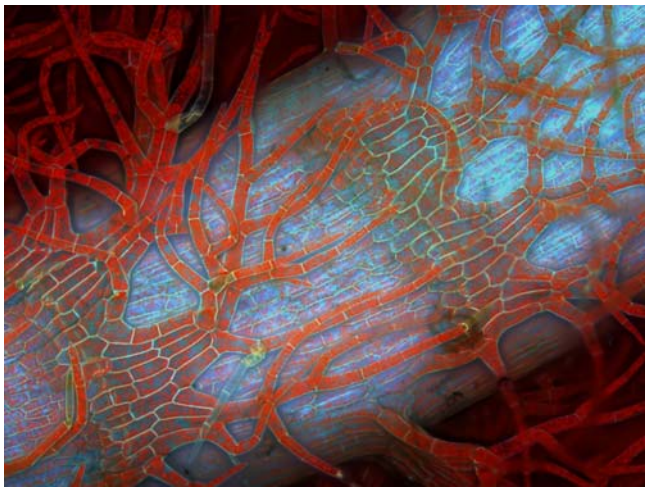

Figure 164. ***Trichocolea tomentella*** with blue cell wall fluorescence. Photo by Magdalena Turzańska.

Figure 165. ***Brachythecium*** fluorescence with leaf cell walls fluorescing aqua and the stems fluorescing bright red. This view makes the leaf bases easy to see. Photo by Magdalena Turzańska.

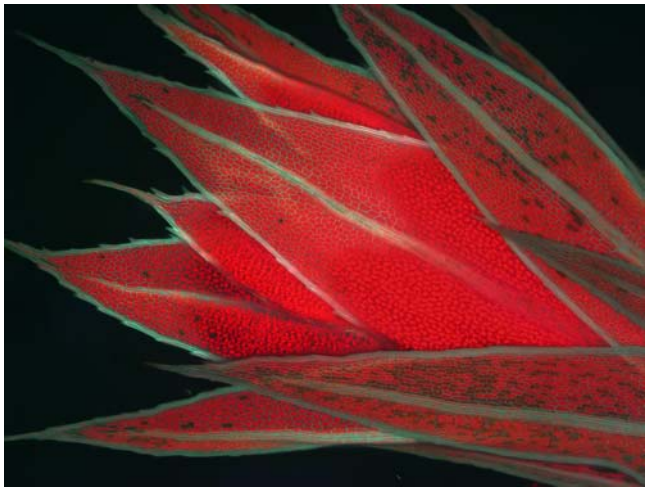

Figure 166. ***Mnium hornum*** leaf border and costa fluorescence with brilliant chlorophyll fluorescence in the leaf cells. Photo by Magdalena Turzańska.

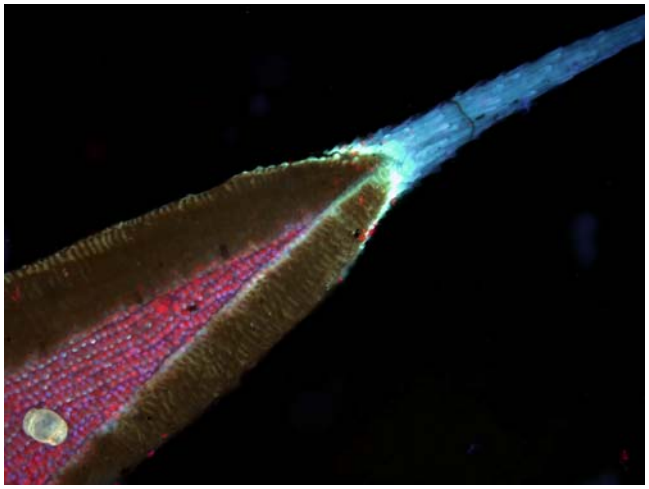

Figure 167. ***Polytrichum piliferum*** leaf fluorescence showing red chlorophyll and blue leaf hair tip. The cell walls of the lamellae can barely be seen fluorescing blue. Photo by Magdalena Turzańska.

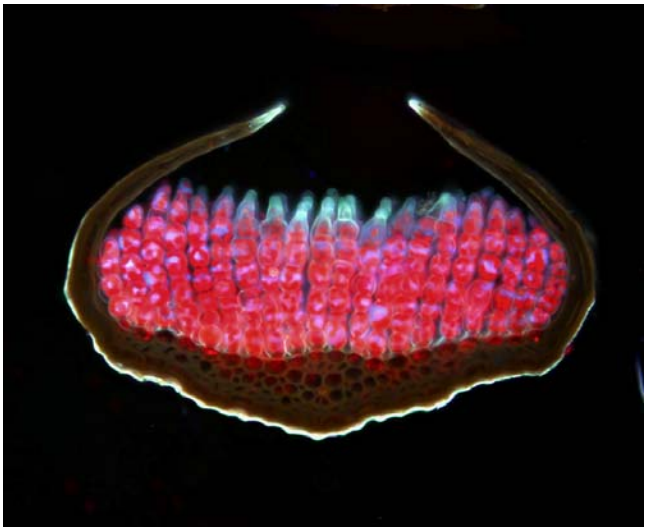

Figure 168. ***Polytrichum piliferum*** leaf cs showing blue fluorescence of the outer cells of lamellae and pale yellow of leaf surface. The lamellae cell walls are fluorescing throughout, but the fluorescence is barely visible due to the strong fluorescence of the chlorophyll. Photo by Magdalena Turzańska.

Figure 169. ***Thuidium tamariscinum*** in sunlight, a species with fluorescent leaf cell walls and contrasting costa fluorescence when illuminated with UV light. Photo by Hermann Schachner, through Creative Commons.

Figure 170. ***Thuidium tamariscinum*** fluorescence in UV light. Photo by Magdalena Turzańska.

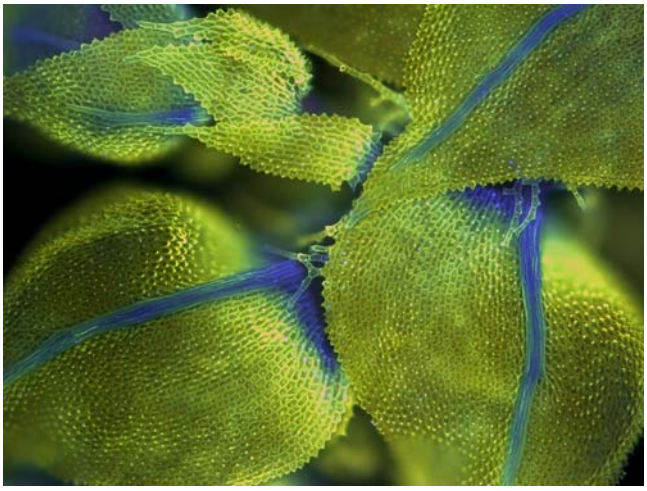

Figure 171. ***Thuidium tamariscinum*** showing a blue fluorescence in the costa and yellow fluorescence in the leaf cell walls, indicating that they have different compounds. These colors have been created by adding berberine to cause the fluorescence. Note the striking difference between the natural fluorescence in Figure 170 and that with berberine stain in this image. Photo by Magdalena Turzańska.

A search of internet images turned up some additional species. One such discovery was a beautiful image of two ***Sphagnum*** species growing together with one (possibly ***Sphagnum divinum***) fluorescing a deep blue-purple and the other lacking fluorescence (Figure 172).

Figure 172. ***Sphagnum*** spp. in white (**upper**) and UV (**lower**) light. The fluorescing moss (**lower**) appears to be ***Sphagnum divinum***, based on its reddish tint (**upper**) and larger, fleshy appearance. Photo ©Damon Noe, with permission.

Sources of Fluorescence

These examples raise the question of the compound(s) causing the fluorescence in bryophytes and why do some have it and others do not. For example, Tamás Pócs (Bryonet 24 March 2022) recalled that ***Bazzania vittata*** (Figure 173-Figure 174) was the only liverwort with fluorescence among those present on the summit of Bellenden Ker in Queensland, Australia.

The two best-known molecules exhibiting fluorescence are chlorophyll and lignin (Donaldson 2020). However, numerous others also exist. These elicit a variety of colors and some (ferulates – one of phenolic compounds) change color with a change in *p*H or chemicals such as Naturstoff reagent (flavonoids). Use of glutaraldehyde as a fixing agent can also induce autofluorescence and permit the imaging of proteins in organelles in the cell protoplast.

It is unclear which structures in bryophytes are responsible for the fluorescence. Andi Cairns (pers. comm. 30 March 2022) suggested that the fluorescence might be due to surface quality. To support this idea, she cited the glaucous surface with minute papillae on both ***Bazzania vittata*** (Figure 173-Figure 174) and ***B. tayloriana*** (Figure 175-Figure 176) (Meagher 2019). ***Zygodon rupestris*** (Figure 59) also has multiple papillae per cell (Figure 177).

Figure 173. ***Bazzania vittata*** in LED light, a species that exhibits fluorescence Photo by Will Cairns, courtesy of Andi Cairns.

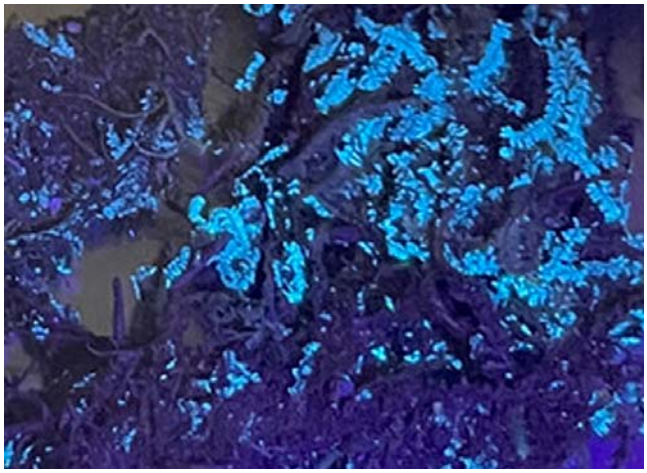

Figure 174. ***Bazzania vittata*** fluorescing. Photo courtesy of Andi Cairns.

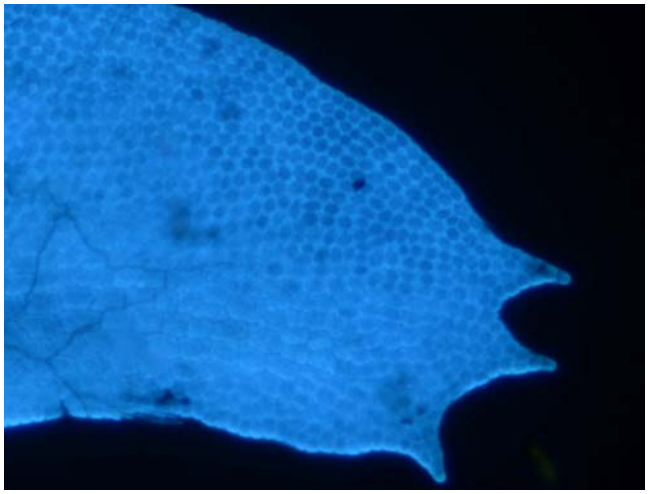

Figure 175. ***Bazzania tayloriana*** leaf showing minute papillae visible on the margins and blue fluorescence. Photo courtesy of David Glenny.

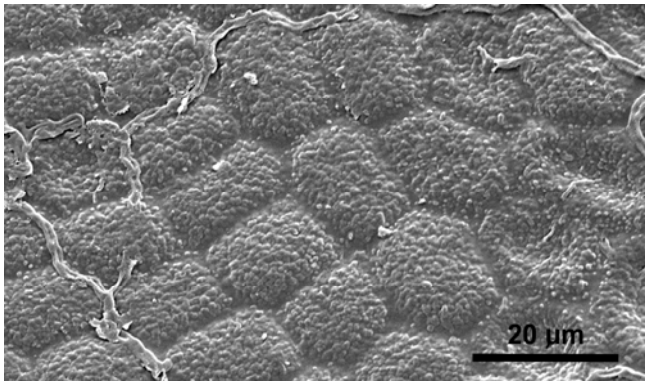

Figure 176. ***Bazzania tayloriana*** dorsal surface cells showing minute papillae. Photo courtesy of John Braggins.

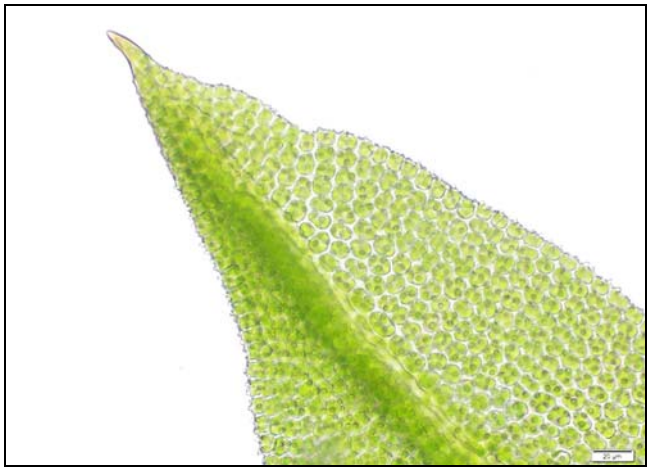

Figure 177. ***Zygodon rupestris*** leaf cells showing papillae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

It is interesting that McClure and Miller (1967) explored the flavonoids causing fluorescence at such an early date without precipitating more studies on this property in a wider range of bryophytes. They found that most of the fluorescence came from flavonoids and some phenolics, as reported by Dave Kofranek (Bryonet 23 April 2022). It is further interesting that none of the pleurocarpous mosses tested exhibited fluorescence, an observation consistent with that of Ken Kellman (Bryonet 21 April 2022) for ***Antitrichia*** (Figure 145) and ***Homalothecium*** (Figure 146). The study only listed blue and purple reactions, so perhaps there was no testing for those that fluoresce red, yellow, or other colors. There is so much remaining for us to understand.

Magdelena Turzańska has found only weak fluorescence in pleurocarpous mosses, ass seen here in ***Hypnum*** sp. (Figure 178).

Figure 178. ***Hypnum*** sp., a pleurocarpous moss showing a golden cell wall fluorescence. Photo by Magdalena Turzańska.

Role

Fluorescence can help to attract pollinators in flowering plants and thus aid in dispersal, but its role in bryophytes is unknown and unexplored. Andi Cairns speculated on the function of fluorescence in bryophytes as agents of antiherbivory (Andi Cairns, pers. comm. 2 June 2022), and J. K. Oliver suggested that they might just be **spandrels** (phenotypic trait that is byproduct of evolution of some other characteristic, rather than direct product of adaptive selection) – a term introduced by Gould and Lewontin (1979) (Andi Cairns, pers. comm., 24 March 2022).

In tracheophytes, Body *et al*. (2019) found that the yellow fluorescent protein that causes yellow fluorescence was produced in response to **jasmonic acid**, a compound produced in response to herbivory. But we thus far have no evidence that this, or any other fluorescence in bryophytes, is a response to herbivory.

But it is always fun to speculate. It is the start of hypotheses that can be tested. Tom Ottley (pers. comm. 5 May 2022) speculated about the potential role in dispersal of gemmae. Musing that the bryophytes could just make blue pigments instead, he realized that bryophytes are not known to make blue pigments. He suggested that perhaps the compound responsible is able to convert UV light to blue. On the other hand, insects are able to see reflected UV light itself (Turpin 2012). This might be a way of making gemmae and other propagules visible amid the maze of non-emitting leaves, just as it helped Gisela Nordhorn-Richter to locate them for her taxonomic studies. For leafy liverworts, the gemmae are more easily

discernable because of their locations at leaf margins. So far, I have found no information to indicate widespread presence of fluorescence in leafy liverwort gemmae. Perhaps the leaf fluorescence helps the insects to find the plants themselves, with contact with gemmae being almost inevitable.

Lloyd (1924) suggested that the taxonomist could use fluorescent color differences to identify **Cyanobacteria**, especially between closely related species. This seems to be possible with some bryophytes, often being a presence-absence difference. But we need many more UV views of bryophytes to really understand the color variation and its potential use in identification.

Perhaps a more important question needs to be answered. Which of these fluorescent colors can other organisms see? Are the colors we see with UV light under the microscope visible to organisms in nature?

For example, in cross section, a species of ***Leucobryum*** (Figure 179) demonstrated cell wall fluorescence. On the other hand, when viewed in the field with a UV light source, ***Leucobryum aduncum* var. *aduncum*** (Figure 132-Figure 133, Figure 136) exhibited no fluorescence.

Figure 179. ***Leucobryum glaucum*** leaf cs showing fluorescence of the cell walls. Photo by Magdalena Turzańska.

As I saw the color of fluorescence in more and more species of bryophytes, I was inclined to think that these are indeed spandrels. The compounds that produce them are often secondary compounds that serve in functions of structure, antiherbivory, and antibiotics. The fact that they fluoresce is likely just a product of the class of compounds that have these functions. At the same time, there is no evolutionary rule that a compound cannot have more than one adaptive quality. It would be interesting to see if the various colors have any correlation with habitat conditions and if they are inducible or always present.

Methodology

For most of our purposes, the field equipment can be simple and relatively inexpensive. Andi Cairns and colleagues used an LED white light head torch (ASD $3.00) and a small UV torch (ASD $14.99, no name, made in China). For their photography they used a combination of the two lights to obtain both fluorescence of one species while showing lack of fluorescence in the other species present. The photos were taken with an iPhone.

For microscopic work, Magdalena Turzańska uses UV light and an Olympus BX50 fluorescence microscope with an Olympus DP 71 camera.

Staining bryophytes can help to make fluorescence visible in some weakly fluorescing structures. Magdalena Turzańska uses berberine (extracted from *Chelidonium majus* roots) for cell wall staining. These are shown below in ***Diplophyllum albicans*** (Figure 180) and ***Nowellia curvifolia*** (Figure 181). Other stains can be used for special purposes.

Bryophytes have been used to develop methods for detecting fluorescent compounds present in small quantities (Delépée & Pouliquen 2002; Zhao *et al*. 2007). Delépée and Pouliquen (2002) used ***Fontinalis antipyretica*** (Figure 65, Figure 70-Figure 71) to develop a method for detecting oxolinic acid. Cerovic *et al*. (1999) reviewed the potential of using fluorescence signals for remote sensing of vegetation. Can this application be used for bryophytes?

Figure 180. ***Diplophyllum albicans*** female shoot showing fluorescence of the dye berberine in the leaf and perianth cell walls. This is not natural fluorescence. The fluorescence is too weak to be visible without the dye. Photo by Magdalena Turzańska.

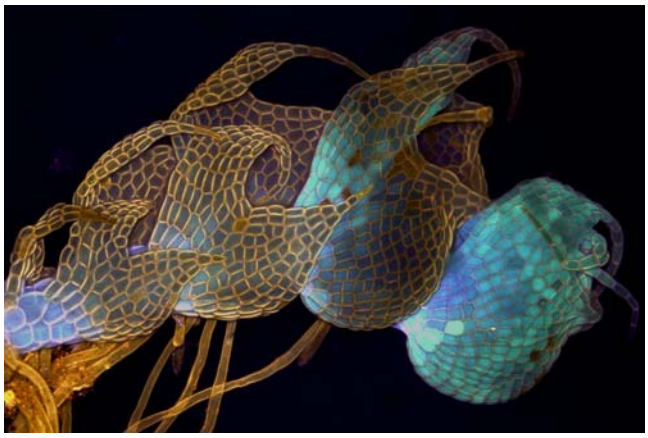

Figure 181. ***Nowellia curvifolia*** showing golden cell wall fluorescence in the leaves after staining with berberine. Photo by Magdalena Turzańska.

Prospects

It appears that fluorescence in bryophytes is a field wide open for study. So many evolutionary questions remain unanswered. How widespread is it among bryophytes? Are the compounds involved the same as those in tracheophytes? Which structures fluoresce? Does this location differ among species or habitats? Which compounds predominate in the bryophytes, and are there phylogenetic patterns to their presence? Can the colors of fluorescence be used to help in identification? Can it help us find some of the tiny species growing among larger species? Does the fluorescence attract arthropods, especially would-be dispersal agents? If so, to what degree does it improve dispersal chances? Does the phenomenon have any adaptive value in particular habitats? Does the fluorescence change with seasons? with temperature? [we know that chlorophyll fluorescence can change with temperature (Deltoro *et al*. 1999)], with drying? Is fluorescence lost over time in herbarium specimens?

Pigments

As in the algae, one can use the chlorophyll-to-phaeophytin ratio to assess physiological stress in bryophytes (Lopez *et al*. 1997). This ratio proved to be a better indicator of environmental stress than presence-absence data for species in 188 stretches of river in northwest Spain. Organic pollution was indicated most strongly, with *p*H also strongly correlated.

As discussed in other chapters, pigments can respond to changes in light intensity. Dark-colored wall or cytoplasmic pigments are present in genera like ***Frullania*** (Figure 123) that are able live high in the canopy or at high elevations (Li *et al*. 1989; Glime *et al*. 1990). Aquatic bryophytes that grow in cold water and full sunlight likewise may produce red cytoplasmic pigments, as seen in ***Fontinalis*** (Figure 182).

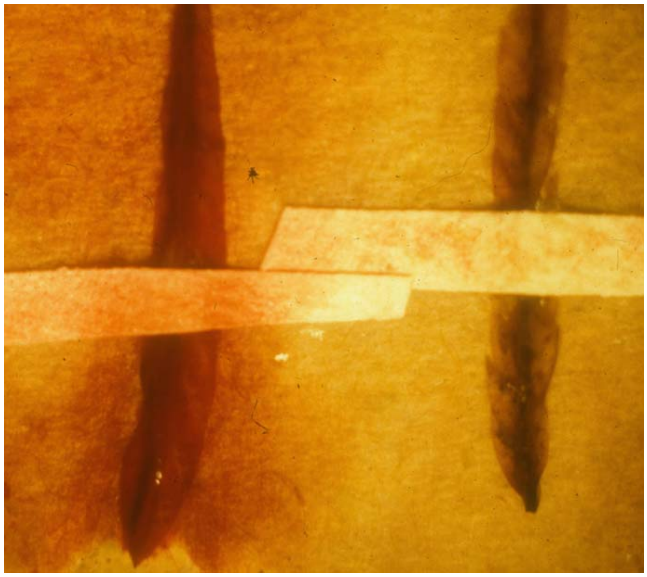

Figure 182. ***Fontinalis antipyretica*** producing red cytoplasmic pigments under water stress in high light. Photo by Janice Glime.

One can only speculate about the advantages of color. Red pigments can be a bit of an enigma. They can respond to both high light and low light. In bright light they are protectors, being positioned between the light source and chlorophyll, often in cell walls where they can protect the entire cell. In low light they seem to work best on the lower surface, or the side away from the light source.

In tropical forests some of the flowering plants have purplish-red coloration on the undersides of leaves. Botanists have considered this to be an adaptation to the low light there. Red algae live in the ocean depths and absorb green light using red pigments (Ritz *et al*. 2000), with most of the red light absorbed by the water itself. These deep water algae are able to activate the red pigments and transfer the energy to the chlorophyll antenna system (photosynthetic light-harvesting antennae) where it activates the chlorophyll electrons (Bag 2021). The chlorophyll antenna system works in bryophytes as well. In bryophytes, thee most frequent of the antenna pigments are α- and β-carotene, lutein, zeaxanthin, violaxanthin, and neoxanthin (Taylor *et al*. 1972). See Chapter 11-1 of this volume for a more thorough discussion of the role of antenna pigments in bryophytes.

Deep forest plants such as bryophytes are able to absorb the green light that filters through the canopy (Neill & Gould 2000; Ruberti *et al*. 2012) and reflect it, presumably to the chlorophyll. In the red alga *Rhodella violacea*, the genes for the production of the red and blue-green pigments phycoerythrin and phycocyanin, respectively, are down-regulated in bright light (Ritz *et al*. 2000). Since chlorophyll is most active in the red end of the spectrum (Wang & Folta 2013), such red reflectance could offer a light enhancement under a green canopy. In ***Arabidopsis thaliana***, when both green and blue light are present, the anthocyanin (red) level is lower than when only blue light is present (Bouly *et al*. 2007; Zhang & Folta 2012) and the degree of reduction of the anthocyanin depends on the rate at which the green light is delivered with the blue light (Zhang & Folta 2012). Melati *et al*. (2019) demonstrated that shaded plants of the Luja plant (*Peristhrophe bivalvis*) has a higher red pigment concentration in shade plants than in full light intensity.

More relevant to the purplish liverwort scales is the red coloration on the undersurfaces of rainforest extreme shade plants. Increased anthocyanin coloration on tracheophyte leaf undersurfaces correlates with the increased absorption of light at the upper (violet) end of the photosynthetic action spectrum (Lee & Graham 1986). Whereas increased red pigments can be a stress response to shade plants exposed to high light intensity, it appears that red pigments on the lower surfaces of photosynthetic organs might have a different function in light capture.

Since anthocyanin is often the pigment responsible for a purplish color, it is possible this mechanism is at work in the liverworts as well, reflecting the limited light that manages to penetrate that far and thus increase that which activates the chlorophyll. It is not an antenna pigment because it is not near the chlorophyll. Such a potential advantage has not, to my knowledge, been explored in the liverworts.

Coloration can also be used as a diagnostic tool. In tracheophytes, pigment variations are indicators for several nutrient deficiencies, toxicities, or antagonisms (Martínez-Abaigar & Núñez-Olivera 1998). Little has been done with color as a nutrient status indicator in bryophytes.

We know that the flavonoid pathway is a specialized metabolic pathway in plants (Davies *et al*. 2020). In flowering plants, flavonoids signal pollinators and dispersal organisms, but they also assist in tolerance to abiotic stresses. We have presumed that this pathway arose during the colonization of land, suggesting that it may have arisen in bryophytes as a defense against UV and drought. It is, nevertheless, absent in hornworts. The bryophyte pathway and its regulation are similar in some ways and differ in others when compared to that seen in flowering plants. One proposal is that flavonoids helped early land plants cope with increased exposure to UVB. But they also helped overcome the dangers imposed by desiccation and extreme temperatures (Markham 1988; Jorgensen 1994; Kenrick & Crane 1997; Cockell & Knowland 1999; Rozema *et al*. 2002; Ligrone *et al*. 2012; Mouradov & Spangenberg 2014; Demarsy *et al*. 2017; Davies *et al*. 2018; de Vries & Archibald 2018; Rensing 2018). Alternatively, Stafford (1991) proposed that these compounds regulated auxin action as well as signalling to mycorrhizal and symbiotic fungi, *i.e.*, serving in communication between complementary organisms. Stafford argued against the UVB-screening role because early concentrations would probably have been low, thus limiting their efficiency at a time when UV-B was particularly high.

I have long been confounded by the one-purpose approach of so many biologists, especially ecologists. It seems to me that these compounds could very well have been as Stafford proposed, serving to signal both auxins and fungi, but at the same time contributing to protection from UV-B. As time proceeded, those individuals that produced more flavonoids would have greater survival rates in the face of extreme temperatures, drought, and UV-B, permitting them to occupy habitats not available to those individuals that produced lesser concentrations of flavonoids. Most likely starting as primitive anthocyanins in the liverworts, the flavonoids have kept adding roles and become more effective at them (Berland *et al*. 2019).

Jumping to the 21st Century, researchers have discovered **auronidins** in ***Marchantia polymorpha*** (Berland *et al*. 2019). But Berland and coworkers discovered that the red pigments in the liverwort ***Marchantia*** (Figure 102, Figure 110, Figure 183-Figure 184) are not anthocyanins, but rather are phenylpropanoids that they have named **auronidins**, a previously unknown and distinct flavonoid class. Liverworts produce red cell-wall-bound pigments called **riccionidins** (now known to be auronidins) as a response to stresses, including UV-B, drought, and nutrient deficiency. Berland and coworkers suggest that these may have been the first anthocyanidins formed in the early land plants and distinct from the anthocyanins. They provide red coloration similar to that of anthocyanins, but they also have a strong fluorescence. Their antioxidant properties could be important in several pathways, but they seem to restricted to cell walls.

This suggests that we should look at fluorescence in our consideration of early evolutionary relationships among bryophytes. Martínez-Abaigar and Núñez-Olivera (2022) have reviewed UV effects on bryophytes, noting that these effects depend on species and evolutionary lineage. Mosses are more UV-tolerant than are liverworts. It should be enlightening to discover where fluorescence exists and how it relates to current habitats and that of the ancestors.

The discovery of auronidins raises so many questions for me. What organs have them? What are the adaptive values, if any, in these organs? Can they tell us an evolutionary story? How do they relate to habitats? Does their fluorescence give the plants any advantage, or is it simply a consequence of having the compound be useful for other characteristics? Are the colors seasonal?

Figure 183. ***Marchantia polymorpha*** with gemmae, showing distribution of red pigmentation, presumably auronidins. Photo by Dick Haaksma, with permission.

Figure 184. ***Marchantia polymorpha*** with red archegoniophores, but green thalli, Laxarbakki, Myvatn, Iceland, 26 July 1987. These red pigments are most likely auronidins. Photo by Janice Glime.

Yet another advantage of the auronidins is their ability to enhance resistance to the fungus ***Phytophthora palmivora*** (Carella *et al*. 2019). Hyphae are unable to penetrate in highly pigmented regions of these plants.

Leaf Canopy

It is well known that chlorophyll concentration increases in response to reduced light availability (Niinemets & Tobias 2014). But within the bryophyte canopy, older tissues are lower on the plant and thus receive less light. In this case, the chlorophyll

concentration decreases with not only age, but also with decreasing light availability (Davey & Ellis-Evans 1996; Niinemets & Tobias 2014). Furthermore, in lower light, the plants are less dense and the leaves are usually farther apart, decreasing the density (Niinemets & Tobias 2014). This reduction in density increases the light interception per leaf area. Pleurocarpous mosses are able to acclimate structurally to light levels by adjusting the density of leaves and branches, whereas non-branching acrocarpous mosses lack the ability to change branching density. In addition, mosses under low water conditions have a greater degree of aggregation, thus further reducing light penetration. But as mosses desiccate they have greater light penetration further down the stem than the same mosses when hydrated, increasing productivity in older parts (Davey & Ellis-Evans 1996).

Absorption is not equal throughout the spectrum. Davey and Ellis-Evans (1996) observed that the greatest attenuation occurred at wavelengths corresponding to the peaks of chlorophyll absorption (675 nm and below 450 nm). Other factors that affect absorption include stem orientation, stem density, leaf size and orientation, and pigment content.

Leaf Angle

Angle of incidence (Figure 185) is the angle formed between the direction of light and the vertical (difference from straight on), so a low sun has a higher angle of incidence. **Leaf angle** (Figure 186) is the angle made by the axil of the leaf and the axis. It affects the reflectance of light in plants. Therefore, a small leaf angle (approaching vertical) creates the effect of a large angle of incidence.

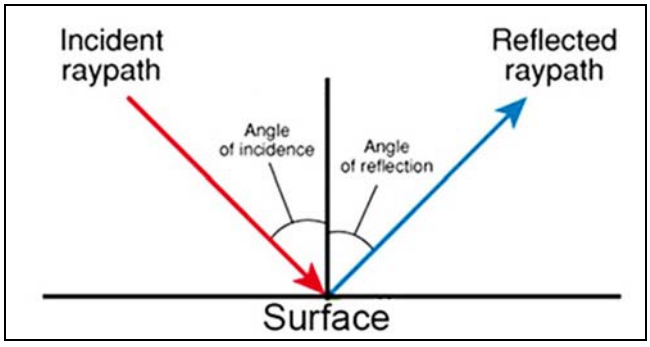

Figure 185. Angle of incidence and reflection pathway. Drawing modified from Clive Dexter at <http://ezbackgrounds.com/blog/ezlighting-guide-angle-incidence.php>.

Howard (1967) demonstrated that leaf angles in four tracheophyte species of 0-30° (=90-60° angle of incidence) made little difference in reflectance, but when the angle of incidence was smaller, the reflectance increased rapidly, consequently rapidly reducing photosynthesis. In the tree leaves of *Eucalyptus regnans*, photosynthesis begins to decrease at ~72° leaf angle, and at 45°, photosynthesis drops to 70% of values of horizontal leaves. At 5° leaf angles it approaches 0% (Kriedmann *et al*. 1964).

In bryophytes, many moss species raise their leaves and wrap them around the stem as they dry, effectively providing greater protection to the chlorophyll by greater overlapping of leaves. In the desert moss ***Syntrichia caninervis*** (Figure 187), leaf angle changes (Figure 188) are an important means of protecting against the effects of high light intensity during long periods of desiccation (Wu *et al*. 2014). First, the leaf movement helps to slow drying, permitting the plant to adjust physiologically in preparation for desiccation (see Chapters 7-5 and 7-6 in Water Relations). Second, the acute leaf angle of only 30° of a dry plant protect the photosynthetic cells. And third, when the leaf rehydrates, it returns in 7 seconds to an angle of 69-84°, with the first leaves reaching normal position in only 1 second. The hyaline cells at the leaf base are thin-walled and facilitate rapid uptake of water, swell, and push the leaf away from the stem. The leaf hair also play a role in reflecting light and reducing its impact on the chlorophyll. But the leaf hairs (**awns**) play another role that thus far has not been explained. They somehow are important in adjusting the leaf angle. When these awns are removed, the angle adjustment is retarded.

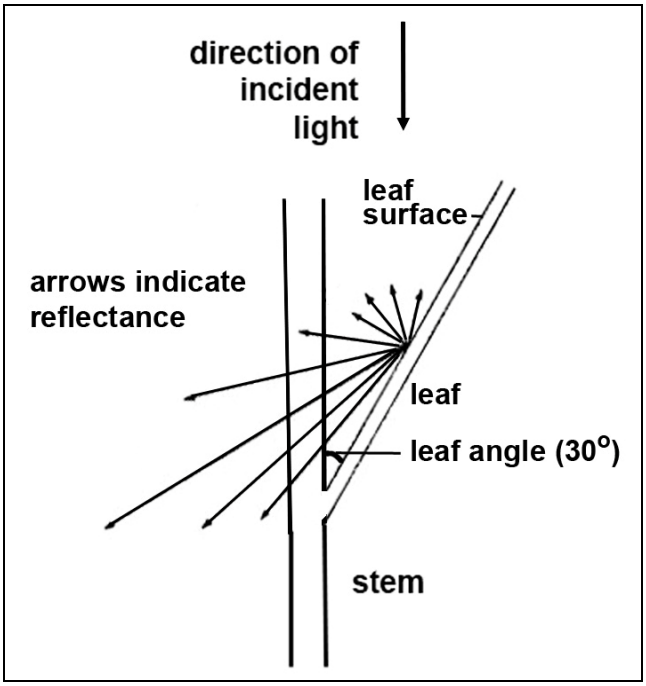

Figure 186. Incidence light and reflectance on a leaf at an acute angle. In this case, the incident light strikes the leaf at an angle of 60° from the straight up light that would strike the leaf from a perpendicular direction. Redrawn from Howard 1967.

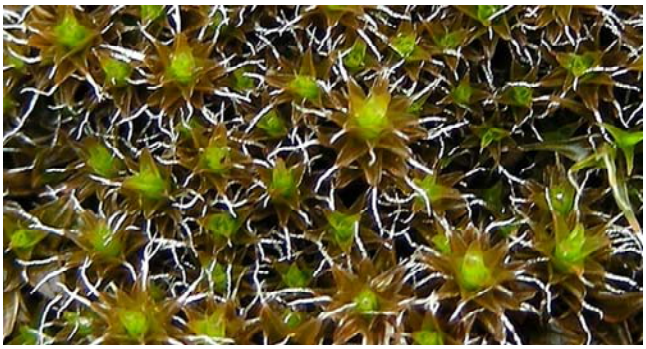

Figure 187. ***Syntrichia caninervis***, a species that changes leaf angles in response to drying. Photo by Michael Lüth, with permission.

Figure 188. ***Syntrichia caninervis*** dry exhibiting twisted leaves with a small leaf angle. Photo by Sheri Hagwood, through public domain.

Xerophytic mosses like ***Syntrichia ruralis*** (Figure 53) can look much darker and expose less surface area to the atmosphere, whereas the wet cells change the optical properties, making the cell walls more translucent (Glime & Church, unpubl.).

Summary

Protonemata of some mosses, such as ***Schistostega pennata***, are able to position their chloroplasts to receive maximum available light and the lens-shaped cells help to focus the light. Their high reflectance provides a luminescence in caves. Similar reflective abilities are present in ***Mittenia plumula*** that lives in wombat holes. ***Cyathodium*** species that live in caves have a similar reflective ability in their thalli.

Some bryophytes are able to live in the dim light surrounding light bulbs in visitor caves, exceeded in their low-light survival only by the algae. Many of the cave bryophytes are also typical of other habitats of greater light intensity, including high-light tolerators like ***Ceratodon purpureus*** and ***Pohlia nutans***. Some are the **tufa formers** that often are so encrusted with limestone that only their tips are able to get sufficient light for photosynthesis. ***Amblystegium serpens*** seems able to live in the lowest light at only 232 lux.

One response to bryophytes in deep caves is **etiolation**, which spaces leaves further apart, thus exposing more surface area to the little light available. In some species, the number of chloroplasts and size of grana can increase and growth can occur even in the dark. Long, thin "exploratory" branches may form. In ***Atrichum undulatum*** the starch disappeared in winter but reappeared in spring, in the dark! When placed in the light, photosynthesis began without delay.

Various plant parts may exhibit fluorescence. So far this ability is known from leaf cell walls, stems, spores, antheridia, archegonia, paraphyses, capsules, peristomes, elaters, gemmae, and bulbils, in addition to the chlorophyll fluorescence known from all photosynthetic organisms. Fluorescence under the microscope has been exhibited in many bryophyte species, but few seem to have been documented in the field. Fluorescence may be caused by a number of compounds, including flavonoids, fatty acids, and lignin-like compounds. Its colors vary widely, but are not visible to the human eye when bright sunlight is present. Nevertheless, many kinds of insects are able to see these colors even in daylight. Its role remains unknown, and it may simply be a property of the cell wall components and antibiotic compounds, but its value in attracting dispersal agents should be explored.

Some mosses develop pigments in response to increased light intensity, although chlorophyll concentrations usually decrease. Others change the leaf angles, decreasing the damage to chlorophyll. Antenna pigments help to transfer light energy to the chlorophyll in low light and pigments on the lower surface may help by reflecting red light back to the chlorophyll.

The light intensity diminishes as it penetrates the bryophyte canopy, but when the leaves dry, more light may reach older portions.

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CHAPTER 10-1

TEMPERATURE: EFFECTS

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CHAPTER 10-1
TEMPERATURE: EFFECTS

Figure 1. Snow on the peak of Mount Edith Cavell, Canadian Rockies, in Jasper National Park, Alberta, Canada. Few plants can grow in this harsh, rocky habitat, but lichens and bryophytes may be found in microsites. Photo by Janice Glime.

Temperature

The temperatures experiences by various microhabitats on the Earth vary widely, from volcanic lava to exposed rock in the Antarctic. Temperatures at which bryophytes exist also vary widely, from those of geothermal fields to glacial polsters (Figure 1). But the daily temperature of a bryophyte may vary more than we had imagined. Gabriel (2000) points out the importance of microclimate temperatures to the growth rate for Azorean forest bryophytes. And on a single sunny afternoon in the Keweenaw Peninsula of Michigan, with an air temperature of ~28ºC, we measured moss leaf temperatures up to 41ºC, whereas a nearby black rock, also in the sun, registered only 31ºC! (Hribljan & Glime, unpublished data).

Proctor (2014) includes cooling as one of basic needs of plants on land. Emphasizing the importance of scale, he contends that for large plants (tracheophytes) convective cooling is most important. For low-growing plants such as bryophytes, evaporative cooling is sufficient.

As C_3 plants, bryophytes are adapted to have a net photosynthetic gain at a relatively low temperature, some (*e.g.* ***Racomitrium lanuginosum***; Figure 2-Figure 3) as low as -10°C (Kallio & Heinonen 1973), but would seldom be expected to do as well at temperatures above 25°C. Even tropical bryophytes seem to do poorly above 25°C (Frahm 1990), where their net assimilation rate decreases drastically, respiration rates are high, and they fail to reach their compensation point (Frahm 1987). Those bryophytes that typically experience cool weather during the growing season, as for example ***Hylocomium splendens*** (Figure 4) from Swedish Lapland, fail to benefit by enhanced growth from a mean increase of 1.5-3°C during the growing season (Jägerbrand *et al*. 2003). It seems that at high temperatures, most bryophytes may become dormant, suffer reversible depression of photosynthesis (Weis *et al*. 1986), or die; irreversible damage to photosynthesis can result from damage to photosystem II (Weis *et al.* 1986).

Figure 2. ***Racomitrium lanuginosum*** forming large mounds in Iceland. Photo by Janice Glime.

Figure 3. ***Racomitrium lanuginosum*** showing the awns that help reflect light and reduce the temperature while reducing water loss. Photo by Michael Luth, with permission.

Temperature and seasonal changes can play a significant role in determining the distribution of bryophytes. For example, when comparing bryophyte floras of the French Alps and Britain, Pentecost and Zhang (2002) found that the distribution of ***Palustriella commutata*** (=*Cratoneuron commutatum*; Figure 5) is influenced more by temperature than by water chemistry, despite the need for free CO_2. Dilks and Proctor (1975) have shown that most bryophytes have a relatively narrow range of temperatures for net photosynthetic gain, experiencing a sharp decline just past the optimum. Indeed, for most bryophytes, the optimum is near 20°C, and for many it is much lower.

Figure 4. ***Hylocomium splendens*** from British Columbia, Canada. Photo by Des Callaghan, with permission.

Figure 5. ***Palustriella commutata*** in one of its common habitats (**Upper**) and closeup (**Lower**). Photos by Michael Lüth, with permission.

Bryophyte Alteration of Temperature

The temperature of a bryophyte is not necessarily the temperature we would feel as we walk by. Often it is quite different in the nearby niches, cooled by air from a rockhouse or warmed by a spot of sun on the absorbing bryophyte tissues. It is the temperature of the microclimate that often determines the growth rate and distribution of the bryophytes (Gabriel 2000).

Not only do cushions retain water, but they moderate the temperature (Rod Seppelt, Bryonet 27 June 2022). In the Antarctic, when the temperature drops below 0ºC, the moss cushions likewise drop in temperature. However, when the cushion begins to freeze, latent heat begins to elevate the temperature to as much as 2ºC. This delays the denaturation of the cellular proteins.

Imagine a moss sitting in the forest, still hydrated because of the protection of the forest. Yet as the Earth moves and the position of the sun changes, sunflecks dance about the forest floor like butterflies. One minute the hydrated moss is in the cool shade of the forest, but the next it is beset by the heat of the sun. Proctor (1982) reported sunfleck temperatures up to 39ºC when the air temperature was a mere 20ºC.

In his treatment on the upper temperature limit of life, Kempner stated that there could be "no defense against high temperatures unless the laws of thermodynamics were violated." But the literal meaning of that is simply not true. Animals sweat, taking advantage of evaporative cooling. Tracheophytes transpire, pumping water from below ground to their leaves, then to the atmosphere, cooling by

the heat absorbed as liquid water changes to gas. And bryophytes, too, can take advantage of transferring water from lower parts to their upper parts where it evaporates and cools the growing tips. And plants, like animals, can reflect the sun by presenting white, reflective surfaces to prevent absorption of the sun's rays. In bryophytes, this reflection may be achieved by **hyalocysts** (hyaline cells), as in ***Sphagnum*** (Figure 6-Figure 8) and ***Leucobryum*** (Figure 9-Figure 11), white hair tips on the leaves, as in ***Racomitrium*** (Figure 3), ***Tortula***/***Syntrichia*** (Figure 12-Figure 13), and ***Polytrichum piliferum*** (Figure 16), or possibly even by the refractive nature of papillae (Figure 14-Figure 15) that give the moss a dull appearance to our eyes.

Figure 6. ***Sphagnum papillosum***, a species that lives in full sun that protects its living cells by hyaline cells (hyalocysts). Photo by David Holyoak, with permission.

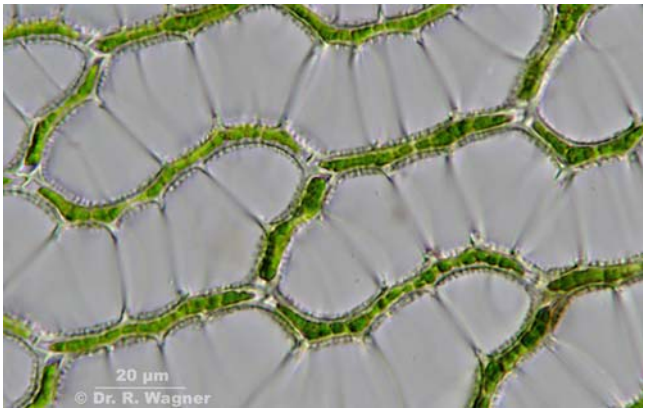

Figure 7. ***Sphagnum papillosum*** leaf cells showing the large hyaline cells that nearly hide the small photosynthetic cells. Photo by Ralf Wagner <www.drralf-waner.de>, with perission.

Figure 8. ***Sphagnum papillosum*** leaf cross section showing hyaline cells that nearly surround the photosynthetic cells. Photo from Botany Website, UBC, with permission.

Figure 9. ***Leucobryum glaucum*** showing its cushion growth form and whitish color. Photo by Janice Glime.

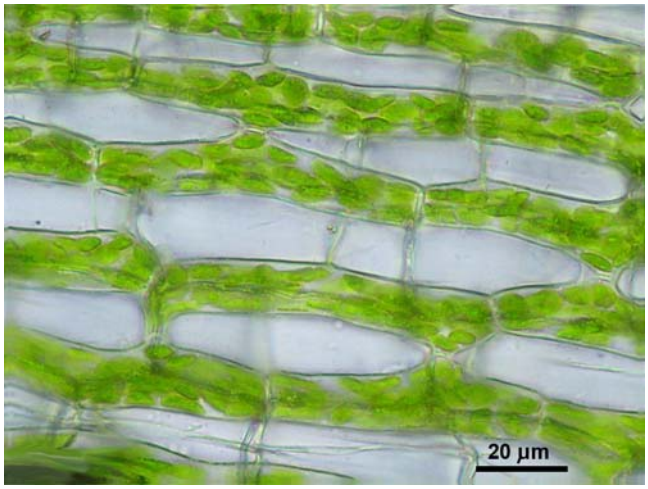

Figure 10. ***Leucobryum glaucum*** leaf cells showing hyaline and photosynthetic cells. Photo by Ralf Wagner <www.drralf-waner.de>, with permission.

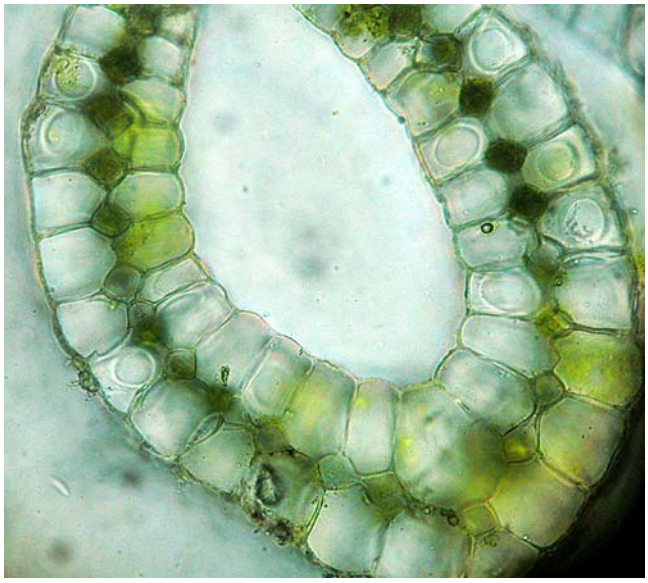

Figure 11. ***Leucobryum glaucum*** leaf cs showing large hyaline cells surrounding the green photosynthetic cells. Photo by Walter Obermayer, with permission.

Figure 12. ***Tortula muralis*** wet, showing awns. Photo by Christophe Quintin, through Creative Commons.

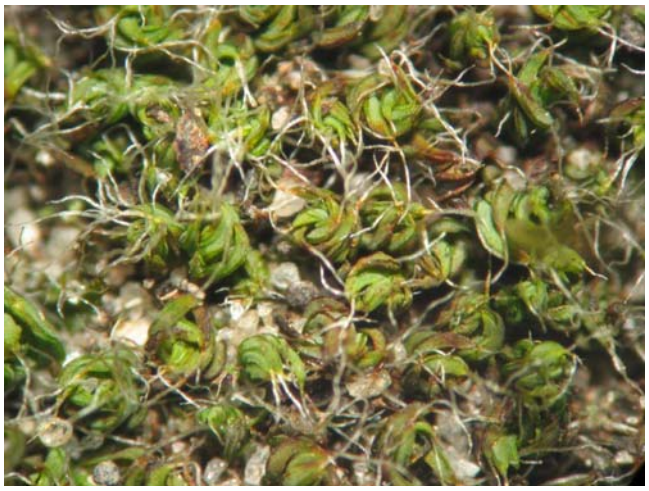

Figure 13. ***Tortula muralis*** dry, showing the twisting of leaves and awns that help to reflect light and protect chlorophyll. Photo by Kristian Peters, with permission.

Figure 14. ***Tortula muralis*** leaf CS showing branched papillae. Photo from Botany Website, UBC, with permission.

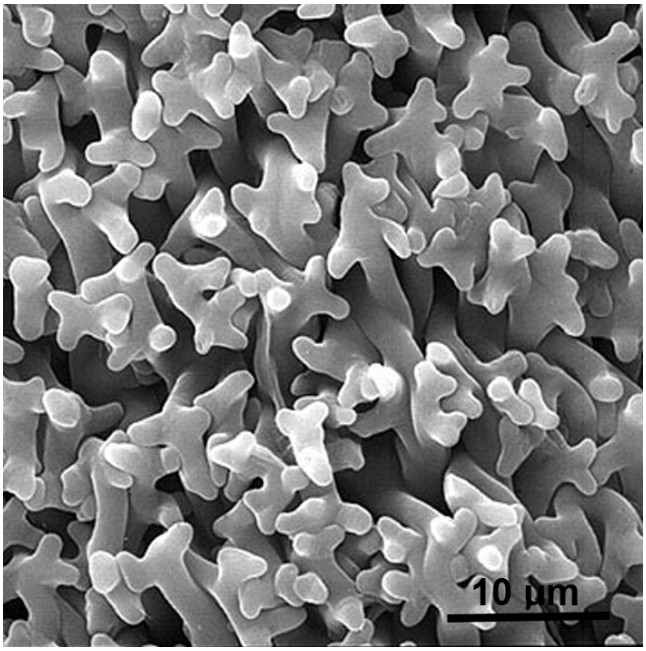

Figure 15. ***Tortula muralis*** leaf SEM image showing branched papillae that reflect and refract light, helping to keep the leaf cool. Photo from Botany Website, UBC, with permission.

Figure 16. ***Polytrichum piliferum*** exhibiting the hyaline hair tips that help to reflect light and hence aid in cooling the moss in the hot sun. Photo from Botany Website, UBC, with permission.

Even as ectothermic animals can modify their temperature by such activities as basking, changing cell shapes, and rearranging scales, bryophytes can survive at sub-zero air temperatures by their own ability to alter the temperature. Lewis Smith (1988) found that in Antarctica the temperature at the surface of a ***Schistidium*** cushion (Figure 17) could vary from -9.2°C to 42.8°C on a single day in January, whereas only 1 m away the temperature 10 cm down into a ***Ceratodon*** turf (Figure 17) had almost no variation (Figure 19). He attributed the lack of change in the ***Ceratodon*** turf to reduction of heat transfer by the moist turf. However, the nearby but typically near-black ***Schistidium*** could operate as a black body that would absorb daytime heat, then re-radiate it at night.

Figure 17. ***Ceratodon purpureus*** (**left**) in depression that maintains a near constant temperature. ***Schistidium antarctici*** (**right**) on ledge where dark color absorbs heat in its dry state. Photo courtesy of Rod Seppelt.

A good example of temperature differences is that of temperatures in the Snowy Mountains of southeastern Australia (Körner & Cochrane 1983). On midsummer days, the maximum leaf-air temperature difference in the trees was a mere 7ºC, rising to 13ºC in the shrubs, 21ºC in the dwarf shrubs, and 24ºC in the grass tussocks and rosette plants. But in an isolated moss cushion, the temperature was 30ºC higher than the air temperature! The differences were less severe at high elevations except for the low plants, where the moss cushion set the record. Temperatures change quickly within the moss cushion, with deeper portions exhibiting less extreme conditions, as seen in the Antarctic (Figure 18-Figure 19). The bare soil, however, reached 81.9ºC! Obviously the mosses must germinate and get established well enough to control their own temperatures before that kind of heat is reached.

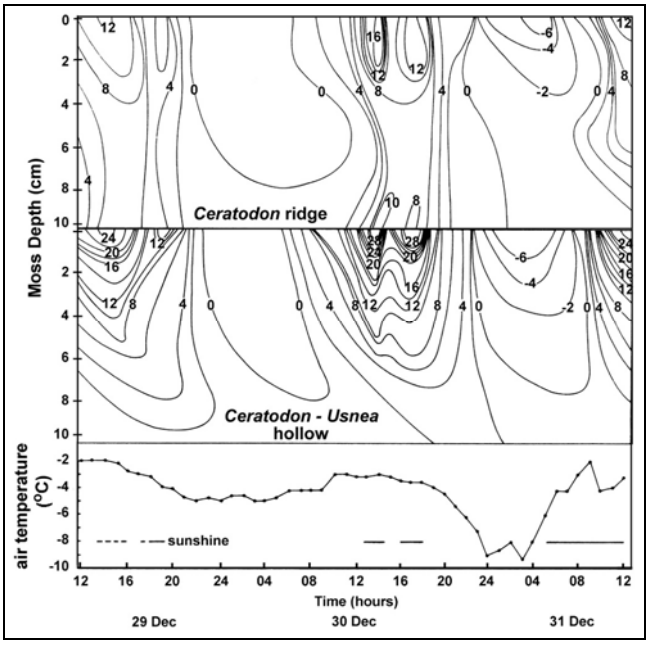

Figure 18. Isotherms for two days in December through a ***Ceratodon*** turf down to 10 cm and a ***Ceratodon*** turf covered by dense *Usnea antarctica.* Redrawn from Lewis Smith 1988.

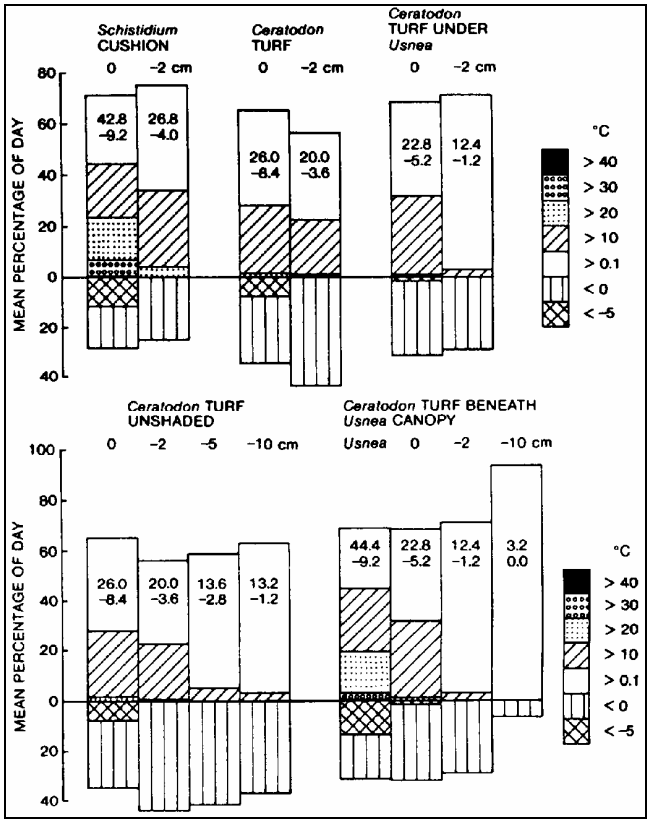

Figure 19. Differences in summer temperatures of surface and subsurface parts of Antarctic moss communities during 13-day period, expressed as mean percentages per day. Absolute maxima and minima for 13-day period appear in bars. From Lewis Smith 1988.

On Mount Fuji, Japan, ***Racomitrium lanuginosum*** (Figure 2-Figure 3) experiences as much as a 42ºC daily temperature range while ***Grimmia elongata*** (Figure 20) nearby has only a 26ºC range. Maruta (1986) suggests that the difference lies in the less dense mat of ***R. lanuginosum***.

Figure 20. ***Grimmia elongata***, illustrating the dense mat that insulates and maintains less temperation variation than loose mats. Photo by Michael Luth, with permission.

The state of hydration, as we might expect, plays a major role in temperature. Water is slow to change its temperature, compared to air, so it is not surprising that Rydin (1984) found the highest temperatures among

Sphagnum (Figure 6) species when they were completely dry. Even shade had little effect on the temperature except when the moss was dry, and under any given set of conditions, there was no difference among ***Sphagnum*** species.

Soil Temperatures

Bryophytes are likewise important in altering the soil temperature. This same ability to act as a black body can add warmth to the soil, but in other cases, the moss could absorb or reflect the heat (or light) and prevent it from reaching the soil beneath.

In the tundra, the bryophytes can prevent warming of the soil. In permafrost areas, mosses contribute to maintaining the permafrost in shallower soils (Van Der Wal & Brooker 2004) compared to bare areas. Van Der Wal and Brooker found that herbivore grazing and trampling by barnacle geese and reindeer reduce the growth of the mosses and hence their depth. This, in turn, increases the soil temperatures. Exclosures that prevented this animal activity and permitted the moss mat to become thicker caused a 0.9ºC decrease in the soil temperature in just seven years (Van der Wal *et al*. 2001). This cooling caused a 50% reduction in biomass of the grass *Poa arctica* and the polar cress *Cardamine nymanii*.

Thick moss cover acts as insulation, preventing the warmth of the sun from reaching the soil. Under cryptobiotic crusts in the alpine tundra basin of the Olympic Mountains, Washington, USA, the soil surface and immediate subsurface was 5-8ºC cooler at midday under moss-dominated crusts (Gold *et al*. 2001) than where crusts were absent. Lichens were even more effective, lowering the temperature by 10-11ºC compared to bare soil. In alpine areas, this lower temperature could deprive roots of needed heat, but in prairies and deserts where cryptogamic crusts occur, it could prove to be essential for root survival. Konis (1949) found the upper thermal limit for normal plant cell activity to range from 45 to 55ºC, although some cells could survive up to 59ºC. Therefore, in the hot climates of prairies and deserts, the bryophyte and lichen crusts could be essential to root survival by ameliorating the soil temperature.

In southern Africa, the crusts are important in providing a habitat where nitrogen fixation occurs, and Aranibar *et al*. (2003) suggest that these crusts permit the survival of these N-fixing systems at high temperatures and through long droughts, providing resilience to the ecosystem.

In the Antarctic, the bryophytes perform the opposite function for the Cyanobacteria. Huntley (1971) reported that they maintained a temperature that was typically more than 10ºC higher than the ambient temperature, often reaching 20ºC during the middle of the day, and providing a suitable temperature for nitrogen fixation activity of the Cyanobacteria. In a Russian study, nitrogen fixation by bacteria in peat did best in the lower layers (20-30 cm) than in the green portion, but could proceed in a range of 5 to 35ºC (Kravchenko & Doroshenko 2003).

The role of the bryophytes in ameliorating soil temperature varies with the ecosystem. For example, in geothermal areas, the bryophytes confine the heat, making soil surface temperatures up to 10ºC higher than it is with them removed (Glime & Iwatsuki unpublished data). In a "moss-lichen pine forest" in Russia, Ipatov and Tarkhova (1983) found that the mosses "soften" the temperature fluctuations more than do lichens and also maintain a higher moisture content, contrasting with the alpine tundra study of Gold *et al*. (2001) where the lichens seemed to do more.

It is no wonder the BOREAS temperature model predicted somewhat poorly until the mosses were added to the model (Pauwels & Wood 1999; Litzgus & Brooks 2000). Moss thickness and moisture content turned out to be important parameters in the sensitivity analysis. But it is complicated. Betts *et al*. (1998) contend that the moss layer makes soil temperature dynamics and water dynamics difficult to track because the moss layer is such a good insulator of the soil. It makes it difficult to predict the temperature of the soil or the thaw date.

Degree Days

Plants often respond to the cumulative effects of temperature, known as **degree days**. That is a measure of the product of the number of days times the mean temperature (ºC) on those days. We know for tracheophytes that these degree days are a factor in germination of seeds, breaking dormancy in bulbs, and ability to reach fruit maturity before the first frost terminates the growing season.

Degree days are seldom mentioned for bryophytes, as few studies have approached their temperature needs in that way. Bates (1989) found that ***Leucobryum glaucum*** (Figure 9) cushions in Great Britain had their highest growth rate in summer, and unlike most bryophytes, growth was more related to temperature than to precipitation. Rather, it seemed to be related to degree days above 5ºC.

While degree days are not mentioned specifically, many studies imply their importance. Callaghan *et al*. (1997) found that the growth of circumarctic populations of ***Hylocomium splendens*** (Figure 21) depends greatly on the early summer temperatures and the length of the growing season (degree days for sure).

Figure 21. The stairstep moss, ***Hylocomium splendens***, exhibiting its steps. Its growth is dependent on a sufficient growing season. Photo by Janice Glime.

Bryophytes can have a profound effect on the **soil degree days** (**SDD**), which are important for root growth and storage organ dormancy, among other things. When moss cover and the canopy were removed from boreal

forests of interior Alaska, the soil warmed, on average, by 345 and 408 soil degree days, respectively (Bonan 1991). These were the two parameters having the highest effect on soil temperature, which normally averaged 851 soil degree days, with elevation and soil drainage patterns being of secondary importance, with deviations of 71 and 66 soil degree days.

Safe Sites

Even turtles can benefit from the ability of the mosses to buffer temperatures. In Georgian Bay, Ontario, Canada, some members of the spotted turtle (***Clemmys guttata***; Figure 22) spend their winter under ***Sphagnum*** (Figure 6) hummocks (Litzgus *et al*. 1999). They enter in early autumn with body temperatures of 12-16ºC and stay there until spring (mid to late April) when the air temperature is 1-5ºC. Within the safety of the hummock, the turtle's body temperature stays 0.3-3.9ºC while air temperatures drop to as low as -35ºC. Such data indicate that ***Sphagnum*** greatly buffers the temperature and creates a very different environment.

Figure 22. ***Clemmys guttata*** hatching amid mosses. Photo courtesy of Steve Soldan.

Mosses may provide safe sites for seed germination. On iron mine tailings in New York, USA, the turf moss ***Polytrichum piliferum*** (Figure 23) became a safe seed bed for a variety of grasses (Delach & Kimmerer 2002). It was especially important for those species that germinate early and become established in cool weather. At that time, the mosses can protect the plants from a late frost and even warm the daytime temperatures due their black-body action. However, they can do little to cool the site sufficiently for continued success on the hot tailings rock during the heat of summer.

Life Cycle Effects

Temperature plays a role in all stages of the life cycle of plants. It potentially affects the physiology of a bryophyte in several ways: photosynthetic rate, respiratory rate, reproductive timing, growth, development, and productivity. These together affect its survivorship. Whereas many animals can maintain a relatively constant internal temperature either through physiological means or by behavioral changes, plants are restricted in their positions and very few have any physiological means by which to change their internal temperatures. Thus, plants, including bryophytes, must adapt structurally, physiologically, or by life cycle alterations to survive periods of extremes of hot and cold. On the other hand, these temperature changes can also signal and initiate changes in life cycle stages (Grime *et al*. 1990), as discussed in the chapters on development and phenology.

Figure 23. ***Polytrichum piliferum***, a moss that becomes a safe site for grass seed germination. Reddish cups are antheridial splash cups. Photo by Janice Glime.

Spore germination is often attuned to temperature. In ***Mnium hornum*** (Figure 24) and ***Plagiomnium undulatum*** (Figure 25), spore germination is dependent on temperature, with more germinating at 20ºC than at 10ºC (Newton 1972). Not surprisingly, it also affects regeneration of fragments, but the surprise is that 77% of the female regenerants survived while all the male regenerants of these two species died.

Figure 24. ***Mnium hornum*** with capsules, a species for which spore germination is best at ~20°C. Photo by Michael Lüth, with permission.

Figure 25. ***Plagiomnium undulatum*** with capsules, a species for which spore germination is best at ~20°C. Photo by Michael Luth, with permission.

McLetchie (2001) also found a temperature sex bias in ***Sphaerocarpos texanus*** (Figure 26), where the spores (Figure 27) that lost dormancy (germinated; Figure 28) on a 25ºC day: 15ºC night schedule were female biased (Figure 29). McLetchie (1999) found a degree-day type of response in spore germination (Figure 28) of ***Sphaerocarpos texanus***, with loss of dormancy increasing with length of time held at a suitable temperature (16/10ºC) and germination conditions. But the interesting thing that he found is that spores held at 35/20ºC during dormancy lost their dormancy more quickly at 16/10ºC than those held at 30/15ºC or at 25/15ºC, whereas those given the moist conditions needed for germination failed to germinate at all at 35/20ºC or 30/15°C. Low temperatures could induce the spores back into a secondary dormancy, much as occurs in seeds of obligate winter annuals.

Figure 26. ***Sphaerocarpos texanus***, a species that changes its development based on temperature. Photo by Martin Hutten, with permission.

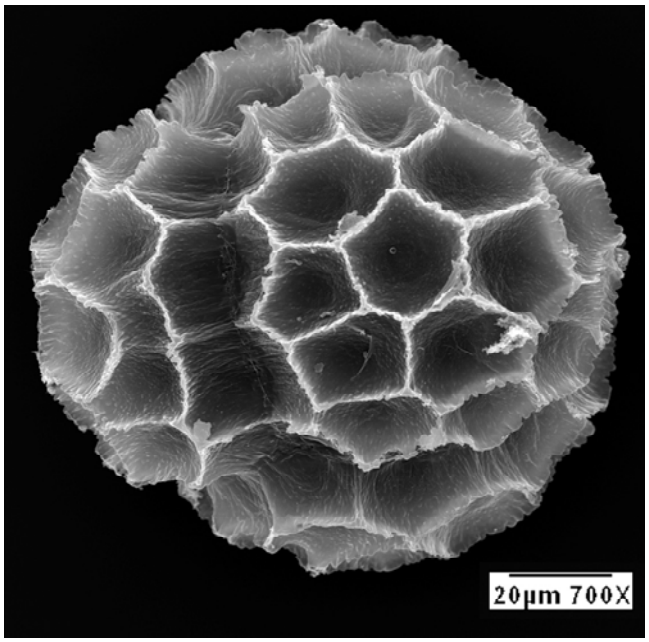

Figure 27. ***Sphaerocarpos texanus*** spore SEM. Dermination is dependent on temperature and with a 25ºC day: 15ºC night the spores that germinate are female biased. Photo courtesy of Karen Renzaglia.

Figure 28. ***Sphaerocarpus texanus*** developing protonema. Germination is dependent on degree days. Photo from Plant actions, with permission.

Figure 29. ***Sphaerocarpos texanus*** female with archegonia. A temperature regime of 25ºC day: 15ºC night creates a female bias in spore germination. Photo by Paul Davison, with permission.

The **protonema** may be affected differently by temperature. Dietert (1980) found that the optimum temperature for germination (Figure 30) of both ***Funaria hygrometrica*** (Figure 31) and ***Weissia controversa*** (Figure 32) was 30ºC, but the optimum for the growth of the protonema was only 25ºC. This higher requirement for germination is not unusual among plants because it insures a smaller probability that a killing frost will occur and kill all the young plants. Thus, a few warm days with spores on a dark soil surface can be sufficient for germination, but the green and hydrated protonema will hopefully enjoy a lower temperature.

Growth is more than just adding biomass and length. It involves producing buds, branches, rhizoids, and vegetative propagules. Most of these were discussed in the chapter on development, but a brief additional discussion is in order here.

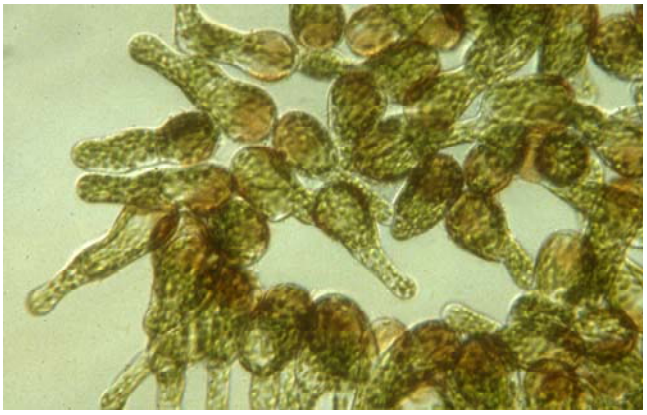

Figure 30. ***Funaria hygrometrica*** spore germination, a stage for which optimum conditions are at 30ºC. Photo by Janice Glime.

Figure 31. ***Funaria hygrometrica***, a species whose life cycle is temperature dependent. Photo by Michael Lüth, with permission.

Figure 32. ***Weissia controversa*** with capsules, a species whose life cycle is temperature dependent. Photo by Michael Luth, with permission.

Gametangia have their own set of temperature requirements as well. In her study on ***Funaria hygrometrica*** (Figure 31) and ***Weissia controversa*** (Figure 32), Dietert found that cooler temperatures were needed for gametangia development than those for germination. Monroe (1965) likewise found that a low temperature (10ºC) stimulated the production of sex organs in ***Funaria*** (Figure 33) and showed that day length had no effect on their timing.

Figure 33. ***Funaria hygrometrica*** young sporophytes, a stage that follows low temperatures needed to stimulate development of archegonia and antheridia. Photo by Michael Luth, with permission.

The **perennial** moss ***Brachythecium rutabulum*** (Figure 34) had its maximum relative growth rate, shoot length, and leaf area at ~19ºC (Figure 35), but these are related to each other and would be expected to increase concurrently (Furness & Grime 1982a).

Figure 34. ***Brachythecium rutabulum***, a common forest floor taxon. Photo by Des Callaghan, with permission.

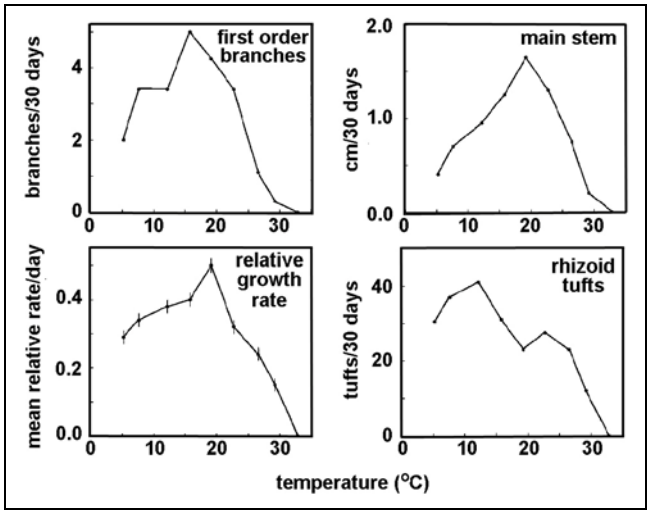

Figure 35. ***Brachythecium rutabulum*** growth at various temperatures. Redrawn from Furness & Grime 1982a.

Rhizoids, on the other hand, do not necessarily develop at the same time as stem and leaf biomass. For ***Fontinalis hypnoides*** (Figure 36), the number of rhizoid clumps (Figure 37) produced increased with temperature in the range of 1-20ºC in both flowing water and pool conditions (Figure 39) (Glime 1980). For ***Fontinalis novae-angliae*** (Figure 38), it increased up to 15ºC in flowing water conditions, but dropped sharply at 20ºC, whereas in pool conditions it continued to rise. The **growth optimum** for these species from the same localities, however, is lower, at 15ºC, for both species (Glime 1987a). **Branching** rose sharply from 1 to 5ºC in ***F. hypnoides*** but exhibited little increase with temperature above that (Figure 39) (Glime 1982).

Figure 36. ***Fontinalis hypnoides***, a species that develops rhizoids in the range of 1-20ºC. Photo by Ivanov, with permission.

Figure 37. ***Fontinalis hypnoides*** rhizoids. Photo by Janice Glime.

The general pattern, however, for branches and total branch and stem growth in ***Fontinalis*** (Figure 36) is that they occur together (Glime 1980). This is reasonable, as in ***B. rutabulum*** (Figure 34), because new branches create a greater total branch and stem length, and in most of these species new branches need new rhizoids (Glime & Raeymaekers 1987). The rhizoids, however, tend to have a strong peak at 15ºC for most of these aquatic species (Figure 39).

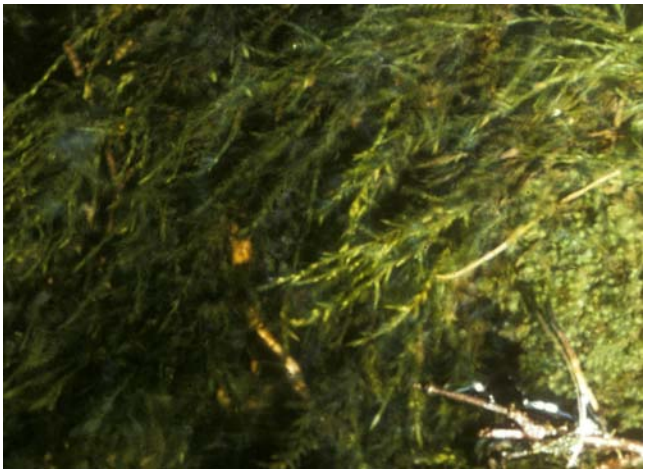

Figure 38. ***Fontinalis novae-angliae*** with capsules. Photo by Janice Glime.

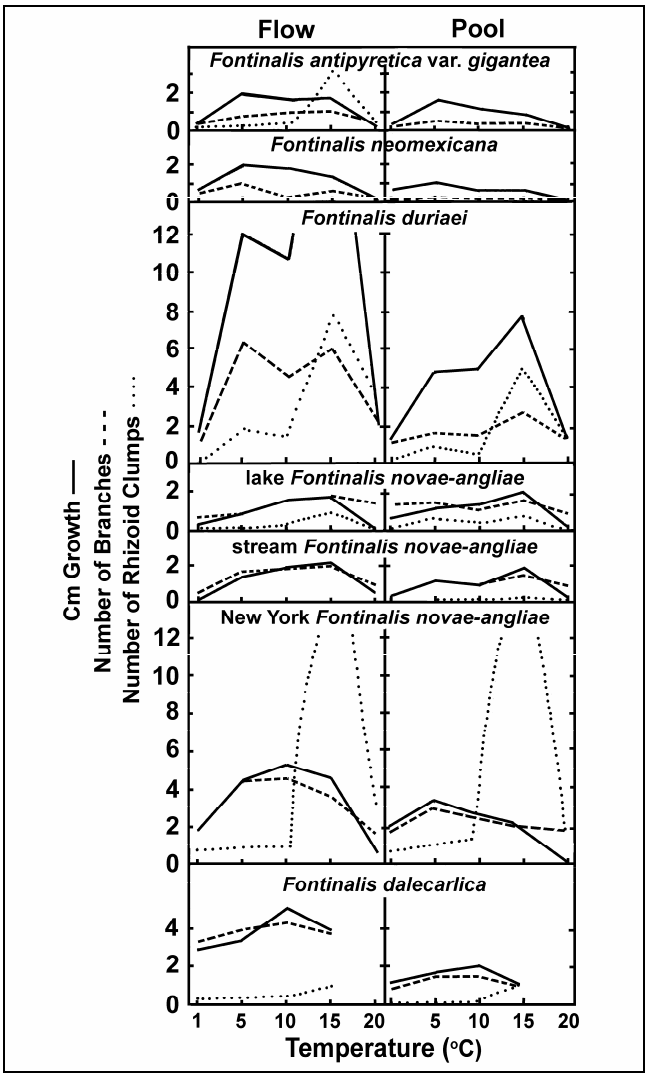

Figure 39. Response of rhizoid clumps, branches, and growth in flowing water (flow) and standing water (pool) conditions to temperatures in the range of 1-20ºC for 15 weeks. Populations at 20ºC were changed to 13ºC after 5 weeks to look for recovery. Numbers represent means of 40 stems. All collections are from the Upper Peninsula of Michigan except the population from New York. Redrawn from Glime & Raeymaekers 1987.

Archegonia of ***Fontinalis*** seemed to respond more like a threshold existed, with the highest production at 15ºC in flowing water, but in pool conditions, that temperature produced the fewest archegonia, with the most at 10° and 15ºC, so few conclusions can be drawn. In an experiment on ***F. dalecarlica*** (Figure 40), production of archegonia (Figure 41) was related to photoperiod (Glime 1984), so temperature may not be an important controlling factor.

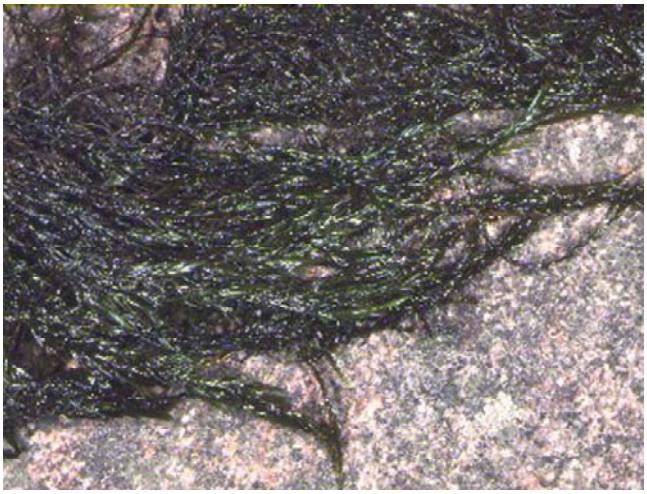

Figure 40. ***Fontinalis dalecarlica***, a species in which different life stages are triggered by different temperatures. Photo by Jan-Peter Frahm.

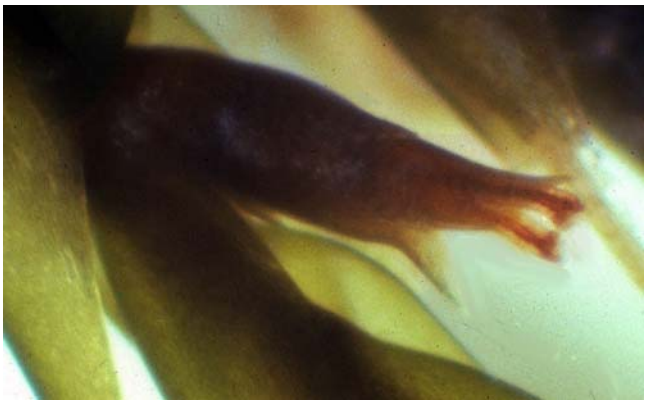

Figure 41. ***Fontinalis dalecarlica*** archegonia produced in greatest numbers at 15°C. Photo by Janice Glime.

Bopp and Bhatla (1990) determined the mean temperatures required for induction of gametangia in several taxa (Table 1). But they also concluded that several of the species were controlled by photoperiod, including ***Pogonatum aloides*** (Figure 42-Figure 43).

Table 1. Mean temperature (ºC) at which gametangia are induced. From Bopp & Bhatla 1990.

Pogonatum aloides	21
Funaria hygrometrica	10
Physcomitrella patens	15
Physcomitrium pyriforme	7
Philonotis turneriana	18

Figure 42. ***Pogonatum aloides***, a species in which photoperiod and temperature trigger life cycle stages. Photo by Michael Luth, with permission.

Figure 43. ***Pogonatum aloides*** with capsules. Photo by Michael Lüth, with permission.

The success of the **sporophyte** first depends on the success of the gametangia, then on the actual fertilization, and finally the requirements for its own development. Hohe *et al*. (2002) found that the highest number of sporophytes in ***Physcomitrella patens*** (Figure 44) were produced at 15ºC, with numbers dropping greatly at 25ºC. Bopp and Bhatla (1990) had similar results, finding the optimal temperature for capsule production to be at 15-19°C, with production droping by 80% at 19-21°C. Vegetative growth, on the other hand, was best at 25ºC. Thus we can understand that temperature is one of the factors that can keep the various energy-requiring activities of the moss, like reproduction and growth, from occurring at the same time.

Bryum argenteum (Figure 45) required 25ºC for capsule development. Bopp and Bhatla (1990) were surprised to find that in ***Funaria hygrometrica*** (Figure 31), capsules were produced at 10-15ºC in 12-16 hours light, but a shorter photoperiod permitted development at higher temperatures.

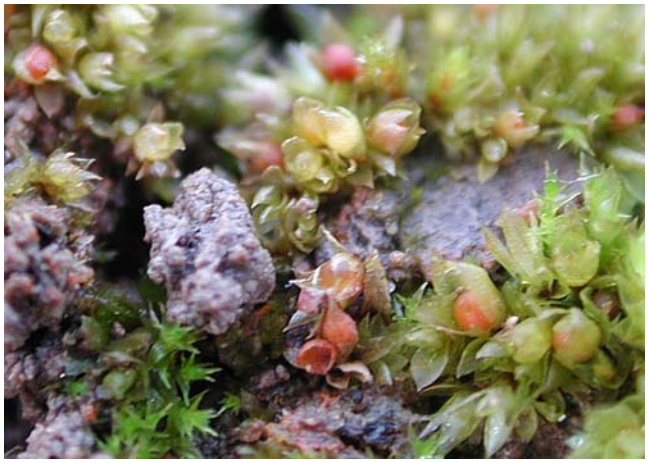

Figure 44. ***Physcomitrella patens*** with capsules that are produced in greatest numbers at 15°C. Photo by Michael Luth.

Figure 45. ***Bryum argenteum*** with capsules. Production of capsules can occur in a range of 10-15ºC in 12-16 hours light per day. Photo by Bob Klips, with permission.

One of the more subtle life cycle effects of temperature is the initiation of **dormancy**. For example, the thallose liverwort ***Lunularia cruciata*** (Figure 46) can be induced into dormancy by temperatures of 24ºC in continuous light, or other high temperature combinations with long days. Since this set of conditions is likely to be a harbinger of forthcoming drought, or already coupled with it, it provides a good signal to go dormant.

Figure 46. ***Lunularia cruciata***, a species than can be induced into dormancy by high temperatures and long days. Photo from <www.aphotofauna.com>, with permission.

Several species of ***Sphagnum*** [***S. magellanicum*** (Figure 47), ***S. capillifolium*** (Figure 48), and ***S. fallax*** (Figure 49) have a quite different dormancy trigger (Gerdol 1995). They are able to grow in summer temperatures if there is sufficient moisture, but they are triggered into dormancy by low night temperatures.

Figure 47. ***Sphagnum magellanicum***, a species that grows in summer temperatures but goes dormant if night temperatures are low. Photo by Michael Luth, with permission.

Figure 48. ***Sphagnum capillifolium***, a species that grows in summer temperatures but goes dormant if night temperatures are low. Photo by J. C. Schou, with permission.

Figure 49. ***Sphagnum fallax***, a species that grows in summer temperatures but goes dormant if night temperatures are low. Photo by David T. Holyoak, with permission.

Even fragments may have their optimum for **regeneration**. Although ***Sphagnum*** (Figure 47-Figure 49) species typically occur in the sun, go dormant in the fall, and grow when enough moisture is available in summer, their fragments do not seem to survive well in heat. Sagot and Rochefort (1996) tested ***S. angustifolium*** (Figure 50), ***S. fallax*** (Figure 49), ***S. fuscum*** (Figure 51), ***S. magellanicum*** (Figure 47), ***S. capillifolium*** (=*S. nemoreum*; Figure 48), and ***S. papillosum*** (Figure 6) and found that only ***S. fallax*** survived temperatures as high as 30ºC for 48 hours of oven drying. The conditions of oven drying may have dried them too quickly, preventing them from entering dormancy. However, the implications are that harvesting peat in the summer may prevent regeneration from fragments that could dry and heat up too quickly once disconnected from the capillary stream of the plants.

Figure 50. ***Sphagnum angustifolium***, a species that does not survive above 30°C of oven drying – perhaps preventing them from the physiological changes normally made during drying. Photo by Michael Luth, with permission.

Figure 51. ***Sphagnum fuscum***, a species that does not survive above 30°C of oven drying – perhaps preventing them from the physiological changes normally made during drying. Photo by Michael Luth, with permission.

Growth of any organism is a competition for energy and nutrients. This is especially true for plants that continue to grow throughout their lifetimes or over a long expanse of years. Bryophytes include both **annual** (regrowing from spores every year) and **perennial** (continuing growth of the same plant for a number of years) growth strategies. This means that some must start the growing season from spores and others simply continue growth from existing plants. Hence we should expect different signals for these two growth processes.

Normal and Extremes for Growth

Aside from these life cycle changes, bryophytes respond physiologically to temperature differences that affect their growth and productivity (Furness & Grime 1982a, b). Most bryophytes have their optimum temperature for growth in the range of 15-25ºC (Furness & Grime 1982b). Yet some bryophytes can have an optimum of less than 10ºC (Furness & Grime 1982b), as in some species of ***Fontinalis*** (Glime 1987a). It is likely that this low temperature optimum, at least in ***Fontinalis***, results from a cumulative effect of increased respiration at higher temperatures. In experiments where the mosses were acclimated to the test conditions for three weeks, the aquatic species ***Fontinalis duriaei*** (Figure 52) exhibited optimum net photosynthesis at 10ºC (Glime & Acton 1979).

Figure 52. ***Fontinalis duriaei***, a species that has optimum photosynthesis at 10°C in the Keweenaw Peninsula of Michigan. Photo by Michael Lüth, with permission.

Furness and Grime (1982a) suggested that bryophytes may be able to compete with tracheophytes because the bryophytes are able to grow over a wider temperature range and to exploit the cool months of spring and autumn for growth. They supported this suggestion by showing that while the optimum temperature for growth, shoot length, and leaf area was 19ºC in ***Brachythecium rutabulum*** (Figure 34), the reduction in relative growth was less than 40% at 5ºC. In southern Finland, ***Sphagnum fuscum*** (Figure 51) had a net productivity gain at any temperature above 0ºC, provided there was sufficient water (Lindholm 1990). This water limit at higher temperatures seems to be a principle for many bryophytes, although ***Sphagnum*** generally has a higher temperature optimum than other bryophytes (Koskimies-Soininen & Nyberg 1987; Li & Glime 1990; Li *et al*. 1992).

A number of factors can affect the optimum temperature for growth, and it is likely that a number of physiological races exist. In ***Fontinalis novae-angliae*** (Figure 38) collected from New Hampshire, USA, the optimum temperature for growth when placed in a common garden was 10ºC, whereas the population from the Upper Peninsula of Michigan had its greatest growth at 15ºC (Glime 1987b; Figure 53). Furthermore, the New

Hampshire populations had considerably more growth at all temperatures below 20ºC than did the Michigan populations. Optima also differed between pool and flowing water conditions, with the New Hampshire population exhibiting its best growth at 5ºC in pool conditions. On the other hand, ***F. hypnoides*** (Figure 36) had almost no difference in growth between pool and flowing water conditions except at 20ºC, where the flowing water conditions produced the best growth (Figure 54). In Japan, Saitoh *et al*. (1970) found the optimum for photosynthesis in ***F. hypnoides*** at 20ºC.

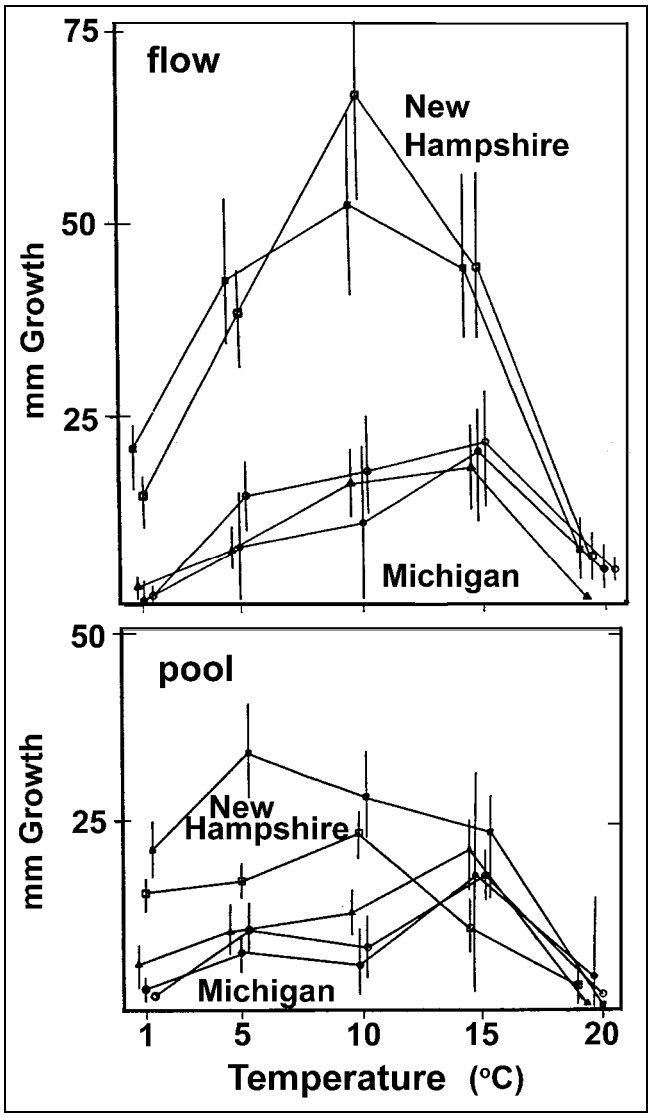

Figure 53. Comparison of growth in flowing water (flow) and standing water (pool) conditions after 15 weeks for ***Fontinalis novae-angliae*** from two geographic areas. Redrawn from Glime 1987b.

Fontinalis novae-angliae (Figure 38) most likely holds the record for high temperature survival of wet mosses. Glime and Carr (1974) boiled it for 14 or more hours a day for two weeks. A year after it was returned to its native stream, a new green leaf appeared on one of the marked stems that had been in the boiling treatment. All the former leaves were gone or brown.

Short-term studies can be misleading, and past history of the bryophyte can influence the temperature for optimum growth. In ***Fontinalis hypnoides*** (Figure 36), spring-collected (June) mosses grew best at 15-20ºC, whereas plants of the same population collected in September ceased growth after 2-3 weeks at 20ºC (Glime 1982). It appears that degree days are at work here.

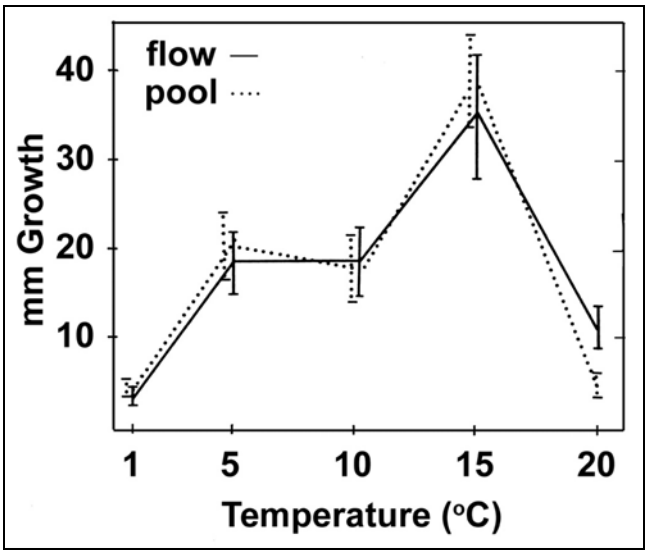

Figure 54. Growth after 15 weeks for ***Fontinalis hypnoides*** from Isle Royale, Michigan, USA, in flowing water (**flow**) and standing water (**pool**) conditions. Redrawn from Glime 1982.

Mosses seem to have the ability to withstand and even take advantage of high temperatures for short periods of time. Liu (2000) showed that ***Plagiomnium acutum*** (Figure 72), ***P. maximoviczii*** (Figure 55), ***Thuidium cymbifolium*** (Figure 56), and ***Chrysocladium retrorsum*** were able to maintain optimum photosynthetic output at 20-35ºC. They actually had a positive net photosynthesis at -15ºC and maintained a net photosynthetic gain for 10-30 minutes at 40-45ºC. However, the 50% injury temperature (IT_{50}) occurred at 44.8°C for ***Thuidium cymbifolium*** and at 45.3°C for ***Plagiomnium acutum***. But even at temperatures less than 45°C, damage to cells and death of the shoot increased with exposure time. None of them survived above 50°C.

Figure 55. ***Plagiomnium maximoviczii***, a species that exhibits optimum photosynthetic output at 20-35ºC. Photo from Hiroshima University Digital Museum of Natural History, with permission.

Figure 56. ***Thuidium cymbifolium*** with capsules, a species that exhibits optimum photosynthetic output at 20-35ºC. Photo by Li Zhang, with permission.

A measurement of air temperature does not present an accurate picture of actual moss temperatures, so both field measurements, which seemingly represent long-term exposure, and lab measurements, which represent only a short-term duration, present problems in realizing the actual tolerances of bryophytes. For example, Kappen and Smith (1980) found that the geothermal moss ***Campylopus praemorsus*** tolerated temperatures up to 29.8ºC in its active parts, while soil temperatures were much higher. We have seen how bryophytes alter the temperature of both the environment and of themselves relative to ambient air temperature. It is important that field measurements reflect the temperature of the leaves in question through the use of microprobes. And laboratory photosynthetic measurements need to mimic temperatures at which the moss has been maintained if they are to tell us the optimum sustained temperature. Nevertheless, these short-term measurements are useful to tell us short-term tolerances that bryophytes may need to sustain in the field. With a soil temperature reaching 81.9ºC in the desert (Körner & Cochrane 1983), they could certainly be subjected to a wide range.

Some more tropical elements of the bryophyte flora seem to find refuge in **rockhouses** (Farrar 1998). These are deep recesses in cliffs and maintain a much buffered temperature regime, but under very low illumination. Although they typically do not get very warm, they seem to be refugia for tropical species that persist there in the absence of extreme winter cold. Perhaps, too, these species are adapted to the low light levels in the lower strata of tropical forests. Although the ferns are more conspicuous in these special habitats, the bryophytes are the most numerous.

Compensation Point

The **temperature compensation point** is that temperature at which photosynthetic gain equals respiratory loss, *i.e.*, net photosynthesis is zero. It is this compensation point, whether for light, temperature, CO_2, or other factor that determines whether a plant is capable of surviving over the long term. While some plants may have a negative gain for a short period of time, they must have a net gain over the annual cycle. In the tropics, low light intensity and high temperatures are major factors in preventing lowland forest bryophytes from reaching their compensation point (Frahm 1987). For most bryophytes, this temperature compensation point is reached somewhere above 20-25ºC, with lowland tropical forest bryophytes having drastic drops in net assimilation above 25ºC, soon reaching and surpassing their temperature compensation point (Frahm 1990). We can assume that if 25ºC is the upper temperature limit for tropical bryophytes in lowlands, this is most likely the upper limit for bryophytes in general, with the exception of those taxa adapted to special habitats like deserts and geothermal areas.

The lower temperature compensation point most likely varies considerably. For two snowbed bryophytes, this limit is not much below freezing, with ***Anthelia*** (Figure 57) reaching it at -4ºC and ***Polytrichum*** (Figure 58-Figure 59) at -5ºC (Loesch *et al*. 1983). Their high temperature compensation point is 30ºC and 32ºC, respectively. It is not surprising that they have a relatively high compensation point at the low end because they are protected by snow during the periods when other bryophytes would most likely be in danger of a late or early season cold spell. Such snowbed habitats seem to be refugia for more northern taxa most likely left behind by the glacier (see Belland 1983).

Figure 57. The whitened branches of ***Anthelia juratzkana*** that most likely protect it from the intense UV light at high elevations while it is still at freezing temperatures from melting snow. Photo by Michael Lüth, with permission.

Figure 58. ***Polytrichum sexangulare*** in late snowbeds. Photo by Michael Lüth, with permission.

Figure 59. ***Polytrichum sexangulare***, a late snowbed moss that continues to photosynthesize down to -5°C. Photo by Martin Hutten, with permission.

Rütten and Santarius (1993) found productivity temperatures in ***Plagiomnium affine*** (Figure 60) and ***P. undulatum*** (Figure 25) with lower limits in the summer at -10 to -15ºC. For Antarctic bryophytes, even lower temperatures are likely for positive photosynthesis. One must wonder what they could achieve if they could be tested in the Antarctic winter.

Figure 60. ***Plagiomnium affine***, a species that can survive temperatures of -10 to -15°C in the summer. Photo by Janice Glime.

As the temperature rises, so do the CO_2 and light compensation points and saturation points (Joliffe & Tregunna 1968). ***Bryum argenteum*** (Figure 45) has a compensation point of 58 ppm at 20.5ºC (Rastorfer 1970). In the moss ***Sanionia uncinata*** (Figure 61), temperatures of 5ºC, 15ºC, and 25ºC have corresponding CO_2 compensation points of 32, 50, and 82 ppm (mg L^{-1}), respectively (Rastorfer 1971). In other words, as the temperature rises, the moss uses more CO_2 to achieve a net gain. This rise in CO_2 requirement is predicted, because these C_3 plants have photorespiration, which increases more rapidly than photosynthesis as the temperature rises. Hence, more fixation would be required to overcome the photorespiratory losses.

Figure 61. ***Sanionia uncinata*** with capsules, a species that is able to use more CO_2 as the temperature rises. Photo by Michael Lüth, with permission.

Compensation points among tracheophytes are generally considered low at approximately 5 ppm or less (Jackson & Volk 1970) and high at 32-122 ppm in moderately bright light and temperatures of 20-30ºC (Heath 1962; Goldsworthy & Day 1970).

Antarctic and Arctic

Even Antarctic mosses seem to survive well at higher temperatures. Rastorfer and Higginbotham (1968) reported that the ratio of photosynthesis to respiration in ***Roellia roellii*** (Figure 62) ranged 11-27:1 in the temperature range of 4-24ºC, dropping to lower values at 34ºC. Nevertheless, 34ºC is a relatively high temperature. Ino (1990) found that the maximum rate of net photosynthesis at saturating light levels occurred at approximately 10ºC in East Antarctic populations of ***Ceratodon purpureus*** (Figure 63) and ***Bryum pseudotriquetrum*** (Figure 64-Figure 65). These were one- or three-day measurements.

Figure 62. ***Roellia roellia***, an Antarctic species that has an abrupt drop in photosynthesis at temperatures of 34°C and higher. Photo by Martin Hutten, with pernission.

Figure 63. ***Ceratodon purpureus***, a species that has its maximum photosynthesis at 10°C in Antarctica. Photo by Janice Glime.

Figure 64. ***Bryum pseudotriquetrum*** in the Antarctic. Photo courtesy of Catherine Beard.

Figure 65. ***Bryum pseudotriquetrum***, a species that has its maximum photosynthesis at 10°C in Antarctica. Photo by Michael Luth, with permission.

Figure 66. ***Marchantia polymorpha*** with gemmae cups, a species that has its maximum photosynthesis at 10°C in Antarctica. Photo by Brenda Dobbs, through Creative Commons.

Racomitrium lanuginosum (Figure 67), on the other hand, had its photosynthetic optimum in high light intensities at 5ºC, with a minimum net gain at -8 to -10ºC (Kallio & Heinonen 1973). In short-term experiments the maximum temperature was generally 25-30ºC. Furthermore, even though the moss was not productive at -30ºC, it quickly became active, reaching 60% activation within three hours of warming.

Figure 67. Spring melt reveals ***Racomitrium lanuginosum*** ready to photosynthesize. Photo by Michael Lüth, with permission.

Acclimation

Acclimation is the gradual and reversible adjustment of an organism to environmental fluctuations, not to be confused with **adaptation**, which is a persistent genetic change that provides the organism with a better ability to survive its environmental conditions. The adjustment to winter cold or summer heat is a result of acclimation.

Many bryophytes seem to be pre-adapted to low temperatures, but have some degree of ability to adjust to high temperatures. Antropova (1974) suggested this for species in seven genera of bryophytes [***Atrichum*** (Figure 68), ***Calliergon*** (Figure 69), ***Chiloscyphus*** (Figure 70), ***Funaria*** (Figure 31), ***Marchantia*** (Figure 66), ***Mnium*** (Figure 24), ***Riccia*** (Figure 71), based on ability to **plasmolyze**. Loss of plasmolysis is an indication of membrane damage. As might be expected, incubation at

their tolerant temperatures (10 and 20ºC) does not affect their thermostability or cold resistance. However, incubation for three hours at temperatures above their optimum does result in increased thermostability. Unlike typical cold acclimation, this increased thermostability is not accompanied by increased cold hardiness. This response is similar to that of flowering plants but different from that of algae.

Figure 68. ***Atrichum undulatum***, in a genus that seems to be pre-adapted to low temperatures. Photo by Brian Eversham, with permission.

Figure 69. ***Calliergon cordifolium***, in a genus that seems to be pre-adapted to low temperatures. Photo by Janice Glime.

Figure 70. ***Chiloscyphus polyanthos***, in a genus that seems to be pre-adapted to low temperatures. Photo by Michael Lüth, with permission.

Figure 71. ***Riccia gougetiana*** var ***armatissima***, in a genus that seems to be pre-adapted to low temperatures. Photo by Michael Lüth, with permission.

Rütten and Santarius (1993) defined **frost tolerance** as the lowest temperature at which no more than 50% irreversible damage occurred in net photosynthetic activity relative to unfrozen plants. They found that optimum productivity temperatures in ***Plagiomnium affine*** (Figure 60) and ***P. undulatum*** (Figure 25) ranged 10-20ºC with lower limits in the summer at -10 to -15ºC. Their hardiness to cold increased progressively during autumn, reaching temperatures below -35ºC by winter. And, as already known from seed plants, the increase in cold hardiness was coupled with an increase in thermostability at high temperatures. But there was no correlation with an increase in total sugar content (sucrose, glucose, and fructose) of the shoots, despite the considerably higher sucrose content than that of less frost-hardy plants. Rütten and Santarius suggest that the accumulation of sucrose may contribute to frost hardiness of these two species, but felt that the seasonal differences could not be accounted for solely by the alterations in sugar concentrations.

Using ***Plagiomnium acutum*** (Figure 72) and ***P. maximoviczii*** (Figure 55) from China, Liu *et al*. (2001) showed that the optimum temperature for photosynthesis rose from winter to summer, ranging 20-35ºC; the mosses could maintain positive net photosynthesis for 20-30 minutes at -10 to -15ºC and from 40-45ºC. Their $\mathbf{Q_{10}}$ (change in rate of reaction per 10ºC change in temperature) in the range of 0-20ºC was only 1.15-1.23. The "average" for non-biological chemical reactions is 2.0. Uchida *et al*. (2002) found that the photosynthetic Q_{10} for the moss ***Sanionia uncinata*** (Figure 61) was nearly 1 in the range of 7 to 23ºC, whereas the respiratory Q_{10} was 3.0, causing net photosynthetic loss as the temperature rose.

Figure 72. ***Plagiomnium acutum*** from China. Photo by Yingdi Liu, with permission.

But bryophytes apparently do have at least limited ability for short-term heat acclimation. Using chlorophyll *a* fluorescence and electrolyte leakage (evidence of membrane damage) to indicate thermal stability, Meyer and Santarius (1998) showed short-term acclimation of hydrated shoots of ***Atrichum undulatum*** (Figure 68) and ***Polytrichastrum formosum*** (Figure 73) to elevated, sublethal temperatures within a few hours. This acclimation lasted several days. Declining water content, on the other hand, caused a dramatic rise in heat resistance.

Figure 73. ***Polytrichastrum formosum*** 1 Des Callaghan, with permission.

Hicklenton and Oechel (1976) found that the moss ***Dicranum fuscescens*** (Figure 72) in subarctic Canada raised its temperature optimum for photosynthesis from 0-10ºC in the beginning of June to 10-20ºC by 7 July, with net productivity dropping drastically by 29 July (Figure 75), but its dark respiration rates showed no evidence of acclimation. The tissue temperatures fluctuated between a low of 3ºC and a high of 26ºC during that period. The remarkable drop in productivity by the end of July suggests that the moss could not sustain the high temperature respiratory cost and eventually lost net productivity. At the other end, net productivity was negative at temperatures above 15ºC on 5 June.

Figure 74. ***Dicranum fuscescens***, a species that raises its temperature optimum as summer progresses from June to July in the subarctic. Photo by Michael Lüth, with permission.

In a field study, Oechel (1976) found a close correlation between the minimum temperature at which 85% of maximum photosynthesis was achieved and the mean maximum tissue temperature for the five days preceding the measurement, further supporting an acclimation to the temperature.

Fornwall and Glime (1982) found evidence of acclimation to cold vs warm in ***Fontinalis duriaei*** (Figure 52). Using mosses that were collected in the same section of stream every eight weeks from 27 November until 3 December of the following year, they demonstrated that those individuals that were collected in January at 0-1ºC had their peak assimilation rate at 10ºC. Those mosses collected in June, before the heat of summer, had a peak at 35ºC, the highest optimum found in the 1-40ºC temperature range of the experiments. These mosses had already reached an optimum of 30ºC by 3 April, even though the stream temperature was only 1ºC. This suggests that something other than temperature is triggering the change in photosynthetic response to temperature. For aquatic bryophytes, this could be a nutrient pulse during spring runoff, increasing photoperiod, or both.

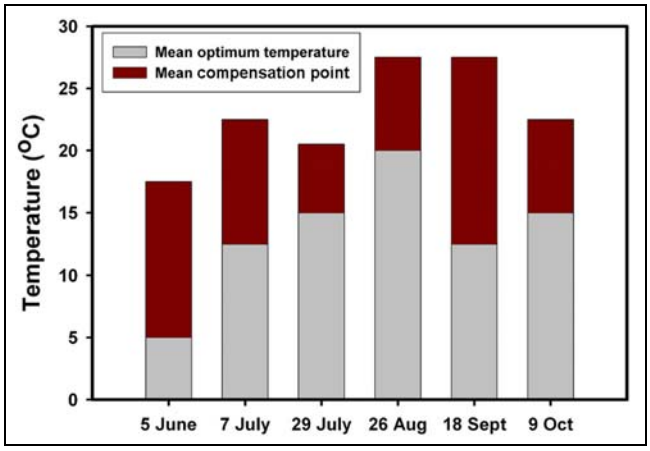

Figure 75. Mean optimum temperatures and upper temperature compensation points for ***Dicranum fuscescens*** photosynthetic activity at Mary Jo lowland near Quebec, Canada, as an effect of acclimation due to increasing and decreasing spring to autumn temperatures. Based on Table 1 in Hicklenton & Oechel 1976.

In the Antarctic populations of ***Sanionia uncinata*** (Figure 61) and ***Polytrichum strictum*** (Figure 76), Collins (1976) demonstrated a shift in the photosynthetic curve depending on the acclimation temperature. Those previously growing at a lower temperature had positive productivity at a lower temperature, had a higher optimum, and had lower productivity at higher temperatures in ***Polytrichum strictum*** (Figure 77). ***Sanionia uncinata*** had a similar low temperature response to that of ***Polytrichum strictum***, with the same optimum in both treatments, but the ones acclimated at higher temperatures exhibited a more rapid photosynthetic decline above the optimum (Figure 77).

Figure 76. ***Polytrichum strictum***, a species whose temperature optimum depends on the previous optimum temperature. Michael Luth, with permission.

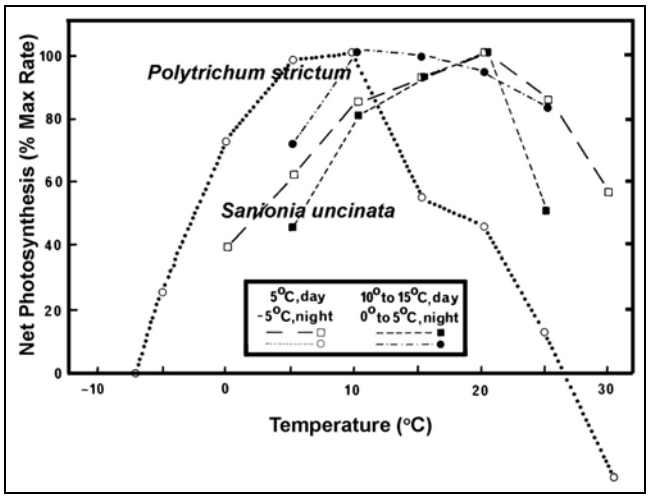

Figure 77. Acclimation responses of two Antarctic moss species at radiant flux density of 500 μeinsteins m^{-2} s^{-1}. Redrawn from Collins 1976.

Cold vs Heat

As seen for the polar regions, those factors that help plants adapt to the cold often incur heat resistance as well. Just as antifreeze in a car keeps it from freezing in winter, it keeps it from boiling in the summer. Such "antifreeze" effects work as well in plants.

In their study of temperature resistance in ***Sphagnum*** (Figure 47-Figure 51), Balagurova *et al*. (1996) found that differences between species were greater for heat resistance than for cold resistance, but there was, nevertheless, a correlation between the two kinds of resistance.

Acclimation Triggers

One factor that could play a role in acclimation is light intensity, although I don't know what physiological mechanisms might be involved. We know that at 140 lux light intensity ***Fontinalis*** sp. (see Figure 40) reaches its compensation point at 20ºC, but when only 40 lux is present, it reaches compensation at 5ºC (Burr 1941). While this should not have been a factor during the lab experiments of Fornwall and Glime (1982), who kept the light intensity constant at 4500 lux, the previous field history of light and photoperiod might have played a role in the temperature performances.

It is often difficult to recognize whether differences are the result of physiological races or of acclimation. For example, Asakawa *et al*. (1991) found that most of the high elevation/high latitude members of several ***Frullania*** taxa synthesized **tamariscol** (***F. tamarisci*** subspecies – Figure 78) and ***F. nepalensis***, whereas those in lower altitudes and latitudes did not. (**Tamariscol** imparts intense "mossy" or pleasant odor.) But we have no evidence that this provides any advantage in cooler climates and may be a geographic variant that travels with a gene that is adaptive. On the other hand, particular conditions of the climate at higher elevations and latitudes (in the north) might cause the gene to be expressed, whereas these triggers may be absent at the time of collection from lower latitudes and altitudes.

Figure 78. ***Frullania tamarisci***, a high elevation species that produces tamariscol. Photo by Michael Luth, with permission.

Kallio and Saarnio (1986) actually transplanted mosses [***Hylocomium splendens*** (Figure 21), ***Pleurozium schreberi*** (Figure 79), and ***Racomitrium lanuginosum*** (Figure 2-Figure 3)] from 60º55'N to 69º45'N and from 69º45'N to 78º13'N to determine their adaptations to cold. The physiological stress of these mosses increased as they were moved northward. Kallio and Saarnio concluded that their adaptations were largely due to their ability to acclimate. Day length and temperature served as important environmental cues to acclimation, and these signals changed as mosses were moved to more extreme latitudes.

Figure 79. ***Pleurozium schreberi***, a species that is apparently able to acclimate when moved to more northern sites. Photo by Janice Glime.

Summary

Bryophytes may experience temperatures far greater than the ambient temperature due to their dark color and ability to act as a black body. Generally bryophytes are only able to tolerate temperatures up to about 40ºC before the temperature becomes lethal. Their optimum, however, is usually much lower than that. They often are able to have photosynthetic gain at temperatures as low as -10ºC, but seldom have a net gain at temperatures above 25ºC. Rather, they typically become dormant in summer heat and drought. For many species, the optimum is 15-25ºC, although it seems to be much lower for stream bryophytes. Even tropical bryophytes have an upper limit of 25ºC.

Bryophytes can alter not only their own temperature, but also the temperature of the soil. Evaporative cooling may lower it, but dark color may raise it. They can protect the root zone of the soil from high temperatures on hot prairies and deserts by shading and insulating. In geothermal areas they can raise the soil temperature by trapping the geothermal heat beneath them. With an atmospheric temperature of 20ºC, a sunfleck may warm a moss to 39ºC. In some locations they may have a temperature 30ºC or more higher than ambient. Their insulating role in the Arctic has a major role in the Arctic temperatures, delaying the thaw cycle by absorbing the heat that would have gone to the soil and decreasing the number of **soil degree days**, and making them essential to the BOREAS temperature model.

Bryophytes can transfer water from lower parts to growing tips and use evaporative cooling much as in tracheophytes. **Awns**, **hyalocysts**, and **papillae** can reflect light to maintain cooler temperatures (See Chapter 7-4). Mosses such as *Sphagnum* retain considerable water, and experience little temperature change. They provide safe sites for small animals such as overwintering turtles and for germinating seeds.

Temperature affects photosynthetic rate, respiratory rate, reproductive timing, growth, development, and productivity. Spore germination temperature is often set higher than that of protonema growth to prevent germination when freeze damage is still likely. Branches, rhizoids, and stem growth may have similar requirements to keep them in consort or may have different temperature requirements to spread out the energy needs or take advantage of suitable conditions for attachment. Gametangia typically have different temperature (or photoperiod) requirements that avoid the competition for energy and to place gametangial maturity at a time when water is available. Sporophyte development may be cued by temperature to delay until after dangers of winter cold. Dormancy is typically triggered by temperature, protecting plants in summer from drought or from being hydrated at a lethal temperature. Even successful development of fragments is dependent on temperature.

Bryophytes seem able to grow over a wider temperature range than tracheophytes, particularly at the low end of the scale. Changes in temperature below their optimum have only modest effects on their productivity, demonstrated by their relatively low $\mathbf{Q_{10}}$ in that range, but net productivity drops off rapidly above their optimum. Physiological races exist within species that can give them quite different temperature responses and optima. However, recent past history of temperatures may be responsible for their **acclimation** rather than their **adaptation**. Optimum temperatures for photosynthesis are typically lower in winter than in summer and may actually rise before the ambient temperature rises, suggesting that temperature is not necessarily the signal.

Some tissues are more resilient that others and may even survive extensive boiling for several weeks, giving rise to new tissues at a later time. Short-term studies may be misleading for testing lethality and optima because of the importance of acclimation and internal tissue protection. Nevertheless, they can tell us the **compensation point** under a specific set of conditions if the recent history is known.

Low temperature acclimation seems to prepare mosses for high temperatures as well, giving Antarctic bryophytes the ability to survive high temperatures. Lack of proper signals for acclimation can prevent bryophytes from extending their ranges into new latitudes.

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Figure 1. ***Racomitrium heterostichum*** mostly imbedded in ice while some branches are free and available for photosynthesis. Photo by Michael Lüth, with permission.

Low Temperature Limits

In general, bryophytes seem able to withstand cold in their leafy state much better than their tracheophyte counterparts. Ochi (1952) found that most mosses (18 species tested) were resistant to cold to -20°C. Seven of these species were resistant to -27°C. He was unable to find any trend in relationships to osmotic value, permeability, or seasonal fluctuations. Ochi's results support the later statement of Kallio and Heinonen (1973), that ***Racomitrium lanuginosum*** (Figure 2), a cosmopolitan moss, is pre-adapted to its abode in the Arctic and Antarctic (see Table 1) and suggest that such pre-adaptation may be a common feature of bryophytes. This contention is supported by the low temperatures that become lethal for bryophytes in the tropics (Table 2).

Figure 2. ***Racomitrium lanuginosum***, a species pre-adapted to living in the polar regions with long, white hair tips. Photo by Janice Glime.

Surprisingly, Arctic liverworts do not seem to be so cold resistant. Among the nine species tested by Biebl (1968), seven were mostly dead at -16ºC, with only the leafy liverworts ***Barbilophozia hatcheri*** (Figure 3) and ***Chandonanthus setiformis*** (Figure 4) surviving well. The moss ***Aulacomnium turgidum*** (Figure 5-Figure 6) also survived at -16ºC. All species survived -6ºC. But these were July responses in Greenland; a quite different picture might emerge in winter. On the other hand, all of them survived up to 42ºC for half an hour, but twelve-hour exposures killed parts of most of them, the same seven, at 38ºC. ***Aulacomnium turgidum*** survived up to 48ºC for half an hour and up to 40ºC for twelve hours. This supports the hypothesis that low temperature survival is coupled with high temperature survival.

Figure 3. ***Barbilophozia hatcheri***, a leafy liverwort that survives to -16°C. Photo by Michael Lüth, with permission.

Figure 4. ***Chandonanthus setiformis***, a leafy liverwort that survives to -16°C. Photo by Michael Lüth, with permission.

Tropical mosses seemed rather similar. After 24 hours of exposure, ***Homaliodendron flabellatum*** (Figure 7) and ***Leucoloma amoene-virens*** survived -14ºC and ***Schistochila commutata*** (Figure 8) survived -11ºC (Biebl 1967). Tropical ***Plagiochila*** (Figure 9), ***Metzgeria*** (Figure 10), and ***Bryum*** (Figure 11) species each survived to at least -4ºC. Try doing that to a tropical *Maranta* (Figure 12).

Figure 5. ***Aulacomnium turgidum*** in a mountainous habitat. Photo by Michael Lüth, with permission.

Figure 6. ***Aulacomnium turgidum***, a moss that survives to -16°C. Photo by Michael Lüth, with permission.

Figure 7. ***Homaliodendron flabellatum***, a tropical species that can survive to -14°C. Photo by Jiang Zhenyu, Mou Shanjie, Xu Zawen, Chen Jianzhi, through Creative Commons.

Figure 8. ***Schistochila*** sp, a tropical species that survives to -12°C. Photo by Jan-Peter Frahm, with permission.

Figure 9. ***Plagiochila*** sp. from the Neotropics. Some tropical members of this genus survive to -4°C. Photo by Michael Lüth, with permission.

Figure 10. The tropical thalloid liverwort, ***Metzgeria claviflora***. Photo by Michael Lüth, with permission.

Figure 11. ***Bryum apiculatum*** from the Neotropics. Some tropical members of this genus survive to -4°C. Photo by Michael Lüth, with permission.

Table 1. Temperature limits for net photosynthesis under natural CO_2 and light saturation. From Larcher 1983, compiled from many authors; *Liu *et al.* 2001.

Plant group	Low-temp limit for CO_2 uptake °C	Temp opt of P_n°C	High-temp limit for CO_2 uptake (°C)
Herbaceous flowering plants			
C_4 plants of hot habitats	+5 to 7	35-45	(50) 50-60
Sun plants (temperate zone)	-2 to 0	20-30	40-50
Shade plants (temperate zone)	-2 to 0	10-20	~40
Desert plants	-5 to 5	20-35 (45)	45-50 (56)
CAM plants (CO_2 fixation at night)	-2 to 0	5-15	25-30
Winter annuals, spring-flowering and alpine plants	-7 to -2	10-20	30-40
Woody plants			
Evergreen trees of the tropics and subtropics	0 to 5	25-30	45-50
Winter-deciduous trees of the temperate zone	-3 to -1	15-25	40-45
Evergreen conifers	- 5 to -3	10-25	35-42
Dwarf shrubs of heath and tundra	~-3	15-25	40-45
Cryptogams			
Arctic and subarctic mosses	**~-8**	**~5**	**~30**
Racomitrium lanuginosum	**-8 to -10**	**5**	**25-30**
Pleurozium schreberi	**-5**	**10-15**	**28-33**
Plagiomnium acutum*	**-10 to -15**	**20-35**	**40-45**
Plagiomnium maximoviczii	**-10 to -15**	**20-35**	**40-45**
Lichens of cold regions	(-25)-15 to -10	5-15	20-30
Desert lichens	~-10	18-20	38-40
Tropical lichens	-2 to 0	~20	
Snow algae	~-5	0-10	30
Thermophilic algae	20 to 30	45-55	65-70

Figure 12. ***Maranta leuconeura***, a tropical plant that dies in cool temperatures well above freezing. Photo by Stickpen, through public domain.

Table 2. Comparison of temperature resistance of leaves of plants from different climatic regions. Limiting temperatures are for 50% injury (TL_{50}) after exposure to cold for 2 or more hours, or after exposure to heat for 0.5 h. Bryophytes appear in **bold**. Tracheophyte data from Larcher 1983, based on data from many authors; cold tracheophytes had been cold-hardened. Data marked by * from Biebl 1967; Data marked by $^{+}$ from Liu *et al*. 2003.

Plants	°C for cold injury	°C for heat injury in growing season
Tropics		
Trees	+5 to -2	45-55
Forest undergrowth	+5 to -2	45-48
Mountain plants	-5 to -10	~45
Schistochila commutata*	**-14**	**44**
Plagiochila* sp.	**-7**	**44**
Homaliodendron flabellatum*	**<-14**	**52**
Leucoloma amoenervis*	**<-14**	
Bryum* sp.	**-11**	**52**
Subtropics		
Sclerophyllous woody plants	-8 to -12	50-60
Subtropical palms	-5 to -14	55-60
Succulents	-5 to -10	58-65
C_4 grasses	-1 to -3(-8)	60-64
Temperate zone		
Evergreen woody plants of coastal regions with mild winters	-6 to -15 (-25)	50-55
Plagiomnium acutum*		**45 (50 dry)**
Arcto-tertiary relict trees	-10 to -25 (-15 to -30)	
Dwarf shrubs of Atlantic heaths	-20 to -30	45-50
Winter-deciduous trees and widely Distributed shrubs	(-25 to -40)	~50
Herbs		
Sunny habitats	10 to -20 (-30)	48-52
Shady habitats	40-45	
Water plants	~-10	38-42
Cold-winter areas		
Evergreen conifers	-40 to -90	44-50
Boreal broad-leaved trees	(-196)	42-45
Arctic and alpine dwarf shrubs	-30 to -70	48-54
Herbs of the high mountains and arctic	(-30 to -196)	44-54

Stress Protection

Bryophytes are well known for their secondary compounds. These defend against competition, microbes, and herbivory, while often protecting against UV radiation, providing drought tolerance, and freezing survival (Xie & Lou 2009). These latter protections can all be associated with cold temperatures. Specifically, bibenzyls and bis(bibenzyls) have provide desiccation tolerance; fatty acid derivatives and phenylpropanoids provide freeze tolerance.

But bryophytes seem to have a large arsenal of protectors against cold stress. They are able to accumulate soluble sugars and abscisic acid (ABA) (Bhyan *et al*. 2012). The latter increases freezing tolerance in plant cells and also is important in desiccation tolerance – a likely consequence of ice crystal formation. During acclimation in ***Physcomitrella patens*** (Figure 13) that was developed to be insensitive to ABA, the cells accumulated sucrose to levels similar to those found in ABA-normal plants. But the trisaccharide theanderose did not accumulate in the ABA-deficient plants. Furthermore, these deficient plants had very limited accumulation of LEA-like boiling-soluble proteins. On the other hand, Minami *et al*. (2005) found an accumulation of several transcripts for LEA proteins and boiling-soluble proteins during freeze-tolerance acclimation. Bhyan *et al*. (2012) concluded that cold acclimation requires an ABA-dependent signalling system. Cold-induced sugar acclimation, however, may or may not be dependent on the ABA system. This ABA dependence is in contrast to the study by Minami *et al*. (2005), which concluded that ABA had no role in cold hardening in ***P. patens***.

Figure 13. ***Physcomitrella patens*** with young sporophytes. Photo by Michael Lüth, with permission.

Freezing

As the external temperature is depressed, the bryophyte cell cools rapidly, presenting a rather different pattern from that of tracheophytes. In tracheophytes, leaf hairs, thick cuticle, and epidermis all serve to insulate the internal leaf cells from rapidly changing temperatures. Bryophyte leaves have none of these.

Freezing presents a number of problems for cells. Formation of crystals can cause physical damage by poking holes in the cell membrane or distorting the cell so that solutes can leak out more easily. Crystals are hygroscopic, attracting the water molecules from the cells to the cell

surface or intercellular spaces where the crystals may reside. This loss of water from the cells causes them to dehydrate. And cell membranes may be damaged or not function properly as fatty acids with higher solidification points become nonpliable.

Despite being perennial above ground, many, perhaps most, bryophytes survive freezing. Fletcher (1982) provided representative species from New Zealand [***Papillaria crocea*** (Figure 14), ***Hypopterygium*** spp. (Figure 15), ***Hymenodontopsis bifaria***, ***Cyathophorum bulbosum*** (Figure 16), ***Calyptrochaeta brownii*** (Figure 17)], South Africa [***Hypopterygium*** sp. (Figure 15)], Australia [***Gigaspermum repens*** (Figure 18), ***Goniomitrium acuminatum*** subsp. ***enerve*** (Figure 19)], and from Florida, USA [***Rhizogonium spiniforme*** (Figure 20)] that survive freezing. In addition, Fletcher demonstrated that ***Takakia lepidozioides*** (Figure 21-Figure 22) remained healthy, as did ***Sphagnum*** spp. (Figure 24) and ***Mnium*** spp. (Figure 23). That number only provides us proof that some species survive, but gives us no idea of the world picture.

Figure 14. ***Papillaria crocea*** in a cloud forest at Mt Budawang, Australia, a species that is able to survive freezing. Photo by Peter Woodard, through Public Domain.

Figure 15. ***Hypopterygium arbuscula***, in a New Zealand and South African genus in which some species are able to survive freezing. Photo by Scott Zona, with permission.

Figure 16. ***Cyathophorum bulbosum***, a New Zealand species that is able to survive freezing. Photo by Peter Woodard, through Creative Commons.

Figure 17. ***Calyptrochaeta brownii***, a South African species that is able to survive freezing. Photo by Tom Thekathyil, with permission.

Figure 18. ***Gigaspermum repens***, an Australian species that is able to survive freezing. Photo by David Tng, with permission.

Figure 19. ***Goniomitrium acuminatum*** subsp. ***.enerve***, a species that survives freezing in Australia. Photo by David Tng, with permission.

Figure 20. ***Rhizogonium spiniforme***, a Florida species that is able to survive freezing. Photo by Janice Glime.

Figure 21. ***Takakia lepidozioides*** habitat, Japan. Photo from Digital Museum, University of Hiroshima, with permission.

Sphagnum capillifolium (Figure 24) exhibits a critical freezing temperature threshold for photosystem II that is identical to its ice nucleation temperature (-1.1°C) (Buchner & Neuner 2010). But frost damage (**LT_{50}**) is not visible until the temperature reaches -16.1°C. The **LT_{50}** is the condition/level at which the condition is lethal to 50% of the population.

Figure 22. ***Takakia lepidozioides***, a high elevation species that survives freezing. Photo by Rafael Medina, through Creative Commons.

Figure 23. ***Mnium thomsonii*** from the Khibiny Mountains, Apatity, Murmansk, member of a genus in which some species survive freezing. Photo by Michael Lüth, with permission.

Figure 24. ***Sphagnum capillifolium***, a species that does not show frost damage above -16°C. Photo by Michael Lüth, with permission.

Something is going on in nature that does not seem to be mimicked in the lab. ***Haplomitrium hookeri*** (Figure 25) from New Zealand and ***H. mnioides*** (Figure 26) from Japan are able to grow in winter in their native habitats, but in cultivation all plants were unhealthy after being subjected to frost (Fletcher 1982). ***Moerckia blyttii*** (Figure 27), ***Symphogyna*** sp. (Figure 28), ***Corsinia coriandrina*** (Figure 29), and ***Asterella*** sp. (Figure 30-Figure 31) became severely bleached by frost in cultivation, but

Corsinia coriandrina remained healthy on an exposed wall top and in an unheated greenhouse down to a temperature of -5.5°C. Blackening occurred in ***Dumortiera hirsuta*** (Figure 32), but the plants survived. ***Asterella*** and ***Monoclea forsteri*** (Figure 33) likewise were blackened by frost in the greenhouse. ***Fossombronia*** (Figure 34) and **Anthocerotophyta** (Figure 35-Figure 36) experienced thallus decay, a phenomenon that they exhibited commonly in winter in nature. Plants of the hornworts ***Anthoceros punctatus*** (Figure 35) and ***Phaeoceros laevis*** (Figure 36) remained healthy in the greenhouse. Likewise, ***Lunularia*** (Figure 37), ***Pellia*** (Figure 38), ***Preissia*** (Figure 39), ***Riccardia*** (Figure 40), ***Riccia*** (Figure 41), and ***Marchantia polymorpha*** (Figure 42) showed no frost damage in the lab.

Figure 25. ***Haplomitrium hookeri***, a species that survives frost in nature, but not in the lab. Photo by Štěpán Koval, with permission.

Figure 26. ***Haplomitrium mnioides***, a species that survives frost in nature, but not in the lab. Photo by Yang, Jia-Dong, through Creative Commons.

Figure 27. ***Moerckia blyttii***, a species that became severely bleached by frost in the lab. Photo by Michael Lüth, with permission.

Figure 28. ***Symphyogyna brasiliensis*** female plant. A species in this genus became severely bleached by frost in the lab. Photo by George J. Shepherd through Creative Commons.

Figure 29. ***Corsinia coriandrina***, a species that became severely bleached by frost in the lab but remained healthy in nature. Photo by Michael Lüth, with permission.

Figure 30. ***Asterella lindenbergiana***, a genus in which some species are blackened by frost in the greenhouse. Photo by Michael Lüth, with permission.

Figure 31. ***Asterella lindenbergiana***, a frost-sensitive genus in the lab. Photo by Martin Hutten, with permission.

Figure 32. ***Dumortiera hirsuta***, a species that survives frost in the lab, but it is blackened. Photo by Michael Lüth, with permission.

Figure 33. ***Monoclea forsteri***, a species that is blackened by frost in the lab. Photo by Jan-Peter Frahm, with permission.

Figure 34. ***Fossombronia angustata***. This genus commonly exhibits winter thallus decay. Photo by Michael Lüth, with permission.

Figure 35. ***Anthoceros punctatus***, a species that remained healthy at temperatures below freezing in the greenhouse. Photo by Tab Tannery, through Creative Commons.

Figure 36. ***Phaeoceros laevis*** with capsules, a species that remained healthy at temperatures below freezing in the greenhouse. Photo by Michael Lüth, with permission.

Figure 37. ***Lunularia cruciata***, a species that remained healthy at temperatures below freezing in the greenhouse. Photo by Des Callaghan, with permission.

Figure 38. ***Pellia epiphylla***, a species that remained healthy at temperatures below freezing in the greenhouse. Photo by Li Zhang, with permission.

Figure 39. ***Preissia quadrata***, member of a genus that remained healthy at temperatures below freezing in the greenhouse. Photo by Janice Glime.

Figure 40. ***Riccardia***, a genus that remained healthy at temperatures below freezing in the greenhouse. Photo by Li Zhang, with permission.

Figure 41. ***Riccia nigrella***, member of a genus that remained healthy at temperatures below freezing in the greenhouse. Photo by Jan-Peter Frahm, with permission.

Figure 42. ***Marchantia polymorpha*** with red edges, a species that remained healthy at temperatures below freezing in the greenhouse. Photo by Brenda Dobbs, through Creative Commons.

This raises the question of how do these exposed bryophytes survive. Why don't they suffer structural damage from internal ice crystals? How are they protected from severe desiccation as crystals on the outsides of leaves draw water from the cells?

Melick and Seppelt (1992) investigated these questions in ***Schistidium antarctici*** (Figure 43), ***Ceratodon purpureus*** (Figure 43, Figure 50), ***Bryum pseudotriquetrum*** (Figure 44-Figure 45), and ***Cephaloziella exiliflora*** (Figure 46) that were collected in late summer in the Antarctic Wilkes Land. Following 16 days of immersion, the plant loss of the carbohydrates glucose and fructose was relatively low (ca. 10-29% of the sugar content) in healthy mosses. However, in the senescing tissues of ***S. antarctici*** 69% of these sugars were lost. Following 16 freeze-thaw cycles the bryophytes experienced a sugar loss 2-3 times as great as in non-frozen controls in all but the dead brown tissue. ***Bryum pseudotriquetrum*** lost 65% of its total sugar content after a freeze-thaw cycle, whereas the other species lost less than 28%. Freezing points varied from -8.3° to -3.5°C, with dead material having the highest freezing temperatures. Freezing temperatures and sugar loss did not correlate and there was no change in the freezing point temperature of tissues after the sugar loss.

Figure 43. ***Schistidium antarctici*** hummock with ***Ceratodon purpureus*** in hollows. Photo courtesy of Rod Seppelt.

Figure 44. ***Bryum pseudotriquetrum*** in Antarctica, a species that loses considerable sugar after a freeze-thaw cycle. Photo by Rod Seppelt, through Creative Commons.

Figure 45. ***Bryum pseudotriquetrum*** in Norway, a species that loses little sugar following 16 days of immersion. Photo by Michael Lüth, with permission.

Figure 46. ***Cephaloziella exiliflora***, a species that loses little sugar following 16 days of immersion. Photo by Tom Thekathyil, with permission.

On Windmill Islands of continental Antarctica, there was almost no seasonal change in the soluble carbohydrate content of the bryophytes and lichens (Melick & Seppelt 1994). The researchers considered that this lack of change

may be the result of the extreme climate and rapid temperature fluctuations.

Desiccation Tolerance

One of the consequences of freezing is dehydration. Consider the loss of moisture from your meat in the freezer when ice crystals form on the meat surface. Ice crystals are hygroscopic, pulling moisture from adjacent tissues. Furthermore, ice within the cell deprives the cell of the use of that water. The desiccation tolerance of bryophytes, therefore, helps them to survive freezing (Segreto *et al*. 2010). In their study of cryopreservation of bryophytes, Segreto and coworkers found that this natural desiccation tolerance negated the need for pretreatment or use of cryoprotectants before preserving live bryophyte tissues through freezing. They also found that longer or larger shoots of the leafy liverwort ***Herbertus*** (Figure 47) were able to regenerate more easily than smaller fragments, a phenomenon that suggests they are either able to transport from healthy cells to those that have been harmed, or that the greater amount of tissue helps to protect some of the cells.

Figure 47. ***Herbertus hutchinsiae***; longer and larger shoots regenerate more easily in this genus. Photo by Michael Lüth, with permission.

Much like their resistance to hot temperatures, at least some bryophytes (***Syntrichia ruralis*** – Figure 48-Figure 49) are more likely to survive freezing if they are dehydrated first (Bewley & Thorpe 1974). Those that were frozen in the hydrated state had lower rates of respiration and showed signs of freeze damage when rehydrated. Nevertheless, the respiration of desiccated mosses and of those desiccated and immersed in liquid nitrogen (frozen) was much higher on recovery than that of the controls that had remained hydrated at room temperature.

Desert species should be particularly adapted to freezing. They are endowed with various adaptations to survive desiccation, and they have a high probability of being desiccated when they experience freezing temperatures. But winter is the active season for the semi-desert grassland mosses in Hungary, with overwintering green shoots that are frequently exposed to temperatures below zero at night (Tuba *et al*. 2008). Daytime temperatures reach 0-5°C, and the dark-colored mosses (***Tortula***/***Syntrichia*** – Figure 48-Figure 49) are even warmer (-2.1° to 6.9°C). The bryophytes were among the 18 out of 20 species that exhibited positive net photosynthesis. The abrupt increase in temperature in March did not affect the productivity rate of the mosses.

Figure 48. ***Syntrichia ruralis***, a species that survives freezing better if it is dry first. Photo by David Holyoak, with permission.

Figure 49. ***Syntrichia ruralis*** dry, showing twisting leaves and awns that help to slow drying and protect at least some leaf cells from UV damage. Photo by Misha Ignatov, with permission.

Lenne *et al*. (2010) found that the ubiquitous moss ***Ceratodon purpureus*** (Figure 50) did not accumulate ice within the moss tissues during freezing. However, external ice induced desiccation. The water-filled hydroid cells cavitated at -4°C. Parenchyma cells of the stem's inner cortex lost 20% of their original volume and exhibited **cytorrhysis** (permanent and irreparable damage to cell wall after complete collapse of plant cell due to water loss and consequent loss of internal positive pressure) at the lowest temperature of -20°C. Nevertheless, following freezing at -20°C, chlorophyll fluorescence showed no damage to the chlorophyll. Once again, desiccation played a major role. In hydrated mosses, internal ice nucleation occurred at -12°C, but desiccated mosses showed no evidence of freezing at the lowest temperature of -20°C. There was nothing left to freeze.

Figure 50. ***Ceratodon purpureus***, a species that experiences **cytorrhysis** due to desiccation that results from freezing, but chlorophyll remains undamaged. Photo by Janice Glime.

Tolerance to desiccation is one feature that helps bryophytes to survive freezing. Since leaves are generally only one cell thick, and most other parts only a few cells thick, water is easily drawn from the tissues during the slow cooling that occurs in nature. This increases the solute concentration and lowers the freezing point. Hence, intracellular freezing does not occur (Mazur 1969, in Smith 1982). In fact, some mosses are able to photosynthesize at temperatures below 0°C. In **nunataks** (area escaping glaciation) of Queen Maud Land, Antarctica, the air temperature rarely exceeds 0°C, yet moss photosynthesis occurs during the summer as long as there is sufficient water availability (Gjessing & Ovstedal 1989). Narrow clefts and stone blocks shield the mosses from desiccation and maintain less heat loss, but they are also shielded from direct solar radiation most of the time. Nevertheless, short-term periods of warming, even to -2ºC, can greatly increase the moss temperature. These microsites permit mosses growing in such severe habitats to have the highest photosynthetic rates.

In the Arctic, ***Racomitrium lanuginosum*** (Figure 2) has an optimum temperature of 5°C at high light intensities (12,000-15,000 lux), but can sustain photosynthesis down to -10°C (Kallio & Heinonen 1973). Even after exposure to -30°C this moss is able to activate quickly (60% within 3 hours) when warmed. Thus, the bryophytes that exist in such harsh environments as the Antarctic and Arctic must have high freezing resistance, a high resistance to light stress, and a low photosynthetic temperature optimum (Alberdi *et al*. 2002).

In ***Marchantia berteroana*** (Figure 51), an Antarctic liverwort, freezing greatly reduces photosynthesis, but the author suggested that photosynthesis was also possible at temperatures below freezing (Davey 1997). Rather than temperature, this species is greatly limited by desiccation stress.

Protection of Photosynthetic System from Light

High light intensities at low temperature levels can be extremely damaging to bryophytes that have leaves only one cell thick. Nevertheless, it appears that many, and perhaps most, bryophytes have mechanisms that protect them. In the Antarctic, where such conditions are common, the reversible inhibition present during freezing suggests that mosses such as ***Schistidium antarctici*** (Figure 43) have processes that protect them from such photoinhibitory damage (Lovelock *et al* 1995a) and thus do not require the repair processes that would require temperatures favorable for such repair enzyme activity. Rather, these mosses, when subjected to snow removal, suffered photoinhibition that was reversed when the temperature became warmer (Lovelock *et al*. 1995b). Nevertheless, the greatest recovery occurred in low light. Lovelock and coworkers (1995b) suggest that the photoinhibition during freezing is a protective process that down-regulates photosystem II when photosynthesis cannot keep up with the light-stimulated excitation of electrons.

Figure 51. ***Marchantia berteroana***, a species limited by desiccation stress, but freezing only reduces photosynthesis. Photo by Andrew Hodgson, with permission.

Pannewitz *et al.* (2003b) showed similar protection for ***Hennediella heimii*** (Figure 52) at Canada Flush in Antarctica. Constant meltwater in the summer kept this moss continuously hydrated at near-freezing temperatures while light levels were frequently high. Yet there were no signs of either light saturation or photoinhibition. Rather, the electron transport rate response to light was linear at all temperatures. Pannewitz and coworkers suggested that the moss might be acclimated by building up non-photochemical quenching systems.

Figure 52. ***Hennediella heimii***, a very cold-tolerant moss while continuously hydrated. Photo by Barry Stewart, with permission.

For those bryophytes that are epiphytes, it is unlikely that enough mechanisms exist to avoid freezing entirely. But living on a dark tree trunk is likely to mean frequent freeze-thaw cycles. This not only presents problems of desiccation, but also presents potential light damage to the photosynthetic system. Working with the Mediterranean epiphytic moss ***Leucodon sciuroides*** (Figure 53), Deltoro *et al*. (1999) found that one aspect of bryophyte freeze-thaw survival could be their ability to enhance their non-radiative dissipation of absorbed light energy by freeze-induced decrease in CO_2 fixation, hence protecting their photosynthetic system from excess excitation. This temporary reduction in CO_2 fixation is quickly returned to normal after freezing.

Figure 53. ***Leucodon sciuroides*** on a tree trunk where it is exposed to atmospheric temperatures all year. Photo by Michael Lüth, with permission.

Rütten and Santarius (1992a) found that photosynthetic apparatus in mature tissues of ***Plagiomnium*** (Figure 55) species was more frost tolerant than that of either young or old leaves. As freezing stress increased, fluorescence decreased and the photosystem II-mediated electron transport system became inactivated. This resulted in inhibition of electron donations to the photochemical reaction of photosynthesis, differing little from the pattern in tracheophytes. Nevertheless, there was little decrease in transfer of excitation energy through antenna pigments to reaction centers of photosystem II as a result of lethal freezing stress.

Role of Calcium

Calcium seems to play a role in cold tolerance through its role in regulation of membrane transport. In ***Physcomitrella patens*** (Figure 13), wild type plants respond to cold shock (0-10°C) by increasing cellular content of calcium (Russell *et al*. 1996). It is most likely not calcium itself, but its effect on membrane permeability and other processes in the cell that provide actual protection. In the thallose liverwort ***Conocephalum conicum*** (Figure 54), Krol *et al*. (2003) likewise found that calcium played a role in climate response. A sudden drop in temperature causes it to generate all-or-none action potentials that appear to be the result of membrane potential changes due to influx of Ca^{++} derived from both internal and external sources.

Figure 54. ***Conocephalum conicum***, a species in which membrane potentials change in response to freezing. Photo by Janice Glime.

The activity and thermosensitivity of superoxide dismutase (SOD) is highly sensitive to ions of Ca^{++} and Zn^{++} (Christov & Bakardjieva 1999). In ***Plagiomnium affine*** (Figure 55), calcium was most important for the one cytosolic and mitochondrial SOD's, whereas zinc was more important for the chloroplastic and two cytosolic SOD's.

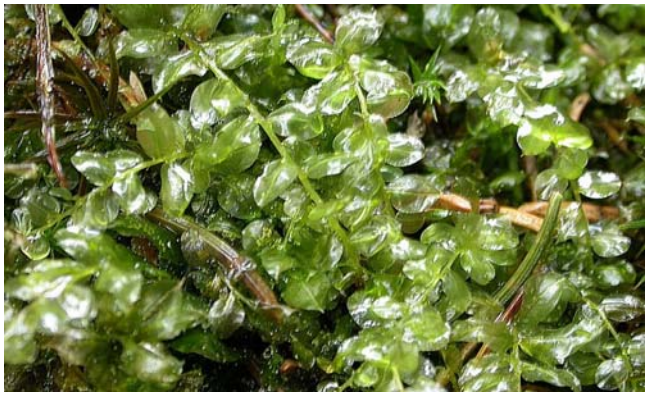

Figure 55. ***Plagiomnium affine***, a species that increases its cold tolerance from summer to winter. Photo by Michael Lüth, with permission.

Abscisic Acid

Physcomitrella patens (Figure 13), as in many studies, has contributed to our understanding of freezing protection in bryophytes. When this species was grown on ABA agar, it accumulated up to 22% of its dry weight as sucrose, compared to 3.7% in control (non-ABA) tissues (Davey 1997). Sucrose serves as a protectant during both freezing and drying, but is insufficient as the only agent for freezing protection. When subjected to temperatures down to -80°C, it survived a freeze-cycle only when provided with the cryoprotectant DMSO, a compound that makes membranes more permeable. This species can only survive slow drying, which it does down to 0.02 g H_2O per g DW. Sugar composition and glass transition temperatures differed little between slow and fast drying. Nevertheless, the strength of the hydrogen bonding in the cell's glassy matrix was greater in the slow-drying conditions.

ABA (abscisic acid) is produced in tracheophytes in preparation for cold temperatures and permits plants to survive to lower temperatures, somewhat like antifreeze.

Nagao *et al*. (2005) have shown that media containing ABA does indeed lower the LT_{50} (temperature at which 50% of cells die) for ***Physcomitrella patens*** (Figure 13) from -2ºC to -10ºC and even lower. They observed that there was a "dramatic" alteration in the appearance of the organelles, manifest in slender chloroplasts with reduced starch grains. The vacuoles became segmented rather than the typical single large vacuole. ABA also protected the cells from membrane lesions that occurred in controls at -4ºC. One of the mechanisms of protection stimulated by the ABA treatment was an increase in the osmotic concentration of cells of the protonema, most likely due to the increased sugar concentration that accompanied the ABA treatment. But that only tells us what ABA can do. Next we need to determine that mosses do indeed produce it or increase its production at the right time, what stimuli cause this production, and can lunularic acid (ABA analog in liverworts) do the same for liverworts.

But the story does not appear to be straight-forward. Although they reported ABA-induced freezing tolerance in ***Physcomitrella patens*** (Figure 13) in 2003, Minami *et al*. (2003, 2005) reported that freezing tolerance was not associated with an increase in the level of endogenous abscisic acid in ***P. patens***, but that it was associated with increases in the expression of stress-related genes. It seems that the role of ABA is to induce the genes, not to offer protection itself (Nagao *et al.* 2001; Minami *et al*. 2003, 2005). When they subjected protonemata of ***P. patens*** to -4ºC, following normal growth conditions, more than 90% of the cells died, indicating that protonema cells are freezing-sensitive (Minami *et al*. 2003, 2004). ABA treatment resulted in a significant increase in the expression of all PPAR genes within 24 h. These genes are known to participate in the increase of freezing tolerance, and indeed, the death rate decreased significantly.

Minami *et al*. (2005) likewise studied freeze tolerance in ***Physcomitrella patens*** (Figure 13). They found that in the temperature range of 10°C and 0°C, and especially at 0°C, freeze tolerance increased significantly. But they found that internal tissue levels of ABA did not increase during that acclimation period. Furthermore, removal of ABA by activated charcoal did not affect the developing freeze tolerance. Hence, they concluded that ABA is unimportant in freeze tolerance. I would guess that it is, however, important in surviving the accompanying desiccation.

Transporter Proteins, ABA, and Ca

Further studies on ***Physcomitrella patens*** (Figure 13) support this conclusion. Two novel transporter-like proteins increase dramatically with low temperature treatment, among other stresses, and increase the cellular tolerance to freezing stress (Takezawa & Minami 2004). It is likely that calmodulin is used by the cell to regulate these novel proteins, and that ABA serves to induce the expression of the necessary genes. However, in ***P. patens***, slow freezing to -4°C caused death of more than 90% of the protonema cells (Minami *et al*. 2003). ABA treatment for 24 hours caused a dramatic increase in the freezing tolerance of this plant, but cold treatment had little effect. This seems to contradict the earlier findings of Nagao *et al*. (2001). They found that both ABA and low temperatures caused an increase in gene expression with concomitant enhancement of freezing tolerance in ***Physcomitrella patens***. The LT_{50} dropped from -2ºC to -10ºC when the protonemata were grown in a medium with enhanced ABA (Nagao *et al*. 2005). It appears that ABA might be the agent needed to effect expression of the freeze-tolerance genes, but how much advance notice does it require?

Sugars and Plasmolysis

But it appears that ABA also is associated with the increase of soluble sugars in the protonemata of ***Physcomitrella patens*** (Figure 13) (Nagao *et al*. 2003). Such sugars increase freezing tolerance, most likely by depressing the freezing point.

Rütten and Santarius (1992b) found an increase in cold tolerance from summer to winter in the mosses ***Polytrichastrum formosum*** (Figure 56), ***Atrichum undulatum*** (Figure 57), ***Plagiomnium undulatum*** (Figure 61), ***P. affine*** (Figure 55), and ***Mnium hornum*** (Figure 58), and the thallose liverwort ***Pellia epiphylla*** (Figure 38). The frost resistance between summer and winter differed by more than 25ºC in some species, but ***Pellia epiphylla*** showed little hardening. Concomitant with this increase in frost tolerance, they found a rise in sucrose concentration (except in ***Mnium hornum***), and those mosses that were highly frost resistant had a total sugar concentration of 90-140 mM, 80% of which was sucrose. The mosses ***Brachythecium rutabulum*** (Figure 59) and ***Hypnum cupressiforme*** (Figure 60) were highly frost tolerant in summer and at that time had high sucrose levels. Furthermore, as sucrose levels declined during artificial exposure to higher temperatures, cold hardiness declined.

Figure 56. ***Polytrichastrum formosum***, a species that increases its frost tolerance from summer to winter. Photo by Michael Lüth, with permission.

Figure 57. ***Atrichum undulatum***, a species that increases its frost tolerance from summer to winter. Photo by Michael Lüth, with permission.

Figure 58. ***Mnium hornum***, a species that increases its cold tolerance from summer to winter. Photo by Michael Lüth, with permission.

Figure 59. ***Brachythecium rutabulum***, a species that is highly frost tolerant in summer. Photo by Michael Lüth, with permission.

Figure 60. ***Hypnum cupressiforme***, a species that is highly frost tolerant in summer. Photo by Michael Lüth, with permission.

Figure 61. ***Plagiomnium undulatum***, a species that increases its cold tolerance from summer to winter. Photo by Michael Lüth, with permission.

However, Rütten and Santarius (1993a) found that different levels of sucrose, glucose, and fructose at the cellular level had no bearing on the frost tolerance of leaves of ***Plagiomnium affine*** (Figure 55) and ***P. undulatum*** (Figure 61). Sucrose seemed to contribute in some way to the tolerance, increasing from summer to winter, while temperature limits increased from -10ºC in summer to less than -35ºC in winter, but there was no correlation between increased sugar content of shoots and frost resistance. They concluded that other factors were also necessary to the increased frost tolerance.

Studies on membrane permeability suggest that sugar uptake and release may be altered as mosses prepare for winter (Rütten & Santarius 1993b). Liu (2000) showed that as the temperature increased above 40ºC in these and other species, the membrane permeability increased. At the cold end of the scale, it appears that protection against an increase in membrane permeability may be a necessary step in cold hardiness. Greater retention of sugars could account for the higher concentrations in cold temperatures.

On the other hand, reversible plasmolysis can protect cells by permitting water loss and preventing crystal damage.

This relationship to membrane permeability is supported by studies on ***Physcomitrella patens*** (Figure 13) (Minami *et al*. 2003). Minami and coworkers subjected protonema cells to hyperosmotic concentrations of NaCl and mannitol, causing an increase in freezing tolerance. They interpreted this increase to indicate that ABA and cold stress trigger the expression of cryoprotectant genes. Oldenhof *et al*. (2006) suggested that sucrose might act as an osmotic spacer in membranes, while at the same time ABA mediates the synthesis of proteins, strengthening the cellular glasses. But we know that ABA can cause membranes to leak. Might there still be a more direct role for ABA than simply a trigger for genes, or is its usual role in membrane leakage one of triggering genes that cause this response?

Aro and Karunen (1988), in studying protonemata of ***Ceratodon purpureus*** (Figure 50), found that the content and unsaturated level of membrane lipids increased significantly in low growth temperatures, apparently contributing to frost hardiness. Hakala and Sewón (1992) found that both drought and low temperatures (6ºC) caused an increased incorporation of ^{14}C into the neutral lipid fraction and decreased its incorporation into the glycolipid fraction in ***Dicranum elongatum*** (Figure 62), suggesting a preferential accumulation of acetylenic triacylglycerols. Such responses, when adaptive, can permit the moss to prepare for the drought of winter through the signal of low temperature.

Figure 62. ***Dicranum elongatum***, a subarctic moss. Photo by Michael Lüth, with permission.

The protonema stage is often ignored in understanding the ecology and physiology of bryophytes. Yet if it is unable to reach a mature state of development and produce gametophores, the species will be greatly limited in its establishment survival. Nagao *et al*. (2006) demonstrated that like the leafy plant, the protonema responds to ABA application, increasing its freezing tolerance. This response includes the accumulation of low-molecular-weight soluble sugars, including **theanderose** (G6-α-glucosyl sucrose). This accumulation was inhibited by an inhibitor of nuclear-encoded protein synthesis (**cycloheximide**), resulting in a marked decrease in freezing tolerance. Theanderose is promoted by cold acclimation and by treatment with hyperosmotic solutes, both of which increase cellular freezing tolerance.

Freezing Longevity

Just how long can a bryophyte remain frozen and survive? In the Antarctic on Signy Island, ***Chorisodontium aciphyllum*** (Figure 63-Figure 64) and ***Polytrichum strictum*** (=*P. alpestre*; Figure 65) form a major part of the vegetation. Recently, Roads and Longton (2013) reported ***C. aciphyllum*** that was extracted from a core at 138 cm depth. This depth remains permanently frozen. There was no great surprise that regrowth occurred from specimens of ***C. aciphyllum*** retrieved from depths of 0-30 cm, but three new shoots grew from specimens extracted from 110 cm! And in addition the leafy liverwort ***Cephaloziella varians*** (Figure 66) regenerated new shoots from the muddy base of that core at 123-138 cm. Based on radiocarbon dating, these plants had been there ~1750 years and had been frozen a good portion of that time!

Figure 63. ***Chorisodontium aciphyllum*** in Antarctica, a species that apparently can remain viable in a frozen state for more than 1700 years! Photo from the Polar Institute through Creative Commons.

Figure 64. ***Chorisodontium aciphyllum***, a species that regenerated from a frozen state after more than 1700 years! Photo from the Jan-Peter Frahm, with permission.

Figure 65. ***Polytrichum strictum***, a major component of the Antarctic flora. Photo by Michael Lüth, with permission.

Figure 66. ***Cephaloziella varians***, a species that regenerated from 1750 year old cores in Antarctica, here nestled among **Polytrichaceae**. Photo by Kristian Peters, with permission.

Internal Cushion Temperatures

The internal temperatures in bryophyte cushions follow the ambient temperature until the cushion temperature drops below 0ºC and the water there begins to freeze (Rod Seppelt, Bryonet 27 June 2022). When the cushion begins to freeze, latent heat is released, elevating the cushion temperature ~2ºC. This slows freezing and provides more time for physiological processes to acclimate, including that of protein partial denaturing. These physiological modifications reduce tissue damage.

Freezing Effects

Freezing can have many consequences on cells of plants. In bryophytes, it can cause disorganization of the chloroplast lamellae, thus damaging the photosynthetic system (Pihakaski & Pihakaski 1979), damage the cell membranes, and cause desiccation and loss of solutes. In the thallose liverwort ***Pellia epiphylla*** (Figure 38) that had been chilled and hardened at -22°C, ultrastructural changes occurred. Vacuoles contained a fine granular substance in hardened tissues. Those that had only been chilled had large electron-dense particles embedded in a finer granular substance. The oil bodies changed, with abundant lipid-like bodies in the cytoplasm. These resembled the oil globules of oil bodies, with oily-looking flecks in the vacuoles. Large starch grains were present in the chloroplasts and the lamellar system lost some of its organization. Interestingly, the net photosynthesis was highest in material that had spent the longest time at -22°C.

Supercooling Intracellular Water

But what is it that permits plants to survive the sub-zero temperatures of winter? One of the first requirements for survival at below freezing temperatures is supercooling of intracellular water (George & Burke 1977). If the water in the cells were to freeze, ice crystals and expansion of water in its frozen state could cause mechanical damage to the cell. We can observe that many trees have as their northern limit the line where -40ºC is rarely reached. This is significant since the lower limit for supercooling of water is -41ºC (Kuiper 1978), and George and Burke (1977) have observed ice formation in xylem at -30 to -40ºC.

Ice Crystals Increase Solutes

Although ice crystals outside the cells can kill plants by desiccation, as in the case of the Florida orange trees, they can also be a means of "winterizing" cells by increasing internal solute concentrations. Molecules have vibrational energy. When an ice crystal forms, the vibrational energy is much reduced, creating an energy gradient between the liquid water molecules in the cell and the crystallized ones outside it (Marchand 1991). The result is that the more active liquid molecules migrate toward the area of less energy on the outside of the cell, adding to the mass of the crystals. Of course the result inside the cell is an increase in concentration of cytoplasmic solutes, thus lowering its freezing point, just as antifreeze does in a car battery. The process of protein denaturation, discussed below, causes the membranes to be leaky, facilitating this emigration of water. In many cells, there seems to be a second change as the temperature continues to decrease, and that change seems to correspond with cell death. One theory suggests that this may be accompanied by failure of water to leave the cell, resulting in internal crystallization and membrane destruction. Even in the absence of internal crystallization, cells still face another problem as the temperature decreases. As additional water is lost, irreversible dehydration may occur and toxic concentrations of solutes may accumulate (Weiser 1970).

Crystal Damage

It is the formation of crystals, not the low temperature itself, that damages cells irreparably, whether it is external crystals that cause dehydration and toxicity, or internal crystals that physically disrupt cell membranes (Schmitt *et al*. 1985). Therefore, another possibility exists for at least some plants to survive the cold, a process called **glass formation** (Marchand 1991). Glass formation results from **vitrification**, in which water solidifies without reorienting into a crystal (Figure 1). This process occurs when we immerse tissue in liquid nitrogen and thus permits us to preserve tissues without ice crystal damage. Balsam poplar trees are known to "form glass" at temperatures below -28°C (Hirsh *et al*. 1985). This means that the contents of

the cell are solid, thus preventing crystal damage, desiccation, and concentration of solutes to toxic levels.

Preventing Ice Crystals

Growers protect oranges by spraying non-nucleating bacteria on them, thus out-competing the bacteria that form the centers for ice crystals on the oranges. Some frogs make tiny proteins that become the centers of small crystals rather than large ones. And it appears that bryophytes and algae may also form special proteins that diminish crystal damage to cells.

One of the means by which plant cells are able to protect themselves from freeze damage is to modify or prevent ice crystals. Crystals form around tiny "nuclei" such as dust particles and bacteria. Being hygroscopic, these crystals grow by taking moisture from their surroundings, including cells. On the outside of the cell, they can desiccate a cell by extracting the water and binding it to the crystal. Inside the cell, they can not only desiccate the cell, but can also cause physical harm by protruding through a cell membrane.

In the Antarctic, Cyanobacteria, algae, and mosses form macromolecular substances that modify growing ice crystals, causing pitting of the crystals, and that cause them to go through an ice phase during freezing (Raymond & Fritsen 2000) – **glass formation** (Figure 67). One Antarctic species of ***Bryum*** (Figure 68) can modify these crystals by using this macromolecular substance to modify the shape of the growing crystals, and it may be that the mechanism of these macromolecules is to prevent recrystallization of ice (Raymond & Fritsen 2001). These substances are absent in temperate Cyanobacteria and mosses, but do occur in mosses from cold North American habitats. Their actual role is unknown, but their ability to be destroyed by temperatures of 45-65ºC suggests that they are protein. It is possible that they may be non-nucleating proteins that reduce crystal formation.

Figure 67. ***Hedwigia ciliata*** with glass formation (ice) on the surface rather than ice crystals. Photo by Michael Lüth, with permission.

Figure 68. ***Bryum cryophilum***, showing the red pigments common in polar regions. One species of ***Bryum*** can modify ice crystals, somehow reducing damage to the plant cells. Photo by Michael Lüth, with permission.

Rate of Freezing

The effectiveness with which these mechanisms can protect the cell are dependent upon the rate of freezing. White and Weiser (1964) found that leaves on the southwest side of a tree could drop in temperature by 9.5°C per minute across the freezing point of cell water at sunset! The result of this rapid freezing was cell death due to crystallization of water trapped inside the cell. Yet the same species was able to tolerate temperatures as low as -87°C when the temperature decreased slowly. Marchand (1991) contends that slow cooling of 10°C per hour is common in nature and permits time for the removal of water from cells by exterior crystal formation.

But what do all these tracheophyte scenarios mean for bryophytes? In 1912 Irmscher reported that at least some mosses were tolerant to desiccation and cold. Antropova (1974) found that temperatures above optimum for 3 hours did not affect cold resistance of moss cells, nor did temperatures within the optimum range influence either thermal stability or cold resistance. From these experiments he deduced that bryophytes respond similarly to tracheophytes but differently from algae to changes in temperature.

But the cooling process in bryophytes is different from that of tracheophytes (Dilks & Proctor 1975). If a tracheophyte cell is cooled rapidly, the cell contents freeze, and this usually causes fatal damage to the cell. However, the normal condition in nature is slow cooling. Because mosses and liverworts lack protective cells or thick, waxy cuticles, and are mostly one cell thick, this process is much more rapid. As the ambient temperature cools to below freezing, bryophyte cell contents will supercool and lose water to the surroundings, depending on the water-potential gradient. Levitt (1972) found that the injurious freezing rate for cell sections of tracheophytes is 60 times as rapid as for whole plants. Since bryophytes are much like a section of tracheophytes, they could experience a similar rapid freeze, one that could occur during a sudden drop in temperature, making bryophytes more vulnerable than tracheophytes. However, as water freezes outside bryophyte cells, the internal freezing point decreases due to loss of water and increasing concentration of cell sap (Dilks & Proctor 1975). And here tracheophytes have a disadvantage compared to bryophytes. Rather, they are

inhibited from water loss by a hydrophobic cuticle, and even if they accomplished this loss, their cells are more likely than those of bryophytes to be damaged by desiccation. Hence, cells high in water content and having little waxy cuticle for protection, like those of lettuce, turn to mush when frozen.

Among the bryophytes compared in Figure 69, the mosses ***Hookeria lucens*** (Figure 70) and ***Plagiothecium undulatum*** (Figure 71) are the most like wet filter paper, with a plateau in cellular cooling as the cell reaches the freezing temperature of water and water leaves the cell. The thallose liverwort (***Conocephalum conicum***, Figure 54), on the other hand, is more similar to the tracheophyte *Arbutus unedo* (Figure 72), with a slow decline in temperature below the freezing point of water.

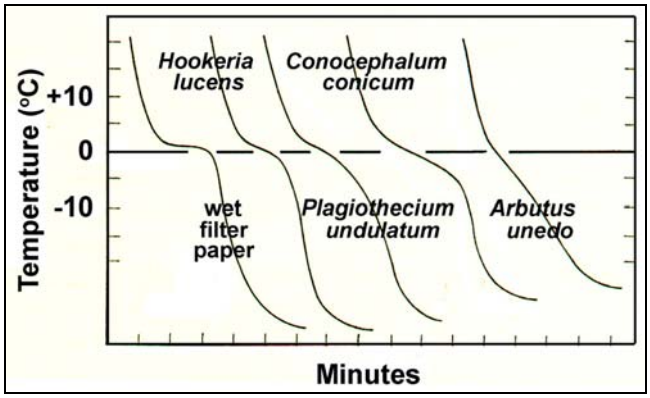

Figure 69. Temperature drop of bryophyte leaf cells compared to that of filter paper and a tree species (*Arbutus unedo* – the strawberry tree). Redrawn from Dilks and Proctor 1975.

Figure 70. ***Hookeria lucens***. Photo by Michael Lüth, with permission.

Figure 71. ***Plagiothecium undulatum***. Photo by Michael Lüth, with permission.

Figure 72. *Arbutus unedo* strawberry tree). Photo by Richie Steffen, courtesy Great Plant Picks, with online permission.

Hydration State

The state of hydration is an important consideration in the tolerance of bryophytes to temperature. It is well-known that they tolerate much higher temperatures in the dry state, but they also often tolerate lower temperatures in the dry state as well. This is predictable because of the danger of water forming crystals that can harm membranes.

Dilks and Proctor (1975) subjected nine moss species and one thallose liverwort species to sub-zero temperatures in a desiccator at 32% relative humidity. All survived to -30ºC in this dry state except the cushion moss ***Leucobryum glaucum*** (Figure 73) and leafy liverwort ***Plagiochila asplenioides*** (Figure 74) var. ***major***, both of which died in the desiccator with and without the cold treatment. In the wet state, however, of the 27 mosses tested, 20 had 50% or more death at -10ºC and lower. For three of the taxa (***Andreaea*** spp., Figure 75), the status could not be determined. ***Hylocomium splendens*** (Figure 76), ***Racomitrium aquaticum*** (Figure 77), ***R. lanuginosum*** (Figure 2), and ***Scorpiurium circinatum*** (Figure 78) survived to -10ºC. ***Hookeria lucens*** (Figure 71), ***Leucobryum glaucum*** (Figure 73), ***Mnium hornum*** (Figure 58), and ***Plagiopus oederianus*** (Figure 79) were dead or mostly dead at -5ºC. Among the liverworts, none of the thallose liverworts survived at -5ºC. Among the leafy liverworts, four species survived as well as the mosses, but two had more than 50% mortality at -5ºC. Only ***Plagiochila spinulosa*** (Figure 80) survived to -10º, with 50% survival. It is interesting that such epiphytes as ***Porella platyphylla*** (Figure 81) had poor survival when moist at -5ºC, because that leafy liverwort lives in northern habitats where it is likely to experience such conditions in the winter, but perhaps acclimation and physiological races differ.

Figure 73. ***Leucobryum glaucum***, a species that died in the desiccator (32% RH) in a cold treatment to -30°C. Photo by Janice Glime.

Figure 74. ***Plagiochila asplenioides***, a species that died in the desiccator (32% RH) in a cold treatment to -30°C. Photo by Michael Lüth, with permission.

Figure 75. ***Andreaea nivalis***. In experiments to -30°C and 32% RH, effects on three species in this genus were inconclusive. Photo by Michael Lüth, with permission.

Figure 76. ***Hylocomium splendens***, a species that survived to -10°C in the lab. Photo by Michael Lüth, with permission.

Figure 77. ***Racomitrium aquaticum***, a species that survived to -10°C in the lab. Photo by Michael Lüth, with permission.

Figure 78. ***Scorpiurium circinatum***, a species that survived to -10°C in the lab. Photo by Michael Lüth, with permission.

Figure 79. ***Plagiopus oederianus***. Photo by Michael Lüth, with permission.

These data suggest that mosses are more tolerant of wet cold than liverworts and that the thallose liverworts are the most vulnerable.

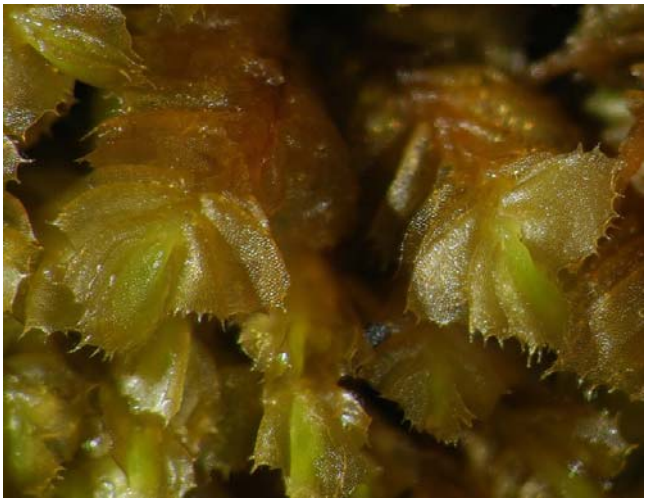

Figure 80. ***Plagiochila spinulosa*** in Scotland, a species with more than 50% survival at -10°C. Photo by Michael Lüth, with permission.

Figure 81. ***Porella platyphylla***, a species that has poor survival if moist at -5°C. Photo by Michael Lüth, with permission.

Lipids in Membranes and Protein Denaturation

We know that bryophytes are able to exist farther north (and south) than woody plants and yet lack the insulating effects of a thick layer of bark. Furthermore, the plasma membrane must remain intact if cellular nutrients and other solutes are to be contained upon thawing. As the temperature drops, the lipid matrix of a plasma membrane can crystallize, and the degree of crystallization depends upon the types of lipids. Saturated lipids crystallize first, with less saturated ones crystallizing at lower temperatures. The crystallization causes membrane proteins to aggregate, setting off a chain reaction. These aggregated proteins make possible the oxidation of sulfhydryl groups of the protein molecules because the close contact permits the formation of disulfide bridges (Levitt 1969). This denaturation of the membrane protein is irreversible and results in membrane destruction, often leading to cell death. It seems then that bryophytes must have some means to prevent this series of events from occurring.

Tracheophytes typically increase their lipid content in response to decreasing temperatures, resulting in winter hardiness. The lipids phosphatidyl choline and phosphatidyl ethanolamine in particular seem to contribute to increased resistance to cold (Kuiper 1970; Yoshida 1974; Siminovitch *et al*. 1975; De La Roche *et al*. 1972, 1975; Willemot 1975). The unsaturated fatty acid linolenic acid likewise seems to play a major role in reducing frost damage (Kuiper 1978).

Unsaturated Lipids

Gellerman and coworkers (1972) reported highly unsaturated lipids in several genera of bryophytes. When Al-Hasan and coworkers (1989) examined ***Bryum bicolor*** (Figure 82) to determine the effects of temperature on cold hardening, they found that the lipids of this species contained higher proportions of digalactosyldiacyl glycerols and sulfoquinovosyldiacyl glycerols when incubated at 5°C than when plants were incubated at 25°C. An interesting and seemingly non-adaptive aside is the greater production of linolenic acid under continuous illumination at 5°C, since low temperatures generally coincide with short days.

Figure 82. ***Bryum bicolor***, a species that has higher concentrations of digalactosyldiacyl glycerols and sulfoquinovosyldiacyl glycerols when incubated at 5°C than when incubated at 25°C. Photo by Michael Lüth, with permission.

Fatty Acid Alterations

One of the means by which organisms prepare for changes in temperature is to alter fatty acid components to those with lower solidification points. Lemmings change the fatty acids in their foot pads by eating bryophytes that contain lots of arachidonic acids, thus providing these tissues with cell membranes that are more pliable at low temperatures (Prins 1981). Meanwhile, the bryophytes are also preparing for winter in a different way.

The protonema of the common moss ***Ceratodon purpureus*** (Figure 50) prepares for winter by increasing its content and unsaturated level of membrane lipids (Aro & Karunen 1988). The galactolipids typically found in chloroplast membranes increased; phospholipids nearly doubled when plants were acclimated at 4ºC vs 20ºC. But this seems to have little effect on the frost hardiness. Rather, it permits these acclimated protonemata to retain a high phospholipid content. If, as is typical of unhardened protonemata, the phospholipids had been lost, that would have caused irreversible damage to CO_2 fixation following freezing and thawing. Aro and Karunen concluded that while the changes in membrane lipids were themselves not an important component of hardening, they were somehow involved in other factors that contributed to frost hardiness.

In ***Sphagnum fimbriatum*** (Figure 83-Figure 84), when the temperature decreases in the range of 5-15ºC, the amounts of linoleic, α linolenic, and arachidonic acids in their glycolipids [both monogalactosyldiacyl glycerols (MGDG) and digalactosyldiacyl glycerols (DGDG)] also decrease (Koskimies-Soininen & Nyberg 1991). These are replaced with increased proportions of palmitic, stearic, and oleic acids, especially in MGDG. However, if light intensity also decreases, as it would as winter approaches, this species exhibits an increase not only of palmitic and stearic acids, but also of linolenic and arachidonic acids, in MGDG, while oleic and α-linolenic acids decrease. But this pattern is certainly not universal. Even the related ***S. magellanicum*** (Figure 85) responds differently (Koskimies-Soininen & Nyberg 1987). It had its largest changes in fatty acid composition at lower temperatures (0-5ºC) and short photoperiods (3-6 hrs daylight). But, unlike ***S. fimbriatum***, in decreasing light and temperatures, ***S. magellanicum*** exhibited a decrease in linolenic acid.

Figure 83. ***Sphagnum fimbriatum*** frozen in its habitat. Photo by Dick Haaksma, with permission.

Figure 84. ***Sphagnum fimbriatum***, a species that decreases its concentrations of various fatty acids, including arachidonic acids, when the temperature decreases in the range of 5-15°C. Photo by Michael Lüth, with permission.

Figure 85. ***Sphagnum magellanicum***, a species that has its largest changes in fatty acids at 0-5°C. Photo by Michael Lüth, with permission.

There are indications that the fatty acid composition of bryophyte cells change as the temperatures do (Saruwatari *et al*. 1999). ***Marchantia polymorpha*** (Figure 42) exhibited changes in the percentages in linolenic acid, arachidonic acid, and eicosapentaenoic acid when the temperature was changed from 25°C to 15°C. Both linolenic acid and eicosapentaenoic acid increased greatly. However, the changes were not equal throughout the cell. Arachidonic acid and eicosapentaenoic acid increased in the chloroplast fraction but not in the rest of the cell, while the level of linolenic acid was increased in both fractions. We need to understand this in the context of the high levels of arachidonic acids known in bryophytes and the suggestion that some animals eat bryophytes to prepare for winter because of these high levels. Prins (1982) has proposed that they provide more fluid fat pads for animals that run around on frozen ground in winter.

One study on lichens might help us predict the way in which bryophytes could respond (Dertien *et al*. 1977). In forested areas, both bryophytes and lichens can be found on tree trunks as well as on the forest floor and in open soil areas. In their study of lichens, Dertien and coworkers (1977) found that lichens of tree trunks contained high levels of the unsaturated linoleic and linolenic acids; however, nearby sand dune species had large quantities of cyclic acids rather than unsaturated acids. This may relate

to the greater likelihood of low temperatures on the tree trunks.

Fatty Acids and N

Using ***Ctenidium molluscum*** (Figure 86), ***Pogonatum urnigerum*** (Figure 87), ***Dichodontium pellucidum*** (Figure 88), and ***Tortella tortuosa*** (Figure 89), Al-Hasan *et al*. (1991) demonstrated that increasing the nitrogen concentration of the medium causes a decrease in the dominant unsaturated fatty acids arachidonic acid (in ***C. molluscum***), eicosatrienic acid (in ***P. urnigerum***), and linoleic acid (***D. pellucidum***, ***T. tortuosa***). Nitrogen availability generally decreases as the growing season progresses in forests, so it is possible that such a decrease could serve as a signal for mosses to store more unsaturated fatty acids. Arachidonic acid and eicosapentaenoic acid are widespread in mosses (Hansen & Rossi 1990), but arachidonic acid never occurs in angiosperms (Karunen 1990).

Figure 86. ***Ctenidium molluscum*** in a rock canyon in Europe. This species seems to switch to more unsaturated fatty acids when N concentrations decrease at the end of the growing season. Photo by Michael Lüth, with permission.

Figure 87. ***Pogonatum urnigerum***, a species that seems to switch to more unsaturated fatty acids when N concentrations decrease at the end of the growing season. Photo by Janice Glime.

Figure 88. ***Dichodontium pellucidum***, a species that seems to switch to more unsaturated fatty acids when N concentrations decrease at the end of the growing season. Photo by Michael Lüth, with permission.

Figure 89. ***Tortella tortuosa***, a species that seems to switch to more unsaturated fatty acids when N concentrations decrease at the end of the growing season. Photo by Michael Lüth, with permission.

Triglycerides

The role of triglycerides in low temperature survival seems yet to be explored. Karunen (1981) found that in the subarctic moss ***Dicranum elongatum*** (Figure 62) triglycerides commonly increased only at low temperatures of 1-6°C. But what might they do for frost hardiness?

Polyribosomes

In the desiccation-tolerant moss ***Syntrichia ruralis*** (Figure 48-Figure 49), temperatures down to 2ºC cause a proliferation of polyribosomes, accompanied by a decrease in single ribosomes (Malek & Bewley 1978). The number of ribosomal subunits does not change. Mosses that have not been desiccated exhibit leucine uptake and were able to synthesize protein at 2° and -2.5°C. However, slowly dried mosses do not contain polyribosomes and instead reform them upon rehydration. There seems to be no change in the

rate of protein synthesis in mosses kept at cold temperatures (2ºC) or winter collected. Rather, the moss appears to be pre-acclimated or pre-adapted to freezing year-round. Malek and Bewley concluded that this moss does not have any seasonal cold hardening.

Age Difference to Freezing

Hudson and Brustkern (1965) found that old and young leaves of mosses may differ in their responses to sub-zero temperatures. They found that ***Plagiomnium undulatum*** (Figure 61) mature leaves experienced extracellular freezing when cooled slowly, thus preventing intracellular freezing. Young shoots, on the other hand, could not tolerate temperatures below 12°C. When subjected to freezing temperatures, young leaves of ***P. undulatum*** do not experience extracellular ice formation, thus making intracellular freezing more likely. Rütten and Santarius (1992a) found that not only young leaves, but also old leaves of ***Plagiomnium***, had much less frost tolerance than mature leaves.

Freezing Effect on Distribution and Niche

Green *et al*. (2007) reported that freeze-thaw cycles are extremely common in parts of Antarctica, with up to 110 occurring in a single year in the northern maritime. Some lichens adapt to this by growing in the pores of rocks, so we should look for bryophytes that have similar safety mechanisms.

The ability to survive freezing will influence both geographic and habitat distribution of bryophytes. Shirasaki (1984) found that ***Bryoxiphium norvegicum*** (Figure 90) subsp. ***japonicum*** is distributed in southern Japan at altitudes of 80 m to 2350 m, whereas further north the upper limit declines. Although this species occurs in areas where there is deep snow for a long period of time, it lives mostly on the vertical faces of overhanging rocks in ravines where it is not likely to be covered directly by snow. However, it is positioned where the overhanging soil and snow protect it from the cold wind.

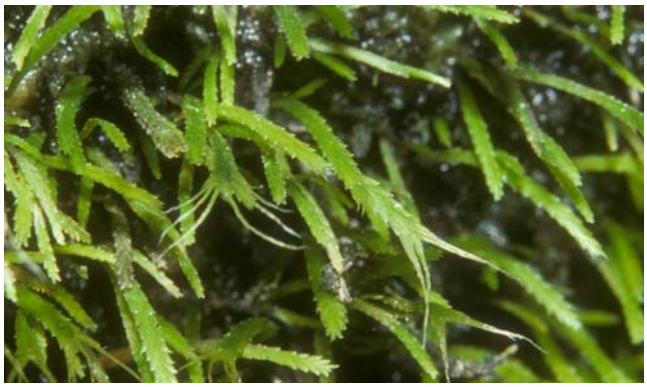

Figure 90. ***Bryoxiphium norvegicum*** growing on a rock face. Some varieties of this species are able to grow at high elevations. Photo by Janice Glime.

Shirasaki (1987) also found that the distributions of the leafy liverworts ***Bazzania trilobata*** (Figure 91) and ***B. yoshinagana*** (Figure 92) in Japan seem to relate to differences in cold and related desiccation tolerance. ***Bazzania trilobata*** grows on soil that receives sunshine and good drainage. It is able to survive in areas with little snow where early spring subjects it to severe cold and desiccation. By contrast, ***B. yoshinagana*** lives primarily on the floor of dense conifer forests where deep snow covers it all winter, thus maintaining moisture and insulating it from the sub-freezing air.

Figure 91. ***Bazzania trilobata***, a species that grows in areas that have little snow where early spring subjects it to severe cold and desiccation. Photo by Michael Lüth, with permission.

Figure 92. ***Bazzania yoshinagana***, a species is covered by deep snow all winter. Photo by Real thing X 0.3. The copyright of the photograph of this site belongs to the author. Please reprint without permission.

As was seen for ***Fontinalis*** (Figure 123-Figure 124) species in the previous subchapter on temperature, adaptation to cold can be a contributing difference between species, permitting them to live where they do. It seemed that for centuries we concentrated on morphological differences between species and attempted to see their geographic separations in that perspective. However, physiological differences are much more likely to determine where plants live than are their morphological differences. In some cases, morphology can cause

physiological differences, such as growth forms that alter temperature, but we should not stop there in our quest for niche delineation.

A good demonstration of these physiological differences is seen in the genus ***Sphagnum***. In their study of five species, Balagurova *et al*. (1996) found that the photosynthetic leaf cells of ***Sphagnum balticum*** (Figure 93), ***S. subsecundum*** (Figure 94), and ***S. teres*** (Figure 95) were more frost-resistant than were those of ***S. magellanicum*** (Figure 85) and ***S. fuscum*** (Figure 96).

Figure 93. ***Sphagnum balticum***, a species that is more frost-resistant than the hummock species ***S. magellanicum*** and ***S. fuscum***. Photo by Michael Lüth, with permission.

Figure 94. ***Sphagnum subsecundum***, a species that is more frost-resistant than the hummock species ***S. magellanicum*** and ***S. fuscum***. Photo by Michael Lüth, with permission.

Figure 95. ***Sphagnum teres***, a species that is more frost-resistant than the hummock species ***S. magellanicum*** and ***S. fuscum***. Photo by Michael Lüth, with permission.

Figure 96. ***Sphagnum fuscum***, a hummock species that is somewhat frost-sensitive. Photo courtesy of Andres Baron Lopez.

For the sunny species of ***Sphagnum magellanicum*** (Figure 85) and ***S. papillosum*** (Figure 97), short days induce dormancy and long days induce growth (Li & Glime 1990; Gerdol 1995). This corresponds well to their optimum growth temperature of 30-35°C, a high optimum for bryophytes. Nevertheless, ***Sphagnum magellanicum*** can grow actively whenever it has sufficient moisture and the nighttime temperature exceeds 0°C (Gerdol 1996). It appears that nighttime temperature can be critical to the growth of ***Sphagnum*** species. ***Sphagnum capillifolium*** (Figure 24) suffered a five-fold reduction in growth at low nighttime temperatures (Gerdol *et al*. 1998). There seemed to be no alteration in photosynthetic pigments or pigment ratios, but rather enzymatic reactions were limited at low temperatures.

Figure 97. ***Sphagnum magellanicum*** (**red**) and ***S. papillosum*** (**olive-green**) growing together on a sunny hummock. Those on the right are wet and on the left they are dry. Photo by Janice Glime.

Regulation of Mammal Reproduction?

There is interesting evidence that some plants stimulate reproductive activity in small mammals that eat them by providing to them their own growth substances. Gibberellic acid, common in germinating seeds, and 6-methoxybenzoxazolinone (6-MBOA, a glycoside derivative) have such an effect. Is it possible that bryophytes, developing under the snow, provide a source of

green food to small mammals, such as voles and lemmings, under the snow pack and help to regulate their reproductive cycle?

Overwintering under Snow

Snow affords great protection from the ravages of winter, and we might have a very different polar and boreal flora without it. Flock (1978) found that it was the areas with deep, late-season snow where bryophytes reached their highest species indices on the Niwot Ridge of Colorado, USA, an alpine area. An interesting separation of acrocarpous and pleurocarpous mosses occurred, with acrocarpous mosses being the most abundant ones in the dry areas that had only a light snow cover. Pleurocarpous mosses were nearly restricted to the wet sites with deep snow, where they outnumbered the acrocarpous taxa. Only ***Hypnum vaucheri*** (Figure 98-Figure 99), ***H. revolutum*** (Figure 100), and ***Abietinella abietinum*** (Figure 101) among the pleurocarpous mosses ventured into the dry areas with little snow. Lichens dominated the rocks. Liverworts were rare. This distribution may be more one of moisture needs than of temperature, but at least the possibility exists for some mosses to enjoy the greater protection from extreme cold when most of the area may be free of snow.

Figure 98. ***Hypnum vaucheri*** habitat in Averstal Graubünden, a species that survives winter in areas with little snow. Photo by Michael Lüth, with permission.

Figure 99. ***Hypnum vaucheri*** in Norway. Photo by Michael Lüth, with permission.

Figure 100. ***Hypnum revolutum***, a species that is able to survive in cold but dry areas with little snow. Photo by Michael Lüth, with permission.

On the other hand, snow cover can be a detriment when the growing season is short, preventing sufficient productivity to complete a life cycle. In the Antarctic, Pannewitz *et al*. (2003a) found that indeed the snow cover was a good insulator, but late-lying snow retained the winter cold that kept the bryophytes inactive long after the ambient air temperature was warm enough for activity. Unlike some north temperate areas where the sub-surface soil may be 10ºC in the winter (Jiquan Chen, University of Toledo, unpublished data), temperatures under the Antarctic snow were typically less than -10ºC while snowmelt was complete in surrounding areas.

Figure 101. ***Abietinella abietina***. Photo by Michael Lüth, with permission.

Snow Temperatures

In the temperate and boreal zones, winter cold and snow can play a major role in ecosystem behavior. Snow cover can be an essential factor in protecting plants from severe cold and wind, while in many cases providing a steady stream of water and nutrients to the soil. Soil temperatures at 5 cm beneath the surface under deep snow in Houghton, Michigan, USA, can remain above freezing for an entire winter while air temperatures plummet to -10ºC or lower (Jiquan Chen, University of Toledo, unpublished data). Longton (1979) reported temperatures at the moss level (***Polytrichum strictum***; Figure 65) at Pinawa, Manitoba, Canada, to remain between 0° and -10°C under the winter snow, but in summer sun the diurnal temperatures fluctuated widely. The mosses clearly ameliorate the temperature in spring and autumn, with

fewer freeze-thaw cycles and higher minimum temperatures at moss levels than at 200 cm above the ground.

We have mostly ignored winter ecology in bryophytes. Do they photosynthesize under the snow? How will they respond to shorter winters as the climate warms? Are any or all of them dormant in cold winters? What is the effect of snow depth on their physiological behavior?

Pannewitz *et al*. (2003a) found that it was possible to measure photosynthetic activity of lichens under undisturbed snow. The snow cover provides a good insulator for both lichens and mosses. But this insulation works at both warming and cooling temperatures. These lichens were inactive at subzero temperatures, even when the air temperatures had warmed enough to allow metabolic activity. For lichens, the maximum activity occurred during the 10-14 days following the final disappearance of the snow. But some species were activated at temperatures below -10ºC when water became available from the high air humidity. Similar accounts of bryophyte responses are largely lacking in most winter ecosystems.

Nutrients from Snow

Inputs and losses of soil nutrients change as temperatures slow processes and snow melt leaches nutrients from collected dust. During January to March, nitrate export can increase from 0 to 1 kg ha^{-1} as the temperature increases from -10 to -3ºC (Park *et al.* 2004 in Campbell *et al.* 2005).

These processes will certainly affect the mosses, positioned at the interface between snow and soil. In her studies on ***Sphagnum russowii*** (Figure 102) in a Jack pine forest (*Pinus banksiana*), Scafone (unpubl) found that the mosses were frozen in a block of ice under the snow as the melt season began in April. But is this the case all winter? Do the mosses receive nutrients that trickle through the snow, trapping them and sequestering them for an early spring surge of growth? Or do they remain frozen until after the snow is gone, facilitating the movement of nutrients past them to breaks in the ice-covered moss carpet? Figure 103 suggests that they don't. How little we know of their winter ecology!

Figure 102. ***Sphagnum russowii***, a species that can freeze in a block of ice and survive. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 103. ***Racomitrium lanuginosum*** emerges from the snow unfrozen and in good health. Photo by Michael Lüth, with permission.

Epiphytes

Mosses in the North Temperate Zone seem to appear in the spring in a much fresher condition than they were in the previous fall, and some of them seem to be further developed. Our data on epiphytes in Keweenaw County, Michigan, USA, suggest that perhaps winter affords them an opportunity to grow in a moist, light environment, protected from winter winds (Trynoski & Glime 1982). We suggested this possibility because, contrary to the popular misconception, the mosses were more abundant on the south side of the trees at 1 m above the ground. In Keweenaw County, the winds come predominately from the north and northwest, bringing desiccation to mosses on that side of the tree. Of course, the south side of the tree is subject to the drying heat of the sun in the summer, but only if the canopy allows it to pass. Our conjecture is that in winter the deep snow (1 m or more) provides a haven. Snow cover does not hug a tree all the way to the surface of the snow. Instead, it forms **tree wells**, where snow is separated from the tree trunk by a small funnel of air, caused at least in part by the reradiation of heat from the dark trunk of the tree (Figure 104). Within this funnel, there is little air movement, and if our theory about the reradiation is correct, the temperature must be near melting, *i.e.* 0°C. Under such conditions, we would assume that the funnel must be moist in winter, at least on sunny days. On the south side of the tree, the temperature would be higher, causing more hours of moist air and above freezing temperatures. Furthermore, sun penetration through the snow should provide ample light at this low temperature. Under such circumstances, we conjecture that mosses could achieve a slow but steady growth during 4-5 months of winter.

Figure 104. Tree well at the base of ***Acer platanoides***. Although the snow has melted considerably, this shows the funnel that can form. Photo by Janice Glime.

As we pondered the tree funnels, we also considered that mosses on rocks and soil under the snow probably receive a relatively steady moisture supply, ample light, and a 0°C temperature, permitting the cold-adapted ones to achieve photosynthesis, little respiratory loss, and some level of growth during at least part of the winter. This raises the interesting question as to what role the snow on the side of a tree trunk might play in the distribution of mosses, providing moisture and light for growth in winter and probably occurring on the side that receives the most direct rain in summer, assuming the prevailing wind direction does not change seasonally. But how much, if any, light penetrates several feet of snow?

Light through Snow

Fortunately, Marchand (1993) has provided proof that many of our theories about snow are possible. He was trying to explain how voles managed to be reproductively active just 10 weeks before the snow melted, and when the snow pack was deeper, they delayed their reproductive activity, again being active just 10 weeks before the snow melt, which occurred a full month later. Assuming they had no more ability to see into the future than do we, he began taking measurements under the snow. Some startling facts were discovered (although, I suspect some physicists would not be surprised).

As expected, the more dense the snow at a given depth, the less light penetrated. However, what Marchand did not predict was that as the snow melted and filled in the spaces between the snow crystals, the light penetration increased. (See transparency in Figure 1). Hence, the voles could use light intensity as an indicator of the coming of clear ground, and our bryophytes could carry out photosynthesis and grow or develop well before the snow was gone in the spring.

He found that any combination of depth:density that was greater than 200 gave maximum thermal protection, resulting in a near 0°C temperature under the snow. Thus, 20 cm of snow with a density of 0.1 g cm^{-3} (very fresh snowfall) would completely buffer most temperature fluctuations. When the density increases to 0.2 g cm^{-3}, twice as much snow is required for the same thermal protection. This means that additional snowfall can ameliorate the lowered temperature effects of increasing density of compacted older snow.

But what of light? Marchand knew that only a small amount of light, principally in the blue and blue-green range (Figure 105), could penetrate the deep snow pack. Under only 3-4 mm of older, crystalline snow, no infra-red radiation penetrates (Gates 1962).

Photosynthesis is greatest in the red range, with a smaller second peak in the blue range. When the snow density reaches 0.3 - 0.4 g cm^{-3}, typical of the upper part of the snow pack in late winter, only 2 - 3% of the surface light reaches a depth of 15 cm. When Marchand's group compacted the snow as much as they could, attaining a density of 0.5 g cm^{-3}, the light penetration was nearly zero. That seemed to be the critical density – the density possible by compaction alone. It was following that experiment when they discovered that melting snow actually increased in transmission of light. Instead of refracted, scattered light passing through tiny ice grains, the light was now passing through larger, fused grains that caused much less scattering and absorption. Although less than 0.1% of incident light seems to reach the ground from late December to early April when the snow depth is greater than 40 cm and density > 0.25 g cm^{-3}, the late season snow provides an insulating source of water as it melts, increasing the transmission of light.

Figure 105. Ice cave at Athabasca Glacier, Jasper, British Columbia, Canada, demonstrating the blue-green color of light penetrating ice. Photo by Janice Glime.

Late Snowbeds

Unique communities of bryophytes occur adjacent to summer snowfields, taking advantage of the cooler temperatures and most likely greater moisture. In such cool habitats, one might find red mosses that increase their leaf temperatures by absorbing the light rays and reradiating them as heat. These mosses might have their lower parts in meltwater at 0ºC while their growing tips are much warmer in the rays of the sun with this "red body" heating. Such mosses include ***Andreaea nivalis*** (Figure 106), ***Bryum muehlenbeckii*** (Figure 107), and ***Racomitrium sudeticum*** (Figure 108) (Bailey 1933; Belland 1983). Others are white, perhaps being protected from the bright light reflecting from the nearby snow, while

being subjected to temperatures that do not allow rapid use of excited electrons among the chlorophyll antenna pigments (see Figure 2 of ***Racomitrium lanuginosum*** for an example). The genus that once was ***Webera***, and now most likely is ***Pohlia*** (Figure 109-Figure 110), seems to have several species that thrive in this unique habitat (Bailey 1933; Woolgrove & Woodin 1994). Bailey comments that in the Cascade Range, Washington, USA, all of these taxa are acrocarpous. Only ***Isopterygiopsis pulchella*** (Figure 111) among these is a pleurocarpous moss.

Figure 106. ***Andreaea nivalis***, illustrating the red color of this arctic/alpine species. Photo by Michael Lüth, with permission.

Figure 107. ***Bryum muehlenbeckii***, a species that uses "red body" heating in the sun. Photo by Michael Lüth, with permission.

Figure 108. ***Racomitrium sudeticum***, a species that uses "red body" heating in the sun. Photo by Michael Lüth, with permission.

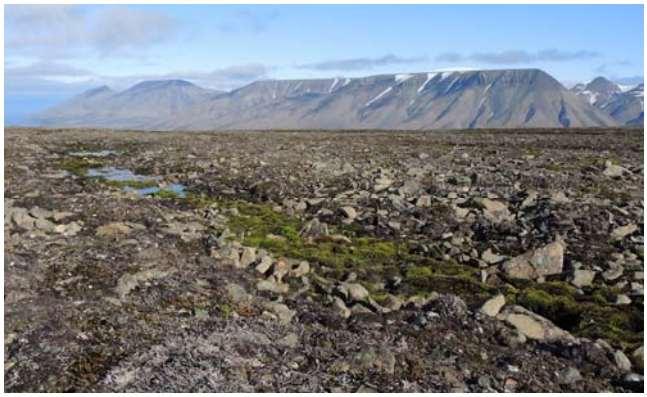

Figure 109. ***Pohlia ludwigii***, a late snowbed bryophyte. Photo by Michael Lüth, with permission.

Figure 110. ***Pohlia ludwigii***, a late snowbed bryophyte. Photo by Michael Lüth, with permission.

Lösch *et al*. (1983) reported that only the top 4 mm of the late snowbed liverwort ***Anthelia juratzkana*** (Figure 112-Figure 113) has enough chlorophyll to be capable of net gain in photosynthesis. This species reaches its low temperature compensation point at -4°C. It easily sustains life in 9 months of darkness, cold, and wetness. However, its respiration rate increases, causing the net photosynthetic rate to decrease following snow melt. In ***Polytrichum sexangulare*** (Figure 114-Figure 115), also a snowbed moss, the low temperature compensation point is -5°C. However, this species did not tolerate being wet and cold in

the dark for so long. Both species survive in these snowbed communities because of their ability to use low light intensities at low temperatures (optimum of 6-11°C). ***Anthelia juratzkana*** is able to grow at the edge of snowbanks at very cold temperatures. ***Polytrichum sexangulare*** succeeds because of its more rapid growth rate, permitting it to outcompete the seed plants. But this evades the question, how do these bryophytes survive the alternating warm and freezing temperatures at the edge of the snowbeds, or do they?

Figure 111. ***Isopterygiopsis pulchella***, a late snowbed pleurocarpous moss. Photo by Michael Lüth, with permission.

Figure 112. ***Anthelia juratzkana*** in a recently melted late snowbed. Photo by Michael Lüth, with permission.

Figure 113. ***Anthelia juratzkana***, a late snowbed leafy liverwort that reaches its low temperature compensation point at -4°C and is able to exhibit growth at the edge of a snowbed. Photo by Michael Lüth, with permission.

Figure 114. ***Polytrichum sexangulare*** with capsules, a late snowbed species. Photo by Michael Lüth, with permission.

Figure 115. ***Polytrichum sexangulare***, a species that grows rapidly, permitting it to outcompete other species. Photo by Michael Lüth, with permission.

Acclimation and Adaptation

Could the Antarctic climate be so severe that the bryophytes are always ready? Melick and Seppelt (1994) found little or no change in soluble carbohydrate levels. However, as already noted, both chlorophyll and carotenoids did respond to seasons. But are bryophytes elsewhere ready both to remain dormant when conditions are too cold and to grow during periods that are warm enough?

Winter Growth

I have long suspected that a number of bryophyte species are able to grow in cold winter months, perhaps even under the snow. For example, mosses like ***Brachythecium rutabulum*** (Figure 59) have better growth at temperatures below 18°C in winter collections than those from summer collections (Furness & Grime 1982).

In a study of 40 bryophyte species in Europe, Furness and Grime (1982) found that most species had an optimum growth temperature of 15°-25°C. Nevertheless, many species continued to grow at temperatures less than 10°C.

Winter Warming Events

What happens to a frozen moss when those sunny days take its temperature above freezing? We know that tracheophytes can be severely damaged when "spring

comes early" and then winter returns. Buds may begin to open, then the tender young leaves killed when frost returns. This expensive energy loss uses stored resources and cannot be tolerated frequently. But what happens to bryophytes under these same circumstances?

Bjerke *et al*. (2011) simulated such events in a sub-Arctic heath using infrared heat lamps and soil warming cables. Among the dominant cryptogamic flora, they subjected the boreal moss ***Hylocomium splendens*** (Figure 76) to such warming events for three consecutive winters. Unlike the lichen ***Peltigera aphthosa*** (Figure 116), ***H. splendens*** exhibited a significant decrease in summertime net photosynthesis (up to 48%) and growth rate (up to 52%). The lichen does not have seasonal life cycle stages, but ***H. splendens*** has seasonal stages when it produces new branches and leaves. The most critical of these responding to winter warm periods is the initiation of growth. These young shoots are vulnerable if the cold period returns shortly thereafter. Such winter warm periods have been experienced in areas such as my home in the Keweenaw Peninsula of Michigan and are likely to increase in frequency as the global climate changes.

Figure 116. ***Peltigera aphthosa***, a lichen that lacks a seasonal life cycle. Photo by Steven K. Sullivan, through Creative Commons.

Snowbed bryophytes are not likely to experience winter melt, but in the spring the bryophytes at the edge of the snowbed may experience alternating warming and freezing periods. We have seen above that late snowbed bryophytes like ***Anthelia juratzkana*** (Figure 112-Figure 113) and ***Polytrichum sexangulare*** (Figure 114-Figure 115) survive the short growing season and long period of snow cover because of their ability to have a net photosynthetic gain in low light at low temperatures (Lösch *et al*. 1983). But how do these bryophytes, especially ***A. juratzkana***, fare at the edge of the snowbed if it melts, then freezes again? Our knowledge of bryophytes in winter, and especially when experiencing intermittent warming, is extremely meager.

Pigments and Color Changes

One protection against high light intensity is development of red pigments (Quinn 2008). Just as high elevation mosses may be red, like those discussed as living in late snowbeds, and snow algae such as *Chlamydomonas nivalis* (Figure 117), are red, some bryophytes produce red pigments to provide protection against UV radiation and may even receive an added bonus of warmer daytime temperatures due to color. Anthocyanins, known in both bryophytes and tracheophytes, convert light to heat; this is especially important in the cooler days at the beginning and end of the growing season (Quinn 2008).

Several species of ***Sphagnum*** (Figure 102) have this color response, wherein cold temperatures induce production of the red cell wall pigment **sphagnorubin**, a flavonoid (Tutschek 1982).

Figure 117. Pink snow caused by the alga ***Chlamydomonas nivalis*** in the Arctic. Photo through Creative Commons.

Bendz *et al*. (1962) pointed out that the color of a bryophyte can vary widely, depending on solar radiation and nutrient availability. These red pigments appear to be anthocyanins. ***Bryum cryophilum*** (Figure 68) exhibits deep red color in the Arctic along stream borders. These proved to be anthocyanins in the cytoplasm. Red cell wall pigments occur in ***Sphagnum magellanicum*** (Figure 85) and ***S. capillifolium*** (***S. nemoreum***; Figure 24). Likewise, ***Warnstorfia pseudosarmentosa*** has red anthocyanin cell wall pigments. One of its pigments chemically resembles those of ***B. cryophilum*** and the other resembles those of the two aforementioned ***Sphagnum*** species.

In the Antarctic, Post and Vesk (1992) found that the leafy liverwort ***Cephaloziella exiliflora*** (Figure 46) was green in shaded sites and dark purple in sunny locations. this red color was due to an anthocyanin-like pigment bound in the chick cell walls of the sun plants. These plants grew in dense turfs and their leaves were larger and more closely spaced, most likely increasing moisture-holding capacity and reducing sun damage. It is interesting that the chlorophyll *a*/*b* ratio did not vary, but the green shade plants had more chlorophyll per unit weight.

Charlie Campbell (Bryonet 12 December 2013) found that the red ***Sphagnum magellanicum*** (Figure 85) was more photosynthetically active after freezing than the yellow-brown ***S. papillosum*** (Figure 97). Others (Quinn 2008) have reported that more highly colored species live in colder mountainous regions, compared to those close to the sea. Other color changes are noted in response to sun. ***Hypnum imponens*** (Figure 118-Figure 120) and ***Thuidium delicatulum*** (Figure 121-Figure 122) definitely change from medium green (Figure 119, Figure 121) to yellow-green or vivid yellow tones (Figure 120, Figure 122) when exposed to more sunlight (Annie Martin, Bryonet 12 December 2013).

Figure 118. ***Hypnum imponens*** in forest showing green color. Photo by Janice Glime.

Figure 119. ***Hypnum imponens*** from forest showing light green color. Photo by Janice Glime.

Figure 120. ***Hypnum imponens*** showing typical golden sun colors. Photo by Michael Lüth, with permission.

Figure 121. ***Thuidium delicatulum*** in shaded location at Hocking Hills Ohio, USA. Photo by Janice Glime.

Figure 122. ***Thuidium delicatulum*** showing golden color indicative of a sunny location. Photo by David Holyoak, with permission.

In ***Sphagnum capillifolium*** (Figure 24), Gerdol *et al*. (1998) found no trigger for the formation of red wall pigments when nighttime temperatures were 5°C and above

One principle to keep in mind in this discussion is that being cold and in bright light at the same time is a problem for plants, especially bryophytes. The light excites the chlorophyll electrons, but the cold temperature slows down the physiological processes. Hence, pigments that absorb some of that light energy can help to protect the chlorophyll from damage. These should not be part of the chlorophyll antenna system because that would transfer even more energy to the chlorophyll. Rather, they can be cytoplasmic or cell wall pigments. In the chapter on light, I have already discussed the reaction of ***Fontinalis antipyretica*** (Figure 123-Figure 124) in cold water exiting an underground stream into full sunlight. The moss was crimson!

Exposure to UV-B radiation is often the trigger for higher levels of pigmentation (Robinson *et al*. 2005). However, the Antarctic species ***Schistidium antarctici*** (Figure 43) did not increase UV-B absorbing pigmentation under higher UV-B radiation, unlike many other species in the Antarctic.

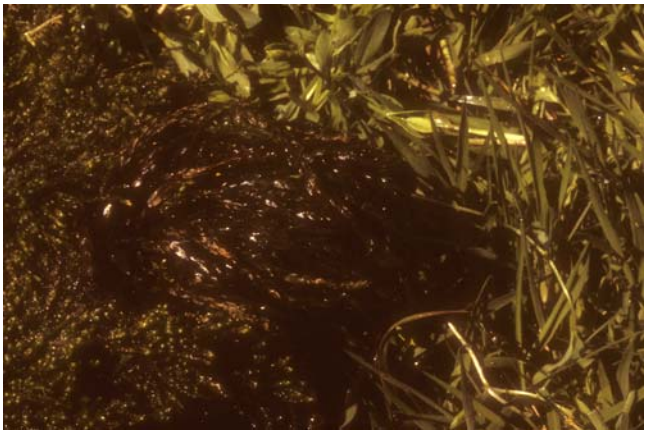

Figure 123. ***Fontinalis antipyretica*** exhibiting red color from the stress of high light levels and cold temperatures. Photo by Janice Glime.

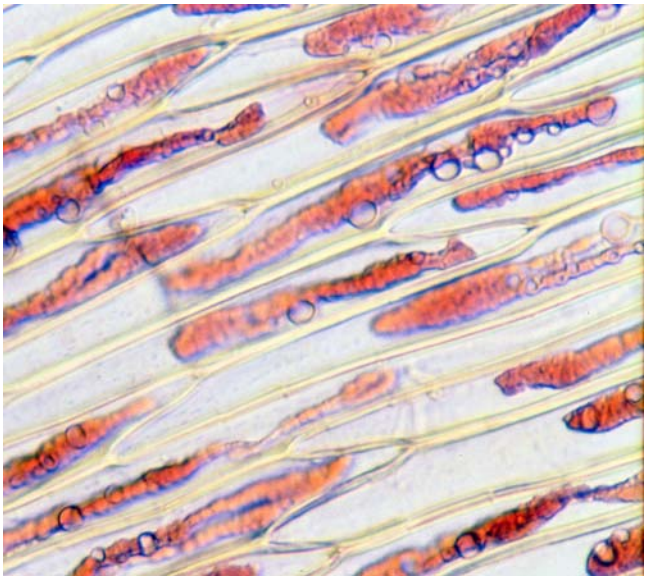

Figure 124. ***Fontinalis antipyretica*** red cells that result from stress. Photo by Janice Glime.

Dunn and Robinson (2006) suggest that ***Bryum pseudotriquetrum*** (Figure 44-Figure 45) will have an advantage over other species under conditions of high UV-B radiation that occurs with low temperatures. This will be mediated in ***B. pseudotriquetrum*** by the presence of UV-B absorbing and anthocyanin pigments that limit physiological activity during periods of low temperatures and desiccation, but also limiting photoprotective and repair mechanisms.

In the same study (Dunn & Robinson 2006), ***Ceratodon purpureus*** (Figure 50) is intermediate among the three species studied. Rather than responding to high levels of UV-B, it has a stable, constitutive concentration of UV-B- absorbing pigments. However, the anthocyanin pigments in this species were more responsive than those of ***Bryum pseudotriquetrum*** (Figure 44-Figure 45), most likely providing antioxidant protection during periods of high UV-B radiation (Turnbull & Robinson 2009). ***Bryum pseudotriquetrum*** did decrease the accumulation of photosynthetic product as the temperature rose. Of the three species, ***Schistidium antarctici*** (Figure 43) presents the least protection and seems to have no UV-B protective response (Dunn & Robinson 2006).

In a different Antarctic study, Melick and Seppelt (1994) found that pigment levels varied seasonally. Total chlorophyll and the chlorophyll *a*/*b* ratio dropped during winter. Carotenoids increased in the summer, presumably responding to the higher light intensity.

Summary

The optimum growth temperature for most bryophytes lies between 15 and 25ºC, but it can go much lower in habitats that remain cold for most of the year. The lowest extreme for photosynthesis appears to be about -15ºC and the uppermost around 40-45ºC. However, it is unlikely that there would be a sustained photosynthetic gain at these higher temperatures.

Snow provides insulation and may serve as a source of nutrients and moisture during the winter. Acrocarpous mosses seem more able to tolerate dry areas with only light snow cover, whereas pleurocarpous mosses are more common on wet sites with deep, long-lasting snow. Some epiphytes may benefit from the moist, protected funnels of air between the snow and tree trunk. Light quality is altered through the snow to principally blue and blue-green and diminishes rapidly from the surface.

Bryophytes near late snowbeds remain cold from melt water while experiencing high light intensities and, like bryophytes from regions of extreme cold, are often red, deriving protection from UV and possibly benefitting from warming. White tips also seem to help in reflecting the bright light. Like the exposed bryophytes, these typically are acrocarpous, with ***Isopterygiopsis pulchella*** being a notable exception.

Freezing of cells can result in damage from crystals that poke holes in membranes, loss of solutes, and desiccation. Hence, desiccated cells are more likely to survive freezing than hydrated cells. Some bryophytes have net photosynthetic gain on nunataks and other areas where the temperature rarely exceeds 0ºC. Net gain at -10ºC is not uncommon.

But low temperature and high light intensity can cause photoinhibition. Bryophytes gain protection through colored pigments and down-regulation of photosystem II to prevent over-excitation of electrons. Mature tissues seem to exceed both young and senescing tissues in their frost tolerance.

Calcium and ABA seem to have a role in cold tolerance, although the mechanism is incompletely understood. ABA stimulates the activity of genes that code for stress proteins. These, in turn, increase freezing tolerance and decrease the death rate. Presence of ABA protects cells from membrane lesions and causes an increase in the sugar concentration of cells, but this may be an indirect effect through activation of genes that code for the production of stress proteins. Ca alters membrane permeability, thus affecting membrane transport. Cold temperatures seem to increase the cellular content of Ca^{++}, which comes from both internal and external sources. An increase in soluble sugars could lower the freezing point or provide energy for rapid repair. Depressed temperatures stimulate the

bryophytes to prepare for winter by activating these mechanisms.

Membrane integrity may be maintained by alteration of fatty acids and lipids, with those having high freezing points being replaced with ones having lower freezing points. There seems to be a change to more unsaturated fatty acids as weather cools. Decreasing N levels may signal this change to occur. Some experiments suggest that arachidonic acids diminish as the temperature cools, but if light intensity decreases, as it would as winter approaches, at least some mosses exhibit an increase not only of palmitic and stearic acids, but also of linolenic and arachidonic acids. Such fatty acids as arachidonic acid may even be important in protecting the footpads of lemmings that eat the mosses prior to the onset of winter.

Bryophytes respond differently from tracheophytes to freezing. Because they are only one cell thick and lack internal air spaces, their external surfaces are able to form ice rather than crystals. This helps to insulate the cell. Furthermore, cellular loss of water in preparation for winter deprives the external surfaces from drawing water from the cells to grow crystals. Presence of macromolecular substances, most likely proteins, help polar and cold region bryophytes to form ice rather than crystals. The rapid cooling achieved by the one-cell-thick leaves also causes water loss from the cell, increasing solute concentration and lowering the freezing point inside the cells. This also contributes to the prevention of internal crystal formation. Thallose liverworts with multiple cell layers are more likely to suffer freezing damage.

The ability to accomplish the various means of surviving freezing plays an important role in the niche width and distribution of closely related species.

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I must again acknowledge all the photographers who have made their images available to me either through Creative Commons or by giving me permission.

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CHAPTER 10-3

TEMPERATURE: HEAT

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TEMPERATURE: HEAT

Figure 1. Condensation of moisture in heated air emerging from geothermal vents at Namakolla, Myvatn, Iceland. Note the green covering of bryophytes that endure this warm, moist environment. Photo by Janice Glime.

Heat Stress and Heat Resistance

Since air temperatures rarely exceed 40°C, it might seem unlikely that bryophytes ever experience the high temperatures often used in experiments. But such levels are not as uncommon as supposed (Larcher 1995). Black mosses on rocks of cliffs and exposed boulders can attain considerable internal heat, and even forest mosses can get hot in sunflecks. When the air temperature is only 20°C, mats of ***Mnium hornum*** (Figure 2) can reach 39°C. ***Sphagnum*** can reach a temperature 10°C higher than air temperature (Longton 1979) and habitats such as freshly burned soil can reach 65°C (Larsen 1980). Yet mosses are known to suffer injury when the temperature exceeds 40ºC (Larcher 1995), and temperatures in the range of 42-51ºC are typically lethal (Nörr 1974; Richardson 1981; Meyer & Santarius 1998; Proctor & Pence 2002). ***Grimmia*** (probably ***Schistidium***; Figure 3-Figure 4) grown at 38ºC produced fewer protonemata and shoots, and more plants turned brown than when grown at 27ºC (Keever 1957). Hence, it is of ecological interest to understand the effects of high temperatures on bryophytes.

Figure 2. ***Mnium hornum*** showing the soft leaves that are exposed to the sun and can reach 39ºC when the air temperature is 20ºC. Photo by Des Callaghan, with permission.

Figure 3. ***Schistidium apocarpum*** showing its dark color that absorbs heat and protects from UV damage. Photo by Michael Lüth, with permission.

Figure 4. ***Schistidium apocarpum*** with capsules, showing white awns that help to keep the plants cool and add protection from UV rays. Photo by Michael Lüth, with permission.

Most bryophytes seem to have a heat tolerance of 39-45ºC (Scheibmair 1938; Dirckson 1964; Nörr 1974). When they are constantly wet, they have an even lower tolerance for continuous warm temperatures, as for example species of ***Fontinalis*** (Figure 5) that lose their vitality and chlorophyll at sustained temperatures of 20ºC (Dilks & Proctor 1975; Glime 1987b, c). On the other hand, the warm soil of geothermal areas permits a haven for some species such as ***Hypnum plumaeforme*** (Figure 6), which reaches its northernmost limits in Japan in a geothermal area (Iwatsuki & Glime 1983). In such areas, bryophytes dominate on warmer soils due to high root zone temperatures that are lethal to roots of tracheophytes. By living on the surface, bryophytes are subject to cooling effects of the atmosphere while insulating the soil and causing it to retain more geothermal heat (Glime & Iwatsuki 1997). This heated ground is particularly important to the Antarctic bryophyte flora.

We can consider two major types of heat-related environmental parameters. In one case, the environment is characterized by permanently high temperatures, and in the other, the plants are subjected to thermal extremes (Kappen 1981). For those plants surviving constant heat, the mode of survival must be physiological. However, for those that must survive heat stress only occasionally when extremes arrive, the plant adaptations may require some degree of physiological tolerance, coupled with mechanisms for avoiding the heat. For many plants, this latter avoidance mechanism often involves a dormant life cycle stage that is metabolically inactive, permitting it to survive physiologically. For bryophytes, this could be accomplished by spores or vegetative diaspores that survive underground or on the surface as inactive tissue. This does in fact aid some flood plain species and other ephemerals that disappear for long periods of time and appear only when conditions are suitable. But for the vast majority of bryophytes, their slow growth makes this annual strategy impractical and they more typically survive in a state of desiccation (in dormancy) in which their temperature tolerance is typically much higher (Hearnshaw & Proctor 1982).

Figure 5. ***Fontinalis antipyretica***, a cool temperature species that loses its vitality and chlorophyll at sustained temperatures of 20ºC. Photo by Andrew Spink, with permission.

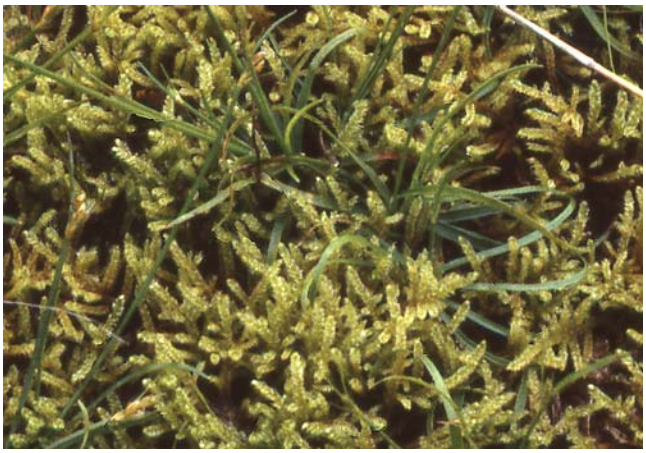


Figure 6. ***Hypnum plumaeforme*** from a geothermal site near Lake Wakoto, Japan. Photo by Janice Glime.

If neither of these strategies is possible, as in wetland bryophytes, their adaptations must include a physiological tolerance to heat, whether it be for short daily periods in summer or for longer duration, or a cooling mechanism. For example, many species of ***Sphagnum*** (Figure 19-Figure 23) have their optimum temperature for growth at 30-35ºC (Li & Glime 1990), whereas most bryophytes have an optimum near 20ºC (Dilks & Proctor 1975). The cosmopolitan ***Bryum argenteum*** (Figure 7) populations, living from the continent of Antarctica through the hot lowland tropics, exhibits heat stress at 30ºC, exhibiting its optimum at 22ºC day/15ºC night (Hedderson & Longton 1999). But air temperature is not indicative of bryophyte temperature, and emergent bryophytes may in fact lower their temperature through evaporative cooling. When that

water is no longer available, the bryophyte is approaching a state of desiccation in which it can become dormant.

Figure 7. ***Bryum argenteum*** with capsules, a cosmopolitan species that exhibits heat stress at 30°C. Photo by Keith Bowman, with permission.

Responses to heat are not immediate in bryophytes. In their study of ***Pohlia wahlenbergii*** (Figure 8), Sandvik and Heegaard (2003) found that the response to nutrient addition was immediate, but that to temperature was delayed. Likewise, ***Fontinalis*** (Figure 5) species can continue to look healthy for several weeks at temperatures above 15 and even 20°C in the field, but after prolonged additional exposure in the lab, they lose their green color and cease growing (Glime 1987b). Such behavior permits them to weather the daily fluctuations as well as the day-night differences in their environments and to sustain short periods of hot weather in summer.

Figure 8. ***Pohlia wahlenbergii***, a species that responds immediately to nutrient addition, but has a delayed response to temperature. Photo by Michael Lüth, with permission.

Heated Habitats

Tropical areas and geothermal habitats present special constraints on bryophytes due to their persistent high temperatures (see Makinde 1993). One would therefore expect that such bryophytes would possess unique adaptations to permit their survival. However, even tropical bryophytes seem to do poorly above 25°C (Frahm 1990). Such high (but not uncommon) temperatures cause their net assimilation rate to decrease drastically, their respiration rates to rise to high levels, and they fail to reach their compensation point (Frahm 1987).

Bryophytes growing in geothermal areas must be capable of tolerating prolonged high temperatures (Given 1980; Hearnshaw & Proctor 1982). For some, this can be done in a dry state, when heat tolerance is much greater. During periods of rain or dew, evaporative cooling can help to maintain a tolerable temperature and permit photosynthetic activity. ***Bryum japonense*** has been found growing at 40°C, ***Philonotis falcata*** (Figure 9) and ***Bryum cyclophyllum*** (Figure 10) at 38°C (Watanabe 1957), and ***Campylopus*** (Figure 11) at 53°C (Glime & Iwatsuki 1994), although the temperature of the actively growing apical region may be much less (*e.g.* 30°C in ***Campylopus praemorsus***; Kappen & Smith 1980). Although liverworts are often considered intolerant, Volk (1984) demonstrated tolerance up to 80°C dry and 50°C wet in ***Riccia*** (Figure 12). Other geothermal taxa, for example ***Bryum argenteum*** (Figure 7) (Hedderson & Longton 1999) and ***Polytrichum*** (Figure 33) species (Loesch *et al*. 1983), exhibit a wide latitudinal range, yet exhibit thermal stress at a mere 30°C and 32°C, respectively. One must exercise caution in interpreting temperature data, however, because they may represent only the soil or air temperatures, which can differ significantly from that of the growing tip of the bryophyte.

Figure 9. ***Philonotis falcata***, a species that can grow in a geothermal area with a soil surface temperature at 38°C. Photo from Digital Museum, Hiroshima University, with permission.

Figure 10. ***Bryum cyclophyllum***, a species that can grow in a geothermal area with a soil surface temperature at 38°C. Photo Janice Glime.

Figure 11. ***Campylopus introflexus*** with water drops that are typical at geothermal sites. Photo by Michael Lüth, with permission.

Figure 12. ***Riccia austinii***, representative of a genus in which some members are able to tolerate temperatures up to 80°C dry and 50°C wet. Photo by Janice Glime.

Sporophyte Stress

Little attention has been paid to temperature relationships of the sporophyte. But in desert mosses, this can be a limiting part of the life cycle. And it appears that post-embryonic sporophytes in at least some desert mosses can only develop in the cooler, wetter months (McLetchie & Stark 2006). It is the perennial gametophytes that permit these plants to survive from year to year. In the desert species ***Microbryum starckeanum*** (Figure 13), all gametophytes survived temperatures of 35-75°C for 1-3 hours, subsequently producing protonemata and shoot buds in a 35-day recovery period. Some leaves exhibited symptoms of stress at 55°C, including leaf burning and discoloration of shoots. However, sporophyte recovery was poor, with reduction in growth and maturation. No sporophytes reached meiosis after exposure for one hour at 75°C. Furthermore, maternal shoots suffered more than did those that aborted their sporophytes in the 35° and 55°C treatments. These shoots took longer to regenerate through protonemata. The reason for this susceptibility of the sporophyte remains unknown. It might be simply less thermotolerance in the sporophyte, or it might that the gametophyte in some way affects the thermotolerance of the sporophyte.

Figure 13. ***Microbryum starckeanum***, a xerophyte for which the sporophyte is more likely to be damaged by heat than is the gametophyte. Photo by Richard Zander, with permission.

Plant and Cellular Responses

Effects of heat stress can include loss of membrane integrity (Liu *et al*. 2003), color change to brown (Keever 1957), shoot damage (Liu *et al*. 2004), and enzyme and pigment destruction (Larcher 1995; Meyer & Santarius 1998; Liu *et al*. 2004). Liu *et al*. (2004) found that ***Plagiomnium acutum*** (Figure 14) survived well at 35-40ºC, exhibiting no cellular damage, but at 45ºC both wet and dry moss cells were damaged (Figure 15). They could find no differences with leaf age, as assessed by position on stem.

Figure 14. ***Plagiomnium acutum***, a species that tolerates temperatures up to 40°C, but suffers damage at 45°C. Photo by Show Ryu, through Creative Commons.

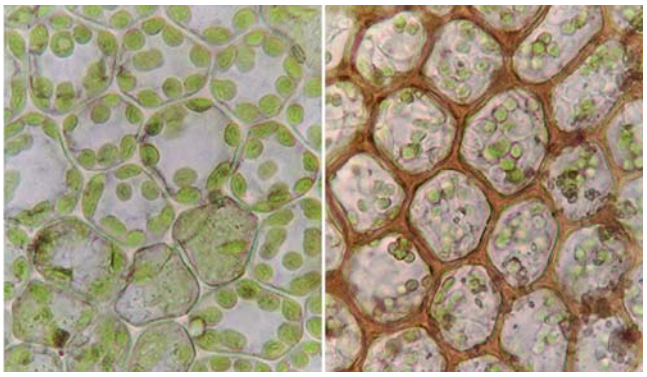


Figure 15. Cells of ***Plagiomnium acutum*** following wet heat treatment. **Left:** 35ºC for 8 hours. **Right:** 45ºC for 1 hour. Photos by Yingdi Liu, with permission.

It appears that membrane permeability varies with temperature even within a normal range of daily temperature fluctuations. Liu *et al*. (2003) demonstrated a temporal fluctuation in cell membrane permeability for ***Thuidium cymbifolium*** (Figure 16) and ***Plagiomnium acutum*** (Figure 14) submersed in water through a 94-hour period. The permeability tracked the temperature almost perfectly (Figure 17).

Figure 16. ***Thuidium cymbifolium*** with capsules, a species in which cell membrane permeability tracks the temperature. Photo by Li Zhang, with permission.

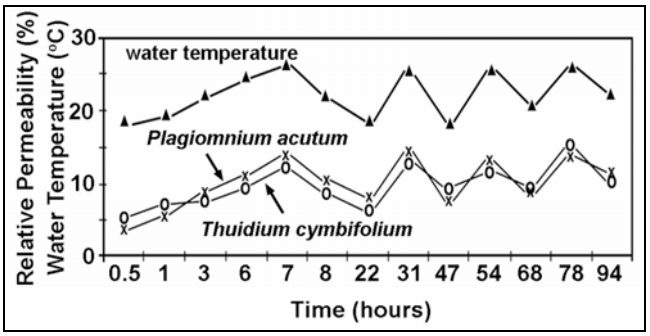


Figure 17. Effect of surrounding temperature on the membrane permeability of two mosses. Redrawn from Liu *et al*. 2003.

In a series of studies, Glime (1980, 1982, 1984, 1987a, b, c) and coworkers (Glime & Knoop 1986; Glime & Raeymaekers 1987) have shown that temperature affects rhizoid production, growth, branching, and gametangia formation in several species of the aquatic moss ***Fontinalis*** (Figure 5; see subchapter on Temperature Effects). And certainly elevational restrictions imply physiological effects that preclude many taxa from growing at higher elevations. These restrictions may even be gender-specific, as in ***Macromitrium*** (Figure 18), where the dwarf male plants are restricted to lower latitudes and altitudes (below the 6ºC January isotherm in Japan), presumably due to low-temperature stress (Une 1985; Une & Yamaguchi 2001).

It appears that even the aquatic moss ***Fontinalis antipyretica*** (Figure 5) may have physiological races adapted to high temperatures. Long exposures to a high temperature could eliminate all but the hardy, and eventually develop a population that is able to withstand the higher temperatures. Such might seem to be the case for this moss growing in a river with abnormally high temperatures due to heated water from hot springs. But when Carballeira *et al*. (1998) transplanted the moss from a normal river site (16ºC) to the heated river (34ºC), there was no notable change in pigment ratio, photosynthetic rate, or respiratory rate after 25 days at the new high temperature. Furthermore, after 2, 4, and 10 days of exposure of mosses from the 16ºC river to 30ºC, then back to 16ºC, these parameters recovered to 50% of their normal values within 10 days. Photosynthesis and respiration both recovered more slowly than did the pigment ratios.

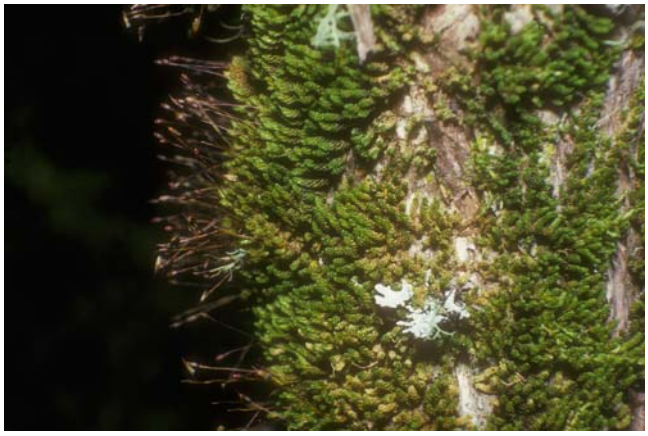


Figure 18. ***Macromitrium microstomum***, member of a genus in which at least some species have dwarf males that are more sensitive to cold temperatures than are females. Photo by Janice Glime.

The ability to tolerate heat is important in dispersal and establishment in a new habitat. Whole colonies can regulate their temperature through insulation. But fragments, often the best means of propagation, lack this protection. When fragments (stem pieces) of several species of ***Sphagnum*** were air dried at 20°C and a relative humidity of ~60%, they survived up to 14 days without water. ***Sphagnum fallax*** (Figure 19) and ***S. magellanicum*** (Figure 20) resisted desiccation better than did ***S. fuscum*** (Figure 21). As one might expect, desiccation delayed the onset of regeneration, most likely due to the need to repair damaged membranes and recover lost nutrients. Oven drying of for 48 hours at 20°C and above was lethal at all temperatures in ***S. angustifolium*** (Figure 22), ***S. fuscum***, ***S. magellanicum***, ***S. capillifolium*** (=***S. nemoreum***; Figure 25), and ***S. papillosum*** (Figure 23). Only ***S. fallax*** was able to survive up to 30°C.

Figure 19. ***Sphagnum fallax***, a species in which fragments can survive up to 14 days at 20°C without water. Photo by Michael Lüth, with permission.

Figure 20. ***Sphagnum magellanicum***, a species in which fragments can survive up to 14 days at 20°C without water. Photo by Michael Lüth, with permission.

Figure 21. ***Sphagnum fuscum***, a species whose fragments can survive up to 14 days at 20°C without water, but that does not resist desiccation as well as ***S. fallax*** and ***S. megellanicum***. Michael Lüth, with permission.

Figure 22. ***Sphagnum angustifolium***, a species that dies when dried in an oven at 20°C. Photo by Jan-Peter Frahm, with permission.

Li and Glime (1990), on the other hand, demonstrated an optimum growth temperature of 30-35ºC for clumps of ***S. magellanicum*** (Figure 20) and ***S. papillosum*** (Figure 23) from the Keweenaw Peninsula of Michigan, USA. Rydin (1984) found no temperature-tolerance differences among ***Sphagnum*** species from Europe. It is likely that the rate of drying differed among these studies so that moisture state may have contributed to the contrasting results, but geographic races may also have been involved in these distant populations. ***Sphagnum fuscum*** (Figure 21) responded to summer warming with enhanced length increment (42-62%) and greater biomass increase, while bulk density decreased (Dorrepall *et al*. 2004). Added snow in winter increased the biomass gain by 33%, but growth in length and bulk density did not change significantly. These changes suggest that not only is the health of the plant affected by temperature, but the structure and moisture-holding capacity are altered, potentially having a major impact on the ecosystem.

Figure 23. ***Sphagnum papillosum***, a species that dies when dried in an oven at 20°C. Photo by Janice Glime.

Biochemical Responses

The observed variations in responses among bryophyte species undoubtedly also result from biochemical differences. Al-Hasan & coworkers (1989) demonstrated a greater concentration of glycerols in ***Bryum bicolor*** (Figure 24) incubated at 5°C than in those at 25°C. It appears, from work with the tracheophyte *Arabidopsis thaliana*, that a reduction in polyunsaturated lipids enhances the thermal stability of the photosynthetic electron transport system (Hugly *et al*. 1989).

Figure 24. ***Bryum bicolor*** decreases its concentration of glycerols when incubated at 25°C compared to those plants at 5°C. Photo by Michael Lüth, with permission.

Isoprene

More recently, Hanson & coworkers (1999) have suggested that heat tolerance in mosses may be due, at least in part, to the production of isoprene, a mechanism of thermal tolerance that seems to have been lost multiple times among more advanced plants. Although little is known thus far about its universality among bryophytes, we do know that at least some bryophytes produce isoprene in response to high temperatures or high light intensities, at considerable cost in carbon – greatly exceeding 2% at temperatures above 30°C (Harley *et al*. 1999). These responses suggest that isoprene may have a role in ameliorating the stresses associated with high temperatures, a role consistent with the physiological evidence. On the other hand, isoprene may contribute to human stress, because it plays a major role in the formation of ozone in forested regions (Harley *et al*. 1999). Isoprene is widespread within the plant kingdom, but it seems to exercise no phylogenetic affinities, is not stored in the leaves, and has no antiherbivory role. Its production in conditions of high light or temperature suggests its protective role in those conditions.

Although isoprene emission is common among mosses and ferns, it is absent in liverworts and hornworts and less predictable among other tracheophytes (Hanson *et al*. 1999). It may be especially useful in certain habitats. Bryophytes growing in the open, such as many ***Sphagnum*** species, are more likely to suffer from thermal stress. This stress could be particularly important when these mosses, with their lower parts in water, may still be in a hydrated state. ***Sphagnum capillifolium*** (Figure 25) from a northern Wisconsin, USA, bog is subject to these large temperature fluctuations and enjoys the benefits of isoprene as a means of increasing its thermotolerance (Hanson *et al*. 1999).

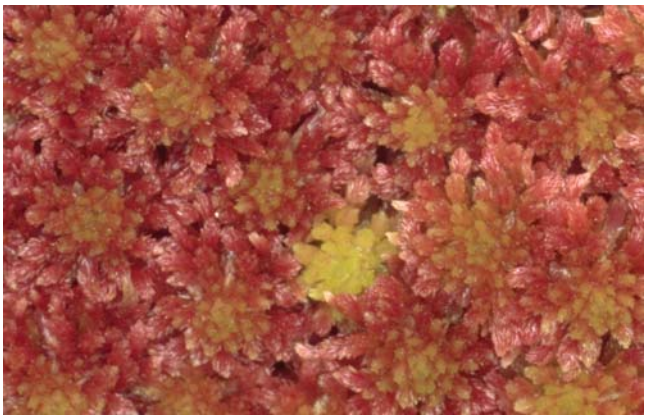


Figure 25. ***Sphagnum capillifolium***. Photo by Jan-Peter Frahm, with permission.

Sugars

In some temperate mosses, sucrose declines upon exposure to high temperatures, resulting in a decline of cold hardiness (Rütten & Santarius 1992), but its loss seems to imply no apparent advantage for heat hardening.

Peroxidase

Marchantia polymorpha (Figure 26) contains a peroxidase that has been characterized as a glycoprotein that is different from any known tracheophyte peroxidase (Hirata *et al*. 2000). Hirata and coworkers demonstrated that it is able to perform oxidative polymerization of lunularin, the liverwort counterpart of ABA. It may play a role in stabilizing the cell membrane during desiccation events. The thallose liverwort ***Marchantia polymorpha*** contains a peroxidase that has been characterized as a glycoprotein that is different from any known tracheophyte peroxidase. Little seems to be known about peroxidases in mosses. In ***Mnium*** sp. (Figure 2), peroxidase appeared to be relatively stable up to 70ºC, but then dropped rapidly as the temperature rose (Bakardjieva *et al*. 1996). Addition of Ca helped to stabilize the peroxidase at higher temperatures. Zinc ions helped to stabilize its activity at high temperatures but inhibited the activity at lower temperatures. When these responses were compared to those of the fern *Polypodium vulgare* (Figure 27), zinc had little effect on that plant at 70ºC. The stability of peroxidase at relatively high temperatures may help the bryophytes to survive the desiccation occurring as the bryophyte approaches high temperatures.

Figure 26. ***Marchantia polymorpha***, a species that produces lunularin that may play a role in stabilizing the cell membrane during desiccation events. Photo by David Holyoak, with permission.

Figure 27. ***Polypodium vulgare***, a plant is unresponsive to zinc as a membrane stabilizer at 70°C, unlike the moss ***Mnium*** sp. Photo by Anneli Salo, through Creative Commons.

Heat Shock Proteins

Early identification of genes and gene function in ***Physcomitrella patens*** (Figure 28) revealed the presence of at least two heat shock protein genes (Machuka *et al*. 1999). It appears that heat shock proteins were present early among the bryophytes (Waters & Vierling 1999a). ***Funaria hygrometrica*** (Figure 29) has at least six such small heat shock proteins (Waters & Vierling 1999a, b). Waters and Vierling considered that genes for these cytosolic proteins must have originated at least 450 million years ago, much earlier than genes for phytochromes. Interestingly, the patterns and rates of evolution in ***F. hygrometrica*** seem different from those of angiosperms. Some, but not all, of the amino acid sequences are the same in both groups.

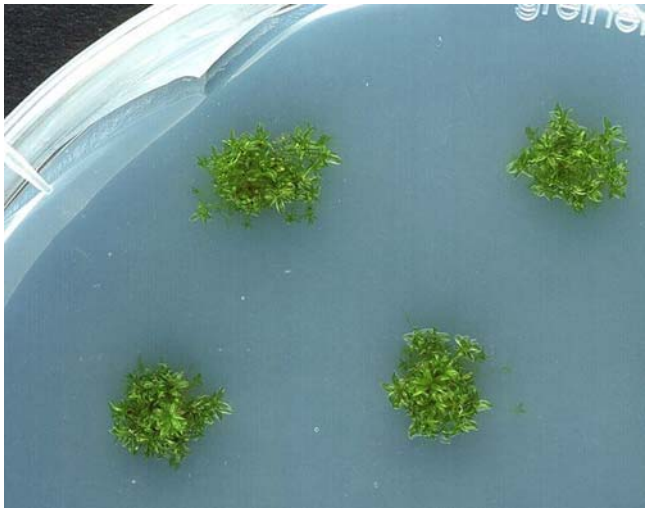


Figure 28. ***Physcomitrella patens*** culture where at least two heat shock proteins were revealed. Photo by Anja Martin in Ralf Reski Lab, through Wikimedia Commons.

Figure 29. ***Funaria hygrometrica***, a species in which we know at least six small heat shock proteins. Photo by Brian Eversham, with permission.

It appears that these ancient bryophyte heat shock proteins have been largely ignored, at least if Cambridge Scientific Abstracts is a good test. We know from the fungus *Phycomyces blakesleeanus* (Figure 30) that blue light and high heat will induce them in that organism (Rodriguez-Romero & Corrochano 2004). Perhaps light, as well as temperature, also plays a role in the photosynthetic bryophytes. But what is that role?

Figure 30. *Phycomyces blakesleeanus*, a fungal species in which heat shock proteins are induced in blue light and high temperatures. Photo by Phil Bendle, through Creative Commons.

Heat shock proteins help the cells to survive the stress induced on other proteins in the cells (Feder & Hofmann 1999). These authors concluded that all species have heat shock proteins and that their expression is correlated with the natural levels of stress they encounter in their environment. From this, it follows that they also are correlated with resistance to stress.

Basile *et al*. (2013) found that heat shock proteins induced by atmospheric pollution cause effects similar to those under the stress of heavy metals in the thallose liverwort ***Conocephalum conicum*** *s.l.* (Figure 31), including severe alterations to the organelles. The implication is that it is the heat-shock proteins that make this liverwort tolerant of heavy metals. When subjected to stress, newly translated proteins can be unstable. The heat shock proteins serve as chaperones that remain attached to these unstable proteins for an extended period of time (Kültz 2005). This chaperone permits the correct folding of denatured proteins, thus stabilizing them and providing defense against damage or dysfunction. It is this capability that labelled them as stress proteins (Wang *et al*. 2004). Furthermore, Neumann *et al*. (1995) concluded that small heat shock proteins protected cells against heavy metal and other stresses by creating a more resistant membrane or improved repair mechanisms.

Figure 31. ***Conocephalum conicum*** *s.l.*, a species in which heat shock proteins are produced in response to heavy metal stress. Photo by Robert Klips, with permission.

Saidi *et al*. (2005) have helped us to understand this role. They found that in ***Physcomitrella patens*** (Figure 28), a temperature of 38°C promoted expression of heat shock genes over three orders of magnitude, whereas at 25°C there was little expression of the promoter genes. This increase in expression permitted the accumulation of GUS (β-glucuronidase) and demonstrated labelled F-actin cytoskeleton in all cell types in all tissues.

In the aquatic moss ***Fontinalis antipyretica*** (Figure 5), temperatures between 20° and 30°C induced production of heat shock proteins. The mean annual temperature of this moss is ~9.5°C (Rau *et al*. 2007). When subjected to heavy metals, this moss produced heat shock proteins, but these did not correspond to any known proteins.

But how does the cell "sense" that the temperature is increasing? Using ***Physcomitrella patens*** (Figure 28), Saidi *et al*. (2011) indicated that physiological and biochemical evidence suggest that the primary sensory role may be Ca^{++} ions. The primary sensor seems to relate to the plasma membrane and may result from the fluidity-sensitive Ca^{++} channels in plasma membranes.

Light vs Dark

Light vs dark can affect response to heat, with plants of ***Plagiomnium acutum*** (Figure 14) in the dark requiring a longer time to exhibit cell damage and death than those in the light, perhaps because of light damage and higher photorespiratory rates at high temperatures (Liu *et al.* 2004).

Acclimation

Evidence on heat acclimation in bryophytes provides conflicting scenarios and clearly more studies are needed. Some studies indicate that bryophytes have little ability to acclimate to near lethal temperatures and that high temperature hardening may be effectively absent. For example, Meyer and Santarius (1998) found only a 1ºC increase for membrane thermal stability from short-term acclimation to sublethal temperatures in two genera. ***Fontinalis antipyretica*** (Figure 5) exposed to a prolonged near-lethal temperature of 30°C exhibited little difference in response between populations previously grown at normal river temperatures and those grown in a river with abnormally high temperatures resulting from hot springs (Carballeira *et al*. 1998).

Both acclimation temperature range and duration influence the acclimation response. Antropova (1974) found that incubation of bryophytes for 72 hours at tolerance temperatures (10 & 20°C) did not influence thermal stability or cold resistance, but that exposure to above optimum temperatures for only 3 hours did increase heat resistance in a behavior similar to that of flowering plants. Glime (1987) found that members of the genus ***Fontinalis*** (Figure 32) were able to tolerate elevated temperatures (above 15°C) for several weeks, but that after prolonged exposure of months they ceased growth and become yellow.

Based on laboratory studies, there is evidence that at sublethal temperatures acclimation to high temperatures occurs (*e.g.* ***Fontinalis duriaei***, Figure 32, Glime & Acton 1979; Fornwall & Glime 1982; ***Polytrichum commune***, Figure 33, Sveinbjörnsson & Oechel 1983), but results are conflicting. Weis *et al*. (1986) found that the thallose liverworts ***Preissia quadrata*** (Figure 34), ***Conocephalum conicum*** *s.l.* (Figure 31), and ***Marchantia polymorpha*** (Figure 26) survived mild heat treatment with a reversible depression of photosynthesis. However, more severe heat caused irreversible damage to photosystem II, much as in higher plants. Nevertheless, these thalli did not have any significant increase in thermal stability of their photosynthetic apparatus as a result of exposure to high sublethal temperatures.

Figure 32. ***Fontinalis duriaei*** in a stream in Japan. Photo by Janice Glime.

Figure 33. ***Polytrichum commune***, a species that has demonstrated acclimation to high temperatures. Photo by Michael Lüth, with permission.

Figure 34. ***Preissia quadrata***, a species that experiences reversible damage at mild heat treatments, but at higher temperatures it is irreversible. Photo by Michael Lüth, with permission.

Contrasting with the delayed response of temperature acclimation in ***Pohlia wahlenbergii*** (Figure 8) (Sandvik & Heegaard 2003), Antropova (1974) found that exposure of

only 3 hours at temperatures above their optimum increased heat resistance in bryophytes in a manner similar to that of flowering plants, whereas incubation within their optimum range of 10-20°C had no effect. Whereas Carballeira and coworkers (1998) found that when exposed to 30°C ***Fontinalis antipyretica*** (Figure 5) showed little difference in pigment ratio, photosynthetic rate, or respiration rate between populations previously grown at normal river temperatures and those grown in a river with abnormally high temperatures resulting from hot springs, Glime (1987) found that this species (collected in Houghton, Michigan, USA) became chlorotic after several weeks of exposure to temperatures above 15°C.

Balagurova *et al*. (1996) found that differences in heat resistance among several ***Sphagnum*** (Figure 19-Figure 23) species was less than that for their cold resistance, but that those differences were correlated. In the case of ***Sphagnum***, environmental conditions strongly affected the thermal resistance. Clearly, the causes and mechanisms of response are complex.

Night Temperature

It is interesting that it is nighttime temperature that is the limiting factor for growth of ***Sphagnum magellanicum*** (Figure 20) in the southern Alps of Italy (Gerdol 1996). It exhibited active growth whenever the night temperature was above 0ºC. This is consistent with the concept that IAA is inhibited by light and therefore most growth occurs at night. Long-day photoperiod promoted growth of all ***Sphagnum*** species [***S. capillifolium*** (Figure 25), ***S. magellanicum***, and ***S. fallax*** (Figure 19)] in an earlier study, with induction requiring both short days and low nighttime temperatures (Gerdol 1995).

Gerdol *et al*. (1998) likewise found that low nighttime temperature limited the growth of ***Sphagnum capillifolium***, causing a five-fold reduction in growth. A nighttime temperature of 5ºC triggers production of red wall pigments, which may contribute to reduced productivity by lowering light intensity reaching the chlorophyll. No degradation of the chlorophyll itself occurred.

Hydration State

The state of hydration is of great importance in the thermal tolerance of bryophytes and their ability to acclimate (Table 1). Dry bryophytes have much greater thermal tolerance than hydrated ones (Figure 35; Figure 42). Alpert (2000) contended that desiccated plants are able to endure temperatures from -272 to 100ºC. But hydrated ***Fontinalis novae-angliae*** (Figure 36) had at least some stem tissue that survived intermittent boiling for more than one week (Glime & Carr 1974). In the moss ***Homalothecium lutescens*** (Figure 37), a decrease in the water content was responsible for an increase in heat tolerance (Dulai *et al*. 2002). An osmotic treatment of only 30 minutes shifted the lethal temperatures upward. But if the plants were kept in the dark, the curves did not shift upward as the water deficit increased, suggesting that the thermal stability of PS II may occur only in the energized photosynthetic membranes. On the other hand, Li *et al*. (1999) found that dark respiration decreased as temperature increased (and hydration state decreased) in ***Herpetineuron toccoae*** (Figure 38) and ***Plagiomnium acutum*** (Figure 14), perhaps explaining part of the greater heat tolerance of dry mosses.

Table 1. Wet and dry 50% lethal temperatures (LT_{50} – ºC) for various mosses, based on Nörr 1974 and Kappen 1981.

	wet	dry
Hylocomium splendens	43	91
Rhytidiadelphus loreus	42	92
Mnium hornum	44	99
Pleurozium schreberi	42	92
Hypnum cupressiforme	44	102
Dicranum scoparium	45	103
Racomitrium lanuginosum	48	105
Sphagnum capillifolium	46	
mosses	41-51	85-110
liverworts	39-45	70-110

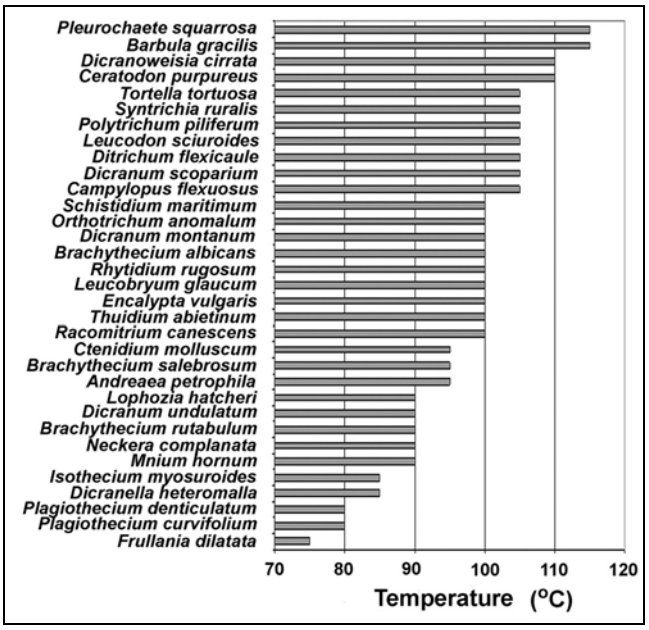


Figure 35. Lethal temperatures for various dry mosses. Based on Lange (1955), using the highest temperature below which most of the mosses first survived for 30 minutes.

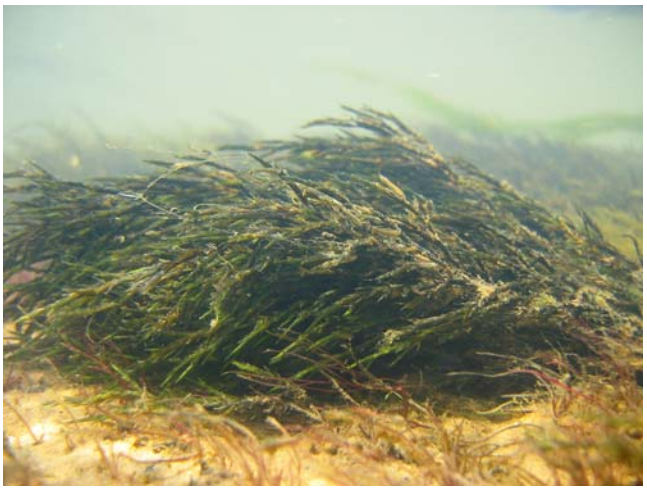


Figure 36. ***Fontinalis novae-angliae***, a species in which some stem tissues survived being in intermittent boiling for more than one week. Photo by John Parker, with permission.

Figure 37. ***Homalothecium lutescens***, a species that becomes more heat tolerant at lower moisture levels. Photo by Michael Lüth, with permission.

Figure 38. ***Herpetineuron toccoae***, a species in which dark respiration decreases at higher temperatures with lower moisture levels. Photo by Michael Lüth, with permission.

In two Polytrichaceae [***Atrichum undulatum*** (Figure 39) and ***Polytrichastrum formosum*** (Figure 40)], short-term acclimation of hydrated shoots occurred within a few hours and provided a small but significant increase in the stability of the cellular membranes and photosynthetic apparatus (Meyer & Santarius 1998). By contrast, it required several days to deharden the tissues. Contrasting with this minimal resistance of hydrated tissues, the increase of heat tolerance in desiccating tissues was dramatic, with an inverse relationship between hydration and heat tolerance.

As one might expect, water use efficiency (WUE) plays a role in heat tolerance in bryophytes. In the moss ***Herpetineuron toccoae*** (Figure 38), transpiration usually is lower and water use efficiency higher than that of ***Plagiomnium acutum*** (Figure 14) in the same habitat (Li *et al*. 1999). This seems to endow ***H. toccoae*** with a greater capacity for heat tolerance and dry habitats.

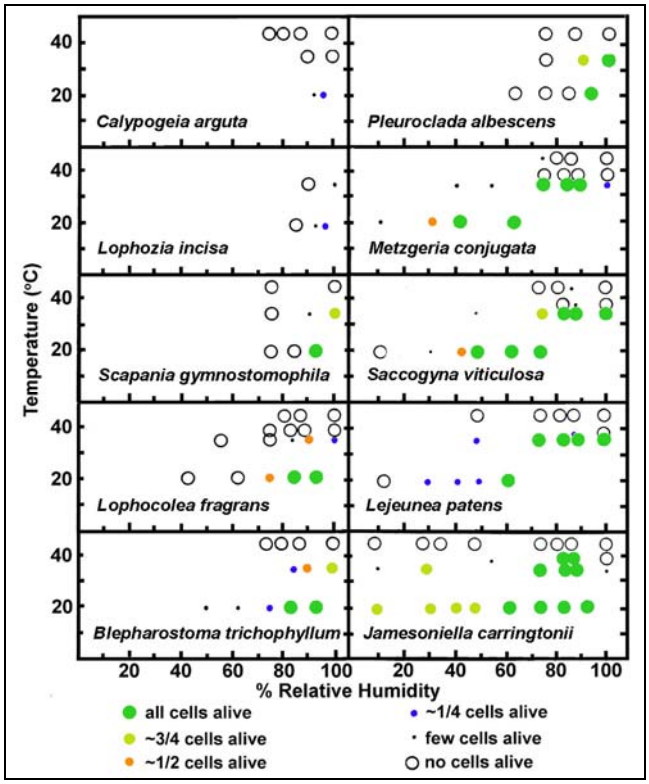
Clausen (1964) explored the relationship between temperature and humidity in 20 species of liverworts from a wide range of locations throughout the globe (Figure 42).

Figure 39. ***Atrichum undulatum***, a species that is able to acclimate to temperature changes within a few hours. Photo by Brian Eversham, with permission.

Figure 40. ***Polytrichastrum formosum***, a species that is able to acclimate to temperature changes within a few hours. Photo by Michael Lüth, with permission.

A common method of drying mosses in the laboratory for temperature experiments has been to place the plants in a sugar or salt solution until they plasmolyze (Figure 43). This pretreatment induces heat resistance, most likely by suspending cellular metabolism.

Figure 41. ***Plagiochila asplenioides***, a species that exhibits plasmolysis when pretreated with a sugar solution and heated to 55°C, but exhibits loss of membrane integrity when pretreated with salt. Photo by Michael Lüth, with permission.



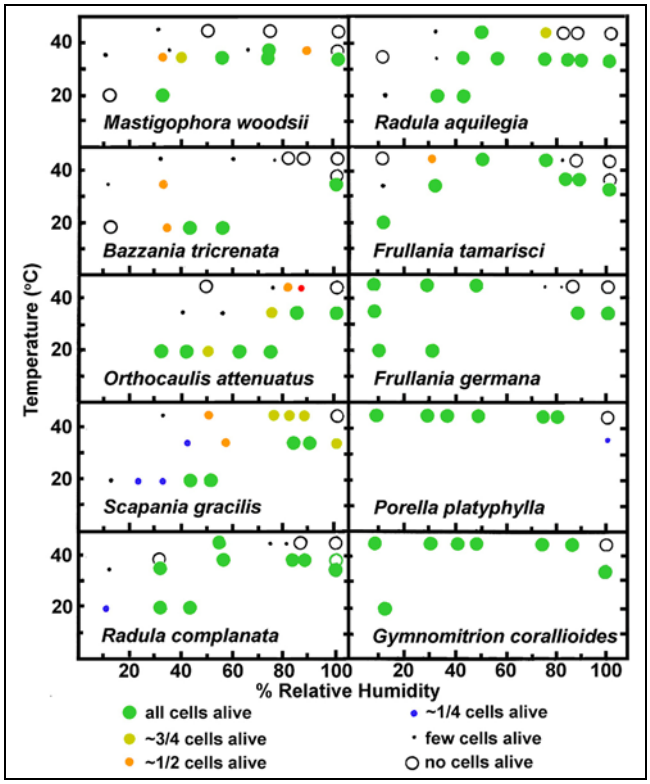


Figure 42. Effects of temperature and state of hydration on 20 leafy liverworts from Europe. Redrawn from Clausen 1964.

Duration

Not only is the actual temperature important, but the duration is also important. Just as we might walk through a hot boiler room unscathed, but be unable to stay for an hour in there without getting sick, bryophytes likewise are able to tolerate short-term bursts of heat as might come from dancing sunflecks. For example, the tropical liverwort ***Schistochila commutata*** dies at 32ºC in water with 12 hours exposure, but survives at 42ºC (but not 44ºC) with only 1/2 hour exposure (Biebl 1967). The tropical mosses ***Homaliodendron flabellatum*** (Figure 44) and ***Bryum*** sp. (Figure 7) tolerate temperatures up to 50ºC in water for half an hour, contrasting with the 25ºC limit for tropical bryophytes reported by Frahm (1990). Figure 45 demonstrates the effect of time in the moss ***Plagiomnium acutum*** (Figure 14).

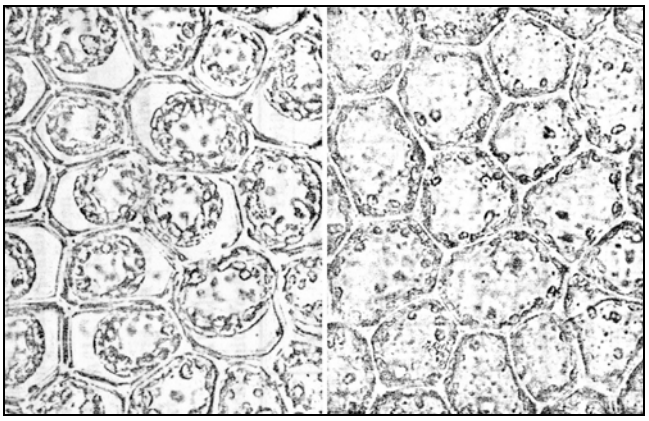


Figure 43. Leaf cells of ***Plagiochila asplenioides*** (Figure 41) demonstrating the effect of heat on desiccated cells. **Left:** Cells plasmolyzed, indicating intact membranes, in 2.5 M sugar solution at 55°C for 1.5 minutes. **Right:** Cells after 1.5 minutes at 55°C with no pretreatment in the salt solution. Lack of cell shrinkage upon drying suggests loss of membrane integrity, suggesting that these cells are dead. Photos from Scheibmair 1938.

Figure 44. ***Homaliodendron flabellatum***, a species that can tolerate temperatures up to 50ºC in water. Photo by Jiang Zhenyu, Mou Shanjie, Xu Zawen, Chen Jianzhi, through Creative Commons.

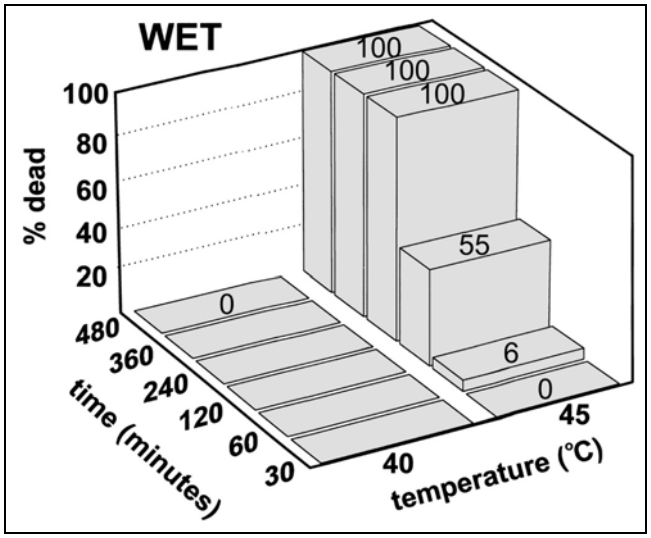


Figure 45. Effect of time on the lethality of temperature in ***Plagiomnium acutum*** (Figure 14). n=30. From Liu *et al*. 2004.

Age and Structure

In some cases, age is a factor in temperature tolerance of tissues, as shown for two ***Plagiomnium*** species in response to low temperatures, with mature tissues being more tolerant than young or senescent ones (Rütten & Santarius 1992, 1993). Yet there seems to be no effect of age on the lethal high temperature of ***Plagiomnium acutum*** (Figure 14) treated wet at 30-60°C for up to 240 minutes (Liu *et al*. 2004). Known cellular damage of high temperatures on bryophytes mainly includes destruction of the plasma membrane as evidenced by loss of electrolytes (Liu *et al* 2003), loss of differential permeability, chemical disorganization, and death of cells or tissue (Liu 20044), all factors where one might expect young and old tissues to respond differently. In studying ***Plagiochila asplenioides*** (Figure 41), Scheibmair (1938) did indeed find that young leaves survived better than older leaves. The older cells died, protoplasm became deformed, and the membrane and cytoplasm became colored. The young leaves survived up to 53°C for 10 hours, whereas the older leaves died after 6 hours at 48°C.

Although a variety of measures have been used to assess damage in bryophytes, the actual physiological responses of bryophytes to temperature are not well understood. One complication is that optimal temperatures for one aspect of a bryophyte life cycle might be detrimental for another, as shown for example in *Fontinalis* rhizoid production, gametangia formation, growth, and branching (Glime 1984, 1987a, b, c; Glime & Knoop 1986; Glime & Raeymaekers 1987). Chlorophyll content (Miyata & Hosokawa 1961; Melick & Seppelt 1994), photosynthesis (Shimizu *et al*. 1983), growth, weight, and number of branches (Bengtson *et al*. 1982; Bakken 1993) are often used as measures of bryophyte health.

It appears that we know almost nothing about the effect of temperature on the development of the sporophyte. Working with desert bryophytes, Stark (personal communication, April 2005) suggested that stress on the gametophyte might trigger the plant to abort its sporophyte, making it difficult to determine independent stress on the sporophyte itself. It appears that once expansion has been initiated, they are very stress tolerant when dry.

HP

Reversible Effects

In thallose liverworts, heat-stress depression of photosynthesis can be reversible (Weis *et al*. 1986). ***Preissia quadrata*** (Figure 34), ***Conocephalum conicum*** *s.l.* (Figure 31), and ***Marchantia polymorpha*** (Figure 26) all were able to recover from mild heat stress, with the recovery period dependent on the extent of the damage. With severe damage, Photosystem II suffered irreversible damage. Nevertheless, unlike in tracheophytes, treatment with high sublethal temperatures had no significant effect on their heat stability.

Decomposition

Few studies have examined bryophyte decomposition, and many misconceptions occur among ecologists about bryophyte decomposition. It is quite a different thing to be decaying from the bottom up on a live plant than to drop leaves and branches that henceforth decay. By being still connected to living plant tissue, decaying portions of a bryophyte are able to move internal and external constituents upward or outward to living portions. Such movement can be influenced by temperature.

Thormann *et al*. (2004) compared decomposition between the sedge *Carex aquatilis* (Figure 46) and the moss ***Sphagnum fuscum*** (Figure 21) in the boreal peatlands. They found a 5 to 17-fold decrease in bog ***Sphagnum fuscum*** litter decomposition with elevated temperature, whereas decomposition of the sedge litter was either enhanced 2- to 30-fold or was unaffected by elevated temperatures. Fungal decay was favored over bacterial decay in elevated temperature conditions. The fungi were able to use polyphenolic polymers as their carbon source, hence favoring their existence over the bacteria in the peat. Nutrient quality seemed to play a major role, favoring the nutrient-rich litter of sedges (8.0-25.7%) over that of bryophytes (0.2%) at higher temperatures. Hence, increases in temperature may not cause the positive feedback to temperature that has been anticipated for all peatlands. Rather, intermediate and rich fens may cause a positive feedback, but poor fens and bogs may actually cause a negative feedback that reduces the input of carbon to the atmosphere.

Figure 46. ***Carex aquatilis***, a species with high nutrient content that decomposes much more rapidly at elevated temperatures than does bog litter (which decreases its decomposition rate). Photo by Max Licher, SW Biodiversity, with online permission.

Summary

Although the air temperature seldom exceeds 40ºC, bryophyte temperatures can reach 60-70ºC in some circumstances. Most bryophytes have a hydrated tolerance limit of 45ºC or less.

Bryophytes can survive the heated periods as spores or other dormant propagules, by becoming dormant (if desiccated), or by physiological adaptations to the elevated temperatures, including desiccation that leads to dormancy. Emergent bryophytes can use evaporative cooling to maintain lower tissue temperatures.

Despite potentially high temperatures, tropical bryophytes typically do poorly above 25ºC, due to high respiration rates. Geothermal bryophytes often provide their own insulation, with hot bases but cool growing tips. The record for wet heat tolerance seems to be ***Riccia*** at 50ºC, although ***Fontinalis*** stem tissue survived more than a week of intermittent boiling. Colors, evaporative cooling, and physical properties can alter the temperature of the growing region of a bryophyte, so air and substrate temperature data may not reflect tissue temperatures.

Heat stress can cause loss of membrane integrity, color changes, shoot damage, enzyme denaturation, pigment destruction, and negative photosynthetic gain. Temperature can promote differential development times for spores, gemmae, rhizoids, branching, growth, gametangia, and sporophyte maturation. Some of these effects are gender specific and may restrict the male and female plants or expression of sexual organs to different elevations or microclimates. **Cryptic species**, **microspecies**, or **physiological races** may exist that are not mirrored by differences in morphology, permitting a species to occupy a wide range of climatic conditions.

It appears that heat is may damage bryophytes in the light more than in the dark, perhaps due to energy loss to photorespiration. Nighttime temperatures may be important for some taxa, with minimal temperatures required for growth.

Known biochemical responses to elevated temperatures include an increase in **glycerols**, **isoprenes**, and **heat shock proteins**, whereas **sugars** decrease, but we know little about any of their roles. **Peroxidase** may play a role in stabilizing cell membranes during thermal stress and desiccation, with Ca and Zn contributing to its stabilization at high temperatures.

Many bryophytes seem to lack the ability to acclimate to high temperatures. Nevertheless, heat resistance can increase in as little as three hours of exposure to above-optimum temperatures, but plants may take several days to **deharden**. It appears that some physiological processes such as photosynthesis may acclimate, but that thermal stability does not change as easily. Even *Sphagnum* exhibited more change in its cold resistance than in its heat resistance, but the two acclimations were correlated.

Desiccated bryophytes have far greater thermal tolerance than hydrated ones, with some apparently surviving the entire temperature range from -272 to 100ºC. In fact, one mechanism for increased heat tolerance is for the plant to decrease its water content, whether by changing its osmotic relationships or by coincidence with a drying atmosphere. One explanation for this is that dark respiration can decrease in response to increased temperatures and concomitant drying. Duration is important, with short durations being tolerable when longer ones are not. Greater **water use efficiency** seems to endow mosses with a greater heat tolerance, but may not be helpful to thallose liverworts.

Age plays a role in heat tolerance in some species, with mature tissues being the most tolerant, and young and senescent ones being less so. Sporophyte responses are poorly known, but some evidence suggests that heat may cause embryo abortion in some taxa.

Decomposition may be altered differently among bryophytes compared to that of tracheophytes. Elevated temperatures can favor fungal over bacterial decay, promoting the decay of the polyphenolic polymers in bryophyte cell walls. High nutrient litter increases decay more with temperature increases than does bryophyte litter. This results in some habitats losing bryophyte litter more quickly while others lose it more slowly.

Acknowledgments

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CHAPTER 10-4

TEMPERATURE: SPECIES AND ECOSYSTEMS

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CHAPTER 10-4

TEMPERATURE: SPECIES AND ECOSYSTEMS

Figure 1. Mountainous habitats provide a wide range of temperatures. Here ***Ditrichum flexicaule*** grows in the foreground. Photo by Michael Lüth, with permission.

Species and Distributions

Importance of Climate

In his study of the Gulf of St. Lawrence region of Canada, Belland (2005) found that climatic variables were the most important factors determining moss species distributions, with warmth of the growing season being the most important. Acebey *et al*. (2003) likewise found that climate accounted for the reduced bryophyte species diversity and changes in growth forms from submontane rainforest in Bolivia to the 4-15-year-old fallows at 500-650 m elevation. In central Belgium, species composition could be predicted based on four life-history traits (minimum spore size, life expectancy, type of gametophyte, and papillose leaf cell walls) and three ecological traits (indicator values of light, temperature, and soil acidity) (Vanderpoorten & Engels 2002). For bryophytes of the eucalypt-dominated forests in Tasmania, minimum temperature in the coldest month and precipitation were the most important variables predicting bryophyte cover, richness, and composition (Pharo *et al*. 2005). These were reduced by the cover of vascular plants. Certainly temperature plays an important role at all stages of the life cycle.

While some species are limited in their extension toward the poles by cold temperatures, others are unable to survive further away from the poles due to the heat. ***Grimmia torquata*** (Figure 2-Figure 3) is an arctic-montane moss that reaches its southern limit in Newfoundland, where further southward expansion seems to be limited by high summer temperatures (Hedderson & Brassard 1990). On the other hand, ***Aulacomnium androgynum*** (Figure 4) and ***Isothecium myosuroides*** (Figure 5-Figure 6) reach their northern limit there due to low winter temperatures and water availability.

Figure 2. ***Grimmia torquata*** in Norway, a species limited by heat south of Newfoundland. Photo by Michael Lüth, with permission.

Figure 3. ***Grimmia torquata***, a northern species that is limited in distribution by heat. Photo by Michael Lüth, with permission.

In nearly every study, however, the importance of water availability is the major limiting factor for growth of bryophytes within a region. Temperature may define the bounds of their distribution, but water availability determines their growth rate within that suitable temperature range. For example, in their study of nine bryophytes [***Racomitrium lanuginosum*** (Figure 7), ***Pleurozium schreberi*** (Figure 8), ***Sphagnum austinii*** (Figure 9), ***S. fuscum*** (Figure 10), ***S. rubellum*** (Figure 11), ***S. papillosum*** (Figure 12), ***S. lindbergii*** (Figure 13), ***S. tenellum*** (Figure 14), and ***S. pacificum*** (Figure 15)] in a coastal peatland in British Columbia, Canada, Asada *et al*. (2003) found that growth was most strongly correlated with precipitation and less so with temperature. Surprisingly, temperature thresholds for ***Sphagnum*** were lower than those for ***Pleurozium schreberi*** and ***Racomitrium lanuginosum***, and winter growth was important for these ***Sphagnum*** species. But we must keep in mind that temperature often co-varies with precipitation, with cooler summer temperatures in a suitable range occurring when there is precipitation.

Figure 4. ***Aulacomnium androgynum***, a species for which the northern limit is determined by temperature and moisture availability. Photo by Janice Glime.

Figure 5. ***Isothecium myosuroides*** on tree at Swallow Falls, Wales, a species that is limited north of Newfoundland by low winter temperatures and water availability.

Figure 6. ***Isothecium myosuroides*** near Swallow Falls Wales, where warmer temperatures and sufficient moisture permit it to live. Photo by Janice Glime.

Figure 7. ***Racomitrium lanuginosum***, a species for which growth responds more to precipitation than to temperature. Photo by Juan Larrain, with permission.

Figure 8. ***Pleurozium schreberi***, a species for which growth responds more to precipitation than to temperature. Photo by Bob Klips, with permission.

Figure 9. ***Sphagnum austinii*** in Scotland, a species for which growth responds more to precipitation than to temperature. Photo by Michael Lüth, with permission.

Figure 10. ***Sphagnum fuscum***, a species for which growth responds more to precipitation than to temperature. Photo by Jutta Kapfer, with permission.

Figure 11. ***Sphagnum rubellum***, a species for which growth responds more to precipitation than to temperature. Photo by Michael Lüth, with permission.

Figure 12. ***Sphagnum papillosum***, a species for which growth responds more to precipitation than to temperature. Photo by Michael Lüth, with permission.

Figure 13. ***Sphagnum lindbergii*** in Norway, a species for which growth responds more to precipitation than to temperature. Photo by Michael Lüth, with permission.

Figure 14. ***Sphagnum tenellum***, a species for which growth responds more to precipitation than to temperature. Photo by Michael Lüth, with permission.

Figure 15. ***Sphagnum pacificum*** in Alaska, a species for which growth responds more to precipitation than to temperature. Photo by Vita Plasek, with permission.

Warming Studies

Studies on effects of global warming (to be discussed in detail in a later chapter) are helping us to understand how bryophytes are affected by temperature and how they affect the temperatures of the soil beneath them. In a species-poor Icelandic moss heath where ***Racomitrium lanuginosum*** (Figure 7) dominated, mean daily surface temperatures were 1-2°C higher under a simulated warming regime, but the soil temperatures tended to be lower than in the control plots (Jonsdottir *et al*. 2005). In several other habitats that were more species-rich, changes were more moderate. In the Arctic, it appears that warming temperatures are likely to decrease bryophyte relative cover as graminoids increase (Hollister *et al*. 2005). Wahren *et al.* (2005) found a similar increase in sedges (*Eriophorum vaginatum* – Figure 16) and decrease in bryophytes in Alaska after eight years of increased temperatures, but even the control plots had a similar response. Ironically, plots with additional snow cover were actually warmer due to the greater insulating effect. They also benefitted by the additional moisture available.

Figure 16. ***Eriophorum vaginatum*** (cottongrass), a species that increases in abundance after warming for eight years. Photo by Martin Olsson, through Creative Commons.

In northern habitats, the moss ***Hylocomium splendens*** (Figure 17) has been studied in many contexts, permitting us to understand its biology well. In a study on circumarctic populations, its growth was strongly correlated with both the early summer temperatures and the length of the growing season (Callaghan *et al.* 1997). The mildest of the subarctic sites fostered the greatest annual segment mass increase, growth rates, and degeneration rates, whereas the lowest were at the high arctic site. Conversely, longevity increased as the climate became more harsh at the more northern sites. Growth between years at two contrasting sites correlated significantly with the temperatures of June and July. This moss is tolerant of a wide range of daily temperature variation, so it is not likely to be seriously affected by global warming. However, not all Arctic systems are likely to respond in the same way. Even ***Hylocomium splendens*** responded negatively to perturbations of climate at a sub-Arctic site, perhaps due to lower humidity and non-equilibrium responses in the relatively short term of the study (Callaghan *et al.* 1999).

Figure 17. ***Hylocomium splendens***, a species whose growth responds to early summer temperatures and the length of the growing season. Photo by Daniel Mosquin, Botany Website, UBC, with permission.

Figure 18. ***Sphagnum squarrosum*** in its typical forest habitat. Photo by J. C. Schou, with permission.

Seasonal Fluctuations

As seen in the previous chapters, temperature can invoke changes in the biochemical constituents of the bryophyte cells. In a study on bryophytes of Windmill Islands, Antarctica, Melick and Seppelt (1994) found that pigment levels varied seasonally, with total chlorophyll and chlorophyll *a*/*b* ratios decreasing in winter, most likely as a light response. Total carotenoids increased in summer, primarily in response to the greater light intensity. Water content was greatest in summer. Soluble carbohydrate levels, on the other hand, varied little among seasons, contrasting with fluctuations seen in bryophytes from other polar regions. This lack of change in carbohydrates may be due to the rapid temperature fluctuations seen on a daily basis during the Antarctic growing season.

Figure 19. ***Sphagnum squarrosum*** with capsules, a shade species that is sensitive to high temperatures and full sun.. Photo by Michael Lüth, with permission.

Species Differences

Within a genus, the responses of different species to temperature vary (Koskimies-Soininen & Nyberg 1991). For example, in the predominantly sun-adapted ***Sphagnum***, the shade-tolerant species ***S. squarrosum*** (Figure 18-Figure 19) suffered loss in its photosynthetic capacity and chlorophyll content when exposed to the heat and bright light following canopy removal (Harley *et al*. 1989), although this may have been strictly a light response. ***Sphagnum fimbriatum*** (Figure 20) responded in very different ways from ***S. magellanicum*** (Figure 21) to changes of temperature (Koskimies-Soininen & Nyberg 1987, 1991). When ***Sphagnum*** species [***S. austinii*** (Figure 9), ***S. fuscum*** (Figure 10)**,** ***S. rubellum*** (Figure 11)**,** ***S. papillosum*** (Figure 12)**,** ***S. lindbergii*** (Figure 13)**,** ***S. tenellum*** (Figure 14), and ***S. pacificum*** (Figure 15)] were compared to other boreal bryophytes, they exhibited lower temperature thresholds than did ***Pleurozium schreberi*** (Figure 8) or ***Racomitrium lanuginosum*** (Figure 7) (Asada *et al*. 2003). These differences often relate to habitat in ways that are obvious, such as hummock vs hollow. Despite the tolerance for heat in some ***Sphagnum*** taxa, winter growth was important for these species.

Figure 20. ***Sphagnum fimbriatum***, a species that responds differently to elevated temperature from ***S. magellanicum***. Photo by Michael Lüth, with permission.

Figure 21. ***Sphagnum magellanicum*** hummock, a species that responds differently to elevated temperature from ***S. fimbriatum*** to elevated temperature. Photo by Michael Lüth, with permission.

Cryptic Species

Many more species most likely have physiological races (cryptic species, microspecies) that differ in their ability to cope with a variety of environmental differences. It is these physiological races that may some day become different species if they remain isolated from each other long enough to become reproductively isolated. Until then, they confound the ecologist by responding to environmental parameters differently.

Physiological races provide physiological differences among populations that appear to be morphologically identical, permitting them to take advantage of a wider range of ecological conditions. A number of cryptic species permit the cosmopolitan ***Grimmia laevigata*** (Figure 23) to survive the extremes of temperature, UV light, and desiccation in its rock habitat (Fernandez *et al*. 2006), often fully exposed to the sun where its black color can cause extremely high temperatures.

Figure 22. A green form of ***Grimmia laevigata*** that may also differ in physiological responses to temperature and desiccation. Photos by Michael Lüth, with permission.

Production of gametangia must be attuned to the growing season, which becomes shorter as one moves toward the poles or to higher elevations. Two species of ***Pohlia*** [***P. nutans*** (Figure 24), ***P. cruda*** (Figure 25)], widely separated in the sub-Arctic and Britain, exhibited shorter maturation periods for both gametangia and sporophytes in the Arctic and sub-Arctic than they did in Britain (Clarke & Greene 1970). One cannot rule out, however, the longer days as compensation for the shorter growing season.

Figure 23. A dark, strongly awned form of ***Grimmia laevigata*** that may also differ in physiological responses to temperature and desiccation from the green form in Figure 22. Photo by Michael Lüth, with permission.

Figure 24. ***Pohlia nutans***, a species that has shorter maturation periods for both gametangia and sporophytes in the Arctic and sub-Arctic than they do in Britain. Photo by Michael Lüth, with permission.

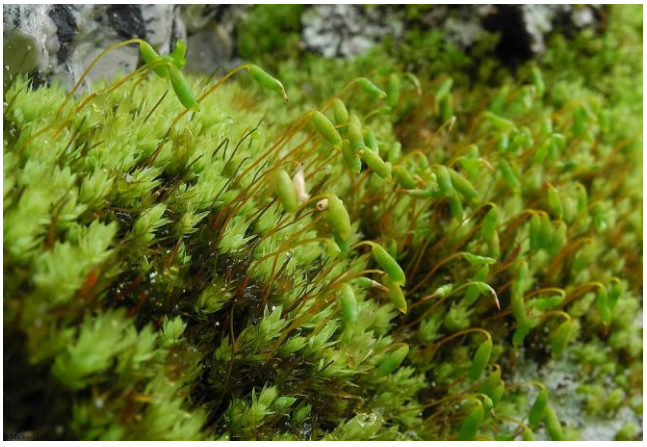

Figure 25. ***Pohlia cruda***, a species that has shorter maturation periods for both gametangia and sporophytes in the Arctic and sub-Arctic than they do in Britain. Photo by Michael Lüth, with permission.

Ecosystem Relationships

Even within a small geographic region, **aspect** (compass direction a slope faces) can have significant effects on the microclimate. On the Cushetunk Mountain of New Jersey, USA, the south slope experiences heavy shade with a nearly isothermal air temperature at 2 m (Cantlon 1953). Under light shade, in small openings, and during the leafless season, this same 2 m in height experiences sharp changes in temperature, with the highest daytime temperatures being near the ground. The north slope, on the other hand, has its lowest temperatures near the ground in all seasons. The greatest differences between the two slopes are in the 5 cm zone above the ground, where soil bryophytes would grow. Furthermore, the greatest vegetation differences between the two slopes were seen in the bryophyte layers, with the fewest between tree layers.

Altering Ecosystems

Bryophytes play a significant role in their ecosystems in altering soil temperatures. Serving as insulation, they keep the soil cooler in summer and warmer in winter. Dark-colored soil serves as a heat-absorbing body, but covered by a moss mat, that soil is protected from the direct radiation that could raise its temperature. In other words, bryophytes buffer the soil temperature (Figure 26).

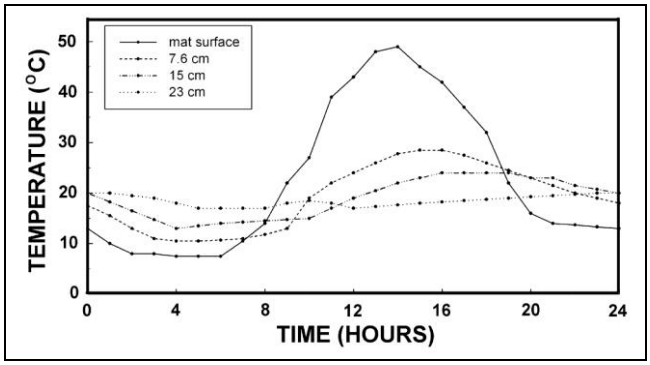

Figure 26. Effects of moss mat on soil temperature. Modified from Richardson 1958.

Especially in northern climates, bryophytes may be instrumental in altering soil temperatures and retarding nutrient turnover, *i.e.*, serving as ecosystem engineers (Eckstein 2000). Not only do they slow the rate of turnover through their insulating effect, but they retard it through their contributions of organic acids and low nutrients that discourage the growth of decomposer microorganisms.

Mosses themselves are very resistant to decomposition, whereas grasses are among the highest (Hobbie 1996). Therefore, any climate change that favors the growth of mosses will reduce the availability of stored nutrients, whereas their decrease will accelerate nutrient turnover and release more carbon to the atmosphere.

Disturbed Habitats

Liverworts are often colonizers of disturbed habitat such as flood plains, where they are subjected to very high temperatures as the soil dries. Genera such as ***Riccia*** (Figure 27) can withstand temperatures of more than 80°C dry and up to 50°C wet (Bolk 1984).

Figure 27. ***Riccia ciliata***, a drought tolerant species of disturbed habitats. Photo by Michael Lüth, with permission.

Grassland

Grasslands generally do not have many bryophyte species, but some taxa may be relatively abundant there. Some grasses can buffer temperatures and hold moisture near the ground by providing a canopy.

In a study of limestone grasslands in the southern Pennine Hills of the United Kingdom, Bates *et al*. (2006) subjected bryophytes to 3°C winter warming. Responses were relatively minor. Drought was the greatest problem, with total bryophyte cover and cover of ***Calliergonella cuspidata*** (Figure 28) and ***Rhytidiadelphus squarrosus*** (Figure 29) responding negatively. ***Fissidens dubius*** (Figure 30) increased in drought-simulated plots. Winter warming caused ***R. squarrosus*** and ***Lophocolea bidentata*** (Figure 31) to decrease, along with overall species richness, but ***Campylium chrysophyllum*** (Figure 32) increased.

Figure 28. ***Calliergonella cuspidata*** at Swallow Falls, Wales, a species that experiences reduced cover when experiencing drought. Photo by Janice Glime.

Figure 29. ***Rhytidiadelphus squarrosus***, a species that experiences reduced cover when experiencing drought. Photo by Michael Lüth, with permission.

Figure 30. ***Fissidens dubius***, a drought-tolerant species. Photo by Michael Lüth, with permission.

Figure 31. ***Lophocolea bidentata***, a species that decreased in the United Kingdom with winter warming. Photo from <www.aphotofauna.com>, with permission.

In a different grassland study, Ingerpuu *et al*. (2005) found rather different results. They planted typical forbs [*Trifolium pratense* (Figure 33), *Festuca elatior* var. *pratensis* (Figure 34), *Prunella vulgaris* (Figure 35)] in pots with either of two bryophyte species [***Brachythecium rutabulum*** (Figure 36), ***Rhytidiadelphus squarrosus*** (Figure 37)]. Using four different densities of tracheophytes, they found that bryophyte cover increased with tracheophyte density, presumably due to creation of more favorable temperatures.

Figure 32. ***Campylium chrysophyllum***, a species that increased in the United Kingdom with winter warming. Photo by David Holyoak, with permission.

Figure 33. *Trifolium pratense*, a species that increases bryophyte cover in pots. Photo by Masaki Ikeda, through Creative Commons.

Figure 34. ***Festuca elatior*** var. ***pratensis***, a species that increases bryophyte cover in pots. Photo by T. Voekler, through Creative Commons.

Figure 35. ***Prunella vulgaris***, a species that increases bryophyte cover in pots. Photo by Zeynel Cebeci, through Creative Commons.

Figure 36. ***Brachythecium rutabulum***. Photo by Michael Lüth, with permission.

Figure 37. ***Rhytidiadelphus squarrosus***. Photos by Michael Lüth, with permission.

Tropics

Within a given tropical ecosystem, temperature ranges are less extreme than in most other regions of the world. This homogeneity of temperature makes water and light availability of paramount importance to distributions of many species. But loss of energy to respiration at frequent high temperatures can be severe. In aquatic habitats, where bryophytes may remain hydrated despite high temperatures, few temperate aquatic taxa are able to survive.

Greater temperature variation is seen when one compares the lowlands with the montane areas. In the tropical areas of Pernambuco State, Brazil, the submontane forest is more favorable for bryophyte growth than is the lowland forest (Cavalcanti Porto 1992). This can be attributed to the lower temperatures of the higher elevations, coupled with additional moisture that results from condensation, despite the lower actual precipitation at the higher elevation. These cooler, more moist conditions favor considerably greater bryophyte diversity than can be found in warmer lowlands.

Polar and Alpine

Polar and alpine regions maintain cool temperatures favorable to C_3 plants such bryophytes throughout the growing season. Even on days that may exceed temperatures favoring net carbon gain, most of the day is generally cool enough to favor fixation over respiration. Such temperature conditions, when coupled with sufficient moisture, are highly favorable to the growth of bryophytes.

The dominant bryophytes [***Bryum argenteum*** (Figure 38), ***B. pseudotriquetrum*** (Figure 39), and ***Ceratodon purpureus*** (Figure 40)] on the Antarctic continent all are cosmopolitan and are widespread in the habitable terrain of Antarctica (Lewis Smith 1999). Each of these species predominates in its specific hydrologic zone. But the hydrologic conditions strongly influence the thermal regime for its moss dwellers. There are frequent long periods of 24-hour sunshine, during which temperatures within the moss turf remain above freezing. These long warming periods can result in more than 3.5 mm annual growth in each of these species. Despite the fact each of these species has an optimum temperature of 15°C for photosynthesis, they are able to maintain significant photosynthesis at 5°C. At 5°, 10°, and 20°C, photosynthetic rates were ***B. argenteum*** > ***B. pseudotriquetrum*** > ***C. purpureus***.

Figure 38. ***Bryum argenteum*** with capsules, one of the dominant bryophytes on Antarctica. Photo by Ivanov, with permission.

Figure 39. ***Bryum pseudotriquetrum*** in Norway, one of the dominant bryophytes on Antarctica. Photo by Michael Lüth, with permission.

Figure 40. ***Ceratodon purpureus***, one of the dominant bryophytes on Antarctica. Photo by Jiří Kameníček (BioLib, Obázek), with permission.

Jonasson *et al*. (1999) predict that warming trends in the Arctic will elicit positive responses of tracheophytes under a regime of both increased warming and higher nutrient levels, causing a decline of bryophytes. In the Antarctic, however, experiments in which soils were incubated at temperatures ranging 2 to 25ºC caused rapid development of algae, mosses, and lichens (Kennedy 1996). Some of the species that grew from these propagule banks at warmer temperatures were species not currently known from Antarctica. Further evidence of the importance of temperature in the Antarctic is the dense cover of bryophytes from temperate areas (*e.g.* ***Campylopus introflexus*** (Figure 41), ***Marchantia polymorpha*** (Figure 42), ***Philonotis acicularis***) in the geothermal areas, while other areas support only sparse cover of any vegetation. Continued dominance and increased cover of bryophytes in the Antarctic will, at least initially, be sustained through bryophytic propagules in the soil bank and the near absence of sources of tracheophyte propagules.

Figure 41. ***Campylopus introflexus***, a cosmopolitan moss that survives in geothermal areas in Antarctica. Photo by Jan-Peter Frahm, with permission.

Figure 42. ***Marchantia polymorpha*** with archegoniophores, a species that survives in geothermal areas in Antarctica. Photo by Janice Glime.

Like the polar regions, alpine areas experience extremes of temperature on a single day. On Mt. Fuji, ***Racomitrium lanuginosum*** (Figure 43) experiences up to 42ºC temperature range in a single day, whereas differences in microhabitat permit ***Grimmia elongata*** (Figure 44) to experience only 26ºC difference at the same time. This microhabitat difference is at least in part orchestrated by the moss itself – ***R. lanuginosum*** has a less dense mat than ***G. elongata***, but the former experiences a small increase in storage heat that results in a large increase in its daily temperature.

Figure 43. Exposed habitat with ***Racomitrium lanuginosum***. Photo by Michael Lüth, with permission.

Figure 44. Somewhat protected habitat with denser cushions of ***Grimmia elongata***. Photo by Michael Lüth, with permission.

Predictions of the effects of warming on the cold tundra have varied from increasing productivity of the bryophyte heath to decreasing productivity, and from increasing CO_2 loss to the atmosphere to increasing it. Johnson *et al*. (1996) found that elevated temperature alone did not change the net CO_2 storage because losses of CO_2 from respiration were offset by gains in photosynthetic uptake. However, methane (CH_4) losses are temperature-dependent and could be a substantial source of transfer from carbon sinks to the atmosphere, further amplifying global warming. Such predictions are further complicated by the availability of water and the type of vegetation.

The presence of permafrost is strongly influenced by the type of vegetation present (Camill 1999a). Changes in temperature would influence these vegetation patterns and impact the locations of permafrost and availability of surface water. Plateau regions characterized by black spruce (*Picea mariana* – Figure 45) with little ***Sphagnum*** and high cover of feather mosses (***Pleurozium schreberi*** (Figure 8), ***Hylocomium splendens*** (Figure 17), and ***Ptilium crista-castrensis*** (Figure 46)] may change considerably in character if their underlying permafrost were to diminish. Cores in these habitats suggest that thawed aquatic habitats progress to aquatic lawn areas, then to hummock communities (Camill 1999b). Such hummock communities can form permafrost in less than 80 years, but such permafrost formation in today's landscape is unlikely due to the climate-warming trend.

Figure 45. *Picea mariana* forest in Northern Alberta, Canada, with the feather mosses ***Pleurozium schreberi*** and ***Hylocomium splendens*** Richard Caners, with permission.

Figure 46. ***Ptilium crista-castrensis***, a species that is likely to diminish if the permafrost melts. Photo by Janice Glime.

Some mosses that are relatively cosmopolitan extend into the Antarctic. On a continent that is only 2% ice free, 24 species of mosses and 1 of liverworts are known (Seppelt & Ochyra 2008). One such moss, ***Hennediella heimii*** (Figure 47-Figure 48) finds its southern limit for sporophyte production (Figure 48) in Antarctica (Seppelt *et al*. 1992).

Figure 47. ***Hennediella heimii*** in a dense turf as one might find in Antarctica. Photo through Creative Commons.

Figure 48. ***Hennediella heimii*** with capsules, with its southern limit for capsule production in Antarctica. Photo by David T. Holyoak, with permission.

Lakes

Although being spared the extremes of the Antarctic terrestrial habitats, the Arctic lakes are a less than favorable habitat. They are both cold and nutrient-poor, with a short growing season (Sand-Jensen *et al*. 1999). These conditions provide the advantage of clear water to great depths, but the attenuation of light, especially red light, makes growth of bryophytes on the bottom of these lakes extremely slow. However, slow growth (~10 mm per shoot per year) is accompanied by slow decomposition, giving these bryophytes an "unprecedented" longevity, compared to other macrophytic vegetation. Because of their ability not only to tolerate these extreme conditions, but to persist for long periods of time, bryophytes are often the exclusive macrophytes in these lakes.

Seppelt (pers. comm. 7 April 2015) reports that ***Ricciocarpus natans*** (Figure 49) and ***Riccia fluitans*** (Figure 50), both floating aquatic liverworts, are common in Alaskan lakes. They survive winter under a layer of snow or encased in ice. But he points out that under the snow is actually the warmest place in the area. He supports the concept that hot dry adaptations may be the same as those for cold and dry.

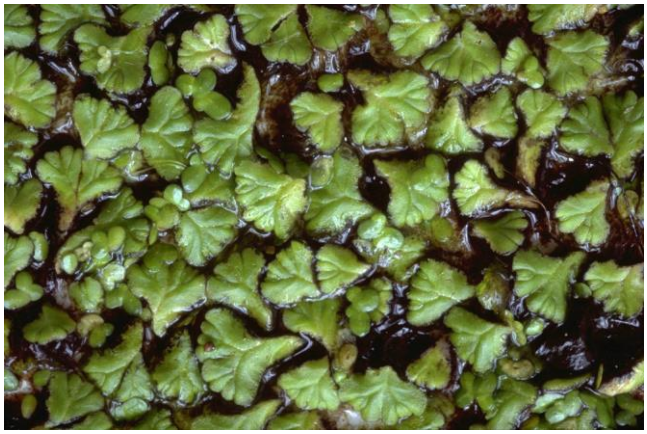

Figure 49. ***Ricciocarpos natans***, a species that can survive winter in ice or under snow. Photo by Jan-Peter Frahm, with permission.

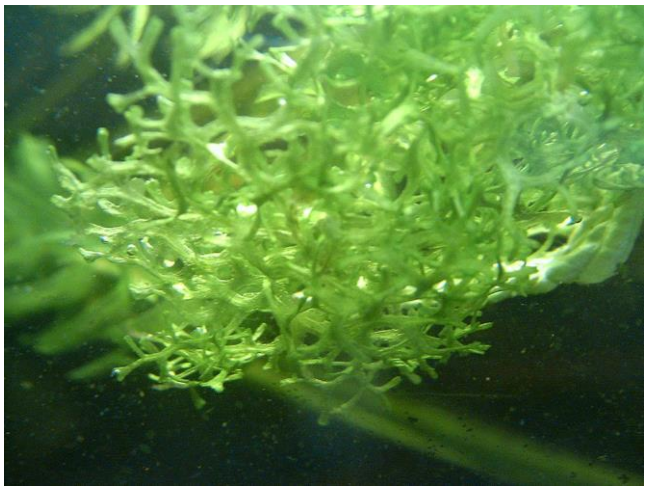

Figure 50. ***Riccia fluitans***, a species that can survive winter in ice or under snow. Photo through Creative Commons.

Streams

In riverbeds, strong gradients of temperature and moisture exist, providing excellent testing grounds for hypotheses related to moisture, light, and temperature. Arscott *et al*. (2000) used mosses from Alaska streams to test the hypothesis that ***Schistidium agassizii*** (Figure 51-Figure 52) would have greater tolerance to desiccation and that ***Hygrohypnum*** [***H. alpestre*** (Figure 53), ***H. ochraceum*** (Figure 54-Figure 55)] would have greater tolerance to elevated temperatures. ***Hygrohypnum*** spp. not only had greater tolerance to temperatures above 20ºC, but also had significantly higher photosynthetic rates at light saturation at all temperatures measured. ***Schistidium agassizii***, on the other hand, had little response to increased light and was inhibited by high temperatures, but recovered rapidly from desiccation. Such studies as these indicate the importance of temperature coupled with other variables, especially light and moisture availability.

Figure 51. ***Schistidium agassizii*** in Norway, a species that recovers well from desiccation but is inhibited by high temperatures. Photo by Michael Lüth, with permission.

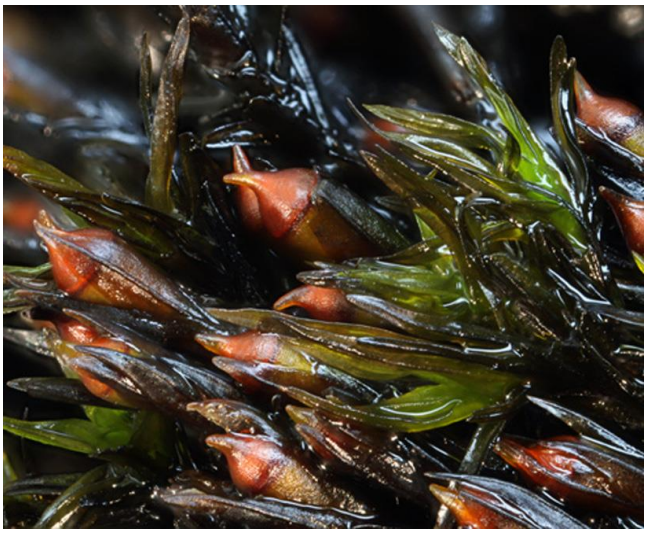

Figure 52. ***Schistidium agassizii***, a species that recovers well from desiccation but is inhibited by high temperatures. Photo by Des Callaghan, with permission.

Figure 53. ***Hygrohypnum alpestre*** in Norway, a species that tolerates temperatures above 20°C and higher photosynthetic rates at light saturation. Photo by Michael Lüth, with permission.

Figure 54. ***Hygrohypnum ochraceum*** in a typical habitat. Photo by Michael Lüth, with permission.

Figure 55. ***Hygrohypnum ochraceum***, a species that tolerates temperatures above 20°C and higher photosynthetic rates at light saturation. Photo by Michael Lüth, with permission.

Warmer temperatures of aquatic habitats not only challenge the carbon gain of photosynthesis over carbon loss to respiration, but they can alter solubility of some contaminants. In an Arctic stream (Alaska, USA), ***Hygrohypnum alpestre*** (Figure 53) and ***H. ochraceum*** (Figure 54-Figure 55) were able to take advantage of added phosphorus by having greater productivity, but ***Schistidium agassizii*** (Figure 51-Figure 52) was not (Arscott *et al*. 2000). The ***Hygrohypnum*** had greater tolerance to temperatures above 20ºC, with significantly higher productivity at all temperatures, perhaps accounting for its greater P uptake, whereas ***S. agassizii*** recovered more easily from desiccation but lacked tolerance for high temperatures.

There are most likely differences among species in their response to heavy metals at different temperatures. If a plant is temperature stressed, one might expect it to be more easily damaged by heavy metals, much as humans are more vulnerable to new infections when they are already sick. Nevertheless, Claveri and Mouvet (1995) found that when ***Platyhypnidium riparioides*** (Figure 56) was moved from 7ºC to 29ºC, both control and copper-contaminated (80 g L^{-1}) mosses exhibited chlorophyll denaturation, but copper uptake kinetics did not change.

Figure 56. ***Platyhypnidium riparioides***. Photo by Michael Lüth.

Peatlands

Peatlands provide a good test for temperature effects because the mosses are so abundant and they are widespread in the northern part of the northern hemisphere. Furthermore, they provide a gradient of microclimates from hollows to hummocks within the same macroclimate (Figure 57). Nicholson *et al*. (1996) examined the climatic relationship of peatlands along a north-south gradient in the Mackenzie River Basin, Canada. Surprisingly, in this system climate was secondary to surface water chemistry, *p*H, solute concentration, and height above water table. Among the climatic variables, temperature and length of growing season shared importance with precipitation, a major factor in height of water table. Hummock species such as ***Aulacomnium palustre*** (Figure 58), ***Dicranum undulatum*** (Figure 59), ***Hylocomium splendens*** (Figure 17), ***Pleurozium schreberi*** (Figure 8), ***Polytrichum strictum*** (Figure 60), ***Sphagnum fuscum*** (Figure 10), and ***Tomenthypnum nitens*** (Figure 61) had the widest ecological amplitude (Nicholson & Gignac 1995). Permafrost in northern habitats has created higher peat surfaces, permitting more hummock species to survive. Lawn and hollow species, on the other hand, have narrower ecological amplitude and are therefore less frequent in more northern peatlands due to continuously frozen hollows.

Figure 57. Peatland with ***Sphagnum flexuosum***, illustrating the numerous microhabitats available to create varied microclimates. Photo by Michael Lüth.

Figure 58. ***Aulacomnium palustre***, a hummock species with wide ecological amplitude. Photo by Kristian Peters through Creative Commons.

Figure 59. ***Dicranum undulatum***, a hummock species with wide ecological amplitude. Photo by Jan-Peter Frahm, with permission.

Figure 60. ***Polytrichum strictum*** with capsules, a hummock species with wide ecological amplitude. Photo by Michael Lüth, with permission.

Figure 61. ***Tomentypnum nitens*** in Norway, a hummock species with wide ecological amplitude. Photo by Michael Lüth, with permission.

Diversity seems to depend less on climate and more on habitat heterogeneity (Vitt *et al*. 1995). Nevertheless, habitat heterogeneity (46%) and temperature (15%) explain 61% of the variation in peatland diversity in 96 peatlands of continental western Canada. Vitt *et al*. (1995) found that habitat heterogeneity, coupled with *p*H or temperature, can predict biodiversity in some peatland types. For example, ***Sphagnum fuscum*** (Figure 10, Figure 57) is a hummock species. For ***Sphagnum fuscum*** in southern Finland, growth was limited to the time when the temperature was above 0ºC, but was further limited to times with ample moisture (Lindholm 1990) and thus would be affected by its height above the water table.

Although we tend to think of ***Sphagnum*** microhabitats as being defined by moisture, temperature can play an important role in competition between ***Sphagnum*** species. In a competition experiment among ***S. fuscum*** (Figure 10, Figure 57) and ***S. balticum*** (Figure 62) from a site in northern Sweden and ***S. magellanicum*** (Figure 21) and ***S. cuspidatum*** (Figure 62) from southern Sweden, all four species grew more in height and biomass production with an increase in temperature, using 11.2°, 14.7°, 18.0°, and 21.4°C, but bulk density decreased (Breeuwer *et al*. 2008). The hollow species ***S. cuspidatum*** was the least responsive. The hummock species ***S. fuscum***, on the other hand, increased biomass production 13-fold from the lowest to highest temperature when in **monoculture** (only one

species in culture). ***Sphagnum balticum*** proved to be the better competitor against ***S. magellanicum*** and ***S. fuscum***, but it lost its competitive advantage at the highest temperature.

Figure 62. ***Sphagnum balticum*** (brownish) and ***S. cuspidatum*** (green), species that increase in height and biomass production with an increase in temperature. Photo by Jan-Peter Frahm, with permission.

Summary

Climate, and especially temperature and water availability, is the primary determinant in the distribution of bryophytes. Temperature typically defines the boundaries of distribution, but water availability defines their growth and distribution within those boundaries. The ability of a species to cope with these two parameters determines, to a large degree, the breadth of the niche for a species and is often a determining difference among species and among **physiological races** (**microspecies**, **cryptic species**).

Studies on potential effects of global warming have provided us with much of what we know about bryophyte responses to temperature. In polar regions, specific habitats may respond differently, with bryophytes increasing where sufficient water is available, but decreasing where conditions favor tracheophytes. Bryophytes in non-polar regions will most likely increase, whereas those in warmer regions will most likely decrease.

Bryophytes experience seasonal changes in temperature yearly. These usually are accompanied by temperature and light/photoperiod changes. Responses may include concentration changes in chlorophyll and other pigments, soluble carbohydrate content, and in water content. Where daily fluctuations are extreme in the Antarctic, carbohydrate content changes little on an annual basis.

Bryophytes can play a major role in altering the soil temperature of an ecosystem, hence altering nutrient turnover rates. Their own decomposition is slowed by cold temperatures.

Disturbance often exposes bryophytes to intolerable heat, but other taxa, such as *Riccia* species, are adapted to survive in such areas. Grasslands can buffer temperatures enough to permit survival of some species. Tropical habitats are too warm for most aquatic bryophytes, but high elevations, where it is cooler and usually moist, there may be considerable diversity. Polar and alpine regions generally favor bryophyte growth relative to tracheophyte growth, causing dominance of bryophytes in many areas. Cold Arctic and alpine lakes may be populated exclusively by bryophytic macrophytes that have very slow growth, but exceptional longevity. Cold streams favor the growth of bryophytes, whereas warm ones favor tracheophytes. Peatlands provide a wide range of moisture and temperature combinations that favor a high diversity of species within the genus *Sphagnum*.

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CHAPTER 11-1

PHOTOSYNTHESIS: THE PROCESS

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CHAPTER 11-1
PHOTOSYNTHESIS: THE PROCESS

Figure 1. ***Antitrichia curtipendula*** on a good photosynthetic day in late spring. Photo by Michael Lüth, with permission.

Photosynthesis: The Productivity Engine

In **primary productivity** of plants, solar energy is transformed to biomass. Using photosynthesis, green plants convert solar energy, carbon dioxide, and water to glucose and other carbon-based compounds and eventually to plant tissue. **Gross primary productivity** is the product of that photosynthetic fixation of carbon, whereas **net primary productivity** is the carbon that is actually converted into biomass, *i.e.*, the fixed carbon that remains once one subtracts that lost to respiration. Consider it like your income. The gross value is your salary, but the net is what is left after taxes, social security, and other "maintenance" deductions. Respiration is the maintenance tax the plant must pay from its gross carbon fixation.

Productivity might be considered the measure of success of a plant. As stated by Anderson *et al*. (1996), photosynthesis provides energy, organic matter, and oxygen for nearly all biotic processes, and it is the only renewable energy source on Earth. If productivity is reduced in the presence of another species, we assume a competitive interaction that deprives the species of some needed resource. Thus, we might think of productivity as being the central issue in ecology around which all other issues revolve.

In order to understand bryophyte productivity, it is necessary to understand the differences in the bryophyte photosynthetic apparatus, especially the structure of the leaf or **phyllid**, compared to that of higher plants. I included the term phyllid here because technically, the bryophyte has no true leaves. This is because bryophytes lack lignified vascular tissue. However, few bryologists use the term phyllid, but rather have chosen to retain the term leaf, recognizing that the structure is different.

The CO_2 concentration in the atmosphere of early land plants was much higher than that found today (Raven & Edwards 2014). This would have supported much higher rates of photosynthesis than the current ones. Since those early times, bryophytes have evolved, adjusting to drastic climatic changes, "surviving and thriving through an incredible range of climatic and environmental variation" (Hanson & Rice 2014). Even some of the early growth forms of bryophytes are still present today, whereas many other groups of early land plants lack any presence today.

Early Studies

Much of our basic knowledge about the process of photosynthesis was learned through studies including bryophytes. In 1910, Blackman and Smith published their

work on effects of CO_2 concentration on photosynthesis and respiration, including ***Fontinalis antipyretica*** (Figure 2) in the study. In fact, ***F. antipyretica*** was included in a number of early landmark studies (Plaetzer 1917; Harder 1921, 1923). One of the most important but overlooked of these early studies on bryophytes is the one by Bode (1940) in which he described a kind of respiration that occurred in the light and that was different from that occurring in the dark. He further described that the greatest respiration occurred in blue light and the greatest photosynthesis in red light. Dilks (1976) further elaborated on this **photorespiration** in bryophytes in a study of many species, demonstrating a lower rate of $^{14}CO_2$ loss in light compared to dark that he attributed to partial reassimilation of the $^{14}CO_2$ produced, a partial inhibition of dark respiration by light, or a low rate of glycolate synthesis and oxidation. We now know that photorespiration typically is greater than dark respiration in **C_3 plants** (see below), and that dark respiration is suppressed in the light, and during the day it occurs mainly in darkened organs of plants, like roots.

Figure 2. ***Fontinalis antipyretica***, the subject of many classical studies on photosynthesis. Photo by Michael Lüth, with permission.

In the higher plants, especially seed plants, photosynthesis occurs inside a complex leaf structure that both limits and protects its activity. Only the internal structures of the leaf are involved in photosynthesis, and these are protected by an epidermis on each surface. For photosynthesis to occur in these tracheophyte plants, CO_2 must enter the leaf, which it does through openings called **stomata**. This imposes a limit based on the capacity for holding gases and the speed with which the stomata can open to admit the gases. Furthermore, when the leaf begins to dry, the stomata close, thus ending the entry of new CO_2.

The tracheophyte method of obtaining water can both limit and enhance tracheophyte photosynthesis. It means that the plant can obtain its water from the soil after the dew has gone and the rain has stopped. On the other hand, replacement of water, and its contained nutrients, is a somewhat slow process that can take minutes to hours following the addition of water by rainfall.

Bryophytes do not have these restrictions. The small size of a bryophyte leaf creates some fundamental differences in the way they achieve photosynthesis. Their ability to dry to 5-10% of their wet weight (Proctor 1990) and recover is unrivaled by most tracheophytes. Their one-cell-thick leaves have no epidermis, little or no waxy cuticle, and no stomata. Therefore, the photosynthetic cells are directly exposed to light for photosynthesis and have direct access to atmospheric gases. They furthermore have no midrib with lignified vascular conduction, but rather usually absorb their water directly through all their leaf surfaces. This means that they are able to respond to the addition of water from dew or fog and can immediately take advantage of a brief rainfall, but they have limited means of obtaining additional water from the soil to replenish that which is lost to evaporation and use. Nevertheless, many bryophytes do have a **costa**, which is the moss version of a midrib, and which at least in some species can conduct limited amounts of water and most likely other substances as well. The role of the costa and other water-responsive cells has been discussed in the chapter on water.

With these gross morphological structures in mind, we can examine the internal workings of the photosynthetic organ, the leaf. It is here that most of the chlorophyll resides and it is here that most of the photosynthesis occurs.

Structural Adaptations

Based on the foregoing discussion of tracheophyte leaves, one might assume that a plant like ***Marchantia polymorpha*** (Figure 3) would be well adapted to photosynthesis. It has a thallus with tissue arranged like the spongy mesophyll of a maple leaf, abundant air chambers, pores surrounded by tiers of cells that function somewhat like guard cells, and a cuticularized epidermis (Figure 4) (Green & Snelgar 1982). But when compared to the functioning of a solid thallus in ***Monoclea forsteri*** (Figure 5), ***Marchantia foliacea*** (Figure 6) achieves little photosynthetic advantage over the simple ***Monoclea forsteri***. Furthermore, although the chambering of ***Marchantia*** provides an advantage for water relations, ***Monoclea*** still seems to have the photosynthetic advantage in very moist habitats. Woodward (1998) asked if plants really need stomata, and answered this question by citing evidence that the number per unit area has increased in geologic time as the CO_2 concentration has decreased. It would be interesting to see if the number of pores in thalli of the **Marchantiaceae** is affected by CO_2 concentration.

Figure 3. ***Marchantia polymorpha***, a species with a chambered thallus and pores. Photo by David Holyoak, with permission.

Figure 4. Cross section of the thallus of ***Marchantia polymorpha*** showing a pore and the chambered photosynthetic tissue beneath it. Photo by Jennifer Steele, Botany Website, UBC, with permission.

Figure 5. ***Monoclea forsteri***, a solid thallose liverwort. Photo by Jan-Peter Frahm, with permission.

Figure 6. ***Marchantia foliacea***, a thallose species with a solid thallus. Photo by Jan-Peter Frahm, with permission.

But our suggestion that internal spaces and an epidermis should benefit photosynthesis is not all wrong. Some bryophytes do benefit from added internal spaces that contribute to surface area for gas exchange. In ***Polytrichum commune*** (Figure 7), leaf lamellae (Figure 8) increase the surface area 2.4-fold (Thomas *et al*. 1996). This seed plant "want-to-be" also has a waxy cuticle to prevent water loss and repels water that could block the movement of CO_2 into the leaf. Proctor (2005) demonstrated that this arrangement of lamellae seemed to protect these mosses from non-photochemical quenching that occurred in other mosses in exposed habitats. He showed that unistratose leaves are limited in their photosynthetic output by their CO_2 diffusion resistance, especially at high light levels. Mosses in the **Polytrichaceae**, on the other hand, enjoy more than a six-fold increase in leaf area, reducing the CO_2 diffusion constraint. The importance of these lamellae can be illustrated by ***Atrichum undulatum*** (**Polytrichaceae;** Figure 9-Figure 12) compared to non-polytrichaceous mosses (Krupa 1984). Leaves of this species had a higher photosynthetic rate per cm^2 than did leaves of ***Rhizomnium punctatum*** (Figure 13) or ***Funaria hygrometrica*** (Figure 14) with single-layered leaves. And the tiny ***Aloina rigida*** (Figure 15-Figure 16) with succulent, lamellose leaves had a photosynthetic rate nearly 4.5 times that of ***Funaria hygrometrica***, a moss of similar size.

Figure 7. ***Polytrichum commune***, a plant with leaf lamellae and no rolled over leaf edges. Photo by James K Lindsey, with permission.

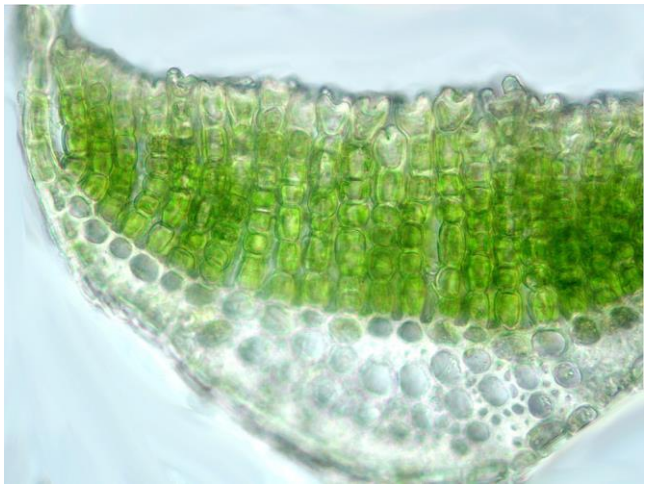

Figure 8. ***Polytrichum commune*** leaf cross section showing lamellae. Photo by Michael Lüth, with permission.

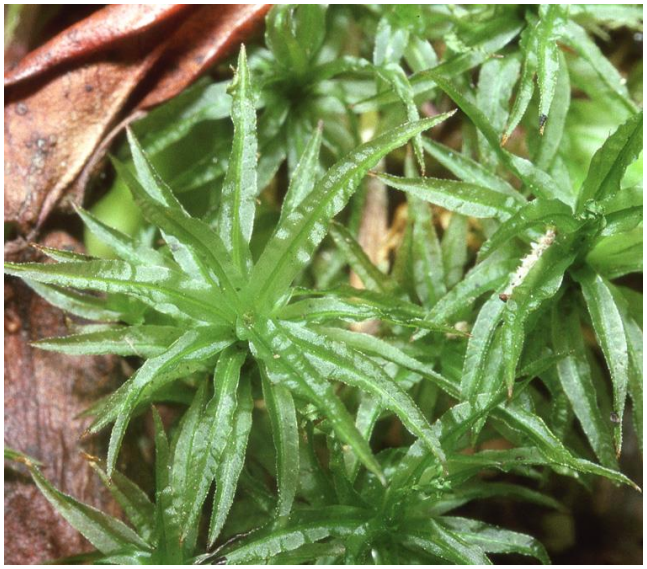

Figure 9. ***Atrichum undulatum***, a species with photosynthetic leaf lamellae. Photo by Janice Glime.

Figure 10. ***Atrichum undulatum*** leaf with lamellae showing their platelike structure. Photo by Walter Obermayer, with permission.

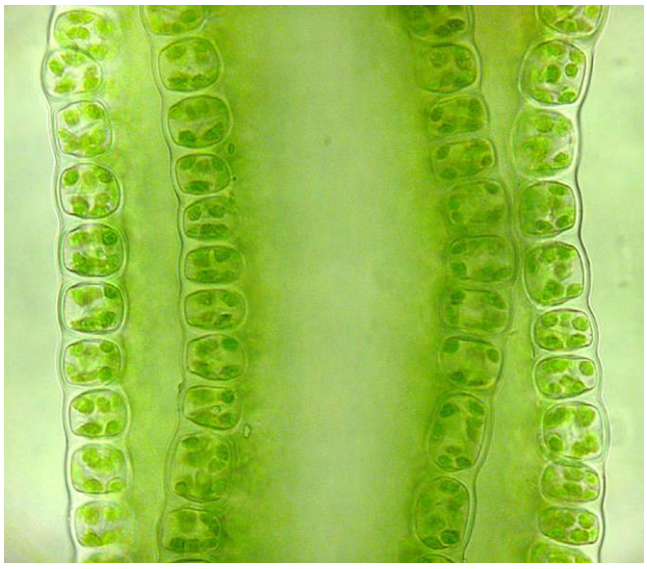

Figure 11. ***Atrichum undulatum*** leaf lamellae showing chloroplasts in the lamellae. Photo by Walter Obermayer, with permission.

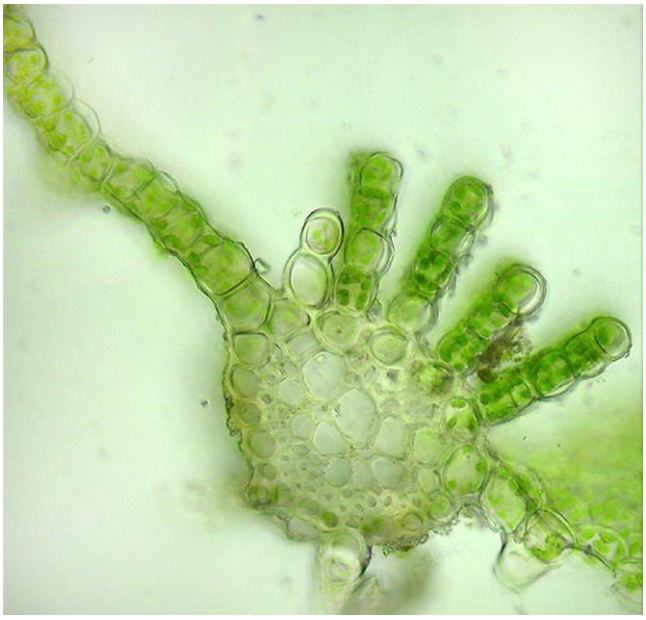

Figure 12. ***Atrichum undulatum*** leaf cs showing lamellae. Photo by Walter Obermayer, with permission.

Figure 13. ***Rhizomnium punctatum***, a species with single-layered leaves and lower photosynthetic rates than species with lamellae. Photo by Bob Klips, with permission.

Figure 14. ***Funaria hygrometrica***, a species with single-layered leaves and lower photosynthetic rates than species with lamellae. Photo by Janice Glime.

Figure 15. ***Aloina rigida***, a species with inrolled leaf margins that cover lamellae. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

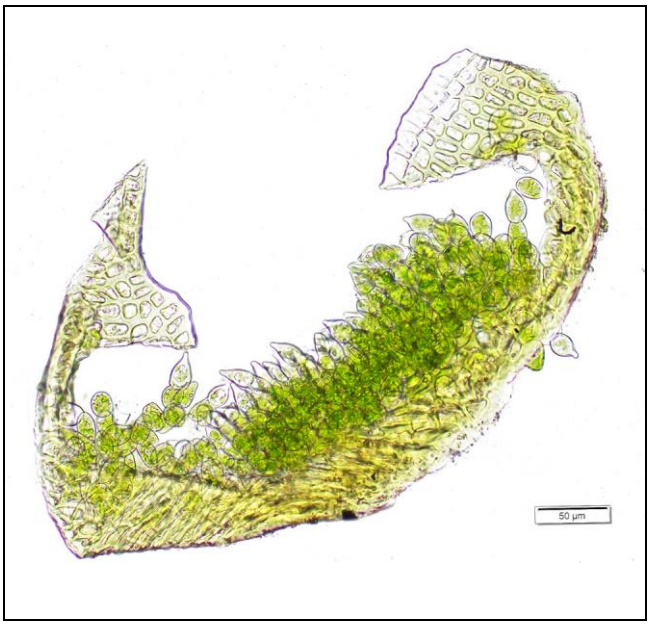

Figure 16. ***Aloina rigida*** leaf cs showing lamellae that add to its photosynthetic capability, and inrolled leaf margins that give this species its succulent look. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Some species of ***Polytrichum*** have an additional adaptation similar to that of ***Aloina rigida*** (Figure 15-Figure 16). They have colorless margins that fold over the leaf lamellae (Figure 20). In alpine populations of ***Polytrichum juniperinum*** (Figure 17-Figure 20), this margin forms a greater part of the leaf than in the woodland populations. Bazzaz *et al.* (1970) suggested that this is an adaptation to the alpine habitat. This interpretation is consistent with the higher light saturation intensity for the alpine population (10,000 lux) compared to that of the woodland population (5000 lux).

Figure 17. ***Polytrichum juniperinum*** showing leaves with overlapping edges. Photo by Michael Lüth, with permission.

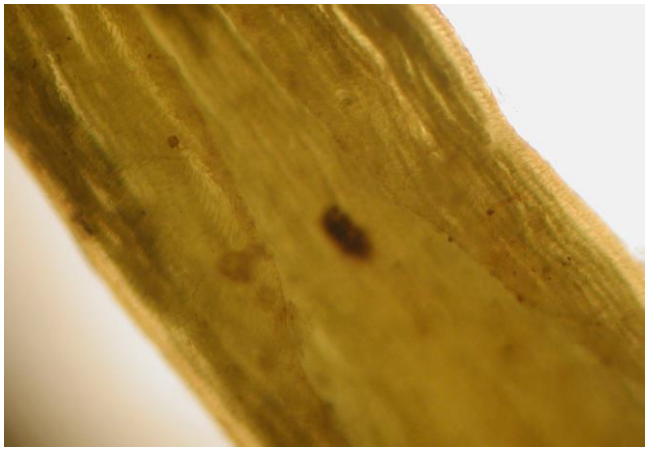

Figure 18. ***Polytrichum juniperinum*** leaf section showing tops of lamellae. Photo courtesy of John Hribljan.

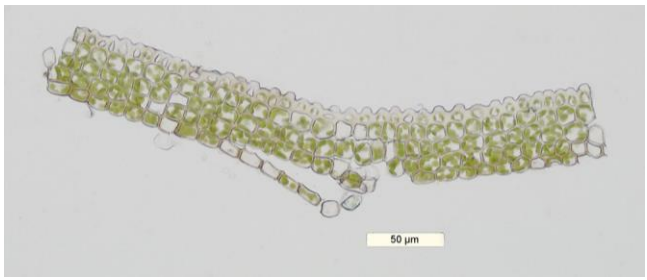

Figure 19. ***Polytrichum juniperinum*** lamella showing photosynthetic tissue. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

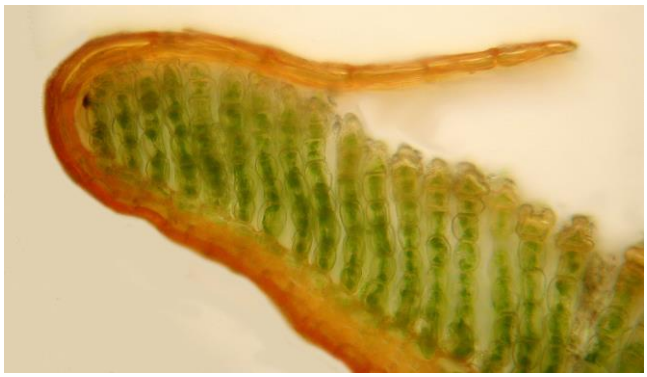

Figure 20. Leaf cross section of ***Polytrichum juniperinum*** showing leaf lamellae and rolled over leaf edge. Photo courtesy of John Hribljan.

Mosses can actually change the structure of their chloroplasts in response to different **wavelengths** of light. In ***Funaria hygrometrica*** (Figure 14), the chloroplasts responded to red light by an increase in area and a decrease in thickness, shrinking in volume by about 10% (Zurzycki 1974). In low intensity of blue light, the effects were similar, but in high levels of blue light, there was a strong reduction of the surface area and a 35% shrinkage in volume. Both effects were reversible. In ***Marchantia polymorpha*** (Figure 3-Figure 4), far-red light at the end of the photoperiod caused 20-30% drop after only a 5-minute exposure following 8-hour days for one week (Fredericq & DeGreef 1968). Longer days caused less reduction.

CO_2 concentration can also modify the size and shape of chloroplasts (Bockers *et al*. 1997). In ***Marchantia polymorpha*** (Figure 3-Figure 4), high CO_2 concentrations caused a modification of the chloroplast shape, and the cell had ~70% more chloroplasts. However, the chlorophyll content differed little, indicating that the greater number of chloroplasts exhibited less chlorophyll per chloroplast. The cells themselves were ~37% smaller in the high (2.0%) CO_2 concentrations compared to the 0.4% concentrations. These changes did not imbue the cells with any greater photosynthetic capacity or efficiency. Furthermore, the CO_2 levels are very high compared to an atmospheric concentration of less than 0.04%, so the responses may be somewhat meaningless. Sonesson *et al*. (1992) reported only 0.04-0.045% CO_2 around ***Hylocomium splendens*** (Figure 21) plants growing on soil.

Figure 21. ***Hylocomium splendens***, a plant that grows in a relatively low CO_2 environment on the forest floor. Photo through Wikimedia Commons.

Despite their small size, bryophytes respond to light much as do tracheophytes. Bryophytes increase their chlorophyll content as the light intensity decreases and increase their mean leaf area as light intensity increases (Sluka 1983).

Water is clearly a factor that limits photosynthesis. ***Sphagnum*** (Figure 22-Figure 26) has a unique way of avoiding a water problem most of the time, making photosynthesis possible long after other bryophytes are too dry (Rice & Giles 1996). It maintains its own reservoir. Each photosynthetic cell is in contact with a large **hyaline** (transparent) cell (Figure 23, Figure 25-Figure 26) that holds water. When Rice (1995) compared three species pairs, the submerged member of the pair always had greater allocation to photosynthetic tissue and greater relative growth rates than did the non-aquatic member of the pair. This can be accomplished by allocating more tissue to photosynthetic cells rather than to hyaline cells and by increasing the light-harvesting chlorophyll proteins.

Figure 22. ***Sphagnum papillosum***, a sun-dwelling hummock species. Photo by David Holyoak, with permission.

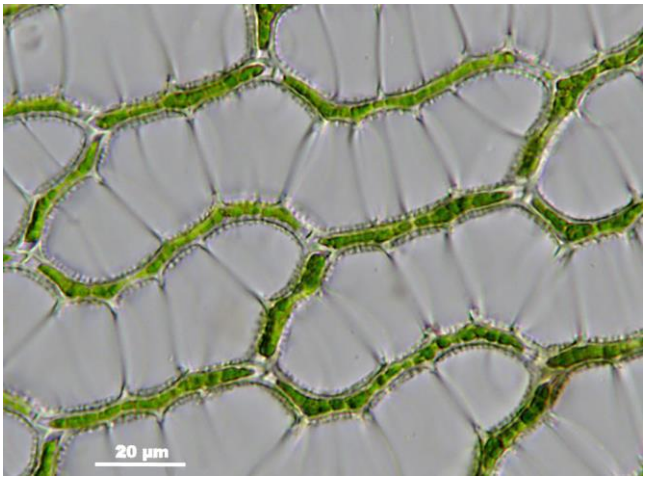

Figure 23. ***Sphagnum papillosum***, a hummock species, showing large hyaline leaf cells. Photo by Ralf Wagner <www.drralf-wagner.de>, with permission.

Figure 24. ***Sphagnum palustre***, a species of wet habitats. Photo by Bernd Haynold, through Creative Commons.

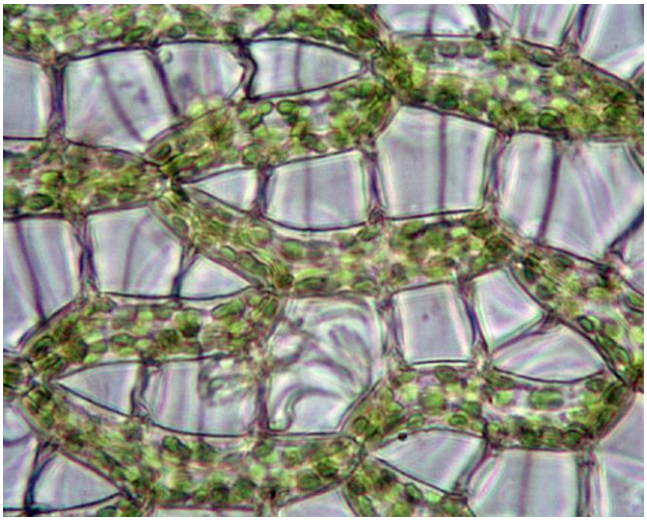

Figure 25. ***Sphagnum palustre***, an aquatic species, showing hyaline leaf cells that are reduced in size. Photo by Malcolm Storey through Creative Commons.

But obtaining **CO_2** is especially problematic in the aquatic environment. In ***Sphagnum***, reduction in the water-filled hyaline cells (Figure 23-Figure 26) helps. Additional adaptations include larger, thinner branch leaves with fewer per length of branch, reducing the boundary layer resistance to CO_2 diffusion (Rice & Schuepp 1995). Aquatic photosynthetic cells have more surface exposure than those in leaves of above-water plants. A biochemical adaptation complemented this structural adaptation by a shift that favors light-reaction proteins (Rice 1995). Proctor *et al*. (1992) demonstrated that the $\Delta 13$ for ***Sphagnum*** photosynthetic cells with hyaline enclosure on both sides (compare Figure 26 to Figure 27) is significantly lower than for other terrestrial species, being consistent with the greater resistance to CO_2 uptake with increasing submersion.

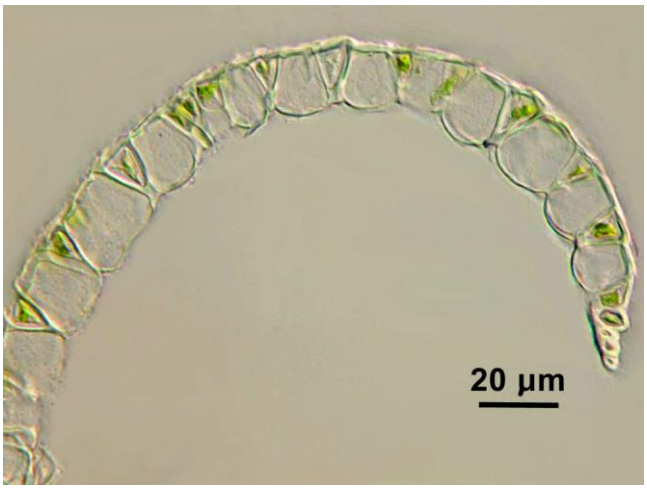

Figure 26. ***Sphagnum obtusum*** branch leaf cs showing photosynthetic cells that are exposed on the outer side of the leaf. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 27. ***Sphagnum centrale*** leaf cross section showing photosynthetic cells completely surrounded by hyaline cells. This species lives on the forest floor and on logs. Photo by Jutta Kapfer, with permission.

Bryophytes have a variety of ways to trap air within or among the leaves. Interestingly, some of our evidence comes from fossils in amber (Robinson 1985). Fossil ***Octoblepharum*** (Figure 28-Figure 29) shows trapped air in the leaves. Live ***Sphagnum*** (Figure 22-Figure 27), on the other hand, does not have air trapped in the hyaline cells – or does it? ***Leucobryum*** (Figure 30-Figure 33) has large air bubbles in its hyaline cells, with bubbles that actually extend through many cells. Unlike ***Octoblepharum***, ***Leucobryum*** leaves develop air pockets as they enlarge, but non-functional older leaves lose their air-entrapment ability. Furthermore, older leaves at the base of the plant use the hyaline cells to hold water.

Figure 28. ***Octoblepharum albidum***, a moss that is white due to hyaline cells. Photo by Michael Lüth, with permission.

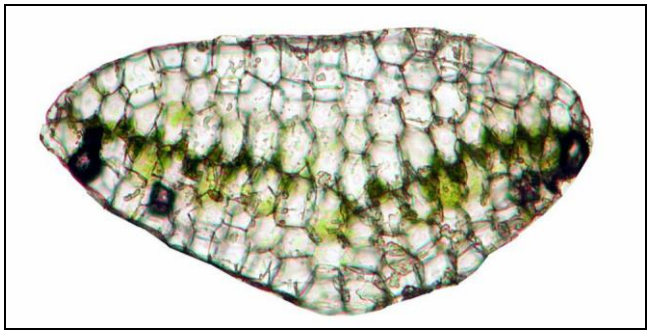

Figure 29. ***Octoblepharum albidum*** leaf cs showing a single layer of photosynthetic cells surrounded by hyaline cells. Photo by Michael Lüth, with permission.

Figure 30. ***Leucobryum glaucum*** showing its whitish color due to hyaline cells. Photo by Janice Glime.

Figure 31. ***Leucobryum glaucum*** showing its thick leaves due to the extra layers of hyaline cells. Photo by Bob Klips, with permission.

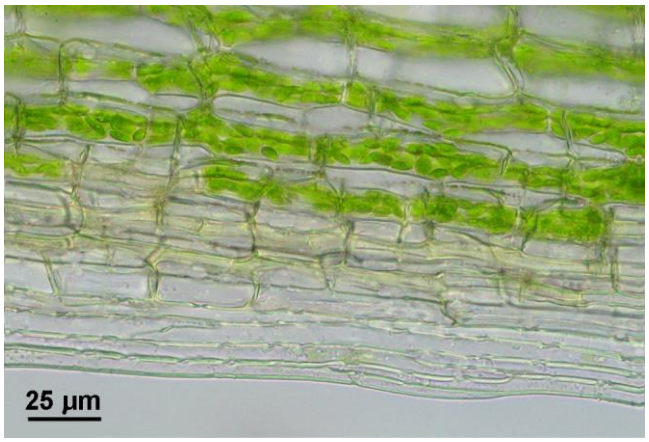

Figure 32. ***Leucobryum glaucum*** leaf section showing hyaline and photosynthetic cells. Photo by Ralf Wagner <www.drralf-wagner.de>, with permission.

Figure 33. ***Leucobryum glaucum*** leaf cs showing layer of photosynthetic cells surrounded by hyaline cells. Photo by Walter Obermayer, with permission.

One possibility to consider is that as air bubbles from photosynthesis form on the surfaces of the plants, CO_2 may enter the bubble by diffusion, much like the diving bell or the plastron used by some aquatic insects. But it would seem this would provide very small amounts indeed.

Photosynthetic Apparatus – the Chloroplast

Chloroplast Structure

Bryophytes, like tracheophytes and green algae (among others), have **chlorophylls *a*** and ***b*** and these chlorophyll molecules are organized within a complex structure called the **chloroplast**. These two photosynthetic pigments are supplemented by the **chlorophyll antenna system** of **xanthophylls** and **carotenes** that serve to trap light energy and transfer it to the chlorophyll *a* action center, all within the **chloroplast**. In all plants and green algae, **starch** is stored within the chloroplast, but it will disappear after as little as 24 hours in darkness (Raven *et al*. 1992).

Chlorophyll in all plants resides in special double-membrane-bound structures called **chloroplasts** (Figure 34). These chloroplasts have within them stacks of membrane-bound structures called **thylakoids**, and it is within these thylakoid membranes and the surrounding fluid, the **stroma**, that the photosynthetic reactions take place (Figure 35).

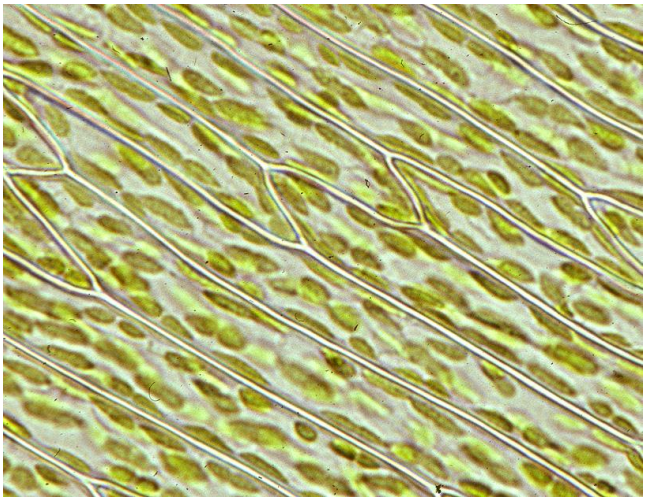

Figure 34. Cells of ***Fontinalis antipyretica*** showing chloroplasts in cells. Photo by Janice Glime.

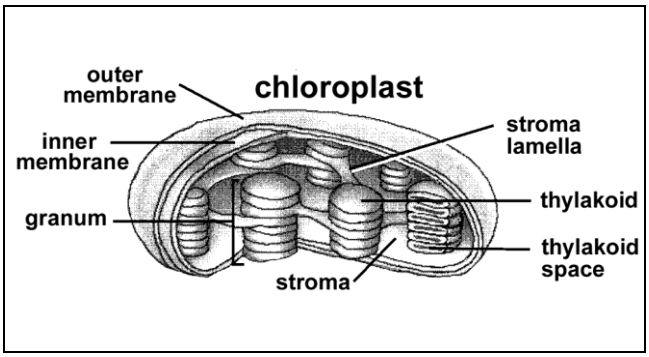

Figure 35. Structure of a single chloroplast. The chlorophyll molecules occur in the thylakoid membranes. Drawn by Janice Glime.

Associated Proteins

Associated with the chlorophyll molecules are proteins, known as **light-harvesting chlorophyll proteins** (**LHCP**). There is some evidence that the protein association with chloroplasts in bryophytes might be unique. Aro (1982a) demonstrated differences in the protein complexes associated with photosystems I and II, using ***Ceratodon purpureus*** (Figure 36), ***Pleurozium schreberi*** (Figure 37), and ***Marchantia polymorpha*** (Figure 3-Figure 4). This is suggested by their ability to survive desiccation and freezing much more easily than plastids of tracheophytes (Tuba 1985). Further evidence came from their limited solubility in acetone when dry, but ability to dissolve much more easily if rehydrated for 15 seconds first (personal observation). Genetic evidence also supports the presence of chlorophyll proteins that are unique to bryophytes. ***Marchantia polymorpha*** has an frxC gene that codes for the sequence for an ATP-binding, Fe-protein that is a bacterial type not present in the tobacco chloroplast (Fujita *et al*. 1989). Furthermore, Neuhaus *et al*. (1990) found only 94% sequence conservation of I polypeptide of Photosystem II between ***Marchantia*** and mustard (*Sinapis alba*, Figure 38).

Figure 36. ***Ceratodon purpureus***, a species with protein complexes associated with PS I and PS II. Photo by Michael Lüth, with permission.

Figure 37. ***Pleurozium schreberi*** on the forest floor of a northern forest, a species with protein complexes associated with PS I and PS II. Photo by Janice Glime.

Figure 38. ***Sinapis alba***, a species with photosystem II polypeptides that differ from those of ***Marchantia***. Photo by Ariel Palmon, through Creative Commons.

Aro (1982b) compared bryophyte chlorophyll protein composition to that of the floating aquatic plant duckweed (*Lemna*, Figure 39) and cucumber (*Cucurbita*, Figure 40). Both the moss ***Ceratodon purpureus*** (Figure 36) and the thallose liverwort ***Marchantia polymorpha*** (Figure 3-Figure 4) had more chlorophyll associated with the light-harvesting chlorophyll protein (LHCP) complexes and fewer with reaction center complexes than did the two tracheophytes. Harrer (2003) supported that observation with his study on ***Marchantia polymorpha***, demonstrating that more than 50% of the PS II particles from ***Marchantia polymorpha*** carry one or two additional masses in the protein complex. So it is possible that bryophytes may have both differences in their kinds of chlorophyll protein, and have different amounts associated in different ways, giving their chlorophyll unique protection.

Figure 39. ***Lemna minor***, member of a genus for which chlorophyll associations differ from those of the tested bryophytes. Photo through Creative Commons.

Figure 40. ***Cucurbita***, a species in which chlorophyll associations differ from those of the tested bryophytes. Photo by Maja Dumat, through Creative Commons.

Fatty Acids

Valanne (1984) and Gellerman *et al*. (1972) have suggested that the C_{20} polyunsaturated fatty acids increase the ability of mosses to adapt to extreme conditions. Those taxa living in shaded habitats have larger grana and contain even more polyunsaturated fatty acids than do sun-adapted species (Karunen & Aro 1979). It appears that polyunsaturated lipids play a role in maintaining structure and thermal stability of chloroplast membranes (Hugly *et al*. 1989), but little has been done to help us understand this relationship in bryophytes. Current studies on the genome and its function in the moss ***Physcomitrella patens*** (Figure 41) and liverwort ***Marchantia polymorpha*** (Figure 3-Figure 4) (*e.g.* Ikeuchi & Inoue 1988) are likely to help us understand these roles in the near future.

Figure 41. ***Physcomitrella patens***, a species that permits us to test gene function. Photo by Michael Lüth, with permission.

Need for Light

Color Retention in the Dark

Light is required to make chlorophyll. In the dark, chlorophyll can degrade, and dry mosses can lose chlorophyll in the light. Hence, when bryophytes first encounter light after a prolonged period of darkness, one might expect them to be pale and have reduced photosynthetic activity. But Valanne (1977) found that protonemata of ***Ceratodon purpureus*** (Figure 36) that had been in darkness for 1-2 months were able to produce starch within 30 minutes. Maximum photosynthesis, however, was not reached until the second day, providing enough time for the development of light-type chloroplasts. PS I had much higher activity in the dark-adapted protonemata than in that grown in light, whereas the activity of PS II was greater in light-grown protonemata.

Chloroplast Replication

Chloroplast replication requires light. Hahn and Miller (1966) demonstrated this in ***Polytrichum commune*** (Figure 7) by showing that in the light chloroplasts replicated, but in the dark, chloroplasts would only replicate when sucrose was present in the medium. Rather, in continuous dark, and when given 15 minutes of far-red light per six hours, chloroplasts became larger. Electron micrographs revealed that the increase in size was due at least in part to the synthesis and degradation of starch.

Photosynthetic Capacity

In general, bryophytes are considered to have lower photosynthetic capacity than that of tracheophytes (Martin & Adamson 2001). In support of this, Rao *et al*. (1979) demonstrated that the Hill reaction (light-driven splitting of water in PS II) rates of three marchantialian liverworts are lower than those of seed plants. But Martin and Adamson (2001) have challenged this view. They too found that, when expressed on the basis of dry weight, net CO_2 uptake

was considerably lower in mosses than in the six tracheophytes they studied. But the differences disappear when expressed on the basis of chlorophyll content. It would appear that the photosynthetic capacity of moss chloroplasts at light saturation and normal CO_2 levels is as great as that of tracheophytes.

One factor to be considered in the photosynthetic rate of bryophytes is their photosynthetic enzyme, ribulose bis-phosphate carboxylase/oxidase (RUBISCO). In a study by Rintamäki and Aro (1985) on a wide range of plant species, it was the moss ***Ceratodon purpureus*** (Figure 36), along with the grass *Deschampsia flexuosa* (Figure 42), that had the highest ratios of activity of RuBP carboxylase/oxidase to RuBP oxidase, suggesting yet another adaptation for a high photosynthetic capacity. But ***Ceratodon purpureus*** is a sun moss and is only one example. It is premature to generalize from this single study.

Figure 42. ***Deschampsia flexuosa***, a grass that has one of the highest ratios of activity of RuBP carboxylase to RuBP oxidase, as did ***Ceratodon purpureus***. Photo by Kelly O'Donnell, through Creative Commons.

Antenna Pigments

The actual trapping of light energy results in a rapid spin on one of the electrons of a pigment. But this initial pigment need not be chlorophyll. Rather, it can be one of the pigments (chlorophyll *b*, carotene, xanthophyll) in the **chlorophyll antenna system** (Figure 43). These pigments occur in the thylakoid membranes within the chloroplasts and are part of Photosystem I and Photosystem II. This extra spin puts the electron in a higher energy state than before and the electron spins off the pigment molecule and is transferred to another and another of the pigment molecules until it reaches the reaction center, chlorophyll *a*.

The antenna pigments permit the chloroplasts to absorb energy in the regions where chlorophyll *a* has little ability to absorb. The two dimers of chlorophyll *a* absorb best at 680 and 700 nm and very poorly between 450 and 650 nm (Martínez Abaigar & Núñez Olivera 1998). Chlorophyll *b* helps to absorb in this latter range. The carotenoids extend the absorption spectrum farther into the 450-490 nm range. Furthermore, **zeaxanthin**, a xanthophyll pigment, can deactivate singlet chlorophyll, and other carotenoids can deactivate both triplet chlorophylls and singlet oxygen that result from excess light energy. Thus, these serve as protective mechanisms against photo-inhibition and protect the chlorophylls from photooxidation, as discussed below.

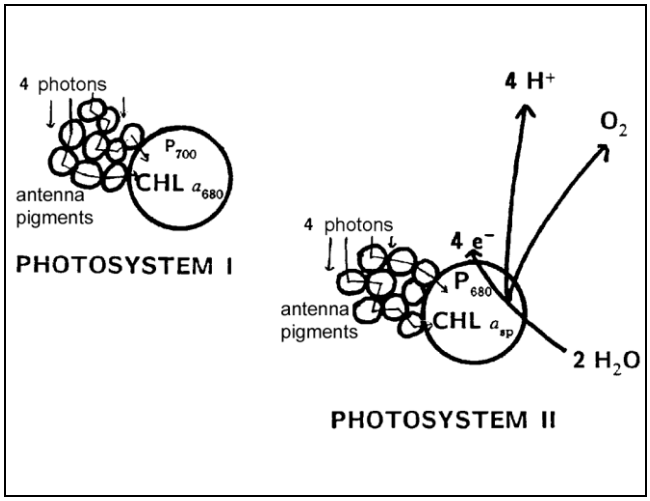

Figure 43. Antenna pigments such as carotene, xanthophyll, and chlorophyll *b* in Photosystem I and Photosystem II transfer light energy to chlorophyll *a* within a single thylakoid membrane. Excitation of electrons in chlorophyll *a* occurs in both photosystems. Modified by Janice Glime from Goodwin & Mercer 1983 and Jensen & Salisbury 1984.

The most frequent of the antenna pigments in bryophytes include α- and β-carotene, lutein, zeaxanthin, violaxanthin, and neoxanthin (Taylor *et al*. 1972; Schmidt-Stohn 1977; Czeczuga 1980, 1985; Czeczuga *et al*. 1982; Huneck 1983; Farmer *et al*. 1988; Boston *et al*. 1991). Because these antenna pigments include yellow, orange, and sometimes red, as well as the different green of chlorophyll *b*, they are able to trap energy from different wavelengths of light instead of just the red that excites chlorophyll *a*. This is advantageous for the many species that inhabit locations that are low in red light. Among ~60 species tested, pigment types differ little between aquatic and terrestrial habitats (Martínez Abaigar & Núñez Olivera 1998). Among the exceptions is the unusual pigment **auroxanthin** found in the obligate aquatic ***Fontinalis antipyretica*** (Figure 2) (Bendz *et al*. 1968).

Heber *et al*. (2005) demonstrated that **zeaxanthin** was necessary for the dissipation of light energy in hydrated mosses. They suggest that only a few molecules of zeaxanthin are needed to suppress the excess energy at the dissipation centers in the antenna system of Photosystem II. Desiccation-dependent quenching, on the other hand, does not require zeaxanthin and apparently is a property of the reaction center complex of Photosystem II.

Many more antenna pigments actually exist among the bryophytes. In a single study on only ten species of liverworts, Czeczuga (1985) found nineteen carotenoids. In addition to the seven named above, he found lycopene, lycoxanthin, α-cryptoxanthin, β-cryptoxanthin, lutein epoxide, β-carotene epoxide, antheraxanthin, α-doradexanthin, adonixanthin, mutatoxanthin, rhodoxanthin, and apo-12'-violaxanthal. All but three of these pigments were already known from mosses. Of the three new ones, α-cryptoxanthin was known in algae, lichens, and higher plants, α-doradexanthin is common in Crustacea and fish, and rhodoxanthin is known in club mosses, horsetails, ferns, conifers, and some species of the pondweed, *Potamogeton*, a flowering plant (Figure 44).

Figure 44. ***Potamogeton gramineus*** showing a red pigment, possibly rhodoxanthin. Photo by Pellaea, through Creative Commons.

Type of Photosynthetic Pathway

Among the tracheophytes, the **C_3 photosynthetic pathway** is most common, but some have a **C_4 pathway**, and some have a **CAM pathway**, neither of which seems to be available to bryophytes. These pathway names are based of the initial placement of the CO_2 when it is taken into the plant. The **C_3 pathway** is assumed to be the primitive pathway, known from algae and bryophytes, as well as tracheophytes, in which the carbon of CO_2 is fixed into a 3-carbon compound in its initial fixation within the plant. In tracheophytes, photosynthesis occurs in the mesophyll tissue of the leaf. There are no special adaptations for internal storage of the carbon for later use in photosynthesis – it must be used immediately and thus is placed immediately into the photosynthetic pathway to form **PGA** (phosphoglyceric acid; Figure 45), the 3-C compound. This immediate use is apparently characteristic of all bryophytes. This distinction of immediate use versus later use in photosynthesis is best understood by comparison with the other two pathways.

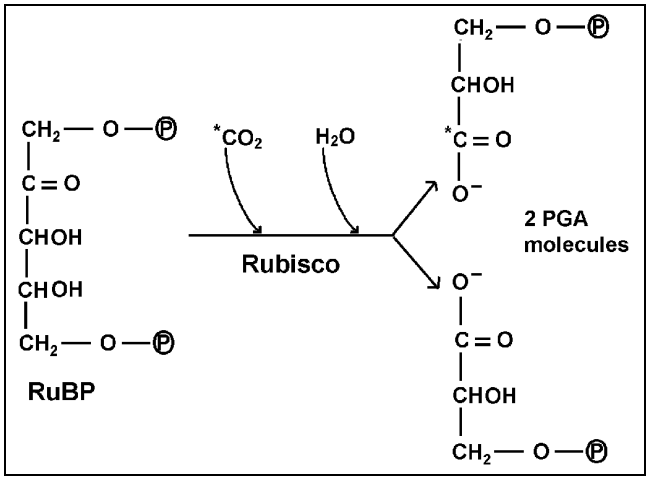

Figure 45. Melvin Calvin and associates found that the carbon from CO_2 is placed into RuBP to make a 6-carbon compound that immediately splits to form two molecules of 3-phosphoglycerate (PGA). This is the first step of the Calvin cycle and is the carbon fixation step for C_3 plants.

The **C_4 pathway** in tracheophytes permits storage of carbon from CO_2 into a 4-carbon compound such as malic or oxalic acid in the mesophyll, to later be transported to the bundle sheath around the vascular tissue, where CO_2 is released and put into the photosynthetic pathway in the bundle sheath. The advantage is that stomata of a C_4 plant can remain open for a short time, CO_2 can be stored rapidly, and photosynthesis can continue for an extended period of time after the stomata are closed. Since the stomata are the major source of water loss from the plant, this is a tremendous savings in water loss and permits the plant to be more productive in dry regions than C_3 plants.

The **CAM pathway** is similar except that stomata open at night instead of daytime as in other plants. Since photosynthesis cannot occur at night, CAM plants survive because carbon from CO_2 is stored in malic acid or other C_4 compound in the mesophyll for use in the daytime. However, in the CAM plant, the CO_2 is released in the mesophyll and photosynthesis takes place in the mesophyll tissue. Table 1 compares many of the structural and physiological attributes of plants with these three pathways.

Each of these has certain ecological advantages and disadvantages (Table 1). The C_3 pathway requires the least energy as ATP and is thus the most energy-efficient. The others, however, impart ecological advantages in hotter and/or drier climates and are more efficient in use of CO_2.

Table 1. Comparison of tracheophyte plants with different types of CO_2 fixation. From Larcher 1983, compiled from many authors.

Characteristic	C_3	C_4	CAM
Leaf structure	Laminar mesophyll, bundle sheaths	Mesophyll radially around chlorenchymatic bundle sheaths (Kranz-type anatomy)	Laminar parenchymatic arranged mesophyll large vacuole
Chlorophyll *a*/*b*	~3:1	~4:1	<3:1
CO_2-compensation concentration at optimal temperature	30-70 µl l^{-1}	<10 µl l^{-1}	in light: 0-200 µl l^{-1} in dark: <5 µl l^{-1}
Primary CO_2 acceptor	RuBP	PEP	In light: RUBP in dark: PEP
First product of photosynthesis	C_3 acids (PGA)	C_4 acids (malate, aspartate)	In light: PGA in dark: malate
Photorespiration	Yes	Not measurable	Yes
Photosynthetic depression by O_2	Yes	No	Yes
CO_2 release in light (apparent photo-respiration)	Yes	No	No
Net photosynthetic capacity	Slight to high	High to very high	In light: slight in dark: medium
Light-saturation of photosynthesis	At intermediate intensities	No saturation at highest intensities	At intermediate to high intensities
Temperature optimum	10-25°C	25-35°C	20-35ºC?
Redistribution of assimilation products	Slow	Rapid	Variable
Dry-matter production	Medium	High	Low

In fact, some bryophytes are capable of photosynthesis at temperatures below freezing, and some species of ***Fontinalis*** (Figure 2) (and probably others) have a temperature optimum near 5ºC (Glime 1987a, b). Their light saturation point is less than full sunlight, and they are capable of net photosynthetic gain at very low light intensities (such as caves and deep water). These characteristics are unknown in C_4 plants. These capabilities greatly extend the growing season for mosses and undoubtedly contribute to their success in ecosystems such as the tundra and boreal forest.

In the aquatic system, CAM photosynthesis seems to be an adaptation of some tracheophytes to the low CO_2 concentration, permitting them to gain CO_2 at night when most of the algae and other aquatic plants are respiring CO_2. The cooler atmosphere may likewise contribute to a reduced loss of the CO_2 from the body of water. It is amazing to me to learn that the C_3 ***Fontinalis antipyretica*** (Figure 2) has a higher carbon uptake rate than does the CAM plant *Isoetes bolanderi* (Figure 46) (Sandquist & Keeley 1990). Does this relate to its lack of cuticle and epidermis, permitting the immediate availability of CO_2 at any time of the day regardless of the light intensity? Perhaps a storage mechanism is not needed if uptake is always possible.

Figure 46. *Isoetes bolanderi*, a CAM plant that sequesters CO_2. Photo by Steve Matson, through Creative Commons.

C_3 Evidence

Several studies have attempted to locate a pathway other than the C_3 pathway among bryophytes, examining the most likely deviants, the aquatic and xerophytic taxa. Thus far, there is no conclusive evidence for any pathway other than C_3. It appears that bryophytes have all the earmarks of C_3 plants, exhibiting higher CO_2 compensation points than those of tracheophytes (Rudolph 1990). Since C_3 plants are unable to sequester CO_2 and have only RUBISCO to help incorporate it into their photosynthetic pathway, they require higher concentrations of CO_2 than plants with C_4 or CAM pathways.

Raven *et al*. (1998) have reviewed the evidence for the C_3 pathway in bryophytes. Biochemically, bryophytes are C_3 plants, as far as is known. Their first carboxylation reaction accounts for more than 95% of the CO_2 incorporation. The ratio of *in vitro* RUBISCO carboxylase activity to that of *in vitro* PEP carboxylase activity is far higher than that known for C_4 or CAM plants (Rintamäki & Aro 1985; Farmer *et al*. 1986; Keeley *et al*. 1986). There is insufficient PEP carboxylase activity to support the observed photosynthetic carbon flux (Rintamäki *et al*. 1988; Madsen *et al*. 1993).

The CAM pathway can be excluded because there is no evidence of nighttime activity and there is no increase in acidity or accumulation of malic acid in the dark (Keeley & Morton 1982; Keeley *et al*. 1986; Raven *et al*. 1987).

Raven *et al*. (1987) then evaluated the physiological evidence, which is primarily based on the CO_2 compensation point. These data support the relatively high CO_2 compensation point of a C_3 plant (Fock *et al*. 1969; Ruttner 1947; Allen & Spence 1981; Raven *et al.* 1987).

Further evidence to support that bryophytes use a C_3 pathway comes from the $^{13}C/^{12}C$ discrimination values. Although there are difficulties with boundary layer resistance, especially in aquatic bryophytes, overall these values are consistent with a C_3 pathway (Raven *et al*. 1987, 1994; Keeley & Sandgren 1992; Rice & Giles 1994, 1996; Smith & Griffiths 1996a, b).

CO_2-concentrating Mechanisms – Exceptions to C_3?

Although bryophytes are considered C_3 plants (Rundel *et al*. 1979, James 1981; Raven *et al*. 1998), certain evidence makes us wonder if there are other variations among them. ***Fissidens cf. manateensis*** (see Figure 47) and ***Fontinalis antipyretica*** (Figure 2) seem to have some sort of CO_2-concentrating mechanism (Salvucci & Bowes 1981; Bowes & Salvucci 1989; Raven *et al*. 1998). CO_2-concentrating mechanisms permit the plant to obtain CO_2 at a higher concentration than conditions would normally allow for a C_3 plant. This can be especially important for plants living in aquatic habitats with *p*H values in the range where the equilibrium shifts from CO_2 to bicarbonate or carbonate.

Figure 47. ***Fissidens grandifrons***, a species that might have some sort of CO_2-concentrating mechanism that permits it to live in alkaline water. Photo by Janice Glime.

Raven (1991) summarized the ecological relationships of CO_2-concentrating mechanisms in plants. He found them to be negatively correlated with areas of CO_2 enrichment caused by respiration of organic carbon that had been produced elsewhere, such as the respiration of

bacteria and other organisms in sediments. Less pronounced relationships seem to exist with low temperatures during the growing season, low *p*H external to the plant, and rapid water movement over the plants that could replace the CO_2 as it is used in photosynthesis.

When growing submerged in Florida, USA, winter conditions (12ºC, 10 h day length), ***Fissidens cf. manateensis*** (see Figure 47) had a typical C_3 compensation point (Salvucci & Bowes 1981). However, when grown in Florida summer conditions (30ºC, 14 h day length), it had the ability to concentrate CO_2. This concentrating ability can be accomplished either by concentrating CO_2 around the RUBISCO to a greater concentration than that of the medium, using a C_4-like mechanism, or by using active transport of inorganic carbon across the membrane.

But ***Fissidens cf. manateensis*** (see Figure 47) is not the only aquatic moss that appears to have some sort of CO_2-concentrating mechanism. Peñuelas (1985) found two more aquatic mosses [***Fissidens grandifrons*** (Figure 47) and ***Fontinalis antipyretica*** (Figure 2)] that could carry out net photosynthesis in high inorganic carbon concentrations with high *p*H values that should have shifted the CO_2 – bicarbonate equilibrium toward the bicarbonate or carbonate end, providing less free CO_2 than that required to reach the compensation point. Several possibilities exist. As suggested earlier, there might be a mechanism for moving this inorganic carbon across the membrane by active transport. Or the moss could use its carbonic anhydrase (Steeman Nielsen & Kristiansen 1949; Arancibia & Graham 2003) externally to convert the HCO_3^- to free CO_2. I suggest a third possibility, that H^+ ions available from cation exchange sites might be sufficient to lower the *p*H and shift the equilibrium toward CO_2 at the moss surface, despite the *p*H being too high elsewhere in the water for that shift to occur. The latter explanation would be consistent with the observations that the CO_2 compensation point and the $^{13}C/^{12}C$ discrimination values for central and Northern European populations of ***Fontinalis antipyretica***, ***Fissidens rufulus*** (Figure 48), ***Riccia fluitans*** (Figure 49), and ***Ricciocarpos natans*** (Figure 50-Figure 51) are consistent with a C_3 pathway (Ruttner 1947; Osmond *et al*. 1981; Allen & Spence 1981; Raven *et al*. 1987, 1994, 1998).

Figure 48. ***Fissidens rufulus***, a moss species with a CO_2 compensation point consistent with a C_3 plant. Photo by Hermann Schachner, through Creative Commons.

Figure 49. ***Riccia fluitans***, a floating liverwort species with a CO_2 compensation point consistent with a C_3 plant. Photo by Štěpán Koval, with permission.

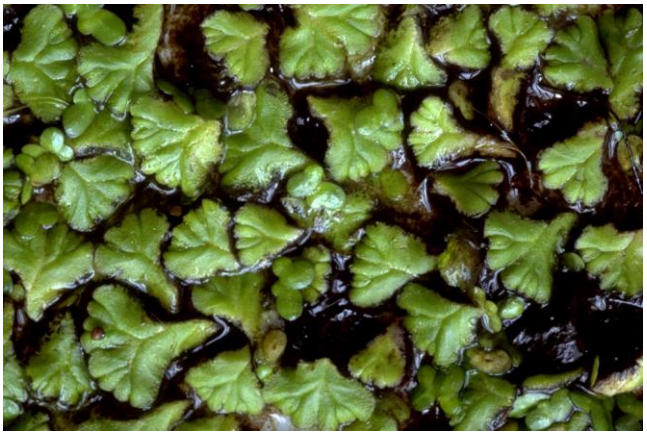

Figure 50. ***Ricciocarpos natans***, a floating thallose liverwort species with a CO_2 compensation point consistent with a C_3 plant. Photo by Jan-Frahm, with permission.

Figure 51. ***Ricciocarpos natans*** section showing internal chambering and photosynthetic cells. Photo by Norbert Stapper, with permission.

This concentrating mechanism, whatever its nature, could explain the presence of bryophytes in calcareous water of streams and lakes where the *p*H would suggest there would be insufficient free CO_2 for mosses to reach their CO_2 compensation point. And, in fact, some bryophytes of calcareous streams seem to be limited to

waterfalls where high turbulence permits gaseous atmospheric CO_2 to come in contact with the moss surface.

One of the most intriguing finds, mentioned above, is that ***Fontinalis antipyretica*** (Figure 2) has a higher C uptake rate from the water column than does its CAM companion, *Isoetes bolanderi* (Figure 46) (Sandquist & Keeley 1990). It appears that even aquatic bryophytes, contrasting with other aquatic macrophytes, lack or have only poorly developed CO_2-concentrating mechanisms (Raven 1991). But what about ***Fontinalis***? Steeman Nielsen and Kristiansen (1949) have demonstrated the presence of carbonic anhydrase in that genus. Is it able to concentrate CO_2? Can it convert bicarbonate to CO_2, perhaps through a *p*H-lowering mechanism? And how should we explain the delay in carbon fixation in ***Fontinalis antipyretica*** (Søndergaard & Sand-Jensen 1979)? Aquatic plants like *Elodea* (Figure 52) have internal air chambers that can delay the emission of respiratory CO_2 and slow the time from uptake to the time it actually enters photosynthesis. But ***F. antipyretica*** has no air chambers. However, it has the lowest delay (0.2%) of the three plants tested, with *Elodea* having 8% and *Littorella* (Figure 53) having 14%. Some researchers have treated this delay in ***Fontinalis*** as evidence of a concentrating mechanism, but the low percent seems insignificant.

Figure 52. *Elodea canadensis*, an aquatic flowering plant species with a delay in carbon fixation. Photo by Kristian Peters, through Creative Commons.

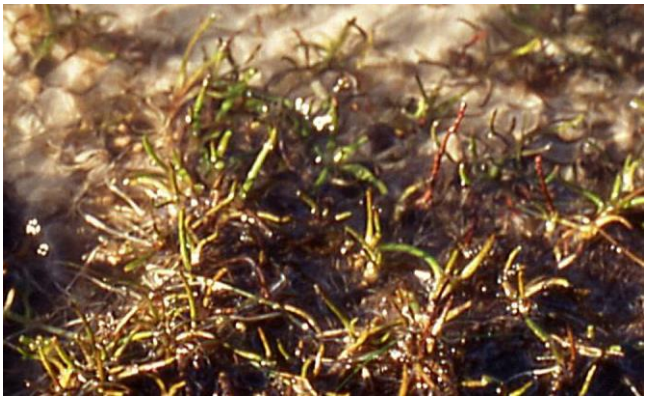

Figure 53. *Littorella uniflora*, an aquatic flowering plant species with a delay in carbon fixation. Photo by Christian Fischer, through Creative Commons.

In a separate comparison between the aquatic moss ***Leptodictyum riparium*** (Figure 54) and the tracheophyte *Elodea canadensis* (Figure 52), the moss had nearly double the RuBPcase activity (11.8 vs 6.0 µM mg^{-1} chl h^{-1}) of the tracheophyte, but also had approximately double the PEPcase activity (0.7 vs 0.3 µM mg^{-1} chl h^{-1}) (Keeley *et al*. 1986). Keeley *et al*. concluded that it is very unlikely that ***Leptodictyum riparium*** can utilize bicarbonate, whereas *Elodea* has been reported to use it freely.

Figure 54. ***Leptodictyum riparium***, an aquatic moss. Photo by Michael Lüth, with permission.

Bicarbonate Uptake

Aquatic tracheophytes typically are able to take in bicarbonate for use in the photosynthetic pathway (Farmer *et al*. 1986). Some aquatic tracheophytes, in particular species of *Isoetes* (Figure 46), have a CAM photosynthetic pathway that permits them to take in CO_2 at night. But in their study of 15 species of aquatic macrophytes, Farmer *et al*. found that the aquatic moss ***Fontinalis antipyretica*** (Figure 2) had no PEP carboxylase, took in no CO_2 at night, and used RUBISCO for its photosynthetic CO_2 fixation. Steeman Nielsen (1947) stated outright that ***Fontinalis antipyretica*** "is unable to utilize HCO_3^- in the surrounding water for photosynthesis." On the other hand, Harder (1921) showed that as bicarbonate concentration increased from 0.01% to 0.64%, the assimilation plus respiration of ***Fontinalis antipyretica*** increased from 0.66 to 3.14. Burr (1941) likewise found that ***Fontinalis*** was more productive in water with bicarbonate than that with CO_2. But what does this genus use as a mechanism to get its CO_2, especially in water with a high *p*H where bicarbonates or carbonates predominate? Steeman Nielsen and Kristiansen (1949) suggested that there is evidence that CO_2 enters the photosynthetic reactions in hydrated form (bicarbonate?). But how is that accomplished?

Perhaps Peñuelas (1985) has discovered the differences behind these contrasting conclusions. He demonstrated that ***Fontinalis antipyretica*** (Figure 2) from the River Muga in N.E. Spain was able to have a positive net photosynthesis up to a *p*H of 11.8-12.0 in a $NaHCO_3$ solution, a remarkably high *p*H and indicative of use of a carbon source other than CO_2. Further support of this conclusion is that this population of ***Fontinalis antipyretica*** increased its photosynthetic rate when higher HCO_3^- concentrations at constant CO_2 were used. But in populations from other localities, this same researcher did

not find evidence of its use of bicarbonates, suggesting that physiological races exist. This is consistent with my observations in eastern United States that it is absent in limestone streams and streams with *p*H high enough to preclude free CO_2, but in other parts of the world I have observed it growing on concrete and in alkaline streams.

Bain and Proctor (1980) tested twenty bryophytes from a variety of aquatic habitats to look for evidence of bicarbonate uptake. The ability of some bryophytes, such as ***Scorpidium*** (Figure 55), to live in water with high *p*H suggests that such a mechanism might exist. However, they found that the *p*H compensation points were in the range expected for C_3 plants dependent on free CO_2 for their carbon source. Only ***Anthoceros husnotii*** succeeded in having photosynthetic gain up to *p*H 9.5 in 2.0 mM $NaHCO_3$. For the others, the equilibrium clustered around *p*H 9.0 for 2.0 mM and 8.0 for 0.2 mM $NaHCO_3$. The four species of bicarbonate-using tracheophytes had final *p*H values ranging 10.1 – 10.9. As suggested above, there may be physiological races with different capabilities. The other possibility is that the mechanism for using bicarbonates may be inducible and was not sufficiently activated during the short-term lab experiments to make a difference.

Figure 55. ***Scorpidium scorpioides*** with capsules, a species that is able to live in high *p*H water. Photo by Michael Lüth, with permission.

Pyrenoids

The slightly elevated *p*H compensation point for ***Anthoceros husnotii*** is consistent with other data on ***Anthoceros*** that suggest the **pyrenoids** (proteinaceous bodies serving as nucleus for starch storage) have a role in concentrating CO_2 in some hornworts. Members of the **Anthocerotophyta** (hornworts; Figure 59) with pyrenoids [***Anthoceros*** (Figure 56), ***Phaeoceros*** (Figure 57)] exhibit a well-developed ability to concentrate CO_2 (Raven 1997; Smith 2000). However, it appears that among land plants, only ***Notothylas*** (Figure 58), ***Phaeoceros***, and ***Anthoceros***, all members of the phylum **Anthocerotophyta**, have such a mechanism (Smith & Griffiths 2000; Hanson *et al*. 2002). When a number of bryophytes were subjected to carbonic anhydrase inhibitors, only ***Phaeoceros laevis*** (Figure 57), a member of **Anthocerotophyta**, exhibited reduced CO_2 affinity and its CO_2 compensation point rose from 2.5 Pa to 20 Pa. No depression occurred in the other liverworts or mosses in the study. These results suggest the role of carbonic anhydrase as a CO_2-concentrating mechanism.

Figure 56. ***Anthoceros crispulus***, member of a genus that uses pyrenoids to concentrate CO_2. Photo by Manju Nair, through Creative Commons.

Figure 57. ***Phaeoceros laevis***, a species that seems to use carbonic anhydrase as a CO_2-concentrating mechanism. Photo by Robert Klips, with permission.

Figure 58. ***Notothylas orbicularis***, member of a genus that uses pyrenoids to concentrate CO_2. Photo by Michael Lüth, with permission.

Raven *et al*. (1998) have reviewed the evidence supporting a CO_2-concentrating mechanism in the pyrenoids of some members of the **Anthocerotophyta**. Such a mechanism was already known in algae with pyrenoids (Vaughn *et al*. 1990, 1992). Pyrenoid-containing hornworts exhibited a $^{13}C/^{12}C$ discrimination of 7.2-11.7% compared to 16.4-35.1% in hornworts lacking pyrenoids

(Smith & Griffiths 1996a, b). The higher values are consistent with a C_3 pathway, whereas the low values of the pyrenoid-containing hornworts are consistent with some sort of CO_2-concentrating mechanism. The CO_2 compensation point has only been investigated in ***Anthoceros crispulus*** (Figure 56), with a value of 26 µM CO_2 $mole^{-1}$, a value higher than that typical of C_4 plants, but lower than that for C_3 liverworts and mosses in the Smith and Griffiths studies (49-68 µM $mole^{-1}$).

Figure 59. ***Phaeoceros carolinianus***. Photo by Michael Lüth, with permission.

Plants with a CO_2-concentrating mechanism have a higher affinity for external CO_2 than do typical C_3 plants. ***Notothylas*** (Figure 58) and ***Phaeoceros*** (Figure 57) exhibit CO_2 compensation points of 11-13 ppm CO_2 compared to 31 ppm for ***Megaceros*** (Figure 62) and 64 ppm for ***Marchantia polymorpha*** (Figure 3-Figure 4) (Hanson *et al*. 2002), where no concentrating mechanism seems to be present.

Those plants with a CO_2-concentrating mechanism can maintain a pool of CO_2 that is immediately available after dark-light transition. ***Anthoceros crispulus*** (Figure 56) exhibited a pool size of 17.6 µmol CO_2 g^{-1} chlorophyll, whereas four of the five C_3 pathway bryophytes had no pool, and the thallose liverwort (with internal air chambers), ***Conocephalum conicum*** (Figure 60-Figure 61), had only 5.5 µmol CO_2 g^{-1} chlorophyll (Raven *et al*. 1998). ***Notothylas*** (Figure 58) and ***Phaeoceros*** (Figure 57) have an inorganic carbon pool of 19-108 µM g^{-1} chlorophyll; ***Megaceros*** (Figure 62) does not maintain any dissolved inorganic carbon pool (Hanson *et al*. 2002).

Figure 60. ***Conocephalum conicum***, a thallose liverwort with pores and air chambers. Photo by Michael Lüth, with permission.

Figure 61. Cross section of thallus of ***Conocephalum conicum*** showing the pore, air chamber, and photosynthetic vs non-photosynthetic cells. Photo from Botany Website, UBC, with permission.

Figure 62. ***Megaceros*** sp., member of a genus in **Anthocerotophyta** that seems to have no CO_2 concentrating mechanism. Photo by Juan Larrain, with permission.

But what is this CO_2-concentrating mechanism? The concentrating mechanism of the pyrenoid suppresses the oxygenase activity of RUBISCO, hence reducing the loss of CO_2 and energy through photorespiration. We do not know the immediate CO_2-fixation products in these pyrenoid-bearing hornworts. Nor do we know the PEP carboxylase to RUBISCO ratios. Is this some primitive C_4 plant struggling between relative amounts of PEP carboxylase and RUBISCO?

The Bottom Line

Nevertheless, no one has been able to demonstrate any direct evidence of a C_4 pathway, and consideration of a CAM pathway seems illogical since there are no stomata in the leaves. Therefore, we can only infer certain characteristics of bryophyte photosynthetic physiology. Like the tracheophytes, we should expect bryophytes to have low photosynthetic temperature optima, ranging 10-20ºC in most species. This is in part due to the loss of CO_2 beyond that gained in photosynthesis at higher temperatures. This loss is from photorespiration, which occurs only in light and increases with temperature more rapidly than does photosynthesis. C_4 plants either lack photorespiration or immediately grab the lost CO_2 and store it as malate. As C_3 plants, all mosses must have photorespiration and would therefore have more photosynthetic gain at low temperatures relative to C_4

plants. It appears that the first record of photorespiration in any plant was in the aquatic moss ***Fontinalis*** (Figure 2) (Bode 1940), yet the best evidence we have for the possibility of an alternative pathway of CO_2 uptake in bryophytes is in this genus. The bottom line – we still don't understand how these CO_2-concentrating mechanisms work, especially in bryophytes lacking pyrenoids.

Diurnal Patterns in Photosynthesis?

Strong daily patterns exist in some bryophytes. ***Pohlia wahlenbergii*** (Figure 63), in a sub-alpine habitat in midsummer, had its highest light-saturated photosynthetic uptake early in the morning (8 mg CO_2 g^{-1} hr^{-1}) (Coxson & Mackey 1990). By late afternoon, this had declined to ~5 mg CO_2 g^{-1} hr^{-1}. The plants showed full recovery during late evening and nighttime. The authors considered that these daily oscillations could be recurring photodestruction and repair of the pigment complexes – an unusual response for plants in high light habitats such as this. They suggested that instead these fluctuations may represent a daily, endogenous photosynthetic rhythm as known in some phytoplankton populations. Although this is an intriguing idea that would permit the moss to gain CO_2 at a time when tracheophytes are slowed by the reduced light intensity and cool temperatures, much more evidence is needed to conclude that any endogenous rhythm exists.

Figure 63. ***Pohlia wahlenbergii***, a species of wet habitats that strong daily photosynthetic patterns. Photo by Michael Lüth, with permission.

I would be more inclined to attribute these morning and evening increases to the increased moisture in the atmosphere. In some parts of the world, fog and dew are the only sources of water for bryophytes. Bryophytes taken from a desiccator will rapidly gain weight on a balance as they absorb atmospheric moisture. A similar phenomenon may permit these plants to have low levels of photosynthetic gain in the low light but higher moisture levels of early morning and pre-dusk conditions.

Products of CO_2

Generally, textbooks present glucose as the final product of photosynthesis, but in fact, this is misleading. Photosynthesis makes PGA that can then be converted to a variety of products, glucose being one of them. In bryophytes, other products are likewise possible. Valanne (1984) reported that the principal sugars made by bryophytes are sucrose, glucose, fructose, and mannose. She pointed out that evidence for notable exceptions in carbohydrate metabolism of bryophytes compared to that of tracheophytes is lacking (Allsopp 1951; Eschrich & Steiner 1967; Huneck 1969; Margaris & Kalaitzakis 1974; Valanne 1984). In the leafy liverwort ***Plagiochila asplenioides*** (Figure 65), volemitol, sucrose, and starch are the principal photosynthetic storage products (Suleiman & Lewis 1980).

Lipids are also an important photosynthetic product (Valanne 1984) in bryophytes. In the Arctic, growing shoots typically contain more lipids than carbohydrates (Rastorfer 1972).

Koskimies-Soininen and Nyberg (1991) found that the types of lipids were dependent on temperature and light. In ***Sphagnum fimbriatum*** (Figure 64), the amount of total lipid increased in dim light conditions at both 15 and 25°C. Conversely, in darkness at 25°C the lipids decreased. Under normal light levels, a decrease in temperature in the range of 5-15°C causes a decrease in the amounts of linoleic, α-linolenic, and arachidonic acids. Concomitantly, concentrations of palmitic, stearic, and oleic acids increase. When light intensity is also decreased, there is an increase in palmitic, stearic, linoleic, and arachidonic acids and a decrease in oleic and α-linolenic acids. Both temperature and light decreases elicit similar responses in total fatty acid desaturation and concentration of α-linolenic acid.

Figure 64. ***Sphagnum fimbriatum***, a species that stores more lipids in low light. Photo by David T. Holyoak, with permission.

Dark CO_2 Fixation

These newly incorporated carbohydrates don't necessarily remain in the same products as are initially stored. In as little as two hours, a number of other products are possible. Within two hours in the leafy liverworts ***Plagiochila asplenioides*** (Figure 65) and ***Scapania undulata*** (Figure 66), the amino acids asparagine, glutamine, and glutamic acid were dominant products (Gupta 1976). Citric acid and malic acids, along with an unknown acidic compound, were also common in both. In addition, ***Plagiochila*** contained fumaric, glycolic, and succinic acids, although the fumaric and glycolic acids took longer than two hours to show $^{14}CO_2$. Soluble carbohydrates included sucrose, glucose, mannitol, fructose, and a series of fructans, differing little from the ones reported by Valanne (1984). But concentrations

differ, with volemitol being the most labelled soluble carbohydrate in ***Plagiochila asplenioides*** and sucrose in ***Scapania undulata***. Interestingly, malic acid, a product associated with CAM photosynthesis, was the most labelled organic acid in both species.

Figure 65. ***Plagiochila asplenioides***. Photo by Michael Lüth, with permission.

Figure 66. ***Scapania undulata***. Photo by Michael Lüth, with permission.

In the dark, non-photosynthetically fixed carbon is incorporated into amino acids (>60% of total non-photosynthetic carbon fixation), making primarily aspartate, alanine, and glutamate (Dhindsa 1985). Most of the remaining non-photosynthetic fixation incorporates carbon into organic acids (<40%). This dark fixation permits rehydrated mosses in the dark to repair damage due to desiccation.

Transport of Photosynthate

Little is known about the movement of most substances in mosses and liverworts, but we do have evidence that both nutrients and photosynthate are indeed moved about. Alpert (1989) reported that within 26 hours, at least 10% of the photosynthate was translocated out of the leafy shoot of ***Grimmia laevigata*** (Figure 67).

Transport of photosynthate in the bryophyte is often similar to that in tracheophytes. In ***Polytrichastrum alpinum*** (Figure 68), photosynthate is translocated from the above ground shoots to the rhizomes (Hobbs & Pritchard 1987). It does not move in the **hydroids** (water-conducting cells, but rather moves in the phloem-like **leptoids**, as demonstrated in ***Polytrichum commune*** (Figure 7) (Eschrich & Steiner 1967). Hébant (1975) demonstrated that a cut stem will exude a clear liquid from the leptoids and associated parenchyma. The associated parenchyma cells seem to function much like companion cells of phloem. These cells have high enzyme activity and most likely are responsible for the movement of substances into and out of the leptoids (Richardson 1981).

Figure 67. ***Grimmia laevigata***. Photo by Michael Lüth, with permission.

Figure 68. ***Polytrichastrum alpinum***. Photo by Michael Lüth, with permission.

While tracheophyte botanists are still trying to understand the mechanisms of xylem and phloem transport in the tracheophytes, bryologists are struggling with much smaller systems in bryophytes. One bryophyte stem is little larger than a single vascular bundle in one of these lignified plants. And the aphids that live on the fluids in the tracheophytes are larger than the diameters of bryophyte stems. So how do bryologists measure something so small when mechanisms of movement in its larger counterpart have been such an enigma for plant physiologists?

For measuring phloem transport, the old adage that if there is a niche, there is an insect to fill it, comes to the rescue of the bryologists. There are indeed tiny aphids (for example ***Myzodium***, Figure 69) that live on the fluids in the phloem of ***Polytrichum*** (Figure 7, Figure 70) species. And Bob Thomas, with his coworkers, has used them to help us understand how mosses transport things from place to place internally.

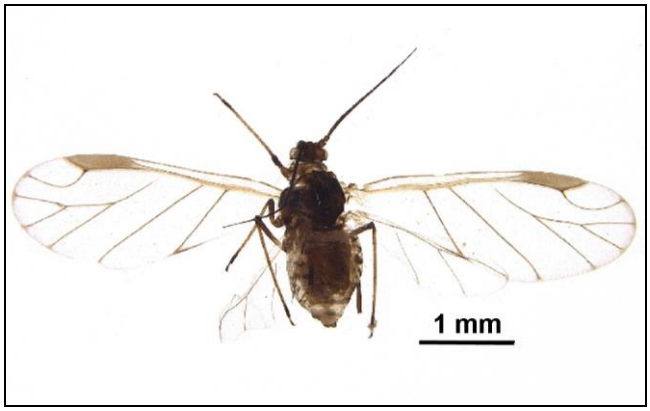

Figure 69. ***Myzodium modestum***, an aphid genus with members that feed on substances in leptoids of ***Polytrichum*** species. Photo by CBG Photography Group, through Creative Commons.

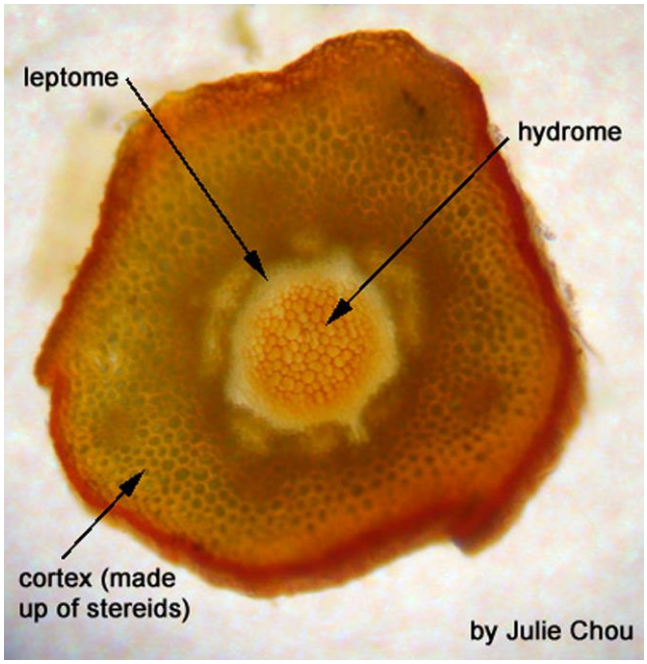

Figure 70. ***Polytrichum commune*** stem cross section, showing location of the leptoids that carry the sugars. Photo from Botany Website, UBC, with permission.

Thomas and coworkers (1990) found that ***Polytrichum commune*** (Figure 7, Figure 70) transports things from **source-to-sink**, just as we find in those other plants. Through some of their early experiments, Thomas *et al*. (1988) found glucose, fructose, and sucrose in pulse-labelled stems 30 minutes after treatment in ***Polytrichum commune***. The translocated carbon appeared in starch and cell wall polysaccharide pools within 1-6 weeks after treatment and could be used or stored. Perhaps the greater surprise is that 3.3% of the labelled sugar appeared later in neighboring stems, presumably following a source-to-sink gradient. This seems to be attributable to the transport of sugars in the leptome through perennating rhizomes, which often connect multiple stems.

But does it work the same way as in those other plants? Leaf conducting cells of ***Polytrichum commune*** (Figure 7, Figure 70) have high solute concentrations, as revealed by incipient plasmolysis, and high ATPase activity at membrane surfaces (Thomas *et al*. 1990). Thomas and coworkers concluded that this permits the moss leaf to use a process analogous to **phloem loading** in minor veins of flowering plants. Furthermore, this sugar loading seems to be coupled with proton transport, suggesting a **proton pump** to get things across cell membranes.

Just how effective is this movement in transporting sugars and other substances from leaves to basal regions? Using petroleum jelly across leaf bases to prevent external capillary movement, Thomas and Lombard (1991) found that 17-38% of the translocated label could be detected in feeding aphids within four hours – not a very rapid rate by tracheophyte standards, where rates are more commonly about 30 cm per hour (Saupe 2005). In fact, the ***Myzodium*** had to divert nutrients away from the food-conducting tissues of the stem and alter the normal source-to-sink flow in order to get enough. Even then, the aphids had to aggregate in order to compete with the natural source-to-sink travel within the moss. In ***Polytrichastrum alpinum*** (Figure 68), the photosynthate reached underground rhizomes at a rate of 3 mm h^{-1} (Collins & Oechel 1974). On the other hand, this moss can move things upward at 32 cm h^{-1} (Eschrich & Steiner 1967).

All this discussion has been on **Polytrichaceae**! We know almost nothing beyond their successful lives to tell us about the other bryophytes in which the conducting system is less well developed. ***Hylocomium splendens*** (Figure 21), a predominately ectohydric moss, moved its photosynthate so slowly that 98% remained at the fixation site 48 hours later (Callaghan *et al*. 1978).

Skré *et al*. (1983) have helped to demonstrate some of the differences and consistencies between the endohydric **Polytrichaceae** and the more common ectohydric pattern of other mosses. ***Polytrichum commune*** (Figure 7) behaved much like the C_4 plants and retained most of its labelled ^{14}C after two hours. However, after 35 days it had sequestered a large portion (second highest of the four species) in its brown tissues. The ectohydric ***Sphagnum subsecundum*** (Figure 71) retained the least of its labelled ^{14}C, but moved the highest portion to its brown tissues after 35 days. ***Hylocomium splendens*** (Figure 21) and ***Pleurozium schreberi*** (Figure 37) had inconsistent patterns of translocation, but all four species accumulated ^{14}C in their growing shoot tips and senescent brown tissues and all four experienced high losses of ^{14}C through respiration during the peak summer growing season.

Figure 71. ***Sphagnum subsecundum***, a species that moves large portions of its carbon to its brown tissues. Photo by Michael Lüth, with permission.

Storage of Photosynthate

Mosses and liverworts differ in their storage of photosynthate. In liverworts, sugar alcohols are important (Suleiman *et al*. 1979). In the mosses, the soluble product is primarily sucrose (Margaris & Kalaitzakis 1974; Suire 1975). Although most of the carbohydrates in aboveground portions of mosses are soluble sugars, the belowground parts are typically richer in starch (Hicklenton & Oechel 1977; Sveinbjörnsson & Oechel 1981). Witt and Teubert (1992) noted the contributions of phosphorylase in starch synthesis in all the sinks for starch in young gemmalings of the thallose liverwort ***Riella helicophylla*** (Figure 72). This included gemmae, meristems, and regenerating cells.

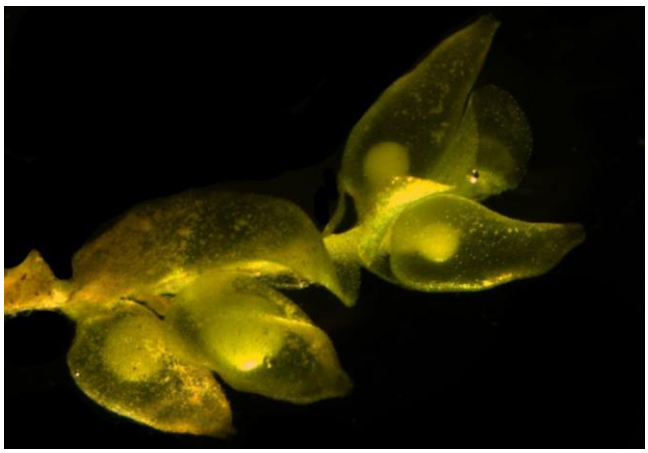

Figure 72. ***Riella helicophylla***, a species that uses phosphorylase in starch synthesis in starch sinks of gemmalings. Photo by NACICCA through Creative Commons.

In ***Polytrichum*** (Figure 7), which may not be typical, the green, photosynthesizing shoot has the largest amount of nonstructural carbohydrate and the stem the least (Sveinbjörnsson & Oechel 1981). Sugars are highest in the green shoots; starches are highest in the belowground parts. The above ground portion can move more than 30% of its daily carbon gain to the below ground rhizome. In a more ectohydric ***Dicranum fuscescens*** (Figure 73), the green part of the shoot has ~7.0-10.5% ash-free tissue dry mass as carbohydrate (Hicklenton & Oechel 1977), approximating about 0.7-1.3% of its fresh weight (Rastorfer 1972).

Figure 73. ***Dicranum fuscescens***, showing lower, light brown, senescent portion near lower portion of picture on right. Photo by Michael Lüth, with permission.

As already seen, even senescent tissue is able to store carbon products (Skré *et al*. 1983). The senescent portion of ***Dicranum elongatum*** (Figure 74) incorporates labelled carbon into lipids (Hakala & Sewón 1992). Hakala and Sewón concluded that the ability of the moss to transport such substances both upward and downward permitted this senescent portion of the moss to serve as an energy store. However, in ***Dicranum fuscescens*** (Figure 75) little change is seen in the starch content of brown, senescing parts of the shoot, while the green, leafy part increases its total carbohydrate content during the growing season. Even so, the starch content of the leafy shoots of this species, as well as ***Polytrichum commune*** (Figure 7) and ***Polytrichastrum alpinum*** (Figure 68), is less than 2% (Hicklenton & Oechel 1977), with similar values in ***Pleurozium schreberi*** (Figure 37) and ***Ceratodon purpureus*** (Figure 36) (Aro & Valanne 1979).

Figure 74. ***Dicranum elongatum***, a species in which senescent portions incorporate carbon into lipids. Photo by Michael Lüth, with permission.

Figure 75. ***Dicranum fuscescens***, a species that does not seem to store energy in its senescing parts, but rather in the green leafy part. Photo by Michael Lüth, with permission.

Sphagnum (Figure 71) increases its lipid content in the spring in growing parts but decreases it in the senescent parts (Rastorfer 1972; Karunen & Salin 1981). ***Dicranum elongatum*** (Figure 74), on the other hand, stores large quantities of lipids in its senescent parts (Karunen & Mikola 1980; Karunen & Liljenberg 1981). In cold weather, mosses, at least in the Arctic, store high quantities of triglycerides (Karunen & Kallio 1976; Swanson *et al.* 1976; Karunen 1981; Karunen & Salin 1981). Both triglycerides and unsaturated fatty acids diminish in elevated temperatures (Karunen 1981).

Illumination affects the ratio of starch to protein, with ***Pleurozium schreberi*** (Figure 37) and ***Ceratodon purpureus*** (Figure 36) in continuous illumination showing an increase in starch content and decrease in protein in the leafy shoots (Aro & Valanne 1979).

During periods of darkness, both the older, senescent portions and active photosynthetic portions of the mosses can lose stored products. In ***Racomitrium barbuloides*** (Figure 76), the concentrations of ethanol-soluble sugars and lipids in green portions decreased in the dark, indicating their use as storage substances (Sakai *et al*. 2001). However, sugars and lipids in the brown, senescent portions did not decrease and starches remained constant in both portions. Continuous light caused initial increase of sugars and lipids in the green portion, but later these decreased in these conditions. This regime caused a significant decline in photosynthetic capacity.

Figure 76. ***Racomitrium barbuloides***, a species that uses ethanol-soluble sugars and lipids as storage products. Photo by Digital Museum, Hiroshima University, with permission.

The type of carbohydrate stored determines its rate of turnover from storage. In the leafy liverwort ***Plagiochila asplenioides*** (Figure 65), breakdown of starch in the dark is rapid, but much carbon still remains as sucrose and volemitol due to their very slow turnover (Suleiman & Lewis 1980).

In limiting habitats where light limits photosynthesis, exogenous sugars may help the plants to maintain a positive carbon balance (Graham *et al*. 2010). In peat mosses, a 1% glucose solution increased photoautotrophic growth by a factor of 1.7. Air-grown mosses exhibited a 28X biomass with a 1% emendment and 39X with a 2% emendment of glucose. Similarly, fructose enhanced growth by 21X at 1% and sucrose at 2% enhanced it by 31X. Graham and coworkers suggest that this **mixotrophy** is a trait that evolved early in evolution of photosynthetic organisms. This ability to use external sugars correlates with the development of protective cell wall polyphenolics, suggesting that the sugars may "subsidize" the cost of producing these protective compounds.

Sporophyte Photosynthesis

Although mature sporophytes are seldom green, they are typically green during the earlier stages of their development. This is easy to suppose in mosses, and confirmed in such mosses as ***Funaria hygrometrica*** (Figure 14) (Krupa 1969), but liverworts do not elongate their setae until the sporophyte is mature, and the developing capsule is confined within the perianth (Figure 77). Nevertheless, Thomas *et al*. (1979) confirmed photosynthesis in liverwort sporophytes of ***Fossombronia foveolata*** (Figure 78-Figure 79), ***Lophocolea heterophylla*** (Figure 80), ***Pellia epiphylla*** (Figure 81), ***Ptilidium pulcherrimum*** (Figure 82), and ***Riella affinis***. In the leafy liverwort ***Lophocolea heterophylla***, 40% of this photosynthetic activity was attributable to spores. They confirmed that the gametophyte tissue surrounding the young sporophyte did inhibit the photosynthesis of the sporophyte by up to 50%.

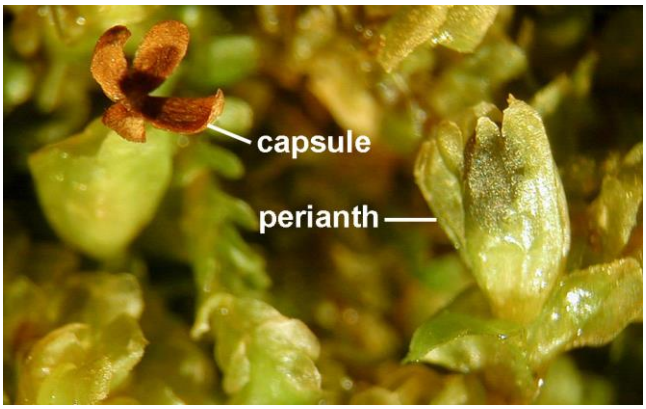

Figure 77. ***Scapania gracilis*** illustrating the complete covering of the perianth over the immature capsule and loss of green color of the capsule at maturity. Photo by Michael Lüth, with permission.

Figure 78. ***Fossombronia foveolata*** with young, green capsules. Photo by David T. Holyoak, with permission.

Figure 79. ***Fossombronia foveolata*** with mature capsules that are no longer green. Photo by Bob Klips, with permission.

Figure 80. ***Lophocolea heterophylla*** with mature capsules that have lost their green color. Photo by David T. Holyoak, with permission.

Figure 81. ***Pellia epiphylla*** young capsule emerging from perianth and losing its green color. Photo from Biopix, through Creative Commons.

Figure 82. ***Ptilidium pulcherrimum*** perianths with some of the young, green sporophytes beginning to emerge. Photo by Michael Lüth, with permission.

Krupa (1969) found that at certain stages in development, the sporophyte of ***Funaria hygrometrica*** (Figure 14) is photosynthetically self-sufficient. Nurit and Chevallier (1978) confirmed this, finding that the ***F. hygrometrica*** gametophyte has a constant production of oxygen in the light throughout its development, but that the production of oxygen in the sporophyte decreases as the capsule matures. Although the weight of the seta (Figure 83) decreases as the weight of the capsule increases (Figure 84-Figure 85) in ***Polytrichum*** (Figure 7), this is not the case in ***Funaria*** (Paolillo & Bazzaz 1968), suggesting that in ***Funaria*** the capsule does its own photosynthesizing. Nevertheless, the gametophyte makes a major contribution to sporophyte biomass in bryophytes.

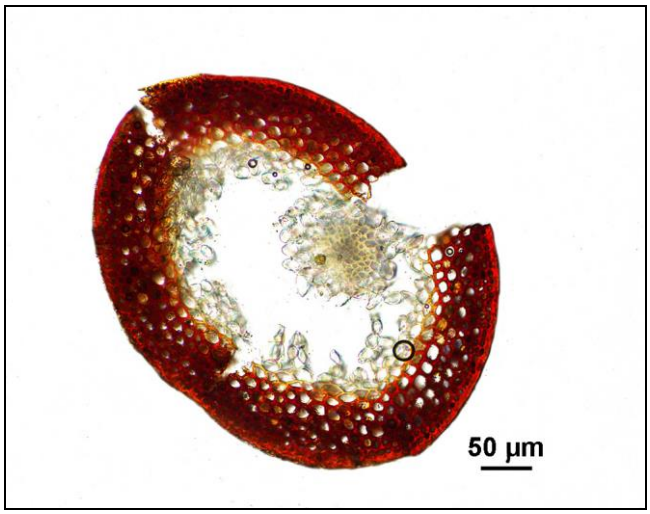

Figure 83. ***Polytrichum juniperinum*** seta cross section showing conducting tissue in circular cluster of cells just inside the break in the stem. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University.

Figure 84. ***Polytrichum juniperinum*** with expanding seta, before capsule formation. Photo by Janice Glime.

Figure 85. ***Polytrichum juniperinum*** capsules with one on left showing mature seta that is thinner than young ones. Photo by Des Callaghan, with permission.

Atanasiu (1975) compared the gametophyte and sporophyte of ***Dicranum scoparium*** (Figure 86) and ***Tortella tortuosa*** (Figure 87). The ratios of net photosynthesis to dark respiration were 0.77-0.97 in the sporophyte and 3.50-5.17 in the gametophyte, suggesting little or no net photosynthetic gain by the sporophyte. These differences were supported by the determination that the gametophytes had 3-4 times the chlorophyll content of the sporophytes. Atanasiu concluded that in these two species the sporophyte is not capable of supporting itself photosynthetically.

Figure 86. ***Dicranum scoparium*** gametophytes and sporophytes showing green capsules. Photo by Michael Lüth, with permission.

Figure 87. ***Tortella tortuosa***. Photo by Michael Lüth, with permission.

Respiration

Bryophytes, like C_3 tracheophytes, have two types of respiration. The productivity of photosynthesis creates an environment in which ATP is produced and dark respiration is suppressed. This respiration, however, occurs in the dark to produce ATP and maintain the biological process of the plant. I am aware of no studies to determine if dark respiration occurs in rhizoids in the daytime, but one might suppose that it does, as it does in roots. But whereas photosynthesis suppresses dark respiration, the presence of the RUBISCO enzyme catalyzes not only photosynthesis, but also catalyzes photorespiration, both in the light. It is this photorespiratory process that causes C_3 plants to have such a low temperature optimum for net photosynthetic gain. As the temperature rises, the rate of photorespiration increases more rapidly than does the rate of photosynthesis, until ultimately the plant loses more CO_2 and energy than it gains. For example, in the High Arctic Svalbard populations of ***Sanionia uncinata*** (Figure 88), photosynthesis at near light saturation remained nearly constant in the range of 7 to 23ºC, suggesting a Q_{10} near 1.0, but the respiratory Q_{10} in that range was 3.0 (Uchida *et al*. 2002). For this reason, most plants, including bryophytes, that have survived the test of time are those that become dormant as the temperature rises, causing both processes to cease. In bryophytes, this is often effected by drying that occurs at higher temperatures.

Figure 88. ***Sanionia uncinata***, a species that in the high Arctic does not seem to alter its photosynthetic rate in response to temperature, but that has a respiratory Q_{10} of 3.0. Photo by Michael Lüth, with permission.

Even dark respiration, which is generally only about 1/2 to 1/3 that of photorespiration, can result in a significant carbon loss. In studying tropical bryophytes, Zotz *et al*. (1997) found that more than half the carbon gained by photosynthesis in the daytime was lost during the night as respiratory loss. This left the bryophytes to gain only about 45% of their initial carbon in new carbon per year. As is common, water was the primary limiting factor for carbon gain.

In early experiments on the effects of light on respiration, Egle and Fock (1965) used, among others, the thallose liverwort ***Conocephalum conicum*** (Figure 60-Figure 61). They found that the results were similar in the liverwort and tracheophyte leaves, but that the curves for the liverwort were more pronounced. They learned that increasing oxygen concentrations (1, 25, & 75%) severely depressed photosynthesis. Following darkening, the CO_2 output increases steadily for about 5 minutes, at which time the stationary dark respiration rate is reached. Initially, high O_2 concentrations caused a strong burst of CO_2 in the dark, but within 15 minutes the thallus reaches the same equilibrium level of dark respiration. The level of oxygen from 1-99% does not influence the dark respiration. Higher light intensities increase the intensity of the CO_2 outburst at the onset of the next dark period. Using experiments that inhibited photosynthesis in the light, Egle and Fock demonstrated that the liberation of CO_2 in the light is greater than that in the dark. High O_2 concentrations cause this photorespiration to greatly exceed

the uptake of CO_2 by photosynthesis. Furthermore, old leaves exhibit more light respiration than do young leaves, contrasting with the reverse effect in dark respiration (Zelitch & Barber 1960; Fock 1965). Egle and Fock were convinced that this process was not the same respiratory process of decomposing assimilates that occurred in the dark. Rather, they discouraged the terminology "light respiration," considering that the light liberation of CO_2 might be only a side reaction of metabolism.

Peñuelas *et al*. (1988) compared the respiration rates of different parts of aquatic plants with that of the shoots of bryophytes. For the aquatic bryophytes studied, shoots had a respiratory rate of 53-66 µmol O_2 g^{-1} dry mass h^{-1}. The green alga *Cladophora glomerata* (Figure 89) had 96 µmol O_2 g^{-1} dry mass h^{-1} respiration. The algae and bryophytes had rates higher than those of flowering macrophyte stems (13-71 µmol O_2 g^{-1} dry mass h^{-1}), but lower than that of their leaves (30-142 µmol O_2 g^{-1} dry mass h^{-1}).

Figure 89. *Cladophora glomerata* filament, a green alga that, along with bryophytes, has a higher respiratory rate than the flowering aquatic plants. Photo by Noora Hellen, through Creative Commons.

Summary

Net productivity is the photosynthetic gain, measured as CO_2 uptake or O_2 emission, of a plant, whereas gross photosynthesis is the total CO_2 fixation, frequently obtained by adding respiratory loss to measured CO_2 uptake. However, photorespiration occurs in the light and cannot be measured by the dark respiration method. Photorespiration, apparently first discovered in bryophytes, contributes to CO_2 loss, and its rate is generally higher than that of dark respiration.

Bryophyte photosynthesis can respond quickly to moisture from dew and fog as well as from rain. It likewise responds quickly to light. The structural simplicity of bryophyte leaves, with only a single cell layer and no need to bring CO_2 in through stomata that close in dry atmospheres, permits bryophytes to take advantage of photosynthetic opportunities immediately. In some cases, leaf lamellae increase the surface area and chlorophyll available for photosynthesis. Pores in some liverwort thalli may control CO_2 uptake. In some cases the chloroplast structure changes in response to changes in wavelengths of light.

Bryophyte chloroplasts are typical of plants, but their chlorophyll proteins and fatty acids appear to be somewhat different from those of tracheophytes. Furthermore, the chlorophyll is conserved for long periods in the dark, whereas it is not in tracheophytes.

Bryophyte productivity is generally low, but the photosynthetic capacity, when measured on the basis of chlorophyll concentration, is similar to that of tracheophytes.

The chlorophyll antenna system, as in tracheophytes, permits bryophytes to use and transmit energy in a variety of wavelengths, directing it to chlorophyll *a*. The most common of these antenna pigments are α- and β-carotene, lutein, zeaxanthin, violaxanthin, and neoxanthin.

Although some bryophytes seem to be able to enhance CO_2 uptake, for example through pyrenoids in many of the Anthocerotophyta, their photosynthetic pathway seems to be entirely C_3. Some aquatic bryophytes, such as ***Fontinalis antipyretica***, seem to be able to take up CO_2 in high *p*H conditions that should permit only very little free CO_2, suggesting some sort of concentrating mechanism.

Photosynthate is transported in the phloem, as demonstrated by tiny aphids. It can be stored in a variety of forms, particularly sugar alcohols (liverworts) and sucrose (mosses). Lipids may be stored in senescent portions and used later for spring growth.

Sporophytes of mosses are photosynthetically active in their young stages, but liverworts do not elongate their setae until the capsule matures, causing little light to reach the developing sporophyte.

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CHAPTER 11-2
PHOTOSYNTHESIS: PHOTOINHIBITION

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CHAPTER 11-2
PHOTOSYNTHESIS: PHOTOINHIBITION

Figure 1. ***Conostomum tetragonum*** exposed to the high light intensity of an alpine area. Photo by Michael Lüth, with permission.

Photoinhibition

In high light intensities, chlorophyll can be damaged by the enhanced activity of electrons beyond that which it can process. This results in **photoinhibition** by decreasing the photosynthetic capacity. In tracheophytes, this is particularly pronounced in dehydrated plants, but in bryophytes, it seems the pattern is quite different.

Seel *et al*. (1992) compared the desiccation-tolerant moss ***Syntrichia ruralis*** var. ***arenicola*** (=*Tortula ruraliformis*) (Figure 2) with the desiccation-intolerant moss ***Dicranella palustris*** (Figure 2). It appeared that desiccation in the dark had no effect on total concentrations of chlorophylls or carotenoids in either moss, but in *D. palustris* it resulted in loss of protein and accumulation of TBA, suggesting lipid peroxidation. ***Dicranella palustris*** was unable to recover its photosynthesis during rehydration, whereas photosynthesis of ***Syntrichia ruralis*** var. ***arenicola*** had only marginal depression in photosynthesis upon rehydration, and only at the highest irradiance. In the light, ***D. palustris*** likewise lost not only protein, but also chlorophyll and carotenoids, while lipid peroxidation increased. Again, ***S. ruralis*** var. ***arenicola*** suffered little damage. Greater damage occurred to this species when hydrated and exposed to high irradiance. Thus we can include that desiccation tolerance affords some protection to the chlorophyll in the presence of high light intensities, at least in some bryophyte species.

Figure 2. **Upper:** ***Syntrichia ruralis*** var. ***arenicola***. **Lower:** ***Dicranella palustris***. Photos by Michael Lüth, with permission.

Temperature plays a major role in photoinhibition and light damage. At low Antarctic temperatures with exposure to high light intensity, ***Schistidium antarctici*** (Figure 3) experienced reduction in its **photosynthetic capacity** (light-saturated rate), **photosynthetic efficiency** (ratio of energy stored to energy of light absorbed), ratio of **variable to maximum fluorescence**, and rate of **fluorescence quenching** when exposed to moderate light (Adamson *et al*. 1988). Adamson *et al*. suggested that photoinhibition may play a major role in limiting photosynthesis and productivity in the Antarctic region. On the other hand, Alpert (1988) showed that ***Grimmia laevigata*** (Figure 4-Figure 5) exhibits no chlorophyll damage during 20 months of desiccation if it is shielded from potential photodamage.

Figure 3. ***Schistidium antarctici***, a high light species that experiences reduced photosynthetic potential in moderate light. Photo courtesy of Rod Seppelt.

Figure 4. ***Grimmia laevigata*** in its typical habitat. Photo by Alan Cressler, with permission.

Figure 5. ***Grimmia laevigata***, a species that can survive 20 months of desiccation without chlorophyll damage. Photo by David Holyoak, with permission.

Quenching

Two means, known as **quenching**, seem to be available to plants, or at least to bryophytes, to reduce excessive activation energy and avoid damage from high light activity. In higher plants and bryophytes, this can be done by the reaction center itself. But bryophytes seem to behave somewhat differently from tracheophytes. For example, the leafy liverwort ***Bazzania trilobata*** (Figure 6) exhibits no decrease in quantum yield in its open reaction centers when oversaturated with light, whereas both peas and barley do (Horton *et al*. 1988), suggesting that the behavior of the reaction center is not essential to prevent photoinhibition in at least some bryophytes. Rather, at least some bryophytes seem to be able to accomplish photoquenching by use of accessory pigments (Paulsen 1998).

Figure 6. ***Bazzania trilobata***, a species that does not decrease its quantum yield when oversaturated with light. Photo by Dick Haaksma, with permission.

One might expect such quenching activities to be especially important in alpine bryophytes. Fluorescence in bryophytes in alpine areas with high UV light intensity can result in different effects from those on tracheophytes (Heber *et al*. 2000). When dehydrated, alpine populations of ***Grimmia alpestris*** (Figure 7) had very low chlorophyll

fluorescence while alpine tracheophytes had high levels. On the other hand, mosses and lichens increase their chlorophyll fluorescence upon rehydration, whereas tracheophytes experience a decrease. Heber *et al*. considered this increase in mosses and lichens to relate to their lack of photodamage in a dry state. Nevertheless, tracheophytes, bryophytes, and lichens all can form chlorophyll fluorescence quenchers as a response to desiccation, but only the bryophytes and lichens exhibit a decrease in fluorescence in response to light energy transfer while dehydrated. Thus, among the alpine taxa they examined, only the bryophyte *Grimmia alpestris* used deactivation to avoid photodamage in both its hydrated and dehydrated states.

Figure 7. ***Grimmia alpestris***, a species with low chlorophyll fluorescence. Photo by Henk Greven, with permission.

Zeaxanthin

One explanation for photo-protective quenching is that in high intensity light, the carotenoid violaxanthin, which itself inhibits quenching, is de-epoxidized to form **zeaxanthin** (Paulsen 1998). The theory is that this transformation to zeaxanthin lowers the energy level sufficiently to permit it to trap energy from the chlorophyll excited state. However, **auroxanthin**, a diepoxy xanthophyll, has an even higher energy level than that of violaxanthin, but it promotes fluorescence quenching and aggregation in isolated major light-harvesting complex II, similar to the effect of zeaxanthin. Ruban *et al*. (1998) have challenged this interpretation of trapping chlorophyll energy because auroxanthin behaves similarly to zeaxanthin as a stimulator of quenching. Rather, Ruban *et al*. contend that it is the flat shape of zeaxanthin and auroxanthin, compared to the perpendicular shape of violaxanthin, that permits them to perform their quenching function.

Sunflecks can initiate rapidly reversible photoprotection within minutes to elicit non-photochemical chlorophyll fluorescence quenching (Matsubara *et al*. 2005). This is vitally important to bryophytes living in forests where low light is supplemented by these ephemeral bursts of bright light. Detectable conversion of the violaxanthin pigment to the protective antheraxanthin or zeaxanthin takes longer, suggesting that there may be more than one mechanism for photoprotection.

In prolonged strong light, photoprotection is usually stabilized within hours of exposure through this reversible violaxanthin cycle, but there is also a slowly reversible conversion of the pigment lutein epoxide to lutein. Matsubara *et al*. suggested that the lutein "locks in" a primary photoprotective mechanism in some species, causing light-harvesting antenna pigments to serve as centers for dissipating excitation energy in high light. Czeczuga (1985) found that lutein epoxide accumulated in ***Marchantia polymorpha*** (Figure 8) thalli in late summer, autumn, and after winter. However, thus far we have no evidence of the specific role of lutein or lutein epoxide in bryophytes.

Figure 8. ***Marchantia polymorpha***, a species that accumulates lutein epoxide seasonally. Photo by Jan-Peter Frahm, with permission.

Bukhov *et al*. (2001a) found that light quenching of chlorophyll fluorescence in the moss ***Rhytidiadelphus squarrosus*** (Figure 9) apparently originated in the pigment antenna system, but in the tracheophytes *Arabidopsis thaliana* (Figure 10) and *Spinacia oleracea* (Figure 11) it appeared to originate in the reaction center. The quenching in ***R. squarrosus*** was strongly enhanced by the pigment **zeaxanthin** (Bukhov *et al* 2001b). Short bursts of light were sufficient to cause an increase in levels of zeaxanthin in this moss, albeit in a 20% CO_2 atmosphere. In fact, only one molecule of zeaxanthin was needed to quench the efficiency of charge separation in Photosystem II by 50%.

Figure 9. ***Rhytidiadelphus squarrosus***, a moss that quenches high light energy with the pigment **zeaxanthin.** Photo by Michael Lüth, with permission.

Figure 10. ***Arabidopsis thaliana*** basal rosette, where light quenching originates in the reaction center. Photo through Creative Commons.

Figure 11. ***Spinacia oleracea*** female plant, a species in which light quenching originates in the reaction center. Photo by Rasbak, through Creative Commons.

Heber *et al*. (2001) concluded that the absence of ATP consumption in reactions associated with the coupled electron transport of PS II permitted the acidification needed in the thylakoids for binding zeaxanthin to the chlorophyll-containing thylakoid protein. These form energy-dissipating traps in the antennae of PS II. Furthermore, the competition for energy capture decreases the activity of PS II. Both mosses and lichens benefit from the protein protonation and zeaxanthin availability in the dissipation of energy in PS II, whereas this is not the case in tracheophytes. The energy dissipation in mosses and lichens in the dry state is not related to protonation and zeaxanthin availability, as indicated by the absence of chlorophyll fluorescence. For mosses and lichens, the big advantage is that excitation of PS II by sunlight is not destructive when they are dry, whereas dry leaves of tracheophytes rapidly lose their PS II activity under strong illumination.

Rintamäki *et al*. (1994) found that strong light induced the PS II centers to increase their capacity for repair of photochemical damage in the moss ***Ceratodon purpureus*** (Figure 12). This increased tolerance was associated with a rapid turnover of the D1 protein, apparently mediated by lincomycin. In the absence of lincomycin, strong light resulted in a net loss of this D1 protein, suggesting that the rapid degradation of the protein was independent of the resynthesis of polypeptide. They interpreted this to mean that synthesis was the limiting factor in the turnover of the D1 protein during photoinhibition. Furthermore, the initial level of fluorescence was correlated with the production of inactive PS II reaction centers that were depleted of the D1 protein. The higher the fluorescence level, the greater the depletion of the D1 protein. Addition of lincomycin facilitated the recovery of the D1 protein, and the rate of D1 protein synthesis after photoinhibition exceeded that of control plants during the first hours under recovery conditions.

Figure 12. ***Ceratodon purpureus***, a species in which strong light induces PS II centers to increase their capacity for repair of photochemical damage. Photo by Janice Glime.

Deltoro *et al.* (1998) compared a desiccation-tolerant (***Frullania dilatata***, Figure 13) and desiccation-intolerant (***Pellia endiviifolia***, Figure 14) liverwort to examine the effects of desiccation and light on non-photochemical quenching. In ***F. dilatata***, there was a rise in the concentration of de-epoxidized xanthophylls that can protect the cells from chlorophyll damage when photosynthesis cannot occur to trap the excited electrons. Dry ***Pellia endiviifolia***, on the other hand, experienced less dissipation of electron activity and did not experience a rise in de-epoxidized xanthophylls. The increase in de-epoxidized xanthophylls appears to be induced by desiccation and mediated by zeaxanthin.

Figure 13. The desiccation-tolerant ***Frullania dilatata*** exhibiting colored protective pigments. Photo by Michael Lüth, with permission.

Figure 14. The desiccation-intolerant ***Pellia endiviifolia*** lacking any visible protective pigments. Photo by Michael Lüth, with permission.

Chloroplast Position

The position of the chloroplasts plays a role not only in maximizing the light capture by the cell in low light, as in protonemata of ***Schistostega pennata*** (Figure 15), but also in minimizing chlorophyll fluorescence during desiccation. Grouping of the plastids during drying may enhance the effect of chlorophyll reabsorption, causing a notable decrease in the F685/F735 ratio in the chlorophyll fluorescence spectrum, as shown in ***Rhizomnium punctatum*** (Figure 16) leaves (Bartosková *et al*. 1999).

Figure 15. ***Schistostega pennata*** protonemata, a species that moves its chloroplasts to maximize light absorption. Photo courtesy of Martine Lapointe, with permission.

Figure 16. ***Rhizomnium punctatum***, a species that groups its plastids during drying. Photo by Janice Glime.

Sun and Shade Plants

Photosynthetic organs of plants typically adjust their chlorophyll concentrations as light conditions change (Martin & Churchill 1982). Hence, those organs in high light intensity tend to have lower concentrations of chlorophyll *b* and total chlorophyll than those in the shade (Valanne 1977; Martin & Churchill 1982). The chlorophyll *b* serves as one of the antenna pigments to trap light energy and transfer it to the chlorophyll *a* reaction center.

Within the bryophytes, there are both chlorophyll and plastid structural differences between plants typical of shade and those of sun, but these may not necessarily be accompanied by photosynthetic differences (Aro *et al*. 1981). For example, ***Marchantia polymorpha*** (Figure 8) has a plastid structure characteristic of shade plants, and ***Ceratodon purpureus*** (Figure 12) of sun plants, but both have the photosynthetic kinetics of shade plants.

Chlorophyll Concentration

Bryophytes in general have chlorophyll concentrations typical of shade plants (Tieszen & Johnson 1968; Table 1). Deora and Chaudhary (1991) examined the chlorophyll content in a number of Indian bryophytes and reported the ranges. Chlorophyll *a* ranged 0.402±0.052 to 2.002±0.700 mg g^{-1} dry mass. Chlorophyll *b* ranged 0.265±0.067 to 1.634±0.070 mg g^{-1} dry mass. The highest level of chlorophyll was in the cave moss ***Cyathodium tuberosum*** (Figure 17) (3.636 mg g^{-1} dw) and the lowest in ***Entodon prorepens*** (Figure 18) (0.667 mg g^{-1} dw). They found that, like the tracheophytes, high solar irradiances corresponded with low chlorophyll content and high *a*:*b* ratios. Martínez Abaigar and Núñez Olivera (1998) compiled data from a number of studies to show that on either a weight or areas basis, bryophytes have lower chlorophyll concentrations than do tracheophytes (Figure 19). They attributed this higher level in tracheophytes to the more complex structure of these plants.

Figure 17. ***Cyathodium*** sp.; ***C. tuberosum*** has the highest chlorophyll concentration of a number of Indian bryophytes. Photo by Li Zhang, with permission.

Figure 18. ***Entodon prorepens***, a species with the lowest chlorophyll concentration of a number of Indian bryophytes. Photo by Li Zhang, with permission.

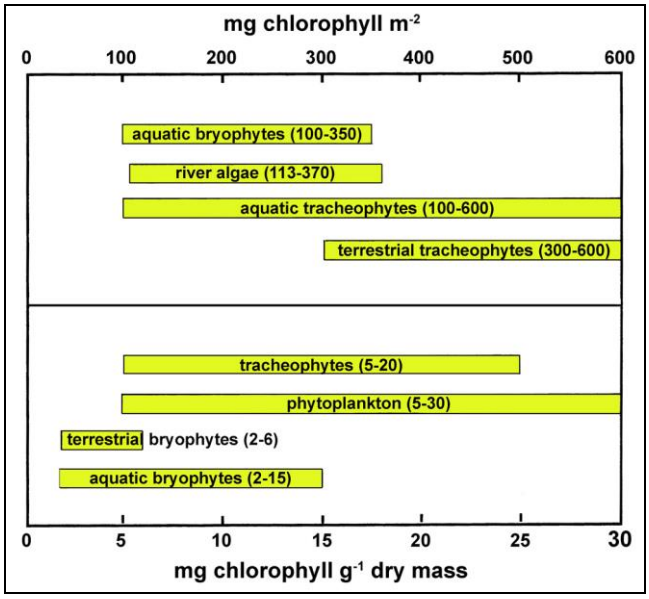

Figure 19. Comparisons of chlorophyll concentrations on an area (**upper**) and biomass (**lower**) basis. Redrawn from Martínez Abaigar and Núñez Olivera (1998), based on data from Martínez Abaigar *et al*. 1994.

Marschall and Proctor (2004) examined 39 moss and 16 liverwort species to compare chlorophylls and carotenoids in relation to light intensity and light saturation. They found a median total chlorophyll concentration of 1.64 mg g^{-1} for mosses and 3.76 mg g^{-1} for liverworts. Mean chlorophyll *a*:*b* ratios were 2.29 and 1.99, respectively. The chlorophyll:carotenoid ratio mean was 4.74 for mosses and 6.75 for liverworts. Light saturation values were low, with almost all less than 1000 µmol m^{-2} s^{-1}; the median for mosses was 583 and for liverworts 214 µmol m^{-2} s^{-1}. These numbers suggest that liverworts, in general, are more shade-adapted than are mosses. Deora and Chaudhary (1991) reached the same conclusion in their study of Indian bryophytes. Pande and Singh (1987) also compared mosses and liverworts during the rainy season in Nainital, Kumaun Himalaya, finding the liverworts to be more prominent in the shade and mosses in the sun, likewise having more chlorophyll and carotenoids in the liverworts. However, they found no chlorophyll:carotenoid differences between liverworts and mosses.

Marschall and Proctor (2004) concluded that bryophytes are **not** "inherently" shade plants and do include sun plants. For example, species of ***Polytrichum*** have lamellae that provide additional surface area for gas exchange, permitting greater CO_2 uptake; these species had the highest **photosynthetic photon flux density** (**PPFD**). Masarovičová and Eliás (1987) supported this conclusion by showing that ***Polytrichum commune*** (Figure 20-Figure 21), with well-developed lamellae, had a higher saturation photosynthetic rate (3.67-5.62 mg CO_2 g^{-1} dry mass h^{-1}) and higher photosynthesis per chlorophyll concentration (0.53 mg CO_2 chl h^{-1}) than did ***Atrichum undulatum*** (Figure 22-Figure 23) (which has less-well-developed lamellae; Figure 23) (3.41 mg CO_2 g^{-1} dry mass h^{-1}) or ***Hypnum cupressiforme*** (Figure 24) (which has no lamellae) (2.56 mg CO_2 g^{-1} dry mass h^{-1}). Marschall and Proctor found that chlorophyll concentration, chlorophyll *a*:*b* ratios, and chlorophyll:carotenoid ratios all were significantly correlated with PPFD at 95% saturation in the bryophytes tested. Nevertheless, the light saturation levels of all bryophytes were lower than those for tracheophytes of open sun habitats. Marschall and Proctor attributed the lower saturation levels to the difficulty of obtaining CO_2 into the cells of bryophytes.

Figure 20. ***Polytrichum commune***, a species with well-developed leaf lamellae. Photo by Michael Lüth, with permission.

Figure 21. ***Polytrichum commune*** showing tall lamellae over entire cross section of leaf. Photo from Botany Website, UBC, with permission.

Figure 22. ***Atrichum undulatum***, a species with lamellae over the leaf costa. photo by Janice Glime.

Figure 23. ***Atrichum undulatum*** leaf cross section showing low lamellae over costa of leaf. Photo by Walter Obermayer, with permission.

Figure 24. ***Hypnum cupressiforme***, a species with no leaf lamellae. Photo by J. C. Schou, with permission.

Chlorophyll degrades into phaeophytin. Chlorophyll *a* degrades more easily than does chlorophyll *b*; hence, phaeophytin *a* has been used as an indication of chlorophyll damage that can result from pollution or other stress. Bastardo (1980) suggests that a chlorophyll *a* to phaeophytin ratio of less than 1.0 in the aquatic moss ***Fontinalis*** (Figure 25) indicates irreversible damage to the chlorophyll component. However, in their study of submerged mosses, Martínez Abaigar *et al*. (1994) found that chlorophyll of aquatic mosses did not degrade into phaeopigments.

Figure 25. ***Fontinalis antipyretica*** var ***gracilis***, a species that exhibits irreversible damage when its chlorophyll *a* to phaeophytin ratio is <1.0. Photo by David Holyoak, with permission.

Deep lakes provide some of the darkest habitats for bryophytes. Fully hydrated, bryophytes are able to take advantage of the CO_2 emitted from the sediments for a slow but steady growth without competition from other macrophytes. These plants are highly shade adapted and have a low light saturation level. The leafy liverwort ***Chiloscyphus rivularis*** (see Figure 26) in Crystal Lake, Wisconsin, USA, is saturated at ~50 µM photons m^{-2} s^{-1} (Farmer *et al*. 1988). This leafy liverwort has high concentrations of chlorophylls *a* and *b* as well as carotenoids. The carotenoids produced consist mostly of **lutein**, a yellow-orange pigment that has most of its absorption at 470-500 nm (blue light). The light energy is transferred through the pigment antenna system to chlorophyll *a*. Table 1 compares chlorophyll levels of a number of bryophyte species.

Figure 26. ***Chiloscyphus polyanthos***; ***C. rivularis*** has high concentrations of chlorophylls *a* and *b* and carotenoids. Photo by Bernd Haynold, through Creative Commons.

In seemingly sharp contrast to this deep-water lutein production, Czeczuga (1987) grew bryophyte leaves under various light intensities with seemingly conflicting results. As in other studies, in the shade the total carotenoid content and β-carotene increased, along with chlorophyll, but in the sunlight there was a marked increase in the lutein content of the leaves. Why should these leaves increase their antenna pigments, particularly lutein, in the sunlight? Is it serving as a filter, unconnected to the antenna function?

Table 1. Chlorophyll concentration (mg g^{-1} dry mass) in a variety of bryophytes, ordered by *a*/*b* ratio.

Species	***a***	***b***	**Total**	***a*/*b***	**Date/ Intensity**	**Location**	**Reference**
Polytrichum piliferum				3.63			Krupa 1984
Plagiomnium undulatum	7.21	2.62	9.82	2.75	27 Jul	SW Slovakia	Masarovičová & Eliás 1987
Atrichum undulatum	6.06	2.27	8.34	2.67	3 Jul	SW Slovakia	Masarovičová & Eliás 1987
Ditrichum flexicaule	2.66	1.06	3.72	2.51	27 Jul	SW Slovakia	Masarovičová & Eliás 1987
Hypnum cupressiforme	4.87	1.91	6.60	2.44	27 Jul	SW Slovakia	Masarovičová & Eliás 1987
Pohlia sp.	8.22	3.46	11.68	2.38	27 Jul	SW Slovakia	Masarovičová & Eliás 1987
Polytrichum formosum	6.37	2.67	9.04	2.38	27 Jul	SW Slovakia	Masarovičová & Eliás 1987
Rhizomnium punctatum			14				Krupa 1984
Polytrichum commune	7.74	3.82	11.56	2.14	3 Jul	SW Slovakia	Masarovičová & Eliás 1987
Hyophila involuta	1.210	0.713	1.923	1.697	50 klux		Deora & Chaudhary 1991
Riccia billardieri	1.465	0.897	2.362	1.632	12-14 klux		Deora & Chaudhary 1991
Plagiochasma appendiculatum	1.934	1.231	3.165	1.571	12 klux		Deora & Chaudhary 1991
Atrichum angustatum				1.5			Martin 1980
Plagiochasma articulatum	1.651	1.112	2.763	1.485	12 klux		Deora & Chaudhary 1991
Cyathodium tuberosum	2.002	1.630	3.636	1.225	10 klux		Deora & Chaudhary 1991
Tortula muralis	1.801	1.388	3.189	1.297	50-70 klux		Deora & Chaudhary 1991
Gymnostomiella vernicosa	1.102	0.687	1.789	1.604	60 klux		Deora & Chaudhary 1991
Fissidens geminiflorous var *nagasakinus*	1.060	0.663	1.723	1.598	55 klux		Deora & Chaudhary 1991
Fissidens curvato-involutus	0.969	0.552	1.521	1.755	45-55 klux		Deora & Chaudhary 1991
Philonotis revoluta	0.964	0.864	1.828	1.115	75 klux		Deora & Chaudhary 1991
Fabronia minuta	0.956	0.891	1.847	1.068	40-50 klux		Deora & Chaudhary 1991
Fissidens diversifolius	0.913	0.645	1.558	1.424	50 klux		Deora & Chaudhary 1991
Bryum cellulare	0.889	0.629	1.518	1.413	50 klux		Deora & Chaudhary 1991
Funaria hygrometrica	0.837	0.587	1.424	1.425	70 klux		Deora & Chaudhary 1991
Bryum capillare	0.544	0.514	1.098	1.058	70 klux		Deora & Chaudhary 1991
Entodon myurus	0.544	0.371	0.915	1.613	80-90 klux		Deora & Chaudhary 1991
Funaria nutans	0.514	0.479	1.020	1.129	70 klux		Deora & Chaudhary 1991
Barbula vinealis	0.406	0.279	0.685	1.455	90 klux		Deora & Chaudhary 1991
Entodon prorepens	0.402	0.265	0.667	1.516	80-90 klux		Deora & Chaudhary 1991
Marchantia polymorpha			0.462*	1.23			Rao et al. 1979
Marchantia polymorpha tips	7.7	2.33	10.03	3.30			Fredericq & De Greef 1968
Marchantia polymorpha bases	6.25	1.88	8.13	3.32			Fredericq & De Greef 1968
Marchantia palmata			0.207*	1.07			Rao et al. 1979
Reboulia hemisphaerica			0.234*	1.11			Rao et al. 1979
Ceratodon purpureus			6.8	2.2	rhythmic lt, 1400 µW cm^2		Valanne 1977
Ceratodon purpureus			3.0	2.0	contin lt, 1400 µW cm^2		Valanne 1977
Ceratodon purpureus			8.5	2.0	rhythmic lt, 200 µW cm^2		Valanne 1977
Ceratodon purpureus			8.1	1.9	contin lt, 200 µW cm^2		Valanne 1977
Dicranum scoparium			1.7				Martin 1980
Brachythecium velutinum			1.8				Martin 1980
Grimmia laevigata			1.6				Martin 1980
Leucobryum glaucum			1.4				Martin 1980
Leucodon julaceus			1.9				Martin 1980
Plagiomnium cuspidatum			1.6				Martin 1980
Polytrichum ohioense			1.8				Martin 1980
Sphagnum lescurii			1.8				Martin 1980
Thelia asprella			1.9				Martin 1980
Thuidium delicatulum			2.1				Martin 1980

*Fresh weight

Age Differences

Masarovičová and Eliás (1987) showed that chlorophyll concentrations differ with age. One need only look at bryophytes in the spring to observe that older parts are typically dark and new growth is a light (Figure 27), almost chartreuse, green. However, storage of other substances in senescing parts contributes to their dark color.

Figure 27. ***Polytrichum commune*** with new, green growth from splash cups and darker, brownish lower parts. Photo by Štěpán Koval, with permission.

Chlorophyll *a*:*b* Ratio

Chlorophyll *a*:*b* ratios can vary considerably, depending on the light available, time of year, and the adaptations of the bryophytes. Martin and Churchill (1982) reported a mean of 2.69 (2.29-2.99) for 20 moss species in an oak-hickory (*Quercus-Carya*, Figure 28) woods in Kansas, USA. But in his study of North Carolina, USA, Martin (1980) reported only 1.14-2.1 for 11 moss species. Masarovičová and Eliás (1987) found a range of 2.14-2.85 for woodland mosses in SW Slovakia in July.

The genus ***Riccia*** frequents a variety of disturbed habitats as well as living on the water surface of lakes and ponds. Patidar *et al*. (1986) found that within this genus, the highest chlorophyll concentrations occurred in shade-grown ***Riccia discolor*** (Figure 29). The lowest concentrations occurred in ***Riccia fluitans*** (Figure 30), a species that floats on the water surface, often in direct sunlight. But surprisingly, the chlorophyll *a*:*b* ratios did not differ among the species in these different habitats.

Figure 28. Oak-hickory forest. Photo by Brian Stansberry, through Creative Commons.

Figure 29. ***Riccia discolor***. When growing in the shade, this species has the highest chlorophyll content among the ***Riccia*** species tested. Photo by Jan Ševčik, through Creative Commons.

Figure 30. ***Riccia fluitans***, the species with the lowest concentration of chlorophyll, in its sunny floating habitat. Photo by Jan-Peter Frahm, with permission.

An increase in irradiance will cause an increase in productivity up to the point where light saturation is reached. In a 36-day laboratory experiment using seven different light levels, Rincòn (1993) demonstrated this concept with six bryophyte species [***Brachythecium rutabulum*** (Figure 31), ***Eurhynchium praelongum*** (Figure 32), ***Lophocolea bidentata*** (Figure 33), ***Plagiomnium***

undulatum (Figure 34), ***Pseudoscleropodium purum*** (Figure 35), ***Thuidium tamariscinum*** (Figure 36)]; all responded to the higher light intensities with greater biomass increase. But they also demonstrated (except for ***Lophocolea bidentata***) that lower light intensities resulted in greater shoot length increase, a response suggesting that IAA was being inhibited by the greater intensity of light. Like Patidar *et al*. (1986), they found that all species had higher chlorophyll levels at low irradiances, but there were no distinct changes in chlorophyll *a*:*b* ratios with light intensity.

Figure 31. ***Brachythecium rutabulum***, a species with greater productivity in high light, but with greater elongation in low light. Photo through Creative Commons.

Figure 32. ***Eurhynchium praelongum***, a species with greater productivity in high light, but with greater elongation in low light. Photo by Michael Lüth, with permission.

Figure 33. ***Lophocolea bidentata***, a species with greater productivity in high light, but no greater elongation in low light. Photo by Michael Lüth, with permission.

Figure 34. ***Plagiomnium undulatum***, a species with greater productivity in high light, but greater elongation in low light. Photo by Michael Lüth, with permission.

Figure 35. ***Pseudoscleropodium purum***, a species with greater productivity in high light, but greater elongation in low light. Photo by Michael Becker, through Creative Commons.

Figure 36. ***Thuidium tamariscinum***, a species with greater productivity in high light, but greater elongation in low light. Photo by Janice Glime.

Tieszen and Johnson (1968) pointed out the importance of bryophytes in tundra ecosystems by examining the chlorophyll distribution within several

communities. Those communities with the lowest overall chlorophyll had the greatest amount of it in their moss and ericaceous components. In the Dry Sedge tundra, about one-third of the chlorophyll was in the moss component. However, in the Wet Sedge tundra, only about 2% was in the moss component. Like other studies discussed earlier, they found that the moss layer had the lowest chlorophyll *a*:*b* ratio, which ranged 1.5-2.5 for all plants. These are relatively low chlorophyll *a*:*b* ratios overall and correspond with the lower light intensities of Arctic latitudes.

Yang *et al*. (1994) compared bryophyte chlorophyll *a*:*b* ratios in 17 species from Yuan-Yang Lake. The minimum ratio was 2.17, with a mean of 2.41. This mean was lower than that found for the two aquatic tracheophytes (3.08), but was nevertheless somewhat higher than most bryophyte values reported (Table 1).

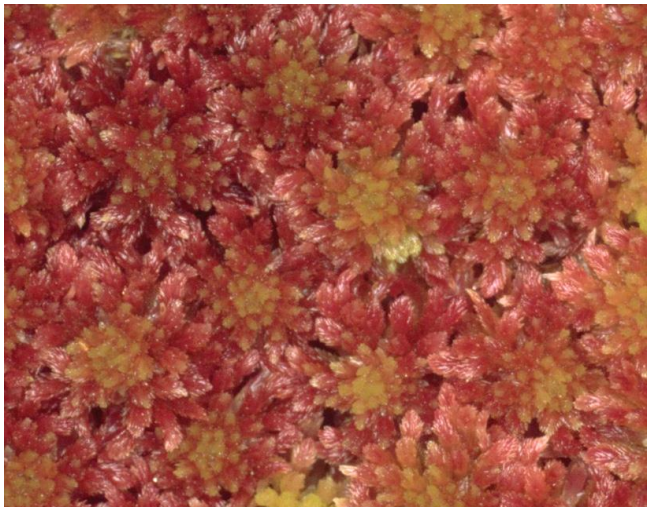

Figure 37. ***Sphagnum capillifolium***, exhibiting its colorful pigments. Photo by Jan-Peter Frahm, with permission.

Czeczuga (1985) quantified the carotenoid pigment concentration in ***Marchantia polymorpha*** (Figure 8) from March until November. Percentage of total pigments were close to or more than double in June, July, and August (17.8-25.0%) compared to the other sampled months (1.8-9.3%). At the same time, the chlorophyll *a*:*b* ratio dropped steadily from 1.41 on 1 April to 1.00 by 14 October.

In a study of aquatic bryophytes the chlorophyll *a* and *b* values ranged widely from 1.52 to 6.67 mg chl *a* g^{-1} dry mass and from 0.61 to 2.70 chl *b* (Martínez Abaigar *et al*. 1994; Figure 38). In autumn and winter, chl *a* ranged 2.11-6.27 and chl *b* ranged 0.91 to 2.95. The ranges of *a*:*b* ratio remained nearly the same in all four seasons (1.95-3.25). But when the bryophytes were separated by habitat, several patterns emerged. Those from habitats subject to summer desiccation had a low summer concentration of chlorophyll and *a*:*b* ratio with an increase in the carotenoid portion. Those from under a dense tree canopy increased in chlorophyll content from spring to summer, and some continued that increase into autumn, while others dropped down again. Those that were continuously submerged demonstrated the smallest seasonal pigment variations.

Seasonal Differences

As light intensity changes, antenna pigments, cytoplasmic water-soluble pigments, and wall pigments change. This results in seasonal changes in the color of the bryophytes.

Martin and Churchill (1982) found that total chlorophyll content of woodland mosses increased from early spring (1.45 mg g^{-1} dry mass) before canopy closure to that attained after full canopy closure (4.36 mg g^{-1} dry mass), demonstrating the wide range of plasticity in the chlorophyll content in these plants. Kershaw and Webber (1986) found a similar relationship in ***Brachythecium rutabulum*** (Figure 31), with chlorophyll concentrations increasing from 1.70 mg g^{-1} on 8 May to 11.1 mg g^{-1} on 11 October. During this time, light saturation declined from 200 µM m^{-2} s^{-1} to 30 µM m^{-2} s^{-1} by 6 July, with the light compensation point likewise falling from 65 µM m^{-2} s^{-1} to 4 µM m^{-2} s^{-1}. It is clear that at least some bryophytes have a large capacity to adjust to changing light levels.

Epiphytes are subject to almost constant drying in both summer and winter. Their highest chlorophyll production is in the autumn, October to November, in Japan (Miyata & Hosokawa 1961), when autumn rain and temperatures suitable for C_3 plants make photosynthesis possible. Their lowest concentrations are in summer.

Gerdol *et al*. (1994) took a novel approach to determining seasonal differences in pigment concentrations in ***Sphagnum capillifolium*** (Figure 37). They compared plant segments and found that both chlorophylls were highest in the midsummer segment. Carotenoids were fairly stable except in spring. Chlorophyll degradation products (phaeophytin, pheophorbide, and chloride) accumulated in the autumn capitulum segment. They interpreted this autumn segment to indicate a rapid degradation of chlorophyll coincident with the night chilling of the end of the growing season.

Habitat Differences in Chlorophyll

Desert and Dry Areas

In the desiccation-tolerant ***Syntrichia ruralis*** (Figure 39) from the Organ Mountains of southern New Mexico, Mishler and Oliver (1991) found that the total chlorophyll on a dry weight basis was higher in late summer and winter than in early summer. The chlorophyll *a*:*b* ratios were relatively low (1.00-2.50), compared to those of tracheophytes, and seemed to have no regular variation pattern.

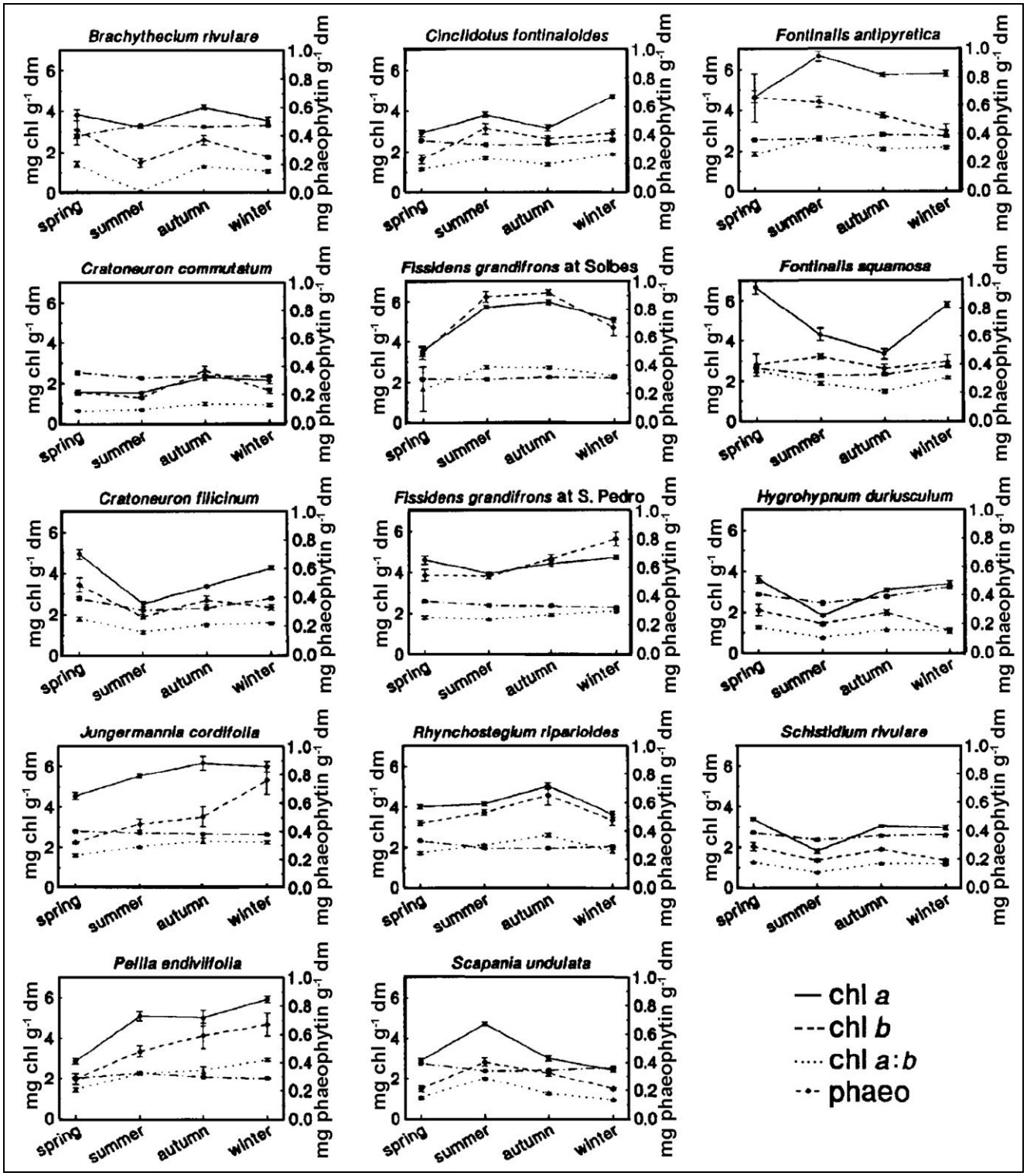

Figure 38. Seasonal changes in chlorophyll in thirteen species of aquatic bryophytes. Based on Martinez Abaigar *et al*. 1994.

Figure 39. ***Syntrichia ruralis***, a species in which total chlorophyll on a dry weight basis is higher in late summer and winter than in early summer. Photo by Michael Lüth, with permission.

Figure 40. ***Cephaloziella exiliflora***, a species that produces a purple anthocyanin-like pigment in response to high light. Photo by Tom Thekathyil, with permission.

Aquatic

Martínez Abaigar *et al*. (1994) compared stream bryophytes to tracheophytes and found that the chlorophyll concentrations were higher (2.2-92. mg g^{-1} dry mass and 97-351 mg m^{-2}) than those of terrestrial bryophytes and comparable to those values for epilithic river algae, but lower than for the tracheophytes. The chlorophyll *a*:*b* ratio of 2.1-2.8 was significantly lower than they found for tracheophytes. Of note is their find that chlorophyll degradation in underwater bryophytes did not produce phaeopigments. This is an important consideration for those persons who would choose a measure of phaeophytin to indicate damage to the bryophytes in pollution studies.

Antarctic

In a habitat where light is obscured by snow for more than six months of the year, it is not surprising that chlorophyll levels diminish. In the Antarctic, bryophyte chlorophyll levels decrease in winter, as does the chlorophyll *a*:*b* ratio (Melick & Seppelt 1994). In summer the rise in carotenoid levels corresponds to the period of high light intensity. The only Antarctic liverwort, ***Cephaloziella exiliflora*** (Figure 40), copes with the high light exposure in the Antarctic summer by producing a purple anthocyanin-like pigment (Post & Vesk 1992). Compared to more protected and shaded plants of the species, these plants had higher carotenoid:chlorophyll ratios, more dispersed thylakoids with fewer grana, fewer appressed thylakoids, more closely spaced leaves, and were larger, growing in a dense turf. Shaded plants had more chlorophyll per unit weight, but their *a*:*b* ratios did not seem to vary much.

Summary

Photoinhibition results from over excitation of electrons under conditions when the plant is unable to use all of those electrons in photosynthesis. It is a common occurrence under high light intensities, especially at low temperatures. This temperature relationship may account for the limitations of some species that prevent their surviving in polar regions. Desiccation-tolerant species seem to be able to dissipate this energy better than the desiccation-intolerant species. Unlike tracheophytes, bryophytes can suffer greater damage when hydrated than when dehydrated.

Quenching is the ability of the plant to redirect the energy in a way that it does not damage the chlorophyll. Accessory pigments can do this by filtering the light or stabilizing the energy level. In bryophytes, the pigment **zeaxanthin** has been implicated in this role, along with a number of other pigments that depend on the species, reacting in some cases almost instantaneously and in others taking hours.

In some cases, clumping of chloroplasts and changes in shape permit the plastids to protect each other.

Bryophytes are typical shade plants, although some species do have adaptations to sun. Under low light intensity, bryophytes increase their chlorophyll *b* concentrations, providing more locations for trapping the light energy. Chlorophyll *a*:*b* ratios generally range between 2 and 3, but can be as low as 1 in some habitats and as high as 3.6 in others.

Lutein is commonly produced in aquatic bryophytes, but also in sunlight, causing its function to be uncertain.

Chlorophyll concentrations change seasonally, with highest concentrations generally being during the rainy growing season.

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CHAPTER 11-3
PHOTOSYNTHESIS: LIMITING FACTORS

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CHAPTER 11-3
PHOTOSYNTHESIS: LIMITING FACTORS

Figure 1. ***Schistidium maritimum*** growing on rocks where desiccation and salt spray exceed the limits of most bryophytes. Photo by Michael Lüth, with permission.

Limiting Factors

"The actual magnitude of assimilation in a leaf at any moment is determined by one or other of the main controlling conditions, light, temperature, or CO_2-supply, acting as a limiting factor." That was the conclusion of Blackman and Smith (1910-1911) in the ninth of their series of papers on vegetable assimilation and respiration. We know that water is another important parameter, but we are still trying to understand completely just how these parameters limit bryophyte photosynthesis. Perhaps Blackman and Smith again best sum it up in their statement that studies on photosynthesis "are more harmoniously interpreted from the point of view of interacting limiting factors than by the conception of optima."

Gerdol *et al*. (1998) illustrated this principle of interacting factors in their study of ***Sphagnum capillifolium*** (Figure 2). They found that low nighttime temperatures could lower growth five-fold, that nutrients limited growth when nighttime temperatures were high, that N and P limited growth at optimum temperatures. Different enzymes are turned on at different temperatures and different *p*H levels, and Gerdol *et al*. suggested that enzymatic reactions could be limited at unfavorable temperatures.

Figure 2. ***Sphagnum capillifolium***, a species in which productivity is affected by nighttime temperatures, nutrients, and N and P at optimum temperatures. Photo by Li Zhang, with permission.

Compensation Point

The **compensation point** is that point at which plant assimilation and respiration are compensated, so that gas exchange is null (Harder 1923). The compensation point can be expressed in terms of temperature, CO_2, or light. When plants are at their compensation point, they have reached a limiting factor for that parameter.

Water Availability

Water as a limiting factor is probably the best understood. Productivity on a worldwide scale seems to be correlated with water availability, at least in ***Polytrichum strictum*** (Figure 3) (Longton 1994). ***Sanionia uncinata*** (Figure 4) in Svalbard, Norway, living on the glacial foreland of the high Arctic, has its highest photosynthetic activities only on rainy days or soon after, indicating that it is not light, but water, that limits the productivity (Uchida *et al*. 2002). Collins (1976) related net productivity to water content in these two species, likewise demonstrating its importance (Figure 5).

Figure 3. ***Polytrichum strictum*** with capsules, a species in which water limits productivity. Photo by Michael Lüth, with permission.

Figure 4. ***Sanionia uncinata***, a species in which water limits productivity. Photo by Janice Glime.

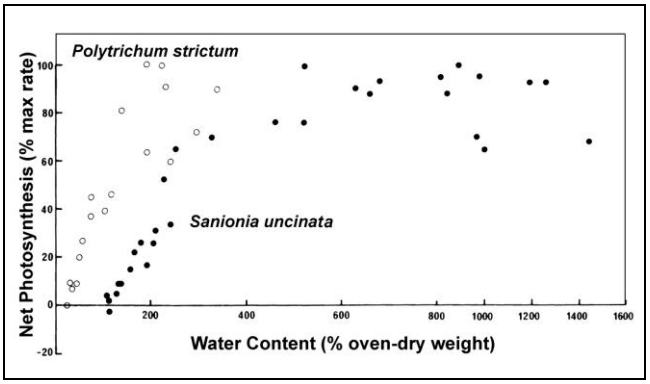

Figure 5. Effect of water content on the net productivity of two mosses from Signy Island. Measurements were at 10ºC, 500 µe m^{-2} s^{-1} (400-700 nm). Redrawn from Collins 1976.

Even in bogs, moisture is limiting. Backéus (1988) found that moisture conditions in August explained about 60% of the variation in ***Sphagnum*** growth the following year. He concluded that the distribution of moisture within the growing season was more important than the mean values. The importance of water in the growth of various ***Sphagnum*** species is well documented (Asada *et al*. 2003). Rydin and McDonald (1985b) examined the **WC_{50}** (% water content at which 50% of the plants would recover if dried to their compensation point) in several ***Sphagnum*** species (Table 1). These ranged from 198% for ***S. balticum*** (Figure 6) to 283% for ***S. tenellum*** (Figure 7). ***Sphagnum*** typically requires more than 100% water content for photosynthesis.

Table 1. WC_{50} values for ***Sphagnum***. Based on references given in Rydin & McDonald 1985b.

Species	% WC_{50}	Reference
S. fuscum	227	Rydin & McDonald 1985b
S. fuscum	400	Silvola & Aaltonen 1984
S. balticum	198	Rydin & McDonald 1985b
S. tenellum	283	Rydin & McDonald 1985b
S. nemoreum	400-620	Titus et al. 1983
S. fallax	250-470	Titus et al. 1983
S. angustifolium	600	Silvola & Aaltonen 1984
S. nemoreum	520	Grace 1970

Figure 6. ***Sphagnum balticum***, a hollow species that cannot survive in hummocks. Photo by Michael Lüth, with permission.

Figure 7. ***Sphagnum tenellum***, a hollow species that cannot survive in hummocks. Photo by Michael Lüth, with permission.

The strange phenomenon in ***Sphagnum*** is that there seems to be no correlation between habitat (hummock vs hollow) and photosynthetic rate at low water contents. Titus *et al*. (1983) found the expected relationship was reversed in ***S. fallax*** (Figure 8) and ***S. capillifolium*** (***S. nemoreum***, Figure 9), with the hollow-dwelling ***S. fallax*** having the higher photosynthetic rates at low water content. Silvola and Aaltonen (1984), on the other hand, found that the hummock species ***S. fuscum*** (Figure 10) was less desiccation-sensitive than the hollow species ***S. angustifolium*** (Figure 11). Rydin and McDonald (1985a) found that the hollow species ***S. balticum*** (Figure 6) and ***S. tenellum*** (Figure 7) cannot grow in hummocks, but that the hummock species ***S. fuscum*** and ***S. rubellum*** (Figure 12) can tolerate the wet hollows. It appears that some species have wide niches for water availability.

Figure 8. ***Sphagnum fallax***, a hollow-dwelling species that has greater productivity at lower water levels. Photo by Michael Lüth, with permission.

Figure 9. ***Sphagnum capillifolium***, a hollow-dwelling species that has greater productivity at lower water levels. Photo by Michael Lüth, with permission.

Figure 10. ***Sphagnum fuscum***, a hummock species that is less desiccation-sensitive than are hollow species. Photo by Michael Lüth, with permission.

Figure 11. ***Sphagnum angustifolium***, a desiccation-sensitive hollow species. Photo by Michael Lüth, with permission.

Figure 12. ***Sphagnum rubellum***, a hummock species that can tolerate wet hollows. Photo by Michael Lüth, with permission.

Part of this dependency on water relates to the contact the plant is able to make with its substratum, or at least the water level below its capitulum. Schipperges and Rydin (1998) found that contact between capitula and the basal portion of the moss is essential to the survival of the moss, with isolated capitula being unable to recover from complete desiccation. They determined that the limit seems to be 10-20% of the water content of the compensation point. Maintenance of this level is accomplished by avoidance of desiccation through high capillarity and dense growth forms.

Hanslin *et al*. (2001) examined the effects of plant density on growth rate and water relationships. Increasing the density negatively impacted the relative growth rate and production of green biomass in both boreal forest mosses examined [***Dicranum majus*** (Figure 13), ***Rhytidiadelphus loreus*** (Figure 14)]. However, in the mid-density range and low relative humidity, some of the watering treatments resulted in the best relative growth rates and green biomass production. Although there were no consistent patterns for most treatments, the length of the wet-dry cycle positively affected the relative growth rate when the number of wet-dry days remained equal. This is most likely due to the high cost of repair, with the longer cycles providing more time for positive productivity after the repair. The length of the dry cycle is far less important than having the needed time for repair and gain.

Figure 13. ***Dicranum majus***, a species in which density impacts growth. Photo by Janice Glime.

Figure 14. ***Rhytidiadelphus loreus*** with capsules, a species in which density impacts growth. Photo by David Holyoak, with permission.

Alpert and Oechel (1987) studied the responses of bryophytes on granitic boulders in the chaparral of San Diego County, California, USA. Even in this dry habitat, the various bryophyte species had significantly different responses to water content, desiccation, and light. Those species in microsites with low water availability achieved maximum net photosynthesis at lower water contents and had a greater ability to recover from prolonged desiccation. Species from microsites with lower light availability achieved higher net photosynthetic rates at lower light intensities. Such studies illustrate the adaptability of bryophytes to a variety of conditions. In this chapter we will examine those limiting factors and the ways that bryophytes cope with them.

Bryophytes adapted to xeric habitats can regain photosynthesis upon rewetting in incredibly short periods of time. In ***Grimmia montana*** (Figure 15), this occurs in 6-10 minutes (McKay 1935). Equilibrium is reached in 30-40 minutes.

Figure 15. ***Grimmia montana***, a xeric species that can regain photosynthesis in 6-10 minutes of rewetting. Photo by Michael Lüth, with permission.

Loss of water can affect not only photosynthesis, but the actual photosynthetic apparatus. As a result, those bryophytes with the ability to achieve non-photochemical quenching have a better chance of survival. In their study of three mosses, Csintalan *et al*. (1999) found that the two rock-dwelling mosses ***Grimmia pulvinata*** (Figure 16) and

Anomodon viticulosus (Figure 17) had a sharp peak of non-photosynthetic quenching when rewet, whereas quenching seemed to recover slowly in the less desiccation-tolerant ***Rhytidiadelphus loreus*** (Figure 14). On the other hand, Deltoro *et al*. (1998) suggested that loss of membrane integrity and subsequent loss of potassium might account for the inability to recover its photosynthetic rate.

Figure 16. ***Grimmia pulvinata***, a rock dweller that has a sharp peak of non-photosynthetic quenching when rewet. Photo by Michael Lüth, with permission.

Figure 17. ***Anomodon viticulosus***, a rock dweller that has a sharp peak of non-photosynthetic quenching when rewet. Photo by Janice Glime.

The moss ***Rhizomnium punctatum*** (Figure 18) experiences damage to PS II at 85% relative humidity (Bartosková *et al.* 1999). This is followed by a functional disconnection of the P680 reaction center from the antenna systems that is evident at higher rates of disconnection.

Figure 18. ***Rhizomnium punctatum***, a species in which PS II is damaged at a reduction to 85% relative humidity. Photo by Jan-Peter Frahm, with permission.

Water Excess

Silvola (1991) demonstrated that the water needed for photosynthesis varies widely among species. Even within a single boreal forest and peatland system, the minimum water content before net photosynthesis declines ranges from 170% to 500%. On the other hand, these mosses, except for ***Polytrichum commune*** (Figure 19), also had an upper limit at which photosynthesis would also decline. This limit was imposed by the difficulty of absorbing CO_2 through a water barrier, a phenomenon also observed in ***Sphagnum*** (Murray *et al*. 1989). Presumably ***P. commune*** managed to maintain internal air spaces in its leaves among the photosynthetic lamellae (Figure 20), hence permitting it to continue photosynthesis.

Figure 19. ***Polytrichum commune*** with capsules, a species that maintains photosynthesis at high moisture contents. Photo by David T. Holyoak, with permission.

Figure 20. ***Polytrichum commune*** leaf cross section showing spaces between lamellae. Photo by Amelia Merced, with permission.

Liu *et al.* (2001b) found that in the mosses ***Thuidium cymbifolium*** (Figure 21) and ***Chrysocladium retrorsum*** (Figure 22) photosynthesis increased in the range of 20-70% water content. Their optimum water content was 70-80%, but then decreased from 80-95%. ***Plagiomnium acutum*** (Figure 23) had a somewhat broader range, increasing photosynthesis in the water content range of 20-80%, maintaining its highest photosynthetic level in the 80-95% range.

Figure 21. ***Thuidium cymbifolium*** with capsules, a species in which photosynthesis increases in the range of 20-70% water content. Photo by Li Zhang, with permission.

Figure 22. ***Chrysocladium retrorsum***, a species in which photosynthesis increases in the range of 20-70% water content. Photo by Yao Kuiyu, through Creative Common.

Figure 23. ***Plagiomnium acutum***, a species that maintains its highest photosynthetic level in the 80-95% water content. Photo by Show Ryu, through Creative Commons.

In ***Sphagnum***, needed water content is much higher. The limiting water level depends on habitat and associated construction of the leaf. For example, in the hummock species ***S. fuscum*** (Figure 10), optimum conditions for photosynthesis occurred at 600-1000% water content, with higher water levels causing a decline in photosynthesis (Silvola & Aaltonen 1984). ***Sphagnum angustifolium*** (Figure 11), which occurred in wetter locations, had its optimum at a wetter 900-1300%. Nevertheless, it often was too wet for optimum CO_2 absorption, whereas in ***S. fuscum*** it rarely was. But the relationship is never so simple. Using ***Sphagnum***, Jauhianen *et al*. (1998) demonstrated that the negative effect of high water content on photosynthesis disappears at higher CO_2 concentrations, with the optimum water concentration increasing as the CO_2 level increases. At 3000 ppm (10X normal atmospheric CO_2 concentrations), there is no decrease in photosynthetic rate with increasing water content in ***S. fuscum*** (Figure 10) (Silvola 1990), supporting the conclusion that greater water content creates a barrier to the entry of CO_2.

Similar water content responses occur in ***Sphagnum*** species from New Zealand (Maseyk *et al*. 1999). Green plants of ***S. cristatum*** (Figure 24) had an optimum water content of 1200-2000%, whereas brown mosses had a higher optimum content of 1400-3000%. Brown coloration in mosses occurs in response to high light intensity, which usually is accompanied by higher temperatures. This suggests that there is a coordinated suite of responses.

Figure 24. ***Sphagnum cristatum***, a species with an optimum water content of 1200-2000%. Photo by Janice Glime.

Seasonal Water Differences

In the tundra of the foothills north of the Brooks Range, Alaska, USA, up to two-thirds of the annual precipitation occurs during summer thunderstorms. In the boreal spruce (*Picea*) forest (Figure 25) in Manitoba, Canada, evapotranspiration was lowest in spring when the ground was still frozen (Betts *et al*. 1999). It was highest in the summer, dropping again in autumn after frost. Evaporation is, predictably, higher when the surface is wet, but it falls with an increase in light level at all temperatures in the summer because of the transpiration resistance of the forest system (*i.e.* guard cells close). But mosses also play a major role in the water evaporation. A wet moss surface lowers the vegetation resistance to water loss at its midmorning minimum by factor of 4. Mosses keep the soil wet and the atmosphere dry by inhibiting evaporation, particularly when they cover pools of standing water.

Figure 25. ***Picea mariana*** forest in Northern Alberta, Canada, with ***Pleurozium schreberi*** and ***Hylocomium splendens*** on the forest floor. Photo by Richard Caners, with permission.

Photosynthetic rate can be directly related to the length of dehydration period (Davey 1997a, b). However, even some bryophytes from very wet habitats in the Antarctic can exhibit some desiccation tolerance. Hydrophytic mosses were more likely to be harmed by repeated wet-dry cycles than were mesophytic or xerophytic bryophytes. Particularly in hydrophytic bryophyte species, the increase in percentage loss of photosynthetic rate following these wet-dry cycles occurred from spring to summer and from summer to autumn sampling periods. Nevertheless, Davey (1997a) could find only broad scale relationships to water availability and drew the same conclusion as Blackman and Smith (1910-1911), that other factors must be important in explaining the distributions of individual species.

Species differ in their responses to humidity. ***Plagiomnium acutum*** (Figure 23) has higher photosynthetic rates on cloudy and rainy days than does ***Herpetineuron toccoae*** (Figure 26), but lower rates on sunny days (Li *et al*. 1999). ***Herpetineuron toccoae*** has a lower rate of transpiration and higher water use efficiency than does ***P. acutum***, permitting it to have a higher photosynthetic rate on sunny days. It also has a higher temperature tolerance. Interestingly, both species decrease their dark respiration with increases in temperature and decreases in relative humidity.

Figure 26. ***Herpetineuron toccoae***, a species that has reduced photosynthesis in low light. Photo by Li Zhang, with permission.

Nighttime Absorption

Nighttime can be an important time for water absorption in bryophytes. Condensation resulting in dew provides moisture on the surfaces of these small plants and can rehydrate them from the desiccation of daytime. Such moistening will reach its maximum just before dawn, preparing the bryophytes to take advantage of the cool temperatures in the early morning light.

Csintalan *et al*. (2000) demonstrated this phenomenon in the desert moss ***Syntrichia ruralis*** (Figure 27). They found that water was absorbed progressively by this moss throughout much of the night. This provided sufficient water for the moss to have positive net photosynthesis for about 1.5 hours immediately after dawn. Although the cumulative carbon balance between dark and light on the day of measurement was negative, on those days with greater dew the balance would be positive. They suggested that this short time period was sufficient to permit repair following long-term desiccation damage.

Figure 27. ***Syntrichia ruralis***, a species that absorbs moisture from the atmosphere at night. Photo by Des Callaghan, with permission.

CO_2

With all the talk about the greenhouse effect due to elevated CO_2 in the atmosphere, it is hard to think in terms of CO_2 limits on plant productivity. But indeed it is often what limits productivity. In aquatic systems, CO_2 is usually limiting, except perhaps in deep water where sediment decomposition provides CO_2 but light levels are low (Maberly 1985; Wetzel *et al*. 1985).

Zotz *et al*. (2000) found that gas exchange of CO_2 is negatively correlated with cushion size in ***Grimmia pulvinata*** (Figure 16). Larger cushions have lower rates of photosynthesis and dark respiration, but alternating dark and light periods cause a complicated response that depends at least in part on the state of hydration.

Despite our increasing CO_2 concentrations in the atmosphere, this gas is often limiting to plants, including bryophytes. For this reason, gas spaces associated with the photosynthetic tissue is important (Raven 1996).

Compensation Point

The bottom line on the CO_2 limit for a species is its CO_2 compensation point. But this changes with the water content, temperature, and light intensity. A plant cannot use more CO_2 if there is insufficient excitation of electrons

due to low light levels. Dilks and Proctor (1975) reported compensation points from published studies (Table 2).

Table 2. CO_2 compensation points for bryophytes.

	µl/L	
Pellia epiphylla	75	Egle & Schenk 1953
Conocephalum conicum	70-105	Egle & Schenk 1953
Bryum argenteum	58	Rastorfer 1970
27 species	25-145	Dilks & Proctor 1975

Hanson *et al*. (2002) compared bryophytes with pyrenoids (hornworts) with ***Marchantia polymorpha*** (Figure 28), a liverwort with no pyrenoids. Pyrenoids are known for their ability to concentrate CO_2, permitting them to store inorganic carbon for later use when levels may diminish. The CO_2 compensation points of the two hornworts with pyrenoids was 11-13 ppm CO_2, whereas in ***M. polymorpha*** it was 64 ppm, a difference consistent with C_3 photosynthesis in the latter.

Figure 28. ***Marchantia polymorpha*** with archegoniophores, a species with much higher CO_2 compensation points than hornworts with pyrenoids. Photo by Rudolf Macek, with permission.

CO_2 Environment

The CO_2 environment around a terrestrial plant may be different from that generally found in the atmosphere. Soil bryophytes benefit from CO_2 emitted from soil decomposition. For example, in a New Zealand temperate rainforest where bryophytes blanket the forest floor, those bryophytes had an annual net uptake of carbon of 103 g m^{-2}, whereas the carbon emitted from the forest floor by bryophytes plus soil respiration was 1010 g m^{-2} (Delucia *et al*. 2003). This meant that the bryophytes used only about 10% of the CO_2 coming from the forest soil microbes. The bryophyte contribution to carbon fixation would be considerably higher in the boreal forest.

Bryophytes can actually affect the turbulent fluxes of CO_2 in the forest. The combined effects of moss photosynthesis and respiration reduced those fluxes by a mean of 0.6 µM m^{-2} s^{-1} (Janssens *et al*. 2001).

For the ground-dwelling ***Hylocomium splendens*** (Figure 25, Figure 29) in a subarctic habitat, the CO_2 concentration around the plants was 400-450 ppm during the hours when the light intensity was above the compensation point (30 µM m^{-2} s^{-1}) (Sonesson *et al*. 1992). Throughout the growing season, it is light, temperature, and water availability that limit the CO_2 uptake.

Figure 29. Ground-dwelling ***Hylocomium splendens***. Photo by Michael Lüth, with permission.

Epiphytes compete with tree leaves for limited CO_2 in the canopy. But wherever the bryophytes are growing, no individual limiting factor is able to work alone. The photosynthetic limits of one are dependent on the levels of the others. Examples of this can be seen in a variety of habitats.

The aquatic moss ***Fontinalis antipyretica*** (Figure 30) has an especially low CO_2 compensation point, but it was consistent with that of C_3 plants (Maberly 1985). The relationship between the photosynthetic rate and the CO_2 concentration showed a photosynthetic increase as the temperature was increased, typical of plants suffering from boundary layer resistance. It is puzzling that this species had a higher assimilation rate in bicarbonate than in pure CO_2 at the same partial pressure (James 1928). This seems to contradict the studies by Bain and Proctor (1980) that indicate its inability to use bicarbonate. Allen and Spence (1981) independently determined this once more for ***Fontinalis antipyretica***. Therefore, in aquatic systems at higher levels of *p*H, when the CO_2 equilibrium shifts toward bicarbonate or carbonate, CO_2 becomes less available to almost non-existent. In these conditions, perhaps the CO_2 is transformed from bicarbonates in some taxa by lower *p*H values at the moss-water interface, but no experimental evidence has verified this hypothesis. Thus, the number of mosses growing in alkaline waters is limited, and it seems that many of the ones that do occur in alkaline waters are adapted to grow in the highly aerated water of waterfalls and rapids, as, for example, ***Fissidens grandifrons*** (Figure 31) (pers. obs.). Others are restricted to the splash zone at the edge of the water, where CO_2 is trapped as the water moves through the air, as in ***Cratoneuron*** (Figure 32) species (Vitt *et al*. 1986; Glime & Vitt 1987).

Figure 30. ***Fontinalis antipyretica***, a species with a low CO_2 compensation point. Photo by Andrew Spink, with permission.

Figure 31. ***Fissidens grandifrons***, a species able to live in alkaline waters. Photo by Janice Glime.

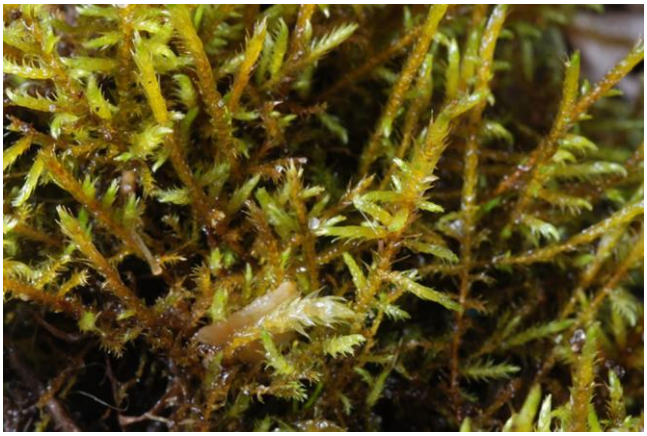

Figure 32. ***Cratoneuron filicinum***, in a genus in alkaline areas is restricted to the splash zone. Photo by J. C. Schou, with permission.

Silvola (1990) examined the effects of CO_2 on the hummock moss ***Sphagnum fuscum*** (Figure 10) productivity and determined that maximum productivity occurred at 600-800% dry mass water content at ambient CO_2 levels of about 380 mg L^{-1}, but that at the saturating CO_2 level of 8000 mg L^{-1}, a saturated water content was needed (Figure 33). Since a CO_2 level of 8000 mg L^{-1} is unrealistic in nature, the curves for 300-1200 mg L^{-1} CO_2 are more instructive. One might speculate that the present success of ***Sphagnum*** in full sun and a temperature of 35ºC, where most other bryophytes cannot survive, might be related to the elevated CO_2 emitted from peat.

The conclusion from all these studies is that one cannot look at the limits of CO_2, or any other factor, in absolute terms. They must be examined as they are affected by the other potential limiting factors (Maberly 1985). So what does that mean for a statement like the title of a paper by Adamson *et al*. (1990), "Photosynthesis in ***Grimmia antarctica*** (= *Schistidium antarcticum*; Figure 34), an endemic Antarctic bryophyte, is limited by carbon dioxide"? When considering limits, it is appropriate to consider the range of the natural conditions of the plant and to express the limits that affect those plants under those conditions. Thus, a plant that is limited by CO_2 in the Antarctic might be limited by light if it were growing in England.

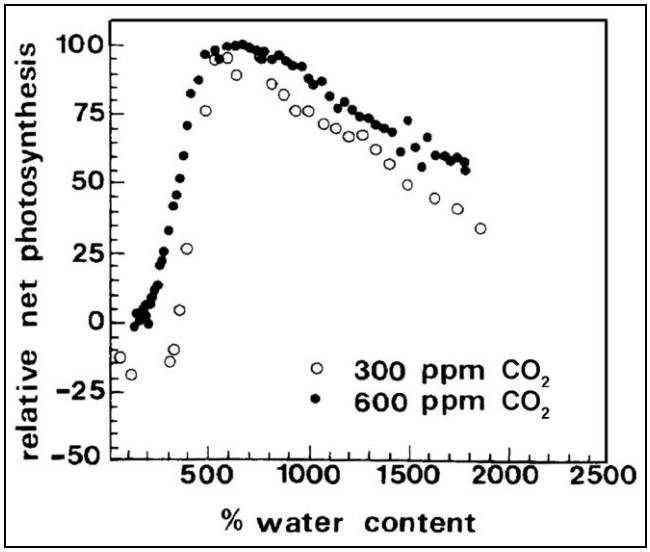

Figure 33. The relationship between net photosynthesis and water content (as percent dry mass) in ***Sphagnum fuscum*** (Figure 10) at two CO_2 concentrations. Constant conditions were maintained at 20ºC, 300 µmol m^{-2} s^{-1} PAR photon flux density, and drying at 70% relative humidity. Redrawn from Silvola 1990.

Figure 34. Saturated ***Schistidium*** (formerly *Grimmia*) ***antarcticum*** with ***Ceratodon purpureus*** between the hummocks. Photo courtesy of Rod Seppelt.

Silvola (1985) showed that bryophytes can be limited by CO_2 in their natural habitat. In the light range of 70-500 µM m^{-2} s^{-1}, raising the CO_2 concentration from 320 ppm to

640 ppm caused a 1.6-2.6-fold increase in the net daily CO_2 exchange.

But short-term studies in the lab or the field may be misleading. Van der Heijden *et al.* (2000) found that initially photosynthesis of ***Sphagnum fallax*** (=*Sphagnum recurvum* var. *mucronatum*) (Figure 8) was stimulated by elevated CO_2 (700 µL L^{-1}), but that after only three days it had returned to the levels of the controls. Furthermore, at low N deposition levels (6 g m^{-2} yr^{-1}) and elevated CO_2, these plants had 17% more biomass after six months, but at high N deposition levels (up to 23 g m^{-2} yr^{-1}), there was little effect on biomass increase. High levels of CO_2 caused a suppression of dark respiration, resulting in an accumulation of soluble sugars in the capitulum. Doubling the CO_2 also reduced the total nitrogen content of the capitula, but not the stems, possibly as a result of the increased sugar content. This reduction was seen in reduced amino acid content, but not in protein content. Such shifts in the carbohydrate to amino acid content has sobering implications for the food web, necessitating that more of the same food be eaten to gain the same amino acid content, and consequently increasing the sugar content. Can invertebrates get diabetes?

Within the bryophyte layers, the CO_2 environment differs from ambient. The forest floor efflux of CO_2 beneath ***Sphagnum*** (Figure 53) and feather mosses such as ***Hylocomium splendens*** (Figure 25, Figure 29) in the boreal black spruce forest (Figure 25) is ~7 M m^{-2} s^{-1}, a loss from the forest floor of 255.4 g C m^{-2} during May-October (Swanson & Flanagan 2001). In ***H. splendens***, the upper parts may have 400-450 ppm CO_2 while the light conditions are above the compensation point (*i.e.*, while photosynthesis is occurring), but light levels below saturation during most of the growing season limit CO_2 uptake (Sonesson *et al*. 1992). Nevertheless, the higher than normal atmospheric levels of CO_2 that occur within the mat permit the plants to have photosynthetic levels that are higher than would normally occur at the reduced (below saturating) light levels.

As the CO_2 concentration of the atmosphere increases, productivity of various groups of plants are likely to be affected differently. The rate of net photosynthesis in the hummock peatmoss ***Sphagnum fuscum*** (Figure 10) increases as the CO_2 concentration increases in the range of 350-2000 ppm CO_2 during half-hour exposures (Jauhiainen & Silvola 1999). The rate at light saturation likewise increases. The effect of radiation fluxes, however, is independent of the level of CO_2. When the exposure to high CO_2 is maintained for longer times, the rates of net photosynthesis gradually decrease compared to those at 350 ppm. On the other hand, at high CO_2 levels, the depression of net photosynthesis found at high water contents is no longer present.

Tropical forests have huge competition for CO_2 in the canopy, but so little light reaches the forest floor that competition is greatly reduced. In a submontane tropical rainforest in Panama, diel variations in water content of six studied bryophytes were great, with both high and low water content limiting photosynthesis (Zotz *et al*. 1997). Low photon flux density is less important in limiting CO_2 exchange. More than half of the carbon gained in the daytime (2.9 mg C per g plant) is lost at night as respiration. If the productivity of this study is representative, the bryophytes gain 45% of their initial carbon content in a year in this environment.

CO_2-Concentrating Mechanisms

Since CO_2 is frequently a limiting resource, a means of concentrating CO_2 for use later or for grabbing it from water is a useful mechanism. Although bryophytes are known only as C_3 plants (Smith & Griffiths 1996), at least some seem to have such mechanisms. Furthermore, both **Cyanobacteria** and many algae are able to accumulate dissolved inorganic carbon through CO_2-concentrating mechanisms (Smith & Griffiths 1996). In the green algae (**Chlorophyta**), this is accomplished by a proteinaceous structure associated with chloroplasts, the **pyrenoid**. And indeed, this structure is present in the phylum **Anthocerotophyta** (Figure 35), but not in all genera.

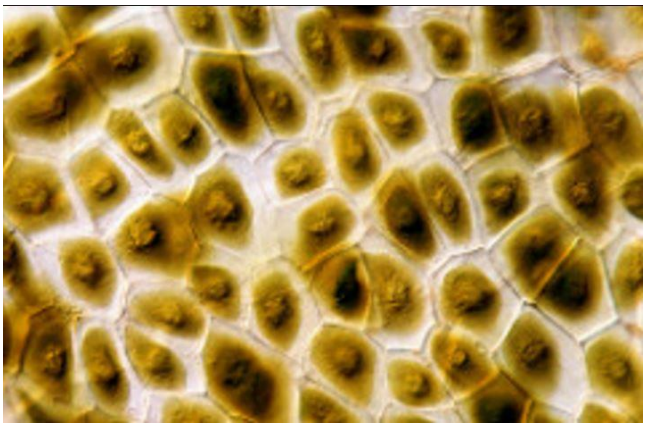

Figure 35. ***Phaeoceros*** cells with pyrenoids associated with chloroplasts. Photo by George Shepherd, with permission.

I find it interesting that it is a primarily terrestrial group that has this mechanism. Living on the soil permits bryophytes to take advantage of CO_2 emitted through soil respiration. But living in the water, attaining CO_2 can be a severe problem for some bryophytes not receiving CO_2 from the sediments and unable to use the carbonates and bicarbonates in water with non-acid *p*H. Something is working to permit some bryophytes to live in these conditions, and the mechanism remains unknown.

*p*H

On land it is likely that *p*H has only minimal influence on the uptake of CO_2 from the atmosphere. However, in the aquatic system, *p*H can be a serious limiting factor. The CO_2 that is dissolved in water seeks equilibrium with the bicarbonate and carbonate. This equilibrium is dependent on *p*H:

$$CO_2 + H_2O \xleftrightarrow{\text{carbonic anhydrase}} H_2CO_3 \leftrightarrow HCO_3^- + H^+$$

$$H_2O \leftrightarrow H^+ + OH^-,\ pK_w = 14.0$$

$$CO_2\ (g) \leftrightarrow CO_2\ (aq)$$

$$CO_2\ (aq) + H_2O \leftrightarrow H_2CO_3,\ pK_a \approx 2.8$$

$$H_2CO_3 \leftrightarrow H^+ + HCO_3^-,\ pK_1 = 6.35$$

$$HCO_3^- \leftrightarrow H^+ + CO_3^{-2},\ pK_2 = 10.3$$

where the *p*K values are those at 25°C

The *p*K is the *p*H at which the dissociated and undissociated forms have the same activity, *i.e.*, the two sides of the arrows in the above equations. It is the equilibrium between the two forms. From this we can derive the level at which inorganic carbon exists in the bicarbonate state. At *p*H 6.35, the solution would be expected to have half CO_2 and half bicarbonate. Above that it becomes predominately bicarbonate. At even higher levels of 10.3, the bicarbonate and carbonate levels are equal. Above *p*H 10.3, the carbon is predominately in the form of carbonate. Allen and Spence (1981) calculated that at *p*H 4.4, 99% of the inorganic carbon is present as H_2CO_3 (making free CO_2 available); only 1% is HCO_3^-, and there is virtually no CO_3^{-2}. At *p*H 8.4, this reverses and 99% of the total inorganic carbon is HCO_3^{-1}; less than 1% is in H_2CO_3; less than 0.03% is in CO_3^{-2}. At any given moment, some CO_2 will exist as biological and chemical reactions occur to release CO_2 into the water, but as time continues, those small amounts will enter into the equilibrium. Nevertheless, metals and other buffering acids and bases can alter the concentrations.

In aquatic systems, CO_2 is spontaneously hydrated to H_2CO_3, but this hydration occurs about 2 orders of magnitude slower than the hydration which occurs in the carbonic anhydrase-catalyzed reaction. But remember that the carbonic anhydrase is in the cell where the *p*H is generally above 6.5. Or is it? There is evidence that carbonic anhydrase acts extracellularly in some algae (Hobson *et al*. 2001), including *Chlamydomonas* (Figure 36) and some diatoms. Thus it is possible that there is extracellular activity in some aquatic mosses. Furthermore, the *p*H of the cell wall is typically lower than that of the cell, ranging 3-6.

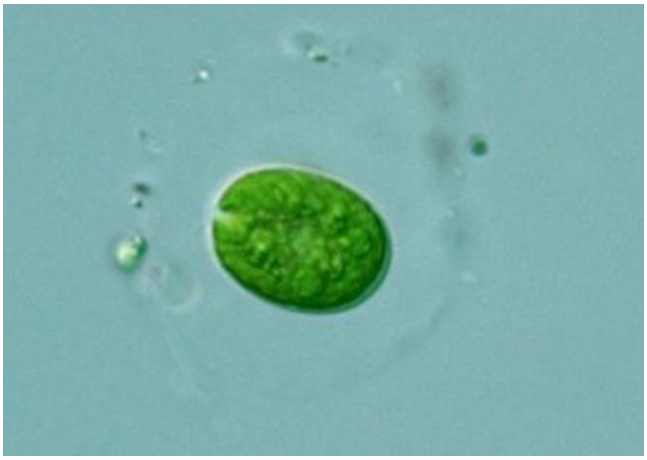

Figure 36. ***Chlamydomonas***, a genus that uses carbonic anhydrase extracellularly. Photo by Yuuji Tsukii, with permission.

I am aware of no evidence that this carbonic anhydrase is able to act on water outside the cell in any bryophyte, but then, no one seems to have looked. With such an elevated *p*H within the cell, the H_2CO_3 is rapidly converted to bicarbonate and the level of carbonic acid is miniscule. But the enzyme RUBISCO is present in the plant photosynthetic cell, ready to place the CO_2 into the photosynthetic pathway where it is bound into the 3-carbon compound, PGA (Rintamäki 1989). Thus, the problem is getting the miniscule amounts of CO_2 from the water in systems where the *p*H is too high for the equilibrium to shift toward free CO_2 or H_2CO_3.

Sphagnum (Figure 7-Figure 12) and other bryophytes have the ability to lower the *p*H through cation exchange, thus keeping more CO_2 in their environment in readily usable form. Consequently, low *p*H values in the proximity of bryophytes with polyuronic acid in the cell walls are most likely common, and the cation exchange properties of these acids would provide H^+ ions in the immediate surroundings. This could provide the free CO_2 needed for photosynthesis. In plants living in cool water and low light, such as many aquatic bryophytes, even such low levels of CO_2 are probably adequate. As discussed in the nutrient chapter, this cation exchange and *p*H-lowering ability have a number of ecological and physiological implications in the peatland habitat. The *p*H-lowering ability and requirements differ with ***Sphagnum*** species, with hummock species tending to have requirements for the lowest *p*H (Haraguchi 1996; Haraguchi *et al*. 2003). After all, it is difficult to have much effect on the *p*H of an entire lake, but having an effect on the immediate microenvironment of a hummock is not.

Limits to Entry

Water limits the entry of CO_2 into cells. For ***Sphagnum fuscum*** (Figure 10), Silvola (1990) found the optimal water content at ambient CO_2 levels to be 600-800%. However, if the CO_2 level was raised, that optimal water content increased, an observation consistent with the difficulty of getting CO_2 into a wet cell through the water boundary. By increasing the concentration of CO_2, more of it is able to penetrate the barrier. At 3000 ppm CO_2, there was no decrease in the photosynthetic rate with increasing water content.

In aquatic habitats, bryophytes may gain CO_2 from that evolved from sediment respiration. Wetzel *et al*. (1985) found that 25-40% of the CO_2 fixed in leaves of tracheophytes comes from the **rhizosphere** (root area). Bryophytes do not have the **lacunae** (minute cavities) to transmit gases in the manner used by many aquatic tracheophytes, but due to their small size, they are able to incorporate the evolving CO_2 as it escapes from the sediments and before it reaches the awaiting phytoplankton.

Methane

Sphagnum (Figure 7-Figure 12) seems to have an alternative source for gaining carbon (Raghoebarsing *et al*. 2005). It is able to obtain carbon through a symbiotic relationship with endophytic methanotrophic bacteria living in the hyaline cells of both stems and leaves. These bacteria oxidize the carbon from the methane to CO_2 that is then used by the ***Sphagnum***. This appears to supply about 10-15% of the carbon used by ***Sphagnum***. This and other processes in the peatland system recycle the methane in ways that cause little of the methane to reach the atmosphere.

Light

The majority of bryophytes grow in habitats where the light intensity is less than that of full sunlight. Therefore, it is not surprising that Rincòn (1993) found that six forest floor bryophytes all increased their biomass relative to

controls when the light intensity was increased for 36 days. But shoot elongation can have the opposite response. In this study, all species [***Brachythecium rutabulum*** (Figure 37), ***Eurhynchium praelongum*** (Figure 38), ***Plagiomnium undulatum*** (Figure 39), ***Pseudoscleropodium purum*** (Figure 40), ***Thuidium tamariscinum*** (Figure 41)] but ***Lophocolea bidentata*** (Figure 42) had greater elongation in the lower light intensities. ***Dicranum majus*** (Figure 13) likewise had its greatest elongation at the lowest light level tested (20 μM m^{-2} s^{-1}) (Bakken 1995).

Figure 37. ***Brachythecium rutabulum***, a species with greater elongation in lower light. Photo by J. C. Schou, with permission.

Figure 38. ***Eurhynchium praelongum***, a species with greater elongation in lower light. Photo by Blanka Shaw, with permission.

Figure 39. ***Plagiomnium undulatum***, a species with greater elongation in lower light. Photo by Janice Glime.

Figure 40. ***Pseudoscleropodium purum***, a species with greater elongation in lower light. Photo by Janice Glime.

Figure 41. ***Thuidium tamariscinum***, a species with greater elongation in lower light. Photo by Janice Glime.

Figure 42. ***Lophocolea bidentata***, a leafy liverwort that exhibits greater elongation in low light. Photo by Michael Lüth, with permission.

Murray *et al*. (1993) found a similar elongation response among Alaskan Arctic tundra ***Sphagnum*** (Figure 7-Figure 12) species. They experimented by removal of tracheophytes in some plots and by use of shade cloth of others, compared to controls. Moss growth in shaded plots was 2-3 times that of mosses in control plots, whereas significant growth reduction was evident in the canopy removal plots. They suggested that those mosses in the canopy removal plots suffered from photoinhibition. In the

laboratory, such inhibition occurred after only two days of high light treatment and the photosynthetic capacity did not recover during the 14 days of the experiment. They suggested that the low tissue nitrogen levels may have prevented the ***Sphagnum*** from acclimating to the high light intensity.

Compensation and Saturation Points

Bryophytes in general are shade-adapted plants with low light compensation points and low saturation levels. Gabriel and Bates (2003) showed that bryophytes of the evergreen laurel forest in the Azores were likewise shade-adapted plants that reached their light saturation at 30 µM m^{-2} s^{-1}. ***Andoa berthelotiana*** (Figure 43) had the lowest compensation point at 20 µM m^{-2} s^{-1} and ***Myurium hochstetteri*** (Figure 44) had the highest at 68 µM m^{-2} s^{-1}. The deep shade species ***Fissidens serrulatus*** (Figure 45) had the extremely low compensation point of 7 µM photons m^{-2} s^{-1}. With leaves remaining on the trees, the low light levels of winter often limit the photosynthetic activity of these bryophytes. Contrasting with these evergreen forest species, the pendulous moss ***Pilotrichella ampullacea*** (Figure 46) in Uganda has a saturating light intensity of 400 µM m^{-2} s^{-1} (Proctor 2002).

Figure 43. ***Andoa berthelotiana***, a shade-adapted moss in the Azores with the lowest light compensation point there. Photo by Jan-Peter Frahm, with permission.

Figure 44. ***Myurium hochstetteri***, a shade-adapted moss in the Azores with the highest light compensation point there. Photo by Michael Lüth, with permission.

Figure 45. ***Fissidens serrulatus***, a deep-shade-adapted moss in the Azores with the lowest light compensation point there. Photo by David Holyoak, with permission.

Figure 46. ***Pilotrichella ampullacea***, a pendent moss with a very high light saturation point. Photo by Jan-Peter Frahm, with permission.

It is difficult to compare results from different studies because the units cannot easily be converted to other forms of measure, as discussed in the chapter on light. Older measurements were typically in foot candles or lux, whereas more recent ones are in energy units or PAR (photosynthetically active radiation) units. Conversion is complicated by the composition of the wavelengths of light. For example, Vashistha and Chopra (1989) determined that the optimal growth of the disturbed habitat liverwort ***Riccia frostii*** (Figure 47) occurred at 3500 lux of continuous light in the lab. But lab light quality differs considerably from that in the field and under fluorescent lights it typically lacks the normal proportion of red light that achieves the highest level of photosynthesis. A light level of 3500 lux is quite low when one considers that full

sunlight is about 70,000 lux. It is likely that at that level of light some other factor became limiting in the lab, perhaps CO_2.

Figure 47. ***Riccia frostii***, a species of disturbed habitats. Photo by Rosemary Taylor, with permission.

The interplay of limiting factors becomes the means of niche partitioning in many of the bryophytes. ***Plagiomnium acutum*** (Figure 23) and ***Herpetineuron toccoae*** (Figure 26) occupy different niches because of this interplay. In ***P. acutum***, photosynthesis is lower on sunny days but higher on cloudy and rainy days than that of ***H. toccoae***, indicating its greater ability to absorb and use weak light while having a higher CO_2 assimilation efficiency (Li *et al.* 1999). The greater water use efficiency of ***H. toccoae*** and lower rate of transpiration permits that species to tolerate higher temperatures and desiccating conditions. One reason for this is the higher respiratory rate of ***P. acutum***.

The mosses ***Plagiomnium acutum*** (Figure 23) and ***P. maximoviczii*** (Figure 48) have light compensation points of 20-40 µM m^{-2} s^{-1} and saturation points of 200-400 µM m^{-2} s^{-1}, with lower values in winter and higher ones in summer (Liu *et al*. 2001a). Thus it appears that they acclimate to the conditions of light or temperature or both.

Figure 48. ***Plagiomnium maximoviczii***, a species with lower compensation and saturation points in winter. Photo from Hiroshima University Digital Museum of Natural History, with permission.

It is intuitively obvious that light intensity will decrease as one penetrates further into the moss layer. In a study on Antarctic mosses, Davey and Ellis-Evans (1996) found that not only did the light intensity decrease, but the attenuation maxima were at the wavelengths where chlorophyll has the greatest absorption peaks (675 nm and <450 nm). That again seems intuitive, since it is the green plant that is blocking the light penetration, and that green is the result of the chlorophyll pigments. But it is not quite that simple. Species differ in their absorption spectra, with stem orientation, stem density, leaf size, orientation, and pigment content all affecting absorption. While bryophytes all tend to have similar pigments, the relative proportions differ. Drying causes the wavelength variation to disappear and light to penetrate further into the clump or mat. These light penetration and wavelength changes resulted from both structural changes in the cells and pigment changes. This is adaptive, permitting deeper layers to carry out photosynthesis as the upper parts of the plants dry beyond the point where they can photosynthesize.

Because of its thin ozone layer, the Antarctic has some of the highest UV intensities on Earth. Among fourteen species of mosses, the light saturation level was 30-270 µM m^{-2} s^{-1} (Davey & Rothery 1997). Nevertheless, these shade-adapted bryophytes exhibited no photoinhibition at any light intensity tested, up to 700 µM m^{-2} s^{-1}.

The thallose liverwort ***Marchantia polymorpha*** (Figure 28) is generally a shade plant, but tolerates at least some direct sun. Nevertheless, its light saturation level was only 2000-3000 lux, with inhibition occurring at higher levels (Mache & Loiseaux 1973). This is a very low saturation level when one considers that full sunlight in the temperate zone is typically about 70,000 lux. Isolated chloroplasts had a rate of photosynthesis about one tenth that of those in whole plants, suggesting that the plant may reduce the light level considerably to achieve its optimum low light level. Furthermore, high light stimulates changes in the chloroplast structure, inducing formation of continuous grana instead of the more typical small grana. By contrast, ***Hypnum cupressiforme*** (Figure 49), an epiphyte, had not reached saturation at any temperature (0-15ºC) at light intensities of 12,000 lux (Kallio & Kärenlampi 1975).

Figure 49. ***Hypnum cupressiforme*** epiphytic habitat, a species with a wide range of temperatures without reaching light saturation. Photo by Dick Haaksma, with permission.

Rastorfer and Higginbotham (1968) measured the light saturation of ***Bryum sandbergii*** from Idaho, USA, at 20ºC in 3% CO_2 and found that photosynthesis attenuated at

about 8 m watts per cm^2 (Figure 50). However, at 4ºC, the photosynthetic rate declined at 8 m watts per cm^2, suggesting photoinhibition at that low temperature (Figure 51).

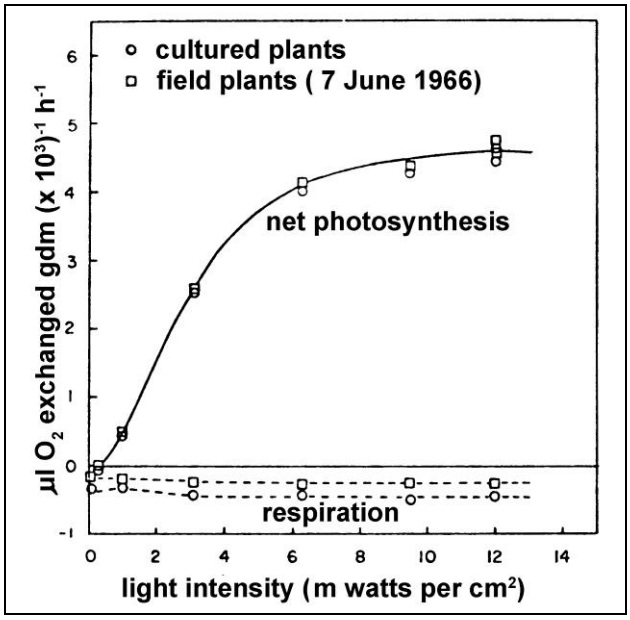

Figure 50. Mean effects of light intensity on net photosynthetic rates of ***Bryum sandbergii*** in the lab and field at 20ºC, 3% CO_2. n=5. Redrawn from Rastorfer and Higginbotham 1968.

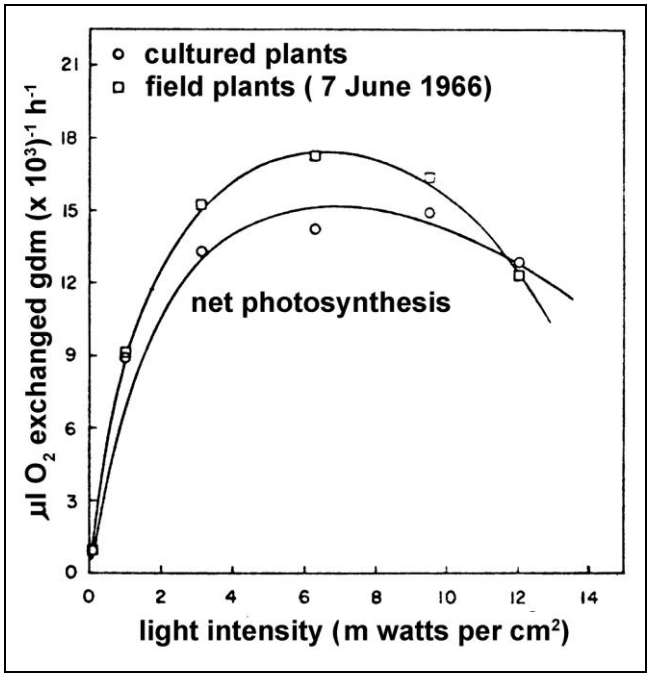

Figure 51. Mean effects of light intensity in the lab and field on net photosynthesis of ***Bryum sandbergii*** at 4ºC, 3% CO_2. n= 5. Redrawn from Rastorfer and Higginbotham 1968.

In ***Sphagnum cristatum*** (Figure 24) and ***S. australe*** (Figure 52) from New Zealand, the light saturation point ranges from 111 to 266 µM m^{-2} s^{-1} (Maseyk *et al*. 1999). Color affected the saturation point of ***S. cristatum***, with brown coloration causing an elevated saturation point. This, in turn, resulted in lower photosynthetic rates, lower quantum efficiencies, and higher light compensation points than those of green plants.

Figure 52. ***Sphagnum australe***, a species with a wide range of light saturation points. Photo by Tom Thekathyil, with permission.

In the Alaskan foothills of the Philip Smith Mountains, ***Sphagnum angustifolium*** (Figure 11) has a light compensation point of 37 µM m^{-2} s^{-1} and light saturation between 250 and 500 µmol m^{-2} s^{-1} at 10°C (Harley *et al*. 1989). At 20°C, this relationship shifted upward, with the compensation point increasing to 127 µM m^{-2} s^{-1} and the saturation point to 500 µM m^{-2} s^{-1}. ***Sphagnum squarrosum*** (Figure 53) experienced decreased photosynthetic capacity and chlorophyll bleaching when the tracheophyte cover was removed.

Figure 53. ***Sphagnum squarrosum*** 1 J. C. Schou, with permission.

Shade mosses have a light compensation point of 20-400 lux and sun species of 1000-2000 lux (Bazzaz *et al*. 1970). Saturation points generally run 10,000-30,000 lux for sun bryophytes (Proctor 1981). The epiphytic ***Ulota cripsa*** (Figure 54) has a saturation point of 40,000 lux (Miyata & Hosokawa 1961). Thus, sun species of bryophytes have compensation and saturation levels about ten times as high as those of shade mosses. In Kansas, USA, the saturating light level for ***Dicranum scoparium*** (Figure 55), ***Leucobryum glaucum*** (Figure 61), and ***Thuidium delicatulum*** (Figure 62) is 200 µM m^{-2} s^{-1} (McCall & Martin 1991).

Figure 54. ***Ulota crispa***, an epiphyte with a high light saturation point. Photo by Janice Glime.

Figure 55. ***Dicranum scoparium***, a forest floor species. Photo by Janice Glime.

Aquatic plants from deep water are likely to have the lowest compensation points due to the low levels of light penetrating to depths. ***Fontinalis*** (Figure 30) exhibited a compensation point of 150 lux at 20°C, but this declined to 40 lux at 5°C (Burr 1941). Wetzel *et al*. (1985) found extremely low light compensation points for ***Sphagnum auriculatum*** var. ***inundatum*** (Figure 56) and *Juncus bulbosus* (a seed plant; Figure 59) from deeper water and higher values for the red alga *Batrachospermum* (Figure 60) from shallower areas.

Figure 56. ***Sphagnum auriculatum***, a species with a very low light compensation point. Photo by Jan-Peter Frahm, with permission.

More recent measurements have put light measurements in terms of energy units or photosynthetically active radiation (PAR). Using energy units, Krupa (1978) found a compensation point of 0.6 and saturation point of 15 W m^{-2} for the shade plant ***Rhizomnium punctatum*** (Figure 18). For the sun plants ***Polytrichum piliferum*** (Figure 57) and ***Funaria hygrometrica*** (Figure 58), the compensation points were 1.8 and 1.4 W m^{-2}, respectively, and the saturation points 55 and 100 W m^{-2}, respectively.

Even the bryophytes seem to operate below their light saturation points for most of the growing season. ***Hylocomium splendens*** (Figure 29) in the subarctic had a compensation point of 30 µM m^{-2} s^{-1} and a saturation point of 100 µM m^{-2} s^{-1} during the growing season, but it only experienced its light saturation level 65% of the time in July, 76% in August, and 96% in September (Sonesson *et al*. 1992).

Figure 57. ***Polytrichum piliferum***, a sun species showing its hyaline hair points. Photo by Michael Lüth, with permission.

Figure 58. ***Funaria hygrometrica***, a sun species. Photos by Michael Lüth, with permission.

Figure 59. ***Juncus bulbosus***, a species with low light compensation point in deep water. Photo by Krzysztof Ziarnek, Kenraiz, through Creative Commons.

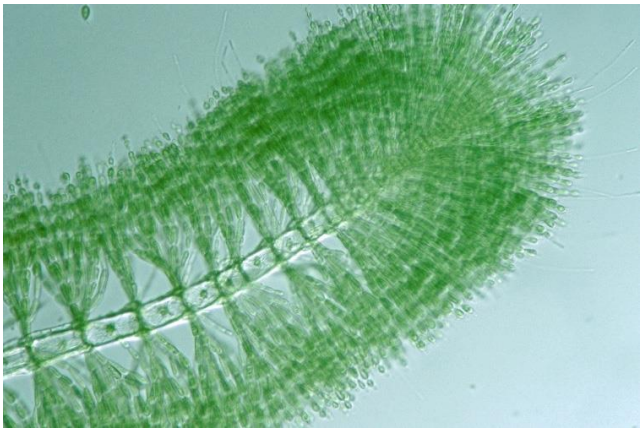

Figure 60. ***Batrachospermum***, a shallow-water red alga with a high light compensation point. Photo by Yuuji Tsukii, with permission.

Light intensity, coupled with air humidity, seems to be a limiting factor for distribution of tropical epiphytic bryophytes in the Amazon (Frahm 1987). The low light intensities, coupled with high temperatures in the lowland forests, do not permit the bryophytes to reach their compensation points. Energy lost to respiration at such temperatures is greater than that gained in the low light levels of the lowlands. This relationship accounts for the increasing number of taxa and biomass with increased elevation.

Figure 61. ***Leucobryum glaucum***, a forest floor species. Photo by Janice Glime.

Figure 62. ***Thuidium delicatulum***, a species of open and forest. Photo by Janice Glime.

Excess Light

Excess light can limit bryophyte productivity by causing photoinhibition and damage to the chlorophyll. Dehydration usually protects the bryophytes from this damage by making the plants dormant. When dehydrated, ***Grimmia alpestris*** (Figure 63) from an alpine habitat had little chlorophyll fluorescence when subjected to high UV light intensity, whereas tracheophytes had high levels of fluorescence under the same conditions (Heber *et al*. 2000). When these mosses were rehydrated, their fluorescence increased, but that of the tracheophytes decreased upon rehydration. These mosses typically do not experience photodamage while dry, apparently using the same protective mechanism while dry as they are able to use successfully while hydrated.

Figure 63. ***Grimmia alpestris***, a species that loses its chlorophyll fluorescence at high light intensities. Photo by Michael Lüth, with permission.

Experiments in canopy removal consistently indicate that high light intensities are not favorable to moss growth. In the Alaskan Arctic tundra, Murray *et al*. (1993) found that ***Sphagnum***-dominated moss growth (Figure 53) increased by 2-3 times in shaded plots, but had a significant growth reduction in plots where the tracheophyte canopy had been removed. They suggested that the reduced growth was due to photoinhibition.

It is not uncommon for bryophytes to become pale in bright sunlight. Others develop red or other energy-absorbing pigments. But some of the effects of greater exposure to light, such as that seen in canopy removal experiments, is that the temperature and moisture conditions change. More of the daylight hours are at temperatures above that which is suitable for C_3 photosynthesis, forcing the plants to become dormant. And the added light and heat cause a greater loss of water by evaporation.

Continuous Light

As already discussed in Chapter 9-4, we know that continuous light may be deleterious to photosynthesis, causing mosses to lose their chlorophyll (Kallio & Valanne 1975). The stroma thylakoids are destroyed, much like the destruction seen in continuous dark in the cave experiments of Rajczy (1982). However, the continuous light damage observed by Kallio and Valanne occurred in laboratory experiments. Plants living in Polar Regions may acclimate to the seasonal change in continuous photoperiod (Richardson 1981).

It appears that continuous light alters the proportions of sugars and lipids. Sakai *et al*. (2001) found that green portions of the moss ***Racomitrium barbuloides*** (Figure 64) initially increased their storage of both sugars and lipids, but then they decreased. This decrease was accompanied with a significant decline in photosynthetic capacity. They suggested that the green tissue plays a major role in photoassimilate storage. It appears that accumulation of photoassimilates inhibits photosynthesis, but that such accumulation is unlikely under natural conditions.

Figure 64. ***Racomitrium barbuloides***, a species that stores sugars and lipids, depending on environmental conditions. Photo from Digital Museum, Hiroshima University, with permission.

Bryophyte Canopy Structure

A bryophyte canopy is constructed differently from that of tracheophytes. Yet, while the leaf structure is very different, the mat structure may in many ways resemble the leaf structure of a tree leaf. Rice *et al*. (2008) investigated the trait relationships in ten species of ***Sphagnum*** (Figure 7-Figure 12). They found no relationship between N content and maximum photosynthesis per mass or area, differing from relationships in tracheophytes. Only capitulum area seemed to be relevant to N storage and maximum photosynthesis. Water content and carotenoid concentration were the strongest predictors of maximum photosynthesis.

Tobias and Niinemets (2010) noted the large variation of light availability within the moss canopy. Furthermore, the lowest light levels are in the lower portions where the oldest tissues reside. Variation within the temperate-boreal forest moss ***Pleurozium schreberi*** (Figure 25, Figure 65) canopy can be greater than that between locations. Chl, Chl/N, and Chl/Carotenoid ratios increase with decreasing light availability between locations. Upper layers of the moss within habitat vary similarly, but after the light diminishes to 50-60% of the above-canopy levels, the layers demonstrate characteristics of senescence. At these depths, pigment and N concentration and photosynthetic capacity decrease with light availability. Thus, younger tissues are able to acclimate, but older ones do not.

Figure 65. ***Pleurozium schreberi***, a common boreal feather moss. Photo by Janice Glime.

Waite and Sack (2010), in studying ten Hawaiian moss species, found that the moss species had low leaf mass per area and low gas exchange rates. The light-saturated photosynthetic rate per mass did not correlate with light levels in the habitat. Rather, microhabitat irradiance had the greatest influence on other photosynthetic parameters and structural traits, causing correlations of traits of leaf area, cell size, cell wall thickness, and canopy density. Costa size, canopy height, and light-saturated assimilation rate per mass correlated with structural allocation. N concentration correlated negatively with canopy mass per area (replacing leaf mass per area used in tracheophytes). The structures are different from those of tracheophytes, but the leaf size and function have been replaced with canopy mass and function.

Photoperiod Effects on Physiology

The effects of photoperiod as an event trigger are well known, but their effects on physiology of vegetative plants has been largely ignored (Cvetić *et al*. 2009). In the forest moss ***Atrichum undulatum***, day length had no noticeable effect on photosynthetic pigments in the lab. Protein content and malate dehydrogenase activity were both higher in long day (16h light/8h dark) than in short day (8h light/16h dark) growth conditions. Long days produced higher concentrations of total phenolic compounds, greater peroxidase activity, and higher total antioxidative capacity.

Temperature

Once again we see evidence that limiting factors do not act alone. In ***Fontinalis antipyretica*** (Figure 30), photosynthesis increases with CO_2 concentration, but the level achieved is further dependent upon temperature (Maberly 1985). As the temperature goes up, boundary layer resistance decreases, permitting more CO_2 to enter the plants.

Aquatic mosses seem to be especially sensitive to high temperature, failing to sustain a healthy state for a prolonged period. Their lethal temperature can be quite low, as illustrated by ***Leptodictyum riparium*** (Figure 66) with a photosynthetic optimum at 23°C and death at 33°C (Sanford 1979). Several ***Fontinalis*** (Figure 30) species can do well at 20°C for a period of time; then they lose their green color and stop growing (Fornwall & Glime 1982; Glime 1982, 1987a, 1987b, 1987c, Glime & Acton 1979).

Figure 66. ***Leptodictyum riparium***, a species that dies at 33°C. Photo by David Holyoak, with permission.

Interestingly, cold resistance seems to be related to heat resistance, as shown by Balagurova *et al*. (1996) for ***Sphagnum*** species. For ***S. subsecundum*** (Figure 67), the lethal temperature of cells was 60.3ºC. Lethal cold temperatures ranged -16.1ºC to -21.8ºC.

Figure 67. ***Sphagnum subsecundum***, a species that demonstrates both low and high temperature tolerance. Photo by Michael Lüth, with permission.

But temperature seems to have less detrimental effect on photosynthesis in bryophytes than we might expect from its role in other processes and organisms. While bryophytes have little ability to control temperature physiologically, they do have the ability to respond through alteration of color that may be induced by day length, light intensity, or temperature itself. Could it be that the red color of the antheridial splash cups of ***Polytrichum piliferum*** (Figure 68) keeps the sperm warm on cool days in spring?

Figure 68. Antheridial splash cups of ***Polytrichum piliferum***. Photo by Janice Glime.

Photosynthetic levels in some Arctic mosses seem to be similar over a wide temperature range. Vilde (1988) interpreted the mosses of the Arctic to be well adapted to their temperature regime. He found that photosynthesis has little temperature limitation and even high light intensity has little effect on these Arctic mosses. Uchida *et al*. (2002) found that the net photosynthetic rate in *Sanionia uncinata* in the high Arctic of Svalbard, Norway, was nearly constant at near-saturating light levels across the range of 7 to 23ºC, but these same plants exhibited the extraordinarily high Q_{10} of 3.0 for respiration in that range. This means that the gross photosynthesis must likewise have experienced a large increase with temperature in that range, with respiration using an increasing differential of that newly fixed carbon.

Temperature can have a threshold effect on bryophyte productivity. Asada *et al*. (2003) found that ***Sphagnum*** (Figure 7-Figure 12) species in a coastal British Columbia, Canada, peatland had lower temperature thresholds than did ***Pleurozium schreberi*** (Figure 25, Figure 65) and ***Racomitrium lanuginosum*** (Figure 69). Winter growth was important in this community, most likely because of greater availability of water; growth was more strongly correlated with precipitation than with temperature.

Figure 69. ***Racomitrium lanuginosum***. Photo by Michael Lüth, with permission.

Kallio and Heinonen (1973) found that ***Racomitrium lanuginosum*** (Figure 69) could photosynthesize at -10ºC (compensation point) and that it returned to 60% of its normal photosynthetic rate within three hours after storage at -30ºC. Its optimum was at 5ºC. They interpreted this moss to be pre-adapted to the wide range of temperatures in which it exists, lacking any clear physiological races with respect to temperature response.

Bryophytes acclimate to temperature, altering their optimum temperature for photosynthesis. This is likely to be accompanied by a shift in the light saturation level. However, the respiration rate does not necessarily acclimate at the same time. Both lowland and highland ***Dicranum fuscescens*** (Figure 70) showed photosynthetic acclimation to higher temperatures of mid summer, with highland plants having maximum rates of 2.1 mg CO_2 g^{-1} dry mass h^{-1} and lowland plants having only 0.74 mg CO_2 g^{-1} dry mass h^{-1} (Hicklenton & Oechel 1976). The optimum temperature shift can occur in as little as 48 hours in this species. The light saturation levels increased from spring to midsummer, then lowered again toward autumn. Dark respiration, however, did not acclimate.

Figure 70. ***Dicranum fuscescens***, a species that acclimates to the higher temperatures of summer. Photo by Michael Lüth, with permission.

But even within the normal range of temperatures, bryophytes perform poorly at higher temperatures that favor most tracheophytes, as shown by the rapid drop in growth rate of the temperate pleurocarpous moss ***Brachythecium rutabulum*** (Figure 37) at temperatures above 15ºC (Furness & Grime 1982). On the other hand, at only 5°C their growth is still 40% of their maximum rate at ~19°C. This moss achieved a growth rate exceeding the maximum reported for seedlings of ten tracheophytes. Furness and Grime show the strong seasonal effects of temperature that help to explain some of the phenology of bryophytes. These results are consistent with its peaks of growth in spring and autumn, allowing it to compete with its tracheophyte neighbors in the British tall herb communities where they grow.

Frahm (1990) determined that high temperatures in tropical lowlands result in high respiration rates. Consequently, at temperatures above 25°C, net assimilation drops sharply. It is that high respiratory loss that limits much of bryophyte distribution in the tropics.

In the New Zealand species ***Sphagnum cristatum*** (Figure 24) and ***S. australe*** (Figure 52), the optimum temperatures for photosynthesis are 20 to 25°C (Maseyk *et al*. 1999). Liu *et al*. (2001a) found that ***Plagiomnium acutum*** (Figure 23) and ***P. maximoviczii*** (Figure 48) could maintain net photosynthetic gain for 10-30 minutes from -15°C to 45°C. Despite their cold climate, fourteen bryophytes in the Antarctic have a temperature optimum for gross photosynthesis of 10-20°C and of 0-20°C for net photosynthesis (Davey & Rothery 1997). With the relatively high Antarctic light intensity, these bryophytes are usually temperature limited during the growing season.

Like the experiments on ***Fontinalis duriaei*** (Figure 71) of Glime and Acton (1979), Dilks and Proctor found that prolonged exposure to high temperatures caused a drop in productivity (Figure 72), thus demonstrating that duration of an experiment would influence the determined optimum temperature. While these curves may indicate the general trend of the response, we must exercise caution because the higher than atmospheric level of CO_2 used would most likely push the temperature optimum to a higher level.

Figure 71. ***Fontinalis duriaei***, a species that experiences a drop in productivity after prolonged high temperatures. Photo by Michael Lüth, with permission.

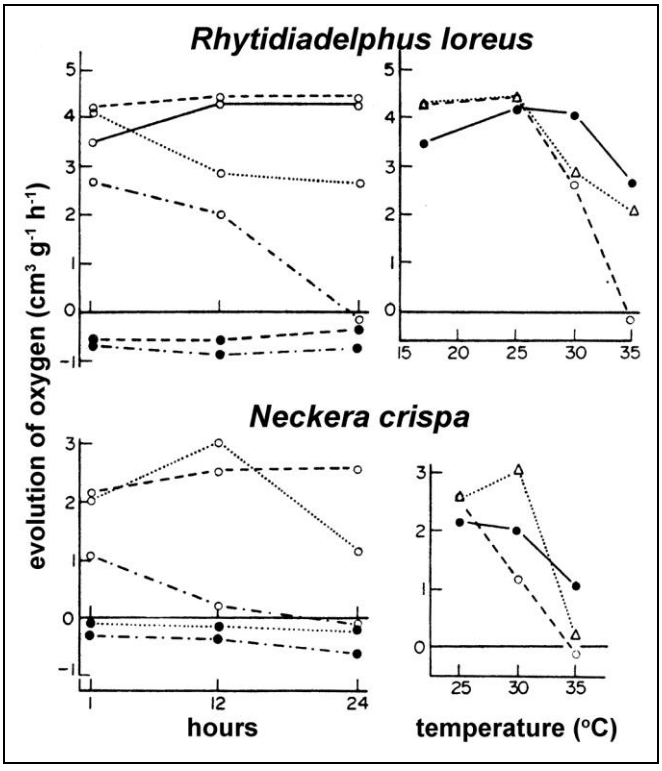

Figure 72. Effect on photosynthesis of prolonged exposure at various temperatures (— 17ºC; - - 25ºC; **....** 30ºC; -.-.- 35ºC) and responses for net assimilation after 1 hour (•), 12 hours (Δ), and 24 hours (o). Redrawn from Dilks & Proctor 1975.

Rastorfer and Higginbotham (1968) demonstrated an increase in net photosynthesis of ***Bryum sandbergii*** in the range of 4-24°C, with a drop at 34°C. Dilks and Proctor (1975) compared twenty-three mosses and five liverworts at temperatures varying 5-45ºC. These bryophytes typically exhibited fourth order polynomial curves that rose to an optimum, then dropped abruptly (Figure 73). However, not all species showed such a sudden drop and some exhibited a broad optimum, as seen in Figure 74. It is interesting that the more Arctic ***Racomitrium lanuginosum*** (Figure 69) exhibits the opposite curve shape – a sharp rise with temperature to its optimum at 5ºC, and a slow decline above the optimum (Kallio & Heinonen 1973; Kallio & Kärenlampi 1975). ***Pleurozium schreberi*** (Figure 25, Figure 65) seems to exhibit a nearly bell-shaped curve with temperature, exhibiting an optimum at 10-15ºC (Kallio & Kärenlampi 1975).

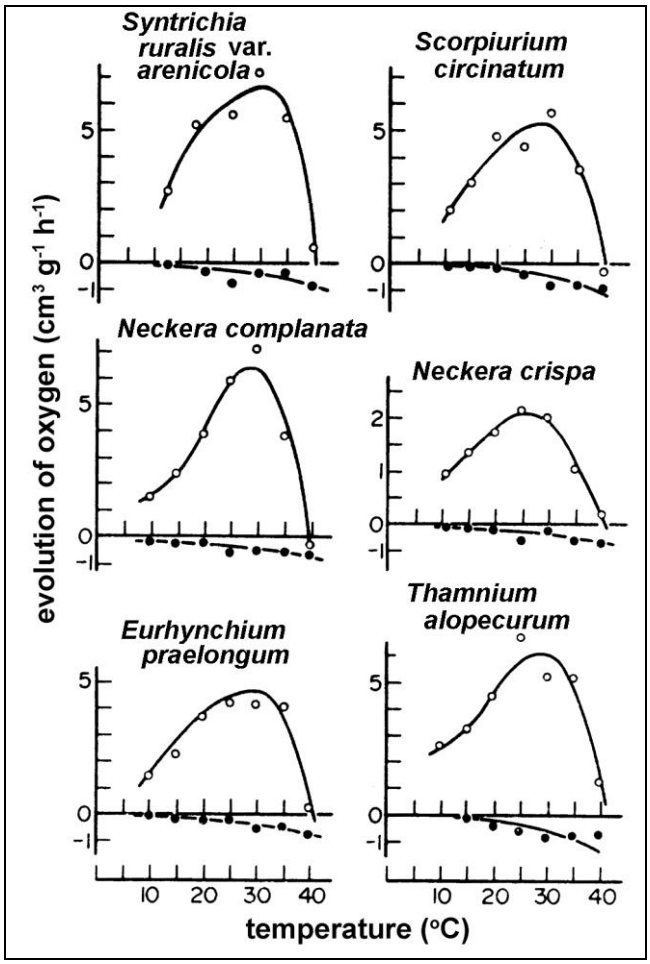

Figure 73. Photosynthesis at various temperatures. o = net assimilation; • = respiration. These responses are modelled with a fourth order curve. Redrawn from Dilks & Proctor 1975.

In the harsh conditions of the Antarctic, we can find some novel responses to temperature and light intensity. The ubiquitous moss ***Bryum argenteum*** (Figure 75) had a strong dark respiration response to temperature, causing significant chances in CO_2 exchange rates (Green *et al*. 1998). This species had a strong linear correlation between gross photosynthesis and electron-transport rate in PS II. Green and coworkers suggested that this deviation from the curvilinear relationship in tracheophytes might result from some sort of suppression of dark respiration in the light. In fact, it seems that both bryophytes and C_3 tracheophytes experience photorespiration in the light. Nevertheless, the relationship appears to be different in the bryophytes.

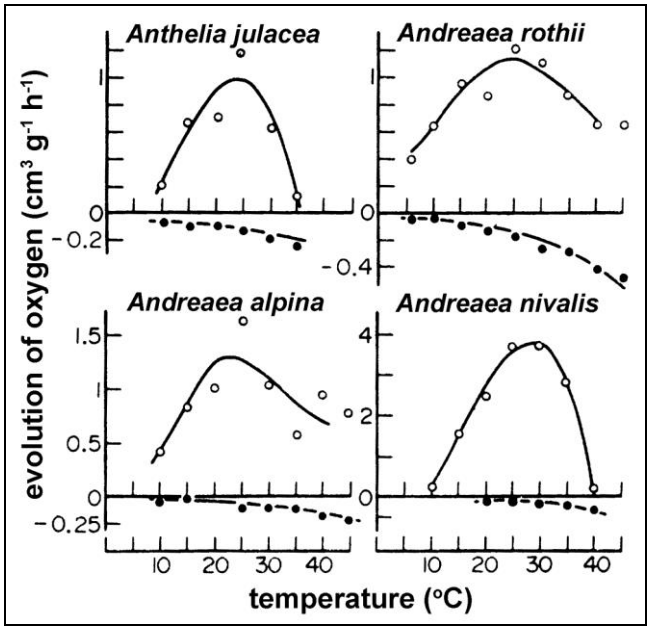

Figure 74. Photosynthesis at various temperatures for several mosses with a northern range. o = net assimilation; • = respiration. These responses are modelled with a fourth order curve but lack the sudden drop seen in Figure 73. Redrawn from Dilks & Proctor 1975.

Figure 75. ***Bryum argenteum***, a species with a strong respiratory response to rising temperatures. Photo by Michael Lüth, with permission.

Compensation Point

In studying 27 temperate bryophytes, Dilks and Proctor (1975) found the high temperature compensation point to be about 35-40ºC. However, temperature compensation points are affected by both light intensity and CO_2 concentration and vice versa (Rastorfer 1971).

Acclimation

Acclimation is a physiological change that adjusts to new conditions. It differs from adaptation in that the ability to change is programmed in the genetic code and the changes are temporary and non-heritable. For example, low temperatures can slow down the photosynthetic

apparatus, but in some habitats high light intensities may still cause high excitation of the photosynthetic apparatus. There is evidence [in ***Leucodon sciuroides*** (Figure 76)] that low temperatures may induce non-radiative dissipation of the absorbed light energy (Deltoro *et al*. 1999). This dissipation is necessary to protect the photosynthetic apparatus from excess excited electrons. This ability to dissipate energy and recover photosynthetically almost immediately upon return to temperatures above freezing permits this bryophyte to survive high light intensity at considerably lower temperature limits. The moss has become acclimated to the new temperature. This moss is one of many examples of preadaptation observed in mosses. This Mediterranean moss is capable of surviving light and temperature conditions that might be encountered in the Antarctic.

Figure 76. ***Leucodon sciuroides***, an epiphyte, showing dry branches to the left and wet ones in the middle. Photo by Michael Lüth, with permission.

Even changes in CO_2 concentrations can elicit acclimation in bryophytes. ***Riccia fluitans*** (Figure 77) lives part of its life floating on lakes and ponds. But some of these plants end up stranded on soil out of water. This environment is much higher in both light and CO_2 than the floating environment from which they came. The relative growth rate under low light and low CO_2 was 0.011 day^{-1}, whereas under high light intensity and high CO_2 it was 0.138 day^{-1} (Andersen & Pedersen 2002). Interestingly, maximum photosynthesis decreased with increasing light intensities, but it increased with increasing CO_2. The CO_2 compensation point was very low at high light and low CO_2 levels, increasing at low light and high CO_2 levels. These shifts in compensation point are an advantage for plants that live in dense mats in the water with low CO_2 availability and high light intensity at the surface and greater CO_2 and lower light intensity on the lower side of the floating mat.

Figure 77. ***Riccia fluitans***, a species in which photosynthetic rate decreases in high light. Photo by Jan-Peter Frahm, with permission.

Glime and Acton (1979) used mosses conditioned for three weeks to a range of temperatures in the lab to demonstrate the effect of temperature on the photosynthesis of ***Fontinalis duriaei*** (Figure 71). These experiments indicated that the prior history of the moss affected its productivity at a given temperature. Maximum growth occurred in spring and fall and peak assimilation occurred at 5400 lux at 10ºC.

Fornwall and Glime (1982) approached the same seasonal question by using field-acclimated plants and showed that ***Fontinalis duriaei*** (Figure 71) altered its maximum temperature for photosynthesis seasonally. When mosses were brought from the field and their photosynthesis measured in the range of 0.5-40ºC, optimal temperatures shifted from 10ºC in January to 35ºC in August. However, these were short-term measurements of photosynthesis with one hour of acclimation to the respirometer flask and two hours of measurement time. Other experiments with growth at these temperatures over a 15-week period showed that the mosses could only sustain this high level of productivity for a short time and that in fact, temperatures above 20ºC caused the mosses to cease growth in the lab (Glime 1982, 1987a, b, c). A more thorough discussion of temperature acclimation is in Chapter 10-1.

The color of these mosses changed with the seasons as well, with the most deep green color in March and April and a brown color in September (Fornwall & Glime 1982). The puzzling result of this study is that not only did mosses from a stream with wide seasonal fluctuations show this acclimation, but those mosses that resided in a stream that maintained a summer temperature of 8.5ºC likewise shifted their summer optimum temperature to 35ºC in the lab photosynthetic experiments. This suggests that the optimum may not result from acclimating to temperature but that it instead may be stimulated by the lengthening photoperiod or other environmental parameter associated with the seasons.

One might expect temperature acclimation in more northern regions. Oechel *et al*. (1975) demonstrated that subarctic populations of ***Dicranum fuscescens*** (Figure 70) exhibited a high temperature acclimation (Figure 78). Acclimation to warm temperatures caused a higher temperature optimum (similar to mean field temperatures,

ranging 5-15°C), higher maximum net photosynthetic rate, and a lower photosynthetic max at 0°C.

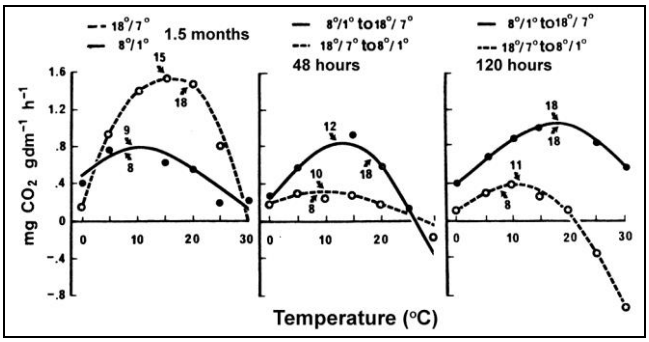

Figure 78. Acclimation responses of net photosynthesis to temperature in ***Dicranum fuscescens*** (Figure 70) at Schefferville, Quebec (55ºN) after cultivation at warm (18º/7ºC) and cool (8º/1ºC) temperatures for 1.5 months. Modified from Oechel *et al*. 1975.

Dicranum fuscescens (Figure 70) in subarctic Canada raised its temperature optimum for photosynthesis from 0-10ºC in the beginning of June to 10-20ºC by 7 July, with net productivity dropping drastically by 29 July (Figure 79), but its dark respiration rates showed no evidence of acclimation (Hicklenton & Oechel 1976). The tissue temperatures fluctuated between a low of 3ºC and a high of 26ºC during that period. The remarkable drop in productivity by the end of July suggests that the moss could not sustain the high temperature respiratory cost and eventually lost net gain in productivity. At the other end, net productivity was negative at temperatures above 15ºC on 5 June. On the other hand, Arctic populations had an optimum temperature that was generally higher than the mean maximum tissue temperature with optima ranging from 12-19°C (Oechel *et al*. 1975). This high optimum commonly accompanies tolerance for lower temperatures.

Even short-term adjustments to changing light levels are possible. The drought-tolerant ***Syntrichia ruralis*** (Figure 27) experienced increases in F_v/F_m, NPQ, and light-adapted PS II yield [phi (PS II)] in sun plants transplanted to the shade, and concurrent decreases in shade plants transplanted to the sun (Hamerlynck *et al.* 2002). But these plants also seemed to have a memory of their old habitat; sun plants performed at a consistently lower level in the shade than did non-transplanted shade plants. Nonetheless, the ability to adjust its photosynthetic apparatus to changing light conditions permits this species to take advantage of a habitat in which the canopy above it changes, changing its exposure to sun vs shade.

One of the changes that occurs on a seasonal basis is a change in the light compensation point and light saturation point. In ***Plagiomnium acutum*** (Figure 23) and ***P. maximoviczii*** (Figure 48) from the temperate zone in China, light compensation points switch from 20 µM m^{-2} s^{-1} in the winter to 40 µM m^{-2} s^{-1} in the summer (Liu *et al*. 2001a). Likewise, the light saturation ranges from 200 µM m^{-2} s^{-1} in winter to 400 µM m^{-2} s^{-1} in summer. The temperature optimum also ranges from a low of 20°C in winter to a high of 35°C in summer.

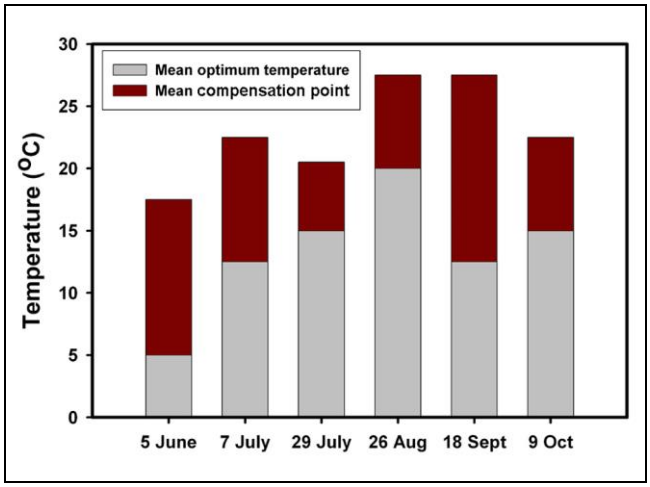

Figure 79. Mean optimum temperatures and upper temperature compensation points for ***Dicranum fuscescens*** (Figure 70) photosynthetic activity at Mary Jo lowland near Quebec, Canada, as an effect of acclimation due to increasing and decreasing spring to autumn temperatures. Based on Table 1 in Hicklenton & Oechel 1976.

Aquatic Differences

In streams, the availability of CO_2 varies widely, dependent on the temperature, *p*H, and rate of flow. In standing water, CO_2 can be even more limiting as temperatures rise and the CO_2 goes out of solution and is lost into the atmosphere. These CO_2 conditions are typically limiting to plant growth, including bryophytes (Madsen *et al*. 1993; Rice & Schuepp 1995). However, structural modifications of leaf spacing, leaf size, and exposure of photosynthetic cells among hyaline cells in ***Sphagnum*** (Figure 80-Figure 81) all contribute to making aquatic taxa less resistant to CO_2 uptake than are non-aquatic taxa (Rice & Schuepp 1995).

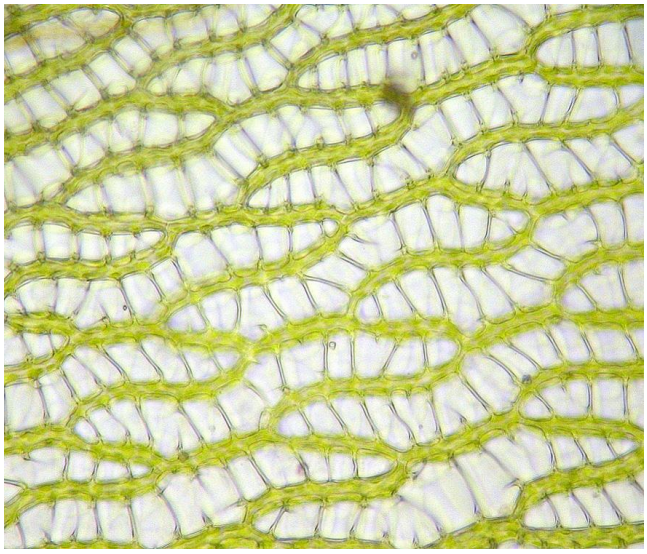

Figure 80. ***Sphagnum novo-zelandicum*** leaf cells showing hyaline cells and photosynthetic cells. Photo by David Tng, with permission.

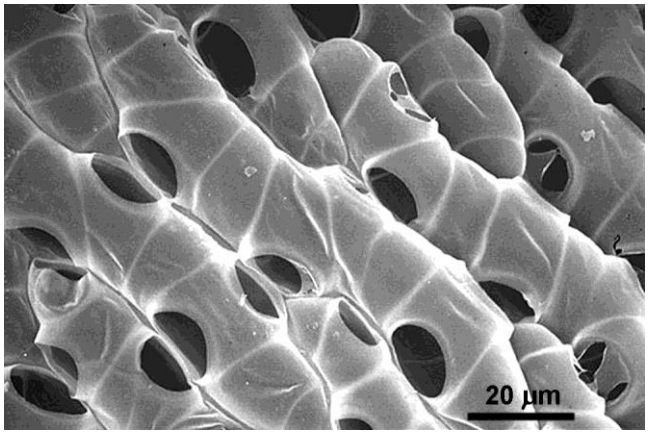

Figure 81. ***Sphagnum*** hyaline cells and pores. Photo from Botany Website, UBC, with permission.

In the aquatic environment, it is the deep water that has the highest CO_2 concentration (Maberly 1985), a product of microbial activity in the sediments. But deep water has the lowest light intensity. A testimony to the CO_2 limits imposed on aquatic mosses is their ability to grow well at extremely low light levels in the bottoms of lakes. These limits change seasonally, with productivity of ***Fontinalis antipyretica*** (Figure 30) in the North Bay of Esthwaite Water, England, being limited by light in November and by temperature in March. In August, despite microbial decomposition, intense competition for CO_2 from dense phytoplankton limits the moss productivity.

Another problem for aquatic bryophytes is that not only does the intensity of light decrease, but the spectral quality changes with depth. A reduction in water clarity due to increased load of dissolved organic carbon in Grane Langsoe caused a greater attenuation of blue light, relative to red light (Schwarz & Markager 1999). Photosynthesis is most active in red light, with its second peak in blue. However, red light has long wavelengths with low energy and thus is readily absorbed by water, making it diminish quickly with depth. The additional decrease in blue light, which has a short, high-energy light wave, means that the bryophytes are deprived of both of the most active wavelengths. The most abundant moss (70% of biomass) in these conditions was ***Warnstorfia exannulata*** (Figure 82), which exhibited its maximum absorption in the young parts that were most highly pigmented.

Figure 82. ***Warnstorfia exannulata***, a species with relatively low productivity in deep water. Photo from Biopix, through Creative Commons.

Riis and Sand-Jensen (1997) showed that this species and ***Sphagnum subsecundum*** (Figure 67) grew faster in deep than in shallow water in a low-nutrient lake in Denmark. Their study supported the hypothesis that supersaturated CO_2 as well as low temperatures and higher nutrient concentrations on the bottom of the lake supported the faster growth, despite the lower light intensity. One advantage of the lower temperature is that gases such as CO_2 stay in solution more easily. ***Sphagnum subsecundum*** exhibited lower dark respiration (1.3-fold) and higher photosynthesis (3.3-fold) at 9.5 m than at 0.7 m conditions.

In lakes, light attenuates with depth, often creating a photosynthetic desert at the bottom. Bryophytes, already adapted to low light, typically grow to greater depths than their macrophytic tracheophyte counterparts. In the Karelia Republic of northwestern Russia, bryophytes dominate at depths in three acidified lakes (*p*H of water 5.3-5.9) (Ilyashuk 2002). One lake was dominated by a dense carpet of ***Sphagnum denticulatum*** (Figure 83) at a depth of 5.0-7.6 m, covering about 50% of the bottom. A second lake had only ***Warnstorfia exannulata*** *s.l.* (Figure 82) at 5.0-7.0 m, covering 20% of the bottom. The third had only ***Fontinalis hypnoides*** (Figure 84) at 4.5-5.5 m, covering 13% of the bottom. In these latter two lakes, the net annual production by the mosses was 32-41 g air-dry mass m^{-2} yr^{-1}. In the ***Sphagnum***-dominated lake, however, the rate was much higher (157 g m^{-2}).

Figure 83. ***Sphagnum denticulatum***, a species with a high rate of annual production in deep water. Photo by Michael Lüth, with permission.

Figure 84. ***Fontinalis hypnoides***, a species with relatively low productivity in deep water. Photo by Ivanov, with permission.

Summary

Photosynthesis is limited by light intensity, temperature, CO_2 availability, and water availability. The compensation point is the level of any of these variables at which the CO_2 assimilation is equal to the CO_2 respired by the plant. These are influenced not only by the environment and seasons, but also by plant density and the plants themselves.

Limits are at both ends of the scale. There is a minimal level needed for successful net gain, but there are also upper limits beyond which the plants will lose energy. The saturation level is that level at which increase causes no further photosynthetic gain.

During the growing season, water is typically the limiting factor. However, some bryophytes are able to use water from fog and dew. Given enough water, CO_2 is often limiting. However, in some habitats, such as lake sediments, CO_2 emissions from bacteria and various invertebrates may elevate the CO_2 levels above ambient air CO_2. And some bryophytes, especially ***Sphagnum***, may use methane, converted to CO_2 by bacteria, to supply their CO_2. Aquatic bryophytes may use cation exchange to lower the *p*H in their immediate vicinity, permitting the use of bicarbonate by shifting the equilibrium toward free CO_2. Furthermore, it is possible that some may use external carbonic anhydrase to capture bicarbonate, but experiments to support this in bryophytes are lacking. Light may be limiting, but bryophytes seem to have the lowest light compensation point of any plant group. High light intensity can cause photodamage.

Net photosynthetic activity in many, perhaps most, bryophytes exhibits an abrupt drop above its optimum due to the loss of CO_2 through photorespiration.

Bryophytes acclimate to temperature, CO_2 level, and light intensity. This permits changes in the optimum, compensation point, and upper level limit or saturation point.

Acknowledgments

I appreciate the help of Don Lueking and Heather Youngs, both of Michigan Technological University, in my understanding of *p*K as it might apply to bryophyte CO_2 uptake. Thank you to Weng Zhe for correcting my error.

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CHAPTER 12
PRODUCTIVITY

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CHAPTER 12
PRODUCTIVITY

Figure 1. ***Pohlia wahlenbergii*** var**. *glacialis***, a wetland moss that is among the more productive of the acrocarpous mosses. Photo by Michael Lüth, with permission.

Productivity

It is within the framework of productivity that bryophytes are often considered unimportant as components of the ecosystem. As Martin and Adamson (2001) have pointed out, the photosynthetic capacity of mosses is generally considered to be much lower than that of the tracheophytes. However, they contend that this may be a misleading conclusion based on the method of calculating rates of net CO_2 uptake. Rather, they demonstrate that when productivity of bryophytes is calculated on the basis of chlorophyll, differences in rate disappear. It is only when dry mass is used to calculate productivity that bryophytes appear to have a much lower productivity rate than that of tracheophytes. And this depends on whether the senescent portions are included in the calculations.

Ecological Factors

Ability to Invade

There are so many ways in which to measure productivity that one must be careful to consider the purpose for which it is being measured. If it is measured to determine how soon it will grow enough to overtake the pebble path through the garden, a consideration of the linear growth of the stem pointed in that direction is most relevant. But if it is to determine what that particular species is capable of doing, in its own right, we would look at it quite differently, most likely at its biomass gain or CO_2 fixed on an hourly or annual basis. And if we want to know how soon it will fill in as ground cover, we need to know its lateral growth – the growth of its branches as well as its main stem. But it is even more complex than that.

New plants could arise from gemmae or fragments, requiring yet other measurements.

These measures are not easily convertible. For example, Gerdol (1996) expressed the linear growth of ***Sphagnum magellanicum*** (Figure 2) as 28-31 mm during the growing season, giving a sense of its ability to add to the depth of the peatland. Its dry matter production, however, was 12-13 mg per plant, giving us less of a mental picture of what effect it has on the ecosystem appearance. Does this latter measure reflect new capitula? How much has it increased the mat vertically? Despite these questions, for a peatland harvester, the biomass increase is of more value than the height of the plant.

Figure 2. ***Sphagnum magellanicum***, a major peat accumulator. Photo by Michael Lüth, with permission.

Niche Differences

Conditions that favor one species of bryophyte may be detrimental to another. This permits the slow-growing bryophytes to co-exist for a long time, with one species, in this case ***Pleurozium schreberi*** (Figure 3), advancing more in one year and the other, ***Dicranum polysetum*** (Figure 4), advancing more in another (Zhang 1998). Arscott *et al*. (2000) demonstrated this with their 13-year experiment in two Arctic streams. An increase in phosphorus caused little difference in the clump-forming ***Schistidium agassizii*** (Figure 5), whereas the formerly rare mat-forming species of ***Hygrohypnum*** (Figure 6) increased rapidly. Furthermore, ***Hygrohypnum*** species had greater tolerance to elevated temperatures (>20ºC) than did ***S. agassizii***, whereas the latter recovered easily from desiccation, while ***Hygrohypnum*** was susceptible to damage.

Figure 3. ***Pleurozium schreberi***, a slow-growing forest floor species. Photo by Janice Glime.

Figure 4. ***Dicranum polysetum***, a slow-growing species that competes with ***Pleurozium schreberi*** (Figure 3). Photo by Michael Lüth, with permission.

Figure 5. ***Schistidium agassizii*** forming clumps. Photo by Michael Lüth, with permission.

Figure 6. ***Hygrohypnum ochraceum*** forming mats. Photo by Michael Lüth, with permission.

Growth

Growth is one measure of productivity, but it has two components: **biomass gain** and **increase in length** (including branches). As Schwinning (1993) pointed out, unequal growth rates within a species can result from environmental and other factors independent of the productivity. She attributed these unequal rates to genetic differences, site differences, and competition (both infra- and interspecies).

Growth Measurements

Growth measurement is never easy in a non-linear subject such as a pleurocarpous moss. For example, several authors (Rincon & Grime 1989; Zechmeister 1995; Stark *et al.* 2001) have concluded that measuring stem elongation only may provide an inaccurate picture of true productivity. In fact, biomass accumulation and shoot elongation are uncoupled events and biomass is a better predictor of productivity than is elongation (Stark 2002). As a result, the methods used for measuring bryophyte growth are varied, each having its own purpose for a particular growth habit.

In larger, perennial mosses it is possible to determine growth because the plant provides natural markers (**innate** markers of Russell 1988; Figure 7). In their seminal papers on phenology of bryophytes, Longton and Greene (1969a, b) estimated annual growth rates using attached cotton markers to measure each stem, measuring distances between innate markers (inflorescence position), and measuring the length of the green apical portion of the stem. Hagerup (1935) used the alternating leaf sizes of taxa such as ***Ceratodon purpureus*** (Figure 8) to measure annual growth.

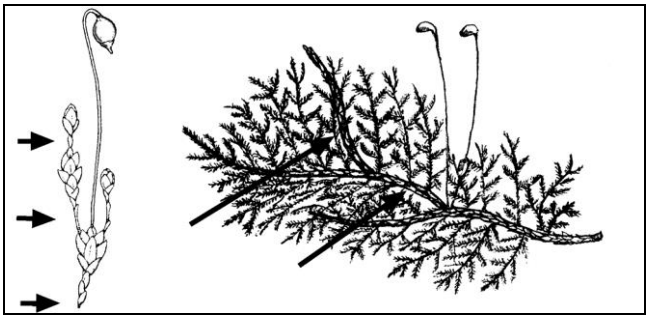

Figure 7. **Left:** Alternating regions of large and small leaves illustrating natural markers of growth on a species of ***Bryum***, based on Hagerup (1935). **Right:** ***Hylocomium splendens*** – arrows indicate region markers for a new season of growth. Drawings by Margaret Minahan.

Figure 8. ***Ceratodon purpureus***, a species with reduced leaf sizes marking the annual growth. Photo by Michael Lüth, with permission.

In others, such as ***Philonotis fontana*** (Figure 9) and ***Aulacomnium palustre*** (Figure 10), **innovations** (new branches just below the apex) often mark new growth, but the first leaves of new growth also cause a constriction compared to the smaller (or larger) leaves ending the previous growing season. In other taxa, there is a wider spacing of the leaves at the beginning of each new season, again causing a clear demarcation between years.

Figure 9. ***Philonotis calcarea*** showing multiple innovations just beneath the antheridial splash cup. Photo by Michael Lüth, with permission.

Figure 10. ***Aulacomnium palustre*** showing the branches near the tip. Photo by Kristian Peters through Creative Commons.

In males of **Polytrichaceae** (Figure 11, Figure 13) and others, new growth can arise from a splash cup so that one can trace back through a series of splash cups to measure growth (Figure 11). These various interruptions are useful in many of the acrocarpous moss taxa and at least some leafy liverworts. In pleurocarpous taxa, a new set of branches may arise, providing a marker, as is most exquisitely exhibited in the stair-step moss, ***Hylocomium splendens*** (Figure 7, Figure 12). But these markers tell us only the total growth for the year, and not the season of growth, and in many pleurocarpous mosses, more than one set of branches can arise in a single year, as in ***Fontinalis*** (Figure 14) (Glime 1982).

Figure 11. ***Polytrichastrum*** showing new growth from splash cups (arrows). Photo by Michael Lüth, with permission.

Figure 12. ***Hylocomium splendens***, showing annual branching. Photo by Amadej Trnkoczy through Creative Commons.

Changes in color can demarcate the growth of the current season, but these are difficult to discern for more than one year (Figure 13).

Figure 13. ***Polytrichum commune*** showing change in color from dark green to light green where the current year's growth begins. Photo by Michael Lüth, with permission.

Hawes *et al*. (2002) determined the ages of mosses in a lake bed of the Canadian High Arctic by using annual **growth bands**. These bands were 10-30 mm in length and were apparent due to changes in leaf density and size. The most recent growth provided four – five bands with recognizable leaves and measurable concentrations of chlorophyll *a*. Another twelve bands were recognizable from leaf scars. However, their attempt to correlate effects of ice cover with growth in a given year failed, and they suggested that the relationship of ice cover to growth (and growth bands) was more complex.

Figure 14. ***Fontinalis*** showing branching. Photo by Andrew Spink <www.andrewspink.nl>, with permission.

Russell (1988) described eight methods for measuring growth (Figure 15), including innate markers. The **cranked wire** technique is commonly employed for ***Sphagnum*** (Figure 2), but suffers from the problem of compaction of the mat, particularly as a result of snow, thus underestimating growth, particularly for more than one year. **Tags** can be used to mark a specific point on the moss from which future measurements are taken, but one must be careful not to injure the stem or interfere with water movement. A modification of this method works well for ***Fontinalis*** (Figure 16) and other aquatics (Glime 1980, 1982); narrow strips of white velcro are placed around the stem as markers (Figure 16) (black velcro seems to have a toxic dye); for terrestrial mosses, the velcro may interfere with water transport, spacing, and drying.

Nets placed over the mosses (Figure 15) likewise provide a starting point for measurements but suffer problems similar to the compaction problems with the cranked wire, although generally it is the older parts that get compacted most. And these might also interfere with water movement, hence giving unnatural readings. **Vital stains** that are not water soluble can serve as markers, including fluorescent dyes and powders; these must be selected not to interfere with photosynthesis or alter nutrient concentrations. **Bags** constructed of nylon mesh can be used to mark a starting point, with an initial measurement of the protruding stems. Russell (1988) recommends cutting the stems to a known length and putting them in the bag, neatly arranged upright; note that this is a flat bag, and the growing tip should not be removed. Gremmen *et al*. (1975) and Russell (1984) used a **coring** method in which they cut horizontally through the

soil beneath the bryophytes, then spread small pieces of polystyrene pellets or other marker before replacing the moss, thus providing a marker from which to measure. This method could again suffer from compaction problems, depending on the species of bryophyte. **Photography** can give rates of advancement of a colony but cannot provide details of growth and provides only horizontal growth (cover), not vertical assessment. Similarly, sheets of clear plastic can be placed over the moss patch and outlines drawn for future comparison. Zhang (1998) used the latter method to show that location of moss patches on the forest floor is quite dynamic.

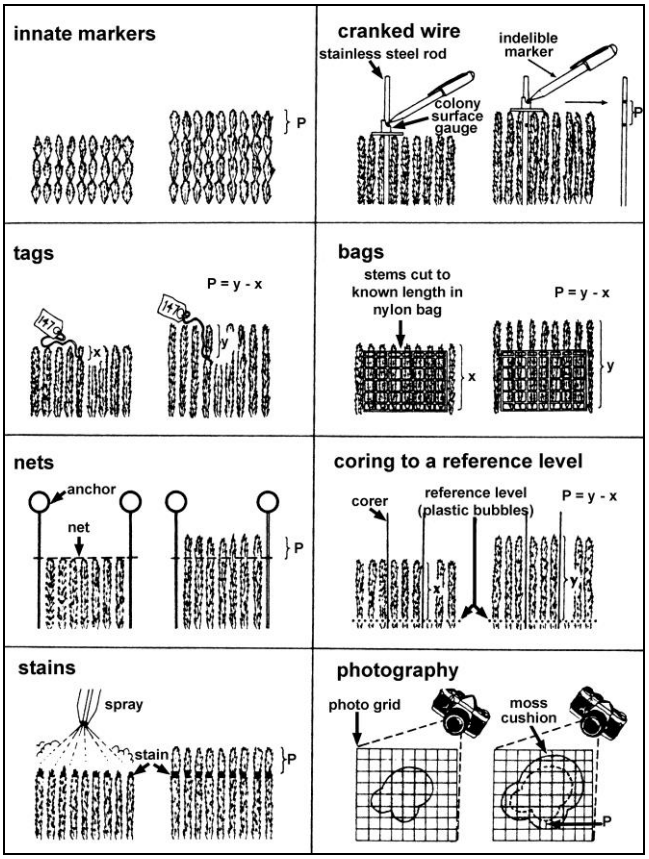

Figure 15. Methods usable for measuring bryophyte shoot extension growth. **Left** figure of each pair represents the starting condition and time; **right** figure represents end of measuring period. Modified from Russell 1988.

Figure 16. ***Fontinalis novae-angliae*** on velcro, permitting measurement of growth. Photo by Janice Glime.

Growth rates may include only the dominant stem, or the sum of all the branches as well. Smith (1982) found that the epiphytic ***Isothecium myosuroides*** (Figure 17) in England never grew more than 16 mm per year. In an even drier habitat, on dry, exposed, granite ledges in northwestern Ontario, Vitt (1989) measured a yearly growth rate of 2.3-3.1 mm yr^{-1} for ***Racomitrium microcarpon*** (Figure 18). Vitt (1990) also measured growth as lateral expansion of a clone. In clumps of ***Pylaisia polyantha*** (Figure 19) on the bases of poplars, the yearly increase was about 6-8 mm yr^{-1}.

Figure 17. ***Isothecium myosuroides*** on tree. Photo by Michael Lüth, with permission.

Figure 18. ***Racomitrium microcarpon***, a species of exposed granite ledges. Photo by Michael Lüth, with permission.

Figure 19. ***Pylaisia polyantha*** with young sporophytes. Photo by Michael Lüth, with permission.

Biomass measurements for living bryophytes are often meaningless because of their tremendous ability to sequester water, not only internally but also externally. Wet mass can be up to 20 times the dry mass of ***Sphagnum*** (Figure 2), making any wet mass measure meaningless for comparison purposes. Drying the moss, however, creates a new variable that necessarily terminates the experiment and may therefore not be practical. Furthermore, dry mosses can gain sufficient atmospheric moisture to show measurable mass gain during the short time required to weigh them (personal observation). In cases where light availability is the same for all members of a population, biomass and growth in length can be correlated and either might be chosen as a measure of productivity, depending on the goals of the study.

How does the growth occur within the plant and what are the sources of the needed resources? Bisang *et al*. (2008) investigated this question in ***Pseudocalliergon trifarium*** (Figure 20). This species has discrete annual segments. They found that growth in mass correlates with the segment mass of the previous two years. This relationship declines linearly for the older years. Hence, it appears that growth is limited by reallocation of resources.

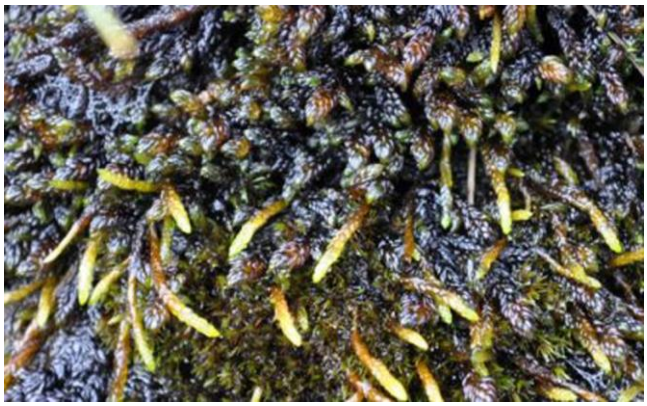

Figure 20. ***Pseudocalliergon trifarium***, a species with discrete annual segments. Photo by Andrew Hodgson, with permission.

Figure 21. Annual growth marker of ***Pseudocalliergon trifarium*** showing end of a season of growth where leaves become smaller on left and remain small for new growth on right. Photo courtesy of Lars Hedenäs.

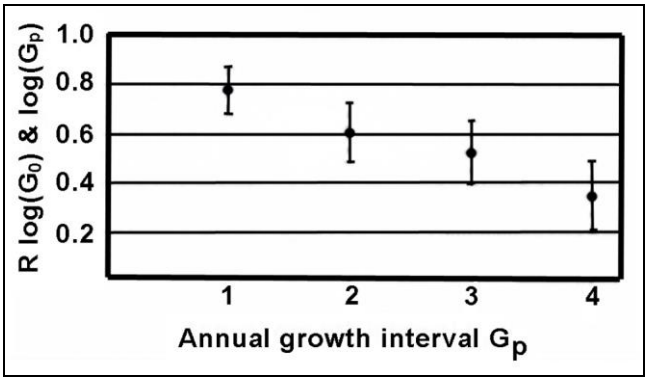

Figure 22. Pearson's Product Moment correlation coefficients R between the most recent growth interval (G_0) and consecutively older annual intervals, G_1 to G_4. Shoots from 12 populations were pooled (n=44). Bars indicate ± 1 standard error of R. Data for biomass were log transformed prior to analyses. Redrawn from Bisang *et al*. 2008.

In ***Bryum laevigatum***, growth bands are evident, marked by a dark brown color and smaller leaves (Rod Seppelt, Bryonet 16 February 2013). New growth exhibits light green, larger leaves. Rhizoids are often more prominent among the smaller leaves. Are these best referenced as growth bands, responsive to changes in the weather, or are they truly markers of annual increments?

Aquatic forms demonstrate markers that may be indicators of seasonal changes in water level, with cessation or near cessation of growth occurring when the water level is low in summer and they are stranded above water. These seasonal changes may be manifest as changes in leaf size or stem length or branching (Rod Seppelt, Bryonet 16 February 2013).

In Antarctica, ***Bryum argenteum*** (Figure 23) and ***Ceratodon purpureus*** (Figure 8) exhibit banding patterns (Rod Seppelt, Bryonet 16 February 2013). These may represent differences between the spring-summer growth and winter dormancy. The internode distance and hyaline leaf apex length differ between Antarctic populations of ***B. argenteum*** and those of Tasmania. Both produce clusters of branches.

Figure 23. ***Bryum argenteum***, a species that exhibits banding patterns. Photo by Rui-Liang Zhu, with permission.

Annual Length Increase

Length increase is generally related to growth form, with acrocarpous mosses exhibiting slow rates of growth in length compared to pleurocarpous mosses (Table 1). The pleurocarpous taxa further increase their biomass by development of new branches, creating an exponential growth pattern. Among these pleurocarpous bryophytes, some can become very long and have high growth rates, with some ***Fontinalis*** (Figure 24) (Glime 1987b) and ***Sphagnum*** (Figure 2) species growing 400 mm in a season. ***Taxiphyllum barbieri*** (Figure 25; Java moss, often mistakenly called *Vesicularia dubyana*) can quickly fill a 50 gallon aquarium through extensive branching and length gain.

Figure 24. ***Fontinalis antipyretica***, a genus that branches multiple times in a growing season. Photo by Michael Lüth, with permission.

Figure 25. ***Taxiphyllum barbieri***, a fast-growing species in an aquarium. Photo by Buchling through Creative Commons.

On Signy Island in the Antarctic, the upright ***Polytrichum strictum*** (Figure 26) grows 2-5 mm, whereas at Pinawa, Manitoba it grows 15-55 mm per year, exhibiting differences due to microclimate and habitat (Longton 1974, 1979). Pitkin (1975) showed wide variation in growth of ***Hypnum cupressiforme*** (Figure 27), depending on its height on the tree trunk, with mm of growth at 30-100 cm above ground doubling that at 150-200 cm from 23 May to 6 October. Not surprisingly, growth of the upper side of a sloping trunk was more than double that on the lower side.

Figure 26. ***Polytrichum strictum***, a species that has 10X as much growth in Manitoba compared to that on Signy Island. Photo by Sture Hermansson, through online permission.

Figure 27. ***Hypnum cupressiforme***, a species whose growth varies with height on the tree trunk. Photo by Jan-Peter Frahm, with permission.

Table 1. Comparison of growth in length of various mosses from a variety of locations and habitats.

Species	mm yr^{-1}	Location	Reference
Forsstroemia trichomitria	3.85-4.45	Virginia	Stark 1986
Calliergon	10-30	Arctic	Hawes *et al*. 2002
lake species	10	Canadian Arctic	Sand-Jensen *et al*. 1999
Leucobryum glaucum	9.1	S. England	Bates 1989
Meesia triquetra	3.7-14.8	Devon Island	Vitt & Pakarinen 1977
Ptilidium pulcherrimum	3.5-6.3	N. Sweden	Jonsson & Söderström 1988
Sphagnum magellanicum	28-31	S. Alps, Italy	Gerdol 1996
Sphagnum papillosum	33		Gaberscik & Martincic 1987
Sphagnum spp.	4-24	northern Quebec	Moore 1989
Polytrichum strictum	2-5	Antarctic	Longton 1979
Polytrichum strictum	15-55[1]	Pinawa, Manitoba, Canada	Longton 1979
Fontinalis duriaei	400 (incl branches)	N. Michigan	Glime 1987a
Rhynchostegium riparioides	33.4-73.3	streams, Northern Pennines, England	Kelly & Whitton 1987
Racomitrium lanuginosum	5.4-6.7	Marion Island	Russell 1984
Racomitrium lanuginosum	2.3	Mt Fuji	Nakatsubo 1990
Racomitrium lanuginosum	5-15	England	Tallis 1959, 1964
Racomitrium microcarpon	2.3-3.1	NW Ontario	Vitt 1989

Uncoupling

In bryophytes, as in some other plants, the increase in height/length may not be well correlated with increase in biomass. For example, in loblolly pine, branching becomes denser in low-density populations, but in high-density populations the trees grow taller. Likewise, self shading or other causes of low light cause elongation without a concomitant gain in biomass, as illustrated by grass elongation under a board on your lawn. It is an interesting phenomenon that biomass increases and elongation may not occur at the same time. Rincon and Grime (1989) showed very clearly that growth in length and increase in biomass of ***Brachythecium rutabulum*** (Figure 28, Figure 31), ***Thuidium tamariscinum*** (Figure 29, Figure 31), and ***Lophocolea bidentata*** (Figure 30, Figure 31) may be almost inverse relationships. When dry matter production declined, there was an increase in length, causing a negative biomass production (Figure 31). This, however, is not true for all species, as seen by ***Plagiomnium undulatum*** (Figure 31, Figure 32) and ***Pseudoscleropodium purum*** (Figure 31, Figure 33).

Figure 29. ***Thuidium tamariscinum*** with capsules, a species in which growth in biomass and length do not occur together. Photo by Michael Lüth, with permission.

Figure 28. ***Brachythecium rutabulum*** with capsules, a species in which growth in biomass and length do not occur together. Photo by Tim Waters, through Creative Commons.

Figure 30. ***Lophocolea bidentata***, a species in which growth in biomass and length do not occur together. Photo by Des Callaghan, with permission.

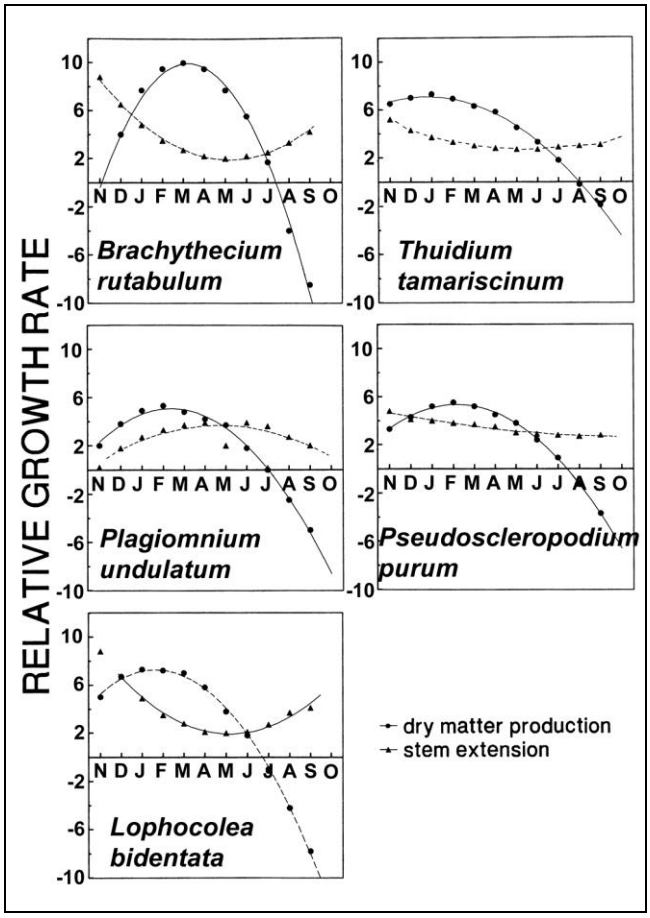

Figure 31. Comparison of relative growth rates in length and dry matter production in five bryophytes from calcareous grasslands. Redrawn from Rincon & Grime 1989.

Figure 32. ***Plagiomnium undulatum***, a species in which weight gain and elongation can occur together. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

The uncoupling of growth rate in length with that of branches is not surprising. As branches elongate, more distance is available for branch buds to form. In ***Leptodictyum riparium*** (Figure 34), total growth and growth of branches increase together (Sanford 1979). The rate of main axis growth, on the other hand, decreases as the rate of branch growth increases.

Figure 33. ***Pseudoscleropodium purum***, a species in which weight gain and elongation can occur together. Photo by Michael Lüth, with permission.

Figure 34. ***Leptodictyum riparium***, an aquatic species in which total growth and that of branches occur together, but main axis growth rate decreases at that time. Photo by Michael Lüth, with permission.

At least in ***Sphagnum*** (Figure 36-Figure 37), this uncoupling seems to be reflected in seasonal carbohydrate content as well (Shiraishi *et al*. 1996). In the Hakkoda Mountains of Japan, the glucose content of three ***Sphagnum*** species was highest in summer. Shiraishi *et al.* (1996) attributed this to an uncoupling between the active periods of matter production and growth. Sucrose, however, peaked in autumn in ***S. capillifolium*** (***S. nemoreum***; Figure 35) and ***S. papillosum*** (Figure 36), presumably in preparation for winter, and the seasonal changes were different between these two hummock species and ***S. tenellum*** (Figure 37), a hollow species.

Figure 35. ***Sphagnum capillifolium***, a hummock species in which growth and weight increase are uncoupled. Photo by Michael Lüth, with permission.

Figure 36. ***Sphagnum papillosum***, a hummock species in which growth and weight increase are uncoupled. Photo by Michael Lüth, with permission.

Figure 37. ***Sphagnum tenellum*** with capsules, a hollow species in which growth and weight increase are uncoupled, but sucrose production differs from the timing of the two previous hummock species. Photo by Dick Haaksma, with permission.

Gaberscik and Martincic (1987) likewise found that net photosynthesis did not correlate with growth. In August, when photosynthesis was maximal, biomass accumulation actually decreased. Chlorophyll content correlated positively with this period of high net photosynthesis, and consequently did not correlate with growth. Rather, the most intensive dry mass increase was at the beginning of the growing season. Winter was a low period for both photosynthesis and growth.

Seasonal Differences

We have assumed maximum growth of most temperate bryophytes to be in the spring when moisture is usually abundant and temperatures are cool. In their study of standing crops, Al-Mufti *et al.* (1977) supported this premise, showing that the peak standing crop in bryophytes occurred in May, the culmination of spring growth, and again in December, following cooler and more moist weather of autumn. The lowest biomass was in August when bryophytes would have suffered respiratory loss in the heat of summer. Zotz and Rottenberger (2001) likewise found this for three moss species [***Grimmia pulvinata*** (Figure 38), ***Schistidium apocarpum*** (Figure 39), ***Syntrichia ruralis*** (Figure 40)] on an exposed limestone wall in temperate Europe, with a strong seasonal pattern showing highest carbon fixation in autumn and near zero in summer.

Figure 38. ***Grimmia pulvinata***, a rock-dwelling species that is typically dormant in summer. This shows white awns that are common among xerophytic bryophytes. Photo by Michael Lüth, with permission.

Figure 39. ***Schistidium apocarpum***, a rock-dwelling species that is typically dormant in summer. Photo by Christophe Quintin, with permission.

Figure 40. ***Syntrichia ruralis***, a rock-dwelling species that is typically dormant in summer. Photo by Darkone, through Creative Commons.

However, we need more field studies to corroborate this assumption of spring growth on a broad scale. Growth in bryophytes has been difficult to measure because it is slow and increments are small, with yearly increments measuring in mm in many taxa.

Kershaw and Webber (1986) approached the seasonal behavior from a different angle, showing that in a forest habitat, chlorophyll was highest in ***Brachythecium rutabulum*** (Figure 28) in summer when light intensity was lowest. Low light, coupled with high temperatures, contributes to low summer productivity.

In a temperate, semi-arid, sandy grassland, ***Syntrichia ruralis*** (Figure 40) was strongly dependent on its microclimatic conditions and followed the same general principles I have suggested (Juhász *et al*. 2002). Its highest productivity, however, was in December and January, with carbon gain beginning in October. It was dormant throughout the hot, dry summer. In a different study where the temperate grassland had cover provided by *Juniperus communis* (Figure 41) shrubs, those species that occurred in the open exhibited a decline in photosynthetic efficiency from the humid spring to the hot, dry summer and exhibited lower efficiency (F_v/F_m) than those bryophytes growing in the shade of the shrubs (Kalapos & Mázsa 2001).

Figure 41. ***Juniperus communis***, a species that provides shade for bryophytes, permitting them to have greater photosynthesis than plants in the open. Photo by Neva Micheva, through Creative Commons.

Using transparencies to map coverage, Jansová (2006) found that **epixylic** bryophytes in a Bohemian old-growth forest grow faster in winter (October – April) than they do in summer, although some species did not differ in percentage growth (Jansová 2006). Both expansion and local extinction were greater in winter, making stability greater in summer.

But not all habitats create such pronounced seasonal differences. In the subarctic, ***Dicranum fuscescens*** (Figure 42) exhibited no clear seasonal differences in daily CO_2 uptake, nor were there any apparent differences between lowland and highland sites (Hicklenton & Oechel 1977). Melick and Seppelt (1994) found no seasonal differences in carbohydrate levels in continental Antarctica, although chlorophyll levels did decrease during winter. One reason for this apparent lack of seasonality is the high degree of daily variation that is experienced by bryophytes in Arctic and Antarctic areas.

Figure 42. ***Dicranum fuscescens***, a species with no clear seasonal differences in CO_2 uptake. Photo by BBS, with permission.

Nevertheless, seasonal water availability can impose seasonal differences, even in these northern regions. In peatland habitats, productivity may respond to greater water availability in summer, but decrease if the moss becomes submerged (Suyker *et al*. 1997), increasing again as they achieve greater CO_2 exchange with receding water. Skré and Oechel (1981) demonstrated, in their two years of study of the Alaskan taiga, that increased amounts of young, photosynthetically active tissue near the end of the growing season in the mosses ***Polytrichum commune*** (Figure 13), ***Pleurozium schreberi*** (Figure 3), ***Hylocomium splendens*** (Figure 12), and ***Sphagnum subsecundum*** (Figure 43) accounted for their highest maximum net photosynthesis occurring in August. Williams and Flanagan (1998) reported maximum photosynthetic rates of boreal ***Sphagnum*** in summer (14 μmol m^{-2} s^{-1}) compared to spring (5 μmol m^{-2} s^{-1}) and autumn (6 μmol m^{-2} s^{-1}). In the same habitat, however, ***Pleurozium schreberi*** had no seasonal variation, with mean rates of 7, 5, and 7 μmol m^{-2} s^{-1} during spring, summer, and autumn, respectively.

Figure 43. ***Sphagnum subsecundum***, a fen species with maximum photosynthetic rates in August. Photo by Jean Faubert, with permission.

Asada *et al*. (2003) showed that winter growth was important for the ***Sphagnum*** species [***S. austinii*** (Figure 44), ***S. fuscum*** (Figure 45), ***S. rubellum*** (Figure 46), ***S.***

papillosum (Figure 36), ***S. lindbergii*** (Figure 47), ***S. tenellum*** (Figure 37), and ***S. pacificum*** (Figure 48)] in the hypermaritime coastal peatland of British Columbia, Canada. Position in the hummock seemed to be important, with lower productivity on the hummocks than in the hollows, again emphasizing the importance of water availability.

Figure 44. ***Sphagnum austinii***, a species that has important winter growth in coastal British Columbia. Photo by Michael Lüth, with permission.

Figure 45. ***Sphagnum fuscum*** hummock, a species that has important winter growth in coastal British Columbia. Photo by Oscar Gran, through Creative Commons.

Figure 46. ***Sphagnum rubellum***, a species that has important winter growth in coastal British Columbia. Photo by Michael Lüth, with permission.

Figure 47. ***Sphagnum linbergii*** in Lapland, a species that has important winter growth in coastal British Columbia. Photo by Michael Lüth, with permission.

Figure 48. ***Sphagnum pacificum***, from Alaska, a species that has important winter growth in coastal British Columbia. Photo by Vita Plasek, with permission.

In the maritime Antarctic (Figure 49), respiration in ***Brachythecium*** (Figure 50) is highest in summer and lowest in winter, regardless of temperature, whereas in ***Chorisodontium*** (Figure 51-Figure 52) and ***Andreaea*** (Figure 53), there is little difference, perhaps relating to their drier habitats (Davey & Rothery 1996). Photosynthesis rates are generally higher in summer. The optimum temperature for photosynthesis does not change between summer and winter.

Figure 49. Maritime Antarctic and mosses. Photo by Matt Amesbury, through Creative Commons.

Figure 50. ***Brachythecium glaciale***, a species with greater in summer than in winter in the Antarctic. Photo by Michael Lüth, with permission.

Figure 51. ***Chorisodontium aciphyllum***, an Antarctic species in which respiration rate differs little between summer and winter. Photo by Peter Convey, with permission.

Figure 52. ***Chorisodontium aciphyllum***, an Antarctic species in which respiration rate differs little between summer and winter. Photo by Jan-Peter Frahm, with permission.

Figure 53. ***Andreaea depressinervis***, an Antarctic genus in which respiration rate differs little between summer and winter. Photo by through Creative Commons.

False Growth Markers

Growth markers come in many types. C. Robin Stevenson (pers. comm.) reports using sand as a marker in ***Campylopus introflexus*** (Figure 54-Figure 56). Each growth increment was demarcated by a layer of sand; changes in leaf size also marked the same increments. But are these truly growth markers? Stevenson suggests that they might also be triggered by heavy rain events. This could supply multiple markers in one year, or it could represent the winter growth surge.

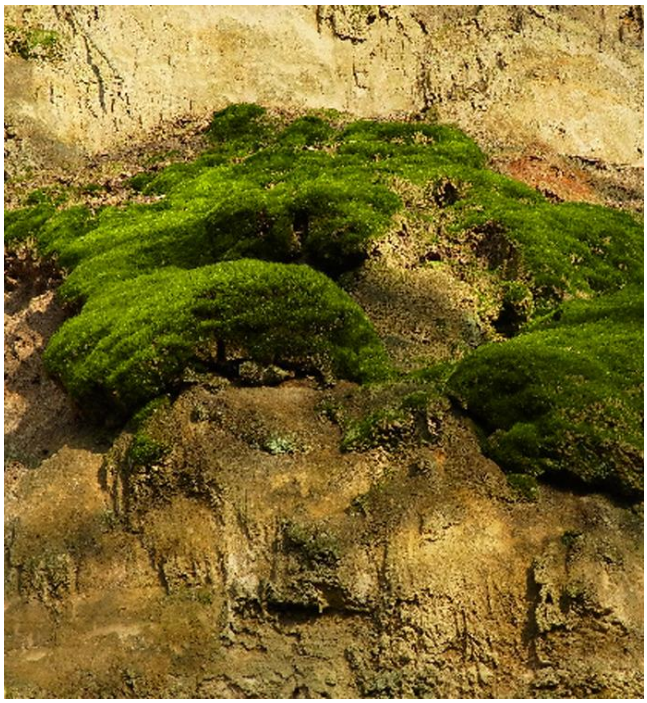

Figure 54. ***Campylopus introflexus***, a species that shows definite growth markers. Photo courtesy of C. Robin Stevenson.

Figure 55. ***Campylopus introflexus*** showing growth markers. Photo courtesy of C. Robin Stevenson.

Figure 56. ***Campylopus introflexus*** showing growth markers. Photo courtesy of C. Robin Stevenson.

Growth Control

Using the open-habitat moss ***Physcomitrella patens*** (Figure 57), Chodok *et al*. (2010) determined that *p*H and temperature significantly affected both biomass and a number of polyunsaturated fatty acids (linoleic acid, LA; γ-linolenic acid, GLA; α-linolenic acid, ALA; eicosadienoic acid, EDA; di-homo-γ-linolenic acid, DHGLA; arachidonic acid, ARA; eicosapentaenoic acid, EPA). Sucrose, $CaCl_2$, and $MgSO_4$ affected only some of the polyunsaturated fatty acids. Higher concentrations of sucrose positively affected LA, ARA, and EPA production; higher concentrations of the metals $CaCl_2$ and $MgSO_4$ negatively affected ARA and EPA.

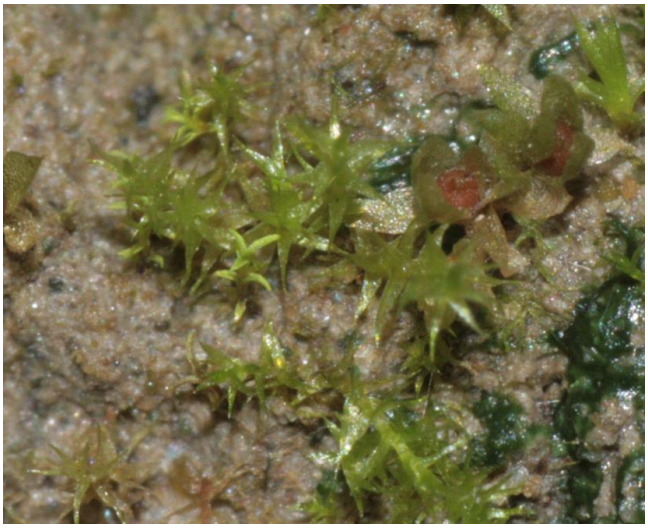

Figure 57. ***Physcomitrella patens*** with capsules, a species in which *p*H and temperature affect both biomass and polyunsaturated fatty acids. Photo by Hermann Schachner, through Creative Commons.

Growth Tradeoffs

Horsley *et al*. (2011) demonstrated that the allocation to asexual vs sexual reproduction in ***Bryum argenteum*** (Figure 23) is under genetic control. The allocation to asexual reproduction is negatively correlated with vegetative growth. Protonemal growth rate, on the other hand, is positively correlated with both asexual and sexual reproduction. The sexes did not differ in growth traits, asexual traits, sexual induction times, or biomass, but female sex-expressing shoots were longer than the males. Males, on the other hand, had a much higher number of reproductive structures, causing a much greater rate (24X) of investment in prezygotic tissue in males compared to females.

Etiolation

Elongation can be misleading. Low radiation causes greater elongation, with the highest elongation in ***Dicranum majus*** (Figure 58) from various polluted areas occurring at the lowest irradiance (20 μM m^{-2} s^{-1}) (Bakken 1995). **Etiolation** (excessive elongation and loss of chlorophyll due to insufficient light) can easily be observed if mosses are collected fresh, then put into a sealed plastic bag and stored in a nearly dark place. More on this phenomenon is discussed in the chapter on light.

Figure 58. ***Dicranum majus*** exhibiting a large plant size typical of low light conditions. Photo by Michael Lüth, with permission.

Belowground Productivity

It is rather presumptuous to title anything related to bryophytes as "Belowground Productivity" because data reporting such values are woefully lacking. Yet, bryophytes have rhizoids, and much of that biomass exists below ground, so such a title is not absurd. Furthermore, bryophytes have underground rhizomes, particularly in the **Polytrichaceae** (Figure 60). Sveinbjörnsson and Oechel (1981) have shown the respiration in the rhizome relative to whole plant CO_2 gain (Figure 59). Nevertheless, this is but an indirect indication that biomass is in place and active there with no indication of the carbon needed to put it there.

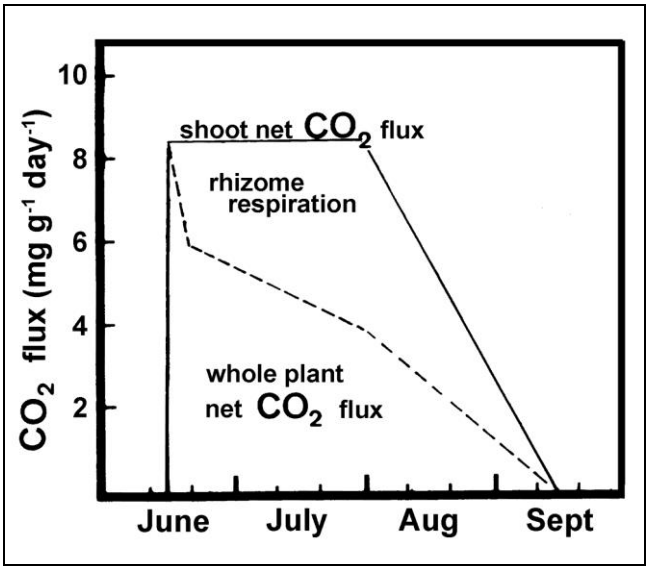

Figure 59. Relationship of aboveground and belowground CO_2 flux in ***Polytrichastrum alpinum*** (Figure 60) and ***Polytrichum commune*** (Figure 13) in the Alaskan tundra. Redrawn from Sveinbjörnsson & Oechel 1981.

Figure 60. ***Polytrichastrum alpinum*** with capsules. Photo by Michael Lüth, with permission.

Sporophyte Productivity

A discussion of the ability of the sporophyte to carry out photosynthesis is in Chapter 2-7, Bryopsida, and in Chapter 5-9, Ecophysiology of Development: Sporophyte. We know that bryophyte sporophytes have chlorophyll, even in thallose liverworts (Bold 1948), but few independent measurements of their rates of productivity seem to exist. These are further complicated by the photosynthetic capacity of the spores inside and the ability of the gametophyte to transport photosynthate to the sporophyte.

Nevertheless, Paolillo and Bazzaz (1968) demonstrated in ***Funaria*** (Figure 61) and ***Polytrichum*** (Figure 61) that the shape of the light saturation curve of the sporophyte is close to that of the gametophyte. For ***Polytrichum***, the weight of the gametophyte decreases as that of the sporophyte increases and there is no net photosynthetic gain by the sporophyte, but such is not the case in ***Funaria***. In ***Funaria***, there is a net photosynthetic gain. In ***Funaria*** the calyptra is perched at the end of the capsule and covers little of it, whereas in ***Polytrichum*** the capsule is completely covered (Figure 61). The authors conclude that the seta serves as a reservoir for the developing capsule.

Figure 61. **Left:** ***Polytrichum*** calyptra covering capsule completely. Photo by Janice Glime. **Right:** ***Funaria*** calyptra covering only the end of the capsule. Photo by Michael Lüth, with permission.

Polytrichum (*s.l.*) species in particular depend on the gametophyte for their carbon nutrition (Renault *et al.*

1992). The members of this group have large calyptrae (Figure 61) that completely cover the capsule and they are densely covered with hairs. This permits little light to reach the capsule. In ***Polytrichastrum formosum*** (Figure 62) sucrose is the primary soluble sugar in both generations, with the highest concentrations (~230 mM) occurring in the **haustorium** (cells at base of sporophyte foot; functions in absorption of nutrients from gametophyte to sporophyte). The **vaginula** (part of archegonium of moss enveloping base of embryo or seta after upper part has been torn away), on the other hand, has primarily hexoses.

Figure 62. ***Polytrichastrum formosum***, a species that uses sucrose in both generations. Photo by Martin Grimm, through Creative Commons.

Productivity and Aging

The current year's tissues seem to be the primary site of photosynthesis for most mosses. Collins and Oechel (1974) found that early in the season, the photosynthesis of Alaskan mosses relied on tissues produced the previous year, or even previous two years, but those rates were lower than for tissues produced in the current year (75% and 40% for 1 and 2 years earlier, respectively). Callaghan and coworkers (1978) found an even greater reduction in Swedish Lapland mosses. One-year-old tissues had rates 55% lower in ***Hylocomium splendens*** (Figure 12) and 58% lower in ***Polytrichum commune*** (Figure 63) than those tissues produced in the current year.

Figure 63. ***Polytrichum commune***, a species that has less productivity in the tissues formed the previous year than in that of the current year. Photo by A. J. Silverside, with permission.

Life Span

We have expressed productivity in measurements from seconds to annual, but in consideration of the ecosystem, it is also appropriate to speak in terms of a lifetime. Although our knowledge of life spans is still meager, we do have indications in some species, although they may be minimal rather than maximal ages. For example, Frye (1928) found specimens of ***Eurhynchium oreganum*** (Figure 64) that were up to six years old. Ulychna (1963) reported mean ages for ***Polytrichum commune*** (Figure 63) of 3-4 years, with dead parts of 15-17 years age, although if they were not growing in hummocks the dead parts seemed to be only 4-5 years old. (Perhaps that is the age when it starts to become a hummock?)

Figure 64. ***Eurhynchium oreganum***, a species that has tissues at least six years ole. Photo by Matt Goff <www.sitkanature.org>, with permission.

Corollary to the importance of life span is the effect that age has on growth rate. Ulychna (1963) found no effect in ***Hylocomium splendens*** (Figure 12) or ***Polytrichum commune*** (Figure 63). In the same two species, Callaghan *et al*. (1978) found that ***Hylocomium splendens*** grows its fronds for two years, then produces new segments, a factor that would be misleading in determining its age by its branching. Other factors can mislead age determinations based on growth markers. ***Polytrichum commune*** continues to have photosynthesis in dry conditions, whereas in ***H. splendens*** it ceases.

New growth may keep pace with dying portions (Callaghan *et al.* 1978). In ***Hylocomium splendens*** (Figure 12), normally the new shoot replaces the decomposing distal portion, but if the young segment is damaged, the whole shoot dies. On the other hand, ***Polytrichum commune*** (Figure 63) has a finite life expectancy which may differ with geographic area, but it also has an underground proliferation that can give rise to new shoots and compensate for lack of branching and death of aboveground parts.

In the maritime Antarctic, ***Polytrichum strictum*** (Figure 65) can have the extremely high annual mortality rate of 32% in young turfs (Collins 1976). However, in pure older turfs it is closer to 13%.

Figure 65. ***Polytrichum strictum*** illustrating the protection plants give each other in older tufts. Photo by Michael Lüth, with permission.

In the Arctic, longevity may compensate for the slow growth rates. Sand-Jensen *et al*. (1999) found that the slow, but steady-growing lake bottom mosses could persist for up to 17 years, retaining green leaves for several years, and decomposing slowly. Their growth rate, however, was only 10 mm per year, a relatively slow rate compared to pleurocarpous aquatic mosses elsewhere.

Leaf Production and LAI

Vitt (1990) decided to investigate the number of leaves and other leaf parameters that have been ignored for bryophytes. He did this to illustrate the complexity of moss populations, a fact often not realized by ecological observers. Using ***Drummondia prorepens*** (Figure 66), a small moss with large leaves, he found about 90 stems per cm^2. The stems averaged *ca*. 65 leaves each, resulting in 6000 leaves per cm^2. Considering the available leaf area for photosynthesis, he determined that one cm^2 has ~15 cm^2 of photosynthetic moss surface.

Figure 66. ***Drummondia prorepens*** on wood, a species in which one cm^2 of substrate has ~15 cm^2 of photosynthetic moss surface. Photo by Dale Vitt, with permission.

The **leaf area index** (**LAI**) has been used to express the relationship of the leaf-to-light interception (Smith 1990). It is the ratio of the leaf area to ground area, using the same units. Thus, a low LAI indicates wasted sunlight. A value of 1 indicates full usage, and a value of greater than 1 permits maximum usage at more angles of the sun. Since bryophyte leaves generally are not perpendicular to the sun, a higher LAI is required to obtain the same amount of light.

Simon (1987) estimated LAI measurements on ***Syntrichia ruralis*** (Figure 40), with 2030 leaves cm^{-2}, and ***Ceratodon purpureus*** (Figure 8), with 27,966 leaves cm^{-2}. These had leaf area indices (LAI) of 44 and 129 respectively. We can state the LAI for ***Drummondia prorepens*** (Figure 66), based on Vitt's (1990) data, as 15, discounting the portion of the leaf that is non-photosynthetic. Vitt (1990) reported a mean leaf area of 1960 mm^2 cm^{-2} (LAI = 19.6) for mosses in the boreal biome.

Energy Content

One distinction among plants is the amount of their tissue used for storage vs that used for photosynthesis. In this regard, the bryophyte uses nearly all of its tissue for photosynthesis, although I question whether it is as high as the 95% shown in

Table 2. Using the category of cryptogams includes the lichens, club mosses, horsetails, and ferns, complicating the interpretation of the number.

Fungal Partners

Although most bryophytes are self-reliant, photosynthetic organisms, some do benefit from fungal partners. The achlorophyllous thallose liverwort ***Cryptothallus mirabilis*** (Figure 67) relies totally on an endophytic fungus for its carbon input (Ligrone *et al*. 1993). The fungus is associated with the bases of the rhizoids and does not penetrate the thallus. There is no evidence that a third partner is involved; associated trees have a different fungal partner. Rather, it most likely gains its carbon from the organic nutrients in the soil and litter. Its dependency on this fungal carbon source is supported by its failure to develop beyond a few cells in sterile culture.

Figure 67. ***Cryptothallus mirabilis***, an achlorophyllous thallose liverwort. Photo by Michael Lüth, with permission.

In ***Aneura pinguis*** (Figure 68; Ligrone *et al*. 1993), ***Conocephalum conicum*** (Figure 69) (Ligrone & Lopes 1989), and ***Phaeoceros laevis*** (Figure 70) (Ligrone 1988),

it appears that it is the fungus that benefits, not the liverwort.

Table 2. Comparison of biomass devoted to photosynthesis vs storage and respiration for plants from major biomes. From Larcher 1983 and compiled from many sources.

Plant	Green mass (photo-synthetically active organs) shoots	Purely respiratory organs	
		Woody stems above ground	Roots and subterranean
Evergreen trees of tropical and subtropical forests	ca. 2%	80-90%	10-20%
Deciduous trees of the temperate zone	1-2%	ca. 80%	ca. 20%
Evergreen conifers of the taiga and in mountain forests	4-5%	ca. 75%	ca. 20%
Alpine scrubwood	ca. 25%	ca. 30%	ca .45%
Young conifers	50-60%	40-50%	ca. lo%
Ericaceous dwarf shrubs	10-20%	ca. 20%	60-70%
Grasses	30-50%		50-70%
Steppe plants			
Wet years	ca. 30%		ca. 70%
Dry years	ca. 10%		ca. 90%
Desert plants	10-20%		80-90%
Arctic tundra			
Tracheophytes	15-20%		
Cryptogams (including bryophytes)	**>95%**		
Plants of the high mountains	10-20%		80-90%

Figure 68. ***Aneura pinguis***, a thallose liverwort. Photo by Michael Lüth, with permission.

Figure 69. ***Conocephalum conicum***, a species that can suffer photosynthate loss due to a fungus. Photo by Janice Glime.

Figure 70. ***Phaeoceros laevis***, a species that can suffer photosynthate loss due to a fungus. Photo by Bob Klips, with permission.

Recent History Effects

Previous conditions have a strong influence on the photosynthetic performance of plants, at least among some Alaskan mosses (Alpert & Oechel 1987). Assemblages of mosses having recent experience with low water availability achieved maximum net photosynthesis at lower water contents than did those that had remained hydrated. Likewise, those mosses that occurred in sites with low light availability achieved higher net photosynthesis at lower light intensities than mosses that had recent history in high light intensities. And a close relationship exists between the lower temperature limit for 85% photosynthesis and the mean maximum tissue temperature for the previous five-day period (Oechel 1976).

Recent history of weather conditions most likely accounts for the considerably lower productivity in spring, compared to summer, in ***Atrichum undulatum*** (Figure 71), ***Plagiomnium affine*** (Figure 72), and ***Polytrichum formosum*** (Figure 62) (Baló 1967). One reason for this is the much higher chlorophyll *a* content in summer, compared to spring. Such previous histories can account for much of the variation we see between measurements of the same species and even the same individuals.

Figure 71. ***Atrichum undulatum*** fresh growth, a species with lower productivity in spring, compared to summer. Photo by Michael Lüth, with permission.

Figure 72. ***Plagiomnium affine***, a species with lower productivity in spring, compared to summer. Photo by Janice Glime.

Mitotic Activity

It appears that mitotic activity, the initial step in new growth, has its own clock. In a study on ***Pellia borealis***, a thallose liverwort, the greatest activity occurs between 11:00 and 14:00 hours (Szewczyk 1978). However, further studies are needed to determine if this is an endogenous rhythm or is tied to a daily ecological event in its habitat.

Respiration

Nearly every photosynthetic study includes respiration measurements. However, these may not be reported separately. **Net photosynthesis** is that incorporated carbon that remains after carbon is lost as CO_2 in respiration.

Bryophytes, as C_3 plants, exhibit both dark respiration and photorespiration. **Photorespiration** (respiration in the light) is difficult to measure because of the ability of a plant to put that same lost CO_2 immediately back into carbohydrate through the photosynthetic pathway. Photorespiration in C_3 plants is generally up to three times greater than dark respiration and accounts for the loss of energy at high temperatures. But even dark respiration increases in summer, as noted in ***Plagiomnium acutum*** (Figure 73) and ***P. maximoviczii*** **(**Figure 74**)** in China (Liu *et al*. 2001).

Figure 73. ***Plagiomnium acutum***, a species in which dark respiration increases in summer. Photo by Show Ryu, through Creative Commons.

Figure 74. ***Plagiomnium maximoviczii***, a species in which dark respiration increases in summer. Photo by Hiroshima University Digital Museum of Natural History, with permission.

Priddle (1980b) found that dark respiration of two Antarctic species of aquatic mosses [***Warnstorfia sarmentosa*** (Figure 75) and ***Drepanocladus*** *s.l.* sp. (Figure 76) differed little from that of algal communities in the same lake. At normal lake temperatures (up to 5ºC), the mosses respired approximately 0.3 g mg^{-1} ash-free dry mass h^{-1}.

Figure 75. ***Warnstorfia sarmentosa***, a species with respiration rates similar to those of algae in the same Antarctic lake. Photo by David Holyoak, with permission.

Figure 76. ***Warnstorfia fluitans***, a genus with respiration rates similar to those of algae in the same Antarctic lake. Photo by Michael Lüth, with permission.

In the high Arctic Svalbard, ***Sanionia uncinata*** (Figure 77) exhibits a high $\mathbf{Q_{10}}$ (ratio of reaction rates for a 10ºC rise) of 3 for respiration in the range of 7-23°C (Uchida *et al*. 2002). In the same range, photosynthesis exhibits very little difference, resulting in low temperature optima.

Figure 77. ***Sanionia uncinata***, a species that experiences a rapid rise in respiration with temperature in the Arctic Svalbard. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Habitat and Geographic Comparisons

Because of the length of the growing season, temperatures during the growing season, day length, available water, and other geographic and climatic factors, productivity in various biomes differs. Table 3 compares the various biomes to provide a framework for the discussion of habitat differences among bryophytes. Table 4 and Table 5 compare rates on biomass and area bases, respectively.

Although **water** may be a good indicator of productivity of a habitat, the general water availability of the habitat is not a good indicator of the productivity at the time that water is available. In fact, the relationship seems to be inverse. As can be seen in Table 3, the highest productivity seems to be from the driest habitats and from the plants adapted to those habitats. On the other hand, Suba *et al*. (1982) found that hygrophytic and mesophytic mosses of a beechwood community had more photosynthetic intensity than more xerophytic rock-inhabiting mosses. History is probably important here.

In the boreal forest, it appears that the **light use efficiency** of ***Pleurozium schreberi*** (Figure 3) (102 mM CO_2 M^{-1}) is well above that of most of the plants there (70-80 mM CO_2 M^{-1}), but its productivity is still lower (1.9 µM m^{-2} s^{-1} (Whitehead & Gower 2001). Other understory shrubs and herbaceous plants had productivity mostly between 9 and 11 µM m^{-2} s^{-1}.

For aquatic bryophytes, **depth** affects light intensity. Growth rates of deepwater mosses can be quite slow (10 mm per year in Canadian High Arctic lakes), and vary little between years (Sand-Jensen *et al*. 1999). Martínez Abaigar *et al*. (1994) found that ***Scapania undulata*** (Figure 78) had a leaf specific area of 317 cm^2 g^{-1} **DM** (dry mass) at 5 cm depth, but at 45 cm depth, the **LSA** (whole-plant leaf surface area) increased to 399 cm^2 g^{-1} DM. Concomitantly, the leaf specific weight (mass) was reduced from 3.16 mg cm^{-2} to 2.50 mg cm^{-2}. These differences can be interpreted as a response to the lower light availability at 45 cm. Canopy leaf fall, on the other hand, caused an increase in accessory pigments relative to chlorophyll *a*.

Figure 78. ***Scapania undulata***, a species in which whole-plant leaf surface area increases with water depth. 1 Michael Lüth, with permission.

Furness and Grime (1982) found that species of disturbed habitats (**ruderal species**) such as ***Funaria hygrometrica*** (Figure 79) had high relative growth rates, as did perennial pleurocarpous species such as

Brachythecium rutabulum (Figure 28) from fertile habitats. Most species grew best at temperatures of 15-25°C, whereas temperatures above 30ºC eventually killed moist mosses.

Figure 79. ***Funaria hygrometrica***, a ruderal species with a high growth rate. Photo by Michael Lüth, with permission.

Rates of Productivity

Productivity varies with habitat (Table 3). Mosses, typically living in shaded habitats, are low in productivity compared to other plant groups (Table 6). In the Antarctic, Davey and Rothery (1996) found greater seasonal variation in bryophytes from hydric habitats than from the less hydric sites.

Probably the highest productivity ever measured for a bryophyte is that of ***Sphagnum*** (Figure 43-Figure 48), with a productivity of 12 tons per hectare per year (Schofield 1985). C_4 plants average a CO_2 uptake of up to 80 mg dm^{-2} hr^{-1}, whereas C_3 plants seem to have a max of about 45 (Larcher 1983). Mosses, on the other hand, have a max of only 3! For some reason, perhaps the thick cuticle and other adaptations that reduce the light, CAM plants have a maximum of only 20. However, since measurement time may not coincide with the period of photosynthesis, we may need to interpret these numbers somewhat differently.

Table 3. Comparison of net primary production, biomass, chlorophyll, and leaf surface area in major biomes. From Whittaker *et al*. 1974; Larcher 1983.

		Net Primary Production			Leaf Surf Area Biomass (dry matter)			Chlorophyll		LAI	
Ecosystem Type	Area 10^6 km^2	Normal range g m^{-2} yr^{-1}	Mean g $m^{-2}yr^{-1}$	Total 10^9 t yr^{-1}	Normal range kg m^{-2}	Mean kg m^{-2}	Total 10^9t	Mean g m^{-2}	Total 10^6t	Mean m^2m^{-2}	Total 10^6 km^2
Tropical rain forest	17.0	1000-3500	2200	37.4	6-80	45	765	3.0	51.0	8	136
Tropical seasonal forest	7.5	1000-2500	1600	12.0	6-60	35	260	2.5	18.8	5	38
Temperate forest:											
Evergreen	5.0	600-2500	1300	6.5	6-200	35	175	3.5	17.5	12	60
Deciduous	7.0	600-2500	1200	8.4	6-60	30	210	2.0	14.0	5	35
Boreal forest	12.0	400-2000	800	9.6	6-40	20	240	3.0	36.0	12	144
Woodland and shrubland	8.5	250-1200	700	6.0	2-20	6	50	1.6	13.6	4	34
Savanna	15.0	200-2000	900	13.5	0.2-15	4	60	1.5	22.5	4	60
Temperate grassland	9.0	200-1500	600	5.4	0.2-5	1.6	14	1.3	11.7	3.6	32
Tundra and alpine	8.0	10-400	140	1.1	0.1-3	0.6	5	0.5	4.0	2	16
Desert and semidesert scrub	18.0	10-250	90	1.6	0.1-4	0.7	13	0.5	9.0	1	18
Extreme desert-rock, sand, ice	24.0	0-10	3	0.07	0-0.2	0.02	0.5	0.02	0.5	0.05	1.2
Cultivated land	14.0	100-4000	650	9.1	0.4-12	1	14	1.5	21.0	4	56
Swamp and marsh	2.0	800-6000	3000	6.0	3-50	15	30	3.0	6.0	7	14
Lake and stream	2.0	100-1500	400	0.8	0-0.1	0.02	0.05	0.2	0.5		
Total continental:	149	782	117.5	12.2	1837	1.5	226	4.3	644		
Open ocean	332.0	2-400	125	41.5	0-0.005	0.003	1.0	0.03	10.0		
Upwelling zones	0.4	400-1000	500	0.2	0.005-0.1	0.02	0.008	0.3	0.1		
Continental shelf	26.6	200-600	360	9.6	0.001-0.04	0.001	0.27	0.2	5.3		
Algal beds and reefs	0.6	500-4000	2500	1.6	0.04-4	2	1.2	2.0	1.2		
Estuaries (excluding marsh)	1.4	200-4000	1500	2.1	0.01-4	1	1.4	1.0	1.4		
Total marine	361	-	155	55.0	-	0.01	3.9	0.05	18.0		
Full total	510	336	172.5	3.6	1841	0.48	243				

Table 4. Productivity rates for bryophytes based on bryophyte mass, ordered from most productive to least. Values refer to CO_2 incorporated; dm refers to dry mass – if dm is not indicated, dry or wet mass is not known for certain.

Species	Productivity Value	Conditions/Location	Reference
Sphagnum auriculatum	232 mg g^{-1} h^{-1}	submersed at light comp point	Wetzel *et al*. 1985
Platyhypnidium riparioides	20.24 mg g^{-1} h^{-1}	max; converted from mM O_2 g^{-1} h^{-1}	Allen & Spence 1981
Fontinalis antipyretica	15.4 mg g^{-1} h^{-1}	max; converted from mM O_2 g^{-1} h^{-1}	Allen & Spence 1981
Plagiomnium acutum	19.9 mg g^{-1} h^{-1}	summer; converted from µM kg^{-1} s^{-1}	Liu *et al*. 2001
Plagiomnium maximoviczii	15.0 mg g^{-1} h^{-1}	summer; converted from µM kg^{-1} s^{-1}	Liu *et al*. 2001
Plagiomnium maximoviczii	9.86 mg g^{-1} h^{-1}	winter; converted from µM kg^{-1} s^{-1}	Liu *et al*. 2001
Plagiomnium acutum	9.20 mg g^{-1} h^{-1}	winter; converted from µM kg^{-1} s^{-1}	Liu *et al*. 2001
Hygrohypnum spp.	2.3-8.7 mg g^{-1} dm h^{-1}	Alaska stream	Arscott *et al*. 2000
Polytrichum formosum	8 mg g^{-1} dm h^{-1}	Hungary, summer, light saturation	Baló 1967
Plagiomnium affine	6 mg g^{-1} dm h^{-1}	Hungary, summer, light saturation	Baló 1967
Atrichum undulatum	5 mg g^{-1} dm h^{-1}	Hungary, summer, light saturation	Baló 1967
Calliergon sarmentosum	4.4 mg g^{-1} dm h^{-1}	max, Alaska Arctic tundra	Oechel & Sveinbjörnsson 1978
Polytrichastrum alpinum	4.4 mg g^{-1} dm h^{-1}	max, Alaska Arctic tundra	Oechel & Sveinbjörnsson 1978
Rhytidiadelphus squarrosus	3.5 mg g^{-1} dm h^{-1}	max, South Sweden	Stålfelt 1937
Ptilium crista-castrensis	3.4 mg g^{-1} dm h^{-1}	max, South Sweden	Stålfelt 1937
Hylocomium splendens	3.2 mg g^{-1} dm h^{-1}	max, South Sweden	Stålfelt 1937
Sphagnum girgensohnii	3.0 mg g^{-1} dm h^{-1}	max, South Sweden	Stålfelt 1937
Polytrichum commune	2.79 mg g^{-1} h^{-1}	max, mature veg, Fairbanks, AK	Skré & Oechel 1981
Sphagnum balticum	2.7 mg g^{-1} dm h^{-1}	subarctic mire	Johansson & Linder 1980
Polytrichum commune	2.65 mg g^{-1} h^{-1}	max, mature veg, Fairbanks, AK	Skré & Oechel 1981
Hylocomium splendens	2.5 mg g^{-1} h^{-1}	max, subarctic Finland	Kallio & Kärenlampi 1975
Rhytidiadelphus triquetrus	2.5 mg g^{-1} h^{-1}	max, South Sweden	Stålfelt 1937
Sphagnum magellanicum	2.2 mg g^{-1} dm h^{-1}		Petersen 1984
Pleurozium schreberi	2.0 mg g^{-1} dm h^{-1}	max, South Sweden	Stålfelt 1937
Pohlia drummondii	2.0 mg g^{-1} h^{-1}	max, subarctic Finland	Kallio & Kärenlampi 1975
Sphagnum papillosum	1.95 mg g^{-1} dm h^{-1}	max, Aug	Gaberscik & Martincic 1987
Sphagnum fuscum	1.7 mg g^{-1} dm h^{-1}	subarctic mire	Johansson & Linder 1980
Polytrichum juniperinum	1.6 mg g^{-1} h^{-1}	max, subarctic Finland	Kallio & Kärenlampi 1975
Schistidium agassizii	0.59-1.6 mg g^{-1} dm h^{-1}	AK stream, converted O_2 to CO_2	Arscott *et al*. 2000
Dicranum fuscescens	0.1-2 mg g^{-1} dm h^{-1}	Arctic, 10 Oct & 7 July, respectively	Hicklenton & Oechel 1976
Dicranum fuscescens	1.5 mg g^{-1} dm h^{-1}	max, Alaska Arctic tundra	Oechel & Sveinbjörnsson 1978
Pterobryum arbuscula	1.5 mg g^{-1} h^{-1}	max, epiphyte, Japan	Hosokawa *et al*. 1964
Thuidium kanedae	1.4 mg g^{-1} h^{-1}	max, epiphyte, Japan	Hosokawa *et al*. 1964
Leucobryum neilgherrense	1.4 mg g^{-1} h^{-1}	max, epiphyte, Japan	Hosokawa *et al*. 1964
Hylocomium splendens	1.39 mg g^{-1} h^{-1}	max, mature veg, Fairbanks, AK; moist?	Skré & Oechel 1981
Dicranum elongatum	1.3 mg g^{-1} dm h^{-1}	max, Alaska Arctic tundra	Oechel & Sveinbjörnsson 1978
Macromitrium gymnostomum	1.3 mg g^{-1} h^{-1}	max, epiphyte, Japan	Hosokawa *et al*. 1964
Sphagnum nemoreum	1.2 mg g^{-1} dm h^{-1}	lake, New York, USA	Titus *et al*. 1983
Ulota crispula	1.2 mg g^{-1} h^{-1}	max, epiphyte, Japan	Hosokawa *et al*. 1964
Pleurozium schreberi	1.20 mg g^{-1} h^{-1}	max, mature veg, Fairbanks, AK	Skré & Oechel 1981
	1.1 mg g-1 h-1	max, south Finland	Kallio & Kärenlampi 1975
Hylocomium splendens	1.08 mg g^{-1} h^{-1}	max, mature veg, Fairbanks, AK	Skré & Oechel 1981
Dicranum bonjeanii subsp *angustum*	1.0 mg g^{-1} dm h^{-1}	max, Alaska Arctic tundra	Oechel & Sveinbjörnsson 1978
Neckera konoi	1.0 mg g^{-1} h^{-1}	max, epiphyte, Japan	Hosokawa *et al*. 1964
Calliergon austrostramineum	1.0 mg g^{-1} h^{-1}	max, Antarctica	Rastorfer 1972
Sphagnum rubellum	0.9 mg g^{-1} dm h^{-1}	max, moorland	Grace 1970
Anomodon giraldii	0.9 mg g^{-1} h^{-1}	max, epiphyte, Japan	Hosokawa *et al*. 1964
Macrosporiella scabriseta	0.9 mg g^{-1} h^{-1}	max, epiphyte, Japan	Hosokawa *et al*. 1964
Boulaya mittenii	0.9 mg g^{-1} h^{-1}	max, epiphyte, Japan	Hosokawa *et al*. 1964
Pohlia nutans	0.9 mg g^{-1} h^{-1}	max, Antarctica	Rastorfer 1972
Dicranum elongatum	0.9 mg g^{-1} h^{-1}	max, subarctic Finland	Kallio & Kärenlampi 1975
Sanionia uncinata	0.9 mg g^{-1} h^{-1}	max, Antarctica	Rastorfer 1972
	0.9 mg g-1 h-1	max, subarctic Finland	Kallio & Kärenlampi 1975
Neckera pennata	0.8 mg g^{-1} dm h^{-1}	May, Adirondack Mt. Forest on tree	Tobiessen *et al*. 1977
Racomitrium lanuginosum	0.8 mg g^{-1} h^{-1}	max, Antarctica	Kallio & Kärenlampi 1975
Polytrichum strictum	0.7 mg g^{-1} h^{-1}	max, Antarctica	Rastorfer 1972
Racomitrium lanuginosum	0.6 mg g^{-1} dm h^{-1}	Fennoscandia tundra	Kallio & Heinonen 1975

Thuidium cymbifolium	0.6	mg g^{-1} h^{-1}	max, epiphyte, Japan	Hosokawa *et al*. 1964
Hylocomium brevirostre var. *cavifolium*	0.6	mg g^{-1} h^{-1}	max, epiphyte, Japan	Hosokawa *et al*. 1964
Homaliodendron flabellatum	0.6	mg g^{-1} h^{-1}	max, epiphyte, Japan	Hosokawa *et al*. 1964
Sphagnum subsecundum	0.57	mg g^{-1} h^{-1}	max, mature veg, Fairbanks, AK	Skré & Oechel 1981
Pleurozium schreberi	0.46	mg g^{-1} h^{-1}	max, mature veg, Fairbanks, AK	Skré & Oechel 1981
Sphagnum nemoreum	0.25	mg g^{-1} h^{-1}	max, mature veg, Fairbanks, AK	Skré & Oechel 1981
Mnium cuspidatum	0.16	mg g^{-1} dm h^{-1}	July, Adirondack Mt. Forest on tree	Tobiessen *et al*. 1977
Anomodon rugelii	0.00	mg g^{-1} dm h^{-1}	July, Adirondack Mt. Forest on tree	Tobiessen *et al*. 1977
Neckera pennata	no PS		July, Adirondack Mt. Forest on tree	Tobiessen *et al*. 1977
Ulota crispa	no PS		July, Adirondack Mt. Forest on tree	Tobiessen *et al*. 1977
Calliergon sarmentosum & *Drepanocladus* spp.	6	mg g^{-1} dm d^{-1}	max, Antarctica lake bottoms	Priddle 1980a
Calliergon giganteum	48.8	mg g^{-1} dm d^{-1}	0.03% CO_2, Arctic mineral sedge marsh	D'Yachenko 1976
	293.0	mg g^{-1} dm d^{-1}	1% CO_2, Arctic mineral sedge marsh	D'Yachenko 1976
Lophozia quinquedentata	25.4	mg g^{-1} dm d^{-1}	0.03% CO_2, Arctic mineral sedge marsh	D'Yachenko 1976
	155.2	mg g^{-1} dm d^{-1}	1% CO_2, Arctic mineral sedge marsh	D'Yachenko 1976
Polytrichum juniperinum	14.5	mg g^{-1} dm d^{-1}	dry, 0.03% CO_2, Arct mineral sedge marsh	D'Yachenko 1976
	87.2	mg g^{-1} dm d^{-1}	dry, 1% CO2, Arctic mineral sedge marsh	D'Yachenko 1976
Sphagnum squarrosum	13.0	mg g^{-1} dm d^{-1}	0.03% CO_2, Arctic mineral sedge marsh	D'Yachenko 1976
	77.8	mg g^{-1} dm d^{-1}	1% CO_2, Arctic mineral sedge marsh	D'Yachenko 1976
Dicranum fuscescens	7	mg g^{-1} dm d^{-1}	max, subarctic	Hicklenton & Oechel 1977

Table 5. Productivity rates for bryophytes on an area basis. Values refer to CO_2 incorporated.

Species	Productivity Value		Conditions/Location	Reference
Sphagnum spp.	14	µM m^{-2} s^{-1}	max, summer	Williams & Flanagan 1998
Sphagnum spp.	6	µM m^{-2} s^{-1}	max, autumn	Williams & Flanagan 1998
Sphagnum spp.	5	µM m^{-2} s^{-1}	max, spring	Williams & Flanagan 1998
Pleurozium schreberi	1.9	µM m^{-2} s^{-1}	Canadian boreal forest	Whitehead & Gower 2001
Ceratodon purpureus & *Bryum pseudotriquetrum*	4	µM m^{-2} s^{-1}	max, Langhovde, E Antarc, 9-17 Jan	Ino 1990
Hypnum cupressiforme	0.045	g m^{-2} s^{-1}	Southern Finland, 5°C	Kallio & Kärenlampi 1975
Pleurozium schreberi	0.045	g m^{-2} s^{-1}	Southern Finland, 15°C (optimum)	Kallio & Kärenlampi 1975
Hydrogonium consanguinium	0.88	g m^{-2} d^{-1}	July, India	Munshi 1974
Hydrogonium consanguinium	1.05	g m^{-2} d^{-1}	August, India	Munshi 1974
Hydrogonium consanguinium	1.05	g m^{-2} d^{-1}	September, India	Munshi 1974
Physcomitrium spp.	0.17	g m^{-2} d^{-1}	December	Munshi 1974
Physcomitrium spp.	0.08	g m^{-2} d^{-1}	January	Munshi 1974
Physcomitrium spp.	0.07	g m^{-2} d^{-1}	February	Munshi 1974
Hydrogonium consanguinium	31.53	g m^{-2} mo^{-1}	August, India	Munshi 1974
Hydrogonium consanguinium	26.60	g m^{-2} mo^{-1}	July, India	Munshi 1974
Hydrogonium consanguinium	14.80	g m^{-2} mo^{-1}	September, India	Munshi 1974
Physcomitrium spp.	5.13	g m^{-2} mo^{-1}	December	Munshi 1974
Physcomitrium spp.	2.44	g m^{-2} mo^{-1}	January	Munshi 1974
Physcomitrium spp.	2.10	g m^{-2} mo^{-1}	February	Munshi 1974
bryophyte cover	754	g m^{-2} yr^{-1}	Marion Island (45º54'S) drainage line	Russell 1985
Hypnum cupressiforme	188	g m^{-2} yr^{-1}	Austria	Zechmeister 1998
Pleurozium schreberi	161	g m^{-2} yr^{-1}	Austria	Zechmeister 1998
Abietinella abietina	144	g m^{-2} yr^{-1}	Austria	Zechmeister 1998
Hylocomium splendens	129.8	g m^{-2} yr^{-1}	Norway, Sweden	Tamm 1953
Hylocomium splendens	127	g m^{-2} yr^{-1}	Austria	Zechmeister 1998
Sphagnum papillosum	101.0	g m^{-2} yr^{-1}	moor	Newbould 1960
Hydrogonium consanguinium	72.93	g m^{-2} yr^{-1}	net production, India	Munshi 1974
Calliergon sarmentosum & *Drepanocladus* (*sensu lato*) spp.	40	g m^{-2} yr^{-1}	max, Antarctica lake bottoms	Priddle 1980a
Sanionia uncinata	30	g m^{-2} yr^{-1}	max, High Arctic, Svalbard (79°N)	Uchida *et al*. 2002
bryophyte cover	21	g m^{-2} yr^{-1}	Marion Island (45º54'S) fellfield	Russell 1985
bryophyte cover	12.8	g m^{-2} yr^{-1}	max, East Ongul Island, Antarctica	Ino 1983
Physcomitrium spp.	11.30	g m^{-2} yr^{-1}	Annual net production	Munshi 1974
Polytrichum strictum	2-5	mm yr^{-1}	Antarctic	Longton 1974?
Polytrichum strictum	15-55	mm yr^{-1}	Pinawa, Manitoba	Longton 1979?

Table 6. Mean maximum values for photosynthesis (CO_2 uptake) and biomass (DM) increase at natural CO_2 levels, saturating light intensity, optimal temperature, and adequate water availability. From Larcher 1983.

Plant group	CO_2 uptake mg dm^{-2} h^{-1}	mg gDM^{-1} h^{-1}
Land Plants		
Phanerogams		
Herbaceous plants		
C_4 plants	30-80 (108)	60-140
C_3 plants		
Crop plants	20-45 (60)	30-60
Plants of sunny habitats (heliophytes)	20-40 (94)	30-60
Shade plants (sciophytes)	4-20	10-30
Plants of dry habitats (xerophytes)	20-45	15-33
Grain and fodder grasses	15-35 (40)	
Wild grasses and sedges	8-20 (25)	8-35
CAM plants		
In the light	3-20	0.3-2
In the dark	10-15	1-1.5
Woody plants		
Tropical and subtropical trees		
Fruit trees	18-22	10-25
Forest canopy trees	12-24	
Understory trees	5-10	
Broad-leaved evergreens of the Subtropics and warm-temperate regions		
Sun leaves	10-18	
Shade leaves	3-6	
Seasonally deciduous trees		
Sun leaves	15-25 (35)	
Shade leaves	5-10	
Conifers		
Winter-deciduous		10-40
Evergreen	5-18	4-18
Mangrove trees	6-12 (20)	
Sclerophylls of periodically dry regions	5-15	3-10
Bamboos	5-10	
Palms	6-10	(12)
Desert shrubs	(4) 6-20 (30)	(2) 5-15 (35)
Dwarf shrubs of heath and tundra		
Winter- deciduous	10-25	15-30
Evergreen	5-10(15)	2-10
Cryptogams		
Ferns	3-5	
Mosses	**up to 3**	**0.6-3.5**
Lichens	0.5-2 (6)	0.3-2.5 (4)
Aquatic Plants		
Swamp plants, emersed hydrophytes	20-40 (50)	
Submersed cormophytes	2-6	5-25
Seaweeds	3-10	1-20 (30)
Planktonic algae		2-3

Although the biomass of bryophytes is small, their carbon sequestration is not inconsequential. Cryptogamic covers sequester ~3.9 Pg of carbon per year (Elbert *et al.* 2012). This equals about 7% of the net primary production in the terrestrial ecosystem. The uptake of N is ~49 Tg per year, accounting for nearly half of the biological N fixation on land.

Latitude Differences

It is difficult to determine if responses of populations in different parts of the world are the result of genetic differences or differences in acclimation history (Sveinbjörnsson & Oechel 1983). ***Polytrichum commune*** (Figure 13) from five diverse regions from Alaska (71°N) to Florida (29°N) were grown under common garden conditions in constant temperature conditions of 5 and 20°C. In this common set of conditions, plants from lower latitudes had higher photosynthetic rates except for the temperate St. Hilaire population. There was a sevenfold difference between the extreme values. Populations from the lower latitudes had more maximum photosynthetic response to the two temperatures than did populations from higher latitudes. On the other hand, bryophytes from higher latitudes had higher energy contents than those from lower latitudes (Russell 1990; Figure 80).

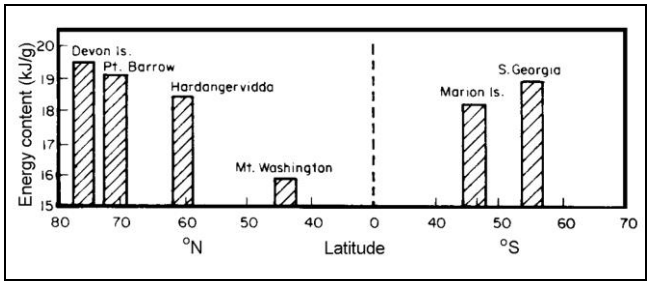

Figure 80. Comparison of mean energy content of bryophytes related to latitude in several tundra sites in Devon Island and Point Barrow, Alaska; Hardangervidda, Denmark; Mt. Washington, New Hampshire; and Marion Island and South Georgia, Antarctica. Reprinted from Russell 1990.

Antarctic

Temperatures in the Antarctic (Figure 81) have rather large daily fluctuations during the growing season. Therefore, it is not surprising to find that bryophytes growing there show little response to changes in temperature and little acclimation to any temperature (Davey & Rothery 1996). Nevertheless, the species exhibit summer maxima in productivity; no seasonal variation seems to exist for optimum temperature of gross or net photosynthesis.

Figure 81. Antarctic ice on Green Island. Photo by Matt Amesbury, through Creative Commons.

But temperature is not the only limiting factor in the Antarctic climate (Bramley-Alves *et al*. 2014). In addition to temperature, water availability likewise limits productivity. More recently, the ozone hole is limiting productivity, in part due to the increased UV-B radiation, but also because of the associated increase in wind in the ozone hole.

Frigid Antarctic

The **frigid Antarctic**, with mean air temperatures generally below 0ºC and very dry air, is entirely vegetated by cryptogams: **Cyanobacteria**, algae, lichens, and mosses. The most conspicuous vegetation is small turf and cushion-forming mosses including ***Bryum*** (Figure 23) and ***Grimmia*** (probably ***Schistidium***; Figure 82) species (Longton 1979). Standing biomass is similar to the annual production of the tundra, reaching 1000 g m^{-2}, but more typically 5-200 g m^{-2} (Longton 1974, Kappen 1985). Annual production seems to be less than 5 g m^{-2} yr^{-1} (Longton 1974, Ino 1983).

Figure 82. ***Schistidium antarctici***, a species with very limited annual production in Antarctica. Photo courtesy of Rod Seppelt.

The **cold Antarctic**, with summer mean air temperatures of 0-2ºC, has a production of 200-900 g m^{-2} in the larger moss turfs and carpets (Longton 1970, Davis 1981), comparable to temperate grassland (Longton 1992)! In this area, the biomass is more commonly 300-1000 g m^{-2} for green shoots, and reaches 20,000 - 30,000 g m^{-2} for total biomass, including older brown parts (Longton 1992). It is interesting that the production here is generally higher than in the Arctic tundra (Longton 1988, Russell 1990), exceeding 1000 g m^{-2} yr^{-1} (Russell 1990), perhaps due to greater precipitation and enhanced soil N and P from the marine environment (Longton 1992).

Arctic

Even in the cold Arctic (Figure 83), water is a major controlling factor in photosynthesis. ***Sanionia uncinata*** (Figure 77) has high photosynthetic activity only when water content is high during or following rainfall (Uchida *et al*. 2002). Temperature has little effect on net photosynthetic rates in this species, with photosynthetic rate being constant in the range of 7-23°C.

Figure 83. Arctic Lapland. Photo by Michael Lüth, with permission.

In Arctic habitats, bryophytes are often poorly represented in models on climate change and carbon balance (Street *et al*. 2012). Nevertheless, they are important components of the vegetation, and their seasonal dynamics are poorly understood. In a system dominated by ***Polytrichum piliferum*** (Figure 84) and ***Sphagnum fuscum*** (Figure 45). Street and coworkers found that seasonal changes in bryophyte photosynthetic capacity are important in determining gross primary productivity for both species and in contributing to the Arctic carbon balance. Gross primary productivity of ***Polytrichum piliferum*** was ~360 g C m^{-2} for one year, for ***S. fuscum*** 112 g C m^{-2}, figures that represent 90% and 30% respectively of the productivity of tracheophytes in the same area. Furthermore, the bryophytes are not significantly affected by the turf water content during the growing season.

Figure 84. ***Polytrichum piliferum***, a species with differences in photosynthetic capacity in different seasons in the Arctic. Photo by Jessica, through Creative Commons.

Wetlands

In the Arctic wetlands (Figure 85), mosses account for 91% of the above ground biomass (Oechel & Sveinbjörnsson 1978). Grasses and sedges usually arise from a bed of mosses, including the turf-forming ***Meesia*** (Figure 86) and ***Cinclidium*** (Figure 87) and carpet-forming ***Calliergon*** (Figure 88) and ***Drepanocladus*** *s.l.* (Figure 76)

species (Longton 1992). The annual production of 100-300 g m^{-2} can be 20-45% bryophyte (Longton 1992) and the biomass is up to 150 g m^{-2} (Oechel & Sveinbjörnsson 1978).

Figure 85. Arctic wetlands. NOAA, through public domain.

Figure 86. ***Meesia longiseta*** in Lapland, a genus that forms Arctic turfs where grasses and sedges grow. Photo by Michael Lüth, with permission.

Figure 87. ***Cinclidium arcticum***, a genus that forms Arctic turfs where grasses and sedges grow. Photo by Michael Lüth, with permission.

Figure 88. ***Calliergon sarmentosum***, an Arctic carpet-forming genus. Photo by Michael Lüth, with permission.

Tundra

In the tundra (Figure 89), mosses exhibit about 10% of the productivity of higher plants, despite occupying 50% of the above ground biomass. Whereas ***Polytrichum strictum*** (Figure 65) can have an annual production of 450-500 g m^{-2} in the cool Antarctic grassland (Figure 90), it reaches only 100-150 g m^{-2} in the Arctic spruce woodland (Figure 91) (Longton 1979). However, in some areas, the production reaches 50-90% of higher plant production and values up to 1000 g dry wt m^{-2} yr^{-1} can be measured (Clarke *et al*. 1971, Kallio & Kärenlampi 1975, Oechel & Sveinbjörnsson 1978, Russell 1990). More typical values are 1-50 g dry wt m^{-2} yr^{-1}. Ratios of biomass to production can be exceedingly high, up to 70:1, illustrating the slow growth and the extreme longevity of the plants (Longton 1992). In heath communities in the tundra of northern Sweden, biomass reaches 156 g m^{-2} (Jonasson 1982). However, in below ground biomass, the phanerogams far exceed the bryophytes, with underground parts contributing more than 50% of the total production of all plants (Longton 1984).

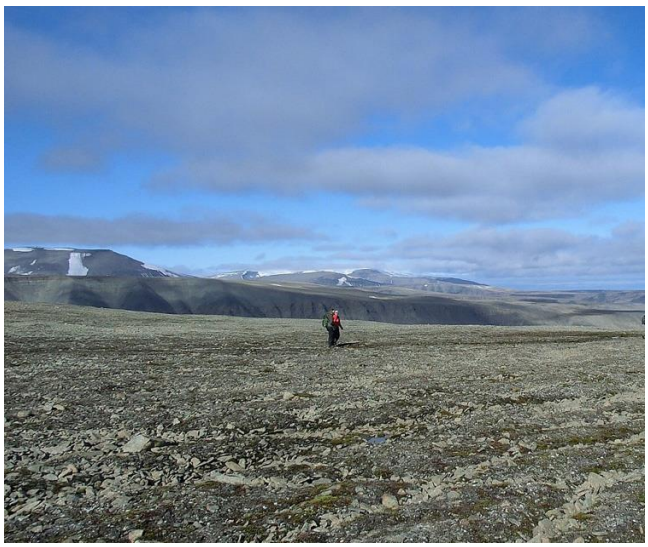

Figure 89. Tundra at Svalbard. Photo by Michael Lüth, with permission.

Figure 90. Tussock grass with Antarctic Fur Seal pups. Photo by Liam Quinn, through Creative Commons.

Figure 91. ***Picea*** in Alaska. Photo by Vita Plasek, with permission.

Coxson and Mackey (1990) found that the subalpine ***Pohlia wahlenbergii*** (Figure 1) exhibited strong diel periodicity in midsummer conditions, declining from 8 mg CO_2 g^{-1} hr^{-1} to ~5 mg CO_2 g^{-1} hr^{-1}.

Boreal Forest

In the boreal forest (Figure 92), the dominant mosses are feather mosses, especially ***Hylocomium splendens*** (Figure 12) and ***Pleurozium schreberi*** (Figure 93) (Longton 1992). Biomass can reach 170-290 g m^{-2} under spruce in Alaska (Figure 92), but only 4-6 g m^{-2} under *Betula* (Figure 94) and *Populus* species. Likewise, production was hardly measurable in the *Betula* and *Populus* forests, but reached 70-150 g m^{-2} under spruce, often exceeding the productivity of the spruce itself (Longton 1992)! Similar rates to those under spruce are found for feather mosses in other coniferous forests (Tamm 1953; Weetman 1968; Pakarinen 1978). ***Pleurozium schreberi*** in black spruce forests in New Brunswick, Canada, had an annual productivity of 44-66 g m^{-2} (Timmer 1970). Tamm (1953) reported 45-60 g m^{-2} for ***Hylocomium splendens*** in a Swedish spruce forest and Damman reported 50 g m^{-2} for it in Newfoundland black spruce forests. Van Cleve and coworkers (1983), for black spruce forests near Fairbanks, Alaska, reported an even higher value of 100 g m^{-2}.

Figure 92. ***Picea mariana*** boreal forest with ***Pleurozium schreberi*** on the forest floor. Photo by Richtid, through Creative Commons.

Figure 93. ***Pleurozium schreberi***. Photo by Jan-Peter Frahm, with permission.

Figure 94. ***Betula papyrifera*** forest. Photo by Nicholas A. Tonelli, through Creative Commons.

In addition to feather mosses, ***Sphagnum*** (Figure 43-Figure 48) is a prominent member of many boreal communities. In a black spruce forest, Swanson and Flanagan (2001) found that ***Sphagnum*** had higher maximum rates of gross photosynthesis than did the feather mosses and exhibited distinct seasonal changes in its photosynthetic capacity.

Several species of ***Dicranum*** occur in boreal forests, and Kellomäki *et al.* (1978) found that they differ physiologically in their ability to tolerate desiccation and photosynthesize. Even within the same species, two varieties can differ substantially. For example, the photosynthetic rate of ***D. fuscescens*** var. ***congestum*** (see Figure 42) increases more rapidly at 12.5ºC than at 17.5ºC with increasing light than does that of ***D. fuscescens*** var. ***flexicaule*** (see Figure 42), in which the rates at the two temperatures are essentially identical. In ***D. fuscescens*** var. ***congestum***, the rate at 12.5ºC is nearly double that at 17.5ºC. However, water deficit has a strong effect on the photosynthetic rate. The best photosynthesis seems to occur in the morning when the plants are able to use morning dew while the temperature is still relatively cool.

Figure 96. ***Quercus*** forest understory habitat of Illacme plenipes. Photo by P. Marek, W. Shear, and J. Bond, through Creative Commons.

Temperate Forest

Ground cover of bryophytes in temperate forests (Figure 95) varies widely. In oak forests (Figure 96) in Hungary, production is only 4.3 g m^{-2} (Smith 1982). Oceanic European oak forests may reach 35.5 g m^{-2} (Pócs 1982). Forman (1969) reported a scant 2-3 g m^{-2} in deciduous forests in New Hampshire (Figure 97), USA, whereas Rieley and coworkers (1979) reported 1600-2900 g m^{-2} in a Welsh ***Quercus petraea*** (Figure 98) woods. In these oakwoods, the production was 170-210 g m^{-2} for the mosses, whereas the herbs had a production of only 120 g m^{-2}. Many of the oakwoods in England are on rocky hillsides where litter accumulation is small, whereas many North American temperate forests bury the mosses in litter (Figure 99) just as the fall growth season for mosses begins (Pitkin 1975). However, Rieley and coworkers (1979) offer another explanation. Sheep eat the grasses selectively and leave the mosses behind. On tree trunks and logs (Figure 100), above the litter, temperate forest bryophytes can be significant.

Figure 97. Deciduous forest, NH. Photo by Ben Kimball, through public domain.

Figure 95. Temperate deciduous forest. Photo by Paul Bolstad, through Creative Commons.

Figure 98. ***Quercus petraea***. Photo by Rosser, through Creative Commons.

Figure 99. Deciduous forest floor in spring Chestnut Ridge Metro Park, Ohio. Photo by Janice Glime.

Figure 100. Epiphytes on trees in California. Photo by Michael Lüth, with permission.

In the temperate rainforest (Figure 101) of Washington, USA, biomass can be as great as 800 g m^{-2} of tree surface, translating to 500 g m^{-2} of forest floor. In the Douglas fir forests (Figure 102) of Oregon, USA, bryophyte biomass can be as high as 8.9 kg on a single 65 m tall tree (Pike *et al*. 1972). On Mt. Baker (Figure 103) in Washington, bryophyte biomass averages ca 180 g m^{-2} (Edwards *et al.* 1960). However, in pine forests (Figure 104) in France, the moss ***Pseudoscleropodium purum*** (Figure 33) has a relatively low annual production of only 39 g m^{-2} (Kilbertus 1968).

Figure 101. Hoh National Rainforest, a temperate rainforest in Washington, USA. Photo by Molonecr7, through Creative Commons.

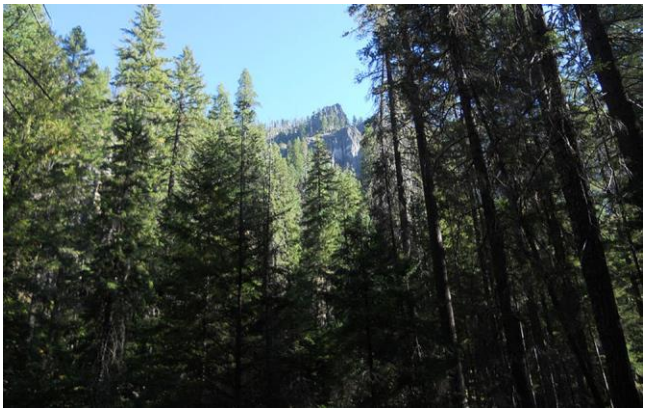

Figure 102. Douglas fir and Ponderosa pine forest, southern Oregon. Photo by Jsayre64, through Creative Commons.

Figure 103. Forest habitat on Mt. Baker. Photo from Wild Earth Guardians, through Creative Commons.

Figure 104. ***Pinus halepensis***, Aleppo Pines grove, Pinet, Hérault, France. Photo by Christian Ferrer, through Creative Commons.

Epiphytes

Neckera pennata (Figure 105) demonstrates that colony growth in area is proportional to colony size, thus exhibiting exponential growth (Wiklund & Rydin 2004). Precipitation was an important parameter in determining colony growth. Presence of other species reduced growth. Wiklund and Rydin estimated that the colony needs to attain a size of 12-79 cm^2 before reproducing sexually, taking 19-29 years to attain that size.

Figure 105. ***Neckera pennata***, an epiphytic moss. Photo by Michael Lüth, with permission.

Peatlands

Peatlands (Figure 106) are often 3-d habitats with hummocks and hollows (Figure 107). Grigal (1985) projected that the surface area is 35% greater in a Minnesota peatland due to this 3-d microtopography. In addition to the increase in surface area, three other factors seem to be important in carbon sequestration:

- differences in dominant plant functional type
- interactions between temperature and water table depth
- ecosystem succession (Flanagan 2014).

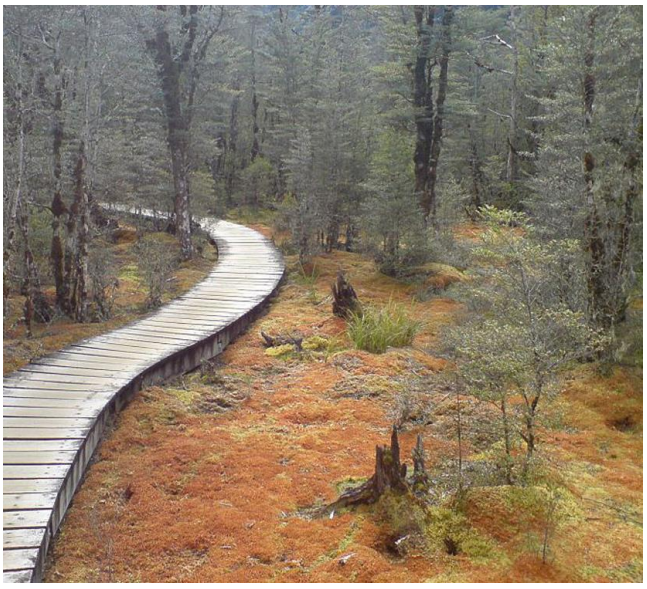

Figure 106. Bog with ***Sphagnum*** in Fiordland, NZ. Photo through Creative Commons.

Figure 107. Bohemia bog with ***Sphagnum cuspidatum*** and ***S. denticulatum***, showing hummocks and hollows. Photo by Jonathan Sleath, with permission.

Moore (1989) found a slight tendency for production of ***Sphagnum*** (Figure 106) to decrease as temperatures decrease northward. Wider differences, however, occur within a single peatland. Hummocks (Figure 108) can have annual production of 100-150 g m^{-2}, lawns 500 g m^{-2}, and pools 600-800 g m^{-2} (Clymo 1970, Clymo & Hayward 1982), suggesting that water availability is the limiting factor for production. Vitt (1990) reported that production varies from 70 to 400 g m^{-2} per year, with fen mosses at the lower half of the range. The highest productivity measured in peatlands seems to be that of ***Sphagnum*** (868 g m^{-2} yr^{-1}) in a recently burned *Eriophorum* (Figure 109) community in Great Britain (Heal *et al*. 1975). Grigal (1985) found a productivity of 320-380 g m^{-2} yr^{-1} in a forested Minnesota bog (Figure 110) and Elling & Knighton (1984) found slightly higher results (390 g m^{-2} yr^{-1}) in an open Minnesota bog (Figure 111). These figures of production compare with a standing crop of 500 g m^{-2} in west Norway (Laennergren & Oevstedal 1983). Somewhat lower values have been reported for Moor House, England, ***Sphagnum***, where the productivity was 213 g m^{-2} yr^{-1} (Forrest & Smith 1975).

Figure 108. ***Sphagnum papillosum*** hummock. Photo by James K. Lindsey, with permission.

Figure 109. ***Eriophorum scheuchzeri***. Photo by Meneerke Bloem through Creative Commons.

Figure 110. Spruce forest, Minnesota bog. Photo by Justin Melssen, through Creative Commons.

Figure 111. Minnesota open bog with early stages of tamarack. Photo by Katy Chayka, through online permission.

Surprisingly, rich fen production is lower. Vitt (1990) found that in Alberta, Canada, at higher elevations it was 47-93 g m^{-2} yr^{-1}, whereas in the lower boreal sites it was 125-131 g m^{-2} yr^{-1}. Vitt attributes the lack of increased productivity in rich fens to the similarity of N and P concentrations in the poor, rich, and extreme-rich fens. Nevertheless, in poor fens, Bartsch and Moore (1985) found that productivity of ***Sphagnum*** (Figure 36-Figure 37) in Quebec was only 58-73 g m^{-2} yr^{-1} in hummocks and 9-19 g m^{-2} yr^{-1} in lawns. It is somewhat puzzling that bog hummocks have less production than carpets, but that poor fen hummocks have double the production of lawns (Vitt 1990).

In peatlands, bryophytes are major contributors to the primary productivity. At a peatland in West Virginia, bryophytes covered 68% of the ground and contributed 43% of the aboveground net primary productivity, with 20, 10, and 27% contributed by herbaceous species, trailing shrubs, and upright shrubs, respectively (Wieder *et al*. 1989). Bryophytes covered 68% of the ground. Precipitation plays a major role in the productivity. Moore (1989) found that growth at the lawn sites was higher than that of hummocks in an average rainfall year, but in a dry year, growth in two of the three lawn sites was less than that in the hummocks.

Species can differ widely in their photosynthetic activity. Dry matter accumulated 141-206 g m^{-2} in ***Sphagnum tenellum*** (Figure 37), 32-190 g m^{-2} in ***S. papillosum*** (Figure 36), and 187-219 g m^{-2} in ***S. capillifolium*** (***S. nemoreum***; Figure 35) at the Takadayachi Moor in Hakkoda Mountains, Japan (Fukushima *et al*. 1995).

Temperature influences the light compensation point of peatland mosses in Alaska (Harley *et al*.). The light compensation point increased from 37 µM m^{-2} s^{-1} at 10°C to 127 µM m^{-2} s^{-1} at 20°C, despite little increase in the maximum CO_2 uptake rate. Laboratory experiments indicated that responses could be quite different from that in the field, with considerably lower light compensation points and higher light saturation rates of assimilation.

Peatlands can serve as important carbon sinks. In restored peatlands, Waddington and Warner (2000) found that the peatlands resulted in considerable decrease in the atmospheric CO_2 (~70% decrease due to gross productivity, 30% to decreased respiration). Unfortunately, restoration did not restore the peatlands to a net carbon sink, but it greatly improved the sequestration of carbon.

The peatland bryophytes, especially ***Sphagnum*** (Figure 36-Figure 37), are particularly sensitive to the direct sunlight of their habitat (Hájek (2014). Due to the wetness of their habitat, they are unable to go dormant to escape its potential damage, and it can be difficult to obtain CO_2 due to diffusion resistance through water. Many ***Sphagnum*** species are desiccation avoiders, but are quite sensitive to drought when they actually do dry out. While hydrated, they are subject to photodamage. Slow growth rates are partly the result of allocation of resources to water-holding tissues.

Desert

In the Chihuahuan (Figure 112), Sonoran (Figure 113), and Mojave Deserts (Figure 114) in North America, the highest biomass of mosses (2.24 g m^{-2}) occurred on the north slope of the Mojave (Nash *et al.* 1977).

Figure 112. Chihuahuan Desert at Big Bend. Photo by Adbar, through Creative Commons.

Figure 113. Sonoran Desert at sunset. Photo by Bob Wick, through Creative Commons.

Figure 114. Mojave Desert on Hualapai American Indian Reservation. Photo by Richard Martin, through Creative Commons.

In a sandy semidesert, Juhász *et al*. (2002) found that ***Syntrichia ruralis*** (Figure 40) exhibited their highest daily carbon fixation rates in December and January, whereas in the summer it went dormant. A net carbon gain did not occur until October. This species is able to maintain its physiological integrity and net photosynthetic gain by changing the surface reflectance and exhibiting thermal dissipation of excess light energy (Hamerlynck *et al*. 2000).

Grimmia laevigata (Figure 115) from the inland chaparral of California, USA, is unable to survive in the most xeric sites because it is unable to maintain a positive carbon balance during repeated wet-dry cycles (Alpert & Oechel 1985).

Figure 115. ***Grimmia laevigata***, a species that cannot maintain a positive carbon balance in the most xeric habitats. Photo by Michael Lüth, with permission.

In these dry habitats, cryptogamic crusts (Figure 116) are important producers and protectors of the soil (Coe *et al*. 2014). These are mixed communities of **Cyanobacteria** (Figure 117), algae, fungi, lichens, and bryophytes. Mosses comprise up to 30% of this crust cover. They are highly tolerant of desiccation and may remain dry for extended periods of time. They also are able to tolerate larger ranges of temperature, light, and cellular water content than mesic species.

Figure 116. Cryptogamic crust. Photo by Nihonjoe, through Creative Commons.

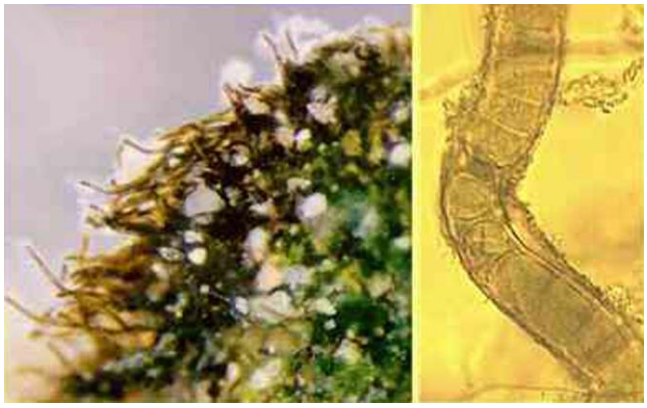

Figure 117. ***Scytonema*** (**Cyanobacteria**) in cryptogamic crusts. Photo from inactive website on Desert Ecology.

Elevated CO_2 stimulates the biocrust mosses, but it appears that they do not acclimate to long-term exposure by continued high rates of photosynthesis (Coe *et al*. 2014). Rather, the elevated levels might favor stress tolerance at the expense of growth, especially at high temperatures. Nitrogen appears to be an important limiting factor, but N deposition can be toxic, increase competition by tracheophytes, and interfere with nitrogen fixation by **Cyanobacteria** (Figure 117).

Dulai *et al*. (2014) used cryptogamic crusts containing **Cyanobacteria** (Figure 117) to test survival under Mars-like conditions. Those organisms that survived best were the ones from very salty and very dry habitats.

Savannah

In such dry habitats as the savannah (Figure 118), the life cycle can be shortened to accommodate the lack of water. Mosses such as ***Archidium ohioense*** (Figure 119), ***Bryum coronatum*** (Figure 120), ***Fissidens minutifolius***, and ***Trachycarpidium tisserantii*** develop protonemata and gametophytes in March – April; by September and October the spores are being dispersed (Makinde & Odu 1994). All of these events occur within the rainy season, permitting maximum photosynthesis.

Figure 118. Savanna grassland with oryx in Samburu National Reserve, Kenya. Photo through Creative Commons.

Figure 119. ***Archidium ohioense*** with capsules, a savannah species. Photo by Li Zhang, with permission.

Figure 120. ***Bryum coronatum***, a species that lives in dry savannahs. Photo by Michael Lüth, with permission.

Temperate Rainforest

Although the rainforest has its season of daily rain, it also has periods of continued dryness. Under these circumstances, respiration may exceed photosynthesis, causing negative photosynthetic gain (DeLucia *et al*. 2003). Forest floor bryophytes in a New Zealand rainforest (Figure 121) have an annual net carbon uptake of 103 g m^{-2}, compared to annual carbon efflux from the forest floor (bryophyte + soil respiration) of -1010 g m^{-2}. Bryophytes were unable to recover more than 10% of carbon lost from the forest floor. Water is the most likely limiting factor in their productivity.

Figure 121. New Zealand rainforest. Photo by Stomac, through Creative Commons.

Tropical Rainforest

The biomass of bryophytes in the tropics rises sharply with elevation. Frahm (1990a) found standing biomass of bryophytes to be less than 10-12 g m^{-2} of tree trunk at low elevations (up to 1000 m), up to 140 g m^{-2} in Peru (Figure 122), and 400-800 g m^{-2} in Borneo (Figure 123). Exceptionally high biomass of bryophytes, up to 1030 g m^{-2}, can occur in high altitude epiphytes in Tanzania (Figure 124) (Pócs 1982). The astonishingly high figure of 1400 g m^{-2} productivity occurs among the epiphytic bryophytes of a Tanzanian cloud forest (Figure 125) (Pócs 1980).

Figure 122. Amazon rainforest. Photo through Creative Commons.

Figure 123. Bornean rainforest. Photo by Willo Eurlings, through Creative Commons.

Figure 124. Western Usambara Mountains and rainforest in Tasmania. Photo by David Ashby, through Creative Commons.

High temperatures and low light place severe limitations on tropical net productivity (Frahm 1990b). Temperatures above 25°C drastically decrease the net assimilation. Coupled with the low light, temperature causes productivity of bryophytes in tropical lowlands to be the lowest of any tropical altitude, with high rates of respiration often resulting in no net carbon gain.

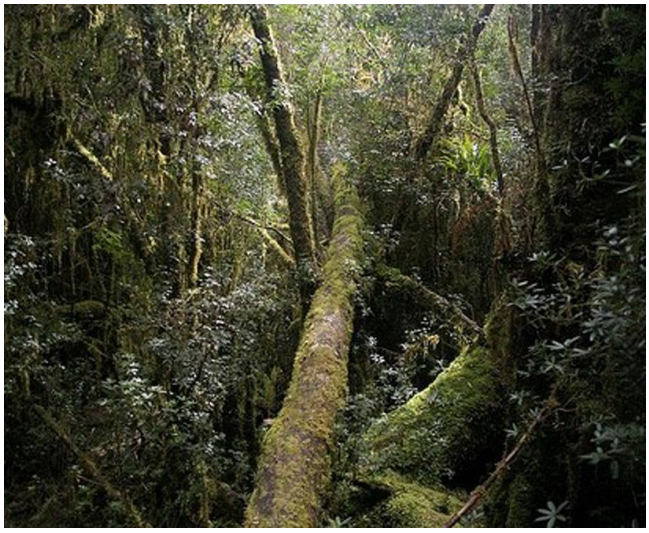

Figure 125. Rain forest Tasmania. Photo by Owen Allen, through Creative Commons.

Tropical Altitudinal Relationships

Wagner *et al*. (2014) emphasized the importance of altitude (Figure 126) in affecting bryophyte diversity and productivity in the tropics, asserting that the bryophytes and lichens demonstrate a conspicuous increase with altitude in the tropics (Wagner *et al.* 2013). In the lowland rainforests (Figure 127), frequent fast drying events and low light greatly limit productivity, even for bryophytes (Wagner *et al*. 2014). These detriments are further enhanced by the warm, moist conditions at night, promoting high dark respiration. The optimum temperatures for net photosynthesis of the species at sea level, 500 m asl, and 1200 m asl in Panama were closely related to the mean temperatures in their habitats at each of those elevations (Wagner *et al*. 2013). However, the ratio of dark respiration to net photosynthesis did not decrease with altitude. Water, light, and CO_2 responses did not vary systematically with altitude. Lowland species often had near-zero carbon balances, most likely due to the rapid evaporation rate that restricts the time available for photosynthesis. This relationship seems to be consistent on a worldwide scale.

Figure 126. Gannett Peak alpine. Photo by Summitcheese, through Creative Commons.

Figure 127. Lowland Rainforest, Masoala National Park, Madagascar. Photo by Frank Vassen, through Creative Commons.

When comparing bryophytes across an elevation gradient on Mauna Loa (Figure 128), Hawaii, Waite and Sack (2011) found that nutrient concentrations in the bryophytes increased with soil nutrient availability. Nutrient concentrations on an area basis were related to irradiance, mediated by the bryophyte canopy mass per area. N and P behaved similarly to those nutrients in tracheophytes. Phosphorus increased and the N:P ratio decreased with elevation, a relationship that is consistence with increasing cold tolerance.

Figure 128. Mauna Loa. Photo by Joe Parks, through Creative Commons.

Problems in the Water

Productivity in aquatic systems is dependent on sufficient CO_2, suitable temperatures, and sufficient light (Glime 2014). Red light becomes negligible in deeper water, and even the CO_2 that is present is slowed by boundary layer resistance, all problems that are greater in water than in terrestrial habitats. Even *p*H is important in the availability of CO_2, with little or no dissolved CO_2 in alkaline water. Temperature becomes a problem when the bryophytes are wet and hot at the same time, a problem that can occur when the bryophytes are moist but not submersed (Figure 129). N and P are often limiting as well. The already limited light can be further reduced by sediments and algae on the plants (Figure 130-Figure 131).

Figure 129. ***Platyhypnidium riparioides*** experiencing hydrated conditions but not submersed. Photo by Michael Lüth, with permission.

Figure 130. ***Fontinalis hypnoides*** with sediments and detritus. Photo by Janice Glime.

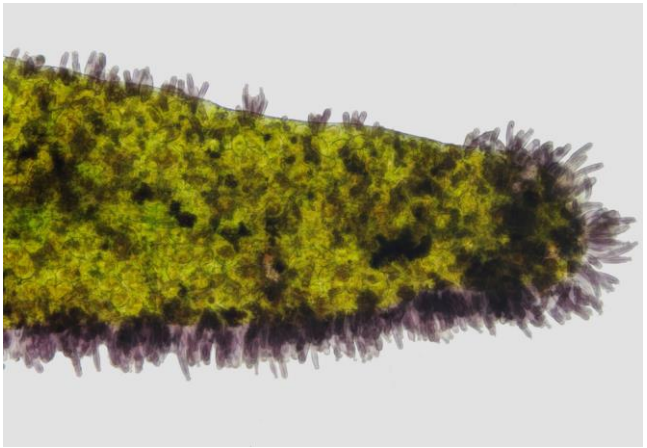

Figure 131. ***Fissidens fontanus*** with periphyton (algae) on its leaf. Photo by Dick Haaksma, with permission.

But there are some advantages not known in terrestrial systems (Glime 2014). The water serves as a UV filter. This can be enhanced in high light by production of protective pigments.

Rivers and Streams

Naiman (1983) considered mosses in 4th order or higher streams to be the most productive autotrophic members of the stream community in boreal forest

watersheds (Figure 132), producing 3.9 x 10^{10} g yr^{-1}. This compares to periphyton productivity of only 2.1 x 10^{10} g yr^{-1} in the same watersheds. These higher order streams occupy 76.8% of the lotic surface area and are responsible for 86.3% of the gross productivity, demonstrating the importance of bryophytes in the stream ecosystem.

Figure 132. Boreal forest in Canada. Photo by Rich Bard, with permission.

But stream habitats can be rather unfavorable, especially for mosses. In one study in Oregon, ***Fontinalis*** (Figure 24) only had positive photosynthesis in the winter (Naiman & Sedell 1980). It was negative the rest of the year.

Despite their slow growth and low nutrient requirements, higher nutrients can favor enhanced growth in some bryophyte taxa. In Alaskan streams (Figure 134), ***Hygrohypnum alpestre*** (Figure 133) and ***H. ochraceum*** (Figure 135) increased in cover following phosphorus enrichment, whereas ***Schistidium agassizii*** (Figure 136-Figure 137) showed little response (Arscott *et al*. 2000). Although the ***Hygrohypnum*** species were intolerant of desiccation, they were more tolerant of high temperatures than ***S. agassizii***, having the higher productivity (1676-6342 µg O_2 g^{-1} dry mass h^{-1}) compared to that of ***S. agassizii*** (428-1163 µg O_2 g^{-1} dry mass h^{-1}).

Figure 133. ***Hygrohypnum alpestre*** in Norway. Photo by Michael Lüth, with permission.

Figure 134. Alaska mountain and stream. Photo by Dhilung, through Creative Commons.

Figure 135. ***Hygrohypnum ochraceum***. Photo by Michael Lüth, with permission.

Figure 136. ***Schistidium agassizii*** Norway 1 Michael Lüth, with permission.

Figure 137. ***Schistidium agassizii***. Photo by Des Callaghan, with permission.

Lakes and Ponds

Bryophytes in lakes enjoy the presence of constant water, permitting photosynthesis at any time other factors are favorable. Instead of being at the mercy of water availability like most bryophytes, these bryophytes face the limits of low light intensity, rapidly attenuated red light, and limited CO_2 availability. In most lakes, temperature is not a problem, with bottom temperatures of deep lakes generally not going below 4ºC, and summer temperatures often not exceeding 10ºC. In more shallow lakes and ponds, summer temperatures may become a problem if they reach 20ºC and sustain that temperature for extended periods. Under those conditions, hydrated bryophytes not only lose more energy to respiration than they gain by photosynthesis, but they must compete with aquatic tracheophytes and algae that benefit from the higher temperatures. Sediment CO_2 can often contribute to the productivity of bottom-dwelling bryophytes in lake systems.

The floating liverwort ***Riccia fluitans*** (Figure 138) increased its relative growth rate from 0.011 d^{-1} at low light and CO_2 to 0.138 d^{-1} at high light and CO_2 (Andersen & Pedersen 2002). There was strong acclimation to light and CO_2 conditions. Nevertheless, high light intensities resulted in decreased maximum net photosynthesis while increasing CO_2 continued to increase the maximum net photosynthesis. The CO_2 compensation point for photosynthesis was strongly depressed by high light and low CO_2 and increased in low light and high CO_2. High levels of CO_2 within the floating mat permits photosynthesis at greater depths where the light intensity attenuates.

Wagner *et al.* (2000) found that in Waldo Lake, Oregon, liverworts, comprising 98% of the bryophyte biomass, exhibited growth similar to that of upland plants (1.5-3 cm annually).

Problems with Bryophyte Measurement

The first problem one faces is measuring productivity in the field vs the lab. In the field, logistics are difficult and effects of CO_2 from the soil may be measured along with respiratory CO_2 from the bryophyte. Even putting the equipment in place can disrupt the bryophyte canopy morphology and change light, temperature, moisture, and CO_2 relationships within the canopy. On the other hand, if we take the mosses into the laboratory, we have disrupted the canopy morphology, lost the normal variation of the field, altered light quality, and in other ways failed to mimic the conditions that occur in the field. And furthermore, laboratory experiments often use only a branch, losing all the effects of the bryophyte canopy and mechanisms of external transport. While these may be useful for physiological studies, they can be misleading when measuring productivity is the objective.

Figure 138. ***Riccia fluitans***, a floating thallose liverwort. Photo by Michael Lüth, with permission.

Past history matters. Some bryophytes have inducible desiccation tolerance. Others provide it as a constitutive trait. Hence responses to various manipulations will behave differently depending on the recent environmental weather.

Summary

Productivity can be considered in many ways, including ability to invade, linear growth, biomass increase, CO_2 uptake, O_2 production, C^{14} incorporation, chlorophyll concentration, and surface expansion. Biomass gain may often be uncoupled from linear growth, with the former typically occurring first.

Likewise, annual growth of the plant can be measured in many different ways, including length of branch internodes; distance between splash cups on a stem; height above a cranked wire, tag, nylon net, plastic bubbles, or dye, growth out of a nylon bag; photographic record of expansion on a grid. Pleurocarpous mosses typically exhibit exponential growth, whereas unbranched acrocarpous mosses have linear growth, thus requiring different measures of growth.

Etiolation (excessive elongation and loss of chlorophyll due to insufficient light) may occur in low-light environments, giving a false measurement of length as an indication of productivity.

Productivity is generally highest when there is a good supply of water and ceases when the bryophyte is desiccated, causing seasonal differences. Once the moisture requirement is met, temperature and light are important in determining maximum productivity, with most bryophytes diminishing in productivity above 20-25ºC and dying at prolonged exposure above 30ºC if hydrated. The lower limit varies geographically and

with species, with some species having their compensation point as low as -10ºC. In water, bryophytes are limited by low light and low concentrations of CO_2, but those on the bottom can take advantage of CO_2 from the sediments.

Belowground productivity may be extensive in some bryophytes, such as those in the Polytrichaceae. Capsules, and even spores, can contribute to overall productivity, but at the same time, they typically reduce productivity of the leafy gametophyte.

Life span may be months to centuries, but unlike tracheophytes, generally only the upper portion of the stem supports active productivity. Mortality of the whole stem can be high, reaching 32% in Antarctic young populations of ***Polytrichum strictum***. On the other hand, longevity may reach 17 years in the Arctic, compensating for the slow growth, and apparently is even higher in some cold lakes.

The **Leaf Area Index** (LAI) indicates that bryophytes are well adapted to take advantage of the many angles of the sun, reaching such levels as 44 and 129 for sun-adapted species, whereas a value of 1 indicates full usage; anything higher than 1 permits maximum usage at more angles of the sun. Mosses in the boreal biome have an LAI of about 20. Light use efficiency can be very high, but productivity still remains low, perhaps due to CO_2 limitation. Mosses have a maximum CO_2 uptake of about 3 mg dm^{-2} hr^{-1}, whereas C_3 tracheophytes reach 45 and C_4 plants reach 80.

Some bryophytes, especially ***Cryptothallus mirabilis***, rely on fungal partners for their carbon input. Other thallose liverworts can lose energy to fungi.

The **highest productivity**, when it occurs, seems to be from bryophytes in the driest habitats. On the other hand, yearly productivity seems to be highest in ***Sphagnum***, reaching 12 tons per hectare.

Striking differences occur among **latitudes** and **habitats**. For example, Antarctic bryophytes have drastic daily temperature fluctuations and show little response temperature differences. Cool tundra populations of ***Polytrichum strictum*** may have only 1/4 – 1/3 the production they exhibit in the cool Antarctic grassland. The ultimate limit to productivity, hence to distribution, is achieving a positive carbon balance. Heat causes respiratory loss and frequent wet-dry cycles require excessive repair, both reducing the net carbon gain in some habitats to 0 and ultimate death.

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Klaus Weddeling, Brian O'Shea, and Marshall Crosby helped me find the new name for *Hylocomium parietale*. It appears to have been *H. parietinum*, now *Pleurozium schreberi*. Several bryonetters helped me locate the current name of *Homaliodendron scalpellifolium*, which is now *H. flabellatum*.

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CHAPTER 13
DECOMPOSITION

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CHAPTER 13
DECOMPOSITION

Figure 1. ***Adelanthus decipiens*** with fresh, green branches and older, decomposing brown branches. Photo by Michael Lüth, with permission.

Decomposition

If you were to ask the average person to name a plant that decays at the bottom while the top is green and continues to grow, most would have no clue or tell you that's not possible. These people, like most of my beginning students, when defining plants, have forgotten about bryophytes. This group of plants is unique in its ability to die at its base and continue life for years, or even centuries, from the parts above.

Although bryophytes are generally quite small, their slow rate of decomposition and their effect on decomposition of other plants can be important influences on ecosystem dynamics. For example, the genus ***Sphagnum*** (Figure 2), well known for its preservative properties, occupies 1/3 of the land on the planet and stores more carbon than any other single genus of plants (Turetsky *et al*. 2002). Decomposition in that system necessarily is important.

Although they lack the lignin that resists decay in tracheophytes, bryophytes are replete with many kinds of secondary compounds – compounds with no known metabolic function, but that seem to deter herbivores from consuming them. These same compounds, including many phenolics, are likewise active in inhibiting the organisms that would normally facilitate decomposition. In fact, bryophytes do have a slower decomposition rate than do tracheophytes (Scheffer *et al.* 2001). Turetsky (2003) considers this to result not only from the secondary compounds, but also from the low nitrogen concentrations in many taxa, an interpretation shared by Aerts *et al.* (1999), who demonstrated that ***Sphagnum*** (Figure 2)

leaves had lower N and P concentrations than other taxa and likewise had lower rates of litter decomposition.

Figure 2. ***Sphagnum fuscum*** hummock. Photo by Oscar Gran, through Creative Commons.

Aerts *et al*. (1999) also found that cellulose decomposition in bogs was lower than in fens and that the nutrient mineralization rate was greater in forested peatlands than in herbaceous peatlands. On the other hand, Coulson and Butterfield (1978) found that the rate of decomposition depended not on the substrate of peatland vs. mineral substrate, but on the kinds of plants being decomposed. Peat mosses can play a major role in determining what kinds of plants can live there, so they do play a role in the sequestration of carbon and the decomposition rate by limiting available nutrients and encouraging growth of evergreen shrubs.

It is not surprising that decomposition rates are affected by nutrient levels in the plants. The availability of nutrients influences the kinds of decomposers and the rate at which they act. Aerts *et al.* (2001) found that higher N concentrations caused higher potential rates of decay of ***Sphagnum*** litter (Figure 3); the rates were actually not significantly affected by nutrient additions. Rather, the higher N levels in ***Sphagnum*** and other litter led to lower P concentrations. Changes in these ratios can have serious effects on the carbon balance. ***Sphagnum***, as an ecosystem engineer, seems quite important in the decomposition process.

Figure 3. ***Sphagnum fimbriatum*** with capsules and senescent tissues. Photo by J. C. Schou, with permission.

Tsuneda *et al*. (2001) studied the degradation of cell walls in ***Sphagnum fuscum*** (Figure 2). They found that the **Ascomycota** fungi ***Acremonium cf. curvulum*** (Figure 4) and ***Oidiodendron maius*** were able to degrade the leaf cell walls in this species. ***Acremonium cf. curvulum*** first fragmented the outer wall layer, then removed it. Then the inner wall was mostly degraded and removed, the middle wall layer, consisting of bundles of microfibrils embedded in an amorphous matrix, experienced degradation and disappearance of the amorphous matrix. Finally, the microfibrils were degraded, causing holes in the cell wall. ***Oidiodendron maius***, on the other hand, did not degrade the wall in layers. Rather, it degraded all the components in a nearly simultaneous manner.

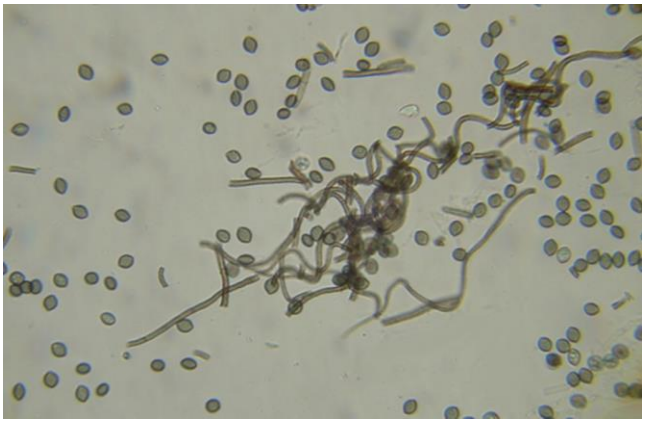

Figure 4. ***Acremonium*** ascospores, a fungus able to degrade ***Sphagnum fuscum*** leaf cell walls. Photo by Ninjatacoshell, through Creative Commons.

Decomposers

A wide array of organisms typically contribute to decomposition of plant material, with invertebrates, especially arthropods, breaking up the tissues into smaller fragments, and fungi and/or bacteria attacking the cellulose and other parts. This is not necessarily the order of activities, which can vary with habitat and available species. **Protozoa** can contribute in some habitats and complete the major groups generally involved.

But bryophytes do not seem to encourage all of these organism groups. Consumption of bryophytes is limited, most likely due to the many secondary compounds they produce (Asakawa 1990). Among liverworts, a variety of volatile oils may be the deterrent (Lohmann 1903, in Frankland 1974). It appears that animals play little role in the decomposition process of bryophytes (Frankland 1974; Coulson & Butterfield 1978).

On the other hand, a wide variety of parasitic and saprophytic fungi are known from bryophytes. Frankland (1974), reporting on earlier work of Racovitza (1959, in Frankland 1974), considered the decreasing order of importance of fungi to be **Ascomycetes** > **Fungi Imperfecti** > **Phycomycetes** > **Basidiomycetes** > **Mycelia Sterilia** > **Archimycetes**. Although some common fungi, like the Loculoascomycetes, may not penetrate the bryophyte host (Henderson 1972, in Frankland 1974), other studies have demonstrated the ability of fungi to penetrate and decompose bryophyte cells (Parke & Linderman 1980; Redhead 1981; Grasso & Scheirer 1981).

There are some indications that the number of fungal species on bryophytes is lower than the number on tracheophytes (Frankland 1974). Longton (1992) found that more than 50% of the bryophytes tested produced microbial inhibitors, perhaps explaining the reduced number of decomposer species found on ***Sphagnum*** (Figure 2), where *p*H is often too low for most bacteria to survive.

However, it appears that even on ***Sphagnum*** (Figure 2), the number of taxa can be large. In a boreal bog in Alberta, Canada, 55 species of fungi were identified on *S. fuscum*, 36 of which were new records for ***Sphagnum*** (Thormann *et al*. 2001). It appears that this may be a poorly investigated habitat for fungi with many more taxa awaiting discovery. One reason for the large number of fungal taxa on ***Sphagnum*** may be their ability to utilize a wide range of carbon sources, including cellulose, tannic acid, and pectin.

The concentration of ergosterol is an indication of fungal presence (Uchida *et al.* 2001). Fungi are common among bryophytes, and Uchida *et al*. found that not only the brown moss litter of ***Hylocomium splendens*** (Figure 5), but also its living green shoots exhibited ergosterol. The interesting relationship for this species is that the ergosterol content of its litter from boreal and subalpine forests was about twice that of the cool temperate forest where the decomposition rate was faster.

Figure 5. ***Hylocomium splendens***, showing senescing brown portions and green shoots. Photo by Michael Lüth, with permission.

Penicillium (Figure 6) seems to be a common inhabitant of bryophytes. Mikola and Hintikka (1956) found it to be one of the more abundant fungi (3 species) on ***Pleurozium schreberi*** (Figure 7), along with ***Mucor*** (Figure 8) (3 species; 50% of the number of molds) and ***Trichoderma*** (see Figure 9-Figure 10) (40% of the number of molds). In the same experiment, a grass had the same species plus four more genera. Leaf litter lacked ***Trichoderma***, but had 8 species not found on the ***P. schreberi***, suggesting certain fungi may have a specificity for bryophytes.

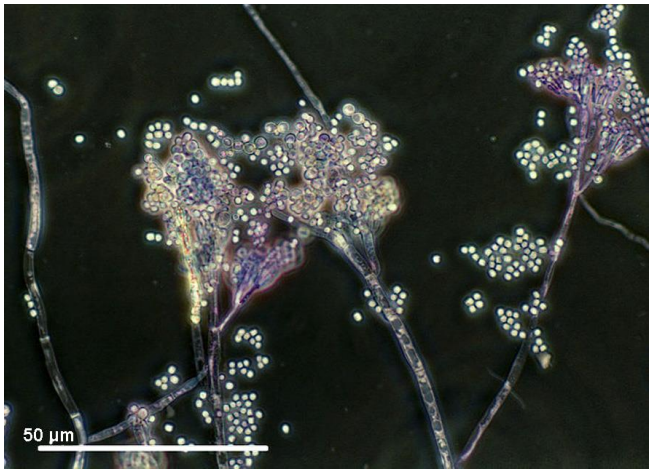

Figure 6. ***Penicillium*** sp. ***Penicillium spinulosum*** is inhibited by culture with ***Sphagnum***. Photo by Josef Reischig, through Creative Commons.

Figure 7. ***Pleurozium schreberi***, a common boreal forest species with several abundant fungal associates. Photo by Janice Glime.

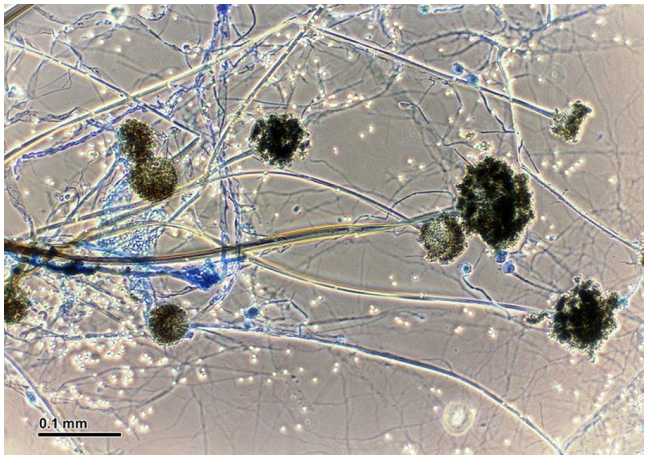

Figure 8. ***Mucor***, a common genus on ***Pleurozium schreberi***. Photo by Josef Reischig, through Creative Commons.

Figure 9. ***Trichoderma*** *aureoviride*. ***Trichoderma lignorum*** is inhibited by culture with ***Sphagnum***. Photo by Paul Cannon, through Creative Commons.

Figure 10. ***Trichoderma*** *harzianum*. ***Trichoderma lignorum*** is inhibited by culture with ***Sphagnum***. Photo by Andre Rodrigues, through Creative Commons.

Clymo (1965) concluded that micro-organisms were the chief agents in ***Sphagnum*** (Figure 2) decomposition, albeit slowly. As suggested earlier, the acidic conditions in most ***Sphagnum*** habitats do not encourage bacterial growth (Frankland 1974). Williams and Gray (1974) found that when the *p*H drops below 5, decomposers drop proportionally to the drop in *p*H. Nevertheless, in an acid peatland, even a four-year addition of simulated acid rain had no effect on the decomposition rate (Rochefort *et al*. 1990). Furthermore, ***Sphagnum*** itself is bacterial resistant, as noted by those using it for bandages in World War I. For example, only 6-8% of dry weight was lost in six months incubation of ***Sphagnum*** inoculated with ***Trichoderma lignorum*** (see Figure 9-Figure 10) or ***Penicillium spinulosum*** (see Figure 6) (Minchevich 1969, in Frankland 1974). ***Collybia dryophila*** (Figure 11), a fungus, causes a 30% loss of bryophyte dry mass in only four months; this fungus caused 53-56% loss in bryophytes while angiosperm litter lost only 46-69% (Mikola & Hintikka 1956, in Frankland 1974). Benda (1957, in Frankland 1974) found that associated organisms could be important. In her experiments, bacterial decomposition of ***Sphagnum*** protein occurred only when fungal symbionts of *Erica* were present.

Figure 11. ***Collybia dryophila***, a species that is able to decompose bryophytes. Photo by Dan Molter, through Creative Commons.

Küster (1968), on the other hand, did not consider peat to be the microbe-poor community that its antibacterial properties might suggest, reporting that the numbers were "much higher than originally assumed." He concluded that chemical composition, structure, moisture, and other factors determined the occurrence and nature of the microorganisms on peat.

Satake and Miyasaka (1984) reported the penetration of bacteria into the cell walls of the leafy liverwort ***Jungermannia vulcanicola*** (Figure 12-Figure 13). Satake and Shibata (1986) supported the role of bacteria in at least some bryophytes by demonstrating that the leafy liverwort ***Scapania undulata*** (Figure 14) exhibits bacterial invasion of its cell walls at both *p*H 6.4 and *p*H 4.2. Furthermore, they found no evidence of fungal presence on these aquatic leafy liverworts.

Figure 12. ***Jungermannia vulcanicola*** habitat. Photo courtesy of Angela Ares.

Figure 13. ***Jungermannia vulcanicola***, a species in which leaf cells are penetrated by bacteria. Photo courtesy of Angela Ares.

Figure 14. ***Scapania undulata***, an aquatic leafy liverwort that seems to be free of fungi. Photo by Michael Lüth, with permission.

Frankland (1974) suggested that *p*H may not be the limiting factor and concluded that the chemical composition of ***Sphagnum*** (Figure 2-Figure 3, Figure 16, Figure 18) walls determined its rate of decomposition. They are rich in pectin. Their cellulose and "lignin" are unusual. The cellulose actually hydrolyzes more readily than that of seed plants, but phenolic compounds such as sphagnol may serve as a microbial retardant. Reports of a lignin of unusual composition probably represent another phenolic compound, but its resistance to decay is still of importance.

Decomposition is not the only factor contributing to the disappearance of bryophyte tissue. Other factors in the Antarctic and elsewhere include wind erosion, leaching, and removal by skuas (Davis 1981). The losses to invertebrates are assumed to be minimal, but for some bryophyte taxa, it could be significant.

Phaeopigments

Phaeopigments have been used to indicate the degree of decomposition in algae and bryophytes. Bastardo (1980) examined ***Fontinalis*** (Figure 15) and other aquatic plants, demonstrating that the ratio of chlorophyll *a* to phaeopigment can be used to indicate plant vitality, with a ratio of less than 1 indicating irreversible decomposition. On the other hand, use of phaeopigments as an indicator of decomposition may be misleading. Martínez Abaigar *et al.* (1994) found that the degradation of chlorophyll in immersed bryophytes did not produce phaeopigments.

Figure 15. ***Fontinalis antipyretica***, a species in which a high phaeophytin to chlorophyll ratio can be an indicator of decomposition. Photo by Misha Ignatov, with permission.

Influential Factors

We have already seen that water is a major factor in the rate of photosynthesis. It appears that it may be the major factor in decomposition as well, with different taxa having different moisture requirements. Belyea (1996) showed that for ***Sphagnum capillifolium*** (Figure 16) this ideal water content was achieved in the zone of water fluctuation; for ***Racomitrium lanuginosum*** (Figure 17), it was just above the highest water level. For epiphytes, it appears that living on the north side of a tree may incur an advantage that increases the decomposition rate (Van Tooren 1988).

Figure 16. ***Sphagnum capillifolium***, a species for which the zone of water fluctuation is ideal for decomposition. Photo by Li Zhang, with permission.

Figure 17. ***Racomitrium lanuginosum***, a species that decomposes best just above the water level. Photo by Janice Glime.

Depth in the peat profile seems to have a major influence on ***Sphagnum*** (Figure 16) decomposition (Hogg 1993; Johnson *et al*. 1990). At a depth of 7-10 cm, nearly all hollow species had completely fragmented into stems and leaves. On the other hand, the hummock species, especially ***S. fuscum*** (Figure 2), remained completely intact to a depth of at least 25 cm. This relationship further supports the contention that hollow species decompose more rapidly than do hummock species (Limpens & Berendse 2003). But as observed by Belyea (1996), those in the zone of water fluctuation disintegrated the most rapidly and completely. Even when samples were moved from deep peat (50-100 cm), the hummock species still decomposed more slowly than did the hollow species (Hogg 1993). In older peat, decomposition reduces to 0%.

Peat seems generally to resist decay. Karunen (1981) demonstrated that ***Sphagnum*** (Figure 2) cell walls were resistant to both **autohydrolysis** and microbial decomposition. Some organisms, such as insects and fish, accomplish autohydrolysis by releasing enzymes (from dead cells) that cause them to digest themselves from the inside out. Nevertheless, not all species of ***Sphagnum*** exhibit equal resistance. Johnson and Damman (1991) indicated that the species are important in determining the decay rate. ***Sphagnum cuspidatum*** (Figure 18) in the hollows have a decay rate (16.9% mass loss) 1.5 times as fast as that of ***S. fuscum*** (Figure 2) (11.3% mass loss) in the hummocks. Even when the species were placed in each others' habitats, ***S. cuspidatum*** continued to have the faster rate. They suggested that the more rapid decay rate of hollow species like ***S. cuspidatum*** may initiate and maintain the hummock and hollow complex. In a separate experiment, Johnson *et al.* (1990) found that among three species, ***S. fuscum*** stems were the most decay resistant, ***S. rubellum*** (Figure 19) next, and ***S. balticum*** (Figure 20) least. Rochefort *et al.* (1990) likewise found that the decomposition rate was least at the top of the hummock and greatest for hollow species, suggesting that it was the slower decomposition rate that maintained the hummocks, not high production.

Figure 18. ***Sphagnum cuspidatum***, a hollow species with a faster decay rate than that of the hummock species ***S. fuscum***. Photo by Jutta Kapfer, with permission.

Figure 19. ***Sphagnum rubellum***, a species with a moderate decay resistance. Photo by Michael Lüth, with permission.

Figure 20. ***Sphagnum balticum***, a species with lower decay resistance than ***S. fuscum*** or ***S. rubellum***. Photo by Michael Lüth, with permission.

Water is not the only factor that differs at the top of the hummock. Because the hummock is not submersed often, if at all, it has only the small task of lowering the *p*H of the adhering water, whereas the hollow species may have their efforts of acidifying diluted by an entire lake. The result is that the hummocks exhibit the lowest *p*H in the peatland (Clymo 1963, Vitt *et al*. 1975; Clymo 1986), and this acidity most likely contributes greatly to the lower breakdown rate there.

Kälviäinen *et al*. (1985) supported the difference between species by demonstrating biochemical differences. The two ectohydric forest mosses underwent a rapid decay and possessed a dominance of short-chain hydroxy acids. The two ectohydric ***Sphagnum*** species were highly resistant to decay and possessed a dominance of long-chain hydroxy acids in their walls. Changes in biochemistry may result in differences in rates. ***Sphagnum fuscum*** (Figure 2) has considerably more hydroxy acids in the 9-12 cm segments than in the 0-0.5 cm segment (Ekman & Karunen (1982).

Fontinalis seems to be somewhat different in this regard. The sterolesters of ***Fontinalis antipyretica*** (Figure 15) are rapidly hydrolyzed during decay (de Leeuw *et al*. 1976).

Rate

Decomposition rates of bryophytes have been difficult to measure. The tiny bryophyte leaves are often lost through the holes of mesh bags, making the litter bag method used for tree leaves less reliable for bryophytes. Nakatsubo *et al*. (1997) used the annual rate of litter production and the amount of litter accumulated to calculate the decomposition rate in ***Hylocomium splendens*** (Figure 5) in boreal and subalpine forests. They estimated the litter production rate based on the moss shoot growth. While this method gave larger estimates than those usually obtained by the litter bag method, it relies on the assumption that litter production occurs at the same rate as shoot production. Over a long period of time, this assumption probably provides a fairly accurate estimate, but in any given year the estimate could be quite disparate.

Bryophytes are known for their slow decomposition. For example, ***Pseudoscleropodium purum*** (Figure 21) has a much slower rate than does the grass *Brachypodium pinnatum* under the same conditions (Kilbertus 1968). The feather moss ***Pleurozium schreberi*** (Figure 7) can require 5-12 years to decay (Weetman & Timmer 1967). But ***Hylocomium splendens*** (Figure 5) lost 10-24% of its biomass per year in Northern Hemisphere boreal and subalpine forests (Nakatsubo *et al*. 1997).

Figure 21. ***Pseudoscleropodium purum***, a species with a much slower decay rate than the grass *Brachypodium pinnatum*. Photo by Janice Glime.

All indications are that bryophyte decomposition is slow [Russell 1990 – tundra (Figure 22); Verhoeven & Toth 1995 – ***Sphagnum*** (Figure 2-Figure 3, Figure 16, Figure 18); Hobbie 1996 – tundra; Sand-Jenson *et al*. 1999 – Arctic lakes (Figure 23); Liu *et al*. 2000 – montane moist evergreen broad-leaved forest (Figure 24); Moore *et al*. 2007 – temperate peatlands (Figure 25); Turetsky *et al*. 2008 – ***Sphagnum*** in boreal peatlands (Figure 23); Lang *et al*. 2009 – subArctic]. As a result, bryophytes become a nutrient sink compared to other plant species in most ecosystems. This implies that they get most of their decomposition nutrients from litter decomposition of tracheophytes, not from recycled nutrients from their own tissues.

Figure 22. Arctic tundra at Svalbard. Photo by Gary Bembridge, through Creative Commons.

Figure 23. Arctic tundra lakes and peatlands. Photo by Sphinx through Creative Commons.

Figure 24. Broadleaf evergreen Laurel forest Photo by Inkaroad, through Creative Commons.

Figure 25. Temperate peatland. Photo by Janice Glime.

Rejment-Grochowska and Misztal-Cieliczko (1975) examined the decomposition of the moss ***Climacium dendroides*** (Figure 26). They found that moss decay increases with depth in the 12 cm examined. Temperature undoubtedly plays a role, with an increase from April to August, then decreasing to November when the study ended. Nakatsubo *et al*. (1997) demonstrated that rates of decomposition of the moss ***Hylocomium splendens*** (Figure 5) decreased with altitude, but at boreal sites the rates were similar to those of the subalpine sites, despite the lower mean annual temperatures. They found a log-linear relationship between the annual mass loss rate and the cumulative value of monthly mean air temperatures higher than 0°C.

Figure 26. ***Climacium dendroides***, a species in whih decay increases with depth. Photo by Michael Lüth, with permission.

In the Antarctic, where ground at 20-30 cm is permanently frozen, decomposition above the frozen portion is less than 1% per year. By the time it becomes part of the permafrost zone, about half the original material has decomposed (Fenton 1980). It took approximately 40 years to decompose half of the moss ***Polytrichum strictum*** (Figure 27) in the upper 15 cm. But this low rate may not be representative. This species has an intrinsically low decomposition rate.

Time, of course, has an effect on the rate. Johnson and Damman (1991) found a much faster rate during the first 10 months than in the months 10-22 after the onset of the experiment. When tested in the anoxic (submerged) zone, ***Sphagnum fuscum*** (Figure 2) actually had less total decomposition (9.1%) in months 10-22 than in the first 10 months (10.6%), whereas ***Sphagnum cuspidatum*** (Figure 18) increased slightly from 15.1% to 16.1%.

Figure 27. ***Polytrichum strictum***, a moss that forms deep cushions. Photo by Michael Lüth, with permission.

Extreme heat may have a negative effect on decomposition in bryophytes (Ohlson 1987). In a Swedish mire, rates of decomposition differ spatially. This may in part be due to temperature differences. Clymo (1965) showed that ***Sphagnum papillosum*** (Figure 28) that was dried at 105° C exhibited less subsequent decay than did material that dried in air. This may have been due to death of associated microorganisms.

Figure 28. ***Sphagnum papillosum***, a species that decays less after being subjected to 105°C. Photo by 1 James K. Lindsey, with permission.

One explanation for the slowdown in decay rate may be types of constituents that still remain (Coulson & Butterfield 1978). In ***Hylocomium splendens*** (Figure 5), the oldest and most decomposed tissues exhibited a slight increase in polymerized lipid monomers (Kälviäinen *et al*. 1985).

Cellulose and hemicellulose content change during decomposition (Küster 1968). For ***Sphagnum*** (Figure 2-Figure 3, Figure 16, Figure 18) the hemicelluloses changed from 16% in relatively undecomposed peat to 10% in well-decomposed plants. Celluloses had a similar decline from 19% to 11%. Such changes affect the kinds of organisms required for or attracted to the moss for decomposition and these changes affect the rate of decay.

As readily obtainable nutrients are consumed by the decomposers, more recalcitrant kinds become a greater proportion of the remaining components. Nadkarni (1984) demonstrated considerably higher nutrient content of N, P, Ca, Mg, K, and Na in live compared to dead parts of epiphyte mats [including bryophytes, *Selaginella* (Figure 29-Figure 30), and *Polypodium* (Figure 31) on *Acer macrophyllum* (Figure 32). However, these changes in concentrations could reflect re-distribution of nutrients to growing parts of the plants. But one of the biggest decreases is in Ca, an insoluble nutrient that is not readily moved within plants, suggesting that some of these changes may result from loss during decomposition. During (1990) demonstrated that bryophytes in calcareous grasslands released nutrients in summer as a result of partial die-back and decomposition. Damman (1988) found that as the age of decomposing ***Sphagnum*** (Figure 2-Figure 3, Figure 16, Figure 18) increases, tissue N concentrations increase. Malmer and Wallén (1993) supported this observation with their evidence that N is conserved in decomposing ***Sphagnum***. N becomes depleted in the litter at the bottom layer where decomposition has led to disintegration, but below that layer (litter deposition level) the concentration of N increases once more with depth (in the decay decrease level).

Figure 29. ***Selaginella oreganum***, a common epiphyte in the Olympic Peninsula, WA . Photo by Janice Glime.

Figure 30. ***Selaginella oreganum***, a tracheophyte species that accompanies bryophytic epiphytes on *Acer macrophyllum*. Photo by Janice Glime.

Figure 31. ***Polypodium glycyrrhiza***, a species that often accompanies epiphytic bryophytes on *Acer macrophyllum*. Photo by Keir Morse, through Creative Commons.

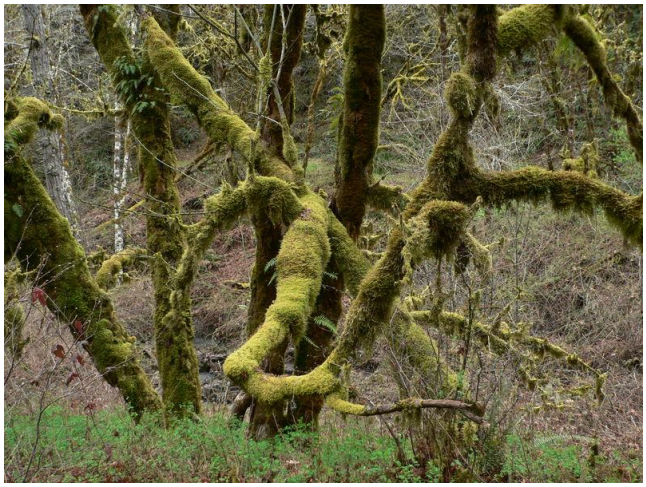

Figure 32. ***Acer macrophyllum*** with bryophytic epiphytes. Photo by Walter Siegmund, through Creative Commons.

Damman suggested that P deficiency might limit the decomposition rate. However, Coulson and Butterfield (1978) found that for ***Sphagnum*** (Figure 2-Figure 3, Figure 16, Figure 18), increased concentration of P caused a reduction in its decomposition rate. Such releases could favor different groups of organisms for subsequent decomposition. Increased N levels, on the other hand, seemed to increase the decomposition rate.

It appears that in ***Sphagnum*** (Figure 2-Figure 3, Figure 16, Figure 18) the ratio of N:C is more important than the absolute level of N in the plants (Limpens & Berendse 2003). This ratio affects the litter quality, with greater decomposition when the N:C ratio is higher.

Habitat within an ecosystem can play a significant role. Decomposition of epiphytic bryophytes in a tropical montane forest at Monteverde, Costa Rica, was significantly less than that of forest floor taxa (Clark *et al*. 1998). The first year, the epiphytes were reduced by 17%, reaching only 19% reduction by the end of the second year. At the same time, forest floor bryophytes lost 29% to decomposition the first year and 45% by the end of the second year. These differences most likely reflect differences in water availability, but they also support the N story. Within the first three months the bryophyte forest floor litter lost 47% of its N; the remaining N seemed to be

recalcitrant. Similar recalcitrance occurred in epiphytes, which typically trap significant amounts of N-containing dust from the atmosphere, then convert it to biomass and lock it up. Reduction in available N could contribute to the slowdown of decomposition with time.

The decomposer population likewise changes with time, further modifying the decay rate. For ***Pleurozium schreberi*** (Figure 7), Mikola and Hintikka (1956) found bacterial densities of 10 million per ml after 20 days, a reduction to 1 after 50 days, up to 40 after 80 days, and back down to 10 after 130 days. The molds had a more consistent pattern, exhibiting declining numbers with time.

The decline in decomposition rate with time seems to be a fairly common occurrence among bryophytes. Clark *et al*. (1998) showed a decline in rate from the first to second year in various northern hemisphere populations of ***Sphagnum*** (Figure 2-Figure 3, Figure 16, Figure 18), ***Dicranum*** (Figure 33), mixed bryophytes (from Costa Rica), and ***Calliergonella*** (Figure 34). Only a population of ***Sphagnum*** from North Sweden deviated, increasing its decomposition rate in the second year. Van Tooren (1988) likewise demonstrated a decline in the decomposition rate of ***Calliergonella cuspidata*** (Figure 34) after six months. Concomitantly, there was a drastic drop within the first two months in both N and P as a percent of that originally present. Nevertheless, after the first two months, both the N and P content eventually increased as a percent of the remaining dry weight.

Decomposition rates of ***Hylocomium splendens*** (Figure 5) varied with site (Uchida *et al*. 2001). The most recent two years of growth were green from all sites. However, two-year-old segments were green in the Canadian boreal forest and the Mt. Fuji subalpine forest, but were senescing from Mt. Tsurugi. By the third year, decomposition had slowed in the boreal and subalpine forests, with the 5-year-old segments on Mt. Fuji exhibiting ~80% of the weight of the largest segment. On Mt. Tsurugi, on the other hand, rapid decomposition had rendered the 5-year-old segment to be less than half the weight of the largest segment.

Figure 33. ***Dicranum fragilifolium*** showing older brown parts that will decompose slowly over time. Photo by Michael Lüth, with permission.

As we can see from these examples, decomposition rates vary widely between habitats and geographic areas. Likewise, the onset of senescence and decomposition varies with locality and habitat. ***Eurhynchium oreganum*** (Figure 35) in Douglas fir forests (Figure 36) of Oregon, USA, begins decomposition at age 3 (Binkley & Graham 1981), whereas those in Washington don't turn brown until age 6 (Frye 1928). In the same Washington forest, ***Hylocomium splendens*** (Figure 5) lives 8 years before its lower parts begin to decompose. But moss tissue may remain alive even after it has become brown (Longton 1972), moving nutrients to younger parts (Eckstein & Karlsson 1999).

Figure 34. ***Calliergonella cuspidata***, a species that experiences a decline in decomposition after six months. Photo by David Holyoak, with permission.

Figure 35. ***Eurhynchium oreganum***, a species that begins decomposition at age 3 in Oregon and age 6 in the neighboring Washington. Photo by Adolf Ceska, with permission.

Figure 36. Douglas fir forest in Vancouver, BC, Canada. Photo by Janice Glime.

We might expect decomposition in the Antarctic to be slow. Baker (1972) found that ***Chorisodontium aciphyllum*** (Figure 37-Figure 38) on Signy Island had an approximately linear decomposition rate, averaging 2% per year.

Figure 37. ***Chorisodontium aciphyllum***, a species that decays at approximately 2% per year in the Antarctic! Photo by Peter Convey, with permission.

Figure 38. ***Chorisodontium aciphyllum***, a species that decays at the rate of 2% per year in the Antarctic. Photo by Jan-Peter Frahm, with permission.

It may be fairly typical that decomposition of forest floor bryophytes is at a pace similar to that of growth. For example, ***Hylocomium splendens*** (Figure 5) exhibits apical growth equivalent to the loss from the distal segments (Callaghan *et al*. 1978). Zhang (1998) used mapped permanent plots on Isle Royale, Michigan, to track yearly changes in boreal bryophytes for four years. He likewise found that decomposition was approximately replaced by new growth, resulting in little change in cover from one year to the next, but often considerable change in position of the clump.

As might be expected, temperature is an important contributor to the rate of decomposition, as shown for peat decomposition in Scotland (Chapman & Thurlow 1998).

Habitat Differences

Forests

Forests are known for their relatively rapid decomposition of deciduous leaf litter. Decomposition in conifer forests is notably slower (Berg 1984). But where do the bryophytes fit in?

Liu *et al*. (2000) compared decomposition of bryophytes [***Homaliodendron scalpellifolium*** (Figure 39), ***Symphyodon perrottetii***, ***Herbertus*** sp. (Figure 40), and ***Bazzania albicans***] with that of three dominant non-conifer tall tree species and an understory bamboo in southwest China. The tracheophyte decomposition rates seem to be controlled by initial concentrations of lignin, N, and P rather than by leaf morphology. Nutrient and lignin concentrations were less important in bryophyte decomposition. Furthermore, the trees all decayed faster than the bamboo, and the bamboo decayed faster than the bryophytes. The rate constants of canopy litter ranged 0.50-0.64, that of bamboo 0.40, and that of bryophytes 0.22. Turnover time for the canopy species ranged 1.55-2.0 years, for bamboo 2.50 years, and for bryophytes 4.55 years.

Figure 39. ***Homaliodendron flabellatum***. ***Homaliodendron scalpellifolium*** decays more slowly than the bamboo or three tree species studied in southwest China. Photo by Jiang Zhenyu, Mou Shanjie, Xu Zawen, Chen Jianzhi, through Creative Commons.

Figure 40. ***Herbertus*** sp., a genus that decays more slowly than the bamboo or three tree species studied in southwest China. Photo by David Elckhoff, through Creative Commons.

Peatlands

It seems that more is known about decomposition of bryophytes in peatlands than from all other ecosystems combined (Collins 1973; Heal & French 1974; Heal *et al*. 1981; Davis 1986; Grandmaison & Laflamme 1986; Lieffers 1988; Russell 1990; Chmielewski 1991; Johnson & Damman 1991; Santelmann 1992; Gignac & Vitt 1994; Bowden *et al*. 1999; Table 1). That is attributable to the

large area of the Earth's surface covered by peatlands and their importance in those ecosystems.

Table 1. Percent decompositional rates of peatland bryophytes. From Bowden *et al*. 1999.

Rate (% y^{-1})	Species	Location	Reference
0.04-3	moss	Arctic	Russell 1990
5	*Sphagnum fuscum*	Arctic	Roswall *et al*. 1975
4	*S. balticum*		
7	*S. lindbergii*		
5	*Drepanocladus schulzii*		
7	*Dicranum elongatum*		
1.5	moss	Antarctic	Davis 1986
1.3-2.4			Baker 1972
0.1-8.3			Fenton 1980
2	*Chorisodontium aciphyllum*	Signy Island	Collins 1973
14	*Sanionia uncinata* (dry)		
25	*S. uncinata* (wet)		

Thomas and Pearce (2004) suggest that cation exchange may be responsible for preventing decay in deep peat. Conditions in the deep peat are anoxic. When mono- and di-valent cations were added to deep peat, a reduction in emissions of methane and CO_2 follows. Decay could be stimulated by adding a carbon source, but not by added NH_4^+. The researchers concluded that the cation limitation is limited to the deep peat and could explain the decay rate differences between anoxic surface and deep peat.

In northern peatlands, the maintenance of unfrozen bogs and fens creates habitat heterogeneity where these wetlands are interspersed among areas of permafrost mounds. Thus, their presence affects the hydrology, topography, thermal regime, and community structure (Turetsky 2004). Turetsky determined that the internal lawn peat produces more CO_2, hence has more decomposition, than other peatland types. The composition of the peat, as suggested earlier, plays a major role in the rate of decomposition, with acid-insoluble material and the ratio of this material to nitrogen being of primary importance when looking at the broadscale of peatlands. However, within a given peatland, the soluble proximate fractions are better predictors of the decompositional rate. Permafrost stability is important in determining the plant and soil environment, which in turn controls litter inputs, quality of organic matter, and ultimately, decomposition rates.

Peatlands are famous for their emission of methane, causing concerns that global warming will raise the methane emission, which will in turn increase the global warming effect (Weltzin *et al*. 2001). But peatlands can also consume methane. Yavitt *et al.* (1990) demonstrated that ***Sphagnum*** (Figure 2-Figure 3, Figure 16, Figure 18) -derived peat from 0-40 cm exposed to aerobic conditions consumed methane (CH_4), presumably due to consumption by aerobic microorganisms, whereas the same peat maintained under anaerobic conditions at 19ºC for 40 hours produced 0.5-1.0 µM L^{-1} peat h^{-1}. Under these two conditions, CH_4 emission of 6.8 mmol m^{-2} d^{-1} and CH_4 consumption of 5.4 mmol m^{-2} d^{-1} demonstrate a net increase of CH_4 to the atmosphere.

Methane emission could experience further enhancement due to various environmental pollutants that enhance the rate of decay. among these concerns are increaing temperaturea and acid precipitation. Rochefort *et al*. (1990) examined the effects of simulated acid rain on ***Sphagnum fuscum*** (Figure 41), ***Sphagnum magellanicum*** (Figure 42), and ***Sphagnum angustifolium*** (Figure 43). During the first two years, production of ***Sphagnum*** was enhanced, but after that it declined to its original rates. Decomposition was unaffected during the four years of application. Furthermore, it appears that the hummocks are maintained by a higher rate of production and lower rate of decomposition than that of the hollows in that Ontario, Canada, poor fen.

Figure 41. ***Sphagnum fuscum***, a hummock top species. Photo by Michael Lüth, with permission.

Figure 42. ***Sphagnum magellanicum***, a species in which acid rain does not affect decomposition rate. Photo courtesy of Betsy St. Pierre.

Figure 43. ***Sphagnum angustifolium***, a species in which acid rain does not affect decomposition rate. Photo by Jan-Peter Frahm, with permission.

In a *Betula*-carr, conditions were suitable for growth of ***Sphagnum recurvum*** var. ***mucronatum*** (Figure 44) (Brock & Bregman 1989). This species proved to have one of the highest productivity rates of peatmosses. On the other hand, loss of mass during breakdown in this species in the wetland forest was low. N, P, and especially K reduced faster than did the biomass during decomposition, but a large proportion of N and P remained after 12 months. This was consistent with the observation that little damage had occurred to the cells, and colonization by micro-organisms was poor.

Figure 44. ***Sphagnum recurvum*** var ***mucronatum***, a species in which N, P, and especially K reduce faster than the biomass during decomposition. Photo by Jan-Peter Frahm, with permission.

The role of ***Sphagnum*** (Figure 42-Figure 45) in slowing decomposition is emphasized by the experiments of Verhoeven and Toth (1995). Using litter bags and laboratory experiments, they compared the decomposition rates of *Carex* litter from a base-rich fen with that of ***Sphagnum fallax*** (Figure 45) from a base-poor fen. In all experiments, the *Carex* litter decomposed significantly faster than did the ***Sphagnum*** litter. But more to the point, when ***S. fallax*** was added to *Carex* litter, the rate of loss of *Carex* mass slowed significantly. They concluded that *Sphagnum* acid, a phenolic compound, was responsible by inhibiting the growth of microorganisms.

Figure 45. ***Sphagnum fallax*** with capsules, a species that has not only a slow decomposition rate, but it reduces decomposition in litter of other species in contact with it. Photo by David T. Holyoak, with permission.

Arctic

Mass loss of non-***Sphagnum*** Arctic mosses correlated with the initial N in the plants, a phenomenon that may relate to their nutritive value to the decomposers (Lang *et al*. 2009).

Tundra

Freeze-thaw cycles in the tundra can affect the microbial activity on peat and other bryophytic substrata. Wynn-Williams (1982) compared dry and wet sites in the Signy Islands of Antarctica under ***Polytrichum strictum*** (Figure 27) and ***Chorisodontium aciphyllum*** (Figure 37-Figure 38). In the tundra biome, bryophytes are of major biomass importance, averaging 30% cover, but often reaching 100% in wetter areas (Russell 1990), so their decomposition rates have a major influence on those ecosystems. A high standing crop biomass results from low decompositional loss rates, with initial annual loss rates commonly below 10%. The long growing season at sub-Antarctic wet sites can support up to 1000 g m^{-2} yr^{-1}.

Antarctic

In the Antarctic, it appears that substrate and moisture are the primary regulators of the decompositional rate, with temperature having little effect (Wynn-Williams 1985; Smith & Walton 1986). Using ***Polytrichum*** (Figure 27) and ***Drepanocladus*** (*sensu lato*) (Figure 46) peat, Wynn-Williams demonstrated consistent differences in respiration rates. Furthermore, the lack of correlation between O_2 uptake and CO_2 release suggests that anaerobic CO_2 production occurs under wet conditions.

Figure 46. ***Drepanocladus longifolius***. In theAntarctic, CO_2 production in this genus occurs under wet conditions and temperature has little effect on rate. Photo by John Game, through Creative Commons.

Davis (1986) examined the decomposition of Antarctic mosses using litter bags. In a 2-year period, ***Polytrichum strictum*** (Figure 27) and ***Chorisodontium aciphyllum*** (Figure 37-Figure 38) from a moss turf community and ***Sanionia uncinata*** (Figure 47), ***Calliergon sarmentosum*** (Figure 48), and ***Cephaloziella varians*** (Figure 49) from a moss carpet community exhibited a decomposition rate of 1.5% per year. This was consistent with the low rate of decomposition of cotton strips inserted into the bryophyte clumps, indicating a low decomposition potential. The decomposition potential, from highest to lowest, for the

five species was ***S. uncinata***, ***C. aciphyllum***, ***C. sarmentosum***, ***P. strictum***, and ***C. varians***. The time required for 50% decomposition of the cotton strips buried among these bryophytes varied from 1-2 years for ***S. uncinata*** and ***C. aciphyllum*** to 3-4 years for ***P. strictum*** and ***C. varians***, with low temperatures, low *p*H, and short active season contributing to their slowness. Other differences affecting differing rates among sites, depth, and species resulted from temperature, nutrient status, water content, and available oxygen.

Figure 47. ***Sanionia uncinata***, a species that has an decomposition rate of 1.5% per year in the Antarctic. Photo by Michael Luth, with permission.

Figure 48. ***Calliergon sarmentosum*** emerging from the water. Photo by Michael Lüth, with permission.

Figure 49. ***Cephaloziella varians***, a species that has an decomposition rate of 1.5% per year in the Antarctic. Photo by Kristian Peters, with permission.

Streams

While impacts of grazers and other decomposers on leaf litter in streams are relatively well known, virtually nothing is known about decomposition of bryophytes in streams (Bowden *et al*. 1999). Yet bryophytes often comprise the predominant in-stream vegetation and must therefore play a significant role in its internal nutrient cycling.

Bowden *et al*. (1999) suggested that stream bryophytes may not produce litter in the traditional sense. Rather, biomass is lost to fragmentation, consequently dispersing tissues that could potentially form new plants in new locations. But in slower streams, fragmentation is less extensive, and accumulations of senescing and dead tissues could contribute significantly to ecosystem structure.

Suren and Winterbourn (1991) compared common bryophytes in and near New Zealand streams, revealing that content of lipids, carbohydrates, and N is similar to that of grasses, shrubs, and tree foliage. However, content of holocellulose, crude fiber, and ash may be slightly higher overall in bryophytes, suggesting there might be slightly more resistance to decomposition. Furthermore, antibiotic compounds such as phenolics, terpenes, and flavonoids may inhibit decomposition (Markham & Porter 1983; Geiger 1990; Gorham 1990; Herout 1990; Markham 1990; Russell 1990; Glime 2006).

It appears that the only study designed to measure the rate of decomposition of stream bryophytes [***Schistidium agassizii*** (Figure 50); ***Hygrohypnum*** spp. (Figure 51)] is that described in Bowden *et al*. (1999) for the Kuparuk River, Alaska, USA (Figure 52). These bryophyte rates are far faster than the yearly rates presented in Table 1 and furthermore show that the rates do not differ greatly from those of the tracheophyte leaves in the same study.

Figure 50. ***Schistidium agassizii***, a species with decomposition rates similar to those of the tracheophyte leaves nearby. Photo by Michael Lüth, with permission.

Figure 51. ***Hygrohypnum ochraceum*** in a stream waterfall. Photo by Michael Lüth, with permission.

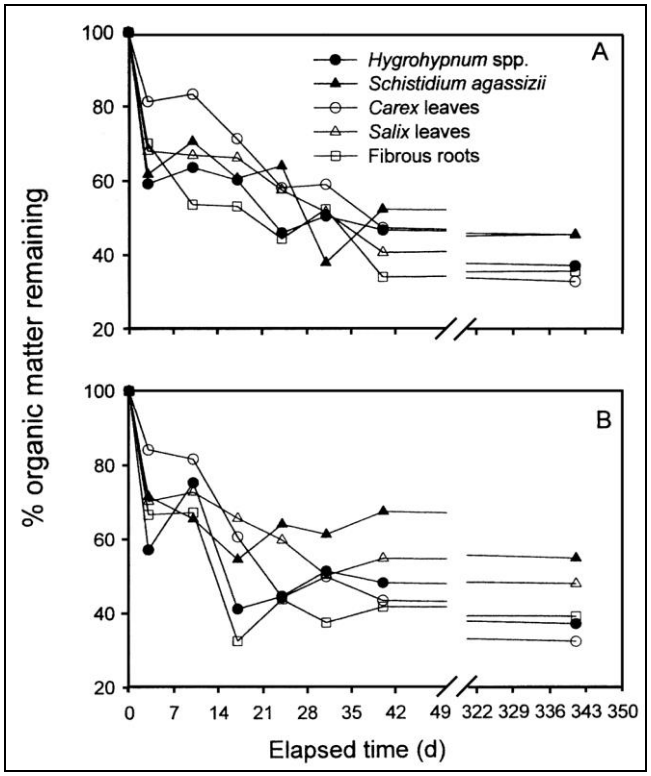

Figure 52. Mean percent of original organic matter of bryophytes, tracheophyte leaves, and roots remaining after six weekly intervals and one year when placed under rocks in the Kuparuk River, Alaska, USA. n = 5. **A =** control; **B =** fertilized portion of stream. Modified from Bowden *et al*. 1999.

Ecologists have traditionally considered that consumption of bryophytes by invertebrates was minimal. Nevertheless, consumption does occur and contributes to the removal of bryophyte tissue. Suren and Winterbourn (1991) found that of 23 invertebrate taxa in alpine streams in New Zealand, only 14 contained bryophytes in their guts. Furthermore, only the cranefly ***Limonia hudsoni*** (Figure 53; **Tipulidae**) and caddisflies ***Zelandopsyche ingens*** and ***Oeconesus similis*** (Figure 54) commonly consumed them. Suren and Winterbourn (1991) showed that bryophytes (***Fissidens rigidulus*** (Figure 55), ***Cratoneuropsis relaxa*** (Figure 56), ***Bryum blandum*** (Figure 57), ***Plagiochila retrospectans*** (Figure 58), and ***Hepatostolonophora paucistipula***) contained more refractory and indigestible compounds than did the common riparian tracheophyte plants nearby (*Chionochloa pallens*, *C. flavescens*, *Hebe subalpina*, *H. odora*, *Nothofagus solandri* var. *cliffortioides*, *Blechnum capense*, and *Marsippospermum gracile*), making the bryophytes less nutritious.

Figure 53. ***Limonia phragmitidis*** adult. Larvae in this genus are among the few insects that consume aquatic bryophyte litter. Photo by James K. Lindsey, with permission.

Figure 54. ***Oeconesus*** larva, one of the few insects that consume aquatic bryophyte litter. Photo by Landcare Research, through Creative Commons.

Figure 55. ***Fissidens rigidulus***, an aquatic species with more indigestible compounds than nearby riparian tracheophytes. Photo by Bill & Nancy Malcolm, with permission.

Figure 56. ***Cratoneuropsis relaxa***, an aquatic species with more indigestible compounds than nearby riparian tracheophytes. Photo by Jan-Peter Frahm, with permission.

Figure 57. ***Bryum blandum***, an aquatic species with more indigestible compounds than nearby riparian tracheophytes. Photo by Niels Klazenga, with permission.

Figure 58. ***Plagiochila asplenioides***, an aquatic species with more indigestible compounds than nearby riparian tracheophytes. Photo by Tim Waters through Creative Commons.

Lakes

In cold lakes, particularly those in polar regions, bryophytes may be the only form of macrovegetation (Sand-Jenson *et al*. 1999). In these frigid waters, with their low nutrients and short ice-free season, bryophytes are able to form dense stands, occupying great depths. Sand-Jenson and coworkers used changes in the size and density of leaves as markers to indicate growth and decomposition in Char Lake and North Lake in the Canadian High Arctic. The annual growth was remarkably constant (~10 mm shoot^{-1}), combined with slow decomposition. The slow growth rate, however, is at least partly offset by the greater longevity of the mosses in these communities.

Epiphytes

Of all the ignored bryophytes in the world, epiphytic taxa (Figure 59) have probably been most ignored by ecologists. However, in the tropics, a number of ecologists have recognized their importance in nutrient retention and cycling. Clark *et al*. (1998) examined the ecological role of epiphytic bryophytes in a tropical montane forest of Monteverde, Costa Rica. They found net production to be 122-203 g m^{-2} yr^{-1} while decomposition from litterbags after one and two years in the canopy was 17 ± 2% and 19 ± 2% mean ± 1 SE), suggesting that the bryophytes may have a significant retention time for nutrients. However, approximately 30% of the N content was released rapidly, contributing short-lived spikes in the N input to the underlying ecosystem. On the forest floor, approximately 47% of the N was lost in fhe first three months from green shoots! However, the N that remained in the litter was recalcitrant. Since bryophytes retain inorganic N from atmospheric deposition, they play a major role in altering the amount of available N to the system by transforming it to highly recalcitrant forms.

Figure 59. In the tropics even small branches can sport bryophytic epiphytes like ***Schlotheimia tecta*** growing with a bromeliad. Photo by Michael Lüth, with permission.

Role

It is too early to define a clear role for bryophytes in nutrient cycling through decomposition in ecosystems. Evidence from epiphytes suggests that leakage of N compounds from senescing bryophytes may be a significant

contribution of the nutrient pool for other epiphytes and throughfall recipients (Clark & Nadkarni 1992).

While our understanding of such roles in the terrestrial ecosystems is meager, our understanding in aquatic systems is nearly non-existent, as noted by Bowden *et al*. (1999). Their role in the regeneration of nutrients in streams is essentially unknown and there seem to be almost no published rates of bryophyte decomposition in stream ecosystems.

Summary

Bryophytes, unlike tracheophytes, die from the bottom up, with apical regions continuing to live and grow as their lower parts decompose. Compared to tracheophytes, their decomposition rate is relatively low, most likely due to recalcitrant cell wall components and secondary metabolites acting as antiherbivore/antibiotic compounds. Loss of nitrogen appears to be initially rapid, then becomes relatively unavailable, further limiting attractiveness to decomposers. Changes in the internal composition of the decomposing bryophyte appear to slow its rate of decomposition after the first year.

Bacterial decomposition may be limited in peatlands by the low *p*H, but it appears that fungi can be abundant, some being unique to bryophytes. Nevertheless, bacteria are able to penetrate the cell walls of at least some aquatic leafy liverworts, presumably contributing to their decomposition.

Phaeopigments may be an indicator of degree of decomposition, but their use for such purposes appears to be unreliable in aquatic systems.

Water seems to be the primary factor affecting rate of decomposition, but it acts in consort with *p*H, cell constituents, temperature, species of bryophyte, and available microorganisms.

Rates of decomposition vary widely, with peatland decomposition ranging from 0.04 to 25% per year. Similarly, the Antarctic exhibited a low rate of 1.5-2% per year. Tropical epiphytes may reach about 18% in a year.

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CHAPTER 1
THE FAUNA: A PLACE TO CALL HOME

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CHAPTER 1
THE FAUNA: A PLACE TO CALL HOME

Figure 1. A bird nest of the New Zealand fantail (***Rhipidura fuliginosa***) in a New Zealand *Nothofagus* forest, exhibiting a potpourri of vegetal material, including bryophytes. Could that be ***Dawsonia*** on the left? Photo by Rosemary Lovatt, with permission.

Types of Interactions

When I first became interested in bryophytes, I turned to the aquatic habitat, a place I had loved as a child and young adult. This soon led me to the organisms that lived among them. But literature on the subject was extremely difficult to find. This did not seem to be a high priority topic among bryologists, and those who studied animals seemed to think bryophytes were unimportant.

It is with great pleasure that I write this book, because there are now many fascinating stories of bryophyte – animal interactions, from housing to building materials (Figure 1) to food to safe sites. It appears that ecologists are beginning to recognize the importance of bryophytes, including them in studies, and publishing their studies in a very wide array of journals. That literature is easier to find now due to the internet, and when contacted, these wonderful scientists have been willing to share their stories and their photographs with all of us.

Bryological Fauna

Imagine yourself as a tiny mite in the forest. Everything around you must seem gigantic! But there, amidst the rocks and pine needles, a miniature forest beckons. It is a moss. This moss is your home. Here you can feel secure, protected from the drying wind and flecks of sun, hidden from the hungry birds, yet able to find tiny morsels for your own diet.

The bryophyte world is full of life, creating a habitat unlike any other (Ramazzotti 1958). Yet we know almost nothing of it. What loss might there be if the mosses were to disappear? What bird might be unable to construct a nest? What ant would have no place to hide its winter cache of seeds? What lemming might freeze its feet? The animals of the forest and field, stream and rock, have a very different view of the mosses and liverworts from that of the human inhabitants of the planet. These relationships will begin to unfold in this volume.

The habitats provided by mosses and liverworts are widely varied and worldwide, from mosses on roofs (Corbet & Lan 1974) to epiphytes (Fly *et al.* 2002) to turf-forming moss polsters (von der Dunk & von der Dunk 1979). In this volume we will explore the wide-ranging sizes and uses of the bryophyte dwellers and users. We will compare the terrestrial habitat, where nematodes are often most abundant, closely followed by rotifers (Figure 2), to the aquatic habitat, which can be quite different, and where Chironomidae (midges) are often the most abundant.

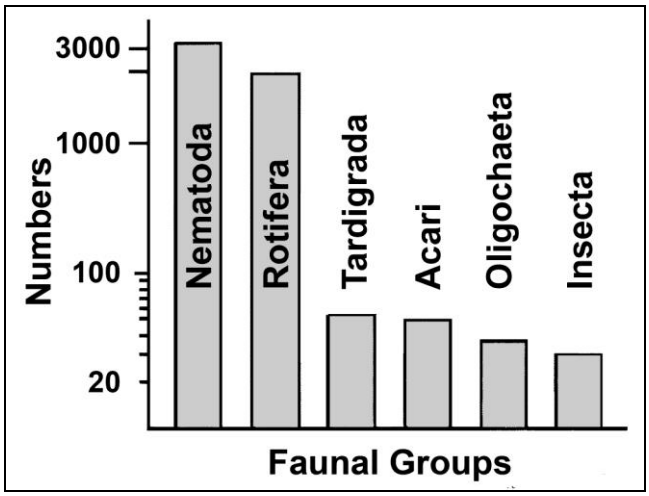

Figure 2. Comparison of relative abundance (log scale) of common bryophyte-inhabiting invertebrate fauna. Redrawn from Sayre & Brunson 1971.

Dispersal

Dispersal is necessary for both bryophytes and their inhabitants. Some, perhaps most of the microinhabitants, ride on a magic flying carpet, transported to their new location as a passenger on the bryophyte. Janiec (1996) trapped microfauna that were transported by the wind to areas with estabishedplants near a glacier on King George Island of the South Shetland Islands. After six weeks of exposure, 859 individuals were trapped. Nematodes comprised 71%, tardigrades 22%, and rotifers 7%. The number of individuals caught depended on the distance from a colonized area and the presence of plant parts, suggesting that the plant parts contributed to their dispersal.

Limitations

Bryophytes provide a habitat with a number of constraints that can prove to be of value to their tiny inhabitants. Most obviously, their small size limits the organisms that can live there. This affords small organisms protection from larger predators. And the bryophytes have a slow growth rate, permitting them to be a nursery to organisms that are initially small, but forcing these youngsters to leave before they are large enough to turn cannibal and consume their own offspring. The perennial nature of most bryophytes, rendering them present when many tracheophytes are absent or unable to provide cover, also provides a suitable overwintering habitat for numerous organisms, from the small ones living among the stems and leaves to the larger ones that live under them or use them as nesting material. Their C_3 habit permits the bryophytes to survive and sometimes even grow when the environment is cold and other plants are dormant, often absent above the substrate surface. Thus, in a world of predators, the bryophytes offer a safe site to numerous organisms that dominate this miniature world.

In the Antarctic, water limits the flora and fauna (Kennedy 1993). Kennedy suggested that water, rather than dispersal or temperature may limit many organisms from colonizing in the Antarctic. He demonstrated that there was a close relationship between the substrate biota and gradients in meltwater, seepage, and upwelling. Furthermore, microarthropod abundance is "directly proportional" to microvariation in relative humidity. Even the algal food source migrates upward in response to added water.

The Inhabitants

Large bryophyte mats typically host a wide variety of micro and macroinvertebrates (Ino 1992; Glime 1994; Peck & Moldenke 1999). The presence of a wide diversity of feeding strategies in a moss community suggests that the moss serves as a site of multiple pathways for nutrient cycling (Merrifield & Ingham 1998).

Fauna of bryophytes may be divided between those that are **bryophilous**, *i.e.*, those that typically live among bryophytes, and the casual visitor, sometimes referred to as **bryoxenous** (Ramazzotti 1958; Gadea 1964). Gerson (1982) divided these bryofauna into four categories:

bryobionts: animals that occur exclusively associated with bryophytes, *e.g.* ***Cyclidium sphagnetorum*** (a ciliate protozoan) on ***Sphagnum*** (*cf* Figure 3)
bryophiles: animals that are usually associated with bryophytes but can be found elsewhere
bryoxenes: animals that regularly spend part of their life cycle among bryophytes
occasionals: animals that may at times be found associated with bryophytes but do not depend on them for survival

Figure 3. ***Cyclidium*** sp. This genus includes ***C. sphagnetorum***, a species that occurs only on ***Sphagnum***. Photo by Yuuji Tsukii, with permission.

Chernov (1985) named the bryophyte-dwelling invertebrates **semi-edophores**, a term that means partly living in soil. This naming is consistent with the treatment of mosses as part of the litter, a practice common in soil biology. In aquatic systems, those tiny organisms that live on the bed of a river or lake and are barely visible to the human eye are termed **meiofauna** – those that pass through a 0.500 mm sieve and are retained on a 0.045 mm sieve (International Association of Meiobenthologists 2008).

Usage of this term has expanded to include organisms living on bryophytes that provide a moist film of water during at least part of the year. Maggie Ray (Bryonet 7 July 2005) stated that there are three groups of meiofauna that commonly live in the film of water on the bryophyte surface and that can achieve an **ametabolic** state. These are tardigrades, free-living nematodes, and rotifers. This **cryptobiotic** or **ametabiotic** state permits them to join the bryophytes in being dormant during those periods when the bryophyte is dehydrated or under a blanket of snow. She states that these cryptobiotic animals are "virtually indestructible." This permits them to survive environmental extremes such as high and low temperatures, high and low *p*H, very high pressure and very low vacuum, and low moisture. Upon return of the habitat to a "livable" and hydrated state, the animals absorb water, expand, and return to an active life. Hence, one might find eggs, "**tuns**" (stage in which body metabolism is undetectable), and cysts. Maggie points out that they do not age while they are in their cryptobiotic state and can remain that way for decades, making ideal study organisms for those interested in space travel and cellular research.

Bryophytes are such an important part of the **niches** of some invertebrates that their name indicates they are "of the moss." A Google search for *muscorum* has revealed 33 of these names among the protozoa and invertebrates (Table 1), and there are probably more, as well as those with *bryophila* or *muscicola* and other bryological epithets such as ***Cyclidium sphagnetorum*** or ***Bryometopus sphagni***.

One particularly important **xerophytic** community is the **cryptogamic crust** (Figure 4) found in prairies and deserts. These bryophyte masses are associated with lichens and algae and inhabited by fungi, bacteria, and other micro-organisms. Among 38 taxa (nematodes, tardigrades, mites, arachnids, springtails, other small insects) in New Mexico, 29 occurred on mossy patches (Brantley & Shepherd 2002). Twenty-seven species occurred on mixed lichen and moss patches, and 21 on lichen patches. Fifteen taxa occurred on all three types. Mosses supported the highest abundance, followed by mixed lichen and mosses, then by lichens. Richness and abundance were both higher in winter (March) than in summer (August) for all crust types in these dry habitats, reflecting differences in moisture stress.

Figure 4. Hydrated cryptogamic crust of ***Syntrichia ruralis*** and other desiccation-tolerant organisms. Photo by Michael Lüth, with permission.

Table 1. Names of protozoa and invertebrates including ***muscorum*** as the specific epithet. The list was derived from an internet Google search, especially ITIS search, for *muscorum*. Accessed on 7 October 2008 at <http://www.itis.gov/servlet/SingleRpt/SingleRpt>.

Protozoa

Assulina muscorum (Rhizopoda)
Chilodontopsis muscorum (Ciliophora)
Gastrostyla muscorum (Ciliophora)
Histriculus muscorum (Ciliophora)
Holosticha (=*Keronopsis*) *muscorum* (Ciliophora)
Oxytricha (=*Opistotricha*) *muscorum* (Ciliophora)
Pusilloburius (=*Pseudoglaucoma*) *muscorum* (Ciliophora)
Rhabdostyla muscorum = Opercularia coarctata (Ciliophora)
Sathrophilus (=*Saprophilus*) *muscorum* (Ciliophora)
Steinia muscorum (Ciliophora) name validity not verified
Strongylidium muscorum (Ciliophora) name validity not verified
Stylonychia muscorum (Ciliophora)
Urostyla muscorum (Ciliophora)

Nematoda

Hemiplectus muscorum (nematode)
Prionchulus muscorum (nematode)

Arthropoda: Arachnida

Gnaphosa (=*Pithonissa*) *muscorum* (Araneae – spider)
Liochthonius muscorum (Araneae – spider)
Tegeocranellus muscorum (Acari – mite)

Arthropoda: Isopoda

Philoscia (=*Oniscus*) *muscorum* (moss wood louse)

Arthropoda: Pseudoscorpiones

Neobisium muscorum (Neobisiidae – moss scorpion)

Arthropoda: Insecta

Acerella muscorum (Protura)
Acrotona muscorum (Coleoptera: Staphylinidae)
Bombus (=*Apis*) *muscorum* (Hymenoptera: Bombidae – moss carder bee)
Anthrenus museorum = Byrrhus (=*Anthrenus*) *muscorum* (Coleoptera: Dermestidae)
Entomobrya (=*Degeeria*) *muscorum* (Collembola – springtails)
Leptothorax (=*Myrmica*) *muscorum* (Hymenoptera: Formicidae)
Liothrips muscorum (Thysanoptera: Thripidae)
Lissothrips muscorum (Thysanoptera: Thripidae)
Mniophila muscorum (Coleoptera – leaf beetle)
Neanura muscorum (Collembola: Neanuridae)
Peromyia muscorum (Diptera: Cecidomyiidae
Tetramorium muscorum (Hymenoptera: Formicidae – Guinea ant)

Mollusca

Pupilla muscorum (Gastropoda – snails)

Bryophytes can be especially important in contributing to species diversity of ecosystems. Sudzuki (1971) found that among 17 stations along five lakes on Mt. Fuji in Japan, the populations of rhizopods, gastrotrichs, rotifers, and nematodes were richest in the mosses. The mosses by Lake Kawaguchi had the highest overall species richness, ranging as high as 77 species, whereas gravels had richness as low as 19 species.

Varga (1992a, b) has found that some rare bryophytes in Sweden [***Plagiobryum zierii*** (Figure 5) & ***Saelania glaucescens*** (Figure 6)] harbor a bryofauna that helps in monitoring air pollution. Not only do the invertebrates have high concentrations of lead, but the fauna in polluted

cushions is diminished compared to that from unpolluted sites.

Figure 5. Lead accumulates in the fauna of this ***Plagiobryum zierii***. Photo by Michael Lüth, with permission.

Figure 6. ***Saelania glaucescens*** is a moss whose bryofauna can be used to monitor air pollution. Photo by Michael Lüth, with permission.

Cover and Nesting Materials – Terrestrial

Moss mats and cushions can make ideal cover and nesting material for a variety of organisms. They serve to buffer both temperature and moisture, while providing sufficient spaces for gas exchange. There are many tiny spaces ideal for laying eggs and protecting young larvae from predators or desiccation. For larger organisms, the leafy stems are easily woven into suitable nests, and the projecting leaves render stability to the completed product. Thus it is not surprising to find that many organisms actually depend on bryophytes for their homes and shelters.

Bryophyte Individuality

But to what extent do individual bryophyte species differ in their provisions for these animals? Learner *et al*. (1990) found no relationship between taxon richness and macroinvertebrate fauna on bank slopes of river corridors where bryophytes were included in the assessment. This suggests that bryophytes might form functional groups that differ in their form from other plants but otherwise differ little within the functional group in the means by which they shelter organisms.

Two communities of bryophytes on Signy Island in the Antarctic support this growth form or functional group suggestion for richness. Davis (1981) found that there was little difference in assimilation or respiration of the plant and faunal components of the ***Polytrichum strictum*** (Figure 7) and ***Chorisodontium aciphyllum*** (Figure 8) turf compared to the ***Calliergidium austro-stramineum*** (Figure 9), ***Calliergon sarmentosum*** (Figure 10), and ***Sanionia uncinata*** (Figure 11) mat with ***Cephaloziella varians*** (Figure 12), but among the faunal taxa (protozoa, Rotifera, Tardigrada, Nematoda, Acari, and Collembola) of these bryophytes, the standing crops of Collembola and Acari differed between the two associations. Thus, while richness differed little, the types of species did differ. Interestingly, it appeared that no bryophytes were eaten by these organisms. Rather, the bryophytes form unique habitats that provide safe sites for the small invertebrates that seek shelter there.

Figure 7. ***Polytrichum strictum***, a turf-former that provides habitat for invertebrates on Signey Island in the Antarctic. Photo by Michael Lüth, with permission.

Bryophytes can play a role in the larger ecosystem picture as well, affecting organisms in other niches. Some mosses in the Antarctic provide habitat for a variety of arthropods indirectly rather than directly by modifying the underlying soil (temperature, moisture, structure) in ways that make it suitable for a variety of arthropods (Gerson 1969).

Figure 8. ***Chorisodontium aciphyllum***, a common invertebrate habitat on Signy Island in the Antarctic. Photo by Jan-Peter Frahm, with permission.

Figure 9. ***Calliergidium austro-stramineum***, a moss that forms a functional group for fauna similar to that of ***Chorisodontium aciphyllum*** (Figure 8). Photo by Bill Malcolm, with permission.

Figure 10. ***Calliergon sarmentosum***, a common invertebrate habitat on Signy Island in the Antarctic. This moss forms a functional group for fauna similar to that of ***Chorisodontium aciphyllum*** (Figure 8). Photo by Michael Lüth, with permission.

Figure 11. ***Sanionia uncinata***, a moss that forms a functional group for invertebrate fauna similar to that of ***Chorisodontium aciphyllum*** (Figure 8). Photo by Michael Lüth, with permission.

Figure 12. Leafy liverwort ***Cephaloziella varians***, growing here with a member of the **Polytrichaceae**. Photo by Kristian Peters, with permission.

Are Bryophytes an Important Food Source?

The answer to that question seems to depend on who you are. But there is clear evidence that some organisms do eat bryophytes. And they seem to have their preferences for both species and parts.

For example, in ***Ulota phyllantha*** (Figure 13), the consumer (apparently an isopod) has a preference for the lamina, leaving behind hair-like structures that are the costa remains (Robin Stevenson, pers. comm. 19 February 2014). In others, gemmae are preferred. Stevenson has suggested that in ***Orthotrichum lyellii*** (Figure 14), where gemmae are prolific, being edible might be an adaptation for dispersal of the gemmae.

Figure 13. ***Ulota phyllantha*** very badly affected by grazing. Those hair-like structures are remaining costae – the leaf lamina has been eaten. Photo courtesy of Robin Stevenson.

Figure 14. ***Orthotrichum lyellii***, a moss with prolific gemmae. Photo by Malcolm Storey, through Discover Life.

Figure 15. Orthotrichum lyellii leaf with gemmae. Photo by Hermann Schachner, through Creative Commons.

Food Value of Bryophytes

Because most bryophytes exist uneaten in herbaria around the world, biologists have long held the view that bryophytes are not effectively a part of the food chain. They have low caloric value (3.7-4.8 Kcal/g; Forman 1968, 1969; Rastorfer 1976a, b), large quantities of holocellulose and crude fiber (Walton 1985) that makes them hard to digest, and are often endowed with a plethora of secondary compounds (Asakawa 1981; see chapter on antiherbivory).

In comparison to evergreen and deciduous shrubs in the alpine tundra, with ~5,560 cal/g ash-free dry mass, bryophytes would seemingly provide considerably less energy (Bliss 1962). Nevertheless, the caloric values for twenty herbaceous tracheophyte species had a mean of 4,601±29 cal/g ash-free dry mass, whereas seven species of moss averaged 4,410±70cal/g, ranging from a high of 4,780 in ***Polytrichum juniperinum*** (var. ***alpestre***) (Figure 16) to 4,211 in ***Sphagnum girgensohnii*** (Figure 17), a difference hardly worth noting.

Figure 16. ***Polytrichum juniperinum***, a moss with 4780 measured calories/g ash free dry mass. Photo by Janice Glime.

Ecologists have long considered that bryophytes had little to offer in nutritional quality (Pakarinen & Vitt 1974). Furthermore, some bryophytes even prevent their consumers from obtaining the nutrition from the non-bryophyte food they have just eaten by complexing the protein in ways that make it indigestible. Liao (unpublished) has found lignin-like protein-complexing tannin compounds in all the boreal forest mosses, except for ***Sphagnum*** (Figure 17), in his study.

In further support of this concept of low food value, we find that in the Antarctic, where bryophytes form the bulk of the vegetation, the invertebrates (protozoa, Rotifera, Tardigrada, Nematoda, Acari, & Collembola) form a diverse fauna among the bryophyte cushions. Yet despite the paucity of non-bryophyte plant food organisms, most invertebrates apparently do not eat the bryophytes (Davis 1981).

Nevertheless, some animals seem to include liverworts (Barthlott *et al*. 2000), mosses (Smith 1977), and hornworts (Bisang 1996) in their diets. Even among the **apparent** (conspicuous) Antarctic bryophytes, which should be expected to have the highest quantity of antifeedant secondary compounds, some invertebrates are adapted to consume them. Weevils (***Ectemnorrhinus similis***) eat 37% of their body weight daily of the moss ***Brachythecium rutabulum*** (Figure 18), consuming 1.67 mg per day per individual weevil on Marion Island (Smith 1977). Tardigrades worldwide are adapted to living among and consuming mosses. Perhaps antifeedants are not as

important to these organisms as we might suppose. How little we know of the physiological mechanisms that make these feeding relationships successful!

Figure 17. ***Sphagnum girgensohnii***. Photo by Janice Glime.

Figure 18. ***Brachythecium rutabulum*** with capsules, a moss that provides 37% of the body weight daily to the weevil ***Ectemnorrhinus similis***. Photo by Andrew Spink, with permission.

We know even less about the nutritive value of sporophytes. Yet several instances are known where capsules are a preferred food, especially for snails and slugs (Davidson *et al*. 1990). Stark (1983) found that 14% of the expanded capsules of ***Entodon cladorrhizans*** (Figure 19) exhibited signs of grazing. Spores can have a lipid content of 30% while vegetative portions may have only 5% (Gellerman *et al.* 1972; Pakarinen & Vitt 1974). Even flowering plants have a lipid content of only 5% in the Arctic (Pakarinen & Vitt 1974).

Figure 19. ***Entodon cladorrhizans***, a moss where capsules are grazed. Photo by Bob Klips, with permission.

Not all functions of food are directly for nutrition. Particularly in northern climates, mammals, and perhaps other animals, seem to benefit from the large quantities of arachidonic acid in bryophytes (Al-Hasan *et al*. 1989). With a melting point of -49.5ºC, this fatty acid provides greater pliability for cell membranes at low temperatures. Prins (1981) suggested that this property may help to keep foot pads of Arctic rodents from freezing.

In any case, bryophytes appear to form an important component of the diet for a number of invertebrates and some Arctic mammals and birds. Gerson (1969) included among these the **Collembola**, **Diptera**, **Hemiptera**, **Hymenoptera**, **Orthoptera**, **Cryptostigmata**, and **Acarina**. These and many others will be discussed further in the succeeding chapters on individual groups.

Vitamins

Bryophytes may fill specific needs of animals when fresh food is scarce. For example, vitamin B_2 is not available in most plants, but ***Barbella pendula*** has a high content and causes no noticeable side effects when fed to puppies and chickens (Sugawa 1960). In fact, Sugawa claims that the animals thrive. Asakawa (1990) lists the species used by Sugawa, citing ***Barbella pendula***, ***B. enervis***, ***Floribundaria nipponica*** (Figure 20), ***Hypnum plumaeforme*** (Figure 21), ***Neckeropsis nitidula*** (Figure 22), and ***Ptychanthus striatus*** (Figure 23) as all resulting in weight gain in chickens and puppies, implying that the presence of B_2 in these bryophytes may have been instrumental in that gain.

Figure 20. ***Floribundaria nipponica***, a moss source of Vitamin B_2 and potential food for puppies and chickens. Photo courtesy of Zen Iwatsuki.

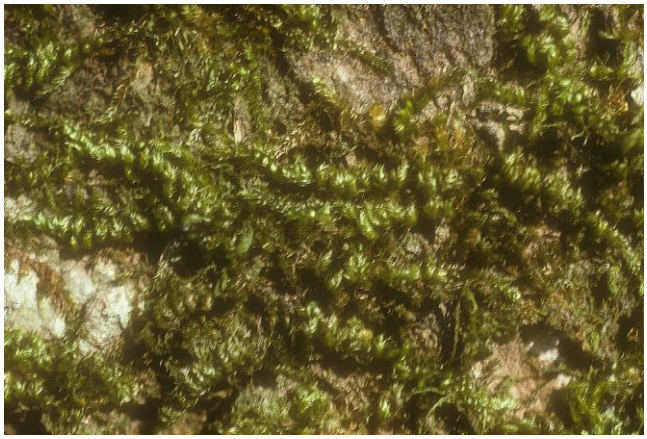

Figure 21. ***Hypnum plumaeforme***, a source of Vitamine B_2 and potential food for puppies and chickens. Photo by Janice Glime.

Figure 22. ***Neckeropsis nitidula***, a moss source of Vitamine B_2 and potential food for puppies and chickens. Photo by Hyun Ji Huon, through Creative Commons.

Figure 23. ***Ptychanthus striatus***, a leafy liverwort source of Vitamin B_2 and potential food for puppies and chickens. Photo by Li Zhang, with permission.

Food Chain Effects

Of concern when bryophytes enter the food web is the ability of bryophytes to retain high levels of radiation. When the Chernobyl accident occurred, bryophytes for hundreds of miles had elevated radiation (Daroczy *et al*. 1988), measurable in mosses two years after the accident (Elstner *et al*. 1987, 1989). These concentrated levels are further concentrated when they enter the food web, and lemmings, which consume them rather extensively in areas affected by the high radiation (Ericson 1977), are but one step into the food web of higher carnivores.

Seasonal Differences in Habitat and Diet

We know virtually nothing about the seasonal changes in diet of invertebrates that might involve bryophytes. And it is likely that bryophytes also change their nutritive value seasonally, but again we are ignorant. We do know that both invertebrates and vertebrates change habitats to survive or take advantage of the seasons (Ovezova 1989). Crafford and Chown (1991) hypothesized that curculionid beetles (**Curculionidae**: Ectemnorhinini) would gain a nutritional advantage by eating bryophytes at low temperatures. Indeed, the cryptogams provided the main source of energy for five out of six of these species on sub-Antarctic Marion Island.

While we seem to know nothing about seasonal diet changes of moss-dwelling invertebrates, we have, however, observed changes in the eating habits of the more conspicuous rodents. Lemmings are known to switch to bryophytes as winter approaches (Prins 1982a), perhaps taking advantage of the high content of arachidonic acid in bryophytes to maintain pliability of cell membranes in their footpads as they run around on frozen ground and snow.

Habitat Differences in Nutrient Availability

Even desert mosses form habitats for a variety of invertebrates (Kaplin & Ovezova 1986). Habitat can play a major role in food value (Figure 24). The avoidance of bryophytes as food seems to be supported where bryophytes form a dominant feature of the physiognomy, *i.e.* the Antarctic, so perhaps apparency theory, the theory that more visible plants contain more antiherbivory compounds, does apply.

Davis (1981) reported that moss was eaten at a rate of less than 0.2 g m^{-2} yr^{-1} by two Antarctic moss invertebrate communities, despite tardigrades, nematodes, rotifers, protozoa, mites, and insects living among them. If such is the case, it supports the model of **apparency**, discussed regarding antiherbivory later in this volume, where the Antarctic bryophytes indeed are the most conspicuous photosynthetic food items available. One would suppose that to avoid herbivory where the slow-growing bryophyte is so conspicuous to would-be consumers, it must either have a high component of secondary compounds to inhibit feeding or lack sufficient food value to make consumption profitable.

This nutritional profitability, as in tracheophytes, differs with habitat. In the high Arctic, not only do the percentages of N and C differ (Figure 24), but the hydric mosses tend to have a higher caloric value (4.57-4.97 kcal/g) and lipid content than do the mesic and terrestrial ones (4.50-4.69 kcal/g) (Pakarinen & Vitt 1974).

Caloric contents likewise differ among terrestrial habitats, with those of alpine regions seemingly lower than those of either coniferous forests (4169 cal/gdw) or northern hardwoods (4179 cal/gdw) (Figure 25; Forman

1968). Oakwoods have the least (3773 cal/gdw) among these studies.

Despite their seemingly lower caloric content, Arctic bryophytes seem to experience greater consumption by mammals than elsewhere (Prins 1982b). Prins (1982a) reported that mosses were found in 20% of Arctic stomach analyses but were only about 1% of the total amount of food consumed. It is clear that a lower proportion of net bryophyte production is grazed than for tracheophytes, and Longton (1984) concluded that bryophytes are utilized primarily via the detritus pathway. Ugh! If they have little caloric content when alive, it would seem that only the microbes could benefit when they are dead. Of course, once eaten they can go up the food chain. It appears that certain temperate animals eat mosses in very limited amounts. Unfortunately, our knowledge of feeding relationships with bryophytes in the tropics is meager.

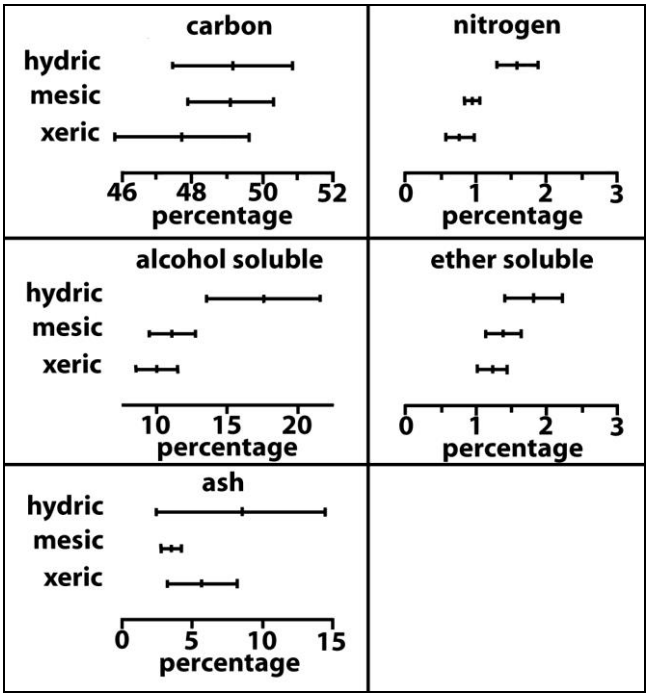

Figure 24. Mean food values (± 95% C.I.) of green (living) tissues based on ash-free dry mass of 35 species of Arctic bryophytes. Redrawn from Pakarinen & Vitt 1974.

Markham and Porter (1978) were among the first to take a global approach to examining the constituents of bryophytes. The differences are strongly influenced by the climate, especially temperature. In the Antarctic, bryophytes have higher C:N ratios than do tracheophytes, with larger amounts of holocellulose and crude fiber and lower energy levels, contributing to their undesirability as a food source (Walton 1985). Pakarinen and Vitt (1974) found that even within the Arctic, ratios could differ considerably, with mesic habitats having a higher carbon ratio (Figure 24). Furthermore, as the moss ages, its cellulose content increases, whereas in grasses it decreases (Walton 1985).

Long after Bliss (1962) initiated the study of Arctic and alpine plants and their nutritional value by examining the caloric and lipid content of alpine tundra plants. Sveinbjornsson and Oechel (1991) found little seasonal difference in lipid or carbohydrate content of ***Polytrichum commune*** (Figure 26) or ***Polytrichastrum alpinum*** (Figure 27). Nevertheless, the variability they did find suggests that seasonality of nutrients bears further investigation. Sugar and starch content were negatively associated with each other, with high starch contents occurring in rhizomes and high sugar contents in shoots, suggesting that starch serves as a storage compound.

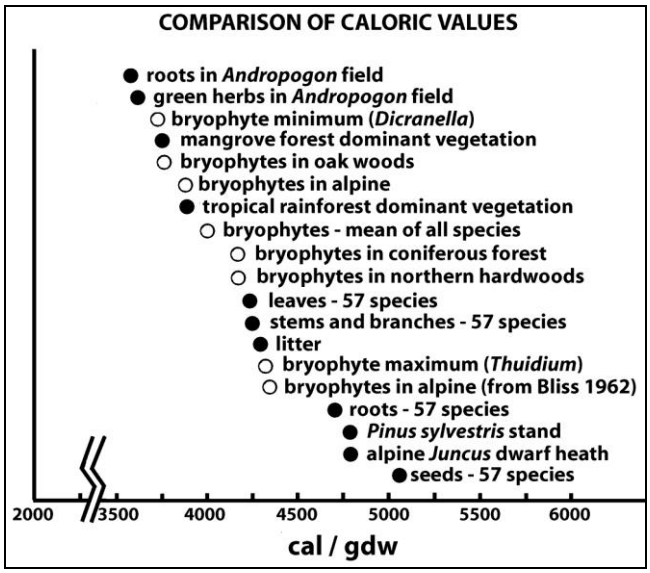

Figure 25. Caloric values (per gram dry weight) of bryophytes (open circles) compared to other plants and plant parts (solid circles). Non-bryophyte data are from Golley 1961; redrawn from Forman 1968.

Figure 26. ***Polytrichum commune*** with capsules. Photo by Michael Lüth, with permission.

Figure 27. ***Polytrichastrum alpinum*** with dew. Photo by Tom Thekathyil, with permission.

Consumption Rates

There are few quantitative studies of bryophyte consumption. Duke and Crossley (1975) calculated that a rock grasshopper, ***Trimerotropis saxatilis*** (Figure 28), consumed the moss ***Grimmia laevigata*** (Figure 29) at a rate of 391 mg m^{-2} yr^{-1} in SE USA. On Marion Island in the Antarctic, an individual beetle, ***Ectemnorrhinus similus***, ate a mean of 1.67 mg of ***Brachythecium rutabulum*** (Figure 18) per day in feeding trials, equivalent to 37% of its body weight (Smith 1977). Davidson and Longton (1987) quantitatively investigated the consumption of several moss species by slugs [***Arion rufus*** (Figure 30-Figure 31) and ***A. subfuscus*** (Figure 32)], as discussed in the chapter on invertebrates.

Figure 28. ***Trimerotropis saxatilis***, a grasshopper well camouflaged among lichens, also eats the moss ***Grimmia laevigata*** in southeastern USA. Photo by Carmen Champagne, through Creative Commons.

Figure 29. ***Grimmia laevigata*** with capsules, food for the grasshopper ***Trimerotropis saxatilis***. Photo by Michael Lüth, with permission.

Figure 30. ***Arion rufus***, black phase of a slug that eats mosses. Photo © Dr. Roy Anderson, with permission.

Figure 31. ***Arion rufus***, a rusty-colored phase of a slug that eats mosses. Photo by James K. Lindsey, with permission.

Figure 32. ***Arion subfuscus***, a slug that consumes mosses. Photo © Dr. Roy Anderson, with permission.

Moss litter is not easily broken down and depends on the moss fauna for consumption, returning to the ecosystem as feces (Frak & Ponge 2002). In alpine areas, other litter generally does not depend on fauna for its breakdown. The same secondary compounds that discourage herbivory also interfere with bacterial and fungal decomposition.

New and Exciting Directions

I am excited – a young researcher decided to examine ***Funaria hygrometrica*** (Figure 33) to see who lived there. This was a great challenge because there are few resources to help in the identification of terrestrial protozoa and algae, especially those that might find mosses to be particularly suitable as homes. But Alen Alex Philip ventured into the realm of the microscopic to explore this cryptic fauna.

What Philip (Philip & Thomas 2016) found was more than he could identify among the 120 kinds of organisms, including Cyanobacteria, algae, Protozoa, Rotifera, Nematoda, and Tardigrada, but he did manage to identify

16 of them to genus. In each of the 15 Indian locations of ***Funaria hygrometrica*** (Figure 33) collections he found six constant genera: **Cyanobacteria** – ***Oscillatoria*** (Figure 34); **Protozoa – *Aspidisca*** (Figure 35), ***Chilodonella*** (Figure 36), ***Holosticha*** (Figure 37), and **Rotifera – *Habrotrocha*** (Figure 38), ***Philodina*** (Figure 39). For a short-lived fugitive moss species of exposed, disturbed habitats, this is to me a surprising number of constant genera!

Figure 33. ***Funaria hygrometrica***, home to 120 different kinds of meiofauna! Photo by Michael Lüth, with permission.

Figure 34. ***Oscillatoria*** sp., a genus that is a constant member of the meiofauna community of ***Funaria hygrometrica*** in India. Photo through Creative Commons.

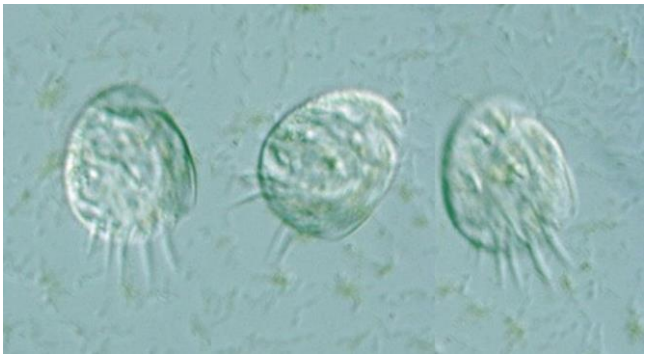

Figure 35. ***Aspidisca*** sp., a genus that is a constant member of the meiofauna community of ***Funaria hygrometrica*** in India. Photo by Yuuji Tsukii, with permission.

Figure 36. ***Chilodonella*** sp., a genus that is a constant member of the meiofauna community of ***Funaria hygrometrica*** in India. Photo by Wolfgang Bettinghofer, through Creative Commons.

Figure 37. ***Holosticha*** sp., a genus that is a constant member of the meiofauna community of ***Funaria hygrometrica*** in India. Photo by Yuuji Tsukii, with permission.

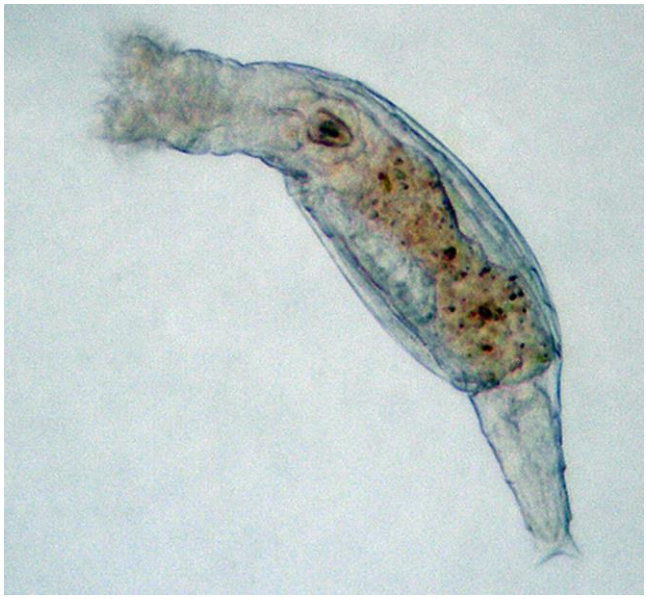

Figure 38. ***Habrotrocha*** sp., a genus that is a constant member of the meiofauna community of ***Funaria hygrometrica*** in India. Photo by Rkitko, through Creative Commons.

Figure 39. ***Philodina*** sp., a genus that is a constant member of the meiofauna community of ***Funaria hygrometrica*** in India. Photo by Wim van Egmond, with permission.

This volume will be a new adventure. In the words of Donald Rumsfeldt, then US Secretary of Defense, in a statement to the press in February 2002, "There are known knowns: there are things we know we know. We also know there are known unknowns; that is to say we know there are some things we do not know. But there are also unknown unknowns – the ones we don't know we don't know." This volume will certainly venture toward the ones we don't know we don't know, and hopefully it will take us to places where we begin to discover those unknowns.

Summary

The small size of bryophytes affords protection from predators to small organisms. This also makes them a good nursery for many kinds of invertebrates. Their perennial nature also provides winter cover, not only for tiny invertebrates, but for larger amphibians and reptiles. Therefore, their potential for contributing to the biodiversity of the planet is enormous.

Bryophyte inhabitants may be classified as **bryobionts** (animals occurring exclusively on bryophytes), **bryophiles** (animals usually but not exclusively among bryophytes), **bryoxenes** (animals that spend part of their lives among bryophytes), and **occasionals** (animals that occur among bryophytes but do not depend on them for survival). **Meiofauna** are the tiny organisms on the bed of a river or lake, or in the moist film of a bryophyte.

One reason for the success of many invertebrate inhabitants is their ability to achieve an **ametabolic** or **cryptobiotic** state, thus becoming dormant when the bryophyte becomes dehydrated or frozen.

Bryophytes buffer both temperature and moisture, not only within the bryophyte community, but in the soil beneath them. Bryophytes differ considerably in their form, yet we know little about differences in communities among different species of bryophytes.

Scientists have assumed that bryophytes have little or no food value, but, nevertheless, isopods, lemmings, and a variety of other organisms do eat them. We know virtually nothing about seasonal changes in nutritive value of bryophytes, nor of seasonal diets of animals that feed on them. Only a few small rodents are known to switch to bryophytes in preparation for winter. Dangers lurk in areas with radiation accumulation in the bryophytes.

Habitat may select for nutritional quality, with alpine taxa having lower caloric values, hydric mosses having higher values and also higher lipid content. Coniferous and northern hardwood forest bryophytes have higher caloric values, bryophytes of oakwoods the least. As bryophytes age, cellulose content increases, further reducing palatability and energy availability.

Acknowledgments

Thank you to Rod Morris for providing the name of the bird that made the nest in the frontispiece. Throughout this volume, Google and Wikipedia have been invaluable. Without the search capabilities of Google, I would never have discovered many of the stories in this volume. With Wikipedia, I could find general information and leads to important primary literature. Members of Bryonet have kindly sent me stories and publications. This volume is the product of worldwide cooperation of scientists of many kinds. Without their help in providing literature, comments, and images, the richness of the forthcoming stories would be lost.

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CHAPTER 2-1
PROTOZOA DIVERSITY

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CHAPTER 2-1
PROTOZOA DIVERSITY

Figure 1. ***Actinophrys sol***, a heliozoan that can sometimes be found among mosses in quiet water, with a diatom. Photo by Yuuji Tsukii, with permission.

Moss-Dwelling Micro-organisms

Bryophytes are truly an elfin world, supporting diverse communities of organisms that we often can't see without a microscope. As one might expect, micro-organisms abound (Figure 1) (*e.g.* Leidy 1880; Maggi 1888; Penard 1908; Heinis 1910; Sandon 1924; Bartos 1946, 1949a, b; Ramazotti 1958; Torumi & Kato 1961; Matsuda 1968; Smith 1974a, b; Schönborn 1977; Sudzuki 1978; Bovee 1979), traversing the crevices like fleas among a dog's hairs. Bovee (1979) reported 145 taxa of protozoa from bogs in the Lake Itasca region, Minnesota, USA. In fact, there are sufficient of these organisms associated with ***Sphagnum*** that there have been books published on their identification (*e.g.* Hingley 1993). From forest bryophytes, Bovee found only 68 taxa. Ciliates and testate amoebae dominate the protozoa in both habitats. Even floating liverworts like ***Ricciocarpos natans*** have their associated microfauna (Scotland 1934).

Gerson (1982) suggests that protozoa have evolved into the bryophyte habitat. Water that wets the mosses permits the protozoa to complete their life cycles. Moist bryophytes easily accumulate windborne dust, providing even epiphytic species with a source of nutrient matter to serve as food for bacteria and ultimately protozoa. Colonization of aerial bryophytes by micro-organisms could likewise be accomplished by wind. Dispersal of these small organisms may be similar to dispersal of spores of mosses, and the implications of their small size will be discussed later in this chapter.

Terminology

It has been a while since I examined the classification of the micro-organisms, so organizing this chapter turned out to be a bigger mire than I had bargained for. I am sure some of my classification is old-fashioned, but practicality has won out if I am ever to approach completion of this volume. I have tried to update where possible, but some things just don't fit there in my mind, or seem more appropriate to write about in a different place. I have decided to avoid kingdom arrangements completely, so you may find some traditional algae here and others in a chapter labelled algae.

Organisms living "firmly attached to a substratum," but not penetrating it, are known by the German term **Aufwuchs** (Ruttner 1953), introduced in 1905 by Seligo (Cooke 1956). Later the term **periphyton** (literally meaning "around plants") was introduced for organisms growing on artificial objects in water. This term was later expanded to refer to all aquatic organisms growing on submerged surfaces. Young (1945) restricted the definition to "that assemblage of organisms growing upon free surfaces of submerged objects in water and covering them with a slimy coat" (in Cooke 1956). The use of the term has varied, including not only **epiphytes** (those living on plants and algae), but also organisms on non-plant substrata. Although the term Aufwuchs has enjoyed a less confusing history of meanings, Americans tend to use periphyton more frequently to refer to those micro-organisms living upon a substrate. By whatever term, this group of micro-organisms often creates a rich community in association with bryophytes. This chapter will concentrate on the protozoa.

Abundance

One difficulty in describing the micro-organisms of bryophytes is the tedious task of sorting through and finding the organisms. Methods for finding and enumerating protozoa are discussed later in this chapter. Often identification and quantification requires culturing the organisms, which will bias the counts to those most easily cultured. Testate rhizopods are most easily located because the presence of the test permits recognition even after death. These limitations must be remembered in any discussion of abundance.

Tolonen and coworkers (1992) found up to 2300 individuals per cm^3 among the bryophytes in Finnish mires. These include **rhizopods** – those with movement by protoplasmic flow, **ciliates**, and **flagellates** (Gerson 1982). The most abundant seem to be the rhizopods (Beyens *et al*. 1986b; Chardez 1990; Balik 1994, 2001), especially those with shells (**testate**) (Beyens *et al*. 1986a, b; Chardez & Beyens 1987; Beyens & Chardez 1994). Among these, ***Difflugia pyriformis*** (Figure 2), ***D. globularis***, ***Hyalosphenia*** (Figure 3), and ***Nebela*** (Figure 4) are the most common among ***Sphagnum*** at Itasca, Minnesota, USA (Bovee 1979). In Pradeaux peatland in France, ***Nebela tincta*** (Figure 4) numbered an average of 29,582 L^{-1} active individuals, with another 2263 in encysted form (Gilbert *et al*. 2003).

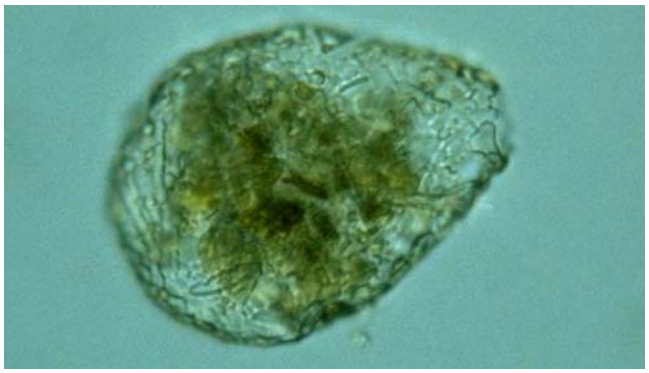


Figure 2. ***Difflugia pyriformis*** test. Photo by Yuuji Tsukii, with permission.

Schönborn (1977) actually estimated the production of protozoa on the terrestrial moss ***Plagiomnium cuspidatum*** (Figure 5) and found a yearly mean of 145 x 10^6 individuals per m^2 (0.11 g m^{-2} d^{-1}). Rainfall played an important role in the dynamics of protozoa among the mosses, contributing to dislocation and modifying production. Many of the protozoa were testate amoebae that carry sand houses around with them. Heavy rains easily knock these loose and carry them to deeper layers in the soil. On the other hand, the daily death rate of these testate amoebae is lower (only 3.0% per day) than in the river itself. Furthermore, the turnover rate in mosses is much lower than in the river. The higher drying rate (higher than in soil) decreases the number of generations to about half that in soil in the same time period.

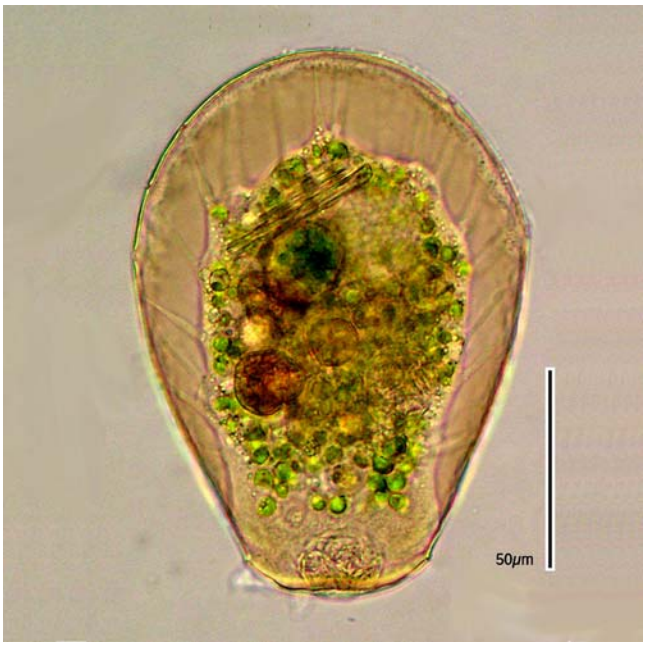


Figure 3. ***Hyalosphenia papilio*** showing test and ingested algae. Photo by Ralf Meisterfeld, with permission.

Figure 4. ***Nebela tincta*** test. Photo by Yuuji Tsukii, with permission.

In temperate forests of northeastern USA, Anderson (2008) identified 50 morphospecies of non-testate amoebae, averaging 17 per sample, based on lab cultures. Densities ranged 3.5 x 10^3 to 4.3 x 10^4 gdm^{-1} of moss. As in other studies, numbers were highly correlated with

moisture content of the mosses ($p < 0.001$). These numbers exceeded those of soil, perhaps due to the heavier weight of soil per unit volume. As expected, number of encysted forms was inversely related to moisture content.

Figure 5. ***Plagiomnium cuspidatum***, a terrestrial moss habitat. Photo by Michael Lüth, with permission.

Peatlands

Peatlands are unique habitats dominated by mosses. Because of their moist nature, they are home to numerous micro-organisms (Warner 1987; Kreutz & Foissner 2006) and will warrant their own sections as we talk about many of the groups of organisms that inhabit mosses.

In addition to the moist habitat of the peatland mosses, peatlands provide numerous small pools, hollows, channels, and small lakes that are ideal habitats for some micro-organisms. Using glass slides, Strüder-Kypke (1999) examined the seasonal changes in these micro-organisms in dystrophic bog lakes at Brandenburg, Germany. May brought ciliates and choanoflagellates and the highest degree of species diversity for the year. This community was replaced by one dominated by peritrich ciliates from August to October. Their decline coincided with early frost, yielding to a winter periphyton of small heterotrophic flagellates. The pioneers on the slides were bacterivorous ciliates.

Peatlands typically have **vertical community** differences, as will be seen as we discuss the various groups. Diminishing light restricts the photosynthetic organisms and those protozoa with **zoochlorellae** (algal symbionts) to the upper portion of the ***Sphagnum***. In the German bog lakes, Strüder-Kypke (1999) found that this zone was characterized by autotrophic cryptomonads and mobile ciliates. Deeper portions were colonized by heterotrophic flagellates and sessile peritrich ciliates.

Cyclidium sphagnetorum (Figure 6) is known only from *Sphagnum* and is thus a **bryobiont** (Grolière 1978 in Gerson 1982). In fact, ***Sphagnum*** usually has the richest bryofauna of any moss, as shown by Bovee (1979) in Minnesota. In Canada, a single gram of ***Sphagnum girgensohnii*** (Figure 7) housed up to 220,000 individuals of protozoa, mostly flagellates, while ***Campylium chrysophyllum*** (Figure 8) had a maximum of only 150,000 in the same habitat (Table 1; Fantham & Porter 1945), suggesting there might be important microhabitat differences among bryophyte species. In Westmorland, the numbers translate to a mere 16 million of these animals in a single square meter of ***Sphagnum*** (Heal 1962).

Figure 6. ***Cyclidium*** sp. (Ciliophora). Photo by Yuuji Tsukii, with permission.

Sphagnum is a particularly common habitat for micro-organisms (Chacharonis 1956; deGraaf 1957). It appears that even the surface of ***Sphagnum*** may offer a unique community. Gilbert *et al.* (1998, 1999) considered that these surface organisms might play an important role in recycling nutrients using the **microbial loop,** an energy/carbon pathway wherein dissolved organic carbon re-enters the food web through its incorporation into bacteria. Changes in these bryophyte protozoan communities could alter the return of nutrients through the microbial loop and indicate the degree of human disturbance.

Figure 7. ***Sphagnum girgensohnii***, a peatmoss that can house up to 220,000 individuals in 1 gram of protozoa. Photo by Michael Lüth, with permission.

Figure 8. ***Campylium chrysophyllum***, a peatland species that may be less hospitable to protozoa than ***Sphagnum***, but still can house 150,000 in just 1 gram. Photo by Michael Lüth, with permission.

Table 1. Number of individuals occupying ***Sphagnum*** per gram dry moss. From Fantham & Porter 1945 in Hingley 1993.

	naked amoebae	testate rhizopods	flagellates	ciliates	rotifers	nematodes
S. papillosum	440	3640	9920	1000	160	120
S. subsecundum	1344	1712	26672	2224	176	64
S. palustre	240	3360	5880	2080	120	360
S. girgensohnii	——————over 220,000——————				1160	4680

In their comparison of the protozoan groups and other small invertebrates on four ***Sphagnum*** species, Fantham and Porter (1945) found that ***Sphagnum girgensohnii*** supported the most protozoa, rotifers, and nematodes, and that flagellates were the most common on all four ***Sphagnum*** species (Table 1). Unfortunately, most extraction techniques do not work well for examining the flagellates, so it is likely that they are more common than most studies indicate.

We might well ask why ***Sphagnum girgensohnii*** was the preferred moss. This species tends to occur on higher ground and in forests where it is not submersed for significant periods of time and it is usually possible for protozoa and other small invertebrates to seek out higher parts of the plants to escape drowning. Water is not always a good thing.

The richness of the invertebrate fauna in peatlands is rather astounding in view of the antibiotic properties of ***Sphagnum***. Its polyphenolic compounds could not only discourage herbivory on the moss, but reduce the availability of micro-organisms, especially bacteria, that might otherwise live there and serve as food for invertebrate inhabitants (Verhoeven & Liefveld 1997). Smirnov (1961) could find only one invertebrate species that ate the ***Sphagnum*** – ***Psectocladium psilopterus*** – a chironomid (midge) larva. Other fauna ate mostly algae from the surface. Nevertheless, microfauna seem to abound in a wide diversity of species and numbers among the ***Sphagnum*** (Smirnov 1961; Tolonen *et al* 1992; Gilbert *et al*. 1999), despite the fact they are on the menu at this mossy restaurant.

Protozoa

Although **Protozoa** was once a recognized taxonomic unit, it is now only a convenient name used to describe the heterotrophic flagellates, ciliates, and amoebae. Of the now-recognized four major groups of protozoa, three can be found in association with bryophytes. These are **Sarcodina** – rhizopods (amoebae), **Ciliophora** – ciliates, and **Mastigophora** – flagellates (Chiba & Kato 1969; Gerson 1982). Bamforth (1973) described two nutritional protozoan groups associated with plant communities. The naked taxa are primarily **bacterivores** (consume bacteria) and depend on the decomposability of the litter (including bryophytes) where they live. The **Testacea** (those rhizopods living in a shell of their own making) are more slow growing, associate with humus and mosses, and live where the humus is of slow decomposability. These characteristics make bryophytes suitable substrates.

The most important factor in determining the habitation by the protozoa is moisture. This determines which species can occur there, what food is available, and whether the protozoan is active or dormant. Mosses act much like a sponge, absorbing water that is available from the soil, rain, and atmosphere, and retaining it. As such, they provide a moist safe haven for protozoans to continue an active life long after other surfaces are dry. But they also help to slow the drying of their underlying substrate and provide insulation against heat, cold, and wind, increasing the utility of the substrate, especially soil, as well (Das 2003).

Gerson (1982) has described four categories of bryophyte fauna, based on their occurrence among bryophytes: **bryobionts –** animals that occur exclusively in association with bryophytes; **bryophiles** – animals that are usually found among bryophytes but may survive elsewhere; **bryoxenes –** animals that regularly spend part of their life cycle on bryophytes; **occasionals** – animals that may at times be found among bryophytes but do not depend on them for survival.

In a study of Polish peatlands, Mieczan (2006) named four categories of protozoa that inhabited the peatlands, based on percent presence: **very constant species** (in 61-100 percent of the samples), **constant species** (in 41-60 percent), **accidental species** (in 21-40 per cent), **accessory species** (in less than 20 per cent). Although this system aligns closely with that of Gerson (1982), it has the advantage that one does not need to know the occurrence of the species elsewhere and it is more quantitative. On the other hand, that quantification requires considerable time to determine.

As already noted, the richest protozoan habitat among the mosses is considered to be ***Sphagnum***, with up to 16 million individuals m^{-2} (Richardson 1981). Whereas ***Sphagnum*** provides a moist habitat, ***Drepanocladus*** (*sensu lato*; Figure 9), a rich fen species, may be a better habitat by trapping more nutrients (Gerson 1982). In that habitat, the amount of available nutrients determined the numbers of protozoa, due to the greater availability of microbes and organic matter that served as food sources.

Figure 9. ***Drepanocladus*** (=*Limprichtia*) ***revolvens***, a species among the brown mosses that live in rich fens. Photo by Michael Lüth, with permission.

In his study of Polish peatlands, Mieczan (2006) found 24 taxa of ciliates and 6 of testate amoebae among mosses. But he considered the majority of these to be accidental or accessory species.

Even dry cryptogamic crusts of prairies and deserts sport a diverse fauna of protozoa. In the Grand Canyon, Arizona, USA, 51 species of ciliates, 28 of amoebae, 17 of Testacea, 4 metazoan taxa, and a number of flagellate morphotypes were present in the water film among just 28 microbiotic crust samples (Bamforth 2003). These crusts were composed of Cyanobacteria, lichens, and bryophytes. In the predominating non-flagellated protozoan groups, **r-selected** (high level of reproduction, small body size, short generation time) bacterivores respond rapidly to wetting, quickly exploit resources, then encyst when unfavorable conditions return. It seems that these protozoan groups and bryophytes were made for each other (Kunz 1968).

Zoomastigophora (Flagellates) and flagellated Chlorophyta

Like Euglenophyta, flagellated green algae (flagellated Chlorophyta) are placed in this sub-chapter because of their movement capability and ecological relationships, especially with peat.

The flagellates, known as Zoomastigophora, swim by means of 1-4 long flagella and thus require at least a film of water. Fortunately, some are able to encyst, enabling them to become dormant when that film of water is absent.

As one might suspect, ***Sphagnum*** can provide long periods when leaves have a thin film of water. Numbers of flagellates can reach 10^7 cells L^{-1} (Gilbert & Mitchell 2006). For the green alga ***Carteria sphagnicola*** (Figure 10) ***Sphagnum*** provides an unique habitat, with its cation exchange making its surrounding water acid. This would be particularly true of a thin film of water that is not diluted by lake or fen water.

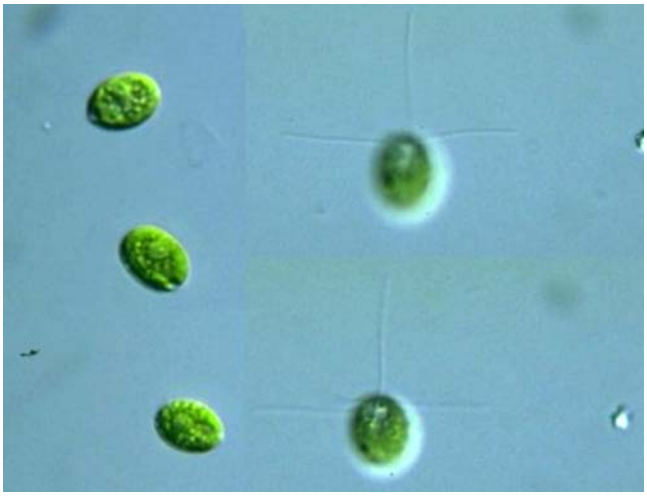


Figure 10. ***Carteria sphagnicola***, a peatland inhabitant. Photo by Yuuji Tsukii, with permission.

Chlamydomonas (Figure 11), a green alga, is a relatively common genus in peatlands. ***Chlamydomonas acidophila***, as its name implies, lives at low *p*H and is common among ***Sphagnum*** plants with a *p*H of 2-6, where as many as 50,000 individuals may exist per cm^2 (Hingley 1993). Another ***Chlamydomonas*** species, known first from ***Sphagnum***, has been named ***C. sphagnicola***.

Figure 11. ***Chlamydomonas moewusii***. Photo by Yuuji Tsukii, with permission.

One advantage that the widely known genus ***Chlamydomonas*** shares with many of the bryophyte-inhabiting protozoa is the ability to form a **palmelloid** stage (Figure 12) – a stage that can remain dormant during dry spells (Rajan 202). This stage is named because of its resemblance to the green algal genus ***Palmella***. In ***Chlamydomonas***, to form the palmella stage, the cells lose their flagella, divide, and form a gelatinous ball in which the cells are embedded. Each cell is still capable of individual function. When favorable conditions return, individual cells are freed and continue an active life.

Figure 12. ***Chlamydomonas***, a genus that can inhabit the hyaline cell of ***Sphagnum***. **Upper:** vegetative cell. **Lower:** palmelloid stage. Photos by Jason Oyadomari, with permission.

Chlamydomonas reinhardtii is known to form gelatinous masses or a **palmelloid** stage (Figure 13) when confronted by the predator ***Brachionus calyciflorus***, a rotifer (Lurling & Beekman 2006). The reaction to form a palmelloid stage can occur within 25 hours and apparently affords some protection against rotifer grazing. The low *p*H of the ***Sphagnum*** habitat may contribute to this ability; calcium can cause the palmelloid stage to dissociate, but phosphorus can negate the dissociation (Iwasa & Murakami

1969). Iwasa and Murakami suggest that organic acids (such as those produced by ***Sphagnum***) chelate calcium and permit the formation of the palmelloid stage. Nakamura *et al*. (1976) have shown that there are other biochemical/chemical interactions that can inhibit the formation of the palmelloid stage in ***Chlamydomonas eugametos***, suggesting that rotifers, and other organisms, could emit biochemicals that stimulate or interfere with palmelloid formation. Among bryophytes, cohabitation with rotifers is likely to occur frequently, so one should look for these special reactions.

Figure 13. ***Chlamydomonas*** close view of palmelloid stage. Photo by Jason Oyadomari, with permission.

Henebry and Cairns (1984) found the flagellated Chlorophyta ***Chilomonas***, ***Monas***, and ***Monasiga*** associated with ***Sphagnum*** in peatlands. Additional members of bryophyte associations are listed in Table 2.

Euglenophyta

Euglena (Figure 14) is one of those organisms that caused consternation among early classifiers because of its combination of animal and plant traits. It can engulf food, but it also has chlorophyll and a flagellum. I have stubbornly used its algal name here but am writing about it with the protozoa because of its flagella. Additional Euglenophyta are listed in Table 2.

Figure 14. ***Euglena*** in a poor fen collection at Perrault Fen, Houghton County, Michigan, USA. Photo by Jason Oyadomari, with permission.

Euglena mutabilis (Figure 15) can withstand *p*H as low as 1.8, numbering 50,000-70,000 per cm^2 of ground surface (Hingley 1993). Its numbers, like those of many other ***Sphagnum*** organisms, correlate positively with moisture content of the peat. ***Euglena mutabilis***, common in the upper 2 cm of peat, lacks the flagellum that is typical of euglenoids and has only two chloroplasts. Of special interest is its ability to live inside hyaline cells of the *Sphagnum* leaves (Figure 16, Figure 17). ***Sphagnum*** species with hooded leaves seem to house more euglenoids than do other kinds of ***Sphagnum***. The "hood" most likely helps to create a micro-basin for trapping water. Some of these tiny unicellular organisms, like *Euglena mutabilis*, enter through the ***Sphagnum*** leaf pores and live within the hyaline cells (these are non-living), dining on organic debris left by former residents.

Figure 15. ***Euglena mutabilis***. Photo by Yuuji Tsukii, with permission.

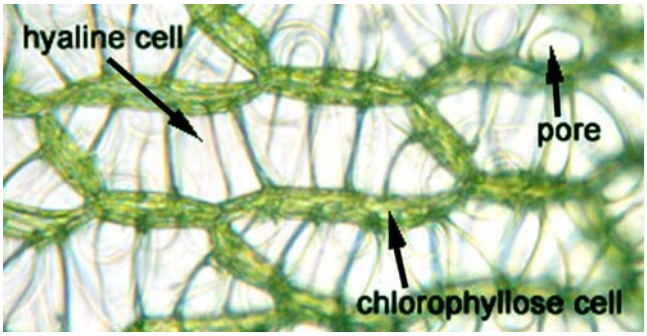


Figure 16. Microscopic view of ***Sphagnum*** leaf showing hyaline cells and pores. Photo with permission from <http://www.botany.ubc.ca/bryophyte/LAB8.htm>.

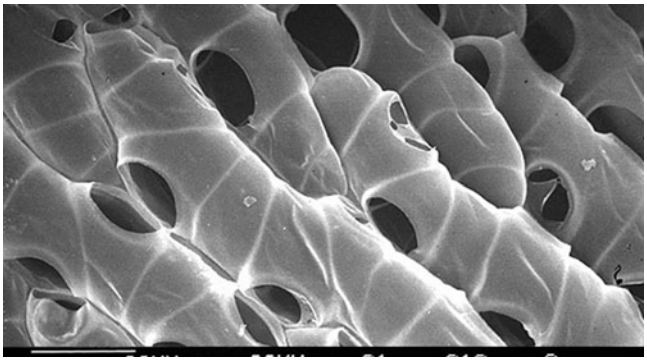


Figure 17. SEM of ***Sphagnum*** hyaline cells, showing pores. Photo from <http://www.botany.ubc.ca/bryophyte/LAB8.htm>, with permission.

Despite their lack of a **test**, ***Euglena acus*** (Figure 18) and ***Phacus longicaudatus*** (Figure 19) can survive desiccation for more than seven years with no test to protect them (Hingley 1993).

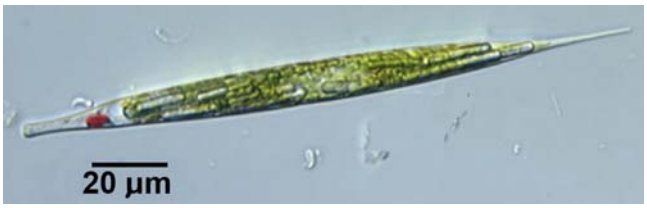


Figure 18. ***Euglena acus*** showing distinctive red eyespot that permits it to respond to light. Photo by Jason Oyadomari, with permission.

Figure 19. ***Phacus longicauda***, a not-so-common member of the bryophytic protozoan fauna. Photo by Yuuji Tsukii, with permission.

Pyrrophyta (=Dinophyta)

The name **Pyrrophyta** literally means fire plants, and these organisms are so-named because of the ability of some species to produce flashes of light through bioluminescence. Sadly, these spectacular show-offs are rarely known from bryophytes (Table 2). I have located only one Pyrrophyta species known commonly to inhabit bryophytes – ***Hemidinium ochraceum*** (Hingley 1993; Figure 20). But that gives me an excuse to write about these remarkable organisms, also known as **dinoflagellates**. ***Hemidinium ochraceum*** lives among the ***Sphagnum*** in hollows of peatlands where they give the ***Sphagnum*** a yellowish-rusty color (Hingley 1993).

Figure 20. The dinoflagellate ***Hemidinium*** sp. Photo by Yuuji Tsukii, with permission.

Whereas some **dinoflagellates** (so-named because of their twirling motion) attract attention by their brilliant displays, others attract it by their deadly toxins. They are the apparent cause of the water that "turned to blood" as reported in Exodus of the *Bible* – red tide organisms known today for the resulting unpleasant odors of dying fish and in some cases very strange effects on humans. Some wear plates of armor and others do not. Their two flagella lie in grooves, one around the middle of the cell like a sash and the other extending from that line down the "back" and up the "front," resulting in their characteristic twirling motion. It is not surprising that they avoid peatlands because most of them prefer alkaline conditions (Hingley 1993).

Ciliophora (Ciliates)

These organisms use a series of fine cilia instead of flagella to achieve movement. Some of these, despite their cilia, attach themselves to ***Sphagnum*** leaves (Hingley 1993). The cilia can serve more than one function. Whereas the primary one is to direct food into the cell, many also use them for locomotion.

Numbers of ciliates among ***Sphagnum*** water range 0-4.2 x 10^6 cells L^{-1} (Gilbert & Mitchell 2006). Many of these organisms may simply use the bryophytes as a substrate. Such is probably the case for the stalked ***Vorticella*** (Figure 21, Figure 22). Nevertheless, detrital matter that accumulates and algae and bacteria that take up residence among the leaves most likely provide food for ciliates, whether confined by an attachment or free-moving.

Some ciliates occur only among ***Sphagnum*** (Figure 23), including ***Bryometopus*** (Figure 24) and ***Climacostomum*** (Figure 25), the latter often with **symbionts** (Figure 26) (Gilbert & Mitchell 2006). Other taxa that Mieczan (2006) found to be very constant in Polish peatlands include ***Askenasia*** sp., ***Chlamydonella*** spp., ***Enchelyomorpha vermicularis*** (70%), ***Gastronauta*** spp. (89%), ***Paramecium putrinum***, and ***Trochilia minuta***.

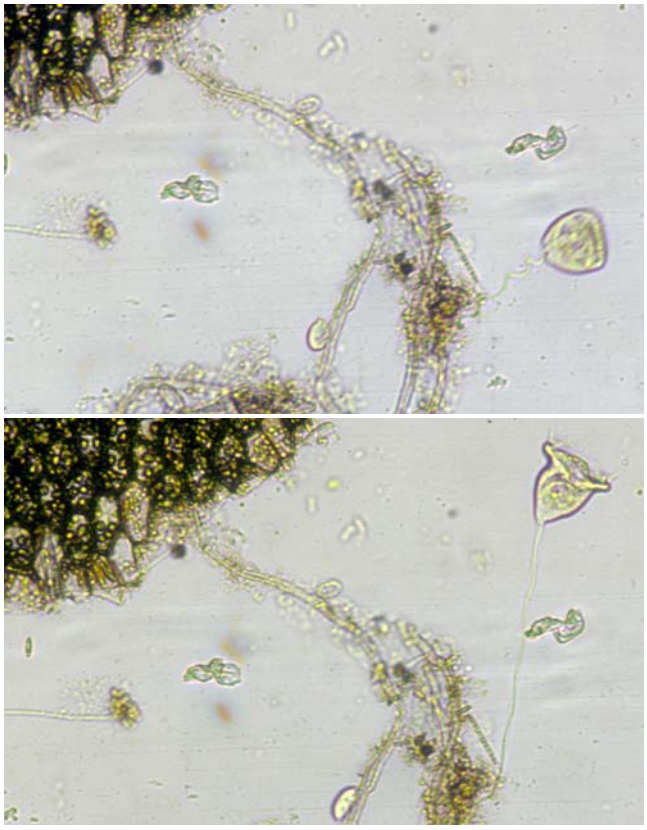


Figure 21. **Upper:** A member of the genus ***Vorticella*** that was living on the leaves of the leafy liverwort ***Jungermannia cordifolia***. **Lower:** This same ***Vorticella*** is shown here with its stalk extended. Photos courtesy of Javier Martínez Abaigar.

Figure 22. ***Vorticella***, a stalked ciliate that inhabits bryophyte leaves and other aquatic substrates. Photo by Jason Oyadomari, with permission.

Figure 23. ***Sphagnum obtusum*** showing the wet capillary spaces among the leaves that support ciliate protozoan communities on these drooping branches. Photo by Michael Lüth, with permission.

The ciliates have a distinct zonation within the peatland, and different communities, fewer in number of individuals and species, occur at the depth of the non-green ***Sphagnum*** parts (Hingley 1993). Those with **symbiotic** algal partners require light and are thus restricted to areas near the surface where the ***Sphagnum*** likewise is green. However, some symbiotic ciliates are also able to ingest food and can thus also live farther down the stems.

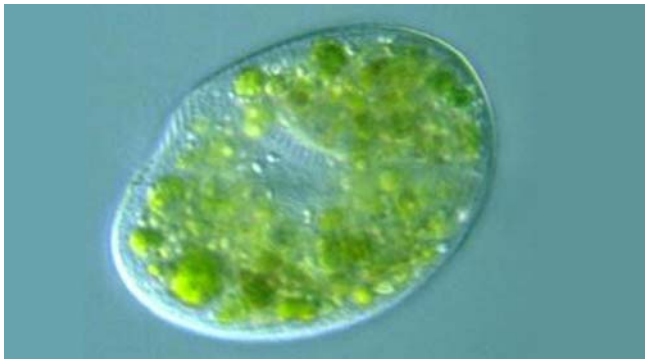


Figure 24. A ciliate, possibly ***Bryometopus***, a bryobiont of ***Sphagnum***, showing photosynthetic symbionts. Photo by Yuuji Tsukii, with permission.

Figure 25. ***Climacostomum virens*** with no symbionts. Photo by Yuuji Tsukii, with permission.

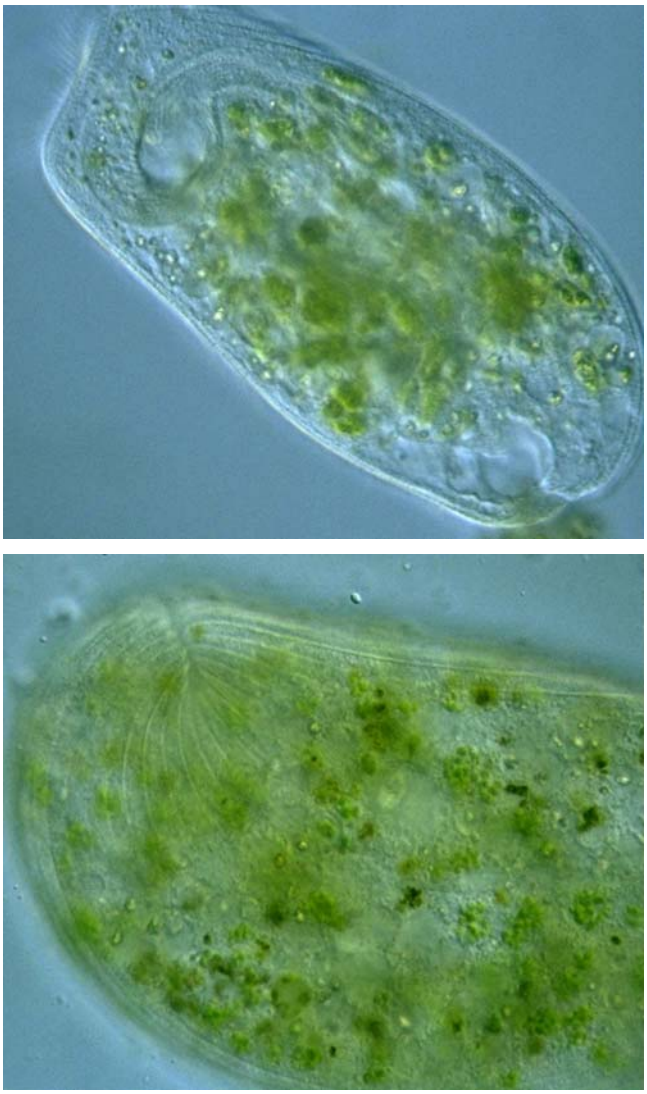


Figure 26. ***Climacostomum virens*** with dense symbionts. Photos by Yuuji Tsukii, with permission.

Like many other protozoa, the ciliates can survive drought by encysting. ***Paramecium aurelia*** (see Figure 27-Figure 28 for genus) can survive more than seven years with no test to protect it (Hingley 1993).

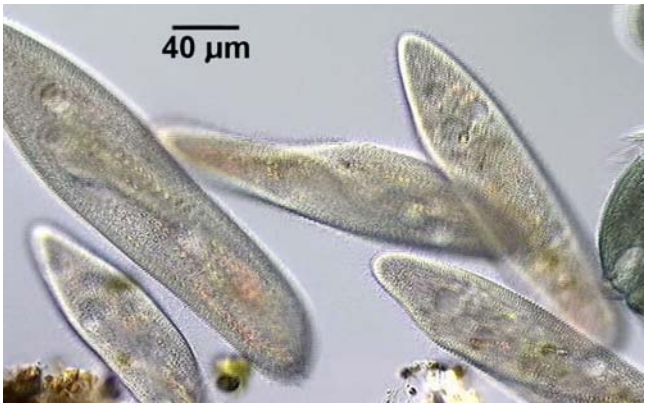


Figure 27. ***Paramecium***, the slipper animal, is a ciliate that is larger than most protozoa. Photo by Jason Oyadomari, with permission.

Figure 28. ***Paramecium*** showing two of its round contractile vacuoles that permit it to regulate its water content. Photo by Jason Oyadomari, with permission.

The ***Sphagnum***-dwelling ciliate ***Podophyra*** sp. (Figure 29) has tentacles that are necessary in its capture of prey. These have a knob at the end that excretes substances that narcotize the prey (Samworth). The interesting part of this trapping mechanism is that the cytoplasm is sucked down these tentacle arms to the body and the prey, such as the ciliate ***Colpidium*** (Figure 30), remains alive during the journey! The prey organism is finally absorbed into the body of the ***Podophyra***. But stranger still it is that the prey organism may be released, still alive, after the ***Podophyra*** has finished feeding!

Figure 29. ***Podophyra***, a ciliate found in Perrault Fen, Houghton County, Michigan, USA. Photo by Jason Oyadomari, with permission.

Figure 30. ***Colpidium campylum***. Photo by Yuuji Tsukii, with permission.

Michael Plewka (Michael Plewka, pers. comm. 29 November 2016) finds the ciliate ***Phacodinium metchnikoffi*** (Figure 31-Figure 33) to be common among mosses. Other inhabitants include ***Bryophyllum tegularum*** (Figure 34-Figure 35) and ***B. loxophylliforme*** (Figure 36).

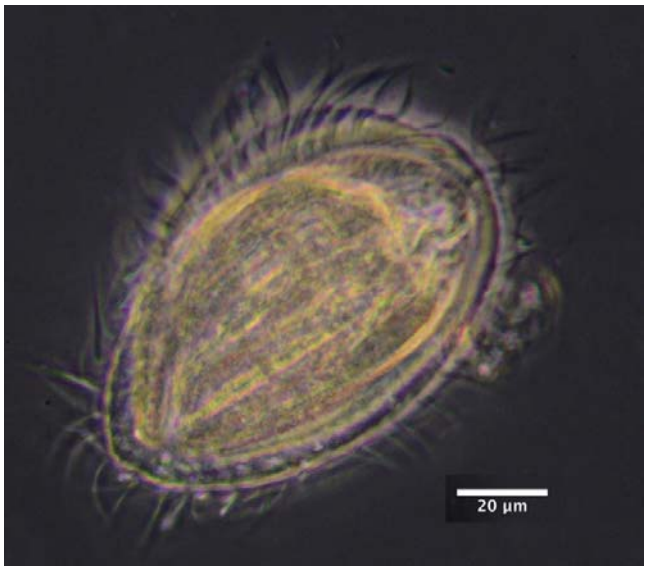


Figure 31. ***Phacodinium metchnikoffi***, a common moss inhabitant in Europe. Photo by Don Loarie, through Creative Commons.

Figure 32. ***Phacodinium metchnikoffi***, a common moss inhabitant in Europe. Photo by Michael Plewka, with permission.

Figure 33. ***Phacodinium metchnikoffi***, a common moss inhabitant in Europe. Photo by Michael Plewka, with permission.

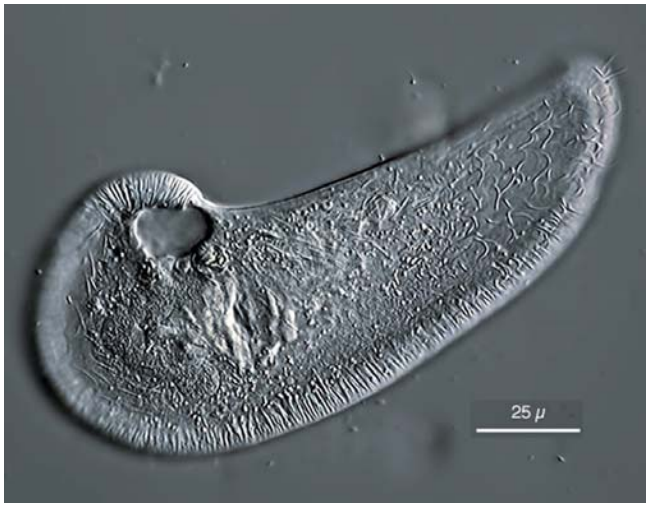


Figure 34. ***Bryophyllum tegularum***, a moss inhabitant in Europe. Photo by Michael Plewka, with permission.

Figure 35. ***Bryophyllum tegularum***, a moss inhabitant in Europe. Photo by Michael Plewka, with permission.

Figure 36. ***Bryophyllum loxophylliforme***, a moss inhabitant in Europe. Photo by Michael Plewka, with permission.

Symbionts

Many of the ciliates have their own **symbiotic** residents. Those ciliates living near the surface of bryophyte communities where there is ample light often incorporate photosynthetic algae inside their cells (Figure 37), benefitting from the oxygen and photosynthate, and contributing CO_2 to the algae (Hingley 1993). The algae can also transfer organic nitrogen, phosphorus, and sulfur and excrete glycerol, glucose, alanine, organic acids, and carbohydrate released as maltose (Arnold 1991; Dorling *et al*. 1997). In return, the symbiotic algae can gain inorganic forms of nitrogen, phosphorus, and sulfur and may gain vitamins, while enjoying the safety of a moist cell. Wang (2005) reported that protozoa with algae seemed to be favored by higher oxygen concentrations with concomitant higher concentrations of CO_2. This higher CO_2 undoubtedly aided the algae in their photosynthesis inside the diffusion barrier of the protozoan cell.

Figure 37. ***Colpoda*** with Chlorophyta symbionts. Photo by Yuuji Tsukii, with permission.

When the alga is to be used as a symbiont, it is protected within a vacuole by a double membrane. Somehow the host cell knows not to digest these, whereas those doomed as food are located in vacuoles that merge with lysosomes and are digested (Karakashian &

Rudzinska 1981). In ***Hydra***, it is the maltose that apparently signals the host not to digest its symbiont (McAulay & Smith 1982 in Arnold 1991), and this may also be the means of recognition in the protozoa. Anderson (1983) suggests that the protozoan may still later digest some of the symbionts, making these photosynthetic organisms into an internal garden to be harvested as needed.

In ***Frontonia***, the alga may survive with or without symbionts (Figure 38). Among the ciliate symbiotic hosts, ***Cyclidium sphagnetorum*** (see Figure 39) is one of the common ciliate species among peatland bryophytes (Groliére 1977). The common ***Paramecium bursaria*** is likely to be home for numerous cells of ***Chlorella*** (Figure 40), but it can also have the alga ***Scenedesmus*** (Figure 41) as a partner (Arnold 1991). Others include ***Frontonia vernalis*** (Figure 42), ***Platyphora similis*** (Figure 43), and ***Prorodon viridis*** (Figure 44). Additional species are listed in Table 2.

Figure 38. ***Frontonia***, a peatland-dwelling ciliate. **Upper:** Cell shape and nucleus. **Lower:** ***Frontonia vernalis*** cell with ***Chlorella*** symbionts and desmids (food items?) in the cell. Photos by Yuuji Tsukii, with permission.

Figure 39. ***Cyclidium***, a genus that often lives on bryophytes. Photo by Yuuji Tsukii, with permission.

Figure 40. ***Paramecium bursaria*** (left), a common ciliate that can inhabit bryophytes, showing its ***Chlorella*** symbionts. Photo by Yuuji Tsukii, with permission.

Figure 41. ***Scenedesmus quadricauda***; a species of ***Scenedesmus*** can be a partner in ***Paramecium bursaria***. Photo by C. Whittaker1000, through Creative Commons.

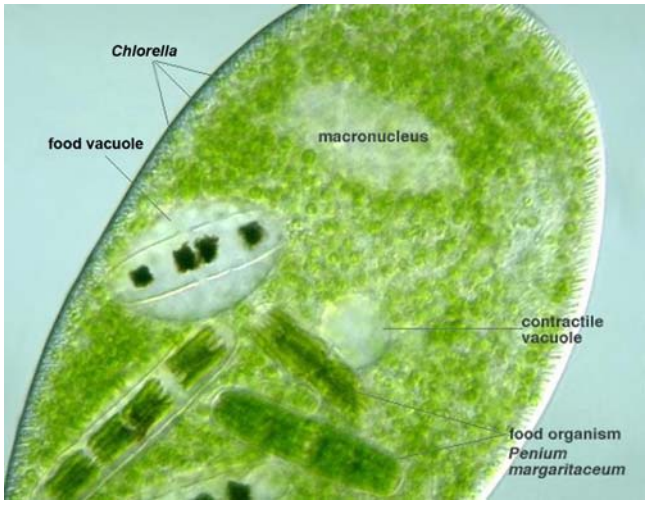


Figure 42. ***Frontonia vernalis***, a peatland-dwelling ciliate with ***Chlorella*** symbionts and desmids in the cell. Photo by Yuuji Tsukii, with permission.

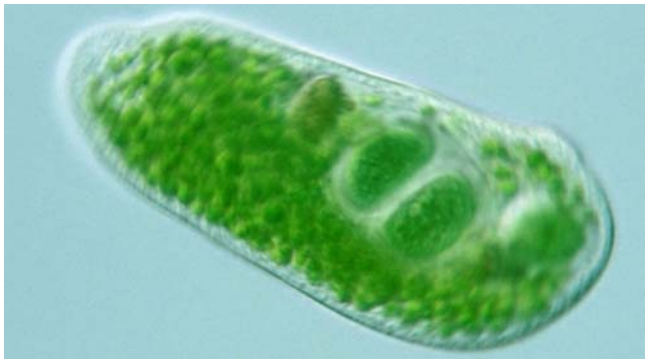


Figure 43. ***Platyophora similis***, a ciliate known from ***Sphagnum*** in Poland (Mieczan 2006). It appears to have both small algal symbionts and larger ingested algae or Cyanobacteria. Photo by Yuuji Tsukii, with permission.

One possible additional advantage to having symbionts, aside from the added energy availability, is that it permits these ciliates to live where the oxygen supply is low, deriving their oxygen from their symbionts (Lawton 1998). This strategy provides them the opportunity to avoid the more oxygen-dependent larger metazoans that might otherwise have them for dinner. In the words of Lawton, it provides "enemy-free space."

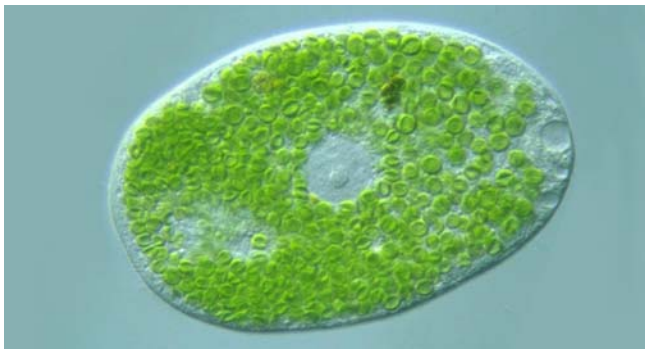


Figure 44. ***Prorodon viridis***, a ciliate that inhabits ***Sphagnum*** in peatlands of Poland (Mieczan 2006). It is packed with algal symbionts with a colorless nucleus in the center. Photo by Yuuji Tsukii, with permission.

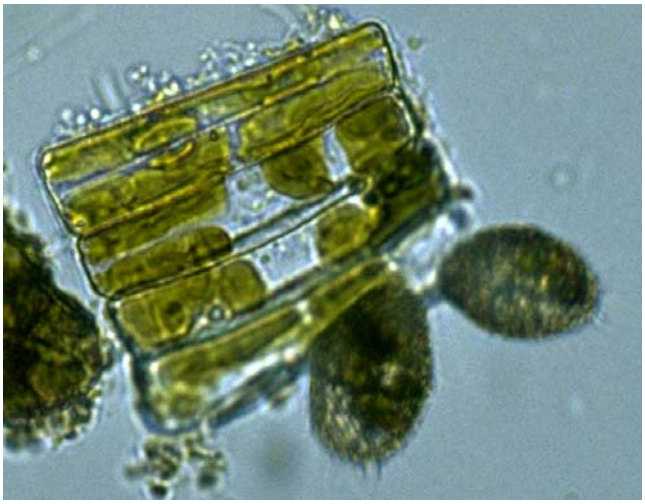
Coleps hirtus (Figure 46-Figure 47) is a facultative host to the ***Chlorella*** symbiont (Auer *et al*. 2004), but it grows faster when it is in the light and endowed with endosymbionts (Stabell *et al*. 2002). Even when it has endosymbionts, it will ingest organic matter, including smaller protozoa and algae (Figure 48-Figure 49; Auer *et al*. 2004). The alga maintains a coordinated growth rate with the host by its rate of leakage of products to the host.

Figure 45. ***Coleps hirtus*** test, showing spines, with diatom. Photo by Yuuji Tsukii, with permission.

Figure 46. ***Coleps hirtus***, a peatland inhabitant found by Mieczan (2006) in Poland. Cells have internal symbiotic algae. Photo by Yuuji Tsukii, with permission.

Figure 47. ***Coleps hirtus*** with internal symbiotic algae. Photo by Yuuji Tsukii, with permission.

Figure 48. ***Coleps*** ingesting the green alga ***Chlorogonium***. Photo by Yuuji Tsukii, with permission.



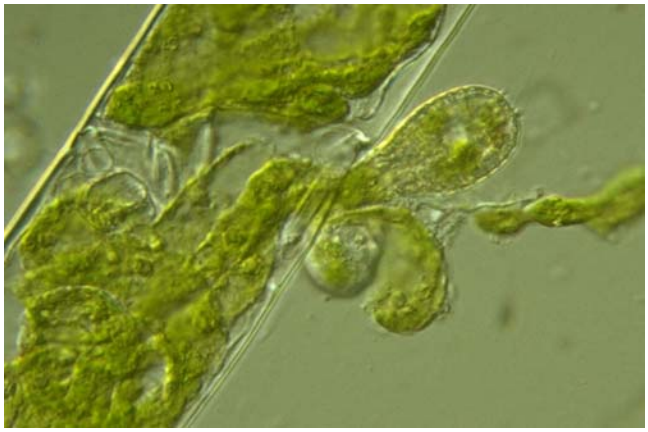


Figure 49. ***Coleps*** feeding on the diatom ***Diatoma***. Photos by Yuuji Tsukii, with permission.

Table 2. Species and genera of Zoomastigophora, flagellate Chlorophyta, Euglenophyta, Pyrrophyta, armored flagellates, Ciliophora, Heliozoa, Cryptophyta, and Ochrophyta I have located in the literature and from observations of protozoologists as those known from bryophytes. Those reported by Hingley are known from peatlands. *Indicates closely associated with ***Sphagnum***. Additional photographs are in Chapter 2-2 of this volume.

Zoomastigophora	
Distigma proteus	Hingley 1993
Flagellate Chlorophyta	
Carteria globosa	Hingley 1993
Carteria sphagnicola	Compére 1966
Chilomonas	Henebry & Cairns 1984
*Chlamydomonas acidophila**	Hingley 1993
*Chlamydomonas sphagnicola**	Hingley 1993
Gonium pectorale	Hingley 1993
Gonium sociale	Hingley 1993
Hyalogonium klebsii	Hingley 1993
Monas	Henebry & Cairns 1984
Monasiga	Henebry & Cairns 1984
Platydorina	Hingley 1993
Polytoma uvella	Hingley 1993
Spermatozopsis	Hingley 1993
Euglenophyta	
Astasia	Hingley 1993
Distigma	Hingley 1993
Euglena acus	Hingley 1993
Euglena deses	Hingley 1993
*Euglena mutabilis**	Hingley 1993
Euglena oxyuris	Hingley 1993
Euglena pisciformis	Hingley 1993
Euglena sanguinea	Hingley 1993
Euglena spirogyra	Hingley 1993
Euglena tripteris	Hingley 1993
Euglena viridis	Hingley 1993
Lepocinclis	Hingley 1993
Phacus longicaudatus	Hingley 1993
Trachelomonas aculeata	Hingley 1993
Trachelomonas bulla	Hingley 1993
Trachelomonas hispida	Hingley 1993
Pyrrophyta & Armored Flagellates	
Amphidinium	Hingley 1993
Ceratium hirundinella	Hingley 1993
*Cystodinium conchaeforme**	Hingley 1993
Dinococcales – epiphytes	Hingley 1993
Glenodinium	Hingley 1993
Gymnodinium caudatum	Hingley 1993
Gyrodinium	Hingley 1993
*Hemidinium ochraceum**	Hingley 1993
Katodinium stigmatica	Hingley 1993
Katodinium vorticella	Hingley 1993
Peridinium cinctum	Hingley 1993
Peridinium inconspicuum	Hingley 1993
Peridinium limbatum	Hingley 1993
Peridinium umbonatum	Hingley 1993
Peridinium volzii	Hingley 1993
Peridinium willei	Hingley 1993
Sphaerodinium	Hingley 1993
Woloszynskia	Hingley 1993
Ciliophora	
Amphileptus pleurosigma	Bourland pers. obs.
Askenasia	Mieczan 2006
Blepharisma lateritium	Hingley 1993
Blepharisma steini	Hingley 1993
Blepharisma musculus	Hingley 1993
*Blepharisma sphagni**	Hingley 1993
Bryometopus pseudochilodon	Hingley 1993
*Bryometopus sphagni**	Hingley 1993
Bryophyllum armatum	Hingley 1993
Bryophyllum loxophylliforme	Plewka 2016
Bryophyllum penardi	Hingley 1993
Bryophyllum tegularum	Plewka 2016
Bryophyllum vorax	Hingley 1993
Bursaria truncatella	Hingley 1993
Chaenea	Hingley 1993
Chilodonella bavariensis	Hingley 1993
Chilodonella cucullus	Hingley 1993
Chilodonella uncinata	Hingley 1993
Chilodontopsis depressa	Bourland pers. obs.
Chlamydonella	Mieczan 2006
Cinetochilum margaritaceum	Bourland pers. obs.
Climacostomum virens	Gilbert & Mitchell 2006
Climacostomum – zoochlorellae	Hingley 1993
Coleps	Hingley 1993
Colpidium	Hingley 1993
Colpoda steinii	Mieczan 2006
Cyclidium glaucoma	Hingley 1993
Cyclidium sphagnetorum – zoochlorellae	Hingley 1993
Cyclogramma protectissima	Hingley 1993
Cyrtolophosis mucicola	Hingley 1993
Didinium nasutum	Bourland pers. obs.

Dileptus tenuis	Hingley 1993
Drepanomonas dentata	Hingley 1993
Drepanomonas exigua	Hingley 1993
*Drepanomonas sphagni**	Hingley 1993
Enchelyodon ovum	Hingley 1993
*Enchelyodon sphagni**	Hingley 1993
Enchelyomorpha vermicularis	Mieczan 2006
Euplotes patella	Hingley 1993
Frontonia vernalis	Groliére 1977
Gastronauta (Ciliophora)	Mieczan 2006
Gonostomum affine	Hingley 1993
Halteria grandinella	Hingley 1993
Hemicyclostyla sphagni	Hingley 1993
*Histriculus sphagni**	Hingley 1993
Holophrya – zoochlorellae	Hingley 1993
Keronopsis monilata	Hingley 1993
Keronopsis muscorum	Hingley 1993
Keronopsis wetzeli	Hingley 1993
Lacrymaria olor	Hingley 1993
Lembadion	Hingley 1993
Leptopharynx costatus – zoochlorellae	Hingley 1993
Litonotus fasciola	Hingley 1993
*Malacophrys sphagni**	Hingley 1993
Microthorax spiniger	Hingley 1993
Monodinium	Bourland pers. obs.
Ophrydium versatile – zoochlorellae	Hingley 1993
Opisthotricha muscorum	Hingley 1993
Opisthotricha parallela	Hingley 1993
Opisthotricha sphagni	Hingley 1993
Oxytricha fallax	Bourland pers. obs.
Oxytricha ludibunda	Hingley 1993
Oxytricha minor	Hingley 1993
Oxytricha variabilis	Hingley 1993
Parahistriculus minimus	Hingley 1993
Paraholosticha nana	Hingley 1993
Paramecium aurelia	Hingley 1993
Paramecium bursaria – zoochlorellae	Hingley 1993
Paramecium putrinum	Mieczan 2006
Pardileptus conicus	Hingley 1993
Perispira ovum	Hingley 1993
Phacodinium metchnikoffi	Plewka 2016
Platyophora similis	Groliére 1977
Platyophora viridis – zoochlorellae	Hingley 1993
Podophyra	Oyadomari pers. obs.
Prorodon cinereus – zoochlorellae	Hingley 1993
Prorodon gracilis	Hingley 1993
Prorodon pyriforme	Hingley 1993
Prorodon viridis	Groliére 1977
Pseudoblepharisma crassum	Hingley 1993
Psilotrocha teres	Hingley 1993
Pyxidium invaginatum	Van der Land 1964
Pyxidium tardigradum	Morgan 1976
Pyxidium urceolatum	Hingley 1993
Rhabdostylum muscorum	Van der Land 1964
Sathrophilus havassei	Hingley 1993
Sathrophilus vernalis	Hingley 1993
Spathidium amphoriforme	Hingley 1993
Spathidium lionotiforme	Hingley 1993
Spathidium muscicola	Hingley 1993
Spirostomum ambiguum	Hingley 1993
Spirostomum minus	Hingley 1993
Steinia sphagnicola	assumed
Stentor coeruleus	Hingley 1993
Stentor multiformis	Mieczan 2006
Stichtricha aculeata	Hingley 1993
Strombidium viride	Mieczan 2006
Stylonichia	Hingley 1993
Thylacidium truncatum – zoochlorellae	Hingley 1993
Trachelius	Hingley 1993
*Trachelophyllum sphagnetorum**	Hingley 1993
Trichopelma sphagnetorum	Hingley 1993
Trochilia minuta (Ciliophora)	Mieczan 2006
Uroleptus longicaudatus	Hingley 1993
Urostyla caudata	Hingley 1993
Urotricha agilis – zoochlorellae	Hingley 1993
Urotricha ovata	Hingley 1993
Urozona buetschlii	Hingley 1993
Vaginicola	Hingley 1993
Vasciola picta	Hingley 1993
Vorticella muralis – zoochlorellae	Hingley 1993
Colorless Flagellates	
Ancyromonas contorta	Hingley 1993
Astasia longa	Hingley 1993
Bodo parvus	Hingley 1993
Bodo saltans	Hingley 1993
Distigma proteus	Hingley 1993
Dinema sulcatum	Hingley 1993
Dinema entosiphon	Hingley 1993
Dinema mastigamoeba	Hingley 1993
Dinema mastigella	Hingley 1993
Notoselenus apocamptus	Hingley 1993
Oikomonas termo	Hingley 1993
Peranema trichophorum	Hingley 1993
Pleuromonas jaculans	Hingley 1993
Heliozoa	
Acanthocystis aculeata	Hingley 1993
Acanthocystis erinaceus	Hingley 1993
Acanthocystis pectinata	Hingley 1993
Acanthocystis penardi – with zoochlorellae	Hingley 1993
Acanthocystis turfaceae – with zoochlorellae	Hingley 1993
Actinophrys sol	Hingley 1993
Actinosphaerium eichhorni	Hingley 1993
Chlamydaster sterni	Hingley 1993
Clathurina einkowski	Hingley 1993
Clathurina elegans	Hingley 1993
Heterophrys fockei	Hingley 1993
Heterophrys myriopoda	Hingley 1993
Lithocolla globosa	Hingley 1993
Piniaciophora stammeri	Hingley 1993
Pompholyxophrys exigua	Hingley 1993
Pompholyxophrys ovuligera	Hingley 1993
Raphidocystis glutinosa	Hingley 1993
Raphidocystis tubifera	Hingley 1993
Raphidophrys ambigua	Hingley 1993
Raphidophrys intermedia	Hingley 1993
Cryptophyta	
Cryptomonas	Hingley 1993
Ochrophyta	
Gonyostomum semen	Hingley 1993
Myxochloris sphagnicola (monotypic)	Hingley 1993
Ochromonas	Hingley 1993
Perone dimorpha (monotypic)	Hingley 1993

In Addition to the taxa listed here, Kreutz and Foissner (2006) have listed many additional taxa from ***Sphagnum*** ponds in Germany. Many of these are figured with wonderful color images, but pool species are not distinguished from those actually on mosses in or adjoining pools.

Summary

There is a rich diversity of protozoans among the bryophytes, much of which has never been explored. **Ciliates** and **testate amoebae** (rhizopods with houses) predominate in both peatlands and forests, but some flagellates and other minor groups occur as well. Bryophytes are especially suitable habitats for these organisms that can **encyst** when dry. And both depend largely on wind for dispersal, with protozoa often dispersing with fragments of their hosts.

Aufwuchs, or **periphyton**, are those organisms that live on aquatic substrata, including bryophytes, without being parasites. **Epiphyte** is a broader term that includes terrestrial associates as well. Identification is difficult and often requires culturing. But more than 2000 organisms per cm^3 make the effort worthwhile.

Rainfall can dislocate the protozoa, especially those with heavy testae, and modify their production. Not surprisingly, numbers are highly correlated with moisture.

Some taxa, known as **bryobionts**, occur only on mosses (*e.g.* ***Cyclidium sphagnetorum***). The naked taxa are mostly **bacterivores**. In ***Sphagnum*** the numbers of protozoa are so high (up to 220,000 per gram) that they are important in the **microbial loop**.

In addition to bryobionts, **bryophiles** are usually found among bryophytes, **bryoxenes** live elsewhere but regularly spend part of the life cycle among bryophytes, and **occasionals** are typical elsewhere, but occasionally are found among bryophytes.

The **Zoomastigophora** (flagellates) include ***Chlamydomonas***, ***Euglena***, and ***Phacus*** among the bryophyte inhabitants. These organisms can swim around in the hooded tips of ***Sphagnum*** leaves and may inhabit the hyaline cells. The low *p*H may contribute to the formation of the **palmelloid** stage in their life cycle, protecting them from rotifer predation. Among the **Ciliophora** (ciliates), ***Stentor*** and ***Vorticella*** may attach themselves to bryophyte leaves. Other members swim about in the surface water film. Some of these have chlorophyll-bearing **symbionts** and thus must live near the surface; the symbionts leak maltose and provide oxygen while gaining CO_2.

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Edward Mitchell provided me with a large number of papers and photographs and William Bourland provided me with wonderful photographs of taxa on my special needs list. Yuuji Tsukii and Jason Oyadomari permitted me to use any of their numerous images. Edward Mitchell and Paul Davison were invaluable in helping me with areas where I was often not personally familiar with the subject.

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PROTOZOA: CILIOPHORA AND HELIOZOA DIVERSITY

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Other Ciliophora Known from Bryophytes

Figure 1. ***Amphileptus pleurosigma***, a free-swimming, predatory ciliate. Photo by William Bourland, with permission.

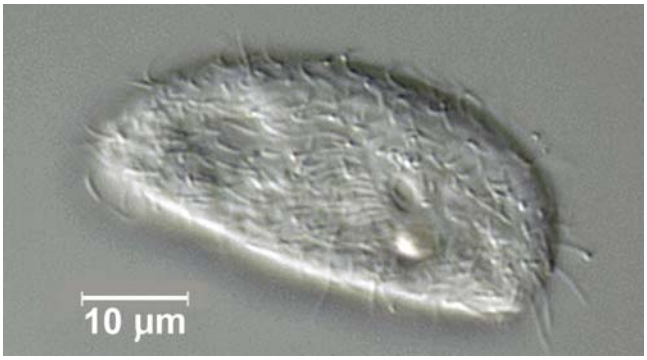

Figure 2. ***Chilodontopsis depressa***, an algivorous ciliate (Risse-Buhl & Küsel 2008). Photo by William Bourland, with permission.

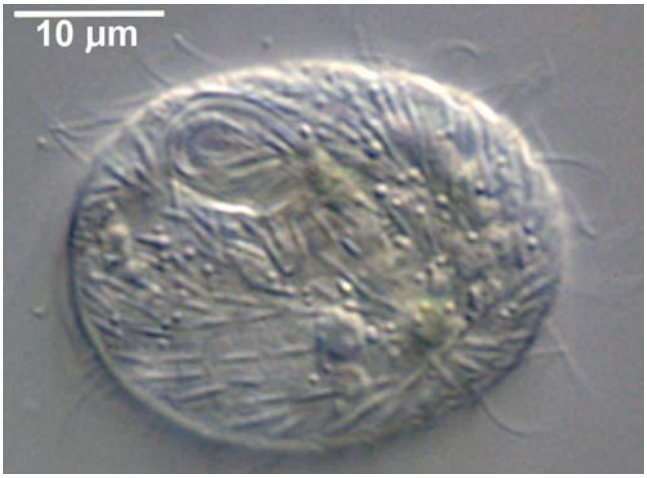

Figure 3. ***Cinetochilum margaritaceum***, a bryophyte-inhabiting ciliate that Mieczan (2007) found in peatland ponds of Poland with *p*H of 5.0. Photo by William Bourland, with permission.

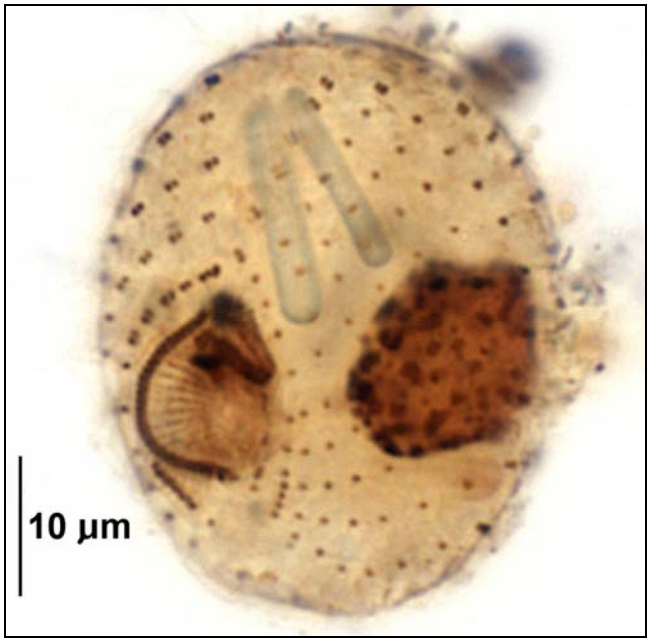

Figure 4. ***Cinetochilum margaritaceum*** stained to show organelles. Photos by William Bourland, with permission.

Figure 5. ***Didinium nasutum***, a bryophyte-dwelling ciliate that feeds on ***Paramecium***. This species is capable of encysting to avoid unfavorable conditions. Photo by William Bourland, with permission.

Figure 6. ***Oxytricha fallax***, a ciliate, has a complex grouping of cilia that are used for sweeping food into the gullet. It lives among bryophytes, as well as other habitats. Lower organism has been stained. Photos by William Bourland, with permission.

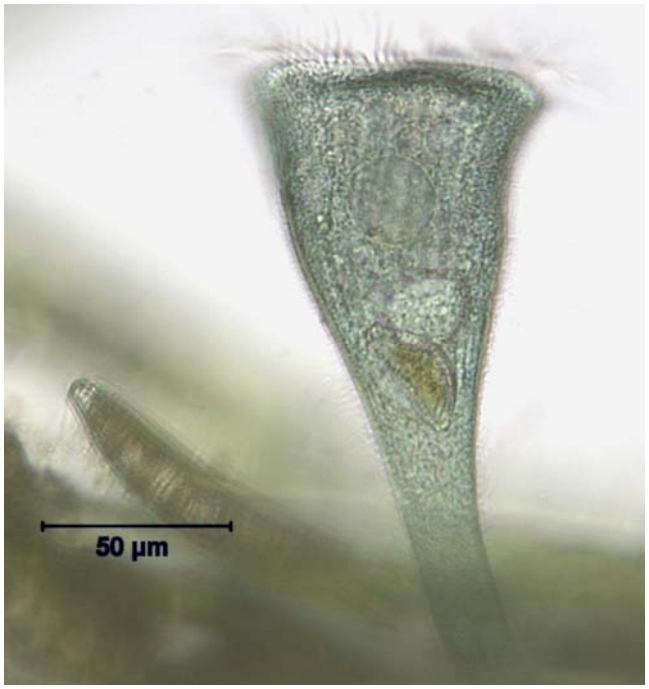

Figure 7. ***Stentor multiformis***, a ciliate that occurs in peatlands (Mieczan 2006) and can attach to moss leaves. Photo by William Bourland, with permission.

Figure 8. ***Stentor*** showing green algal symbiont. Photo by Wim van Egmond, with permission.

Figure 9. ***Colpoda steinii***, a constant member of ***Sphagnum*** communities in two Polish peatlands (Mieczan 2006). Photo by Yuuji Tsukii, with permission.

Figure 10. Two ***Holophyra*** species, ciliates that can inhabit ***Sphagnum*** in peatlands (Mieczan 2006). Photos by Yuuji Tsukii, with permission.

Figure 11. ***Monodinium***, a ciliate that sometimes occurs on ***Sphagnum*** in peatlands (Mieczan 2006), showing ring of cilia. Photo by Yuuji Tsukii, with permission.

Figure 12. ***Monodinium*** dividing. Photo by Yuuji Tsukii.

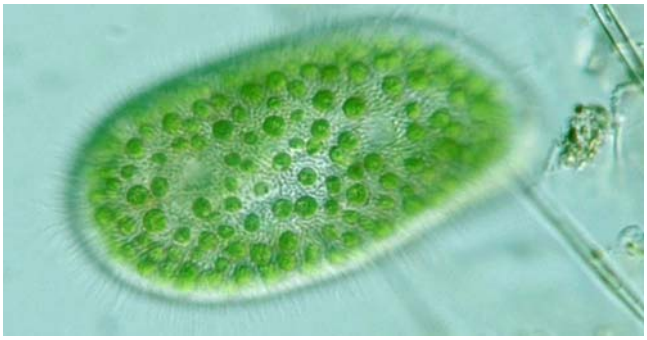

Figure 13. ***Paramecium bursaria***, a common species that can occur on ***Sphagnum*** in peatlands in Poland (Mieczan 2006). This one has algal symbionts. Photo by Yuuji Tsukii, with permission.

Figure 14. ***Spathidium muscicola***, a ciliate that can live among mosses. Photo by Yuuji Tsukii, with permission.

Figure 15. ***Steinia sphagnicola***. Normal cell. Photo by Yuuji Tsukii, with permission.

Figure 16. ***Steinia sphagnicola*** cell dividing. Photo by Yuuji Tsukii, with permission.

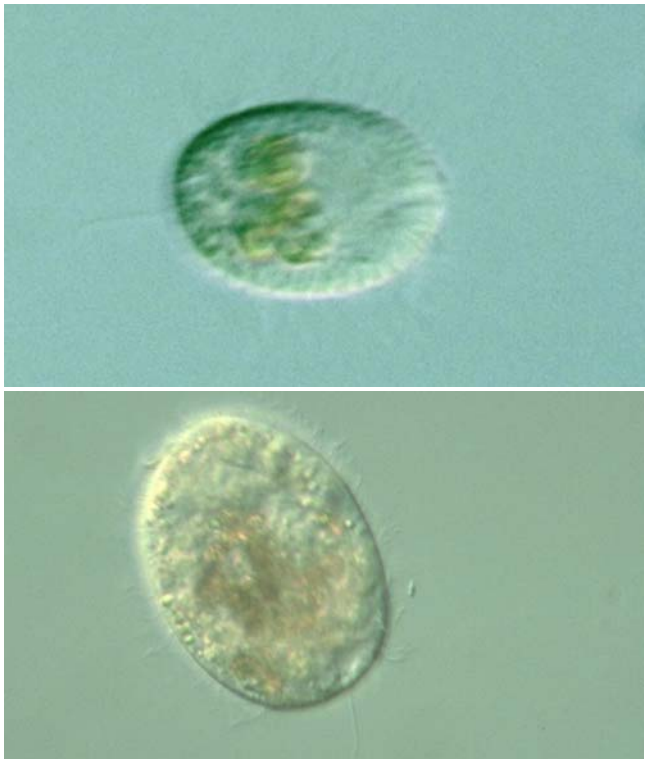

Figure 17. **Upper:** ***Urotricha farcta***. **Lower:** ***Urotricha platystoma***. This genus occurs on mosses in Polish peatlands (Mieczan 2006). Photo by Yuuji Tsukii, with permission.

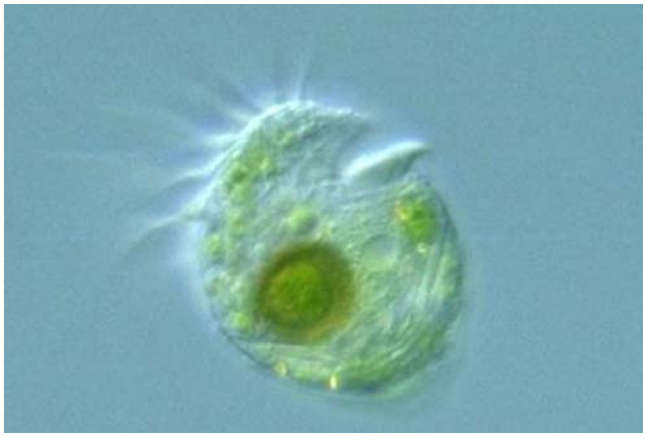

Figure 18. ***Strombidium viride***, a ciliate that occurs occasionally on mosses in peatlands in Poland (Mieczan 2006). Photo by Yuuji Tsukii, with permission.

Michael Plewka kindly sent me the names of several **Ciliophora** that commonly occur on bryophytes. These include ***Phacodinium metchnikoffi*** (Figure 19-Figure 20), ***Bryophyllum tegularum*** and ***B. loxophylliforme*** (Figure 21).

Figure 19. ***Phacodinium metchnikoffi***, a common species on wet moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 20. ***Phacodinium metchnikoffi*** showing ribs. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 21. ***Bryophyllum loxophylliforme***, a common species on wet moss. ***Bryophyllum tegularum*** likewise is common there. Photo by Michael Plewka <www.plingfatory.de>, with permission.

Heliozoa

The heliozoans look like a sunburst with their sticky, wirelike pseudopods. About 20 species live among ***Sphagnum*** in pools with *p*H ranging 5-5.6 (Hingley 1993). The sticky pseudopods, known as **axopods**, are used to ensnare food such as algae and smaller protozoa, and to protect the organisms. They also facilitate a slow movement, since these organisms lack cilia or flagella. The beautiful and delicate moss dwellers include *Actinophrys sol* (Figure 23) and ***Actinosphaerium eichhorni*** (Figure 24-Figure 25).

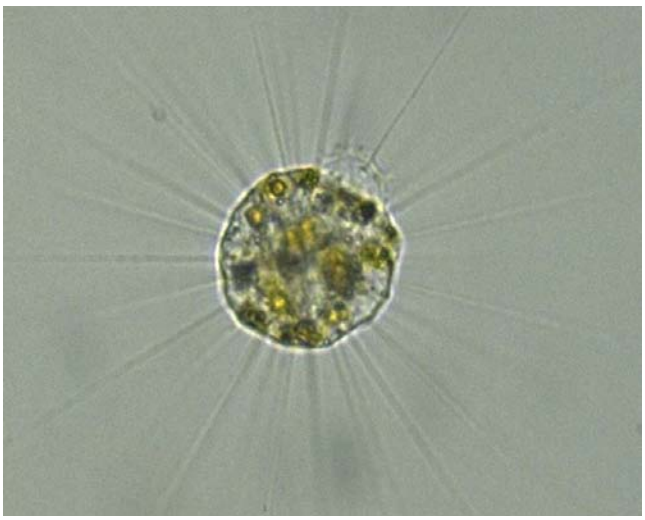

Figure 22. ***Actinophrys sol***, a moss dweller, showing radiating pseudopodia. Photo by Yuuji Tsukii., with permission

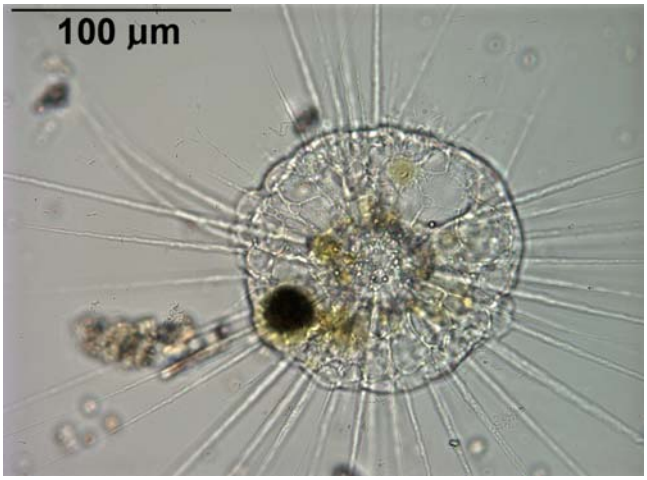

Figure 23. ***Actinophrys sol*** showing radiating pseudopodia. Photo by William Bourland, with permission.

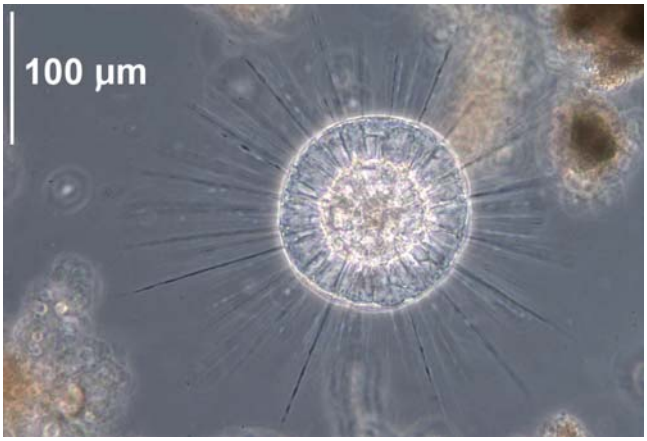

Figure 24. ***Actinosphaerium eichhorni***. Photo by William Bourland, with permission.

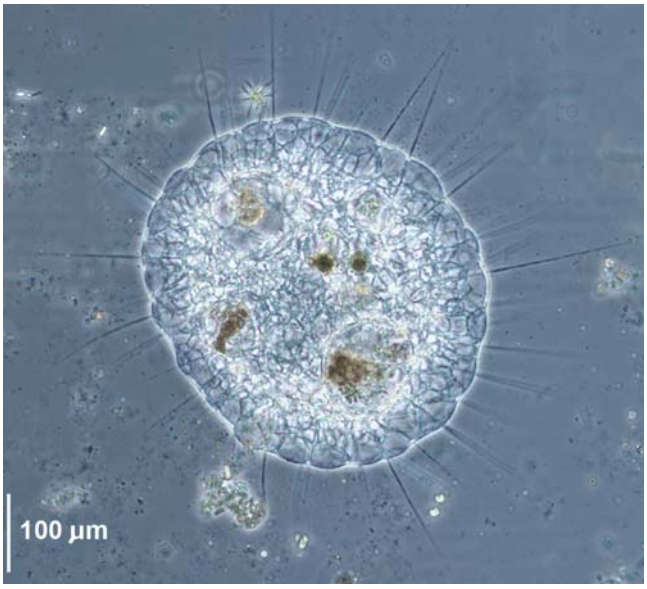

Figure 25. ***Actinosphaerium eichhorni***. Photo by William Bourland, with permission.

Summary

Although they are more difficult to detect, the **Ciliophora** are quite common among bryophytes. They are best detected by culturing, and then the many species seen in this chapter become active. **Heliozoa** are not common among bryophytes, and only the few species shown here are familiar ones in a bryophyte habitat.

Acknowledgments

This chapter would not have existed without my new, but never seen, friends, William Bourland and Yuuji Tsukii. William Bourland provided me with a set of his pictures of bryophyte inhabitants. Yuuji Tsukii gave me unlimited permission to use his many, many images on the Protist Information Server website. Michael Lüth reported his observations on Protozoa on bryophytes.

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CHAPTER 2-3
PROTOZOA: RHIZOPOD DIVERSITY

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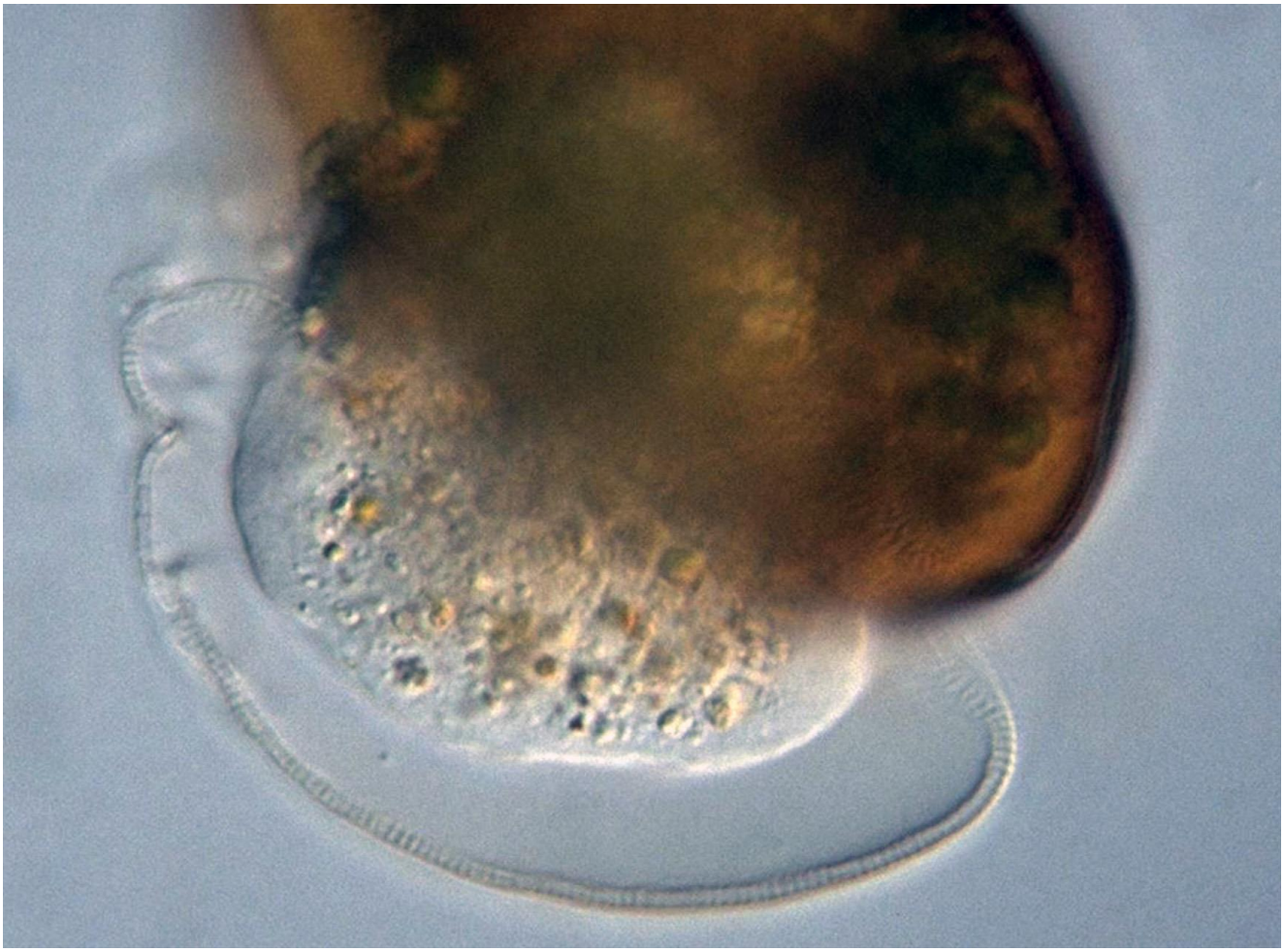

Figure 1. ***Arcella vulgaris***, a testate amoeba (**Rhizopoda**) that is dividing. Photo by Yuuji Tsukii, with permission.

Rhizopoda (Amoebas)

The **Rhizopoda** are a phylum of protozoa with a name that literally means "root feet" (Figure 1). They include both **naked** and **testate** amoebae. **Testate amoebae** are encased in "houses" of their own making (Figure 2) by way of organic secretions (Hoogenraad & Groot 1953; Wilmshurst 1998). Imagine a tiny pile of sand grains moving across a liverwort leaf.

Despite being only one-celled, testate species construct houses made of various materials such as small sand grains cemented by their own secretions, and even diatoms (Figure 4) may be included among the sand grains. Some even manufacture silica plates that they meticulously arrange into housing. Others may include such items as mineral particles, pollen grains, and the recycled plates and remains of their microscopic food organisms. Such testate rhizopods include ***Difflugia*** (Figure 5-Figure 6), ***Arcella vulgaris*** (Figure 8-Figure 9), and ***Centropyxis*** (Figure 11) among the most common moss-dwellers (Bartos 1949a).

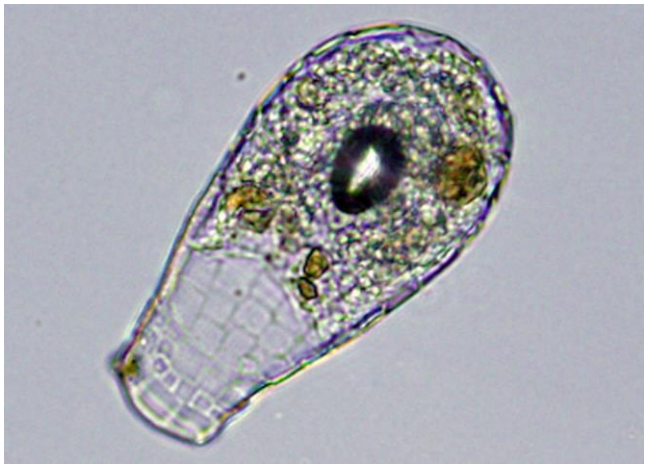

Figure 2. This testate amoeba is among the many testate amoebae that live among the bryophytes. This one dwelt on the moss ***Sanionia uncinata*** (Figure 3) on the Barton Peninsula of King George Island, Antarctica. Photo by Takeshi Ueno, with permission.

Figure 3. ***Sanionia uncinata***, home to testate amoebae in the Antarctic. Photo by Michael Lüth, with permission.

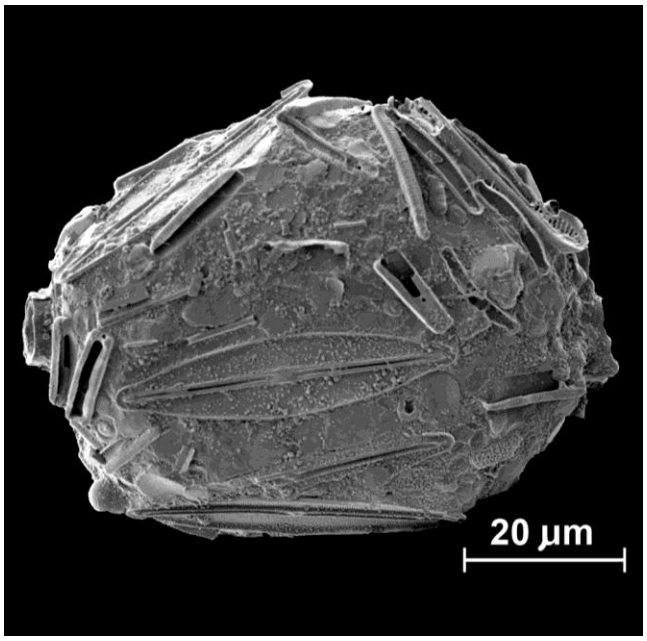

Figure 4. SEM photo of ***Amphitrema wrightianum*** showing diatoms used in making the test. Photo by Edward Mitchell, with permission.

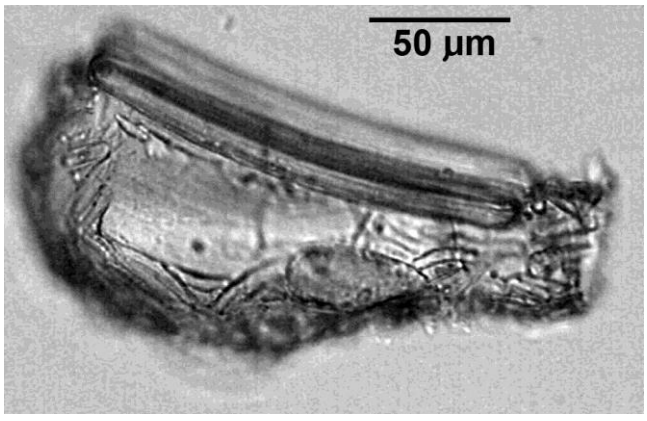

Figure 5. ***Difflugia bacillifera*** test with incorporated diatoms. Photo by Edward Mitchell, with permission.

Figure 6. ***Difflugia bacillifera*** test with incorporated diatoms. Photo by Yuuji Tsukii, with permission.

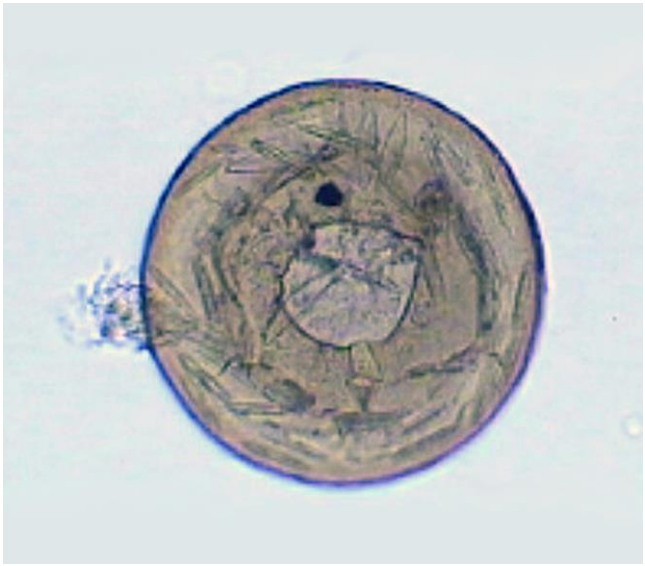

Figure 7. Empty shell of ***Arcella vulgaris***, a testate amoeba that forms donut shapes on moss leaves. Photo courtesy of Javier Martínez Abaigar, with permission.

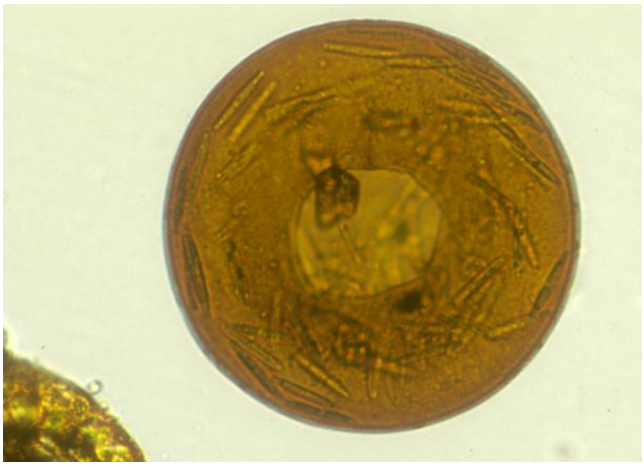

Figure 8. ***Arcella vulgaris***, a testate amoeba that forms donut shapes on moss leaves. Photo courtesy of Javier Martínez Abaigar, with permission.

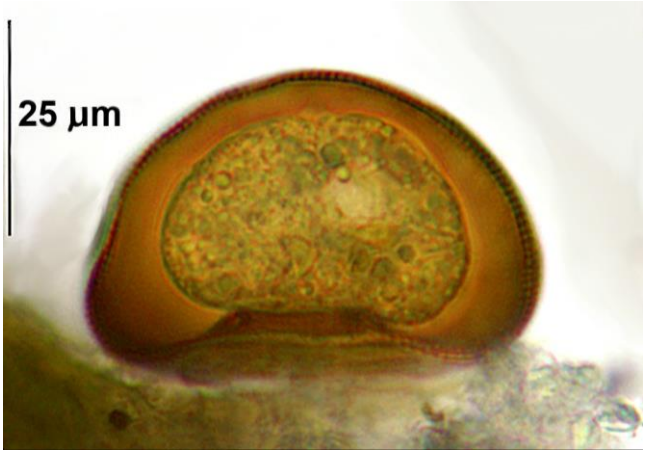

Figure 9. ***Arcella vulgaris*** showing protoplast inside test. Photo by William Bourland, with permission.

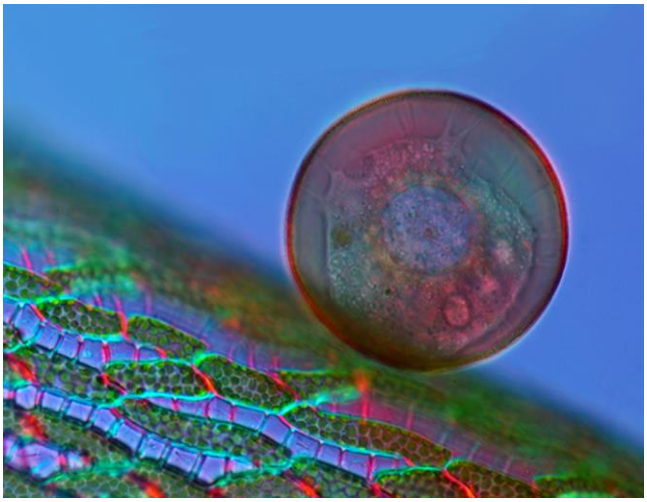

Figure 10. ***Arcella*** sp. on a ***Sphagnum*** leaf. Photo by Marek Miś at <http://www.mismicrophoto.com/>, with permission.

Figure 11. ***Centropyxis aculeata***, a testate amoeba with sand grains in its case. Photo courtesy of Javier Martínez Abaigar.

Although naked amoebae are sometimes numerous on submerged ***Sphagnum*** (Figure 13) plants, the testate amoebae seem to be particularly common among the bryophytes (Richters 1908 a, b, c, d, e; Heinis 1908, 1910, 1911, 1914, 1928; Penard 1909; Roberts 1913; van Oye 1936; Bartos 1938a, b, c, 1939, 1940, 1946a, b, 1947, 1949a, b, 1950, 1951, 1963a, b, c; Jung 1936 a, b; Jung & Spatz 1938; Hoogenraad & Groot 1940, 1948, 1951, 1952a, b; Fantham & Porter 1945; Bonnet 1961, 1974, 1978; del Gracia 1964, 1965a, b, c, 1966, 1978; Chardez 1965, 1990; Golemansky 1967; Chiba & Kato 1969; Coûteaux 1969; Decloître 1970, 1974; Corbet 1973; Chardez 1976, 1979; Coûteaux & Chardez 1981; Richardson 1981; Beyens & Chardez 1982; Tolonen *et al*. 1985; Schönborn & Peschke 1990; Charman & Warner 1992; Balik 1996; Mitchell *et al*. 2004, 2008; Mieczan 2007). In one Swedish bog, 40 species of testate amoebae were found (Mitchell *et al*. 2000). However, it is interesting that in two Polish peatlands, Mieczan (2006) found only six taxa, compared to 24 ciliate taxa.

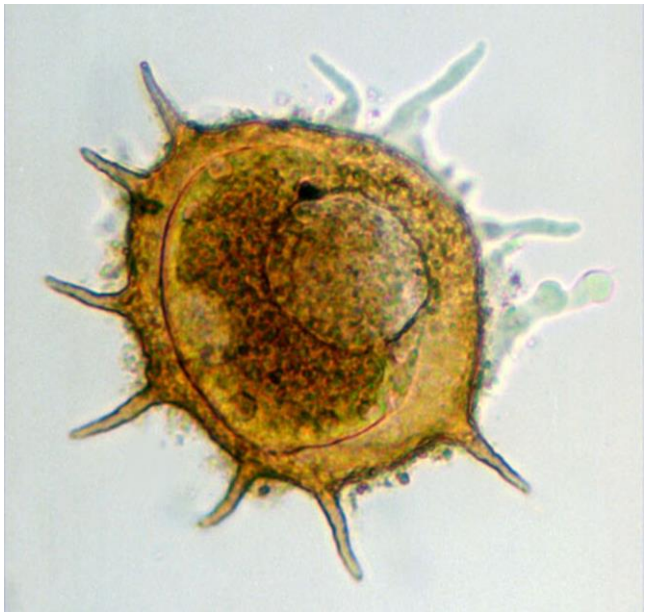

Figure 12. Live ***Centropyxis aculeata*** showing natural colors. Photo by Ralf Meisterfeld, with permission.

Figure 13. Peatland with ***Sphagnum cuspidatum***, an important submersed species that serves as home for many protozoans. Photo by Michael Lüth, with permission.

Species Diversity

The diversity of testate amoebae among mosses is quite remarkable. Those dwelling in peatlands are so species-rich and numerous that I have devoted an entire subchapter to them. But terrestrial bryophytes have rhizopods as well.

Török (1993) examined six species of terrestrial mosses in Hungary to compare their rhizopod fauna species diversity. He found 46 testate species, six of which were new for Hungary. The dominant taxa are reviewed in Table 1. The Hungarian diversity exceeded that reported for Arctic mosses (Beyens *et al*. 1986b). Török found ***Plagiopyxis labiata*** on most of the mosses in the study as well as finding them on ***Sphagnum***. Some differences in protozoan species composition seemed evident among moss species. For example, ***Phryganella acropodia***, a soil species, had its highest moss occurrence in ***Brachythecium velutinum*** (Figure 14). ***Trinema penardi***, a common ***Sphagnum*** inhabitant, was a characteristic species to be found in ***Cirriphyllum tommasinii*** (Figure 15). The rhizopod genera with the most species among these six mosses were ***Centropyxis*** (Figure 11-Figure 12) and ***Euglypha*** (Figure 18). The six mosses are listed with their diversity and numbers in Table 2.

Table 1. Eudominant (X) and dominant (x) rhizopods on six bryophyte species in Hungary (Török 1993).

	Plagiomnium undulatum	***Plagiothecium platyphyllum***	***Leptodictyum riparium***	***Cirriphyllum tenuinerve***	***Brachythecium velutinum***	***Atrichum undulatum***
Tracheleuglypha dentata	X	X				
Trinema enchelys	X	X	X			X
Difflugia lucida	X				x	
Corythion dubium		X				
Euglypha laevis			X		x	
Trinema lineare			X			x
Plagiopyxis declivis	x			X		x
Microcorycia flava		x	x	X		
Euglypha rotunda			x	x	X	
Trinema penardi				x		
Trinema complanatum						X
Difflugiella oviformis						x
Centropyxis aerophila var. *sphagnicola*						x

Figure 14. ***Brachythecium velutinum***, the moss where ***Phryganella acropodia*** is most common in Hungary. Photo by Michael Lüth, with permission.

Table 2. Total Shannon diversity and species numbers in each of the collections of mosses from Hungary (Török 1993).

Moss Species	**Diversity**	**# Spp**	**# Indivs**
Plagiomnium undulatum	4.36	34	216
Plagiothecium platyphyllum	3.65	26	471
Amblystegium riparium	2.60	14	375
Cirriphyllum tenuinerve	2.98	21	485
Brachythecium velutinum	3.52	27	844
Atrichum undulatum	2.80	14	285

Figure 15. ***Cirriphyllum tommasinii***, a moss where ***Trinema penardi*** is a characteristic species in Hungary. Photo by Michael Lüth, with permission.

In the southeastern Alps in Italy 25 species occurred on the forest moss ***Hylocomium splendens*** (Figure 16) in the altitudinal range from 1000-2200 m asl (Mitchell *et al*. 2004). The most frequent taxa on ***H. splendens*** included ***Assulina muscorum*** (Figure 17), ***Centropyxis aerophila*** (Figure 18), ***Corythion dubium*** (Figure 19), ***Euglypha ciliata*** (Figure 20), ***Euglypha laevis***, ***Nebela tincta*** (Figure 21), ***Phryganella acropodia***, and ***Trinema enchelys*** (Figure 22), all with a frequency greater than 10 among 21 samples. Densities per gram of a single species were as high as 12,666 (***Corythion dubium***, Figure 19). It is interesting that every one of these species is also among the common peatland taxa elsewhere (Table 3); they are all cosmopolitan, a phenomenon suggested by Vincke *et al*. (2004) and discussed in a later subchapter. ***Nebela collaris*** (*sensu lato*) is not only common on the leaf surfaces of

Sphagnum, but can occur within the hyaline (colorless) cells as well (Gilbert *et al*. 2003).

Figure 16. ***Hylocomium splendens***, a host for many protozoa. Photo by Michael Lüth, with permission.

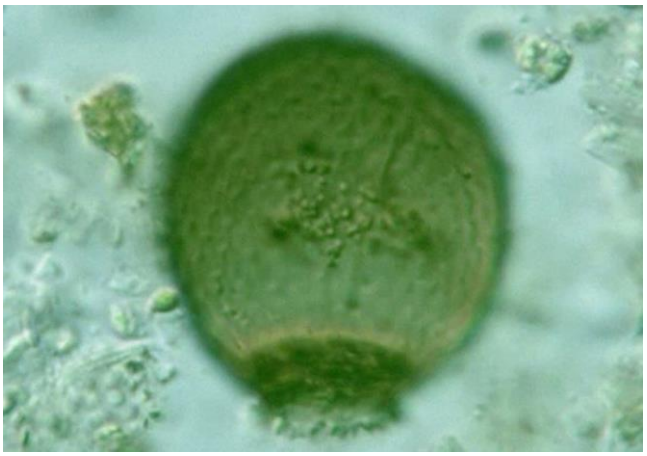

Figure 17. ***Assulina muscorum*** with pseudopodia showing. Photo by Yuuji Tsukii, with permission.

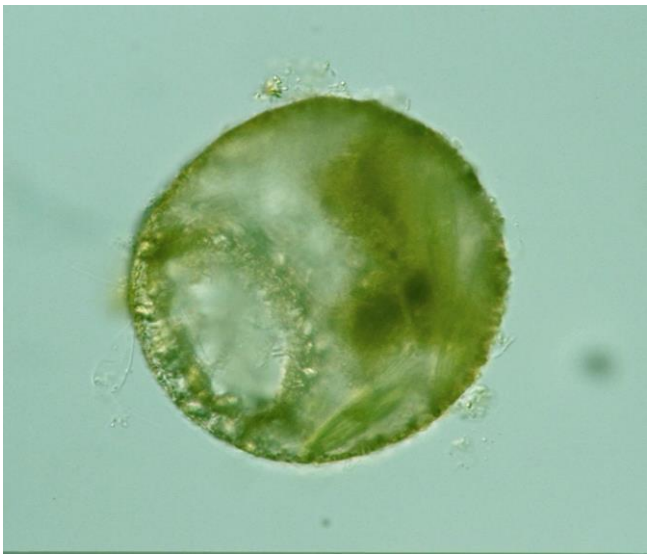

Figure 18. ***Centropyxis aerophila*** test. Photo by Yuuji Tsukii, with permission.

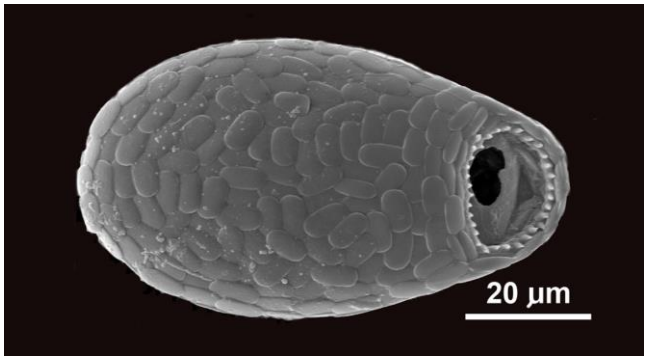

Figure 19. Test of ***Corythion dubium***. Photo by Edward Mitchell, with permission.

Figure 20. ***Euglypha ciliata*** showing cell contents. Photo by Yuuji Tsukii, with permission.

Figure 21. ***Nebela tincta*** showing ingested diatom. Photo by Yuuji Tsukii, with permission.

Table 3. Comparison of similarities in common testate amoebae communities occurring in several locations around the Northern Hemisphere. Note that the list for Bulgaria includes only the most common; others indicate presence. Photos of most follow the table.

	Jura Mtns Switzerland Mitchell & Gilbert 2004	**S Cen Alaska** Payne *et al.* 2006	**Sweden**	**Finland**	**Netherlands**	**Britain**	**Bulgaria** Davidova 2008	**Eur & NA** Martini *et al.* 2006
			Mitchell *et al.* 2000					
Amphitrema (*Archerella*) *flavum*	x	x	x	x	x	x	x	
Amphitrema wrightianum		x						
Arcella arenaria	x	x	x	x		x		x
Assulina muscorum	x	x	x	x	x	x		x
Assulina seminulum	x	x	x	x	x	x		x
Bullinularia indica	x	x	x	x	x	x		x
Centropyxis aculeata		x						
Centropyxis aerophila	x						x	
Corythion dubium	x	x	x	x	x	x	x	x
Cryptodifflugia ovaliformis	x							
Difflugia leidyi			x	x	x	x		x
Euglypha ciliata	x		x	x		x		x
Euglypha compressa	x		x	x	x	x		x
Euglypha laevis			x	x	x	x		x
Euglypha rotunda	x	x					x	x
Euglypha strigosa	x		x	x	x	x		x
Heleopera petricola		x						x
Heleopera rosea	x		x					x
Heleopera sphagni	x	x	x	x	x	x		x
Heleopera sylvatica			x	x	x	x		
Hyalosphenia elegans	x	x	x	x	x	x		x
Hyalosphenia papilio	x	x	x	x	x			x
Nebela flabellulum						x		
Nebela (*Physochila*) *griseola*			x	x	x	x		x
Nebela militaris	x	x	x	x	x	x		x
Nebela tincta	x	x	x	x	x	x		x
Phryganella acropodia	x		x	x	x	x		x
Phryganella hemisphaerica							x	
Placocista spinosa		x						
Pyxidium tardigradum	x							
Trigonopyxis arcula	x	x		x	x	x		x
Trinema enchelys	x						x	
Trinema lineare	x						x	
Trinema sp.			x					

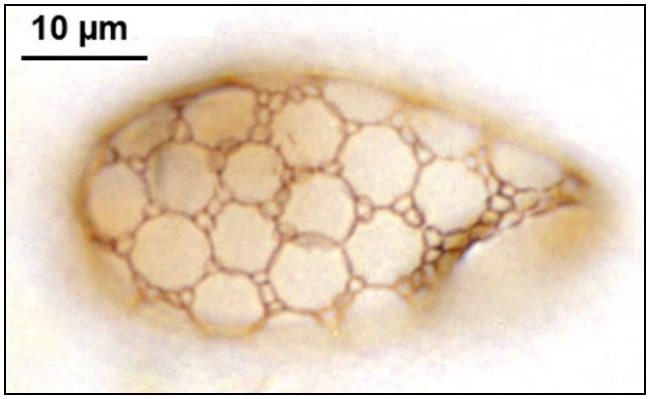

Figure 22. Test of ***Trinema enchelys***. Photo by William Bourland, with permission.

Mieczan (2006) found that the testate species ***Difflugia oblonga*** (Figure 23), ***Euglypha*** sp. (Figure 24), and ***Nebela longeniformis*** comprised more than 25% of the total numbers in the two Polish peatlands he studied.

In contrast to studies on moist peatland bryophytes (*e.g.* Table 3), Nguyen *et al*. (2004) found only 9 rhizopod species in 30 samples of the xerophytic moss ***Syntrichia ruralis*** (Figure 25). Mitchell *et al*. (2004) attributed this depauperate number to the dry conditions and restriction of samples to the photosynthetic tips of the moss.

Figure 23. ***Difflugia oblonga***, a testate amoeba that was common in the Polish peatlands studied by Mieczan (2006). Photo by Yuuji Tsukii, with permission.

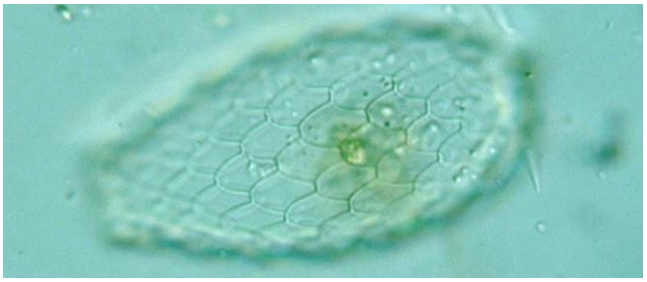

Figure 24. Test of ***Euglypha bryophila***, a species whose name means "moss loving." Photo by Yuuji Tsukii, with permission.

Other studies on species richness generally include mosses as a group, rather than examining individual species, with rhizopod richness ranging 9-53 species (Beyens *et al*. 1986a, b; 1990; Beyens & Chardez 1994; Todorov & Golemansky 1996; Van Kerckvoorde *et al*. 2000). Additional bryophyte inhabitants from around the world are shown in Figure 26 - Figure 59. A complete list of bryophyte-inhabiting rhizopods is in Table 4.

Figure 25. ***Syntrichia ruralis***, a dry habitat moss that frequently dries out and goes dormant. It is part of the cryptogamic crust, among other habitats. Photo by Michael Lüth, with permission.

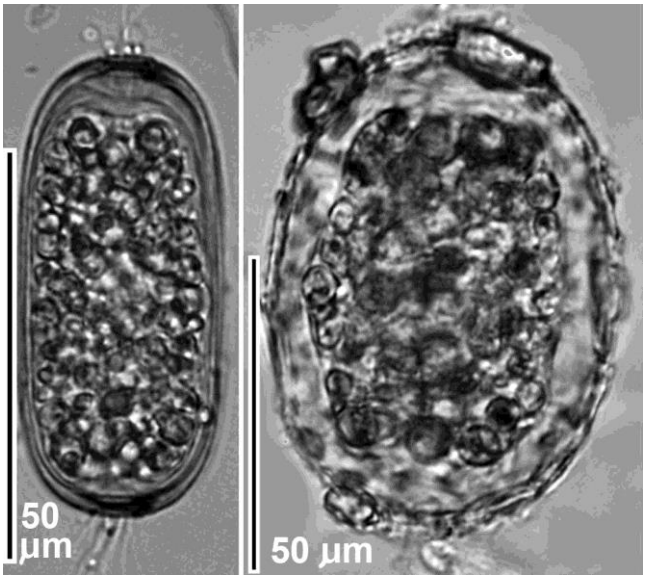

Figure 26. Tests of ***Amphitrema*** (=*Archerella*) ***flavum***. Photos by Edward Mitchell, with permission.

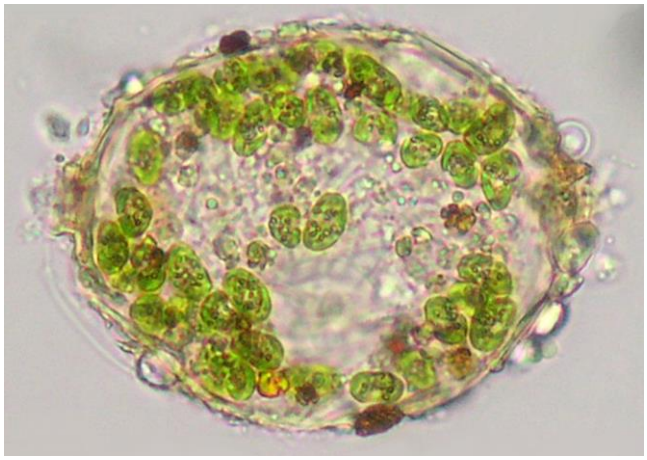

Figure 27. ***Amphitrema wrightianum***, a common bryophyte inhabitant, with included chloroplasts. Photo by Edward Mitchell, with permission.

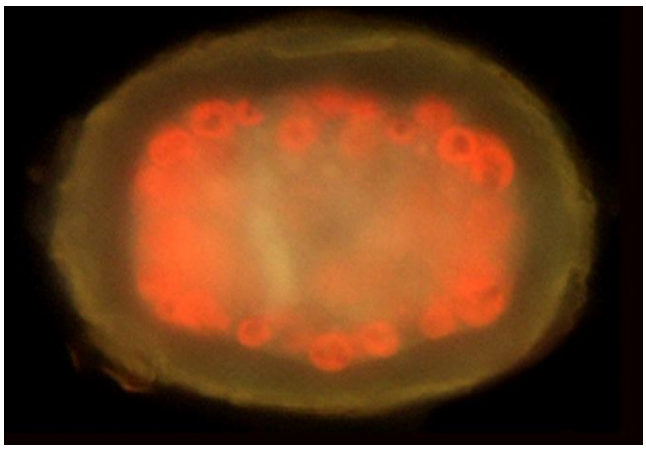

Figure 28. ***Amphitrema wrightianum*** living cell with chlorophyll fluorescence. Photo by Edward Mitchell, with permission.

Figure 29. ***Arcella arenaria***. Photo by Yuuji Tsukii, with permission.

Table 4. The following taxa are those I have found in the literature and by corresponding with protozoologists as known rhizopods inhabiting bryophytes. Peatland taxa that are I have not found listed for other bryophytes are in the Peatland Rhizopod subchapter. This list is undoubtedly incomplete. *Indicates those not mentioned elsewhere in this chapter and that are found on ***Barbula indica*** (Figure 30), as listed by Nguyen-Viet *et al*. 2007.

Amphitrema (*Archerella*) *flavum*
Arcella arenaria
Arcella artocrea
Arcella catinus
Arcella crenulata
Arcella vulgaris
Assulina muscorum
Centropyxis aerophila
Centropyxis constricta
Centropyxis ecornis
Centropyxis eurystoma
Centropyxis kahli
Centropyxis platystoma
Chlamydomyxa montana
Codonella cratera
Coleps hirtus
Corythion dubium
Cyphoderia trochus
Difflugia leidyi
Difflugia lucida
*Difflugia pristis**
Difflugiella crenulata
Diplochlamys timida
Euglypha bryophila
Euglypha ciliata
Euglypha compressa
*Euglypha diliociformis**
Euglypha laevis
Euglypha rotunda
*Nebela scotica**
Nebela tincta
Paraquadrula irregularis
Phryganella acropodia
Phryganella hemisphaerica
Pyxidium tardigradum
Tracheleuglypha dentata
Trinema enchelys
Trinema lineare
Trinema sp.

Figure 30. ***Barbula indica***, home of several testate protozoans listed in Table 4. Photo by Li Zhang, with permission.

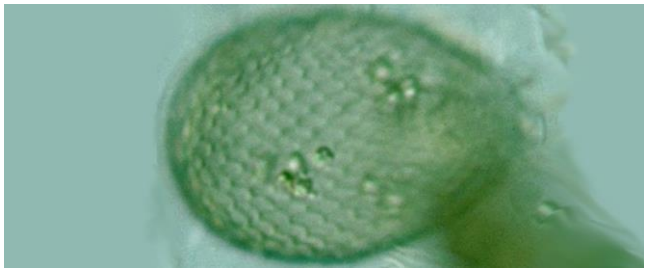

Figure 31. ***Assulina muscorum*** test. Photo by Yuuji Tsukii, with permission.

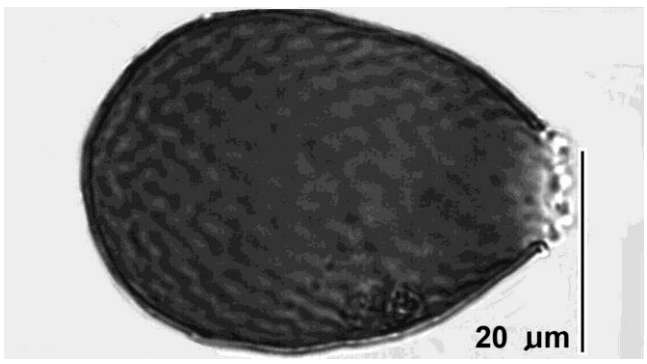

Figure 32. ***Assulina muscorum*** test. Photo by Edward Mitchell, with permission.

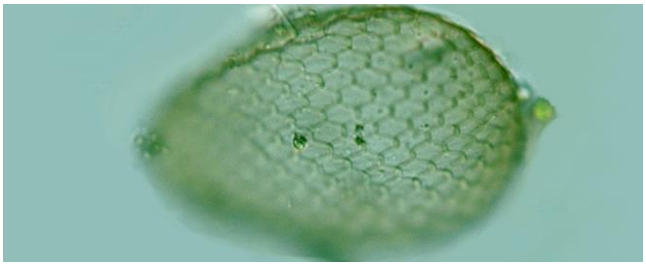

Figure 33. ***Assulina seminulum*** test. Photo by Yuuji Tsukii, with permission.

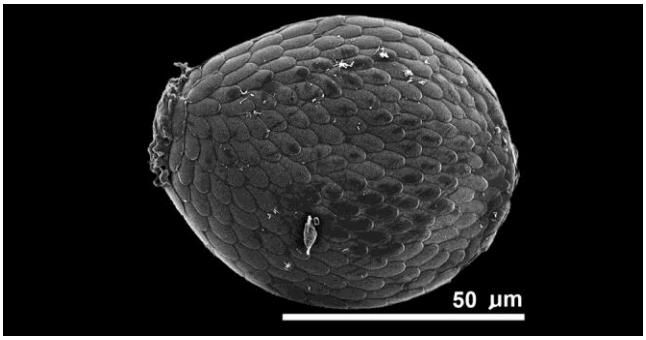

Figure 34. SEM photo of ***Assulina seminulum*** test. Photo by Edward Mitchell, with permission.

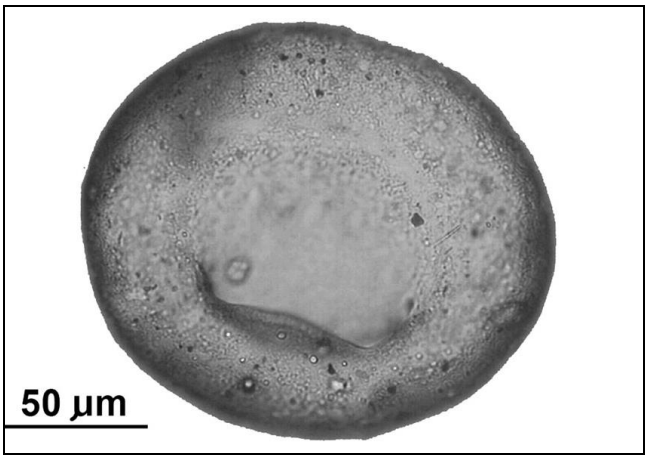

Figure 35. ***Bullinularia indica*** test. Photo by Edward Mitchell, with permission.

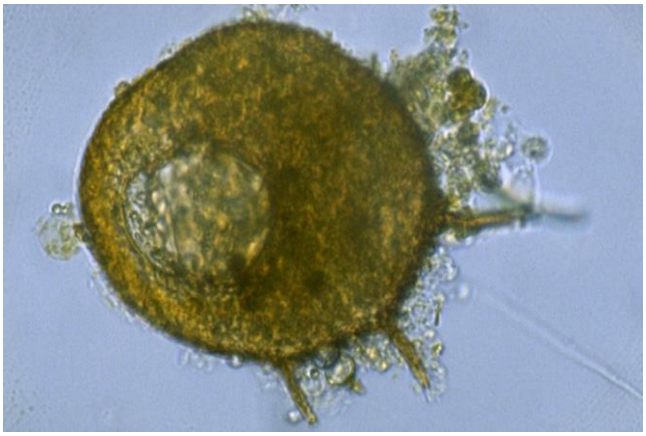

Figure 36. ***Centropyxis aculeata*** test showing spines. Photo by Yuuji Tsukii, with permission.

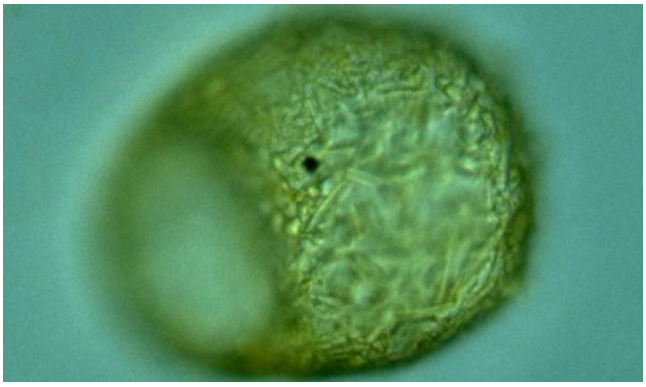

Figure 37. ***Centropyxis aerophila***, a terrestrial protozoan. Photo by Yuuji Tsukii, with permission.

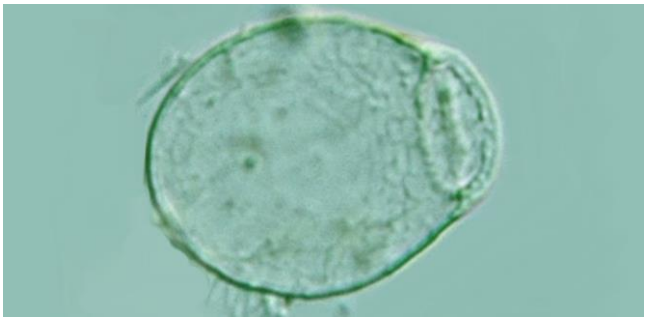

Figure 38. ***Corythion dubium*** test. Photo by Yuuji Tsukii, with permission.

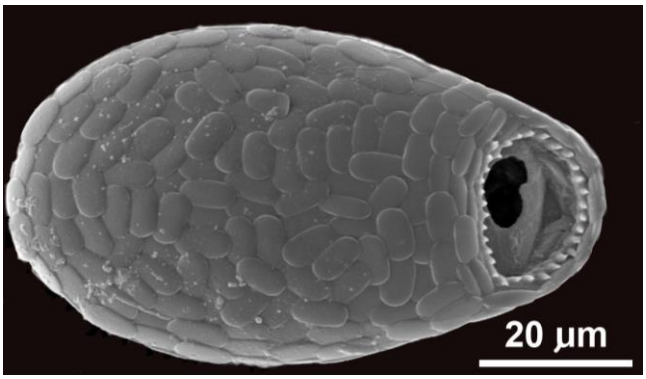

Figure 39. ***Corythion dubium*** test showing opening. **Upper:** Photo by Yuuji Tsukii. **Lower: SEM** photo by Edward Mitchell, both with permission.

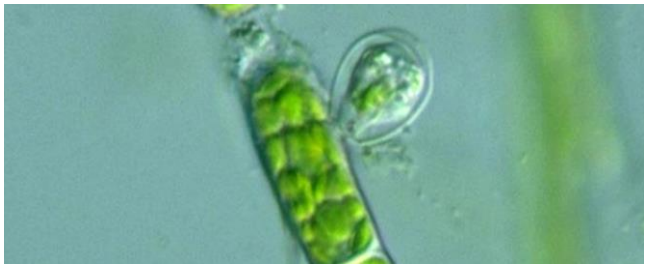

Figure 40. ***Cryptodifflugia ovaliformis*** *g*rowing on filamentous alga. Photo by Yuuji Tsukii, with permission.

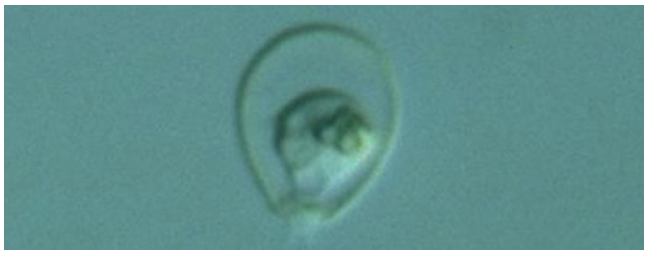

Figure 41. ***Cryptodifflugia ovaliformis*** test and protoplast. Photo by Yuuji Tsukii, with permission.

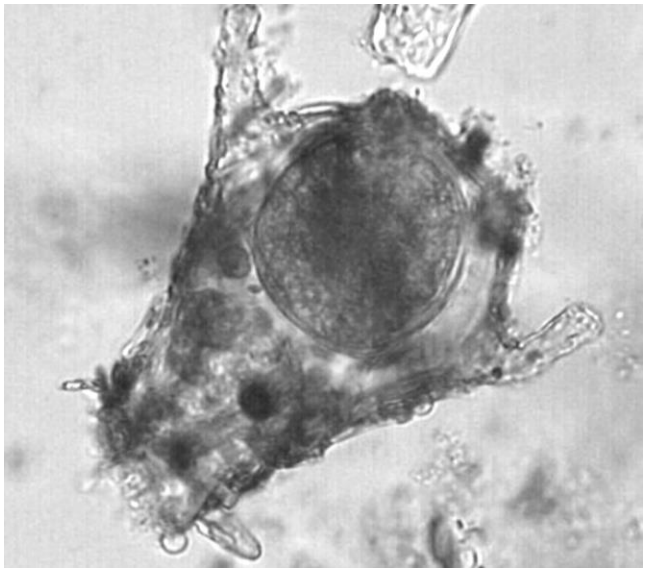

Figure 42. Encysted ***Difflugia leidyi***. Photo by Edward Mitchell, with permission.

Figure 43. ***Euglypha ciliata*** live cell. Photo by Yuuji Tsukii, with permission.

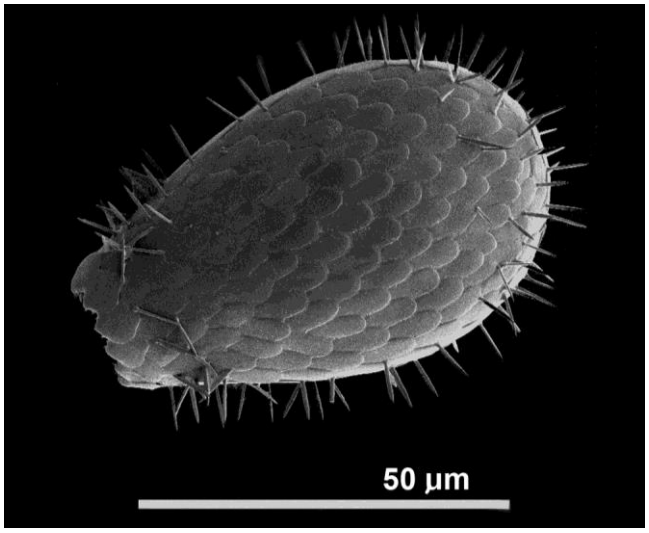

Figure 44. ***Euglypha ciliata*** test. Photo by Edward Mitchell, with permission.

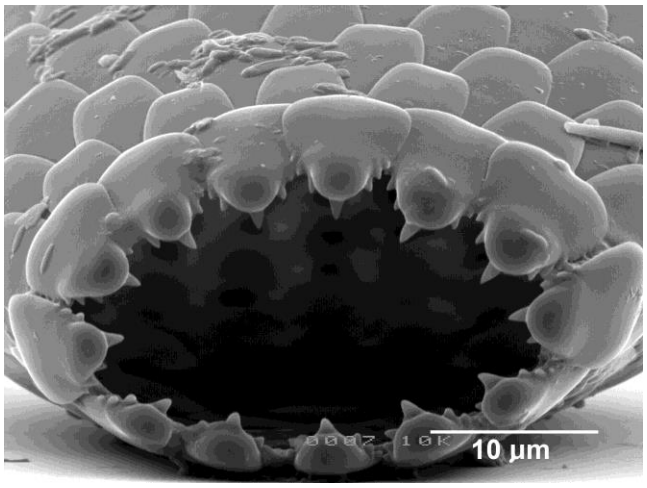

Figure 45. ***Euglypha compressa*** opening in test. Photo by Edward Mitchell, with permission.

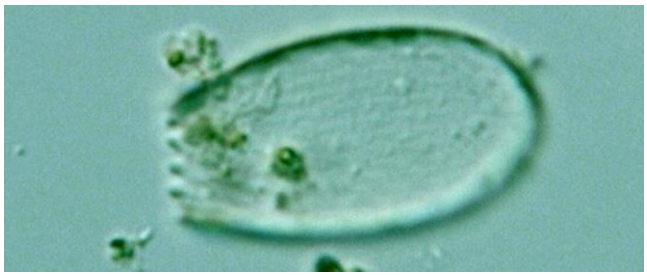

Figure 46. ***Euglypha rotunda*** test. Photo by Yuuji Tsukii, with permission.

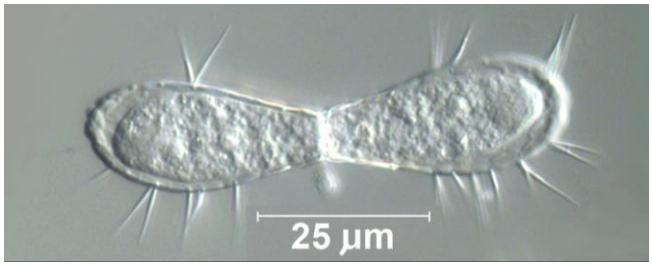

Figure 47. ***Euglypha strigosa*** duplicating cell. Photo by William Bourland, with permission.

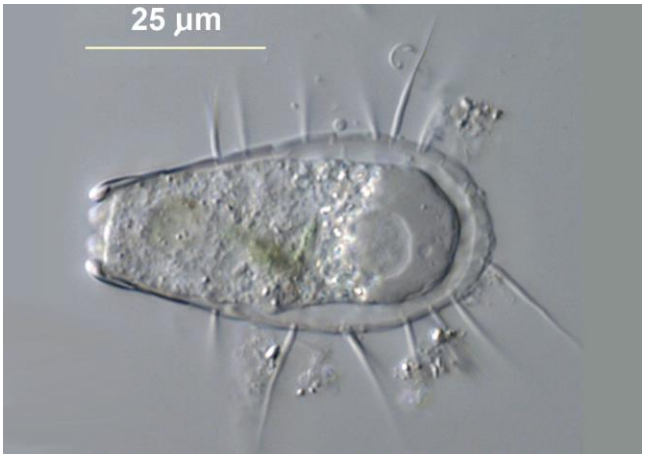

Figure 48. ***Euglypha strigosa*** single cell with test. Photo by William Bourland, with permission.

Figure 49. ***Heleopera petricola*** with diatom. Photo by Yuuji Tsukii, with permission.

Figure 50. ***Heleopera sphagni*** living cell. Photo by Yuuji Tsukii, with permission.

Figure 51. Live cell of ***Heleopera sylvatica*** showing pseudopodia. Photo by Yuuji Tsukii, with permission.

Figure 52. Test of ***Heleopera sylvatica*** with protoplast. Photo by Yuuji Tsukii, with permission.

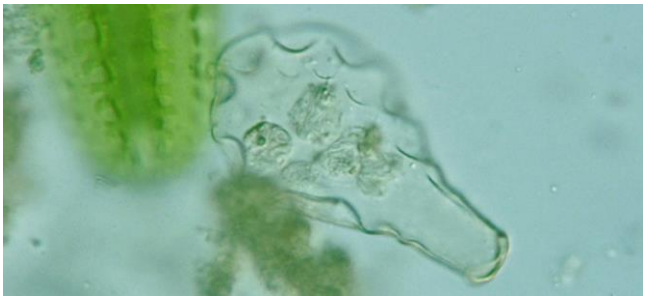

Figure 53. ***Hyalosphenia elegans*** test with remains of protoplast. Photo by Yuuji Tsukii, with permission.

Figure 54. ***Hyalosphenia papilio*** test with protoplast and chloroplasts. Photo by Yuuji Tsukii, with permission.

Figure 55. ***Nebela flabellulum*** living cell and test. Photo by Yuuji Tsukii, with permission.

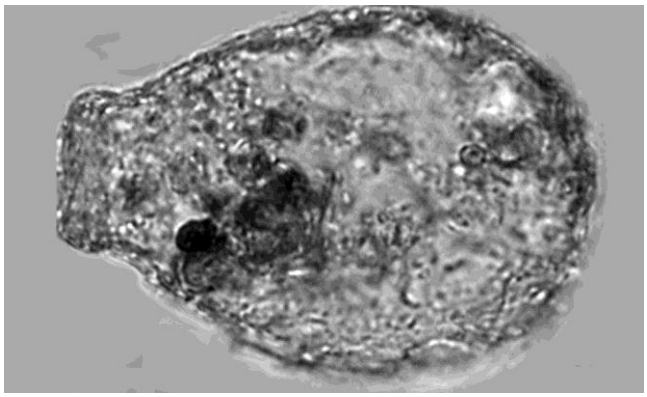

Figure 56. ***Nebela*** (*Physochila*) ***griseola***. Photo by Edward Mitchell, with permission.

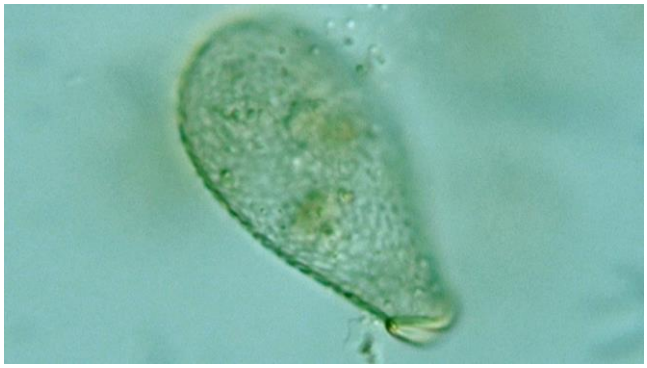

Figure 57. ***Nebela militaris*** test. Photo by Yuuji Tsukii, with permission.

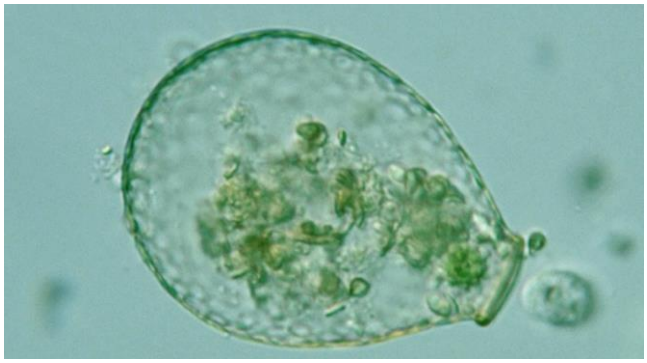

Figure 58. ***Nebela tincta*** test and protoplasm. Photo by Yuuji Tsukii, with permission.

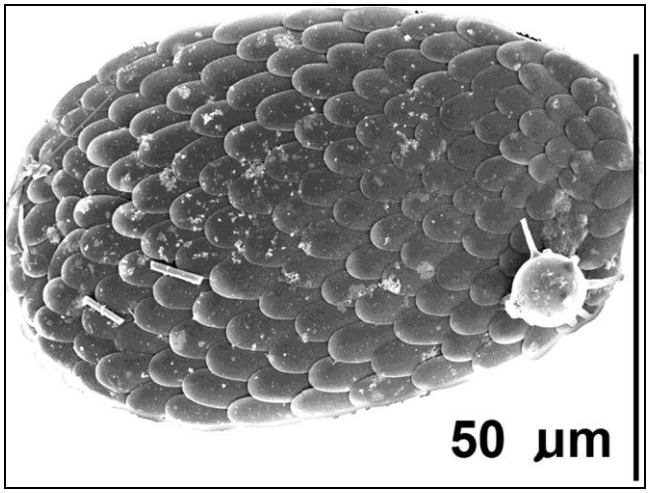

Figure 59. Test of ***Placocista spinosa***. Photo by Edward Mitchell, with permission.

Testate amoebae that live on bryophytes are mostly cosmopolitan taxa (see discussion of the Baas Becking hypothesis in Chapter 2-5). Even more remarkable than the Northern Hemisphere similarities seen in Table 3 is that the Antarctic displays similar communities. In the Antarctic, where mosses are the dominant flora, testacean protozoa are particularly rich in species. Vincke *et al*. (2004) found 83 taxa, representing 21 genera, among the mosses on Île de la Possession of the sub-Antarctic. Smith (1974) found them in carpets of the moss ***Sanionia uncinata*** (Figure 3) in the severe climate of the South Orkney Islands and near Rothera Station, Adelaide Island, both in the Antarctic.

On Île de la Possession of the sub-Antarctic, the bryophyte communities were dominated by ***Euglypha laevis***, ***E. rotunda*** (Figure 60), ***Trinema enchelys*** (Figure 61), and ***T. lineare*** (Figure 62, Figure 63), (Vincke *et al*. 2004). These four taxa are among those listed in Table 3 as common in the Northern Hemisphere.

Figure 60. Test of ***Euglypha rotunda***. Photo by Yuuji Tsukii, with permission.

Figure 61. ***Trinema enchelys*** test and living cell. Photo by Yuuji Tsukii, with permission.

Figure 62. ***Trinema lineare*** test and protoplasm. Photo by Yuuji Tsukii, with permission.

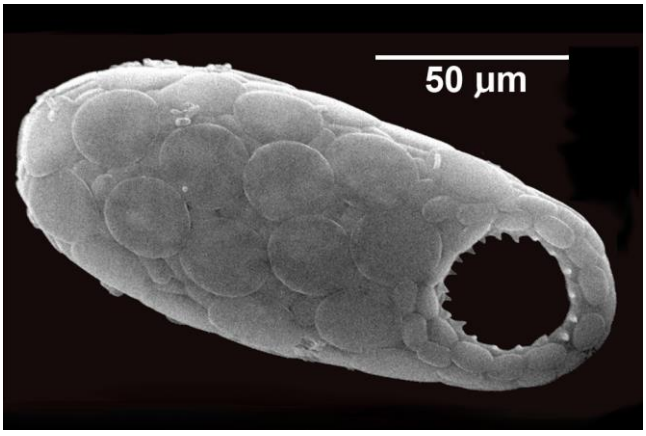

Figure 63. SEM photo of ***Trinema lineare*** test. Photo by Edward Mitchell, with permission.

Upon analysis, three communities of testate amoebae emerged for Île de la Possession: the ***Corythion dubium*** (Figure 39) **community** occurred in drier and slightly acidic terrestrial moss communities; the ***Arcella arenaria*** (Figure 29) and the ***Difflugiella crenulata*** **communities** were both in wetter, circumneutral habitats, with the former occurring in standing water and the latter community typically on submerged mosses of running water. In those habitats, the bryophyte species was important in describing the testate protozoan community. Among these dominant organisms, only ***Difflugiella crenulata*** is absent from the Northern Hemisphere taxa listed in Table 3. A word of caution, though: the taxa are difficult to distinguish and one name may have been applied to several taxa, or several names from different regions may actually apply to the same taxon. Morphologies can differ between regions, making the same species appear different (Bobrov *et al*. 1995). And within a region, cryptic species ("hidden" species that look the same but are reproductively isolated and genetically distinct) can exist.

Many of the known bryophyte inhabitants are never reported as such in the literature. In gathering information for this chapter, I have been able to add several taxa to the published literature I uncovered. Some, like ***Euglypha bryophila*** (Figure 64), are suggested by their names. Others, like ***Tracheleuglypha dentata*** (Figure 65), have come to me among the images of bryophyte-inhabiting protozoans sent by protozoologists. William Bourland has provided me with images of several moss inhabitants that I

have not found in the literature: ***Cyphoderia trochus*** (Figure 66); ***Quadrulella symmetrica*** (Figure 67). I also found many among the Perrault Fen, Michigan, USA images of Jason Oyadomari. Many more taxa are probably lurking among the **non-*Sphagnum*** taxa.

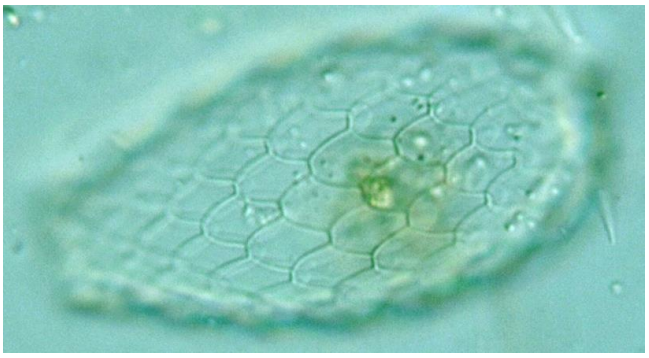

Figure 64. ***Euglypha bryophila***, a bryophyte inhabitant with a name that means moss-loving. Photo by Yuuji Tsukii, with permission.

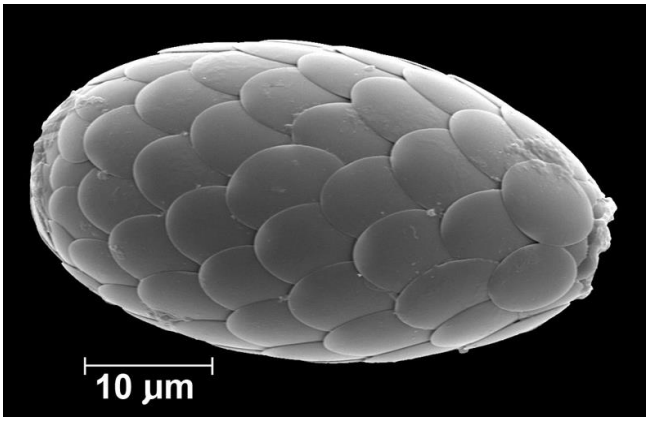

Figure 65. ***Tracheleuglypha dentata*** test with scales. Photo by Edward Mitchell, with permission.

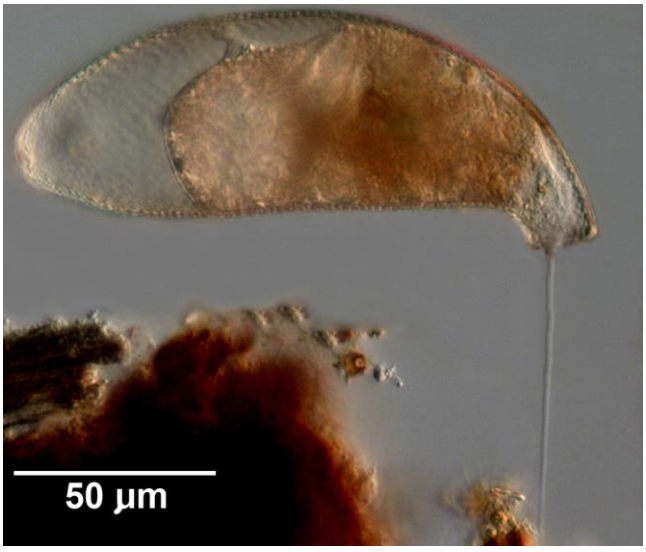

Figure 66. ***Cyphoderia trochus***, another member of the Euglyphidae. Photo by William Bourland, with permission.

Figure 67. ***Quadrulella symmetrica***, a testate rhizopod that can be found among bryophytes. Photo by William Bourland, with permission.

Summary

The rhizopods (amoebae) can be naked or testate (living in a self-made house), with testae made of sand, diatoms, pollen, or mineral particles put together with secretions. Testate species are cosmopolitan and are particularly common on bryophytes, especially in peatlands. These common species even extend to the Antarctic. ***Euglypha laevis***, ***E. rotunda***, ***Trinema lineare***, and ***T. enchelys*** are among the dominant taxa in both hemispheres. More taxa may be in common but are currently understood as multiple species. Many others undoubtedly remain to be discovered, especially among the **non-*Sphagnum* bryophytes**.

Acknowledgments

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CHAPTER 2-4
PROTOZOA: RHIZOPOD ECOLOGY

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PROTOZOA: RHIZOPOD ECOLOGY

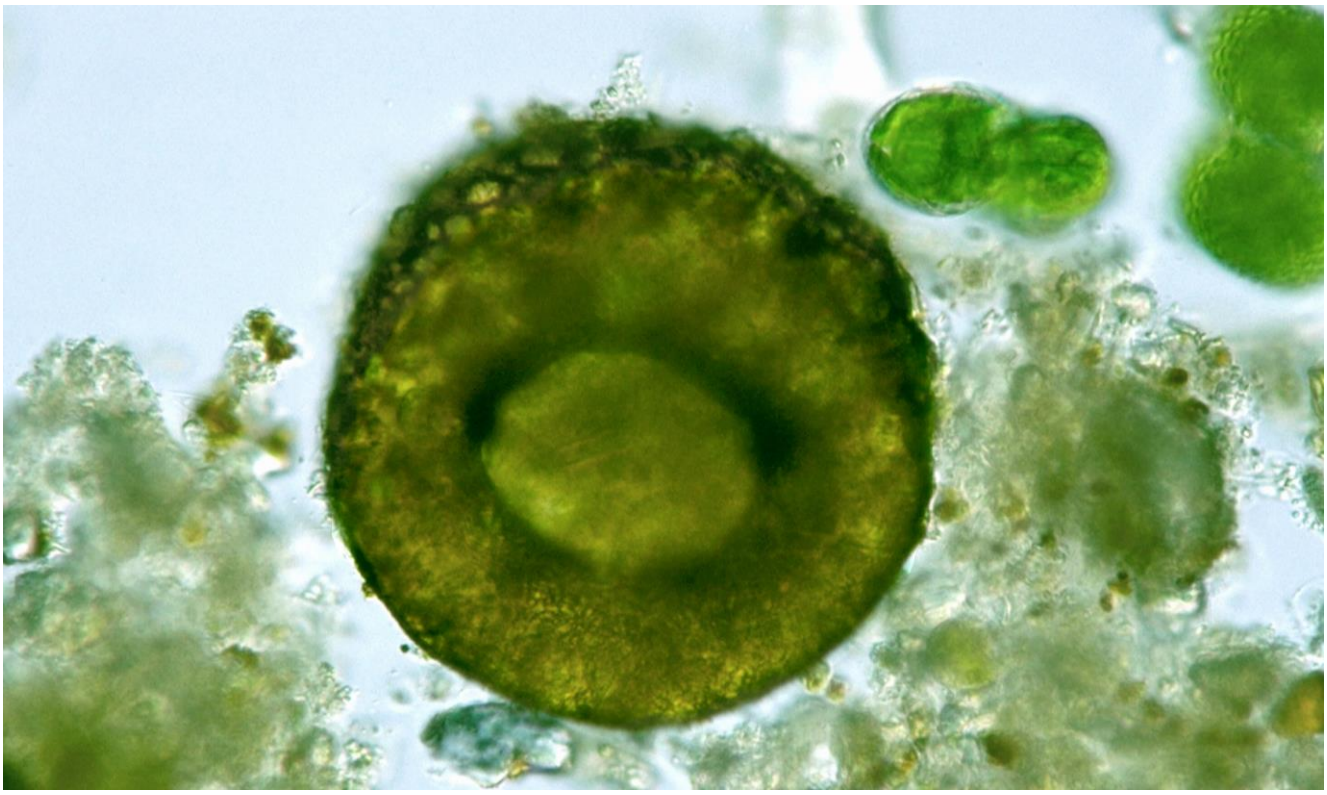

Figure 1. Test of ***Centropyxis ecornis*** with desmids that are common cohabitants in peatlands. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Geographic Distribution

Testate amoeba communities not only are diverse in themselves, but they typically occur with a diversity of algae and other micro-organisms (Figure 1). Moss-dwelling testate amoebae have been reported from the Antarctic (*e.g.* Richters 1904, 1908a, b; Sudzuki 1964; Smith 1973a, b, c, 1974a, b, 1986; Beyens *et al.* 1988; Balik 1994), to The Czech Republic (Balik 2001), to the Canadian Arctic (Beyens *et al.* 1986a, b), to name only a few. Beyens and Chardez (1994) thought that the amoebae formed specific assemblages related to the moss habitats. Working in the Mt. Kurikoma district of Japan, Chiba and Kato (1969) likewise suggested that the testacean community structure is related to the bryophyte habitat.

Bartos (1949) reported on the moss-dwelling Rhizopoda of Switzerland. Most of his samples were from aerial mosses, but the Rhizopoda belonged to damp moss associations. The largest numbers of individuals belonged to the testate amoeba genus ***Centropyxis***, including ***C. aerophila*** (Figure 3), ***C. eurystoma***, ***C. kahli***, and ***C. ecornis*** (Figure 4), in all the mosses. Smith (1992) reported ***Arcella arenaria*** (Figure 2), ***Centropyxis aerophila*** (Figure 3), ***Corythion dubium*** (Figure 5), ***Difflugia lucida***, ***Diplochlamys timida***, ***Heleopera petricola*** (Figure 6), and ***Trigonopyxis arcula*** (Figure 7) from Antarctica, where numbers were generally low compared to Northern Hemisphere studies. Only ***Bryum*** exhibited larger populations, those of ***Arcella arenaria***. ***Centropyxis aerophila*** seems to prefer more calcareous situations (Coûteaux 1969), although its distribution in South Georgia (Antarctica) occurs at *p*H 4.5-5.6 (Smith & Headland 1983). This species is variable, whether due to geography or ecology (Chardez 1979).

Figure 2. ***Arcella arenaria***. Photo by Yuuji Tsukii, Protist Information Server, with permission.

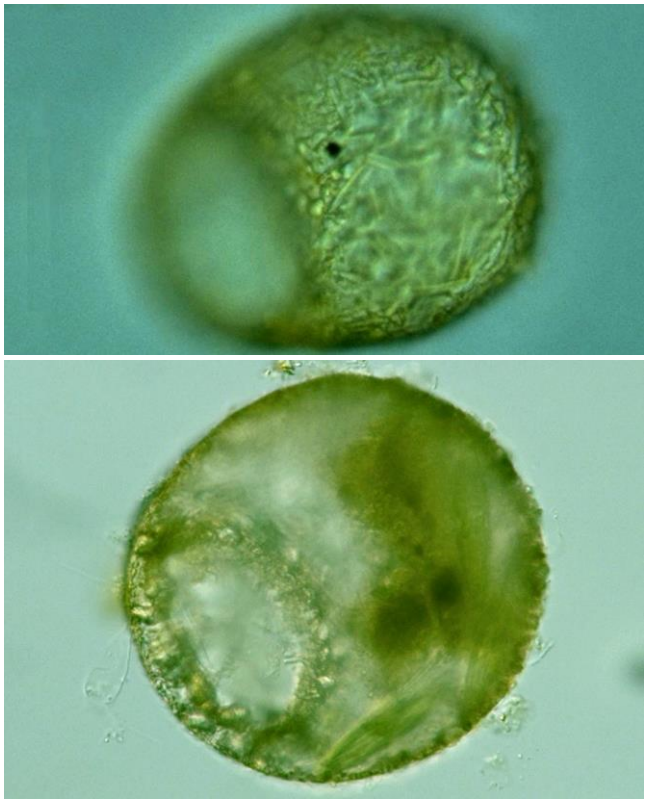

Figure 3. ***Centropyxis aerophila***, an aerial protozoan that lives on damp mosses. Photos by Yuuji Tsukii, Protist Information Server, with permission.

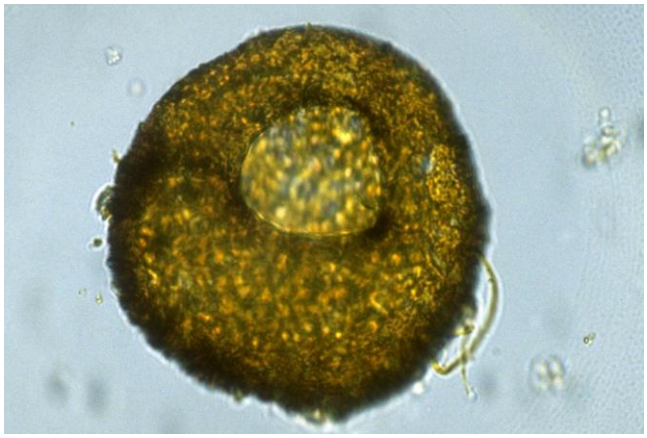

Figure 4. ***Centropyxis ecornis***, a doughnut-shaped testate amoeba that is common among mosses. Photo by Yuuji Tsukii, with permission.

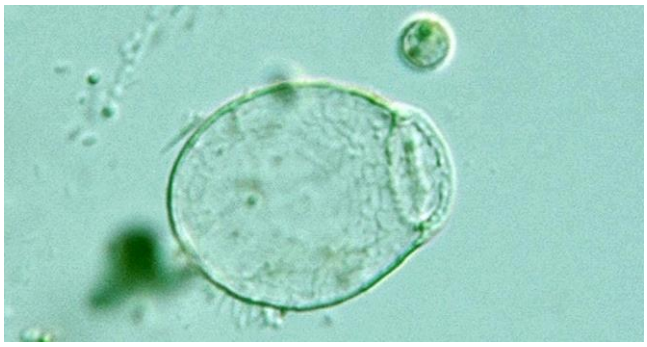

Figure 5. ***Corythion dubium*** test. Photo by Yuuji Tsukii, with permission.

Figure 6. ***Heleopera petricola***. Photo by Yuuji Tsukii, Protist Information Server, with permission.

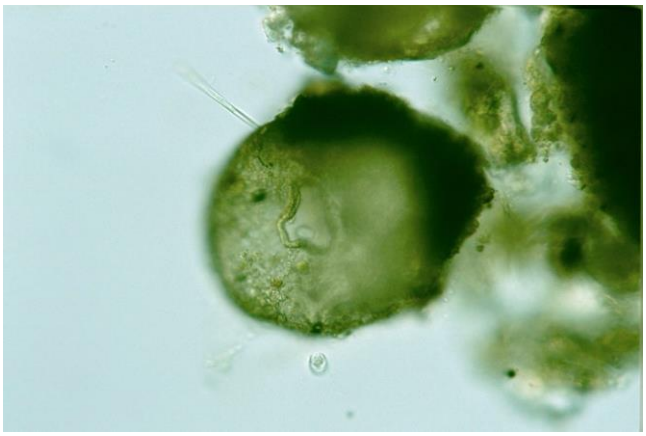

Figure 7. ***Trigonopyxis arcula***. Photo by Yuuji Tsukii, Protist Information Server, with permission.

As for most of the invertebrates, the highest numbers seem to occur in peatlands. Gilbert *et al.* (2003) reported 29,582 ± 9650 active individuals per liter of *Nebela vas* and 2263 ± 1620 for the encysted ones at Pradeaux peatland (Puy de Dôme, France), with the greatest abundance at the end of June (almost 40,000), dropping to the lowest number in July (less than 15,000).

Communities

Although most of the information regarding rhizopod communities is for peatlands (Subchapter 2-5), a few studies have discussed communities in other types of bryophytes. Beyens *et al*. (1990) compared communities from the coastal lowlands on Devon Island, NWT, Canadian Arctic. These encompassed 57 taxa on mosses, soils, and lichens. The dry, acidic moss habitats were characterized by ***Assulina muscorum*** – ***Corythion dubium*** assemblages. In wet, neutral *p*H habitats, ***Paraquadrula irregularis*** was dominant. Sedge moss meadows had a soil fauna association of ***Plagiopyxis callida*** – ***Plagiopyxis declivis***. ***Centropyxis minuta*** was mostly on coarsely textured soils in this study, but is known from mosses elsewhere.

Mazei and Belykova (2011) found 29 rhizopod species/forms associated with mosses at the water edge in seven streams of the Sura River basin (Middle Volga region, Russia). The dominant species are ***Centropyxis aerophila***, ***Centropyxis cassis***, ***Crythion dubium***,

Euglypha ciliata glabra, ***Tracheleuglypha dentata***, ***Trinema complanatum***, ***Trinema enchelys***, and ***Trinema lineare***. The species richness in these communities varies from 2 to 11 per sample, with an abundance of 100 to 4000 individuals per gram dry moss. Mazei and Belykova suggested that the character of the community could be influenced by forest cover, water hardness, "biogenic elements," stream size, and environmental contamination.

Davis (1981) reported that the testate rhizopods were the dominatform of non-photosynthetic life among mosses in the maritime Antarctic. Smith (1986) reported ten species on the moss ***Sanionia uncinata***: ***Assulina muscorum***, ***Corythium dubium***, ***Difflugia lucida***, ***Nebela lageniformis***, ***Nebela wailesi***, ***Phryganella acropodia***, ***Trigomopyxis arcula***, and a species of ***Difflugia***, possibly ***D. mica***. The most abundant of these were ***Difflugia lucida*** and ***Assulina muscorum***. The species richness was low, similar to that found in other southern latitudes.

Moisture Relationships

Moisture plays an important role in survivorship. Like many other bryophyte inhabitants, the testate amoebae among the bryophytes survive the wet-dry changes so common among the bryophytes (Chardez 1990). When conditions are dry, many rhizopod amoebae can **encyst** (Sacchi 1888 a, b; Heal 1962), thus escaping the need for water during long periods of drought (Hingley 1993). Some have survived 5-8 years in dry moss (Hingley 1993).

Chlamydomyxa montana is one such encysting protozoan. In its amoeboid state it feeds on diatoms, but it is photosynthetic in bright light in its encysted state (Pearlmutter & Timpano 1984). Cysts of this unusual amoeba occur on the branches of ***Sphagnum*** (Lankester 1896). These cause the moss to be ruddy brown, with a glistening surface due to olive-brown disk-like or ovoid cysts about 1-2 mm in diameter. When these are awakened, a network of threads appears, signifying the amoeboid stage.

In Germany, the death rate of testaceans in the river exceeded that in mats of the terrestrial ***Plagiomnium cuspidatum*** (Figure 8) (3%/day) (Schönborn 1977). This is perhaps due to the greater resistance to desiccation among the terrestrial taxa and represents a time of optimal conditions. With ***Euglypha ciliata*** (Figure 9, Figure 10) (429,000 individuals/m^2; 15.5 mg/m^2) and *Assulina muscorum* (Figure 11) (406,000 individuals/m^2; 2.9 mg/m^2) dominating, the production rate on the mosses is 40,600 individuals m^{-2} day^{-1} and a biomass of 0.3 mg m^{-2} day^{-1}. In drier times, generation time increases as amoebae go dormant, causing fewer generations to be produced and reducing the productivity. Soil organisms spend only half the time for one generation compared to those living on the bryophytes. Not only is the moss subject to more frequent drying, but the number of ***Aufwuchs*** on the mosses is lower, thus providing less food.

Rhizopod communities are determined by the moisture and temperature conditions available to them (Chiba & Kato 1969). This affects not only the clumps of moss they inhabit, but also their vertical distribution within the clump. For example, in the Canadian Arctic, ***Trinema lineare*** (Figure 12) occurs deep in the moss mat where conditions are more humid (Beyens *et al*. 1986b).

Rhizopods are able to inhabit ponds, lakes, marshes, and swamps where there is likewise sufficient moisture to support moss growth (Cash *et al*. 1905). They are constant members of the community near ponds among the mosses ***Drepanocladus*** spp. (*sensu lato*), ***Philonotis fontana***, and ***Aulacomnium palustre***, where they are typically associated with diatoms. Rhizopods also subsist among mosses on tree trunks and roots in shaded forests.

Figure 8. ***Plagiomnium cuspidatum***, a safe site compared to soil. Photo by Michael Lüth, with permission.

Figure 9. ***Euglypha ciliata*** showing the cilia that give it its name. Photo by Yuuji Tsukii, Protist Information Server, with permission.

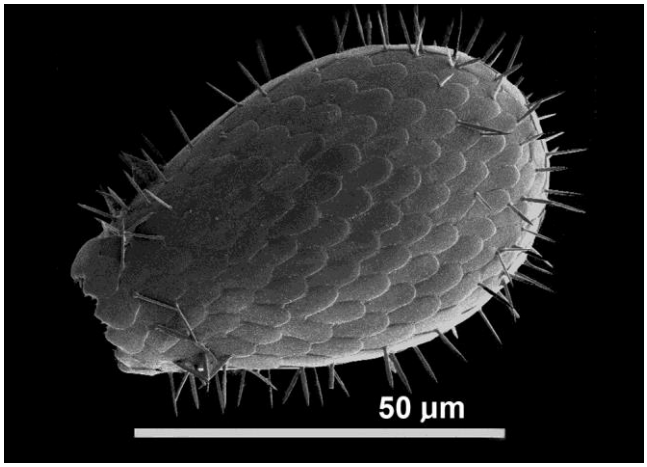

Figure 10. Test of ***Euglypha ciliata***. Photo by Edward Mitchell., with permission

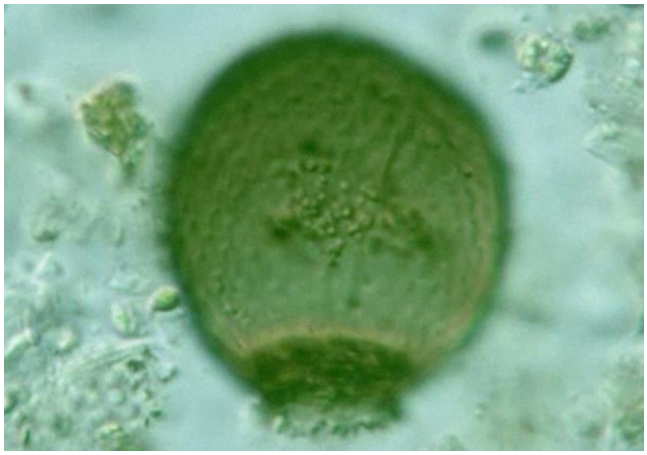

Figure 11. ***Assulina muscorum***, a common bryophyte inhabitant. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Figure 12. ***Trinema lineare***. Photo by Yuuji Tsukii, PIS, with permission.

Bartos (1949) found that in those mosses that were often dry, ***Centropyxis labiata*** occurred, with ***C. platystoma*** and ***C. constricta*** (Figure 13) in somewhat damper ones. The very dry mosses housed ***Trigonopyxis arcula*** (Figure 14) and ***Bullinularia indica*** (Figure 15). Several species occurred in all moss probes: ***Trinema enchelys*** (Figure 16), ***Nebela collaris*** (Figure 17), ***Euglypha ciliata*** (Figure 10), and ***Assulina muscorum*** (Figure 11).

Figure 13. Test of ***Centropyxis constricta***, a common protozoan among damp mosses. Photo by Yuuji Tsukii, with permission.

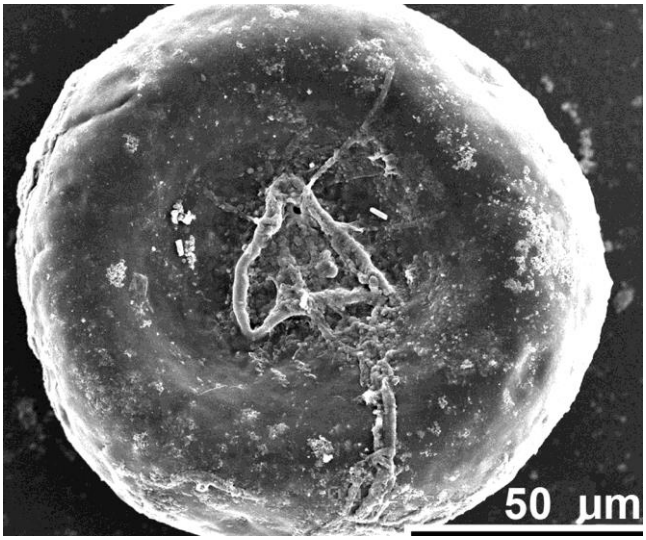

Figure 14. Test of ***Trigonopyxis arcula***. Photo by Edward Mitchell, with permission.

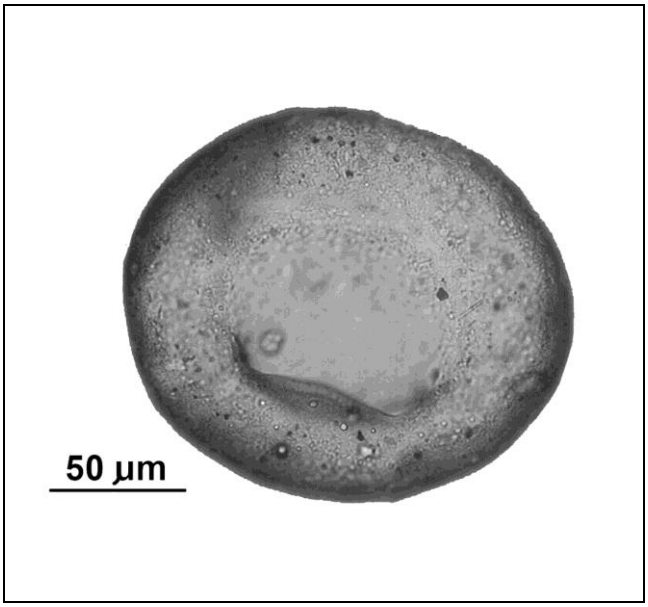

Figure 15. Test of ***Bullinularia indica***, a protozoan that lives on dry mosses. Photo by Edward Mitchell, with permission.

Figure 16. ***Trinema enchelys*** test with living protoplasm. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Figure 17. ***Nebela collaris***, a common species among mosses. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Case Building

The large, shell-forming ***Arcella*** is a common genus among bryophytes, particularly ***Sphagnum*** (Hoogenraad & De Groot 1979; Chardez & Beyens 1987). ***Arcella*** builds a case that is completely organic (Meisterfeld & Mitchell 2008; Figure 18) and resembles a tiny doughnut in bottom view (Figure 19). ***Arcella crenulata*** and ***A. mitrata*** (Figure 20) tend to occur together on ***Sphagnum*** that is constantly wet, low in nutrients, and in a *p*H range of 4-6. Others such as ***A. arenaria*** (Figure 19), ***A. catinus*** (Figure 21), ***A. artocrea*** (Figure 22, Figure 23), and ***A. microstoma*** "prefer" ***Sphagnum***, but also occur elsewhere.

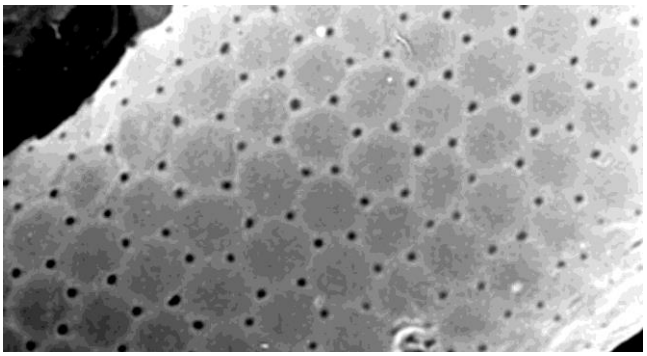

Figure 18. SEM image of test of ***Arcella hemisphaerica*** showing organic construction. Photo by Ralf Meisterfeld, with permission.

Figure 19. Test of ***Arcella arenaria***. Photo by Yuuji Tsukii, with permission.

Figure 20. Living ***Arcella mitrata***. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Food

The Rhizopoda have long been considered to be bacterivores, but it appears that this conclusion may be somewhat short-sighted. Although most are heterotrophic, a few are mixotrophic, housing photosynthetic algae as symbionts (Gilbert *et al.* 2000). The ability of some taxa to ingest a wide size range (0.2-1000 µm) of organisms and particulate organic matter (POM) offers a potential competitive advantage.

Figure 21. Test of ***Arcella catinus***. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Wilmshurst (1998) found protozoa so common in New Zealand ***Sphagnum*** peatlands that she estimated that more than 50,000 protozoans could "eke out a living" in a gram of fresh moss. The amoebae survive by consuming particulate organic matter, algae that grow epiphytically on the mosses, bacteria, fungi, plant cells, and even smaller amoebae (Richardson 1981; Gilbert *et al*. 2000). Although bacterivorous taxa are the most frequent, some taxa eat algae and other protozoa almost as large as they are.

Deriu *et al.* (1995) challenged earlier studies that suggested that ***Sphagnum*** served as a reservoir of mycobacteria as a food source, citing the medicinal properties of ***Sphagnum*** as evidence of the near absence of mycobacteria. Nevertheless, it is likely that bacteria serve

as the primary food source. Mieczan (2006) found that among the ***Sphagnum*** in Poleski National Park in Poland the bacterivorous protozoa had the greatest numbers, whereas those that ate algae were least common.

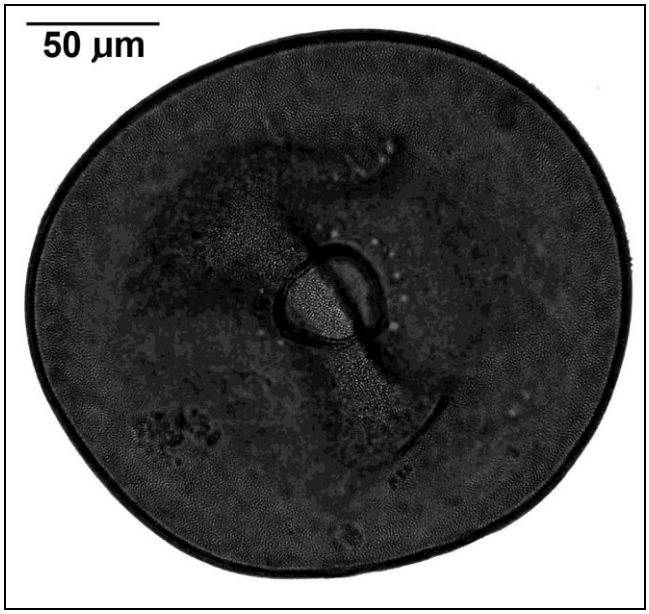

Figure 22. Test of ***Arcella artocrea***. Photo by Edward Mitchell, with permission.

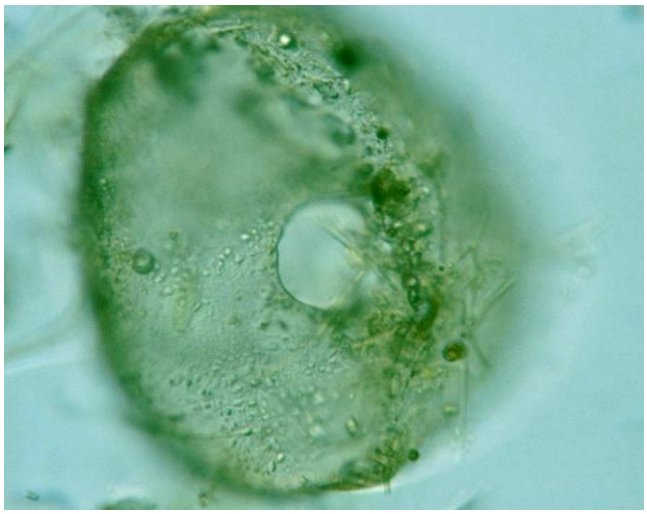

Figure 23. Test of ***Arcella artocrea***. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Symbionts

Despite their habitation within a case or test, some of the Testacea also have **symbionts**. Among those inhabiting bryophytes, symbiotic taxa include ***Amphitrema flavum*** (Figure 24), ***Difflugia oblonga*** (Figure 25), ***Hyalosphenia papilio*** (Figure 26), and ***Heleopera sphagni*** (Figure 27) (Burkholder 1996; Charrière *et al*. 2006; Meisterfeld & Mitchell 2008). Their dependency on light forces them to live in the upper few cm where the algae live both independently and within the rhizopod, and are able to photosynthesize. A more detailed discussion of algal symbionts is in the subchapter on Protozoa Diversity (Chapter 2-1).

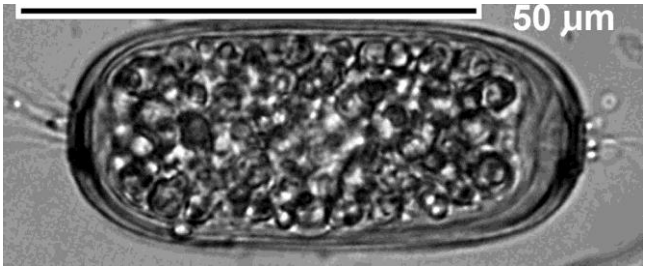

Figure 24. ***Amphitrema flavum***, a protozoan that incorporates green algal symbionts. Photo by Edward Mitchell, with permission.

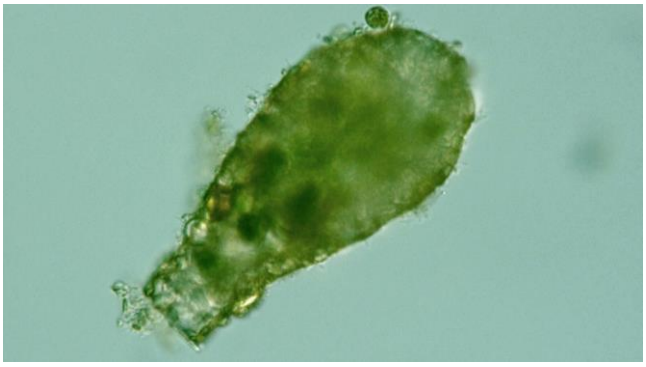

Figure 25. ***Difflugia oblonga*** with green algae, possibly living as symbionts. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Bryophyte Chemistry

Moss chemistry appears to play an important role in at least some cases in determining species richness. Testate amoebae occupying ***Hylocomium splendens*** (Figure 28) in the Italian Alps were distributed largely in accordance with differences in C, P, Ca, Mg, Al, Fe, and Na of the moss tissues (Mitchell *et al*. 2004). The researchers suggested that the chemistry affected the prey organisms, thus affecting their consumers, the amoebae. Surprisingly, there was no relationship to the important nutrients N and K. Both Mitchell *et al*. (2004) and Bonnet (1973b) concluded that distribution of testate amoebae among wefts of *H. splendens* was independent of soil type.

Figure 26. ***Hyalosphenia papilio*** densely impregnated with symbiotic algae. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Figure 27. ***Heleopera sphagni*** with what appear to be algal symbionts. Photo by Yuuji Tsukii, Protist Information Server, with permission.

In addition to the taxa mentioned above, Mieczan (2006) also found ***Codonella cratera*** (Figure 29) in two Polish peatlands. There is surely a wealth of species waiting to be discovered in the little-explored bryophyte microcosm. Corbet (1973) managed a 38-page article on the testate species of ***Sphagnum*** at a single location, Malham Tarn, Yorkshire. Other bryophytes have received much less attention.

Figure 28. ***Hylocomium splendens***, a terrestrial habitat for protozoa. Photo by Michael Lüth, with permission.

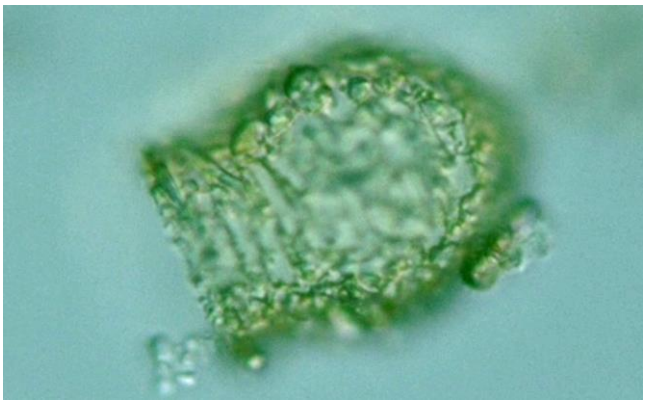

Figure 29. Test of ***Codonella cratera***. Photo by Yuuji Tsukii, Protist Information Server.

Pollution – Heavy Metals

Rhizopods, as well as bryophytes, can serve as indicators of pollution damage to a community. In a study of the moss ***Barbula indica*** in Viet Nam, both richness and abundance of rhizopods were reduced by lead (Nguyen-Viet *et al*. 2007). Shannon diversity was negatively correlated with cadmium. Although several species of rhizopods were negatively correlated with lead, cadmium, zinc, and nickel, lead was the only pollutant that caused a significant change at the community level. Other effects will be discussed in the sub-chapter on Peatland Rhizopods.

Summary

Centropyxis and ***Arcella*** are among the most common of the testate amoebae among epiphytic bryophytes. Communities vary seasonally as moisture changes. Moisture is also the greatest determinant of the choice of bryophyte and vertical location within it, but for some *p*H also plays a role. Construction of cases may help them to survive brief dry periods, but most encyst until favorable moisture returns. Terrestrial taxa are more resistant to desiccation than are aquatic ones. Generation time is longer on mosses because of the time spent encysted.

Many of the rhizopods are bacterivores, but they also consume fungi, algae, plant cells, and smaller amoebae. Chemistry may affect the available food organisms, but N & K do not seem important. Several of the rhizopods harbor ***Chlorella*** as symbionts. Their need for light causes these taxa to live in the upper few cm of the bryophyte layer.

Rhizopods often have a negative correlation with pollutants, especially some of the heavy metals.

Acknowledgments

Yuuji Tsukii was most helpful in giving me permission to use his images from the Protist Information Server. Edward Mitchell helped me to find literature and provided me with a number of images I couldn't find elsewhere.

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CHAPTER 2-5
PROTOZOA: PEATLAND RHIZOPODS

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CHAPTER 2-5
PROTOZOA: PEATLAND RHIZOPODS

Figure 1. A peatland with ***Sphagnum magellanicum*** that serves as habitat for protozoa. Photo by Michael Lüth, with permission.

Peatlands Taxa: *Sphagnum*

Protozoa, and especially Rhizopoda, are apparently most abundant in peatlands (Figure 1) and were among the earliest of the moss fauna to be examined (Jung 1936). But few other bryophyte protozoans have been studied in detail. Among the abundant **sphagnicolous** taxa (growing in ***Sphagnum*** moss) are ***Nebela*** (Figure 2), ***Hyalosphenia*** (Figure 3), ***Difflugia pyriformis*** (Figure 4), and ***D. globularis*** (Bovee 1979; Gerson 1982). Table 1 summarizes the species I have found in the literature.

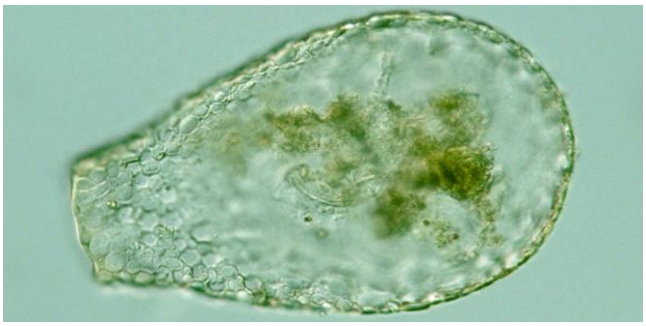

Figure 2. ***Nebela collaris***, a sphagnicole. Photo by Yuuji Tsukii, with permission.

Figure 3. ***Hyalosphenia papilio***, a sphagnicole. Photo by Yuuji Tsukii, identified by Matthieu Mulot, with permission.

Mitchell *et al*. (2000b) compared testate (with a house) amoebae in peatlands of Switzerland, the Netherlands, Great Britain, Sweden, and Finland. They found that the plant species differed more than the species of amoebae. The high number of rhizopod species among ***Sphagnum***, compared to that of other mosses or tracheophytes, supported the usefulness of rhizopods as indicators of both past and present conditions. Furthermore, the mosses were

less affected by the chemistry of the ground water than were such taxa as *Carex* and *Eriophorum*. But when Booth and Zygmunt (2005) compared the testate amoeba communities of the Great Lakes in North America with those of the Rocky Mountains of North America, the communities differed, perhaps due to differences in climate and the trophic state of the peatlands. Even so, these two regions had many species in common, and these species occupied similar moisture positions in both regions. In the Rocky Mountains, USA, distribution of these testate amoebae in ***Sphagnum***-dominated peatlands is dictated primarily by surface moisture (Zygmunt *et al*. 2003). Communities in the western Great Lakes region are similarly distributed, with 50% of the species also occurring in the Rocky Mountain peatlands, and similar communities exist for Yellowstone National Park.

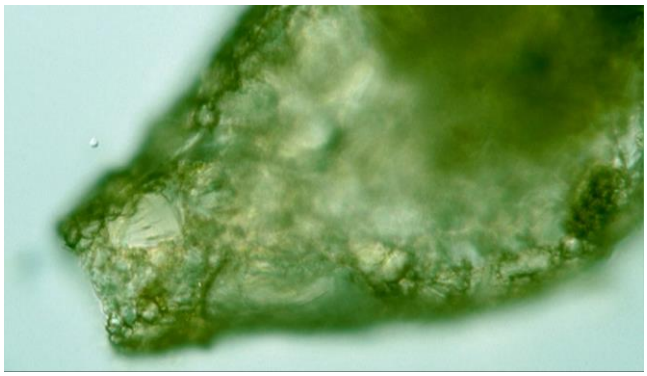

Figure 4. ***Difflugia pyriformis***, a sphagnicole. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Testate amoebae abound in peatlands all over the world. Because of their abundance there, testate amoebae have been widely studied in peatlands all over the world (*e.g.* Leidy 1879; Harnish 1924, 1925, 1927, 1948, 1950, 1951; Hoogenraad 1934, 1935; Jackzo 1941; van Oye 1941, 1951; Conra, 1943; Heinis 1945; Hoogenraad & de Groot 1946; Paulson 1953; Rose 1953; Hoppman 1954; Chacharonis 1956; Varga 1956; Bonnet 1958; Thomas 1959; Heal 1961, 1964; Schönborn 1962, 1963, 1965; Martin 1963; Buttler *et al*. 1966 a, b; Tolonen 1966, 1994; Coûteau 1969; Bovee 1979; Seis 1971; Corbet, 1973; Laminger 1975; Vucetich 1975; Grospietsch 1976; Ruitenburg & Davids 1977; Meisterfeld 1978, 1979a, b; Beyens & Chardez 1984; Tolonen *et al*. 1985, 1992, 1994; Warner 1987; Hendon & Charman 1997; Gilbert *et al*. 1998a, b, 2003; Woodland *et al*. 1998; Bobrov *et al*. 1999; Strüder-Kypke & Schönborn 1999; Mitchell *et al*. 1999, 2000a, b; Charman *et al*. 2000; Booth 2002; Langdon *et al*. 2003; Laggoun-Défarge *et al*. 2008).

Bobrov *et al*. (1999) studied their ecology in peatlands of Russia. Bousquet (1950) studied them in southwestern France, Mieczan (2006) in Poland, and Wilmshurst (1998) in New Zealand. Robson *et al*. (2001) reported on ***Sphagnum*** bog microfauna in Tierra del Fuego, South America, demonstrating several of the same familiar genera as those in Switzerland (Bartos 1949a). Among those Northern Hemisphere taxa also identified in Tierra del Fuego were ***Assulina*** (Figure 5), ***Corythion*** (Figure 6), ***Euglypha*** (Figure 7), and ***Heleopera*** (Figure 8). Just as peatland plants are more cosmopolitan than other plants, these rhizopod assemblages seem to be more affected by ecology than by geography. This is reflected in the small-scale vertical gradients seen among the amoebae, rotifers, and other invertebrates. As noted above, it appears that the number of species of these rhizopods is generally much greater among ***Sphagnum*** (Figure 1) than among other mosses or tracheophytes (Mitchell *et al*. 2000b). Nevertheless, Tolonen *et al*. (1992) found little difference in rhizopod taxa between ***Sphagnum*** communities and those of bryalean mosses in Finnish mires. Unfortunately, few studies have compared fauna on these two groups of bryophytes at the same location.

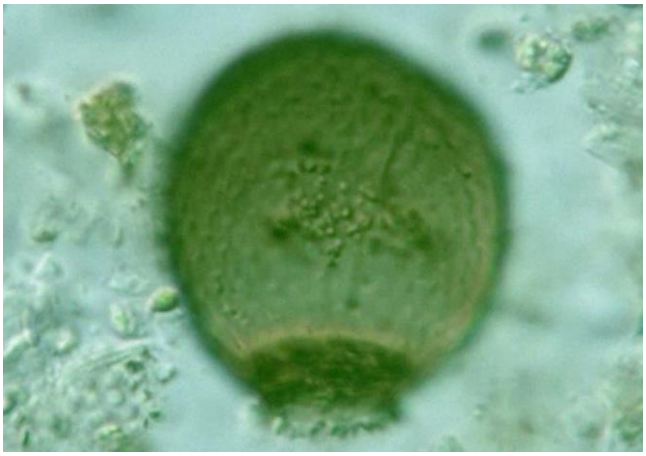

Figure 5. ***Assulina muscorum*** showing pseudopodia and test. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Figure 6. ***Corythion pulchellum*** showing lower surface. Photo by Yuuji Tsukii, Protist Information Server, with permission.

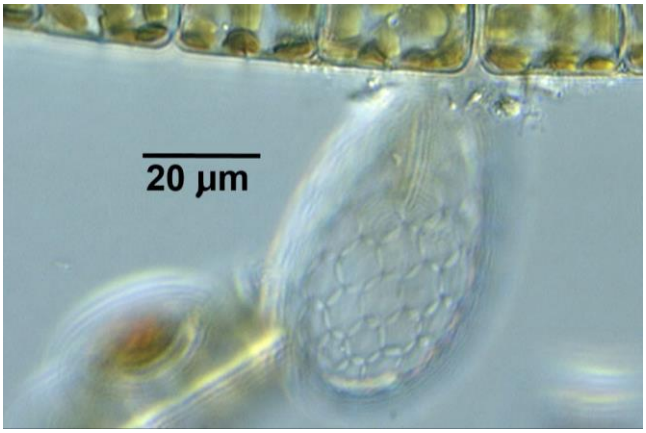

Figure 7. ***Euglypha*** test sitting on algal filament. Photo by Jason Oyadomari, with permission.

Table 1. Species of testate amoebae known from peatlands. *Indicates species closely associated with *Sphagnum*.

*Amphitrema flavum** - zoochlorellae	Hingley 1993	*Heleopera rosea**	Hingley 1993
Amphitrema stenostoma * - zoochlorellae	Hingley 1993	*Heleopera sphagni** - zoochlorellae	Hingley 1993
*Amphitrema wrightianum** - zoochlorellae	Hingley 1993	*Heleopera sylvatica**	Hingley 1993
*Arcella discoides**	Hingley 1993	*Hyalosphenia cuneata*	Hingley 1993
*Arcella gibbosa**	Hingley 1993	*Hyalosphenia elegans** - zoochlorellae	Hingley 1993
*Arcella hemisphaerica**	Hingley 1993	*Hyalosphenia minuta*	Hingley 1993
Arcella mitrata	Hingley 1993	*Hyalosphenia ovalis*	Hingley 1993
Arcella polypora	Hingley 1993	*Hyalosphenia papilio** - zoochlorellae	Hingley 1993
*Arcella vulgaris**	Hingley 1993	*Lecythium hyalinum*	Hingley 1993
*Assulina muscorum**	Hingley 1993	*Lecythium mutabile*	Hingley 1993
*Assulina seminulum**	Hingley 1993	*Lesquereusia epistomium*	Hingley 1993
*Bullinularia indica**	Hingley 1993	*Lesquereusia inaequalis*	Hingley 1993
Campascus minutus	Hingley 1993	*Lesquereusia modesta**	Hingley 1993
Centropyxis aculeata group*	Hingley 1993	*Lesquereusia spiralis**	Hingley 1993
*Centropyxis arcelloides**	Hingley 1993	*Nebela barbata**	Hingley 1993
*Centropyxis cassis**	Hingley 1993	*Nebela bigibbosa**	Hingley 1993
*Corythion dubium**	Hingley 1993	*Nebela carinata**	Hingley 1993
Corythion pulchellum	Hingley 1993	*Nebela collaris**	Hingley 1993
Cryptodifflugia compressa	Hingley 1993	*Nebela dentistoma**	Hingley 1993
Cryptodifflugia eboracensis	Hingley 1993	*Nebela flabellum**	Hingley 1993
Cryptodifflugia ovalis	Hingley 1993	*Nebela galeata**	Hingley 1993
Cryptodifflugia oviformis	Hingley 1993	*Nebela griseola**	Hingley 1993
Cryptodifflugia penardi	Hingley 1993	*Nebela lageniformis**	Hingley 1993
Cryptodiflugia pulex	Hingley 1993	*Nebela marginata**	Hingley 1993
Difflugia amphoralis	Hingley 1993	*Nebela militaris**	Hingley 1993
*Difflugia bacilliarum**	Hingley 1993	*Nebela minor**	Hingley 1993
*Difflugia bacillifera**	Hingley 1993	*Nebela parvula**	Hingley 1993
Difflugia constricta	Hingley 1993	*Nebela penardiana**	Hingley 1993
Difflugia curvicaulis	Hingley 1993	*Nebela tenella*	Mazei & Tsyganov 2007/08
Difflugia globularis	Bovee 1979	*Nebela tincta**	Gilbert *et al*. 2003
Difflugia globulus	Hingley 1993	*Nebela tubulosa**	Hingley 1993
*Difflugia oblonga**	Hingley 1993	*Nebela vitraea**	Hingley 1993
Difflugia pyriformis	Bovee 1979	*Phryganella acropodia*	Hingley 1993
*Difflugia rubescens**	Hingley 1993	*Placocista jurassica*	Hingley 1993
*Difflugia tuberculata**	Hingley 1993	*Placocista spinosa**	Hingley 1993
*Difflugia urceolata**	Hingley 1993	*Portigulasia rhumbleri*	Hingley 1993
*Euglypha ananthophora**	Hingley 1993	*Pseudochlamys patella*	Hingley 1993
Euglypha brachiata	Hingley 1993	*Quadrulella symmetrica**	Hingley 1993
*Euglypha ciliata**	Hingley 1993	*Pseudodifflugia compressa*	Hingley 1993
Euglypha cristata	Hingley 1993	*Pyxidicula cymbalum*	Hingley 1993
Euglypha filifera	Hingley 1993	*Sphenoderia dentata*	Hingley 1993
*Euglypha rotunda**	Hingley 1993	*Sphenoderia fissirostris*	Hingley 1993
Euglypha scutigera	Hingley 1993	*Sphenoderia lenta**	Hingley 1993
*Euglypha strigosa**	Hingley 1993	*Sphenoderia macrolepis*	Hingley 1993
*Euglypha tuberculata**	Hingley 1993	*Trigonopyxis arcula**	Hingley 1993
Heleopera lata	Hingley 1993	*Trinema enchelys**	Hingley 1993
*Heleopera petricola**	Hingley 1993		

Figure 8. ***Heleopera*** sp. test with protoplast. Photo by Yuuji Tsukii, Protist Information Server, with permission.

The nature of peatlands may account for their prominent testate amoeba fauna (Booth & Zygmunt 2005). ***Sphagnum*** itself is particularly rich in species (Hingley 1993; Mazei *et al*. 2007). The amoebae are able to live in the thin film of water in the concavity of ***Sphagnum*** leaves (Figure 9; Corbet 1973). Mazei *et al*. (2007) found 59 species of testate amoebae among the ***Sphagnum*** plants of a bog in Volga Highland in Russia. Among these, 24 were common and the minimal richness was three species in a sample. Interestingly, the highest densities of organisms occurred in the driest bog habitats, but predictably, the diversity was lowest (3 species), with ***Arcella arenaria*** (Figure 10) the most common. At medium levels of humidity, the number of species was greater (13-16), with ***Nebela tenella*** (Figure 11) and ***Hyalosphenia elegans*** (Figure 12) being the most common. Low oxygen concentrations reduced densities by 50-65%. When oxygen was not limiting, however, both abundance and species richness increased with depth. At high humidity, the dominant taxa were ***Hyalosphenia papilio*** (Figure 13) and ***Heleopera sphagni*** (Figure 14). But not all of these testae were occupied by live amoebae. The number of living individuals ranged 35-75% of the testae found.

Figure 9. ***Sphagnum papillosum*** showing the hood leaf tips that provide a concavity for water that houses amoeboid protozoa. Photo by Michael Lüth, with permission.

Lamentowicz and Mitchell (2005) found 52 taxa of testate amoebae in ***Sphagnum*** peatlands of northwestern Poland. In a later study, in Poland's largest peatland complex, Lamentowicz *et al*. (2007) found 32 taxa of testate amoebae. In most of the ten sites in this complex, species composition was dominated by ***Hyalosphenia papilio*** (Figure 13), ***Cyclopyxis arcelloides*** (see Figure 15), and ***Hyalosphenia elegans*** (Figure 12); ***Amphitrema flavum*** (Figure 16, Figure 17) was among the most numerous.

Figure 10. ***Arcella arenaria*** test. Photo by Yuuji Tsukii, Protist Information Server, with permission.

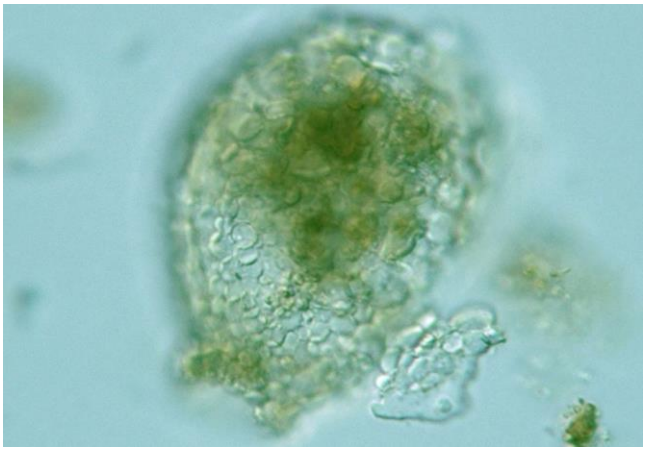

Figure 11. ***Nebela tenella*** test with protoplast. Photo by Yuuji Tsukii, Protist Information Server, with permission.

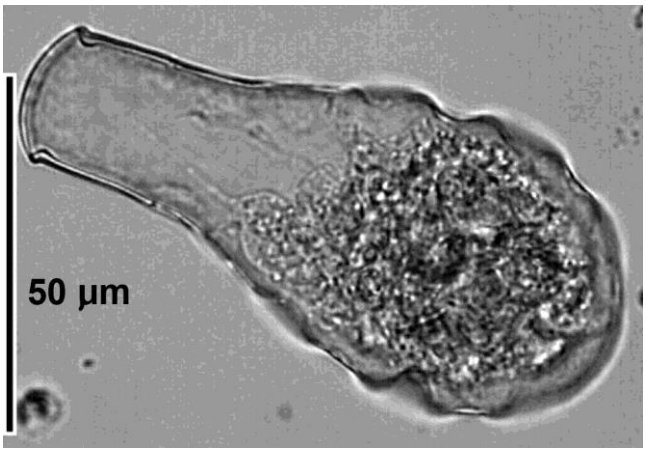

Figure 12. ***Hyalosphenia elegans*** test. Photo by Edward Mitchell, with permission.

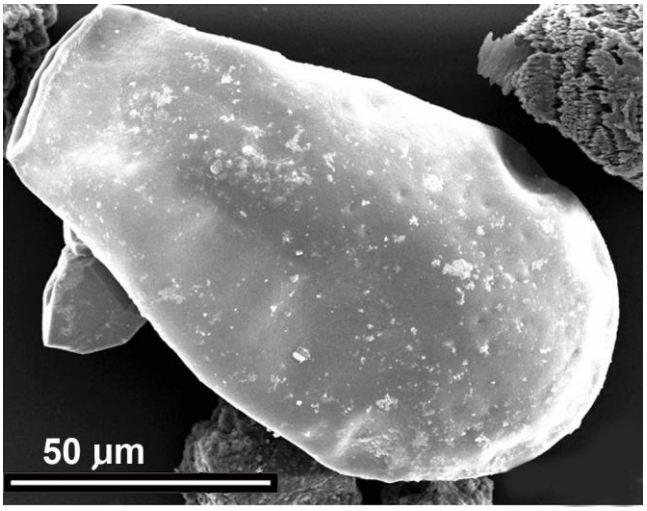

Figure 13. ***Hyalosphenia papilio*** test. Photo by Edward Mitchell, with permission.

Figure 14. ***Heleopera sphagni*** living cell and test. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Lamentowicz and Mitchell (2005) identified three groups of testate taxa, based on depth to water table (DWT) and *p*H: **high DWT & low *p*H**, **low DWT & low *p*H**, and **high *p*H & mid-range DWT**. Species tolerance increases with dryness, with a pattern that reflects that of ***Sphagnum***. That is, changes in the water table depth have more effect on those species in wet habitats than on those in drier microhabitats. This appears to indicate that those in dry microhabitats are specialists for drought.

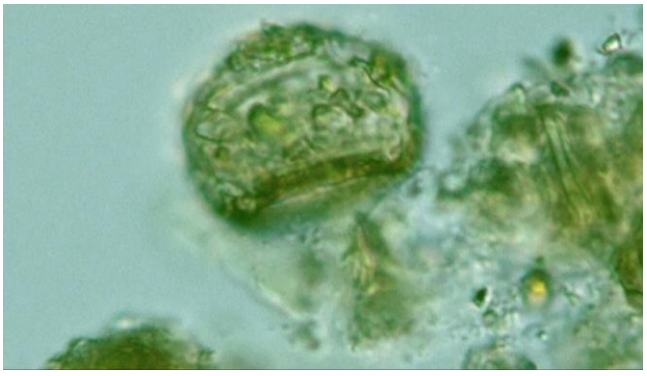

Figure 15. ***Cyclopyxis***, a testate rhizopod. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Corbet (1973) found several species that are apparently confined to the ***Sphagnum*** habitat: ***Amphitrema flavum*** (Figure 16-Figure 17), ***A. wrightianum*** (Figure 18-Figure 19), ***A. stenostoma*** (Figure 20), ***Hyalosphenia elegans*** (Figure 12), and ***H. papilio*** (Figure 13). ***Cryptodifflugia ovalis*** (Figure 21) and ***Amphitrema flavum*** (Figure 16) can live within the hyaline cells of ***Sphagnum*** leaves, entering through the pore and experiencing constant moisture.

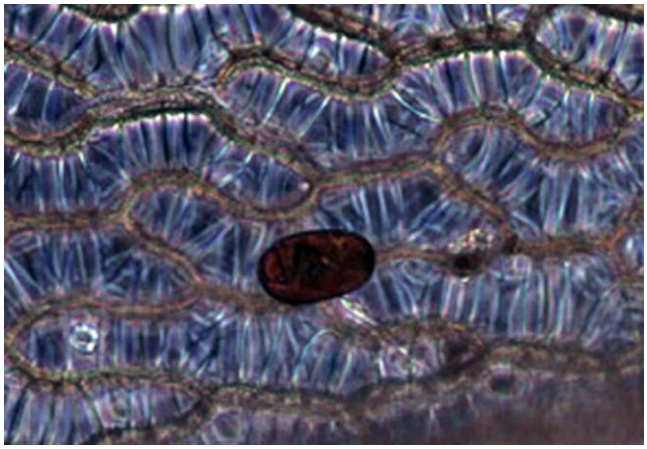

Figure 16. Several species, such as this rhizopod [***Amphitrema*** (=*Archerella*) ***flavum***] are confined to the ***Sphagnum*** habitat. It is shown here in a ***Sphagnum*** leaf. Photo by Edward Mitchell, 2004. From Genome News Network, The Wet World of Moss <http://www.genomenewsnetwork.org/articles/2004/03/04/moss.php>, with permission.

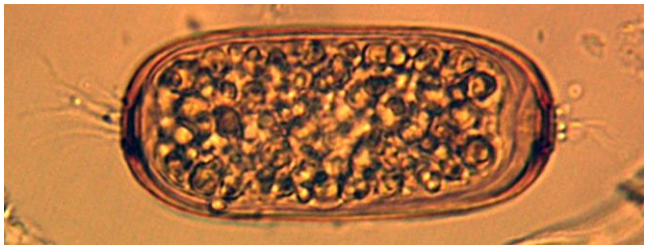

Figure 17. ***Amphitrema*** (*Archerella*) ***flavum*** showing pseudopods. Photo by Edward Mitchell, with permission.

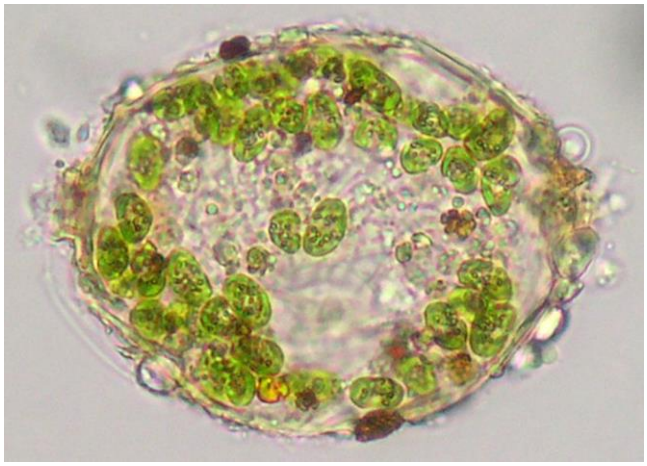

Figure 18. ***Amphitrema wrightianum*** showing ingested chloroplasts. Photo by Edward Mitchell, with permission.

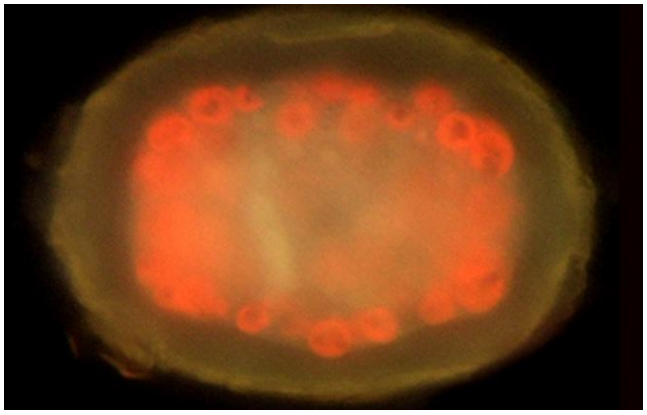

Figure 19. ***Amphitrema wrightianum*** using fluorescence to show ingested chloroplasts. Photo by Edward Mitchell, with permission.

Figure 20. ***Amphitrema stenostoma*** test with sand grains and living protoplast with included chloroplasts. Photo by Yuuji Tsukii, Protist Information Server, with permission.

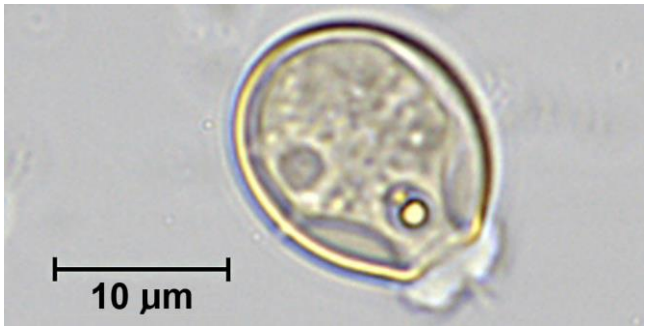

Figure 21. ***Cryptodifflugia ovalis*** showing living cell and extruded protoplasm. Photo by William Bourland, with permission.

Those species that characterize ***Sphagnum*** hummocks (Figure 22) in the western Carpathians [***Nebela militaris*** (Figure 23), ***N. tincta*** (Figure 24), ***Assulina muscorum*** (Figure 25), ***Heleopera petricola*** (Figure 26)] seem intolerant of the mineral-rich fens (Opravilová & Hájek 2006). Only ***Corythion dubium*** (Figure 27) and ***Nebela bohemica*** occupy both. The Euglyphidae were dominant in all these habitats and were nearly the exclusive testate inhabitants of the moderately rich fens. Hyalospheniidae, on the other hand, characterized the extremely acid habitats, particularly in ***Sphagnum*** hummocks. The overall vegetation was the best predictor of the testate protozoan composition, and the composition of the bryophyte assemblage was the second most important predictor.

Figure 22. ***Sphagnum warnstorfii*** hummock. Photo by Michael Lüth, with permission.

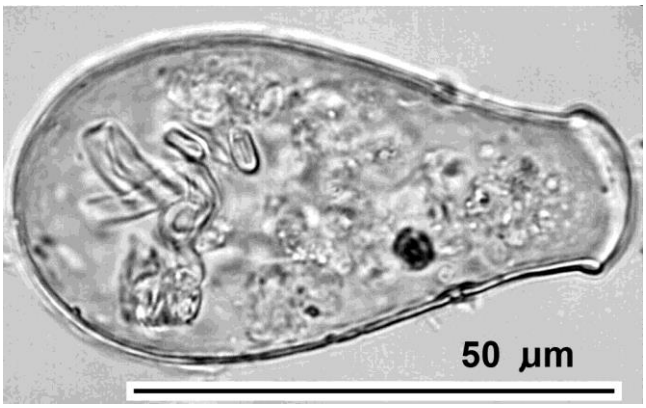

Figure 23. Test of ***Nebela militaris***. Photo by Edward Mitchell, with permission.

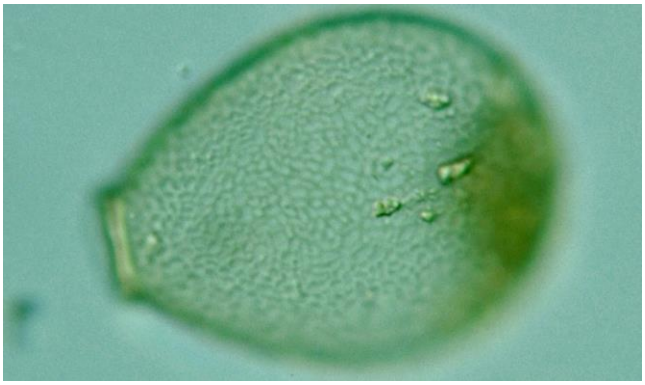

Figure 24. ***Nebela tincta*** test. Photo by Yuuji Tsukii, Protist Information Server, with permission.

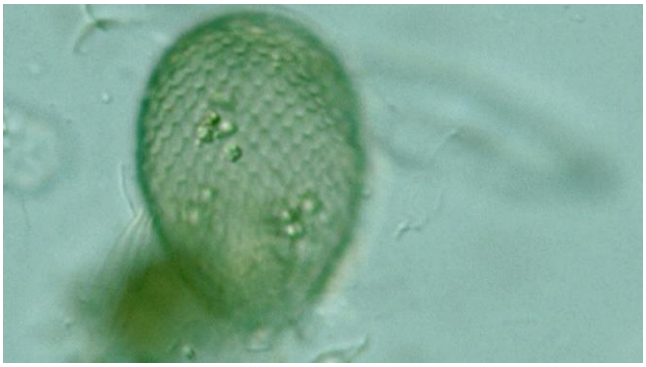

Figure 25. ***Assulina muscorum*** test. Photo by Yuuji Tsukii, with permission.

Figure 26. ***Heleopera petricola*** test beside a desmid. Photo by Yuuji Tsukii, with permission.

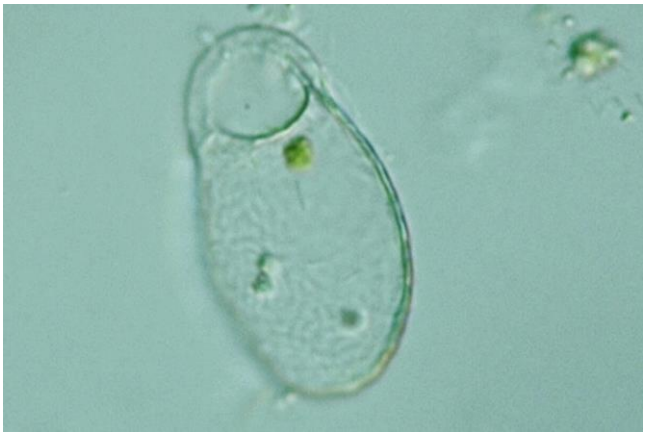

Figure 27. ***Corythion dubium***. Photo by Yuuji Tsukii, with permission.

Mazei and Tsyganov (2007/08) reported on a number of taxa in the ***Sphagnum*** peatlands of Russia. In a single bog, they found 63 taxa comprising 21 genera. They found two different communities, one that lived in the ***Sphagnum*** "quagmire" and one that lived in the bottom sediments of the drainage. The detritivores from the bottom sediments included ***Arcella gibbosa***, ***A. vulgaris***, ***A. hemisphaerica***, ***A. discoides***, ***A. intermedia***, ***A. mitrata***, ***Centropyxis aculeata sphagnicola***, ***Cyclopyxis kahli***, ***Difflugia glans***, ***Lesquereusia spiralis***, ***Netzelia tuberculata***, and ***Phryganella hemisphaerica***. Those species typical of ***Sphagnum*** were ***Archerella flavum***, ***Euglypha cristata***, ***Difflugia juzephiniensis***, ***Cryptodifflugia compressa***, ***Nebela militaris***, and ***Sphenoderia fissirostris***. Those inhabiting both the ***Sphagnum*** mats and the quagmire included ***Assulina seminulum***, ***A. muscorum***, ***Bullinularia indica***, ***Centropyxis aculeata***, ***Difflugia globulosa***, ***D. parva***, ***Euglypha ciliata***, ***Hyalosphenia elegans***, ***Nebela tenella***, and ***N. tincta***. Other species are not so specific and occur in both of the major bog communities: ***Arcella arenaria***, ***Euglypha laevis***, and ***Trigonopyxis arcula***.

But even within the ***Sphagnum*** quagmire, Mazei and Tsyganov (2007/08) found three types of testate amoebae communities. The **xerophilous** (dry-loving) community could be found in hummocks made of ***Polytrichum strictum***, ***Sphagnum papillosum***, and ***S. angustifolium***. These dry hummocks house a community characterized by ***Assulina muscorum***, ***A. seminulum***, and ***Cryptodifflugia compressa***. The lawns of ***Sphagnum palustre*** and ***S. magellanicum*** make a wet community characterized by ***Heleopera sphagni***, ***Hyalosphenia papilio***, ***H. elegans***, and ***Nebela tenella***. Submerged ***Sphagnum riparium*** is characterized by an association of ***Cyclopyxis eurystoma***, ***Heleopera sphagni***, ***Hyalosphenia papilio***, and ***Phryganella hemisphaerica***. Available moisture, determined by depth from the water table, separated the communities. The greatest homogeneity occurs in the moist areas in the middle of the quagmire, whereas dry habitats have the greatest diversity. On the other hand, a greater proportion of amoebae were alive in the moist areas (36-45%) compared to 22-27% of those in dry habitats.

Medium and Rich Fens

Bryophytes of rich fens (Figure 28) differ greatly from those of ***Sphagnum*** bogs and poor fens, and so do the protozoa. To utilize fully the testate protozoa to reconstruct peatland history, as discussed later in this chapter, it is important to understand these faunal differences. Opravilová and Hájek (2006) studied the spring fens of the Western Carpathians in the Czech Republic and Slovakia to fill in this rather large gap in our knowledge. They found that two species [***Paraquadrula irregularis*** (Figure 29, Figure 30) and ***Centropyxis discoides*** (see Figure 31)] were essentially restricted to fens, while seven rhizopod species characterized the bryophytes there. In moderately rich ***Sphagnum*** fens, ***Arcella discoides*** (Figure 32) was characteristic. In poor fens, testate protozoan species of bryophyte lawns were closely tied to moisture and overlapped widely with those of poor fen sediments and moderately rich fens: ***Nebela collaris*** (Figure 33), ***Phryganella acropodia***, ***Sphenoderia fissirostris***.

Figure 28. ***Limprichtia*** (=*Drepanocladus*) ***revolvens*** in a rich fen. Photo by Michael Lüth, with permission.

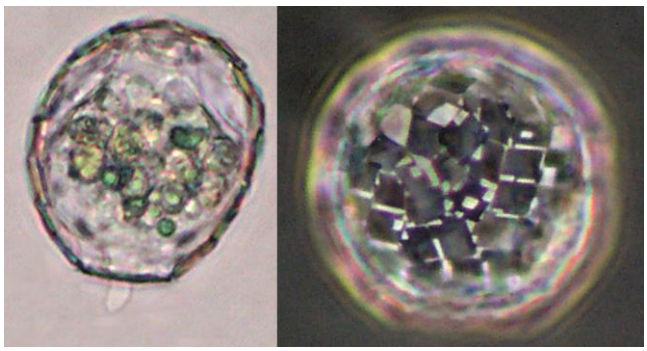

Figure 29. ***Paraquadrula*** sp. showing test. Photos by Edward Mitchell, with permission.

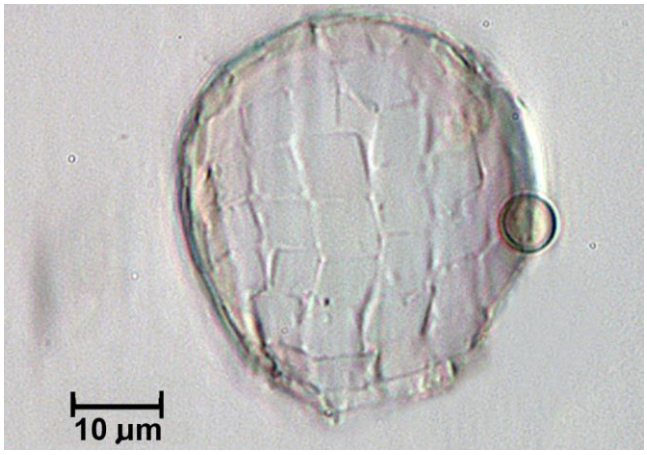

Figure 30. ***Paraquadrula irregularis***. Photo by William Bourland, with permission.

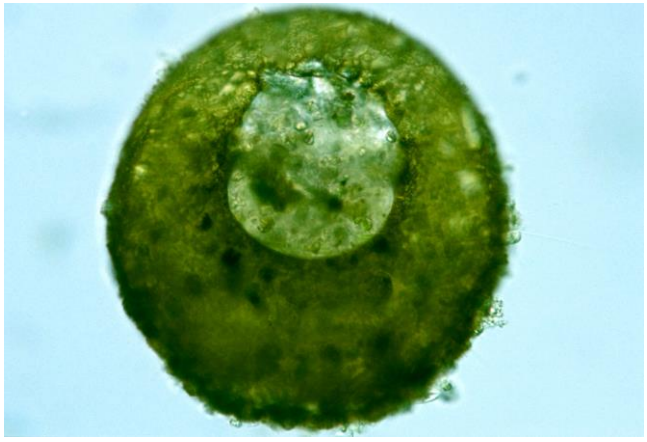

Figure 31. ***Centropyxis ecornis***. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Figure 32. ***Arcella discoides*** test and protoplast. Photo by Yuuji Tsukii, Protist Information Server, with permission.

The protozoan species of ***Sphagnum*** fens in the Czech Republic and Slovakia are very similar to those known elsewhere, with ***Amphitrema flavum*** (Figure 34), ***A. wrightianum*** (Figure 34), and ***Hyalosphenia papilio*** (Figure 35), being optimal in wet microhabitats, but also tolerating higher mineral concentrations (Meisterfeld 1979b; Charman & Warner 1992; Tolonen *et al.* 1992; Booth 2001; Schnitchen *et al.* 2003; Booth & Zygmunt 2005; Lamentowicz & Mitchell 2005; Opravilová & Hájek 2006). In the drier poor fens, the dominant species are ***Assulina muscorum*** (Figure 25), ***A. seminulum*** (Figure 36), ***Arcella catinus*** (Figure 37), ***Nebela militaris*** (Figure 23), ***N. bohemica***, ***Trigonopyxis arcula*** (Figure 38), and ***Corythion dubium*** (Figure 39). ***Corythion dubium*** also occurs in moderately rich fens (Beyens *et al.* 1986; Tolonen *et al.* 1994; Bobrov *et al.* 1999; Mitchell *et al.* 2000b; Opravilová & Zahrádková 2003; Vincke *et al.* 2004).

Figure 33. ***Nebela collaris*** test and cell. Photo by Yuuji Tsukii, Protist Information Server, with permission.

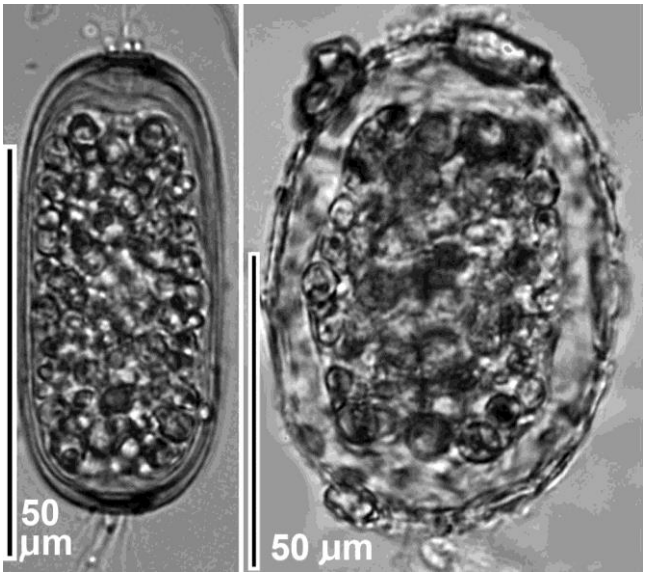

Figure 34. **Left:** ***Amphitrema flavum***. **Right:** ***Amphitrema wrightianum***. Photos by Edward Mitchell, with permission.

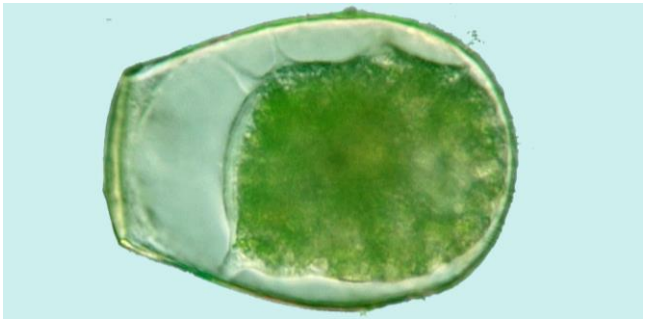

Figure 35. ***Hyalosphenia papilio***. Photo by Yuuji Tsukii, with permission.

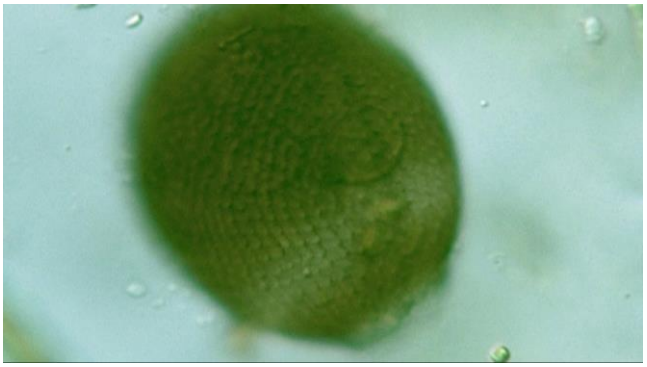

Figure 36. ***Assulina seminulum***. Photo by Yuuji Tsukii, with permission.

Figure 37. ***Arcella catinus*** test. Photo by Yuuji Tsukii, Protist Information Server, with permission.

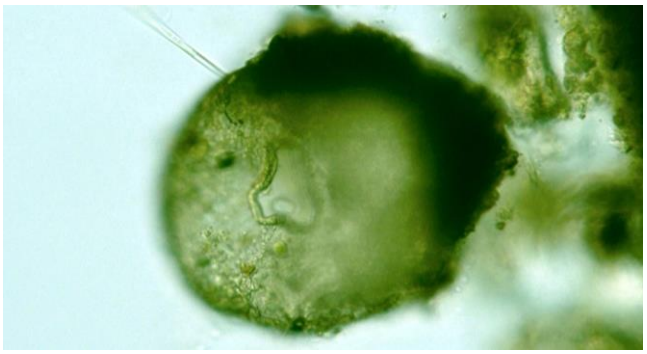

Figure 38. ***Trigonopyxis arcula***. Photo by Yuuji Tsukii, Protist Information Server, with permission.

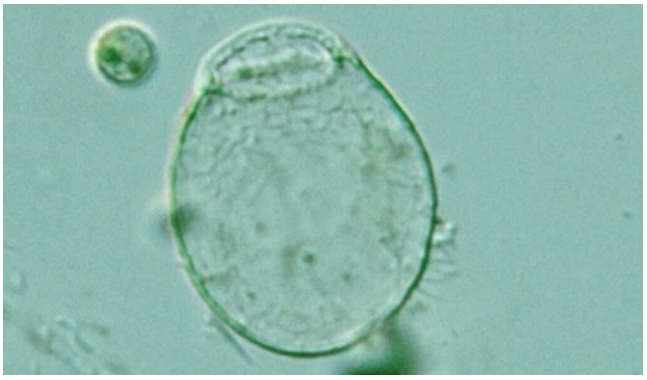

Figure 39. Test of ***Corythion dubium***. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Among the "brown mosses" (Figure 40, Figure 41,) of calcareous fens, ***Centropyxis cassis***, ***Cyclopyxis kahli***, ***Cyphoderia ampulla*** (Figure 42), ***Difflugia glans***, ***Quadrulella symmetrica*** (Figure 43), and ***Trinema enchelys*** (Figure 44) often predominate (Mattheeussen *et al.* 2005; Opravilová & Hájek 2006). There is indeed a gradient of species from poor to rich fens, with moisture being an important variable in the poor fens and bogs (Opravilová & Hájek 2006; Hájek *et al.* 2011). Interestingly, the sediments of poor acidic fens support a species composition similar to that of bryophyte tufts of mineral rich fens (Opravilová & Hájek 2006).

Figure 40. ***Tomentypnum nitens***, a brown moss common in fens. Photo by Michael Lüth, with permission.

Figure 41. ***Scorpidium scorpioides***, a brown moss common in fens. Photo by Michael Lüth, with permission.

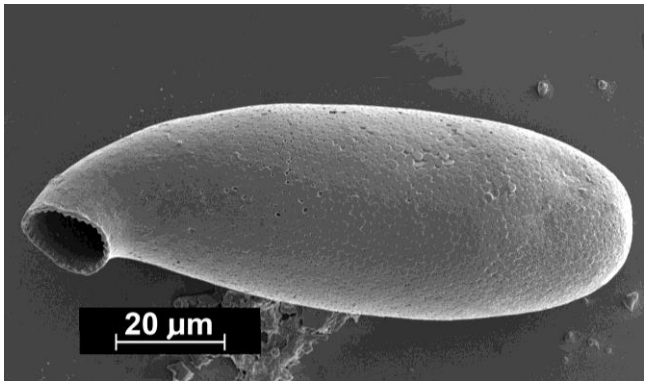

Figure 42. ***Cyphoderia ampulla*** test. Photo by Edward Mitchell, with permission.

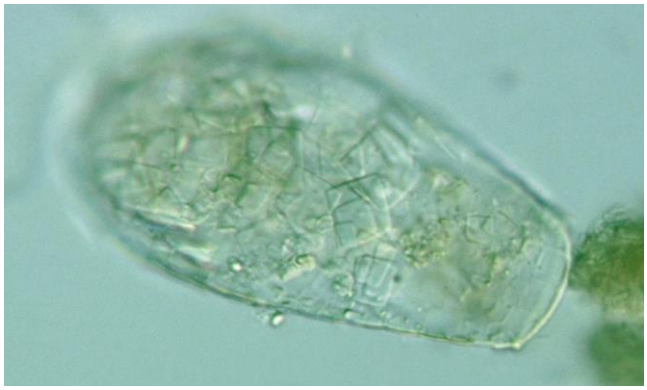

Figure 43. ***Quadrulella symmetrica***. Photo by Yuuji Tsukii, with permission.

Figure 44. ***Trinema enchelys***. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Successional Stages

Differences occur not only between peatlands, but also in different stages of the same peatland, an important factor in permitting us to reconstruct the past history of peatlands. Mazei and Bubnova (2007) demonstrated 42 species in the initial stage of a transitional bog. Early stages were characterized by widespread species such as ***Assulina muscorum***, ***Arcella arenaria***, ***Phryganella hemisphaerica***, and ***Euglypha laevis***, whereas the sphagnobionts such as ***Nebela***, ***Hyalosphenia***, and ***Heleopera*** were absent. Vertical differences had not developed because the species that characterize the different depths had not yet become established.

Kishaba and Mitchell (2005) carried out a 40-year study on the ***Sphagnum***-inhabiting rhizopods to determine successional trends in the Swiss Jura Mountains. They took their first samples in 1961 following peat cutting and lateral drainage that resulted in an increase in tree cover, especially at the edges. By the second sampling date in 2001, three species had increased significantly in mean relative abundance: ***Nebela tincta*** *s. l.* (+97%), ***Bullinularia indica*** (+810%), and ***Cyclopyxis eurystoma*** (+100%; absent in 1961), while two species decreased significantly: ***Assulina muscorum*** (-63%) and ***Euglypha compressa*** (-93%). Furthermore, testate amoebae communities differed among hummocks, lawns, and hollows. Nevertheless, there were no significant changes in the overall community structure between the two sampling dates.

Recent, moist stages of succession in the Jura Mountains of Switzerland were dominated by ***Hyalosphenia papilio***, with ***Archerella flavum*** indicating wet, acidic conditions at one site (Laggoun-Défarge *et al*. 2008). Drier acid conditions supported a greater abundance of ***Nebela tincta*** and ***Assulina muscorum***. ***Corythion dubium*** also indicated dry, acid conditions.

Habitat Needs

Mieczan (2007) examined the habitat preferences of eleven testate amoebae in Eastern Poland peatlands. He found that low *p*H (4.5) favored the amoebae (see also Warner & Chmielewski 1992; Tolonen *et al*. 1994; Charman & Warner 1997; Mitchell *et al*. 1999; Bobrov *et al*. 2002; Booth 2002; Lamentowicz & Mitchell 2005). These acidophilic taxa were dominated by ubiquitous and common taxa, with ***Arcella vulgaris***, ***Assulina muscorum***, ***Euglypha*** sp., and ***Hyalosphenia*** sp. having a distinct preference for low *p*H. The distribution pattern seemed to be controlled by moisture (no surprise there), whereas the total numbers and biomass had a positive correlation with *p*H and total organic carbon content of the water. Heal (1964) found that *p*H was a major factor accounting for differences between bog and fen communities in Great Britain. In addition to moisture and *p*H, the trophic status and concentration of mineral nutrients, including calcium, can play a role in determining numbers (Tolonen *et al* 1992).

In the Western Carpathians along the border between the Czech Republic and Slovakia, Hájková *et al*. (2011) attempted to ascertain the factors that determined which micro-organisms comprised communities at two sites within mineral-rich ***Sphagnum***-fens and four within mineral-poor ***Sphagnum***-fens. They found that community composition correlated with water *p*H, conductivity, calcium concentration, and ***Sphagnum*** dominance. The types of mosses often played a major role, with a significant positive correlation between testate amoebae and ***Sphagnum*** (***S. fallax***, ***S. flexuosum***, ***S. palustre***, ***S. papillosum***). On the other hand, there was a significant negative correlation with "crawling dense tufts" of bryophytes (***Cratoneuron filicinum***, ***Palustriella commutata***, ***P. decipiens***). There was no correlation with crawling loose tufts (***Brachythecium rivulare***, ***Calliergonella cuspidata***, ***Plagiomnium ellipticum***, ***P. elatum***) or erect species (***Bryum pseudotriquetrum***, ***Fissidens adianthoides***, ***Philonotis caespitosa***). These community distinctions suggest that growth form was an important factor. Growth form often determines water-holding ability, a strong factor in distribution of testate amoebae.

Food

Although many of the protozoa associated with bryophytes are detritus/bacterial feeders, some common species prefer a different diet. In one ***Sphagnum*** peatland 17.4% of ***Nebela collaris*** *sensu lato* most frequently preyed upon micro-algae (45%, with diatoms comprising 33% of total prey), spores and fungal mycelia (36%), and large ciliates, rotifers, and small testate amoebae in smaller numbers (Gilbert *et al*. 2003). However, 71% of the food content could not be identified because it was partially decomposed. It appears that when the mosses are

sufficiently wet, most of the food organisms are immobile, senescent, or dead. However, as the water film on the moss becomes thin, it constrains the ciliates and micro-Metazoa, causing them to be a more easily consumed part of the diet.

Vertical Distribution

Peatlands have both horizontal and vertical differences in moisture, light availability, nutrient availability, and *p*H (Figure 45). The testate rhizopods are distributed both vertically and horizontally with respect to these differences (Meisterfeld 1977).

Figure 45. ***Sphagnum teres***, demonstrating the zonation from light to dark within the peat. Photo by Michael Lüth, with permission.

Perhaps because of the multiple factors involved in vertical and horizontal distribution, distinct patterns are difficult to discern. Mazei and Tsyganov (2007/8) considered the aggregations of species to blend into each other in patches of varying sizes. For ***Assulina muscorum*** and ***A. seminulum***, patch size seemed to correlate with shell size. As sample size increases, heterogeneity increases. Communities can be distinct on as small as a 1-cm patch, but more typically the minimum size does not exceed several cm. In their study in the Middle Volga region of Russia, Mazei and Tsyganov found that associated with the upper parts of ***Sphagnum*** the typical species were ***Assulina flavum***, ***A. muscorum***, ***A. seminulum***, ***Heleopera sphagni***, and ***Hyalosphenia papilio***. Among these, ***Assulina flavum***, ***Heleopera sphagni***, and ***Hyalosphenia papilio*** were mixotrophs, requiring light for their algal symbionts (see sub-chapter 2-4), whereas ***Hyalosphenia elegans*** lacked symbionts and lived in a deeper community. The upper 0-3 cm layer typically had low rhizopod species richness but the highest abundance in the peatlands. And among those tests the proportion of living organisms was highest (75%). Species of ***Amphitrema*** likewise occur in the upper layer because of the need for light by their symbionts (Gilbert & Mitchell 2006).

When conditions are somewhat drier, the vertical structure of the communities is more pronounced (Mazei & Tsyganov 2007/08). Low moisture typically resulted in empty tests, especially in ***Assulina*** species. Survival of the rhizopod species is facilitated by the **r-strategies** of reproduction in which these small organisms are able to increase rapidly in response to the return of favorable conditions.

One additional factor that may play a role in distribution for some species is available nitrogen (Mitchell & Gilbert 2004). In cutover peatlands fertilized with N for three years, richness of the peatland was high (22 taxa of testate amoebae), but diversity of individual samples was low (6.6), attesting to the diversity of the habitat. Species richness increased with depth, but there was little response to differences in N levels in the tested range of additions of 0, 1, 3, or 10g N m^{-2} yr^{-1} for three years. Only ***Bullinularia indica*** was significantly more abundant in N-fertilized plots. Although the vertical distributions differed among species, there seemed to be no relationship to either shell type or metabolism type. In the top segment (0–1 cm), ***Assulina muscorum*** was most abundant. At 3–5 cm ***Heleopera rosea***, ***Nebela militaris***, and ***Phryganella acropodia*** were most abundant.

It is not surprising that the taxa with zoochlorellae occur in the green portions of ***Sphagnum***. In Obersee near Lunz, Austria, the dominant taxa hosting zoochlorellae are ***Amphitrema flavum***, ***Heleopera sphagni***, ***Hyalosphenia papilio*** (Laminger 1975). ***Centropyxis aculeata*** likewise lives there, but without zoochlorellae. Activity among the rhizopods extended down to 18 cm, with some of the less mobile testate species extending to a depth of 45 cm. Some of the species that lived down to depths of 12 cm were species that also inhabited forest mosses (***Euglypha laevis***, ***Trinema enchelys***, and ***T. lineare***). At 18 cm, several sediment species of ***Difflugia*** occurred (***D. amphora***, ***D. corona***, ***D. acuminata***, ***D. lebes***). Furthermore, the populations of ***Centropyxis aculeata*** exhibited characteristics of sediment-inhabiting taxa, *i.e.* tests covered with mineral particles and no spines.

Horizontal Differences

Not only do the testate amoebae have a vertical zonation in peatlands, but their horizontal distribution varies as well, reflecting habitat patchiness (Meisterfeld 1977; Mitchell *et al*. 2000a; Mazei and Tsyganov 2007/8). In the Swiss Jura Mountains, spatial structure accounted for 36% of the observed variation. Imbedded in the horizontal variability, Mitchell *et al.* found that microtopography played an important role, indicating that in just 0.25 m^2 conditions are not uniform and present a different picture from that seen on a macroscale. In this case, the horizontal scale responds to differences in distance from the water table, whereas vertically within a ***Sphagnum*** mat, light, moisture, and detrital accumulation all differ. The horizontal scale also differs in *p*H and ion concentrations, both of which are lower on hummocks than in hollows. These differences in turn cause differences in the bacteria, fungi, algae, and other protozoa available for food. And hummock ***Sphagnum*** species are usually different from hollow species, having different morphologies that provide different sorts of spaces and different abilities to retain water and detritus.

Seasonal Differences

Communities of protozoa can differ among seasons, just as moisture and other conditions change in their habitat. As a result, species richness will fluctuate, as will abundance. In a ***Sphagnum*** bog in the Middle Volga region of Russia, species richness increases as the vegetation increases during May to September (Mazei &

Tsyganov 2007/2008). At the same time, evenness and species diversity have little variation. Species abundance changes are less well defined seasonally, most likely being more responsive to available moisture that is not directly tied to season.

Spring brings melting snow in most peatlands (Figure 46), with dormant protozoa awakening as the environment becomes more hospitable. In spring, dominant **hygrophilous** (water-loving) species in the Middle Volga region included ***Heleopera sphagni***, ***Hyalosphenia papilio***, and ***Nebela tincta*** (Mazei Tsyganov 2007/08). This dominance is replaced in summer and autumn by ***Hyalosphenia elegans*** and ***Nebela tenella***. The **xerophilous** (dry-loving) community is slightly different and the diversity is somewhat greater. In spring, ***Assulina muscorum***, ***Heleopera sphagni***, and ***Nebela tincta*** dominate, being replaced in summer by a community of ***Assulina seminulum***, ***Euglypha ciliata***, ***Hyalosphenia elegans***, and ***Nebela tenella***. Yet another community appears in autumn, dominated by ***Assulina seminulum***, ***Cryptodifflugia compressa***, and ***Trigonopyxis arcula***.

Figure 46. As the snow recedes, the ***Sphagnum*** habitat will witness the awakening of water-loving protozoa that have remained dormant throughout the winter. Photo courtesy of Andres Filipe Baron Lopez in Alaska.

Heal (1964) found slightly different species in his study of six fen and bog sites in Great Britain, but the patterns were similar. Three species – ***Amphitrema flavum***, ***Hyalosphenia papilio***, and ***Nebela tincta*** *sensu lato* – had peak numbers from May until October. They then either encysted or died. For ***Hyalosphenia papilio***, light is a controlling factor because this protozoan typically contains photosynthetic zoochlorellae (Figure 47). Although many of these rhizopods can reproduce every eight days by cell division, field evidence suggests that they have fewer than ten generations per year. This low number of generations limits their ability to respond to improved environmental conditions. These three species thus accounted for a biomass of 1.0 g m^{-2} and 30.2 x 10^6 individuals m^{-2} in Great Britain. Nevertheless, Heal found 98 species and varieties in these six sites with a distribution similar to that found in northern fens and bogs.

One mechanism that maintains closely related species in different niches is their seasonal requirements. For example, ***Hyalosphenia papilio*** is dominant in spring, ***H. elegans*** in summer-autumn. ***Nebela tincta*** occurs in spring, ***N. tenella*** in summer. ***Assulina muscorum*** appears in spring, ***A. seminulum*** in summer.

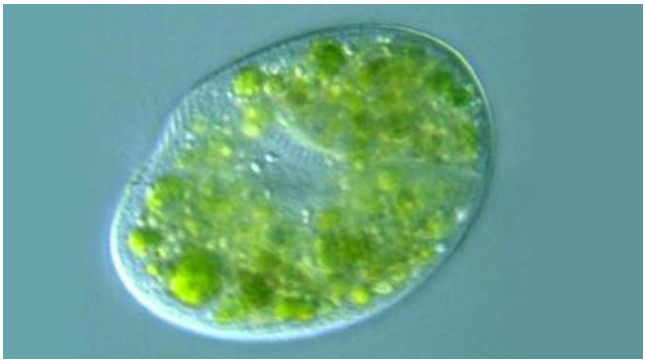

Figure 47. This protozoan, possibly ***Bryometopus***, contains zoochlorellae. Photo by Yuuji Tsukii, with permission.

Pollution

Pollution can alter the peatland rhizopod communities. Mitchell *et al*. (2003) found that CO_2 enrichment caused a change in structure, but not in total biomass. Heterotrophic bacterial biomass increased by 48%, whereas that of the testate amoebae decreased by 13%. They suggested that the increase in CO_2 may have caused an increase in ***Sphagnum*** exudates that in turn stimulated an increase in bacterial biomass.

Ozone Loss and UV-B Radiation

One of the effects of pollution with refrigerants has been the destruction of ozone in the upper atmosphere. This loss of ozone itself is not dangerous; it is not an oxygen source for life on Earth. But it is a critical shield of the UV rays from the sun, high energy wavelengths that are lethal to many forms of life. This is especially realized in polar regions.

Searles *et al*. (1999) examined the effects of this "ozone hole" in regions of Tierra del Fuego, southern Argentina, and Chile. Their study was experimental. They chose areas with an ozone hole and used plastic film filters to reduce the UV-B reaching the habitat, in this case a ***Sphagnum*** bog. The growth and pigment concentrations of ***Sphagnum*** (***S. magellanicum***) were virtually unaffected during the three months of the experiment. The surprise was that both **testate amoebae** and **rotifers** in this ***Sphagnum*** habitat became more numerous under the near-ambient UV-B radiation (*i.e.*, under the reduced ozone filter of the ozone hole) than they were under reduced UV-B radiation resulting from the plastic filter (Figure 48). The protozoa were dominated by ***Assulina muscorum*** with some individuals of ***A. seminulum***, ***Nebela***, ***Heleopera***, and ***Euglypha*** species.

Protozoan communities are also sensitive to other pollutants (Nguyen-Viet *et al*. 2008). As in testate amoebae on ***Barbula indica*** in Viet Nam, the testate amoebae on ***Sphagnum fallax*** declined in species richness, total density, and total biomass and community structure was altered with added lead (Nguyen-Viet *et al*. 2007, 2008). NO_2 also caused a decline in diversity, but not in density in the more heavily polluted city center of Besançon, France (34.8 ± 9.5 µg m^{-3}) compared to the peripheral area (14.6 ± 4.7 µg m^{-3}) (Nguyen-Viet *et al*. 2004). ***Paraquadrula irregularis*** differed dramatically, being present in all peripheral samples and completely

absent in the city; no other species differed significantly between the two areas.

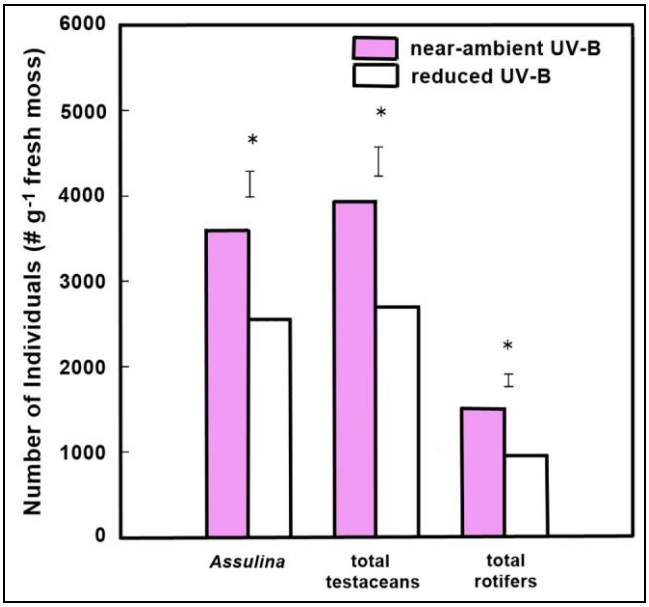

Figure 48. Effects of UV-B radiation on **protozoa** and **rotifers** living among ***Sphagnum magellanicum*** in the Antarctic ozone hole. Vertical lines represent standard error of differences between treatments. Redrawn from Searles *et al*. 1999.

Reconstruction of Past Climate

Diatoms and siliceous protozoan plates and scales are common in peat preparations (Douglas & Smol 2001). However, these are seldom used in peatland reconstruction because it is nearly impossible to identify the species from these fossils. Fortunately, rhizopod tests are often present in the same samples and require the same preservation techniques as the diatoms and scales. Since the species are generally identified by their shells, there has been considerable recent interest in using these testate shells for determining the past history of the peatlands.

Both the mosses and the amoebae are well conserved over time, ***Sphagnum*** because of its resistance to decay, and for testate amoebae it is the unique test (housing) that likewise resists decay (Meisterfeld & Heisterbaum 1986; Coûteaux 1992). Both can be identified thousands of years later.

Even fossil evidence supports the richness of the ***Sphagnum*** fauna (Douglas & Smol 1988). Fortunately, the species are cosmopolitan (Smith & Wilkinson 2007) and community structure varies little with geography (Mitchell *et al*. 2000b; Booth & Zygmunt 2005), differing much less between geographic areas than does the tracheophyte community (Mitchell *et al.* 2000b). Even if species have diverged into sister species and become endemic (Mitchell & Meisterfeld 2005), it will often be possible to use these species complexes as indicators. On the other hand, we may be plagued by species that have diverged physiologically without changing morphologically, thus permitting them to live under different conditions but without being recognizable as different taxa.

As already implied, the testate amoebae have a distribution pattern that mimics that of ***Sphagnum*** (Lamentowicz & Mitchell 2005). Wet habitat species of both are more sensitive to changes in the water table depth than are those of dry habitats such as hummocks. Species of dry habitats are more tolerant of desiccation. Consequently, the testate amoeba shells from the past permit us to reconstruct the past history of peatlands (van Geel 1976; Beyens & Chardez 1987; Warner 1991; Wilmshurst 1998; Bobrov *et al*. 1999; Charman *et al*. 1999; McGlone & Wilmshurst 1999a, b; Foissner 1999; Mauquoy & Barber 2002; Schnitchen *et al*. 2003; Zygmunt *et al*. 2003; Booth *et al*. 2004; Gilbert & Mitchell 2006; Payne *et al*. 2006; Payne & Mitchell 2007; Mitchell *et al*. 2008). Payne *et al*. (2008) demonstrated that even such diverse regions as Turkey, North America, and Europe have similar testate communities. Because of the unique assemblages of testate amoebae associated with moisture conditions of the peat mosses worldwide and the effects of climate change on them, the testate amoebae are useful for reconstructing past climate.

Surface moisture of **bogs** (with only precipitation as a water source), in particular, is controlled by climate. Reconstruction of the testate amoeba history permits reconstruction of the historic surface moisture, and that permits reconstruction of past rainfall. The amoebae are so fine tuned to the water table that they can help a researcher to predict the water table within less than 2 cm (Payne & Mitchell 2007). For example, Hughes *et al*. (2006) used testate amoebae to identify fourteen distinct phases of near-surface water tables in a coastal plateau bog in eastern Newfoundland, with corresponding time periods beginning 8270, 7500, 6800, 5700, 5200, 4900, 4400, 4000, 3100, 2500, 2050, 1700, 600, and 200 calibrated years BP. The final drainage of glacial Lake Agassiz accounts for the first major phase of pool development at 8400 calibrated years BP, followed by the Ungava lakes ca 7500-6900 calibrated years BP. From 7500 BP to the present the reconstructed bog surface water and the stacked ice rafted debris of the North Atlantic Ocean correlate well. At the same time, long-term changes in air masses may have been a contributing factor. Records of "cosmogenic isotope flux," when compared to the bog surface wetness reconstruction, suggest that reduced solar radiation presents a consistent link with increased bog surface wetness during the Holocene.

But the models are not always so accurate. Payne *et al.* 2006) were only able to estimate within 9.7 cm of water table depth, and that was after exclusion of selected data. They attributed the less than ideal fit to inaccuracies in water-table measurements, very large environmental gradients, and recent climatic change in the study area. Their *p*H estimates were only off by 0.2, which is within the error range of many *p*H measuring techniques.

Using weighted averaging to model species abundance as measures of water table depth and soil moisture, Bobrov *et al*. (1999) calculated optima and tolerance of species niches. They found that each group of taxa tends to have a gradient of hydrological preference. For example, a wet to dry gradient is exhibited among species of the ***Trigonopyxis arcula*** group: ***T. arcula*** var. ***major*** > ***T. arcula*** > ***T. minuta***. Likewise, the ***Assulina-alkanovia*** group exhibits wet to dry as ***A. seminulum*** > ***A. muscorum*** > ***Hyalosphenia elegans*** and the ***Trinema*** *lineare* group appears as ***T. lineare*** var. ***truncatum***/***T. lineare*** > ***T.***

lineare var. ***terricola***. Interestingly, these species gradients also follow a large to small size gradient, indicating that small taxa survive better than large ones under dry conditions. It appears that having spines is a disadvantage in dry habitats. Within the genera ***Euglypha*** and ***Placocista***, the spined forms (Figure 49) are typical of wetter habitats than are those with shorter spines or no spines. These relationships suggest that the most effective use of these rhizopods for reconstruction of the past water regime is to use the lowest possible level of identification, *i.e.* species and varieties.

One interesting question that arises is whether these spined taxa are really different species and varieties, *i.e.*, genetically different, or if they represent ecotypes – morphological representations of the microenvironment where they occur. For example, Laminger (1975) found that ***Centropyxis aculeata*** from greater depths lacked spines and their tests were covered with mineral particles. To test the possibility of ecological morphs, Booth (2001) examined four of the most common taxa in two Lake Superior coastal wetlands: ***Arcella*** spp., ***Assulina*** spp., ***Centropyxis cassis*** type, and the ***Nebela tincta-parvula-collaris*** group. Using 74 microsites, Booth compared testate amoeba assemblages based on percent moisture, depth to water table, *p*H, porosity, depth of living moss, and associated bryophyte and tracheophyte species. He used such parameters as test length and aperture diameter for amoebae from at least ten microsites. In general, there was little correlation between morphological variation and microenvironmental parameters. However, in the ***Nebela tincta-parvula-collaris*** group, the test size correlated significantly with *p*H ($r^2 = 0.68$). Booth concluded that these testate rhizopods are sensitive indicators of water-level and *p*H changes.

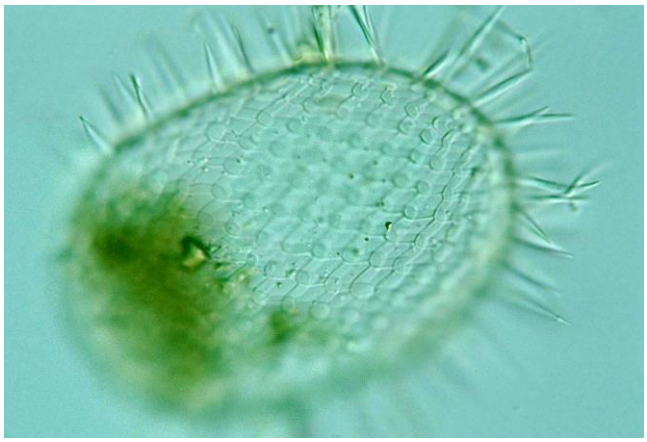

Figure 49. ***Placocista spinosa***, a rhizopod typical of wet habitats. Photo by Yuuji Tsukii, with permission.

Many more studies on testate amoeba ecology have been conducted in the Northern Hemisphere than elsewhere (Mitchell & Meisterfeld 2005), making their comparisons somewhat easier. In the East Carpathian peatlands of eastern Europe, species such as ***Amphitrema flavum*** (Figure 17) and ***Hyalosphenia papilio*** (Figure 12) indicate wet conditions were present (Schnitchen *et al*. 2003). ***Assulina muscorum*** (Figure 50), ***Difflugia pulex***, and ***Nebela militaris*** (Figure 23) indicate that conditions were dry.

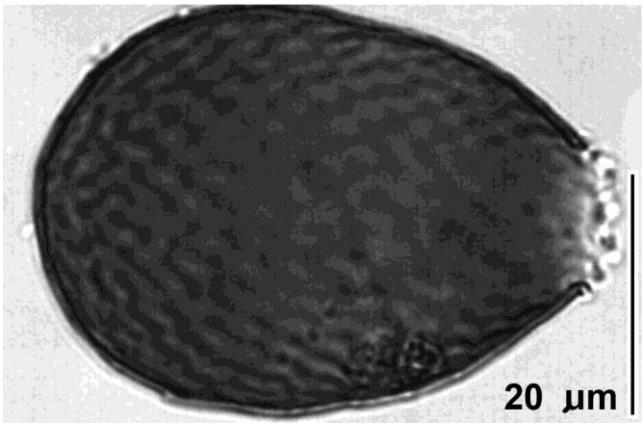

Figure 50. Test of ***Assulina muscorum***. Photo by Edward Mitchell, with permission.

In ***Sphagnum*** peatlands of the Rocky Mountains, USA, surface moisture determines the distribution of fossil rhizopods (Zygmunt *et al*. 2003). As suggested by the ecological studies of Lamentowicz and Mitchell (2005) and others (Booth & Zygmunt 2005), Booth and Jackson (2001) could track the history of an ombrotrophic peatland in northeastern Lower Michigan, USA, through 2800 years of changes using the moisture preferences of these organisms. Such fossils as these testae of rhizopods permit us to determine past changes in water table depth (Warner 1991; Woodland 1998; Woodland *et al*. 1998). Booth and Zygmunt (2005) further argued that the widespread geographic nature of the rhizopod relationships makes interpretation of their community structure widely applicable.

Charman and Warner (1997) used 60 samples from 14 peatlands in Newfoundland, Canada, and found 40 species that occurred in more than six samples. They used these to model the relationships between the species and the water table depth. Species with narrow tolerances provided the best indicators. These include ***Amphitrema stenostoma***, ***Arcella discoides***, ***Cryptodifflugia sacculus***, ***Difflugia bacillifera***, ***Nebela carinata***, ***Nebela griseola***, ***Nebela marginata***, ***Quadrulella symmetrica***, and ***Sphenoderia lenta***. Charman and Warner recommend that for most accurate results modern constructs from wide regions should be used to interpret the data from peatland cores that represent palaeoecological time series.

Fortunately, most of the testate amoeba taxa are cosmopolitan, permitting the studies from the Northern Hemisphere to be used in less-studied areas such as New Zealand (Charman 1997; Wilmshurst 1998). In fact, Charman (1997) modelled the hydrologic relationships of protozoa and ***Sphagnum*** in peatlands of New Zealand and suggested that "palaeohydrology could be accurately inferred from fossil faunas."

Schoning *et al*. (2005) used peatland amoebae to reconstruct 125 years of peatland amoebae in Sweden. Unlike the cases in other areas in Europe, the changes in water table correlated primarily with changes in mean annual temperature, whereas in most other studies, precipitation was also an important factor. They caution that spatial differences must be considered in these historic interpretations and thus more study is needed on these influences.

In a Michigan, USA, study, Booth (2002) found that most of the eleven peatlands he studied had similar testate assemblages. As in most other studies, depth to water table was the best predictor of the protozoan assemblages. Nevertheless, within a given peatland, community variability was correlated with environmental heterogeneity, adding support to the suggestion of Schoning *et al.* (2005) regarding spatial considerations. But the testate amoebae in bog/fen habitats also had distinct differences in species between May and late summer-early autumn. Testate amoebae in the swamp community, on the other hand, had no clear difference in community structure between dates. They attributed these differences to the more constant water table and moisture conditions in the swamp.

Warner *et al*. (2007) add further support to the importance of considering seasons, particularly for living rhizopods. In southern Ontario, Canada, the usual factors of soil water content and water table influenced the distribution of amoeboid species and these differ with seasons. But the big differences were in the open bog/fen community, whereas in the swamp community there was no clear seasonal difference between May and August or October.

The historical record will not take us back forever. In their study on bogs in Ontario and Minnesota, Warner and Charman (1994) found that cores spanning the entire Holocene era only exhibited rhizopods present in the last 6500 years. They indicated that the fauna changed from the early rich fens with sedges and brown mosses. At those early stages, the protozoan communities were dominated by ***Cyclopyxis*** and ***Centropyxis***. By 5000 BP, the habitat had become ***Sphagnum***-dominated and the predominant protozoan taxa had shifted to ***Amphitrema flavum***, ***Assulina muscorum***, ***Heleopera sphagni***, and ***Hyalosphenia subflava***. As the habitat became drier, taxa again shifted to ***Nebela griseola***, ***N. militaris***, and ***Trigonopyxis arcula***.

Geographic Differences

Despite a considerable number of studies indicating usefulness of these organisms, use of testate amoebae to determine past habitats can at times be misleading. Harnish examined mires in Central Europe (1927 in Paulson 1952-53) and in Lapland, North Sweden (1938 in Paulson 1952-53), and found that the communities were not similar. Rather, associations from Central Europe did not exist in raised bogs in Lapland. In fact, the ***Amphitrema*** association existed in Lapland, but in different habitats, not raised bogs, whereas in Central Europe it was confined to raised bogs. The ***Hyalosphenia*** type was also absent in the Lapland raised bogs.

Problems in Using Rhizopods

There are caveats in using fossilized amoeba tests to assess past communities of testate rhizopods. Not all tests are equally preserved (Mitchell *et al*. 2007). The Euglyphida, which includes the common ***Euglypha*** species (Figure 51), are an **idiosome** group that secretes its own test and its biosilica plates (Beyens & Meisterfeld 2001). This biological test decays more readily than the testae of the other groups (Mitchell *et al*. 2007). In ***Sphagnum*** peatlands, this differential decay seems to make little difference in the estimations of water table depth. However, in minerotrophic peatlands, with large numbers of this Euglyphida group, the loss of these tests leads to an underestimation of the water table depth. Data on more alkaline fens are lacking, and the community structure there is not well known. If this idiosome group is not dominant there, reconstruction may be more accurate.

Swindles and Roe (2007) likewise found that under conditions of low *p*H, such as found in peatlands, the degree of dissolution was highly variable, but it did not seem to relate to **xenosomic** (using "foreign" materials) vs. **idiosomic** tests. ***Euglypha*** (Figure 51) is particularly susceptible, whereas ***Assulina muscorum*** (Figure 50), ***Amphitrema flavum*** (Figure 34), and ***Trigonopyxis arcula*** (Figure 52) are affected little by acidity. Payne (2007) found similar results by subjecting rhizopod tests to weak acid, nutrient enrichment, and desiccation over 28-months, and used shorter-term experiments with stronger acids in peatlands. He determined that during dry periods the record may be altered by differential preservations of the tests, as demonstrated by significant effects of long-term desiccation and short-term acid treatment at two different concentrations. This consequence could lead to over-estimating water table depths.

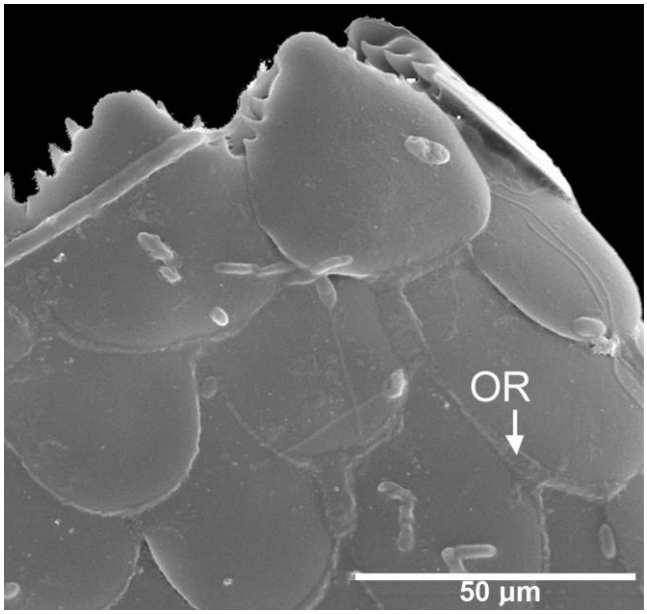

Figure 51. SEM detail of biosilica plates of ***Euglypha penardi***, a protozoan for which the test is especially susceptible to dissolution. Photo by Edward Mitchell, with permission.

Human Influence on Development

In New Zealand, it appears development of ***Sphagnum*** bogs has been dependent on human activity such as clearing or modifying the vegetation, resulting in ***Sphagnum*** dominance (Wilmshurst 1998). In other places, clearing of a peatland means that without human intervention it is gone forever. After such loss, it is often desirable to reconstruct the peatland. Testate amoebae have been used to define the past nature of the peatland for reconstruction purposes (Charman 1997; Charman & Gilbert 1997).

In a Polish peatland, a rapid shift in peat accumulation and lower *p*H occurred ~110-150 years ago, with a shift to

a ***Sphagnum***-dominated poor fen (Lamentowicz *et al*. 2007). The protozoa supported this history. Researchers interpreted this to be a result of forest clearance in surrounding areas. Whereas peatlands are often destroyed by human activity, in some cases those activities make conditions more favorable to peatland development. In this case, ***Sphagnum*** peatland replaced a species-rich poor fen.

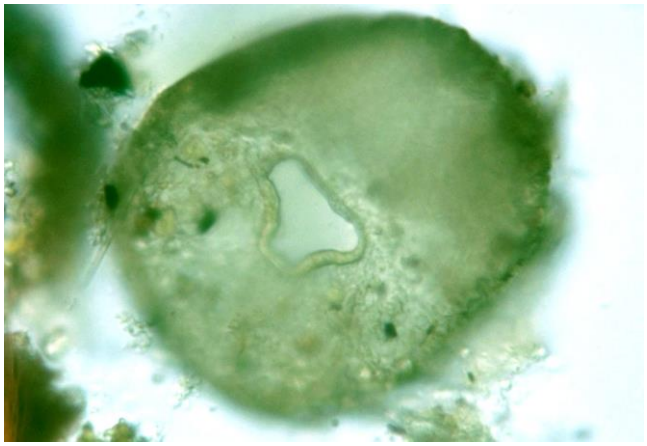

Figure 52. ***Trigonopyxis arcula*** test showing opening for pseudopod. This test is more stable than that of ***Euglypha***. Photo by Yuuji Tsukii, with permission.

Laggoun-Défarge *et al*. (2008) found testate amoebae can be used to reflect disturbances that result from peat harvesting. Where better carbohydrate preservation was present, along with more heterogeneous peat composition, the testate amoebae exhibited a higher diversity, thus serving as a biological indicator of conditions.

Use in Peatland Regeneration

Regeneration of peatlands can use remains of testate amoebae to determine the species to re-introduce or to follow the progress in a less labor-intensive fashion by monitoring the amoebae. In the Jura Mountains, Switzerland, Laggoun-Défarge *et al*. (2008) examined a peatland that had been mined for heating fuel until World War II and found that amoeba communities changed as peatlands changed during regeneration. The *Sphagnum* habitat shifted from moderately acidic, wet conditions to more acidic, drier conditions. During these changes, biomass and mean size of amoebae declined while remaining higher at the undamaged site. At the same time, species richness and diversity increased while density declined. As reported by Mitchell *et al*. (2004), changes in the amoeba community lagged behind that of the returning ***Sphagnum*** community. Moreover, during the forty years of 1961-2001, overall amoeba richness (33) remained unchanged, but richness per sample decreased from 11.9 to 9.6 (Kishaba & Mitchell 2005). Relative abundance changed, with three species increasing significantly [***Bullinularia indica*** (Figure 53) (+810%), ***Cyclopyxis eurystoma*** (+100%, 0 in 1961), ***Nebela tincta*** (Figure 54) (+97%)] and two species declining [***Assulina muscorum*** (Figure 50) (-63%), ***Euglypha compressa*** (Figure 55) (-93%)]. The researchers concluded the expected changes in richness were complete before the 1961-2001 study began.

Jauhianinen (2002) demonstrated in an ombrotrophic bog that the testacean shells were present throughout the vertical profile, whereas in the minerotrophic fen they were numerous only at the surface. As in other studies, moisture conditions were important, but peat composition and minerals also played important roles. Following restoration, species that indicated dry conditions disappeared, whereas the moisture gradient seemed to result in less defined community differences. In fact, the minerals seemed to have a greater effect.

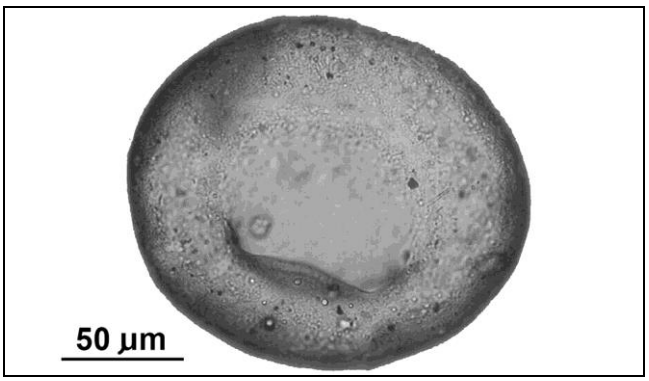

Figure 53. ***Bullinularia indica***. Photo by Edward Mitchell, with permission.

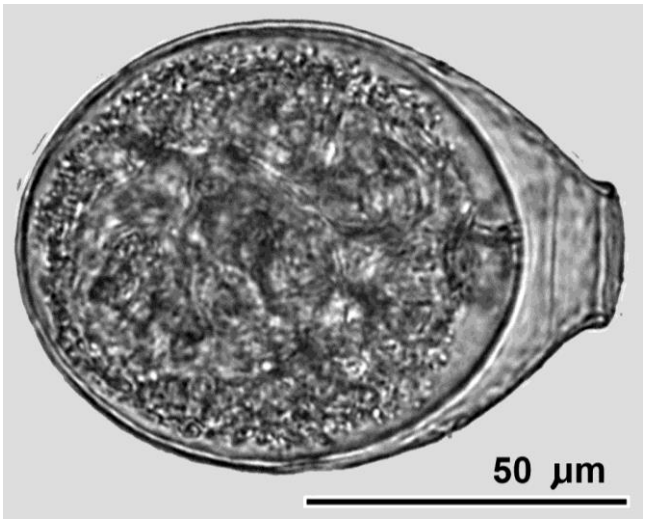

Figure 54. ***Nebela tincta*** test with living amoeba. Photo by Edward Mitchell, with permission.

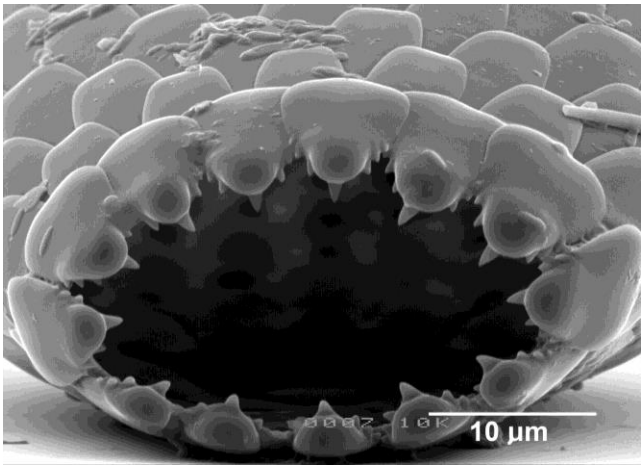

Figure 55. Opening of test of ***Euglypha compressa***. Photo by Edward Mitchell, with permission.

Lamentowicz *et al*. (2008) demonstrated that the testate amoebae record in a Baltic coast peatland in Northern Poland correlated well with the stable isotope data in the same core. The large number of testate protozoans known from peatlands, their relatively cosmopolitan distribution, and the understanding we have of the water table requirements for many of these species provide us with a useful tool for understanding the past history of many peatlands.

Summary

Peatlands support an abundant bryophyte fauna, with ***Amphitrema***, ***Assulina***, ***Corythion***, ***Difflugia***, ***Euglypha***, ***Heleopera***, ***Hyalosphenia***, and ***Nebela*** typically being the most common genera. ***Sphagnum*** sports more species than those found among other mosses or tracheophytes. These taxa are widespread and thus are very reliable indicators of moisture conditions in the peatlands and are less affected by water chemistry than are the tracheophytes.

Diversity is lowest in the driest peatland habitats, but the number of individuals is highest. Abundance increases with depth if oxygen is not limiting. Dry habitat species are more tolerant of changes in water depth than are wet habitat species. Rich fen amoeba species differ from those of acid bogs, but Euglyphidae are prominent in all these habitats. ***Paraquadrula irregularis*** and ***Centropyxis discoides*** are restricted to fens, with ***Arcella discoides*** indicative of rich fens. Detritus forms a major portion of the protozoan diet in the peatlands.

Vertical zonation presents the symbiotic taxa in the light zone at the top of the moss, with those requiring more moisture occurring at the greatest depths. Shell size, *p*H, moisture, light, nutrients, and available food all contribute to the distribution. Horizontal variation results from differences in bryophyte species and microtopography, resulting in differences in distance from water table and in *p*H. Seasonal differences reflect some of these same changes in moisture and food availability and are effective in separating niches of closely related species.

CO_2 enrichment may cause a reduction in testate amoebae while at the same time increasing bacterial biomass. Loss of the ozone filter and consequent increase in UV-B radiation may actually favor some testate amoebae in *Sphagnum* peatlands.

Amoebae form more constant associations in peatlands than do the plants. And testate species, with few exceptions, are well preserved even after death. Therefore, they can serve as appropriate markers of past climates as well as indicators of predisturbance conditions, although tests of some species, especially Euglyphidae, decompose more easily than others and can skew the results. The best indicators are those with narrow tolerance ranges, especially for moisture.

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CHAPTER 2-6
PROTOZOA ECOLOGY

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CHAPTER 2-6
PROTOZOA ECOLOGY

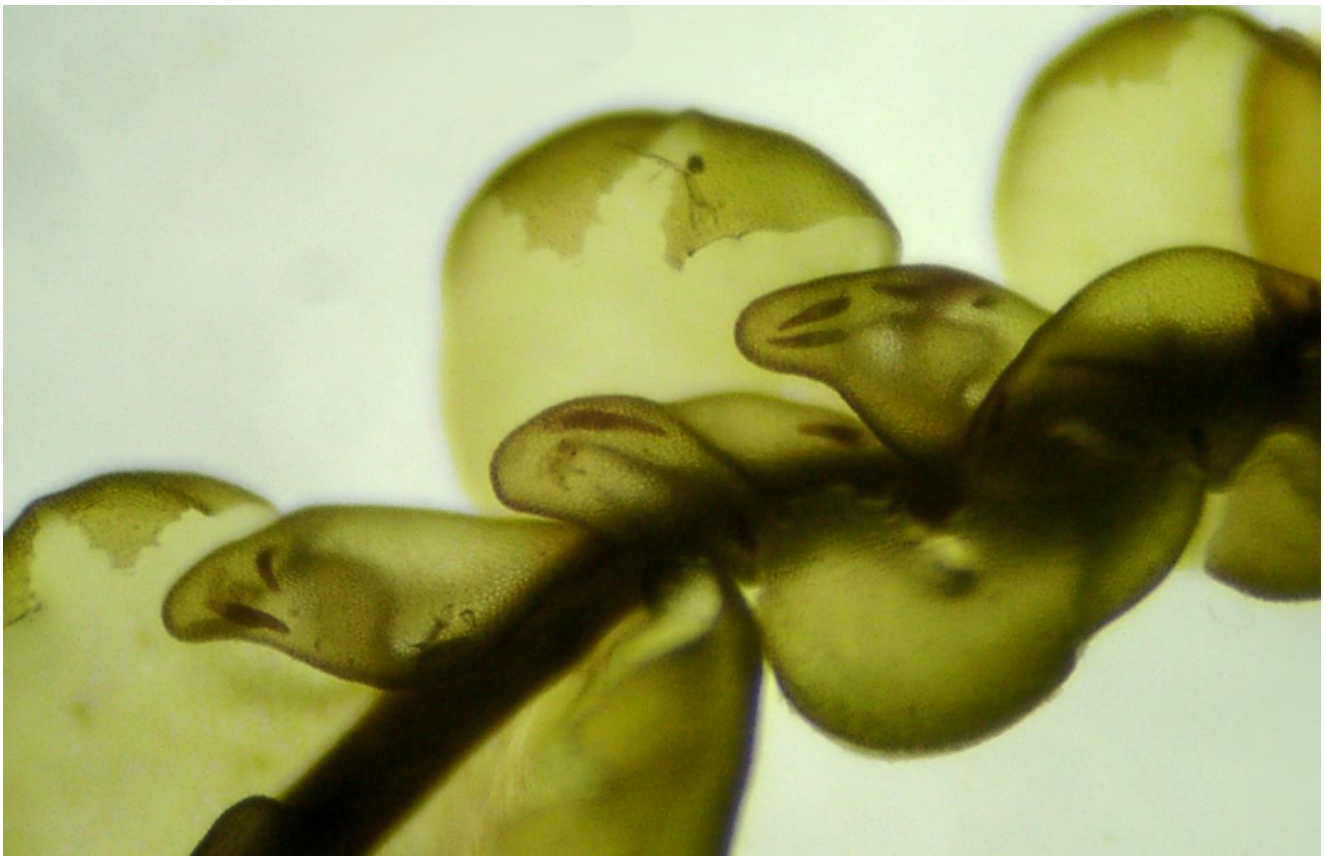


Figure 1. The ciliate protozoan ***Blepharisma americana*** inhabits the lobules of the liverwort ***Pleurozia purpurea***. Photo by Sebastian Hess, with permission.

General Ecology

Protozoa can probably be found on almost any bryophyte if one just looks carefully (Figure 1). Larger protozoa tend to occur in bog habitats (Chardez 1967; Bovee 1979). As drier habitats are examined, the species are smaller and smaller. ***Difflugia*** (Figure 2) species are typical of aquatic mosses; ***Cyclopyxis*** species occur on terrestrial mosses. ***Centropyxis*** species distribution depends on the habitat, with ***C. aculeata*** (Figure 3, Figure 4) in wet locations and ***C. platystoma*** in dry ones. ***Corythion dubium*** (Figure 5), ***Assulina muscorum*** (Figure 6), and ***Trinema lineare*** (Figure 7) occur generally on forest mosses (Chardez 1957; Bovee 1979; Beyens *et al*. 1986), although ***A. muscorum*** also is known from the cells of living ***Sphagnum recurvum*** (Figure 8) (BioImages 1998). ***Corythion pulchellum*** (Figure 9) and ***Trinema complanatum*** (Figure 10) occur only on forest mosses (Chardez 1960; Bovee 1979). ***Nebela collaris*** (Figure 11), ***Centropyxis aculeata***, and ***Hyalosphenia papilio*** (Figure 12) occur on ***Sphagnum*** and other bog mosses, but not on forest mosses (Chardez 1960; Chiba & Kato 1969; Bovee 1979).

Figure 2. ***Difflugia bacillifera*** with diatoms in the test. Note the small desmid beside it. Photo by Yuuji Tsukii, with permission.

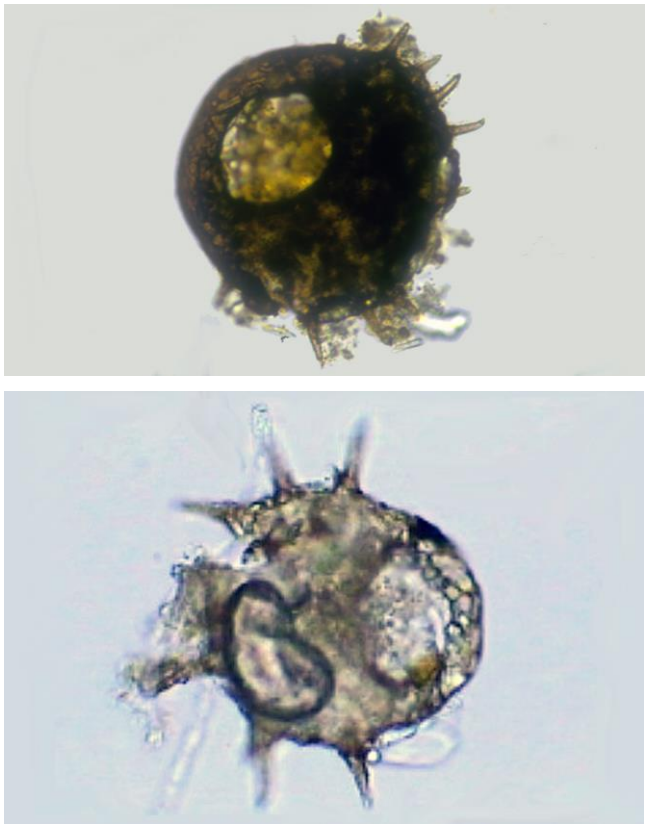


Figure 3. ***Centropyxis aculeata***, a testate amoeba that commonly occurs on bryophyte leaves. Photo courtesy of Javier Martínez Abaigar, with permission.

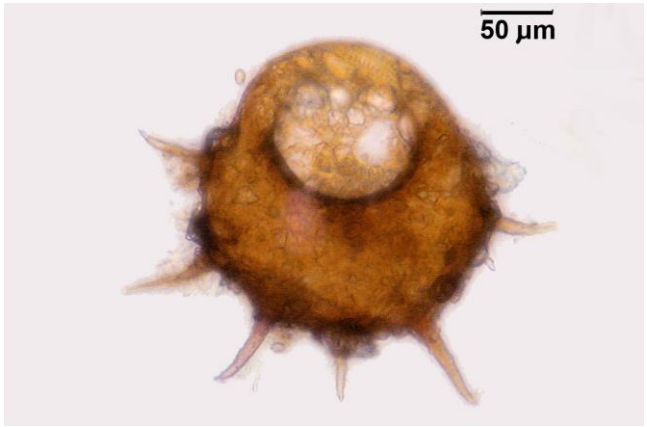


Figure 4. ***Centropyxis aculeata*** test. Photo by William Bourland, with permission.

Figure 5. ***Corythion dubium*** test. Photo by Yuuji Tsukii, with permission.

Figure 6. ***Assulina muscorum***. Photo by Yuuji Tsukii, with permission.

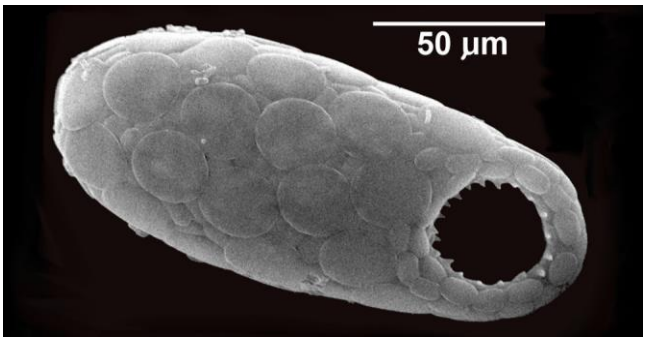


Figure 7. Test of ***Trinema lineare***. Photo by Edward Mitchell, with permission.

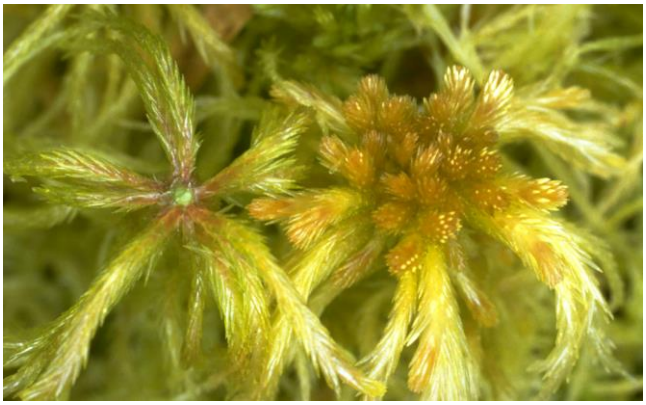


Figure 8. ***Sphagnum recurvum* var. *tenue***, a peatmoss that supports living protozoa in its hyaline cells. Photo by Jan-Peter Frahm, with permission.

Figure 9. ***Corythion pulchellum***. Photo by Yuuji Tsukii, with permission.

Figure 10. ***Trinema complanatum***. Photo by Yuuji Tsukii, with permission.

Figure 11. ***Nebela collaris***. Photo by Yuuji Tsukii, with permission.

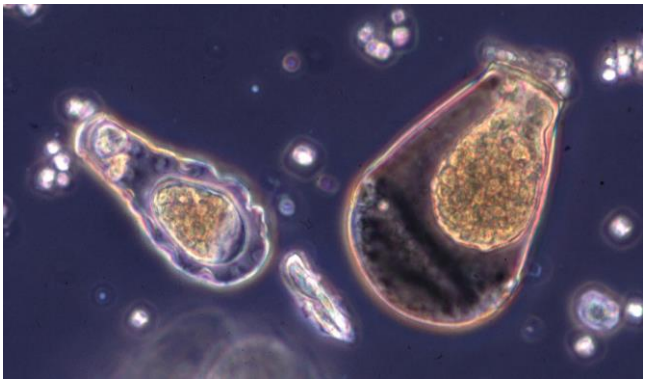


Figure 12. ***Hyalosphenia papilio*** and ***H. elegans***. Photos by Edward Mitchell, with permission.

Protozoa are generally the most numerous invertebrates among the ***Sphagnum*** plants (Figure 8; ntham & Porter 1945). In a Canadian study, flagellates were the most numerous, but testate amoebae are often the most numerous.

Epiphytes

Despite the dryness of aerial habitats, protozoa are common among epiphytic bryophytes, drying and encysting as the bryophytes dry, then reviving, eating, and reproducing when the bryophytes are moist. This habitat may hold many species as yet undiscovered because it is a habitat less frequently studied by protozoologists. Nevertheless, a number of taxa are known from this unique habitat (Golemansky 1967; Casale 1967; Bonnet 1973a, b).

Antarctic

The role of protozoa is particularly important in the Antarctic. On Elephant Island of the South Shetland Islands in the Antarctic, moss carpets and turf form a major part of the habitat available to protozoa (Smith 1972). Mastigophoran (flagellate) moss inhabitants include 15 species. The Mastigophora are not unique to this habitat. Those that were in most of the moss samples also were in samples of grass/soil, clay, or **guano** (accumulation of feces). Furthermore, none of the species that was abundant in the other habitats was absent among bryophytes except ***Tetramitus rostratus***, which was abundant only on guano. The Rhizopoda, including the testate amoebae, seemingly avoided the guano on Elephant Island, whereas 16 species occurred in the bryophyte habitats (Smith 1972). Several of those Rhizopoda present in the grass/soil habitat were not found among the moss samples. Fourteen species of Ciliata occurred among mosses.

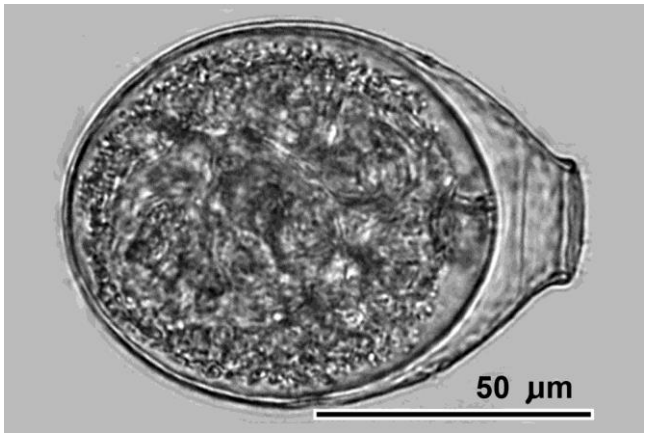


Figure 13. ***Nebela tincta*** test with living amoeba. Photo by Edward Mitchell, with permission.

The small number of Elephant Island moss samples (4 in ***Polytrichum–Chorisodontium*** turf & 5 in ***Brachythecium–Calliergon–Drepanocladus*** carpet) precludes comparison of moss preferences (Smith 1972). The most abundant ciliate, ***Urotricha agilis*** (see Figure 14), was abundant in both turf and carpet. In samples of turf, mean numbers per gram of fresh weight ranged 170-4,500. In carpet they ranged 250 to 7,700. On Signey Island species numbers were higher in moss turf (40), whereas on Elephant Island they were higher in moss carpet (37) than in turf.

Figure 14. ***Urotricha platystoma***. Photo by Yuuji Tsukii, with permission.

Nutrient Cycling

Protozoa are common predators on bacteria and fungi (Hausmann *et al.* 2003), having the role of nutrient cyclers (Mitchell *et al*. 2008). In the Pradeaux peatland in France, the testate ***Nebela tincta*** (Figure 13) consumed mostly micro-algae, especially diatoms, associated with mosses (Gilbert *et al*. 2003). In summer they also consumed large ciliates, rotifers, and other small testate species. Micro-organisms collect between leaves and along stems of ***Sphagnum***. When the system is wet, prey organisms are mostly immobile and often dead, but when conditions are drier and the water film is thin, testate fauna are able to ingest more mobile organisms than usual because these prey are slowed down by lack of sufficient free water for rapid swimming. Although we know little about their role among bryophytes, it is likely that at least in peatlands the role of moss-dwelling protozoans in nutrient cycling is significant (Gilbert *et al*. 1998a, b; Mitchell *et al*. 2008).

Habitat Effects

When protozoa and other inhabitants live on a host, they can alter the host. Insects are well known for the many forms of galls that develop on the host plant. Gradstein *et al*. (2018) discovered a white colony of protozoa, resembling gnathifers, in the swollen shoot tips of the liverwort ***Herbertus sendtneri***. This resulted in cessation of the tip growth and subsequent development of innovations below the tip.

Moss Effects on Soil Habitat

The presence of mosses also affects the micro-organisms found in the underlying soil. Miroschnichenko and coworkers (1975) found that the greatest numbers of micro-organisms were under mosses (compared to other soil substrata) in a community in Russia, and Smith and Headland (1983) found similar results for testate rhizopods on the sub-Antarctic island of South Georgia. Smith (1974a, 1986) found protozoa living among the bryophytes in the South Orkney Islands and Adelaide Island of the Antarctic. Ingole and Parulekar (1990) found that the faunal density, including protozoa, was high in moss-associated sediments. These micro-organisms may account for the ability of some macrofauna to remain within the moss mat throughout a major part of their development by serving as a food source (Smith 1974a, 1986).

Epizoites

Some of the fauna, such as ***Pyxidium tardigradum*** (Figure 17), an **epizoite**, are hitch-hikers. This protozoan is recorded as a **symphoriont** (organism carried by and often dispersed by its host) on two species of tardigrades (Figure 15) [***Hypsibius oberhaeuseri*** (Figure 16) and ***Milnesium tardigradum***] that live among mosses (Land 1964; Morgan 1976). It can be so common on them (up to 35, but more typically 1-3) as to have negative effects on the tardigrade host that must expend extra energy to carry them around (Vicente *et al*. 2008). For this reason, Vicente *et al*. (2008) suggest that it should perhaps be considered a parasite.

Figure 15. **Tardigrade**. Photo courtesy of Filipe Osorio.

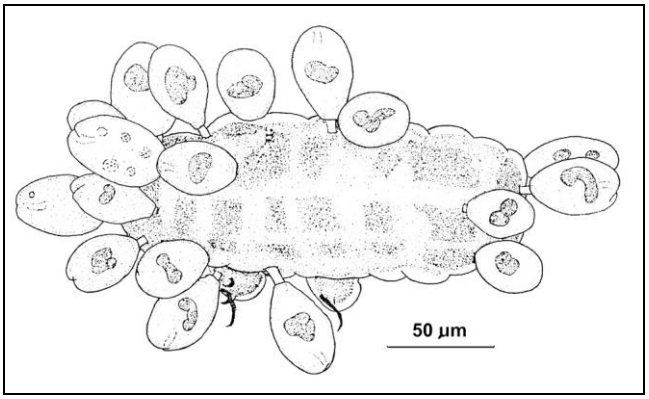


Figure 16. ***Hypsibius oberhaeuseri*** with ***Pyxidium tardigradum*** growing as a symphoriont. Redrawn from Van Der Land 1964.

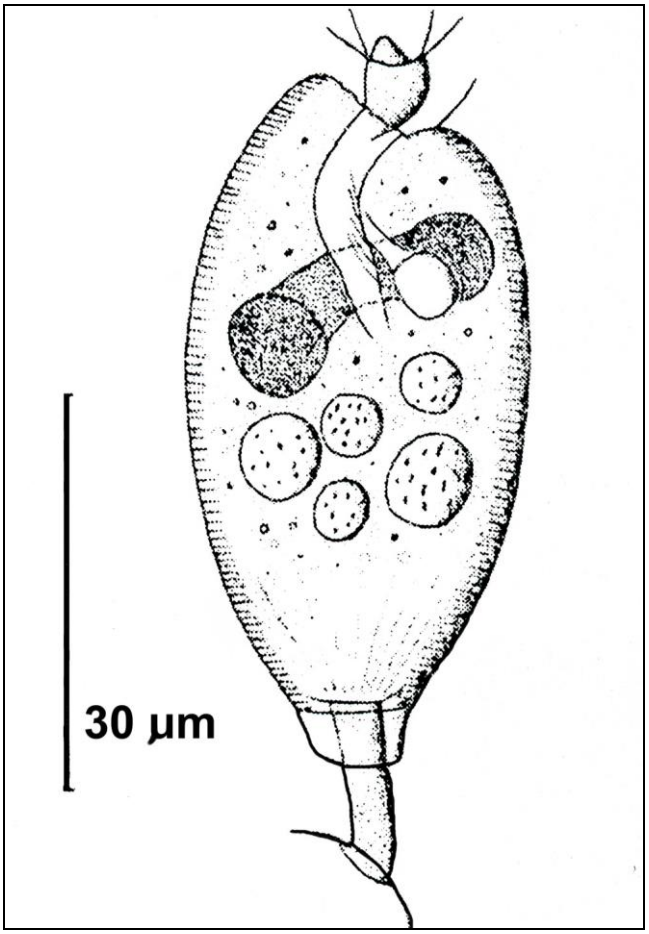


Figure 17. ***Pyxidium tardigradum***, a tardigrade symphoriont. Redrawn from Van Der Land 1964.

Soil Crusts

Protozoan communities associated with cryptogamic soil crusts (Figure 18) have hardly been studied. In a study of only five crusts in southeastern Utah, Bamforth (2008) found 28 species of amoebae, 45 ciliates, and 19 testate amoebae. The number of amoebae ranged 680-2500, ciliates 20-460, and testate amoebae 2400-2500 per gram dry mass of crust. As crusts succeeded from *Microcoleus* (Cyanobacteria) to lichens to bryophytes, numbers of protozoa increased, perhaps reflecting longer periods of internal moisture in the crusts. Predominant taxa are somewhat different from cosmopolitan ones we have seen elsewhere, comprised mostly of ***Acanthamoeba*** (Figure 19), ***Hartmanella*** (Figure 20), **Vahlkampfidae** (Figure 21), two species of ***Colpoda*** (Figure 22), several other colpodids, ***Polyhymenophora*** sp., and species of ***Cryptodifflugia*** (Figure 23) and ***Difflugiella***.

Figure 18. Soil crust with the moss ***Syntrichia ruralis***. Photo by Michael Lüth, with permission.

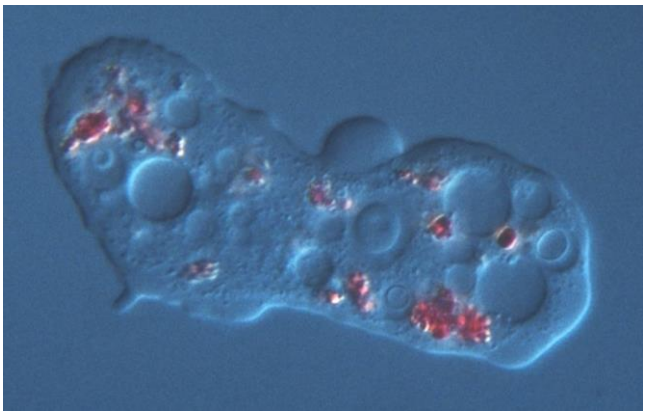


Figure 19. ***Acanthamoeba*** showing ingested carmine particles. Photo by Akira Kihara, with permission.

Figure 20. ***Hartmanella***. Photo by Yuuji Tsukii, with permission.

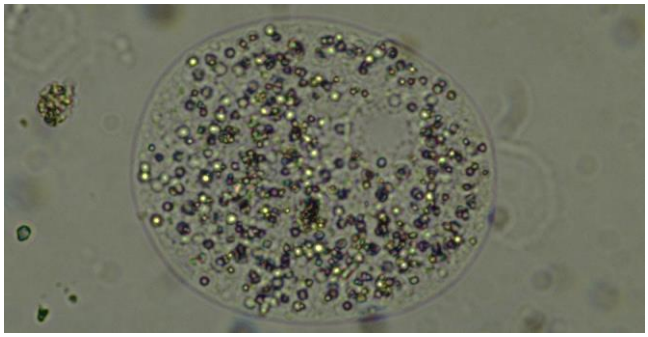
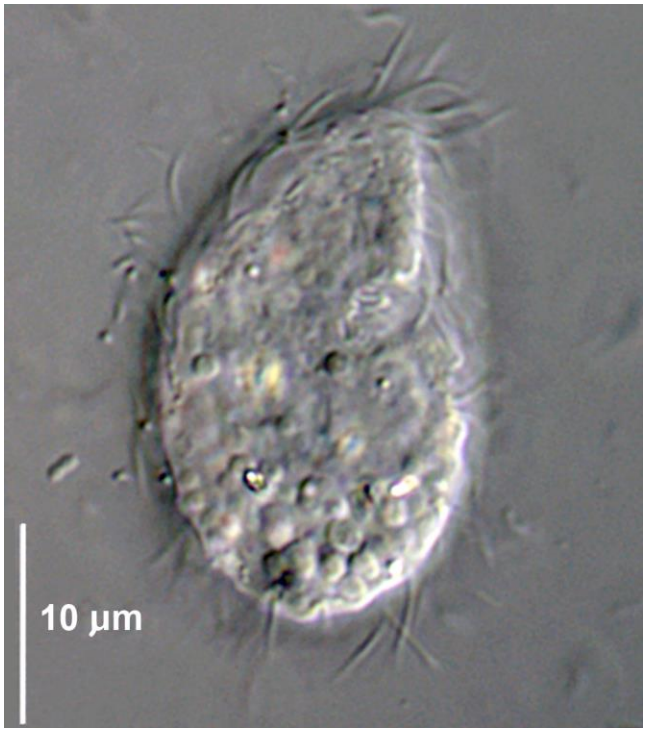


Figure 21. ***Valkampfia***. Photo by Yuuji Tsukii, with permission.



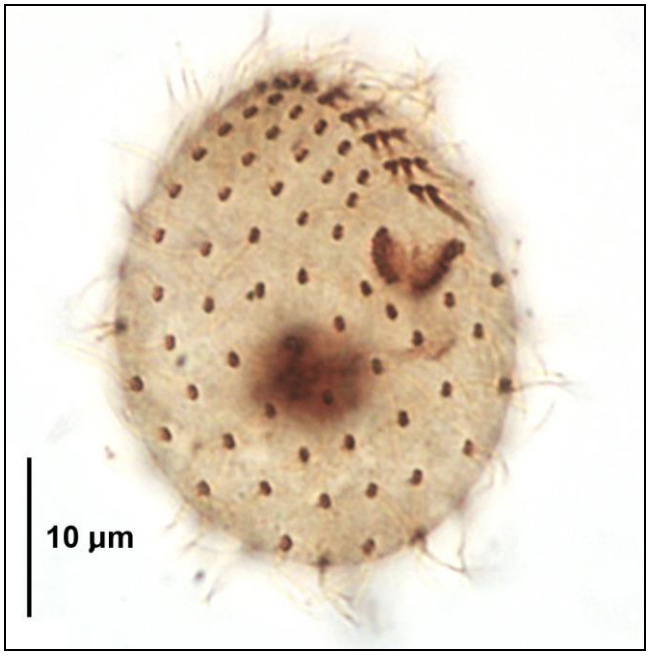


Figure 22. ***Colpoda aspera***. Photos by William Bourland, with permission.

Figure 23. ***Cryptodifflugia ovaliformis*** on an alga filament. Photo by Yuuji Tsukii, with permission.

Vertical Zonation

Bryophyte suitability as a protozoan habitat differs in both time and space. Bryophytes offer a vertical series of habitats (Figure 24) that differ in temperature, moisture, and light, and presumably food quality and quantity. Horizontally, the substrate or height above the water table can differ, causing species differences. Hence, the micro-organisms distribute themselves in different communities both seasonally and spatially, particularly in the *Sphagnum* peatlands (Schönborn 1963; Heal 1964; Meisterfeld 1977; Mazei and Tsyganov 2007).

Figure 24. ***Sphagnum subnitens*** showing tips and lower branches that create habitat zones for protozoa. Photo by Michael Lüth, with permission.

Spaces: Several studies indicate that the sizes of spaces within the bryophyte habitat influence the sizes of organisms and influence the available food (Dalenius 1962; Corbet 1973; Bovee 1979; Robson *et al*. 2001). Capillary spaces among branches and leaves hold water. Gilbert *et al*. (2003) suggested that as the ***Sphagnum*** becomes drier, ciliate protozoa are easier to catch for food because the thin film of water slows them down. As the moss becomes too dry, rather than migrating to lower, moister areas, many of these taxa, like several invertebrate groups, can encyst, permitting them to survive desiccation (Heal 1962; Gerson 1982). And when the moss resumes activity under the stimulation of rain (or fog), the rhizopods do likewise.

Nitrogen: **N**itrogen from guano seemingly deterred all the testate amoebae on Elephant Island (Smith 1972). Nitrogen distribution affects the vertical distribution of at least some testate amoebae in ***Sphagnum*** communities, but nitrogen availability does not seem important for most testate amoebae in the upper centimeters of *Sphagnum* mats in the Swiss Jura Mountains (Mitchell & Gilbert 2004). There were 22 testate taxa among these mosses, although mean diversity of a typical sample was only 6.6. The species richness increased with depth. The moss-dwelling ***Assulina muscorum*** (Figure 25) was most abundant in the top 0-1 cm; ***Phryganella acropodia***, ***Heleopera rosea*** (see Figure 26), and ***Nebela militaris*** (Figure 27) were the most abundant taxa at 3-5 cm depth. In this case, species richness increased with depth in the mat. Only *Bullinularia indica* (Figure 28) appeared to be more abundant in plots fertilized with nitrogen.

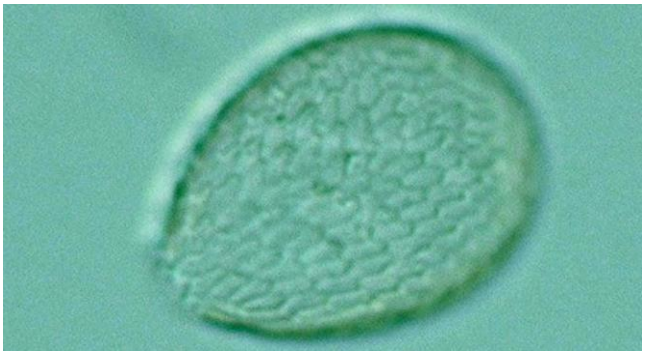


Figure 25. ***Assulina muscorum***. Photo by Yuuji Tsukii, with permission.

Figure 26. ***Heleopera sylvatica*** showing pseudopods. Photo by Yuuji Tsukii, with permission.

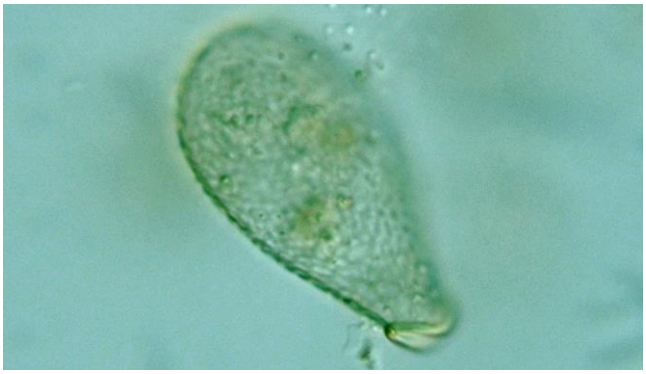


Figure 27. ***Nebela militaris***. Photo by Yuuji Tsukii, with permission.

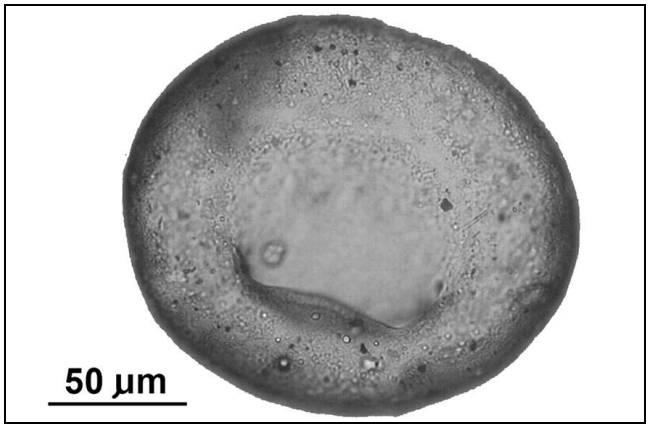


Figure 28. Test of ***Bullinularia indica***. Photo by Edward Mitchell, with permission.

Temperature: The Antarctic fauna is dominated by moss-dwelling micro-organisms, including protozoa, rotifers, nematodes, and tardigrades (Schwarz *et al.* 1993). Here, temperature may play a role as important as that of moisture. This need for adequate heat results in a vertical zonation of the fauna. For example, at the Canada Glacier, in southern Victoria Land, the majority of moss-dwelling organisms were in the top 5 mm in the post-melt samples, rather than in the pre-melt samples. However, while temperatures differed, so did the available moisture, making it difficult to determine controlling factors.

Light: As one might expect, light determines the absence of protozoa with chlorophyllous symbionts in the lower strata (Chacharonis 1956). Only those surface species contain chlorophyll, either as symbiotic algae or that of their own possession. However, some with chlorophyllous symbionts may occur as deep as 6-10 cm in ***Sphagnum*** mats (Richardson 1981). Of the 27 species lacking symbionts in a ***Sphagnum*** mat, all but two exhibited maximum abundance below 6 cm. But even within the first 5 cm, vertical zonation exists. Mitchell and Gilbert (2004) demonstrated a significant difference in number of species between the first 3 cm and the 3-5 cm depth in ***Polytrichum strictum*** (Figure 29) of a Swiss peatland (Figure 30).

Figure 29. ***Polytrichum strictum***. Photo by Michael Lüth, with permission.

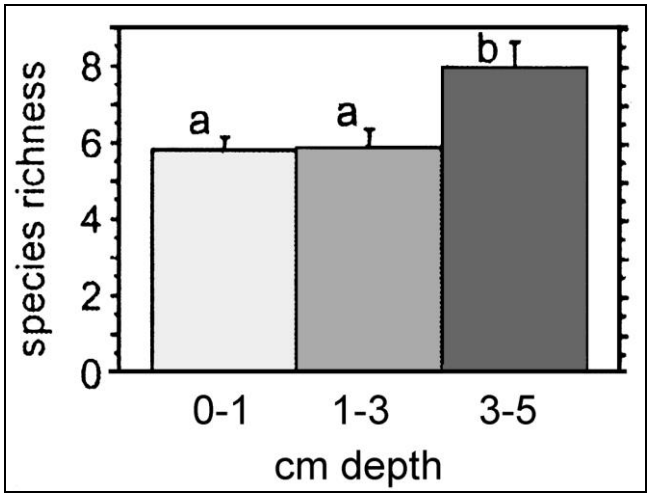


Figure 30. Vertical distribution of species richness of testate amoebae in a ***Polytrichum strictum*** "carpet" of a Swiss peatland. Redrawn from Mitchell & Gilbert 2004.

Community Differences: As for a number of other moss habitats, the *Sphagnum* peat mat provides vertical differences in microhabitat that are further expressed as vertical community differences (Meisterfeld 1977; Strüder-Kypke 1999; Mitchell *et al*. 2000). Strüder-Kypke found that even in the upper 30 cm of the mat, two very different protistan communities are dictated by the strong vertical zonation. Both light and nutrients differ, causing the upper region to support a denser colonization, mostly of autotrophic cryptomonads and vagile ciliates (able to move about or disperse in a given environment). On the other hand, deeper samples exhibited heterotrophic flagellates and sessile peritrich ciliates.

Presence of testate amoebae at greater depths within the moss mat does not always indicate a retreat to a location of greater moisture. Schönborn (1977) demonstrated that 15% of the shells can be transported to lower depths by 550 mm rainfall, but 400 mm generally does not seem to cause a noticeable downward loss.

Zoophagy by Liverworts?

Carnivorous plants are well known among the flowering plants, but the ability of bryophytes to attract and trap organisms has been questionable. Who would guess that these seemingly primitive organisms can attract their own prey? But one interpretation is that the leafy liverwort genera ***Colura*** (Figure 31, Figure 32) and ***Pleurozia*** (Figure 33) have **lobules** (water sacs) that do just that (Hess *et al*. 2005). And this is not an isolated example. In the Aberdare Mountains, Kenya, Chuah-Petiot and Pócs (2003) found many protozoa inhabiting the lobules of the epiphytic ***Colura kilimanjarica*** (Figure 31, Figure 32).

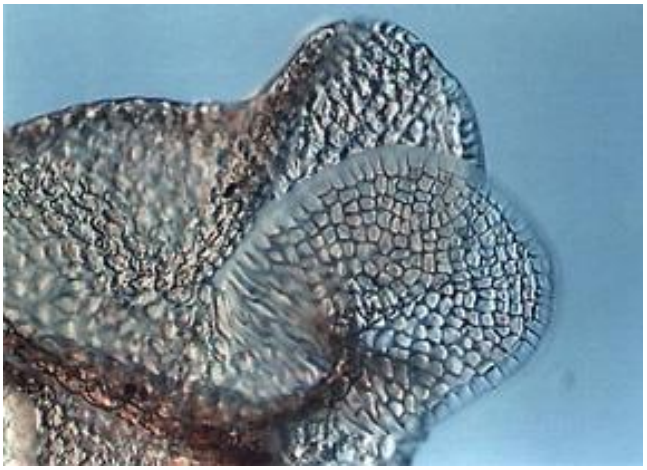
Figure 31. **Upper:** The leafy liverwort, ***Colura***. **Lower:** This lobule of ***Colura*** houses the ciliate protozoan ***Blepharisma americana***. Photos by Jan-Peter Frahm, with permission.

Figure 32. **Upper:** SEM of lobule of ***Colura***. **Lower:** Living lobule. These lobules of ***Colura*** are inhabited by the reddish ciliate protozoan ***Blepharisma americana***. Photos by Jan-Peter Frahm, with permission.

Figure 33. Underside of ***Pleurozia purpurea*** showing lobules where invertebrates often live – and die. Photo by Sebastian Hess, with permission.

Lobules are usually considered to be water storage organs. However, in these genera, they might also serve as traps. Goebel (1888, 1893, 1915) did not consider it likely that these were real traps. He argued that insectivorous plants have attractants in order to lure their prey into their traps. Although the lobule resembles the trap of the bladderwort, *Utricularia*, Goebel argued that that does not mean it is used the same way. He furthermore argued that the benefit gained by the excrement from animals (and dead animals?) would be less than that gained from the water. Since having the animals does not preclude also providing a water reservoir, it would seem that zoophagy would simply be an added benefit. Schiffner (1906) even reported chironomid larvae in the lobules, suggesting an even larger source of fecal matter. But the openings in ***Pleurozia*** are small, only about 300 µm, and closed by a round "lid" of hyaline cells (Hess *et al*. 2005). What causes these organisms to enter in the first place?

Figure 34. ***Pleurozia purpurea***, a leafy liverwort with lobules that can house a variety of invertebrates, including the ciliate ***Blepharisma americana***. Photo by Sebastian Hess, with permission.



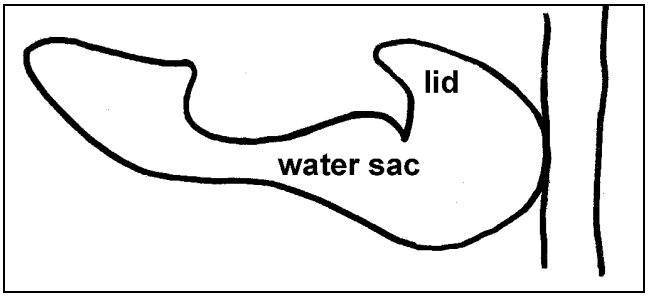


Figure 35. **Upper:** Lobule of ***Pleurozia purpurea*** showing lid. Photo by Sebastian Hess, with permission. **Lower:** Lobule redrawn from Hess *et al*. (2005). This lobule of ***Pleurozia purpurea*** serves as home and apparently ultimately as a trap for a wide range of protozoa and invertebrates.

Barthlott *et al*. (2000), using feeding experiments with the ciliate protozoan ***Blepharisma americana*** (Figure 1, Figure 36-Figure 38), demonstrated that ***Colura*** does indeed catch protozoa with its lobules. Hess and coworkers (2005) set out to determine if ***Pleurozia purpurea*** (Figure 33-Figure 35) is likewise carnivorous.

Figure 36. The ciliate ***Blepharisma americana*** that inhabits "zoophagous" liverworts. Photo by Yuuji Tsukii, with permission.

Again using ***Blepharisma americana***, a cohabitant of *Sphagnum* mats with ***Pleurozia purpurea***, Hess *et al*. (2005) performed dozens of experiments in Petri dishes to see if the dispersion of the protozoan remained random. Indeed, the protozoa gradually accumulated around the *Pleurozia*! Within only 30 minutes, 86% of the lobules contained the protozoa. After several hours, up to 16 protozoans were trapped, and further observation failed to reveal any that escaped.

The mode of attraction is only speculation. Barthlott *et al*. (2000) found that older parts of ***Colura*** were more effective at attracting ***Blepharisma americana*** (Figure 37, Figure 38) than were younger parts, suggesting that concentrations of bacteria may have been a factor. In fact, in experiments on ***Colura***, Barthlott *et al*. (2000) found that ***B. americana*** moves over the bryophyte surface "like a vacuum cleaner," devouring the bacteria.

Figure 37. A stained ***Blepharisma americana***. Photo by Yuuji Tsukii, with permission.

The shade provided by the plants could also contribute to the higher concentrations of protozoa near the branches of ***Pleurozia purpurea*** (Hess *et al*. 2005), but if so, the liverwort would probably be less effective as a refuge in the field where other mosses were also present.

Hess and coworkers (2005) claim that the large number of organisms in the lobules in such a short time is too great to be attributed to chance. However, they fail to provide any statistical evidence or probability to support this claim, for example, alternative liverworts or mosses. They furthermore state that the organisms die there, but they provide no data on the deaths of the organisms. They do point out that there is no direct evidence that any nutrients provided by the organisms are used by the liverworts, but there is likewise no evidence to the contrary. In any case, the liverworts could benefit from the cleaning of bacteria that block light and compete for nutrients.

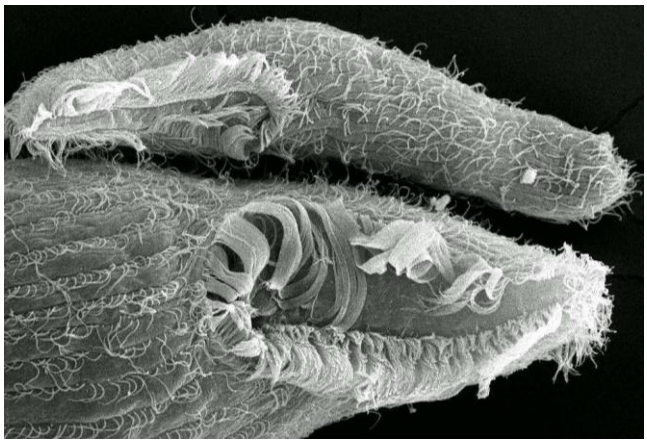


Figure 38. SEM photo of ***Blepharisma*** demonstrating small cell on top and large, cannibalistic cell below. Under starvation conditions, larger individuals become cannibalistic. Photo by Pauline Gould, with permission.

Zoophagy is the process of eating animals (*phag* = eat, devour; Hanson 1962; Lincoln *et al.* 1998). There is a fine distinction in what constitutes just eating compared to true carnivory, wherein living organisms are killed (or not) and digested. In this case, it seems that the animals may be trapped, but there is no real proof that they are consumed by the plant. Does admitting the animals into the trap (lobule) then make the liverworts zoophagous? Hess *et al.* (2005) argue that animals die in the traps and subsequently release their cell contents, bursting in the case of ***Blepharisma americana***. These dead animals are then decomposed by bacteria. Surely some of the nutrients released are absorbed by the liverworts. Is this not a process parallel to that of the pitcher plant ***Sarracenia purpurea***? Many so-called carnivorous plants, like ***S. purpurea***, seem to lack enzymes to digest all or some of the parts of their prey and depend on resident bacteria to accomplish the task. With this broad definition of carnivory, could we not call the liverworts **carnivorous**? I think I want more data on whether this is a chance event or true trapping before I make that claim. Such experiments would need controls of leafy liverworts with no "traps" to see if the protozoa simply accumulate wherever there is shelter. On the other hand, I wonder how many leafy liverworts with locules provide preferred housing for protozoa.

Dispersal

For any organism to succeed, it must have a means of dispersal. Protozoans can't go very far on their own. They are too small to crawl far on pseudopods or paddle their way with a flagellum or cilia, the common means of transportation for the majority of protozoan moss dwellers. But they can travel reasonable distances as passengers on the mosses, riding on fragments that establish a new home where they land.

Sudzuki (1972) conducted experiments using electric fans to determine the success of wind as a dispersal agent, using mosses as one of the sources of invertebrate fauna. He found that the smaller organisms – micro-organisms, including protozoa, were easily dispersed by light breezes as well as wind. Larger organisms such as gastrotrichs, flatworms, rotifers, nematodes, oligochaetes, tardigrades, crustaceans, and arachnomorphs, on the other hand, rarely were dispersed at wind velocities of less than 2 m per second [tornadoes are generally 27-130 m per second (Allaby 1997)]. In the field, colonization progressed from flagellates to ciliates to rhizopods, suggesting that passive dispersal was not the only factor controlling their colonization rates.

Once an organism becomes airborne, turbulent air may take them 3,000 to even 17,000 m on thermal drafts, with winds carrying them much higher and farther (Maguire 1963). Puschkarew (1913) found that protozoan cysts average about 2.5 per cubic meter, making these organisms readily available for dispersal and colonization on suitable bryophytes.

Smith (1974b) likewise considered that the mosses themselves served as dispersal agents for the protozoa. In particular, moss invasions of volcanic tephra on Deception Island in the Antarctic greatly increased the protozoan fauna. Not only do the mosses provide a great increase in suitable niches, but since they were most likely colonized by protozoa in their former locations, fragments arriving on the island could easily carry communities of fauna as passengers.

Rain can carry many algae and protozoa (Maguire 1963). Rain-borne organisms seem to originate predominantly from splash, typically from plants and soil, and do not travel far vertically, so that mechanism is most likely only suitable for local habitat travel.

In streams, the water movement itself serves as an effective dispersal agent, and aerial dispersal from waterfalls and rapids can carry algae and other *Aufwuchs* to new locations.

Raccoons are very effective in carrying whole communities of organisms, particularly protozoa, and can accomplish distances of at least 60 meters (Maguire 1963). Both terrestrial and aquatic birds contribute to dispersal, and other mammals contribute, but their relative role is not known.

Several scientists have discussed the dispersal of micro-organisms by insects (Maguire 1963; Parsons *et al.* 1966). Such mechanisms could easily contribute to the colonization of bryophytes by their micro-inhabitants. The many aquatic insect inhabitants will be discussed in an upcoming chapter. Consider the activity of insects among bryophytes, especially in streams, and their subsequent relocation due to swimming or stream drift. The *Aufwuchs* could easily be carried from one location to another by these mobile inhabitants (Figure 39). Emerging insects may also swipe micro-organisms trapped by the surface tension and carry them to resting locations, including bryophytes, on land.

Figure 39. Dragonfly ***Aeshna grandis*** female ovipositing and exposing herself to possible transport of protozoa. Photo by David Kitching, with permission.

Although few studies seem to have directly addressed the dispersal of micro-organisms by insects to bryophytes, we can infer at least some possibilities from more general studies on dispersal by insects. Maguire (1963) examined the distance both horizontally and vertically to which organisms were dispersed from a pond in Texas and another in Colorado. Dragonflies (Figure 39) and wasps, in particular, carried several species of protozoa and one species of rotifer. Parsons *et al.* (1966) found amoeboid and other protozoan cysts on adult Odonata, suggesting the possibility of a relatively long dispersal range. Odonata in

a short-term experiment dispersed up to 860 m to the farthest pond in the experiment (Conrad *et al.* 1999). Michiels and Dhondt (1991) estimated that 80% of adult dragonfly ***Sympetrum danae*** had migrated 1.75 km or more to their study site. But more importantly, evidence suggests they can migrate 3500 km or more across the Indian Ocean (Anderson 2009). This and other long-distance migrations provide a potential yearly means of dispersal for the micro-organisms.

Cosmopolitan

'Everything is everywhere, but, the environment selects' (in Wit & Bouvier 2006; O'Malley 2008). This statement, often called the Baas Becking Principle, has been applied to microscopic organisms that are globally distributed by high dispersal, and that lack biogeographic patterns (Fontaneto *et al.* 2008). But Wit and Bouvier made it clear that the original hypothesis "did not disregard the biogeography of free-living microorganisms." Finlay *et al*. (1996) extend the concept to suggest global species diversity is inversely related to body size. Therefore, the huge number of protist individuals makes global dispersal inevitable through normal events such as ocean circulations, groundwater connections, hurricanes, damp fur, dust storms, etc. (Weinbauer & Rassoulzadegan 2003). This argument is supported by the fact that the estimated number of free-living ciliates is about 3000, whereas there are about 10,000 species of birds and 120,000 species of Lepidoptera (butterflies and moths) (Lawton 1998).

The concept of global distribution describes well the major protozoa associated with bryophytes. This concept does not preclude, however, the presence of cryptic species that differ in less recognizable traits (Richards *et al*. 2005; Fontaneto & Hortal 2008; Fontaneto *et al*. 2008; Kooistra *et al*. 2008), and in recent detailed studies distinct genetic species have been found in disparate parts of the world (Telford *et al*. 2006; Fontaneto *et al*. 2008; Kooistra *et al*. 2008).

One consideration to support "everything is everywhere" is the small number of species of protozoa relative to 750,000 species of insects and 280,000 species of other animals (Papke & Ward 2004). Morphological data support the concept that dispersal is worldwide, suggesting there would be fewer than 5000 morphological protozoan species. Could this also be the explanation for the small number of bryophytes relative to other plants? In both cases, molecular evidence is starting to suggest that there may be cryptic species with genetic differences that are not expressed morphologically (Logares 2006), revealing distributions that are much more restricted.

Bryophyte protozoan communities are remarkably similar no matter where the bryophytes occur and consist primarily of cosmopolitan species. Davidova (2008) compared the testacean communities of epiphytic bryophytes to those of soil bryophytes in Strandzha Natural Park, South-Eastern Bulgaria, and found them to be quite similar in their taxonomic richness, species diversity, and community structure. The most common taxa in both habitats were ***Centropyxis aerophila*** var. ***sphagnicola***, ***C. aerophila*** (Figure 40), ***Phryganella hemisphaerica***, ***Euglypha rotunda*** (Figure 41), ***Corythion dubium*** (Figure 5), ***Trinema enchelys*** (Figure 42), and ***T. lineare*** (Figure 7). Among these, only ***Phryganella hemisphaerica*** is missing from the sites in Switzerland, Alaska, Sweden, Finland, Netherlands, Britain, Bulgaria, and North America as summarized in Table 1 of Chapter 2-2. The epiphytic community had 34 taxa in 13 genera, whereas the soil mosses had 31 taxa in 13 genera.

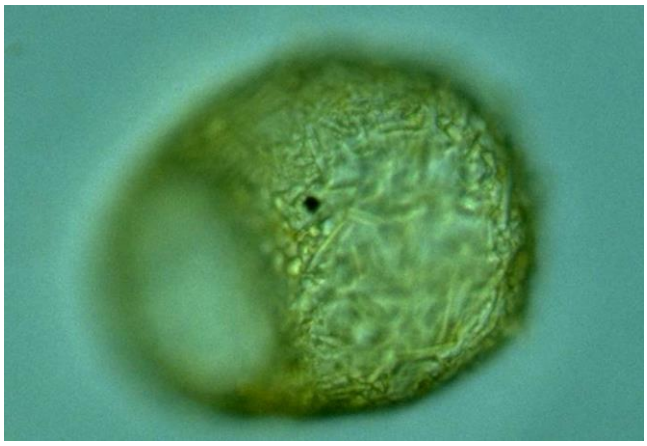


Figure 40. ***Centropyxis aerophila*** test. Photo by Yuuji Tsukii, with permission.

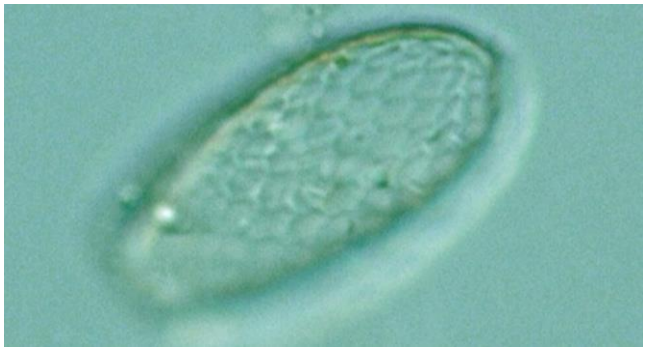


Figure 41. ***Euglypha rotunda***. Photo by Yuuji Tsukii, with permission.

Figure 42. ***Trinema enchelys***. Photo by Yuuji Tsukii, with permission.

The moss-dweller ***Nebela*** (*Apodera*) *vas* (Figure 43) has been touted to refute the Baas Becking Principle (Mitchell & Meisterfeld 2005; Smith & Wilkinson 2007). In 89 collections, representing 25 publications, mosses represented 59% of its habitat, with ***Sphagnum*** being the most common (Smith & Wilkinson 2007). Its distribution

is throughout the equatorial region at high altitudes, southern cool-temperate, and sub-Antarctic zones, but it is conspicuously absent in the Holarctic northern hemisphere. Its absence from hundreds of samples from seemingly suitable habitats in the northern hemisphere support the contention that its absence is not a fluke of sampling (Mitchell & Meisterfeld 2005) This distribution is definitely not cosmopolitan, despite its wide *p*H range (3.8-6.5) (Smith & Wilkinson 2007). Although it has a rather defined climatic range (temperate to sub-Antarctic), its absence in this climate throughout most of the more frequently studied northern hemisphere cannot support the concept of "everything is everywhere." Evidence such as this has been used to argue that micro-organisms are dispersed following the same principles as macro-organisms (BioMed Central 2007). Genetic differences that are not detectable from morphology suggest that global diversity of micro-organisms may be greater than has been suspected (BioMed Central 2007; Fontaneto *et al*. 2008). Such evidence suggests that care is needed in assigning names to microbial/protozoan collections.

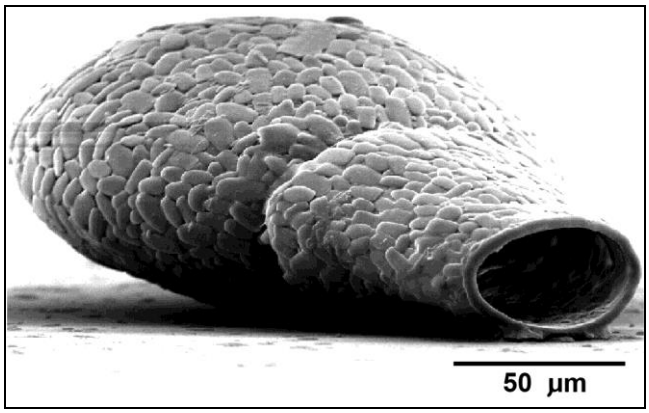


Figure 43. SEM view of ***Apodera*** (*Nebela*) ***vas*** showing test. Photo by Edward Mitchell, with permission.

Jenkins *et al.* (2008) have tested the size hypothesis, using 795 data values on dispersal units from published research. They found that active dispersal vs. passive dispersal matters greatly, with active dispersers dispersing significantly farther ($p<0.001$) while having a significantly greater mass ($p<0.001$). They showed that size does make a difference, but not always as predicted by the Baas Becking Principle. Among active dispersers, it is the larger dispersers that go the greater distances, perhaps related to required energy. The principle does not even hold well for the passive dispersers. The distances travelled by these dispersal units were random with respect to mass.

How well does the size:dispersal distance relationship hold for bryophytes that travel by spores? One might argue that as a group, they are more cosmopolitan than seed plants and less cosmopolitan than the protozoa. Fortunately for the protozoa, they are not very specialized for particular bryophytes.

Communities as Biological Monitors

Ciliates living among bryophytes in Czechoslovakia are sensitive to air pollution, giving us another way to assess the effects of air pollutants (Tirjakova & Matis 1987). Testate amoebae, including ***Assulina*** (Figure 25), ***Corythion*** (Figure 5, Figure 9), ***Euglypha*** (Figure 41), and ***Heleopera*** (Figure 26), as well as ***Euglena*** (Figure 44) and Cyanobacteria, in a ***Sphagnum*** bog of Tierra del Fuego, South America, were sensitive to UV-B radiation (Robson *et al*. 2001). But surprisingly the testate amoebae and rotifers were significantly more abundant and had greater species diversity under current levels of UV-B radiation than those that received reduced UV-B. The fungal component likewise had significantly greater abundance and species diversity under the current dosage than under the reduced dosage.

Figure 44. ***Euglena mutabilis***, a common euglenoid among bryophytes, particularly in peatlands. Photo by Yuuji Tsukii, with permission.

Because pollution affects the entire community, moss-dwelling protozoans can often be a more efficient means of assessing pollution damage than other biological components. In a study in France, Nguyen-Viet *et al.* (2007a, b) assessed the response of the protozoan community under simulated lead pollution. Using Pb^{+2} concentrations ranging from 0 to 2500 µg L^{-1}, they found that biomass decreased significantly for bacteria, microalgae, testate amoebae, and ciliates at 625 and 2500 µL^{-1} Pb^{+2} after six weeks. The microbial biomass decreased as the densities of testate and ciliate protozoa decreased, but the relative biomass of bacteria to that of the protozoa remained constant. The correlation between the two groups increased as the lead concentration increased. Hence, the protozoa provided an effective and relatively inexpensive means of assessing the community response.

Enhanced CO_2 had the opposite effect on the community relationships (Mitchell *et al*. 2003). Biomass of the testate amoebae decreased by 13% while the heterotrophic bacteria increased by 48% when the CO_2 was increased to 560 ppm, compared to those at an ambient CO_2 concentration of 360 ppm. Mitchell *et al*. (2003) suggest that the increase in bacterial biomass may be a response to increased exudation from ***Sphagnum*** under the higher CO_2 regimen.

As discussed in an earlier sub-chapter, the testate amoebae can serve as indicators of drainage in *Sphagnum* mires, as noted by Warner and Chmielewski (1992) in northern Ontario, Canada. As the water level falls, some species increase while others decrease.

Collecting and Sorting

There are lots of references for collecting, preserving, and enumerating aquatic and soil taxa of protozoa, but few on methods for bryophyte fauna. However, many methods for soil will apply equally well to the bryophyte fauna. A thorough coverage of methods is in Adl *et al*. (2008), with methods for peatland microfauna in Gilbert and Mitchell (2006). A special method for holographic viewing of live testate amoebae is presented by Charrière *et al*. (2006).

Collecting

Collecting protozoa that live among mosses is simple and requires no special equipment. In thick cushions or mats of bryophytes, extraction can be achieved with a stainless steel corer. In some circumstances, a knife can be used to cut a core and the core then placed into a cylindrical plastic container (Lamentowicz & Mitchell 2005). Stream bryophytes should be collected in a way that avoids as much loss downstream as possible. This can be achieved by shielding the bryophyte from most of the flow and especially shielding it as it breaks through the surface. One's hands are often sufficient to achieve this, but a container might be used over the bryophyte, enclosing as much of its depth as possible while dislodging it from the substrate. For non-quantitative collections in almost any habitat, a hand-grab is usually sufficient. For diversity studies, it is important to get the moss down to its substrate because zonation often occurs.

Storage & Preservation

Bryophytes and adhering water/moisture can be kept in jars or polyethylene bags until they are returned to the lab. If the weather is warm, it is desirable to place the containers in a cooler with ice. Oxygen is a problem, so open containers or vials with loose lids will help. For aquatic collections, some free water might be needed, making it necessary to confine the water by such means as a wad of paper towel or cloth above the water level to avoid splashes out of the jar. Parafilm may suffice for short time periods, or two, separated layers of screen or mesh.

The most rewarding experience is to observe the protozoa live as they swim about in the water film, gyrate from a stalk, or engulf a food item. Some species will remain alive only a few hours after collection (Samworth 1995). If the organisms are to be kept for a few days, place them in a refrigerator (not freezer) or incubator that is set in the range of 5-15ºC (Glime pers. obs.). The container should be covered to reduce evaporation, but not sealed. Jars with lids should have the lid on loosely to permit air exchange. If the jar is opened and a foul odor escapes, there has not been enough air exchange, and many of the organisms will be dead – and perhaps subsequently eaten by the more hardy ones.

Preservation

If the sample is to be kept for long in the field before returning to the lab, and the weather is hot, it might be necessary to preserve the organisms. This is fine for testate amoebae, but may make counting and identification of other protozoans difficult or impossible.

Preservation of bryophyte protozoan samples is like that of other protozoa, using 2% glutaraldehyde (final solution) (Mitchell *et al*. 2003), formaldehyde (Fisher *et al*. 1998; Gilbert *et al*. 1998a, b), or glycerol (Hendon & Charman 1997b), but the water content of the bryophyte must be considered in calculating the dilution. For example, saturated ***Sphagnum*** typically has 95% water content (Gilbert & Mitchell 2006).

Long-term Storage of Cysts

One choice for long-term storage is to let the mosses and their fauna dry slowly in air for several days. This can be done in open paper bags, a method typically used for drying bryophytes, or in open jars. Cool drying is preferable for many species, but survivorship will vary depending on the climate of origin and should be tested against fresh samples if the samples will be used for quantitative or diversity work.

Once the samples are dry and the protozoa have encysted, they can be sealed in containers and stored at 4ºC. Again, the effects of storage should be tested for any quantitative or diversity work. Tropical taxa may require a warmer storage temperature (Acosta-Mercado & Lynn 2003). This method will only work for species that readily encyst and for testate rhizopods.

Extraction

Organisms can be extracted from the bryophyte-water matrix with a teat pipette (*i.e.* volume is unimportant) and placed as a drop on a glass microscope slide. Bryophyte inhabitants can be squeezed into a sample bottle with little danger to them, but this may have disastrous results for larger fauna that may be of interest. Protozoa can be concentrated in a centrifuge or by running the water through a fine nylon mesh (Samworth 1995), but smaller organisms will be lost and adhering organisms will remain behind on the bryophyte.

Gilbert *et al*. (2003) reduced the negative effects of squeezing by pressing a sieve (1.5 mm mesh) on the moss surface and sucking the water up with a syringe. They were unable to solve the problem of adhering organisms, including some microbial groups. Others are missed because they live inside *Sphagnum* cells. This method creates minimal destruction of the *Sphagnum* mat, even through repeated sampling, except for the trampling by the people doing the sampling.

In their book on ***Sphagnum*** ponds, Kreutz and Foissner (2006) suggest a slide on slide method (Figure 45). Mosses can be washed in a small amount of suitable water, preferably rainwater or other water that won't kill the fauna. In most cases, lots of detrital matter will come off the mosses, along with many members of the fauna. Dense material will collect on the bottom of the container and can be drawn into a pipette/dropper (ca 2 mL). Material can be transferred onto a glass slide to cover most of the slide. A second slide is then used at an angle to push the flocculent detratil matter to the end of the slide. When the edge of the top slide reaches near the end of the bottom slide, the top slide is lowered onto the bottom one and used as a coverslip. A smaller version of this method (*i.e.* a smaller sample of water and detritus) can be done in the same way with a drop of the water and detritus in the middle. In this case, a coverslip of the desired size can be used in the same manner as the top slide described above. Note that both

methods will be biased toward mobile organisms. Tardigrades, rotifers, sessile protozoans, and other attached organisms will be poorly represented, if at all, by this method (and most others!). To see these, branches of moss ned to be examined under the microscope.

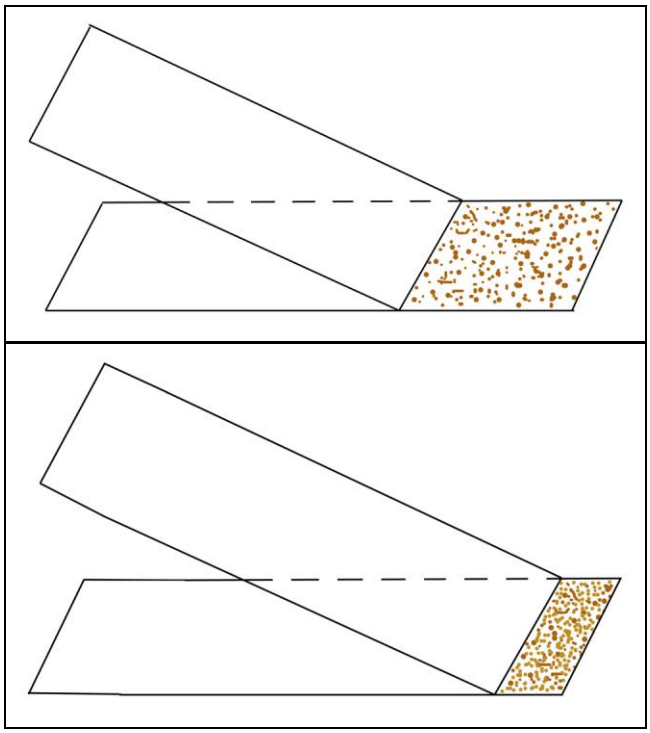


Figure 45. Slide on slide method of concentrating and extracting micro-organisms. Drawing by Janice Glime based on images in Kreutz and Foissner 2006.

Testate Amoebae

The non-flooded Petri dish method (below) can be used to culture testate amoebae as well, but a longer time may be needed to wake up the cysts (Adl *et al*. 2008).

One method to extract **testate** organisms is to dry the bryophytes at 65ºC, then sieve and back-sieve them with a sieve that retains all particles in the range of 10-300 µm. The standard method seems to be that of Hendon & Charman (1997b). A standard length of moss is cut and boiled for 10 minutes to loosen the amoebae. The boiled samples are filtered first at 300 µm, then back filtered through 20 µm. The organisms retained by the 20 µm filter are stored in 5 ml vials with glycerol.

Another method for extracting testate species is to put single shoots of bryophyte samples in a vial and shake them with a vortex mixer (Nguyen-Viet *et al*. 2004). This solution can be filtered through a 40 µm mesh filter and washed with deionized water to remove larger organisms. The tiny testate species will most likely all go through the filter due to the force of the water. The filtered water can then be placed in a plankton-settling chamber for 24 hours so the testae will settle to the bottom. For this method, Nguyen-Viet *et al*. (2004) used 20 samples of approximately 0.3 g fresh weight of living moss, placed in a glass vial with 7 ml of 4% formaldehyde.

A different approach to extraction is to boil the living bryophyte stems in distilled water for 20 minutes, stirring occasionally (Lamentowicz & Mitchell 2005). This solution with moss is then sieved through a 300 µm sieve to remove large constituents. The filtrate can then be concentrated with a centrifuge at 3000 rpm for 4-6 minutes. The tests can be stored in glycerol.

Non-testate Taxa

The non-testate taxa are somewhat more difficult to work with because they are best seen while active. One alternative is to culture them, using the non-flooded Petri dish protocol described by Adl *et al*. (2008):

1. Place bryophyte sample in a 5- or 10-cm Petri dish. Several Petri plates can be set up initially and drained on different days to avoid depleting nutrients with the wash.
2. To culture, moisten sample with distilled water or wheat grass medium.
    a. To make wheat grass medium, combine 1 g wheat grass powder and 1 L distilled or deionized water in a 2-L Erlenmeyer flask.
    b. Boil at a gentle rolling boil for 2 minutes, then let settle and cool for 1 hour.
    c. Filter into a new flask through several layers of cheesecloth to remove the grass residue.
    d. Adjust the *p*H to appropriate level (based on sample *p*H) with a phosphate buffer.
    e. Autoclave in screw top bottles for 20 minutes.
    f. Bacteria growth can be reduced by diluting to 1/10 or 1/100 strength.
3. Alternatively, a culture can be made from a dilute solution of detritus from the moss.
4. Incubate at 15ºC in the dark or at ambient field temperature. Be sure plates do not desiccate.
5. Observe every few days for signs of activity, up to about 30 days. Some testate amoebae will take several weeks or even months to leave the encysted stage and become active.
6. To observe, moisten the culture plate with a squeeze bottle of distilled or deionized water.
7. Tilt the plate until there is enough to drain the water into a new plate.
8. Observe the drained water in the new plate with a dissecting microscope and oblique transmitted illumination; capture organisms with micro-dissecting tools or a micropipette, then observe with an inverted microscope with phase contrast if possible (see observation section below). Most will require 100-400X to be seen well.
9. Note that the often abundant cercomonads form thin filopodia that explore tiny pores (<1 µm diameter). These adhere to flat surfaces and are not easily seen or dislodged. They may require staining (see below).
10. The original plate can be returned to the incubator.

Observation

Live observations can be done with a small branch, a leaf, or just a drop of adhering water on a glass slide with a compound microscope. A few larger protozoa might be observed with a dissecting microscope. A cavity slide will avoid crushing as the slide dries. Further confinement can

be achieved with this type of slide by putting a drop of water on the cover slip, then inverting it over the cavity, making a **hanging drop** slide. Alternatively, putting Vaseline at the corners of a cover slip on a standard flat slide will keep the cover slip from crushing them. More water can be added at the edge of the cover slip and will be drawn under by capillary action.

Ciliates and flagellates can be slowed down by a viscous substance such as methyl cellulose. Observing them in the interstitial water of intact bryophytes also tends to slow them down. Note that these organisms are mostly transparent and viewing may be improved by using darkfield and/or closing down the diaphragm of the microscope. An inverted microscope has the advantage of giving you a better view of those protozoa that settle on the bottom, especially testate amoebae.

Start your observations with a low magnification and move up after you have found a quiet one you want to observe, preferably surrounded by a bryophyte leaf or other confinement.

For testate amoebae, observation of dead material is not a problem, albeit not so interesting. The test is well-preserved and can be observed and identified at the convenience of the observer.

Staining

Staining can make the organisms easier to see (Figure 46), and vital stains may help to provide behavioral information. For example, neutral red can be used to follow digestion (Howey 2000). Newly formed vacuoles will stain bright red. As digestion proceeds, the vacuole will become yellowish, indicating a change in *p*H toward alkaline. Powdered carmine can also be used to indicate the location of the vacuole. Subsequent observation with Nomarski differential interference contrast can provide clear visibility. The observer should experiment with brightfield, darkfield, India ink in the solution, oblique illumination, phase contrast, or whatever types of optical contrast may be available. Unfortunately, all stains appear eventually to be toxic, so the viewing time is limited (Howey 2000; Table 1). WARNING: Read the labels carefully; many stains are also highly toxic to humans!

Figure 46. ***Oxytrichia fallax*** stained with Protargol. Photo by William Bourland, with permission.

Table 1. Concentrations needed to stain ***Paramecium*** and toxicity after one hour. Table from Howey 2000.

Stain	Min Conc to Stain	Toxicity - % dead in hour
bismarck brown	1:150,000	0
methylene blue	1:100,000	5
methylene green	1:37,500	5
neutral red	1:150,000	3
toluidine blue	1:105,000	5
basic fuchsin	1:25,000	30
safranin	1:9,000	30
aniline yellow	1:5,500	0
methyl violet	1:500,000	20
Janus green B	1:180,000	40
Nile blue	1:30,000	
Rhodamine	1:20,000	

Identification

There are some specialty keys available, and lots of pictures on the internet. However, internet pictures and keys should be used with caution and the source of information evaluated because these are unrefereed and often contain errors. A good general reference for identification is the publication by Lee *et al.* (2002), "The Illustrated Guide to the Protozoa." Its nomenclature is in places outdated, so usage should be checked in Adl *et al*. (2005). A more recent aid is a book by Kreutz and Foissner (2006). This book has wonderful color pictures, but there is no designation to tell which were on bryophytes and which were in open water.

Quantification

Adl *et al*. (2008) advised that taxa must be counted within one or two days of collection because temperature and moisture changes will shift the bacterial communities and this will, in turn, cause a change in community structure of the protozoa.

To quantify the sample size, the bryophyte can be weighed after drying. However, some amoebae will become glued to the bryophyte by the attending algae and detrital matter, thus contributing to the weight. Biovolumes can be estimated by using the geometrical shapes and an appropriate formula for that shape, then multiplying by the number obtained (Mitchell 2004).

Adl *et al*. (2008) provided a method to estimate protozoa per gram of dry soil. It could be modified for bryophyte purposes. For any quantification, the method must be consistent among those communities being used for comparison. One can use stem length, wet weight, or dry weight, but these have different biases for different bryophytes and those must be dealt with. Furthermore, different methods may favor the observations of some protozoan taxa. For example, larger organism are more easily seen, testate organisms are more likely to fall from the moss upon shaking, sessile organisms will most likely not fall at all.

Charman (1997) suggested a method for quantifying the testate amoebae and warned of its shortfalls. You may be familiar with methods of determining pollen density by including a known number of *Lycopodium* spores in the sample (for example, 200) and using the ratio of those

observed on the slide to those put in the sample. Unfortunately, in the testate samples extracted from mosses, the number of tests estimated was reduced by up to 80% and the number of taxa was reduced by 60%, probably due to differences in weight, making this a less than desirable method. Using KOH to digest the organic matter did not destroy the tests, and permitted extraction of more tests, but they were damaged and more difficult to identify. Charman concluded that a water-based preparation with sieving was the best method.

Various combinations of filtration, vortex, and centrifuge can be used to get the best results for particular circumstances. Different mesh sizes can be used with back filtration to classify the organisms into size groups (Kishaba & Mitchell 2005). The organisms collected between 15 and 350 µm are a typical size group of Testacea examined (*e.g.* Warner & Charman 1994; Booth & Zygmunt 2005).

Summary

Larger protozoa tend to occur in moist or bog habitats, whereas drier habitats have smaller ones. Some even occur within the hyaline cells of *Sphagnum*. Some protozoa are exclusive to *Sphagnum*; others occur only on forest mosses. Those on epiphytic bryophytes are able to dry with the mosses and encyst during periods of drought. Moisture also contributes to the vertical zonation of protozoa in peatlands. Soil crusts can have some of the highest numbers of species. Moisture is the major determining factor on species distribution and survivorship, with terrestrial species able to withstand drying more than wet habitat species can. Over 400,000 individuals can occur in one square meter of terrestrial mosses. Studies in the Antarctic suggest that temperature and moss growth form play roles in the number of species.

Drying slows the mobile organisms and permits larger protozoa to capture them. Their consumption of micro-organisms places the moss-dwelling protozoa in the role of nutrient cycling. The bryophytes further contribute to ecosystem processing by affecting the moisture and temperature, hence altering the protozoan fauna, in the underlying soil.

Some protozoa are hitch-hikers on other bryophyte inhabitants, such as those that ride around on tardigrades. Others have green algae as symbionts and are thus restricted to photic zones on the bryophytes, whereas those without these symbionts typically occur below 6 cm depth. Yet others (***Pleurozia***, ***Colura***) seem to trap protozoan prey in leaf lobules. In fact, it appears that the leafy liverwort ***Pleurozia purpurea*** may actually attract ***Blepharisma americana***.

Dispersal is likely to be as passengers on bryophyte fragments. A successional pattern from flagellates to ciliates to rhizopods suggests that other factors determine colonization rates. Some colonization comes from dormant cysts awaiting suitable conditions. Dispersal of cysts and living organisms can be facilitated by splashing raindrops. Some may even be facilitated by insects, birds, raccoons, and other mammals.

The small size of protozoans and other micro-organisms led to the assumption of cosmopolitan distribution, a concept known as the Baas Becking Principle, or "everything is everywhere." However, recent studies on distribution and genetic differences have brought this principle into question.

Bryophyte-inhabiting protozoa are sufficiently sensitive to some types of air pollution that they can be used as monitors, but not all are sensitive to the same things, so community structure is likely to change.

Collecting is relatively simple, but quantification is tricky. Testate species can be separated by physical means, but other taxa often require culturing to awaken cysts. Some may be amenable to staining to further clarify identification.

Acknowledgments

Paul Davison has been wonderful in helping me with the methods portion of this chapter, including the suggestion to include it. Edward Mitchell provided me with a large number of papers and photographs. Both of these researchers were invaluable in helping me with areas where I was often not personally familiar with the subject.

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CHAPTER 3-1
SLIME MOLDS: BIOLOGY AND DIVERSITY

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CHAPTER 3-1
SLIME MOLDS: BIOLOGY AND DIVERSITY

Figure 1. Orange slime mold on moss, Blue Lake Creek valley, Washington, USA. Photo by Matt Goff, Sitka Nature, with permission.

What are Slime Molds?

Slime mold or slime mould is an informal name given to three kinds of unrelated eukaryotic organisms. While the bryophytes were undergoing classification changes at the familial and ordinal levels, **Protista** were jumping to new kingdoms and phyla. Hence, anyone whose knowledge about these organisms is as old as mine needs a road map to understand who now belongs where. Slime molds are no longer considered fungi, but instead seem to be protozoa.

The protozoa have been joined by other groups to form the current concept of the paraphyletic kingdom **Protista**, also known as **Protozoa**, a grouping that is one of convenience. One such group to join them is the slime molds (Figure 1). Once classified as fungi, they have been booted out of that kingdom due to their lack of chitin and their feeding by engulfing food. They are now considered **Protista** due to their motile stages that look and behave like protozoa. Within the **Protozoa**, we will consider here the phylum known as **Eumycetozoa** or **Amoebozoa** (Shadwick *et al*. 2009; Kang *et al*. 2017).

The slime molds are comprised of more than 1000 species from all seven continents (Lloyd 2011). The life cycle is one reason for their current classification position. They can live freely as single cells, but in dictyostelids they can later aggregate to form multicellular reproductive structures.

Using 18S rDNA and cladistics, Leontyev *et al*. (2019) revised the classification of the **Myxomycetes**. Noting that "Myxomycetes show a higher within-group genetic divergence than true fungi, higher animals, or vascular plants," they divide the slime molds into three classes, giving the groups taxonomic status according to the International Code of Nomenclature:

- **CLASS MYXOMYCETES** (Figure 2-Figure 9)

  The **Myxomycetes**, also known as **Myxogastria**, are the **acellular** slime molds, referring to the plasmodium that is multinucleate with no cell separation. These form the largest group of slime molds and contain almost all of the slime molds that associate with bryophytes. Based on the list of genera in nomen.eumycetozoa.com (5 May 2019), I have found all but three of the genera with at least one species that has been found on bryophytes to be in this class. The **plasmodium** (Figure 22, Figure 24) moves by amoeboid movement with rapidly streaming protoplasm, reaching speeds up to 1.35 mm per second (Alexopoulos 1962, 1964). The mass can migrate when it streams to an advancing position and

withdraws its protoplasm from the rear area. When food becomes scarce, this mass will migrate to the surface of the substrate and form its rigid fruiting bodies. These produce spores that hatch into amoebae to continue the life cycle (Ling 1999).

Figure 2. ***Physarum decipiens*** young fruiting bodies on leafy and thallose liverworts. Photo by David Mitchell, from The Eumycetozoan Project, DiscoverLife.org, with permission.

Figure 3. ***Physarum decipiens*** mature fruiting bodies on leafy liverwort. Photo by Alain Michaud, from The Eumycetozoan Project, DiscoverLife.org, with permission.

Figure 4. ***Physarum cinereum*** immature fruiting bodies. Photo from Denver Botanical Garden, from The Eumycetozoan Project, DiscoverLife.org, with permission.

Figure 5. ***Physarum cinereum*** mature fruiting bodies. Photo by David Mitchell, from The Eumycetozoan Project, DiscoverLife.org, with permission.

Figure 6. ***Physarum globuliferum*** with immature fruiting bodies. Photo by Ray Simons, from The Eumycetozoan Project, DiscoverLife.org, with permission.

Figure 7. ***Physarum globuliferum*** with mature fruiting bodies releasing spores. Photo by Dmitry Leontyev, from The Eumycetozoan Project, DiscoverLife.org, with permission

Figure 8. ***Physarum leucophaeum*** with immature fruiting bodies. Photo by Denver Botanical Garden, from The Eumycetozoan Project, DiscoverLife.org, with permission.

Figure 9. ***Physarum leucophaeum*** with mature fruiting bodies emitting spores. Photo by Alain Michaud, from The Eumycetozoan Project, DiscoverLife.org, with permission.

- **CLASS DICTYOSTELIOMYCETES** (Figure 12)

  Dictyostelids are cellular slime molds. I have found only two genera with any species reported on these slime molds. The **Dictyosteliomycetes** do not form huge plasmodia (Figure 22, Figure 24) and remain as individuals, feeding on microorganisms. When they run out of food, they form fruiting bodies, first releasing signal molecules that enable them to find each other and then aggregating as swarms. They join to form a tiny multicellular coordinated slug-like creature (Figure 10). They can aggregate about 100,000 cells in ***Dictyostelium discoideum*** (Figure 11-Figure 12) (Kessin *et al*. 1996). This aggregate crawls to an open place in the light to form a fruiting body (Kakiuchi *et al.* 2001). While some of the amoeboid cells actually become spores, others become part of the dead stalk that lifts the spores upward. About 20% of the cells of the ***Dictyostelium discoideum*** die as they form the stalk (Kessin *et al*. 1996). This group is largely unrecorded from bryophytes. The only record I found was for ***Dictyostelium quercibrachium*** from the margin of a small bog in Ohio, USA (Cavender *et al*. 2005), and it is not clear if was actually on a moss.

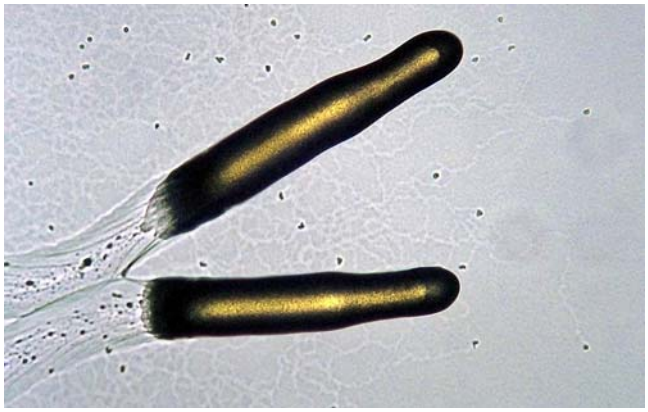

Figure 10. ***Dictyostelium mucoroides*** pseudoplasmodial slug on agar. Note their slug-like appearance. Photo by Dmitry Leontyev, through Creative Commons.

Figure 11. ***Dictyostelium discoideum*** development. Photo by Usman Bashir, through Creative Commons.

Figure 12. ***Dictyostelium discoideum*** fruiting in an open place. Photo by Usman Bashir, through Creative Commons.

- **CLASS CERATIOMYXOMYCETES**

The **Ceratiomyxomycetes** is a small group of only three genera (Leontyev *et al*. 2019). Their typical substrates are dead plant material, especially decaying wood. The genus ***Ceratiomyxa*** has at some time been in each of these three classes. It is the only genus of this new class that I have found reported from bryophytes. These slime molds have a complex life cycle, usually with a sexual phase, and the cycle includes amoeboflagellates that do not divide but instead convert into amoebae or to form a plasmodium (Spiegel *et al*. 2018). The plasmodium most likely follows sexual reproduction and formation of a zygote, although the sexual reproduction has not been verified in all genera. Fructification produces one, two, four, or eight spores at the top of a relatively long stalk.

Figure 14. ***Trichia varia*** with orange sporangia. Photo by Lebrac, through Creative Commons.

Identification Difficulties

Identification of species can be difficult for a number of reasons. Not only are there different color phases during the development of the sporangia, but there are different sexual strategies within currently perceived species (Clark & Haskins 2010; Feng & Schnittler 2015). One example of this is the widespread ***Trichia varia*** (Figure 13-Figure 17; **Myxomycetes**), an occasional bryophyte dweller (Feng & Schnittler 2015). Within this "species" there are three distinct sexual biospecies that are reproductively isolated from each other, based on 197 specimens collected from throughout Eurasia. In this case, the genotypes are distinct, but the phenotypes are not. Furthermore, there appear to be numerous sibling species that are biologically distinct, unable to mate, but morphologically indistinguishable, and these are spread throughout the world (Clark & Haskins 2010).

Figure 15. ***Trichia varia*** with yellow sporangia on moss. Photo from Bite.Your.Bum Photography, through Creative Commons.

Figure 13. ***Trichia varia*** with white young sporangia on mosses. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 16. ***Trichia varia*** with brown sporangia. Photo from EOL, through Creative Commons.

Figure 17. ***Trichia varia*** with mature brown sporangia, dehiscing and dispersing spores. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.com, with online permission

Reproduction and Colonization

Slime molds sound like nasty things that grow in the corners of your refrigerator, but in fact they are beautiful and fascinating organisms that really aren't molds at all. For centuries we thought they were, but unlike true fungi, they eat bacteria and other micro-organisms. Hence, they have been reclassified into the **Protista**. Stephenson and Stephenson (2022) found that although bryophyte mats are appropriate substrata for slime molds in temperate deciduous forests, the species richness and abundance are both relatively low. Their unique call to fame is their rather strange life cycle in which they try to be fungi when fruiting and protozoa when active.

General Life Cycle

The **Myxomycetes** are the **plasmodial slime molds** and with few exceptions are the only group large enough to be noticed easily (Wikipedia: Slime Molds 2019). In these **acellular** slime molds, the **plasmodia** (Figure 18, Figure 22, Figure 24) have many nuclei with no dividing cell membranes and can form a plasmodial mass that may be several meters in size. One of the most obvious of these is the slimy yellow plasmodium of ***Fuligo septica*** (Figure 19-Figure 20) on rotting logs – a species that also can occur on bryophytes (Figure 18). Both the amoeboid and the plasmodial stages can engulf microorganisms as food.

Figure 18. ***Fuligo muscorum*** on **Polytrichaceae**. Photo by James K. Lindsey, with permission.

Figure 19. ***Fuligo septica*** plasmodium on log. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 20. ***Fuligo septica*** on mosses (**Polytrichaceae**) in Orekhovo, Russia. Photo by Alexey Sergeev <asergeev@asergeev.com>.

When slime mold spores germinate, amoeba-like cells form (**myxamoebae**; Figure 21, Figure 24) (Wikipedia: Slime Molds 2019). These are typically **haploid** (have one set of chromosomes), can move about, and feed on bacteria. If these amoebae encounter the correct mating type, they can mate to form **zygotes** that develop into **plasmodia** (Figure 19, Figure 22, Figure 24). The protoplasm within the plasmodium can stream at speeds up to 1.35 mm per second, the fastest rate known for any organism (Alexopoulos 1962). When food becomes limiting, the plasmodium moves to the surface and begins to form its rigid fruiting bodies (**sporangia**; Figure 6-Figure 12, Figure 24) (Wikipedia: Slime Molds 2019). It is this stage that caused us to originally think they were fungi, but it lacks the chitin that is present in fungi. The life cycle is completed when these sporangia produce spores, usually by meiosis, for the next generation of amoebae. Some of these species go from spore to fruiting structure very quickly (Alexopoulos 1964).

Figure 21. ***Didymium*** myxamoebae hatched from spores. Brown structures are spores. Photo by George Barron, modified, with permission.

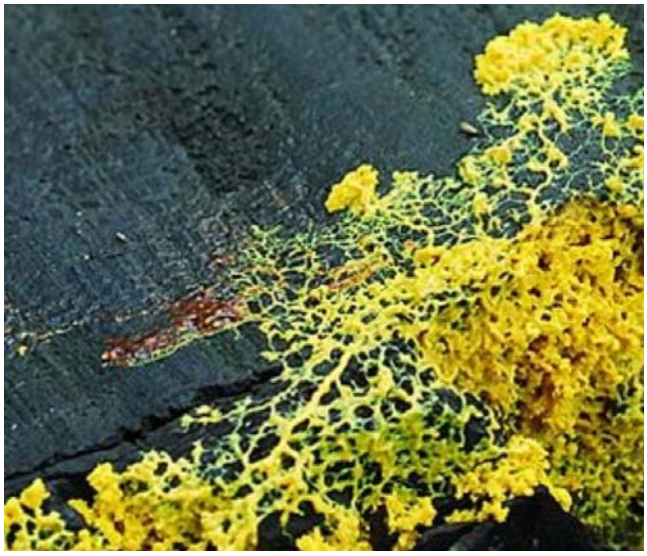

Figure 22. ***Fuligo aurea*** plasmodium. Photo through Creative Commons.

If free water is available, **myxamoebae** (Figure 21) form **swarm cells** (Figure 24) by developing flagella – one long and one very short (Myxomycota 2019). Some species mate as myxamobae (Figure 24) and others as swarm cells. Although adjoined myxamoebae are ready to mate, they generally cannot mate with the same strain, *i.*e. no sibling mating.

If conditions become too dry for the plasmodium (Figure 22), it will form a **sclerotium** (Figure 23, Figure 24), which is a dry dormant state (Wikipedia: Slime Molds 2019) and sometimes resembles the slime left by a slug. When this sclerotium once again becomes moist, it returns to the active plasmodium state. An alternative to this is that some species can form a **microcyst** (Figure 24) (Myxomycota 2019). This stage occurs when the amoeboid cells or swarm cells round up and form a thin wall, then become dormant, surviving unfavorable conditions.

Figure 23. Sclerotium. Photo courtesy of Steve Stephenson.

The multinucleate, diploid plasmodium (Figure 22) moves and feeds until conditions are right (or wrong) and it reorganizes into sporangia (Myxomycota 2019). The spores that are produced generally undergo meiosis to produce four nuclei. Three of these abort, leaving a single haploid nucleus, in a cell that becomes the haploid spore.

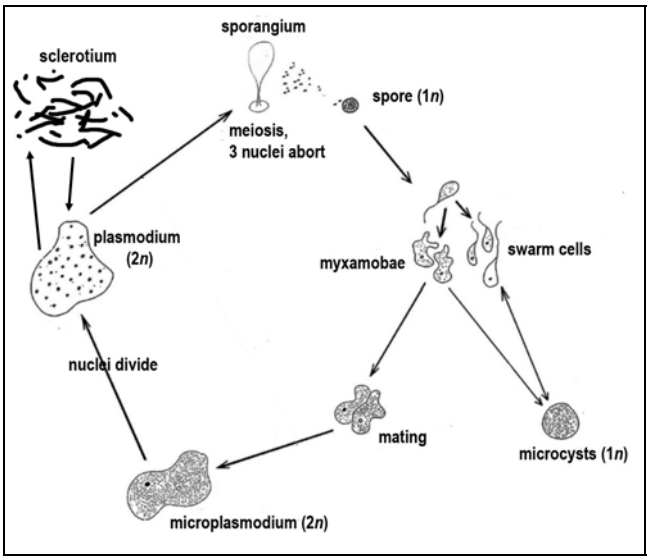

Figure 24. Generalized slime mold life cycle. Modified from Hoppe & Schwippert 2014.

Some species can produce **diploid** (having 2 sets of chromosomes) **amoeboflagellates** (includes flagellated cells and amoeboid cells) that develop directly into the plasmodium (Figure 22) without having any crossing with another cell (Clark & Haskins 2010). This appears to be the result of a failure of meiosis, resulting in **diploid** spores (**apomixis**). Thus a single spore of some species can complete a life cycle without any mating occurring.

Seasonal Changes

Reproduction in the **Myxomycetes** is typically seasonal. Eliasson (1980) recorded the times of **fructification** (producing sporangia) in several Swedish species over the course of four years. Those **Myxomycetes** fruiting in May-June include ***Amaurochaete atra*** (Figure

25), ***A. tubulina*** (Figure 26; not known from bryophytes), ***Reticularia jurana*** (Figure 27-Figure 28; a species close to the sometimes bryophyte dweller ***R. lycoperdon*** and that sometimes occurs close to bryophytes), and ***Symphytocarpus flaccidus*** (Figure 29-Figure 30; sometimes occurs on bryophytes). Those fruiting in June-August include ***Ceratiomyxa fruticulosa*** (Figure 31-Figure 32), ***Fuligo septica*** (Figure 33), ***Stemonitis axifera*** (Figure 34), ***S. fusca*** (Figure 35-Figure 36), and ***Stemonitopsis hyperopta*** (Figure 37; image on moss seen, but further documentation not available), all of which are known sometimes to associate with bryophytes. In September-October, those fruiting include ***Colloderma oculatum*** (Figure 38), ***Fuligo muscorum*** (Figure 39), ***Trichia botrytis*** (Figure 40-Figure 42), and ***T. decipiens*** (Figure 43-Figure 45). ***Lycogala epidendrum*** (Figure 46) spans May to October. Some of the species fruiting in spring may fruit again in autumn. All of these species occasionally occur associated with bryophytes.

Figure 25. ***Amaurochaete atra***, a slime mold that fruits in May-June in Sweden. Photo from UkrBIN.com, with online permission.

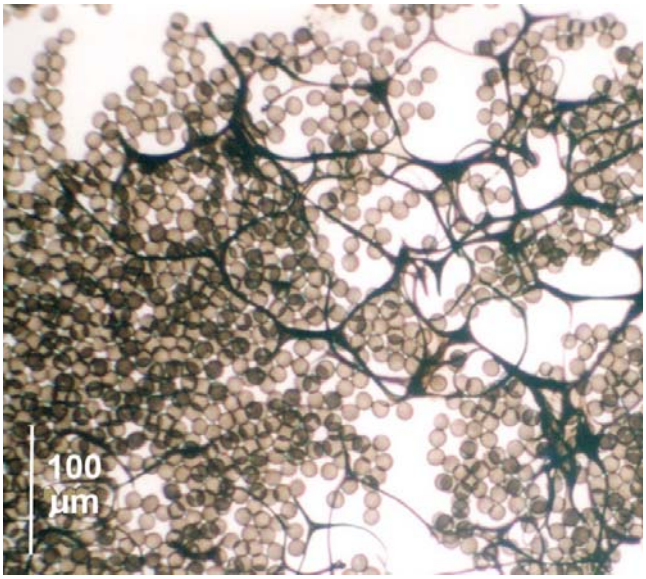

Figure 26. ***Amaurochaete tubulina*** spores and capillitium, a slime mold that fruits in May-June in Sweden. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 27. ***Reticularia jurana***, a species that fruits in May to June in Sweden. From Amadej Trnkoczy, through Creative Commons.

Figure 28. Habitat of ***Reticularia jurana*** on a mossy bank. Photo by Amadej Trnkoczy, through Creative Commons.

Figure 29. ***Symphytocarpus flaccidus*** on mosses. Photo by Dmitry Leontyev, with online permission.

Figure 30. ***Symphytocarpus flaccidus*** with maturing capsules. Photo by Thomas Laxton, through Creative Commons.

Figure 31. ***Ceratiomyxa fruticulosa*** fruiting bodies on bryophytes. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 32. ***Ceratiomyxa fruticulosa*** fruiting bodies. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 33. ***Fuligo septica*** plasmodia growing on mosses at the base of a tree. Photos by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 34. ***Stemonitis axifera*** fruiting bodies growing on moss. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 35. ***Stemonitis fusca*** fruiting bodies on log. Photo from Encyclopedia of Life, through Creative Commons.

Figure 36. ***Stemonitis fusca* var. *fusca*** on mosses. Photo from Denver Botanical Gardens, with online permission.

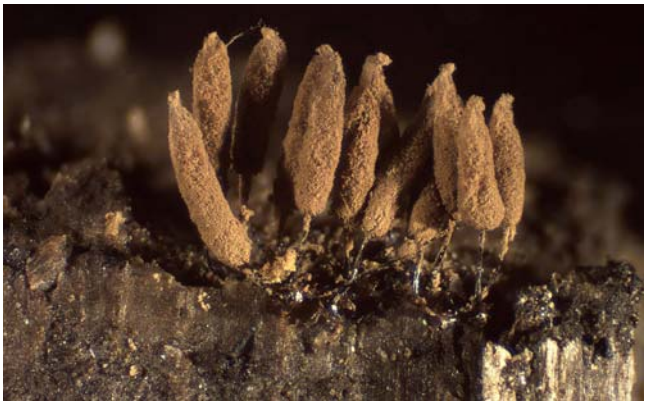

Figure 37. ***Stemonitopsis hyperopta*** on rotting wood. Photo through Creative Commons.

Figure 38. ***Colloderma oculatum*** fruiting bodies on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 39. ***Fuligo muscorum*** fruiting structure on bryophyte. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

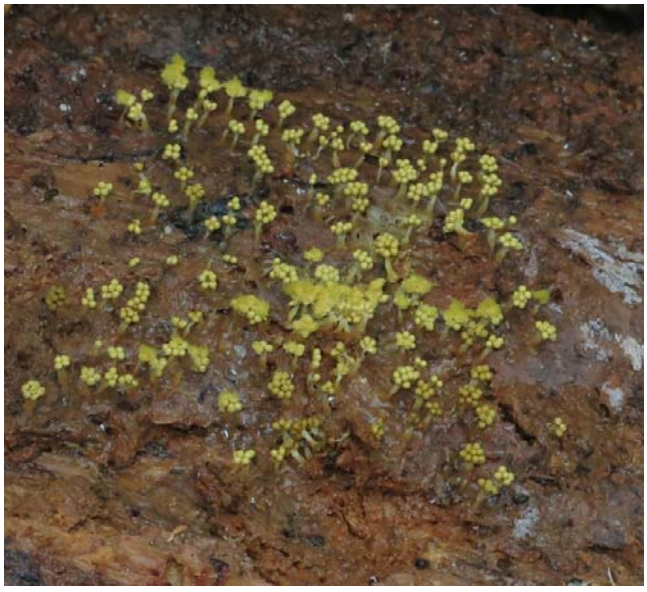

Figure 40. ***Trichia botrytis*** cf. **var. *flavicoma*** fruiting on rotten wood. Photo by John Barkla, through Creative Commons.

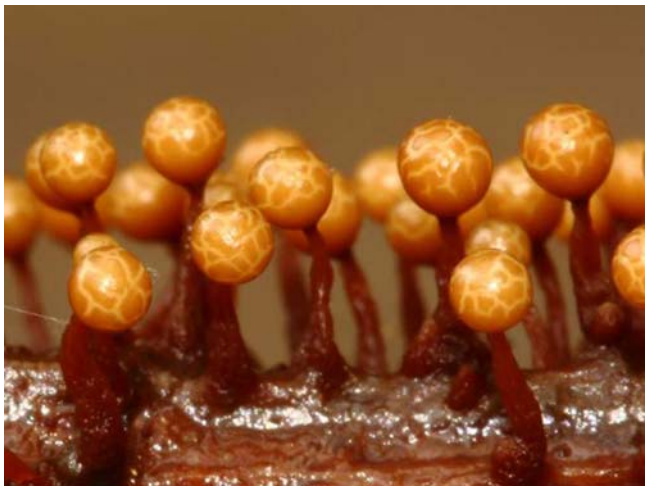

Figure 41. ***Trichia botrytis*** fruiting on wood. Photo by Sarah Lloyd, with permission.

Figure 42. ***Trichia botrytis*** old and dry fruiting structures on wood. Photo by Bernard Dupont, through Creative Commons.

Figure 43. ***Trichia decipiens*** young fruiting bodies. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 44. ***Trichia decipiens***. Mature fruiting bodies. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 45. ***Trichia decipiens*** empty fruiting bodies. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 46. Fruiting bodies of ***Lycogala epidendrum*** (wolf's milk; toothpaste slime) on mosses. The plasmodia are composed of small, red amoeboid cells (Wikipedia: *Lycogala epidendrum* 2019). When the conditions change, these rarely seen cells find each other by chemical signals and aggregate into the fruiting body, as seen here. Photos by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Some of the other seasonal records for the occasional **Myxomycetes** bryophyte dwellers include ***Arcyria ferruginea*** (Figure 47; known from bryophytes – based on photos by Iyp-tala at <https://hiveminer.com/Tags/arcyria>; Dawn & Jim at <https://hiveminer.com/Tags/arcyria>), ***A. obvelata*** (Figure 48; known from bryophytes – based on photo from <https://www.alamy.com/stock-photo-arcyria-obvelata-slime-mold-73514471.html>, ***Collaria arcyrionema*** (Figure 49; syn=***Lamproderma arcyrionema***; known from bryophytes – Ranade *et al*. 2012), and ***Physarum viride*** (Figure 50; known from bryophytes – Stephenson & Studlar 1985), all of which appeared early in the year. ***Stemonitopsis hyperopta*** (Figure 37; known from bryophytes based on online image; attribution not available), ***Cribraria intricata*** (Figure 51; known from mosses – Ranade *et al*. 2012), ***Cribraria cribrarioides*** (Figure 52; on bryophytes in photograph), ***Lamproderma columbinum*** (Figure 53; known from bryophytes – Stephenson & Studlar 1985), ***Tubifera ferruginosa*** (Figure

54-Figure 55; known from bryophytes – Stojanowska & Panek 2004), and ***Trichia verrucosa*** (Figure 56; known from bryophytes based on image) appeared later in the year.

Figure 47. ***Arcyria ferruginea*** fruiting bodies. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 48. ***Arcyria obvelata***, a species that has been photographed elsewhere growing on bryophytes. Photo by Patrick Schifferli, through Creative Commons.

Figure 49. ***Collaria arcyrionema*** fruiting, a species reported from bryophytes. Photo by Guang-Bao Xiang and Quan-Nian Jun, through Creative Commons.

Figure 50. ***Physarum viride*** fruiting bodies. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 51. ***Cribraria intricata***, a species known to grow on bryophytes. Photo by Clive Shirley, The Hidden Forest <www.hiddenforest.co.nz>, with permission.

Figure 52. ***Cribraria cribrarioides*** on bryophytes, and fruiting late in the year. Photo from Myxotropic, through Creative Commons.

Figure 53. ***Lamproderma columbinum*** growing with bryophytes, showing the slime mold's fruiting bodies. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 54. ***Tubifera ferruginosa*** on mossy wood. Photo by Sarah Lloyd, with permission.

Figure 55. Mature sporangia of ***Tubifera ferruginosa*** on moss. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 56. ***Trichia verrucosa*** with liverworts, and fruiting late in the year. Photo by Sarah Lloyd, with permission.

Environmental Stimuli

Kazunari (2010) examined the succession of slime mold communities in a forest setting in southwestern Japan and found that the seasonal factors of the slime mold communities were related to the decay state of the wood. Kazunari also showed that certain species were visible at only certain times of the year. But what are the factors that trigger these responses?

Light

Many of the slime molds migrate to light before initiating development of sporangia. Loss of bark during decay could provide a light signal for amoeboid and swarm cells under the loose bark of a decaying log. Reinhardt (1968) explored the effect of light on the cellular slime mold ***Acrasis rosea*** (Figure 57-Figure 58), a taxon that might not be representative of the **Myxomycetes** of interest here. Both continuous light and continuous dark failed to stimulate the production of sporangia. Reinhardt was able to stimulate sporangia production by exposing the cultures to light, followed by a minimum of 7-8 hours of darkness. Hence, we see that seasonal changes in day length could synchronize the fruiting of the slime molds.

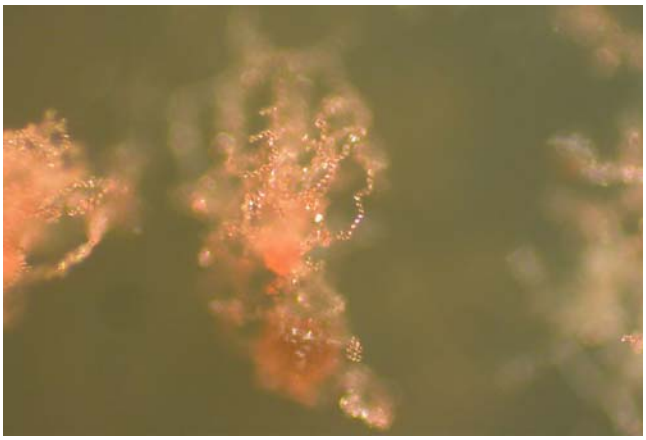

Figure 57. ***Acrasis rosea*** sporangia; this cellular slime mold responds to light to produce sporangia. Photo from Biology of Fungi Lab UC Berkeley, California, through Creative Commons.

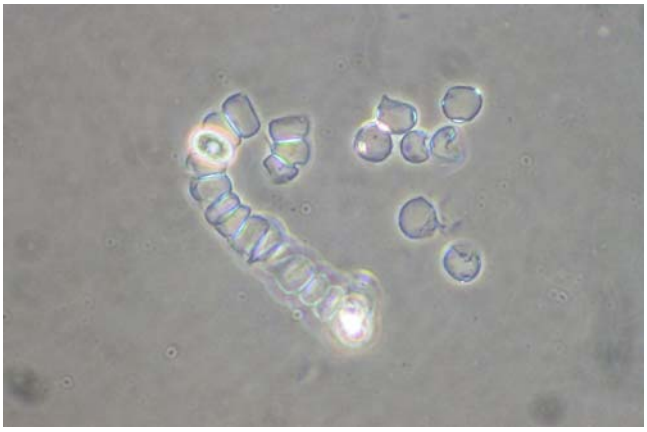

Figure 58. ***Acrasis rosea*** amoebae, a cellular slime mold, emerging from spores. Photo by Chirley Chio at Mushroom Observer, California, through Creative Commons.

Kakiuchi *et al.* (2001) demonstrated the role of the colors of light in the initiation of reproduction in the **Myxomycetes** slime mold ***Physarum polycephalum*** (Figure 59). Light initiates the breakup of the plasmodium (Figure 22) into equal-sized spherical pieces within about five hours. Blue and far-red light both initiate this behavior, whereas red light (but not blue) inhibits the far-red induction. These fragments develop the sporangia and spores. When it is time to develop sporangia, plasmodia can creep out from under bark or the bases of bryophytes and seek higher ground and more light.

Figure 59. ***Physarum polycephalum*** on leafy liverworts. Photo by Bernard Spragg, through Creative Commons.

*p*H and Volatile Substances

Researchers have found that bark *p*H is important in determining slime mold distribution on bark, but that it might be masked by geographic location (Everhart *et al.* 2008; Keller & Everhard 2010). It is reasonable to ask, then, if substrate *p*H is important in the reproductive cycle.

Early work by Reinhardt (1968) demonstrated that *p*H was important for fruiting in ***Acrasis rosea*** (Figure 57-Figure 58); a cellular slime mold in an entirely different clade), with growth occurring at *p*H 3.5-7.6, but fruiting only at 5.0-6.6. Such differences in *p*H could occur as a result of changes in the decay state of a log or litter. Of course this is only one species, and not even in the **Myxomycetes**, but it illustrates the mechanisms that might be used by other slime molds as well.

Gray (1939) found that temperature and *p*H are closely interrelated, at least in the **Myxomycetes** slime mold ***Physarum polycephalum*** (Figure 59). When *p*H remains constant, the time required for fruiting varies directly with the temperature, requiring longer times at higher temperatures. Furthermore, the higher the temperature, the fewer cultures produce fruiting bodies. When *p*H also varies, higher temperatures require greater acidity to produce fruiting bodies. At a constant temperature, the greatest fruiting occurs at *p*H 3.0. The maximum temperature at which this species will produce sporangia is 32.5º-35.0ºC. **Sclerotia** will not form at low temperatures (8º-12ºC) or high temperatures (32.5º-35.0ºC). Light still seems to be necessary for fruiting at all temperatures.

While the change in *p*H could be a seasonal phenomenon, research by Newell *et al.* (1969) suggests a different relationship. In the slime mold ***Dictyostelium discoideum*** (Figure 11-Figure 12; **Dictyosteliomycetes)**, a dweller of shallow soil, also known from bryophytes and litter, the amoebae form multicellular aggregates from which they are able to form fruiting bodies with stalks and spores. This change of state may occur at the same microsite, or it can change its structure into a form that can migrate to a more favorable location. This migration can be stimulated by the accumulation of metabolites from the slime mold or a low ionic strength in its substrate. This migration is inhibited by the presence of a buffer or overhead illumination. In an unbuffered system, the stimulus for fruiting is "appreciably volatile." In the presence of a buffer, the slime molds transformed from a migrating **slug** (Figure 10) and sat still, producing fruiting bodies on that spot. The strong base NaOH was completely ineffective in preventing the formation of the moving slug. Furthermore, the transformation into a moving slug was inversely related to the density of the slime mold cells, indicating that it was something produced by the slime mold that signalled the migration. Others (Bonner *et al.* 1950; Francis 1964) have observed that this species moves toward heat, following a very low temperature change gradient (as little as 0.05º C per cm). This behavior could decrease the volatile substance produced by the slime mold – an indicator that it is not too dense a population. But a heat gradient also would lead the moving slug form toward the light, which would then stop the migration and cause it to form the fruiting bodies.

Using the unicellular slime mold ***Dictyostelium mucoroides*** (Figure 10; **Dictyosteliomycetes**), Filosa (1979) similarly demonstrated the presence of a volatile substance by using charcoal as an absorbent. In the dark, this species produced **macrocysts** (encysted, resting plasmodium), but in the light it produced fruiting bodies. But if the dark cultures were grown over activated charcoal, they likewise would form fruiting bodies. When grown in light with KOH (a CO_2 absorbent), they produced macrocysts, but if activated charcoal was added, they again only produced fruiting bodies.

All of these responses to heat, light, *p*H, and an exudate from the slime molds themselves could optimize their reproductive potential. These stimuli cause the slime molds to move to a location where spores are more easily dispersed and will have less competition for space during fruiting and food for the next generation.

Water

In the cellular slime molds, surface water is a key factor as well (Bonner *et al*. 1982). When the plasmodial slug tip reaches above the water film, it usually causes the slime mold to shift gears and produce the fruiting structures. Among the cellular slime molds, light seems to be less important, promoting fructification only in those phototactic slugs that orient away from the surface.

Reproduction in Myxomycetes

Some slime molds are particularly associated with bryophytes (Ing 1994), and almost all of these are in the **Myxomycetes**, the acellular or plasmodial slime molds. ***Myxo*** means slime. They gain their energy by engulfing and digesting bacteria, yeasts, fungal spores, and decaying material in their amoeboid stage (Wikipedia: Slime Molds 2019), food sources that are often available on bryophytes. Spores are formed in a capsule-like structure. When the spores germinate, they release the amoeboid cells, referred to as the **myxamoebae** (Figure 21). If there is sufficient water for swimming, the myxamoeba may develop flagella and become a **swarm cell**. This process can be reversed, the flagellum retracted, and the amoeboid stage returned. Unlike the **Dictyosteliomycetes**, the **Myxomycetes** are sexual. When two different mating strains find each other, they join to form a **zygote**. Even in forming the **plasmodium** (Figure 22), the **Myxomycetes** differ from the **Dictyosteliomycetes**. In **Myxomyceyes**, the zygote does not form an amoeba, but instead divides only its nucleus. These nuclei continue to divide to form the **plasmodium** – a large, multinucleate body composed of a single cell.

In their **plasmodium** (Figure 22) stage, the **Myxomycetes** can flow like an amoeba, feeding as they traverse their substrate (Wikipedia: Slime Molds 2019). The plasmodium prefers darkness, and when it ventures into the light it is likely to go into its **sclerotium** (Figure 23, Figure 24) stage – a dormant stage that can remain so for years; this stage is also imitated by drying conditions. That shiny dry covering that looks like a slug's slime trail on the surface of a moss might be a sclerotium. The sclerotium is particularly likely to form if the plasmodium dries out. If, on the other hand, it runs short on food first, it goes into its fruiting stage. Such factors as light and temperature can induce the plasmodium to transform into fruiting structures (Figure 61 that produce **meiospores**, hence returning the organism to its 1*n* state (having only one set of chromosomes). The subsequent spores may germinate into flagellated cells or amoeboid cells that multiply vegetatively and engulf food to gain energy.

Figure 60. ***Didymium squamulosum*** sporangia. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 61. ***Trichia subfusca*** mature fruiting bodies on bark. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Temperature plays an important role in maintaining the active state of the amoeboid stage, and any habitable site must have sufficient moisture, making bryophytes necessary for survival of any that venture onto rocks (Ing 1994). The behavior of the slime mold under adverse conditions is reminiscent of the bryophytes and many of the fauna found there. When the going gets rough, they sleep like Rip Van Winkle! For the slime molds, it is the sclerotium (Figure 23, Figure 24); for many fauna it is a cyst; and for the bryophytes it is a simple dormancy without any change of state.

The **Physarales** (Figure 2-Figure 9; Figure 60-Figure 68), and especially ***Diderma*** (Figure 62-Figure 68), frequently fruit extensively where bryophytes and lichens cover the bark (Brooks *et al*. 1977). We know substrate is important for finding food in the mobile stages, but is it important for fruiting? Do the bryophytes offer the advantage of a higher perch for dispersal of these tiny beings?

Figure 62. ***Diderma*** sp. on liverwort. Ken-ichi Ueda, through Creative Commons.

Figure 63. ***Diderma cinerea*** sporangia on moss. Photo by Sarah Lloyd, with permission.

Figure 64. ***Diderma imperialis*** fruiting bodies on moss. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 65. ***Diderma montanum*** fruiting bodies on bryophytes. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 66. ***Diderma sessile*** fruiting bodies on mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 67. ***Diderma sessile***. fruiting bodies on bryophytes. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 68. ***Diderma umbilicatum*** fruiting bodies on mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Dispersal

Using 18S rDNA variants from 125 specimens from 91 localities of the myxomycete ***Badhamia melanospora*** (sometimes a moss dweller; Figure 69-Figure 70), Aguilar (2014) set out to determine if the Baas-Becking hypothesis of "everything is everywhere" can be applied to **Myxomycetes**. They found two distinct groups within this

species: one group comprises all populations from Argentina and Chile; the other is formed by populations from North America together with human-introduced populations from other parts of the world. For this species, they concluded that everything is not everywhere. Instead, the taxon consists of a complex that has at least two cryptic species that probably diverged as **allopatric** (having non-overlapping distributions) in North and South America. But as will be seen in this chapter, many of the slime molds do have widespread distributions on several continents.

Figure 69. ***Badhamia melanospora***, a species that sometimes grows on bryophytes. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

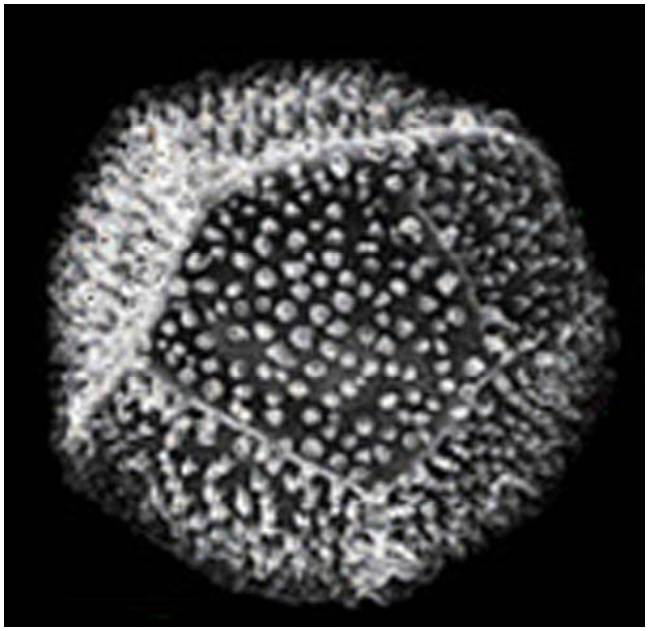

Figure 70. ***Badhamia melanospora*** spore SEM. Can it travel around the world? The Eumycetozoan Project, DiscoverLife.org, with permission.

It appears that some slime molds occur in the same places for multiple years, but their propensity for living on logs and even living trees means that at some time they must disperse to survive. Schnittler and Tesmer (2008) asked if the habitat colonization model for spore-dispersed organisms works for slime molds. They found spore numbers per sporangium ranging from 1 to 106. Average spore size ranges 10.3 µm to 14.8 µm in the studied taxa. Culture data suggest that the number of spores required to create the observed frequencies (as a percent of successfully colonized habitat islands) is generally three orders of magnitude higher. Species with sexual reproductive systems typically produce more spores than do asexual ones.

The presence of individual species is limited not by dispersal, which seems to be efficient, but by suitable substrate (Ing 1994). We have seen that the species are seasonal, but as we might expect, the time of year for the conspicuous fruiting varies with climatic zone. The dispersal is primarily tied to the onset of rain after a long warm period. This is typically autumn in the temperate regions, whereas in parts of the tropics it begins with the monsoon season. Dispersal does not determine species presence, except perhaps among the corticolous species. Rather, it is suitable substrates that determine presence.

One factor in dispersal of the spores is their surface structure. Three types exist in the **Myxomycetes**: spiny, reticulate, and smooth surfaces (Hoppe & Schwippert 2014). Using spores from 17 species, including ***Metatrichia floriformis*** (Figure 71) (reticulate; see Figure 72), ***Fuligo septica*** (Figure 33) (spiny; see Figure 73), and ***Licea parasitica*** (smooth; see Figure 74) as well as ***Ceratiomyxa fruticulosa*** (Figure 31-Figure 32; **Ceratiomyxomycetes**) (smooth) (all known from bryophytes as well as other substrata), they determined the wettability of the spores. Spiny spores would half sink into the water but nevertheless they floated. Reticulate spores are superhydrophobic and float on the surface tension of the water. Spores with no ornamentation sink to the bottom rather quickly.

Figure 71. ***Metatrichia floriformis*** sporangia. Photo by Clive Shirley, The Hidden Forest, with permission.

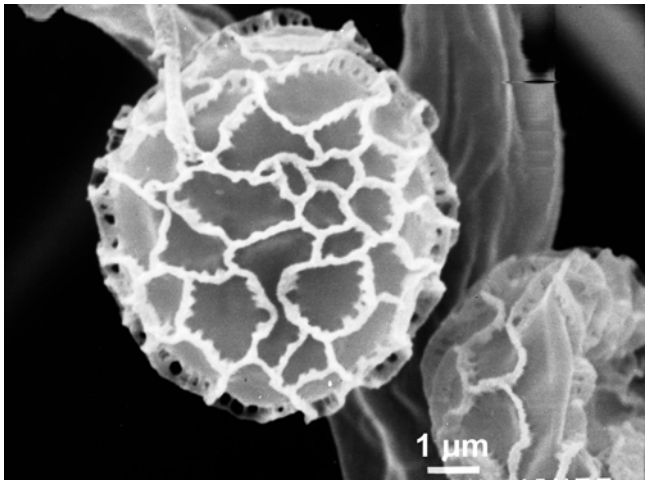

Figure 72. ***Stemonitis fusca***, sometimes a moss dweller, reticulate spores. SEM photo courtesy of Yuri Novozhilov.

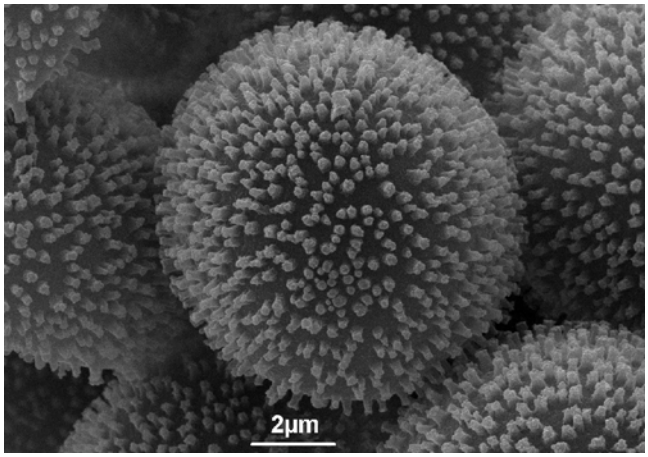

Figure 73. ***Physarum notabile***, sometimes a moss dweller, spiny spores. SEM photo courtesy of Yuri Novozhilov.

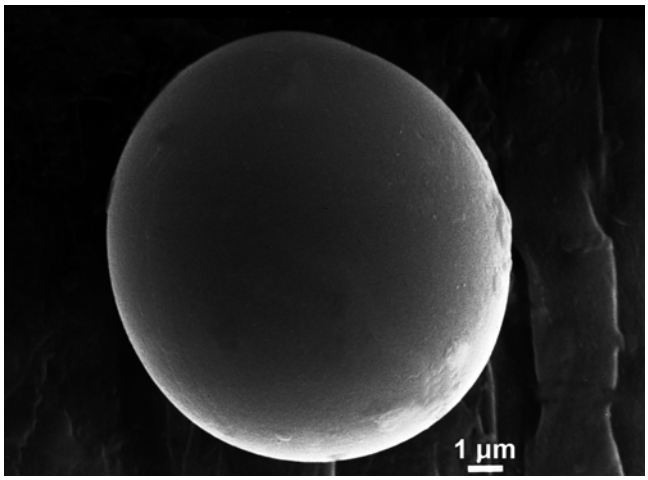

Figure 74. ***Licea deplanata***, not a known bryophyte dweller, smooth spore. SEM photo courtesy of Yuri Novozhilov.

Dispersal by wind seems to predominate (Keller & Smith 1978). Underlying bryophytes can become covered in spores (Figure 75). Dispersal may be aided by the **capillitium** (Figure 76) that in some species twists in response to changing moisture conditions. The capillitium also is likely to act like a salt shaker, doling out a few spores at a time instead of releasing all of them in a single burst of wind, a function similar to that of the peristome in mosses.

Figure 75. ***Tubulifera ferruginosa***. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

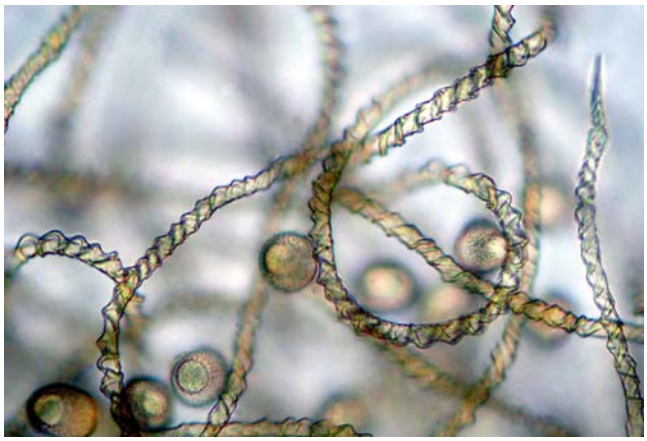

Figure 76. ***Trichia varia*** spores and capillitium. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

In some species, insects and mites seem to be important dispersal agents (Keller & Smith 1978; Eliasson 1977). Beetles are abundant on ***Amaurochaete*** (Figure 25) species and spores that cling to the body and legs would get a free ride for dispersal (Eliasson 1977).

Eliasson (1980) indicated that invertebrates are important in the dispersal of several species of slime molds. This is sometimes accomplished through predation by snails and insects that carry the spores on their bodies or in their digestive tracts (Ing 1967; Angela Newton, Bryonet, 20 November 2006).

The isopod ***Philoscia muscorum*** (Figure 77) appears to spread the cellular slime mold ***Didymium bahiense*** (Figure 78) (Ing 1004). Huss (1989) verified the potential of dispersal by earthworms (Figure 79) and pillbugs (**Isopoda**; Figure 77). Some of these invertebrate species are bryophyte dwellers, although typically not the ones used in the experiments. These invertebrates were fed both spores and myxamoebae of slime molds. Although percentages of both survived, the spores survived better

than the myxamoebae. When invertebrate feces were cultivated, the species the invertebrates had eaten developed in the cultures.

Figure 77. The isopod ***Philoscia muscorum***, a likely dispersal agent for the cellular slime mold ***Didymium bahiense***. Photo by Malcolm Storey, through Creative Commons.

Figure 78. ***Didymium bahiense*** on bryophytes. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 79. The earthworm ***Octolasion cyaneum***; some species in this genus ingest slime molds and disperse them. Photo by Chih-Han Chang, through Creative Commons.

A similar relationship was found between the cellular slime mold ***Dictyostelium discoideum*** (Figure 11-Figure 12; **Dictyosteliomycetes**), an occasional bryophyte dweller, and the nematode ***Caenorhabditis elegans*** (Figure 80) (Kessin *et al*. 1996). This nematode is an inhabitant of the moss ***Sphagnum*** (Figure 81) (Glatzer & Ahlf 2001) and feeds on slime molds, including consumption of the spores. It kills the amoeboid stage, but the spores survive the digestive tract, making this another organism capable of moving the spores from one place to a new location for germination.

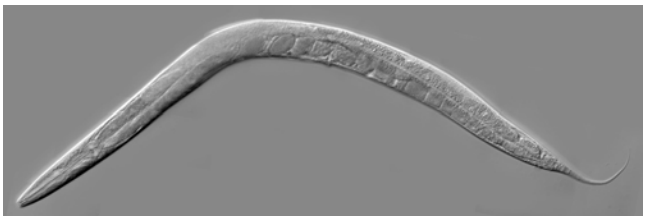

Figure 80. ***Caenorhabditis elegans***, a nematode that seems to benefit from some properties of ***Sphagnum***, and that also can disperse slime molds living there. Photo by Kbradnam, through Creative Commons.

Figure 81. ***Sphagnum recurvum***, in a genus that is home for the nematode ***Caenorhabditis elegans***. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Habitat Needs

Publications on slime molds are in no short supply. Gray and Alexopoulos (1968) published a treatise on the biology. Martin and Alexopoulos (1969) wrote a general treatise on the group. Ing (1994) summarized the phytosociology, arranged according to major vegetation types. Rollins and Stephenson (2011) summarized the global distribution and ecology.

As of 2011, Sarah Lloyd reported that only 1000 species of slime molds had been described. Their greatest abundance is in temperate forests, where they occur on living and dead trees and rotting wood, but also in some unusual habitats, including on dung and on living animals (Stephenson & Rojas 2017).

Moisture

Ing (1994) related the slime molds to their habitat factors, surmising that temperature is an important limiting factor in tropical, subtropical, Mediterranean, and alpine species. There is a consistent distinction between the corticolous, lignicolous, and epiphyllous species, and the lignicolous species have a preference for either conifers or deciduous trees. Ing even referred to bryophyte associations, noting that a few slime molds are particularly

associated with them. This may be due to water relations, with Ing noting that water and water-retaining substrates are of prime importance. The presence of fruiting structures (sporangia) is dependent on the arrival of rain after a prolonged warm period, making their presence most common in autumn in temperate regions. In the tropics, capsules form when the monsoon season begins. Fruiting seems to be independent of substrate.

Eliasson (1980) noted that species that have large plasmodia (Figure 22) typically are rare under arid conditions. This would suggest that the slime molds on bryophytes are the larger species in most habitats because of the moisture-holding capacity of the bryophytes.

On the other hand, Schnittler *et al*. (2013), based on observations in Xinjiang Province, China, concluded that corticolous **Myxomycetes** are some of the most drought-tolerant organisms in that habitat. They are opportunistic, permitted by their ability to survive in a dormant state for decades and to complete their life cycles in a few days of appropriate conditions.

Latitude

Stephenson *et al*. (1993) found recognizable patterns in the latitudinal variation of slime molds. The species assemblages in the tropical-subtropical regions is distinctly different from that found in temperate regions. Furthermore, the species differ in their substrate usage at different latitudes. Some species that are rare outside the Arctic and subArctic can be relatively common in these northern regions (Stephenson *et al*. 2000).

Food and Light

Naturally, available food is of importance in the location of active slime molds. Slime molds frequently make "decisions" for location based on the quality of food available. The common **Myxomycetes** slime mold ***Physarum polycephalum*** (Figure 59, Figure 82; sometimes a bryophyte dweller), in its amoeboid phase and if both locations are shaded, will choose the higher food quality 100% of the time (Latty & Beekman 2010). When a much higher quality food is in the light, it is selected, but when the difference in quality is small, the slime mold will select the shade over the light location, even if its food is of lesser quality.

Figure 82. ***Physarum polycephalum*** plasmodium or rotting wood. Photo by Frankenstoen, through Creative Commons

Role of Bryophytes as Slime Mold Habitat

Stephenson and Studlar (1985) found representatives of all six orders (at that time) of slime molds, exclusive of the **Labyrinthulomycota** and the **Plasmodiophorids** in their study of bryophyte-dwellers in the United States and Canada. The **Physarales** (Figure 2-Figure 9; Figure 60-Figure 68) (38% of all collections) were the most abundant, but members of the **Stemonitales** (Figure 34-Figure 37) (23%), **Trichiales** (Figure 13, Figure 40-Figure 45) (18%), and **Liceales** (Figure 83-Figure 84) (17%) were also commonly bryophyte associates. The order **Echinosteliales** (Figure 99-Figure 100) and the class **Ceratomyxomycetes** (Figure 31-Figure 32) comprised only 4% and 1%, respectively. All four of the major types of slime mold fruiting bodies (sporangia, aethalia, plasmodiocarps, and pseudoaethalia) were represented in their 170 collections.

Figure 83. ***Licea floriformis*** fruiting bodies on moss leaves. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 84. ***Licea retiformis*** plasmodium. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

But are these slime molds preferential colonists of bryophytes? Stephenson and Studlar (1985) set out to try to answer this question. By examining 170 collections throughout North America, they found that three species were particularly common: ***Fuligo septica*** (Figure 33), ***Stemonitis axifera*** (Figure 34), and ***S. fusca*** (Figure 35).

Furthermore, they found that some bryophytes were more likely than others to be suitable substrata: ***Nowellia curvifolia*** (Figure 85), ***Brotherella recurvans*** (Figure 86), ***Thuidium delicatulum*** (Figure 87), and ***Hypnum imponens*** (Figure 88). The slime mold order **Physarales** (Figure 2-Figure 9; Figure 60-Figure 68) was the most commonly represented. Taxa producing sporangia were the most abundant, representing 79% of the collections, but this is also the most common type of slime mold fruiting body (Gray & Alexopoulos 1968).

Figure 85. ***Nowellia curvifolia*** on log, a leafy liverwort that is a suitable substrate for some slime molds. Photo from <www.aphotofauna.com>, with permission.

Figure 86. ***Brotherella recurvans***, one of the more common moss substrata for the slime molds ***Fuligo septica***, ***Stemonitis axifera***, and ***S. fusca***. Photo by Bob Klips, with permission.

Figure 87. ***Thuidium delicatulum***, one of the more common moss substrata for the slime molds ***Fuligo septica***, ***Stemonitis axifera***, and ***S. fusca***. Photo by Janice Glime.

Figure 88. ***Hypnum imponens***, one of the more common moss substrata for the slime molds ***Fuligo septica***, ***Stemonitis axifera***, and ***S. fusca***. Photo by Jason Hollinger, through Creative Commons.

Most of the slime molds examined by Stephenson and Studlar (1985) occurred only one or two times among the 170 bryophyte collections that had slime molds, suggesting that there is little specificity involved. They suggest that three cases warrant further examination: ***Stemonitis axifera*** (Figure 34) with ***Thuidium delicatulum*** (Figure 87), ***Barbeyella minutissima*** (Figure 89) with ***Nowellia curvifolia*** (Figure 85) and ***Lepidozia reptans*** (Figure 90), and ***Lepidoderma tigrinum*** (Figure 91) with ***Nowellia curvifolia***. Certainly ***S. axifera*** (Figure 34) is not specific for bryophytes; 78% of those examined were from decorticated areas of logs. Likewise, the second and third most common species were more commonly collected from other substrata. ***Barbeyella minutissima*** was only associated with liverworts, but it is so small that it was not seen in the field. Therefore, it was found only on liverwort samples that were examined in the lab. In the Stephenson and Studlar study, **smooth mats** support more slime molds than other life forms. And slime molds that live on rotten wood seem to be the most common bryophyte associates.

Figure 89. ***Barbeyella minutissima*** on bryophytes. Photo by David Mitchell, The Eumycetozoan Project, with permission.

Figure 90. The liverwort ***Lepidozia reptans***. Photo by Michael Lüth, with permission.

Figure 91. ***Lepidoderma tigrinum*** immature on moss with slug. Photo by Marianne Meyer, through Creative Commons.

But other studies suggest there really are some bryophyte-specific slime molds. ***Fuligo muscorum*** (Figure 39), named for a mossy habitat, is common on ***Polytrichum*** (Figure 92), ***Dicranum*** (Figure 93), and ***Hypnum*** (Figure 88) species (Ing 1994). ***Elaeomyxa cerifera*** (Figure 94), although very rare, is known only from terrestrial bryophytes, including the liverwort ***Pellia epiphylla*** (Figure 95) (Hadden 1921).

Figure 92. ***Polytrichum juniperinum***; the slime mold ***Fuligo muscorum*** is common on the genus ***Polytrichum***. Photo by Bob Klips, with permission.

Figure 93. ***Dicranum scoparium***; the slime mold ***Fuligo muscorum*** is common on the genus ***Dicranum***. Photo by Janice Glime.

Figure 94. ***Elaeomyxa cerifera*** fruiting bodies on bryophytes. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 95. ***Pellia epiphylla*** is a suitable substrate for ***Elaeomyxa cerifera***, a species only known from bryophytes. Photo by Bernd Haynold, through Creative Commons.

If bryophytes are indeed a preferred substrate for some species, the next question is why. Stephenson and Studlar (1985) suggest that bryophytes serve as spore traps, increasing the chances of the trapped species becoming residents here. The bryophytes then provide a moist habitat, again favoring growth of slime molds. These same conditions provide a habitat for numerous protozoa and bacteria, providing food for the slime molds, and even the detritus produced by tardigrades, annelids, and arthropods can serve as food sources (Gerson 1969, 1982; Richardson 1981).

In a single study, Bovee (1979) reported 68 species of protozoa (particularly shelled amoebae and ciliates) among mosses, mostly the mosses ***Brachythecium salebrosum*** (Figure 96), ***Plagiomnium cuspidatum*** (Figure 97), and ***Pylaisiella selwynii*** (Figure 98) on a rotten log in Minnesota. Many of these protozoa provide suitable food for the slime molds in their mobile phase.

Figure 96. ***Brachythecium salebrosum***, home of many protozoa. Photo by Michael Lüth, with permission.

Figure 97. ***Plagiomnium cuspidatum***, home of many protozoa. Photo by Janice Glime.

Bryophytes may provide a preferred location for forming sporangia. Slime molds migrate to the highest position available before making sporangia (Stephenson & Studlar 1985), and bryophytes on a log could very well be that place.

Figure 98. ***Pylaisia selwynii***, home of many protozoa. Photo by Jan-Peter Frahm, with permission.

In any case, the slime molds, like the tardigrades, rotifers, and protozoa, seem to be well-adapted to the **poikilohydric** (having no mechanism to prevent desiccation) existence of living among bryophytes (Gerson 1982). When the bryophyte and the slime mold dry out, the myxamoebae and swarm cells of the slime mold can form **microcysts**; plasmodia (Figure 22) are able to form **sclerotia** (Figure 23, Figure 24). These structures are all resistant and survive well under desiccating conditions. They can quickly resume activity when water becomes available. The tolerance of slime molds to alternate wetting and drying that typically accompanies the bryophytes provides us with another reason to suspect that they can live within, as well as sporulate upon, bryophyte clumps.

But not all slime molds benefit from the moist environment of the bryophytes. The genus ***Echinostelium*** (Figure 99-Figure 100) is comprised of tiny slime molds that live on bark (Keller & Brooks 1976). But in areas that support the growth of algae, mosses, and leafy liverworts, larger aphano- and phaneroplasmodial slime molds are favored. Keller and Brooks surmised that the tiny protoplasmodial ***Echinostelium*** species were unable to compete.

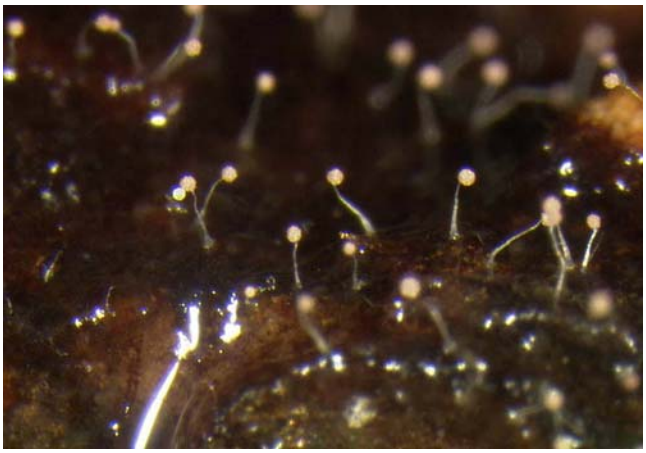

Figure 99. ***Echinostelium minutum***, a tiny species that is probably unable to compete. Photo by Satyendra Rajguru, The Eumycetozoan Project, DiscoverLife.org, with online permission.

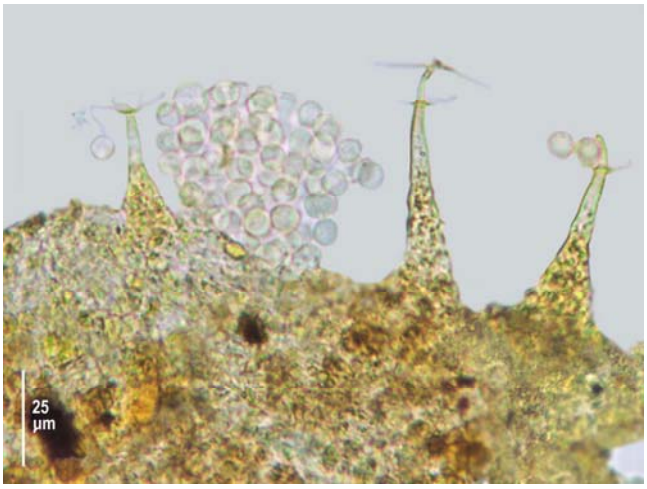

Figure 100. ***Echinostelium arboreum*** showing stalks left when spores are dispersed. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Slime Mold Effects on Bryophytes

A takeover by slime molds on mosses is apparently a rare occurrence (Coker 1966). Nevertheless, at least one example exists. Coker reported that the slime mold ***Cribraria rufa*** (Figure 101) had apparently destroyed a patch of the moss ***Orthodontium lineare*** (Figure 102-Figure 103) on a rotten conifer stump.

Figure 101. ***Cribraria rufa*** fruiting, a species that apparently can destroy the moss ***Orthodontium lineare***. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 102. ***Orthodontium lineare*** on rotting log, a moss that can be destroyed by the slime mold ***Cribraria rufa***. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 103. ***Orthodontium lineare*** with capsules, a moss that can be destroyed by the slime mold ***Cribraria rufa***. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Almost 100 compounds have been identified from the slime molds (Dembitsky *et al*. 2005). These include lipids, fatty acid amides (pigments) and derivatives, alkaloids, amino acids and peptides, naphthoquinone pigments, aromatic compounds, carbohydrate compounds, terpenoid compounds, and arcyriaflavin derivatives (alkaloids). Some of these give the slime molds their unique colors. But some have antimicrobial activity against bacteria like ***Bacillus cereus*** (Figure 104) (Pereira *et al*. 1996). These compounds might permit them to compete with other slime molds, but do they have any effect on the bryophytes?

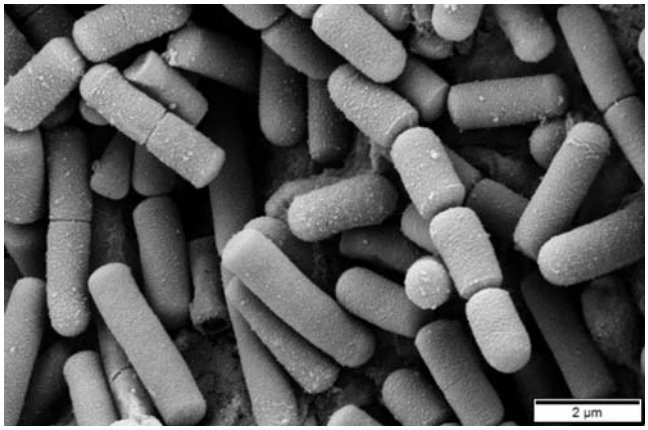

Figure 104. ***Bacillus cereus*** SEM, a species that is inhibited by some of the secondary compounds produced by slime molds. Photo by Mogana Das Murtey and Patchamuthu Ramasamy, through Creative Commons.

Slime molds do not usually appear to be any threat to the bryophytes. However, in some cases, it appears that the slime molds are aggressive enough to overgrow and destroy the bryophytes (Coker 1966). ***Fuligo intermedia*** (Figure 105) seems to be harmful (Pant & Tewari 1982), most likely due to its density of fruiting bodies that can cover patches several centimeters in diameter. Such growths would deprive the moss of light and may interfere with gas exchange.

Figure 105. ***Fuligo intermedia*** fruiting bodies on bryophytes. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Bryophytes Growing on Slime Molds

In some species, the fruiting bodies of slime molds can persist. That can lead to a reverse relationship with bryophytes. It gives the bryophytes sufficient time to grow over the slime molds, as observed by Sarah Lloyd (2011). She found a growth of leafy liverworts on the stalk of a slime mold on decaying wood, undoubtedly a very rare occurrence.

Epizooites

One of the most unusual habitats for slime molds is on living lizards, ***Corytophanes cristatus*** (Figure 106), in Mexico and Costa Rica (Lloyd 2011). This lizard is a sit-and-wait predator and therefore moves around little. It uses its head to dig its nest and often has residual soil in the scoop on the top of its head. This microenvironment is home to the tiny liverwort ***Lejeunea obtusangula*** (see Figure 107) (Gradstein & Equihua 1995). But this lizard is also sometimes home to the slime mold ***Physarum pusillum*** (Figure 108). The co-occurrence of the liverwort and the slime mold, if at all, is most likely one of chance resulting from the scooping behavior of the lizard.

Figure 106. ***Corytophanes cristatus***, the crested lizard that sometimes has the slime mold ***Physarum pusillum*** or the leafy liverwort ***Lejeunea obtusangula*** growing on it. Photo by Simon J. Tonge, through Creative Commons.

Figure 107. ***Lejeunea*** sp. from the Neotropics; ***L. obtusangula*** sometimes occurs on the lizard ***Corytophanes cristatus***. Photo by Michael Lüth, with permission.

Figure 108. ***Physarum pusillum*** fruiting bodies, a species known to live on the lizard ***Corytophanes cristatus***. Photo by Gustavo F. Morejón J., through Creative Commons.

Potential for Symbiosis?

In sharp contrast to the casual and accidental associations of most slime molds with their substrates and neighbors, some relationships might be more directly beneficial. In pure cultures of the slime mold ***Fuligo cinerea*** (Figure 109; sometimes a bryophyte dweller) (and the green alga ***Chlorella xanthella*** – Figure 110), sodium radiophosphate accumulated in them both from the medium. When these were separately mixed with the opposite species, both species were able to accumulate the radiophosphorus from the other species cultured with it. While this suggests the potential for a symbiosis, it fails to demonstrate any dependency or benefit. Nevertheless, a **protocooperation** could exist with nutrients, moisture, or other conditions that enhance the environment created by a bryophyte and a slime mold living together. Adding algae or **Cyanobacteria** to the mix might make it even better.

Figure 109. ***Fuligo cinerea*** on lichens and leafy liverworts, a slime mold that is able to exchange substances with the alga ***Chlorella xanthella***. Photo by Alexey Sergeev, with permission.

Figure 110. ***Chlorella*** sp.; ***C. xanthella*** is able to exchange substances with the slime mold ***Fuligo cinerea***. Photo by Barry H. Rosen, through Creative Commons.

Interactions with Invertebrates

Both bryophytes and slime molds often host a variety of invertebrates. Among the inhabitants of slime molds, nematodes can be numerous, as they are among some bryophytes. In ***Dictyostelium discoideum*** (Figure 12; **Dictyosteliomycetes**), the aggregate of slime mold cells protects the formation from nematode predation, whereas nematodes readily feed on the individual cells (Kessin *et al*. 1996). Nematodes are also known from the **Myxomycetes** slime molds ***Trichia varia*** (Figure 13-Figure 17) and ***Stemonitopsis typhina*** (Figure 111; both can occur on bryophytes) on rotten wood (Ing 1967).

Figure 111. ***Stemonitopsis typhina*** sporangia, a species where nematodes can thrive. Photo from George Barron, with online permission.

Snails (Figure 112) and slugs (Figure 113) also can feed on slime molds, and these slime molds may be moss inhabitants. Snails and other invertebrates feed on the fruiting bodies of ***Lycogala epidendrum*** (Figure 46) (Eliasson 1980; Pant & Tewari 1982).

Some tardigrades (water bears) feed selectively on slime molds (Kylin 1991). Since tardigrades are common on bryophytes, it is likely that this three-way association occurs, with bryophytes providing the substrate for the slime molds and the slime molds providing food for the tardigrades. ***Milnesium tardigradum*** (Figure 114), used in the experiments, is a moss inhabitant (see Chapter 5 in this volume). Kylin demonstrated that it not only will consume some slime molds and spurn others, those consumed can be moss inhabitants. These include the **Myxomycetes** ***Diderma*** cf. ***testaceum*** (Figure 115; an inhabitant of species of mosses, leaves, and twigs), ***Trichia botrytis*** (Figure 40-Figure 42), and ***Clastoderma debaryanum*** (Figure 116-Figure 117). The response of ***D.*** cf. ***testaceum*** is interesting. The tardigrade typically attacks the vein where protoplasm is streaming. The slime mold responds by streaming away from the bite. The tardigrade seldom takes a second bite, causing little damage to the slime mold. But when the slime mold begins forming sporangia, the tardigrade once again attacks, burrowing into the developing sporangium. This causes the sporangial development to cease. Occasionally the sporangium will collapse onto the tardigrade, trapping it. ***Trichia botrytis*** elicits similar responses when the plasmodium (Figure 22)

is attacked, usually feeding for about 12 hours, but has a sporangium that is too small for the tardigrade to burrow into it. ***Clastoderma debaryanum*** is a much smaller slime mold and the tardigrade usually consumes the entire plasmodium.

Figure 112. Fruiting bodies of ***Arcyria stipata*** with one of its enemies – a snail. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 113. Slug and the slime mold ***Lamproderma*** on mosses. Photo by Keller, through Creative Commons.

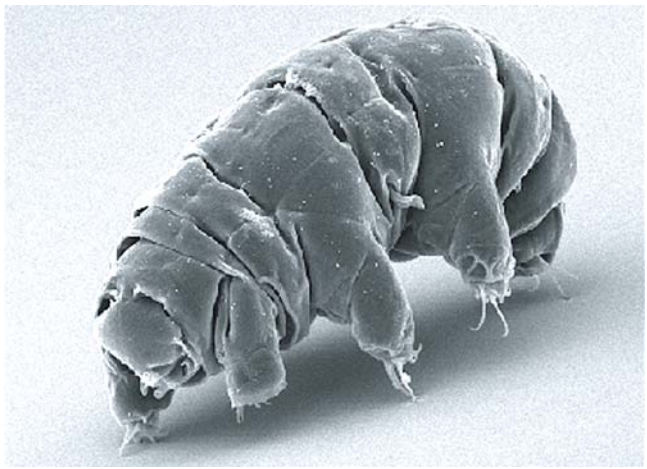

Figure 114. ***Milnesium tardigradum*** SEM, a species that feeds on the moss-inhabiting slime molds ***Diderma*** cf. ***testaceum***, ***Trichia botrytis***, and ***Clastoderma debaryanum***. Photo from Schokraie *et al*. 2012, through Creative Commons.

Figure 115. ***Diderma testaceum*** fruiting structures, with lichens, a slime mold that serves as food for the tardigrade ***Milnesium tardigradum***. Masse (1892) indicated that this species grows on leaves, mosses, and twigs. Photo by James K. Lindsey, through Creative Commons.

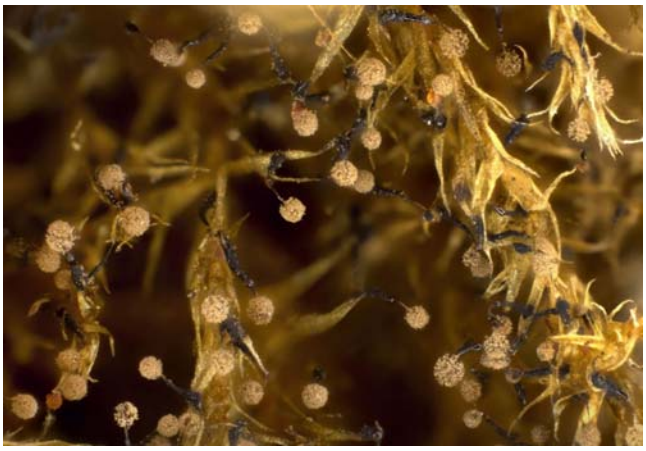

Figure 116. ***Clastoderma debaryanum*** on moss, a slime mold that serves as food for the tardigrade ***Milnesium tardigradum***. Photo from Myxotropic, through Creative Commons.

Figure 117. ***Clastoderma debaryanum*** fruiting body on moss, a slime mold that serves as food for the tardigrade ***Milnesium tardigradum***. Photo from Myxotropic, through Creative Commons.

Isopods are common inhabitants on bryophytes and will readily consume them (Hames & Hopkin 1989). They likewise can occur on slime molds (Ing 1967). They eat both plasmodia (Figure 22) and fruiting bodies of the **Myxomycetes** slime molds. The isopods ***Trichoniscus pusillus*** (Figure 118) and ***Oniscus asellus*** (Figure 119) feed on the slime molds ***Trichia varia*** (Figure 13-Figure 17) and ***Arcyria denudata*** (Figure 120). The isopod ***Androniscus dentiger*** (Figure 121) eats both plasmodia and sporangia of ***Didymium iridis*** (Figure 122), at the same time dispersing this species across the substrate. Spores have been found in the isopod digestive tracts undigested. All of these three slime molds are known from bryophytes.

Figure 118. ***Trichoniscus pusillus***, an isopod that feeds on the slime molds ***Trichia varia*** and ***Arcyria denudata***. Photo by Malcolm Storey, EOL, through Creative Commons.

Figure 119. ***Oniscus asellus*** with moss on log, an isopod that feeds on the slime molds ***Trichia varia*** and ***Arcyria denudata***. Photo by Kurt Kulac, through Creative Commons.

Figure 120. ***Arcyria denudata*** fruiting bodies. Photo by Kim Fleming, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 121. ***Androniscus dentiger***, an isopod that feeds on the slime mold ***Didymium iridis***. Photo by Gilles San Martin, through Creative Commons.

Figure 122. ***Didymium iridis*** sporangia, food for the isopod ***Androniscus dentiger***. Photo by through Creative Commons.

Millipedes are likely known from both bryophytes and slime molds. The millipede ***Cylindroiulus punctatus*** (Figure 123) consumes the sporangia of the slime mold ***Trichia varia*** (Figure 13-Figure 17) on wet, rotten wood (Ing 1967).

Figure 123. ***Cylindroiulus punctatus***, a millipede that feeds on the slime mold ***Trichia varia***. Photo by Saxifraga-Ab H Baas, through Creative Commons.

Collembola (springtails; Figure 124) are avid consumers of small slime molds on bark (Ing 1967). Some of these springtails eat ***Stemonitopsis typhina*** (Figure 111; sometimes a bryophyte dweller) and ***Cribraria piriformis*** (Figure 125-Figure 126) on rotten wood. Both ***Stemonitopsis typhina*** and ***Cribraria piriformis*** can occur on or with bryophytes, making it likely that a 3-way association sometimes occurs among the bryophytes, slime molds, and springtails.

Figure 124. ***Isotoma caerulea*** on moss and a potential consumer of slime molds. Photo by Andy Murray, through Creative Commons.

Figure 125. ***Cribraria piriformis*** sporangia with contained spores, food for springtails. Photo from Myxotropic, through Creative Commons.

Figure 126. ***Cribraria piriformis*** sporangia with spores gone, perhaps being eaten by springtails. Photo by Myxotropic, through Creative Commons.

Insects are common on both bryophytes and slime molds. Some **Coleoptera** (beetles) may be occasional or accidental feeders on **Myxomycetes** (Ing 1967). Among these, the beetle ***Anisotoma humeralis*** (Figure 127) seems to be confined to large slime molds such as ***Fuligo septica*** (Figure 33), ***Reticularia lycoperdon*** (Figure 128-Figure 129), ***Stemonitis fusca*** (Figure 35-Figure 36), ***Symphytocarpus flaccidus*** (Figure 29-Figure 30), and ***Tubifera ferruginosa*** (Figure 55); all of these slime molds can sometimes be found associated with bryophytes. The spores are held in the capillitium and are relatively accessible (Figure 130).

Figure 127. ***Anisotoma humeralis***, a beetle that feeds on slime molds that are known to inhabit mosses. Photo by Boris Loboda, through Creative Commons.

Figure 128. Pink ***Reticularia lycoperdon*** on mossy log. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 129. White ***Reticularia lycoperdon*** on mossy bark. Photo by Marion Zãller, through Creative Commons.

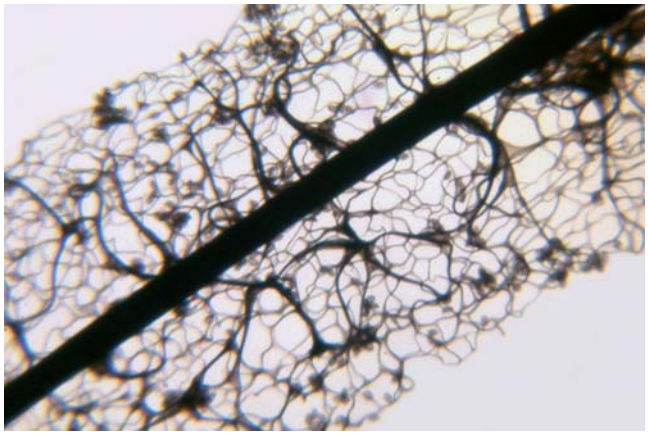

Figure 130. Capillitium of sporangium of ***Stemonitis***. Photo by Janice Glime.

Some beetles even seem to be obligate feeders on slime molds (Dudka & Romanenko 2006). Lawrence and Newton (1980) reported on about 35 beetle species, mostly from North American, that feed on slime mold spores. Dudka and Romanenko (2006) found that slime mold spores occurred in 19 of the 25 beetle (**Latridiidae**) guts they examined from Crimea. These included ***Latridius hirtus*** (Figure 131), ***Enicmus rugosus*** (Figure 132), and ***E. fungicola*** (Figure 133) as obligate slime mold feeders. On the other hand ***Corticarina truncatella*** (Figure 134) is a facultative slime mold feeder. The most common 13 species of slime molds, including ***Fuligo septica*** (Figure 33), ***Mucilago crustacea*** (Figure 135), ***Stemonitis axifera*** (Figure 34), ***S. fusca*** (Figure 35), and ***S. splendens*** (Figure 136), were inhabited by five species of **Latridiidae**; all of these slime molds can occur on bryophytes.

Figure 131. ***Latridius hirtus*** adult, a beetle that feeds on slime mold spores. Photo by Stefan Schmidt, through Creative Commons.

Figure 132. ***Enicmus rugosus*** adult, a beetle that feeds on slime mold spores. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 133. ***Enicmus fungicola*** adult, a beetle that feeds on slime mold spores. Photo by Tim Faasen, with permission.

Figure 134. ***Corticarina truncatella*** adult, a beetle that facultatively feeds on slime mold spores. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 135. ***Mucilago crustacea*** on mosses. Photo by Drew Henderson, through Creative Commons.

Figure 136. ***Stemonitis splendens***, one of the slime molds eaten by the beetle family **Latridiidae**. Photo by Dan Molter, through Creative Commons.

Some **Coleoptera** (beetles) in the **Leiodidae** can be considered slime mold beetles (Wheeler & Miller 2005). ***Stetholiodes*** sp. (Figure 137) is a slime mold beetle that was originally described from moss in northern Indiana (Blatchley 1910). Several species of ***Agathidium*** (Figure 138) are known moss inhabitants, including ***A. brevisternum***, ***A. rhinocerellum***, and ***A. cavisternum*** (Figure 139) (Wheeler & Miller 2005). The only known host for ***Agathidium rhinocerellum*** is the **Myxomycetes** slime mold ***Fuligo septica*** (Figure 33, Figure 140), a widespread generalist species that includes bryophytes among its substrates. It is likely that other moss dwellers in this family also feed on slime molds.

Figure 137. ***Stetholiodes laticollis*** adult; some members of this genus are slime mold beetles that live on mosses. Photo by Museum of Comparative Zoology, Harvard University, through Creative Commons.

Figure 138. ***Agathidium*** sp. adult; some members of this genus are both moss and slime mold inhabitants. Photo by Joyce Gross, with permission.

Figure 139. ***Agathidium cavisternum***, a moss dweller and possible slime mold feeder. Photo from Museum of Comparative Zoology, Harvard University, through Creative Commons.

Figure 140. ***Fuligo septica*** on moss, a slime mold that is host for the beetle ***Agathidium rhinocerellum***. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Some **Diptera** larvae live on the slime mold plasmodia (Figure 22) and feed on them, with some remaining there as pupae. ***Bradysia*** (Figure 141) species feed on plasmodia of ***Fuligo septica*** (Figure 33) and sporangia of ***Lycogala epidendrum*** (Figure 46) and ***Arcyria incarnata*** (Figure 142-Figure 143), all occasional bryophyte dwellers. In fact, some flies can be reared on slime molds as their only food.

Figure 141. ***Bradysia*** larvae, a species that feeds on slime mold plasmodia of ***Fuligo septica*** and sporangia of ***Lycogala epidendrum*** and ***Arcyria incarnata***. Photo by David Cappaert, through Creative Commons.

Figure 142. ***Arcyria incarnata*** fruiting bodies, food for ***Bradysia***. Photo by Stu's Images, through Creative Commons.

Figure 143. ***Arcyria incarnata*** fruiting bodies on mosses, food for ***Bradysia***. Photo by Dan Molter, through Creative Commons.

Summary

Slime molds are really not molds, but protozoa, with an amoeboid feeding stage and a spore-producing, non-feeding stage. They also lack chitin, a compound found in true molds. The bryophyte dwelling members are included in the **Eumycetozoa** or **Amoebozoa** and classified into the classes **Myxomycetes**, **Dictyosteliomycetes**, and **Ceratiomyxomycetes**.

The life cycle has a dormant spore that will germinate when adequate water is available and develop into **swarm cells** or **amoeboid cells**. This stage feeds like an amoeba. In **Myxomycetes**, either of these cell types can form a zygote that divides to form a **plasmodium**. This stage likewise feeds on bacteria, algae, and protozoa. It can dry out to form a **sclerotium** that can remain dormant for years, or move to higher ground in the light to form sporangia and spores. Either stage can occur on bryophytes, but the plasmodium stage is likely to be unnoticed. The life cycle is usually keyed to seasons, with autumn being the more favorable fruiting season for most species. Dispersal is most likely primarily by wind, but animals are also dispersal vectors, either by carrying spores on the outside or by digesting them or plasmodia and dispersing them in the feces.

The slime molds respond to light, *p*H, volatile substances, temperature, and water availability to trigger fruiting. We know most slime molds seek higher positions with more light before forming sporangia. Do bryophytes provide a more suitable location for that event? Do slime molds benefit in their dispersal by the activities of moss fauna?

The slime molds known to associate with mosses are predominantly in the **Myxomycetes**. The mosses may provide prolonged moisture and a place to get above the prevailing substrate for better dispersal, or they may be dispersed by some of the invertebrates living among the bryophytes. Little is known about the effect the slime molds have on the bryophytes. Some slime molds live on animals, and these may be the same animals that have bryophytes growing on them. The potential for symbiosis exists, but little evidence supports any symbiotic relationship.

Acknowledgments

Thank you to Sarah Lloyd for challenging my organization of this subchapter and to Steve Stephenson for providing me with recent literature that helped me untangle the classification of these slime molds. The Eumycetozoan website has been invaluable for checking current nomenclature and finding suitable images. Thank you to Yuri Novozhilov for providing me with images to illustrate the three spore surface types.

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CHAPTER 3-2
SLIME MOLDS: BRYOPHYTE ASSOCIATIONS

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CHAPTER 3-2
SLIME MOLDS: BRYOPHYTE ASSOCIATIONS

Figure 1. Slime mold, probably ***Fuligo septica***, on mosses in New Zealand. Photo by Bernard Spragg, through public domain.

Bryophyte Associations

Slime-mold-bryophyte associations can occur for a number of reasons. These can be accidental associations in which spores find favorable conditions to germinate, *i.e.*, sufficient moisture. Others are facultative, living on logs, but creeping onto mosses as the plasmodium moves about to feed and be able to survive there. Still others may climb up the bryophytes, as indicated in the previous subchapter, to emerge from bark crevices and reach the light for fruiting. Others germinate within the bryophyte mat where moisture conditions are maintained and bryophytes hide the slime mold plasmodium from our searching eyes. It is not until the slime mold is ready to produce sporangia that it climbs out where it is visible on the bryophyte. And finally, there are those slime molds that live only on bryophytes – the **bryophiles**. This latter group is a small one, but of the most interest to a bryologist. This chapter is a gathering of all sources I could find to demonstrate slime molds that ever occur on or with bryophytes.

Bryophiles

Dudka and Romanenko (2006) described a variety of cases in which slime molds interact or co-exist with other organisms. They found 13 species of slime molds on 9 species of mosses and 3 species of liverworts on decaying wood or bark in the Crimean Nature Reserve. These included their relationships with bryophytes and they noted that the slime mold **sporophores** (sporangial stalks) at the surface of mosses and liverworts are rather widespread in nature (Stephenson & Stempen 1994; Härkönen *et al.* 2002; Stojanowska & Panek 2004). But it appears that the best known bryophiles include only ***Barbeyella minutissima*** (Figure 2-Figure 3), ***Colloderma oculatum*** (Figure 4), and ***Lepidoderma tigrinum*** (Figure 5) (Schnittler & Novozhilov 1996; Dudka & Romanenko 2006).

Figure 2. Fruiting bodies of ***Barbeyella minutissima*** on bryophytes. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

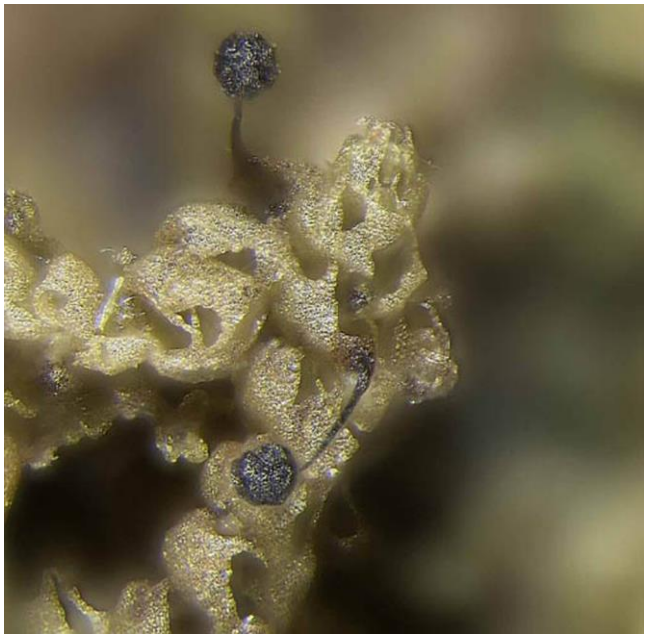

Figure 3. Fruiting bodies of ***Barbeyella minutissima*** on a leafy liverwort. Photo by Steve Stephenson, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 4. ***Colloderma oculatum*** on bryophytes. Photo from the Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 5. Fruiting bodies of ***Lepidoderma tigrinum*** on bryophytes. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Barbeyella minutissima (Figure 2-Figure 3) is a rare slime mold with a disjunct distribution in the northern Alps of Germany and several states in the Appalachian Mountains of the eastern USA (Schnittler *et al*. 2000). The distribution of this species is centered in montane spruce-fir forests, where it commonly associates with ***Colloderma oculatum*** (Figure 4), ***Lamproderma columbinum*** (Figure 6), and ***Lepidoderma tigrinum*** (Figure 5). ***Barbeyella minutissima*** is associated with several leafy liverwort species. In particular, the leafy liverwort ***Nowellia curvifolia*** (Figure 7-Figure 8) serves as an indicator for the presence of ***Barbeyella minutissima***.

Figure 6. ***Lamproderma columbinum*** on mosses. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 7. ***Nowellia curvifolia*** on a decorticated log, an indicator for the slime mold ***Barbeyella minutissima***. Photo from Bioimages, through Creative Commons.

Figure 8. ***Nowellia curvifolia***, a leafy liverwort substrate for the slime mold ***Barbeyella minutissima***. Photo from Bioimages, through Creative Commons.

One very rare slime mold (***Elaeomyxa cerifera*** – Figure 9) is known primarily from the soil-dwelling thallose liverwort ***Pellia epiphylla*** (Figure 10) (Hadden 1921; Ing 1994), a soil-dwelling liverwort that is common on stream banks, but also occurs on decorticated logs, often in association with bryophytes. Similarly, ***E. reticulospora*** (Figure 11) is known only from its type locality on bryophytes in the tropics (Moreno *et al*. 2008).

Figure 9. ***Elaeomyxa cerifera*** with sporangia on bryophytes. Photo by Sarah Lloyd, with permission.

Figure 10. ***Pellia epiphylla*** with capsules. Photo by Li Zhang, with permission.

Figure 11. ***Elaeomyxa*** *cf.* ***reticulospora***, a tropical slime mold known only from bryophytes in its type locality. Photo by Sarah Lloyd, with permission.

Little study of tropical slime molds has occurred, with most of it in the last 20 years. One of these more thorough studies is that of Rojas *et al*. (2010) in Costa Rica. They determined that elevation was a key factor in determining distribution. Lowland substrate preferences include litter, inflorescences, and bryophytes (Schnittler & Stephenson 2000, 2002; Schnittler 2001). Species of these substrates tend to be specialized and have narrow niches. ***Lamproderma columbinum*** (Figure 6) and ***L. scintillans*** (Figure 12) seem to prefer bryophytes. ***Stemonitis fusca*** (Figure 13-Figure 14) and ***Lycogala epidendrum*** (Figure 15), both known from bryophytes, prefer higher elevation forests.

Figure 12. ***Lamproderma scintillans*** sporangia. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 13. ***Stemonitis fusca*** sporangia on moss. Photo by Richard Orr, with permission.

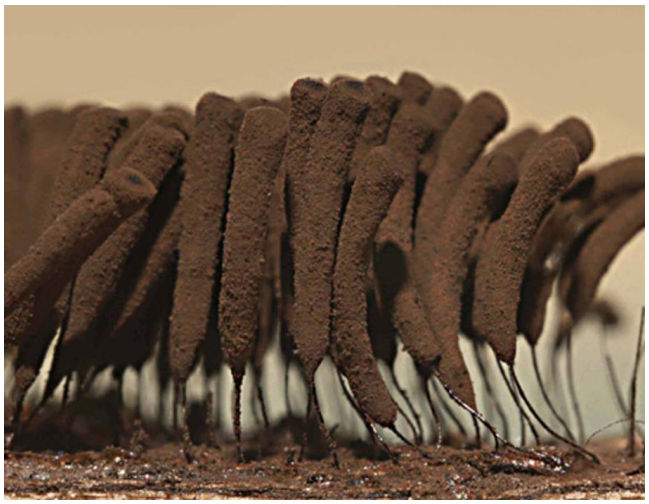

Figure 14. ***Stemonitis fusca*** with mature sporangia. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 15. Fruiting bodies of ***Lycogala epidendrum*** (wolf's milk; toothpaste slime) on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Commonly Associated Slime Molds

Despite the apparently limited number of true bryophilous species, other coincidental associations may offer some moisture advantages. ***Arcyria cinerea*** (Figure 16-Figure 17; see also Robbrecht 1974), ***Echinostelium arboreum*** (Figure 18), ***E. minutum*** (Figure 19), ***Macbrideola cornea*** (Figure 20), ***Perichaena vermicularis*** (Figure 21), and ***Physarum cinereum*** (Figure 22-Figure 23) in the montane Crimea are most commonly associated with the mosses ***Hypnum cupressiforme*** (Figure 24) and ***Leucodon sciuroides*** (Figure 25), and leafy liverwort ***Porella platyphylla*** (Figure 26).

Figure 16. ***Arcyria cinerea***. fruiting bodies. Photo by George Barron, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 17. ***Arcyria cinerea*** fruiting on mosses. Photo by Dan Molter, through Creative Commons.

Figure 18. ***Echinostelium arboreum*** fruiting body. Photo from Myxotropic, through Creative Commons.

Figure 19. ***Echinostelium minutum*** fruiting body, a species frequently associated with bryophytes. Myxotropic, through Creative Commons.

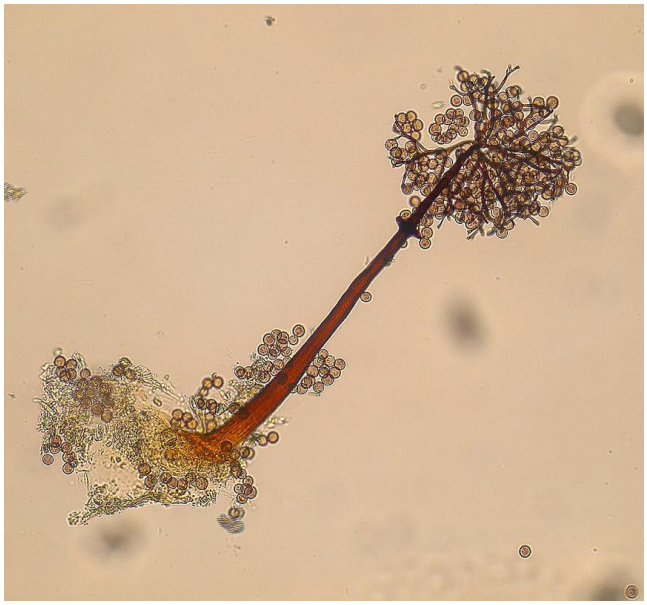

Figure 20. ***Macbrideola cornea***, a species frequently associated with bryophytes. Photo by Shirokikh, through Creative Commons.

Figure 21. ***Perichaena vermicularis***, a species frequently associated with bryophytes. Photo by Sarah Lloyd, with permission.

Figure 22. ***Physarum cinereum*** mature sporangia on log. Photo from Denver Botanical Gardens, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 23. ***Physarum cinereum*** var ***aureonodum*** with dehiscing capsules. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 24. ***Hypnum cupressiforme***, a moss that often provides the substrate for a number of slime mold species. Photo by Janice Glime.

Figure 25. ***Leucodon sciuroides*** dry, a moss that often provides the substrate for a number of slime mold species. Photo by Kai Vellak, through Creative Commons.

Figure 26. ***Porella platyphylla***, a leafy liverwort that often provides the substrate for a number of slime mold species. Photo by Janice Glime.

The following **Myxomycete**-bryophyte associations are also known, but more rarely (Dudka & Romanenko 2006):

Didymium trachysporum (Figure 27) on ***Ctenidium molluscum*** (Figure 28)
Licea minima (Figure 29-Figure 30) on ***Hypnum cupressiforme*** (Figure 24)
Perichaena chrysosperma (Figure 31) on ***Frullania dilatata*** (Figure 32)
Stemonitis fusca (Figure 14) on ***Leucodon sciuroides*** (Figure 25)
Symphytocarpus amaurochaetoides (Figure 33-Figure 34) on ***Pterigynandrum filiforme*** (Figure 35-Figure 36)
Symphytocarpus impexus (Figure 37) on ***Porella platyphylla*** (Figure 26)
Trichia varia (Figure 38-Figure 39) on ***Anomodon viticulosus*** (Figure 40-Figure 41)

In addition to these, ***Physarum cinereum*** (Figure 22-Figure 23) occurs on fallen leaves and decaying wood, but it occurs more frequently on bryophytes.

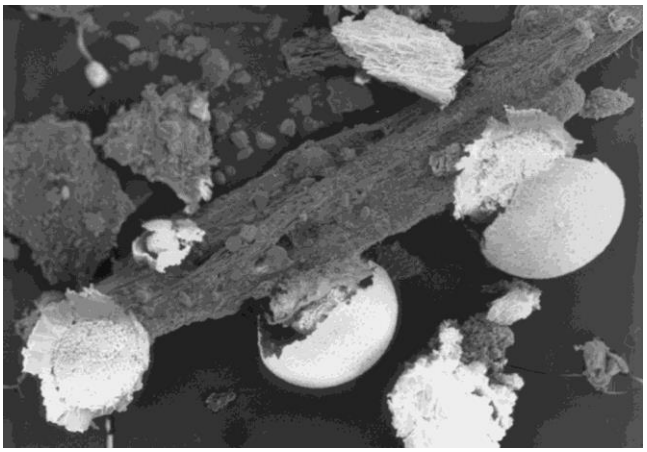

Figure 27. ***Didymium trachysporum***, a species known from the moss ***Ctenidium molluscum***. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 28. ***Ctenidium molluscum***, a moss occasionally serving as a slime mold substrate. Photo by Michael Lüth, with permission.

Figure 29. ***Licea minima*** fruiting body, a species occasionally using the moss ***Hypnum cupressiforme*** as a substrate. Photo from Myxotropic, through Creative Commons.

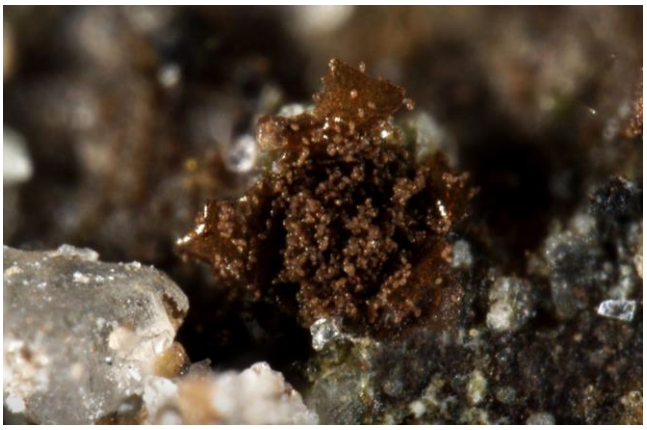

Figure 30. ***Licea minima*** fruiting body showing spores. Photo from Myxotropic, through Creative Commons.

Figure 31. ***Perichaena chrysosperma*** fruiting bodies, a species occasionally using a bryophyte substrate. Photo from Myxotropic, through Creative Commons.

Figure 32. ***Frullania dilatata***, a known leafy liverwort substrate for ***Perichaena chrysosperma***. Photo by Barry Stewart, with permission.

Figure 33. ***Symphytocarpus amaurochaetoides*** on moss, a species also known from the moss ***Pterigynandrum filiforme***. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 34. ***Symphytocarpus amaurochaetoides*** and snails eating the fruiting bodies of slime molds on a decorticated log. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 35. ***Pterigynandrum filiforme*** on tree, a known but uncommon moss substrate for ***Symphytocarpus amaurochaetoides***. Photo by Dick Haaksma, with permission.

Figure 36. ***Pterigynandrum filiforme*** a known but uncommon substrate for ***Symphytocarpus amaurochaetoides***. Photo by Michael Lüth, with permission.

Figure 37. ***Symphytocarpus impexus*** on log, a species that can sometimes occur on the leafy liverwort ***Porella platyphylla***. Photo by Thomas Laxton, through Creative Commons.

Figure 38. ***Trichia varia*** fruiting bodies, a species known to occur on the moss ***Anomodon viticulosus***. Photo by Harley Barnhard, The Eumycetozoan Project, DiscoverLife.org, with online permission.

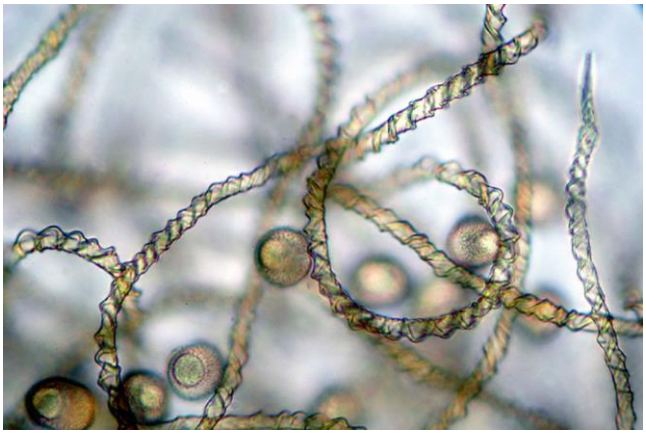

Figure 39. ***Trichia varia*** capillitia and spores. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 40. ***Anomodon viticulosus*** on bark, one of the mosses known to serve as a substrate for ***Trichia varia***. Photo by Michael Lüth, with permission.

Figure 41. ***Anomodon viticulosus***, a suitable substrate for ***Trichia varia***. Photo by Janice Glime.

While some slime molds prefer bryophyte substrates, lichens are rarely preferred (Ing 1999; Leontyev 2010). Among these bryophyte inhabitants in the Ukraine are ***Metatrichia vesparia*** (Figure 42; probably should be ***Trichia***) and ***Tubifera ferruginosa*** (Figure 43-Figure 44), two slime molds typically found on decaying wood that is covered with mosses (Leontyev 2010).

Figure 42. ***Metatrichia vesparia*** fruiting on mosses. Photo by Alexey Zakharinskij, through Creative Commons.

Figure 43. ***Tubifera ferruginosa*** with mosses and liverworts. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 44. ***Tubifera ferruginosa*** with mature sporangia on mosses and wood. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Novozhilov *et al*. (2006) reported slime mold diversity and ecology from arid regions in Russia. They noted that ***Physarum bivalve*** (Figure 45), ***Physarum leucophaeum*** (Figure 46), and ***Didymium melanospermum*** (Figure 47-Figure 48) occurred on living mosses. It is likely that the mosses lengthened the period of available moisture in these dry habitats.

Figure 45. ***Physarum bivalve*** on wood, a slime mold known to inhabit mosses. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 46. ***Physarum leucophaeum***, a slime mold known to grow on mosses. Photo by Jerry Cooper, through Creative Commons.

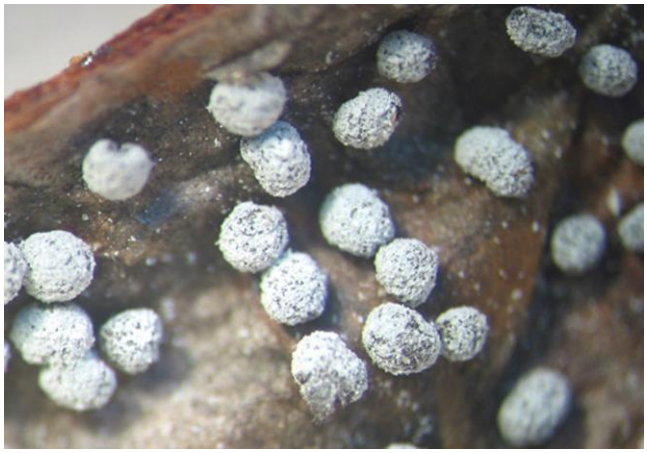

Figure 47. ***Didymium melanospermum*** fruiting bodies. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 48. ***Didymium melanospermum*** fruiting bodies. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Although I have found few Asian records, Ukkola *et al*. (2001) reported ***Physarum album*** (Figure 49) on moss-covered rotting logs and ***P. pusillum*** (Figure 50-Figure 51) on moss-covered bark of a living tree in China. In Nainital, India, ***Fuligo intermedia*** (Figure 52) occurs on mosses (Pant & Tewari 1982).

Figure 49. ***Physarum album***, a species known from moss-covered rotting logs. Photo by George Shepherd, through Creative Commons.

Figure 50. ***Physarum pusillum*** fruiting bodies on leaf litter. Photo by Gustavo F. Morejón J., through Creative Commons.

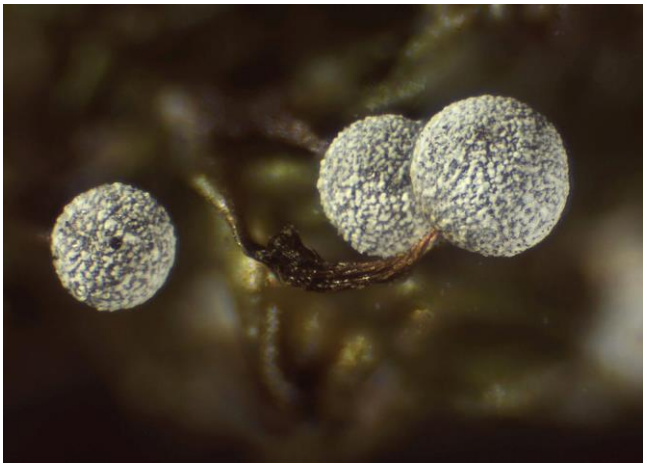

Figure 51. ***Physarum pusillum*** sporangium on mosses. Photo by TAO92, through Creative Commons.

Figure 52. ***Fuligo intermedia*** on ***Polytrichum***. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

It is clear that slime molds are often associated with bryophytes (Sean Edwards, pers. comm. 7 December 2013). But these associations may simply be two organisms with similar environmental requirements, particularly for moisture. Among these, Edwards was able

to list several of these moss-slime mold associations from England:

Fuligo septica (Figure 53, Figure 62) pulsing plasmodium with ***Hypnum andoi*** (Figure 54)
Physarum leucophaeum (Figure 46) encrusted sporangia, dehiscing on ***Leptodictyum riparium*** (Figure 55)
Diderma deplanatum (Figure 56-Figure 58) on ***Mnium hornum*** (Figure 59).

Figure 53. ***Fuligo septica*** on ***Hypnum andoi***. Photo by Sean Edwards, with permission.

Figure 54. ***Hypnum andoi***, a moss known to form a substrate for ***Fuligo septica***. Photo by Michael Lüth, with permission.

Figure 55. ***Leptodictyum riparium***, a moss known to form a substrate for ***Physarum leucophaeum***. Photo by Michael Lüth, with permission.

Figure 56. ***Diderma deplanatum*** fruiting bodies on moss. David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 57. ***Diderma deplanatum*** fruiting bodies on moss. David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 58. ***Diderma deplanatum*** fruiting on moss. David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 59. ***Mnium hornum***, a moss known to provide a substrate for ***Diderma deplanatum***. Photo by Tim Waters, through Creative Commons.

Elsewhere in Europe, Eliasson and Adamonyte (2009) reported ***Licea operculata*** on mosses in Sweden.

Figure 60. ***Licea operculata*** sporophytes, a species also known from mosses. Photo by Clive Shirley, The Hidden Forest, with permission.

Stephenson and Studlar (1985) found that a number of species of slime molds are associated with bryophytes in temperate North America (Table 1). Although their study was targetted and extensive, revealing a number of bryophytes that have slime mold associates, the data were insufficient to determine any preferences.

Table 1. Slime molds occurring among the 17 most frequent species of bryophytes with sporulating slime molds (120 collections) from 20 localities in Tennessee, Kentucky, West Virginia, Virginia, Pennsylvania, Colorado, and Montana, USA, and one from British Columbia, Canada. Number of collections indicates the number of times the slime mold species was collected among the 120 collections. Based on table in Stephenson & Studlar 1985.

	Numb. Bryo. Host Taxa	**Numb. Collections**	**Fig. Numb.**
Stemonitis axifera	8	19	Figure 61
Fuligo septica	6	13	Figure 62
Stemonitis fusca	8	11	Figure 14
Trichia favoginea	3	9	Figure 63
Lepidoderma tigrinum	4	8	Figure 5
Lycogala epidendrum	10	8	Figure 15
Tubifera ferruginosa	5	7	Figure 64-Figure 65
Barbeyella minutissima	2	6	Figure 2
Didymium melanospermum	4	6	Figure 47-Figure 48
Arcyria cinerea	3	5	Figure 16-Figure 17
Physarum viride	4	5	Figure 66
Didymium iridis	0	4	Figure 67
Physarum album	3	4	Figure 49
Trichia decipiens	2	4	Figure 68
Diderma effusum	2	3	Figure 69
Lamproderma columbinum	4	3	Figure 6
Physarum cinereum	3	3	Figure 22
Physarum globuliferum	3	3	Figure 70
Physarum leucophaeum	3	3	Figure 46
Trichia subfusca	2	3	Figure 71
Ceratiomyxa fruticulosa	2	2	Figure 72
Stemonitopsis typhina	1	2	Figure 74
Cribraria spp.	2	2	Figure 75
Cribraria cancellata	2	2	Figure 76
Hemitrichia calyculata	1	2	Figure 77-Figure 79
Leocarpus fragilis	2	2	Figure 81
Physarum braunianum	2	2	Figure 82
Physarum rubiginosum	2	2	Figure 83-Figure 84
Trichia varia	2	2	Figure 39
Others	11		

Figure 61. ***Stemonitis axifera*** on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 62. ***Fuligo septica***, a species that can live on bryophytes. Photo by Kim Fleming, through Creative Commons.

Figure 63. ***Trichia favoginea***, a slime mold with three known bryophyte host taxa in North America. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 64. Young ***Tubifera ferruginosa*** sporangia on moss. Photos by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 65. Old sporangia of ***Tubifera ferruginosa*** on moss. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 66. ***Physarum viride*** dehiscing fruiting bodies. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 67. ***Didymium iridis***, a species here on decaying wood, but that may coincide with bryophytes. Photo by Willa Schrlau, through Creative Commons.

Figure 68. ***Trichia decipiens*** with sporangia, on moss. Photo by Anneli Salo, through Creative Commons.

Figure 69. ***Diderma effusum***. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 70. ***Physarum globuliferum*** on decaying wood. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

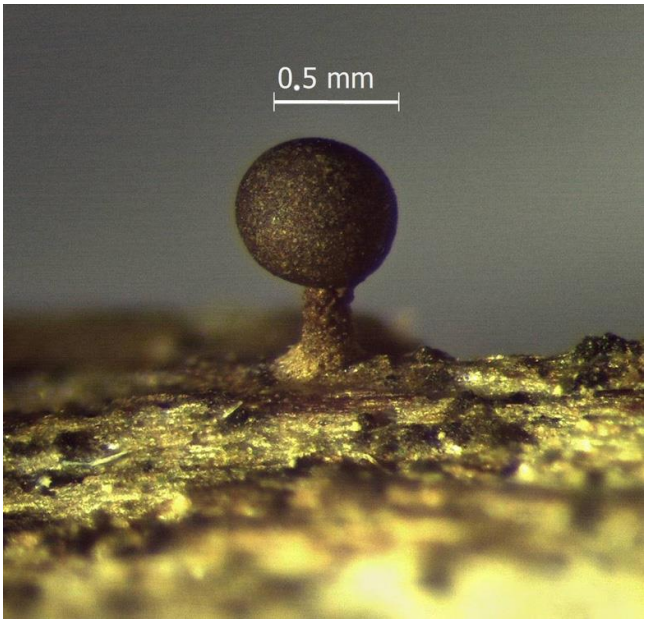

Figure 71. ***Trichia subfusca*** sporangium, a slime mold known to grow on mosses. Photo from Flora of Russia, Moscow State University, through Creative Commons.

Figure 72. ***Ceratiomyxa fruticulosa*** on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 73. ***Ceratiomyxa fruticulosa*** on mosses. Photo by MK, through Hiveminer.

Figure 74. ***Stemonitopsis typhina*** sporangia on rotting wood. Photo by George Barron, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 75. ***Cribraria*** sp. fruiting on bryophytes. Photo by Sarah Lloyd, with permission.

Figure 76. ***Cribraria cancellata*** fruiting bodies. Photo by Lawrence Leonard, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 77. ***Hemitrichia calyculata***. Young fruiting bodies on bryophytes. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 78. ***Hemitrichia calyculata***. Young fruiting bodies. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 79. ***Hemitrichia calyculata***. Mature sporophyte dispersing spores and showing capillitium. Photo by Lawrence Leonard, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 80. ***Leocarpus fragilis*** with young sporangia on moss. Photo by Boris Loboda, with permission.

Figure 81. ***Leocarpus fragilis*** mature fruiting bodies. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 82. Mature fruiting bodies of ***Physarum braunianum***. Photo by Denver Botanical Garden, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Others, collected in Maine, USA, that may have a moss preference are ***Trichia subfusca*** (Figure 85), cultured from mosses in a moist chamber, and ***Paradiachea rispaudii*** (Figure 86), a rather rare species that Stephenson collected only twice in 30 years, both times with mosses on the forest floor (Zoll & Stephenson 2013).

Figure 83. ***Physarum rubiginosum*** on moss, possibly **Hylocomiaceae**. Photo by Scott Darbey, through Creative Commons.

Figure 84. ***Physarum rubiginosum*** fruiting on moss. Photo by John Davis, with permission.

Figure 85. ***Trichia subfusca*** fruiting on bark. Photo by Alain Michaud, Eumycetozoan Project, DiscoverLife.org, with online permission.

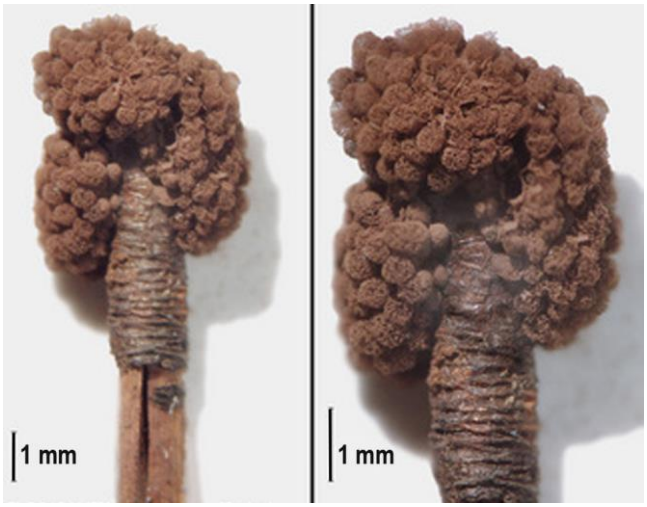

Figure 86. ***Paradiachea rispaudii***, possibly an obligate moss dweller. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Lado *et al*. (2003) examined slime molds in two Neotropical forest reserves in Mexico. ***Physarum alvoradianum*** occurred on mosses along with the slime mold ***Diderma rugosum*** (Figure 87). Other slime molds are sometimes associated with dead or living bryophytes, including ***Diderma chondrioderma*** (Figure 88), ***Didymium bahiense*** (Figure 89), ***Licea*** sp. (Figure 29-Figure 30, Figure 90-Figure 91), ***Physarum album*** (Figure 92), ***P. crateriforme*** (Figure 93), ***P. didermoides*** (Figure 94), and ***Stemonitis flavogenita*** (Figure 95-Figure 96).

Figure 87. ***Diderma rugosum*** fruiting structure, a slime mold that is often associated with bryophytes. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 88. ***Diderma chondrioderma*** on moss. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 89. ***Didymium bahiense*** fruiting on bryophyte detritus. Photo from EOL, through Creative Commons.

Figure 90. ***Licea retiformis*** plasmodium on bryophytes. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 91. ***Licea floriformis*** fruiting bodies on moss leaves. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 92. ***Physarum album***, a slime mold sometimes associated with mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission..

Figure 93. ***Physarum crateriforme*** fruiting bodies on moss leaves. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

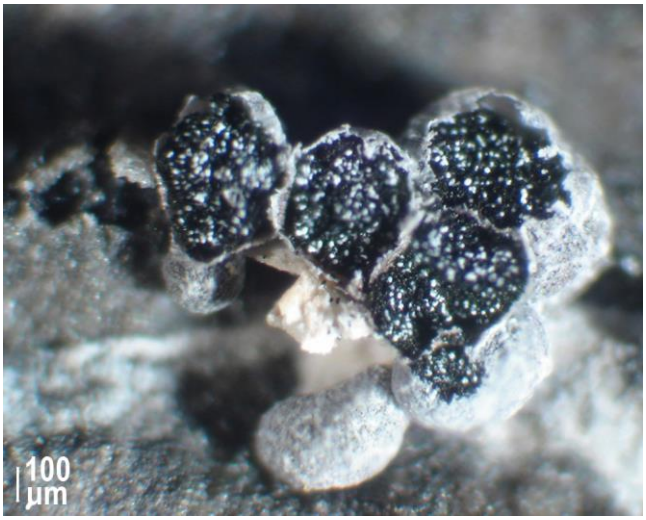

Figure 94. ***Physarum didermoides*** fruiting bodies, a slime mold sometimes associated with mosses. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 95. ***Stemonitis flavogenita*** early sporangial development on log and mosses. Photo by Chris Wagner, through Creative Commons.

Figure 96. ***Stemonitis flavogenita*** fruiting on decaying wood. Photo by Kathawk, through Creative Commons.

Even in the Antarctic, bryophytes, in this case the leafy liverwort ***Lepidozia*** (Figure 97), support the growth of the slime mold ***Lamproderma*** (Figure 6) (Stephenson *et al*. 1992).

Figure 97. ***Lepidozia glaucophylla***; the genus ***Lepidozia*** is a substrate for slime molds in the genus ***Lamproderma*** in the Antarctic. Photo by Janice Glime.

Collection Records in Floras

Most of the records of slime molds associated with bryophytes are in floristic treatments where species are listed, described, and known habitat affinities provided. Hence, I was able to add a number of bryophyte associates to this chapter by searching this body of literature, albeit not extensively. Unfortunately, these usually fail to state where the bryophyte is growing, much less the species. Thus we cannot separate those that expand from a log onto the moss from those that become established on the moss by preference or even restriction. When the more specific substrate is known, the relationship is in the Slime Mold subchapter on Ecology and Habitat.

A further difficulty is that the plasmodial stage may reside in a different place from the fruiting stage. The plasmodial stage can usually only be identified by culturing it until it produces sporangia. Even then, beginners will be confounded by the many color phases seen in some species (Figure 98-Figure 104).

Figure 98. ***Arcyria affinis***, a known log species, on liverworts. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 99. ***Arcyria affinis*** 1 October. This and the following series of this species indicate the color changes as the slime mold matures on the same rock. Photo by Sarah Lloyd, with permission.

Figure 100. ***Arcyria affinis*** 2 October. Photo by Sarah Lloyd, with permission.

Figure 101. ***Arcyria affinis*** 3 October. Photo by Sarah Lloyd, with permission.

Figure 102. ***Arcyria affinis*** 4 October as the color darkens. Photo by Sarah Lloyd, with permission.

Figure 103. ***Arcyria affinis*** 6 October as the outer covering (**periderm**) begins to break. Photo by Sarah Lloyd, with permission.

Figure 104. ***Arcyria affinis*** 9 October, with capsules dehiscing and revealing the capillitium. Photo by Sarah Lloyd, with permission.

Among the early North American records, Sturgis (1893) in Massachusetts, USA, reported that ***Paradiachea caespitosa*** (syn=*Comatricha caespitosa*; Figure 105-Figure 111) occurred on moss and the lichen ***Cladonia*** (Figure 112). Ricker (1902) reported ***Craterium obovatum*** (Figure 113) on moss and sticks, ***Physarum leucophaeum*** (Figure 46) on moss, ***Lepidoderma tigrinum*** (Figure 5) in moss on tree, ***Diachea thomasii*** (Figure 114) on moss, and ***Cribraria argillacea*** (Figure 115) among mosses in Maine, USA. Gilbert (1927) reported ***Physarum virescens*** (Figure 116) on moss in eastern Massachusetts, USA. Greene (1929) reported ***Diderma deplanatum*** (Figure 56-Figure 58), ***Diderma radiatum*** (Figure 117), ***Didymium melanospermum*** (listed in publication as *D. melanosporum*; Figure 118), ***Physarum bivalve*** (syn=*Physarum sinuosum*; Figure 45), and ***P. contextum*** (Figure 119) on moss in western Washington, USA. Gray (1938) added ***Physarum gyrosum*** (Figure 120) as a species fruiting on living moss in Indiana, USA.

Figure 105. ***Paradiachea caespitosa*** 6:11 am 12 December. Photo by Sarah Lloyd, with permission.

Figure 106. ***Paradiachea caespitosa*** 4:42 pm 12 December. Photo by Sarah Lloyd, with permission.

Figure 107. ***Paradiachea caespitosa*** 6:48 am 13 December. Photo by Sarah Lloyd, with permission.

Figure 108. ***Paradiachea caespitosa*** 4:16 pm 13 December. Photo by Sarah Lloyd, with permission.

Figure 109. ***Paradiachea caespitosa*** 7:06 am 15 December. Photo by Sarah Lloyd, with permission.

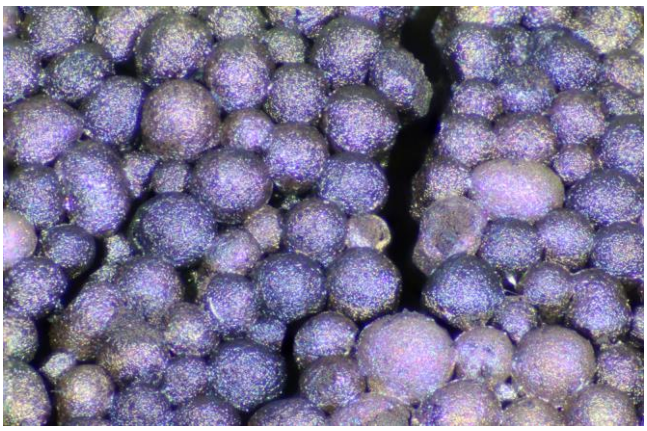

Figure 110. ***Paradiachea caespitosa*** sporangia 26 January. Photo by Sarah Lloyd, with permission

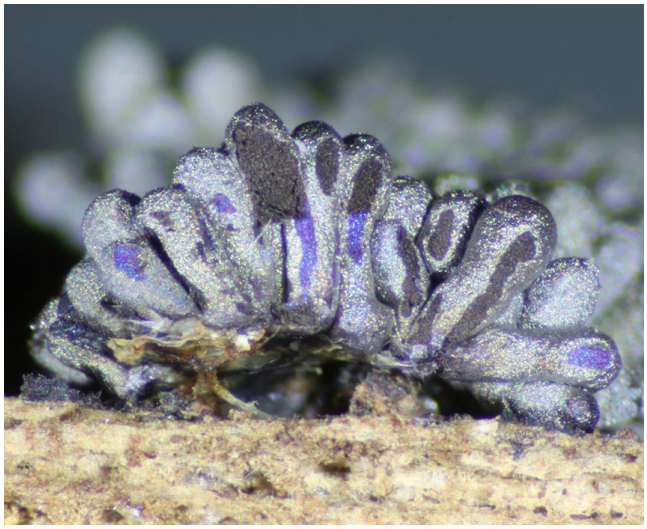

Figure 111. ***Paradiachea caespitosa*** sporangia. Photo by Sarah Lloyd, with permission.

Figure 112. ***Cladonia chlorophaea*** with ***Polytrichum***; the genus ***Cladonia*** can serve as a substrate for the slime mold ***Paradiachea caespitosa***. Photo by Tim Sage (NMNR), through Creative Commons.

Figure 113. ***Craterium obovatum*** or ***Trichia erecta*** yellow plasmodium. Kim Fleming, through Creative Commons.

Figure 114. ***Diachea thomasii*** sporangia, sometimes a moss dweller in Maine, USA. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 115. ***Cribraria argillacea*** sporangia on moss on log. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 116. ***Physarum virescens*** on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 117. ***Diderma radiatum*** on wood with bryophytes. Photo by Clive Shirley, <www.hiddenforest.co.nz>, with permission.

Figure 118. ***Didymium melanosporum*** sporangia on mosses. Photo by J. C. Schou, with permission.

Figure 119. ***Physarum contextum*** on wood, a slime mold known to inhabit mosses. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

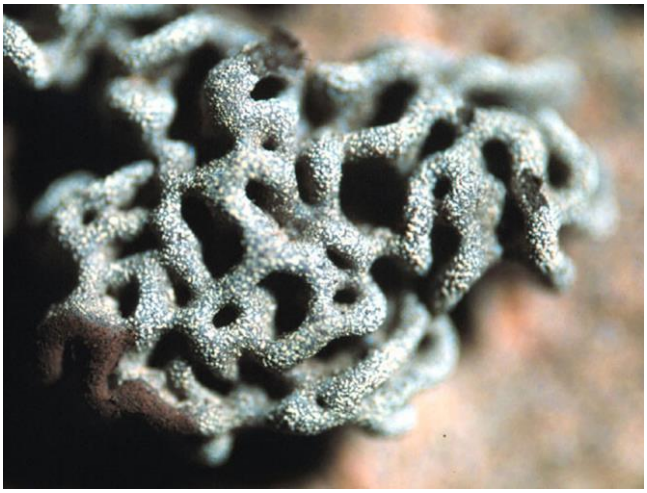

Figure 120. ***Physarum gyrosum***, a slime mold that sometimes occurs on bryophytes. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Lister (1917) cultured the slime mold ***Colloderma*** sp. (Figure 4) from mosses in the UK, maintaining it until the slime mold produced spores. More recent references include a greater number of records of moss dwellers, and often more details of the habitat. Doidge (1950) reported ***Lamproderma scintillans*** (Figure 12) growing on mosses and roots of epiphytic orchids in a greenhouse.

Based on collections from Lake ltasca State Park, Minnesota, USA, Palm *et al*. (1979) listed bryophytes as the substrate for a number of slime molds, but they did not give the substrate of the bryophytes. These bryophyte-dwelling slime molds included ***Arcyria oerstedtii*** (Figure 121), ***Craterium leucocephalum*** (Figure 122), ***C. minutum*** (Figure 123-Figure 124), ***Diderma crustaceum*** (Figure 125), ***Didymium melanospermum*** (Figure 48), ***D. nigripes*** (Figure 126), ***D. squamulosum*** (Figure 127), ***Fuligo septica*** (Figure 53, Figure 62), ***Hemitrichia serpula*** (Figure 128-Figure 129), ***Leocarpus fragilis*** (Figure 81), ***Metatrichia vesparia*** (Figure 42), ***Mucilago crustacea*** (Figure 130), ***Physarum bivalve*** (Figure 45), ***P. cinereum*** (Figure 22-Figure 23), ***P. notabile*** (Figure 131), ***P. album*** (Figure 49), ***Stemonitis fusca*** (Figure 14), and ***Tubifera ferruginosa*** (Figure 65).

Figure 121. ***Arcyria oerstedti*** on mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 122. ***Craterium leucocephalum*** sporangia ready to dehisce. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 123. ***Craterium minutum*** immature sporangia on mosses in New Zealand. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 124. ***Craterium minutum*** with dehiscing sporangia. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 125. ***Diderma crustaceum*** sporangia. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 126. ***Didymium nigripes*** sporangia, a species known from bryophytes. Photo by Sarah Lloyd, with permission.

Figure 127. ***Didymium squamulosum*** on mosses. Photo by James K. Lindsey, with permission.

Figure 128. ***Hemitrichia serpula***, a known moss dweller. Photo by John Carl Jacobs, through Creative Commons.

Figure 129. ***Hemitrichia serpula*** with moss and snail. Photo by Amadej Trnkoczy, through Creative Commons.

Figure 130. ***Mucilago crustacea*** on bryophytes. Photo by Drew Henderson, through Creative Commons.

Figure 131. ***Physarum notabile*** sporangia. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with permission.

New records continue to appear. Baba and Er (2018) added ***Craterium dictyosporum*** (Figure 132) to the records from Turkey by finding this species on mosses. In 2013, Mishra and Phate added the new species ***Badhamiopsis stipitata*** to the slime molds of Maharashtra, India, noting its fruiting occurrence on living mosses, but that species does not seem to appear in any checklists or nomenclatural lists.

Figure 132. ***Craterium dictyosporum*** sporangia on moss. Photo by John Davis, with permission.

Perhaps the most interesting recent study for bryologists (since that of Stephenson and Studlar in 1985) is that of Yatsiuk *et al*. (2018) in the Ukraine. They not only noted the species of slime molds, but also identified the moss species substrate in many cases. They found ***Didymium melanospermum*** (Figure 48) on the living moss ***Atrichum undulatum*** (**Polytrichaceae**; Figure 133). ***Didymium ovoideum*** (Figure 134) and ***Stemonitis axifera*** (Figure 135) were restricted to species of ***Sphagnum*** (Figure 136) and/or **Polytrichaceae**.

Figure 133. ***Atrichum undulatum***, substrate for ***Didymium melanospermum*** in peatlands. Photo by Hugues Tinguy, through Creative Commons.

Figure 134. ***Didymium ovoideum*** sporangium on wood. Photo by Thomas Laxton, through Creative Commons.

Figure 135. ***Stemonitis axifera***, a species that has been reported from bryophytes several times and is restricted to them in a Ukrainian peatland. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 136. ***Sphagnum palustre***; the genus ***Sphagnum*** is a known substrate for slime molds. Photo by Bob Klips, with permission.

Ranade *et al*. (2012) also reported ***Stemonitis axifera*** (Figure 135; as ***S. smithii***) from bryophytes in India. ***Didymium*** species are typically organisms of litter and parts of living plants (Liu *et al*. 2015), but several species have already been reported in this subchapter as living on bryophytes. Furthermore, ***D. melanospermum*** seems to prefer acid substrates (Stephenson & Studlar 1985; Ing 1994), explaining its presence in a ***Sphagnum*** habitat. Yatsiuk *et al*. (2018) found ***Stemonitis axifera*** (Figure 61) not only on living mosses, but also on litter and wood debris, as was the case for ***Arcyria cinerea*** (Figure 16).

Photographic Indicators

One way to determine which slime molds are able to live on bryophytes is to search for images that show them with bryophytes. This doesn't work for most animal relationships because photographers are likely to pose their animals on bryophytes to provide a pleasing background, but it seems unlikely that this happens with slime molds, particularly when it appears to be taken in the field.

The following images (Figure 137-Figure 173) provide such pictures to increase our knowledge of slime molds one might find on bryophytes. Some of these are adjacent, but not intermingled, suggesting that they do well in similar habitats and on the same substrate, frequently indicating similar moisture and *p*H requirements.

Figure 137. ***Alwisia bombarda*** with sporangia on mosses. Photo by Sarah Lloyd, with permission.

Figure 138. ***Arcyria stipata***, a known log species, associated with leafy liverworts and mosses on wood, but not actually growing on the bryophytes. This suggests they both might simply like the same habitats. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 139. Fruiting bodies of ***Badhamia delicatula*** with mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 140. ***Badhamia macrocarpa*** sporangia on mosses. Photo by David Mitchell, with permission.

Figure 141. ***Badhamia melanospora*** fruiting bodies with mosses on bark. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 142. ***Badhamiopsis ainoae*** open fruiting body, growing with mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 143. ***Brefeldia maxima*** plasmodium with moss. Photo through Creative Commons.

Figure 144. ***Comatricha alta*** sporangia on mosses. Photo by Sarah Lloyd, with permission.

Figure 145. ***Cribraria confusa*** sporangia with bryophytes. Photo by Sarah Lloyd, with permission.

Figure 146. ***Cribraria macrocarpa*** on bark with mosses, possibly ***Neckera*** sp. Photo by Alejandro Huereca, through Creative Commons.

Figure 147. ***Cribraria piriformis*** sporangium, a species that sometimes fruits on bryophytes. based on image from <http://www.gorjanski-gobar.si/wp/?p=14163>. Photo from Myxotropic, through Creative Commons.

Figure 148. ***Dictydiaethalium plumbeum*** on bryophytes. Photo by Ray Simons, The Eumycetozoa Project, DiscoverLife.org, with online permission.

Figure 149. ***Diderma*** sp. on liverwort. This is a common genus on bryophytes. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 150. ***Diderma globosum*** fruiting on mosses. Photo from Mushroom Observer.org, through Creative Commons.

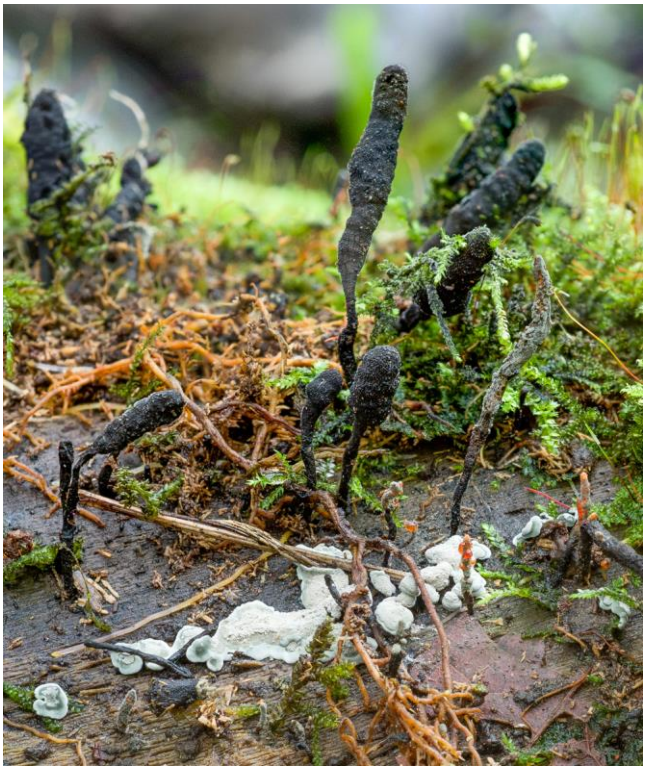

Figure 151. ***Diderma globosum*** fruiting on mosses. Photo from Mushroom Observer.org, through Creative Commons.

Figure 152. ***Diderma*** *cf.* ***niveum*** sporangia on mosses. Photo by Sarah Lloyd, with permission.

Figure 153. ***Diderma*** *cf* ***subincarnatum*** with capsules on mosses. Photo by Sarah Lloyd, with permission.

Figure 154. ***Fuligo septica*** on moss. Photo by Mikel A. Tapia, with permission.

Figure 155. ***Fuligo septica*** on mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 156. ***Lamproderma piriforme*** sporangia on bryophytes. Photo by Sarah Lloyd, with permission.

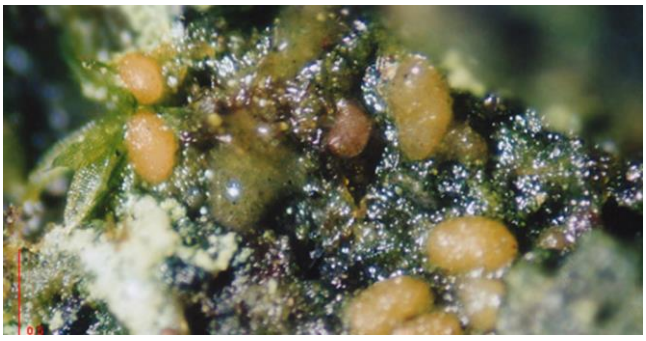

Figure 157. ***Licea sambucina*** on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 158. ***Lindbladia tubulina*** on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 159. ***Lindbladia tubulina***; upper image is on bryophytes. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 160. ***Lindbladia tubulina*** on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 161. ***Lycogala conicum*** on decaying wood with a leafy liverwort. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 162. ***Lycogala conicum*** on mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 163. ***Physarum bogoriense*** with mosses. Photo from the Denver Botanical Garden, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 164. ***Physarum flavidum*** on moss. Photo from Denver Botanical Garden, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 165. ***Physarum leucopus*** on moss. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 166. ***Stemonitis herbatica*** on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 167. ***Stemonitis herbatica*** with mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 168. ***Stemonitopsis typhina*** with mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 169. ***Stemonitopsis typhina*** sporangia. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 170. ***Symphytocarpus amaurochaetoides*** on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 171. ***Trichia contorta*** on mosses. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 172. ***Trichia munda*** with mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 173. ***Tubifera microsperma*** with mosses. Photo by Lawrence Leonard, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Generalists – Bryophytes Are Okay

Many of the slime molds that occur with or on bryophytes are **generalists**. This is not to be confused with those species that prefer bryophytes and that are typically **specialists**. Lado and de Basanto (2008) highlighted the abundance and widespread distribution of generalist ***Arcyria cinerea*** (Figure 16) in their review of Neotropical slime molds, indicating its presence in 28 of 30 countries. Tropical generalists include ***Arcyria denudata*** (Figure 174; known from bryophytes – Stojanowska & Panek 2004), ***Cribraria cancellata*** (Figure 175; known to associate with bryophytes on logs – Schnittler & Novozhilov 1998), ***Didymium nigripes*** (Figure 126; known from bryophytes – Palm *et al*. 1979), ***D. squamulosum*** (Figure 127; known from bryophytes – Palm *et al*. 1979), ***Fuligo septica*** (Figure 53, Figure 62; known from bryophytes – Stephenson & Studlar 1985), ***Hemitrichia calyculata*** (Figure 77-Figure 79; known from bryophytes – Stephenson & Studlar 1985), ***H. serpula*** (Figure 128-Figure 129; known from mosses – Ranade *et al*. 2012), ***Lycogala epidendrum*** (Figure 15; known from bryophytes – Stephenson & Studlar 1985), ***Perichaena chrysosperma*** (Figure 31; known from liverworts – Dudka & Romanenko 2006), ***Physarum album*** (Figure 92; known from bryophytes – Lado *et al*. 2003), ***Ph. viride*** (Figure 66; known from bryophytes – Stephenson & Studlar 1985), ***Stemonitis fusca*** (Figure 14; known from bryophytes – Palm *et al*. 1979; Dudka & Romanenko 2006), and ***Trichia favoginea*** (Figure 63; known from bryophytes – Stephenson & Studlar 1985).

Figure 174. ***Arcyria denudata*** on bryophytes. Photo by Sarah Lloyd, with permission.

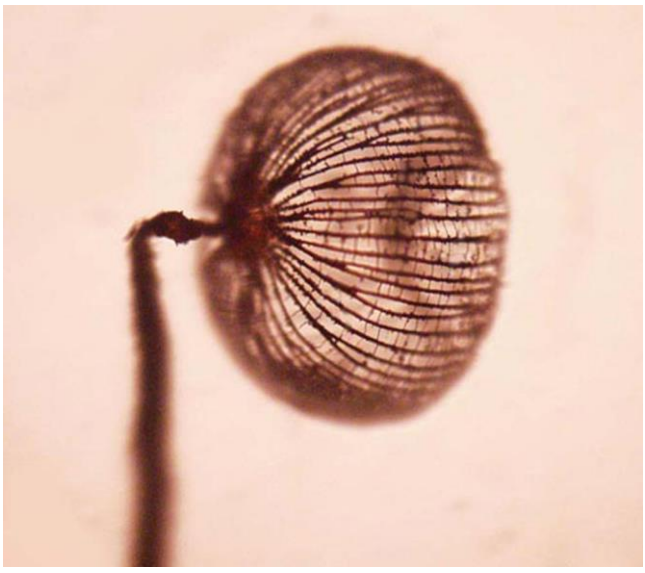

Figure 175. ***Cribraria cancellata*** fruiting body showing threadlike capillitium. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Härkönen and Ukkola (2000) considered the occasional moss dwellers ***Arcyria cinerea*** (Figure 16), ***A. pomiformis*** (Figure 176) and ***Echinostelium minutum*** (Figure 19) to be indifferent to substrate.

Figure 176. ***Arcyria pomiformis*** with mosses. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Interactions Can Be Helpful or Hindering

Despite the number of associations between bryophytes and slime molds, the relationship is often negative. Schnittler and Stephenson (2000) found that the higher the epiphytic coverage was, the lower the number of slime mold records obtained in culture (Figure 177). In Costa Rica, both slime mold species diversity and abundance decreased with increasing elevation, as well as with higher moisture levels, relationships that suggest they should not correlate well with bryophytes, which typically increase with altitude. Furthermore, on litter, the slime mold species with robust plasmodia increased with increasing elevation, further supporting the hypothesis of a negative relationship with bryophytes. On the other hand, Schnittler and Stephenson suggest that excess moisture of tropical forests does not favor the slime mold development. This conclusion is supported by the observation that the two seasonal dry forest types accounted for 90% of the total slime mold diversity. Nevertheless, the typical wood inhabitant ***Ceratiomyxa fruticulosa*** (Figure 72) was recorded twice from mossy bark in the wet forest. Schnittler and Stephenson suggested that a possible explanation for the decreasing slime molds with altitude (Figure 177) is that a closed epiphyte (bryophytes and lichens) cover interferes with slime mold growth.

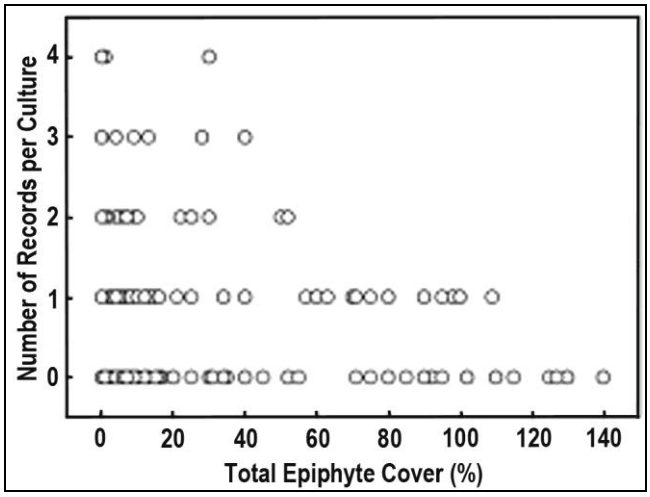

Figure 177. Myxomycete species richness vs epiphyte (including bryophyte) cover. Modified from Schnittler & Stephenson 2000.

Novozhilov *et al*. (2000) considered that the bryophilous slime molds, or at least the plasmodial slime molds (**Myxogastria**), albeit associated with mosses, were probably there due to slime algae (Figure 178), wood, or rocks that occurred where moisture was maintained by humid ravines. The ravine taxa include less than 5% of the slime molds and are mostly macroscopic taxa of temperate and boreal zones. Their fructification and spore release typically occurs in late autumn. The ravine species are all but impossible to grow in culture, making it likewise all but impossible to identify those not fruiting at the time of collection.

Figure 178. ***Cribraria persoonii*** fruiting bodies; the substrate appears to have algae with the slime molds growing on them. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

On the other hand, Landolt *et al*. (1992) suggested that the antibiotic properties of bryophytes might inhibit the growth of slime molds on or among many kinds of bryophytes. This could be particularly important for those slime molds that might use the bryophytes as feeding grounds for bacteria and other micro-organisms (Banerjee & Sen 1979). Landolt and coworkers observed that slime molds exhibited greater numbers in forests with a groundcover of deciduous litter than in those with a bryophyte ground cover. But is that due to inhibition or to differences in habitat requirements?

Schnittler and Stephenson (2000) commented further on the decreasing abundance and diversity of slime molds with elevation, whereas bryophytes increase in both. They suggested that competition for nutrients could cause bryophytes, especially in the tropics, to outcompete the slime molds for nutrients.

But as also noted by Schnittler and Stephenson (2000), slime mold species diversity is positively correlated with substrate *p*H on both litter and bark. Since conifer litter and conifer forests tend to be acidic, could that explain the absence of slime molds on bryophytes there, as observed by Landolt *et al*. (1992)? On the other hand, studies in the conifer *Cryptomeria japonica* forests in Japan indicate a negative correlation between slime mold abundance and *p*H, particularly for some species (Takahashi 2018; Takahashi & Harakan 2018).

Summary

Few bryophytes seem to be restricted to bryophytes (**bryophiles**). These include ***Barbeyella minutissima*** on leafy liverworts (especially ***Nowellia curvifolia***), ***Colloderma oculatum***, and ***Lepidoderma tigrinum***, the latter two often in association with ***B. minutissima***. This raises so many questions about the relationship between bryophytes and slime molds. Why is ***Barbeyella minutissima*** so restricted in its substrate? Does it derive some benefit from the liverworts? Could it really be elsewhere but in a form we have recognized as a different species?

And why do some slime molds seem to grow to the edges of moss mats and stop? Does the moss produce an inhibitory substance? Or is it the darkness at the base of the moss mat that stops the plasmodium in its tracks?

Other slime molds with a preference for bryophytes include ***Lamproderma columbinum*** and ***L. scintillans***. But most of the associations seem to be coincidental – the bryophytes are in the preferred habitat and nothing stops the expansion of the slime molds simply grow onto the bryophytes. And how many associations are we missing in the amoeboid, swarm cell, and plasmodial stages because they are hard to find and require culturing for identification? And even if they grow in culture and produce identifiable sporangia, would they do this in nature on or among the bryophytes?

Stemonitis axifera may be a candidate that prefers bryophytes, being restricted to ***Sphagnum*** and **Polytrichaceae** in a peatland study.

Checklists and photographs can be used to find some of those species that sometimes occur on bryophytes. From these, one can surmise that most of the bryophyte dwellers are **generalists** that can live on a bryophyte, whereas those that prefer or only live on bryophytes are **specialists**.

Evidence from elevational studies suggests that bryophytes might actually inhibit or outcompete the slime molds at higher altitudes by overgrowing them, shading them, or competing for nutrients. Antibiotics produced by the bryophytes could inhibit the micro-organisms needed by the slime molds as food or even inhibit the slime molds themselves. In some cases, *p*H is a deterrent for many slime mold species. Presence of algae and Cyanobacteria, as well as protozoa and bacteria, may enhance the suitability of bryophytes as a substrate for slime molds.

Acknowledgments

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CHAPTER 3-3
SLIME MOLDS: ECOLOGY AND HABITATS – BARK AND LOGS

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CHAPTER 3-3
SLIME MOLDS: ECOLOGY AND HABITATS – BARK AND LOGS

Figure 1. ***Fuligo** cf. **septica*** growing on bryophytes on a log. Photo by Janice Glime.

Habitats

It is well known that many slime molds have a substrate preference (Eliasson 1980), including dead wood, bark, twigs, dead leaves, and dung (Stephenson *et al*. 2000). But are there truly species that prefer bryophytes? It would appear that some may prefer leaves with bryophyte associations, as described in the ecology subchapter. But there are a number of species that are likely to be found in bryophyte associations, particularly in the high latitudes of the Northern Hemisphere (Kaiser 1913; Gray & Alexopoulos 1968; Farr 1979; Ing 1994; Stephenson *et al*. 2000). Martin and Alexopoulos (1969) reported 49 different species on some sort of mossy substrate.

Rollins and Stephenson (2011) identified five substrate types for slime molds: soil, leaf litter, twigs, bryophytes, and snow. For some reason, they did not list logs as a habitat/substrate, although the paper did discuss slime molds on logs.

Döbbeler & Nannenga-Bremekamp (1979) suggest that some slime molds may indeed be unique to bryophytes, or at least use them as primary substrate. Similarly, Ing (1994), in studying the phytosociology of slime molds, reported that a few species are "particularly associated" with bryophytes. Likewise, several other authors have reported that some (few) bryophytes appear almost invariably in association with bryophytes (Gray & Alexopoulos 1968; Ing 1983, 1994).

However, the majority of slime mold associates most frequently encountered by Stephenson and Studlar (1985) in the USA and Canada include ***Brotherella recurvans*** (Figure 2), ***Thuidium delicatulum*** (Figure 3), ***Hypnum imponens*** (Figure 4), and ***Hypnum curvifolium*** (Figure 5) – species that show a broad ecological amplitude, and characteristically grow not only on rotten wood but also on soil, living trees, and rocks.

Figure 2. ***Brotherella recurvans***, a frequent slime mold substrate in North America. Photo by Bob Klips, with permission.

Figure 3. ***Thuidium delicatulum***, a frequent slime mold substrate in North America. Photo by Hermann Schachner, through Creative Commons.

Figure 4. ***Hypnum imponens***, a frequent log dweller and slime mold substrate in North America. Photo by Jason Hollinger, through Creative Commons.

Figure 5. ***Hypnum curvifolium***, a frequent slime mold substrate in North America. Photo by Bob Klips, through Creative Commons.

Stephenson and Studlar (1985) found that most of the bryophyte species that support the development of slime mold colonies are low-growing. Their life forms include **smooth mat**s (58%) > **short turfs** (19%) > **rough mat**s (13%) > **wefts** (9%) > **tall turf**s (2%) > **turfs with creeping primary stem** (1%) > **small cushion** (1%). The only species that exceeded 2 cm in height were ***Polytrichum commune*** (Figure 6) and ***Sphagnum recurvum*** (Figure 7) (both **tall turfs**) and ***Pleurozium schreberi*** (Figure 8) (**weft**). Longton (1980) determined that **short turfs** retain more capillary water than do the other life forms, perhaps explaining that these were the second most abundant life form.

Figure 6. ***Polytrichum commune***, one of the few taller moss species used as a substrate by slime molds. Photo by Bob Klips, with permission.

Figure 7. ***Sphagnum recurvum***, one of the few taller moss species used as a substrate by slime molds. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 8. ***Pleurozium schreberi***, one of the few taller moss species used as a substrate by slime molds. Photo by Bob Klips, with permission.

Bark Associations

Ing (1994) concluded that slime molds are more likely to be found on bryophytes in woodlands having high humidity. This is probably more important on standing tree bark associations than on fallen logs. Bryophytes on the bark can help to retain moisture and to trap airborne spores, thus making it likely that at least some slime molds should be favored by or restricted to mossy areas. This affinity might also differ with the moisture availability in the habitat.

In addition to water-holding capacity of bark, the general shape of the tree, surface texture of the tree bark, (fibrous, furrowed, ridged, scaly, smooth) along with epiphytic cover of algae, mosses, liverworts, and lichens may also influence the presence of corticolous slime molds (Brooks *et al*. 1977).

Diderma corrugatum (Figure 9) is a slime mold that seems to be restricted to moss-covered bark, occurring in the southeastern United States (Brooks *et al*. 1977). It typically occurs in the top part of the canopy on branches and on the upper trunk, in both places where bryophytes form extensive cover. It has a watery white phaneroplasmodium often associated with mosses and liverworts (Brooks *et al*. 1977). Although it can live on several kinds of trees, elms (***Ulmus***; Figure 10) seem to be the more common substrate. Everhart and Keller (2008) suggested that bryophytes may contribute to the necessary moisture for this species.

Figure 9. ***Diderma corrugatum*** sporangia, a species that seems to be restricted to moss-covered bark when it grows in the southeastern USA. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 10. ***Ulmus americana*** bark, a preferred substrate for ***Diderma corrugatum***. Photo by Downtowngal, through Creative Commons.

The closely related ***Diderma rugosum*** (Figure 11) differs in microhabitat from ***D. corrugatum*** (Figure 9), but still is often associated with mosses (Brooks *et al*. 1977). It occupies leaf litter and the basal part of tree trunks. Unlike ***D. corrugatum***, it seems to prefer mossy bark of the sycamore (***Platanus occidentalis***; Figure 12) along streams. Ing (1982) reported ***Diderma chondrioderma*** (Figure 13) as a rare species from mossy bark of living trees in the UK. Ranade *et al*. (2012) contributed to our knowledge of bryophyte-***Diderma*** associations in India. In their checklist, they reported ***Diderma badhamioides*** on mosses growing on the bark of a tree; ***Diderma chondrioderma*** occurs on live mosses as well tree bark in India.

Figure 11. ***Diderma rugosum*** fruiting structure, a species that seems to prefer mossy bark of the sycamore (***Platanus occidentalis***). Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

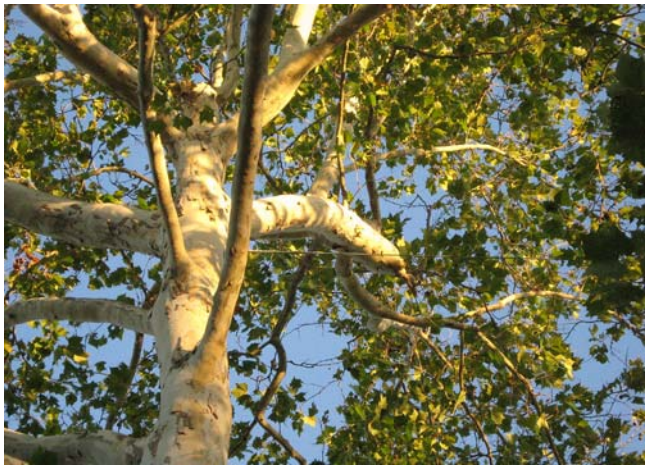

Figure 12. ***Platanus occidentalis*** (sycamore); ***Diderma rugosum*** seems to prefer the bark of this tree, often with mosses. Photo by Bill McChesney, through Creative Commons.

Figure 13. ***Diderma chondrioderma***, a rare species in the UK, living on the mossy bark of trees. Photo by James K. Lindsey, with permission.

Diderma cinereum likewise lives on bark, including sometimes living on the epiphytic mosses (Figure 14-Figure 15). So far I have found only a photographic record of this.

Figure 14. ***Diderma cinereum*** sporangia on bryophytes. Photo by James K. Lindsey, with permission.

Figure 15. ***Diderma cinereum*** sporangia on bryophytes. Photo by James K. Lindsey, with permission.

Doidge (1950) noted ***Badhamia affinis*** (Figure 16-Figure 17) on both mosses and bark of dead and living trees in Africa. ***Badhamia versicolor*** (Figure 18) usually occurs on bark of living trees, and similarly it often uses mosses and lichens as a substrate (Ing 1982; Poulain *et al.* 2011). Ing (1982) reported that ***Badhamia versicolor*** is a rare species on mossy bark of living trees in the UK. Keller and Brooks (1975) described ***Badhamia rugulosa*** from bark and moss-covered tree substrata and grape vines (***Vitis***). They noted that this slime mold tends to occur in flowways and in areas of the bark that retain moisture, with both mosses and liverworts, as well as algae, satisfying that need for moisture retention. In Taiwan, ***Badhamia formosana*** occurs on bark of living trees where it often appears also on the epiphytic mosses (Liu *et al.* 2002).

Figure 16. Fruiting bodies of ***Badhamia affinis*** with bryophytes. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 17. Mature fruiting bodies of ***Badhamia affinis*** with bryophytes. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 18. Fruiting bodies of ***Badhamia versicolor*** on a moss. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org with online permission.

Figure 20. ***Physarum tesselatum*** sporangia, a species of bark and living mosses. Photo from Myxotropic, through Creative Commons.

Ranade *et al*. (2012) contributed to our knowledge of bryophyte-slime mold associations on bark in India. In their checklist, they reported ***Physarum mortonii*** (Figure 19) and ***P. tesselatum*** (Figure 20) on bark and living mosses, whereas ***Physarum album*** (Figure 21) occurs not only on moss growing on bark of trees, but also on dead twigs; this species is also known from moss-covered rotting logs in China (Ukkala *et al*. 2001). Ukkala *et al*. (2001) found that in Hunan, China, the slime mold ***Physarum pusillum*** (Figure 22) is sometimes associated with mosses on the bark of broad-leaved trees.

Figure 21. ***Physarum album*** sporangia on decaying wood, a species that also lives on mosses of bark and dead twigs. Photo by George Shepherd, through Creative Commons.

Figure 19. ***Physarum mortonii*** sporangia, a species of bark and living mosses. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 22. ***Physarum pusillum*** sporangia, a species that sometimes is associated with epiphytic mosses. Photo by Clive Shirley, The Hidden Forest, with permission.

Stemonitis axifera (Figure 23-Figure 24) and ***Trichia botrytis*** (Figure 25) both occur on bark of trees and mosses growing on them in India (Ranade *et al*. 2012).

Figure 23. ***Stemonitis axifera*** sporangia on decorticated log, a species that also occurs on bark and epiphytic mosses. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 24. ***Stemonitis axifera*** with liverworts, a species of bark and epiphytic mosses. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 25. ***Trichia botrytis*** on mosses, a species that occurs both on bark and bark mosses. Photo by Dragiša Savić, with permission.

Gilert and Neuendorf (1991) reported ***Elaeomyxa reticulospora*** (Figure 26; as *Lamproderma reticulosporum*) from its type locality in western Java in Indonesia, where it was found on the moss-covered trunk of a huge evergreen tree.

Figure 26. ***Elaeomyxa reticulospora***, a species known from moss-covered bark. Photo by Sarah Lloyd, with permission.

Large colonies of ***Colloderma oculatum*** (Figure 27) occur on the moss-covered bark of living trees in coastal Central Europe (Schnittler & Novozhilov 1996). ***Clastoderma pachypus*** occurs on bark covered with mosses in Lithuania (Adamonyté 2007).

Figure 27. ***Colloderma oculatum*** on bryophytes, a typical habitat for it on bark of living trees. Photo by The Eumycetozoan Project, DiscoverLife.org, with online permission.

Schnittler *et al*. (2002) reported ***Didymium floccosum*** (Figure 28) from the densely moss-covered bark of a living tree. The single large colony grew among mosses and small amounts of leafy debris.

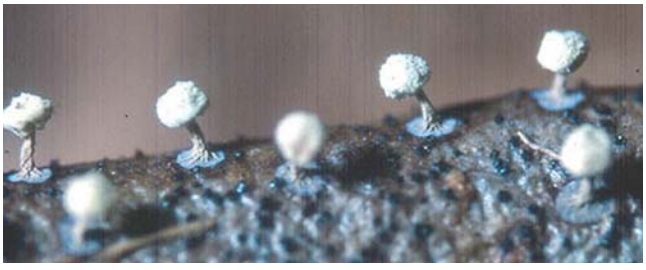

Figure 28. ***Didymium floccosum*** sporangia, a species that can occur on dense moss cover on bark. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

The slime mold ***Paradiacheopsis solitaria*** (Figure 29; syn.=*Comatricha solitaria*) occurs on bark, often with mosses and lichens, in the UK (Ing 1982). Eliasson and Gilert (2007) found ***Paradiacheopsis solitaria*** on mosses and lichens on bark of living ***Malus*** (apple) in Sweden. ***Perichaena chrysosperma*** (Figure 30) occurs in Sweden as solitary, globose or subglobose sporangia on bark or mosses on bark of living trees.

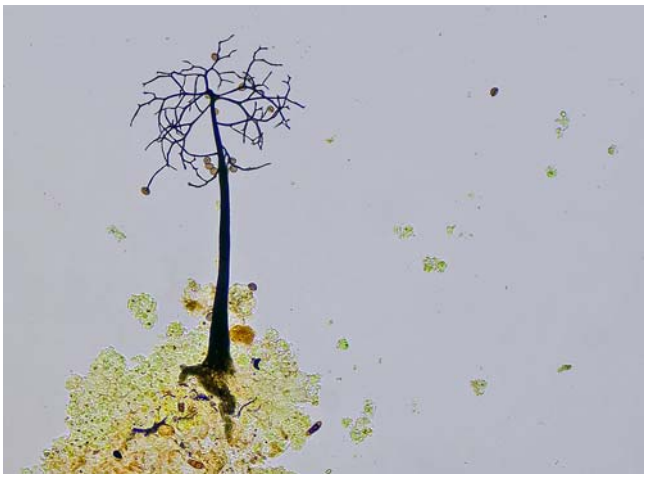

Figure 29. ***Paradiacheopsis solitaria*** sporangium that has lost its spores, a bark and moss-dwelling species. Photo by Dmitry Leontyev, through Creative Commons.

Figure 30. ***Perichaena chrysosperma***, a species of bark and mosses on living trees. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Some corticolous species of slime molds may invade the bryophytes from their bark substrate (Brooks *et al*. 1977). On the other hand, some taxa may start on mosses and then invade the bark. If a plasmodium lives under the bark, it may sometimes be difficult to avoid mosses when it crawls out to produce sporangia (Figure 31).

In their study of corticolous taxa in Costa Rica, in four different forest types, Schnittler and Stephenson (2000) found that those species found on bark at higher elevations also occurred on lush bryophyte mats that covered the bark: ***Arcyria cinerea*** (Figure 32-Figure 33), ***Physarum cf. roseum*** (Figure 34-Figure 35), ***Ceratiomyxa fruticulosa*** (Figure 36), ***Cribraria oregana*** (Figure 37), and ***Didymium iridis*** (Figure 38). Nevertheless, they found that when no bare bark was present, the growth of slime molds was diminished. But, in culture, bark with no epiphytes failed to provide successful slime mold cultures. Perhaps the bryophytes act as a trap, but the sporelings quickly migrate to a more open surface in this habitat.

Figure 31. ***Brefeldia maxima*** on mosses on bark. With mosses everywhere, plasmodia emerging from bark crevices will undoubtedly crawl onto mosses. Photo by Dick Culbert, through Creative Commons.

Figure 32. Fruiting bodies of ***Arcyria cinerea***. Photo by Kim Fleming, The Eumycetozoan Project, DiscoverLife.org, with permission.

Figure 33. ***Arcyria cinerea*** fruiting on mosses. Photo by Dan Molter, through Creative Commons.

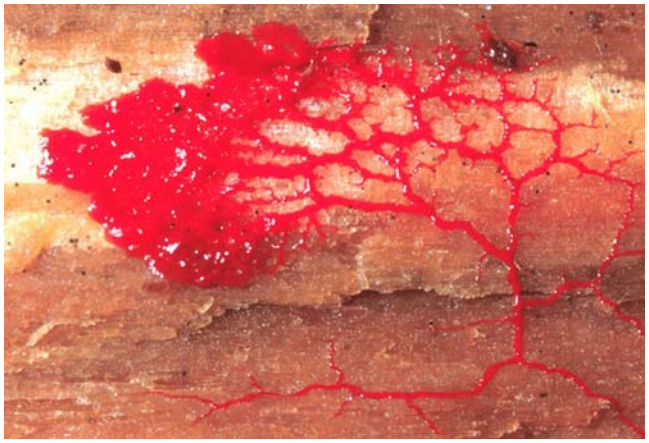

Figure 34. ***Physarum roseum*** plasmodium, a species that occurs on lush moss mats at higher elevations in North America. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 35. ***Physarum roseum*** sporangia. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 36. ***Ceratiomyxa fruticulosa*** fruiting bodies on bryophytes. Photo by Richard Droker, through Creative Commons.

Figure 37. ***Cribraria oregana*** sporangia, a species that can occur on lush bryophyte mats. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 38. ***Didymium iridis*** on decaying log. Photo by Willa Schrlau, through Creative Commons.

Among these Costa Rican bryophyte inhabitants, only ***Arcyria cinerea*** (Figure 32-Figure 33) was also present in Virginia (Schnittler & Stephenson 2000). The most common species in each of these two areas were absent in the other. ***Arcyria cinerea*** is a widespread species tolerant of an array of substrates, including mossy bark of living trees, especially oak (Ing 1982). Furthermore, as elevation increased, the number of species of slime molds decreased (Schnittler & Stephenson 2000), contrasting with the elevational relationship of bryophytes in the Colombian Andes (Gradstein *et al*. 1989; Wolf 1993).

Everhart and Keller (2008) examined the life history strategies of slime molds that live on bark, including six tree species and two vine species in Kentucky and Tennessee, USA. They cultured 580 samples and found 46 slime mold species in 20 different genera. The majority of

these had stalked sporangia. They concluded that the corticolous slime molds in the tree canopy are **r-selected** (optimized for high reproduction). Their resistant, dormant, resting stages permit them to survive the irregular wet periods interspersed with prolonged dry periods in their habitat. The most abundant species, especially the **Echinosteliales** (Figure 39-Figure 40), have a plasmodial stage that exhibits the smallest surface to volume ratio (**protoplasmodium**) and produces spores quickly over 2-4 days by producing a single, tiny, stalked sporangium (Figure 40). Their spore release is efficient, with an rapidly disappearing **periderm** (outer covering of the sporangium).

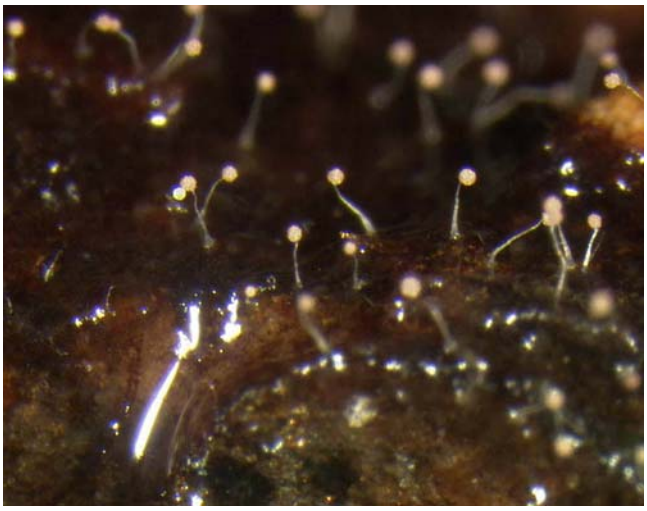

Figure 39. ***Echinostelium minutum***, showing the tiny, stalked sporangia. Photo by Satyendra Rajguru, The Eumycetozoan Project, DiscoverLife.org, with online permission.

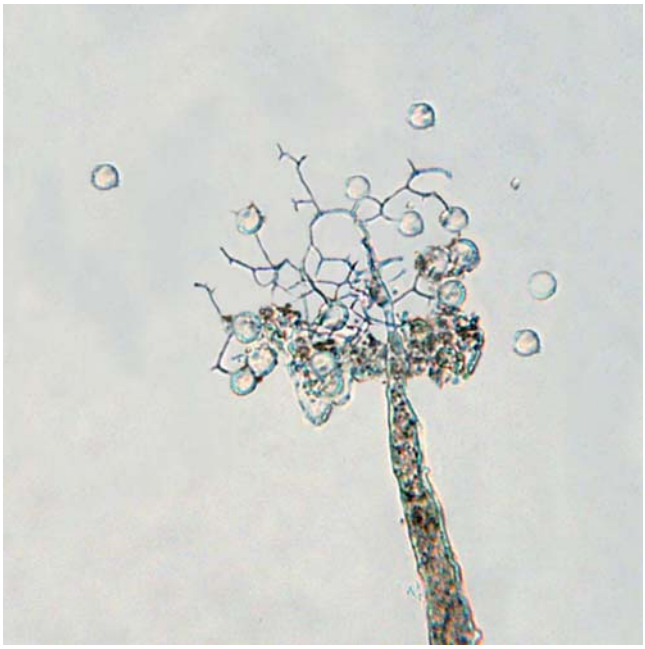

Figure 40. ***Echinostelium minutum*** sporangium showing absence of periderm when spores are dispersing. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Slime mold specialists are using rope-climbing techniques like those used by bryologists in the tropics. Snell and Keller (2003) collected slime molds from bark at 3-m increments to the tops of five different tree species in the Great Smoky Mountains National Park, USA. They identified 84 species from their 418 cultures, representing 25 trees. They found similar slime mold community composition among the five tree species, but occurrence and abundance differed and were related to differences in bark *p*H. No height differences were apparent, nor did bark moisture seem to make any difference.

Melissa Skrabal found a new myxomycete species (plasmodial slime mold) ***Diachea arboricola*** (Figure 36) in the tree canopy using rope-climbing techniques (Keller & Skrabal 2002). Although these slime molds occur primarily on bark, one collection developed on bark-dwelling bryophytes (Keller et al. 2004). Observations of this species may help to explain the occasional occurrence of some slime molds on bryophytes. The plasmodium (jelly-like slime stage) of ***Diachea arboricola*** moves great distances across the bark surface, but is apparently confined to the tree canopy. In order to traverse the canopy, the plasmodium often encounters bryophytes living there. This behavior was also observed in a Petri dish, where a large plasmodium covered the moss in a moist chamber. Thus, when cultures of slime molds include bryophytes, mosses and liverworts, they serve as a substratum to renew the myxomycete life cycle and develop sporangia. A possible explanation for the bryophyte occurrence of ***Diachea arboricola*** sporangia, and that of other occasional slime mold species on bryophytes, is that the bryophyte dries while the slime mold is on it, and on a sunny day, may trigger fruiting body formation.

Figure 41. ***Diachea arboricola*** sporangium, a bark species that migrates on the tree as a plasmodium. Photo by Kenny Snell, courtesy of Harold W. Keller, from Keller & Skrabal 2002; Keller & Barfield 2017; Keller 2019.

Liverwort vs Moss Associations

In humid forests, the epiphytic liverworts often serve as substrates for slime molds (Ing 1994). Coincidentally, they also serve as substrates for myxobacteria, providing a food source for the slime molds and permitting their development. Schuster (1957) reported fruiting bodies of ***Lamproderma columbinum*** (Figure 42), ***Collaria arcyrionema*** (Figure 43), ***Physarum flavidum*** (Figure 44), and ***Cribraria violacea*** (Figure 45) on both stems and leaves of leafy liverworts. Ing (1994) considered the epiphytic liverworts to be frequent developmental substrates for slime molds. ***Hemitrichia minor*** is typically associated with ***Metzgeria furcata*** (Figure 46) and ***Radula complanata*** (Figure 47). Isabelle Mazaud photographed ***Diacheopsis synspora*** (Figure 48-Figure 49) from ***Metzgeria furcata*** on the bark of ***Quercus robur*** (Figure 50). ***Licea bryophila*** (Figure 51) seems to be confined to bark-dwelling liverworts, and ***L. gloeoderma*** is found only on the epiphytic leafy liverwort ***Frullania*** (Figure 52) species in Bavaria (Döbbeler & Nannenga-Bremekamp 1979).

Figure 42. ***Lamproderma columbinum*** on moss. Photo from Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 43. ***Collaria arcyrionema***, a species that fruits on leafy liverworts. Photo by Taibif.tw, through Creative Commons.

Figure 44. ***Physarum flavidum*** sporangia, a species that can occur on stems and leaves of leafy liverworts. Photo by Sarah Lloyd, with permission.

Figure 45. ***Cribraria violacea***, a species that can occur on stems and leaves of leafy liverworts. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 46. ***Metzgeria furcata***, a species that is a typical substrate for ***Hemitrichia minor***. Photo from <www.aphotofauna.com>), with permission.

Figure 47. ***Radula complanata***, a species that is a typical substrate for ***Hemitrichia minor***. Photo by Hermann Schachner, through Creative Commons.

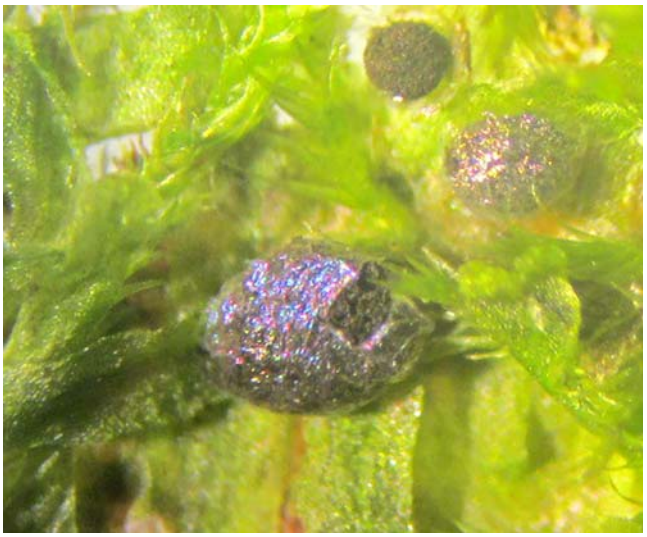

Figure 48. ***Diacheopsis synspora*** on ***Metzgeria furcata*** on ***Quercus robur***. Photo courtesy of Isabelle Mazaud.

Figure 49. ***Diacheopsis synspora*** from ***Metzgeria furcata*** on bark of ***Quercus robur***. Photo courtesy of Isabelle Mazaud.

Figure 50. ***Quercus robur*** with bryophytes on bark, home for ***Diacheopsis synspora*** on the liverwort ***Metzgeria furcata***. Photo by Robert Vidéki, through Creative Commons.

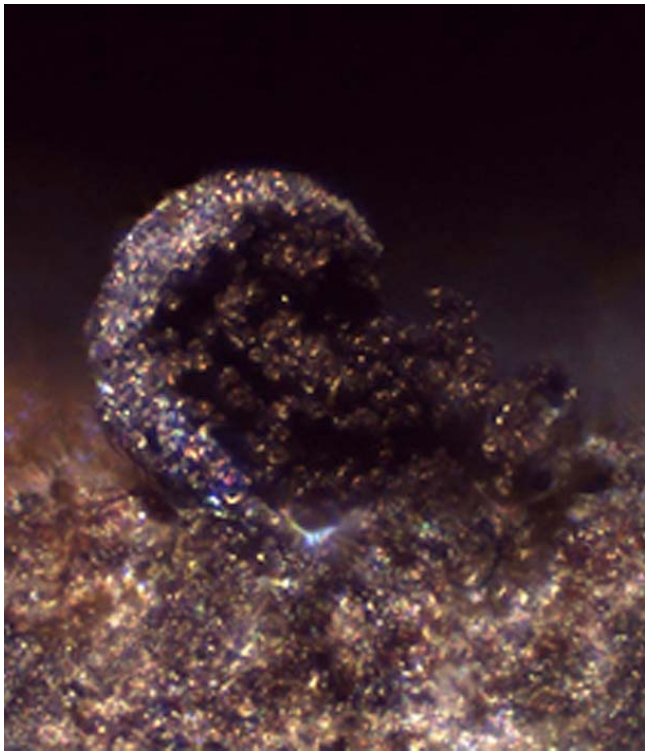

Figure 51. ***Licea bryophila*** sporangia, a species that seems to be confined to liverworts on bark. Photo by Thomas Laxton, through Creative Commons.

Figure 52. ***Frullania*** sp.; ***Licea gloeoderma*** is found exclusively on this genus of leafy liverworts. Photo by Felipe Osorio-Zúñiga, with permission.

The slime mold ***Diacheopsis mitchellii*** grows on epiphytic bryophytes in Flanders, Belgium (de Haan 2017). De Haan included an image of it growing on ***Lophocolea heterophylla***.

Diderma chondrioderma (Figure 13) is commonly associated with the moss ***Hypnum andoi*** (Figure 53; syn.=***Hypnum mammillatum***) and the slime mold ***Macbrideola cornea*** (Figure 54) occurs with several acrocarpous moss species (Ing 1994). ***Macbrideola cornea*** forms a single plasmodium that can migrate to the tips of moss leaves and form stalked sporangia (Harold Keller, pers. comm. 22 April 2019). Unlike most of the known moss dwellers, the common ***Licea parasitica*** (Figure 55) is not confined to mosses in fructification, but its **microcysts** (resistant dormant stage) can become conspicuous on the moss leaves.

Figure 53. ***Hypnum andoi***, a common substrate for ***Diderma chondrioderma***. Photo by Michael Lüth, with permission.

Figure 54. ***Macbrideola cornea*** sporangia, a species that associates with several acrocarpous moss species. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

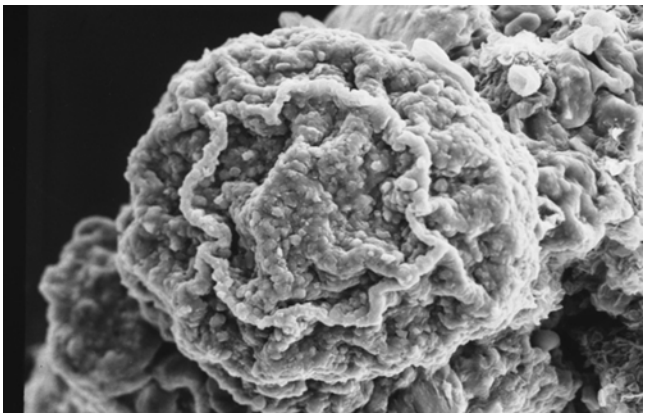

Figure 55. SEM of ***Licea parasitica*** sporangium, a species that forms conspicuous coverings on moss leaves in its microcyst stage. The Eumycetozoan Project, DiscoverLife.org, with online permission.

It is likely that slime mold preferences for mosses vs liverworts relate to moisture or other bark preferences of these two groups of bryophytes. There has been no experimental work to attempt to find the determining factors.

Limiting Factors

Studlar (1982) examined host specificity of epiphytic bryophytes, reporting on 54 moss and 18 liverwort species on 120 trees comprised of 6 species. She found that among those bryophytes with a frequency of 20% or more on tree trunks up to 1.8 m, only three species were restricted to just one host, with another 21 exhibiting a strong single-host preference. She found that the bryophyte species richness and frequency decreased with decreasing bark *p*H, with water absorption capacity of the bark having a lesser effect. It would be interesting to see if slime molds associated with bryophytes have the same gradients on these trees.

Everhart *et al.* (2009) evaluated the bark characteristics and canopy epiphytes (mosses, lichens, and algae) associated with corticolous slime molds in three temperate forests in the southeastern USA. They used rope-climbing techniques to sample trees and grapevines up to 15 m above the ground. They used five 2 x 2 cm quadrats, resulting in 187 sample sites, for determining percent

cover. They found no association between epiphytic percent cover and slime molds. Rather, like Studlar (1982), they found that bark *p*H was the major factor apparently influencing the presence of the corticolous slime mold species. They considered the patchy distribution to be the result of the small plasmodium typical of most of the corticolous species. They concluded that rather than improving the growing conditions for the slime molds, bryophytes had a negative correlation with them, albeit not a significant one.

Härkönen (1977) actually measured *p*H at the locations of slime molds living on bryophytes. Overall, the bark-dwelling slime molds occurred on a wide range of *p*H from 2 to 9. Specifically, ***Perichaena chrysosperma*** (Figure 30) occurred on *Populus tremula* (Figure 56) with a *p*H of 5.5; ***Stemonitis pallida*** (Figure 57) occurred on *Juniperus communis* (Figure 58) with a *p*H of 4.5.

Figure 57. ***Stemonitis pallida*** sporangia, a species that occurs on *Juniperus communis* with a bark *p*H of 4.5. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 58. ***Juniperus communis***, a species with a bark *p*H of 4.5. Photo by Chris Cant, through Creative Commons.

Figure 56. ***Populus tremula***, home for ***Perichaena chrysosperma***, with a bark *p*H of 5.5. Photo by J. R. Crellin, through Creative Commons.

Härkönen *et al*. (2004) found that slime mold species richness on bark of forests in Hunan, China, was highest when the bark was relatively acidic and had a high water-retention capacity. The bryophytes, on the other hand, had a higher diversity on less acidic, relatively smooth bark. It is assumed that smooth bark holds less water.

Härkönen (1977) inferred that the mosses trapped the spores of the slime molds. To test this hypothesis, he cultured bark from living trees at three localities in Finland. In these moist chambers, 19 species of slime molds appeared on the pieces of bark. He found that ***Comatricha nigra*** (Figure 59) preferred an acid substrate, whereas others like ***Arcyria cinerea*** (Figure 32-Figure 33) preferred a less acid one. Fructification in the cultures varied from a few days to more than 40 days. Source of origin affected the species diversity, with the urban locality samples producing only six species. Interestingly, the virgin forest samples exhibited more species, but fewer fructifications. *Salix caprea* and *Alnus incana* have very few epiphytic mosses, presumably greatly reducing the capture of slime mold spores.

Figure 59. ***Comatricha nigra*** young sporangia, a species that prefers an acid substrate. Photo by Bjorlil, through Creative Commons.

Interestingly, Ing (1994) found that temperature was the only significant factor limiting tropical, subtropical, Mediterranean, and alpine species. Nevertheless, water is of prime importance, with water-retaining substrates being essential. They considered only "a few species" to be particularly associated with terrestrial bryophytes. The slime molds tended to prefer either coniferous or angiospermous wood.

Unlike bryophyte diversity, slime mold diversity and abundance decrease with elevation and associated higher moisture levels in the tropical Costa Rica (Gradstein *et al.* 1989; Wolf 1993; Schnittler & Stephenson 2000). Furthermore, it is in two seasonally dry forests where 90% of the slime mold diversity occurs. The negative correlation between slime molds and bryophytes suggests that the bryophytes may actually out-compete the slime molds in the more moist, bryophyte-dominant ecosystems at higher elevations. Nevertheless, higher species diversity seems to be correlated with higher substrate *p*H. On the other hand, litter-inhabiting slime molds with robust phaneroplasmodia increase with increasing elevation. It also appears that the continuously moist forests at higher elevations are not favorable for slime mold growth and development. These factors all contribute to the fact that biodiversity of slime molds does not reach its highest levels in tropical forests.

Schnittler and Stephenson (2000) found ***Ceratiomyxa fruticulosa*** (Figure 36) twice on mossy bark in the wet Costa Rican forest. All the species found on bark at higher elevations occurred not only on bark, but also on lush epiphytic moss and liverwort mats on the bark. These were ***Arcyria cinerea*** (Figure 32-Figure 33), ***Physarum*** *cf.* ***roseum*** (Figure 34-Figure 35), ***Ceratiomyxa fruticulosa***, ***Cribraria oregana*** (Figure 37), and ***Didymium iridis*** (Figure 38). The culture studies made it "obvious" that a closed cover of epiphytes hampers growth of slime molds. Nevertheless, many cultures prepared with bark having low cover of epiphytes likewise produced no slime molds. In any case, the number of slime mold records, based on cultures, clearly decreased with increasing elevation. Schnittler and Stephenson suggested that the abundant bryophytes use the bark nutrients, hence making them unavailable for bacterial growth, thus making less bacterial food available for the slime molds. But they pointed out that slime molds were often absent at low elevations where bryophytes were likewise rare.

In addition to bark-dwellers, some slime molds find substrates of liverworts growing on leaves to provide a suitable substrate (Schnittler *et al*. 2006). In the tropical forest, these habitats typically have a poor species richness of slime molds (Schnittler *et al.* 2006), but an assemblage dominated by members of the **Physarales** (Figure 19-Figure 22) is common (Schnittler 2001).

Log and Stump Associations

The most common habitat for slime molds seems to be that of logs (see, for example, Stephenson & Studlar 1985). These include a variety of stages of decay, and the logs often have a dense cover of bryophytes. Stumps offer similar habitats, but may differ in having exposed wood before decay sets in.

Doidge (1950), in her African report, included more detail on substrate than many of the early studies. She reported ***Cribraria cancellata*** (Figure 60) on dead wood and moss. ***Trichia affinis*** (Figure 61) occurred on decayed wood and moss. While it is likely that some of these slime molds grew from a primary substrate onto the mosses, that cannot be discerned from the report.

Figure 60. ***Cribraria cancellata*** sporangia on bryophytes. Photo by George Barron, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 61. ***Trichia affinis*** sporangia. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

A number of species are common on rotten wood, where they are able to provide food for a number of invertebrate organisms (Ing 1967). These slime molds include ***Arcyria denudata*** (Figure 62-Figure 63), ***Stemonitopsis typhina*** (Figure 64), ***Cribraria piriformis*** (Figure 65), ***Didymium iridis*** (Figure 38), ***Fuligo septica*** (Figure 1, Figure 66), ***Lycogala epidendrum*** (Figure 67), ***Reticularia lycoperdon*** (Figure 68), ***Stemonitis fusca*** (Figure 69), ***Symphytocarpus flaccidus*** (Figure 70-Figure 71), ***Trichia varia*** (Figure 72), ***Tubifera ferruginosa*** (Figure 73-Figure 74). All of these slime mold species occur on the same substrata preferred by a number of bryophyte species and are known to occasionally occur on the bryophytes.

Figure 64. ***Stemonitopsis typhina*** mature sporangia. Photo by George Barron, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 62. ***Arcyria denudata*** plasmodium, a common species on rotten wood. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 65. ***Cribraria piriformis*** sporangia, a slime mold that provides food for log-dwelling organisms. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 63. ***Arcyria denudata*** sporangia in their dispersal stage, with mosses. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 66. ***Fuligo septica*** plasmodium, a slime mold that provides food for log-dwelling organisms. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 67. ***Lycogala epidendrum*** sporangia, a species that provides food for invertebrates on logs, on the moss ***Thuidium***. Photo by Andrew Khitsun, with online permission.

Figure 68. ***Reticularia lycoperdon*** on log with moss, a slime mold that provides invertebrates with food. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 69. ***Stemonitis fusca*** sclerotium and sporangia; ***S. fusca*** provides food for invertebrates on logs. Photo by Deryni, through Creative Commons.

Figure 70. ***Symphytocarpus flaccidus*** sporangia, a slime mold that provides invertebrates with food. Photo Sarah Lloyd, with permission.

Figure 71. ***Symphytocarpus flaccidus*** sporangia. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 72. ***Trichia varia*** sporangia on mosses, a slime mold that provides food for invertebrates on logs. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 73. ***Tubifera ferruginosa*** sporangia on mosses on a log, a species that provides food for invertebrates. Photo by Dohduhdah, through Creative Commons.

Figure 74. ***Tubifera ferruginosa*** immature sporangia among mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Rojas and Stephenson (2007) examined **Myxomycetes** at high elevations in Costa Rica. They determined that ***Didymium squamulosum*** (Figure 75), ***Lycogala epidendrum*** (Figure 67), and ***Metatrichia floriformis*** (Figure 76) seem to group together at high *p*H levels and lower substrate heights. The sometimes-moss-dwellers ***Cribraria mirabilis*** (Figure 77) and ***Trichia botrytis*** (Figure 25) prefer more acidic substrates and higher substrates. They concluded that while bryophytes are important on the ground there, but not on logs, the bryophytes are not the reason for the presence of these slime molds at greater heights. As seen elsewhere, ***Lamproderma columbinum*** (Figure 42) is strongly associated with bryophytes. ***Cribraria piriformis*** (Figure 65), ***Ceratiomyxa fruticulosa*** (Figure 36) (on stumps overgrown with mosses – see also Stojanowska & Panek 2004), ***Cribraria mirabilis***, and ***Cribraria vulgaris*** (Figure 78) exhibited most of their fruitings on logs, twigs, and bryophytes. Rojas and Stephenson concluded that most of these slime molds were generalists that are able to survive changing microenvironmental conditions.

Figure 75. ***Didymium squamulosum*** on moss. Photo by James K. Lindsey, with permission.

Figure 76. ***Metatrichia floriformis*** sporangia, a species that occurred together with ***Trichia varia*** on a moss-covered aspen log. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 77. ***Cribraria mirabilis*** sporangia, a species that prefers acidic substrates and sometimes occurs on mosses. Photo by Rod Nelson, The Eumycetozoa Project, DiscoverLife.org, with online permission.

Figure 78. ***Cribraria vulgaris*** sporangia, a species occurring on moss-covered stumps and logs. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

The slime mold ***Hemitrichia minor*** is relatively common on logs covered with the leafy liverwort ***Lophocolea heterophylla*** (Figure 79). As shown in many studies cited herein, ***Barbeyella minutissima*** (Figure 80) occurs on such small liverworts as ***Lepidozia reptans*** (Figure 81) and ***Nowellia curvifolia*** (Figure 82) on montane forest logs in such distant locations as Japan, Europe, and North America (Kowalski & Hinchee 1972; Stephenson & Studlar 1985), with a similar relationship shown by the rare ***Licea hepatica*** (Kowalski 1972). ***Lepidoderma tigrinum*** (Figure 83) forms a strong association with both lichens and liverworts, the latter including ***Anastrophyllum michauxii*** (Figure 84), on damp coniferous logs. The frequent association of ***Perichaena corticalis*** (Figure 85) and ***P. depressa*** (Figure 86) with species of ***Hypnum*** (Figure 4) on ash (***Fraxinus***; Figure 87) fallen trunks that haven't "quite reached the ground" is notable (Ing 1982, 1994). I have already noted that ***Cribraria rufa*** (Figure 88) actually seems to damage the moss ***Orthodontium lineare*** (Figure 89) where both grow on conifer logs (Coker 1966).

Figure 79. ***Lophocolea heterophylla***, apparently overgrowing old slime molds. Photo by Sture Hermansson, with online permission.

Figure 80. ***Barbeyella minutissima*** sporangia on leafy liverwort. Photo by Randy Darrah, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 81. ***Lepidozia reptans***, one of the preferred substrates for ***Barbeyella minutissima***. Photo by David T. Holyoak, with permission.

Figure 82. ***Nowellia curvifolia***, a leafy liverwort that is an indicator for the presence of ***Barbeyella minutissima*** in that habitat. Photo by Hermann Schachner, through Creative Commons.

Figure 83. ***Lepidoderma tigrinum*** with sporangia on moss, a slime mold found on conifer logs with a thick cover of mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 84. ***Anastrophyllum michauxii***, a common leafy liverwort substrate for ***Barbeyella minutissima***. Photo by Michael Lüth, with permission.

Figure 85. ***Perichaena corticalis*** with mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 86. ***Perichaena depressa***, a slime mold species frequently associated with the moss genus ***Hypnum***. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 87. ***Fraxinus americana*** bark. ***Perichaena corticalis*** and ***P. depressa*** often occur with ***Hypnum*** species on fallen trunks of ***Fraxinus***. Photo by Keith Kanoti, through Creative Commons.

Figure 88. ***Cribraria rufa*** sporangia, a species that seems to damage the moss ***Orthodontium lineare***. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 89. ***Orthodontium lineare*** with capsules, a moss that seems to be damaged by the slime mold ***Cribraria rufa***. Photo by David T. Holyoak, with permission.

Clissmann *et al*. (2015) considered the diversity of slime molds on decaying beech (***Fagus sylvatica***; Figure 90) logs. They found that the conspicuous slime molds with large fruiting bodies displayed a strong preference for well-decayed, moist wood. These included ***Fuligo septica*** (Figure 1, Figure 66), ***Lycogala epidendrum*** (Figure 67), and ***Reticularia lycoperdon*** (Figure 68), all of which are known from mosses. DNA identifications revealed that the majority of representatives were in the genera ***Arcyria*** (Figure 32; Figure 62-Figure 63), ***Trichia*** (Figure 72, Figure 92), and ***Lycogala*** (Figure 67). The most common species on these logs were ***Arcyria cinerea*** (Figure 32-Figure 33), ***Hemitrichia clavata*** (Figure 91), ***Trichia scabra*** (Figure 92), and ***T. varia*** (Figure 72). It is notable that all the species named here by Clissmann and coworkers are also known from bryophytes on logs.

Figure 90. ***Fagus sylvatica***; well-decayed logs of this species host large slime molds. Photo by Roger Culos, through Creative Commons.

Figure 91. ***Hemitrichia clavata*** sporangia on log, one of the most common species on ***Fagus sylvatica*** logs. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 92. ***Trichia scabra*** sporangia on mosses, one of the most common slime mold species on ***Fagus sylvatica*** logs. Photo by Fotky, through Creative Commons.

There are even new species to be found in this common Myxomycetes habitat. Sarah Lloyd collected a new species, ***Alwisia lloydiae*** (Figure 93-Figure 94) (Leontyev *et al*. 2014). This species grows on logs, stumps, and mossy logs in New South Wales and Tasmania in Australia.

Figure 93. ***Alwisia lloydiae*** sporangia on mosses. Photo by Sarah Lloyd, with permission.

Figure 94. ***Alwisia lloydiae*** dehiscing capsules with mosses. Photo by Sarah Lloyd, with permission.

Figure 95. ***Tubifera*** cf. ***applanata*** with bryophytes on decaying wood. Photo by Sarah Lloyd, with permission.

Figure 96. ***Tubifera applanata*** dispersing spores onto bryophytes. Photo by Sarah Lloyd, with permission.

It is with this background of the strong relationship between slime molds and logs, and with the most common taxa occurring with bryophytes, that we must evaluate the relationship, if any, of slime molds with the bryophytes that grow on the logs. Are they simply benefitted by the same growing conditions? Or is the relationship **commensalism**, wherein one benefits and one is neither benefitted nor harmed? The slime molds could benefit from the moisture-holding capacity of the bryophytes, or the food organisms they house. It is harder to imagine any benefit to the bryophyte. Or do the slime molds provide food for invertebrates that in turn disperse the bryophyte spores?

Comparison of Checklists

Many researchers have reported slime molds growing on or over bryophytes on logs. Greene (1929) reported ***Tubifera ferruginosa*** (Figure 73) on mossy logs. Hagelstein (1941), using specimens added to the ***Tubifera applanata*** (Figure 95-Figure 96) similarly grows on decaying logs (Yatsiu, *et al*. 2018) and can grow on the bryophytes there (Figure 95). Herbarium of the New York Botanical Garden, reported a number of species from logs, noting those of conifer logs with a thick cover of mosses, lichens, and liverworts. These bryophyte associates included ***Colloderma oculatum*** (Figure 27), ***Lepidoderma tigrinum*** (Figure 83), ***Diderma roanense***, and ***Lamproderma columbinum*** (Figure 42). Others only indicated mossy logs, including ***Diderma roanense*** and ***Lepidoderma tigrinum***. Thus the short-comings of collections in herbaria deprive us of detailed information from which to draw inferences regarding specificity of the substrate, moisture and light levels, and *p*H. Hagelstein further pointed out that even in the sporangial stage, mosses can conceal the slime molds, so at best the ecology of slime molds associated with bryophytes is poorly represented.

Critchfield and Demaree (1991) reported ***Badhamia nitens*** (Figure 97-Figure 98) from dead wood and bark, but sometimes on mosses (and lichens) in California. Singer *et al*. (2005) reported ***Diderma montanum*** (Figure 99; syn.=*Chondrioderma montana*) and ***Diderma asteroides*** (Figure 100) on mosses on decayed wood. Robbrecht (1974) noted that ***Arcyria*** (Figure 101) occurs on diverse substrates, but mostly on dead wood (including alder, poplar, beech, oak, spruce, willow) at various stages of decay, but also on mosses, presumably on decaying wood. Ing (1982) reported ***Physarum psittacinum*** (Figure 102-Figure 103) on mossy rotten logs and ***Trichia affinis*** (Figure 104) on moss and rotten wood. Nissan (1997) found ***Physarum decipiens*** (Figure 105) on dead branches in association with mosses. Johannesen (1984) found ***Didymium ochroideum*** on mosses on dead wood of the Norway spruce (***Picea abies***; Figure 106). Stephenson

(1985) found ***Licea pusilla*** on the moss ***Hypnum imponens*** (common on logs; Figure 4) and on decaying coniferous wood.

Figure 97. ***Badhamia nitens*** sporangia, a species of dead wood and bark, but that sometimes occurs on mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 98. ***Badhamia nitens*** sporangia on mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 99. ***Diderma montanum*** sporangia, a slime mold species of dead wood and bark, but also sometimes on mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 100. ***Diderma asteroides*** sporangia, a slime mold species of dead wood and bark, but also sometimes on mosses. Photo from Myxotropic, through Creative Commons.

Figure 101. ***Arcyria nutans*** with capsules on decaying wood with mosses. Photo by Lairich Rig, through Creative Commons.

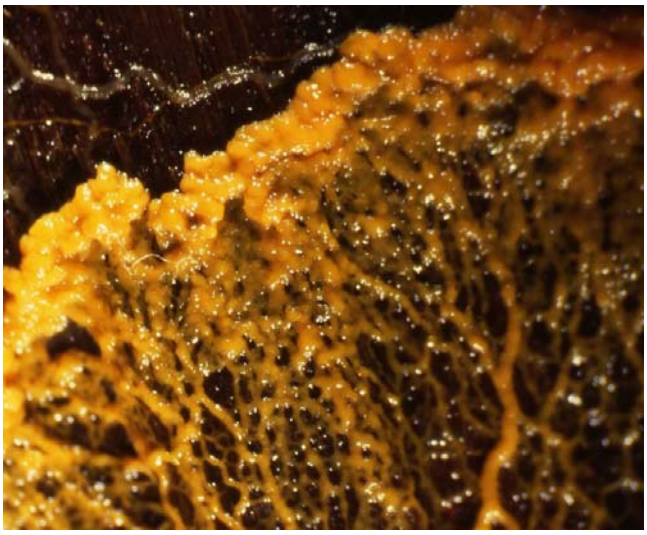

Figure 102. ***Physarum psittacinum*** plasmodium, a species known to occur on mossy rotten logs. Photo by Helen Ginger, through Creative Commons.

Figure 103. ***Physarum psittacinum*** sporangia on moss. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 104. ***Trichia affinis*** sporangia, a species known to occur on mossy rotten logs. Photo by Malcolm Storey, through Creative Commons.

Figure 105. ***Physarum decipiens*** on bryophytes, a species that also occurs on dead branches with mosses. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 106. ***Picea abies***; the slime mold ***Didymium ochroideum*** occurs on mosses on logs of this species. Photo by Qgroom, through Creative Commons.

As we entered the 21st Century, new records continued. Adamonyte (2000) found ***Cribraria argillacea*** (Figure 107) and ***Trichia favoginea*** (Figure 108-Figure 109) on very rotten, moss-covered logs, ***Hemitrichia clavata*** (Figure 91) and ***H. serpula*** (Figure 110) together on a moss-covered deciduous log, ***Metatrichia floriformis*** (Figure 76) with ***Trichia varia*** (Figure 72) on a moss-covered aspen log, ***Stemonitis axifera*** (Figure 23) on a moss-covered log in Estonia. Ukkala *et al*. (2001) reported several ***Physarum album*** (Figure 21) on decayed wood covered with mosses in China. Similarly, Castillo *et al*. (2009) reported ***Physarum leucophaeum*** (Figure 111) "in" moss on wood of the oak ***Quercus pyrenaica*** (Figure 112) in Cabañeros National Park, Spain. Working on Pantelleria, a volcanic island located 110 km southwest of the island of Sicily, Italy, Compagno *et al*. (2016) found ***Trichia persimilis*** (Figure 113-Figure 114) on rotten stumps and mosses.

Figure 107. ***Cribraria argillacea*** among mosses on log; this species is known from well-rotted, moss-covered logs. Photo by Malcolm Storey, through Creative Commons.

Figure 108. ***Trichia favoginea*** with mosses. Photo from Denver Botanical Garden, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 109. ***Trichia flavoginea***, an occasional bryophyte-dweller. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 110. ***Hemitrichia serpula*** producing spores, a species known to occur on a moss-covered deciduous log. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

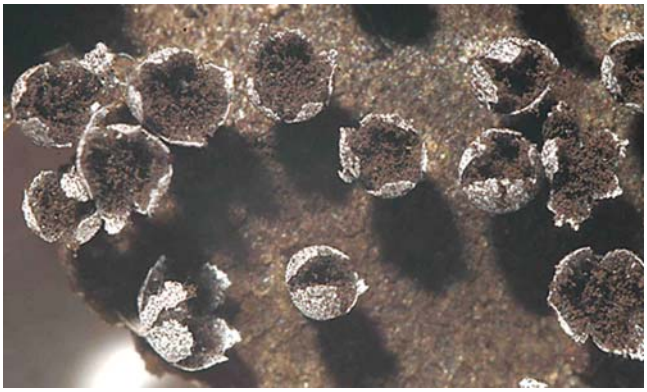

Figure 111. ***Physarum leucophaeum*** expelling its spores. This slime mold species occurs among mosses on wood of the oak ***Quercus pyrenaica***. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 112. ***Quercus pyrenaica*** bark, substrate for the slime mold ***Physarum leucophaeum***. Photo by Xemenendura, through Creative Commons.

Figure 113. ***Trichia persimilis*** with mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 114. ***Trichia persimilis*** fruiting. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

The interesting thing in these lists of slime molds reported by various researchers in diverse parts of the world is that in my limited perusal of various checklists, searching for bryophyte associations, a species has rarely been listed on bryophytes in more than one list. While this perusal is far from extensive, it nevertheless suggests to me that the slime molds on the bryophytes are not unique to that substrate. A more thorough study of the published records, backed up by field studies, will be necessary to support that hypothesis.

A more extensive study of slime molds and their substrates is that of Schnittler and Novozhilov (1996) in the boreal forests of northern Karelia in Russia. Some of these weren't picky about the type of wood, but others seemed to be more specific. Many occurred insufficiently to generalize. For example, ***Badhamia foliicola*** (Figure 115) occurred only once, in that case on a strongly decayed deciduous, moss-covered, decorticated log lying on the forest floor of a spruce-birch-aspen forest. ***Physarum globuliferum*** (Figure 116) produced only two records, both from moderately decayed coniferous wood that was partially covered with mosses. ***Physarum leucophaeum*** (Figure 117) was likewise not very common, but was always on dead wood, mostly aspen (***Populus***; Figure 56), but less commonly on spruce, and was often associated with mosses; lab cultures came from mossy living or dead bark of aspen.

Figure 115. ***Badhamia foliicola*** sporangia, a species known from a strongly decayed deciduous, moss-covered, decorticated log. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 116. ***Physarum cf. globuliferum***, a species in Russia from moderately decayed coniferous wood that was partially covered with mosses. Photo by George Shepherd, through Creative Commons.

Figure 117. ***Physarum leucophaeum***, a species that in Russia was not common, occurred on dead aspen wood, but occasionally occurred on bryophytes. Photo by Jerry Cooper, through Creative Commons.

On the other hand, the common ***Physarum album*** (Figure 21) and ***Stemonitis fusca*** (Figure 69) occurred on all kinds of well-decayed wood, but despite records of these species on bryophytes elsewhere, none were mentioned in this Karelian study (Schnittler & Novozhilov 1996). ***Physarum viride*** (Figure 118) likewise occurred on decayed wood, mostly of conifers, but occasionally on deciduous trees; there was no mention of bryophytes, although it has been associated with them in other studies. ***Comatricha laxa*** (Figure 119) was very frequent, and displayed a strong preference for coniferous wood, usually on small branches that had lost their bark and were lying on wet mosses. Might these have spent their plasmodial stage among the mosses, crawling up onto the branches to produce their sporangia?

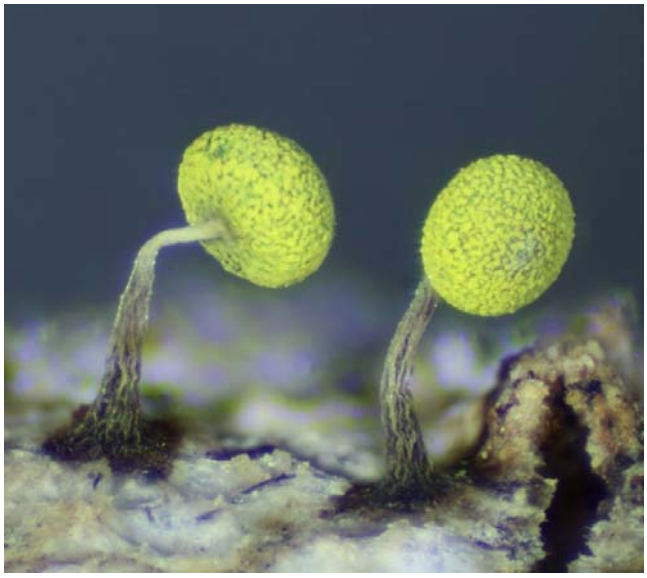

Figure 118. ***Physarum viride*** sporangia, a species of decaying wood, especially conifers. Photo by Sarah Lloyd, with permission.

Figure 119. ***Comatricha laxa*** sporangia on decaying log, a slime mold that also occurs on logs lying on wet moss. Photo by Clive Shirley, The Hidden Forest, with permission.

Schnittler and Novozhilov (1998) conducted another extensive study on slime molds on those fruiting in the late autumn in the Northern Ammergauer Alps on the Bavarian-Tyrolean border. Some of these indicated successional stages, as discussed below. Others related to bryophytes include ***Lamproderma columbinum*** (Figure 42) on thick moss beds of fallen logs (see also Ing 1982) and rocks. The ***Licea pygmaea*** (Figure 120) group, mostly rare, prefer strongly decayed (37% of records), moss-overgrown (31%), or algae-covered wood (22%). But some [***Hemitrichia clavata*** (Figure 91), ***H serpula*** (Figure 110), ***Collaria arcyrionema*** (Figure 43; syn.=*Lamproderma arcyrionema*), ***Lamproderma cf. sauteri*** (Figure 121), ***Lepidoderma tigrinum*** (Figure 83), ***Trichia varia*** (Figure 72)] occurred on wood without bryophytes, despite all of these being known elsewhere from bryophytes as well. For example, Ing (1982) reported ***Lepidoderma tigrinum*** from mossy wood.

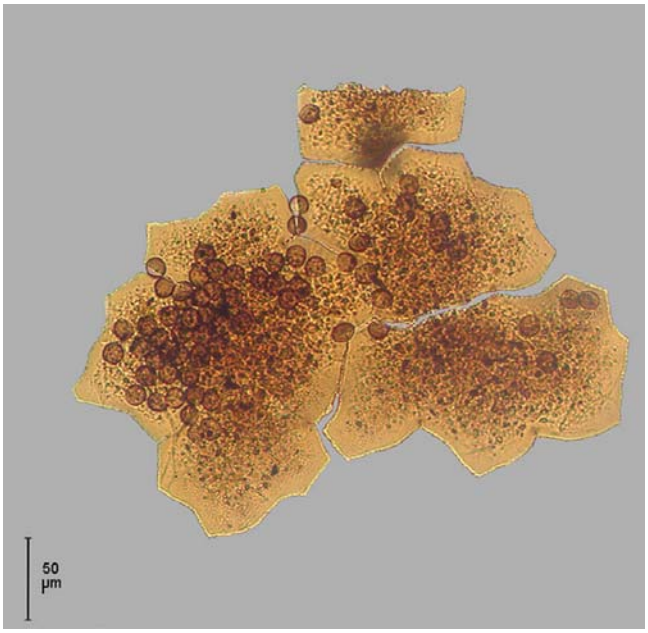

Figure 120. ***Licea pygmaea*** peridium with sporangia, a species with a moderate frequency with mosses. Photo from The Eumycetozoan Project, DiscoerLife.org, with online permission.

Figure 121. ***Lamproderma sauteri*** sporangia. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

A number of biologists have considered ***Barbeyella minutissima*** (Figure 80) to be restricted to bryophytes. Kowalski and Hinchee (1972) found it in relatively good abundance on the slopes of Mount Baker and Mount Rainier, Washington, USA. There it formed associations with the leafy liverworts ***Anastrophyllum michauxii*** (Figure 84), ***Blepharostoma trichophyllum*** (Figure 122), ***Cephalozia bicuspidata*** (Figure 123), ***Plagiochila asplenioides*** (Figure 124), and ***Scapania bolanderi*** (Figure 125). The small size of this slime mold makes it easy to overlook, especially with its very restrictive habitat. Kowalski and Hinchee hypothesized that it is usually overlooked, and that it is likely to occur in any montane area. They suggested searching for it among the leafy liverworts, using a hand lens or dissecting microscope.

Figure 122. ***Blepharostoma trichophyllum***, a common leafy liverwort substrate for ***Barbeyella minutissima***. Photo by Hermann Schachner, through Creative Commons.

Figure 123. ***Cephalozia bicuspidata***, a common leafy liverwort substrate for ***Barbeyella minutissima***. Photo from Botany Website, UBC, with permission.

Figure 124. ***Plagiochila asplenioides***, a common leafy liverwort substrate for ***Barbeyella minutissima***. Photo by Hermann Schachner, through Creative Commons.

Figure 125. ***Scapania bolanderi***, a common leafy liverwort substrate for ***Barbeyella minutissima***. Photo from Botany Website, UBC, with permission.

Barbeyella minutissima (Figure 80) seems to be distributed primarily in montane spruce-fir forests (Schnittler *et al*. 2000). It typically is associated with three other slime molds, ***Colloderma oculatum*** (Figure 27), ***Lamproderma columbinum*** (Figure 42), and ***Lepidoderma tigrinum*** (Figure 83). The leafy liverwort ***Nowellia curvifolia*** (Figure 82) is such a common substrate for it that the liverwort can serve as an indicator species for its presence.

Working in India, Ranade *et al*. (2012) added a different group of species. On living mosses and bark of stumps they found ***Badhamia capsulifera*** (Figure 126), whereas ***B. utricularis*** (Figure 127-Figure 129) seemed to prefer dead wood and mosses; ***Trichia affinis*** (Figure 104) likewise occurred on wood of a stump and live mosses growing on it. Similarly, ***Hemitrichia serpula*** (Figure 110) occurred on both mosses and dead wood, but the researchers specifically stated that ***Arcyria stipata*** (as *Hemitrichia stipitata*; Figure 130) and ***Stemonitis axifera*** (Figure 24) occurred on dead wood and living mosses. ***Trichia botrytis*** (Figure 25) occurs on the bark of trees and mosses growing on it, on dead coniferous wood, and on living mosses. ***Diderma cor-rubrum*** and ***Lamproderma columbinum*** (Figure 42) occurred on a moss-covered stump. ***Physarum stellatum*** (Figure 131), instead, occurred on dead wood, mosses, and an oak stump. As might be expected, ***Barbeyella minutissima*** (Figure 80) was associated with mosses and liverworts on decaying logs. ***Stemonaria nannengae***, ***Stemonitis farrensis***, and ***Trichia favoginea*** (Figure 132) were seemingly more particular about the wood, occurring on decaying gymnosperm wood covered with mosses, whereas ***Diderma alexopouli*** and ***D. indicum*** occurred on a moss-covered conifer stump, with the latter also occurring on mosses. ***Physarum flavidum*** (Figure 44, Figure 133) was found in coniferous forests, where it occurred on decorticated logs and mosses. ***Fuligo aurea*** (Figure 134) was even more specific (or maybe the collectors were able to be more specific), growing on moss covering the decaying wood of the fir, ***Abies pindrow*** (Figure 135-Figure 136). ***Cribraria rubiginosa*** (Figure 137) occurred on mosses on a log.

Figure 126. ***Badhamia capsulifera***, a species that occurs on living mosses and stumps. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 129. Plasmodium stage of ***Badhamia utricularis*** invading shelf fungi. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 127. Young fruiting bodies of ***Badhamia utricularis*** invading shelf fungi. Are those moss protonemata? Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 130. ***Arcyria stipata*** with sporangia on wood and mosses. Photo from The Eumycetozoan Project, DiscoverLife.com, through online permission.

Figure 128. Mature fruiting bodies of ***Badhamia utricularis*** invading shelf fungi. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

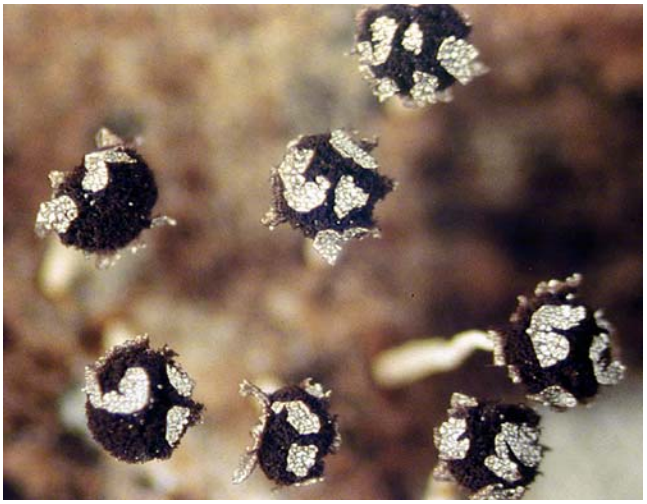

Figure 131. ***Physarum stellatum*** sporangia ready to disperse spores, a species of dead wood and mosses. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 132. ***Trichia favoginea*** on log with liverworts. Photo by Jerry Cooper, through Creative Commons.

Figure 133. ***Physarum flavidum*** sporangia on log, a species also known from mosses. Photo by Sarah Lloyd, with permission.

Figure 134. ***Fuligo aurea*** plasmodium on wood. Photo through Creative Commons.

Figure 135. ***Abies pindrow*** in Manali, India. The slime mold ***Erionema aureum*** grows on the decaying wood of this species. Photo by Vyacheslav Argenberg, through Creative Commons.

Figure 136. ***Abies pindrow*** in India. Photo by Gaurav Verma, through Creative Commons.

Figure 137. ***Cribraria rubiginosa***, a species known from mosses on a log. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Joshaghani *et al.* (2013) added to our knowledge of both slime mold geography and their substrate uses by studying the slime mold flora of Iran. He named ***Arcyria cinerea*** (Figure 32-Figure 33), ***A. incarnata*** (Figure 138), ***Fuligo septica*** (Figure 1, Figure 66), ***Hemitrichia clavata*** (Figure 91), ***H. serpula*** (Figure 110), ***Lycogala epidendrum*** (Figure 67), ***Lycogala exiguum*** (Figure 139-Figure 140), ***Metatrichia vesparia*** (Figure 141), ***Physarum didermoides*** (Figure 142), ***Stemonitis axifera*** (Figure 24), ***S. fusca*** (Figure 69), ***S. splendens*** (Figure 143), ***Stemonitopsis typhina*** (Figure 144), ***Trichia decipiens*** (Figure 145-Figure 146), ***T. favoginea*** (Figure 132), and ***T. scabra*** (Figure 92) as occurring on rotten wood and mosses.

Figure 138. ***Arcyria incarnata*** mature sporangia, a slime mold of rotten wood and mosses. Photo by Stu's Images, through Creative Commons.

Figure 139. ***Lycogala exiguum*** developing sporangia, a species that occurs on rotten wood and mosses. Photo by Katja Schulz, through Creative Commons.

Figure 140. ***Lycogala exiguum*** mature sporangia. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 141. ***Metatrichia vesparia*** sporangia, a species that occurs on rotten wood and mosses. Photo by George Barron, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 142. ***Physarum didermoides*** on mosses, a species that occurs on rotten wood and mosses. Photo by Andrew Khitsun, with online permission.

Figure 143. ***Stemonitis splendens***, a species that occurs on rotten wood and mosses. Photo by Jennifer Linde, through Creative Commons.

Figure 144. ***Stemonitopsis typhina*** sporangia, a species that occurs on rotten wood and mosses. Photo by Sarah Lloyd, with permission.

Figure 145. ***Trichia decipiens*** developing sporangia on decaying wood, a species that occurs on rotten wood and mosses. Photo by Jerzy Opiola, through Creative Commons.

Figure 146. ***Trichia decipiens*** mature sporangia, a species that occurs on rotten wood and mosses. Photo by Fungi07, through public domain.

Stephenson *et al*. (1993) carried out the unusual comparison between slime molds of the two locations in the middle Appalachian Mountains in eastern USA with those of two regions in India. Using 3788 collections, covering 1954-1990, they compared slime molds from tropical-subtropical southern India and three temperate sites. As one might expect, the tropical-subtropical site had the least similarity to the other three sites. The **Physarales** (Figure 19-Figure 22) formed a greater proportion of the southern India collections (63%), whereas the **Liceales** (Figure 51, Figure 55, Figure 120) were much better represented in the three more northern sites. Furthermore, the typical substrata differed, with more than 63% of the southern collections coming from leaf litter and other non-woody debris. On the other hand, more than 80% of the temperate collections were from woody substrates. These differences in slime mold species groups and substrate preferences may help to explain differences seen in their associations with bryophytes. With 80% of the northern species occurring on woody substrates, and the common presence of bryophytes on such substrates, we should expect them to be associated frequently. It is the nature of that association that remains to be defined.

Where Bryophyte and Slime Mold Meet

Stephenson and Studlar (1985) attempted to determine if the association of slime molds with bryophytes, particularly on logs and stumps, was a preference or just a coincidence. They included only those plasmodial slime molds for which bryophytes served as the primary substrate for fruiting. They concluded that most of the 52 slime mold species occurring on 55 bryophyte species that they were able to sample in North America were coincidental. Only ***Barbeyella minutissima*** (Figure 80) and ***Lepidoderma tigrinum*** (Figure 83) exhibited a preference for leafy liverworts on rotten conifer logs. In fact, ***B. minutissima*** occurred only on the leafy liverworts ***Nowellia curvifolia*** (Figure 82), ***Lepidozia reptans*** (Figure 81), and ***Cephalozia lunulifolia*** (Figure 147) on decorticated logs of ***Picea rubens*** (red spruce; Figure 148). This is a tiny slime mold and was not even seen until collections were examined in the lab with a microscope. ***Lepidoderma tigrinum*** was usually associated with leafy liverworts, especially ***Nowellia curvifolia*** and ***Lepidozia reptans***, but also occasionally with the mosses ***Dicranum montanum*** (Figure 149) and ***Dicranodontium denudatum*** (Figure 150). This species also was fruiting on parts of the logs that were devoid of bryophytes. Kowalski (1971) likewise reported ***L. tigrinum*** on badly decayed coniferous wood growing over and among the mosses and liverworts.

Figure 147. ***Cephalozia lunulifolia***, one of the preferred substrates for ***Barbeyella minutissima***. Photo by Štěpán Koval, with permission.

Figure 148. ***Picea rubens*** (red spruce); liverwort-covered logs of this species are preferred habitats of ***Barbeyella minutissima***. Photo by Keith Kanoti, through Creative Commons.

Figure 149. ***Dicranum montanum***, a moss that is an occasional substrate for ***Lepidoderma tigrinum***. Photo by Bob Klips, with permission.

Figure 150. ***Dicranodontium denudatum***, a moss that is an occasional substrate for ***Lepidoderma tigrinum***. Photo by David T. Holyoak, with permission.

Dudka and Romanenko (2006) considered the relationships between the slime molds and bryophytes to be spatial when they occur together on woody substrata, not trophic. Rather, they may be regulated by their specific microclimatic conditions within the bryophyte colonies. Nevertheless, they considered most of the slime mold associations with bryophytes to be accidental. They seem to develop more extensively and occur more frequently on fallen decaying logs overgrown with bryophytes because of the high humidity that both thrive in (Stojanowska & Panek 2004).

What Do These Associations Offer?

Life Cycle Relationships

It appears that bryophytes might play a role in the life cycle of slime molds. Stephenson and Studlar (1985) found a number of slime molds fruiting on bryophytes in temperate North American forests. They considered that 52 of the slime mold species occurring with the 55 bryophytes species were "coincidental." However, the slime molds ***Barbeyella minutissima*** (Figure 80) and ***Lepidoderma tigrinum*** (Figure 83) appear to be truly bryophilous, particularly on leafy liverworts on rotten conifer logs. ***Barbeyella minutissima***, ***Colloderma oculatum*** (Figure 27), and ***Lepidoderma tigrinum*** are not only truly bryophilous, but ***Barbeyella minutissima*** is especially associated with ***Nowellia curvifolia*** (Figure 82) and members of ***Cephalozia*** (Figure 147) (Dudka & Romanenko 2006), species that can completely cover a decaying coniferous log (Schnittler & Novozhilov 1998; Schnittler *et al.* 2000; Novozhilov 2005). Stephenson and Studlar (1985) suggested that in most cases the bryophytes provide exposed surfaces that are convenient for slime mold spore production. On the other hand, the plasmodial stages might reside there without being noticed. ***Barbeyella minutissima*** and ***Lepidoderma tigrinum*** are often associated with the bryophytes aligned with algal layers on decorticated wood (Stephenson & Studlar 1985; Schnittler 2001; Smith & Stephenson 2007; Rollins & Stephenson 2011).

Stephenson and Studlar (1985) were unable to determine if the bryophytes provided a sustainable food source by harboring microorganisms useful for the feeding stages (swarm cells, myxamoebae, plasmodia) of the life cycle. They did consider the bryophytes to be obvious exposed surfaces "convenient for sporulation." Their conclusion was that plasmodia do not avoid bryophytes, but that their sampling was inadequate to determine exclusivity or preference for bryophytes.

Algae and Cyanobacteria

Algae and **Cyanobacteria** (Figure 152-Figure 153), in addition to bryophytes, are common on decorticated logs. In their investigation of decaying red spruce (***Picea rubens***; Figure 148) logs with both leafy liverworts and slime molds, Smith and Stephenson (2007) found nine **Cyanobacteria** species, two **Chlorophyta** (Figure 154, Figure 156, Figure 157) species, and one **Bacillariophyta** (diatom; Figure 151) species. Of these, two **Cyanobacteria** [***Chroococcus tenax*** (Figure 152) and ***Aphanothece saxicola*** (Figure 153)] and one green alga (***Chlorococcum humicola***; Figure 154) dominated. In addition to potential nitrogen addition through N-fixation, these **Cyanobacteria** and algae could provide a food source for the slime molds.

Figure 151. Mixed diatoms (**Bacillariophyta**). Photo by Janice Glime.

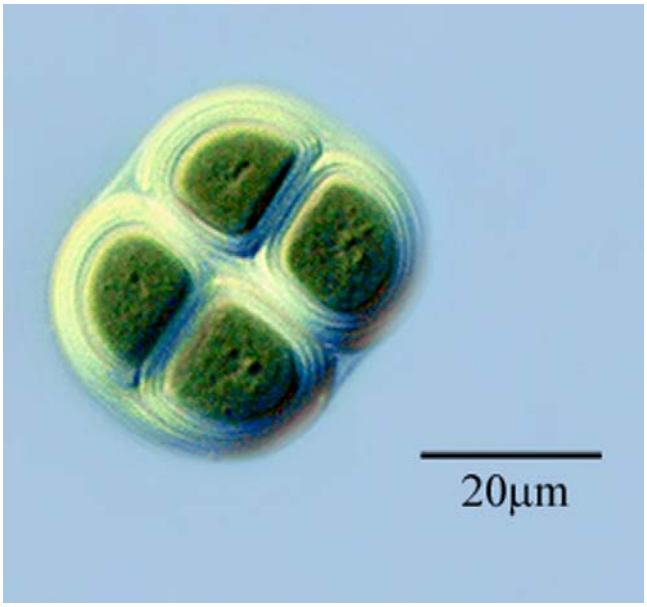

Figure 152. ***Chroococcus tenax***, a species that accompanies both leafy liverworts and slime molds on decaying logs. Photo from Proyecto Agua, through Creative Commons.

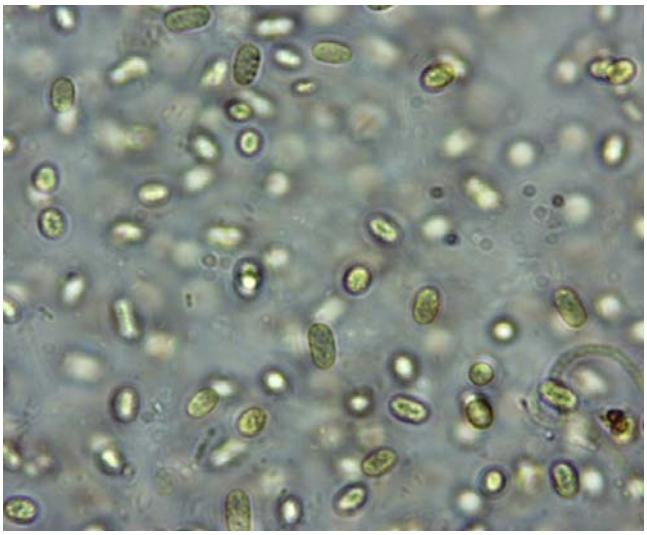

Figure 153. ***Aphanothece*** sp.; ***A. saxicola*** accompanies both leafy liverworts and slime molds on decaying logs. Photo by Karolina Fucikova, through Creative Commons.

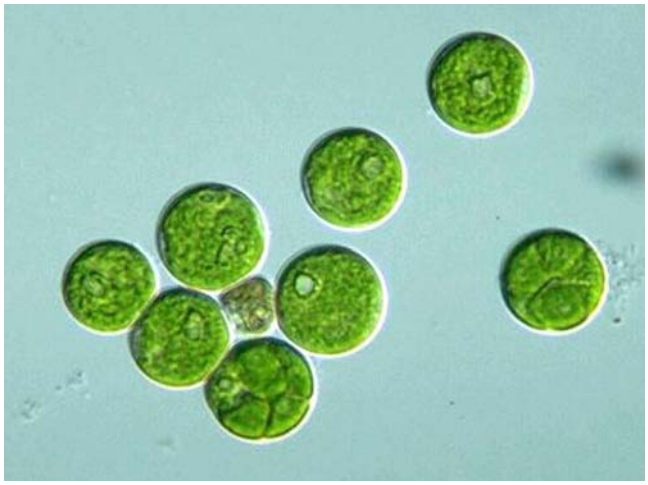

Figure 154. ***Chlorococcum*** sp.; ***C. humicola*** accompanies both leafy liverworts and slime molds on decaying logs. Photo by Yuuji Tsukii, with permission.

The slime mold ***Clastoderma debaryanum*** (Figure 155) occurs on Norway spruce (***Picea abies***; Figure 106) logs in Lithuania (Adamonyté 2007). These logs are covered with algae and some mosses. In other cases, slime molds occur on dead wood covered with a scanty growth of liverworts and algae, or with only algae. This slime mold species is unusual in its ability to grow on substrates with a wide *p*H range of 3.8 to 7.5 (Rosing *et al*. 2007).

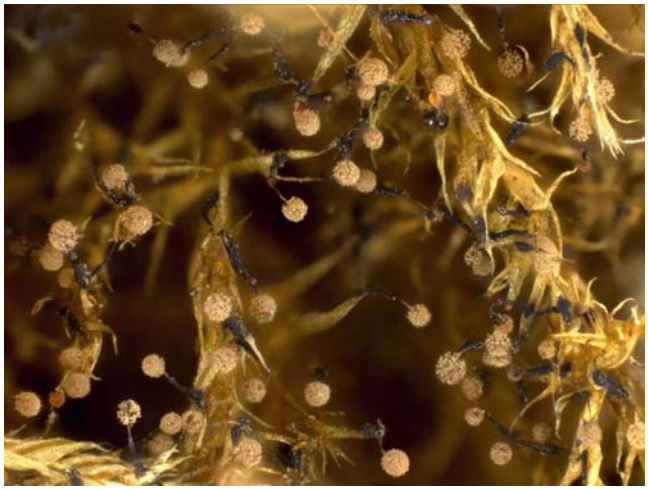

Figure 155. ***Clastoderma debaryanum*** on mosses. Photo from Myxotropic, with online permission.

Interestingly, ***Barbeyella minutissima*** (Figure 80) grows on leaf tips that protrude above the water film (Schnittler & Novozhilov 1998). Association with algae was "obvious" in 70% of the collections and in 60% of the collections of ***Colloderma oculatum*** (Figure 27). The late season fruiting insures cool nights that provide extended dewfall, keeping the logs moist enough for algal/Cyanobacterial growth for weeks. On the other hand, ***Barbeyella minutissima*** and ***Licea pygmaea*** (Figure 120), accompanied by scattered sporocarps of ***Colloderma*** and ***Lepidoderma*** (Figure 83), occur primarily on the lower sides of logs directed towards the rivulet but preserved from rainfall itself.

Slime molds are known to feed on algae (Zabka & Lazo 1962). In fact, Lazo demonstrated that the slime

mold ***Physarum didermoides*** (Figure 142) can incorporate cells of the green alga ***Chlorella*** (Figure 156), a common symbiont in lichens and even *Hydra*, into its plasmodium, causing the plasmodium to be green. In addition to these examples, the plasmodium of occasional moss dweller ***Didymium iridis*** (Figure 38) is known to contain the green alga ***Trebouxia*** (Figure 157) (Keller & Braun 1999), a common lichen symbiont. But who benefits in this relationship with slime molds, and how?

Figure 156. ***Chlorella***, an apparent symbiont in the plasmodium of ***Physarum didermoides***. Photo by Barry H. Rosen, through Creative Commons.

Figure 157. ***Trebouxia***, an apparent symbiont in the plasmodium of ***Didymium iridis***. Photo by Alan J. Silverside, with permission.

Decay Stages

As noted by Leontyev (2010), most slime molds tend to be limited to a particular type of substrate. Some become more specific, occupying only a particular stage of wood decay. For example, ***Arcyria incarnata*** (Figure 138) and ***Comatricha nigra*** (Figure 158-Figure 159) prefer the second stage, one of firm, decorticated wood. ***Trichia favoginea*** (Figure 132) and ***T. scabra*** (Figure 92) prefer the third stage in which the wood has an average degree of decomposition, but is still not colonized by mosses. In the fourth stage, the wood is fully decomposed and covered by mosses, a stage preferred by the slime molds ***Metatrichia vesparia*** (Figure 141) and ***Tubifera ferruginosa*** (Figure 160).

Figure 158. ***Comatricha nigra*** young sporangia. Photo by Bjorlil, through Creative Commons.

Figure 159. ***Comatricha nigra*** sporangia on firm, decorticated wood. Photo by Helen Ginger, through Creative Commons.

Figure 160. ***Tubifera ferruginea*** on bryophytes, a slime mold that prefers fully decomposed wood covered with mosses. Photo by Amadej Trnkoczy, through Creative Commons.

As wood decays, its structure and moisture content change. Initially, the logs have the species that were present on the living trunk. However, as the log changes,

the bark falls off, and the species of mosses, liverworts, lichens, and algae go through a successional process that results in very different assemblages from those on the living tree (Ing 1994).

Schnittler and Novozhilov (1998) describe the decay stages of the wood from decorticated logs, thicker than 15 cm, that are slightly to moderately decayed. These come from very moist (water-saturated air) and shady places and are covered by a thin, slimy layer of algae and liverworts. The moist wood stage is mostly decorticated, with a moderate to strong decay, and are covered with a thicker cover (>1 cm thick) of mosses, frequently ***Paraleucobryum*** sp. (Figure 161) and sometimes species of the leafy liverwort ***Mylia*** (Figure 162). This association is typically enriched with detritus. Differing from ***Barbeyella minutissima*** (Figure 80) and ***Colloderma oculatum*** (Figure 27) that occur almost entirely on the decorticated spruce and fir logs that have coverings of slimy algae and **Cyanobacteria**, ***Cribraria cancellata*** (Figure 163) and ***Diderma montanum*** (Figure 164) tend to occur in the cooler valley bottoms, where they produce sporangia on moderately decayed wood of spruce and beech, often on logs with mossy, loose bark.

Figure 161. ***Paraleucobryum longifolium***, a moss of the moist wood stage of mostly decorticated logs. Photo by Hermann Schachner, through Creative Commons.

Figure 162. ***Mylia taylorii***; the genus ***Mylia*** often occurs on the moist wood stage of the mostly decorticated logs. Photo by David T. Holyoak, with permission.

Figure 163. ***Cribraria cancellata*** sporangia, a species that occurs on moderately decayed wood of spruce and beech, often on logs with mossy, loose bark. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 164. ***Diderma montanum*** sporangia, a species that occurs on moderately decayed wood of spruce and beech, often on logs with mossy, loose bark. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Stephenson and Studlar (1985) concluded that ***Barbeyella minutissima*** (Figure 80) and ***Lepidoderma tigrinum*** (Figure 83) are bryophilous, being almost invariably associated with bryophytes, and in particular with leafy liverworts. Schnittler *et al*. (2000) examined collections from 27 localities in the Northern Hemisphere. They concluded that these two species are restricted to decorticated coniferous wood covered by 40-100% leafy liverworts, based on 41 collections. They furthermore noted the importance of a "thin, slimy layer" of algae.

Stojanowska and Panek (2004) reported a number of bryophyte-slime mold-log associations from a nature reserve in southwest Poland. ***Cribraria vulgaris*** (Figure 78) and ***Lycogala epidendrum*** (Figure 67) occur there on moss-covered stumps and logs. ***Fuligo septica*** (Figure 1, Figure 66), ***Lycogala exiguum*** (Figure 139-Figure 140), ***Metatrichia vesparia*** (Figure 141), ***Stemonitis fusca*** (Figure 69), ***S. pallida*** (Figure 57), ***Trichia botrytis*** (Figure 25), ***T. persimilis*** (Figure 113-Figure 114), ***T. varia*** (Figure 72), and ***Tubifera ferruginosa*** (Figure 73) occur on bryophyte-covered stumps. ***Diderma radiatum*** (Figure 165-Figure 166) occurs on stumps overgrown with the moss ***Brachythecium rutabulum*** (Figure 167). ***Arcyria cinerea*** (Figure 32-Figure 33), ***A. denudata*** (Figure 62-Figure 63), ***Physarum compressum*** (Figure 168-Figure 169), ***Physarum gyrosum*** (Figure 170-Figure 171), ***Stemonitis axifera*** (Figure 24), and ***Trichia scabra*** (Figure 92) occur on bryophyte-covered logs. ***Lepidoderma tigrinum*** (Figure 83) occurs on decaying logs densely

overgrown with ***Dicranum montanum*** (Figure 149) (see also Neubert *et al.* 1993), whereas ***Badhamia panicea*** (Figure 172-Figure 173) occurs on bark of a recent log with ***Brachythecium rutabulum***. ***Reticularia lobata*** (syn.=***Enteridium lobatum***; Figure 174) occurs on bryophyte-covered conifer wood. They also mentioned that ***Lamproderma columbinum*** (Figure 42) occurs on ***Tetraphis pellucida*** (Figure 175), a moss species most typical of decaying stumps, but that also occurs on rocks. The co-occurrence of particular slime molds with specific mosses may reflect a preference of both for the same microclimate.

Figure 165. ***Diderma radiatum*** sporangia on log with mosses. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 166. ***Diderma radiatum*** sporangia, ready for dispersal. Photo from Myxotropic, through Creative Commons.

Figure 167. ***Brachythecium rutabulum***, a common substrate for ***Diderma radiatum***. Photo by Arnoldius, through Creative Commons.

Figure 168. ***Physarum compressum*** on bryophytes. Photo courtesy of Sarah Lloyd.

Figure 169. ***Physarum compressum*** fruiting. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 170. ***Physarum gyrosum*** fruiting; this slime mold can be found on logs covered with bryophytes. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

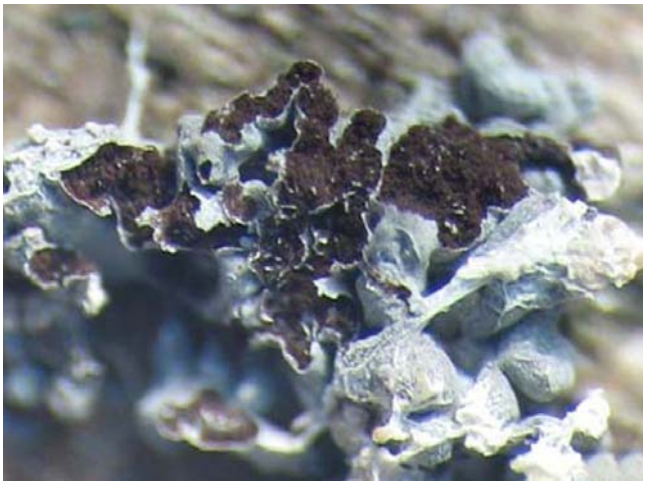

Figure 171. ***Physarum gyrosum*** fruiting and dispersing spores. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 172. ***Badhamia panicea*** sporangia, a species that occurs on bark of a recent log with the moss ***Brachythecium rutabulum***. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 173. ***Badhamia panicea*** sporangia. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 174. ***Reticularia lobata***, a species of bryophyte-covered conifer wood. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 175. ***Tetraphis pellucida***, a moss that is sometimes a substrate for the slime mold ***Lamproderma columbinum***. Photo by Hermann Schachner, through Creative Commons.

Spore Traps

We know from studies on dwarf males that some bryophyte spores successfully germinate on leaves of the same species. This raises the questions of what other kinds of propagules are successful there, and how widespread are these relationships with other kinds of organisms.

Stephenson and Rojas (2020) raised this question regarding slime molds associated with bryophytes. Most spores are dispersed by wind; some are dispersed by animals. The wind dispersal appears to be very efficient within distances of at least 50 meters (Schnittler *et al*. 2006; Schnittler & Tesmer 2008). The spores seem able to travel until they meet a physical surface where they can rest (Stephenson & Rojas 2020). Since mosses can provide such surfaces, Stephenson and Rojas used nylon bags containing sterilized mosses from the tropics in Costa Rica (predominantly ***Pilotrichella flexilis*** – Figure 176) and the temperate deciduous forest of northwest Arkansas, USA (predominantly ***Thuidium delicatulum*** – Figure 3). The mosses in the bags were collected after more than four months and cultured. Of the 40 moist chamber cultures from the tropics, 95% showed growth of **Myxomycetes** and 90% of these produced fruiting bodies. However, the temperate cultures produced **Myxomycetes** growth in only 70% of the cultures, with only 18% producing fruiting

bodies. The Costa Rica cultures similarly had 91 specimens appearing; the Arkansas cultures had only three species, representing three different genera. ***Diderma effusum*** (Figure 177) was the only species present in cultures from both locations. From Arkansas, only ***Diderma effusum*** (3 records) and ***Cribraria microcarpa*** (2 records; Figure 178) were present in at least two cultures. Interestingly, the most abundant species in Costa Rican cultures were ***Diderma effusum*** (16 records) and ***Cribraria violacea*** (16 records; Figure 45, Figure 179), as well as ***Perichaena dictyonema*** (16 records; Figure 180) and ***Gulielmina vermicularis*** (15 records; Figure 181-Figure 182). Furthermore, 44% of the 91 Costa Rican specimens were members of the genus ***Perichaena***/***Gulielmina***. However, many of these species occurred only once. Those cultures from Costa Rica had a mean of 2.3 specimens per culture; those from Arkansas had only 0.2 per culture.

Figure 176. ***Pilotrichella flexilis***, a spore trap for slime molds in Costa Rica. Photo by Claudio Delgadillo Moya, with permission.

Figure 177. ***Diderma effusum*** on rotting wood. Photo by Clive Shirley, Hidden Forest (hiddenforest.co.nz), with permission.

Figure 178. ***Cribraria microcarpa*** on log with mosses. Photo by Tyson Ehlers, through Creative Commons.

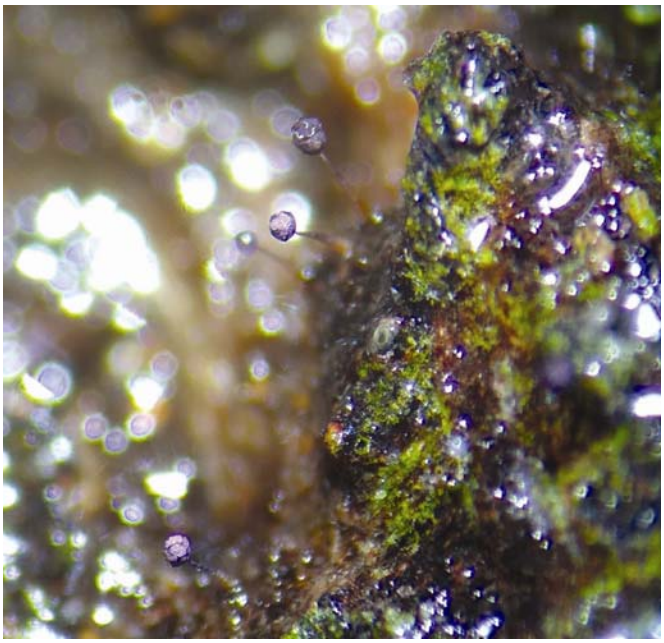

Figure 179. ***Cribraria violacea*** with mosses. Photo by Peta McDonald, through Creative Commons.

Figure 180. ***Perichaena dictyonema*** on rotting wood. Photo by Allison K. Pollack, through Creative Commons.

Figure 181. ***Gulielmina vermicularis*** transforming to its sporangial phase. Photo by Merlu, through Creative Commons.

Figure 182. ***Gulielmina vermicularis*** on rotting wood. Photo by Alejandro Huereca, through Creative Commons.

Differences in environmental factors may be responsible for the differences in species abundance between the two sites (Stephenson & Rojas 2020). The Arkansas site had a lower mean *p*H and was drier during the study period. Sporangia of **Myxomycetes** are more common in moist periods. There are insufficient data from the two regions to make a comparison of number of species present in the area. This study demonstrates the potential role of mosses as spore traps that increase the diversity of slime molds and remind us of the moss potential to serve a similar role for other kinds of organisms with small propagules.

Summary

Bark and logs are the two most common substrata for slime molds. And both of these substrates frequently have bryophytes on them. The motile slime molds therefore encounter bryophytes as they move about and may traverse them or stay and form sporangia. On logs in particular, leafy liverworts are common, and these seem to be suitable substrates for a number of slime molds. In some cases, the underlying algae might contribute to this association, providing fixed nitrogen or food.

Slime molds that move upward and into the light to produce sporangia may gain some advantage on the slightly elevated bryophytes. This positioning can provide greater access to dispersal agents, including wind and invertebrates. Nevertheless, the bryophytes used are of low stature, with **smooth mats** being the most frequent.

Diderma corrugatum seems to be restricted to moss-covered bark, whereas ***D. chondrioderma*** seems only to prefer it. Some of the slime molds seem to be confined to liverworts, including ***Barbeyella minutissima*** on logs, ***Licea bryophila*** on bark, and ***Licea gloederma*** on bark. ***Licea parasitica*** seems to prefer mosses in its **microcyst** stage. ***Colloderma oculatum***, ***Lamproderma columbinum***, and ***Lepidoderma tigrinum*** are common only associated with ***Barbeyella minutissima*** on bryophyte-covered logs, especially with the liverwort ***Nowellia curvifolia***. On the other hand, most of the bryophyte dwellers seem to be accidentals – generalists that tolerate the substrate with no preference for it. Others occur on mossy logs or bark, but not directly on the bryophytes.

In some cases, the slime mold seems to start on bark and invade the bryophyte. In other cases, it germinates on the bryophyte and moves onto the bark or wood. In the latter case, the bryophyte might benefit from the greater moisture in the bryophyte mat, in addition to the ability of the bryophyte to trap the spores.

Both of bark and logs have periods of drying out, especially tree boles. The slime molds and mosses are both tolerant of these events, but mosses are able to slow the drying process due to their capillary spaces. In addition to moisture, *p*H seems to be important in separating substrata among slime mold species. Decay stages are likewise important, with different stages providing different moisture levels, but also typically having more bryophytes as they decay more. Slime molds on logs with bryophytes are often also associated with algae and Cyanobacteria, especially ***Chroococcus tenax***, ***Aphanothece saxicola***, and ***Chlorococcum humicola***.

Bryophytes are important as spore traps for slime molds, but many questions remain regarding the importance of this relationship.

Acknowledgments

Marianne Meyer and Isabelle Charissou were very helpful in providing me with pictures of slime molds on mosses and Marianne helped me with identification of some images contributed by others. Harold W. Keller provided additional information and images to support the story on ***Diachea arboricola***. Steve Stephenson provided me with the paper on spore traps and helped me sort out the nomenclature.

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CHAPTER 3-4
SLIME MOLDS: ECOLOGY AND HABITATS – LESSER HABITATS

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SLIME MOLDS: ECOLOGY AND HABITATS – LESSER HABITATS

Figure 1. ***Lophocolea heterophylla*** with slime molds. Photo by Sture Hermansson, with online permission.

Epiphyllous Leafy Liverwort Associations

In the tropics, **epiphyllous** (growing on leaves) liverworts (Figure 2) are common, typically associated with lichens, fungi, algae, and bacteria. Mosses are rare in this association. But some associations also include slime molds.

Schnittler (2001) found eleven species of slime molds associated with epiphyllous liverworts (Figure 2) in Ecuador, Costa Rica, and Puerto Rico. He found 11 species, with 97% of the 131 cultures producing growths of slime molds. One of his finds, ***Arcyria afroalpina*** (Figure 3-Figure 4), was a new find for the Neotropics (Schnittler *et al*. 2002). When samples of 15 leaf pieces were cultured in moist chambers, the most frequent slime mold species (59-66%) were ***Arcyria cinerea*** (Figure 5), ***Didymium iridis*** (Figure 6), and ***D. squamulosum*** (Figure 7). These most likely occur with the epiphylls as myxamoebae. Lowland rainforests that have a high annual rainfall provide the greatest numbers of slime molds. However, the habitat appears to be less than ideal, as evidenced by the atypically small sporocarps.

Figure 2. ***Leptolejeunea epiphylla*** on leaf. Photo by Tom Thekathyil, with permission.

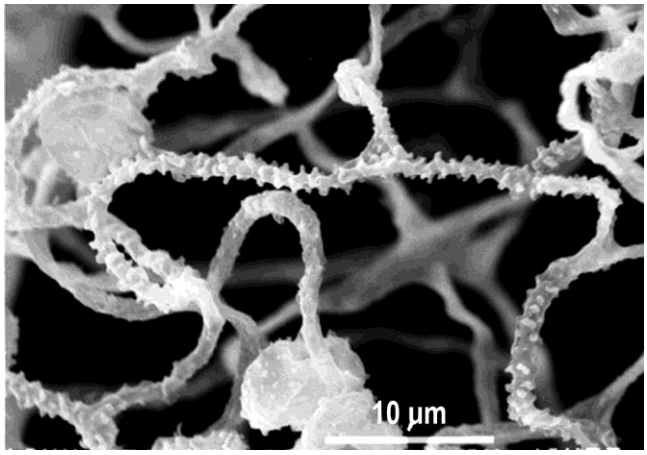

Figure 3. ***Arcyria afroalpina*** spores and capillitia. Photo by Yuri Novozhilov, Eumycetozoan Project, DiscoverLife.org, with online permission.

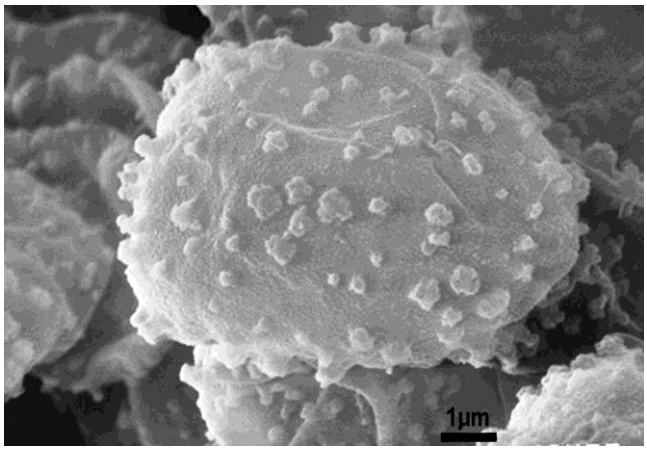

Figure 4. ***Arcyria afroalpina*** spore, SEM. Photo by Yuri Novozhilov, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 5. ***Arcyria cinerea***, one of the most frequent epiphyllous species of slime molds cultured from leaves with epiphyllous liverworts. Photo by Kim Fleming, through Creative Commons.

On the other hand, all six sites clearly share an assemblage of common species (Fig. 2) (Schnittler 2001). The average frequency of the three most common species on epiphyllous liverwort covers was surprisingly high, with 0.59 for ***Arcyria cinerea*** (Figure 5) and 0.66 for both ***Didymium iridis*** (Figure 6) and ***D. squamulosum*** (Figure 7). At least the three most common species of slime molds (***Arcyria cinerea***, ***Didymium iridis***, and ***D. squamulosum***) are very probably regular inhabitants of liverwort-covered leaves. Several lines of evidence seem to support this. First, all three species were found with very scattered and often solitary sporocarps considerably smaller than typical for fructifications of these species in other microhabitats. In addition, tiny **phaneroplasmodia** (conspicuous plasmodia, as in the **Physarales**; Figure 8), 1-3 mm in extent were frequently observed in the first two weeks of culture. Plasmodia migrating from the litter layer to fruit on living plants are much larger.

Figure 6. ***Didymium iridis*** sporangia, one of the most frequent epiphyllous species of slime molds cultured from leaves with epiphyllous liverworts. Photo through Creative Commons.

Figure 7. ***Didymium squamulosum***. Photo by John Shadwick, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 8. Phaneroplasmodium. Photo by Sarah Lloyd, with permission.

There is a potential for direct leaf-to-leaf dispersal of myxamoebae as well as their dormant stages (**microcysts**) by rainwater or leaf-dwelling insects (Schnittler 2001). Occasional cultures produce growths of ***Diderma effusum*** (Figure 9), ***D. hemisphaericum*** (Figure 10), ***Lamproderma scintillans*** (Figure 11), and ***Physarum compressum*** (Figure 12); all other recorded slime molds are rare. None of the slime molds found in this study seems to be specialized for living leaves as a microhabitat. The leaf microflora most likely supplies ample food for successful colonization. However, some differ sufficiently from non-epiphyllous populations that they might be separate races.

Figure 9. ***Diderma effusum*** on moss, a slime mold that occasionally occurs with epiphyllous liverworts. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 10. ***Diderma hemisphaericum***, a slime mold that occasionally occurs with epiphyllous liverworts. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 11. ***Lamproderma scintillans*** sporangia, a slime mold that occasionally occurs with epiphyllous liverworts. Photo by Ray Simons, The Eumycetozoa Project, DiscoverLive.com, with online permission.

Figure 12. ***Physarum compressum***, a slime mold that occasionally occurs with epiphyllous liverworts. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Camino *et al*. (2008) reported on the slime molds in the mountains of central Cuba. There they found two species associated with epiphyllous liverworts: ***Arcyria afroalpina*** (Figure 4-Figure 3) and ***Comatricha laxa*** (Figure 13).

Figure 13. ***Comatricha laxa*** sporangia on decaying log, a species known to also associate with epiphyllous leafy liverworts. Photo by Clive Shirley, The Hidden Forest, with permission.

Non-Epiphyllous Liverwort Associations

Stephenson and Studlar (1985) reported ***Arcyria cinerea*** (Figure 5), ***Physarum viride*** (Figure 14), ***Stemonitis axifera*** (Figure 15-Figure 16), ***Trichia decipiens*** (Figure 17), and ***T. favoginea*** (Figure 18) associated with non-epiphyllous leafy liverworts, but they were not restricted to this substrate. As already noted, ***Barbeyella minutissima*** (Figure 19) and ***Lepidoderma tigrinum*** (Figure 20) exhibited a preference for leafy liverworts on rotten conifer logs. In fact, the rare ***B. minutissima*** is mostly known from the leafy liverworts ***Nowellia curvifolia*** (Figure 19, Figure 21), ***Lepidozia reptans*** (Figure 22), and ***Cephalozia lunulifolia*** (Figure 23-Figure 24).

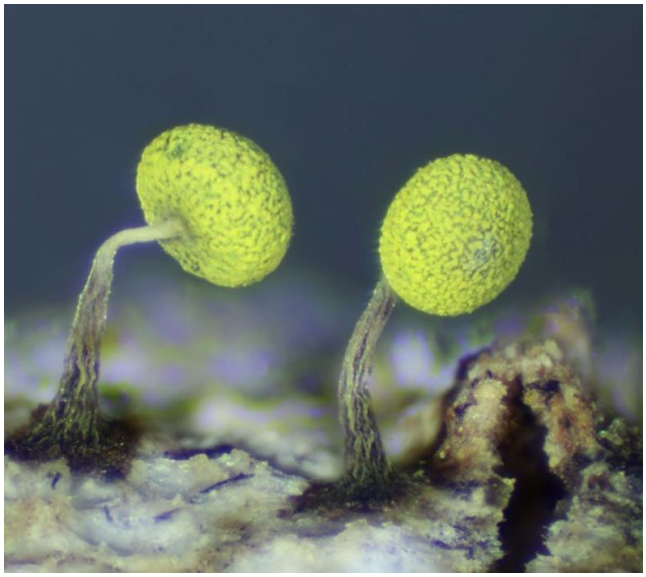

Figure 14. ***Physarum viride*** sporangia, a species that can be associated with leafy liverworts on logs and elsewhere. Photo by Sarah Lloyd, with permission.

Figure 15. ***Stemonitis axifera*** plasmodium starting to produce sporophytes, a species that can be associated with leafy liverworts on logs and elsewhere. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 16. ***Stemonitis axifera*** with liverworts, a species that can be associated with leafy liverworts on logs and elsewhere. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 17. ***Trichia decipiens*** sporangia, a species that can be associated with leafy liverworts on logs and elsewhere. Photo by Fungi07, through public domain.

Figure 18. ***Trichia favoginea*** on log with liverworts. Photo by Jerry Cooper, through Creative Commons.

Figure 19. ***Barbeyella minutissima*** sporangia on the leafy liverwort ***Nowellia curvifolia***. Photo by Randy Darrah, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 20. ***Lepidoderma tigrinum*** with sporangia on moss, a species that is more common on leafy liverworts. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 21. ***Nowellia curvifolia*** on log, a suitable substrate for a number of species of slime molds. Photo by Bernd Haynold, through Creative Commons.

Figure 22. The liverwort ***Lepidozia reptans***. Photo by Michael Lüth, with permission.

Figure 23. ***Cephalozia lunulifolia***, a suitable substrate for a number of species of slime molds. Photo by Michael Lüth, with permission.

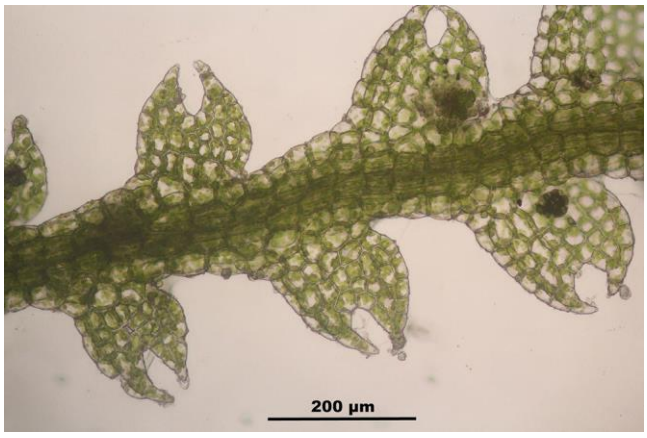

Figure 24. ***Cephalozia lunulifolia***, a suitable substrate for a number of species of slime molds. Photo by Hermann Schachner, through Creative Commons.

Nowellia curvifolia (Figure 19, Figure 21) is the most common slime mold associate (Stephenson & Studlar 1985); it is a liverwort found almost exclusively on rotten logs (Schuster 1957). Hence, the preference in the rotting log habitat for leafy liverworts may simply be that leafy

liverworts are common on rotting logs. The mosses ***Tetraphis pellucida*** (Figure 25) and ***Dicranum montanum*** (Figure 26-Figure 27) are also common associates of slime molds, and likewise are characteristic of rotting wood (Stephenson & Studlar 1985). It is likely that the slime molds are opportunists or simply have broad enough habitat requirements to permit their survival **on** the potentially competing bryophytes.

Figure 25. ***Tetraphis pellucida*** with gemmae, a common rotten wood moss. Photo by Hermann Schachner through Creative Commons.

Figure 26. ***Dicranum montanum***, a suitable substrate for some slime molds, on rotting log. Photo by Janice Glime.

Figure 27. ***Dicranum montanum*** showing the curly leaves when dry. Photo by Janice Glime.

Leaf Litter

Some moss dwellers are also litter slime molds. Compagno *et al*. (2016) reported ***Didymium melanospermum*** (Figure 28) on mosses or litter. Moreno *et al*. (2018) found ***Didymium nigripes*** (Figure 29) on moss debris in Spain. Doidge (1950) reported ***Diderma subdictyospermum*** on moss and dead leaves. Similarly, Ranade *et al.* (2012) reported ***Diderma alpinospumarioides*** on dead leaves and twigs, but sometimes on living moss in India. Renade and coworkers found that ***Physarum melleum*** (Figure 30) occurs on dead leaves as well as among living mosses. Sarah Lodge photographed ***Collaria aff. rubens*** (Figure 31) on mosses; this is a species that typically is associated on deciduous leaf litter (Takahashi 2015).

Figure 28. ***Didymium melanospermum*** on leaves of a soil moss (**Mniaceae**). Photo by Armand Turpel, through Creative Commons.

Figure 29. ***Didymium nigripes*** sporangia, a species known from moss debris. Photo by Christophe Quintin, with online permission.

Figure 30. ***Physarum melleum*** sporangia, a species of dead leaves and living mosses. Photo by Clive Shirley, The Hidden Forest, with permission.

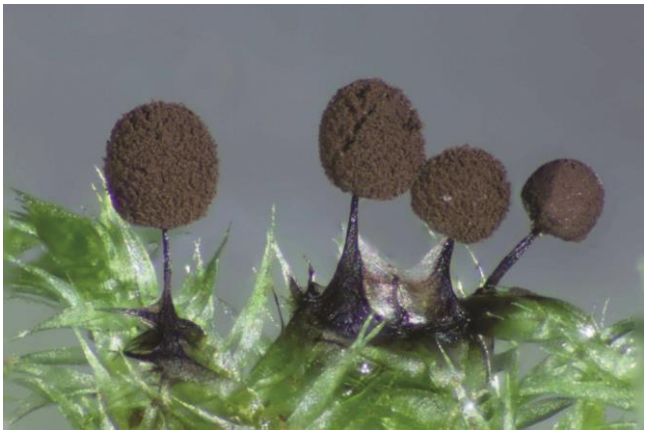

Figure 31. ***Collaria aff. rubens*** on mosses, a species associated with leaf litter. Photo by Sarah Lloyd, with permission.

Soil Associations

Soil associations between bryophytes and slime molds seem to be much less common than associations in other habitats. In temperate forests, mosses of **Polytrichaceae** (Figure 32, Figure 36), **Dicranaceae** (Figure 33-Figure 34), and **Hypnaceae** (Figure 35) are common, with the slime molds ***Fuligo muscorum*** (Figure 36), ***Physarum citrinum***, ***P. confertum*** (Figure 37), and ***P. virescens*** (Figure 38-Figure 39) occasionally occurring on them (Ing 1994). One very rare slime mold (***Elaeomyxa cerifera*** – Figure 40-Figure 41) is known from the soil-dwelling thallose liverwort ***Pellia epiphylla*** (Figure 42) (Hadden 1921; Ing 1994) and from decaying wood, usually in association with bryophytes (Steven Stephenson, pers. comm. 1 June 2019).

Figure 32. ***Polytrichum*** sp. on the forest floor, habitat for ***Fuligo muscorum*** and several species of ***Physarum***. Photo by Janice Glime.

Figure 33. ***Dicranum scoparium*** on the forest floor, habitat for ***Fuligo muscorum*** and several species of ***Physarum***. Photo by Janice Glime.

Figure 34. ***Dicranum scoparium***, habitat for ***Fuligo muscorum*** and several species of ***Physarum***. Photo by Janice Glime.

Figure 35. ***Hypnum curvifolium***, a species of the forest floor and logs and a common substrate for moss-dwelling slime molds. Photo by Bob Klips, through Creative Commons.

Figure 36. ***Fuligo muscorum*** on **Polytrichaceae**. Photo by James K. Lindsey, with permission.

Figure 37. ***Physarum confertum***, a slime mold species that occurs on forest mosses in the families **Polytrichaceae**, **Dicranaceae**, and **Hypnaceae**. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 38. ***Physarum virescens*** in early fruiting stage on moss. Photo by Alexey Sergeev, with permission.

Figure 39. ***Physarum virescens*** on the moss ***Dicranum***. Photo by Alexey Sergeev, with permission.

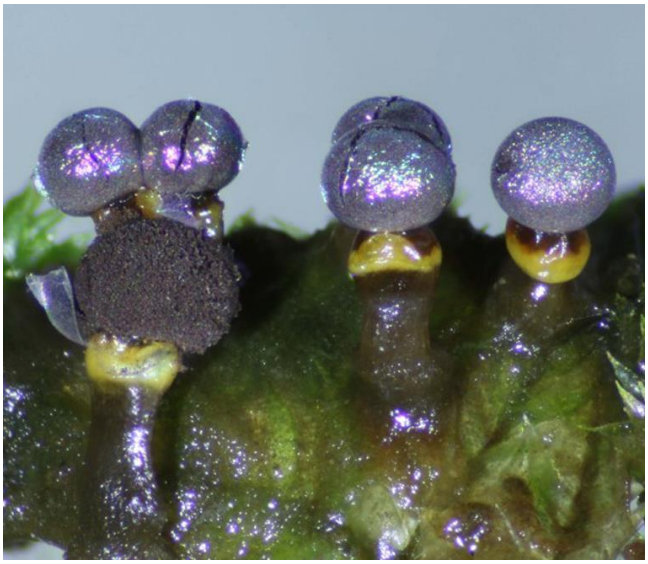

Figure 40. ***Elaeomyxa cerifera*** with sporangia on mosses. Photo by Sarah Lloyd, with permission.

Figure 41. ***Elaeomyxa cerifera*** sporangium beginning to dehisce. Photo from Myxotropic.org, through Creative Commons.

Figure 42. ***Pellia epiphylla*** with capsules, substrate for ***Elaeomyxa cerifera***. Photo by Li Zhang, with permission.

Pant and Tewari (1982) described the growth of ***Fuligo intermedia*** (Figure 43) on mosses in Nainital in the Himalayan region of India. These slime molds occurred on the mosses ***Atrichum obtusulum***, ***Pogonatum aloides*** (Figure 44), ***Barbula*** sp. (Figure 45), and ***Leucodon secundus***. Only the green tips of the mosses appeared above the yellowish-white of the ***Fuligo intermedia*** (Figure 43). They suspected that the growth of the mosses was retarded. A related species, ***Fuligo cinerea*** (Figure 46-Figure 47) occurs on dead leaves, yeast, and rotten cloth pieces, as well as on mosses and lichens.

Figure 43. ***Fuligo intermedia*** on ***Polytrichum***. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 44. ***Pogonatum aloides*** (**Polytrichaceae**), one of the substrates for the slime mold ***Fuligo intermedia***. Photo by Hermann Schachner, through Creative Commons.

Figure 45. ***Barbula convoluta***; the genus ***Barbula*** is one of the substrates for the slime mold ***Fuligo intermedia***. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman and Karen Blisard.

Figure 46. ***Fuligo cinerea*** on lichens and leafy liverworts on bark. Photo by Alexey Sergeev, with permission.

Figure 47. ***Fuligo cinerea*** on a mossy forest floor. Photo by Ramsés Pérez, through Creative Commons.

It is not unusual to find that species cannot be put into their proper substrate heading when using the descriptions. This is not necessarily the fault of the author. Information is often based on herbarium labels and material present with the specimen, but not seen in the field by the author(s). ***Physarum citrinum*** occurs on terrestrial mosses in woodlands, but were the mosses on soil (Ing 1982)? Later, Ing (1994) reported this species from soil. Ing (1982) was able to be more specific in reporting ***Physarum virescens*** (Figure 38-Figure 39) as mostly on terrestrial mosses in woodlands and characteristic of sessile oakwoods, a species that elsewhere is also almost always associated with bryophytes (Steven Stephenson, pers. comm, 1 June 2019). In Spain, ***Physarum bivalve*** (Figure 49) occurs on mosses (Castillo *et al*. 2009), but in what habitat?

Figure 48. ***Typhula lutescens*** with sporangia on mosses. Photo by Tomasz Pachlewski, with permission.

Figure 49. ***Physarum bivalve***, a species known from mosses in Spain. Photo by Rod Nelson, DiscoverLife.org, with online permission.

Schnittler and Novozhilov (1996) described several slime mold-bryophyte associations that appear to be on soil in their study of the northern Karelia of Russia. One they noted as a very scanty collection of ***Physarum*** *cf.* ***carneum*** on mosses. They were more specific in noting ***Physarum virescens*** (Figure 38-Figure 39) as preferring big moss tussocks on the ground, especially ***Dicranum*** (Figure 103). ***Stemonitis fusca*** (Figure 50) was represented by a single collection on moss tussocks in a spruce-birch-aspen woodland. ***Didymium melanospermum*** (Figure 28) typically occurs on thick moss tussocks on soil, but it also occurs at the base of rocks, or even more rarely on litter.

Similarly, ***Leocarpus fragilis*** (Figure 51-Figure 52) can grow on the ground, on mosses, and on litter, but it can only be located in autumn.

Figure 50. ***Stemonitis fusca*** with sclerotia and sporangia on mosses. Photo by Deryni, through Creative Commons.

Figure 51. ***Leocarpus fragilis*** on moss. Photo by Matt Goff, Sitka Nature, with permission.

Figure 52. ***Leocarpus fragilis*** on a soil moss in the **Polytrichaceae**. Photo by Boris Loboda, with permission.

Ranade *et al*. (2012) reported several species that are likely to be associated with soil or litter. ***Cribraria intricata*** (Figure 53; syn.=*C. dictydioides*) occurs not only on rotten wood, but also on roots and dead mosses. ***Cribraria languescens*** (Figure 54-Figure 55) occurs on rotten stems and mosses, presumably on the ground. They reported that ***Physarum didermoides*** (Figure 56; syn.=*Diderma spumarioides*) occurs on living moss, presumably on soil mosses. ***Collaria arcyrionema*** (Figure 57; syn.=*Lamproderma arcyrionema*) occurs not only on wood, but also on dead leaves and mosses. ***Lamproderma echinulatum*** (Figure 58) and ***Metatrichia floriformis*** (Figure 59; syn.=*Trichia floriformis*) likewise occur on mosses, presumably on the forest floor. ***Physarum brunneolum*** (Figure 60) occurs not only on mosses, but also on lichens and decaying wood; again, the substrate of the mosses and lichens is not provided. The most unusual substrate is that of ***Stemonitis flavogenita*** (Figure 61) on a dead archegoniophore of the thallose liverwort ***Marchantia*** sp. (Figure 62), presumably with the latter growing on soil.

Figure 53. ***Cribraria intricata*** sporangia on bark with a few mosses. Photo by Fluff Berger, through Creative Commons.

Figure 54. ***Cribraria languescens***, a species that occurs on rotten wood, roots, and dead mosses. Photo from Myxotropic, through Creative Commons.

Figure 55. ***Cribraria languescens*** sporangium. Photo from Myxotropic, through Creative Commons.

Figure 56. ***Physarum didermoides*** on mosses. Photo by Andrew Khitsun, with online permission.

Figure 57. ***Collaria arcyrionema***, a species that occurs on dead wood and mosses. Photo by Taibif.tw, through Creative Commons.

Figure 58. ***Lamproderma echinulatum*** sporangia on bryophytes. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 59. ***Metatrichia floriformis*** with mosses on bank. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 60. ***Physarum brunneolum***, a species of mosses, lichens, and decaying wood. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 61. ***Stemonitis flavogenita***, a species that has been found on a dead archegoniophore of ***Marchantia***. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 62. ***Marchantia polymorpha*** archegoniophores, one of the substrates for ***Stemonitis flavogenita***. Photo by Janice Glime.

Figure 63. ***Diachea leucopodia*** on leaf litter, a species that also occurs on mosses. Photo by Rosser1954, through Creative Commons.

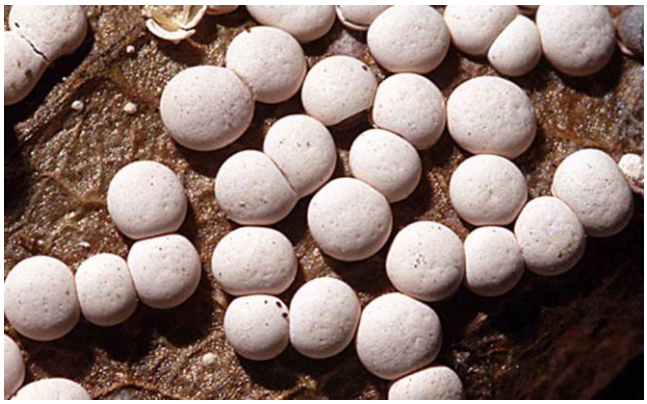

Figure 64. ***Diderma testaceum*** on leaf litter, a species that also occurs on mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Joshaghani *et al*. (2013) reported ***Badhamia ovispora*** as occurring on forest mosses in Iran. This suggests that they grew on soil mosses as the other records were more specific in referring to wood or rotten wood.

Stojanowska and Panek (2004) were specific about a number of species of slime molds that occurred on mosses on logs or stumps, but they reported some simply from mosses. Presumably, these were forest floor mosses, including ***Diachea leucopodia*** (Figure 63), ***Diderma testaceum*** (Figure 64), and ***Physarum virescens*** (Figure 38-Figure 39) (plasmodial stage). They described ***Diderma deplanatum*** (Figure 65) as surrounding mosses. ***Lamproderma columbinum*** (Figure 66) occurred on the moss ***Tetraphis pellucida*** (a species of rocks and decaying wood; Figure 25), but also on the moss ***Dicranum scoparium*** (Figure 33-Figure 34) – a moss that could occur on soil, rocks, logs, or tree bases.

Figure 65. ***Diderma deplanatum*** on mosses. Photo by The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 66. ***Lamproderma columbinum***, with fruiting bodies of slime mold on bryophytes. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Rock Associations

Among the earliest moss-slime mold associations reported is that of Kaiser (1913). Brown capsules of the slime mold ***Leocarpus fragilis*** (Figure 51) occurred on the moss ***Dicranum fulvum*** (Figure 67) in the southern Catskill Mountains of New York. The substrate was not reported, but this moss commonly occurs on sandstone rocks (Seltzer & Wistendahl 1971). The slime mold is not bryophilous, being common on dead leaves (Kaiser 1913).

Figure 67. ***Dicranum fulvum***, sometimes a substrate for the slime mold ***Leocarpus fragilis***. Photo by Bob Klips, with permission.

Schnittler and Novozhilov (1996) reported on a number of slime molds using bryophytes as a substrate in the northern Karelia of Russia. One of the most common species, ***Physarum album*** (Figure 68) appears to be a generalist and includes moss tussocks on rocks among its substrata. ***Physarum viride*** (Figure 14) likewise accepts a number of substrata, including moss and liverwort layers of rocks, where "it prefers medium-wet places between the pure slimy algae layers and the big moss tussocks."

Figure 68. ***Physarum album*** sporangia on decaying wood, a generalist that also occurs on mosses. Photo by George Shepherd, through Creative Commons.

On granite rocks Schnittler and Novozhilov (1996) found two subassociations of slime molds. One prefers the thicker tussocks (> 0.5 cm), especially the mosses ***Sanionia uncinata*** (Figure 69), ***Dicranum fuscescens*** (Figure 70), and ***Cynodontium strumiferum*** (Figure 71). These tussocks have dry leaf tips, but the tussocks have a wet interior and are enriched with small particles of detritus. The slime molds ***Lamproderma columbinum*** (Figure 66), ***L. sauteri*** (Figure 72), and ***Didymium melanospermum*** (Figure 28) fruit here, the latter often at the bases of the rocks. The second sub-association occurs in thin water films and will be discussed below under the Wet Habitat Associations.

Figure 69. ***Sanionia uncinata***, a species forming thick mats with dry tips but moist interiors and collections of detritus. It serves as substrate for the slime molds ***Lamproderma columbinum***, ***L. sauteri***, and ***Didymium melanospermum***. Photo by Hermann Schachner, through Creative Commons.

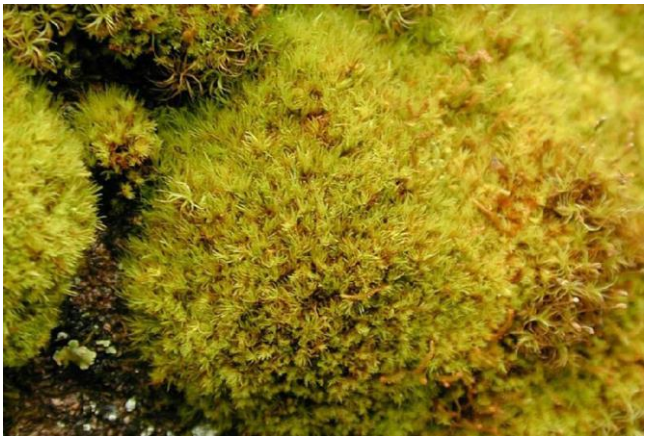

Figure 70. ***Dicranum fuscescens***, a rock-dwelling moss that serves as substrate for the slime molds ***Lamproderma columbinum***, ***L. sauteri***, and ***Didymium melanospermum***. Photo by Michael Lüth, with permission.

Figure 71. ***Cynodontium polycarpon*** with capsules, a rock-dwelling moss that serves as substrate for the slime molds ***Lamproderma columbinum***, ***L. sauteri***, and ***Didymium melanospermum***. Photo by Štěpán Koval, with permission.

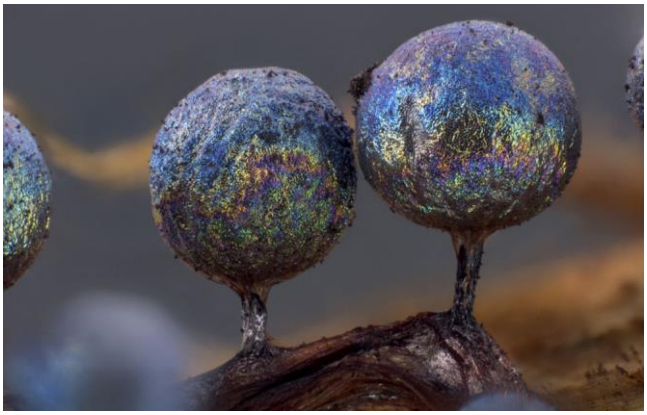

Figure 72. ***Lamproderma sauteri*** sporangia that can occur on moss-covered rocks. Photo by The Eumycetozoan Project, DiscoverLife.org, with online permission.

Diderma lucidum seems to be restricted to mossy rocks (Brooks *et al*. 1977).

Few studies seem to have included the rock habitat. Schnittler and Novozhilov (1996), studying the boreal woodlands of northern Karelia in Russia, have contributed a number of records of slime molds that seemingly are able to live on rocks by using bryophytes as their immediate substrate. ***Lamproderma columbinum*** (Figure 66) occurred almost exclusively on moss-covered rocks, where it was often accompanied by ***L. sauteri*** (Figure 72) and ***Colloderma oculatum*** (Figure 73), but preferring drier and thicker moss tussocks than the substrate preferred by these two slime molds. ***Lamproderma columbinum*** forms large and conspicuous colonies on thick moss beds on rocks (as well as on moss-covered logs). ***Lepidoderma tigrinum*** (Figure 20) fruits in autumn after the first frosts and snowfalls, when it is visible in a rock association of very wet, thin liverwort and algae mats. In summer the plasmodia are visible.

Figure 73. ***Colloderma oculatum*** on bryophytes. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Sand Dunes

Sand dunes are inhospitable habitats for both bryophytes and slime molds. But where there is a niche, some bryophyte will usually fill it. Hence, the slime mold ***Physarum didermoides*** (Figure 56; syn.=*Diderma spumarioides*) is common in sand dunes and often forms "plaques of sporangia up to a square meter" on carpets of the moss ***Syntrichia ruralis*** (Ing 1994).

Alpine and Polar

When investigating the alpine and Arctic/Antarctic areas, researchers have often been surprised at the low diversity of slime molds. They are both less abundant and exhibit fewer species than in other areas, but some rarer species elsewhere can be present more commonly in the Arctic (Stephenson *et al*. 2000).

Although the cold regions do not appear to be friendly toward slime molds, the most bryophyte-exclusive (perhaps leafy liverwort-exclusive) slime mold, ***Barbeyella minutissima*** (Figure 19) is a common alpine slime mold (Kowalski & Hinchee 1972). Similarly, Kowalski (1972) found that in the mountains of Washington, USA, ***Licea***

hepatica seems to be restricted to leafy liverworts, a species that seems to be unknown from other substrata (Steven Stephenson, pers. comm. 1 June 2019).

This may cause us to be hopeful of special bryophyte associations high in the mountains, but beyond these two limited cases, that does not appear to be the case.

Elaeomyxa australiensis (Figure 74) is known from an alpine snowbank habitat in Australia (Moreno *et al*. 2009; Stephenson & Shadwick 2009). There it grows on litter in association with bryophytes, with only 3 collections out of 300 actually occurring on bryophytes (Stephenson & Shadwick 2009). In these Australian alpine areas, ***Meriderma cribrarioides*** (reported as ***Lamproderma atrosporum***; Figure 75) also occurs on bryophytes.

Figure 74. ***Elaeomyxa*** *cf.* ***australiensis***, an alpine snowbank species that grows with litter in association with bryophytes. Photo by Sarah Lloyd, with permission.

Figure 75. ***Meriderma cribrarioides*** sporangium, a species that sometimes occurs on bryophytes in alpine areas of Australia. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Stephenson *et al*. (2000) set out to determine what factors limit slime mold distribution in high-latitude and cold-dominated regions in the Northern Hemisphere. They collected 938 specimens and cultured 1453 substrate samples from 12 study areas in Iceland, northern Russia, Alaska, and Greenland. They identified 150 species, with 33 being widely distributed in at least five study areas. With only 41 species having a frequency greater than 1%, most of the species seemed to have only limited distribution or low frequency. Although the Arctic species seem to have a depauperate representation of species known from the temperate region, as already noted, some species that are considered rare in temperate areas are common in the Arctic, supporting the conclusion that the Arctic slime mold communities are different from those in temperate regions.

Novozhilov *et al*. (1999) reported 56 species of slime molds from the Taimyr Peninsula in north-central Siberia. Among these, only two species apparently were found ever associated with bryophytes. ***Didymium melanospermum*** (Figure 28) typically occurs on mossy coarse woody debris. ***Mucilago crustacea*** (Figure 76) is even less associated, occurring in a moss- and grass-rich, open patch of the forest tundra. It is notable that slime mold species numbers decrease progressively from the northern taiga, northward to the tundra subzone. This study supports the contention that the tundra is represented by an impoverished flora from the northern taiga subzone.

Figure 76. ***Mucilago crustacea***, a species that occurs in moss-rich habitats in the forest tundra. Photo by Alexey Sergeev, with permission.

Stephenson *et al*. (1991) expressed their disappointment at the small number of species they were able to find on the soils of the Alaskan tundra. After collecting from nine different study sites, their cultures yielded only ***Dictyostelium mucoroides*** (Figure 77; **Dictyosteliomycetes**) and ***D. sphaerocephalum*** (Figure 78). The total number of slime mold colonies per gram of wet soil averaged more than 100 for all samples and was more than 200 at three of the four Arctic tundra sites. These values are similar to those they found for forest soils in two spruce study sites of interior Alaska.

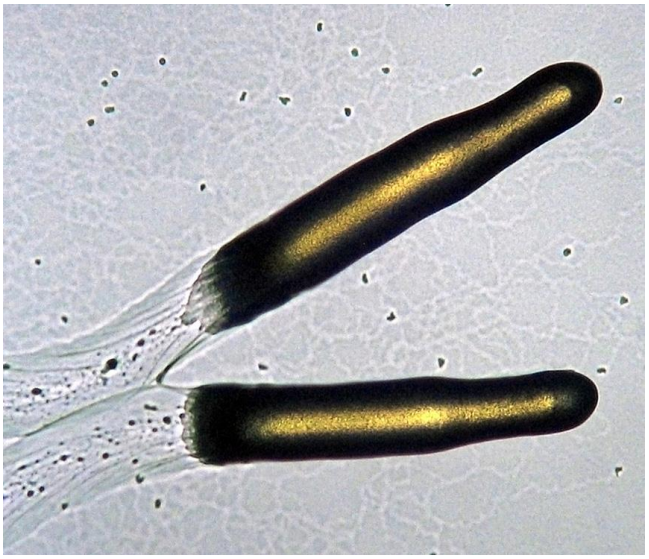

Figure 77. ***Dictyostelium mucoroides*** (**Dictyosteliomycetes**) plasmodial slug, a tundra species. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

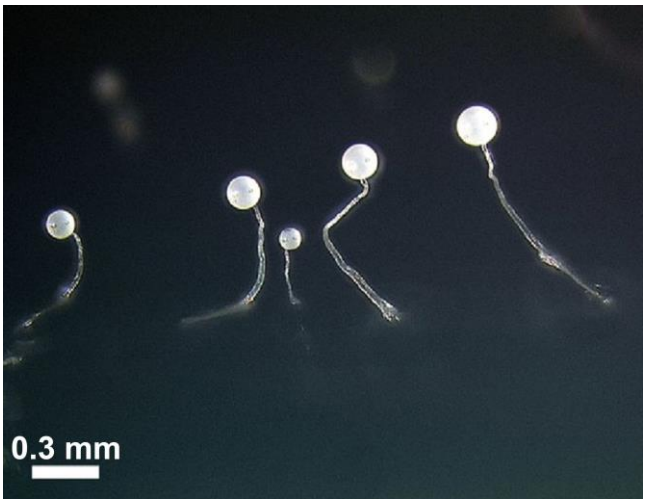

Figure 78. ***Dictyostelium sphaerocephalum*** fruiting body, sometimes the only slime mold present in the Alaskan tundra. Photo by Andy Swanson, with permission, image provided by Steve Stephenson.

The report from Stephenson *et al*. (1991) is similar to that of Benson and Mahoney (1977). But the latter authors considered ***Dictyostelium mucoroides*** (Figure 77) to be conspecific with ***D. sphaerocephalum*** (Figure 78). They found the latter inclusive species to be dominant above 1700 m in Southern California.

Cavender conducted a number of studies in Arctic and high altitude locations. He found a new Alaskan tundra species of ***Dictyostelium***, ***D. septentrionale***, along with ***D. mucoroides*** (Figure 77), ***D. sphaerocephalum*** (Figure 78), and ***D. giganteum*** in that tundra habitat (Cavender 1978). He considered ***D. sphaerocephalum*** and ***D. mucoroides*** to have sufficiently large populations to play a role in tundra ecology. When Cavender (1983) sampled slime molds in the Rocky Mountains, USA, he found that the soil slime molds were 29.5% ***Dictyostelium sphaerocephalum*** and 68% ***D. mucoroides*** when appearing in cultures. Cavender (1980, 1983) concluded that the altitudinal distribution of slime molds is similar to that of latitude. In the Appalachian Mountains, eastern USA, Cavender (1980) found that the dictyostelid slime molds predominate, with 15 species. The greatest ***Dictyostelium*** richness occurred at 590 - 820 m.

Landolt *et al*. (1992) found ***Dictyostelium mucoroides*** (Figure 77) and ***D. sphaerocephalum*** (Figure 78) to be overwhelmingly dominant in the Kantishna Hills of Denali National Park (formerly Mt. McKinley), Alaska, USA, with the number of clones per gram of wet soil ranging 0-1203. Some of these sites were restoration sites; the natural sites had far greater slime mold density. The mean number of clones per gram of wet soil was 259 clones for the 14 study sites, with the seven natural sites having a mean of 430. ***Dictyostelium mucoroides*** was the dominant species (59-98%) in the natural sites. In the restoration sites, ***D. sphaerocephalum*** was dominant (50-100% of all clones) in the six restoration study plots where slime molds were found.

But none of the preceding studies reported any ***Dictyostelium*** species on bryophytes.

Emphasizing the paucity of species in these cold habitats, Kanda and Sato (1982) were unable to find any cellular slime molds in the alpine tundra of Mt. O-Akan, Hokkaido, Japan. Hence, we should not be surprised that most of these polar and alpine studies did not report any slime molds growing on bryophytes.

In the Carpathians of Poland, other species emerge as nivicolous species (Ronikier *et al*. 2008). These include 18 species, of which 10 are reported for the first time in Poland. ***Diderma niveum*** (Figure 79), ***Lepidoderma chailletii*** (Figure 80), and ***Lamproderma ovoideum*** (Figure 81) are very abundant, particularly in the spring in glades and shrub communities. ***Diderma alpinum*** (Figure 82) and ***D. niveum*** occur on mosses.

Figure 79. ***Diderma cf. niveum*** sporangia on mosses. Photo by Tom Thekathyil, with permission.

Figure 80. ***Lepidoderma chailletii*** sporangia. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

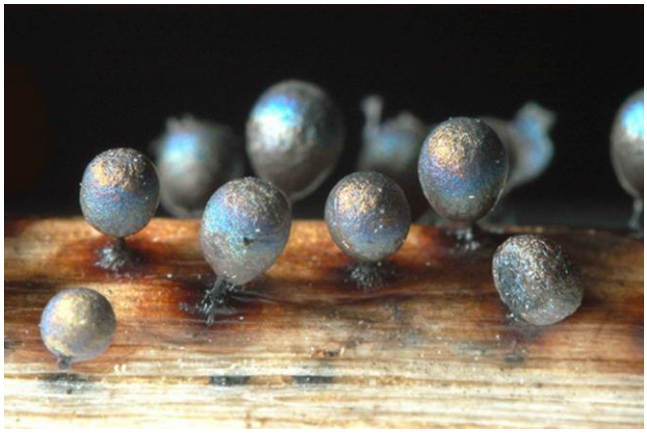

Figure 81. ***Lamproderma ovoideum*** sporangia. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 82. ***Diderma alpinum*** sporangia, a species that occurs on mosses in the Carpathian Mountains. Photo by The Eumycetozoan Project, DiscoverLife.org, with online permission.

Stephenson *et al*. (1992) noted the paucity of reports of slime molds from Antarctica and the subAntarctic islands. Several genera occurring there are known from bryophytes elsewhere, but many of the Antarctic species are different. ***Diderma effusum*** (Figure 9) is known from mosses in the Antarctic (unpublished record from Steven Stephenson, pers. comm. 1 June 2019).

Lepidoderma crustaceum (Figure 83) is among the bryophyte dwellers found on the subAntarctic Macquarie Island in the Antarctic region (Stephenson *et al*. 2007a). ***Lamproderma ovoideum*** (Figure 84) similarly occurs on the leafy liverwort ***Lepidozia*** sp. (Figure 22) on Macquarie Island (Stephenson *et al*. 1992). But most of the species in the Antarctic region are **niveal** (subject to actions of snow and ice) species, and their fruiting is associated with winter snow packs. ***Lamproderma ovoideum*** is typical of such habitats in alpine areas. Whereas only 6 slime mold species were known in 1990 from the Antarctic region, 32 were known from Iceland and 54 from Greenland (Gøtzsche 1989, 1990). In an intensive study, Stephenson *et al*. (2007b) located 22 species on Macquarie Island.

Figure 83. ***Lepidoderma crustaceum*** sporangia, one of the bryophyte dwellers on Macquarie Island. Photo from Myxotropic, through Creative Commons.

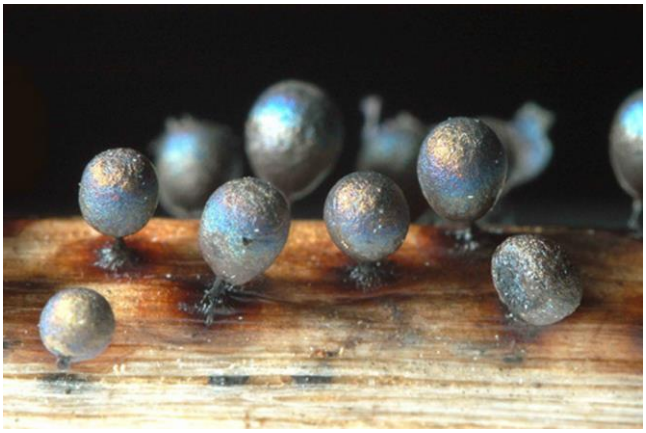

Figure 84. ***Lamproderma ovoideum*** sporangia, a late snowmelt species in alpine areas, sometimes occurring on bryophytes. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Stephenson *et al*. (2007b) reported a more diverse slime mold fauna on Macquarie Island, including several that occurred on bryophytes. These bryophyte dwellers included 6 of 80 collections of ***Trichia verrucosa*** (Figure 85), 1 of 78 of ***Diderma alpinum*** (Figure 86-Figure 87), 2 of 59 of ***Craterium leucocephalum*** (Figure 88), 2 of 48 ***Didymium cf. dubium*** (Figure 89-Figure 90), 7 of 15 ***Lamproderma arcyrioides*** (Figure 91-Figure 92), and 13 of 68 of all other species. ***Diderma radiatum*** (Figure 93-

Figure 94) had a higher ratio, but poor representation, with 1 of the 3 collections being on bryophytes. ***Lamproderma ovoideum*** (Figure 84) is considered **nivicolous** (associated with snow), but the only collection of this species was on bryophytes. ***Lepidoderma crustaceum*** (Figure 84) also was reported from bryophytes. The most common bryophytes serving as slime mold substrates on Macquarie Island are the mosses ***Brachythecium salebrosum*** (Figure 95), ***Achrophyllum dentatum*** (Figure 96-Figure 97), and the leafy liverwort ***Lophocolea bidentata*** (Figure 98).

Figure 85. ***Trichia verrucosa*** mature and dispersing sporangia, a Macquarie Island slime mold that occasionally fruits on bryophytes. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 86. ***Diderma alpinum*** sporangia, a Macquarie Island slime mold that occasionally fruits on bryophytes. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

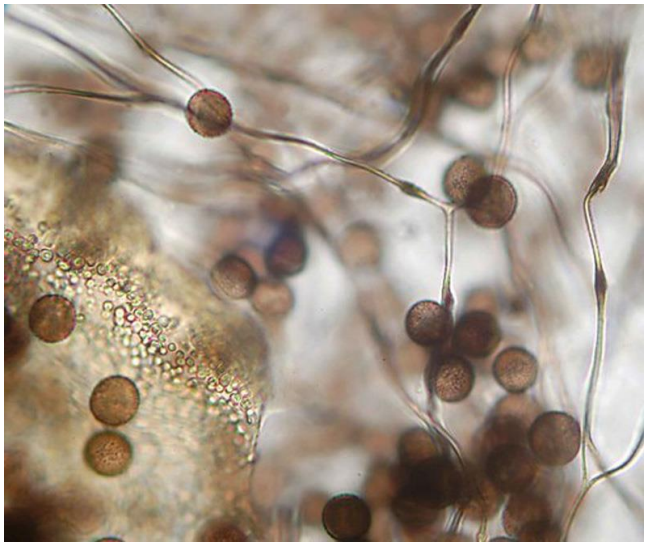

Figure 87. ***Diderma alpinum*** spores and capillitium. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 88. ***Craterium leucocephalum***, a slime mold that occasionally appears on bryophytes on Macquarie Island in the Antarctic. Photo by Clive Shirley, the Hidden Forest, with permission.

Figure 89. ***Didymium dubium*** on leaf litter, a species that can also occur on bryophytes on Macquarie Island. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

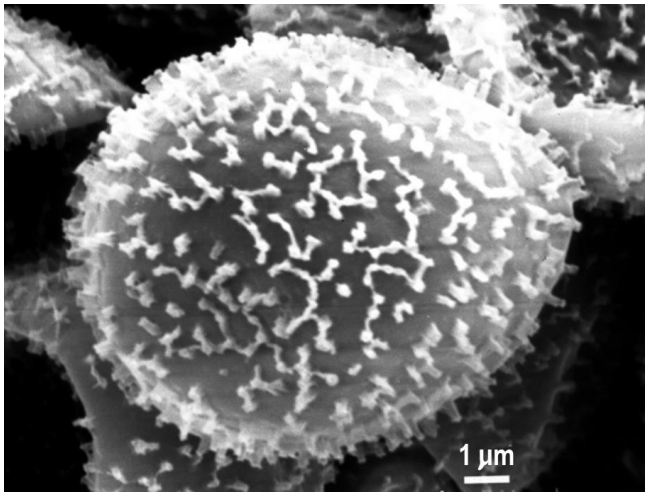

Figure 90. ***Didymium dubium*** spore SEM. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 93. ***Diderma radiatum*** sporangia with mosses on decaying wood, a slime mold that occasionally appears on bryophytes on Macquarie Island in the Antarctic. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 91. ***Lamproderma arcyrioides*** sporangia with moss, sometimes a bryophyte inhabitant on Macquarie Island. Photo by James K. Lindsey, with permission.

Figure 94. ***Diderma radiatum*** after the capsules dehisce. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 92. ***Lamproderma arcyrioides*** mature sporangia. Photo by Randy Darrah, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 95. ***Brachythecium salebrosum***, one of the preferred bryophyte substrates for slime molds on Macquarie Island. Photo by Michael Lüth, with permission.

Figure 96. ***Achrophyllum dentatum***, one of the preferred bryophyte substrates for slime molds on Macquarie Island. Photo by David Tng, through Creative Commons.

Figure 97. ***Achrophyllum dentatum*** with leaf gemmae. Photo by Des Callaghan, through Creative Commons.

Figure 98. ***Lophocolea bidentata***, one of the preferred bryophyte substrates for slime molds on Macquarie Island. Photo by Hermann Schachner, through Creative Commons.

Wet-Habitat Associations

Lindley *et al*. (2007) remarked on the paucity of information on slime molds in aquatic habitats. They found that the distributions of slime molds above and below the water level were different.

Ravines

Krziemiewska (1934) reported ***Colloderma oculatum*** (Figure 73; as *C. dubium*) from wet wood covered with mosses and liverworts in her study in the Zarocelak forest, eastern Carpathians. But studies that concentrate on ravine slime molds are still very limited.

One reason for the lack of study in this interesting habitat is that they can only be identified during their fruiting season. In most habitats, bark and other substrate samples can be taken to the lab and cultured. But Novozhilov *et al*. (2000) lamented the difficulty of culturing the slime molds that prefer the trickling water of humid ravines. This lack of success forces researchers to be in the field when the slime molds are producing sporangia, noting that this is predominately in the late autumn, a time when most slime mold specialists, who are also academicians, are busy with their educational responsibilities. With all this difficulty in being at the right place at the right time, Novozhilov and coworkers estimate that less than 5% of the species occur in such habitats.

Whereas most of the slime molds seem to prefer rotting logs, some prefer more moist or even wet habitats. One reason for this may be the associated algae that can serve as a food source. Ing (1994) noticed that algae were typically abundant in association with the mats of bryophytes that served as substrate for slime mold fruiting bodies in cool, moist ravines of the western British Isles (Ing 1983). In another European study, Schnittler and Novozhilov (1998) reported the slime molds ***Colloderma oculatum*** (Figure 73) fruiting on wet, moss-covered rock surfaces that presented a continuous layer of algae.

Craterium muscorum (Figure 99; syn.=*Badhamia rubiginosa* var. *globosa*) and ***Diderma lucidum*** are rare Atlantic species that can be found on moss-covered rocks in wooded ravines (Ing 1982). ***Lamproderma columbinum*** (Figure 66) and ***Lepidoderma tigrinum*** (Figure 20), both species noted elsewhere from bryophytes, are characteristic of ravines. ***Fuligo muscorum*** (Figure 100) occurs in wet, terrestrial mossy habitats.

Figure 99. ***Craterium muscorum*** sporangia on mosses, a species that occurs in wet, terrestrial mossy habitats. Photo by Janet Graham, through Creative Commons.

Figure 100. ***Fuligo muscorum*** on the moss ***Hypnum***. Photo by Charles Hipkin, with permission from Barry Stewart.

Lamproderma sauteri (Figure 72) occurs on bryophyte layers on rocks and boulders where there is running water (Novozhilov *et al*. 2000). These occurrences seem to be mostly in association with the Arctic-alpine leafy liverwort, ***Gymnomitrion concinnatum*** (Figure 101). ***Colloderma oculatum*** (Figure 73) and ***Lepidoderma tigrinum*** (Figure 20) seem to benefit from living on thin, slimy layers of liverworts under a thick cover of mosses and having a covering of water film.

Figure 101. ***Gymnomitrion concinnatum***, an Arctic-alpine leafy liverwort that serves as substrate for ***Lamproderma sauteri***. Photo by Michael Lüth, with permission.

In his 1983 study of ravines in the UK, Ing found that slime molds were associated with the moist bryophytes near waterfalls and dripping areas that kept the mosses moist. Novozhilov *et al*. (2000) reported a similar relationship on wood and rocks near trickling water in humid ravines. In fact, ***Lamproderma columbinum*** (Figure 66; **Stemonitidaceae**) is an ecotype that is associated with mosses in such habitats. Ing (1983) found that sporangia of slime molds occur most commonly on the mosses ***Cratoneuron commutatum*** (Figure 102), ***Dicranum majus*** (Figure 103), ***D. scoparium*** (Figure 33-Figure 34), ***Hyocomium armoricum*** (Figure 104), ***Hypnum cupressiforme*** (Figure 105), ***Isothecium myosuroides*** (Figure 106), ***Plagiothecium undulatum*** (Figure 107), and ***Rhytidiadelphus loreus*** (Figure 108), and the liverworts ***Bazzania trilobata*** (Figure 109), ***Lepidozia reptans*** (Figure 22), ***Plagiochila asplenioides*** (Figure 110), ***P. spinulosa*** (Figure 111), ***Saccogyna viticulosa*** (Figure 112), and ***Scapania gracilis*** (Figure 113). The most common slime molds that occur on these ravine bryophytes are ***Craterium muscorum*** (Figure 99), ***Diderma lucidum***, ***D. ochraceum*** (Figure 114), ***Lamproderma columbinum*** (Figure 66), and ***Lepidoderma tigrinum*** (Figure 20).

Figure 102. ***Cratoneuron commutatum***, one of the more common mosses serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 103. ***Dicranum majus***, a large ***Dicranum*** where slime molds commonly form sporangia. Photo by Michael Lüth, with permission.

Figure 104. ***Hyocomium armoricum***, one of the more common mosses serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 105. ***Hypnum cupressiforme***, one of the more common mosses serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 106. ***Isothecium myosuroides***, one of the more common mosses serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 107. ***Plagiothecium undulatum***, one of the more common mosses serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 108. ***Rhytidiadelphus loreus***, one of the more common mosses serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 109. The leafy liverwort ***Bazzania trilobata***, one of the more common liverworts serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 110. ***Plagiochila asplenioides***, one of the more common liverworts serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 111. ***Plagiochila spinulosa***, one of the more common liverworts serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 112. ***Saccogyna viticulosa***, one of the more common liverworts serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 113. ***Scapania gracilis***, one of the more common liverworts serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 114. ***Diderma ochraceum*** sporangia on moss, a common slime mold on ravine bryophytes. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

A very detailed study of slime molds in ravines and their associated bryophytes, using 127 small-scale relevés, is that of Schnittler *et al*. (2010) in sandstone gorges of Switzerland. They followed the methods developed by Holz (1997) for ravine bryophyte communities. Only five taxa account for 87% of the records, and all of these except ***Lamproderma puncticulatum*** (Figure 115-Figure 116) are reported elsewhere in this chapter from bryophyte associations: ***Colloderma robustum*** (Figure 117), ***Diderma ochraceum*** (Figure 114), ***Lamproderma columbinum*** (Figure 66), ***L. puncticulatum*** agg., and ***Lepidoderma tigrinum*** (Figure 20). They determined that the community is relatively unique, occurring only in the deep, narrow ravines on nearly vertical rocks, mostly on northern exposures. The substrate has a very acidic *p*H with a mean of 3.35. The fruiting season, in the beginning of October, has a very constant microclimate with nearly 100% relative humidity and ~10ºC. Green algae, most commonly ***Coccomyxa confluens*** (Figure 118), were associated with all the slime mold collections. The mosses ***Dicranodontium denudatum*** (Figure 119) (59%) and ***Tetraphis pellucida*** (Figure 25) (50%) and leafy liverworts ***Mylia taylorii*** (Figure 120) (64%) and ***Diplophyllum albicans*** (Figure 121) (40%) had high indicator values for the community. Nevertheless, the five most common slime molds had high niche overlap values, but low niche width values, indicating their high degree of specialization. I have to wonder if these slime molds were cryptospecies because they are relatively well known outside ravines and are among species more frequently cited as associated with bryophytes. For example, Hoffmann (1795) originally described ***Diderma ochraceum*** from mosses. On the other hand, sufficient habitat information is often lacking.

Figure 115. ***Lamproderma puncticulatum*** immature sporangia on bryophytes. Photo by Mireille Lenne, courtesy of Marianne Meyer.

Figure 116. ***Lamproderma puncticulatum*** on the liverwort ***Pellia***. Photo courtesy of Isabelle Mazaud.

Figure 117. ***Colloderma robustum***, a species associated with ravine bryophytes. Photo by Sarah Lloyd, with permission.

Figure 118. ***Coccomyxa confluens*** on mosses. Photo by James K. Lindsey, with permission.

Figure 119. ***Dicranodontium denudatum***, a common substrate for slime molds in ravines. Photo by David T. Holyoak, with permission.

Figure 120. ***Mylia taylorii***, a common ravine substrate for slime molds. Photo by Hermann Schachner, through Creative Commons.

Figure 121. ***Diplophyllum albicans***, a common ravine substrate for slime molds. Photo by David T. Holyoak, with permission.

Ing (1983) described a ravine slime mold community having a preference for bryophytes on rocks in numerous Atlantic locations in the British Isles. But the species differed somewhat from those in Switzerland: ***Craterium muscorum*** (Figure 99), ***Diderma lucidum***, ****D. ochraceum*** (Figure 114), ****Lamproderma columbinum*** (Figure 66), and ****Lepidoderma tigrinum*** (Figure 20), with *species being common in ravines of both countries. Later he (Ing 1994) recognized the ravine slime mold community as a distinct community.

Schnittler *et al*. (2010) did note that even when the inclination was suitable, pure turfs of ***Tetraphis pellucida*** (Figure 25) rarely had slime molds, but also tended to have less trickling water or algae. The leafy liverwort ***Mylia taylorii*** (Figure 120), on the other hand, is a good indicator organism for the presence of ravine slime molds. These researchers concluded that most of the ravine species are rare outside the ravines, citing ***Colloderma robustum*** (Figure 117) and ***Diderma ochraceum*** (Figure 114), two species closely associated with ***Mylia taylorii***. ***Lamproderma puncticulatum*** (Figure 115-Figure 116) agg. was likewise closely associated with ***M. taylorii***. Other common ravine species, specifically ***Lamproderma columbinum*** (Figure 66) and ***Lepidoderma tigrinum*** (Figure 20), occur elsewhere in forests with constantly humid conditions; in the British ravines they are closely associated with ***Tetraphis pellucida*** (Figure 25). As noted earlier in this chapter, they may be true bryophiles. ***Diderma umbilicatum*** (Figure 122) was always "in close neighborhood" with ***Mylia taylorii*** and ***Dicranodontium denudatum*** (Figure 119), suggesting that this slime mold preferred similar conditions to these two bryophytes. The moving plasmodia of ***D. umbilicatum*** were a conspicuous bright yellow. These segregate to form distinct sporangia on the tips of the bryophyte shoots, often forming a doughnut shape around the narrow leaves of ***Dicranodontium***.

Other species preferring ***Tetraphis pellucida*** (Figure 25) in ravines include ***Diderma lucidum*** and ***Lamproderma columbinum*** (Figure 66), the latter occurring there in 73% of the ***Tetraphis*** turf records where green algae were present in Saxonian Switzerland (Schnittler *et al*. 2010). ***Lamproderma puncticulatum*** (Figure 115-Figure 116) prefers thicker bryophyte tufts [64% with ***Mylia taylorii*** (Figure 120), 56% with ***Tetraphis pellucida***]. ***Lepidoderma tigrinum*** (Figure 20) prefers ***Dicranodontium denudatum*** (Figure 119) (74% of all records) and ***Mylia taylorii*** (65%), but occurred several times on ***Sphagnum*** (Figure 128-Figure 129) tufts at the base of large rocks; ***Diderma umbilicatum*** (Figure 122) had a similar preference for these two species. ***Physarum album*** (Figure 123) was less common, with only three records on ***Tetraphis pellucida*** and one on ***Dicranodontium denudatum***. Overall, the slime molds seem to prefer the closed turfs of ***Mylia taylorii*** and ***Dicranodontium denudatum***, but not the common pure short turfs of ***Tetraphis pellucida***.

Figure 122. ***Diderma umbilicatum*** on mosses, a species often near bryophytes in ravines. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 123. ***Physarum album***, a species that occasionally occurs on mosses in ravines. Photo by Sarah Lloyd, with permission.

Schnittler *et al*. (2010) agreed with Ing (1994) that nitrogen-fixing activity of the **Cyanobacteria** may be beneficial in some way to the slime molds, possibly as nutrients for their food source, or directly as a food source. But experimental evidence to support this is lacking. They in fact suggested that bryophilous slime molds may instead be phycophilous.

Wet Rocks

One of the early reports on slime mold-bryophyte associations in wet habitats is that of Lister (1918) in the UK. He found ***Lamproderma scintillans*** (Figure 11) on stones in a shallow stream. He surmised that they had migrated to these rocks from mosses and leaf litter on the stream bank.

Schnittler and Novozhilov (1996) described a granite rock community that is comprised of ***Colloderma oculatum*** (Figure 73) and ***Lepidoderma tigrinum*** (Figure 20). These two species fruit on very thin (< 0.5 cm), slimy layers of liverworts, covered with a water film. These microhabitat films are found at 1-3 m height on rocks that are provided with trickling water. The large moss tussocks on the upper margins of the rocks can function as a water reservoir. Both slime mold species produce sporangia directly on the water film of the liverworts. The researchers assumed that the plasmodia lived within the bryophyte layers because of their location on the rocks. The huge colonies, especially of ***Colloderma oculatum***, suggest that moss layers are a normal microhabitat. The **Cyanobacteria** (Figure 124-Figure 127) present are a possible food source for the plasmodia. In the northern Ammergauer Alps, Schnittler and Novozhilov (1998) also found ***Colloderma oculatum*** on wet rock surfaces where they were associated with mosses and a continuous layer of algae (probably including **Cyanobacteria**).

One such bryophyte dweller that may really be an algae/**Cyanobacteria** dweller is ***Physarum viride*** (Figure 14). This species occurs on two substrate types, one of which is on the moss and liverwort layers of rocks (Schnittler & Novozhilov 1996). It prefers medium-wet places between the pure slimy algae layers and the big moss tussocks.

One advantage to living on a wet rock is the presence of **Cyanobacteria**. Not only do the rocks present slimy layers of these nitrogen-fixing organisms, but so also do the bryophytes (Ing 1994). In the study by Ing, these encrustations are predominantly ***Nostoc muscorum*** (Figure 124-Figure 125) or ***N. commune*** (Figure 126-Figure 127). For the slime molds, these can be a food source, whereas for the bryophytes, they may improve the nitrogen availability. The beneficial aspects of this association are supported by the frequency with which this assemblage of species coincides with the ***Nostoc*** growths. In this case, the rocks are base-rich, and Ing hypothesized that the nitrogen-fixing activity of the ***Nostoc***, enhanced by a high *p*H, may be beneficial for the slime molds. ***Craterium muscorum*** (Figure 99), ***Lamproderma columbinum*** (Figure 66), and ***Lepidoderma tigrinum*** (Figure 20) typically develop plasmodia that have close contact with the ***Nostoc*** on these wet rocks.

Figure 124. ***Nostoc muscorum*** gelatinous ball, a **Cyanobacterium** frequently associated with wet bryophytes and of likely benefit to slime molds. Photo from Protist Information Server, with permission.

Figure 125. ***Nostoc muscorum*** individual filaments. Photo by Charles Krebs, with online permission.

Figure 126. ***Nostoc commune*** on mosses. Yamamaya, through Creative Commons.

Figure 127. ***Nostoc commune*** individual filaments. Photo by David Wagner, with permission.

Sphagnum and peatland Dwellers

Sphagnum (Figure 128) offers both a habitat modifier that maintains a high moisture level, and a substrate. Carr (1939) provided an early record of ***Didymium iridis*** (Figure 6; as *Didymium nigripes* var. *xanthopus*) growing in abundance on ***Sphagnum***.

Figure 128. ***Sphagnum fallax*** with capsules. Photo by David T. Holyoak, with permission.

Schnittler and Novozhilov (1996) noted species of slime molds that were in some way associated with ***Sphagnum*** (Figure 128) in the northern Karelia of Russia. Nevertheless, they observed that the ***Sphagnum***-rich spruce (***Picea***; Figure 129) woodland, despite its nearly continuously moist environment, served as a poor habitat for slime molds. Only ***Physarum virescens*** (Figure 38-Figure 39) appeared to be adapted sufficiently to live on the large moss tussocks.

Figure 129. ***Sphagnum*** in spruce forest. Photo courtesy of Kim Barton.

In his examination of mosses of wet habitats, Ing (1994) found two slime molds that are mostly restricted to growing on ***Sphagnum*** (Figure 128). These are ***Symphytocarpus trechispora*** (Figure 130) and ***Amaurochaete trechispora***. On the other hand, Salamaga *et al*. (2014) concluded that in Poland ***S. trechispora*** is acidophilic. Whereas it frequently occurs on ***Sphagnum***, it is not restricted to that substrate. They reported it also from ***Polytrichum*** sp. (Figure 131) (growing with ***Sphagnum fallax*** – Figure 128). It is also known from ***Sphagnum*** in Scotland, England, and Germany (Ing 1999; Schnittler *et al*. 2011).

Figure 130. ***Symphytocarpus trechispora*** on moss. Photo by Thomas Laxton, through Creative Commons.

Figure 131. ***Polytrichum commune***, a common substrate for ***Symphytocarpus trechispora***. Photo by Christopher Tracey through Creative Commons.

In the same study, Ing (1994) found that two bryophiles, ***Lamproderma columbinum*** (Figure 66, Figure 132) and ***Lepidoderma tigrinum*** (Figure 20), occur on ***Sphagnum*** (Figure 128) as well as other bryophytes. ***Diderma simplex*** (Figure 133) is a moorland species that includes bog mosses among its substrates. Hagelstein (1941) reported ***Paradiachea caespitosa*** (Figure 134) growing on the tips of ***Sphagnum***. But Ing (1994) concludes that in general, the low *p*H and low oxygen availability make many mires and bogs unsuitable for the growth of slime molds.

Figure 132. ***Lamproderma cf. columbium***, on ***Sphagnum***, Catfield Fen. Photo courtesy of Isabelle Masaud.

Figure 133. ***Diderma simplex***, a species that can grow on bog mosses. Photo by Bruce Watt, University of Maine, Bugwood.org, through Creative Commons.

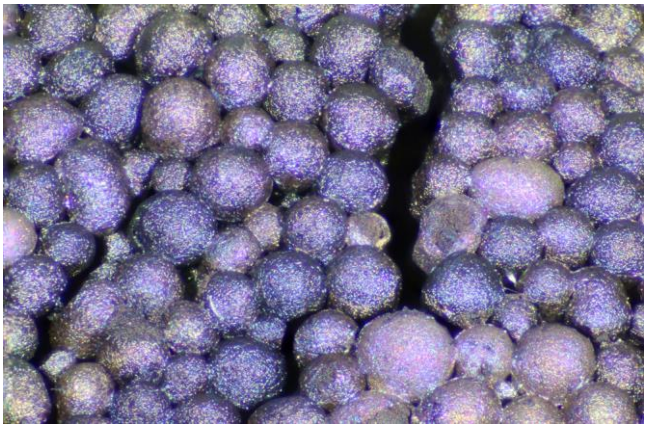

Figure 134. ***Paradiachea caespitosa***, a species that grows at the tip of ***Sphagnum***. Photo by Sarah Lloyd, with permission.

Cavender *et al*. (2005) reported a new species of cellular slime mold, ***Dictyostelium quercibrachium*** (**Dictyosteliomycetes**), from the margin of a small bog in Ohio, USA. Cavender and Vadell (2006) likewise reported the cellular slime mold ***Acytostelium magniphorum*** from the margin of a small bog in Ohio. Landolt *et al*. (2006) suggested that bog margins provide relict habitats that have been under explored for slime molds and therefore may hold more unknown species or range extensions.

In a more recent study in the Ukraine, Yatsiuk *et al*. (2018) found ***Didymium ovoideum*** (Figure 135) on ***Sphagnum*** (Figure 128). ***Didymium melanospermum*** (Figure 28) and ***Stemonitis axifera*** (Figure 136) occurred on species of ***Sphagnum*** and **Polytrichaceae** (Figure 131). ***Didymium melanospermum*** typically occurs on acid substrates, including mosses (Stephenson & Studlar 1985; Nannenga-Bremekamp 1991; Ing 1994). On the other hand, ***Stemonitis axifera*** does not appear to be bryophilous in most locations.

Figure 135. ***Didymium ovoideum*** sporangium on wood, a species that sometimes occurs on ***Sphagnum***. Photo by Thomas Laxton, through Creative Commons.

Figure 136. ***Stemonitis axifera*** sporangia on decorticated log, a species that also occurs on ***Sphagnum*** and **Polytrichaceae**. Photo by Clive Shirley, The Hidden Forest, with permission.

In ***Sphagnum*** (Figure 128) bogs, ***Badhamia lilacina*** (Figure 137-Figure 138) seems to prefer aquatic areas, but their fruiting occurs on moss leaves (Tamayama & Keller 2013). Others, like the ***Leocarpus fragilis*** (Figure 139) in occur in peatlands but seem to avoid the ***Sphagnum***. Only one tiny patch of this one is on the moss.

Figure 137. ***Badhamia lilacina*** plasmodium on ***Sphagnum***. Photo from <www.vestrehus.dk>, with implied permission.

Figure 138. ***Badhamia lilacina*** on ***Sphagnum***. Photo by Janet Graham, through Creative Commons.

Figure 139. ***Leocarpus fragilis*** on ***Sphagnum*** and twigs. Photo by Boris Loboda, with permission.

Summary

Habitats for the slime molds are arguably as diverse as those of bryophytes. Some of the "less important" habitats, in terms of number of species, are on epiphyllous leafy liverworts, on liverworts elsewhere, on leaf litter, on soil, on rocks, on sand dunes, in alpine and polar regions, in ravines, on wet rocks, and in peatlands, including on ***Sphagnum***. These habitats contrast with the higher richness and abundance on bark and rotting wood. In all of these habitats, some slime molds exist on bryophytes. Our understanding of this slime mold-bryophyte relationship is almost non-existent. The presence of plasmodia on bryophytes is even less well understood than the presence of sporangia. In contrast to the bryophytes, the species richness and abundance changes of slime molds with increasing elevation mimic those seen for increasing altitude.

Alpine areas seem have some of the bryophiles, such as ***Barbeyella minuta***. Polar regions, on the other hand, are often dominated by **Dictyosteliomycetes**. Records of bryophyte dwellers are rare or non-existent in the polar regions.

Ravines provide a unique assemblage of species, and many of these occur on bryophytes, probably in part because bryophytes provide a high cover there. ***Craterium muscorum***, ***Diderma lucidum***, ***D. ochraceum***, ***Lamproderma columbinum***, and ***Lepidoderma tigrinum*** are common on bryophytes there. The presence of ***Mylia taylorii*** is a good indicator organism for the presence of ravine slime molds, and many also occur on the moss ***Dicranodontium denudatum***. The **Cyanobacteria** ***Nostoc muscorum*** and ***N. commune*** are common associates on wet rocks and may provide food for the slime molds. Slime molds occurring in peatlands in association with ***Sphagnum*** may be there because of the low *p*H.

Of the 79 genera of slime molds in the **Mxyomycetes**, **Dictyosteliomycetes**, and **Ceratiomyxomycetes** listed by nomen.eumycetozoa.com as of 5 May 2019, 44 have at least one member that has been found on a bryophyte. I have found no records among the protostelids.

Summarizing this chapter raises more questions than answers. Do either the bryophytes or the slime molds, or both, benefit from their association? If so, how? Do the bryophytes and slime molds simply prefer the same environmental conditions? It seems likely that moisture is a major factor, but experiments are needed on a sponge or other non-biological material to provide moisture with no nutrients. Do some bryophytes inhibit the growth of slime molds? Do some provide food through the microflora and fauna of the bryophyte, and do others fail to provide it because of growing conditions or inhibitors? Are some slime molds inhibited while others are not by the same bryophyte species? Experiments with bryophyte extracts on cultures of slime molds could be illuminating.

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Marianne Meyer and Isabelle Charissou were very helpful in providing me with pictures of slime molds on mosses and Marianne helped me with identification of some images contributed by others. Sarah Lloyd and Steve Stephenson were very helpful in providing images, references, and critiques.

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CHAPTER 4-1
INVERTEBRATES: INTRODUCTION

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CHAPTER 4-1
INVERTEBRATES: INTRODUCTION

Figure 1. ***Marchantia polymorpha*** that has been nibbled by an unknown organism. Note holes in the thallus. Photo by C. R. Stevenson, with permission.

The Invertebrate Fauna

Einstein is credited with saying that the most incomprehensible fact about nature is that it is comprehensible (Miller 1992). The invertebrate community associated with bryophytes, especially in terrestrial habitats, needs still to be comprehended.

Dendy (1895) coined the term **cryptozoic fauna** to describe "the assemblage of small terrestrial animals found dwelling in darkness beneath stones, rotten logs, the bark of trees, and in other similar situations." Although not specifically mentioned, bryophytes surely belong among the "other similar situations," as evidenced by the browsed patches on the liverwort in Figure 1. A comparable term for such bryophyte dwellers in the aquatic realm is **meiofauna**, defined as "**benthic** (living on the bottom of a body of water) animals that can fit a mesh size of 1 mm and be retained on a mesh size of 42 µm" (Brave New Biosphere 1999). Although living among bryophytes directly contradicts being on the bottom, the bryophytes do occupy the bottom, and one might think of the habitat they create as simply an extension of that bottom.

For many of the invertebrates, the bryophytes represent a moist island among the drier sites. Invertebrates living there because they are able to survive in interstial collections of water droplets are considered **limnoterrestrial**, and this **limnoterrestrial habitat** houses many organisms better known in aquatic habitats, such as copepods, gastrotrichs, rotifers, and tardigrades (Thorp & Covich 2010).

The invertebrate fauna are likely to play an important role in nutrient cycling within the bryophyte community, thus facilitating return of detrital matter to ecosystem level nutrient cycling. Merrifield and Ingham (1998) suggested that the diversity of feeding strategies found in moss invertebrate communities provides evidence of within-bryophyte-community nutrient cycling. Studies by Davis (1981) seem to support this suggestion. He found that the moss turf community and the moss carpet community in the maritime Antarctic on Signy Island showed similar levels of productivity, trophic structure, and efficiencies of organic matter transfer, but they differed in **Collembola**

(springtails) and **Acari** (mites) standing crops, turnover of mosses, and accumulation of dead organic matter. Both communities [turf of ***Polytrichum strictum*** (= *P. alpestre*; Figure 2-Figure 3) and ***Chorisodontium aciphyllum*** (Figure 4-Figure 5) and carpet of ***Calliergon sarmentosum*** (Figure 6), ***Calliergidium austro-stramineum*** (Figure 7), ***Sanionia uncinata*** (Figure 8), and ***Cephaloziella varians*** – a liverwort (Figure 9)] had fauna of **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola**. Despite the diverse fauna, Davis found no evidence that the mosses would have been eaten. However, he based this on known feeding groups of the organisms and not on direct evidence. Nevertheless, it is likely that detrital matter and predation were primary food pathways, permitting nutrient cycling.

Figure 2. ***Polytrichum strictum*** cushions in Alaska, home for **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola** in the Antarctic. Photo courtesy of Andres Baron Lopez.

Figure 3. ***Polytrichum strictum***, home for **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola** in the Antarctic. Photo by Jan-Peter Frahm, with permission.

Figure 4. ***Chorisodontium aciphyllum*** in Antarctica, home of **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola**. Photo from Polar Institute, through Creative Commons.

Figure 5. ***Chorisodontium aciphyllum***, home of **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola**. Photo by Jan-Peter Frahm, with permission.

Figure 6. ***Calliergon sarmentosum***, home for **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola** in the Antarctic. Photo by David T. Holyoak, with permission.

Figure 7. ***Calliergidium austro-stramineum***, home for **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola** in the Antarctic. Photo by Bill Malcolm, with permission.

Figure 8. ***Sanionia uncinata***, home for **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola** in the Antarctic. Photo by Michael Lüth, with permission.

Figure 9. ***Cephaloziella varians*** (among mosses), home for **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola** in the Antarctic. Photo by Kristian Peters, with permission.

Nelson and Hauser (2012) examined what would seem to be a very different habitat from that of the Antarctic samples of Davis (1981) – epiphytic mosses and liverworts of the Pacific Northwest, USA. Despite that seeming difference in climate, the same six groups were dominant: Acari, Tardigrada, Collembola, Nematoda, and Rotifera, in that order. Protozoa were also abundant, but they did not quantify those. They found no differences in major groups between mosses and liverworts, but suggested that there may have been differences between species.

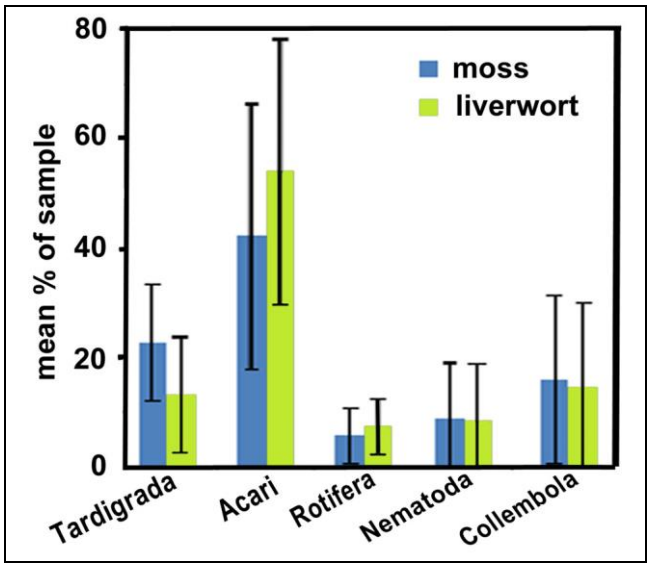

Figure 10. Mean percent and standard deviation of organisms for each of the five dominant taxa groups in epiphytic mosses and liverworts at Tryon Creek State Natural Area, 1, 7, and 17 October 2011, calculated for all samples together. Redrawn from Neslon & Hauser 2012.

In the Czech Republic, Božanić *et al*. (2013) attempted to illucidate the factors that determined which invertebrates inhabited bryophyte clumps. They examined the fauna on 15 bryophyte species (61 total samples) and identified 45 invertebrate species in 13 higher taxonomic groups. They found that the two most important factors determining the invertebrate fauna were the size of the moss clump (Figure 12) and the height above ground (Figure 13). The moss genus ***Brachythecium*** housed the most invertebrate taxa, with the species ***Brachythecium curtum*** (Figure 11) on rotten trees housing the most.

Figure 11. ***Brachythecium curtum*** on rotten wood, home for the most invertebrate taxa in a Czech Republic study. Photo by Janice Glime.

Millipedes preferred bryophyte habitats higher above ground, with ***Nemasoma varicorne*** (Figure 14) being the most abundant (Božanić *et al*. 2013). Mites (**Acarina**), pseudoscorpions (**Pseudoscorpiones**), and ants (**Formicidae**) were only in the lower levels. Interestingly, tree diameter also played a role in locations, with the isopods ***Trichoniscus pusillus*** (Figure 15) and ***Porcellium collicola*** (Figure 16) occupying mosses on smaller trees, whereas the isopod ***Trachelipus rathkii*** (Figure 17) and centipedes ***Lithobius mutabilis*** and juveniles of other ***Lithobius*** species preferred larger trees.

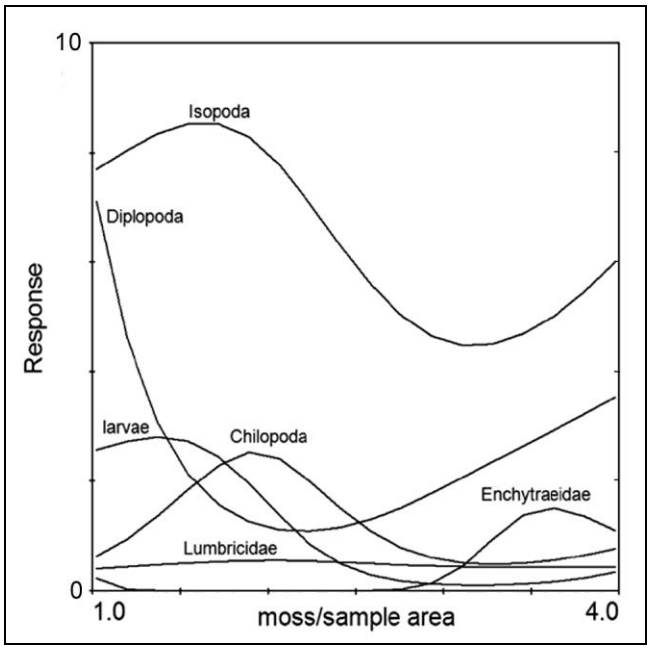

Figure 12. Relative numbers of invertebrate groups on bryophytes vs moss sample area. Redrawn from Božanić *et al*. 2013.

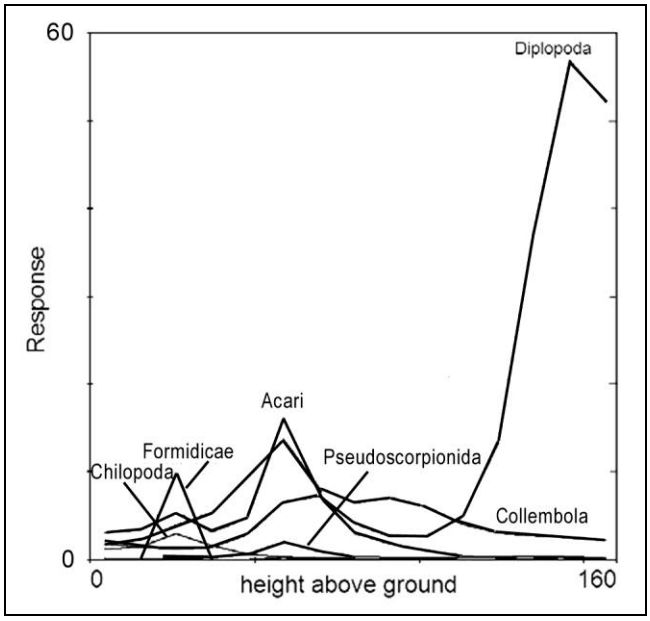

Figure 13. Relative numbers of invertebrate groups on bryophytes vs height above ground. Redrawn from Božanić *et al*. 2013.

Figure 14. ***Nemasoma varicorne*** female, an abundant above ground millipede that can be found among bryophytes. Photo by Walter Pfliegler, with permission.

Figure 15. ***Trichoniscus pusillus***, a species among mosses on smaller trees. Photo by Andy Murray, through Creative Commons.

Figure 16. ***Porcellium collicola***, a species among mosses on smaller trees. Photo by Dragisa Savic, with permission.

Figure 17. ***Trachelipus rathkii***, a species among mosses on larger trees. Photo by Joerg Spelda, SNSB, Zoologische Staatssammlung Muenchen, through Creative commons.

Figure 18. ***Lithobius mutabilis***, a species among mosses on larger trees. Photo by Joerg Spelda, SNSB, Zoologische Staatssammlung Muenchen, through Creative Commons.

Dražina *et al*. (2011) examined the mieofauna of bryophytes in Europe. These included **Turbellaria** (flatworms), **Rotifera** (rotifers), **Nematoda** (nematodes), **Gastrotricha**, **Oligochaeta** (segmented worms), **Tardigrada** (tardigrades), and **Crustacea**, as well as small, immature insects. They found more than 100 taxa, with rotifers dominating (52 taxa) and nematodes second (27 taxa). In fast water, rotifers averaged an abundance of 219 individuals cm^{-3}. Velocity accounted for much of the variation in locations, with rotifers being most abundant in high velocity and gastrotrichs, tardigrades, and microturbellarians having a negative relationship to flow velocity.

Perić *et al*. (2014) studied the invertebrate drift and found that the meiofauna formed a "considerable" portion of it among moss-rich areas in a karst stream. They found 60 invertebrate taxa in the drift. Only six taxa, all in the annelid and arthropod meiofauna, comprised 35% of the total drift density. Most of the Macroinvertebrates were immature insects. The **Cladocera** (***Alona*** spp.; Figure 19) comprised 26,7%, ***Riolus*** spp. (**Coleoptera**: **Elmidae**; Figure 20) comprised 13.2%, ***Simulium*** spp. (**Diptera**: **Simuliidae**; Figure 21) 12.2%, **Enchytraeidae** (**Annelida**; Figure 22) 10.4%, **Hydrachnidia** (mites; Figure 23) 6.3%, **Orthocladiinae** (**Diptera**: **Chironomidae**; Figure 24) 3.9%, and **Naididae** (**Annelida**; Figure 25) 3.6%.

Figure 19. ***Alona***, a bryophyte dweller that is most common among them in the drift. Photo by Yuuji Tsukkii, with permission.

Figure 20. ***Riolus subviolaceus*** adult, a genus that is common in mosses and common in stream drift. Photo from Naturalis Biodiversity Center, through Creative Commons.

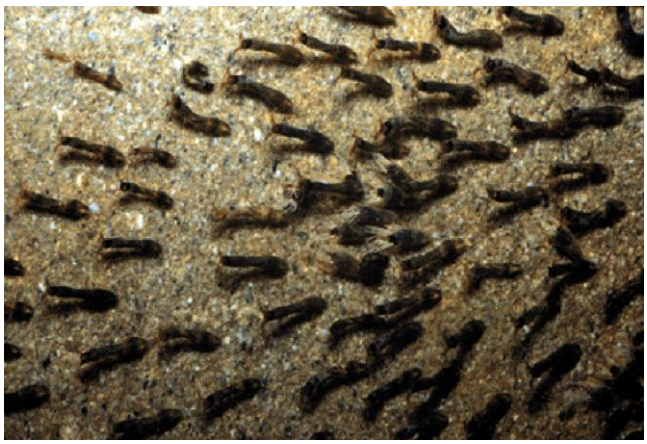

Figure 21. ***Simulium*** larvae, bryophyte dwellers that are common in the drift. Photo from USDA, through Public Domain.

Figure 22. **Enchytraeidae**, a family with bryophyte dwellers that are common in the drift. Photo by Aina Maerk Aspaas, NTNU University Museum, Department of Natural History, through Creative Commons.

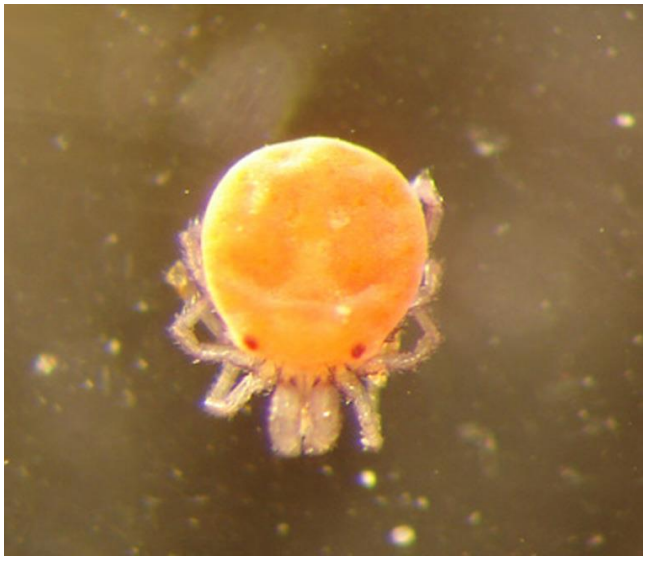

Figure 23. **Hydrachnidia**, a mite group with bryophyte dwellers that are common in the drift. Photo by Mnolf, through Creative Commons.

Figure 24. *Synorthocladius* larva, a member of **Orthocladiinae**; members of this subfamily are common among stream mosses and stream drift. Photo from Stroud Water Research Center, through Creative Commons.

Figure 25. **Naididae**, a family with bryophyte dwellers that are common in the drift. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Drozd *et al*. (2009) conducted studies in bryophyte fauna in the forests of the submountain and mountain areas of the Czech Republic. They concluded that moisture, bryophyte presence, and surprisingly, bryophyte species were the important characteristics determining total abundance. Their study area bryophytes included the mosses ***Polytrichum commune*** (Figure 26), ***Polytrichastrum formosum*** (Figure 27), ***Sphagnum teres*** (Figure 28), ***Sphagnum girgensohnii*** (Figure 29, ***Sphagnum fallax*** (Figure 30), ***Pleurozium schreberi*** (Figure 31-Figure 32), ***Eurhynchium angustirete*** (Figure 33), ***Oligotrichum hercynicum*** (Figure 34), and the leafy liverwort ***Bazzania trilobata*** (Figure 35-Figure 36).

Figure 26. ***Polytrichum commune*** habitat, a species of the submountain and mountain areas of the Czech Republic. Photo by Sten Porse, through Creative Commons.

Figure 27. ***Polytrichastrum formosum***, a species of the submountain and mountain areas of the Czech Republic. Photo by David T. Holyoak, with permission.

Figure 28. ***Sphagnum teres***, a species of the submountain and mountain areas of the Czech Republic. Photo by J. C. Schou, with permission.

Figure 29. ***Sphagnum girgensohnii***, a species of the submountain and mountain areas of the Czech Republic. Photo by Martin Hutten, with permission.

Figure 30. ***Sphagnum fallax***, a species of the submountain and mountain areas of the Czech Republic. Photo from <www.aphotofauna.com>, with permission.

Figure 31. ***Pleurozium schreberi***, a species of the submountain and mountain areas of the Czech Republic. Photo by Bob Klips, with permission.

Figure 32. ***Pleurozium schreberi***, a species of the submountain and mountain areas of the Czech Republic. Photo by Michael Lüth, with permission.

Figure 33. ***Eurhynchium angustirete***, a species of the submountain and mountain areas of the Czech Republic. Photo by Hermann Schachner, through Creative Commons.

Figure 34. ***Oligotrichum hercynicum***, a species of the submountain and mountain areas of the Czech Republic. Photo by David T. Holyoak, with permission.

Figure 35. ***Bazzania trilobata***, a species of the submountain and mountain areas of the Czech Republic. Photo by Michael Lüth, with permission.

Figure 36. ***Bazzania trilobata***, a species of the submountain and mountain areas of the Czech Republic. Photo by Barry Stewart, with permission.

Sampling

Drozd *et al*. (2009) lamented the paucity of comprehensive studies, citing many studies that included only one taxonomic group. They studied the bryophyte fauna using 66 traps in three mountain ranges in the Czech Republic. These traps collected more than 55,000 individuals in 5 sites with a mean of 850 individuals per trap. Litter saples had higher arthropod abundance than did moss cushions. They suggested this was probably influenced by the behavior of the detritivorous arthropods that do not have to move about in search of food. They also suggested that the arthropods might use the bryophytes only as a temporary shelter against predators and desiccation.

Quantitative field sampling of bryophytes is a challenge, and what works for one species may not work for another. Hynes (1961) collected mosses by hand and stuffed them into a 180 cc jar until it reached capacity, a sample of ca 300 cm^2. But this may not work well for some large growths of *Fontinalis* spp and produces a large sample to be sorted. Furthermore, adding material from other locations in the clump or different clumps diminishes the ability to detect variability and prevents examining subtle effects of stream location. Pulling the moss from the water generally loses few animals because they are adapted to clinging within the moss mat, but pulling the moss apart to make a smaller sample to fit into 180 cc will dislodge even some of the best adapted. Cutting the moss into smaller segments would be less disruptive, but if no bases are samples, some organisms with preferences for bases may be missed. And increasing the sample size of all collections to one suitable for large clumps of ***Fontinalis*** (Figure 37) would create a prohibitive sorting size. I found that collecting a handful, preferably to fit into a baby food jar, worked well (Glime1994). The samples were quantified on the basis of moss dry weight after sorting by hand. Frost (1942) used 200 g wet weight for her moss sample size. Since many of the invertebrates disintegrate quickly, 90-95% ethanol should be added immediately. Lower concentrations become too dilute. This method worked well for insects, but may not be suitable for all the non-chitonous invertebrates. These methods will be discussed with the various groups.

Figure 37. ***Fontinalis antipyretica***, a large aquatic moss that is difficult to sort through. Photo by Bernd Haynold, through Creative Commons.

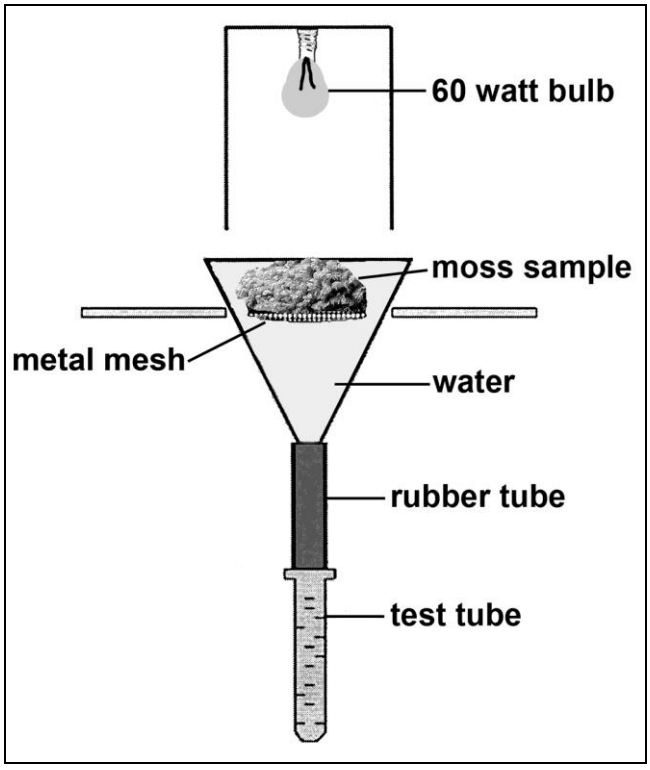

Figure 38. Baermann funnel using moss sample. Water can be replaced with air for non-aquatic organisms, thus making it similar to the Berlese funnel. Modified from Briones 2006.

Hynes (1961) solved the sorting problem by floating the organisms with a saturated solution of calcium chloride. Even with repeated stirring, those organisms with spines and clinging legs may remain in the mosses, as will those nestled at the bases of leaves that curl around them, creating a bias in the sampling.

Determining the faunal composition and community structure of these microhabitats is not an easy task. The most obvious method of sampling invertebrates is sorting them from the bryophytes under the dissecting microscope. But this method is tedious, very time-consuming, and often misses the smaller organisms (personal experience!). The method of wringing and squeezing is much less tedious and faster, a method used by Morgan (1977), but certainly many get left behind, and attached organisms are likely to be preferentially left behind, not to mention damage to larger organisms. To help in this time-consuming task, Paul Davison (pers. comm. 21 June 2006) modified the **Baermann funnel** (Figure 38) for extracting turbellarians (as well as nematodes, copepods, and tardigrades) from bryophytes. A piece of cheese cloth, muslin, or tissue paper is placed in a funnel to hold a sample (Tylka Nematology Lab 2005). This is usually supported by a piece of screening (Figure 38). Then water is run through the sample with rubber tubing clamped at the end of the funnel. After the sample sits overnight or longer, the water is released from the funnel and collected. The first few drops will have a concentration of nematodes, which are heavier than water.

Another method is use of the **Berlese funnel**, which does not have water, using a light and/or temperature gradient that separates mobile organisms such as **arthropods** and **annelids**, but that method leaves the non-mobile ones behind, and doesn't work for nematodes (ED-STEEP). If it is too hot, organisms die before they can drop.

Nelson and Hauser (2012) discovered that the Berlese funnel and soaking in water gave very different results. For the water extraction, they placed the bryophytes in 200 mL water and allowed to settle for at least two hours, following the protocol for tardigrades described by Thorpe and Covich (2010). The sample was taken by sucking up sediment with a dropper and placing two drops on a depression slide. The Berlese funnel method has a strong bias toward arthropods, in this case mites (Acari), whereas the water method found at least 6 types of tardigrades and many algae and protozoa. They found "almost no taxa overlap" between the two extraction methods!

Kreutz and Foissner (2006) likewise used liquid extraction. They placed mud on a slide, but for bryophytes it is necessary to wash the bryophytes into water in something like a Petri plate. Detritus and unattached organisms will be dislodged if the bryophytes are stirred into the water. The precipidated detritus can be placed on a slide and separated using the slide-on-slide method described in Chapter 2-6, Protozoa Ecology.

Jennings (1979) used the Baerman funnel to extract invertebrates from mosses on Signy Island in the Antarctic. Fairchild *et al*. (1987) have taken advantage of the behavior of these invertebrates to develop an extraction method. By creating a vertical temperature and oxygen gradient in samples of ***Sphagnum*** (Figure 28-Figure 30), they were able to obtain an 85% efficiency. Merrifield and Ingham (1998) compared several methods of extracting invertebrates. In a study of ***Eurhynchium oreganum*** (Figure 39) in the Oregon Coast Range, USA, Merrifield and Ingham first verified extraction efficiency for **nematodes** and other invertebrates using the Baermann funnel. First, invertebrates were collected from the funnel

apparatus, then more were collected from the mosses on subsequent days, and finally more were collected by squeezing and agitation of the moss. More than 90% of cumulative final counts of the nematodes ***Monhystera*** spp. (Figure 40) and ***Prionchulus muscorum*** (Figure 41) were extracted by the Baermann funnel technique by day 4 of extraction. Tardigrade extraction was even more efficient, reaching 95% by day 4. Rotifers, however, were less efficiently extracted, with only 42% by day 4 and 55% by day 7.

Figure 39. ***Eurhynchium oreganum***, home for nematodes. Photo by Matt Goff, with permission.

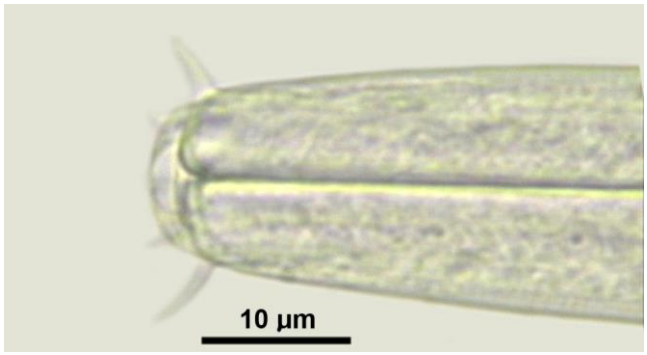

Figure 40. ***Monhystera*** sp., a nematode that is extracted effectively from bryophytes by a Baerman funnel. Photo by Peter Mullin, with permission.

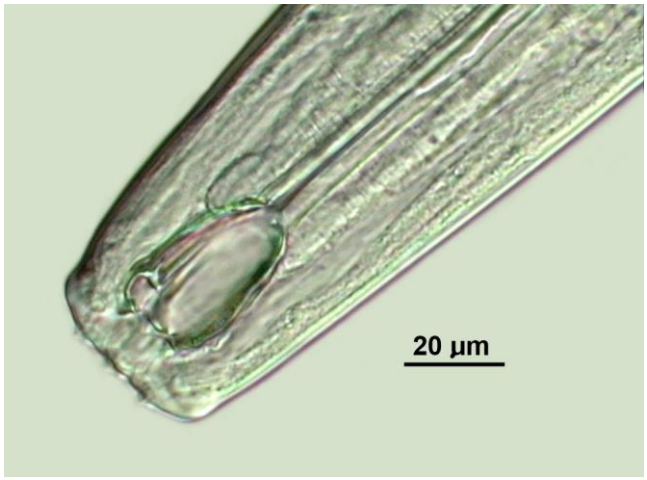

Figure 41. ***Prionchulus muscorum***, a nematode that is extracted effectively from bryophytes by a Baerman funnel. Photo by Peter Mullin, with permission.

Andrew and Rodgerson (1999) investigated diversity gradients of invertebrates on bryophytes on two mountains in Tasmania. they compared two extraction techniques for their effectiveness in representing diversity – Tullgren funnels and sugar flotation – with a new technique using kerosene phase separation. When using two samples bulked together, they found that the kerosene phase separation extracted more total individuals and more Acari (mites) and Collembola (springtails). When they compared single samples (1.5 cm x 2.5 cm), the abundance results were the same, but only three of the nine taxa found in the bulked samples were extracted from the single samples. They therefore recommended that two samples be taken and used as replicates (not bulked).

Preservation of Specimens

Ecologists take note. Simply identifying and counting the faunal organisms and getting someone to identify the bryophytes isn't enough! Whereas you may be confident that your expert has identified everything correctly, it is likely that the expert is less confident and has provided you with the "best" determination possible with the material provided. But ecological specimens typically lack reproductive organs, are not well preserved, and may not even be the whole organism. Systematists always pay careful attention to keeping specimens and publishing their location. Ecologists and physiologists should also. Both the bryophytes and the fauna should be preserved and their locations in permanent, reputable herbaria and museums should be part of any publication based on the data. Furthermore, the specimens should be clearly labelled as voucher specimens, referencing the study.

Species concepts change; often physiological and ecological properties are not uniform among members of the earlier species concept. In the absence of a specimen, the data become useless. Yet, in 1950, Fosberg examined 270 ecological publications with discussions of species. Locations of preserved specimens were provided in only five of these publications! I decided to see if the situation had improved by using a much smaller sample size of three recent ecological journals and three recent bryological journals. In the 15 papers I examined from ecological journals, there was no mention of preserving or keeping specimens. In the three bryological journals, all 15 papers dealing with systematics or checklists provided the herbaria locations. However, even among this group of biologists who share the same journals, none of the six ecological papers in the same issues mentioned any preservation of specimens from the species included in the study. This practice of providing no preserved reference material defies the concept that scientific data must be verifiable.

I disagree with Fosberg (1950) when he pokes fun at stating the source of the nomenclature. Unlike his concept that this is presented to "verify" the identity of the organism, the source of nomenclature demonstrates the species concept used and provides a link to a source where a description may be found. Thus, if one uses ***Drepanocladus*** from Crum 1973, we know that a broad concept of the genus is used and that ***Sanionia***, ***Warnstorfia***, or other genus might now apply instead.

Community Patterns

When only aquatic vs terrestrial are considered, we find a difference in groups dominating the bryophytes. In terrestrial habitats, arthropods dominate (Kinchin 1992). Nevertheless, few arthropods spend their entire life cycle among mosses (Kinchin 1990a). The aquatic fauna, Kinchin (1992) contends, is dominated by nematodes, tardigrades, and rotifers. It is not clear if he includes the peatlands in this aquatic grouping, but I have examined the preserved fauna of stream bryophytes, where I have found **insects** to be the dominant organisms (Glime 1994). I must admit, however, that my bias was to describe the insect communities.

A particularly good reference for the identification of species in ***Sphagnum*** pools (Figure 42), particularly in Germany, is that of Kreutz and Foissner (2006). However, those on mosses are not distinguished from those in open water.

Figure 42. ***Sphagnum cuspidatum*** and S. denticulatum with bog pools. Photo by Jonathan Sleath, with permission

Terrestrial/Limnoterrestrial

Kinchin (1992) reviewed the invertebrate fauna among bryophytes in the British Isles and provided us with a summary of the "moss" habitat. He found that acrocarpous cushions support a richer fauna than the more loosely packed pleurocarpous mosses, attributing this to the greater ability of acrocarpous cushions to hold water. He demonstrated this ability experimentally, showing that at 100% saturation a cushion of the acrocarpous ***Bryum argenteum*** (Figure 43) held 277% of its "dry" weight in water. The pleurocarpous moss ***Hypnum cupressiforme*** (Figure 44), on the other hand, held 1496%. ***Bryum argenteum*** held 85% of its dry weight as soil trapped among the rhizoids, whereas ***H. cupressiforme*** has less than 1%. But perhaps most importantly, ***B. argenteum*** required 180 hours to reach steady dryness, whereas ***H. cupressiforme*** required only 132, and this was in a moss starting with more than 5X as much water!

Figure 43. ***Bryum argenteum*** showing its compact habit. Photo by Dick Haaksma, with permission.

Figure 44. Mat of ***Hypnum cupressiforme***. Photo by Dick Haaksma, with permission.

Slow drying, as you will soon see, is a prerequisite for survival in many of these faunal organisms. Supporting his argument, Kinchin found that the ***Bryum argenteum*** (Figure 43) fauna was much richer than that of ***Hypnum cupressiforme*** (Figure 44). Interestingly, he found that mosses such as ***Tortula muralis*** (Figure 45) and ***Grimmia pulvinata*** (Figure 46) with long hair points have particularly rich fauna, which might again result from a mechanism for slow drying.

Figure 45. ***Tortula muralis*** in a rock crevice. Photo by Michael Lüth, with permission.

Figure 46. ***Grimmia pulvinata*** on boulder. Photo by Michael Lüth, with permission.

The wonderful fauna of bryophytes led Gadsby (1926) to publish his paper, "Meanderings 'mong mosses." Even after a fire bryophytes such as ***Funaria hygrometrica*** (Figure 47) and ***Ceratodon purpureus*** (Figure 48) accumulate organic matter and dust, permitting invertebrates to colonize (Clément & Touffet 1981). Others are quick to colonize areas of harvested peat (Curry *et al*. 1989). Even glacial land in the Antarctic (Schwarz *et al*. 1993) and geothermal areas of Iceland (Elmarsdottir 2003) and Ireland (Fahy 1974) sport their own bryophyte invertebrate fauna, most likely facilitated by the ameliorating effect of the microclimate within the bryophyte clone. In the Antarctic, Sohlenius *et al*. (2004) found highest invertebrate densities where there were moss communities.

In addition to the protozoa already discussed, these leaves are home to large numbers of rotifers, nematodes, and oribatid mites, and the associated bacteria, fungi, and algae provide their sustenance. Some of the species, particularly ***Sphagnum*** (Figure 41) inhabitants, are not found elsewhere. Many live as epiphytes on the leaf, but some live as endophytes, gaining entrance to the cells through pores in ***Sphagnum*** leaf and stem cells. These specialists are often elusive by standard sampling techniques. Nevertheless, Hingley showed that 50% of the taxa were present in a single drop of water!

Figure 47. ***Funaria hygrometrica***, a common colonizer after fires that collects organic matter, permitting invertebrates to colonize. Photo by Michael Lüth, with permission.

Figure 48. ***Ceratodon purpureus***, a common colonizer after fire, accumulates organic matter, permitting invertebrate fauna to develop. Photo by Michael Lüth, with permission.

Jones *et al*. (1994) described mosses as ecosystem engineers that provide living spaces by providing a suitable physical structure. Although ***Sphagnum*** (Figure 42) is the most cosmopolitan engineer, bryophytes create habitats for invertebrates in many ecosystems. Sayre and Brunson (1971) compared the moss inhabitants in a variety of habitats to determine what faunal taxa were most common (Figure 49).

One of the primary determinants of faunal inhabitants is the film of water surrounding moss leaves, especially ***Sphagnum*** (Hingley 1999). Bryophyte habitats generally influence the faunal community structure based on their moisture availability. Five classes can be recognized (Hofmann 1987; Hofmann & Eichelberg 1987):

I	Submerged mosses
II	Mosses that are permanently moist
III	Mosses that are only rarely dry
IV	Mosses that are frequently dry
V	Exposed mosses that are often dry for long periods

In desert cryptogamic crusts, bryophytes seem to be important to the soil fauna (Brantley & Shepherd 2004). Among these invertebrates are **arachnids**, **mites**, **nematodes**, **springtails**, **tardigrades**, and other small **arthropods**. Mixed lichen and moss patches supported 27 taxa at sites in New Mexico, whereas mosses had 29 taxa. Abundance and diversity were higher in winter than in summer, most likely due to a lower water stress. Even the moss ***Syntrichia ruralis*** var. ***pseudodesertorum*** (Figure 50) may have its own invertebrate community (Kaplin & Ovezova 1986; Ovezova 1989).

In ***Vaccinium*** **heaths**, the moss litter is difficult to break down (Frak & Ponge 2002). The invertebrate fauna process the litter, convert it to animal feces, and transform the soil to mor.

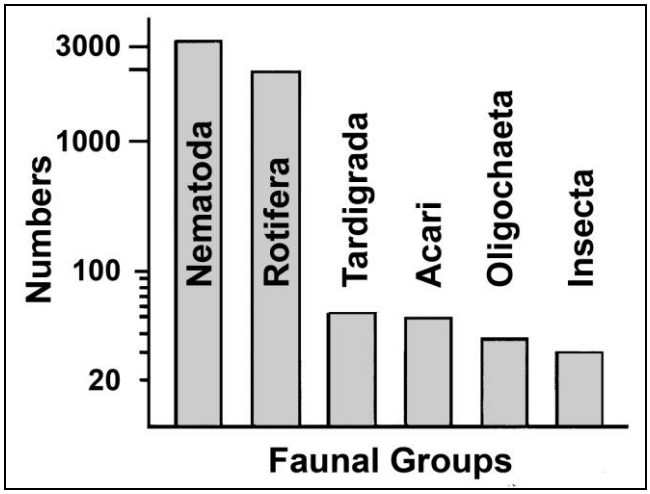

Figure 49. Mean population numbers of faunal groups from 3 2.5-cm diameter cores per moss sample, plotted on a logarithmic scale. Samples represent a variety of habitats from 26 locations in Maryland and Virginia, USA. Redrawn from Sayre & Brunson 1971.

Figure 50. ***Syntrichia ruralis*** var. ***pseudodesertorum*** may have its own invertebrate community. Photo by Paul Slichter, with permission.

In the Antarctic, the structure of the mosses [***Calliergon sarmentosum*** (Figure 51), ***Drepanocladus*** sp. (possibly ***Sanionia uncinata***)] provides a complex community where epiphytic algae and invertebrates form a higher diversity than the surrounding algal community (Priddle & Dartnall 1978). For example, ***Calliergon sarmentosum*** provides the site of most abundant algae in leaf axils. Six stem zones result from deterioration of basal portions. Benthic invertebrates move actively among these mosses. Six species of **rotifers** are common in the middle stem zones where there is the greatest abundance of epiphytes. Of these, two colonize the bare underside of leaves whereas four live mostly in leaf axils. Wind-induced mixing in the summer provides transportation for at least some of the epiphytes from the shallow portions of the lake. **Rotifers** settle there as larvae.

Figure 51. ***Calliergon sarmentosum***, a common component of the moss-invertebrate community in the Antarctic. Photo by Michael Lüth, with permission.

The invertebrate representation can be more limited in the Antarctic than in many other parts of the world. Schwarz *et al*. (1993) found that the moss-dominated flushes near the Canada Glacier supported a community where **Protozoa**, **rotifers**, **worms**, and **tardigrades** dominated, with all but the **Protozoa** occurring at 5-10.83 mm depth in the moss. Following melt, more of the organisms were found in the upper 5 mm of the moss habitat. **Mites** occurred in lesser quantities and **Collembola** were nearly absent. On the other hand, a catenulid **flatworm** in that habitat was a rare find; **microturbellarians** are quite rare in Antarctica.

Bryophytic epiphytes are important habitats for invertebrates. Kellar (1999) and Milne and Short (1999) demonstrated this for ***Dicranoloma*** in the cool temperate rainforest of Victoria, Australia. Nadkarni and Longino (1990) have demonstrated this for the neotropics.

Lobules as Habitat

As discussed in the chapters on micro-organisms and rotifers, the water-holding lobules of some leafy liverworts may house a variety of invertebrates. In fact, these invertebrates seem in some cases to be attracted to the plants and readily enter the lobules (Hess *et al*. 2005). In the leafy liverwort ***Pleurozia purpurea*** (Figure 52-Figure 53), the fauna include **Ciliata**, **Rhizopoda** (protozoans), **flatworms**, **nematodes**, **annelids**, **rotifers**, **tardigrades**, and **copepods**. A detailed discussion of the "trapping" mechanism of the lobules is in sub-Chapter 2-6 on protozoa. Whether these invertebrates are truly trapped and consumed by the liverworts remains unknown. Decaying inhabitants provide food for other members of the community and provide a proximal source of nutrients for the liverwort leaves. These organisms form a unique faunal community where organisms live, consume, die, and decay.

Aquatic

Bryophytes can offer communities that mimic those of riffles, or house very different communities. In her study of the River Liffey, Ireland, Frost (1942) found that the

numbers of organisms found in 23 bryophyte samples differed little between an acid (ca 282,000 organisms) and an alkaline (ca 306,900 organisms) stream, but the composition of the organism differed. On the other hand, Elgmork and Sæther (1970) found that at least some species exhibited larger numbers of individuals at locations with moss cover on the stones than those without mosses, suggesting that the mosses could accommodate a much larger number of invertebrates.

Figure 52. The leafy liverwort ***Pleurozia purpurea***, showing the protective nature of the curved leaves. The lobules are underneath. Photo by Sebastian Hess, with permission.

Figure 53. **Left:** Worm, probably an **oligochaete**, from the lobule of the leafy liverwort ***Pleurozia purpurea***. **Right:** Lobule of the liverwort, ***Pleurozia purpurea***. Photos by Sebastian Hess, with permission.

In a study of Doe Run, Meade County, Kentucky, USA, Minckley (1963) found that the invertebrate abundance in beds of the moss ***Fissidens fontanus*** (Figure 54) "strongly reflected the fauna of unvegetated riffles." This seems to be almost a contradiction since the same study demonstrated that the closely matted ***F. fontanus*** created a "pool environment in the midst of riffles." Minckley suggested that those animals that were relatively scarce in the moss beds but much more abundant in the rubble of smaller riffles may have been driven there by the preference of crustaceans for the mosses. Inhabiting the riffles permitted the smaller invertebrates to avoid being dinner for the crustaceans.

Figure 54. ***Fissidens fontanus***, an aquatic moss that creates a quiet refuge in the middle of riffles. Photo by Tan Sze Wei Aquamoss website <www.aquamoss.net>, with permission.

Kinchin (1992) considered the faunal inhabitants to grade from unspecialized among the submerged mosses to more specialized, drought-resistant or drought-tolerant toward the dry end. Carpenter and Lodge (1986) found that submerged plants, including bryophytes, affect the physical environment through light extinction, temperature modulation, hydrodynamics, and substrate. They alter the chemistry by providing oxygen, altering inorganic and organic carbon, and sequestering nutrients. Nevertheless, some habitats, while appearing suitable, are not colonized by any species.

Aquatic bryophytes in streams generally house the largest and probably the most diverse fauna among the various stream communities (see *e.g.* Percival & Whitehead 1929; Frost 1942; Badcock 1953; Hynes 1961; Minckley 1963; Thorum 1966; Stern & Stern 1969; Michaelis 1977; Cowie & Winterbourn 1979; Carpenter & Lodge 1986; Suren 1988, 1991a, b; Vlčková *et al.* 2001/2002; Paavola 2003). Amos (1999) described the torrent among the ***Fontinalis*** branches (Figure 55) in a poetic fashion: "All was quiet at the bottom of the torrent moss world, despite the storm of rushing water overhead." Here one could find zones of algae – diatoms, desmids, and filamentous species. Inhabitants included **round** and **segmented worms**, **rotifers**, **gastrotrichs**, **water fleas**, **copepods**, **scuds**, and a variety of larval **insects** as well as adults of tiny species. The **mountain midge** larva anchors there with suction cups that are even better than those of the squid and octopus. Yet Kinchin (1990b, 1992) paints a different picture of the waterfalls in Ein Gedi Nature Reserve, Israel, where the fauna is relatively poor.

Figure 55. ***Fontinalis antipyretica*** houses a wide range of invertebrates in streams and lakes, giving them a refuge from rapid flow and predators. Photo by Michael Lüth, with permission.

Specificity for particular bryophytes may be more a result of the habitat where each bryophyte lives. Paavola 2003) attempted to show the relationship between bryophytes, macroinvertebrates, and fish, with a goal to show concordance and usefulness in predictive power. Bryophytes and macroinvertebrates showed a weak congruence with weak predictive power, but neither had a good congruence with fish. Cowie and Winterbourn (1979) found distinct preferences for certain bryophyte species among the invertebrates in a New Zealand stream, but these differences also reflected habitat differences such as position in sream. ***Fissidens rigidulus*** occurred in the torrential water in mid channel. ***Pterygophyllu quadrifarium*** occurred where it was water saturated by the inner spray zone of a waterfall. ***Cratoneuropsis relaxa*** grew in the outer spray zone. Cowie and Winterbourn suggested that the invertebrates responded to differences in water saturation, flow rates, and detritus-trapping ability by the mosses, the latter also relating to flow rate but including aspects of the moss morphology.

In aquatic habitats, bryophytes are particularly important in contributing to faunal diversity (Priddle & Dartnall 1978; Suren & Winterbourn 1992a). In the Antarctic, these faunal groups are dominated by **Protozoa**, **Rotifera**, **Nematoda**, **Turbellaria**, **Tardigrada**, **Oligochaeta**, and **Acari** (Ingole & Parulekar 1990). In alpine streams of New Zealand, bryophytes provide shelter with reduced flow (Suren 1991b) and catchment for algae and detritus, thus creating a habitat with both shelter and food (Suren 1992), and in some cases materials for constructing larval cases (Suren 1987). Among 23 invertebrate taxa, 14 were found with bryophyte fragments in their gut, but their presence in the gut was only common in several of the aquatic insects (Suren & Winterbourn 1991). Bryophytes contained more indigestible compounds than did other plants, making them less nutritious. Rather, it appears that detritus and periphyton were the primary food sources (Suren & Winterbourn 1992b).

In these New Zealand streams, the bryophyte faunal communities were greater in streams above the treeline (Suren 1993). Greater invertebrate density occurred within bryophyte communities with periphyton than those with detritus (Suren 1993). Bryophyte communities were dominated by aquatic **insects** and **Nematoda**, **oribatid mites**, **Hydracarina**, **Copepoda**, and **Ostracoda** (Suren 1988). When artificial mosses were used in place of real ones, similar invertebrate communities developed, but some, *e.g.* **Nematoda**, **Acarina**, **Tardigrada**, **Ostracoda**, seemed to suffer from loss of the food supply (Suren 1991a).

Linhart *et al*. (2002) examined the fauna of ***Fontinalis antipyretica*** (Figure 55) growing on rocks used to stabilize a side channel of the Morava River in the Czech Republic. The means of moss-dwelling meiofauna were 253,917 ± 178,335 (± SD) per 10 g dry weight of moss and 7,160,461 ± 5,029,047 per 1 m^2 of the bottom area during October 1999-November 2000. **Bdelloidea** (rotifers) formed the dominant group (76%), followed by **Monogononta** (rotifers) (11.23%), **Nematoda** (6.38%), **Chironomidae** (midges) (4.08%), and **Oligochaeta** (worms) (1.06%). Linhart and coworkers (2002) considered that fine particulate matter trapped by the mosses would serve as both a habitat and a food source. They found that about 4% of the trapped matter was coarse matter (500-1000 µm), 14% medium (10-500 µm), and 82% fine (30-300 µm). Only 10% of the trapped matter is organic. The size and content of the trapped matter were significantly correlated (P<0.05) with densities of **Oligochaeta** (segmented worms), **Hydrachnidia** (mites), **Cladocera**, **Copepoda**, and **Chironomidae**. They reported that the bryophyte habitat houses considerably greater numbers of meiofauna compared to the stream gravel bed. Table 1 compates the numbers of moss-dwelling organisms in streams.

Even in the Antarctic, bryophytes are important habitats for invertebrates. In the flushes of meltwater, moss-dwelling invertebrates are dominated by protozoa, rotifers, nematodes, and tardigrades that live at moss depths of 5-10.8 mm. The upper 5 mm of the moss housed more members of all groups in post-melt samples than in pre-melt samples. Mites were less important than in more temperate climates. On the other hand, a flatworm, which is rare in the Antarctic, occurred there.

Altitudinal Gradients

Altitudinal gradients are often followed by community and diversity gradients. But surprisingly, the greatest diversity often occurs at mid altitudes rather than decreasing toward the summit. Andrew *et al.* (2003) investigated diversity gradients of invertebrates on bryophytes on mountains in Tasmania and New Zealand. Although they found altitudinal relationships, these were not consistent among the four mountains they studied. Rather, there were strong geographic differences. Mt. Field in Tasmania had the highest invertebrate and bryophyte diversity at 750 m, whereas Mt. Rufus had low diversity of both throughout its entire altitudinal gradient. In New Zealand, Otira had the highest bryophyte and invertebrate diversity at low altitudes, but Kaikoura had the highest invertebrate diversity at the highest altitude where the bryophyte diversity was lowest.

Food Webs

The aquatic food web is quite complex. It appears that detritus and periphyton may play a major role in the presence and abundance of invertebrates on the bryophytes (Percival & Whitehead 1929). Suren (1988) experimented with artificial bryophytes made of nylon cord woven into a

4 mm mesh mat. In the stream where the mat was highly colonized by periphyton and detritus, the invertebrates were far more abundant than in the stream with little periphyton and detritus on the mat. There was little difference between the number of inertebrates on the artificial and real mosses. But some groups were significantly reduced on the artificial mosses: **Acarina** (mites), **Collembola** (springtails), **Tardigrada** (water bears), **Dorylaimoidea** (nematode worms), and **Ostracoda**, possibly due to the loss of the bryophytes as a food source. It appears that the **aquatic insects** do not depend on the bryophytes for food, but some of the other invertebrates do. Aquatic insect relationships will be discussed in the chapter on aquatic insects, since they are major players in the aquatic bryophyte realm.

Much less is known about the terrestrial food webs in bryophyte microcosms. Sayre and Brunson (1971) pointed out that these ecosystems have the same four basic food units as larger ecosystems described by Odum (1963): abiotic, producer, consumer, and decomposer. In fact, there are often secondary consumers and even some tertiary consumers.

The **abiotic** portion of the habitat includes dust and other particles gained from the atmosphere, organic leachates from the bryophytes (and host trees for epiphytes), decaying bryophyte parts, and the remains of dead inhabitants. The water film enveloping the bryophytes is essential to their survival in active states, but like the bryophytes, most of the organisms living here are capable of dormancy when the water dries up. They gain the advantage that the bryophytes dry slowly compared to most other available substrata.

The bryophytes themselves are **producers**, but they often also have algae on them (yes, even those on trees) and may have lichens associated with them, both of which add to the carbon fixation.

Table 1. Comparison of numbers of invertebrate organisms in moss collections from streams. **NR** means not reported.

	Sample Size	Hydrozoa	Platyhelminthes	Nematoda	Annelida	Rotifera	Gastrotricha	Tardigrada	Non-Insect Arthropoda	Insecta	Mollusca	Reference
Straffan, River Liffey, Ireland	200 g	NR	0.1	56.0	48.0	NR	NR	NR	489	12755	0.7	Frost 1942
Ballysmuttan, River Liffey, Ireland	200 g	NR	0.1	38.0	36.0	NR	NR	NR	160	12051	+	Frost 1942
Cold Springbrook, Tennessee, USA	0.1 m²	NR	1.1	NR	NR	NR	NR	NR	18.9	255	NR	Stern & Stern 1969
Bystřice, Czech Republic	10 g dry	34	319	18305	1355	54561	1347	736	1817	46426	NR	Vlčková *et al.* 2001-2002
Mlýnský náhon, Czech Republic	10 g dry	0.0	37	16198	3602	222084	189	277	427	11229	NR	Vlčková *et al.* 2001-2002
Welsh Dee Tributary, Wales	~300 cm²	NR	0.5	1.8	11.5	NR	NR	NR			NR	Hynes 1961
Mouse Stream, alpine, New Zealand	1 m²	NR	NR	87430	NR	NR	NR	5640			NR	Suren 1991a
Tim's Creek, alpine, New Zealand	1 m²	NR	NR	6810	NR	NR	NR	0			NR	Suren 1991a
West Riding, Yorkshire, GB - loose moss	%	NR	NR	NR	4.6	0.0	NR	NR	4.6	90	0.4	Percival & Whitehead 1929
West Riding, Yorkshire, GB - thick moss	%	NR	NR	NR	0.0	0.0	NR	NR	4.7	63	4.1	Percival & Whitehead 1929
alpine unshaded stream, New Zealand	% top 10	NR	NR	22.1	NR	NR	NR	2.4	12.9	61		Suren 1991b
alpine shaded stream, New Zealand	% top 10	NR	NR	12.5	NR	NR	NR	0.0	8.1	74		Suren 1991b

The **consumer** component of the bryophyte community has seldom been investigated. We know that **tardigrades** are often specifically adapted to sucking contents from bryophyte cells and may be the primary consumers (Pennak 1953; LeGros 1958). However, many **tardigrades** are also carnivores; Sayre and Brunson (1971) suggest that most of those in their study were secondary consumers, *i.e.* predators/carnivores. Higgins (1959) suggested **rotifers** were a food source for **tardigrades**. As one of the two most abundant invertebrates in samples of Sayre and Brunson (1971), **rotifers** are a good source of food. **Tardigrades** also feed on **nematodes** (Sayre 1969).

As in other habitats, fungi and bacteria break down the debris that accumulates among the bryophytes. The bacteria and the by-products of their decomposition provide food for **nematodes**, **rotifers**, and **oligochaetes** (Sayre & Brunson 1971). Hence, one could hypothesize a simple food web (Figure 56).

Frost (1942) considered the mosses in some habitats to be a fallback substrate. She thought that those organisms that reach large numbers on other kinds of plants could colonize the moss when the other plants became overcrowded. This would increase the importance of the mosses in the food web. In other cases, they provide a winter substrate when tracheophytes are dormant.

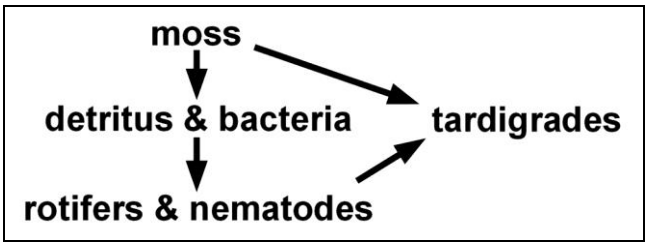

Figure 56. Theoretical food web involving mosses and lower invertebrates. **Mollusks**, **insects**, and other **arthropods** could form secondary and tertiary consumers in this web.

Pollution

One predicted consequence of acidification is a shift from tracheophytes to bryophytes, especially in lakes (Carpenter & Lodge 1986). This may also be so in slow streams, whereas fast streams are typically dominated by bryophytes from the start. A consequence of this shift is likely to be a decrease in rates of decomposition in the sediment and an increasse in the diffusion of phosphorus, iron, and possibly other metal ions into the water column. These chemical changes relate to the inability of bryophyte rhizoids and shoots to oxidize the sediments. These changes are likely to result in changes to the faunal community, but the interactions are too complex to make good predictions.

Mosses are well known for their ability to monitor and indicate pollution. But it appears that their fauna may also be important indicators of the assault by heavy metals and other air pollutants (Steiner 1994a, b, c). Zullini and Peretti (1986) found that lead pollution affects **nematodes** living among mosses. Species richness declines and communities become more uniform as pollution levels rise, especially for the **oribatid mites** (Figure 58) (Steiner 1995a). Moss communities of **nematodes**, **rotifers**, and **tardigrades** change composition in response to SO_2 fumigation (Steiner 1995b). Both **nematodes** and **tardigrades** were greatly reduced in numbers by the highest SO_2 levels (0.225 ppm), particularly the nematodes ***Chiloplectus*** *cf.* ***andrassyi*** and ***Paratripyla intermedia***. Nevertheless, the tardigrade ***Macrobiotus persimilis*** (Figure 57) actually increased with increasing SO_2 levels. More attention should be paid to these organisms whose population numbers can serve as suitable indicators of pollution.

Figure 57. ***Macrobiotus*** cf. ***furciger***, a tardigrade that seems to thrive in higher SO_2 levels. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Although the **arthropods** in aquatic systems have often been used as indicators, in terrestrial moss communities they seem to be less sensitive to pollution than **nematodes** and **tardigrades** (Steiner 1995b).

Harvesting Dangers

It would be irresponsible to include this and the succeeding chapters without reminding the readers of the dangers lurking in harvested mosses. Such mosses, like their living counterparts, harbor numerous invertebrates (Peck *et al.* 1996), many that can become dormant for extended periods of time. The danger is not one to your safety, but to safety of ecosystems that may be disturbed, first in one from which you remove the bryophytes, and second to one to which they are transported.

Muir (2004) reported 81 million pounds of moss per year, the equivalent of about 10,500 semi-trucks, harvested in the Pacific Northwest. This massive harvest on logs can take 10-23 years to recover (Peck 2006). Most likely a greater recovery time is needed for epiphytes.

Using a Berlese funnel for extraction, Peck and Moldenke (1999) identified 125 invertebrate taxa from 200 moss mats in Oregon, USA. Greater overall numbers were present at shrub bases than at tips. However, this pattern did not exist for all organism groups (Peck & Moldenke 1999). **Coleoptera** (beetles) and **Thysanoptera** (thrips) exhibited greater numbers per gram at the base, as did detritivores in general, but spiders and predators in general were actually lower in numbers at the bases. Turtle-mites characterized basal samples [***Ceratoppia*** sp. (Figure 58), ***Hermannia***, and ***Phthiracarus*** sp. (Figure 60)], whereas microspiders (**Micryphantidae**) and springtails (***Sminthurus***; Figure 61) were typical of tips.

Figure 58. ***Ceratoppia*** sp., a genus that lives among bryophytes at the bases of shrubs in Oregon, USA. Photo by Dragiša Savić, with permission.

Figure 59. ***Hermannia*** sp., a turtle-mite that lives among bryophytes at the bases of shrubs in Oregon, USA. Photo by Tom Murray, through Creative Commons.

Figure 60. ***Phthiracarus*** sp., a mite species that lives among bryophytes at the bases of shrubs in Oregon, USA. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 61. ***Sminthurus viridis***; ***Sminthurus*** is typical of bryophytes at the tips of shrub branches in Oregon, USA. Photo by AfroBrazilian, through Creative Commons.

Moss harvesting therefore creates two problems. At first it creates the possibility of endangering specific inhabitants that thrive only among bryophytes. Secondly, transport of harvested mosses will undoubtedly also transport the invertebrate fauna, providing the possibility for these creatures to invade areas where they did not exist before, most likely altering their new ecosystem, often to the detriment of the native fauna and flora. Details of harvesting will be discussed in a different volume.

Summary

The invertebrate fauna living among bryophytes can be variously categorized as **cryptozoic fauna** (hidden animals), **meiofauna** (retained on a mesh size of 42 µm, and **benthic** (living on the bottom of a body of water). The non-arthropod fauna include primarily **nematodes**, **rotifers**, **tardigrades**, and **annelids**, generally in that order of abundance. Their diverse feeding strategies engage them in nutrient cycling.

Sampling can be difficult and often requires extraction by hand or use of a **Baermann or Berlese funnel**. Whenever possible, specimens should be preserved in a recognized museum and that location published along with any studies involving them.

In aquatic habitats, the bryophytes provide a safe site away from torrents and large predators, where invertebrates are known to number as much as 25,400 per g dry weight of ***Fontinalis***. Detrital matter trapped by the moss is a ready food source. In prairies and desert regions, bryophytes may provide the most important suitable habitat. In the Antarctic, epiphytic algae provide food for the meiofauna.

Most of the organisms do not eat bryophytes and depend on adhering detritus and bacteria for food (**rotifers** & **nematodes**). **Tardigrades**, however, may also eat bryophytes.

Because of their ability to respond to heavy metals and other pollutants, the invertebrates provide a suitable group to monitor air pollution, along with their bryophyte habitat.

On one hand, harvesting of bryophytes can remove endangered invertebrate species, and on the other may distribute species to new areas where they may become invasive or disruptive to new ecosystems.

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CHAPTER 4-2
INVERTEBRATES: SPONGES, GASTROTRICHS, NEMERTEANS, AND FLATWORMS

Figure 1. This **planarian, *Polycladus gayi***, is navigating a mat of the liverwort ***Lepidozia cordulifera***. The planarian is a native of Valdivian rainforests of southern Chile, where it hunts for food on bryophytes and other substrata. Photo courtesy of Filipe Osorio.

Cnidaria

Members of the **Hydrozoa** (hydroids) are not common among bryophytes, but they can occur there. Jones (1951) reported ***Hydra viridissima*** (Figure 2) from ***Fontinalis antipyretica*** (Figure 3) on bedrock in the River Towy, Wales.

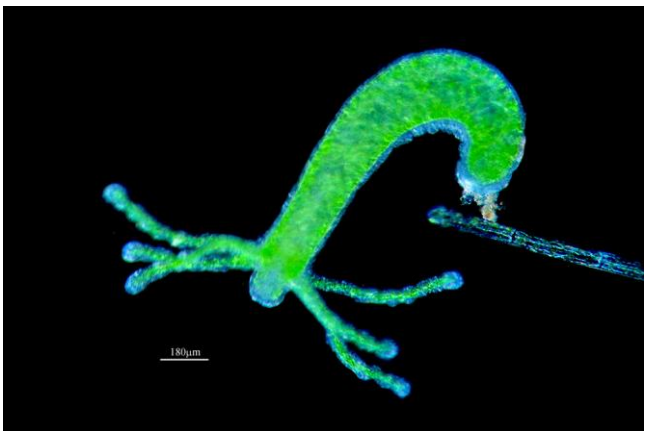

Figure 2. ***Hydra viridissima***, occasional bryophyte dweller. Photo from Proyecto Agua, with permission.

Figure 3. ***Fontianlis antipyretica*** growing in a stream where it can offer a protected substrate for a number of invertebrates. Photo by Andrew Spink, with permission.

Porifera – Sponges

Sponges don't seem to have any particular appreciation of bryophytes, being unknown from that habitat. However, it appears that the moss genus ***Fissidens*** has a special fondness for sponges. I know of no other bryophyte genus

that finds this a suitable habitat, but ***Fissidens fontanus*** (Figure 4) in Europe is epizootic on **sponges** (Sowter 1972) and ***F. brachypus*** lives only on freshwater sponges in the Amazon (Buck & Pursell 1980). ***Fissidens*** seems to like animal habitats, living on the openings of wombat holes, termite mounds, and in this case, on a sponge.

Although a moss-sponge combination in nature is rare, humans seem to have found this combination useful. A patent application by Albert G. Morey, dated 13 October 1968, for an "improved mattress" extols the virtues of placing a large **sponge** (mattress) over a layer of only slightly spongy material such as moss. A three-layer mattress is considered to be superior, with the lower layer of moss sustaining the middle layer of woody fiber or excelsior, again with a layer of elastic **sponge** on top. It appears that this was a real sponge (or lots of them) and predates the use of cellulose sponges. The improvement seems to have been the addition of the moss and fibrous layers.

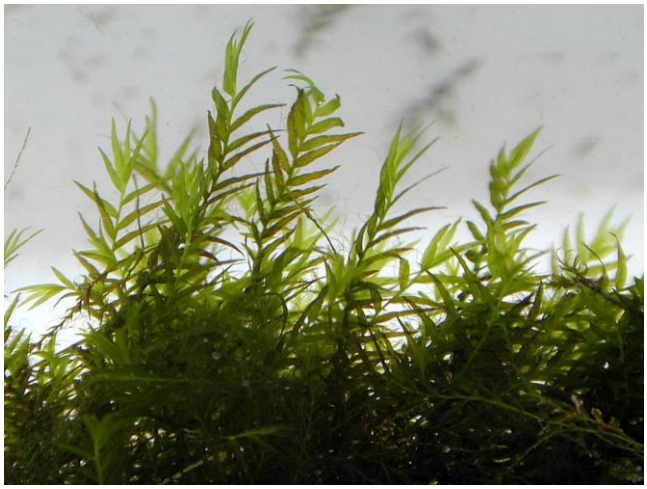

Figure 4. ***Fissidens fontanus***, a species that can be epizootic on **sponges**. Photo by Michael Lüth, with permission.

Gastrotrichs

These small animals with "hairs on their stomachs" use them to beat against such surfaces as moss leaves to glide forward (Figure 5-Figure 11; Hingley 1993). They lack a coelom, like flatworms, and move in a similar motion. Like nematodes, rotifers, and tardigrades, freshwater **gastrotrichs** are all **parthenogenetic**, producing viable unfertilized eggs. Adults are unable to go dormant, but when unfavorable conditions arise, they produce larger eggs with heavier shells that survive not only desiccation, but also low and high temperatures. They adhere using cement glands in two terminal projections (Gastrotrich 2009). One of the glands conveniently secretes a de-adhesion to release them.

They may be found occasionally on aquatic bryophytes. The **Dichaeturidae** is a rare family that has been found in cisterns, in underground water, and among mosses (Remane 1935-1936; Ruttner-Kolisko 1955). In the Czech Republic, Vlčková *et al.* (2001/2002) reported 2823 of these invertebrates on 100 ml of the aquatic moss ***Fontinalis antipyretica*** (Figure 3) in Bystřice, whereas in Mlýnský náhon there were only 371 per 100 ml. In Bystřice the mosses held a food source of organic matter in the size range of 30-100 µm. Linhart *et al.* (2002) found that abundance was negatively influenced by flow velocity in both of these streams, and the gastrotrichs were significantly fewer in riffles, suggesting that bryophytes could act as refugia in areas of high flow. On the other hand, sediment also was reduced in areas of high velocity, resulting in more available food in sediments in low velocity areas.

In a peatland complex in northern Italy, Balsamo and Todaro (1993) identified 21 species of **gastrotrichs**. Hingley (1993) found the following gastrotrichs among the peatlands mosses in her study of the British Isles:

Chaetonotus heterocanthus	*Chaetonotus zelinkai*
Chaetonotus maximus	*Heterolepidoderma ocellatum*
Chaetonotus ophiogaster	*Ichthydium forcipatum*
Chaetonotus polyspinosus	*Lepidodermella squamatum*
Chaetonotus voigti	*Stylochaeta fusiformis*

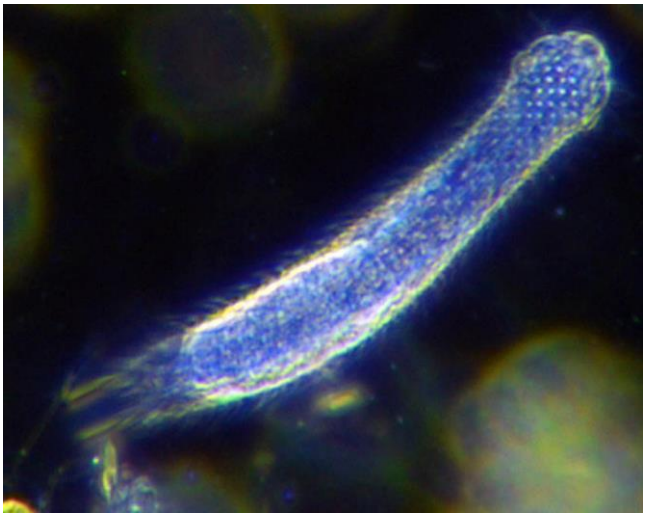

Figure 5. **Gastrotrich** showing two tails and cilia. Photo by Jasper Nance through Wikimedia Commons.

Figure 6. **Gastrotrichs** awakened from dry soil. Photo by Paul G. Davison, with permission.

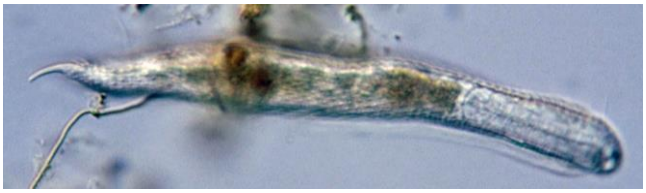

Figure 7. ***Heterolepiderma***, a genus that has moss-dwelling gastrotrichs. Photo by Yuuji Tsukii, with permission.

Figure 8. ***Chaetonotus cordiformis*** next to a desmid. Photo by Yuuji Tsukii, with permission.

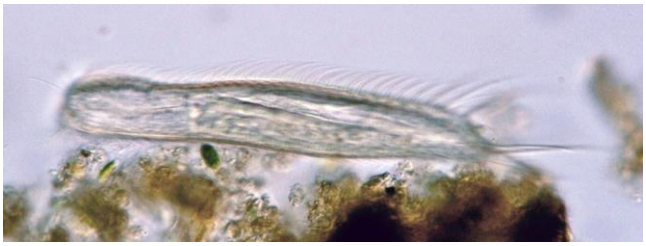

Figure 9. ***Chaetonotus zelinkai***, a moss-dwelling gastrotrich. Photo by Yuuji Tsukii, with permission.

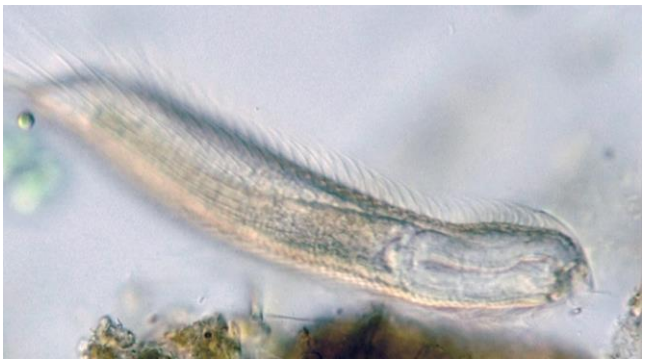

Figure 10. ***Chaetonotus zelinkai***, a peatland gastrotrich. Photo by Yuuji Tsukii, with permission.

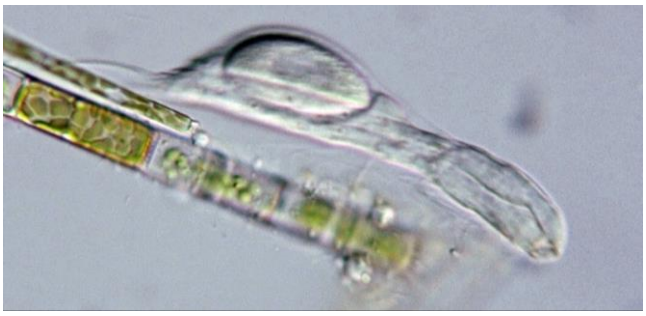

Figure 11. ***Ichthydium forficula***, a member of a genus that can occupy peatlands. Photo by Yuuji Tsukii, with permission.

Nemertea – Ribbon Worms

The ribbon worms are an unknown phylum to most of us. But those nemertines that live on land have learned about bryophytes. In 1915, Dakin described one of these as a new species *Geonemertes dendyi*, later moved to ***Argonemertes dendyi*** (Figure 12), from Western Australia. Anderson (1980) reported this species from Ireland, where it can be found among a thin layer of mosses on branches. Later, Anderson (1986) reported it from mosses and under bark in Ireland. Ribbon worms are clandestine species that one can rarely find in the open (Winsor 2001, pers. comm. 29 February 2012).

Argonemertes dendyi (Figure 12) is among the small fauna, measuring only 15 mm (Dakin 1915). It has multiple eyes, numbering as many as 30 or 40. As descendents from marine organisms, one of the major adaptations required by terrestrial nemerteans was a way to maintain sufficient hydration (Moore & Gibson 1985). The physiological mechanisms are not well understood but seem to involve mucous glands, blood and excretory system, and modulation of osmotic properties. These worms often travel with potted plants, and consequently they can be found in far-flung parts of the planet (Gibson 1995; Moore *et al*. 2001). Their hermaphroditic reproduction makes establishment of these travellers more likely to succeed.

Figure 12. ***Argonemertes dendyi***. Photo by Malcolm Storey through Creative Commons.

Leigh Winsor (pers. comm., 16 February 2012) is an avid seeker of terrestrial flatworms, but occasionally he also finds nemertines (Winsor 1985). He reports finding ***Argonemertes australiensis*** (Figure 13) under a thick mat of moss where it resided on a rotting log in a closed forest in southwest Tasmania. That is impressive for a worm that is 40 mm long (Hickman 1963; Moore 1975; Mesibov 1994). The egg capsules typically occur in rotting logs in August and March (Winsor 1996/97). These eggs are clear, jelly-like, and oblong, ca 10 mm long X 3 mm diameter.

Figure 13. ***Argonemertes australiensis*** extracted from moss on a log. Photo by Leigh Winsor, with permission.

This strange nemertine uses its proboscis to escape. When in a hurry, the worm quickly everts the proboscis and uses it as a muscled anchor to pull its body forward rapidly

as the proboscis once again returns to its internal lodging (Figure 14). This rapid proboscis also out-paces its Collembola and other prey, permitting the worm to capture its dinner. This species comes in three very distinct color varieties (Mesibov 1994), most likely permitting it to survive in its diverse habitat where different predators may lurk in different locations, a phenomenon we will discuss later for tropical frogs.

Figure 14. ***Argonemertes australiensis*** with an extended proboscis. Photo by Leigh Winsor, with permission.

Platyhelminthes – Flatworms

Most of us in the pre-DNA-biology generations learned about flatworms in high school because it was easy to do experiments with ***Dugesia*** (see *e.g.* Saló & Baguñà 2002), known to most of us as *Planaria*. This animal has a distinguishable head with two eyes, and it was relatively easy to cut the head in half and watch two heads develop. This novel exercise opened discussions about development and other topics and provided a memorable experience that endeared the flatworms to us for life.

Most of the **turbellaria** (Figure 1), formerly a class within the phylum **Platyhelminthes**, are nocturnal and free-living, and it is among this group that one finds a small number of bryophyte-dwellers. The group is not monophyletic and is no longer recognized taxonomically, but the concept of **turbellaria** is useful for our purposes as all the bryophyte dwellers are in this group of non-parasites. The **turbellaria** lack a true body cavity and are shaped like a large ciliate protozoan and actually have a covering of cilia that permits them to glide (Hingley 1993). But they are multicellular, somewhat flattened, as their phylum name implies, where *platy* means flat and *helminth* means worm. This flattening permits them to obtain oxygen throughout their bodies, which lack circulatory and respiratory organs. They sport a simple digestive system, nervous system, and excretory system, and they seem to lack any sort of physiological or anatomical adaptations for conserving water, but they may be able to conserve water through alternative biochemical excretory pathways (Winsor *et al*. 2004). They even have eyespots and a simple brain (Hingley 1993).

Reproduction in the phylum may be by simple division (fission), whereas almost all turbellarians are **simultaneous hermaphrodites** (have both sexes at the same time). Among the family Typhloplanidae, the eggs may be thin-shelled in summer and hatch within days of being laid, but winter eggs are often thick-shelled and may be dormant (Pennak 1953; Domenici & Gremigni 1977; Hingley 1993). In the Typhloplanidae, these thick-shelled eggs can survive desiccation, whereas mature individuals might migrate to more moist, deeper levels. In other terrestrial flatworms, egg shells are typically thick (Figure 15), but the process of laying down the shell is different from those of the Typhloplanidae, and their ability to survive harsh conditions is unknown. These process differences may relate to differences between freshwater and terrestrial triclads (Winsor 1998a).

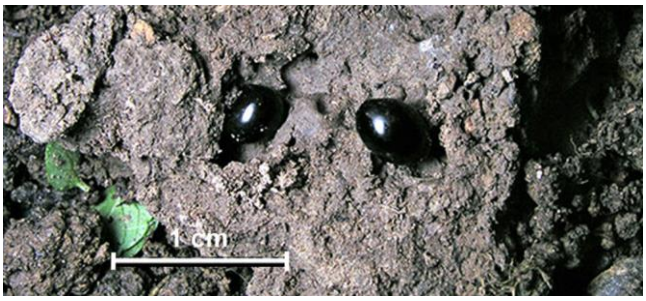

Figure 15. Eggs of a terrestrial flatworm. Photo by Alastair Robertson and Maria Minor, Massey University, Copyright SoilBugs, published by permission.

Bryophyte Habitat Constraints

Leigh Winsor, who has spent more than 40 years studying terrestrial flatworms, says that in wet forests the bryophytes are generally too adherent to the substrate to permit the (large) flatworms to move beneath the moss (Leigh Winsor, pers. comm. 16 February 2012).

Furthermore, unlike many of the invertebrates that seek mosses to maintain moisture, the flatworms seek a fairly smooth surface to which they can adhere their ventral surface, thus minimizing water loss. I would suggest further that the hygroscopic mosses might actually absorb surface water from the flatworms in drying conditions, further drying them. Nevertheless, the bryophyte mats do offer a substrate where the flatworms can pursue their prey (Leigh Winsor, pers. comm. 16 February 2012). And some seem to solve the problem of water loss by twisting into a knot that glues the ventral surface to itself (Figure 16). On the other hand, in excessively wet conditions, the terrestrial flatworms may use mosses to prevent getting too wet by crawling up into the moss and away from **frank water** (obvious pools of water).

Figure 16. ***Australopacifica*** sp. in knot on moss in New Zealand. Photo by Alastair Robertson and Maria Minor, Massey University, Copyright SoilBugs, published by permission.

Following Schultze (1857), who suggested that terrestrial planarians are likely to exhibit a rich fauna concealed in damp mosses, under stones, and other habitats where moisture is sufficient to maintain them, Davison *et al*. (2008, 2009) report on bryophilous microturbellarians from northwest Alabama, USA. These smaller versions are able to live among mosses on tree trunks and rocks.

The terrestrial flatworm ***Tasmanoplana tasmaniana*** (Figure 17), a species widespread in a variety of habitats throughout Tasmania, has also been found beneath moss in a temperate rainforest near Fourteen Mile Creek, SW Tasmania (Leigh Winsor, pers. comm. 16 February 2012). The area was very wet and the bryophytes and logs were saturated with water.

Figure 17. ***Tasmanoplana tasmaniana***, a flatworm that lives in mosses in Tasmania. Photo by Leigh Winsor, with permission.

Bryophytes provide a moist habitat where zoospores of such parasites as the **chytridiomycosis** fungus ***Batrachochytrium dendrobatidis*** can survive (Dewel *et al.* 1985). This fungus can be lethal to some amphibians. One must wonder how bryophytes may play a role in harboring other parasites, or conversely, in providing antibiotics that deter them.

One mossy habitat that may be suitable for larger planarians is on leaves covered with epiphylls, as seen in ***Pseudogeoplana panamensis*** (Figure 18). The surface is relatively flat, and the mosses, liverworts, and other epiphylls can maintain greater moisture levels than a "clean" leaf surface. This relationship remains unstudied.

Figure 18. This flatworm, possibly ***Pseudogeoplana panamensis***, is on a palm leaf covered with lichens. Photo by Brian Gratwicke through Creative Commons.

Food Sources

When active, **microflatworms** feed on **protozoa**, **nematodes**, **rotifers**, **tardigrades**, **insect** larvae (Figure 19), and **algae** (Kolasa 1991; Davison *et al*. 2008) with which they share their mossy home. As suggested by Davison, it appears that one attraction for these **flatworms** in moss communities is the available **tardigrades** (Figure 20). **Flatworms** are known to eat **mosquito** larvae (Figure 19), so it is likely that they are able to eat **Chironomidae** (**midge**) larvae that live among the leaves of aquatic mosses and liverworts. Some **microturbellarians** are known to house green **algae** as symbionts (Kolasa 1991), presumably contributing to oxygen, but possibly also contributing carbohydrates. Such a relationship is unknown among moss-dwellers, but certainly it would be worthwhile to search for such symbionts. We do know that some of the tardigrades eat diatoms, a group of algae common on bryophytes, even in some terrestrial habitats, making algae part of the food chain (Bartels 2005).

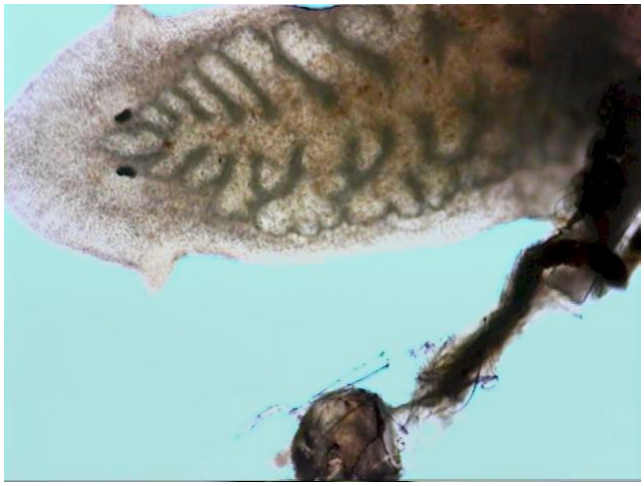

Figure 19. **Flatworm** feeding on a **mosquito** larva. Photo by Paul G. Davison, with permission.

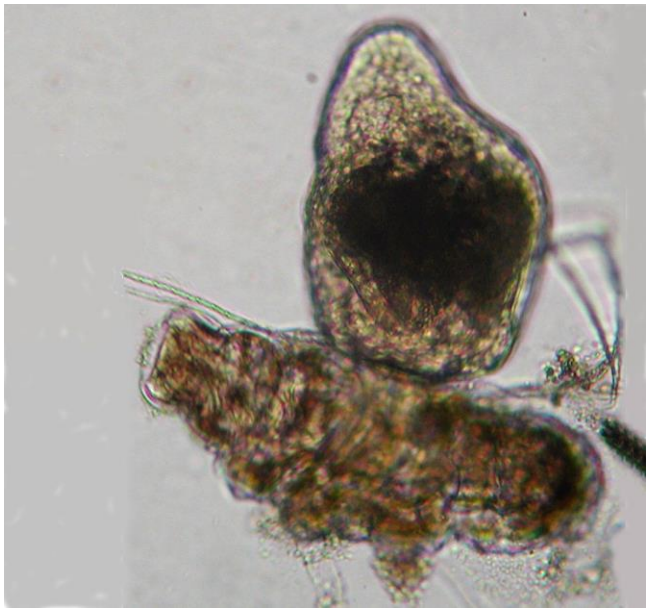

Figure 20. **Flatworm** eating **tardigrade**. Photo by Paul G. Davison, with permission.

Davison *et al*. (2009) experimented with prey choice among flatworms from epiphytic mosses in Alabama, USA. The flatworms had a strong preference for the rotifer ***Philodina roseola*** (Figure 21) over the nematode ***Panagrolaimus***, both of which occur on bryophytes (Hirschfelder *et al*. 1993; Shannon *et al*. 2005). They either ingested these prey or sucked the contents out.

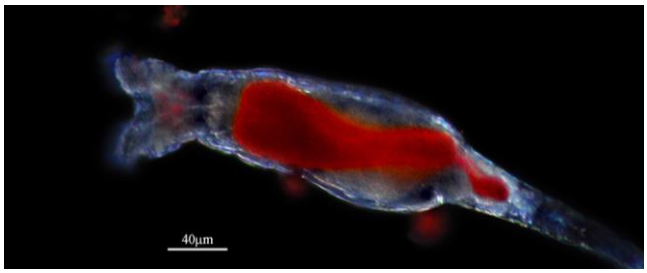

Figure 21. ***Philodina roseola***, a preferred prey organism for some flatworms. Photo from Proyecto Agua, with permission.

Protection or Predation?

The terrestrial flatworms seem to be relatively well protected from predation. Vertebrates seem to avoid them, most likely due to their mucous secretions when disturbed (Arndt & Manteufel 1925; McGee *et al*. 1996; Cannon *et al*. 1999). ***Arthurdendyus triangulatus*** (Figure 22) invokes violent reactions in earthworms when they make contact (Blackshaw & Stewart 1992 in Winsor *et al.* 2004). The flatworm wraps itself around the earthworm and secretes strong enzymes that turn the poor earthworm into soup! But then, earthworms are their primary source of food (Winsor *et al*. 2004). When this species is unable to find any food, it can survive more than 15 months at 12°C by digesting its own tissues – and shrinking (Blackshaw 1992, 1997; Christensen & Mather 1998a, 2001). However, at 20°C it dies within three weeks without food (Blackshaw 1992), so its presence at warmer temperatures needs to be timed with availability of a food source.

Figure 22. ***Arthurdendyus triangulatus*** on a bed of damp mosses. Photo © Roy Anderson, with permission.

Mosses can deprive the stoneflies of their flatworm prey. Wright (1975) found that flatworms in streams of North Wales were scarce on the undersides of stones and spent their lives confined to patches of mosses. Those that emerged from the mosses to venture to the undersides of rocks became easy prey for the stonefly *Dinocras cephalotes*.

Watch Out for Invasive Species

Arthurdendyus triangulatus (New Zealand flatworm, formerly *Artioposthia triangulata*; Figure 22) lives in damp terrestrial habitats such as those under logs, decaying wood, mosses, and leaves (Willis & Edwards 1977). ***Arthurdendyus triangulatus*** is a flatworm about 50 mm long, but can extend to 200 mm when in motion. Unlike the lab planaria with two large eyespots, ***Arthurdendyus triangulatus*** has a row of tiny black eyes extending down the pale-colored margin. These, as in planaria, are light sensitive and aid the animal in its navigation.

Arthurdendyus triangulatus (Figure 22) originated in New Zealand, but most likely hitch-hiked its way to Ireland among nursery plants, where it was able to spread to Scotland and Britain (Willis & Edwards 1977; Christensen & Mather 1998b; Baird *et al.* 2005). A member of this genus has also found its way to Macquarie Island in the subAntarctic (Winsor 2001). With its ability to travel at the rate of 28 cm per minute (Mather & Christensen 1995) and migrate as much as 20 m (Mather & Christensen 1998), there is concern about its spread in the British Isles where its habit of eating earthworms may be detrimental to their role in aerating the soil (Willis & Edwards 1977; Blackshaw 1990, 1997; Christensen & Mather 1995; Boag & Yeates 2001; Mather & Christensen 2001; Baird *et al.* 2005). One individual can eat about 1.4 *Eisenia foetida* earthworms each week (Blackshaw 1991) and has no species preference among earthworms. Furthermore, ***Arthurdendyus triangulatus*** thrives better in habitats with more earthworms (Mather & Christensen 2003).

Baird *et al*. (2005), concerned with its potential to drastically reduce the earthworm populations, studied the survival strategies of ***Arthurdendyus triangulatus*** (Figure 22) and its reproductive behavior under multiple conditions. As noted, planarians can survive for long periods of time without food, utilizing reabsorbed body tissue instead (Calow 1977; Ball & Reynoldson 1981). This permits them to survive winter and even allows them to lay eggs during that season (Baird *et al*. 2005). Whereas Christensen and Mather (1995) demonstrated that these flatworms could survive at least 15 months at 12°C without food, at lower temperatures (8°C), there was even less weight loss. In the lab, they had 100% survival under starvation for 4 weeks at 10°C, but at 15°C, 30% died during that time (Blackshaw & Stewart 1992). This greater loss of weight at temperatures above 14°C and the reduced survival at the warmer temperatures explains the greater spread seen in the northern compared to southern parts of the UK (Blackshaw 1992; Boag *et al.* 1993, 1995, 1998; Baird *et al.* 2005).

Because of these low temperature requirements, it is often necessary for these flatworms to burrow into the soil or travel down tunnels made by other invertebrates. The presence of bryophytes is likely to enhance the habitat by moderating the temperature and maintaining a greater level of moisture, but such bryophyte linkages have not been explored.

This species is a **K strategist** and is a hermaphrodite. Baird *et al*. (2005) demonstrated that ***Arthurdendyus triangulatus*** (Figure 22) could lay nine egg capsules in four months, with a mean of 4 eggs per capsule, producing 45 eggs per individual per year. It is able to store sperm after copulation (Baird 2002). Individuals cultured alone

were able to produce eggs for up to eight months, indicating that sperm could be stored at least that long (Baird *et al*. 2005).

At temperatures above 10°C, there was a considerable decrease in hatching success, but eggs took longer to hatch at 10°C (Baird *et al*. 2000, 2005). These eggs, like the adults, can easily travel with potted plants from one country to another, and although the nursery trade is highly regulated, internet sales usually escape this close scrutiny.

Desiccation Tolerance

If there is a niche, there is most likely an organism to fill it. And eventually, there is most likely a biologist to study it, but for moss-dwelling **flatworms**, this has been a long time in coming. Although **flatworms**, known to most of us as human parasites and freshwater organisms, can be quite abundant among bryophytes, their presence there is barely known (Paul Davison, pers. comm., 8 August 2007).

Unlike rhizopods and other kinds of protozoa, moss-dwelling **microflatworms** are not known to enter a state of **cryptobiosis**. Davison has collected several ***Bryoplana xerophila*** (Figure 23) from mosses on a concrete wall and taken them to room-dry conditions, then revived them (Figure 24). These relatively unknown members of the bryophyte community do form cysts and resistant eggs (Figure 25-Figure 26) that permit them to survive the alternating wet and dry conditions found among bryophytes, especially those on tree trunks, despite the thinness of their mucous covering (Davison *et al*. 2008, 2009; Van Steenkiste *et al*. 2010). But for the Australian and New Zealand fauna, these cysts do not seem to occur on the bryophytes (Leigh Winsor, pers. comm. 16 February 2012). Winsor considers the bryophyte habitat there to be too exposed for the cysts or eggs and young to survive.

Figure 23. ***Bryoplana xerophila***, a moss-dwelling **microturbellarian** from Alabama. Photo by Paul G. Davison.

But for ***Bryoplana xerophila*** (Figure 23-Figure 26) survival on rocks is facilitated by the ability to encyst (Van Steenkiste *et al*. 2010). The cysts typically occur in concavities between moss leaves and the stem connection where interstitial water slows water loss. Once rewet, they begin moving within the cyst and within minutes (up to 15 minutes) break through the cyst wall and are on their way to an active life once again. They further ensure survival of the species by laying one or two eggs as they go into encystment.

Figure 24. Recently excysted terrestrial flatworm**,** ***Bryoplana xerophila***, and empty cysts. The dark brown eggs formed during encystment provide a second means of surviving. These **flatworms** were living in the moss ***Entodon seductrix*** (Figure 44) from a concrete block wall in Florence, Alabama, induced to encyst on a glass slide, then brought back to an active state. Photo by Paul G. Davison, with permission.

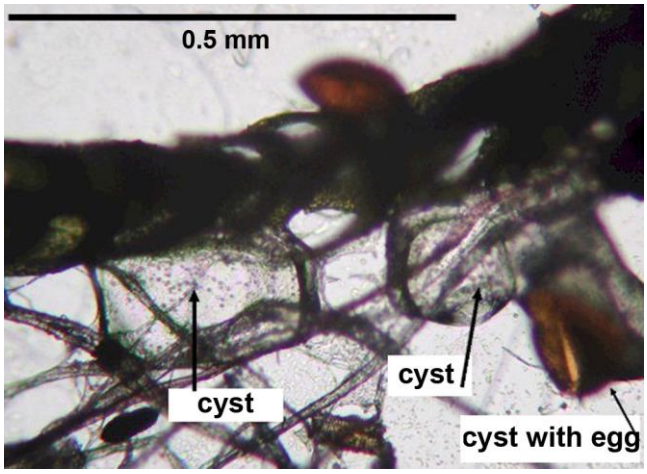

Figure 25. Cysts of flatworms, ***Bryoplana xerophila***, in desiccated state on moss. Photo by Paul G. Davison, with permission.

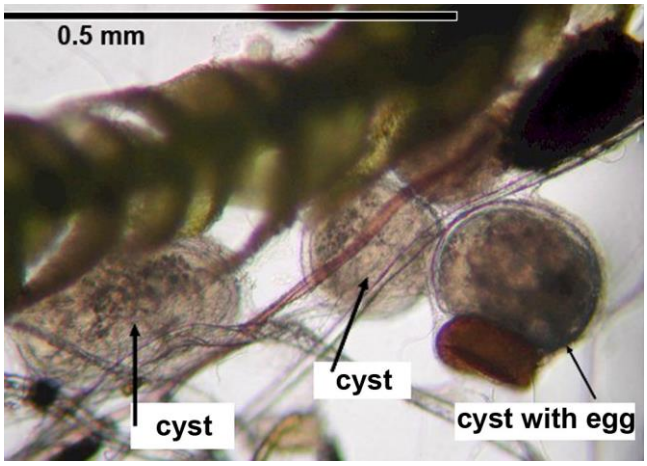

Figure 26. Cysts of flatworms, ***Bryoplana xerophila***, on a moss after rehydration. Photo by Paul G. Davison, with permission.

Terrestrial (Limnoterrestrial)

Fletchamia sugdeni (**Sugden's flatworm**, also known as **canary worm**; Figure 27-Figure 28) is a native of wet and dry forests in Victoria and Tasmania, Australia

(Winsor, 1977; Ogren & Kawakatsu 1991), where it can sometimes be found among bryophytes. Dendy (1890) noted that ***Fletchamia sugdeni*** was "remarkable for its habit of wandering about in broad daylight." That is truly remarkable for this bright yellow planarian. But the bright color might actually be a warning color that would be more useful in daylight.

Figure 27. ***Fletchamia sugdeni*** (**Sugden's flatworm**, **canary worm**), Victoria, Australia. Photo by Leigh Winsor, with permission.

Figure 28. ***Fletchamia sugdeni*** (**Sugden's flatworm, canary worm**) traversing a moss-covered substrate in Tasmania. This planarian certainly does not have camouflage on this bryophyte with its bright yellow color, but may gain protection with this warning coloration. Photo courtesy of Sarah Lloyd.

The bright yellow ***Caenoplana citrina*** (*C. barringtonensis* syn.; Figure 29) is known from mosses at Barrington Tops, New South Wales (Wood 1926). It resembles ***Fletchamia sugdeni*** (Figure 27-Figure 28), but has two stripes down its dorsal surface.

Wood (1926) noted that ***Caenoplana coerulea*** (Figure 30-Figure 31) was the commonest species collected near the Barrington River, New South Wales, being found on rocks, damp moss, the trunks of trees, and under rotten logs. Its thick-walled egg is in Figure 32.

Figure 29. A bright-colored flatworm, probably ***Caenoplana citrina*** (formerly *C. barringtonensis*), on a bed of mosses. Photo by Ian Sutton through Flickr Creative Commons.

Figure 30. ***Caenoplana coerulea***, a moss-dweller, among other habitats, displaying its blue color. Photo by Peter Woodard through Wikimedia Commons.

Figure 31. ***Caenoplana coerulea***, a moss dweller in a darker form. Photo from <www.aphotofauna.com>, with permission.

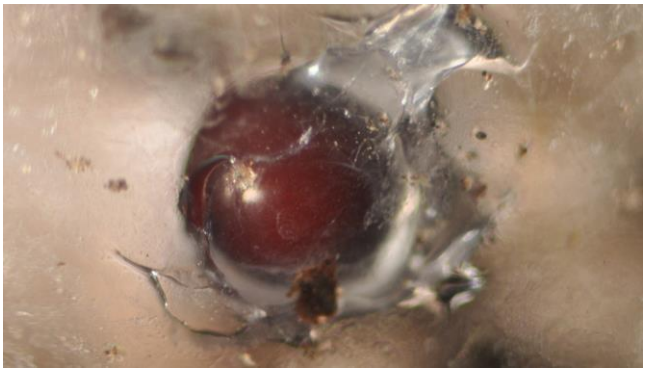

Figure 32. ***Caenoplana coerulea*** egg laid in captivity. Photo by Jacobo Martin through Flickr Creative Commons.

Elsewhere in Great Britain, McDonald and Jones (2007) compared habitat and food preferences for two species of ***Microplana***, a terrestrial flatworm. The habitat choices in the experiment were not germane to bryophytes, but in addition to the artificial cover, they did find cocoons at a 7 cm depth in ***Sphagnum*** in the garden. This genus is likely to occur among bryophytes elsewhere and thus should be sought there. The food preferences of ***Microplana terrestris*** (Figure 33) were gastropods [***Arion hortensis*** (slugs, Figure 34) and ***Discus rotundatus*** (snail, Figure 36)]. ***Microplana scharffi*** (Figure 37) preferred earthworms but also ate slugs. Both of these species avoided eating live animals and instead fed on damaged animals (see Figure 35). McDonald and Jones suggested that centipedes may contribute to that damage in nature.

Figure 33. ***Microplana terrestris*** in its grey form. Photo by Brian Eversham, with permission.

Figure 34. ***Arion hortensis***, a food source (when dead) for ***Microplana terrestris***. Photo © Roy Anderson, with permission.

Figure 35. Land planarians eating dead earthworm and dead springtails in a rainforest gully, Canberra, Australia. Photo by Andras Keszei, with permission.

Leigh Winsor (pers. comm. 16 February 2012) reports that some terrestrial flatworms have a "most unpleasant taste" (he tasted some species!) that may have a repugnatorial function. Whether brightly colored Australian flatworm species have a repugnant or toxic taste to birds or other predators is not presently known, but the yellow coloration could serve as either Batesian or Muellerian mimicry.

Figure 36. ***Discus retundatus***, a food source (when dead) for ***Microplana terrestris***. Photo by Francisco Welter Schultes through Creative Commons.

Figure 37. ***Microplana scharffi***, a flatworm that eats dead earthworms and slugs among bryophytes and elsewhere. Photo from <www.aphotofauna.com>, with permission.

Hyman (1957) reported the planarian ***Gigantea cameliae*** (identified at that time as *Geoplana cameliae* and moved to *Gigantea* by Ogren & Kawakatsu 1990) on wet mosses at night in Trinidad. This 25 mm, up to 50 mm (Hyman 1941), planarian is larger than most moss dwellers, especially among the terrestrial taxa. This species is also present in Panama (Hyman 1941), but there seem to be no reports of it from bryophytes there.

One mossy habitat where these **microturbellarians** seem to be quite rare, however, is in the Antarctic. Nevertheless, Schwarz *et al*. (1993) did find one **catenulid flatworm** inhabiting the mosses of flushes near the Canada Glacier on continental Antarctica.

Epiphyte Dwellers

The **microturbellarians** are those free-living flatworms (Platyhelminthes) generally <1 mm in length (*e.g.* Figure 23; Davison *et al*. 2008). They typically live in water films, making them essentially aquatic (**limnoterrestrial**). Bryophytes can provide such water films, so it is no real surprise that they (**Rhabdocoela**,

Typhloplanidae) are common 1-2 m above ground among epiphytic mosses. Davison *et al.* (2008) sampled longleaf pine-mixed hardwoods, *Juniperus* in limestone cedar glades, northern hardwoods above 1600 m elevation, dwarf oak forest, upland hardwoods-pine, and planted roadside pecan trees in the southeastern USA. They found that the tree trunk dwellers are rare in cool, mossy stream ravines, where one might have expected them, but are common in areas prone to rapid drying following rainfall – mosses on tree trunks fit this need well. In such locations, Davison *et al*. have found that flatworms are quite common in association with mosses on hackberries and other trees in Florence, Alabama, USA. These mosses include ***Leucodon julaceus*** (Figure 38) on *Cornus florida* and ***Clasmatodon*** (Figure 39) on *Paulownia tomentosa*, all at least 0.3 m above ground, as well as on trees of open, urban habitats, including *Catalpa* sp., *Celtis* sp., *Cornus florida*, *Fraxinus* sp., *Liquidambar*, *Magnolia grandiflora*, *Quercus* spp., and *Ulmus* spp. They survive these habitats by forming thin-coated transparent mucous cysts, a mechanism not familiar in other habitats.

Figure 38. Epiphytic ***Leucodon julaceus***, a known habitat for flatworms. Photo by Janice Glime.

Figure 39. ***Clasmatodon parvulus*** with capsule, a home for flatworms. Photo by Paul G. Davison, with permission.

Davison later collected **flatworms** from mosses on two white oaks in northern Tennessee, suggesting that they may be widespread, at least in these south temperate areas (Paul Davison, pers. comm. 12 January 2008). The collections were from the mosses ***Forsstroemia trichomitria*** (Figure 40) and ***Haplohymenium triste*** (Figure 41) growing 1.7-2 m above the ground. Although these had 10 and 6 turbellarians, a sample of ***Hypnum curvifolium*** (Figure 42) from the tree base produced only one flatworm. Davison suggests that the **water bears** (tardigrades) are important determinants of the location of the **flatworms** as a food source, and **water bears** were much less abundant at the tree base.

Figure 40. ***Forsstroemia trichomitria*** on a tree trunk, providing a suitable habitat for flatworms. Photo by Janice Glime.

Figure 41. ***Haplohymenium triste*** on bark, a suitable habitat for flatworms. Photo by Robert Klips, with permission.

Figure 42. ***Hypnum curvifolium*** on bark at base of tree, a habitat unsuitable for tardigrades and flatworms. Photo by Robert Klips, with permission.

Although **flatworms** are known from dry mosses on rocks, these observations by Davison and coworkers (2008, 2009) appear to be the first discovery of their living among epiphytic bryophytes. There is at least one report of moss-dwelling turbellarians (on ***Eurhynchium oreganum***, Figure 43) on a wet log (Merrifield & Ingham 1998), but that is hardly similar to the dry habitat of a tree trunk. The **flatworms** are seldom abundant, with four or fewer from a clump being common. However, they can be as abundant as 20 in a palm-sized patch of moss. Although they are not abundant, they are frequent, despite the apparent dispersal problems they are likely to have.

Figure 43. ***Eurhynchium oreganum***, sometimes home to flatworms. Photo by Matt Goff, with permission.

Epilithic Dwellers

The **epilithic** (rock) dwellers, like the epiphytic dwellers, must tolerate frequent drying on a very xeric habitat. For these limnoterrestrial microturbellarians, a bare rock is a challenge beyond their means. But bryophytes hold moisture and accumulate soil, making this austere habitat more turbellarian friendly. It was from this habitat that Van Steenkiste and co-workers (2010) described the new genus – ***Bryoplana***. They appropriately named the new species, the first in the genus, ***Bryoplana xerophila*** (Figure 23-Figure 26). This one was found among mosses, including ***Entodon seductrix*** (Figure 44), and soil on a concrete wall in northern Alabama, USA. Not only is it a new genus, but it is the first limnoterrestrial member of the **Protoplanellinae** to be found in North America and is among only a few rhabdocoels from a dry habitat. This species is easy to miss, measuring only 0.4-0.5 mm long.

Figure 44. ***Entodon seductrix***, a moss where the flatworm ***Bryoplana xerophila*** is known to encyst. Photo by Robert Klips, with permission.

These particular **microturbellarians** had guts filled with **bdelloid rotifers**, common inhabitants of mosses (Van Steenkiste *et al*. 2010). They ingested small ones within a minute, but for larger rotifers, they drained them instead, using a sucking action by the pharynx.

Other genera and species of limnoterrestrial turbellarian moss-dwellers include ***Acrochordonoposthia***, ***Adenocerca***, ***Chorizogynopora***, ***Haplorhynchella paludicola***, ***Olisthanellinella***, ***Olisthanellinella rotundula***, ***Perandropera***(?), and ***Rhomboplanilla bryophila*** (Van Steenkiste *et al.* 2010). Association of ***Acrochordonoposthia conica*** with mosses seems to be particularly well documented (Reisinger 1924; Steinböck 1932; Luther 1963). ***Rhomboplanilla bryophila*** is even named for its preference for a bryophyte habitat. The absence of images of these taxa on the internet is a testimony to how little we know of them.

Aquatic Bryophyte Habitats

Most of the non-parasitic **flatworms** (formerly **Turbellaria**) are known from aquatic habitats. Stern and Stern (1969) found numbers among cold springbrook mosses (***Fontinalis antipyretica***, Figure 3) in Tennessee to be similar to those on stones, ranging 1-5 per 0.1 m^2 on stones and 1-4 per 0.1 m^2 among the moss-algae associations. Frost (1942) found the fauna of **turbellarians** among mosses [mostly ***Fontinalis squamosa*** (Figure 45), ***F. antipyretica*,** and ***Platyhypnidium riparioides*** (Figure 46)] in her River Liffey Survey, Ireland, to be less than 0.1% of the non-microscopic fauna. Berg and Petersen (1956) reported ***Schmidtea lugubris*** (formerly *Planaria lugubris*; Figure 47) and ***Dendrocoelum lacteum*** (Figure 48-Figure 49) from beds of ***Fontinalis dalecarlica*** (Figure 51) in Store Gribsø Lake, Denmark. **Turbellarians** are not generally a dominant component of the aquatic bryophyte fauna.

Figure 45. ***Fontinalis squamosa***, a common habitat for stream fauna, including flatworms. Photo by Michael Lüth, with permission.

In a springbrook in Meade County, Kentucky, USA, flatworms were very abundant at one sampling station on the flattened moss ***Fissidens fontanus*** (Figure 52), ranging from ~92 per 0.1 m^2 in June to ~1200 in January, but at another station, the same moss had numbers ranging from ~7 to ~300 in November and March respectively. In the marl riffles, the highest number was 1, and in rubble riffles it was not found. The flatworm ***Phagocata velata*** (see Figure 53) was the most abundant flatworm on ***Fissidens fontanus*** as well as under flat stones, logs, twigs, and debris, always in fast currents.

Figure 46. ***Platyhypnidium riparioides*** in Europe. This species can be submerged or emergent. Photo by Michael Lüth, with permission.

Figure 47. ***Schmidtea lugubris*** **(**formerly ***Dugesia lugubris***) from Crowland, Lincs, UK. Photo by Roger S Key, with permission.

Figure 48. ***Dendrocoelum lacteum*** female in extended position. Crowland, Lincs, UK. Photo by Roger S. Key, with permission.

Figure 49. ***Dendrocoelum lacteum*** female in contracted position. Note the two eyes. Crowland, Lincs, UK. Photo by Roger S. Key, with permission.

Figure 50. ***Dendrocoelum lacteum*** female with recently deposited egg. Crowland, Lincs, UK. Photo by Roger S. Key, with permission.

Figure 51. ***Fontinalis dalecarlica***, suitable home for the flatworm ***Dendrocoelum lacteum***. Photo by Janice Glime.

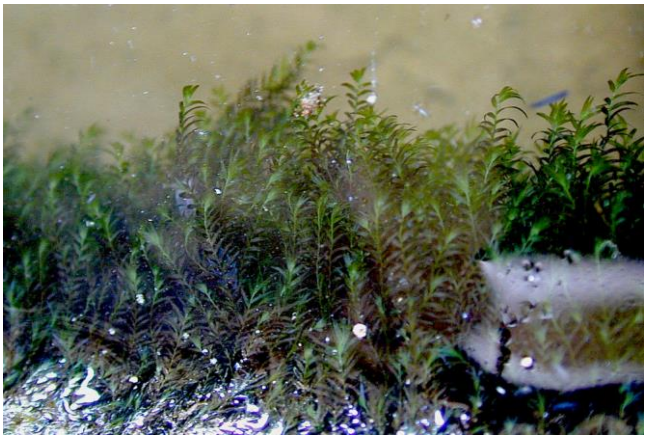

Figure 52. ***Fissidens fontanus***, showing the flat fronds. Photo by Michael Lüth, with permission.

The well-known planarian ***Dugesia dorotocephala*** finds "moss and sand quite acceptable," preferring them over silt, but less than rocks or leaves (Figure 54; Speight & Chandler 1980). ***Phagocata gracilis***, a moss-preferring species, selected temperatures of 4-22°C, preferring 14.8°C on rocks and 12.6°C on moss. I have to wonder if that was oxygen-related, with mosses taking up oxygen at night. ***Phagocata velata***, on the other hand, preferred living on rocks and migrated mostly to a temperature range of 16.0-20.5ºC, with a temperature preference of 17.8ºC.

Figure 53. ***Phagocata vitta***. Photo by Malcolm Storey through Creative Commons.

Figure 54. ***Dugesia*** sp. in its rock habitat, which is usually preferred to mosses. Photo by Janice Glime.

In a New Zealand springbrook, ***Neppia montana*** (Figure 55) seemed to have a preference for the ***Achrophyllum quadrifarium*** (=***Pterygophyllum quadrifarium***; Figure 56) over the other two mosses in the stream (***Fissidens rigidulus***, ***Cratoneuropsis relaxa***) (Cowie & Winterbourn 1979). The ***A. quadrifarium*** occurred in a zone extending from the stream margins on up the banks where it received spray from the rapidly moving water. This is a large, pleurocarpous moss with flattened branches.

Figure 55. ***Neppia montana***, a flatworm that prefers ***Achrophyllum quadrifarium*** over other moss species in its stream. Photo by Paddy Ryan, with permission.

Figure 56. ***Achrophyllum quadrifarium***, home of the flatworm ***Neppia montana*** in a New Zealand springbrook. Photo by Jan-Peter Frahm, with permission.

Extraction and Observation Techniques

The **flatworms** represent a little known fauna of terrestrial bryophytes. Brigham (2008) suggests that one reason for this may be the lack of a satisfactory extraction technique. She compared the traditional beaker extraction method with a Baermann funnel method modified by Paul Davison (see Vol 2, Chapter 4-1). Using the beaker

method, she was unable to find any **microturbellarians** among the mosses. However, she found them in multiple samples using the modified Baermann funnel.

Since these organisms are too small and too numerous for quantification in the field, they must be transported to the laboratory for extraction. Examination of live organisms makes them both easier to locate and easier to identify (Kolasa 2000). Warm temperatures and lack of oxygen quickly become lethal, not to mention confined but hungry predators, so samples must be kept in a cooler (Stead *et al*. 2003) and processed within a few hours of collection. Preserved animals usually cannot be identified.

Winsor (1998b) suggests narcotizing the flatworms with 10% ethanol, then preserving them with a formaldehyde calcium cobalt fixative. They can be cleared for examination in terpineol, imbedded in paraffin wax, and serially sectioned. The sections can be stained to make internal systems more visible. Long-term storage may require 80% ethanol, and those for DNA extraction should be fixed in 100% ethanol.

Slowing down live animals for identification can be challenging, but Thorp and Covich (1991) recommend placing them in a small volume of water on ice. Alternatively, they can be anaesthetized with a mix of 7% ethanol, 0.1% chloretone, and 1% hydroxylamine hydrochloride.

One trick to help in identification of soft-bodied taxa when time is at a premium is to use a video camera on a sample under appropriate microscope magnification (Stead *et al*. 2003). Davison and Kittle (2004) suggest making a miniature aquarium using microscope slides as a housing for both culturing these organisms and examining them (Figure 57-Figure 59).

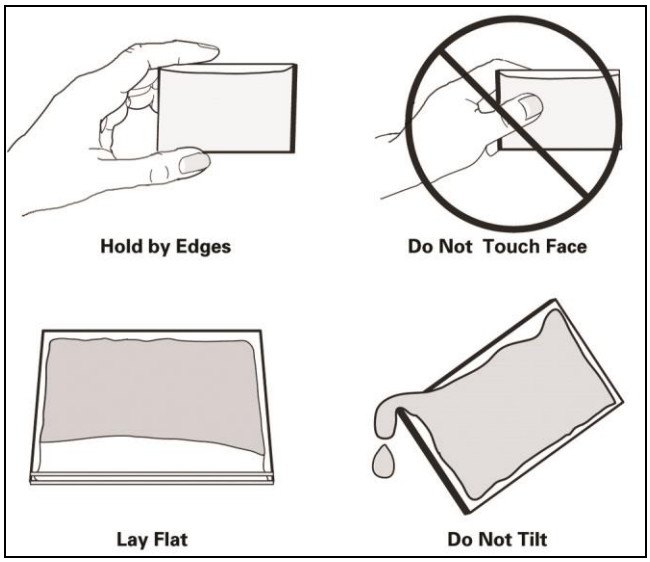

Figure 57. Method for constructing a microchamber for observing flatworms and other small invertebrates. Modified from Davison 2006.

Food choices in the lab may differ from those in the field where a wider array of choices is available. Gut analyses are used for larger organisms to determine diet in the field. But obtaining samples for gut analysis in flatworms and other tiny invertebrates is a bit more tricky than that used for insects and larger invertebrates. One can't pull or dissect the gut from the animal. Instead, Young (1973) sacrificed the animals another way. He squashed them with a coverslip on a glass slide. But first the flatworms had to take a bath by crawling around in tap water to remove adhering items that might look like food in the squash. Then they were placed on the "squash" slide, all within an hour of collection to avoid extensive digestion of the food items.

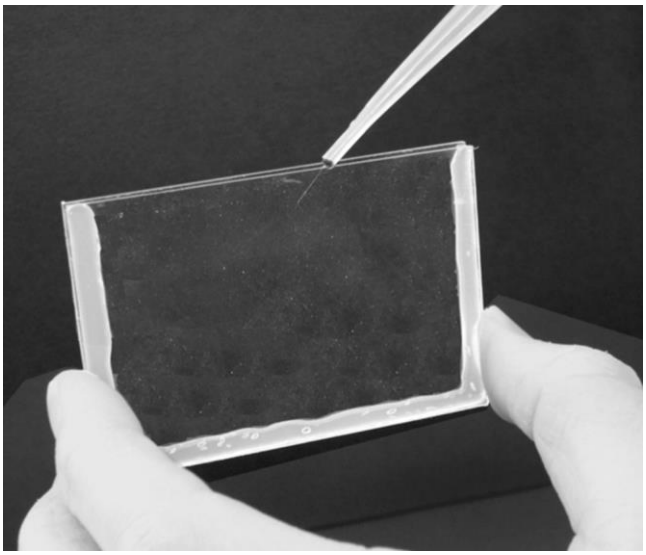

Figure 58. Filling completed microchamber built by above construction. Photo by Paul G. Davison from Davison 2006.

In 1979, Feller *et al*. demonstrated the usefulness of immunological techniques for identifying major taxonomic groups in the guts of these small organisms. Young and Gee (1993) used the precipitin test, a serological technique, to identify major taxonomic groups in the gut. Schmid-Araya *et al*. (2002) first anaesthetized the organisms with CO_2 to prevent regurgitation, although it was not clear if this method was used to identify flatworm gut contents. More recently, DNA extraction and amplification provide a means of identifying gut material from such small meiofauna (Martin *et al*. 2006), providing a potential tool for flatworms.

Figure 59. Occupied microchamber (with flatworms and moss). Image modified from Davison 2006.

Summary

Fissidens fontanus and ***F. brachypus*** can grow epizootically on **sponges**. Humans may enjoy a mattress made with mosses and sponges.

Gastrotrichs survive the dry stages of mosses by producing larger eggs that survive due to heavier shells. They seem to prefer lower velocity areas where sediments can accumulate and can be relatively common in peatlands.

Microflatworms are mostly from aquatic habitats where they are known from ***Fontinalis antipyretica***, ***F. squamosa***, and ***Platyhypnidium riparioides***. They survive winter and dry periods like the **gastrotrichs**, as thick-shelled eggs, but they can also form cysts, particularly among epiphytic mosses. They are actually more abundant on tree trunks that are prone to drying out than they are in cool, mossy stream ravines. These terrestrial species seem to be most abundant among the mosses where they can find **tardigrades** to eat. The triclad flatworm ***Phagocata gracilis*** actually prefers moss habitats.

A Baermann funnel seems to work best for extracting microturbellarians from terrestrial mosses.

Acknowledgments

Paul Davison kept me informed of new finds, which were especially important for these groups where so little is known of their bryophyte relationships. Filipe Osorio added information on tropical Platyhelminthes. Sarah Lloyd has kept me in mind as she finds new invertebrates and takes pictures for me, including the canary worm. Yuuji Tsukii gave me permission to use his wonderful collection of images. Leigh Winsor has been invaluable in helping me to identify the flatworm and nemertine worm pictures, to understand these species better, and to review the revised chapter (February 2012). Thank you to Larry Williams for catching some of my errors and notifying me.

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CHAPTER 4-3
INVERTEBRATES: NEMATODES

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CHAPTER 4-3
INVERTEBRATES: NEMATODES

Figure 1. Nematode taken from epiphytic bryophytes. Photo by Paul G. Davison, with permission.

Nematoda – Roundworms

The failure of many soil biologists to distinguish between bryophytes and what the rest of us think of as soil (*i.e.* not including bryophytes) has made researching the bryophyte-dwelling nematodes and annelids particularly difficult. Although we usually think of the nematodes (roundworms as soil organisms, they join the many other invertebrates in living among bryophytes as well (Allgén 1929; Overgaard-Nielsen 1948, 1949; Zullini 1970, 1977; Wood 1973; Yeates 1979; Caldwell 1981a, b; Zullini & Peretti 1986; Kinchin 1989; Merrifield 1992; Steiner 1994a, b, c, 1995a, b; Gadea 1964a, b, 1995; Linhart *et al*. 2000a, b, 2002a). Even the pendant moss ***Barbella asperifolia*** (see Figure 2) can be inhabited by nematodes (Noguchi 1956). The most common moss-dwelling nematodes worldwide are ***Plectus*** (Figure 3) (named for its twisted excretory tract) and ***Eudorylaimus*** (Figure 4; Overgaard-Nielsen 1948; Brzeski 1962a, b; Gadea 1964b; Eliava 1966, Spaull 1973).

Figure 2. ***Barbella*** sp., demonstrating the aerial habitat of some **nematodes**, with another pendant moss, ***Meteorium*** sp. Photo by Janice Glime.

Figure 3. The tail end of the nematode genus ***Plectus***. Photo by Peter Mullin, with permission.

Figure 4. Head of ***Eudorylaimus*** juvenile from Costa Rica. Photo by Melianie Raymond, with permission.

Most of the nematodes that inhabit mosses are less than 1 cm in length (Poinar 1991). Their digestive tract has a. mouth and anus, and it is the structure of this tract that determines many species differences in these animals. They get their gases by simple diffusion, and thus living deep in mosses can present a problem. The head possesses sensory papillae. Reproduction may be sexual or by parthenogenesis. No known species is hermaphroditic.

Densities and Richness

Kinchin (1992) claims that nematodes are common in most moss samples and are easy to see while they are alive due their thrashing movements. Fantham and Porter (1945) reported up to 480 per gram of moss. In their survey of Canadian moss fauna, they considered them to be the most abundant of the (terrestrial) metazoan fauna. Frost (1942) reported a mean of 56 and 38 individuals per stream sample (200 g). These represented only 0.41 and 0.3% of the fauna, respectively. In a high mountain brook, in the Colorado Rocky Mountains, Elgmork and Sæther (1970) reported that nematodes, primarily from the family Tylenchidae, were most abundant in the locations where there were mosses, but were not necessarily on the mosses – they were in all locations in the stream.

Despite the large numbers, not many species are known from bryophytes. Hingley (1993) reported that only 30 species were known from ***Sphagnum*** (Figure 5), despite 30,000 species known from soil or fresh water. One reason for the small number of species known is that they are quite difficult to identify. Table 1 indicates species richness of nematodes in a number of locations, demonstrating several habitats.

Figure 5. Mix of ***Sphagnum*** typical of that found in north temperate bogs and providing suitable nematode habitat. Photo by Janice Glime.

Table 1. Comparison of species richness of nematodes among mosses in various habitats. Table based on Hoschitz 2003.

Locality	# spp	Reference
Grassland & other non-woody		
Seeland, Denmark	48	Micoletzky 1929
Signy Island, Antarctic	30	Spaull 1973
Mols, Denmark	27	Nielsen 1949
Pamir, Asia	10	Micoletzky 1929
Polar		
Ross Island, Antarctica	6	Wharton & Brown 1989
Dry Valleys, Antarctica	4	Freckman & Virginia 1993
Ross Island, Antarctica	2	Yeates 1970
Alpine Summit		
Dachstein, Austria	2	Hoschitz 2003

Habitat Needs

Some of the mossy habitats, especially in streams, might make it easy for a nematode to become dislodged. Kinchin (1989) points out that many of the moss taxa have a caudal adhesive organ that permits them to anchor themselves.

Moisture Requirements

The moss cushion is not homogeneous. Generally, one can identify a leafy canopy layer, a stem layer with reduced leaf cover, and the rhizoid layer (Kinchin 1989). Many nematodes are able to migrate vertically through these layers diurnally to escape the dry upper canopy in the daytime (Overgaard-Nielsen 1948, 1949). Overgaard-Nielsen recognized three ecological groups, based on their behavior in dealing with moisture needs:

1. Members of the largest group, including ***Plectus*** (Figure 3), migrate from the rhizoid layer to the canopy layer when the moss is damp.

2. Worms such as ***Aphelenchoides*** (Figure 6) with modest migrations move only from the rhizoid layer to the stem layer and only when the moss is saturated.
3. Non-migrating worms such as ***Dorylaimus*** (Figure 7) never venture from the rhizoid layer, regardless of the moisture level.

Figure 6. ***Aphelenchoides*** sp., a moss dweller in the rhizoid layer. Photo by Peter Mullin, with permission.

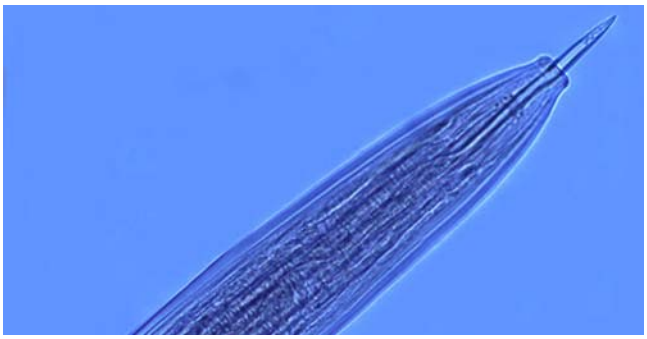

Figure 7. ***Dorylaimus*** sp. Photo by Aldo Zullini, with permission.

Moist mosses have more nematode species than dry ones (Kinchin 1989). Mosses that experience frequent desiccation episodes tend to have a more specialized moss fauna. In the ones that are dry most of the time, the fauna is primarily comprised of ***Plectus rhizophilus*** (Figure 8), a species that does not occur in the soil beneath the moss (Overgaard-Nielsen 1948, 1949). **Acrocarpous** moss cushions typically have more nematodes than **pleurocarpous** feather mosses (Kinchin 1989). Kinchin suggests that the water content in cushions is more favorable for movement.

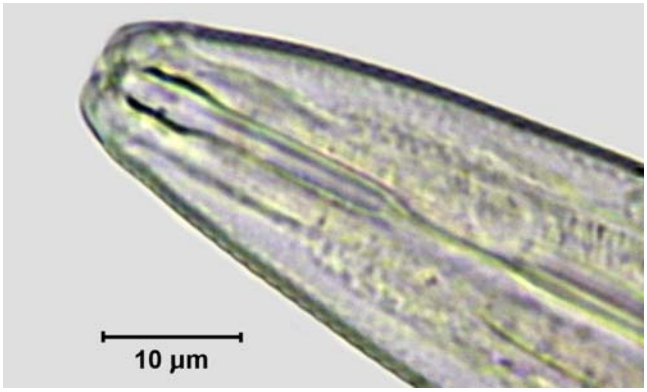

Figure 8. ***Plectus rhizophilus***, a nematode that specializes in dry moss habitats. Photo by Peter Mullin, with permission.

As in most non-arthropod invertebrates, water can be a limiting factor for nematodes. Womersley (1987) (in Wharton 2004) considered most of the moss-dwelling nematodes to be slow-dehydration strategists, whereas other nematodes may tolerate rapid dehydration of the habitat by having mechanisms that make their own dehydration slow. Hence, despite their need for water, they can be common in cryptogamic crusts. In just one of its faunal genera, the Konza Prairie crusts support 16 species in the genus ***Plectus*** (Figure 3; Figure 8). Beasley (1981) and Kinchin (1990) suggested that some nematodes actually require a dry phase in their life cycle.

Food Supply

Food supply may at times be an overriding factor in determining locations of moss-dwelling nematodes. Several researchers have suggested that food supply was a major controlling factor for nematode density in soil (Bunt 1954; Winslow 1964; Yeates 1967). Spaull (1973) suggested that food was likely to also be a determining factor in the moss community, at least in the Antarctic. Predominant food strategies of bryophyte-dwelling nematodes include predators (Barbuto & Zullini 2006) and bacteriovores (Lazarova *et al*. 2000) and food includes bacteria, algae, and protozoa (Poinar 1991). Mosses usually collect detrital matter that provides suitable habitat for Protozoa and bacteria.

Quality of Food

However, it is possible that it is the quality of food that matters. Spaull (1973) found that nematode abundance was not related to water content on Signy Island, but correlated with a low ratio of C:N (favoring bacteria) in the soil (including mosses), seemingly explaining the greater numbers associated with the grass *Deschampsia antarctica*, where C:N ratios were the lowest. Hingley (1993) indicated that the peatland nematodes did not eat the moss ***Sphagnum*** (Figure 5). Rather, they are likely to eat bacteria, protozoa, and small invertebrates.

Warming Effect among Bryophytes

Spaull (1973) and Holdgate (1964) consider the warming effect of solar radiation within the upper portion of the moss mat to determine activity of nematode moss dwellers. But this influence is only important near the surface, with its influence diminishing with depth (Longton & Holdgate 1967; Cameron *et al*. 1970). Nevertheless, bryophytes buffer the temperature of the soil beneath them, keeping it cooler in summer and insulating it against an early frost or cold when there is no snow cover.

Unusual Bryophyte Dwellings

It appears that some nematodes have found a cozy niche in **antheridia** of mosses (Figure 9). Lars Hedenäs (pers. comm. Aug. 2007) has found such nematodes in old perigonia of ***Homalothecium lutescens*** (Figure 10) collected in France by Gillis Een with one actually inside the spent antheridium. Could this be a common niche for some nematode taxa, or was this just an opportunist and rare occurrence?

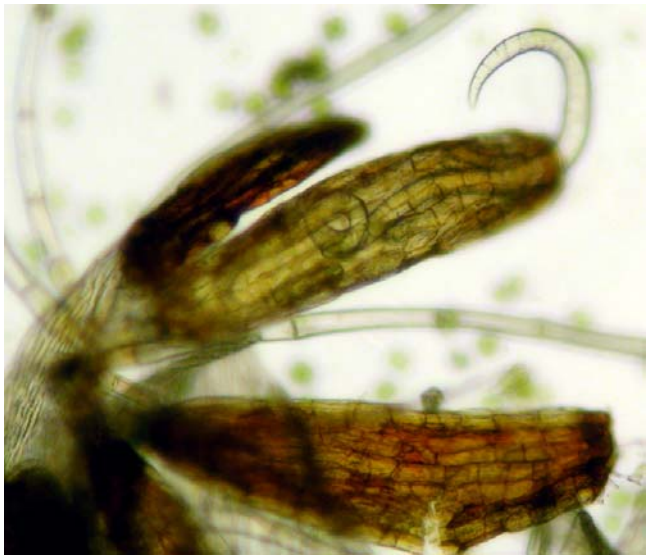

Figure 9. This nematode chose an antheridium of the moss ***Homalothecium lutescens*** for its home. Photo by Lars Hedenäs, with permission.

Figure 10. ***Homalothecium lutescens***, a moss where nematodes may dwell in the antheridia. Photo by Michael Lüth, with permission.

Substrate Preferences

Barbuto and Zullini (2006) found that despite highly variable densities of nematodes between samples and substrate of the mosses, the diversity and trophic group structure varied little. Predators dominated in these Italian samples. Soil as a substrate for the mosses seemed to favor a greater species richness and biomass, particularly for large species such as ***Aporcelaimellus obtusicaudatus*** (Figure 11-Figure 12; most likely a species complex; Mike Hodda, personal communication). In their study, ***Tripylella intermedia*** seemed to occur exclusively on mosses on rocks, but any other relationship to substrate was not clear. On the other hand, Eyualem-Abebe *et al*. (2006) reported it as a species of both mosses and soil. As in many other geographic areas, Barbuto and Zullini (2006) found that the two most common species were ***Prionchulus muscorum*** (Figure 13) and ***Plectus acuminatus***, occurring in nearly all samples. The greatest differences among European communities seemed to be between continental and Mediterranean communities.

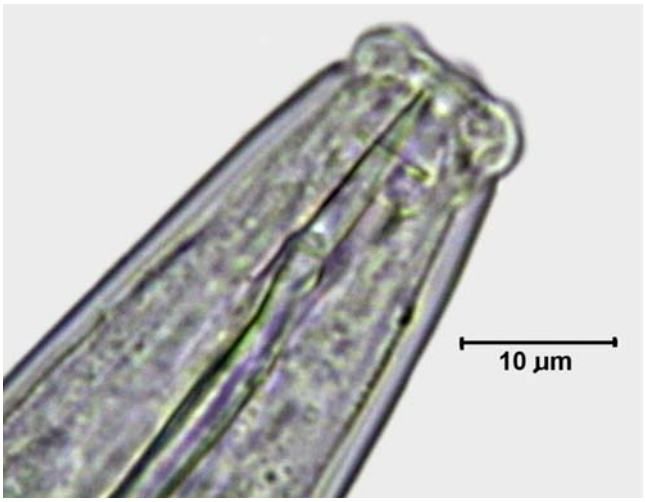

Figure 11. Head view of ***Aporcelaimellus***, a genus with the large ***A. obtusicaudatus*** preferring mosses on soil in an Italian study. Photo by Peter Mullin, with permission.

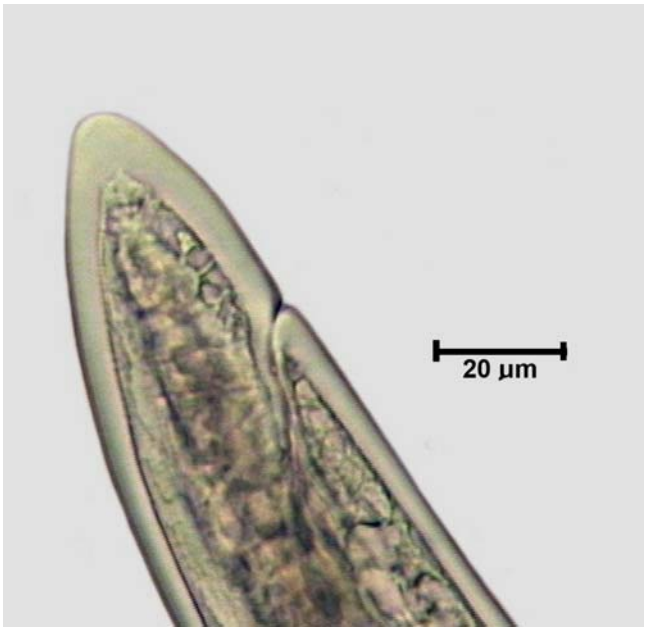

Figure 12. Tail view of ***Aporcelaimellus***. Photo by Peter Mullin, with permission.

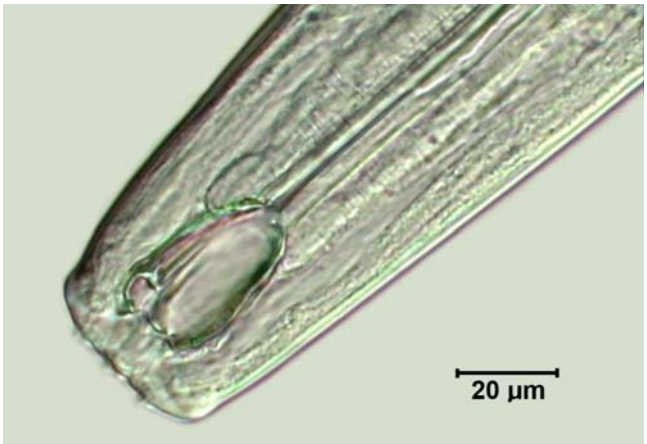

Figure 13. ***Prionchulus muscorum***, one of the two most common species among mosses in an Italian study. Photo by Peter Mullin, with permission.

Lazarova *et al*. (2000), in comparing nematode communities on the moss ***Hypnum cupressiforme*** (Figure 14) in Bulgaria, likewise found that abundance was quite variable among substrata (soil, stone, & tree trunks) and samples, and these likewise were similar in diversity, trophic group structure, and generic composition. They did, however, vary in species composition. Contrasting to the predatory dominance of nematodes in the broader range of European mosses studied by Barbuto and Zullini (2006), they found that the most abundant ***H. cupressiforme*** nematodes were bacteriovores. The proportion of predatory and omnivorous nematodes was quite low. They also found no clear substrate dependence of any species except for ***Chiloplectus andrassyi*** (Figure 15), which was most abundant among ***H. cupressiforme*** on stone.

Figure 14. ***Hypnum cupressiforme***, a preferred habitat for ***Chiloplectus andrassyi***. Photo by Michael Lüth, with permission.

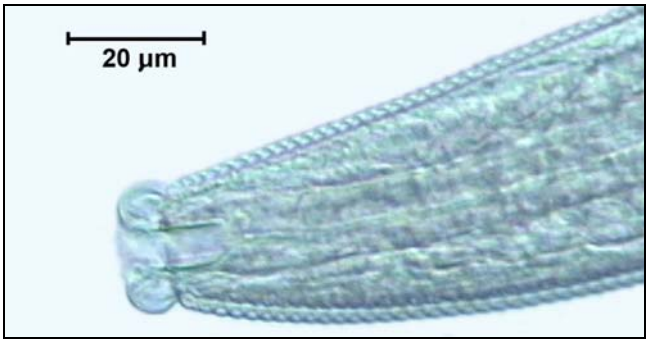

Figure 15. ***Chiloplectus*** sp., a member of a genus in which ***C. andrassyi*** seems to prefer ***Hypnum cupressiforme*** on stone. Photo by Peter Mullin, with permission.

Motility Constraints

Merrifield and Ingham (1998) considered that low densities of nematodes in some mosses may result from interference by the moss with the motility efficiency of the nematodes. Kinchin (1992) commented that live nematodes in mosses were easy to locate because of their thrashing movements. Overgaard-Nielsen (1948) described the genera ***Aphelenchoides*** (Figure 6), ***Monhystera*** (Figure 16), ***Plectus*** (Figure 8), ***Prionchulus*** (Figure 13), ***Teratocephalus*** (Figure 17), and ***Tylenchus*** (Figure 18) as moving by swimming (a rare event for most nematodes), thus requiring an accumulation of large quantities of water, but more likely they crawl in a thin film of water (Mike Hodda, personal communication). Nematodes are heavier than water and thus sink. The members of ***Eudorylaimus*** (Figure 19) are "powerful benders" that can move in a thin film of water. Although ***Eudorylaimus*** species are unable to inch or swim where they live on the moss, their bending ability permits them to attain a patchy distribution (Merrifield & Ingham 1998). The genera ***Monhystera*** and ***Plectus*** move like inchworms, using their caudal and labial gland adhesives (Overgaard-Nielsen 1948). But ***Tylenchus***, lacking the caudal glands, cannot creep, and basically becomes confined to its original location.

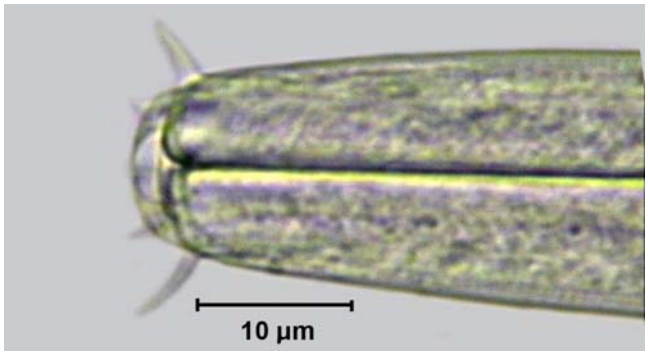

Figure 16. ***Monhystera*** sp., a nematode that moves like an inchworm among the mosses. Photo by Peter Mullin, with permission.

Figure 17. ***Teratocephalus terrestris***, representing a genus that is abundant in the Antarctic moss turf. Photo by Peter Mullin, with permission.

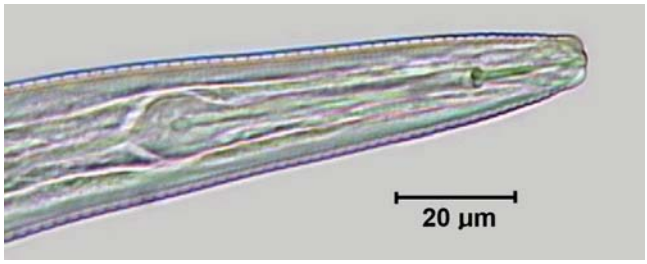

Figure 18. ***Tylenchus davainei***, in a genus where ***Tylenchus polyhypnus*** sets the record for a long dormancy of 39 years on a moss herbarium specimen. Photo by Peter Mullin, with permission.

Figure 19. ***Eudorylaimus*** juvenile. Photo by Peter Mullin, with permission.

Drought Strategies

As one would expect in a diverse group of organisms, the strategies for survival in a widely varying environment are also diverse. Like their mossy substrate, nematodes are able to go dormant for long periods of time (McSorley 2003). The record seems to be that of ***Tylenchus polyhypnus*** (literally meaning many sleeps). This moss-dweller became active again after 39 years of sleeping on a moss herbarium specimen! (Figure 18; Steiner & Albin 1946).

Eggs have a long longevity that permits them to remain quiescent until favorable conditions for growth and development return (Hingley 1993). They can survive drought, lack of oxygen, and a series of freeze-thaw cycles. Sex ratios can change to provide a more favorable ratio for the conditions at hand. And worms can cluster together in great aggregations in the soil, although I know of no reports of this phenomenon within moss habitats. Even adults can survive long periods of **anhydrobiosis**, a dormant state in which some invertebrates can survive desiccation. The lack of water prevents all enzymatic metabolic reactions (Clegg 1973; Barrett 1982).

Panagrolaimus (Figure 20) is known from a wide range of niches, including bryophytes, and they are bacterial feeders, a strategy that suits them well for dwelling among bryophytes (Shannon *et al*. 2005). They furthermore have the ability to survive extreme desiccation by entering the dormant state of **anhydrobiosis**, thus being able to dry as the bryophytes dry. Many of the ***Panagrolaimus*** species require preconditioning through slow desiccation. ***Panagrolaimus superbus***, on the other hand, has a fast desiccation strategy in which it can survive rapid desiccation, but whose chance of survival increases with preconditioning. Just as found for freezing tolerance (Crowe *et al*. 1984), there is a high correlation between **trehalose** induction and desiccation/anhydrobiosis survival (Shannon *et al*. 2005). It is therefore not surprising that ***P. superbus*** maintains a high level of trehalose even in its fully hydrated state, *i.e.*, 10% of its dry mass! It is possible, then, that it is this ready supply of trehalose that preadapts this species to survival of desiccation.

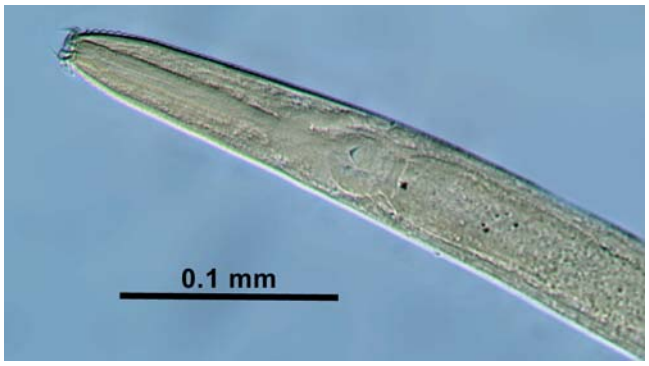

Figure 20. ***Panagrolaimus davidi***. Photo by Smithsonian Institution, National Museum of Natural History, Invertebrate Zoology through Creative Commons.

Panagrolaimus (Figure 20) species also exhibit behavioral adaptations to drying. They coil their bodies (Figure 21) and clump with other nematodes, both of which reduce the surface area from which water can be lost (Shannon *et al*. 2005).

Figure 21. This moss-dwelling nematode is attempting to move with its longitudinal muscles. Coiled positions like this also reduce the rate of water loss as the habitat dries. Photo courtesy of Andi Cairns.

Both moss-dwelling nematodes and bryophytes have been described as **poikilohydrous**, meaning their water content will vary with that of the environment (Proctor 1979). Like most mosses, some nematodes can enter an anhydrobiotic state or become dormant. Unlike ***Panagrolaimus superbus***, most nematodes must dry slowly to survive (Crowe & Madin 1974) and eventually lose most of their water. ***Plectus*** (Figure 3), a common moss dweller, is a notable exception, being known as a "quick drier" (Mike Hodda, personal communication). Coiling their bodies (Figure 21) helps many nematodes to slow the water loss (Demeure *et al*. 1979), but Kinchin (1989) indicated that there are no observations to indicate whether or not this behavior is present in moss inhabitants Fortunately, Andi Cairns has photographed a moss-dwelling nematode doing just that (Figure 21).

Habitation of mosses themselves is a survival strategy. Mosses, especially cushions, dry slowly. A boundary layer of still air forms over the cushion. Evaporation must occur through this boundary layer. Thicker layers mean slower evaporation rates. The nematodes are nestled in the axils of leaves, so those in a cushion experience slower evaporation than those in more open habitats (Richardson 1981).

Some mosses may contribute to slowing evaporation not only of themselves, but also their inhabitants by curling their leaves, as in ***Atrichum*** spp. (Figure 22). Others, such as ***Syntrichia princeps*** (Figure 23) or ***S. intermedia*** (Figure 24), may wind their leaves helically around the stem.

Figure 22. ***Atrichum undulatum*** with moist leaves (upper right) and dry, curled leaves (lower middle). Curled leaves help to slow evaporation, permitting the nematodes to acclimate as they go dormant. Photo by Michael Lüth, with permission.

Figure 23. ***Syntrichia princeps***. Photo by Martin Hutten, with permission.

Figure 24. ***Syntrichia intermedia***, illustrating the twisting of leaves that can protect nematodes from rapid drying. Photo by Michael Lüth, with permission.

Kinchin (1992) observed that luxuriant growths of epiphytic bryophytes often had fewer species and reduced numbers compared to those bryophytes in lesser abundance. He suggested that the more open growth habit of these mosses in higher humidity were perhaps not suitable for the nematodes. He further suggested that some nematodes require alternate dry and wet phases in their life cycles, thus not faring well in the more moist dense moss growths (see also Kinchin 1990).

Succession

Moss age not only affects probability of arrival, but also influences the moisture of the habitat. The most specialized nematode species arrive first because they are adapted to the changing moisture regime. These include ***Plectus rhizophilus*** (Figure 25), a moss canopy species (Kinchin 1989). Members of the rhizoidal group (*e.g.* ***Dorylaimus***, Figure 7) are the last to arrive because they require the more stable moisture climate of a larger cushion. Although ***Dorylaimus*** is an aquatic genus, it can survive on very wet mosses (Aldo Zullini, pers. comm. 18 March 2009). On the other hand, Mike Hodda (personal communication) considers that they may arrive last because they have long life cycles and are slow to breed, whereas ***Plectus*** (Figure 27) is short-lived, fecund, and moves much more quickly.

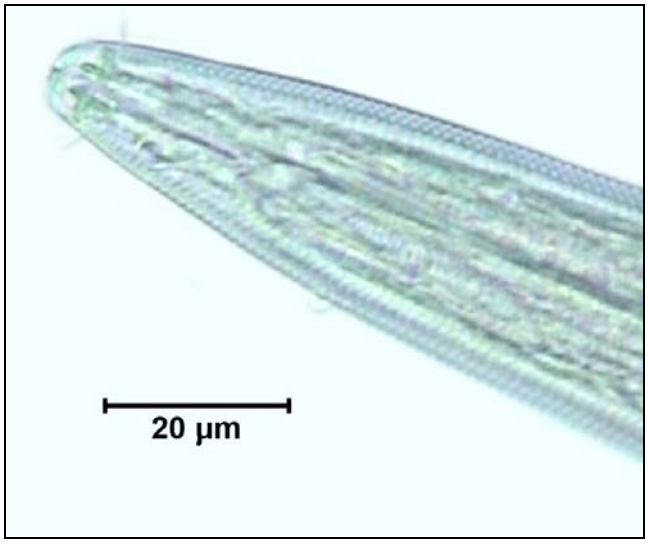

Figure 25. ***Plectus rhizophilus***, a nematode found among roof mosses. Photo by Peter Mullin, with permission.

Nematode communities in moss cushions are so sensitive to moisture regimes that they can be used to ascertain the moisture history of the cushion (Kinchin 1989). Fewer species would be present in cushions that are frequently desiccated. Thus even among populations of the same species, communities will differ based on the moisture history of the cushion. Overgaard-Nielsen (1967) demonstrated this by comparing communities associated with ***Ceratodon*** sp. (Figure 26) on north- and south-facing sides of a thatched roof (Table 2).

Figure 26. ***Ceratodon purpureus***, a common roof moss that has its own nematode fauna. Photo by Michael Lüth, with permission.

Table 2. Comparison of nematode densities (numbers per cm^2) in cushions of ***Ceratodon*** sp. (Figure 26) on a single thatched roof (Overgaard-Nielsen 1967).

	S-facing	N-facing	Figure
Plectus rhizophilus	330	51	Figure 25
Plectus cirratus	0	47	Figure 27
Aphelenchoides parietinus	0	8	Figure 28
Paraphelenchus pseudoparietinus	0	1	Figure 29
Prionchulus muscorum	0	1	Figure 13

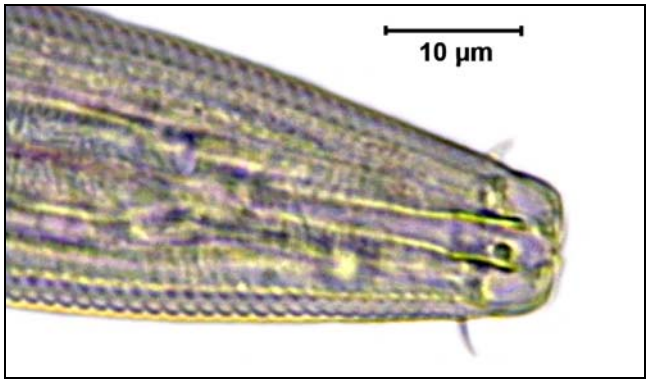

Figure 27. ***Plectus cirratus***, known from roof mosses. Photo by Peter Mullin, with permission.

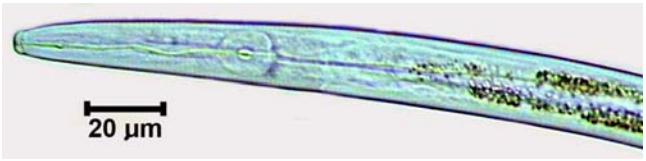

Figure 28. ***Aphelenchoides parietinus***, a roof moss dweller. Photo by Peter Mullin, with permission.

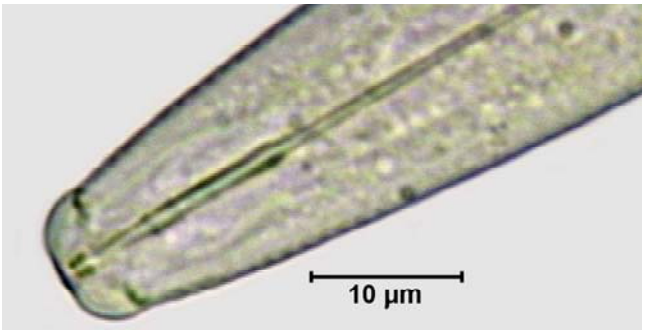

Figure 29. ***Paraphelenchus*** (=*Paraphelenchoides*) ***pseudoparietinus***, a roof moss inhabitant. Photo by Peter Mullin, with permission.

Seasonal Changes

Seasonal differences among the moss-dwelling nematodes can be pronounced, as reported by Steiner (1994d in Boag & Yeates 2004) for the Swiss Alps. In a study of nematodes dwelling on ***Eurhynchium oreganum*** (Figure 30) in the Oregon Coast Range, USA, comparison indicated that the densities of ***Eudorylaimus*** spp. (Figure 19) and ***Plectus*** spp. (Figure 25, Figure 27) differed between sampling dates, but that densities of ***Monhystera*** spp. (Figure 16), ***Prionchulus muscorum*** (Figure 13), and ***Tylenchus*** spp. (Figure 18) did not differ, resulting in total densities of nematodes that varied little between dates (Figure 31; Merrifield & Ingham 1998). Nevertheless, ***Monhystera*** (Figure 16) species reached a mean of 35 individuals per gram in August, but only 1 or fewer in winter and spring. Members of other genera occurred sporadically in low numbers: ***Aphelenchus*** (Figure 32), ***Acrobeles*** (Figure 33), ***Cuticonema***, ***Ecphyadophora***, ***Leptolaimus*** (Figure 34), ***Teratocephalus*** (Figure 17), and members of the order **Cromadorida**. The number of nematodes per gram of dry moss ranged from 21 in February to 64 in July, a density somewhat lower than that found in other studies on moss-dwelling nematodes.

Figure 30. ***Eurhynchium oreganum***, home to nematodes and other invertebrates in Oregon, USA. Photo by Matt Goff, <www.sitkanature.org>, with permission.

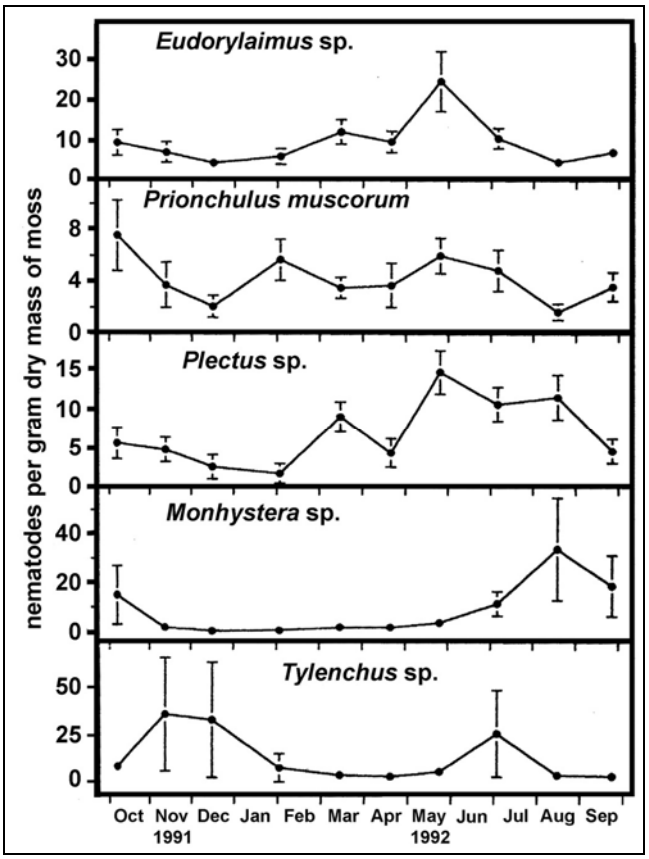

Figure 31. Seasonal changes in densities of nematodes on the moss ***Eurhynchium oreganum*** (Figure 30) from Mary's Peak, Oregon Coast Range, Oregon, USA. Vertical bars represent standard errors. Redrawn from Merrifield & Ingham 1998.

Figure 32. ***Aphelenchus avenae***, a member of a genus where some members live among mosses. Photo by Peter Mullin, with permission.

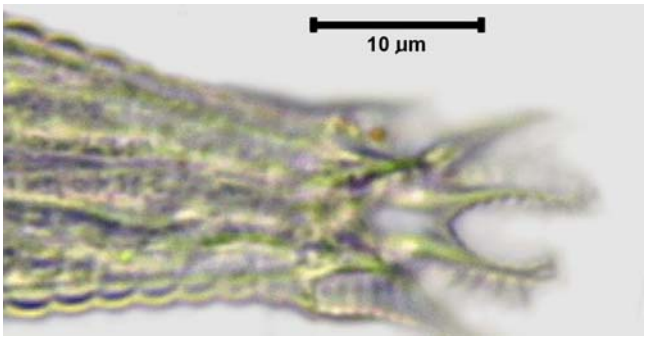

Figure 33. Head end of ***Acrobeles***, a sporadic genus on the moss ***Eurhynchium oreganum*** on the Oregon coast. Photo by Peter Mullin, with permission.

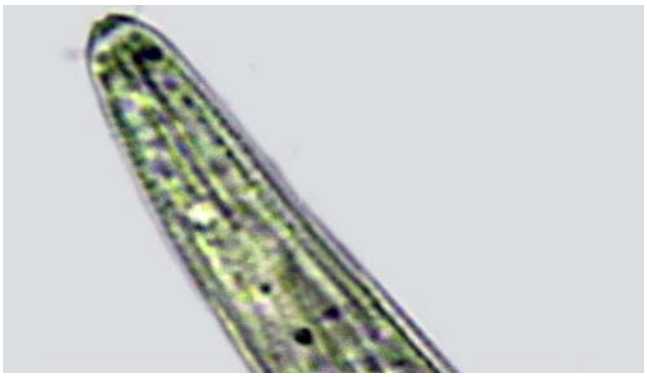

Figure 34. Head end of ***Leptolaimus***, an occasional dweller on the moss ***Eurhynchium oreganum*** (Figure 30). Photo by Peter Mullin, with permission.

Merrifield and Ingham (1998) suggested peaks of ***Eudorylaimus*** (Figure 19) and ***Plectus*** (Figure 3) species in association with the moss ***Eurhynchium oreganum*** (Figure 30) in the Oregon Coast Range in late May, continuing until August, could indicate optimal conditions during that time of year (Figure 31). It is not clear if food is a limiting factor because feeding habits of some species are not clear. In fact, these nematodes are often polyphagous, with some switching food items from bacteria to prey items as they grow (Yeates *et al*. 1993; Mike Hodda, personal communication). Merrifield (1994) examined the relationship between spore production of the moss ***Schistidium maritimum*** (Figure 35) and the omnivorous nematode ***Eudorylaimus*** at Yachats, Lincoln County, Oregon, USA, in a year-long study. She found a lag of one month between the peak of mature sporophytes and the maximum density of nematodes. Since there were no other invertebrates to serve as food, she suggested that the spores might serve as a food source.

Plectus sp. (Figure 3), a bacteriovore, ranged from 4 to 12 per gram dry weight (gdw) of moss on the northwest slope of Mary's Peak, Oregon, USA, throughout most of an October 1990-October 1991 sampling period, but reached 25 per gdw in June (Merrifield 1992). ***Monhystera*** sp. (Figure 16), on the other hand, peaked in September with 35 per gdw, whereas it remained mostly below 1 per gdw throughout the Oregon winter. The possibly fungus and plant feeder ***Tylenchus*** sp. (Figure 18) had a bimodal seasonal distribution, with highs in November (35) and July (25). ***Prionchulus*** sp. (Figure 13), a predator, peaked at 6-8 in summer and winter, with fluctuations throughout the year.

Figure 35. ***Schistidium maritimum*** in a typical shoreline habitat. Photo by Michael Lüth, with permission.

Spaull (1973) likewise found a vertical migration of moss-dwelling nematodes on Signy Island. In the summer and first half of winter the nematodes remained in the 3 cm nearest the surface, but when the cold of winter set in, they could be found primarily in the 3-6 cm layer. Spaull speculated that the freeze-thaw cycle near the surface resulted in a decline in numbers there, but that the lower positions also experienced slightly higher daytime temperatures in the autumn. Despite earlier studies suggesting the importance of moisture (Tilbrook 1967a, b), there seemed to be no relationship between vertical position and moisture in the mosses (Figure 36).

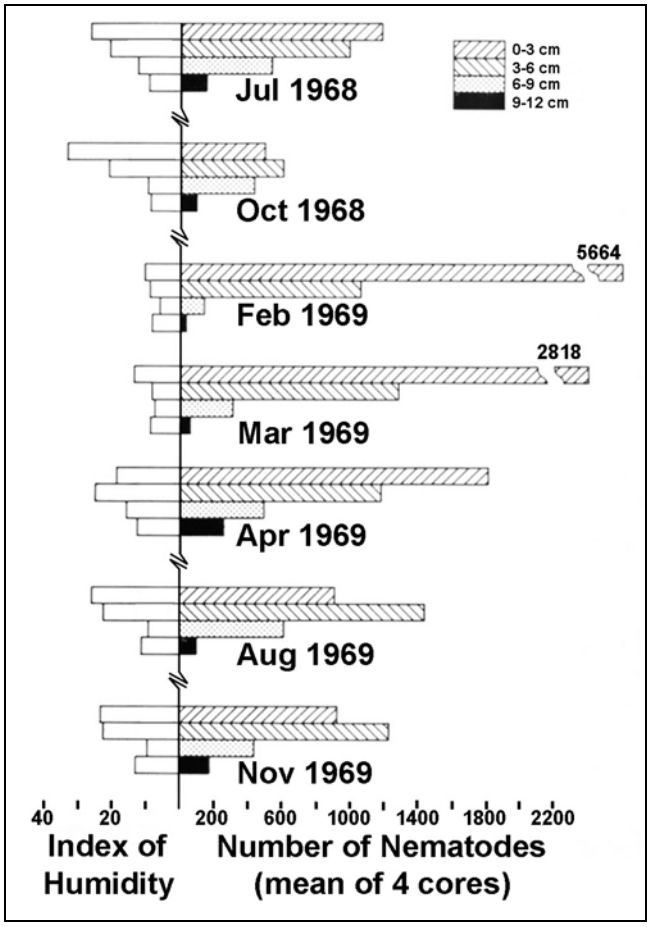

Figure 36. Seasonal depth distribution of nematodes compared to humidity levels in ***Calliergon*** (Figure 37)-***Calliergidium*** (Figure 38) cores on Signy Island, Antarctic region. Redrawn from Spaull (1973).

Figure 37. ***Calliergon sarmentosum***, a known host of nematode-trapping fungi on Signy Island in the Antarctic. Photo by Michael Lüth, with permission.

Some moss-dwelling nematodes can respond to seasonal changes by migrating. Of course they can't travel long distances like birds can. Whereas some nematodes migrate vertically on a daily basis, others move vertically within the moss community to survive changing seasons (Wharton 2004). In the Antarctic, Caldwell (1981b) and Maslen (1981) found that a seasonal migration existed in moss carpets, wherein the nematodes moved deep into the carpet in autumn and returned to the surface in spring. But it is interesting that they found no similar migration pattern in moss cushion forms.

Figure 38. ***Chorisodontium aciphyllum***, home to nematodes in the Antarctic. Photo by Jan-Peter Frahm, with permission.

Freeze Tolerance

Nematodes range at temperatures from snow pools to hot springs, with a species of ***Aphelenchoides*** (Figure 28) occurring at 61.3ºC (Hebert 2008). In fact, some Antarctic nematodes can withstand freezing at -80°C for more than six years (Newsham *et al*. 2006). On the liverwort ***Cephaloziella varians***, there were more live ***Coomansus gerlachei*** nematode individuals than of ***Rhyssocolpus paradoxus***. Nematodes had much greater survival (49%) than did tardigrades (13%) or rotifers (2%).

One factor that permits nematodes to succeed in climates of the Antarctic, alpine areas, and other areas with harsh winters is their ability to survive freezing conditions. But how does this tiny, watery worm do it? Several species in the genus ***Panagrolaimus*** (Figure 39-Figure 41) have been studied to reveal their freeze-tolerance secrets. Some day we may be able to freeze and thaw humans from what we learn about these moss inhabitants.

The transparency of the nematode body enabled Wharton and Ferns (1995) to discover that ***Panagrolaimus davidi*** (Figure 20) froze not only in its extracellular spaces, but also formed ice in living cells (Figure 39). They found that all body parts could experience freezing and thawing, including within cells (Figure 39). Freezing extends inward through body openings, mostly through the excretory pore. These nematodes, with intracellular freezing, can revive, grow, and reproduce, at least in culture (Figure 41-Figure 41).

Figure 39. Frozen female ***Panagrolaimus davidi*** that survives intracellular ice formation (Wharton & Ferns 1995). This female was frozen on a light microscope cold-stage. Freezing causes darkening in appearance, and ice can be seen throughout this nematode, except the egg, which remains unfrozen due to its protective shell. Photo by Melianie Raymond, with permission.

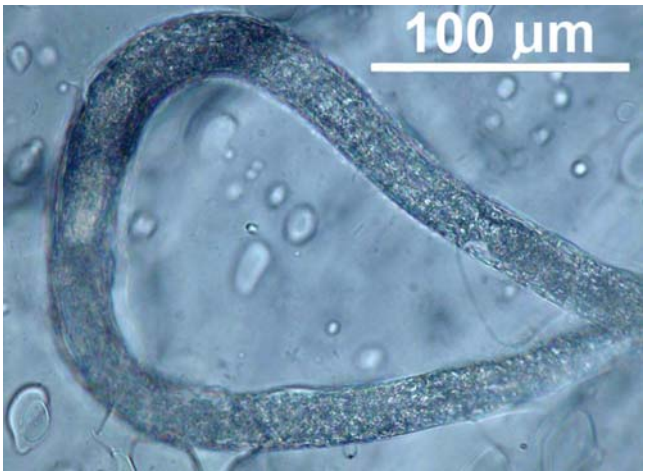

Figure 40. The same female ***Panagrolaimus davidi*** as in Figure 39, thawing from being completely frozen. Photo by Melianie Raymond, with permission.

But ***Panagrolaimus davidi*** (Figure 20) has more possibilities to survive freezing, and these may play a role in its desiccation story as well. These nematodes can avoid freezing by dehydration (Wharton *et al*. 2007). If nucleation of their surrounding medium occurs at a high subzero temperature, *e.g.* -1°C, the nematodes dehydrate instead of freezing. This occurs as a result of difference in vapor pressure between ice and super-cooled water at the same temperature. When they are cooled slowly, there is sufficient time for them to lose enough water to prevent freezing. It is only when they are cooled rapidly or at a

lower nucleation temperature that they actually freeze internally, but still survive. These multiple strategies permit them to survive the harsh Antarctic environment.

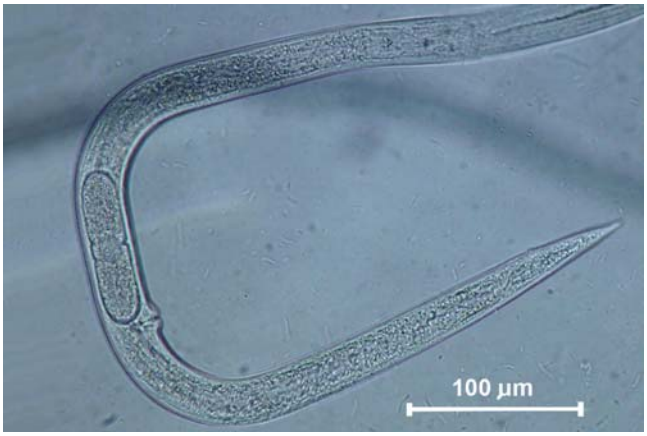

Figure 41. The same female ***Panagrolaimus davidi*** as in Figure 39, after thawing from being completely frozen, but undamaged. Photo by Melianie Raymond, with permission.

However, when these nematodes are in water, they are seeded by exogenous ice nucleation, a process in which a dust particle, protein, or other small particle (the "nucleus") forms the center for ice crystallization – the same process used for making artificial snow. Even under these conditions, some of the nematodes of this species do survive. One reason for their survival is that the formation of the ice seems to be restricted to the **pseudocoel** – the "false" body cavity. A major danger from ice crystallization is that the crystals are sharp and poke holes in cell membranes, or distort them, changing permeability. However, the pseudocoel is fluid and **acellular**, thus avoiding that danger.

Thermal history and age are important in determining which individuals survive (Wharton & Brown 1991). In arthropods, supercooling and freeze tolerance are thought to be mutually exclusive, but in nematodes, that is not the case. In the Antarctic, sub-zero temperatures can occur on any day of the year, making tolerance a necessity for survival. Even in the summer, moss temperatures can go down to -8.4ºC (Block 1985). The moss environment is usually saturated with water (Pickup 1990a, b), requiring that the nematodes either prevent ice nucleation or survive exogenous nucleation and subsequent freezing.

Panagrolaimus davidi (Figure 20; Figure 39-Figure 42) freezes when it is seeded by exogenous ice nucleation and is freezing tolerant (Wharton & Brown 1991). In the moss habitat, nematodes will usually experience low water loss rates; hence, an interaction between water loss and cold tolerance may occur under some conditions. This slow water loss rate may be a vital factor in its choice of the moss as a habitat (Wharton *et al*. 2003). When nucleation begins at subzero temperatures near -1ºC, this nematode dehydrates (Wharton *et al*. 2003). The difference in vapor pressure of ice and supercooled water, at the same temperature, drives the water loss from the nematode. If the process is slow enough, the nematode loses enough water to prevent freezing (Figure 42). It is likely that **trehalose**, an important molecule during dehydration, also acts to prevent or reduce freezing within the worm (Wharton 2003).

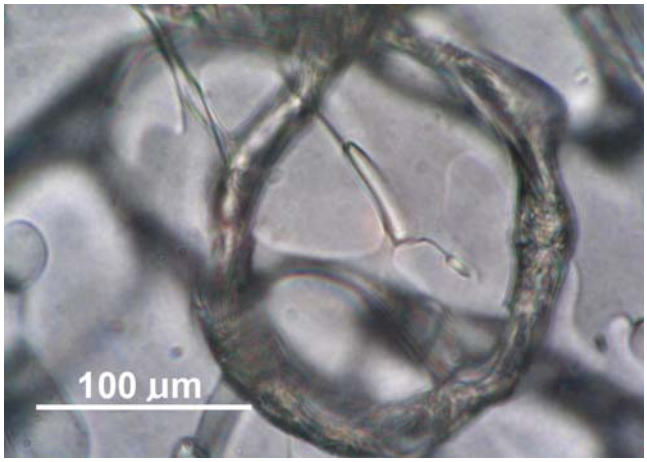

Figure 42. ***Panagrolaimus davidi*** showing cryoprotective dehydration. ***Panagrolaimus davidi*** can also survive exposure to freezing conditions by undergoing cryoprotective dehydration (Wharton *et al*. 2003). This photo shows a nematode encased in ice, unfrozen but dehydrated. Photo by Melianie Raymond, with permission.

To further combat its frigid environs, ***Panagrolaimus davidi*** (Figure 20; Figure 39-Figure 42) produces **ice-active proteins** (Wharton *et al*. 2005a). These proteins seem to have the ability to stabilize the ice after freezing by preventing **recrystallization** during minor freeze-thaw temperature fluctuations within the organism. Wharton *et al*. (2005b) examined the survival of these nematodes under several freezing scenarios. At sub-zero temperatures near 0ºC, three patterns of ice formation were evident: no ice, extracellular ice, and intracellular ice (Wharton *et al*. 2005b). In a slow-freezing regime (at -1ºC) mainly extracellular ice (70.4%) formed, with most of the ice in the pseudocoel. Cryoprotective dehydration accounted for ~25% of the individuals with no ice within their bodies. However, under a fast-freezing regime (at -4ºC) both intracellular (54%) and extracellular (42%) ice formed. Fortunately, the intracellular ice only formed in the cytoplasm of cells, while organelles remained in unfrozen spaces between the crystals. Nevertheless, those nematodes that experienced the fast freezing had only 53% survival compared to 92% for those that underwent slow freezing.

We have also learned that the Antarctic ***Panagrolaimus davidi*** (Figure 20; Figure 39-Figure 42) is able to survive freezing temperatures by supercooling when it is in air that permits it to be free of surface water (Figure 42) (Wharton & Brown 1991; Wharton *et al*. 2003). But, in these conditions, it is intolerant of freezing. In fact, it can survive better at sub-zero temperatures than other individuals of the species that have been kept at 15ºC in 99% relative humidity – not unlike the moisture relationships of bryophytes and their tolerance to temperature extremes.

The importance of mosses to the life cycle of ***Panagrolaimus davidi*** (Figure 20; Figure 39-Figure 42) is evidenced by the nematode's optimum temperature range of 25-30ºC (Brown *et al*. 2004). Population growth ceases at about 6.8ºC. Fortunately, egg incubation requires only 4.1-7.6ºC. This bacteriovore is **r-selected** (typically short-lived with lots of offspring like bacteria), more like temperate nematodes than its Antarctic compatriots. However, the

cold polar environment forces it to become dormant for long periods of time and to grow in spurts; such longevity is more like that of **K-selected** organisms (long life span and few offspring, like humans), but is it right to count that dormancy period as part of its longevity?

Scientists have known about freezing of juveniles and eggs of other nematodes for some time, but the mechanisms were not understood. In some species (***Trichostrongylus colubriformis***), a sheath protects at least some juveniles from formation of exogenous ice nucleation, although this species also survives freezing (Wharton & Allan 1989). Worms of ***Ditylenchus dipsaci*** and the eggs of ***Globodera rostochiensis*** are able to survive freezing in wet conditions, but the researchers were unable to distinguish between survival of freezing and prevention of ice nucleation (Wharton *et al*. 1984; Perry & Wharton 1985).

But not all cold temperatures are in the high elevations and latitudes. In peatlands, freezing is common, yet nematodes survive. Some protection is afforded by their behavior of coiling (Hingley 1993). But the greater protection is most likely their chemical alteration. As unfavorable conditions approach, they decrease their concentrations of **fats**, **glycogen**, and **glucose** and increase **glycerine** and **trehalose** (Crowe *et al*. 1984). In addition to its probable role in preventing or reducing freezing (Wharton 2003), trehalose is able to stabilize dry membranes, a consequence of freezing as well as drought conditions (Crowe *et al*. 1984).

Gall-formers

Some of bryophyte-dwelling nematodes are free-living and some are parasitic on the bryophytes (Gadea 1977, 1978a, b; Duggal & Koul 1985; Georgievska 1990). Nematode galls on bryophytes have been known since before 1905 (Dixon 1905; Marchal 1906). Dixon reported that others had found them on ***Warnstorfia fluitans*** (Figure 43), ***Drepanocladus aduncus*** (Figure 44), ***Hypnum cupressiforme*** (Figure 14), and several species of ***Dicranum*** (Figure 45). Dixon himself found them on ***Thamnobryum alopecurum*** (Figure 46). After reading the descriptions of others, he concluded that he had also seen them on ***Eurhynchium hians*** (Figure 47) as well. These galls typically occur at the shoot and branch apices. Dixon observed numbers up to 50 adorning a single stem of ***Thamnobryum alopecurum***.

Figure 43. ***Warnstorfia fluitans***, a widespread aquatic moss that gets nematode galls. Photo by Michael Lüth, with permission.

Figure 44. ***Drepanocladus aduncus***, a host species for nematode galls. Photo by Hermann Schachner, through Creative Commons.

Figure 45. ***Dicranum scoparium*** with capsules; several species o ***Dicranum*** host nematode galls. Photo by Hermann Schachner, through Creative Commons.

Figure 46. ***Thamnobryum alopecurum***, a host to the gall-forming nematode ***Tylenchus davainii***. Photo by Michael Lüth, with permission.

Figure 47. ***Eurhynchium hians***, a species that can be home to gall-forming nematodes. Photo by Michael Lüth, with permission.

Schiffner (1906) noted that the nematode galls were typically associated with the apices where one should find sporophytes (Figure 48). But those shoots with galls did not produce sporophytes. Kitagawa (1974) observed apical galls in leafy liverworts and concluded that the nematode gallers induced a protective appendage resembling a perigynium or marsupium. This structure originally enveloped a young sporophyte and he concluded that the nematode galls are associated with the sporophytes of the liverwort.

Figure 49. ***Orthotrichum*** nematode galls showing their position where the sporophyte should be. Photo courtesy of Martin & Rosie Godfrey.

Akiyama (2010) found nematode galls on the leafy liverwort ***Lejeunea tuberculosa*** in the upper montane forest of northern Thailand. The galls consisted of tightly gathered abnormal leaves at the apex of shoots. Unlike Dixon's suggestion that all the moss galls were the same species, Akiyama determined that two nematode species could be found within a single gall. The numerous one of these was filamentous and lacked any ornamentation. The other was much thicker, had curved tails (see Figure 1), a vent, and ring-like ornamentation at the terminal position. This second species occurred in only small number. Eggs were present, and because of their size, Akiyama considered them to belong to the former, filamentous species. But he also suspected that those nematodes with the curved tails might not be a gall-forming species, but rather a usual bryophyte dweller.

Figure 50. ***Lejeunea tuberculosa***, a species that can host nematode galls. Photo courtesy of Gaik Ee Lee.

Many kinds of nematodes induce the formation of galls (Sheldon 1936; Horikawa 1947) on both mosses [*e.g.* ***Racomitrium lanuiginosum*** (Figure 51) and ***R. heterostichum*** (Figure 52) (Deguchi 1977), ***Thuidium delicatulum*** (Figure 53) (Sheldon 1936; by ***Anguina askenasyi***, Steiner 1936, 1937), ***Phascopsis rubicunda*** (Stone 1980 in southern and western Australia), ***Dicranum*** sp., ***Thamnobryum alopecurum*** (Figure 46), ***Eurhynchium*** sp., ***Warnstorfia fluitans*** (Figure 43), and ***Hypnum cupressiforme*** (Figure 14) (Dixon 1905, 1908; Gerson 1982) and liverworts [*e.g.* ***Cheilolejeunea krakakammae*** (Asthana & Srivastava 1993) and ***Anastrophyllum minutum*** (Figure 54; Kitagawa 1974)].

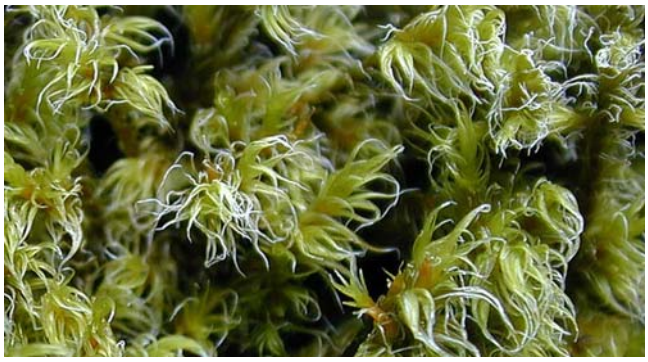

Figure 51. ***Racomitrium lanuginosum***, a moss known for its nematode galls. Photo by Michael Lüth, with permission.

Figure 52. ***Racomitrium heterostichum***, a moss where nematodes are known to from galls. Photo by Michael Lüth, with permission.

Figure 53. ***Thuidium delicatulum***, a pleurocarpous moss that forms nematode galls. Photo by Michael Lüth, with permission.

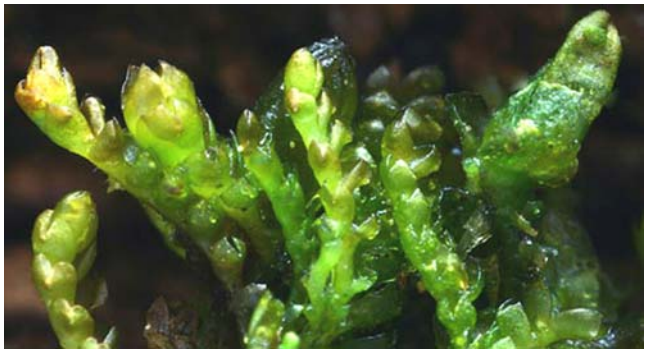

Figure 54. The leafy liverwort ***Anastrophyllum minutum*** a host to nematode galls. Photo by Des Callaghan, with permission.

Dixon (1905) reported the nematode ***Tylenchus davainii*** (Figure 55) to form galls on ***Thamnobryum alopecurum*** (Figure 46), ***Eurhynchium hians*** (=***E. swartzii***; Figure 47), and ***Hypnum cupressiforme*** (Figure 14) in Great Britain. Hedenäs (2000) found 59 individuals of the moss ***Abietinella abietina*** (Figure 56-Figure 57) (6.6% of those examined) to have nematode galls in the apices of their vegetative branches. Typically, where one gall existed, numerous ones could be found.

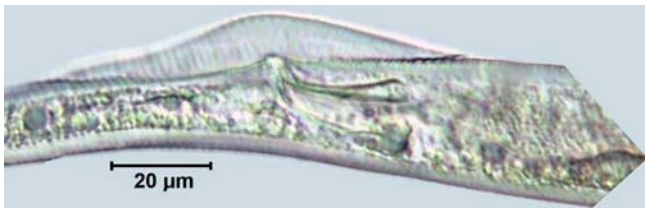

Figure 55. ***Tylenchus davainii***, a gall-forming nematode. Photo by Peter Mullin, with permission.

Figure 56. ***Abietinella abietina***, a moss that can have nematode galls. Photo by Michael Lüth, with permission.

Figure 57. ***Abietinella abietina*** with nematode galls on the branch tips. Photo by Lars Hedenäs, with permission.

Claudio Delgadillo has described to me (Bryonet 18 March 1996) a growth form of ***Bryum argenteum*** (Figure 58) from Mexico that is unusual and may represent the typical result of nematode gall formation (Figure 60). The presence of nematode galls caused the upper part of the stem to be modified. The upper leaves had a modified shape, color, and general structure that had the appearance of a fruiting cleistocarpous moss.

Figure 58. ***Bryum argenteum***, one of the mosses that houses nematode galls. Photo by Michael Lüth, with permission.

Figure 59. ***Bryum argenteum*** with a nematode gall at its tip. Photo courtesy of Claudio Delgadillo Moya.

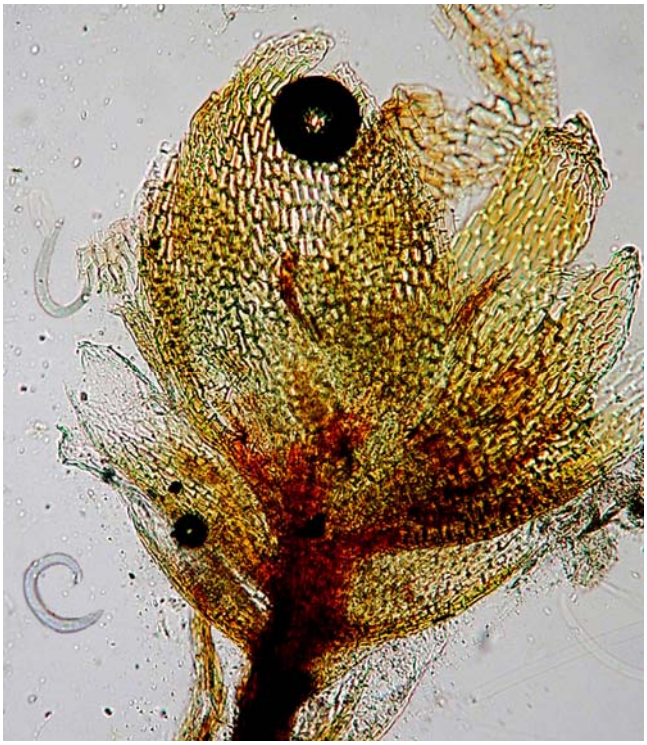

Figure 60. ***Bryum argenteum*** gall. The cell walls are thickened and the leaves and stem apex have a different morphology from uninfected plants. Two C-shaped nematodes can be seen at left, collected near Temascalapa, Mexico. Photo courtesy of Claudio Delgadillo Moya.

Stone (1978) commented that nematodes produced similar galls on male plants of ***Bryum pachytheca*** in Australia, again resembling cleistocarpous capsules. Both Stone (1980) for ***Phascopsis rubicunda*** and Delgadillo (Bryonet 1996) for ***Bryum argenteum*** (Figure 58-Figure 60) reported that the cell walls were thickened. Stone reported that the stems of ***Phascopsis rubicunda*** were hollow and necrosed, cell walls were reddened and glossy, and inner leaves were ecostate, and like Delgadillo, she considered the galls to resemble cleistocarpous capsules.

As I thought I was drawing this chapter to a close, a new report appeared in the Australasian Bryological Newsletter. Jolley and Hodda (2009) found nematode galls on a tiny Australian moss called ***Stonea oleaginosa*** (Figure 61-Figure 63), a fitting name commemorating Ilma Stone, who had reported nematodes in this moss under the moss name of ***Tortula oleaginosa*** (Stone 1978). This moss from the salt bush and mallee in Southern Australia is inconspicuous (<1 mm) as it hides among the sand grains, often nearly buried.

As in ***Phascopsis rubicunda***, Stone (1978) had reported hollow, elongated stems, but she had not observed galls. Like Delgadillo and Stone for other species of moss, Jolley and Hodda (2009) described the galls as resembling cleistocarpous moss capsules (Figure 63). And as in ***Phascopsis rubicunda***, the galls of ***Stonea oleaginosa*** (Figure 62-Figure 63) are modified leaves that are very broad, with thick cell walls. I have to wonder if some of those unidentifiable mosses I have seen in the field with what I thought were developing sessile capsules may have been bearing galls – did I really explore them thoroughly enough?

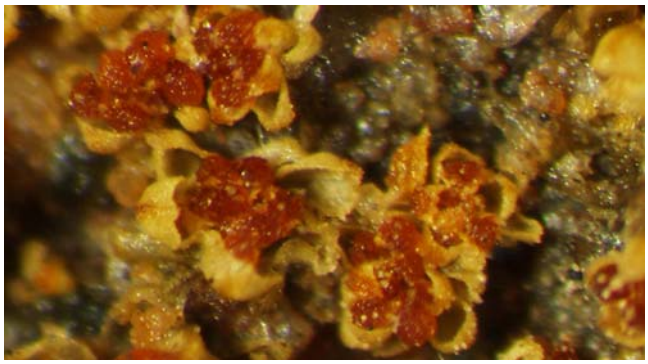

Figure 61. ***Stonea oleaginosa***, a microscopic moss. Photo by Helen Jolley, with permission.

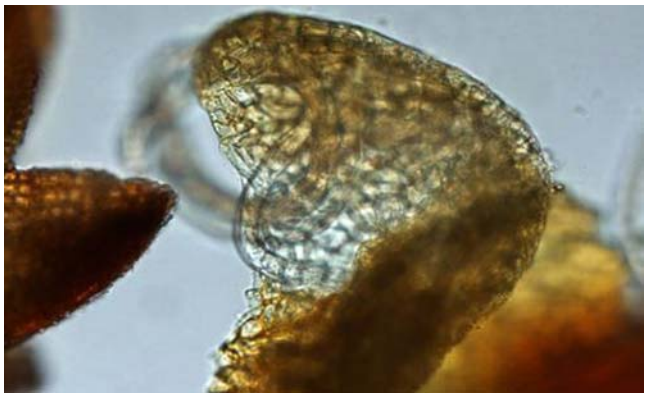

Figure 62. Gall leaf of ***Stonea oleaginosa***, caused by the nematode ***Nothanguina*** sp. nov. Photo by Helen Jolley, with permission.

Figure 63. Leaf gall of the nematode ***Nothanguina*** from the moss ***Stonea oleaginosa***. Note the encysted nematodes within. Photo by Helen Jolley, with permission.

Jolley and Hodda (2009) determined the nematode to be a species of ***Nothanguina*** (Figure 64), a species that occurs on several Australian moss taxa, including ***Phascopsis rubicunda***, and was a species as yet undescribed. (That is coming soon.) The genus is known to house up to five female adults, usually about the same number of males, and numerous eggs and juveniles in one gall. But in galls on ***Stonea oleaginosa*** (Figure 61-Figure 63), only female nematodes are known.

In ***Stonea oleaginosa*** (Figure 61-Figure 63), the galls are placed amid the archegonia of the moss, possibly modifying archegonia to inhibit fertilization. By interesting coincidence, only female plants are known in this moss, and inhibition of fertilization seems unnecessary, unless galls were so frequent that useless males were lost through evolution. Rather, females produce upper leaves that are modified into propagules that are rich in oils and break off the plant easily (Stone 1978). Could it be that some hormone inhibits male development in the moss and subsequently in the nematode? It would be interesting to follow the development of the gall to understand how tissues are modified to make the gall tissues and propagules.

Figure 64. ***Nothanguina*** sp. nov. from ***Stonea oleaginosa***. Photo by Helen Jolley, with permission.

Niklas Lönnell (pers. comm. 26 March 2012) described a nematode gall on ***Microbryum floerckeanum*** (Figure 65). This moss had a structure that looked like a strange capsule, but it proved to be a structure with a nematode resident.

Figure 65. ***Microbryum floerkeanum*** with capsules, home of a nematode gall. Photo by David Holyoak, with permission.

It appears that even ***Buxbaumia aphylla*** (Figure 66) may host nematodes. Misha Ignatov (Bryonet 7 April 2017) observed gametophytes that resembled sea urchins (Figure 67) and had no trace of sporophytes. Instead, a nematode was often present inside (Figure 68). These occurred in September when the temperature was *ca*. 10ºC in their Middle European Russia location.

Figure 66. ***Buxbaumia aphylla*** showing nearly mature capsules. The gametophyte is merely a protonema (threadlike structure) and the leafy plants seen here belong to other mosses. Photo through public domain.

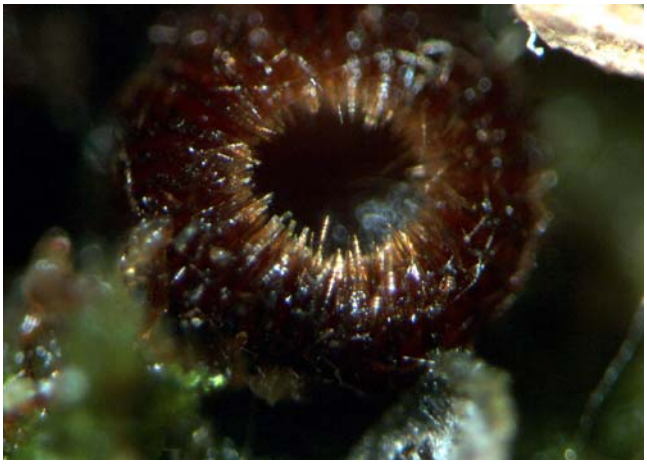

Figure 67. ***Buxbaumia aphylla*** nematode gall. Courtesy of Misha Ignatov.

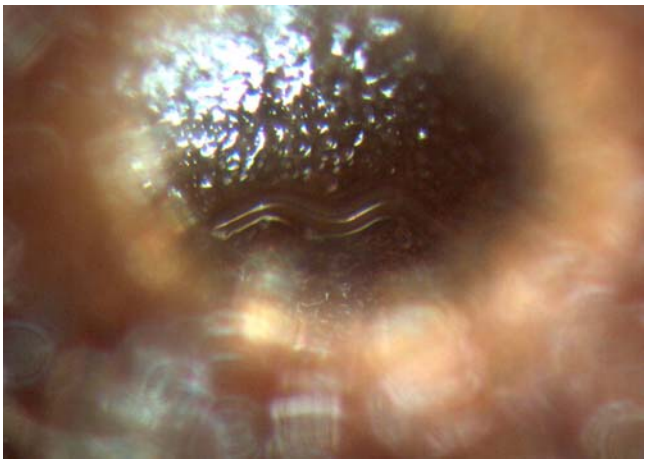

Figure 68. ***Buxbaumia aphylla*** nematode in gall. Courtesy of Misha Ignatov.

Unfortunately, few of the bryophyte gall-formers have been identified, so we don't know if they are unique to bryophytes. It is likely that at least some are. Ernie Bernard at the University of Tennessee is currently working with nematode galls from the moss ***Hypnum***. sp. (Paul G. Davison, pers. comm. 22 January 2012).

Terrestrial Moss Inhabitants

Hodda (2003) lists only three bryophytes as hosts for nematodes: ***Barbula*** sp. (Figure 69) – ***Aphelenchoides*** sp. (Figure 28); ***Tortula*** sp. (Figure 70) – ***Aphelenchus*** sp. (Figure 32), ***Aphelenchoides*** sp.; ***Grimmia pulvinata*** (Figure 71) – ***Laimaphelenchus pini.*** But Kinchin (1992) reported that nearly all moss samples from the British Isles contained nematodes, often in large numbers.

Figure 69. ***Barbula convoluta***, a nematode host. Photo by Michael Lüth, with permission.

Figure 70. ***Syntrichia*** (=*Tortula*) ***intermedia***, a moss that houses nematodes. Photo by Michael Lüth, with permission.

Figure 71. ***Grimmia pulvinata***, a moss that hosts nematodes. Photo by Michael Lüth, with permission.

Eyualem-Abele *et al*. (2006) reported that ***Tripylella arenicola*** occurs on moss as well as in soil. Many aquatic taxa also are able to survive in the wet habitat provided by moisture held in capillary spaces among bryophyte leaves. I was able to document eighteen genera (Table 3) that have species known in and around moss clumps. There are most likely more that have never been identified, or even found.

Peatlands

Some of the ubiquitous nematodes reside in peat, but others are inhibited by the low *p*H. Glatzer and Ahlf (2001) found that the nematode ***Caenorhabditis elegans*** (Figure 72) was inhibited in growth in the sediments. When they tested eighteen different sediment combinations that mimicked those available, the optimum for growth and successful reproduction was a mixture with 5% ***Sphagnum*** peat (Figure 5), suggesting that this nematode may actually benefit from some characteristic of the peat. Nematodes such as the **mycophagous *Aphelenchoides compositicola*** and many **saprophytic** nematodes can be a problem in peat used for culture of mushrooms and must be eliminated with chemicals such as ethylene oxide (Nikandrow *et al.* 1982).

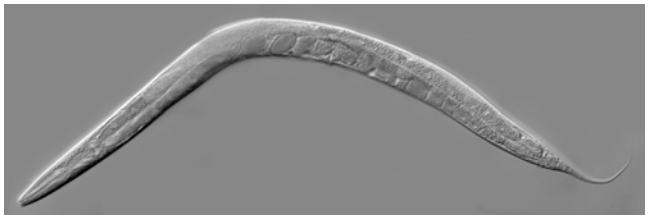

Figure 72. ***Caenorhabditis elegans***, a nematode that seems to benefit from some properties of ***Sphagnum***. Photo by Kbradnam, through Creative Commons.

Some individuals coil up inside the hyaline cells of ***Sphagnum*** leaves (Figure 73), and nematodes even deposit eggs within these cells (Hingley 1993). Eggs of these species survive long periods of drought, anaerobic conditions, and repeated freeze-thaw cycles. Even adult worms can survive unfavorable conditions by encysting and decreasing fats, glycogen, and glucose, increasing glycerine and trehalose, and assuming a coiled position (Crowe *et al*. 1984).

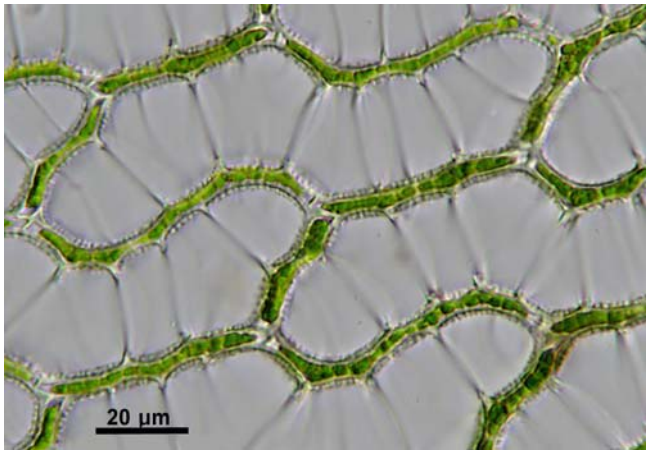

Figure 73. ***Sphagnum papillosum*** leaf cells. Nematodes may live in the hyaline cells. Photo by Ralf Wagner <www.drralf-wagner.de>, with permission.

As noted earlier, although there are about 30,000 species of nematodes worldwide, only about 30 species are known from ***Sphagnum*** (Figure 5) (Hingley 1993). Knowledge about specific taxa on other mosses is likewise limited (Table 3), but Coleman pointed out in 1971 that our knowledge about nonparasitic nematodes in soils in many parts of the USA is nonexistent. With the important role they are perceived to play in soil compared to mosses, it is hardly surprising that knowledge about those among mosses is somewhat scant.

Woodland peat mosses are a somewhat preferred community (Hingley 1993). Some of these worms feed on detritus while others are predatory, feeding on protozoa and small invertebrates. The herbivorous species apparently never feed on the mosses. Nevertheless, nematodes living in the microbiotic soil crusts of prairies are known to eat moss rhizoids, among other things (Bamforth 2003).

Table 3. Nematode genera that are known to inhabit terrestrial bryophytes. Occasional taxa from the Antarctic are not included. *Indicates taxa also on the Table 4 aquatic list.

*Achromadora**	Kinchin 1989
Aphelenchoides	Kinchin 1989
Aphelenchus	Hodda 2003
Caenorhabditis	Glatzer & Ahlf 2001
Chromadorina	Kinchin 1989
Diplogaster	Kinchin 1989
*Dorylaimus**	Kinchin 1989
Monacrosporium	Duddington *et al*. 1973
Monhystera	Kinchin 1989
*Mononchus**	Kinchin 1989
Nothanguina	Jolley & Hodda 2009
Odontolaimus	Kinchin 1989
Paraphelenchoides	Overgaard-Nielsen 1967
*Plectus**	Kinchin 1989
*Prionchulus**	Overgaard-Nielsen 1967
Rhabditis	Kinchin 1989
Thyronectria	Duddington *et al*. 1973
*Tylenchus**	Kinchin 1989
Tripylella	Eyualem-Abebe *et al.* 2006

Global Warming

Global warming has been a concern for the peatland habitat at all levels. Sohlenius and Boström (1999a) investigated the effect a rise in temperature might have on nematode communities of peatlands by transplanting peat blocks from northern Sweden to nine warmer sites within that country. After one year, they found that in all but the northernmost transplant site, these transplants resulted in increased numbers, but had no influence on species composition. The most abundant of the 35 taxa were ***Plectus*** (Figure 3) and ***Teratocephalus*** (Figure 17) (Sohlenius & Boström 1999b).

Hence, it appears that temperature alone may not have a serious effect on nematodes, but they cautioned that other changes in the ecosystem could alter the nematode communities. Furthermore, tardigrades, known to prey on nematodes, also increased in numbers, possibly damping

the effect of temperature on the nematodes (Sohlenius & Boström 1999b). I would consider that one year is insufficient basis for a long-term assessment as the greater temperatures could lie within normal variation from year to year. Even Sohlenius and Boström (1999b) suggested that seasonal differences and the short duration of the experiment could be misleading. Numbers of nematodes increased in autumn, especially in warm sites, with a positive relationship between nematode numbers and temperature in November. Likewise, in spring there were more nematodes in warm sites than in cooler ones.

Population Size

In an ombrotrophic mire in northern Sweden, Sohlenius *et al*. (1997) found high densities of nematodes, especially in the moss surface layer. In fact, the nematodes dominated with a mean abundance of 9.4 million individuals per square meter. These were represented by 34 taxa. The surface layer was characterized by similar numbers of fungal vs bacterial feeders. By contrast, bacterial feeders dominated the underlying peat.

Aquatic Nematodes

In New Zealand alpine streams, nematodes were the most abundant moss-dwelling invertebrate (40.6%), exceeding **all** the insects (Suren 1993). This number was higher above the treeline (43.6%), but was exceeded by the Chironomidae (midges) below the treeline. In an unshaded alpine stream at Arthur's Pass National Park on South Island, NZ, Chironomidae were the most abundant (57.6%), with nematodes in second place (22.1%) (Suren 1991b). The same relationship existed in a shaded stream, but the Chironomidae became more dominant (63.4%) compared to only 12.5% nematodes. Numbers of nematodes were lower and their ranks dropped in the gravel in both streams. This was supported by the significant correlations of nematodes with bryophytes compared to gravels.

In the Czech Republic, Vlčková *et al*. (2001/2002) found similar percentages of nematodes among ***Fontinalis antipyretica*** (Figure 74) plants, with 38,350 per mL (14.6% of total meiofauna) in one stream and 31,813 per mL (6.4%) in another.

Some aquatic mosses have a somewhat unique fauna. In a comparison of communities associated with ***Fontinalis antipyretica*** (Figure 74) and those of associated gravel, Linhart *et al*. (2000b) found six genera only in mosses and five only in gravel. Nine genera occurred in both habitats. The most abundant genera were the same as many terrestrial genera and Linhart *et al*. (2000b) considered that their feeding strategy explained locations of dominant genera: ***Plectus*** (Figure 75) – bacteriophagous, in moss; ***Mononchus*** (Figure 76), ***Tobrilus***, and ***Tripyla*** (Figure 77) – predators, in gravel; ***Eudorylaimus*** (Figure 78) – plant feeders, in moss; ***Dorylaimus*** (Figure 7) – omnivorous, both substrates. Table 4 lists taxa of nematodes known from aquatic bryophytes.

Figure 74. Streambed covered with dangling ***Fontinalis antipyretica***, where nematodes may be numerous. Photo by Andrew Spink, with permission.

Table 4. Taxa of freshwater nematodes known from bryophytes, based on Eyualem-Abebe *et al*. (2006).

Achromadora terricola	*Mononchus*
Alaimus sp.	*Mylonchulus brachyuris*
Anatonchus dolichurus	*Neotobrilus telekiensis*
Clarkus papillatus	*Oncholaimellus campbelli*
Cobbonchus palustris	*Plectus* sp.
Cobbonchus radiatus	*Prionchulus muscorum*
Comiconchus trionchus	*Prionchulus punctatus*
Coomansus intestinus	*Prismatolaimus intermedius*
Coomansus parvus	*Rhabdolaimus terrestris*
Dorylaimus sp.	*Tobrilus zakopanensis*
Enchodelus sp.	*Tripyla affinis*
Eudorylaimus	*Tripyla filicaudata*
Limonchulus bryophilus	*Tripyla glomerans*
Mesodorylaimus spp.	*Tripyla setifera*
Metateratocephalus crassidens	*Tylenchus davainei*
Miconchus studeri	

Figure 75. ***Plectus***, widespread genus with bacteriophagous moss dwellers. Photo by Yuuji Tsukii, with permission.

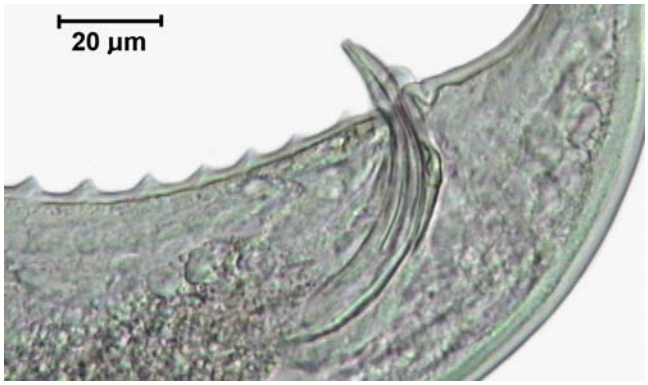

Figure 76. ***Monochus***, a predator. Photo by Peter Mullin, with permission.

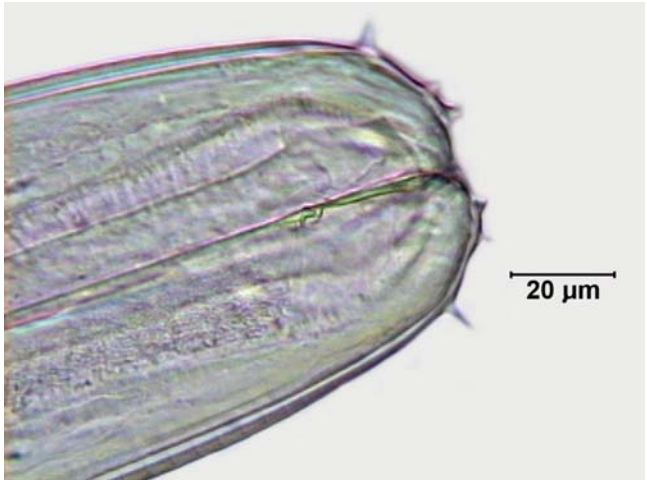

Figure 77. ***Tripyla*** sp. from an alpine habitat in the Rocky Mountains, USA. Photo by Peter Mullin, with permission.

Figure 78. ***Eudorylaimus*** sp., a plant feeder that lives among mosses. Photo by Melianie Raymond, with permission.

A study comparing artificial and real mosses [***Fissidens rigidulus*** (Figure 79), ***Cratoneuropsis relaxa***, ***Bryum blandum*** (Figure 80)] in New Zealand suggests that mosses may indeed have something unique to offer the nematodes (Suren 1991b). In three out of four trials, involving two streams, the artificial mosses made of nylon cord were poor mimics of the bryophyte habitat for the nematodes. Mosses had a mean of 84,000 & 90,000 (2 trials) per m^2 in mosses compared to 1560 & 2400 per m^2 in artificial mosses in one stream and 9840 & 3780 per m^2 in mosses compared to 1760 & 1320 in artificial mosses in a second stream. While it is unlikely that the bryophytes themselves provided food, they are a good source of periphyton and detritus.

On the other hand, when Hynes (1961) used silk in place of mosses, the percentage of organisms that were nematodes associated with the silk differed little from that associated with the mosses.

Figure 79. ***Fissidens rigidulus***. Photo by Bill and Nancy Malcolm, with permission.

Figure 80. ***Bryum blandum***, a moss superior to artificial mosses as a nematode habitat. Photo by Jan-Peter Frahm, with permission.

In streams, mosses can serve as nutrient traps, collecting detrital matter that is readily available to tiny organisms such as these (Suren 1991a; Linhart *et al*. 2002b). Food availability may account for moss-dwelling (***Fontinalis antipyretica***; Figure 74) nematodes whose numbers more closely resembled those in the gravel in that Austrian study: 2,850 per m^2 in the moss and 2,135 per m^2 in the gravel. When Linhart *et al*. (2000a) considered all meiofauna, mean abundances were as follows: moss at locality 1 – 182,672 individuals per 100 mL of moss, gravel at locality 1 – 1,206 individuals per 100 mL substrate, moss at locality 2 – 390,057 individuals per 100 mL moss. Mosses had more than 150 times as great a meiofauna density compared to the nearby mineral substrate. Nematodes were only about 22% of this moss

meiofauna, but that is still greater than the entire meiofauna of the mineral substrate. Differences in fine particulate organic matter (FPOM, >30 µm) may account for differences in nematode densities. At locality 1, mosses trapped 19 times as much FPOM as the gravel and 3 times as much as the moss at locality 2. Likewise, nematodes at locality 2 comprised only 11% of the meiofauna. Everybody has to eat!

Even aquatic habitats dry out from time to time. Aquatic moss-dwelling nematodes are among the dominant invertebrates and tolerate these drying events in a state of **anhydrobiosis** (Overgaard-Nielsen 1949; Gilbert 1974; Crowe 1975; Nicholas 1975; Wright 1991), a capability that is not typical of other aquatic nematodes (Merrifield & Ingham 1998).

The Antarctic

Mosses are an important habitat for nematodes in the Antarctic (Figure 81). But not all mosses are created equal, and biologists in the Antarctic have been very aware of these differences. Caldwell (1981a) compared nematodes in moss turf with those in moss carpet on Signy Island. These two ecosystems differ markedly, with the carpets averaging 220-236 mg m^{-2} of nematode biomass and the turf 105-355 mg m^{-2}, showing a much greater variation. Despite these differences, the annual nematode population respiration was very similar: 1726.1 µL O_2 m^{-2} d^{-1} in the turf and 1761.0 µL O_2 m^{-2} d^{-1} in the carpets, accounting for 16% and 35% of metazoan respiration in the turf and carpet, respectively.

In Wilkes Land, East Antarctica, Petz (1997) found the highest abundance of soil microfauna occurred in mosses, with 513 nematodes per gram dry "soil" (moss). Distribution was non-random because the microfauna were often strongly correlated with each other and were related to water and organic matter. Air temperature and *p*H more likely had indirect effects through the food web, especially the detrital component.

Figure 81. Nematode from the terrestrial moss ***Sanionia uncinata*** on the Barton Peninsula of King George Island, Antarctica. Photo by Takeshi Ueno, with permission.

Spaull (1973) found 30 species in 19 genera among mosses on Signy Island, with summer population densities of 0.48 x $10^6/m^2$ in the upper 6 cm of ***Chorisodontium*** (Figure 38)-***Polytrichum*** (Figure 82) turf compared to 7.47 x $10^4/m^2$ in soil beneath the grass *Deschampsia antarctica*. Nevertheless, in alpine areas in ***Schistidium apocarpum*** (as ***S. grande***; Figure 83), Hoschitz (2003) and in the Antarctic (Figure 84; Caldwell 1981a, b), bryophytes and lichens provide a protected shelter in which nematodes may survive. In the Austrian Alps, ***Plectus*** sp. (Figure 3) and ***Eudorylaimus*** sp. (Figure 78) survive the extreme conditions of the Alps. ***Plectus murrayi*** (Figure 85) is likewise a moss inhabitant at Victoria Land in the Antarctic (Melianie Raymond, pers. comm. 2008). ***Teratocephalus tilbrooki*** and ***Plectus antarcticus*** coexist in the shelter of moss cushions and mats (Pickup 1990b) and were the most abundant taxa on Signy Island in the Antarctic (Spaull 1973). However, on Signy Island ***Plectus*** (Figure 3) reaches its greatest abundance in moss carpets and ***Teratocephalus*** (Figure 17) in moss turf, suggesting that moss form plays a role, most likely in moisture relations, but possibly also in temperature relations.

Figure 82. ***Polytrichum strictum*** in Alaska, a moss where nematodes are known to live in the upper 6 cm in the Antarctic. Photo by Andres Baron Lopez, with permission.

Figure 83. ***Schistidium apocarpum***, a moss that provides a survival refuge in the Antarctic and alpine areas. Photo by David T. Holyoak, with permission.

Figure 84. Moss (reddish) and lichens. This photo shows a typical habitat for ***Plectus murrayi*** and occasionally ***Panagrolaimus davidi*** and ***Eudorylaimus antarcticus***. The photo was taken near Gondwana Station, Terra Nova Bay, Victoria Land. Photo by Melianie Raymond, with permission.

Figure 85. Two individuals of ***Plectus murrayi***, an Antarctic endemic that is often found in moss beds. Photo by Melianie Raymond, with permission.

The common presence of ***Teratocephalus*** (Figure 17) seems to be unique to the Antarctic, where it is abundant in the moss turf (Spaull 1973). It survives the frigid cold by a fast dehydration strategy that reduces damage by ice crystals (Wharton 2003). It would be interesting to determine how this fast dehydration relates to its choices of moss species/form. ***Ditylenchus*** sp. B occurs in more exposed aerial thalli of lichens (Spaull 1973). The latter species exhibits supercooling ability, whereas the moss-dwelling species both have bimodal supercooling point distributions. The high group supercools to ~-7°C and the other at ~-22°C. Pickup (1990b) suggests that field temperatures are likely to reach even lower levels than that.

Spaull (1973) found ***Teratocephalus***, ***Plectus*** (Figure 3), and ***Eudorylaimus*** (Figure 78) in all the bryophyte sampling locations on Signy Island, with the former two accounting for more than 50% of the nematodes among mosses. Cushion-formers such as ***Andreaea*** (Figure 86) and ***Grimmia***, on the other hand, had a nematode community where ***Plectus*** comprised less than 3%. A similar small percentage of ***Teratocephalus*** occurred in ***Bryum***. ***Eudorylaimus*** is more abundant in moss carpets and cushions than elsewhere. ***Eudorylaimus*** sp. C, in particular, seems to prefer cushions of ***Andreaea*** (Figure 86), ***Grimmia***, and ***Tortula***, where it comprises 45% of the individuals in that genus, but it is rare elsewhere (Spaull 1973). ***Antarctenchus hooperi*** is less restricted, being common in cushions of ***Andreaea*** and ***Tortula*** and in carpet-forming ***Calliergon*** (Figure 37)-***Calliergidium*** (probably ***Warnstorfia austrostraminea***), but it is likewise rare or absent elsewhere. The tylenchids [***Antarctenchus***, ***Aphelenchoides***, ***Ditylenchus***, ***Tylenchus*** (Figure 18)] are more abundant in moss turf than elsewhere, whereas the monhysterids [***Monhystera*** (Figure 16), ***Prismatolaimus***] are less numerous in moss turf than in other bryophyte formations.

Figure 86. ***Andreaea gainii*** (blackish) in Antarctica, showing cushion growth where nematodes may lurk. Photo from Polar Institute through Creative Commons.

The genus ***Eudorylaimus*** is particularly common in the Antarctic. Melianie Raymond (pers. comm. 2008) found ***Eudorylaimus antarcticus*** (Figure 87) among mosses in the Antarctic. In the McMurdo Dry Valleys, ***Eudorylaimus*** species are unaffected by vegetation type, including bryophytes (Simmons *et al.* 2009). ***Plectus*** (Figure 3) species, although bryophyte dwellers, are more abundant in algae. Its abundance above ground and below ground were significantly correlated in both the microbial mats and mosses. That is, the above ground abundance was a good indicator of below-ground abundance. The ability of ***Plectus*** species to migrate vertically is likely to benefit it in this changeable and extreme climate (Overgaard-Nielsen 1948; Kinchin 1989).

Kito *et al*. (1996) found a new species of ***Eudorylaimus*** (***E. shirasei***), bringing the Antarctic total in that genus to seven. Some of the specimens for this new species were collected from moss clumps at Cape Ryugu on the Prince Olav Coast, East Antarctica. It is odd among the members of ***Eudorylaimus*** (Figure 78) in having multinucleate intestinal cells, a factor that could simply have been overlooked elsewhere, but that raises questions about the possible effects of the severe Antarctic climate in causing or selecting for this multinucleate state. New species of moss nematodes will most likely continue to be described, particularly in the Antarctic.

Sohlenius and Boström (2006) found that 64% of 91 moss cushion samples from nunataks in East Antarctica had nematodes in them. In this harsh environment, 8% of the samples had no microfauna (nematodes, rotifers, or tardigrades) at all. The researchers considered the patchy distribution of nematodes and other organisms among the mosses to be a product of patch dynamics where stochastic processes determined colonization. They further supported this notion with the fact that nematodes in different cushions had different developmental stages, but it is possible that these may reflect differences in temperature that would affect rate of development. Competition with tardigrades that share their food sources seems also to be a limiting factor within a cushion.

Figure 87. ***Eudorylaimus antarcticus***, a common nematode among Antarctic mosses. Photo by Melianie Raymond, with permission.

In nunataks of Vestfjella, Heimefrontfjella, and Schimacher Oasis in East Antarctica, the faunal communities associated with mosses lacked organization and represented early stages of succession (Sohlenius *et al*. 2004). In these exposed nunatak moss habitats, species of ***Plectus*** (Figure 3) and ***Panagrolaimus*** (Figure 20) were the most frequent of the nematodes, occurring in 26% and 5% of the samples, respectively.

Dangers Lurking among Bryophytes

Fungal Interactions

Who would think that fungal treachery looms amid the mosses! Although nematode-trapping fungi are known worldwide, they were unknown in the Antarctic until 1973. In their examination of Signy Island mosses, Duddington *et al*. (1973) found nematode-trapping fungi on a number of moss species: ***Brachythecium austrosalebrosum***, ***Calliergon sarmentosum*** (Figure 37), ***Sanionia uncinata*** (Figure 88) (all hydrophytic), and ***Andreaea depressinervis*** (mesophytic-xerophytic). These fungi sport rings (Figure 89) that are able to constrict around nematodes that wander through them, thus ensnaring them. Several specimens of the predatory ***Thyronectria antarctica*** var. ***hyperantarctica*** had indeed trapped nematodes within their mossy home. Spaull (in Duddington *et al*. 1973) also noted fungi with such loops in a sample of the leafy liverwort ***Cephaloziella*** sp. (Figure 90) mixed with the lichen ***Cladonia metacorallifera*** from Terra Firma Islands in Marguerite Bay (latitude 68º42'S).

Figure 88. ***Sanionia uncinata***, common home of nematodes and nematode-trapping fungi. Photo by Michael Lüth, with permission.

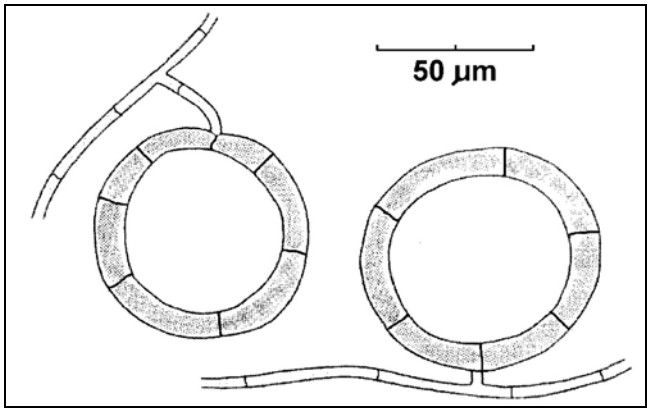

Figure 89. Nematode-trapping fungus, possibly ***Monacrosporium cionopagum***, isolated from the moss ***Calliergidium cf. austro-stramineum*** on Signy Island in the Antarctic. Redrawn from Duddington *et al*. 1973.

Figure 90. Leafy liverwort ***Cephaloziella turneri***, member of a genus that is home to nematode-trapping fungi. Photo by Michael Lüth, with permission.

The Antarctic sports at least 18 taxa that either trap nematodes or become endozoic parasites of members of this phylum (Gray *et al*. 1982). Many of these have been found among the mosses. Among the Hyphomycetes that snare nematodes, ***Monacrosporium ellipsosporum*** and ***M. cionopagum*** were the most widely distributed. The most frequent of the endozoic taxa was ***Harposporium anguillulae*** (Figure 91). These fungi seemed to have some bryological preferences, with ***M. ellipsosporum*** preferring calcicolous mosses. In fact, it appears that acidic habitats might provide a safe haven - the nematophagous fungi were absent from permanently saturated moss carpets and the strongly acidic turf-forming mosses of Polytrichaceae.

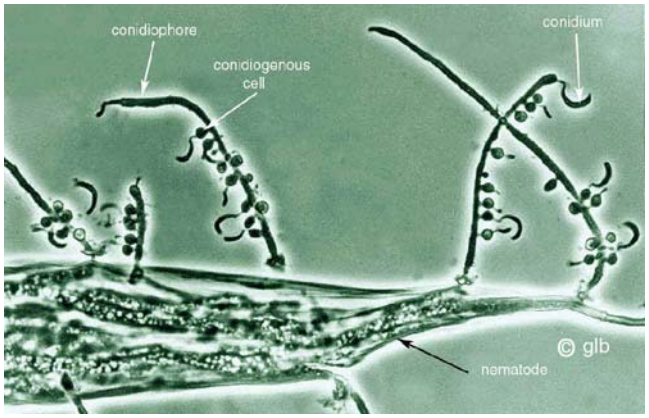

Figure 91. ***Harposporium anguillulae***, fungal parasite with conidiophores and conidia, on a dead nematode. Photo by George Barron, with permission.

These ensnaring fungi are not restricted to the Antarctic. Duddington (1951) considered the abundance of such fungi among mosses to result from the large amount of water among the shoots and leaves, making the environment favorable for both nematodes and fungi. In the Antarctic, the mosses provide the added benefit of being warmer than the air in summer.

Both nematodes and fungi live among ***Sphagnum*** (Figure 5). And here we also find nematode ensnaring fungi. In particular, the genus ***Sporotrichum*** (Figure 92), known for causing **sporotrichosis** in those who handle ***Sphagnum***, is able to trap the nematodes that reside there (Dollfus 1946).

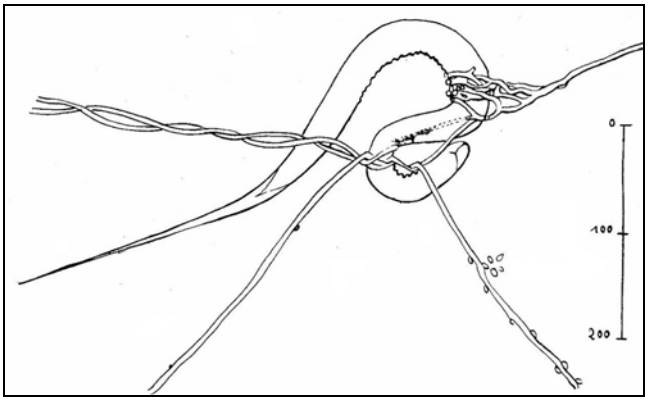

Figure 92. The nematode-ensnaring fungus ***Sporotrichum*** sp. in action. This is the same genus known so well for causing sporotrichosis in people who work with ***Sphagnum***. Image from Dollfus 1946.

Other fungal treachery looms, although not so dramatically. Several species of nematode-dwelling parasites await. Among these on Signy Island in the Antarctic are ***Harposporium*** sp. (Figure 91) and ***Acrostalagmus*** sp.

The widespread fungus ***Catenaria anguillulae*** (Figure 93-Figure 96) parasitizes nematodes (Sayre & Keeley 1969). Its **zoospores** (swimming spores) are attracted to the nematodes by exudates from the mouth, anus, or other opening of the nematode, including wounds. Once attached, the zoospores encyst, typically in clusters. These eventually germinate and penetrate through the nearby orifice to attack their host, the nematode. Success of the fungus is favored by high temperatures (optimum at 28°C) and moisture, the latter provided by bryophytes.

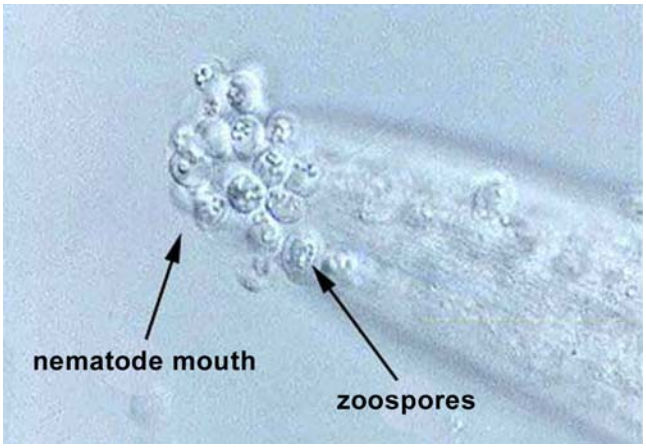

Figure 93. Nematode with zoospores of fungus ***Catenaria anguillulae*** surrounding its mouth. Photo by George Barron, with permission.

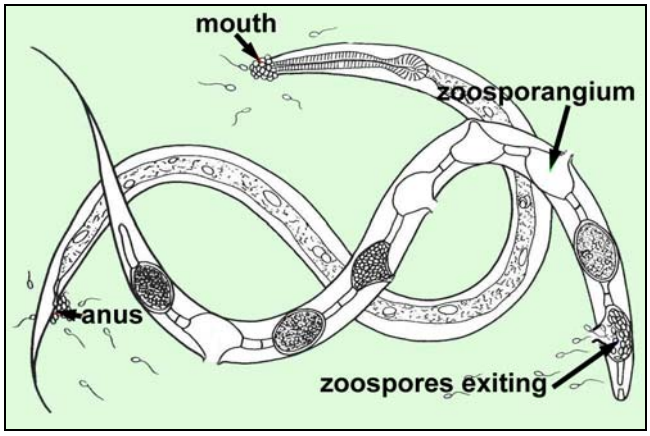

Figure 94. Nematodes showing infestation by ***Catenaria anguillulae***. Modified from George Barron's image, with permission.

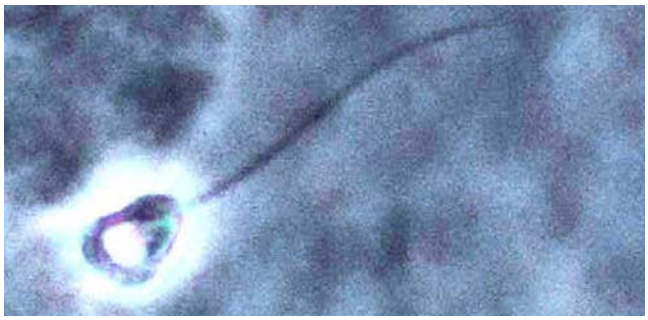

Figure 95. Zoospore of ***Catenaria anguillulae***. Photo by George Barron, with permission.

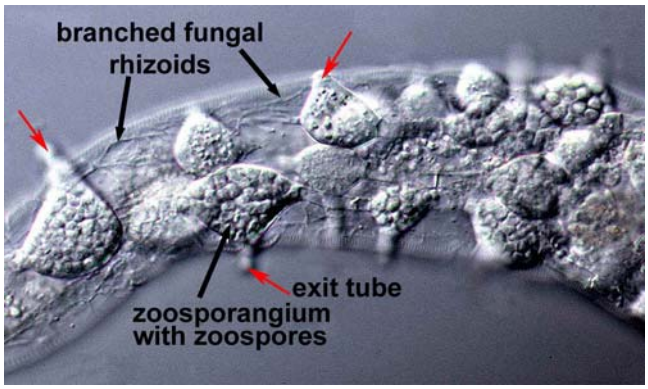

Figure 96. Zoosporangia of ***Catenaria anguillulae*** within a nematode. Red arrows indicate the exit tubes where zoospores escape. Photo by George Barron, with permission.

Safe Site from Predation

One advantage to living in a habitat with only small chambers is that large organisms don't fit. This affords some protection from predation, but nematodes are definitely not free from it. Some are preyed on by co-habiting tardigrades (Doncaster & Hooper 1961); under experimental conditions, one tardigrade, ***Macrobiotus richtersi*** (Figure 97), consumed 61 nematodes per day – no small threat (Sánchez-Moreno *et al*. 2008). Others must surely fall prey to insects. Even the protozoa may be a threat (Yeates & Foissner 1995). The Testacea (amoebae) can ingest nematodes, attacking mostly from the tail. In New Zealand, it was the protozoa ***Nebela*** (*Apodera*) ***vas*** (Figure 98) and ***Difflugia*** sp. (Figure 99) that waged the attacks, mostly on ***Dorylaimus*** (Figure 7) and ***Plectus*** (Figure 3) species among common bryophyte inhabitants.

Figure 97. ***Macrobiotus richtersi***, a moss-dwelling tardigrade that devours numerous nematodes. Photo through Creative Commons.

Pollution

Even aquatic organisms can suffer from air pollution. Steiner (1995b) tested responses of several groups of aquatic moss-dwelling invertebrates to SO_2 pollution. Nematodes, rotifers, and tardigrades changed their community composition. SO_2 at 0.225 ppm for 18 months significantly reduced the numbers of several nematode species. Responses were not so clear at 0.075 ppm, with some species increasing and others decreasing in numbers.

Lead can also considerably alter the moss-dwelling nematode community. Zullini and Peretti (1986) found that increased lead content in the moss resulted in a significant decrease in diversity, richness, and biomass, but not the density. The **Dorylaimina** suborder suffered the most by far.

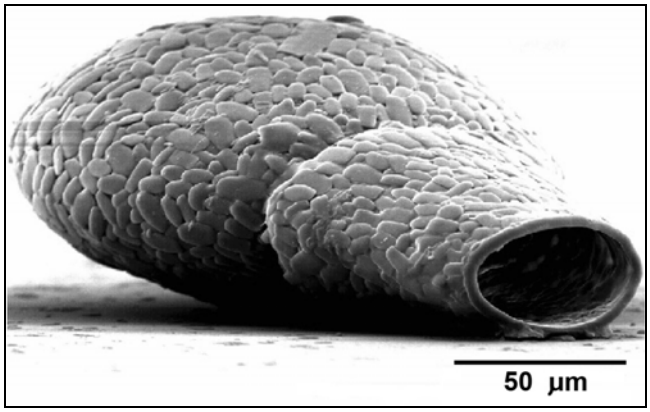

Figure 98. ***Nebela*** (=*Aphodera*) ***vas***, a protozoan that is a nematode predator. Photo by Edward Mitchell, with permission.

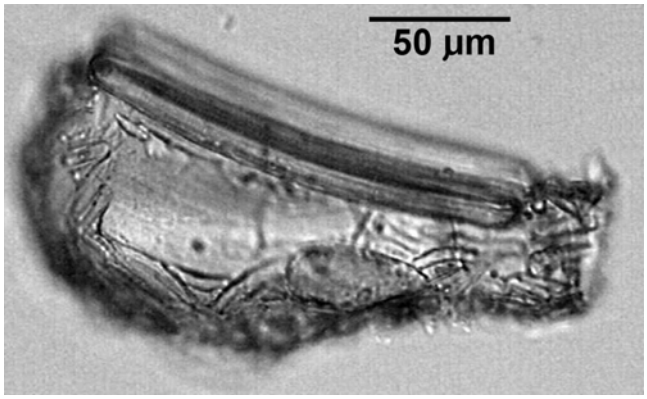

Figure 99. ***Difflugia bacillifera***, a moss-dwelling protozoan that preys on nematodes. Photo by Edward Mitchell, with permission.

Summary

Among the most common bryophyte-dwelling nematodes are members of the genera ***Plectus*** and ***Eudorylaimus***. These nematodes are usually less than 1 cm in length and many are much smaller. Although bryophyte-inhabiting nematodes are rarely studied, they are common there and can reach 480 individuals in just 1 g of moss.

Many nematodes adhere to the mosses with an **adhesive organ**. Water is their most limiting factor. They can migrate vertically among the bryophytes to adjust their moisture level. Some migrate from rhizoids to canopy when the moss is too wet, some move from the rhizoids to the stems when the moss is saturated, and some never leave the rhizoids. The most specialized nematodes, such as ***Plectus rhizophilus***, live in the bryophytes that experience the most events of desiccation, such as the epiphytes.

Members of ***Plectus*** are quick driers. Acrocarpous cushions are more favorable habitats than pleurocarpous feather mosses. Slow dehydration is important to their survival in a state of **anhydrobiosis**; some achieve this by **coiling**. Water is also necessary for their motility, where they can swim, crawl, inch, or bend to move. Some survive by living and reproducing inside the hyaline cells of ***Sphagnum***. **Eggs** likewise have a long survival and can even survive lack of oxygen.

Food strategies are mostly bacteriovores and predators. Some are **mycophagous** or **saprophytic**. Woodland mosses often feed on the detritus. They seem to do best in habitats with a low C:N ratio in the food source. Stream mosses serve as nutrient traps that favor nematodes.

Bryophytes can provide a safe site against would-be predators. However nematode-trapping fungi and fungal parasites may loom there. Bryophytes can also make a safe site by buffering the temperature both in the bryophyte and in the soil beneath. Even antheridia can serve as habitat, and in other cases the nematodes nestle among archegonia to make nematode galls. Galls seem to occur on many species of bryophytes and house nematodes that are often less than 1 mm long.

Numbers usually are highest in summer and lowest in winter, with some species migrating to greater depths in winter. Some species among ***Panagrolaimus*** can freeze and recover. Others, such as one ***Aphelenchoides***, can tolerate temperatures ranging from meltwater to 61.3ºC. **Trehalose** can protect some from freezing damage as well as from dehydration damage, most likely by stabilizing membranes.

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CHAPTER 4-4
INVERTEBRATES: ANNELIDS

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CHAPTER 4-4
INVERTEBRATES: ANNELIDS

Figure 1. ***Aeolsoma***, an aquatic annelid that sometimes inhabits mosses such as ***Fontinalis***. Photo by Yuuji Tsukii, with permission.

Annelida – Segmented Worms

Among the bryophyte-dwelling **Annelida** are worms that qualify as **mesofauna** (Figure 1). These are organisms, also including **mites** (**Acari**) and **springtails** (**Collembola**), that can occupy pore spaces that have a diameter of less than 2 mm (Briones 2006). In other words, these are small annelids, primarily in the subclass **Oligochaeta**.

Among the annelids, the family **Enchytraeidae** is a worldwide but little known family that can be found among the bryophytes. They reach their greatest abundance in the moist temperate soils (Block & Christensen 1985). Unlike the large, pink-red earthworms, these worms are usually grey-white (Briones 2006). Their identification is based primarily on internal characters, hence making them unknowns to the casual observer. And they must be live to be identified because preservatives make them opaque. **Enchytraeids** are important consumers in the Arctic tundra sedge-moss meadow habitat (Ryan 1977).

Although annelids are not as common as some other invertebrates in bryophytic habitats, there are at least some notable exceptions. ***Fontinalis*** (Figure 2) has been known to house 67 **oligochaetes** and 5 **leeches** (**Hirudinea**) in a square meter (Berg & Peterson in Macan 1966). Moss balls of ***Drepanocladus*** (Figure 3) and ***Fontinalis*** also house these annelids. In New Zealand Suren (1993) found **oligochaetes** to occupy 12.3% of the bryophyte fauna.

Three of the most common Enchytraeids in peatlands are ***Cognettia sphagnetorum***, ***Marionina clavata***, and ***Achaeta eiseni*** (Figure 4; Briones *et al.* 1997; Briones pers. comm. 17 March 2009). Nevertheless, Standen and Latter (1977) demonstrated that the common ***C. sphagnetorum*** is less common among ***Sphagnum*** than it is among *Eriophorum* or *Calluna* in a blanket bog at Moor House in Cumbria. ***Marionina clavata*** is aided in its survival by laying two types of eggs, one taking ~112 days and another taking ~271 days for the worms to reach maturity at 10ºC, thus potentially providing them with two different sets of conditions (Springett 1970). A tolerance for low *p*H levels in ***C. sphagnetorum*** and ***M. clavata*** (2.9-4) suggests their suitability for peatland habitation (Graefe & Beylich 2003).

Figure 2. **Brook moss**, ***Fontinalis duriaei***, where **annelids** can be common. Photo by Janice Glime.

In a Dutch Scots pine forest these three had a vertical zonation pattern in the same order, with ***Cognettia sphagnetorum*** (Figure 5) being the first to colonize new needle litter (Didden & de Fluiter 1998).

Figure 3. Moss ball of ***Drepanocladus*** from Lake Kucharo, Japan. Photo by Janice Glime.

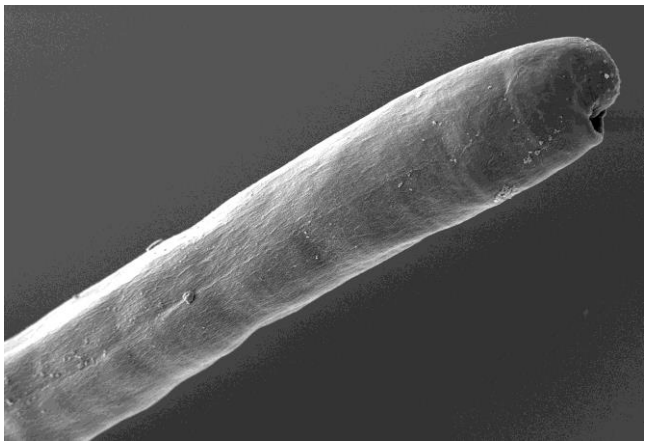

Figure 4. SEM image of *Achaeta* sp. Photo by María Jesús Iglesias Briones, with permission.

Water Relations

Very small annelids (**Enchytraeidae**) occur among ***Sphagnum*** plants. Springett (1970) found six species associated with peat. The moisture changes can result in diurnal vertical migrations (upwards at night), at least in ***Cognettia sphagnetorum*** (Springett *et al*. 1970; Hingley 1993; Briones *et al*. 1997), a widespread species known from aquatic habitats, ***Sphagnum*** peatlands, and on South Georgia in the Antarctic from ***Polytrichum*** (Figure 6) clumps (Block & Christensen 1985).

Cognettia sphagnetorum (Figure 5) has no cocoon stage, thus permitting it to take full advantage of the growing season in cold, wet climates of places like the Antarctic (Hingley 1993).

Several species of ***Achaeta*** (Figure 4) are morphologically adapted to drought by having a thicker cuticle. However, it appears that physiological adaptations to drought in the enchytraeids may be limited.

On the other hand, they seem also to be intolerant of too much water. In a study on the effects of drainage on the mesofauna of peatlands in Finland, Silvan *et al*. (2000) found that water-level drawdown resulting from peatland drainage caused an increase in the numbers of all the mesofauna studied, including the **Enchytraeidae**, with numbers ten times as great after 60 years. Because of a proportionally larger increase in Collembola, the proportion of **Enchytraeidae** in the fauna dropped slightly. More than 60% of the **enchytraeids** occurred in the top 4 cm of the peat. Within two years after water was returned to a drained peatland, the numbers dropped abruptly to levels near that of pre-drainage.

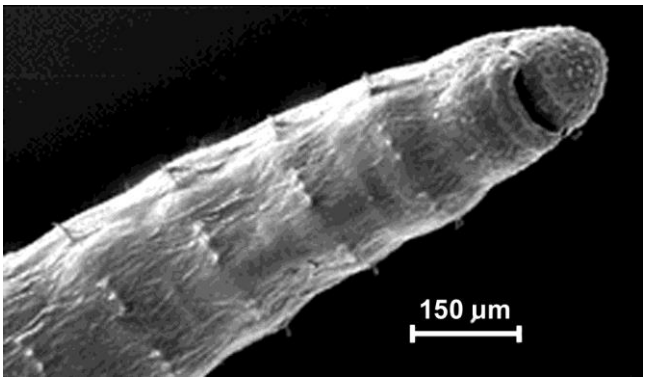

Figure 5. SEM image of ***Cognettia sphagnetorum***. Photo © María Jesús Iglesias Briones, with permission.

Figure 6. Clump of ***Polytrichum*** that could house **annelids**. Photo by Michael Lüth, with permission.

Temperature Tolerance

In peatlands and elsewhere, the **Enchytraeidae** are sensitive to temperature, which seems to be a major differentiating factor for population size. ***Cognettia sphagnetorum*** increases its reproductive rate, most likely through its capability of fragmentation as a reproductive strategy, in response to warmer temperatures (Briones *et al*. 1997). Warming seems to result in greater numbers without a concomitant vertical migration. Despite this advantage, Briones *et al*. (2007) considered that an increase in temperature to a maximum mean annual threshold of 16ºC could cause total loss of this species from some regions.

Achaeta eiseni, also a peatland species, is resistant to higher temperatures, increasing in numbers as temperatures increase, whereas numbers of ***Cernosvitoviella atrata*** (Figure 7) are greatly reduced by higher temperatures (Briones 2006, pers. comm. 17 March 2009). The latter species is inhibited by its inability to avoid dry conditions, resulting in death at high temperatures (Briones *et al*. 1997).

Figure 7. SEM image of ***Cernosvitoviella atrata***. Photo by María Jesús Iglesias Briones, with permission.

Cognettia sphagnetorum and ***C. glandulosa*** (known from moss banks and elsewhere; Block & Christensen 1985) are also prepared for the seasonal inundation of the peatlands. They are able to produce red blood under very wet conditions (Healy & Bolger 1984) to survive the low oxygen conditions that arise. Healy and Bolger showed that 35% of the Irish taxa of **enchytraeids** preferred habitats that were submerged or frequently flooded.

Reproduction

Any successful inhabitant of mosses must have a life cycle that is coordinated with the moss habitat. One advantage to some **Oligochaetes** is their ability to reproduce by fragmentation. Christensen (1959) pointed out that the **Enchytraeidae** contrast with other Oligochaeta in their inability to reproduce by fragmentation. At the same time, he reported on asexual reproduction in three species among the 78 Dutch **Enchytraeidae** studied by that time. In fact, one species apparently had only asexual reproduction, by fragmentation. Honda *et al*. (2003) described fragmentation in ***Enchytraeus japonensis***. This worm uses stem cells to accomplish its regeneration. Segments form as organs regenerate. They showed that cells with newly synthesized DNA appeared first as a ring in the tail area. The labelling then migrated, suggesting that the formation of segments occurs before organ regeneration. This regeneration cycle can take as few as ten days (Myohara *et al*. 1999; Nakamura 2004), and both ends of the worm can regenerate (Nakamura 2004). Nakamura (2004), in a six-and-a-half-year study, determined that the average fragmentation cycle length for the species was 20.4 days. The maximum number of fragmentation events in the life of the worm was 122, with an average of 35.3. The number of fragments in one event was 6.3. The cycle can repeat until the worm is starved or the population density is low, at which time it will differentiate gonads and reproduce once sexually (Honda *et al*. 2003). At this time I don't know how the number of annelid species using fragmentation relates to bryophytes as a habitat.

Food Relations

Springett and Latter (1977) experimented with various fungal diets on agar and found they could not keep many ***Cognettia sphagnetorum*** alive on the combinations they tried. Exudates from the mycelia of Basidiomycetes proved most harmful, resulting in 100% mortality in 20 days. They concluded that micro-organisms did not form any part of the natural diet of moorland Enchytraeidae. Hingley (1993) considered peat to be a poor source for food (Hingley 1993), with the moss itself seemingly of poor quality for annelids; only stem material of ***Sphagnum*** has been found in gut analyses (Figure 8; Standen & Latter 1977). Nevertheless, these worms feed on items that are generally unpalatable to other animals (Hingley 1993). After these are processed by the **annelids**, the feces are colonized by fungi and bacteria, which are in turn ingested by **Protozoa**, **rotifers**, and **nematodes**. Hence a food web emerges and peat is processed.

Briones (pers. comm.) challenged the suggestion that peatlands offered poor food quality, stating that enchytraeids are known to consume bacteria and dead organic matter, both of which are associated with the peatlands. Briones *et al*. (2004) used ^{14}C to match the gut contents with the substrate and found that most of the assimilated food came from sediment that is 5-10 years old. Their vertical movements in response to changing moisture did not affect their food source, but at higher temperatures it seemed that they had altered their carbon source since there was a lower ^{14}C enrichment with depth.

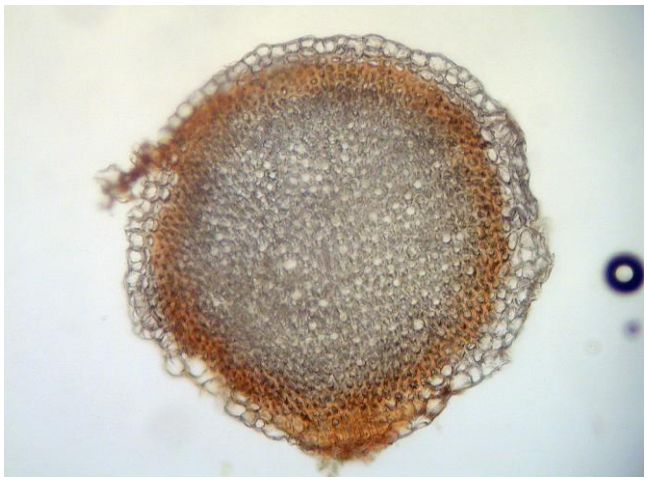

Figure 8. Stem section of ***Sphagnum contortum***, like those found in an annelid gut. Photo by Michael Lüth, with permission.

Guts from worms in substrata of ***Sphagnum***, *Calluna*, and *Eriophorum* at Moorhouse, Great Britain, all contained mixed decomposing litter, including cellulosic or humified plant material, amorphous humus, and associated fungal mycelia, again suggesting equal nutritional availability in the peatlands (Standen & Latter 1977). The ***Sphagnum*** stem material extracted from the gut of ***Cognettia sphagnetorum*** (Figure 5) causes one to question if these stems provide nutrition or merely serve to help in grinding other foods, much like the role of sand. In any case, the very high numbers of worms reached in peatlands provides witness that these are not bad systems for **enchytraeids** (Briones pers. comm.).

In the blanket bog at Moor House, Great Britain, the numbers of ***Cognettia sphagnetorum*** were significantly less in ***Sphagnum*** than they were in *Calluna* and *Eriophorum*, suggesting that ***Sphagnum*** was not an ideal habitat. However, when these were converted to numbers

per gram dry weight of substrate, there were no significant differences among substrata. The species was in greatest numbers in association with older decomposing litter of *Eriophorum* and *Calluna* and with surface layers of ***Sphagnum***. The numbers of worms correlated weakly with unstained fungi, cocci, and moisture.

Sampling

Annelids are generally extracted from core samples. Researchers typically use some modification of a Berlese funnel (Didden *et al*. 1997; See Chapter 4-1). For annelids, a wet funnel is the most common, as suggested by O'Connor (1955) and Overgaard-Nielsen (1948, 1949). The moss samples are placed in a water-filled funnel and the temperature is gradually increased to about 40ºC (~3 hours). The high temperature causes the worms to vacate the mosses and drop down to the funnel. In organic soils, the efficiency is often 95% or more (Healy 1987), but can be less than 50% in some samples (Willard 1972 in Didden *et al*. 1997). Variations on this include soil cores in an earthenware cylinder suspended over a heated water bath (O'Connor 1955). The worms are driven upward to a layer of cool sand on top of the soil core. The worms are recovered by washing them from the sand.

An alternative method is to squeeze water from the mosses onto a microscope slide or into a Petri dish (Hingley 1993). Repeated extraction can be accomplished by soaking the moss in water and squeezing again, repeating this for a standard number of times. A paint brush or strip of filter paper can be used to transfer them to a drop of water on a slide. The sample could be transferred to a test tube, then centrifuged. A concentrated sample can then be removed from the bottom of the test tube with a long pipette.

Andrew and Rodgerson (1999) tested three methods of extracting invertebrates from Tasmanian bryophytes: Tullgren funnels, sugar flotation, and kerosene phase separation. When two samples were combined, the kerosene phase separation method extracted more total individuals, more **mites**, and more **Collembola**. Nevertheless, only three of the nine taxa were found in the single samples, suggesting that replicate samples are needed. Andrew and Rodgerson attributed this to differences caused by spatial scales. They further found that there is site scale variation at 2 km or less that may be more important that altitudinal variation.

Habitats

Aquatic

Aquatic bryophytes can serve as annelid (subclass Oligochaeta) habitat, especially for **Naididae**, reaching as much as 33% of the invertebrate fauna (1968 per dm^2) in thick moss vegetation of streams in the West Riding of Yorkshire, UK (Percival & Whitehead 1929). Their numbers were exceeded only by the Chironomidae (midges). This is a sharp contrast to their apparent absence on *Potamogeton* in those streams. Brusven *et al*. (1990) found that annelids were the most common non-insect invertebrate in the South Fork of the Salmon River, Idaho, USA. In Brazil, Gorni and da Gama Alves (2007) collected ***Fissidens*** and ***Philonotis*** (Figure 9) in winter and spring. Bryophytes adhering to rocks in the rapids of the Jacaré Pepira River, Brotas, São Paulo, Brazil, and to a vertical rock wall of a waterfall near the river provided a home for 191 Naididae individuals of ***Nais communis***, ***Pristinella jenkinae***, and ***P. menoni***. Among the identifiable species, ***P. jenkinae*** was dominant, representing 96.8% of all individuals. This species occupied both the submerged mosses of stream beds and the rock wall mosses with little water. But often the annelids are not very common. In ***Fontinalis antipyretica*** in the Czech Republic, Vlčková *et al*. (2001/2002) found that only about 1.1% of the fauna were annelids in one stream and about 1.4% in another.

Figure 9. ***Philonotis fontana***, representing a genus where ***Nais communis***, ***Pristinella jenkinae***, and ***P. menoni*** dwell in Brazil. Photo by Michael Lüth, with permission.

Naididae occupancy of mosses may provide several benefits to these worms. Mosses provide a safe site where the current is reduced in fast water (Vlčková *et al.* 2001/2002; Habdija *et al.* 2004). This is important for a group of organism that lack any adaptations for clinging or anchoring. Abundance and diversity are likely to increase with an increase in moss biomass, and more biomass makes available more periphyton and detritus (Egglishaw 1969; Suren 1993; Vlčková *et al.* 2001/2002; Linhart *et al*. 2002a, b).

Like Thienemann (1912), I rarely found oligochaetes among the bryophytes in Appalachian Mountain, USA, streams (Glime 1968). But Percival and Whitehead (1929) found that ***Eiseniella teträedra*** was a frequent inhabitant among the mosses in shallow water (3-4 cm). Nevertheless, even in thick moss beds, it reached a density of only 6 per dm^2. The Naididae (***Nais elinguis***), on the other hand, reached as many as 12,000 per dm^2 among the thick moss beds. Thickness of moss growth, as well as time of year and recent history of river conditions, influenced the density of oligochaetes. Percival and Whitehead suggest that the much smaller numbers of these naidids in the loose moss mats may be due to "feeble" setae and no ability to attach to the moss.

Hynes (1961) compared the oligochaetes, including ***Eiseniella teträedra***, on mosses and silk in a Welsh mountain stream and found little difference in the percentage of organisms, suggesting that the moss need not be a living organism and might only provide a substrate, perhaps with trapped detritus as a food source.

Peatlands

Unlike many other kinds of animals, the annelids are not very diverse in peatlands. Hingley (1993) reported that

only three families of **Oligochaeta** occur in peatlands, with the most common being the **Enchytraeidae**. Duinen *et al*. (2006) found that in Estonia and The Netherlands, only ***Cognettia sphagnetorum*** occurred in ombrotrophic raised bogs, *i.e.*, in the most nutrient-poor situations. In Estonia, ***Nais variabilis*** (Figure 10), ***Lumbriculus*** (=*Lumbricus*) ***variegatus*** (Figure 11), and species with sexual reproduction occur only in more minerotrophic water bodies with a higher decomposition rate and consequent higher nutrient content. The lagg zone (marginal area around the bog where nutrients are often higher) fares somewhat better, having ten species of oligochaetes. This zone is absent in The Netherlands due to agriculture.

Figure 10. ***Nais variabilis***, a moss-dwelling annelid. Photo by Yuuji Tsukii, with permission.

Figure 11. ***Lumbriculus*** *(=Lumbricus*) ***variegatus***, an annelid that is used to feed pets and that lives in minerotrophic peatlands. Photo from Wikimedia Commons.

Prairie Worms

It is possible that mosses may provide refugia for one rare species. The giant **Palouse earthworm** (***Driloleirus americanus***; Figure 12), named because it can reach nearly a meter in length, is the subject of a petition to declare it an endangered species and afford it protection (Palouse Prairie Foundation 2007). Few recent reports of its presence exist. In one such report, however, near Moscow, Idaho, USA, two researchers found it in a somewhat mesic area under forest canopy. The area had abundant mosses and these researchers found several of the worms near the surface under moss mats when looking for moss-feeding beetles in the Byrrhidae. In drier times it can burrow down as much as 5 m.

Figure 12. The giant **Palouse earthworm** (***Driloleirus americanus***), an endangered worm that seems to seek moisture under mosses in the Palouse Prairie. Photo by Yaniria Sanchez-de Leon, with permission.

Antarctic

As in the peatlands, the **Enchytraeidae** are common in the Antarctic bryophytes. Block and Christensen (1985) found ***Cognettia sphagnetorum*** in ***Polytrichum*** clumps and ***C. glandulosa*** in moss banks. On South Georgia and Signy Island, they found seven taxa in soil and peat, but suspected that five of those had been introduced by human activity on the islands.

Dispersal Agents?

The presence of bryophyte diaspores in earthworm castings suggests a possible dispersal mechanism (During *et al*. 1987). Van Tooren and During (1988) found various spores and vegetative diaspores in the guts of terrestrial **earthworms** [***Allolobophora caliginosa***, ***A. chlorotica***, and ***Lumbricus terrestris*** (Figure 13-Figure 14)] in The Netherlands. Especially rhizoid tubers and spores occurred. However, it is not clear that these provided any nutritional value to the worms because some remained viable and grew new plants, suggesting digestion was not possible. Rather, they most likely were simply mixed in with the soil that was being consumed.

Figure 13. ***Lumbricus terrestris***, the common earthworm, is able to transport various diaspores, thus being a potential dispersal agent for bryophytes. Photo by Michael Linnenbach through GNU Free Documentation.

Figure 14. ***Lumbricus terrestris*** wending its way in a clump of the moss ***Rhynchostegium confertum***. Photo by Serhat Ursavas, with permission.

From a bryological point of view, it thus appears that the worms might serve as dispersal agents, although it was spores, not the more easily established tubers, that remained viable after traversing the **earthworm** gut (Van Tooren & During 1988). Tubers seemed unable to survive the journey through the gut. Twenty-five species of mosses germinated from diaspores from gut contents, with ***Pottia/Phascum*** (Figure 15) being the most common. This compares to the presence of only eight species of mosses in the samples of **earthworms**, indicating transport from other locations. For buried diaspores, **earthworms** may facilitate their movement from beneath the surface to the castings above ground where they are exposed to light and able to germinate. On the other hand, ***Bryum rubens*** (Figure 16) is not known to produce sporophytes in this area and relies on vegetative diaspores. It is one of the most common species in the area, but is not common above ground. It was also rare in the worm samples, causing Van Tooren and During to suggest that mechanical and chemical processes in the gut cause high mortality of the rhizoidal tubers in this species.

Figure 15. ***Pottia bryoides***, a member of one of the genera that had the highest germination in cultures from earthworm guts. Photo by Michael Lüth, with permission.

Earthworm Culture

Peatmoss is recommended as an additive to rich soil for rearing earthworms (Mascio 2006; How to Grow Your Own Earthworms 2009; Oliver 2009)

Most farmers seem to consider **earthworms** to be their friends because they reputedly aerate the soil. However, they can also be a nuisance. One person complained that the earthworms were the largest deterrent to the establishment of a moss garden. The worms would "plow" up the surface and detach the moss from the soil. It appeared that they also chewed up the moss, but there seems to be only circumstantial evidence of that.

Figure 16. Clump of ***Bryum rubens***, a moss that does not produce sporophytes and relies on dispersal of vegetative diaspores. Photo by Michael Lüth, with permission.

Polychaetes

I completely overlooked this mostly marine group when I wrote this chapter (Figure 17). It was only when two people posted pictures on Bryonet of strange organisms they found among bryophytes that I realized there are terrestrial polychaetes that may inhabit bryophytes. These Bryonet organisms were not polychaetes, but they did raise the question. However, I have been unable to find any published documentation that polychaetes ever occur on bryophytes.

Figure 17. Syllid polychaete undergoing epitoky – becoming sexually mature. Photo by Megan McCuller, through Creative Commons.

Storch and Welsch (1972) described adaptations to air breathing in polychaetes from the mangrove swamps of Sumatra. Their exterior is protected by a cuticle that varies in thickness. The gills have extracellular spaces that have blood lacunae in the epidermis in at least one species. But the terrestrial polychaetes seem to be poorly known.

Thank you to Bryonet and its wonderful subscribers! *Parergodrilus heideri* and *Hrabeiella periglandulata* are the only terrestrial European flatworms, where they live in forest soils (Dumnicka & Rozen 2002) and would seem to be likely candidates for bryophyte dwelling (Juan Larrain,

pers. comm. 29 February 2012). But both Larrain and I searched the web for links to bryophytes to no avail. Rather, Schlaghamerský and Šídová (2009) examined the vertical distribution of a population in the Czech Republic of *Hrabeiella periglandulata* in soil and determined that they avoided the organic layer, which would include bryophytes. Perhaps the minute *Parergodrilus heideri* (Rota 1997) and *Hrabeiella periglandulata* (Rota 1998) are hiding among them somewhere with the right moisture conditions. But it is more likely that the temperature of their environment is modified by the presence of bryophytes at the surface.

Summary

Many bryophyte-inhabiting annelids (segmented worms) are **mesofauna**, *i.e.* able to occupy spaces with a diameter < 2 mm. The **Enchytraeidae** are among the most common. Bryophyte-dwelling annelids may form zones in the soil and bryophytes and some species may migrate up and down daily in response to changing moisture conditions. **Enchytraeids** have a wide tolerance to water, but have little adaptation to drought. Some species produce red blood to survive low oxygen conditions.

Although most **Enchytraeidae** cannot reproduce by fragmentation, some enchytraeids can reproduce by this method in a cycle of ~20.4 days. ***Cognettia sphagnetorum*** increases its reproductive rate when temperatures get warmer, but an annual mean above 16ºC could cause annihilation. Some species thrive in higher temperatures, whereas others are seriously affected.

Neither mosses nor fungi seem to serve as food for the annelids, although ***Sphagnum*** stems have been found in guts. In peatlands, 5-10-year old sediments seem to be an important food source. Bryophytes in streams can provide safe sites where reduced current provides more debris for food. Despite their apparent distaste for bryophytes, annelids may disperse vegetative diaspores by eating them and depositing them elsewhere unharmed, indicating at least some are not digested..

Worms can be extracted from bryophyte samples using funnel systems. Smaller taxa can be extracted by squeezing water onto a microscope slide.

The **Palouse earthworm** (***Driloleirus americanus***) is a rare species that occurs under moss mats in the prairie.

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CHAPTER 4-5

INVERTEBRATES: ROTIFERS

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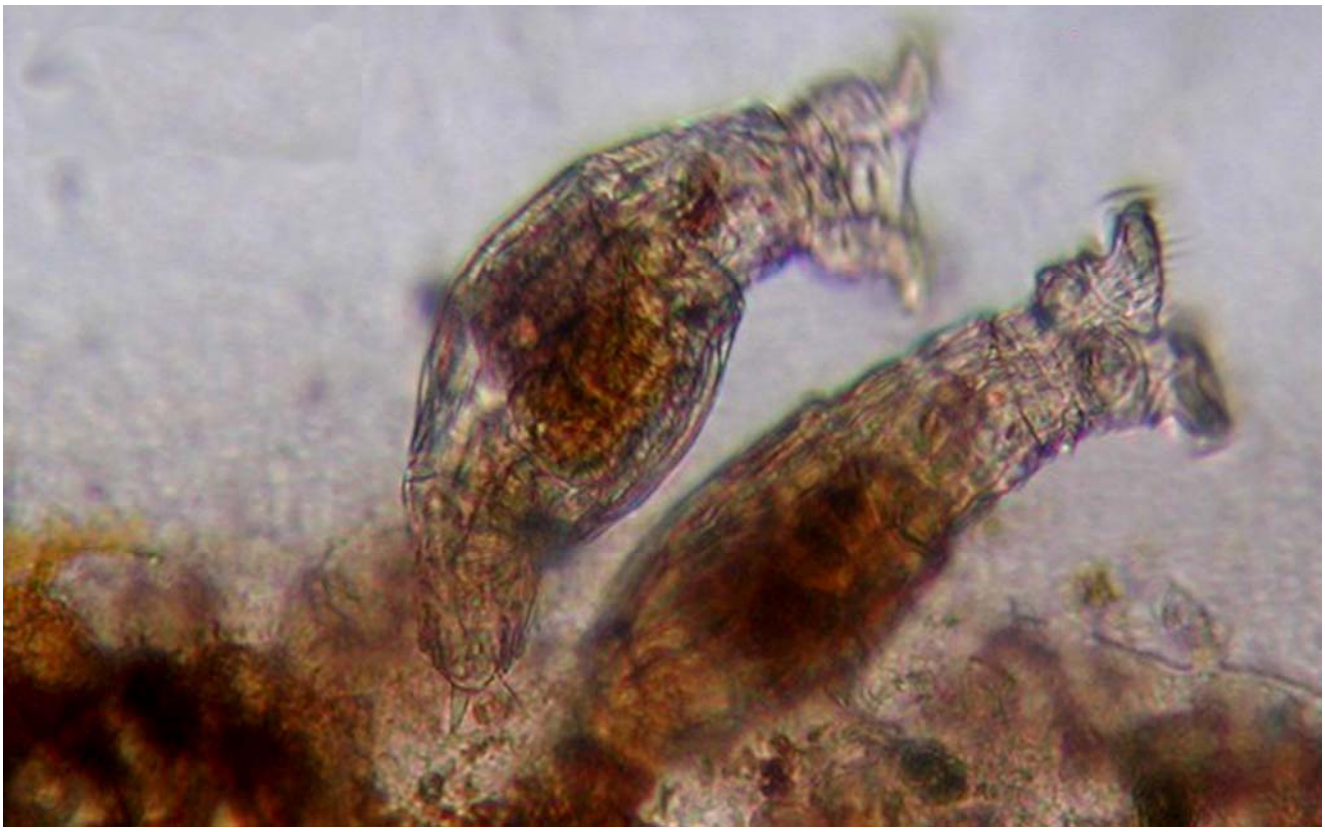

Figure 1. Two **bdelloid rotifers** that commonly inhabit bryophytes. Photo by Paul Davison, with permission.

Rotifera – Rotifers

Rotifers, also known as wheel animals, are so-named because of the ciliated **corona** on the head. The corona creates a circular movement that is used to direct food to the mouth. Rotifers have up to five simple eyes (Figure 2) that are light-sensitive and often are red. This sensitivity to light permits some species to be **phototactic** (moving toward or away from light).

Rotifers are natural partners for organisms like bryophytes that often experience extended periods of drought. Pourriot (1979) considered the number of species that inhabit mosses to be over 200. The number is surely larger now.

Anthony von Leeuwenhoek discovered in 1702 that rotifers could tolerate months in a state of desiccation, hence marking the earliest studies on **cryptobiosis**, or life in a dormant state without water (Alpert 2000). This desiccation tolerance is particularly common in the class **Bdelloidea**. In this dry state, they are easily dispersed along with fragments of the mosses they inhabit.

Not much bigger than some protozoa (mostly 0.1-0.5 mm long, but up to 2 mm), they form a phylum of their own, the **Rotifera**, with at least 2000 species (Howey 1999). They are multicellular and even possess a primitive brain, at least in females (Hingley 1993).

Figure 2. ***Brachionus quadridentatus*** (**Monogononta**) showing red eyespot. Photo by Frank Fox, through Creative Commons.

Rotifers have a variety of means of protection. Some are encased in a **lorica** (rigid case or shell; Figure 3, Figure 13-Figure 14). Others build tubes or cases (Figure 53, Figure 82). Some have sharp spines (Figure 13). And some simply hide, many of which use bryophytes for hiding.

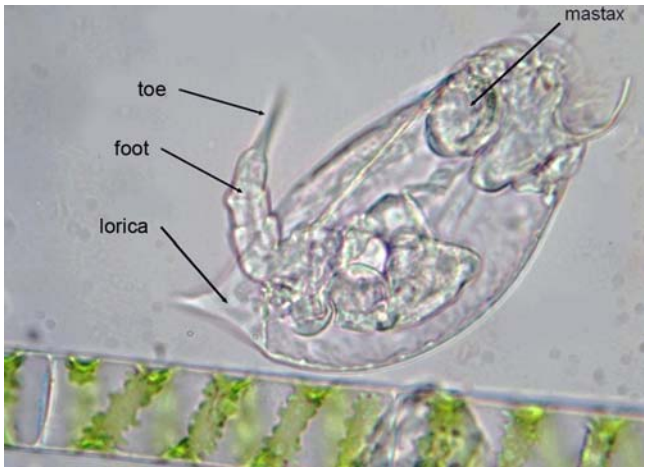

Figure 3. ***Colurella adriatica***, showing location of the mastax and other prominent features. This one is sitting on the green alga *Spirogyra* sp., but it sometimes occurs among mosses. Photo by Michel Verolet, with permission.

Moss-dwelling rotifers have been around for a long time. Waggoner and Poinar (1993) reported on fossil habrotrochid rotifers from Dominican amber. These revealed microfossils from the bracts of a moss from the Eocene-Oligocene (circa 34 million years ago) in the northern Dominican Republic. It is interesting that these match the **thecae** (sheaths) of living moss dwellers in ***Habrotrocha***, being almost identical with ***H. angusticollis*** (Figure 4). These **parthenogenetic** (producing unfertilized eggs) bdelloid rotifers seem to have a well-adapted body plan that has persisted for 35 million years.

Figure 4. ***Habrotrocha angusticollis***, a moss inhabitant. Photo by Yuuji Tsukii, with permission.

It is likely that many species of rotifers remain to be described. The most likely habitat for these discoveries is that of bryophytes. The bryophyte dwellers are often very small, rarely swim, and go dormant (see below) as a **tun** (Figure 61) or a **resting egg**, all characteristics that make them less likely to be noticed and more difficult to identify. Shiel and Green (1996) remarked that considerably more rotifers in New Zealand and the Australasian region remain undescribed. At that time the region had 388 valid species in 66 genera. Yet less than 5% of these were endemic to the Australasian region.

With the potential differences in physiology and biochemistry, it is also likely that DNA analysis will reveal many microspecies and perhaps even different species that are not recognizable based on morphology alone. Kaya *et al*. (2009) compared "DNA species" with morphological species of bdelloid rotifers from mosses in Turkey and the United Kingdom. They found that traditional identification methods underestimate rotifer diversity by factors of 2 at the local level and 2.5 at a regional level. Each moss sample had 3-9 morphospecies, but the DNA species ranged 8-12 per moss sample. These DNA species numbers indicated greater differences in diversity among locations (**gamma diversity**) than within samples (**alpha diversity**). Rotifer biologists consider that the number of cryptic species that can be revealed by DNA taxonomy may be overwhelming (Suatoni *et al*. 2006; Fontaneto *et al*. 2008).

This knowledge that the **Rotifera** include many **cryptic species** (species that look alike but can't interbreed), as demonstrated by DNA, is supported by a diversity of narrow ecological niches (see, for example, Fontaneto *et al*. 2011). This allows for physiological/biochemical differences that permit the species to survive in a wide range of cosmopolitan habitats. This diversity and cosmopolitan distribution has led to superfluous names in many of the rotifer genera. This chapter follows the nomenclature of Segers (2007); for species described after that publication it follows EOL <http://eol.org/>.

Reproduction

The lifespan of many rotifers is as much as 30-40 days, not counting their time in dormant states (Ricci 2001). But Wikipedia (2016) considers it to be much shorter for **Monogononta**, ranging 2 days to 3 weeks for females. And species of these animals can often be found in active or dormant states on both aquatic/wetland (Priddle & Dartnall 1978; Bateman & Davis 1980; Ricci 1983; Ricci *et al*. 1989; Linhart *et al*. 2002a) and terrestrial mosses (Bartos 1949; Ramazotti 1958; Overgaard-Nielsen 1967; Kukhta *et al*. 1990). Several species are even known from the harsh environment of mosses growing on roofs (Hirschfelder *et al*. 1993).

Rotifers (depending on the taxon) have three types of individuals: **mictic** (mixing) females, **amictic** females (not reproducing sexually), and males. Rotifer eggs may be attached to a substrate (Figure 5-Figure 6) or remain attached to the parent (Figure 7) (EOL 2016). The female rotifers themselves live only a few days to a few weeks. The males have no digestive tract, are often sexually mature at birth, and are short-lived, as you might expect when they don't eat. Hence, it is also understandable that males are much smaller than females (Figure 8).

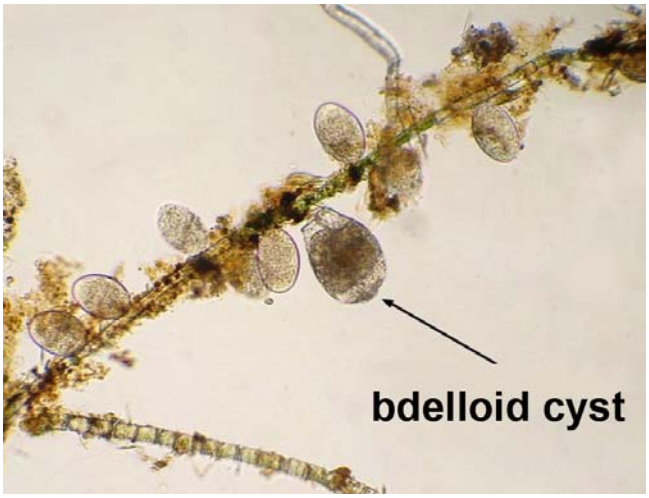

Figure 5. Bdelloid rotifer eggs on alga. Photo by Michel Verolet, with permission.

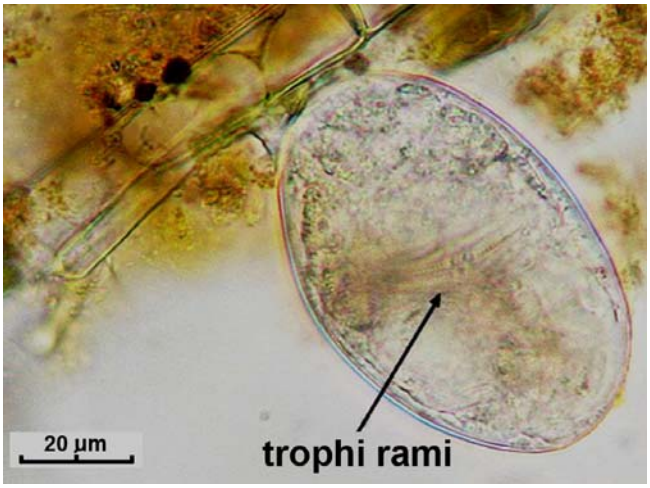

Figure 6. Egg of rotifer on an algal filament. Photo by Michel Verolet, with permission.

Figure 7. ***Brachionus*** with 3 eggs. Photo by Jean-Marie Cavanihac, with permission.

The female reproductive system of rotifers consists of one (**Monogononta**) or two (**Bdelloidea**) ovaries. Each ovary has a **vitellarium gland** (Figure 9) that supplies the eggs with yolk.

Figure 8. ***Cephalodella gibba*** in copulation, male on left. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 9. ***Asplanchna girodi*** **vitellarium**. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Bdelloidea

Bdelloid rotifers (class **Bdelloidea**; Figure 10-Figure 11), known as moss rotifers, are less species rich (over 450 described species) than the **Monogononta** (ca 1500 species). The **Bdelloidea** are the most common rotifers in peatlands (bogs and fens; Bielańska-Grajner *et al*. 2011) and other mosses (Sayre & Brunson 1971; Ricci *et al*. 2003b; Gilbert & Mitchell 2006). All known taxa are **parthenogenetic**, *i.e.*, they have only females that reproduce asexually, giving rise to more females (Hingley 1993). However, Danchin *et al*. (2011) analyzed the genome of one of these, ***Adineta vaga*** (Figure 12), a moss dweller, and found four genotype modifications that suggested rare events of sexual reproduction may have occurred.

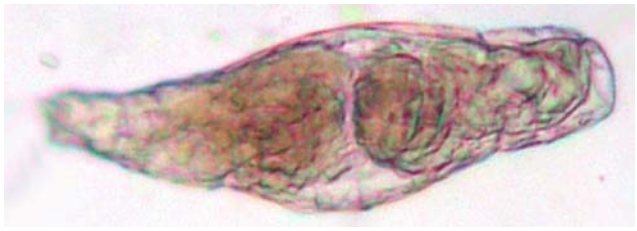

Figure 10. **Bdelloid rotifer** taken from bryophytes. Photo courtesy of Dan Spitale.

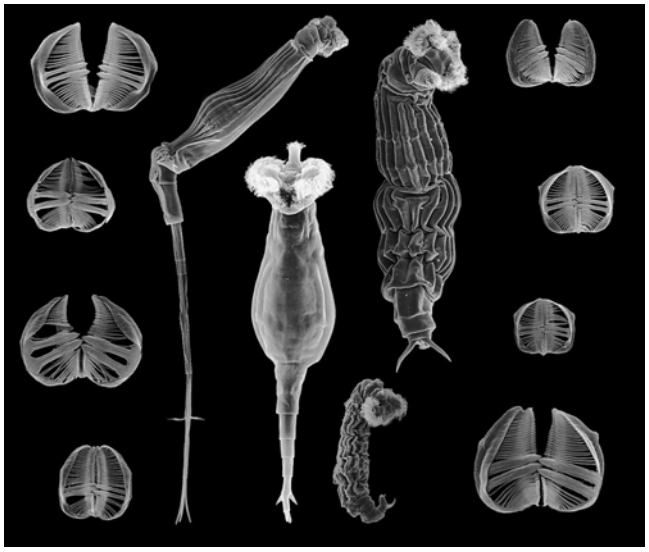

Figure 11. Examples of **bdelloid rotifers** and **trophi**, the hardened part of the **mastax**. Photos by Diego Fontaneto, through Creative Commons

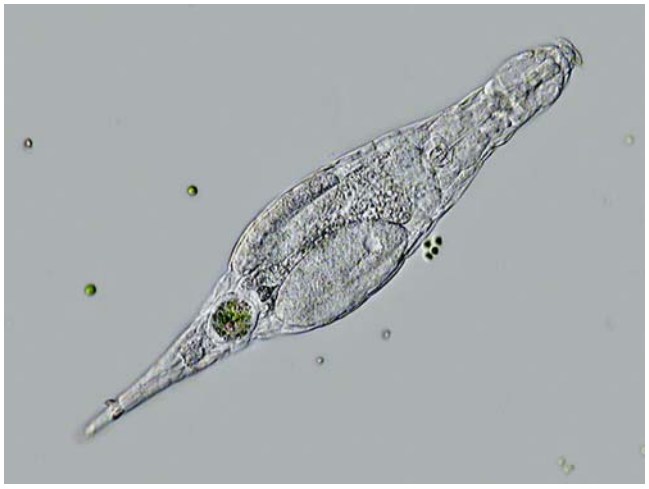

Figure 12. ***Adineta vaga***, a moss dweller that is 0.2-0.3 mm when extended. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Monogononta

The **Monogononta** is the second major class of rotifers, and by far the largest (ca 1500 species) (Wikipedia 2012a). Among these are members that have both sexual and asexual reproduction. The short-lived, uncommon males, however, serve only for reproduction and thus are much smaller than females. Some males are so reduced that they have little more than a bladder and a penis! One such monogonont is the mostly planktonic genus ***Brachionus*** (Wikipedia 2011; Figure 2, Figure 7, Figure 13-Figure 14). In this genus, with some members occurring among bryophytes, increases in population density can induce sexual reproduction. The sexually produced eggs can become resting eggs that survive unfavorable conditions (Plewka 2014). It appears that at least in ***Brachionus*** *calyciflorus* (Figure 13) only one allele is needed to turn off sexual reproduction and force all reproduction to be parthenogenetic. ***Brachionus urceolaris*** (Figure 14) sometimes lives among bryophytes (Figure 7; Hingley 1993), but it is primarily a cosmopolitan planktonic species like the other ***Brachionus*** species (EOL 2016). It is mostly parthenogenetic, but it occasionally produces males.

Figure 13. ***Brachionus calyciflorus***, a species that needs only one allele to turn off sexual reproduction. Academy of Natural Sciences in Philadelphia, through Creative Commons.

Figure 14. ***Brachionus urceolaris***, a bryophyte dweller. Photo courtesy of Emily Toscana Guerra from Rotifer World Catalog, through Creative Commons.

In the **Monogononta**, two types of reproduction occur. In one type, females produce unfertilized eggs that develop into females, just as in the bdelloids (Hingley 1993). But in the second type, sexual females appear only when environmental conditions are unfavorable, such as drought or cold. These females produce a sexual egg that forms a thick-walled resting "egg" when fertilized (Figure 15). That resting egg develops into a female. If the egg is not fertilized, it develops into a male.

Figure 15. ***Euchlanis triquetra*** with expelled resting egg. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Bryophytes as Habitat

Moss-dwelling **rotifers** have attracted the attention of rotifer specialists for some time (Burger 1948). The family **Habrotrochidae** (see Lobule Dwellers below) seems to occur mostly on mosses but is also **benthic** (living on the bottom of a water body) (Wallace & Snell 1991). There are two species in the genus ***Elosa*** (Figure 16) that are common on ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112), and these are considered bog specialists (Pejler & Bērziņš 1993b).

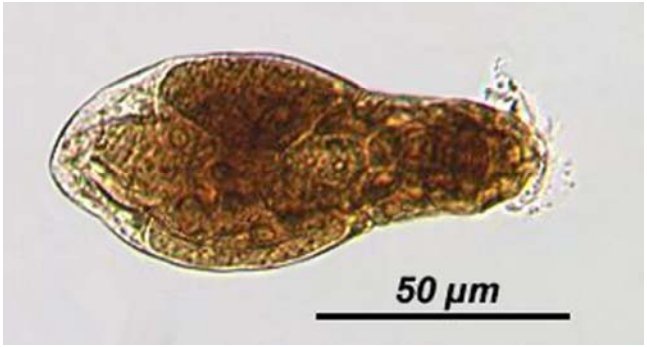

Figure 16. ***Elosa worrallii***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003 from Rotifer World Catalog, through Creative Commons.

Rotifers occur with bryophytes in both aquatic and terrestrial habitats, with bryophytes often providing a water space in the latter. Duggan (2001) points out that the **periphytic** (living on plant surfaces) species of rotifers have received little attention compared to the **planktonic** (drifting in open water) species. Bryophytes are among these **macrophytic** (referring to plants that are visible without a microscope) substrates that support the periphyton, but Duggan did not include them in his study, considering bryophytes to be a separate habitat. **Periphytic** rotifers seem to have preferences among macrophyte species based on differences in physical structure or complexity, food concentration or composition, chemical factors, macrophyte age, and differences in protection from predation they provide (Duggan 2001). The same factors are likely to control bryophyte choices as well.

Terrestrial and wetland rotifers crawl through the spaces among leaves and branches of bryophytes, living in the water film surrounding the plant (Hingley 1993). In her website on rotifers, Jean-Marie Cavanihac (2016) considers ***Rotaria rotatoria*** (formerly ***Rotifer vulgaris***; Figure 17) to be one of the most frequent rotifers on mosses, and as a free-living (unattached) rotifer, it moves like a caterpillar.

Figure 17. ***Rotaria rotatoria***, a bdelloid rotifer from moss. Photo by Christian D. Jersabek, through Creative Commons.

The bryophyte dwellers feed on the bacterial and protozoan inhabitants, swim among the leaves, or nestle between the leaves and branches where they gain more protection against their predators (Hingley 1993). The same is true for those living in terrestrial habitats as well as in ponds, lakes, and waterways.

Habitat Characteristics

Although not restricted to these habitats, rotifers are common on mosses in alpine ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) bogs and in wetlands. Bryophytes may be particularly useful to stream and other aquatic rotifers as a substrate. Pejler and Bērziņš (1989) contend that rather than any chemical attraction for a substrate, some substrates might be avoided, perhaps due to lack of periphyton. The genus ***Lecane*** (Figure 122) is a very large, widespread genus that has little preference for any particular substrate (Pejler & Bērziņš 1994). In fact, it furthermore seems to have good dispersal, as indicated by its rapid ease of colonization on an artificial substrate of cotton. Fontaneto and Ricci (2006) consider that rotifers are probably best dispersed in their dormant state (allowing them to be dispersed along with their bryophytic substrate).

The species on various macrophytes differ, even when a different species of macrophyte is growing in close proximity (Pontin & Shiel 1995; Duggin *et al*. 2001). Likewise, bryophyte species composition explains most of the variation in monogonont rotifers in springs and fens

(Hájková *et al*. 2011). Bryophytes form four functional groups, supporting the importance of plant form in their selection of the bryophyte substrate. Species composition of monogonont rotifers differs significantly (P <0.01) among crawling dense [***Cratoneuron filicinum*** (Figure 18), ***Palustriella commutata*** (Figure 19), ***P. decipiens*** (Figure 20)], crawling loose [***Brachythecium rivulare*** (Figure 21), ***Calliergonella cuspidata*** (Figure 22), ***Plagiomnium affine*** agg. (***P. ellipticum*** – Figure 23, ***P. elatum*** – Figure 24)], and ***Sphagnum*** tufts [***S. fallax*** (Figure 25), ***S. flexuosum*** (Figure 26), ***S. palustre*** (Figure 109), ***S. papillosum*** (Figure 27)]. The fourth group is erect (mostly acrocarpous) species: ***Bryum pseudotriquetrum*** (Figure 28), ***Fissidens adianthoides*** (Figure 29), ***Philonotis caespitosa*** (Figure 30).

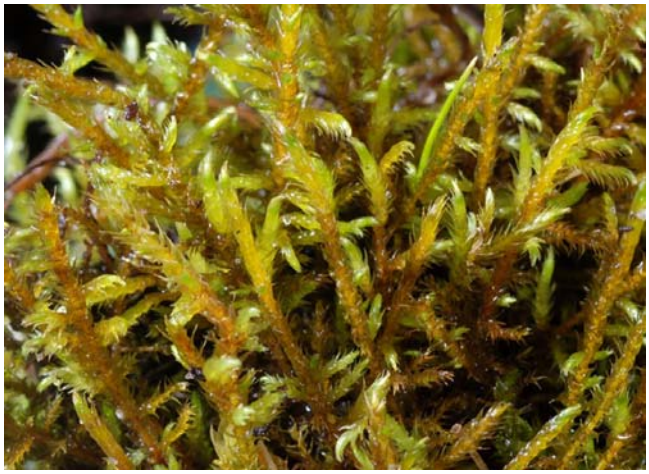

Figure 18. ***Cratoneuron filicinum***, a "crawling dense bryophyte" that serves as home for one group of rotifers. Photo by J. C. Schou, with permission.

Figure 19. ***Palustriella commutata***, a "crawling dense bryophyte" that serves as home for one group of rotifers. Photo by David T. Holyoak, with permission.

Figure 20. ***Palustriella decipiens***, a "crawling dense bryophyte" that serves as home for one group of rotifers. Photo by Michael Lüth, with permission.

Figure 21. ***Brachythecium rivulare***, a "crawling loose bryophyte" that serves as home for one group of rotifers. Photo by Michael Lüth, with permission.

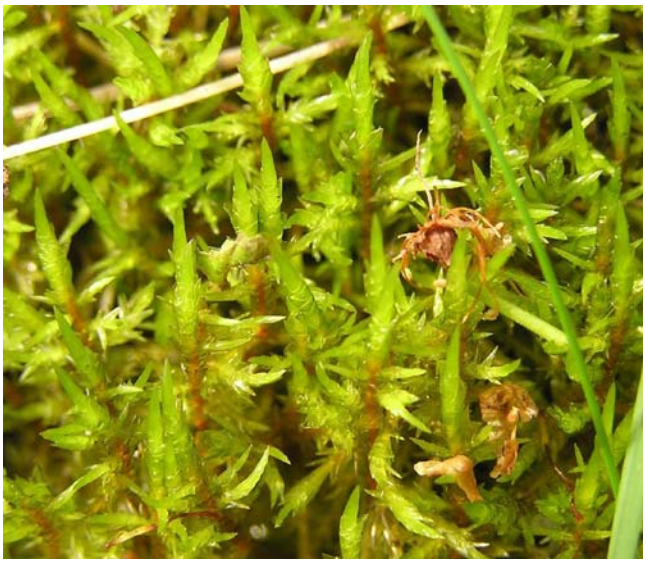

Figure 22. ***Calliergonella cuspidata***, a "crawling loose bryophyte" that serves as home for one group of rotifers. Photo by Michael Becker, through Creative Commons.

Figure 23. ***Plagiomnium ellipticum***, a "crawling loose bryophyte" that serves as home for one group of rotifers. Photo from Biopix, through Creative Commons.

Figure 24. ***Plagiomnium elatum***, a "crawling loose bryophyte" that serves as home for one group of rotifers. Photo by Michael Lüth, with permission.

Figure 25. ***Sphagnum fallax***, home of "***Sphagnum*** tuft" rotifers. Photo from <www.aphotofauna.com>, with permission.

Figure 26. ***Sphagnum flexuosum***, home of "***Sphagnum*** tuft" rotifers. Photo by Michael Lüth, with permission.

Figure 27. ***Sphagnum papillosum***, home of "***Sphagnum*** tuft" rotifers. Photo by Dale H. Vitt, with permission.

Figure 28. ***Bryum pseudotriquetrum***, home of "erect species" rotifers. Photo by Michael Lüth, with permission.

Figure 29. ***Fissidens adiantoides*** with capsules, home of "erect species" rotifers. Photo by Bob Klips, with permission.

Figure 30. ***Philonotis caespitosa***, home of "erect species" rotifers. Photo by Kristian Peters, with permission.

Hájková *et al*. (2011) demonstrated bryophyte-dwelling monogonont rotifers in springs and fens form communities that are strongly correlated with water *p*H and conductivity, Ca concentration, and ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) dominance. The rotifers did not respond to silica, iron, or nutrients, despite the effects of these factors on amoebae, algae, and other microscopic food organisms. Rotifer species composition does not depend on water chemistry, except *p*H and calcium, at least in part because their ***Sphagnum*** substrate selects for these factors. For shell-forming species, these latter chemical factors are often more important.

Aquatic bryophytes may provide a refuge during particularly heavy stream flow. The number of rotifer species among bryophytes in Tatra streams increased during spring runoff from 18 in winter to 24 during runoff (Madaliński 1961). Other factors that contribute to substrate choice include temperature, oxygen content, trophic levels, chemistry, food availability, and predators (Pejler & Bērziņš 1989).

Abundance

An average of 700 **rotifers** can exist per gram on the soil-dwelling mosses ***Ceratodon purpureus*** (Figure 31) and ***Polytrichum juniperinum*** (Figure 32), rock-dwelling moss ***Schistidium apocarpum*** (Figure 33), and bog/fen species of ***Sphagnum*** (Gerson 1982). Consider that a rough estimate for a handful of moss is about 10 grams.

Figure 31. ***Ceratodon purpureus***, a common moss on roofs, roadsides, and other open places. It typically has a large population of **rotifers**. Photo courtesy of Geralyn Merkey.

Figure 32. ***Polytrichum juniperinum***, a common **rotifer** home. Photo by Michael Lüth, with permission.

Figure 33. ***Schistidium apocarpum***, a common moss that can house 700 **rotifers** per gram. Photo by Michael Lüth, with permission.

Aquatic rotifers can occupy a significant portion of the **meiofauna** (minute organisms living in soil and aquatic sediments) of aquatic mosses such as ***Fontinalis antipyretica*** (Figure 34) (Vlčková *et al*. 2002). Out of 20 taxa, **Bdelloidea** formed the dominant group with about 76% of the total meiofauna numbers. Linhart (2000) found that clumps of ***Fontinalis antipyretica*** was inhabited by 151 times the densities of meiofaunal invertebrates

compared to adjacent mineral substrate. During winter in two streams in the Czech Republic, Linhart found 182,672-390,057 individuals per 100 mL of ***F. antipyretica***. That's about a handful of moss. Rotifers (**Bdelloidea**) were the dominant organisms, occupying up to 74% of the meiofauna. The rotifers seemed to be reduced by high amounts of organic matter, whereas **Chironomidae** (Figure 35) benefitted. These differences account for the dominance of rotifers (**Bdelloidea**) in Mlýnský náhon (76% of the community), whereas in Bystřice, the dominant group was **Chironomidae** (34%) (Vlčková *et al.* 2002).

Figure 34. ***Fontinalis antipyretica***, home for a dense fauna of **rotifers**. Photo by Michael Lüth, with permission.

Figure 35. ***Propsilocerus saetheri*** larva, a member of **Chironomidae**. **Chironomidae** benefit from increased detritus, whereas rotifers are reduced in numbers. Photo by NTNU Museum of Natural History and Archaeology, through Creative Commons.

Although the aquatic moss ***Fontinalis antipyretica*** (Figure 34) often lives in relatively rapid water, it can house huge numbers of temporary and permanent meiofauna. In samples taken in October and November, Vlčková *et al*. (2002) found 261,660 individuals per 100 mL of this moss in Bystřice and 498,948 in Mlýnský náhon. More permanent residents contribute approximately 62% and 95% in these locations, respectively. At Mlýnský náhon, the **Bdelloid** rotifers form 76% of the community as permanent residents.

Aquatic mosses can contribute significantly to biodiversity by providing a 3-d habitat. Linhart *et al*. (2002a) and Vlčková *et al*. (2002) found that rock rip-rap overgrown by aquatic mosses (***Fontinalis antipyretica***; Figure 34) in a side channel of the Morava River, Czech Republic, contributed both habitat and food source for the meiofauna. Both the habitat and the food source were realized through the fine particulate matter trapped by the mosses. In this habitat, **Bdelloid** rotifers dominated as 76% of the organisms among 18 meiofaunal taxonomic groups.

Sampling

When comparing numbers of nematodes, tardigrades, mites, and annelids to rotifers among bryophytes, Merrifield and Ingham (1998) found low numbers of rotifers, with no seasonal variation. They suggested that the low numbers of rotifers in moss samples may be due to the use of the Baermann funnel for sampling. This technique is not suitable for immobile organisms like periphytic rotifers, as indicated by comparison with subsequent squeezings and agitation of the moss.

Before we explore this group of organisms, we need to consider potential sampling bias and the effects it may have on the numbers of rotifers in various studies. Because of their tendency to attach, rotifers require different sampling techniques from tardigrades and worms. They do not extract well with the Baermann funnel used so commonly for other invertebrates (Merrifield & Ingham 1998). Merrifield and Ingham tested the efficiency of this funnel technique on the moss ***Eurhynchium oreganum*** (Figure 36) on the Oregon Coast Range, USA, by squeezing and agitating the moss after the funnel extraction and suggested that the sedentary habit of the rotifers might cause them to be under sampled.

Figure 36. ***Eurhynchium oreganum***, a moss where the funnel technique might under-sample the rotifers. Photo by Blanka Shaw, with permission.

Fussmann *et al*. (2000) discussed the problems with using sedimentation chambers of **fixed** (preserved) organisms. These must be analyzed with an inverted microscope and the amount of work required becomes prohibitive. Even for **non-sessile** (unattached) rotifers, using a transparent filtering funnel with appropriate mesh screening misses a large portion of the population (Likens & Gilbert 1970). It is most likely worse for bryophyte dwellers living in the small interstitial spaces.

May (1986) suggests that sampling sediments can be done in one day and the dormant individuals or resting eggs

cultured to permit identification. But this method is not only time-consuming, it may not enable one to see those individuals hiding among the bryophytes, especially in pockets, folds, and cells.

Pennak (1962) reported results from a littoral sampling tube, but cautioned that this method was less effective in sampling rotifers from macrophytes than the use of nets (Pennak 1966). Others (Goddard & McDiffett 1983; Duggan *et al.* 2001) used removal of the macrophytes, a method also appropriate for bryophytes, but the sorting process is tedious and time consuming. For example, removing the rotifers from the surfaces can be accomplished with a syringe (Pontin & Shiel 1995), but for a quantitative study this can be a large project, considering the numbers cited above. It is also a destructive method, and the patchiness of rotifer species would require a large number of samples.

Artificial substrata are a possible alternative (Duggan *et al*. 1998; Duggan 2001), but that method presumes that the bryophyte is being used only as a substrate and that shape of substrate and other organisms in the community don't matter. And this does not seem to be the case – preferred food organisms may be absent and high densities occur in leaf axils and other restricted spaces that are not mimicked by the artificial substrate.

Green (2003) sampled periphytic rotifers with Hydrobios plankton nets, mesh 55 µm. These samples were preserved in formaldehyde, then thoroughly mixed and sub-sampled with a wide-mouthed pipette. The subsamples were mixed with a small volume of lactic acid and mounted on a glass slide for examination. But once again, I question how effective this is for rotifers hiding in pockets, lobules, cells, or attached.

The closest macrophytes to use as models for bryophytes might be sampling of the alga *Chara* and the flowering plant *Utricularia vulgaris* (Figure 38). Kuczyńska-Kippen & Nagengast (2006) sampled periphyton (adhering algae, protozoa, microinvertebrates) on these and other macrophytes by removing a 0.25 x 0.25 m square of the plants. These were first rinsed in distilled water. Then the periphyton remaining was removed manually with a knife and small brush and number of rotifers calculated per volume of water above the sampled area. This is another destructive technique and would be prohibitively costly in time.

Figure 37. ***Chara vulgaris***, a potential model for bryophyte faunal communities. Photo by Mnolf, through Creative Commons.

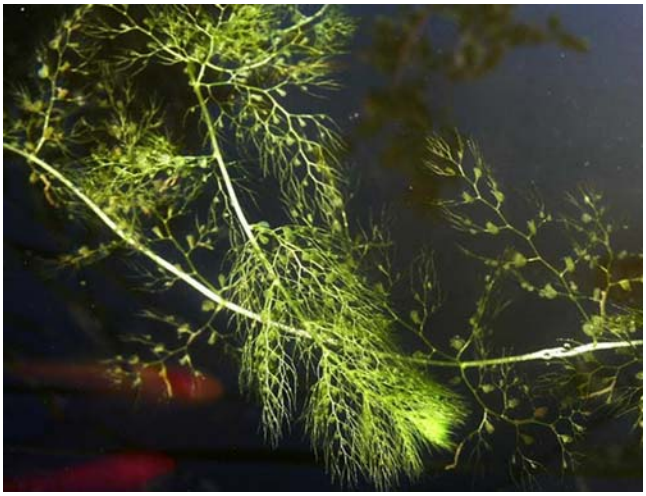

Figure 38. ***Utricularia vulgaris***, a potential structural model for bryophyte rotifer communities. Photo by Erastos Kampouropoulos, through Creative Commons.

Vlčková *et al*. (2002) attempted to sample the aquatic moss ***Fontinalis*** (Figure 34) quantitatively. They removed the moss and its associated fauna with a 30 µm mesh hand net. The associated fauna and detritus were then washed from the moss and sieved through a 1 mm mesh to remove the larger organisms and debris. The organisms that went through the net were retained on a 30 µm mesh filter. The sediment retained by this filter was diluted in a graduated cylinder and 1 ml samples were observed with a dissecting microscope and counted in a Sedgwick Rafter counting chamber. But even this extensive (and destructive) method can fail to sample attached or pocketed fauna.

These difficulties help to explain the paucity of quantitative ecological studies on bryophyte dwellers.

Extraction Techniques

To further complicate finding rotifers even under the dissecting microscope, rotifers respond to disturbance by retracting their corona and toes, appearing like a ball. In this condition, they are difficult to locate, even with a dissecting microscope. And imagine trying to identify these balls! You can place a branch of bryophyte in a Petri dish or watch glass and cover it with water (Fox 2001). Then let it sit quietly, preferably on the stage of a dissecting microscope, for 15-30 minutes until the rotifers become active again. They can then be removed with microforceps by removing several leaves on which you have observed rotifers. If they are placed on a glass slide or hanging drop slide, you can observe these with the compound microscope at 40X.

But some rotifers are too small for this technique and are likely to be missed. Peters *et al*. (1993) suggest a different method that appears to be a somewhat reliable quantitative technique. They tested it on 74 samples of mixed ***Brachythecium rutabulum*** (Figure 39) and ***Ceratodon purpureus*** (Figure 31), both terrestrial mosses. Their criteria for establishing a method were that it should not kill the organisms because some must be alive to be identified, it must be equally effective for all species, it must be quantifiable, and it should be economical in both equipment cost and time. Bryophyte samples 1 cm^2 should be shaken vigorously in a 70 ml vial with 20 ml rainwater

for 15 seconds. If the sample is dry, it should soak for 24 hours in rainwater first. After shaking, put the sample and water in a Petri dish with a grid. Then put the moss back in the vial. Rotifers can be counted with a dissecting microscope at 40-50X. This should be repeated nine more times with material from the same sample, using a new Petri dish each time. From each of these samples, take 50 rotifers at random and make a separate slide for each. These can be stored for weeks in a moist chamber. This method needs more testing to check for attached species, species bias, and reliability of quantitative measures.

Figure 39. ***Brachythecium rutabulum***, a moss used for extracting rotifers by a shaking technique. Photo by J. C. Schou, with permission.

Sakuma *et al*. (2002) tested two methods (covering method; picking-up method) of obtaining epiphytic rotifers from lake vegetation (Figure 40). Their "covering method" involved shaking a vegetation sample in a 2-L jar of filtered lake water (40 µm mesh). The jar lid (cap) is placed on the jar and the jar is placed upside-down in the lake water. The lid is then removed under water and the submerged part of the bryophyte is gently covered from above. The bryophyte is cut with scissors near the lip of the jar and the jar lid is returned to cover the jar. The covered jar is shaken vigorously 50 times, which in testing recovered 90% of the rotifers. Shaking only 10 times recovered only 80%. The water in the jar is then filtered through a 40 µm filter and fixed with sugar formalin (see Haney & Hall 1973).

In the "picking-up method" the jar of lake water is prepared as above (Sakuma *et al*. 2002). It differs in cutting the bryophyte in the lake and picking it up above the water surface. This bryophyte sample is then put in the jar. The epiphytic rotifers are then treated as for the "covering method."

The authors consider the "covering method" to be superior in estimating the abundance, but it requires both hard work in a boat and more time (Sakuma *et al*. 2002). The "picking-up method" (Figure 40) introduces errors in the abundance estimates. The rotifers ***Lecane*** (Figure 41), ***Euchlanis*** (Figure 42), and ***Trichocerca*** (Figure 43) are underestimated, whereas ***Brachionus*** (Figure 13-Figure 14), ***Mytilina*** (Figure 44), ***Lepadella*** (Figure 45), and ***Colurella*** (Figure 46) seem to be accurately estimated. Such differences provide misleading information on community structure. The shaking part of the "covering method" is not without its own creation of bias. ***Lecane*** (Figure 47) and ***Collotheca*** (Figure 48) remained on the plants (*Potamogeton* – Figure 49) at ca. 50% and 70%, respectively.

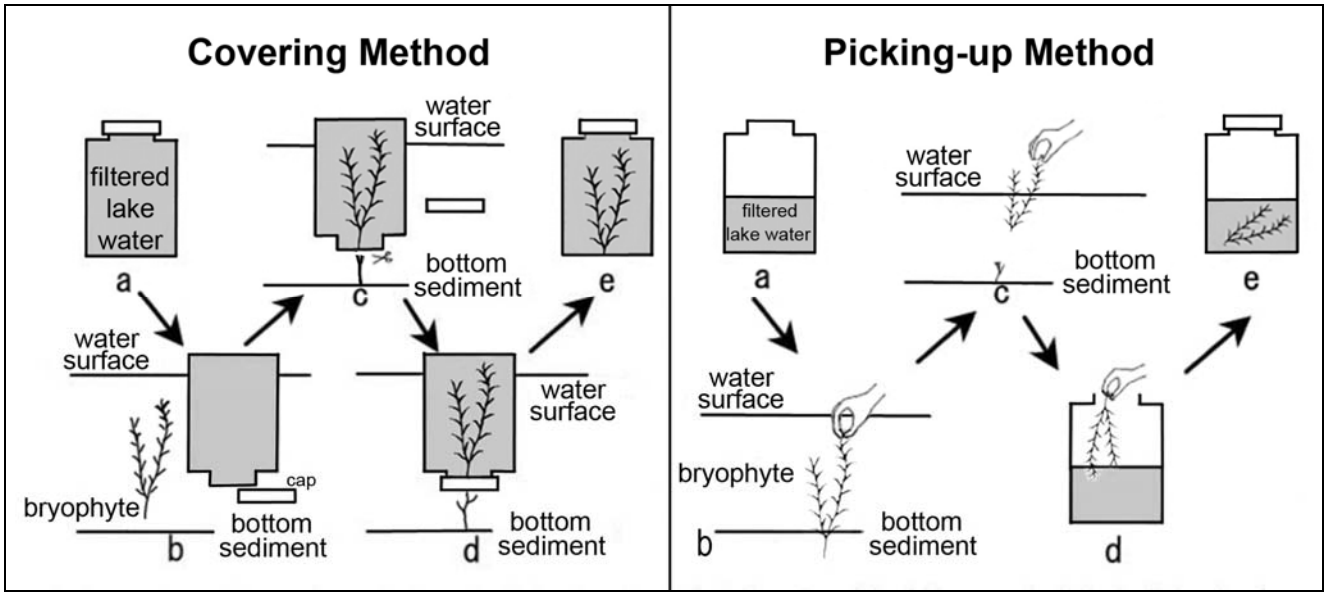

Figure 40. Methodology for the "covering method" and "picking-up method." Modified from Sakuma *et al*. (2002).

Figure 41. ***Lecane crenata***, a genus that is underestimated in the "picking-up method." Photo by Yuuji Tsukii, with permission.

Figure 42. ***Euchlanis***, a genus that is underestimated in the "picking-up method." Photo by Jean-Marie Cavanihac, with permission.

Figure 43. ***Trichocerca rattus carinata***, representing a genus that is underestimated in the "picking-up method." Photo from Jersabek *et al*. 2003, with permission.

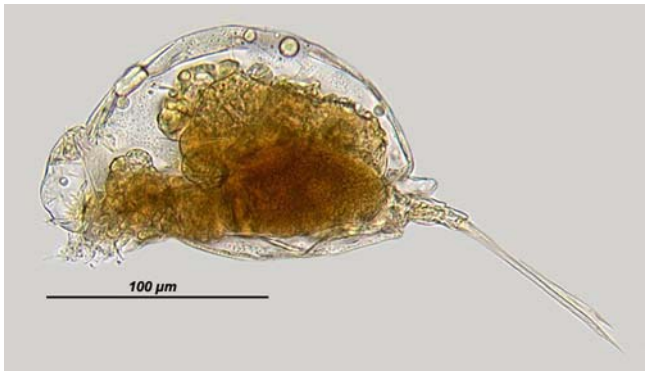

Figure 44. ***Mytilina acanthophora*** ssp. ***trigona***, a genus that seems to be adequately represented by the "picking-up" method. Photo by Jersabek *et al.* 2003, with permission.

Figure 45. ***Lepadella acuminata***, member of a genus that seems to be adequately represented by the "picking-up" method. Photo by Yuuji Tsukii, with permission.

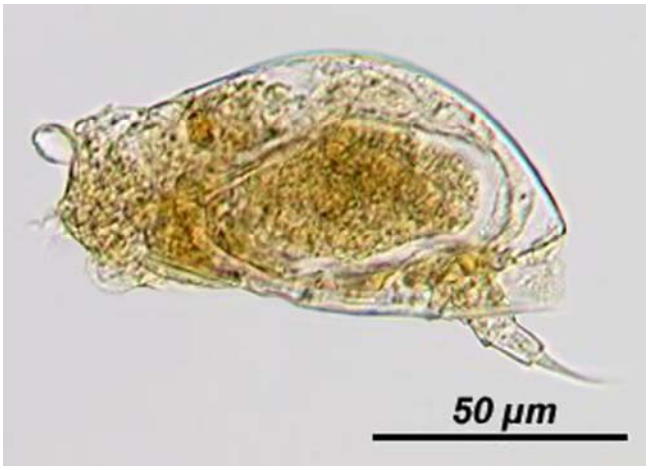

Figure 46. ***Colurella uncinata***, a genus that seems to be adequately represented by the "picking-up" method. Photo by Jersabek *et al*. 2003, through Creative Commons.

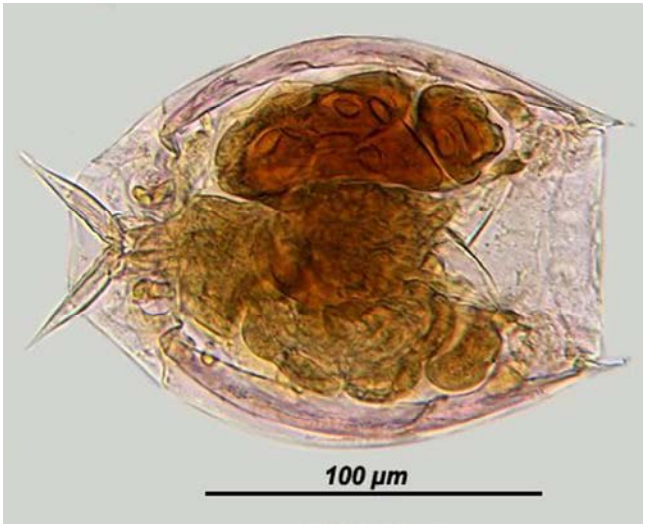

Figure 47. ***Lecane depressa*** subsp ***brachydactyla***. ***Lecane*** is a genus that remains mostly with the substrate when plants are shaken in water. Photo by Jersabek *et al*. 2003, with permission

Figure 48. ***Collotheca*** sp., a genus that does not detach well in shaking techniques. Look carefully to see the cilia. Photo by Yuuji Tsukii, with permission.

Figure 49. ***Potamogeton nodosus***. Shaking ***Potamogeton*** is an ineffective method for removing most individuals of ***Lecane*** and ***Collotheca*** species, suggesting they would likewise not be dislodged from bryophytes. Photo by Jim Conrad, through public domain.

Adaptations

The **Rotifera** are cosmopolitan, including both tropical and polar environments. There is a large number of species, permitting them to occupy a wide range of habitats. This indicates that ecological barriers are more important than geographical barriers in determining their distribution (Pejler 1995). However, many of the species are **euryoecious** (able to live in a variety of conditions), whereas few have strong restrictions on their environments. When an environment has a large number of rotifer species, the species typically differ greatly in their morphology. Therefore, it is difficult to characterize adaptations for a given environment. It is thus not surprising that published literature provides little information about adaptations of **rotifers** to the bryophyte habitat.

Particle Feeders

Rotifers among bryophytes can feed on detrital matter and algae collected by the bryophytes.

Spines

Kellicottia longispina (Figure 50) is a common plankton species that may be well adapted for bryophyte living. It has very long spines on its case (**lorica**) that Madaliński (1961) considered helpful in attaching to bryophytes. Others understand them as serving as a flotation device (De Smet, pers. comm. 3 November 2016), certainly not an adaptation to bryophyte living.

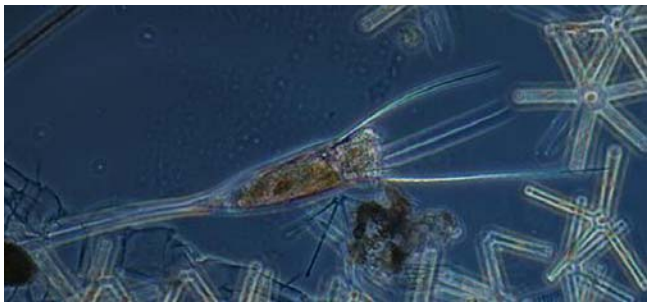

Figure 50. ***Kellicottia longispina*** showing its long spines that permit it to attach to bryophytes. Photo by Philipp Trummer, through Creative Commons.

But Pejler & Bērziņš (1989) have somewhat different ideas about long spines. They claim these are generally found in clear water as a protection against visual predators. This is consistent with defense against predation by small fish as shown by Barnhisel (1991) for *Bythotrephes*, a cladoceran. Rather, Pejler and Bērziņš suggest that adaptations to bryophytic living involve the suitability of the foot, egg-carrying protrusions, and other lorical structures. Certainly diet plays a role, with some bryophytes being suitable food for detrital feeders, but mostly because of the collected detritus and other planktonic and periphyton organisms among the bryophytes.

Small Size

If you are tiny and soft-bodied, you certainly need some sort of protection or a place to hide. Otherwise, you will be somebody's dinner. Wilts *et al*. (2010) discovered one of the smallest rotifers known, ***Bryceella perpusilla***, a new species, concealed on terrestrial mosses in Germany. It is likely that many other small bryophyte-dwelling species remain unknown.

Some rotifers, for example ***Cupelopagis vorax*** (Figure 51), are too large to live among bryophytes (Cavanihac 2004). Cavanihac (2004) considered that this size limitation may be, in part, because the bryophytes cannot house enough detritus and bacteria to meet the food needs of the large rotifers. For ***Cupelopagis vorax***, a consumer of ciliates and smaller rotifers, this may not be the case. This species lacks prominent cilia to draw food toward its mouth (Edmondson 1940, 1949). Therefore, it benefits when it settles on larger leaves where smaller ciliate rotifers bring food into the vicinity of its mouth. On the other hand, Dumont *et al*. (1975) found that the rotifers among the periphyton (which includes most of those associated with bryophytes) tended to be smaller than those living as plankton (see also Ricci *et al*. 2003a).

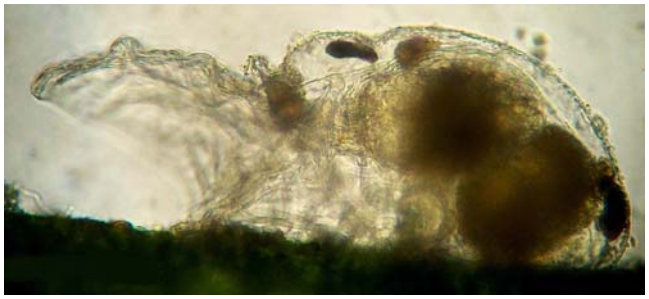

Figure 51. ***Cupelopagis vorax***, a rotifer that finds a **moss** leaf too small for its feeding needs. Photo by Jean-Marie Cavanihac at Micscape, with permission.

Mobility vs Attachment?

Epp and Lewis (1984) demonstrated that speed of motion was related to size in rotifers. Using ***Brachionus*** (Figure 2, Figure 13-Figure 14) and ***Asplanchna*** (Figure 52), they demonstrated that ***Brachionus*** has little size variation during its development, whereas ***Asplanchna*** increases significantly in size as it develops. Nevertheless, both genera decrease their speed of movement significantly as their size increases. ***Brachionus*** uses 62% of its energy for ciliary movement. This is a very inefficient activity, so we might consider one bryophyte adaptation to be attachment instead by crawling, thus saving energy. To observe the rotifers in motion, let the wet moss sit for 30 minutes before observation to provide the rotifers sufficient time to become active.

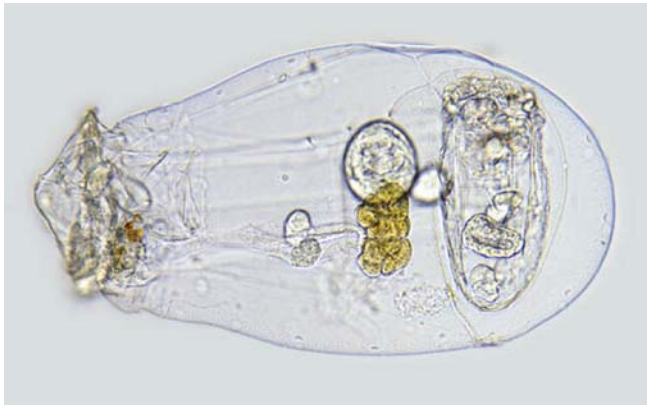

Figure 52. ***Asplanchna*** sp., a species that increases in size as it develops. Photo by Wim von Egmond, with permission.

Living in tune with their mossy environment, **limnoterrestrial** (in habitat providing tiny water reservoirs in terrestrial environment) rotifers exhibit a seasonal dynamic that depends on water availability and air quality (Kukhta *et al*. 1990; Steiner 1994a, b, 1995a, b). Not only is water important for hydration, but it is necessary for locomotion. The bdelloid rotifers (Figure 11) have a contractile body that permits them to creep around on the moss (Sayre & Brunson 1971). And the cilia that form the corona create currents as they beat (Figure 53), directing food particles into the mouth while thrusting the rotifer forward (Hingley 1993). Thus, the corona also contributes to movement.

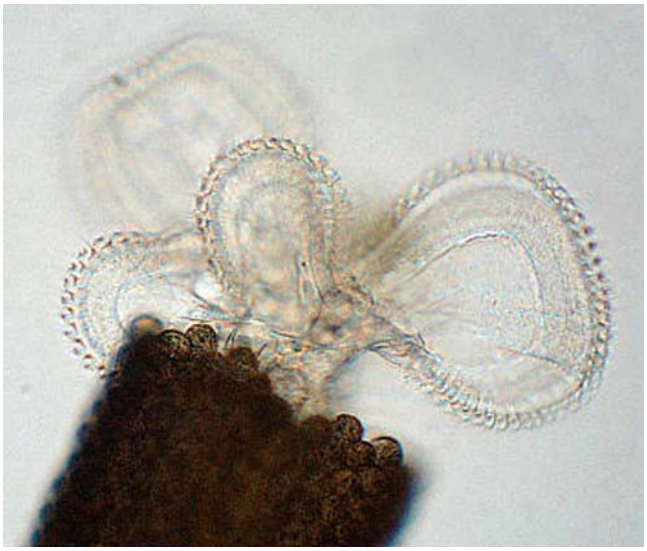

Figure 53. Wheels of cilia (**corona**) on ***Floscularia*** sp. Photo by Martin Mach, with permission.

Members of the periphyton often remain firmly attached to the substrate, be it rock, bryophyte, or other macrophyte. This attachment may use a cement, produced by the toes that have a cement gland (Baqai *et al*. 2000).

Protection

Habrotrocha sp. (Figure 54) secretes a mucus that makes it appear much larger (Figure 54). Wallace and Snell (1991) considered mucus to be an adaptation against predation in the rotifers ***Conochilus*** (Figure 55) and ***Lacinularia*** (Figure 56), but it would seem it would likewise contribute to protection of rotifers such as ***Habrotrocha*** against desiccation in a mossy habitat where some members of the genus are known to live. However, this has not been clearly demonstrated. Others, such as ***Keratella*** (Figure 57-Figure 58), are protected from both desiccation and predation by armor (Figure 57-Figure 58), with spines that may help against predation.

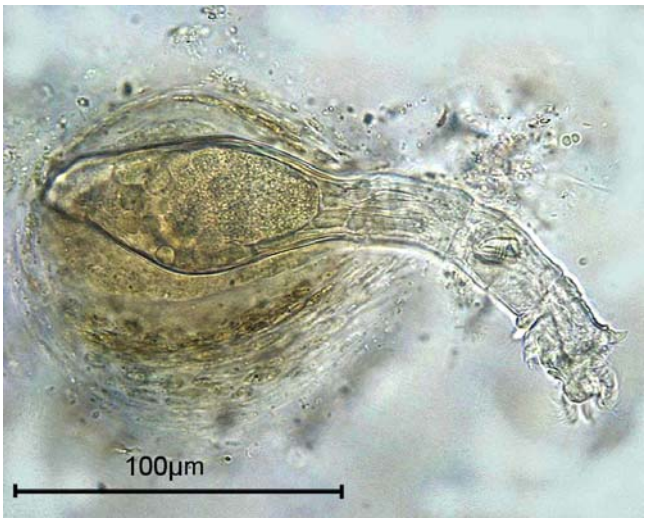

Figure 54. ***Habrotrocha*** sp. surrounded with mucus it has secreted, presumably providing it with protection against desiccation. Photo by Michel Verolet, with permission.

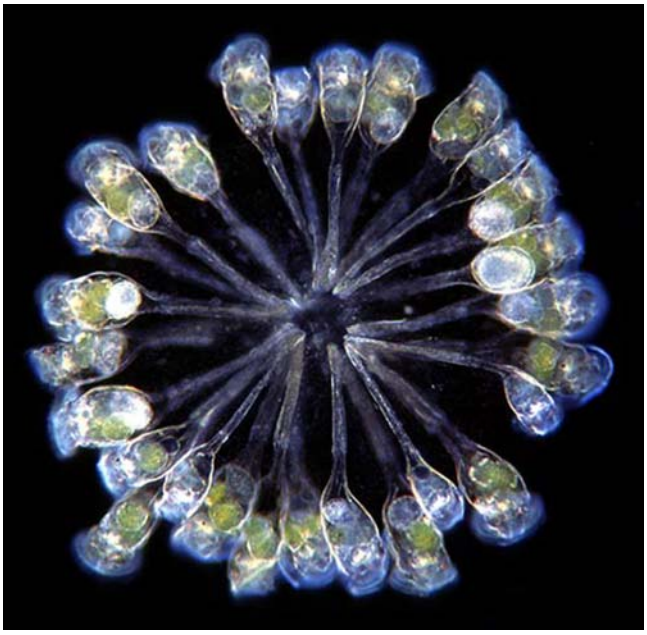

Figure 55. Colonial species of ***Conochilus***, a genus that uses mucus as protection. Photo by Wim van Egmond, with permission.

Figure 56. ***Lacinularia flosculosa***; this genus secretes mucus as protection against predators. Photo courtesy of Phuripong Meksuwan, through Rotifer World Catalog.

Figure 57. ***Keratella serrulata***, showing armor and spines. Photo by Wim van Egmond, with permission.

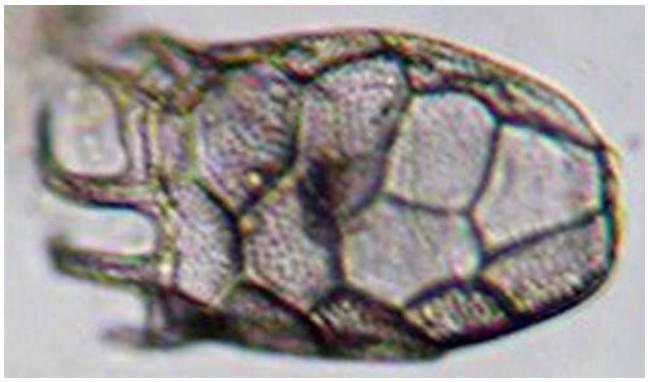

Figure 58. Armor of the rotifer ***Keratella*** sp. Photo by Paul Davison, with permission.

The genus ***Floscularia*** (**Monogononta**; Figure 59) is a tube builder, using tiny pellets, and is known to live on ***Sphagnum*** (Figure 25) (Hingley 1993).

Figure 59. ***Floscularia ringens***, member of a bryophyte-inhabiting genus. Photo by Paul Davison, with permission.

Having parthenogenesis is an advantage for rotifers that travel with a moss fragment and are likely to land where there is no male partner. This advantage is further assured by the predominance of females in the population. In addition to the reproductive adaptations, many adaptations may be physiological.

Dormant States

Of course, a major need for terrestrial moss dwellers is the ability to survive dry periods. The actual mechanisms that permit this survival have been elusive. Some early ideas lack sufficient support and have been discarded as a general mechanism. One such mechanism is the ability to secrete a mucus, as in *Macrotrachela natans* (Bryce 1929). But there is inconclusive evidence that the ability to produce this mucus actually protects the rotifer from the effects of water loss (Tunnacliffe & Lapinski 2003). Rather, it appears that most rely on physiological changes that occur during dehydration.

Physiological Adaptations

Anhydrobiosis

One reason for the abundance of bdelloid rotifers on bryophytes is that they share with the bryophytes the ability to enter dormancy (Gilbert 1974). In the **Bdelloidea**, the most common group of terrestrial rotifers, including those among bryophytes, this dormancy permits the adults to survive when frozen or desiccated. In **Monogononta**, dormancy is restricted to the fertilized resting egg. Hence, the predominant group of moss dwellers (**Bdelloidea**) has two methods of surviving desiccation.

The concept of **anhydrobiosis** was introduced by Giard in 1894 as a highly stable state of suspended animation that an organism enters as a culmination of desiccation (Tunnacliffe & Lapinski 2003). It differs from **desiccation tolerance**, which refers to the ability of a cell or organism to tolerate loss of water, although not necessarily reaching a resting state.

Cryptobiosis (**anhydrobiosis**) is one type of dormancy (Wallace & Snell 1991; Fontaneto & Ricci 2004). **Anhydrobiosis**, a dormant state caused by loss of water, permits some rotifers to live with the same water stresses to which bryophytes are subjected.

Van Leeuwenhoek was the first to recognize the state of anhydrobiosis in a rotifer, the bdelloid ***Philodina roseola*** (Figure 60) (Tunnacliffe & Lapinski 2003). Tunnacliffe and Lapinski (2003) argue that the term **anhydrobiosis** is inappropriate because the organism in not devoid of all water and that it has shut down to a state of suspended animation. They suggested the term **anhydrous cryptobiosis** because it implies the living but inactive state. Nevertheless, the term **anhydrobiosis** has been used for a long time and its intended definition is understood. Hence, I prefer not to introduce a new term and agree with Tunnacliffe and Lapinski that "as 'anhydrobiosis' is firmly established in the literature, it is unlikely that it can now be replaced."

Figure 60. ***Philodina roseola***, a species that is able to regulate its net water balance during dehydration. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Changes During Anhydrobiosis

Desiccation Stages: **Rotifers** enter this state of anhydrobiosis in stages (Ricci & Melone 1984). First they contract into the compact shape known as a **tun** (Figure 61) (Marotta *et al.* 2010). During this contraction, the cephalic and caudal extremities are withdrawn into the trunk. Presumably, this reduces the rate of water loss and minimizes water loss in the dormant state. The tissues and cells become packed, preserving their integrity (Ricci 2001). This preparation requires several hours, and a shorter period can reduce the recovery success (Caprioli & Ricci 2001).

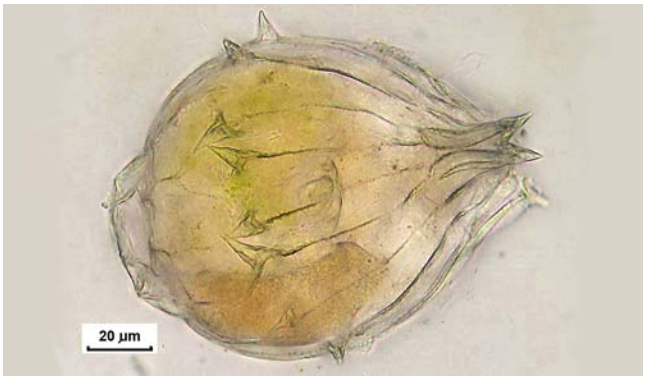

Figure 61. Tun of a **rotifer**, ***Pleuretra brycei***, a moss dweller. Photo by Michel Verolet, with permission.

Ability to contract and fold seems important to the survival of ***Macrotrachela quadricornifera*** (Figure 62) (Ricci *et al*. 2004). Upon drying, the rotifer contracts, drawing its foot and head into the body trunk (Figure 63) (Ricci & Melone 1984). Starved **rotifers** of this species survive better than those fed on concentrated food, with food remaining in the gut when the latter form the **tun** (Figure 64) (Ricci *et al*. 2004). This is in contrast to the loss of survival in ***Philodina roseola*** (Figure 60) when dried after starvation (Jacobs 1909). It is possible that the reason for the reduced survivorship of well-fed ***M. quadricornifera*** is that the food interferes with the necessary folding and contraction.

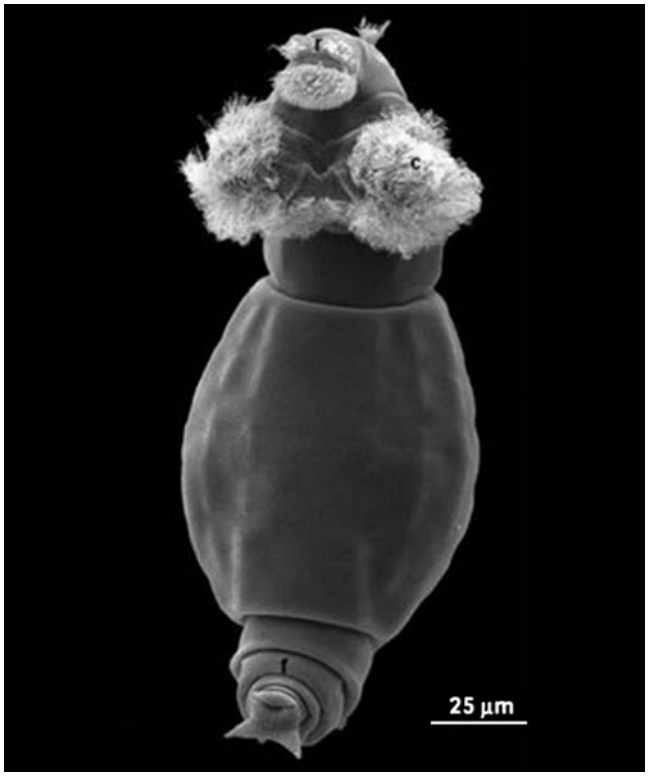

Figure 62. ***Macrotrachela quadricornifera***. Photo by Diego Fontaneto and Giulio Melone, with permission.

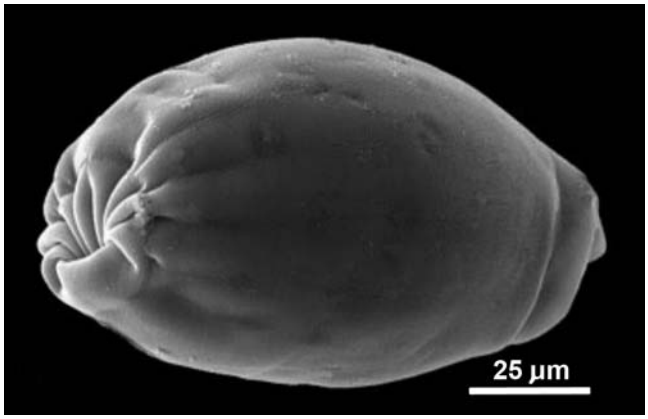

Figure 63. ***Macrotrachela quadricornifera*** contracting as it dries. Photo by Claudia Ricci, with permission.

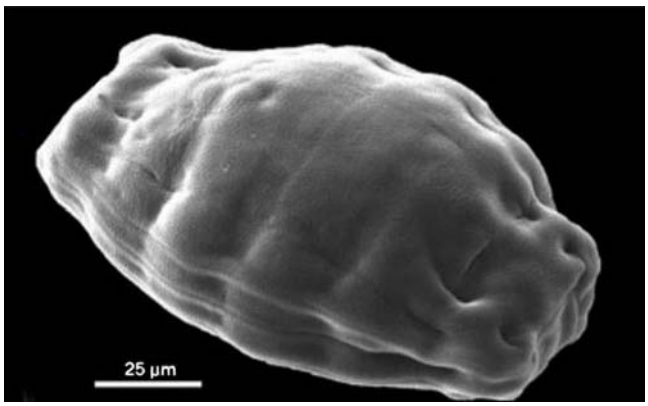

Figure 64. ***Macrotrachela quadricornifera*** tun. Photo by Diego Fontaneto & Giulio Melone, with permission.

Macrotrachela quadricornifera (Figure 62-Figure 64) shrinks considerably in size during dehydration, with the anhydrobiotic animal having only about 60% of the volume of the hydrated form (Ricci *et al*. 2008; see also Marotta *et al.* 2010). The internal organization changes drastically, with body cavities becoming indistinguishable. Even more extreme is its loss of more than 95% of its weight when anhydrobiotic, mostly as water. This water loss is inconsistent with a 60% volume loss and Ricci and coworkers suggest that it may indicate presence of space-filling molecular species in the dehydrated animal.

Dehydration Conditions: Caprioli and Ricci (2001) found that ***Macrotrachela quadricornifera*** (Figure 62) was able to survive rapid desiccation, whereas ***Philodina roseola*** (Figure 60) only survived best when subjected to a slower desiccation rate. Both of these are bdelloid rotifers. Nevertheless, when Caprioli and Ricci (2001) experimented with ***Macrotrachela quadricornifera***, ***Philodina roseola***, and ***Adineta oculata***, they found that these bdelloids are able to somewhat regulate the net water balance during the onset and termination of anhydrobiosis. This would be particularly helpful in a terrestrial environment, even among bryophytes that are in an exposed habitat such as boulders in the sun.

Jacobs (1909) provided an early explanation of the dehydration process that affects the survival rate in ***Philodina roseola*** (Figure 60). He found that when rotifers were dried slowly, their survival rate was higher (75% survival) than those dried rapidly in a desiccator (12%). At 40°C they actually had a slightly higher survival rate (94%) than those dried at 20°C (82%). However, longevity during dry storage was greater in those dried at 20°C. He supported the importance of **anhydrobiosis** by showing that dry storage produced a higher survival rate than storage at high relative humidity.

Jacobs (1909) found that 82% of ***Philodina roseola*** (Figure 60) had no survival after he dried starved individuals, but 82% of the well-fed individuals survived the same treatment. This is in contrast to some macroinvertebrates that survive best when the gut is empty (see terrestrial insect chapters), including the rotifer ***Macrotrachela quadricornifera*** (Figure 62-Figure 64).

The rotifer desiccation process is in some ways similar to that of bryophytes. Both require a lag time between periods of desiccation. Schramm and Becker (1987) found that ***Habrotrocha rosa*** (Figure 65), a bryophyte dweller, required a recovery period of at least one day before it could survive another period of desiccation.

Biochemical Changes: In nematodes and tardigrades, **trehalose** is produced and stored during desiccation. This molecule helps to stabilize cellular structures and preserve molecular integrity. In more modern studies, researchers have identified the non-reducing disaccharides trehalose and sucrose as playing critical roles in anhydrobiotic survival (Tunnacliffe & Lapinski 2003). One or the other of these sugars is typically present in high concentrations as many types of organisms undergo desiccation, leading to the anhydrobiotic state. These sugars seem to act as water replacement molecules, acting as "thermodynamic and kinetic stabilizers of biomolecules and membranes."

Figure 65. ***Habrotrocha rosa***, a bryophyte dweller that requires at least one day of recovery before another desiccation event. Photo by Rkitko at Wikipedia Commons.

But rotifers seem to contradict this wisdom. Protection by trehalose is not the case in the rotifers ***Philodina roseola*** (Figure 60) or ***Adineta vaga*** (Figure 12) (Tunnacliffe & Lapinski 2003). No simple sugars seem to increase at all. Contrary to the high non-reducing disaccharide concentrations found during dehydration in nematodes, brine shrimp cysts, bakers' yeast, resurrection plants, and plant seeds, the rotifers lack these high intracellular sugar concentrations in preparation for desiccation, yet have excellent desiccation tolerance (Tunnacliffe & Lapinski 2003).

Among the **Bdelloidea**, species are either desiccation tolerant or not; the difference is not a matter of degree (Örstan 1998; Ricci 1998). Lacking trehalose, they must have something that permits them to survive. That "something" continued to be elusive. Next, Tunnacliffe *et al*. (2005) found a hydrophilic protein in ***Philodina rosea*** (Figure 60) upon dehydration. This is an LEA protein that also is associated with desiccation tolerance in plants. Furthermore, this protein appears in desiccation-tolerant nematodes and micro-organisms and appears to have a role in desiccation tolerance (Denekamp *et al.* 2010; Hand *et al*. 2011). Hand and coworkers found that these LEA protein genes are expressed in the resting eggs of rotifers such as ***Brachionus plicatilis*** (Figure 66) and the female adults that formed these resting eggs.

Figure 66. ***Brachionus plicatilis*** with egg. Eggs of this species are known to have LEA proteins that are expressed during dormancy. Photo by Sofdrakou, through Creative Commons.

Longevity during Anhydrobiosis

The record for survival after the longest period of anhydrobiosis is that of ***Macrotrachela quadricornifera*** (Figure 62). It survived 59 years on a moss on a herbarium sheet, becoming active when it was rewet (Rahm 1923). But even Rahm questioned his own record, suggesting it may have been the result of more recent contamination from windborne dust carrying dormant rotifers. Furthermore, even in this species the success of recovery decreases with time (Caprioli & Ricci 2001).

Pennak (1953) cites one bdelloid rotifer that was revived from moss after 27 years of dry storage. Unfortunately, no reference is cited and we cannot evaluate whether the moss might have had rotifers introduced from dust or nearby more recently dried mosses.

To determine survival time, Guidetti & Jönsson (2002) examined rotifers that had been kept dry for 9-138 years. The adult stage may have a limited cryptobiotic lifespan in the presence of oxygen, but the rotifer ***Mniobia*** (Figure 67) survived live as eggs for nine years on bryophytes, suggesting that the egg stage (see Figure 68) might have greater longevity than the cryptobiotic adult stage. This appears to be the longest record for **rotifer** survival in anhydrobiosis other than the possible 59 years for an adult ***Macrotrachela quadricornifera*** (Figure 62-Figure 64) reported by Rahm (1923) from a herbarium moss or the undocumented record from Pennak (1953).

Figure 67. ***Mniobia*** sp. with egg. Photo by Walter Dioni, with permission.

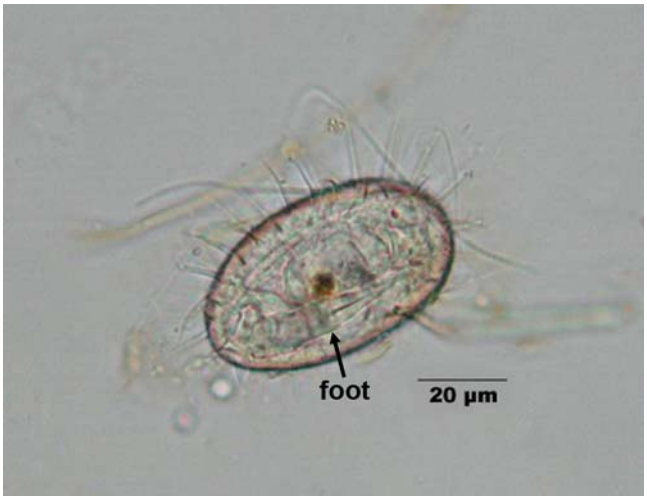

Figure 68. Egg stage of ***Squatinella lamellaris*** showing developing parts. Photo by Ralf Wagner, with permission.

Age Differences

Age affects recovery rate from desiccation but has no effect on the subsequent longevity of ***Macrotrachela quadricornifera*** (Figure 62) that do recover (Ricci *et al*. 1987). In experiments, fertility of 5-day-old stressed **rotifers** had significantly decreased, whereas 14-day-old stressed individuals had decreased life spans. Age also affected ability to survive drying. The highest recovery rate occurred for 8-day-old **rotifers** stressed for 4 days, whereas no rotifers aged 5 days survived 30 days of drying.

Size Differences – Aquatic vs Terrestrial

The moss-dwelling rotifer strains differ slightly in size, with terrestrial moss dwellers being smaller than the aquatic strains of the same species (Ricci 1991). This smaller size may permit them to take advantage of adhering moss water for a longer period of time. Among the ***Macrotrachela quadricornifera*** (Figure 62), eggs and juveniles are less able to recover from desiccation than are mature animals. This species is a good **bet-hedger**, encompassing multiple strategies for survival in a variety of habitats. The moss habitat undoubtedly offers the advantage of slow drying, which increases survivorship upon rewetting (Ricci *et al*. 2003a).

Reproductive Effects

In a study of nine species of **bdelloid rotifers**, Ricci (1983) found that those moss-dwelling terrestrial rotifers living in unpredictable environments had less likelihood of reproducing than aquatic species with a more predictable environment. Thus, it is not surprising that they reproduced less, but lived longer. Moss-dwelling species tend to reproduce throughout their mature lives and never senesce, whereas the aquatic species have a greater reproductive output and are more likely to die after reproduction, having a senescent period at the end of their lives. The strategy of the aquatic species would not serve the terrestrial moss-dwelling taxa well due to the unpredictable nature of the habitat. The terrestrial moss-dwellers, on the other hand, can enter the state of **anhydrobiosis** when the conditions become unfavorable. During this state they can tolerate extremes of temperature and desiccation and do not need food. Frequent reproduction could be detrimental to these animals if they do not have sufficient resources to sustain them during the anhydrobiotic state. Success is further supported by a delay in maturity that reduces reproductive cost. On the other hand, in the water, large adults may be easy prey, favoring a shorter time to maturity.

Furthermore, the aquatic (non-moss) strains of ***Macrotrachela quadricornifera*** (Figure 62-Figure 64) invested maximum resources in reproduction (**r strategists**), consequently reducing their survival, whereas the moss-dwelling strains were long-lived and invested fewer resources in their reproduction (**K strategists**) (Ricci 1991). Ricci points out that the moss habitat experiences a much greater temperature fluctuation in a shorter period of time than would occur in the aquatic non-moss habitats. Ricci suggests that the terrestrial moss habitat has much more important limiting factors – availability of food and moisture, whereas a wide temperature range with sudden changes must be tolerated.

Temperature Protection

Despite all the preparation for anhydrobiosis, these dormant beings are not as well protected as we once thought. On the other hand, Rahm (1923) found that once dry, at least some rotifers can survive 151°C for 35 minutes. Broca (1860) revived rotifers with water after they remained dry in a vacuum for 82 days, then were immediately heated to 100°C for 30 minutes.

The temperature relationships of the moss-dwelling rotifers are interesting. Compared to the non-moss populations, those of ***Macrotrachela quadricornifera*** (Figure 62) living among mosses exhibit an irregular response to increasing temperature in the range of 16-24°C (Ricci 1991).

Recovery Rate

As one might expect, terrestrial rotifers have the greatest desiccation recovery rates compared to aquatic rotifers. When fifteen bdelloid species (6 genera) were collected from water and terrestrial moss environments, the highest recovery rates following anhydrobiosis for seven days were for the adults from terrestrial mosses (Ricci 1998). Activity generally resumed in about one hour after rehydration. Ricci suggests that evolutionarily all bdelloid rotifers originally had the ability to enter anhydrobiosis, but that some species have subsequently lost it. Aquatic species had only 20-50% recovery among young, pre-reproductive individuals, whereas moss-dwelling species had 50-100% recovery among these juveniles. This improved in adults of both groups. Could it be that this group evolved originally in a moss habitat? On the other hand, ***Otostephanos macrantennus***, a moss and soil dweller (Ricci 1998), did not survive desiccation at any life stage, except for one individual older adult. Furthermore, its eggs collapsed and were unable to survive desiccation, whereas the overall viability among these fifteen species was 40-60%. Ricci considered ***Otostephanos macrantennus*** to have "an anomalously low desiccation survival rate."

The Bryophyte Connection

The data for ***Macrotrachela quadricornifera*** (Figure 62) and other species raise the question of how these animals survive on bryophytes. To partially answer this question, Ricci *et al*. (1987) collected mosses from a spring-fed pond in Italy. Hence, it is likely that the humidity remained higher than that of the laboratory. Furthermore, the mosses themselves provide capillary spaces that can lock in water for a longer period of time than that of the surroundings. Unlike the rotifers that depend on eggs for reproduction, bdelloid rotifers in this study had a much lower hatching rate (19%) compared to 40-100% (Pourriot & Snell 1983) reported for those species that depend on resting eggs to colonize new environments. ***Macrotrachela quadricornifera*** (Figure 62-Figure 64) is a parthenogenetic rotifer, requiring no partner to reproduce. Therefore, its life on a moss leaf is not dependent on finding a partner in what can be an isolated habitat. The ability of the moss leaf to disperse in the wind provides a means for the rotifer likewise to disperse.

Certainly one of the most important adaptations of bryophyte dwellers is this ability to withstand drying.

Bdelloid rotifers in particular are common among bryophytes and humus-containing soil (Sládeček 1983). Many of these are able to desiccate for long periods of time and become active again. Pennak (1953) reports that one bdelloid rotifer revived after 27 years of desiccation.

Other Protections during Anhydrobiosis

Once in the state of anhydrobiosis, the rotifer gains protections not available to it in the active state. Among these is the ability to survive strong ultraviolet light (Rahm 1923, 1926, 1937). In its normal hydrated state, strong UV light kills the rotifers "almost instantly." This dehydrated state also confers a high tolerance to low temperatures (-190°C) (Rahm 1923), and Becquerel (1950) showed survival of ***Habrotrocha constricta*** (Figure 69) and ***Philodina roseola*** (Figure 60) at 0.05K (-273.1°C, or close to absolute zero)! Anhydrobiosis also stops the internal clock of the rotifers so that they do not age unless they are in the active state (Ricci *et al*. 1987). This is an advantage for those living among bryophytes that dry periodically.

Figure 69. ***Habrotrocha constricta***, a species of both aquatic and epiphytic mosses that is able to survive at 0.05K. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Gladyshev and Meselson (2008) demonstrated that bdelloid rotifers have extreme resistance to ionizing radiation. Using bryophyte dwellers ***Adineta vaga*** (Figure 12) and ***Philodina roseola*** (Figure 60), they were able to show that the reproduction is much more resistant to ionizing radiation than that of the monogonont ***Euchlanis dilatata*** (Figure 70). They suggest that this resistance is due to the same evolutionary adaptation that permits these rotifers to survive desiccation in their natural habitats. They consider the mechanism to involve DNA breakage that is repaired following rehydration. This breakage/repair sequence may be the mechanism that kept their load of transposable genetic elements low, thus contributing to the success of the asexual species for such a long time rather than suffering from the early extinction suffered by so many other asexual taxa. This connection should be explored in bryophytes that also have survived for a very long time as asexual organisms. Kamisugi *et al*. (2016) found indications of the possibility in ***Physcomitrella patens***, a moss that demonstrates repair genes for damaged chromosomes.

Figure 70. ***Euchlanis dilatata***, a monogonont moss dweller that has poor resistance to ionizing radiation. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Surviving Fungi

Wilson (2011) found yet another advantage to having anhydrobiosis in the life cycle. He pointed out that organisms that lack sexual reproduction usually do not survive evolutionary time. The **Red Queen hypothesis** is that the limited capacity to create new genetic makeup leads to extermination due to rapidly evolving parasites and pathogens. But the asexual **Bdelloidea** have indeed survived under these conditions. Wilson explains this survival of bdelloid rotifers as a result of their ability to disperse while in a desiccated state, arriving in a new location parasite free.

In experiments, wind dispersal during seven days of desiccation successfully removed a fungal parasite from populations of one species and permitted them to disperse independent of their fungal parasite (Wilson 2011). Wilson desiccated a "heavily infected" population of ***Habrotrocha elusa*** on a moss, placed it in a wind chamber, and collected those that landed on target dishes. These were rehydrated after 7 days. In 70% of the dishes, new populations became established and two-thirds of these were free of parasites. However, if the rotifers were "dispersed" while wet, all the new populations were infected and were killed by the fungus.

Wilson (2011) made an additional observation on ***Adineta vaga*** (Figure 12) collected from an **epiphytic** moss. In bryological literature, **epiphytic** moss refers to those mosses living on trees or shrubs; these are often referred to as "tree mosses" in the rotifer literature. Following anhydrobiosis this species had enhanced **fecundity** (reproductive rate) compared to those that had not been dehydrated, even when they were infected with fungal parasites. This suggests that the desiccation-rehydration cycle may serve as a cue to invest heavily in reproduction.

Food

Rotifers obtain their food by rotating **cilia** in the **corona** (Figure 71) that directs the food into the mouth. This enables them to eat small particles of organic matter, bacteria, algae, protozoa, and even other rotifers (Wikipedia 2012b). [These same cilia can be used for

swimming (Fontaneto & Ricci 2004)]. The food is directed to the mouth and the modified pharynx called a **mastax** (Figure 72-Figure 73), the latter consisting of the **trophus** and its musculature. Their menu usually consists of food items that are up to 10 µm in size (Wikipedia 2012b). This ability to filter such small particles from their environment makes them useful in maintaining clean water in aquaria. Clément *et al*. (1980) described the muscle structure and method of controlling the cilia to obtain food for the moss dweller ***Philodina roseola*** (Figure 60, Figure 71) and planktonic *Brachionus calyciflorus* (Figure 74) and their ability to reject some foods.

Figure 71. ***Rotaria*** sp. showing cilia that direct food into the mouth. Photo by Wim van Egmond, with permission.

Figure 72. ***Dissotrocha scutellata*** showing **mastax**. This species has been collected on the moss ***Andreaea rupestris*** growing on a rock in the open. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 73. Mastax, showing the **trophi** of a **rotifer** from the liverwort ***Frullania eboracensis***. This structure is used for crushing food items. Photo courtesy of Mark Pokorski.

Figure 74. *Brachionus calyciflorus*, a species that can reject some foods. Photo from Academy of Natural Sciences in Philadelphia, through Creative Commons.

Food choices differ with habitat, even within the same species. The bdelloid rotifer ***Macrotrachela quadricornifera*** (Figure 62-Figure 64) is a filter feeder whose food preference and survivorship both differ among the habitat strains (Ricci 1991). Moss dwellers were unable to survive on yeast (*Saccharomyces cerevisiae*) alone, whereas the two aquatic strains survived and grew. One of the moss-dwelling strains was unable to eat the one-celled green alga *Chlorella pyrenoidosa* (see Figure 75). The other moss strain did best on the bacterium *Escherichia coli*, which resulted in poor growth of all the other strains. It appears that the habitat may influence the types of enzymes available for digestion of food. We cannot, however, say if this is an environmental response during development or a genetic one that has persisted through a number of moss-dwelling generations.

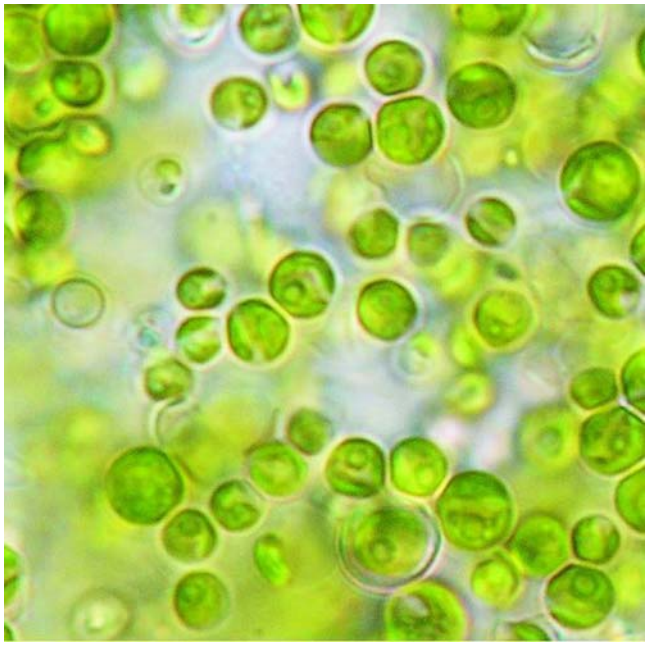

Figure 75. ***Chlorella vulgaris***; ***C. pyrenoidosa*** a rejected food for moss-dwelling ***Macrotrachela quadricornifera***. Photo by Sarah Duff, through Creative Commons.

Most of the **rotifer** inhabitants of ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) feed on small particles of food directed to them by their wheel cilia (Figure 76) (Hingley 1993). They mash their food with their **mastax** (Figure 72-Figure 73, Figure 3), thus modifying these in the ecosystem.

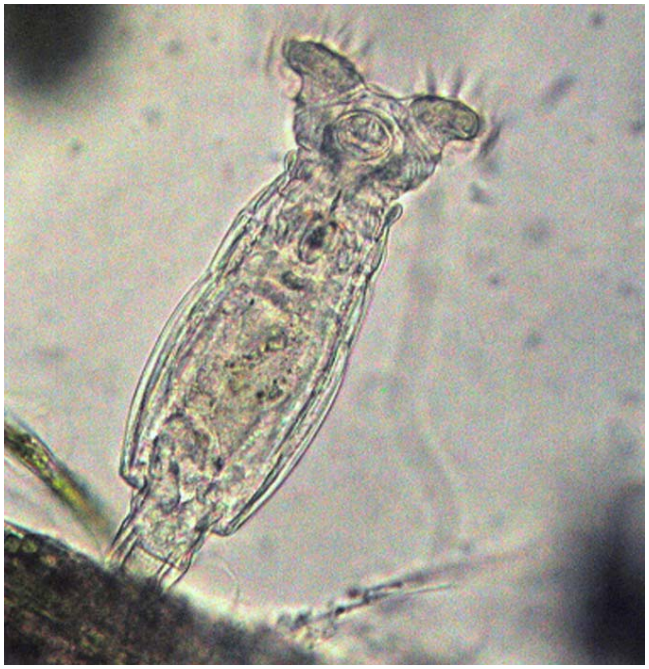

Figure 76. The two "wheels" of cilia on this moss-dwelling rotifer are in full motion. Photo courtesy of Andi Cairns.

A few rotifers actually bite their food. For example, among the moss dwellers, this method is used by ***Lindia torulosa*** (Figure 77-Figure 78) and ***Notommata groenlandica*** (Figure 79), but there are many others as well (Plewka 2016).

Figure 77. ***Lindia torulosa*** biting ***Oscillatoria***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 78. ***Lindia torulosa*** consuming ***Oscillatoria***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 79. ***Notommata groenlandica*** ready to penetrate and eat the desmid ***Netrium*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Role in the Food Web

Tiny animals usually have bigger animals that eat them. The rotifers fall prey to copepods, fish, and Bryozoa, but small rotifers are also eaten by bigger rotifers (Wallace *et al*. 2006). For example, members of the rotifer genus ***Lecane*** (Figure 122, Figure 128) are eaten by the rotifer ***Dicranophorus robustus*** (Figure 80) (Jersabek *et al*. 2003), both known from bryophytes. On the other hand, when the ***Asplanchna*** ate too much ***Keratella*** (Figure 81), the ***Asplanchna*** died, possibly due to the spines and hard lorica of the ***Keratella*** (Figure 57).

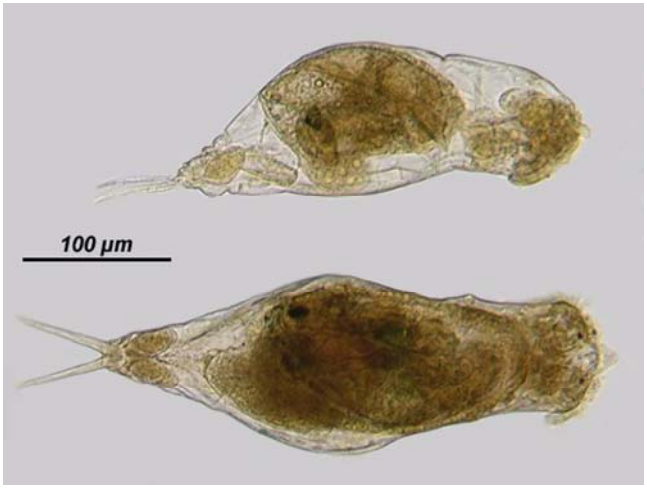

Figure 80. ***Dicranophorus robustus***, a bryophyte dweller that eats smaller rotifers on bryophytes. Photo from Jersabek *et al*. 2003, through Creative Commons.

Figure 81. ***Asplanchna*** sp. overfed on ***Keratella*** sp. This large rotifer died after eating a large quantity of the smaller ***Keratella*** (van Egmond 2003). Photo by Wim van Egmond, with permission.

Some rotifers, especially **sessile** (attached) rotifers, are easy prey for larger invertebrates. For example, Antarctic tardigrades appear to be important predators on rotifers (Sohlenius & Boström 2006). Some rotifers make tubes in which to hide. ***Ptygura velata*** (Figure 82-Figure 83) solves the problem of becoming someone else's dinner by making a tube from its own fecal pellets (Figure 82-Figure 83), where it withdraws from danger (Edmondson 1940).

Figure 82. ***Ptygura*** sp. with its case made of its own fecal pellets, attached to a ***Sphagnum*** leaf. Photo by Wim van Egmond, with permission.

Figure 83. Close view of ***Ptygura*** sp. showing fecal pellets in the case. Photo by Wim van Egmond, with permission.

Rotifers participate in a food web within the moss habitat. Therefore, things that hurt their food items indirectly impact the rotifers. For example, rotifer biomass on ***Sphagnum fallax*** (Figure 25) decreased in response to experimentally added lead (Nguyen-Viet *et al*. 2007). The mechanism, however, appeared to be indirect due to the loss of microbial biomass and not due to the direct effects of lead on the rotifers. The biomass of bacteria, microalgae, testate amoebae, and ciliates decreased significantly and "dramatically." The linkage appears to be that bacteria provided food for the ciliate and testate protozoa, and these in turn provided food for the rotifers. Rotifers do have preferences, and these preferences affect the species composition of algae in their ecosystems (Wikipedia 2012b). They also affect the species composition through competition for food with Cladocera and Copepoda.

Specific Habitats

We would probably make some very interesting discoveries if bryologists and rotifer biologists would join forces. But rotifer folks rarely name the bryophytes where their rotifers dwell, and most bryologists can't name the rotifers they find and are likely to miss the dormant ones. Some rotifers may have very specific habitats, particularly among bryophytes that offer unusual conditions.

Lobule Dwellers

Claudine Ah-Peng expressed surprise to find invertebrates in the lobules of some species of **Lejeuneaceae**, notably in the lobules of the leafy liverwort ***Acrolejeunea emergens*** (Figure 84-Figure 85). These occurred on plants at the Piton de la Fournaise volcano (Réunion in the Indian Ocean) collected on a 1986 lava flow.

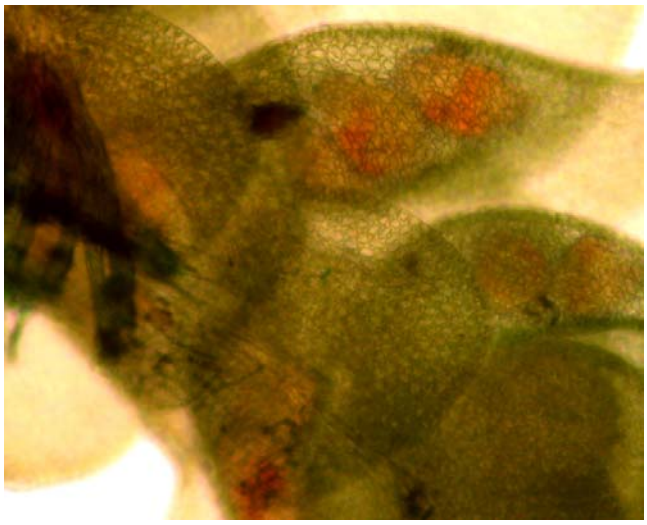

Figure 84. ***Acrolejeunea emergens*** with several orange invertebrates in the lobules. These appear to be resting stages of rotifers. Photo courtesy of Claudine Ah-Peng.

Figure 85. ***Acrolejeunea emergens*** with an emerging invertebrate, apparently a **rotifer**, in a lobule. Photo courtesy of Claudine Ah-Peng.

Bdelloid rotifers seem to be common in lobules, even in the tiny leafy liverwort ***Microlejeunea*** (Figure 86). Blanka Shaw has provided me with pictures of the tiny leafy liverwort ***Microlejeunea ulicina*** (Figure 87) from Whitewater Falls in Transylvania County, North Carolina, USA, with rotifer inhabitants, again in lobules. These initially motionless animals began moving their "wheels" when the warmth of the microscope light activated them.

Figure 86. ***Microlejeunea*** sp. showing lobules. Photo by Paul Davison, with permission.

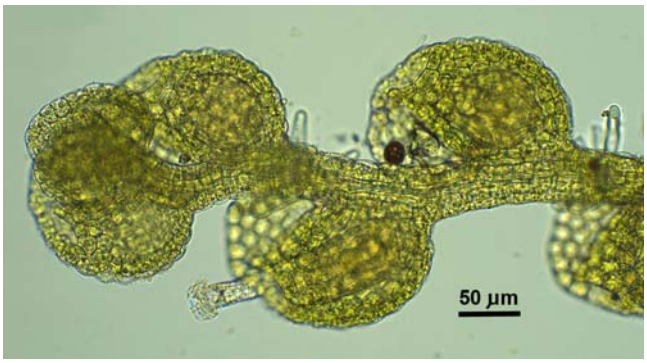

Figure 87. ***Microlejeunea ulicina*** with a rotifer emergent from a lobule. Scale is 50 µm. Photo courtesy of Blanka Shaw.

In North America, Puterbaugh *et al.* (2004) found that rotifers were common in the lobules of the leafy liverwort ***Frullania eboracensis*** (Figure 88-Figure 92). The younger outer portions of the plants had more rotifers in the lobules than did the interior lobules. Sterile plants had a mean ratio of 0.83±0.15 rotifers per lobule. Male and female plants had a mean ratio of 0.38±0.04 rotifers per lobule. Sterile plants likewise tend to be younger. Since we would expect older lobules to have more rotifers due their greater time available for colonization, these findings suggest that older portions may have something, perhaps a chemical exudate, that discourages the colonization by rotifers, or it could be due to lobule size difference, microhabitat differences, or accessibility.

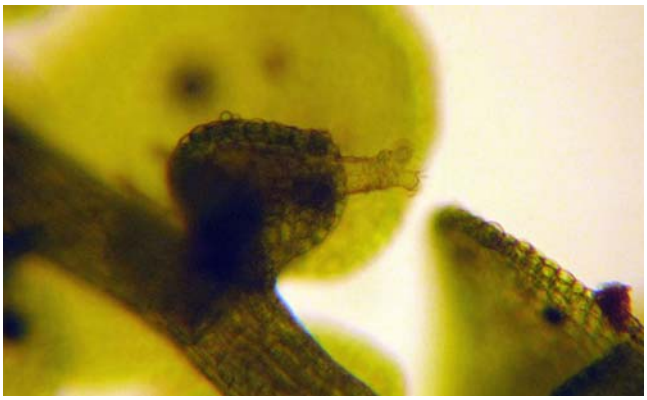

Figure 88. ***Frullania eboracensis*** with a rotifer in its **lobule**. Photo by Robert Klips, with permission.

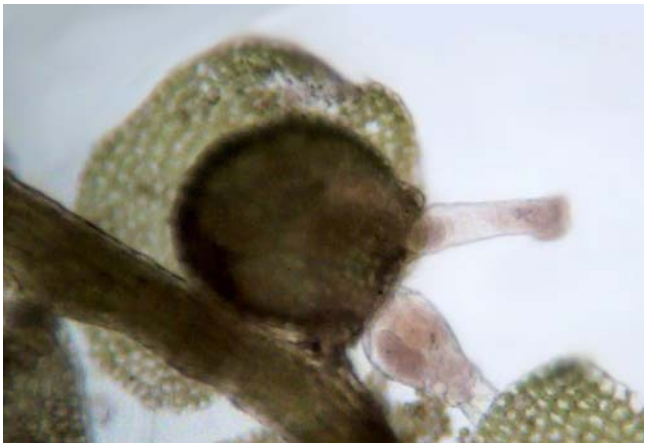

Figure 89. Bdelloid rotifers in lobules of ***Frullania eboracensis***. Photo courtesy of Mark Pokorski.

Figure 90. Bdelloid rotifer on lobule of ***Frullania eboracensis***. Photo courtesy of Mark Pokorski.

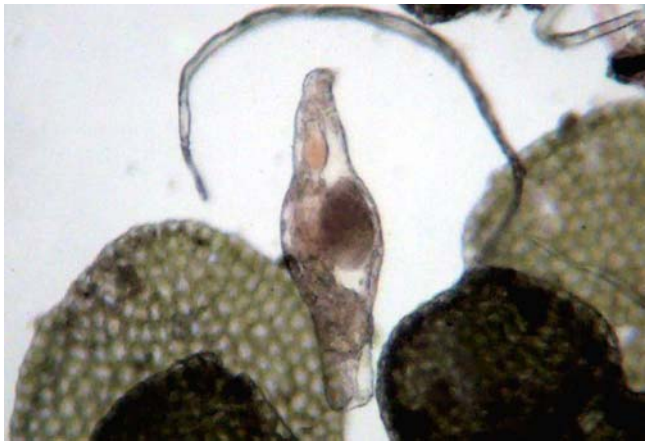

Figure 91. ***Frullania eboracensis*** with bdelloid rotifers as inhabitants. Photo courtesy of Mark Pokorski.

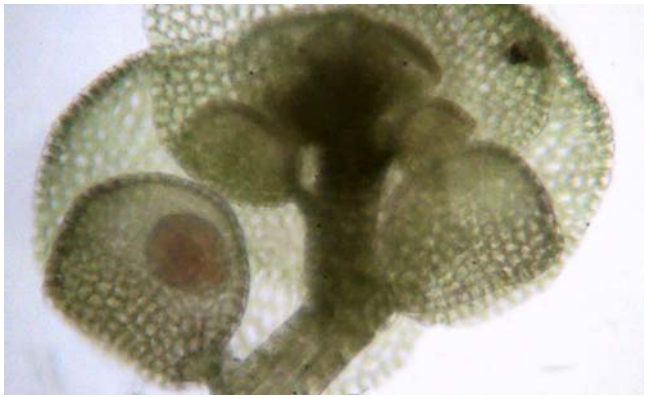

Figure 92. Lobules of ***Frullania eboracensis*** with dormant rotifers. These dormant stages could be resting eggs or cysts. Photo courtesy of Mark Pokorski.

Hess *et al*. (2005) found rotifers in lobules of ***Colura*** sp. (Figure 93-Figure 95) and ***Pleurozia purpurea*** (Figure 96-Figure 100). These liverworts have a trap lid on the lobules, and it appears that the inhabitants might not be able to escape, dying in the lobule (trap) and contributing organic matter that could break down and provide nutrients to the liverworts. However, there does not seem to be any evidence that ***Microlejeunea*** (Figure 86-Figure 87) or ***Frullania*** (Figure 88-Figure 92) species have this trapping action.

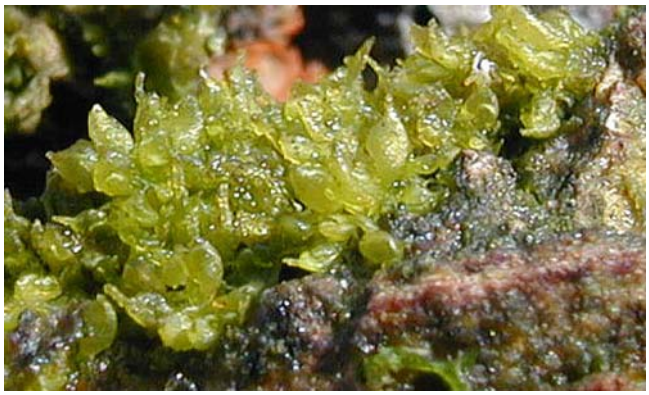

Figure 93. ***Colura calyptrifolia***, a leafy liverwort with lobules where **rotifers** can live. Photo by Michael Lüth, with permission.

Figure 94. ***Colura*** leaf with lobule where rotifers often live. Photo courtesy of Jan-Peter Frahm.

Figure 95. SEM of ***Colura*** leaf lobule where rotifers often live. Photo courtesy of Jan-Peter Frahm.

Figure 96. ***Pleurozia purpurea***, a leafy liverwort with lobules that house, and possibly trap, rotifers and other fauna. Photo by Janice Glime.

Figure 97. Branch of ***Pleurozia purpurea***. Photo courtesy of Sebastian Hess.

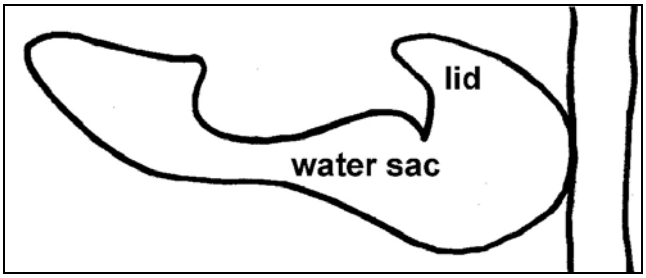

Figure 98. Lobule of ***Pleurozia purpurea*** showing the trap and lid. Redrawn from Hess *et al*. 2005.

Figure 99. Leaf of ***Pleurozia purpurea*** showing lobule and lid. Photo courtesy of Sebastian Hess.

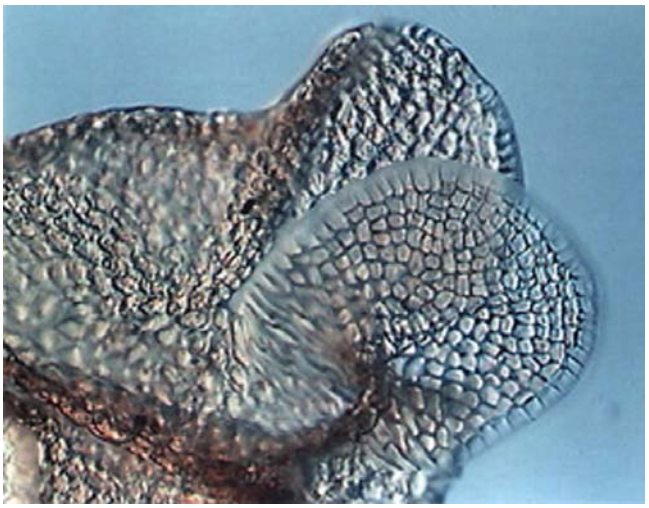

Figure 100. Lobule of ***Pleurozia purpurea*** showing lid. Photo courtesy of Sebastian Hess.

Lobules are not necessary for rotifer habitation of the leafy liverworts. ***Jungermannia cordifolia*** (Figure 101), with only a flat leaf surface to offer, likewise has its fauna of these interesting invertebrates (Javier Martínez Abaigar, pers. comm. 2008), as do mosses that lack similar structures.

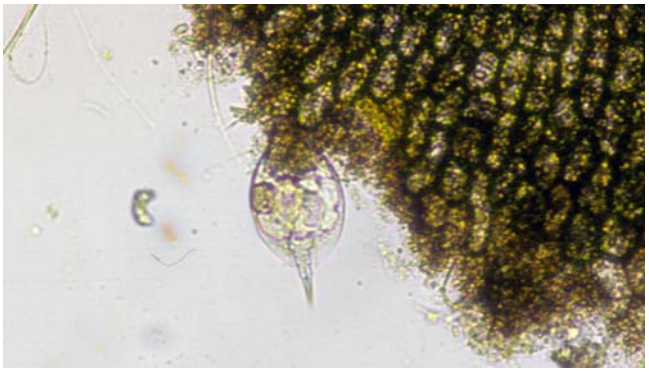

Figure 101. This ***Lepadella*** species, with its "wheels" hidden and its toes showing, is feeding on detrital material associated with the liverwort ***Jungermannia cordifolia***. Photo courtesy of Javier Martínez Abaigar.

Des Callaghan (Bryonet 10 November 2012) kindly provided us with a YouTube video <http://youtu.be/kHhBBppqh_Y> of rotifers feeding from the lobules of the tiny ***Lejeunea patens*** (Figure 102-Figure 103) in Wales and another of rotifers in lobules of ***Harpalejeunea molleri*** (Figure 104). I knew that the ciliated "wheels" directed food into the mouth, but I never realized the speed or the distance of that effect. The particles started outside the field of view and travelled farther than the extended length of the rotifer. Some particles came from near the foot and others shot in like a meteor from the height of the cilia or a little above, but from some distance.

Figure 102. ***Lejeunea patens*** on rocks near Swallow Falls stream, Wales. Photo by Janice Glime.

Figure 103. ***Lejeunea patens***, home of rotifers in Wales. Photo by Michael Lüth, with permission.

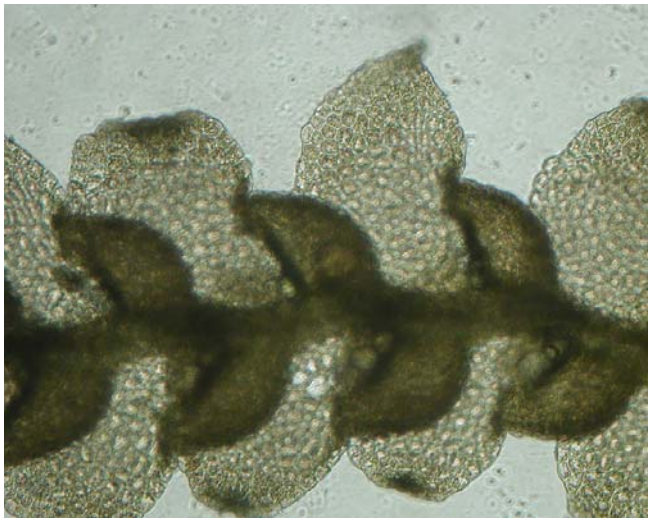

Figure 104. ***Harpalejeunea molleri*** with lobules that are home for rotifers. Photo by Jan-Peter Frahm, with permission.

Retort Cells

Curiously, two species of ***Habrotrocha*** (Figure 105) (***Habrotrocha roeperi***, Figure 106; ***Habrotrocha reclusa***, Figure 107) choose to live in the **retort** cells (Figure 106, Figure 108) of the stems of some species of ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112), entering through the subterminal pore. **Retort** cells differ from other ***Sphagnum*** outer stem (Figure 110) and branch cells by having a terminal neck that terminates in a pore, somewhat like the neck of a leather wine flask. Hingley (1993) found it interesting that these rotifer species seemed to avoid the stem cells of ***Sphagnum palustre*** (Figure 109), ***S. papillosum*** (Figure 27, Figure 110), and ***S. magellanicum*** (Figure 111-Figure 112), all species of the subgenus ***Sphagnum*** that has spiral thickenings in the **cortical** (outer stem) cell walls (Figure 110).

Figure 105. ***Habrotrocha bidens*** from moss on ground; ***Habrotrocha*** is a genus known from retort cells of ***Sphagnum*** and lobules of ***Frullania***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

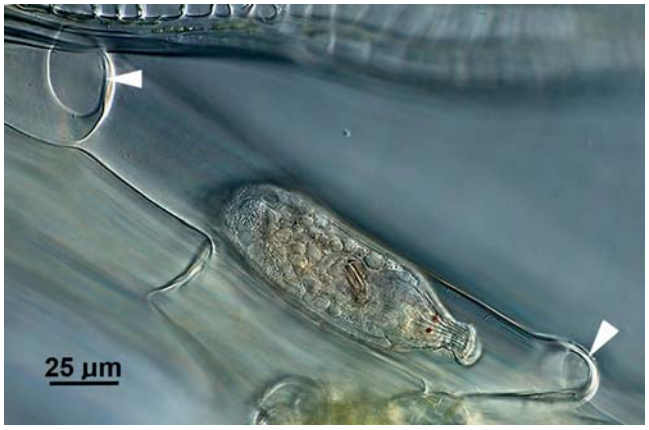

Figure 106. ***Habrotrocha roeperi*** in **retort** cell. Arrows indicate protruding pores. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 107. ***Habrotrocha*** *cf* ***reclusa***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

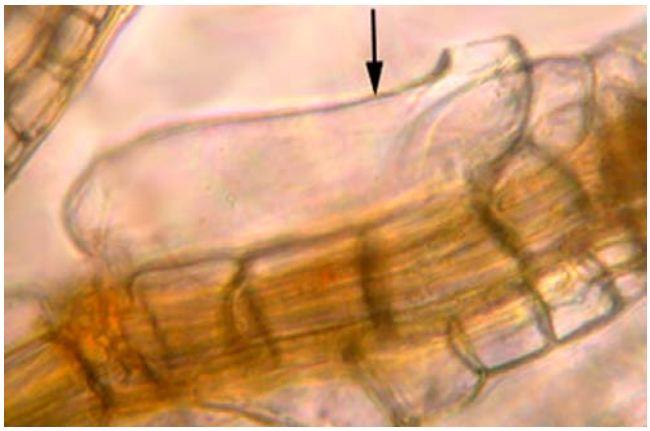

Figure 108. Retort cell of ***Sphagnum***, lacking spiral thickenings. Picture with permission from Wilf Schofield, University of British Columbia botany web site.

Figure 109. ***Sphagnum palustre***, a species with retort cells on the stem that rotifers seem to avoid. Photo by Michael Lüth, with permission.

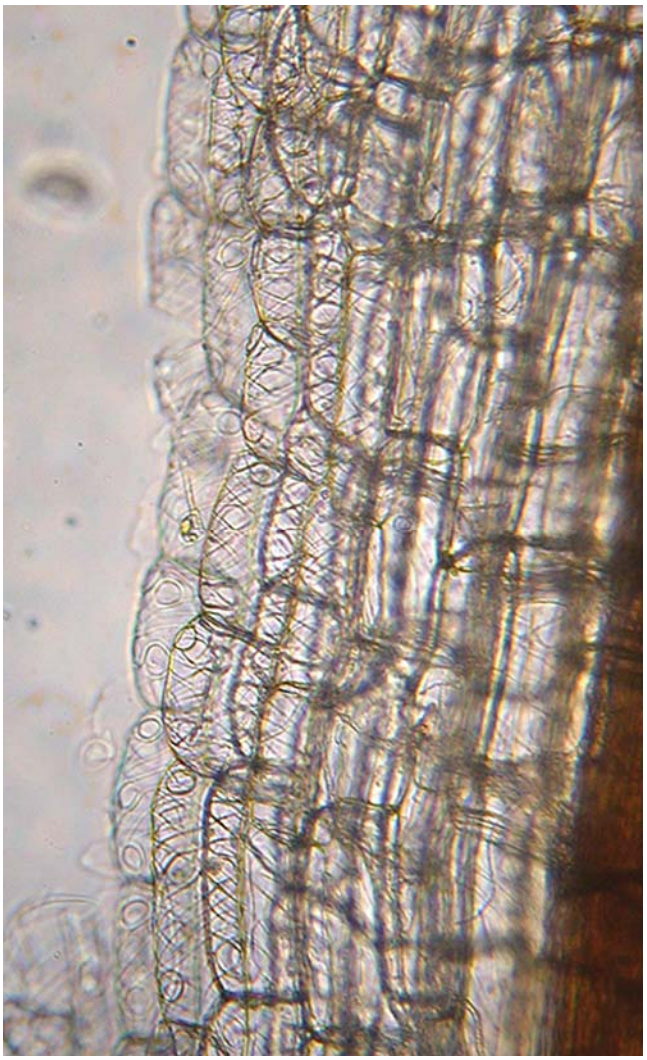

Figure 110. ***Sphagnum papillosum*** outer stem cells in longitudinal view showing fibrils and pores that are flat against the cell surface. Rotifers do not inhabit these. Photo from UBC Botany website, with permission from Shona Ellis.

Figure 111. ***Sphagnum magellanicum*** hummock, a species whose retort cells are avoided by the retort-inhabiting ***Habrotrocha*** species. Photo by James K. Lindsey, through Creative Commons.

Figure 112. ***Sphagnum magellanicum***, a species whose stem cells lack retort cells and are avoided by retort-cell species of ***Habrotrocha***. Photo by Michael Lüth, with permission.

In addition to living in ***Sphagnum*** retort cells, ***Habrotrocha roeperi*** (Figure 106) and ***Habrotrocha reclusa*** (Figure 107) live inside the outer cells of ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) branches (May 1989). May states that these rotifers could be considered as parasites. I have to question what nutrition they get from the ***Sphagnum*** by living in those outer cells. It is more likely that they feed on associated micro-organisms.

Roofs

Colonization of mosses on roofs permitted Hirschfelder *et al*. (1993) to compare species of rotifers on an upright acrocarpous moss (***Ceratodon purpureus***; Figure 31) and a mat-forming pleurocarpous moss (***Brachythecium glareosum***; Figure 113). They collected mosses every two weeks from roofs aged 3-92 years, dried them at 20ºC, and cut them into small pieces. The pieces were re-wet in deionized water and examined for awakening rotifers. The mat-forming moss had significantly more species and greater numbers of rotifers than did the upright moss, but species on ***C. purpureus*** differed little from those that could be found on ***B. glareosum***. They found that rotifer colonization of the mosses continued for decades and that the colonization of the mosses was rapid. Nevertheless, the numbers of rotifer species increased with time (Figure 114).

Figure 113. ***Brachythecium glareosum***, a rotifer habitat on roofs. Photo by Des Callaghan, with permission.

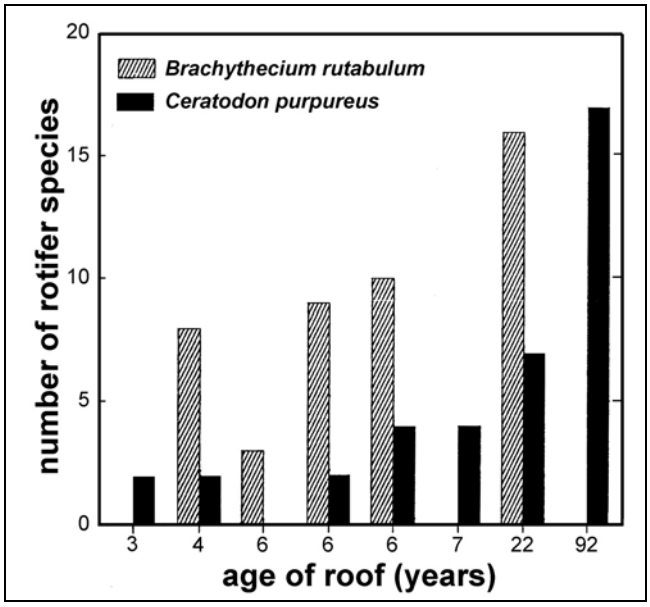

Figure 114. Succession of rotifer species that increase in number with age of roof. Redrawn from Hirschfelder *et al*. 1993.

Arctic and High Altitude

De Smet and Beyens (1995) considered rotifers to be one of the dominant bryophyte dwellers on Devon Island. In the Arctic Spitsbergen, the bdelloid rotifers among mosses had an unexpectedly high species richness – 52 taxa (Kaya *et al*. 2010). Kaya and coworkers concluded that the moisture regime and geographic localization of the mosses were the most important ecological factors in affecting the differences in species composition between samples. (See also De Smet 1988).

Fontaneto and Ricci (2006) examined elevational effects on the rotifer fauna of lichens and mosses across the Italian, French, and Swiss Alps. Distances among the 47 sample sites ranged from 1 m to 420 km. Low elevation sites ranged 850-1810 m asl; high elevation sites were 2984-4527 m asl. They found significant differences in both species richness and species composition between the mosses and lichens at high elevations. Nevertheless, there

was no significant difference in the heterogeneity of the species assemblages. High-elevation **alpha diversity** (diversity of each site, *i.e.* local species diversity) was significantly lower than that at lower elevations. On the other hand, when comparing only species richness, there was no difference between higher and lower elevations.

Alpha diversity in these Alp rotifers was significantly lower at high-elevation than at low-elevation sites, but the estimated number of species was not reduced when compared with sites at low elevations (Fontaneto & Ricci 2006). Geographical distance between sites had no effect on species composition of rotifers in either mosses or lichens. The high elevation sites did not simply represent a reduction in number of species represented at lower elevations. Rather, they indicated that low density of favorable habitat patches, coupled with the low number of available propagules (moss riders), accounts for the heterogeneity of rotifers among the moss patches and the lower richness in individual patches at higher elevations.

Antarctic

In the Antarctic, rotifers share the mosses with tardigrades and nematodes among the microinvertebrates. Early explorations of de Beauchamp (1913) in the Antarctic revealed the bdelloid ***Mniobia*** (Figure 67) among mosses. Most of the bdelloids he located were contracted and could not be identified. In addition, he found the monogononts ***Lindia torulosa*** (Figure 115), ***Colurella adriatica*** (Figure 3), and ***C. colurus***.

Figure 115. ***Lindia torulosa*** head, a species that lives among mosses in the Antarctic. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Petz (1997) found that 95% of the samples from Wilkes Land, East Antarctica, had rotifers, with the highest numbers in mosses (1,311/g), although it was tardigrades that dominated. Water and organic matter seemed to be the most important controlling factors for these invertebrate numbers.

The Antarctic mosses sport an active community of invertebrates that move among the stems and branches. Priddle and Dartnall (1978) showed experimentally that wind caused mixing in summer, resulting in the transport of larval rotifers from shallow portions of the lake. Priddle and Dartnall found six rotifer species along the stems of aquatic mosses [***Warnstorfia sarmentosa*** (Figure 116), ***Drepanocladus*** sp. (probably ***Sanionia uncinata***; Figure 117)]. Two of these rotifers were bdelloids and four were sessile monogonont species. These rotifers preferred the middle stem zones of mosses where the highest growths of epiphytic algae and other epiphytic organisms occurred. Of these, four species chose leaf axils, whereas the other two settled on the bare underside of the leaf.

Figure 116. ***Warnstorfia sarmentosa***, home for a variety of Antarctic rotifers. Photo by David T. Holyoak, with permission.

Figure 117. ***Sanionia uncinatus***, a suitable substrate for Antarctic rotifers. Photo by Michael Lüth, with permission.

These studies were followed by those of Dartnall and Hollowday (1985), Hansson *et al.* (1996), Dartnall (1980, 1995, 1997, 2000, 2005a,b (flooded moss carpets), all providing records of Antarctic bryophytes.

Dartnall and Hollowday (1985) found that ***Macrotrachela concinna*** was most often encountered in terrestrial mosses. An unidentified species of ***Philodina*** (Figure 60) occurred on growing tips of mosses in the lake. ***Notholca salina*** and ***Resticula gelida*** (Figure 118) were most common in the flooded moss carpet. ***Adineta barbata*** (Figure 119) was collected from drying mosses.

Figure 118. ***Resticula gelida***, a plankton species that is common in flooded moss carpets in the Antarctic. Photo by Michael Plewka <www.plingfactory.de>, with permission.

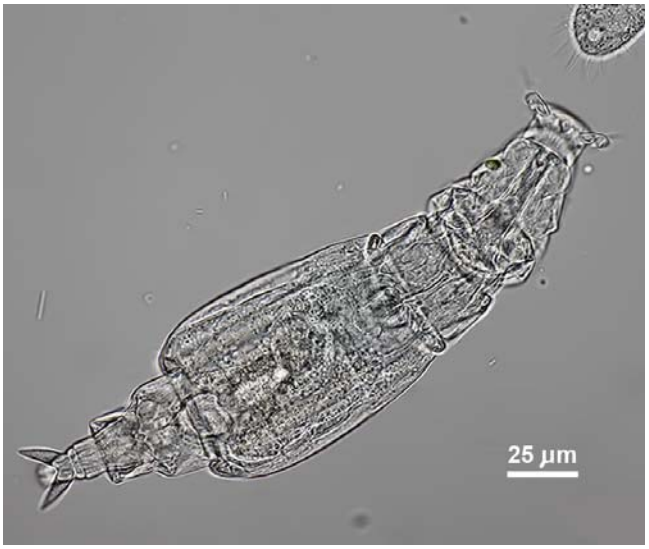

Figure 119. ***Adineta barbata*** from epiphytic moss, a species that occurs among mosses that dry out in the Antarctic. Photo by Michael Plewka <www.pllingfactory.de>, with permission.

Hansson *et al*. (1996) found that rotifers in the Antarctic (South Georgia) were rare in the open water and were restricted mostly to mosses in shallow areas, as well as sediment surfaces. These taxa were varied, including ***Cephalodella auriculata*** [Figure 120; a cold-water species (Segers 2001)], ***C. gibba*** [Figure 121; (see also De Smet 2001)], a cold-water species (Segers 2001) known from habitats with *p*H <3.0 in Germany (Deneke 2000), ***Lecane closterocerca*** (Figure 122; see also Hingley 1993), ***L. lunaris*** (Figure 123), ***Lepadella patella*** (Figure 124; see also Hingley 1993), ***Resticula*** sp. (Figure 125), ***Testudinella*** sp. [perhaps ***Testudinella patina*** (Figure 126) found by Hingley (1993)], ***Tricocerca brachyura*** (Figure 127), and several bdelloid rotifers among the more common ones.

Figure 120. ***Cephalodella auriculata*** (**Notommatidae**), a cold-water benthic and epiphytic moss-dwelling rotifer. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 121. ***Cephalodella gibba***, an aquatic rotifer (Segers 2001), typically occurring in the sediments (Hingley 1993; Schmid-Araya 1995), that is found among the Antarctic mosses (De Smet 2001). Photo from Jersabek *et al*. 2003, through Creative Commons.

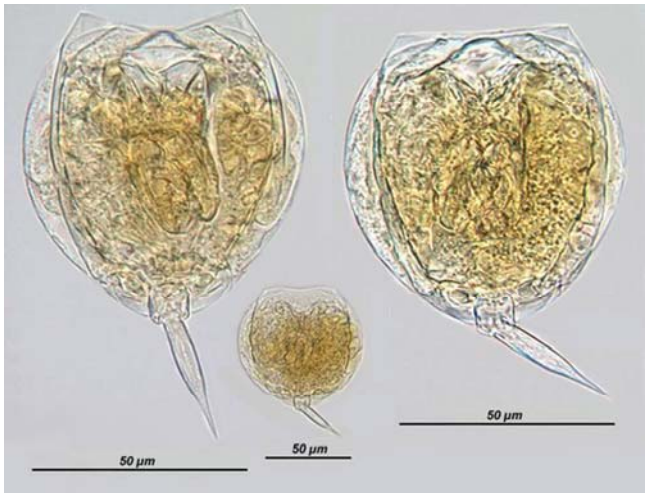

Figure 122. ***Lecane closterocerca***, a species primarily on mosses in the Antarctic. Photo by Jersabek *et al*. 2003 from Rotifer World Catalog, through Creative Commons.

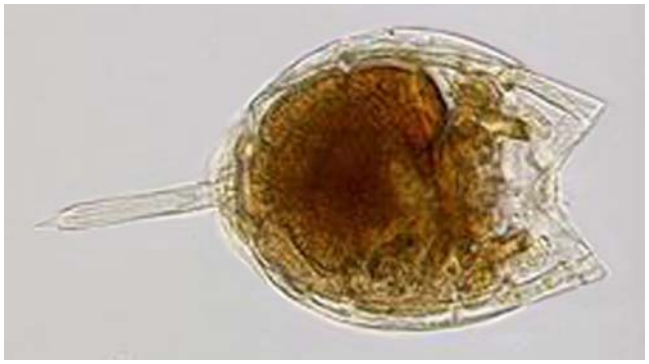

Figure 123. ***Lecane lunaris***, a bryophyte dweller in the Antarctic. Photo from Jersabek *et al.* 2003, with permission.

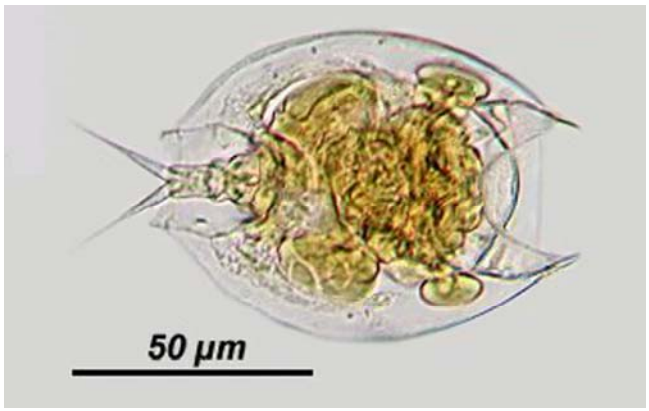

Figure 124. ***Lepadella patella***, an Antarctic moss dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 125. ***Resticula nyssa***; this genus is a common moss dweller in the Antarctic. Photo by Jersabek *et al*. 2003 from Rotifer World Catalog, through Creative Commons.

Figure 126. ***Testudinella patina***, an Antarctic moss dweller. Photo by Yuuji Tsukii, with permission.

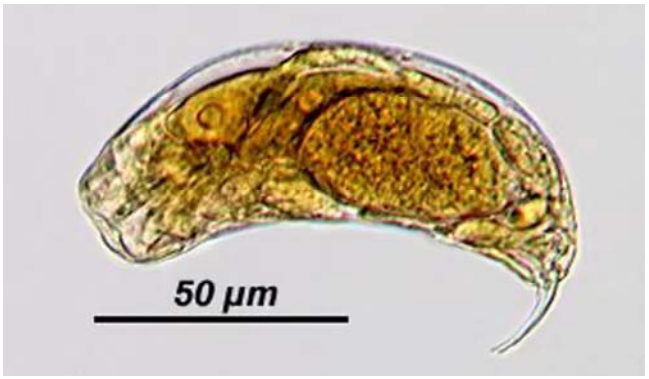

Figure 127. ***Trichocerca brachyura***, an Antarctic moss dweller. Photo by Jersabek *et al.* 2003, with permission.

Hansson *et al*. (1996) found the genus ***Lecane*** (Figure 128), to be one of the more common rotifers on Antarctic bryophytes. This is a widespread genus with one of the largest numbers of species. It includes several endemic species (Segers 1996) and members that are able to live in the contrasting warm climates of southeast Asia (Segers 2001) and Brazil (Turner & Da Silva 1992).

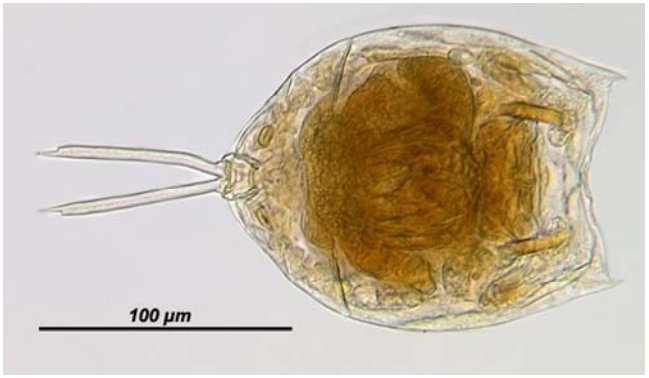

Figure 128. ***Lecane curvicornis***, member of a genus that has several species living on mosses in the Antarctic. Photo by Jersabek *et al*. 2003, with permission.

One of the common habitats for Antarctic rotifers is the moss ***Sanionia uncinata*** (Figure 129). In this habitat, the rotifers (Figure 130) are subject to predation by nematodes (Newsham 2004).

Figure 129. ***Sanionia uncinata***, a common moss in higher latitudes, including the Antarctic, and home for rotifers. Photo by Hermann Schachner, through Creative Commons.

Figure 130. Moss-dwelling ***Adineta*** sp. from the moss ***Sanionia uncinata*** on the Barton Peninsula of King George Island, Antarctica. Photo by Takeshi Ueno, with permission.

Fontaneto *et al*. (2015) determined that the number of monogonont rotifer species decreases toward the poles. The number of bdelloid species, on the other hand, increases toward the poles. Bryophytes play an important role in providing habitats for them farther north and south. The **Bdelloidea** are most common in limnoterrestrial environments – mosses, lichens, and soils (Wallace *et al*. 2006; Fontaneto & De Smet 2015). The **Monogononta**, although sometimes present in limnoterrestrial habitats, including mosses, are mostly aquatic. Hansson *et al*. (1996) found that rotifers were rare in the open water of the Antarctic region, being restricted to the vegetation (mainly mosses) in shallow areas as well as the sediment surface.

Sudzuki (1964) enumerated the moss-water community at Langhovde in the Antarctic region and found that it was "not so unusual." He identified 13 rotifer species in the Antarctic region. These included ***Adineta gracilis*** (Figure 131), ***Adineta*** sp., *Encentrum antarcticum* (invalid species), ***Habrotrocha*** (Figure 105-Figure 107), *Lepadella patella matsuda* (invalid subspecies, ***Macrotrachela*** sp. from Langhovde. However, some of these species are now invalid. Sudzuki (1979) also sampled mosses using polyurethane foam in a variety of Antarctic sites. These added ***Habrotrocha cf. gulosa*** and ***Macrotrachela nixa*** to the moss rotifer fauna.

Figure 131. ***Adineta gracilis***, a moss dweller that lives among Antarctic moss carpets. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Freshwater plankton and submerged mosses supported 13 species of monogonont rotifers in the South Shetland Islands (Janiec 1993, 1996a, b; Janiec & Salwicka 1996).

In their studies of southern Victoria Land, Schwarz *et al*. (1993) found that the protozoa, rotifers, nematodes, and tardigrades dominate the invertebrate fauna of the moss-dominated flushes. These invertebrates, including rotifers, were concentrated at 5-10.83 mm depth in the moss carpets. In post-melt cores, the upper 5 mm of the moss mats had more rotifers (and other invertebrates) than in pre-melt samples.

Nevertheless, whereas the rotifers are common on terrestrial mosses, few studies have gone farther than identifying them as rotifers. It is likely that new species, or at least cryptic species, remain to be described there.

Nunataks

Sohlenius and Boström (1996, 2005) examined samples from **nunataks** (Figure 132; exposed, often rocky portions of ridges, mountains, or peaks that escape snow and glaciation, typically vegetated by algae, mosses, and lichens). Among these samples, 67% contained rotifers, with the most frequent and diverse microfauna group being bdelloid rotifers (19 species).

Figure 132. **Nunatak** in Antarctica. Photo by Stephen Bannister, through Creative Commons.

In moss cushions alone from Antarctic nunataks, Sohlenius and Boström (2006) found that 82% of their 91 samples had rotifers, the highest, above the nematodes (64%) and tardigrades (32%). Jennings (1976) studied the ecology of bdelloid rotifers in moss carpets on Signy Island. He found bdelloid and two monogonont rotifer species. These included ***Adineta gracilis*** (Figure 131), ***A. steineri*** (Figure 133), ***A. vaga*** (Figure 12), ***Habrotrocha constricta*** (Figure 69), ***H. crenata*** (Figure 134, ***H. pulchra***, ***Macrotrachela concinna***, ***M. kallosoma***, ***Mniobia burgeri***, and ***Philodina plena*** (Figure 135-Figure 136; see also Donner 1980).

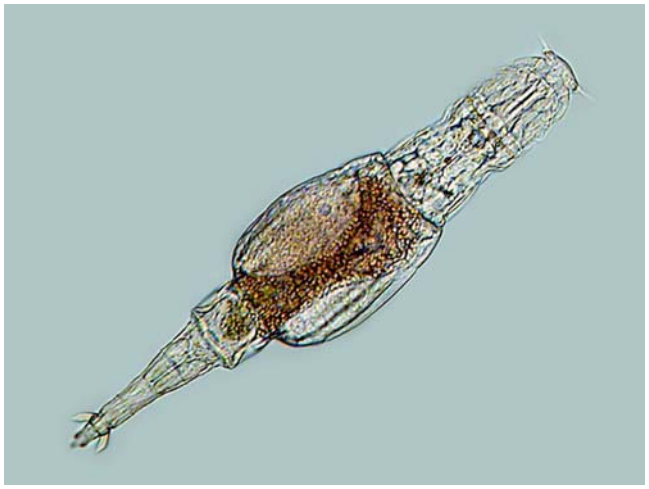

Figure 133. ***Adineta steineri***, an epiphytic moss dweller that also lives in Antarctic moss carpets. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 134. ***Habrotrocha crenata***, a beech litter species that is also known from Antarctic moss carpets. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 135. ***Philodina plena***, a ***Sphagnum*** dweller that lives in Antarctic moss carpets. Photo by Michael Plewka <www.plingfactory.de>, with permission

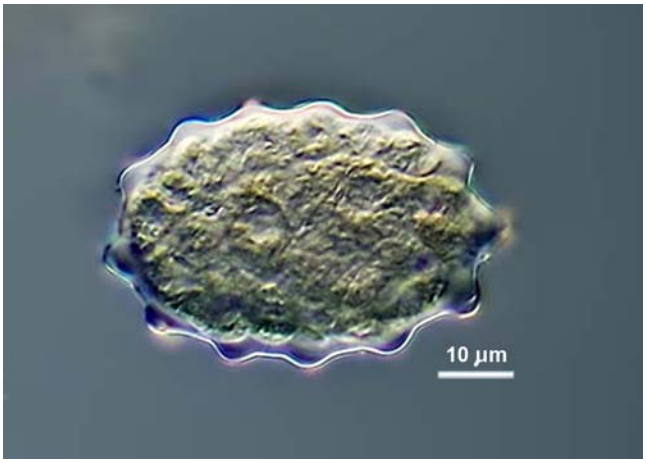

Figure 136. Egg, probably from ***Philodina plena***, a species that occurs in Antarctic moss carpets. Photo by Michael Plewka <www.plingfactory.de>, with permission

Bog and Fen Habitats

The terminology of bog and fen has differed between North America and Europe, with North Americans tending to refer to any habit with dominant ***Sphagnum*** as a bog, whereas the Europeans have considered bogs to be defined by their water sources as only precipitation (*i.e.*, raised bogs or other peatland with no source of mineral-rich water) (Rydin & Jeglum 2013). Those low-nutrient sites with groundwater sources are considered by the Europeans to be poor fens. Other differences in nomenclature exist, making the habitat discussion in this chapter a little fuzzy since I had no way to know which definition the researcher might be using. Fortunately, the rotifers seem to care more about the species of bryophytes than the source of the water, most likely liking the same habitat types as their bryophyte substrates.

The diversity of habitats in bogs and fens results in a number of species preferring these ecosystems. Halsey *et al*. (2000) considered ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) to be a suitable habitat for rotifers due to its large water-holding capacity. Unique communities characterize the various stages in the peatland ecosystem (Francez & Dévaux 1985).

Sayre and Brunson (1971) considered rotifers to be excellent tools for research on the periphyton/epiphyte organisms on mosses in peatlands. Although ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) seems to be important for many species of rotifers, many rotifers are missed during casual observance because their size is less than 200 µm (Gilbert & Mitchell 2006). Some are missed because they hide inside hyaline cells of ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) leaves and stems, entering through the pores (Hingley 1999), or in outer branch cells (May 1989).

Nevertheless, an important deterrent for many rotifers is that ***Sphagnum*** acidifies its surroundings (Clymo 1963, 1964; Williams *et al*. 1998) and may account for a higher species diversity in rich fens than in ***Sphagnum*** peatlands. Since many rotifer species are intolerant of a low *p*H, especially loricate species, the low *p*H limits the rotifer diversity (Nogrady *et al*. 1993) (see Acidity below.) On the other hand, ***Sphagnum*** is important in the phosphorus and nitrogen cycling in bog ecosystems, with the help of

the rotifers that process the detritus (Błedzki & Ellison 1998, 2002).

Some rare species can be common among ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112). For example, the ***Tetrasiphon hydrocora*** (Figure 137) was not uncommon in association with ***Sphagnum*** in Lac des Femmes, Quebec, Canada, yet seemed to be rare on a more general scale (Nogrady 1980). It likewise was one of the rotifers reported in the peatland study by Hingley (1993). One reason for the occurrence of rare species among ***Sphagnum*** may be its ability to serve as a safe site/refugium against predators (Kuczyńska-Kippen 2008). ***Sphagnum*** also provides a source of food such as the desmids seen in the gut of ***Tetrasiphon hydrocora*** (Figure 137). Desmids are common in ***Sphagnum*** peatland pools and among the ***Sphagnum*** plants (personal observation), providing food for many kinds of rotifers. Others may require the alternating wet and dry cycles.

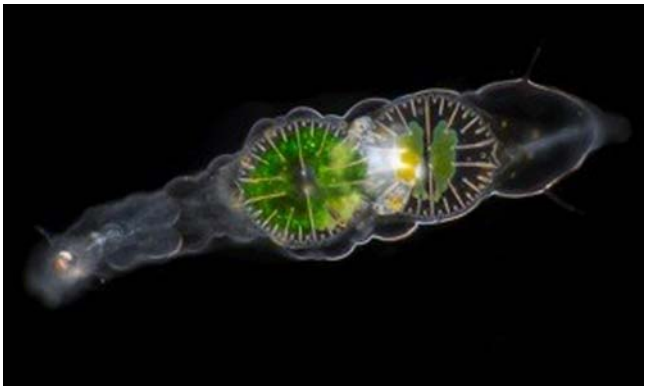

Figure 137. ***Tetrasiphon hydrocora*** with the desmid ***Micrasterias rotata*** in its gut. Photo by Wim von Egmond, with permission.

Species Richness

The abundant peatlands of the Scandinavian countries has resulted in most of our basic knowledge of peatlands arising there.

Pejler and Bērziņš (1993a) found that species richness of rotifers associated with the ***Sphagnum*** (Figure 157) in Swedish peatlands ranged from 33 to 59, including both **Bdelloidea** and **Monogononta**. In an extensive study of peatlands in Poland, Bielańska-Grajner *et al*. (2011) examined the rotifers in eight sampling locations in peatlands, including 2 raised bogs, 2 poor fens, 1 intermediate fen, and 1 rich fen. They found 42 taxa of **Monogononta** and 26 of **Bdelloidea**. **Monogononta** comprised only 4-18% of the numbers among the eight sites sampled. On the other hand, bdelloids were dominant and contributed 80% overall to the number of individuals, ranging 56-85%. Among the **Bdelloidea**, the most abundant rotifers were ***Habrotrocha angusticollis*** (Figure 4), ***H. lata*** (Figure 138), ***H. roeperi*** (Figure 106), ***Macrotrachela quadricornifera*** (Figure 62-Figure 64), ***Rotaria rotatoria*** (Figure 17), ***Lecane elasma*** (Figure 139), ***L. lunaris*** (Figure 123), ***L. scutata*** (Figure 140).

Figure 138. ***Habrotrocha lata*** from ***Sphagnum*** pond. Photo by Michael Plewka <www.plingfactory.de>, with permission.

The large genus ***Lecane*** (Figure 139-Figure 140) enjoys widespread distribution, including the Antarctic. Nevertheless, there are species in this genus restricted to ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) bogs (Pejler & Bērziņš 1994). ***Lecane elasma*** (Figure 139) is considered characteristic of ***Sphagnum*** (Francez & Dévaux 1985).

Figure 139. ***Lecane elasma***, a peatland species. Photo by Jersabek *et al.* 2003, with permission.

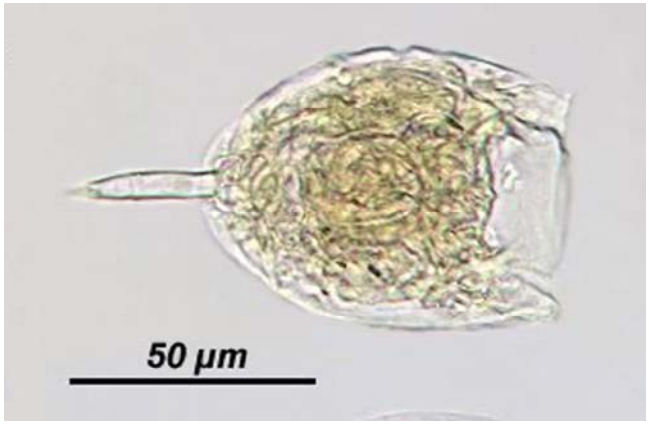

Figure 140. ***Lecane scutata***, one of the abundant bdelloid rotifers in Polish peatlands. Photo by Jersabek *et al.* 2003, with permission.

Bielańska-Grajner *et al*. (2011) selected ***Habrotrocha angusticollis*** (Figure 4), ***Dicranophorus capucinus*** (Figure 141), ***Keratella serrulata*** (Figure 142), and ***Lepadella elliptica*** for further analysis and found that abiotic factors were important determinants of distribution. Nevertheless, the researchers found that the highest density of rotifers occurred in a raised bog dominated by ***Sphagnum angustifolium*** (Figure 157), but this might suggest that a number of rotifer species may prefer the same abiotic conditions as this moss. Francez and Dévaux (1985) similarly found the highest proportion of characteristic rotifer species in a low moor where ***Sphagnum angustifolium*** was dominant.

Figure 141. ***Dicranophorus capucinus*** from among ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

Figure 142. ***Keratella serrulata***, an abundant ***Sphagnum*** associate in Sweden. Photo by Michael Plewka <www.plingfactory.de>, with permission.

As noted, the **Bdelloidea** are the dominant group, in peatlands mostly represented by the genera ***Philodina*** (Figure 143-Figure 144) and ***Habrotrocha*** (Figure 145) (Gilbert & Mitchell 2006). Among the **Monogononta**, peatlands are occupied mostly by ***Colurella*** (Figure 3), ***Euchlanis*** (Figure 146-Figure 148), ***Lecane*** (Figure 139-Figure 140), and ***Trichocerca*** (Figure 149) (Gilbert & Mitchell 2006). Francez (1981), who identified 142 species in peatlands, found that in France both abundance and average size were greater in fens than in bogs. Many kinds of rotifers are unable to live among peat mosses because of the high degree of acidity (Hingley 1993).

Figure 143. ***Philodina*** on the alga *Spirogyra*. Photo by Yuuji Tsukii, with permission.

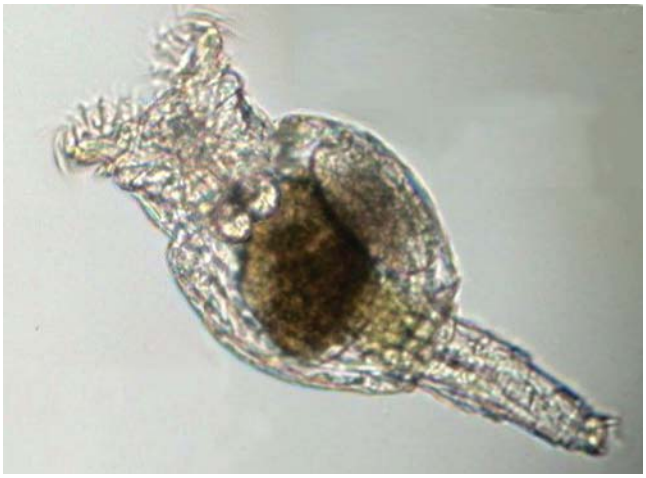

Figure 144. Extended ***Philodina.*** Photo by Jean-Marie Cavanihac at Micscape, with permission.

Figure 145. ***Habrotrocha rosa*** (**Bdelloidea**). Photo by Rkitko from Wikipedia Commons.

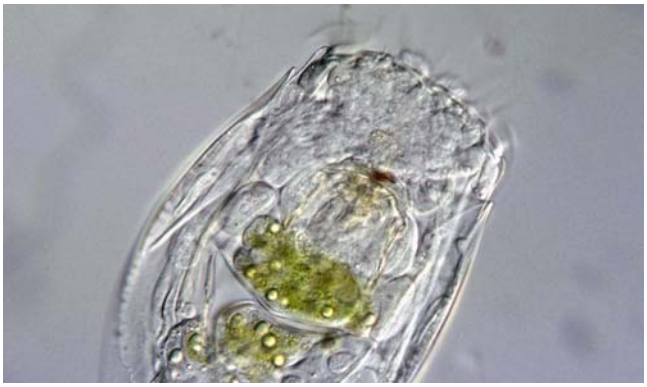

Figure 146. ***Euchlanis***, a genus having species of peatland rotifers. Photo by Yuuji Tsukii, with permission.

Figure 147. ***Euchlanis***. Photo by Jean-Marie Cavanihac at Micscape, with permission.

Figure 148. ***Euchlanis.*** Photo by Jean-Marie Cavanihac at Micscape., with permission.

Figure 149. ***Trichocerca longiseta***, an alpine species but not typically a moss dweller. Photo by Yuuji Tsukii, with permission.

In Australia, Koste and Shiel (1989) identified members of the **Euchlanidae**, **Mytilinidae**, **Trichotriidae**, all members of **Monogononta**. In ***Sphagnum*** pools (Figure 150) they found ***Diplois daviesiae*** and ***Euchlanis meneta*** (Figure 151) in acid water and on submerged ***Sphagnum*** (Figure 150). ***Trichotria truncata*** (Figure 152), an acidophile, occurred among ***Sphagnum***.

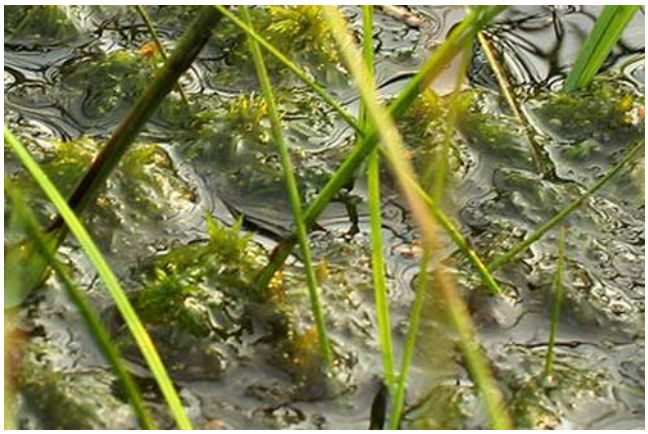

Figure 150. Submersed ***Sphagnum cuspidatum***, potential home for the rotifers ***Diplois daviesiae***, ***Euchlanis meneta***, and ***Trichotria truncata***. Photo by Andrew Spink, with permission.

Figure 151. ***Euchlanis meneta*** female, an inhabitant of acid ***Sphagnum*** pools. Photo by Jersabek *et al.* 2003, with permission.

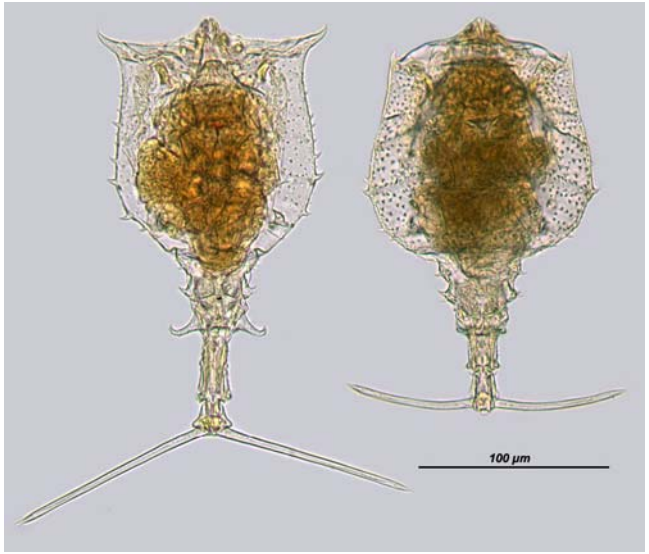

Figure 152. ***Trichotria truncata***, a ***Sphagnum***-dwelling acidophile. Photo by Jersabek *et al.* 2003, with permission.

Rotifer studies in North American bogs have been somewhat limited compared to the number of bogs present in the northern part of the continent. We can safely say that the **Bdelloidea** are the most abundant rotifers among the mosses in peatland habitats (Sayre & Brunson 1971). Some species of rotifers are **tyrphobionts**, restricted to peatlands, but many are also known from other types of habitats (Warner & Asada 2006). Few species seem to be restricted to peatlands, conforming to the typical widespread nature of rotifers.

Most Canadian peatland studies concentrated on the plants and vertebrates. Warner and Asada (2006) were among the first to include invertebrates in an extensive survey. In a **poor fen** (similar to a bog in bryophyte species composition) in Newfoundland, Canada, Bateman and Davis (2007) found 25 **bdelloid** and 39 **monogonont** rotifers. Among these, 27 were new records for Canada and 13 new for North America. They found an average of 354 rotifers per cm^2 and 17 species per formation. These were seasonal, with the **monogononts** almost vanishing in winter. The **bdelloids** decreased, but not so dramatically.

The first extensive study of New England, USA, included 31 bogs from Vermont, Massachusetts, and northwestern Connecticut (Błedzki & Ellison 2003). Błedzki and Ellison collected from **interstitial spaces** (pore water), bog pools, and pitcher plants (see below). These three habitats yielded 38 rotifer species among more than 50,000 individuals. These bogs had a rotifer density that ranged 150-51,250 individuals dm^{-3} (Błedzki & Ellison 2002).

The bog ponds had 16 species; the interstitial spaces had 14 (Błedzki & Ellison 2003). The rotifer species richness increased significantly with bog elevation. On the other hand, latitude, longitude, and bog area made no significant difference in richness. The most frequent species was ***Habrotrocha rosa*** (Figure 65), present in pore water of 30 out of 31 bogs, but never in the bog pools. This species comprised 31% of the collected rotifers (Błedzki & Ellison 2002). The other abundant species were ***Lecane pyriformis*** (Figure 153), ***L. lunaris*** (Figure 123), ***Cephalodella gibba*** (Figure 121), and ***Polyarthra vulgaris*** (Figure 154). The sampling methods involved 50 ml plastic centrifuge tubes pressed into the ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) mat (Błedzki & Ellison 2003). These tubes readily filled with water. While this method may have been effective for those rotifers that swam in the pore water, their methodology most likely missed attached species that rarely enter open water, such as ***Collotheca*** (Figure 48) and ***Lecane*** (Sakuma *et al*. 2002).

Edmondson (1940) explored the rotifers in bogs in Wisconsin, USA. Although he found no species to be restricted to ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112), the rotifer ***Collotheca heptabrachiata*** was known only from ***Sphagnum*** in Wisconsin. In his studies, both ***Ptygura pilula*** (Figure 155) and ***P. velata*** (Figure 156) occurred in "enormous numbers" in one ***Sphagnum*** peatland during the latter part of July and all through August.

For more species associated with ***Sphagnum*** or peatlands, see individual families in the following subchapters.

Figure 153. ***Lecane pyriformis***, a common bog species in association with ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

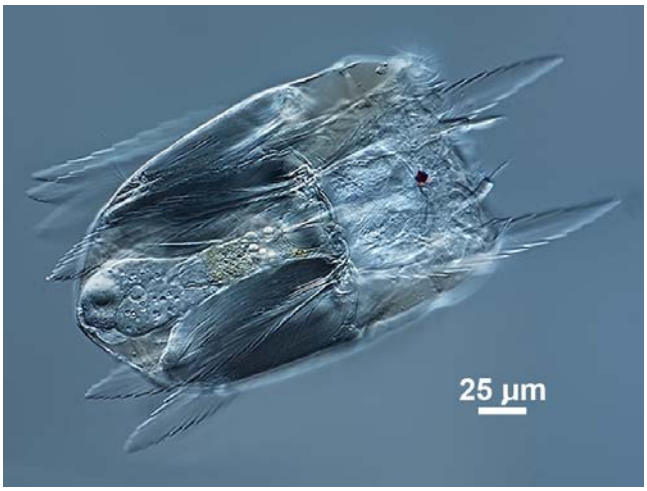

Figure 154. ***Polyarthra vulgaris***, a common bog species in association with ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 155. ***Ptygura pilula***, a species that can reach large numbers on ***Sphagnum***. Photo by Jersabek *et al*. 2003 from Rotifer World Catalog, through Creative Commons.

Figure 156. ***Ptygura velata*** shown here on the macrophyte *Ceratophyllum*, but it can reach large numbers in peatlands. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Abiotic Factors

The hummocks and hollows of bogs and fens present very different moisture and temperature regimes, and this is represented by differences in rotifer species (Bateman & Davis 2007). The summits of the hummocks in a poor (**mesotrophic**) fen (a habitat similar to a bog) in Newfoundland, Canada, house predominately bdelloid rotifers, although these never become desiccated. They found that position on the hummock was important in determining species composition. The **Bdelloidea** were the main rotifers on the tops of the hummocks. The **Monogononta**, on the other hand, increased in number of species and individuals from top to bottom, reaching their greatest number of species in the hollows. Nevertheless, the total numbers of rotifers was greatest at the tops of the hummocks. They determined that desiccation did not occur and that predation was not an important factor in determining distribution.

As the peatland water content decreases, the fauna become less like that of open water. Among peat mosses, the species with the highest percentage of characteristic rotifer species is the **oligotrophic** (low nutrient) ***Sphagnum angustifolium*** (Figure 157) of low moors (Francez & Dévaux 1985). Pejler and Bērziņš (1993a) found most bdelloids need lots of oxygen, commensurate with their limnoterrestrial environment, but some survive in soft bottom sediments.

Figure 157. ***Sphagnum angustifolium***, a commonly dominant peat moss that provides a home for species of ***Habrotrocha***, ***Macrotrachela***, ***Rotaria rotatoria***, and ***Lecane***. Photo by Michael Lüth, with permission.

Acidity

The acidity of the water may play a role in distribution, but it is difficult to determine if it is a direct or indirect effect. Bērziņš and Pejler (1987) found that **oligotrophic** (low nutrient) species occur at a *p*H optimum at or below 7.0, whereas **eutrophic** (rich in nutrients and so supporting a dense population) species are generally at or above this level. The rotifers may be there because of a suitable *p*H and absent elsewhere because the *p*H is too high or too low, or they may be there because they are limited to a particular substrate such as ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112), which is itself limited to that same *p*H range (Edmondson 1940). Edmondson considers the rotifers ***Lecane satyrus*** (Figure 158), ***Notommata falcinella*** (Figure 159), ***Lindia pallida*** (Figure 160), among others, to be limited to ***Sphagnum***. Jersabek *et al*. (2003) also reported ***Notommata falcinella*** from submerged ***Sphagnum*** in Maryland, USA. In these cases, it appears to be the substrate that is important, as these species are not found on other substrates at the same *p*H.

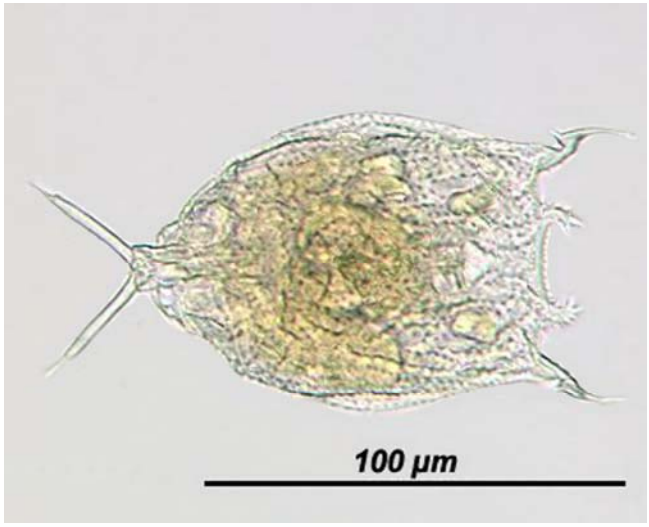

Figure 158. ***Lecane satyrus***, a species that seems to be limited to ***Sphagnum***. Photo by Jersabek *et al*. 2003 from Rotifer World Catalog, through Creative Commons.

Figure 159. ***Notommata falcinella***, a species that seems to be restricted to ***Sphagnum***. Photo by Jersabek *et al*. 2003 from Rotifer World Catalog, through Creative Commons.

Figure 160. ***Lindia pallida***, a species that seems to be limited to ***Sphagnum***. Photo by Christian Jersabek, through Creative Commons.

Lecane lunaris (Figure 123) is tolerant of a broad *p*H range (Pejler & Bērziņš 1993b). This widespread species furthermore occurs in peatlands in both New England, USA (Błedzki & Ellison 2003), and Poland (Bielańska-Grajner *et al*. 2011). ***Habrotrocha angusticollis*** (Figure 4), a characteristic species for peatlands, particularly ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112), generally occurs in a *p*H range of 3.8-6.4 (Warner & Asada 2006). **Bdelloidea** dominate in peatlands. This group is typically dominant in acidified water (Bateman & Davis 1980; Bielańska-Grajner *et al*. 2011), but it has a broad *p*H tolerance range (Bērziņš & Pejler 1987; Bateman & Davis 1980). Their reliance on parthenogenesis makes colonization easier, often evoking the **founder principle** (loss of genetic variation in new population established elsewhere by very small number of individuals from larger population), and may account for this wider range of *p*H tolerance among populations (Bērziņš & Pejler 1987; Ricci 1987).

In the Wisconsin study of Edmondson (1940), ***Ptygura mucicola socialis*** (Figure 161-Figure 162) was found amid a colony of the **Cyanobacterium *Gloeotrichia*** sp. (Figure 163) at the low *p*H of 3.5 in a ***Sphagnum*** peatland. It is interesting that these rotifers are often associated with algae on the mosses, presumably using them as a food source, although it might be other organisms associated with the algae that provide the food.

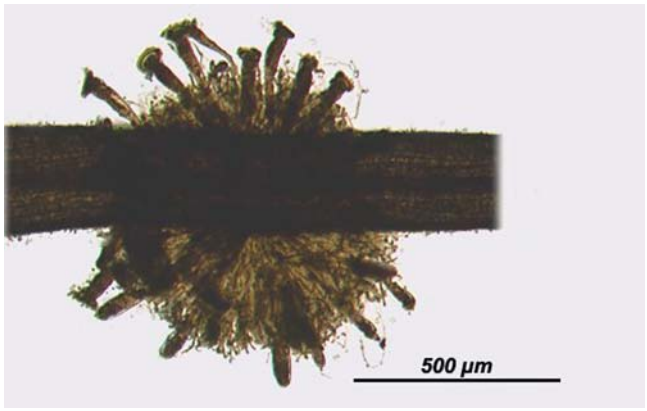

Figure 161. ***Ptygura mucicola***, a species that lives in colonies of ***Gloeotrichia*** amid ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

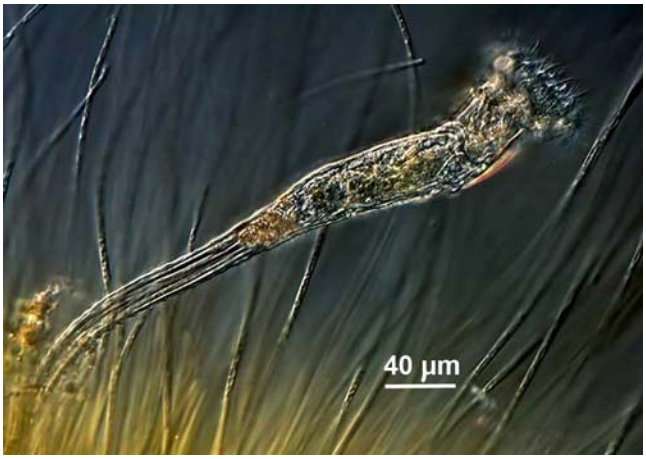

Figure 162. ***Ptygura melicerta*** var. ***melicerta*** with ***Gloeotrichia***. ***Ptygura mucicola***, a moss dweller, is considered by some to be a variety of ***P. melicerta***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

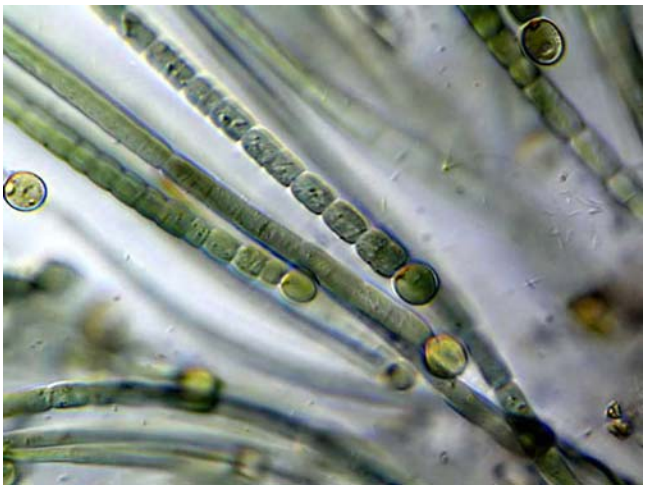

Figure 163. ***Gloeotrichia*** sp. with heterocysts, home for ***Ptygura mucicola socialis*** in peatlands. Photo from <www.diatom.org>, through Creative Commons.

Surface Configuration

Flat, broad surfaces do not seem to be suitable for most sessile rotifers, something to consider when using an artificial substrate. Edmondson (1940) suggested this may relate to their method of feeding. But it could also relate to capillary water.

Sphagnum (Figure 25-Figure 27, Figure 109-Figure 112, Figure 150) leaf morphology seems to play a role in the location of the rotifers. The rotifer ***Collotheca gracilipes*** lived on the concave side of a submerged moss leaf along with the green algae ***Bulbochaete*** (Figure 164) and ***Oedogonium*** (Figure 165) (Edmondson 1940). And ***Collotheca cucullata*** occurred on the concave side of a ***Sphagnum*** leaf (Figure 166) in a different peatland at *p*H 5.6. ***Ptygura velata*** (Figure 156) likewise is found on the concave side of the leaf, suggesting the importance of water held there by capillarity in the interstitial spaces. On ***Sphagnum perichaetiale*** (syn. ***Sphagnum erythrocalyx***; Figure 167-Figure 168), the rolled tip of the leaf provides a similar protection, and Edmondson found more than 200 rotifers residing there!

Figure 164. ***Bulbochaete***, a green alga that shares the ***Sphagnum*** spaces and leaves with the rotifer ***Collotheca gracilipes***. Photo from Proyecto Agua, through Creative Commons.

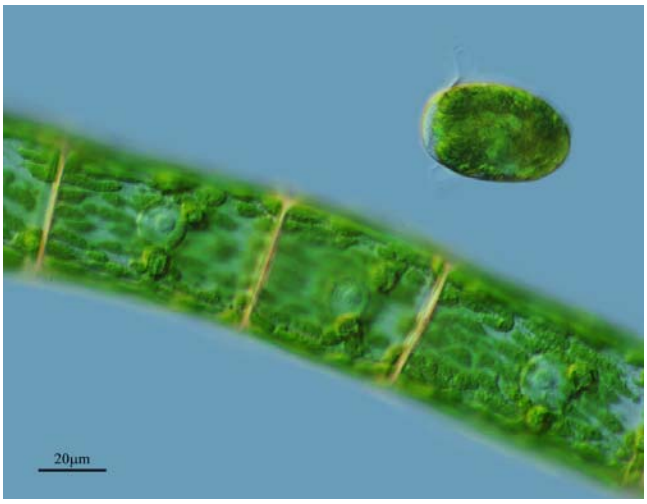

Figure 165. ***Oedogonium***, a green alga that shares the ***Sphagnum*** leaf with the rotifer ***Collotheca gracilipes***. Photo from Proyecto Agua, through Creative Commons.

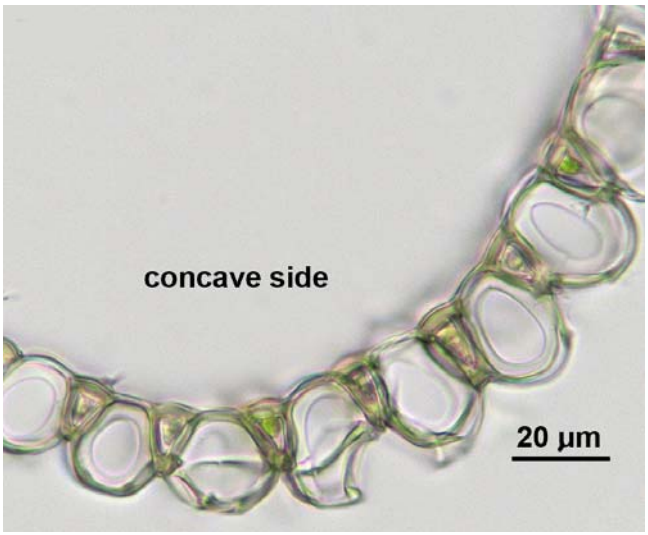

Figure 166. ***Sphagnum subnitens*** leaf cross section showing concave side where some species of ***Collotheca*** live. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

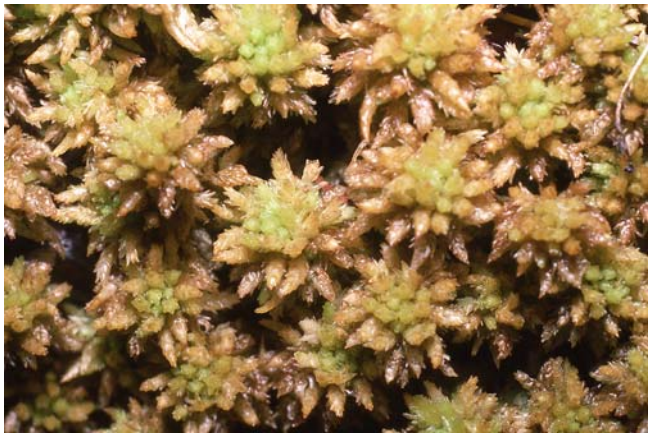

Figure 167. ***Sphagnum perichaetiale***, a species known to house 200 rotifers. Photo by Janice Glime.

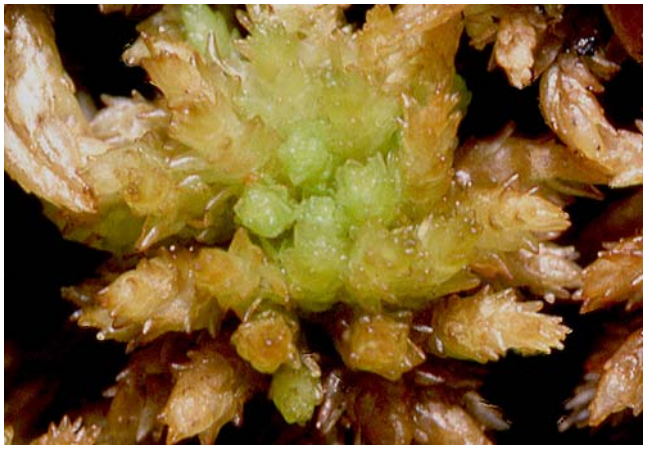

Figure 168. ***Sphagnum perichaetiale***. Note the rolled leaf tip where the rotifers attach. Photo by Janice Glime.

Rotifer and other invertebrate species assemblages change as the peatland develops so that specific associations can be described for each stage (Francez & Dévaux 1985). Likewise, communities differ with position in the hummock-hollow complex (Bateman & Davis 1980). The oligotrophic ***Sphagnum angustifolium*** (Figure 157), a species typical of mineral-rich sites (Hale 2012), seems to have one of the most unique and consistent assemblages of rotifer taxa (Francez & Dévaux 1985). Water content of the moss environment is the major factor determining the fauna, with the wettest mosses having communities most similar to those of the water. This is further supported by changes in protozoa species arising as a result of drainage (Warner & Chmielewski 1992).

Like the **Protozoa** (**Rhizopoda**), rotifers have both horizontal and vertical distribution patterns among the ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) (Meisterfeld 1977) and this may account for some variation in the distribution patterns of animals that prey upon them. But this vertical zonation also reflects the food available to the microfauna (Strüder-Kypke 1999). Differences in light and nutrients result in a denser colonization in the upper part where photosynthetic cryptomonads can provide food and mobile ciliate protozoa can take advantage of these food sources. Lower in the mat, but within the upper 30 cm, sessile ciliates and heterotrophic flagellates predominate. Moisture seems to be the dominant

determiner of species assemblages, with *p*H being secondary (Charman & Warner 1992). As Bērziņš and Pejler (1987) indicated, *p*H may not in itself be a strong determinant of rotifer assemblages in peatlands, but rather may create an environment that supports oligotrophy or eutrophy as determining factors.

Pitcher Plants

The pitcher plants, especially ***Sarracenia purpurea*** (Figure 169), are interesting habitats for rotifers. These plants require the moist habitat of peatlands to become established and grow, growing upward as the moss grows upward. Hence, rotifers that live in the water of their pitcher-like leaves are indirectly dependent on the peat mosses (***Sphagnum***).

Figure 169. ***Sarracenia purpurea*** with water in leaves, home for several rotifer species. Photo by David Midgley, through Creative Commons.

Rotifers in the pitcher plant leaves are important in the cycling of nitrogen and phosphorus (Błedzki & Ellison 1998, 2002). By eating the detritus, they convert these two nutrients into forms usable by the pitcher plants. In their study of Massachusetts, USA, pitcher plants (***Sarracenia purpurea***; Figure 169), Błedzki and Ellison (1998) found that ***Habrotrocha rosa*** (Figure 65) could provide a pitcher plant leaf with 8.8-43 mg of N and 18.2-88 mg of P in a single growing season, far exceeding that supplied by insects and rainfall. The rotifers accomplish this by having populations of ca. 400 individuals per leaf pitcher. These rotifers can excrete ~5.2 µg NO_3-N, ~3.91 µg NH_4-N, and ~18.4 µg PO_4-P per day into a single leaf.

Błedzki and Ellison (2003) compared the rotifers in the pitcher plant leaves [***Sarracenia purpurea*** (Figure 169)] to those of pore water and bog ponds. These three habitats had low species similarity (Jaccard indices of similarity <0.25). The most common species was ***Habrotrocha rosa*** (Figure 65). This species had its highest production at *p*H 4 in culture (Błedzki & Ellison 1998). The pitcher plant water had a *p*H range of 3.5-6.3, dropping from the higher *p*H as the dying trapped insects decompose (Fish & Hall 1978). The ***H. rosa*** is subject to severe predation by the **Diptera** larvae that also live in the pitchers, including several mosquito species (Błedzki & Ellison 1998). Numbers of ***H. rosa*** are inversely related to numbers of these larvae.

Lecane lunaris (Figure 123) and ***Notholca acuminata*** (Figure 170) occurred in water-filled leaves in a Vermont bog. In that same bog ***Cephalodella anebodica*** occurred in a water-filled leaf (Błedzki & Ellison 2003).

Figure 170. ***Notholca acuminata***, a species that lives in water-filled leaves of the northern pitcher plant in bogs. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Aquatic Bryophytes

Most of the studies on rotifers of **lentic** bryophytes are in peatlands. Several studies on littoral species have also been described above because they involved peat mosses. However, there have been a number of studies on the rotifers of stream bryophytes.

Drazina *et al*. (2011) studied both lakes and streams and found that rotifers were the dominant group of meiofauna among aquatic bryophytes, with 52 species among bryophytes in Europe (National Park Plitvice Lakes). In fast water, they averaged 219 individuals per cm^3. Several researchers have found the **Bdelloidea** to be dominant among rotifers associated with submerged mosses (Badcock 1949; Madaliński 1961; Donner 1972).

Streams

In his study of rotifers in German streams, Donner (1964) found that the rotifers were the most numerous as inhabitants of mosses. Fontaneto *et al*. (2005) analyzed an 80-m stretch of a stream in NW Italy to describe the **meta-community** (set of interacting communities linked by dispersal of multiple, potentially interacting species) structure of rotifers that colonized mosses. Mosses were absent in the riffles, but the shoreline was almost continuously covered with submerged mosses (***Brachythecium*** sp. – Figure 171). The same species of moss also occurred in the pools. The researchers concluded that rotifers in pools most likely arrived from other pools by travelling with their moss substrate, whereas within the pool they could move about by themselves. Different movement capabilities of the species within pools could account for small scale differences in communities. The species occupying these habitats in this stream segment were ***Adineta vaga minor*** (Figure 12), ***Embata hamata***, ***Habrotrocha bidens*** (Figure 172), ***H. constricta*** (Figure 69), ***H. gracilis***, ***H. pulchra***, ***Macrotrachela quadricornifera*** (Figure 62-Figure 64), ***Philodina acuticomis odiosa***, ***P. flaviceps*** (Figure 173), ***P. plena*** (Figure 135-Figure 136), ***P. rugosa*** (Figure 174), ***P. vorax*** (Figure 175), ***Pleuretra brycei*** (Figure 61, Figure 176), and ***Rotaria rotatoria*** (Figure 17). There was only a slight trend of differences in species composition from upstream to downstream (Figure 177).

Figure 171. ***Brachythecium rivulare***, potential streamside and in-stream habitat of several rotifer species. Photo by David T. Holyoak, with permission.

Figure 174. ***Philodina rugosa*** from epiphytic moss, a rotifer that also occurs on streamside mosses, especially ***Brachythecium*** sp. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 172. ***Habrotrocha bidens*** from moss on ground; a species that also occurs on mosses in streams. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 175. ***Philodina vorax***, a species that lives on epiphytic mosses, ***Sphagnum***, and streambank mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 173. ***Philodina flaviceps*** from detritus, a stream bryophyte dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

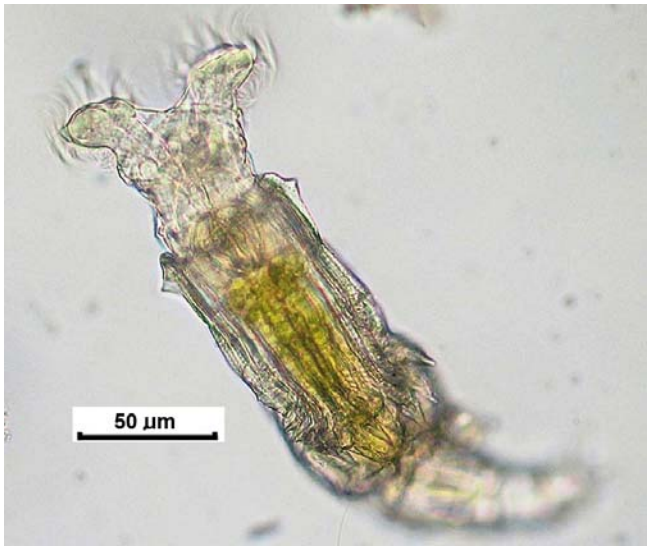

Figure 176. ***Pleuretra*** *cf* ***brycei***, a species that lives among ***Brachythecium***. Photo by Michel Verolet, with permission

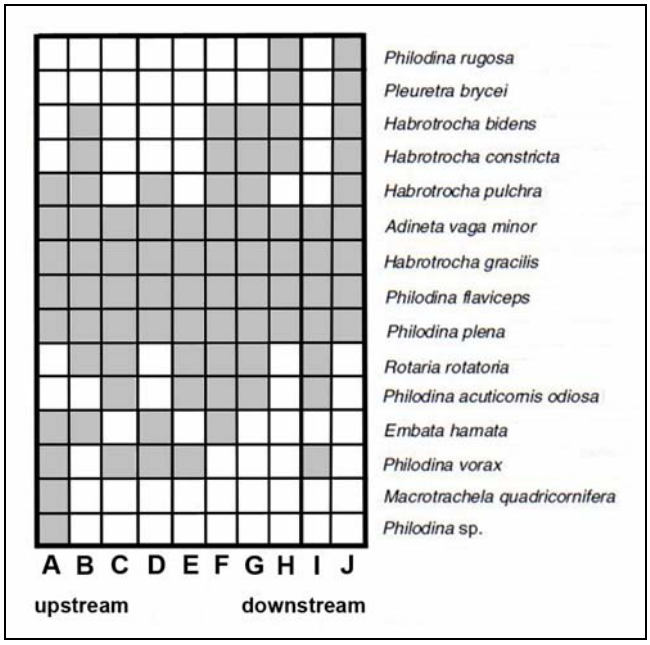

Figure 177. Distribution of moss-dwelling rotifers in a stretch of an Italian stream, arranged from upstream to downstream. Based on Fontaneto *et al*. 2005.

Suren (1992) suggested that the high densities of meiofaunal communities, including rotifers, associated with the bryophytes in New Zealand alpine streams may result from the food value of the large periphyton component and the shelter from fast water currents. In the stream bed, these organisms move into interstitial spaces in the substrate to avoid fast flow. Among the bryophytes, where they occur in high densities, they live among the stems and leaf axils where they are less exposed.

Bryophytes in streams provide a safe harbor within a tumultuous habitat and a substrate for food organisms (Suren 1992). Although the stream has an ameliorated temperature compared to terrestrial systems, its constantly changing water levels and flow rates make it a challenging environment for small organisms, especially attached species. Bryophytes offer a place where flow rate reaches virtually zero at the base, providing a range of flow rates. Furthermore, current can affect where rotifers occur within the moss mat, with some species remaining in lower layers where the current is reduced to zero. Hence, it appears that flow rate has little effect on bryophyte fauna in different parts of mountain streams (Madaliński 1961). However, this ignores the fact that bryophytes themselves may be limited by current.

Linhart *et al*. (2002b) considered the stream bryophyte-rotifer association to result from the exposure of the stream bryophytes to water current (Wulfhorst 1994). Historically, the bryophytes have been considered to be refuge sites from flow (Madaliński 1961; Elliot 1967; Gurtz & Wallace 1984; Suren 1992) due to the reduction of flow within the moss mat (Gregg & Rose 1982; Madsen & Warncke 1983; Sand-Jensen & Mebus 1996). But for small invertebrates, this argument is questionable because the flow rates at the surface layer of gravel or bedrock sediments are similar to those within the moss mats (Williams & Hynes 1974; Gregg & Rose 1982; Angradi & Hood 1998). On the other hand, the **Monogononta** do seem to be affected by the flow within the mats of ***Fontinalis antipyretica*** (Figure 34). Could it be ease of food capture rather than protection from flow that determines where they are able to live? Or refuge from predators?

Some rotifers are able to withstand the flow of a stream, whereas others in streams hide among the bryophytes or other protected areas. Linhart *et al*. (2002b) collected data to compare the **Bdelloidea** and **Monogononta** relative to flow velocity amid the moss ***Fontinalis antipyretica*** (Figure 34) and on the surrounding mineral substrate. The **Monogononta** were unable to withstand the high flow velocities, whereas the **Bdelloidea** did not seem to have a preference. Therefore, the ratio of **Bdelloidea** to **Monogononta** had a strong positive relationship to the flow velocity within the moss with the ratio of **Bdelloidea** to **Monogononta** reaching as high as 13:1 in high flow areas in these streams. A similar relationship did not exist on the mineral substrate. Linhart and coworkers concluded that this does not support the concept of the mosses serving as a refugium from flow.

Bryophytes also serve as traps for drifting rotifers. Madaliński (1961) found that bryophytes in streams that flow out of lakes have a richer fauna than those in torrents arising from springs. Hence, numbers can vary widely between streams, perhaps due to available food and flow rate, as well as differences in sources for new or replacement fauna. Rotifers on the moss ***Fontinalis antipyretica*** (Figure 34) reached over 100,000 per mL in one stream in the Czech Republic and over 400,000 per mL in another (Vlčková *et al*. 2002).

Suren (1992) investigated the role of shade in determining the meiofaunal communities of bryophytes in New Zealand alpine streams. He found that the unshaded site had higher meiofaunal densities than did the shaded site and that bryophytes had higher faunal densities than did gravel habitats. Furthermore, the meiofaunal communities differed between bryophytes and gravel. He suggested that food value within the bryophyte habitat may account for the higher densities of rotifers and other meiofauna there.

In a Wisconsin, USA, study, ***Ptygura linguata*** occurred only on the bladderwort (*Utricularia* sp.; Figure 38) and the brook moss ***Fontinalis*** sp. (Figure 34) (Edmondson 1940). ***Ptygura cristata*** (Figure 178), a species known previously only from Australia, likewise was found on ***Fontinalis*** in the inlet to a Wisconsin lake! Molecular studies may tell us that these long-distance variants are actually different species, or at least microspecies. Or did some limnologist wear the same boots in both places?

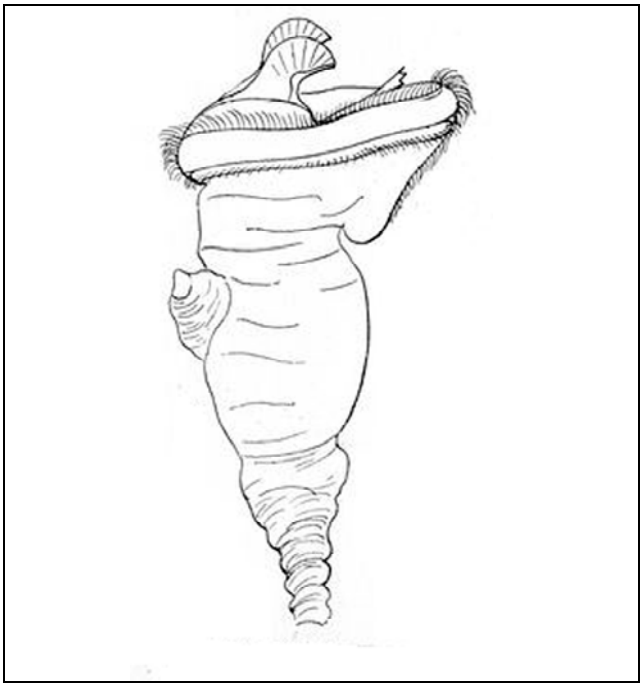

Figure 178. ***Ptygura cristata***, a species known from ***Fontinalis***. Drawing by Murray (1913) from Rotifer World Catalog, through Creative Commons.

Waterfalls

Savatenalinton and Segers (2008) examined the rotifers among the wet mosses of a waterfall in Thailand. Among these, they found the new species ***Lecane martensi*** (Figure 179). They located twelve species in their single day of collection, December 2004. ***Lepadella minuta*** and ***Lecane agilis*** (Figure 180-Figure 181) were new to Thailand. The other species were ***Brachionus angularis*** (Figure 182-Figure 183), ***B. forficula*** (Figure 184), ***Colurella adriatica*** (Figure 3), ***Keratella cochlearis*** (Figure 185), ***K. tropica*** (Figure 186), ***Lecane arcuata***, ***L. lunaris*** (Figure 123), ***L. paxiana***, and ***Trichocerca pusilla*** (Figure 187) among the waterfall mosses.

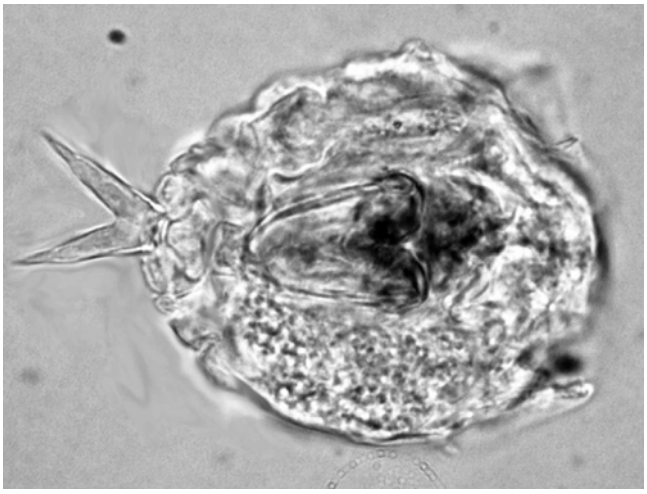

Figure 179. ***Lecane martensi***, a species that was discovered among mosses in a waterfall. Photo by Savatenalinton & Segers 2008, through Creative Commons.

Figure 180. ***Lecane agilis*** from submerged ***Sphagnum***, a rotifer that also occurs among mosses in a waterfall. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 181. ***Lecane agilis*** contracted. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 182. ***Brachionus angularis***, a planktonic species that can occur in waterfalls, perhaps trapped by the mosses of the waterfall. Photo by Michael Plewka <www.plingfactory.de>, with permission.

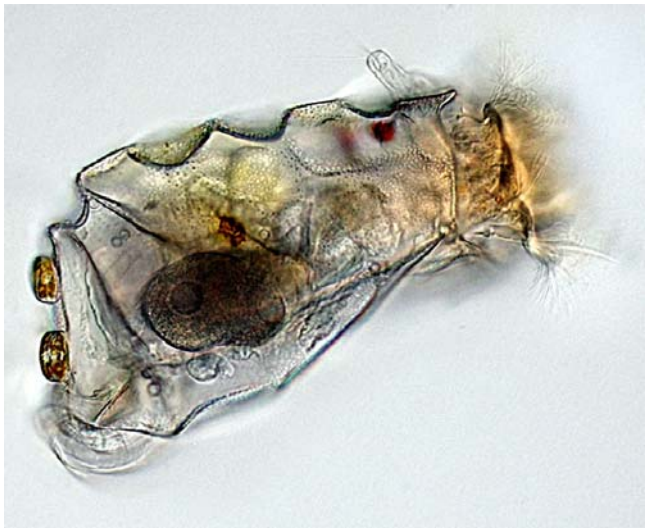

Figure 183. ***Brachionus angularis*** lateral view showing its armored lorica. This is a planktonic species that can occur in waterfalls. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 184. ***Brachionus forficula***, a planktonic species known from mosses in waterfalls where they may have been trapped by the mosses. Photo by Jersabek *et al.* 2003, with permission.

Figure 185. ***Keratella cochlearis*** with two eggs; this planktonic species can occur among mosses in waterfalls. Photo by Michael Plewka <www.plingfactory.de>, with permission.

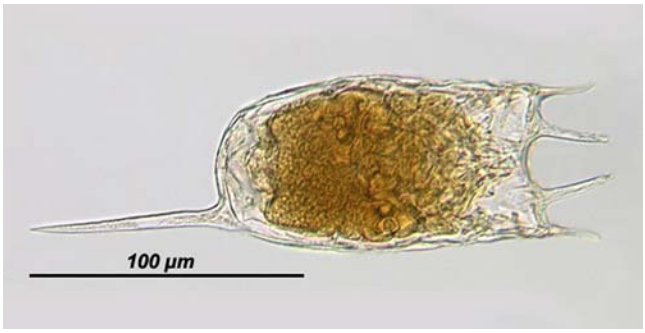

Figure 186. ***Keratella tropica***, a planktonic species that can occur among mosses in waterfalls. Photo by Jersabek *et al.* 2003, with permission.

Figure 187. ***Trichocerca pusilla***, a planktonic species that can occur among waterfall mosses. Photo by Jersabek *et al*. 2003, with permission.

Krakatau

Krakatau is a volcanic island west of Java and south of Sumatra. Heinis (1928) examined the moss fauna of the island. Rotifers were identified on the moss ***Philonotis*** sp. (Figure 30). Heinis found ***Rotaria montana***, ***Habrotrocha angusticollis*** (Figure 188), ***Macrotrachela ehrenbergi*** (Figure 189), ***Macrotrachela papillosa*** (Figure 190), and ***Adineta gracilis*** (Figure 191).

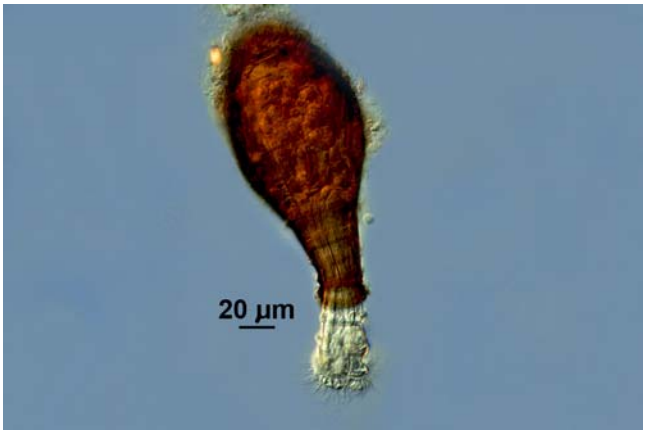

Figure 188. ***Habrotrocha angusticollis***, a moss dweller. Photo by Proyecto Agua, through Creative Commons.

Figure 189. ***Macrotrachela ehrenbergii***, a moss resident on Krakatau. Photo by Jersabek *et al* 2003, with permission.

Figure 190. ***Macrotrachela papillosa***, a moss resident on Krakatau. Photo by Michael Plewka <www.plingfactory.de>, with permission.

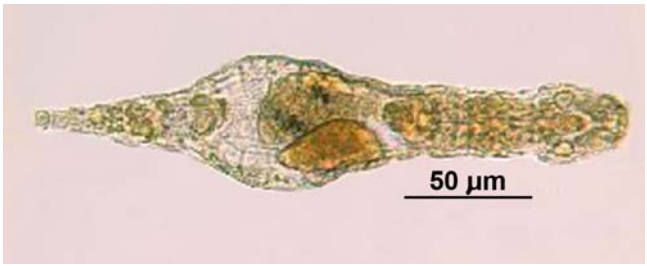

Figure 191. ***Adineta gracilis***, a moss resident on Krakatau. Photo by Jersabek *et al*. 2003, with permission.

Seasons

In Oregon, USA, densities of rotifers did not vary by season in the moss ***Eurhynchium oreganum*** (Figure 36), a tree trunk and log dweller, whereas those of nematodes, tardigrades, mites, and some annelids did (Merrifield & Ingham 1998). They suggested that the low numbers of rotifers in moss samples may be due to the use of the Baermann funnel for sampling. This technique is not suitable for immobile organisms like rotifers, as indicated by their comparison with subsequent squeezings and agitation of the moss.

Periphytic rotifers living on non-bryophytic macrophytes must find a way to survive the winter season in parts of the world where these macrophytes disappear as winter approaches. On the other hand, life is possible on bryophytes because they are present year-round. There are insufficient detailed studies to make any generalizations about differences in life cycles of bryophyte dwellers vs periphyton on other macrophytes and algae.

Bielańska-Grajner *et al.* (2011) assessed the numbers (density) of rotifers in spring, summer, and autumn in peatland types in eastern Poland. They found considerable differences among sites. For example, in one raised bog (DB1) the greatest density of rotifer individuals was in summer, whereas in another (DB2), the greatest density was in autumn (Figure 192).

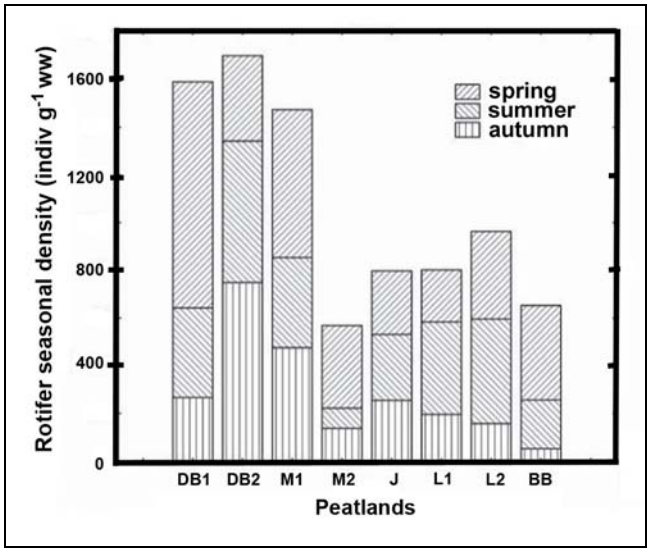

Figure 192. Seasonal changes in moss-dwelling rotifers from eight peatlands in eastern Poland. DB1, DB2, & M1 = raised bogs; M1 & J = poor fens; L1 & L2 = intermediate fen; BB = rich fen. Modified from Bielańska-Grajner *et al.* 2011.

Bateman and Davis (1980) examined the seasonal differences among rotifers in a hummock-hollow complex in a poor fen in Newfoundland, Canada. The **Monogononta** all but disappeared in winter. **Bdelloidea** decreased but still maintained relatively good numbers.

Ricci *et al.* (1989) found no seasonal replacement of clones of ***Macrotrachela quadricornifera*** (Figure 62-Figure 64) from a terrestrial moss in northern Italy. Likewise, the isozyme variant composition was unaffected by temperature changes. Instead, relative humidity seemed to regulate the number of isozyme morphs.

Danger amidst the Bryophytes

The fungi ***Lecophagus longispora*** (Figure 194-Figure 195) and ***L. musicola*** (Figure 196-Figure 199) use adhesive pegs that attract rotifers (George Barron, pers. comm. 25 January 2010). But the rotifers are lured to the fungus, only to be attacked themselves. Once the rotifers are attached, the pegs adhere, using lectin/carbohydrate bonding, and the fungus penetrates the rotifer, ultimately parasitizing it.

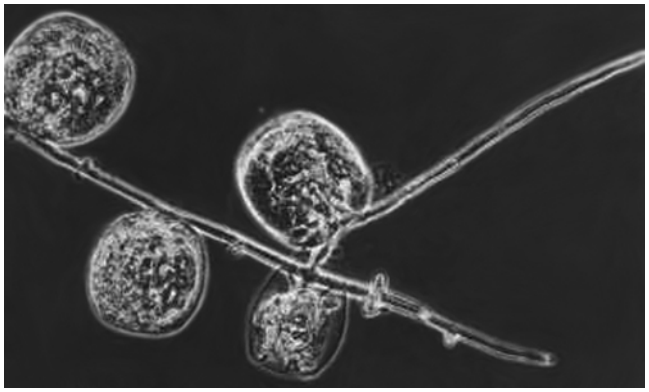

Figure 193. ***Lecophagus longispora*** infecting four rotifers. Photo by George Barron, with permission.

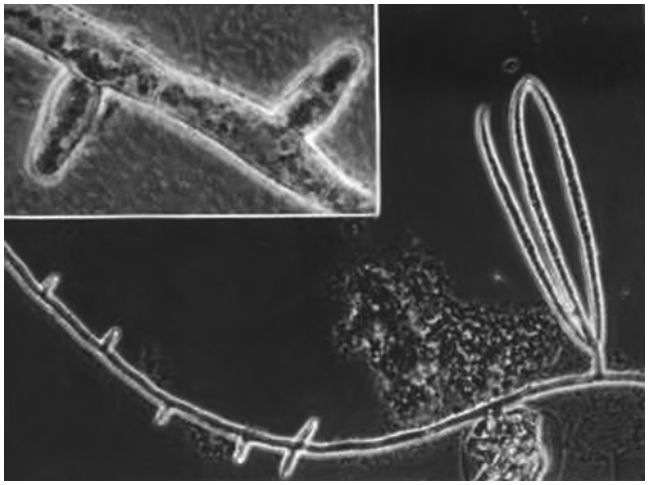

Figure 194. ***Lecophagus longispora***, fungus that traps **tardigrades** and **rotifers** and may be a threat in mosses. Lower image is hypha of fungus with cluster of conidia and adhesive pegs. Inset shows adhesive pegs. Photos by George Barron, with permission.

Figure 195. ***Lecophagus longispora*** infecting rotifers and showing an elongate branch with terminal conidiogenous cell bearing a cluster of developing conidia. (X450). Photo by George Barron, with permission.

Figure 196. ***Lecophagus muscicola*** that has captured two rotifers and two adhesive pegs. Photo by George Barron, with permission.

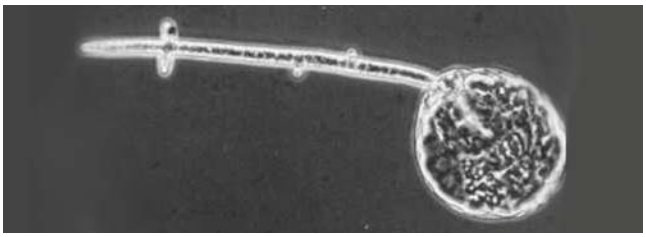

Figure 197. ***Lecophagus longispora*** infecting a rotifer; hypha shows adhering pegs. Such infections are also known for tardigrades. Photo by George Barron, with permission.

Figure 198. **Rotifer** with hyphae of ***Lecophagus muscicola*** inside. Photo by George Barron, with permission.

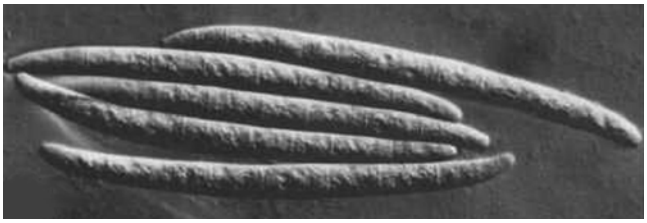

Figure 199. Conidia (X600) of ***Lecophagus muscicola***. Photo by George Barron, with permission.

Another fungus dangerous to some bryophyte-dwelling species is ***Zoophagus insidians*** (Figure 200). Aquatic rotifers attempt to feed on its branch tips, but the adhesive tips bond (possibly lectin/carbohydrate bonding) to the rotifer mouth and inside the oral cavity (Barron 2012). The tip grows there and assimilative hyphae penetrate the body cavity of the rotifer, releasing digestive enzymes that ultimately digest the rotifer from the inside. This attack on the rotifer mouth permits this fungal species to select loricate rotifers (Prowse 1954).

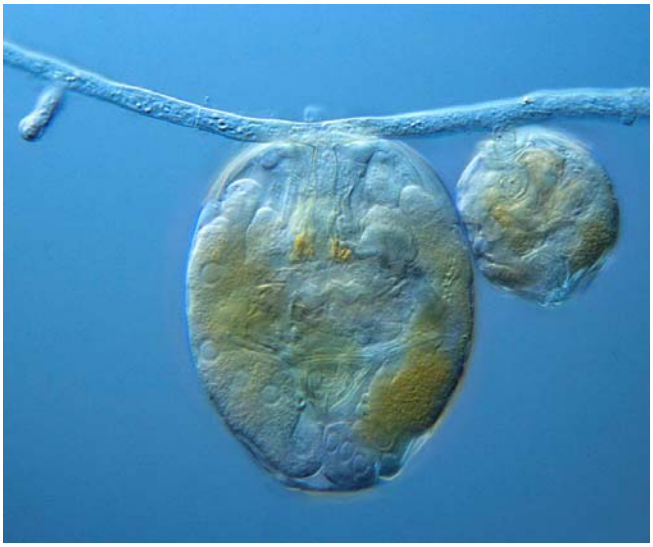

Figure 200. ***Philodina roseola***, sometimes a bryophyte dweller, caught by the fungus ***Zoophagus insidians***. Photo by Wim van Egmond, with permission.

Whisler and Travland (1974) refer to the fungus as "wily" because of its sneak attack on the rotifers. When the **adhesive peg** of the fungus contacts the rotifer (Figure 201), the fungus is stimulated to release a glue from its trap. The traps are branches that are packed with vesicles containing an electron-dense glue, and upon contact the two layers of the fungal wall separate and the vesicles fuse with the cell membrane. The cilia of the rotifer are stuck to the fungal trap by this glue. Growth of the fungal **haustorium** [slender projection from fungal thread (hypha) of parasitic fungus that enables it to penetrate host] proceeds rapidly, digesting the rotifer within a few hours.

Zoophagus (Figure 200-Figure 201) apparently does not produce zoospores, with those few zoospores reported apparently belonging to contaminants (Dick 1990; Powell *et al*. 1990). Instead it reproduces by **fusiform conidiospores** (asexual fungal spores; see Figure 199), and it has been placed in the **Zygomycetes** (Powell *et al*. 1990) due to its reproductive differences. These conidiospores are sometimes referred to as gemmae.

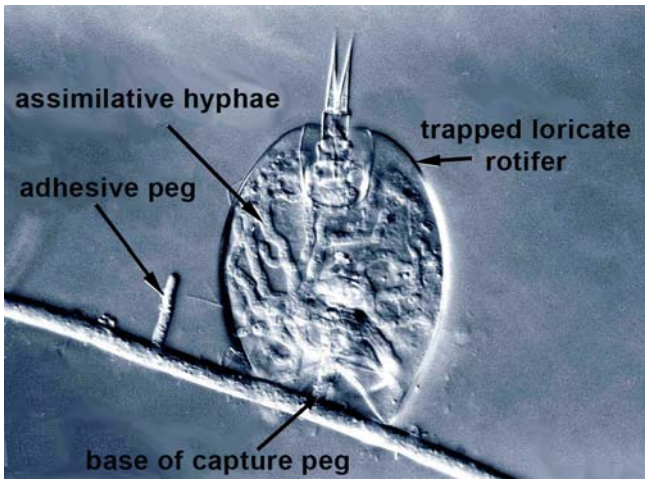

Figure 201. The rotifer ***Lepadella*** caught by the fungus ***Zoophagus insidians***. Photo by Wim van Egmond, with permission.

Ozone Hole and Pollution Dangers?

A number of researchers have chosen the microfauna of terrestrial bryophytes as indicators of air pollution effects (Steiner 1994a, b). Meyer *et al*. (2010) compared the microfauna on transplanted mosses (***Pseudoscleropodium purum*** – Figure 202) in rural, urban, and industrial areas of France. The mosses were placed in jars in open shelters that prevented contamination carried by rain. They found that the biomasses for microalgae, bacteria, rotifers, and testate amoebae were greatest in the rural area. However, at the end of the study there were no significant differences for nematodes or rotifers. Although the mosses absorbed Al, Cr, Cu, Fe, Pb, Sr, and Zn, only Cu and Pb had a significant effect on the biomass of rotifers.

Figure 202. ***Pseudoscleropodium purum***, the moss used in transplant experiments to assess effects of pollution on microfauna, including rotifers. Photo by Hermann Schachner, through Creative Commons.

Responses of functional groups to air pollution is often ignored in favor of simpler studies on single species. Nguyen-Viet *et al*. (2007) examined the effects of

simulated lead pollution by experimenting in controlled laboratory conditions on the microbial communities associated with ***Sphagnum fallax*** (Figure 203). But in this case, the biomass of rotifers was not significantly affected by lead addition. However, the biomass decreased in all treatments (including controls) during the experiment (20 weeks). On the other hand, biomasses of bacteria, microalgae, testate amoebae, and ciliates were dramatically and significantly decreased in both Pb addition treatments (625 & 2,500 μg L^{-1} of Pb^{2+}) compared to the controls. This decrease in microbial food source unbalanced the microcosms, causing significant differences in microfaunal community structure. Trophic links were changed because the testate amoebae and ciliates had strongly reduced biomass, whereas the bacteria had a relatively stable contribution to the microbial biomass. These changes affected the rotifer biomass through the food web.

Figure 203. ***Sphagnum fallax***, a species that absorbs lead but houses rotifers that are not harmed directly by lead additions. Photo by Christian Fischer, through Creative Commons.

Although there seemed to be no differences in growth of ***Sphagnum magellanicum*** (Figure 111-Figure 112) under the ambient UV-B radiation in the ozone hole and reduced UV-B under filters in Tierra del Fuego, southern Argentina, the rotifer fauna of this moss seems to prefer the greater UV-B under ambient conditions (Searles *et al.* 1999). The rotifers were actually more numerous under the ambient conditions of UV-B in the ozone hole than under the reduced UV-B created by the filters.

Summary

Rotifers (**Rotifera**) can enter a state of **cryptobiosis** (dormant state) and survive desiccation right along with bryophytes, also getting dispersed with the fragments of mosses. The **bdelloid rotifers** are the most common among bryophytes and are **parthenogenetic**, hence are all female. In the **Monogononta**, unfertilized eggs develop into a male. In unfavorable conditions, monogononts form thick-walled resting "eggs" (really zygotes and embryos). They depend on water not only for hydration, but for locomotion and directing food to the mouth using cilia in the corona.

The dehydrated state (**anhydrobiosis**) helps to protect them from UV light, high temperatures, cold temperatures, and fungal infection. When confronted with drying conditions, bdelloid rotifers form a compact structure known as a **tun**. Slow drying produces the greatest survival and production of the disaccharide sugar **trehalose** maintains membrane integrity. Activity generally resumes within one hour of rehydration, but they need about a day of active state before they go into another dehydrated state. The record survival for an egg appears to be nine years, whereas an adult of ***Macrotrachela quadricornifera*** mya have survived dry on a moss on a herbarium sheet for 59 years. Mucus appears to deter predation, but it could also protect against or slow dehydration.

Bryophyte-dwelling rotifers tend to be smaller than those in open water. Terrestrial bryophytes provide slow but unpredictable and frequent drying. Adaptations to bryophyte living include small size, ability to attach or crawl in small spaces, parthenogenesis, dormancy by egg and tun, detritus as a food source, and structures such as tubes, mucus, and loricas for protection. Bryophytes contribute cover, water film, slow drying, and periphytic and detrital food sources.

Tardigrades may be significant predators, but rotifers such as ***Ptygura velata*** construct a tube from their own feces for protection. Some rotifers in epiphytic sites live in lobules of leafy liverwort leaves (***Frullania***, ***Microlejeunea***, ***Colura***, ***Pleurozia purpurea***, ***Acrolejeunea***) where desiccation is less frequent and there is a modicum of protection.

Rotifers are common on bryophytes. In the Antarctic the terrestrial species are largely restricted to mosses. Peatland habitats have the highest diversity among the bryophyte habitats, with the **Bdelloidea** predominating. ***Habrotrocha roeperi*** and ***Habrotrocha reclusa*** seem to be restricted to the **retort** cells of some ***Sphagnum*** species. Bog and fen rotifers are mostly widespread species with wide habitat tolerances. A few are restricted to bryophytes in bogs. In ***Sphagnum*** peatlands, acidity seems to discourage many species, with more species and greater abundance in fens. Rotifers in pitcher plants contribute to decomposition and nutrient cycling in the leaves, especially for nitrogen and phosphorus. In aquatic habitats, those occupying ***Fontinalis antipyretica*** can reach densities 151 times that of adjacent mineral substrate. Hundreds of thousands of rotifers can exist in 100 mL of this moss. Unique species can occur among bryophytes in waterfalls. Fine particulate matter trapped by mosses can serve as food. In the Antarctic, many **rotifers** prefer the middle stem zone where epiphytic algae are most abundant.

Acknowledgments

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CHAPTER 4-6

INVERTEBRATES: ROTIFER TAXA – BDELLOIDEA

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CHAPTER 4-6

INVERTEBRATES: ROTIFER TAXA – BDELLOIDEA

Figure 1. **Rotifer** on a ***Sphagnum*** leaf. Photo by Marek Miś at <http://www.mismicrophoto.com/>, with permission.

Taxa on Bryophytes

With about 2200 species, rotifers are a group with a wide range of aquatic, marine, and **limnoterrestrial** (requiring watery matrix in terrestrial habitats, but also subject to desiccation) species, permitting us to analyze habitat relations. This analysis is limited with respect to bryophytes because few studies describe those in the bryophyte habitat, and those that do typically simply indicate "moss." This is demonstrated by the delineation of rotifer habitats in the comprehensive study on the relationship of rotifers to habitat, using only **macrophytes** (housing periphytic rotifers), open water (with planktonic forms), **minerogenous** sediments (with **psammon** and **hyporheos**), **organogenous** sediments, and other organisms (*i.e.* parasites and epizoans) (Pejler 1995). Bryophytes are not given separate attention. Pejler (1995) pointed out that rotifers are mostly cosmopolitan, hence suggesting that ecological barriers are more important in determining their distribution. Nevertheless, Pejler considers rotifers to lack strong restrictions of habitat. Extreme environments do support few species, but can support large numbers of individuals, typically primary consumers. On the other hand, when rotifer species are numerous the differences in their morphology are so great that patterns of adaptations are difficult to define.

Pejler (1995) considered that adaptations to chemical and physical environments may develop rapidly in geologic time, whereas those changes that are more fundamental occur over a longer time period. Differences in structure of **trophi** (tiny, calcified, jaw-like structures in the pharynx) seem to facilitate differences in food type and these differences are most apparent among **Bdelloidea**, but even in extreme environments, differences don't seem to

correlate with habitat and closest relatives seem to occur in "normal" habitats.

Although many taxa can be found on bryophytes, few have been studied relative to the role of the bryophytes, and finding the existing studies among published literature can be a bit hit or miss. I am unable to summarize adaptations except to suggest that being small (which applies to the entire phylum) and being able to attach may be advantages. Movement among bryophytes is mostly inchworm style rather than being accomplished by the cilia. The trophi need to be adapted to the available food, with detritus being abundant among the bryophytes. The species included here most likely provide a very incomplete list, and the ecological information included with the images is likewise very incomplete. Furthermore, the distribution of species is poorly known, although many are considered cosmopolitan. Due to these limitations, these chapters are organized first by classification rather than ecology.

CLASS BDELLOIDEA

The name **Bdelloidea** (the "B" is silent) refers to the method of movement and means "leech-like." The **Bdelloidea** have a **corona** that is split into two, creating two "wheels" to direct food to the mouth (Figure 1). It is the smaller in number of species of the two classes and has only four families (Melone & Ricci 1995), all of which are represented on bryophytes. In fact, Donner (1956, 1975) reported that 95% of the rotifers living on terrestrial mosses, soil, and lichens are in the **Bdelloidea**. The most species on soil and moss are in the genus ***Habrotrocha***, (Figure 14-Figure 25) whereas 30% of the overall species in **Bdelloidea** are in ***Macrotrachela***.

This group is comprised of ~460 species, only one of which Segers (2008) considered to be marine, but Fontaneto (2006) reported several strictly marine species. They are distinguished from the **Monogononta** by the presence of two ovaries (**Monogononta** have only one). This class of rotifers is comprised entirely of females and is exclusively **parthenogenetic** (having offspring from unfertilized eggs), negating the need for males to complete the life cycle.

The bdelloid rotifers are characterized by an elongated body with a telescopically retractable foot, single dorsal antenna, and apical rostrum (Melone & Ricci 1995). The ciliatory apparatus is used for both locomotion and collecting food, making it adaptive based on the animal's life style. The moss dwellers typically have a narrower wheel apparatus, a more rigid cuticle that has cuticular spines or knobs, and smaller toes (Donner 1953, 1956).

The **bdelloids** are known from freshwater and soil, and are common on **bryophytes**. They have a retractable head with a well-developed **corona** that is divided into two parts. Movement includes both swimming and crawling, but they seldom venture into the plankton (Fontaneto & Ricci 2004). Crawling is similar to the movement of inchworms, or some leeches, using the toes and head while arching the mid body, then elongating again forward.

Burger (1948) suggested three regulatory mechanisms to determine the suitability of mosses for the **Bdelloidea**:

1. The age of the moss at the site affects the time during which colonization has been possible, and that in turn affects the number of species present.
2. Water presence and resultant osmotic potential affect activity of the rotifers.
3. Availability of suitable food is important. This includes both size of potential food and food quality (Ricci 1984).

Kutikova (2003) considered their morphological structures, obligate parthenogenesis, and **anhydrobiosis** to be important adaptations to living among mosses and other terrestrial substrata that have sharp environmental fluctuations. Most of the **bdelloids** survive unfavorable periods, particularly drought, by entering a type of dormancy known as **anhydrobiosis,** *i.e.* dry dormancy (Gilbert 1974; Ricci 1987, 1998, 2001). All the bdelloids that live among bryophytes are able to secrete mucus as they dry (Figure 2) and create a case-like structure with adhering particles. It is their ability to withstand drying, along with their parthenogenetic reproduction (Ricci 1992), that fosters their cosmopolitan distribution (Fontaneto *et al.* 2006, 2007, 2008). And this ability of anhydrobiosis may also be the reason that Horkan (1981), in his report on Irish rotifers, found only this group on mosses other than those in bogs. Furthermore, no **Bdelloidea** were present in the Irish bogs, on bog moss, or in bog pools, suggesting they may require those dry periods. On the other hand, Diego Fontaneto (pers. comm. 2 November 2016) finds **Bdelloidea** to be common among mosses in bogs. It could be that hydrology plays an important role, but Fontaneto also finds **Bdelloidea** in habitats that never dry.

Figure 2. ***Habrotrocha pusilla textris*** in mucilaginous nest with 2 eggs, a condition that permits them to survive drought. Photo by Michael Plewka <www.plingfactory.de>, with permission.

In addition to the ability of anhydrobiosis and the addition of mucus, those **Bdelloidea** living in habitats that dry frequently may have thicker integuments that include distinct outgrowths, granules, and spines (***Macrotrachela multispinosa***, ***Dissotrocha aculeata***) (Kutikova 2003). However, the value of these thick integuments is unknown (Diego Fontaneto, pers. comm. 2 November 2016).

Richters (1907) described six bdelloid rotifers from mosses in the Kerguelen Islands in the Antarctic. On the other hand, **Bdelloidea** were conspicuously absent from the littoral mosses on Svalbard (De Smet 1988).

Only one carnivorous **bdelloid** is known, and it is not known from **bryophytes**. Rather, the **bdelloids** filter or scrape or browse their diet of bacteria, one-celled algae, yeast, or particulate organic matter (Ricci 1984).

Adinetidae

Ricci and Covino (2005) demonstrated various aspects of anhydrobiosis in the **Adinetidae**, using ***Adineta ricciae***. Rotifers that recovered from anhydrobiosis had similar longevity and significantly higher **fecundity** (reproductive rate of an organism or population) than did the hydrated controls. Lines of offspring produced after the anhydrobiosis dormancy likewise had significantly higher fecundity and longevity than controls from mothers of the same age. The name ***A. ricciae*** led me on a search to find its connection to the thallose liverwort genus ***Riccia***, one that has several members that are dormant in muds and revive when the area is flooded. But of course, the genus is not named for the liverwort, but for the rotifer biologist, Claudia Ricci.

Adineta

The genus ***Adineta*** has many **cryptic species** (species that look alike but can't interbreed), as demonstrated by DNA and a diversity of narrow ecological niches (Fontaneto *et al*. 2011). This diversity has led to superfluous names in many of the rotifer genera. This text follows the nomenclature of Segers (2007).

Several species of ***Adineta*** are known from bryophytes. ***Adineta barbata*** (Figure 3), ***A. gracilis*** (Figure 4), and ***A. vaga*** (Figure 5) occur in bogs on or among ***Sphagnum*** (Figure 6) (Myers 1942; Hingley 1993; Bielańska-Grajner *et al*. 2011). ***Adineta barbata***, in particular, is associated with ***Sphagnum subsecundum*** (Figure 7) (Horkan 1981; Hingley 1993; Jersabek *et al*. 2003). ***Adineta vaga*** is more widespread, occurring on sandstone, roof, and **epiphytic** (in this case growing on trees) mosses as well. ***Adineta vaga rhomboidea*** occurs on the terrestrial weedy moss ***Ceratodon purpureus*** (Figure 8) (Yakovenko 2000).

Figure 3. ***Adineta barbata***, a species known to live on ***Sphagnum subsecundum*** (Figure 7) and other mosses. Photo by Jersabek *et al*. 2003, with permission.

Figure 4. ***Adineta gracilis***, a species known from ***Sphagnum*** and other mosses. Photo by Jersabek *et al*. 2003, with permission.

Figure 5. ***Adineta vaga***, a **moss** dweller that is 0.2-0.3 mm when extended. It is known from mosses on tree (*Salix*), roof, and sandstone substrates. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 6. ***Sphagnum*** sp., home for a variety of rotifers. Photo by Bernd Haynold, through Creative Commons.

Figure 7. ***Sphagnum subsecundum***. Photo by Michael Lüth, with permission.

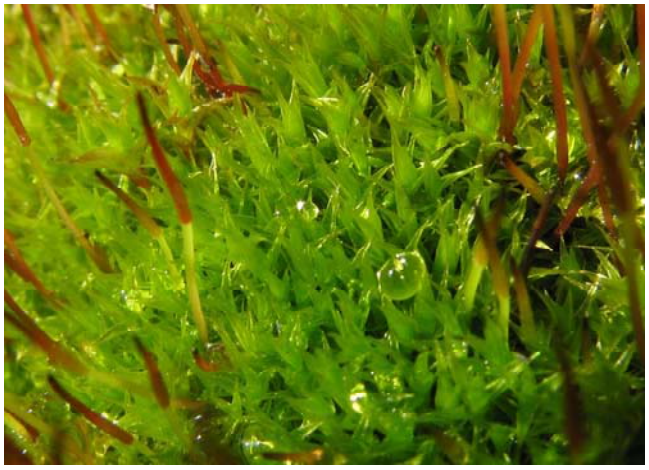

Figure 8. ***Ceratodon purpureus***, home for ***Adineta vaga*** *var*. ***rhomboidea***. Photo by Jiří Kameníček, with permission.

Other species occur on bryophytes in various habitats. In most cases, the habitat is simply listed as moss, or some other non-bryophyte habitat and moss. These include ***Adineta cuneata*** (Figure 9) on moss (Plewka 2016), ***A. steineri*** (Figure 10) on epiphytic mosses (Hirschfelder *et al*. 1993; Plewka 2016), and ***A. tuberculosa*** (Figure 11) on moss (Horkan 1981; Plewka 2016).

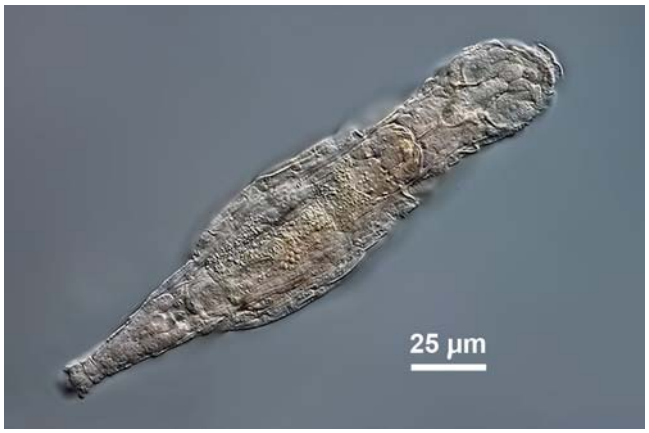

Figure 9. ***Adineta cuneata*** from moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

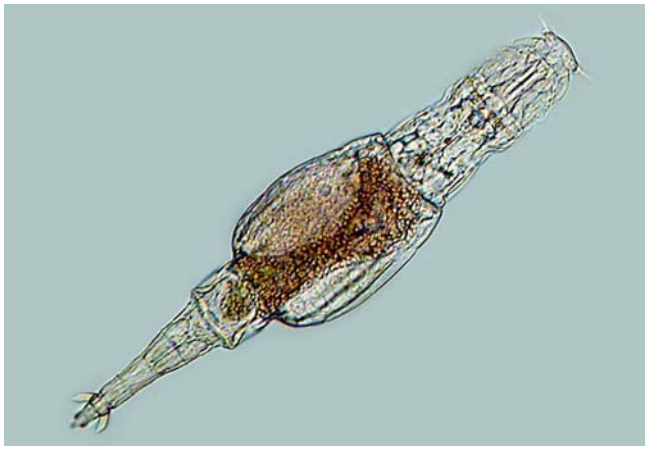

Figure 10. ***Adineta steineri***, a species that lives on epiphytic mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 11. ***Adineta tuberculosa***, a moss inhabitant. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Bradyscela

In addition to the ***Adineta*** species, ***Bradyscela clauda*** (Figure 12) occurs on the terrestrial moss ***Brachythecium rutabulum*** (Figure 13) (Madaliński 1961; Plewka 2016).

Figure 12. ***Bradyscela clauda*** with retracted cilia, from ***Brachythecium rutabulum.*** Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 13. ***Brachythecium rutabulum***, home for ***Bradyscela clauda*** in Europe. Photo by Michael Lüth, with permission.

Habrotrochidae

The **Habrotrochidae** is a family with three genera, all of which occur among mosses.

Habrotrocha

Habrotrocha species are common inhabitants among ***Sphagnum*** (Figure 6) (Bateman 1987; Peterson *et al*. 1997; Błedzki & Ellison 1998) as well as other mosses. ***Habrotrocha*** is able to survive decreasing moisture with the protection of a mucous matrix (Kutikova 2003). This is particularly helpful when mosses are drying. The members of ***Habrotrocha*** accumulate various small adhering particles, thus further providing them a shelter to protect them while they are dry.

Habrotrocha ampulla (Figure 14), ***H. angusticollis*** (Figure 15-Figure 16), ***H. collaris*** (Figure 37-Figure 38), ***H. constricta*** (Figure 28-Figure 29), and ***H. lata*** (Figure 17-Figure 18) live among or on ***Sphagnum*** in ***Sphagnum*** ponds (Myers 1942; Horkan 1981; Hingley 1993; Jersabek *et al*. 2003; Bielańska-Grajner *et al*. 2011; Plewka 2016).

Figure 14. ***Habrotrocha ampulla*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 15. ***Habrotrocha angusticollis***, a bryophyte dweller. Photo by Yuuji Tsukii, with permission.

Figure 16. ***Habrotrocha angusticollis*** from ***Sphagnum*** ponds. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 17. ***Habrotrocha lata***, a species collected from **bryophytes** in more than one location. Photo through Proyecto Agua, with permission.

Figure 18. ***Habrotrocha lata*** from ***Sphagnum*** pond. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Some species of ***Habrotrocha*** use the protection of ***Sphagnum*** **retort** cells (Figure 19-Figure 21) for their homes (Plewka 2016). These are special cells that have a pore in a flask-like neck at the end of the stem epidermal

cell. The rotifers that live there extend outward from the pore to feed. This is particularly true for ***Habrotrocha reclusa*** (Figure 22), known from ***Sphagnum subsecundum*** (Figure 7) (Myers 1942) and ***H. roeperi*** (Figure 23; Bielańska-Grajner *et al*. 2011; Plewka 2016).

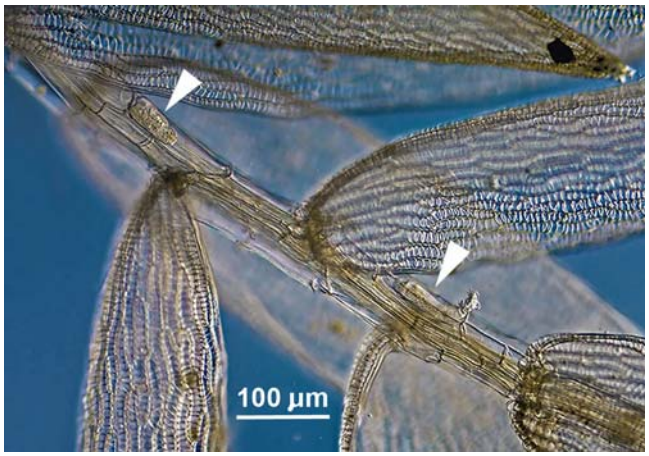

Figure 19. ***Sphagnum*** showing retort cells with ***Habrotrocha roeperi*** (arrows), a retort cell dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

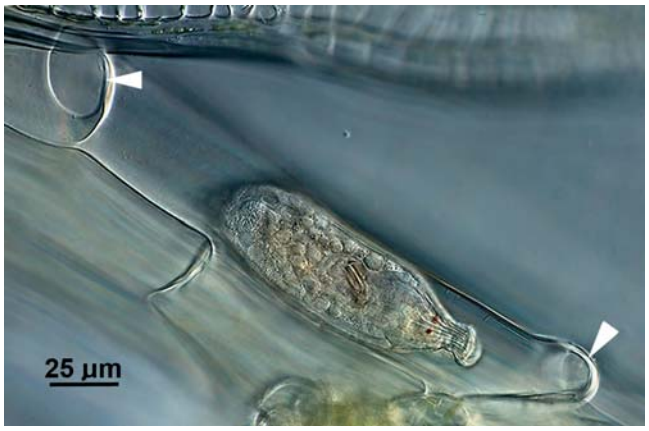

Figure 20. ***Habrotrocha roeperi*** in a retort cell. Arrows indicate the pores. Photo by Michael Plewka <www.plingfactory.de>, with permission.

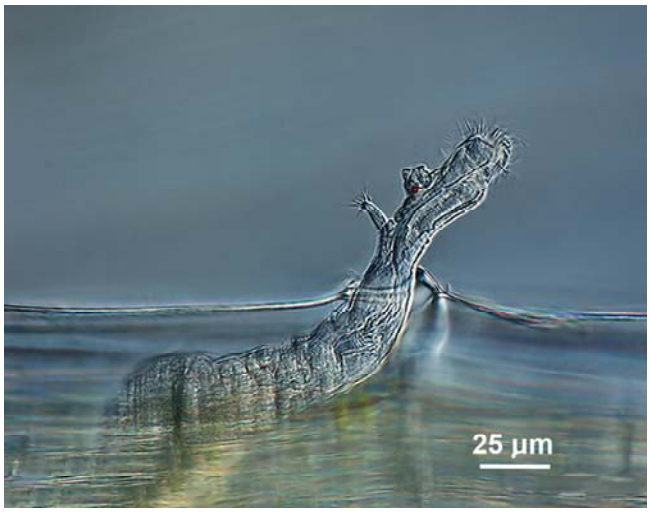

Figure 21. ***Habrotrocha roeperi*** extending out of a retort cell, a position in which it can attempt to trap food. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 22. ***Habrotrocha cf. reclusa***, a retort cell dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 23. ***Habrotrocha roeperi***, a retort cell dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Bog habitats for ***Habrotrocha*** (Figure 24), in particular ***H. rosa*** (Figure 25), include pitcher plants (***Sarracenia purpurea***, Figure 26), where the rotifers are a major food source for co-habiting members of the **Culicidae** (mosquitoes) (Bateman 1987), causing the mosquito population numbers to rise (Błedzki & Ellison 1998). The pitcher plants are common plants among the ***Sphagnum*** (Figure 6) in bogs and provide a pool of water in their leaves. The rotifers are an important source of N and P in the bog/fen-dwelling pitcher plants.

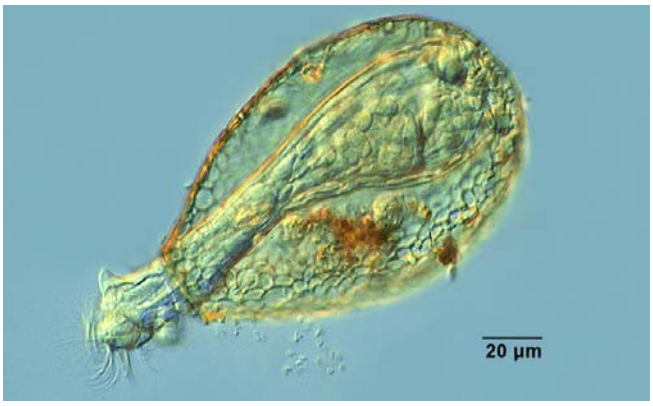

Figure 24. ***Habrotrocha***, a genus with many species that occur on **bryophytes**. Photo by Proyecto Agua Water Project through Creative Commons, with permission.

Figure 25. ***Habrotrocha rosa***, a species that lives in pitcher plants. Photo by Rkitko at Wikipedia Commons.

Figure 26. ***Sarracenia purpurea***, a bog plant that provides a watery home for ***Habrotrocha rosa***. Photo by Pouzin Oliver, through Creative Commons.

There are many species in ***Habrotrocha*** that live among bryophytes. These include ***H. bidens*** (Figure 27) on mosses on the ground (Hingley 1993; Plewka 2016), ***H. constricta*** (Figure 28-Figure 29) on ***Sphagnum***, water mosses, and **epiphytic** bryophytes (those growing on trees) (Myers 1942; Horkan 1981; Hingley 1993; Plewka 2016), ***H. novemdens*** (Figure 30) on mosses (Plewka 2016), ***Habrotrocha pavida*** on the mosses ***Ceratodon purpureus*** (Figure 8) and ***Bryum argenteum*** (Figure 31) (Yakovenko 2000), ***H. pusilla*** (Figure 32) in mucilage on moss (Horkan 1981; Plewka 2016), and ***H. quinquedens*** (Figure 33) on both wet and dry mosses (Plewka 2016). Some species also occur in the lobules of the leafy liverwort ***Frullania*** (Figure 34-Figure 35; Michel Verolet).

Figure 27. ***Habrotrocha bidens*** from moss on ground. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 28. ***Habrotrocha constricta***, a species that lives on both water moss and epiphytic moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 29. ***Habrotrocha constricta***, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 30. ***Habrotrocha novemdens*** from moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 31. ***Bryum argenteum***, home of ***Habrotrocha pavida***. Photo by Manju Nair, through Creative Commons.

Figure 32. ***Habrotrocha pusilla***, a species that lives in mucilage on moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Hirschfelder *et al*. (1993) examined the rotifers among epiphytic bryophytes and added ***Habrotrocha flava***, ***H. fusca***, and ***H. insignis***.

Figure 33. ***Habrotrocha quinquedens***, a species that lives on both wet and dry mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

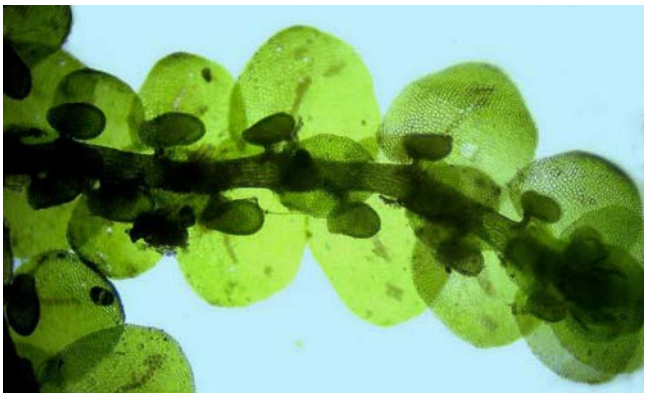

Figure 34. ***Habrotrocha*** on ***Frullania***, peeking out of the hood-shaped lobules. Photo by Michel Verolet, with permission.

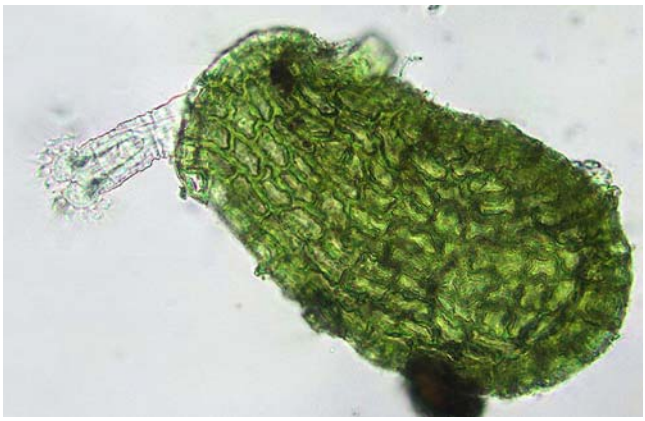

Figure 35. ***Habrotrocha*** in ***Frullania*** lobule. Photo by Michel Verolet, with permission.

A number of additional species are known from bryophytes, but with no additional details. Madaliński (1961) reported ***H. microcephala*** and ***H. tridens*** (see also Bielańska-Grajner *et al*. 2011) from the environs of Tatra streams. Horkan (1981) reported ***Habrotrocha aspera*** (Figure 36; see also Plewka 2016); see also Hingley 1993 for bog mosses), and ***H. pulchra***. Hingley (1993) added ***H. longula***, and ***H. minuta***; Peters *et al*. (1993) added ***H. eremita***. It appears that 1993 was a good year for bryophyte rotifer studies.

Figure 36. ***Habrotrocha aspera***, a moss inhabitant. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 37. ***Habrotrocha collaris***, a species known from bryophytes, including ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

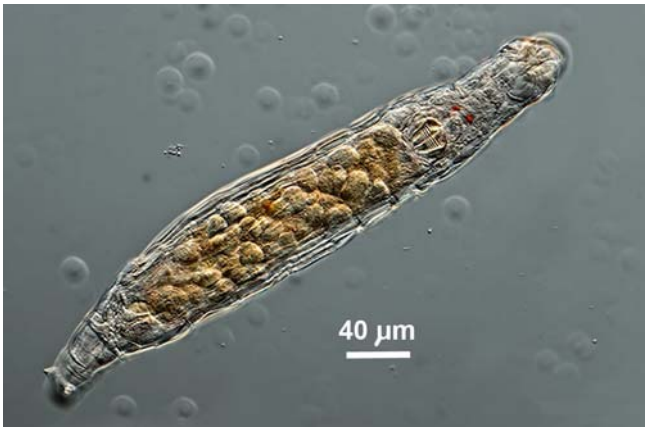

Figure 38. ***Habrotrocha collaris*** with two red eyespots, a bryophyte dweller, including ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Otostephanos

The genus ***Otostephanos*** has species on ***Sphagnum*** (Figure 6), but others occur on terrestrial mosses. ***Otostephanos auriculatus*** (Figure 39-Figure 40) occurs on ***Sphagnum*** and ***O. jolantae*** (Figure 41) occurs in ***Sphagnum*** ponds (Plewka 2016). ***Otostephanos monteti*** (Figure 42) lives on the emergent moss ***Drepanocladus aduncus*** (Figure 43) (Yakovenko 2000). ***Otostephanos cuspidilabris*** is known from "soggy" plants of the moss ***Atrichum*** sp. (Figure 44-Figure 45) (Yakovenko 2000). ***Otostephanos macrantennus*** is a bryophyte dweller (Ricci 1998). Two species live among dry mosses, ***O. regalis*** (Figure 46) on roof mosses (Hirschfelder *et al.* 1993; Plewka 2016) and ***O. torquatus*** (Figure 47) on mosses on concrete (Peters *et al.* 1993; Plewka 2016).

Figure 39. ***Otostephanos auriculatus*** from ***Sphagnum*** pond. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 40. ***Otostephanos auriculatus***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

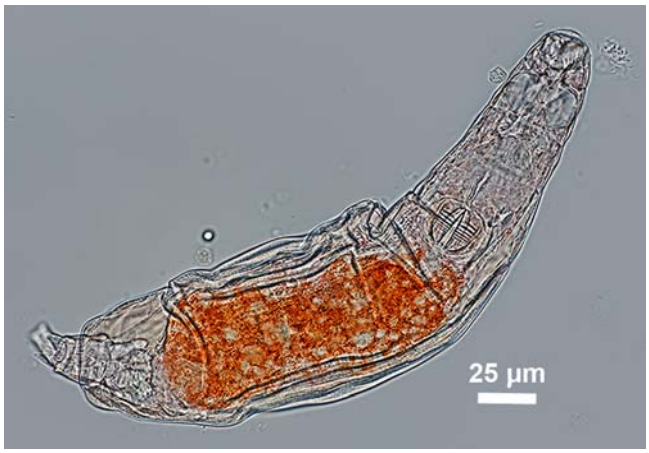

Figure 41. ***Otostephanos jolantae*** from ***Sphagnum*** pond. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 42. ***Otostephanos monteti***, a species that lives on the emergent moss ***Drepanocladus aduncus***. Photo by Michael Plewka <www.plingfactory.de>., with permission.

Figure 43. ***Drepanocladus aduncus***, home for ***Otostephanos monteti***. Photo by Bob Klips, with permission.

Figure 44. ***Atrichum angustatum*** streamside habitat and home of ***Otostephanos cuspidilabris***. Photo by Bob Klips, with permission.

Figure 45. ***Atrichum angustatum***, home of ***Otostephanos cuspidilabris***. Photo by Bob Klips, with permission.

Figure 46. ***Otostephanos*** *cf.* ***regalis*** from dry moss on roof. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 47. ***Otostephanos torquatus*** from dry moss on concrete. Michael Plewka <www.plingfactory.de>, with permission.

Scepanotrocha

Some members of a second genus seem also to find the retort cells of ***Sphagnum*** to be a suitable home. ***Scepanotrocha rubra*** (Figure 48-Figure 49) lives in these cells, extending out of them to feed (Figure 48) (Myers 1942; Plewka 2012).

Figure 48. ***Scepanotrocha rubra*** in a retort cell of a ***Sphagnum*** stem. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 49. ***Scepanotrocha rubra***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

In addition to the retort dwellers, ***Scepanotrocha corniculata*** (Figure 50) lives on mosses, ***S. semitecta*** (Figure 51) is a ***Sphagnum*** (Figure 6) dweller, and ***S. simplex*** (Figure 52) lives on epiphytic mosses as well as ***Sphagnum***, once again demonstrating the seemingly wide range of microhabitats used by a single rotifer species (Plewka 2016).

Figure 50. ***Scepanotrocha cf. corniculata*** from moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 51. ***Scepanotrocha semitecta*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 52. ***Scepanotrocha simplex***, a species that lives on both epiphytic mosses and ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Philodinavidae

Only two species from this family seem to be moss dwellers. ***Philodinavus paradoxus*** (Figure 53) lives in

lakes, rivers, and streams (Madaliński 1961; Ricci & Melone 1998; Plewka 2016) and is preyed upon by flatworms, larger moss-dwelling rotifers, and nematodes (Schmid-Araya & Schmid 1995). It is tiny (200 µm long) and creeps with leech-like movements, being unable to swim (Ricci & Melone 1998). Instead, its strong foot anchors it to its substrate, a feature of importance in streams and rivers. Its corona is poorly developed and it obtains its food by browsing, facilitated by the ciliated buccal field and trophi protruding throughout the mouth. Its disjunct distribution in Europe and New Zealand may indicate a lack of collecting and lack of experts on this group.

Figure 53. ***Philodinavus paradoxus***, a species from stream mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Within its short lifetime of only 20 days, ***Philodinavus paradoxus*** can produce 6-7 eggs (Ricci & Melone 1998). These seem to have about the same resistance to desiccation damage as adults, with only 10% of each surviving 7 days of desiccation, a desiccation intolerance that is typical of aquatic rotifer taxa.

Henoceros falcatus is commonly found in the same mosses in running waters with ***Philodinavus paradoxus*** (Diego Fontaneto, pers. comm. 2 November 2016). Ricci and Melone (1998) reported this species from mosses. They noted that ***H. falcatus*** was first found in mosses submerged in streams in South Africa (Milne 1916). Later ***H. falcatus*** was found in similar habitats in Europe, South America, Asia, and Hawaii (Schmid-Araya 1995; Turner 1996). The two species co-occur in Austria (Schmid-Araya 1995) and in Valle Argentina, Italy. It seems to be common for these two species to co-occur, suggesting similar ecological requirements. In fact, rather than being rare (Schmid-Araya 1995; Ricci & Melone 1998), Fontaneto *et al*. (2007) consider them to be fairly common in their specialized habitat of stream mosses.

Figure 54. ***Henoceros falcatus***, a stream moss dweller. Photo by Michel Verolet, with permission.

Philodinidae

The philodinids use their cilia or foot and rostrum (Figure 55) to facilitate swimming (Hickernell 1917). At high temperatures these rotifers engage in active swimming, but in cold water they creep like a leech with the cilia retracted. During feeding, they attach themselves by the foot and use the cilia to direct food to the pharynx. When drying occurs, the animal forms a ball and dries up. The ball is formed by retracting both the head and the foot into the trunk of the rotifer and losing all the water, pulling the organs together and eliminating spaces. When they get water again, they resume their normal shape in ten minutes or less.

Ceratotrocha and *Didymodactylos*

This family has many bryophyte-dwelling species. ***Ceratotrocha cornigera*** is the only member of its genus documented from bryophytes, including bogs (Horkan 1981; Hingley 1993). ***Didymodactylos carnosus*** (Figure 55) likewise is known from mosses (Ricci & Melone 2000; Plewka 2016).

Figure 55. ***Didymodactylos carnosus***, common in moss. Note the two rings of cilia. Photo by Michel Plewka <www.plingfactory.de>, with permission.

Dissotrocha

Dissotrocha has several known bryophyte-dwelling species. ***Dissotrocha aculeata*** (Figure 56), ***D. macrostyla*** (Figure 57), and ***D. spinosa*** occur on or among ***Sphagnum*** (Figure 6) (Horkan 1981; Hingley 1993; Bielańska-Grajner

et al. 2011; Plewka 2016). ***Dissotrocha scutellata*** (Figure 58-Figure 59) is known from the moss ***Andreaea rupestris*** (Figure 60-Figure 61), a rock dweller that dries out frequently (Plewka 2016).

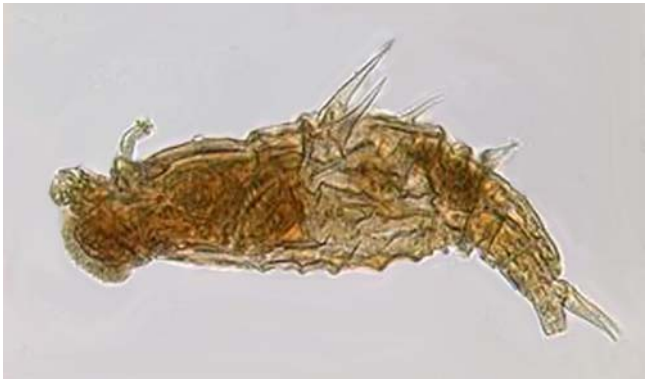

Figure 56. ***Dissotrocha aculeata***, a species known from ***Sphagnum*** and **other mosses**. Photo by Jersabek *et al*. 2003, with permission.

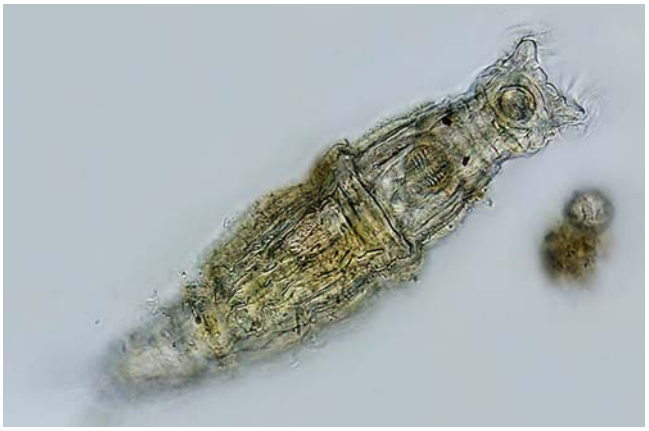

Figure 57. ***Dissotrocha macrostyla*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 58. ***Dissotrocha scutellata***, a dweller on ***Andreaea rupestris***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 59. ***Dissotrocha scutellata***, a species that lives on the exposed rock-dwelling moss ***Andreaea rupestris***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 60. ***Andreaea rupestris***, home for ***Dissotrocha scutellata***. Photo by Michael Lüth, with permission.

Figure 61. ***Andreaea rupestris***, home for ***Dissotrocha scutellata***. Photo by Michael Lüth, with permission.

Macrotrachela

A number of species of the large genus ***Macrotrachela*** occur on mosses. Some of these are from ***Sphagnum*** (Figure 6), including ***Macrotrachela concinna*** (Myers 1942; Hingley 1993), ***M. crucicornis*** (Myers 1942), ***M. decora*** (Figure 62) (Plewka 2016), and ***M. papillosa*** (Figure 63) (Horkan 1981; Hingley 1993).

Figure 62. ***Macrotrachela cf. decora*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 63. ***Macrotrachela papillosa***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Other species occur in contrasting habitats of both ***Sphagnum*** (Figure 6) and mosses growing on trees. These include ***M. multispinosa*** (Figure 64-Figure 65; Myers 1942; Horkan 1981; Hingley 1993; Jersabek *et al*. 2003), ***M. nana*** in stream environs (Figure 67; Madaliński 1961; Bielańska-Grajner *et al*. 2011; Plewka 2016), ***M. plicata*** (Figure 66; Myers 1942; Horkan 1981; Hingley 1993; Jersabek *et al*. 2003; Bielańska-Grajner *et al*. 2011; Plewka 2016), and ***M. quadricornifera*** (Figure 68; Myers 1942; Horkan 1981; Hingley 1993; Jersabek *et al*. 2003; Bielańska-Grajner *et al*. 2011; Plewka 2016).

Figure 64. ***Macrotrachela multispinosa brevispinosa***, a species that occurs on submerged mosses and mosses on limestone and trees. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 65. ***Macrotrachela multispinosa*** from among epiphytic mosses. Photo by Jersabek *et al*. 2003, with permission.

Figure 66. ***Macrotrachela plicata*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 67. ***Macrotrachela nana*** from ***Sphagnum***, tree moss, and other mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 68. ***Macrotrachela quadricornifera***, a species from ***Sphagnum*** and epiphytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Others are known only as epiphytes, including ***M. aculeata*** (Figure 69; Plewka 2016), ***M. magna*** (Figure 70; Plewka 2016), and ***M. tuberilabris*** (Figure 71; Plewka 2016).

Figure 69. ***Macrotrachela aculeata*** from mosses on trees. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 70. ***Macrotrachela magna*** from epiphytic moss, showing its extended position. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 71. ***Macrotrachela tuberilabris*** from moss on tree. Michael Plewka <www.plingfactory.de>, with permission.

Additional members of the genus occurred on various mossy substrates, including ***Macrotrachela ehrenbergii*** (Figure 72) on ***Sphagnum*** (Figure 6), mosses on walls, and epiphytes (Peters *et al.* 1993; Jersabek *et al.* 2003; Plewka 2016), ***M. habita*** (Figure 74) on ***Sphagnum***, moss on trees, rocks, and ground (Myers 1942; Horkan 1981; Hirschfelder *et al*. 1993; Jersabek *et al.* 2003; Plewka 2016), ***M. insolita*** (Figure 75) on mosses submerged in pond (Hirschfelder *et al*. 1993; Plewka 2016) and in peatlands (Bielańska-Grajner *et al*. 2011), ***M. musculosa*** (Figure 76) on ***Sphagnum***, ground mosses, and epiphytic mosses (Myers 1942; Hirschfelder *et al.* 1993; Plewka 2016), ***M. punctata*** (Figure 77-Figure 78) on dry mosses on rocks (Hirschfelder *et al.* 1993; Plewka 2016); ***M. zickendrahti*** (Figure 79) on ***Sphagnum*** and other mosses (Jersabek *et al.* 2003; Plewka 2016). For ***M. muricata***, I have found little information except it occurs on mosses (Horkan 1981).

Figure 72. ***Macrotrachela ehrenbergii***, a species that lives among mosses on walls and trees as well as on ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

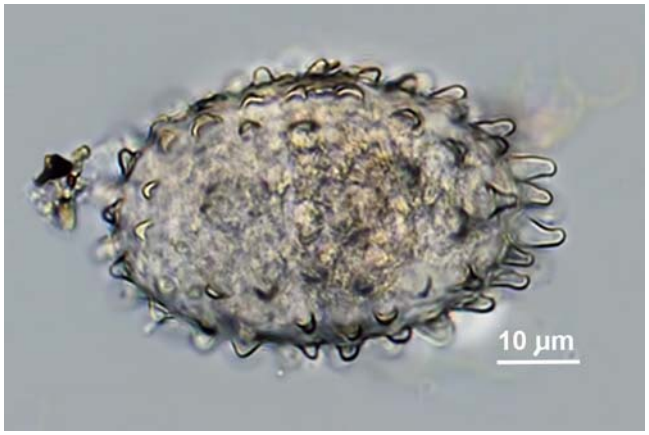

Figure 73. ***Macrotrachela ehrenbergii*** egg. The projections may help to preserve it during drought. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 74. ***Macrotrachela habita***, a species from moss on trees, rocks, and ground. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 75. ***Macrotrachela insolita***, s species that lives in ponds with submerged moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

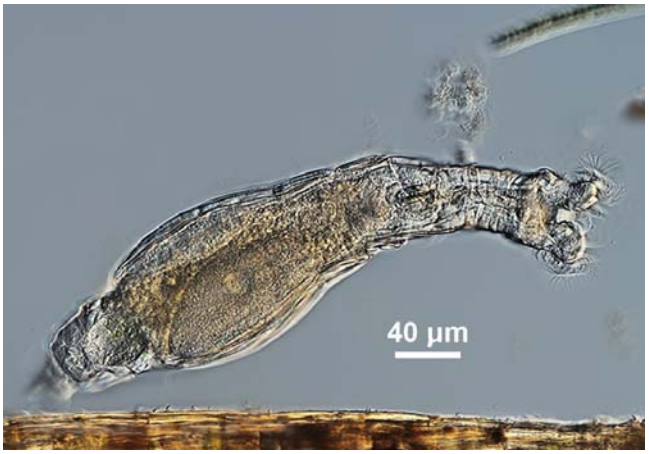

Figure 76. ***Macrotrachela musculosa***, a species from mosses on ground and trees. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 77. ***Macrotrachela punctata***, a species from dry moss on rocks. Here it is contracted with cilia out. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 78. ***Macrotrachela punctata***, a species of dry moss on rocks. Here it is extended with cilia contracted. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 79. ***Macrotrachela zickendrahti***, a species from moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

The absence of records for moss dwellers may be common. For example, Ricci (1980) found ***Macrotrachela plicatula*** (Figure 80) among mosses in Uganda. This was the first time it had been found since its 1911 description as a new species.

Figure 80. ***Macrotrachela plicatula*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Mniobia

Mniobia likewise has its ***Sphagnum*** (Figure 6) dwellers, including those found by Hingley (1993): ***M. incrassata*** (Figure 81-Figure 82), ***M. magna*** (Figure 84), ***M. obtusicornis*** (Figure 85), ***M. symbiotica*** (see also Hudson 1889; Horkan 1981). Among these, ***M. incrassata*** is known from other mosses as well (Plewka 2016). ***Mniobia scarlatina*** (Figure 83; Jersabek *et al*. 2003) and ***M. tetraodon*** (Myers 1942; Horkan 1981) occur on epiphytic mosses. ***Mniobia symbiotica*** also occurs in the lobules of the leafy liverwort ***Frullania eboracensis*** (Figure 86-Figure 88), an epiphyte in eastern USA (Biechele 2014).

Figure 81. ***Mniobia incrassata*** from moss, showing exterior of lorica. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 82. ***Mniobia incrassata*** from moss, showing rotifer inside lorica. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 83. ***Mniobia scarlatina*** from among epiphytic mosses. Photo by Jersabek *et al*. 2003, with permission.

Figure 84. ***Mniobia magna***, a moss inhabitant, including epiphytes, with its body shortened and cilia out. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 85. ***Mniobia cf. obtusicornis***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 86. ***Frullania eboracensis*** on bark – home for ***Mniobia symbiotica***. Photo by Janice Glime

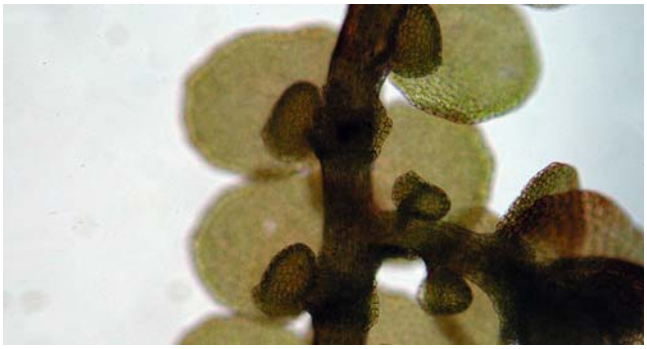

Figure 87. ***Frullania eboracensis*** showing lobules that serve as home for ***Mniobia symbiotica***. Photo by Bob Klips, with permission.

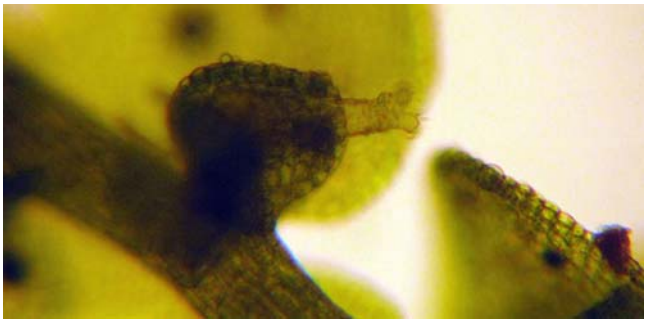

Figure 88. ***Frullania eboracensis*** from Ohio, USA, with a rotifer in a lobule – possibly ***Mniobia symbiotica***. Photo by Bob Klips, with permission.

Mniobia orta (Peters *et al*. 1993) and ***M. russeola*** (Horkan 1981; Hirschfelder *et al*. 1993) are also bryophyte dwellers.

Pleuretra

The genus ***Pleuretra*** seems to prefer habitats that dry out. ***Pleuretra humerosa*** (Figure 89-Figure 90) occurs on dry mosses on granite (Plewka 2016). ***Pleuretra lineata*** (Figure 91-Figure 93) occurs on the mosses ***Andreaea rupestris*** (Figure 60-Figure 61) and ***Grimmia pulvinata*** (Figure 94) (Hirschfelder *et al*. 1993; Plewka 2016), both species of exposed rocks. ***Pleuretra brycei*** (Figure 95-Figure 96) is also a bryophyte dweller, but among ***Sphagnum*** (Figure 6-Figure 7) and demonstrates the spines that help to protect it among the bryophytes (Madaliński 1961).

Figure 89. ***Pleuretra humerosa***, a species of dry mosses on granite. It is shown here in its extended position that is used during its inchworm movement. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 90. ***Pleuretra humerosa***, a species of dry moss on granite, shown here in its contracted shape with cilia out. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 91. ***Pleuretra lineata***, a species that lives on ***Andreaea rupestris*** and ***Grimmia pulvinata***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 92. ***Pleuretra lineata***, a species that lives on the mosses ***Andreaea rupestris*** and ***Grimmia pulvinata***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

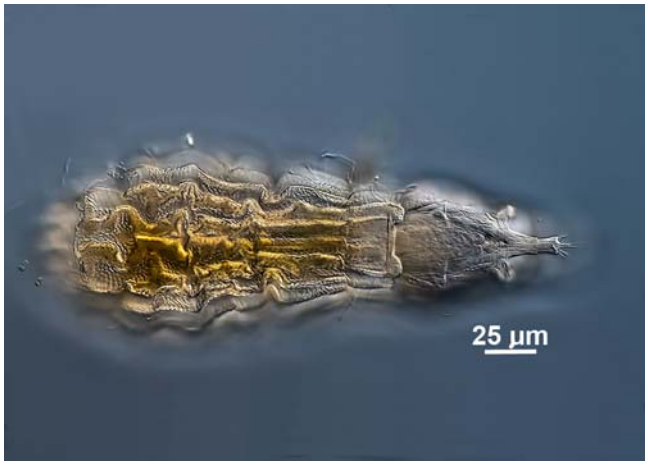

Figure 93. ***Pleuretra lineata***, inhabitant of ***Andreaea rupestris*** and ***Grimmia pulvinata***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 94. ***Grimmia pulvinata***, home of ***Pleuretra lineata***. Photo by Michael Lüth, with permission.

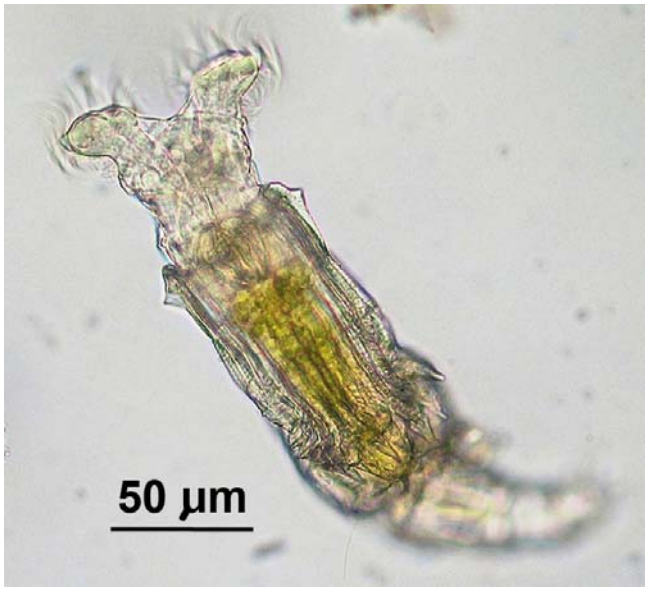

Figure 95. ***Pleuretra cf brycei***, a bryophyte dweller. Photo by Michel Verolet, with permission.

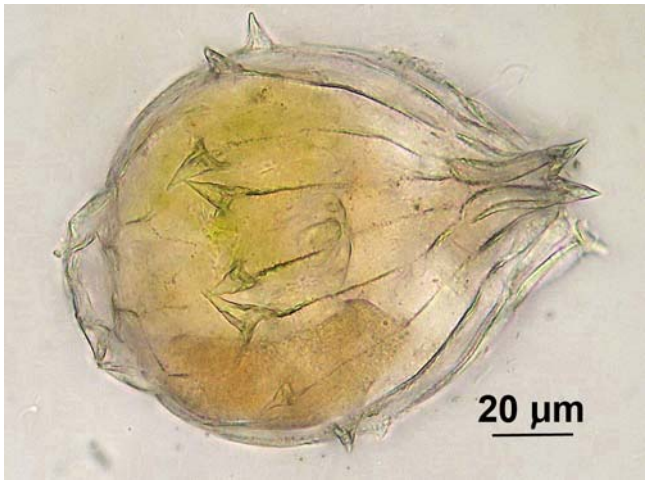

Figure 96. ***Pleuretra*** *cf* ***brycei*** tun, demonstrating the spines that help to protect it. Photo by Michel Verolet, with permission.

Philodina

Philodina acuticornis (Figure 97), ***P. nemoralis*** (Figure 98), and ***P. brevipes*** live on ***Sphagnum*** (Figure 6) (Hingley 1993). ***Philodina citrina*** (Figure 99-Figure 100), ***P. plena*** (Figure 101), ***P. proterva***, and ***P. vorax*** (Figure 102) all occur on ***Sphagnum*** (Figure 6) (Hirschfelder *et al*. 1993; Jersabek *et al*. 2003; Bielańska-Grajner *et al*. 2011; Plewka 2016). But ***P. plena*** also occurs on epiphytes (Myers 1942) and ***P. citrina*** and ***P. vorax*** live on epiphytic mosses and mosses on rock or concrete. ***Philodina nemoralis*** (Figure 103; Plewka 2016) and ***P. rugosa*** (Figure 105; Horkan 1981; Hingley 1993; Fontaneto *et al*. 2007; Plewka 2016) live in contrasting submersed and dry habitats, including on epiphytic mosses. Other rotifers on epiphytic mosses include ***Philodina childi*** (Figure 104; Horkan 1981; Hingley 1993; Plewka 2016). Other members of the genus that are associated with bryophytes include ***P. erythrophthalma***, ***P. flaviceps*** (Figure 106), and ***P. roseola*** (Figure 107-Figure 111) (Horkan 1981; Hirschfelder *et al*. 1993; Madaliński 1961; Plewka 2016).

Figure 97. ***Philodina acuticornis***, a species that likes green algae among ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 98. ***Philodina nemoralis***, a species of submersed, dry, and epiphytic mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 99. ***Philodina citrina*** from ***Sphagnum*** bogs and mosses on stones. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 100. ***Philodina citrina***, a species known from ***Sphagnum*** bogs and epiphytic mosses. Photo by Jersabek *et al.* 2003.

Figure 101. ***Philodina plena*** occurs on ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 102. ***Philodina vorax***, a species that occurs on ***Sphagnum***, epiphytic mosses, and mosses on concrete. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 103. ***Philodina nemoralis***, a species that occurs on submersed, dry, and epiphytic mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 104. ***Philodina childi*** occurs on epiphytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 105. ***Philodina rugosa***, a species that lives on epiphytic mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 106. ***Philodina flaviceps***, a species that occurs on moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 107. ***Philodina roseola***, a species that can be found on bryophytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

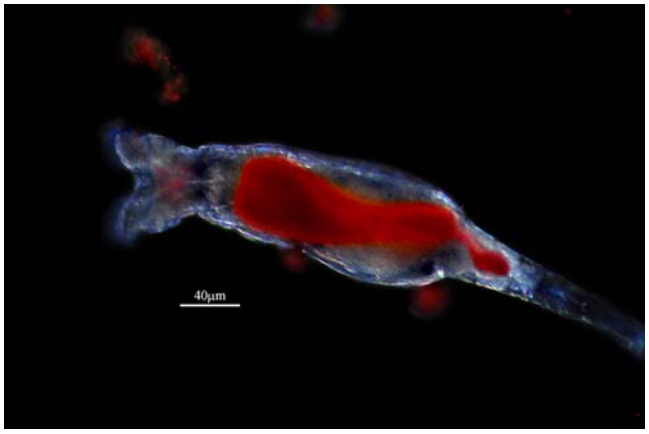

Figure 108. ***Philodina roseola***, a species that can be found on bryophytes. Photo from Proyecto Agua, with permission.

Figure 109. ***Philodina roseola*** with eggs, a species known to inhabit **bryophytes**. Photo by Jersabek *et al*. 2003, with permission.

Rotaria

Rotaria (Figure 110) is a genus that moves like a leech, permitting it to move among bryophytes. The genus ***Rotaria*** is able to move among mosses and other substrata by creeping with its head and foot (van Egmond 1999). The foot is sticky, enabling it to attach to a surface while it feeds (Dickson & Mercer 1966; Schmid-Araya 1998). The anterior cilia (Figure 111) make a current that directs the food toward the pharynx for ingestion.

Figure 110. ***Rotaria***, fully extended as it would be for its leech-like movement. This is a genus with several bryophyte-dwelling species that can move about the bryophytes in this manner. Photo by Wim van Egmond, with permission.

Figure 111. ***Rotaria***, showing the two wheels that direct the food into the gullet. Photo by Yuuji Tsukii, with permission.

Several species of ***Rotaria*** live in association with ***Sphagnum*** (Figure 6). These include ***R. citrina*** (Figure 112-Figure 113), ***R. haptica***, ***R. macroceros*** (Figure 114), ***R. macrura*** (Figure 115-Figure 116; see also Horkan 1981; Bielańska-Grajner *et al*. 2011), ***R. magnacalcarata***, ***R. neptunia*** (Figure 117-Figure 118), ***R. neptunoida*** (Figure 119), ***R. quadrioculata***, ***R. socialis*** (Figure 120), ***R. spicata***, and ***R. tardigrada*** (Figure 121; see also Bielańska-Grajner *et al*. 2011) (Hingley 1993; Plewka 2016). In addition to the ***Sphagnum*** dwellers, ***R. rotatoria*** (Figure 122) and ***R. macrura*** live on mosses (Madaliński 1961; Horkan 1981; Plewka 2016) as well as living in peatlands (Bielańska-Grajner *et al*. 2011). ***Rotaria sordida*** (Figure 123) is unusual in living not only on mosses on limestone, but also in living on the thallose liverwort ***Marchantia polymorpha*** (Figure 124; Horkan 1981; Hirschfelder *et al*. 1993; Plewka 2016) and in peatlands (Bielańska-Grajner *et al*. 2011).

Figure 112. ***Rotaria citrina*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 113. ***Rotaria citrina*** with 2 daughters (see the two mastax), from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 114. ***Rotaria macroceros***, known from **bog pools**. Note the long antenna in the middle of the head. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 115. ***Rotaria macrura***, a ***Sphagnum*** associate. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 116. ***Rotaria macrura*** from among ***Sphagnum*** and other mosses, showing fully extended foot. Photo by Jersabek *et al*. 2003, with permission.

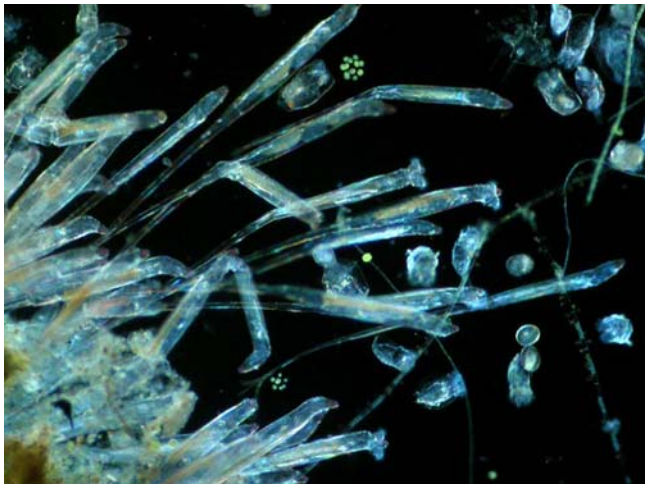

Figure 117. ***Rotaria neptunia*** colony. Photo by Michael Plewka <www.plingfactory.de>, with pernission.

Figure 118. ***Rotaria neptunia*** anterior. Photo by Michael Plewka <www.plingfactory.de>, with pernission.

Figure 119. ***Rotaria neptunoida***, a ***Sphagnum*** dweller, extended while creeping. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 120. ***Rotaria socialis***, an inhabitant of ***Sphagnum*** and other mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 121. ***Rotaria tardigrada*** creeping, with its corona retracted. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 122. ***Rotaria rotatoria***, a species known from bryophytes in more than one location. Photo by Jersabek *et al.* 2003, with permission.

Figure 123. ***Rotaria sordida sordida***, a species that lives on the thallose liverwort ***Marchantia polymorpha*** and moss on limestone. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 124. ***Marchantia polymorpha***, home for ***Rotifera sordida***. Photo by David T. Holyoak, with permission.

Desiccation Tolerance

Ricci (1998) compared the desiccation survival percentage of rotifers in the **Philodinidae** from water vs those from terrestrial mosses. The rotifers from terrestrial mosses survived seven days of desiccation better than did those from the water (Figure 125). The 2-day-old rotifers (juveniles) had poor resistance to desiccation. ***Rotaria rotatoria***, *R. neptunia*, and ***Otostephanos macrantennus***, all from bodies of water that do not dry out, did not recover from desiccation at any life stage. On the other hand, ***Philodina acuticornis*** and ***R. neptunoida*** likewise live in permanent bodies of water (including among mosses) and do withstand desiccation. Ricci also summarized indications of desiccation tolerance of **Bdelloidea** reported in the literature and from her own studies (Table 1).

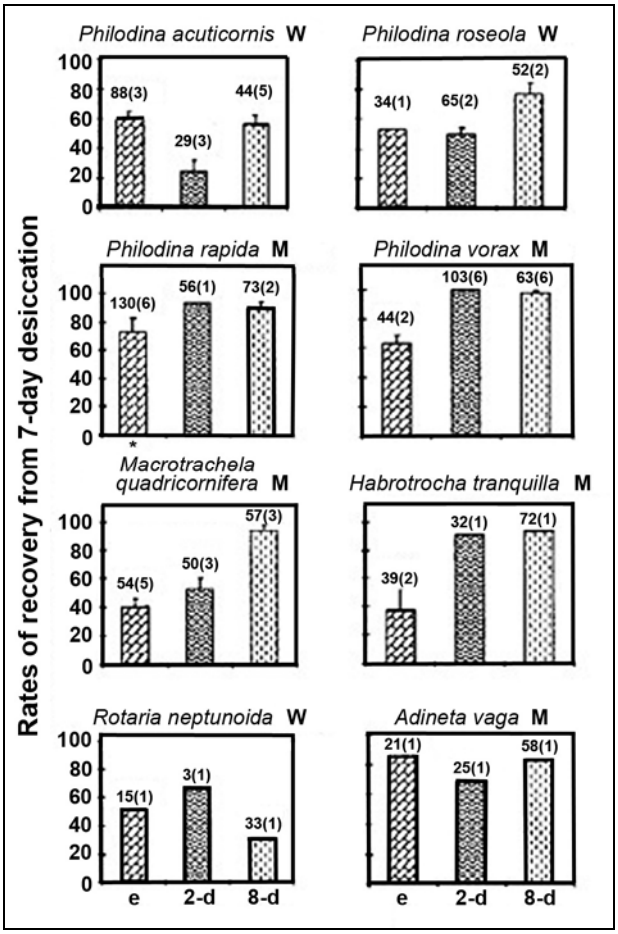

Figure 125. Recovery rates of rotifers collected from terrestrial mosses (**M**) and from water bodies (**W**). Life stages are **e** = newly laid eggs or embryos; **2-d** = 2-day-old juveniles; **8-d** = 8-day-old adults. Numbers above bars = sample size; (number) = number of replicates. Bars represent mean recovery rates among replicates; vertical lines = standard error. *Percentage viability adjusted to control. Redrawn from Ricci (1998).

Table 1. Genera of **Bdelloidea** that inhabit mosses compared to those from water, among genera for which desiccation tolerance is known. Adapted from Ricci (1998). Habitats are based on Donner (1965).

Adinetidae			
Adineta	moss, water	+	Dobers 1915; Örstan 1995
Bradyscela	moss	(+)	Donner 1976
Habrotrochidae			
Habrotrocha	mainly moss & soil	+	Schramm & Becker 1987
Otostephanos	moss, *Sphagnum*	(+)	Murray 1911
Scepanotrocha	moss, soil	(+)	Donner 1976
Philodinavidae			
Abrochtha	water	+	Ricci 1998
Henoceros	water	+	Ricci 1998
Philodinavus	water	+	Ricci 1998
Philodinidae			
Didymodactylos	moss	(+)	Donner 1976
Macrotrachela	moss, water	+	Dobers 1915; Ricci *et al.*1987
Mniobia	moss, soil	+	Dobers 1915
Pleuretra	moss	(+)	Murray 1911
Philodina	moss, water	+	Jacobs 1909; Ricci 1998
Rotaria	mainly water, soil	+	Ricci 1998

Summary

The rotifers in **Bdelloidea** are the most frequently represented rotifers on bryophytes.The bryophyte dwellers are usually not also planktonic and typically attach to the bryophytes by their toes. They move like an inchworm or use their cilia. They obtain their food from the microscopic organisms and detritus among the mosses. Only females exist and the eggs can typically survive desiccation. Mucus helps these rotifers to survive desiccating conditions.

Bryophyte-dwelling **Bdelloidea** include four families known from bryophytes: **Adinetidae**, **Habrotrochidae**, **Philodinavidae**, **Philodinidae**. The **Adinetidae** are known from bogs and other bryophytes. The **Habrotrochidae** have a number of species from bogs and from other bryophytes. Many of the species live in such small niches as ***Sphagnum*** retort cells and liverwort lobules. The **Philodinavidae** has two moss dwelling species that often occur together in streams. The **Philodinidae** creep in cold water and live attached on plants; a number of species occur on bryophytes. The **Philodinidae** terrestrial moss dwellers tested have greater desiccation tolerance than do the aquatic species. Adults are more desiccation tolerant than juveniles.

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CHAPTER 4-7a

INVERTEBRATES: ROTIFER TAXA – MONOGONONTA

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CHAPTER 4-7a
INVERTEBRATES: ROTIFER TAXA – MONOGONONTA

Figure 1. ***Keratella*** sp. among ***Sphagnum*** leaves. Photo by Marek Mis <www.mismicrophoto.com>, with permission.

CLASS MONOGONONTA

This is the largest of the two classes of rotifers, comprised of ~1570 species, ~1488 of which are free-living in fresh water of limnoterrestrial habitats (Segers 2008). It differs from the **Bdelloidea** in having two sexes and having only one ovary. Nevertheless, asexual reproduction occurs over and over until environmental conditions, often related to crowding, trigger the reproduction to become sexual (Welch 2008). At this time, the eggs of the **amictic** (non-sexual) females hatch into **mictic** females that produce their eggs by meiosis. The **haploid** eggs that are not fertilized develop into much smaller males and fertilization of a female by these males produces **diploid** eggs that become resting eggs.

The monogonont rotifers mostly eat small particles and organisms by filtering them, some actually seize them, and some are parasitic.

ORDER COLLOTHECACEA

Many members of this order are **sessile** (attached) and some are colonial. These rotifers have a foot that lacks toes, but they possess many foot glands that are used for adhesion. The females are predominantly sessile, but males and immature rotifers are free-living.. The rotary apparatus surrounds a funnel-like **invagination**. Many are surrounded with a jelly sheath.

Collothecidae

Many members of the Collothecidae are plant and algal inhabitants. The **Collothecidae** provide us with evidence of adaptive strategies embodied in reproduction. An examination of 65 species of rotifers, including this family, revealed that egg volume of rotifers increased as body volume increased, but the relative size of eggs actually decreased as body size increased (Wallace *et al*.

1998). This means that smaller species, typical among planktonic species and bryophytes, invest the most in egg production. The **Flosculariidae** (**Floscullariacea**) species are of intermediate size and their relative investment in egg mass is likewise intermediate. The **Collothecidae** family has the largest species and the lowest relative biomass of egg production among those examined by Wallace *et al*.

Collotheca

Collotheca (Figure 2-Figure 8) is a common genus in peatlands, living in ***Sphagnum*** pools (Figure 5) and on ***Sphagnum*** (Figure 2, Figure 21, Figure 61-Figure 62).

Figure 2. ***Collotheca*** on ***Sphagnum***. Photo by Marek Mis <www.mismicrophoto.com>, with permission.

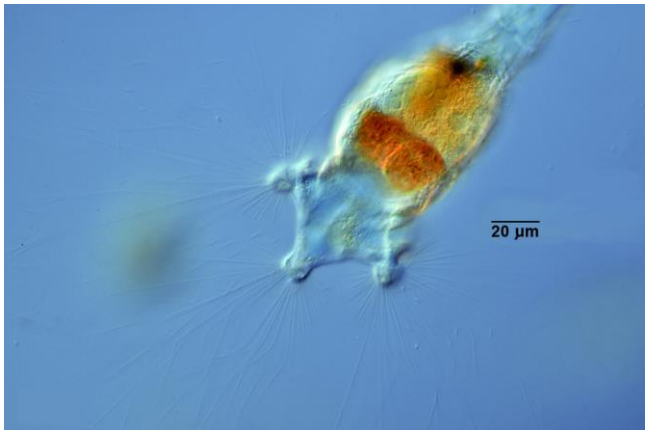

Figure 3. ***Collotheca***, a common genus on ***Sphagnum***. Photo by Proyecto Agua Water Project through Creative Commons.

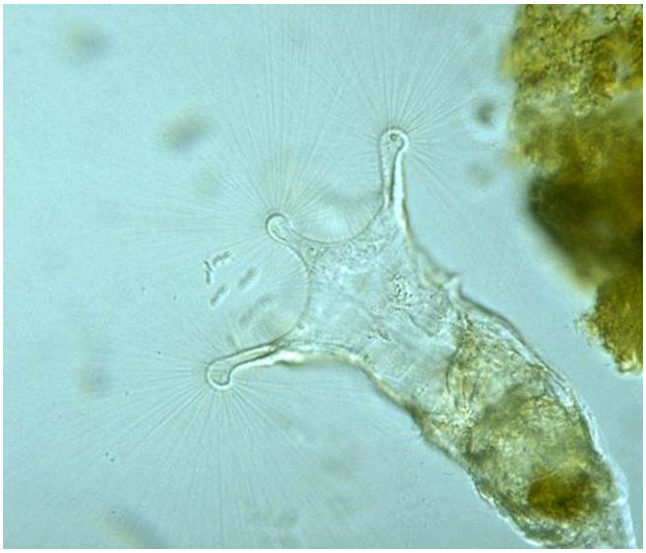

Figure 4. ***Collotheca*** sp., a common genus on ***Sphagnum***. Photo by Yuuji Tsukii, with permission.

Figure 5. ***Sphagnum*** pond, home for rotifers. Photo by Michael Luth.

Collotheca campanulata occurs on wet mosses as well as in the plankton on Svalbard (De Smet 1993). The relationships of this species to aquatic flowering plants can instruct us on relationships to look for among bryophytes. ***Collotheca campanulata*** (***gracilipes***) (Figure 6) is selective in its location on its aquatic plant substrate (Wallace & Edmondson 1986). On plants such as *Elodea canadensis*, it selected (98%) the lower (**abaxial**) surfaces of the leaves. When given equal opportunities for four plant species, it selected *Lemna minor* over *Elodea canadensis*, but in the field more were found on *Elodea canadensis*, with densities reaching more than six individuals per mm^2. Light made a difference, with 91% of the rotifers selecting the **adaxial** (upper) surface in continuous light, but showing no preference in continuous darkness. **Alpha amylase** appears to be the chemical that helps them to identify a plant substrate. Those rotifers that were induced to settle on the abaxial surface produced more eggs than those that were induced to settle on the adaxial surface. It would be interesting to see if these relationships persist on liverworts like ***Riccia fluitans*** (Figure 9) and ***Ricciocarpos natans*** (Figure 10). But what would they do on mosses like ***Fontinalis*** (Figure 11)? They are also known from bog

pools where they attach to ***Sphagnum*** (Figure 2, Figure 21, Figure 61-Figure 62) and algae (Figure 8).

Figure 6. ***Collotheca campanulata***, a rotifer that takes up residence on aquatic plants, ***Sphagnum***, and algae. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 7. ***Collotheca campanulata***, a species that is known as sessile on ***Sphagnum*** and occurs in bog pools. Photo by Yuuji Tsukii, with permission.

Figure 8. ***Collotheca campanulata***, a species that is known as sessile on ***Sphagnum*** in bogs and occurs in bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 9. ***Riccia fluitans***, a substrate for rotifers, stranded here above water. Photo by Janice Glime.

Figure 10. ***Ricciocarpos natans***, potential home for rotifers. Photo by Janice Glime.

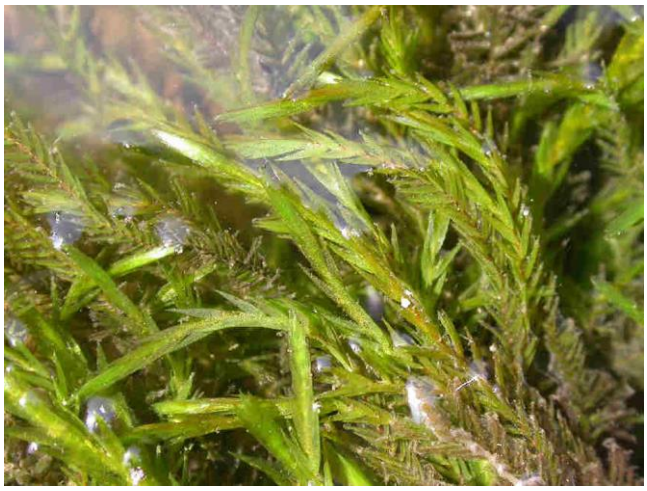

Figure 11. ***Fontinalis antipyretica*** var. ***gracilis***, home for rotifers that are able to feed on the associated detritus. Photo by David T. Holyoak, with permission.

Sphagnum peatlands (Figure 61) are home to several species of ***Collotheca***. ***Collotheca coronetta*** (Figure 12-Figure 13) and ***Collotheca ornata*** (Figure 14) live sessile on ***Sphagnum*** (Figure 21, Figure 62) (Jersabek *et al*. 2003). ***Collotheca ornata*** also occurs on wet mosses and in plankton on Svalbard. ***Collotheca crateriformis*** (Figure 15-Figure 16) and ***C. trilobata*** (Figure 17) live among ***Sphagnum*** (Figure 21). Bielańska-Grajner *et al*. (2011) reported ***C. wiszniewski*** from bogs and fens in Poland.

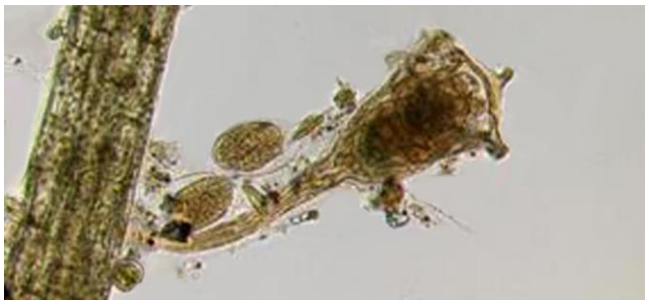

Figure 12. ***Collotheca coronetta***, a species that occurs sessile on ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

Figure 13. ***Collotheca coronetta***, a species that lives sessile on ***Sphagnum***, shown here with mucilage and resting eggs. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 14. ***Collotheca ornata***, a species that lives in bogs and is sessile on ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

Figure 15. ***Collotheca crateriformis*** from among ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

Figure 16. ***Collotheca crateriformis*** from among ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

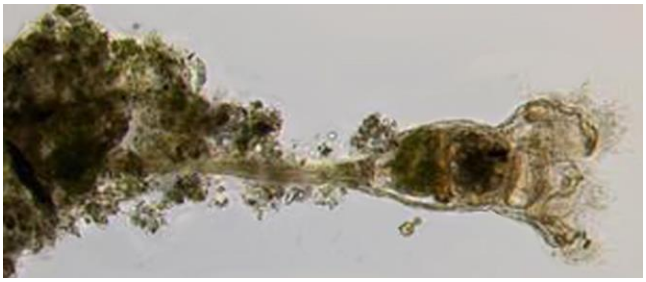

Figure 17. ***Collotheca trilobata*** from among ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

Stephanoceros

So far I have found few reports on ***Stephanoceros*** from bryophytes, but then, it is a genus with only two species (Meksuwan *et al*. 2013), both of which occur on bryophytes. And even the taxonomy is questionable, with the genus arguably belonging to ***Collotheca***. ***Stephanoceros fimbriatus*** (Figure 18-Figure 20) is a sessile species that lives on ***Sphagnum*** (Figure 21) as one of its substrates (Jersabek *et al*. 2003). ***Stephanoceros millsii*** (Figure 22) is known from bryophytes.

Figure 18. ***Stephanoceros fimbriatus***, a sessile species that can occur ln ***Sphagnum***. Photo by Wim van Egmond, with permission.

Figure 19. ***Stephanoceros fimbriatus*** with ***Sphagnum***. Photo by Marek Mis <www.mismicrophoto.com>, with permission.

Figure 20. ***Stephanoceros fimbriatus*** female, a species that occurs sessile on ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 21. ***Sphagnum cuspidatum***, potential home for a variety of rotifers. Photo by David T. Holyoak, with permission.

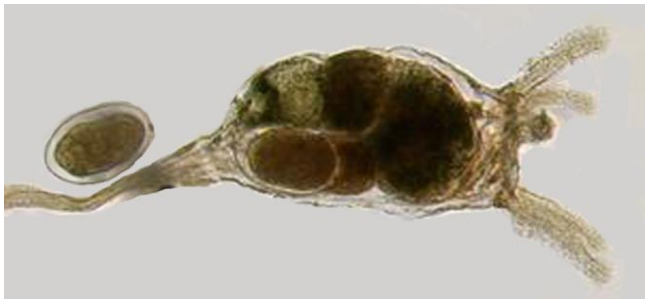

Figure 22. ***Stephanoceros millsii***, a species known from bryophytes. Note the eggs. Photo by Jersabek *et al.* 2003.

ORDER FLOSCULARIACEA

Not only do the members of this order lack toes; some of the planktonic species lack feet as well. Nevertheless, they have multiple **foot glands** to secrete glue. The rotary organ has a double ring of cilia that surrounds the anterior of its lobe-like appendages. Species may be either free-living or sessile and are suspension feeders.

Conochilidae

The species ***Conochilus hippocrepis*** (Figure 23-Figure 24) is typically planktonic in both ponds and large bodies of water, but among these habitats you can find it associated with ***Sphagnum*** (Figure 21) (Jersabek *et al.* 2003). It generally lives in a habitat with a *p*H of 6.3-8.3 and temperature range of 6.4-15.4°C (de Manuel Barrabin 2000). Its colonies can reach 30-60 members that are joined in a gelatinous case (Figure 25). Detritus and bacteria, generally abundant in the habitat, serve as food (Pourriot 1977).

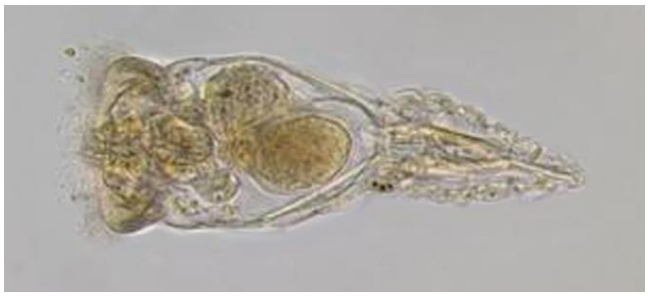

Figure 23. ***Conochilus hippocrepis*** female, member of a genus known on ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 24. ***Conochilus unicornis*** female, member of a genus known to associate with ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

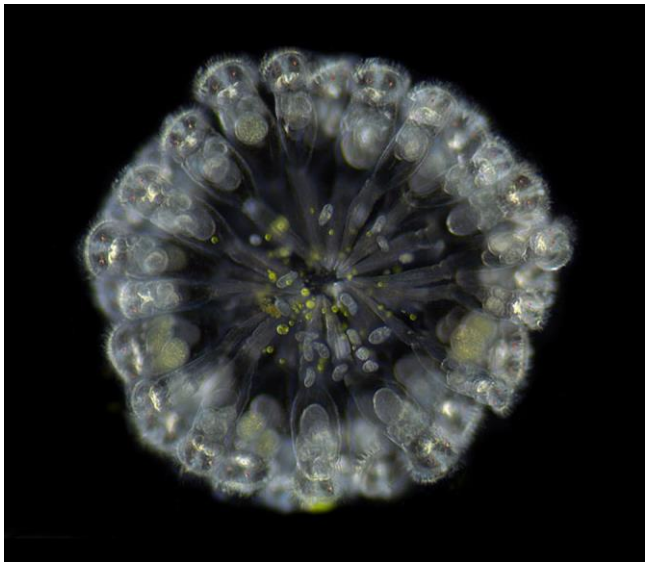

Figure 25. ***Conochilus*** sp. colony. This genus has species that are sessile on ***Sphagnum***. Photo by Wim van Egmond, with permission.

Conochilus hippocrepis (Figure 23-Figure 24) is sensitive to increasing predator pressure from the copepod ***Parabroteas sarsi*** (Figure 26) (Diéguez & Balseiro 1998). As the predator increases in size and begins to prey on the ***C. hippocrepis***, this rotifer responds by increasing its colony size (Figure 25). This seems to be the only member of this family known to associate with bryophytes, in particular ***Sphagnum*** (Figure 21).

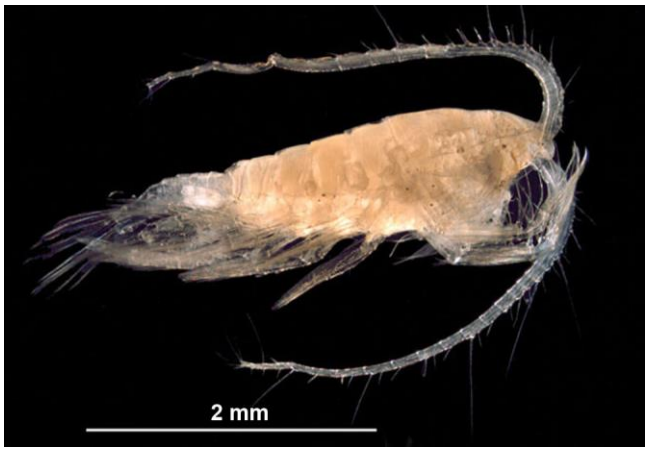

Figure 26. ***Parabroteas sarsi*** male, predator on ***Conochilus hippocrepis***. Photo by Cristián Correa Guzmán, with permission.

Flosculariidae

In this family the male is small and free-swimming, whereas the female lives in a tube and usually attaches by its modified foot. Some of these females (*e.g.* ***Ptygura linguata***) live on the bladders of species of the bladderwort ***Utricularia***. But, sadly for the rotifers, they also constitute part of the diet of these same bladderworts (Mette *et al*. 2000). This habitat affords the rotifers a special aid in getting food as it is sucked into the bladder. Bryophytes can offer no such aid, and although the genera on bryophytes are often the same because they are sessile, species differ.

Floscularia

The genus ***Floscularia*** (Figure 27-Figure 29) is a tube builder and is known to live on ***Sphagnum*** (Figure 66) (Hingley 1993). Jabez Hogg described this tube-building behavior in 1883 (*In* Rotifers 2012). The case is composed of tiny pellets. Gosse, in 1851 (*In* Rotifers 2012), reported a specimen attached to a submerged moss in a pond and observed its case-building behavior. I cannot improve upon the text provided by Hogg (1854, *In* Rotifers 2012): "In November, 1850, Mr. Gosse found a fine specimen of a ***Floscularia*** (Figure 27-Figure 29) attached to a submerged moss from a pond at Hackney; this he watched as it engaged in building its case, and at the same time discovered the use of the curious little rotatory organ on the neck. When fully expanded, the head is bent back at nearly a right angle to the body, so that the [rotary] disc (Figure 29) is placed nearly perpendicularly, instead of horizontally; the larger petals, which are the frontal ones, being above the smaller pair." The terminology has changed, but the observations still provide us with a clear picture of this rotifer on a moss. He discovered the role of these wheels of cilia by adding carmine to the water and observing its pathway.

Figure 27. ***Floscularia conifera*** female, a species that occurs sessile on ***Sphagnum*** and in bog pools. Photo by Jersabek *et al*. 2003, with permission.

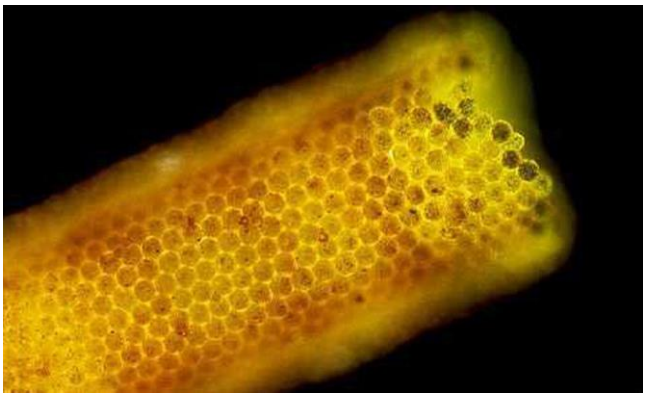

Figure 28. ***Floscularia ringens*** tube. Photo with online permission from <http://www.micrographia.com/>.

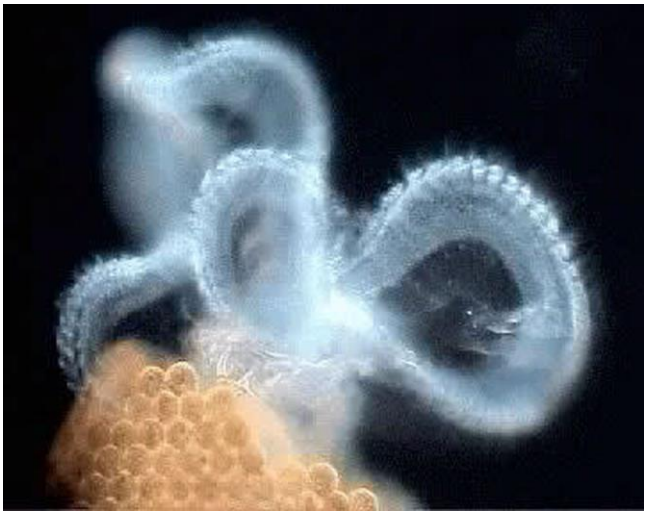

Figure 29. Tip of case of ***Floscularia ringens***, showing the geometric arrangement of pellets and the rotary apparatus. Photo by Martin Mach, with permission.

Gosse (1851 *In* Rotifers 2012) provided a charming description of the feeding as well: "If the atoms be few, we see them swiftly glide along the facial surface, following the irregularities of outline with beautiful precision, dash round the projecting chin like a fleet of boats doubling a bold headland, and lodge themselves, one after another, in the little cup-like receptacle beneath." But these were not used as food. Rather, they were eventually emptied from the cup, which was bent down to the margin of the case and the pellet, mixed with "salivary secretion," added to the margin of the case (Figure 29). Each pellet required 2-3 minutes to be gathered and deposited.

Fontaneto *et al.* (2003) added detail to tube building in ***Floscularia***. They observed that each pellet in the tube has a hole in the middle. The pellets are cemented together with "glue bundles" and the tube is lined with mucus.

Ptygura

As I read through account after account of rotifer sampling, I can't help but wonder if more attention should be given to the bryophyte habitat for locating new rotifer species, especially for sessile groups like this one. A number of these species are sessile on ***Sphagnum*** (Figure 66) and feed on associated algae. De Smet (1990) reported an unidentified species from wet mosses on Svalbard.

Ptygura rotifer (Figure 30) is a free-swimming rotifer (Michael Plewka, pers. comm. 6 August 2016), but Hingley (1993) collected them among ***Sphagnum*** (Figure 66) as well and reported them as sessile there.

Ptygura brachiata (Figure 31-Figure 32) and ***P. velata*** (Figure 33) likewise are species that live on ***Sphagnum*** (Figure 66) (Jersabek *et al*. 2003; Opitz 2016). In addition, a number of species live on other bryophytes as well as living in bogs. For example, ***Ptygura crystallina*** (Figure 34) lives on bryophytes and in bogs in the Pocono Mountains, Pennsylvania, USA. ***Ptygura melicerta*** (Figure 35-Figure 38) forms colonies (Figure 35) in a lake in Wisconsin, USA, but it is also present on bryophytes and in bog pools. It is common among colonies of the **Cyanobacterium *Gloeotrichia*** (Figure 38) (Plewka 2016).

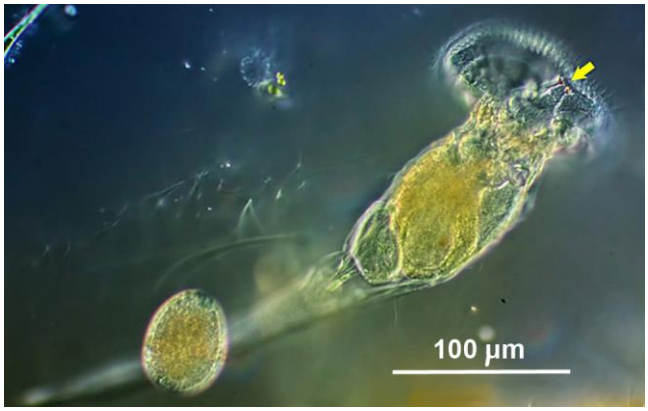

Figure 30. ***Ptygura rotifer***, a species of submersed moss in ponds. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 31. ***Ptygura brachiata*** female, known to be sessile on ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 32. ***Ptygura brachiata***, a species known to be sessile on ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 33. ***Ptygura velata***, typically living on ***Ceratophyllum***, occurs in bogs. Photo by Michael Plewka <www.plingfactory.de>, with permission.

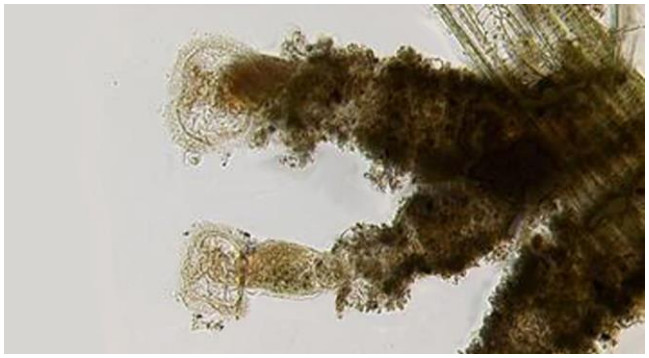

Figure 34. ***Ptygura crystallina*** female, a species from bryophytes and can occur in bogs. Photo by Jersabek *et al.* 2003, with permission.

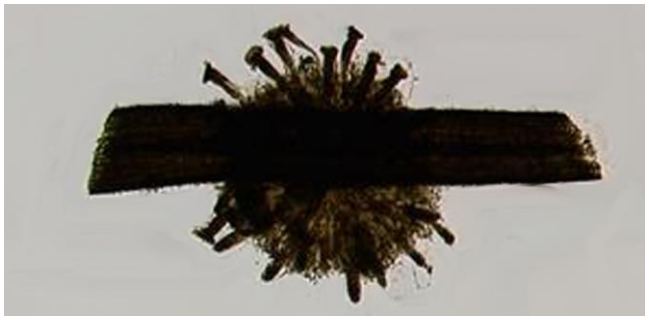

Figure 35. ***Ptygura melicerta*** colony in a lake in Wisconsin, USA. This species can occur among bryophytes and in bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 36. ***Ptygura melicerta*** female from a lake in Connecticut, USA. Here it is among **Cyanobacteria**; it can occur among bryophytes. Photo by Jersabek *et al.* 2003, with permission.

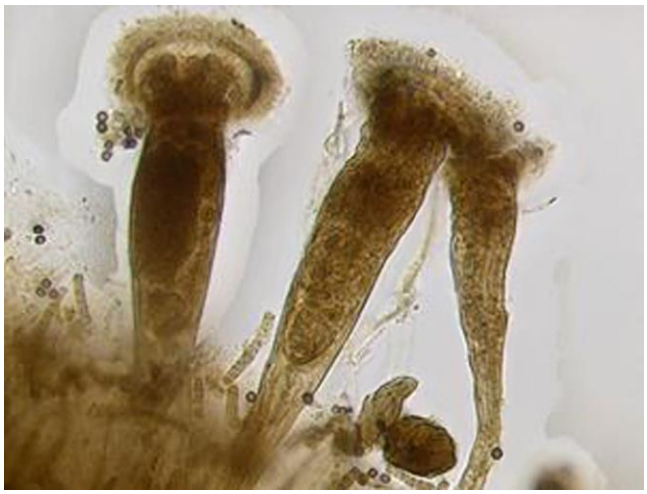

Figure 37. ***Ptygura melicerta*** colony in a lake in Wisconsin, USA. This species is known from bryophytes and bog pools. Photo by Jersabek *et al.* 2003, with permission.

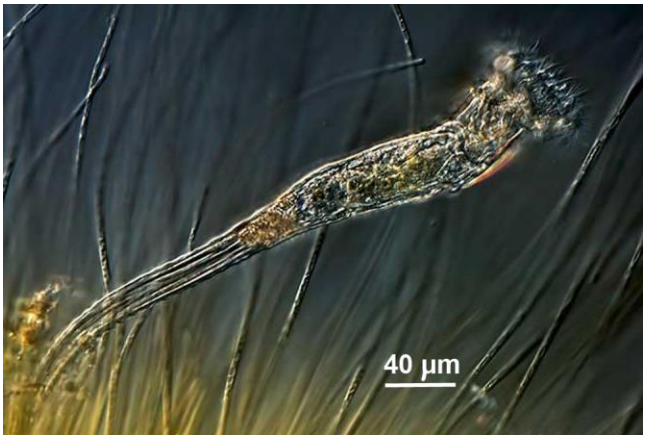

Figure 38. ***Ptygura melicerta*** with ***Gloeotrichia***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Ptygura pilula (Figure 39) seems to be more commonly a moss dweller, including ***Sphagnum*** (Figure 40), where it passes dry periods with a gelatinous covering (Plewka 2016). It incorporates feces (Figure 39-Figure 41) into this tubular housing, further adding to its protection. It also produces resting eggs (Figure 42) that help it to survive dry periods. ***Ptygura stygis*** is also known from submerged mosses (Ptygura 2016).

Figure 39. ***Ptygura pilula*** with feces in gelatinous housing. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 40. ***Ptygura pilula*** female sessile on a ***Sphagnum*** leaf; it also occurs in bog pools. Photo by Jersabek *et al.* 2003, with permission.

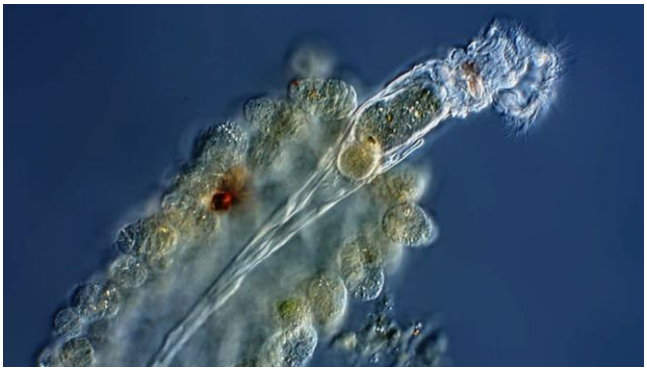

Figure 41. ***Ptygura pilula*** in case, an aquatic moss inhabitant. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 42. ***Ptygura pilula*** resting egg. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Hexarthridae

In a study of a Turkish lake, Gülle *et al*. (2010) found that rotifers were most abundant from June through August and disappeared from November through April. It was a member of the **Hexarthridae**, *Hexarthra fennica*, that was one of the dominant taxa – 51% of the zooplankton. The rotifers were most dense at a depth of 5 m. But it seems that bryophyte dwellers are few. I found only ***Hexarthra mira*** (Figure 43-Figure 44) reported as a bog and occasional bryophyte dweller, but this species is likewise planktonic. It most likely occurred among mosses accidentally from open water. Its amictic eggs become resting eggs (Figure 45-Figure 46), helping to permit its survival as its habitat dries.

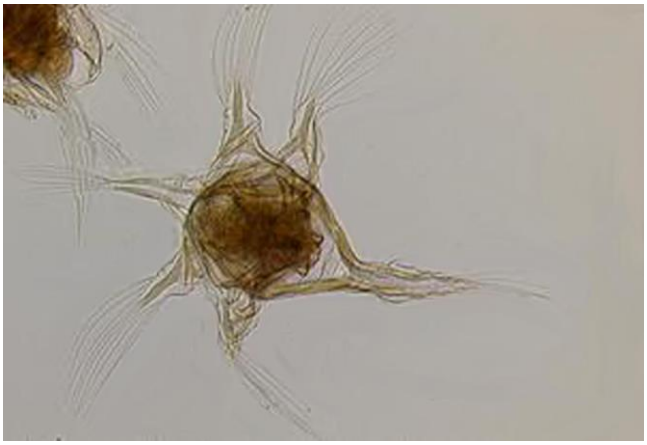

Figure 43. ***Hexarthra mira***, a typically planktonic species known from bryophytes and bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 44. ***Hexarthra mira*** female from Mexico. This planktonic species is sometimes found among bryophytes and in bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 45. ***Hexarthra mira*** with amictic egg. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 46. ***Hexarthra mira*** resting egg. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Testudinellidae

The family **Testudinellidae** includes both saltwater and freshwater species. It is characterized by having dorsal and ventral plates of the lorica that are completely fused laterally. The body is greatly flattened dorsi-ventrally (top-bottom). The foot is long and retractile (see Figure 49 and Figure 50) with a tuft of cilia at its tip. These rotifers are free swimming, typically in the littoral zone, but members of ***Testudinella*** (Figure 48-Figure 59) may also occur on bryophytes and in ***Sphagnum*** pools (Figure 5) as well as on other macrophytes. There are three genera, but only ***Testudinella*** seems to be represented on bryophytes.

Myers (1942) provided one of the more detailed texts on rotifer habitats. Among these are a number of species that live on or among ***Sphagnum*** (Figure 21) or in pools (Figure 5) among the peatlands. One such species is ***Testudinella armiger*** (Figure 47), a species that lives on the emergent species ***Sphagnum cuspidatum*** (Figure 21).

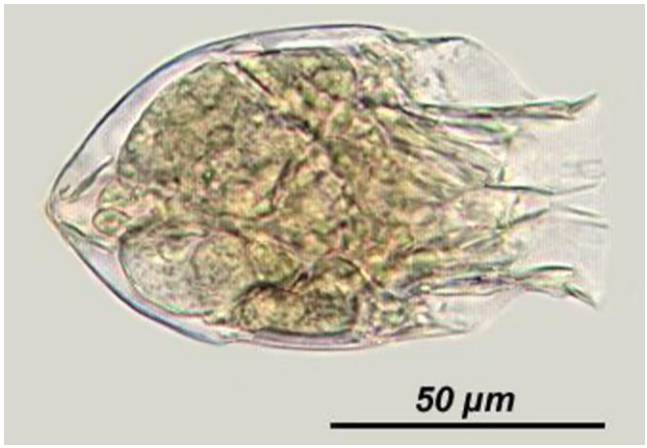

Figure 47. ***Testudinella armiger***, an inhabitant of ***Sphagnum cuspidatum***. Photo by Jersabek *et al.* 2003, with permission.

The records for ***Sphagnum*** (Figure 21) associates include ***Testudinella aspis***, ***T. emarginula*** (Figure 48), ***T. epicopta*** (Figure 49), ***T. tridentata*** (Figure 50-Figure 51), and ***T. truncata*** (Figure 52) (Myers 1942; Jersabek *et al.* 2003). ***Testudinella emarginula*** occurs in ***Sphagnum*** bogs (Figure 66) (Jersabek *et al.* 2003). This cosmopolitan species lives on plant surfaces, although it occasionally occurs in the plankton (de Manuel Barrabin 2000). It is a cold-water species (7.7-7.8°C) with a circumneutral *p*H preference (*p*H 6..8-7.5) and wide alkalinity range.

Figure 48. ***Testudinella emarginula*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 49. ***Testudinella epicopta*** from among ***Sphagnum***. Photo by Jersabek *et al. 2003*, with permission.

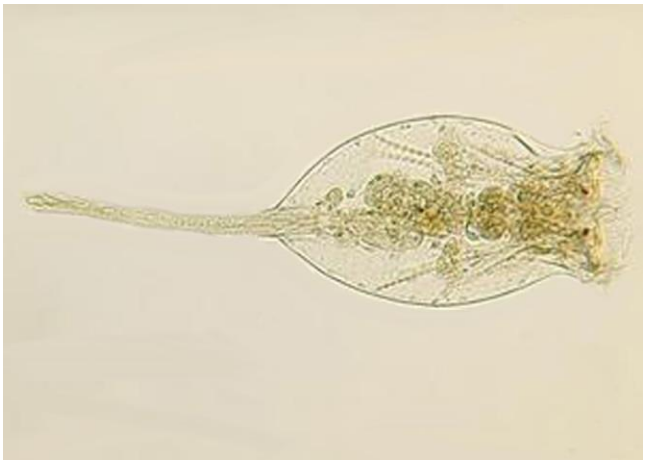

Figure 50. ***Testudinella tridentata*** subsp. ***dicella*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

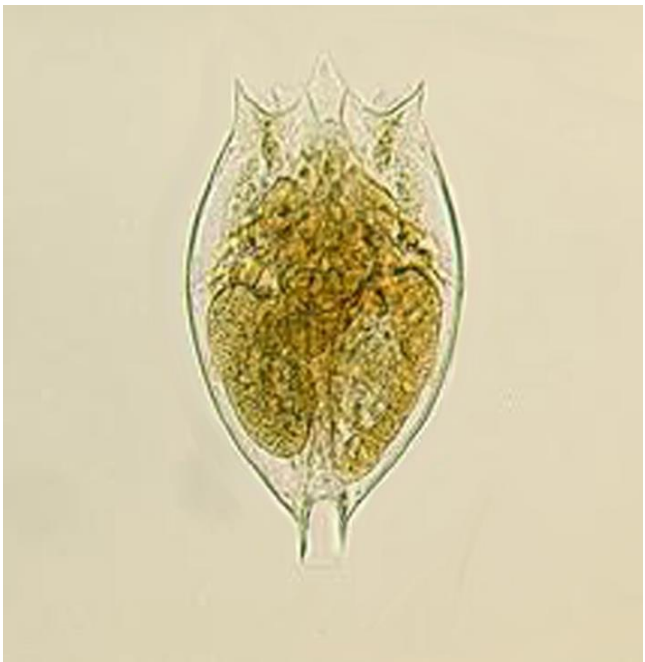

Figure 51. ***Testudinella tridentata*** subsp ***dicella*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

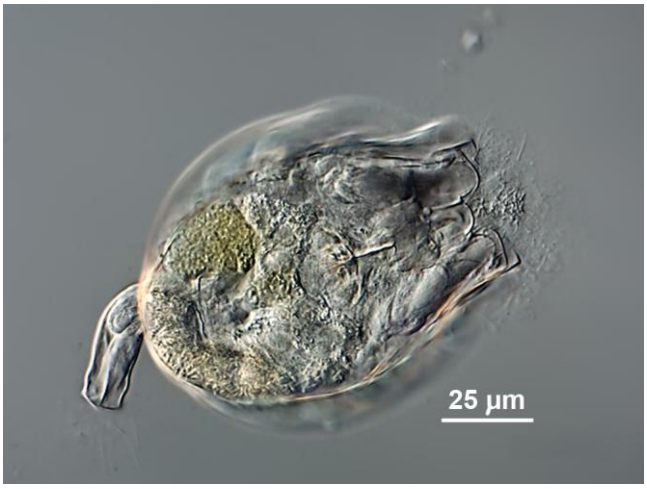

Figure 52. ***Testudinella truncata***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Testudinella incisa (Figure 53) is typically a plankton species (Plewka 2016), but it also occurs in association with ***Sphagnum*** (Figure 54) (Jersabek *et al*. 2003). The former subspecies, ***T. incisa emarginula***, is now considered a separate species, ***T. emarginula***, so it is possible that the reference to the planktonic ***T. incisa*** really belongs to ***T. emarginula***.

Figure 53. ***Testudinella incisa***, a species sometimes associated with ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

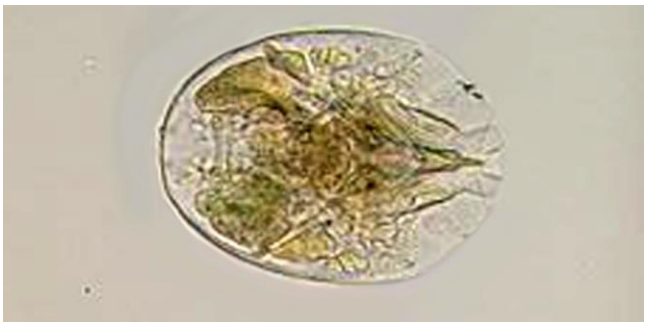

Figure 54. ***Testudinella emarginula*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Some members of ***Testudinella*** (Figure 55) are known from bryophytes outside of bogs. Others, such as ***Testudinella elliptica*** (Figure 56-Figure 57), live among both bog bryophytes and non-bog bryophytes.

Figure 55. ***Testudinella patina***, a genus that occurs on bryophytes. Note the complete retraction of the foot. Photo by Wim van Egmond, with permission.

Figure 56. ***Testudinella elliptica***, a species that lives on both ***Sphagnum*** and other bryophytes. Photo by Michael Plewka <www.plingfactory.de>.

Figure 57. ***Testudinella elliptica***, a species that lives on both ***Sphagnum*** and other bryophytes. Photo by Michael Plewka <www.plingfactory.de>.

Testudinella patina (Figure 58-Figure 59) is a planktonic species that likes small bodies of water where aquatic plants are abundant (de Manuel Barrabin 2000), but it is also known from peatlands (bogs or fens) in Poland (Bielańska-Grajner *et al*. 2011). Bryophytes are among the aquatic plants in some associations where it has been found. The aquatic plant area provides it with its preferred foods of the green alga ***Chlorella*** (Figure 64) and diatoms (Figure 60). It tolerates high salinity and lives in a *p*H range of 6.3-8.89. It enjoys a wide temperature range of 9.5-24.3°C. Some occur on mosses in Antarctica (Figure 59).

Figure 58. ***Testudinella patina*** female, a species that sometimes is associated with aquatic bryophytes. Here its cilia are withdrawn. Photo by Jersabek *et al.* 2003, with permission.

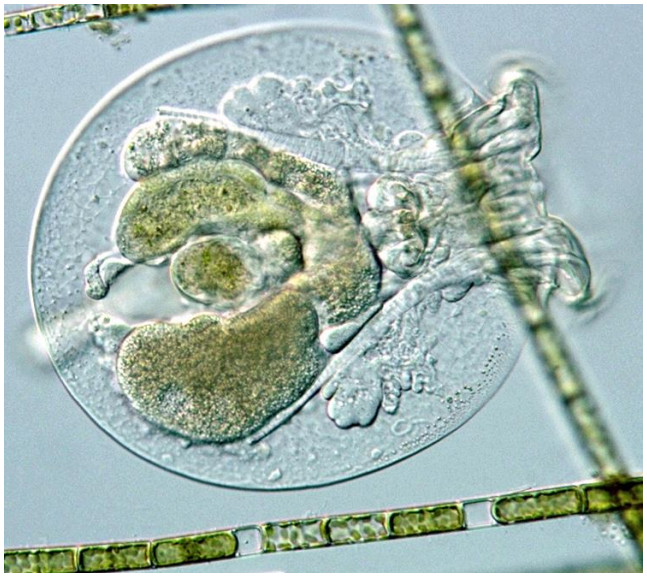

Figure 59. ***Testudinella patina***; some members of this genus are Antarctic moss dwellers. Photo by Yuuji Tsukii, with permission.

Figure 60. Diatoms that can be found among bryophytes, some serving as food for rotifers living there. Photo by Damian H. Zanette, through Public Domain.

ORDER PLOIMIDA

This order has the most families. But are these species ones likely to be on bryophytes? Myers (1942) reported 52 species of ploimate rotifers among ***Sphagnum subsecundum*** (Figure 61-Figure 62) from collections in 1941.

Figure 61. ***Sphagnum subsecundum*** in its habitat, home of ***Pedipartia gracilis***. Photo by Michael Lüth, with permission.

Figure 62. ***Sphagnum subsecundum***, home of ***Pedipartia gracilis***. Photo by Michael Lüth, with permission.

Wallace *et al*. (2008) asked if "everything is everywhere?" They answered this question in the Chihuahua Desert pools in Mexico. They found that indeed the specialized, warm-water habitat of the desert did not support "everything." The microinvertebrate fauna was dominated by rotifer families that are also common on bryophytes: **Brachionidae**, **Lecanidae**, **Lepadellidae**, and **Notommatidae**. Both habitats dry up. The full statement for "everything is everywhere" includes "but the environment selects." The desert pools are actually a similar environment to that of bryophytes that dry out between rain events.

Trochosphaeridae

Cryptic species, morphologically indistinguishable biological groups incapable of interbreeding, are not uncommon in many rotifer families. ***Filinia*** species of **Trochosphaeridae** are highly variable and likely comprise a number cryptic species (Ruttner-Kolisko 1989). This is at least in part due to the parthenogenetic reproduction that can quickly lead to a clone of genetically identical individuals in a **founder population** in a lake or other habitat. This is furthermore complicated by the absence of many good morphological characters by which to distinguish species. In the ***Filinia terminalis-longiseta*** group, ecological properties differ and suggest the existence of these microspecies, or perhaps sister species. Only two members of the **Trochosphaeridae** seem to be known from bryophytes: ***Filinia longiseta*** (Figure 63) and ***F. terminalis*** (Figure 65).

Filinia longiseta (Figure 63) is known from bryophytes in England and Ireland. This is typically a cosmopolitan planktonic species of lakes, ponds, moorland waters, and even brackish water (de Manuel Barrabin 2000). It lives in a wide range of warm temperatures (7.7-26.2°C) and *p*H (6.3-9.9). It is a filter feeder on detritus, bacteria, and small algae like ***Chlorella*** (Figure 64) in a size range of 10-12 µm (Pourriot 1965) and most likely competes for its food with members of the rotifer genus ***Conochilus*** (Figure 23-Figure 25).

Figure 63. ***Filinia longiseta***, a bryophyte dweller in lakes, ponds, and moorland waters. Photo by Jersabek *et al*. 2003, with permission.

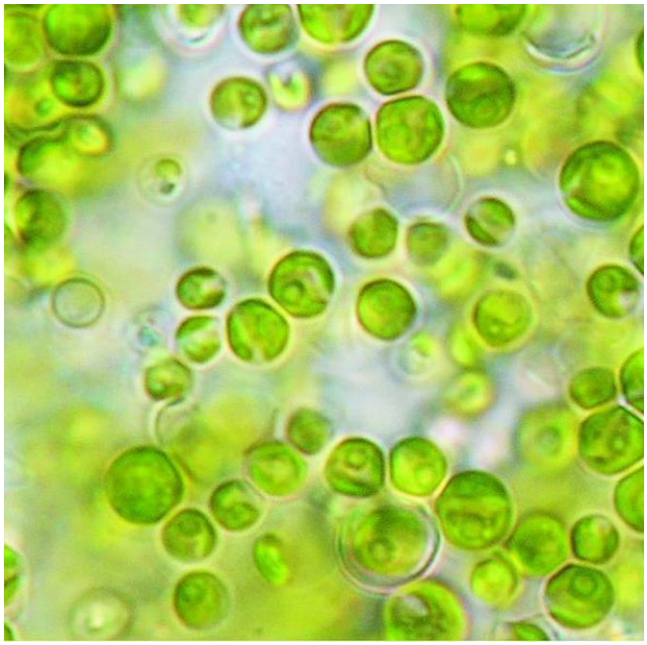

Figure 64. ***Chlorella vulgaris***, a green alga that is often associate with ***Sphagnum*** and that provides food for ***Testudinella patina***. Photo by Sarah Duff, through Creative Commons.

Filinia terminalis (Figure 65) is morphologically variable but seems to occupy a narrow and well-defined niche (Ruttner-Kolisko 1980). At an oxygen content of less than 2 mg L^{-1}, it can reach as many as 1000 individuals per liter. Not surprisingly, it is facultatively anaerobic. Its food sources include bacteria that are chemosynthetic or that decompose plankton.

Figure 65. ***Filinia terminalis*** female, Photo by Jersabek *et al*. 2003, with permission.

Although ***Filinia terminalis*** (Figure 65) is a cosmopolitan, planktonic species, it is known from bryophytes and ***Sphagnum*** bogs (Figure 66) (de Manuel Barrabin 2000). Its preferred conditions are mesotrophic to eutrophic in a *p*H range of 6.64-8.22. Its temperature range is relatively wide: 7.3-22.8°C, although de Manuel Barrabin considers it to be a species of the cool **hypolimnion** (bottom layer of deep lake or ocean; temperature never goes below 4°C). Ruttner-Kolisko (1980) found that it prefers temperatures below 12-15°C.

Figure 66. ***Sphagnum papillosum***, a bog moss. Photo by James K. Lindsey, with permission.

Brachionidae

This is a family dominated by planktonic species and was the family with the most species represented in Spanish reservoirs (de Manuel Barrabin 2000), but a few seem to spend time among bryophytes, perhaps as a place to avoid predation, or just dropped there by moving water. An interesting study by Stenson (1982) demonstrated, however, that an experimental reduction of the fish population led to an increase in larger rotifers and a decrease in the smaller filter-feeding species such as ***Keratella cochlearis*** (Figure 79), a member of the **Brachionidae**. Stenson attributed this to a change in competition for food from rotifers such as ***Polyarthra*** (**Synchaetidae**; Figure 67).

Figure 67. ***Polyarthra major***, a large rotifer that eats smaller rotifers. Note the feather-like blades that are used like paddles in swimming. Photo by Wim van Egmond, with permission.

Anuraeopsis

Anuraeopsis fissa (Figure 68-Figure 71) has been reported from a pond in Pennsylvania, USA (Jersabek *et al.* 2003). This is a planktonic rotifer that has been found among bryophytes and in bog pools. It prefers warm water and a **eutrophic** (nutrient-rich) habitat (Margalef 1955). It frequents small water bodies (de Manuel Barrabin 2000). Its food includes bacteria and detritus (Pourriot 1977) and it may become food for the rotifer ***Asplanchna*** (Figure 72) (Guiset 1977).

Figure 68. ***Anuraeopsis fissa*** with an emerging juvenile from a pond in Pennsylvania, USA. Photo by Jersabek *et al.* 2003, with permission.

Figure 69. ***Anuraeopsis fissa*** showing toes and red eyespot. Photo by Michael Pewka <www.plingfatory.de>, with permission.

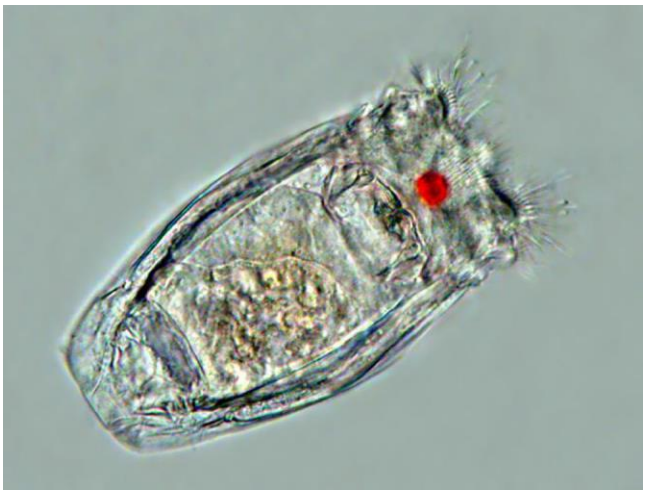

Figure 70. ***Anuraeopsis fissa*** showing a single, light-sensitive red eyespot and cilia, but with toes retracted. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 71. ***Anuraeopsis fissa*** with amictic eggs. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 72. ***Asplanchna***, in this case with a gut of ***Keratella***. It is also a predator on ***Anuraeopsis fissa***. Photo by Wim van Egmond, with permission.

Brachionus

Brachionus urceolaris (Figure 73) is planktonic, common in small, alkaline bodies of water (*p*H 7.25-9) (de Manuel Barrabin 2000). It can occur in moving water and is relatively tolerant of high salinity. It is a cosmopolitan species with a wide temperature tolerance (7.35-24.3°C). Despite its alkaline preference, Hingley (1993) found it closely associated with ***Sphagnum*** (Figure 21) in a bog.

Figure 73. ***Brachionus urceolaris***, a species that is closely associated with bog ***Sphagnum***. Photo from Proyecto Agua, with permission.

Brachionus urceolaris (Figure 74), and probably others, has a survival trick against predation. The eggs survive consumption by predators such as the cladoceran *Leptodora kindtii* (Figure 75) without harm (Nagata *et al*. 2011). Often the cladocerans would eject the eggs, and they typically ejected the lorica while digesting the living contents. There was a negative correlation between the portion of unconsumed (ejected) eggs and the length of the predator. That is, longer predators ejected fewer eggs. Nevertheless, hatching success seemed to be independent of the predator's body length. As many as 75% of the undigested eggs hatched successfully.

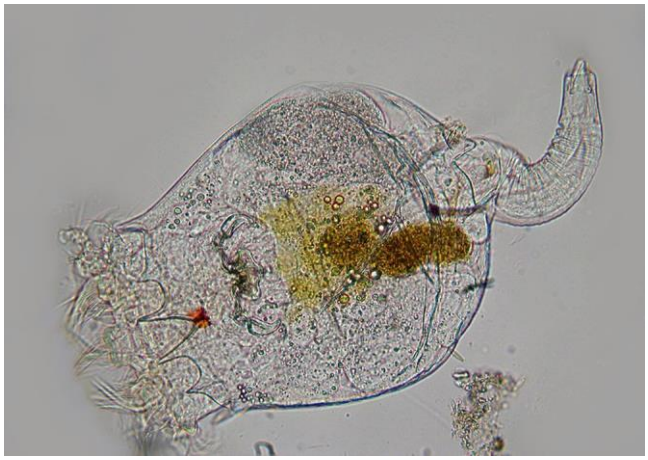

Figure 74. ***Brachionus urceolaris***, a planktonic species that can occur in a ***Sphagnum*** bog. Photo by Michael Verolet, with permission.

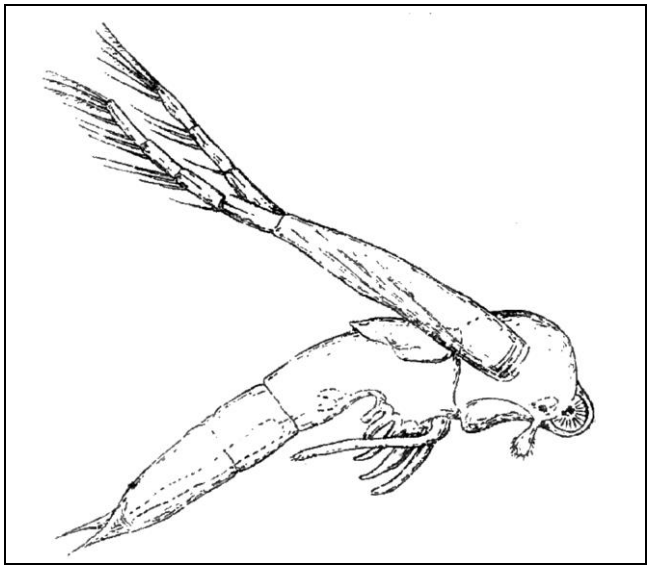

Figure 75. ***Leptodora kindtii***, a large cladoceran that is a predator on ***Brachionus urceolaris***. Drawing by A. Milnes Marshall, through Public Domain.

Kellicottia

Kellicottia is a genus with only two species (Segers 2007). ***Kellicottia longispina*** (Figure 76-Figure 77) is a central European species known from bryophytes, but it is actually typically a planktonic species (Plewka 2016). Its long spines no doubt help to protect it from predation (see Barnhisel 1991), but Madaliński (1961) suggested they

may help attach it to bryophytes. It is active year-round as an inhabitant of oligotrophic lakes with a rather narrow *p*H range of 8.2-8.5, but as expected its temperature range is broad (10.6-21.8°C) and it does not occur in small bodies of water (de Manuel Barrabin 2000). Its food is primarily chrysomonads and centric diatoms (Pourriot 1977).

Figure 76. ***Kellicottia longispina*** female, a planktonic species that has also been found with bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 77. ***Kellicottia longispina*** demonstrating spines that may help in attaching it to bryophytes. Photos by Michael Plewka <www.plingfactory.de>, with permission.

Figure 78. ***Kellicottia longispina*** demonstrating spines that probably protect it from predation. Photos by Michael Plewka <www.plingfactory.de>, with permission.

Keratella

Feeding rates are inversely related to the density of food organisms in ***Keratella cochlearis*** (Figure 79), as well as in the planktonic, but occasional bryophyte-dweller, ***Polyarthra vulgaris*** (**Synchaetidae**), and *Polyarthra dolichoptera* (Bogdan & Gilbert 1982). ***Keratella cochlearis*** preferred the alga ***Chlamydomonas*** (Figure 80) to all other foods offered, perhaps explaining the rarity of this rotifer among mosses, where ***Chlamydomonas*** also is uncommon (pers. obs.). Nevertheless, ***K. cochlearis*** lives in bog/fen habitats (Bielańska-Grajner *et al.* 2011) where some species of ***Chlamydomonas*** occur (Struder-Kypke & Schonborn 1999).

Figure 79. ***Keratella cochlearis*** showing lorica, a species that is mostly planktonic but also occurs in bog/fen peatlands. Photo by Michael Plewka <www.plingfactory.de>, with permission.

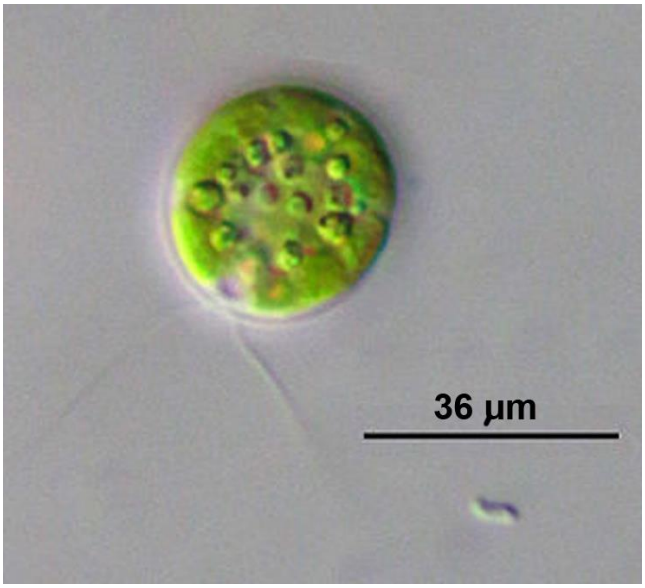

Figure 80. ***Chlamydomonas*** *globosa*, a genus that is food for ***Keratella cochlearis***. Photo by Picturepest, through Creative Commons.

Nevertheless, a number of species of ***Keratella*** live among bryophytes. ***Keratella mixta*** (Figure 81) lives among ***Sphagnum*** (Figure 62) (Jersabek *et al*. 2003). Others live in peatlands (bogs or fens), including ***K. paludosa*** (Figure 82) (Bielańska-Grajner *et al.* 2011).

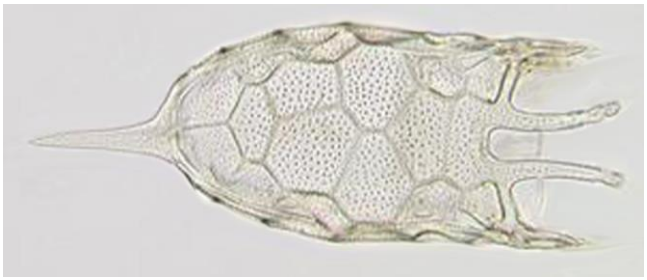

Figure 81. ***Keratella mixta*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 82. ***Keratella paludosa*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Keratella quadrata (Figure 83-Figure 85) is a species known from bryophytes. This is also a cosmopolitan species that is active all year round (de Manuel Barrabin 2000). It is tolerant of mineralization and survives a wide *p*H range of 6.64-10.19. Its temperature range is likewise wide (6.4-26.1°C), as expected for a perennial species. It has broad food preferences, including detritus, bacteria, and algae in the Chlorococcales, Volvocales, Euglenales, Chrysophyceae, and diatoms (Pourriot 1977). As is typical among rotifers, females are larger than males (Figure 84). Resting eggs (Figure 85) help it to survive in this changeable habitat.

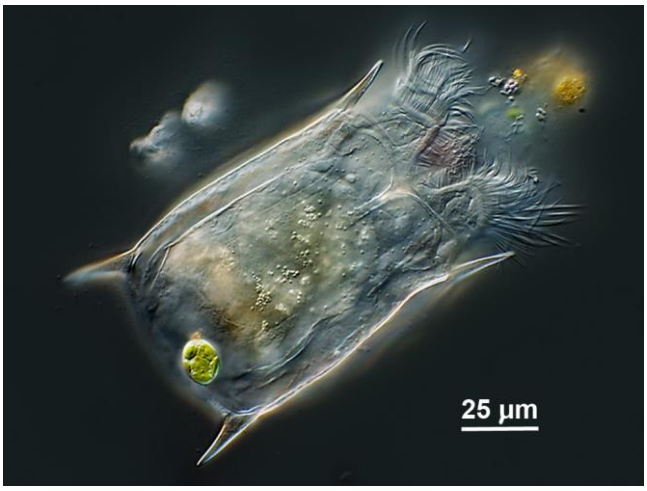

Figure 83. ***Keratella quadrata*** showing lorica and cilia. Photo by Michael Plewka <www.plingfactory.de>, with permission.

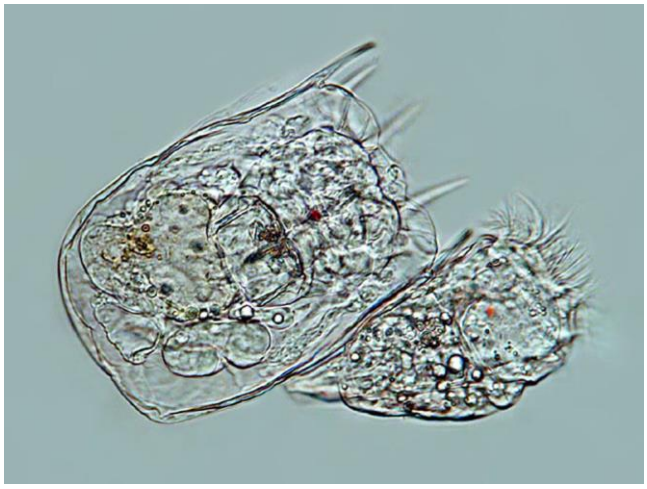

Figure 84. ***Keratella quadrata*** female (larger) and male (smaller), a species known from bryophytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 85. ***Keratella quadrata*** resting eggs. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Keratella serrulata (Figure 86-Figure 88) is the only planktonic brachionid that is a specialist of acid water, particularly water from bogs with ***Sphagnum*** (Figure 21) (Bērziņš & Pejler 1987; Bielańska-Grajner *et al*. 2011). Its known *p*H is around 6.6 and temperature around 18.6°C (de Manuel Barrabin 2000). It feeds on algae in the Chrysophyceae and Volvocales (Pourriot 1977). ***Sphagnum*** is important in creating its acid habitat – it lives especially in the outflow of ***Sphagnum*** bogs and poor fens (Jersabek *et al*. 2003).

Figure 86. ***Keratella serrulata***, an inhabitant of acid bog outflow water. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 87. ***Keratella serrulata***, a ***Sphagnum*** dweller, showing its ventral surface. Photo by Michael Plewka <www.plingfactory.de>, with permission.

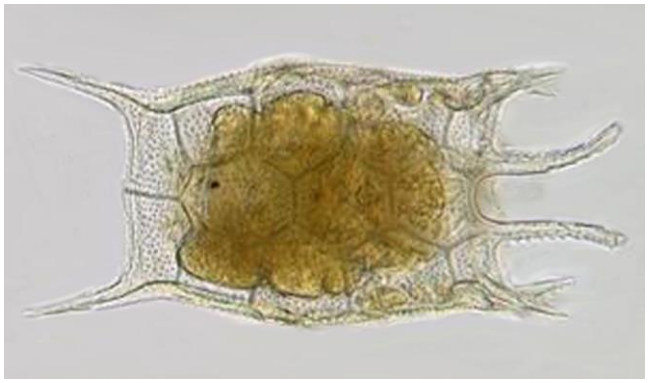

Figure 88. ***Keratella serrulata***, a species known from ***Sphagnum*** bogs and poor fen waters. Photo by Jersabek *et al.* 2003, with permission.

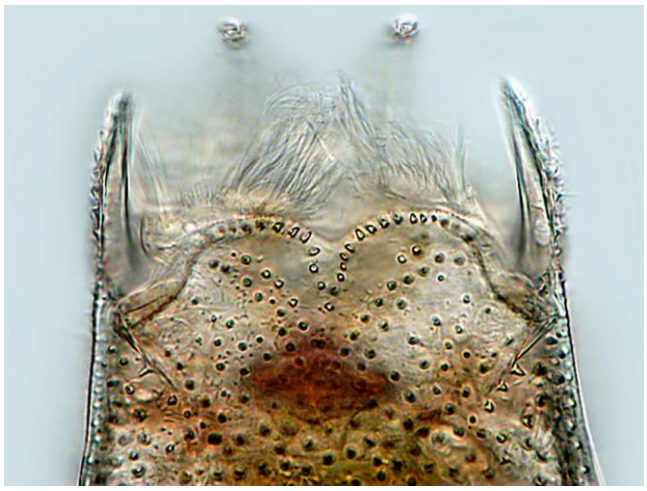

Figure 89. ***Keratella serrulata*** showing rotary cilia. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Keratella also can occur among wet mosses in waterfalls. Savatenalinton and Segers (2008) found ***Keratella cochlearis*** (Figure 79) and ***Keratella tropica*** (Figure 90) in a waterfall in Thailand, but it is likely that these planktonic species were carried there from open water (De Smet, per. comm. 3 November 2016).

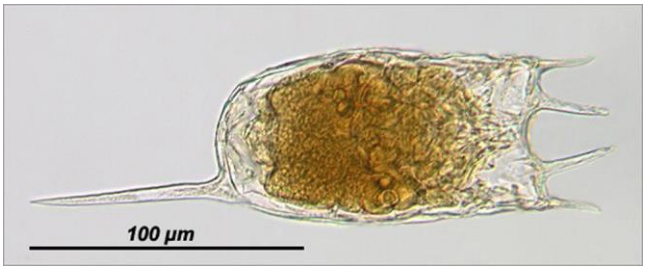

Figure 90. ***Keratella tropica***, a waterfall moss dweller. Photo by Jersabek *et al.* 2003, with permission.

Notholca

Although ***Notholca*** is a relatively large genus, only three species seem to be bryophyte dwellers. ***Notholca foliacea*** (Figure 91) occurs on mosses (Plewka 2016). ***Notholca latistyla*** is restricted to the Arctic and occurs on submerged mosses (De Smet 1990). ***Notholca squamula*** likewise occurs on submerged mosses on Svalbard.

Figure 91. ***Notholca foliacea*** from moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Dicranophoridae

The **Dicranophoridae** are predators and are agile in pursuing and capturing their prey (Pejler & Bērziņš 1993a). Unlike many rotifers, the **Dicranophoridae** are not planktonic – other predatory rotifers exist among the plankton – and they avoid the sediments where their prey organisms are not sufficiently abundant. Unlike many rotifers, these have been documented on two species of bryophytes through a study of their substrata. ***Albertia naidis*** (Figure 92), ***Aspelta angusta*** (Figure 97), ***A. aper*** (Figure 95), ***A. circinator*** (Figure 96), ***Dicranophorus forcipatus*** (Figure 117-Figure 118), ***D. haueri***, ***D. robustus*** (Figure 113-Figure 114), ***Encentrum eurycephalum***, ***E. fluviatile***, ***E. lupus***, and ***E. mustela*** (Figure 134), and ***E. uncinatum*** (Figure 131), were all present on 1-10% of the 122 collections of ***Fontinalis*** (Figure 11). ***Aspelta aper***, ***A. circinator***, ***Dicranophorus epicharis*** (Figure 107), ***D. luetkeni*** (Figure 110-Figure 112), ***Encentrum arvicola***, ***E. elongatum***, ***E. incisum*** (Figure 127), ***E. lupus***, ***E. sutor***, ***E. sutoroides***, ***E. tyrphos***, and ***Wierzejsklella velox*** (Figure

139-Figure 140) were all present on 1-10% of the 194 collections of ***Sphagnum*** (Figure 21). The species differ, but only the genus ***Albertia*** is present exclusively on ***Fontinalis***, and only ***Wierzejsklella*** is present exclusively on ***Sphagnum*** in this comparison. Both sets of bryophyte dwellers occur on a wide variety of other plant substrata – none was specific to bryophytes.

Albertia

Only one species of this relatively small genus is associated with bryophytes. ***Albertia naidis*** (Figure 92) not only occurs among ***Sphagnum*** (Figure 5) and ***Fontinalis*** (Figure 11), but it also is parasitic on ***Stylaria lacustris*** (Figure 93), an oligochaete (segmented worm) (Jersabek 2003).

Figure 92. ***Albertia naidis*** subsp ***intrusor*** from among ***Sphagnum*** and parasitic on ***Stylaria lacustris***. This species is also known from the aquatic moss ***Fontinalis***. Photo by Jersabek *et al.* 2003, with permission.

Figure 93. ***Stylaria lacustris***, an annelid that is parasitized by ***Albertia naidis***. Photo by Niels Sloth, with permission.

Aspelta

Several species of ***Aspelta*** live among ***Sphagnum*** (Figure 5) (*e.g.* ***A. beltista***, Figure 94) (Jersabek *et al.* 2003). Others occur not only with ***Sphagnum***, but also occur with the aquatic moss ***Fontinalis*** (Figure 11). These are ***Aspelta aper*** (Figure 95) (Pejler & Bērziņš 1993a) and ***A. circinator*** (Figure 96) (Plewka 2016). ***Aspelta angustus*** (Figure 97) occurs among mosses on rock and also among the periphyton on ***Sphagnum*** (Figure 21) (Plewka 2016).

Figure 94. ***Aspelta beltista*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 95. ***Aspelta aper***, a rotifer that occurs on both ***Fontinalis*** and ***Sphagnum*** species. Photo by Jersabek *et al.* 2003, with permission.

Figure 96. ***Aspelta cf circinator***, a species of ***Sphagnum*** ponds, but also occurs with ***Fontinalis***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

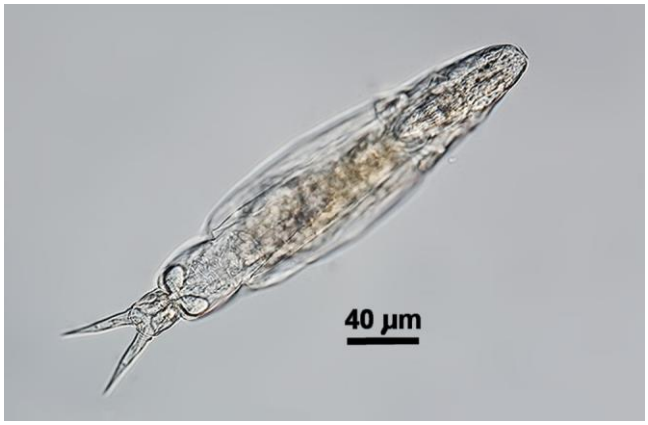

Figure 97. ***Aspelta angusta*** from among mosses on rock but also among the periphyton on ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Aspelta chorista (Figure 98) lives among the moss ***Warnstorfia exannulata*** (Figure 99-Figure 100) (Myers 1942; Jersabek *et al.* 2003).

Figure 98. ***Aspelta chorista*** from among the moss ***Warnstorfia exannulata***. Photo by Jersabek *et al.* 2003, with permission.

Figure 99. ***Warnstorfia exannulata*** habitat where one might find ***Aspelta chorista***. Photo by J. C. Schou, with permission.

One known species of ***Aspelta*** is more terrestrial. ***Aspelta secreta*** is characteristic of mosses on sandstone rocks in firewood habitats (De Smet & Verolet 2009).

Figure 100. ***Warnstorfia exannulata***, home for ***Aspelta chorista***. Photo by J. C. Schou, with permission.

Dicranophorus

Sphagnum (Figure 21) seems to be a common habitat for a number of species of ***Dicranophorus***. These include ***Dicranophorus alcimus*** (Figure 101; Jersabek *et al*. 2003), ***D. artamus*** (Figure 102; Jersabek *et al*. 2003), ***D. biastis*** (Figure 103; Jersabek *et al*. 2003), ***D. capucinus*** (Figure 104-Figure 105; Jersabek *et al*. 2003; Bielańska-Grajner *et al*. 2011), ***D. colastes*** (Figure 106; Jersabek *et al*. 2003), ***D. epicharis*** (Figure 107; Pejler & Bērziņš 1993a), ***D. facinus*** (Figure 108; Myers 1942), ***D. hercules*** (Bielańska-Grajner *et al*. 2011), ***D. isothes*** (Figure 109; Jersabek *et al.* 2003), ***D. luetkeni*** (Figure 110-Figure 112; Jersabek *et al*. 2003; Bielańska-Grajner *et al*. 2011), and ***D. proclastes*** (Myers 1942).

Figure 101. ***Dicranophorus alcimus*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

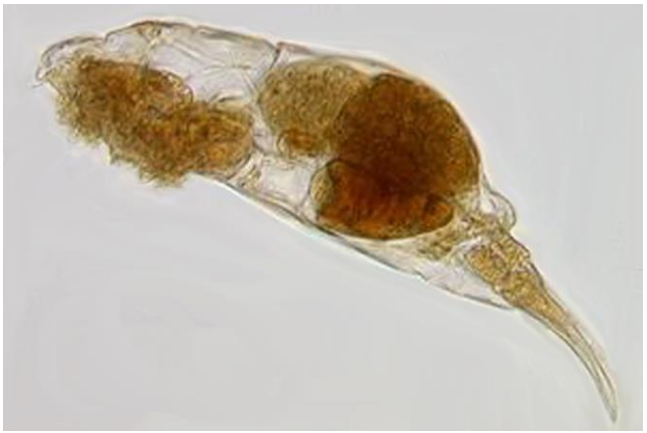

Figure 102. ***Dicranophorus artamus*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 103. ***Dicranophorus biastis*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

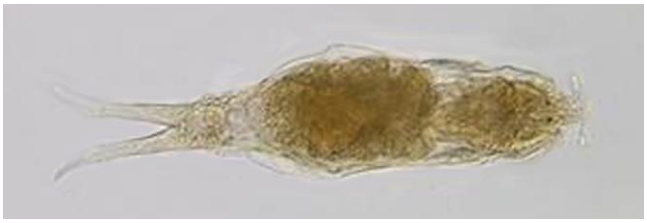

Figure 104. ***Dicranophorus capucinus*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 105. ***Dicranophorus capucinus*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 106. ***Dicranophorus colastes*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

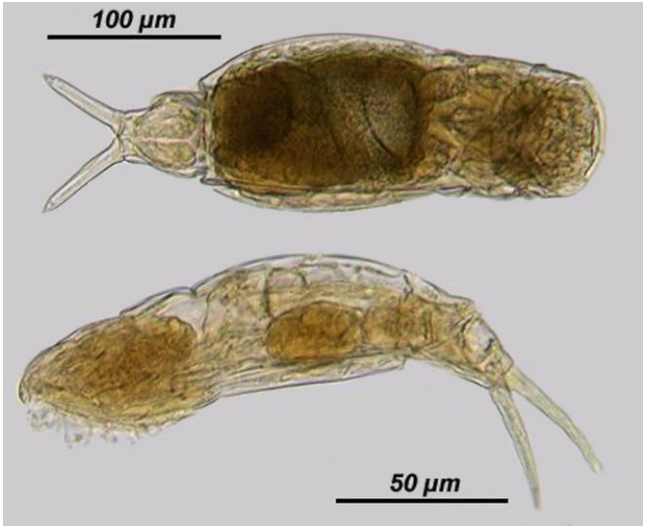

Figure 107. ***Dicranophorus epicharis***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 108. ***Dicranophorus facinus*** lives among ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

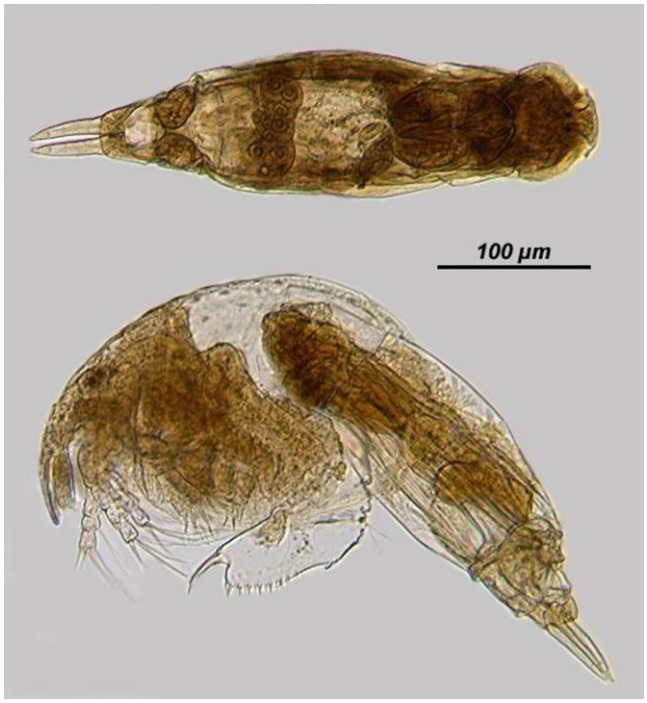

Figure 109. ***Dicranophorus isothes***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

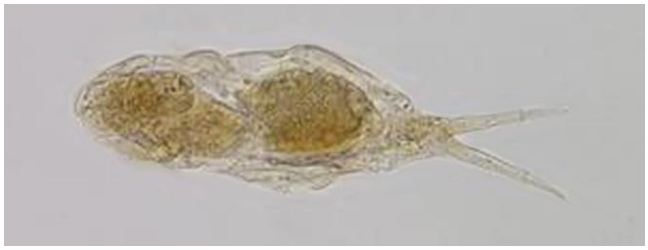

Figure 110. ***Dicranophorus luetkeni*** female, a species known from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 111. ***Dicranophorus luetkeni*** male, a species known from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 112. ***Dicranophorus luetkeni*** female with egg. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Dicranophorus robustus (Figure 113-Figure 114), like several other members of the **Dicranophoridae**, occurs on both the bog moss ***Sphagnum*** (Figure 21) and the brook moss ***Fontinalis*** (Figure 11) (Hingley 1993; Pejler & Bērziņš 1993a). It commonly ingests members of the rotifer genus ***Lecane*** (Figure 115), a very large genus that is abundant on bryophytes (Jersabek *et al*. 2003). This dual habitat of ***Sphagnum*** and ***Fontinalis*** also works for ***D. rostratus*** (Figure 116; Hingley 1993; Jersabek *et al.* 2003).

Figure 113. ***Dicranophorus robustus*** from *Aufwuchs*, a species found with bryophytes, including ***Sphagnum*** and ***Fontinalis***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

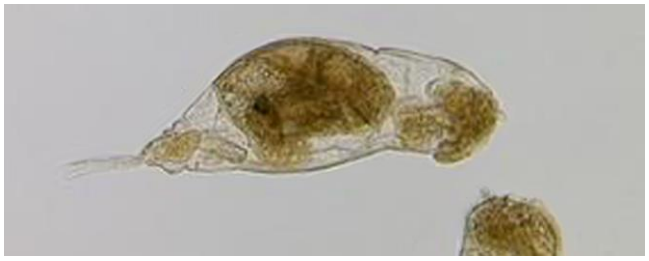

Figure 114. ***Dicranophorus robustus*** female, a species that is known to live among bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 115. ***Lecane clara***, without stiffened lorica. Members of ***Lecane*** serve as food for ***Dicranophorus robustus***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 116. ***Dicranophorus rostratus*** female, a species known from ***Sphagnum*** (Myers 1942) and ***Fontinalis***. Photo by Jersabek *et al.* 2003, with permission.

Some species are known thus far only from ***Fontinalis*** (Figure 11). Among these is ***Dicranophorus forcipatus*** (Figure 117-Figure 118) (Pejler & Bērziņš 1993a; Plewka 2016), including its occurrence on Svalbard exclusively on submerged mosses (De Smet 1993).

Figure 117. ***Dicranophorus forcipatus***, a rotifer found among bryophytes in several studies, including ***Fontinalis***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 118. ***Dicranophorus forcipatus***, a rotifer found among bryophytes in several studies, shown here feeding on the surfacce of ***Spirogyra*** sp. Photo by Michael Plewka <www.plingfactory.de>, with permission.

The aquatic ***Dicranophorus hercules*** (Figure 119) is known from bryophytes (Jersabek *et al*. 2003), but its typical habitat is in the **psammon** (interstitial community among sand grains in fresh water) (Ruttner-Kolisko 1954; Pejler & Bērziņš 1993b). In fact, Wizsniewski (1934, 1937) considered this species to be exclusive to the psammon. Nevertheless, Bielańska-Grajner *et al*. (2011) found it among the peatland bryophytes in Poland.

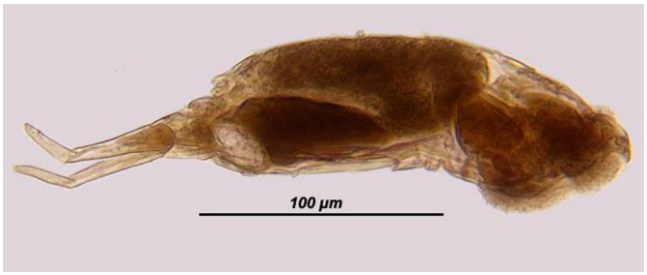

Figure 119. ***Dicranophorus hercules***, a species known from bryophytes. Photo by Jersabek *et al*. 2003, with permission.

Dorria

Dorria dalecarlica (Figure 121) is the only species in the genus (Segers 2007) and is a moss dweller in aquatic habitats, where it lives on dripping and submersed ***Fontinalis dalecarlica*** (Figure 11) (Myers 1942).

Figure 120. ***Dorria dalecarlica***, a species that can occur on submerged mosses in streams. Photos by Jersabek *et al*. 2003, with permission.

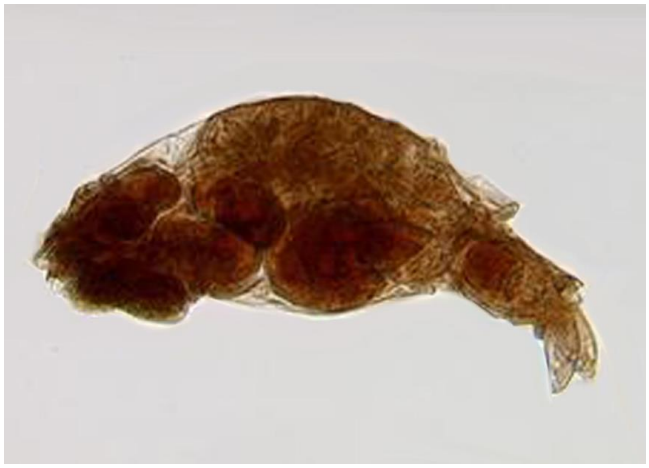

Figure 121. ***Dorria dalecarlica***, a species that can occur on submerged mosses in streams. Photos by Jersabek *et al*. 2003, with permission.

Encentrum

The genus ***Encentrum*** is a large genus with a number of species that live on bryophytes. ***Sphagnum*** (Figure 21, Figure 66) dwellers include ***E. aquilus*** (Figure 122; Jersabek *et al*. 2003), ***E. arvicola*** (Pejler & Bērziņš 1993a), ***E. carlini*** (Figure 123; Jersabek *et al*. 2003), ***E. elongatum*** (Pejler & Bērziņš 1993a), ***E. felis*** (Figure 124-Figure 125; Hingley 1993; Jersabek *et al*. 2003), ***E. glaucum*** (Figure 126; Hingley 1993), ***E. incisum*** (Figure 127; Pejler & Bērziņš 1993a), ***E. saundersiae*** (Figure 128; Myers 1942), ***E. sutor*** (Pejler & Bērziņš 1993a), ***E. sutoroides*** (Pejler & Bērziņš 1993a), ***E. tobyhannaense*** (Figure 129; Jersabek *et al*. 2003), and ***E. tyrphos*** (Pejler & Bērziņš 1993a).

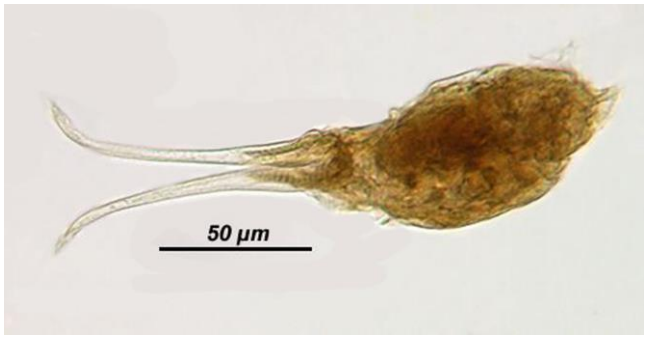

Figure 122. ***Encentrum aquilus***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

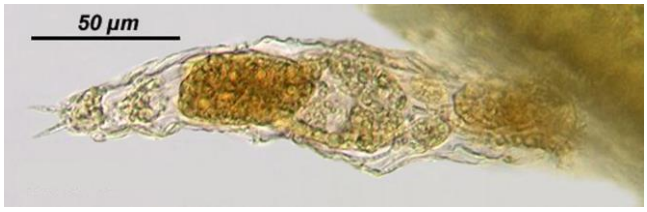

Figure 123. ***Encentrum carlini***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

Figure 124. ***Encentrum felis*** with protruding forcipate trophi. Photo by Michael Plewka <www.plingfactory.de>, with permission.

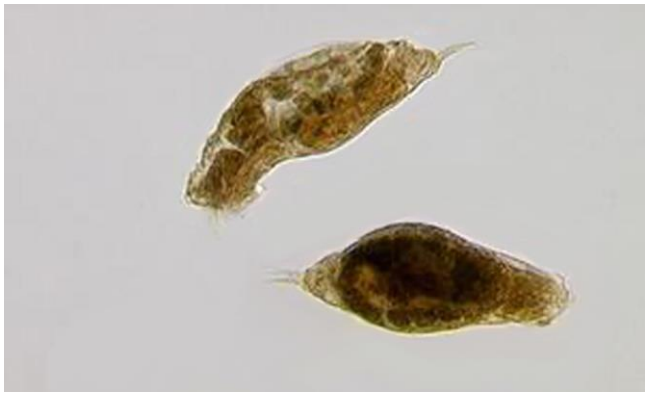

Figure 125. ***Encentrum felis***, a species known from bryophytes, including ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 126. ***Encentrum glaucum*** female, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 127. ***Encentrum oxyodon/E. incisum***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

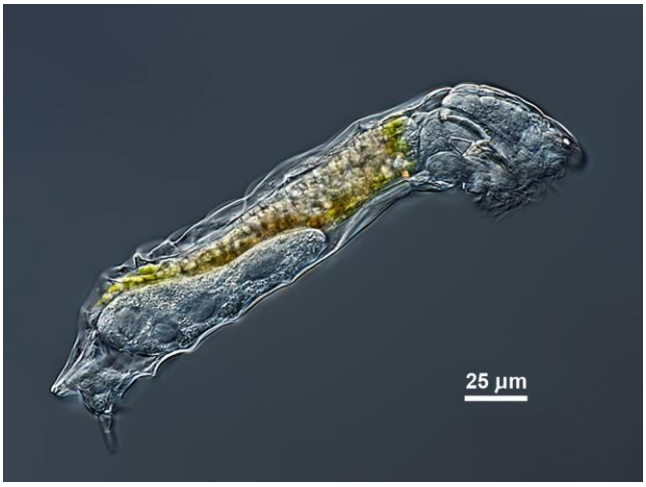

Figure 128. ***Encentrum saundersiae*** lateral view, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 129. Trophus of ***Encentrum tobyhannaensis*** from among ***Sphagnum***. Often this is the only structure that can be recognized in old collections. Photo by Jersabek *et al.* 2003, with permission.

As seems to be a common feature of this family, several species live on both ***Sphagnum*** (Figure 21, Figure 66) and ***Fontinalis*** (Figure 11). These are ***Encentrum lupus*** (Pejler & Bērziņš 1993a), ***E. mustela*** (Figure 130) (Hingley 1993; Pejler & Bērziņš 1993a), and ***E. uncinatum*** (Figure 131; Horkan 1981; Hingley 1993; Pejler & Bērziņš 1993a; Plewka 2016). ***Encentrum eurycephalum*** and ***E. fluviatile***, on the other hand, are only known from ***Fontinalis*** (Pejler & Bērziņš 1993a). ***Encentrum mucronatum*** and ***E. uncinatum*** live on submerged mosses on Svalbard, where the former is one of the most frequent species (De Smet 1990); ***E.*** cf. ***marinum*** (Figure 132) lives exclusively among submerged mosses on Svalbard, whereas ***E. mustela*** occurs on submerged mosses and in the plankton (De Smet 1993).

Figure 130. ***Encentrum mustela***, a species that occurs on both ***Sphagnum*** and ***Fontinalis***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 131. ***Encentrum uncinatum*** swimming. This species is known from the brook moss ***Fontinalis*** and the bog moss ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 132. ***Encentrum marinum***, a species that occurs exclusively among submerged mosses on Svalbard. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Encentrum lutra (Figure 133) also lives in the unpredictable habitat of epiphytic mosses (Plewka 2016). The habitat of ***E. permolle*** (Figure 134) is on moss (Plewka 2016) in Antarctic islands (Fontaneto *et al*. 2015).

Figure 133. ***Encentrum lutra***, a species that lives among epiphytic mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 134. ***Encentrum permolle***, a moss dweller in the Antarctic. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Pedipartia

Pedipartia is a genus with only one species, ***P. gracilis*** (Figure 135) (Segers 2007). This rotifer species is known from just one species of ***Sphagnum***, ***S. subsecundum*** (Figure 61-Figure 62) (Myers 1942; Jersabek *et al*. 2003).

Figure 135. ***Pedipartia gracilis*** from among ***Sphagnum subsecundum***. Photo by Jersabek *et al*. 2003, with permission.

Streptognatha

Streptognatha is another genus known by only one species (Segers 2007). ***Streptognatha lepta*** (Figure 136-Figure 137), a species reported in Great Britain and elsewhere, occurs on ***Sphagnum*** (Figure 21, Figure 66) (Jersabek *et al*. 2003).

Figure 136. ***Streptognatha lepta*** female, lateral view, a species known from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

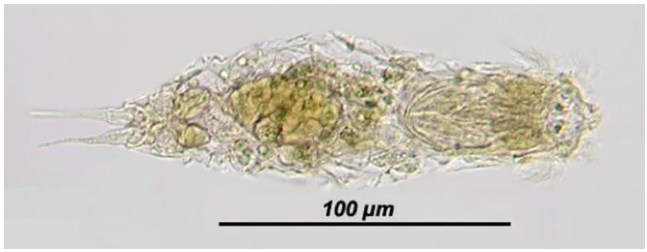

Figure 137. ***Streptognatha lepta*** female, a rotifer known to associate with ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Wierzejskiella

Of the eight species (Segers 2007) of ***Wierzejskiella***, three are known bryophyte dwellers. And all three live on ***Sphagnum*** (Figure 21, Figure 66). ***Wierzejskiella elongata*** (Figure 138) lives among ***Sphagnum*** (Myers 1942). ***Wierzejskiella velox*** (Figure 139-Figure 140) occurs both among ***Sphagnum*** and in ***Sphagnum*** pools (Myers 1942).

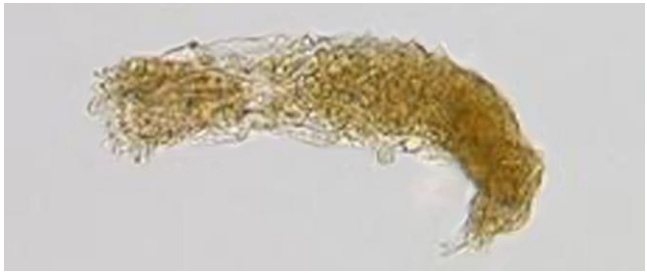

Figure 138. ***Wierzejskiella elongata*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

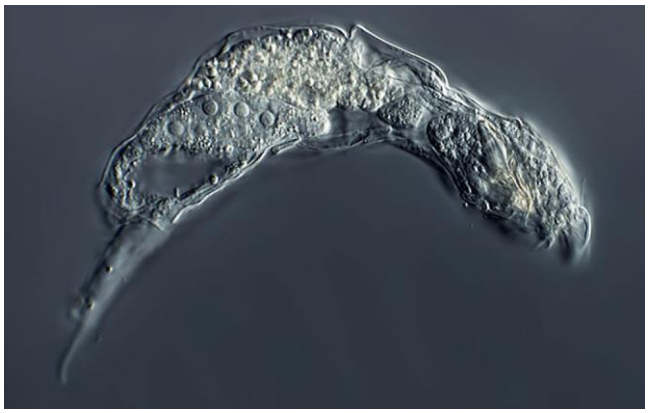

Figure 139. ***Wierzejskiella velox***, a species from ***Sphagnum*** and ***Sphagnum*** pools (Myers 1942). Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 140. ***Wierzejskiella velox*** from ***Sphagnum***, shown here with its forcipate trophi extruded as it approaches the desmid food item.. Photo by Mark Plewka <www.plingfatory.de>, with permission.

Epiphanidae

This family has rotifers that are usually planktonic, so like most of the rotifers on bryophytes, it is likely that the bryophyte is a temporary refuge. Many of the members of this family are marine (Koste 1978; Fontaneto *et al*. 2006, 2008), where no bryophytes are known.

Cyrtonia

Cyrtonia is another genus with only one species (Segers 2007), and that species is a moss dweller – ***C. tuba*** (Figure 141-Figure 142). It is known from ponds, but it has also been collected from mosses (Jersabek *et al*. 2003).

Figure 141. ***Cyrtonia tuba***, a pond and moss dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

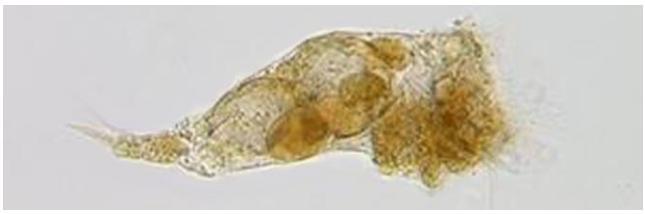

Figure 142. ***Cyrtonia tuba*** from a pond in Ohio, USA. This species has been collected from mosses. Photo by Jersabek *et al.* 2003, with permission.

Epiphanes

This genus of nine species seems to have only one that lives with bryophytes. ***Epiphanes brachionus*** (Figure 143)

lives in ***Sphagnum*** (Figure 21, Figure 66) bogs (Plewka 2016).

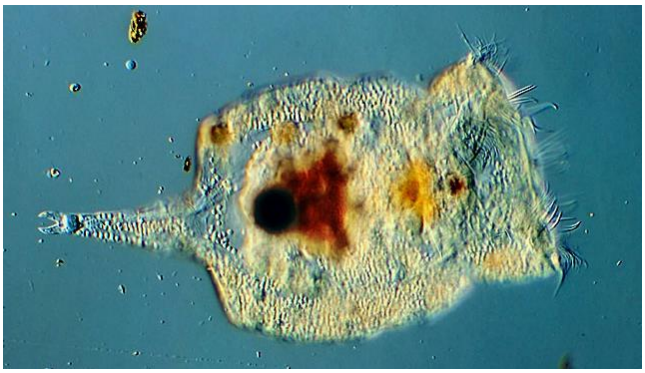

Figure 143. ***Epiphanes brachionus*** from a ***Sphagnum*** bog. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Mikrocodides

Mikrocodides, a genus of three species (Segers 2007), typically occurs in the plankton and among the periphyton. One species, ***Mikrocodides chlaena*** (Figure 144-Figure 146), however, lives among mosses and in bog pools (Plewka 2016).

Figure 144. ***Mikrocodides chlaena***, a species that occurs among mosses and in bog pools. Photo by Michael Plewka <www.plingfactory.de>, with permission.

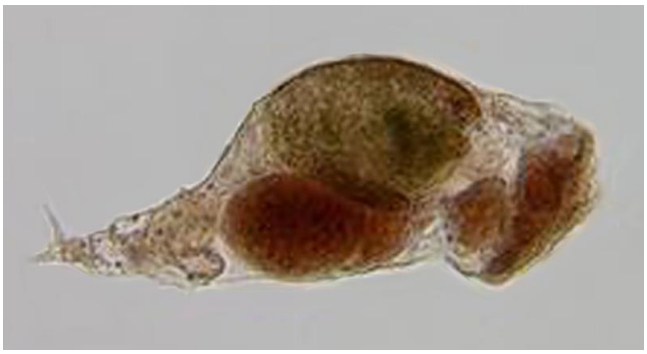

Figure 145. ***Mikrocodides chlaena*** female from New Jersey, USA. This species has been collected from mosses and from bog pools. Photos by Jersabek *et al.* 2003, with permission.

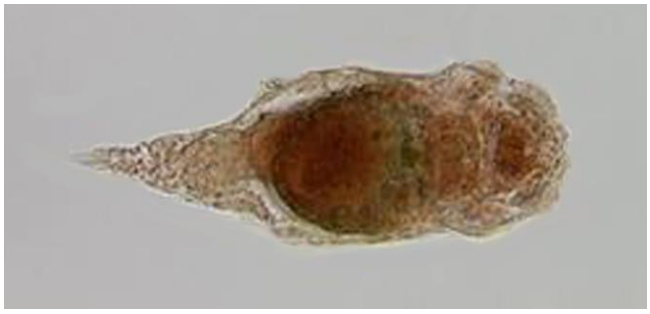

Figure 146. ***Mikrocodides chlaena*** female from New Jersey, USA. This species has been collected from mosses and from bog pools. Photos by Jersabek *et al.* 2003, with permission.

Euchlanidae

This family is characterized by a lorica consisting of connected plates (Koste & Shiel 1989). The toes are elongated. Of the five genera in the family, only ***Euchlanis*** is known from mosses.

Sphagnum (Figure 21, Figure 66), as usual, is a common substrate, with a number of species of ***Euchlanis*** associated with it. These include ***E. callysta*** (Figure 147), ***E. calpidia*** (Figure 148-Figure 149, ***E. dilatata*** (Figure 156-Figure 157), ***E. incisa*** (Figure 150) and ***E. triquetra*** (Figure 151-Figure 155) (Błedzki & Ellison 2003; Jersabek *et al*. 2003).

Figure 147. ***Euchlanis callysta*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 148. ***Euchlanis calpidia*** from among ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

Figure 149. ***Euchlanis calpidia*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 150. ***Euchlanis incisa*** from ***Fontinalis***. Photo by Michael Plewka <www. plingfactory.de>, with permission.

Figure 151. ***Euchlanis triquetra*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 152. ***Euchlanis triquetra*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

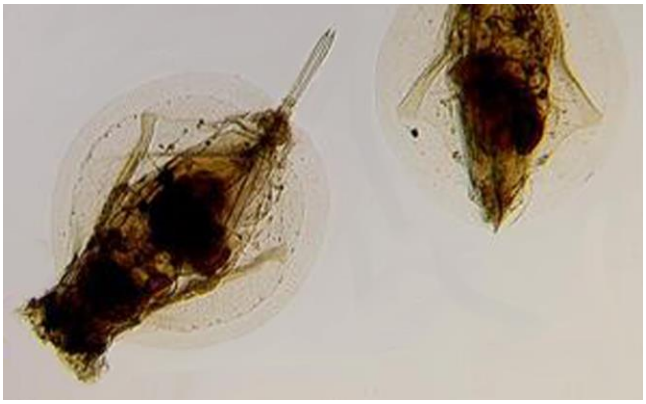

Figure 153. ***Euchlanis triquetra*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 154. ***Euchlanis triquetra***, a species known from ***Sphagnum*** bogs. Photo by Mark Plewka <www.plingfactory.de>, with permission.

Figure 155. ***Euchlanis triquetra*** with expelled resting egg. Photo by Michael Plewka <www.plingfactory.de>, with permission.

There seems to be a paucity of studies on rotifers beyond listing the taxa present in various water bodies. But in the **Euchlanidae**, at least one species that is known from ***Sphagnum*** (Figure 21, Figure 66) seems to have been the subject of several kinds of biological studies. For example, ***Euchlanis dilatata*** (Figure 156-Figure 157) has proven its ability to serve as a sensitive biomonitor (Sarma *et al.*

2001). In an experiment on herbicides, this species experienced a significant reduction in population density and rate of population increase in the presence of methyl parathion. These responses were exacerbated as the concentration of methyl parathion increased, regardless of food (***Chlorella vulgaris*** – Figure 64) concentration. However, higher food concentrations served to mediate the effect on the rate of population increase.

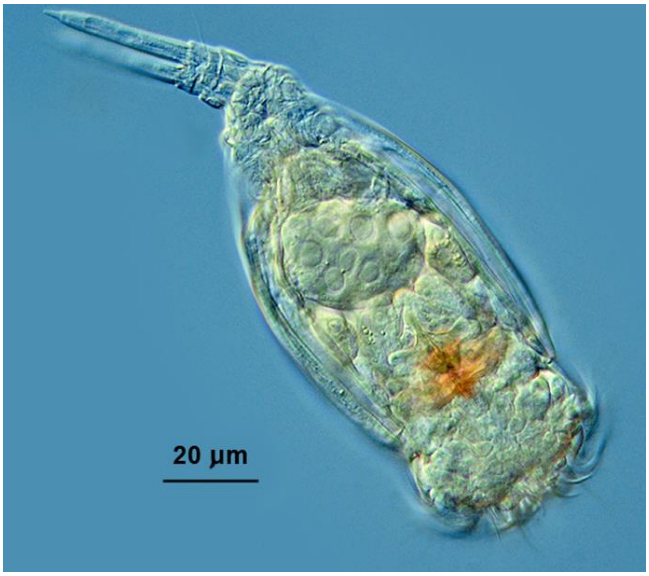

Figure 156. ***Euchlanis dilatata***, a species that can occur on bryophytes and other macrophytes. Photo by Proyecto Agua Water Project, through Creative Commons.

Figure 157. ***Euchlanis dilatata***, a species that has been collected from bryophytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Euchlanis dilatata (Figure 156-Figure 157) is a benthic-periphytic species known from littoral zones of small bodies of eutrophic waters (de Manuel Barrabin 2000), but can occur on bryophytes (Jersabek 2016) and other macrophytes (Plewka 2016). On Svalbard, it occurs exclusively on submerged mosses, along with ***E. deflexa*** (Figure 159) and ***E. meneta*** (Figure 158) (De Smet 1988, 1993). ***Euchlanis dilatata*** occurs in both fresh water and brackish water, preferring water rich in nutrients, especially those favoring **Cyanobacteria** (de Manuel Barrabin 2000). These waters generally have a *p*H range of 6.3-9.6 and a temperature range of 6.4-24°C. Although only 200 µm long, this species is consumed by damselfly naiads (Ejsmont-Karabin *et al*. 1993). In the lab, it is able to survive on **Cyanobacteria** [***Limnothrix*** *redekei* (Figure 160), ***Oscillatoria***. *limnetica* (Figure 161), ***Aphanizomenon*** *flos-aquae* (Figure 162), ***Anabaena*** sp. (Figure 163)], all genera that can be found with ***Sphagnum***, and a prochlorophyte (*Prochlorothrix hollandica*) (Gulati *et al*. 1993). In the field ***E. dilatata*** consumes detritus, bacteria, **Cyanobacteria**, and the diatom ***Cyclotella*** (Figure 164) (Carlin 1943), all likewise present among ***Sphagnum***. It often benefits from the convenience of attaching to planktonic algae colonies (Pejler 1962).

Figure 158. ***Euchlanis meneta***, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 159. ***Euchlanis deflexa***, an occupier of submerged mosses on Svalbard. Photo by Jersabek *et al*., with permission.

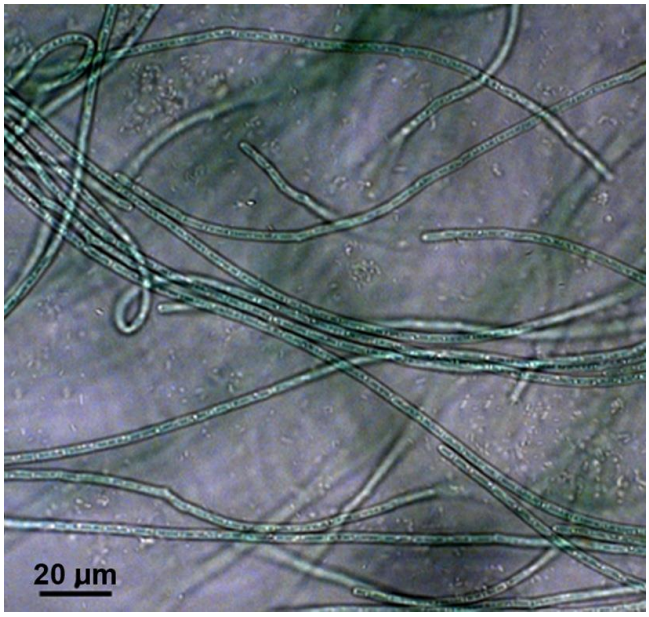

Figure 160. ***Limnothrix redekei***, food for ***Euchlanis dilatata***. Photo by Matt Pano, through Creative Commons.

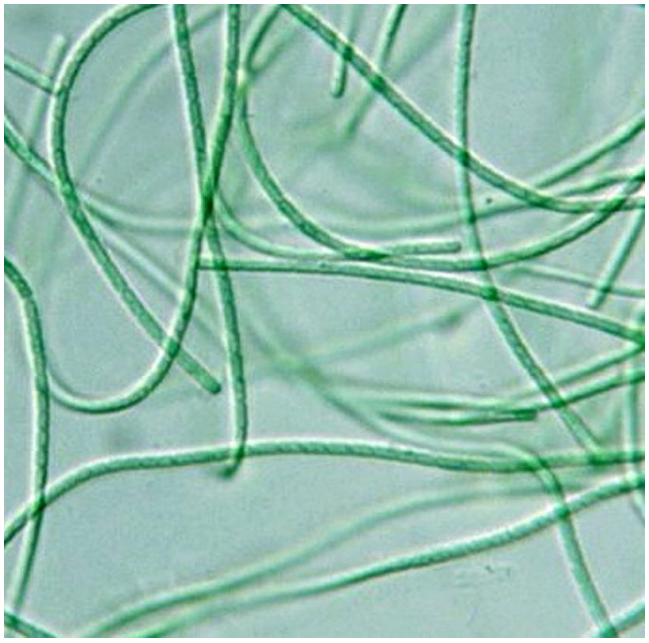

Figure 161. ***Oscillatoria limnetica***, food for ***Euchlanis dilatata***. Photo by Yuuji Tsukii, with permission.

Figure 162. ***Aphanizomenon flos-aquae***, food for ***Euchlanis dilatata***. Photo by Nordic Microalgae <www.nordicmicroalgae.org>, with online permission.

Figure 163. ***Anabaena***, food for ***Euchlanis dilatata***. Photo by Jason Oyadomari, with permission.

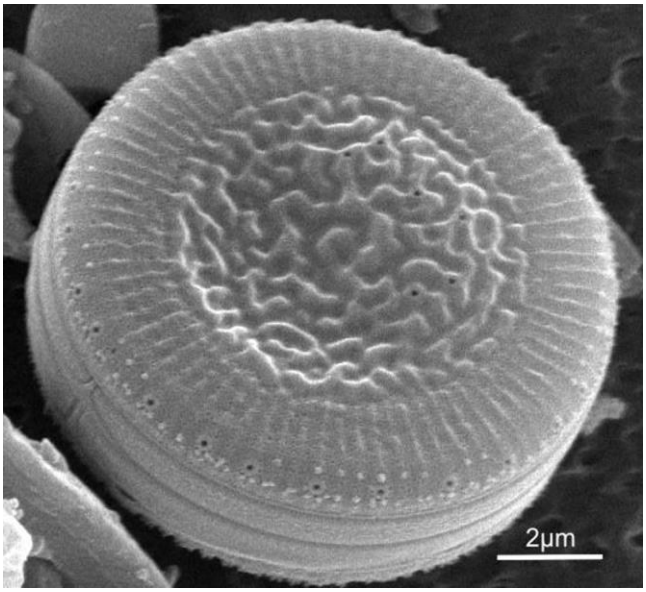

Figure 164. ***Cyclotella caspia***, food for ***Euchlanis dilatata***. Photo by Janina Kownacka, Nordic Microalgae <www.nordicmicroalgae.org>, with online permission.

Euchlanis incisa (Figure 165-Figure 167) is likewise a ***Sphagnum*** (Figure 21-Figure 66) dweller, in the northeastern USA (Błedzki & Ellison 2003), but it is also known from the non-bog aquatic moss ***Fontinalis*** (Figure 11) (Plewka 2016).

Figure 165. ***Euchlanis incisa*** female, a species known from bryophytes. Photo by Jersabek *et al*. 2003, with permission.

Figure 166. ***Euchlanis incisa***, a species known from bryophytes, including ***Fontinalis***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 167. ***Euchlanis incisa***, a species known from bryophytes. Photo by Jersabek *et al*. 2003, with permission.

In addition to ***Sphagnum***, other bryophytes may be substrates for members of ***Euchlanis***. ***Euchlanis meneta*** (Figure 158-Figure 168) is among the dominant rotifers on mosses on Devon Island, Baffin Bay, Canada (De Smet & Beyens 1995). This species is also known from the other end of the Earth, from New Zealand (Shiel & Green 1996).

Figure 168. ***Euchlanis meneta*** female, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Euchlanis oropha (Figure 169) is a widespread **rheophilic** (loving flowing water) species that can occur on mosses, among other substrates.

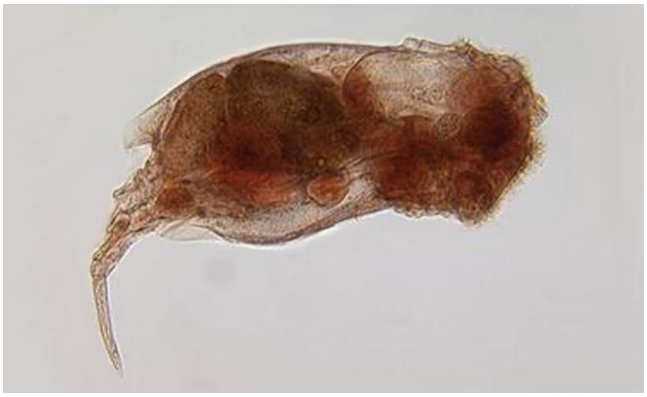

Figure 169. ***Euchlanis oropha*** female, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Gastropodidae

This family is distinguished by its oval shape and sac-like or compressed body plan. It has a thin shell that surrounds the entire body with only a small opening for the head and ventrally located foot (Figure 170-Figure 173) that is sometimes absent. The family occurs primarily in fresh water, with few marine species. There are two genera, but only members of ***Gastropus*** seem to have been collected from bryophytes. Of the three species in this genus, two are known bryophyte dwellers: ***G. hyptopus*** (Figure 170-Figure 171) and ***G. minor*** (Figure 172) (Plewka 2016). ***Gastropus stylifer*** lives on submerged mosses in trenches of Alaskan polygons (Segers *et al.* 1996).

Figure 170. ***Gastropus hyptopus***, a moss dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 171. ***Gastropus hyptopus***, a species known from bryophytes and from bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 172. ***Gastropus minor*** lateral view, a bryophyte dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 173. ***Gastropus minor*** female, a species known from ***Sphagnum*** bogs. Note the ventral foot. Photo by Jersabek *et al.* 2003, with permission.

Summary

The rotifers in **Monogononta** are often represented on bryophytes, especially in peatlands. The Class **Monogononta** has three orders and is the largest class of rotifers. Many members of order **Collothecacea** are sessile. Some members of family **Collothecidae** are known from ***Riccia fluitans***, ***Sphagnum***, and other bryophytes. Members of the order **Flosculariacea** are suspension feeders, and known bryophyte dwellers include members of **Conochilidae**, **Filiniidae**, **Flosculariidae**, **Hexarthriidae**, and **Testudinellidae**. The order **Ploimida** includes both planktonic and non-planktonic families that are known from bryophytes. Those included in this subchapter are **Brachionidae**, **Dicranophoridae**, **Epiphanidae**, **Euchlanidae**, and **Gastropodidae.** Additional families are in the next sub-chapters.

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CHAPTER 4-7b

INVERTEBRATES: ROTIFER TAXA – MONOGONONTA

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CHAPTER 4-7b

INVERTEBRATES: ROTIFER TAXA – MONOGONONTA

Figure 1. Lecane stokesii, a monogonont rotifer that can be found among bryophytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Taxa on Bryophytes, Ploimida continued

Lecanidae

The **Lecanidae** were represented by the second highest number of species among rotifers in the reservoirs in Spain (de Manuel Barrabin 2000) and their species are well represented among those rotifers collected with bryophytes as well (*e.g.* Jersabek et al. 2003). One reason for this is that the family has only one, but a very large, genus – ***Lecane***. The genus ***Lecane*** is the second largest genus of rotifers, with at least 160 species (Segers 1995).

Not surprisingly, there are a number of ***Lecane*** species living in ***Sphagnum*** (Figure 1, Figure 2). One of the early reports including ***Sphagnum*** dwellers was that of Harring (1915) in Panama. These included ***L. bifurca*** (Figure 3; see also Myers 1942), ***L. flexilis*** (Figure 4-Figure 5; see also Bielańska-Grajner *et al*. 2011), ***L. inermis*** (Figure 7-Figure 8), ***L. monostyla*** (Figure 9; see also Bielańska-Grajner *et al*. 2011), and ***L. tenuiseta*** (Figure 10; see also Bielańska-Grajner *et al*. 2011). The ***Sphagnum*** associates include those in bogs and fens. Błedzki and Ellison (2002) found ***Lecane pyriformis*** (Figure 11) and ***L. lunaris*** (Figure 44-Figure 45) to be among the abundant ***Sphagnum*** dwellers in their study. To these, Bielańska-Grajner *et al*. (2011) added ***L. bulla*** (Figure 12-Figure 13), ***L. intrasinuata*** (Figure 14), ***L. luna*** (Figure 15), and ***L. perpusilla*** as bog dwellers. But ***Sphagnum*** fauna records must be viewed with caution. Methods using pore water often miss the relatively immobile rotifers that live on mosses (Sakuma *et al*. 2002).

Figure 2. ***Sphagnum*** and ***Potentilla tridentata***, home for many kinds of rotifers. Photo by Nancy Leonard, with permission.

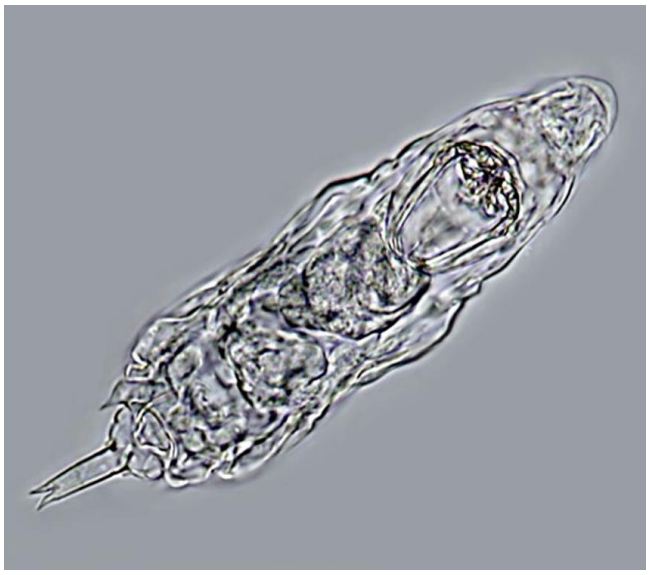

Figure 3. ***Lecane bifurca*** lives among mosses, including ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Hingley likewise found ***Lecane flexilis*** (Figure 4-Figure 5; see also Bielańska-Grajner *et al*. 2011) among ***Sphagnum*** (Figure 2), but Jersabek *et al*. (2003) further reported it from the floating thallose liverwort, ***Riccia fluitans*** (Figure 6). This rotifer species occurs infrequently in the plankton, preferring instead the littoral (near shore) zone (de Manuel Barrabin 2000). It occurs more frequently in alkaline habitats (Pejler 1962; Koste 1978) in a *p*H range of 6.64-7.87, although Koste and Shiel (1990) found it in slightly acidic water. Its wide temperature range (9.50-21.13°C) permits it to be cosmopolitan (de Manuel Barrabin 2000).

Figure 4. ***Lecane flexilis***, a species known from bogs and from the thallose liverwort ***Riccia fluitans*** in ponds. Photo by Jersabek *et al.* 2003, with permission.

Figure 5. ***Lecane flexilis***, a species known from ***Riccia fluitans*** in ponds. Photo by Jersabek *et al.* 2003, with permission.

Figure 6. ***Riccia fluitans***, a floating liverwort that is home to ***Lecane flexilis***. Photo by Jan-Peter Frahm, with permission.

In ***Lecane inermis*** (Figure 7-Figure 8), a ***Sphagnum*** (Figure 2) dweller, **mictic** (producing eggs that without fertilization develop into males but with fertilization form resting eggs that later develop into amictic females) females have the longest lives of 11.1 ± 0.28 days, followed by amictic females with a lifespan of 8.9 ± 0.11 days, and the shortest lifespan in males at 5.7 ± 0.07 days (Miller 1931). In males, death of 83% of the population occurs in the four to six days. Sexual females lay one egg every 8.6 hours, whereas the **amictic** (producing eggs that

develop without fertilization) female lays one every 7.5 hours. Amictic females usually die within 24-36 hours after laying the last egg, but among the mictic females, 19% live six more days after depositing eggs. Typically, ***Lecane inermis*** is a littoral species that also occurs in warm water such as thermal springs and geysers (de Manuel Barrabin 2000). Its typical temperature is around 19.4°C, but it can be found near geysers at temperatures up to 62.5°C. Its environmental *p*H is usually around 7.3.

Figure 7. ***Lecane inermis***, a ***Sphagnum*** dweller. The upper image is in the extended state, the lower one in the contracted state. Photo by Jersabek *et al*. 2003, with permission.

Figure 8. ***Lecane inermis***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 9. ***Lecane monostyla***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

Lecane tenuiseta (Figure 10) is typically a littoral species, known from a *p*H around 7.9 and a temperature around 13.5°C (de Manuel Barrabin 2000). Although it is cosmopolitan, its restricted habitat requirements make it relatively rare.

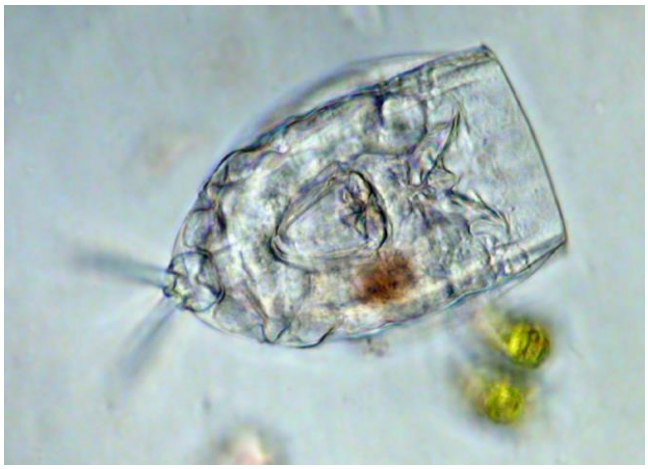

Figure 10. ***Lecane tenuiseta***, typically a littoral species, sometimes living among ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

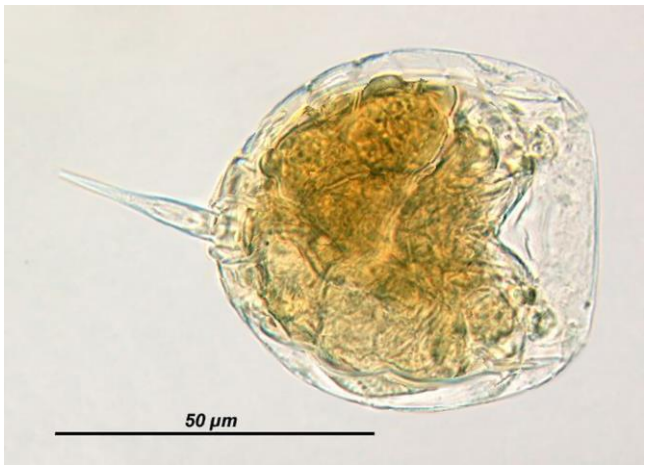

Figure 11. ***Lecane pyriformis***, an abundant bog dweller. Photo by Jersabek *et al.* 2003, with permission.

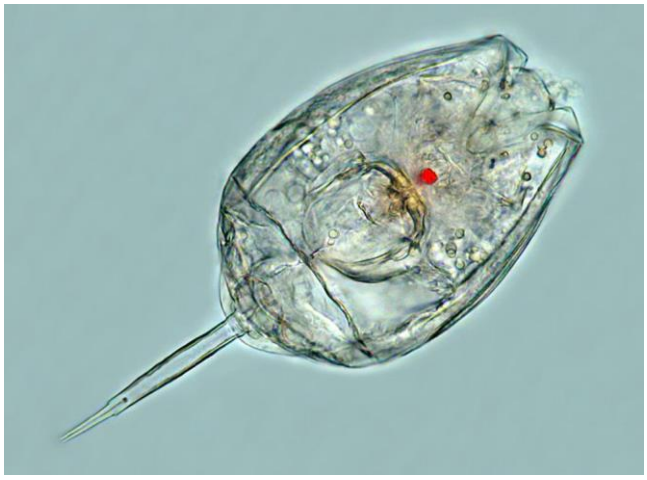

Figure 12. ***Lecane bulla*** from leaf litter, also a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

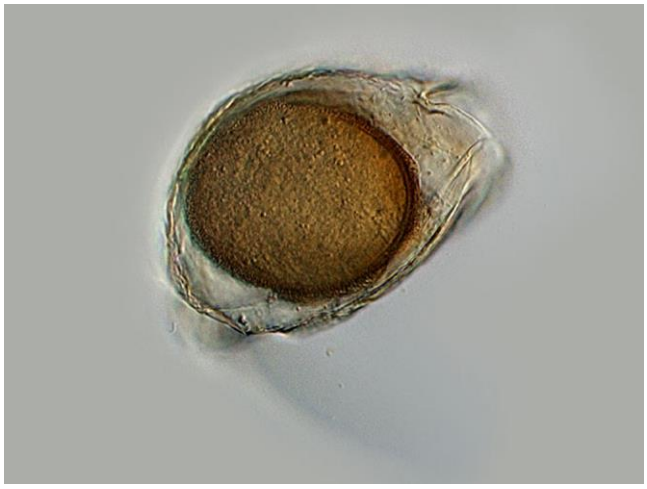

Figure 13. ***Lecane bulla*** resting egg inside its deceased mother. Photo by Michael Plewka <www.plingfactory.de>, with permission.

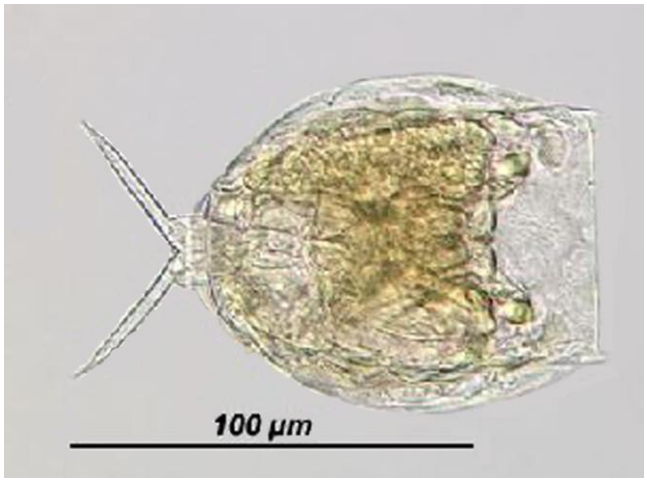

Figure 14. ***Lecane intrasinuata***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

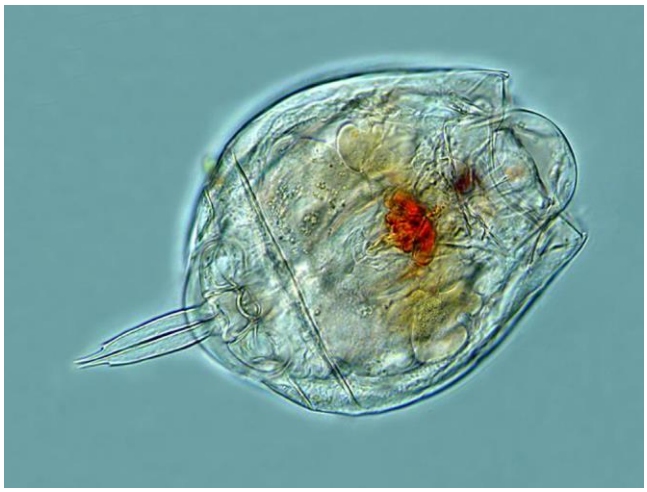

Figure 15. ***Lecane luna*** from among water plants, also a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

One of the most extensive treatments of North American rotifers is that of Myers (1942) for the Poconos in Pennsylvania, USA. He considered ***Lecane obtusa*** (Figure 16), ***L. opias*** (Figure 17; see also Bielańska-Grajner *et al*. 2011), and ***L. subulata*** (Figure 18-Figure 19) to be small species that are common among ***Sphagnum*** (Figure 2). In that same publication, he reported ***L. depressa*** (Figure 20-Figure 21; see also Hingley 1993), ***L. formosa***, ***L. furcata*** (Figure 22), ***L. niothis***, ***L. pumila*** (Figure 23), ***L. rhytida***, ***L. scutata*** (Figure 24; see also Koste & Shiel 1990; Bielańska-Grajner *et al*. 2011), ***L. subtilis*** (Figure 25; see also Bielańska-Grajner *et al*. 2011), ***L. tryphema*** (Figure 26), and ***L. verecunda*** (Figure 27) from ***Sphagnum***. He also reported ***L. dysoarata*** (Figure 28) from the emergent species ***Sphagnum cuspidatum*** (Figure 29). Horkan (1981) reported ***L. quadridentata*** (Figure 30-Figure 31) from bog pools.

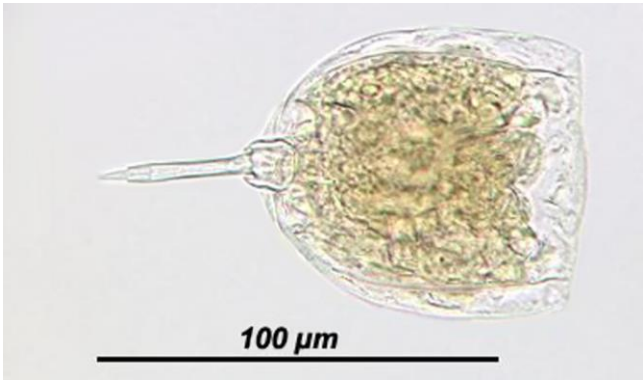

Figure 16. ***Lecane obtusa***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

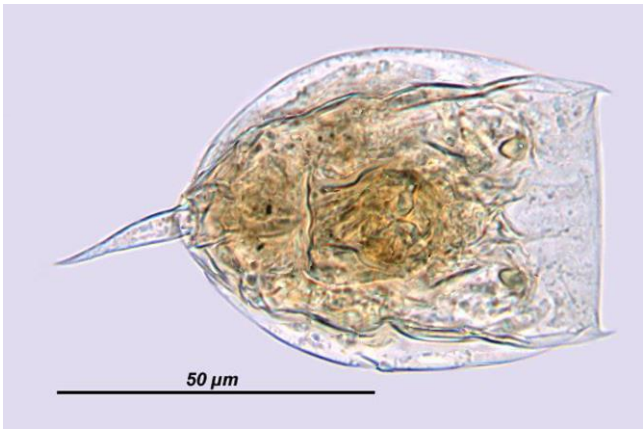

Figure 17. ***Lecane opias***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

Figure 18. ***Lecane subulata*** from among ***Sphagnum*** (Myers 1942). Photo by Jersabek *et al.* 2003, with permission.

Figure 19. ***Lecane subulata*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 20. ***Lecane depressa***, a species known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

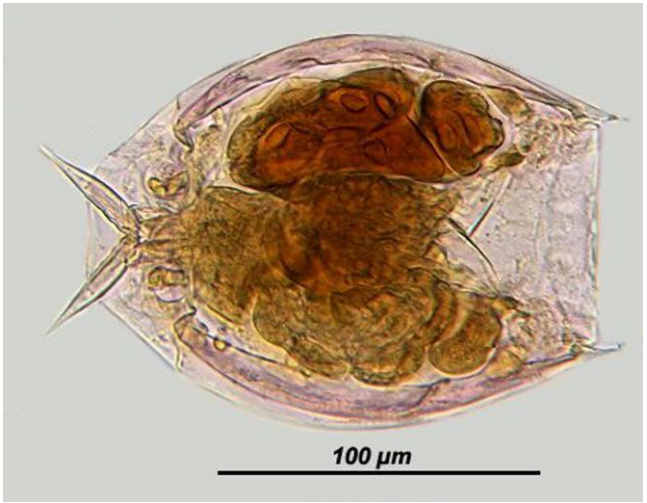

Figure 21. ***Lecane depressa***, a species known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

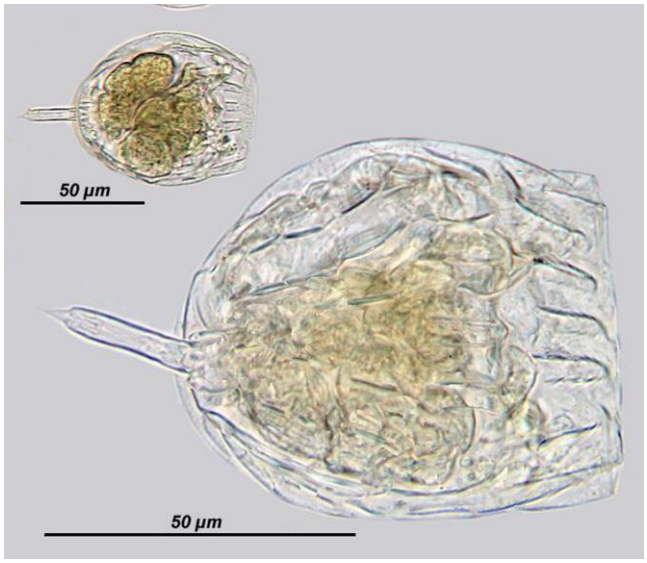

Figure 22. ***Lecane furcata***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 23. ***Lecane pumila***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Lecane scutata (Figure 24) occurs in the littoral zone of lakes where it lives on plant surfaces (de Manuel Barrabin 2000). It is an acidophile, commonly living among ***Sphagnum*** (Figure 2) (Myers 1942; Koste & Shiel 1990), but it is cosmopolitan and probably not restricted to strongly acid habitats (de Manuel Barrabin 2000).

Figure 24. ***Lecane scutata***, a ***Sphagnum*** dweller and acidophile. Photo by Jersabek *et al.* 2003, with permission.

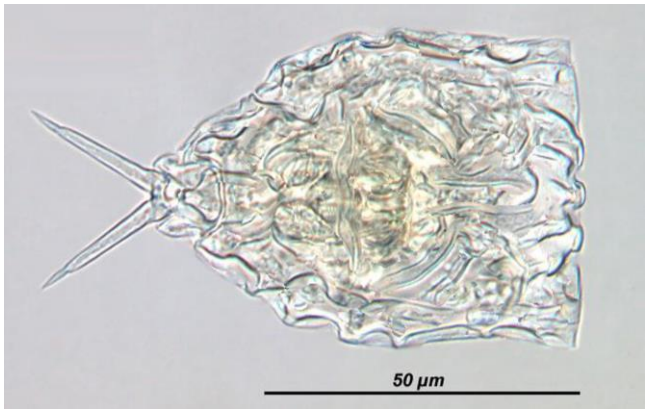

Figure 25. ***Lecane subtilis***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 26. ***Lecane tryphema*** in a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

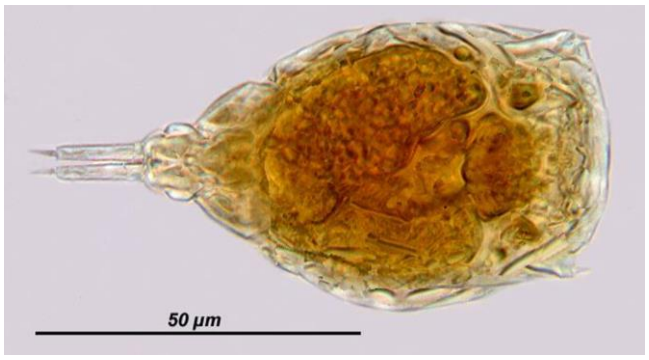

Figure 27. ***Lecane verecunda***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 28. ***Lecane dysoarata***, a ***Sphagnum cuspidatum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

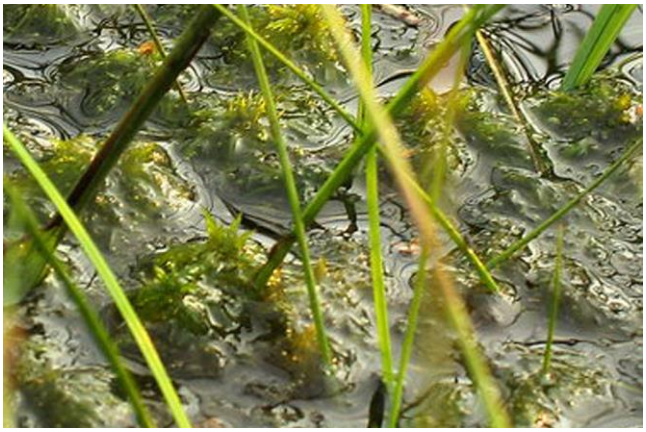

Figure 29. ***Sphagnum cuspisdatum***, home for ***Lecane quadridentata***. Photo by Andrew Spink, with permission.

Figure 30. ***Lecane quadridentata***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 31. ***Lecane quadridentata*** from a lake in Pennsylvania, USA. This species has been collected from bryophytes and from bog pools. Photo by Jersabek *et al.* 2003, with permission.

Hingley (1993) published a manual on the microscopic life in ***Sphagnum*** (Figure 2), including the rotifer fauna. Her records included ***L. agilis*** (Figure 32), ***L. clara*** (Figure 33-Figure 34; see also Bielańska-Grajner *et al*. 2011), ***L. closterocerca*** (Figure 35-Figure 36; see also Bielańska-Grajner *et al*. 2011), ***L. cornuta*** (Figure 37-Figure 39), ***L. galeata*** [Figure 40-Figure 41; see also Jersabek *et al*. 2003 from ***Sphagnum subsecundum*** (Figure 42) and Bielańska-Grajner *et al*. 2011], ***L. hamata*** (Figure 43; see also Bielańska-Grajner *et al*. 2011), ***L. lunaris*** (Figure 44-Figure 45; see also Madaliński 1961; Bielańska-Grajner *et al*. 2011), ***L. pyrrha*** (Figure 46), ***L. signifera*** (Figure 47), ***L. signifera ploenensis*** (Figure 48), and ***L. stichaea*** (Figure 49-Figure 50).

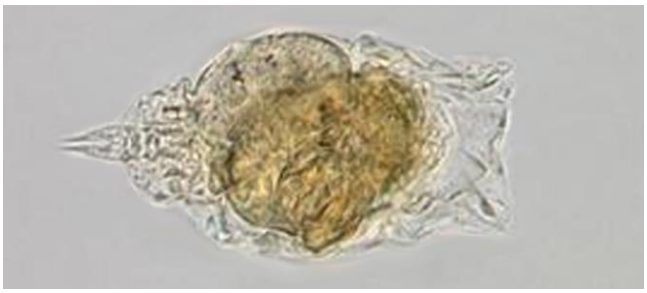

Figure 32. ***Lecane agilis***, a species known from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 33. ***Lecane clara***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 34. ***Lecane clara***, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Lecane closterocerca (Figure 35-Figure 36) is a species known from bryophytes, including ***Sphagnum*** (Figure 2). This cosmopolitan littoral species is common in the plankton in a *p*H range of 6.7-9.1 and temperatures of 7.8-24°C (de Manuel Barrabin 2000). Despite its common presence in freshwater, it has a wide tolerance of salinity.

Figure 35. ***Lecane closterocerca***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 36. ***Lecane closterocerca***, a ***Sphagnum*** dweller with fused toes. Photo by Jersabek *et al.* 2003, with permission.

Figure 37. ***Lecane cornuta***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

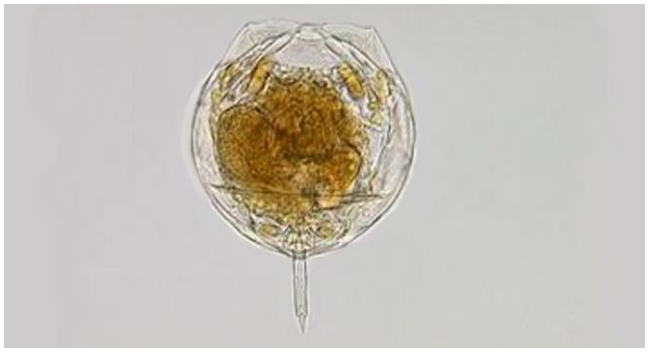

Figure 38. ***Lecane cornuta***, a species known from bryophytes**,** with foot extended. Photo by Jersabek *et al.* 2003, with permission.

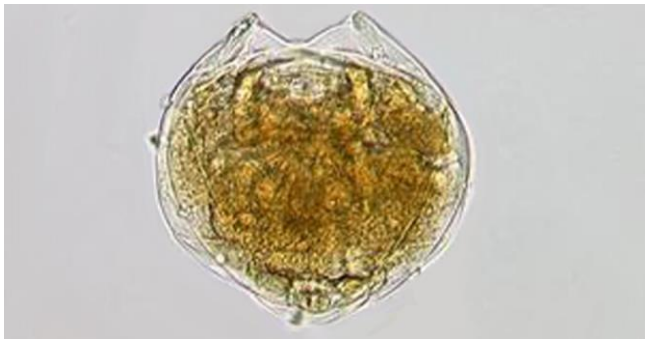

Figure 39. ***Lecane cornuta***, with foot retracted. Photo by Jersabek *et al.* 2003, with permission.

Figure 40. ***Lecane cf galeata***, a species known from ***Sphagnum subsecundum*** (Figure 42) in bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 41. ***Lecane cf galeata***, a species known from ***Sphagnum subsecundum*** (Figure 42) in bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 42. ***Sphagnum subsecudum***, home of ***Lecane galeata***. Photo by Michael Lüth, with permission.

Lecane hamata (Figure 43) is a cosmopolitan, littoral species living on plant substrata and known from bryophytes (de Manuel Barrabin 2000), including ***Sphagnum*** (Figure 2; Hingley 1993). It occurs at *p*H levels around 7.9 with a known from a temperature range of 11.9-13.5°C (de Manuel Barrabin 2000).

Figure 43. ***Lecane hamata***, a species known from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Lecane lunaris (Figure 44-Figure 45) is a cosmopolitan littoral species that is frequent in the plankton (de Manuel Barrabin 2000) and is known to inhabit bryophytes, including ***Sphagnum*** (Figure 2; Hingley 1993). It is known from water that is rich in nutrients with a *p*H of 6.3-9.2 and a temperature range of 7.2-26.2°C (de Manuel Barrabin 2000).

Figure 44. ***Lecane lunaris***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 45. ***Lecane lunaris***, a species known to inhabit bryophytes, including ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 46. ***Lecane pyrrha***, a species known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 47. ***Lecane signifera***, a species known to live among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 48. ***Lecane signifera ploenensis*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

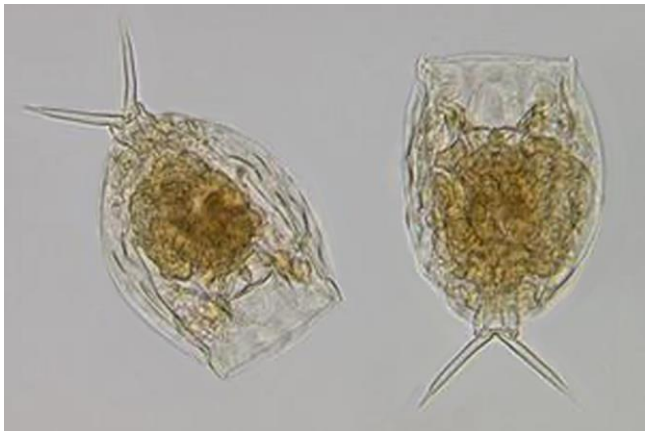

Figure 49. ***Lecane stichaea***, a species known from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

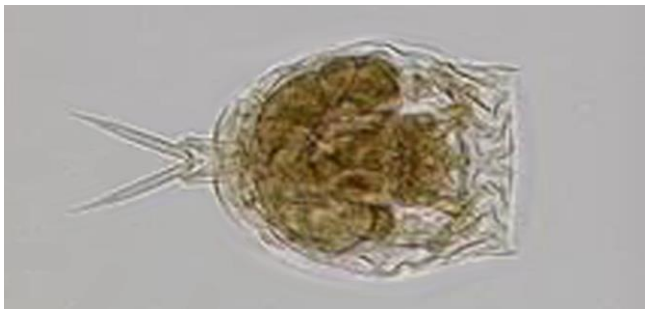

Figure 50. ***Lecane stichaea***, a rotifer associated with ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

To these studies, Jersabek *et al*. (2003) added species from records at the Academy of Natural Sciences of Philadelphia. The ***Sphagnum*** (Figure 2) associates included ***Lecane calcaria*** (Figure 51), ***L. copeis*** (Figure 52), ***L. curvicornis*** (Figure 53), ***L. depressa*** (Figure 54), ***L. mira*** (Figure 55), ***L. mitis*** (Figure 56), ***L. pertica*** (Figure 57-Figure 58), ***L. psammophila*** (Figure 59), ***L. satyrus*** (Figure 60), and ***L. thalera*** (Figure 61-Figure 62). Plewka (2016) included ***L. acus*** (Figure 63) and ***L. arcula*** (Figure 64), two ***Sphagnum*** dwellers not included on the other lists here. Jersabek *et al*. (2003) reported ***L. lauterborni*** (Figure 65) from ***Sphagnum wheeleri*** in Hawaii (Figure 66).

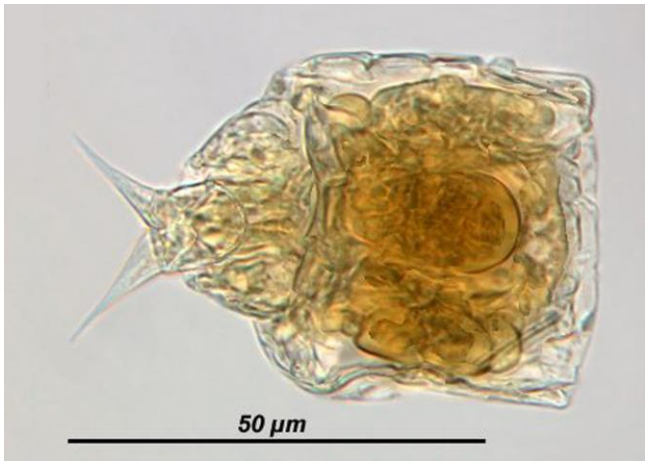

Figure 51. ***Lecane calcaria***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

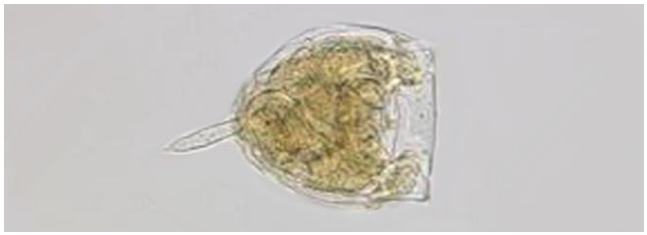

Figure 52. ***Lecane copeis*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

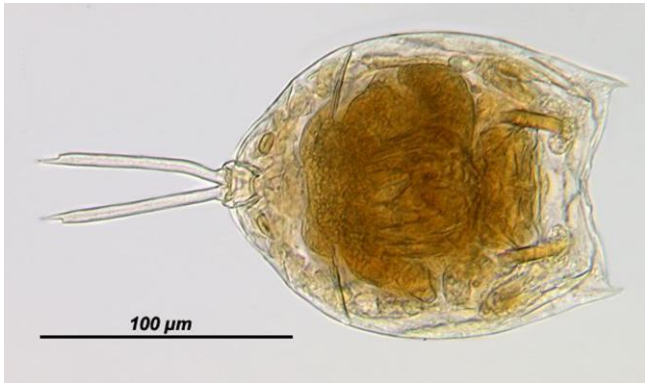

Figure 53. ***Lecane curvicornis***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 54. ***Lecane depressa*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Lecane mira (Figure 55-Figure 56) is a cosmopolitan species that lives on aquatic plants, including ***Sphagnum***, and is common in somewhat acid waters, but can also be common at a *p*H around 7.2 (de Manuel Barrabin 2000). It is known from a temperature around 10.8°C.

Figure 55. ***Lecane mira*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 56. ***Lecane mitis*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 57. ***Lecane pertica*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

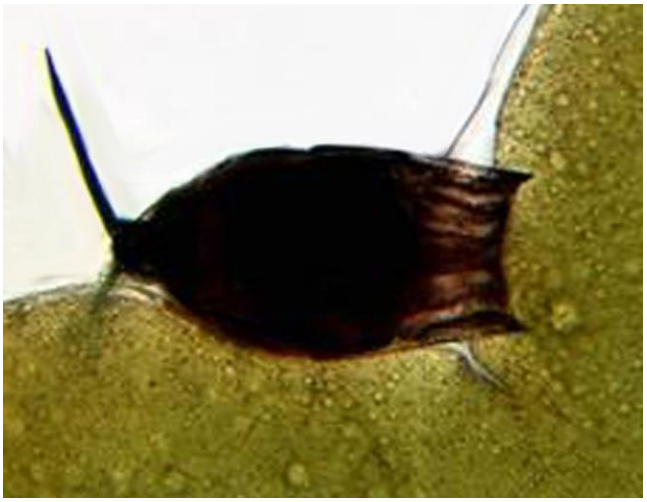

Figure 58. ***Lecane pertica***, shown here on duckweed (*Lemna*), but it also occurs among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

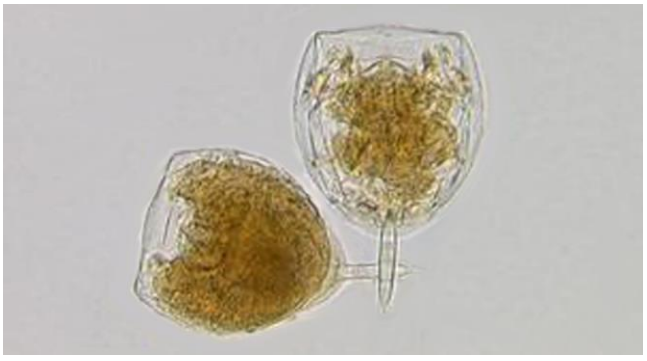

Figure 59. ***Lecane psammophila*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 60. ***Lecane satyrus*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 61. ***Lecane lamellata/thalera***, a ***Sphagnum*** dweller. These two species are difficult to distinguish and might hybridize. Photo by Jersabek *et al*. 2003, with permission.

Figure 62. ***Lecane thalera*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 63. ***Lecane acus***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 64. ***Lecane arcula***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

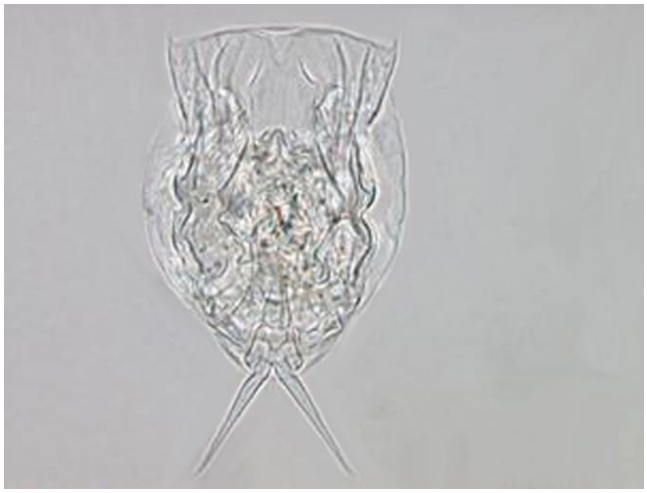

Figure 65. ***Lecane lauterborni*** from among ***Sphagnum wheeleri*** in Hawaii and ***Sphagnum*** in Pennsylvania, USA. Photo by Jersabek *et al.* 2003, with permission.

Figure 66. ***Sphagnum wheeleri***, Home for ***Lecane lauterborni*** in Hawaii. Photo by Jersabek *et al.* 2003, with permission.

Some researchers include ***Sphagnum*** (Figure 2) and "moss" (perhaps meaning ***Sphagnum***) as the rotifer habitats. Among these are ***Lecane elasma*** (Figure 67; Jersabek *et al*. 2003; Bielańska-Grajner *et al*. 2011), ***L. ligona*** (Figure 68; Jersabek *et al*. 2003), and ***L. stokesii*** (Figure 69) living between mosses (Plewka 2016).

Figure 67. ***Lecane elasma*** from among mosses and ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

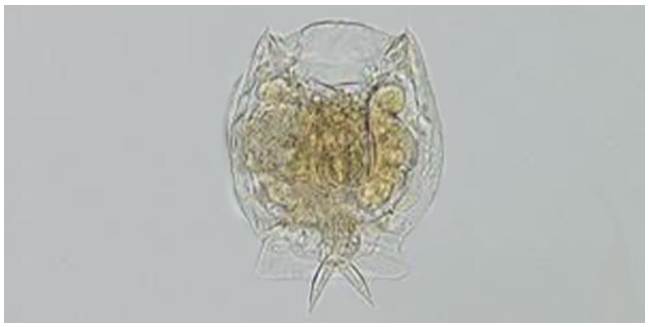

Figure 68. ***Lecane ligona*** from a ***Sphagnum*** pool. Photo by Jersabek *et al.* 2003, with permission.

A few reports simply list "moss": ***L. climacois*** (Figure 70; Myers 1942; Jersabek *et al*. 2003), ***L. rhopalura*** (Figure 71) on submerged moss (Jersabek *et al*. 2003), ***L. ungulata*** (Figure 72-Figure 74; Madaliński 1961). ***Lecane arcuata*** occurs among submerged mosses in trenches of Alaskan polygons (Segers *et al*. 1996) and wet mosses on Svalbard (De Smet 1993).

Figure 69. ***Lecane stokesii*** from between mosses, including ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 70. ***Lecane climacois*** from among mosses. Photo by Jersabek *et al.* 2003, with permission.

Figure 71. ***Lecane rhopalura*** from among submerged moss in a pond. Photo by Jersabek *et al.* 2003, with permission.

Figure 72. ***Lecane ungulata***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 73. ***Lecane ungulata***, a species known to inhabit bryophytes. Photo by Jersabek *et al*. 2003, with permission.

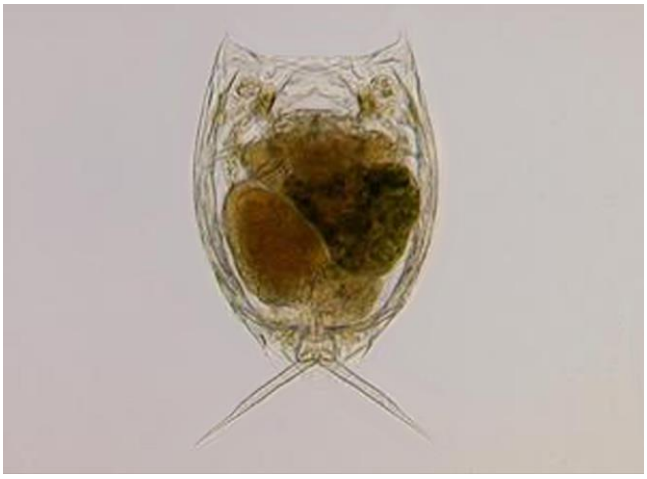

Figure 74. ***Lecane ungulata*** var. ***tenuior***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

One of the undersampled habitats seems to be waterfalls. ***Lecane martensi*** was discovered on wet mosses as a new species in this habitat by Savatenalinton and Segers in 2008. What seems to be most lacking is records of this large genus associated with terrestrial bryophytes.

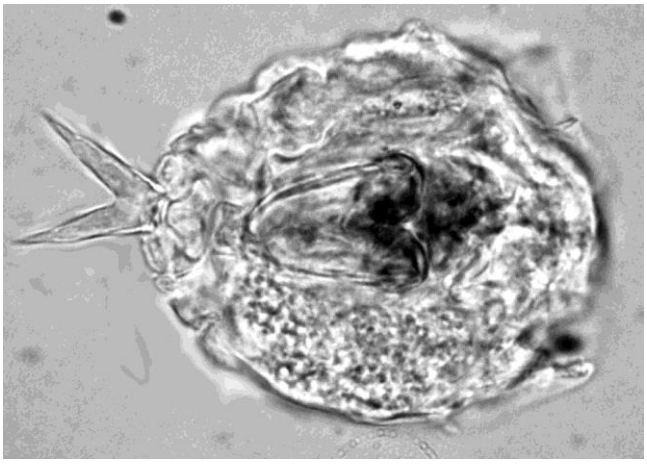

Figure 75. ***Lecane martensi***, a species that was discovered among mosses in a waterfall. Photo by Savatenalinton & Segers 2008, through Creative Commons.

Ituridae

This small family, with only one genus, seems to have little written about it beyond species lists and taxonomic distinctions. Even the map of its distribution showed nothing. I could find only one species, ***Itura aurita*** (Figure 76-Figure 77), that had been collected from mosses, including from bogs (Horkan 1981). De Smet (1993) reported it from submerged mosses on Svalbard.

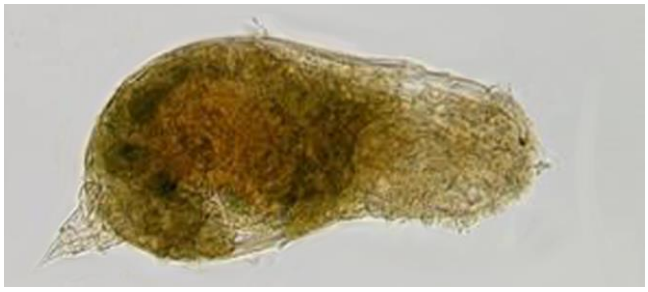

Figure 76. ***Itura aurita*** from Pocono Lake, Pennsylvania, USA. This species is known from bryophytes and from bogs. Photo by Jersabek *et al*. 2003, with permission.

Figure 77. ***Itura aurita***, a moss dweller, with green food in its gut. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Lepadellidae

Many of the **Lepadellidae** are cosmopolitan, often occurring in freshwater habitats (Baribwegure & Segers 2001). In particular, the genera ***Colurella*** (Figure 78-Figure 86, Figure 88), ***Lepadella*** (Figure 91-Figure 112), and ***Squatinella*** (Figure 116-Figure 126) are widespread. These same three genera are well represented among bryophyte collections. A fourth genus, ***Paracolurella*** (Figure 114-Figure 115), also is known from bryophytes.

Colurella

Colurella adriatica (Figure 78-Figure 79) is an uncommon species that may be cosmopolitan (de Manuel Barrabin 2000). It is a planktonic species in small water bodies that lives among plants in the littoral zone and is known from bryophytes. It seems to prefer basic water around *p*H 8.4 and is known from temperatures around 23.5°C. It is known from bryophytes (Madaliński 1961)

and occurs among submerged mosses on Svalbard (De Smet 1990, 1993). ***Colurella colurus*** has similar requirements, but is known from a *p*H level around 7.1 and temperature of 9.7°C (de Manuel Barrabin 2000). It is known from bryophytes (Madaliński 1961) and occurs among submerged mosses and in plankton on Svalbard (De Smet 1993).

Figure 78. ***Colurella adriatica***, a species known from bryophytes and bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 79. ***Colurella adriatica***, a species that lives among plants in the littoral zone and is known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Colurella clausa (Figure 80), ***C. denticauda*** (Myers 1942) and ***C. obtusa*** (Figure 81-Figure 83; Horkan 1981; Hingley 1993; Błedzki & Ellison 2003; Plewka 2016), and ***Colurella tesselata*** (Figure 84-Figure 85; Horkan 1981; Hingley 1993; Jersabek *et al.* 2003) occur with ***Sphagnum*** (Figure 2). ***Colurella obtusa*** occurs on Svalbard, where one can find it among submerged mosses and plankton (De Smet 1993). ***Colurella hindenburgi*** (Figure 86) occurs with ***Sphagnum subsecundum*** (Figure 87) (Myers 1942; Jersabek *et al.* 2003), but it also occurs among terrestrial bryophytes (Bielańska-Grajner *et al.* 2011) and in submerged mosses and plankton on Svalbard (De Smet 1993). Segers *et al.* (1996) found ***Colurella uncinata*** among submerged mosses in trenches of Alaskan polygons.

Figure 80. ***Colurella clausa*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

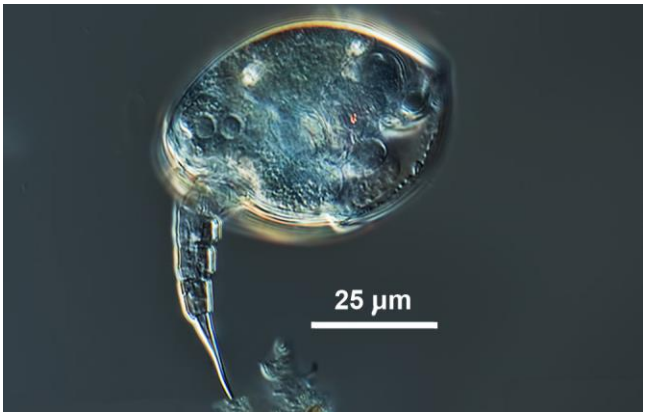

Figure 81. ***Colurella obtusa***, a bog and ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

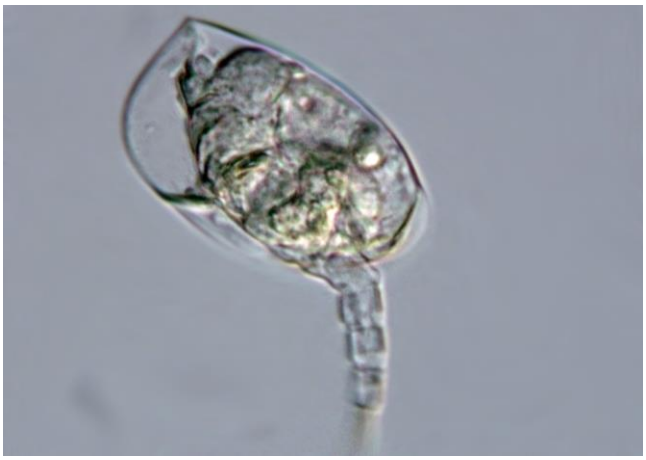

Figure 82. ***Colurella obtusa***, a bog and ***Sphagnum*** dweller. Photo by Yuuji Tsukii, with permission.

Figure 83. ***Colurella obtusa***, a species known from bryophytes and bogs. Photo by Jersabek *et al.* 2003, with permission.

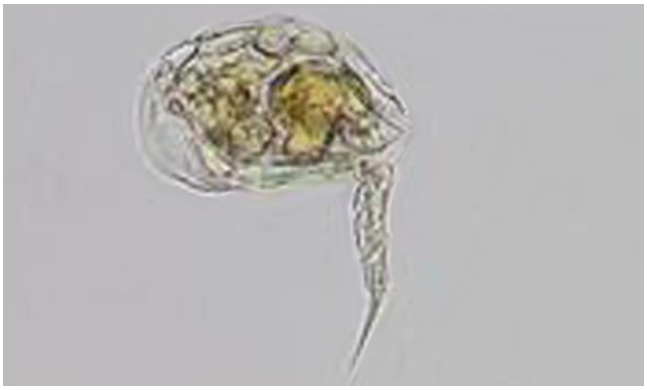

Figure 84. ***Colurella tesselata*** side view, a species known from ***Sphagnum*** bogs. Photo by Jersabek *et al*. 2003.

Figure 85. ***Colurella tesselata***, a species known from more than one location of ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

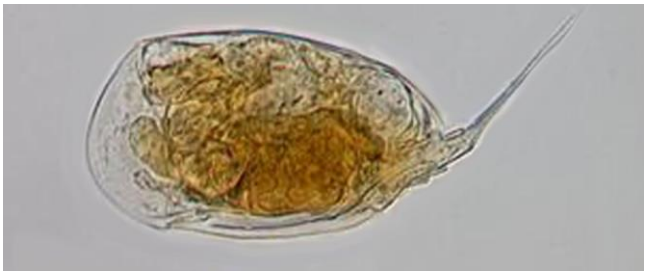

Figure 86. ***Colurella hindenburgi*** from among ***Sphagnum subsecundum*** (Figure 87). Photo by Jersabek *et al.* 2003, with permission.

Figure 87. ***Sphagnum subsecundum*** emersed in a fen. Photo by Michael Lüth, with permission.

The genus ***Colurella*** has several species associated with terrestrial bryophytes. ***Colurella geophila*** (Figure 88) lives on epiphytic mosses (Plewka 2016).***Colurella hindenburgi*** (Figure 89) lives on mosses on the dry habitat of granite rocks (Colurella 2016) as well as in bogs and fens (in Poland; Bielańska-Grajner *et al*. 2011). Bielańska-Grajner *et al*. (2011) likewise found ***C. adriatica*** (Figure 78-Figure 79) and ***C. colurus*** in these bogs and fens. ***Colurella paludosa*** (Figure 90) lives in ***Sphagnum*** ponds (Figure 29) (Plewka 2016).

Figure 88. ***Colurella geophila***, a species that lives on epiphytic moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 89. ***Colurella hindenburgi***, a species that lives on mosses on granite rocks. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 90. ***Colurella paludosa***, a species of ***Sphagnum*** pools. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Lepadella

Lepadella species include several that live among bryophytes. Myers (1942), working in the Poconos, Pennsylvania, USA, listed ***Lepadella apsicora*** (Figure 91), ***L. akrobeles*** (Figure 92-Figure 93), ***L. latusinus*** (Figure 94), ***L. ovalis*** (Figure 95-Figure 96; see also Bielańska-Grajner *et al*. 2011 from Poland), and ***L. zigzag*** (Figure 97) as ***Sphagnum*** (Figure 2) associates (Myers 1942).

Figure 91. ***Lepadella apsicora***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

Figure 92. ***Lepadella akrobeles*** from among ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

Figure 93. ***Lepadella akrobeles*** from among ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

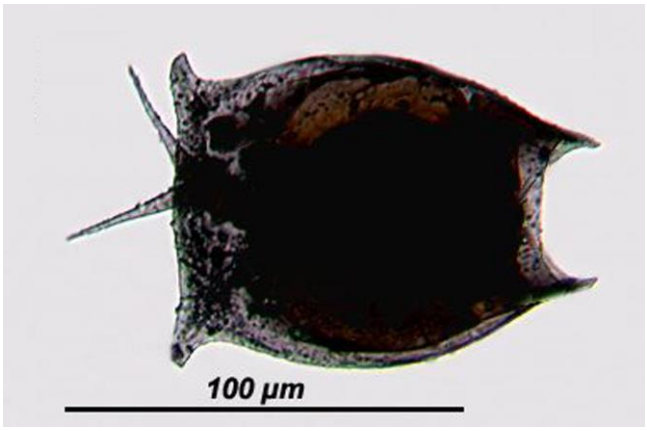

Figure 94. ***Lepadella latusinus***, a species that lives among ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

Lepadella ovalis (Figure 95-Figure 96) is a cosmopolitan species (de Manuel Barrabin 2000). It is a plankton species that occurs among macrophytes in the littoral zone and it can inhabit bryophytes. It is known at *p*H levels of 8.58-9.14 and from the temperature range of 23.6-24°C.

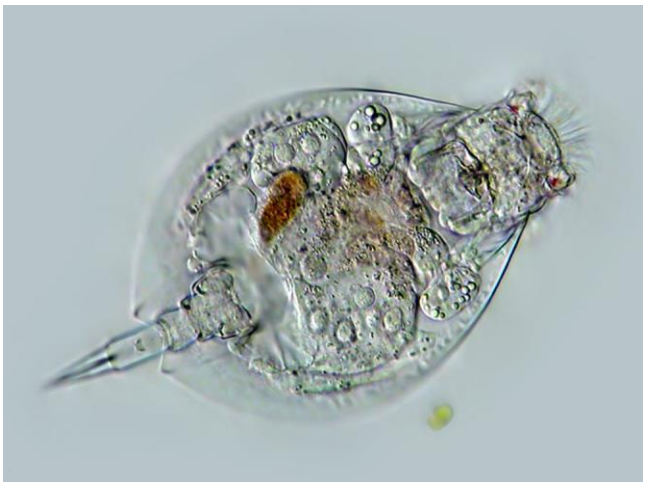

Figure 95. ***Lepadella ovalis***, a bryophyte dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 96. ***Lepadella ovalis*** is a plankton species that can inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

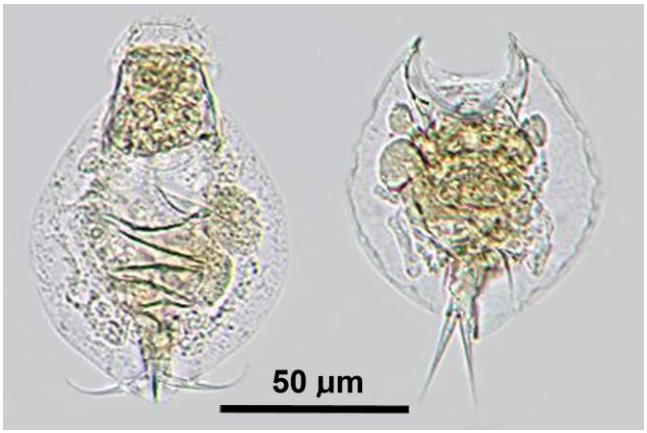

Figure 97. ***Lepadella zigzag***, from ***Sphagnum*** in a pool. Photo by Jersabek *et al*. 2003, with permission.

Lepadella patella (Figure 98-Figure 99) is a littoral species known to inhabit bryophytes (de Manuel Barrabin 2000), including submersed mosses on Svalbard (De Smet 1990, 1993) and on submerged mosses in trenches of Alaskan polygons (Segers *et al*. 1996). This cosmopolitan species lives primarily on plant substrata, but occasionally occurs in the plankton of reservoirs, rivers, and ponds. It is uncommon in large bodies of water. It is known from a *p*H of 6.7-9.3 and temperatures of 9.1-22.3. Bielańska-Grajner *et al*. (2011) and Plewka (2016) reported it from ***Sphagnum*** (Figure 2) peatlands (bogs or fens).

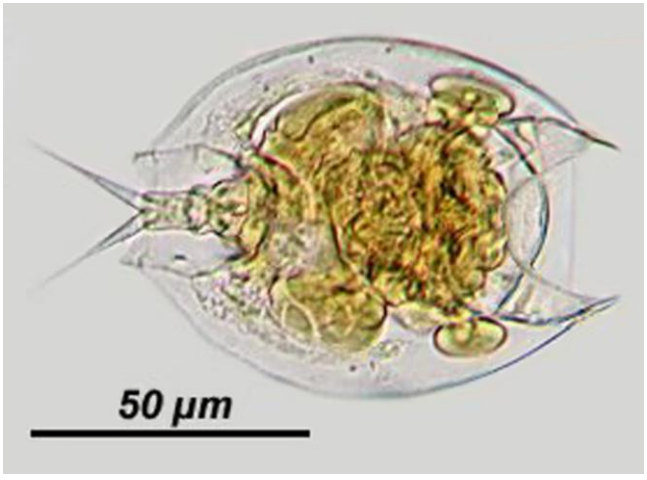

Figure 98. ***Lepadella patella***, a littoral species known to inhabit bryophytes, but also can be found in ***Sphagnum*** bogs Photo by Jersabek *et al.* 2003, with permission.

Plewka (2016) and others include several additional species as ***Sphagnum*** (Figure 2) associates. ***Lepadella acuminata*** (Figure 100-Figure 101; Hingley 1993; Bielańska-Grajner *et al*. 2011) [also with submerged mosses on Svalbard (De Smet 1993)], ***L. elliptica*** (Bielańska-Grajner *et al*. 2011); ***L. heterostyla*** (Figure 102; Plewka 2016), ***L. pterygoida*** (Figure 103; Hingley 1993; Jersabek *et al*. 2003), ***L. triba*** (Figure 104; Hingley 1993; Jersabek et al. 2003), ***L. triptera*** (Figure 105-Figure 108; Horkan 1981; Hingley 1993), and ***Lepadella whitfordi*** (Figure 109; Myers 1942) all are associated with ***Sphagnum*** or occur in bogs. Both ***L. triba*** and ***L. triptera*** occur among submerged mosses on Svalbard (De Smet 1993). ***Lepadella beyensi*** was described from submerged mosses in a puddle in the high Arctic (De Smet 1994). ***Lepadella deridderae*** subsp. ***alaskae*** lives on submerged mosses in trenches of Alaskan polygons (Segers *et al*. 1996). ***Lepadella minuta*** occurs among submerged mosses on Svalbard (De Smet 1993).

Figure 99. ***Lepadella patella***, a rotifer known from a ***Sphagnum*** bog. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Lepadella acuminata (Figure 100-Figure 101) is a species known to inhabit **bryophytes** as well as other plant substrata and is only occasionally found among the plankton (de Manuel Barrabin 2000). It occurs with submerged mosses on Svalbard (De Smet 1993). This species does best in water that is slightly acid (Koste 1978) [*p*H 6.8-8.3 (de Manuel Barrabin 2000)] and has a temperature range of 7.8-19°C (Koste 1978).

Figure 100. ***Lepadella acuminata*** is a species known to inhabit ***Sphagnum*** as well as other plant substrata. Photo by Jersabek *et al.* 2003, with permission.

Figure 101. ***Lepadella acuminata***, a species that sometimes occurs on bryophytes. Photo from Michael Plewka <www.plingfactory.de>, with permission.

Figure 102. ***Lepadella heterostyla***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 103. ***Lepadella pterygoida*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 104. ***Lepadella triba***, a species known to live among ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 105. ***Lepadella triptera***, a species known to inhabit bryophytes and that can occur in bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 106. ***Lepadella triptera***, a species known from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 107. ***Lepadella triptera***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

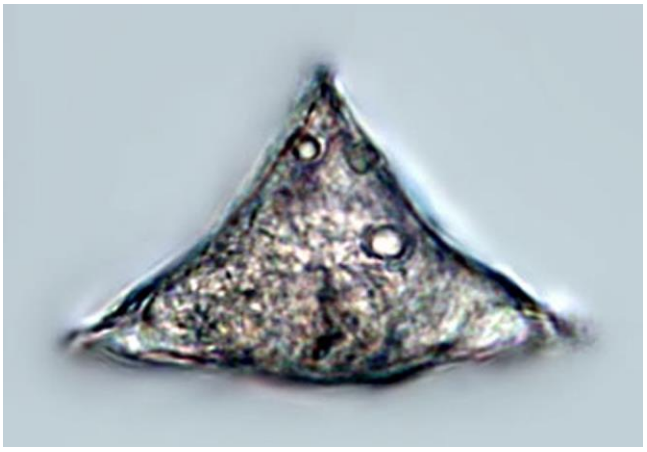

Figure 108. ***Lepadella triptera*** showing three wings of the lorica. Photo by Michael Plewka <www.plingfactory.de>, with permission.

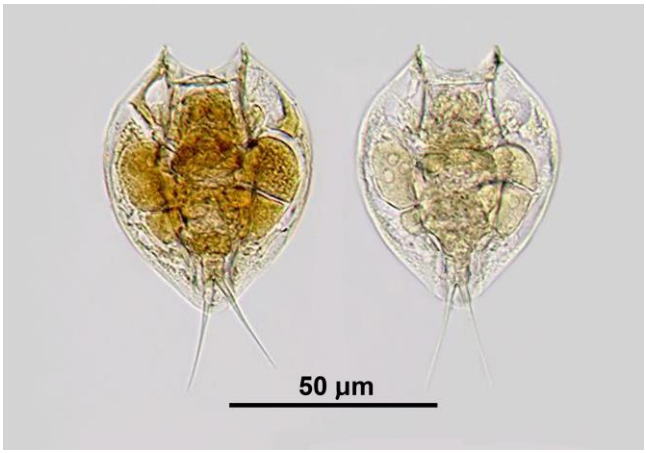

Figure 109. ***Lepadella whitfordi***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

Lepadella venefica (Figure 110-Figure 111) lives on emersed ***Sphagnum subsecundum*** (Figure 87) and in ***Sphagnum*** (Figure 2) bogs (Jersabek *et al*. 2003).

Figure 110. ***Lepadella venefica*** from emersed ***Sphagnum subsecundum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 111. ***Lepadella venefica*** from among emersed ***Sphagnum subsecundum***. Photo by Jersabek *et al.* 2003, with permission.

Lepadella eurysterna (Figure 112) is perhaps the only ***Lepadella*** species known from the aquatic moss ***Fontinalis novae-angliae*** (Figure 113) (Myers 1942).

Figure 112. ***Lepadella eurysterna***, a species that lives among the aquatic moss ***Fontinalis novae-angliae***. Photo by Jersabek *et al.* 2003, with permission.

Figure 113. ***Fontinalis novae-angliae***, home for ***Lepadella eurysterna***. Photo by Janice Glime.

Paracolurella

Paracolurella is among the many rotifer genera represented among the ***Sphagnum*** (Figure 2). It is a genus of only two species, ***P. aemula*** (Figure 114) and ***P. logima*** (Figure 115), and both of these occur among ***Sphagnum*** (Jersabek *et al*. (2003).

Figure 114. ***Paracolurella aemula*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

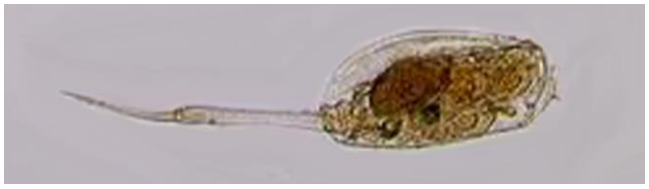

Figure 115. ***Paracolurella logima*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Squatinella

More rotifers from the genus ***Squatinella*** occur on or among ***Sphagnum*** (Figure 2). Myers (1942) reported only ***S. bifurca*** (Figure 116) as a ***Sphagnum*** associate. Hingley (1993) reported ***S. lamellaris*** [Figure 117-Figure 121, typically a periphyton species (Plewka 2016)], ***S. longispinata*** Figure 122), ***S. microdactyla*** [Figure 123; typically a plankton species (Plewka 2016)], and ***S. rostrum*** (Figure 124-Figure 125; see also Bielańska-Grajner *et al*. 2011). Jersabek *et al*. (2003) added the additional species ***S. retrospina*** (Figure 126) from a ***Sphagnum*** bog.

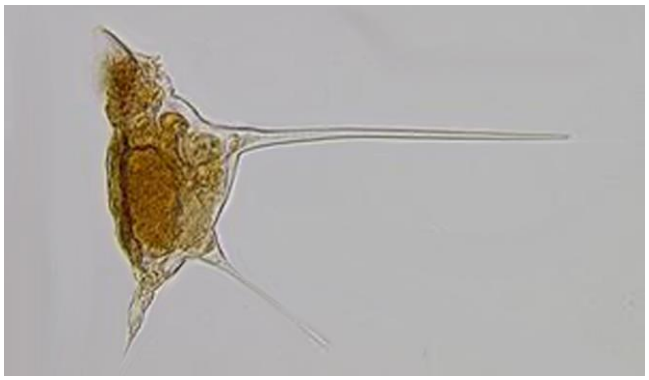

Figure 116. ***Squatinella bifurca*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 117. ***Squatinella lamellaris f. mutica*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 118. ***Squatinella lamellaris*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 119. Side view of ***Squatinella lamellaris*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 120. ***Squatinella lamellaris***, a member of the periphyton, including ***Sphagnum*** as a substrate. Photo by Michael Plewka <www.plingfactory.de>, with permission.

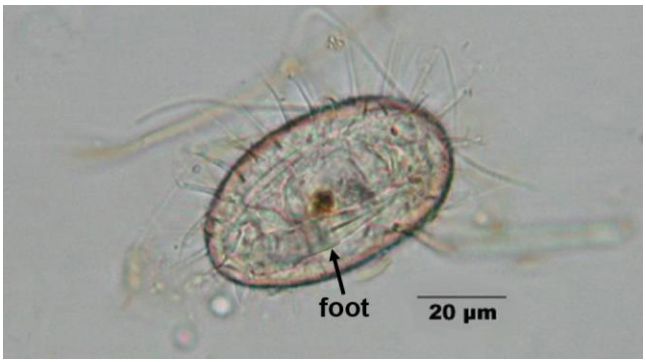

Figure 121. ***Squatinella lamellaris f. tridentata*** egg, showing foot and mastax, a ***Sphagnum*** dweller. Photo by Ralf Wagner, with permission.

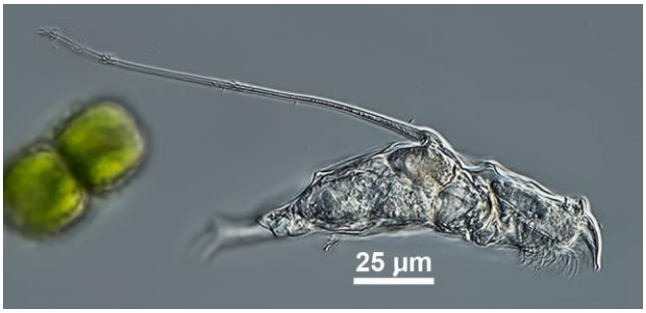

Figure 122. ***Squatinella longispinata***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

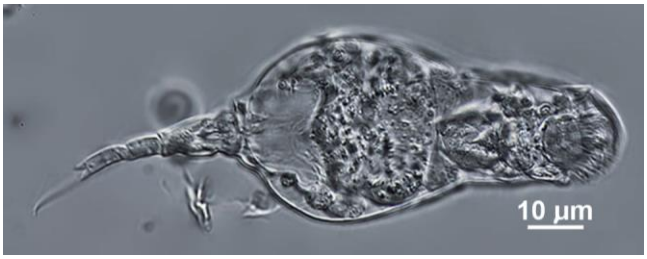

Figure 123. ***Squatinella microdactyla***, typically a plankton species, but one that also occurs among ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 124. ***Squatinella rostrum***, a ***Sphagnum*** associate. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 125. ***Squatinella rostrum***, a ***Sphagnum*** associate. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 126. ***Squatinella retrospina*** from among ***Sphagnum*** in bog. Photo by Jersabek *et al.* 2003, with permission.

Lindiidae

This is a small family with only one genus and at least fifteen species (De Smet 2005). Three of these occur in salt water. Three species are known from bryophytes. ***Lindia annecta*** (Figure 127) is a periphytic species that occurs among ***Sphagnum*** in bogs (de Manuel Barrabin 2000). In reservoirs of Spain it is known at temperatures around 7.9 and a *p*H of around 6.8. Jersabek *et al*. (2003) also reported a collection of this species from a lake in the Pocono Mountains, Pennsylvania, USA.

Figure 127. ***Lindia annecta*** is a periphytic species that commonly occurs in ***Sphagnum*** bogs. Photo from Jersabek *et al*. 2003, with permission.

Lindia pallida (Figure 128) is likewise a ***Sphagnum*** (Figure 2) dweller, living anywhere that wet or partly submerged ***Sphagnum*** occurs (Harrington & Myers 1922). To quote Harrington and Myers, "in such locations it may be collected at any time and any place."

Figure 128. ***Lindia pallida*** from ***Sphagnum***. Photo by Christian Jersabek, with permission.

Lindia torulosa (Figure 129-Figure 133) is a large rotifer (>500 1 µrn) that is cosmopolitan, including records from one sub-Antarctic and four Antarctic locations (Dartnall 1995). ***Lindia torulosa*** is aquatic, but it also inhabits submersed mosses (de Beauchamp 1913) and wet terrestrial mosses (De Smet, pers. comm. 13 November 2016), where it eats the **Cyanobacteria** ***Oscillatoria*** (Figure 130-Figure 131) and ***Anabaena***/***Nostoc*** (Figure 132) (Koste 1979; Plewka 2016). Its trophi are specialized for eating **Cyanobacteria**.

Figure 129. ***Lindia torulosa***, a species known to inhabit bryophytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 130. ***Lindia torulosa***, shown here preparing to eat ***Oscillatoria***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 131. ***Lindia torulosa*** consuming ***Oscillatoria***, using its specialized trophi. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 132. ***Lindia torulosa*** with ***Anabaena*** or ***Nostoc*** in its gut. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 133. ***Lindia torulosa*** showing cilia. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Microcodidae

This family has only one genus, and only a single species, ***Microcodon clavus*** (Figure 134-Figure 135), a plankton species, is also known from bryophytes (Horkan 1981; Hingley 1993; Jersabek *et al.* 2003. It has no **lorica** (shell) and is shaped like a cone with a long, ventral foot (Naberezhnomu 1984).

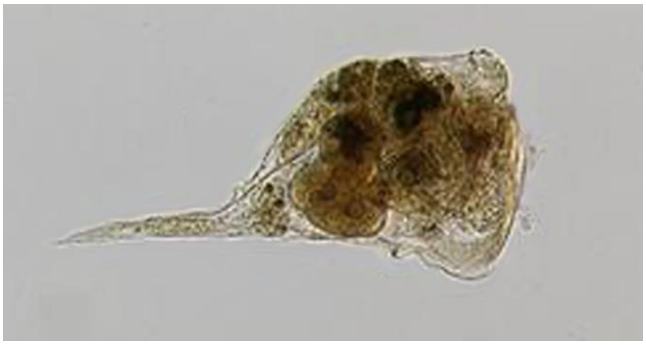

Figure 134. ***Microcodon clavus*** from among ***Sphagnum*** in bogs. Photo by Jersabek *et al.* 2003, with permission.

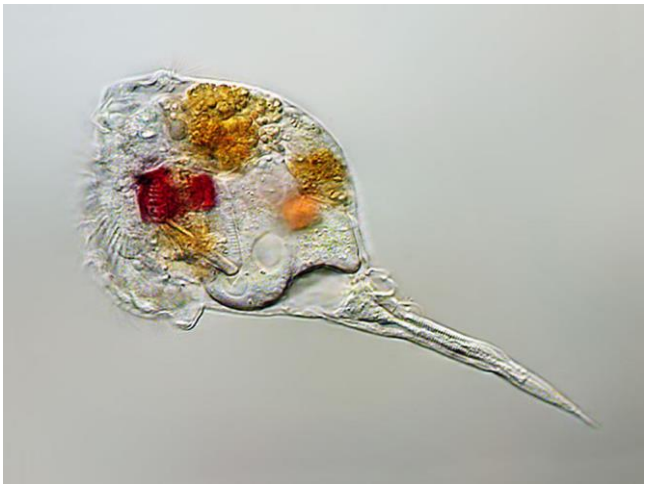

Figure 135. ***Microcodon clavus***, a plankton dweller that can occur among ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Mytilinidae

The **Mytilinidae** are **loricate** rotifers (Koste & Shiel 1989). That is, they have a shell. This lorica is triangular to rhombic in cross section and there is often a double keel on the dorsal side. The species are littoral bottom-dwellers, rarely occurring in the plankton. There are only two genera, but only ***Mytilina*** (Figure 136), a genus with 37 species, is represented among bryophytes, with three species thus far reported here.

Mytilina macrocera (Figure 137) is a ***Sphagnum*** (Figure 2) dweller (Jersabek *et al*. 2003). ***Mytilina mucronata*** (Figure 138-Figure 139) occurs on various substrata, including algal filaments (Figure 138; Photo by Jersabek *et al.* 2003), submerged mosses in trench of Alaskan polygons (Segers *et al*. 1996), and among ***Sphagnum*** in bogs (Horkan 1981; Hingley 1993); on Svalbard, it occurs on wet mosses, but also in the plankton (De Smet 1993). ***Mytilina brevispina*** (Figure 141-Figure 140) is a bryophyte dweller on ***Sphagnum*** (Hingley 1993; Plewka 2016).

Figure 136. ***Mytilina***, a genus with three species known from bryophytes. Note the triangular (top to bottom) shell and dorsal keel. Photo by Jean-Marie Cavanihac, with permission.

Figure 137. ***Mytilina macrocera***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 138. ***Mytilina mucronata***, a species known to inhabit bryophytes and to live in bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 139. ***Mytilina mucronata*** on the filamentous alga ***Oedogonium***. It also inhabits bryophytes and lives among ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 140. ***Mytilina brevispina***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 141. ***Mytilina brevispina*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Summary

The monogonont order **Ploimida** is continued here from the previous sub-chapter. The **Lecanidae** is a large family with only one genus, ***Lecane***. ***Lecane*** has many species associated with bryophytes. The **Ituridae** has one species known from bryophytes. The **Lepadellidae** is a cosmopolitan family of freshwater with four genera known from bryophytes. The **Lindiidae** is a small family with only one documented species among bryophytes. The **Microcodidae** has only one species and it occurs with bryophytes. The **Mytilinidae** are littoral species. Three species of ***Mytilina*** occur among bryophytes.

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CHAPTER 4-7c

INVERTEBRATES: ROTIFER TAXA – MONOGONONTA

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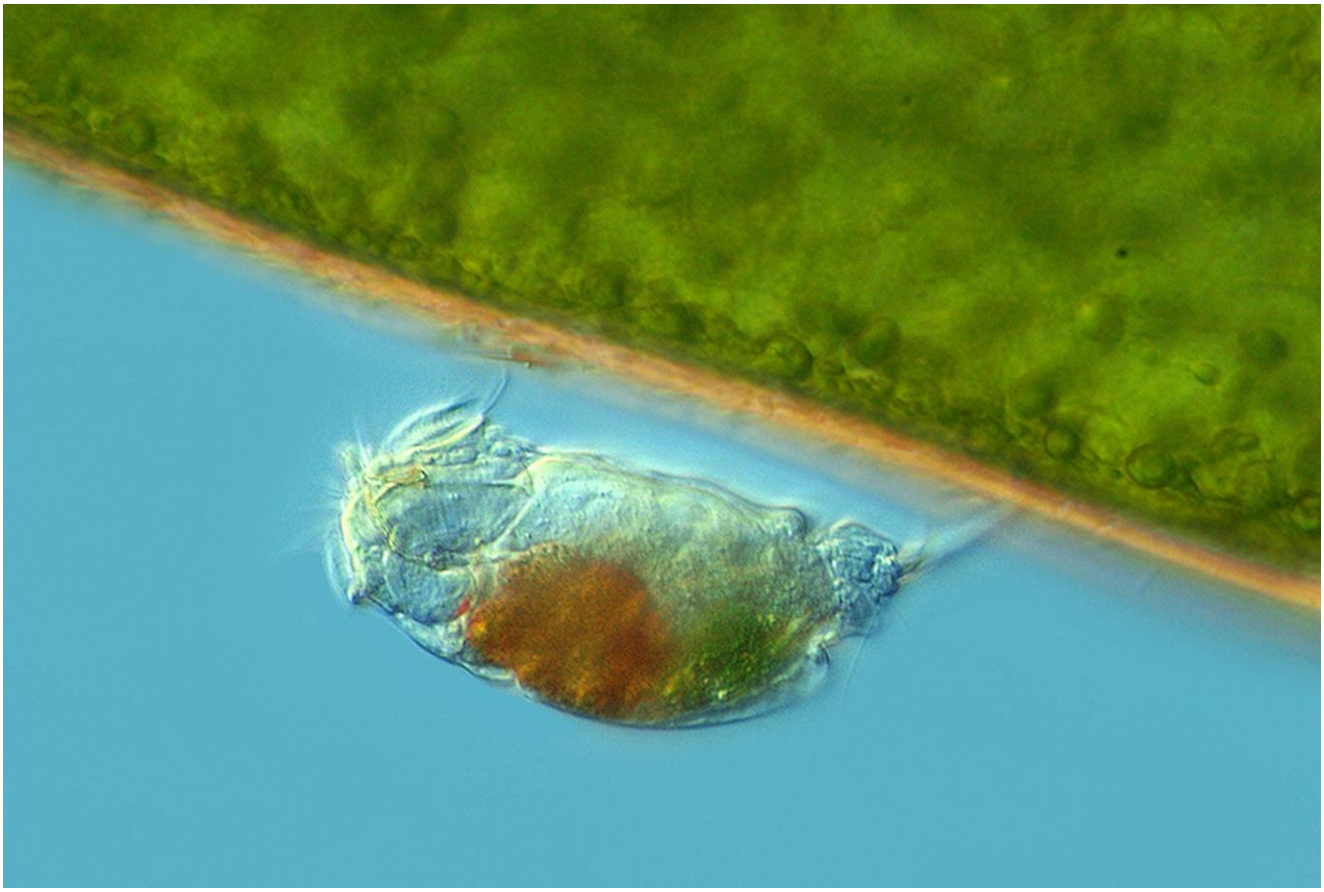

Figure 1. ***Cephalodella***, a common genus among ***Sphagnum***. Photo by Proyecto Agua Water Project Creative Commons.

Notommatidae

The name **Notommatidae** literally means "eyes on the back." The members of this family have a nearly cylindrical body with a thin foot and two toes. Many of its species are known from bryophytes.

Cephalodella

Cephalodella (Figure 1) is a large genus, with many species that occur among bryophytes. Most of these are associated with ***Sphagnum*** (Figure 2). These include ***Cephalodella abstrusa*** (Myers 1942), ***C. anebodica*** from bogs (Figure 2) (Błedzki & Ellison 2003), ***C. apocolea*** (Figure 3-Figure 5; Hingley 1993; Jersabek *et al.* 2003), ***C. auriculata*** (Figure 6-Figure 9; Hingley 1993; Jersabek *et al*. 2003), ***C. belone*** (Figure 10; Jersabek *et al*. 2003), ***C. biungulata*** (Figure 11; Jersabek *et al.* 2003), ***C. catellina*** (Figure 12-Figure 13; Horkan 1981; Hingley 1993), ***C. compressa*** (Figure 28; Jersabek *et al*. 2003), ***C. derbyi*** (Figure 29; Plewka 2016), ***C. elegans*** (Figure 30; Jersabek *et al*. 2003), ***C. forficula*** (Figure 26-Figure 25; Horkan 1981; Hingley 1993), ***C. gibba*** (Figure 15-Figure 17; Horkan 1981; Hingley 1993; De Smet 2001; Jersabek *et al.* 2003; Bielańska-Grajner, *et al*. 2011), ***C. gibboides*** (Bielańska-Grajner *et al*. 2011), ***C. gigantea*** (Figure 31; Plewka 2016), ***C. intuta*** (Figure 21-Figure 22; Hingley 1993), ***C. licinia*** (Figure 32; Jersabek *et al.* 2003), ***C. lipara*** (Figure 33-Figure 34; Jersabek *et al*. 2003), ***C. mira*** (Figure 35-Figure 36; Jersabek *et al*. 2003), ***C. mucronata*** (Figure 37; Jersabek *et al.* 2003), ***C. nana*** (Figure 38-Figure 39; plus other bryophytes; Hingley 1993), ***C. nelitis*** (Figure 40; Jersabek *et al.* 2003), ***C. pheloma*** (Hingley 1993), ***C. plicata*** (Myers 1942), ***C. rotunda*** (Figure 18; Plewka 2016), and ***C. tantilloides*** (Hingley 1993; Bielańska-Grajner *et al*. 2011).

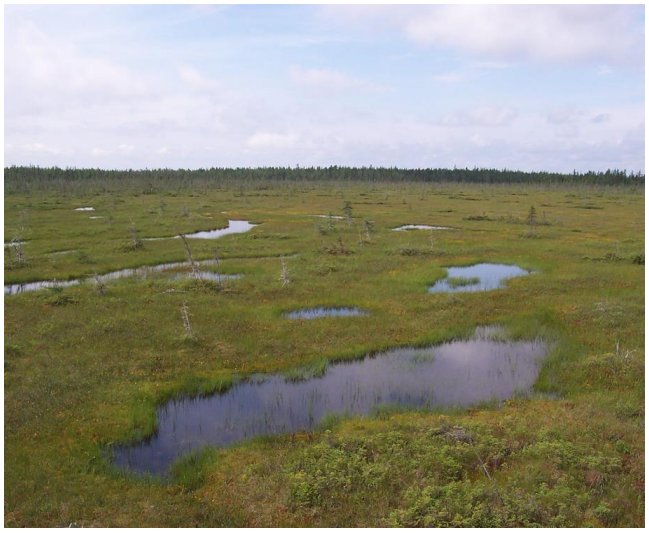

Figure 2. ***Sphagnum*** "bog" (probably a poor fen) with pools. Photo by Boŕeal, through Creative Commons.

Figure 3. ***Cephalodella apocolea***, a ***Sphagnum*** dweller, showing curved toes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 4. ***Cephalodella apocolea*** with diatoms in its gut. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 5. ***Cephalodella apocolea***, a species known from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Cephalodella auriculata (Figure 6-Figure 9) is a bryophyte dweller in northern climates. In Alaska it occurs among the submerged mosses in the trenches between the polygons (Segers *et al*. 1996).

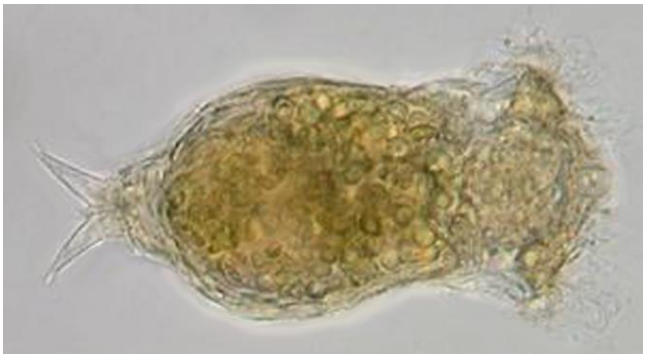

Figure 6. ***Cephalodella auriculata***, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

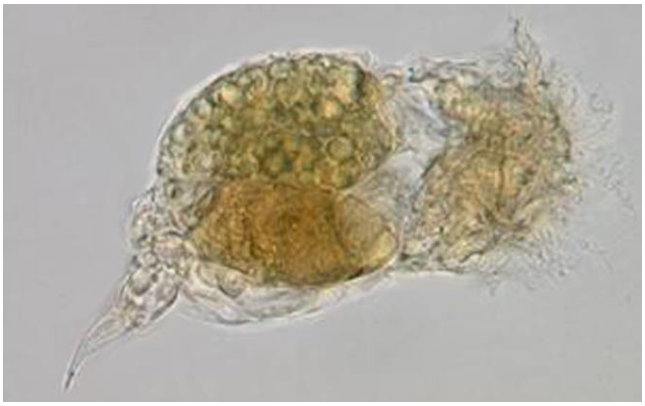

Figure 7. ***Cephalodella auriculata***, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 8. ***Cephalodella auriculata***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

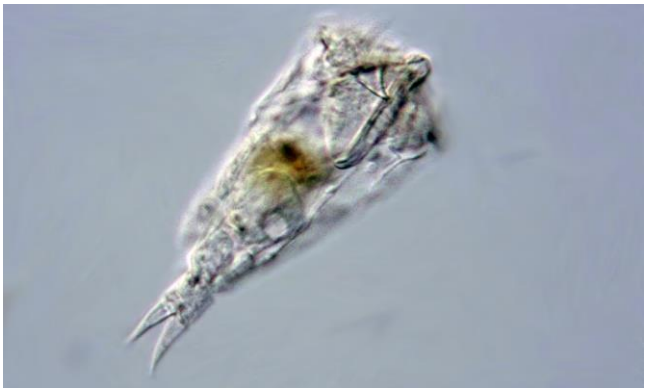

Figure 9. ***Cephalodella auriculata***, a ***Sphagnum*** dweller. Photo by Yuuji Tsukii, with permission.

Figure 10. ***Cephalodella belone*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

On Svalbard ***C. biungulata*** (Figure 11) lives exclusively on submerged mosses (De Smet 1993).

Figure 11. ***Cephalodella biungulata***, a species known from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Cephalodella catellina (Figure 12-Figure 13), ***C. evabroedae***, ***C. gibba*** (Figure 15-Figure 17), ***C. rotunda*** (Figure 18), and ***C. ventripes*** var. ***angustior*** (Figure 19) occur on submerged mosses, but also in the plankton on Svalbard (De Smet 1988, 1990, 1993). ***Cephalodella catellina*** comprised up to 20% of the rotifers on the submerged mosses (De Smet 1988). On the other hand, ***C. biungulata*** (Figure 11), ***C. glandulosa***, ***C. hoodii*** (Figure 20), ***C. intuta*** (Figure 21-Figure 22), and ***C. megalocephala*** (Figure 23) occurred exclusively on mosses (De Smet 1993). ***Cephalodella gibba*** and ***C. sterea*** (Figure 24) are among the most abundant of the submerged, moss-dwelling rotifers on Hopen, Svalbard (De Smet 1990). In Alaska, ***C. gibba*** occurred on submerged mosses in the trenches between polygons (Segers *et al*. 1993). Other species on submerged mosses on Hopen included ***Cephalodella forficula*** (Figure 26-Figure 25) and ***C. misgurnus***.

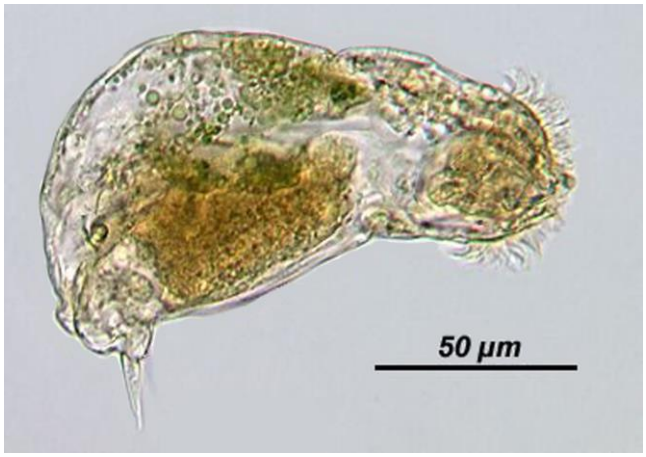

Figure 12. ***Cephalodella catellina*** from a ***Sphagnum*** bog. Photo by Jersabek *et al*. 2003, with permission.

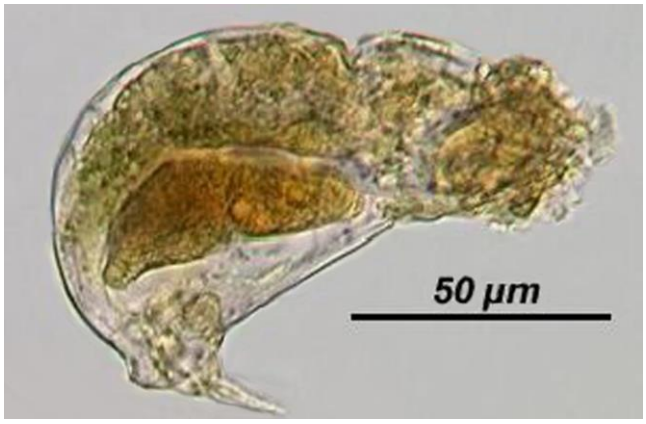

Figure 13. ***Cephalodella catellina*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Cephalodella gibba (Figure 15-Figure 17) is a cosmopolitan planktonic species of small bodies of water (de Manuel Barrabin 2000). It lives in littoral areas of both fresh and brackish water and occasionally lives in branchial chambers of crustaceans. It feeds on single-celled algae, flagellates, and ciliates. It prefers cold water (Segers 2001), but is known from a range of 6.4-18.8°C (de Manuel Barrabin 2000). Its known *p*H range is 6.6-8.48. In Germany, it is known from habitats with *p*H <3.0 (Deneke 2000). It typically occurs in the sediments (Hingley 1993; Schmid-Araya 1995), but it also is found among the Antarctic mosses (De Smet 2001).

Figure 14. ***Cephalodella gibba***, a ***Sphagnum*** associate. Photo by Jersabek *et al*. 2003, through Creative Commons.

Figure 15. ***Cephalodella gibba*** lateral view, a plankton and littoral species that also associates with ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

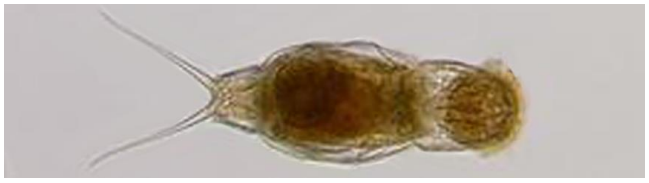

Figure 16. ***Cephalodella gibba***, a species known from bogs and from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 17. ***Cephalodella gibba*** in copulation, with the smaller male on left. Photo by Michael Plewka <www.plingfactory.de>, with permission.

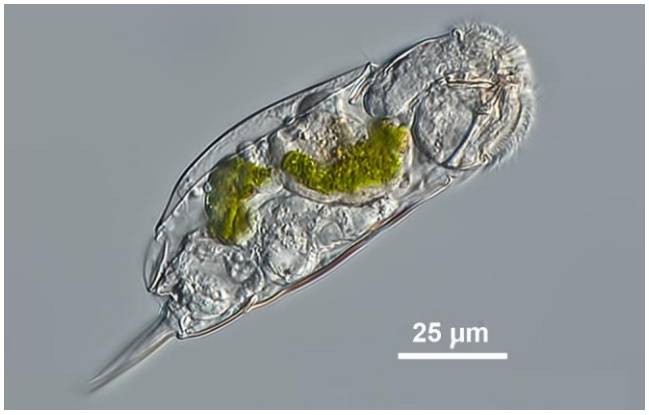

Figure 18. ***Cephalodella rotunda***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 19. ***Cephalodella ventripes***, a species of plankton and submerged mosses. Photo by Michael Plewka <www.plingfactory.de>.

Figure 20. ***Cephalodella hoodii***, a species that occurs exclusively on submerged mosses on Svalbard. Photo by Michael Plewka <www.plingfactory.de>.

Figure 21. ***Cephalodella intuta***, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 22. ***Cephalodella intuta***, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 23. ***Cephalodella megalocephala***, a species that occurs exclusively on submerged mosses on Svalbard. Photo by Michael Plewka <www.plingfactory.de>.

Figure 24. ***Cephalodella sterea*** from a pond in Ontario, Canada. This species also occurs on **bog mosses**. Photo by Jersabek *et al.* 2003, with permission.

Cephalodella forficula (Figure 26-Figure 25) is a free-swimming, tube-dwelling species (Dodson 1984) known to live among bryophytes and in bog pools (Figure 2). It is a cosmopolitan littoral species that lives mostly in small bodies of water, occasionally as part of the plankton (de Manuel Barrabin 2000). It occurs in alkaline habitats but prefers slightly "acid" water in a *p*H range around 8.2 and a temperature near 19°C. Dodson (1984) describes its tubes made of mucus in detritus-rich environments. It closes the tubes at both ends and swims back and forth in its tube, living on bacteria shed from the inner walls. Dodson considers only small rotifers <1 mm can use this feeding strategy because of surface-to-volume considerations. In high food conditions, rotifers removed from the tube immediately build another, but under starvation or low oxygen conditions they leave the tube and swim about.

Figure 25. ***Cephalodella forficula***, a species known to live among bryophytes and in bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 26. ***Cephalodella forficula***, a species known to live among bryophytes and in bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 27. ***Cephalodella forficula*** swimming. Photo by Michael Plewka <www.plingfactory.de>, with permission.

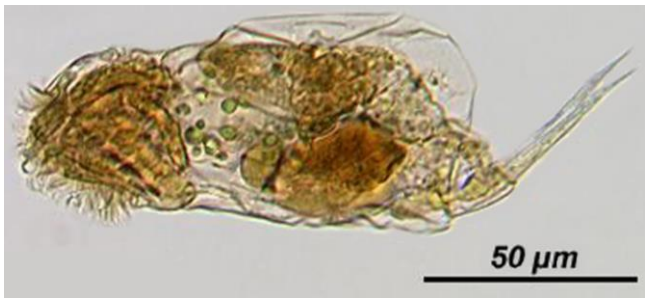

Figure 28. ***Cephalodella compressa*** from among ***Sphagnum.*** Photo by Jersabek *et al.* 2003, with permission.

Figure 29. ***Cephalodella derbyi*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 30. ***Cephalodella elegans*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

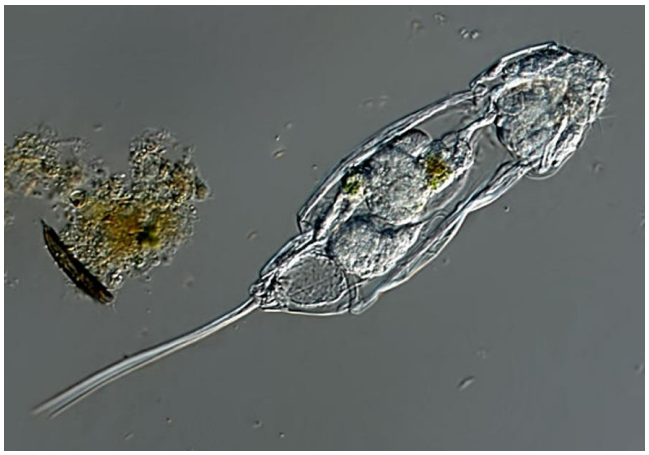

Figure 31. ***Cephalodella gigantea*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 32. ***Cephalodella licinia*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

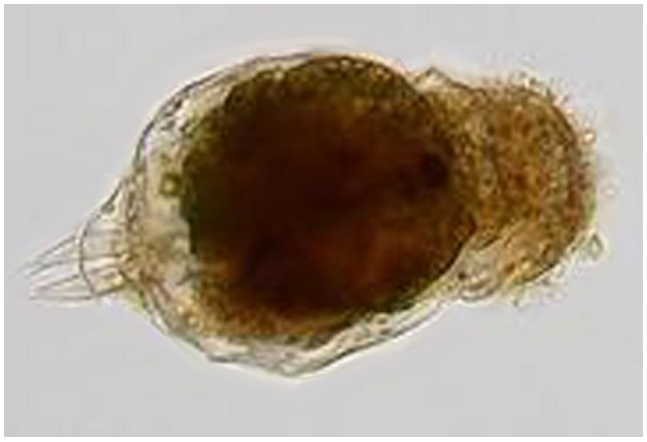

Figure 33. ***Cephalodella lipara*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

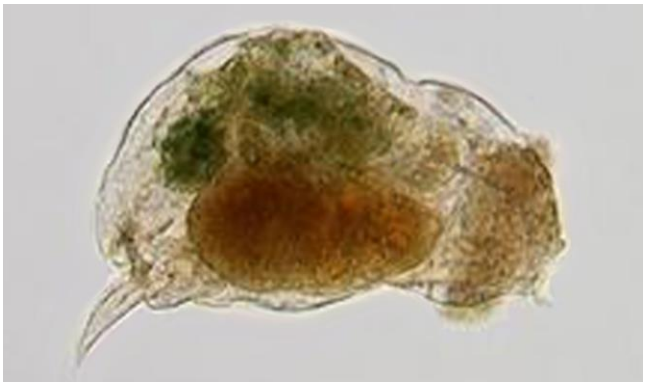

Figure 34. ***Cephalodella lipara*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 35. ***Cephalodella mira*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

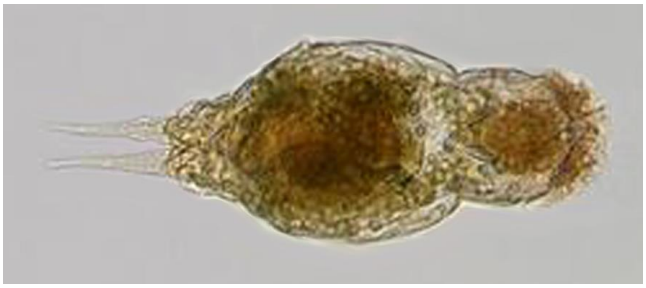

Figure 36. ***Cephalodella mira*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 37. ***Cephalodella mucronata*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 38. ***Cephalodella nana***, a species known from bryophytes, including ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 39. ***Cephalodella nana***, a species known from bryophytes, including ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

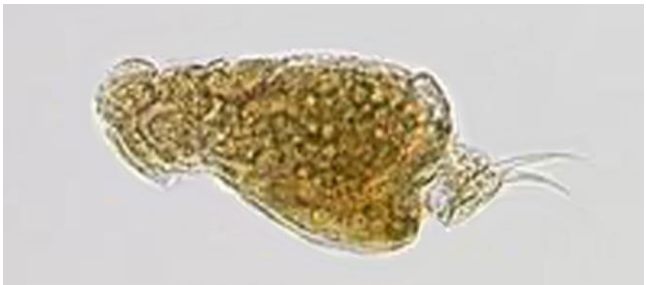

Figure 40. ***Cephalodella nelitis*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

A number of ***Cephalodella*** species live in bogs, but their specific affiliation with ***Sphagnum*** (Figure 41) is not specified. These include ***Cephalodella eva*** (Figure 42-Figure 43; also with stream mosses; Horkan 1981; Jersabek *et al*. 2003), ***C. exigua*** (Figure 44) in bogs (Jersabek *et al.* 2003), ***C. hoodii*** (Figure 20; Horkan 1981), ***C. lepida*** (Figure 45; Jersabek *et al.* 2003), ***C. physalis*** (Figure 46-Figure 48; Hingley 1993; Jersabek *et al.* 2003), ***C. rostrum*** (Hingley 1993), ***C. sterea*** (Figure 24; Horkan 1981), ***C. tachyphora*** (Figure 49-Figure 50; Jersabek *et al.* 2003), and ***C. tantilla*** (Figure 51; Hingley 1993).

Figure 41. ***Sphagnum capillifolium***, member of a genus that is home for many species of rotifers. Photo by J. C. Schou, with permission.

Figure 42. ***Cephalodella eva*** from a stream in Pennsylvania, USA. This species has been collected on mosses. Photo by Jersabek *et al.* 2003, with permission.

Figure 43. ***Cephalodella eva*** from the Pocono Mountains, in Pennsylvania, USA. This species is known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 44. Side view of ***Cephalodella exigua*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 45. ***Cephalodella lepida*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

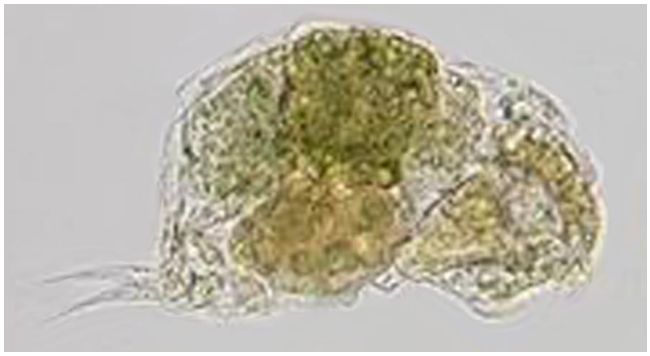

Figure 46. ***Cephalodella physalis***, a species known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 47. ***Cephalodella physalis***, a species known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 48. ***Cephalodella physalis***, a species known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 49. ***Cephalodella tachyphora*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 50. ***Cephalodella tachyphora*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 51. ***Cephalodella tantilla*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Cephalodella subsecunda (Figure 52) is known from ***Sphagnum subsecundum*** (Figure 53) (Jersabek *et al.* 2003). Some ***Cephalodella*** are known from submersed ***Sphagnum*** (Figure 41), including ***C. gracilis*** [Figure 54-Figure 55; Bielańska-Grajner *et al*. 2011; Plewka 2016; in streams Madaliński 1961), and ***C. inquilina*** (Figure 56; Jersabek *et al*. 2003). ***Cephalodella ventripes*** (Figure 19) occurs not only on ***Sphagnum*** (Hingley 1993), but as already noted, it also occurs on submerged moss and among the plankton (De Smet 1993; Plewka 2016). On Svalbard, ***Cephalodella ventripes*** var. ***angustior*** occurs mostly between submerged mosses (De Smet 1988).

Figure 52. ***Cephalodella subsecunda*** from among emergent ***Sphagnum subsecundum*** (Myers 1942). Photo by Jersabek *et al.* 2003, with permission.

Figure 53. ***Sphagnum subsecundum***, home of ***Cephalodella subsecunda*** and other rotifers. Photo by Michael Lüth, with permission.

Figure 54. ***Cephalodella gracilis***, a species from submersed ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 55. ***Cephalodella gracilis***, a species known from bryophytes. Photo by Jersabek *et al*. 2003, with permission.

Figure 56. ***Cephalodella inquilina*** from among submerged ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Other members of ***Cephalodella*** occur on submerged mosses (***Cephalodella cyclops***; Figure 57; Plewka 2016), including ***Fontinalis*** (Figure 58) (***C. dorseyi***; Figure 59; Jersabek *et al*. 2003). ***Cephalodella megalotrocha*** is also a bryophyte dweller (Horkan 1981).

Figure 57. ***Cephalodella cyclops***, a species that occurs in ponds with submerged mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

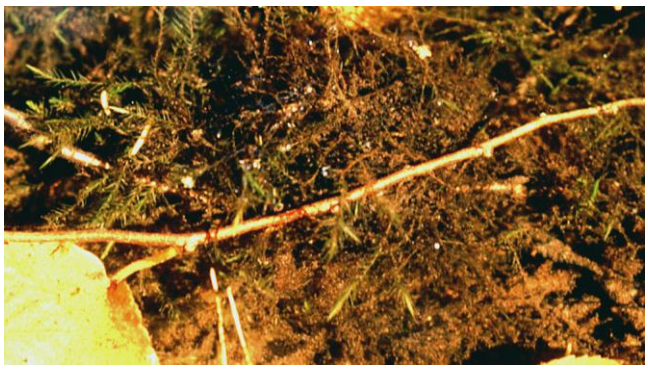

Figure 58. ***Fontinalis hypnoides*** with detritus. ***Fontinalis*** is a suitable home for ***Cephalodella dorseyi***. Photo by Janice Glime.

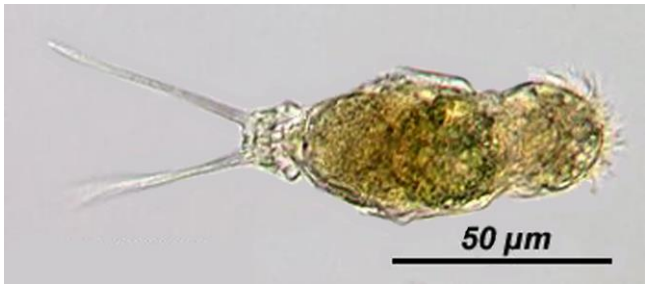

Figure 59. ***Cephalodella dorseyi*** from among ***Fontinalis***. Photo by Jersabek *et al.* 2003, with permission.

Drilophaga

Drilophaga judayi (Figure 60) is an ectoparasitic rotifer (but occasionally free-swimming). In the Poconos Mountains, Pennsylvania, USA, it was found only among

Sphagnum (Figure 41) (Myers 1942). In a genus of only three species, two live in association with ***Sphagnum***. The second of these is ***D. bucephalus*** (Figure 61), an ectoparasite on oligochaetes and a ***Sphagnum*** dweller (Plewka 2016).

Figure 60. ***Drilophaga judayi***, a parasitic rotifer that occurs only among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 61. ***Drilophaga bucephalus*** from ***Sphagnum.*** Photo by Michael Plewka (www.plingfactory.de), with permission.

Enteroplea

Enteroplea lacustris (Figure 62-Figure 63) occurs among ***Sphagnum*** (Figure 41) and in bog pools (Figure 2). Myers (1942) received a collection of a clump of wet ***Sphagnum*** from the Poconos Mountains, Pennsylvania, USA, and kept it in an aquarium for several months. Then a large number of ***E. lacustris*** appeared. There has been no report of it in the Poconos Mountains since.

Figure 62. ***Enteroplea lacustris***, a species that lives among ***Sphagnum*** and in bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 63. ***Enteroplea lacustris*** from among ***Sphagnum*** and in bog pools. Photo by Jersabek *et al.* 2003, with permission.

Eosphora

Eosphora is a genus with only seven known species. Of these, two seem to find bryophytes suitable for habitation. ***Eosphora ehrenbergi*** (Figure 64) occurs in bog pools (Horkan 1981; Jersabek *et al*. 2003). ***Eosphora najas*** (Figure 65) is a littoral-planktonic species that eats detritus (Plewka 2016), but it is known to occur among bryophytes in streams (Madaliński 1961) and ponds (De Smet 1993).

Figure 64. ***Eosphora ehrenbergi*** male from Utah, USA, a species known from bog pools. Photo by Jersabek *et al.* 2003, with permission.

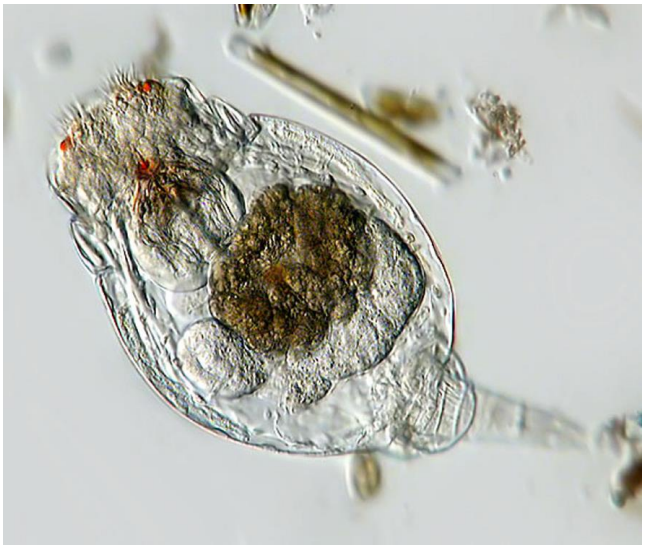

Figure 65. ***Eosphora najas***, showing eyespots, a planktonic species that eats detritus. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Eothinia

Eothinia has only six species. Only one of these, ***Eothinia elongata*** (Figure 66), associates with bryophytes by living in bogs (Horkan 1981).

Figure 66. ***Eothinia elongata*** from Three Lakes, Wisconsin, USA, a species known from bogs. Photo by Jersabek *et al.* 2003, with permission.

Monommata

The bryophyte dwellers in ***Monommata*** are all associated with ***Sphagnum*** (Figure 41). Hingley (1993) reported ***Monommata actices*** (Figure 67), ***M. aeschyna***, ***M. astia*** (Figure 68), ***M. longiseta*** (Figure 69-Figure 70), ***M. maculata*** (Figure 71), and ***M. phoxa*** as ***Sphagnum*** associates. To these, Plewka (2016) added ***M. dentata*** (Figure 72) and Jersabek *et al*. (2003) added ***M. hyalina*** (Figure 73). ***Monommata aequalis*** (Figure 74; Horkan 1981) and ***M. grandis*** (Figure 75; Plewka 2016) occur in bog pools and ***Sphagnum*** ponds (Figure 2), respectively. On Svalbard, De Smet (1993) found a species of ***Monommata*** exclusively on submerged mosses.

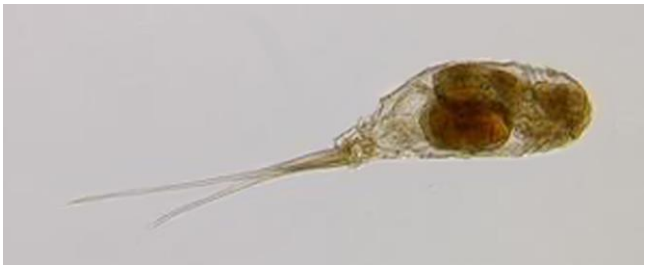

Figure 67. ***Monommata actices***, a species that is known from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

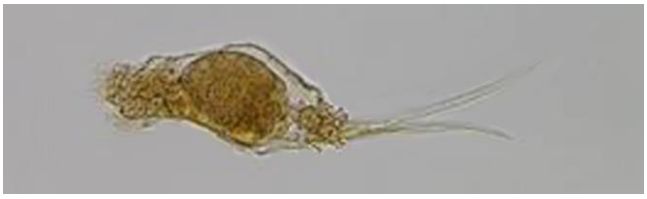

Figure 68. ***Monommata astia***, a species known to inhabit bryophytes, including ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 69. ***Monommata longiseta***, a planktonic species that also inhabits bryophytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 70. ***Monommata longiseta***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

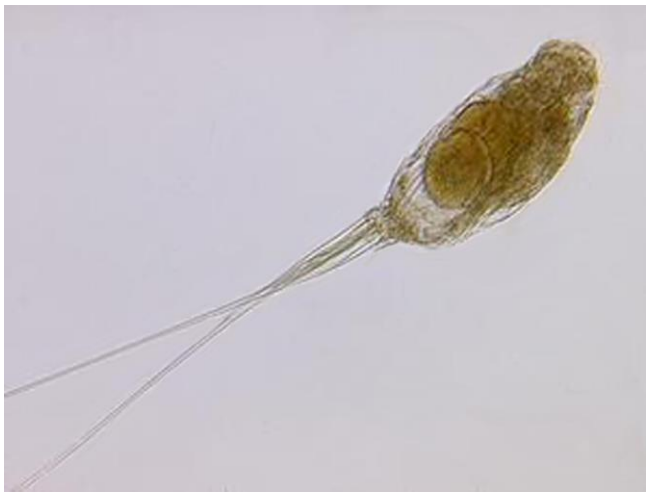

Figure 71. ***Monommata maculata***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 72. ***Monommata dentata***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 73. ***Monommata hyalina*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

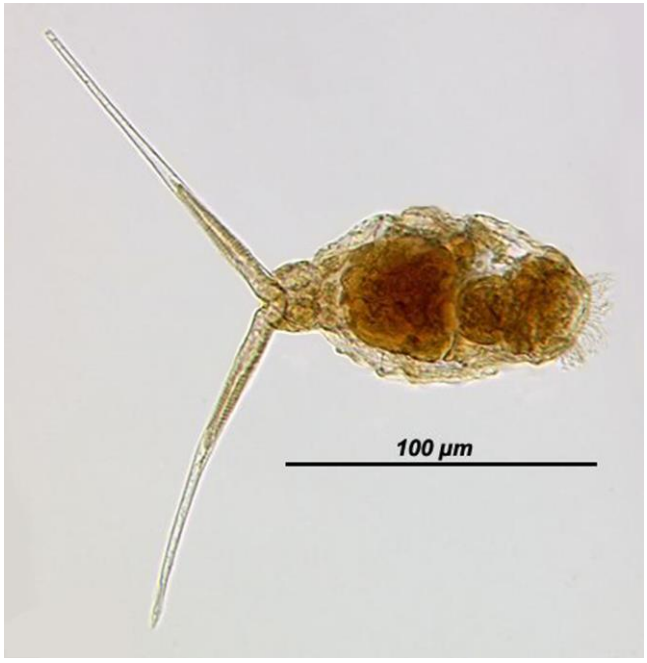

Figure 74. ***Monommata aequalis***, a bog-pool dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 75. ***Monommata grandis***, an inhabitant of ***Sphagnum*** ponds. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Notommata

This genus likewise contributes to the rotifer fauna of ***Sphagnum*** (Figure 41). Among these ***Sphagnum*** associates one can find ***Notommata allantois*** (Figure 76; Hingley 1993; Plewka 2016), ***N. cerberus*** (Figure 77-Figure 78); Horkan 1981; Hingley 1993; Jersabek *et al.* 2003; Plewka 2016), ***N. cherada*** (Figure 79; Jersabek *et al.* 2003), ***N. contorta*** (Figure 80; Hingley 1993; Jersabek *et al.* 2003), ***N. copeus*** (Figure 81-Figure 83; Horkan 1981; Hingley 1993; Plewka 2016), ***N. cyrtopus*** (Figure 87; bog pools and other bryophytes; Horkan 1981), ***N. doneta*** (Myers 1942), ***N. falcinella*** [Figure 88; on ***Sphagnum subsecundum*** (Figure 53; Harrington & Myers 1922; Hingley 1993), ***N. fasciola*** (Figure 89; Jersabek *et al.* 2003), ***N. groenlandica*** (Figure 90-Figure 91; Hingley 1993; Plewka 2016), ***N. pachyura*** (Figure 92-Figure 94; Horkan 1981; Hingley 1993), ***N. peridia*** (Figure 95; Myers 1942), ***N. pygmaea*** (Figure 96; Myers 1942), ***N. saccigera*** (Figure 97-Figure 98; Harrington & Myers 1922; Myers 1942; Hingley 1993), and ***N. tripus*** (Figure 99-Figure 100; bog pools, others; Horkan 1981; Hingley 1993). Horkan (1981) reported ***Notommata brachyota*** from bryophytes.

Figure 76. ***Notommata allantois*** with green gut, a species that occurs in ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Notommata cerberus subsp. ***parvida***; Figure 77-Figure 78) is a cosmopolitan species known to inhabit bryophytes

(de Manuel Barrabin 2000) and to live in bog pools (Horkan 1981). It is an omnivore that consumes other rotifers, desmids, diatoms, and flagellates (de Manuel Barrabin 2000). Its known *p*H is around 8.2 and temperature around 18.8°C.

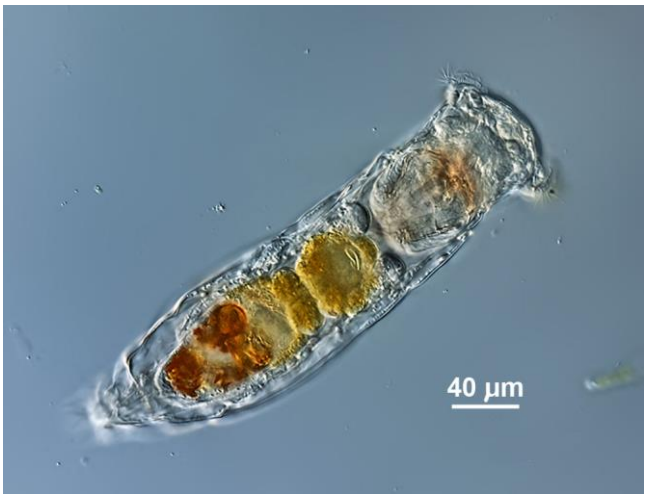

Figure 77. **Notommata cerberus**, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 78. ***Notommata cerberus*** subsp. ***parvida***, a cosmopolitan species known to inhabit bryophytes and to live in bog pools. Photo by Jersabek *et al.* 2003, with permission.

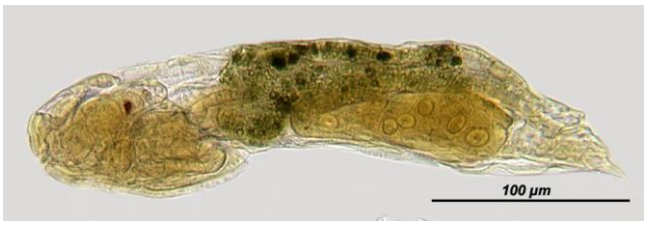

Figure 79. ***Notommata cherada***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

Figure 80. ***Notommata contorta***, known from a ***Sphagnum*** pool. Photo by Jersabek *et al.* 2003, with permission.

Notommata copeus (Figure 81-Figure 83) is a cosmopolitan, littoral species (de Manuel Barrabin 2000) known to inhabit bryophytes. It also occasionally occurs in the plankton (de Manuel Barrabin 2000) and in bog pools (Horkan 1981). It is known from a *p*H around 7 and temperature around 6°C (de Manuel Barrabin 2000). Its food is mostly zygnematalean algae – ***Mougeotia*** (Figure 84), ***Spirogyra*** (Figure 85), and ***Zygnema*** (Figure 86), that occur in these pools.

Figure 81. ***Notommata copeus*** with mucilage & bacteria, giving it a fuzzy look. This is a species from ***Sphagnum***. Note the desmid ***Closterium*** in the upper left, a potential food item. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 82. ***Notommata copeus***, a bryophyte dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 83. ***Notommata copeus***, a species known to inhabit bryophytes and bog pools. Photo by Jersabek *et al.* 2003, with permission.

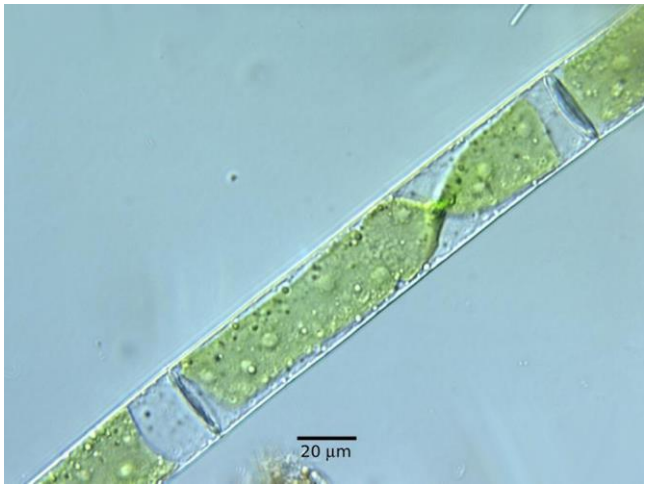

Figure 84. ***Mougeotia***, food for ***Notommata copeus***. Note the twisted chloroplast in the ***Mougeotia***. Photo by Jason Oyadomari, with permission.

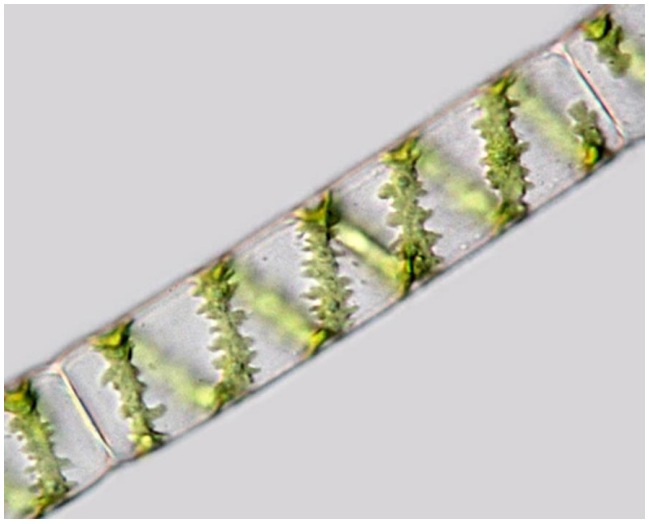

Figure 85. ***Spirogyra***, food for ***Notommata copeus***. Photo from Landcare Research, Manaaki Whenua, through Creative Commons.

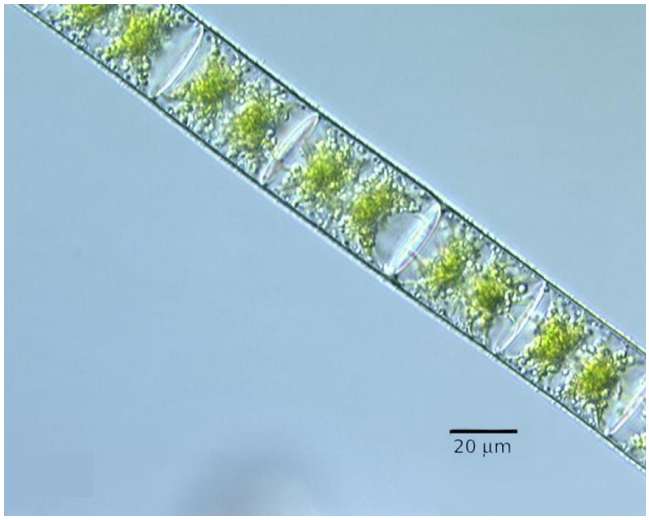

Figure 86. ***Zygnema***, food for ***Notommata copeus***. Photo by Jason Oyadomari, with permission.

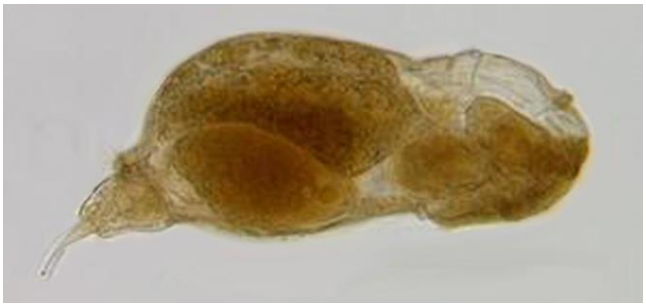

Figure 87. ***Notommata cyrtopus*** from New Jersey, USA. This species has been collected from bryophytes and is known from bog pools. Photos by Jersabek *et al.* 2003, with permission.

Figure 88. ***Notommata falcinella***, a species known from bryophytes, including ***Sphagnum subsecundum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 89. ***Notommata fasciola*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 90. ***Notommata groenlandica*** with the desmid ***Netrium***, a food item from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 91. ***Notommata groenlandica*** from a ***Sphagnum*** bog. Photo by Michael Plewka <www.plingfactory.de>, with permission.

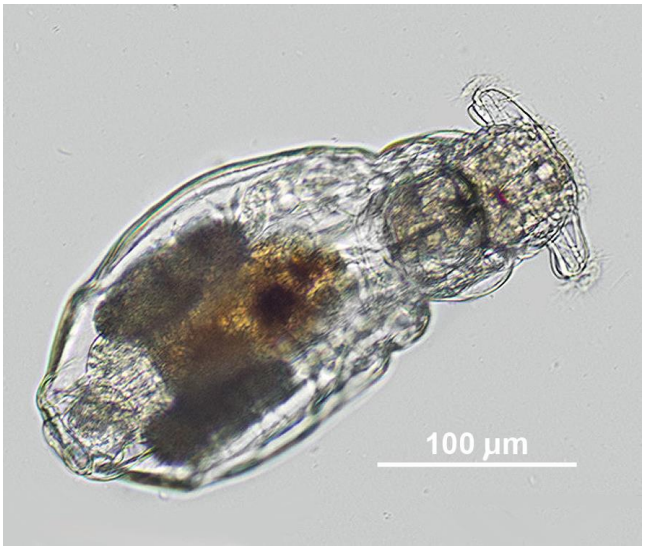

Figure 92. ***Notommata pachyura*** from detritus that it can find among ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 93. ***Notommata pachyura***, a species known to inhabit bryophytes and to occur in bogs. It feeds on non-colonial desmids (GLERL 2009). Photo by Jersabek *et al.* 2003, with permission.

Figure 94. ***Notommata pachyura***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 95. ***Notommata peridia***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 96. ***Notommata pygmaea***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

Figure 97. ***Notommata saccigera***, a species known to inhabit bryophytes, including ***Sphagnum*** (Myers 1942). Photo by Jersabek *et al.* 2003, with permission.

Figure 98. ***Notommata saccigera***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

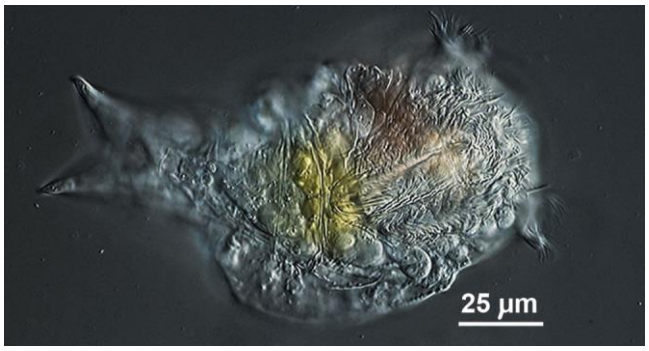

Figure 99. ***Notommata tripus*** from *Myriophyllum*. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 100. ***Notommata tripus***, a species known to inhabit bryophytes in more than one location and also occurs in bog pools. Photo by Jersabek *et al.* 2003, with permission.

On Svalbard ***Notommata glyphura*** (Figure 101) occurs on submerged mosses, but also occurs among the plankton (De Smet 1993).

Figure 101. ***Notommata glyphura***, a species of plankton and submerged mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Pleurata

Of the seven species in ***Pleurata***, three are associated with bryophytes. All of these are associated with ***Sphagnum*** (Figure 41) and include ***P. chalicodes*** (Figure 102), ***P. tithasa*** (Figure 103), and ***P. vernalis*** (Figure 104) (Jersabek *et al*. 2003). In Alaska, ***P. chalicodes*** occurs with submerged mosses in trenches of polygons (Segers *et al*. 1996).

Figure 102. ***Pleurata chalicodes*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

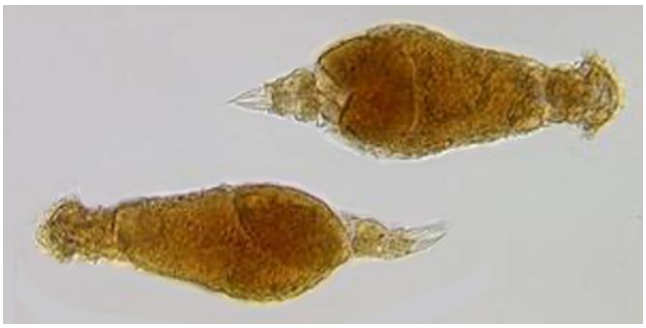

Figure 103. ***Pleurata tithasa*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 104. ***Pleurata vernalis*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Pleurotrocha

Although ***Pleurotrocha*** has eight species, only two of these are associated with bryophytes. ***Pleurotrocha petromyzon*** (Figure 105) occurs with the aquatic moss ***Fontinalis*** (Figure 58) (Plewka 2016). The only

Sphagnum (Figure 41) dweller seems to be ***P. robusta*** (Figure 106-Figure 107; Jersabek *et al*. 2003).

Figure 105. ***Pleurotrocha petromyzon***, a species that occurs on the aquatic moss ***Fontinalis***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 106. ***Pleurotrocha robusta*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 107. ***Pleurotrocha robusta*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Pseudoploesoma

Pseudoploesoma is a small genus with only one species, ***P. formosum*** (Figure 108-Figure 110). It occurs among ***Sphagnum*** in bog ponds (Figure 2) (Myers 1942; Jersabek *et al.* 2003).

Figure 108. ***Pseudoploesoma formosum*** from among ***Sphagnum*** in a bog pond. Photo by Jersabek *et al.* 2003, with permission.

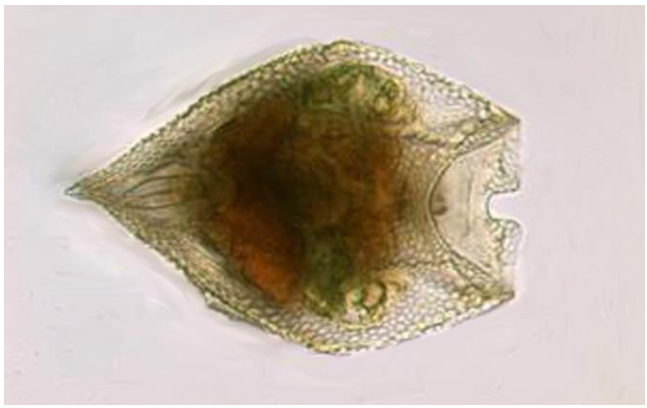

Figure 109. ***Pseudoploesoma formosum*** from among ***Sphagnum*** in a bog pond. Photo by Jersabek *et al.* 2003, with permission.

Figure 110. ***Pseudoploesoma formosum*** from among ***Sphagnum*** in a bog pond. Photo by Jersabek *et al.* 2003, with permission.

Resticula

Three members of ***Resticula*** are associated with bryophytes and other submerged plants. ***Resticula melandocus*** (Figure 111-Figure 113) occurs in ***Sphagnum***

bogs (Figure 2) (Hingley 1993), but also is associated with the alga ***Nitella*** (Jersabek *et al*. 2003; Plewka 2016). ***Resticula nyssa*** (Figure 114-Figure 115) is a littoral species that lives on plant surfaces, including bryophytes (de Manuel Barrabin 2000), including ***Sphagnum*** (Figure 41) (Hingley 1993). On Svalbard, it occurs exclusively on submerged mosses (De Smet 1993). It prefers slightly acidic water, although the measured *p*H was 8.2. Its temperature preference is around 18.8°C (de Manuel Barrabin 2000). ***Resticula plicata*** (Figure 116) lives in ***Sphagnum*** ponds (Figure 2) (Plewka 2016).

Figure 111. ***Resticula melandocus*** from the alga ***Nitella***, but this rotifer also occurs in ***Sphagnum*** bogs. Photo by Michael Plewka <www.plingfactory.de>, with permission.

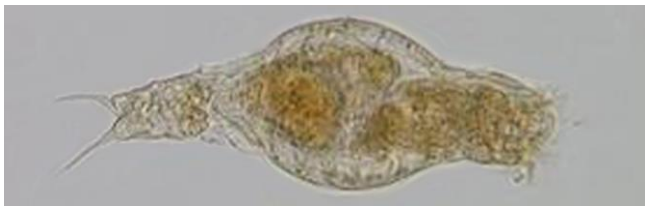

Figure 112. ***Resticula melandocus***, known from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

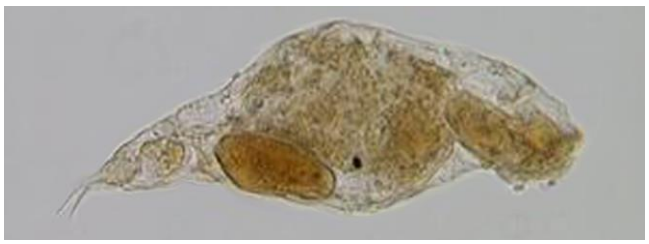

Figure 113. ***Resticula melandocus***, side view, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 114. ***Resticula nyssa***, a littoral species that lives on plant surfaces, including bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 115. ***Resticula nyssa***, known from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 116. ***Resticula plicata***, inhabitant of ***Sphagnum*** ponds. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Taphrocampa

Taphrocampa is a genus with only four species. Of these, two are known from ***Sphagnum*** (Figure 41): ***T. annulosa*** (Figure 117-Figure 118) and ***T. clavigera*** (Figure 119) (Hingley 1993; Jersabek *et al*. 2003).

Figure 117. ***Taphrocampa annulosa***, known from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 118. ***Taphrocampa annulosa***, lateral view, a species known from **bryophytes**. Photo by Jersabek *et al.* 2003, with permission.

Figure 119. ***Taphrocampa clavigera***, a species known from ***Sphagnum*** in more than one location. Photo by Jersabek *et al.* 2003, with permission.

Proalidae

This family lacks a hardened lorica and instead takes on a wormlike appearance. It lives in freshwater and occurs on plants, on the bottom, and among sand grains of the littoral zone as well as in damp terrestrial habitats (EOL 2012). Some are even **epizoic** on other invertebrates and some live parasitically in algae or on invertebrates.

Bryceella

This genus is **oviparous** (producing eggs that are laid and hatch later). All known species of the genus ***Bryceella*** live among ***Sphagnum*** (Figure 41). ***Bryceella tenella*** (Figure 120-Figure 121) seems to be known only from ***Sphagnum*** (Myers 1942; Hingley 1993; Jersabek *et al.* 2003; Bielańska-Grajner, *et al*. 2011). On the other hand, ***Bryceella perpusilla*** (Figure 122; Wilts *et al*. 2010) and ***B. stylata*** (Figure 123-Figure 124; Hingley 1993; Plewka 2016) both occur on ground-dwelling and epiphytic mosses as well as aquatic habitats, illustrating an ability to tolerate a wide moisture range. Segers *et al*. (1996) reports ***B. stylata*** from submerged mosses in trenches of Alaskan polygons; on Svalbard, it occurs exclusively on submerged mosses (De Smet 1993). ***Bryceella pusilla*** (Figure 125), previously known as ***Wierzejskiella vagneri***, is known from a ***Sphagnum*** bog (Plewka 2016).

Bryceella perpusilla (Figure 122) was described as a new species in 2010 from northwest Germany (Wilts *et al.* 2010). Its describers considered it to be one of the smallest rotifers (50-80 µm) and even one of the smallest metazoans known. Even its name, *perpusilla*, means very small. This small size, combined with its narrow body and dorsiventral compression, permits it to live among terrestrial mosses. The individuals glide among the mosses in a "nimble and jerky manner very fast on the moss stalks" and eat the detritus associated with the mosses. Even in the lab, they never leave the moss to swim. But they are not restricted to these terrestrial mosses. They also occur among ***Sphagnum*** (Figure 41) in Lake Gorbacz in Poland. They seem to prefer cold periods at about 10°C.

Figure 120. ***Bryceella tenella***, a ***Sphagnum*** associate. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 121. ***Bryceella tenella***, a ***Sphagnum*** associate. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 122. ***Bryceella perpusilla***, a species that lives among epiphytic mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 123. ***Bryceella stylata*** (stomach stained neutral red), a species that lives in ***Sphagnum*** bogs and on epiphytic mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 124. ***Bryceella stylata***, a species known from **bryophytes**. Photo by Jersabek *et al*. 2003, with permission.

Figure 125. ***Bryceella pusilla*** from a ***Sphagnum*** bog. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Proales

Proales is a somewhat larger genus. A number of its species occur among ***Sphagnum*** (Figure 41). These include ***Proales bemata*** (Figure 126; Myers 1942), ***P. cognita*** [Figure 127-Figure 128; on ***Sphagnum cuspidatum*** (Figure 129); Jersabek *et al*. 2003], ***P. decipiens*** (Figure 130; Horkan 1981; Hingley 1993; Harrington & Myers 1922), ***P. doliaris*** (Figure 131; ***Sphagnum*** bogs; Hingley 1993; Jersabek *et al*. 2003), ***P. fallaciosa*** (Figure 132-Figure 134; Hingley 1993), ***P. latrunculus*** (current name not located; Hingley 1993), ***P. micropus*** (Hingley 1993), ***P. minima*** [Figure 135-Figure 136; on ***Sphagnum subsecundum*** (Figure 53); Hingley 1993; Plewka 2016], ***P. ornata*** (Myers 1942), ***P. palimmeka*** (Figure 137; on submerged ***Sphagnum***; Jersabek *et al*. 2003), and ***P. sordida*** (Horkan 1981).

Figure 126. ***Proales bemata***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

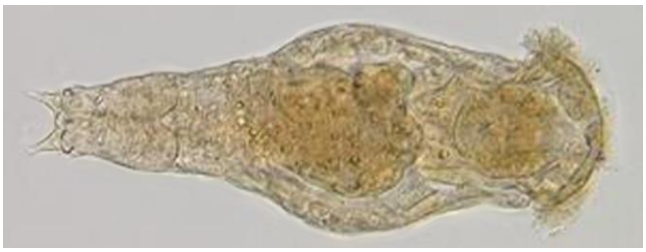

Figure 127. ***Proales cognita*** from among ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

Figure 128. ***Proales cognita*** from among ***Sphagnum cuspidatum***. Photo by Jersabek *et al*. 2003, with permission.

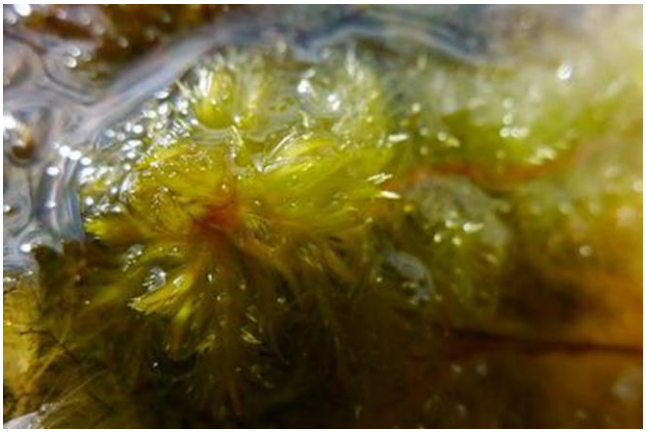

Figure 129. ***Sphagnum cuspidatum***, home of ***Cephalodella subsecunda***. Photo through Creative Commons.

Figure 130. ***Proales decipiens***, a species known to occur in bogs and to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 131. ***Proales doliaris***, a species known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

Proales fallaciosa (Figure 132-Figure 134) is a **cosmopolitan** (in most of world), benthic-periphytic (and planktonic) species of small water bodies (de Manuel Barrabin 2000). It is known to inhabit bryophytes, including ***Sphagnum*** (Figure 41). On Svalbard it inhabits submerged mosses (De Smet 1993). It lives in alkaline to slightly acid water with a *p*H around 8.39 and temperature around 18.8°C (de Manuel Barrabin 2000) where it feeds on bacteria, detritus, algae, and microcrustaceans (Koste & Shiel 1990).

Figure 132. ***Proales fallaciosa***, a cosmopolitan species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 133. ***Proales fallaciosa***, a species known to inhabit bryophytes. Photo by Jersabek *et al*. 2003, with permission.

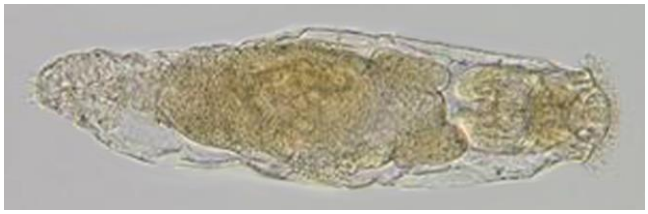

Figure 134. ***Proales fallaciosa***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 135. ***Proales minima*** occurs on submersed moss, including ***Sphagnum subsecundum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 136. ***Proales minima***, a species collected from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

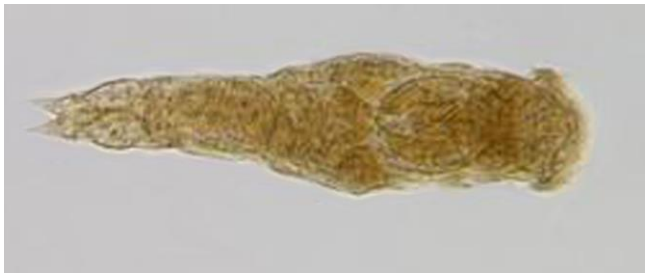

Figure 137. ***Proales palimmeka*** from among ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

In addition to these ***Sphagnum*** dwellers, ***Proales ardechensis*** (Figure 138) lives in a seepage area where wet mosses attach to a vertical rock face that dries up in summer (De Smet & Verolet 2009). The *p*H there is 7.35 and water temperature of 7°C. ***Proales globulifera*** (Figure 139) is part of the periphyton on ***Fontinalis*** (Figure 58) (Plewka 2016), and ***P. theodora*** (Figure 140-Figure 141) associates with bryophytes in streams and rivulets (Madaliński 1961).

Figure 138. ***Proales ardechensis***, a species that lives among wet mosses on rocks in seepage areas. Photo by Michael Verolet, with permission.

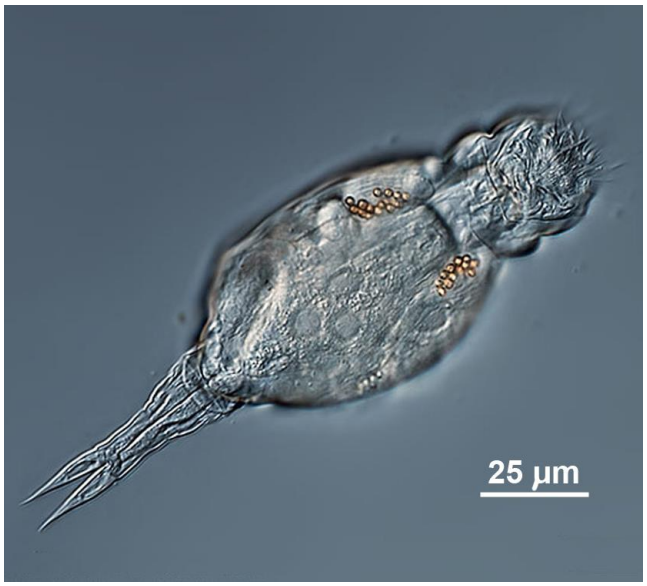

Figure 139. ***Proales globulifera***, a species periphytic on ***Fontinalis***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 140. ***Proales theodora***, a plankton species that also associates with mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 141. ***Proales theodora***, a plankton species that also occurs among mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Proales laticauda (Figure 142) is the only terrestrial member of the genus that I have found. De Smet and Verolet (2009) first described it from moss on sandstone in a firewood area. Plewka (2016) reported it from mosses where it accompanied mucilaginous green algae.

Figure 142. ***Proales laticauda***, a species that occurs on moss with mucilaginous green algae. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Proalinopsis

Proalinopsis is a genus of only seven species. Among these, three are associated with ***Sphagnum*** (Figure 41) or live in bogs. These are ***Proalinopsis caudatus*** (Figure 143-Figure 144) in bog pools (Horkan 1981; Hingley 1993; Plewka 2016), ***P. phacus*** on ***Sphagnum*** (Myers 1942), and ***P. squamipes*** (Figure 145) from a ***Sphagnum*** ditch and bogs (Hingley 1993; Jersabek *et al.* 2003). ***Proalinopsis gracilis*** (Figure 146) is known from the floating thallose liverwort ***Riccia fluitans*** (Figure 147) (Jersabek *et al.* 2003).

Figure 143. ***Proalinopsis caudatus*** from a ***Sphagnum*** pond. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 144. ***Proalinopsis caudatus***, a species known to inhabit bryophytes and to occur in bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 145. ***Proalinopsis squamipes***, known from a ***Sphagnum*** ditch. Photo by Jersabek *et al.* 2003, with permission.

Figure 146. ***Proalinopsis gracilis*** from among the floating thallose liverwort ***Riccia fluitans***. Photo by Jersabek *et al.* 2003, with permission.

Figure 147. ***Riccia fluitans***, home for ***Proalinopsis gracilis.*** Photo by Christian Fischer, through Creative Commons.

Wulfertia

On Svalbard, ***Wulfertia ornata*** occurs exclusively among submerged mosses in a pool (De Smet 1993).

Scaridiidae

This is a segregate family from **Notommatidae** (Segers 1995). At least some of the species are cosmopolitan; some are pantropical. ***Scaridium*** is the only genus and has only seven species. ***Scaridium longicaudum*** (Figure 148-Figure 150) is associated with bryophytes. It is occasionally planktonic (Plewka 2016), but it can occur in bogs (Horkan 1981) and typically occurs between vegetation (De Smet, pers. comm. 14 November 2016). ***Scaridium montanum*** occurs in ***Sphagnum*** ponds.

Figure 148. ***Scaridium longicaudum*** lateral view, a periphytic species that can be found in bogs. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 149. ***Scaridium longicaudum*** from Pocono Lake, Pennsylvania, USA. This species is known from bogs. Photos by Jersabek *et al.* 2003, with permission.

Figure 150. ***Scaridium longicaudum***, a bog species. Photos by Jersabek *et al.* 2003, with permission.

Synchaetidae

To my mind, this family has some of the most unusual-looking rotifers. It has only four genera, three of which include bryophyte associates.

Polyarthra

Polyarthra (Figure 153, Figure 157-Figure 158) reminds me of a Native American headdress. Many of the species have long blade-like flexible appendages – my association with feathers and headdresses. The members of the genus are planktonic, but a few species have been found among bryophytes. They feed by a grabbing and sucking motion.

Gilbert and Schroder (2004) suggested that the **diapause** (resting) eggs (Figure 151) that develop into amictic females in species like ***Polyarthra vulgaris*** (Figure 151-Figure 152), occasionally a moss dweller, may be an adaptation for survival in an environment that is unstable. These amictic females have a higher lipid content, reduced digestive tract, and produce a single large egg within hours of hatching, whereas the normal generation time is six days. The diapause eggs are produced by sexual reproduction of a female and small male (from small eggs; Figure 152), thus producing a **diploid egg** (one having two sets of chromosomes). Like many algae and other plants, this behavior of sexual reproduction occurs when the environment becomes unfavorable. The diapause egg is able to remain viable without hatching for extended periods of time.

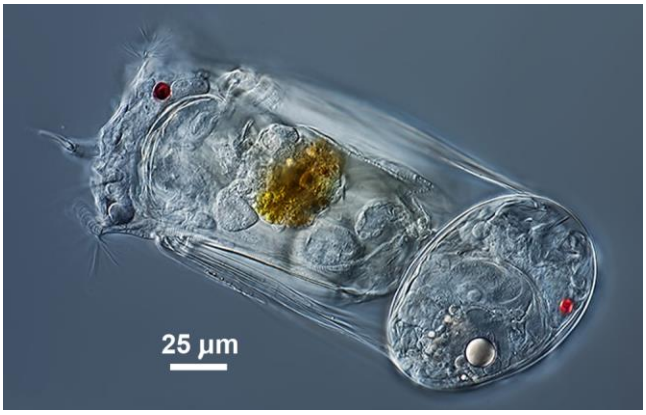

Figure 151. ***Polyarthra vulgaris*** with parthenogenetic diploid amictic egg. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 152. ***Polyarthra vulgaris*** with male eggs (smaller than female eggs). Photo by Michael Plewka (www.plingfactory.de), with permission.

Polyarthra euryptera (Figure 153) is a cosmopolitan planktonic species (de Manuel Barrabin 2000) that is known from bog pools (Horkan 1981). They occur in warm water, but are known from temperatures in the wide range of 5.9-24.9°C (de Manuel Barrabin 2000). They are seasonal, reaching a maximum population size in the summer. They generally do not occur in the hypolimnion, where they would be trapped in cold water. This species may be prey for other rotifers, including ***Asplanchna girodi*** (Figure 154) and ***Ploesoma hudsoni*** (Figure 155-Figure 156) (Guiset 1977). Their known *p*H range is 6.3-9.9.

Figure 153. ***Polyarthra euryptera***, a cosmopolitan planktonic species that is known from bog pools. Photo by Jersabek *et al.* 2003, with permission.

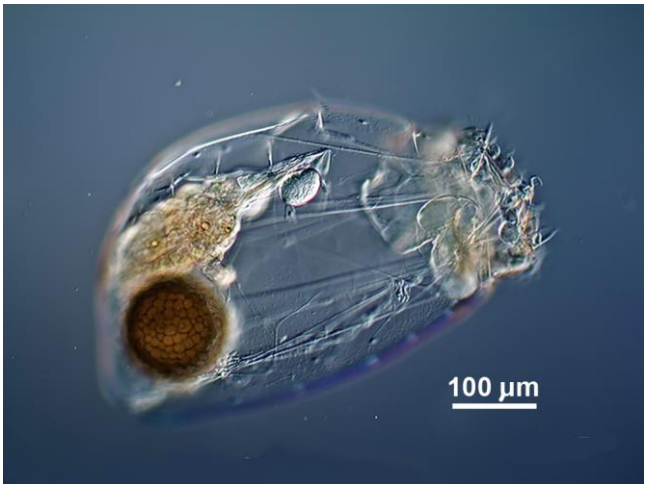

Figure 154. ***Asplanchna girodi*** (with resting egg), a species that preys upon ***Polyarthra euryptera***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

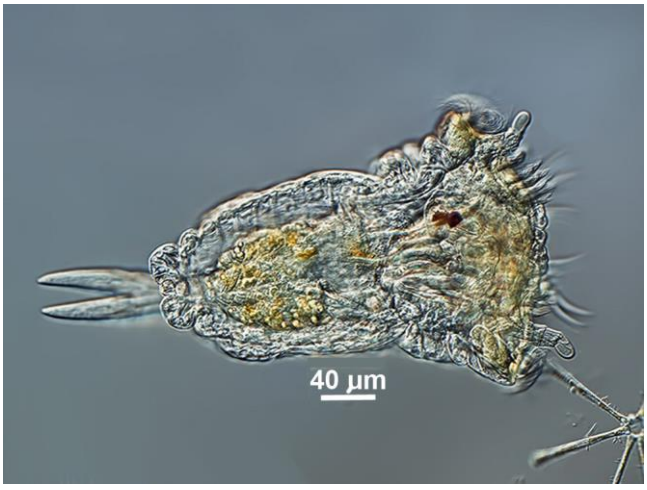

Figure 155. ***Ploesoma hudsoni*** dorsiventral view, a predator on ***Polyarthra euryptera***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 156. ***Ploesoma hudsoni*** (lateral view), a predator on ***Polyarthra euryptera***. Photo by Michael Plewka <www.plingfactory.de>, with pernission.

Polyarthra vulgaris (Figure 157-Figure 158) has likewise been found among mosses, including ***Sphagnum*** (Figure 41), in bogs (Hingley 1993), although it is a planktonic species (de Manuel Barrabin 2000). This species is cosmopolitan and present year-round. To accommodate its year-round activity, it tolerates temperatures 5.9-16-7°C. It prefers high levels of oxygen, a *p*H range of 6.6-6.9, and lives near the water surface, rarely occurring in the hypolimnion. It feeds on centric diatoms and algae in the **Cryptomonadaceae** (Pourriot 1977) and **Chrysophyceae** (Devetter 1998), as well as bacteria and one-celled **Chlorophyta** (Bogden & Gilbert 1987). Bogden and Gilbert (1987) describe the feeding as a suction that uses pharyngeal expansion. The fecundity is positively related to the amount of chlorophyll *a* present (Devetter & Sed'a 2003). They are especially important in the food web, along with other rotifers, when the hydrological conditions are unstable (Keckeis *et al*. 2003).

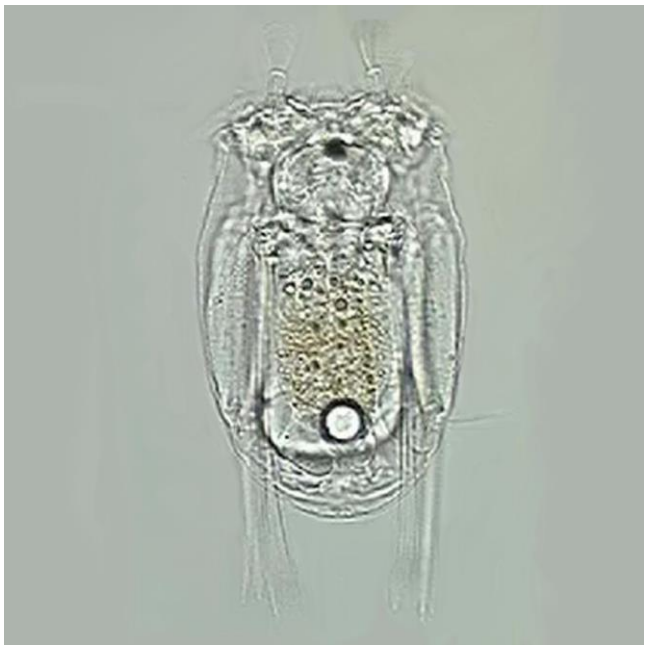

Figure 157. ***Polyarthra vulgaris*** has been found among mosses, although it is a planktonic species. Photo from Malcolm Storey, through Creative Commons.

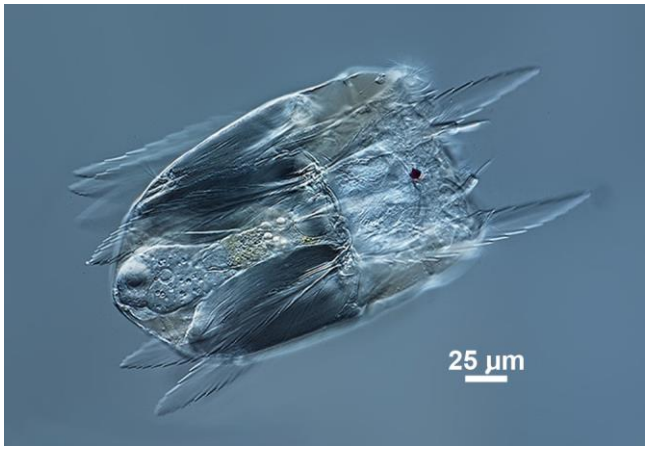

Figure 158. ***Polyarthra vulgaris***, a planktonic species that lives among ***Sphagnum*** in bogs. Photo by Michael Plewka

Synchaeta

The genus ***Synchaeta*** (Figure 159) is typically planktonic in both freshwater and marine environments, it also has members that live on bryophytes in freshwater (Hingley 1993). It also is one of the few rotifers to live in the marine environment (Brownell 1988; Wikipedia 2012), but not on bryophytes there (bryophytes do not occur in the marine environment). It prefers cold water and is absent in the warm water habitats of southeast Asia (Segers 2001).

Figure 159. ***Synchaeta***, a cold-water genus that occurs on bryophytes (Hingley 1993). Photo by Wim van Egmond, with permission.

Synchaeta pectinata (Figure 160-Figure 161) is a cosmopolitan planktonic species (de Manuel Barrabin 2000) that has been collected from bryophytes and can live in bog pools (Horkan 1981; Hingley 1993). Although it survives at temperatures of 5.9-25.5°C, it has its maximum populations at low temperatures (de Manuel Barrabin 2000). It lives in both small and large lakes at *p*H 6.3-9.3. The food is primarily algae of the **Cryptomonadaceae**, **Chrysophyceae**, and centric diatoms (Pourriot 1970). The species is often infected by the fungus *Plistophora* (*Bertramia*) *asperospora*. ***Synchaeta tremula*** (Figure 162) occurs in bogs (Horkan 1981).

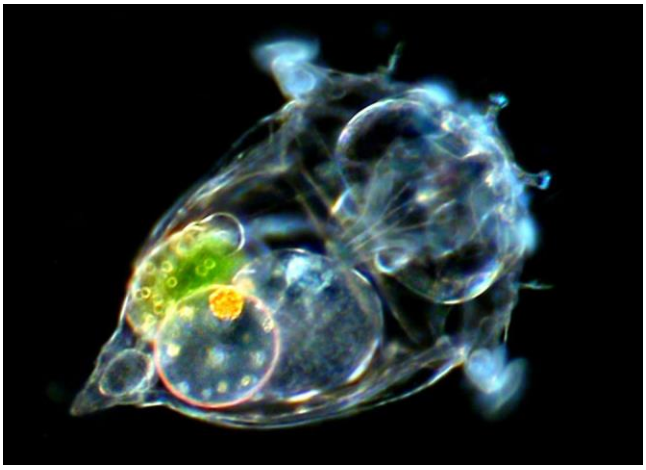

Figure 160. ***Synchaeta pectinata*** from plankton. Photo by Michael Plewka <www.plingfactory.de>), with permission.

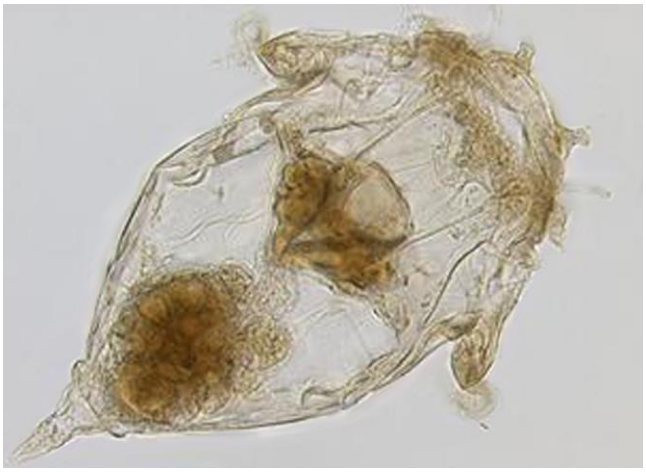

Figure 161. ***Synchaeta pectinata***, typically a cosmopolitan planktonic species, also lives among bryophytes and can live in bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 162. ***Synchaeta tremula*** from a lake in New Jersey, USA. This species also occurs in bogs. Photo by Jersabek *et al.* 2003, with permission.

Tetrasiphonidae

As nearly as I can determine, there is one genus and possibly two species in this family, although Segers (2007) only lists ***Tetrasiphon hydrocora*** (Figure 163-Figure 164); one species remains undescribed. This species is known from ***Sphagnum*** (Figure 41) and submersed mosses (Nogrady 1980; Hingley 1993; Plewka 2016).

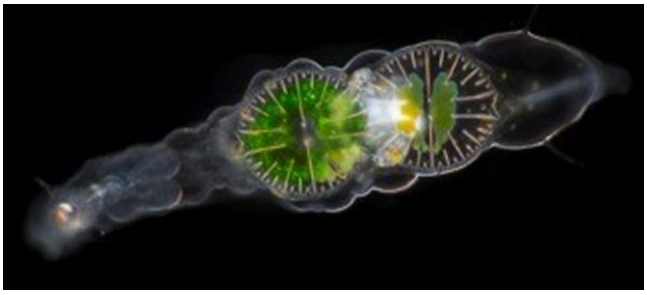

Figure 163. ***Tetrasiphon hydrocora***, a species known from ***Sphagnum***, with the desmid ***Micrasterias*** in its gut. Photo by Wim von Egmond, with permission.

Figure 164. ***Tetrasiphon hydrocora***, a species known from ***Sphagnum***. Note desmids in the gut. Photo by Jersabek *et al.* 2003, with permission.

Trichocercidae

The members of this family usually have a twisted body and strongly asymmetrical trophi. Some members are parasitic. Some live among bryophytes, including ***Sphagnum*** (Figure 41).

Elosa

Elosa has a symmetrical body, but the trophi are asymmetrical. ***Elosa worrallii*** (Figure 165) shares the genus with one other species that is sometimes considered to be conspecific with ***E. worrallii*** (Segers 2007). ***Elosa worrallii*** lives among bryophytes, including ***Sphagnum*** (Myers 1942; Hingley 1993).

Figure 165. ***Elosa worrallii*** with notch in lorica, a species known from bryophytes, including ***Sphagnum*** (Myers 1942). Photo by Michael Plewka <www.plingfactory.de>, with permission.

Trichocerca

By contrast to ***Elosa***, ***Trichocerca*** is a larger genus. ***Trichocerca bicristata*** (Figure 166-Figure 167) is planktonic, but lives in bog pools (Figure 2; Horkan 1981; Hingley 1993). ***Trichocerca brachyura*** (Figure 168) occurs in bogs in the Pocono Mountains, Pennsylvania, USA (Horkan 1981; Jersabek *et al.* 2003). ***Trichocerca cavia*** (Figure 169) is likewise a species known from ***Sphagnum*** bogs, living on submerged mosses (Hingley 1993; Plewka 2016). On Svalbard, ***T. cavia*** occurs among submerged mosses, but also occurs in the plankton (De Smet 1993). Among others known from ***Sphagnum*** bogs, Hingley (1993) included ***T. collaris*** (Figure 170), ***T. elongata*** (Figure 171), ***T. junctipes*** (***T. sejunctipes***?), ***T. longiseta*** (Figure 172-Figure 173), ***T. porcellus*** (Figure 174-Figure 175; see also Bielańska-Grajner *et al*. 2011) [also from ***Fontinalis*** (Jersabek *et al*. 2003)], ***T. rattus*** (Figure 178-Figure 179), (also Horkan 1981; Jersabek *et al*. 2003), and ***T. rosea*** (Figure 180-Figure 181; also Jersabek *et al*. 2003).

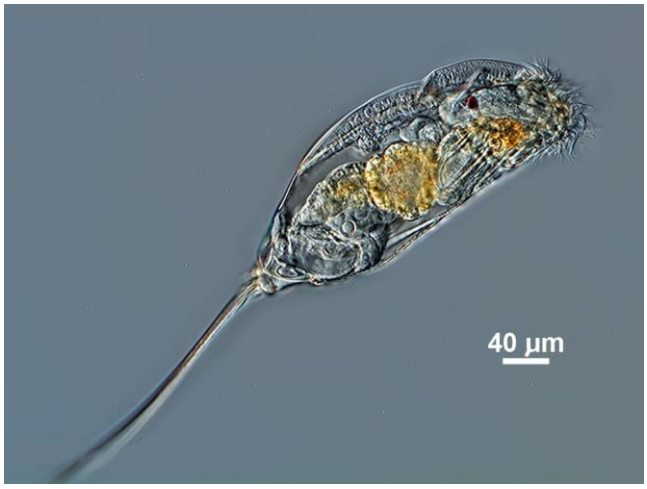

Figure 166. ***Trichocerca bicristata***, a planktonic species that lives in ***Sphagnum*** pools. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 167. ***Trichocerca bicristata***, a rotifer known from bog pools. Photo by Jersabek *et al.* 2003, with permission.

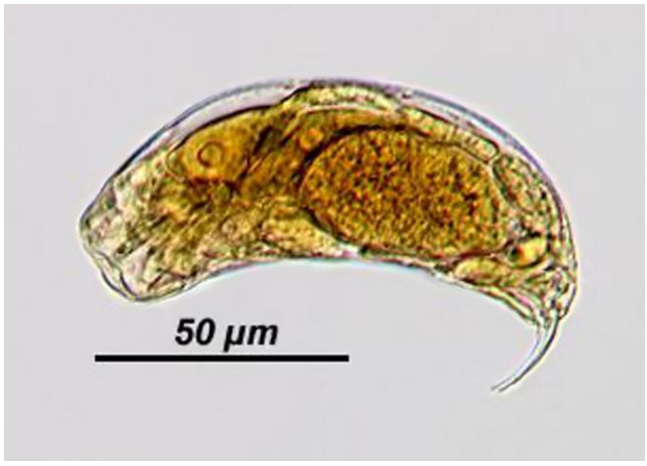

Figure 168. ***Trichocerca brachyura*** from the Pocono Mountains, Pennsylvania, USA. This species is known from bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 169. ***Trichocerca cavia***, a species that lives on submerged moss and in ***Sphagnum*** bogs. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 170. ***Trichocerca collaris***, known from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 171. ***Trichocerca elongata***, a species known from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 172. ***Trichocerca longiseta***, a species known from bogs. Photo by Yuuji Tsukii, with permission.

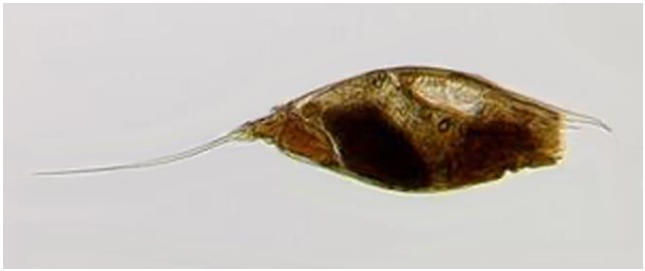

Figure 173. ***Trichocerca longiseta***, known from a bog. Photo by Jersabek *et al.* 2003, with permission.

Trichocerca major (Figure 175) and ***T. porcellus*** (Figure 174) are cosmopolitan species in small water bodies with limited nutrients (de Manuel Barrabin 2000). ***Trichocerca major*** is known from both a bog and ***Fontinalis*** (Jersabek *et al.* 2003). Both species typically occur between vegetation as periphyton (De Smet, pers. comm. 14 November 2016). ***Trichocerca porcellus*** is active in winter at temperatures around 9.5°C and occurs at a *p*H around 7.1. It lays eggs inside algal mats such as ***Aglaucoseria***, ***Fragilaria*** (Figure 176), and ***Dinobryon*** (Figure 177). It is known from bryophytes in multiple locations, including collections of the aquatic moss ***Fontinalis*** (Figure 58).

Figure 174. ***Trichocerca porcellus***, a cosmopolitan periphytic species known from the aquatic moss ***Fontinalis***. Photo by Jersabek *et al.* 2003, with permission.

Figure 175. ***Trichocerca major***, a species known from both a bog and ***Fontinalis***. Photo by Jersabek *et al.* 2003, with permission.

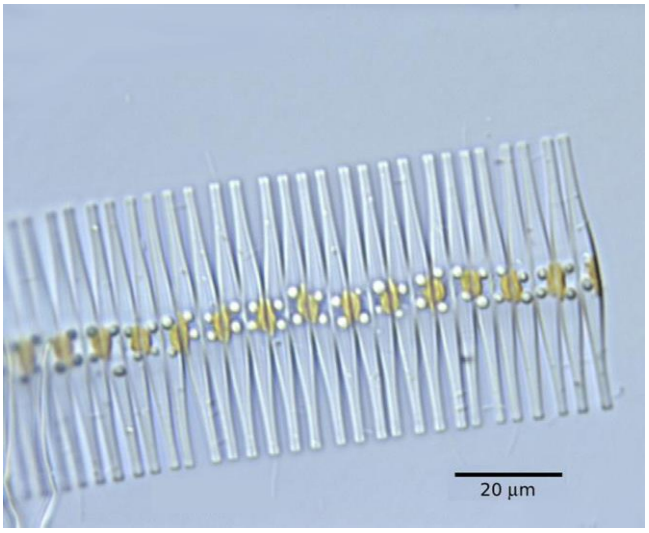

Figure 176. ***Fragilaria***, egg-laying site of ***Trichocerca porcellus***. Photo by Jason Oyadomari, with permission.

Figure 177. ***Dinobryon divergens***, in a genus that is an egg-laying site for ***Trichocerca porcellus*** and food for ***Trichocerca similis***. Photo by Frank Fox, through Creative Commons.

Figure 178. ***Trichocerca rattus*** lateral view. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 179. ***Trichocerca rattus*** f. ***carinata***, a form of a species known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

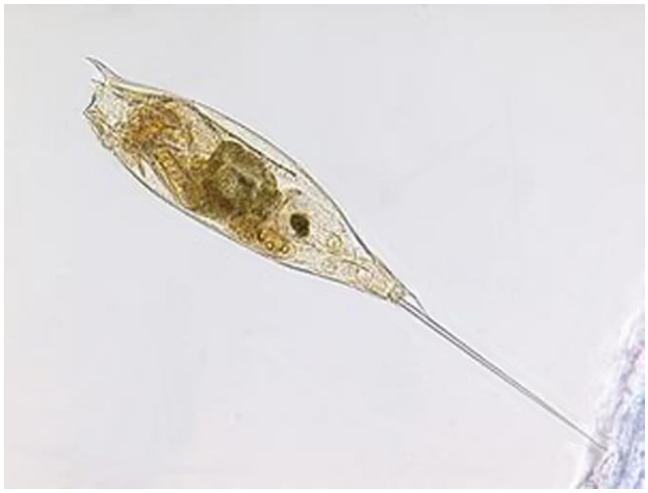

Figure 180. ***Trichocerca rosea***. This species is known from more than one bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 181. ***Trichocerca rosea***, a species that been found in more than one location on ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Trichocerca similis (Figure 182-Figure 183) is a planktonic rotifer, but it also is known from bryophytes and bog pools in Pennsylvania, USA (Myers 1942; Horkan 1981). It is likely to be cosmopolitan, preferring warmer waters (de Manuel Barrabin 2000). It attaches its asexual eggs to other members of the plankton (Pourriot 1970). It prefers a slightly basic *p*H of 7-9.63 and temperatures of 9.5-26.2°C (de Manuel Barrabin 2000). Food is predominantly Cryptomonadaceae and Chrysophyceae, especially *Mallomonas* (Figure 184) and *Dinobryon* (Figure 177). It is a common food item of predator rotifers such as ***Asplanchna*** (Figure 154) and *Ploesoma* (Figure 155-Figure 156) (Guiset 1977).

Figure 182. ***Trichocerca similis***, a planktonic species that also occurs with bryophytes and in bog pools. Photo by Jersabek *et al.* 2003, with permission, with permission.

Figure 183. ***Trichocerca similis***, a plankton species that lives among bryophytes and in bog pools. Photo by Michael Plewka <www.plingfactory.de>, with permission.

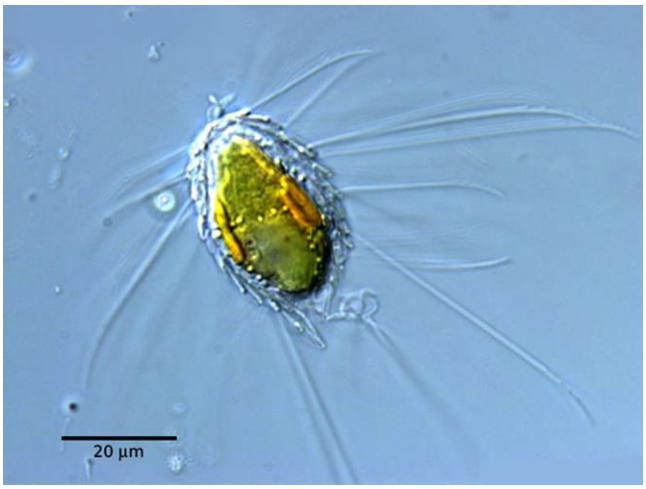

Figure 184. ***Mallomonas***, food for ***Trichocerca similis***. Photo by Jason Oyadomari, with permission.

Jersabek *et al*. (2003) added several ***Sphagnum*** (Figure 41) associates. These included ***Trichocerca edmondsoni*** (Figure 185), ***T. ornata*** (Figure 186) as a bog species and ***T. lata*** (Figure 187), ***T. parvula*** (Figure 188; these two species are easily confused), ***T. platessa*** (Figure 189), ***T. rotundata*** (Figure 190), and ***T. scipio*** (Figure 191) from among ***Sphagnum***.

Figure 185. ***Trichocerca edmondsoni*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 186. ***Trichocerca ornata*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 187. ***Trichocerca lata*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 188. ***Trichocerca parvula*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 189. ***Trichocerca platessa*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

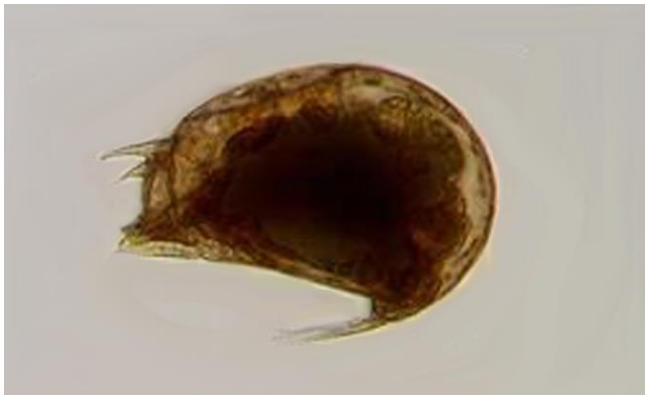

Figure 190. ***Trichocerca rotundata*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 191. ***Trichocerca scipio*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Both ***Trichocerca tenuior*** (Figure 192) and ***T. tigris*** (Figure 193-Figure 195) occur in bogs (Horkan 1981; Hingley 1993), but they also both live on the thallose liverwort ***Riccia fluitans*** (Figure 147) in ponds (Jersabek *et al*. 2003). ***Trichocerca harveyensis*** (Figure 196) lives on ***Fontinalis disticha*** and seems to be the only bryophyte dweller in ***Trichocerca*** not known from ***Sphagnum*** (Figure 41) (Myers 1942; Jersabek *et al.* 2003).

Figure 192. ***Trichocerca tenuior*** from among the thallose liverwort ***Riccia fluitans***. This rotifer also occurs on bog mosses. Photo by Jersabek *et al*. 2003, with permission.

Figure 193. ***Trichocerca tigris***, a species that lives among ***Sphagnum*** and the thallose liverwort ***Riccia fluitans*** in ponds. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 194. ***Trichocerca tigris*** from among ***Sphagnum*** in a bog and ***Riccia fluitans*** in pond. It also occurs in bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 195. ***Trichocerca tigris***, known from ***Sphagnum*** in a bog and from the thallose liverwort ***Riccia fluitans*** in a pond. Photo by Jersabek *et al.* 2003, with permission.

Figure 196. ***Trichocerca harveyensis*** from among ***Fontinalis disticha***. Photo by Jersabek *et al.* 2003, with permission.

On Svalbard, ***T. rattus*** (Figure 178-Figure 179) occurs on submerged mosses, but also in the plankton (De Smet 1993). Horkan (1981) included ***T. similis*** (Figure 183-Figure 182) as a species of bog pools. Bielańska-Grajner *et al*. (2011) added ***T. musculus***. On Svalbard, ***T. intermedia*** (rare; Figure 197), ***T. longistyla***, ***T. obtusidens*** (Figure 198), ***T. uncinata*** (Figure 199), and ***T. weberi*** (Figure 200) occur on submerged mosses, but they also occur in the plankton (De Smet 1988, 1993).

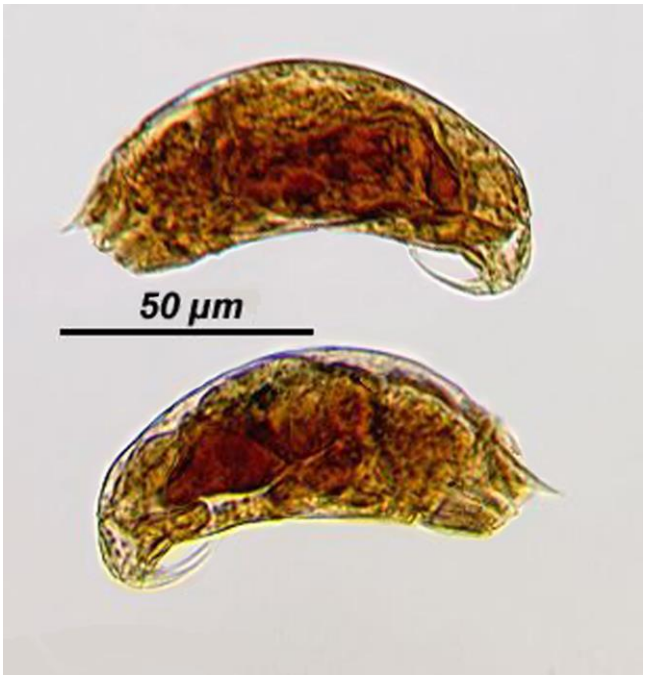

Figure 197. ***Trichocerca intermedia***, a species of submerged mosses on Svalbard. Photo by Jersabek et al. 2003, through Creative Commons.

Figure 198. ***Trichocerca obtusidens*** Jersabek *et al*. 2003, through Creative Commons.

Figure 199. ***Trichocerca uncinata***, a species of submerged mosses and plankton on Svalbard. Photo by Jersabek *et al.* 2003, through Creative Commons.

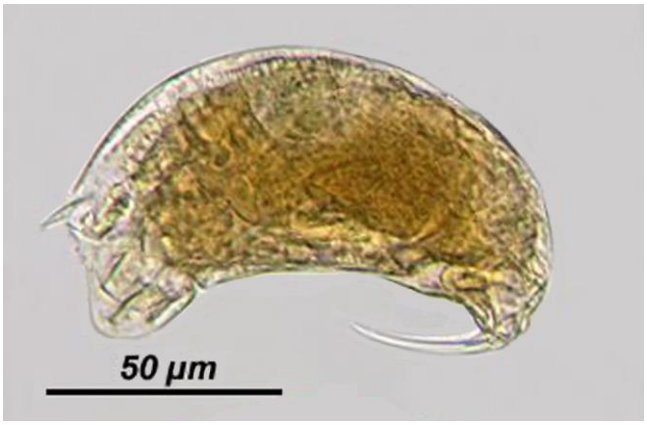

Figure 200. ***Trichocerca weberi***, a species of submerged mosses and plankton on Svalbard. Photo by Jersabek et al. 2003, through Creative Commons.

This family is one that represents the sparse studies on rotifers living on mosses in waterfalls. It is represented by ***Trichocerca pusillus*** (Figure 201) from a waterfall in Thailand (Savatenalinton & Segers 2008), but this species is more typically a plankton species (De Smet, pers. comm. 14 November 2016).

Figure 201. ***Trichocerca pusilla***, a planktonic species that can occasionally occur among wet mosses in waterfalls. Photo by Jersabek *et al.* 2003, with permission.

Trichotriidae

This family is loricate and its surface is marked with facets that have spicules or spines and are mostly granulate (Koste & Shiel 1989). The lorica extends beyond the body to the head, foot, and toes. It typically occurs both on and between aquatic plants, only occurring in the plankton when it is migrating to a new location. There are only three genera, and two of them (***Macrochaetus***, ***Trichotria***) have been collected from **bryophytes**.

Macrochaetus

Macrochaetus collinsii (Figure 203-Figure 202) inhabits bryophytes in bogs (Hingley 1993). ***Macrochaetus multispinosus*** (Figure 204) lives among ***Sphagnum*** (Figure 41; Jersabek *et al.* 2003).

Figure 202. ***Macrochaetus collinsii***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

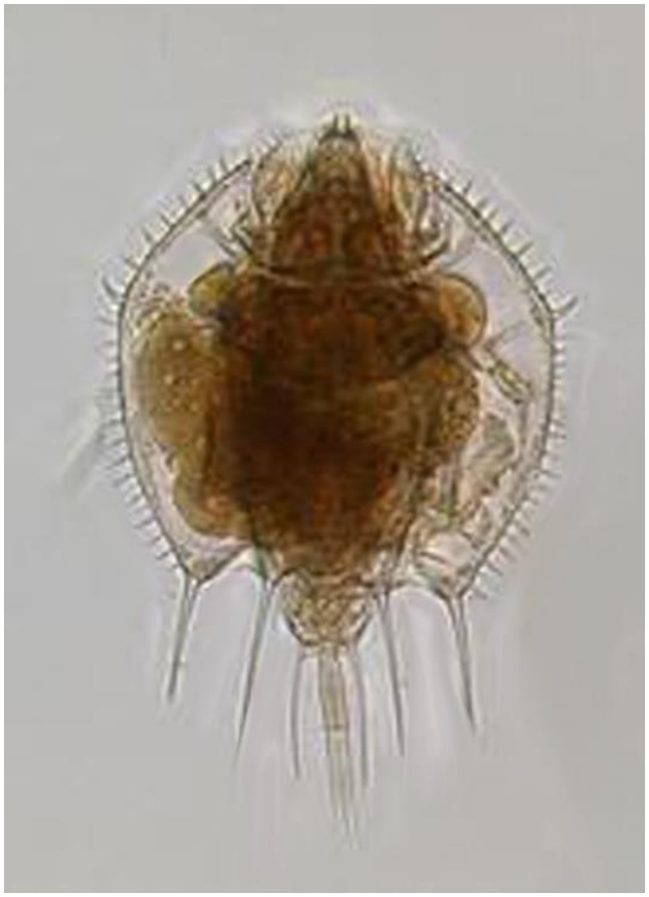

Figure 203. ***Macrochaetus collinsii***, a species known to inhabit bryophytes in bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 204. ***Macrochaetus multispinosus*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Trichotria

Trichotria cornuta (Figure 205), ***T. pocillum*** (Figure 206-Figure 207), ***T. tetractis*** (Figure 209-Figure 212), ***Trichotria tetractis caudata*** (Figure 210), ***T. tetractis similis*** (Figure 211), and ***T. truncata*** (Figure 213-Figure 215) all live among ***Sphagnum*** (Figure 41) in bogs (Horkan 1981; Hingley 1993; Jersabek *et al.* 2003; Bielańska-Grajner *et al*. 2011; Plewka 2016). ***Trichotria pocillum*** is a cosmopolitan species that lives on plant substrata (de Manuel Barrabin 2000), including bryophytes, and can occur in bogs (Horkan 1981). It eats the organic detritus and algae, particularly diatoms, that accumulate among the plants (de Manuel Barrabin 2000). It is widely tolerant of mineralization but prefers a narrow *p*H range of 7.5-8.1. Its known temperatures are in the narrow range of 7.7-9.1, making it active only in winter, at least in Spanish reservoirs. ***Trichotria tetractis*** is a cosmopolitan species and has ecological relationships with ***T. pocillum*** (de Manuel Barrabin 2000). ***Trichotria tetractis*** is known from a *p*H around 8.1 and temperature around 18.8°C.

Figure 205. ***Trichotria cornuta*** from among submerged ***Sphagnum*** in a bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 206. ***Trichotria pocillum***, a plankton and detritus dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 207. ***Trichotria pocillum***, a species that lives on plant substrata (de Manuel Barrabin 2000), including bryophytes, and can occur in bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 208. ***Trichotria similis*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 209. ***Trichotria tetractis*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 210. ***Trichotria tetractis caudata***, a cosmopolitan species from bogs among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 211. ***Trichotria tetractis similis*** (stained) from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

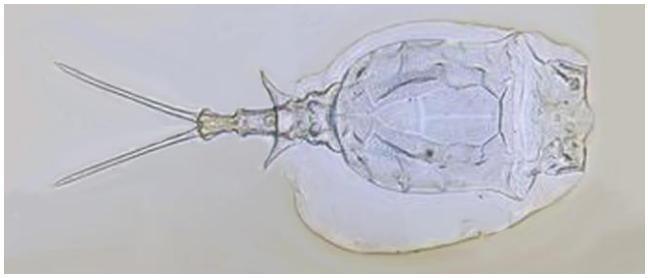

Figure 212. ***Trichotria tetractis***, a species known from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 213. ***Trichotria truncata***, a species known from more than one ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

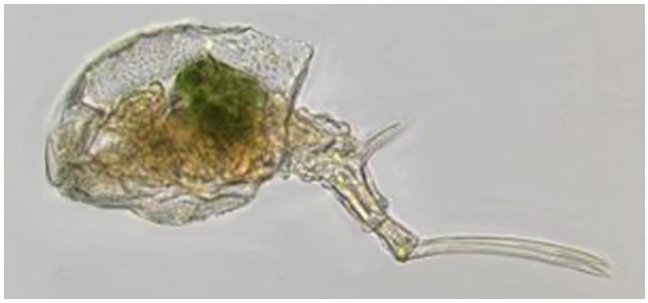

Figure 214. Side view of ***Trichotria truncata***, a species known to associate with ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 215. ***Trichotria truncata***, a species known from more than one location where it is associated with bryophytes, including ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Summary

The monogonont order **Ploimida** is continued here from the previous sub-chapter. The **Notommatidae** is a large family with a number of species collected from bryophytes. The **Proalidae** has no hardened lorica; it occurs on freshwater plants. The **Scaridiidae** is a small family with two species from bryophytes reported here. The **Synchaetidae** has mostly planktonic members, but some have been found among bryophytes. The **Tetrasiphonidae** may have only two species, and they are known from bryophytes. The **Trichocercidae** have a twisted body; two genera have species on bryophytes. The **Trichotriidae** are loricate with spicules or spines; two genera occur on bryophytes.

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CHAPTER 4-8
INVERTEBRATES: MOLLUSCS

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CHAPTER 4-8
INVERTEBRATES: MOLLUSCS

Figure 1. **Slug** on a ***Fissidens*** species. Is it eating, or just a casual visitor? Photo by Janice Glime.

The most familiar of the bryophyte inhabitants among the molluscs are the snails and slugs, but you will see that some bivalves also have an interesting relationship with bryophytes.

Mollusca are considered to be **bilaterally symmetrical** (like humans) (Pratt 1935), but they seem to push the definition to the limit. In bivalves, that is not too difficult to understand, but in snails the twisted body and shell seem to twist the definition as well; even organs normally paired, like kidneys, are not paired (Figure 2).

Gastropoda: Snails and Slugs

Most terrestrial and freshwater snails (**Pulmonata**) have spiral shells and these may be taller than the diameter of the opening (**elongate/conical**; Figure 26) or shorter (Figure 148) (Pratt 1935). The inside body is also a spiral, but it is not the same spiral as the one of the shell. This internal spiral affects the digestive system as well. With its mouth to the ground, the snail is infamous for the positioning of the anus above the mouth on the right side of the head (Figure 2).

In snails, the mantle secretes a shell, and this requires calcium carbonate. For this reason, you will find a number of terrestrial taxa restricted to limestone areas. Slugs (Figure 3), on the other hand, lack shells and exhibit no external twists. Instead they have a thin calcareous plate embedded in the mantle.

Unlike the marine snails, terrestrial gastropods lack an **operculum** to cover the shell opening. Instead, they use a calcified slime (**epiphragm**; Figure 4) for protection in hibernation or aestivation. The **respiratory pore** (Figure 3) is on the right side of the body, and closes to keep out water in aquatic species or to prevent desiccation under dry conditions on land. Both aquatic and terrestrial gastropods have lungs, necessitating return to the surface for aquatic members to get air. Aquatic members have only one pair of non-retractile tentacles, whereas land-dwellers have two pairs and both are retractile. Aquatic species have an eye at the base of each tentacle; the land snails have their eyes on the tips of the rear pair of tentacles.

Most gastropods eat algae and plants, which they scrape with the **radula** (Figure 5), but a few are carnivorous. The radula is made of chitin with rows of minute calcareous teeth. And if you thought bryophytes used minute characters for identification, snail identification is often based on these teeth!

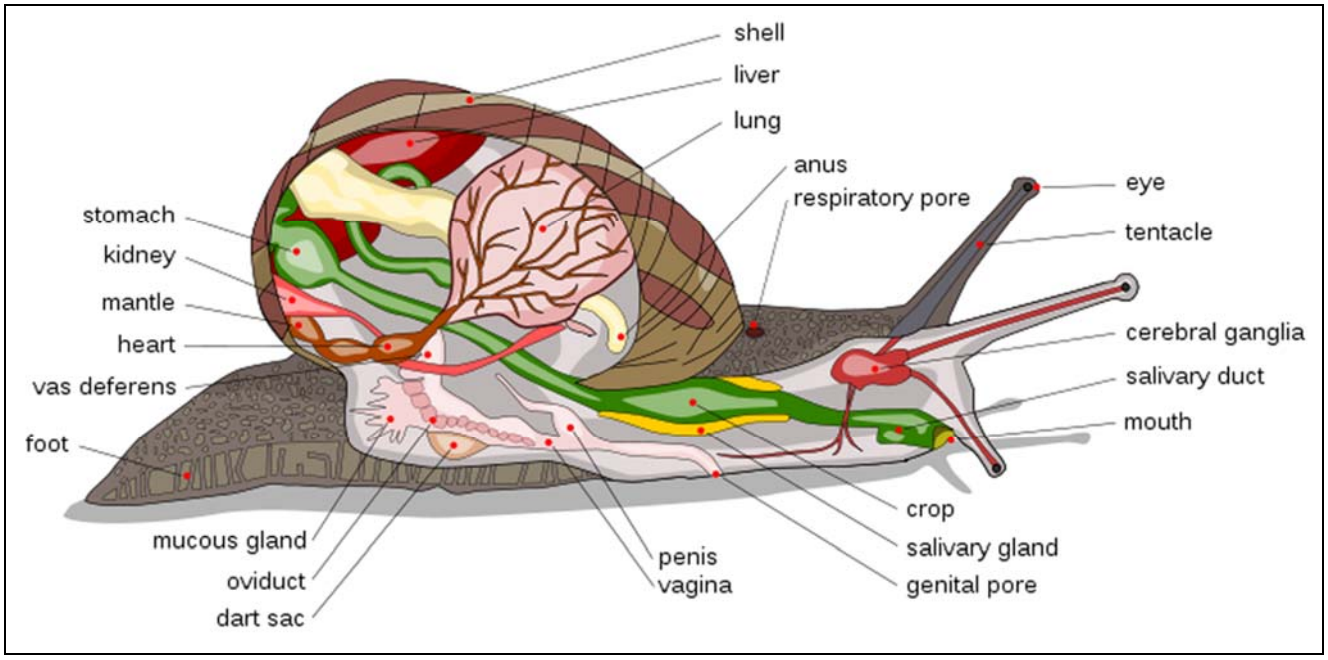

Figure 2. Snail, showing its major internal and external parts. Note the dart sac from which the love dart is ejected. Image from Wikimedia Creative Commons.

Figure 3. Great Red Slug, ***Arion rufus***, dark form, Bishop Middleham Quarry Nature Reserve, Co Durham. Note the large **respiratory pore** on the mantle of this sometimes moss dweller. This snail can travel nearly 0.5 km in search of more suitable conditions (Sandelin 2012). Photo by Brian Eversham, with permission.

Figure 4. *Helix pomatia* **epiphragm**. Photo by Hannes Grobe, through Wikimedia Commons.

Figure 5. *Pomacea canaliculata* mouth showing **radula**. Photo by S. Ghesquiere, through Wikimedia Commons.

Reproduction

Most terrestrial snails and slugs are **simultaneous hermaphrodites**, mutually exchanging gametes during copulation. This is not true for land-dwelling prosobranch snails (including the Pomatiidae, Aciculidae, Cyclophoridae, and others) – families that have separate sexes (Wikipedia 2012b). The prosobranch snails are the ones that have an **operculum** that can be used to cover the opening when they retreat into the shells.

Some land snails are **sequential hermaphrodites**, being first male, then female (Nordsieck 2012b). Others, such as ***Arianta arbustorum*** (**Helicidae**; Figure 6), a moss-dwelling snail, have a mechanism that prevents sperm cells from fertilizing the snail's own egg cells before they reach the sperm pouch of the mate. In the aquatic **Lymneidae**, snails can reproduce using unfertilized eggs, permitting

them to multiply rapidly in a new location and causing invasive species problems when they are introduced as aquarium pets.

The reproductive anatomy of the snail is a bit peculiar, with the **penis** and **vagina** everting from near the head (Figure 7-Figure 8). In the hermaphrodites, the penes wrap around each other, sometimes extending to great lengths (Figure 9).

Figure 6. ***Arianta arbustorum*** on a bed of mosses and leafy liverworts. Photo ©Roy Anderson, with permission.

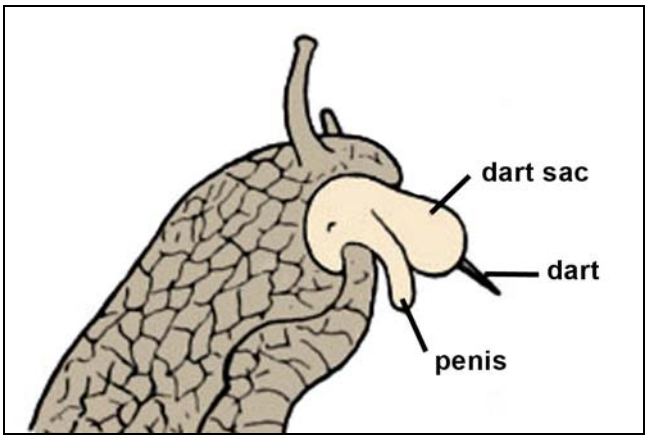

Figure 7. *Helix pomatia* head during mating. Redrawn from Johannes Meisenheimer, through Wikimedia Commons.

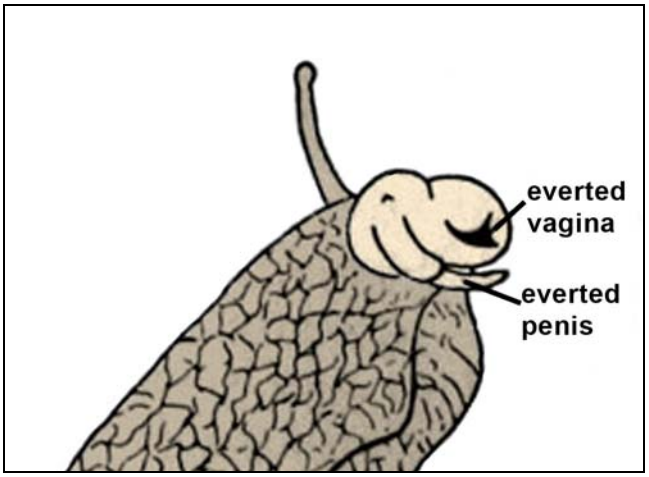

Figure 8. *Helix pomatia* head after mating, showing both male and female parts of this **simultaneous hermaphrodite**. Redrawn from Johannes Meisenheimer, through Wikimedia Commons.

Figure 9. Slugs mating, demonstrating the very long penes. Photo through Wikimedia Commons.

Mating and the Love Dart

The mating process is a combination of love and war (Figure 10). The dart, or more than one in some species, is made of calcium carbonate, chiton, or cartilage (Figure 11). During mating, each snail tries to inject this "dart" into the other snail (Figure 12) (Koene & Chase 1998a; Chase & Blanchard 2006). It might be more appropriate to call this a dagger because it is injected by a thrust, not a shot or a throw. The first mating of a snail stimulates the production of the dart, so it cannot be used until the second mating. Once used, it requires time to generate a new one.

Figure 10. Roman snails (*Helix pomatia*) in full foot contact during mating. This process of contact of foot, lips, and tentacles can take up to 20 hours. Photo through Wikimedia Commons.

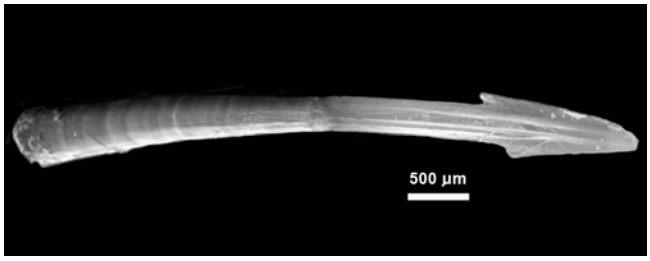

Figure 11. **Love dart** of the snail ***Monachoides vicinus***. Photo by Joris M. Koene and Hinrich Schulenburg through Wikimedia Commons.

Figure 12. Mating garden snails (***Helix aspera***) with **love dart** in snail on right, just above the antenna of the left snail. Photo by Eynar through Wikimedia Commons.

But what does the dart accomplish? Early hypotheses considered it to be a "gift of calcium" to help in the development of the eggs. Leonard (1992) used a theoretical model to support the hypothesis that the love dart induced the partner to act as a male, hence insuring that the thruster would also be fertilized. Koene and Chase (1998a, b) used an experimental approach to disprove the long-held hypothesis of a "gift of calcium."

Through the work of Koene and Chase (1998 a, b), the role of this dart has become clearer. It carries with it a mix of **hormones** that help to move the sperm cells toward the sperm pouch where they are stored until fertilization (Koene & Chase 1998a, b). This is accomplished by causing changes in the structure of the copulatory canal leading ultimately to the sperm pouch. These changes increase the chances, often doubling them, that sperm from that mating snail are successful in fertilizing eggs, since it is likely that the partner will have multiple mating events. But the dart, preferably aimed at the foot, can miss its ideal target and land in a less desirable location, like the base of the antenna. When that happens, the snail is no longer able to retract or extend the antenna.

Each partner goes through gyrations apparently in an attempt to avoid being recipient of the love dart, or at least to avoid receiving it in an undesirable location. So far, Leonard's (1992) hypothesis of stimulating the partner to carry out its male role does not seem to have been tested experimentally, but with the mix of hormones it could still be a viable part of the story. It appears that this love dart, although not understood at the time, could have been the basis for the story regarding Cupid's arrow (Chase 2010).

Egg and Larval Development

Most gastropods lay eggs, with only a few species bearing live young. In aquatic snails, development of the larva occurs as a planktonic stage once it leaves the egg, but in terrestrial pulmonate snails, development is completed within the egg. Some snails (*e.g.* **Clausiliidae**) exhibit **ovoviviparity**, wherein the larvae emerge inside the mother's body and emerge from "her" body as juvenile snails (Nordsieck 2012b). This practice permits these snails to live in dry areas where external eggs could not survive the desiccation. Some species of the **oviparous** (egg-laying) species, such ***Arion flagellus*** (Figure 13), lay their eggs under or among bryophytes (Figure 14).

Figure 13. ***Arion flagellus*** on a sheet of mosses. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 14. ***Arion flagellus*** eggs in Oaks Wood, Cambourne, Cambridgeshire, UK. Note the bit of moss beside the eggs and on the eggs – remnants of the cover that previously protected them. Photo by Brian Eversham, with permission.

Richter (1972) found that the banana slug (***Ariolimax columbianus***, Figure 15) laid 3-4 mm eggs under moss where soil conditions were neither excessively wet nor dry. Placing eggs under mosses and other loose substrata may be an energy-saving strategy for some species. Bauer (1994) considered the behavior of some snails that dig holes to be an investment in **parental care**, but incurring an energy cost. Other than these preparations, snails do not tend their eggs or hatchlings. ***Ariolimax californicus*** (Figure 16) also may occur under bryophytes (Peggy Edwards, pers. comm.).

Figure 15. ***Ariolimax columbianus*** on moss. Photo by Bill Leonard, with permission.

Figure 16. ***Ariolimax californicus*** exiting a mat of mosses, a suitable location for laying eggs. Photo coourtesy of Peggy Edwards.

Bryophyte Interactions

Glistening trails of pearly mucous (Figure 17) criss-cross mats and turfs of green, signalling the passing of snails and slugs on the low-growing bryophytes (Figure 1). In California, the white desert snail ***Eremarionta immaculata*** (Figure 18) is more common on lichens and mosses than on other plant detritus and rocks (Wiesenborn 2003). Wiesenborn suggested that the snails might find more food and moisture there. Are these molluscs simply travelling from one place to another across the moist moss surface, or do they have a more dastardly purpose (as hunters) for traversing these miniature forests?

Figure 17. ***Lehmannia valentiana*** with its slime trail on a moss (upper right) in Swavesey, Cambridgeshire, UK. Photo by Brian Eversham, with permission.

Figure 18. ***Eremarionta immaculata*** in the Riverside Mountains, CA, USA. Photo by William D. Wiesenborn, with permission.

But not all snails and slugs find the bryophyte substrate attractive. Some actually avoid its rough surface. Nevertheless, trails of slime (Figure 19) are not unusual, and we have little insight into the reasons why some find it inviting while others find it repulsive.

Figure 19. Snail or slug trails on ***Dicranum viride*** on big maple trunk. Photo courtesy of Betsy St. Pierre.

Abundance

Snails can sometimes occur in significant numbers in moss habitats. Their need for a moist environment (Pratt 1935) would seemingly attract snails to the mosses as a moist substrate. Quantitative information on snails and slugs among bryophytes is scarce, and often only mentions that bryophytes are abundant in the habitat (*e.g.* Nekola 2002).

The study by Grime and Blythe (1969) is helpful in understanding numbers and dynamics of moss-dwelling snail populations, but we need many more studies. They found average morning populations of up to 8.5 per 100 g dry weight of moss in early September for the copse snail ***Arianta arbustorum*** (Figure 20) at Winnats Pass in Derbyshire, England. In collections totalling 82.4 g of moss, they examined snail populations in a 0.75 m^2 plot each morning on 7, 8, 9, & 12 September 1966. ***Arianta arbustorum*** numbered 0, 7, 2, and 6 on those days, respectively, with weights of 0.0, 8.5, 2.4, and 7.3 per 100 g dry mass of moss. This was surpassed only by those on

Urtica dioica (stinging nettle) reaching 14.4 and *Mercurialis perennis* (dogs mercury) reaching 16.2. Nevertheless, it takes a lot of dry moss to make 100 g.

Figure 20. The moss-dwelling copse snail, ***Arianta arbustorum***. Photo © Roy Anderson <habitas.org.uk>, with permission.

Nighttime activity by many snails is likely to be greater than that during the day, and little snails may actually seek refuge in mosses during the day (Grime & Blythe 1969). Furthermore, snails like ***Arianta arbustorum*** (Figure 20) typically climb, often to a considerable height, to obtain food. Bryophytes just don't fit as a refuge for larger snails, so the behavior of the larger ***Arianta arbustorum*** may not reflect that of the small snails.

Adaptations

Confusing the Predator

In the Pacific Northwest, USA, unusual jumping slugs in the genus ***Hemphillia*** (Figure 21-Figure 24) prefer coarse woody debris or moss mats on decaying logs (Leonard & Ovaska 2003). They have some remarkable adaptations for their log habitats. One such adaptation appears to be to confuse their predators by smearing their slime trail (Figure 17).

Figure 21. ***Hemphillia glandulosa***, the warty jumping slug, on moss. This and the following photo illustrate the variability in its coloration. Photo by Kristiina Ovaska, with permission.

Jumping to Escape

A second adaptation to avoid predation is to "jump." Jumping slugs (***Hemphillia***; Figure 22) don't actually jump. Instead, when they are approached by a predator snail or other predator, they tighten their muscles, coil up, and straighten rapidly, flopping around on their substrate until they are free of it, and fall. This effects a rapid motion that looks like a jump (Leonard 2011). This activity also breaks the slime trail, facilitating their freedom to "jump." The slow-moving predator snails don't have a chance. Leonard says these slugs are potentially successful dispersers of fungal spores. I would think that would work for dispersing bryophytes as well, for spores, asexual structures, and fragments.

Figure 22. ***Hemphillia glandulosa***, the warty jumping slug, on moss. This and the above photo illustrate the variability in its coloration. Photos by Kristiina Ovaska, with permission.

In Canada, some of these ***Hemphillia*** (Figure 21-Figure 24) species seem safe from extinction due to sufficient abundance, but others are endangered due to increasing patchiness of suitable habitats (Leonard & Ovaska 2003). The 1994 NW Forest Plan regulates ground disturbance activities on federal lands in northern California to Washington, protecting "survey and manage" species, including several species of jumping slugs, ***Hemphillia***. ***Hemphillia dromedarius*** (dromedary snail; Figure 23-Figure 24) is officially threatened in both Canada and the United States, where it lives in the state of Washington. Legal protection of these slugs can help in the protection of mosses in these areas. However, the Bush administration was not sympathetic to this protection and it could be lost at any time with a change in administrative philosophy. Perhaps the novelty of its jumping behavior will increase public interest and sympathy and lead to its protection in yet another way.

Figure 23. ***Hemphillia dromedarius***, the dromedary jumping slug. Photo by Kristiina Ovaska, with permission.

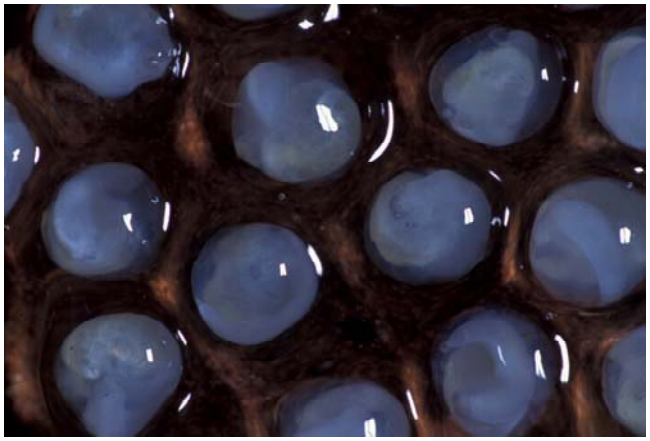

Figure 24. Eggs of ***Hemphillia dromedarius***, the dromedary jumping slug. Photo by Kristiina Ovaska, with permission.

Keeping It Small

If you want to go clambering among the bryophytes, it helps to be small (Figure 26). One would expect that size would also constrain movement among the bryophytes and restrict larger snails to the surface. But some tiny snails actually occur fairly deep within the bryophyte mat. Such is the elongate snail captured by Jan-Peter Frahm deep within a cushion of ***Distichium capillaceum*** (Figure 25).

Figure 25. ***Distichium capillaceum*** with a snail nestled deep within the cushion. Photo by Jan-Peter Frahm, with permission.

Truncatellina cylindrica (Figure 26) is another very small snail. Where it lives at Groomsport, Down, UK, it occurs in yellow dunes among mosses and the roots of vegetation on drier, sunny slopes (Anderson 1996).

Figure 26. ***Truncatella cylindrica*** on ***Tortula*** sp. Note the small size of this conical snail. Photo by Stefan Haller, with permission.

Szlavecz (1986) determined that snail size plays an important role in their behavior, including food searching. Although one might think that larger animals need to eat more, it seems that the larger ***Monadenia hillebrandi mariposa*** (Figure 27) instead spends more time crawling and less time feeding, permitting it to travel farther. Although it prefers leaf litter, it consumes mosses as well (Figure 28). This snail lives in cool, mossy forests and sometimes hibernates among mosses, including thick moss on a bigleaf maple branch (Sandelin 2012).

Figure 27. ***Monadenia hillebrandi***, a consumer of the mosses ***Rhytidiadelphus*** sp. and ***Grimmia trichophylla***. Photo by John Slapcinsky, through Creative Commons.

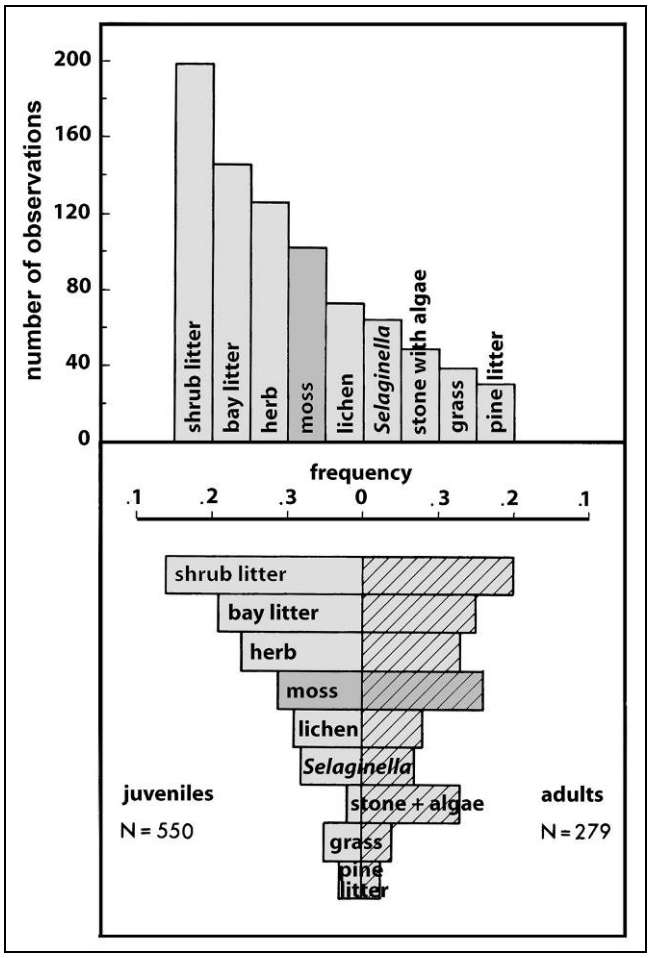

Figure 28. Laboratory selection of foods by the snail ***Monadenia hillebrandi mariposa***. **Upper**: all data combined. **Lower:** juveniles vs adults. Redrawn from Szlavecz 1986.

Monadenia fidelis (Figure 29) lives in dry forests as well as prairie wetlands where its presence is indicative of an unburned prairie (Severns 2005). Loubser *et al*. (2005) found it associated with nearby mosses in 33% of their samples. But like many observations of animals with bryophytes, this may mean that they need bryophytes in their habitat, that they prefer the same habitats as bryophytes, or that the relationship is coincidental – the bryophytes are near something they need. In this case, mosses are one of its winter hibernating sites, where they hibernate under mosses in crotches of maple trees (Monadenia 2016).

Figure 29. ***Monadenia fidelis*** (Pacific sideband snail) on mosses. Photo by Walter Siegmund through Wikipedia Commons.

Conical Shape

The terrestrial conical snails, or at least the smaller of these snails, seem to be more suited to traversing the internal spaces of bryophytes. ***Cochlicopa lubrica*** (Figure 30) and ***Cochlicopa lubricella*** (Figure 31), moss snails, have been known from mosses for a long time. In 1840 Turton reported these snails from mosses and grass on the ground and under stones in the British Isles.

Figure 30. ***Cochlicopa lubrica*** on mosses. Photo by Malcolm Storey, through Creative Commons.

Figure 31. ***Cochlicopa lubricella***, moss snail, on mosses. Photo © Roy Anderson <habitas.org.uk>, with permission.

Turton (1840) also reported another tiny conical snail, ***Ena obscura*** (Figure 32), from mosses and under stones. But this snail has another way to be elusive from would-be predators. It covers itself with mud or debris, rendering it nearly invisible by hiding the shiny shell (The Great Snail Hunt 2012), but might it also provide a means of controlling water loss or temperature?

Figure 32. ***Ena obscura***, a snail that lives in forests or on walls, under stones and moss (Turton 1840) in the Sulehay, Northants, UK. It covers itself with mud as camouflage. Photo by Roger S. Key, with permission.

Avoiding Desiccation

Bryophytes remain moist long after their epiphytic and rock substrata, and even those on dry soil can become moist, collecting fog or light rainfall that never reaches the soil. Hence, they can become a refuge for snails and slugs seeking moisture. Such is often the case for the banana slug, ***Ariolimax columbianus*** (Figure 15), in the Pacific lowlands, USA. This slug leaves its moist cover on a moss-covered fallen log to forage at night, then returns to the moss (Sandelin 2012). Taking advantage of the

moisture at night, this slug can travel nearly 0.5 km in search of more suitable conditions.

The large (up to 13-15 cm) bryophyte-dwelling slug ***Arion ater*** (Figure 33-Figure 35) forms a ball by contracting its body and humping up (Figure 34) (Sandelin 2012). That reduces its surface area and thus reduces water loss. It can also twist on itself to reduce exposed surface area (Figure 35). This twisting ability is probably also helpful as it climbs moss setae and feeds on the capsules.

Figure 33. Black form of ***Arion ater*** in an extended position. Photo by David Perez, through GNU Free Documentation.

Figure 34. Black form of ***Arion ater*** forming a ball by contracting and humping up. Photo by Emőke Dénes, through Wikimedia Commons.

Figure 35. ***Arion ater*** juvenile contracting on itself. Photo © Roy Anderson <habitas.org.uk>, with permission

Bryophytes can offer the snails and slugs yet another means to escape drought and extreme heat or cold. These gastropods can **hibernate** in cold temperatures or **aestivate** in heat or drought (Boss 1974), and this sometimes occurs among bryophytes. Some snails remain dormant for as many as five or six years. Boss suggests that the ability to hibernate and aestivate may play a strong role in the expansion of geographic range, speciation, and extinction.

The European snail species ***Fruticicola fruticum*** (=*Eulota fruticum*, *Bradybaena fruticum*; Figure 36) hibernates from October until a time in spring when the weather is suitable for it to become active (Künkel 1928). It accomplishes this hibernation in dead moss or it may burrow into the ground with its aperture facing upward.

Figure 36. ***Fruticicola fruticum*** with ***Polytrichum*** nearby. Photo by Michael Becker, through Wikimedia Commons.

No Shell – Slugs

Slugs can be somewhat common on bryophytes and seem to have the same adaptations as snails. Their only advantage would seem to be greater flexibility due to the absence of a hardened and bulky shell, but that brings with it a greater chance for desiccation. For that reason, bryophytes may be a source of hydration. For many species, being small helps in permitting them to hide from predators and to maneuver among the bryophytes (Figure 37).

Figure 37. Keeled slug (***Tandonia budapestensis***), common inhabitant of mosses such as this ***Leucolepis*** in the Pacific Northwest, USA. Photo courtesy of Jeri Peck.

The **Limacidae** is a family of slugs, and both common genera (***Deroceras***, ***Limax***) have members that have been found among mosses. In the sub-Antarctic Marion Island, the slug ***Deroceras panormitanum*** (Figure 38; originally described as the separate species ***D. caruanae***) lives in moist bryophyte communities as well as on decaying bryophytes (Smith 1992). With a totally exposed body, slugs in such harsh environments can find shelter and moisture among the bryophytes.

Figure 38. ***Deroceras panormitanum*** on what appears to be a species of the moss ***Campylopus.*** Photo © Roy Anderson <habitas.org.uk>, with permission.

Brain Eversham (pers. comm. 21 March 2012) tells me that the yellow slugs, ***Limax flavus*** (=***Limacus flavus***; Figure 39) and ***L. maculatus*** (Figure 40), live mainly on old walls in Britain, where, like many snails, they are night active. They feed primarily on lichens and algae, but will graze on dead plant material if they run out of lichens. They don't generally eat leafy mosses, but they will browse on the capsules. He has observed ***Tortula muralis*** (Figure 41) and ***Grimmia pulvinata*** (Figure 42) with the setae remaining but all the capsules nibbled off. Ken Adams (Bryonet 18 March 2020) reports that capsules of ***Codonoblepharon forsteri*** (=*Zygodon forsteri*) where he does fieldwork in the UK are mostly eaten before they mature (Figure 43). Eversham suggests that the capsules and spores of bryophytes are more nutritious or more digestible than the leaves and stems.

Figure 39. ***Limax flavus*** on a bed of mosses. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 40. ***Limax maculatus*** on moss at Bridge House, Swavesey, UK. Photo by Brian Eversham, with permission.

Figure 41. ***Tortula muralis***, a species whose capsules serve as food for species of ***Limax***. Photo by Michael Lüth, with permission.

Figure 42. ***Grimmia pulvinata*** with capsules and awns. Photo by Michael Lüth, with permission.

Figure 43. ***Codonoblepharon forsteri*** with young capsules and seta from capsules that were probably lost to herbivory. Photo by Michael Lüth. with permission.

In Search of Food

As just described for two species of ***Limax*** (Figure 39-Figure 40), snails and slugs may browse on bryophytes. They have a rasping tongue (**radula**) that destroys the epidermis of tracheophytes (Grime & Blythe 1969), but what does it do to moss leaves only one cell thick? Apparently in some cases it makes mosses potential food (Szlavecz 1986), and enables some gastropods to consume even the tough capsule (Davidson & Longton 1987, Davidson *et al*. 1990).

Low Palatability?

Often it appears that the palatability index for bryophytes is low (Jennings & Barkham 1975). Furthermore, snails and slugs seem to be less interested in grazing things with awns than those without. Robin Stevenson (pers. comm. January 2008) has seen ***Bryum argenteum*** (Figure 44-Figure 45) that is completely grazed over, but never observed such grazing on an awned ***Grimmia*** species (Figure 42). Could it just be that there is no nutrition in an awn, or do they have trouble gliding across the furry tips of leaves?

Figure 44. ***Bryum argenteum***, a moss with no awns and a food source for snails and slugs. Photo by Michael Lüth, with permission.

Figure 45. ***Bryum argenteum*** showing lack of awns. Photo from UBC website, with permission from Shona Ellis.

But awns, even in ***Grimmia pulvinata*** (Figure 46), may not deter all snails (Figure 46). Szlavecz (1986) was able to identify the awned ***Grimmia trichophylla*** (Figure 47) in feces of the California snail, ***Monadenia hillebrandi mariposa*** (Figure 27) and also demonstrated that the spine tips of the tracheophyte *Selaginella hansenii* (Hansen's spikemoss; Figure 48) did not deter feeding or crawling. Perhaps it depends on the density of the hair tips, since ***Grimmia trichophylla*** (Figure 47) and *S. hansenii* (Figure 48) have much less dense hairs than ***G. pulvinata*** (Figure 46), and on the particular species and size of snail or slug. On the other hand, it appears that the slugs are able to graze the lower margins of a clump, apparently resting on the substrate without the need to traverse the awns (Figure 46).

Figure 46. ***Grimmia pulvinata*** exhibiting grazing that girdles the base of the clump in a pattern typical of snail or slug grazing, but also known for isopods. Photo by Robin Stevenson, with permission.

Figure 47. ***Grimmia trichophylla*** in Bretagne (Brittany), France, showing somewhat less imposing awns than those of ***Grimmia pulvinata***. Photo by Michael Lüth, with permission.

Figure 48. ***Selaginella hansenii***, a spine-tipped tracheophyte eaten by the snail ***Monadenia hillebrandi mariposa***. Photo by J. E. (Jed) and Bonnie McClellan, © California Academy of Sciences, with permission.

Michael Lüth has observed snails grazing on ***Orthotrichum*** (Figure 49) and Terry McIntosh has seen slugs grazing on other bryophytes, with both observers indicating that the damage to the moss was similar to that shown for ***Grimmia pulvinata*** in Figure 46 (Bryonet 12 January 2008). On the other hand, Frank Greven (Bryonet 13 January 2008) has seen this pattern as a result of grazing by isopods (wood lice). Robin Stevenson (pers. comm. 14 January 2008) agrees that isopods might be deterred by the awns, causing them to eat in such a pattern. But in this case, after climbing up a bridge coping, the snail or whatever might have found that this moss provided the best choice available.

Figure 49. ***Orthotrichum urnigerum***, member of a genus known to be grazed by snails. Photo by Michael Lüth, with permission.

Low Nutritional Quality?

That rasping tongue is not always enough to accomplish the task of obtaining nutrients from mosses. Oyesiku and Ogunkolade (2006) experimented with snails and the moss ***Hyophila involuta*** (Figure 50). In their laboratory experiments, the snails (***Limicolaria aurora***; Figure 51) gained the most weight when fed with ***Hyophila involuta*** paste. The snails that had only unground moss actually lost weight. Those in the field experiment (restricted to ***Hyophila involuta***) either lost weight or remained the same. Fecal matter of the field snails had fragments of moss that had lost the chlorophyll from their cells as well as that of abundant algae and Cyanobacteria. The presence of these snails on the moss was seasonal from April until October, when the moisture and lower temperature of the moss may have provided a favorable habitat. This experiment suggests that in this case the snail was unable to penetrate the cells of the moss, making it an unlikely food source in nature. Rather, the researchers suggest that the snails most likely use the moss as a moist and cool habitat.

Oyesiku and Bello (2012) experimented further with the effect of the moss ***Hyophila involuta*** (Figure 50) as a food for the snail ***Limicolaria aurora*** (Figure 51). The study was based on an interest in including mosses as feed when breeding snails. The moss was mixed in various ratios with corn pap powders (*Zea mays*). Overall, there was a significant correlation with the feed ratios of decreasing order of moss 50%:corn 50% > moss 25%:corn 75% > moss 0%:corn 100% > moss 100%:corn 0% > moss 75%:corn 25%. The highest weight gain of 15 g peaked at the fourth day in ***L. aurora*** fed with moss 50%:corn 50%. Furthermore, the snails exhibited a strong positive weight gain correlation with increasing days of feeding with 25% moss to 75% corn.

Figure 50. ***Hyophila involuta***, with a snail; the snail ***Limicolaria aurora*** can thrive on this moss. Photo by Li Zhang, with permission.

Figure 51. Shell of ***Limicolaria aurora***. Photo by David G. Robinson, USDA APHIS PPQ at Bugwood.org, through public domain.

Chemical Deterrents to Herbivory

Longton (pers. comm. 1996) has speculated that phenolic compounds that protect the leafy gametophytes deter herbivory, especially on perennials. This could account for greater herbivory on the annual ***Funaria hygrometrica*** (Figure 52) than on perennial ***Brachythecium rutabulum*** (Figure 66) or ***Mnium hornum*** (Figure 80). The phenolic compounds in the latter two species were released only after severe hydrolysis, leading Davidson *et al*. (1990) to suspect that the phenolic acids might be tightly bound to cellulose in the cell wall. The greater palatability of the ***F. hygrometrica*** supports the general theory that perennials invest more resources in defense against herbivory than do annuals such as ***F. hygrometrica***.

Figure 52. Young sporophytes of ***Funaria hygrometrica*** before spores form. Photo by Michael Lüth, with permission.

Food for Some

Clearly for some slugs and snails there are bryophytes that do indeed seem palatable. Ochi (1960) reported that the thallose liverwort ***Conocephalum conicum*** (Figure 53) served as food for a slug. Merrifield (2000) found evidence of heavy grazing on epiphytic bryophytes, particularly the moss ***Syntrichia laevipila*** (Figure 54), of Oregon white oaks (*Quercus garryana*) in the Willamette Valley, Oregon, USA, and considered that either springtails or slugs were likely responsible. She considered that the abundance of gemmae on ***S. laevipila*** may be a response to this grazing.

Figure 53. ***Conocephalum conicum*** showing feeding damage upper middle) by something, perhaps a slug. Photo by John Hribljan, with permission.

Figure 54. ***Syntrichia laevipila*** on bark. Photo by Jonathan Sleath, with permission.

Algae growing on mosses, especially in the aquatic habitat, could be a prominent source of food for gastropods. In the Negev Desert, adult desert snails (***Sphincterochila zonata***) fed exclusively on algae on the soil surface, creating an algal turnover of 142 kg hectare^{-1}, despite being active for only 8-27 days in winter during the rainy period (Shachak & Steinberger 1980). Other Negev Desert snails feed on the mosses themselves. ***Sphincterochila boissieri*** (Figure 55) feeds on shrubs there, but its feces indicate that it also feeds on the moss ***Tortula atrovirens*** (=***Desmatodon convolutus***; Figure 56) (Yom-Tov & Galun 1971). This is a snail that has color morphs of brown and white, but they apparently don't affect its temperature (Yom-Tov 1971; Slottow *et al*. 1993). However, their rodent predators choose more brown than white snails, enough to exhibit significant differences in their choices (Slottow *et al*. 1993).

Figure 55. ***Sphincterochila boissieri***, a species that is known to eat ***Tortula atrovirens*** in the Negev desert. Photo by Mark A. Wilson, through Creative Commons.

Figure 56. ***Tortula atrovirens***, a moss that is eaten by the Negev Desert snail, ***Trochoidea seetzeni***. Photo by Des Callaghan, with permission.

Szlavecz (1986) examined feeding preferences in 31 individuals of the snail ***Monadenia hillebrandi mariposa*** (Figure 27). Collections of field feces indicated that they consumed the mosses ***Rhytidiadelphus*** sp. (Figure 57) and ***Grimmia trichophylla*** (Figure 58) in nature, among other things. In the lab, they preferred shrub and bay litter over mosses, but preferred mosses and lichens over grasses and pine litter. More green moss than brown occurred in the feces, whereas brown material was more common from consumed tracheophytes (Figure 59).

Figure 57. ***Rhytidiadelphus squarrosus***, a member of a genus that has been found in feces of the snail ***Monadenia hillebrandi mariposa***. Photo by Michael Lüth, with permission.

Figure 58. ***Grimmia trichophylla*** showing awns. Photo by Michael Lüth, with permission.

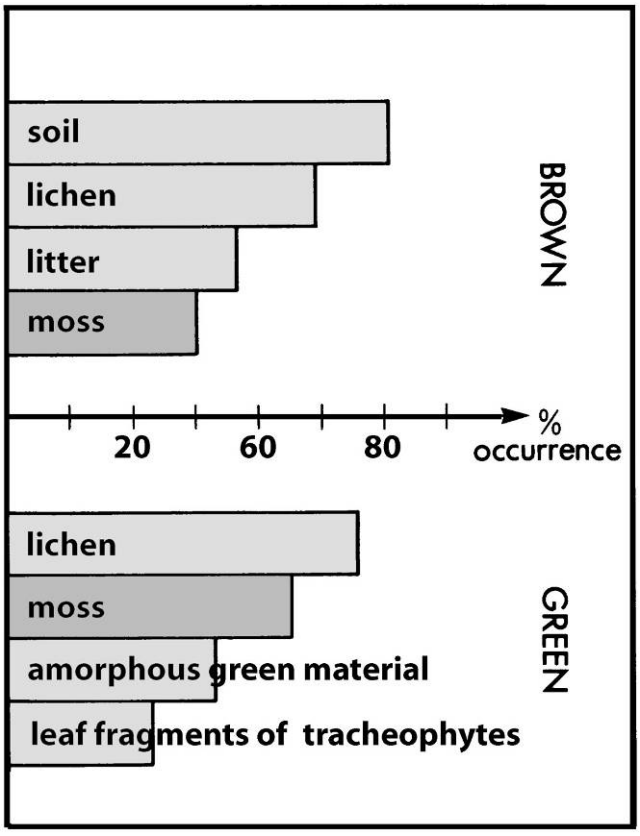

Figure 59. Comparison of green and brown portions of plant material eaten by the **snail *Monadenia hillebrandi mariposa***. Modified from Szlavecz 1986.

Grime and Blythe (1969) found bryophytes in the feces of four species of snails out of the six examined from Winnats Pass, Derbyshire, England, on 13 October. But then, tracheophyte foods are often less nutritious as the plants prepare for winter. Studies by Chatfield (1973), Williamson & Cameron (1976), and Richter (1976) indicate that at least juvenile snails might do best on a mixed diet. But for ***Cepaea nemoralis*** (Figure 60-Figure 61), it appears that even though mosses are part of their habitat, they are seldom part of the diet (Williamson & Cameron 1976).

Figure 60. ***Cepaea nemoralis***, banded snail juvenile at Old Sulehay Forest, UK, a species that lives in a mossy habitat but apparently does not eat them. Photo by Brian Eversham, with permission.

Figure 61. ***Cepaea nemoralis***, a species that lives in a mossy habitat but apparently does not eat them. Photo by Stefan Haller, with permission.

In the tropical montane rainforest of Brazil, those small, flattened snails in the **Charopidae** (Figure 62) eat bryophytes (Maciel-Silva & dos Santos 2011). Both ***Canalohypopterygium tamariscinum*** (syn. = ***Hypopterygium tamarisci***; Figure 63) and ***Lopidium concinnum*** (Figure 64) had evidence of leaf herbivory, mostly in the beginning of the rainy season (September to December). A species of snail in the **Charopidae** and a moth larva in the **Geometridae** were the culprits. Using an index of damage (ID) in 2007, 2008, Maciel-Silva and dos Santos found that ***C. tamariscinum*** had higher damage (68%, 35%) than ***L. concinnum*** (38%, 23%) in these two years (Figure 65). These rates were lower than those for

tracheophytes. They found no correlation with phenols, proteins, or the ratio between them (Figure 65).

Figure 62. **Charopidae** feeding on ***Lopidium concinnum*** from an Atlantic Forest, Brazil. Photo by Adaises Maciel-Silva and Nivea Dias dos Santos, with permission.

Figure 63. ***Canalohypopterygium tamariscinum***, a food source for **Charopidae**. Photo by Niels Klazenga, with permission.

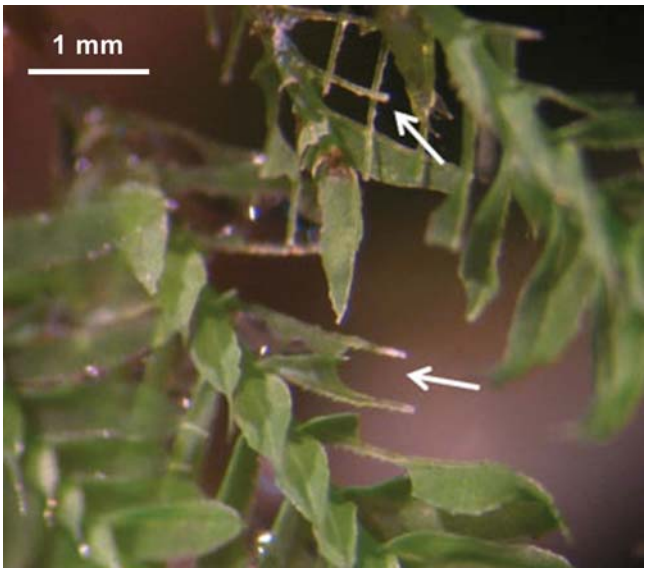

Figure 64. Evidence of **Charopidae** herbivory on ***Lopidium concinnum*** from an Atlantic Forest, Brazil. Photo by Adaises Maciel-Silva and Nivea Dias dos Santos, with permission.

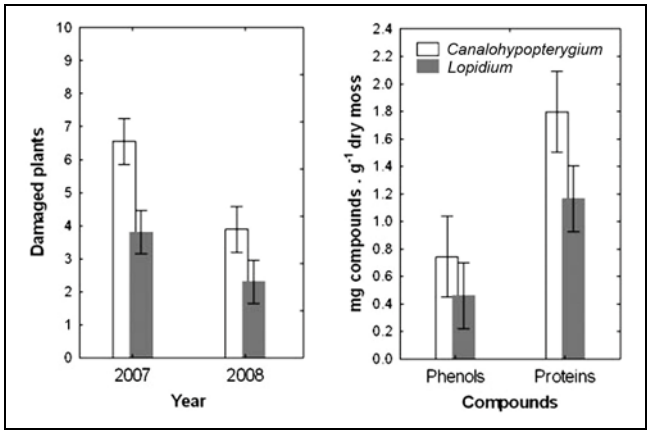

Figure 65. **Charopidae** and **Geometridae** damage to mosses in 10 colonies of plants. Image from Adaises Maciel-Silva and Nivea Dias dos Santos.

An Avoidance of Gametophores?

Davidson and Longton (1985, 1987; Davidson 1988, 1989) reported that several species of generalist slugs consumed bryophytes. In some cases, the **protonema** (threadlike stage that develops from moss spore) is readily consumed (Grime 1979). In Great Britain, capsules and protonemata of several mosses [***Brachythecium rutabulum*** (Figure 66), ***Mnium hornum*** (Figure 67-Figure 68), and ***Funaria hygrometrica*** (Figure 69)] were eaten preferentially to leafy gametophores by slug species in the genus ***Arion*** (Figure 70) (Davidson & Longton 1987; Davidson *et al*. 1990). Cambs (2012) found that the slug ***Limax maculatus*** (Figure 40) likewise would eat capsules, but the leafy parts seemed to serve only as an emergency food. It appears that some may even eat **calyptrae** (covering over capsule; Figure 71). **Ferulic acid**, present in shoots but absent in young capsules of ***Mnium hornum***, is a phenolic compound that is only released after severe hydrolysis. Its antibiotic role as an antifungal agent (Sarma & Singh 2003) and in antiherbivory (Seigler 1983; Smith 2011) may contribute to this preference for capsules, as discussed below. Davidson and coworkers found that older capsules with spores were less preferred than the green ones (Figure 72; Davidson & Longton 1987; Davidson *et al*. 1990).

Figure 66. Slug eating capsules of ***Brachythecium***. Note the number of setae that are missing capsules. Photo by Janice Glime.

Figure 67. Young, green capsules of ***Mnium hornum*** that are preferred by ***Arion* slugs**. Photo by Michael Lüth, with permission.

Figure 68. Mature capsules of ***Mnium hornum***. Photo by Janice Glime.

Figure 69. Capsules of ***Funaria hygrometrica*** – potential snail food. Photo by Michael Lüth, with permission.

Figure 70. ***Arion rufus*** on mosses in a woodland above Poole's Cavern, Buxton, UK. Photo by Brian Eversham, with permission.

Figure 71. Slug on moss calyptra, apparently finding something to eat. Photo courtesy of Sarah Lloyd..

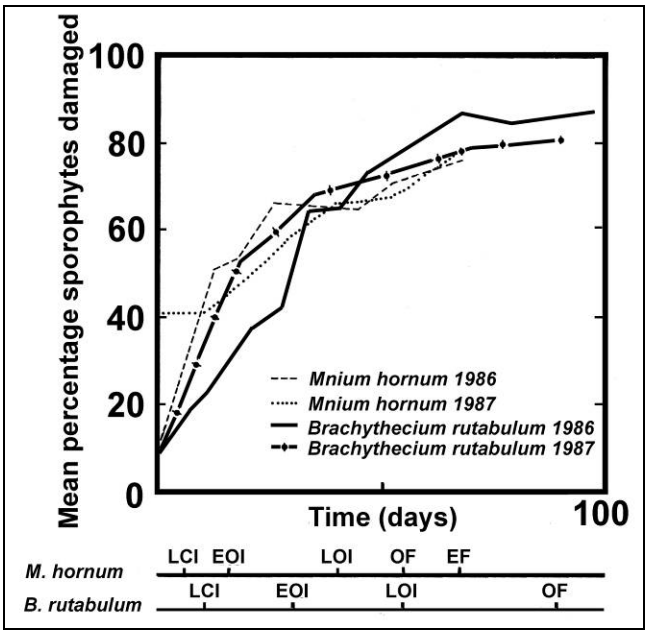

Figure 72. Relative damage by slugs (***Arion*** spp.) of sporophyte stages of two species of bryophytes. n=300-500 at day 0. **LCI** = late calyptra stage; **EOI** = early operculum intact; **LOI** = late operculum intact; **OF =** operculum fallen; **EF** = empty and fresh. Redrawn from Davidson *et al*. 1990.

Davidson (1989) found that slugs consumed only trivial amounts of ***Brachythecium rutabulum*** shoots (Figure 66). ***Mnium hornum*** (Figure 80) was also ignored, but after 5-7 days of starvation ***Arion rufus*** (10-15 cm long; Figure 73) and ***A. subfuscus*** (5-7 cm long; Figure 74) ate significant quantities of shoots of this species. The garden slug ***Arion hortensis*** (Figure 75) still ignored the moss even after 7 days of starvation.

Figure 73. ***Arion rufus*** on a bed of mosses. Photo by Jean Bisetti, with permission.

Figure 74. ***Arion subfuscus***, a slug known to consume ***Mnium hornum***. Photo by Gary Bernon, USDA APHIS at Bugwood.org, through public domain.

Figure 75. ***Arion hortensis*** *s.s.* at Bridge House, Swavesey, UK. Photo by Brian Eversham, with permission.

Given the choice of capsules or vegetative material, both ***Arion rufus*** (Figure 3, Figure 70, Figure 73) and ***A. subfuscus*** (Figure 76) preferred immature capsules (see Figure 77 with a slug on immature capsules of ***Leucolepis acanthoneuron***) of all three mosses, with ***Mnium hornum*** (Figure 80) being top choice (Davidson 1989). Setae were generally ignored, but ***A. subfuscus*** did occasionally eat ***M. hornum*** and ***Brachythecium rutabulum*** (Figure 66) setae. All three slugs also ate protonemata in the laboratory, and for ***B. rutabulum*** and ***Funaria hygrometrica*** (Figure 52) the protonemata were eaten just as much by ***A. rufus*** and ***A. subfuscus*** as were immature capsules. In fact, dry weight consumption exceeded that of immature capsules. Young shoots were also eaten, but less readily.

Figure 76. ***Arion subfuscus***, a slug that prefers immature capsules. Photo by Sanja 565658, through Creative Commons.

Figure 77. Slug browsing on immature capsule of the moss ***Leucolepis acanthoneuron***. Photo from UBC website, with permission.

Davidson and Longton (1987) suggested that ***Arion hortensis*** (Figure 75) was restricted by the physical structure of the capsule to consuming developing spores from broken capsules in ***Polytrichum commune*** (Figure 78); no spores were eaten from unbroken capsules. When approaching ***Mnium hornum*** (Figure 80), the slugs would withdraw their tentacles, then retreat, suggesting some sort of chemical deterrent; they behaved similarly in the presence of extracts from the capsule. It is likely that hydroxycinnamic and phenolic acids in this species and in ***Brachythecium rutabulum*** (Figure 66) provided this chemical protection against herbivory (Davidson *et al*. 1989). Stems of both species were apparently protected by ferulic and possibly m- and p-coumaric acids bound in the cell walls of the shoots (Davidson *et al*. 1989), explaining the preference of the slugs for capsules. On the other hand, when moss extracts were placed on communion wafers, the slugs ate them more readily, suggesting that chemistry alone was not the likely deterrent (Anonymous 1987; Davidson *et al*. 1990). Rather, some physical feature of the mosses, perhaps the cell wall, deterred these slugs.

Figure 78. ***Polytrichum commune*** capsules showing the persistent hairy calyptra and waxy capsule that is only eaten by snails when the capsule is broken. Photo by Michael Lüth, with permission.

Presence of moss cells of ***Brachythecium rutabulum*** (Figure 79) and ***Mnium hornum*** (Figure 80-Figure 81) in the feces of previously starved ***Arion*** suggest that the leafy mosses are not digested well (Davidson *et al*. 1990). On the other hand, all three species of slugs named above readily consumed ***Funaria hygrometrica*** (0.4-6.5 mg wet weight per slug; Figure 69) in overnight feeding trials. The importance of mosses as food may rest with the organisms living on the mosses – fungi, bacteria, protozoa, rotifers, *etc*., making indigestibility of the mosses inconsequential.

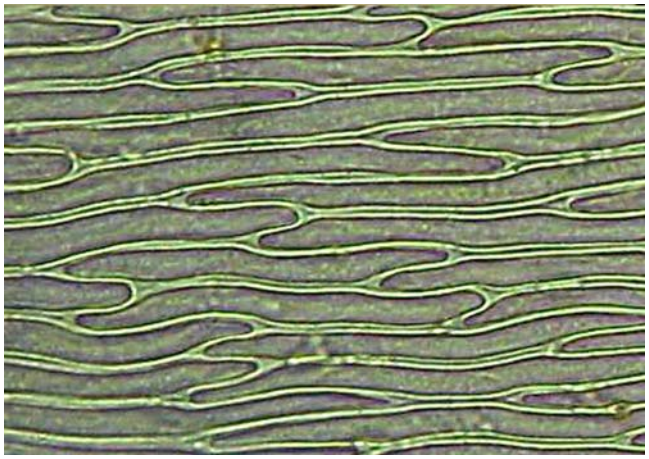

Figure 79. ***Brachythecium rutabulum*** cells as they might be seen in feces. Photo by Tom Thekathyil, with permission.

Mostly indirect evidence suggests that slugs and snails graze capsules of ***Buxbaumia viridis*** (Figure 84) (Gordon Rothero, Birds feeding on moss capsules, Bryonet-l, 10 April 2003; Figure 84). Michael Lüth (Bryonet 23 September 2017) observed and photographed a slug grazing on the capsule of ***Buxbaumia viridis*** (Figure 83). Dave Kofranek reports tasting it – to him it tastes like cucumbers (Bryonet 24 September 2017). Infante Sánchez and Heras Pérez (2015) exlored the herbivory on capsules of ***Buxbaumia viridis*** (Figure 84). They found three types of damage on the sporophytes. In one type the seta and lower part of the capsule remain. For this type, they actually observed slugs feeding on the capsules; the same kind of slug was also feeding on young green capsules of ***Herzogiella seligeri*** (Figure 85). In a second type, the entire capsule is gone, but the seta remains. This could have been slugs as well, but they were unable to observe them and considered that ants or birds might also feed on them. The capsules are grazed in spring before they mature, thus likely being unable to accomplish a successful dispersal. The third type was destruction by a fungus, causing abortion of the capsule development.

Figure 80. ***Mnium hornum*** shoots – a species that was ignored in experiments until the slugs were starved. Photo by Janice Glime.

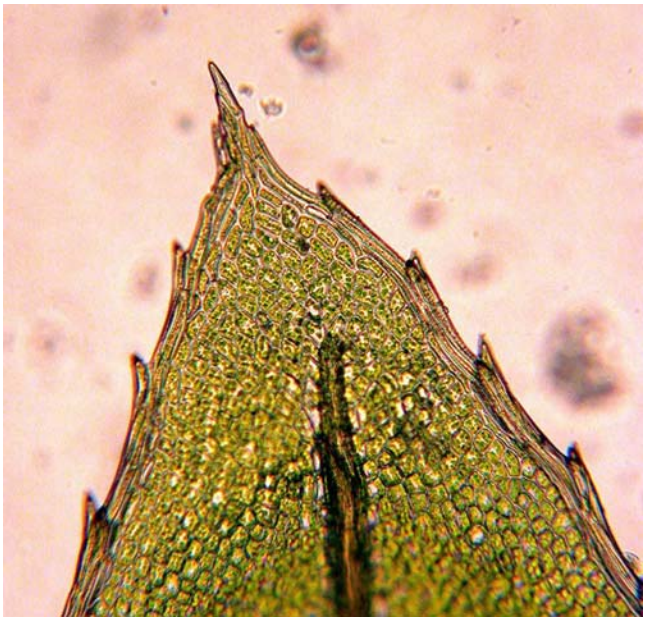

Figure 81. ***Mnium hornum*** leaf tip cells, what one might see in feces. Photo by Bob Klips, with permission.

It is perhaps not surprising that snails eat the capsules of ***Splachnum*** (Figure 82). This genus has odors that attract flies, so they may serve as attractants to gastropods as well. However, no studies have attempted to test this hypothesis with snails.

Figure 82. Snail on setae of ***Splachnum*** capsules in Alaska, eating capsules. Photo courtesy of Blanka Shaw.

Figure 83. ***Buxbaumia viridis*** with slug eating capsule. Photo by Michael Lüth, with permission.

Figure 84. ***Buxbaumia viridis*** capsules. Note that the leafy part belongs to another species of moss. Photo by Adolf Ceska, with permission.

Figure 85. ***Herzogiella seligeri*** with capsules, a species in which young capsules are eaten by slugs. Photo by Hermann Schachner, through Creative Commons.

Guy Brassard reported to me that Stéphane Leclerc has taken a picture of a slug in Quebec, Canada, eating a ***Buxbaumia aphylla*** (Figure 86-Figure 88) capsule!

Figure 86. ***Buxbaumia aphylla*** that are immature and have not been eaten. Photo by Štěpán Koval, with permission.

Stark (1860) relayed a story of the ill fate of collected specimens of ***Buxbaumia aphylla*** (bug-on-a-stick moss; Figure 87) on their journey from Scotland to England. A slug had inadvertently been included in the package and it managed to destroy their prized specimens. On the other hand, ***B. aphylla*** can fool you. After repeated observations with my graduate student, Chang-Liang Liao, we have discovered in the field that what appeared to me to be grazing on capsules of ***Buxbaumia aphylla*** is really only the splitting of the capsule top as it dries (Figure 87), and that this occurs on nearly every capsule.

Figure 87. ***Buxbaumia aphylla*** showing exposed green spores in the capsule that has split open. Photo by Janice Glime.

Figure 88. ***Buxbaumia aphylla*** that may have been damaged by a herbivore. Photo by Janice Glime.

Slugs also eat hornworts (**Anthocerotophyta**; Figure 89). Bisang (1996) reported that they especially eat the green sporophytes.

Figure 89. ***Phaeoceros carolinianus***, a hornwort with mostly green sporophytes, a food source for slugs. Photo by Michael Lüth, with permission.

Digestibility

So what did the slugs derive from the consumed mosses? When they consume preferred foods such as lettuce leaf or carrot root, the resulting feces contain macerated, partially pigmented tissue (Davidson 1989). When they consumed bryophytes, on the other hand, large pieces of leaf, whole leaves, and even stem pieces remained intact. Most cells still contained green chloroplasts. Evidently the moss did little more than fill the gut. Even the preferred capsules were poorly digested, with capsule wall fragments, opercula, and peristome teeth remaining. Mature spores seemed unharmed, but immature spores seemed to have experienced some digestion, appearing broken, colorless, and shrivelled. Likewise, the protonemata seemed to be digestible, resembling the lettuce and carrots in being macerated and colorless or brown.

Caution must be used in conducting laboratory experiments with food choices. Jennings and Barkham (1975) found that bryophytes all gave low palatability scores when six species of slugs, including the three in the Davidson (1989) study, had a choice of foods. The wider range of choices in the field may permit them to avoid the less palatable bryophytes.

Role in Bryophyte Competition with Lichens

Rosso and McCune (2003) found that molluscs on shrubs in the Pacific Northwest, USA, exhibited significant herbivore activity on the lichens. Bryophytes, on the other hand, had little change in cover between stems in exclusions and those available for herbivory. It appears that the mollusc herbivory on lichens (Boch *et al*. 2011) may benefit the bryophytes by contributing to the successful competition of the bryophytes over the lichens in the understory of these forests.

Palatable Gametophytes

Des Callaghan (Bryonet 10 June 2011) reports slugs feasting on the gametophytes of ***Hookeria lucens*** (Figure 90) near a stream. In only six days they completely removed all the plants by dining on them, leaving behind only a stump and a slime trail (Figure 91). This was a research station, so Callaghan needed to find a way to discourage the slugs. Suggestions from Bryonetters included sprinkling ground glass around the study area (Michael Richardson, Bryonet 10 June 2011); putting out cups of beer to attract and drown the slugs or putting curry powder or other hot substance around the mosses (Janice Glime, Bryonet 10 June 2011); copper rings that are effective in gardens and could be made with a coil of wire (David Bell, Bryonet 10 June 2011).

Figure 90. ***Hookeria lucens*** in healthy condition. Photo by Des Callaghan, with permission.

Figure 91. Temperature/humidity data logger with ***Hookeria lucens*** eaten by slugs. Photo by Des Callaghan, with permission.

Annie Martin (Bryonet 11 June 2011) is a professional gardener and described her experience in trying to eliminate slugs. She suggested putting salt on the head (if put on the tail the slug continues to live and eat). Her experience with beer is that it just keeps on attracting snails night after night, even though many of them drown, so it is an ineffective waste of money. Brown mulch seems to provide a favorable habitat, so she eliminated it, a technique that worked, but isn't relevant for discouraging snails on mossy rocks.

Aquatic Grazing

Grazing by gastropods (slugs and snails) can be so severe as to define distribution of a bryophyte species. Lohammar (1954) found that in northern Europe ***Fissidens fontanus*** (Figure 92) was absent in lakes where ***Fontinalis antipyretica*** (Figure 93) was also absent. Gerson (1982) suggested that scarcity of ***Fissidens*** in some places is due to snail grazing. In the presence of ***Fontinalis***, this smaller moss lives among the ***Fontinalis*** fronds where it is presumably protected from snail grazing by the inedible forest of ***Fontinalis*** surrounding it and the density of the ***Fontinalis*** stems.

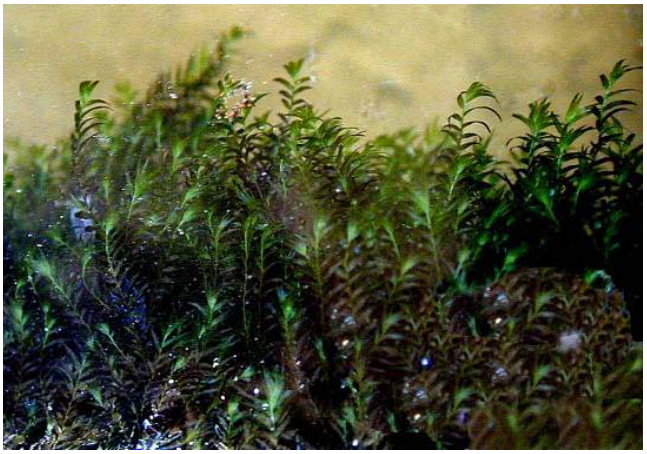

Figure 92. ***Fissidens fontanus***, a moss that seems to be vulnerable to snail grazing except where it is protected by ***Fontinalis*** species. Photo by Michael Lüth, modified by Janice Glime, with permission.

Figure 93. ***Fontinalis antipyretica***, a moss that apparently protects the smaller ***Fissidens*** from grazing by snails. Photo by Bernd Haynold, through Wikimedia Commons.

It may be that in the aquatic habitat the snail effect on some bryophytes is much greater than in the terrestrial habitat. But it is not necessarily all bad. Steinman (1994) opined that snail grazing could account for the apparent unresponsiveness of epiphytes following phosphorus enrichment in a woodland stream in Tennessee, USA, where bryophytes were prominent. And some bryophytes seem prepared to fight back. The thallose liverwort ***Ricciocarpos natans*** (Figure 94) exhibits molluscicidal properties that are active against the snail carrier of **schistosomiasis** (Wurzel *et al*. 1990).

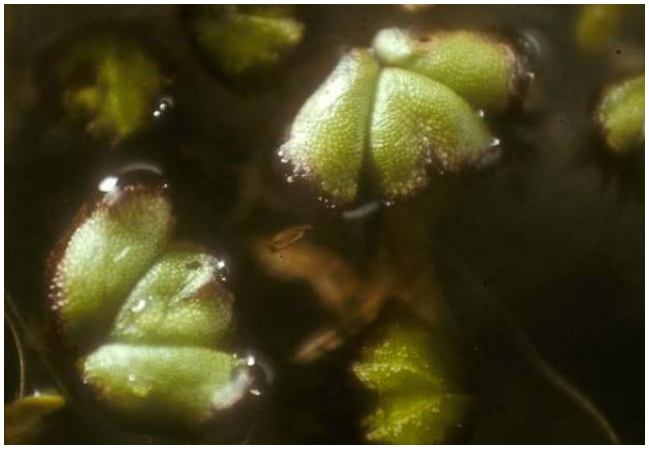

Figure 94. ***Ricciocarpos natans***, a species with molluscicidal properties, floating on the water surface. Photo by Janice Glime.

Bryophyte Antifeedants

Based on the foregoing discussion, it appears that at least some bryophytes are able to discourage browsing by slugs (Frahm & Kirchhoff 2002). Alcohol extracts of the moss ***Neckera crispa*** (Figure 95) and leafy liverwort ***Porella obtusata*** (Figure 96) have antifeedant activity against the slug ***Arion lusitanicus*** (Figure 97). Extracts of 0.5% dry weight of the moss had low activity, whereas

those from the liverwort exhibited moderate activity at only 0.05%. At 0.25% the antifeedant activity of ***Porella obtusata*** was complete. It is likely that this activity is not specific for slugs and may discourage insects, bacteria, and fungi as well.

Figure 95. ***Neckera crispa***, a moss that has antifeedant activity against the slug ***Arion lusitanicus***. Photo by Michael Lüth, with permission.

Figure 96. ***Porella obtusata***. Photo by Jan-Peter Frahm, with permission.

Figure 97. ***Arion lusitanicus***, a slug that traverses mosses, but finds ***Neckera crispa*** and ***Porella obtusata*** unpalatable. Photo by Mogens Engelund, through Wikipedia Commons.

On the other hand, ***Arion lusitanicus*** (Figure 97), also known as the murder slug, easily eats the thallose liverwort ***Marchantia polymorpha*** (Figure 98) (Nils Cronberg, Bryonet 7 April 2016). Cronberg has observed this species feeding on ***Marchantia*** and has noticed that as the slug had invaded the wetland, ***Marchantia polymorpha*** had disappeared in parallel with the invasion.

Figure 98. ***Marchantia polymorpha*** showing a nibbled thallus on the upper left, about 1/3 down and 1/3 over from the corner. It also has a tear that is not likely the result of herbivory. Photo by James K. Lindsey, with permission.

Dispersal Agents

It appears that slugs are not all bad in the bryophyte world and may instead be a necessary vector for some propaguliferous taxa (Stolzenburg 1995). Slugs and snails (Figure 99) leave a trail of mucous as they go, and as you well know if you have handled these molluscs, this secretion can be sticky. It is therefore no surprise that these animals have dispersal abilities.

Figure 99. Snails such as this one traversing epiphytic mosses in Japan may be effective dispersal agents. Photo by Janice Glime.

Slugs are able to disperse the brood branches of ***Dicranum flagellare*** (Figure 100) (Kimmerer & Young 1995). These tiny branches become entrapped in the secretions and are deposited in the ensuing slime trail. Kimmerer and Young found that these can be transported at least 23 cm from the colony, although the mean distance in their study was only 3.7 cm.

Figure 100. ***Dicranum flagellare*** showing the tight flagellate branches that can be dispersed by **slugs**. Photo by Janice Glime.

And it appears that the secretion increases the ability of the propagule to adhere to its substrate without affecting the germination rate. In fact, experiments by Davidson (1989) suggest that passage of spores through the slug's digestive system may enhance germination success. All plates containing mature spores from slug (***Arion*** spp.; Figure 97) fecal pellets produced shoots, whereas only 80% of the plates with uneaten mature ***Mnium hornum*** (Figure 67-Figure 68) spores and 70% of those with uneaten ***Brachythecium rutabulum*** (Figure 101) spores produced shoots.

Figure 101. ***Brachythecium rutabulum***, for which the spores germinate better if they have passed through the gut of a slug (***Arion***). Photo by Michael Lüth, with permission.

For those snails and slugs that nibble on spores, one might assume that not all spores end up inside them. Unless they have perfect aim with that huge foot, their somewhat clumsy feeding method is undoubtedly going to render some spores as passengers in the mucous on the foot. Sooner or later, these will be deposited in a new location.

The ability of snails and slugs to glide across bryophytes and to climb setae to capsules suggests that these animals may be important as dispersal agents. But how widespread are herbivory and dispersal among bryophytes that temporarily host these slow-moving animals?

Although we know that bryophyte spores reach the mollusc gut, experiments are needed to see if spores expelled in feces are able to colonize successfully. Davidson (1989) found that ***Brachythecium rutabulum*** (Figure 101) and ***Mnium hornum*** (Figure 80) spores eaten by ***Arion*** species actually germinated better than controls.

Manfred Türke sent me images of mosses in the feces of the slug ***Arion vulgaris*** (Figure 102). I was amazed at the size of the fragment of moss in the feces (Figure 103-Figure 104). This is a potential means for dispersal, but the various species of bryophytes must be tested for viability. Digestive enzymes and extreme *p*H could damage the moss cells. On the other hand, the pathogenic fungi ***Phytophora*** spp. (Figure 105) survive as both oospores and filaments and are viable after passing through the digestive system of this slug species (Telfer *et al*. 2015). This was demonstrated by culturing the feces on agar.

Figure 102. ***Arion vulgaris***, a slug that eats mosses, potentially dispersing them. Photo by Dilian Georgiev through Creative Commons.

Figure 103. ***Arion vulgaris*** feces with bryophytes and other material in it. Photo courtesy of Manfred Türke.

Figure 104. ***Arion vulgaris*** bryophyte from slug feces. Photo courtesy of Manfred Türke.

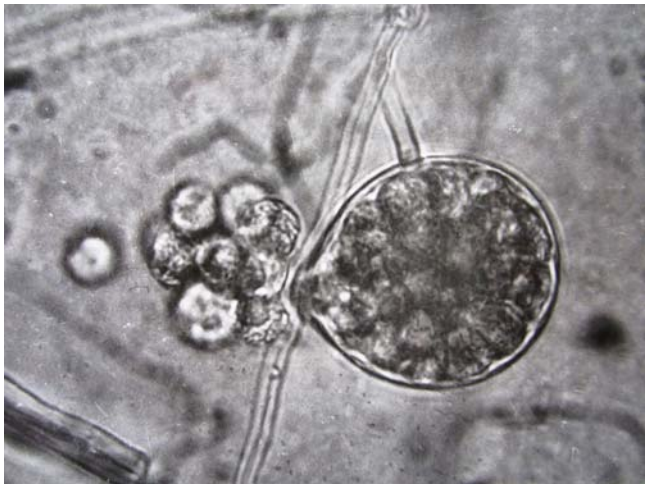

Figure 105. ***Phytophthora parasitica*** zoosporangia, a genus that survives passage through the gut of ***Arion vulgaris***. Photo by Tashkoskip, through Creative Commons.

To provide additional information on the potential dispersal ability of slug feces, Boch *et al*. (2013) fed capsules of four bryophyte species [***Bryum pallescens*** (Figure 106), ***Funaria hygrometrica*** (Figure 69), ***Leptobryum pyriforme*** (Figure 107), ***Pellia endiviifolia*** (Figure 108)] to three slug species [***Arion vulgaris*** (Figure 102), ***A. rufus***; Figure 3, Figure 70, Figure 73), ***Limax cinereoniger*** (Figure 109)]. Among the 117 bryophyte samples, 51.3 % of the spore cultures had germination following gut passage.

Figure 106. ***Bryum pallescens*** with capsules. Spores of this species pass through the guts of several slugs and retain their viability. Photo by David T. Holyoak, with permission.

Figure 107. ***Leptobryum pyriforme*** with capsules. Spores are able to pass through the guts of at least some slugs and remain viable. Photo by Michael Lüth, with permission.

Figure 108. ***Pellia endiviifolia*** with sporophytes. The spores of this species are able to pass through the gut of several slug species and remain viable. Photo by Janice Glime.

Figure 109. ***Limax cinereoniger*** on a mat of moss. Photo by Michal Maňas through Creative Commons.

Boch *et al*. (2013) found that germination rates did not differ among the bryophyte species, but the species of slug

had strong effects. Among these three slugs, ***Limax cinereoniger*** (Figure 109) ate the lowest percentage of the bryophytes provided, and even correcting for that, they had the lowest percentage of feces samples (12.9%) producing protonemata. On the other hand, 76% of those of ***Arion vulgaris*** (Figure 102) and 74% of those of ***Arion rufus*** (Figure 3, Figure 70, Figure 73) produced protonemata (Figure 110).

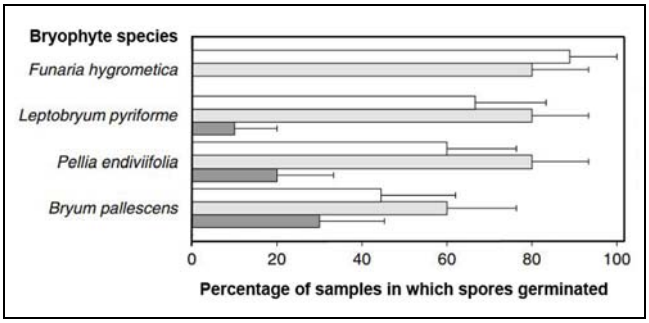

Figure 110. Comparison of spore germination from bryophytes cultured from the feces of three species of slugs. White bars = ***Arion rufus***; light grey bar = ***Arion vulgaris***, dark grey bar = ***Limax cinereoniger***. Redrawn from Boch *et al*. (2013).

Türke *et al*. (2013) provide evidence that slugs do indeed disperse fragments of mosses by consuming spores and fragments. For tracheophyte seeds, they suggested an average of 5 m dispersal distance, exceeding the typical less than 1 m in dispersal by ants. In some slugs, the seeds are destroyed in the digestive tract, but in other cases they remain viable propagules.

Boch *et al*. (2015) discussed several ways that slugs benefit bryophytes. Their herbivory on tracheophytes (lignified vascular plants) permits more light to reach the low-growing bryophytes. But they also crawl across bryophytes and some eat the bryophytes. This puts them in the position to disperse spores, fragments, and other propagules.

Nevertheless, documentation of the effect of the slugs on the bryophyte community is meager. Boch and coworkers (2015) designed a factorial common garden experiment to determine some of the effects of slugs on the bryophyte vegetation. They collected sporophytes of 11 native and 1 invasive bryophyte species [***Barbula convoluta*** (Figure 111), ***Brachythecium rutabulum*** (Figure 101), ***Brachythecium velutinum*** (Figure 112), ***Bryum*** sp. (Figure 106), ***Campylopus introflexus*** (Figure 113), ***Ceratodon purpureus*** (Figure 114), ***Funaria hygrometrica*** (Figure 69), ***Leptobryum pyriforme*** (Figure 115), ***Marchantia polymorpha*** (Figure 98), ***Phascum cuspidatum*** (Figure 116), ***Plagiomnium affine*** agg. (Figure 117), ***Pohlia*** sp. (Figure 118)], representing 8 families. They used three enclosure treatments: slugs previously fed with bryophyte sporophytes, slugs that had not been fed sporophytes, no slugs. The researchers demonstrated that bryophyte **cover** increased in 21 days from 1.4% to 3.9% in plots where slugs had been fed, an increase that was 2.8 times higher than in the other two treatments. After eight months, the **species richness** was 2.6X higher (5.8 vs 2.2) than in the other treatments. The researchers concluded that the slugs contributed to increasing bryophyte cover and diversity by reducing the dominance of tracheophytes. The early increase in cover in the enclosures with slugs fed sporophytes suggests that they also accomplish dispersal.

Figure 111. ***Barbula convoluta*** with capsules. Photo by Kristian Peters, with permission.

Figure 112. ***Brachythecium velutinum*** with unopened capsules. Photo by Michael Lüth, with permission.

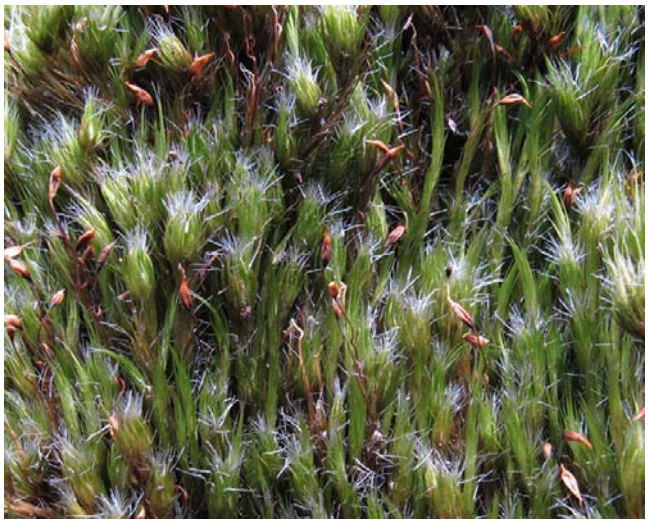

Figure 113. ***Campylopus introflexus*** with capsules. Photo by Michael Lüth, with permission.

Figure 114. ***Ceratodon purpureus*** with young capsules, showing the normal proliferation. Photo by Michael Lüth, with permission.

Figure 115. ***Leptobryum pyriforme*** with numerous immature capsules. Photo by Michael Lüth, with permission.

Figure 116. ***Phascum cuspidatum*** with unopened capsules. Photo by Michael Lüth, with permission.

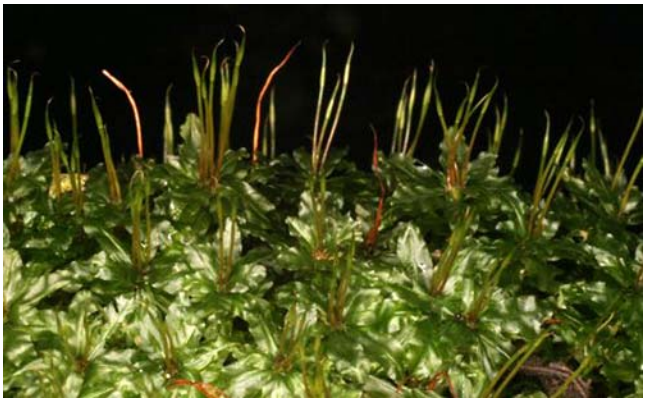

Figure 117. ***Plagiomnium affine*** with developing capsules. Photo by Jan-Peter Frahm, with permission.

Figure 118. ***Pohlia nutans*** with immature capsules. Photo by Michael Lüth, with permission.

When the question of bryophyte dispersal by slugs arose on Bryonet, Scott Redhead (Bryonet 26 August 2016) suggested that this might even occur in the **Splachnaceae**. To that suggestion, Michael Lüth posted an image of ***Tetraplodon mnioides*** (Figure 119) showing one uneaten capsule and one that had been removed by an animal, possibly a slug, documenting his own observations of capsule herbivory. Christian Schröck (Bryonet 26 August 2016) likewise observed grazed capsules in ***Voitia*** and ***Tetraplodon***. However, we need observations of feeding to determine the identity of the herbivores.

Figure 119. ***Tetraplodon mnioides*** with one capsule eaten by an unidentified herbivore. Photo by Michael Lüth, with permission.

Lüth (2010) suggested that the pre-dispersal stage of the capsules on **Splachnaceae** are likely to attract herbivores that differ from the flies that spread the spores. At this earlier stage, the capsules have a different odor from that during the dispersal stage. This odor lasts for only a short time and is therefore often missed by field biologists. On Bryonet (26 August 2016), Lüth explained that ***Splachnum ampullaceum*** smells like *Vaccinium oxycoccos* and occurs in the same habitats, often blending with these cranberries. And ***Tetraplodon mnioides*** (Figure 119) smells like ***Vaccinium myrtillus***. Although not all evolutionary successes are linked to adaptation, it makes one wonder if these early odors are adaptive to facilitate a longer dispersal and subsequent deposition in dung, although one might assume that would require a larger mammal, not a slug.

Figure 120. ***Splachnum ampullaceum*** sporophytes with a cranberry of similar color to the right. Photo by Michael Lüth, with permission.

I think most people would consider dispersal by snails and slugs to be distance-limited. But perhaps, with the help of birds, this is not so limited. Kawakami *et al*. (2003) demonstrated that the Japanese White-eyes (***Zosterops japonicus***; Figure 121) and the Brown-eared Bulbuls (***Hypsipetes amaurotis***; Figure 122) are birds that eat snails. In fact, five species of snails are able to remain in their shells and appear in the feces. If these snails had eaten moss spores, those spores might be transported a considerable distance, yet be viable in the gut of the snail. It is probably a rare event. Lots of questions remain in this relationship, but the scenario brings up interesting hypotheses.

Malone (1965) discovered another possibility, exemplified by the Killdeer (***Charadrius vociferus***; Figure 123). Malone found two species of freshwater snails attached to the feet of the Killdeer. These were able to remain attached and viable long enough to effect dispersal. The snail ***Galba obrussa*** was able to survive 14 hours on Killdeer feet out of water. But the likelihood that an aquatic snail is carrying bryophyte spores is small due the rarity of capsules. Nevertheless, if a wetland snail has similar behavior, it has a better chance of having consumed spores from wetland mosses.

Figure 121. ***Zosterops japonicus***, a bird that passes intact snails through the gut. Photo by Dick Daniels, through Creative Commons.

Figure 122. ***Hypsipetes amaurotis***, a bird that passes intact snails through the gut. Photo by Nubobo, through Creative Commons.

Figure 123. ***Charadrius vociferus***, a species that disperses snails on its feet. Photo by Andrew C, through Creative Commons.

One additional factor determining the suitability of a slug for spore (or fragment) dispersal is the habitat where feces are likely to be deposited. Researchers have made the first steps in understanding the role of slugs in bryophyte dispersal, but much remains to be explored.

Bryophytes as Home

Because of their small movement space, bryophytes can serve as safe sites for smaller snails. Birds can be significant consumers of snails, particularly during migration (Shachak & Steinberger 1980), and bryophytes can make the snails less conspicuous, if not hiding them completely. In terrestrial habitats, arachnids such as spiders and daddy-long-legs (**Opiliones**) are also predators on snails (Nyffeler & Symondson 2001). While some spiders can probably navigate the spaces within the moss mat, it seems unlikely that most mature daddy-long-legs could manage without getting caught. In addition to the arachnids, carabid beetles prey on terrestrial gastropods (Symondson 2004). Some of these beetles use a pump mechanism to extract the gastropod remains from its shell.

Even snails are predators on slugs. The shell of the snail makes navigation among the bryophyte branches more difficult, potentially making the bryophytes a refuge for the smaller of vulnerable slugs.

In a study of bryophyte inhabitants in the Bükk Mountains of Hungary, Varga (2008) found the tiny gastropods ***Punctum pygmaeum*** (Figure 124) and ***Pupilla muscorum*** (Figure 154) among the terrestrial mosses ***Plagiobryum zieri*** (Figure 125), ***Hypnum cupressiforme*** (Figure 126), and ***Tortella tortuosa*** (Figure 127). Standen (1898) found ***Punctum pygmaeum*** from moss shakings. From my own observations, it appears that snails and slugs are common on and even in bryophyte clumps, but finding documentation on the use of bryophytes by these small species evades even the aggressive Google search.

Figure 124. The tiny ***Punctum pygmaeum*** on ***Ena montanum***, both on a moss. Photo by Stefan Haller, with permission.

Figure 125. ***Plagiobryum zieri***, a moss that supports the gastropods ***Punctum pygmaeum*** and ***Pupilla muscorum***. Photo by Michael Lüth, with permission.

Figure 126. Slug on ***Hypnum***. Photo by Janice Glime.

Figure 127. ***Tortella tortuosa*** in Europe. Photo by Michael Lüth, with permission.

The European snails ***Azeca goodalli*** (Figure 128), ***Euconulus fulvus*** (Figure 129), ***Columella edentula*** (Figure 130), ***Discus*** (subgen ***Goniodiscus***) ***rotundatus*** (Figure 131), ***Lauria cylindracea*** (Figure 132-Figure 133, ***Vertigo pusilla*** (Figure 134), and ***Vitrina pellucida*** (Figure

135) live among mosses, among other substrata (Cloudsley-Thompson & Sankey 1961). ***Carychium tridentatum*** (Figure 136), ***Discus rotundatus***, ***Cepaea hortensis*** (Figure 137), ***Oxychilus navarricus*** (formerly *O. helveticus*; Figure 138), and several rare species of ***Aegopinella*** (formerly in *Retinella*) [***A. pura*** (Figure 139), ***A. nitidula*** (Figure 140-Figure 141)] are known under mossy brick rubble (Verdcourt 1954). ***Clausilia bidentata*** (10-11 mm; Figure 142) is also rare, but can be found under moss. Standen (1898) reported on ***Clausilia rugosa*** (Figure 143) swarming on mossy walls in the UK and feeding on mosses and lichens. Standen (1898) found the snail ***Acme lineata*** on a patch of the thallose liverwort ***Marchantia*** sp. (Figure 98).

Figure 128. ***Azeca goodalli*** shell. Photo by Francisco Welter Schultes, through Creative Commons.

Figure 129. ***Euconulus fulvus***. Photo by Brian Eversham, with permission.

Figure 130. ***Columella edentula***. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 131. ***Discus rotundatus*** on moss. Photo by Christophe Quintin, through Creative Commons.

Figure 132. ***Lauria cylindracea*** on bark. Photo by Christophe Quintin, through Creative Commons.

Figure 133. ***Lauria cylindracea***, whose small size can be seen in comparison to this seed. Photo by Christophe Quintin, through Creative Commons.

Figure 134. ***Vertigo pusilla*** on bark. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 135. ***Vetrina pellucida*** on bark. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 136. ***Carychium tridentatum*** on moss-covered branch. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 137. ***Cepaea hortensis*** venturing into one of the **Pottiaceae** mosses. Photo by Stefan Haller, with permission.

Figure 138. ***Oxychilus navarricus*** on the moss ***Rhytidiadelphus squarrosus***. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 139. ***Aegopinella pura*** on leaf litter. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 140. ***Aegopinella nitidula*** on moss. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 141. ***Aegopinella nitidula*** showing shell coils. Photo by Brian Eversham, with permission.

Figure 142. ***Clausilia bidentata*** on moss. Photo by Christophe Quintin, through Creative Commons.

Figure 143. ***Clausilia rugosa*** on bark, a species that eats mosses and lichens. Photo by O. Gargominy, through Creative Commons.

Eucobresia diaphana (Figure 144) lives in humid, cool places on mountains and in forests of Europe, where it is likely to encounter mosses, as seen in Figure 144 (Welter Schultes 2012b), but other than this picture, I can't verify what use it might make of them.

Figure 144. ***Eucobresia diaphana*** on a species of the moss ***Tortula***. Photo by Stefan Haller, with permission.

On the South Pacific Kermadec Islands, Iredale (1913) remarked that in dry weather one must look for the snails among the mosses, where they hide from the dryness. He commented that they are quite variable in choice of trees, with one bole producing a dozen or more while the next half dozen adjoining trees disclose none.

Not surprisingly, new species still lurk amid the bryophytes. Efford (1998) found a new species of the carnivorous New Zealand endemic genus ***Rhytida*** (Figure 145), and reported observations by others of ***R. patula*** and ***R. meesoni perampla*** crawling on mosses and tree trunks at night. These and other New Zealand snails often fall prey to introduced predators. ***Wainuia urnula*** (Figure 146), another night-active snail on mosses, tree trunks, and rocks, was readily eaten by possums, rats, and hedgehogs in captivity. Efford (2000) found that 82% of the 315 ***W. urnula*** snails examined had an unusual food in the feces and gut – terrestrial amphipods. Its relative, ***W. edwardi*** (Figure 147), did not consume amphipods, and no other gastropod is known to consume them. The adaptation for consuming amphipods appeared to be largely behavioral, although there were some differences in the teeth.

Figure 145. ***Rhytida otagoensis***, member of a carnivorous genus that has some moss-dwellers. Image by James Atkinson, with permission.

Figure 146. ***Wainuia urnula***, a tiny night-active New Zealand endemic snail that traverses mosses, as shown here. Photo by Andrew Spurgeon, with permission.

Figure 147. ***Wainuia edwardi***, member of a genus that lives among mosses. Photo by James W. Atkinson, with permission.

Epiphytic

Wiesenborn (2003) observed snails in the Riverside Mountains of California and found that the active snails preferred epiphytic mosses (Figure 148) and lichens compared to plant detritus and four sizes of rocks as habitat. They suggested that the epiphytes could provide these snails with food or moisture. Tree bark soon becomes a desert after the rain dries up, but mosses remain moist much longer, permitting the snails to be active longer and to search there for food where other small invertebrates likewise take refuge from desiccation.

Figure 148. ***Monachoides incarnatus*** on bark where it often encounters bryophytes. Photo by Stefan Haller, with permission.

Tropical islands, especially Hawaii, are particularly vulnerable to invasive species. With all the visitor traffic and import/export business, hitchhikers easily reach the islands. Snails are among these, and may be one of the causes of the apparent extinction of the bird called Po'ouli (***Melamprosops phaeosoma***; Figure 149) (Mountainspring *et al*. 1990). This native Hawaiian bird is especially adapted to feeding on land snails and insects on branches and under mosses, lichens, and bark. Its toes are large and are used for prying up moss and bark to acquire tree snails. The bill is stout, withstanding the force needed for manipulating the snails. Its demise is due largely to increased activity and habitat modification by feral pigs, avian disease, and possible gene pool impoverishment due to low numbers. But it also suffers competition for food by the introduced garlic snail (***Oxychilus alliarius***; Figure 150), a native of northwestern Europe (Welter Schultes 2012a) that emits a garlic odor when it is disturbed. This species is likewise a moss-dweller of mountain slope forests. It feeds on living and dead plant tissue, but it also consumes small snails and the eggs of other snails and slugs (Oxychilus 2011).

Figure 149. Po‘ouli (***Melamprosops phaeosoma***) on a mossy branch. Note the sturdy beak used to pry loose bark or crush snails found under bryophytes. Photo through Wikimedia Commons.

Figure 150. ***Oxychilus alliarius*** on moss on bark. Photo © Roy Anderson <habitas.org.uk>, with permission.

The slug ***Prophysaon vanattae*** (scarletback taildropper; Figure 151) is one of those slugs that seems to find a safe site under mosses on trees on Vancouver Island, Canada (Kristiina Ovaska, pers. comm. 30 June 2009). But it also hangs on epiphytic moss mats in the moist deciduous forest there and may even lay eggs there (Figure 152).

Figure 151. ***Prophysaon vanattae***, the scarletback taildropper, can be found hiding under mosses. Photo by Kristiina Ovaska, with permission.

Figure 152. ***Prophysaon vanattae*** with eggs on a moss. Photo by Kristiina Ovaska, with permission.

Pilsbry (1948) suggested that the pupillid snail ***Bothriopupa variolosa*** in eastern North America might prefer mossy rocks and trees.

Figure 153. ***Bothriopupa tenuidens***; ***B. variolosa*** seems to prefer mossy tree trunks and rocks. Image copyright Gary Rosenberg, www.DiscoverLife.

Calcareous Areas

Because of the need for calcium to make the shell, many snails are dependent on limestone habitats to obtain this important resource. Hence, this is a good place to look for snails on mosses growing there.

Pupilla muscorum (Figure 154) is named for its occurrence among mosses in Great Britain, although it also occurs under stones and in leaf litter (Ehrmann 1956). This tiny (3-4 mm high shell) moss snail often prefers calciferous ground, but others describe it as indifferent to limestone content (Nordsieck 2012a). These snails are **ovoviviparous**. The eggs can survive over winter inside the female's body and are laid in the favorable conditions of spring. At that point, it is not the eggs that must survive because the juveniles usually hatch during oviposition. ***Pupilla triplicata*** (Figure 155) is likewise a moss dweller in Hungary and elsewhere (Deli *et al*. 2002).

Figure 154. ***Pupilla muscorum***. Photo by Malcolm Storey, through Creative Commons.

Figure 155. ***Pupilla triplicata***, a European moss dweller. Photo by O. Gargominy, through Creative Commons.

Another tiny conical snail (2-3 mm) of calcareous areas is ***Acicula fusca*** (Figure 156) in moss on chalk cliffs at Ballycastle, and on chalk underlying basalt at Black Head, Antrim, UK (Anderson 1996). And ***Pomatias elegans*** (Figure 157) occurs on mosses in limestone areas in the Burren, County Clare, UK (Platts *et al*. 2003).

Figure 156. ***Acicula fusca***, a tiny snail that lives among mosses on chalk cliffs. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 157. ***Pomatias elegans*** at Cheddar, Somerset, UK. Photo by Roger S. Key, with permission.

Trochulus (formerly ***Trichia***) ***plebeia*** (Figure 158) occurs in wet mossy areas by springs in limestone areas (Gilbert *et al*. 2005). ***Trochulus villosus*** (Figure 159) lives in the German Alps and requires high moisture (Welter Schultes 2010), making bryophytes useful for maintaining that moisture. This strange genus of snails has hairs on its shell that help to hold it against wet surfaces (Gilbert *et al*. 2005). I don't have any indication that these hairs offer any particular help for living among bryophytes, but if they have any tactile properties, they could help keep it from getting stuck between branches by warning that the passage was getting too narrow.

Figure 158. ***Trochulus plebeia***, a hairy snail, at Sugley Wood, UK. Photo by Brian Eversham, with permission.

Figure 159. ***Trochulus villosus*** on mosses in Germany. Photo by Stefan Haller, with permission.

The European family **Clausiliidae**, known as door snails, derive their name from the "sliding door" that covers the opening of the shell (Wikipedia 2012a). This calcareous door is known as a **clausilium**, hence the family name. It permits the snail to retreat into its shell and seal it off against predators. ***Cochlodina laminata*** (Figure 160), the plaited door snail, lives "between mosses" as well as leaf litter, but may also be found climbing trees in deciduous forests and montane pine forests (Welter Schultes 2012b). ***Clausilia dubia*** (Figure 161) is a calciphilic inhabitant of humid, shady rocks and old walls, but also lives on tree trunks "full of moss." Michael Proctor (pers. comm. 23 April 2016) informed me that this species is very common on Carboniferous limestone in Yorkshire Dales, UK, in the bryophyte and lichen habitats. ***Macrogastra ventricosa*** (Figure 162), the ventricose door snail, lives in places with plentiful mosses on the forest floor or on tree trunks, mostly in the mountains (Welter Schultes 2012b). ***Macrogastra attenuata*** (Figure 163) lives between moss-covered rocks as well as on stones, rocks, and leaf litter in montane forests.

Figure 160. ***Cochlodina laminata*** on bark where it appears to be grazing mosses. Photo by Andrew Dunn, through Creative Commons.

Figure 161. ***Clausilia dubia*** with moss. Photo by O. Gargominy, through Creative Commons.

Figure 162. ***Macrogastra ventricosa*** on moss. Photo by J. C. Schou, Biopix, through Creative Commons.

Figure 163. ***Macrogastra attenuata***, a species of moss-covered rocks in montane forests of Europe. Photo by Niels Sloth, with permission.

Vertigo meramecensis (Meramac River snail), unlike a number of other members of the genus, is a strict calciphile (Nekola & Coles 2010). It is a species of special concern that lives in Iowa and Missouri, USA, and dwells in decomposed leaf litter of moss-covered ledges and shaded carbonate cliffs, among other places.

Bogs and Mires

True bogs are acid, poor fens are acid, intermediate fens have intermediate *p*H levels, and rich fens are basic. For a snail, that *p*H range is an important consideration in choice of habitat because of the need for calcium in forming a shell. Because of this relationship, most malacologists have considered ***Sphagnum*** (Figure 164) peatlands, heathlands, and pine forests as unsuitable habitats for snails and consequently have poor snail biodiversity (Karlin 1961; Kerney & Cameron 1979; Horsák & Hájek 2003).

In fact, Nekola (2010) found that highly and even moderately acidic sites had significantly ($P<0.000000005$) lower richness and abundance than did neutral and calcareous habitats. Nevertheless, the typical acid site supported 5-10 species.

But some snails actually thrive in the low *p*H of bogs and other acid habitats. One such snail is ***Vertigo malleata*** (Figure 165), an extreme **calcifuge**. The degree to which snails have been overlooked in these habitats is exemplified by finding this new species in 60 sites out of 100 acid sites investigated from Maine to Florida, USA (Coles & Nekola 2007). In the bogs it was found primarily in leaf litter on top of the ***Sphagnum*** (Figure 164). Nekola (Jeff Nekola, pers. comm. 16 April 2012) informed me that ***Vertigo malleata*** was virtually absent in the ***Sphagnum*** itself, occurring only where there was leaf litter on top of the ***Sphagnum***. It would be interesting to watch its behavior if it is placed amid the ***Sphagnum***. Is it avoiding ***Sphagnum***, or seeking food only found among the litter? In more northern locations, ***V. cristata*** (Figure 166) or ***V. perryi*** may be present in bogs, but again, they only occur in the leaf litter, not among the ***Sphagnum*** (Jeff Nekola, pers comm. 16 April 2012). ***Vertigo cristata*** is likewise common in pine and spruce forests, heaths, and ***Sphagnum*** peatlands (Nekola & Coles 2010).

Figure 164. ***Sphagnum*** blanket bog, a habitat that does not provide enough calcium for snails. Photo from Creative Commons.

Figure 165. ***Vertigo malleata*** from Lewis Ocean Bay, South Carolina, USA. This snail lives in ***Sphagnum*** peatlands, but avoids the ***Sphagnum***, living in patches of leaf litter on top of it. Photo by Jeff Nekola, with permission.

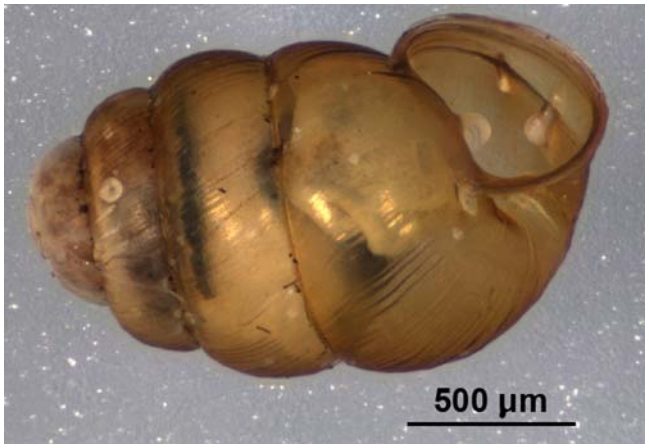

Figure 166. ***Vertigo cristata***, a species that lives on leaf litter, but not ***Sphagnum***, in bogs. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

It appears that other snails that live in bogs and poor fens likewise typically avoid the ***Sphagnum*** (Figure 164). Like ***Vertigo malleata*** (Figure 165), ***Gastrocopta tappaniana*** occurs in decomposing leaf litter of fens, pocosins, and ***Sphagnum*** bogs (Nekola & Coles 2010). Even ***Vertigo perryi***, a resident on the sides of ***Sphagnum*** hummocks, occurs on sedge leaf litter there. And ***Vertigo ventricosa*** (Figure 167) occurs in well-decomposed graminoid and broadleaf plant litter in the ***Sphagnum*** peatlands and poor fens.

Slugs have much less need for that important element – calcium (Ca). In boggy habitats, these gastropods would seem to have little choice but to travel across bryophytes (Stanisic 1996). ***Deroceras laeve*** (Figure 168) is among the slugs that traverse the complicated topography of bogs and mires. But their specific relationships to the bryophytes seems unknown. On the other hand, another member of the genus, ***Deroceras reticulatum*** (Figure 169), is a ubiquitous slug, but Anderson (2010) points out that raised and blanket peat or exposed ground above 300 m are the only habitats where it is not likely to be found. Hence, it appears that physiological differences are important in separating these slugs.

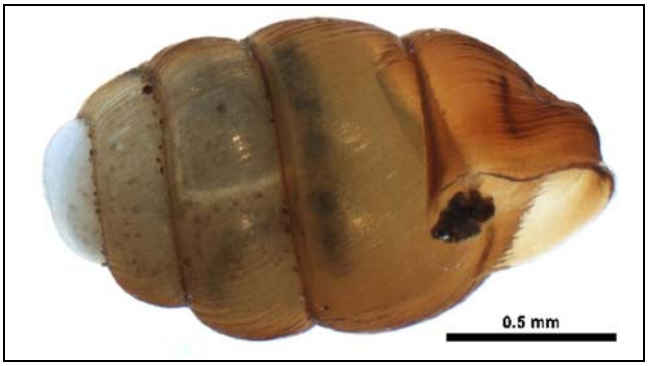

Figure 167. ***Vertigo ventricosa***, a species of litter in peatlands. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 168. ***Deroceras laeve*** (marsh slug) at Flitwick Moor, Bedfordshire, UK. Photo by Brian Eversham, with permission.

Figure 169. ***Deroceras reticulatum*** on a bed of mosses (not ***Sphagnum***). Photo © Roy Anderson <habitas.org.uk>, with permission.

Aquatic

In streams, it is likely that snails find mosses as a safe site from the current. Habdija *et al*. (2004) rarely found any gastropods on bryophytes at velocities of greater than

70 cm s^{-1}, whereas oligochaetes became more abundant at higher velocities. Flow rates are much slower within the moss mats, thus providing a haven for feeding where the current is unlikely to dislodge the snails and slugs. This also provides them protection from predators such as fish (mostly), ducks, shore birds, and amphibians (Pennak 1953).

Frost (1942) found a strong difference in gastropod inhabitants among bryophytes between an acid and an alkaline stream in her River Liffey survey in Ireland. In the limestone stream, she found 17 snails among the bryophytes, but she found none in the acid stream. Moss inhabitants in the limestone stream included ***Ancylus fluviatilis*** (Figure 170) and a species of ***Planorbis*** (Figure 171). She pointed out that these molluscs were only occasionally found among the mosses.

Figure 170. ***Ancylus fluviatilis*** showing its close adherence to the substrate. Photo by Mauro Mariani, through Wikimedia Commons.

Figure 171. ***Planorbarius corneus***. Photo © Roy Anderson <habitas.org.uk>, with permission.

Invasive species such as the carnivorous ***Euglandina rosea*** (Figure 172), a native of tropical North America, can have severe effects on native snail species elsewhere (Kinzie 1992). In Hawaii, this species has endangered the aquatic **endemic** (Hawaii only) lymnaeid snails due to its seek and capture behavior. The few surviving individuals are primarily restricted to streamside seeps or damp mosses and liverworts covering rocks near waterfalls.

Figure 172. ***Euglandina rosea***, an invasive carnivore. Photo through Wikimedia Commons.

Plant Protectors

Not all slugs and snails seem to share a love of bryophyte habitats. As already noted, some seem to avoid them. Heinjo During has shared with me a story that unravelled in the Netherlands, published by Bart van Tooren (1990). To quote van Tooren, an increasing number of *Linum* (flax) seedlings correlates with an increasing number of bryophytes and other plants. Presumably, the slugs that were eating the seedlings would not traverse the bryophytes to get to these vulnerable young plants. They experimented by comparing plots with >70% cover of bryophytes with those having <20% cover. Their results were complicated by superimposing treatments of added water and/or NPK nutrients. In the control plots (no additions), the survival of *Linum* (flax) seedlings was greatest in plots with low bryophyte cover. However, in all three treatments at Vrakelberg the survival was greatest in plots with >70% bryophyte cover, whereas at Laamhel the addition of water plus nutrients was the only treatment that resulted in a large shift to greater survival with high bryophyte cover.

Although van Tooren (1990) was unable to demonstrate significant effects of bryophytes in his 1990 study, he and his coworkers did find them on the same slope in the 1981 study (Keizer *et al*. 1985). Bryophytes under the growing conditions of that year significantly reduced mortality of the tracheophytes *Linum catharticum* and *Carlina vulgaris.* Apparently, bryophytes may serve as deterrents to slugs in some years when weather conditions might otherwise encourage herbivory, but provide little support for them in years when nutrients and/or water availability are different. Such interactions between species that change with the weather require further investigation.

Getting and Staying Connected

Snails require calcium for their shells (Hotopp 2002). Hence, acidic bogs and poor fens with acidic ***Sphagnum*** species are inadequate habitats for them (Peterka *et al*. 2021). Those that are able to find enough calcium to

survive there are further endangered by birds that are unable to find enough calcium for their eggshells, forcing those that are able to do so to seek out snails for food so they can fortify their calcium intake (Mänd *et al*. 2000).

It is therefore not surprising that snails are scarce in acidic bogs and are negatively related to the ***Sphagnum*** (Figure 173) species (Horsák & Hájek 2003; Peterka *et al*. 2021). But when Peterka *et al*. (2021) examined the relationship of snails to age of rich fens, they found no correlation, whereas there was a correlation with tracheophytes. Nevertheless, fen age had a significant effect of snail diversity, and particularly on two dominant snails. These two snails [***Euconulus alderi*** (Figure 174), ***Vertigo geyeri*** (Figure 175)] displayed significant ($P<0.05$) non-random affinity to older fens than would be expected by chance. Peterka and coworkers suggested that the lack of correlation of bryophytes with fen age was due to the ability of their spores to disperse (Frahm 2012; Sundberg 2013) and the ability to establish more quickly through fragments (Mälson and Rydin 2007; Wilkinson et al. 2017) than the seeds of flowering plants and conifers.

Figure 173. ***Sphagnum angustifolium***, a poor fen species that helps to create an acidic habitat that is detrimental to snails. Photo by Hermann Schachner, through Creative Commons.

Figure 174. ***Euconulus alderi***, a snail species for which abundance is significantly affected by rich fen age. Photo by Pekka Malinen, through Creative Commons.

Figure 175. ***Vertigo geyeri*** on moss, a snail species for which abundance is significantly affected by rich fen age. Photo by Roy Anderson, through Creative Commons.

Mussels (Bivalve Molluscs)

Mussels are not common bryophyte inhabitants, but can occasionally occur there in aquatic environs. Frost (1942) found ***Sphaerium corneum*** (Figure 176) and four species of ***Pisidium*** (Figure 177) among the mosses in the limestone stream in her River Liffey, UK, survey, but their typical niches were elsewhere in the stream.

Some bivalve molluscs and other organisms can actually turn the relationship around and provide a home for the bryophytes. Yes, some of these animals actually have mosses growing on them. Neumann and Vidrine (1978) found ***Fissidens fontanus*** (Figure 92) and ***Leptodictyum riparium*** (Figure 178) growing on freshwater mussel shells.

Figure 176. ***Sphaerium corneum*** on an aquatic plant. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 177. ***Pisidium amnicum***. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 178. ***Leptodictyum riparium***, a moss known to grow on freshwater mussels**.** Photo by Michael Lüth, with permission.

ECHINODERMATA

I refuse to create a chapter for this marine phylum, but one observation is interesting enough to note here. Claudio Delgadillo-Moya (pers. comm. 30 March 2016) reported to me that a student who is working on sea urchins has found moss tissue in the gut of one and leafy liverwort fragments in another! There is no bryophyte known to be marine, but some do tolerate sea spray and live near the water. Most likely one of these, no, two of these, fell into the water or washed in from a stream or river. Resourceful urchin!

Summary

Snails and slugs (gastropods) have often been observed on bryophytes. They are adapted to land with a calcified slime **epiphragm** to cover the shell opening and **respiratory pore** in the body. A **radula** of many teeth permits them to scrape their food. Reproduction is mostly by **simultaneous hermaphroditism**. This may be facilitated by a **love dart** that facilitates movement of sperm cells to the sperm pouch by injecting hormones. Larvae develop within the egg in most so that the gastropods are typically **oviparous**. A few are known to deposit eggs in mosses.

The white desert snail, ***Eremarionta immaculata***, is common on bryophytes and seems to prefer them as a habitat. The copse snail, ***Arianta arbustorum*** is a night-active inhabitant. More quantitative studies have shown that some slugs and snails prefer bryophytes. More active snails might be found at night, whereas tiny snails might take refuge in the bryophytes during the day.

Adaptations include "jumping" (***Hemphillia***), small size, conical snail, hibernation/estimation, and no shell (slugs). Snails might use them as a safe site to escape spiders, daddy-long-legs, and beetles, whereas other predators may lurk among the bryophytes. In streams, bryophytes may protect them from fish, ducks, shore birds, and amphibians.

Bryophyte leafy plants and capsules can serve as food for snails and slugs, but some of these molluscs seem to avoid leaves with **awns**. Nutritional quality may be poor in some, and some have antiherbivore compounds that interfere with development, digestion, and palatability. In some cases the moss structure is such that the snails actually lose weight, whereas moss paste fosters a weight gain. But the gastropods may gain their nutrition from adhering algae and Cyanobacteria. In some cases protonemata and green capsules are preferred to leafy plants. ***Fissidens fontanus*** can be virtually eliminated by snails in lakes where there is no ***Fontinalis antipyretica*** to protect it. And some leafy mosses are palatable.

But some slugs won't eat the moss even when they have been starved for 7 days. They have even been observed retreating from a moss. Various phenolic compounds seem to be involved in their reluctance to eat some bryophyte species. ***Ricciocarpos natans*** has molluscicidal properties that are effective against snail vectors of schistosomiasis.

The moss may not offer any nutrition. Intact cells of leaves, capsules, and mature spores pass through the gut, and it seems that only young spores and protonemata become pale during their trip through the digestive system.

Because of their mucous trail, slugs and snails are able to disperse some bryophytes, including brood branches, spores, and leaf fragments. And it appears that the mucous helps the dispersed fragment to adhere to its new substrate. Spores can even pass through the digestive system and survive, thus adding another form of dispersal.

Gastropods can be common among epiphytes, avoid acid habitats, and abound in limestone habitats. The acidity produced by poor fen species can exclude them because of inability to produce a hard shell.

Tiny mussels are able to live among bryophytes in aquatic habitats. ***Fissidens fontanus*** and ***Leptodictyum riparium*** can live on the shells.

Echinoderms generally have no association with bryophytes, but if a bryophyte falls into the marine water it may occasionally be eaten.

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TARDIGRADE SURVIVAL

Figure 1. ***Dactylobiotus*** sp. on the green alga *Spirogyra*. Photo by Yuuji Tsukii, with permission.

Tardigrades – Water Bears

Tardigrades (*tardus* = slow, *gradus* = step, or slow walkers), also known as water bears or moss piglets, are close relatives of the arthropods (Garey *et al*. 1996, 1999; Giribet *et al*. 1996).

Water bears resemble small bears (0.1-1 mm), complete with claws, but a few too many legs (4 pairs) (Figure 1). They are either armored (**Heterotardigrada**) or unarmored (**Eutardigrada**). The aquatic ones are usually a translucent white, whereas the terrestrial ones are often colored. Each of the eight legs has claws, which, when combined with their slow gait, makes them look very much like miniature polar bears with some extra legs. The very common ***Macrobiotus hufelandi*** (Figure 2) lumbers along at a maximum of 17.7 cm h^{-1} (Ramazzotti & Maucci in Mach 2010). Tardigrades are just the right size to move among the bryophyte leaves, they lumber along slowly like bears, and they are downright cute!

Tardigrades, comprising about 900 species (Garey *et al*. 2008), can be found in marine, aquatic, and terrestrial habitats (Goeze 1773; May 1948; Greven 1980; Maucci 1986; Kinchin 1994). On land they frequently live in association with bryophytes (Figure 3; Figure 4) and lichens (Mihelčič 1967; Mehlen 1969; Utsugi 1984; Meininger *et al*. 1985; Mancardi 1988; Szymanska 1994; Bertolani & Rebecchi 1996; Tarter *et al*. 1996; Miller 1997; Jerez Jaimes *et al*. 2002; Boeckner *et al*. 2006; Bartels *et al*. 2009; Meyer & Hinton 2009; Rossi *et al*. 2009; Simmons *et al*. 2009). In water, algae, as well as bryophytes, provide homes.

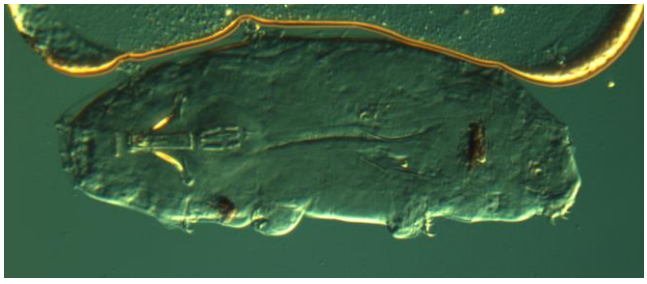

Figure 2. ***Macrobiotus hufelandi***, a common tardigrade that is among those inhabiting mosses. Photo by Paul Bartels, with permission.

These terrestrial tardigrades depend on the water drops that adhere to mosses and liverworts (Hingley 1993) and are therefore often termed **limnoterrestrial** (living in terrestrial habitats, but requiring a water film). Aquatic bryophytes can also house tardigrades (Hallas 1975; Kinchin 1987b, 1988; Steiner 1994a, b), as do the algae. However, of the ~1000 tardigrades reviewed by Guidetti

and Bertolani (2005) and Garey *et al*. (2008), only 62 were truly aquatic. The others depend on water associated with the interstitial spaces of terrestrial algae, lichens, bryophytes, soil, and leaf litter. Water bears are found in habitats from hot springs to layers under the ice (in cryoconite holes in glaciers) and occupy every continent of the world.

Figure 3. This tardigrade resided among the leaves of the moss ***Hypopterygium arbuscula*** (Figure 4). Photo courtesy of Filipe Osorio.

Figure 4. ***Hypopterygium arbuscula***, a known bryophyte habitat for tardigrades in Chile. Photo by Juan Larrain through Creative Commons.

Most of the terrestrial tardigrades are bryophyte inhabitants (Nelson 1991a). These terrestrial bryophyte taxa have a life span ranging 3-4 months (Franceschi *et al*. 1962-1963), 3-7 months for ***Macrobiotus hufelandi*** (Figure 2; Morgan 1977), up to about 3 months for roof-moss-dwelling ***Echiniscus testudo*** (Figure 5; Morgan 1977), to about 2 years (Altiero & Rebecchi 2001) of active life (not counting dormant periods). The bryophyte-inhabiting taxa are more common in temperate and polar zones than in the tropics (Nelson 1991a). Some, as for example ***Echiniscus testudo*** (Figure 5), live almost exclusively on bryophytes (Corbet & Lan 1974).

Despite their cosmopolitan distribution (Romano 2003), broad habitat requirements, and relative visibility (compared to protozoa, for example), the tardigrades remain poorly known. As late as 1985, Hidalgo and Coombs reported that 16 states in the USA had no records of tardigrades. Species not previously described are easily discovered by those who know where to look for them.

The environmental conditions that affect tardigrades are likewise poorly studied (Guil *et al*. 2009), despite the extensive studies on a few species that have become travellers of the universe in space. Among those conditions that have been studied, altitudinal gradients and micro-environmental variables (including substrate choice among vegetation, bryophytes, and leaf litter) seem to have gotten the bulk of the attention (Guil *et al*. 2009). Guil and coworkers found a unimodal distribution relative to altitude for species richness, but it was closely tied to habitat variation. The best predictor of the distribution of tardigrades in the Sierra de Guadarrama Mountain Range, Spain, was bioclimatic classification. Soil, climate, vegetation structure, and leaf litter type worked both separately and in combination to determine species richness, explaining nearly 60% of the species richness in micro-scale plots. Abundance, on the other hand, was significantly influenced only by soil composition and leaf litter type. The macro-environmental gradients seemed to be unimportant in determining abundance (*e.g.* Figure 6).

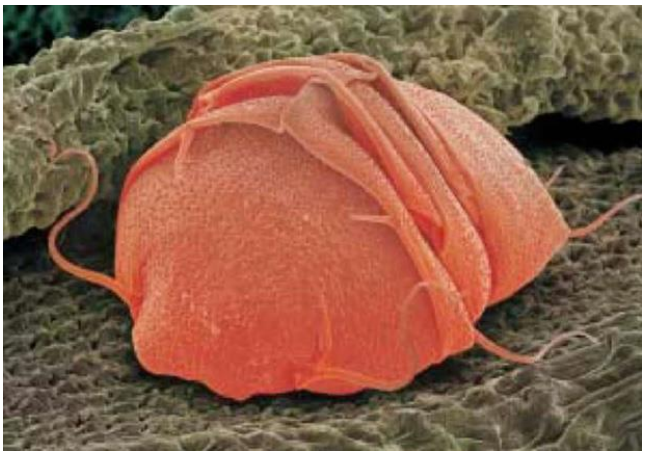

Figure 5. ***Echiniscus testudo*** dormant stage (tun), demonstrating the rigid nature of its armor that prevents it from extensive changes in size. Photo by Power & Syred through Creative Commons.

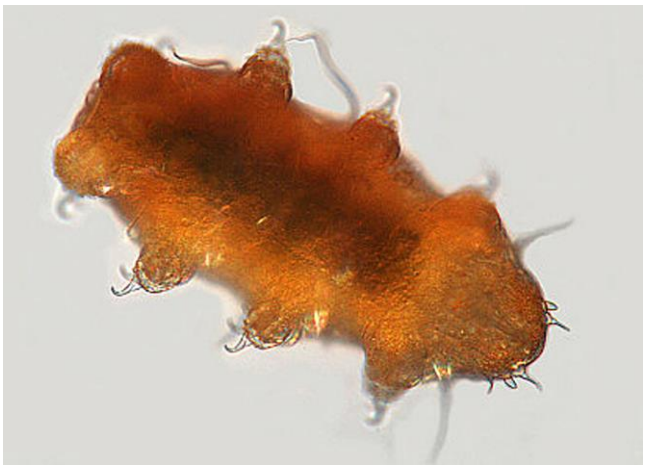

Figure 6. ***Echiniscus*** species (*E. testudo* occurs almost exclusively on bryophytes) seem to be unresponsive to moisture changes. Photo by Martin Mach, with permission.

Suitability of Bryophytes as Habitat

The importance of bryophytes as a tardigrade habitat is evident by the number of publications on "moss" tardigrade fauna: Mihelčič 1967; Hallas 1975; Pilato & Sperlinga 1975; Morgan 1976; Bruegmann 1977; Morgan 1977; Maucci 1978, 1980; Bertolani 1983, 2001; Binda 1984;

Utsugi 1984; Meininger *et al*. 1985; Hofmann 1987; Hofmann & Eichelberg 1987; Kinchin 1987a, b, 1988, 1994; Meininger & Spatt 1988; Mancardi 1988; Bertolani *et al*. 1990; Tarter & Nelson 1990; Kathman & Cross 1991; Nelson 1991a, b; Utsugi & Ohyama 1991; Moon *et al*. 1994; Szymanska 1994; Miller & Heatwole 1995; Adkins & Nelson 1996; Tarter *et al*. 1996; Hooie & Davison 2001; Guidetti & Jönsson 2002; Jönsson 2003; Meyer *et al*. 2003; Hooie 2005), to name a few. It appears that when tardigrade lovers want to collect a lot of them, they collect bryophytes and lichens – or just bryophytes (generally lumped into "mosses").

Unfortunately, the authors rarely name the bryophytes from which their prizes were extracted. However, some evidence suggests that little specificity exists for bryophyte species, and lichens are as suitable as bryophytes, with no apparent differences in tardigrade species (Meyer & Hinton 2007). I have to wonder, however, why reports on tardigrades from liverworts are so scant (Figure 7). Perhaps it is just as suggested to me by Łukasz Kaczmarek, that most zoologists do not understand the differences between mosses and liverworts. (Neither do my students when they begin looking at them.)

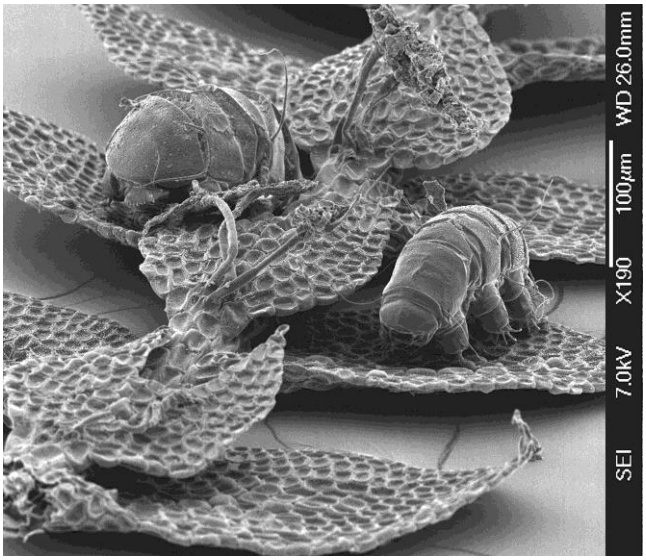

Figure 7. SEM view of tardigrades on the lower sides of leaves of a leafy liverwort. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

Ramazzotti and Maucci (1983) considered mosses suitable habitat based on three needs of the **limnoterrestrial** tardigrades:

1. a structure that allows sufficient oxygen diffusion
2. the ability to undergo alternate periods of wetting and drying resulting from solar radiation and wind
3. a medium that contains sufficient food.

Based on these criteria, bryophytes are particularly good habitats for tardigrades in several ways (Ramazzotti & Maucci 1983; Claps & Rossi 1984; Adkins & Nelson 1996). Their structure permits sufficient oxygen diffusion, both in aquatic and terrestrial habitats. Bryophytes experience drying, which most do slowly, permitting the tardigrades likewise to dry slowly, and both have a tolerance to dehydration that permits them to survive adverse conditions (Kinchin 1994). Furthermore, the tardigrades have a prolonged life span when it is interrupted by such a dormancy period. And bryophytes contain food items, such as algae, protozoa, and nematodes, as well as the bryophytes themselves, sufficient for the tardigrades. Most likely, the small chambers among the bryophyte branches also afford protection from larger would-be predators. And when fragments of bryophytes disperse, they may carry tardigrades with them.

It is the interstitial water of bryophytes that provides the suitable habitat for tardigrades (Hallas 1975). This water is typically found in leaf sheaths of bryophytes. Hallas investigated the drying of "cushions" of ***Hypnum cupressiforme*** (Figure 8). It required 19 hours for the moss to dry to a stable weight. The water retention relative to the weight of the cushion decreased linearly with the density of the cushion. However, the rate of drying can change with the temperature, saturation of the air, and air movement. He concluded that all compartments dry at the same rate, independent of the initial water content of each pocket, and the small variation in drying time is of no consequence for the tardigrades and other inhabitants. The tardigrades were concentrated in the living, chlorophyllous layer (compared to deeper, senescent layers) where there was more moisture. The water pockets connect vertically from one leaf to the next, but only connect horizontally when it rains. Therefore, horizontal migration of the tardigrades is only possible when the moss becomes saturated during rainfall. In ***H. cupressiforme*** (Figure 8), such bridges are formed only when rainfall exceeds 3 mm. Hallas considered that nighttime and morning dew were not sufficient for the most common tardigrade [***Macrobiotus hufelandii*** (Figure 2) – a species that comprised 91% of the 386 tardigrades] to become active, suggesting that it would take ten times that amount of water to bring the moss to saturation levels.

Figure 8. Mat of ***Hypnum cupressiforme***. Photo by Dick Haaksma, with permission.

But bryophytes do pose their problems for the tiny tardigrades. These animals are quite light weight, so imagine their struggle to control their movements when they encounter fully hydrated bryophytes with a continuous bath of water surrounding them. Greven and Schüttler (2001) observed these slow-moving creatures [***Macrobiotus*** sp., ***Echiniscus testudo*** (Figure 5) on ***Encalypta streptocarpa*** [=*E. contorta*] (Figure 9) when the bryophyte was fully hydrated. The poor bears could barely

move and had difficulty maintaining the direction of their movements in the water. They could easily become dislodged by rainwater unless they are able to nestle in a leaf axil or other protected niche. And that is often a good place to look for them.

Figure 9. ***Encalypta streptocarpa***, a tardigrade habitat that can be difficult to navigate when it is fully hydrated. Photo by Michael Lüth, with permission.

On the other hand, ***Polytrichastrum*** [=*Polytrichum*] ***formosum*** (Figure 10) did not sustain a continuous water film and the tardigrades seemed also unable to move in this "dry" habitat (Greven & Schüttler 2001). Rather, they seemed confined to the leaf axils, where water collected. As water receded, the animals ceased movement and formed a **tun** (protective dormant stage of tardigrade that is altered both chemically and physically) right there, permitting it to survive without water for up to 10 years (Jönsson & Bertolani 2001)! Perhaps tardigrades were the inspiration for the Rip Van Winkle story.

Figure 10. ***Polytrichastrum formosum***, a moss that does not maintain a water film and is thus a poor tardigrade habitat. Photo by Des Callaghan, with permission.

Moisture seems to be the greatest determinant of species distribution among bryophytes. Richness among epiphytic bryophytes in the Cincinnati, Ohio, USA area was greatest in areas of high humidity (Meininger *et al*. 1985). Hofmann and Eichelberg (1987) found that the tardigrades lacked correlation with bryophyte species but that their distribution could be predicted by the degree of moisture they prefer. It is therefore not surprising that some bryophytes housed no tardigrades.

Tardigrades in association with roads along the Alaska pipeline demonstrate a moisture relationship (Meininger & Spatt 1988). Dust resulting from gravel roads associated with the pipeline alters the habitat for both mosses and tardigrades. Those tardigrades living among mosses near roads were species adapted to xeric habitats. These species typically fed on fungi and algae, whereas those farther from the road were more likely to be omnivores or carnivores, presumably because they had more freedom to move about in a somewhat more moist environment.

Adaptations of Tardigrades

One might ask if these bryophyte-dwelling creatures have any special adaptations that permit them to live where they do. Their greatest adaptation is that they live in a habitat that permits them to dry slowly and go into a dormant state, as we will discuss shortly – a kind of behavioral/physiological adaptation. In fact, it appears that limnoterrestrial species actually require a habitat where they have dormant periods. And for many, the stylets permit them to suck the contents out of bryophyte cells, among other things, making them one of the few organisms specially adapted for obtaining nutrients from bryophytes.

Like insects, tardigrades have chitin, in this case in the innermost layer of the cuticle. The chitinous armor of some terrestrial tardigrades (heterotardigrades) may slow drying and offer protection from damage while dry. Of course small size is essential for living in the miniature world of bryophytes. And their claws (Figure 11-Figure 13) may permit them to clamber about more easily among the leaves and branches of the bryophytes. But Bertolani and Biserov (1996) consider that the reduction of claws on the fourth pair of legs is an adaptation to moving among the interstitial spaces in the soil. Does this same adaptation pertain to those among bryophytes?

Figure 11. Claws on four of the eight legs of ***Echiniscoides sigismundi*** (a tidal zone species). Photo by Martin Mach, with permission.

Figure 12. Claws of a tardigrade that is most likely ***Cornechiniscus cornutus*** (a bryophyte-dweller). Photo by Martin Mach, with permission.

Figure 13. Claws of ***Echiniscus*** sp., a genus with many bryophyte-dwelling species. Photo by Martin Mach, with permission.

Their light weight facilitates tardigrade dispersal. Their bodies are flexible, permitting them to nestle in leaf axils or move in small spaces. But most of these as adaptations to the bryophyte habitat are speculation. There have been no tests to determine if any of these traits actually increases their survival among bryophytes compared to other habitats. Some very interesting experiments could be designed.

Let's examine one of the bryophyte-dwelling tardigrades as an example of potential adaptations. Martin Mach (The Water Bear) found ***Cornechiniscus cornutus*** (Figure 14) among bryophytes on a mountain top in Hungary. This cute little bear has two horns on its head (Figure 15) and a nice salmon color. But it is slow and clumsy, out-classed by the faster-moving and more abundant ***Ramazzottius*** (formerly ***Hypsibius***) ***oberhaeuseri*** (Figure 25). Do such ornamentations as horns and hairs help to reduce predation in this habitat? Is that an advantage to offset the slower movement? Does the bright color protect the water bear from UV damage, especially while it is dry?

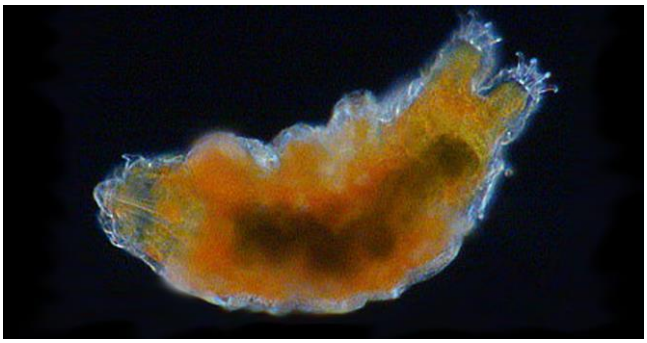

Figure 14. ***Cornechiniscus cornutus***. Photo by Martin Mach, with permission.

Survival of Hazardous Conditions

The biggest hazard a bryophyte imposes on a tardigrade is intermittent desiccation. But in addition to that desiccation, the organism may be subjected to high or low temperatures, low oxygen conditions, and UV light for prolonged periods. With little ability to move elsewhere, it needs some other type of protection.

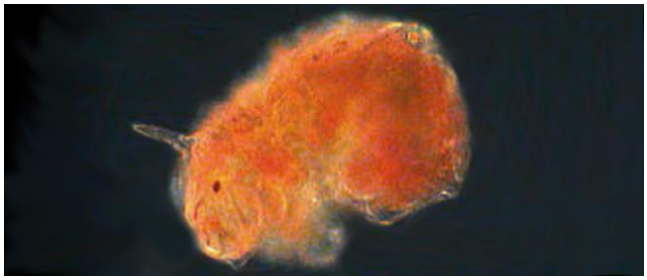

Figure 15. ***Cornechiniscus cornutus*** showing one of its two head horns. Photo by Martin Mach, with permission.

Aquatic organisms rarely need to be concerned with desiccation. However, if an animal is to survive among terrestrial bryophytes, it must be prepared for drying when the bryophyte dries out, and many of the tardigrade habitats are in dry places, including **cryptogamic crusts** (assemblages of Cyanobacteria, algae, lichens, & mosses) in the prairie and desert, and among epiphytes on trees. These bring with them the very hazards mentioned above – UV light in the absence of water for protection, and extremes in temperature. And the watery body must be hydrated for oxygen to enter it.

To unravel the relative importance of these stressors related to desiccation, Wright (1991) studied fifteen species of tardigrades and their responses to insolation, elevation, standardized desiccation rate, and hydration capacity of the plant substrate. There was considerable variation in ecotype among seven species with xeric associations. ***Macrobiotus hufelandi*** (Figure 2) and ***Hypsibius dujardini*** (Figure 16), both hygrophilic species, are absent from habitats that desiccate rapidly. On the other hand, the xerophiles ***Milnesium tardigradum*** (Figure 51) and ***Ramazzottius oberhaeuseri*** (Figure 25) avoid locations with high insolation and rapid desiccation rate, but also avoid poorly drained sites and sites with prolonged hydration. Despite these differences, ***Milnesium tardigradum*** often associates with the two ***Hypsibius*** species and may use them for food. The lack of association among ***Macrobiotus hufelandi***, ***Paramacrobiotus*** (formerly *Macrobiotus*) ***richtersi*** (Figure 17), and ***Hypsibius prosostomus*** may be due to competitive exclusion.

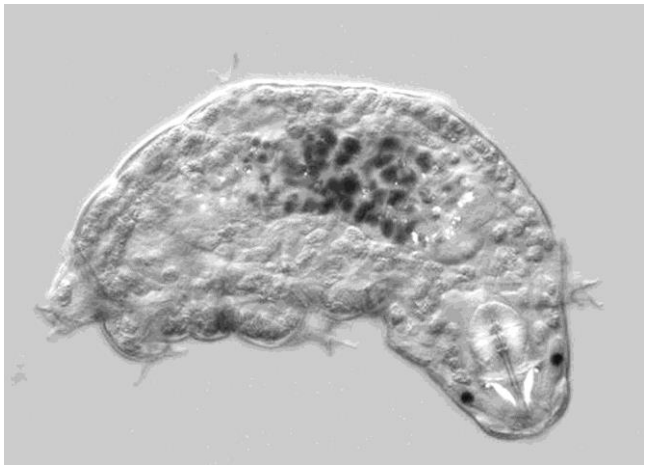

Figure 16. ***Hypsibius dujardini*** with the alga *Chlorococcum* in its gut. Photo by Willow Gabriel through EOL Creative Commons.

Figure 17. ***Paramacrobiotus richtersi***. Photo by Science Photo Library through Creative Commons.

Physical Adaptations

The soft-bodied tardigrades appear to have few structural adaptations to survive drought. Some, like ***Echiniscus***, have long hairs (Figure 18-Figure 19), but the hairs are so few that one can hardly imagine they are of any help to reduce water loss or protect the dry animal. Hmmm...What might their function be? Or are they a non-detrimental left-over? One interesting idea is that they might serve as straws to draw water into the body – a hypothesis requiring both experimentation and TEM examination. But suppose that is true. It could be a way to cause water to enter without drowning the animal – *i.e.*, permitting maintenance of an air layer on the surface. On the other hand, they could serve as fine hairs to collect dew and fog on their surface and direct it to the skin, thus increasing surface area and collection surface for the water. Or the hairs cold act like whiskers on a cat, facilitating navigation among the mosses. More interesting experiments are needed!

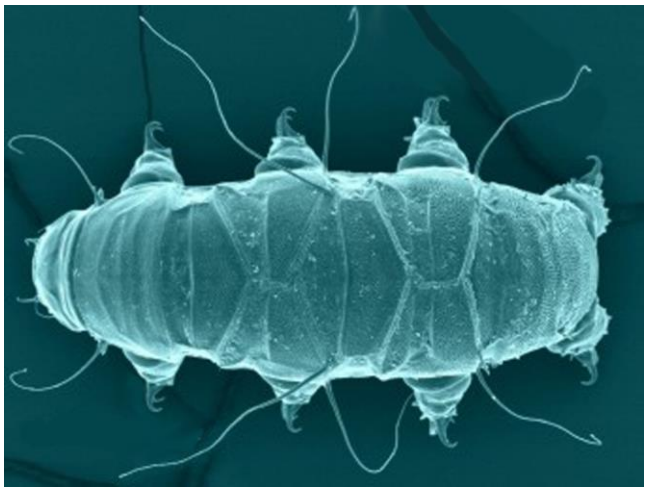

Figure 18. ***Echiniscus trisetosus***, illustrating the sparse but long hairs and plates of armor. Photo by Łukasz Michalczyk and Łukasz Kaczmarek, with permission.

Oxygen availability can be a problem, and for this reason the tardigrades avoid dense bryophytes and usually remain in the top few centimeters of soil where more oxygen is available (Ramazzotti & Maucci 1983). Hence, another possibility for the long hairs is that they could be tactile extensions to warn of an environment that is too tight, or chemical sensors to aid in finding food or sensing predators – or sensing a low-oxygen environment. Hypothesis testing is needed!

Figure 19. Two of the long hairs of ***Echiniscus***. Photo by Martin Mach, with permission.

Echiniscus viridianus (Figure 20) seems to do well among bryophytes. It was originally described from mosses in Alabama USA (20 individuals) and later collected in New Mexico and the Azores Islands, again among mosses (Pilato *et al*. 2007). As in other members of the genus, this species bears armor and long hairs.

Figure 20. ***Echiniscus viridianus***. Photo by Paul J. Bartels, with permission.

Spines/hairs and body armor may offer a bit more protection. Some bryophyte-dwelling species such as ***Cornechiniscus cornutus*** (Figure 21) and some members of the genera ***Echiniscus*** (Figure 22-Figure 23) and ***Ramazzottius*** (Figure 24-Figure 25) (and others) have "**armor**" on their bodies that is somewhat leathery. I am aware of no studies that demonstrate the ability of the armor to reduce water loss, but it would appear to be a good possibility. Other possible advantages of this armor-like **cuticle** may include protection from fungi and other pathogens and some kinds of predators, particularly while in cryptobiosis, and it most likely would afford limited UV protection. How little we know!

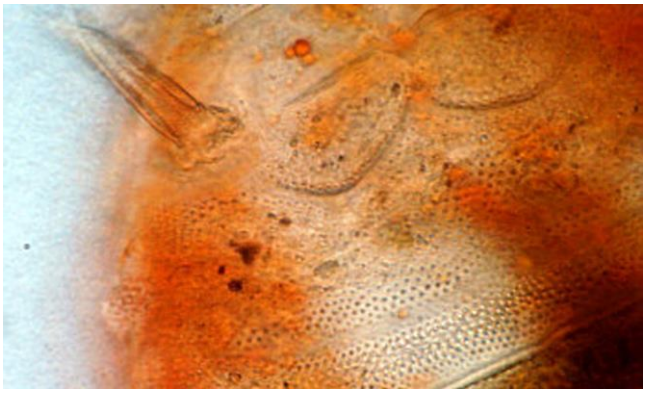

Figure 21. ***Cornechiniscus cornutus*** showing armor. Photo by Martin Mach, with permission.

Figure 22. ***Echiniscus*** sp. posterior dorsal side showing a type of armor. Photo by Martin Mach, with permission.

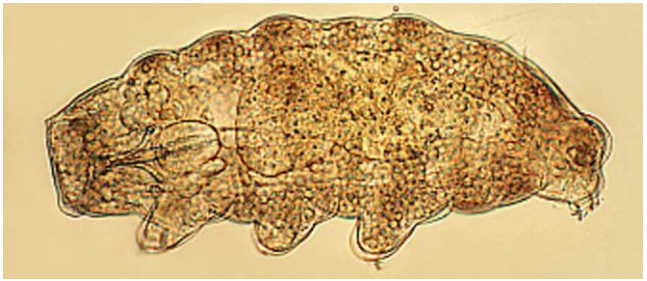

Figure 23. Tardigrade sp. showing a type of armor. Photo by Martin Mach, with permission.

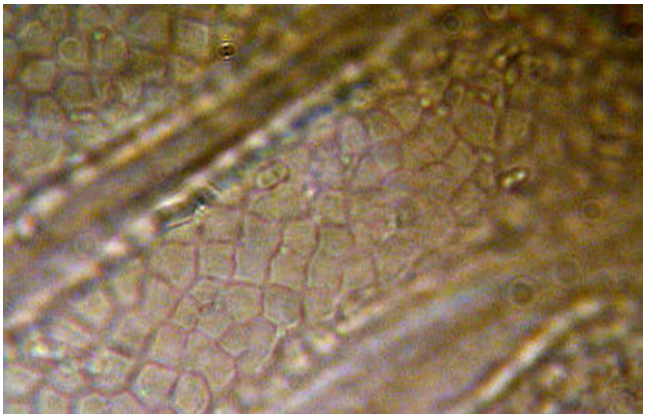

Figure 24. Armor on ***Ramazzottius oberhaeuseri***. Photo by Martin Mach, with permission.

Figure 25. ***Ramazzottius oberhaeuseri***, a tardigrade with armor. Photo by Martin Mach, with permission.

Pigments

Terrestrial tardigrades come in green, brown, yellow, orange, pink, red, purple, or black, whereas aquatic ones are white (Hebert 2008). Bonifacio *et al*. (2012) pointed out that despite the many studies on tardigrades relative to space travel, little is known about the nature or function of their pigments. They described the carotenoid nature of the pigments and the ability of these pigments to decrease under high oxidative stress. They hypothesized that these pigments had an anti-oxidant function and could possibly protect the animals during extreme environmental conditions.

It is possible that the wonderful colors of some tardigrades (Figure 26-Figure 27) are adaptations against UV damage to DNA, especially during prolonged periods in a cryptobiotic state. Such pigmentation advantages have been demonstrated in bryophytes (Martínez Abaigar & Olivera 2007) and copepods (Byron 1982), so it is reasonable to expect them to serve similar functions in tardigrades, particularly in those more open habitats such as **cryptogamic crusts**. It would be an interesting study to examine the relationship of color with habitat in tardigrades. I am aware of no such study, but Martin Mach (pers. comm. 18 October 2012) pointed me to the publication of Ernst Marcus (1929). Marcus suggested that pigments were a response to UV light. He cited as support the findings that pigmentation varies with winter vs summer UV radiation. Experiments are needed to support this hypothesis, and one must wonder how this relates to those living among bryophytes. Marcus pointed out that insolation does not penetrate well into the moss colony, making bright pigments unnecessary for these tardigrades.

Physiological Adaptations

Light Response

Tardigrades have a pair of eyes, although at times they may be "ghost eyes" (Figure 28) that cannot be seen

through ordinary observation (Mach 2012). These eyes respond to light, and at least in ***Macrobiotus hufelandi*** (Figure 2) the response changes with size and age (Beasley 2001). The smaller, younger size group had a significantly negative response to light. Beasley hypothesized that this behavior serves to conserve body moisture in small individuals that have a larger surface area to volume ratio than do larger ones. The response is not a phototaxis (directional response to light), but rather was photokinesis (non-directed, random movement), resulting in either an increase in speed or a change in direction when exposed to light. Such behavior would seem to support finding a "safe" place away from light.

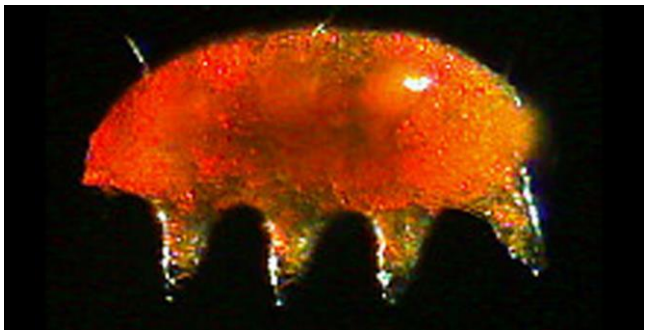

Figure 26. Adult ***Echiniscus*** sp., demonstrating one of the bright colors found in tardigrades. Photo by Martin Mach, with permission.

Figure 27. ***Cornechiniscus cornutus***, a bryophyte-dwelling "horned" species that exhibits brilliant colors that could afford UV protection. Photo by Martin Mach, with permission.

Figure 28. Ghost eyes of ***Ramazzottius oberhaeuseri***. Photo by Martin Mach, with permission.

Cryptobiosis

Albert Szent-Gyorgyi, a 20th Century Hungarian biochemist, once stated "Water is life's mater and matrix, mother and medium. There is no life without water." In their cryptobiotic state, tardigrades come close to disproving that statement. Anthony van Leuwenhoek first described cryptobiosis in 1702, but it was not until 1959 that Keilin coined the term **cryptobiosis** (Wright 2001). Cryptobiosis is a reversible ametabolic state that can be induced by dehydration and cooling, and possibly osmotic stress and anoxia.

Metazoans such as tardigrades use **glycerol** and the disaccharide sugars **sucrose** and **trehalose** (Wright 2001) as protectants. Before entering the cryptobiotic state, these substances must be synthesized from glycogen reserves, hence requiring a preparatory period. Certain behavioral adaptations may help to delay the desiccation, thus permitting these compounds to be synthesized.

One of the factors that contributes to the tolerance of desiccation is the ability to reduce surface area during tun formation (Wright 1991), hence slowing the process. Those that are most desiccation tolerant have the greatest infolding. This means those species with thick dorsal plates (Figure 29) are at a disadvantage. As Wright showed for ***Echiniscus testudo*** (Figure 5), there is very little surface area reduction possible.

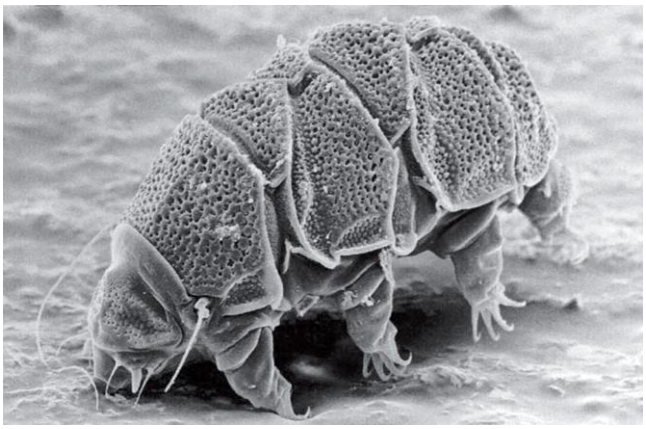

Figure 29. ***Echiniscus mauccii*** showing the plates that make shrinkage during desiccation all but impossible. Photo by Diane Nelson and Paul Bartels, with permission.

Moss cushions help to make survival of this cryptobiotic state possible. The small spaces among mosses hold static air that can slow the dispersion of water vapor (Wright 1989). This permits the slow drying that is necessary for survival of the tardigrade in the desiccated state. Mosses in exposed positions may desiccate rapidly. Some mosses [*e.g.* ***Polytrichum*** (Figure 30), ***Dawsonia*** spp. (Figure 31)] are able to slow this process by folding their leaves (van Zanten 1974).

Wright experimented with tardigrades on mosses in their natural habitat. **Eutardigrada** species were hydrated at least 24 hours before the experiments. As expected, there is considerable variation among species in their ability to tolerate desiccation. But they also differ in the lethal humidities (53-78%) for initial desiccation. Those species that are best able to tolerate rapid initial drying are also those most able to acquire tolerance to low humidities of 25-31% following drying in high humidity.

Figure 30. ***Polytrichum formosum*** showing open leaves (left & right) and folded leaves (center). Photo by Michael Lüth, with permission.

Figure 31. ***Dawsonia superba***, a moss that seems unfavorable for tardigrade feeding and rolls its leaves when dry. Photo by Jan-Peter Frahm, with permission.

Typically, tardigrades are desiccated in 80% relative humidity (Wright 1991). In this condition, they dehydrate rapidly, then abruptly reduce water loss (the **permeability slump**). This slump occurs in both live animals prior to tun formation and in extended dead animals, so it is not a physiological phenomenon. This slump permits the animals to retain considerable water in their desiccated state. Crowe (1972) examined the humidity effects on ***Paramacrobiotus areolatus*** (Figure 32). He found that at humidities lower than 70% this species became flattened and crumpled. Above this level, dehydrating animals form tuns. This appears to be an active process that is not as effective in anesthetized animals. Tuns of active animals lose water at only 0.3 times the rate of anaesthetized animals. The anaesthetized animals reach moisture equilibration with the environment within one hour, whereas tuns do not reach that equilibrium within 100 hours. In dry air, tardigrades can reach as little as 2-3% water content without dying if they are able to dry properly.

Literally meaning "hidden life," **cryptobiosis** is a state of suspended animation in which the organism is able to survive unfavorable conditions while expending little energy. During that state, the organism does not feed, reproduction stops, and metabolism is extremely reduced and may possibly even cease. For the **limnoterrestrial** (living in water films on land) tardigrade, it appears to be an essential part of survival and life, and it stops the aging clock.

Figure 32. Head region of ***Paramacrobiotus*** [=*Macrobiotus*] ***areolatus***. The bulbous oval to the right of the three filaments (stylets and buccal tube) is the pharynx. Photo by Martin Mach, with permission.

Despite the apparent absence of structural adaptations, desiccated tardigrades, like their mossy habitats, have great survival capabilities. They have two forms of **dormancy**: **cryptobiosis** and **encystment** (Guidetti *et al*. 2006). The cryptobiosis of tardigrades is exhibited in several forms:

- **anhydrobiosis** (induced by loss of water)
- **cryobiosis** (induced by declining temperatures)
- **anoxybiosis** (induced by insufficient oxygen)
- **osmobiosis** (induced by loss of water due to higher external salt concentrations) (Bertolani *et al*. 2004).

To be active, tardigrades must stay in a water film in order to breathe (Bordenstein 2008). But in a cryptobiotic state, as discussed below, tardigrades can survive not only desiccation, but temperatures as low as 0.05K (-272.95ºC) for 20 hours or -200ºC for 20 months (Miller 1997). They have even survived 151ºC for a few minutes (Lindahl & Balser 1999). They become active again after living with 0% hydration (Lindahl & Balser 1999). This desiccated dormant state also permits them to survive pressures of 6000 atmospheres (Seki & Toyoshima 1998), *i.e*. six times the pressure of the deepest part of the oceans! Yet they can also survive the vacuum and UV radiation of space (Jönsson *et al*. 2008), a feat not known for any other animal. The ability of tardigrades to undergo **cryptobiosis** is more widely known than their encystment behavior. True cryptobiotic states are survived as a **tun** (Figure 33-Figure 43). The tardigrades will be the ones to survive when everything else is deceased.

Tun Formation

When they undergo desiccation, the **tardigrades** form a **tun** (Figure 33-Figure 43) (Lindahl & Balser 1999). The **tun** is a barrel-shaped, dry, dormant tardigrade. Tuns are

formed in the process of entering true cryptobiosis, *i.e.*, in anhydrobiosis, osmobiosis, and cryobiosis, but not in anoxybiosis. Although the stimulus differs among these, each ultimately involves the loss of free water.

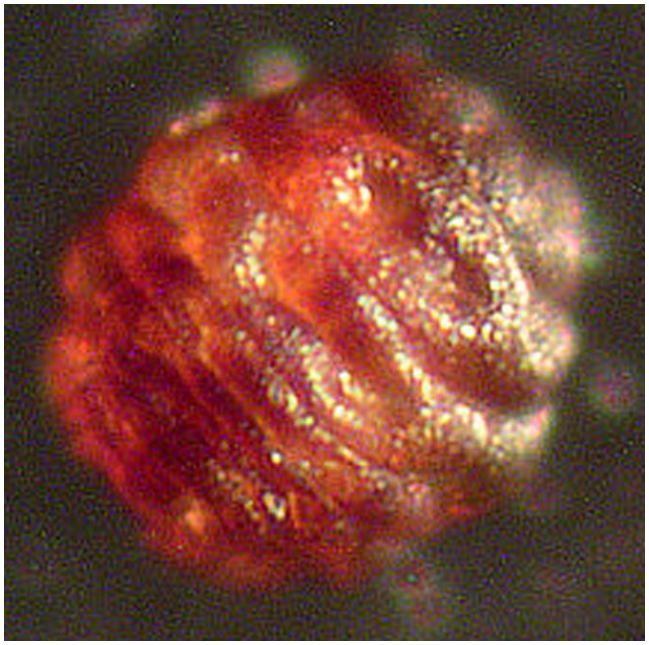

Figure 33. Tun of ***Ramazzottius oberhaeuseri***. Photo by Martin Mach, with permission.

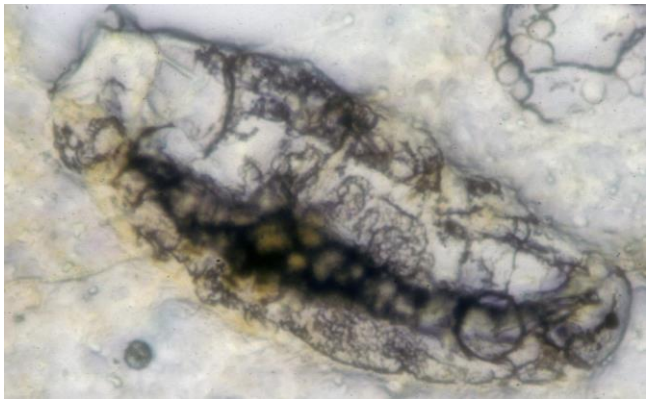

Figure 34. **Tardigrade** tun – water bear in a state of anhydrobiosis. Photo by Janice Glime.

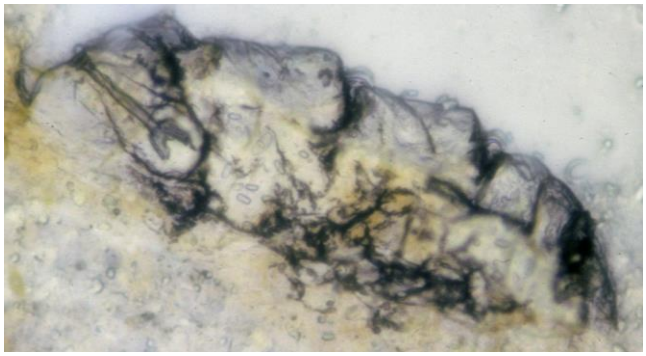

Figure 35. **Tardigrade** tun – water bear in a state of anhydrobiosis. Note the buccal apparatus (resembles a tuning fork on left end). Photo by Janice Glime.

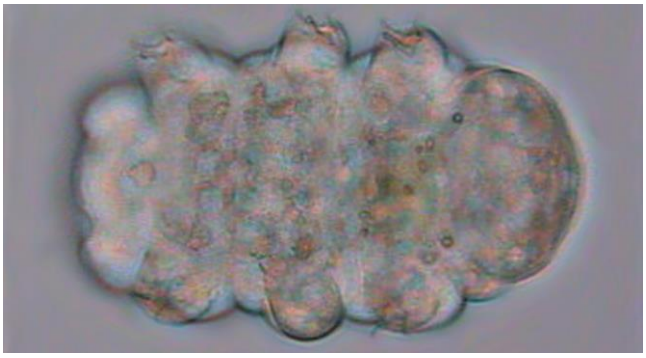

Figure 36. Tun of ***Hypsibius*** sp. Photo by Martin Mach, with permission.

Figure 37. Tun of ***Echiniscus*** sp. Photo by Martin Mach, with permission.

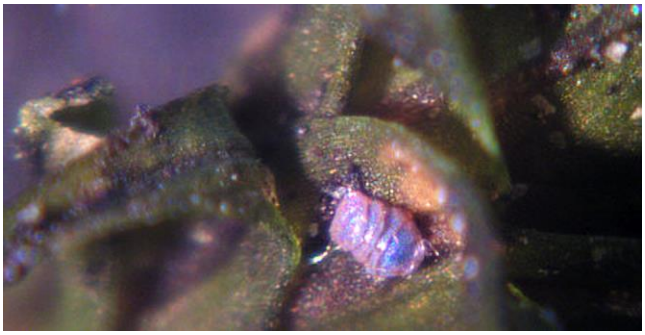

Figure 38. Tun of ***Echiniscus*** sp. on moss leaf. Photo by Martin Mach, with permission.

Figure 39. Multiple tuns of ***Echiniscus*** sp. on a single moss leaf. Photo by Martin Mach, with permission.

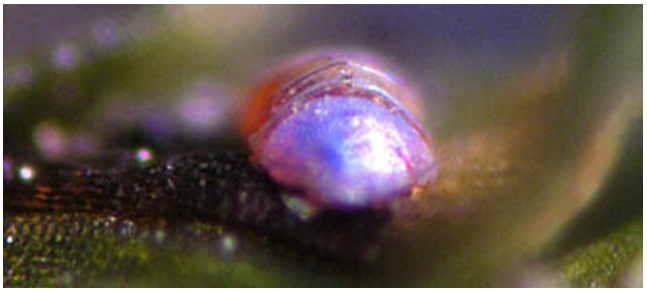

Figure 40. Tun of ***Echiniscus*** sp. on moss leaf. Photo by Martin Mach, with permission.

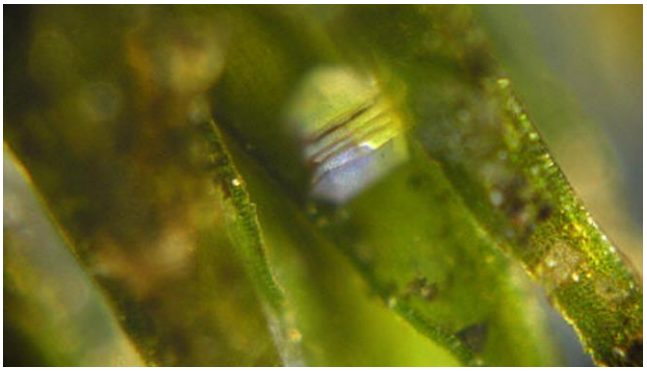

Figure 41. Tun of ***Echiniscus*** sp. on a moss leaf. Photo by Martin Mach, with permission.

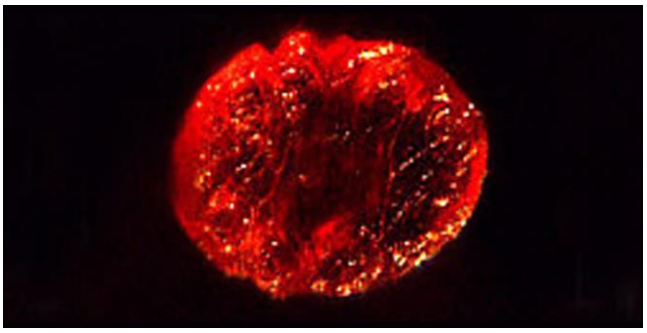

Figure 42. Tun of ***Echiniscus*** sp. Photo by Martin Mach, with permission.

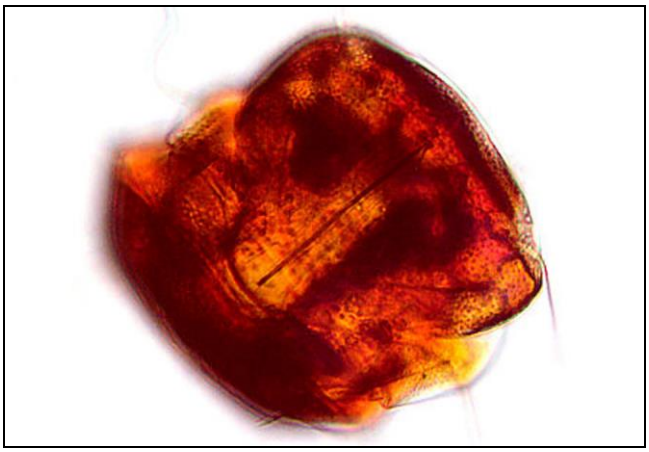

Figure 43. Tun of ***Echiniscus*** sp. Photo by Martin Mach, with permission.

This tun is a little ball in which the tardigrade can survive 0% relative humidity! However, it only requires a reduction to 70-95% humidity to trigger the **tun** formation, a resting form in a cryptobiotic state in which the tardigrade appears to be dead (Crowe 1972). During tun formation, loss of free and bound water is greater than 95% (Bertolani *et al*. 2004). The body folds and the appendages are withdrawn (Lindahl & Balser 1999). Wax is extruded onto the surface and most likely reduces water loss (Wright 1988a, b). Those tardigrades with the most variability in the thickness of this **cuticle**, making them more pliable, are those able to have the greatest surface area reduction when they form tuns (Wright 1988a, 1989). The thin areas would permit greater infolding. Lipids of the inner cuticle are thickest in the species that are best able to tolerate rapid drying. Crowe (1972) demonstrated that the cuticle of ***Paramacrobiotus areolatus*** (Figure 32) is removed from air contact during tun formation and becomes less permeable to water. Crowe likewise suggested that this loss of permeability might be due to a lipid phase change,.

Despite the waxy cuticular protection, the water content is reduced to less than 1% (Lindahl & Balser 1999) and the tun becomes shrivelled and wrinkled (Hingley 1993). ***Echiniscus testudo*** (Figure 5), an armored tardigrade, has much thicker **dorsal** (back) plates, apparently compensating for its limited ability to reduce surface area as it is drying (Wright 1988a, 1989).

The tardigrade bodies synthesize cell protectants such as **trehalose**, **glycerol**, and **heat shock proteins** that contribute to successful recovery from the tun state (Wright 1989). Trehalose is typically found in high concentrations in animals in a state of cryptobiosis (Crowe & Crowe 1984). Trehalose is able to bond with DPPC and alter the spacing of polar head groups, apparently stabilizing the dry cell membranes. Hengherr *et al*. (2008b) determined that levels of trehalose varied considerably among species. In fact, they detected no changes in trehalose levels in any Heterotardigrada, and ***Milnesium tardigradum*** (Figure 51) apparently had no trehalose at all. They did demonstrate that tardigrade embryos can accumulate high levels of trehalose, seemingly explaining the high level of desiccation tolerance in that life cycle stage.

Tun formation is essential to tardigrade survival under desiccating conditions. For ***Paramacrobiotus areolatus*** (Figure 44), and probably most tardigrades, if the humidity is low (<70%) or **anoxic** (lacking oxygen) during its desiccation, it is unable to form a tun and cannot be revived (Crowe 1972). It must have sufficient energy (requiring oxygen), hydration, and time to enter the tun stage.

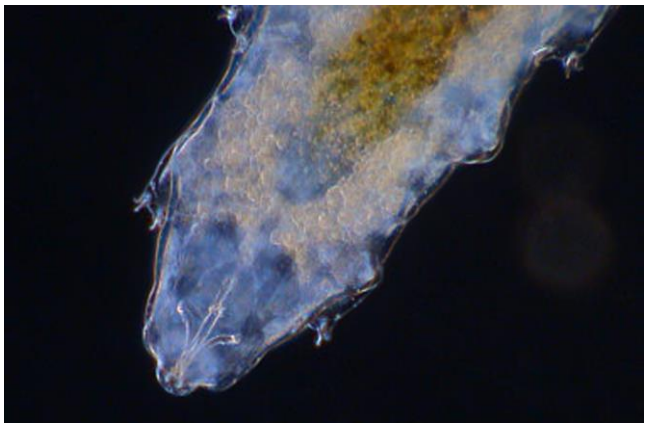

Figure 44. ***Paramacrobiotus areolatus***. Photo by Martin Mach, with permission.

Tardigrades revive (Figure 45) almost as quickly as a moss when water returns (Crowe & Higgins 1967), in as little as 4 minutes (Hingley 1993), or several hours, depending on how long they have been dehydrated (Lindahl & Balser 1999). One marine tardigrade has been induced to alternate between a cryptobiotic state and activity on a 6-hour cycle.

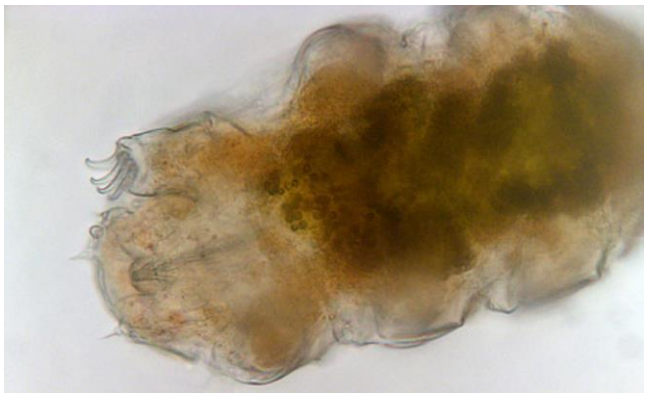

Figure 45. ***Echiniscus*** sp. rehydrated after four years of desiccation. Photo by Martin Mach, with permission.

Dangers in a Tun

One concern that comes to mind is the possible damage that could happen to these organisms while in the tun stage. I am reminded of the frozen frogs and toads during the winter. They are very susceptible to physical damage if they are disturbed. I would think an animal such as the amphibians hiding under a rock or clump of moss would experience no more physical abuse than the tiny tardigrade among the moss leaves. Ice crystals could poke holes in cells, larger animals could eat them, or they could get knocked off into a hole where conditions were not favorable to their maintenance and survival. I have to wonder just what dangers these dormant organisms do face, and how many actually survive these in the wild to become once again active. It seems we currently have no idea.

Certain dangers include cell degradation and DNA damage. As the tardigrades exist longer and longer, they accumulate cell degradation and DNA damage (Rebecchi *et al*. 2009b), ultimately accumulating too much for successful repair. Hence, the tun does not completely protect them, and chances of survival decrease with time.

Effects of Size

Jönsson *et al*. (2001) found that size influenced survival of cryptobiotic tardigrade species, but that direction of influence differed among species. The common ***Ramazzottius oberhaeuseri*** (300 µm length; Figure 46) had a much higher survival rate (66%) (Figure 47) than did ***Richtersius coronifer*** (40%) (up to 1 mm length; Figure 48). ***Ramazzottius oberhaeuseri*** (Figure 46) has a high ability to retain water, perhaps with a physiological adaptation to reduce water loss in this smaller organism with a high surface area to volume ratio.

Within ***Richtersius coronifer*** (Figure 48), large individuals were less likely to survive cryptobiosis than medium-sized ones (Figure 49); reproductive state had no effect (Jönsson & Rebecchi 2002). Better energetic conditions increased survival. Jönsson and Rebecchi suggested that larger organisms had greater energy constraints when entering and leaving anhydrobiosis, decreasing survival rate.

Figure 46. ***Ramazzottius oberhaeuseri***. Photo by Martin Mach, with permission.

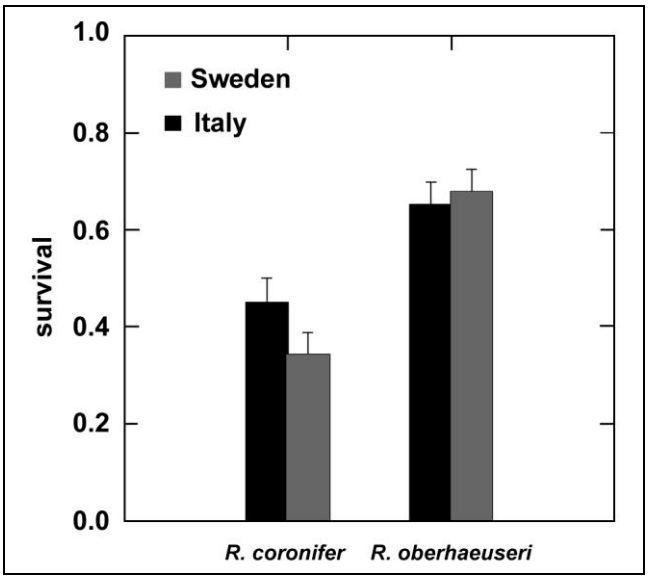

Figure 47. Comparison of survival during encystment for ***Richtersius coronifer*** and ***Ramazzottius oberhaeuseri*** from Italy and Sweden. Vertical line represents standard error. Redrawn from Bertolani et al. 2004, based on Jönsson et al. 2001.

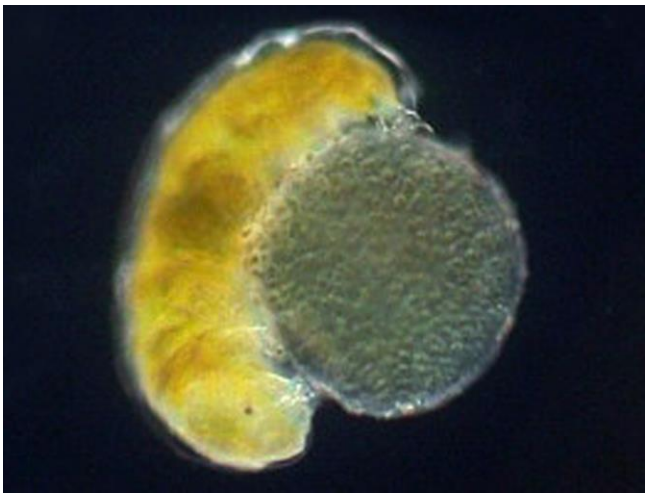

Figure 48. ***Richtersius coronifer***, clinging to an algal cell. Photo by Martin Mach, with permission.

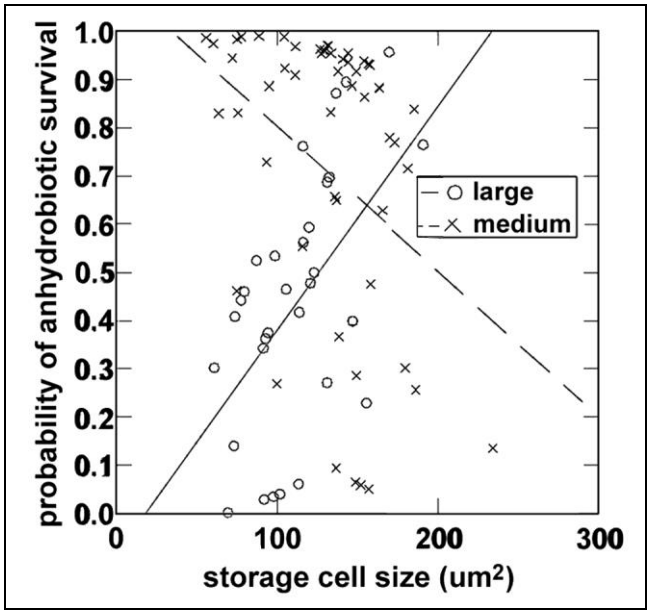

Figure 49. Probability of survival from anhydrobiosis for large and medium-sized ***Richtersius coronifer*** as a function of storage cell size. Probability is based on the predicted values from a logistic regression model, using buccal tube length, category, storage cell size, and interaction between the last two categories. Redrawn from Jönsson & Rebecchi 2002, in Bertolani *et al*. 2004.

Jönsson and Rebecchi (2002) likewise found that medium-sized tardigrades had a better chance of survival than did large ones in ***Richtersius coronifer*** (Figure 48). Large storage cell size was an important parameter to predict greater survival in the large tardigrades (Figure 49).

Reuner *et al.* (2010) described the storage cells as free-floating cells in ***Milnesium tardigradum*** (Figure 51), ***Paramacrobiotus tonollii*** (Figure 50), and ***Macrobiotus sapiens*** that apparently store and release energy as glycogen, protein, and fat. These stores provide energy during cryptobiosis. Storage cell size did not relate to body size, except that the largest tardigrade, ***Milnesium tardigradum*** (Figure 51), also had the largest storage cells. After seven days of anhydrobiosis (tun stage resulting from desiccation), this species had decreased cell size, but the other two species did not. Food sources used in the study did not seem to affect cell size.

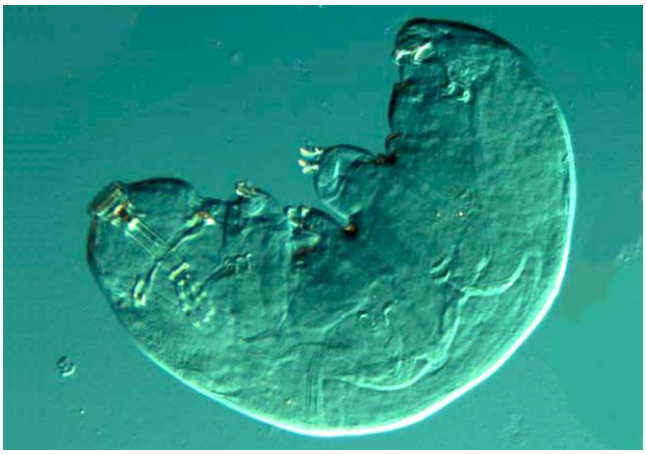

Figure 50. ***Paramacrobiotus tonollii***. Photo by P. J. Bartels, with permission.

Figure 51. ***Milnesium tardigradum***, a large tardigrade. Photo by Yuuji Tsukii, with permission.

Longevity

Tardigrades are often credited with century-long survival in a cryptobiotic state. This is due to the report that one herbarium specimen of a moss housed a tardigrade that began cellular activity after 120 years of being dry in the herbarium (Franceschi 1948; Brusca & Brusca 1990; Jönsson & Bertolani 2001)! But, sadly, this record has been called into question, and the tardigrade never fully recovered despite its cellular activity. At the very best, even this faint degree of survival is probably a rare occurrence (see Jönsson & Bertolani 2001). Jönsson and Bertolani (2001) reviewed the evidence and considered that ten years is a more realistic estimate of survival time for tardigrades in a cryptobiotic state.

Rebecchi *et al.* (2008) decided to test this claim of longevity further, using five species of tardigrades from lichens. They collected wet lichens with active tardigrades and permitted them to dry in the ambient conditions of the lab. Among these, ***Ramazzottius oberhaeuseri*** (Figure 25), ***Echiniscus testudo*** (Figure 5), and ***E. trisetosus*** (Figure 18), species that also occur on bryophytes, were sufficiently abundant to permit statistical conclusions. At the beginning of the experiment 91% of ***R. oberhaeuseri*** and 72% of ***Echiniscus*** spp. were active. ***Ramazzottius oberhaeuseri*** (Figure 25) survived up to 1604 days, whereas ***Echiniscus*** spp. lived only 1085 days. Nevertheless, this may not reflect going into the tun stage under natural conditions, which is likely to be slower among mosses. This could be particularly important for tardigrades that increase trehalose levels.

To test the **longevity** of tuns vs **eggs** under anhydrobiosis, Guidetti and Jönsson (2002) examined 63 different moss samples from stored collections, ranging in anhydrobiotic state 9-138 years. Eggs survived longer than dry adults (tuns), with those of ***Ramazzottius oberhaeuseri*** (Figure 25) surviving nine years. Much more work is needed to determine what factors account for such differences in survivorship and how it relates to individual species and habitats. The ability to survive unfavorable conditions permits the tardigrades to live in such places as ***Grimmia pulvinata*** tufts (Figure 52) on house roofs (Corbet & Lan 1974) or among branches of the epiphyte ***Orthotrichum cupulatum*** (Figure 53) (Jönsson *et al.* 2001).

Figure 52. ***Grimmia pulvinata***, a moss that can support tardigrade communities on roofs. Photo by Michael Lüth, with permission.

Figure 53. ***Orthotrichum cupulatum***, an acrocarpous moss that provides habitats for tardigrades. Photo by Michael Lüth, with permission.

Like the rotifers, tardigrades suspend their aging clock while they are dormant (Hengherr *et al* 2008a). ***Milnesium tardigradum*** (Figure 51) that was subjected to alternating periods of drying and activity exhibited similar longevity of active periods to that of animals of the species that had not experienced dry periods.

Ramazzotti and Maucci (1983) estimated that freshwater species such as those of ***Hypsibius*** (Figure 54) and ***Macrobiotus*** (Figure 55) live about 1-2 years. Terrestrial bryophyte-inhabiting species of the same genera live much longer, averaging 4-12 years. This extended life is due largely to their periods of cryptobiosis, during which the biological clock stops.

Figure 54. ***Hypsibius convergens***, a common bryophyte inhabitant. Photo by Paul Bartels, with permission.

Figure 55. ***Macrobiotus marlenae***, a terrestrial species known from mosses on rock. Photo by Martin Mach, with permission.

Dangers and Protective Mechanisms

One contributing factor in their survival of drying is the ability of tardigrades to alter their cell membranes (Brave New Biosphere 1999). They replace the water in the cell membranes with sugar, thus preventing radiation from causing ionization. Like the nematodes and rotifers, some tardigrades prepare for desiccation by producing **disaccharide** sugars, including **trehaloses** (Bordenstein: Tardigrades; Westh & Ramløv 1991). Disaccharides like trehalose and **sucrose**, as well as **glycerol**, are used as membrane protectants by metazoans such as tardigrades, whereas plants typically use **oligosaccharides** such as **stachyose** and **raffinose** (Wright 2001).

This water replacement by sugars also protects invertebrates during freezing because crystallization cannot occur (Brave New Biosphere 1999). The accumulation of trehalose of 0.1-2.3% of dry weight occurred within 5-7 hours during desiccation in ***Richtersius coronifer*** (Figure 48; Westh & Ramløv 1991). This accumulation was reversed within 6 hours upon rehydration. Both water loss and sugar replacement prevent the rupture of the cell membrane that would result in death. But trehalose has multiple properties that help to stabilize desiccated cells (Table 1).

Table 1. Properties of trehalose that benefit dehydrating cells. From Watanabe 2006.

Non-reducing activity
Low tendency to crystallize
Stable glass formation
High vitrification temperature
High ability of water replacement
Structuring activity of intracellular water with HSP
Stabilization of dry membranes
Antioxidant activity of protein and fatty acids
Free-radical scavenger

Nevertheless, tardigrades accumulate trehalose at the low end of the scale for anhydrobiotic organisms – about 2% (Watanabe 2006). This lower level in tardigrades and absence of trehalose in rotifers is coupled with their ability to enter anhydrobiosis within one hour, whereas organisms with larger accumulations (up to 40%) can take at least two days.

Trehalose is not a cure-all for desiccation effects in tardigrades. High temperatures and high humidity may lead to destruction of trehalose (Rebecchi *et al*. 2009a). In other cases, or in consort, oxidative damage may occur. Using ***Paramacrobiotus richtersi*** (Figure 17) as an experimental organism, Rebecchi *et al.* demonstrated that DNA changes can occur during desiccation. Neumann *et al*. (2009) likewise demonstrated a slight increase in DNA damage during drying, but they also found that DNA damage increased with duration of anhydrobiosis. Furthermore, high temperatures and relative humidity have negative effects on both survival and time to recover after rehydration, with effects increasing with duration of exposure. One reason for this is that damages are not repaired during anhydrobiosis and therefore accumulate with time.

Anhydrobiosis

The most common of the cryptobiotic states is **anhydrobiosis** (state of dormancy brought on by dehydration). In their state of **anhydrobiosis**, tardigrades can remain inactive during unfavorable conditions such as prolonged dryness (Kinchin 1987b). **Anhydrobiosis** is usually restricted to animals less than 1 mm in length (Watanabe 2006). Hence, some invertebrates are only able to enter this state during early developmental stages. Tardigrades and rotifers, being less than 1 mm when fully developed, are able to do so at any developmental stage.

In order to survive anhydrobiosis, tardigrades must dry very slowly (Hingley 1993; Collins & Bateman 2001). To form the tun, they must retract their head, legs, and hind end, forming a rounded tun, thus reducing surface area. In this state of anabiosis, they are able to withstand extremes of temperature and desiccation. Nevertheless, water arouses them in as little as four minutes.

It appears that continuously hydrated conditions may be detrimental to the survival of tardigrades (Jönsson 2007). Using bryophyte populations from Island Öland, Sweden, Jönsson subjected the tardigrades to two treatments of 6-month duration over an 18-month period. These experimental treatments increased hydration, decreased hydration, or remained as controls. The total population was significantly smaller (barely so) under increased hydration. But effects were not the same for all tardigrades. ***Richtersius coronifer*** (Figure 48) and ***Echiniscus spiniger*** failed to respond to the treatment, whereas ***Milnesium tardigradum*** (Figure 51) declined under increased hydration. But even ***Richtersius coronifer*** experienced reduction in the density of eggs (Figure 56-Figure 57) under the watering treatment. Hydration did not significantly increase density in any of the tardigrades. This adds further support to the idea that periods of dormancy (cryptobiosis) are necessary to increase longevity of the tardigrade. This would, in turn, increase variability of conditions, offering an array of conditions for reproduction.

Richtersius coronifer (Figure 48) can increase its survival rate by forming **aggregates**, a mechanism barely known for tardigrades but common in nematodes (Ivarsson & Jönsson 2004). The clustering reduces exposed surface area and thus slows drying. It is possible that this is used more in tardigrades than is realized; its use among bryophyte fauna is as yet unknown.

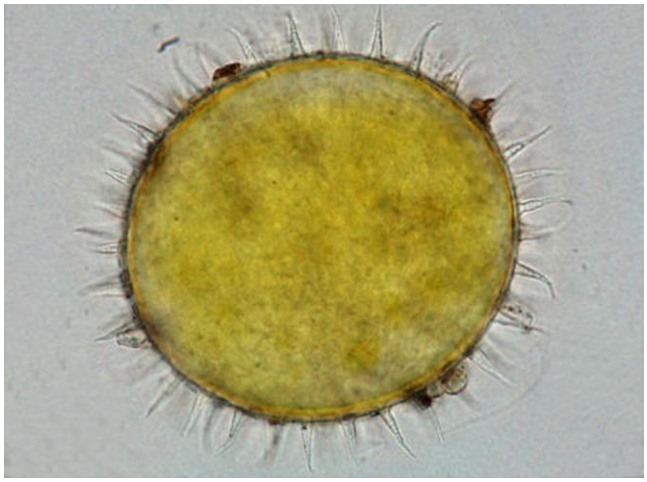

Figure 56. Egg of ***Richtersius coronifer***. Photo by Martin Mach, with permission.

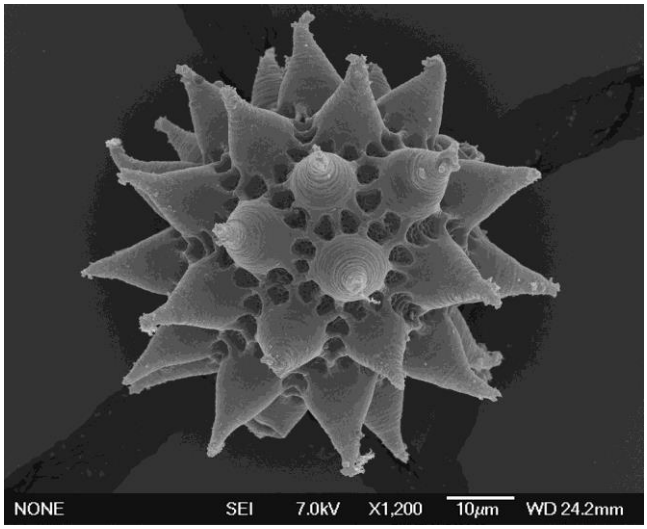

Figure 57. ***Macrobiotus magdalenae*** egg showing the highly decorated nature that is typical of eggs laid free from the **exuvia** (shed body shells). In this state the organism can survive as well as in a tun. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

Schill and Fritz (2008) examined the desiccation tolerance of the embryonic stages of ***Milnesium tardigradum*** (Figure 58), a potential means of surviving desiccation that has been neglected. They rehydrated this species after treatment at eight different humidity levels (10, 20, 31, 40, 54, 59, 72, 81%). They found that the less developed stages were more susceptible to desiccation damage. In the first three days of development, low humidity caused a decrease in hatching rates following rehydration. Later stages fared better, but when older embryos were dried fast at low humidity levels, development was delayed and hatch rates were lower after rehydration. Nevertheless, older embryos fared better than younger ones.

Even in 2011, Schokriae *et al*. still considered the survival mechanisms of tardigrades to be poorly understood. They considered the possibility that heat shock proteins (HSPs) might protect them from irreversible aggregation and degradation during anhydrobiosis. They found that ***Milnesium tardigradum*** (Figure 51) had HSPs in several major chaperone families, suggesting the ability

of the tardigrade to use these for protection when dehydrated.

Figure 58. ***Milnesium tardigradum***, a bryophyte dweller whose younger stages are the most susceptible to desiccation. Photo by Yuuji Tsukii, with permission.

The cryptobiotic state of anhydrobiosis has a significant impact on the ecological role of the tardigrades. It affects their role in the food chain, their ability to disperse, and their survival through a longer period of time (see reviews by Pilato 1979; Wright *et al*. 1992; Kinchin 1994). Bryophytes often play a significant role in achieving that state.

Osmobiosis

Osmobiosis is a special case of cryptobiosis that permits some species to tolerate high salinity and to form a tun (Lindahl & Balser 1999). It is initiated when the animal experiences an external salt concentration that is higher than that inside the organism. However, for tardigrades, while possible, osmobiosis is typically not necessary as most tardigrades already have a high salt tolerance.

Anoxybiosis

Anoxybiosis is another special case where the tardigrade has the ability to survive low oxygen (Lindahl & Balser 1999). Tardigrades are very sensitive to changes in oxygen tension, and prolonged reduction of oxygen leads to **osmoregulatory** failure.

Anoxybiosis is not a true state of cryptobiosis and does not involve tun formation (Figure 59). Unlike true cryptobiosis, anoxybiosis involves the uptake of water. The lack of oxygen results in the inability to control osmosis, causing water to enter the cells in excess. The animals become turgid, immobile, and retain fully extended bodies that are perfectly bilaterally symmetrical (Figure 60). Even animals in a molt can enter anoxybiosis (Figure 61).

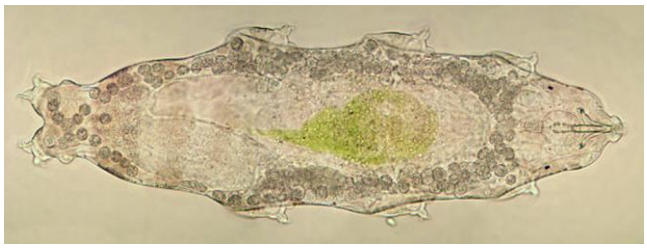

Figure 59. ***Macrobiotus hufelandi*** male in anoxybiotic state, showing lack of tun formation. Photo by Martin Mach, with permission.

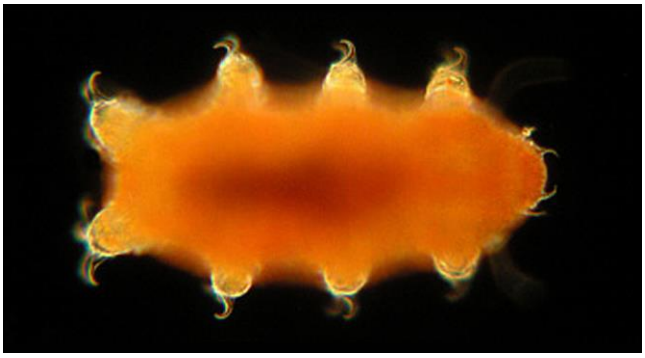

Figure 60. Tardigrade showing **anoxybiosis**, where water has entered through the cuticle by osmosis and caused swelling and turgidity. Note the extended legs and perfectly symmetrical body. The animal cannot move in this state. Photo by Martin Mach, with permission.

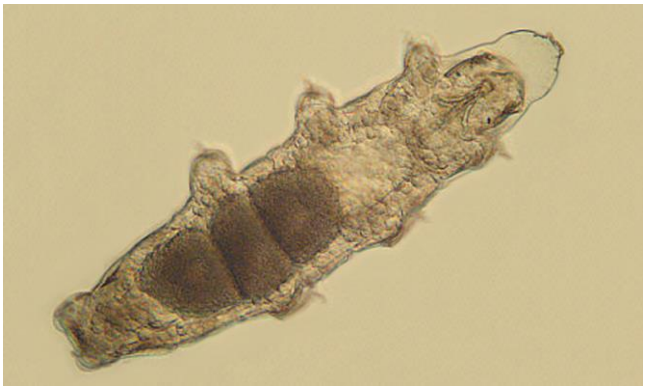

Figure 61. Tardigrade induced into **anoxybiosis** during its molt. Photo by Martin Mach, with permission.

Revival to normal state (Figure 62) relates to the duration of the dormant state. However, the success of that recovery is controversial (Wright *et al*. 1992), with some researchers finding that they can survive for only 3-4 days (Crowe 1975) and others finding survival of *Echiniscoides* (a tidal zone genus) up to six months in closed vials (Kristensen & Hallas 1980).

Figure 62. This tardigrade was caught by low oxygen during molt and entered **anoxybiosis**. Here it has recovered and is moving within the swollen cuticle to complete its molt. Photo by Martin Mach, with permission.

Cryobiosis

Cryobiosis is another special case of cryptobiosis that results when the temperature decreases and the water in the cells has frozen (Wikipedia: Cryptobiosis 2009). Molecular mobility stops (Wikipedia: Cryptobiosis 2009), permitting the tardigrades to survive very low temperatures (Westh *et al.* 1991; Westh & Kristensen 1992; Ramløv & Westh 1992; Sømme 1996; McInnes & Pugh 1998). They do this by actually freezing, but the freezing is ordered (Lindahl & Balser 1999) and the result once again is a tun.

Cryobiosis in tardigrades differs from anhydrobiosis (Wright 2001). First of all, tun formation in not necessary for survival. The important process is that intracellular freezing must be avoided. But tardigrades, unlike many arthropods, are freeze-tolerant. This can be accomplished by **ice-nucleating proteins** that are located outside the cells. These proteins act like water magnets, drawing water out of the cell. Also unlike many other arthropods, the extracellular freezing, promoted by the ice-nucleating proteins, occurs at temperatures near 0°C. In ***Richtersius coronifer*** (Figure 48), **trehalose** synthesis is not part of this process, although there may be other cryoprotectants in the cell. The details of freeze protection are not fully understood, but the loss of water from the cells may cause the cells to become "unfreezable." Glycerol contributes as an antioxidant. Being imbedded in ice probably also prevents oxidation damage. In this cryobiotic state, the tardigrades can survive for decades.

Tardigrades often experience wide temperature fluctuations while in an active state. In particular, they can be subjected to subzero temperatures. Their ability to tolerate these sub-zero conditions requires either tolerance of freezing body water or having a mechanism to lower the freezing point. Hengherr *et al*. (2009) subjected nine species from polar, temperate, and tropical regions to cooling by 9, 7, 5, 3, and 1ºC h^{-1} down to -30ºC, then returning them to ambient temperature at a rise of 10ºC h^{-1}. Survival was better at fast and slow cooling rates, with low survival rates at intermediate cooling rates. Hengherr *et al*. suggested that this relationship may indicate a physical effect during fast cooling and possible synthesis of **cryoprotectants** during slow cooling. The increased survival with slower cooling indicates that tardigrades protect their cellular structure from freezing injury without altering their freezing temperature.

As indicated above, at least some protection seems to be accomplished by using **ice-nucleating proteins** in the body fluids (Westh *et al*. 1991). Such proteins serve as centers for crystal formation, a technique used to make snow for ski hills. This cryoprotective mechanism permits tardigrades to survive rapid freezing and thawing cycles such as those experienced in the Arctic and Antarctic. Usually this type of protection means that the nucleating centers are small, permitting only small crystals to form, consequently reducing damage to the cell membranes.

The ice-nucleating activity in the body fluid from ***Richtersius coronifer*** (Figure 48) is reduced by 50% following *ca* $7x10^3$ times dilution (Westh *et al*. 1991). Heating to temperatures above 68°C induces an abrupt decrease in the activity, suggesting that the nucleators are proteinaceous.

Westh and Kristensen (1992) examined ***Richtersius coronifer*** (Figure 48) and ***Bertolanius*** [=*Amphibolus*] ***nebulosus*** (see Figure 63) and compared their cryoprotective strategies. ***Richtersius coronifer*** (Figure 48) lives in drought-resistant mosses and overwinters in a frozen or dry state (cryptobiosis). ***Bertolanius nebulosus***, on the other hand, lives among moist mosses and algae and spends its winter frozen in a cyst or as eggs. Both species can supercool to as low as -7ºC. But these two species have distinctly different heat stability, resulting from differences in ice-nucleating proteins. In both cases, ice formation is rapid, but crystallization most likely stops within a minute of nucleation. This protects the cells from damage caused by large, sharp crystals. Nevertheless, ice constitutes 80-90% of the body water. Winter acclimatization of ***R. coronifer*** results in a 10% lower ice formation than summer acclimatization. The thaw point was unaffected by winter vs summer, suggesting that there is no accumulation of low molecular weight cryoprotective substances.

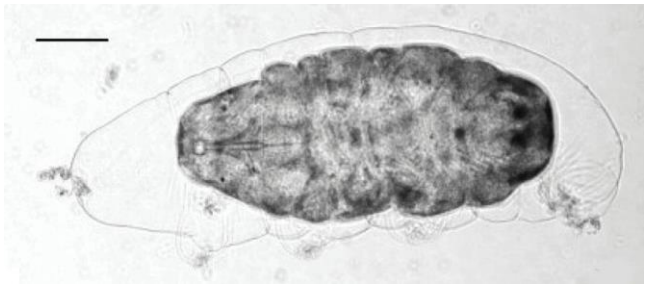

Figure 63. ***Bertolanius volubilis*** type A cyst. Photo by Roberto Bertolani from Bertolani *et al*. 2004, with permission.

Despite their seeming indestructibility, not all tardigrade individuals fare well at low temperatures, and some species fare better than others. Bertolani *et al*. (2004) demonstrated this for three species of tardigrades (Figure 64). ***Ramazzottius oberhaeuseri*** (Figure 25) seems to be almost indestructible down to -80ºC, whereas ***Hypsibius dujardini*** (Figure 16) had only 20% survival at that temperature. In fact, it had less than 80% survival at -9ºC.

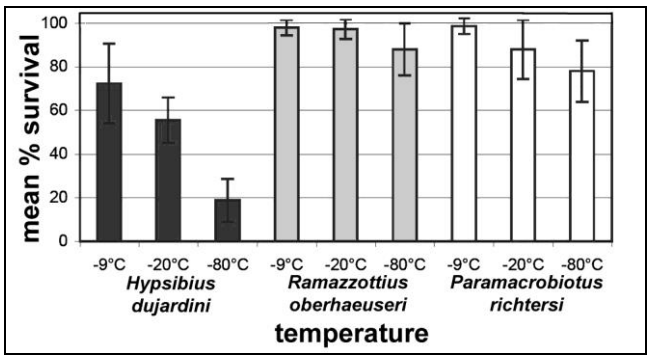

Figure 64. Comparison of survival of three bryophyte-dwelling tardigrades subjected to sub-zero temperatures. Redrawn from Bertolani *et al*. 2004.

Holmstrup *et al*. (2002) considered the problem of low temperatures in soil environments. Most of the work had been done on insects, but tardigrades are ideal for this kind of study. Insects often have the ability to supercool and to retain water in a dry environment. But non-insect soil invertebrates have resistance to desiccation that is orders of

magnitude less than that of terrestrial insects. This suggests that the other invertebrates may use an entirely different mechanism for surviving desiccation and cooling. Dehydration results because the water vapor pressure of supercooled water is higher than that of ice under the same temperature. A drop in temperature of even a few degrees of supercooling will cause considerable water loss. This loss continues until the vapor pressure of body fluids and that of surrounding ice are equal. When this is achieved, there is no longer any danger of ice formation in the tissues, permitting the invertebrate to survive at subzero temperatures. Holmstrup *et al*. (2002) showed that soil invertebrates do not use supercooling to survive. Instead, they dehydrate, changing their body-fluid melting point to that of the ambient temperature. This mechanism works even in the extreme cooling conditions and rapid rates seen in the polar soils.

Tardigrades live in many habitats that experience such cold temperatures. The widely fluctuating temperatures of the polar regions subject them to extremes while they are still in the active state. Thus they must either have the ability to tolerate the freezing of their body tissues or a means to lower their tissue freezing point (Hengherr *et al*. 2009).

Temperature

Rebecchi *et al*. (2009) pointed out that most stress studies on tardigrades had involved terrestrial tardigrades. Hence, they examined the limnic boreo-alpine species ***Borealibius zetlandicus*** for its stress responses. This species is able to survive freezing in lab experiments by entering a cryptobiotic state. Faster cooling rates lead to greater death from freezing. It furthermore is able to survive relatively "hot" water, having an experimental heat-shock LT50 of 33.0 ± 0.5°C. On the other hand, no members of this species were able to survive desiccation in the experiments. It is likely that in its natural habitat it is able to survive drying conditions by behavior – finding locations among moss leaves or in other plants or in muds where it does not dry as completely.

Ramløv and Westh (2001) studied ***Richtersius coronifer*** (Figure 48) and found that when this species enters anhydrobiosis it accumulates the disaccharide **trehalose**, with the maximum content of 2.3% of the dry weight. This species was able to survive temperatures up to 70°C in a moss cushion for an hour with no effect on survival rate. However, above that temperature, survival decreased rapidly, with no survival at 100°C. Ramaløv and Westh suggested that heat shock proteins may be involved in the high temperature survival.

Diapause (Encystment)

Tardigrades are especially endowed with the physiological ability to survive. They are among the few organisms that can use both **anhydrobiosis** and **diapause** (**encystment**) as a means of dormancy to survive unfavorable conditions (Guidetti *et al*. 2008). Diapause is common among aquatic tardigrades, but there are some terrestrial species that experience diapause (Westh & Kristensen 1992; Nelson 2002). Whereas cryptobiosis is well studied, the role of diapause (encystment) is not well known in tardigrades. It appears that it is not an essential part of the life cycle – only a means to survive some unfavorable conditions.

Węglarska (1957) found that ***Dactylobiotus dispar*** (Figure 65-Figure 68) was induced to encyst by environmental conditions that gradually became worse. Interestingly, when there was a rapid change to poor conditions, this tardigrade went into **anoxybiosis**. When a tardigrade is about to encyst, it ingests large amounts of food that is stored in the body cavity cells (Nelson 1991a). The remaining material in the gut is defecated.

Figure 65. ***Dactylobiotus*** sp. Photo by Yuuji Tsukii, with permission.

Encystment is more complex than **tun** formation (Bertolani *et al*. 2004). The **cysts** are ovoid and are composed of a series of cuticles that surround the sleeping animal (Figure 69; Guidetti *et al*. 2006). They are described as resembling an onion or a Matrioshka Russian doll.

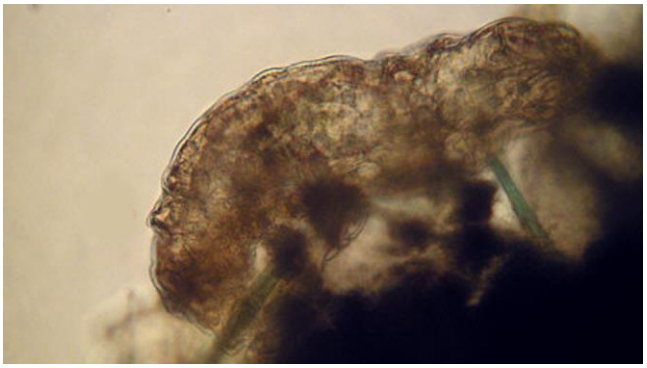

Figure 66. ***Dactylobiotus dispar***. Photo by Martin Mach, with permission.

Figure 67. Eggs of ***Dactylobiotus dispar***. Photo by Martin Mach, with permission.

During encystment, new cuticular structures are synthesized (Guidetti *et al*. 2006). Encystment starts with the discharge of the sclerified portions of the buccal-pharyngeal apparatus without the loss of cuticle. Rather, they produce two or three new cuticles. In ***Bertolanius*** [=*Amphibolus*] ***volubilis*** (Figure 69), the new cuticle is similar to that found on the non-encysted organisms, whereas in ***Dactylobiotus parthenogeneticus*** (Figure 70-Figure 72) the ultrastructure of the new cuticle differs. The tardigrade retracts within the cuticle (Nelson 1991a).

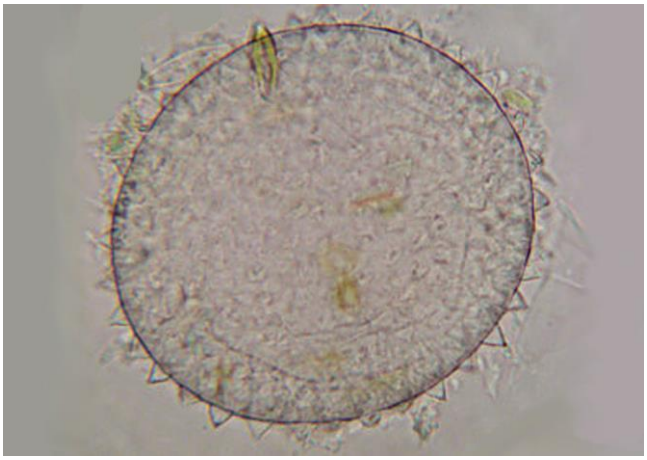

Figure 68. Egg of ***Dactylobiotus dispar***. Photo by Martin Mach, with permission.

Tardigrade encystment is known for only a few species, although it may be more widespread than is currently known. There are at least three types of cysts (Guidetti *et al*. 2006). ***Bertolanius volubilis*** has two types (Figure 69); ***Dactylobiotus parthenogeneticus*** (Figure 70-Figure 72) exhibits only one. Having two types of cysts in the same species seems to be a terrestrial character (Bertolani *et al*. 2004). Type 2 cysts have an additional layer of cuticle compared to type 1 cysts. Although only a few species have been described, it appears that a type 1 cyst never shows a modified buccal-pharyngeal apparatus, whereas a type 2 cyst does.

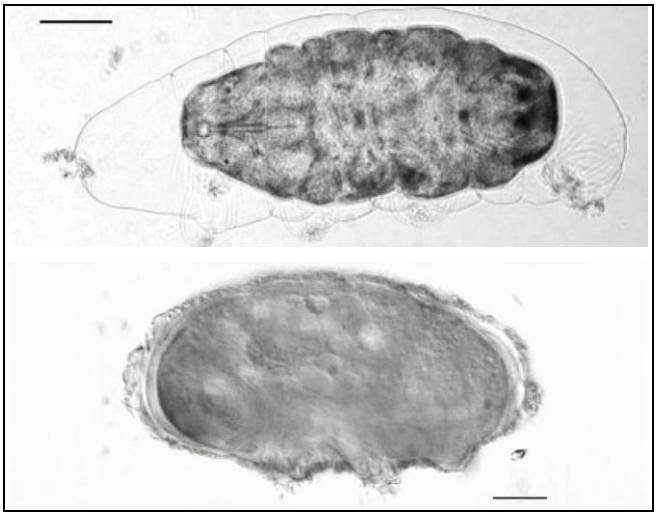

Figure 69. **Upper:** Type 1 cyst. **Lower:** Type 2 cyst (surrounded by several layers of cuticle), both of ***Bertolanius volubilis***. Photos by Roberto Bertolani in Bertolani *et al*. 2004, reproduced with permission.

Figure 70. ***Dactylobiotus*** sp., a member of a genus with only one type of diapause. Photo by Yuuji Tsukii, with permission.

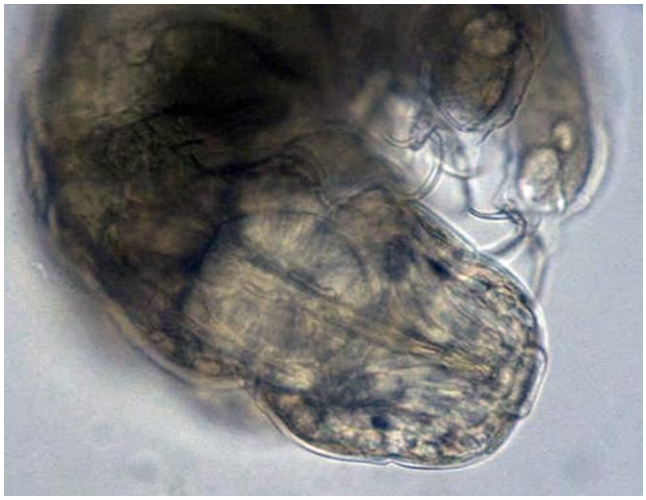

Figure 71. ***Dactylobiotus*** sp., a tardigrade with only one type of diapause cyst. Photo by Martin Mach, with permission.

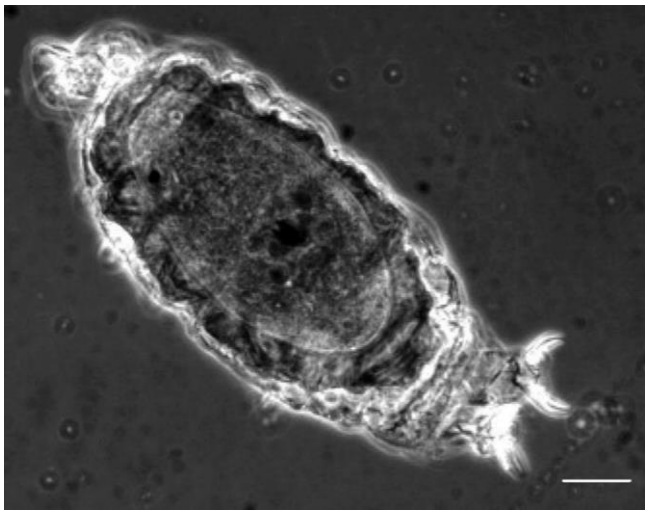

Figure 72. ***Dactylobiotus*** sp. cyst. Photo by Roberto Bertolani in Bertolani *et al*. 2004, reproduced with permission.

Conditions that cause emergence from the cysts are not understood. Unlike those in an anhydrobiotic state, the encysted tardigrades are not drought-resistant. Nor can they withstand high temperatures, because they have continuous water content. Nevertheless, the cysts can survive in nature for more than a year on their food reserves (Westh & Kristensen 1992).

Using the tardigrade ***Bertolanius volubilis*** (Figure 69) from the mosses ***Racomitrium sudeticum*** (Figure 73) and ***R. elongatum*** (Figure 74) on sandstone in the Northern Apennines of Italy, Guidetti *et al*. (2008) examined the factors involved in the inducement of diapause. They learned that in ***B. volubilis*** the type of diapause cysts produced in April differed from those produced in November. The April cysts are produced during a warm season, whereas the other type is present during the cold season. Temperature is responsible for induction, maintenance, and termination of the cyst. Both exogenous (temperature) and endogenous (physiological) factors serve as stimuli.

Figure 73. ***Racomitrium sudeticum***, where ***Bertolanius volubilis*** in the Northern Apennines of Italy undergoes diapause, forming spring cysts that differ from winter cysts. Photo by Michael Lüth, with permission.

Figure 74. ***Racomitrium elongatum***, a moss habitat in the Northern Apennines of Italy where ***Bertolanius volubilis*** makes different cysts in spring and winter. Photo by Michael Lüth, with permission.

Eggs

Eggs that are laid externally are typically ornamented (Figure 75-Figure 76) (Nelson 1991a). These may be laid singly or in groups.

Figure 75. Egg of a tardigrade, a stage that helps it survive desiccation. Photo by Martin Mach, with permission.

As already noted, eggs can provide a long-lasting escape from unfavorable conditions. At least some tardigrades can produce both **subitaneous** (non-resting) and **resting eggs** (Bertolani *et al*. 2004). Altiero *et al*. (2009) examined the eggs of ***Paramacrobiotus richtersi*** (Figure 17) and found that the percentage of hatching was high (75-93%), but that four different patterns were discernible. Subitaneous eggs hatched in 30-40 days. Delayed hatching eggs hatched in 41-62 days. Some eggs required 90 days or more if the culture was wet and 13% of these (**diapause resting eggs**) required a dry period followed by rehydration. The remainder (87% of this last >90-day category) never hatched. They considered this variable hatching time to be a form of **bet-hedging**.

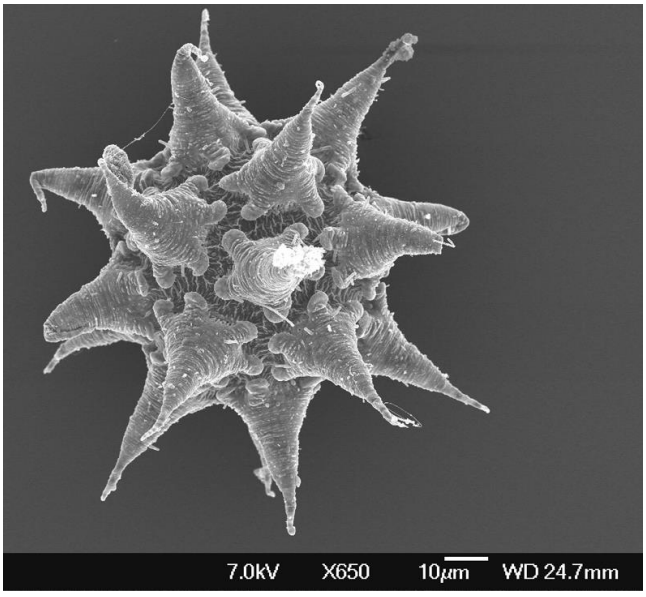

Figure 76. ***Macrobiotus szeptyckii*** egg showing the highly decorated surface of eggs laid free from the exuvia. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

Migration?

Anhydrobiosis is not the only strategy available to organisms to escape drying conditions. Some organisms migrate to deeper levels of the moss or soil to escape

drought. However, it appears that this option might not be available to many of the slow-moving tardigrades.

Wright (1991) found that those tardigrades living in the interstices of the moss habitat migrate vertically to the **soil C-zone** (layer just above bedrock) as a means of escaping or slowing desiccation. The exception to this behavior is ***Echiniscus testudo*** (Figure 5).

Nelson and Adkins (2001) examined this depth relationship in cushions of the moss ***Schistidium rivulare*** (=*Grimmia alpicola;* Figure 77). They found that among five species, only one (***Echiniscus viridissimus***) was more frequent in the top layer, regardless of the wet or dry condition of the moss. (Hmmm... Could the green that gives it its name indicate it has a photosynthetic symbiont that requires light, or just a penchant for green food?)

Nelson and Adkins (2001) concluded that none of the ***Schistidium*** (Figure 77) inhabitants used migration as a means to escape reduction in moisture. They speculated that for tardigrade inhabitants of xeric mosses, there was no advantage to migration. Rather, they stayed put and went into a state of anhydrobiosis in both upper and lower layers.

Figure 77. ***Schistidium rivulare***, a moss where excessive hydration can cause death to its tardigrade inhabitants. Photo by Michael Lüth, with permission.

Summary

Tardigrades (water bears) are common in both aquatic and terrestrial bryophytes. The land dwellers require a water film and thus are called **limnoterrestrial** tardigrades. Despite their worldwide distribution, they are not well known.

The bryophyte habitat offers sufficient oxygen, wetting and drying, sufficient food, a dispersal vehicle, and protection. Moisture is probably the most important factor in their distribution. Species of bryophytes do not seem to affect the types of tardigrades species.

Tardigrades are adapted to the bryophyte habitat by their small size, stylets that permit sucking contents from bryophyte cells, flexible bodies, and a very responsive life cycle. Colored **pigments** in some may offer UV protection, especially during dry periods. Tardigrades can **encyst** or go into a **cryptobiotic** state as a **tun**. Cysts may differ between summer and winter. Tardigrades must dry slowly to survive the cryptobiotic state. While in it, they are resistant to high and low temperature extremes, absence of water, extreme pressure, vacuum, and radiation. **Anhydrobiosis** is induced by diminishing hydration; **cryobiosis** is induced by low temperatures near 0ºC; **osmobiosis** is induced by a change in salinity; **anoxybiosis** is induced by low oxygen. Tardigrades form **trehaloses** that protect the cell membranes while dehydrated or at low temperatures. They typically can survive about 10 years in the tun, but one specimen resumed physiological activity after 120 years on a herbarium moss specimen, then died. Nevertheless, **DNA damage** accumulates during cryptobiosis; survival seems to be based on **DNA repair**. Furthermore, high temperatures and high humidity destroy trehalose.

Another means of long-term survival is by producing resistant eggs. Variable hatching times may provide a form of **bet-hedging** in some species.

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CHAPTER 5-2
TARDIGRADE REPRODUCTION AND FOOD

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CHAPTER 5-2
TARDIGRADE REPRODUCTION AND FOOD

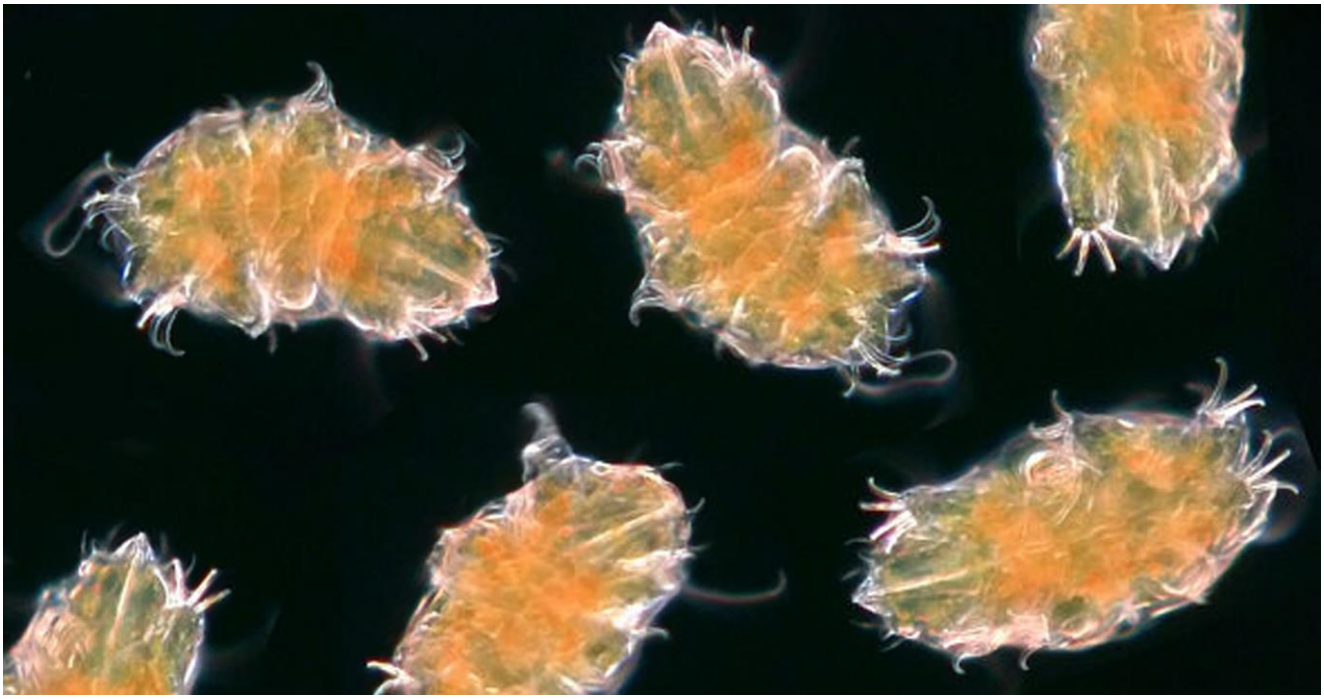

Figure 1. ***Echiniscus***, a parthenogenetic genus with at least 146 described species (Guidetti & Bertolani 2005). This genus is common on bryophytes and reproduces there. Photo by Martin Mach, with permission.

Life Cycle and Reproductive Strategies

One means by which organisms survive in such changeable habitats as bryophytes is by progressing to a different life cycle stage to wait out the storm – or lack of one. Tardigrades are especially adept at this, as seen in Chapter 5-1 (diapause and cryptobiosis). In tardigrades, diapause and cryptobiosis can occur at any time and developmental stage. Here we will look at reproduction and its role in further providing an escape route, at least for the species, if not the individual, an even that often occurs on bryophytes (Figure 1).

Hofmann (1987) considers that tardigrades must be able to reproduce quickly and in sufficient numbers when conditions are favorable because their life style is one of intermittent activity and inactivity, the latter in either a state of dormancy or cryptobiosis. This constraint of brief reproductive periods and the necessity for a few individuals to have sufficient offspring makes them **r-strategists**. They lack a defined carrying capacity and the population density is dependent upon the length of time since establishment in that location.

Life history of tardigrades can differ among species, presumably providing somewhat different adaptive strategies. For example, ***Paramacrobiotus tonollii*** (Figure 2) requires 16 days for its embryonic development whereas ***Macrobiotus sapiens*** requires only 12 days (Lemloh *et al.* 2011). ***Paramacrobiotus tonollii*** is larger than ***M. sapiens*** but the latter has a longer life span of 83 days.

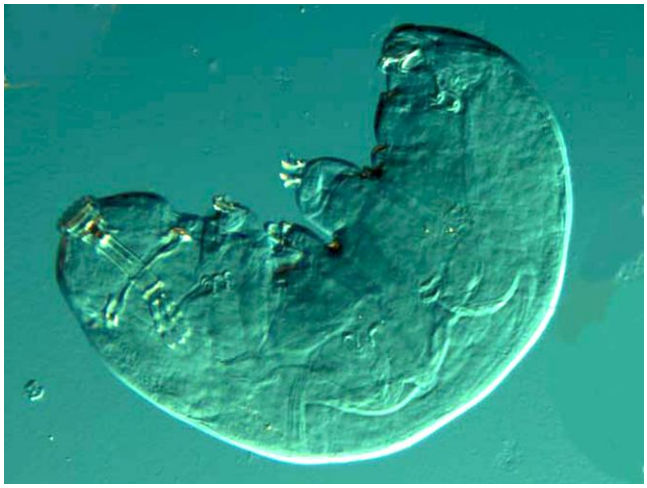

Figure 2. ***Paramacrobiotus tonollii***. Photo by Paul Bartels, with permission.

Reproductive Strategies and Habitat

Reproductive mechanisms do differ among tardigrades in different habitats (Bertolani 2001). Those living among bryophytes, as well as those of freshwater, leaf litter, and soil, commonly are **parthenogenetic** (Figure 1), or more rarely **hermaphrodites** that self-fertilize. Marine species, on the other hand, have separate sexes. Bertolani hypothesized that organisms living in isolated and unstable habitats (including bryophytes) have evolved **cryptobiosis**, **parthenogenesis**, **self-fertilization**, and **passive dispersal**, benefitting them in their challenging living conditions.

Passive wind dispersal of tardigrades with mosses is already known and may be their primary dispersal strategy (Pilato 1979). As is common among many mosses, those tardigrades that have **parthenogenesis** (equivalent to vegetative reproduction in mosses, *i.e.* reproduction without males) do not also have self-fertilization. These reproductive strategies, as in bryophytes, permit tardigrades to reproduce when only one individual, or its egg (Figure 3), arrives to colonize a new location.

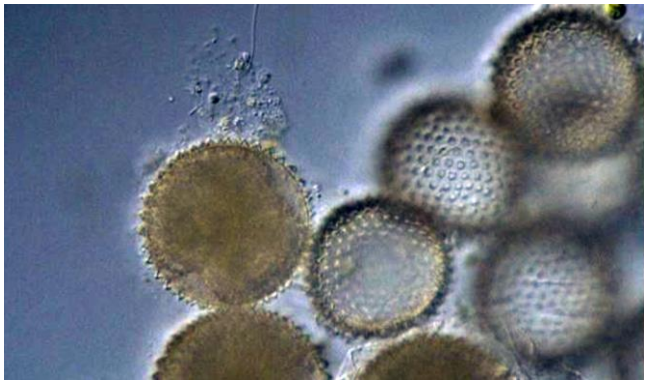

Figure 3. Eggs of a species of ***Dactylobiotus***. The clustering of eggs may be beneficial in protecting each other, but their inherent resistance to almost everything suggests that is probably not important. Photo by Yuuji Tsukii, with permission.

Dispersal in tardigrades seems independent of the tardigrade because it is passive dispersal. But Bertolani *et al*. (1990) considered that the differences in distribution and frequency of members of the genus ***Ramazzottius*** relate to their differences in reproductive modes. In their study of ***Ramazzottius*** species on bryophytes and lichens, they found that the sex ratio was strongly influenced by the type of reproduction, but also differed when samples were collected from tree trunks and limited rocky areas versus extensive rocky outcrops. Bertolani *et al*. found that bryophyte-dwelling ***Ramazzottius*** tardigrades from tree trunks or slightly rocky areas exhibited parthenogenesis and absence of male tardigrades. Among the rocky outcrops, there were always at least some males, although some parthenogenesis still occurred. Males are only useful if there is sufficient opportunity for contact with females. Perhaps the rocky outcrops provided less of a labyrinth and permitted the needed contact? Eggs provide light-weight, windborne propagules to disperse the species (Figure 3).

[To clarify for botanists, some references tend to use the term egg for the zygote and sometimes even the developing organism (embryo) until it has hatched, like the hatching of a bird egg. Since I found the term egg used in my references, I shall use egg here as well.]

Eggs

Depending on the species, there are two ways tardigrade eggs (including embryos) may be deposited. Some lay free eggs on their substrate (Figure 3), but others deposit them in the shed **exuvia** of a molt (Mach: The Water Bear; Figure 4).

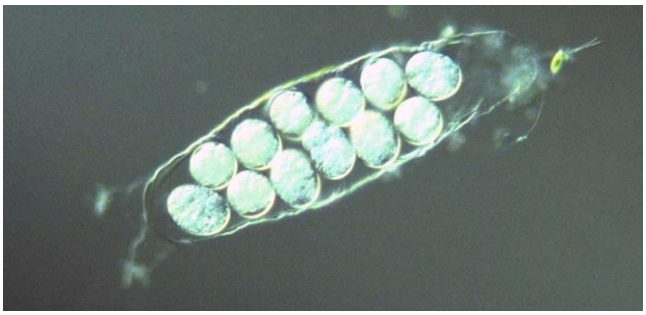

Figure 4. A number of eggs can develop within one shed **exuvia**, as shown here for ***Hypsibius*** sp. Photo by Yuuji Tsukii, with permission.

Macrobiotus hufelandi (Figure 5) has two sexes – males do exist (Figure 5) (Mach 2010). It is one of the species having free eggs (Figure 6). Eggs deposited outside the exuviae generally have decorative processes (Figure 7) (Mach 2010). Kinchin (1994) suggests that the functions of the egg processes include anchorage of the egg to a substrate or a transporting medium, defensive structure against being eaten by other animals, water reservoir which slows down the desiccation process, and regulation of gas exchange between egg and environment.

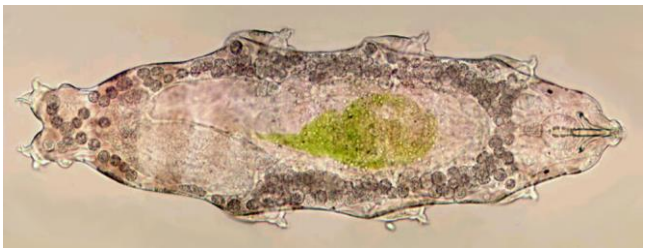

Figure 5. ***Macrobiotus hufelandi*** male. Photo by Martin Mach, with permission.

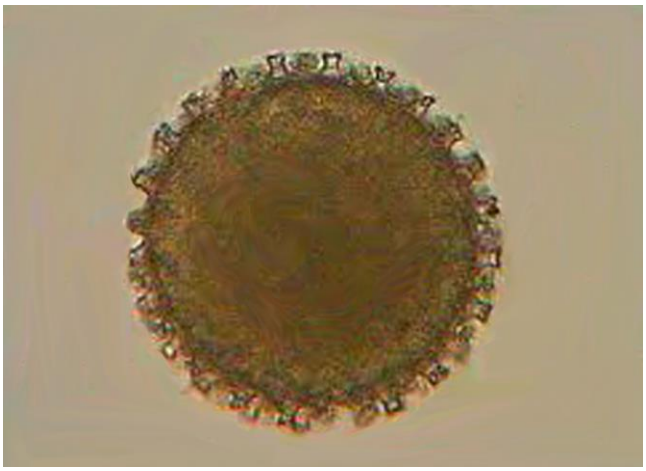

Figure 6. Egg of ***Macrobiotus hufelandi***, demonstrating the decorative processes on this free-egg deposit. Photo by Martin Mach, with permission.

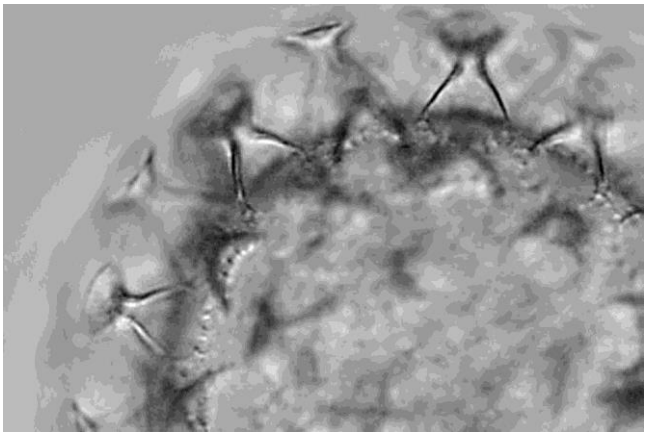

Figure 7. Egg of ***Macrobiotus*** sp., demonstrating the highly decorative surface that is typical of eggs laid free of the organism. Photo by Martin Mach, with permission.

When healthy adult tardigrades discard their outer covering, many taxa deposit eggs in these shed **exuviae** (outer "skins") (Figure 8-Figure 11) (Bertolani *et al*. 2009). The eggs may be few or many (up to 30-40) and may differ even within the same species, as can be seen for ***Milnesium tardigradum*** in Figure 9-Figure 11 (Altiero *et al*. 2006). The number of eggs depends on the species, but also on the nutritional status of the individual female (Mach: The Water Bear). And it seems that some bears may even ingest their own eggs to improve their nutritional status.

Egg development is poorly known. In ***Paramacrobiotus*** [=*Macrobiotus*] ***richtersi*** (Figure 12) it can be prolonged to 90 days or more if the eggs undergo desiccation and become resting eggs (Altiero *et al*. 2009). The non-resting (**subitaneous**) eggs may hatch in as little as 30-40 days.

Figure 8. These eggs reside in the shed exuvial "armor" of the parent and permit the tardigrade species to survive winter and desiccation. Photo by Martin Mach, with permission.

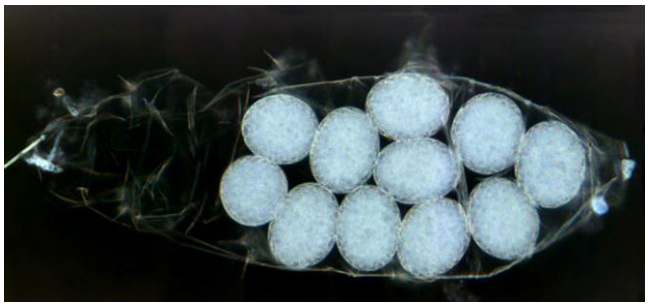

Figure 9. Individual of ***Milnesium tardigradum*** with eleven eggs in the shed exuvia. Photo by Martin Mach, with permission.

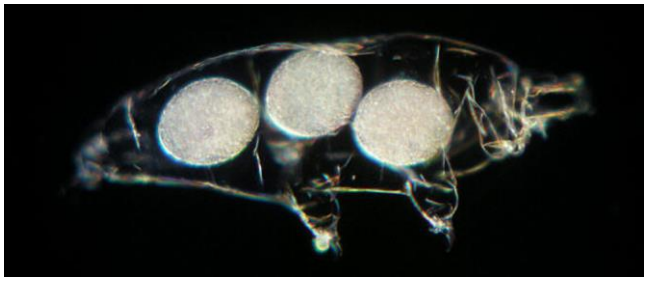

Figure 10. Individual of ***Milnesium tardigradum*** with only three large eggs in the exuvia. Photo by Martin Mach, with permission.

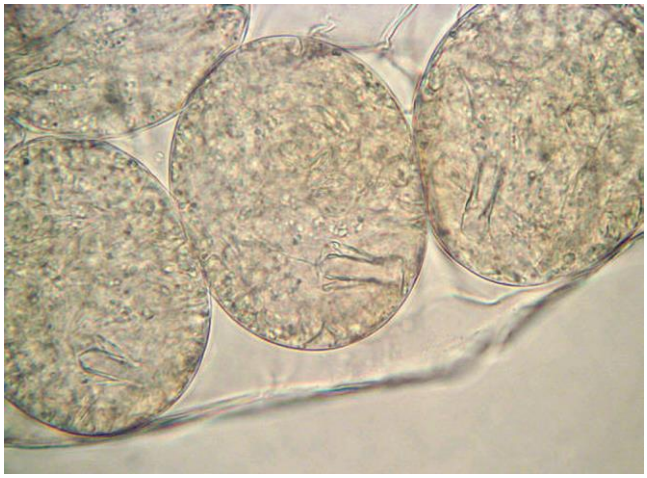

Figure 11. Developed eggs of ***Milnesium tardigradum*** with the buccal apparatus visible, indicating nearness to maturity. Photo by Martin Mach, with permission.

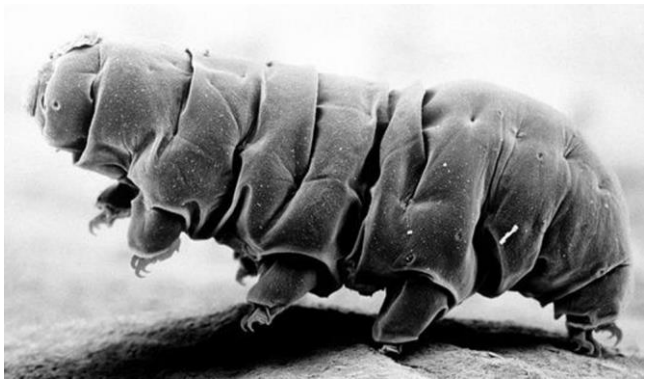

Figure 12. ***Paramacrobiotus richtersi***. Photo from Science Photo Library, through Creative Commons.

The eggs generally develop within the exuvia until the fully-formed tardigrade is ready to leave the egg, as shown here for individuals in the genus ***Echiniscus*** (Figure 13-Figure 19), requiring several weeks for completion (Mach: The Water Bear). The eggs are able to survive the same drying conditions as the adult; development stops during that dry state. The young tardigrades resemble the adults (Figure 20-Figure 23), but are smaller, requiring a series of molts as they grow. Growth occurs by cell enlargement rather than by addition of cells. Since the eggs often remain in the exuvia until they hatch (Figure 21), size would tend to reduce wind-dispersal of the pollen-grain-sized eggs except when they are dispersed along with a substrate such as mosses.

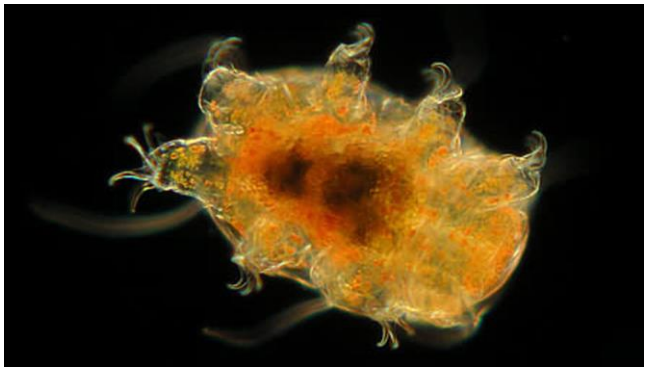

Figure 13. ***Echiniscus*** adult. Photo by Martin Mach, with permission.

Figure 14. ***Echiniscus*** exuvia with eggs (embryos) after first division. Photo by Martin Mach, with permission.

Figure 15. ***Echiniscus*** embryo after two divisions. Photo by Martin Mach, with permission.

Figure 16. Multicellular ***Echiniscus*** embryo Photo by Martin Mach, with permission.

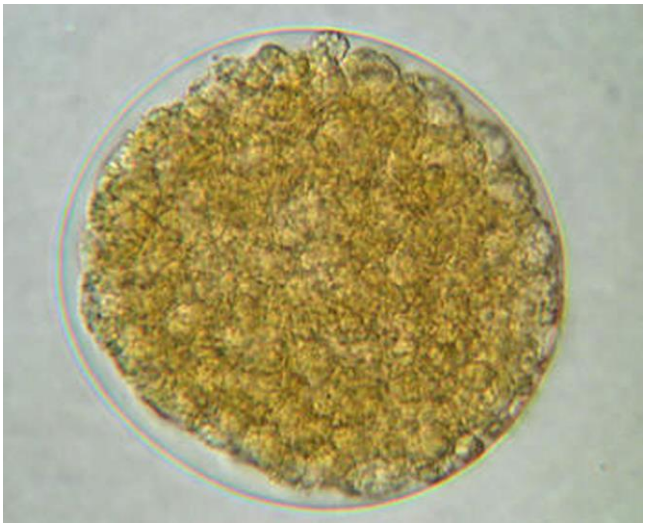

Figure 17. Morula stage in the embryo development of ***Echiniscus***. Photo by Martin Mach, with permission.

Figure 18. This mature "egg" of ***Echiniscus*** can be found among bryophytes, and its smooth surface is typical of eggs that are kept within the exuvia. Note the buccal apparatus that signifies its late developmental stage. Photo by Martin Mach, with permission.

In soil-dwelling ***Paramacrobiotus richtersi*** (Figure 12; also a known bryophyte dweller), temperature played a role in rate of development, survival rate, body growth, and generation time (Figure 24; Hohberg 2006). On the other hand, hatching time, first to fourth molts, and maturation time were dependent upon body size alone.

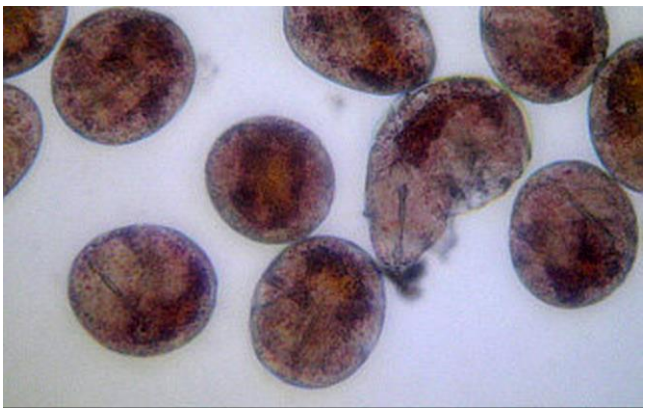

Figure 19. ***Echiniscus*** hatching from its eggs. Photo by Martin Mach, with permission.

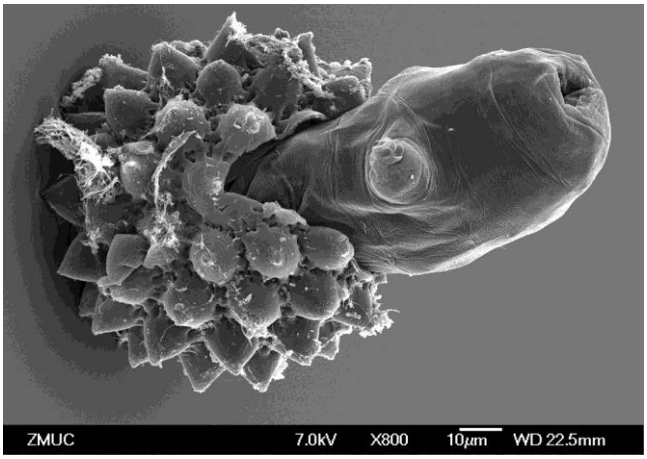

Figure 20. Moss-dweller ***Macrobiotus derkai*** hatching. from a free "egg." Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

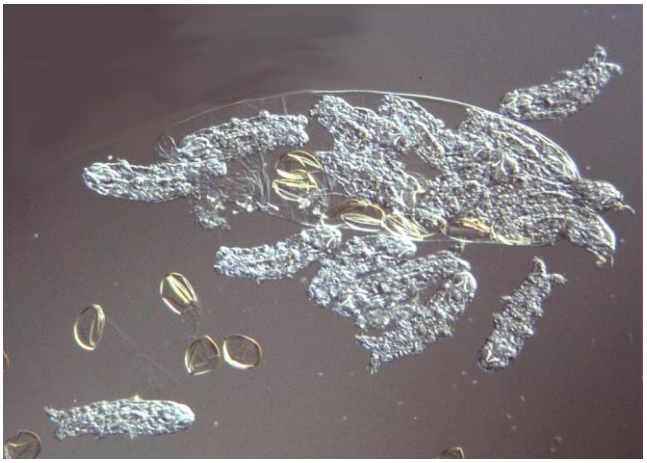

Figure 21. Despite the large number of eggs/embryos, it appears that most of them are successful in hatching into young tardigrades, as seen here for a species of ***Hypsibius***. Photo by Yuuji Tsukii, with permission.

Figure 22. ***Echiniscus*** young and old. Note the long "hairs" extending from the body, giving the genus its name. Photo by Martin Mach, with permission.

Figure 23. ***Echiniscus*** young. Photo by Martin Mach, with permission.

Some tardigrades have found another safe site for their eggs. They can use the capsule of a moss as an egg depository (Mach: The Water Bear; Figure 25-Figure 26).

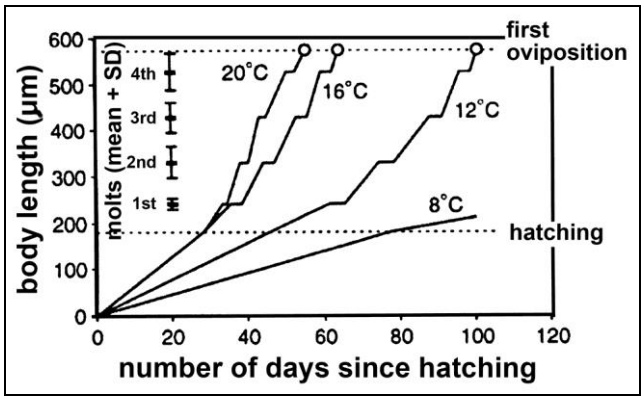

Figure 24. Effects of temperature on the development of ***Paramacrobiotus richtersi*** (Figure 12), starting with the day the tardigrades hatched. Body lengths are for hatching and first oviposition only. Redrawn from Hohberg (2006).

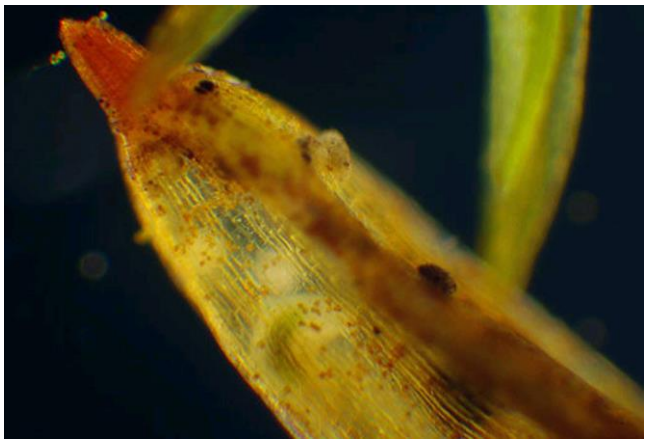

Figure 25. Moss capsule with tardigrade (with green gut) and two white eggs. Photo by Martin Mach, with permission.

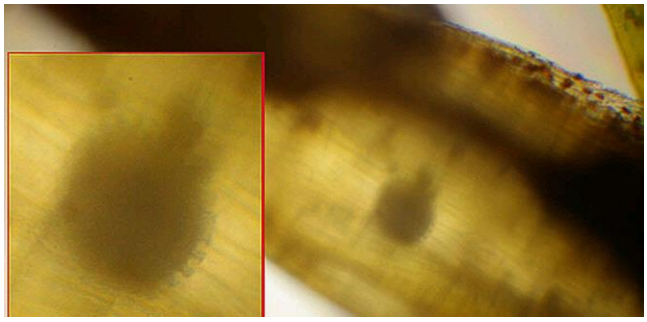

Figure 26. This egg is protected by a moss capsule. Based on the decorations on the eggs, they appear to be close to ***Macrobiotus hufelandi***. Photos by Martin Mach, with permission.

Molting

Like its relatives in the Arthropoda, the tardigrade must **molt** (Figure 27-Figure 35). This process usually requires 5-10 days and occurs several times throughout its life (Walz 1982), including after sexual maturity while the body is still increasing in size (Nelson 1982). During molting, the old cuticle, claws, and lining of the fore- and hindgut are shed (Figure 28), causing a stage known as the **simplex** stage (Figure 35). Lacking its sclerified parts of the buccal-pharyngeal apparatus, the tardigrade cannot feed. It appears that tardigrades molt 4-12 times during their 3-30 months of active lives (Nelson 2002).

Figure 27. ***Milnesium tardigradum*** as it recedes from its cuticle in preparation for molting. Note the dark brown eggs that will soon be left behind. Photo by Martin Mach, with permission.

Figure 28. ***Milnesium tardigradum*** emerging from its exuvia during molting, leaving its claws, eggs, and various other parts behind. Photo by Martin Mach, with permission.

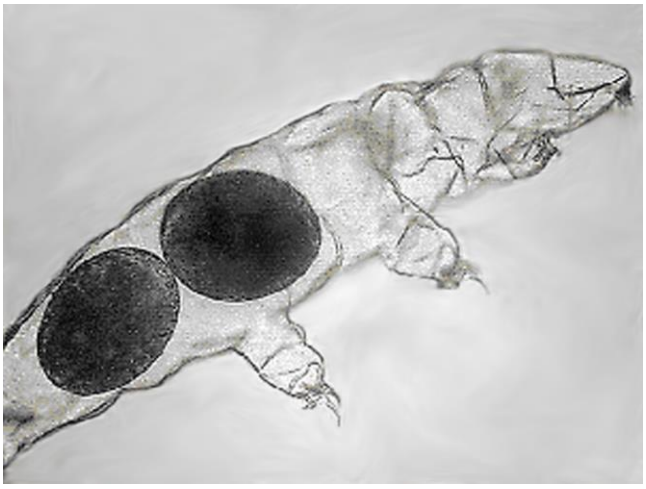

Figure 29. Eggs in the shed exuvia of ***Milnesium tardigradum***. Photo by Martin Mach, with permission.

Figure 30. ***Milnesium tardigradum*** eggs in its shed exuvia. Photo by Martin Mach, with permission.

Cyclomorphosis

It appears that **cyclomorphosis** (annual cycle of morphological change) occurs in tardigrades, although it has been demonstrated in only a few species. It has been documented in the marine species *Halobiotus crispae* (Kristensen 1982; Halberg *et al*. 2009). Likewise, Dastych (1993) demonstrated cyclomorphosis in a cryoconite-dwelling species of ***Hypsibius*** (Figure 31), and in a bryophyte dweller. Furthermore, Rebecchi and Bertolani (1994) did demonstrate it for one species in the genus ***Bertolanius*** [=*Amphibolus*] (Figure 33), which does have moss-dwelling species.

Kristensen (1982) studied the marine *Halobiotus crispae* cycle and found two morphs. In winter there is a **pseudosimplex** stage that hibernates and is sexually immature. These winter forms gather in large **aggregations** in protected areas where the aggregations increase chances for survival of the freezing temperatures. The population experiences synchronous development of gonads, hence all reaching sexual maturity and breeding simultaneously. But the cycle for other taxa and habitats, including bryophytes, remains to be explored (Nelson 2002).

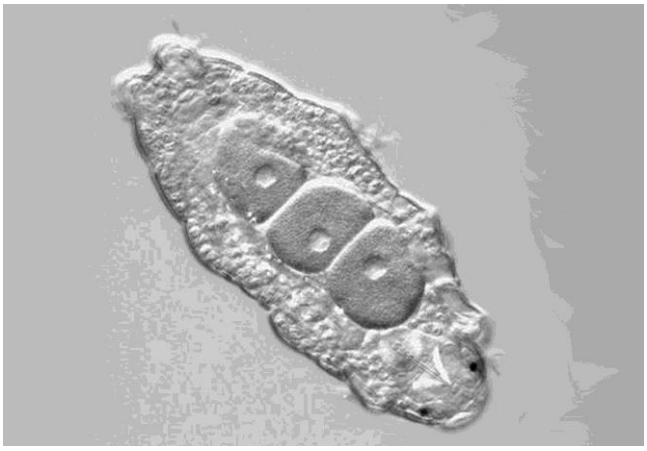

Figure 32. ***Hypsibius dujardini*** with 3 oocytes. Photo by Willow Gabriel, through EOL Creative Commons.

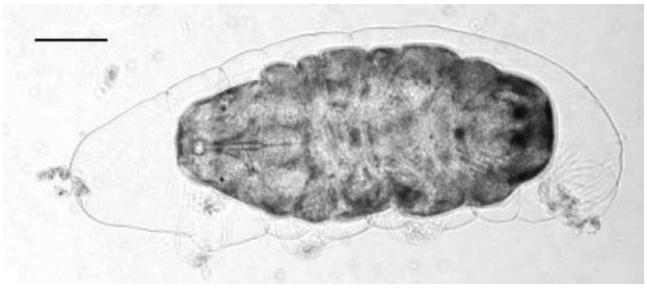

Figure 33. ***Bertolanius volubilis*** cuticle with a type A cyst inside. Photo by Roberto Bertolani, with permission.

Figure 34. ***Ramazzottius oberhaeuseri*** completing its molt out of its old cuticle. The emerging organism will remain in this **simplex** stage until it rebuilds its cuticular parts. Photo by Martin Mach, with permission.

Bryophytes as Food Reservoirs

Bryophyte-dwelling tardigrades include both bryophyte-eating tardigrades and those with a variety of other feeding strategies, including carnivory. The tardigrade has a specially adapted pair of **stylets** (Figure 49) and a muscular pharynx (Figure 50-Figure 52) that produces a suction into the gut, permitting the tardigrade to suck fluids from the interior of a bryophyte or algal cell (Figure 53) or even small animals such as rotifers (Figure 54) and nematodes [Tardigrada (Water Bears) 2005]. In the family Echiniscidae (Figure 36), a common family on bryophytes, the stylet may be very long, permitting penetration of the thick cellulose walls of bryophytes. For example, ***Echiniscus testudo*** (Figure 37) feeds primarily on bryophytes (Morgan 1977). ***Diphascon*** (Figure 52), also a bryophyte dweller, has a flexible buccal tube with spiral rings resembling the extension on a vacuum cleaner. Small bryophyte dwellers may subsist on diatoms and bacteria that live epiphytically among the bryophytes [Bartels 2005; Tardigrada (Water Bears) 2005].

Figure 35. *Pseudobiotus* sp. shedding its cuticular exuvia and leaving its eggs/embryos behind. Photo by Paul Davison, with permission.

Figure 36. ***Echiniscus perviridis*** with green color, most likely due to its vegetarian diet. ***Echiniscus testudo*** is known to feed primarily on bryophytes. Photo by Łukasz Kaczmarek, with permission.

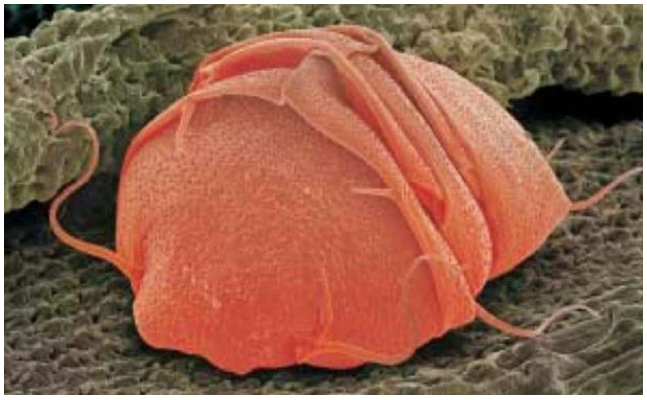

Figure 37. ***Echiniscus testudo*** tun. Photo by Power & Syred through Creative Commons.

Schill *et al*. (2011) consider the bryophytes to be a "rich food supply for both carnivorous and herbivorous species." These food sources include nematodes, rotifers, plant cells, algae (Figure 38), yeast, and bacteria, and for some, bryophytes. Schill and coworkers conducted a genetic tracer study (rbcL) on the guts of tardigrade species from various sites in Europe that demonstrated the presence of mosses from the **Erpodiaceae [*Aulacopilum hodgkinsoniae*, *Venturiella sinensis*** (Figure 39)] and **Pottiaceae** [***Syntrichia*** (=*Tortula*) ***obtusissima*** (Figure 40)] in the guts of field-collected ***Macrobiotus sapiens***, **Grimmiaceae** [***Grimmia elongata*** (Figure 41), ***Coscinodon cribrosus*** (Figure 42), ***Schistidium strictum*** (Figure 43)] from ***Macrobiotus persimilis*** and ***Echiniscus granulatus***, and the green alga ***Trebouxia*** (Figure 44) from ***Richtersius coronifer*** (Figure 38). For ***Macrobiotus sapiens*** they found no rbcL sequence demonstrating presence of the families **Pottiaceae** or **Orthotrichaceae**. It appears that ***Macrobiotus sapiens*** will only eat these latter two moss families when **Grimmiaceae** is not available, or that others had been digested completely before samples were extracted. The small tardigrade stylet makes it difficult for them to obtain cell contents from the moss genera ***Polytrichum*** (Figure 45), ***Dicranum*** (Figure 46), ***Leucobryum*** (Figure 47), and ***Racomitrium*** (Figure 48). Digestion in tardigrades is aided by the gut *p*H, with the foregut having an acidic environment and the midgut having a basic environment (Marcus 1928).

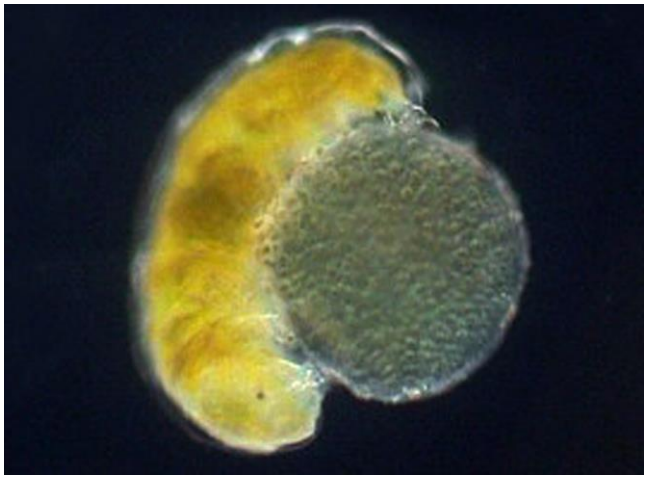

Figure 38. ***Richtersius coronifer***, clinging to an algal cell. Photo by Martin Mach, with permission.

Figure 39. ***Venturiella sinensis***, a moss eaten by ***Macrobiotus sapiens***. Photo from Digital Museum, Hiroshima University, with permission, with permission.

Figure 40. ***Syntrichia obtusissima*** showing hair points. Photo by Claudio Delgadillo, with permission.

Figure 41. ***Grimmia elongata***, a moss eaten by ***Macrobiotus persimilis*** and ***Echiniscus granulatus***. Photo by Michael Lüth, with permission.

Figure 42. ***Coscinodon cribrosus***, a moss that is suitable habitat and food for ***Macrobiotus persimilis*** and ***Echiniscus granulatus***. Photo by Michael Lüth, with permission.

Figure 43. ***Schistidium strictum***, a moss that is eaten by ***Macrobiotus persimilis*** and ***Echiniscus granulatus***. Photo by Jan-Peter Frahm, with permission.

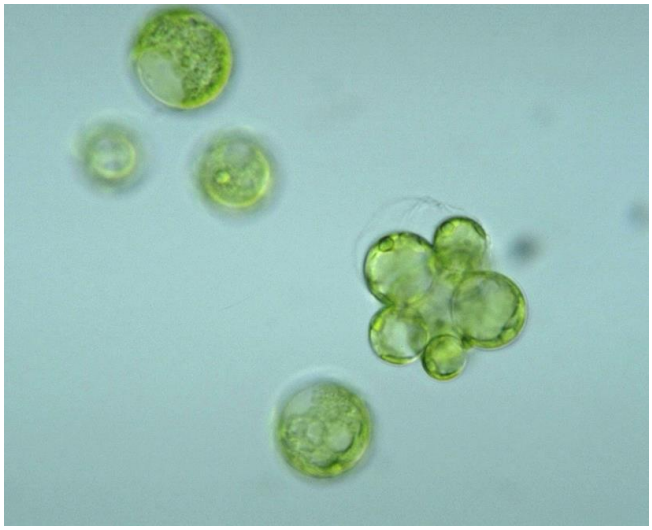

Figure 44. *Trebouxia*, a lichen symbiont that appeared in the guts of field collected ***Macrobiotus persimilis*** and ***Echiniscus granulatus***. Photo by Yuuki Tsukii, with permission.

Figure 45. ***Polytrichum commune***, a moss with thick leaves that make feeding by tardigrades difficult. Photo by Michael Lüth, with permission.

Figure 46. ***Dicranum scoparium***, a moss with leaves that seem to make feeding by tardigrades difficult. Photo by Janice Glime.

Figure 47. ***Leucobryum glaucum***, showing thick leaves that make tardigrade feeding difficult. Photo by James K. Lindsey, with permission.

Figure 48. ***Racomitrium macounii*** ssp ***macounii***, a moss with leaves that seem to make feeding by tardigrades difficult, in Europe. Photo by Michael Lüth, with permission.

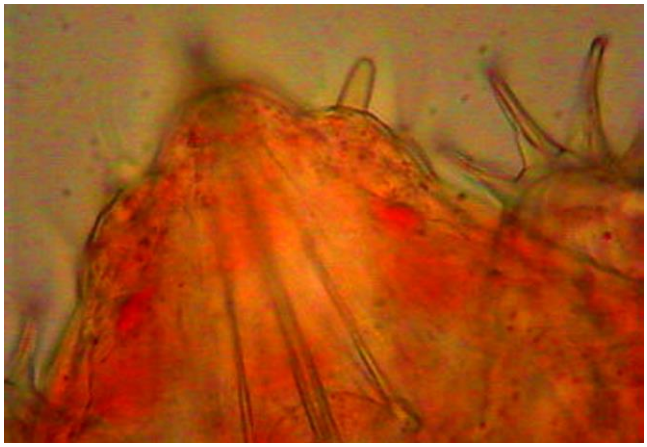

Figure 49. ***Echiniscus*** with the stylets protruding (out of focus). Photo by Martin Mach, with permission.

Tardigrades even consume smaller tardigrades. Larger species such as those of ***Macrobiotus*** (Figure 5) and ***Milnesium*** (Figure 9, Figure 51) consume smaller members such as ***Diphascon*** (Figure 52) and ***Hypsibius*** (Figure 64), as exhibited by remains of claws and buccal apparati (Figure 57) in the gut (Nelson 2002). Large carnivorous Eutardigrada such as ***Paramacrobiotus richtersi*** (Figure 12), ***Milnesium tardigradum*** (Figure 9, Figure 10, Figure 51, Figure 54), and ***Bertolanius nebulosus*** are widespread in many habitats, including bryophytes [Tardigrada (Water Bears) 2005]. They eat nematodes, rotifers, and smaller tardigrades, but still use the stylet to suck out cell contents. Suzuki (2003) reared ***Milnesium tardigradum*** from the moss ***Bryum argenteum*** (Figure 55), using only rotifers [***Lecane inermis***, common in wet ***Sphagnum*** (Miller 1931)] as food.

Figure 50. This tardigrade has the stylets withdrawn into its head. The pharynx is in the center behind the stylets. Photo by Paul Davison, with permission.

Figure 51. "Head" region of ***Milnesium tardigradum*** showing the pharynx. Photo by Martin Mach, with permission.

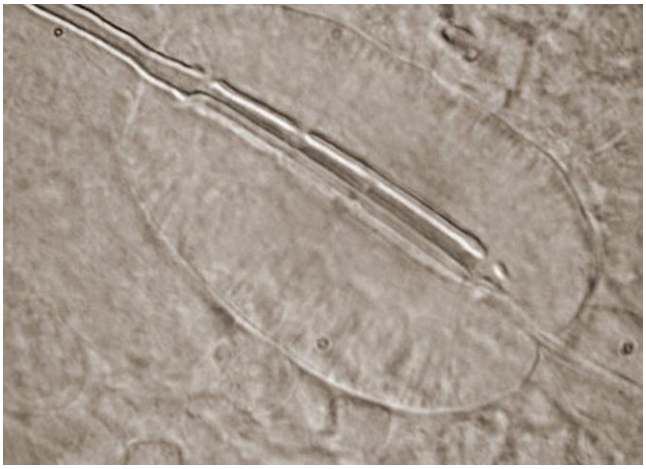

Figure 52. Pharynx (oval) of ***Diphascon***, the organ that produces the suction for the stylets. Photo by Martin Mach, with permission.

Figure 53. The green in this tardigrade is likely to be algae or moss. Photo by Paul Davison, with permission.

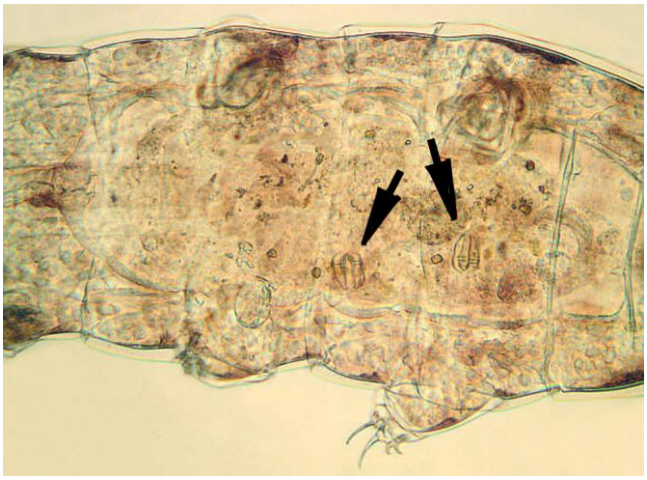

Figure 54. ***Milnesium*** with the mastax of rotifers visible in the gut (black arrows). Photo by Martin Mach, with permission.

Figure 55. ***Bryum argenteum***, a moss known to house ***Milnesium tardigradum***. Photo by Michael Lüth, with permission.

Suren (1988) attempted to determine the importance of bryophytes as food vs. simply substrate by using artificial mosses in high alpine New Zealand streams. When artificial structures were used, similar communities of invertebrates developed, but tardigrades appeared to be affected negatively by the absence of the bryophytes, a difference Suren interpreted to reflect a loss of bryophytes as a food source. It seems to be one of the few animals specifically adapted to obtaining the good stuff from the insides of the cells of bryophytes. Its stylets (Figure 49-Figure 50) serve as a miniature needle and straw to puncture the cell and suck the nutrients from it. The pharynx (Figure 52) serves as a pump to draw fluids in through the stylets (Tardigrades, Bears of the Moss).

It appears that eating bryophytes requires more than just the equipment to suck the good stuff out of the cell. The excretory system seems also to be altered. Węglarska (1990) found that in four genera of tardigrades, those that live among bryophytes have larger excretory organs relative to body size than do the freshwater species. The purpose of this added size remains a mystery.

Ramazzotti and Maucci (1983) suggested that excretion probably occurs in four ways in tardigrades. At molting it occurs through the salivary glands. Likewise, when the cuticle is shed it removes accumulated excretory granules. It can occur through the wall of the midgut. And in the eutardigrades, it occurs through excretory glands. There is no study to determine how these various mechanisms might relate to a diet of bryophytes.

Role in Food Web

As seen above, tardigrades typically are either plant eaters or are carnivorous (Garey *et al*. 2008), including protozoa, nematodes, and rotifers (Figure 54), but also consume bacteria and fungi (Kinchin 1988). As noted in the earlier chapter on nematodes, they can be predators on nematodes that live in the same clump of moss (Sánchez-Moreno *et al*. 2008), making them important consumers and often the top carnivore.

Both ***Paramacrobiotus*** [=*Macrobiotus*] ***richtersi*** (Figure 12) and ***Macrobiotus harmsworthi*** (Figure 56-Figure 57) caused significant declines in the nematode populations, thus regulating the food web. In fact, a single ***P. richtersi*** dined on an average of 61 nematodes in a day! Unlike many of the slow-walking water bears, these carnivorous water bears are able to move swiftly to attack and devour their prey (Kristensen & Sørensen 2005).

Davison (2005) reports that tardigrades lumber across the substrate, swinging their heads back and forth in search of food. When he offered them nematodes and rotifers, the tardigrades made no attempt to eat them. When he offered them a larger choice, the annelid ***Lumbriculus*** sp., a genus with known members that inhabit mosses, he found that they immediately approached it and began eating it.

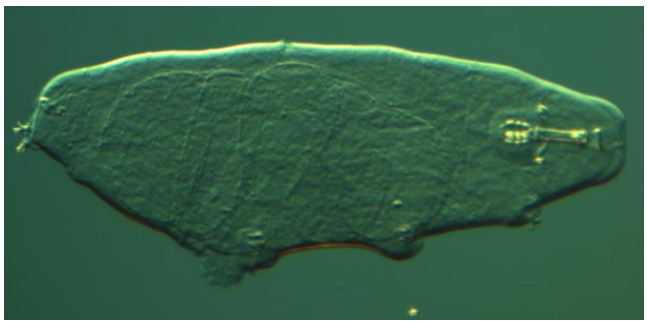

Figure 56. ***Macrobiotus harmsworthi***, a nematode predator. Photo by Paul J. Bartels, with permission.

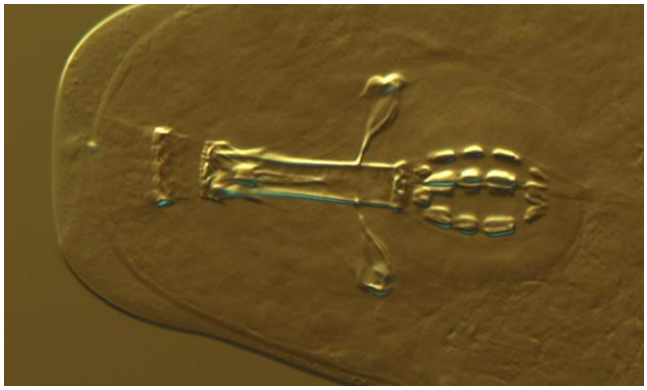

Figure 57. ***Macrobiotus harmsworthi*** buccal apparatus. Photo by Paul Bartels, with permission.

Tardigrade specialists have assumed that the **buccal apparatus** (Figure 58-Figure 60) indicates characteristics of the food, but no studies exist on the relationships of buccal apparati among the limnoterrestrial taxa (Nelson 2002).

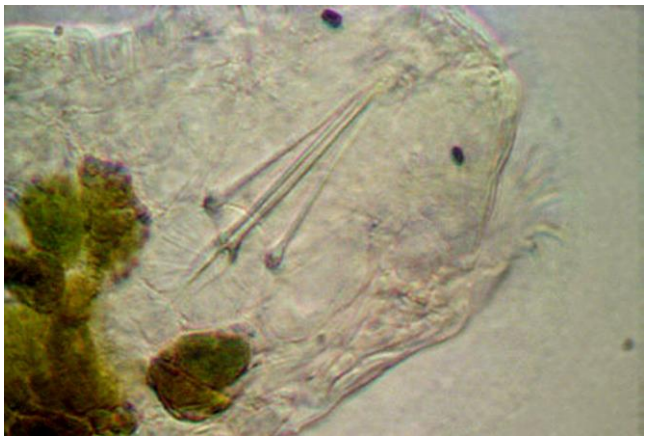

Figure 58. The three "filaments" and pharynx are the buccal apparatus of this ***Echiniscoides sigismundi***. The **pharynx** resembles a pair of kidneys in contact with the three filaments. The outer two filaments are the stylets; the inner one is the buccal tube. The gut contains algal or plant material that has been ingested by this tidal zone species. Photo by Martin Mach, with permission.

Figure 59. The three "filaments" and oval behind them are the buccal apparatus of ***Paramacrobiotus*** [=*Macrobiotus*] ***areolatus***. The bulbous oval to the right of the three filaments (stylets and buccal tube) is the pharynx. Photo by Martin Mach, with permission.

Figure 60. ***Dactylobiotus dispar*** has a buccal apparatus similar to that of ***Paramacrobiotus areolatus***. Photo by Martin Mach, with permission.

But tardigrades can have their predators too. Snails that live among the moss leaves could enjoy a meal of tardigrades (Fox 1966). The land snail ***Bulimulus guadalupensis*** (Figure 61) from Puerto Rico had evidence that all life cycle stages of the tardigrade ***Echiniscus molluscorum*** (see Figure 62) live in its feces (Fox & Garcia-Moll 1962). It is not clear if these passed unharmed through the gut or if they took advantage of the feces as a food source after defecation. It is even possible that eggs passed through the gut and hatched in the feces.

Figure 61. The land snail ***Bulimulus guadalupensis*** is a known predator on moss-dwelling tardigrades. Photo by Gary Rosenberg at <www.discoverlife.org>.

Tardigrades have smaller predators as well. The fungus ***Ballocephala pedicellata*** (Figure 63) is known from the tardigrades ***Hypsibius dujardini*** (Figure 64) and ***Diphascon pingue*** complex (Figure 65) living in the moss ***Atrichum angustatum*** (Figure 66) (Pohlad & Bernard 1978). In this study, tardigrades with the fungus were only

present in January and February in the collecting area in southeastern USA.

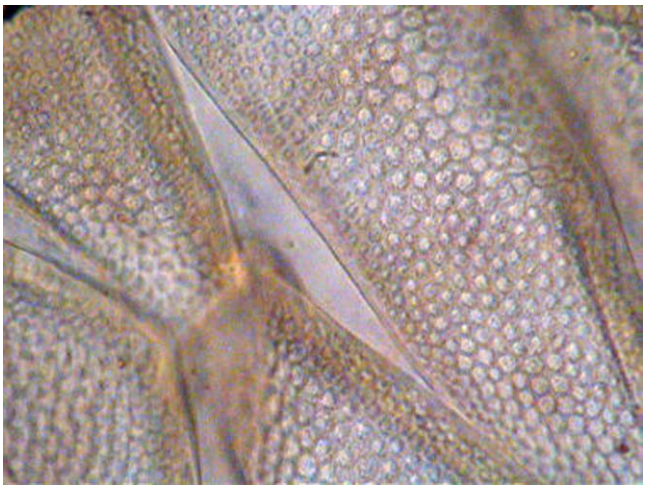

Figure 62. Armor of ***Echiniscus*** sp. Material such as this is easy to identify in the feces of predators. Photo by Martin Mach, with permission.

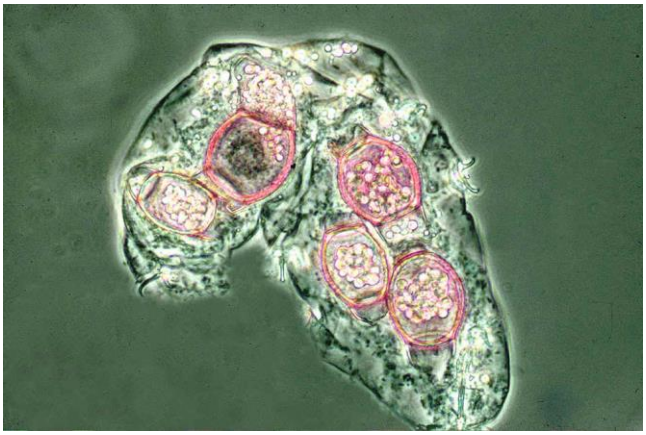

Figure 63. ***Ballocephala sphaerospora*** zygospores in a tardigrade. Photo by George Barron, with permission.

Figure 64. ***Hypsibius dujardini***, a host for the fungus ***Ballocephala pedicellata***. Photo from Rpgch Wikimedia Commons.

Figure 65. ***Diphascon pingue***. Photo by Michael Collins, with permission.

Figure 66. ***Atrichum angustatum***, a habitat for tardigrades, and in winter, their parasitic fungus ***Ballocephala pedicellata***. Photo by Michael Lüth, with permission.

Summary

Life cycle stages often provide a means of surviving changes in the environment. Bryophyte-dwelling tardigrades are usually **parthenogenetic**. They rarely are **hermaphrodites**, and parthenogenetic individuals do not self-fertilize.

Tardigrade species may either lay free eggs or deposit them inside the exuvia as it is shed. External eggs are usually highly decorated, whereas those laid inside the exuvia tend toward smooth. The number of eggs varies up to 40, with the number depending on the species and nutritional status. Time required for development of the fertilized egg may be up to 90 days. Variability in development time permits **bet-hedging**. Temperature affects development rate, survival rate, and body growth, as well as affecting generation time. Young tardigrades resemble the adults and continue to grow by cell enlargement. Molting permits the tardigrade to expand its size and requires 5-10 days during which the tardigrade cannot eat and is less protected. Some species have more than one morph, where the winter morph may form aggregations that enhance survival of freezing conditions.

Tardigrades consume algae, bryophytes, fungi, protozoa, nematodes, rotifers, and smaller tardigrades. In many cases this is accomplished using a **stylet** that forms a straw for sucking cell contents. They suck in their prey with the pair of stylets, with the muscular pharynx producing suction. For whatever reason, bryophyte dwellers also have larger excretory organs than do tardigrades of other substrata.

They play an important role in regulating the food web of bryophytes in some circumstances. Tardigrades are subject to predation by snails and even larger tardigrades. Fungi may extract nutrition from them.

Acknowledgments

Like all of my chapters, this one is really the product of the efforts of many biologists. Roberto Bertolani provided an invaluable update to the tardigrade taxonomic names and offered several suggestions on the text to provide clarification or correct errors. Bryonetters have been wonderful in making their photographs available to me and seeking photographs from others. Paul Davison has been helpful in providing suggestions and offering images. Martin Mach and Yuuji Tsukii have given permission to use images that illustrate the species and life cycle stages. Łukasz Kaczmarek has provided me with references and contact information. Claudio Delgadillo was kind enough to take the picture of *Syntrichia obtusissima* just for this chapter. Martin Mach was kind enough to send me corrections for typos in the previous online version. My sister, Eileen Dumire, read and edited an earlier version of the chapter for me from the viewpoint of a non-biologist. And a big thank you goes to Michael Lüth for permission to use his many images and to all those who have contributed their images to Wikimedia Commons for all to use. I fear I have forgotten some who have helped – I have worked on this chapter for too many years.

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CHAPTER 5-3
TARDIGRADE HABITATS

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CHAPTER 5-3
TARDIGRADE HABITATS

Figure 1. ***Echiniscus*** sp., member of a genus that is common on bryophytes. Photo by Martin Mach, with permission.

Bryophyte Habitats

Tardigrades exist in both aquatic and terrestrial habitats worldwide, and in both cases can be found with bryophytes (Figure 1) (and lichens and leaf litter) (Utsugi *et al*. 1997). The tropics seem unfavorable (Mathews 1938), perhaps for the same reasons that temperate stream bryophytes are uncommon in lowland tropical waters – they are warm and wet at the same time, encouraging bacterial and fungal growth.

Most of the more than 900 known tardigrade species are **limnoterrestrial** (Garey *et al* 2008). That is, they live in a thin surface film of water, most commonly on bryophytes, lichens, algae, and other plants. They can only remain active while this film of water exists. Of the 910 species reviewed by Garey *et al*. (2008), only 62 species, in 13 genera, are truly aquatic and unknown from limnoterrestrial habitats. Nevertheless, many of the limnoterrestrial species can at least occasionally be found in freshwater. In these terrestrial habitats, *p*H of the substrate, oxygen tension, moisture content of the bryophyte, thickness of the bryophyte mat or cushion, and altitude (and its attendant conditions) all contribute to the habitat distribution.

I have taken the liberty of changing the word "moss," used in many tardigrade studies, to "bryophyte." I have learned from one of my kind tardigrade reviewers that people who study tardigrades often do not understand leafy liverworts and lump them into mosses. Hence, unless I could determine that the researcher definitely had in mind only mosses (and not also liverworts), I used the term bryophytes. I also learned that many ecologists include mosses in the category of "soil"! Others include them in "litter." While this lumping can be a useful concept for some aspects of functional ecology, one needs to be aware of it when searching for bryological literature or interpreting soil literature.

Tardigrades are especially common on tree bark bryophytes (**epiphytes**), presumably due to having similar tolerances to drying (Crum 1976). They are known from all seven continents and up to 6600 m altitude in the Himalayas (Ehrenberg 1859 in Fontoura *et al*. 2009). Collins and Bateman (2001) examined factors affecting tardigrade distribution in Newfoundland and learned that in this case altitude and type of bedrock were important in determining tardigrade distribution. Moisture and rate of drying further defined their distribution. And in some cases, competitive exclusion or interspecific competition seemed to be determining factors for community composition.

Specificity

Species assemblages seem to be similar throughout the world. Is this due to lack of taxonomic understanding or to widespread dispersal? In the following sections we will examine what we know about factors affecting tardigrade communities under different circumstances.

It appears that many tardigrades have little preference for bryophytes versus lichens (Meyer & Hinton 2007). But even those cryptogams, supporting their wet-dry requirements, are usually not unique habitats for the tardigrades, with the same species of bryophytes and lichens also present in soil, leaf litter, and additional habitats. Several studies have attempted to show any species preferences for bryophytes, but typically with no success (Kathman & Cross 1991; Miller & Heatwole 1995; Meyer & Hinton 2007). Further evidence of non-specificity is in their distribution. Meyer and Hinton (2007) report that the Nearctic realm shares 82 species of tardigrade with the Neotropical realm. Everything is everywhere! On the other hand, 30% of the Nearctic species are known from only one site. One of the problems in describing the tardigrade habitat is that substrate records are inconsistent or absent for many collections.

But some studies have indicated that lichens and mosses may be preferred over other substrata. Working in China, Beasley *et al*. (2006) found 18 species of tardigrades from three provinces, primarily in lichens and bryophytes.

One of the most common tardigrades among bryophytes is ***Milnesium tardigradum*** (Figure 21) and the less common ***Macrobiotus hibiscus***. Hinton and Meyer (2008) reported these among liverworts (***Jungermannia*** sp.; Figure 2) in a suburban lawn in central Georgia (USA).

Figure 2. ***Jungermannia atrovirens***, member of a genus where tardigrades have been found in a lawn in Georgia, USA. Photo by Michael Lüth, with permission.

Liverworts are rarely mentioned in tardigrade studies. However, Hinton and Meyer (2007) reported ***Echiniscus virginicus*** and ***Milnesium tardigradum*** from liverworts. In their study, they collected handfuls of mosses, liverworts, and lichens from 54 parishes in Louisiana, USA. They found 51 species in the region: 19 in Texas, 16 in Louisiana, 10 in Mississippi, 33 in Alabama, 3 in Georgia, and 15 in Florida. Of these 51 cryptogam dwellers, 20 are widely distributed in the region and 18 are apparently cosmopolitan. Hinton and Meyer suggested that ***Biserovus bindae***, ***Echiniscus cavagnaroi***, ***Echiniscus kofordi***, ***Hexapodibius christenberryae***, ***Minibiotus fallax***, and ***Parhexapodibius pilatoi***, along with a new variant of ***Macrobiotus*** cf. ***hufelandi***, may represent a distinctive southeastern USA regional fauna living among cryptogams. On the other hand, ***Echiniscus cavagnaroi*** and ***Echiniscus kofordi*** are known only in the Neotropical Region and in the Galapagos Islands, but ***Minibiotus fallax*** was described in Australia. These three species are frequently encountered in mosses and lichens.

Habitat Differences

Several tardigrade researchers have considered five types of bryophyte habitats (Mihelčič 1954/55, 1963; Ramazzotti 1962; Hofmann 1987):

- bryophytes that are submerged
- bryophytes that are permanently moist
- bryophytes growing in shady places and rarely dry
- bryophytes that dry out frequently and receive direct sunlight regularly
- bryophytes that are extremely exposed and often dry for a longer period.

Ito (1999) was able to identify six groupings of tardigrades, based on habitat preference, in his altitudinal study on Mt. Fuji, Japan. Kaczmarek *et al*. (2011) likewise found altitudinal relationships in Costa Rica. They furthermore found a higher diversity among mosses than among lichens or liverworts, although they admitted to a possible bias due to unequal sampling. Tardigrades from these substrates were most common from 2000 to 2400 m asl and above 3200 m asl.

Tardigrades do not have much control over their dispersal, typically depending on dispersal of the substrate. This may help to explain the observations on two morphotypes of the moss ***Grimmia***. In this case, the tardigrade distribution was very patchy. There were no differences in distribution patterns on the two ***Grimmia*** morphotypes, despite their representation of different moisture conditions (Bettis 2008). Bettis suggested that the greater rainfall during the winter of observation might account for the lack of difference. But tardigrades are well known for their great tolerance of extremes, so their greatest limitation may be dispersal.

Acid or Alkaline?

Bartels (2005) reported greater diversity in limestone habitats than elsewhere. It appears that acid can be an uncomfortable or lethal milieu. ***Hypsibius dujardini*** (Figure 13) had reduced activity after only five minutes at *p*H 3 and died at *p*H 2.8. Even at *p*H 4.0, it had reduced activity after 30 hours.

But in Giessen, Germany, Hofmann (1987) found a somewhat different relationship. The four most abundant species [***Macrobiotus hufelandi*** (Figure 7), ***Ramazzottius*** (formerly in *Hypsibius*) ***oberhaeuseri*** (Figure 3), ***Milnesium tardigradum*** (Figure 21), and ***Echiniscus testudo*** (Figure 4)] had similar preferences for alkaline substrata, but the remaining species, as a group, had a preference for the acidic habitats, thus presenting greater tardigrade species diversity among the acid substrata and the mosses that inhabited them.

Figure 3. ***Ramazzottius oberhaeuseri***, a bryophyte dweller that cannot tolerate constant moisture. Photo by Martin Mach, with permission.

Hingley (1993) found only two genera in her acid peatland studies: ***Diphascon*** (***D. scoticum***) (Figure 29) and ***Macrobiotus*** (Figure 6). To that Pilato (2009) added ***Bindius triquetrus*** from ***Sphagnum*** (Figure 5) in Sicily. Distribution is patchy (Romano *et al*. 2001), requiring greater sampling effort. One must wonder, is the paucity of reports of aquatic tardigrades on bryophytes a realistic representation of a meager aquatic fauna, or are there simply too few studies that have looked for them?

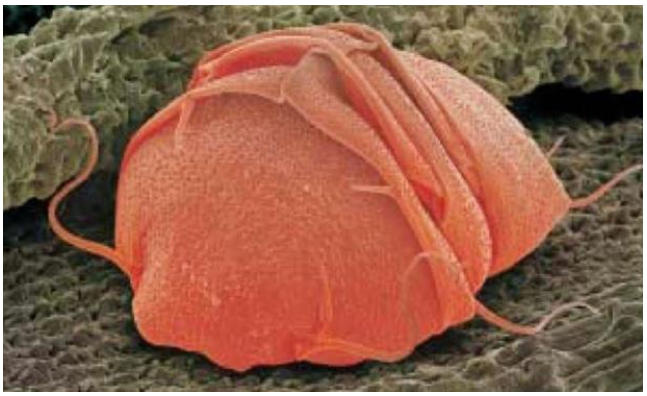

Figure 4. ***Echiniscus testudo*** tun on a bryophyte leaf. Photo by Power & Syred, through Creative Commons.

Figure 5. ***Sphagnum fuscum***, a species that forms hummocks where a tardigrade could find moisture but usually avoid being flooded. Photo by Michael Lüth, with permission.

Altitude

Many researchers have shown a relationship between altitude and the distribution of tardigrades (Rodriguez-Roda 1951; Nelson 1973, 1975; Ramazzotti & Maucci 1983; Dastych 1985, 1987, 1988; Beasley 1988), suggesting that species richness increases with altitude. Bertolani and Rebecchi (1996) found that some species were typical of high altitudes or latitudes. Some researchers have even classified the tardigrades based on altitudinal groupings (lowland, upland, montane, etc.) (Ramazzotti & Maucci 1983; Dastych 1987, 1988). Collins and Bateman (2001) found that in Newfoundland, Canada, the lowland class could be further divided into locations up to100 m and those above (101-200 m).

Table 1 compares the altitudinal abundance of 45 species of tardigrades associated with bryophytes on mountains in British Columbia, Canada (~48-60ºN), with those of **riparian** epiphytes (inhabiting trees on banks of natural water courses) in Alabama, USA (~33ºN). Although the latitudes are quite different, six species are common to both), but six species differ. The three most abundant Alabama species were common to both, but the very common ***Macrobiotus hufelandi*** (Figure 7) was absent in the Alabama collections. These data suggest that there may be more than just chance determining the species and abundance differences.

But not all altitudinal studies have supported these conclusions (*e.g.* Kathman & Cross 1991). It is interesting that Meininger and Spatt (1988) found that altitude was not influential in determining distribution and abundance of moss-dwelling tardigrades in Alaska, USA. Likewise, Guil *et al*. (2009) found that the altitudinal differences could be explained by differences in soil, climate, vegetation structure, and litter type. Nevertheless, Ramazzotti and Maucci (1983) considered certain species to occur only above 500 m. This may simply be a lack of sufficient collecting – they claimed that ***Macrobiotus harmsworthi*** (Figure 6) was one of these "montane" species, but Dastych (1985) later reported it from locations between 0 and 1100 m altitude on Spitsbergen Island, Norway. Furthermore, Dastych (1980, 1988), showed a large correlation between Tardigrada species and altitude in the Tatra Mountains in Poland. Certainly latitude must be considered in making comparisons of altitude. And local moisture regimes are likely to play a major role in altitudinal relationships.

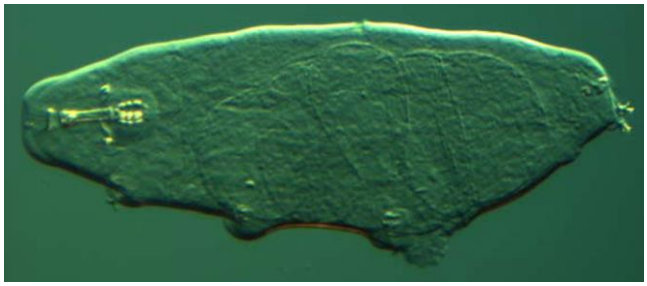

Figure 6. ***Macrobiotus harmsworthi***, a common tardigrade on bryophytes and elsewhere. Photo by Paul J. Bartel, with permissions.

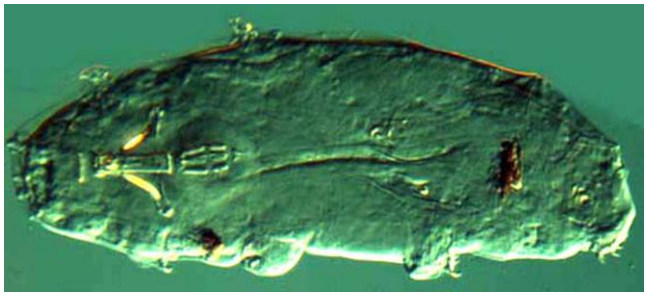

Figure 7. ***Macrobiotus hufelandi***, one of the most abundant tardigrades on bryophytes. Photo by Paul J. Bartels, with permission.

Table 1. Altitudinal distribution of numbers of tardigrades in eleven bryophyte samples each, from six altitudes on five mountains on Vancouver Island, British Columbia, Canada, from Kathman & Cross 1991, and from 108 riparian epiphytic bryophyte samples representing 6 sites at Choccolocco Creek, Alabama, USA, from Romano *et al*. 2001. Those highlighted in grey occur in both sites.

	Altitude (m)						
	150	**450**	**750**	**1050**	**1350**	**>1525**	**riparian**
Astatumen trinacriae							3
Bertolanius [=*Amphibolus*] *weglarskae*	0	0	0	0	0	2	
Calohypsibius ornatus	0	3	10	4	2	3	
Diphascon [=*Hypsibius*] *scoticum*	22	18	11	13	30	16	
Diphascon belgicae	1	0	0	6	2	1	
Diphascon iltisi	0	1	0	0	0	0	
Diphascon modestum	12	0	1	4	0	0	
Diphascon nodulosum	14	4	1	16	17	26	
Diphascon pingue sl	70	318	45	7	40	27	
Diphascon prorsirostre	4	38	16	3	8	5	
Diphascon recamieri	49	47	2	3	13	1	
Echiniscus cf. *arctomys*							28
Echiniscus horningi	2	1	1	3	3	5	
Echiniscus mauccii	6	3	0	3	1	7	16
Echiniscus quadrispinosus	0	0	2	14	4	1	
Echiniscus sp. n.							24
Echiniscus wendti	2	3	3	0	38	3	
Hypechiniscus gladiator	0	0	0	0	0	0	
Hypsibius convergens	199	203	188	78	54	26	
Hypsibius dujardini							1
Insuetifurca arrowsmithi	0	0	40	0	1	0	
Isohypsibius lunulatus	6	9	0	0	0	0	
Isohypsibius sattleri	96	49	28	4	8	0	
Isohypsibius woodsae	0	0	0	2	0	0	
Itaquascon pawlowskii	1	0	0	2	0	1	
Macrobiotus crenulatus	1	0	0	0	0	0	
Macrobiotus echinogenitus (Figure 8)	0	0	10	79	48	0	737
Macrobiotus harmsworthi	177	459	284	44	8	10	
Macrobiotus hufelandi	3039	1710	2061	1116	1586	662	
Macrobiotus islandicus							1
Macrobiotus lazzaroi	10	0	0	0	0	0	
Macrobiotus sp. A	1	0	0	0	0	0	
Mesocrista spitzbergensis	5	1	0	2	2	0	
Milnesium tardigradum	21	24	2	0	2	4	87
Minibiotus cf. *intermedius*							27
Minibiotus intermedius	2	1	12	3	0	0	
Murrayon hibernicus	0	0	0	14	1	0	
Paramacrobiotus [=*Macrobiotus*] *areolatus*	31	16	0	0	0	0	476
Paramacrobiotus[=*Macrobiotus*] *richtersi*	0	0	0	0	0	1	4
Platicrista cheleusis	8	1	2	13	10	13	
Pseudechiniscus goedeni	0	5	0	0	0	2	
Pseudechiniscus juanitae	0	0	3	0	0	0	44
Ramazzottius baumanni	18	44	8	7	5	3	
Ramazzottius oberhaeuseri	11	2	0	1	1	0	
Testechiniscus laterculus	0	0	0	0	39	0	
SUM OF INDIVIDUALS	3808	2960	2730	1421	1923	819	1448
NUMBER OF SPECIES	27	23	21	24	24	22	12

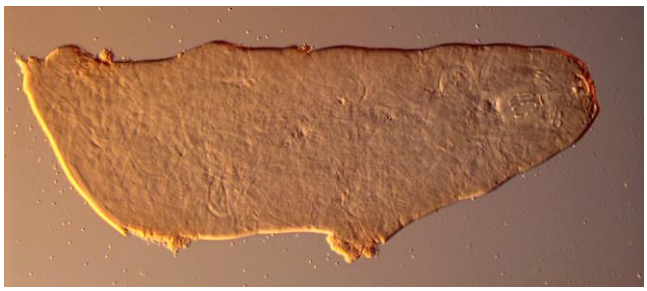

Figure 8. ***Macrobiotus echinogenitus***, a tardigrade living on riparian bryophytes at Choccolocco Creek Alabama, USA. Photo by Paul J. Bartels, with permission.

Using PCA analysis, Kathman and Cross (1991) also reported no relationship between altitude and abundance on Vancouver Island, British Columbia, on the western coast of Canada (Table 1 suggests a decreasing trend in number of individuals might be present). Collins and Bateman (2001) later reported that altitude was one of the major determining factors in tardigrade distribution in Newfoundland, eastern coast of Canada. Rodriguez-Roda (1951 in Kathman & Cross 1991) found that altitude had a distinct effect on the abundance of tardigrades in Spain, with numbers increasing with altitude and reaching a maximum between 1000 and 2000 m. Dastych (1980) likewise found that tardigrades in the Tatra Mountains of Poland increased with altitude, again with the maximum numbers between 1000 and 2000 m. In one of his later studies, Dastych (1985) reported a seemingly opposite effect, demonstrating that the number of species and individuals decreased with increasing altitude in West Spitsbergen, Norway. The differences between studies may be a matter of scale and the fact that only some species are affected by altitude within the study range, but moisture regimes are likely to differ as well.

Nelson (1973, 1975) found that only seven of the 21 bryophyte-dwelling species on Roan Mountain, Tennessee, USA, were affected by altitude. Bertrand (1975) found three altitudinal groups in the Aigoual Mountains of France. Beasley (1988) divided the tardigrades from 1052-3567 m in New Mexico, USA, into altitudinal ranges. Ito (1999) examined tardigrades at 17 stations on Mt. Fuji, Japan, finding little distributional pattern related to altitude (950-2380 m). Rather, the distribution related to habitat.

Collins and Bateman (2001) found that tardigrades of Newfoundland, Canada, were affected by both altitude (Table 2) and type of bedrock, but that moisture content and rate of desiccation of the mosses and lichens where they live also contributed to their distributional pattern.

Table 2. Decline in number of species with increasing altitude in Newfoundland. From Collins and Bateman 2001.

Altitude	Total number of species found at each altitude	Mean number of tardigrade species at each site
0->100 m	28	2.75
101->200 m	15	1.75
200+ m	8	1.88

Differences in techniques, lack of or differences in statistical analyses to support purported differences, and misidentification could contribute to the apparent differences in relationships among these studies, but moisture regimes most likely play a major role. In some cases, competitive exclusion appears to play a role (Collins & Bateman 2001). Nevertheless, it is likely that the effect of altitude, if it exists, depends in part on both latitude and scale.

Polar Bryophytes

Because of their relative abundance, and the predominance of mosses and lichens in the Antarctic flora, we have learned some interesting aspects of their faunal ecology and physiology there.

As early as 1976, 23 species of tardigrades were known from Antarctica (Jennings 1976). That's not bad for that early date in a place with limited vegetation, harsh climate, and limited opportunity for collecting, not to mention the distance to be travelled for colonization. Most of these tardigrade species have worldwide distribution (Venkataraman 1998). In the short Antarctic summers, the tardigrades multiply quickly, using parthenogenesis.

Unlike most habitats elsewhere, the tardigrades in the Antarctic moss turf do exhibit a vertical zonation pattern. Schwarz *et al*. (1993) found that protozoa, rotifers, nematodes, and tardigrades dominated the moss-dominated flushes at Canada Glacier, southern Victoria Land, Antarctica. Mites were of less importance. These invertebrates occurred in the range of 5 to 10.83 mm depth in the moss clumps. Post melt samples had a greater percentage of all groups of organisms in the upper 5 mm of mosses compared to those at that depth range in the pre-melt samples, suggesting either migration or rapid reproduction once melting occurred.

Venkataraman (1998), in clumps of ***Bryum argenteum*** (Figure 9) from continental Antarctica, found that the tardigrades only live down to 15 cm depth in the 30 cm deep turfs. If they prefer to eat rotifers, they can only find those down to 10 cm. Their slow movement could limit the distance they can reasonably move downward and still return for food in a timely manner. Ramazzotti (1972) estimated that tardigrades could travel an average of 17.7 cm h^{-1}, seemingly enough speed to travel another 10 cm, but perhaps not in the cold and not during the daytime feeding period when downward movement would be most beneficial to avoid drying.

Temperature may play a role in the zonation of these Antarctic bryophytes. Bryophyte temperatures in the Antarctic can differ considerably from those of the air and may provide a warm refuge for activity even on cold days. Bryophytes exhibit a sharp temperature zonation on sunny days when there is no snow cover (Jennings 1979). The surface is subject to evaporative cooling in the polar winds while the moss layer immediately below that interface is quiet and often dark in color, absorbing the heat like a black body, as seen by the temperatures shown in Figure 10. Hence, in summer the moss turf has temperatures much higher than that of the air and at the beginning and end of the summer season the temperatures fluctuate around freezing for a considerable time, even if the mosses are snow-covered.

Sohlenius and Boström (2006) described tardigrade communities from moss cushions on four ice-free mountains (nunataks) in Antarctica. Tardigrades occurred in 32% of the 91 samples of mosses. No invertebrates at all occurred in 8% of the samples. They considered stochastic processes (random events) accounted for the uneven colonization of the moss cushions, most likely as a result of random dispersal. They suggested that nematodes seem to offer competition, whereas the rotifers seem to provide a food choice.

Figure 9. ***Bryum*** sp. cushions in Antarctica, demonstrating the deep turfs that can house tardigrades. Photo courtesy of Catherine Beard.

Figure 11. ***Richtersius coronifer***, a tardigrade that survives Arctic winters on mosses in a frozen state. Photo by Martin Mach, with permission.

Tardigrades manage to survive the extreme cold of the long Antarctic winter as a **tun** (see Chapter 4-6). But other physiological adaptations are needed to combat the extremes of temperature that can be experienced in a single Antarctic day (see for example Figure 10).

Both ***Bertolanius nebulosus*** and ***Richtersius coronifer*** (Figure 11) endure ice formation as they proceed through the onset of freezing temperatures (Westh & Kristensen 1992). Both are able to supercool to -6 or -7ºC before they succumb to freezing. These two tardigrades are common in Polar areas, as well as elsewhere. ***Richtersius coronifer*** (Figure 11) spends its Arctic winters in drought-resistant mosses as a frozen or dry individual. ***Bertolanius nebulosus*** has adopted a somewhat different strategy, spending its cold period in moist mosses and algae as a frozen cyst, or occasionally as an egg or adult.

It appears that adapted tardigrades can survive extreme conditions for a long time. Newsham *et al*. (2006) experimented in a way that might be considered cruelty to animals (but not unlike Mother Nature herself). They partially dried a bit of the leafy liverwort ***Cephaloziella varians*** from Rothera Point on the Wright Peninsula, Adelaide Island, western Antarctic Peninsula, then stored it frozen at -80ºC for six years and two months. They then rapidly thawed the liverwort at 10ºC. You guessed it! Tardigrades survived, along with nematodes and a bdelloid rotifer. Only two individuals [***Diphascon*** sp. (see Figure 12), ***Hypsibius*** cf. ***dujardini*** (Figure 13)] out of fifteen tardigrades (13%) made it, but that is still remarkable! The eleven individuals of ***Macrobiotus furciger*** (Figure 14) and one of ***Echiniscus*** sp. did not. Nematodes fared a bit better, with 31% survival out of 159 individuals.

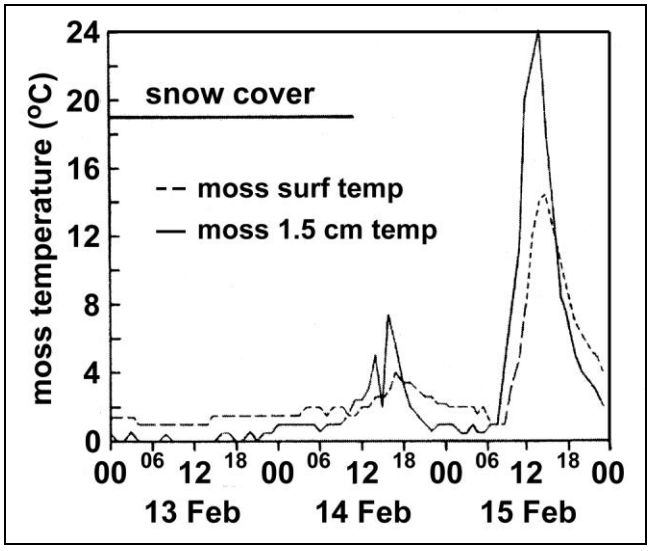

Figure 10. Comparison of moss surface temperature with that of 1.5 cm depth in moss cover on Signy Island in the Antarctic on three days in February, 1973. Redrawn from Jennings 1979.

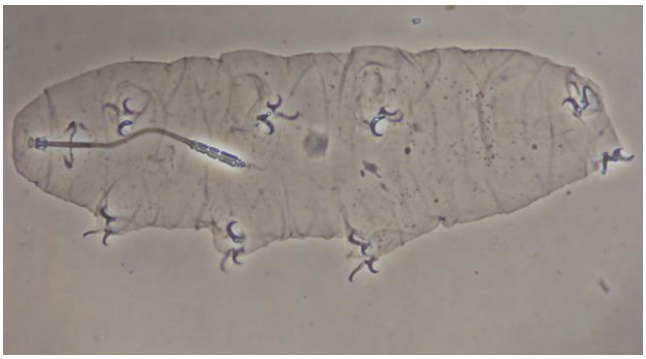

Figure 12. ***Diphascon scoticum***, a moss-dwelling representative of a genus in which one member survived storage at -80ºC for six years! Photo by Łukasz Kaczmarek, with permission.

Figure 13. ***Hypsibius dujardini***, a species that survived -80ºC for six years. Photo by Rpgch, through Wikimedia Commons.

Figure 14. ***Macrobiotus furciger***. Photo by Smithsonian Institution, through EOL Creative Commons.

Sømme and Terje Meier (1995) examined ***Echiniscus jenningsi*** (Figure 15), ***Macrobiotus furciger*** (Figure 14), and ***Diphascon chilenense*** from Müihlig-Hofmannfjella, Dronning Maud Land, Antarctica to ask similar winter survival questions. They compared both hydrated and dehydrated individuals. After 600 days at -22ºC, both hydrated and dehydrated tardigrades had high survival rates. After 3040 days, the dry individuals still had a high rate of survival. However, at -80ºC hydrated ***Echiniscus jenningsi*** (Figure 15) did not fare as well as the others, decreasing in survivorship as time increased from 7 to 150 days. At -180ºC, all hydrated individuals of these three species rapidly died, but all dehydrated species had good survivorship after 14 days at -180ºC.

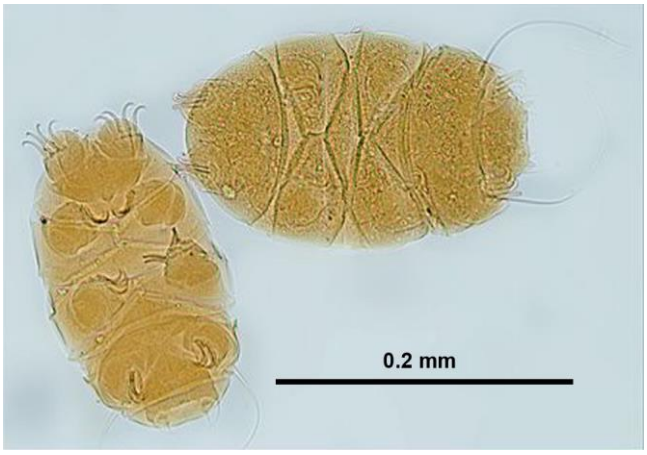

Figure 15. ***Echiniscus jenningsi***. Photo by Smithsonian Institution, through EOL Creative Commons.

It is incredible that some Antarctic tardigrades can survive temperatures as low as -80ºC in a **hydrated** state (Sømme & Meier 1995; Sømme, 1996)! The ability to survive short periods in a hydrated condition just below a freezing temperature is important to survival in bryophyte clumps that regularly warm in the day and freeze at night. Ice crystals on the bryophytes would most likely help to dehydrate the tardigrades as temperatures plummeted to well below freezing, facilitating their survival during the long and very cold winters. Furthermore, the ability to survive low temperatures for years would permit tardigrades to survive dispersal across the ice or remain viable within it until a suitable habitat or conditions are reached.

But how do the rapidly changing temperatures of the environment affect the ability of the tardigrade to move about on the bryophyte to seek food? The **beneficial acclimation hypothesis** (BAH) predicts that animals will have their best performance at the temperature to which they are acclimated. Li and Wang (2005) tested this hypothesis with the moss-dwelling species ***Macrobiotus hufelandi*** (Figure 7, Figure 19), collected from the Qinling Mountains in central China. They acclimated the water bears to 2 and 22ºC for two weeks. Using walking speed and percentage of time moving, they compared performance at the acclimation temperature with that at the alternate temperature. They found that both walking speed and percentage of time moving was significantly faster when the tardigrades were kept at their acclimation temperature than when they were placed at the higher or lower experimental temperature.

But in the Antarctic, we have seen that such extreme temperature fluctuations within a single day are not unusual. Could this be a threat to the water bears, who must find food, often adhering bacteria and algae, on the moss? And others eat nematodes and other moving targets. One factor to consider is that in the experiments of Li and Wang, only 1.5 minutes acclimation were provided at the new temperature before measurements began, lasting another 3-5 minutes. This seems unrealistic as a representation of nature. The next question to ask is how fast can the tardigrades acclimate to a new temperature?

Danger may lurk among the Antarctic bryophytes. Gray *et al*. (1982) isolated eighteen taxa of predaceous fungi from among Antarctic mosses and soil samples. Among these eight different trapping mechanisms were present. The fungus ***Monacrosporium ellipsosporum*** seemed to be associated primarily with calcicolous mosses. Although these are nematode-trapping fungi, they may also catch the occasional tardigrade. More importantly, it indicates that the moss habitat is suitable for parasitic fungi that might attack other invertebrate groups such as tardigrades.

Miller *et al*. (1996) actually looked at the role of bryophytes vs other cryptogamic substrata in harboring tardigrades on the Windmill Islands in East Antarctica. ***Pseudechiniscus suillus*** (Figure 16), ***Macrobiotus*** sp. (see Figure 7, Figure 19), ***Hypsibius antarcticus***, ***Ramajendas frigidus***, ***Diphascon chilenense***, and ***Diphascon pingue*** (Figure 17) occurred among mosses and lichens. Three of these had positive associations with each other and with bryophytes: ***Pseudechiniscus suillus***, ***Hypsibius***

antarcticus, and ***Diphascon chilenense***. These three species had a strong negative association with algae and lichens.

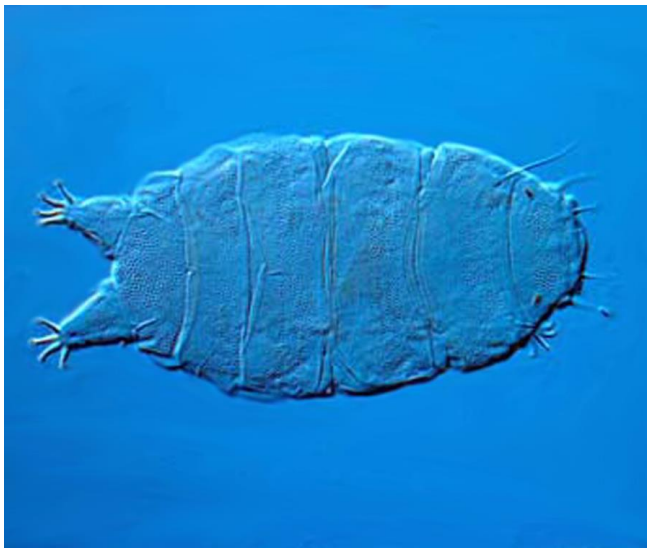

Figure 16. ***Pseudechiniscus suillus*** group, an Antarctic bryophyte dweller that avoids lichens. Photo by P. J. Bartels, with permission.

Figure 17. ***Diphascon pingue***, a moss and lichen dweller Swedish forests and in the Antarctic. Photo by Michael Collins, with permission.

Forest Bryophytes

Forests have a much more tempered climate than the Antarctic. Trees reduce the rate of water loss and shade the bryophytes and their fauna from the heat of the bright sun.

Jönsson (2003) examined bryophytes in Swedish forests and found sixteen species of tardigrades, five of which were previously undescribed for that region [***Murrayon dianeae*** (Figure 36), ***Isohypsibius sattleri***, ***Platicrista angustata*** (Figure 18), ***Diphascon belgicae***, ***D. pingue*** (Figure 17)]. Jönsson found that the pine forest had the most species compared to clearcut areas, but that abundance differed little from that of clearcut areas. Of the sixteen species of tardigrades recorded, the cosmopolitan ***Macrobiotus hufelandi*** (Figure 19) was by far the most abundant. The weft growth form seemed to harbor more tardigrades than did other bryophyte growth forms.

Figure 18. ***Platicrista angustata***. Photo by Michael Collins, with permission.

Figure 19. ***Macrobiotus hufelandi***. Photo by Martin Mach, with permission.

Schuster and Greven (2007) conducted a 54-month study of the tardigrade fauna of the moss ***Rhytidiadelphus squarrosus*** in the Black Forest of Germany. They found 24 species, dominated by ***Macrobiotus hufelandi*** (56%), ***M. richtersi*** (18%), and ***Diphascon pingue*** (12%). Diversity tended to be higher in winter, but the three dominant species generally declined in winter and increased from spring until fall. Rainfall, humidity. and temperature seemed to play a major role in changes in seasonal abundance.

Epiphytes

Whereas forest floor bryophyte dwellers are protected by snow in winter, bryophytes on trees (**epiphytes**) are often above the winter snow level. In summer they have intermittent wet and dry periods and in winter they often have exposures to extreme temperatures, lacking the protective cover of snow. In the Cincinnati, Ohio, USA area, bark-inhabiting bryophytes provide homes to numerous tardigrades, with the greatest species richness in environs of high humidity and clean air (Meininger *et al.* 1985). Hence, cities afford a less hospitable environment due to the lower humidity and decreased air quality.

Despite their seemingly unfriendly habitat, epiphytic bryophytes are particularly suitable as a tardigrade habitat. Indeed, this habitat seems to house the most species. The frequency of wetting and drying of these bryophytes seems to be most suitable to the tardigrade life cycle. Richness seems to run about 4-16 species. Hooie and Davison (2001; Hooie Tardigrade diversity) found the following tardigrades associated with the epiphytic moss ***Ulota crispa*** (Figure 20) on four tree species (*Acer saccharum*, *Acer rubrum*, *Betula lenta*, *Tilia americana*) in the Great Smoky Mountains National Park, USA:

Echiniscus cf. ***oihonnae***
Echiniscus virginicus
Hypechiniscus gladiator
Macrobiotus hufelandi (Figure 19)
Milnesium tardigradum (Figure 21)
Minibiotus cf. ***pustulatus***
Paramacrobiotus tonollii (Figure 23)
Pseudechiniscus (Figure 22)

Figure 20. ***Ulota crispa***, an epiphytic moss that houses a number of tardigrade species. Photo by Michael Lüth, with permission.

In a study of riparian tardigrades, Romano *et al*. (2001) reported on the tardigrades on epiphytic bryophytes in Alabama, USA. Using 108 samples, they extracted 1588 tardigrades from three tree species on six sampling dates. Like Riggin (1962) for forest bryophytes, Romano *et al*. (2001) found that ***Macrobiotus*** species (Figure 6-Figure 8) were the most abundant (1358 of the 1588 tardigrades, 86%). They found no differences among tree species, bryophyte species, or seasons, but there were site differences, possibly suggesting dispersal limitations. Although relative humidity and temperature did not seem to influence abundance, precipitation did. Interestingly, as precipitation increased, the number of tardigrades decreased. Beasley (1981) found that higher humidity resulted in lower tardigrade abundance in the Caribbean National Rain Forest at Luquillo, Puerto Rico. This further supports the hypothesis that periods of anhydrobiosis are required in the life of a tardigrade and that lack of them shorten the length of life. However, if only active periods are considered, there may be little difference.

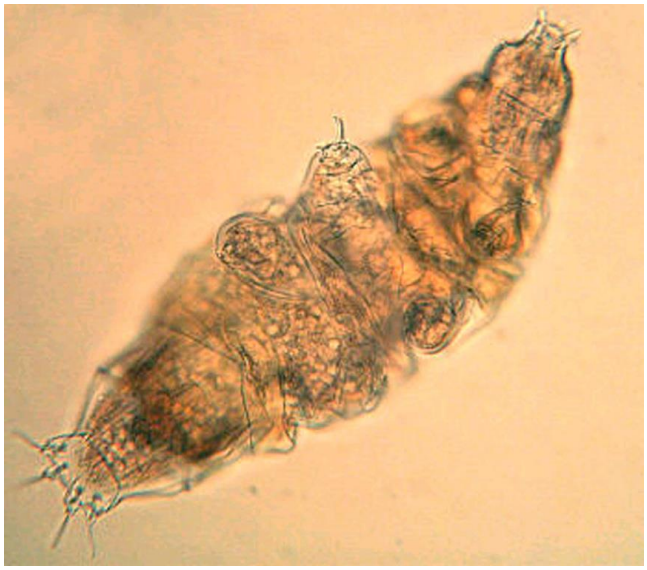

Figure 21. ***Milnesium tardigradum***. A cosmopolitan bryophyte inhabitant. Photo by Martin Mach, with permission.

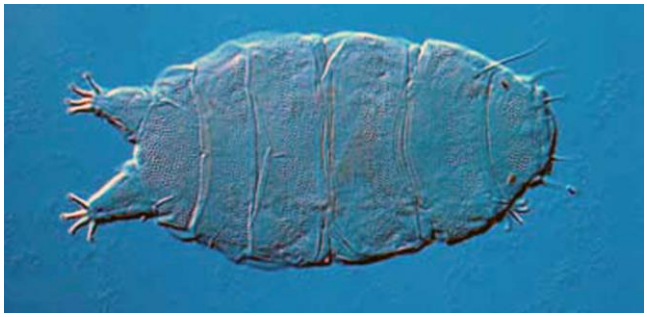

Figure 22. ***Pseudechiniscus juanitae***. Photo by Paul J. Bartels, with permission.

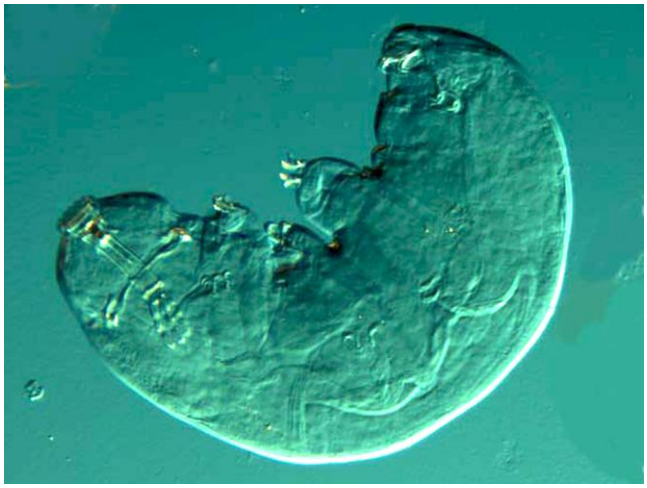

Figure 23. ***Paramacrobiotus tonollii***, a tardigrade known from ***Ulota crispa*** in the Smoky Mountains. Photo by Martin Mach, with permission.

Briones *et al*. (1997) suggested that during periods of high precipitation the film of water surrounding the bryophytes may become anoxic, killing the tardigrades. This could especially be a problem in the riparian zone, where the bryophytes, and hence the tardigrades, were under water during several collection periods. Diversity of tardigrades was somewhat low in the Alabama, USA,

riparian sites (Table 1), with only twelve species overall (Romano *et al*. 2001). Mosses included ***Anomodon*** (Figure 24), ***Leucodon*** (Figure 25), and ***Schwetschkeopsis*** (Figure 26), all epiphytes.

Figure 24. ***Anomodon rugelii***, an epiphytic moss. Photo by Michael Lüth, with permission.

Figure 25. ***Leucodon sciuroides***, an epiphytic moss that compresses and curls its branches upward when it dries. Photo by Michael Lüth, with permission.

Figure 26. ***Schwetskeopsis fabronia*** , an epiphyte from Asia and North America, and home for tardigrades. Photo by Misha Ignatov, with permission.

As in the Alabama study, Jerez Jaimes (2002) found a low diversity of only seven species on the moss ***Calymperes palisotii*** (Figure 27) on six species of trees on the campus of the University of Puerto Rico at Mayagüez. The highest species richness was on *Mangifera indica* (mango) and *Swietenia macrophylla* (mahogany).

When collections came from trees and shrubs from all 67 counties in Florida, only 20 species of tardigrades were found (Meyer 2006, 2008). Meyer also found no specificity for a particular bryophyte (47 species included) or ecological region, but there was specificity for bryophytes as opposed to foliose lichens.

There seemed to be an avoidance of one moss species, ***Aulacomnium heterostichum*** (Figure 28), with no tardigrades occurring on it (Meyer 2008). Bartels and Nelson (2006), working in the Great Smoky Mountains National Park, USA, increased the number of known species in the park from three to 42 from multiple substrates, a further testimony to how little known these organisms are. Bartels and Nelson found that more tardigrades occurred in bryophytes at breast height on a tree than at the tree bases, perhaps again relating to longer or more frequent dry periods.

Diphascon [=*Hypsibius*] ***scoticum*** (Figure 29), a very common tardigrade, inhabits mosses on logs (Cushman, pers. comm. 1970). It would be interesting to compare the log-dwelling tardigrade taxa with those living on epiphytic bryophytes of the same species. Presumably, the log habitat would have longer moist periods. Based on the findings discussed above of Bartels and Nelson (2006) and Romano *et al.* (2001), one might expect more on the epiphytes, where alternating wet and dry periods might fit better with the apparent dormancy requirements of the tardigrades.

Figure 27. ***Calymperes palisotii***, a moss that had the lowest tardigrade diversity on the University of Puerto Rico campus, Mayagüez. Photo by Claudio Delgadillo Moya, with permission.

Figure 28. ***Aulacomnium heterostichum***, a moss that seems to be avoided by tardigrades. Photo by Janice Glime.

Figure 29. ***Diphascon scoticum***, a very common tardigrade, one that has been found among mosses on logs. Photo by Paul J. Bartels, with permission.

Aquatic

Few truly aquatic tardigrades seem to exist. Garey *et al*. (2008) reported that of the more than 900 species of tardigrades they reviewed, most live in the water film on the surface of bryophytes, lichens, algae, and other photosynthetic organisms. Of their 910 species of tardigrades, only 62 (in 13 genera) were truly aquatic. In New Zealand, tardigrades represented only 2.4% of the fauna among the bryophytes of an unshaded stream in the alpine zone on South Island (Suren 1991a). In a more extensive study there, they represented only 1.2% of the invertebrates collected among mosses in 103 streams in one study (Suren 1993). Similar small numbers were present among the moss ***Fontinalis antipyretica*** (Figure 34) in the Czech Republic, where one stream had 1541 per mL of moss (0.6% of the fauna in the moss) and another stream had only 545 per mL (0.1%) (Vlčková *et al*. 2001/2002). In the Colorado Rocky Mountains, Elgmork and Sæther (1970) found most of the tardigrades ***Dactylobiotus*** cf ***macronyx*** (formerly ***Macrobiotus macronyx***) associated with algae, but they also reported them from ***Fontinalis*** beds (Figure 34) and other submerged mosses.

In streams, flow velocity may cause tardigrades to seek refuge among mosses. Suren (1992) reported high densities of tardigrades (***Dactylobiotus*** [=*Macrobiotus*] ***dispar***; Figure 30-Figure 31) associated with mosses in alpine streams of New Zealand. In an earlier study Suren (1991b) found that the colonization of this species on artificial mosses was at a reduced density compared to that on mosses [***Fissidens rigidulus*** (Figure 32), ***Cratoneuropsis relaxa***, ***Bryum blandum*** (Figure 33)].

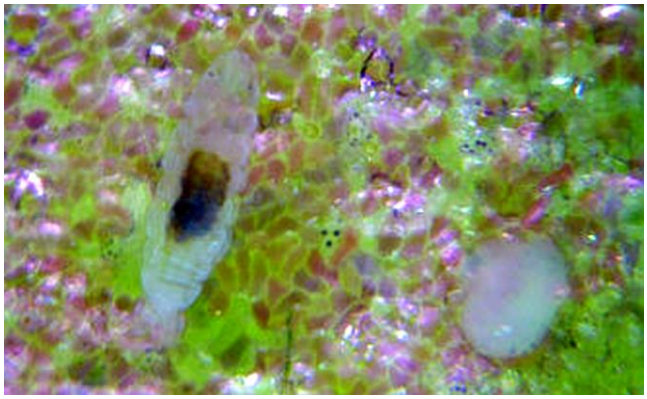

Figure 30. ***Dactylobiotus*** [=*Macrobiotus*] ***dispar***. Photo by Martin Mach, with permission.

Figure 31. ***Dactylobiotus*** [=*Macrobiotus*] ***dispar***. Photo by Martin Mach, with permission.

Figure 32. ***Fissidens rigidulus*** from New Zealand, a good tardigrade habitat. Photo by Bill and Nancy Malcolm, with permission.

Figure 33. ***Bryum blandum*** from New Zealand, where tardigrade density is greater than that on artificial mosses. Photo by Jan-Peter Frahm, with permission.

Suren (1992) reported densities of 3120 and 8160 per m^2 on the mosses in two trials, whereas they reached only 1760 and 1600 on the artificial substrata. He suggested that the high periphyton biomass among mosses provided a good food source that made this a good habitat for the tardigrades. This suggestion is supported by the largest percentage of variation (24.2%) being explained by the ultra-fine particulate matter (UFPOM). The abundance of tardigrades on bryophytes was 10 times that found on stream gravel.

Linhart *et al*. (2002) examined scattered clumps of the aquatic moss ***Fontinalis antipyretica*** (Figure 34) and found that whereas several groups of invertebrates were distributed among the clumps in relation to stream flow, this was not the case for tardigrades. Even though the researchers showed that fine organic matter trapped within the moss mat was determined by flow velocity, this did not seem to be a determining factor in tardigrade distribution.

Figure 34. ***Fontinalis antipyretica*** in flowing water. Photo by Michael Lüth, with permission.

In the Italian Alps ***Borealibius zetlandicus*** occurred on ***Warnstorfia exannulata*** (Figure 35; Rebecchi *et al*. 2009). This tardigrade species is known only from boreo-alpine areas, where it typically occurs in sediment, submerged aquatic mosses, or ***Sphagnum*** (Figure 5). But like many other tardigrades, this one has a wide habitat range, including the Barents Sea and terrestrial mosses and soil that rarely dry out. This boreal habitat distribution for this species is possible because this species is able to survive freezing. But the populations of the species studied are unable to survive desiccation.

Figure 35. ***Warnstorfia exannulatus***, home for the tardigrade ***Borealibius zetlandicus*** in the Italian Alps. Photo by Michael Lüth, with permission.

Suren (1992) also considered the possibility that the mosses offered shelter from the rapid flow of water elsewhere. These tiny organisms are often in the leaf axils of the mosses, where they have almost no effect from the strong flow, yet the oxygen diffusion could be fairly rapid. But as yet, no data seem to support cause and effect of flow velocity and tardigrade distribution.

Living in a stream is challenging for a tardigrade. Using 22 animals, Shcherbako *et al*. (2010) found that ***Milnesium tardigradum*** (Figure 21) could manage in water with a mean velocity of 23.3 mm/h, moving at a mean speed of 19.8 mm/h in the light and 29 mm/h in the dark, making snails look like track stars! Bryophytes provide a safe refuge from fast-moving waters. Eles and Repas (2009) described the stream tardigrades as having faster motion and longer claws than their terrestrial counterparts.

In New Zealand, Suren (1992) found that the tardigrade ***Dactylobiotus dispar*** (Figure 31) represented about 6.6% of the fauna on mosses in unshaded streams compared to 0.6% on gravel. In shaded streams they occupied only 5.3% of the bryophyte fauna compared to 0.4% on gravel. But not all wet habitats seem to be very suitable for tardigrades.

Kaczmarek (pers. comm. 29 January 2010) has reminded me that most of the water-dwelling tardigrades are in fact marine. Those that are truly freshwater aquatic species live on algae or plants (including bryophytes), in the sand, or in sediments. The genus ***Murrayon*** (Figure 36) is unusual among the water-dwelling tardigrades in that some aquatic individuals lay their eggs in the shed shells of cladocerans (Bertolani *et al*. 2009).

Figure 36. ***Murrayon dianeae***, an aquatic tardigrade. Photo by Michael Collins, with permission.

Emergent bryophytes may be especially comfortable for some species of tardigrades. One of the more "friendly" environments is in association with ***Barbula*** [=*Didymodon*] ***tophacea*** (Figure 37-Figure 38), a well-known rock-forming moss, above the wet zone.

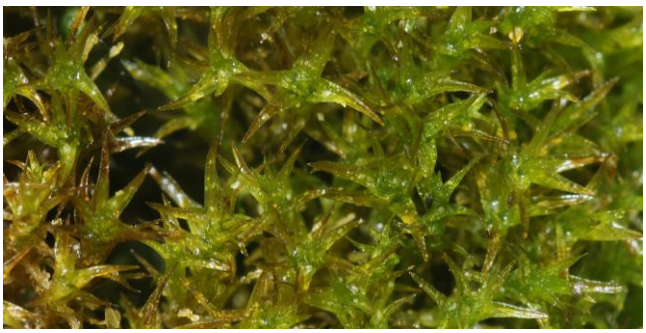

Figure 37. ***Barbula*** [=*Didymodon*] ***tophacea***, an emergent moss known to house 84 tardigrades per gram. Photo by Barry Stewart, with permission.

The aquatic habitat is also sometimes hospitable to hygrophilous species that are more typical among moist mosses or species with a wide tolerance range for moisture conditions (Nelson & Marley 2000). On the other hand, ***Hypsibius dujardini*** (Figure 13) is known from moist mosses, but it is primarily aquatic (McFatter *et al*. 2007). ***Parhexapodibius pilatoi*** was found among mosses on a stream bank in central Georgia (McFatter *et al*. 2007), but otherwise is known only from Michigan (Bernard 1977).

Figure 38. ***Barbula*** [=*Didymodon*] ***tophacea***, an emergent moss showing the numerous possibilities for resting in leaf axils. Photos by Michael Lüth, with permission.

Dry Habitats

Although collectors looking for a rich bryophyte flora would most likely ignore the desert, some bryophytes depend on its predominately dry nature. The cryptogamic crust of prairies and deserts has its own tardigrade fauna (Brantley & Shepherd 2002). In this habitat of bryophytes, lichens, Cyanobacteria, and algae, long dry periods are guaranteed. The occasional wet periods make it a suitable tardigrade habitat.

As already discussed, Meininger and Spatt (1988), working along Dalton Highway in the tundra adjacent to the trans-Alaska Pipeline, found that road dust had a major impact on both the mosses and the tardigrades. The mosses near the road represented xerophytic species tolerant of high calcium. Consequently, the tardigrades likewise were taxa tolerant of drier conditions. Because of the moisture limitations on other kinds of taxa, the tardigrades near the road were mostly fungivorous and algal feeders; those farther from the road, where ***Sphagnum*** (Figure 5) was able to grow, tended to be more omnivorous and carnivorous. These habitat differences caused differences in tardigrade fauna between roadside bryophytes and more distant ***Sphagnum*** species.

Vertical and Horizontal Distribution

It seems likely that some vertical distribution within the bryophyte mat should occur. These could be defined by light levels. The presence of eyespots (Figure 41) in at least some members of Tardigrada was reported by Greven (2007), with responses to light varying from none to both positive and negative. Beasley (2001) reported negative photokinesis in the common tardigrade ***Macrobiotus hufelandi*** (Figure 19), a common moss dweller. Rather than being attracted to or from the light, they increased their rate of movement. Since light indicates sun intensity, it also is an indicator of the likelihood of drying, making the response to move quickly away from light an adaptive one. Vertical differences in tardigrade distribution are known from soil (Leetham *et al*. 1982). Nevertheless, as noted elsewhere, there seems to be little evidence for vertical position differences or migration of tardigrades in mosses; only one tardigrade (***Echiniscus viridissimus***) seems more common near the upper portion of the moss (Nelson & Adkins 2001). Wright (1991) found that in xeric habitats this species does not migrate vertically to the C zone as the moss dehydrates, even though other species do at the same time.

Data from the Antarctic suggest that temperature may play a role in the vertical positioning of tardigrades there. On Signy Island, 80% of the tardigrades occurred in the upper 6 cm of moss, and usually 70% were in the top 3 cm (Jennings 1979). One factor that contributes to this limited distribution is that the turf below 7-8 cm is **anaerobic** (lacking oxygen), making it inhospitable for the tardigrades. In moss-dominated flushes near the Canada Glacier in southern Victoria Land, Antarctica, the invertebrates, including tardigrades, occurred at a mean depth ranging 5-10.83 mm (Schwarz *et al*. 1993). As discussed above, the relative number of organisms increased near the surface in post-melt mosses. This is not necessarily a direct temperature response; it could result from changes in light or humidity associated with the melt.

Schuster *et al*. (2009) examined the microclimate within a cushion of the moss ***Rhytidiadelphus loreus*** (Figure 39). They found that the deep layers had lower daytime and higher nighttime temperatures than **ambient** (in this case, air temperature). Oxygen was similar throughout the cushion, but CO_2 increased greatly with depth. The six species of tardigrades were concentrated in the green-brown layer of the moss. The authors suggested that light and oxygen had little impact on the distribution but that CO_2 kept the tardigrades from occupying lower positions and that temperature might cause migrations within the upper portion.

Figure 39. ***Rhytidiadelphus loreus***. Photo by Michael Lüth, with permission.

Differences in horizontal distribution may be the result of microhabitat differences such as shade vs sun or distance from water. But they can also be a simple result of passive, random dispersal and the slow-moving nature of the animal. Degma *et al*. (2011) sampled ***Hypnum cupressiforme*** (25 samples; Figure 40) to try to determine

the causes of horizontal positioning of tardigrades on that species. They found 224 tardigrades in the species ***Milnesium tardigradum*** (Figure 41), ***Hypsibius convergens*** (Figure 42), ***H. microps***, ***Diphascon pingue*** (Figure 17), ***Astatumen trinacriae*** (Figure 43), ***Macrobiotus hufelandi*** (Figure 7), and ***Minibiotus*** sp. (Figure 44) They found no significant moisture gradient among the moss plants. The distribution of the tardigrade species was aggregated, but the number of species (richness) was random. There was no relationship of tardigrade species distribution to moisture.

Figure 40. ***Hypnum cupressiforme***, home of seven species of tardigrades. Photo by Michael Lüth, with permission.

Figure 41. Eyespots of ***Milnesium tardigradum***. Photo by Martin Mach, with permission.

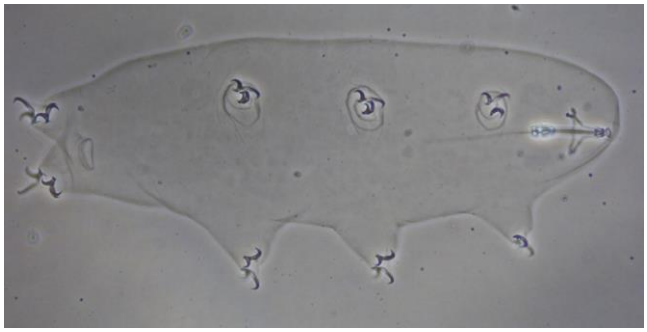

Figure 42. ***Hypsibius convergens***. Photo by Łukasz Kaczmarek, with permission.

But even these species may not be able to tolerate desiccation. ***Macrobiotus hufelandi*** (Figure 7) and ***Hypsibius dujardini*** (Figure 13) are unable to live in habitats that desiccate quickly, perhaps explaining their association with the slow-drying bryophytes (Wright 1991). Other bryophyte dwellers [***Milnesium tardigradum*** (Figure 41) and ***Ramazzottius*** (formerly *Hypsibius*) ***oberhaeuseri*** (Figure 3)] may not tolerate constant moisture, but these two species avoid high insolation and rapid desiccation, again making bryophytes a suitable habitat.

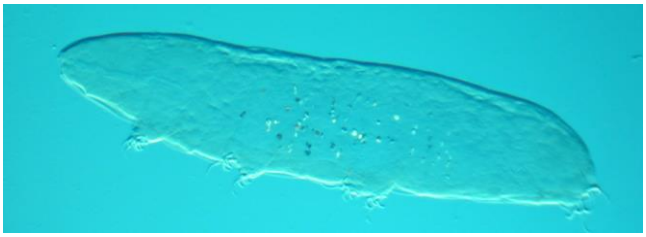

Figure 43. ***Astatumen trinacriae***. Photo by Paul J. Bartels, with permission.

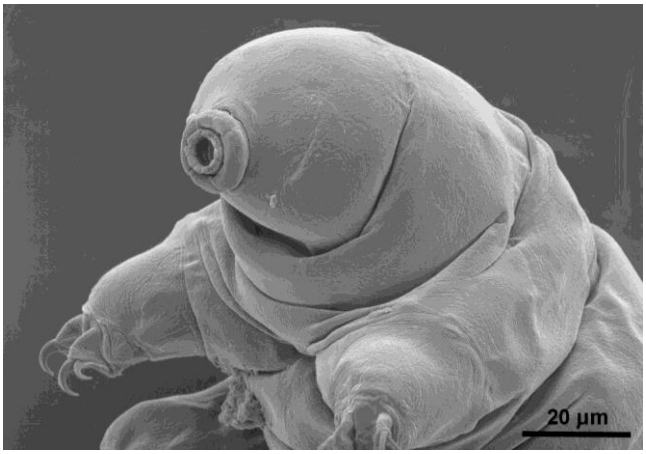

Figure 44. ***Minibiotus intermedius***. Photo by William Miller, through Flickr.

Competition and food relations are often determinants of the species assemblages. For example, ***Milnesium tardigradum*** (Figure 41) may be found with two ***Hypsibius*** species that it can use for food (Wright 1991). Competition may account for the negative associations among ***Macrobiotus hufelandi*** (Figure 7), ***Paramacrobiotus richtersi*** (Figure 45), and ***Isohypsibius prosostomus*** (see Figure 46) in xeric habitats.

Figure 45. ***Paramacrobiotus richtersi***. Photo through Creative Commons.

Figure 46. ***Isohypsibius asper***. Photo by Smithsonian Institution through EOL Creative Commons.

Summary

Tardigrades live on both terrestrial and aquatic bryophytes, with the lowest numbers in the tropics. Epiphytic mosses seem to be especially suitable for them. Altitude is influential on species and numbers in some cases, but in others researchers were unable to find any differences. There are indications that the greatest numbers on higher mountains occur at mid elevations. Latitude, scale, and moisture availability most likely play a role.

Numbers of species in most studies are modest. In forests, studies reported herein range 7-42 species. In one study, the number of species was greater in the pine forest, but the number of individuals differed little from that of clearcut areas. ***Macrobiotus hufelandi*** seems to be the most common species just about everywhere. The most common genera are ***Echiniscus***, ***Macrobiotus***, ***Diphascon***, and ***Hypsibius***, and the genera recently segregated from them. Tardigrades comprised only 1.2% of the invertebrates in an expansive New Zealand study and Hingley found only two taxa in peatlands. Dry habitats may pose food limitations; constantly wet ones may be unfavorable to their longevity.

Although mosses get wet and dry on top first, it appears that tardigrades have little ability to migrate and do not even seem to be arranged in vertical assemblages. But, they have eyespots, indicating that light may play some role in their locations.

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CHAPTER 5-4
TARDIGRADES: SPECIES RELATIONSHIPS

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CHAPTER 5-4
TARDIGRADES: SPECIES RELATIONSHIPS

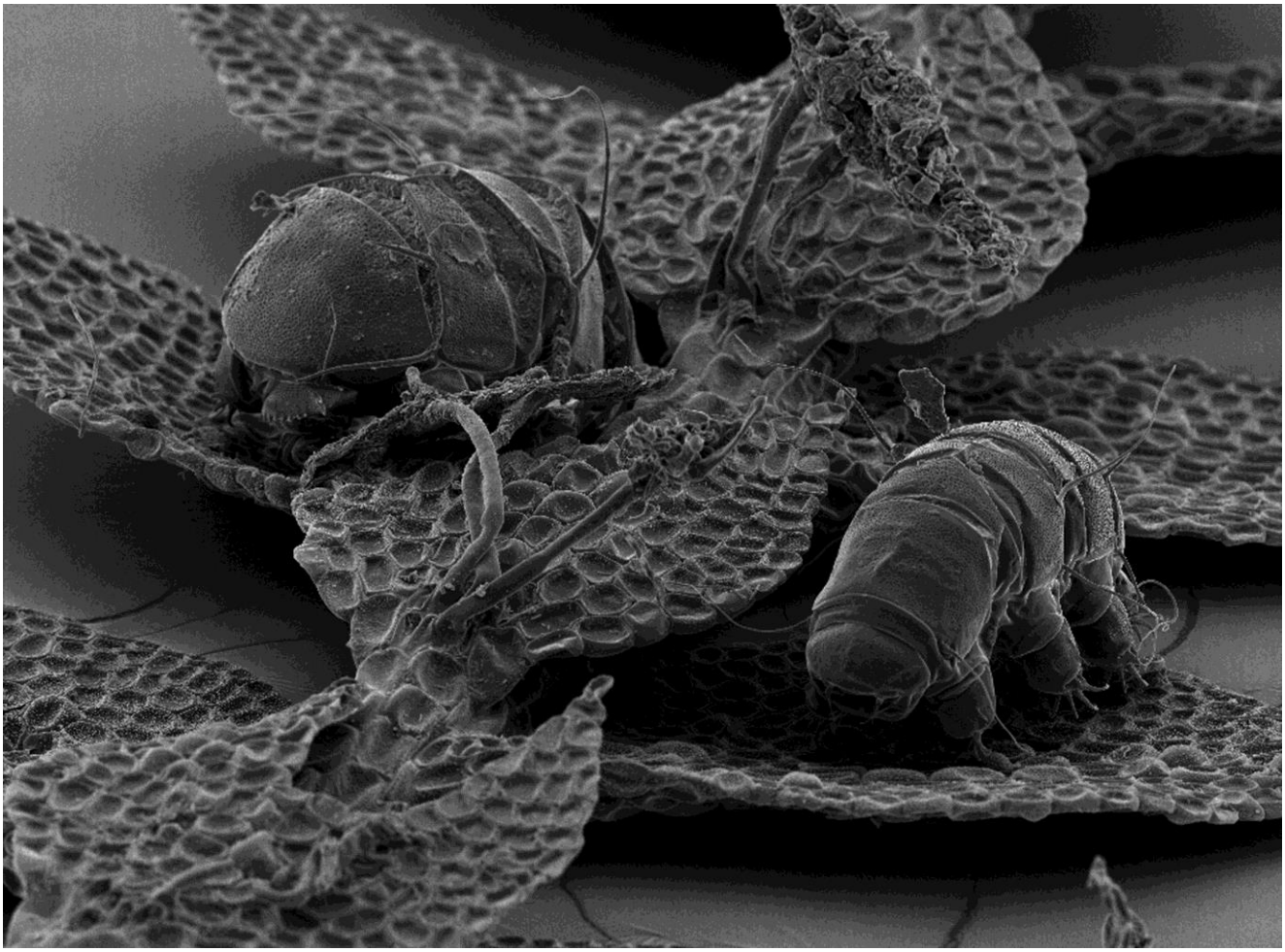

Figure 1. SEM of tardigrades on a leafy liverwort. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

Species Relationships

Tardigrades occur on both mosses and liverworts (Figure 1). Since bryophytes vary widely in structure, compactness, and moisture-holding nature, one would expect that some bryophytes would be more suitable for tardigrades than others, causing specificity. But is that really the case?

Although Hofmann and Eichelberg (1987), in Lahnau near Giessen, Germany, found a correlation between species of tardigrade and degree of moisture in their preferred mosses, there seemed to be no example of a single species of tardigrade preferring a single species of moss. It appeared that species of bryophyte was not an important factor for most tardigrades.

A number of studies name the bryophytes where the tardigrades have been found, but quantitative approaches are limited. For example, Degma (2006) found ***Echiniscus reticulatus*** on the moss ***Ctenidium molluscum*** (Figure 2) and ***Testechiniscus spitsbergensis*** from the mosses ***Tortella tortuosa*** (Figure 3), ***Ctenidium molluscum*** (Figure 2), ***Distichium capillaceum*** (Figure 4), and ***Ditrichum flexicaule*** (Figure 5-Figure 6) in Slovakia.

Baxter (1979) did find differences in the tardigrades on several moss species in Ireland. These represented different life forms as well as habitats. Some of their more specific finds include stream bank mosses that had ***Diphascon oculatum*** (Figure 7). ***Polytrichum*** (Figure 8), with its more open structure, had ***Diphascon scoticum*** (Figure 9). ***Hypsibius dujardini*** (Figure 1) was abundant, accompanied by ***Isohypsibius tuberculatus***, on the turfs of ***Rhytidiadelphus squarrosus*** (Figure 10).

Figure 2. ***Ctenidium molluscum***, a moss that is home to ***Echiniscus reticulatus***, among others. Photo by Michael Lüth, with permission.

Figure 3. ***Tortella tortuosa***, a Slovakian habitat for ***Testechiniscus spitsbergensis***. Photo by Michael Lüth, with permission.

Figure 4. ***Distichium capillaceum***, a known tardigrade habitat. Photo by Michael Lüth, with permission.

Figure 5. ***Ditrichum flexicaule***, a habitat for ***Testechiniscus spitsbergensis***. Photos by Michael Lüth, with permission.

Figure 6. View inside cushion of ***Ditrichum flexicaule***, a habitat for ***Testechiniscus spitsbergensis***. Photos by Michael Lüth, with permission.

Figure 7. ***Diphascon oculatum***, an inhabitant of streambank mosses. Photo by Björn Sohlenius, Swedish Museum of Natural History, with permission.

Figure 8. ***Polytrichum***, a moss with spreading leaves that provide limited tardigrade habitat. Photo by Michael Lüth, with permission.

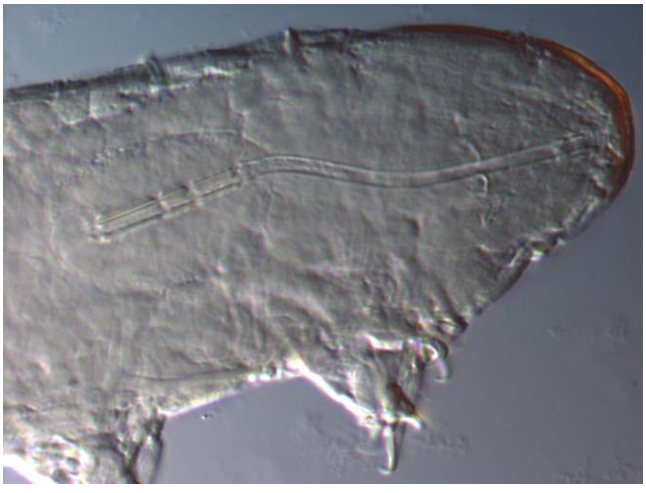

Figure 9. ***Diphascon scoticum***, a tardigrade that is able to inhabit ***Polytrichum***. Photo by Paul J. Bartels, with permission.

Figure 10. ***Rhytidiadelphus squarrosus***, where Baxter (1979) found ***Isohypsibius tuberculatus*** and ***Diphascon scoticum***. Photo by Michael Lüth, with permission.

Figure 11. ***Lembophyllum divulsum***, a home for 16 tardigrade species in New Zealand. Photo by Li Zhang, with permission.

Figure 12. ***Hypnum cupressiforme***, the moss with the most tardigrade species in the New Zealand study by Horning *et al*. (1978), shown here on rock and as a pendant epiphyte. Photos by Michael Lüth, with permission.

Horning *et al*. (1978) examined the tardigrades on 21 species of mosses in New Zealand and listed the tardigrade species on each (Table 1). Some moss species clearly had more tardigrade species than others, ranging from 1 on ***Syntrichia rubra*** to 17 on ***Hypnum cupressiforme*** (Figure 12). ***Lembophyllum divulsum*** (Figure 11) had 16 species.

Hopefully lists like the one provided by Horning *et al*. (1978) will eventually permit us to determine the characteristics that foster tardigrade diversity and abundance. Perhaps the moss ***Hypnum cupressiforme*** (Figure 12) had the most tardigrade species among the mosses in New Zealand because of its own wide habitat range there. However, Degma *et al*. (2005) found that distribution of the number of tardigrade species on this moss in their Slovakia sites was random, as supported by a Chi-square goodness of fit test. But this still does not preclude the assertion that its ubiquitous nature on a wide range of habitats in New Zealand may account for the greater number of species of tardigrades on ***Hypnum cupressiforme*** in the New Zealand study.

A kind of vertical zonation occurs among tardigrades on trees that is the reverse of that sometimes found within a moss cushion. In the Great Smoky Mountains National Park, the number of tardigrade species among epiphytes at breast height was greater than the number of species found at the base (Bartels & Nelson 2006). This may relate to the need for dry periods, but it could also relate to differences in predators and possibly even to dispersal patterns.

In their study of Chinese mosses Beasley and Miller (2007) found that **Heterotardigrada** (armored tardigrades) were better represented than were **Eutardigrada** (unarmored tardigrades), a factor the authors attribute to the **xerophilic** moss samples and the locality, which has hot, dry summers, very cold, dry winters, low summer rainfall, and high winds (Fullard 1968). The Heterotardigrada have armor, which may account for their ability to withstand the dry habitat. These tardigrades also have **cephalic** (head) appendages with a sensorial function, a character lacking in the Eutardigrada, but so far their function has not been related to a bryophyte habitat. Beasley and Miller found little specificity, but most of the mosses were xerophytic and exhibited similar moisture requirements. They did find that ***Echiniscus testudo*** (Figure 13) occurred on a wider variety of mosses than did other tardigrade species.

On Roan Mountain in Tennessee and North Carolina, Nelson (1973, 1975) found no specificity among 21 tardigrade species on 25 bryophyte species. Hunter (1977) in Montgomery County, Tennessee, and Romano *et al*. (2001) in Choccolocco Creek in Alabama, USA, again were unable to find any dependence of tardigrades upon a particular species of bryophyte in their collections.

Table 1. Tardigrade species found on the most common moss taxa in New Zealand. From Horning *et al*. 1978.

Breutelia elongata	*Macrobiotus hibiscus*
	Macrobiotus liviae
	Milnesium tardigradum
	Minibiotus intermedius
Breutelia pendula	*Diphascon prorsirostre*
	Diphascon scoticum
	Doryphoribius zyxiglobus
	Hypechiniscus exarmatus
	Macrobiotus hibiscus
	Macrobiotus liviae
	Milnesium tardigradum
Bryum campylothecium	*Hypsibius convergens*
	Isohypsibius sattleri
	Minibiotus intermedius
Bryum dichotomum	*Hypsibius wilsoni*
	Macrobiotus coronatus
	Macrobiotus liviae
Bryum truncorum	*Diphascon chilenense*
	Diphascon scoticum
	Isohypsibius sattleri
	Isohypsibius wilsoni
	Macrobiotus coronatus
	Macrobiotus furciger
	Macrobiotus liviae
	Macrobiotus recens
	Paramacrobiotus areolatus
	Paramacrobiotus richtersi
	Ramazzottius oberhaeuseri
Dicranoloma billardieri	*Hypechiniscus exarmatus*
	Macrobiotus hibiscus
Dicranoloma grossialare	*Diphascon prorsirostre*
	Hypechiniscus exarmatus
	Hypsibius dujardini
	Isohypsibius cameruni
	Isohypsibius sattleri
	Limmenius porcellus
	Macrobiotus anderssoni
	Macrobiotus hibiscus
	Macrobiotus liviae
	Milnesium tardigradum
	Pseudechiniscus novaezeelandiae
Dicranoloma menziesii	*Macrobiotus hibiscus*
	Macrobiotus liviae
	Paramacrobiotus areolatus
Dicranoloma robustum	*Echiniscus bigranulatus*
	Macrobiotus anderssoni
	Macrobiotus furciger
	Macrobiotus liviae
	Milnesium tardigradum
	Pseudechiniscus juanitae
Dicranoloma trichopodum	*Echiniscus quadrispinosus*
	Echiniscus q. brachyspinosus
	Macrobiotus furciger
	Pseudechiniscus lateromamillatus
Hypnum cupressiforme	*Diphascon alpinum*
	Diphascon bullatum
	Echiniscus quadrispinosus
	Echiniscus spiniger
	Hypsibius dujardini
	Macrobiotus anderssoni
	Macrobiotus coronatus
	Macrobiotus furciger
	Macrobiotus hibiscus
	Macrobiotus liviae
	Macrobiotus recens
	Milnesium tardigradum
	Oreella mollis
	Paramacrobiotus areolatus
	Pseudechiniscus novaezeelandiae
	Pseudechiniscus juanitae
	Ramazzottius oberhaeuseri
Lembophyllum divulsum	*Diphascon alpinum*
	Doryphoribius zyxiglobus
	Hypsibius convergens
	Isohypsibius sattleri
	Macrobiotus anderssoni
	Macrobiotus coronatus
	Macrobiotus furciger
	Macrobiotus hibiscus
	Macrobiotus liviae
	Macrobiotus recens
	Milnesium tardigradum
	Minibiotus intermedius
	Paramacrobiotus areolatus
	Pseudechiniscus juanitae
Macromitrium erosulum	*Macrobiotus furciger*
	Macrobiotus hibiscus
	Macrobiotus liviae
	Pseudechiniscus juanitae
Macromitrium longipes	*Doryphoribius zyxiglobus*
	Hypsibius convergens
	Macrobiotus recens
	Minibiotus intermedius
Porotrichum ramulosum	*Diphascon alpinum*
	Diphascon scoticum
	Doryphoribius zyxiglobus
	Echiniscus bigranulatus
	Hypsibius convergens
	Macrobiotus anderssoni
	Macrobiotus coronatus
	Macrobiotus furciger
	Macrobiotus hibiscus
	Macrobiotus liviae
	Macrobiotus rawsoni
	Minibiotus aculeatus
	Pseudechiniscus lateromamillatus
	Pseudechiniscus novaezeelandiae
	Pseudechiniscus juanitae
Racomitrium crispulum	*Calohypsibius ornatus*
	Diphascon alpinum
	Echiniscus quadrispinosus
	Echiniscus zetotrymus
	Hebesuncus conjungens
	Hypsibius convergens
	Isohypsibius wilsoni
	Macrobiotus anderssoni
	Macrobiotus coronatus
	Macrobiotus furciger
	Macrobiotus hibiscus
	Macrobiotus orcadensis
	Milnesium tardigradum
	Oreella minor
	Paramacrobiotus areolatus
	Pseudechiniscus juanitae
Racomitrium lanuginosum	*Diphascon scoticum*
	Echiniscus quadrispinosus brachyspinosus
	Echiniscus vinculus
	Hebesuncus conjungens
	Macrobiotus furciger
	Milnesium tardigradum
	Minibiotus intermedius
	Oreella mollis
	Pseudechiniscus juanitae
Racomitrium ptychophyllum	*Echiniscus quadrispinosus*
	Echiniscus velaminis
	Hebesuncus conjungens
	Hypechiniscus exarmatus
	Hypsibius dujardini
	Macrobiotus furciger
	Milnesium tardigradum
	Minibiotus intermedius
	Oreella mollis
Syntrichia princeps	*Hypsibius convergens*
	Ramazzottius oberhaeuseri
	Isohypsibius wilsoni
	Macrobiotus coronatus
	Macrobiotus recens
	Milnesium tardigradum
	Pseudechiniscus novaezeelandiae
Syntrichia rubra	*Diphascon scoticum*
Tortula subulata var. *serrulata*	*Diphascon scoticum*
	Paramacrobiotus areolatus

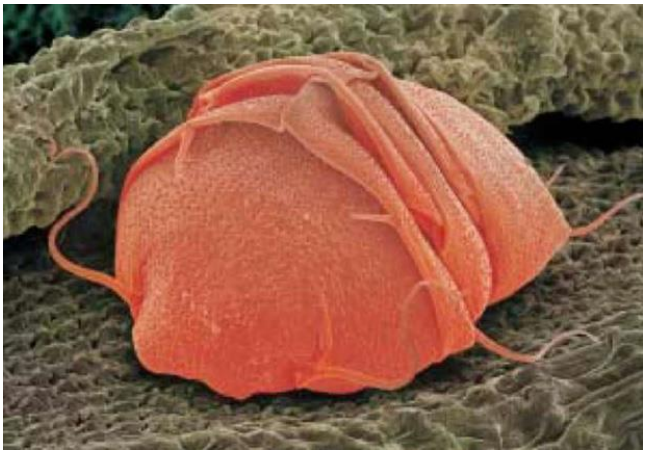

Figure 13. ***Echiniscus testudo*** tun. Photo by Power & Syred through Creative Commons.

Hofmann developed a preference coefficient:

$$P_n = (T_n/S_n) \sum_{i=1}^{n} 100(T_i/S_i)$$

where P = preference index for category n of observed factor
n = index of observed category
T = number of tardigrade populations of a single species
S = number of samples in category

The preference indices will add up to 100%. The categories can be the five bryophyte habitat groups listed by Mihelčič 1954/55, 1963; Ramazzotti 1962, and Hofmann 1987 or other groupings defined for the purpose.

Table 2. Distribution of tardigrades on specific mosses in Xinjiang Uygur Region, China, based on herbarium specimens. From Beasley & Miller 2007.

tardigrade	**numb/samples**	**moss**
Bryodelphax asiaticus	1/1	*Pseudoleskeella catenulata*
Cornechiniscus holmeni	18/5	*Grimmia tergestina*
		Mnium laevinerve
		Schistidium sp.
Echiniscus blumi	4/4	*Abietinella abietina*
		Schistidium sp.
Echiniscus canadensis	82/7	*Grimmia laevigata*
		Grimmia ovalis
		Grimmia tergestina
Echiniscus granulatus	8/3	*Grimmia longirostris*
		Schistidium trichodon
		Schistidium sp.
Echiniscus testudo	11/4	*Grimmia anodon*
		Grimmia longirostris
		Grimmia tergestina
		Lescuraea incurvata
		Pseudoleskeella catenulata
		Schistidium sp.
Echiniscus trisetosus	33/5	*Abietinella abietina*
		Grimmia ovalis
		Pseudoleskeella catenulata
Macrobiotus mauccii	2/2	*Schistidium* sp.
Milnesium asiaticum	10/4	*Grimmia anodon*
		Grimmia tergestina
		Grimmia ovalis
		Schistidium sp.
Milnesium longiungue	4/2	*Grimmia laevigata*
		Grimmia ovalis
Milnesium tardigradum	5/4	*Grimmia tergestina*
		Grimmia ovalis
		Orthotrichum sp.
Paramacrobiotus alekseevi	5/4	*Brachythecium albicans*
		Schistidium sp.

Table 3. Preference of moss species by tardigrades, using five moss species plus the remaining species combined (total = 43 species) as the habitat categories, based on 106 samples from Giessen, Germany (Hofmann 1987).

	Ceratodon purpureus	***Grimmia pulvinata***	***Bryum argenteum***	***Syntrichia ruralis***	***Syntrichia montana***	Other
samples (%)	19	9	7	7	6	52
Macrobiotus hufelandi	16	18	18	18	21	8
Ramazzottius oberhaeuseri	18	27	29	17	0	8
Milnesium tardigradum	13	23	15	20	23	6
Echiniscus testudo	11	20	20	9	34	6
mean	14.5	22.0	20.0	16.0	19.5	7.0
empty samples	25	7	9	9	11	38

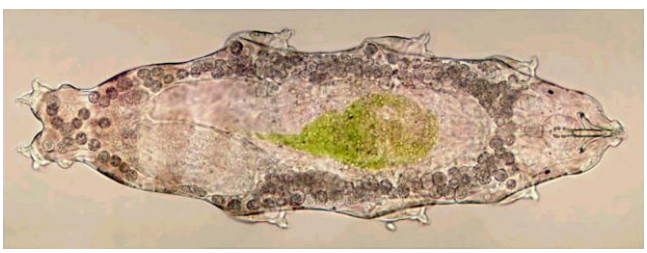

Figure 14. ***Macrobiotus hufelandi***. Photo by Martin Mach, with permission.

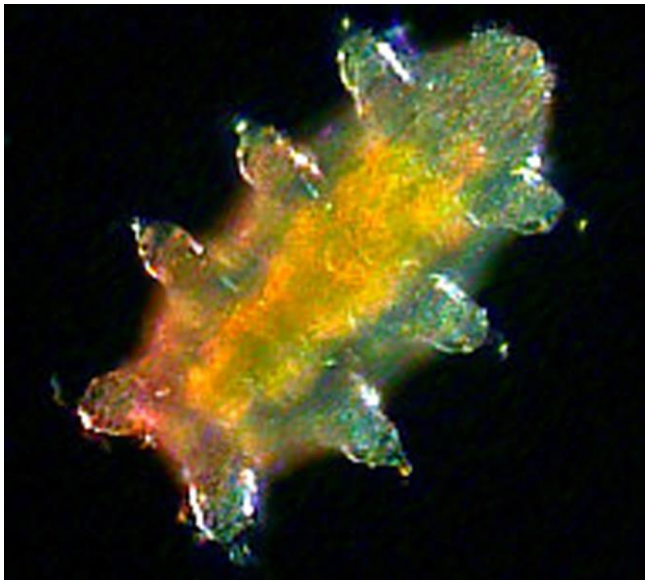

Figure 15. Adult ***Echiniscus*** sp.. Photo by Martin Mach, with permission.

Kathman and Cross (1991) found that species of bryophyte had no influence on the distribution or abundance of tardigrades from five mountains on Vancouver Island, British Columbia, Canada. In fact, Kathman and Cross (1991) were unable to find any correlation with altitude or aspect throughout a span from 150 to 1525 m. They concluded that it was the presence of bryophyte that determined tardigrade presence, not the species of bryophyte, altitude, or locality. Despite a lack of specificity among the tardigrades, 39 species inhabited these 37 species of mountain bryophytes, comprising 14,000 individuals. Several researchers contend that any terrestrial species of tardigrade can be found on any species of moss, given the "appropriate microhabitat conditions" (Bertrand 1975; Ramazzotti & Maucci 1983). If these tardigrade bryophyte specialists find no differences among the bryophytes, can we blame the ecologists for lumping all the bryophytes in their studies as well?

In collections from Giessen, Germany, the most common tardigrade species, the cosmopolitan ***Macrobiotus hufelandi*** (Figure 14), had no preference for any moss species (Hofmann 1987). But lack of influence of bryophyte species may not always be the case. Hofmann (1987) used a preference index to show that four out of sixteen tardigrades from Giessen had distinct preferences among five moss species and that they seemed to prefer cushion mosses over sheet mosses. Also contrasting with the above researchers, Bertolani (1983) found that there seemed to be a species relationship between tardigrades and coastal dune mosses. It is possible that this is again related to moisture. The moisture relationship might also explain why mosses on rotten logs seem to have few tardigrades. Could it be that they are too wet for too long?

Meyer (2006a, b, 2008) found 20 species of tardigrades among 47 species of mosses, liverworts, lichens, and ferns in Florida. There were some tardigrade species that were significantly associated with either mosses or lichens, but, as in most other studies, there was no convincing evidence for associations with any plant species substratum. Despite the lack of substrate specificity, there were three significant negative associations and one positive association between species of tardigrades. Likewise, in Georgia and the Gulf Coast, USA, Hinton and Meyer (2007) found ***Milnesium tardigradum*** (Figure 16), ***Minibiotus intermedius*** (Figure 39), and ***Minibiotus furcatus*** among mosses, whereas ***Echiniscus cavagnaroi***, ***E. kofordi*** (see Figure 15), and ***Minibiotus fallax*** were in both mosses and lichens.

Figure 16. ***Milnesium tardigradum***, an inhabitant of both mosses and liverworts. Photo by Björn Sohlenius, Swedish Museum of Natural History.

Life Forms

There is some indication that species differences may exist, based on life form. The bryophyte form can affect the moisture-holding capacity and rate of loss of moisture. That foregoing evidence suggests that the moisture-holding capacity of cushion mosses was probably a desirable trait in that habitat. On the other hand, Beasley (1990) found that more samples of clubmosses (Lycopodiaceae – tracheophytes) (75%) had tardigrades than did mosses (46%) or liverworts (0%) in Gunnison County, Colorado.

There seems to be a preference for cushions among the most common species [***Macrobiotus hufelandi*** (Figure 14), ***Ramazzottius oberhaeuseri*** (Figure 17), ***Milnesium tardigradum*** (Figure 16), and ***Echiniscus testudo*** (Figure 13)] (Hofmann 1987). But the less frequent species are commonly found among sheet mosses. The ubiquitous ***Macrobiotus hufelandi*** seems to have no preference for moss shape.

Figure 17. ***Ramazzottius oberhaeuseri***. Photo by Martin Mach, with permission.

Jönsson (2003), working in the forests of Sweden, found that wefts had more tardigrades than other moss forms. Kathman and Cross (1991) likewise found that tardigrades from Vancouver Island were more common on weft-forming mosses than on turfs, suggesting that the thick carpets of the wefts were more favorable habitat than the thinly clustered turfs with their thick rhizoidal mats and

attached soil. Contrasting with some of these findings, and the preference for cushion mosses in the study by Hofmann (1987), Diane Nelson (East Tennessee State University, Johnson City, pers. comm. in Kathman & Cross 1991) found no preference for sheet or cushion mosses in her Roan Mountain, Virginia, USA study. Rather, those tardigrades were more common in thin, scraggly mosses or in small tufts than in thick cushion mosses.

Sayre and Brunson (1971) compared tardigrade fauna on mosses in 26 North American collections from a variety of habitats and substrata (Figure 18). They found that mosses of short stature in the **Thuidiaceae** (Figure 19) and **Hypnaceae** (Figure 20) had the highest frequencies of tardigrades. Other moss-dwellers were found in fewer numbers on members of the moss families **Orthotrichaceae** (epiphytic and rock-dwelling tufts; Figure 21), **Leucobryaceae** (cushions on soil and tree bases; Figure 22), **Polytrichaceae** (tall turfs on soil; Figure 23), **Plagiotheciaceae** (low mats on soil and tree bases; Figure 24), and **Mniaceae** (mats & wefts on soil; Figure 25).

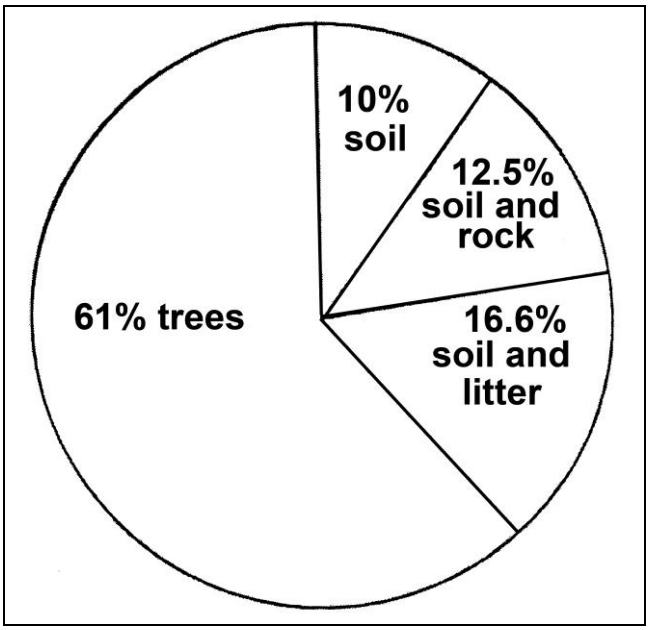

Figure 18. Relative frequency of tardigrades on bryophytes of various North American substrata. Redrawn from Sayre & Brunson 1971.

Figure 19. ***Thuidium delicatulum*** (Thuidiaceae), a low-stature moss that is a good tardigrade habitat. Photo by Michael Lüth, with permission.

Figure 20. ***Hypnum revolutum*** (Hypnaceae), representing a family that includes low-stature mosses that had among the highest frequencies of tardigrades in 26 North American collections (Sayre & Brunson 1971). Photo by Michael Lüth, with permission.

Figure 21. ***Orthotrichum pulchellum***, an epiphytic moss in the **Orthotrichaceae**. This family is among those with lower numbers of tardigrades in the North American study of Sayre & Brunson (1971) compared to families of mat-forming species. Photo by Michael Lüth, with permission.

Figure 22. ***Leucobryum glaucum***, a cushion moss in the **Leucobryaceae**. This family of mosses had lower numbers of tardigrades than those found in the mat-forming mosses in 26 North American collections (Sayre & Brunson 1971). Photo by Michael Lüth, with permission.

Figure 23. ***Polytrichum juniperinum***, a moss in the Polytrichaceae. This family of mosses tends to have low numbers of tardigrades (Sayre & Brunson 1971). The tardigrades do live among them often nestle in the leaf bases where water evaporates more slowly. Photo by Michael Lüth, with permission.

Figure 24. ***Plagiothecium denticulatum***, a low-growing soil moss in **Plagiotheciaceae**, a family with limited numbers of tardigrade dwellers (Sayre & Brunson 1971). The flattened growth habit provides few protective chambers, perhaps accounting for the lower numbers. Photo by Michael Lüth, with permission.

Figure 25. ***Plagiomnium cuspidatum***, a soil moss in the **Mniaceae**, a family with limited numbers of tardigrade dwellers (Sayre & Brunson 1971). The spreading nature of the vertical shoots and the flattened nature of the horizontal shoots would most likely not provide many protective chambers for the tardigrades. Photo by Michael Lüth, with permission.

Collins and Bateman (2001), studying tardigrade fauna of bryophytes in Newfoundland, Canada, found that rate of desiccation of the mosses affected distribution of tardigrades, and this suggests that bryophyte species and life forms that dehydrate quickly should have fewer individuals and probably different or fewer species than those that retain water longer. In different climate regimes, that rate will differ. This may explain a preference for cushions in some locations and not in others. Data are needed on humidity within the various life forms of bryophytes, correlated with tardigrade densities, to try to explain why different life forms seem to be preferred in different locations.

Liverworts

I would expect liverworts, with their flat structure, to have at least some differences in tardigrade communities (Figure 1). But reports on liverwort inhabitants are limited, at least in part due to lack of knowledge about bryophytes on the part of the tardigrade specialists and an equal lack of knowledge of tardigrades by bryologists. Hinton and Meyer (2009) found two species of tardigrades [***Milnesium tardigradum*** (Figure 16) and ***Macrobiotus hibiscus***], both also common among mosses, in samples of the liverwort ***Jungermannia*** sp. (Figure 26). In the Gulf Coast states, USA, Hinton and Meyer (2007) found ***Echiniscus virginicus*** among liverworts.

Figure 26. The leafy liverwort ***Jungermannia sphaerocarpa***, representing a genus from which tardigrades are known. Photo by Michael Lüth, with permission.

Liverworts may actually house some interesting differences as a result of their underleaves (Figure 27) and flattened life form (Figure 28). In their New Zealand study, Horning *et al*. (1978) found that among the liverworts (Table 4), ***Porella elegantula*** (Figure 27) had the most species (16). The folds and underleaves of this genus form tiny capillary areas where water is held, perhaps accounting for the large number of species. Interestingly, the tardigrade ***Macrobiotus snaresensis*** occurred on several liverwort species [4 ***Lophocolea*** species, ***Plagiochila deltoidea*** (Figure 29)], but did not appear in any moss collections. Of 150 liverwort samples (26 species), 27% had tardigrades, with a total of 16 species, mean of 2.8 species, range 1-9. In 107 samples of foliose lichens, 60.7% had tardigrades, mean 2.2 species, range 1-11.

Figure 27. ***Porella elegantula***, showing the underleaves and folds that create numerous capillary spaces. Photo by Jan-Peter Frahm, with permission.

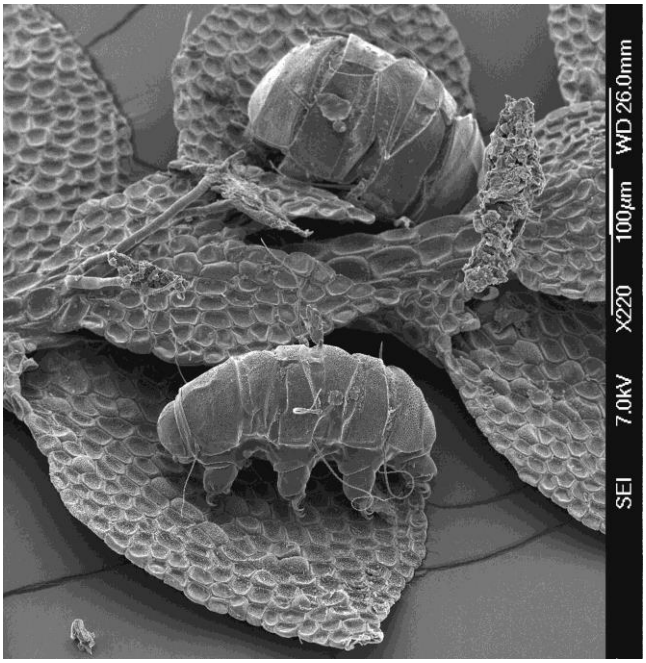

Figure 28. Underside of leafy liverwort with two tardigrades. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

Figure 29. ***Plagiochila deltoidea***, a leafy liverwort that forms large patches in wet ground in New Zealand. This is a known habitat for tardigrades. Photo by Clive Shirley, Hidden Forest <http://www.hiddenforest.co.nz>, with permission.

It appears that at least some other researchers have paid attention to liverworts. Christenberry (1979) found ***Echiniscus kofordi*** and ***E. cavagnaroi*** on liverworts in Alabama, USA. Hinton and Meyer (2009) found ***Milnesium tardigradum*** (Figure 16) and ***Macrobiotus hibiscus*** in a liverwort sample from Georgia, USA. Michalczyk and Kaczmarek (2006) found a new species, ***Paramacrobiotus magdalenae*** (Figure 30, Figure 31), on liverworts in Costa Rica. Newsham *et al.* (2006) identified the tiny leafy liverwort ***Cephaloziella varians*** and used it to experiment on the effects of low temperature storage on tardigrades and other Antarctic invertebrates.

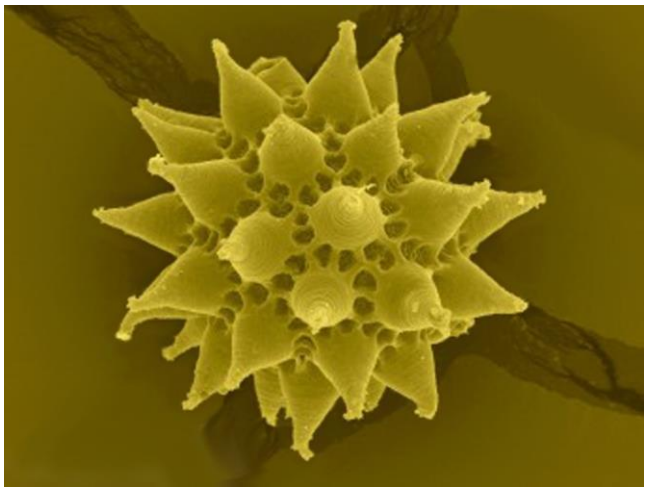

Figure 30. ***Paramacrobiotus magdalenae*** egg. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

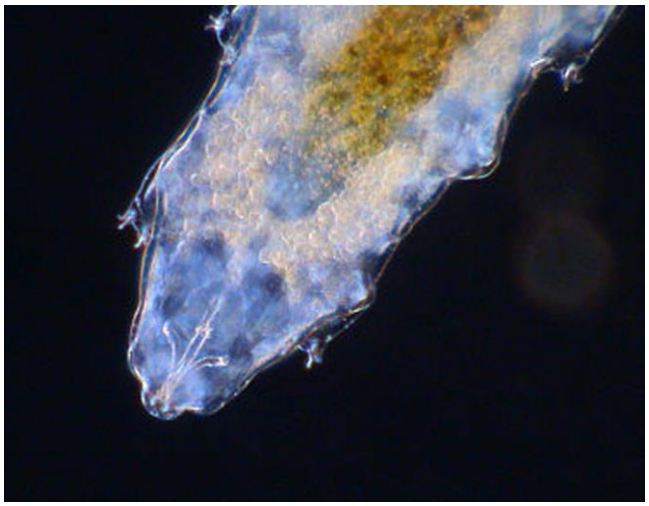

Figure 31. ***Paramacrobiotus areolatus***. Photo by Martin Mach, with permission.

Just what do we mean by "appropriate habitat conditions"? The bryophytes only occur in conditions that are appropriate for them, hence defining the conditions for the tardigrades. And the bryophytes create habitat conditions of moisture due to their morphology and substrate preference. Lack of species preference in many studies may result from methods that were insensitive to subtle differences or that failed to control for microhabitat differences. Usually no statistical tests were employed, sample sizes were small, and enumeration was often simple presence/absence data.

Table 4. Species of tardigrades found on 13 liverwort species in New Zealand and surrounding islands. From Horning *et al.* 1978.

Liverwort Species	Tardigrade Species
Lophocolea innovata	*Macrobiotus snaresensis*
Lophocolea. minor	*Macrobiotus snaresensis*
Lophocolea. subporosa	*Macrobiotus snaresensis*
Lophocolea semiteres	*Diphascon chilenense*
	Macrobiotus coronatus
Lophocolea subporosa:	*Diphascon scoticum*
	Hypsibius dujardini
	Macrobiotus snaresensis
Lophocolea sp.	*Macrobiotus liviae*
Metzgeria decipiens	*Echiniscus spiniger*
	Isohypsibius sattleri
	Paramacrobiotus areolatus)
	Macrobiotus furciger
	Macrobiotus coronatus
	Minibiotus intermedius
	Macrobiotus liviae
	Macrobiotus snaresensis
	Milnesium tardigradum
	Pseudechiniscus novaezeelandiae
Metzgeria decrescens	*Diphascon scoticum*
	Macrobiotus recens
	Macrobiotus snaresensis
	Milnesium tardigradum
Plagiochila deltoidea	*Echiniscus bigranulatus*
	Hypechiniscus exarmatus
	Hypsibius convergens
	Isohypsibius cameruni
	Macrobiotus anderssoni
	Macrobiotus liviae
	Macrobiotus recens
	Macrobiotus snaresensis
Plagiochila fasciculata	*Diphascon scoticum*
	Macrobiotus furciger
Plagiochila obscura	*Macrobiotus coronatus*
	Macrobiotus liviae
	Pseudechiniscus juanitae
Plagiochila strombifolia	*Macrobiotus anderssoni*
	Macrobiotus furciger
Porella elegantula	*Doryphoribius zyxiglobus*
	Echiniscus vinculus
	Diphascon alpinum
	Diphascon bullatum
	Diphascon prorsirostre
	Hypsibius convergens
	Isohypsibius sattleri
	Macrobiotus anderssoni
	Macrobiotus furciger
	Macrobiotus coronatus
	Macrobiotus hibiscus
	Minibiotus intermedius
	Minibiotus aculeatus
	Macrobiotus liviae
	Milnesium tardigradum
	Pseudechiniscus novaezeelandiae

Substrate Comparisons

Meyer (2006b) extended the comparison of substrata in Florida, USA, to include not only liverworts, mosses, and foliose lichens, but also ferns. He found 20 species of tardigrades on 47 species of plants and lichens. They found that some species were positively associated with mosses or with foliose lichens, but as in most other studies, there was no association with any particular plant or lichen species.

Guil *et al*. (2009a) reviewed tardigrades and their habitats (altitude, habitat characteristics, local habitat structure or dominant leaf litter type, and two bioclimatic classifications), including bryophytes and leaf litter at various elevations. They were able to show some habitat preference. Species richness was most sensitive to bioclimatic classifications of macroenvironmental gradients (soil and climate), vegetation structure, and leaf litter type. A slight altitude effect was discernible. These relationships suggest that differences among bryophyte species should exist where bryophyte species occupy different environmental types or maintain different microenvironments within a habitat. But it also suggests that within the same habitat, bryophytes of various life forms should provide different moisture regimes, hence creating species relationship differences.

In a different study in the Iberian Peninsula (extreme southwestern Europe), Guil *et al*. (2009b) found that leaf litter habitats showed high species richness and low abundances compared to rock habitats (mosses and lichens), which had intermediate species richness and high abundances. Tree trunk habitats (mosses and lichens) showed low numbers of both richness and abundances. One might conclude that the moisture of these habitats is the overall determining factor, and this should coincide with bryophyte species groups on the large scale.

Miller *et al*. (1996) found six species of tardigrades in lichen and bryophyte samples on ice-free areas at Windmill Islands, East Antarctica. The tardigrade species ***Diphascon chilenense*** (see Figure 32), ***Acutuncus antarcticus*** (formerly ***Hypsibius antarcticus***; see Figure 33), and ***Pseudechiniscus juanitae*** (=***Pseudechiniscus suillus***; Figure 34) showed a positive association with bryophytes and a negative association with algae and lichens.

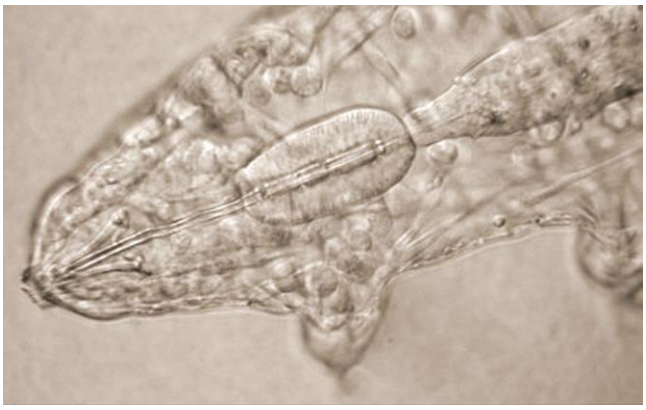

Figure 32. ***Diphascon*** sp., member of one of the most common bryophyte-dwelling genera. Photo by Martin Mach, with permission.

Meyer and Hinton (2007) reviewed the Nearctic tardigrades (Greenland, Canada, Alaska, continental USA, northern Mexico). They found that one-third of the species occur in both cryptogams (lichens and bryophytes) and soil/leaf litter (Table 5). Few tardigrades occurred exclusively in soil/leaf litter habitats. Although many

occurred among both bryophytes and lichens, 18 species occurred only in bryophytes. It is likely that bryophytes offer a better moisture environment, but this has not been tested.

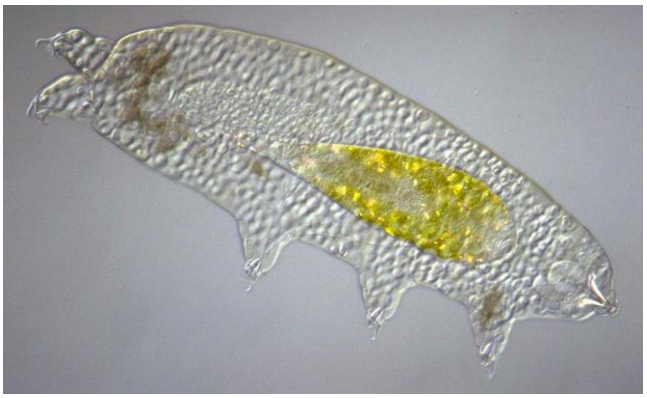

Figure 33. ***Hypsibius***. Photo by Yuuji Tsukii, with permission.

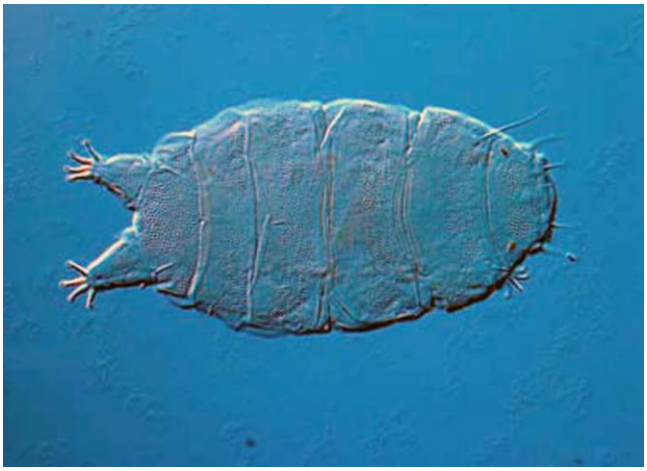

Figure 34. ***Pseudechiniscus juanitae***. Photo by Paul J. Bartels, with permission.

Table 5. Comparison of tardigrades inhabiting their primary substrates in the Nearctic realm. Only species present on that substrate in at least three sites are included. From Meyer & Hinton 2007.

Substrate category	number of species
Cryptogams only	64
Both cryptogams and soil/leaf litter	27
Soil/leaf litter only	3
Both bryophyte and lichen	50
Bryophyte only	18
Lichen only	5

Beasley (1990) conducted a similar study in Colorado, USA. Out of 135 samples of liverworts, mosses, lichens, and club mosses (Lycopodiaceae), they found 20 species in 55 samples. There were no tardigrades on liverworts (!), but they were on 46% of mosses and 43% of lichens. The big surprise is that 75% of the clubmosses had tardigrades.

In the Great Smoky Mountains National Park, Bartels and Nelson (2006) found that the number of species differed little among the substrates they sampled (soil, lichen, moss, & stream habitats). Whereas it is not unusual for the soil, lichens, and mosses to have similar fauna and richness, it seems a bit unusual for the stream habitat to be as rich. ***Amphibolus*** cf. ***weglarskae*** and ***Diphascon*** cf. ***ramazzottii*** were the only species found only on bryophytes among those four substrates.

Horning *et al*. (1978) collected from soil, fungi, algae, bryophytes, lichens, marine substrata, freshwater substrata, and litter in New Zealand and surrounding islands. From bryophyte and lichen habitats, they found that all 14 of the most abundant species occurred in at least three of the five "plant" categories (three lichen forms, liverworts, and mosses). Among these, the highest occurrence was among mosses. Although ***Milnesium tardigradum*** (Figure 16) was slightly more abundant on lichens than on mosses, the combined numbers on mosses and liverworts was still higher. Horning *et al*. identified the bryophytes and lichens and presented the species of tardigrades on each (Table 1, Table 4, Table 6). In 559 moss samples, 45.8% had tardigrades, mean of 1.8 species, range 1-8 (Table 1). Of 55 species of tardigrades known for New Zealand, 45 occurred on mosses.

Finding New Species

The common appearance of tardigrades among bryophytes causes those who seek to describe new taxa to go first to the mossy habitats. In this spirit, Kaczmarek and Michalczyk (2004a) found the new species of moss-dwelling ***Doryphoribius quadrituberculatus*** in Costa Rica. From mosses in China they described the new species ***Bryodelphax brevidentatus*** (Kaczmarek *et al.* 2005) and ***B. asiaticus*** (Figure 35; Kaczmarek & Michalczyk 2004b), as did Li and coworkers for ***Echiniscus taibaiensis*** (Wang & Li 2005), ***Isohypsibius taibaiensis*** (Li & Wang 2005), ***Isohypsibius qinlingensis*** (Li *et al*. 2005a), ***Pseudechiniscus papillosus*** (Li *et al*. 2005b), ***Pseudechiniscus beasleyi***, ***Echiniscus nelsonae***, and ***E. shaanxiensis*** (Li *et al*. 2007), and Tumanov (2005) for ***Macrobiotus barabanovi*** and ***M. kirghizicus***. Pilato and Bertolani (2005) described ***Diphascon dolomiticum*** from Italy.

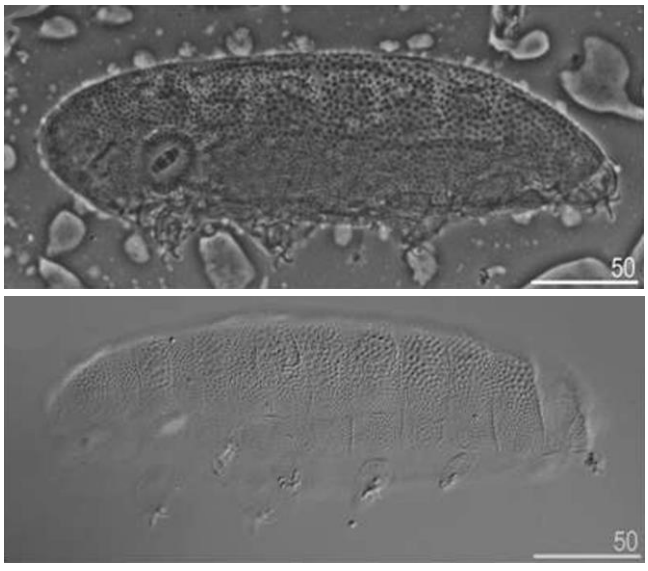

Figure 35. ***Bryodelphax asiaticus***. Photo through Creative Commons.

Table 6. Comparison of numbers of individuals and percentage of individuals of each of 14 tardigrade species on liverworts, mosses, and lichens in collections from New Zealand and surrounding islands. The remaining ones were on other non-plant substrata. Number of samples is in parentheses. From Horning *et al*. 1978.

	n	liverworts % (150)	mosses % (559)	lichens % (239)
Pseudechiniscus novaezeelandiae	46	8.70	56.50	23.90
Pseudechiniscus juanitae	43	6.98	44.19	27.91
Macrobiotus harmsworthi	89	5.62	55.06	34.83
Macrobiotus hibiscus	90	7.78	60.00	17.78
Minibiotus intermedius	65	7.69	41.54	32.30
Milnesium tardigradum	143	7.69	35.66	37.06
Hypsibius dujardini	32	10.53	50.00	2.63
Paramacrobiotus areolatus	58	3.45	60.34	18.97
Echiniscus bigranulatus	18	5.56	38.89	38.89
Hypechiniscus gladiator	21	19.05	61.90	9.50
Diphascon scoticum	35	11.43	65.71	11.43
Macrobiotus liviae	72	8.33	56.94	18.06
Macrobiotus anderssoni	63	11.11	42.86	22.22
Macrobiotus furciger	89	12.36	50.56	22.47

New species from South Africa are no surprise, as enumeration of small organisms in that country is barely out of its infancy. Kaczmarek and Michalczyk (2004c) described the new species ***Diphascon zaniewi*** in the Dragon Mountains there. Other species found there were more cosmopolitan: ***Hypsibius maculatus*** (previously known only from Cameroon and England), ***H. convergens*** (Figure 36), ***Paramacrobiotus*** *cf*. ***richtersi*** (Figure 37), and ***Minibiotus intermedius*** (Figure 38-Figure 39).

Figure 36. ***Hypsibius convergens***, a common moss-dweller. Photo by Björn Sohlenius, Swedish Museum of Natural History, with permission.

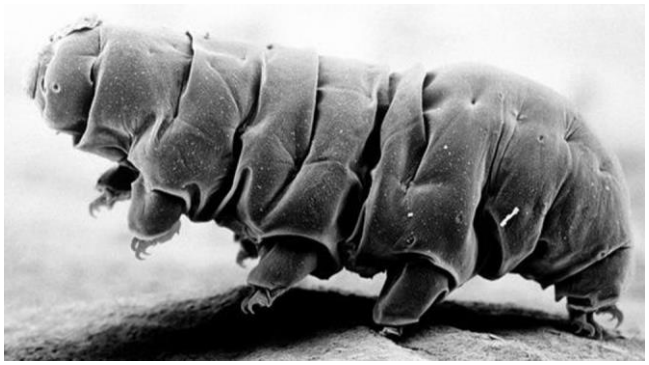

Figure 37. ***Paramacrobiotus richtersi***, a common bryophyte dweller. Photo by Science Photo Library through Creative Commons.

Figure 38. ***Minibiotus intermedius***. Photo by William Miller through Flickr.

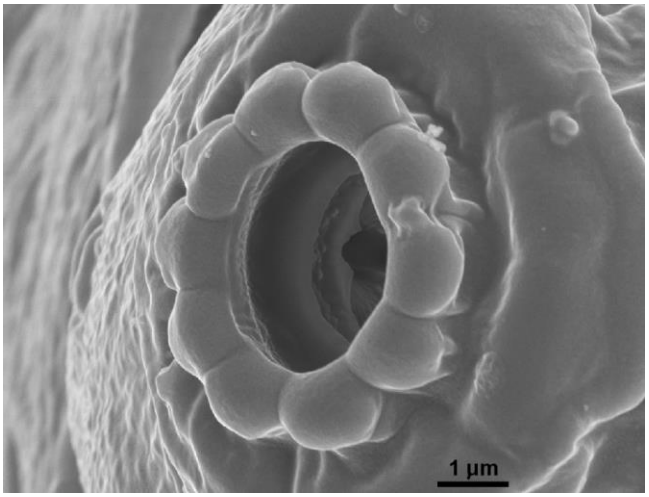

Figure 39. ***Minibiotus intermedius*** mouth. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

Likewise, in South America, Michalczyk and Kaczmarek (2005) described ***Calohypsibius maliki*** as a new species from Chile; Michalczyk and Kaczmarek (2006) described ***Echiniscus madonnae*** (Figure 40) from

Peru, all from bryophytes. In Argentina they described ***Macrobiotus szeptyckii*** and ***Macrobiotus kazmierskii*** (Kaczmarek & Michalczyk 2009). In 2008 Degma *et al*. described another new species [***Paramacrobiotus derkai*** (Figure 41)] from Chile, a country where only 29 species had previously been described.

Figure 40. ***Echiniscus madonnae***, a moss dweller from Peru. Photo by Łukasz Kaczmarek & Łukasz Michalczyk, with permission.

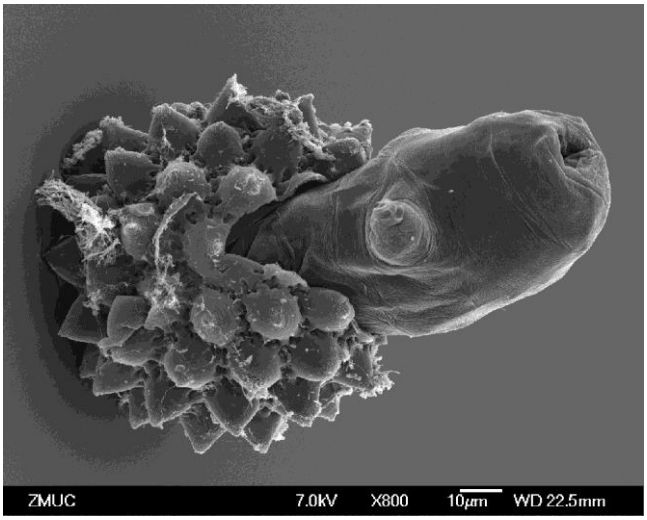

Figure 41. ***Paramacrobiotus derkai*** emerging from egg. Photo by Łukasz Kaczmarek, with permission.

In Portugal, lichens and mosses provided the new species ***Minibiotus xavieri*** to Fontoura and coworkers (2009). In Cyprus, Kaczmarek and Michalczyk (2004d) described ***Macrobiotus marlenae*** (Figure 42). ***Macrobiotus kovalevi*** proved to be a new species from mosses in New Zealand (Tumanov 2004). Clearly, mosses have been a favorite sampling substrate for tardigrade seekers (Kaczmarek & Michalczyk 2009) and most likely hold many more undescribed species around the world.

Even when new species are collected, they are not always identified or diagnosed in a timely manner. This can result in their ultimate description from multiple locations. Such is the case for ***Echiniscus viridianus*** (Figure 43), a new species described by Pilato *et al*. (2007) from Alabama and New Mexico, USA, and from the Azores Islands, all from mosses.

Figure 42. ***Macrobiotus marlenae***. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

Figure 43. ***Echiniscus viridianus***. Photo by Paul J. Bartels, with permission.

Summary

Most studies indicate no correlation between bryophyte species and tardigrade species. There is limited indication that cushions may have more species, but in other studies thin mats have more than cushions. Other studies indicate they are more common on weft-forming mosses than on turfs. Open mosses like ***Polytrichum*** seem to be less suitable as homes. There may be some specificity for liverworts rather than mosses, as for example ***Macrobiotus snaresensis*** in New Zealand. Unfortunately, many researchers have not identified the bryophyte taxa in tardigrade faunistic studies. A common garden study including several bryophyte species and tardigrades of the same or different species could be revealing.

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Roberto Bertolani provided an invaluable update to the tardigrade taxonomic names and offered several suggestions on the text to provide clarification or correct errors. Łukasz Kaczmarek has provided me with references, images, contact information, and a critical read of an earlier version of the text. Martin Mach and Yuuji Tsukii have given permission to use images that illustrate the species. Michael Lüth has given permission to use his many bryophyte images, and my appreciation goes to all

those who have contributed their images to Wikimedia Commons for all to use. Martin Mach was kind enough to send me corrections for typos in the previous online version. Thank you to my sister, Eileen Dumire, for providing the view of a novice on the readability of the original text (it has been much expanded since then). Tardigrade nomenclature is based on Degma *et al*. 2010.

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CHAPTER 5-5
TARDIGRADE DENSITIES AND RICHNESS

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CHAPTER 5-5
TARDIGRADE DENSITIES AND RICHNESS

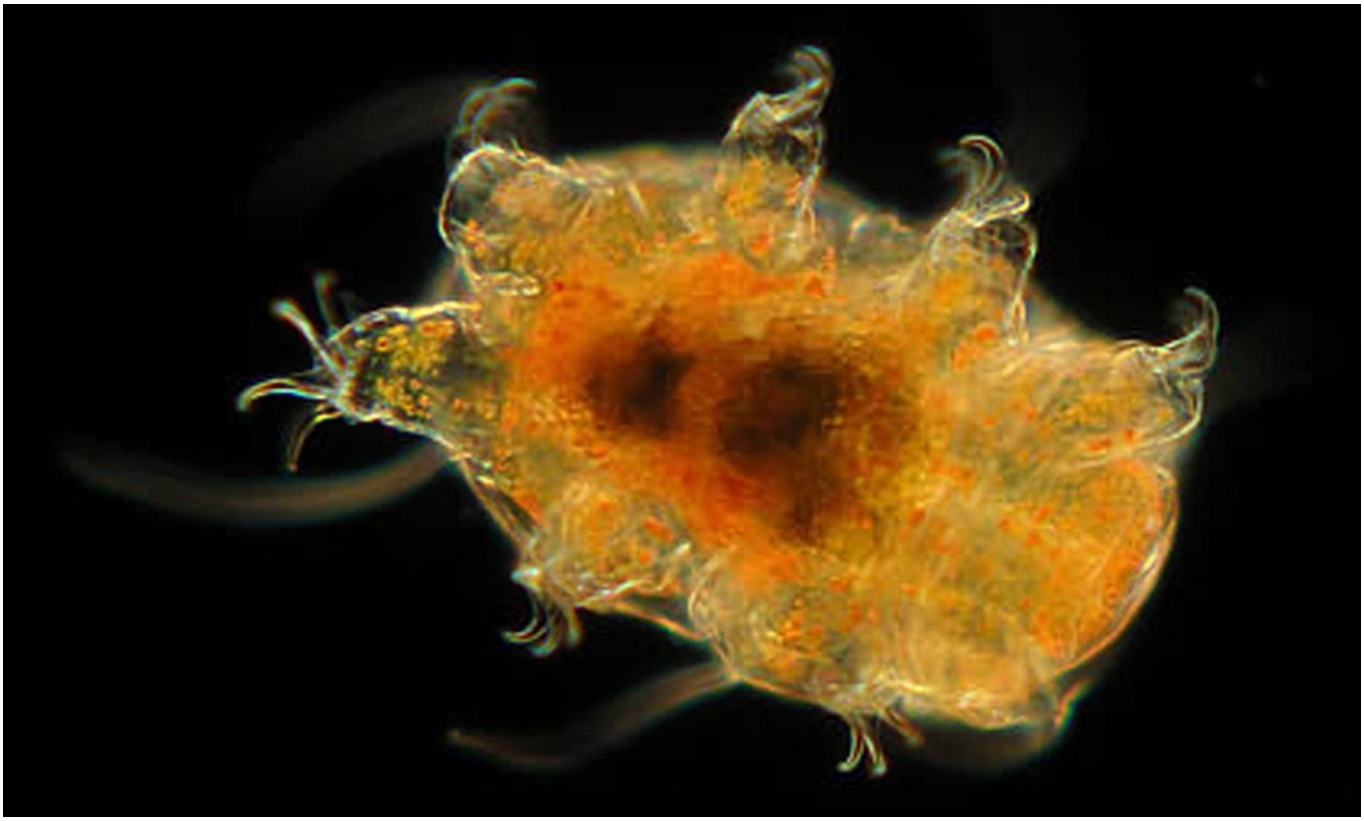

Figure 1. ***Echiniscus***, the genus with the most species among mosses. Photo by Martin Mach, with permission.

Densities and Richness

But just how common are these bryophyte-dwelling tardigrades (Figure 1)? I think the largest reported density I have found in the literature is 22,000 individuals per gram of dry moss (Mathews 1938), but that is an old number and may well have been replaced. These animals seem to be especially adapted for the bryophyte habitat (Jerez *et al.* 2002), achieving densities as great as 2,000,000 individuals per square meter of ***Bryum argenteum*** (Figure 2) (Brusca & Brusca 1990). (Is that greater than 22,000 per gram?) Nelson (2002) reminds us that densities of these animals are highly variable and conditions for optimum development of the population are unknown (see also Kinchin 1994). Factors such as temperature and moisture (Franceschi *et al.* 1962-1963; Morgan 1977; Briones *et al.* 1997), air pollution (Steiner 1994a, b, c, 1995), and food availability (Hallas & Yeates 1972) all influence population density. And it appears that random dispersal may be a major factor, since both population density and species diversity vary considerably between adjacent microhabitats that appear to be identical (Nelson 2002).

Figure 2. ***Bryum argenteum*** exhibiting the tight leaves that provide capillary spaces where tardigrades can enjoy prolonged water retention. Photo by Michael Lüth, with permission.

Among the more extensive studies is that of Kathman and Cross (1991) on Vancouver Island, British Columbia, Canada. They collected from mosses at six altitudes on five mountains and found 39 species among 37 moss species, with 13,696 individuals in all. However, as noted in Bertolani's (1983) study, the species of moss did not seem to be important.

Horning *et al*. (1978) collected from soil, fungi, algae, bryophytes, lichens, marine substrata, freshwater substrata, and litter in New Zealand and surrounding islands. They provide summaries of the tardigrade species from each bryophyte species. From their 1354 collections, they represented 577 terrestrial habitats. All 14 of the more abundant tardigrade species occurred in at least three of the five "plant" categories (three lichen forms, liverworts, and mosses). Among these, the highest occurrence was among mosses, except for ***Milnesium tardigradum*** (Figure 3), which occurred more often among lichens. They reported the number of species on each bryophyte, but not the density of individuals. As in other studies, moisture seemed to play a major role. They considered the "plant" categories, arranged from dry to moist, to be crustose lichen > fruticose lichen > foliose lichen > liverworts & mosses. The foliose lichens and mosses served as habitat for more tardigrade species than did the liverworts, crustose lichens, or fruticose lichens. Liverworts housed 30 tardigrade species on 26 liverwort species.

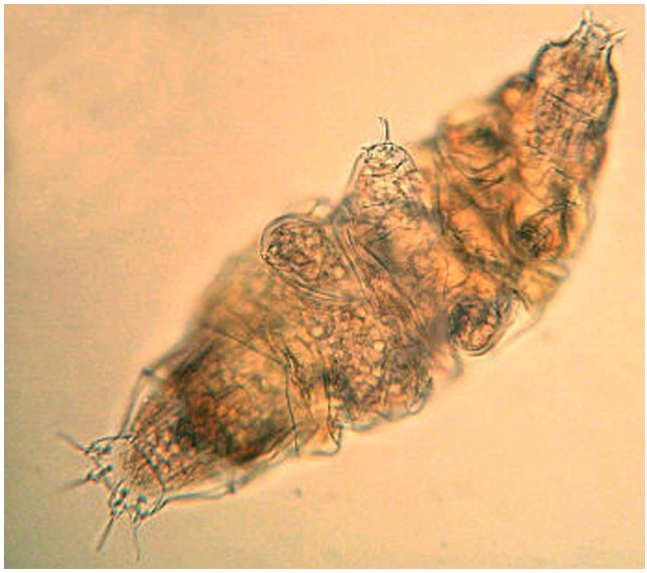

Figure 3. ***Milnesium tardigradum***, a moss dweller that seems to have a slight preference for lichens. Photo by Martin Mach, with permission.

Roof mosses (Figure 4) have their share of tardigrade fauna; Morgan (1977) recorded densities of four tardigrade species [***Macrobiotus hufelandi*** (Figure 15), ***Milnesium tardigradum*** (Figure 3), ***Ramazzottius oberhaeuseri*** (Figure 5), ***Echiniscus testudo*** (Figure 6)] of up to 823 individuals per gram of the mosses ***Ceratodon purpureus*** (Figure 7) and ***Bryum argenteum*** (Figure 8) on roofs in Swansea, Wales. In total, Morgan collected 32,552 tardigrades from these two mosses on just three roof locations at the University College of Swansea.

Even new species might be abundant in many parts of the world. This is an under-collected group, as suggested by finding very common species for the first time in some countries. Kristensen *et al*. (2009) found more than 200 individuals of a new species of ***Bryodelphax*** (see Figure 9) in a "very small moss sample." And these were cohabiting with ***Macrobiotus hufelandi*** (Figure 15) and ***Milnesium tardigradum*** (Figure 3).

Figure 4. Moss-covered roof that has been sampled along the edge. Photo by Susan Moyle-Studlar, with permission.

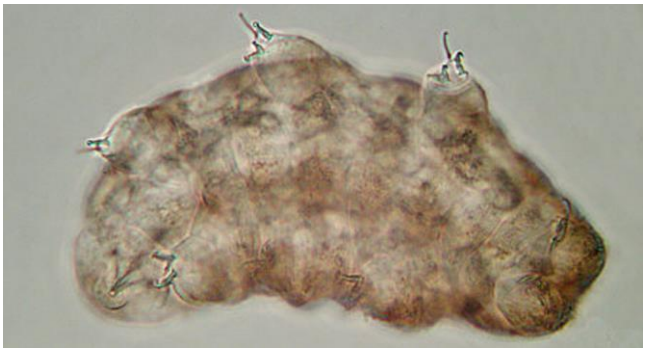

Figure 5. ***Ramazzottius oberhaeuseri***, a common moss-dweller, including those on roofs. Photo by Martin Mach, with permission.

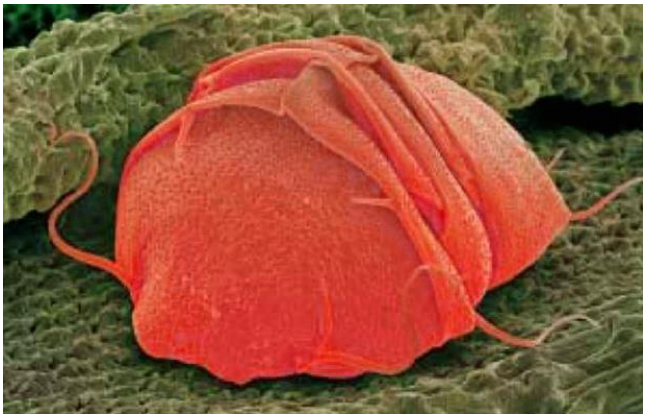

Figure 6. ***Echiniscus testudo*** tun on a moss leaf. Photo by Power & Syred through Creative Commons.

Figure 7. ***Ceratodon purpureus***, another common roof moss that can house innumerable tardigrades. Photo by Michael Lüth, with permission.

Figure 8. ***Bryum argenteum***, a common roof moss that can house innumerable tardigrades. Photo by Michael Lüth, with permission.

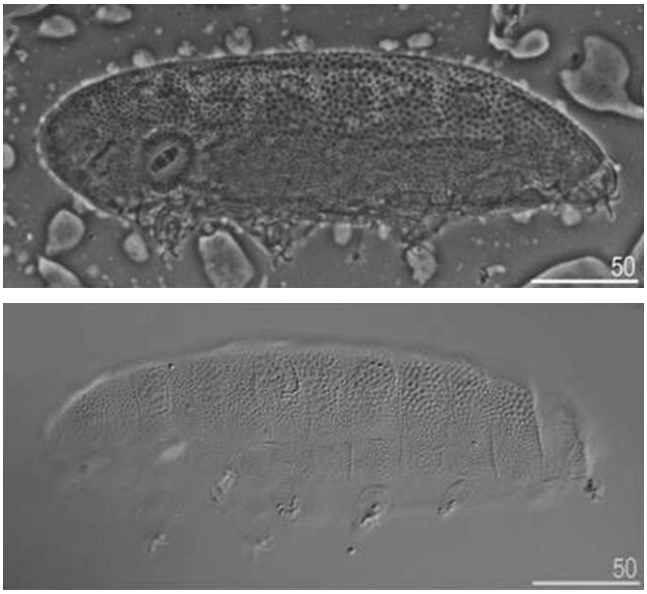

Figure 9. ***Bryodelphax asiaticus***. Photo through Creative Commons.

Europe

One might expect the knowledge of European tardigrades to be the most complete, partly because the taxonomy of the bryophytes has been known longer than in many other countries, including North America, and partly because of the interest of Europeans in natural history.

Some European mosses have abundant tardigrades: ***Hypnum cupressiforme*** (Figure 10), ***Hylocomium splendens*** (=*Hypnum parietinum*) (Figure 11), and ***Sanionia uncinata*** (Figure 12), as well as ***Grimmia*** (might include ***Schistidium***; Figure 13) and ***Tortula*** (Marcus 1928a; probably includes ***Syntrichia***; Figure 14) and may contain up to 20,000 individuals per 1 g of air-dried moss (Marcus 1928b).

Figure 10. ***Hypnum cupressiforme***, home of abundant tardigrades. Photo by Michael Lüth, with permission.

Figure 11. ***Hylocomium splendens***, a good habitat for tardigrades. Photo by Janice Glime.

Figure 12. ***Sanionia uncinata***, a suitable tardigrade habitat. Photo by Janice Glime.

Figure 13. ***Grimmia elongata*** cushions. Photo by Michael Lüth, with permission.

Figure 14. ***Tortula intermedia*** cushion. Photo by Michael Lüth, with permission.

In a boreal forest in Sweden, Jönsson (2003) found sixteen species of tardigrades on mosses, including the widespread ***Macrobiotus hufelandi*** (Figure 15) as the most common. Among these, five were new to Sweden. They also found that the forest tended to have more tardigrade species than did a clear-cut area, but overall abundance within a species differed little between these two habitats.

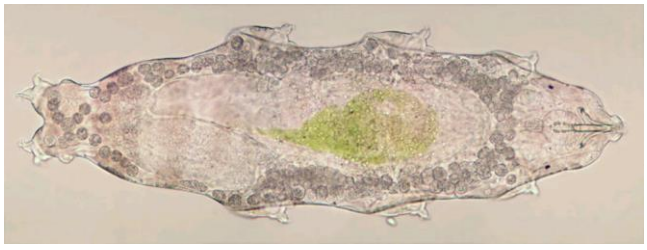

Figure 15. ***Macrobiotus hufelandi***, a dominant species on ***Rhytidiadelphus squarrosus*** (Figure 19) in the Black Forest, Germany. Photo by Martin Mach, with permission.

In the Tihany Peninsula, Hungary, Felföldy and Iharos (1947) found modest numbers, with 38 individuals per gram of the moss ***Eurhynchium swartzii*** (Figure 16) and 84 per gram among clones of ***Barbula*** [formerly in *Didymodon*] ***tophacea*** (Figure 17).

Figure 16. ***Eurhynchium swartzii***, a pleurocarpous moss that is known to house tardigrades. Photo by Kristian Peters through Wikimedia Commons.

Figure 17. ***Barbula tophacea***, an acrocarpous moss that houses tardigrades. Photo by Michael Lüth, with permission.

Hofmann and Eichelberg (1987) found sixteen species, including two undescribed, among mosses at Lahnau, near Giessen, Germany. Maucci (1980) collected 2686 samples of bryophytes and found 23 species of tardigrades.

In Sardinia, Pilato and Sperlinga (1975) likewise found sixteen species of tardigrades among the bryophytes. These included ***Macrobiotus nuragicus*** and ***M. arguei*** as new species. ***Isohypsibius pappi***, ***I. sattleri*** (formerly ***I. bakonyiensis***), and ***Hypsibius convergens*** (Figure 18) were new for Sardinia. It seems that finding new species within tardigrade communities is a fairly common occurrence.

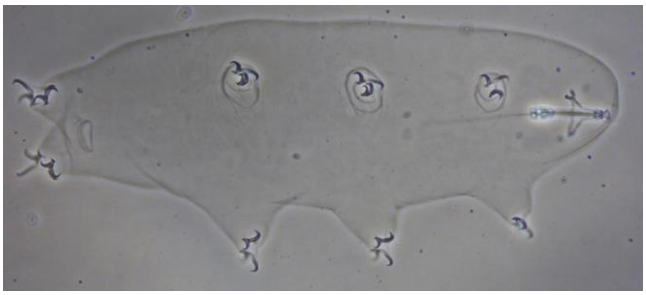

Figure 18. ***Hypsibius convergens***, one of the most common of bryophyte dwellers. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

Schuster and Greven (2007) followed the inhabitants of the moss ***Rhytidiadelphus squarrosus*** (Figure 19) in the Black Forest in Germany for 54 months (Table 1). They uncovered 19,909 individuals comprising 24 species. The dominant species were ***Macrobiotus hufelandi*** (Figure 15; 56%), ***Paramacrobiotus richtersi*** (Figure 20; 18%), and ***Diphascon pingue*** (Figure 21; 12%). In contrast to the Oregon study, the highest diversity occurred in winter, whereas the number of individuals declined in winter, then increased from spring until autumn, as in Oregon. On the other hand, ***D. rugosum*** (Figure 22), ***Hypsibius dujardini*** (Figure 23), and ***H***. cf. ***convergens*** (Figure 18) exhibited peaks in winter. Water-loving species were most numerous in the moist season, whereas **euryhydric** species increased when it was relatively dry and sunny. During the course of the 54 months, 14 of the 24 species remained, whereas species succession/change occurred among the others.

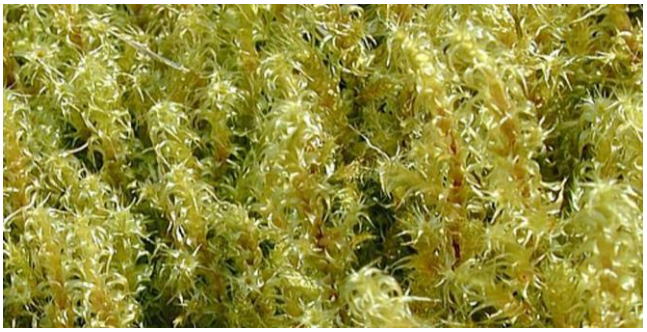

Figure 19. ***Rhytidiadelphus squarrosus***, the home for 24 rotifer species in The Black Forest of Germany. Photo by Michael Lüth, with permission.

Figure 20. ***Paramacrobiotus richtersi***, one of the most common and abundant of the bryophyte tardigrades. Photo by Science Photo Library through Creative Commons.

Figure 21. ***Diphascon pingue***. Photo by Michael Collins, with permission.

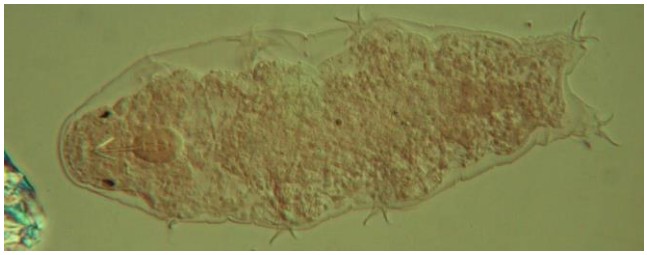

Figure 22. ***Diphascon rugosum***, a tardigrade that peaks in winter in Oregon, USA. Photo by Björn Sohlenius, Swedish Museum of Natural History, with permission.

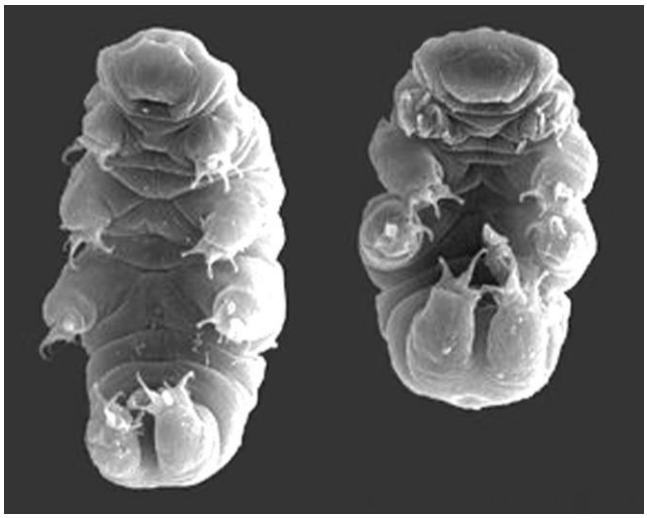

Figure 23. ***Hypsibius dujardini***, a moss dweller that has its peak population in winter in the Black Forest of Germany. Photo by Bob Goldstein, with permission.

Species such as ***Diphascon oculatum*** (Figure 24) that had reasonable numbers on ***Rhytidiadelphus squarrosus*** (Figure 19), but for which no eggs were found (Schuster & Greven 2007), might deposit eggs at a different season than those sampled. It is unlikely that they would deposit eggs in a different habitat/location from that of the adults because of their limited mobility. On the other hand, rare species occurring only once, *e.g.* ***Mesocrista spitzbergensis*** (Figure 25) [note – this is a name change from *M. spitzbergense*, required to make the gender agree with that of the genus (Degma *et al.* 2010)], may have been an accidental arrival on ***Rhytidiadelphus squarrosus***, or generally rare. It would be interesting to know the longevity and life cycle of rare species.

Figure 24. ***Diphascon oculatum***, an inhabitant of ***Rhytidiadelphus squarrosus*** (Figure 19). Photo by Björn Sohlenius, Swedish Museum of Natural History, with permission.

Table 1. Comparison of total number of individuals (in order of dominance), eggs in exuviae, dominances, and frequencies for each tardigrade species collected on ***Rhytidiadelphus squarrosus*** (Figure 19) in the Black Forest of Germany within the investigation period of 54 months. Asterisks indicate species found at least once in each year of study. From Schuster & Greven 2007.

Species	N. individuals	Eggs / Exuviae	Dominance (%)	Frequency (%)
**Macrobiotus hufelandi* (Schultze 1833)	11118	448	55.84	100
**Paramacrobiotus richtersi* (Murray 1911)	3600	179	18.08	100
**Diphascon pingue* sl (Marcus 1936)	2359	170	11.85	100
**Hypsibius scabropygus* (Cuénot 1929)	429	15	2.15	78.5
**Macrobiotus patiens* (Pilato *et al*. 2000)	403	7	2.02	87.9
**Hypsibius dujardini* (Doyère 1840)	390	58	1.96	72.9
**Diphascon rugosum* (Bartos 1935)	348	22	1.75	48.6
**Isohypsibius prosostomus* (Thulin 1928)	294	29	1.48	67.3
**Hypsibius convergens* (Urbanowicz 1925)	246	18	1.24	46.7
**Hypsibius pallidus* (Thulin 1911)	246	13	1.24	65.4
**Hypsibius* cfr. *convergens*	164	8	0.82	31.8
**Milnesium tardigradum* (Doyère 1840)	101	4	0.51	48.6
**Diphascon oculatum* (Murray 1906)	77	0	0.39	41.1
**Diphascon prorsirostre* (Thulin 1928)	63	1	0.32	39.3
Isohypsibius pappi (Iharos 1966)	24	7	0.12	16.8
Hypsibius sp.	12	0	0.06	2.8
Diphascon nobilei (Binda 1969)	8	0	0.04	2.8
Minibiotus cfr. *poricinctus*	8	0	0.04	3.7
Minibiotus cfr. *scopulus*	6	0	0.03	5.6
Diphascon scoticum (Murray 1905)	5	0	0.03	2.8
Minibiotus intermedius (Plate 1888)	5	0	0.03	3.7
Diphascon bullatum (Murray 1905)	1	0	0.01	0.9
Diphascon higginsi (Binda 1971)	1	0	0.01	0.9
Mesocrista spitzbergensis (Richters 1903)	1	0	0.01	0.9
Sum	19909	979	100.00	

Figure 25. ***Mesocrista spitzbergensis***, an inhabitant of ***Rhytidiadelphus squarrosus***. Photo by Björn Sohlenius, Swedish Museum of Natural History, with permission.

In Scotland, Morgan (1976) found that bryophyte and lichen dwellers represented the highest number of tardigrades as well as having the greatest species diversity. In Wales, Morgan (1974) found tardigrades numbering $2287x10^3$ m^{-2} among mosses. By contrast, Hallas and Yeates (1972) found only $12x10^3$ m^{-2} in soil and litter in Danish forests.

Studies on abundance reveal a wide range of densities. Degma and coworkers (2003, 2006; & Pecalková 2003; *et al*. 2004, 2005) have provided us with records of tardigrades on named species of mosses in Slovakia. On ***Hypnum cupressiforme*** (Figure 10) in Central European oak-hornbeam forests of Slovakia, Degma *et al*. (2005) found 3050 tardigrades [21 species in two families (**Hypsibiidae** & **Macrobiotidae**)] from 79 moss samples. As in many other studies they were unable to demonstrate any of 12 environmental variables that accounted for the distribution of the tardigrades. Rather, they found that the distribution of species was random.

Nevertheless, in his 2003 study, Degma found particular tardigrades on particular bryophytes (Figure 26-Figure 43): ***Eremobiotus alicatai*** on mosses ***Brachythecium rutabulum*** (Figure 26) and ***Eurhynchium hians*** (Figure 27); ***Isohypsibius pappi*** on these two as well as on ***B. reflexum*** (Figure 28), ***Homalothecium sericeum*** (Figure 29), ***Hypnum cupressiforme*** (Figure 10), ***Mnium stellare*** (Figure 31), and ***Rhynchostegium megapolitanum*** (Figure 32); ***Isohypsibius josephi*** on ***Amblystegium serpens*** (Figure 33) and ***Brachythecium starkei*** (Figure 34); ***Diphascon iltisi*** on ***Campylium halleri*** (Figure 35); ***Astatumen trinacriae*** (Figure 36) on ***Brachythecium rutabulum*** (Figure 26), ***Homalothecium sericeum*** (Figure 29), ***Hypnum cupressiforme*** (Figure 10), ***Isothecium alopecuroides*** (Figure 30), ***Leskeella nervosa*** (Figure 37), ***Paraleucobryum longifolium*** (Figure 38), and ***Pterigynandrum filiforme*** (Figure 39); ***Isohypsibius dastychi*** in unidentified moss. Degma and Pecalková (2003) reported ***Diphascon belgicae*** in ***Brachythecium reflexum*** (Figure 28); ***Calohypsibius schusteri*** and ***Itaquascon pawlowskii*** in ***Hypnum cupressiforme*** (Figure 10). In 2006 Degma reported ***Echiniscus*** *cf.* ***reticulatus*** on ***Ctenidium molluscum*** (Figure 40); ***Testechiniscus***

spitsbergensis on ***Ctenidium molluscum*** (Figure 40), ***Distichium capillaceum*** (Figure 41), ***Ditrichum flexicaule*** (Figure 42), and ***Tortella tortuosa*** (Figure 43). But are these just chance findings, or is there a preference? It is interesting that all but the last three and ***Paraleucobryum longifolium*** (Figure 38) are mat-forming mosses. Was this a preference of the tardigrade or the collector? Or simply a consequence of the habitat?

Figure 26. ***Brachythecium rutabulum***, a mat-forming moss that is home to ***Astatumen trinacriae***, ***Eremobiotus alicatai***, and ***Isohypsibius pappi***. Photo by Michael Lüth, with permission.

Figure 27. ***Eurhynchium hians***, a mat-forming moss that is home to ***Eremobiotus alicatai*** and ***Isohypsibius pappi***. Photo by Michael Lüth, with permission.

Figure 28. ***Brachythecium reflexum***, a mat-forming moss that is home to ***Diphascon belgicae*** and ***Isohypsibius pappi***. Photo by Michael Lüth, with permission.

Figure 29. ***Homalothecium sericeum***, a mat-forming moss that is home to ***Astatumen trinacriae*** and ***Isohypsibius pappi***. Note the branches turned to one side. Photo by Michael Lüth, with permission.

Figure 30. ***Isothecium alopecuroides***, home to ***Astatumen trinacriae*** and ***Isohypsibius pappi***. Photo by Biopix through EOL Creative Commons.

Figure 31. ***Mnium stellares***, home to ***Isohypsibius pappi***. Photo by Michael Lüth, with permission.

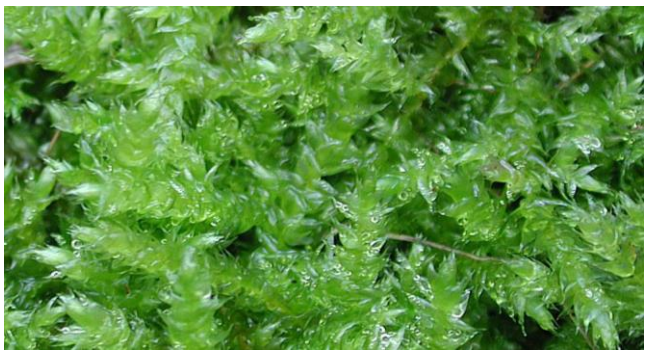

Figure 32. ***Rhynchostegium megapolitanums***, home to ***Isohypsibius pappi***. Note the droplets of water adhering to the leaves, making this a good limnoterrestrial habitat. Photo by Michael Lüth, with permission.

Figure 33. ***Amblystegium serpens***, home to ***Isohypsibius josephi***. Photo by Michael Lüth, with permission.

Figure 34. ***Brachythecium starkei***, home to ***Isohypsibius josephi***. Photo by Michael Lüth, with permission.

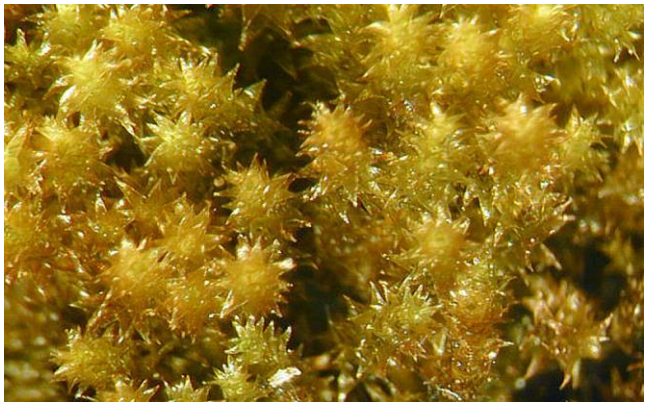

Figure 35. ***Campylium halleri***, home to ***Diphascon iltisi***. Photo by Michael Lüth, with permission.

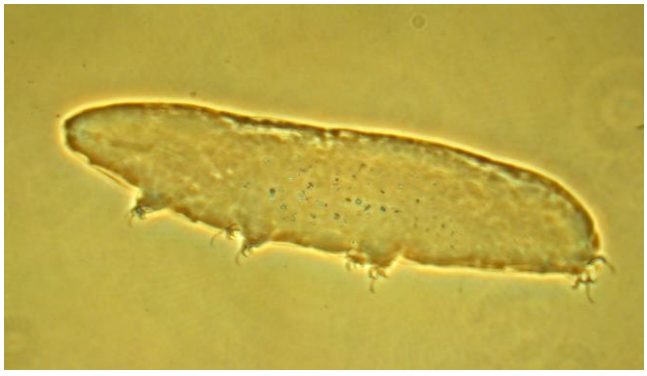

Figure 36. ***Astatumen trinacriae***. Photo by Paul J. Bartels, with permission.

Figure 37. ***Leskeella nervosa***, home to ***Astatumen trinacriae***. Note the bulbils at the tips of branches. Photo by Michael Lüth, with permission.

Figure 38. ***Paraleucobryum longifolium***, a cushion former on rocks, home to ***Astatumen trinacriae***. Photo by Michael Lüth, with permission.

Figure 39. ***Pterigynandrum filiforme***, home to ***Astatumen trinacriae***. Photo by Michael Lüth, with permission.

Figure 40. ***Ctenidium molluscum***, home to ***Echiniscus*** *cf.* ***reticulatus*** and ***Testechiniscus spitsbergensis***. Photo by Michael Lüth, with permission.

Figure 41. ***Distichium capillaceum***, a cushion former, home to ***Testechiniscus spitsbergensis***. Photo by Michael Lüth, with permission.

Figure 42. ***Ditrichum flexicaule***, exhibiting tight vertical leaves, home to ***Testechiniscus spitsbergensis***. Photo by Michael Lüth, with permission.

Figure 43. ***Tortella tortuosa***, a cushion former, home to ***Testechiniscus spitsbergensis***. Photo by Michael Lüth, with permission.

North America

The neglect of tardigrades has not escaped North America. Meyer (2006a) lamented that only one species of tardigrade had been reported from Florida. By sampling 47 species of mosses, liverworts, lichens, and ferns from trees and shrubs in all 67 counties of Florida, he found 20 species of tardigrades. Like other studies discussed here, he could find no association between tardigrade species and any particular bryophyte or lichen species. He did, however, find differences between species occurring on lichens and mosses in general.

It is clear that neglect of the bryophyte habitat is neglect of tardigrades in general. Based on species-area curves, Bartels and Nelson (2007) estimated the greatest species richness among bryophytes in their comparison of habitats in the Great Smoky Mountains, USA, although their actual numbers showed about equal numbers of species among the terrestrial habitats:

Aquatic	29
Soil	39
Lichen	35
Moss	37
Total	140

Among the additional species most likely to contribute to the predicted number of bryophyte dwellers are a number of species found there on other substrata, that are known from bryophytes elsewhere but not found in the necessarily limited sampling in this study.

Meyer *et al.* (2003) examined populations among a variety of habitats in central Florida and Ouichita Mountains, Arkansas, USA. They found the tardigrades to be both diverse and abundant, varying greatly within the same species among mosses on different rocks and trees. For example, in an extreme case a tree exhibited three species with numerous individuals while the adjacent tree had none. Four adjacent cores yielded from 0 to 86 individuals, totalling 5 species. This type of distribution is consistent with the patchiness discussed below and supports the hypothesis of random dispersal followed by aggregation resulting from reproduction without migration.

Paul Davison (pers. comm. 21 June 2006), working in Alabama, USA, contends that tardigrades are best found on "scrappy mosses" that occur in harsh environments. These include those on the face of concrete steps or rock and concrete walls, rooftops, or bark of city trees. In fact, some researchers have suggested that the tardigrades might require a dry period during their lives to survive. Using such mosses, drying, and crumbling them through a 0.5 cm screen over a dish pan can yield as many as 70 tardigrades in just 5 mL of processed extract.

A more modest flora was in evidence in the collections from Southwestern Virginia, USA (Riggin 1962). In 434 collections of mosses and lichens, Riggin found only 694 individual tardigrades – hardly a story of high densities on a broad scale. These were represented by 26 species. ***Macrobiotus*** seems to be among the most common genera on bryophytes, including North American collections where Riggin found 63% of the Virginia bryophyte (moss?) and lichen collections housing members of this genus.

In a study of both the Upper and Lower Peninsulas of Michigan, USA, Meyer *et al.* (2011) revealed 28 species of tardigrades from mosses, liverworts, lichens, and leaf litter, of which 19 were from bryophytes [***Echiniscus blumi***, ***E. merokensis***, ***E. virginicus***, ***E. wendti***, ***Pseudechiniscus facettalis***, ***P. suillus*** (Figure 44), ***Milnesium tardigradum*** (Figure 3), ***Hypsibius arcticus*** (Figure 45), ***Ramazzottius baumanni***, ***R. oberhaeuseri*** (Figure 5), ***Diphascon alpinum***, ***D. nodulosum*** (Figure 46), ***Astatumen trinacriae*** (Figure 36), ***Macrobiotus echinogenitus***, ***M. hufelandi*** (Figure 15), ***Minibiotus intermedius*** (Figure 47), ***Fractonotus caelatus***, ***Paramacrobiotus areolatus*** (Figure 48), ***P. tonollii*** (Figure 49)]. Of the 28, 18 species were considered to be cosmopolitan. They found only one new

species, and it was not a bryophyte dweller. Although Ramazzotti and Maucci (1983) reported that more than ten taxa of tardigrades can often occur in a single bryophyte sample, and the range is generally 2-6, Meyer *et al*. found diversity on Michigan bryophytes to usually be at the lower end of this range.

Figure 44. ***Pseudechiniscus juanitae***. Photo by Paul J. Bartels, with permission.

Figure 45. ***Hypsibius arcticus***. Photo from Smithsonian Institution through EOL Creative Commons.

Figure 46. ***Diphascon nodulosum***. Photo by Michael Collins, with permission.

Figure 47. ***Minibiotus intermedius***. Photo by William Miller through Flickr.

Figure 48. ***Paramacrobiotus*** [=*Macrobiotus*] ***areolatus***. Photo by Martin Mach, with permission.

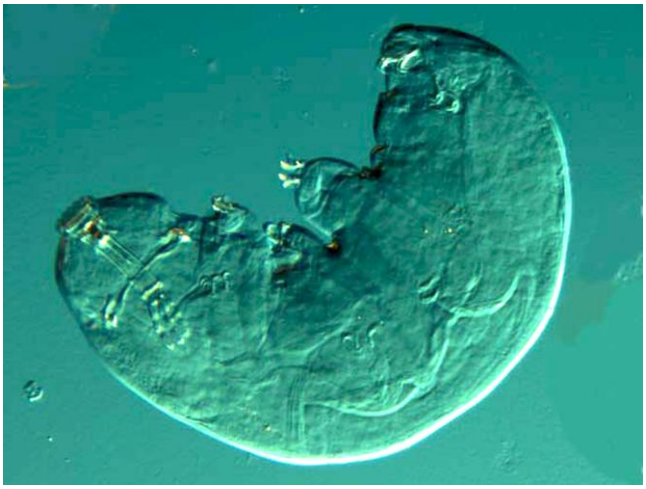

Figure 49. ***Paramacrobiotus tonollii***. Photo by Paul J. Bartels, with permission.

Nelson and Hauser (2012) collected epiphytic mosses and liverworts in a natural area in Oregon, USA. Out of 1102 invertebrates collected, the tardigrades ranked second, exceeded only by the mites (**Acari**). They pointed out the need for water sampling (washing samples) to find tardigrades. These animals did not show up in the Berlese

extraction used by many collectors. Their collections reveal at least six or seven different taxa of tardigrades from each epiphytic moss water sample, a number that brings the patchy distribution of tardigrades into question. They considered the tardigrades to be well represented for a group with approximately 1000 species, compared to mites with approximately 50,000 species.

South America and Neotropics

Numbers of species and density varies widely among tardigrade collections. Claps *et al*. (2009) found 28 species in 10 genera in a sub-Antarctic *Nothofagus* forest (18) and plateau (13) in the Rio Negro province of Argentina. In Costa Rica, Kaczmarek *et al*. (2009, 2011) found more than 7000 tardigrade individuals in 700 samples of lichens, mosses, and liverworts. These comprised 64 species in 18 genera, but the average number of species per sample was not more than three. They found altitude to be an important factor in distribution, with the highest diversity in the range of 1400-2000 m asl (35 species, 55% frequency). Only 18 species (28% frequency) occurred in the range of 2400-2800 m asl. In the range of 2000-2400 m asl the number of individuals was high. Then at 3200 m asl the frequency (70%) and abundance increased again. Surprisingly, they found a significantly higher presence in the urban and agricultural habitats than they did in natural habitats. Although 24 species had very defined habitat preferences, with the highest frequency in humid habitats, substrate and plant type were not important in their habitat choice.

Asia

Unfortunately, much of the Asian literature is lost to the western world because of our lack of skill in reading the languages. But according to Beasley *et al*. (2006), the knowledge of tardigrades in China is meager. And ecological studies seem to be totally wanting. Many of the studies are simply reports of collections made by outsiders (*e.g.* Mathews 1937a, b; Bartos 1963; Pilato 1974; Beasley *et al*. 2006). Pilato (1974) found six species of tardigrades in Chinese bryophyte communities and identified three new species: ***Bryodelphax*** [=*Echiniscus*] ***sinensis***, ***Macrobiotus mandalaae***, and ***Macrobiotus mauccii***. Yang (2002) reported on tardigrades from bryophytes in Yunnan Province. Beasley *et al*. (2006) reported only 18 species from a wide geographic range (3 provinces) in China, with 12 of these species occurring on mosses [***Echiniscus nepalensis***, ***Pseudechiniscus jiroveci***, ***Murrayon hibernicus***, ***Hypsibius pallidus***, ***Isohypsibius sattleri***, ***Doryphoribius flavus***, ***Diphascon pingue*** (Figure 21), ***Diphascon scoticum*** (Figure 50), ***Diphascon prorsirostre***, ***Mesocrista spitsbergensis*** (Figure 51), ***Platicrista angustata*** (Figure 52), ***Milnesium tardigradum*** (Figure 3)] and 1 on a liverwort [***Cornechiniscus lobatus*** (see Figure 53)]. Of the 18 species reported, 8 were new to China! It is likely that a much larger fauna exists but has not been explored – or translated.

In 2007, Beasley and Miller published a list of tardigrades from Xinjiang Uygur Autonomous Region, China, based on bryophyte specimens from the Missouri Botanical Garden. They found only 78 tardigrades among the 270 specimens of bryophytes, comprising 12 species. Of these 12, 7 were new to China. Several additional species could not be identified. The best known bryophyte dweller among these was ***Milnesium tardigradum*** (Figure 54). ***Echiniscus testudo*** (Figure 6) was found among the greatest number of bryophyte species. The majority of species were in the **Heterotardigrada**, possibly due to the higher elevation of the samples and the arid nature of the habitats.

Figure 50. ***Diphascon scoticum***. Photo by Łukasz Kaczmarek, with permission.

Figure 51. ***Mesocrista spitsbergensis***. Photo by Björn Sohlenius Swedish Museum of Natural History, with permission.

Figure 52. ***Platicrista angustata***, a species that occurs on mosses in China. Photo by Michael Sullivan, with permission.

International knowledge of the Japanese tardigrade fauna suffers from the same language barrier. Mathews, who also named a number of Chinese taxa, reported on the Japanese tardigrades in 1936/37. More recently, Ito (1999) made an ecological study on the north slope of Mt. Fuji,

sampling soil, mosses, and lichens. The number of soil tardigrades ranged 8,050 m^{-2} to 75,500 m^{-2}. Their density was as high as the density of soil arthropods such as mites (Acari) and springtails (Collembola). A few of these showed a relationship with altitude (950-2380 m asl), but typically the dominant species for a habitat did not change much among locations. On the other hand, they changed considerably between habitats at a single location.

Figure 53. ***Cornechiniscus cornutus***. Photo by Martin Mach, with permission.

The Japanese certainly have not ignored the tardigrades. They have made important contributions to the physiology (Horikawa & Higashi 2004; Horikawa *et al.* 2006) and space biology (Horikawa 2008; Ono *et al*. 2008) of these organisms. There are also good studies on the ecology of soil species. But ecological studies on bryophyte-dwelling taxa are hard to find.

Africa

Although little is known about them, Africa sports its share of moss-dwelling tardigrades. Pilato and Pennisi (1976) reported 21 species of tardigrades among the mosses in their collections from Cyrenaica (eastern coast of Libya), two of which represented the first members of their genera in Africa. A third, ***Isohypsibius brulloi***, was a new species. Binda (1984) found thirteen species of moss-dwelling tardigrades in South Africa and Mozambique.

Meyer and Hinton (2009) found only nine species of tardigrades among mosses and lichens in KwaZulu-Natal, South Africa, bringing the total number of species from soil, mosses, and lichens to 61 in southern Africa. But aside from species records, tardigrade-bryophyte ecological studies seem to be rare or non-existent for Africa.

Antarctic and Arctic

Unlike Asia, Africa, and South America (McInnes 1994), tardigrades are fairly well studied in polar climates, especially in the Antarctic. In the Antarctic, bryophytes, as well as lichens and algae, provide important habitats for tardigrades, rotifers, and nematodes (Utsugi & Ohyama 1991; Sohlenius *et al*. 2004). Most invertebrates decrease in abundance as one approaches the poles, but Jennings (1979) found that tardigrades actually increase in abundance in the Antarctic tundra. Peters and Dumjahnn (1999) found 15 species in ten genera in their 249 cushion moss samples from Disko Island, West Greenland. On the other hand, in his moss studies on the Antarctic Schirmacher Oasis, Mitra (1999) examined 36 sites and found only two tardigrade species.

Here they are also patchily distributed, nevertheless usually having the highest densities among these three groups of organisms. The ubiquitous and very common moss inhabitant, ***Macrobiotus*** sp., is present there, on the sub-Antarctic Marion Island (McInnes *et al*. 2001). Other tardigrades present include ***Milnesium*** *cf.* ***tardigradum*** (Figure 54) and ***Echiniscus*** sp. (Figure 55). Gut analysis of ***M. tardigradum*** revealed the presence of bdelloid rotifers and even other tardigrades (***Diphascon*** sp.). Sohlenius and Boström (2006) also noted predation by tardigrades on rotifers in East Antarctica.

On the **nunataks** (mountain peaks that penetrate the ice sheet) in continental Antarctica, distribution of tardigrades is patchy, with the greatest abundance occurring within moss cushions and **guano** (accumulated excrement of seabirds and bats) from bird colonies (Swedish Museum of Natural History 2009). Nine tardigrade taxa have been identified in the Swedish studies.

Figure 54. ***Milnesium tardigradum***, a cosmopolitan moss inhabitant. Photo by Yuuji Tsukii, with permission.

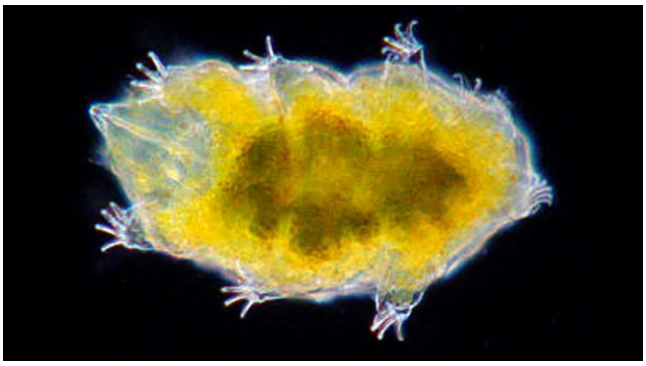

Figure 55. ***Echiniscus***, a ubiquitous genus that occurs on mosses in the Antarctic. Photo by Martin Mach, with permission.

On Signy Island off the coast of Antarctica, Jennings (1979) found five species of tardigrades that occurred at both of the sampling sites: ***Echiniscus capillatus***, ***E. meridionalis***, ***Hypsibius dujardini*** (Figure 23), ***Diphascon alpinum***, ***Diphascon pingue*** *sensu lato* (Figure 21; or may be *Diphascon polare*, *D. dastychi*, or *D. victoriae*), and ***Macrobiotus furciger*** (Figure 56). Other less common taxa were ***Diphascon scoticum*** (Figure 50), ***Isohypsibius renaudi*** (Figure 57), and ***Isohypsibius asper*** (Figure 58). Jennings conducted sampling for two years and found maximum populations of $309x10^3$ m^{-2} in moss communities of ***Polytrichum strictum*** - ***Chorisodontium aciphyllum*** (Figure 59-Figure 61). In the ***Calliergidium austro-***

stramineum – ***Calliergon sarmentosum*** – ***Sanionia uncinata*** communities (Figure 12; Figure 62; Figure 63) they found a maximum of $71x10^3$ m^{-2}. Reproductive potential is high, with increases of 3- to 4-fold in a single year. Hallas and Yeates (1972) found they could reach as high as 10- to 20-fold increases. ***Echiniscus*** increased 100-fold at one Signy Island site (Jennings 1979).

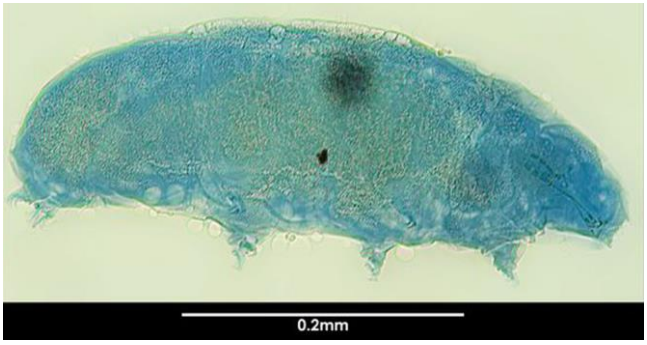

Figure 56. ***Macrobiotus furciger***. Photo by Smithsonian Institution through EOL Creative Commons.

Figure 57. ***Isohypsibius renaudi***. Photo through EOL Creative Commons.

Figure 58. ***Isohypsibius asper***. Photo by Smithsonian Institution through EOL Creative Commons.

In their Antarctic study, Utsugi and Ohyama (1989) found five species of tardigrades in 15 out of 31 samples from Ongul Island, Langhovde, Skarvsnes, Einstoingen, and Rundvagshetta, including algae, lichens, and mosses. ***Hypsibius arcticus*** (Figure 45) was common in all their samples. The other four species were rare.

Figure 59. ***Polytrichum strictum*** and ***Chorisodontium aciphyllumn*** in the Antarctic, where Jennings (1979) found $309x10^3$ tardigrades per m^2. Photo by Tim Hooker, with permission.

In a different study on Wilkes Land, East Antarctica, Petz (1997) found tardigrades in more than 74% of the collections of fellfield mosses. These were the most abundant of the invertebrates, with 4,607 in just one gram of moss. Rotifers were the most abundant in other habitats. Ottesen and Meier (1990) likewise found that tardigrades were more abundant among mosses on South Georgia, compared to other habitats.

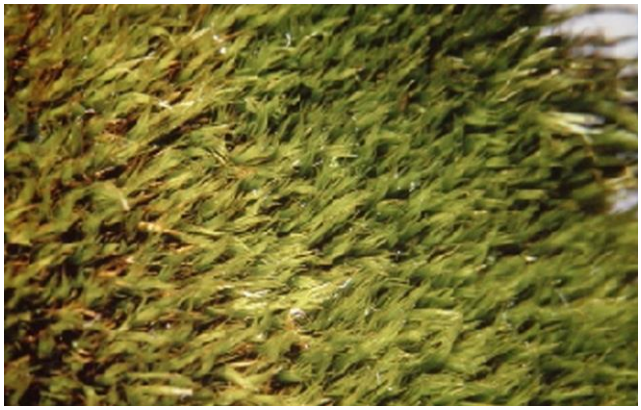

Figure 60. ***Chorisodontium aciphyllumn*** in the Antarctic. Photo by Tim Hooker, with permission.

Figure 61. ***Polytrichum strictum***, a moss habitat in the Antarctic and other cool, wet areas. Photo by Michael Lüth, with permission.

Figure 62. ***Calliergon sarmentosum***, of the ***Calliergidium austro-stramineum*** – ***Calliergon sarmentosum*** – ***Sanionia uncinatus*** association in the Antarctic. Photo by Michael Lüth, with permission.

Figure 63. ***Sanionia uncinata***, a cosmopolitan moss that provides tardigrade habitat in the Antarctic. Photo by Jan-Peter Frahm, with permission.

Seasonal Variation

Densities may vary with seasons (Figure 66). ***Hypsibius convergens*** (Figure 18) exhibits temporal variation in pool and meadow moss habitats (Marcus 1929). In city mosses, the numbers of individuals of ***Macrobiotus hufelandii*** (Figure 15) and ***Pseudechiniscus pseudoconifer*** correlated with meteorological factors during a 3-month winter/early spring study (Franceschi *et al*. 1962-63). It appears that ***Echiniscus*** (Figure 55) and its segregate genera may commonly have seasonal variations. Jennings (1979) found that ***Echiniscus*** (possibly considered a segregate genus now) was the only tardigrade with seasonal variation among the eight species in his Signy Island study.

This is at least in part a reflection of changes in moisture. As already seen for ***Diphascon rugosum*** (Figure 22), ***Hypsibius dujardini*** (Figure 23), and ***Hypsibius cf. convergens*** (Figure 18), there were clear population peaks in winter in a carpet of the soil moss ***Rhytidiadelphus squarrosus*** (Figure 19) in the Black Forest, Germany (Schuster & Greven 2007). Species diversity and evenness was generally higher for the tardigrade communities in winter and least in summer (Figure 64). On the other hand, ***Macrobiotus hufelandi*** (Figure 15), ***Diphascon pingue*** (Figure 21), and to a lesser degree ***Paramacrobiotus richtersi*** (Figure 20), declined in winter, increasing in spring through fall (Figure 65). ***Macrobiotus hufelandi*** had its peaks in summer and lows in January (Schuster & Greven 2007), as shown for total tardigrades by Merrifield and Ingham (1998), but the other major species did not follow that pattern (Schuster & Greven 2007).

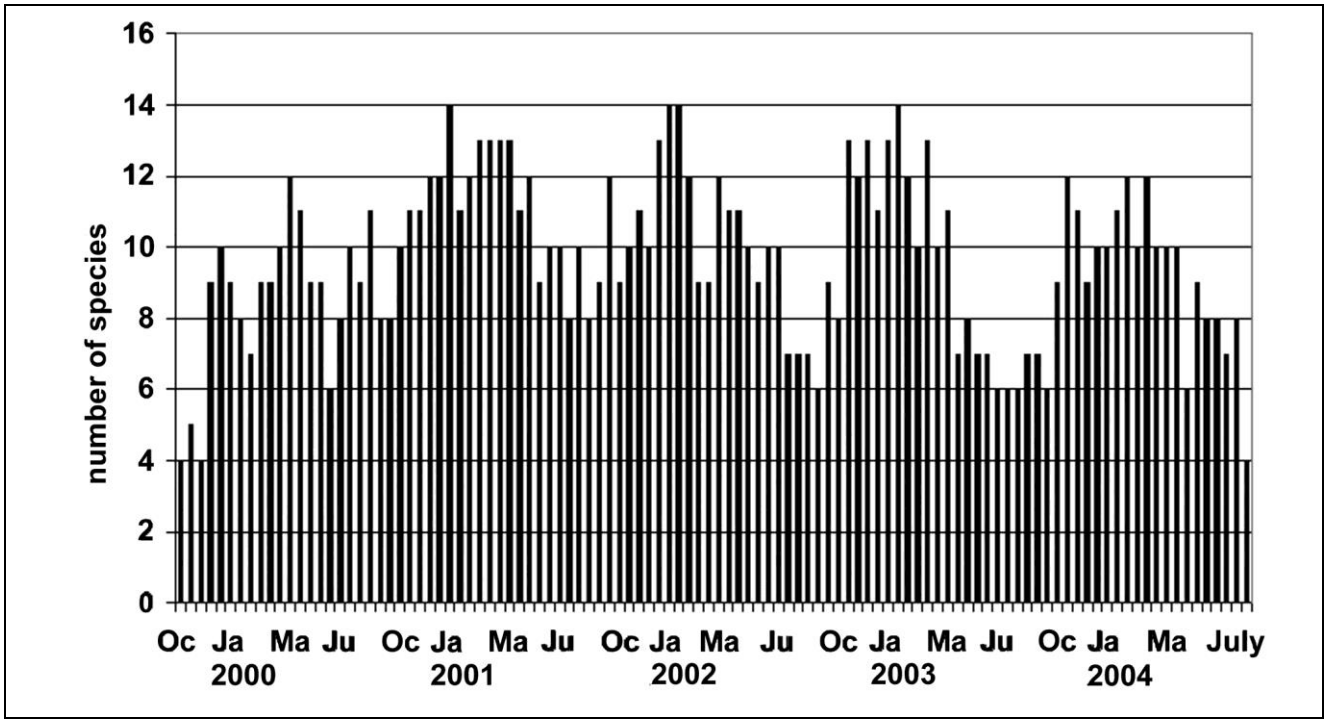

Figure 64. Seasonal changes in number of species of tardigrades found in ***Rhytidiadelphus squarrosus*** (Figure 19) clumps. (n = 108). Redrawn from Schuster & Greven 2007.

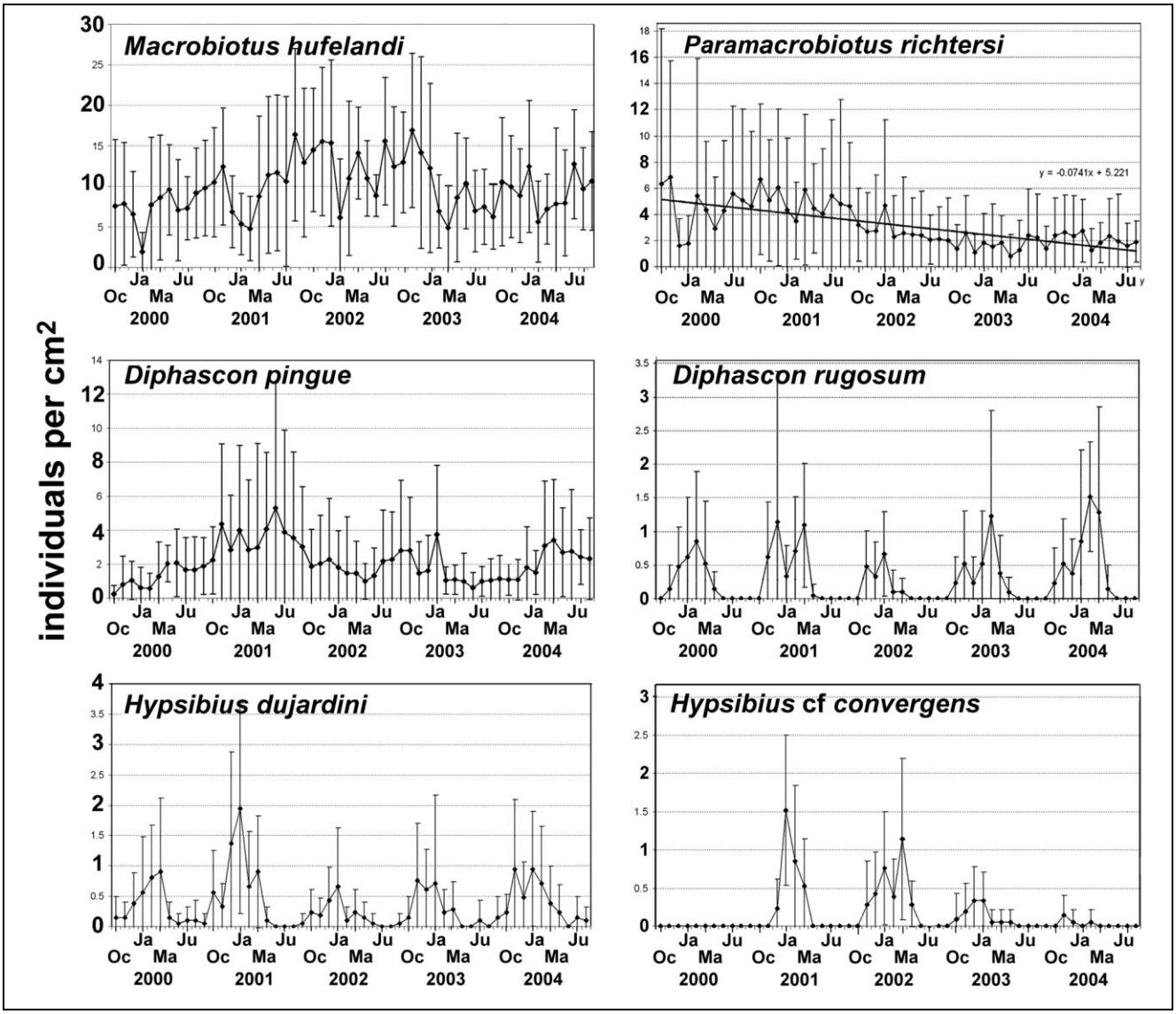

Figure 65. Seasonal changes in number of individuals of the dominant tardigrades found in ***Rhytidiadelphus squarrosus*** (Figure 19). ***Paramacrobiotus richtersi*** shows a trend of decline during the sampling years, as shown by the regression line. Modified from Schuster and Greven 2007.

Using a Baermann funnel (Merrifield & Ingham 1998), Merrifield (1992) reported 5 tardigrades per gram on ***Eurhynchium oreganum*** (Figure 67) in Oregon, USA, from April to August, with an increase to 15 in September and October, then a crash to 1 for winter months of November through March (Figure 66). Were the bears hibernating elsewhere, or were numbers crashing in the damp Oregon winter?

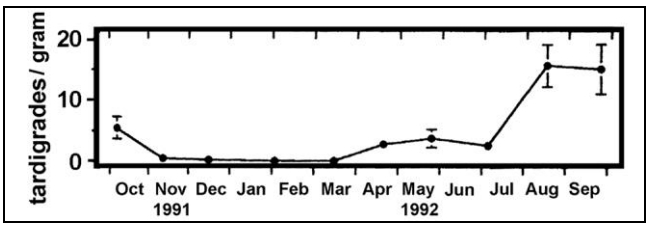

Figure 66. Seasonal changes in numbers of tardigrades on mosses at Mary's Peak, Oregon, USA. Redrawn from Merrifield & Ingham 1998.

Figure 67. ***Eurhynchium oreganum***, a non-winter habitat for tardigrades. Photo from University of British Columbia bryophyte website, with permission.

Romano *et al*. (2001) attempted to determine the seasonal effects on tardigrades among mosses along Choccolocco Creek, Alabama, USA. They surveyed mosses on three trees each in six sites for 18 months and found no correlation between occurrence and season. However, they did find seasonal differences in the number of species and abundance when they pooled samples.

Patchiness

A number of studies suggest that the distribution of tardigrades within a given area or on a particular type of substrate is patchy. Degma *et al*. (2005) actually did both cluster analysis and CCA, demonstrating that most of the differences in species diversity were the result of randomly found species and that colonization of any given substrate is a random process. It would appear that the greatest determining factor in their specific location and species composition is their dispersal to that location, a process that is as random as it is for the mosses and liverworts they sit on. Further support for this randomness is their random distribution among populations of the moss ***Hypnum cupressiforme*** (Figure 68), supported by a Chi-square goodness of fit test.

Figure 68. ***Hypnum cupressiforme***, a ubiquitous moss that seems suitable for many taxa of tardigrades. Photo by Michael Lüth, with permission.

Degma *et al*. (2009, 2011) found that the horizontal distribution of the tardigrades on a moss clump is aggregated, but that aggregation is not related to moisture in the moss cushion. They hypothesized that once a tardigrade arrives through random recruitment it is able to establish a micro-population. From that beginning slow radiation occurs. The result is that large substrates have more tardigrades but some parts of these larger patches will lack tardigrades while other parts will house aggregations. They continued their study (Degma *et al.* 2011) using ***Hypnum cupressiforme*** (Figure 68) with a 5x5 matrix of circular plots and determined that there was no significant moisture gradient along that moss slope. Nevertheless, the tardigrades existed in clumps or patches. With a large number of individuals (224) in seven species [***Milnesium tardigradum*** (Figure 3), ***Hypsibius convergens*** (Figure 18), ***H. microps***, ***Diphascon pingue*** (Figure 21), ***Astatumen trinacriae*** (Figure 36), ***Macrobiotus hufelandi*** (Figure 15), ***Minibiotus*** sp. (Figure 47)], they found that species number was random, but that species distribution was aggregated. That aggregated distribution was NOT related to moisture in the moss mat. They concluded, therefore, that the best hypothesis to explain the patchy distribution of the tardigrades within the moss cushion was that recruitment of eggs and specimens on the moss was random and that these recruits subsequently reproduced, creating micro-populations where density gradually increased over time. This hypothesis makes the assumption that tardigrades migrate little from the location of their birth. Following this reasoning on a larger scale would account for the patchy distribution observed on larger moss clumps. Larger patches of mosses are more likely to be the recipients of dispersed tardigrades or their eggs and hence are more likely to have tardigrades than would small patches. This would also account for the high degree of variation encountered in random sampling from various moss cushions in the same location. While the individuals are aggregated, the aggregations are random.

Meyer (2006b) did a careful study on the spatial variability of tardigrade populations among moss patches on trees and rocks at three locations in the USA. He examined the fauna on patches ranging 0.1 to >5 cm^2. He found very high variation among the patches. One interesting discovery was that very small patches rarely had tardigrades. Could it be that they did not retain moisture long enough, or was it a matter of dispersal, with small patches having endured too short a time for colonization to be common?

Perhaps it is predictable that patchiness would characterize Antarctic moss dwellers. In the Antarctic, bryophytes, as well as lichens and algae, provide an important habitat for tardigrades, rotifers, and nematodes (Utsugi & Ohyama 1991; Sohlenius *et al*. 2004). Here tardigrades are also patchily distributed, nevertheless having the highest densities among these three groups of organisms. One might assume that bryophytes must arrive first, or that the tardigrades arrive with their bryophyte home. Hence, dispersal to the continent and its remote islands most likely plays a major role in their location.

Studies by the Swedish Museum of Natural History (2009) likewise found patchy distribution of tardigrades on the nunataks of the Antarctic. These windswept peaks emerge above the ice sheets and provide the substrate needed for bryophytes, lichens, and inhabiting tardigrades. Moss cushions and humus enriched by bird colonies provided the greatest numbers of tardigrades, with 400 samples yielding only nine tardigrade taxa. Nevertheless, 32% of the samples had tardigrades (Sohlenius & Boström 2006). The importance of the stochastic process of colonization is supported by the presence of different developmental stages in various samples, suggesting that dispersal may be a dynamic, albeit random, process occurring constantly on the windy peaks. Further population control may exist through competition with the co-occurring nematodes, whereas it appears that the poor rotifers serve as dinner for at least some of these tardigrades.

Bettis (2008) tested differences in tardigrade distribution on ***Grimmia*** (Figure 69) on exposed granitic outcrops vs protected seasonally riparian forms in California, USA. Again, the distribution was "very patchy" and did not support the hypothesis that more tardigrades would be on the more protected, more moist mosses.

Figure 69. ***Grimmia laevigata*** in Europe. Photo by Michael Lüth, with permission.

Both Meyer (2006b) (in the terrestrial system) and Romano *et al*. (2001) (in the aquatic system), emphasized the importance of accounting for this patchiness in designing a sampling strategy. Meyer suggested that the variability of a given location should be understood before determining the number of samples to take. Romano emphasized the need for a greater sampling effort.

In short, it appears that the major factor accounting for tardigrade distribution and patchiness is dispersal. If the tardigrade lands in an appropriate habitat, it is able to withstand considerable environmental variation there, and the habitat itself seems to offer little to discriminate against any tardigrade species. Rather, factors like reproductive potential may play the greater role in determining the abundance, and possibly even the diversity, once the tardigrades arrive.

I was excited to make new friends among newcomers to the bryophyte-tardigrade relationship. I hope this chapter has inspired more young researchers to include the bryophyte microcosm in their studies. Jaime Jiménez, a vertebrate zoologist, summarizes his conversion to tardigrade study in the box below:

Statement by Jaime Jiménez

While working on the seedsnipe and geese feces with Nick [Nick Russo] and Mike [Robertson] on Navarino Island, examining for bryophytes fragments to cultivate, they found a few small water bears. Nick and Mike were my first cohort students from my IRES-NSF grant (Bernard [Goffinet] was the US co-mentor). We were all captivated to see these creature for the first time. It happened that Peter Convey (BAS that used to examine tardigrades from Antarctica) was at the lab during these days and he offered to bring these samples to Cambridge to the tardigrade world expert Sandra McInnes. She put me in contact with William Miller (KS, one of the US tardigrade experts), as she recently reviewed a paper of him on tardigrades found in bird nests. Simultaneously, with Mike, Nick and Sandra we presented a poster in Copenhagen and then in British Columbia (American Ornithological Societies conference). I invited William to UNT, and since then we have been collaborating. As a result, I "rearranged my lab" to add microscopes, dissecting scopes and cameras to mammal traps, camera traps, mist nests and binoculars. This triggered my enthusiasm to collect many bryophytes/moss samples throughout southern Chile from which I am "hunting" tardigrades to study their biogeography and habitat associations. I also have one graduate student working on tardigrade biotic homogenization.

Summary

Tardigrades can range in numbers from none to 22,000 individuals per gram of dry moss. More than 2 million are known from a single square meter. On Vancouver Island in Canada, 39 species have been found among bryophytes. They do not seem to prefer any particular moss, and they often occur equally as frequently on lichens and liverworts as they do on mosses. In New Zealand, 30 species are known from liverworts.

Macrobiotus and ***Echiniscus*** (and their more recent segregates) are among the most abundant tardigrades in the bryophyte fauna. Although most invertebrates decrease in numbers toward the poles, tardigrades actually increase. However, their numbers are highly variable from one place to another. Here, even more so than elsewhere, distribution of the tardigrades is patchy. Even adjacent trees in some localities are known to differ greatly in their tardigrade fauna. Yet, on Wilkes Land in the Antarctic, 74% of the fellfield mosses had tardigrades.

They are known to increase up to 100-fold, but it appears that 3- to 4-fold is more typical. Their abundance can be seasonal, with some peaking in winter and others in summer or spring/fall. Some respond to the rainy season. Others don't seem to respond to season.

Dispersal plays a large role in both geographic distribution and local patchiness. Within the cushions the tardigrades are often aggregated, but there appears to be no relationship with moisture. On the other hand, small patches seem to lack tardigrades, suggesting that moisture is important. But arrival is a major factor, and from that arrival of one tardigrade, a population develops. Since their movement is slow, they accumulate. But small patches of mosses indicate a short time in which arrival could have occurred.

Acknowledgments

Like all of my chapters, this one is really the product of the efforts of many biologists. Roberto Bertolani provided an invaluable update to the tardigrade taxonomic names and offered several suggestions on the text to provide clarification or correct errors. Bryonetters have been wonderful in making their photographs available to me and seeking photographs from others. Paul Davison and Des Callahan have been helpful in providing suggestions and offering images. Bob Goldstein, Bjorn Sohlenius, Martin Mach, and Yuuji Tsukii have given permission to use images that illustrate the species and life

cycle stages. Łukasz Kaczmarek has provided me with references and contact information. As always, a big thank you goes to Michael Lüth for permission to use his many images and to all those who have contributed their images to Wikimedia Commons and other public domain sources for all to use. I must admit that this chapter would have been far less interesting without the help of Google to locate the tardigrade stories. I fear I have forgotten some who have helped – I have worked on this chapter for too many years. Nomenclature follows Degma *et al*. (2010).

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TARDIGRADE ECOLOGY

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CHAPTER 5-6
TARDIGRADE ECOLOGY

Figure 1. ***Echiniscus***, the genus with the most species among mosses. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

Dispersal

As already discussed, one suggested reason for patchy distribution of tardigrades is the difficulty of dispersal for this small organism. Miller *et al*. (1994) concluded that tardigrade distribution in the Antarctic is influenced more strongly by dispersal limitations than it is by climate or habitat interactions. McInnes and Convey (2005) found a low species richness of tardigrades (6 taxa) in the South Sandwich Islands in the sub-Antarctic. They found indications that the tardigrades originated from both sub-Antarctic and maritime Antarctic populations.

Wind dispersal is considered the major means by which tardigrades move to new locations (Christenberry & Higgins 1979; Bertolani *et al*. 2009). The anhydrobiotic state is very light weight and can easily survive the various dangers of space (see below).

Faurby *et al*. (2008) suggested dispersal rate may be coupled with survival in the anhydrobiotic state. Based on these assumptions, Bromley (2009) has considered the possibilities that habitats such as rooftops with mosses serve as islands for tardigrades.

Sudzuki (1972) experimented with wind dispersal to moss mats and found that smaller micro-organisms (<10x30x50 µm) were easily blown from their location to reach the mosses 100-500 cm away. Tardigrades, on the other hand, almost never reached the mosses during two months of experimentation with the fan-generated wind operating alternate days.

Although wind is probably the most common means, other means of dispersal may be afforded by water, insects, and other invertebrates. Resting eggs offer another dispersible propagule. Eggs of tardigrades are about the same size as a pollen grain and may similarly be dispersed by wind (Ramazzotti 1972). Many species have eggs with decorations on them (Figure 2) reminiscent of allergenic pollen grains, *i.e.*, those adapted for wind pollination.

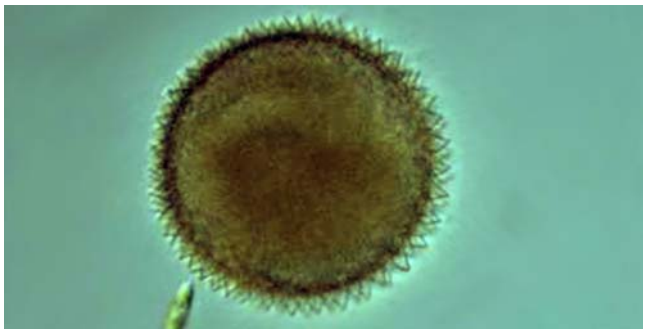


Figure 2. Egg of ***Dactylobiotus*** sp. showing decorated wall similar to that of a pollen grain. Photo by Yuuji Tsukii, with permission.

Whereas tardigrades don't seem to be dispersed very easily by themselves, their dispersal as hitch-hikers on bryophytes is a more feasible means (Janiec 1996). Not only live animals, but also tuns, cysts, and eggs can be dispersed when their bryological home is dispersed. Storms, animals, wind, and water are all means by which the substrate and fauna could travel together.

Most recently, we find that a combination of seedsnipes, bryophytes, and tardigrades may contribute to their dispersal (Robertson *et al*. 2020). Robertson and coworkers demonstrated that tardigrades can live in the feces of the White-bellied Seedsnipe (***Attagis malouinus***, Figure 3). These included the tardigrades ***Adropion*** (Figure 4), ***Isohypsibius*** (Figure 26), and ***Macrobiotus*** (Figure 11, Figure 17, Figure 25). Since at least some of these genera are known to live among bryophytes, and ***Attagis malouinus***, as well as two species of the geese ***Chloephaga picta*** (Figure 5) and ***C. poliocephala*** (Figure 6) are known to ingest bryophytes (Russo *et al*. 2020), dispersal of mosses and their adherent tardigrades might very well be dispersed by **endozoochory** – that is, dispersal by passing through the gut of the birds.

Figure 3. ***Attagis malouinus*** in rocky area with mosses nearby. Photo courtesy of Nick Russo.

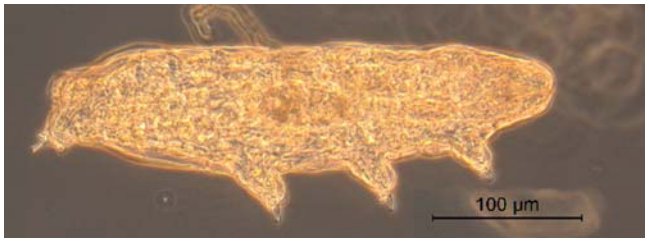


Figure 4. ***Adropion scotticum***, a tardigrade found in an embryonic stage in the feces of ***Attagis malouinus***. Photo by Aina Maerk Aspaas, NTNU University Museum, through Creative Commons.

Figure 5. ***Chloephaga picta***, a species known to eat mosses. **Female** on left, **male** on right. Photo by Fabien Khan, through Creative Commons.

Figure 6. ***Chloephaga poliocephala*** adult in Patagonia, a species known to eat mosses. **Female** on left, **male** on right. Photo by Alex Proimos, through Creative Commons.

Peninsula Effect

The **peninsula effect** postulates that the number of species will decrease as one approaches the tip of a peninsula. This presumably is the case because of the lack of opportunity for invasion of new species from the more seaward positions. Simpson (1964) suggested that there is a peninsular effect in animal distribution similar to that seen in island biogeography. Jenkins and Rinne (2008) defined the peninsula effect as "the prediction that the number of species declines from a peninsula's base to its tip." They considered whether this concept might be a "red herring" and expressed concern that most studies had not controlled for other possible explanations or from unequal sampling effort. In the Florida, USA, peninsula, they found that 82.5% of variation in freshwater microcrustacean species richness was attributed to habitat and sampling effort, and there was no peninsular effect. In fact, they suggest that the evidence previously published only supported the concept for mammals.

Taylor and Regal (1978) tested the concept of extinction and recolonization, a tenet of the peninsular effect, for rodents in Baja California and concluded that for an effective peninsular effect the habitable sites "are few and widely spaced." Brown (1987) examined the effect on butterflies (Lepidoptera) in the Baja peninsula and determined that there was no peninsular effect for that group. Likewise, Busack and Hedges (1984) found no peninsular effect for lizards and snakes on the Baja peninsula.

Taylor and Regal (1978) suggest that changes in vegetation in Florida that are due to rising water levels and climate change may account for the decline in species richness southward on that peninsula. They argue that other large peninsulas where Simpson demonstrated a peninsular effect represent major topographic changes or harsh climate gradients that could account for changes in species number.

Nevertheless, Meyer (2008) found a peninsular effect in tardigrades when bryophyte and lichen epiphytes in all 67 Florida counties were sampled, with species richness diminishing from north to south. If we combine the information gained from the above studies, it appears that Taylor and Regal (1978) may have been correct in suggesting that the peninsular effect required few and

widely spaced habitable sites. And widely spaced for one species may be a lazy day's walk for another. To put this into the perspective of bryophyte-dwelling tardigrades, isolation and difficulty of dispersal are typical, *i.e.*, widely spaced habitable sites (see dispersal discussion above), and would make tardigrades more likely to have the extinction-recolonization limits required for the peninsular shape to have a "peninsular effect." The apparent need for wind dispersal of tardigrades is further complicated by their residence within the bryophyte mat, and it seems they would most likely be dispersed only when they and their bryophyte substrate are dry and fragments to which they adhere become airborne. This dispersal limitation has been discussed earlier (Chapter 5-5 of this volume) in relation to the patchiness of populations within a given small area.

There is a possible caveat to this discussion. The definition of a peninsular effect seems to have drifted from that of Simpson (1964). He considered peninsulas to have fewer species (lower richness) than continental areas and did not treat them as having fewer species toward the tip. However, he did consider that spread of species could occur in one direction only (*i.e.*, no new mammal species were likely to arrive from the tip in the short term). He suggested that this would make them more liable to local extinctions (*i.e.*, reducing the density of species richness).

Distribution

Tardigrades, like the protozoa, have many taxa with worldwide distributions (McInnes 1994; McInnes & Pugh 1998). With so little attention paid to this group, relative to that for the protozoa, it is difficult to draw distributional conclusions. There are hints of the "**everything is everywhere**" principle (in Wit & Bouvier 2006) for these small, lightweight creatures. (See Chapter 2-6 on Protozoa Ecology.) Their ability to become anhydrobiotic for long periods of time increases their chances for successful dispersal over great distances.

Among the moss dwellers, we find that ***Doryphoribius flavus*** has been found in Europe, Asia, Africa, and Central America (McInnes 1994). It is now known from Tennessee, USA (Bartels *et al*. 2007). Its original discovery was in moss subjected to desiccation (Iharos 1966). On the other hand, ***Doryphoribius polynettae*** had been found only in Russia in a small lake and in mosses [***Sphagnum*** sp. (Figure 7), ***Polytrichum juniperinum*** (Figure 8)] near the lake, but was likewise recently found in Tennessee (Bartels *et al*. 2007).

Figure 7. ***Sphagnum warnstorfii***. Photo by Michael Lüth, with permission.

Meyer (2008) found ***Minibiotus fallax***, previously known only from Australia (Pilato *et al*. 1989), in moss and lichen collections from Florida, USA. Other surprising disjunctions are likely to appear because the group is poorly known and sampling is spotty.

Jørgensen *et al*. (2007) explored the microspecies concept in ***Echiniscus testudo*** (Figure 9), using DNA sequences. Their study included 13 localities on three continents. They found high haplotype diversity and low sequence diversity, suggesting that this species had haplotype evolution with distinct asexual lineages and a high dispersal, as suggested by lack of isolation by distance. Although there were geographic differences, there was low genetic diversity. ***Echiniscus*** (Figure 10) is the largest genus, and the authors suggest that the high number of species may result from the combination of large potential for dispersal coupled with the lack of need of a partner for reproduction. Bryologists might benefit from understanding the distribution of these organisms as bryophytes and tardigrades seem to have similar dispersal advantages and disadvantages and both are capable of asexual reproduction.

Figure 8. ***Polytrichum juniperinum***. Photo by Michael Lüth, with permission.

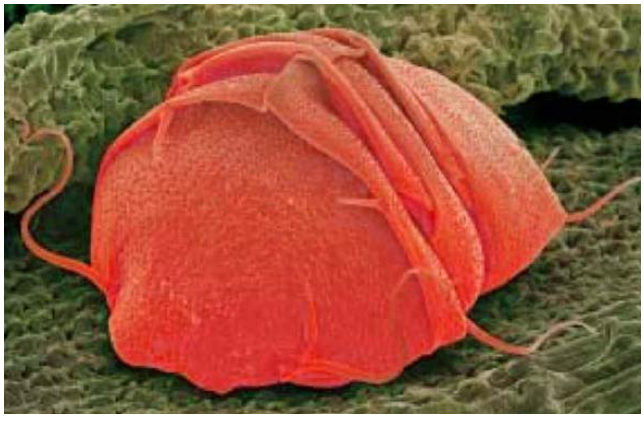


Figure 9. ***Echiniscus testudo*** tun. Photo by Power & Syred through Creative Commons.

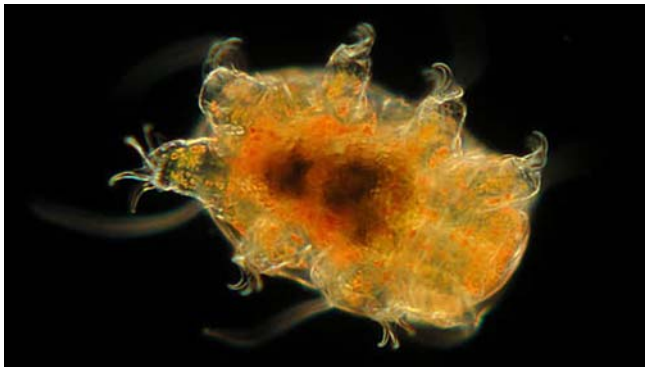


Figure 10. ***Echiniscus***, the largest tardigrade genus and a common bryophyte inhabitant. Photo by Martin Mach, with permission.

Although it does not appear that ***E. testudo*** (Figure 9) has a large number of microspecies, it is likely that some of the more common species may actually be species complexes, further complicating our understanding of species distributions and diversity. These include taxa such as ***Macrobiotus hufelandi*** (Figure 11), ***Minibiotus intermedius*** (Figure 12), ***Diphascon scoticum*** (Figure 13), and ***Milnesium tardigradum*** (Figure 14) (Bertolani & Rebecchi 1993; Claxton 1998, 1999; Pilato 1987).

Figure 11. ***Macrobiotus hufelandi***. Photo by Martin Mach, with permission.

Figure 12. SEM of ***Minibiotus intermedius***. Photo by William Miller through Flickr Commons.

Figure 13. ***Diphascon scoticum***. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

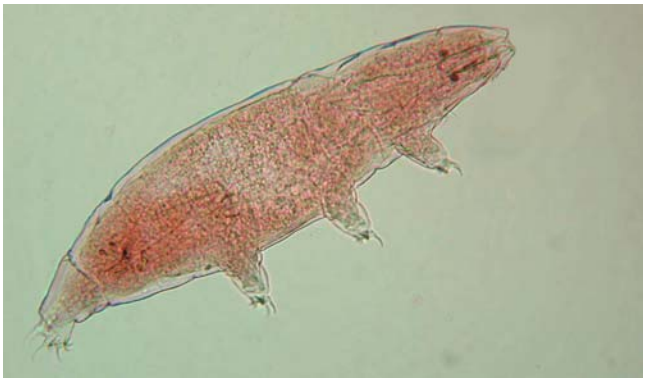


Figure 14. ***Milnesium tardigradum***. Photo by Björn Sohlenius at Swedish Museum of Natural History, with permission.

Blaxter *et al*. (2004) examined the Scottish tardigrade fauna for genetic differences. They found that some **Molecular Operational Taxonomic Units** (**MOTU**) were shared between the two rural collections in the study, but that none were found in both the one urban and two rural sites. This lack of commonality conflicts with the generally accepted concept of ubiquity of this faunal group. They described the high variability among the specimens as representing "**taxon flocks**." It suggests to me that once arriving at a new site, the tardigrades are likely to reproduce asexually and eventually diverge from their ancestors, creating **cryptic** species. **Genetic drift**, **Founder Principle**, and **microselection** factors could all contribute to enhancing this noted variability. I suspect we will find many similar examples among bryophytes.

Such possibilities of genetic variation without obvious morphological indicators demonstrate the folly of attempting to present a reasonable distribution pattern for the moss-dwelling tardigrades at this stage. Look for them. You will probably find a new species, or at least a new cryptic species, and certainly expand our understanding of their distributions and their ecology.

Distribution is the product of many factors, including dispersal, climate, niches available, microclimate, and attending factors such as altitude, rainfall, temperature range, and severity and length of winter or summer. Guil *et al*. (2009) sampled mosses and other vegetation to determine the effects of micro- and macro-environmental factors on the distribution of tardigrades in those habitats in the central Iberian mountain areas of Spain. They found that bioclimatic classification was the best predictor for

species richness. Altitude had a relationship, but its effects could not be separated from the macro-environmental gradients of soil, climate, vegetation type, and litter type. Within the micro-scale plots, the micro- and macro-environmental variables could explain ca 60% of the species richness, particularly litter type and vegetation type. On the other hand, abundance was not explained by the macro-environment, but rather was explained by soil composition and litter type. I have to wonder if soil composition affected the availability of bryophytes and their growth forms.

Common Species

Among the many collections of bryophytes, species of ***Echiniscus*** (Figure 15), ***Hypsibius*** (Figure 16), ***Macrobiotus*** (and segregate genera; Figure 17), ***Milnesium*** (Figure 14), and ***Ramazzottius*** (Figure 18) seem particularly common.

Table 1 lists some of the taxa known from the literature, but many more exist and would be an endless task to include here. A complete list of all tardigrade names with updated nomenclature (used here) is in Degma *et al*. 2010.

Figure 15. ***Echiniscus*** sp., member of one of the most common genera among bryophytes. Photo by Martin Mach, with permission.

Figure 16. ***Hypsibius dujardini***, member of one of the most common moss-dwelling genera of tardigrades. Photo by Bob Goldstein, with permission.

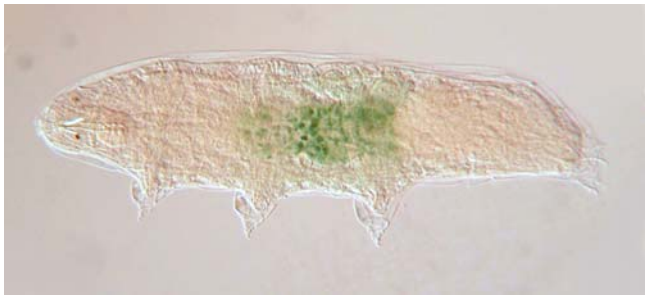


Figure 17. ***Macrobiotus blocki***, an Antarctic member of one of the most common moss-dwelling genera. Photo by Martin Mach, with permission.

In Sweden, Jönsson (2003) found that ***Macrobiotus hufelandi*** (Figure 11) is far more common among mosses than are other tardigrade species. This species seems to be abundant in most bryophyte studies. It seems remarkable that as late as 2003, the common bryophyte dwellers ***Murrayon dianae***, ***Isohypsibius sattleri***, ***Platicrista angustata*** (Figure 22), ***Diphascon belgicae***, and ***Diphascon pingue*** (Figure 19) were recorded from Sweden for the first time (Jönsson 2003).

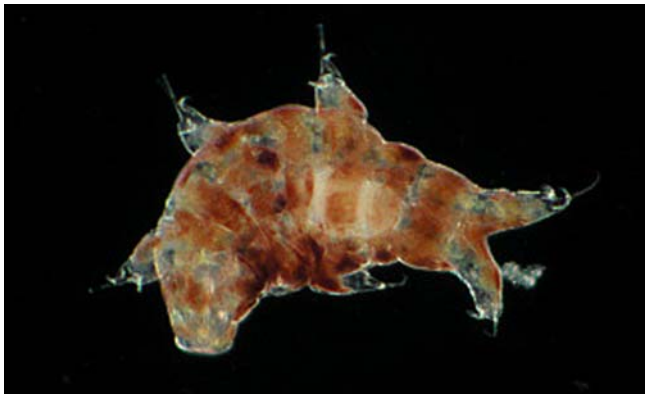


Figure 18. ***Ramazzottius*** sp., member of a common moss-dwelling genus. Photo by Martin Mach, with permission.

Figure 19. ***Diphascon pingue***. Photo by Michael Collins, with permission.

A major problem in trying to define tardigrade distributions and habitats is the lack of sufficient study of this entire group of organisms. Guil and Cabrero-Sañudo (2000) stated that the "tardigrade species description process fails to show an asymptotic tendency." Meyer and Hinton (2007) reported that "30% of the Nearctic species have been reported from a single site!" In other words, it will be a long time before we even know most of the species in existence or even make reasonable estimates of

how many species there are. And ecological descriptions necessarily lag behind the descriptions of the species.

Beasley *et al*. (2006) lamented the difficulty of assessing diversity of tardigrades in China because of the limited data available. In their report on 18 tardigrades of Sichuan, Yunnan, and Xizang Provinces, eight were new records for China. Among the 86 species known from China, 82 are terrestrial. Among these, ***Echiniscus nepalensis***, ***Pseudechiniscus jiroveci***, ***Murrayon hibernicus***, ***Hypsibius pallidus***, ***Isohypsibius sattleri***, ***Doryphoribius flavus***, ***Diphascon pingue*** (Figure 19), ***D. scoticum*** (Figure 13), ***D. prorsirostre*** (Figure 20), ***Mesocrista spitsbergensis*** (Figure 21), ***Platicrista angustata*** (Figure 22), ***Milnesium tardigradum*** (Figure 14) were from mosses. Only ***Cornechiniscus lobatus*** (see Figure 23) was found on liverworts.

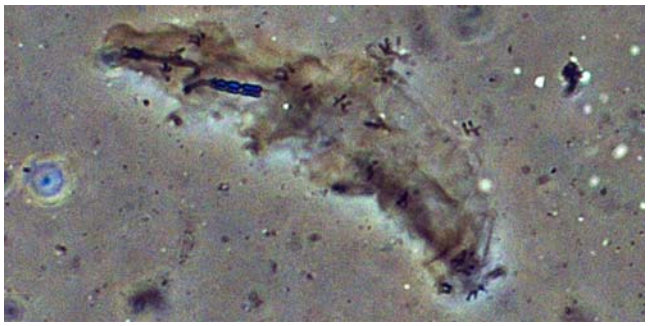


Figure 20. ***Diphascon prorsirostre***. Photo by Michael Collins, with permission.

Figure 21. ***Mesocrista spitsbergensis***. Photo by Björn Sohlenius, Swedish Museum of Natural History, with permission.

Figure 22. ***Platicrista angustata***. Photo by Michael Collins, with permission.

Figure 23. ***Cornechiniscus cornutus.*** Photo by Martin Mach, with permission.

Communities

Séméria (1982) found that a typical bryophyte-dwelling (and lichen-dwelling) tardigrade had one predator and several detritivorous or herbivorous species in its community. Typical communities of bryophyte-dwellers have 2-6 tardigrade species, and sometimes even more than ten (Ramazzotti & Maucci 1983).

Specific bryophyte communities have rarely been identified, but Miller *et al*. (1996) identified significant positive associations between the three most common of the tardigrade species and certain bryophyte species in the Antarctic. On the other hand, these same three species had a strong negative association with algae and lichens. In Britain, Wright (1991) suggested that ***Milnesium tardigradum*** (Figure 14) might have a selective predatory association with ***Hypsibius dujardini*** (Figure 16) and ***Ramazzottius oberhaeuseri*** (Figure 28).

Among the Florida epiphytes, Meyer (2008) typically found one predatory species [***Milnesium tardigradum*** (Figure 14, Figure 50), ***Paramacrobiotus richtersi*** (Figure 24)], ***Macrobiotus*** cf. ***harmsworthi*** (Figure 25), or one other ***Macrobiotus*** species, one ***Minibiotus*** species, and one echiniscid species. One or more of these niches is frequently unoccupied, but when occupied the species followed this trophic hierarchy. In only one sample were there two predatory species.

Figure 24. SEM of ***Paramacrobiotus richtersi***. Photo through Creative Commons.

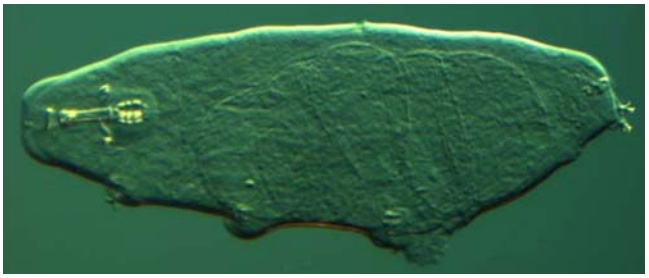


Figure 25. ***Macrobiotus harmsworthi***, a common tardigrade on bryophytes and elsewhere. Photo by Paul J. Bartels, with permission.

Collins and Bateman (2001) found that ***Isohypsibius prosostomus*** (Figure 26) did not occur with ***Diphascon scoticum*** or ***Minibiotus intermedius*** (Figure 12) and only rarely occurred with ***Diphascon pingue*** (Figure 19) or ***Hypsibius convergens*** (Figure 27), attributing these negative associations to trophic overlap.

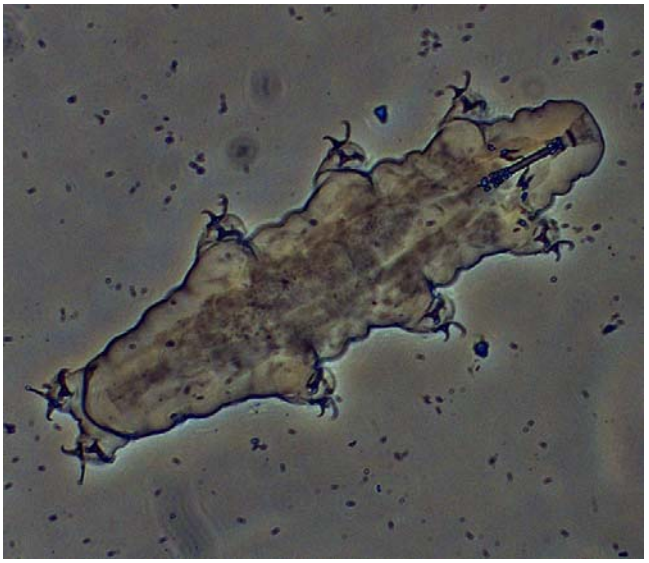


Figure 26. ***Isohypsibius prosostomus***. Photo by Michael Collins, with permission.

Figure 27. ***Hypsibius convergens***. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

Competitive exclusion, most likely for food, also drives community associations. Wright (1991) found that ***Macrobiotus hufelandi*** (Figure 11), ***Paramacrobiotus richtersi*** (Figure 24), and ***Isohypsibius prosostomus*** (Figure 26) avoid each other's company.

But food webs are not the only controlling factors. Bryophytes can play a major role through the climate they create. For example, ***Macrobiotus hufelandi*** (Figure 11) and ***Hypsibius dujardini*** (Figure 16) are absent when the habitat desiccates rapidly, making some bryophytes ideal for them (Wright 1991). ***Milnesium tardigradum*** (Figure 14, Figure 50) and ***Ramazzottius*** (formerly ***Hypsibius***) ***oberhaeuseri*** (Figure 28) likewise avoid areas with a high rate of desiccation, as well as locations with high insolation, but also avoid poorly drained sites, excluding them from bryophytes in low-lying, wet areas. These limitations can result in predictable associations. Among these is a significant association among ***Milnesium tardigradum*** (Figure 14, Figure 50) – a predator – and two ***Hypsibius*** species among the British fauna. Further temporary community differences can be driven by the behavior of some species to migrate vertically in the moss cushion to a position of greater moisture, while other species such as ***Echiniscus testudo*** (Figure 9) remain behind. And of course this inability to migrate may limit the mosses it occupies in the first place.

But despite the importance of moisture in the continuing life cycle of the tardigrades, there is not always agreement on the moisture level needed In Newfoundland, only ***Hypsibius dujardini*** (Figure 16) seems to follow a consistent relationship to a moisture category (Collins & Bateman 2001). It appears that rate of desiccation must be considered along with moisture level in determining the community structure.

Even on the same moss species or growth form, macrohabitat makes a difference. Jönsson (2003) found that tardigrade abundance of the same species differed between a forest and a clearcut area, with greater numbers of species in the forest. Nevertheless, abundances were similar.

Unique Partnerships?

Despite the tiny size of this moss community, its relationships can be complex. The tardigrades ***Ramazzottius oberhaeuseri*** (Figure 28) and ***Milnesium tardigradum*** (Figure 14) both can carry the protozoan ***Pyxidium tardigradum*** (Figure 29) on their surface, a relationship known as that of a **symphoriont** (Morgan 1976). Morgan found both of these tardigrades with their passengers living among mosses. Van der Land (1964), who first discovered these protozoa on lichens, revived the dried tardigrades there, only to discover these protozoa that also were dormant became active after being placed in water. The accompanying rotifers and oribatid mites had no protozoan passengers, but Van der Land (1964) could not determine if these companions were alive at the time he rehydrated them. As noted earlier, this protozoan can at times be so abundant (up to 35 on a single water bear) that they slow down the tardigrade and might more appropriately be considered a parasite (Vicente *et al*. 2008). Although such symphoriont/parasitic(?) relationships have rarely been observed among the moss dwellers, we simply have not spent much time looking for them.

Figure 28. ***Ramazzottius oberhaeuseri***. Photo by Martin Mach, with permission.

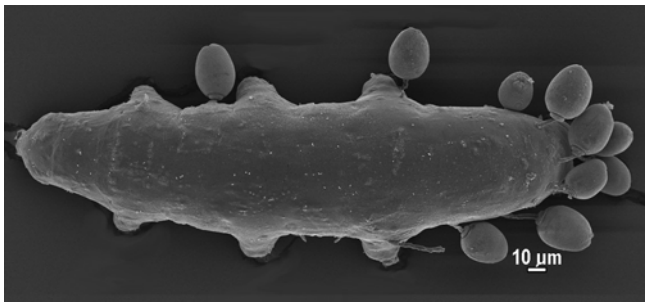


Figure 29. Tardigrade infected with the protozoan ***Pyxidium*** sp. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

Bryophyte Dangers – Fungal Parasites

This wonderful bryophyte home is not without its dangers to the moss-dwelling tardigrades. The phycomycetous fungus ***Catenaria anguillulae*** (Figure 30) is a widespread parasite on living, senescent, and dead microscopic animals (Barron 2009). The motile zoospores are attracted to exudations from openings on the bodies of nematodes and rotifers (Jansson & Thiman 1992), and it is likely that this opportunist also occurs on tardigrades (George Barron, pers. comm. 2010). The zoospores encyst on the cuticular covering near the opening or a wound. Hence, it is typical for them to colonize around the mouth or other opening. They subsequently germinate and penetrate through the orifice or wound to attack the animal on the inside.

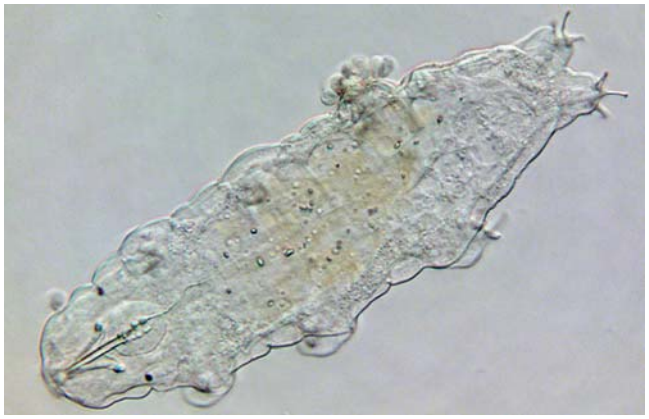


Figure 30. Tardigrade with fungus on its side. It is likely that this fungus is ***Catenaria anguillulae*** and that the attack location is a wound. Photo by Martin Mach, with permission.

Two fungi in the Ascomycota, ***Lecophagus*** [=*Cephaliophora*] ***muscicola*** (Figure 31-Figure 32) and ***Lecophagus*** [=*Cephaliophora*] ***longispora*** (Figure 33-Figure 34), capture rotifers and possibly tardigrades within the bryophytes and bryophyte-covered soil (Barron *et al*. 1990). This rather strange pair of fungi is endowed with elongate, hyaline, multiseptate, canoe-shaped conidia produced in small clusters at the apex of the conidiophores. When rotifers are present, the conidia germinate and produce one or several adhesive pegs that capture rotifers and tardigrades. Such fungal predators have been identified from moss-covered soil and forest debris in New Zealand and mosses in Canada, as well as from leaf mold in Japan, but their actual attack on tardigrades dwelling in mosses lacks documentation.

McInnes (2003) reports that the predatory fungus *Lecophagus antarcticus* attacks tardigrades that occur on cyanobacterial mats in lake sediments. Since ***Lecophagus muscicola*** (Figure 31-Figure 32) and ***L. longispora*** (Figure 33) are in the same genus and occur in wet or mossy soil (Barron *et al*. 1990; George Barron, pers. comm. 25 January 2010), it is reasonable to suggest that they might attack tardigrades in the same habitat, but can they? In fact, rotifers are attracted to the adhesive pegs of the fungus and then attach to the tip of the peg. That is their downfall, as the predator becomes the prey when the host (rotifer, nematode, or tardigrade) adheres to these adhesive pegs, possibly by lectin/carbohydrate bonding. But instead of providing a meal for the invertebrate, the fungus penetrates and parasitizes it, making it a host. Barron considers this "a stretch" to consider that the tardigrades would attack the fungi just as readily as would the rotifers. But tardigrades are known to consume other filaments such as those of algae, so it is at least a possibility.

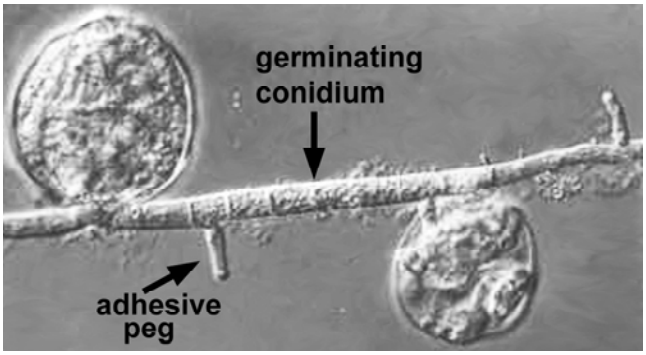


Figure 31. ***Lecophagus muscicola*** with two captured rotifers and two adhesive pegs. Photo by George Barron, with permission.

Figure 32. Conidia (X600) of ***Lecophagus muscicola***. Photo by George Barron, with permission.

Figure 33. ***Lecophagus longispora*** infecting rotifers. Note also the elongate branch with terminal conidiogenous cell bearing a cluster of developing conidia. (X450). Photo by George Barron, with permission.

Several species of fungi in the genus ***Ballocephala*** (Zygomycota) (Figure 35-Figure 37) are known to attack tardigrades (Pohlad & Bernard 1978; Barron 2007). ***Ballocephala pedicellata*** was first described from individuals attacking the tardigrades ***Hypsibius dujardini*** (Figure 16) and the ***Diphascon pingue*** (Figure 19) complex living among mosses (Pohlad & Bernard 1978).

Adhesive conidia of ***Ballocephala*** species (Figure 35) attach to the cuticle surrounding the mouth of the tardigrade (Figure 35). These adhesive spores then encyst on the outside of their host. The spores extend long, narrow penetration pegs that are used to "snake" their way into the host, bypassing the defense mechanisms of the animal (Barron 2007). As the hyphae grow they penetrate the host and fill it with hyphae (Figure 36) that secrete extracellular enzymes to digest the tardigrade and assimilate its tissue.

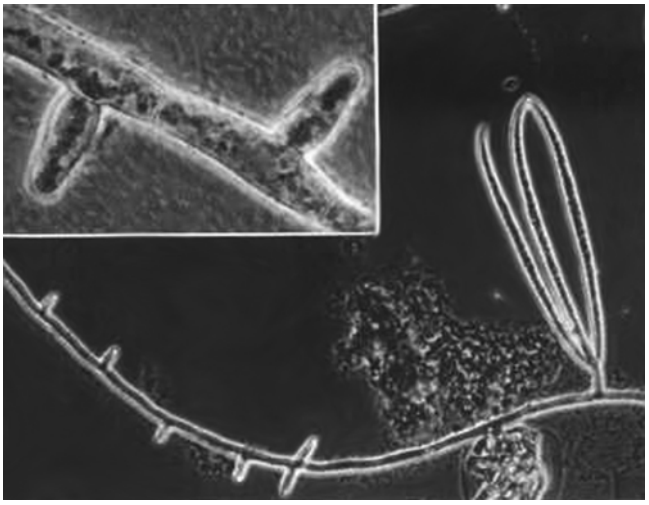


Figure 34. Hypha of ***Lecophagus longispora*** with a cluster of conidia and adhesive pegs, a fungus that traps rotifers and that may be a threat to some tardigrades living in mosses. Inset shows the adhesive pegs. Photos by George Barron, with permission.

Eventually the fungus breaks from the inside to the outside where it produces asexual spores (**conidiospores**) (Figure 38) that attack additional hosts. The fungus even has its own means to survive when the environment dries up and the tardigrade with it. Like many algae faced with declining conditions, this fungus undergoes sexual reproduction and produces zygotes that in turn form a thick wall and become **zygospores** (Figure 37). These resting spores permit the fungus to survive long periods of time (weeks to years) until favorable growing conditions return. Upon germination the zygospores presumably will divide to produce conidiophores and conidia that infect later generations of the tardigrade, but so far, this event has not been witnessed.

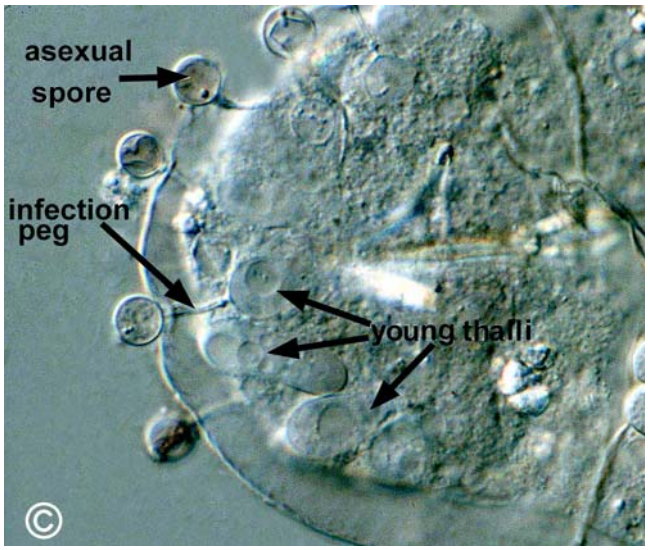


Figure 35. Spores of the fungus ***Ballocephala sphaerospora*** surrounding the mouth of a tardigrade. Photo by George Barron, with permission.

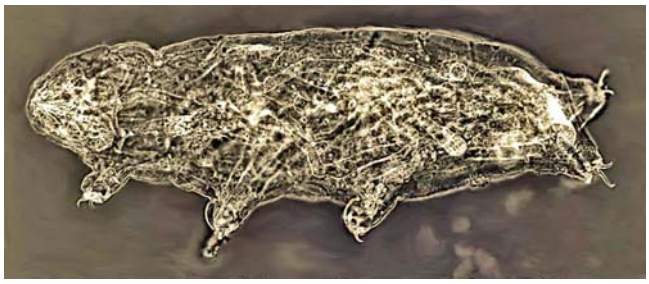


Figure 36. Tardigrade with hyphae of fungus ***Ballocephala*** sp. that have completely taken over its body. Photo by George Barron, with permission.

Figure 37. Zygospores of the parasitic fungus ***Ballocephala sphaerospora*** filling a tardigrade. The tiny balls inside the cells are oil droplets used as a reserve food supply. Photo by George Barron, with permission.

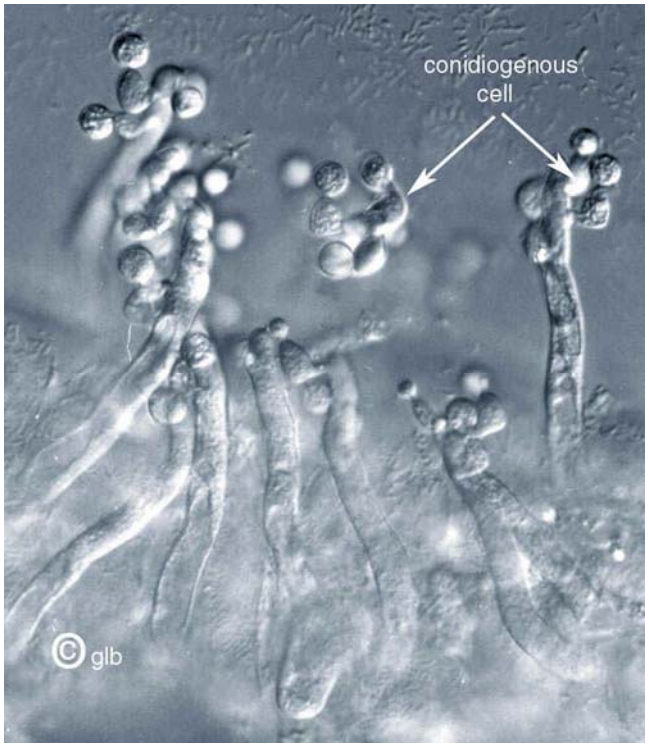


Figure 38. Conidiospores of the fungus ***Ballocephala sphaerospora*** on a tardigrade. Photo by George Barron, with permission.

The parasitic fungus ***Haptoglossa mirabilis*** (Figure 39) attacks tardigrades using the most complicated cellular mechanism known among the fungi (Robb & Barron 1982). It uses a gun-shaped attack cell that "shoots" into the host (Figure 40-Figure 41). At the anterior end of its cell is an elongated, barrel-shaped form. It is invaginated deeply into the cell, forming a bore. At the base of the bore is a walled chamber to house a missile-like attack apparatus. Robb and Barron hypothesize its mechanism:

This apparatus is able to fire the projectile at a high speed like a hypodermic needle, penetrating and injecting the host with the sporidium that infects the host. To accomplish this it has a basal vacuole with very high osmotic power. Water enters it rapidly and pumps the protoplasm and nucleus from the gun cell, through the hypodermic tube, and into the body of the host. If rotifers touch this fungus, they are hit within 0.1 second! But the proficiency of this apparatus doesn't end there. The head of this "harpoon" projectile is laminated, making it compressible. Thus, once it penetrates its host, it expands to seal the wound.

Once within the tardigrade, the fungus forms a cylindrical thallus (Figure 39) that consumes the poor tardigrade in a matter of days (Robb & Barron 1982). The hyphae eventually form zoospores. These exit through tubes and swim away to encyst. When the cysts germinate they form new clusters of gun cells. Some species can attack rotifers and nematodes as well.

George Barron (personal communication 1 March 2010) has commented to me that parasitic and predatory fungi are likely if both stylet-feeding and ingestion-feeding tardigrades coexist among mosses. But he finds it surprising that they have not yet been discovered.

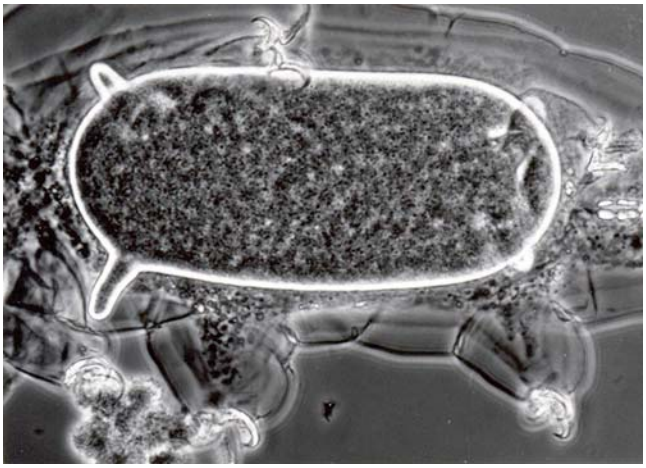
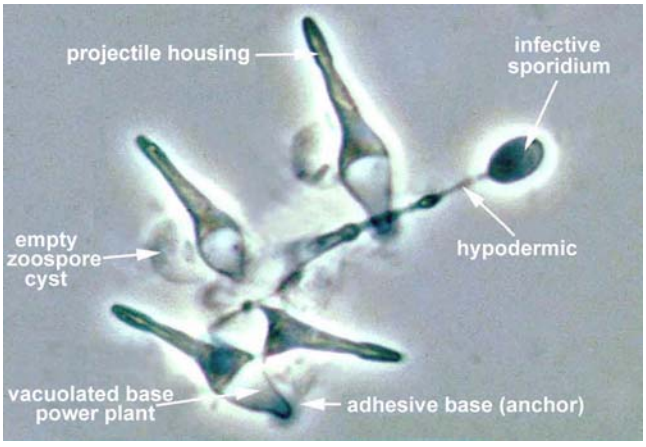


Figure 39. Fungus ***Haptoglossa mirabilis*** in a tardigrade, where it has formed a single thallus. Photo by George Barron, with permission.

The parasitic fungal genus ***Harposporium*** (Figure 42) has members that attack tardigrades (Saikawa *et al*. 1991), but the fungus must be ingested to function (George Barron, pers. comm. 25 January 2010). Barron (2008) suggests, as a hypothesis, that the spore is pumped down the oesophagus, where "it spirals and screws into the muscle fibres, thus lodging in the oesophagus."



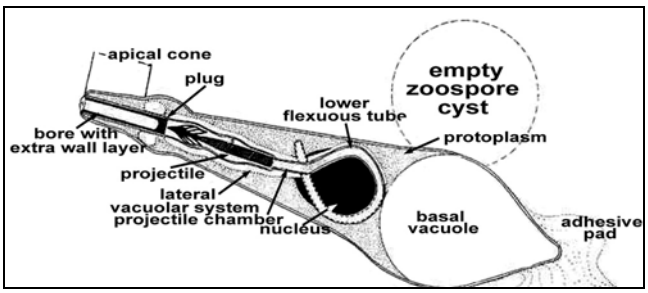


Figure 40. ***Haptoglossa mirabilis*** attack cells. Photo and diagram by George Barron, with permission.

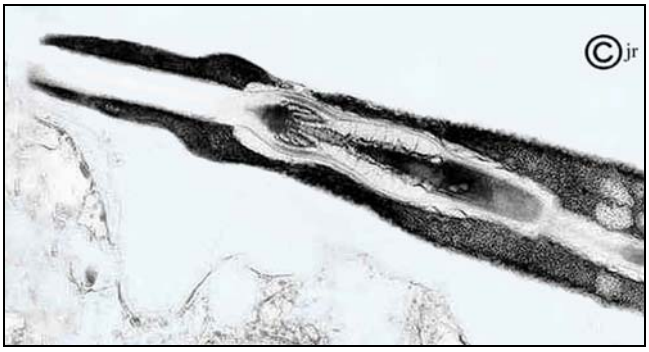


Figure 41. ***Haptoglossa mirabilis*** attack cell. Photo by Jane Robb and George Barron, with permission.

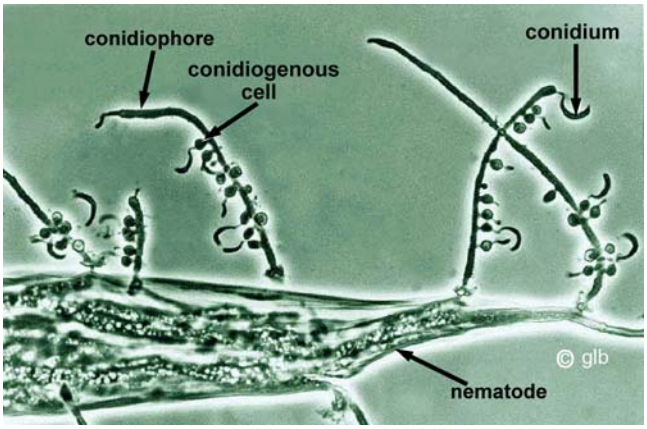


Figure 42. ***Harposporium anguillulae***, a parasite on nematodes and tardigrades. Photo by George Barron, with permission.

Role of Bryophytes in Fungal Interactions

Milnesium tardigradum (Figure 14) can be parasitized by a chytridiomycetous fungus, a zoosporic fungus that is common in soil (Dewel & Dewel 1987). Letcher and Powell (2002) attempted to determine the role that mosses play in the establishment of **Chytridiomycota** in four sites in the Blue Ridge and Allegheny Mountains of Virginia, USA. They first determined that frequency of **Chytridiomycota** was greatest in soil under and surrounding the rhizoids of two moss species [***Polytrichastrum*** (formerly in *Polytrichum*) ***ohioense*** (Figure 43), ***Dicranum polysetum*** (Figure 44)]. They also found that random point sampling suggested differences existed in zoosporic fungal frequency between the moss-covered soil and the exposed soil adjacent to these mosses, as well as between the two taxa. Similar differences were demonstrated using linear transect sampling. But, at last, the statistical analysis of the random point samples failed to demonstrate that the differences were significant for frequency of zoosporic fungi between the exposed soil and the moss-covered soil. However, they did find a significant difference between different moss/soil complexes for the frequency of the 15 common zoosporic fungal species they identified.

Figure 43. ***Polytrichastrum ohioense*** males with new growth. Photo by Janice Glime.

Figure 44. ***Dicranum polysetum***. Photo by Robert Klips, with permission.

One reason to suspect fungal differences under mosses compared to exposed soil is moisture. Using a scale of 0-10 (dry to saturated), Letcher and Powell found that the 48 moss-covered soil samples had a mean soil moisture content of 1.89, whereas the 24 exposed soil samples had a mean of 1.33.

Pollution

In addition to fungal dangers, the bryophytes also become dangerous to tardigrades when they become polluted (Steiner 1994b). Vargha *et al*. (2002) found that the concentrations of metals in tardigrades bore a relationship to the concentrations in the mosses. Elevated concentrations of heavy metals correlated with a decrease in tardigrade fauna. Meininger *et al*. (1985) found that poor air quality (SO_2) could reduce the number of tardigrades in otherwise suitable moisture regimes among epiphytic mosses in the area of Cincinnati, Ohio, USA (Figure 45).

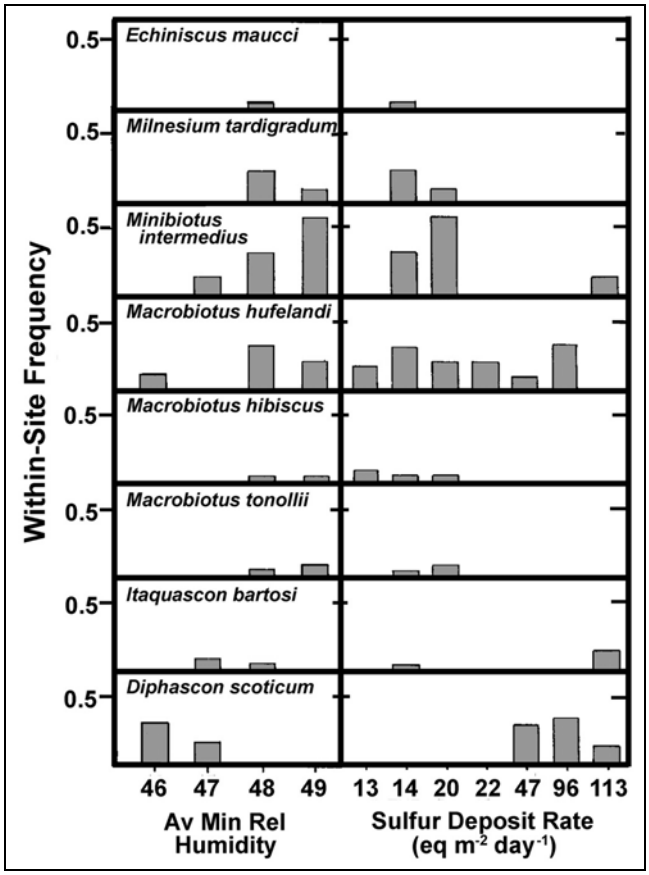


Figure 45. Effects of relative humidity and sulfur deposits from SO_2 on the frequency of **tardigrades** inhabiting lichens and mosses on red oak (*Quercus rubra*) in the Cincinnati area of Ohio, USA. n=20. Redrawn from Meininger *et al*. 1985.

Just as bryophytes and lichens have often been used as indicators of clean air or biomonitors of air pollution, so have their tardigrade inhabitants in both aquatic (Steiner 1994a) and terrestrial (Steiner 1995) conditions. And their responses are much the same. In a study in the Cincinnati, Ohio, USA area, Meininger *et al*. (1985) found that both epiphytic (tree-dwelling) bryophytes and their tardigrade fauna had the greatest species richness in areas with high humidity and clean air. Humidity is typically depressed in urban areas, and depression is likewise more rapid there, resulting from the more open environment (fewer trees) and reradiation of heat trapped by buildings and asphalt. Two moss-dwelling tardigrades provided good indicators. ***Diphascon scoticum*** (Figure 13) was dominant in urban park sites with low air quality and reduced humidity. They feed on protococcal algae on the tree bark, and the low *p*H tolerance of this species may have played a role in its prevalence there. ***Minibiotus intermedius*** (Figure 12), on the other hand, occurs more often in the more humid rural sites and is apparently unable to tolerate the rapid evaporation rates that may characterize more urban environments.

Hohl *et al*. (2001) investigated tardigrades upwind and downwind of a coal-burning power plant in Missouri, USA. They found that the tardigrade density was greater upwind, but *Echiniscus* sp. was found only downwind. The more sensitive ***Ramazzottius*** sp. occurred only upwind. ***Macrobiotus*** sp., ***Minibiotus*** sp., and ***Milnesium tardigradum*** occurred in both locations, but in different numbers. Although these species were mostly named only to genus, all were in genera or species known from bryophytes.

Acid Rain, SO_2, and NO_2

Acid rain poses a threat to at least some tardigrades. ***Hypsibius dujardini*** (Figure 16) has reduced activity at *p*H 4.0 (Bartels 2005). Even at *p*H 5, activity is reduced compared to controls at *p*H 7 (Thompson 2008). At *p*H 2.8 they are killed (Bartels 2005). Acevedo (2008) examined one of the most common bryophyte dwellers, ***Milnesium tardigradum*** (Figure 14), for its tolerance to *p*H, as measured by activity. Although ***M. tardigradum*** could survive from *p*H 1.54 to 12.5 for 1 minute, this species, like ***Hypsibius dujardini*** (Figure 16), had increased survival time as the *p*H approached 7. This species proved to be more sensitive at the higher *p*H levels.

Nevertheless, Steiner (1994a) found that neither tardigrades nor rotifers seemed to vary in abundance in response to SO_2 or NO_2. But in 1995, Steiner reported that the community composition did change in response to SO_2.

In the aquatic environment, using both experiments and air quality at 12 sites, Steiner (1995) showed that changes to the tardigrade and other aquatic fauna composition correlated negatively with the SO_2 concentrations. They used untreated control mosses and those subjected to concentrations of 0.025, 0.075, and 0.225 ppm SO_2 for 18 months and found that the highest level caused significant decreases in the numbers of several tardigrade species. SO_2 caused a significant decrease in *p*H in the moss cushions. The populations of ***Macrobiotus persimilis*** actually increased as pollution increased. Steiner (1994a) suggested that the tardigrade (and other invertebrate) fauna of epilithic moss cushions could be appropriate biomonitors for air quality.

Urban Environment

Even if the urban habitat is not always polluted in the usual sense, it is a drastic contrast in environment to that of more natural rural areas. Cities themselves both create and hold heat. That makes them susceptible to rapid drying, a condition lethal to many tardigrades.

Johansson *et al*. (2011) compared tardigrades from 73 urban and 24 rural locations in Fresno County, California. Only 22% of the urban samples had tardigrades, whereas 74% of the rural samples had tardigrade inhabitants. The urban samples likewise had fewer species, but the densities of these species differed little from that of the rural sites. Of the 26 species found, 7 were found only in the urban samples, 16 only in rural samples, and 3 in both. The rural communities differed more among themselves than did the urban samples. Interestingly, tardigrades seemed to prefer lower *p*H levels in both community types. Hence, the researchers excluded acid rain as the cause of differences. It is likely that the microclimate of the city is less favorable due to greater exposure and heat, leading to more rapid drying.

Moly de Peluffo *et al*. (2006) conducted a more controlled study of urban conditions by using samples from the same tree species from the city of General Pico in Central Argentina. They included paved areas with different traffic intensities, non-paved areas, an industrial area, and a bus station. They examined 11 mm diameter

samples of lichens and mosses from the trees. Only 5 tardigrade species were collected in total [***Echiniscus rufoviridis***, ***Milnesium cf. tardigradum*** (Figure 14), ***Ramazzottius oberhaeuseri*** (Figure 28), ***Paramacrobiotus areolatus*** (Figure 46), ***Macrobiotus*** sp.]. ***Milnesium cf. tardigradum*** and ***Ramazzottius oberhaeuseri*** were the most abundant. Mean density of tardigrades was 10, but the maximum reached 50 per cm^2. ***Milnesium cf. tardigradum*** dominated along paved streets where there was intense traffic, suggesting that it was the most tolerant species. In periurban areas, ***Ramazzottius oberhaeuseri*** dominated despite the high suspension dust and high sun exposure. In the Neotropical region of Santa Rosa, Argentina, Peluffo *et al*. (2006) found the same five species. Again, only ***Milnesium cf. tardigradum*** occurred in areas with high levels of vehicle traffic.

Figure 46. ***Paramacrobiotus areolatus*** head region. Photo by Martin Mach, with permission.

Dust can be a factor in tardigrade distribution. Meininger and Spatt (1988) found that both tardigrades and their bryophyte environment are affected by road dust such as that created by the trans-Alaska Pipeline haul road (Dalton Highway). In this case, the dust is calcium-rich. ***Sphagnum*** (Figure 7) is absent within 10 m of the road. Instead, calcium-tolerant moss species such as ***Aulacomnium turgidum*** (Figure 47) and ***Dicranum angustum*** (Figure 48) occupy these alkaline areas. The tardigrades that survive here are xeric species such as ***Diphascon scoticum*** (Figure 13) and ***Hypsibius dujardini*** (Figure 16). Farther from the road, these fungal and algal feeding species are replaced by omnivores and carnivores [***Macrobiotus hufelandi*** (Figure 11) and ***M. harmsworthi*** (Figure 25), respectively].

Tardigrades in Space

Imagine living through conditions of 151ºC, -273ºC, the vacuum of space, radiation 500 times that humans can tolerate, 2000X normal atmospheric pressure, and ten years with no water! (Ramløv & Westh 2001; Jönsson *et al*. 2008; ZAMP Wiki 2009). Tardigrades are sometimes considered to be **extremophiles**, and their ability to survive these conditions would seemingly put them among the champions. But extremophiles are organisms that *live* at extremes; tardigrades must become dormant to survive these, and the longer they are in this condition, the lower their chances of survival (Mullen 2002). These abilities to become dormant - enter **cryptobiosis** - have made them popular animals for space travel, surviving and carrying back the evidence of the effects of space on subcellular components. And they were the first space travellers without space suits to survive.

Figure 47. ***Aulacomnium turgidum***, a calcium-tolerant species, in Norway. Photo by Michael Lüth, with permission.

Figure 48. ***Dicranum angustum***, a calcium-tolerant species. Photo by Jan-Peter Frahm, with permission.

The ability to shut down makes tardigrades ideally suited for space travel (Jönsson *et al*. 2008; Rebecchi *et al*. 2009a). They can survive a vacuum (Gavaret 1859) and its resulting extreme dehydration (Jönsson *et al*. 2008). They also survive both solar and cosmic radiation. They survive extreme ionizing radiation (570,000 roentgens kills only 50%; humans can be killed by 500) (May *et al*. 1964) and can return from space travel under these extremes and become active again with no reduction in survival (Jönsson *et al*. 2008; Rebecchi *et al*. 2009a). They have even survived temperature extremes from -200ºC to 151ºC (Doyère 1842; Rahm 1923, 1937; Becquerel 1950; Keilin 1959; Seki & Toyoshima 1998; Lindahl & Balser 1999).

Richtersius coronifer (Figure 49), ***Milnesium tardigradum*** (Figure 50) (Jönsson 2008), and ***Paramacrobiotus richtersi*** (Figure 24) (Rebecchi *et al*. 2009a, b) began their space adventure on 17 September 2007. They arrived back from their adventure in space on 26 September, and not only were they alive, but they could

also reproduce! ***Milnesium tardigradum*** did better than ***R. coronifer***. About 12% of those exposed to UV-A and UV-B managed to recover, although they exhibited reduced egg production compared to the control animals that stayed on Earth. Those exposed to the full range of UV radiation only partially recovered, then died. Jönsson *et al*. (2005) suggested that during anhydrobiosis there are no biochemical protectants to protect against radiation. Rather, it appears that survival of tardigrades may be due to efficient DNA repair.

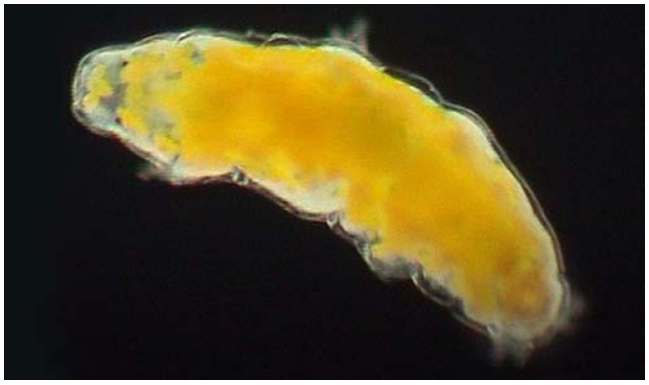


Figure 49. ***Richtersius coronifer*** and its close relatives have a beautiful deep yellow color. This species has been a successful space traveller. Photo by Martin Mach, with permission.

Paramacrobiotus richtersi (Figure 24) and ***Ramazzottius oberhaeuseri*** (Figure 28) were able to withstand high doses of ultraviolet radiation in both active and anhydrobiotic states (Altiero *et al*. 2011). Nevertheless, the survival rate of hydrated or desiccated specimens was inversely related to the UV doses, with ***P. richtersi*** tolerating the increase of UV dose better than ***R. oberhaeuseri***.

The survival of ***Richtersius coronifer*** (Figure 49) in the adventure beginning 17 September 2007 (Jönsson 2008) was at least somewhat predictable. In the lab, this species survived instant freezing to -195.8ºC and vacuum conditions with 96-100% survival (Persson *et al*. 2009). In low Earth orbit it experienced little effect from cosmic radiation or microgravity (68, 89, 82% survival). On the other hand, when Persson *et al*. (2009) subjected ***R. coronifer***, ***Ramazzottius oberhaeuseri*** (Figure 28), and ***Echiniscus testudo*** (Figure 9) to desiccation on moss, the survival rate was very low (0-22.5%). They emphasized that the protocol for desiccation is important and may not have been appropriate for survival.

Another moss-dweller (among other substrata), ***Hypsibius dujardini*** (Figure 16), was scheduled to be travelling in space on a Russian spacecraft as I write (Milstein 2009). Following its liftoff in October 2009, it was scheduled to reside there for three years! Its habitat is a bit of polymer microcosm with conditions mimicking those of a bit of meteor rock. But, alas, technical and safety issues have caused a two-year delay before lift off (Madrigal 2009). The objective is to determine if life can survive interplanetary space travel, a test of the **Transpermian Theory**. The Transpermian Theory suggests that life might have travelled on a bit of meteoric rock from Mars or other planet and landed on Earth billions of years ago. The tough part, both for the real meteoric rock traveller and the spacecraft test subjects may be the landing event on Earth.

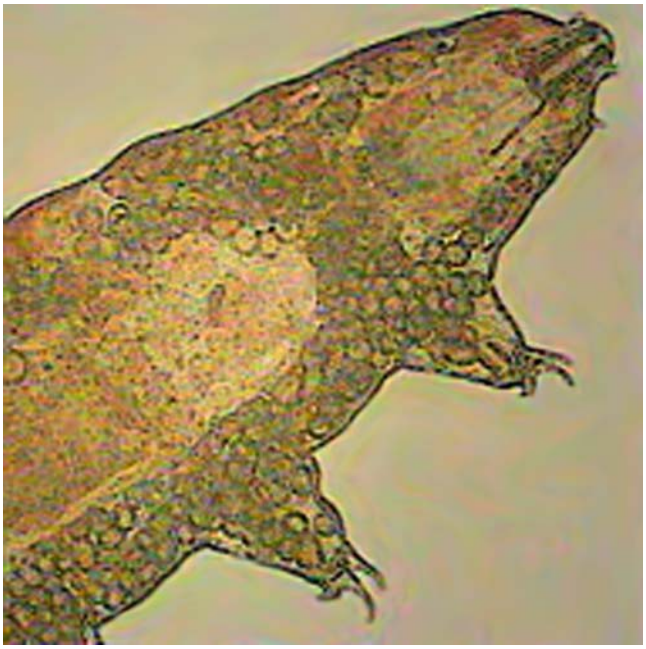


Figure 50. ***Milnesium tardigradum***, a space traveller. Photo by Martin Mach, with permission.

Most tardigrades have gone on their space adventure in an anhydrobiotic state. Rebecchi *et al*. (2011) used ***Paramacrobiotus richtersi*** (Figure 24) to determine the effects of the anhydrobiotic state on survivorship in space. They flew these animals for twelve days in a low-earth orbit (250-290 km altitude). The desiccated animals had high survival rate (79-95%), similar to that of non-desiccated ground controls. There was no visible damage to their double-stranded DNA, but their heat shock proteins (HSP expression at 70 and 90 kDa) increased compared to ground controls.

Persson *et al*. (2011) assessed the effects of cosmic radiation on tardigrades, as well as rotifers. The tardigrades spent time in a low Earth orbit where they were exposed to cosmic radiation and microgravity. ***Richtersius coronifer*** (Figure 49) was dried for two years on Whatman-3 filters during its space travel. However, none of the members of this species could be revived. In a different microcosmos experiment, Persson *et al*. desiccated ***R. coronifer***, ***Ramazzottius oberhaeuseri*** (Figure 28), and ***Echiniscus testudo*** (Figure 9) as well as rotifers and nematodes on a moss substrate. Species in this experiment had some, but very low, survival. Embryos of ***Milnesium tardigradum*** (Figure 14), on the other hand, all survived cosmic radiation from space flight. ***Richtersius coronifer*** also survived extreme cold and vacuum while in anhydrobiosis.

Evolutionary Similarities to Bryophytes

What could tardigrades and bryophytes possibly have in common? Their habitat requirements, for one thing. Hence, both do well with asexual reproduction (Pilato 1979). And both do well under circumstances requiring dormancy. Pilato points out that there is marked

uniformity in both size and morphology in the four invertebrate groups of rotifers, gastrotrichs, nematodes, and tardigrades. That character does not seem to fit so well with bryophytes, but if one compares them to tracheophytes, perhaps it does. Both groups have "a less common pattern of geographic distribution than usually believed" for organisms having only passive transport. They furthermore have maintained their antiquity and have given rise to entire orders. But there are also some strong differences. Compared to tardigrades, bryophytes do not have a constant cell number, have no marine members, and are capable of regeneration. Pilato suggests that parthenogenesis would have significantly delayed evolution, a concept that has come into question for bryophytes. He furthermore suggests that by entering cryptobiosis, these invertebrate organisms escape the variability of the environment and thus escape many of the selection pressures that drive evolution.

Sampling and Extraction

Sampling from mosses is not a very standardized procedure. The moss must first be collected from its substrate. What works for a flat mat does not work for a thick mat, weft, or tall turf. Sayre and Brunson (1971) suggested using a metal test-tube cap 2.5 cm in diameter to cut a core from the moss (see also Guil *et al*. 2009) – a technique that should work well for thin mats with stems that are not tough, but many growth forms would not sample well by this method. Since tardigrades are slow-moving, one need not worry about their escaping during the cutting procedure. However, I prefer the hand removal, followed by a dry weight of bryophyte for quantification. Fortunately, both bryophytes and tardigrades can survive such drying. A large clump could later be cut down the middle and still permit sampling of all the sub-habitats.

Fortunately, mosses need little care once collected and can easily be kept in small paper bags – the kind that was once used in the candy store (~10 x 20 cm when folded). If it is not too hot or severely dry, these will permit the mosses to dry slowly, provided they are not in the path of a fan or other drying agent. Using plastic bags can foster growth of fungi if the bag is kept for more than a day or two, and it will not permit the drying needed for both kinds of organisms. Morgan and King (1976 in Clifford 2005) suggested using an open plastic bag that would permit air drying.

Obtaining tardigrades from mosses may be a bit tedious. One method is to immerse the bryophytes in water (Claxton 1998; Guidetti *et al*. 2008) in something like a finger bowl or Petri dish. Tap water may be okay, depending on chlorine levels; if pond water is used, it should be boiled and filtered to avoid contamination. Distilled water should NOT be used because it will cause the tardigrade to take on water by osmosis and it is likely to become too extended to move. Placing the bryophyte upside down with the soil portion above the water will give the best results; muddy water makes it difficult to spot the bears (Sayre & Brunson 1971). If you are interested in vertical positioning, place aluminum foil or other cover over the container to keep it dark.

Sayre and Brunson (1971) recommend keeping the moss submersed for 24 hours at room temperature. The moss should then be removed and the absorbed water squeezed into the dish. The water in the dish should then be stirred and poured into a counting dish. After the tardigrades have settled they can be counted with a dissecting microscope. They recommend 60X, but most dissecting microscopes don't go that high, so one might need a pair of 20X oculars. If there is too much water, they suggest decanting off the excess, but for quantitative purposes, I suspect that will lead to inaccuracies for these light-weight animals.

Nelson (1991) considered this to be a common method. She recommended letting the collected bryophytes dry in paper bags for at least several days, then placing them in water for several hours to awaken the tardigrades. The wet bryophytes are then squeezed to remove water with water bears into a Petri dish or other container. As in the Sayre and Brunson method, excess water can be decanted off and the sediment examined.

Guidetti *et al*. (2008) recommend that after immersing the bryophytes, the water should be sifted repeatedly to collect the tardigrades. From there, the animals can be extracted while observing them with a dissecting microscope.

Schuster *et al*. (1977) used a similar method. Collection material (bryophytes, soil, detritus) was swirled in water and once the dense particles settled, the water was decanted and poured through a US Standard #325 filter, pore size ~44 µm. These were then washed from the filter into a preservation jar or onto a glass slide. Specimens can be preserved by adding 5% formalin or glutaraldehyde, or alcohol, as discussed later.

Other researchers choose to use the Baermann funnel to extract the animals (Hohberg 2006) as already described for invertebrates (Chapter 4-1 of this volume).

A slight modification of these methods is to clean a bryophyte clump of its loose soil and place it into a Petri plate upside down (Deep Data 2009). Fill the plate with water. When the bryophyte absorbs all the water, add more. Maintain a few mm of water in the plate after the bryophyte is fully hydrated. The bryophyte should be kept hydrated for several hours or overnight before examination. Remove the bryophyte from the water and examine it with a dissecting microscope at 20X or higher. Alternatively, this website also recommends squeezing out the water and examining the liquid. Look for yellow, red, or whitish animals that move "like puppies."

Nelson and Bartels (2007) used a different method when working with samples from soil, lichens, mosses, and leaf litter from the Smoky Mountains. They extracted the tardigrades using centrifugation with Ludox AM™ and mounted them on microscope slides in Hoyer's medium.

Tardigrades can be put to sleep with $MgCl_2$ or shocked with freshwater, then decanted into a fine mesh (20-40 µm) net (Nelson 2002). An intriguing method is to use an aquarium air stone to bubble the tardigrades that can then be collected with a piece of paper towel laid on the surface of the water. (If that works, I doubt that decanting is good for quantitative studies.) The towel should then be rinsed through a 30-40 µm net. For aquatic samples, water can be used from the habitat.

Clifford (2005) draws heavily on the experience of Morgan and King (1976) in his Tardigrada website. He suggests narcotizing the water bears with 20% alcohol in a volume equal to that of the bryophyte plus water. The

bears will no longer be able to cling to the bryophytes and can be more easily dislodged into the alcohol/water solution. The bryophyte and associated organisms can be removed after about 10 minutes and wrung into a Petri dish to remove the adhering water and bears. This immersion and wringing should be repeated several times, with immersion up to 15 minutes. The extracted water can be examined at about 50X magnification. (As you can see, recommendations for magnification vary from 20X to 60X. You will have to see what works for you.)

Clifford (2005) suggests that a somewhat simpler method is to flood the bryophyte with enough water to cover it for 48-72 hours. Then remove the moss to a new dish and start with the alcohol at 70%. Force the alcohol through the bryophyte clump with a pipette that has a strong bulb. A baster might work for larger mosses, but I haven't tried it. This alcohol method seems a bit cruel to the bears.

Nelson and Hauser (2012) complain that extraction from the limnoterrestrial habitats, those habitats of water adhering in spaces such as the ones among bryophytes, is often done with the Berlese funnel. They contend that this method has a strong bias toward arthropod diversity and does not work well for relatively slow-moving or immobile animals such as tardigrades. Rather, they found much more diversity among the microscopic invertebrates such as tardigrades when they used water flooding for extraction. In fact, they found almost no taxa overlaps when comparing these two methods!

Tardigrades can be preserved in 70% alcohol, but they can be difficult to locate again, and one must check periodically to be sure the alcohol isn't about ready to dry up. A few drops of glycerine in the vial of alcohol helps when the alcohol does dry out. The preferable method seems to be to mount them in one of the standard mounting media used for bryophytes and other things. Pennak (1953) gives instructions for various media. Unfortunately (or fortunately) a number of these media have been declared carcinogenic or toxic and are no longer available.

Checklist of Bryophyte Dwellers

I won't even pretend that I can provide a complete list of these taxa. I have not covered all the literature, and certainly many have yet to be discovered, but at least Table 1 is a start.

Table 1. Partial list of tardigrades known to inhabit bryophytes, based on literature.

Heterotardigrada (armored tardigrades)

Bryodelphax aaseae	Kristensen *et al*. 2010
Bryodelphax asiaticus	Kaczmarek & Michalczyk 2006
Bryodelphax brevidentatus	Kaczmarek *et al*. 2005
Bryodelphax mateusi	Guil 2002
Bryodelphax parvulus	Guil 2002
Bryodelphax sinensis	Pilato 1974
Bryodelphax tatrensis	Guil 2002
Cornechiniscus cornutus	Mach, The Water Bear
Cornechiniscus lobatus	Guil 2002
Cornechiniscus holmeni	Beasley & Miller 2007
Cornechiniscus subcornutus	Guil 2002
Echiniscus arctomys	Mehlen 1969
Echiniscus barbarae	Kaczmarek & Michalczyk 2002
Echiniscus bigranulatus	Horning *et al.* 1978
Echiniscus bisculptus	Guil 2002
Echiniscus blumi	Kaczmarek & Michalczyk 2006
Echiniscus brachyspinosus	Horning *et al*. 1978
Echiniscus canadensis	Kaczmarek & Michalczyk 2006
Echiniscus capillatus	Jennings 1979
Echiniscus cavagnaroi	Christenberry 1979
Echiniscus ganczareki	Michalczyk & Kaczmarek 2007
Echiniscus granulatus	Kaczmarek & Michalczyk 2006
Echiniscus horningi	Kathman & Cross 1991
Echiniscus jenningsi	Margulis & Chapman 1998
Echiniscus kofordi	Christenberry 1979
Echiniscus laterosetosus	Ito 1993
Echiniscus lichenorum	Guil 2002
Echiniscus madonnae	Michalczyk & Kaczmarek 2006a
Echiniscus marinellae	Guil 2002
Echiniscus mauccii	Kathman & Cross 1991
Echiniscus mediantus	Guil 2002
Echiniscus merokensis	Kaczmarek & Michalczyk 2006
Echiniscus multispinosus	Guil 2002
Echiniscus nelsonae	Li *et al*. 2007
Echiniscus cf. *oihonnae*	Hooie & Davison 2001
Echiniscus palmai	Dastych 1997
Echiniscus perarmatus	Binda *et al*. 2001
Echiniscus perviridis	Nelson & Adkins 2001
Echiniscus polygonalis	Ito 1993
Echiniscus quadrispinosus	Kathman & Cross 1991
Echiniscus reticulatus	Kaczmarek & Michalczyk 2006
Echiniscus scabrospinosus	Guil 2002
Echiniscus semifoveolatus	Ito 1993
Echiniscus shaanxiensis	Li *et al*. 2007
Echiniscus sinuloides =???	Guil 2002
Echiniscus spiniger	Horning *et al.* 1978
Echiniscus spinulosus	Guil 2002
Echiniscus taibaiensis	Wang & Li 2005
Echiniscus testudo	Beasley & Miller 2007
Echiniscus trisetosus	Kaczmarek & Michalczyk 2006
Echiniscus velaminis	Horning *et al.* 1978
Echiniscus vinculus	Horning *et al.* 1978
Echiniscus virginicus	Hooie & Davison 2001
Echiniscus viridianus	Pilato *et al*. 2007
Echiniscus viridissimus	Nelson & Adkins 2001
Echiniscus wendti	Kathman & Cross 1991
Echiniscus zetotrymus	Horning *et al.* 1978
Hypechiniscus exarmatus	Horning *et al.* 1978
Hypechiniscus gladiator	Kathman & Cross 1991
Oreella minor	Horning *et al.* 1978
Oreella mollis	Horning *et al.* 1978
Parechiniscus chitonides	Guil 2002
Parechiniscus unispinosus	Guil 2002
Pseudechiniscus beasleyi	Li *et al*. 2007
Pseudechiniscus brevimontanus	Nelson & Bartels 2007
Pseudechiniscus clavatus	Guil 2002
Pseudechiniscus facettalis	Ito 1993
Pseudechiniscus goedeni	Kathman & Cross 1991
Pseudechiniscus gullii	Pilato & Lisi 2006
Pseudechiniscus insolitus	Guil 2002
Pseudechiniscus jiroveci	Kaczmarek & Michalczyk 2006
Pseudechiniscus juanitae	Pilato & Lisi 2006
Pseudechiniscus lateromamillatus	Horning *et al.* 1978
Pseudechiniscus novaezeelandiae	Horning *et al.* 1978
Pseudechiniscus papillosus	Li *et al*..2005
Pseudechiniscus pseudoconifer	Franceschi *et al*. 1962-63
Pseudechiniscus spinerectus	Pilato *et al*. 2001
Testechiniscus laterculus	Kathman & Cross 1991
Testechiniscus meridionalis	Jennings 1979
Testechiniscus spitsbergensis	Kaczmarek & Michalczyk 2006

Eutardigrada (unarmored/naked tardigrades)

Acutuncus antarcticus	Miller *et al*. 1996
Amphibolus weglarskae	Bartels & Nelson 2007
Astatumen trinacriae	Nelson & Bartels 2007
Bertolanius nebulosus	Westh & Kristensen 1992
Bertolanius volubilis	Guidetti *et al*. 2008
Bertolanius weglarskae	Kathman & Cross 1991
Bindius triquetrus	Pilato 2009

Biserovus bindae Christenberry & Higgins 1979
Calohypsibius maliki Michalczyk & Kaczmarek 2005
Calohypsibius ornatus Kaczmarek & Michalczyk 2006
Calohypsibius placophorus Guil 2002
Calohypsibius schusteri Nelson & Bartels 2007
Calohypsibius verrucosus Guil 2002
Dactylobiotus ambiguus Guil 2002
Dactylobiotus dispar Suren 1992
Dactylobiotus macronyx Guil 2002
Diphascon alpinum Horning *et al*. 1978
Diphascon belgicae Kathman & Cross 1991
Diphascon bullatum Horning *et al*. 1978
Diphascon carolae Bartels & Nelson 2009
Diphascon chilenense Horning *et al*. 1978
Diphascon dolomiticum Pilato & Bertolani 2005.
Diphascon granifer Bartels & Nelson 2009
Diphascon higginsi Nelson & Bartels 2007
Diphascon iltisi Kathman & Cross 1991
Diphascon modestum Kathman & Cross 1991
Diphascon nobilei Schuster & Greven 2007
Diphascon nodulosum Kathman & Cross 1991
Diphascon oculatum Schuster & Greven 2007
Diphascon patanei Nelson & Bartels 2007
Diphascon pingue Kaczmarek & Michalczyk 2006
Diphascon prorsirostre Kaczmarek & Michalczyk 2006
Diphascon ramazzottii Bartels & Nelson 2007
Diphascon recamieri Kathman & Cross 1991
Diphascon rugosum Schuster & Greven 2007
Diphascon scoticum Kaczmarek & Michalczyk 2006
Diphascon sexbullatum Kaczmarek & Michalczyk 2006
Doryphoribius flavus McInnes 1994
Doryphoribius gibber Pilato & Lisi 2006
Doryphoribius huangguoshuensis Wang *et al.* 2007
Doryphoribius mexicanus Beasley *et al*. 2008
Doryphoribius picoensis Fontoura *et al.* 2008
Doryphoribius polynettae Bartels *et al*. 2007
Doryphoribius quadrituberculatus Kaczmarek & Michalczyk 2004a
Doryphoribius zappalai Wang *et al*. 2007
Doryphoribius zyxiglobus Horning *et al.* 1978
Hebesuncus conjungens Kaczmarek & Michalczyk 2006
Hypsibius arcticus Utsugi & Ohyama 1989
Hypsibius camelopardalis Guil 2002
Hypsibius convergens Kaczmarek & Michalczyk 2006
Hypsibius dujardini Kaczmarek & Michalczyk 2006
Hypsibius maculatus Kaczmarek & Michalczyk 2004b
Hypsibius microps Guil 2002
Hypsibius pallidus Kaczmarek & Michalczyk 2006
Hypsibius roanensis Nelson & Bartels 2007
Hypsibius scabropygus Schuster & Greven 2007
Insuetifurca arrowsmithi Kathman & Cross 1991
Insuetifurca xiae Li 2009
Isohypsibius arbiter Binda *et al*. 2001
Isohypsibius archangajensis Kaczmarek & Michalczyk 2006
Isohypsibius asper Jennings 1979
Isohypsibius baslovi Bartels & Nelson 2009
Isohypsibius bertolanii Manicardi 1989
Isohypsibius brevispinosus Bartels & Nelson 2009
Isohypsibius brulloi Pilato & Pennisi 1976
Isohypsibius cameruni Horning *et al*. 1978
Isohypsibius josephi Guil 2002
Isohypsibius lunulatus Kathman & Cross 1991
Isohypsibius mammillosus Guil 2002
Isohypsibius mihelcici Kaczmarek & Michalczyk 2006
Isohypsibius monstruosus Guil 2002
Isohypsibius montanus Guil 2002
Isohypsibius pappi Pilato & Sperlinga 1975
Isohypsibius prosostomus Schuster & Greven 2007
Isohypsibius qinlingensis Li *et al*. 2005
Isohypsibius sattleri Kaczmarek & Michalczyk 2006
Isohypsibius taibaiensis Li & Wang 2005
Isohypsibius tuberculatus Nelson & Bartels 2007
Isohypsibius wilsoni Horning *et al*. 1978
Isohypsibius woodsae Kathman & Cross 1991
Itaquascon bartosi Meininger *et al*. 1985
Itaquascon mongolicus Kaczmarek & Michalczyk 2006
Itaquascon pawlowskii Kathman & Cross 1991
Itaquascon unguiculum Pilato *et al.* 2002
Limmenius porcellus Horning *et al.* 1978
Macrobiotus almadai Fontoura *et al.* 2008
Macrobiotus anderssoni Horning *et al*. 1978
Macrobiotus arguei Pilato & Sperlinga 1975
Macrobiotus baltatus Guil 2002
Macrobiotus barabanovi Tumanov 2005
Macrobiotus barbarae Kaczmarek *et al.* 2007
Macrobiotus blocki Bertolani pers. comm. 2010
Macrobiotus bondavallii Manicardi 1989
Macrobiotus contii Pilato & Lisi 2006
Macrobiotus coronatus Horning *et al*. 1978
Macrobiotus crenulatus Kathman & Cross 1991
Macrobiotus echinogenitus Kathman & Cross 1991
Macrobiotus furciger Horning *et al*. 1978
Macrobiotus grandis Guil 2002
Macrobiotus harmsworthi Kaczmarek & Michalczyk 2006
Macrobiotus hibiscus Meininger *et al*. 1985
Macrobiotus hufelandi Kaczmarek & Michalczyk 2006
Macrobiotus islandicus Kathman & Cross 1991
Macrobiotus kazmierskii Kaczmarek & Michalczyk 2009
Macrobiotus kirghizicus Tumanov 2005
Macrobiotus kovalevi Tumanov 2004
Macrobiotus lazzaroi Nelson & Bartels 2007
Macrobiotus liviae Nelson & Bartels 2007
Macrobiotus lusitanicus Guil 2002
Macrobiotus magdalenae Michalczyk & Kaczmarek 2006b
Macrobiotus mandalaae Pilato 1974
Macrobiotus marlenae Kaczmarek & Michalczyk 2004c
Macrobiotus martini Bartels & Nelson 2009
Macrobiotus mauccii Pilato 1974
Macrobiotus montanus Kaczmarek & Michalczyk 2006
Macrobiotus nuragicus Pilato & Sperlinga 1975
Macrobiotus occidentalis Guil 2002
Macrobiotus orcadensis Horning *et al*. 1978
Macrobiotus pallarii Guil 2002
Macrobiotus patiens Schuster & Greven 2007
Macrobiotus persimilis Fontoura *et al.* 2008
Macrobiotus polaris Venkataraman 1998
Macrobiotus polyopus Kaczmarek 2003
Macrobiotus priviterae Binda *et al*. 2001
Macrobiotus pseudofurcatus Guil 2002
Macrobiotus radiatus Guil 2002
Macrobiotus ragonesei Binda *et al*. 2001
Macrobiotus rawsoni Horning *et al*. 1978
Macrobiotus recens Horning *et al*. 1978
Macrobiotus reinhardti Michalczyk & Kaczmarek 2003
Macrobiotus sapiens Bertolani pers. comm. 2010
Macrobiotus sklodowskae Michalczyk *et al*. 2006
Macrobiotus snaresensis Horning *et al*. 1978
Macrobiotus spectabilis Kaczmarek & Michalczyk 2006
Macrobiotus subjulietae Horning *et al*. 1978
Macrobiotus szeptyckii Kaczmarek & Michalczyk 2009
Mesocrista spitzbergensis Kathman & Cross 1991
Milnesium asiaticum Beasley & Miller 2007
Milnesium cf. *eurystomum* Kaczmarek & Michalczyk 2006
Milnesium longiungue Beasley & Miller 2007
Milnesium tardigradum Kaczmarek & Michalczyk 2006
Minibiotus aculeatus Horning *et al*. 1978
Minibiotus africanus Binda *et al*. 2001
Minibiotus continuus Pilato & Lisi 2006
Minibiotus fallax Claxton 1998
Minibiotus gumersindoi Fontoura *et al.* 2008
Minibiotus hufelandioides Guil 2002
Minibiotus intermedius Kaczmarek & Michalczyk 2006
Minibiotus cf. *poricinctus* Schuster & Greven 2007
Minibiotus pustulatus Hooie & Davison 2001
Minibiotus cf. *scopulus* Schuster & Greven 2007
Minibiotus weglarskae Kaczmarek & Michalczyk 2006
Minibiotus xavieri Fontoura *et al*. 2009
Murrayon dianae Jönsson 2003
Murrayon hibernicus Kaczmarek & Michalczyk 2006
Murrayon pullari Guil 2002
Murrayon stellatus Bartels & Nelson 2009
Parhexapodibius pilatoi Hinton & Meyer 2009
Paramacrobiotus alekseevi Beasley & Miller 2007
Paramacrobiotus areolatus Kaczmarek & Michalczyk 2006
Paramacrobiotus danielae Pilato *et al*. 2001
Paramacrobiotus derkai Degma *et al.* 2008
Paramacrobiotus halei Bartels & Nelson 2009
Paramacrobiotus huziori Michalczyk & Kaczmarek 2006b
Paramacrobiotus richtersi Kaczmarek & Michalczyk 2006

Paramacrobiotus tonollii	Hooie & Davison 2001	*Ramajendas frigidus*	Miller *et al.* 1996
Parhexapodibius pilatoi	Hinton & Meyer 2009	*Ramazzottius baumanni*	Kathman & Cross 1991
Platicrista angustata	Jönsson 2003	*Ramazzottius novemcinctus*	Guil 2002
Platicrista cheleusis	Kathman & Cross 1991	*Ramazzottius oberhaeuseri*	Kaczmarek & Michalczyk 2006
Platicrista horribilis	Nelson & Bartels 2007	*Richtersius coronifer*	Kaczmarek & Michalczyk 2006
Platicrista ramsayi	Marley 2006	*Thulinius augusti*	Guil 2002
Ramajendas renaudi	Jennings 1979		

Summary

The patchy distribution of tardigrades may be due to dispersal. The tardigrades (unlike their mossy habitats) are not easily blown 100 cm by typical winds. Nevertheless, they easily survive space travel during those uncommon events of dispersal. Highly resistant eggs may be a common means of dispersal. Bryophytes and feces of bryophyte consumers may provide means of dispersal.

The most common genera are ***Echiniscus***, ***Hypsibius***, ***Macrobiotus*** and segregate genera, ***Milnesium***, and ***Ramazzottius***. Many taxa are widespread, and many more are likely to be discovered. Cryptic species are likely.

Despite their cosmopolitan distribution and widespread occurrence in moss, lichen, and certain soil habitats, it is relatively easy to find new species anywhere in the world. Whole states in the USA (16!) lack any tardigrade records.

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CHAPTER 6-1
ONYCHOPHORA

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CHAPTER 6-1
ONYCHOPHORA

Figure 1. ***Euperipatus rowelli***, a velvet worm that is being cultured on ***Sphagnum***. Photo by Andras Keszei, with permission.

Phylum Onychophora (Velvet Worms)

Onyches is the Greek word for claws and ***pherein*** means to carry, *i.e.*, claw bearers. The phylum Onychophora (Figure 1) derives its name from the pair of retractable, chitinous claws on each foot (Figure 2-Figure 3). It is interesting that the mandibles (jaws), deep within the throat, resemble these claws. This is a phylum of wormlike creatures, 0.5-20 cm long, closely related to the arthropods and tardigrades, classified into a super group known as the Panarthropoda (Wikipedia 2010). These functionally segmented animals have antennae (Figure 4), tiny eyes (Figure 4), many paired legs (Figure 2; Figure 6), and slime glands, but they lack the chitinous exoskeleton of the arthropods. Because of their legs, they more closely resemble caterpillars, but the fleshy antennae distinctly set them apart. And they are not jointed in the same way as arthropods. Their slow movements are not unlike those of caterpillars.

Figure 2. ***Euperipatus rowelli***, revealing the feet with chitinous claws. Note the two bluish slime glands beneath the antennae and the barely visible mouth in the center of the head.. Photo by Andras Keszei, with permission.

Figure 3. Close view of foot and claws of ***Euperipatus rowelli***. Photo by Andras Keszei, with permission.

Figure 4. ***Euperipatoides rowelli*** showing antennae with tiny eyes near their bases. Photo by Andras Keszei, with permission.

The phylum is rare. This is in part due to the restricted ranges of the species and their very narrow and restricted habitat needs. But part is due to industrialization and the loss of suitable habitat. Only eleven species have been studied in detail, and three of those are critically endangered or in one case possibly extinct (Wikipedia 2010).

They are circumtropical, but are most common in the Southern Hemisphere tropics, where they prey on small insects. Because of their sensitivity to drying out, they are most common in humid forests such as the tropical rainforests, where mosses seem to be an important part of their habitat (Figure 5) (Onychophora 2005). On the other hand, Brues (1948) reported that Dr. P. J. Darlington collected a specimen of ***Paraperipatus*** in the Bismarck range of New Guinea in moss at 10,000 ft. (3048 m), which is above timberline. ***Epiperipatus biolleyi*** (Figure 6) is often associated with mosses, especially in the early stages of succession (Brinck 1956; Ruhberg 1985; Mayer 2006). Mayer and Harzsch (2007) collected this species from mosses in Costa Rica for their study of the nervous system. The onycophorans use the moss as cover to protect them from the radiation.

Figure 5. ***Peripatus*** sp. amid mosses on a rock. Photo by Robbin Moran, with permission.

Figure 6. ***Epiperipatus biolleyi***. Photo by Georg Mayer, Creative Commons license of BMC.

Feeding Habits

These are slow walkers (1 cm s^{-1}) (Monge-Nájera *et al*. 1993) and thus cannot realistically use aggression for protection or capture. They sense their prey by air movements caused by the movement of the prey; they are nearly blind. To catch their prey, they squirt a sticky slime, generally about 1 cm, but up to 30 cm from the onychophoran (Read & Hughes 1987; Wikipedia 2010; BBC 2010). The glue dries very quickly and immobilizes the prey. For larger prey, they may target the limbs, immobilizing them with the glue-like slime. This slime comprises up to 11% of the dry weight of the velvet worm and is 90% water. Its constituents include mostly collagen proteins. It also includes sugars, lipids, and nonylphenol, a surfactant known only in the Onychophora. This makes a super glue, and the nature of the lipid and nonylphenol suggests that these two substances may be used to prevent the organism from being glued by its own secretions by stopping or slowing the drying process. Haritos *et al*. (2010) examined the mechanism in ***Euparipatoides rowelli*** (Figure 4) and proposed that when the slime is expelled from the gland, evaporative water loss triggers a "glass transition change in the protein solution, resulting in adhesive and enmeshing thread formation, assisted by cross-linking of the complementary charged and hydrophobic regions of the protein." That is, this species, and probably other onychophorans, uses disordered proteins rather than the structured silk-like proteins used by some other kinds of invertebrate predators. The large percentage of body mass accounted for by this substance is

somewhat balanced by the organism's behavior of eating and reusing the dried slime of its prey (Read & Hughes 1987; Wikipedia 2010; BBC 2010). It requires 24 days to replenish the supply provided by the repository (Read & Hughes 1987). This glue also seems to be their only form of defense.

Moisture and Light Relations

The Onychophora have a covering of α chitin that seems to do little to prevent desiccation, forcing them to live in areas with high humidity – mosses and leaf litter of rainforests (Wikipedia 2010). Their sensitivity to desiccation is counteracted by having their activity primarily at night or in rainy weather (Monge-Nájera *et al*. 1993). And at least some also prefer soil that has been covered by moss, most likely because that soil has a higher moisture content. When suddenly exposed to light and its drying effects, they may roll into a ball like some isopods, forming a position that conserves moisture (Figure 7).

Figure 7. ***Euperipatoides rowelli*** enrolled after being exposed from its log habitat. Photo by Andras Keszei, with permission.

It appears that desiccation is not the only problem for exposed onychophorans. ***Epiperipatus biolleyi*** (Figure 6) is phototactic and hides from direct sunlight, avoiding light in the range of 470-600 nm (Monge-Nájera *et al*. (1993).

Monge-Nájera *et al*. (1993) reported that the field preference of the onychophoran ***Epiperipatus biolleyi*** (Figure 6) was either the moss-substrate interface or in burrows in the soil. Using a series of experiments, Monge-Nájera *et al*. demonstrated the preference of the ***E. biolleyi*** for bryophytes over grass (Figure 10). The researchers covered half a Petri dish with the thallose liverwort ***Marchantia polymorpha*** (Figure 8) and half with blades of grass. When subjected to light, nearly 80% of the animals curled up under the bryophytes within a mean time of 189 seconds (n=9). The ones on soil continued searching by inserting their antennae and head among soil particles, but they never came to rest or made any burrow (Figure 10). The researchers suggested that in nature these animals may be limited to areas where there are suitable burrows or cover such as bryophytes that provide cover similar to that in a burrow. It appears that ***Macroperipatus torquatus*** (Figure 9) has a similar restriction (Read 1985) to such habitats.

Figure 8. ***Marchantia polymorpha***. James K. Lindsey, with permission.

Figure 9. ***Macroperipatus torquatus***, shown here crossing young bryophytes, used the liverwort ***Marchantia polymorpha*** as cover from light in the lab. Photo by Mr. Spanky, through Creative Commons.

Moisture, as well as light, were most likely driving forces in these experiments. Monge-Nájera *et al*. (1993) measured the humidity in the two vegetation choices (Figure 10) by drying them to a constant weight. Moisture was significantly higher in the bryophyte portions (bryophytes: 84.2±3.4, 76.5-87.9%; grass: 71.1±4.4, 66.8-80.0%) using Mann-Whitney U with $p<0.001$ and 10 replicates.

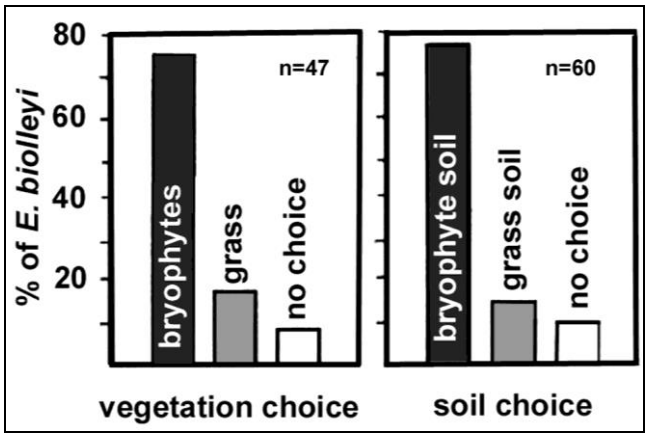

Figure 10. Comparison of percentage of ***Epiperipatus biolleyi*** in bryophyte cover vs grass blade cover (**left**) and on soil from under bryophytes vs soil from under grass (**right**) in 8 cm diameter Petri plates. These onychophorans were 5 cm long, so some straddled the two areas, having no clear choice. Modified from Monge-Nájera *et al*. 1993.

The onychophorans most likely also use the mosses as cover to avoid predators, which include the Clay-colored Robin (***Turdus grayi***; Figure 11) and Hemprich's Coral Snake (***Micrurus hemprichii***; Figure 12) (Monge-Nájera *et al*. 1993).

Figure 11. Clay-colored Robin, ***Turdus grayi***, a predator on onycophorans. Photo by Amado Demesa, through Creative Commons.

Figure 12. Yellow-banded Coral Snake, ***Micrurus hemprichii***, a predator on onycophorans. Photo by Rich Hoyer, through Creative Commons.

Mating and Reproduction

Finding suitable habitat or finding a mate requires considerable time for such slow-moving creatures and puts them at risk of desiccation. Thus, an efficient system for locating their habitat increases their chances for survival. Eliott *et al*. (1993) demonstrated for the first time in onychophorans, using ***Cephalofovea tomahmontis***, that the crural glands at the bases of the legs in males produce a pheromone that attracts females of the same species. It appears that pheromone-producing glands not only help in locating males, but may also prevent desiccation in females seeking new locations.

Peat moss is a typical substrate for culturing ***Euperipatus rowelli*** (Figure 13) (Barclay *et al*. 2000; Reinhard & Rowell 2005; Haritos *et al*. 2010; Andras Keszei, pers. comm. 7 March 2013). Keszei finds that ***Sphagnum*** (Figure 15) is the only suitable substrate he has found for culturing these onychophorans because it prevents mold while keeping them moist. This is perhaps due to the antibiotic properties of ***Sphagnum***. He says that this species does not normally live among the ***Sphagnum*** [they live in decaying logs, including *Eucalyptus* (Figure 14)], but that he has collected them from less than 100 m away and considers ***Sphagnum*** as a possible hunting ground for them.

Figure 13. ***Euperipatus rowelli*** being cultured on peatmoss, a medium that helps to limit fungal infection. Photo by Andras Keszei, with permission.

Figure 14. ***Euperipatus rowelli*** on decaying wood in NSW where they live in habitats ranging from rainforest to dry sclerophyll forests in decomposing logs. Photo by Andras Keszei, with permission.

Figure 15. ***Sphagnum cristatum***, a suitable substrate for culturing onycophorans. Photo by Janice Glime.

Eggs of at least some species are laid under mosses (Mayer & Tait 2009). On Mt. Macedon, Victoria, Australia, Mayer and Tait found ***Ooperipatellus insignis*** (see Figure 16) in leaf litter and under moss.

Figure 16. ***Ooperipatellus viridimaculatus*** on moss. Photo by Chris Morse, through Creative Commons.

Barclay *et al*. (2000) demonstrated that in ***Euperipatoides rowelli*** (Figure 13-Figure 19), males are the first dispersers. They secrete a pheromone that attracts both males and females of the same species. Thus, when these males disperse to decomposing logs, the females are able to locate this suitable habitat with a much lower water loss and expenditure of energy. It would be interesting to know if such a pheromone signal is equally used and effective among those onychophorans dwelling among bryophytes.

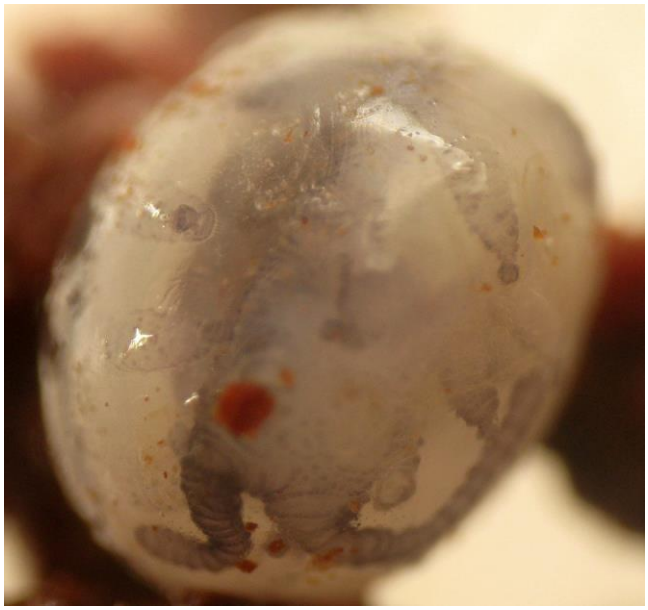

Figure 17. Oviviparous egg of ***Euperipatoides rowelli*** at time of "birth." Photo by Andras Keszei, with permission.

Figure 18. Newborn ***Euperipatoides rowelli***. Photo by Andras Keszei, with permission.

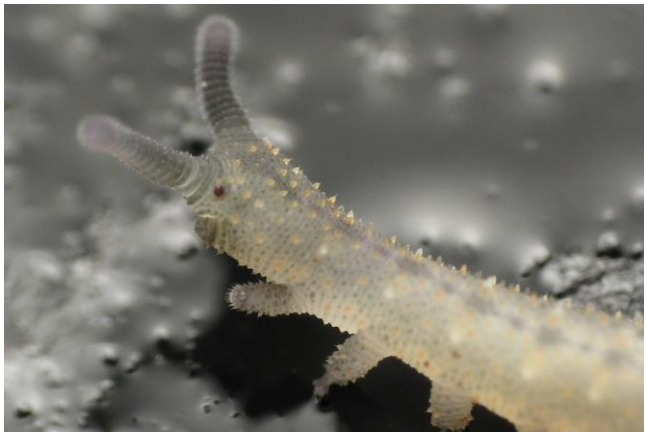

Figure 19. ***Euperipatus rowelli*** baby that has not yet developed its pigmentation. Photo by Andras Keszei, with permission.

Figure 20. ***Euperipatoides kanangrensis***. Photo by Martin Smith through Wikimedia Commons.

Like most of the onychophorans, ***Euperipatoides rowelli*** (Figure 1-Figure 2, Figure 7) is secretive. However, Reinhard and Rowell (2005) suggest that their behavior is nevertheless complex. They form aggregations as large as 15, comprised of females, males, and young. The female is dominant, and despite collective hunting, the dominant female eats first – alone. Behavior of aggressive dominant and passive-subordinate establishes a hierarchy. This structured group will defend its log aggressively against any invasion by onychophorans from another location.

Monge-Nájera and Alfaro (1995) hypothesized that onychophorans might find mosses because of some odor contributed by the mosses. However, when they provided them with filter paper with water on one end and macerated moss on the other end, the onychophorans showed no preference. Furthermore, while the preference of this species for moist habitats was greater than for dry habitats in Costa Rica, more specific preferences were not clear. Habitats included sandy soil, under moss, in and under logs, under stones, and in soil of crevices.

Reproduction is sexual in all but ***Epiperipatus imthurmi***, a species lacking males and using **parthenogenesis** (reproduction from an unfertilized egg) instead (Wikipedia 2010). Interestingly, the females are typically fertilized only once during their lives. If they are fertilized before the egg cells are mature, the sperm will be stored in a special reservoir. Sperm are released from their packets when amoebocytes from the female's blood collect inside the deposition site and decompose the packets. The young may be born live or laid as eggs, depending on the species.

Birds and rodents prey on the velvet worms. Their foraging activities may account for some of the disturbances to the mossy habitat.

Peripatoides novaezelandiae (Figure 21-Figure 23) is the most common peripatus species in New Zealand (Ryan 2012). I have not been able to verify that it lives among mosses, but it is commonly cultured on ***Sphagnum*** (Figure 15). However, a discussion on YouTube indicated that one of the posters photographed this species on ***Sphagnum***, and he stated that he photographed it in a culture that used the moss where it had been found.

Figure 21. ***Peripatoides novaezelandiae*** on moss. Photo by Paddy Ryan, with permission.

Figure 22. ***Peripatoides novaezelandiae*** showing feet. Photo by Paddy Ryan, with permission.

Figure 23. ***Peripatoides novaezelandiae*** on liverwort. These are likely traversed in search of food and soil beneath them is often sought to avoid dehydration. Photo by Paddy Ryan, with permission.

Mimics?

In the cloud forests of Ecuador, an onycophoran and a lepidopteran mimic live in the arboreal bryosphere (Zitani *et al*. 2018). The onycophorans are unable to close their many traheal spiracles and thus lose water easily. Therefore, bryophytes may serve as a moist habitat to maintain the moisture of the onycophorans. They are nocturnal and hav limited dispersal, further conserving thir moisture. In these arboreal moss cushions, they cohabit with annelids, molluscs, curstaceans, millipedes, centipedes, arachnids, and insects. But in one of the mosses samples there was a caterpillar that resembled th onycophoran in size, shape, and coloration. Is it really a mimic, or are both addapted by cryptic coloration to the same habitat? Is one of them unfit for would-be predators?

Summary

Among the bryophyte inhabitants are members of the relatively rare phylum Onychophora. Little is known about their behavior, but it appears that bryophytes are important in maintaining moisture in the soil beneath them where onychophorans may live. It is likely that we will discover that many more species make use of the bryophytes in some capacity.

Sphagnum is an important culture medium for onychophorans because they do not develop fungal infections when it is used.

Acknowledgments

I appreciate the helpful comments and images of Andras Keszei that have greatly enhanced the clarity of this chapter. Bernard Goffinet kindly sent me the article on the Onychophoran by Zitani *et al*.

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CHAPTER 7-1
ARTHROPODS: HABITAT RELATIONS

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CHAPTER 7-1
ARTHROPODS: HABITAT RELATIONS

Figure 1. The epiphytic moss ***Orthotrichum lyellii*** that has been chewed, most likely by an arthropod, partially stripping the stems. Photo by C. Robin Stevenson, with permission.

Arthropods (Phylum Arthropoda)

The most conspicuous group of organisms living in the shelter of bryophytes are the arthropods (Bonnet *et al*. 1975; Kinchin 1990, 1992). McKenzie-Smith (1987) contended that animal densities among bryophytes often were greater than those we might expect simply on the basis of the greater surface area, implying that they provided more than just space. Yet, as Gerson (1969) so aptly pointed out, ecologists, both botanical and zoological, had dismissed the bryophyte habitat, as Cloudsley-Thompson (1962) put it, because "it is clear that moss does not form a biotope with a stable microclimate." Humph! To what were the ecologists comparing it?

Not only do the bryophytes modify their internal climate relative to the ambient conditions, they also modify the soil conditions, permitting some of the arthropod species to survive there when the ambient atmospheric conditions are extreme and uninhabitable (Gerson 1969). Acting like a spongy insulator, they buffer soil temperatures and reduce water evaporation from the soil. But they also can interfere with water reaching the soil in short spates or very light rainfall. They provide a humid environment when the sun dries the atmosphere. And some species act like a black box, absorbing heat with dark-colored leaves and reaching temperatures higher than those in the atmosphere. With these varying conditions, we might hypothesize that bryophytes can serve as a refuge at times while being inhospitable at others, and for some, provide a source of food (Figure 1).

The abundance of arthropods among bryophytes may in part relate to their concurrent venture onto land in the early Ordovician (Anissimov 2010). Once on land, they have invaded the three main strata: subterranean, forest floor debris, and arboreal (Grimmett 1926). Among these, we will generally not be concerned with the subterranean stratum as it is rarely a habitat for bryophytes. The stratum of forest floor debris reminds us that soil scientists often consider the moss layer as part of the soil, and most certainly Grimmett included it with the forest floor debris.

Yanoviak *et al.* (2004) considered such habitats as epiphytic mosses to enhance species richness of the arboreal arthropods by increasing the available types of niches. The bryophytes provide a structural component to

the arboreal habitat and function to buffer the moisture and protect against the wind. They furthermore provide a foraging location and a place to deposit eggs (Gerson 1982; André 1983; Nadkarni 1994; Kitching *et al*. 1997; Drozd *et al*. 2009).

The bryophytes can serve as food for a wide range of arthropods and at the same time they provide excellent camouflage. Fischer (2005) estimated that 300 species of animals, many of which are arthropods, live among mosses in the Pacific Northwest and Appalachian Mountains, North America. These arthropods, in turn, can serve as food for a wide range of larger animals.

In their *Science* article, "The Forgotten Megafauna," Hansen and Galetti (2009) state that "In any given ecosystem, the largest vertebrates have ecosystem impacts that are similar on a relative scale to those of the largest vertebrates in another ecosystem: One ecosystem's mesofauna is another ecosystem's megafauna." This concept can be extended to comparing the bryophyte habitats. In this case, it would usually be the arthropods that occupy this position of megafauna. Although most of these top predators are insects, other arthropods are likewise important. As will become evident, we know almost nothing about these relationships in the bryophyte habitat.

Arthropods were so-named because they have jointed legs (Hingley 1993). Some arthropods are small enough to inhabit the water film in a leaf concavity, and small crustaceans and mites are able to live in that film between the leaves. Larger arthropods such as spiders and insects can run across the surface or navigate among the stems and leaves.

Bryophytes in all sorts of habitats house a varied arthropod fauna. Smrž (1992) studied the microarthropods inhabiting mosses on roofs. Block (1985) described arthropods in a terrestrial community on Signy Island in the maritime Antarctic. In the Antarctic, mosses modify soil moisture and temperature, permitting arthropods to live there (Gerson 1969). Curry *et al*. (1989) studied the invertebrate fauna of reclaimed peatlands in Ireland. De Graaf (1957) examined both the macrofauna such as arthropods and the microflora of a quaking bog in the Netherlands. Varga (1992) examined the communities associated with two protected moss species [***Plagiobryum zierii*** (Figure 2) & ***Saelania glaucescens*** (Figure 3)] in Hungary and found that mosses with high lead concentrations near roads were associated with poorer bryofauna than mosses from unpolluted control sites, as already noted for micro-organisms. Protozoa, small metazoa, bacteria, organic debris, and plant material serve as food for the inhabiting arthropods, permitting the arthropods to sustain life within the protection of a bryophyte clump.

Insects, the largest group of arthropods and the largest single group of animals on the planet, have many members small enough to navigate within the moss clumps, and are therefore a major component of the fauna. They can be so numerous as to require special extraction methods (Andrew & Rodgerson 1999). Their abundance and diversity have earned them separate chapters in this book.

Figure 2. ***Plagiobryum zierii***, a moss where lead accumulations can lead to a depauperate fauna. Photo by Michael Lüth, with permission.

Figure 3. ***Saelania glaucescens***, a lead accumulator that becomes unsuitable for many invertebrates. Photo by Michael Lüth, with permission.

Habitat Relations

Since I first began, early in my career, studying arthropods associated with aquatic bryophytes, numerous studies have addressed the fauna of the protective bryophyte habitat (see Borges *et al.* 2005). Yet, the relationships of the bryological fauna to the bryophytes remains poorly known (Drozd *et al*. 2008). Drozd and coworkers (2009) were able to demonstrate that significant relationships exist between the microhabitat conditions within the bryophyte cushions and the patterns of abundance of the invertebrate community (Figure 4).

In comparison to litter habitats, Drozd *et al*. (2009) were surprised to find that nearly all arthropod groups were in greater abundance in the litter than in moss cushions ($p = 0.0003$; *e.g.* Figure 5). But as they identify species, we may find this relates to available space for larger organisms that cannot navigate well among the bryophytes. Drozd *et al*. (2009) found that moss presence, moss species, and moisture were very important in determining arthropod abundance.

Much remains for us to understand about the arthropod fauna of these unique habitats.

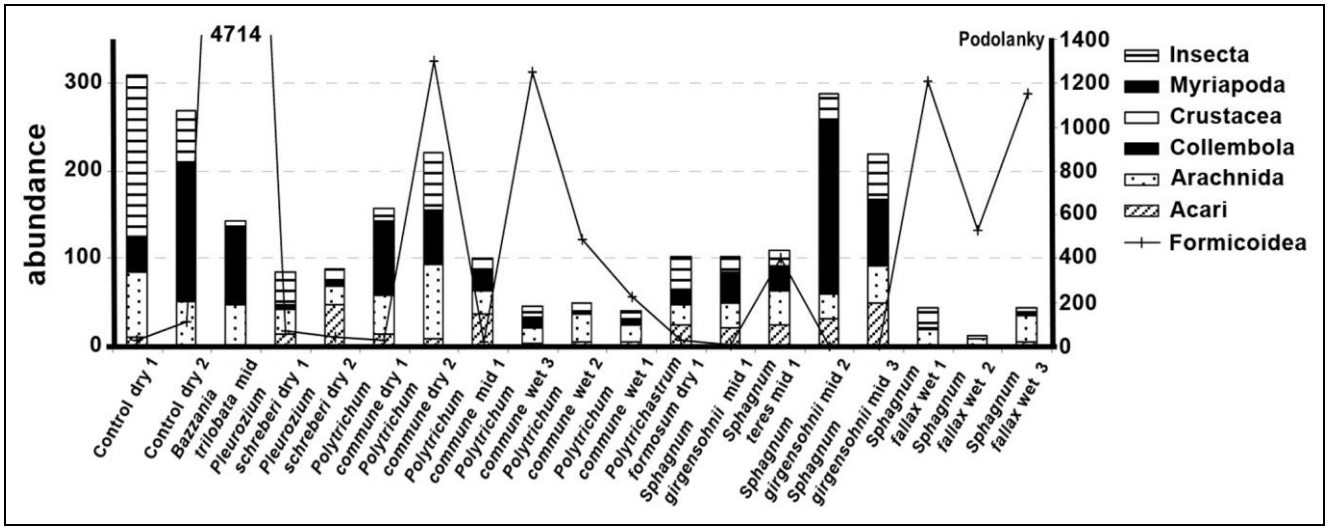

Figure 4. Abundance of arthropod taxonomic groups in pitfall traps in the mountains of the Czech Republic. Ants (Formicoidea) from Podolánky were drawn separately because of their high numbers. Control = litter; moisture categories are wet (high), middle, and dry (low). Redrawn from Drozd *et al*. 2009.

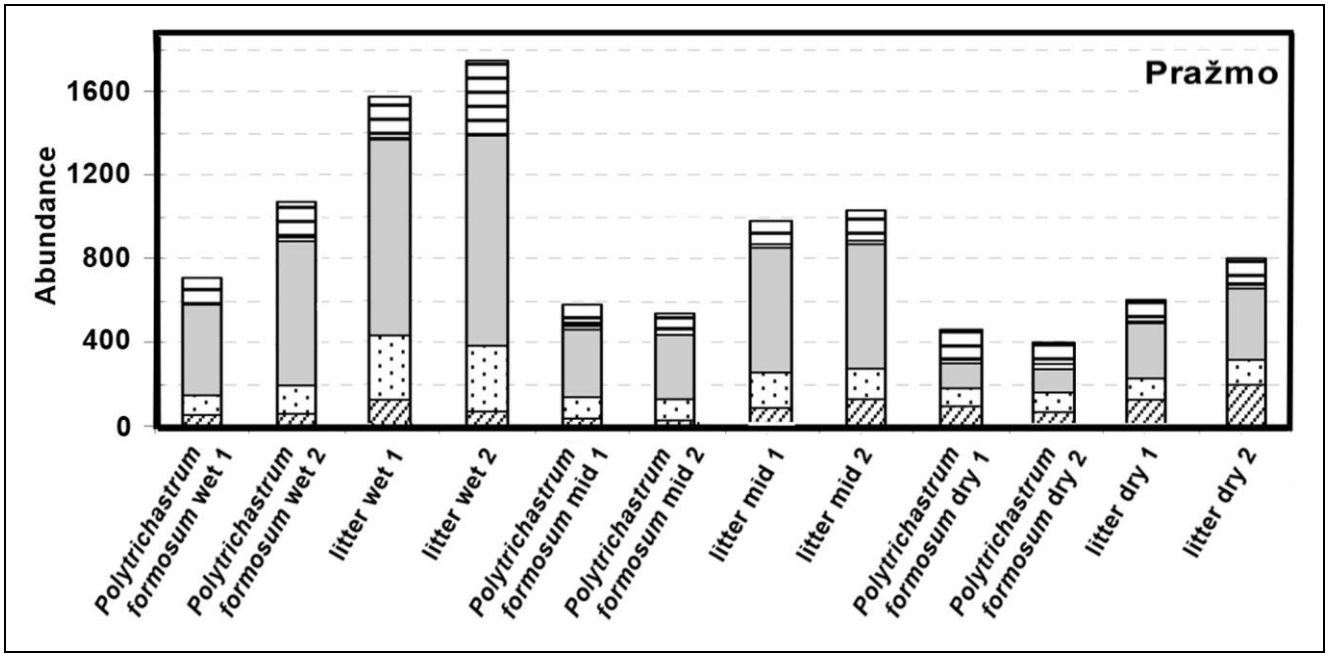

Figure 5. Abundance of arthropod taxonomic groups in pitfall traps at Pražmo in the mountains of the Czech Republic. Moisture categories are wet (high), middle, and dry (low). Redrawn from Drozd *et al*. 2009.

Epiphytes

The importance of bryophytes to the arthropod community is suggested by a positive correlation between bryophyte abundance and arthropod morphospecies in a study in Maine, USA (Miller *et al*. 2007). Epiphytes, especially in the tropics, are a habitat for a number of arthropod inhabitants (Nadkarni & Longino 1990). Nadkarni and Longino found that canopy "soils" in Costa Rica included Coleoptera, Collembola, Acari, insect larvae, ants, Amphipoda, and Isopoda. And disturbance that removes bryophytes typically results in a decrease in arthropods, at least temporarily.

Zytynska *et al*. (2011) found that genetic variation in species of tropical trees could affect associated epiphytes and invertebrates. They found that greater genetic diversity among the trees led to greater diversity among epiphyte and invertebrate communities. The very limited specificity of bryophytes for host trees suggests there may not be a strong influence on bryophyte diversity, but we must ask how much influence the genetic differences in the trees may have on the invertebrate communities living among those bryophytes. Peck and Moldenke (2010) found that there were no significant differences among arthropods between the two tree species they sampled, but rather arthropod communities related more to location of the mats.

Pettersson *et al*. (1995) found that the number of larger invertebrates, important food sources for birds, was greatest among arboreal lichens in the boreal forest of Sweden, compared to habitats in managed forests that lacked

abundant lichens. The predominant invertebrates were spiders (**Araneae**), **Lepidoptera**, and **Diptera** larvae. Thus, decline in bird populations have been linked to loss of food organisms that depend on lichens in that habitat. Similar studies for bryophytes (Nadkarni 1994), indicate that it is likely that loss of spiders from disturbed habitats that previously had more bryophytes might likewise be a cause for bird decline.

Secondary forests developed after deforestation are recolonized slowly by bryophytic epiphytes (Pettersson *et al.* 1995). Hence, the arthropods and other invertebrates are necessarily delayed in their arrival. Absence of suitable habitat nearby will further delay colonization of new growth. Pettersson *et al.* (1995) demonstrated that natural boreal forests (i.e., those without harvesting) supported five times as many invertebrates per tree branch as the mature secondary forests as well as a greater diversity. Spiders were among the dominant organisms. Non-migrating birds often depend on these invertebrates during the winter when small differences in food abundance can be critical to sustaining their lives. Furthermore, only the invertebrates larger than 2.5 mm form suitable prey for overwintering passerine birds, a size that was consistently higher in unlogged forest. Although most epiphytes in this case were lichens, bryophytes are likely to present a similar story.

Typical tropical sampling methods, including fogging, tend to miss many of the bryophyte-dwelling arthropods (Yanoviak *et al*. 2003). Nevertheless, tropical studies indicate the importance of epiphytic bryophytes as habitat for numerous arthropods (Yanoviak *et al.* 2007). In Monteverde, Costa Rica, secondary forests had thinner mats that were less structurally diverse than those in primary forests. Although species richness differed little between the two forest types, abundance of arthropods was significantly higher in the secondary forest, primarily because of the presence of ants. During the dry season (February – May), the number of taxa was lower, with arthropods becoming dormant or seeking places with greater moisture, including deep in mats. Nadkarni and Longino (1990) demonstrated the invertebrates that were dominant in the Costa Rican canopy as well as the forest floor: adult beetles (**Coleoptera**), **amphipods**, ants (**Hymenoptera**), springtails (**Collembola**), insect larvae, **isopods**, and mites (**Acari**). The ground fauna exhibited 2.6 times the density of that found in the canopy, but this does not diminish their importance for canopy-dwelling birds. Temperate bryophytic epiphytes can be suitable habitats for arthropods as well (Voegtlin 1982).

Forest Floor

It is likely that bryophytes, like litter, influence the kinds of spiders and other arthropods on the forest floor. Willett (2001) demonstrated in the Santa Cruz Mountains of California, USA, that forest floor spiders indicated such characters as old growth vs logged forest. Both diversity and abundance of spiders decreased with herb cover. Those spiders that live in association with moss mats are likely to decrease as well in disturbed (logged) forests, often due to a decrease in prey abundance.

Rock Zonation

Bonnet *et al*. (1975) examined the ecology of 26 bryophyte-dwelling species of springtails (**Collembola**) and 45 species of mites (**Acari**, Figure 6). These arthropods exhibited a population gradation from soil to aerial mosses. Likewise, there was a gradation from drier mosses on the south face of the forest rock to the deep soil communities on the north face. This study pointed to the importance of humidity and temperature in determining the distribution of these two arthropod groups.

Figure 6. Mite (**Acari**). Photo by Alan R. Walker, through Creative Commons.

Cryptogamic Crusts

The cryptogamic crust is a mix of lichens, algae, Cyanobacteria, and bryophytes that form a crust on dry soil. In prairies and semidesert lands they may occupy as much as 70% of the soil (Brantley & Shepherd 2004) and provide a means of conserving moisture, providing a suitable habitat for arthropods. In the piñon-juniper woodland of central New Mexico, mosses provided a better habitat (greater faunal abundance) than did lichens or mixed lichen crusts (Brantley & Shepherd 2004). Likewise, mosses housed the most taxa (29 species, then mixed lichens and mosses (27), then lichens (21). Fifteen taxa occurred on all three of these substrata, suggesting possible specificity, but with a greater degree of generalists than specialists among cryptogamic taxa. Shepherd *et al*. (2002) found that the fauna of crust mosses were active following winter precipitation, exhibiting significant increases in both richness and abundance. This period may introduce arthropods when other fauna are absent, thus having an important impact on soil nutrient cycling.

In the Little Desert National Park, northwest Victoria, Australia, the soil crusts (nine mosses and nine liverworts) housed only the phylum Arthropoda among the invertebrates (Milne *et al*. 2006). Diversity was low; diversity was greater in the wetter periods.

Streams

Bryophytes in streams greatly increase substrate available to arthropods (Suren 1988; Figure 7). Sometimes they house communities that mimic those of riffles, but in other cases they harbor very different communities. And the *p*H conditions can affect the faunal composition. In the River Liffey, Ireland, Frost (1942) compared 23 bryophyte samples each between an acid and alkaline stream and found that the numbers of organisms differed little between them (acid ca 282,000; alkaline ca 306,900 organisms), but the composition of the organisms differed. In a mountain

stream in Nara Prefecture in Japan, Tsuda and Nakagawa (1959) likewise found that communities of moss-covered rocks differed from those of bare rock.

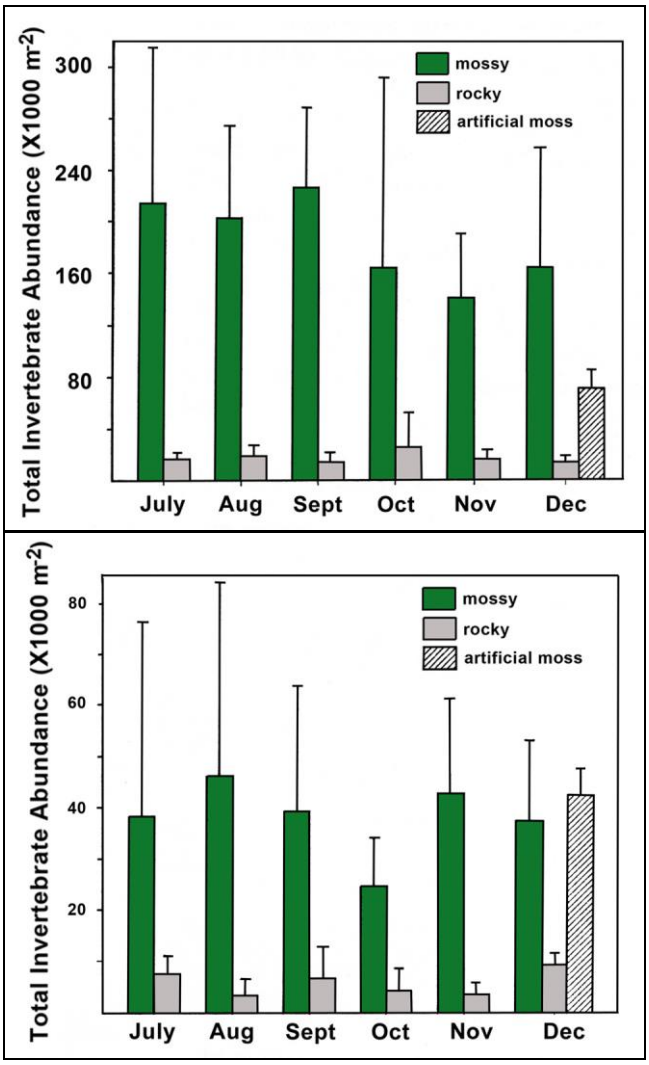

Figure 7. Comparison of invertebrate abundance in mossy habitats, rocky habitats, and artificial mosses made of nylon twine in two streams in New Zealand. Redrawn from Suren 1988.

In streams, bryophytes house not only numerous aquatic insects, but also amphipods like ***Gammarus*** (Figure 8, Figure 11) (Badcock 1949). And this invertebrate eats its own home. ***Gammarus*** lives among ***Fissidens*** (Figure 9) and eats its leaves (Minckley & Cole 1963).

Figure 8. ***Gammarus*** sp., a scud that is often found among aquatic bryophytes. Photo by Janice Glime.

Bryophytes in streams serve as a perennial refuge for many arthropods in a habitat where other plants usually disappear for the winter or are absent altogether because the flow rate is too rapid for them to survive at some times during the growing season. Such ephemeral plants prevent the establishment therein of such arthropods as ***Asellus*** (Figure 10) and ***Gammarus*** (Figure 11) (Fontaine & Nigh 1983), but the more permanent bryophytes often house these taxa.

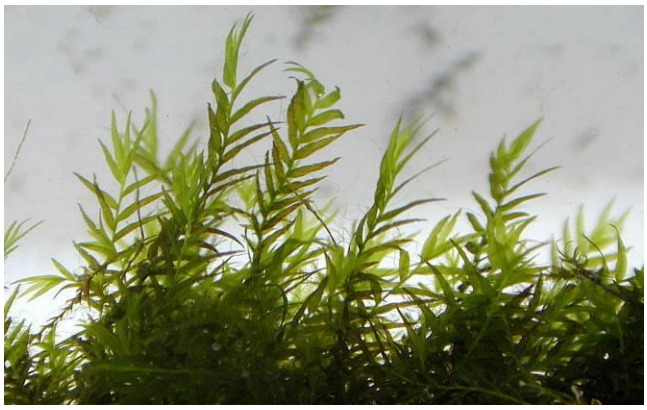

Figure 9. ***Fissidens fontanus***, a moss that serves as both home and food for ***Gammarus***. Photo by Michael Lüth, with permission.

Even in raging water of snowmelt, chambers within the bryophyte mat tend to be quiet (Dorier & Vaillant 1954; Kamler & Riedel 1960). This depends in part on the form and depth of the moss. The heavy flow often relegates the bryophytes to the downstream sides of rocks. The flow dynamics cause the water to arch over the bryophytes, creating the negligible flow within the moss mat (Kamler & Riedel 1960). These factors determine the quantity and composition of the fauna (Kamler & Riedel 1960).

Figure 10. ***Asellus aquaticus***, a common inhabitant of aquatic bryophytes. Photo by Jacob LaCroix, with pernission.

Referring to the stream bryophyte fauna, Suren (1992a) stated that "these invertebrates are traditionally neglected in stream surveys and their ecological roles poorly understood." He found that densities of meiofauna were greater than those in stream gravel habitats. Faunal communities among bryophytes were different from those in gravel. As in many other cases, the availability of periphyton as food seems to be an important factor in the distribution of these fauna (Glime & Clemons 1972;

Johnson 1978; Devantry 1987; Suren 1988, 1990; Suren & Winterbourn 1992b). But shelter from fast current among stems and in leaf axils is most likely important for many species (Suren 1992a; Suren & Winterbourn 1992a, b).

Figure 11. The scud ***Gammarus*** sp., sometimes an abundant inhabitant of aquatic bryophytes. Photo by Janice Glime.

Organic matter (FPOM and UFPOM) fractions in bryophyte samples differ between shaded and unshaded sites (Suren 1992a, b; Suren & Winterbourn 1992b). At the unshaded site the food source was primarily periphyton, but at the shaded site it was primarily fine amorphous detritus (Figure 12). This greater detritus accumulation was largely due to the position of this portion of the stream below timberline (Suren 1992b).

Figure 12. ***Hygroamblystegium fluviatile*** showing detritus (grey areas) trapped among the branches. Photo by Michael Lüth, with pernission.

There have been many discussions about the importance of bryophytes as a food source. Until relatively recently, ecologists considered bryophytes to be unfit food, hence rendering them unimportant in many ecosystem studies. More recent studies suggest that at least some organisms use them as food, but it is likely that their role as a substrate for epiphytic algae might be more important than their direct use, at least in aquatic systems. McWilliam-Hughes *et al*. (2009) examined the role of various components as carbon sources in two temperate rivers. Epilithic algae were primary food sources. They found that 98% of the scrapers (primarily insects) exhibited enriched δ13C values relative to those of bryophytes, and that values in these two components were correlated. This relationship was not so obvious in slow-water habitats. In headwater streams, the brook moss ***Fontinalis*** (Figure 36) was abundant. In low order streams (a first-order stream is a headwater stream), ***Drepanocladus*** (*sensu lato*?; Figure 13-Figure 14) was abundant. McWilliam-Hughes and coworkers suggested that when rivers had low productivity and were nutrient limited, scrapers compensated for the limited food availability by switching to "marginal" foods, including bryophytes. They based this suggestion on the scrapers in low-order streams that depended more on ***Fontinalis*** than did the scrapers in high-order streams depend on ***Drepanocladus***.

Figure 13. ***Warnstorfia fluitans*** (formerly *Drepanocladus fluitans*). Photo by Michael Lüth, with pernission.

Figure 14. Close-up of ***Warnstorfia fluitans*** (formerly *Drepanocladus fluitans*). Photo by Michael Lüth, with pernission.

Linhart *et al*. (2002) support yet another means by which bryophytes support the food pyramid in streams. ***Fontinalis antipyretica*** on rock rip-rap in a channel of the Morava River, Czech Republic, trapped particulate matter that provided a food source for arthropods. Seasonal variation in the arthropod groups of **Hydrachnidia** (=Hydracarina – mites), **Cladocera** (Figure 15), **Copepoda**, and **Chironomidae** (midges) correlated significantly with trapped matter and specifically with organic matter. Linhart and coworkers concluded that aquatic bryophytes on rip-rap increase spatial diversity that supports considerably greater numbers of **meiofauna** (component of fauna of sea or lake bed comprising small, but not microscopic, animals; defined by size based on standard mesh width of sieves with 500-1000 µm as upper and 32-63 µm as lower limit; all animal life of any particular region or time) than the gravel bed.

Abundance of various types of arthropods varies widely among stream locations. Table 1 demonstrates a few of these differences from a wide range of studies. Unfortunately, the methods of reporting abundance vary as widely as the invertebrates, but relative numbers are useful. Those not reported often mean the investigators did not include them in the study.

Table 1. Comparison of arthropod abundance (exclusive of Insecta) in various locations around the world. NR = not reported.

	Sample Size	Hydracarina	Copepoda	Cladocera	Ostracoda	Amphipoda	Isopoda	Decapoda	Reference
Straffan, River Liffey, Ireland	200 g	147	329	0.4	4	6	2	0.3	Frost 1942
Ballysmuttan, River Liffey, Ireland	200 g	114	45	0.4	0.3	0	0	0	Frost 1942
Cold Springbrook, Tennessee, USA	.1 m²	+	NR	NR	NR	13.4	5.5	NR	Stern & Stern 1969
Bystřice, Czech Republic	10 g dry	880	582	180	175	NR	NR	NR	Vlčková *et al* . 2001-2002
Mlýnský náhon, Czech Republic	10 g dry	95	269	48	15	NR	NR	NR	Vlčková *et al* . 2001-2002
Welsh Dee Tributary, Wales	~300 cm²	1.7	6.8	0.1	0.4	NR	NR	NR	Hynes 1961
Mouse Stream, alpine, New Zealand	1 m²	NR	15470	NR	NR	NR	NR	NR	Suren 1991a
Tim's Creek, alpine, New Zealand	1 m²	NR	1120	NR	NR	NR	NR	NR	Suren 1991a
West Riding, Yorkshire, GB - loose moss	%	2.82	NR	NR	NR	0.8	NR	NR	Percival & Whitehead 1929
West Riding, Yorkshire, GB - thick moss	%	3.25	NR	NR	NR	1.35	NR	NR	Percival & Whitehead 1929
alpine unshaded stream, New Zealand	%	1.1	9	NR	2.8	NR	NR	NR	Suren 1991b
alpine shaded stream, New Zealand	%	5.9	1.5	NR	0.7	NR	NR	NR	Suren 1991b

Figure 15. **Cladoceran**, a member of the aquatic bryophyte fauna that feed on trapped organic matter. Photo by Yuuji Tsuki, with pernission.

Heino and Korsu (2008) reminded us that there are few studies that address the species-area concept of stream bryophyte fauna (macroinvertebrates). Contrary to 2-d substrates, only one significant species-area relationship existed among the six that they tested.. They found two significant individuals-area relationships, but both were nevertheless weak. Rather, they found strong significant relationships between both species richness and the number of individuals with bryophyte biomass in all six sampling locations. Furthermore, disturbance by a bulldozer resulted in a stronger species-bryophyte biomass relatioships. The species-area relationships on stones were weak. Heino and Korsu suggest that bryophyte biomass has a "pivotal role" both species richness and number of individuals among stream macroinvertebrates. They recommended experimental testing to determine the importance of passive sampling, provision of more food, more niche space, and flood disturbance refugia in these bryological-faunal relationships.

Peatlands

Be careful when you pull that handful of ***Sphagnum*** from the crimson mat in the peatland. It might bite! And you might be crushing hundreds of lives – rotifers, ants, mites, spiders, and more, not to mention the numerous protozoa (Chacharonis 1956; de Graaf 1957; Heal 1962, 1964; Corbet 1973; Bninska *et al*. 1976; Bateman & Davis 1980; Clymo & Hayward 1982; Borcard 1986, 1993; Schönborn & Peschke 1990; Hingley 1993).

The bog provides a wide range of niches. The surface layer can experience a 30°C temperature variation in a single day, with humidity ranging 40-100% (Gerson 1969). But down in the layer of stems the temperature variation drops to only 5°C per day and the humidity is stable at 100%.

One ***Sphagnum*** site housed 145 species of invertebrates, whereas a nearby forested site housed only 65 (Schofield 1985). Chiba and Kato (1969) suggested that the testacean (protozoan) community in the Mt. Kurikoma district of Japan is related to the habitat of the bryophytes there.

Since ***Sphagnum*** is a habitat of large scale, it is not surprising that Biström and Pajunen (1989) found some of the larger invertebrates – the multipedes (animals with many feet, mostly used for millipedes, centipedes, and symphylans, but also sometimes applied to spiders and insects), including **Araneae** (mites; also Gerson 1972; Seyd 1988), **Pseudoscorpionida**, **Opiliones** (harvestmen), **Diplopoda** (millipedes), **Chilopoda** (centipedes), and **Symphyla** (blind, white multipedes; Figure 20) among both the ***Sphagnum*** and ***Polytrichum commune*** in the Finnish peatlands. ***Sphagnum*** and ***Polytrichum commune*** (Figure 16) habitats housed numerous spiders (1368 individuals/77 species), as well as **pseudoscorpions** (35/1) (Figure 17), **harvestmen** (157/5), **centipedes** (43/3) (Figure 18), **millipedes** (39/4) (Figure 19), and **Symphylans** (multipedes; 9/1) (Figure 20) (Biström & Pajunen 1989). It is interesting that despite high variability overall, ***Sphagnum girgensohnii*** (Figure 21) has its own characteristic species, with a high proportional similarity among samples, indicating that the faunal communities of this species are fairly consistent and suggesting the possibility of some characteristic favoring this species group (Biström & Pajunen 1989).

Figure 16. ***Polytrichum commune***, a habitat for a wide range of arthropods. Photo by Michael Lüth, with pernission.

Spiders can actually characterize the various biotopes within a peatland (Villepoux 1990). Lycosid spiders (wolf spiders) such as ***Lycosa pullata*** (Figure 22) and ***Pirata piraticus*** (Figure 23) seem to be common in peatlands (Nørgaard 1951), no doubt benefitting from the abundant invertebrates clambering about among the mosses. In poor pine fens, one can find the wolf spider ***Pardosa maisa*** in the ***Sphagnum*** layer (Itaemies & Jarva 1983). At the Massif Central, France, spiders in the ***Sphagnum*** bog were so diverse and common that they could be used to characterize the different biotopes making up the bog (Villepoux 1990). And not surprisingly, at least in Sweden, there is a rare spider wasp, ***Anoplius caviventris*** (Hymenoptera: Pompilidae), there to take advantage of the situation (Berglind 1993).

Figure 17. **Pseudoscorpion**, a group that often lives among mosses. Photo by Llnoba from Wikimedia Commons.

Figure 18. ***Geophilus***, a centipede that is common among ***Sphagnum*** and ***Polytrichum commune***. Photo by Fritz Geller-Grimm through Wikimedia Commons.

Figure 19. **Millipede** similar to those found among bryophytes. Photo by Dan L. Perlman through Creative Commons.

Figure 20. A symphylan (white multipede) that can inhabit mosses. This one is probably a species of ***Scutigerella***. Photo by Sonia Martinez through Wikimedia Commons.

Figure 21. ***Sphagnum girgensohnii***, home to many kinds of arthropods that seem to have a high consistency among samples. Photo by Michael Lüth, with pernission.

Figure 22. Wolf spider (**Lycosidae**), relative of ***Lycosa pullata*** that occurs in peatlands. Photo by Janice Glime.

Figure 23. ***Pirata piraticus***, a lycosid spider that inhabits peatlands. Photo by Michael Hohner, with pernission.

Arthropods can encounter difficulty in the base-poor environment of peatlands. Normally, calcite ($CaCO_3$) is used to harden the cuticle, but this compound is generally not available in the acid environment of the peatland. Norton and Behan-Pelletier (1991) found that the ***Sphagnum***-dwelling mites ***Eniochthonius minutissimus***, ***Archoplophora rostralis***, and ***Prototritia major*** deposit whewellite, a form of calcium oxalate that may originate as precipitation from the fungal food eaten by the mites, using the whewellite as a cuticular hardening agent.

Removing invertebrates from ***Sphagnum*** can be a laborious task. While sifting may be viable for tiny beetles, it is impractical for many taxa. Providing a vertical gradient of temperature and O_2 (Fairchild *et al*. 1987) can drive the invertebrates to a common location at the top or bottom of the moss column for easy removal, suggesting to us that these organisms in the peatlands must balance the heat near the surface with the diminished oxygen but cooler temperatures further down in the ***Sphagnum*** mat.

Antarctic

Even the Antarctic and sub-Antarctic have their share of arthropod moss-dwellers (Goddard 1979; West 1984; Block 1985). Booth and Usher (1986) examined the life history of mites living among moss turfs. They (Booth & Usher 1984) found that ***Polytrichum*** (s.l.?) cover was somewhat important, but percentage water content was consistently important, a factor discussed already for other invertebrates. Calcium and potassium were likewise important in the arthropod distribution. It is also likely that the warmer temperatures in the bryophytes encouraged arthropod colonization (Gerson 1969). Gerson (1969) suggested that, particularly in the Antarctic, the moss-arthropod associations were the result of modifications of the soil. The mites sometimes feed on mosses as well.

The bryophyte habitat is very important for diversity of Antarctic arthropods (Gerson 1969; Block 1985; Kennedy 1994), although diversity can be somewhat low (Block 1985). Mats of ***Polytrichum-Dicranum*** harbor more arthropods than do ***Pohlia*** mats. They are less wet and cold in summer had have more open texture. ***Ceratodon purpureus*** (Figure 24) and ***Distichium capillaceum*** (Figure 25) have larger numbers of microarthropods compared to communities of ***Andreaea*** (Figure 26). Kennedy suggests that the paucity of invertebrates in ***Andreaea*** may relate to its lack of convolutions or internal spaces compared to the other aforementioned species.

Figure 24. ***Ceratodon purpureus***. Photo by Michael Lüth, with pernission.

Figure 25. ***Distichium capillaceum*** showing chambering at base where arthropods can hide. Photo by Michael Lüth, with pernission.

Figure 26. ***Andreaea rupestris***, a compact moss possessing less chambering than that found among ***Distichium capillaceum*** stems. Photo by Michael Lüth, with pernission.

Altitude

On four mountains in New Zealand, Andrew *et al*. (2003) found that although diversity varied with altitude, there was no trend along the altitudinal gradient. For example, Otira had the highest diversity among both invertebrates and bryophytes at low altitudes, whereas Kaikoura had its highest invertebrate diversity coupled with the lowest bryophyte diversity at the highest altitudes. However, on Mt. Field, Andrew and Rodgerson (1999) found a mid-altitudinal peak in abundance of invertebrates living among bryophytes. On Mt. Rufus they found an altitudinal abundance gradient but no differences in species richness with altitude. They determined that scale variation was a greater contributor to richness than altitude on Tasmanian mountains.

Temperature Protection for Arthropods

Bryophyte mounds and turfs provide an insulating layer that is important for a number of organisms. Some insects, like the Mecopterans ***Boreus westwoodi*** (Figure 27) and ***B. hyemalis*** in southeast Norway, are active on the snow in the winter (Hagvar 2001). These insects lay their eggs among mosses in **subnivean** (under snow) air space, thus protecting the larvae from exposure. **Collembola** (springtails) are likewise winter active and are common both on the surface and in the moss mats (Hagvar 2001).

Figure 27. ***Boreus westwoodi*** on mosses. Photo by Barbara Thaler-Knoflach, with pernission.

In peatlands, ***Sphagnum*** hummocks may maintain a nearly constant temperature just below freezing (-2.5 to -8.5°C) while the air temperature drops to as low as -20°C (Longton 1979a). Nevertheless, in the cold Antarctic, Booth and Usher (1984) found that the cover of ***Polytrichum*** was usually less important than percentage water content and calcium content for the inhabiting arthropods.

In summer, bryophytes in some locations provide a cool haven from the summer heat (Gold *et al*. 2001). Under the moss-dominated crusts in the Olympic Mountains of Washington, USA, soil surface and near-surface temperatures are 5-8°C cooler at midday than in bare soil. Lichens cool the soil surface even more, by 10-11°C. ***Sphagnum***, on the other hand, can reach temperatures as much as 10°C above ambient (Longton 1979a), forcing its inhabitants to move further down into the mat. And in the boreal forest at Pinawa, Canada, temperatures in ***Bryum argenteum*** (Figure 28) reached as high as 55°C! (Longton 1979b). It is likely that dark pigments contribute to the warming of bryophyte habitats, even under light snow cover.

Disturbance

Disturbance of bryophyte habitats creates islands that may limit faunal dispersion. Using experiments, Lawton (1999) found that bryophyte islands support all the predictions for isolated micro-arthropod communities. That is, Lawton found that fragmentation would lead to species extinctions, corridors will reduce extinctions, and abundance will decrease in those species that survive.

Hoyle and Gilbert (2004) examined the effects of fragmentation on the microarthropod microcosms in a temperate ecosystem. Earlier evidence had suggested that the species richness and abundance are maintained if moss patches are connected by corridors. While this may be true, Hoyle and Gilbert found that species richness (including microarthropods) actually varies little between landscapes of various sizes and connectivity with other moss landscapes. Furthermore, there seemed to be no differences in responses between predators and non-predators. However, they suggested that corridors might be more important in more extreme environments, such as the Antarctic.

Figure 28. ***Bryum argenteum***. Photo by Michael Lüth, with pernission.

But not all small patches are doomed to extinction of their arthropod fauna. As exhibited by many studies on Antarctic mosses (discussed in a later chapter), new fauna will arrive. This is typically achieved by passive transport (**aerobiology**) for both the bryophytes and their microfauna (Mandrioli & Ariatti 2001). And the smaller arthropods might just hitch a ride on bryophyte fragments.

Role of Life Form

Kinchin (1992) found that acrocarpous cushions house a richer fauna than the more open pleurocarpous mosses. This suggests that moisture-holding capacity of the habitat is an important attribute. For example, at 100% relative humidity, the acrocarpous ***Bryum argenteum*** had a water

content equaling 277% of its dry weight. This contrasted with the pleurocarpous ***Hypnum cupressiforme***, which held 1496% of its weight as water. Whereas ***B. argenteum*** held 85% of its dry weight as soil among its rhizoids, ***Hypnum cupressiforme*** held less than 1%. This soil difference could have contributed to the differences in fauna, but it is more likely that rate of water loss played a more important role. ***Hypnum cupressiforme*** reached steady dryness in 132 hours, whereas ***B. argenteum*** required 180 hours, despite starting at a much lower moisture content. Further support for the moisture hypothesis is provided by ***Tortula muralis*** and ***Grimmia pulvinata***. These mosses have long hair points, most likely contributing to slow drying, and are inhabited by an especially rich fauna. But greater protection from UV light and heat of the sun could also play a role in accounting for the greater number of species within acrocarpous cushions.

Chemical Refuge

More recently, researchers have investigated the role of bryophytes as a chemically defended refuge. Because the bryophytes are well defended by secondary compounds, larger generalist feeders do not consume them. This results in an avoidance of the bryophytes so that they likewise do not consume the smaller invertebrates that live among them. Parker *et al*. (2007) demonstrated that crayfish (***Procambarus spiculifer***, Figure 29) and Canada geese (***Branta canadensis***, Figure 30) selectively consumed ***Podostemum ceratophyllum*** (riverweed, a tracheophyte; Figure 31) in preference over the brook moss ***Fontinalis novae-angliae*** (Figure 36), despite the fact that the moss made up 89% of the total plant biomass. Extracts of the moss demonstrated the presence of a **C18acetylenic acid**, octadeca-9,12-dien-6-ynoic acid, that discouraged feeding by crayfish. Experiments with pellets demonstrated that it was not plant structure that determined which plant was eaten. On the other hand, the moss supported a community of macroinvertebrates twice the size of that on riverweed. By being unpalatable to large carnivores, the moss could provide a refuge for smaller animals, especially arthropods.

Figure 29. ***Procambarus spiculifer***, a crayfish that won't eat ***Fontinalis novae-angliae***. Photo by Josh Geyer through Creative Commons.

The deterrents, as in this case, may not be general deterrents. While crayfish rejected it, the amphipod ***Crangonyx gracilis*** (Figure 32) and isopod ***Asellus aquaticus*** (Figure 33) consumed the moss but not the riverweed. Such chemical defenses thus create enemy-free space for these smaller invertebrates and can influence the community structure.

Figure 30. Canada geese (***Branta canadensis***), a species that avoids eating invertebrates from among ***Fontinalis antipyretica***. Photo by Janice Glime.

Figure 31. ***Podostemum ceratophyllum*** (riverweed), a flowering plant that looks like an overgrown liverwort when it does not have flowers, and that is not avoided by Canada geese as a source for invertebrate food. Photo by Alan Cressler, with pernission.

Figure 32. ***Crangonyx gracilis*** (amphipod). Photo from Discover Life through Creative Commons.

Figure 33. ***Asellus aquaticus*** (isopod). Photo by Morten D. D. Hansen, with pernission.

The study by Parker *et al*. (2007) supported a further advantage of the bryophyte habitat (Figure 34 & Figure 35). The geese were often swept downstream by the rapid water where the bryophytes grew. The smaller invertebrates, however, were able to navigate safely within the protection of the moss, taking advantage of the reduced flow there.

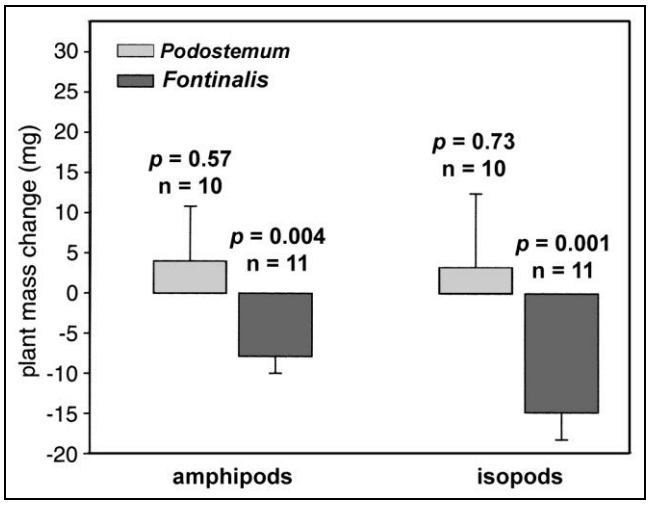

Figure 34. Mean loss or gain (± SE) of plant mass in the moss ***Fontinalis novae-angliae*** vs tracheophyte ***Podostemum ceratophyllum*** due to grazing by amphipods (***Crangonyx gracilis***) and isopods (***Asellus aquaticus***). Probability level indicates whether change in biomass is significantly different from zero when the two plant species were offered individually to amphipods and isopods. Redrawn from Parker *et al*. 2007.

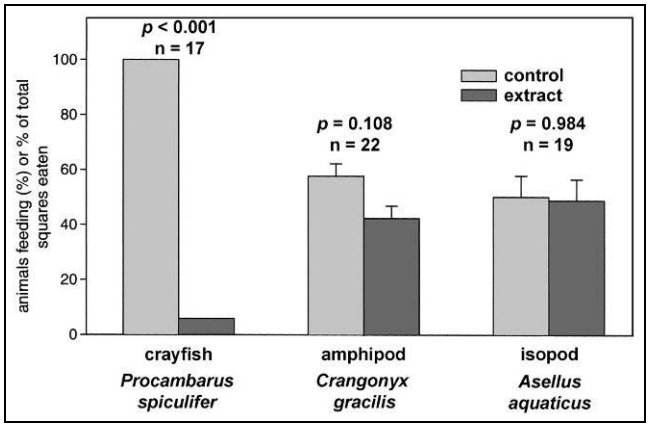

Figure 35. Comparison of feeding by geese on control pellets (freeze-dried, powdered broccoli & lettuce) vs pellets enhanced with crude extracts of the brook moss ***Fontinalis novae-angliae***. Squares refer to number of window screen squares from which pellets were eaten. Redrawn from Parker *et al*. 2007.

Food Value

Despite traditional thinking, terrestrial bryophytes can serve as food for some arthropods (Lawrey 1987). Catching them in the act can be difficult as many of these herbivores are nocturnal (Hribljan 2009). A common pattern of eating seems to be to strip all but the border and costa (Wyatt & Stoneburner 1989, Davidson *et al*. 1990), not unlike insects that skeletonize tree leaves.

Contrary to many statements in the literature about poor nutritional value of mosses (*e.g.* Pakarinen & Vitt 1974; Suren & Winterbourn 1991), Parker *et al*. (2007) found that ***Fontinalis novae-angliae*** (Figure 36) had the highest dry mass, ash-free dry mass, and protein content among the available plants in their study stream at Chattahoochee River National Recreation Area near Atlanta, Georgia, USA.

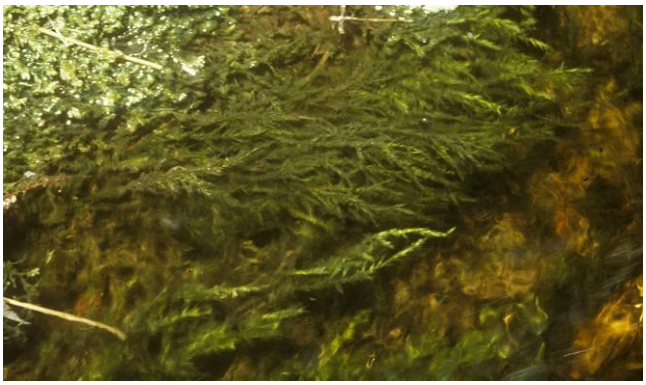

Figure 36. ***Fontinalis novae-angliae***. Photo by Janice Glime.

It is not just aquatic mosses that provide nutrition. Lawrey (1987) provided us with a review of moss and lichen nutritional value for arthropods. He contends that the nutritional composition is similar to that of the tracheophytes, containing the same sugars (Lawrey 1987), but with the addition of some unknown ones in at least some mosses (Maass & Craigie 1964). The caloric content is likewise similar to that of higher plants (Bliss 1962; Forman 1968; Pakarinen & Vitt 1974; Rastorfer 1976). Elemental concentrations are similar (and vary among species), with only potassium and magnesium being at lower levels than in tracheophytes (Prins 1981). Spores have the highest lipid concentrations, resulting in their consumption by some arthropods such as ants (Plitt 1907) and other animals.

Thus, we must ask why there is so little evidence of consumption of bryophytes by arthropods. Lawrey (1987) suggests several explanations. Low digestibility has been suggested several times, in part based on the high ratio of cell wall to cell contents. Furthermore, liverworts are well known for their secondary compounds (Adam & Becker 1994; Adio & König 2005; Veljić *et al*. 2008), and recent studies likewise indicate that other bryophytes, including mosses, are highly endowed with antifeedant secondary compounds as well (Davidson 1988; Mueller & Wolf-Mueller 1991; Frahm & Kirchoff 2002; Asakawa 2005). But it is not just the high ratio of cell walls or the antifeedants that make the bryophytes less digestible. They have lower concentrations of easily digested soluble carbohydrates and hemicelluloses than do tree leaves, and, supporting the cell wall to contents ratio hypothesis, they have higher concentrations of structural components such as cellulose and lignin-like polyphenolic compounds that are not easily digested than do their tracheophyte counterparts (Table 2) (Skre *et al*. 1975; Lawrey 1987).

Lawrey actually compared these components in the moss ***Polytrichastrum*** (=*Polytrichum*) ***ohioense*** (Figure 37-Figure 39) with those of a conifer and angiosperm. My concern with using this study as a basis for understanding bryophyte herbivory is that Polytrichaceae has a more highly structured body plan than most bryophytes and I

suspect its content of lignin-like polyphenolic compounds is greater than that of many kinds of moss. Furthermore, the cuticle, at least in ***Polytrichum commune*** (Figure 40), seems likewise to be more developed than that of many other moss taxa (Proctor 1979), so it may not be representative of the edibility of mosses.

Table 2. Comparison of percentage of structural components of tree leaves and of plants of the moss ***Polytrichastrum*** (=*Polytrichum*) ***ohioense***. From Lawrey 1987.

Litter type	soluble carb	hemi-cellulose	cellulose	"lignin"	ash
Pinus resinosa leaves	35.41	13.44	19.37	23.56	3.68
angiosperm tree leaves	43.89	11.59	20.43	11.04	6.97
Polytrichastrum ohioense	16.51	14.07	24.37	12.90	4.24

Figure 37. ***Polytrichastrum ohioense***. Photo by Bob Klips, with pernission.

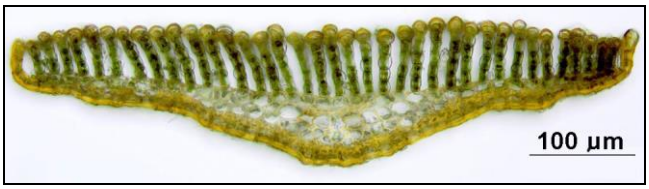

Figure 38. Leaf cross section of ***Polytrichastrum ohioense***, showing the complex structure of the leaf. Photo by Amelia Merced through Duke University Herbarium, with permission.

Figure 39. ***Polytrichastrum ohioense***. Photo by Morgan L. Vis and Kathy Aleric.

Figure 40. ***Polytrichum commune*** showing waxy surface. Photo by James K. Lindsey, with permission.

Not only are the polyphenolic compounds difficult to digest, but they typically have antibiotic activity (*e.g.* Madsen & Pates 1952; Pates & Madsen 1955; Ramaut 1959; McCleary *et al*. 1960; Wolters 1964; McCleary & Walkington 1966; Gupta & Singh 1971; Banerjee & Sen 1979; Asakawa 1990, 2007; Basile *et al*. 1995; Verhoeven & Liefveld 1997; Frahm & Kirchoff 2002). Lawrey (1987) suggests that these antibiotics could affect both palatability and digestion for the arthropods. Since the microflora of the gut aids digestion in a number of arthropods (not many have been examined carefully), antibiotics could kill these important digestive components, to the detriment of the host. Hence, not only would the bryophytes be difficult to digest, but so would other food eaten with them.

But bryophytes can serve as food sources for arthropods indirectly. Their many invertebrate inhabitants (Yanoviak *et al*. 2003, 2006) provide food for birds, especially in the tropics (Nadkarni & Matelson 1989). In discussing the role of lichens in boreal forests, Pettersson *et al*. (1995) suggested that this habitat could be critical for passerine birds in winter, citing the loss of spiders and insects in managed forests compared to natural forests. It is likely that bryophyte communities in many forests serve as a similar refuge of importance during seasons of limited access to arthropods as food.

Bryophytes most likely play a major role in the locations and activity of soil organisms, hence facilitating movement of nutrients through that ecosystem, although little definitive study seems to exist. Organisms such as pillbugs migrate downward in the daytime and back up at night, feeding on the mosses, then returning downward where their feces ultimately rest (Hribljan 2009). This results in cycling of nutrients from one location to another, undoubtedly causing these recycled nutrients to reach the soil more easily. It is likely that insects and other invertebrates actually retreat into the soil to escape predation, desiccation, and UV light, then venture upward into moss mats at night to forage. In some cases, mosses may be essential as part of the habitat. They therefore contribute, through these migrant invertebrates, to aeration, nutrient movement, biodiversity, and water movement in the soil. While this role is an intriguing notion for soil properties and nutrients, its importance needs to be tested.

Collection and Extraction Techniques

When I first tried to publish my doctoral work on insects associated with stream mosses, I listed numbers like 12,064 Chironomidae per gram of moss. The reviewer wanted to know how I had developed these numbers because I "obviously had not counted them." But I did!

The variety of invertebrates makes a single technique impractical – and biased. The 6 or more legs of arthropods easily get caught on the stems and leaves. Mine were necessarily preserved because I would have a collecting day and come back with 30-40 collections of mosses that needed to have arthropods removed. I had no way to provide the cold, oxygenated water they required to stay alive, and many of them would disintegrate quickly once dead. In fact, many insects release enzymes when their cells die that cause the cells to break down quickly, a process known as **autolysis**.

Collection

One problem one must face during collection is the loss of organisms during the collection. Borcard (1986) used a cylindrical sampler mounted on a hand drill to make a core of ***Sphagnum*** for collecting mites. These samples were not deformed or compressed and thus provided uniform samples suitable for statistical comparisons.

For epiphyte dwellers, particularly in the tropics, insecticide fogging (**Pyrethrin** insecticide) is commonly used for arthropods (Yanoviak *et al*. 2003), but this method is often not effective for arthropods that hide in crevices, tree holes, humus pockets, and epiphytes, including bryophytes. Instead, most of the bryophyte inhabitants are trapped within the mats. The smaller of these arthropods are the least likely to be knocked down by fogging. Mites, in particular, are missed when the fogging method is used for sampling.

Loss of organisms could be especially problematic in streams where the escapees are quickly washed downstream. On the other hand, these stream bryophyte-dwelling organisms are adapted to clinging to the bryophytes against the drag of stream flow, so it appears that few escape. I tested this occasionally during my own research by putting a collection net downstream as I used hand grabs to sample. Few organisms, compared to the large number present, actually escaped, so I abandoned the downstream nets.

Suren (1993) was more cautious in his mountain stream sampling. He placed a **Surber sampler** (area =10x10 cm, 100 µm mesh) (Figure 41) around the bryophyte clump to be sampled. A Surber sampler has a square frame that must be placed on the bottom of the stream, and a net extends downstream from that, usually about 50 cm or more. Suren used a razor blade to dislodge the bryophytes, but one could use a knife or scalpel. I used my hands – fortunately, I have strong fingernails. Its disadvantage is that it is often difficult to make the entire frame touch the substrate, and the stream may be too deep to reach from substrate to surface, hence permitting some organisms to float away and others to escape along the bottom. It is, perhaps, better than a simple hand grab, except that one can clasp the hand around the mosses, seemingly preventing many escapes.

Figure 41. Surber sampler, showing the investigator removing a rock from the sampling area. The opening of the net faces upstream and the net catches organisms dislodged during sampling. Photo by Ray Drenner, with permission.

A modification of Suren's method is to use a screen with handles. This device usually has a wooden support or pole on each end with the mesh extended between them. The base is placed as snuggly as possible against the stream substrate and bryophytes are dislodged to flow into the screen. The ones I have used are made of metal window screening, giving them rigidity, but perhaps one with a fine cloth mesh would work, permitting a closer fit around rocks in the streambed and capturing smaller organisms. The big disadvantage of the window screening is that the mesh size is large enough for mites and others of the smallest organisms to go right through the mesh, creating a sampling bias toward larger organisms. Furthermore, for collecting bryophyte communities, both the screening and fine cloth mesh samplers would require two people, one to hold the device and one to dislodge the moss.

Extraction

There are extraction techniques that are usable to get estimates of various groups if you are willing to live with their biases. The Winkler technique is still useful (Nadkarni & Longino 1990), but relies on the movement of the arthropods away from heat or light, thus creating a bias against less mobile organisms. Trägårdh (1929) recognized the limitations of this method to small soil invertebrates such as mites that are sensitive to evaporation. He found that if the moss dries too quickly they are likely to die before they can escape the heat. Instead, he chose to use a warm water funnel such at that used by chemists to filter colloidal matter. He covered this with sieves of different mesh sizes, depending on the material to be sampled.

Andrew and Rodgerson (1999) used multiple extraction techniques to sample small invertebrates living among bryophytes in Tasmania. They used Tullgren Funnels and sugar flotation (Pask & Costa 1971), but also tried a new method using kerosene phase separation (Andrew & Rodgerson 1999). They determined that the phase separation freed more total individuals and more **Acari** (mites) and **Collembola** (springtails) in particular. The technique works because the kerosene attaches to the cuticles of insects, causing the insects to float. Their procedure is to "pickle" the insects and their moss housing for two weeks in 95% ethanol. This mix is then put into a

test tube, filling it to 3/4 full. This is topped off with 1 cm of kerosene and shaken vigorously until the solutions are fully mixed. After the mix settles for 10-15 minutes, the tube is rolled to release trapped bubbles from the sides and bottom. The insects and other arthropods collect on the interface between the alcohol and kerosene. The kerosene must be removed with a pipette, then the remaining kerosene plus interface can be removed. To get the arthropods from the sides of the test tube, they washed the sides with 95% ethanol and repipetted to collect the arthropods. The entire process should be repeated to increase the efficiency (about 16% more). A fume hood should be used to examine the organisms safely. Brantley and Shepherd (2004) used heptane flotation to avoid the desiccation problems caused by alcohol and other flotation media.

Taxonomic Difficulties

Bryologists are very familiar with the difficulties of making determinations in the field. The myriad of arthropod species creates even greater taxonomic problems, particularly when dealing with the tiny organisms living among bryophytes. It is rare to find a person with taxonomic expertise in both groups (spanning two kingdoms!), and within the huge group of arthropods, scientists typically are experts in only one class or for insects, only one order. In 1996, Walter *et al*. estimated that the 45,000 species described represented only 5% of the number of species actually **extant**. Among those 95% of undescribed, unnamed species, the bryophyte dwellers may represent an even higher percentage of undescribed members. Instead, crop and other economic pests are usually the first taxa to be investigated.

Such taxonomic challenges explain in large part the lack of detailed information about the faunal arthropod communities among bryophytes. Facing this challenge, Oliver and Beattie (1993) suggested another method that would permit an assessment of biodiversity without requiring taxonomic expertise, large expenditures of time, or high cost. They compared the estimates of species richness (number of species) made by both experts and technicians. The technicians were trained for only a few hours so that they could separate organisms into **recognizable taxon units (RTUs).**

Using the same sampling methods, the specialists for each taxonomic group of spiders, ants, polychaetes, and mosses identified and separated the taxa to species (Oliver & Beattie 1993). Interestingly, for the three animal groups the experts determined there to be 147 taxa, whereas the technicians separated their organisms into 165 groups. Among the ants and spiders, the technicians had an error rate of 13% or less. When 13 undergraduate students repeated the procedure, the average error was only 14.4%. Some of the differences arose from splitting or lumping by the experts – taxonomic concepts that will continue to plague the ecologists trying to describe ecosystems and communicate their findings. It seems that the results for mosses were more difficult to interpret. The results in numbers had greater similarity between experts and technicians, but splitting and lumping of taxa made the comparisons more difficult.

Such methods as that of Oliver and Beattie (1993) are useful for rapid assessment of biodiversity, but they do not tell us about community shifts. When comparing two ecosystems, the composition of the species may tell us more than the numbers of species. Further problems arise due to differences in sexes and juvenile vs adult life forms, perhaps accounting for some of the greater diversity reported by the technicians. We have thus far no reason to expect that these age and sex-related within-species morphological differences are habitat related, and they do have significance in assessing functional groups. On the other hand, as we will see for amphibian taxa, various color morphs of adults can indeed relate to habitat and niche differences. Technicians are not likely to be aware of these variations, and even the experts disagree over whether to consider some of them to be different species.

Summary

Bryophytes form a habitat for many kinds of arthropods. They serve this function well by providing moisture, cover, protection from UV exposure, temperature modification, and a habitat for smaller invertebrates that serve as food. Even the soil habitat is enhanced when covered by bryophytes. They provide a refuge under some conditions and are suitable egg-laying sites for some arthropods, but are unsuitable for habitation at others. In winter they provide insulation and protection. In their role as a habitat or a refuge, they can greatly enhance species richness. This amplifies the food source for predators such as birds.

Despite the presence of secondary compounds (antifeedants, antibiotics) in many bryophytes, some still serve as food and are able to contribute protein and dry mass. Smaller organisms living there serve as food items, and the fauna serve as nutrient cyclers, moving nutrients back toward the soil.

The arthropods often form gradations of communities from soil to treetops, with mosses being present in each of those habitat zones. These ranges reflect differences in temperature, light, and humidity preferences. Disturbance of the epiphytic communities can impact food sources for non-migrating birds, especially in winter.

In dry habitats such as prairies, mosses in cryptogamic crusts provide a refuge from the sun and desiccation. These arthropods in turn contribute to soil nutrient cycling.

In streams bryophytes provide a safe site against predators that don't like the taste of the bryophytes, but these bryophytes are also a safe site against the rapid flow of streams and rivers. Furthermore, they provide this habitat during winter when tracheophytes disappear from the streams. They furthermore increase surface area that collects periphyton and detritus, suitable food sources for many arthropods, a role most likely much more important than the role of the bryophyte itself as a food source.

Sphagnum sites are particularly rich in species, sometimes having double the number of species found in forested areas. Lycosids are common. Spiders have unique niches within the peatlands and often characterize biotopes there. Nevertheless, the low *p*H and need for basic compounds to harden the cuticle make the peatlands inhospitable for many taxa.

In the Antarctic, water content in and under bryophyte cover is important, but in some cases the bryophytes are important for providing suitable temperatures. This can be especially important for overwintering of eggs and larvae, as well as some adults. Nevertheless, higher altitudes in New Zealand do not seem to influence species richness.

Bryophytes in many habitats can provide refuge from the heat of summer, but upper layers of mosses such as ***Sphagnum*** or ***Bryum argenteum*** can reach temperatures 10°C or more above ambient. A further protection by bryophytes is the chemical defense that discourages larger predators and protects the microarthropods hiding among the bryophytes.

Disturbance and fragmentation seems to have little effect on the microarthropod fauna remaining in the bryophyte islands. Recolonization can occur by passive transport.

Acrocarpous cushions can house more arthropods than pleurocarpous mosses, perhaps due to greater moisture-holding capacity in the former. But cushions also hold much more soil. And cushions generally afford more protection from UV light and heat of the sun.

Secondary compounds that prevent herbivory may also defend the small inhabitants living among the bryophytes. Crayfish and Canada Geese tend to avoid feeding on bryophyte inhabitants.

Collecting and extracting is somewhat problematic because not all arthropods can be collected and extracted by the same techniques. Collection includes fogging, hand grabs, Surber samplers, and kick nets. One can accomplish extraction with a Tullgren funnel, sugar flotation, or kerosene phase separation, as well as hand picking. Once the arthropods are extracted, the difficult task of identification begins. For purposes of assessing diversity, morphotypes will suffice, but for comparing actual community composition, species names are important.

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CHAPTER 7-2
ARTHROPODS: ARACHNIDA – SPIDER BIOLOGY

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Figure 1. ***Arctosa*** *cf*. ***alpigena*** female on moss, showing disruptive coloration that makes it more difficult to see. It has been reported from mosses in more than one study (Harvey *et al.* 2002; Almquist 2005). Photo by Walter Pfliegler, with permission.

SUBPHYLUM CHELICERATA

The subphylum **Chelicerata** includes the spiders and mites, both having members associated with bryophytes. Both spiders and mites are in the class **Arachnida**, along with scorpions, harvestmen, ticks, and Solifugae. The **Chelicerata** are characterized by four pairs of walking legs, a pair of chelicerae, and a pair of pedipalps. Although the arachnids are not as small as many of the organisms in preceding chapters, many are small enough that the bryophytes still provide sufficient space for many of these taxa to navigate easily among the stems and leaves. Hence, we should expect to find the bryophytes to be a suitable habitat for a number of these.

Following the concept of a niche, bryophytes can provide a number of important "resources" for arachnids. The most obvious of these are shelter and protection. With **disruptive coloration** on their backs, spiders and other small arachnids can hide among the bryophytes undetected by would-be predators such as birds. This shelter may provide a safe site when an arachnid is being chased or provide a protected niche for an egg case during incubation. The protection also extends to anchorage and shelter from wind, diffusion of raindrops (avoiding the impact of a free-fallen drop), temperature buffering, and retention of humidity. Further possibilities include having

a place to lie in wait for a walking meal to meander by, or perhaps even eating the bryophyte itself, a menu item that is poorly documented (and unlikely) for spiders.

But bryophytes may also extend their benefits to those arachnids not living among the branches. Bryophytes help to keep the soil beneath humid, soft, and pliable for longer periods than that experienced by bare soil. They permit an arachnid to emerge from a burrow and look around while remaining hidden beneath a canopy of loose bryophytes. Even those arachnids traversing the surface of bryophytes may benefit from the disruptive coloring of mosses that make the disruptive colors of arachnid backs less conspicuous. Or they may simply add a place where humidity is greater, helping arachnids to travel greater distances before risk of drying. And who knows if these arachnids might take advantage of the early morning dew captured by bryophyte leaves to gain a drink of water.

With all these possibilities, we would expect some arthropods to have distinct adaptations to that bryophytic habitat. Indeed some do, but I feel certain many stories remain to be discovered.

Class Arachnida

The arachnids include the spiders (order **Araneae**), mites (subclass **Acarina**), ticks (subclass **Acarina**), and harvestman or daddy-long-legs (order **Opiliones**). These are creatures that somewhat resemble insects, but as adults they have eight legs. They have one or two main body regions, not three as in insects. Among these, the mites are fairly common residents in moss clones. Although the other arachnids are not very common among bryophytes, there are, nevertheless, some interesting stories about all of these inhabitant groups.

Arachnid Trapping Limitations

Little quantitative work exists for any arachnids except that for the moss-dwelling mites. One limitation that might suggest that bryophytes are unimportant is the typical sampling method used for forest floor arthropods, including arachnids. Pitfall traps are typically used for those arthropods that are active above the surface during some part of the 24-hour cycle (Curtis 1980). But if arthropods spend most of their time within the bryophyte mat rather than on the surface, they are not likely to fall into such traps.

Curtis found that responses of spider species to four pitfall trapping methods differed, causing distortions in the community species frequency curves. Hence, we should expect even greater differences among a wider range of methods. For example, Komposch (2000) studied the spiders in wetlands of Austria using pitfall traps, light traps, soil sifters, and hand collections. As will be seen in studies cited in this chapter, this broader set of methods gets better representation of groups like the **Linyphiidae**, a very species-rich family of small spiders with many species living among bryophytes.

Pitfall traps are sunken into the ground with water or other liquid to trap the fallen arthropods. The top is covered with a wide mesh screen to keep out debris and possesses a second raised cover to keep rain out. The container can be simple, like a cereal bowl (Figure 2) or can (Figure 3). Although bait is shown in the diagrams, it is not necessary and may introduce a bias if the study is quantitative.

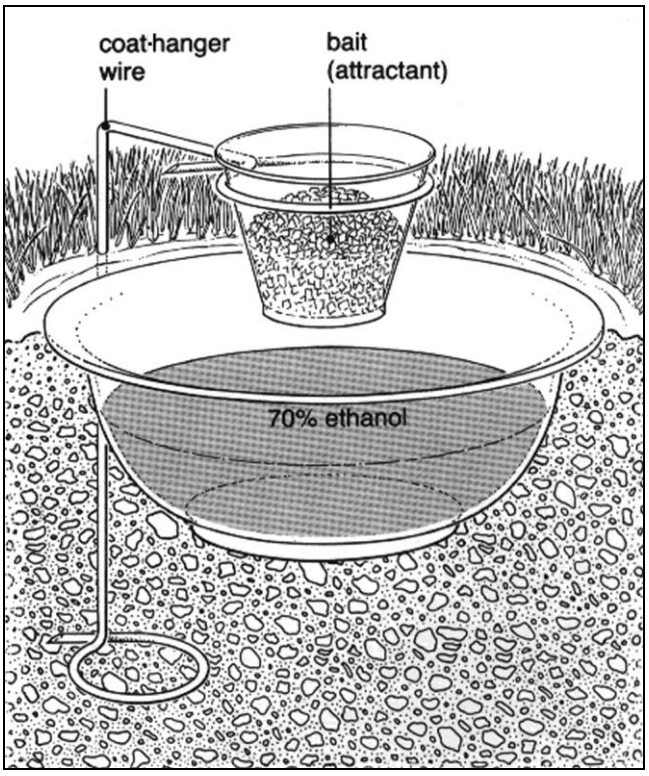

Figure 2. Pitfall trap with cereal bowl holding alcohol. The bait will bring the organisms to the trap, but most will fall into the alcohol before reaching the wire that gives them access. Drawing from USDA website.

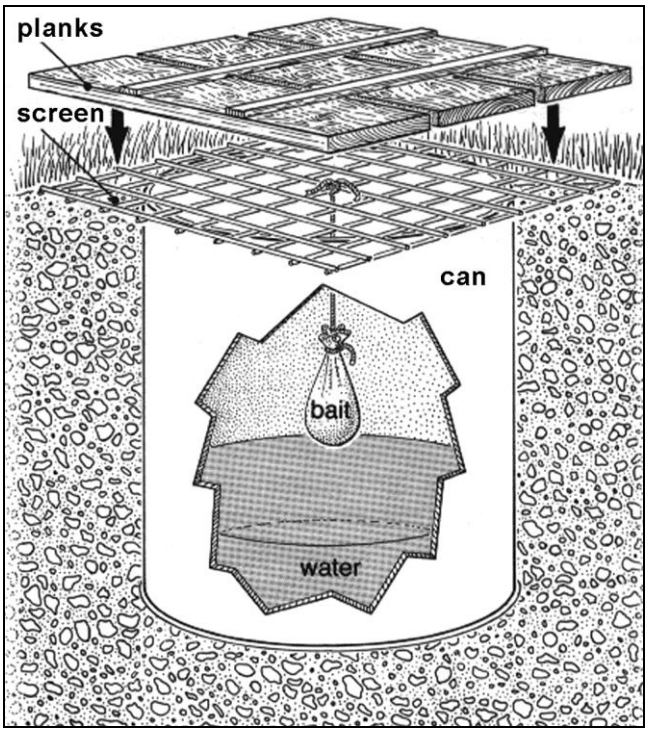

Figure 3. Pitfall trap using a can with water to trap arthropods. Drawing from USDA website.

In the tropics, fogging with pesticides (Pyrethrin) can reveal a number of canopy arthropod fauna. However,

most of the bryophyte dwellers remain trapped within the bryophyte clumps (Yanoviak *et al*. 2003). The smaller ones, like the **Linyphiidae,** are the least likely to drop from the canopy into the collecting containers, giving a biased representation of the community and even missing some species entirely.

Such trapping limitations tend to limit the habitat descriptions of spider fauna. For example, Koponen (1999) described the fauna of the Finnish taiga, but only mentioned the mosses ***Pleurozium schreberi***, ***Dicranum***, and ***Hylocomium splendens*** as the dominant ground cover without relating the spider locations to them.

Sieving might be a somewhat better technique for bryophyte dwellers, but for many species that live among the branches of the mosses, only hand picking is likely to uncover some of the species sufficiently to represent their abundance. We need to examine the efficacy of typical trapping and other sampling methods on enumeration of bryophyte-dwelling arthropods.

Order Araneae – Spiders

"Once upon a time Anansi the Spider was walking, walking, walking through the forest when something caught his eye. It was a strange moss-covered rock. "How interesting!" Anansi said. "Isn't this a strange moss-covered rock!" (Kimmel 1988).

Kimmel (1988) uses mosses and a spider to build a children's story. In this story, a spider uses "strange moss-covered rock" to trick the other animals, but Little Bush Deer decides the spider needs to learn a lesson.

Spiders in nature use mosses to provide cover and camouflage against predation. Rocks with mosses are indeed interesting, although not quite in the way of trickery that Anansi used them. They house many kinds of arthropods, spiders among them.

Nomenclature for spiders follows Platnick (2000-2013).

Spider Biology

There are approximately 40,000 species of spiders in the world (Wikipedia 2012a; InsectIdentification 2013). Spiders are 8-legged creatures that have chitinous coverings and two body regions, the **cephalothorax** (head and thorax as one external unit) and abdomen. Unlike the insects, they lack antennae. Instead, they have various hairs that penetrate their chitinous covering (Wikipedia 2010d). Some of these may be sensitive to the slightest movement, such as that of wind. Others are sensitive to chemicals, thus achieving the role of insect antennae and our noses and tongues.

The legs originate on the underside of the cephalothorax. Instead of muscles, they use hydraulic pressure to extend their legs, although they have muscles to flex them. This explains why dead spiders always have the legs drawn in – no pressure to extend them. And any puncture to the chitin of the cephalothorax causes loss of water pressure and certain death.

Spiders have chelicerae (claws) with fangs that they use to inject venom into their forthcoming dinner. Most of these poisons are not serious dangers for humans, although they can cause itching or painful swelling locally. Only one herbivorous spider is known (Meehan *et al*. 2009), all others being predators. Therefore, we should not expect them to consume bryophytes.

Spiders excrete uric acid, a very concentrated form of nitrogen waste, thus permitting them to conserve water for long periods of time. This reduction of need for water may help to explain their reticence to live among mosses where humidity is often high, but there are at least some spiders that live in the water, so one would expect some to be adapted to the higher humidity of bryophytes in other habitats.

While bogs probably host the majority of spider species associated with bryophytes, many spiders live among bryophytes also in drier habitats. Humid forests are often rich in bryophytes. But dry habitats such as coastal dunes may also have a high coverage of bryophytes serving as habitats for spiders, even though these bryophytes are dried up much of the time.

Although at times the Linyphiidae may be somewhat numerous, in other cases spiders are a minor component of the bryophyte habitat. In the epiphyte mats of Costa Rican cloud forests, where bryophytes are only one component, Yanoviak *et al*. (2007) found spiders among the lowest in representation among 10 groups of arthropods, occupying about 1% of the fauna in the cloud forests in the wet season and 1-2% in the dry season.

Growth Forms and Life Forms

Bryophytes are often lumped together as if they are all the same to their animal communities, but growth and life forms can make quite a difference to the living space within. Gimingham and Birse (1957) related growth form response to decreasing levels of moisture, from dendroid and thalloid mats in high moisture to short turfs and cushions in low moisture. Vilde (1991) showed that differences in life form can reduce evaporative rate by 5.3-46 times, depending on the species and site conditions.

The two terms of **life form** and **growth form** have been confused in the literature (La Farge 1996), as discussed in Chapter 4-5. To reiterate briefly here, **growth** form is a purely morphological term and although genetically determined, it can be modified by the environment, as opposed to **life form**, which is more encompassing and describes the result of life conditions, including growth form, influence of environment, and assemblage of individuals (Warming 1896; Mägdefrau 1982). La Farge-England (pers. comm. 1996) sums it up by stating that **life form** is the **assemblage** of individual shoots, branching pattern, and directions of growth as modified by the habitat, whereas **growth form** is a property of an **individual**, the structures of the shoots, direction of growth, length, frequency and position of branches.

Mägdefrau (1969) defined the following **life forms**, to which I have added examples and habitats:

annuals: ***Phascum***, ***Riccia*** – disturbed habitats
short turf: ***Trichostomum brachydontium***, ***Barbula*** – epiphytes; tundra
tail: ***Prionodon densus***, ***Leucodon***
cushion: ***Leucobryum*** – deciduous & conifer forests; epiphytes; alpine; desert
mat: ***Hypnum***; ***Plagiothecium*** – moist forests; conifer forests; epiphytes; alpine; tundra
fan: ***Neckeropsis*** – humid tropical forests; epiphytes
tall turf: ***Dicranum*** spp.; ***Polytrichum*** – conifer forests; alpine; tundra

weft: ***Hylocomium***, ***Pleurozium*** – conifer & deciduous forests; desert; alpine; tundra
dendroid: ***Climacium***, ***Hypnodendron*** -
pendant: **Meteoriaceae** – humid tropical forests; epiphytes

Sphagnum does not fit well into these categories because of its loose interior with an expanded apex. It perhaps most closely fits into the tall turf.

A comparison of these categories as spider habitats may provide interesting relationships. However, few studies address the moisture benefits of various life forms to the bryophytes and none seem to address this question experimentally for the spiders. Therefore, we can only theorize. Life forms will be mentioned occasionally throughout this chapter, but they should be viewed with some caution because the vocabulary used seems to be primarily confined to mat vs cushion.

Bryophytes as Cover

As early as 1896, Banks recognized the importance of mosses for spiders, including the **Linyphiidae** ***Eridantes*** (as *Lophocarenum*) ***erigonoides***, ***Islandiana flaveola*** (as *Tmeticus flaveolus*), and ***Scylaceus*** (as *Tmeticus*) ***pallidus*** in moss on Long Island, NY, USA. Bryophytes form important cover for many kinds of spiders. Es'kov (1981) found that an abundant moss cover is important for spider populations in the Russian taiga; Vilbaste (1981) likewise found spider fauna in mires of Estonia. Diverse invertebrate bryophyte communities similar to those found in the soil are common in the tundra (Chernov 1964), so it is possible that the bryophyte habitat is an important feeding area for spiders there. Bonte *et al*. (2003) found a significant correlation between spiders and moss cover in the coastal grey dunes along the North Sea. Larrivée *et al*. (2005) found a correlation between spiders and moss/lichen cover in burned areas, but not in clearcut areas, suggesting that the two types of deforestation elicit very different responses from the spider populations.

Pearce *et al*. (2004) compared the microhabitats of spiders in boreal forests of northwestern Ontario, Canada. They found that among the four stand types, spiders did not view mosses as simply mosses. Rather, ***Agyneta olivacea*** (see Figure 4; **Linyphiidae**) and ***Pardosa uintana*** (see Figure 22; **Lycosidae**) occupied microhabitats associated with feather mosses (wefts; Figure 5) rather than those of ***Sphagnum*** (tall turf; Figure 6), suggesting the possibility that life or growth form may be important.

Figure 4. Male ***Agyneta ramosa*** on a moss, giving one an idea of its small size. Photo by Jørgen Lissner, with permission.

Figure 5. ***Hylocomium splendens***, a weft-forming feather moss. Photo by Michael Lüth, with permission.

Figure 6. ***Sphagnum russowii***, where a variety of spiders might take advantage of the humidity. Photo by Michael Lüth, with permission.

Among the few studies to consider the bryophyte habitat specifically, that of Biström and Pajunen (1989) compares the fauna in two forest locations in southern Finland. In these forests, they considered the fauna on ***Polytrichum commune*** (Figure 7) and several species of ***Sphagnum*** (Figure 6). They found seven generalist spiders, all **Linyphiidae** [***Centromerus arcanus*** (Figure 16), ***Dicymbium tibiale*** (Figure 8), ***Semljicola faustus*** (as *Latithorax faustus*; Figure 9), ***Lepthyphantes alacris*** (Figure 10), ***Minyriolus pusillus*** (Figure 11-Figure 12), ***Tapinocyba pallens*** (Figure 13), and ***Walckenaeria cuspidata*** (Figure 14)], that occurred with these mosses at all five of the main collecting sites during the May to October collecting season.

Figure 7. ***Polytrichum commune***, a moss with a measureable cuticle. Photo by Des Callaghan, with permission.

Figure 8. ***Dicymbium tibiale*** on mosses. Photo by Jørgen Lissner, with permission.

Figure 9. ***Semljicola faustus*** female. Photo by Jørgen Lissner, with permission.

Figure 10. ***Lepthyphantes alacris***, one of the common spiders associated with bryophytes in forests of Finland. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 11. ***Minyriolus pusillus*** male on mosses. Photo by Jørgen Lissner, with permission.

Figure 12. ***Minyriolus pusillus*** male on ***Polytrichum***, a small generalist spider that is common among forest mosses of Finland. Photo by Jørgen Lissner, with permission.

Figure 13. ***Tapinocyba pallens*** male on moss. Photo by Jørgen Lissner, with permission.

Figure 14. ***Walckenaeria cuspidata*** female on moss. Photo by Jørgen Lissner, with permission.

Drozd *et al*. (2009) sampled under moss "cushions" and in litter, obtaining 55,000 invertebrate specimens. They found that the arthropod association, including spiders, reflects interaction between presence of mosses (***Polytrichum commune***, ***Polytrichastrum formosum***, ***Sphagnum teres***, ***Bazzania trilobata***, ***Pleurozium schreberi***, ***Eurhynchium angustirete***, ***Oligotrichum hercynicum***) and other features of the microhabitat. Moss presence, moss species, and moisture are very important characters for both total arthropod abundance and abundance of various arthropod groups. On the other hand,

the total arthropod abundance and that of most groups is actually higher in the litter than in moss cushions (p = 0.0003). Although the surface activity is considerable, the dense moss cushion prevents them from moving effectively or with due speed. Hence the larger arthropod taxa avoid the dense interior by staying on the surface.

Trampling

Few studies on trampling effects on bryophytes or on spiders exist. Nevertheless, one can imagine that anything that squashes the spaces where spiders move about in search of food would have a negative impact on the spider community. Duffey (1975) studied the effects of trampling on invertebrates in grassland litter and found that the air space dropped from 63% to 38% as a result of 10 treads per month. Although there was little difference in the invertebrate fauna between two levels of trampling, there was significant reduction in the spider fauna. Furthermore, spiders were sensitive at a much lower trampling level than the vegetation itself. It is possible that spiders living among bryophytes would suffer similarly from compaction. On the other hand, it could be that the bryophytes would spring back, offering patches of refuge following trampling of other vegetation. This would make an interesting study.

Abundance, Richness, and Specificity

Quantitative studies are not as common as species richness studies, but one can, nevertheless, find a number of studies with species numbers. For our purposes, however, it is difficult to identify which of those species is associated directly with bryophytes rather than just occurring in a habitat that has bryophytes.

In the study by Biström and Pajunen (1989) in two forest locations in southern Finland, there were 23 species that occurred in at least one of the main sites with a density of at least one individual per square meter. At Borgå they found approximately 57 species associated with ***Polytrichum commune*** (Figure 7), some of which were juveniles and could not be identified to species. In association with ***Sphagnum girgensohnii*** (Figure 15) they found only 43 species. ***Centromerus arcanus*** (Figure 16) and **Erigoninae** juveniles were among the most abundant at both sites. The most abundant of bryophyte-associated species, ***Centromerus arcanus*** (Figure 16), is only 1.5-2.6 mm long (Roberts 1987) and exhibited mean densities of 8.7-24.4 individuals per square meter (Biström & Pajunen 1989). Somewhat less abundant were ***Dicymbium tibiale*** (1.8-11.9 mm; Figure 8) and ***Lepthyphantes alacris*** (0.7-2.0 mm; Figure 10).

Figure 15. ***Sphagnum girgensohnii***, a common woodland species. Photo by Michael Lüth, with permission.

Figure 16. ***Centromerus arcanus***, the most abundant spider associated with ***Sphagnum*** in a Finish study. Photo by Jørgen Lissner, with permission.

I found the greater number of species associated with ***Polytrichum commune*** (Figure 7) (Biström & Pajunen 1989) to be somewhat surprising because the ***Polytrichum*** species do not have the high moisture-holding capacity available with species of ***Sphagnum*** (Figure 15). Perhaps the ***Polytrichum commune*** is too dry for some spiders, as suggested by the moisture data of Biström and Pajunen (1989), but for others some of the wetter mosses are less desirable. Too much water can affect the ability to exchange gasses through the tiny spider tracheae, causing the spiders to drown. ***Polytrichum commune*** provides a high spot out of the wet environment. It would be interesting to monitor the behavior of the spiders as water levels change in the bog and fen ecosystems. Such moisture and morphological differences are not exclusionary for most of the generalist spiders, but may be of importance in the distributions of rarer species.

I also wonder which of these mosses provides a habitat where maneuverability is greater. It would appear to me that it would be easier to move among ***Sphagnum*** stems (Figure 15) than among those of ***Polytrichum commune*** (Figure 7), but perhaps the spider does not perceive it that way. It would be interesting to experiment with the environmental variables vs the morphological characters that differ among these species to see just what factors are important to the location of the spiders. One must also consider the possibility of sampling bias. Although the sieve technique used by the researchers in this study seems to be the most appropriate for bryophytes, it may have differed in effectiveness between moss genera.

No spider species seemed to be especially abundant on just one bryophyte species and rare on the others, suggesting that they either had relatively wide tolerances for the conditions available or that they were sufficiently mobile to be found in the range of species locations due to transit between preferred sites. For example, some species of the **Linyphiidae** subfamily **Erigoninae** may be numerous in an area one day and gone the next (Wikipedia 2010b). This lack of specificity is consistent with observations by Graves and Graves (1969) in North Carolina, USA. They found no habitat specificity for the spiders among mosses, fungi, *Rhododendron* leaf litter, and other microhabitats.

Isaia *et al.* (2009) present us with a very useful study from the Abruzzo Apennines in Central Italy. They used a Berlese apparatus to extract spiders from "wet" mosses.

Not surprisingly, the **Linyphiidae** were the most prominent family. This is a large family of tiny spiders and was represented by 22 of the 38 species.

In all, Isaia and coworkers (2009) found 494 spiders among wet mosses from the Apennines in Central Italy, representing 38 species in 36 genera and 14 families, an interesting distribution where lack of multiple species in the same genus suggests niche separation. Some were more generalists, occurring in mosses and elsewhere [***Robertus lividus*** (Figure 17-Figure 18; **Theridiidae**), ***Caracladus leberti*** (**Linyphiidae**), ***Diplocephalus arnoi*** (*cf.* Figure 19; **Linyphiidae**), and ***Antistea elegans*** (Figure 20; **Hahniidae**)]. Juveniles of ***Lepthyphantes*** (Figure 10), ***Parachtes***, ***Cryphoeca*** (Figure 21), ***Pardosa*** (Figure 22), ***Pirata*** (Figure 23), and ***Xysticus*** (Figure 24), all rather common genera, likewise included the mosses among their habitats.

Figure 17. ***Robertus lividus*** female on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 18. ***Robertus lividus***. Photo by Trevor & Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 19. ***Diplocephalus latifrons*** male on moss, a spider sometimes associated with bryophytes. Photo by Jørgen Lissner, with permission.

Figure 20. ***Antistea elegans***, a known moss dweller. Photo by Jørgen Lissner, with permission.

Figure 21. ***Cryphoeca silvicola***, a species whose young have been found among mosses in the Abruzzo Apennines of Central Italy (Isaia *et al*. 2009). Photo by Glenn Halvor Morka, with permission.

Figure 22. ***Pardosa monticola***, representing a genus with moss-dwelling members. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 23. ***Pirata piraticus***, a moss-dwelling spider. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 24. ***Xysticus cristatus*** (ground crab spiders), member of a genus known from mosses. Photo by Trevor & Dilys Pendleton <www.eakringbirds.com>, with permission.

Parachtes siculus (**Dysderidae**) prefers wet places, so mosses proved to be a suitable place for this species (Isaia *et al*. 2009). Not surprisingly, they found a new species of **Linyphiidae** (***Diplocephalus arnoi***) from wet mosses, with 96 out of 103 specimens from mosses associated with the film of water on rocks (**petrimadicolous** mosses). ***Mecopisthes latinus*** (**Linyphiidae**) also occurred among these mosses. The **Hahniidae** in wet mosses were represented by ***Antistea elegans*** (Figure 20), the most abundant, followed by immature members of ***Cryphoeca*** (Figure 21). One male of ***Cryphoeca silvicola*** (Figure 21) could be identified, and one male of ***Hahnia ononidum*** (Figure 25), known elsewhere from mosses, as well as ***Ozyptila claveata*** (or possibly ***O. trux***?) (see Figure 26; **Thomisidae**) from wet mosses. This small number of males may be an artifact due to their smaller size and greater difficulty of finding them.

Figure 25. ***Hahnia ononidum*** female. Photo by Glenn Halvor Morka, with permission.

Figure 26. ***Ozyptila trux*** on ***Plagiomnium*** sp. This genus is sometimes represented on or among wet mosses. Photo by Glenn Halvor Morka, with permission.

Moisture Relationships

Many spiders are particularly prone to desiccation, whereas some species from arid climates are able to survive without water for months and even years. Entling et al. (2007) found that spider β-diversity was strikingly higher in open habitats than in forests, suggesting that they have either behavioral or physiological means to protect them from desiccation. Many spiders are night-active, permitting them to enter more exposed areas without the danger of desiccation from daytime sun. Anyone who has put a living spider in a jar knows that spiders easily dehydrate, leading to their death. Their legs contract due to the loss of hydrostatic pressure.

But in a study of five species of spiders from various habitats, Vollmer and MacMahon (1974) could find no relationship with habitat. Likewise, Gajdo and Toft (2000), using pitfall traps, found no relationship between epigeic spiders and moisture in a heathland-marsh gradient in Denmark. In the latter case, the habitat ranged from 100% cover of mosses to near zero.

Rather, body size seemed to be a better determinant of the rate of water loss (Vollmer & MacMahon 1974), with small spiders losing moisture more rapidly due to their larger surface area to volume ratio. This water loss leads to reduced survivorship in smaller individuals (Vincent 1993).

One adaptation for survival of these small species and individuals is behavioral – living among bryophytes or taking periodic refuge there. As will be seen in many of the examples in this chapter, bryophyte-dwelling spiders are frequently small.

On the other hand, the critical activity point does correlate with the moisture of the habitat (Vollmer & MacMahon 1974), suggesting that bryophytes may permit spiders, especially small ones, to be more active.

Nonetheless, DeVito *et al*. (2004) found that within the spider genus ***Pardosa***, distribution did indeed follow a moisture gradient related to a stream. But even these were not restricted by proximity to the shoreline. Bruun and Toft (2004) were able to demonstrate a moisture gradient in two Danish peat bogs, with ***Pardosa sphagnicola*** (Figure 27-Figure 29) and ***Oedothorax gibbosus*** (Figure 30) at the moist end of the gradient and ***Haplodrassus signifer*** (Figure 31) and ***Zelotes*** spp. (Figure 32) at the dry end. They concluded that moisture and vegetation density were the determining factors for community composition.

Figure 27. ***Pardosa sphagnicola*** on mosses. Photo by Walter Pfliegler, with permission.

Figure 28. ***Pardosa sphagnicola*** female with egg sac. Photo by James K. Lindsey, with permission.

Figure 29. ***Pardosa sphagnicola*** female with young spiderlings. Photo by James K. Lindsey, with permission.

Figure 30. ***Oedothorax gibbosus*** female on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 31. ***Haplodrassus signifer*** male on moss. Photo by Jørgen Lissner, with permission.

Once we understood the mechanisms of water loss by spiders, size became a logical explanation. The **tracheae** are the respiratory organs where oxygen enters the body (Davies & Edney 1952). Thus they are also exit points for water, but also cause drowning if too much water is present to block them. Humphreys (1975) pointed out that water loss is influenced by the size of the spider, temperature, saturation deficit, and by relative humidity per se. Davies and Edney demonstrated that up to 30°C the rates of water

loss in mg cm^{-3} hr^{-1} were low, never more than 1.6 (dead spiders with free spiracles) and usually <0.6.

Figure 32. ***Zelotes latreillei***. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Hence, temperature is also important in conserving moisture. Animals exposed at 2°C intervals from 40-50°C show a steep rise in water loss starting at 42°C (Davies & Edney 1952). The species are ordered by critical temperatures (lowest to highest): *Zygiella* (as *Zilla*) *atrica* [outsides of houses (Emerton 1902); woodlands (Elton 1928)], ***Pardosa amentata*** (Figure 45; **Lycosidae**; bogs), ***Metellina segmentata*** (as *Meta*) [Figure 33; **Tetragnathidae**; some species in breaks in blanket bogs (Cherrett 1964)]; *Tegenaria domestica* (as *T. derhami*) [wooded areas, deserts, coastal areas, grassy fields, inside man-made structures (Hunt 2012)]. *Zygiella* (as *Zilla*) *x-notata* [outsides of houses (Emerton 1902); woodlands (Elton 1928)] shows a less defined critical temperature and a lower rate of evaporation than any other study species at higher temperatures. Experiments with dusting caused a six-fold increase in the evaporation rate of ***Pardosa amentata***, causing Davies and Edney (1952) to conclude that a wax layer might be present in the cuticle. Since living organisms lost water more slowly than dead ones, it is likely that this cuticle is secreted by living organisms. There are no experimental data on bryophyte-dwelling spiders and any cuticular relationship relative to temperature.

Figure 33. ***Metellina segmentata***. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

In the Morr House National Nature Reserve, Westmorland, GB, Cherrett (1964) found ***Metellina*** (as *Meta*) ***merianae*** (Figure 34; **Tetragnathidae**) and ***Larinioides*** (as ***Araneus***) ***cornutus*** (Figure 35-Figure 36; **Araneidae**) only in breaks in the blanket bog (Cherrett 1964). ***Metellina merianae*** was mostly in peat overhangs, suggesting that it was avoiding either sun (heat, light) or finding a moist site that was open enough for easy movement. Cherrett attributed this distribution to avoidance of light. Four other species, however, were distributed in a way suggesting they had the ability to withstand desiccation.

Figure 34. ***Metellina merianae***. Photo by Glenn Halvor Morka, with permission.

Figure 35. ***Larinioides cornutus*** spiderling, an inhabitant of blanket bogs. Photo by James K. Lindsey, with permission.

Figure 36. ***Larinioides cornutus*** female, an inhabitant of blanket bogs. Photo by James K. Lindsey, with permission.

I don't know of any direct observations of spiders drinking water from mosses, but I consider it likely that it occurs. The water in soil capillary spaces provides a source of water, even for the larger Lycosidae. Parry (1954) experimented with ***Alopecosa*** (as *Tarentula*) ***barbipes*** (Sundevall), a species of heathlands and one of the larger British lycosids, and *Hogna* (as *Lycosa*) *radiata*. Parry demonstrated that when these spiders had lost about 10% of their normal weight, they would nearly always take advantage of an opportunity to drink from these capillary spaces. It would seem that water adhering in the capillary spaces of bryophytes would be even easier to obtain than that within the soil and may be an important source of water in places such as sand dunes. ***Alopecosa barbipes*** occurs on calcareous coastal dunes in Flanders, Belgium, where the ground cover is predominately mosses (***Syntrichia ruralis***, ***Hypnum cupressiforme*** var. ***lacunosum***), low grasses, and low herbs (Bonte *et al*. 2000). The mosses in this habitat may be important as a source of drinking water.

Importance of Temperature

We have seen the importance that temperature holds for two lycosid spiders living on and in the ***Sphagnum*** mat. In geothermal areas, bryophytes often form the dominant vegetation. Studies of spiders living there may produce new records, or at the very least, range extensions, but a search with Google Scholar produced nothing on this relationship.

But spiders also inhabit cool areas. Růžička and Hajer (1996) found that spiders in North Bohemia lived on mountain tops and peat bogs as well as on the lower edges of boulders where the air stream created "an exceedingly cold microclimate." They found ***Diplocentria bidentata*** (Figure 37; **Linyphiidae**) in pitfall traps laid among mosses at the edge of the stony debris. ***Semljicola*** (as ***Latithorax***) ***faustus*** (Figure 9; **Linyphiidae**), a species known previously only from peat bogs, and ***Theonoe minutissima*** (Figure 38; **Theridiidae**), also a known bog dweller, occurred in moss at the lower edge of the debris.

Figure 37. ***Diplocentria bidentata*** on moss. Photo by Jørgen Lissner, with permission.

Figure 38. ***Theonoe minutissima*** female on moss. Photo by Jørgen Lissner, with permission.

Temperature can be important at the microclimate scale for nest and web site selection. Riechert and Tracy (1975) showed that there was an 8-fold increase in obtaining energy for *Agelenopsis aperta* (**Agelenidae**), a desert spider, from selection of a favorable thermal environment, compared to only 2-fold for selecting for greater numbers of prey. This is at least partly due to the increased spider activity in more favorable temperatures. Riechert (1985) suggested that shade might provide a cue to sites with favorable temperatures, whereas olfactory and vibratory cues help them to locate prey.

Humphreys (1975) showed that for *Geolycosa godeffroyi* (**Lycosidae**) water loss was a function of temperature. Humphreys suggested that this burrowing spider might be able to obtain water in the soil when it was greater than 11% by using heat differentials as a source of water, even though the spider was unable to extract it from near-saturated air. This heat differential extraction would seem to be a possibility among mosses as well.

The need for temperature optimization can cause spiders to select certain vegetational attributes. In a sagebrush community, spiders selected the most dense foliage form that had been experimentally modified by tying the branches together (Hatley & Macmahon 1980). The species diversity and number of **guilds** (any groups of species that exploit same resources, or that exploit different resources in related ways) were greater there. Should we expect a similar relationship for the scaled down community of small spiders that live among bryophytes? If

so, we might expect the communities to differ based on bryophyte life forms.

Hygrolycosa rubrofasciata (**Lycosidae**; Figure 39), a forest species, may choose its habitat for conditions conducive to attracting a mate. The male makes its mating "call" by drumming its abdomen on dry leaves, hence making the bog habitat unsuitable (Kotiaho *et al*. 2000). Kotiaho and coworkers found a positive correlation between dry leaves and presence of spiders. Furthermore, the drumming rate and both male and female mobility were correlated with temperature.

Figure 39. ***Hygrolycosa rubofasciata*** on moss. Photo by Arno Grabolle, with permission.

Food Sources

If you have wondered how those spiders in your cellar find food to survive the winter, perhaps they don't need any, at least for a long time. Forster and Kavale (1989) found that the Australian redback spider (*Latrodectus hasselti*) can survive more than 300 days as adults with no food. Their longevity is greatest at 10°C, making your cellar or cool attic a suitable place to wait out the low food period. This suggests that within a bryophyte mat such spiders could survive a long winter without danger of death by starvation. Apparently most spiders can recover after 2-3 months with no food.

Reports on bryophytes as food for arachnids are relatively rare, although some recent studies have demonstrated that at least some mite taxa consume them (See Chapt 9-1). One suggestion that appears frequently in the literature is that bryophytes either have too little nutritional value, or that it is too difficult to extract that nutritional value from cells that have a large ratio of cell wall (cellulose) to cell contents. But for the arachnids, both the mouth parts and the digestive systems are adapted to eating animal prey.

Spiders may trap their prey or actively hunt for them. Many have poisons that anaesthetize or kill the prey. For example, the **Thomisidae** have their first two pairs of legs modified for grabbing the prey (Lissner 2011a). Their third and fourth legs help to anchor the spider to its substrate during the ensuing, but short, struggle. Once the spider has the opportunity to bite the prey, the prey dies within seconds from the highly potent venom. The longer first two pairs of legs permit the spider to walk sideways like a crab, albeit slowly (Stewart 2001).

Prey size is important to spiders. Whereas they are able to eat captured prey that is larger than they are, this is not necessarily their preferred prey size. Nentwig and Wissel (1986) found that the preferred size ranged 50-80% the size of the spider. Only two of the thirteen spiders in the experiments accepted prey (crickets) that were double their size. Nentwig (1989) found that season had little or no effect on prey size selection. Rather, the important influences were properties of the web, microhabitat, physiological, and behavioral differences among the spider species.

Hunting spiders can be **polyphagous**, feeding on a wide range of prey, or **oligophagous**, specializing on few kinds of organisms (Nentwig 1986). The **monophagous** species are rare, but their single food choice is usually a selection from only a few prey taxa – ants, bees, termites, and other spiders.

Despite the size relationships, the relationship between predator and prey may be unimportant in habitat choice. In one dune system, the relationship between dwarf spiders and their **Collembola** (springtail) prey seems to be a matter of common microhabitat preferences (Bonte & Mertens 2003). In this habitat that experiences severe microclimate fluctuations, both predator and prey aggregate. Both groups are negatively affected by grass coverage, but rather aggregate as a function of moss coverage and not of soil moisture.

Some spiders choose to live among the mosses in trees. When Miller *et al*. (2007, 2008) found a correlation between bryophytes, **Collembola** (springtails), and spiders in Maine, USA, they suggested that spiders depended on the **Collembola** living among the bryophytes for food. When the bryophytes were lost due to gap harvesting of the forest, the arthropod communities were affected, with various responses among the members. Height on the tree influenced the communities (Wagner *et al*. 2007). Bryophytes were most abundant near the tree base. At that level they primarily housed **Acari** (mites), **Araneae** (spiders), and **Collembola**, whereas at 2 m the Diptera (flies) were the most abundant. Loss of trees, and consequent loss of tree-base mosses, resulted in loss of **Collembola** and subsequent reduction in food for spiders.

Other organisms housed among bryophytes are also important as spider food. Among these are **earthworms**. Although predation of spiders on **earthworms** has rarely been observed (Figure 40), it appears that those spioders that do choose these as part of their diet are the ones that live on the ground in leaf litter, moss-covered patches, and under stones and logs (Nyffeler *et al*. 2001). These **earthworms** have a high protein content (~60-70%, dry weight) (MacDonald 1983; Lee 1985) that complements the typical insect diet of spiders. In the non-web-building genus ***Xysticus*** (Figure 41; **Thomisidae**), a crab spider only 7 mm long was able to consume parts of an **earthworm** of 2 cm length (Nyffeler 1982). This was no doubt possible because of the powerful front legs and a potent venom. Even web-building spiders feed on earthworms (Nyffeler *et al*. 2001). These include those making sheet webs (*e.g.* ***Amaurobius*** – **Amaurobiidae**) and silk tubes (*e.g.* ***Atypus*** – **Atypidae**) (Nyffeler *et al.* 2001), both bryophyte dwellers (Blackwell 1857).

By reviewing the literature, Nyffeler *et al*. (2001) found that members of eleven different families of spiders

are known to feed on other spiders. As you might expect, these predators belong mostly to larger species (>10.0 mm) that live near the ground in woodlands and grasslands. Among these are species that live in and under clumps of mosses.

Figure 40. ***Leptorhoptrum robustum*** male, a spider that is known from mosses, eating worm. Photo by Jørgen Lissner, with permission.

Figure 41. ***Xysticus cristatus*** among mosses. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Reproduction

Spider mating can be hazardous for the males. Females are usually larger than males, sometimes much larger (Wikipedia 2012a). Hence, males are easily overcome and can serve as dinner for the female. Males, on the other hand, express a number of complex courtship rituals that help them avoid predation by the females. They usually manage to have several matings, being limited by their short two-year life span (but much longer in some species like the tarantula).

Most spiders build nests where they deposit their eggs (Figure 42), often numbering around 1000 (Biodiversity Explorer 2012). When the eggs are expelled, they become surrounded in a viscous liquid that cements the eggs together when they dry (Figure 43). The female provides them with a fluffy silk that covers and insulates them, and she attaches this to vegetation or includes it in her web. This cocoon also serves as protection against ant predation. Eggs laid in summer usually hatch in 1-2 weeks, whereas those laid at the end of summer will over-winter and hatch the following spring or summer. **Lycosidae** (wolf spiders) carry the cocoon attached to the rear of the abdomen (Figure 44) and later carry their young around on their backs (Figure 45), presumably providing further protection.

Figure 42. ***Xysticus ulmi*** (**Thomisidae**) female with eggs among mosses. Photo by Jørgen Lissner, with permission.

Figure 43. *Ero* sp. cocoon, showing attachment. Photo by Walter Pfliegler, with permission.

Figure 44. ***Pardosa pullata*** (**Lycosidae**) female, a bog dweller, on ***Sphagnum***, carrying egg sac on her abdomen, as is typical in her family, Lycosidae. Photo by Jørgen Lissner, with permission.

Figure 45. ***Pardosa amentata*** female with spiderlings. Photo by James K. Lindsey, with permission.

In the **Thomisidae**, no webs or retreats are used for oviposition (Figure 42; Lissner 2011c). The males are much smaller and darker than the females. During courtship, males touch the female in a way that causes her to recognize him as a male spider and she assumes a submissive posture. Once eggs are produced, the female guards the egg sack. Members of the genus ***Xysticus*** (Figure 41) are known from bryophytes (Isaia *et al.* 2009).

Some spiders use mosses as the substrate for depositing their cocoons. Hajer *et al*. (2009) found that ***Theridiosoma gemmosum*** (Figure 46; **Theridiosomatidae**) maintained its egg sac (Figure 47) on ***Hypnum cupressiforme*** (Figure 48) during their study. Alexander (2003) found this spider species among fen vegetation in Cornwall, UK, where it presumably deposits its cocoons. This species has a rather unusual mating behavior. The male releases silken threads between successive copulations (Hajer *et al*. 2009, 2011). The females unwind these draglines, then roll them into a bundle which they ingest before copulating again. Hence this nuptial gift transfers nutrients from the male to the female. Barrows (1918) reported that this species can "always" be found among wet mosses on cliff faces and other wet situations in deep woods.

Figure 46. ***Theridiosoma gemmosum*** adult male on moss. Photo by Jørgen Lissner, with permission.

At least some members of the **Linyphiidae** are known to care for their young by providing food (Willey & Coyle 1992). On the other hand, they may eat their own eggs, at least in captivity – a phenomenon that has rarely been reported for spiders and may not exist in nature. The even smaller size of the young may dictate the need for a more protective environment, *i.e.*, buffered against temperature and moisture fluctuations, during the "child-rearing" period of their lives.

Figure 47. ***Theridiosoma gemmosum*** egg cocoon. Photo by Jørgen Lissner, with permission.

Figure 48. ***Hypnum cupressiforme***. Photo by David Holyoak, with permission.

Scotina celans (Figure 49; **Liocranidae**) lives in both mosses and detritus in woodlands, where it makes a funnel tube for its nest, lying in wait there for prey (Harvey *et al*. 2002). Females regurgitate food to feed the young.

Figure 49. ***Scotina celans*** (**Liocranidae**) on mosses. Photo by Morten D. D. Hansen, with permission.

Nests and Webs

Among the potential uses of bryophytes, some spiders may choose them as a nesting site. This can be a home for the adult who, in most families, lies in wait for its prey. The spider has a unique set of structures called **spinnerets** that produce the silken thread used for making the webs and nests (Figure 50). These webs can be funnels (Figure 51), 3-d structures (Figure 52), or the more commonly figured sheet structures (Figure 53) such as those seen in Halloween decorations. The common moss dwellers in the **Linyphiidae** make horizontal doily webs, sometimes covering large areas (Figure 54-Figure 55). ***Frontinella***, (**Linyphiidae**) the bowl and doily spider, makes an upper bowl-shaped web and a lower, flattened web (Figure 56). The spider rests under the bowl (Figure 57), above the doily, to await prey. ***Eresus sandaliatus*** (Figure 58; **Eresidae**) is one of those that will at least at times use mosses as a location for its food web (Figure 59).

Figure 50. ***Achaearanea riparia*** (**Theridiidae**), occasional moss-dweller (Logunov *et al*. 1998), showing silken thread from spinnerets. Photo by Glen Peterson, through Creative Commons.

Figure 51. This nest of ***Amaurobius ferox*** (**Amaurobiidae**) provides evidence that mosses can be used for its housing. Photo by James K. Lindsey from <www.commonaster.eu>, with permission.

Figure 52. Three-dimensional spider-web. Photo ©<www.free-images.org.uk>, with permission.

Figure 53. Sheet spider web with dew drops. Photo by Fir0002/Flagstaffotos through Wikimedia Commons.

Figure 54. Doily webs of **Linyphiidae**. These occupied over 1000 m^2 in California, USA. Photo by John A. Basanese through Creative Commons.

Figure 55. Doily webs of **Linyphiidae**. Photo by John A. Basanese through Creative Commons.

Figure 56. ***Frontinella*** (**Linyphiidae**) bowl and doily web with spider on under side of web. Some species of ***Frontinella*** occur on mosses. Photo ©Gary Vallé, with permission.

Figure 57. ***Frontinella*** (**Linyphiidae**) spider on under side of bowl part of bowl and doily web. Photo ©Gary Vallé, with permission.

Figure 58. ***Eresus sandaliatus*** (**Eresidae**) male among mosses. Photo by Jørgen Lissner, with permission.

Figure 59. ***Eresus sandaliatus*** (**Eresidae**) food web among bryophytes and lichens. Photo by Jørgen Lissner, with permission.

In the southern part of its range, ***Atypus affinis*** (Figure 60-Figure 62; **Atypidae**) is a rare spider (Jonsson 1998), sometimes building its tubes under mosses with the opening in the mosses. Using a sieving technique, Jonsson was able to distinguish the actual locations of the spiders. He found 90 nest tubes in just one square meter on the tops and sides of stony screes in southern Sweden, often among mosses. These tubes serve as traps for food items. Prey items fall into the trap and are captured and eaten by the spider attacking them from beneath. Only young spiderlings and males ever leave the tube, the males only in search of a female.

Figure 60. ***Atypus affinis*** (**Atypidae**) among grasses, most likely a male in search of a female tube. Photo by Manuel Valdueza through public domain.

Figure 61. ***Atypus affinis*** (**Atypidae**) eggs and spiderlings. Only the spiderlings and female-searching males leave the tube. Photo by Jørgen Lissner, with permission.

Figure 62. ***Atypus affinis*** (**Atypidae**) male. The male in this image is the exoskeleton of a dead male that has been eaten by the female. Photo by Jørgen Lissner, with permission.

In the genus ***Arctosa*** (Figure 1; **Arctosidae**)**,** these medium to large spiders make burrows in mosses, sand, detritus, or under stones (Figure 63) (Lissner 2011c). But some spiders do not make any sort of retreat (Lissner 2011c). The **Thomisidae** make no webs or retreats for any purpose.

Figure 63. ***Arctosa cinerea*** (**Lycosidae**) digging burrow, which members of the genus sometimes do among mosses. Photo copyright by Evan Jones, Spider Recording Scheme/British Arachnological Society (2012) Website and on-line database facility <http://srs.britishspiders.org.uk>.

Hahniidae live close to the ground and construct their small sheet webs among mosses as well as other areas that exhibit small depressions (Lissner 2011b). ***Hahnia nava*** (Figure 64), a sheet-web maker, places its nets in mosses and other low plant forms (Harvey *et al.* 2002). ***Hahnia helveola*** even makes its webs in pine needles, as well as leaf litter, mosses, and low plant forms.

On the southern Appalachian peaks, USA, the tiny size (3-4 mm) of the endangered spruce-fir moss spider ***Microhexura montivaga*** (Figure 65; **Dipluridae**) permits it to live in flattened tube webs under mosses and litter mats of the spruce-fir forests (Coyle 1985). ***Microhexura montivaga***, the smallest of the tarantulas, was first discovered in North Carolina (USFWS 2012). It lives in high elevation remnants of Fraser fir and red spruce forests on shaded boulders exclusively within mats of damp, well-drained mosses and liverworts (Geatz 1994). Its 2-3 mm size permits it to move easily among the branches. Springtails within the moss mats may serve as a primary food source (USFWS 2012). The spider is endangered because its spruce-fir habitat is being destroyed by the balsam woolly adelgid (Hemiptera) (Geatz 1994; Tarter & Nelson 1995; Smith & Nicholas 1998). This canopy destruction results in drying of the mosses, making them unsuitable for this spider.

Figure 64. ***Hahnia nava***, a sheet-web maker that places its webs among mosses and other low vegetation. Photo by Glenn Halvor Morka, with permission.

Figure 65. The moss spider ***Microhexura montivaga*** (**Dipluridae**). Photo by Joel Harp, US Fish & Wildlife Service.

Spiders that live above ground typically produce a security thread by which they can relocate to their webs. It would be interesting to see if this is done among bryophyte-dwelling spiders.

In some cases, the bryophyte seems to play an important role that cannot be served as well as the tracheophyte counterparts. This role is in helping to form the trap door of the trapdoor spiders (Moggridge 1873) including **Ctenizidae** and **Liphistiidae** (Wikipedia 2014) and the lesser known **Cytraucheniidae** (Eiseman & Charney 2010). ***Cyclocosmia torreya***, known primarily from Guatemala, Thailand, and China, builds burrows in moss banks along the Apalachicola River in Florida, USA (Wikipedia 2014). ***Stasimopus mandelai*** (Ctenizidae; see Figure 66), in the Eastern Cape Province of South Africa, makes its trap door of silk and soil with a very light covering of moss (Hendrixson & Bond 2004).

Figure 66. ***Stasimopus robertsi*** at the entrance of its burrow. Another spider in this genus, ***S. mandelai*** incorporates mosses in a trapdoor that covers its burrow. Fritz Geller-Grimm through Creative Commons.

Bits of bryophytes are often added to the door as camouflage (Cloudsley-Thompson 1989), but based on images on the web, growing mosses often comprise part of the lid and appear to help in holding the lid together (Figure 67-Figure 69). The spider hides beneath the lid, and when it sees a prey organism, it darts out from the protective lid to grab the prey. It would seem that a tracheophyte would be too heavy to serve as a network to hold this door together.

Figure 67. Trapdoor spider ***Liphistius malayanus*** (**Liphistiidae**), from China, Japan, and Southeast Asia, under a moss-covered trapdoor. Photo by Amir Ridhwan, Malaysian Spider website, through Creative Commons.

Figure 68. Trapdoor spider (**Ctenizidae**) with bryophytes surrounding it and covering the "door." Photo by Hankplank through Creative Commons.

Figure 69. Trapdoor for the spider ***Hebestatis*** sp. (**Ctenizidae**) under moss. Photo by Marshal Hedin through Creative Commons.

Dormant Stages

One might find a greater site selectivity for the immobile dormant or egg stages. For spiders whose cocoons are not incorporated into the web constructed for trapping prey, the web/feeding site may have very different characteristics from that of the oviposition site (Suter *et al*. 1987). Suter *et al*. (1987) examined the site selection of the linyphiid ***Frontinella communis*** (as *F. pyramitela*) (Figure 56, Figure 70-Figure 71). This species, as far as I know, does not typically use mosses, but the female deposits her eggs in a loosely woven cocoon on or near the soil, whereas many members of this family deposit their eggs aerially where the humidity is usually much lower. It appears that the ***Frontinella communis*** cocoon loses water at approximately double the rate lost by three common aerial species (*Achaeranea tepidariorum*, *Argyrodes trigonum*, and *Uloborus glomosus*). Fritz and Morse (1985) contend that selection of the oviposition site is "one of the most important decisions made" by organisms that deposit eggs externally. Hieber (1985) demonstrated this same importance in the cocoon-carrying ***Argiope aurantia***, where the outer cocoon layer provides the air space that does most of the insulating.

Figure 70. ***Frontinella communis*** (**Linyphiidae**), a spider that deposits her eggs near the soil where water loss is less than at the aerial position of her food web. Here she is on the underside of the web. Photo by William DuPree, with permission.

Figure 71. ***Frontinella communis*** (**Linyphiidae**), the bowl and doily spider, on its web. This species makes a double web, hence its common name. Photo by Robert Klips, with permission.

Hence, we should look at moss-dwelling species for differences in the ability of their cocoons to maintain adequate moisture levels and to prevent excess moisture compared to aerial species. We know that ***Hickmanapis minuta*** (**Anapidae**) will attach its egg sacs to mosses (Hickman 1943). It is likely that a number of others do the same.

Overwintering

Spiders typically live only about two years, so it would not seem expedient for their overwintering strategy to be a strong evolutionary driver. Nevertheless, they must survive at least one winter, and strategies vary. In the **Thomisidae**, there seems to be no special overwintering structure – no web or burrow (Lissner 2011c).

But for some spiders, mosses are essential to winter survival. ***Larinia jeskovi*** (**Araneidae**), living among the sedge *Carex rostrata*, is rare in Europe (Kupryjanowicz 2003). It builds no winter retreat, but females overwinter in areas with a thick, loose layer of mosses. When the moss layer is absent, the abundance of this species is low. In peatlands, ***Sitticus floricola*** (Figure 72-Figure 73; **Salticidae**) overwinters deep in the ***Sphagnum*** (Harvey *et al*. 2002).

Figure 72. ***Sitticus floricola*** (**Salticidae**) among mosses. Photo ©Pierre Oger, with permission.

Figure 73. ***Sitticus floricola*** (**Salticidae**) on web. Photo by Peter Harvey, Spider Recording Scheme-British Arachnological Society.

Spider Guilds

Root (1967) defined a guild as "a group of species that exploit the same class of environmental resources in a similar way." This uses terminology familiar from the niche concept, but confines members of a guild to a class of resources rather than all of them.

The concept of guild may be useful in describing the spider communities of bryophytes, but such a description has not yet been constructed. Cardoso *et al*. (2011) defined spider guilds in large scale view for the first time. They used foraging strategy (type of web and method of active hunting), prey range (narrow or wide diversity), vertical stratification (ground or vegetation) and circadian activity (diurnal or nocturnal). This resulted in eight guilds, based on feeding strategy: (1) sensing weavers; (2) sheet weavers; (3) space weavers; (4) orb web weavers; (5) specialists; (6) ambush; (7) ground; and (8) other hunters. Using this classification, Cardoso and coworkers found that the correlation of guild richness or abundances was generally higher than the correlation of family richness or abundances. Nevertheless, guilds tended to include related species because among spiders the web-building strategy and form of the feeding apparatus are the basis of higher classification. Therefore, it is not surprising that families serve as good surrogates, forming similar groupings.

If we attempt to describe the predominant spider guilds among bryophytes, it might provide a framework for examining the habitats where they live. Certainly the **ground-hunting guild** is common on the surface of bryophytes in bogs and open habitats such as sand dunes and grasslands or meadows. Cardoso *et al*. (2011) found that **ground hunters** formed the largest guild (number of families) worldwide. The **sheet-weavers** and **other hunters**, including the **Linyphiidae**, are predominant among bryophytes in most habitats. Surprisingly, the **ground hunters** have the largest family representation among the bryophytes, but the number of species is not large, and representation differs with habitat. Each of the guilds is represented by one or more families among the bryophytes:

Sensing web: Atypidae
Sheet web: Amaurobiidae, Dipluridae, Eresidae, Hahniidae, Linyphiidae (Linyphiinae, Micronetinae)

Space web: Dictynidae (Dictyninae), Micropholcommatidae
Orb web: Anapidae, Araneidae, Symphytognathidae
Specialist: Mimetidae
Ground hunters: Corinnidae, Gnaphosidae, Liocranidae, Lycosidae, Zoridae
Other hunters: Clubionidae, Linyphiidae (Erigoninae), Philodromidae, Salticidae
Ambush hunters: Thomisidae

I have omitted the **Cybaeidae** because the one species (***Argyroneta aquatica***) reported herein uses an underwater nest and darts out to catch prey, not catching them with a web as used for the guild classification.

Adaptations to Bryophytes

For spiders, living among bryophytes seems to be mostly an advantage for the spiders, not the bryophytes. The provision of cover and moisture by the bryophyte is complemented by providing avoidance of larger predators. Loss of water would result in loss of hydrostatic pressure in the legs, making it impossible to extend their legs, hence making them unable to escape. The moisture within a moss mat should therefore make mobility easier than in a drier location.

In other groups of animals, color patterns have presented good adaptations. There seems to be little discussion of this as an adaptation for bryophyte-living, and certainly green spiders are rare. However, coloring of spiders is often disruptive, as seen for ***Sitticus floricola*** (Figure 72-Figure 73; **Salticidae**) and the disruptive pattern of the spider in Figure 74.

But to live among bryophytes can be somewhat demanding on the construction of the spider. Bryophytes do not provide an easy landscape for navigation for larger spiders. Within the protective cover, jumping is usually not an option. The higher moisture content could save energy that might be needed to provide a thicker cuticle for spiders living in drier habitats. But being small is an important adaptation, permitting easy navigation and being compensated by the higher moisture levels available. The moss furthermore buffers the rain so that it does not easily dislodge the spider, and spiders are able to move about sufficiently to avoid drowning in areas of water collection such as leaf bases.

Figure 74. This spider blends well as it traverses the moss ***Didymodon cordatus*** in Europe. Photo by Michael Lüth, with permission.

Several families stand out among bryophyte dwellers. The one with the greatest number of bryophyte-dwelling species is the **Linyphiidae**, a family of spiders generally less than 2 mm long. Bryophyte-dwelling spiders are also found within many other spider families, especially including the **Gnaphosidae** (ground spiders), **Clubionidae** (foliage spiders), and **Theridiidae** (comb-footed spiders), some of which are considerably larger. In New Zealand, the **Micropholcommatidae** have a number of bryophyte-dwelling species.

Anapidae

The **Anapidae** are orb weavers, often with webs less than 3 cm. Given the small size (mostly less than 2 mm) and habits (Wikipedia 2010a) of this family, we should look for heretofore unknown species among the bryophytes. Kropf (1997) has shown that one member, *Comaroma simoni* (Figure 75), a member of the **Anapidae**, is born without a hardened covering, a characteristic that likely applies to other species as well. Such species are thus subject to greater desiccation than adults (Kropf 1997), a problem that could be ameliorated by bryophytes. Nonetheless, this species is a soil dweller in Austria and in the scree areas of mountains in Europe, it occurs exclusively in association with bare rock (Růžička & Klimeš 2005). Kropf suggests that in the beech (*Fagus sylvatica*) forests of Austria this species most likely undergoes vertical migration to reach the best moisture and temperature conditions. In many habitats, such behavior could make the bryophyte an important part of a daily and seasonal cycle for some taxa, even if only to increase the soil moisture.

The **Anapidae** live primarily in tropical rainforests of New Zealand, Australia, and Africa, with scattered occurrences on other continents, where bryophytes (and leaf litter) commonly provide them a home on the ground (Wikipedia 2013). ***Pseudanapis aloha*** (**Anapidae**), is known from mosses in the mountains of Hawaii, USA.

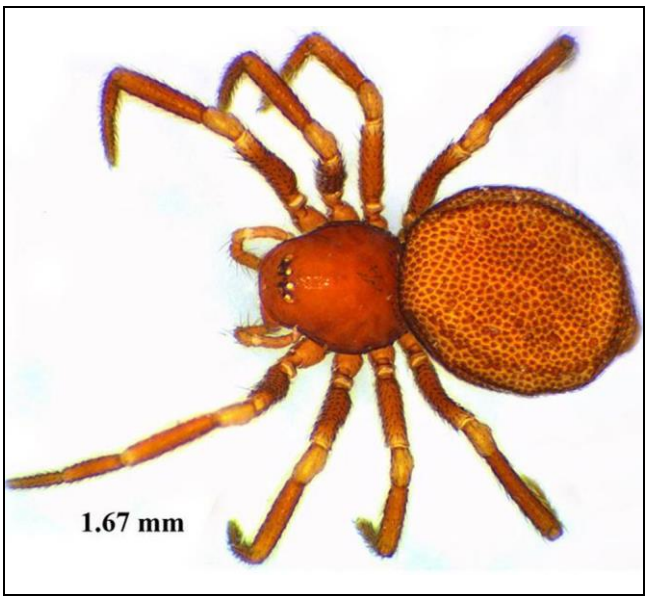

Figure 75. ***Comaroma simoni***. Photo ©Pierre Oger, with permission.

Clubionidae (Sac or Tube Spiders)

These spiders make tubes where they hang out during the day. These tubes are located under stones, loose bark, between moss, and between leaves. At night they are hunters. On Mount Kilimanjaro, Denis (1950) found the 12 mm ***Clubiona abbajensis kibonotensis*** under moss [(see *C. reclusa* (Figure 76-Figure 78) and *C. pallida* (Figure 79)].

Figure 76. ***Clubiona reclusa***, a generic relative of ***Clubiona abbajensis kibonotensis***, in nest with egg sac on a fern frond. Photo by Jørgen Lissner, with permission.

Figure 77. ***Clubiona reclusa*** egg sac from fern frond. Photo by Jørgen Lissner, with permission.

Figure 78. ***Clubiona reclusa*** male. Photo by Jørgen Lissner, with permission.

Figure 79. ***Clubiona pallidula***, a generic relative of ***Clubiona abbajensis kibonotensis*** that lives under mosses on Mount Kilimanjaro. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Gnaphosidae (Ground Spiders)

The **Gnaphosidae** (Figure 80) form a worldwide family with over 2000 species (Wikipedia 2012c). They do not construct a web for capturing prey, but instead are night-active hunters. They spend the daylight hours in a silken retreat. The females guard their thick-walled eggs until the spiderlings hatch.

Figure 80. ***Gnaphosa muscorum*** (**Gnaphosidae**) on leaf. Photo by Tom Murray, with permission.

Linyphiidae (Sheet Spiders)

If any family may be considered adapted to living among bryophytes, it is the **Linyphiidae**. This is the largest family of spiders [more than 4,300 described species in 578 genera worldwide (Wikipedia 2012b)], so it is not surprising that its species comprise the majority of bryophyte dwellers. Their tiny size (1-10 mm) makes them difficult to find and identify. Hence, there are likely many more species than those already described.

The shape of the **Linyphiidae** is somewhat different from that in many other spider families. The thorax is reduced relative to the abdomen, and the abdomen is humped or globular, making it the conspicuous part of the spider (Figure 81). Is this an adaptation that permits a relatively large amount of the body to be available for

reproduction while making a smaller size possible for the animal overall?

Figure 81. ***Linyphia triangularis*** showing body shape. Photo by James K. Lindsey, with permission.

Linyphiidae build sheet or dome-shaped webs (Figure 82), hence the common names of sheet weavers or sheet spiders, with no retreat, and spend their time hanging upside down on the underside of the sheet (Nieuwenhuys 2010). Flying insects become ensnared by the web and fall to its lowest point where the awaiting spider bites it through the net (Lissner 2011c). In Jutland, Denmark, the female shadow hammock spider, ***Labulla thoracica*** (Figure 83), is known to weave her web under a moss mat (Hormiga & Scharff 2005).

Figure 82. Horizontal webs at Shiretoko Goko, Japan, such as those manufactured by members of the **Linyphiidae**. Photos by Janice Glime.

Figure 83. ***Labulla thoracica***, a spider that weaves webs beneath moss mats. Photo by Ondřej Machač, with permission.

Dispersal in the **Linyphiidae** is often accomplished by **ballooning**, a phenomenon in which the spider ascends to something taller, like a fence, points the spinnerets upward, then secretes a thread (Pratt 1935; Lissner 2011c). It jumps or is blown with the thread serving as an anchor. On a good wind, it can accomplish a greater distance. For these small spiders, this is more than could be accomplished by walking, and the thread provides an anchor so that they don't get too far from their current suitable habitat. It is a lot like bungee jumping, except a lot of their travel is horizontal. These spent bungee cords can actually be noticeable when many spiders balloon in a short period of time, as may occur in late summer. Individuals will also keep trying if they are unsuccessful in travelling very far, contributing to the accumulation of threads on the ground.

Within the **Linyphiidae**, the subfamily **Erigoninae** is a group of small spiders that are mostly less than 3 mm long. In some members of ***Walckenaeria***, including a number of moss dwellers, eyes of males are located on a pedestal or turret (Figure 84-Figure 85), creating a periscope. But this would-be periscope provides little visual contribution. Rather, it serves a sexual function, possibly secreting sexual pheromones (Millidge 1983). There is some evidence that the female grabs it during courtship or mating, as known in the linyphiid ***Hypomma bituberculatum***.

Figure 84. ***Walckenaeria acuminata*** male on a moss, showing the stalk that houses the eyes. Photo by Jørgen Lissner, with permission.

Figure 85. ***Walckenaeria cucullata*** male on moss, providing a front view of the stalk with eyes. Photo by Jørgen Lissner, with permission.

Lycosidae (Wolf Spiders)

Contrasting with these small species, the larger ***Pardosa maisa***, a wolf spider (*cf.* Figure 86), lives in a poor pine fen where there is a "rich" ***Sphagnum*** layer (Itaemies & Jarva 1983). Peatlands and mires have their unique fauna of spiders (Vilbaste 1981). Villepoux (1990) found that ground-level spiders in a French peat bog formed several representative groups, each helping to define a biotope. In fact, he felt that only a few species of spiders were sufficient to estimate the diversity of the plant communities in this habitat. In bog and fen habitats, several members of this family are dominant, running about on the surface rather than within the mat, and no doubt taking advantage of the moist mosses to retain their moisture in the drying rays of the sun. Other sunny habitats for moss inhabitants of this family include the open tundra (Dondale *et al*. 1997), sand dunes (Merkens 2000), and as invaders after fires (Larrivée *et al*. 2005).

Figure 86. ***Pardosa amentata*** female with egg sac, a wolf spider related to the ***Sphagnum*** spider ***P. maisa*****.** Photo by James K. Lindsey, through Wikimedia Commons.

Symphytognathidae and Micropholcommatidae

The family includes some very small spiders, some of which are known moss-dwellers. The Samoan moss spider (***Patu marplesi***; **Symphytognathidae**) is often considered to be the world's smallest spider (Alphonse 2010), having a leg span of only 0.5 mm (King 2004). However, in other members of this genus only the female is known. Since the male is typically smaller, it is possible that other species may be smaller, in particular *Patu digua* (Wikipedia 2010c) that is often designated as the smallest. ***Patu marplesi*** is known from mosses in New Zealand (Forster 1959). The family **Micropholcommatidae** is a segregate of **Symphytognathidae** and includes ***Textricella*** a genus with a number of known moss dwellers. ***Textricella nigra*** (**Micropholcommatidae**) is known from moss on tree trunks at 1000 m asl and the type is known from moss, both in New Zealand; ***T. propinqua***, ***T. pusilla***, ***T. salmoni***, ***T. scuta***, ***T. signata***, ***T. tropica***, ***T. vulgaris*** (many records), ***Micropholcomma bryophilum***, ***Parapua punctata***, ***Pua novaezealandiae***, ***Zealanapis australis*** (as ***Chasmocephalon armatum***), all members of **Micropholcommatidae,** occur among mosses in New Zealand. ***Patu woodwardi*** (as *Mismena woodwardi*; **Symphytognathidae**) from New Guinea and ***Textricella hickmani*** and ***T. parva*** from Tasmania are known from mosses.

Theridiidae (Tangle-web Spiders, Cobweb Spiders, and Comb-footed Spiders)

This family (Figure 87) is likewise among the larger families with over 2200 species (Wikipedia 2012d). The females often build a tangle web (3-d) instead of a simpler sheet. Their web construction uses a sticky silk to capture prey instead of the more common woolly silk. Many other theridiids trap ants and other ground-dwelling insects with their elastic sticky silk trap lines that lead to the soil surface. It would be worth searching for these traplines among bryophytes. The family includes the well-known widow spiders. The largest genus is ***Theridion***, which includes some members among mosses (Logunov *et al*. 1998).

Figure 87. ***Robertus pumilus***, member of a genus in which some members inhabit bryophytes. Photo by Tom Murray, through Creative Commons.

Summary

Spiders are in the subphylum **Chelicerata**, Class **Arachnida**, Order **Araneae**. Spiders have eight legs attached ventrally to the **cephalothorax**. Some occur on the surface of moss beds where mosses provide moisture, but others live within moss beds and cushions. Because of their tiny size and habit of living within moss mats or cushions, some, perhaps many, spiders never go near pitfall traps commonly used for collecting. More diversity is likely if one uses a combination of pitfall traps, light traps, soil sifters (sieving), and hand collections. Because of widespread use of only pitfall traps, our knowledge of bryophyte-dwelling spiders most likely underestimates the importance of the bryophyte habitat for diversity. Spiders considered rare are likely to occur among bryophytes, in part due to inadequate sampling, and in other cases due to rarity of a particular habitat.

The growth form of bryophytes may play a role in the choice of habitat, but no study specifically tests this hypothesis, although different spider communities have been found on different growth forms. Small members of **Linyphiidae** have the most moss-dwelling species in most habitats, with **Lycosidae** having more biomass in open habitats of bogs, tundra, dunes, and sites after fire.

Spiders are susceptible to water loss and may use bryophytes as a moist retreat as well as a hideaway from predators. The bryophyte cover also protects them from the heat and UV rays of the sun, with higher temperatures causing a greater water loss. Bryophytes serve as sites for reproduction, nests, and food webs. Some spiders use mosses as a winter refuge. Spiders will locate their nests to optimize temperature, thus optimizing energy gain.

Spiders use claws with fangs to inject venom into their prey. Some use webs to trap and others hunt their prey. Spiders are carnivores and most likely never eat bryophytes. However, bryophytes can serve as a source of food by harboring food organisms, including other spiders, insects (esp Collembola), and earthworms.

The most common spider families to be found associated with bryophytes are Anapidae, Clubionidae (sac or tube spiders), Gnaphosidae (ground spiders), Linyphiidae (sheet spiders), Lycosidae (wolf spiders), Symphotognathidae, Micropholcomatidae, Theridiidae (tangle-web spiders, cobweb spiders, and comb-footed spiders). All eight spider guilds are present among mosses. The adaptations of spiders to living among bryophytes may include disruptive coloration and small size, with maneuverability limiting larger spiders. Bryophytes are the sites for webs of some species and for placing eggs for others. They provide buffered temperature and humidity locations for dormant stages, including overwintering. Some members of the **Linyphiidae**, the most species-rich family among bryophytes, care for their young by providing food, but most young spiderlings are on their own.

Dispersal in large spiders is typically accomplished by running, but in the tiny **Linyphiidae**, ballooning and bungee jumping can help them to get to greater distances than is feasible for their tiny legs.

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CHAPTER 7-3
ARTHROPODS: ARACHNIDA – SPIDER HABITATS

Janice M. Glime and Jørgen Lissner

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CHAPTER 7-3
ARTHROPODS: ARACHNIDA - SPIDER HABITATS

Figure 1. ***Gnaphosa nigerrima*** (**Gnaphosidae**) male on moss. Photo by Jørgen Lissner, with permission.

Habitats

Although the smallest spiders are somewhat common among bryophytes, this habitat is one that has not been studied extensively. Because these small spiders are not very mobile, they are often missed by pitfall traps, and even those that do fall into the traps cannot be specifically associated with the bryophytes. It is likely that in most habitats one can find new or rare spider species among the bryophytes.

Pommeresche (2002) used pitfall traps to examine spiders in fifty different sites in the Geitaknottane Nature Reserve in western Norway, including open forests, shady pine forests, humid deciduous forests, and dry deciduous forests. He found a good correlation between the spider communities and the plant communities. The bog and forest habitats of the Nature Reserve had a number of species varying from 21 to 51 per site. They identified five groups of spider communities on the reserve: wet, open areas; open forests; shady pine forests; humid deciduous forests. The communities correlated well with vegetation, having significant correlations with productivity of wood, soil humidity, tree cover, bush cover, and heat index. As will be seen later, vegetation type is likewise important in determining the spider fauna of bogs and fens (subchapters 7-3, 7-4).

Oliger (2004) used studies from northwest Russia to assert that species such as ***Arctosa alpigena*** (as *Tricca alpigena*; **Lycosidae**; Figure 2), ***Antistea elegans*** (**Hahniidae**; Figure 3), and ***Gnaphosa nigerrima*** (**Gnaphosidae**; Figure 1, Figure 4) were common in bogs but rare in forests, whereas ***Agroeca brunnea*** (**Liocranidae**; Figure 5; a leaf litter species), ***Hygrolycosa rubrofasciata*** (**Lycosidae**; Figure 6), ***Pirata hygrophilus*** (**Lycosidae**; Figure 7), ***Trochosa spinipalpis*** (**Lycosidae**; Figure 8), and ***T. terricola*** (Figure 127) were 5-10 times more abundant in forests than in bogs. Nevertheless, ***Trochosa spinipalpis*** occurs almost exclusively in bogs in

Great Britain (Boyce 2004) and Pommeresche (2002) reported ***T. terricola*** to be among the five most active spiders in the bog at Geitaknottane Nature Reserve, western Norway. Clearly the relationships of spiders to habitat are complex. Hence, we might expect the presence of bryophytes to make a difference in the spider diversity of the ecosystem and their presence of absence might influence the type of spider fauna there.

Figure 2. ***Arctosa*** *cf.* ***alpigena*** (**Lycosidae**) female. Photo by Walter Pflieigler, with permission.

Figure 3. ***Antistea elegans*** (**Hahniidae**). Photo by Jørgen Lissner, with permission.

Figure 4. ***Gnaphosa nigerrima*** (**Gnaphosidae**) on mosses. Photo by Jørgen Lissner, with permission.

Figure 5. ***Agroeca brunnea*** (**Liocranidae**), a forest leaf litter species. Its relationship to mosses may be occasional. Photo ©Pierre Oger, with permission

Figure 6. ***Hygrolycosa rubrofasciata*** (**Lycosidae**) on mosses. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.

Figure 7. ***Pirata hygrophilus*** (**Lycosidae**), a forest species. Photo by Ondřej Machač, with permission.

Figure 8. ***Trochosa spinipalpis*** (**Lycosidae**) female on moss. Photo by Jørgen Lissner, with permission.

On the other hand, Graves and Graves (1969) found that the spiders collected from mosses and other substrata on the forest floor in a high-rainfall area at 1300 m in the southern Appalachian Mountains, USA, were mostly generalists, occupying several types of humid forest microcommunities. Habitat specificity seems to be lacking for many of the bryophyte dwellers.

Forests, Heaths, and Meadows in Denmark (observations by Jørgen Lissner)

Bryophytes have adapted to nearly all types of habitats and apart from forming the dominant ground cover in bogs, they are also often dominant (at least locally) in forests, heaths, and meadows. Coniferous forests frequently possess a thick layer of bryophytes on the forest floor as well as on stems and branches of bushes and trees. Some moss species are acting as pioneer plants on heaths, such as the invasive moss ***Campylopus introflexus*** (Figure 9), which may increase significantly after burning or other management practices that expose raw humus. Other moss species such as ***Hypnum cupressiforme*** (Figure 10) may increase in abundance as the heath grows older and provides shadier and moister conditions suitable for the moss underneath the heather. Mosses may also serve as habitat for spiders in wet heathland and various types of grassland, including unimproved grasslands, *e.g. Molinia* meadows on calcareous, peaty or clayey-silt-laden soils. Even cultivated lawns may have a dense coverage of mosses such as ***Brachythecium rutabulum*** (Figure 11) and ***Rhytidiadelphus squarrosus*** (Figure 12).

Figure 9. ***Campylopus introflexus***. Photo by David Holyoak, with permission.

Figure 10. ***Hypnum cupressiforme*** var. ***cupressiforme***. Photo by David Holyoak, with permission.

Figure 11. ***Brachythecium rutabulum*** in Europe. Photo by Michael Lüth, with permission.

Figure 12. ***Rhytidiadelphus squarrosus*** in Europe. Photo by Michael Lüth, with permission.

Just a few samples of spiders inhabiting mosses in these habitats are shown here. ***Haplodrassus moderatus*** (Figure 13; **Gnaphosidae**) uses mosses as hiding places during the day and perhaps also hunts its prey among mosses during the night. ***Gnaphosa leporina*** (Figure 14-Figure 15; **Gnaphosidae**) is frequent on wet heathland whereas ***Scotina celans*** (Figure 16; **Liocranidae**) is sometimes found in mosses of dry heathland. ***Scotina***

celans also lives in both mosses and detritus in woodlands, where it makes a funnel tube for its nest. ***Asthenargus paganus*** (Figure 17; **Linyphiidae**) is found rather rarely among mosses of moist open coniferous forest. Arne Grabolle (pers. Comm. 1 November 2012) told me of finding this species deep within mosses in Germany. ***Agyneta ramosa*** (Figure 19; **Linyphiidae**) has been recorded from a variety of habitats, often from mosses. ***Ceratinella brevipes*** (Figure 20; **Linyphiidae**) and its close relative ***Ceratinella brevis*** (Figure 21) are found in a wide array of habitats, including wet woodland with ***Sphagnum*** (Figure 45) and various types of grasslands and meadows.

Figure 13. The nocturnal ground spider, ***Haplodrassus moderatus*** (7 mm; **Gnaphosidae**), has been recorded from a range of damp habitats, ranging from moist meadows and fairly dry ***Sphagnum*** bogs, such as degraded raised bogs. Photo by Jørgen Lissner, with permission.

Figure 14. The ground spider, ***Gnaphosa leporina*** (8 mm; **Gnaphosidae**), shown here on the invasive moss ***Campylopus introflexus***, is common in damp heathlands of Northern Europe. During the daytime this nocturnal species can be found in cracks and cavities underneath ***Campylopus introflexus*** mats, an introduced and invasive moss that has now become widely distributed in heathland and dunes in many parts of Europe. Photo by Jørgen Lissner, with permission.

Figure 15. ***Gnaphosa leporina*** (**Gnaphosidae**) submale on mosses. Photo by Jørgen Lissner, with permission.

Figure 16. ***Scotina celans*** belongs to the spider family **Liocranidae** (spiny-legged sac spiders). The female shown here measures ca 4.5 mm. Specimens may be found by sifting dense mats of ***Hypnum cupressiforme/jutlandicum*** moss on *Calluna* heathland, but it may also be found among leaf litter. Photo by Jørgen Lissner, with permission.

Figure 17. The Palaearctic line-weaving spider, ***Asthenargus paganus*** (1.6 mm; **Linyphiidae**), is sometimes found rather abundantly in dense mats of red-stemmed feather moss (***Pleurozium schreberi***, Figure 18). This moss is very common in the ground layer of moist, open coniferous forest of Northern Europe, such as in the transition zones between forests and wet heathland. Photo by Rudolf Macek, with permission.

Figure 18. ***Pleurozium schreberi***. Photo by John Hribljan, with permission.

Figure 19. ***Agyneta ramosa*** (**Linyphiidae**), here a male measuring 2.2 mm. This Palaearctic species is mainly found in mosses of damp areas such as deciduous woodland and among leaf litter and mosses in forested edges of raised bogs. Photo by Jørgen Lissner, with permission.

Figure 20. ***Ceratinella brevipes*** (**Linyphiidae**) on moss. Photo by Jørgen Lissner, with permission.

Figure 21. ***Ceratinella brevis*** is a small species of the line-weaving spiders (**Linyphiidae**) with rather short legs and globular, coriaceous abdomen. The female shown here measures slightly less than 2 mm. It occurs in similar situations to those of the smaller congener, ***Ceratinella brevipes*** (Figure 20). Both species may be collected from mosses in a wide array of habitats. Photo by Jørgen Lissner, with permission.

Forests and Woodlands

Often we learn about organisms and their reliance on microhabitat features following a disturbance by examining what has disappeared and what correlates with that disappearance. Huber *et al*. (2007) did just that following clear-cutting of a Norway spruce forest (*Picea abies*) in Germany. They found that the control, uncut forest, spider fauna was dominated by one species, ***Coelotes terrestris*** (49% of the spider fauna) (Figure 22-Figure 23; **Amaurobiidae**), a species noted by Sereda *et al.* (2012) to be positively related to moss cover and negatively related to litter cover on the forest floor. They did not demonstrate what this relationship entailed, so it could be a matter of both preferring similar environmental conditions. In Denmark ***C. terrestris*** (8-15 mm) is found under large, rotten wood in very dark, moist places, but this primarily woodland species sometimes also occurs in mossy banks (Harvey *et al*. 2002; Nieuwenhuys 2011).

Figure 22. ***Coelotes terrestris*** (**Amaurobiidae**), a forest species that correlates positively with moss cover. Photo by Ed Nieuwenhuys, with permission.

Figure 23. ***Coelotes terrestris*** retreat among mosses and litter. Photo by James K. Lindsey, with permission.

During the two years following cutting, the families **Linyphiidae**, **Amaurobiidae**, **Agelenidae**, and **Clubionidae** all decreased drastically (Huber *et al*. 2007). These were replaced by the wolf spider family, the **Lycosidae** – large spiders that hunt their food. The disappearing species were characterized by those that were small (<3.0 mm) and large (>10.5) web builders with a preference for hygrophilic to medium moisture. These disappearing species typically live below ground or associated with the moss layer. As expected, the spiders that prefer open habitat increased in number. Huber and co-workers specifically pointed out that individuals that preferred a humus layer with mosses decreased. They interpreted this decrease to be the result of a higher light intensity.

On the other hand, some forest spiders seem to avoid bryophytes. Sereda *et al*. (2012) found that ***Tenuiphantes zimmermanni*** (Figure 24; **Linyphiidae**), a spider known from mosses elsewhere (Holm 1980), and *Tapinocyba insecta* (Figure 25; **Linyphiidae**) were negatively related to cover of mosses on the forest floor in a *Fagus sylvatica* forest in Europe, whereas Arne Grabolle (pers. comm. 1 November 2012) found ***Tapinocyba pallens*** (Figure 26) deep among mosses in Germany. *Tapinocyba insecta* was also negatively correlated with availability of prey, which could account for its negative correlation with mosses. Sereda and coworkers concluded that a patchy habitat was important in increasing the diversity of spiders on the forest floor.

Figure 24. ***Tenuiphantes zimmermanni*** female. Photo by Jørgen Lissner, with permission.

Figure 25. *Tapinocyba insecta* (**Linyphiidae**) female. This species is negatively correlated with bryophytes in a *Fagus sylvatica* forest. Photo by Jørgen Lissner, with permission.

Figure 26. ***Tapinocyba pallens*** male, a species that may occur deep withing mosses. Photo by Jorgen Lissner, with permission.

By comparing interiors and edges of old-growth forest and managed forests in southern Finland, Pajunen *et al*. (1995) were able to describe some of the specific habitats of spiders. They concluded that there were no habitat specialists among these forest species, with no species being strictly an old-growth species. Rather, differences in tree canopy cover accounted for differences in species assemblages. The **Lycosidae** (wolf spiders – hunters) and **Gnaphosidae** benefitted from clear-cutting, whereas small species, especially **Linyphiidae**, decreased from the greater exposure in plantations and open forests.

Nevertheless, a few species may be moss specialists. Jackson (1906) reported two members of **Theridiidae** [***Theonoe minutissima*** (as *Onesinda minutissima*; Figure 27), ***Robertus neglectus***] and three of **Linyphiidae** [***Palliduphantes pallidus*** (as *Lepthyphantes pallidus*; Figure 28), and ***Saaristoa firma*** (as *Tmeticus firmus*; Figure 29) as species of mosses in woods of the Tyne Valley, but mentioned no other habitat for them. ***Minyriolus pusillus*** (Figure 30; **Linyphiidae**) only seemed to occur among mosses in damp woods.

Figure 27. ***Theonoe minutissima*** (**Linyphiidae**). Photo by Jørgen Lissner, with permission.

Figure 28. ***Palliduphantes pallidus*** (**Linyphiidae**). Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 29. ***Saaristoa firma*** (**Linyphiidae**) on moss. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.

Figure 30. ***Minyriolus pusillus*** male on moss. Photo by Jørgen Lissner, with permission.

Among the moss-dwelling spiders in Yukon forests, Dondale *et al*. (1997) found ***Hackmania prominula*** **(Dictynidae**) in moss and litter in coniferous woods. This family is seldom recorded from mosses, but is known from tundra mosses (Koponen 1992; Logunov *et al.* 1998).

Atypidae

The **Atypidae** is not typically a moss-dwelling family. Nevertheless, when Jonsson (1998) used a sieving technique to distinguish the actual locations of the spiders in the Skäralid Gorge, southern Sweden, a forested location with a microclimate affected by the gorge, he found that mosses could be used by this spider. He found ***Atypus affinis*** (Figure 31) in its tube beneath the soil with its opening extending into the leaf litter, soil, stones, and mosses of the gorge. However, in British heathland this species tends to avoid soil covered by mosses (Dallas 1938) and it is not usually considered a bryophyte dweller elsewhere. Hence, it appears that some spiders, such as this one, are facultative bryophyte dwellers.

Figure 31. ***Atypus affinis*** (**Atypidae**) male exoskeleton; the insides have been eaten by a female of the species. Photo by Jørgen Lissner, with permission.

Clubionidae (Sac Spiders)

The sac spiders (**Clubionidae**) are represented by only one genus among the forest mosses. ***Clubiona lutescens*** (Figure 32) lives in a broad range of habitats and has been collected from mosses and litter of woodlands in the UK (Crocker & Daws 1996).

Figure 32. ***Clubiona lutescens*** on moss. Photo by Ed Nieuwenhuys, with permission.

Gnaphosidae (Ground Spiders)

This family has a wide range of sizes, as small as 3 mm and as large as 16 mm or more. Of the 2000 species, few are known from mosses. Two **Gnaphosidae** occurred among forest mosses at the Lesni Lom Quarry (Hula & Šťastná 2010). ***Micaria pulicaria*** (Figure 33), another non-specialist of warm, dry places, occurred among both grass and mosses in more open habitats of forest edges, clearings, and mountain corries (cirques). ***Zelotes clivicola*** (Figure 34), another abundant spider, can be found in pine and birch forests under stones and among mosses at the quarry. In the Arctic Yukon, Dondale *et al*. (1997) found ***Gnaphosa microps*** (Figure 35) in litter and moss in coniferous woods.

Figure 33. ***Micaria pulicaria*** (**Gnaphosidae**), one of the ant mimics. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.

Figure 34. ***Zelotes clivicola*** (**Gnaphosidae**) male. Photo by Glenn Halvor Morka, with permission.

Figure 35. ***Gnaphosa microps*** (**Gnaphosidae**). Photo by Glenn Halvor Morka, with permission.

Hahniidae (Dwarf Sheet Spiders)

The **Hahniidae**, a family of small spiders of about 2 mm, also can be found among woodland mosses. ***Hahnia helveola*** (Figure 36) builds its webs in mosses in woodlands and a variety of other UK habitats (Harvey *et al*. 2002). It lives at the roots of conifers, among needles, or concealed among the mosses, whereas ***Hahnia montana*** (Figure 37) lives among dead leaves and mosses (Jackson 1906;), where it also lives in the mountain forests of Tatras National Park, southern Poland (Svatoň & Kovalčík 2006); it places its small sheet web close to the ground among the mosses or under stones. ***Hahnia ononidum*** (as *H. H. mengei*) (Figure 38) occurred in association with *Vaccinium myrtillus*, *V. vitis-idaea*, and *Empetrum* sp. in a range of 100-400 m asl in Norway and used the cover of leaf litter as well as mosses (Hauge 1969). This species was active in Norway for the relatively long period of May to September.

Figure 36. ***Hahnia helveola*** (**Hahniidae**) on leaf litter. Photo by Jørgen Lissner, with permission.

Figure 37. ***Hahnia montana*** (**Hahniidae**). Photo by Jørgen Lissner, with permission.

In the Czech Republic, ***Cryphoeca silvicola*** (Figure 39; **Hahniidae**) lives in forest litter, mosses, and stone rubble, but it mainly occurs on lichens on tree bark (Szymkowiak & Górski 2004). We might find it among epiphytic bryophytes there as well.

Figure 38. ***Hahnia ononidum*** (**Hahniidae**) female. Photo by Glenn Halvor Morka, with permission.

Figure 39. ***Cryphoeca silvicola*** (**Hahniidae**) on bark. Photo by Rudolf Macek, with permission.

Linyphiidae

There are several subfamilies common among mosses in the species-rich Linyphiidae: **Erigoninae, Linyphiinae,** and **Micronetinae**. In the moist older forests, Huhta (1971) found that the typically smaller **Erigoninae** spiders occupied deeper positions in smaller cavities among mosses and humus than the somewhat larger **Linyphiinae** spiders.

The **Linyphiidae**, the largest spider family with moss-dwelling members, enjoys large numbers in moist, closed forests, especially where there is a well-developed cover of the moss ***Dicranum majus*** (Figure 40) (Pajunen *et al*. 1995). They also found that the smaller members in the subfamily **Erigoninae** are able to penetrate the smaller cavities deeper in the moss layer, the primary home of this subfamily. Small spiders such as **Linyphiidae** are able to attach their webs between the stems of mosses. The well-established mosses in older forests provide suitable websites for linyphiid species such as those of ***Lepthyphantes*** (possibly now in ***Palliduphantes***) and ***Macrargus rufus*** (Figure 41). As the canopy declines, larger (medium-sized) members of the **Linyphiidae** are able to take advantage of the improved growth of mosses. ***Porrhomma convexum*** (Figure 42) is a widespread linyphiid spider that commonly occurs in moss and in ground vegetation in woods (Agnarsson 1996).

Figure 40. ***Dicranum majus*** with capsules. Photo by David Holyoak, with permission.

Figure 41. ***Macrargus rufus*** (**Linyphiidae**) male on moss. Photo by James K. Lindsey, with permission.

Figure 42. ***Porrhomma convexum*** (**Linyphiidae**). Photo by Tom Murray, with permission.

In the Finnish forest study on spiders of the mosses ***Polytrichum*** (Figure 43-Figure 44) and ***Sphagnum*** (Figure 45), the **Linyphiidae** had the most species represented – far more than any other family (Biström & Pajunen 1989). Because of the large number of species in this family, and the small size of most members of the family, this high representation is predictable.

Figure 43. ***Polytrichum*** in bog at Azuma Yama, Japan. Photo by Janice Glime.

Figure 44. ***Polytrichum strictum*** cushion. Photo by Michael Lüth, with permission.

Figure 45. ***Sphagnum*** sp. in birch-hemlock forest, Michigan, USA. Photo by Janice Glime.

Several **Linyphiidae** were typical of both leaf litter and mosses in the Tyne Valley woodlands: ***Microneta viaria*** (Figure 46; more typical of dry leaves and sandy places where it escapes some predators by mimicking ants), ***Porrhomma cambridgei*** (as *Porrhomma oblongum*), ***Centromerus dilutus*** (as *Sintula diluta*), and ***Tapinocyba praecox*** (Figure 47). Several other species of Linyphiidae were present among both mosses and grasses in woodlands there: ***Dicymbium tibiale*** (damp areas; Figure 48), ***Micrargus herbigradus*** (as *Lophomma herbigradum*; Figure 49), and ***Agyneta cauta*** (as *Microneta cauta*).

Figure 46. ***Microneta viaria*** (**Linyphiidae**) male. Photo by Glenn Halvor Morka, with permission.

Figure 47. ***Tapinocyba praecox*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Figure 48. ***Dicymbium tibiale*** male on bryophytes. Photo by Jørgen Lissner, with permission.

Figure 49. ***Micrargus herbigradus*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Maelfait *et al*. (1990) found ***Eriogonella hiemalis*** and ***Minyriolus pusillus*** in wet woodlands where they were associated with a well-developed moss layer. They were abundant in wet Douglas fir (*Pseudotsuga menziesii*) stands.

In a study in Norway, Hauge (1969) found several linyphiid spiders that seemed to prefer mosses. The small (ca 1.38 mm) ***Diplocentria rectangulata*** (as *Microcentria pusilla*; Figure 50; **Linyphiidae**) occurred June – September, when it was "very abundant" in mosses, occurring only in mosses and in association with *Vaccinium myrtillus*, *V. vitis-idaea*, and *Empetrum* sp. as the dominant plants in the birch forests at 150-350 m asl. ***Macrargus multesimus*** occurred as ground dwellers in mosses and among dead leaves in birch forests at 150-300 m asl.

Figure 50. ***Diplocentria rectangulata*** female. Photo by Glenn Halvor Morka, with permission.

The small (<2 mm) ***Lepthyphantes antroniensis*** (as *L. exiguus*) seemed somewhat seasonal in Norway, appearing in collections June – September 1967 and June – August 1968 (Hauge 1969). It likewise occurred in mosses and

among dead leaves on the forest floor of birch at 150-250 m asl. The somewhat larger (ca 4 mm) ***Tmeticus nigriceps*** (as *Gongylidium nigriceps*; **Linyphiidae**) occurred at lower elevations (10-200 m asl) and was likewise collected in the summer months of June – August in mosses and among dead leaves in the birch forest. Hauge (1976) reported three new species of spiders in Norway. One of these, ***Meioneta saxatilis*** (**Linyphiidae**), occurred in moss cover in mixed deciduous and pine forests. Arne Grabolle (pers. comm. 1 November 2012) often finds ***Meioneta mossica*** (Figure 51) deep within mosses in Germany.

Figure 51. ***Meioneta mossica***, a deep moss dweller in Germany. Photo by Marko Mutanen, University of Oulu, through Creative Commons.

A large number of species of the linyphiid genus ***Walckenaeria*** are known from mosses in a variety of habitats, and the forest is no exception. ***Walckenaeria cuspidata*** (Figure 52) occurs among mosses in a wide range of habitats, including woods (Harvey *et al*. 2002). Jackson (1906) found ***W. cuspidata*** (as *Cornicularia cuspidata*; Figure 52) not only among mosses and grass in woods, but also in fields and marshes in the Tyne Valley of northern England. Jackson listed ***Walckenaeria dysderoides*** (as *Wideria fugax*; Figure 53) from mosses, but no habitat was given. ***Walckenaeria dysderoides*** (Figure 53) likewise was abundant in moss and detritus at the Lesni Lom Quarry in the Czech Republic, where it preferred humid habitats (Hula & Šťastná 2010).

However, in Flanders, Belgium, ***W. dysderoides*** was rare in forested sites, but occurred in well-developed moss carpets (Maelfait *et al*. 1990. ***Walckenaeria nodosa*** (Figure 54) seems to have a smaller range of habitats, but lives among mosses in woods (Harvey *et al*. 2002). In the Tyne Valley, UK, Jackson (1906) found ***W. obtusa*** (Figure 55) only from mosses, but Harvey *et al*. (2002) reported ***W. obtusa*** from mosses and grass in broad-leaved forests of the UK (Harvey *et al*. 2002). In addition to these UK species, Millidge (1983) reported species from Arctic and North American forested sites: ***W. anceps*** from mosses and conifer litter; ***W. communis*** (Figure 56) from moss in fir woods and also from a frog's stomach in Alaska (this species was one of only three **Linyphiidae** from mosses in the Arctic Yukon forests); ***W. faceta*** from moss on logs and deciduous litter; ***W. tricornis*** from mosses in high ground of the northeastern USA and in the Northwest Territories.

Figure 52. ***Walckenaeria cuspidata*** (**Linyphiidae**) female on moss. Photo by Jørgen Lissner, with permission.

Figure 53. ***Walckenaeria dysderoides*** (**Linyphiidae**) female on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 54. ***Walckenaeria nodosa*** (**Linyphiidae**) male on moss, where it lives in wet woods. Photo by Jørgen Lissner, with permission.

Figure 55. ***Walckenaeria obtusa*** (**Linyphiidae**), a moss dweller in broad-leaved forests. Photo by Ruth Ahlburg, with permission.

Figure 56. ***Walckenaeria communis***, one of many moss-dwelling ***Walckenaeria*** species. Photo by Tom Murray, through Creative Commons.

Logs can be important as habitats for both bryophytes and spiders. In some cases, these mosses serve as home for the spiders. Such is the case for ***Eremaeus stiktos***, an inhabitant of moss-covered logs in Washington, USA (Higgins 1962).

At the Lesni Lom Quarry in the Czech Republic, Hula and Šťastná (2010) found that the linyphiid ***Centromerus sylvaticus*** (Figure 57) was especially abundant in autumn and early spring, living among mosses and detritus in both open and forested sites. Jackson (1906) found this species among mosses, grasses, and leaf litter in the Tyne Valley of England.

In other locations, although the **Linyphiidae** usually predominate, species differ from the above studies. This is not surprising for animals with a short life span and limited dispersal ability. Pickavance and Dondale (2005) reported three Holarctic linyphiid spider species from Newfoundland, where they lived among mosses. ***Carorita limnaea*** (Figure 58) occurred in mixed coniferous woods as well as peatlands. ***Hilaira canaliculata*** lived among litter and mosses in shrub thickets. ***Sciastes dubius*** lived in damp mosses in mixed coniferous woods.

Figure 57. ***Centromerus sylvaticus*** (**Linyphiidae**) female. Photo by Jørgen Lissner, with permission.

Figure 58. ***Carorita limnaea*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

The linyphiid ***Diplocephalus latifrons*** (Figure 59) is a dominant species in the forests in the moist, shaded bottom of the Skäralid Gorge, southern Sweden, where it occurs among mosses in that dark habitat (Jonsson 1998). Accompanying it in this area is another linyphiid, ***Monocephalus castaneipes***, living among mosses on south-facing slopes, as well as on trees and ground.

Figure 59. ***Diplocephalus latifrons*** (**Linyphiidae**) male crossing a bryophyte. Photo by Jørgen Lissner, with permission.

The linyphiid ***Thyreosthenius parasiticus*** (Figure 60) is common in the northern hemisphere temperate region, occurring in mosses of woodlands and litter of old beech forests (Szymkowiak & Górski 2004). In the Geitaknottane Nature Reserve, western Norway, ***Gonatium rubellum***

(Figure 61) is typically found among mosses in the bilberry-pine and deciduous forests (Pommeresche 2002).

Figure 60. ***Thyreosthenius parasiticus*** female on thallose liverwort. Photo by Jørgen Lissner, with permission.

Figure 61. ***Gonatium rubellum*** on moss. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.

The Palaearctic linyphiid ***Centromerus arcanus*** (Figure 62) occurs among moss, grass, and leaf litter in coniferous forests and in acid bogs, especially in mountainous areas of the UK (Harvey *et al*. 2002). ***Diplocentria bidentata*** (Figure 63-Figure 64) is likewise a species of northern climates and is rare in lowland areas south of 59°N. It occurs in moss, as well as in grass, under stones, and in woodland litter (Locket & Millidge 1953; Harvey *et al*. 2002; Lissner 2011). It was common among mosses in the colder portions of the Skäralid Gorge, southern Sweden at 56°N, 13°E (Jonsson 1998). In their study of spiders of the scree slopes in the Czech Republic, Růžička and Klimeš (2005) found this species to be an exclusive inhabitant of mosses, and it never occurred in deep layers. Růžička (2011) likewise found it to occur exclusively among mosses on lower margins of scree slopes that had a permafrost-like microclimate at the mid altitudes (300-550 m asl) in the Czech Republic.

It is interesting that in their study of Arctic Yukon forests, Dondale *et al.* (1997) found only three members of **Linyphiidae**. ***Ceratinopsis stativa*** lives there in moss in deciduous or mixed woods. ***Lepthyphantes alpinus*** lives in moss in coniferous and birch woods. The third linyphiid species was the more widely known moss-dweller, ***Walckenaeria communis*** (Figure 56) on moss and litter in moist coniferous woods.

Figure 62. ***Centromerus arcanus*** female on moss. Photo by Glenn Halvor Morka, with permission.

Figure 63. ***Diplocentria bidentata*** female on moss. Photo by Jørgen Lissner, with permission.

Figure 64. Close view of ***Diplocentria bidentata*** female. Photo by Jørgen Lissner, with permission.

Neotropical and South American Forests

Tropical communities, even in higher elevations, are quite different from those at higher latitudes. Like other forests, forests in South America have their share of **Linyphiidae**, but these are not well studied. In general, the species reported from one tropical area differ from those in another. This is in part due to limited collecting and insufficient communication and observation among collecting groups, but it also speaks to the dispersal limitations between higher mountain areas in the tropical areas.

Miller (2007) reviewed the records of Neotropical erigonine spiders, providing many records of spiders among mosses in forests there. These included ***Scolecura propinqua*** in the humid mossy Chaco forest, Argentina, eastern Bolivia, and Paraguay, but its relationship to the mosses there is not clear. ***Intecymbium antarcticum*** and ***Sphecozone bicolor*** have been found in disturbed forests in Chile, where they live among mosses (Miller & Hormiga 2004; Miller 2007). The latter species was also found in dung traps in ***Sphagnum*** (Miller 2007). ***Millidgella*** (as *Valdiviella*) ***trisetosa*** occurs in mossy forest floor litter of *Nothofagus* and *Araucaria* forests at 1250 m in Chile, as well as litter from moss on the forest floor at 460 m and in wet forest moss at 500 m. ***Onychembolus anceps*** occurs in moss on logs in Chile.

Sphagnum in forests has its own unique species, including ***Microplanus odin*** from the cloud forest of western Panama at 1860 m, whereas ***Microplanus mollis*** was found by sifting mosses at 3450-3650 m asl at Laguna Iguaque, Colombia (Miller 2007). Also at Laguna Iguaque, Miller reports ***Gonatoraphis lysistrata*** and ***Triplogyna major*** from mosses. ***Labicymbium sturmi*** occurred on mosses and tracheophytes at 3600 m in the Cordillera Oriental region of Colombia.

In the far south, including southern Chile and South Georgian Islands, mosses shelter additional unique bryophyte-dwelling spiders. These include ***Notiomaso australis*** (Figure 65) in association with leaf litter, debris, and rocks, as well as among and under mosses (Miller 2007). ***Onychembolus subalpinus*** occurs in central and southern Chile and adjacent Argentina on the mossy forest floor among the litter, low shrubs, and moss near Chorio Hermoso at 350 m asl. Pitfall traps revealed that ***Neomaso claggi*** is widespread in this region, occurring among mosses that live in the shade among the tussock grass and from mosses on a wet streambank, as well as among low shrubs.

Figure 65. ***Notiomaso australis*** (possibly) from South Georgia. Photo by Roger S. Key, with permission.

Lycosidae

This family seems to be poorly represented among forest mosses, preferring sunny locations. Pajunen *et al*. (1995) report ***Pardosa riparia*** Figure 66) as numerous in ***Polytrichum commune*** (Figure 67) in swampy forests, but it appears that in drier forests this family is not typically a moss dweller.

Figure 66. ***Pardosa riparia*** female on moss. Photo by Walter Pflieigler, with permission.

Figure 67. ***Polytrichum commune*** var ***commune.*** Photo by David T. Holyoak, with permission.

But the forest following cutting in the Yukon Arctic region seems to be an exception, perhaps due to the greater light penetration, having a species-rich representation of the family. Dondale *et al*. (1997) found eight species of this family on or in mosses:

Arctosa alpigena on moss in spruce woods
Pardosa concinna in moss in coniferous woods
Pardosa furcifera in moss in coniferous woods
Pardosa hyperborea in moss in coniferous woods
Pardosa mackenziana in moss in coniferous woods, more rarely in deciduous woods
Pardosa moesta on moss in mixed woods
Pardosa uintana in moss in coniferous woods
Pardosa xerampelina somewhat rarely on moss in coniferous woods.

Malkaridae

This is a family of small spiders (Figure 68) that live mostly in leaf litter and mosses in temperate and tropical wet forests in Australia and New Zealand (Hormiga & Scharff 2020). Little is known about their life history. They are rarely observed in their natural habitat, so bryologists can contribute to our knowledge of their natural history.

Figure 68. ***Tingotingo tokorera*** (**Malkaridae**) male, member of a family of tiny spiders that live in leaf litter and mosses. Photo by S. E. Thorpe, through public domain.

Salticidae

Nieuwenhuys (2009) reports that ***Pseudicius encarpatus*** (Figure 69; **Salticidae**) can occur among mosses and leaf litter in forests of northwest Europe, although it typically occurs under bark. In the Tyne Valley of northern England, Jackson (1906) reported mosses from various substrata, demonstrating that most bryophyte-dwelling spiders are not bryophyte specialists. It is likely that the spiders treat the mosses in the same way many soil biologists do – as part of the litter layer. Hence, many species are common to both litter and mosses. ***Neon reticulatus*** (Figure 70), also in the **Salticidae**, lived among pine needles and mosses. In Iran, Logunov *et al*. (2006) found ***Chinattus caucasicus*** among mosses and liverworts in moist forest.

Figure 69. ***Pseudicius encarpatus***, a spider that occurs mostly on bark but can also occur among mosses and leaf litter in woodlands. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.

Figure 70. ***Neon reticulatus*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Theridiidae

Robertus lividus (Figure 71), a member of the **Theridiidae**, occurred among both mosses and stones; this genus occurs among mosses in a variety of habitats, but thus far the known species are different among the habitats. Hauge (1969) reported ***Robertus lyrifer*** (**Theridiidae**) from 150-350 m asl in Norway, only in mosses and in association with *Vaccinium myrtillus*, *V. vitis-idaea*, and *Empetrum* sp. as the dominant plants.

Figure 71. ***Robertus lividus*** (**Theridiidae**) female on moss. Photo by Jørgen Lissner, with permission.

Thomisidae

This family is not common among forest mosses. But in the Arctic Yukon three members are known (Dondale *et al*. 1997). ***Ozyptila sincera*** occurs in moss in coniferous woods. ***Xysticus britcheri*** occurs in moss in coniferous woods, whereas it occurred among lichens on the tundra. ***Xysticus emertoni*** (Figure 72) occurs in moss and litter under shrubs and trees.

Figure 72. ***Xysticus emertoni*** (**Thomsiidae)** female. Photo by John Sloan, with permission.

Rock Outcrops

Some forest spiders find their refuge among mosses on rock outcrops, and these may represent different families from the usual forest moss dwellers. ***Microhexura montivaga*** (Figure 73), in the **Dipluridae**, lives in moss mats that are damp but well drained in well-shaded areas of North Carolina, USA, forests (Coyle 1981, 1997, 1999; Harp 1992; Tarter & Nelson 1995; USFWS 2012). If the moss mat is too dry, the spider suffers desiccation, and if it is too wet, the large drops of water can interfere with absorption of air through the spiracles (USFWS 2012). Springtails (Collembola) are abundant in these moss mats and are the most likely food source (Coyle 1981, Harp 1992).

Figure 73. ***Microhexura montivaga***. Photo by Joel Harp, US Fish and Wildlife Service, through public domain.

Epiphytic Bryophytes

Epiphytic bryophytes have their spider fauna as well. In Hungary, Horváth and Szinetár (2002) used trunk-traps at 3 m height to compare the fauna in forest and urban habitats. They found that these mountain forest biotopes had a characteristic fauna, influenced by higher prey density, warmer climate, and lower predation in towns. Epiphytic moss fauna included ***Phrurolithus festivus*** (Figure 74; **Corinnidae**) and ***Clubiona comta*** (**Clubionidae**), but these species are not restricted to bryophyte habitats. It is likely that other spiders use the dense moss cover in the canopy of parts of the tropical rainforest and cloud forest, but these remain to be studied.

Figure 74. ***Phrurolithus festivus***. Photo by Trevor and Dilys Pendleton <http://www.eakringbirds.com/>, with permission.

Epiphytes reach their greatest density in the rain forests, including the tropics. Tropical spiders seem to have finer resource partitioning than those in the temperate regions, with both species and family diversity being higher in the tropics (Cardoso *et al*. 2011). Nevertheless, functional diversity there is also influenced by altitude and habitat structure. This finer niche partitioning is undoubtedly at least in part the result of the greater number of niches, coupled with the greater variety of both predator and prey organisms. Bryophytes in that region therefore might provide opportunities for greater specialization and diversity.

Peck and Moldenke (1999) have been concerned about invertebrates being spread to new areas in harvested mosses. In their study of these invertebrate communities, they found that the microspiders, **Micryphantidae** (**Linyphiidae**, *e.g.* Figure 46-Figure 50), were among the most abundant invertebrates in moss mats at the tips of shrub branches. The other abundant group was the springtail ***Sminthurus*** (Figure 75), a food item for spiders.

Figure 75. ***Sminthurinus aureus*** *forma* ***maculata***, a moss dweller that is spider food. Photo by Jan van Duinen, with permission.

Heath and Heather

Heathlands (Figure 76) are dominated by *Erica* and *Calluna*, among other shrubs, but they may also have a dense cover of mosses, including ***Sphagnum*** (Figure 45). These mosses can have their own fauna of spiders. In northwestern Europe, these habitats seem to be losing their ability to support their typical fauna. At the nature reserve Lüneburger Heide, Germany, the ladybird spider, ***Eresus kollari*** (Figure 77; **Eresidae**) (often included in ***Eresus cinnaberinus***), is one of these diminishing species (Krause *et al*. 2011). This species, a native of southern Europe, usually lives under rocks or in mosses (Wikipedia 2012a) where it requires a balance between exposure and warming (Krause *et al*. 2011). Krause *et al*. (2011) found that they could not separate the effects of *Calluna* cover from that of the moss layer in determining the suitability of the habitat. Both sexes dig their burrows in the organic layer, and the heat of insolation needs to penetrate to 10 cm (Krause *et al*. 2011). This spider subsists on millipedes (Figure 78) and beetles, and the successful male moves into the nest with the female and shares in eating the prey (Wikipedia 2012a).

Figure 76. Heath and heather occur with bryophytes among the boulders at Cwm Idwal National Nature Reserve in northern Wales. Photo by Janice Glime.

Figure 77. ***Eresus kollari***. Photo by Josef Mikuška, through EOL Public Domain.

Figure 78. ***Eresus cinnaberinus*** eating a millipede. Photo by Janos Bodor, through public domain at CalPhotos.

Gajdo and Toft (2000) used pitfall traps to examine spider fauna on a moisture transect from heathland to marsh in Denmark. They could find no clear relationship between vegetation structure or soil moisture and the pattern of spider species composition. This habitat extended from 100% moss cover to areas that had next to no mosses. But the mobility, especially of larger spiders, could easily make it difficult to detect preferences by using pitfall traps. This lack of relationship could even be the result of day-night migrations to optimize moisture, at least for the larger species.

Hauge (2000) used pitfall traps in a coastal heathland in western Norway to examine habitat distribution. The area included variation from plant associations dominated by the shrub *Calluna vulgaris* with several moss species to areas with a continuous, humid ***Sphagnum*** (Figure 45) mat and little *Calluna.* During an especially dry spring and early summer, the spiders, and particularly the **Linyphiidae**, diminished drastically toward mid-summer in the *Calluna vulgaris* area. In that habitat, linyphiids ***Minyriolus pusillus*** (Figure 30; already reported from forests), ***Erigonella hiemalis***; Figure 79), ***Gongylidiellum latebricola*** (Figure 80), and ***G. vivum*** (Figure 81) comprised 59% of the spider fauna. ***Gongylidiellum*** and ***Gonatium rubens*** (Figure 82) occurred among the *Calluna* habitat in damp places among moss, grass, and leaf litter (Bengtson & Hauge 1979; Holm 1980).

Figure 79. ***Erigonella hiemalis*** on moss. Photo by Jørgen Lissner, with permission.

Figure 80. ***Gongylidiellum latebricola*** on moss. This species occurs among mosses in heathlands. Photo by Jørgen Lissner, with permission.

Figure 81. ***Gongylidiellum vivum*** female on moss. Photo by Jørgen Lissner, with permission.

Figure 82. ***Gonatium rubens*** female on moss. Photo by Jørgen Lissner, with permission.

In the ***Sphagnum*** area of Norwegian heathlands, dominance shifted, and ***Robertus arundineti*** (45%; Figure 83; **Theridiidae**) and ***Minyriolus pusillus*** (10%; **Linyphiidae**) represented 55% of the species (Hauge 2000). Nevertheless, ***Sphagnum*** bogs are among the habitats that have some species in common with heathlands. In Great Britain, ***Hypselistes jacksoni*** (Figure 84; **Linyphiidae**) and ***Trochosa spinipalpis*** (Figure 8; **Lycosidae**) occur almost exclusively in bogs and wet heaths (Boyce 2004).

Figure 83. ***Robertus arundineti*** male. Photo by Jørgen Lissner, with permission.

Figure 84. ***Hypselistes jacksoni***. Photo by Jørgen Lissner, with permission.

On the Faroe Islands, several families are represented in association with mosses on the heathlands, with a new one, the **Zoridae**, present. ***Zora nemoralis*** (Figure 85) is found on the Faroe Islands and likewise is found among moss and heather in the UK (Harvey *et al*. 2002). ***Haplodrassus signifer*** (Figure 86; **Gnaphosidae**) lives among heather and moss at Kletsbrúgv, Faroe Islands, at 125 m altitude (Lissner 2011). ***Hahnia montana*** (Figure 37; **Hahniidae**), a spider also of woodlands, nests among mosses in the heathland (Harvey *et al*. 2002; Lissner 2011). But as usual, the **Linyphiidae** is the most diverse family among the bryophytes and is discussed below.

Figure 85. ***Zora nemoralis*** nymph on leaf litter. Photo by Walter Pfliegler, with permission.

Figure 86. ***Haplodrassus signifer*** sub-adult female on moss. Photo by Jørgen Lissner, with permission.

Clubionidae

The Clubionidae are the sac spiders, so-named because they build sac-like structures which serves as retreats. This once-large family now has only 15 genera and about 500 species. Few of these are represented on bryophytes. ***Clubiona trivialis*** (Figure 87) is known from mosses among heather and from moss in meadows and pastures (Schenkel, 1925; Holm 1980, Lissner 2010, 2011). Harvey *et al*. (2002) report ***Clubiona norvegica*** (Figure 88) from among mosses in the high moorland of the UK, a habitat similar to heathland.

Figure 87. ***Clubiona trivialis*** (**Clubionidae**) on leaf. Photo by Holger Gröschl, through Wikimedia Creative Commons.

Figure 88. ***Clubiona norvegica*** (**Clubionidae**) male on moss. Photo by Walter Pfliegler, with permission.

Linyphiidae

The **Linyphiidae** is a common family among mosses of heathlands. ***Oreonetides vaginatus*** (Figure 89) lives among moss in moist heaths, but it also lives in snow beds with *Salix herbacea* (Holm 1967). ***Poeciloneta variegata*** (Figure 90) lives under stones and among grass, moss, and heather (Brændegaard 1928). ***Semljicola faustus*** (Figure 91) is known from mosses and occurs on heather (Bengtson & Hauge 1979; Holm 1980), but I cannot document that it occurs on mosses in heather. Some species, such as ***Sintula comigera*** occurs in the wet heathlands of Flanders, Belgium, but also occurs in ***Sphagnum*** bogs (Maelfait *et al.* (1990).

Figure 89. ***Oreonetides vaginatus*** (**Linyphiidae**) female among mosses and litter. Photo by Jørgen Lissner, with permission.

Figure 90. ***Poeciloneta variegata*** (**Linyphiidae**) female on leaf. Photo ©Pierre Oger, with permission.

Figure 91. ***Semljicola faustus*** (**Linyphiidae**) female. Photo by Jørgen Lissner, with permission.

In the Faroe Islands, Lissner (2011) reported ***Agyneta subtilis*** from similar habitats to those of ***A. decora*** (Figure 92) in Britain, where it lives among mosses in a variety of habitats, including mosses in heathlands. However, in Iceland ***A. decora*** is known only from mossy grassland and meadows, not heathlands (Agnarsson 1996). ***Centromerus arcanus*** (Figure 62) lives in mosses and can be found in grass and shrub heath (Bengtson & Hauge 1979; Bengtson *et al*. 2004), as well as mosses in forests. ***Ceratinella brevipes*** (Figure 20) was located by sweeping heather and sifting moss amongst grass on a slope (Holm 1980); it also occurs on mosses in forests and other habitats.

Figure 92. ***Agyneta decora*** (**Linyphiidae**) female on moss. Photo by Jørgen Lissner, with permission.

Mecynargus morulus (Figure 93) occurs on high ground (200-880 m) among mosses, grass, gravel, and under stones (Lissner 2011). Previously, Holm (1967) had reported this species to be common in ***Hylocomium*** (***splendens***?) (Figure 94) on moss heaths in the Faroes. It is typically a high ground species in the Faroe Islands, found at 200-880 m asl in moss, grass, gravel, and under stones (Lissner 2011). ***Palliduphantes ericaeus*** (Figure 95) likewise occurred in ***Hylocomium***, but at altitudes below 200 m (Holm 1980). Jackson (1906) reported ***P. ericaeus*** (as *Lepthyphantes ericaceus*) among mosses, heather, and leaves in the Tyne Valley, UK.

Figure 93. ***Mecynargus morulus*** (**Linyphiidae**) on moss. Photo by Jørgen Lissner, with permission.

Figure 94. ***Hylocomium splendens***, showing its weft life form, in the Keweenaw Peninsula of Michigan. Photo by Janice Glime.

Figure 95. ***Palliduphantes ericaeus*** (**Linyphiidae**) on moss. Photo by Jørgen Lissner, with permission.

Lissner (2011) found ***Tiso vagans*** among moss and rocks on the Faroe Islands. In Britain, it is known from a wide variety of habitats, including moss, grass and detritus in heathland (Harvey *et al*. 2002).

Improphantes complicatus (Figure 96) occurs in both Greenland (Lissner 2011) and the Yukon tundra (Dondale *et al*. 1997) in a variety of damp and dry habitats, including among moss, litter, and under stones on heaths (Figure 76). ***Leptorhoptrum robustum*** (Figure 97) has been found in moss among heather vegetation up to 750 m (Brændegaard 1928; Bengtson & Hauge 1979; Holm 1980).

Figure 96. ***Improphantes complicatus*** (**Linyphiidae**). Photo by Gergin Blagoev, through Creative Commons.

Figure 97. ***Leptorhoptrum robustum*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Tenuiphantes mengei (Figure 98) has several habitats, including grass and moss of dry heath in Britain (Harvey *et al*. 2002). ***Tenuiphantes zimmermanni*** (Figure 24) has an even broader range of habitats where it is associated with bryophytes, including forests and moorland with heather (Holm 1980), where it occurs among the heather, grasses, sedges, and mosses (Harvey et al. 2002).

Figure 98. ***Tenuiphantes mengei*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

As in the woodlands, the most species-rich linyphiid moss-dweller genus in the heathlands is ***Walckenaeria***. ***Walckenaeria antica*** (Figure 99), also in woodlands, lives below 300 m in the Faroe Islands (Holm 1980), where it is known from mosses among heather (Lissner 2011). ***Walckenaeria clavicornis*** (Figure 100) occurs at 50-600 m in the Faroes, living among mosses, gravel, and stones, but in Greenland it occurs among mosses in "luxuriant heaths" (Holm 1967; Millidge 1983). ***Walckenaeria karpinskii*** (as *W. holmi*) lives among ***Sphagnum*** and other mosses in North America and Greenland, as well as under stones, in the moist dwarf-bush heath (Millidge 1983). ***Walckenaeria nodosa*** (Figure 54), also found in the Faroes, is known from damp heathland in southern England (Harvey *et al*. 2002). ***Walckenaeria nudipalpis*** (Figure 101) occurs below 300 m in the Faroes (Holm 1980), occurring among mosses in heather (Lissner 2011). Jackson (1906) reported ***W. monoceros*** (as *Prosopotheca monoceros*) and ***W. acuminata*** (Figure 102) in the Tyne Valley, UK, among moss in moorlands, a landform that can have vegetation closely related to heath. Maelfait *et al*. (1990) considered ***W. dysderoides*** (Figure 53) to be rare, but typical of open heath with well-developed moss carpets in Flanders, Belgium.

Figure 99. ***Walckenaeria antica*** (**Linyphiidae**) on sand. Photo ©Pierre Oger, with permission.

Figure 100. ***Walckenaeria clavicornis*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Figure 101. ***Walckenaeria nudipalpis*** (**Linyphiidae**) male on bryophytes. Photo by Jørgen Lissner, with permission.

Figure 102. ***Walckenaeria acuminata*** (**Linyphiidae**) male on moss. Notice the projection on the head where the eyes are located. Photo by Jørgen Lissner, with permission.

Marshes and Moist Meadows

Cattail marshes generally lack bryophytes, but some marshes have their own bryophyte flora. Kupryjanowicz (2003) described the spider fauna of sedge marshes and sedge-moss marshes in Poland. In these two habitats, he collected 14,566 individuals, comprising 173 species. The family mix in these Polish marshland locations is rather different from that of the previously discussed habitats, and certainly many of the species differ. Among these, ***Pardosa sphagnicola*** (Figure 103; **Lycosidae**) and ***Pirata tenuitarsis*** (Figure 104; **Lycosidae**) inhabit mosses in the sedge-moss marshes; these two species are active hunters and are able to run across the surface of water in hunt of food (Figure 105).

It is not surprising that some sphagnophilous species [***Pardosa sphagnicola*** (Figure 103), ***Pirata uliginosus*** (Figure 106), ***P. tenuitarsis*** (Figure 104), and ***Antistea elegans*** (Figure 3; **Hahniidae**)] live in sedge moss marshes, along with other peat-bog related species, *e.g.* ***Aphileta misera*** (Figure 107; **Linyphiidae**; reported by Jackson to live only among mosses and only in marshes in the Tyne Valley of England), ***Gnaphosa nigerrima*** (Figure 4; **Gnaphosidae**), and ***Neon valentulus*** (Figure 108; **Salticidae**). ***Drassyllus lutetianus*** (Figure 109; **Gnaphosidae**) likewise occurs among mosses in marshes as well as in bogs (Koponen 2002).

Figure 103. ***Pardosa sphagnicola*** (**Lycosidae**) on moss. Photo by James K. Lindsey, with permission.

Figure 104. ***Pirata tenuitarsis*** (**Lycosidae**) female among ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 105. ***Pirata tenuitarsis*** (**Lycosidae**) on the water surface. Photo by James K. Lindsey, with permission.

Figure 106. ***Pirata uliginosus*** (**Lycosidae**) male subadult. Photo by Walter Pflieigler, with permission.

Figure 107. ***Aphileta misera*** (**Linyphiidae**) on moss. Photo by Morten D. D. Hansen, with permission.

Figure 108. ***Neon valentulus*** (**Salticidae**). Photo by Sarefo through Wikimedia Commons.

Figure 109. ***Drassyllus lutetianus*** (**Gnaphosidae**), a moss-dweller in marshes and bogs. Photo by Jan Barvinek, through Creative Commons.

At one marsh site, three species dominated in the mosses: ***Erigonella ignobilis*** (Figure 110; **Linyphiidae**) (8%), ***Porrhomma pygmaeum*** (Figure 111; **Linyphiidae**) (6.7%) – also reported by Storey (2012), and ***Sitticus caricis*** (Figure 112; **Salticidae**) (9%). At another site, dominant species typical of mosses were ***Ozyptila gertschi*** (**Thomisidae**), ***Neon valentulus*** [Figure 108; **Salticidae** (***N. reticulatus*** occurs in forests on mosses)], and ***Sitticus caricis*** (**Salticidae**), species that were subdominant in the pitfall trap catches. ***Larinia jeskovi*** (**Araneidae**) is a rare species elsewhere, but survives in the marshlands by overwintering among the mosses.

Figure 110. ***Erigonella ignobilis*** (**Linyphiidae**). Photo by Jørgen Lissner, with permission.

Figure 111. ***Porrhomma pygmaeum*** (**Linyphiidae**) on moss. Photo by Jørgen Lissner, with permission.

Figure 112. ***Sitticus caricis*** (**Salticidae**) on moss. Photo by Jørgen Lissner, with permission.

Linyphiidae

Some of the earliest records of spiders among mosses in marshland are those of Jackson (1906) for the Tyne Valley, UK, who listed only two, both in the Linyphiidae.

Cnephalocotes obscurus (Figure 113) occurs among both mosses and rushes in marshes, whereas ***Oedothorax gibbosus*** (as *Gongylidium gibbosum*; Figure 114) lives among mosses and grasses in marshes.

Figure 113. ***Cnephalocotes obscurus*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Figure 114. ***Oedothorax gibbosus*** (**Linyphiidae**). Photo by Morten D. D. Hansen, with permission.

Holm (1980) found a number of **Linyphiidae** in moist meadows of the Faroe Islands. He found ***Palliduphantes ericaeus*** (Figure 95) at altitudes below 200 m by sifting moss, mostly ***Hylocomium*** (Figure 94). ***Centromerus arcanus*** (Figure 62) occurred in moss in a meadow at 180-200 m altitude (Holm 1980); it is a **eurytopic** (able to tolerate a wide range of habitats and conditions) species also occurring in forests and heathland. ***Leptorhoptrum robustum*** (Figure 97) occurs among moss and grass in meadows up to 750 m (Holm 1980; Brændegaard 1928). Lissner (2011) reported a number of species from wet meadows there, including the linyphiid ***Hypomma bituberculatum*** (Figure 115) from a very wet, gently sloping meadow with abundant mosses.

The common moss-dwelling linyphiid genus ***Walckenaeria*** is again represented in marshes, including the Faroe Islands (Lissner 2011), with species repeating several found in the forest: ***Walckenaeria cuspidata*** (Figure 52) among mosses in wet meadows at 260 and 290 m altitude (Holm 1980), also in marshes of the Tyne Valley, northern England (Jackson 1906); ***W. nodosa*** (Figure 54) among mosses in marshes in the Faroes and in southern England (Harvey *et al*. 2002). ***Walckenaeria nudipalpis*** (Figure 101), known also from heathlands elsewhere, in the Faroe Islands is mostly below 300 m among mosses in moist meadows and bogs (Holm 1980; Lissner 2011). Jackson (1906) reported ***W. nudipalpis*** (Figure 101) among moss in "swampy" places, which may include several habitat types. ***Walckenaeria acuminata*** (Figure 102) lives among moss, grass, and dead leaves in marshes and other habitats, including heathland (Jackson 1906).

Figure 115. ***Hypomma bituberculatum*** (**Linyphiidae**) female among mosses. Photo by Jørgen Lissner, with permission.

Swampy Places

The term swamp has a myriad of definitions, and I cannot pretend to understand what definition was intended by the various researchers over a century or more from all over the globe. For example, Hula and Šťastná (2010) reported that the linyphiid ***Walckenaeria dysderoides*** (Figure 53) occurs among mosses and detritus in "humid habitats," leaving the habitat open to some interpretation. Likewise, Maelfait *et al*. (1990) reported that ***Agyneta ramosa*** (Figure 19) was rare in Flanders, Belgium, but it occurred in open "marshy" situations that had a thick moss layer. Therefore, I have included this section only as a place to represent those spiders from habitats identified by the researchers as swamps or swampy.

As already discussed for marshes and forests, bryophyte-dwelling spiders often occur in other habitats and on other substrata in those habitats. For example, in the Tyne Valley, UK, Jackson (1906) reported a number of **Linyphiidae**. ***Hilaira excisa*** lives among grass, rushes, and moss in swamps. Grasses often seem to provide alternative habitats to mosses, with ***Bathyphantes nigrinus***, ***Gongylidiellum vivum*** (Figure 81; also in heathland), ***Tenuiphantes cristatus*** (as *Lepthyphantes cristatus*; Figure 116), and ***Semljicola faustus*** (as *Sintula fausta*; Figure 91) among both mosses and grasses in swamps. But Jackson also reported some species only from mosses: ***Diplocephalus permixtus*** (Figure 117), ***Drepanotylus uncatus*** (as *Hilaira uncata*; Figure 118), ***Erigonella ignobilis*** (as *Troxochrus ignobilis*; Figure 110), ***Erigonella hiemalis*** (as *Troxochrus hiemalis*; Figure 79). I have found only one species thus far, ***Robertus neglectus*** from among moss in swamps, but also in woods, that belongs to a different family, the **Theridiidae**. But this may be an artifact of the way people have described or named the habitat.

Figure 116. ***Tenuiphantes cristatus*** (**Linyphiidae**) male on detritus. Photo by Walter Pfliegler, with permission.

Figure 117. ***Diplocephalus permixtus*** (**Linyphiidae**) female on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 118. ***Drepanotylus uncatus*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Aquatic

Few spiders are aquatic, and even fewer have any known association with mosses. Pickard-Cambridge (1860) mentioned that ***Argyronecta aquatica*** (Figure 119-Figure 120; **Cybaeidae**) is an occasional spider in Southport, UK, where it can be found in moss dykes. This unique spider is the only one known to spend its entire life under water (Wikipedia 2012b). This is possible for this air breather because of unique behavior similar to that of some aquatic insects. It uses a **diving bell**. It traps air in a bubble (or grabs an air bubble) and holds the bubble with hairs on its abdomen and legs. It is then able to exchange CO_2 with the O_2 from the bubble. The bubble loses CO_2 and gains O_2 from the water by diffusion. When the diffusion rate is unable to replace the oxygen to a sufficient amount, the spider grabs another air bubble.

Females of ***Argyroneta aquatica*** (Figure 119-Figure 120) go a step farther (Schütz & Taborsky 2003). They build an underwater diving bell web that they fill with air. This nest is used for molting, mating, raising offspring, and even for digesting prey. They leave the bells only to dart out to catch prey that have the misfortune of touching the bell or the threads that anchor it. The male bell is smaller, and males are more active in pursuing prey. Since their nets serve fewer purposes, the air supply lasts longer.

Figure 119. ***Argyroneta aquatica*** (**Cybaeidae**) female water spider, inhabitant of fens and bogs. Photo by Jørgen Lissner, with permission.

Figure 120. ***Argyroneta aquatica*** (**Cybaeidae**) showing air bubble on underside. Photo by Norbert Schuller, through Wikimedia Commons.

Insects often get the air for their diving bells from the photosynthetic air bubbles on plant leaves. It would be interesting to determine if the spiders that live among or near bryophytes likewise use this source of oxygenated air.

Sand Dunes

One does not usually think about sand dunes as a bryophyte habitat, but in fact, bryophytes, particularly

mosses, can be important stabilizers on the sand. For spiders, they are important refuges for moisture and cover, especially from both the heat and light of the sun.

Merkens (2000) divided inland dunes in northern Germany into four categories in an attempt to delimit habitats for spiders there: lichen cover, grass cover, herb cover, moss cover. He found that not only the type of vegetation cover (especially lichen, moss, and herbs), but also the kind of neighboring habitat, play important roles to influence the species composition of the inland dunes. Among the 286 species on the dunes, he found among the 34 species with significant ($p<0.05$) habitat correlations, nine species were significantly correlated with moss cover. These were in families familiar from forest studies, but are mostly species not previously cited. **Salticidae**: ***Aelurillus v-insignitus*** (Figure 121-Figure 122); **Lycosidae**: ***Alopecosa fabrilis*** (Figure 123-Figure 126), ***Trochosa terricola*** (Figure 127); **Linyphiidae**: ***Bathyphantes gracilis*** (Figure 129), ***Centromerita concinna*** (Figure 130), ***Centromerus sylvaticus*** (Figure 57; also occurs on mosses in forests), ***Typhochrestus digitatus***; **Gnaphosidae**: ***Drassyllus pusillus*** (Figure 131); **Hahniidae**: ***Hahnia nava*** (Figure 132-Figure 133). Merkens found that on these dunes, the spider community seems to follow the successional stage. Some are restricted to the initial stage of open sand and little plant cover, whereas others depend on a dense cover of mosses and herbs that represent the advanced stages of succession.

Figure 121. ***Aelurillus v-insignitus*** (**Salticidae**) male, a species correlated with moss cover in northern Germany dunes. Photo by Ed Nieuwenhuys, with permission.

Figure 122. ***Aelurillus v-insignitus*** (**Salticidae**) female blending with color among rocks. Photo by Ed Nieuwenhuys, with permission.

Figure 123. ***Alopecosa fabrilis*** (**Lycosidae**) male on lichens. Photo by Jørgen Lissner, with permission.

Figure 124. ***Alopecosa fabrilis*** (**Lycosidae**) head of male showing eyes. Photo by Jørgen Lissner, with permission.

Figure 125. ***Alopecosa fabrilis*** (**Lycosidae**) female. Photo by Jørgen Lissner, with permission.

Figure 126. ***Alopecosa fabrilis*** (**Lycosidae**) female with spiderlings on back. Photo by Jørgen Lissner, with permission.

Figure 127. ***Trochosa terricola*** (**Lycosidae**) male on moss. Photos by Jørgen Lissner, with permission.

Figure 128. ***Bathyphantes gracilis*** (**Linyphiidae**) on its web. Photos by Jørgen Lissner, with permission.

Figure 129. ***Bathyphantes gracilis*** (**Linyphiidae**) on its web. Photos by Jørgen Lissner, with permission.

Figure 130. ***Centromerita concinna*** male on moss. Photo by Jørgen Lissner, with permission.

Figure 131. ***Drassyllus pusillus*** (**Gnaphosidae**) male on sand with moss. Photo by Jørgen Lissner, with permission.

Figure 132. ***Hahnia nava*** (**Hahniidae**) male. Photo by Jørgen Lissner, with permission.

Figure 133. ***Hahnia nava*** (**Hahniidae**) female. Note that the white marks are reflections on the shiny black thorax. Photo by Jørgen Lissner, with permission.

In coastal dunes of Belgium, marram grass (*Ammophila arenaria*) and mosses often dominate the dunes (Bonte *et al*. 2002). As in Germany, ***Alopecosa fabrilis*** (Figure 123-Figure 126; **Lycosidae**) dominated the spider fauna, particularly in areas with a dominance of lichens and mosses near the inner dune front. ***Alopecosa fabrilis*** was the only one of the German dune species with habitat correlations that correlated only with moss cover (Merkens 2000). On the other hand, *Oedothorax apicatus* and *Arctosa perita* had a significant negative correlation with moss cover.

In these Belgian dunes, families were similar, but fewer, than those in forests. In addition to ***Alopecosa fabrilis*** (**Lycosidae**), mosses served as habitat to ***Micaria dives*** (Figure 134; **Gnaphosidae**), ***Zelotes longipes*** (Figure 135; **Gnaphosidae**), and ***Walckenaeria stylifrons*** (Figure 136; **Linyphiidae**) – a species different from that of previously discussed habitats (Bonte *et al*. 2002). The genus ***Micaria*** is **diurnal** (active in daytime) and runs about rapidly in the bright sunshine, hunting for food (Lissner 2011). Bell *et al*. (1998) found a different species of ***Zelotes***, the widespread European spider species ***Zelotes latreillei*** (Figure 137). This native of chalk and coastal areas of Europe is positively correlated with the number of plant species in sand dunes. It lives in areas with a rich, compact "thatch" of low vegetation where bare ground is partly replaced with cover of moss, debris, and other vegetation.

Figure 134. ***Micaria dives*** (**Gnaphosidae**) female, a diurnal sand dune spider that lives where lichens and mosses are dominant. This genus mimics ants, perhaps discouraging some predators. Photo ©Pierre Oger, with permission.

Figure 135. ***Zelotes longipes*** female on moss. Photo by Jørgen Lissner, with permission.

Figure 136. ***Walckenaeria stylifrons*** (**Linyphiidae**) female. Photo by James K. Lindsey, with permission.

Figure 137. ***Zelotes latreillei*** (**Gnaphosidae**) on sand. Photo by James K. Lindsey, with permission.

Clubiona lutescens (Figure 32; **Clubionidae**) occurs in a wide variety of habitats, including woodlands, grasslands, marshes, gardens, waste places, and stony seashores (Crocker & Daws 1996), where it can be found among bryophytes.

For any bryophyte habitat to be suitable, it must not only provide appropriate heat, moisture, and cover, but it must be a place where there is also food available. In the coastal dunes of Belgium, Bonte and Mertens (2003) found that both spiders and springtails (family **Isotomidae**) diminish in numbers as grass coverage increases and soil

formation increases. It is their conclusion that species aggregations of both groups are driven by these changes, resulting in their aggregation in areas with high moss coverage.

Grasslands and Pastures

Although grasslands are not considered mossy habitats, close examination will often reveal species like those of ***Brachythecium*** (Figure 138), ***Bryum*** spp. (Figure 139), ***Racomitrium canescens*** (Figure 140), ***Syntrichia ruralis*** (Figure 141), and ***Tortella flavovirens*** (Figure 142-Figure 143) (Jun & Rozé 2005). Krajak *et al*. (2000) considered the moss and litter layers in grasslands to be important for the spider communities. They found that the soils under the mosses in the sedge-moss community of grasslands had the highest water-holding capacity and maintained a stable moisture level throughout the year.

Figure 138. ***Brachythecium albicans***, a moss that is an ephemeral colonist in sand dunes. Photo by Michael Lüth, with permission.

Figure 139. ***Bryum algovicum*** on sand, a species that stabilized dunes. Photo by David T. Holyoak, with permission.

Figure 140. ***Racomitrium canescens***, a dry grassland moss in Europe. Photo by Michael Lüth, with permission.

Figure 141. ***Syntrichia ruralis***, a moss that helps to stabilize foredunes. Photo by David T. Holyoak, with permission.

Figure 142. ***Tortella flavovirens***, a moss that survives on sand dunes, in its hydrated state. Photo by Michael Lüth, with permission.

Figure 143. ***Tortella flavovirens*** in its desiccated state. Photo by Michael Lüth, with permission.

Pastures are often wetter than wild grasslands, but one might consider these two habitats as a continuum, with "fields" occurring somewhere in that continuum. Nevertheless, I have found little evidence of overlapping species, albeit based on a very small sample.

Clubionidae

As mentioned earlier, ***Clubiona lutescens*** (**Clubionidae**; Figure 32) occupies a wide range of habitats in the UK and elsewhere, with mosses in grasslands among these (Harvey *et al*. 2002).

Gnaphosidae

Micaria pulicaria (Figure 33) is likewise very abundant among grass and moss in various open habitats at the Lesni Lom Quarry (Hula & Šťastná 2010), but occurs in forests in the Tyne Valley of England.

Linyphiidae

This habitat has its own fauna of spiders, and some may depend on bryophytes for cover or moisture. As usual, a number of these are in the **Linyphiidae**. In grasslands of Essex, UK, ***Cnephalocotes obscurus*** (Figure 113) lives among the detritus, mosses, and other herbaceous vegetation (Spider and Harvestman Recording Scheme 2012), in addition to swampy places cited above. Roberts (1987) reported ***Peponocranium ludicrum*** (Figure 144) from mosses and grasses in the UK. Johnston and Cameron (2002) reported ***Sintula corniger*** (Figure 145) among mosses, grasses, and litter in the UK. It is not clear if these species occur among mosses in grassland.

Figure 144. ***Peponocranium ludicrum*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Figure 145. ***Sintula corniger*** (**Linyphiidae**) female on moss. Photo by Jørgen Lissner, with permission.

Also in Britain, ***Savignia frontata*** (Figure 146), ***Tenuiphantes zimmermanni*** (Figure 24), and ***Tiso vagans*** live in grasslands and among mosses (Harvey *et al*. 2002); ***T. zimmermanni*** is also known from forests and heathlands, as discussed above.

Figure 146. ***Savignia frontata*** male. Photo by Jørgen Lissner, with permission.

Holm (1980) reports ***Ceratinella brevipes*** (Figure 20), a moss inhabitant in many of its habitats, from sifting mosses growing among grasses on a slope and ***Gongylidiellum vivum*** (Figure 81; also from heath, swampy land, and grassland) from grass heaths in the UK. ***Leptorhoptrum robustum*** (Figure 97) also occurred in open grass heaths, more rarely in other habitats (Bengtson & Hauge 1979).

Jackson (1906) found a number of members of **Linyphiidae** in the Tyne Valley, England. ***Panamomops sulcifrons*** (as *Panamomops bicuspis*) occurred among mosses in fields or pastures. Members of the ubiquitous ***Walckenaeria*** included ***W. acuminata*** (Figure 102) and ***W. cuspidata*** (Figure 52), both previously discussed from other bryophyte habitats, occurring in fields and pastures. ***Walckenaeria cuspidata*** (Figure 52) in Iceland prefers moist grassland and moss there as well (Agnarsson 1996).

At the Lesni Lom Quarry (Brno-Hady), a nature preserve in the Czech Republic, ***Centromerus sylvaticus*** (Figure 57), also on mosses in sand dunes and forests, is a very abundant species in autumn and early spring in grasslands there; it is common in open habitats (Hula & Šťastná 2010).

Grasslands in the Arctic can be quite different from those in the temperate zone. In Iceland, ***Agyneta decora*** (Figure 92), also known from heathlands, occurs there in mossy grasslands (Agnarsson 1996) and ***A. subtilis***, likewise known from mosses in heathlands, occurs among both mosses and grasses (Harvey *et al*. 2002).

Improphantes complicatus (Figure 96) occurs over a wide range of altitudes in Iceland, where it occupies mosses and wet grasslands (Agnarsson 1996); it also occurs in heathlands in Greenland. ***Porrhomma montanum*** (Figure 160) occurs among grassland and moss in Iceland (Agnarsson 1996).

Sunny banks often have different vegetation and thus different spiders from the main habitat. For example, Jackson (1906) reported ***Syedra gracilis*** (as *Syedra pholcommoides*) as rare among mosses and grasses on sunny banks. Miller and Hormiga (2004) found ***Myrmecomelix leucippus*** among mosses on a xeric slope in the Neotropics in Peru.

Lycosidae

Among the bryophyte dwellers, the **Lycosidae** are most common in marshes and bogs, but they also occur in grasslands. In the Faroe Islands, ***Pardosa palustris*** (Figure 197) occurs among mosses and in grassy heaths (Schenkel 1925; Bengtson and Hauge 1979; Holm 1980; Lissner 2011), and most likely occurs among mosses in those heaths.

Thomisidae

The **Thomisidae** are represented by several genera. Jackson (1906) found the rare ***Trichopternoides thorelli*** (as *Entelecara thorelli*) and ***Xysticus bifasciatus*** (Figure 147) among mosses in fields or pastures of the Tyne Valley, England. ***Ozyptila pullata*** (Figure 148) occurs among mosses in calcareous grassland in the UK (Harvey *et al*. 2002).

Figure 147. ***Xysticus bifasciatus*** (**Thomisidae**). Photo by Ed Nieuwenhuys, with permission.

Figure 148. ***Ozyptila pullata*** (**Thomisidae**). Photo ©Pierre Oger, with permission.

Mountains and Altitudinal Relations

Mountains create a series of climate zones in which plant communities differ. Increased elevation changes light intensity, increases UV-radiation (a problem for spiders), shortens the growing season, promotes lower temperatures, creates moisture differences, and can have different substrata. All of these differences promote differences in bryophyte communities as well, and the role of bryophytes for spiders is likely to change in consort with these differences.

Unfortunately, few studies connect substrate such as mosses with the mountain habitat or with elevational differences in climate and plant communities. In the Tyne Valley, UK, Jackson (1906) alludes to it when he states that ***Ceratinella brevis*** (Figure 149; **Linyphiidae) –** a species known from mosses in forests – occurs to a "considerable altitude" among grass, **mosses**, and dead leaves. A major contributor to altitudinal records, Lissner (2011) frequently cites altitude in his collections from the Faroe Islands.

Figure 149. ***Ceratinella brevis*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Svatoň and Kovalčík (2006) provided an extensive spider study in the Tatras National Park, southern Poland, with a number of peaks over 2500 m asl, although elevational effects are not discussed. Mountain forest

mosses house ***Cryphoeca carpathica*** (Figure 150; **Hahniidae**), ***Hahnia difficilis*** (**Hahniidae**), and the common moss-dweller, ***Hahnia montana*** (Figure 37). Other muscicolous species include ***Robertus truncorum*** (Figure 151; **Theridiidae**) and the rarer ***Alopecosa pinetorum*** (Figure 152; **Lycosidae**). Boggy areas there support ***Pardosa sordidata*** (**Lycosidae**) and ***Robertus scoticus*** (Figure 153). It is interesting that ***Robertus*** occurs in several different habitats described above, but each is reported as a different species.

Figure 150. ***Cryphoeca carpathica*** (**Hahniidae**). Photo by Biopix, through Creative Commons.

Figure 151. ***Robertus truncorum*** (**Theridiidae**) female on moss. Photo by Walter Pfliegler, with permission.

Figure 152. ***Alopecosa pinetorum*** (**Lycosidae**) female. Photo by Walter Pfliegler, with permission.

Figure 153. ***Robertus scoticus*** (**Theridiidae**) female on moss. Photo by Walter Pfliegler, with permission.

Araneidae

This family is not often represented among bryophytes. However, in the Tatra Mountains Svatoň and Kovalčík (2006) found ***Araneus nordmanni*** (Figure 154) in a peat bog. This species is more common in the USA and Canada; it is rare in Europe.

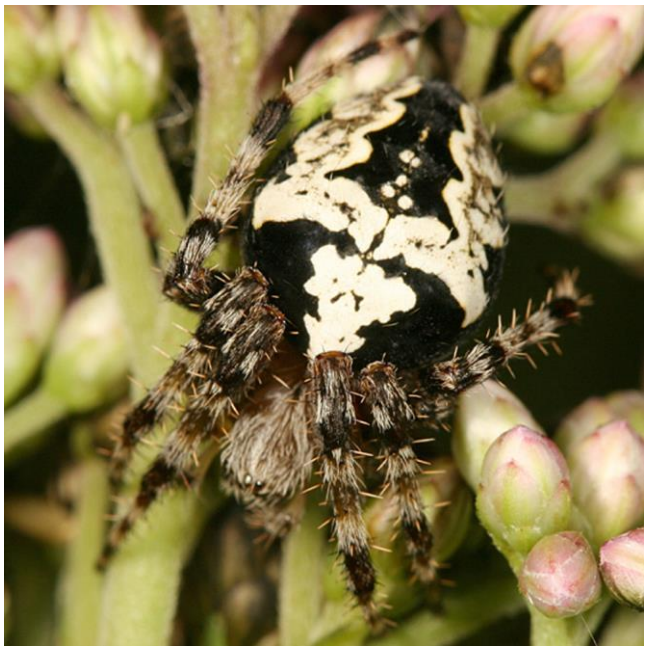

Figure 154. ***Araneus nordmanni*** (**Araneidae**) on flower buds. Photo by Tom Murray, through Creative Commons.

Clubionidae

A 12 mm spider, ***Clubiona abbajensis kibonotensis***, was found under moss on Mount Kilimanjaro, Africa (Denis 1950).

Gnaphosidae

The family **Gnaphosidae** is represented in many habitats among the moss dwellers. In the Faroe Islands, two species have been reported. ***Micaria alpina*** (Figure 155) occurs above 750 m on the Faroe Islands, likewise in mosses, but also under stones and among grasses (Holm 1980). ***Haplodrassus signifer*** (Figure 86) occurs at 125 m asl (Lissner 2011), and is also present among mosses in the heather. In the Yukon and elsewhere in the Arctic and alpine regions, ***Gnaphosa borea*** occurs primarily above 1000 m asl (Dondale *et al*. 1997).

Figure 155. ***Micaria alpina*** (**Gnaphosidae**) female. Photo by Walter Pfliegler, with permission.

Hahniidae

In Caribou Mountains Wildland Provincial Park, Canada, members of the **Hahniidae** occur in mosses and other damp places (Nordstrom & Buckle 2006). They sometimes make webs among mosses and usually hide under bits of soil at the edge of the web (Lissner 2011; Framenau 2012).

In the Tatras Mountains, Svatoň and Kovalčík (2006) likewise found **Hahniidae** to live among mosses. These included ***Cryphoeca carpathica*** (Figure 150), ***Hahnia difficilis***, and ***H. montana*** (Figure 37). ***Hahnia montana*** has been mentioned for several other habitats above.

Linyphiidae

This family comprises a strong majority among the reported Arctic and alpine moss-dwelling spiders. In the East Alps, Thaler (1999) reported three bryophyte-dwellers, all **Linyphiidae**, that were confined to cushions (mosses and other plants): ***Erigone tirolensis*** (Figure 156), ***Walckenaeria clavicornis*** (Figure 100) [also among mosses at 50-600 m in the Faroe Islands (Holm 1980; Lissner 2011) and in Britain mostly above 650 m altitude, but also in raised bogs at low elevations (Harvey *et al*. 2002), and in heathlands, grasslands, and pastures], and ***Oreoneta montigena*** (as *Hilaira montigena*), a species also found among mosses in the Carpathians by Svatoň and Kovalčík (2006). ***Gonatium rubens*** (Figure 157) occurs among mosses in the mountains of the Faroe Islands (Holm 1980), but also occurs in heathlands elsewhere.

Figure 156. ***Erigone tirolensis*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Figure 157. ***Gonatium rubens*** (**Linyphiidae**) female on moss. Photo by Jørgen Lissner, with permission.

Holm (1980) and Lissner (2011), working in the Faroe Islands, are among the few to include both elevations and moss habitats in their reports. Most of those spiders reported here are in the **Linyphiidae.** For those spiders living among mosses at lower elevations, they reported the eurytopic ***Centromerus arcanus*** (Figure 62) [known from mosses on mountains in Britain (Harvey *et al.* 2002)]; ***Hilaira nubigena*** (Figure 158) [also from altitudes of 400-750 m asl in Britain (Brændegaard 1928; Bengtson & Hauge 1979; Holm 1980)]; ***Walckenaeria antica*** (Figure 99) below 300 m and also from heathlands elsewhere (Lissner 2011); ***Walckenaeria cuspidata*** (Figure 52) at 260 m and 290 m asl (Holm 1980), also occurring in the mountains of Britain (Harvey et al. 2002) and noted above from forests, marshes, ad grassland. ***Walckenaeria nudipalpis*** (Figure 101) has a somewhat more intermediate distribution, being found from 45 m up to 400 m asl in the Faroes (Lissner 2011); it also occurs in heathland and marshes elsewhere.

From higher altitudes, one can find **Linyphiidae**, including ***Mecynargus morulus*** (Figure 93), a species also known from heathlands, which occurs from 200-880 m asl in the Faroes (Lissner 2011). ***Meioneta nigripes*** (Figure 159) occurs above 500 m asl in Britain, but at lower altitudes in Orkney and Shetland (Harvey *et al*. 2002). ***Scotinotylus evansi*** occurs at 600 m asl in the Faroe Islands (Lissner 2011) and is found in altitudes up to 1000 m asl in Iceland (Agnarsson 1996).

Figure 158. ***Hilaira nubigena*** (**Linyphiidae**). Photo by Glenn Halvor Morka, with permission.

Some moss dwellers are wide-ranging species. Among these is the linyphiid ***Porrhomma convexum*** (Figure 42) from 0-900 m asl in Iceland (Agnarsson 1996) and from mosses in forests elsewhere. ***Porrhomma montanum*** (Figure 160; also from mosses in grasslands elsewhere) occurs from sea level to the highest point in the Faroes (882 m asl at Slættaratindur) (Lissner 2011) and from 0-900 m asl in Iceland (Agnarsson 1996). As expected for a species of many habitats, ***Tenuiphantes zimmermanni*** (Figure 24) likewise occurs among mosses from sea level to "high levels in the mountains" (Holm 1980) and in forests, heath, and grasslands elsewhere.

Figure 159. ***Meioneta nigripes*** (**Linyphiidae**). Photo by Michael Hohner, with permission.

Snowfields provide unique communities of spider species that either tolerate or require cool temperatures and elevated moisture. Here, the **Linyphiidae** are likewise common (Svatoň & Kovalčík 2006), but their associations with bryophytes adjoining the snowfields are not known. In the Tatra Mountains Svatoň and Kovalčík (2006) found that the **Linyphiidae** is the most frequently represented.

Figure 160. ***Porrhomma montanum*** (**Linyphiidae**). Photo by Glenn Halvor Morka, with permission.

Lycosidae

In Sweden, ***Arctosa alpigena*** (Figure 161) is found in ***Sphagnum*** (Figure 162) bogs in subalpine and alpine regions (Almquist 2005). ***Arctosa alpigena*** occurs above 1000 m in the mountains of the UK, where it lives both in and under the moss ***Racomitrium lanuginosum*** (Figure 195) (Harvey *et al*. 2002).

Figure 161. ***Arctosa alpigena*** (**Lycosidae**) on ***Sphagnum***. Photo by Barbara Thaler-Knoflach, with permission.

Figure 162. ***Sphagnum magellanicum*** from Cape Hope. Photo from NY Botanical Garden, through public domain.

Svatoň and Kovalčík (2006) found the rare lycosid ***Alopecosa pinetorum*** among mosses in the Tatra Mountains, the highest range in the Carpathian Mountains. In addition, ***Pardosa sordidata*** occurred in boggy areas.

Tundra and Arctic

A number of spider species appear to be very tolerant of cold, but few cases of physiological adaptation are documented. In their study of Alaskan arthropods, Dunman *et al*. (2004) identified three spiders that had antifreeze proteins (AFPs). Most of the terrestrial arthropods are freeze avoiders, and this seems to include those AFP-producing species. The proteins do, however, function to prevent freezing.

Sherriffs (1934) was among the first to identify the tundra mosses where spiders were found, but he reported only two species of bryophyte dwellers. ***Thanatus arcticus*** (Figure 163-Figure 164; **Philodromidae**) from Greenland guards its large white flattened egg cocoon that it deposits under stones. Logunov *et al*. (1998) also reported this species from the moss-tussock-shrubby wet tundra of southern Siberia.

Dondale *et al*. (1997) have added many more species to the list of moss-dwelling tundra species. All but one (***Sisis rotundus***, **Linyphiidae**) of these also occur in litter or other habitats. Those living in bogs and fens will be discussed in the next sub-chapter.

Figure 163. ***Thanatus arcticus*** (**Philodromidae**) female. Photo by Jørgen Lissner, with permission.

Figure 164. ***Thanatus arcticus*** (**Philodromidae**) female. Photo by Jørgen Lissner, with permission.

Of those species listed for the Yukon, 57 are known to occur in or associated with mosses (Dondale *et al*. 1997). ***Alopecosa*** (**Lycosidae**) species, known elsewhere from mosses, were present among lichens, but not reported among mosses. The following species occur with mosses in the tundra or alpine areas of the Yukon and elsewhere: **Theridiidae** – ***Robertus vigerens*** (Figure 165); **Thomisidae** – ***Xysticus emertoni*** (Figure 166); **Salticidae** – ***Phidippus borealis*** (Figure 167). Additional Yukon species are discussed below with families having more representation.

Figure 165. ***Robertus vigerens*** (**Theridiidae**) on moss. Photo by Kyrontf, through Creative Commons.

Figure 166. ***Xysticus emertoni*** (**Thomisidae)** female. photo by John Sloan, with permission.

Figure 167. ***Phidippus borealis*** (**Salticidae**) eating moth. Photo by David A Burke, with permission.

Koponen (1992) found juvenile ***Dictyna*** (Figure 168; **Dictynidae**) among the moss ***Racomitrium*** in the low Arctic of the Belcher Islands, Hudson Bay, but reported no adults.

Figure 168. ***Dictyna*** sp. (**Dictynidae**). Photo by Christophe Quintin, through Creative Commons.

It is interesting that several species that live among mosses in forested sites live instead under stones in the open tundra (Dondale *et al*. 1997).

In their study of the tundra spiders in Tuva, South Siberia, Logunov *et al*. (1998) reported on habitats that had little prior study. These researchers compared the species found in mountain moss-tussock-shrubby wet tundra, the mountain moss tussock, and mountain moss-lichen-stony tundra. The most represented families in the wet, mossy tundra were **Gnaphosidae** (5 spp.), **Linyphiidae** (33 spp.) – they formed the highest proportion of species exclusive to the mountain moss-lichen-stony tundra and had the highest species richness in both habitats, **Lycosidae** (12 spp.), **Philodromidae** (3 spp.), **Salticidae** (6 spp.), **Theridiidae** (3 spp.), and **Thomisidae** (7 spp.), plus one other (Logunov *et al*. 1998). In the stony tundra, the most represented families were similar, with **Dictynidae** (1 sp.), **Gnaphosidae** (8 spp.), **Linyphiidae** (12 spp.), **Lycosidae** (4 spp.), **Salticidae** (3 spp.), and **Thomisidae** (2 spp.). The moss-lichen-stony tundra had the most exclusive species among the 23 habitat types studied, but the number may represent under collection, with only 14 species collected in the scree.

Logunov *et al*. (1998) demonstrated that at Tuva, differing from species at the moss-tussock shrubby tundra, the species in the mountain moss-lichen-stony tundra included: ***Agyneta olivacea*** (**Linyphiidae**), ***Monocerellus montanus*** (**Linyphiidae**), ***Euophrys proszynskii*** (**Salticidae**), ***Talaera*** sp. 2 (**Salticidae**), ***Gnaphosa*** species (**Gnaphosidae**), ***Mongolicosa pseudoferruginea*** (as *Acantholycosa triangulata*; **Lycosidae**), and ***Pardosa baraan*** (**Lycosidae**). This diversity of family representation seems to represent specialization of individual species and even includes large spiders (**Lycosidae**).

A surprisingly small number of Siberian species were found in both the mountain moss-lichen-stony tundra and the moss-tussock shrubby tundra habitats (Logunov *et al*. 1998): ***Euophrys flavoatra*** (**Salticidae**), ***Parasyrisca logunovi*** (**Gnaphosidae**), ***Tibioplus diversus*** (Figure 169; **Linyphiidae**), ***Typhochrestoides baikalensis*** (**Linyphiidae**), ***Victorium putoranicum*** (**Linyphiidae**), ***Xysticus austrosibiricus*** (**Thomisidae**).

Figure 169. ***Tibioplus diversus*** on moss. Photo by Walter Pfliegler, with permission.

Centromerus clarus (**Linyphiidae**), ***Parasyrisca ulykpani*** (**Gnaphosidae**), and ***Thaleria sajanensis*** (**Linyphiidae**) were unique to the mountain moss-tussock-shrubby wet tundra (Logunov *et al*. 1998).

On the other hand, the species in the mountain moss-tussock-shrubby wet tundra included many of the same species as the mountain moss tussock (Logunov *et al*. 1998). These were mostly members of the **Linyphiidae**: ***Agyneta fuscipalpus***, ***Agyphantes sajanensis*** (as *Lepthyphantes sajanensis*), ***Anguliphantes sibiricus*** (as *Lepthyphantes sibiricus*), ***Bathyphantes simillimus*** (Figure 170), ***Bolyphantes distichus*** (as *Lepthyphantes distichus*), ***Ceratinella wideri***, ***Decipiphantes decipiens***, ***Episolder finitimus***, ***Erigone atra*** (Figure 171), ***Hilaira herniosa*** (Figure 172), ***Hylyphantes nigritus*** (Figure 173-Figure 174), ***Improphantes flexilis***, ***Lepthyphantes luteipes*** (a genus represented among mosses elsewhere by different species), ***Mecynargus monticola*** (Figure 175) [also in the Yukon tundra (Dondale *et al*. 1997)], ***Meioneta affinisoides*** (as *Agyneta affinisoides*), ***Mughiphantes cornutus*** (as *Lepthyphantes cornutus*), ***Panamomops dybowskii*** (a genus represented by different species in grasslands), ***Panamomops tauricornis***, ***Pelecopsis dorniana*** (Figure 176), ***Savignia frontata*** (Figure 146; also among mosses in grasslands of the UK), ***Scotinotylus protervus***, ***Semljicola latus,*** and ***Silometopus uralensis*** (see Figure 177). Only ***Semljicola*** matched a genus also found in the Hudson Bay study (Koponen 1992).

Figure 170. ***Bathyphantes simillimus*** (Linyphiidae), a tundra moss tussock dweller in South Siberia. Photo by Jørgen Lissner, with permission.

Figure 171. ***Erigone atra*** maneuvering among the dead portions of mosses. Photo by Jørgen Lissner, with permission.

Figure 172. ***Hilaira herniosa*** female in its detritus and moss habitat. Photo by Walter Pfliegler, with permission.

Figure 173. ***Hylyphantes nigritus***, a tundra moss-dweller. Photo ©Pierre Oger, with permission.

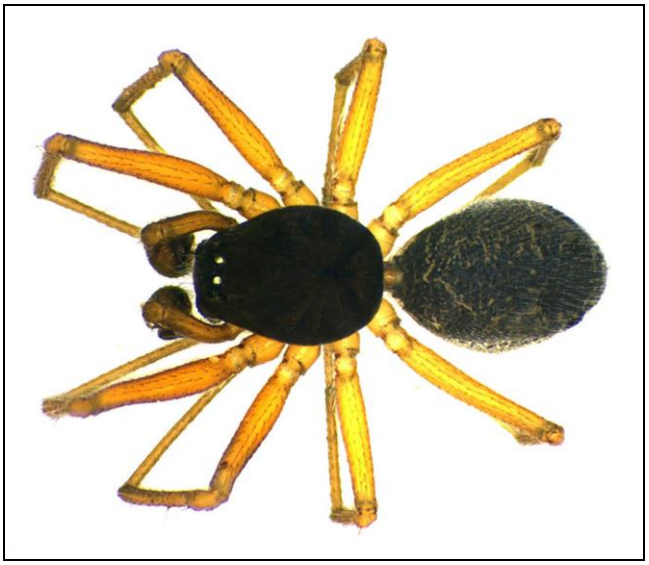

Figure 174. ***Hylyphantes nigritus***, a tundra moss-dweller. Photo ©Pierre Oger, with permission.

Figure 175. ***Mecynargus monticola*** female habitus. Photo by Glenn Halvor Morka, with permission.

Figure 176. ***Pelecopsis dorniana***. Photo by Gergin Blagoev, Bold Systems, through Creative Commons.

Figure 177. ***Silometopus reussi*** male showing its small size relative to a moss. This is a species primarily of straw, undergrowth, manure heaps, and other garden habitats. Photo by Jørgen Lissner, with permission.

Another Siberian spider that shares its habitat with bryophytes is ***Chalcoscirtus hyperboreus*** (see Figure 178; **Salticidae**), which occurs in humid moss-shrub tundra (Danilov & Logunov 1993).

Figure 178. ***Chalcoscirtus alpicola***, a relative of ***C. hyperboreus*** that lives among bryophytes in the tundra. Photo by Barbara Thaler-Knoflach, with permission.

Clubionidae

Non-linyphiid spiders include ***Clubiona trivialis*** (Figure 87) in moss in meadows and pastures (Schenkel 1925; Holm 1980; Lissner 2010, 2011), a species also from heathland mosses.

Gnaphosidae

The **Gnaphosidae** were represented in the Siberian tundra by ***Gnaphosa borea, G. leporina*** (Figure 15), also in wet heathland in Denmark, and ***G. sticta*** (Figure 179), all unique to the mountain moss-tussock-shrubby wet tundra at Tuva, South Siberia (Logunov *et al*. 1998). However, in the mountain moss-lichen-stony tundra in the same area, ***G. muscorum*** (Figure 180) and ***G. pseudoleporina*** were the species present among the mosses. Another represented genus of **Gnaphosidae** among mosses at Tuva was ***Micaria***, including ***M. alpina*** (Figure 155), also found among mosses in the mountainous locations elsewhere and ***M. viaria*** (Figure 46) also known from woodland mosses elsewhere (Logunov *et al*. 1998). In the Arctic Yukon, ***Micaria*** is represented among mosses by ***M. constricta*** (Dondale *et al*. 1997). Dondale and coworkers also reported ***Drassodes neglectus*** (Figure 181) from the Arctic Yukon. ***Zelotes potanini***, also in the **Gnaphosidae**, was present in the mountain moss-lichen-stony tundra at Tuva (Logunov *et al*. 1998).

Figure 179. ***Gnaphosa sticta*** (**Gnaphosidae**) female. Photo by Glenn Halvor Morka, with permission.

Figure 180. ***Gnaphosa muscorum*** (**Gnaphosidae**). Photo by Dorothy Pugh <http://www.dpughphoto.com/contact_us.htm>, with permission.

Figure 181. ***Drassodes neglectus*** (**Gnaphosidae**). Photo by John Sloan, with permission.

Hahniidae

The **Hahniidae**, including eurytopic ***Hahnia montana*** (Figure 37; also known from forest mosses elsewhere), live among mosses in the Faroes (Lissner 2011). The spiders in this family hunt on the upper side of the sheet web, unlike the Linyphiidae, and apparently have no retreat. ***Hahnia cf. ononidum*** (Figure 38) lives in the mountain moss-tussock-shrubby wet tundra of Siberia (Logunov *et al*. 1998).

Linyphiidae

Dondale *et al*. (1997) report that most of the tundra members of the **Linyphiidae** occur among mosses. Some moss-dwelling genera seem to be represented by different species in different places in the tundra as already seen at Tuva, South Siberia. One such genus is ***Erigone***. In Tuva, Logunov *et al*. (1998) found ***Erigone atra*** (Figure 171) in the mountain moss-tussock-shrubby wet tundra as well as in the mountain moss tussock, whereas in the mountain moss-lichen-stony tundra they found ***E. remota***. Sherriffs (1934) found ***Erigone arctica*** var. ***maritima*** (Figure 182) with ***Polytrichum*** sp. (Figure 43-Figure 44) in Iceland. And Lissner (2011) found ***Erigone psychrophila*** (Figure 183) among mosses on the Faroe Islands. These all differ from ***Erigone tirolensis*** reported from mosses in the East Alps.

Figure 182. ***Erigone arctica*** female on mosses. Photo by Jørgen Lissner, with permission.

Figure 183. ***Erigone psychrophila*** female in moss. Photo by Jørgen Lissner, with permission.

One of the **Linyphiidae**, ***Scotinotylus***, is a northern latitude genus with several species endemic to North America (Millidge 1981). ***Scotinotylus bicornis*** is known from several specimens at only one location, at 1400 m in British Columbia, Canada, where a single female was reported from moss on a rock slide (Millidge 1981); no habitat was given for the other collections. ***Scotinotylus evansi*** was present among mosses on the Faroe Islands (Lissner 2011) and also in Iceland (Agnarsson 1996). The genus ***Scotinotylus*** was one of the more diverse genera among mosses in the South Siberian tundra (Logunov *et al*. 1998), where ***Scotinotylus alpigenus***, ***Scotinotylus altaicus***, and ***Scotinotylus protervus*** were present among mosses in both mountain moss-tussock-shrubby wet tundra and the mountain moss tussock.

Some ***Walckenaeria*** species in the mountain moss-lichen-stony tundra of Siberia are different from those in other habitats reported herein. Entling *et al*. (2007) considered that the niche of spiders evolved faster than the physiological or morphological characters. Based on 244 published spider communities representing 70 habitat types, they reported that the greatest variation was between species within genera. Like ***Erigone*** and ***Scotinotylus***, the genus ***Walckenaeria*** supports this concept with representation among many habitats but with differences in represented species. In the tundra, this genus includes ***Walckenaeria koenboutjei*** and ***Walckenaeria korobeinikovi*** (Logunov *et al*. 1998), not reported from other habitats in this chapter. To these, Dondale *et al*. (1997) added ***W. exigua***, ***W. karpinskii*** [as *W. holmi* – also in North America and Greenland (Millidge 1983)], and ***W. spiralis*** from the Yukon tundra. However, other species of this genus that are more common elsewhere also occur among mosses on the Faroe Islands (Lissner 2011): ***Walckenaeria antica*** (Figure 99), ***W. clavicornis*** [Figure 100; also among mosses in Greenland (Holm 1967)], ***W. cuspidata*** [Figure 52; also among mosses in Iceland (Agnarsson 1996)], ***W. nodosa*** (Figure 54), ***W. nudipalpis*** (Figure 101), and ***W. obtusa*** (Figure 184). Several species of ***Walckenaeria*** were also present among ***Racomitrium*** (Figure 194-Figure 195) in the low Arctic of the Belcher Islands, Hudson Bay (Koponen 1992).

Figure 184. ***Walckenaeria obtusa***. Photo by Ruth Ahlburg, with permission.

Several additional linyphiid genera were present among mosses on the Faroe Islands as well as in the Siberian tundra, but the species were different. Lissner (2011) reported ***Improphantes complicatus*** (Figure 96), a species also found among mosses in Iceland (Agnarsson 1996), Yukon tundra (Dondale *et al*. 1997), and Greenland (Lissner 2011) in heathlands and grasslands. He also found ***Ceratinella brevipes*** (Figure 74; also known from mosses in forests, heath, grasslands, and mountains elsewhere) and ***Semljicola faustus*** (Figure 91), also known from mosses in heathland and swampy places elsewhere.

In the low Arctic of the Belcher Islands, Hudson Bay, Koponen (1992) sieved the thick ***Racomitrium*** moss layer (Figure 194-Figure 195). This method frequently revealed ***Semljicola obtusus*** (as *Latithorax obtusus*). Koponen also found ***Horcotes quadricristatus*** by hand-picking in the moss-lichen layer. ***Diplocephalus sphagnicola*** occurred on moss at the dry rock site of the moss-lichen tundra and shore in central Flaherty Island, also in the Hudson Bay.

Although the volcanic Kurile Islands in the Ring of Fire are not in the Arctic, the northernmost islands have tundra vegetation, and the volcanic activity and location create a severe climate on the islands. Most of the precipitation falls as snow, but the summers are foggy. Here one can find the linyphiid ***Oreoneta kurile*** in moss and meadow litter (Saaristo & Marusik 2003).

Faroe Islands

Lissner (2011) and Holm (1967) investigated the spiders of the Faroe Islands, citing many bryophyte associations. The islands are in a tundra biome, so many of these species might be considered tundra species. Most, however, have been discussed under other habitats, especially mountains and altitudinal effects, and will not be repeated here.

It appears that most of the moss dwellers are in **Linyphiidae**. Among those linyphiid genera not located in Siberia, Lissner found ***Centromerita bicolor*** (Figure 185), ***Gonatium rubens*** (Figure 157; including mosses in mountains of the Faroes and heathlands elsewhere), ***Hypomma bituberculatum*** (Figure 115), ***Leptorhoptrum robustum*** (Figure 97), ***Oreoneta frigida***, ***Palliduphantes ericaeus*** (Figure 95; known from mosses of heathlands and moist meadows), ***Poeciloneta variegata*** (Figure 90), and ***Porrhomma montanum*** (Figure 160; also from mosses in grasslands and mountains) [also in Iceland (Agnarsson 1996)]. ***Porrhomma convexum*** (Figure 42) occurred at 0-900 m asl in Iceland and in the Faroe Islands (Lissner 2011). ***Porrhomma egeria*** occurred in Iceland tundra (Agnarsson 1996), whereas in Britain, it was often found in deeper parts of caves, less frequently outside caves within moss (Harvey *et al.* 2002).

Figure 185. ***Centromerita bicolor***. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.

Agyneta decora (Figure 92) is found among mosses in the Faroe Islands (Lissner 2011) and Iceland (Agnarsson 1996). ***Agyneta subtilis*** and ***A. ramosa*** (Figure 186-Figure 187) both occur in mosses in the Faroe Islands, but are also known from mosses in non-tundra habitats in Britain (Harvey *et al*. 2002). All three of these species are known from mosses outside the tundra, with ***A. decora*** and ***A. subtilis*** from heathlands and ***A. ramosa*** from forests. In the Yukon, this genus is represented among tundra mosses by ***Agyneta olivacea*** (Dondale *et al*. 1997).

Figure 186. ***Agyneta ramosa*** male on moss. Photo by Jørgen Lissner, with permission.

Figure 187. ***Agyneta ramosa*** male on moss detritus. Photo by Jørgen Lissner, with permission.

Lissner (2011) reported ***Meioneta nigripes*** (Figure 159) from tundra mosses of the Faroe Islands; this species is also known from mosses in the mountains of the UK. ***Meioneta affinisoides*** was listed earlier from the Siberian tundra. Dondale *et al*. (1997) reported ***Meioneta lophophor*** from tundra mosses in the Yukon. Bengtson *et al*. (1976) recognized the importance of bryophytes for the Icelandic spider fauna and suggested that more species might be found in the thick moss layer of the grass meadow. But they only specifically identified one spider, ***Meioneta saxatilis*** (Figure 188; **Linyphiidae**), from mosses there.

Figure 188. ***Meioneta saxatilis***. Photo ©Pierre Oger, with permission.

Oreonetides vaginatus (Figure 89; also in mosses of heathlands elsewhere) occurs in the Faroes among moss in snow beds with *Salix herbacea* and other habitats (Holm 1967; Lissner 2011). This is among the few bryophyte-dwelling spiders in common with those of the Yukon tundra (Dondale *et al*. 1997), where it occurs in bogs and alpine areas. Holm (1980; Lissner 2011) found ***Saaristoa abnormis*** (Figure 189) among ***Sphagnum*** (Figure 162) and the weft-forming feather moss ***Hylocomium*** (Figure 94) in the Faroe Islands.

Figure 189. ***Saaristoa abnormis*** male on moss. Photo by Jørgen Lissner, with permission.

Centromerus arcanus (Figure 62) occurs among mosses in the Faroe Islands, but also occurs in mountainous regions of Britain (Harvey *et al*. 2002). ***Diplocentria bidentata*** (Figure 64), also known from forest mosses – see above, ***Gongylidiellum vivum*** (Figure 81), a eurytopic species discussed above for bryophytes in a number of other habitats, ***Hilaira nubigena*** (Figure 158), also known from bryophytes in mountains in the UK, ***Savignia frontata*** (Figure 146) also known from grassland mosses in the UK, ***Tenuiphantes mengei*** (Figure 98), ***Tenuiphantes zimmermanni*** (Figure 24) (both ***Tenuiphantes*** species occur among mosses in other habitats as well), ***Tiso vagans***, and ***Tmeticus affinis*** (Figure 190) likewise occur among mosses in the Faroes (Lissner 2011). ***Tenuiphantes zelatus*** is known from mosses in the Yukon tundra and alpine areas (Dondale *et al*. 1997).

Figure 190. ***Tmeticus affinis*** on leaf. Photo by Jørgen Lissner, with permission.

Several species of ***Mecynargus*** occur among mosses in the tundra. ***Mecynargus morulus*** (Figure 93) occurs on the Faroe Islands (Lissner 2011), as well as among bryophytes in the heathlands and mountains elsewhere. Koponen (1992) reported ***Mecynargus borealis*** (as *Conigerella borealis*) from sieving the thick ***Racomitrium*** mat in the low Arctic of the Belcher Islands, Hudson Bay. ***Mecynargus monticola*** (Figure 175) occurred among mosses in Tuva, South Siberia (Logunov *et al*. 1998).

Yukon

Many of the species reported from the Yukon tundra mosses have been discussed above, but a number of species have not been reported elsewhere herein. These include ***Ceraticelus alticeps***, ***C. bulbosus***, ***C. laticeps***, ***Ceratinopsis labradorensis***, ***Cnephalocotes obscurus*** (Figure 113; also in the Ural Mountains and widespread in other habitats where it lives in mosses as shown above), ***Hybauchenidium gibbosum*** (Figure 191), ***Incestophantes washingtoni*** (Figure 192) also in alpine mosses), ***Ivielum sibiricum***, ***Macrargus multesimus*** (Figure 193) also in birch forests), ***Procerocymbium sibiricum*** (also among alpine mosses elsewhere), and ***Sisis rotundus*** (Dondale *et al*. 1997).

Figure 191. ***Hybauchenidium gibbosum*** male. Photo by John Sloan, with permission.

Figure 192. ***Incestophantes washingtoni***. Photo by Gergin Blagoev, through Creative Commons.

Figure 193. ***Macrargus multesimus*** male. Photo by John Sloan, with permission.

Lycosidae

This family of hunters is able to run across the open spaces of the tundra, and in the Yukon they are better represented than they are among most other mossy habitats. Koponen (1992) reported juveniles from sifting through the moss ***Racomitrium*** from hummocks (Figure 194-Figure 195). Dondale *et al*. (1997) has contributed a number of Arctic tundra records for lycosids (wolf spiders) associated with bryophytes:

Arctosa alpigena	Holarctic; alpine
Arctosa raptor	Nearctic; alpine
Pardosa furcifera	Nearctic; alpine
Pardosa fuscula	Nearctic; alpine
Pardosa hyperborea	Holarctic; alpine
Pardosa nordicolens	Arctic
Pirata piraticus	Holarctic; lake & stream margins

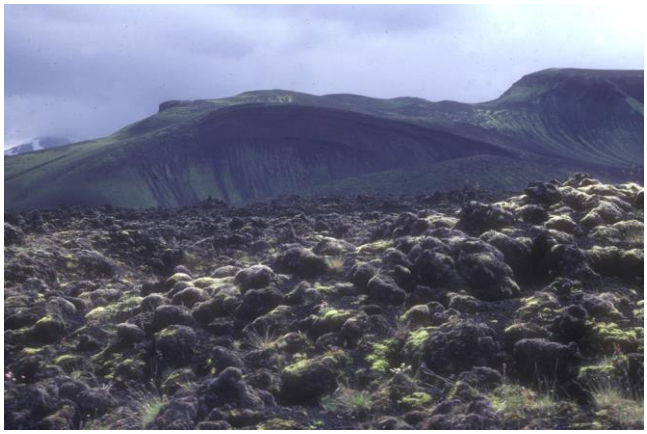

Figure 194. ***Racomitrium*** heath in Iceland. Photo by Janice Glime.

Figure 195. ***Racomitrium lanuginosum***, a spider habitat in the tundra. Photo by Michael Lüth, with permission.

Sherriffs (1934) reported ***Arctosa alpigena*** (Figure 161; **Lycosidae**) among ***Calliergon*** sp. (Figure 196) in Iceland, a species later located by Lissner (2011) among mosses in the Faroe Islands and by Almquist (2005) in Sweden. In Iceland and other tundra locations, extensive areas are covered by the moss ***Racomitrium*** (Figure 194-Figure 195), where ***Arctosa alpigena*** also occurs in ***Racomitrium*** "heaths" (Harvey *et al.* 2002).

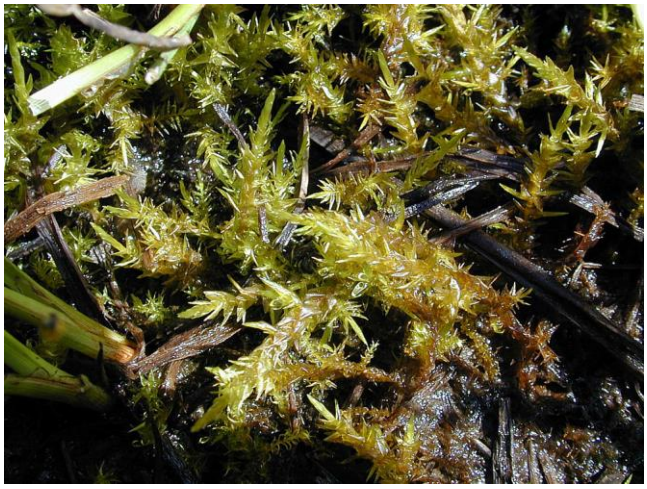

Figure 196. ***Calliergon giganteum*** in Europe. Photo by Michael Lüth, with permission.

Pardosa palustris (Figure 197) occurs among mosses in a wide range of habitats on the Faroe Islands, including grassy heath (Schenkel 1925; Bengtson & Hauge 1979; Holm 1980), but differs from ***Pardosa baraan*** found among mosses in the mountain moss-lichen-stony tundra of Siberia (Logunov *et al*. 1998).

Figure 197. ***Pardosa palustris*** on a fern leaf. Photo by James K. Lindsey, with permission.

Bryophytes vs Lichens

In many cases, such as cryptogamic crusts, lichens seem to offer many of the same benefits as bryophytes. They provide small crevices where small organisms can hide from would-be predators and escape the rays of the sun. But if it is protection from moisture loss, many kinds of lichens often do not provide the safe haven that spiders can find among the bryophytes. This is especially true for crustose lichens that would seem to offer only a disruptive coloration that makes the tiny spiders less conspicuous (Figure 198). For the Northern Hemisphere ***Zygiella atrica*** (Figure 199; **Araneidae**), mosses may play a role as a disruptive habitat when the spider has been disturbed from its aerial habitat, typically of bushes. When disturbed, it drops quickly to the ground (Roberts 1985), and if mosses are there, they could make it less conspicuous. However, the coloration on its abdomen suggests it might fare better among leaf litter.

Figure 198. ***Zygiella atrica*** female sitting on a covering of crustose lichens on bark. This lichen offers little in the way of protection and may add only a disruptive background where the spider is less conspicuous. This species apparently is not known from bryophytes (Wikipedia 2011). For spiders adapted to dry habitats, this location can be an advantage, whereas the damper and more convoluted habitat of a bryophyte might hinder rapid escape and be too damp. Photo by Jørgen Lissner, with permission.

Figure 199. ***Zygiella atrica*** male on bark. Photo by Jørgen Lissner, with permission.

Although it seems like mosses and lichens could offer similar habitats, in their report on Yukon bryophytes Dondale *et al*. (1997) report several spider species on lichens, but not on bryophytes, and many on bryophytes but not on lichens. When they occurred on both, the two substrates were sometimes in different habitats, suggesting possible moisture differences.

Casual Users

The list of spiders that may nest in or hide in bryophyte patches is surely a long one. Our knowledge is insufficient to know if there is any preference among these spiders, although at least a few seem to exist, but it appears that most of them are like some of the non-bryologists – they find no particular role for bryophytes vs any other short-statured substrate, including litter.

In many studies, the authors mention the presence of bryophytes and may even compare presence of spiders in mossy vs non-mossy areas at a research site. But one must guess that often the correlation of spiders with the presence of bryophytes is one of mutual need for the conditions that

promote the establishment of bryophytes, rather than a need for the bryophytes.

In any case, when bryophytes are present in the habitat, spiders will most likely traverse them from time to time. In some cases this will benefit the spider as a camouflaged background, whereas in others the bryophyte may provide a drink of water or rehydration site. But for some spiders, bryophytes are just part of the terrain and will be traversed when between the spider and its destination, hence creating the casual user.

The orb weaver spider, ***Cercidia prominens*** (Figure 200; **Araneidae**) is among those that can occasionally be found on mosses, but its relationship to them is poorly known and that is not its typical habitat. It is known to occur "at the base of mossy or heathery banks" along footpaths and makes orb webs among low vegetation (Roberts 1985). When disturbed, the spider drops into the litter layer, and this layer may likewise include mosses in some locations.

Figure 200. ***Cercidia prominens*** male, known from mosses, but most likely only as accidental visitors. Photo by Jørgen Lissner, with permission.

Amaurobius ferox (Figure 201; **Amaurobiidae**) might be one of these casual users. This unusual spider makes me glad I am not its mother! The species practices matriphagy (Kim & Roland 2000; Kim *et al.* 2000). That's right, the young eat their mother, and she actually encourages it! This ungrateful behavior ensures a greater survival of the young by giving them, apparently, a good nutritional start in life. But that is not all she does to ensure their success. The first generation of offspring may eat her eggs for her next set of offspring, giving the first clutch a greater chance for success, and increasing the success of matriphagy in that first clutch (Kim & Roland 2000). The young spiderlings can stimulate the release of the second clutch of eggs from the mother at an earlier developmental stage than usual. In experiments, survival success was greater when this first clutch had access to the eggs than when it was the second clutch that procured eggs as food. Bryophytes can occur in the neighborhood, but do not seem to provide any particular function in this spider's life.

In other cases, the spiders live in boggy areas where the moss creates the habitat needed for the trees and shrubs they inhabit. For example, ***Araneus nordmannii*** (Figure 202; **Araneidae**) lives in boggy areas of the Tatras National Park, southern Poland (Svatoň & Kovalčík 2006), but typically it occurs in dense forests, making its webs between tree trunks and branches. It is more common in the USA and Canada than in Europe.

Figure 201. ***Amaurobius ferox***, a casual inhabitant of mosses, seen here "in the neighborhood." However, its nest among mosses suggests that it is at least not adverse to a mossy habitat. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

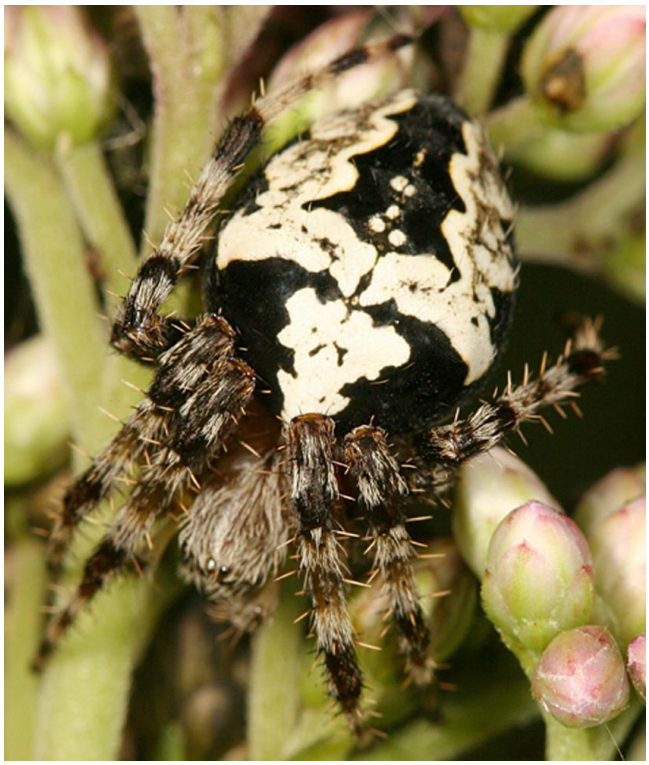

Figure 202. ***Araneus nordmannii***, a species known from boggy areas in the Tatras National Park, southern Poland, but typically from dense forests, making webs between tree trunks. Photo by Tom Murray, through Creative Commons.

The list in Table 1 includes those species I have determined as bryophyte dwellers. However, a few, as indicated, were identified by their images on bryophytes, where they may be casual visitors or even posed.

Table 1. Species of spiders known to me that occur in association with bryophytes. Most of these have been collected by methods that targeted bryophytes. None has specifically identified liverworts, although they presumably were included in some cases. The number of citations are an indication of the frequency of the species among locations, but the same is not true for genera. If only the genus was named, it has not been listed separately from a known species, albeit sometimes from a different location. + indicates species for which I have seen photographs of the spiders associated with a moss, but the association may be spurious or staged.

Acantholycosa norvegica	Logunov *et al*. 1998
Acantholycosa triangulata	Logunov *et al*. 1998
Achaearanea riparia	Logunov *et al*. 1998
Aelurillus v-insignitus	Merkens 2000
Agroeca brunnea	Koponen 2002
Agroeca proxima	Koponen 2002
Agyneta affinis	Koponen 2002
Agyneta affinisoides	Logunov *et al*. 1998
Agyneta cauta	Koponen 2002
Agyneta fuscipalpus	Logunov *et al*. 1998
Agyneta mossica	Koponen 2002
Agyneta olivacea	Logunov *et al*. 1998
Agyneta ramosa	Lissner 2011b
Alopecosa aculeata (Lycosidae)	Logunov *et al*. 1998
Alopecosa fabrilis	Merkens 2000
Alopecosa pulverulenta	Koponen 2002
Amaurobius ferox	Pendleton & Pendleton; Lindsey
Antistea elegans (Hahniidae)	Isaia *et al*. 2009
Aphileta (*Hillhousia*) *misera*	Kupryjanowicz 2003
Araneus cornutus	Cherrett 1964
Araneus marmoreus	Lissner this volume
Arctosa alpigena	Harvey *et al*. 2002; Almquist 2005
Arctosa lamperti	Kupryjanowicz 1998
Argyroneta aquatica	Pickard-Cambridge 1860
Asthenargus paganus	Lissner this volume
Atypus affinis	Jonsson 1998
Bathyphantes gracilis	Merkens 2000; Koponen 2002
Bathyphantes parvulus	Koponen 2002
Bathyphantes simillimus	Logunov *et al*. 1998
Bolyphantes luteolus	Koponen 2002
Caracladus leberti (Theridiidae)	Isaia *et al*. 2009
Carorita limnaea	Pickavance & Dondale 2005
Centromerita concinna	Merkens 2000
Centromerus arcanus	Biström & Pajunen 1989
Centromerus clarus	Logunov *et al*. 1998
Centromerus levitarsis	Koponen 2002
Centromerus sylvaticus	Merkens 2000
Ceratinella brevis (Linyphiidae)	Jackson 1904-1907
Ceratinella brevipes	Holm 1980
Ceratinella wideri	Logunov *et al*. 1998
Cercidia prominens	Roberts 1985
Chalcoscirtus alpicola	Logunov *et al*. 1998
Chalcoscirtus hyperboreus	Danilov & Logunov 1993
Clubiona abbajensis kibonotensis	Denis 1950
Clubiona lutescens	Crocker & Daws 1996
Clubiona germanica	Komposch 2000
Clubiona norvegica	Harvey *et al*. 2002
Cnephalocotes obscurus	Jackson 1904-1907
Comaroma simonii	Kropf 1997
Cryphoeca silvicola (Hahniidae)	Isaia *et al*. 2009
Decipiphantes decipiens	Logunov *et al*. 1998
Dendryphantes czekanowskii	Logunov *et al*. 1998
Dictyna (Dictynidae)	
Dicymbium tibiale	Biström & Pajunen 1989
Diplocentria bidentata	Jonsson 1998
Diplocephalus arnoi (Theridiidae)	Isaia *et al*. 2009
Diplocephalus dentatus	Brunn & Toft 2002
Diplocephalus helleri	Komposch 2000
Diplocephalus latifrons	Jonsson 1998
Diplocephalus permixtus	Jackson 1904-1907
Dipoena prona	Koponen 2002
Drassodes pubescens	Koponen 2002
Drassyllus pusillus	Merkens 2000
Drepanotylus uncatus	Koponen 2002
Dysdera (Dysderidae)	
Enoplognatha caricis	Komposch 2000
Episolder finitimus	Logunov *et al*. 1998
Erigone atra	Logunov *et al*. 1998
Erigone psychrophila	Lissner 2011b
Erigone remota	Logunov *et al*. 1998
Erigonella ignobilis	Kupryjanowicz 2003
Euophrys flavoatra	Logunov *et al*. 1998
Euophrys proszynskii	Logunov *et al*. 1998
Frontinella communis	Suter *et al*. 1987
Glyphesis cottonae	Kupryjanowicz *et al*. 1998
Gnaphosa borea	Logunov *et al*. 1998
Gnaphosa lapponum	Koponen 2002
Gnaphosa leporina	Logunov *et al*. 1998
Gnaphosa microps	Koponen 2002
Gnaphosa muscorum	Logunov *et al*. 1998
Gnaphosa nigerrima	Kupryjanowicz 2003
Gnaphosa pseudoleporina	Logunov *et al*. 1998
Gnaphosa sticta	Logunov *et al*. 1998
Gnathonarium dentatum (Linyphiidae)	Lissner this volume
Gonatium rubens	Holm 1980
Gongylidium nigriceps	Hauge 1969
Gongylidiellum vivum	Lissner this volume
Hahnia nava	Merkens 2000
Hahnia ononidum	Hauge 1969; Isaia *et al*. 2009
Haplodrassus moderatus	Koponen 2002
Haplodrassus signifer	Koponen 2002
Heliophanus dampfi	Komposch 2000
Hickmanopsis minuta	Hickman 1943
Hilaira excisa	Jackson 1904-1907
Hilaira herniosa	Logunov *et al*. 1998
Hylyphantes nigritus	Logunov *et al*. 1998
+Hypomma bituberculatum	Lissner 2011b
Hypselistes jacksoni	Boyce 2004
Improphantes flexilis	Logunov *et al*. 1998
Labulla thoracica	Hormiga & Scharff 2005
Lepthyphantes alacris	Biström & Pajunen 1989
Lepthyphante angulatus	Koponen 2002
Lepthyphantes bergstroemi	Logunov *et al*. 1998
Lepthyphantes cornutus	Logunov *et al*. 1998
Lepthyphantes distichus	Logunov *et al*. 1998
Lepthyphantes exiguus	Hauge 1969
Lepthyphantes luteipes	Logunov *et al*. 1998
Lepthyphantes mengei	Koponen 2002
Lepthyphantes sajanensis	Logunov *et al*. 1998
Lepthyphantes sibiricus	Logunov *et al*. 1998
Lophomma punctatum	Lissner this volume
Lycosa pullata	Nørgaard 1951
Macrargus carpenteri	Koponen 2002
Macragus multesimus	Hauge 1969

Maro lepidus Koponen 2002
Maro minutus Koponen 2002
Maro sublestus Koponen 2002
Maso sundevalli Lissner this volume
Mecopisthes latinus (Linyphiidae) Isaia *et al*. 2009
Mecynargus monticola Logunov *et al*. 1998
Meta Cherrett 1964
Metellina merianae Cherrett 1964
Metopobactrus prominulus Lissner this volume
Micaria alpina Logunov *et al*. 1998
Micaria constricta Nordstrom & Buckle 2006
Micrargus herbigradus Lissner this volume
Microcentria pusilla Hauge 1969
Microhexura montivaga Coyle 1985
Microneta viaria Logunov *et al*. 1998
Minicia marginella Koponen 2002
Minyriolus pusillus Biström & Pajunen 1989
Monocephalus caastaeipes Jonsson 1998
Monocerellus montanus Logunov *et al*. 1998
Neon valentulus Koponen 2002
Notioscopus sarcinatus Kupryjanowicz *et al*. (1998
Oryphantes angulatus Spuògis *et al*. 2005
Ozyptila arctica Logunov *et al*. 1998
Ozyptila claveata (Thomisidae) Isaia *et al*. 2009
Ozyptila orientalis Logunov *et al*. 1998
Pachygnatha (Tetragnathidae)
Palliduphantes ericaeus Lissner 2011b
Panominops dybowskii Logunov *et al*. 1998
Panominops tauricornis Logunov *et al*. 1998
Parachtes siculus (Dysderidae) Isaia *et al*. 2009
Parasyrisca logunovi Logunov *et al*. 1998
Parasyrisca ulykpani Logunov *et al*. 1998
Pardosa baraan Logunov *et al*. 1998
Pardosa bifasciata Logunov *et al*. 1998
Pardosa bukukun Logunov *et al*. 1998
Pardosa eiseni Logunov *et al*. 1998
Pardosa fulvipes Komposch 2000
Pardosa hyperborea Koponen 2002
Pardosa indecora Logunov *et al*. 1998
Pardosa maisa Itaemies & Jarva 1983
Pardosa oksalai Logunov *et al*. 1998
Pardosa oljunae Logunov *et al*. 1998
Pardosa pullata Nørgaard 1951
Pardosa schenkeli Logunov *et al*. 1998
Pardosa sphagnicola Oliger 2004
Patu marplesi Alphonse 2010
Pardosa biphasciata Logunov *et al*. 1998
Pardosa bukukun Logunov *et al*. 1998
Pardosa indecora Logunov *et al*. 1998
Pardosa oksalai Logunov *et al*. 1998
Pardosa oljunae Logunov *et al*. 1998
Pardosa sphagnicola Oliger 2004
Pelicopsis dorniana Logunov *et al*. 1998
Pelecopsis parallela Koponen 2002
Pellenes lapponicus Logunov *et al*. 1998
Pirata insularis Koponen 2002
Pirata latitans Lissner this volume
Pirata piraticus Nørgaard 1951
Pirata piscatorius Koponen 2002
Pirata tenuitarsis Kupryjanowicz 2003
Pirata uliginosus Brunn & Toft 2002
Poeciloneta petrophila Logunov *et al*. 1998
Robertus arundineti Koponen 2002
Robertus kastoni Logunov *et al*. 1998
Robertus lividus (Theridiidae) Biström & Pajunen 1989
Robertus lyrifer Hauge 1969
Robertus scoticus Svatoň & Kovalčík 2006
Robertus ungulatus Lissner this volume
Savignia frontata Logunov *et al*. 1998
Scotina celans Jackson 1904-1907
Scotina palliardi Koponen 2002
Scotinotylus alpigenus Logunov *et al*. 1998
Scotinotylus altaicus Logunov *et al*. 1998
Scotinotylus protervus Logunov *et al*. 1998
Semljicola (=*Latithorax*) *faustus* Biström & Pajunen 1989
Semljicola latus Logunov *et al*. 1998
Silometopus uralensis Logunov *et al*. 1998
Sintula corniger Cameron 2002
Sitticus caricis Kupryjanowicz 2003
Sitticus lineolatus Logunov *et al*. 1998
Stemonyphantes lineatus Koponen 2002
Talaera sp. 2 Logunov *et al*. 1998
Talavera westringi Kupryjanowicz, *et al*. 1998
Tallusia experta Koponen 2002
Tapinocyba pallens Biström & Pajunen 1989
Taranucnus setosus Koponen 2002
Tetragnatha nigrita Lissner this volume
Thaleria sajanensis Logunov *et al*. 1998
Thanatus arcticus Logunov et al. 1998
Thanatus bungei Logunov *et al*. 1998
Thanatus coloradensis Logunov *et al*. 1998
Thanatus formicinus Koponen 2002
Theonoe minutissima Koponen 2002
Theridion sibiricum Logunov *et al*. 1998
Tibioplus diversus Logunov *et al*. 1998
Tiso vagans Harvey *et al*. 2002
Tricca alpigena Logunov *et al*. 1998
Trochosa spinipalpis Koponen 2002
Trochosa terricola Merkens 2000
Typhochrestoides baikalensis Logunov *et al*. 1998
Typhochrestus digitatus Merkens 2000
Victorium putoranicum Logunov *et al*. 1998
Walckenaeria acuminata (Linyphiidae) Lissner this volume
Walckenaeria alticeps (Linyphiidae) Palmgren, P. 1982
Walckenaeria antica Koponen 2002
Walckenaeria capito Koponen 2002
Walckenaeria cucullata Lissner this volume
Walckenaeria cuspidata Biström & Pajunen 1989
Walckenaeria karpinskii Logunov *et al*. 1998
Walckenaeria koenboutjei Logunov *et al*. 1998
Walckenaeria korobeinikovi Logunov *et al*. 1998
Walckenaeria nodosa Harvey *et al*. 2002
Walckenaeria nudipalpis Koponen 2002
Xysticus (Thomsiidae) Isaia *et al*. 2009
Xysticus austrosibiricus Logunov *et al*. 1998
Xysticus bonneti Logunov *et al*. 1998
Xysticus britcheri Logunov *et al*. 1998
Xysticus emertoni Logunov *et al*. 1998
Xysticus kaiserlingi Nordstrom & Buckle 2006
Xysticus lineatus Koponen 2002
Xysticus rugosus Logunov *et al*. 1998
Xysticus triguttatus Nordstrom & Buckle 2006
Zelotes latreillei Koponen 2002
Zelotes potanini Logunov *et al*. 1998
Zora parallela Koponen 2002

In some cases, there is a negative correlation of spiders with bryophytes. This could be again be a habitat need for particular taxa, but it is also possible that there is some chemical interaction that discourages some spider species from nearing the bryophytes. Certainly this is an unanswered question that could lead to some practical uses in deterring some spiders in houses and may warrant investigation. But it is also certain that at least in most cases, not all spiders are deterred.

Invasive Bryophytes

While tracheophytes have numerous invasive species, few invasive species among bryophytes have concerned ecologists. One reason for this is their apparent ability to travel well on their own, hence not often being solely the result of human activities. But some species are indeed invasive and can even be aggressive. In some cases, they may bring their fauna with them, as is true for those used in the horticulture industry, but more recently the moss garden trade has become another possible source. Even bryologists are likely to introduce species, often inadvertently when a bit is pulled from a pocket or by other means escapes its human vector. These invasive species have the potential to create new niches and to outcompete and replace old ones, not to mention introducing a new fauna from their hitch-hikers. One way to get implications for the role of bryophytes in an ecosystem is to compare habitats where mosses have either disappeared or have been introduced.

Schirmel *et al*. (2011) examined the impact of the invasive moss ***Campylopus introflexus*** (Figure 203) on spider communities of acidic coastal dunes along the Baltic Sea. This moss species can quickly build dense carpets in such habitats, creating new environmental conditions. Schirmel and co-workers chose to examine the carabid beetle and spider communities because of their known indicator value. They compared the spider fauna on non-invaded native, lichen-rich (*Cladonia* spp.) acidic coastal dunes with those that had been invaded by the moss ***Campylopus introflexus***, the latter creating a moss-rich community. Using pitfall traps, they found 2682 spiders (66 species). Both activity levels and species richness decreased in the invaded areas. Both web-building and wolf spiders (Lycosidae) were more abundant among the native ground cover. They attributed the change in fauna to differences in vegetation structure, microclimate, and a reduced food supply. It will be interesting to see if the decrease in species richness persists as time permits invasion of species more suited to the new habitat, including appropriate food species.

Schirmel and Buchholz (2013) found that the invasion of ***Campylopus introflexus*** (Figure 203-Figure 204) in acidic coastal dunes altered the functional diversity of the spider fauna and altered the pattern of life history traits of the faunal community. The invasive moss caused shifts in hunting mode of the spiders, permitting larger individuals than did the native vegetation. Furthermore, the percentages of web-building spiders were reduced while the trait composition of spiders became more heterogeneous with more functional diversity.

Known Associates

It is difficult to put together a list of known associates with any reliability, and after finding hundreds with only limited effort, I decided that publishing a list was beyond the need for this book. Photographs on the web suggest possible relationships, but may be posed or represent only casual association on the way to another location. Additional records, particularly indicating the role of the bryophytes, will be welcomed.

Figure 203. ***Campylopus introflexus***, an invasive bryophyte in many parts of the world, including this one in Wales. Photo by Janice Glime.

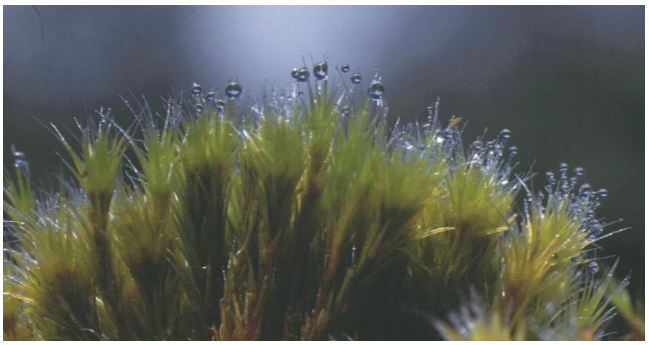

Figure 204. ***Campylopus introflexus*** from New Zealand, where it is native. Photo by Jan-Peter Frahm, with permission.

Summary

In addition to ***Sphagnum***, ***Polytrichum***, ***Hylocomium***, and ***Racomitrium*** have been cited as habitats where spiders live. But in most cases, the actual bryophyte is not named and the role of the bryophyte is seldom known.

Forests mosses are characterized by **Linyphiidae**, **Lycosidae** (not abundant), **Salticidae**, **Theridiidae**, and **Thomsiidae**. Forest rock outcrop bryophyte communities differ from those of the forest floor and of the epiphytic bryophytes, the latter often being quite important in tropical rainforests. Those bryophyte fauna of forested areas are often species with broad habitat distribution.

Many of the same spiders occur in mosses in heathland, mountains, and tundra, with **Linyphiidae** being especially important for both diversity and numbers, but also having **Clubionidae** as a common inhabitant.

Marshes, moist meadows, and swampy places often share common species with each other and with bogs and fens. The **Linyphiidae** is again the predominant family. Grasslands and pastures likewise have **Linyphiidae**, but have a greater representation of the larger **Lycosidae**, a character they share with the tundra, in both cases probably due to greater sunlight and openness. Mountains and the tundra share genera, but often the species are different not only between these two habitats, but also between locations of the same habitat. The **Linyphiidae** predominate among the bryophytes. The **Lycosidae** are more common here than in forests, heath, and marshland.

Hence, the most common family in most habitats is the **Linyphiidae**, with ***Walckenaeria*** seemingly the most diverse and frequent genus among the mosses.

Lichens seem to share few species with bryophytes and have fewer spider inhabitants, perhaps not offering the moisture available among bryophytes. Some spiders may be seen on bryophytes only because the bryophyte is there and must be crossed to reach a destination. But many species of spiders seem to use bryophytes at least some of the time for moisture, drinking, hiding, and egg sites. When a habitat changes to dominance of one type of vegetation such as grasses to dominance by bryophytes, the types of spiders changes as well and thus the invader may prove to be a detriment to the spider community. Considerable experimental work is needed to determine the importance and role of the bryophytes for the spider community.

Invasive bryophyte species, such as ***Campylopus introflexus***, can change not only the appearance of the vegetation, replacing the lichen-dominated community, but also alter the spider communities associated with the ground vegetation.

Acknowledgments

My co-author, Jørgen Lissner, actually collected data and took numerous photographs to help make the forest portion of this chapter more complete; he also served as a critical reviewer that prompted me to re-organize the chapter. Norm Platnick helped me to find current names for species from older literature. Jeremy Miller provided me with a paper on tropical Erigoninae that included many moss dwellers. John Steel alerted me to the moss-dwelling Malkaridae and provided me with the paper. Many photographers contributed images, as noted in the captions.

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CHAPTER 7-4
ARTHROPODS: SPIDERS AND PEATLANDS

Janice M. Glime and Jørgen Lissner

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CHAPTER 7-4
ARTHROPODS: SPIDERS AND PEATLANDS

Figure 1. A spider's view of ***Sphagnum capillifolium***. Photo by Michael Lüth, with permission.

A number of studies have investigated the spider fauna of peat bogs, *e.g.* Villepoux (1990), Kupryjanowicz *et al.* (1998), Koponen (2000), and Scott *et al.* (2006). Some studies have been aimed at ecological aspects such as investigating the spider fauna assemblages of different bog types, others have been aimed at comparing assemblages as a function of shading or assessing spider indicator species of conservation value. Rëlys and Dapkus (2002) demonstrated the high degree of dissimilarity between spiders in pine forests and bogs in southern Lithuania. Few studies dealing directly with spiders and preferred moss species are known to us. Most information is scattered in the literature, and in most instances only relate spider habitats in respect to mosses to higher taxonomical levels such as "among moss" or "in ***Sphagnum*** bogs" (Figure 1).

Bogs and Fens

The nomenclature used for labelling the various types of bogs and fens has been inconsistent among the continents and even within continents, especially when considered over time. This makes it somewhat difficult to make adequate comparisons between studies when one is not familiar with the specific location. The fact that current usage is based on water and nutrient source to define these habitats into **bog** (raised bog with only precipitation as water and nutrient input), vs **fen** (nutrients and water sources include ground water) makes it even more difficult to determine the category based on published studies alone. The fen is further divided into **poor**, **intermediate**, and **rich fen**, again based on nutrient levels. These distinctions may influence the spider fauna, but as will be documented in some of the studies below, the flora (usually described by the tracheophytes) may be the more important character for describing the spider habitat.

Many studies have catalogued the spiders in peatlands around the world, but especially in Europe. This even broader term of peatlands can include grasses and sedges with no or few mosses and lacking ***Sphagnum*** completely. Although authors often did not distinguish the substrate used by the spiders, it is reasonable to surmise that the spiders' presence was because the mosses that dominate the ground surface of the bog or fen provided the conditions needed for their lives (Figure 1), even if that is to provide a habitat suitable for shrubs and trees that the spiders inhabit. ***Sphagnum*** (Figure 2), especially, plays a large role in creating those conditions.

Figure 2. ***Sphagnum subsecundum*** showing spider webs. Photo by Michael Lüth, with permission.

Bryophytic Accommodations

Humans need to explain things, being curious and asking why. So we ask here why spiders associate with peatlands and their mosses. An obvious consideration is moisture, but the mosses also provide an escape from the sun (heat and light), a location for food, and a refuge from predation. These are the same characteristics typical of bryophyte interactions for most invertebrates. We will examine just how important they are for spiders in the bog and fen habitats.

Moisture Relationships

Moore and Bellamy (1974) discuss maintaining moisture as being among the adaptations of arachnids in "mire" habitats. Mires, bogs, and the various types of ***Sphagnum*** (Figure 1) peatlands have an increasing temperature upward and an increasing humidity downward. Nørgaard (1951) presented this gradient for a Danish ***Sphagnum*** bog (Table 1). Kajak *et al*. (2000) found that moss and litter layers were important for spiders in both natural and drained fens, with mosses causing the soil under them in the sedge-moss community to have the highest water-holding capacity and the greatest moisture stability throughout the year.

Table 1. Gradation of temperature and humidity in a Danish ***Sphagnum*** bog. From Nørgaard 1951.

	Diurnal Temperature Fluctuation	Relative Humidity
100 cm above surface	26°C	<40%
At mire surface	33°C	<40%
100 cm below surface	5°C	100%

A particularly helpful study is one by Biström and Pajunen (1989) examining the arachnid fauna occurring in association with ***Polytrichum commune*** (Figure 3), ***Sphagnum girgensohnii*** (Figure 4), and ***S. squarrosum*** (Figure 5) during May – October 1988 at two locations in southern Finland. All three of these mosses can occur in light shade with high water content. The life forms of these three mosses differ, with the sun-loving ***P. commune*** being slender and upright, forming tall turfs, and sometimes having limited space between the stems, especially for larger spiders; it furthermore has a waxy leaf surface that does less to maintain surface moisture. ***Sphagnum girgensohnii*** is more shade-loving and provides relatively open spaces among the stems while creating a much greater canopy to intercept light and protect from UV radiation than one would expect from within the ***P. commune*** turf. ***Sphagnum squarrosum*** has a similar life form to that of ***S. girgensohnii***, but it has larger leaves and a more succulent appearance.

Figure 3. ***Polytrichum commune***, illustrating the waxy appearance of the leaves that hold little water compared to ***Sphagnum***. Photo by Michael Lüth, with permission.

Figure 4. ***Sphagnum girgensohnii***, a treed fen species that provides habitat for spiders. Photos by Janice Glime.

Figure 5. ***Sphagnum squarrosum***, a woodland species that harbors spiders. Photo by Janice Glime.

When Biström and Pajunen sieved the mosses they retrieved 1671 arthropod specimens. Among these were 1368 Araneae represented by 77 species, 35 Pseudoscorpionida represented by 1 species, and 157 Opiliones represented by 5 species. Other arthropods included Diplopoda (39/4), Chilopoda (43/3), and Symphyla (9/1). Mites (Acarina) were not included in the study. Our climate in the Keweenaw Peninsula, Michigan, USA, is similar to the climate of Finland, but I (Glime) must confess that I have never found pseudoscorpions or harvestmen among any moss collections. Perhaps I simply was not observant at the right times.

Biström and Pajunen identified three moisture content levels (dry, moist, and wet) among these Finnish mosses and estimated the number of individuals per sample in each of these three conditions. They then estimated the number of individuals of each major spider species per sieved sample in each category (Table 2). Species that tended to occur in drier stands included the **Linyphiidae** ***Dicymbium tibiale*** and ***Tenuiphantes alacris***. Those that seemed to prefer moister mosses included the **Linyphiidae** ***Centromerus arcanus***, ***Minyriolus pusillus***, and ***Tapinocyba pallens***. They found that the spider ***Walckenaeria kochi*** (Figure 61; **Linyphiidae**) occurred only on ***Polytrichum commune***, suggesting a preference for a drier habitat than that afforded by the five ***Sphagnum*** species present. Palmgren (1975) considered the optimum habitat for ***Centromerus arcanus*** to be moist spruce forest with a ***Sphagnum*** (Figure 1) carpet. The only spider community that seemed to differ significantly was that of ***Sphagnum girgensohnii***, a grouping that was revealed by cluster analysis.

In addition to the moisture contained within the ***Sphagnum*** (Figure 1) mat, peatlands can give spiders a convenient access to open water, particularly for amphibious and "aquatic" species. Amphibious spiders that live in bogs are able to run along the surface of the water (Figure 6) until they reach a plant (Figure 7) (Nørgaard 1951). They can then climb down the plant, using the leverage gained from the plant attachment to break through the surface tension and climb down into the water.

Table 2. Abundance (individuals per sample) of widespread spider taxa in each of three moisture categories in Finnish forested boggy areas. From Biström & Pajunen 1989.

	dry	**moist**	**wet**
Dicymbium tibiale	0.87	0.39	0.24
Semljicola faustus	0.10	0.14	0.28
Minyriolus pusillus	0.03	0.10	0.23
Tapinocyba pallens	0.05	0.09	0.13
Walckenaeria cuspidata	-	0.04	0.04
Centromerus arcanus	0.82	0.95	1.45
Tenuiphantes alacris	0.48	0.28	0.11
Macargus rufus	0.13	0.12	0.06
Neon reticulatus	0.02	0.04	0.06
Robertus scoticus	0.03	0.18	0.09

Figure 6. ***Pirata piraticus*** walking on the water surface. Photo by Trevor and Dilys Pendleton at <http://www.eakringbirds.com/>, with permission.

Figure 7. ***Pirata piraticus*** climbing on a plant at the water surface. Photo by Michael Hohner, with permission.

But spiders in bogs are not just about water. Rather, this specialized fauna reflects not only the microclimate

and physical factors, but also the lack of disturbance, the age of the habitat, and the surrounding vegetation that may supply new fauna or serve as a refuge during certain times of the year (Bruun & Toft 2004). For the small spiders like the **Linyphiidae**, where long distance travel is difficult, stability is key. And ability to maintain body moisture is part of that.

Regular flooding effectively prevents some species from inhabiting various wetlands. In particular, Bruun and Toft (2004) found that the **Linyphiidae** were absent at Gjesing Mose, Denmark, attributing the absence to frequent flooding. On the other hand, they were present in other locations where the moss was floating, hence avoiding flooding of the spider habitat. Under moderate fluctuations in water level, some spiders are able to retreat upward into the hummocks. Other spiders such as ***Maro lepidus*** (Figure 38; **Linyphiidae**) take advantage of the water, preferring hollows over hummocks (Koponen 2004). This species was also found by Komposch (2000) in wetlands of Austria.

Kupryjanowicz *et al*. (1998) found a large proportion of **hygrophilous** (water-loving) species in the raised peat bogs of Poland. Humidity and illumination were the major determinants of the spider fauna. In the sunlit areas of the bog, two wolf spiders (**Lycosidae**), ***Pardosa sphagnicola*** (Figure 8) and ***Arctosa alpigena lamperti*** (Figure 51) dominated the spider fauna. Since these are larger spiders, it is likely that they are more tolerant of the drying sun because of their lower surface area to volume ratio. Their dominance in peatlands is a shift from the dominance of **Linyphiidae** among mosses in most drier habitats. The somewhat loose arrangement of the ***Sphagnum*** (Figure 1) branches below the surface might permit them to retreat there when they need to replenish moisture, avoid UV light, or escape from predators.

Figure 8. ***Pardosa sphagnicola*** female on ***Sphagnum***. Photo by Walter Pfliegler, with permission.

The moisture relations of spiders in bogs are reflected in the ability of the bogs to support species that are also common in marshes and other wetlands. For example, in Poland Kupryjanowicz (2003) found some of the most common **sphagnophilous** species, including **Hahniidae:** ***Antistea elegans*** (Figure 9), **Lycosidae**: ***Pardosa sphagnicola*** (Figure 8), ***Pirata tenuitarsis*** (Figure 10), and ***P. uliginosus*** (Figure 33) in the sedge-moss marshes. Other peat bog species present in these marshes were the **Gnaphosidae:** ***Drassyllus lutetianus*** (Figure 11) and ***Gnaphosa nigerrima*** (Figure 12) – a species mostly restricted to ***Sphagnum*** carpets of moors in Germany (Platen 2004), and **Salticidae**: ***Neon valentulus*** (Figure 13). The **Linyphiidae** were also present, represented by ***Aphileta misera*** (Figure 36), but this family is much more species-rich elsewhere.

Figure 9. ***Antistea elegans*** (**Hahniidae**). Photo by Jørgen Lissner, with permission.

Figure 10. ***Pirata tenuitarsis*** (**Lycosidae**) male among ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 11. ***Drassyllus lutetianus*** (**Gnaphosidae**). Photo by Jan Barvinek, through Creative Commons.

Figure 12. ***Gnaphosa nigerrima*** (**Gnaphosidae**) on moss. Photo by Jørgen Lissner, with permission.

Figure 13. ***Neon valentulus*** (**Salticidae**), a known peat bog species. Photo by Sarefo, through Wikimedia Commons.

On the other hand, it appears that many of the spiders in bogs are actually **xerophiles** (dry-loving), permitting them to survive the dry heat of summer in exposed areas of the bog. For example, ***Walckenaeria furcillata*** (Figure 14; **Linyphiidae**) is a widespread species that occurs not only under heather and scrub, and among mosses and grasses on acid heathland, but also occurs in deciduous woodlands, calcareous grassland, and fens (Dawson *et al*. in prep). ***Synageles hilarulus*** (Figure 15; **Salticidae**) is a sub-boreal species (Logunov 1996) that runs about in search of food, but in the Mediterranean region, it occurs in grassland (Telfer *et al*. 2003). ***Trochosa robusta*** (Figure 16; **Lycosidae**) lives predominately on dry grassland of limestone, but can also be found on the oligotrophic moors (Platen 2004). These spiders can escape excessive moisture by climbing plants or hummocks.

Figure 14. ***Walckenaeria furcillata*** (**Linyphiidae**). Photo by Jørgen Lissner, with permission.

Figure 15. ***Synageles hilarulus*** (**Salticidae**) among bryophyte and needle litter. Photo by Stefan, Schmidt through Creative Commons.

Figure 16. ***Trochosa robusta*** (**Lycosidae**) female, a species that lives in bogs but is adapted to dry habitats. Photo by Jørgen Lissner, with permission.

Temperature Relationships

Although it is sometimes difficult to separate the effects of temperature from those of moisture, certainly the ***Sphagnum*** (Figure 1) mat provides a gradient of both, as seen in Table 1. The surface experiences greater extremes of both (Figure 87), making the mat a suitable refuge for some spider species. The differences between surface

conditions and those within the peat layer can provide adequate niche separations in a short vertical distance. Nørgaard (1951) cites the vertical separation of two members of **Lycosidae**, ***Pirata piraticus*** (Figure 17) and ***Pardosa pullata*** (as *Lycosa pullata*; Figure 18-Figure 19), in a Danish ***Sphagnum*** (Figure 1) bog in relation to temperature and humidity. ***Pirata piraticus*** lives among the ***Sphagnum*** stalks (Figure 4) where the relative humidity remains a constant 100% and the temperature varies only about 5°C within a day. At the surface (Figure 1), however, where ***Pardosa pullata*** lives, the humidity varies between 40 and 100% on a single day with temperature variations up to 30°C within a day. ***Pardosa pullata*** is physiologically adapted to this fluctuation, with a higher temperature preference and a higher thermal death point than those of ***Pirata piraticus***. The latter species also has a greater sensitivity to low humidities. This relationship is described in greater detail later in this sub-chapter.

Figure 17. ***Pirata piraticus*** (**Lycosidae**) female with egg sac. Photo by Jørgen Lissner, with permission.

Figure 18. ***Pardosa pullata*** (**Lycosidae**) male on mosses. Photo by Jørgen Lissner, with permission.

Figure 19. ***Pardosa pullata*** (**Lycosidae**) female with egg sac on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Spider Mobility

Perhaps one limiting factor for spiders among bog and fen bryophytes is the problem of mobility. First, they must arrive, so that for restored peatlands, this can be a serious detriment to species diversity and the specialists are likely to be the last to arrive because they must traverse unfriendly territory to get there. Some spiders are highly mobile compared to others. The larger spiders like **Lycosidae** (wolf spiders) are able to run across the surface, and as most of us have witnessed, these can run fairly quickly and traverse considerable distances compared to such spiders as the tiny **Linyphiidae**. Hence, the larger spiders, especially the **Lycosidae**, are more common on peatlands, especially during restoration, than in other bryological habitats. ***Gnaphosa nigerrima*** [6.7-9.1 mm (Grimm 1985); Figure 12; **Gnaphosidae**] is widespread in northern Europe and Asia, where it is common on ***Sphagnum*** lawns (Figure 1). Its presence in pitfall traps among ***Sphagnum*** (Harvey *et al.* 2002) reflects its ability to run about swiftly at night. Nevertheless, it is unable to cross a fragmented landscape to reclonize restored wetlands. This is evident in Denmark, where it only occurs in the very best (undisturbed) bogs. This species demonstrates the importance of broad ecological amplitude in enabling spider dispersal.

Abundance and Dominance

Peatlands seem to have a better commonality of dominant species over widespread geographic areas than some of the other communities. This is especially true for the **Lycosidae**, where the genera ***Arctosa***, ***Pirata***, ***Pardosa***, and ***Trochosa*** are common and often the most abundant, but species vary geographically. Nevertheless, as large spiders, they can be less abundant in numbers than small spiders like the **Linyphiidae**. Biomass comparisons might tell a different story.

Komposch (2000) used a variety of sampling methods (pitfall traps, light-traps, soil-sifter, hand-collecting) to study the spiders in wetlands at Hörfeld-Moor, Austria. This study assessed the spider fauna of alder forest, willow shrub, hay meadow, moist meadow, sedge swamp, reed bed, meadowsweet fen, floating mat, and raised bog. Surprisingly, the bog had the smallest percentage of red data species (17% endangered) among the habitats sampled. Komposch suggested that the small number of endangered

species in the raised bog may relate to the small size of this habitat in the study area. Fourteen species occurred only in the bog, but were not necessarily bryophyte inhabitants and were often represented by only one or two individuals. The dominant species were members of the **Lycosidae**: ***Trochosa terricola*** (Figure 20-Figure 21) (30%), ***Trochosa spinipalpis*** (Figure 22) (22%), and ***Pirata hygrophilus*** (Figure 23) (10%), all reported elsewhere in this chapter as important species in bogs or fens. ***Gnaphosa nigerrima*** (Figure 12; **Gnaphosidae**), likewise reported elsewhere in this subchapter, occurred on hummocks (Komposch 2000) in an area where peat was formerly harvested (Rupp 1999).

Figure 20. ***Trochosa terricola*** female (**Lycosidae**). Photo by Jørgen Lissner, with permission.

Figure 21. ***Trochosa terricola*** (**Lycosidae**) male on moss. Photo by Jørgen Lissner, with permission.

Kupryjanowicz *et al*. (1998) reported 203 species of spiders in the raised peat bogs of Poland, where ***Sphagnum magellanicum*** (Figure 24) and ***S. rubellum*** (Figure 25) dominate the moss layer. The ***Sphagnum magellanicum*** habitat was dominated by **Lycosidae**: ***Pardosa sphagnicola*** (Figure 8) (14, 32, and 34% of spiders at three sites) and in the *Vaccinium uliginosum* pinetum, ***Pirata uliginosus*** (Figure 33) with 19 and 24% at two sites and 39% at another site. ***Pardosa sphagnicola*** comprised 18% at the latter site. But even rare species were relatively numerous here and in other bogs, especially on more sunlit peat bogs: ***Arctosa alpigena lamperti*** (Figure 51; **Lycosidae**) (7% in one site), ***Gnaphosa microps*** (Figure 26; **Gnaphosidae**) (3% in one site), ***Pardosa hyperborea*** (Figure 52) (3% in one site), ***P. maisa*** (8% in one site), and ***Scotina palliardi*** (**Liocranidae**) (3%, 0.03%, 4% in three sites) – a species new to Poland.

Figure 22. ***Trochosa spinipalpis*** (**Lycosidae**) among ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 23. ***Pirata hygrophilus*** (**Lycosidae**). Photo by Kjetil Fjellheim, through Creative Commons.

Figure 24. ***Sphagnum magellanicum***. Photo by Michael Lüth, with permission.

Figure 25. ***Sphagnum rubellum***. Photo by Michael Lüth, with permission.

Figure 26. ***Gnaphosa microps*** (**Gnaphosidae**). Photo by Glenn Halvor Morka, with permission.

In bogs of Geitaknottane Nature Reserve, western Norway, the **Lycosidae** again dominated. ***Pirata hygrophilus*** (Figure 23) showed the highest activity abundance (49.2%), followed by ***Pardosa pullata*** (Figure 18-Figure 19) (17.2%); ***Notioscopus sarcinatus*** (Figure 27; **Linyphiidae**) (3.9%), ***Pardosa amentata*** (Figure 28) (3.3%), and ***Trochosa terricola*** (Figure 20-Figure 21; **Lycosidae**) (3.3%) were also among the most abundant (Pommeresche 2002). However, activity can be misleading, with the distance travelled by the tiny **Linyphiidae** being quite short and often confined to the mosses, keeping them out of pitfall traps.

Figure 27. ***Notioscopus sarcinatus*** (**Linyphiidae**) on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 28. ***Pardosa amentata*** (**Lycosidae**). Photo by Jørgen Lissner, with permission.

Biström and Pajunen (1989), in their study of two Finnish peatlands, found 23 species with densities of 1 or more individuals per square meter. They found that in the forested boggy areas they studied, the spider fauna was represented by a few very abundant species and many rarely sampled species. Seven species comprised 66% of the total number of spiders. ***Centromerus arcanus*** (**Linyphiidae**) was the most abundant spider, with 8.7-24.4 individuals per square meter, and tended to be more frequent in ***Sphagnum girgenoshnii***. Other **Linyphiidae** included ***Dicymbium tibiale*** (1.8-11.9) and ***Lepthyphantes alacris*** (0.7-8.6). Larger spiders such as ***Pirata uliginosus*** (Figure 33; ***Linyphiidae***) are somewhat less dense (1.4), but more easily seen. ***Theonoe minutissima*** (Figure 29; **Theridiidae**) is small like a linyphiid but was not as abundant (1.1).

Figure 29. ***Theonoe minutissima*** (**Theridiidae**) female on moss. Photo by Jørgen Lissner, with permission.

Koponen (2002) compared the spider fauna of Sweden, Finland, and northern Norway. He found that spider communities of the southern sites (hemiboreal) differed from the boreal sites of coniferous taiga and those north of the taiga. In the hemiboreal zone, the **Lycosidae** were dominant, led by ***Pirata uliginosus*** (Figure 33), along with ***Pardosa pullata*** (Figure 18-Figure 19), whereas the **Lycosidae** ***Pardosa sphagnicola*** (Figure 8) and ***P. hyperborea*** (Figure 52) were dominant in the boreal zones. ***Hilaira nubigena*** (Figure 30; **Linyphiidae**) and ***Pardosa atrata*** were dominant north of the taiga. No one species

dominated throughout the study area. In Finland, near the northern limit of the hemiboreal zone, the 20 most abundant species were nine **Lycosidae**, nine **Linyphiidae**, one **Hahniidae**, and one **Philodromidae**. The three boreal zones all had ***Pardosa sphagnicola*** and ***P. hyperborea***, both **Lycosidae,** as their two most abundant species. ***Arctosa alpigena*** (Figure 51; **Lycosidae**) (as *Tricca alpigena*) was also typical there. In the two northernmost zones [**palsa** (low, often oval, frost heaves occurring in polar and subpolar climates, containing permanently frozen ice lenses) and **coastal hemiarctic bogs**], ***Hilaira nubigena*** (Figure 30; **Linyphiidae**) and ***Pardosa atrata*** were also common.

In a similar study Koponen (1994) found 169 species of spiders in 14 families in the peatlands of Quebec, Canada. Of these, 73 species occurred only in the temperate-boreal region, 58 only in the subarctic-arctic region, and 38 in both regions. The **Linyphiidae** were the most species-rich family (58.3% of species), an interesting observation in a study using pitfall traps. This family was typical of the subarctic region, with the **Erigoninae** being especially important there. The linyphiid ***Ceratinella brunnea*** occurred in six of the seven study areas. Typical of peatlands, the **Lycosidae** comprised 12.4% of the species, with ***Alopecosa aculeata*** (Figure 94) and ***Pardosa hyperborea*** occurring in six of the seven study areas; **Gnaphosidae** comprised 7.1%. The **Hahniidae**, **Dictynidae**, **Salticidae**, **Liocranidae**, and **Theridiidae** were mostly confined to the temperate and to a lesser extent to boreal regions, although ***Theonoe stridula*** (**Theridiidae**) occurred in six of the seven study areas. Quebec and southern Ontario bogs had 64% of their species in common in the temperate region, whereas only 27% were in common in the subarctic region. The species from bogs in the Manitoba taiga and Quebec were intermediate with 50% of the species in both. About one-third of the spiders in the Quebec bog are Holarctic.

Figure 30. ***Hilaira nubigena*** (**Linyphiidae**). Photo by Glenn Halvor Morka, with permission.

In Russia, open ***Sphagnum*** bogs and bog moss pine forests supported 97 species of spiders (Oliger 2004). The most abundant of these was ***Pardosa sphagnicola*** (Figure 8; **Lycosidae**). The most common families in pitfall traps were **Lycosidae**, **Gnaphosidae**, and **Liocranidae**, whereas the **Linyphiidae** was represented by the most species. It is possible that the **Linyphiidae** were more abundant than indicated by the pitfall traps. Members of this family of tiny spiders are likely to spend little time venturing outside their moss habitat.

As in most of the other habitats discussed in Chapter 7-2, the linyphiid genus ***Walckenaeria*** plays an important role in species diversity. This subchapter likewise includes a number of species of ***Walckenaeria*** from bogs and fens. In addition to these, Millidge (1983) reported several from "boggy areas" in North America and Greenland, including ***W. clavicornis*** (Figure 63), ***W. redneri***, ***W. castanea*** (Figure 31), and ***W. prominens***. Among these, only ***W. castanea*** was identified as being in a ***Sphagnum*** bog.

Figure 31. ***Walckenaeria castanea*** (**Linyphiidae**). Photo by Tom Murray, through Creative Commons.

Tyrphobionts

Peus (1928) coined the term **tyrphobiont** to define those species that are confined to living in peat bogs and mires. Following this definition, Casemir (1976) listed eight species of spiders as true tyrphobionts in Europe: ***Heliophanus dampfi*** (Figure 32; **Salticidae**), ***Pirata uliginosus*** (Figure 33; **Lycosidae**), ***Clubiona norvegica*** (Figure 34; **Clubionidae**), ***Theonoe minutissima*** (Figure 35; **Theridiidae**) – a species listed as rare in Slovakia. Representing the **Linyphiidae**, he found ***Aphileta*** (as ***Hillhousia***) ***misera*** (Figure 36), ***Drepanotylus uncatus*** (Figure 37), ***Hilaira excisa***, and ***Maro lepidus*** (Figure 38).

Figure 32. ***Heliophanus dampfi*** (**Salticidae**) on a leaf. Photo by Jørgen Lissner, with permission.

Table 3. The most abundant spider species (>10 individuals), and other interesting bog spider species from Karevansuo bog, Finland. Total number of individuals = 3670; total number of species = 98. From Koponen 2002.

	Indivs.	%		Indivs.	%
Pirata uliginosus (Lycosidae)	885	24.1	*Agroeca proxima* (Liocranidae)	19	0.5
Pardosa hyperborea (Lycosidae)	802	21.9	*Tenuiphantes mengei* (Linyphiidae)	18	0.5
Arctosa alpigena (Lycosidae)	159	4.3	*Haplodrassus signifer* (Gnaphosidae)	17	0.5
Trochosa spinipalpis (Lycosidae)	116	3.2	*Scotina palliardi* (Liocranidae)	15	0.4
Agyneta cauta (Linyphiidae)	112	3.1	*Zelotes latreillei* (Gnaphosidae)	15	0.4
Walckenaeria antica (Linyphiidae)	110	3.0	*Agroeca brunnea* (Liocranidae)	13	0.4
Pardosa sphagnicola (Lycosidae)	99	2.7	*Walckenaeria nudipalpis* (Linyphiidae)	13	0.4
Alopecosa pulverulenta (Lycosidae)	93	2.5	*Lasaeola prona* (Theridiidae)	12	0.3
Macrargus carpenteri (Linyphiidae)	5	2.3	*Bathyphantes parvulus* (Linyphiidae)	11	0.3
Oryphantes angulatus (Linyphiidae)	0	2.2	*Centromerus arcanus* (Linyphiidae)	11	0.3
Antistea elegans (Hahniidae)	5	1.5	*Xysticus lineatus* (Thomisidae)	7	
Maro lepidus (Linyphiidae)	5	1.5	*Neon valentulus* (Salticidae)	6	
Drepanotylus uncatus (Linyphiidae)	49	1.3	*Minicia marginella* (Linyphiidae)	6	
Pirata piscatorius (Lycosidae)	47	1.3	*Zora parallela* (Zoridae)	5	
Centromerita concinna (Linyphiidae)	46	1.3	*Haplodrassus moderatus* (Gnaphosidae)	5	
Pardosa pullata (Lycosidae)	42	1.1	*Drassyllus pusillus* (Gnaphosidae)	4	
Pirata insularis (Lycosidae)	38	1.0	*Pelecopsis parallela* (Linyphiidae)	3	
Thanatus formicinus (Philodromidae)	34	0.9	*Taranucnus setosus* (Linyphiidae)	3	
Meioneta affinis (Linyphiidae)	34	0.9	*Pirata piraticus* (Lycosidae)	2	
Bathyphantes gracilis (Linyphiidae)	33	0.9	*Theonoe minutissima* (Theridiidae)	2	
Stemonyphantes lineatus (Linyphiidae)	33	0.9	*Gnaphosa microps* (Gnaphosidae)	1	
Gnaphosa lapponum (Gnaphosidae)	30	0.8	*Maro sublestus* (Linyphiidae)	1	
Drassodes pubescens (Gnaphosidae)	26	0.7	*Maro minutus* (Linyphiidae)	1	
Robertus arundineti (Theridiidae)	21	0.6	*Centromerus levitarsis* (Linyphiidae)	1	
Tallusia experta (Linyphiidae)	20	0.5	*Meioneta mossica* (Linyphiidae)	1	
Bolyphantes luteolus (Linyphiidae)	20	0.5	*Walckenaeria capito* (Linyphiidae)	1	

Figure 33. ***Pirata uliginosus*** (**Lycosidae**) male subadult among ***Sphagnum***. Photo by Walter Pflieigler, with permission.

Figure 34. ***Clubiona norvegica*** (**Clubionidae**) on mosses. Photo by Walter Pfliegler, with permission.

Figure 35. ***Theonoe minutissima*** (**Theridiidae**) on ***Sphagnum***. The female of this small comb-footed spider, measures just 1.2 mm. Photo by Rudolf Macek, with permission.

Figure 36. ***Aphileta misera*** (**Linyphiidae**) on ***Sphagnum***. Females are 2 mm. Photo by Morten D. D. Hansen, with permission.

Figure 37. ***Drepanotylus uncatus*** (**Linyphiidae**), another widespread Palaearctic moss inhabitant, where it occurs in bogs and more rarely in neutral or alkaline mesotrophic fens. Photo by Rufolf Macek, with permission.

Figure 38. ***Maro lepidus*** (**Linyphiidae**) female on moss. Photo by Jørgen Lissner, with permission.

Are these tyrphobiont designations supported by other studies? We find that the suitability of the designation can vary by country. It is interesting that Casemir (1976) considered ***Drepanotylus uncatus*** (Figure 37; **Linyphiidae**) and ***Maro lepidus*** (Figure 38; **Linyphiidae**) to be tyrphobionts, whereas at Hörfeld-Moor in Austria, these species were present in some habitats, but not in the bog (Komposch 2000). And even in Great Britain, ***Clubiona norvegica*** (Figure 34; **Clubionidae**) occurs in wet places of the high moorland in other mosses as well as ***Sphagnum*** (Harvey *et al*. 2002). ***Hilaira excisa*** (**Linyphiidae**) is even more puzzling, for we were unable to find any other record of this species from ***Sphagnum*** bogs, although our search was definitely not comprehensive. In Denmark it occurs in mossy springs with seeping cold groundwater (cold in the summer). Furthermore, in the Tyne Valley, UK, ***Hilaira excisa*** lives among grass, rushes, and moss in swamps (Jackson 1906).

Neet (1996) hypothesized that the tyrphobionts should serve as indicators of "good-state" peat bogs. However, the analysis was confounded by the strong relationship between peat bog area and number of tyrphobiont species (Kendall's rank correlation Tau = 0.65). Neet (1996) showed that the number of tyrphobiont species of seven European peat-bogs increased as the area of the bog increased. He pointed out that in addition to the species-area relationship, insufficient sampling effort, biogeographical effects and isolation, and perturbations causing local extinctions all contribute to absent tyrphobionts. As in the analysis above, Neet (1996) pointed out that later evidence does not support all members of Casemir's (1976) list as tyrphobionts. He found that under conditions where the preferred peatland habitat is scarce, some of these tyrphobionts could occur in other habitats, including ***Pirata uliginosus*** (Figure 33; **Lycosidae**) and ***Drepanotylus uncatus*** (Figure 37; **Linyphiidae**) (Hänggi 1987; Hänggi *et al*. 1995). I (Lissner) likewise found ***Drepanotylus uncatus*** in non-peatland habitats in Denmark, but less reliably, among mosses of neutral or alkaline mesotrophic fens. Hence, these are not strict tyrphobionts.

Specialists and Rare Species

Bogs are often the home of rare species, and their rarity increases as more bogs get destroyed. One such example of rarity is ***Heliophanus dampfi*** (Figure 32; **Salticidae**). ***Heliophanus dampfi*** is a rare jumping spider, known in the United Kingdom only from Flanders Moss (Stewart 2001) and two other mires, one each in Wales and Scotland (Harvey *et al*. 2002). Nevertheless, it is known as a bog inhabitant in studies elsewhere [Casemir 1976 (Germany); Kupryjanowicz *et al*. 1998 (Poland)].

In a study of the ***Sphagnum*** (Figure 1) habitats of northwest Russia, Oliger (2004) reported that ***Antistea elegans*** (Figure 9; **Hahniidae**), ***Arctosa alpigena*** (Figure 51; **Lycosidae**) (as *Tricca alpigena*), and ***Gnaphosa nigerrima*** (Figure 12; **Gnaphosidae**), all species reported for bogs elsewhere in this subchapter, were numerous in bogs but rare in forests. Biström and Pajunen (1989) considered that the hahniid ***Antistea elegans*** (Figure 9) might be a bog specialist, with 1.4 individuals per square meter in one site in Finland, but Kupryjanowicz (2003) has reported it from marshes in Poland.

In England, the rare ***Maro lepidus*** (Figure 38; **Linyphiidae**) is only known from acid mires, generally with abundant ***Sphagnum*** (Boyce 2004). ***Erigone psychrophila*** (Figure 39; **Linyphiidae**), ***E. dentigera*** (as ***E. capra***), and ***Semljicola faustus*** (as *Latithorax faustus*) (Figure 40; **Linyphiidae**) similarly are bog specialists in upland blanket mires in England, living in saturated ***Sphagnum*** at the margins of pools. But ***Semljicola faustus*** is known from mosses among heather in the Faroe Islands (Bengtson & Hauge 1979; Holm 1980) and from peat bogs

as well as among stony debris in North Bohemia (Růžička & Hajer 1996). ***Glyphesis cottonae*** (Figure 41; **Linyphiidae**) and ***Centromerus levitarsis*** (Figure 42; **Linyphiidae**) are specialists among ***Sphagnum*** in acid mires; Dawson *et al*. (in prep.) report ***C. levitarsis*** from ***Sphagnum*** in damp woodlands and moors in Great Britain.

Figure 39. ***Erigone psychrophila*** (**Linyphiidae**) female on bryophytes. This species prefers saturated ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 40. ***Semljicola faustus*** (**Linyphiidae**) female. Photo by Jørgen Lissner, with permission.

Figure 41. ***Glyphesis cottonae*** (**Linyphiidae**) on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 42. ***Centromerus levitarsis***. Photo by Jørgen Lissner, with permission.

Later Boyce (2011) explored the invertebrate fauna of Dartmoor, UK, bogs. He considered ***Walckenaeria nodosa*** (Figure 43) to be frequent in bogs and wet heaths. And like others, he found the ***Linyphiidae*** to be well represented. He considered the linyphiid ***Aphileta misera*** (Figure 36) to be a specialist in acid mires. ***Bolyphantes luteolus*** (Figure 44) is likewise an obligate acid mire associate, occurring in litter and mosses of blanket bogs. It is "scarce" in the UK. ***Meioneta mossica*** (Figure 45) occurs exclusively on ***Sphagnum*** (Figure 1) lawns where adults build small webs among upper parts of moss cushions. This species requires abundant bog mosses to make suitable homes. ***Araeoncus crassiceps*** (Figure 46), ***Drepanotylus uncatus*** (Figure 37), and ***Pirata uliginosus*** (Figure 33) live in litter and moss in blanket bogs.

Figure 43. ***Walckenaeria nodosa***, a species of bogs and wet heaths. Photo by Rudolf Macek, with permission.

Figure 44. ***Bolyphantes luteolus***, an obligate acid mire associate Rudolf Macek, with permission.

Figure 45. ***Meioneta mossica***, a species restricted to ***Sphagnum*** lawns. Photo by Eveline Merche, through Creative Commons.

Figure 46. ***Araeoncus crassiceps***, a species that lives among litter and mosses in blanket bogs. Photo by Jørgen Lissner, with permission.

Erigone welchi (Figure 47; **Linyphiidae**) lives in saturated ***Sphagnum***, making its webs in the moss cushions just above the water surface (Boyce 2004). ***Meioneta mossica*** (**Linyphiidae**) builds small webs among the upper layers of the moss cushions in open ***Sphagnum*** lawns. ***Pirata piscatorius*** (Figure 48; **Lycosidae**) lives in very wet areas of ***Sphagnum*** bogs, where the females build a vertical silken tube in the moss, leading down beneath the water surface and providing an escape when the spider is disturbed.

Figure 47. ***Erigone welchi*** (**Linyphiidae**). Photo by Marko Mutanen, through Creative Commons.

Figure 48. ***Pirata piscatorius*** (**Lycosidae**) female with egg sac. Photo by Jørgen Lissner, with permission.

Komposch (2000) demonstrated the uniqueness of spider **coenoses** of bogs in the wetlands of Austria. He used pitfall traps, light traps, soil sifters, and hand collections to assess the spider fauna of alder forest, willow shrub, hay meadow, moist meadow, sedge swamp, reed bed, meadowsweet fen, floating mat, and raised bog. The dendrogram of communities showed the greatest separation of the bog spiders from those of all other habitats in the study. Nevertheless, the three dominant species were not specialists. ***Pirata hygrophilus*** (Figure 49; **Lycosidae**) was the most frequent species in the area, but it has a widespread habitat range, including the ground layer of damp woodlands, raised bogs, lowland heaths, marshy grassland, but especially associated with open water (Harvey *et al*. 2002). ***Trochosa terricola*** (Figure 20-Figure 21; **Lycosidae**) was the most abundant and is known from woodland, grassland, heathland and industrial sites, hiding under stones and logs; it prefers dry, heathy conditions to bogs and marshes (Harvey *et al*. 2002). Only ***T. spinipalpis*** (Figure 22) among these abundant spiders prefers damp places, but even it occurs widely in bogs, wet heath, damp meadows, fens, and marshland. On the Austrian raised bogs, ***Trochosa terricola*** (Figure 20-Figure 21) and ***T. spinipalpis*** were **sympatric** (have overlapping distributions) and formed the spider coenosis there. The floating mat bog seemed to be the preferred habitat for ***Pirata piscatorius*** (Figure 48).

Figure 49. ***Pirata hygrophilus*** (**Lycosidae**) female with egg sac. Photo by Jørgen Lissner, with permission.

Stewart (2001) sheds light on the niche questions for some of these bog species from Flanders Moss, Scotland. Species that were common in some areas seemed to be absent in many others. This is the case for ***Clubiona diversa*** (Figure 50; **Clubionidae**), a common bog dweller in Scotland, but preferring drier sites in southern England (Stewart 2001); in Denmark it is common in wet and dry heathland, but not in places with a peat layer. But what is it that causes these spiders to inhabit such disparate habitats in different places?

In Poland, Kupryjanowicz *et al*. (1998) found that the rarest species and those that could be labelled tyrphobionts were present on the more sunlit peat bogs. Among the most numerous of these rare species were **Gnaphosidae**: ***Gnaphosa microps*** (Figure 26); **Linyphiidae**: ***Glyphesis cottonae*** (Figure 41) and ***Meioneta mossica***; **Liocranidae**: ***Scotina palliardi***; **Lycosidae**: ***Arctosa alpigena lamperti*** (Figure 51), ***Pardosa hyperborea*** (Figure 52), and ***P. maisa*** [also from ***Sphagnum*** in poor pine fens (Itaemies & Jarva 1983)]; **Salticidae**: ***Heliophanus dampfi*** (Figure 32) and ***Cobanus cambridgei***? (as *Talavera westringi*; see Platnick 2013); and **Theridiidae:** ***Theonoe minutissima*** (Figure 35). But in the mountains of the UK, ***Arctosa alpigena*** lives both in and under the moss ***Racomitrium lanuginosum***. And ***Theonoe minutissima*** occurs among mosses in woods of the Tyne Valley, UK (Jackson 1906) and in peat bogs as well as among stony debris in North Bohemia (Růžička & Jaher 1996). Other rare species in Poland bogs incuded **Clubionidae:** ***Clubiona norvegica*** (Figure 34 – also in moorland in the UK); **Gnaphosidae**: ***Haplodrassus moderatus*** (Figure 53 – also in mosses of forests in Denmark) and ***Zelotes aeneus*** (Figure 54); **Linyphiidae:** ***Aphileta misera*** (Figure 36 – also in marshes in the UK), ***Centromerus semiater*** (Figure 55), and ***Ceraticelus bulbosus*** (as *Ceraticelus sibiricus*) (Figure 56); **Lycosidae:** ***Pirata insularis***, ***P. tenuitarsis*** (Figure 10 – also in marshes in Poland), and ***Zora armillata*** (Figure 57); and **Mimetidae**: ***Ero cambridgei*** (Figure 58-Figure 59). The percentage of rare species ranged from 3.5% to 18.3%.

Figure 51. ***Arctosa alpigena lamperti*** (**Lycosidae**) on ***Sphagnum***. Photo by Rudolf Macek, with permission.

Figure 52. ***Pardosa hyperborea*** (**Lycosidae**) on ***Sphagnum***. Photo by Tom Murray, BugGuide, through Creative Commons.

Figure 50. ***Clubiona diversa*** (**Clubionidae**) on dead moss. Photo through Creative Commons.

Figure 53. The nocturnal ground spider, ***Haplodrassus moderatus*** (**Gnaphosidae**) (7 mm), has been recorded from a range of damp habitats, ranging from moist unimproved grassland (e.g. *Molinia* meadows) to fairly dry ***Sphagnum*** bogs, such as degraded raised bogs. Photo by Jørgen Lissner, with permission.

Figure 54. ***Zelotes aeneus*** (**Gnaphosidae**). Photo ©Pierre Oger, with permission.

Figure 55. ***Centromerus semiater*** (**Linyphiidae**) habitus. Photo by Glenn Halvor Morka, with permission.

Figure 56. ***Ceraticelus bulbosus*** (**Linyphiidae**). Photo by Chuck Parker, through Creative Commons.

Figure 57. ***Zora armillata*** (**Zoridae**). Photo by Rudolf Macek, with permission.

Figure 58. ***Ero cambridgei*** (**Mimetidae**) on leaf. Photo by Jørgen Lissner, with permission.

Figure 59. ***Ero cambridgei*** (**Mimetidae**) on leaf. Photo by Jørgen Lissner, with permission.

Mosses as Spider Habitats in Bogs and Fens

Is *Sphagnum* Special?

One factor that creates tyrphobionts is having a special requirement. For example, ***Pirata hygrophilus*** (Figure 23;

Lycosidae) is a prominent species in a number of European bogs (Casemir 1976; van Helsdingen 1976; Almquist 1984; Kupryjanowicz *et al*. 1998; Svaton & Pridavka 2000). Unlike the sun-loving rare species described by Kupryjanowicz *et al*. (1998), ***Pirata hygrophilus*** seems to occur only in areas of shaded ***Sphagnum*** (Nørgaard 1952). ***Pirata piscatorius*** (Figure 48) also seems to be confined to the ***Sphagnum*** area of the habitat (Bruun & Toft 2004).

Some species seem to require the bogs for their winter retreat (Boyce 2004). For example, ***Sitticus floricola*** (Figure 38; **Salticidae**) spends the winter deep in the ***Sphagnum*** hummocks (Harvey *et al*. 2002; Boyce 2004).

Boyce (2004) found that for some species, the acid nature of the habitat seemed to be important, but was it the *p*H (acidity) or the vegetation associated with it? For example, ***Hilaira pervicax*** (Figure 62; **Linyphiidae**) is an acid mire dweller among ***Sphagnum*** and rushes in acid flushes and blanket mires (Boyce 2004). ***Hilaira nubigena*** (Figure 30) lives above 400 m and is likewise associated with ***Sphagnum*** and rushes in acid flushes and blanket mires. ***Semljicola caliginosus*** (**Linyphiidae**) lives in ***Sphagnum*** and wet litter on blanket mires. ***Clubiona norvegica*** (Figure 34; **Clubionidae**), ***Walckenaeria kochi***, (Figure 61) and ***W. clavicornis*** (Figure 63; **Linyphiidae**) are primarily known from acid (***Sphagnum***) mires in Britain, but they are not restricted to this habitat (see Chapter 7-2). ***Pirata tenuitarsis*** (Figure 10; **Lycosidae**) usually lives among ***Sphagnum*** near bog pools. Do they require this habitat, or do they benefit from lack of a predator or competing species?

Figure 60. ***Sitticus floricola*** (**Salticidae**). Photo by Peter Harvey, Spider Recording Scheme-British Arachnological Society.

Figure 61. ***Walckenaeria kochi*** on ***Polytrichum*** sp. Photo by Rudolf Macek, with permission.

Figure 62. ***Hilaira pervicax*** (**Linyphiidae**). Photo by Marko Mutanen, through Creative Commons.

Figure 63. ***Walckenaeria clavicornis*** (**Linyphiidae**) on moss. Photo by Jørgen Lissner, with permission.

On the other hand, some spider species prefer ***Sphagnum*** habitats, but are not necessarily confined to bogs. At the Lesni Lom Quarry (Brno-Hady) in the Czech Republic, ***Zelotes clivicola*** (Figure 64; **Gnaphosidae**) was abundant among mosses in peat bogs, but it also occurred under stones in peat bogs and among mosses in pine and birch forests (Hula & Šťastna 2010).

Figure 64. ***Zelotes clivicola*** (**Gnaphosidae**) male. Photo by Jørgen Lissner, with permission.

Maelfait *et al*. (1995) found that ***Gongylidiellum latebricola*** (Figure 65; **Linyphiidae**) was one such species, with its presence correlating with the presence of ***Sphagnum*** in riverine forests in Flanders, Belgium. But what is the role of ***Sphagnum*** in such habitats? Is it a winter retreat? Or could it be a moist refuge in the heat or drought of summer? I (Lissner) have found it commonly among ***Hypnum*** mats in forests in Denmark and about equally common from acidic fens (with or without ***Sphagnum***). Hence, whatever role ***Sphagnum*** has for this species, it is apparently not unique. Furthermore, not all ***Sphagnum*** species are equal, with some occurring in forests in shallow turfs, some submerged, and others at varying water levels in the open.

In Russia, two members of **Lycosidae**, ***Pardosa atrata*** and ***Pirata piscatorius*** (Figure 48), occur commonly in bogs, but are absent from forests (Oliger 2004). ***Antistea elegans*** (Figure 9; **Hahniidae**), ***Gnaphosa nigerrima*** (Figure 12; **Gnaphosidae**), and ***Arctosa alpigena*** (Figure 51; **Lycosidae**) (as *Tricca alpigena*) were numerous in bogs, rare in forests. On the other hand, four **Lycosidae** were dominant in both bogs (48%) and forests (52%) in this study: ***Alopecosa pulverulenta*** (Figure 66), ***Pardosa sphagnicola*** (Figure 8), ***P. hyperborea*** (Figure 52), and ***Pirata uliginosus*** (Figure 33).

Figure 65. ***Gongylidiellum latebricola*** (**Linyphiidae**) on moss. Photo by Jørgen Lissner, with permission.

Figure 66. ***Alopecosa pulverulenta*** (**Lycosidae**) with spiderlings on moss. Photo by Walter Pfliegler, with permission.

Pommeresche (2002) found that bog spider communities in Norway had more species in common with the open *Calluna*-pine forests than with other types of forests, perhaps indicating an acid preference. **Lycosidae**, **Liocranidae**, and **Tetragnathidae**, for example, dominated both bogs and *Calluna*-pine forests. Some species indicated open areas: ***Trochosa terricola*** (Figure 20-Figure 21; **Lycosidae**), ***Gonatium rubens*** (Figure 67; **Linyphiidae**), and ***Pardosa pullata*** (Figure 18-Figure 19; **Lycosidae**). ***Pirata hygrophilus*** (Figure 23; **Lycosidae**) was an indicator species for bogs. ***Pirata hygrophilus*** and ***Notioscopus sarcinatus*** (Figure 27; **Linyphiidae**) (in wet ***Sphagnum*** and ***Polytrichum*** under scrub) only occurred in the bogs, whereas elsewhere in Europe ***P. hygrophilus*** frequently occurs in humid forests (Maelfait *et al*. 1995; Thaler 1997) and ***Notioscopus sarcinatus*** (Figure 68) occurs in fens (Boyce 2004), supporting the observation that the preferred habitat may differ geographically.

Figure 67. ***Gonatium rubens*** (**Linyphiidae**). Photo by James K. Lindsey, with permission.

Figure 68. ***Notioscopus sarcinatus*** on moss. Photo by Jørgen Lissner, with permission.

Heathlands, another acid habitat, have some species exclusively in common with the bog habitats. For example, ***Hypselistes jacksoni*** (Figure 69; **Linyphiidae**) and ***Trochosa spinipalpis*** (Figure 22; **Lycosidae**) occur almost exclusively in bogs and wet heaths in Great Britain (Boyce 2004).

Figure 69. ***Hypselistes jacksoni*** (**Linyphiidae**) on moss. Photo by Jørgen Lissner, with permission.

As might be expected, marshlands can have similar species to those of bogs. ***Gnaphosa nigerrima*** (Figure 12; **Gnaphosidae**) occurs in ***Sphagnum*** lawns (Boyce 2004) as well as in marshes (Kupryjanowicz 2003). On the other hand, ***Carorita limnaea*** (Figure 70); **Linyphiidae**) not only lives in very wet acid ***Sphagnum*** mires (Boyce 2004), but also in mixed coniferous woods (Pickavance & Dondale 2005), another typically acid habitat.

Figure 70. ***Carorita limnaea*** (**Linyphiidae**) suspended from moss. Photo by Jørgen Lissner, with permission.

The foregoing studies imply the importance of the vegetation structure, at least as a complement to the niche provided by ***Sphagnum***. But how do we explain that some spider species occur in what appear to be very different habitats? For example, ***Satilatlas britteni*** (**Linyphiidae**) lives in ***Sphagnum*** bogs and salt marshes (Boyce 2004). In the Faroe Islands, ***Centromerita bicolor*** (Figure 71; **Linyphidae**) not only occurs in ***Sphagnum*** wetlands, but also on a sand dune, as well as many other habitat types (Lissner 2011). Clearly some of these are generalists, but some, like ***Satilatlas britteni*** occupy only two very different habitats.

Figure 71. ***Centromerita bicolor*** on moss. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.

The Bog and Fen Habitat

Hummocks and Hollows

Topogenous ***Sphagnum***-dominated, acidic fens are frequently developed into a topographic mosaic of hollows and hummocks. Hollows only provide a thin layer of non-flooded moss as habitat and may become seasonally flooded. Hummocks provide a deeper layer of moss/peat, including subsurface air spaces that spiders may occupy. Not surprisingly, a higher number of spider species is associated with the hummocks than in the surrounding hollows, at least when it comes to spiders living within the moss layer (Koponen 2004). Hummocks are less susceptible to flooding and provide more stable environments than the hollows. The structures of hummocks are more complex due to the thickness of the moss layer and the presence of a higher number of moss and plant species. Thus, they offer lots of hiding and hunting places per unit of area. They may also exhibit a more uniform climate internally except for the upper few centimeters. Ant colonies (*e.g.* ***Formica***, ***Myrmica*** spp.) are common features of hummocks and the activities of ants may diversify habitats, providing internal runways, and increasing the number of spider species sustained by the hummocks. According to Lesica and Kannowski (1998) the activities of ants may provide an environment for plants that has better aeration and is warmer, as well as nutrient-enriched, allowing more plant species to colonize the hummock. This undoubtedly affects the properties of the spider habitats. Cavities produced by ants may be exploited by web-building spiders, *e.g.* the small comb-footed spider, ***Theonoe minutissima*** (Figure 35; **Theridiidae**), a spider mostly found within hummocks. Densities in moist hollows, low hummocks, and higher ***Sphagnum fuscum*** hummocks are 1.7-2.1- fold higher than in wet hollows (Koponen 2004). ***Drepanotylus uncatus*** and ***Pardosa sphagnicola*** were more abundant in moist hollows in southern Finland and ***Robertus arundineti*** in hummocks.

Indirect Association with *Sphagnum*

Many spiders found in bogs and fens are indirectly associated with mosses. For example the stunted trees sometimes found on open or scarcely wooded **ombrogenous** bogs or on poor fens provide microhabitats suitable for spiders (Figure 72). Usually they contain plenty of loose bark and rotten wood, much preferred

hiding places for many spider species. The orb weaver ***Araneus marmoreus*** (Figure 73-Figure 75; **Araneidae**) is frequently found in wooded wetlands, constructing its web usually at heights above 1.5 m (Harvey *et al*. 2002). The long-jawed orb weaver, ***Tetragnatha nigrita*** (Figure 76; **Tetragnathidae**), is largely confined to branches of birch and other trees growing on ***Sphagnum*** bogs and fens, and is only rarely found on the same tree species growing outside bogs and fens. The spider fauna associated with the herb layer of bogs and fens is also distinctly different from that of the herb layer of nearby drier places. For example, the jumping spider ***Heliophanus dampfi*** (Figure 32; **Salticidae**) can be swept from the herb layer and from tree saplings in ***Sphagnum*** bogs, but is very rare in other types of wetlands.

Figure 72. ***Sphagnum*** bog with stunted birch, near Lake Salten Langsø, Denmark. Photo by Jørgen Lissner, with permission.

Figure 73. ***Araneus marmoreus*** (**Araneidae**) showing disruptive coloration. Photo by Trevor and Dilys Pendleton <http://www.eakringbirds.com/>, with permission.

Figure 74. ***Araneus marmoreus pyramidatus*** (**Araneidae**) on moss at Hatfield Moors. Photo by Brian Eversham, with permission.

Figure 75. ***Araneus marmoreus*** (**Araneidae**) showing pyramid design on the dorsal side of the abdomen. Photo by Jørgen Lissner, with permission.

Figure 76. ***Tetragnatha nigrita*** (**Tetragnathidae**) female on leaf. Note the abdominal patterning that resembles that of dead leaves. Photo by Walter Pfliegler, with permission.

Differences among Bogs and Fens

Individual **ombrogenous** (dependent on rain for its formation) bogs as well as poor fens seem to possess rather different spider assemblages even if located relatively close to one another. Many moss-associated spider species of the bogs appear to have a very scattered distribution, being found only in a few widely separated bogs, *e.g.* ***Robertus ungulatus*** (Figure 77; **Theridiidae**), ***Clubiona norvegica*** (Figure 34; **Clubionidae**), ***Glyphesis cottonae*** (Figure 41; **Linyphiidae**), and ***Carorita limnaea*** (Figure 70; **Linyphiidae**). This is puzzling since the dispersal capacity usually is high for spiders. Perhaps this is a combination of low dispersal capacity, inhospitable land between sites, and local extinction exceeding recolonization.

Figure 77. ***Robertus ungulatus*** male on moss. Photo by Jørgen Lissner, with permission.

One of the spiders that seems to prefer the ***Sphagnum*** habitat is ***Pardosa sphagnicola*** (Figure 79-Figure 81; **Lycosidae**; Oliger 2004). In the Lake Ladoga region of Russia, this species is the most abundant and is nearly ubiquitous among the peatlands. Oliger found that there was significant similarity in the taxa of spiders in peatlands in NW Russia, Finland, and Lithuania. These especially included **Lycosidae**, **Gnaphosidae**, and **Liocranidae**. The latter were frequently encountered in pitfall traps.

Figure 78. ***Pardosa sphagnicola*** (**Lycosidae**) on ***Sphagnum***. Photo by Barbara Thaler-Knoflach, with permission.

Figure 79. Male ***Pardosa sphagnicola*** (**Lycosidae**), an inhabitant of ***Sphagnum***. Photo by James K. Lindsey, through Wikimedia Commons.

Figure 80. ***Pardosa sphagnicola*** (**Lycosidae**) female with egg sac. Photo by James K. Lindsey, through Wikimedia Commons.

Figure 81. ***Pardosa sphagnicola*** (**Lycosidae**) female with spiderlings among ***Sphagnum*** branches. Photo by James K. Lindsey, through Wikimedia Commons.

Niche Separation – Lycosidae

Nørgaard (1951) reported on the common lycosid spiders ***Pardosa pullata*** (as *Lycosa pullata*; Figure 82; **Lycosidae**) and ***Pirata piraticus*** (Figure 83; **Lycosidae**) in Danish ***Sphagnum*** bogs. These two spiders live in close proximity to each other, but their microdistribution

vertically is very different. ***Pardosa pullata*** (4-6 mm length) prefers moist habitats, where it runs about on the surface of the closely knit ***Sphagnum*** capitula (plant tops; Figure 1), although in Great Britain the maritime climate permits it to be quite ubiquitous. In Denmark, Nørgaard found a mean of 12 individuals per square meter on the surface of the ***Sphagnum*** carpet in mid July. ***Pirata piraticus*** (up to 9 mm long; Figure 83) likewise prefers moist habitats. Stewart (2001) considers ***Pirata piraticus*** to be the commonest wolf spider of wet, marshy areas with ***Sphagnum*** moss, where it dwells beneath the surface among the much more open realm of ***Sphagnum*** stems (Nørgaard 1951). Nevertheless, it stays close to a free water surface (Nørgaard 1951). As discussed above, temperature can account for the separation of these two species. In the topographic depression bog used for this study, daily air temperatures vary widely from 6°C at night (due to cold air masses streaming down from higher ground) to 32°C in the daytime sun (Figure 84). At the ***Sphagnum*** surface it is even higher, reaching 39°C. Such wide variation is not, however, the case among the stems within the ***Sphagnum*** mat. During the same time period, temperatures ranged only 17 to 22°C at 10 cm below the surface.

Figure 82. ***Pardosa pullata*** (**Lycosidae**) female on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 83. ***Pirata piraticus*** (**Lycosidae**) male. Photo by Jørgen Lissner, with permission.

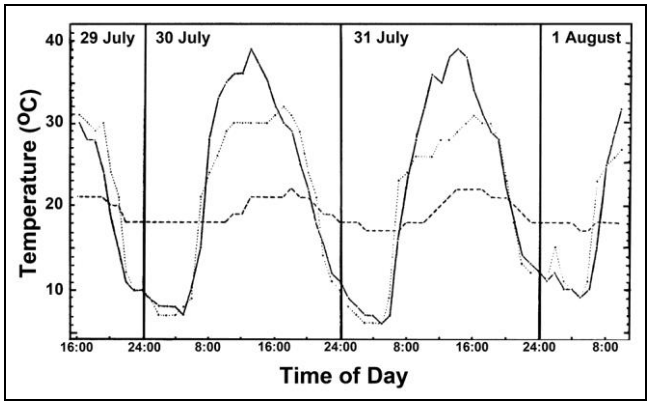

Figure 84. Daily fluctuations in temperature during mid summer in a ***Sphagnum*** bog in Denmark at 10 cm below surface (– – –), surface (——), and 100 cm above surface (· · · · ·). Redrawn from Nørgaard 1951.

Further separation of the two species is provided by the differences in relative humidity, especially in summer. During the three days at the end of July when the temperature was measured, the humidity at the surface where ***Pardosa pullata*** (Figure 82) resides dropped to as low as 40% in the daytime (Nørgaard 1951). On the other hand, the stem layer habitat of ***Pirata piraticus*** (Figure 83) remained a constant 100%. In experiments, Nørgaard demonstrated that ***P. pullata*** has a greater tolerance for low humidity than does ***P. piraticus***. The former species had 100% survival for the 8 hours of the experiment at ≥85% humidity in the temperature range of 20-35°C, whereas ***P. piraticus*** survived only 2.5 hours at 85% humidity. At lower humidity levels (64 & 43%), ***P. piraticus*** generally did not survive for 8 hours at any of these temperatures.

For these two spider species, the life cycle is closely tuned to the conditions of the bog (Nørgaard 1951). Both species hibernate while they are still immature. ***Pardosa pullata*** (Figure 82) hibernates in tussocks of rush, sedge, and ***Polytrichum*** turfs (Figure 85). These locations keep it safely above the water surface even during winter floods. In spring the female carries its egg cocoon attached to its spinnerets. This species spends its days running about the ***Sphagnum*** surface, particularly while the sun is shining. It can hide from enemies among the irregularities of the carpet and hunches up between the capitula at night and during cold spells, never entering the stalk layer. Both males and females have disappeared by mid September.

Figure 85. Bog with ***Polytrichum*** cushions. Photo by James K. Lindsey, with permission.

Pirata piraticus (Figure 83) actually survives in an active state through the winter (Figure 86) and must face some severe conditions. Nørgaard (1951) observed young ***P. piraticus*** under the frozen ***Sphagnum*** capitula (Figure 86). Although their movements when disturbed in the field were sluggish, they became quite active when the clumps of moss were thawed in the lab. In this species, the female spider builds a retreat tube vertically in the stem layer (Figure 87). This tube is 6-8 cm tall and open at both ends. The upper end opens at the surface of the ***Sphagnum*** carpet. The eggs are deposited in the tube and wrapped in a spherical dirty-white cocoon, still attached to the spinnerets. The female takes advantage of the upper opening to position her attached eggs at the surface on sunny days. Disturbance causes the visible cocoons to disappear into the retreat as the female responds to the motion. If they are further persecuted, they exit the tube at the lower end and run on the water surface until they can find a stem to climb down below the water surface.

Figure 86. ***Sphagnum squarrosum*** showing frosted branches during early winter. Photo by Michael Lüth, with permission.

It appears that the location of the tube among the ***Sphagnum*** stems is ideal for the female spider to incubate her eggs. Nørgaard (1951) experimented with the temperature preferences of newly captured ***Pirata piraticus*** (Figure 83) and found that both males and females without cocoons preferred temperatures of 18-24°C. However, when the females had egg cocoons, their temperature preference changed to 26°-32°C. By positioning themselves upside down in the tube with the egg cocoon at the surface of the ***Sphagnum***, the females could maintain a comfortable body temperature while keeping the eggs at their needed higher temperature. Nørgaard also determined that the temperature was more important than the humidity. In a strong temperature gradient, the spiders would go to 21°C in a moist area or a dry area, depending on where that temperature was available. By contrast, ***Pardosa pullata*** (Figure 82) does not change its temperature preference when carrying egg cocoons and prefers temperatures of 28°-36°C, making the surface of the ***Sphagnum*** its location of choice.

Temperature further plays a role in mortality. In the experiments by Nørgaard (1951), ***Pirata piraticus*** (Figure 83) suffered heat stupor at 35°-36°C, whereas ***Pardosa pullata*** (Figure 82) experienced heat stupor at 43°C. It is interesting that ***Pardosa pullata*** females with cocoons began normal movements at 12-14°C, whereas ***Pirata piraticus*** began at 14-19°C. Clearly the spaces among ***Sphagnum*** stems provide the buffered temperature range that is necessary for the life cycle of ***Pirata piraticus***. Nørgaard suggests that construction of the tube permits ***Pirata piraticus*** to move more quickly to the deeper, cooler part of the mat than would movement through the capitulum layer from the surface of the ***Sphagnum*** mat when the temperature at the surface approaches the spider's lethal temperature. Even though adults in this family may be too large to move easily among bryophytes, juveniles may find this habitat ideal.

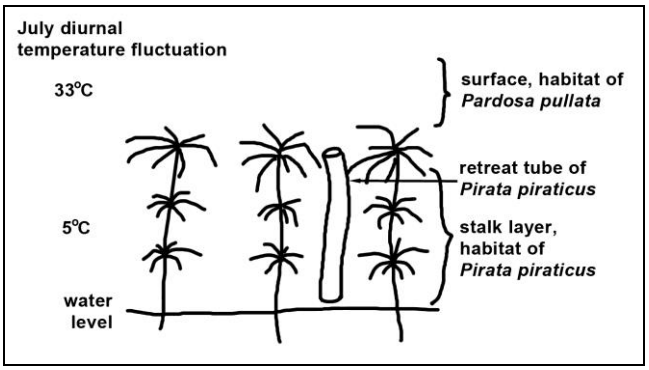

Figure 87. Comparison of temperature niches of two **Lycosidae** spiders from Danish ***Sphagnum*** bogs. Based on Nørgaard 1951.

Bryophytes and Trap-door Spiders

Bog habitats are also home to some trap-door spiders (**Ctenizidae**) that lie in wait for their prey. They make themselves inconspicuous by hiding in a burrow with a trap-door opening (Cloudsley-Thompson 1989). These trap doors are often further camouflaged by bits of lichen or moss incorporated into them.

Bryophytes Hide New Species

Reports describing new species can provide additional species that live in boggy habitats, sometimes giving more detailed habitat information. Efimik and Esyunin (1996) described ***Walckenaeria korobeinikovi*** (Figure 88; **Linyphiidae**) as a new species from a boggy habitat in the Urals. Palmgren (1982) described the ecology of ***Walckenaeria alticeps*** (Figure 89) as new to Finland, where it is restricted to very wet, deep ***Sphagnum*** or wet debris in areas with some canopy cover. We should expect to find more species as researhers look more carefully at the multiple layers of the bryophytes in bogs and fens.

Figure 88. ***Walckenaeria korobeinikovi*** (**Linyphiidae**). Photo by Gergin Glagoev through Bold Systems, through Creative Commons.

Figure 89. ***Walckenaeria alticeps*** (**Linyphiidae**) male on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

It appears that a ***Racomitrium*** hummock in the middle of a ***Sphagnum*** bog can afford a different habitat from its surroundings. For example, ***Micaria alpina*** (Figure 90; **Gnaphosidae**) occurs among grass, moss, and under stones above 750 m in Great Britain, but it also is known from a ***Racomitrium*** hummock (Figure 91) in the middle of a ***Sphagnum*** bog (Harvey *et al*. 2002).

Figure 90. ***Micaria alpina*** (**Gnaphosidae**) female. Photo by Walter Pfliegler, with permission.

Figure 91. ***Racomitrium lanuginosum*** hummock, refuge for spiders above the water. Photo by Peter J. Foss <http://www.fossenvironmentalconsulting.com/>, with permission.

Conservation Issues

When peatlands are endangered, so are their spiders. The spider species are as unique as those of the plants (Bruun & Toft 2004). Scott *et al*. (2006) found that the number of spider bog indicator species can serve as a surrogate for conservation value of the total invertebrate fauna of bogs. They used three parameters to assess their indicator value: naturalness index, species quality, and species rarity curve. The **naturalness index** has a scale of 1-10, with 0 being totally artificial (Machado 2004). The **species quality index** requires assigning a numerical score to all species present according to their rarity. The index is equal to the sum of the quality scores divided by the number of species. Scott *et al*. used the Red Data Book classification as indicated in Harvey *et al*. (2002) to develop those assignments. These categories were assigned as follows: Common = 1, Local = 2, Notable B = 4, Notable A = 8, RDB3 = 16, RDB2 = 32 and RDB1 = 64. For example, ***Heliophanus dampfi*** (Figure 32; **Salticidae**) was assigned 32 points and ***Gnaphosa nigerrima*** (Figure 12; **Gnaphosidae**), the rarest species, 64 points (Harvey *et al*. 2002). The **species-area curve** indicates the steepness of the curve as each species is added to the list. In developing their criteria for indicator species, they considered that three criteria must be met to indicate a good indicator species of a good peatland site:

1. the naturalness index exceeds 0.5
2. the species quality is greater than 2.8
3. the indicator species-area relationship is above the trend line (see Figure 92).

Hence, tracking spider fluctuations can serve as a warning system for peatlands in decline.

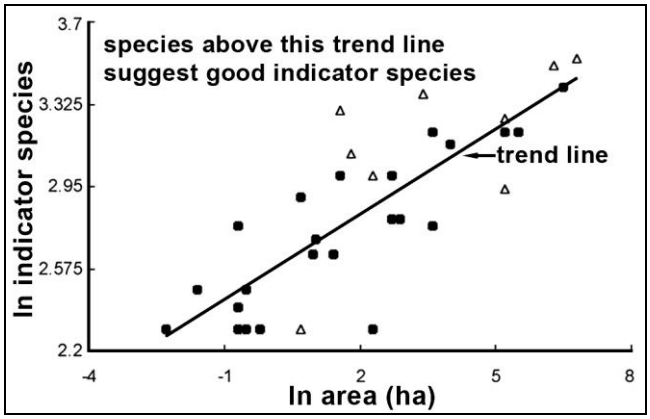

Figure 92. Species-area curve for spiders from 32 bogs in western Britain. Redrawn from Scott *et al*. 2006.

Platen (2004) demonstrated that spider communities can be used to assess the state of degradation of oligotrophic moors. DECORANA demonstrated differences between the lowest and highest stages of degradation, but failed to distinguish the four stages between those. Platen attributed this to the predominance of eurytopic species occurring in the middle stages. However, the Kruskal-Wallis test did discriminate among all the stages. Forest species increased with increasing degradation. Typical species of oligotrophic moors (less hygrophilic) had the greatest abundance at medium stages of degradation.

Peatland Fire Communities

Studies indicate that loss of peatlands can precipitate a serious loss of spider species. As seen above, a number of rare species occur in bogs and fens. In the following example, fire destroyed the peatland of Sudas Bog in Latvia and this study examined the spider fauna the first season afterwards (Spuògis *et al*. 2005). A surprisingly large number of species (48), compared to 40 in the unburned areas, occupied the peatlands after this short time. The invading community was somewhat different from the previous peatland community. The dominant colonizers were ***Agroeca proxima*** (Figure 93; **Liocranidae**), a species typical of pine bogs (Koponen *et al*. 2001; Rëlys *et al*. 2002), and ***Alopecosa aculeata*** (Figure 94; **Lycosidae**), two species with good mobility. Nevertheless, most of the species were typical of the original pine bog. Activity levels likewise were similar to those on the unburned bog. It is possible that some of these species were able to survive the fire from deep within the moss layer, but many colonized from the surrounding bog habitats, possibly travelling up to 120 m.

One interesting phenomenon was that the spiders, even though they were the same species, were darker in color in the burned over bog (Spuògis *et al*. 2005). This was especially true in ***Ozyptila trux*** (Figure 95; **Linyphiidae**), a slow-moving spider (Stewart 2001) that probably survived the fire. Spuògis and coworkers suggested that this darker color was in response to the dark color of the burned peat, perhaps due to greater predation on more visible light-colored individuals. It is also possible that more dark-colored individuals survived the increased exposure to UV light better.

Figure 93. ***Agroeca proxima*** on moss. Photo by Jørgen Lissner, with permission.

Figure 94. ***Alopecosa aculeata*** (**Lycosidae**) female from under moss. Photo by John Sloan, with permission.

Figure 95. ***Ozyptila trux*** (**Linyphiidae**) male among mosses. This species is darker in burned areas. Photo by Jørgen Lissner, with permission.

The **Gnaphosidae**, with ***Drassyllus pusillus*** (Figure 96), ***Gnaphosa microps*** (Figure 26), and ***Zelotes latreillei*** (Figure 97) typically occurring in unburned bogs, were notably absent after the fire (Spuògis *et al*. 2005). Typical species that colonized and were also present in the unburned bogs included ***Trochosa spinipalpis*** (Figure 22; **Lycosidae**) and ***Oryphantes angulatus*** (Figure 98; **Linyphiidae**) from various depths of ***Sphagnum***, ***Agroeca proxima*** (Figure 93; **Liocranidae**), ***Alopecosa aculeata*** (Figure 94; **Lycosidae**) [also known after fire in Canada (Aitchison-Benell 1994)], and ***Euryopis flavomaculata*** (Figure 99; **Theridiidae**) (another slow-moving spider that probably survived the fire). Species such as the **Linyphiidae** ***Agyneta cauta***, ***Micrargus apertus*** (Figure 100), and ***Oryphantes angulatus***, and ***Robertus lividus*** (Figure 101; **Theridiidae**), live in deep layers of moss and probably are able to survive fire (Spuògis *et al*. 2005). ***Agyneta cauta*** (**Linyphiidae**), ***Tenuiphantes cristatus*** (Figure 102; **Linyphiidae**), ***Phrurolithus festivus*** (Figure 103; **Corinnidae**), ***Alopecosa pulverulenta*** (Figure 104; **Lycosidae**), and ***Hygrolycosa rubrofasciata*** (Figure 105; **Lycosidae**) are active in the upper layer of ***Sphagnum***, but it is possible that they likewise retreated deep into the moss to escape the heat and dryness of the fire. ***Gnaphosa bicolor*** (Figure 106; **Gnaphosidae**) and ***Porrhomma pallidum*** (Figure 107; **Linyphiidae**) were probably early invaders – they are species not typical of peatland. ***Aulonia albimana*** (Figure 108; **Lycosidae**) is likewise a probable invader; its activity is restricted to the surface except for its retreat in ***Sphagnum*** (Spuògis *et al*. 2005). The tiny **Linyphiidae** most likely were least able to survive the fire (Hauge & Kvamme 1983); their small size would make them gain heat faster and lose water faster, at the same time preventing them from moving very far. All things considered, the colonizers, whether from outside or from deep in the peat, are still mostly species typical of peat bogs. This is partly because many of the peatland species are actually xerothermic, capable of surviving the dry summer periods.

Figure 96. ***Drassylus pusillus***. Photo by Rudolf Macek, with permission.

Figure 97. ***Zelotes latreillei*** (**Gnaphosidae**). Photo by James K. Lindsey, with permission.

Figure 98. ***Oryphantes angulatus*** (**Linyphiidae**) female on moss. Photo by Walter Pfliegler, with permission.

Figure 99. ***Euryopis flavomaculata*** (**Theridiidae**). Photo by Glenn Halvor Morka, with permission.

Figure 100. ***Micrargus apertus*** (**Linyphiidae**). Photo by Arno Grabolle <www.arnograbolle.de>, with permission.

Figure 101. ***Robertus lividus*** female among mosses. Photo by Jørgen Lissner, with permission.

Figure 102. ***Tenuiphantes cristatus*** (**Linyphiidae**) male on litter. Photo by Walter Pfliegler, with permission.

Figure 103. ***Phrurolithus festivus*** (**Corinnidae**) on moss. Photo by Jørgen Lissner, with permission.

Figure 104. ***Alopecosa pulverulenta*** (**Lycosidae**) male. Photo by James K. Lindsey, with permission.

Figure 105. ***Hygrolycosa rubrofasciata*** (**Lycosidae**) on moss. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.

Figure 106. ***Gnaphosa bicolor*** (**Gnaphosidae**) male on moss. Photo by Jørgen Lissner, with permission.

Figure 107. ***Porrhomma pallidum*** (**Linyphiidae**) female live on ***Sphagnum***. Photo by Glenn Halvor Morka, with permission.

Figure 108. ***Aulonia albimana*** (**Lycosidae**) on moss. Photo ©Pierre Oger, with permission.

In the taiga of southeastern Manitoba, Canada, pitfall traps revealed similar trends to those in Latvia for spider communities of burned and unburned bogs. As in Sudas Bog in Latvia, there were more species in the burned bog after the fire (Aitchison-Benell 1994). The numbers of species remained high for about two months after the fire, then decreased, as one might expect for the usual seasonal activity patterns. In this case, 50 spider species were located in the burned plots and only 45 in the control plots, with 26 species common to both. Species present in burned plots but not in the control bogs included **Lycosidae**: four species of ***Pardosa***, ***Alopecosa aculeata*** (Figure 94), and ***Trochosa terricola*** (Figure 20-Figure 21); **Liocranidae**: ***Agroeca ornata*** (Figure 109); **Linyphiidae**: ***Bathyphantes pallidus*** (Figure 110), ***Erigone atra*** (Figure 111), ***Pocadicnemis americana*** (Figure 112), and ***Tunagyna debilis*** (Figure 113). The control bogs also had unique species that apparently were unable to survive the fire: ***Hogna frondicola*** (Figure 114; **Lycosidae**); ***Gnaphosa microps*** (Figure 26Figure 26; **Gnaphosidae**), and ***Neoantistea agilis*** (Figure 115; **Hahniidae**). ***Gnaphosa microps*** likewise disappeared after fire in Latvian bogs (Spuògis *et al*. 2005).

Figure 111. ***Erigone atra*** maneuvering among the dead portions of mosses. Photo by Jørgen Lissner, with permission.

Figure 109. ***Agroeca ornata*** male. Photo by Yann Gobeil, through Creative Commons.

Figure 112. ***Pocadicnemis americana***. Photo by Gergin Blagoev, through Creative Commons.

Figure 110. ***Bathyphantes pallidus*** (**Linyphiidae**) female. Photo by Tom Murray, through Creative Commons.

Figure 113. ***Tunagyna debilis***. Photo by Bold Systems Biodiversity Institute of Ontario, through Creative Commons.

Figure 114. ***Hogna frondicola*** (**Lycosidae**). Photo by Steve McKechnie, through Creative Commons.

Figure 115. ***Neoantistea agilis*** (**Hahniidae**) male on leaf. Photo by Tom Murray, through Creative Commons.

Maintenance, and even increases, of species richness after fire seem to be common trends among spiders of various habitats (*e.g.* Aitchison-Benell 1994; Neet 1996; Spuògis *et al*. 2005). But Neet points out that early assessment can be misleading, as seen in the Manitoba bogs (Aitchison-Benell 1994). Rare species that survive in the habitat before a fire can disappear as invading species replace them (Neet 1996).

Larrivée *et al*. (2005) clarified some of the disturbance relationships in a Canadian black spruce (*Picea mariana*) forest. Although this was not a bryophyte study, the principles are most likely the same. When comparing clear-cut sites with burned stands, they found that the hunting spiders (**Lycosidae**) were more abundant in the clear-cut stands. Although the **Lycosidae** typically increase after fire, spiders in the clear-cut stands would escape the lethal effects of fire and thus may have retained the original species. This suggestion is supported by the high turnover (2X) of these spiders in the burned areas. Web-building spiders had similar catch rates in these two groups of sites and in uncut controls, but surprisingly had the highest turnover rates and gamma diversity. The clearcuts were characterized by spider comunities typical of dry, open, disturbed forest floor, whereas those in burned stands correlated with high cover of shrubs and dried moss-lichen substrate and deep litter, likely refuges during the fire as well as areas of higher moisture after the fire.

Moretti (2000) examined the effects of winter fires in forests of the Alps and found that 30% of the species occurred only in the burned sites, whereas only 7% were exclusive to the unburned controls. The absence of pioneer species in the burned sites suggests that the spiders were able to survive the fire.

Lycosidae are mobile species and thus are able to invade quickly after a fire, as seen by Spuògis *et al*. (2005) for bogs and Koponen (2005) for forests. **Linyphiidae**, on the other hand, are nearly immobile and may be greatly reduced in numbers after a fire, as seen by Koponen (2005) for a forested site. In bogs, where wet mosses can provide refuge during the fire, **Linyphiidae** can survive and thus be present after the fire (Spuògis *et al*. 2005). But this family can diminish in numbers in succeeding years, while the **Lycosidae** can increase (Koponen 2005).

Summary

Bogs and fens house spiders that benefit from the more constant moisture provided, but also from the moderated temperature, shade, food organisms, and refuge from predation. As in many mossy habitats, the **Linyphiidae** are prominent. But spiders in the **Lycosidae** – hunting spiders – can be seen running across the water surface or the surface of sunny ***Sphagnum***. Nevertheless, many species are xerophiles, living in exposed areas of the bog or fen. The **lycosid** genera ***Arctosa***, ***Pirata***, ***Pardosa***, and ***Trochosa*** are widespread in the peatland habitat, but species vary geographically. They are the most conspicuous, but in smaller numbers than the small **Linyphiidae**. Although there are a few widespread species in the bogs, rare species such as ***Heliophanus dampfi*** and ***Maro lepidus*** may be found somewhat frequently here. Few species seem to be **tyrophobionts** (species that are confined to living in peat bogs and mires), and that status seems to differ by country.

Some spiders use ***Sphagnum*** for a winter retreat. Others seem to benefit from the low *p*H. Some have only an indirect association, living among the tracheophytes that live in the peatlands. Even within the ***Sphagnum*** mat, niche separation can occur in the temperature-moisture-light gradient among the stems.

Trap-door spiders cut a door cover in the surface soil-moss layer, where the mosses seem to hold the soil together and permit the hinge to work. The mosses also provide camouflage.

Spiders can be used to assess the naturalness and degradation of peatlands and serve as a surrogate for other invertebrate taxa. Fires in peatlands cause a serious loss of spider species, especially rare species. The invading community is somewhat different from the original peatland community, partly due to lack of a nearby recolonization source. Other species survive the fire among the damp peat, but these may disappear within a few years due to interactions with invading spider species, especially the mobile **Lycosidae**.

Acknowledgments

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CHAPTER 7-5
ARTHROPODS: SPIDERS OF PEATLANDS IN DENMARK AND TUNDRA

Janice M. Glime and Jørgen Lissner

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CHAPTER 7-5
ARTHROPODS: SPIDERS OF PEATLANDS IN DENMARK AND TUNDRA

Figure 1. ***Sphagnum*** in flush at Cwm Idwal National Nature Reserve, Wales. Flushes at high elevations and in tundra habitats are often carpeted with ***Sphagnum***. Photo by Janice Glime.

Peatlands

Sphagnum, while not the only kind of peatland, forms a variety of habitats in wet areas. Among these are flushes (Figure 1), bogs, poor fens, and intermediate fens. Bogs and poor fens are poor in nutrients, whereas intermediate fens are somewhat more nutrient rich. Flushes can likewise be somewhat richer as nutrients are carried into them from higher elevations. These are mostly northern habitats, with similar habitats occurring in the southern hemisphere at similar latitudes, but deprived of the land mass available in the northern hemisphere.

Two Acidic *Sphagnum* Fens

Below are some examples of quantitatively important mosses and associated spiders in selected minerotrophic fens of low (acidic) and of moderate alkalinity. Only spiders that are believed to be strongly or fairly strongly dependent on mosses for habitat are listed. Species restricted to bogs are known as **tyrphobionts** and include quite a few spiders; however, the inhabitants of bogs are not necessarily associated with the moss layer but may inhabit the herb, shrub or tree layer. Species characteristic of bogs but not confined to them are called **tyrphophiles**.

Sphagnum affine (Figure 2) has become increasingly rare in Denmark, but its presence indicates ombrotrophic conditions and low nutrient availability. Two acidic ***Sphagnum*** fens near Lake Salten Langsø serve as examples as they have been fairly well investigated in respect to the moss flora and spider fauna. This sub-chapter largely represents the research of co-author Jørgen Lissner and includes original unpublished research on those spiders associated with bryophytes in bogs and fens in Denmark.

Figure 2. ***Sphagnum affine***, a moss of ombrotrophic fens. Photo by Jan-Peter Frahm, with permission.

Dalhof Mire (observations by Lissner)

The Dalhof Mire is situated south of Lake Salten Langsø and covers just 1.5 hectare (Figure 3). This acidic ***Sphagnum***-dominated fen has evolved from a formerly overgrown lake. The depth of the peat layer is unknown. As is typical of small acidic mires, it is rather species poor concerning mosses, but nevertheless contains a rich spider fauna, including several very rare species. This undoubtedly relates to the fen being very old and the fact that it is situated in a protected landscape far from direct human influences.

Figure 3. At a distance the Dalhof Mire seems to be dominated by sedges and grasses, but at closer inspection ***Sphagnum*** is found to cover almost the entire surface. Photo by Jørgen Lissner, with permission.

The fen consists of a micro-topographic mosaic of hummocks and hollows (Figure 4). The upper surfaces of hummocks are elevated to 20-30 cm above the surrounding hollows. This level of spatial heterogeneity provides a relatively high number of niches for spiders to occupy, particularly on and within the well-developed hummocks.

There are only a few flowering plants in the hollows, the dominant one being *Eriophorum angustifolium*. A higher number of flowering plant species is found on the hummocks: *Empetrum nigrum*, *Calluna vulgaris*, *Vaccinium oxycoccus*, *Eriophorum vaginatum*, *Molinia caerulea*, and *Pinus sylvestris* are among the commonest.

Figure 4. Hummock in acidic ***Sphagnum*** fen. It is quite obvious that hummocks provide spider habitats that are very different from those of the surrounding hollows. Photo by Jørgen Lissner, with permission.

The hollows of the Dalhof Mire are dominated by ***Sphagnum cuspidatum*** (Figure 5) and ***S. fallax*** (Figure 6). ***Sphagnum papillosum*** (Figure 15) and ***S. rubellum*** (Figure 7) are also present in the lawn and/or carpet. Moss-associated spiders found here include ***Erigonella ignobilis*** (Figure 8; **Linyphiidae**), ***Carorita limnaea*** (Figure 9; **Linyphiidae**), and ***Robertus ungulatus*** (Figure 10-Figure 11; **Theridiidae**). At least three other ***Robertus*** species [***R. lividus*** (Figure 13), ***R. arundineti*** (Figure 54), ***R. scoticus*** (Figure 14)] are also frequently found among mosses in Northern Europe, all three in bogs elsewhere, but also forests (***R. lividus***), heathland (***R. arundineti***), and mountains (***R. scoticus***).

Figure 5. ***Sphagnum cuspidatum*** in Europe. Photo by Michael Lüth, with permission.

Figure 6. ***Sphagnum fallax***. Photo by Michael Lüth, with permission.

Figure 7. ***Sphagnum rubellum***. Photo by Michael Lüth, with permission.

Erigonella ignobilis (Figure 8) is a common line-weaving spider (**Linyphiidae**) that prefers damp habitats and is found among damp or wet moss, including ***Sphagnum*** spp. in many different types of bogs and fens across much of Europe. Cherrett (1964) found that this family exhibited habitat specificity in eight vegetation types that strongly correlated with the availability of other arthropods.

Figure 8. ***Erigonella ignobilis*** (**Linyphiidae**) male (1.4 mm) on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Carorita limnaea (Figure 9; **Linyphiidae**) (1.2 mm) is a rare Palaearctic line-weaving spider, apparently only found in acidic ***Sphagnum*** fens. At the Dalhof Mire it is most common in mosses growing in the transition zone between hummocks and hollows.

Figure 9. ***Carorita limnaea*** (**Linyphiidae**) male (1.2 mm) on moss. Photo by Jørgen Lissner, with permission.

Robertus ungulatus (Figure 10-Figure 11; **Theridiidae**) (~2 mm) is another rare species that lives among very wet moss in hollows of acidic ***Sphagnum*** bogs, but specimens have also been found among wet ***Plagiomnium*** (Figure 12) mosses in rich fens with plentiful seeping groundwater.

Figure 10. ***Robertus ungulatus*** (**Theridiidae**) male (2.2 mm) on moss. Photo by Jørgen Lissner, with permission.

Figure 11. ***Robertus ungulatus*** (**Theridiidae**) on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

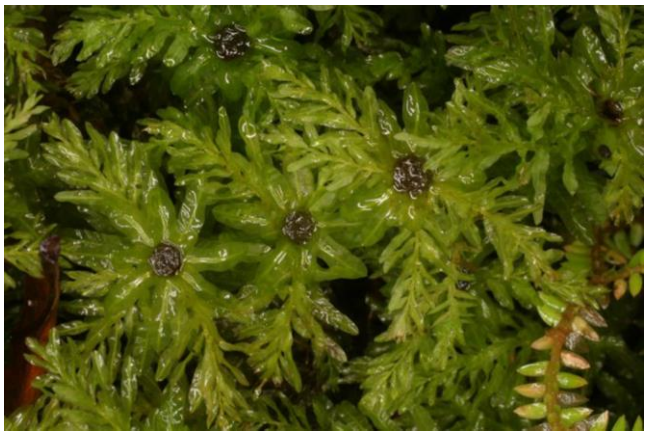

Figure 12. ***Plagiomnium undulatum***. Photo by Jan-Peter Frahm, with permission.

Figure 13. ***Robertus lividus*** (**Theridiidae**) female on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 14. ***Robertus scoticus*** (**Theridiidae**) female, a species listed as vulnerable in Slovakia, on ***Sphagnum***. Photo by Walter Pfliegler, with permission.

The hummocks are more species-rich compared to hollows. The following mosses dominate the hummocks in the Dalhof Mire: ***Sphagnum papillosum*** (Figure 15), ***Sphagnum magellanicum*** (Figure 16), ***Aulacomnium palustre*** (Figure 17), and ***Polytrichum strictum*** (Figure 18), whereas ***Sphagnum angustifolium*** (Figure 18), ***Polytrichum commune*** (Figure 20), ***Straminergon stramineum*** (Figure 21), and ***Sphagnum rubellum*** (Figure 7) are less abundant. The hummocks also provide habitat for the rare pseudoscorpion, ***Microbisium brevifemoratum*** (see Chapter 8).

Figure 15. ***Sphagnum papillosum*** in Europe. Photo by Michael Lüth, with permission.

Figure 16. ***Sphagnum magellanicum***. Photo by Michael Lüth, with permission.

Figure 17. ***Aulacomnium palustre***. Photo by Janice Glime.

Figure 18. ***Polytrichum strictum*** from southern Europe. Photo by Michael Lüth, with permission.

Figure 19. ***Sphagnum angustifolium*** in Europe. Photo by Michael Lüth, with permission.

Figure 20. ***Polytrichum commune*** showing straight stems and no branching. Photo by George Shepherd, with permission.

Figure 21. ***Straminergon stramineum***. Photo by David Holyoak, with permission.

Moss-associated spiders found in the hummocks include ***Minicia marginella*** (Figure 22-Figure 24; **Linyphiidae**), ***Sintula corniger*** (Figure 25; **Linyphiidae**), and ***Theonoe minutissima*** (Figure 26; **Theridiidae**). ***Sintula corniger*** attaches egg sacks within clumps of ***Polytrichum commune*** (Figure 20; Harvey *et al.* 2002).

Figure 22. A male of the linyphiid ***Minicia marginella*** (1.6 mm; **Linyphiidae**) clinging to a ***Polytrichum commune*** leaf. In Denmark, this species is found only in acidic ***Sphagnum*** bogs and fens where it appears to prefer the drier (upper) portions of hummocks or drier bogs such as degraded raised bogs. It can be sifted from mosses such as ***Polytrichum strictum*** and ***P. commune***. Photo by Jørgen Lissner, with permission.

Figure 23. ***Minicia marginella*** (**Linyphiidae**) submale on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 24. ***Minicia marginella*** (**Linyphiidae**) submale on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 25. ***Sintula corniger*** (**Linyphiidae**) male (ca. 1.6 mm). A widespread but very local species found among moss and sedges in wet heathland and ***Sphagnum*** bogs and fens. Photo by Jørgen Lissner, with permission.

Figure 26. ***Theonoe minutissima*** (**Theridiidae**) on moss. Photo by Jørgen Lissner, with permission.

Other Dalhof Mire spider species, which only sometimes utilize mosses or moss-covered areas as habitat include the **Hahniidae**: ***Antistea elegans*** (Figure 96); **Linyphiidae**: ***Aphileta misera*** (Figure 27), ***Ceratinella brevis*** (Figure 28), ***Hypselistes jacksoni*** (Figure 29), ***Metopobactrus prominulus*** (Figure 30), ***Tallusia experta*** (Figure 31), ***Walckenaeria cucullata*** (Figure 32), ***Walckenaeria nudipalpis*** (Figure 33); **Lycosidae**: ***Pirata latitans*** (Figure 34), ***Trochosa spinipalpis*** (Figure 35). The latter species is found in damp habitats ranging from acidic ***Sphagnum*** fens to mineral rich fens. It is frequently found by sifting mosses, which serve as hiding places during the daytime.

Figure 27. ***Aphileta misera*** on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 28. ***Ceratinella brevis*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Figure 29. ***Hypselistes jacksoni*** (**Linyphiidae**) male on a ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 30. ***Metopobactrus prominulus*** (**Linyphiidae**). Photo by Jørgen Lissner, with permission.

Figure 31. ***Tallusia experta*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Figure 32. ***Walckenaeria cucullata*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Figure 33. ***Walckenaeria nudipalpis*** (**Linyphiidae**) male on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 34. ***Pirata latitans*** (**Lycosidae**) female with egg sac on moss. Photo by Jørgen Lissner, with permission.

Figure 35. Female wolf spider ***Trochosa spinipalpis*** (**Lycosidae**) (10 mm) photographed with the moss ***Paludella squarrosa***. Photo by Jørgen Lissner, with permission.

Some spider species may be found in both hummocks and hollows including the **Linyphiidae** ***Centromerus arcanus*** (Figure 36), ***Walckenaeria nodosa*** (Figure 37-Figure 38), ***Walckenaeria acuminata*** (Figure 39), and the **Lycosidae** ***Pardosa sphagnicola*** (Figure 40).

Figure 36. ***Centromerus arcanus*** (**Linyphiidae**) female (2 mm), a common species in a variety of damp habitats, primarily coniferous woodland, wet heathland, and acidic bogs and fens. This tyrphophile species is frequently found among moss, but is not strictly associated with mosses and can be found in wet leaf litter as well. Photo by Jørgen Lissner, with permission.

Figure 37. The male head of ***Walckenaeria nodosa*** (**Linyphiidae**) is elevated into a characteristic bulbous lobe. The species measures ca. 2 mm and is associated with ***Sphagnum*** in poor fens and in depressions of wet heathland. Photo by Jørgen Lissner, with permission.

Figure 38. ***Walckenaeria nodosa*** (**Linyphiidae**) female on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 39. The male ***Walckenaeria acuminata*** (**Linyphiidae**) (ca. 3 mm) with its peculiar head drawn out into a stalk carrying eight eyes, four midway and four at top. This species is found in a wide array of usually damp habitats. Occasionally it has been sifted from ***Sphagnum*** lawn carpets of bogs and fens. Photo by Jørgen Lissner, with permission.

The male of ***Pardosa sphagnicola*** (Figure 40; **Lycosidae**) has a body length of 5 mm. This species is one of many species of wolf spiders found in moss-dominated bogs and fens. Wolf spiders are capable of running rapidly

about during periods with warm and sunny conditions and hunt their prey on the surface of mosses as a well as on water surfaces. When disturbed by trampling they can be observed to run on water surfaces, seeking cover. During cold periods they hide within mosses. Sifting mosses often reveals a high number of wolf spiders of all sizes, mostly belonging to the species-rich genera ***Pardosa*** and ***Pirata***. Many species construct vertical silk tubes within moss clumps. These tubes are used as retreats when the spiders are not running about.

Figure 40. ***Pardosa sphagnicola*** (**Lycosidae**) male (5 mm) on moss. Photo by Jørgen Lissner, with permission.

Naesgaard Mire (observations by Lissner)

The Naesgaard Mire (Figure 41) is a small (0.75 ha) mire formed in a dead-ice depression near the west end of Lake Salten Langsø. There are hardly any hummocks and the entire mire is very wet, particularly during the winter (Figure 41). The moss vegetation is dominated by ***Sphagnum cuspidatum*** (Figure 5), much of which is growing submersed, and ***Sphagnum fallax*** (Figure 6). *Eriophorum vaginatum* dominates among the flowering plants.

Figure 41. The Naesgaard Mire is a very wet ***Sphagnum*** fen dominated by ***Sphagnum cuspidatum*** (Figure 42) and *Eriophorum vaginatum*, the latter species forming the tussocks seen on the image. There are only a few, indistinct hummocks. Photo by Jørgen Lissner, with permission.

The spider fauna is not particularly rich, but it does include some rare species, among these ***Glyphesis cottonae*** (Figure 55; **Linyphiidae**) found in wet ***Sphagnum***. Other species associated with mosses include ***Drepanotylus uncatus*** (Figure 56; **Linyphiidae**), ***Maro lepidus*** (Figure 57; **Linyphiidae**), ***Pirata piscatorius*** (Figure 58; **Lycosidae**), and ***Theonoe minutissima*** (Figure 26; **Theridiidae**).

Figure 42. ***Sphagnum cuspidatum***, a species that typically grows submersed, frequently bordering a lake or pool. Photo by Michael Lüth, with permission.

The female of the small comb-footed spider, ***Theonoe minutissima*** (Figure 26; **Theridiidae**), measures just 1.2 mm. It may be found in a variety of habitats, but is most commonly found in acidic ***Sphagnum*** bogs and fens. At the Dalhof Mire this species is found often deep down in hummocks dominated by ***Sphagnum magellanicum*** (Figure 16). Perhaps it prefers cavities within hummocks just above the water surface.

Other Naesgaard Mire spider species which may not strictly depend on mosses include **Hahniidae**: ***Antistea elegans*** (Figure 96); **Linyphiidae**: ***Cnephalocotes obscurus*** (Figure 44), ***Diplocephalus permixtus*** (Figure 43), ***Erigonella ignobilis*** (Figure 8), ***Gnathonarium dentatum*** (Figure 45), ***Gongylidiellum vivum*** (Figure 46), ***Lophomma punctatum*** (Figure 47), ***Micrargus herbigradus*** (Figure 48), ***Oedothorax gibbosus*** (Figure 49-Figure 50), ***Oryphantes angulatus*** (Figure 51), ***Palliduphantes ericaeus*** (Figure 52-Figure 53), and ***Tallusia experta*** (Figure 31); **Lycosidae**: ***Pirata latitans*** (Figure 34); **Theridiidae**: ***Robertus arundineti*** (Figure 54).

Figure 43. ***Diplocephalus permixtus*** (**Linyphiidae**) female on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

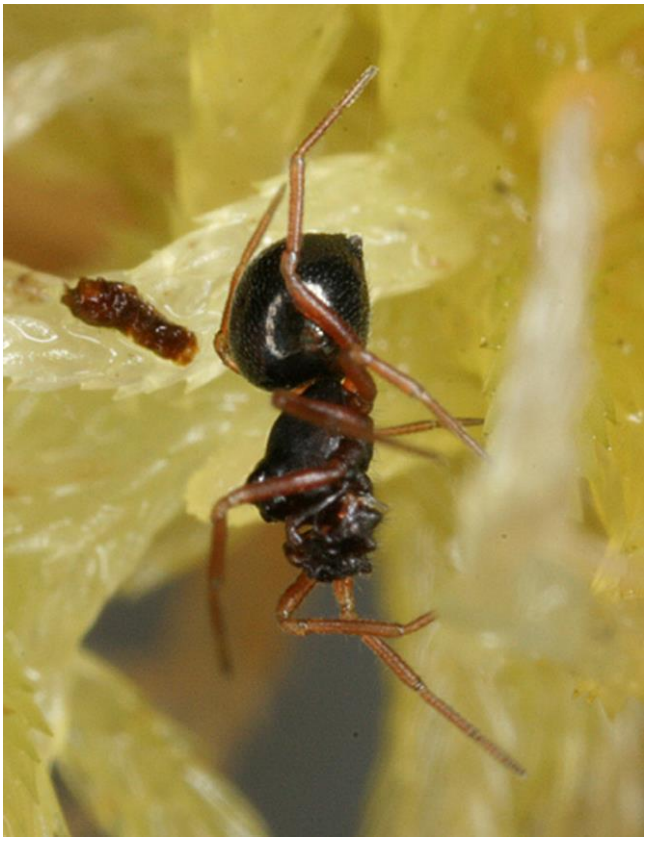

Figure 44. ***Cnephalocotes obscurus*** (**Linyphiidae**) on ***Sphagnum***. Photo by Morten D. D. Hansen, with permission.

Figure 45. ***Gnathonarium dentatum*** (**Linyphiidae**) male on moss. Photos by Jørgen Lissner, with permission.

Figure 46. ***Gongylidiellum vivum*** (**Linyphiidae**) male on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 47. ***Lophomma punctatum*** (**Linyphiidae**) female. Photo by Jørgen Lissner, with permission.

Figure 48. ***Micrargus herbigradus*** (**Linyphiidae**) female on moss. Photo by Jørgen Lissner, with permission.

Figure 49. ***Oedothorax gibbosus*** (**Linyphiidae**) female on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 50. ***Oedothorax gibbosus*** (**Linyphiidae**) male on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 51. ***Oryphantes angulatus*** (**Linyphiidae**) female on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

The rare and very small ***Sphagnum*** mire inhabitant, ***Glyphesis cottonae*** (Figure 55; **Linyphiidae**) (0.9-1.0 mm), has a very scattered occurrence throughout its range, apparently being absent from most ***Sphagnum*** bogs and mires. At the Naesgaard Mire it is found in ***Sphagnum fallax*** (Figure 6) and ***S. cuspidatum*** (Figure 5) in wet parts of the mire. It is unlikely that the species is widely overlooked as it is often abundant where it occurs. Perhaps the dispersal capacity of this species is low since there are plenty of mires having suitable micro-habitats without the presence of this species. Both ***Sphagnum fallax*** and ***S. cuspidatum*** are very common members of the moss flora in northern European acidic fens, so we should expect a more common occurrence of ***Glyphesis cottonae***.

Figure 52. ***Palliduphantes ericaeus*** (**Linyphiidae**) female on moss. Photo by Jørgen Lissner, with permission.

Figure 53. ***Palliduphantes ericaeus*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Figure 54. ***Robertus arundineti*** (**Theridiidae**) male. Photo by Jørgen Lissner, with permission.

Figure 55. ***Glyphesis cottonae*** (**Linyphiidae**) (0.9-1.0 mm) on ***Sphagnum*** in a mire. Photo by Jørgen Lissner, with permission.

Another widespread Palaearctic moss inhabitant, ***Drepanotylus uncatus*** (Figure 56; **Linyphiidae**), reaches a body length of 3 mm. The male is easily recognized by the curved palpal tibial apophysis just visible on the image. This species is found among mosses in acidic bogs and fens. More rarely, records relate to mosses of neutral or alkaline mesotrophic fens.

Figure 56. Male ***Drepanotylus uncatus*** (**Linyphiidae**) (3 mm) on ***Sphagnum***. Note the curved palpal tibial apophysis just visible on the image. Photo by Jørgen Lissner, with permission.

The small male of ***Maro lepidus*** (Figure 57; **Linyphiidae**) measures just 1.2 mm in body length and belongs to the line-weaving spider family. This is a rather uncommon species most often found in wet ***Sphagnum*** of acidic bogs and fens, such as raised bogs and ***Sphagnum*** depressions of wet heathland. In Denmark, this species has been found among ***Sphagnum fallax*** (Figure 6) on several occasions.

Figure 57. ***Maro lepidus*** (**Linyphiidae**) male (1.2 mm) on moss. Photo by Jørgen Lissner, with permission.

As one of the largest members of ***Pirata***, ***P. piscatorius*** (**Lycosidae**) (8 mm) bears resemblance to fishing spiders (*Dolomedes* spp.). The species is confined to very wet habitats and constructs a vertical silken tube (retreat) in ***Sphagnum*** mats which extends down below the water surface. If disturbed the spider will escape down below the water surface (Bristowe 1923 in Harvey *et al.* 2002). It is found in a wide array of wetlands such as carr, mires, bogs and fens, but is more frequent in acidic bogs and fens than in rich fens.

Figure 58. ***Pirata piscatorius*** (**Lycosidae**) (8 mm) bears resemblance to fishing spiders (***Dolomedes*** spp.). Photo by Jørgen Lissner, with permission.

Raised Bogs

In their treatise on spiders of raised peat bogs in Poland, Kupryjanowicz *et al*. (1998) considered the spiders of raised peat bogs to form three groups: 1) inhabiting sunlit peat bog [***Sphagnetum magellanici*** (Figure 16)], 2) occupying moderately illuminated *Ledo-**Sphagnetum***, 3) preferring shaded peat bogs (*Vaccinio uliginosi-Pinetum*). These three habitats are separated by the relative contributions of peat bog and forest species. Forest shading decreases the number of peat bog species. They found that there are a number of **hygrophilous** (water-loving) and **heliophilous** (sun-loving) species that were common to all the study areas.

As discussed earlier, Kupryjanowicz *et al*. (1998) found 203 species of spiders in the six raised bogs of their

Polish study areas. Komposch (2000) found no relationship between percentage of endangered arachnids and diversity or evenness of wetland communities or with percentage of endangered plant species. Some species are not known outside raised bogs. These include **Gnaphosidae**: ***Gnaphosa microps*** (Figure 59); **Lycosidae**: ***Arctosa alpigena lamperti*** (Figure 60); **Linyphiidae**: ***Glyphesis cottonae*** (Figure 55), ***Meioneta mossica*** (see Figure 61); **Liocranidae**: ***Scotina palliardi***; **Salticidae**: ***Heliophanus dampfi*** (Figure 62); and **Theridiidae**: ***Theonoe minutissima*** (Figure 26). Most of the raised bog species are more general peat bog species, including **Linyphiidae**: ***Agyneta cauta***, ***Aphileta misera*** (Figure 27), **Gnaphosidae**: ***Gnaphosa nigerrima*** (Figure 63), **Lycosidae**: ***Pardosa hyperborea*** (Figure 64), ***P. maisa***, and ***P. sphagnicola*** (Figure 65); or hygrophilous species such as **Linyphiidae**: ***Drepanotylus uncatus*** (Figure 56), and ***Notioscopus sarcinatus*** (Figure 98); and **Lycosidae**: ***Pirata uliginosus*** (Figure 66).

Figure 61. ***Meioneta affinis*** (**Linyphiidae**) female on moss. This species lives on moss, grass, and dry stones (Nentwig *et al*. 2012). Photo by Jørgen Lissner, with permission.

Figure 59. ***Gnaphosa microps*** (**Linyphiidae**). Photo by Glenn Halvor Morka, with permission.

Figure 62. ***Heliophanus dampfi*** on leaf. Photo by Jørgen Lissner, with permission.

Figure 60. ***Arctosa alpigena lamperti*** on ***Sphagnum***. Photo by Rudolf Macek, with permission, with permission.

Figure 63. ***Gnaphosa nigerrima*** male on moss. Photo by Jørgen Lissner, with permission.

Figure 64. ***Pardosa hyperborea***. Photo by Walter Pfliegler, with permission.

Figure 65. ***Pardosa sphagnicola***, carrying spiderlings, on ***Sphagnum*** and the lichen ***Cladina***. Photo by Walter Pfliegler,with permission.

Figure 66. ***Pirata uliginosus*** (**Lycosidae**), a bog dweller. Photo by Jørgen Lissner, with permission.

Stewart (2001) found ***Heliophanus dampfi*** (Figure 62); **Salticidae**) in Britain for the first time on a raised bog at Flanders Moss. In all, he found 118 species of spiders at Flanders Moss. Lycosids comprised 41% of the trapped specimens, with ***Pirata uliginosus*** (Figure 66; **Lycosidae**) (177 individuals) overshadowing the usually more common ***Pirata piraticus*** (Figure 67) (2 individuals). But the most common species in traps was the tetragnathid ***Pachygnatha degeeri*** (Figure 68) (440 individuals), most of which were trapped in the drier area at the edge of the moss, in heather and tufts of grass, perhaps not really using the moss habitat.

Figure 67. ***Pirata piraticus*** in bog. Photo by Trevor and Dilys Pendleton at <http://www.eakringbirds.com/>, with permission.

Figure 68. ***Pachygnatha degeeri*** (**Tetragnathidae**) male on moss. Photo by Jørgen Lissner, with permission.

Other species from mosses in Flanders Moss include ***Agroeca proxima*** (Figure 69; **Liocranidae**) (nocturnal hunter), ***Neon reticulatus*** (Figure 70; **Salticidae**), ***Ozyptila*** (Figure 71; slow walkers; **Thomisidae**), ***Pirata piraticus*** (Figure 67; **Lycosidae**), ***Scotina gracilipes*** (Figure 72; **Liocranidae**) (nocturnal hunter), ***Xysticus*** (Figure 73; **Thomisidae**) (slow walkers), ***Zora spinimana*** (Figure 74; **Zoridae**) (daytime hunter) (Stewart 2001).

Figure 69. ***Agroeca proxima*** (**Liocranidae**) male on moss. Photo by Jørgen Lissner, with permission.

Figure 70. ***Neon reticulatus*** (**Salticidae**). Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 71. ***Ozyptila trux*** on moss. Photo by Jørgen Lissner, with permission.

Figure 72. ***Scotina gracilipes*** (**Liocranidae**) female on moss. Photo by Jørgen Lissner, with permission.

Figure 73. ***Xysticus ferrugineus*** (**Thomisidae**) female on moss. Photo ©Pierre Oger, with permission.

Figure 74. ***Zora spinimana*** (**Zoridae**) female on sand. Photo ©Pierre Oger, with permission.

Robertus lividus (Figure 13; **Theridiidae**) is a common spider of a number of grassy and mossy habitats. It appeared in only one of the two bogs in this Danish study. ***Pholcomma gibbum*** (Figure 75; **Theridiidae**) is a 1.5 mm spider common in grass, moss, and detritus at Flanders Moss, but absent in the Danish studies.

Figure 75. ***Pholcomma gibbum*** (**Theridiidae**) female on moss. Photo by Jørgen Lissner, with permission.

Of interest is the presence of ***Pachygnatha clercki*** (Figure 76-Figure 77; **Tetragnathidae**) at Flanders Moss. We did not find this spider listed in any of the other studies included in this chapter, but it is a very common species in many habitats where it is found among low vegetation in places such as bogs or marshes and the edges of ponds, rivers, and streams (Harvey *et al*. 2002). This spider makes no web and hunts at ground level among mosses and low plants in damp places (Stewart 2001).

Figure 76. ***Pachygnatha clercki*** (**Tetragnathidae**) male on leaf. Photo by Ed Nieuwenhuys, with permission.

Figure 77. ***Pachygnatha clercki*** (**Tetragnathidae**) female on leaf. Photo by Ed Nieuwenhuys, with permission.

Raised Bogs in Denmark (observations by Lissner)

The spider fauna of raised bogs is relatively rich, at least when compared to the vegetation, which is rather species poor. A significant fraction of the spider species is associated with higher strata of the vegetation or is mainly confined to leaf litter in the lagg-zone. Three raised bogs situated in Denmark serve as examples here.

Lille Vildmose is the largest raised bog found in northwestern Europe, covering more than 20 sq. km. An additional 2.5 sq. km of degraded raised bog is found in the area. The Kongens Mose raised bog and the Storelung raised bog are much smaller, covering 1.6 sq. km and 0.3 sq. km, respectively, both with degraded parts. Projects aimed at restoring degraded parts of these bogs have been initiated.

The **Lille Vildmose** raised bog in Denmark contains relatively large, undisturbed areas dominated by ***Sphagnum cuspidatum*** (Figure 5) in the hollows and ***S. magellanicum*** (Figure 16) and ***S. rubellum*** (Figure 7) on the hummocks. Unique, raised bog structures have evolved, such as well-developed secondary lakes created over time by relatively higher decomposition rates of ***S. cuspidatum*** dominating the hollows compared to decomposition rates of other ***Sphagnum*** species growing on the hummocks. Plants occurring with some abundance, but otherwise rare in the region include *Scheuchzeria palustris*, *Rubus chamaemorus*, *Drosera anglica*, and ***Sphagnum affine*** (Figure 78). The latter has become increasingly rare in Denmark; its presence indicates ombrotrophic conditions and low nutrient availability. *Calluna vulgaris* is one of the commonest flowering plant species on the bog surface. A range of biotopes adjoin the bog area, including various forest types and open areas with acidic and calcareous grassland as well as dry and wet heathland. As a consequence of the variety of habitats the entire area is

very species rich. About 300 spider species have been recorded at the Lille Vildmose, more than half the number of species known from the entire country of Denmark.

Figure 78. ***Sphagnum affine***. Photo by Jan-Peter Frahm, with permission.

The **Kongens Mose** raised bog contains remnants of undisturbed raised bog but also areas that have been degraded by peat cutting and drainage. The bog is bordered to the east by Draved Forest, one of the best natural forests of Denmark. The combined spider fauna of these two areas is very rich.

The **Storelung** raised bog consists mostly of forested wetland, but about 10 ha is raised bog with degraded parts or recently restored areas.

Spider species found among mosses in these three raised bogs include ***Clubiona norvegica*** (Figure 79; **Clubionidae**), ***Gnaphosa nigerrima*** (Figure 63; **Gnaphosidae**), and ***Centromerus levitarsis*** (Figure 81; **Linyphiidae**).

The female ***Clubiona norvegica*** measures 6.5 mm. It belongs to the family **Clubionidae** (sac spiders), so-named because they make silken sacs (Figure 80) as retreats on plants and rocks. In much of its range it is a rare inhabitant of ***Sphagnum*** bogs, including raised bogs. Here, it can be sifted from moss and ***Sphagnum***, but it may also sometimes be swept from higher vegetation, such as *Salix*.

Figure 79. This female ***Clubiona norvegica*** (**Clubionidae**) measures 6.5 mm. This specimen was found among ***Sphagnum*** with sparse *Molinia* in an wet area of the bog with much open water. Photo by Jørgen Lissner, with permission.

Figure 80. **Clubionidae** retreat sac. Photo by Aniruddha Dhamorikar through Creative Commons.

Figure 81. Ventral view of the female ***Centromerus levitarsis*** (**Linyphiidae**) showing the characteristic long, slender scape of the epigyne. This specimen was sifted from ***Sphagnum palustre*** at the Storelung raised bog and measures ca. 1.8 mm. Photo by Jørgen Lissner, with permission.

Two Spring-Fed Mires

Lake Bredsgård (12 ha) and Lake Rosborg (75 ha, Figure 100) serve as examples of **mesotrophic fens** with a high number of moss species and a diversity of microhabitats. Both fens are the results of failed land reclamation projects which were aimed at draining the lakes for agriculture and pasture. However, the areas remained too wet after drainage due to the presence numerous springs along the former bottoms and lake sides supplying a large and constant amount of cold groundwater. At the fens, seep areas are found with rare, but characteristic, bryophytes, *e.g.* ***Cratoneuron filicinum*** (Figure 82), ***Paludella squarrosa*** (Figure 83), and ***Hamatocaulis vernicosus*** (Figure 84). The two fens are also microrefugia for the yellow marsh saxifrage (*Saxifraga hirculus*), a threatened and declining plant in most of Europe.

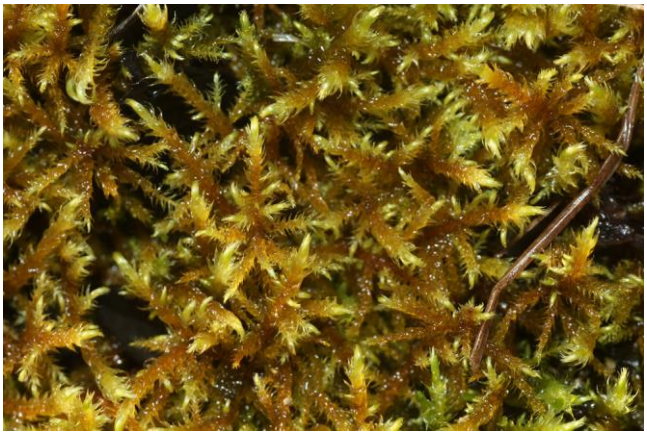

Figure 82. ***Cratoneuron filicinum***. Photo by Barry Stewart, with permission.

Figure 83. ***Paludella squarrosa*** in Europe. Photo by Michael Lüth, with permission.

Figure 84. ***Hamatocaulis vernicosus*** in Europe. Photo by Michael Lüth, with permission.

The combined moss flora of both fens counts to about 65 species, indicating that these fens are of regional importance. A number of liverworts are known from the fens, but only ***Marchantia polymorpha*** (Figure 85) occurs with some abundance. At least twelve ***Sphagnum*** species occur in the fens. ***Sphagnum palustre*** (Figure 86), ***Sphagnum teres*** (Figure 87), ***Sphagnum fimbriatum*** (Figure 88), and ***Sphagnum warnstorfii*** (Figure 89) are quantitatively important and form mats of some sizes locally. ***Aulacomnium palustre*** (Figure 17), ***Calliergonella cuspidata*** (Figure 90), ***Climacium dendroides*** (Figure 91), ***Dicranum bonjeanii*** (Figure 92), and ***Polytrichum commune*** (Figure 20) dominate among the other bryophyte species. In addition, ***Helodium blandowii*** (Figure 93) and ***Tomentypnum nitens*** (Figure 94) may locally dominate seep areas.

Figure 85. ***Marchantia polymorpha***. Photo by James K. Lindsey, with permission.

Figure 86. ***Sphagnum palustre*** in Europe. Photo by Michael Lüth, with permission.

Figure 87. ***Sphagnum teres*** in Europe. Photo by Michael Lüth, with permission.

Figure 88. ***Sphagnum fimbriatum*** in Europe. Photo by Michael Lüth, with permission.

Figure 89. ***Sphagnum warnstorfii*** in Europe. Photo by Michael Lüth, with permission.

Figure 90. ***Calliergonella cuspidata*** in Bretagne. Photo by Michael Lüth, with permission.

Figure 91. ***Climacium dendroides***. Photo by Janice Glime.

Figure 92. ***Dicranum bonjeanii*** in Europe. Photo by Michael Lüth, with permission.

Figure 93. ***Helodium blandowii*** in Europe. Photo by Michael Lüth, with permission.

Figure 94. ***Tomentypnum nitens***. Photo by J. C. Schou, with permission.

Lake Bredsgård (observations by Lissner)

The spider fauna of Lake Bredsgård is not thoroughly investigated. Moss-associated spider species include **Hahniidae**: ***Antistea elegans*** (Figure 96); **Linyphiidae**: ***Ceratinella brevis*** (Figure 95), ***Erigonella ignobilis*** (Figure 8), ***Maso sundevalli*** (Figure 97), ***Notioscopus sarcinatus*** (Figure 98), ***Oedothorax gibbosus*** (Figure 49-Figure 50), ***Walckenaeria cuspidata*** (Figure 103); **Salticidae**: ***Sitticus caricis*** (Figure 102); **Theridiidae**: ***Robertus arundineti*** (Figure 54).

Figure 95. ***Ceratinella brevis*** (**Linyphiidae**) on moss. Photo by Jørgen Lissner, with permission.

Antistea elegans (Figure 96; **Hahniidae**) belongs to the lesser cobweb spiders, characterized by having the spinners arranged in a transverse row. The male has a body length of about 3 mm. The species builds a small sheet over depressions at ground level (Cattin *et al*. 2003). It has been recorded from a variety of damp habitats, including bogs with wet ***Sphagnum***.

Figure 96. ***Antistea elegans*** (**Hahniidae**) on ***Sphagnum***. The male shown here has a body length of 3 mm. Photo by Jørgen Lissner, with permission.

Figure 97. ***Maso sundevalli*** (**Linyphiidae**) female on moss. Photo by Jørgen Lissner, with permission.

Figure 98. ***Notioscopus sarcinatus*** (**Linyphiidae**) male (2 mm) positioned on ***Cinclidium stygium*** (Figure 99), a rare moss of minerotrophic fens. The spider is found in a variety of mosses, perhaps most numerously in ***Sphagnum warnstorfii*** (Figure 89), a common species of minerotrophic fens. Note the peculiar conical process on the carapace separated from the head by a narrow slit. Photo by Jørgen Lissner, with permission.

Figure 99. ***Cinclidium stygium***. Photo by Kristian Peters through Wikimedia Commons.

Lake Rosborg (observations by Lissner)

Moss-associated spiders of Lake Rosborg (Figure 100) include **Linyphiidae**: ***Aphileta misera*** (Figure 27), ***Gnathonarium dentatum*** (Figure 45), ***Lophomma punctatum*** (Figure 47); **Gnaphosidae**: ***Gnaphosa nigerrima*** (Figure 63); and **Salticidae**: ***Sitticus caricis*** (Figure 102).

Figure 100. Lake Rosborg, a spring-fed mire with a rich moss flora. Photo by Jørgen Lissner, with permission.

Aphileta misera (Figure 27; **Linyphiidae**) is a small and indistinct species of the line-weaving spiders. The female shown measures ca. 2 mm. The species is fairly common in various types of acidic bogs. Some records from rich fens could relate to mineral poor areas of heterogeneous rich fens. Egg sacks have been found affixed within clumps of ***Polytrichum commune*** (Figure 20) (Harvey *et al*. 2002).

Another ground spider, ***Gnaphosa nigerrima*** (Figure 101) is found in among mosses in both acidic bogs and rich fens. The male measures ca. 7 mm. The species can be found in wet ***Sphagnum***-dominated hollows of raised bogs as well as within dense clumps of ribbed bog moss [***Aulacomnium palustre*** (Figure 17)] in rich fens, mosses of quite different bryological life forms. This nocturnal spider emerges at night to hunt actively, but hides during the day in a silken retreat within the moss carpet. The spider is rather rare in much of its range, which is peculiar considering it is frequently found among common moss species. One of its favorites, ***Aulacomnium palustre***, is very common in a wide array of mire habitats. Nevertheless, this spider species (at least in Denmark) is only found in the very best bogs and mires with high species diversity.

Figure 101. ***Gnaphosa nigerrima*** (**Gnaphosidae**) on mosses. Photo by Jørgen Lissner, with permission.

Figure 102. The jumping spider ***Sitticus caricis*** (4 mm, **Salticidae**) inhabits bogs and fens and hunts among low vegetation and on the surface of ***Sphagnum*** mats. Photo by Jørgen Lissner, with permission.

Figure 103. ***Walckenaeria cuspidata*** (**Linyphiidae**) male on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Tundra Peatlands

Tundra peatlands are extensive and the influence of ***Sphagnum*** on the water regime and nutrient cycling is extensive. The ***Sphagnum*** acts like a sponge, holding water until its capacity is reached, then releasing it suddenly, causing rushes because the permafrost beneath it is impenetrable. In the summer, this vast peat carpet becomes a safe site for spiders, providing moisture and a refuge from the high UV light of the tundra sunshine.

In the Arctic tundra, the tundra influence may be greater than the influence of bogs and ***Sphagnum***. The Arctic bogs of the Yukon have more **Linyphiidae** than do the forests there (Dondale *et al*. 1997). Dondale *et al*. found ***Ceratinopsis stativa*** in moss and litter (and also in mosses in forests), ***Erigone blaesa*** in bog litter, ***Hybauchenidium gibbosum*** (Figure 104) in moss and plant litter, ***Kaestneria rufula*** (Figure 105) in moss and plant litter, ***Oreonetides vaginatus*** (Figure 106) in plant litter, ***Procerocymbium sibiricum*** in moss and litter in spruce bogs, ***Scotinotylus sacer*** in bog litter, and ***Walckenaeria clavicornis*** (Figure 107) in moss in bogs and heaths.

Figure 104. ***Hybauchenidium gibbosum***. Photo by John Sloan, with permission.

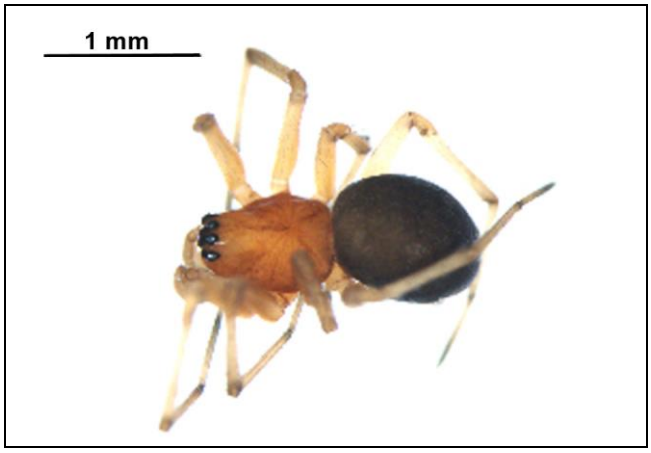

Figure 105. ***Kaestneria rufula***. Photo by Gergin Blagoev through Bold Systems Creative Commons.

Figure 106. ***Oreonetides vaginatus*** on leaf. Photo by Rudolf Macek, with permission.

Figure 107. ***Walckenaeria clavicornis*** with closeup of cephalothorax in lower image. Photos by Jørgen Lissner, with permission.

Not surprisingly, due to the open nature of the habitat, the Yukon **Lycosidae** are represented by a number of species (Dondale *et al*. 1997). ***Arctosa raptor***, ***Pardosa sodalis*** in moss in larch or spruce bogs, ***Pirata piraticus*** (Figure 67) in moss and herbs in bogs, and ***Pirata zelotes*** in bogs and swamps. These are probably only surface relationships, but the mosses undoubtedly play a role in creating a suitable habitat. Likewise, in the **Salticidae** ***Cobanus cambridgei*** (as *Sitticus finschii*) occurs in litter in spruce bogs. The **Gnaphosidae** are represented by ***Micaria pulicaria*** and ***M. tripunctata*** among bog mosses, the latter in spruce bogs.

In the Faroe Islands, many of the species are found in bogs or with ***Sphagnum***, but most are also in other habitats. These multi-habitat species associated with ***Sphagnum*** or bogs included **Hahniidae**: ***Hahnia montana*** (Figure 108) (Harvey *et al.* 2002; Lissner 2010, 2011), **Linyphiidae**: ***Centromerita bicolor*** (Figure 109) (Lissner 2011), ***Centromerus arcanus*** (Figure 36) [bogs (Harvey *et al*. 2002)], ***Erigone psychrophila*** (Figure 110) [***Sphagnum*** at the edge of bog pools (Harvey *et al*. 2002), ***Hilaira nubigena*** (Figure 111) [***Sphagnum*** bog; also in Britain (Holm 1980; Lissner 2011)], ***Improphantes complicatus*** (Figure 112) [***Sphagnum*** bogs (Lissner 2011)], ***Saaristoa abnormis*** (Figure 113) [among ***Sphagnum*** (Holm 1980)], ***Semljicola faustus*** (Figure 114) [among ***Sphagnum*** in bog of pine forest (Bengtson & Hauge 1979; Holm 1980)], ***Walckenaeria clavicornis*** (Figure 107) [in bogs of Greenland (Holm 1967) and in ***Sphagnum*** in Britain (Harvey *et al*. 2002)]. ***Walckenaeria nodosa*** (Figure 37-Figure 38) [a moss dweller in the Faroes (Lissner 2011), occurs in lowland bogs in Britain (Harvey *et al*. 2002)] and ***Walckenaeria nudipalpis*** (Figure 33) in bogs (Holm 1980). The **Lycosidae**, as in lower latitude bogs and tundra in general, are relatively common, including ***Arctosa alpigena*** (Figure 115) [in ***Racomitrium*** (Figure 116-Figure 117) of the Faroes (Harvey *et al*. 2002) and ***Sphagnum*** bogs of Sweden (Almquist 2005)], and ***Pardosa palustris*** (Figure 118) [***Sphagnum*** bogs (Schenkel 1925; Holm 1980; Bengtson & Hauge 1979)].

Figure 108. ***Hahnia montana*** (**Hahniidae**). Photo by Jørgen Lissner, with permission.

Figure 109. ***Centromerita bicolor*** female on moss. Photo by Jørgen Lissner, with permission.

Figure 110. ***Erigone psychrophila*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Figure 111. ***Hilaira nubigena*** (**Linyphiidae**). Photo by Glenn Halvor Morka, with permission.

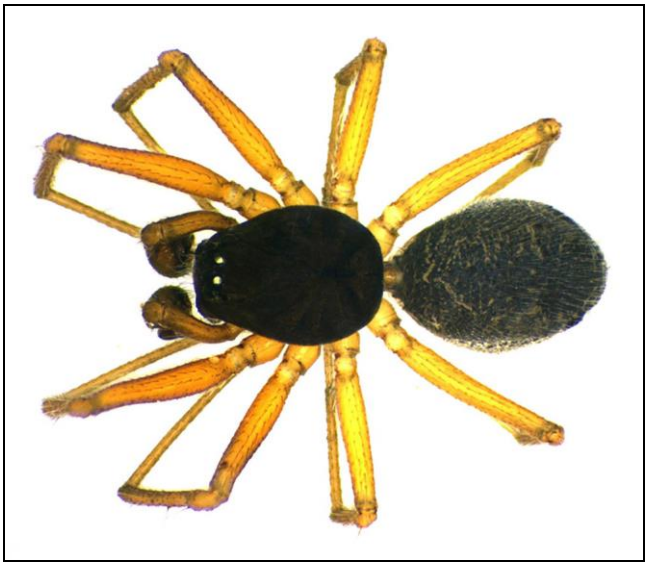

Figure 112. ***Hylyphantes nigritus*** (**Linyphiidae**). Photo ©Pierre Oger, with permission.

Figure 113. ***Saaristoa abnormis*** (**Linyphiidae**). Photo ©Pierre Oger, with permission.

Figure 114. ***Semljicola faustus***. Photo by Jørgen Lissner, with permission.

Figure 115. ***Arctosa alpigena*** (**Lycosidae**) from ***Sphagnum***. Photo by Barbara Thaler-Knoflach, with permission.

Figure 116. ***Racomitrium*** hummocks in Iceland. Photo by Janice Glime.

Figure 117. ***Racomitrium canescens*** hummocks in Iceland. Photo by Janice Glime.

Figure 118. ***Pardosa palustris*** female with spiderlings. Photo by Walter Pfliegler, with permission.

The Arctic/alpine ***Micaria constricta*** (Figure 119; **Gnaphosidae**) and ***Xysticus keyserlingi*** (see Figure 120; **Thomisidae**), as well as the more widespread ***X. triguttatus***, were collected from peatlands in the Wenztel Lake area, Alberta, Canada (Nordstrom & Buckle 2006).

Figure 119. ***Micaria constricta*** (Gnaphosidae). Photo by Biodiversity Institute of Ontario through Creative Commons.

Figure 120. ***Xysticus*** sp. (**Thomisidae**) preying on an insect. Photo by Hectonicus through Wikimedia Commons.

The US Fish and Wildlife Service (Global Species 2013) constructed a food web for the fauna of ***Sphagnum fuscum*** (Figure 121) in the Alaskan tundra. Among the organisms featured in this web was the spider ***Pirata piraticus*** (Figure 67; **Lycosidae**). He indicated that the springtail (**Collembola**) ***Bourletiella hortensis*** served as a primary food source for this spider in the ***S. fuscum*** hummocks. On the other hand, birds were the main predators of the spiders, including the Lapland Longspur (***Calcarius lapponicus***), Common Redpoll (***Carduelis flammea***), and Boreal Chickadee (***Poecile hudsonica***). While this food web serves only to provide examples, it does emphasize the importance of tundra ***Sphagnum*** habitats as a source of food for spiders, in this case emphasizing springtails.

This tundra moss species synusium was described by Popp in 1962. He found ***Limnozetes ciliatus*** and ***L. rugosus*** in association with it.

Figure 121. ***Sphagnum fuscum*** hummock. Photo by Michael Lüth, with permission.

Summary

Peatlands include flushes, bogs, poor fens, and intermediate fens, as well as moors and mires. They are extensive in the Arctic, where they are important in controlling the hydrology and temperature.

The Danish mires are represented by spider families that are typical in mires elsewhere, including the **Linyphiidae**, **Theridiidae**, **Hahniidae**, and **Lycosidae**. Many of these are small spiders that live among the stems of the ***Sphagnum***. Some Lycosidae make tubes that permit them to move quickly from the surface of the moss mat to below the water surface, providing a quick escape route.

Raised bogs represent true bogs where water input is entirely from precipitation. Their communities of spiders depend on the amount of sunlight reaching the moss canopy, with shading causing a decrease in bog species. In addition to the families common in the Danish mires, they also house the **Gnaphosidae** and **Salticidae**, and even the **Tetragnathidae**. Others may be **Liocranidae**, Thomisidae, and **Zoridae**. In Denmark, **Clubionidae** join the fauna.

Springfed mires are fens with more nutrients than bogs but still have at least twelve species of ***Sphagnum***. The spider families are similar, despite the differences in plant species. ***Gnaphosa nigerrima*** hides in a silken retreat in the moss carpet, especially ***Aulacomnium palustre***, but is rare despite its widespread preferred moss species.

The tundra peatlands often have unique flora, perhaps due to their geographic isolation. Their species sometimes coincide with those of lowland bogs. Due to the open nature and available sunshine, **Lycosidae** are common. ***Racomitrium*** hummocks are common and can be in habited by ***Arctosa alpigena***. Other arthropods, especially **Collembola**, are important as food for the spiders.

Of the 112 families of spiders, the number of families typical of peatlands are only a small representation.

Acknowledgments

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Table 1. Species of spiders known to me that occur in association with bryophytes. Most of these have been collected by methods that targeted bryophytes. None has specifically identified liverworts, although they presumably were included in some cases. The number of citations are an indication of the frequency of the species among locations, but the same is not true for genera. If only the genus was named, it has not been listed separately from a known species, albeit sometimes from a different location. + indicates species for which I have seen photographs of the spiders associated with a moss, but the association may be spurious or staged.

Acantholycosa norvegica	Logunov *et al*. 1998
Acantholycosa triangulata	Logunov *et al*. 1998
Achaearanea riparia	Logunov *et al*. 1998
Aelurillus v-insignitus	Merkens 2000
Agroeca brunnea	Koponen 2002
Agroeca proxima	Koponen 2002
Agyneta affinis	Koponen 2002
Agyneta affinisoides	Logunov *et al*. 1998
Agyneta cauta	Koponen 2002
Agyneta fuscipalpus	Logunov *et al*. 1998
Agyneta mossica	Koponen 2002
Agyneta olivacea	Logunov *et al*. 1998
Agyneta ramosa	Lissner 2011b
Alopecosa aculeata (Lycosidae)	Logunov *et al*. 1998
Alopecosa fabrilis	Merkens 2000
Alopecosa pulverulenta	Koponen 2002
Amaurobius ferox	Pendleton & Pendleton; Lindsey
Antistea elegans (Hahniidae)	Isaia *et al*. 2009
Aphileta (*Hillhousia*) *misera*	Kupryjanowicz 2003
Araneus cornutus	Cherrett 1964
Araneus marmoreus	Lissner this volume
Arctosa alpigena	Harvey *et al.* 2002; Almquist 2005
Arctosa lamperti	Kupryjanowicz 1998
Argyroneta aquatica	Pickard-Cambridge 1860
Asthenargus paganus	Lissner this volume
Atypus affinis	Jonsson 1998
Bathyphantes gracilis	Merkens 2000; Koponen 2002
Bathyphantes parvulus	Koponen 2002
Bathyphantes simillimus	Logunov *et al*. 1998
Bolyphantes luteolus	Koponen 2002
Caracladus leberti (Theridiidae)	Isaia *et al*. 2009
Carorita limnaea	Pickavance & Dondale 2005
Centromerita concinna	Merkens 2000
Centromerus arcanus	Biström & Pajunen 1989
Centromerus clarus	Logunov *et al.* 1998
Centromerus levitarsis	Koponen 2002
Centromerus sylvaticus	Merkens 2000
Ceratinella brevis (Linyphiidae)	Jackson 1904-1907
Ceratinella brevipes	Holm 1980
Ceratinella wideri	Logunov *et al*. 1998
Cercidia prominens	Roberts 1985
Chalcoscirtus alpicola	Logunov *et al*. 1998
Chalcoscirtus hyperboreus	Danilov & Logunov 1993
Clubiona abbajensis kibonotensis	Denis 1950
Clubiona lutescens	Crocker & Daws 1996
Clubiona germanica	Komposch 2000
Clubiona norvegica	Harvey *et al*. 2002
Cnephalocotes obscurus	Jackson 1904-1907
Comaroma simonii	Kropf 1997
Cryphoeca silvicola (Hahniidae)	Isaia *et al*. 2009
Decipiphantes decipiens	Logunov *et al*. 1998
Dendryphantes czekanowskii	Logunov *et al.* 1998
Dictyna (Dictynidae)	
Dicymbium tibiale	Biström & Pajunen 1989
Diplocentria bidentata	Jonsson 1998
Diplocephalus arnoi (Theridiidae)	Isaia *et al*. 2009
Diplocephalus dentatus	Brunn & Toft 2002
Diplocephalus helleri	Komposch 2000
Diplocephalus latifrons	Jonsson 1998
Diplocephalus permixtus	Jackson 1904-1907
Dipoena prona	Koponen 2002
Drassodes pubescens	Koponen 2002
Drassyllus pusillus	Merkens 2000
Drepanotylus uncatus	Koponen 2002
Dysdera (Dysderidae)	
Enoplognatha caricis	Komposch 2000
Episolder finitimus	Logunov *et al*. 1998
Erigone atra	Logunov *et al*. 1998
Erigone psychrophila	Lissner 2011b
Erigone remota	Logunov *et al*. 1998
Erigonella ignobilis	Kupryjanowicz 2003
Euophrys flavoatra	Logunov *et al*. 1998
Euophrys proszynskii	Logunov *et al*. 1998
Frontinella communis	Suter *et al*. 1987
Glyphesis cottonae	Kupryjanowicz *et al*. 1998
Gnaphosa borea	Logunov *et al*. 1998
Gnaphosa lapponum	Koponen 2002
Gnaphosa leporina	Logunov *et al*. 1998
Gnaphosa microps	Koponen 2002
Gnaphosa muscorum	Logunov *et al*. 1998
Gnaphosa nigerrima	Kupryjanowicz 2003
Gnaphosa pseudoleporina	Logunov *et al*. 1998
Gnaphosa sticta	Logunov *et al*. 1998
Gnathonarium dentatum (Linyphiidae)	Lissner this volume
Gonatium rubens	Holm 1980
Gongylidium nigriceps	Hauge 1969
Gongylidiellum vivum	Lissner this volume
Hahnia nava	Merkens 2000
Hahnia ononidum	Hauge 1969; Isaia *et al*. 2009
Haplodrassus moderatus	Koponen 2002
Haplodrassus signifer	Koponen 2002
Heliophanus dampfi	Komposch 2000
Hickmanopsis minuta	Hickman 1943
Hilaira excisa	Jackson 1904-1907
Hilaira herniosa	Logunov *et al*. 1998
Hylyphantes nigritus	Logunov *et al*. 1998
+Hypomma bituberculatum	Lissner 2011b
Hypselistes jacksoni	Boyce 2004
Improphantes flexilis	Logunov *et al*. 1998
Labulla thoracica	Hormiga & Scharff 2005
Lepthyphantes alacris	Biström & Pajunen 1989
Lepthyphante angulatus	Koponen 2002
Lepthyphantes bergstroemi	Logunov *et al*. 1998
Lepthyphantes cornutus	Logunov *et al*. 1998
Lepthyphantes distichus	Logunov *et al*. 1998
Lepthyphantes exiguus	Hauge 1969
Lepthyphantes luteipes	Logunov *et al*. 1998
Lepthyphantes mengei	Koponen 2002
Lepthyphantes sajanensis	Logunov *et al*. 1998
Lepthyphantes sibiricus	Logunov *et al*. 1998
Lophomma punctatum	Lissner this volume
Lycosa pullata	Nørgaard 1951
Macrargus carpenteri	Koponen 2002
Macragus multesimus	Hauge 1969

Maro lepidus Koponen 2002
Maro minutus Koponen 2002
Maro sublestus Koponen 2002
Maso sundevalli Lissner this volume
Mecopisthes latinus (Linyphiidae) Isaia *et al*. 2009
Mecynargus monticola Logunov *et al*. 1998
Meta Cherrett 1964
Metellina merianae Cherrett 1964
Metopobactrus prominulus Lissner this volume
Micaria alpina Logunov *et al*. 1998
Micaria constricta Nordstrom & Buckle 2006
Micrargus herbigradus Lissner this volume
Microcentria pusilla Hauge 1969
Microhexura montivaga Coyle 1985
Microneta viaria Logunov *et al*. 1998
Minicia marginella Koponen 2002
Minyriolus pusillus Biström & Pajunen 1989
Monocephalus caastaeipes Jonsson 1998
Monocerellus montanus Logunov *et al*. 1998
Neon valentulus Koponen 2002
Notioscopus sarcinatus Kupryjanowicz *et al*. (1998
Oryphantes angulatus Spuògis *et al*. 2005
Ozyptila arctica Logunov *et al*. 1998
Ozyptila claveata (Thomisidae) Isaia *et al*. 2009
Ozyptila orientalis Logunov *et al*. 1998
Pachygnatha (Tetragnathidae)
Palliduphantes ericaeus Lissner 2011b
Panominops dybowskii Logunov *et al*. 1998
Panominops tauricornis Logunov *et al*. 1998
Parachtes siculus (Dysderidae) Isaia *et al*. 2009
Parasyrisca logunovi Logunov *et al*. 1998
Parasyrisca ulykpani Logunov *et al*. 1998
Pardosa baraan Logunov *et al*. 1998
Pardosa bifasciata Logunov *et al*. 1998
Pardosa bukukun Logunov *et al*. 1998
Pardosa eiseni Logunov *et al*. 1998
Pardosa fulvipes Komposch 2000
Pardosa hyperborea Koponen 2002
Pardosa indecora Logunov *et al*. 1998
Pardosa maisa Itaemies & Jarva 1983
Pardosa oksalai Logunov *et al*. 1998
Pardosa oljunae Logunov *et al*. 1998
Pardosa pullata Nørgaard 1951
Pardosa schenkeli Logunov *et al*. 1998
Pardosa sphagnicola Oliger 2004
Patu marplesi Alphonse 2010
Pardosa biphasciata Logunov *et al*. 1998
Pardosa bukukun Logunov *et al*. 1998
Pardosa indecora Logunov *et al*. 1998
Pardosa oksalai Logunov *et al*. 1998
Pardosa oljunae Logunov *et al*. 1998
Pardosa sphagnicola Oliger 2004
Pelicopsis dorniana Logunov *et al*. 1998
Pelecopsis parallela Koponen 2002
Pellenes lapponicus Logunov *et al*. 1998
Pirata insularis Koponen 2002
Pirata latitans Lissner this volume
Pirata piraticus Nørgaard 1951
Pirata piscatorius Koponen 2002
Pirata tenuitarsis Kupryjanowicz 2003
Pirata uliginosus Brunn & Toft 2002
Poeciloneta petrophila Logunov *et al*. 1998
Robertus arundineti Koponen 2002
Robertus kastoni Logunov *et al*. 1998
Robertus lividus (Theridiidae) Biström & Pajunen 1989
Robertus lyrifer Hauge 1969
Robertus scoticus Svatoň & Kovalčík 2006
Robertus ungulatus Lissner this volume
Savignia frontata Logunov *et al*. 1998
Scotina celans Jackson 1904-1907
Scotina palliardi Koponen 2002
Scotinotylus alpigenus Logunov *et al*. 1998
Scotinotylus altaicus Logunov *et al*. 1998
Scotinotylus protervus Logunov *et al*. 1998
Semljicola (=*Latithorax*) *faustus* Biström & Pajunen 1989
Semljicola latus Logunov *et al*. 1998
Silometopus uralensis Logunov *et al*. 1998
Sintula corniger Cameron 2002
Sitticus caricis Kupryjanowicz 2003
Sitticus lineolatus Logunov *et al*. 1998
Stemonyphantes lineatus Koponen 2002
Talaera sp. 2 Logunov *et al*. 1998
Talavera westringi Kupryjanowicz, *et al*. 1998
Tallusia experta Koponen 2002
Tapinocyba pallens Biström & Pajunen 1989
Taranucnus setosus Koponen 2002
Tetragnatha nigrita Lissner this volume
Thaleria sajanensis Logunov *et al*. 1998
Thanatus arcticus Logunov et al. 1998
Thanatus bungei Logunov *et al*. 1998
Thanatus coloradensis Logunov *et al*. 1998
Thanatus formicinus Koponen 2002
Theonoe minutissima Koponen 2002
Theridion sibiricum Logunov *et al*. 1998
Tibioplus diversus Logunov *et al*. 1998
Tiso vagans Harvey *et al*. 2002
Tricca alpigena Logunov *et al*. 1998
Trochosa spinipalpis Koponen 2002
Trochosa terricola Merkens 2000
Typhochrestoides baikalensis Logunov *et al*. 1998
Typhochrestus digitatus Merkens 2000
Victorium putoranicum Logunov *et al*. 1998
Walckenaeria acuminata (Linyphiidae) Lissner this volume
Walckenaeria alticeps (Linyphiidae) Palmgren, P. 1982
Walckenaeria antica Koponen 2002
Walckenaeria capito Koponen 2002
Walckenaeria cucullata Lissner this volume
Walckenaeria cuspidata Biström & Pajunen 1989
Walckenaeria karpinskii Logunov *et al*. 1998
Walckenaeria koenboutjei Logunov *et al*. 1998
Walckenaeria korobeinikovi Logunov *et al*. 1998
Walckenaeria nodosa Harvey *et al*. 2002
Walckenaeria nudipalpis Koponen 2002
Xysticus (Thomsiidae) Isaia *et al*. 2009
Xysticus austrosibiricus Logunov *et al*. 1998
Xysticus bonneti Logunov *et al*. 1998
Xysticus britcheri Logunov *et al*. 1998
Xysticus emertoni Logunov *et al*. 1998
Xysticus kaiserlingi Nordstrom & Buckle 2006
Xysticus lineatus Koponen 2002
Xysticus rugosus Logunov *et al*. 1998
Xysticus triguttatus Nordstrom & Buckle 2006
Zelotes latreillei Koponen 2002
Zelotes potanini Logunov *et al*. 1998
Zora parallela Koponen 2002

CHAPTER 8-1
ARTHROPODS: HARVESTMEN AND PSEUDOSCORPIONS

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CHAPTER 8
ARTHROPODS: HARVESTMEN AND PSEUDOSCORPIONS

Figure 1. ***Phalangium opilio*** on the moss ***Tortula*** sp. Photo by Christophe Quintin through Creative Commons.

Order Opiliones – Harvestmen

These long-legged arachnids are variously known as daddy-long-legs, granddaddy-long-legs, and harvestmen (Figure 1). The name harvestmen most likely derives from their peak abundance around harvest time. They live on every continent but Antarctica. The adults are usually too big to live within the moss mat, but some do, and some have discovered other uses.

Adaptations

The harvestman typically lives among vegetation, including gardens, where it obtains droplets of water resting on the plants. I have not found any discussion of harvestmen adaptations to bryophytes, but we can consider these based on those seen in other groups of organisms. Camouflage would not seem to be a problem. These arthropods are the shape and size of a medium-sized seed and typically are some shade of brown, often with disruptive patterns, seemingly regardless of habitat. This coloration makes them relatively inconspicuous. Their legs are long and thin, making those appendages all but invisible among the bryophyte branches (Figure 2-Figure 4).

Harvestmen range in body size from less than 1 mm to 7 mm, but their long legs make them appear to be much larger. The long legs and their "push-up" positioning makes maneuvering within moss mats a difficult

proposition. On the other hand, these long legs permit them to move quickly across the surface without attracting undue attention. They are light weight, and their long legs act like a spring board, softening their impact as they run, another feature that is useful for running across loose vertical bryophyte structures.

Figure 2. ***Leiobunum rotundum*** male on mosses, demonstrating the slender black legs of this species. Photo by Morten D. D. Hansen, with permission.

An adaptation for living **within** the bryophyte community might be to have short legs that would enable them to enter the bryophyte domain without getting their legs tangled or caught. In fact, being smaller in all ways could help. For example, ***Siro carpathicus*** (Sironidae; see Figure 3) is one of the few harvestmen known from within moss clumps and is among the smaller species of harvestmen (Rafalski 1956, 1958). But this species has the disadvantage that it is easy prey for the larger arthropods.

Figure 3. ***Siro*** sp. on mosses. ***Siro carpathicus*** is a species that lives among mosses. Note how short the legs are on this harvestman, compared to the more familiar garden species. Photo by M. Hedin, through Creative Commons.

A native of Great Britain and other areas of western Europe, the moss visitor ***Leiobunum rotundum*** (Sclerosomatidae), like many, has scent glands that discourage predators (Wikipedia 2011). For years I watched my dog chase daddy-long-legs. One day he actually caught one, but he was quick to spit it back out. After that, he still chased them, but he didn't attempt to catch them anymore.

Figure 4. This harvestman, in Inohae Valley, Japan, is relatively inconspicuous among the mosses on the tree trunk, with its thin legs blending with the small bryophyte branches. Bryophytes in this environment could provide a source of water, obtained from droplets, in this rather dry habitat. Photo by Janice Glime.

The harvestmen have gotten the reputation of being venomous, a long-perpetuated myth. They have no venom glands, no fangs, and cannot pierce human skin. This reputation may have been based on the smell that emanates when they are handled (Opiliones Internet Discussion Group 2011). At the sides of the eyes are two pores that secrete a foul-smelling fluid. This is most likely what discouraged my dog. The chemical can burn the eyes and mouth, encouraging the would-be predator to release the captured harvestman. In a cave in southwestern Canada, cohabiting cricket, frog, and salamander guts were examined, but no harvestmen were in evidence (Holmberg *et al*. 1984). Bats, on the other hand, do eat Opiliones (Whitaker *et al*. 1977).

This moss visitor, ***Leiobunum rotundum***, is one of the harvestmen that can release a leg if it gets caught, but

generally this leg cannot regenerate (Figure 5). If one watches this process, a surprise ensues. The detached leg continues to twitch! This can last from as little as a minute to as long as an hour, depending on the species (Opiliones Internet Discussion Group 2011). There are "pacemakers" in the ends of the femur of the leg that signal the muscles to extend the leg. The leg relaxes between signals, causing a repeated twitching motion. This could draw the attention of the predator away from the harvestman, allowing it to escape.

Figure 5. ***Leiobunum rotundum*** male on mosses, demonstrating the detachable legs of this species. This fellow seems to have sacrificed one of its eight legs already. Photo by Morten D. D. Hansen, with permission.

Some species of harvestmen are known for their aggregation behavior (Figure 6; Coddington *et al*. 1990). When in these masses, they can sometimes resemble a moss until closer inspection is possible (Bugs in the News 2011). Aggregations of ***Leiobunum*** in southeastern USA have as many as a thousand individuals (Cockerill 1988). Wagner (1954) reported 70,000 individuals in aggregations of ***Leiobunum cactorum*** (*nomen nudum*). Mukherjee *et al.* (2010) reported up to 300,000 individuals of ***Pseudogagrella*** sp. (Sclerosomatidae) in a winter aggregation in a rainforest in China, although the individual patches had only 10-30 individuals.

Figure 6. Aggregation of harvestmen. Photo by Luis Fernández García through Creative Commons.

The function of these aggregations remains unknown, and research has served largely to negate hypotheses (Holmberg *et al* 1984; Machado & Vasconcelos 1998). Machado and Vasconcelos (1998) examined aggregation behavior of three species at 1200 m elevation in Brazil. Among these, only ***Holoversia nigra*** (Gonyleptidae) released repugnatory substances when disturbed. The other two species fled or hid. Yet, among some species elsewhere, disturbance elicits a pulsating behavior among the members of the aggregation (Cockerill 1988), giving the appearance of a larger, more foreboding organism (Opiliones Internet Discussion Group 2011). Other possible advantages may include regulation of temperature, humidity, or light. Cockerill (1988) found several species of ***Leiobunum*** (Figure 5) that aggregated during the day but not at night, lending support for this microclimate hypothesis.

Holmberg *et al*. (1984) suggested that the aggregation behavior of ***Leiobunum paessleri*** in southwestern Canada provided a safe microenvironment. When day length exceeded 14 hours, they migrated into caves, where they formed vertical aggregations. Mating occurred after they vacated the caves in spring. In lab experiments, survival below freezing was poor. For organisms that are hibernating or resting, aggregation behavior could offer environmental protection as well as providing an alarm system when predators approach. On tree trunks and other exposed places, the stacking of individuals, as in Figure 6, could not only offer protection from predators, but reduce wind velocity, reducing desiccation.

The Harvestman Presence

Edgar (1990) mentions that harvestmen occur in mosses, as well as in leaf litter, under logs, and in caves. Biström and Pajunen (1989) investigated the arthropods, including harvestmen, in two forested areas near "boggy" sites in southern Finland. They visited the Borgå sites 8 times between early May and early October and the Esbo sites 21 times during approximately the same period. Samples of moss measuring 25x25 cm and 10 cm deep were sieved to find the organisms. The bryophyte samples were primarily ***Polytrichum commune*** (Figure 19), ***Sphagnum girgensohnii*** (Figure 20), and ***S. squarrosum***. Among the arthropods, the Opiliones were the third most abundant (157 individuals among 1671 arthropods) and were represented by five species. ***Nemastoma lugubre*** (Nemastomatidae; Figure 7-Figure 8) was a generalist harvestman found at all five of the main sites, ranging in abundance from 0.2 to 3.7 individuals per square meter. When the researchers divided the samples into wet, moist, and dry, three of the harvestmen species [***Mitopus morio*** (Phalangiidae; Figure 9-Figure 12), ***Oligolophus tridens*** (Phalangiidae; Figure 13-Figure 14), ***Lacinius ephippiatus*** (Phalangiidae; Figure 16-Figure 16)] had a "tendency" to occur in the drier stands. ***Rilaena triangularis*** (Phalangiidae; formerly ***Platybunus triangularis***; Figure 17-Figure 18) also occurred among these mosses, but there were insufficient data to determine any preferences.

Further evidence of the abundant and widespread nature of some of these species is that one can find ***Mitopus morio***, ***Nemastoma lugubre***, ***Rilaena triangularis***, and ***Lacinius ephippiatus*** in the Faroe Islands (Kauri 1980). The ***Oligolophus*** species there is a different one named ***O. meadii***.

Figure 7. ***Nemastoma lugubre***, a harvestman that can be found among mosses. Photo by Ruth Ahlburg, with permission.

Figure 8. ***Nemastoma lugubre***, a harvestman that lives among mosses as well as other substrata. Photo by Ed Nieuwenhuys, with permission.

Figure 9. Dark color form of ***Mitopus morio***. Photo by James K. Lindsey, with permission.

Figure 10. Two color forms of ***Mitopus morio***. Photo by Ed Nieuwenhuys, with permission.

Figure 11. Close view of ***Mitopus morio*** with a red mite on its leg. Photo © Stuart Dunlop <www.donegal-wildlife.blogspot.com>, with permission.

Figure 12. ***Mitopus morio*** with a background of lichens on bark. Photo by Morten D. D. Hansen, with permission.

Figure 13. ***Oligolophus tridens***, a harvestman that seems to prefer drier sites in boggy areas. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 14. ***Oligolophus tridens***, a harvestman that seems to prefer drier sites in boggy areas. Photos by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 15. ***Lacinius ephippiatus*** female. Photo by Morten D. D. Hansen, with permission.

Biström and Pajunen (1989) found a slight indication that the fauna of ***Sphagnum girgensohnii*** (Figure 20) could be distinguished from that of the other moss stands, but this may be due to habitat differences that suited both the moss and the harvestmen rather than a preference for this ***Sphagnum*** species. At Borgå, there was a significant difference in arachnid species richness between ***Polytrichum commune*** (Figure 19) and ***S. girgensohnii*** (Figure 20). These differences may relate to moisture differences between the microhabitats since ***Sphagnum*** species are much better adapted to hold water than are those of ***Polytrichum***.

Figure 16. ***Lacinius ephippiatus*** mating. Note the red mite. Photo by Morten D. D. Hansen, with permission.

Figure 17. ***Rilaena triangularis*** resting on crustose lichens. Photo by Trevor & Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 18. ***Rilaena triangularis*** resting on tree bark next to a patch of mosses. Photo by Trevor & Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 19. ***Polytrichum commune***, showing its stiff leaves. Photo by Des Callaghan, with permission.

Figure 20. ***Sphagnum girgensohnii*** with ***Polytrichum commune*** at the upper edge, forming a harvestman habitat. Photo by Michael Lüth, with permission.

Sampling such as that of Biström and Pajunen (1989) are suitable for finding inhabitants within a moss mat, but one needs to be more clever to achieve representative sampling of those organisms that live on the surface. The harvestmen can move fairly rapidly, so those living in peatlands on the surface are unlikely ever to be sampled by removing cores. Differences in day/night habitat may also hinder sampling efforts, particularly for those that might migrate between shrubs/trees and the moss layer. Some harvestmen hang from the undersides of branches and leaves in the daytime, taking advantage of the shade to avoid overheating and desiccation, but become active at night. I have been constantly amazed at the number of species that are preferentially nocturnal in their activities, a concept that day-active humans like myself often fail to embrace. I am convinced that unless we develop and use a good sampling protocol for dusk and nightfall sampling we will not have a good understanding of those organisms that utilize the bryophyte habitat in their daily activities.

In Poland, the endangered ***Siro carpathicus*** (Figure 3) lives in mosses, under rocks, and in grass in the deciduous forests (Błaszak 2011). This small species may be one of the few species actually adapted to moving about within the moss clumps. In the Tyne Valley, UK, ***Obisium muscorum*** lives among mosses in marshes (Jackson 1904-1907).

Mating Sites

It appears that mosses play a role in the mating of at least some harvestmen, such as the striped harvestman ***Leiobunum vittatum*** (Figure 21). This species is common in the eastern United States. The males position themselves on moss-covered rocks, often remaining there for days at a time (Macías-Ordóñez 2000). One might suppose that being on a moss prevents desiccation during this prolonged visit. Following copulation, the female investigates potential sites for her eggs by injecting her ovipositor into cracks and crevices until she finds a suitable place to deposit the eggs (Machado & Macías-Ordóñez 2007). It would be interesting to investigate whether the state of hydration of the moss determines selection of location and timing.

Figure 21. ***Leiobunum vittatum***, a harvestman that uses mossy rocks for mating. Photo by Hugh Yemen, with permission.

As a prelude to mating, the female must actually touch the male before recognizing him as a male harvestman (Macías-Ordóñez 2000). The male then pounces on the female and mates with her. The moss continues to play a role as the female ***L. vittatum*** completes the reproductive process by laying her eggs on or under the rock, but not on large, vertical rocks. This may just be convenience – presumably rocks with mosses are selected for the moisture of the moss, but that particular rock is most likely used for laying eggs because of its proximity. The male continues to follow her as she searches for crevices and other suitable places to lay her eggs.

For some species of harvestmen, bryophytes are included among egg-laying sites (Juberthie 1964; Bumblebee.org 2011). This appears to be the case for an invading ***Leiobunum*** species in Europe (Wijnhoven 2011). The female inserted her ovipositor into mosses on the tree trunk at about 30 cm above the ground. This was the only observation of oviposition on a tree, but other individuals did deposit eggs on mosses in crevices.

Species with short ovipositors lay their eggs on mosses or rock walls (Juberthie 1964). The eggs are protected by a mucous layer that prevents desiccation. ***Leiobunum rotundum*** (Figure 22-Figure 24), ***Mitopus morio*** (Figure 10), and ***Oligolophus tridens*** (Figure 14) hide their eggs (Juberthie 1964; Kaestner 1968). ***Leiobunum vittatum***

(Figure 21) not only hides its eggs, but deposits a "repugnant" substance on them (Edgar 1971; Clawson 1988; Macías-Ordóñez 1997).

Figure 22. ***Leiobunum rotundum***, a species that hides its eggs. Photo by Ed Nieuwenhuys, with permission.

Figure 23. Close views of ***Leiobunum rotundum*** on bark. Photo by Ed Nieuwenhuys, with permission.

Figure 24. Close view of ***Leiobunum rotundum***. Photo by Trevor & Dilys Pendleton <www.eakringbirds.com>, with permission.

Often the harvestmen must walk a tightrope between moisture and dryness (Edgar 1971). Too little moisture causes the eggs to develop incompletely; too much encourages the growth of mold. While it would seem that bryophytes might be able to ameliorate the extremes of this moisture gradient compared to soil, documentation that such is the case, or even that bryophytes are used, is lacking.

Seasons

Life cycles tend to dictate the presence or absence of many species. Eggs are essentially invisible to most people, or impossible to identify, so only active invertebrates are noted. Seasonal behavior of bryophyte-dwelling harvestmen does not seem to have attracted the attention of arachnologists, but we can derive indications from seasonal studies in other contexts.

The name harvestman refers to the many species that spend the winter as eggs, hence disappearing about the time harvest ends. Swain and Usher (2004) studied seasonal behavior of harvestmen as part of a restoration study at Flanders Moss, United Kingdom. The bog-dwelling ***Mitopus morio*** (Figure 11) has its peak abundance there in summer to early autumn, followed by ***Paroligolophus agrestis*** (Phalangiidae; Figure 25-Figure 26) in late autumn to early winter. This results from the appearance of ***M. morio*** several weeks before, and its disappearance likewise several weeks before, ***P. agrestis***.

Figure 25. ***Paroligolophus agrestis*** (formerly *Oligolophus agrestis*) among mosses. Photo by Trevor & Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 26. ***Paroligolophus agrestis*** (formerly ***Oligolophus agrestis***) among mosses. Photos by Trevor & Dilys Pendleton <www.eakringbirds.com>, with permission.

Other species had much shorter active periods (Swain & Usher 2004). Forest-dwelling species like ***Oligolophus hanseni*** (Phalangiidae; Figure 27-Figure 28) and ***Lophopilio palpinalis*** (Phalangiidae; Figure 29) appeared for only a few weeks each year, with strong abundance peaks in early winter for ***O. hanseni*** and in late summer for ***L. palpinalis***. Bog-dwelling species with year-long presence, like ***Rilaena triangularis*** (Figure 18), lack a strong abundance peak; in this species there was a very small spring peak. ***Nemastoma bimaculatum*** (Nemastomatidae; Figure 30-Figure 31), likewise a bog dweller, had a peak in autumn, and likewise exhibited low density throughout the year, as also demonstrated for ***Nemastoma lugubre*** by Vanhercke (Figure 32; Vanhercke 2004). These various phenologies combined to create the highest diversity in summer and autumn, when abundance likewise was at its highest. Winter diversity was the lowest, as one might expect.

Figure 27. ***Oligolophus hanseni*** on bark. Photos by Ruth Ahlburg, with permission.

Figure 28. ***Oligolophus hanseni*** on lichens. Photos by Ruth Ahlburg, with permission.

But these trends may not be indicative of harvestmen living among bryophytes elsewhere. Bryophytes can buffer the temperature and moisture fluctuations, so it is possible that these harvestmen may have longer activity periods than plant/tree-dwelling species, and possibly even longer than those living in litter or soil.

Figure 29. ***Lophopilio palpinalis*** on decaying wood. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 30. ***Nemastoma bimaculatum***. Photo by James K. Lindsey, with permission.

Figure 31. ***Nemastoma bimaculatum*** among mosses and litter. Photo by Trevor & Dilys Pendleton <www.eakringbirds.com>, with permission.

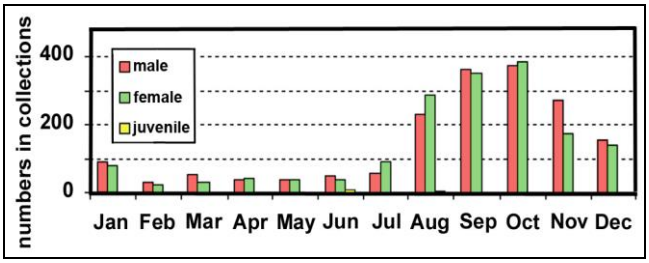

Figure 32. Seasonal dynamics of ***Nemastoma bimaculatum***, based on abundance in museum collections. Absence of juveniles, except a few in June and August, is most likely due to collector bias. Redrawn from Vanhercke 2004.

The liverwort host ***Neosadocus maximus*** (Gonyleptidae; Figure 33) has behavioral activities that can be grouped into five categories (Osses *et al*. 2008). Osses and coworkers found in their Brazilian study that 53% of the time was spent at rest and 31% in exploration. Females spent more time resting than did males. Unlike the human species, it was the males who spent more time grooming. This species was most active at night and during summer, and had increased activity at warmer temperatures, but not at higher humidities.

Epizoic Liverworts on Harvestmen

On quite another note, tropical liverworts (and Cyanobacteria) are known to grow epizootically on the backs of harvestmen (Machado & Vital 2001). On Cardoso Island in Southeastern Brazil, ***Aphanolejeunea subdiaphana*** (see Figure 34) and ***Lejeunea*** (Figure 35) aff. *confusa* joined the Cyanobacteria on the backs of at least four specimens of ***Neosadocus maximus*** (Figure 33 & Figure 36), but only two occurred out of 130 specimens in the coastal sand forest. On the other hand, out of only ten individuals in the rainforest, two had liverworts on their backs.

Figure 33. ***Neosadocus maximus*** from Intervales State Park, São Paulo state, southeastern Brazil, with liverworts on its back. Photo by Bruno A. Buzatto, with permission.

These liverworts seem especially adapted for such habitats. They have adhesive cells on their **propagules** (dispersal units, in this case **gemmae**) that aid attachment and they colonize rapidly (Machado & Vital 2001). The harvestmen seem to accommodate the colonization by having depressions in the dorsal scutes, similar to those of the beetles that are colonized by bryophytes. Setae, pubescent areas, and tubercles may also help by retaining moisture (Gressitt *et al.* 1968; Gradstein *et al.* 1984). And, like the beetles, these harvestmen have a long life span (3-4 years) (Juberthie & Munoz-Cuevas 1971, Cokendolpher & Jones 1991, Gnaspini 1995) that may aid establishment (Gradstein & Equihua 1995). Both are slow-moving and widespread. The female harvestmen lay 26-64 eggs on vegetation and remain to tend the eggs, which mature rapidly (Machado & Vital 2001). Machado and Vital suggest that the reluctance shown by this species to exude its repugnant odor (Cokendolpher 1987, Machado & Vasconcelos 1998) may be an additional adaptation to invite bryophyte establishment.

Figure 34. ***Aphanolejeunea truncatifolia*** from Uganda, showing the small size of this genus. Photo by Martin Wigginton, with permission.

Figure 35. ***Lejeunea*** sp., member of a genus that is known to grow on the backs of harvestmen. Photo by Michael Lüth, with permission.

In ***Neosadocus variabilis***, the females guard the eggs and young (Machado & Vital 2001). It is possible the same behavior occurs in ***N. maximus***. The role of liverworts in nesting of ***N. maximus*** is unknown.

Figure 36. The harvestman ***Neosadocus maximus*** from Cardoso Island, São Paulo state, southeastern Brazil, with liverworts on its back. Photo by Ricardo J. Sawaya.

Predators on Bryophyte Inhabitants

Although the connection is speculative, it is likely that some harvestmen are predators on unsuspecting fauna of epiphytic bryophytes. Castanho and da Rocha (2005) found that ***Neosadocus maximus*** (Figure 36), in the **Gonyleptidae**, eats tree frogs (Hylidae) in the rainforest of southeastern Brazil. However, it is possible that they were being detritivores, feeding on dead treefrogs rather than capturing living ones. But one must wonder, since this same harvestman blends in well with its bryophytic surroundings, making it possible to lie in wait without itself becoming dinner.

One discovery of a food item for harvestmen that was rather unexpected is their ability to eat earthworms (**Lumbricidae**). Halaj and Cady (2000) discovered that among 1032 night-active ***Leiobunum*** sp., they consumed earthworms as about 47% of their diet. ***Leiobunum rotundum*** (Figure 2) is a moss dweller and could find earthworms among the mosses. But trials with another species, *Habrobunus maculosus*, indicated that they might not be able to kill the earthworms, but instead eat ones already dead.

Harvestmen are often prey of parasitic mites, as seen in Figure 37 (Cokendolpher 1993).

Figure 37. Harvestman with parasitic mites. Photo © Stuart Dunlop <www.donegal-wildlife.blogspot.com>, with permission.

Peatlands

It is interesting that the harvestmen found in Flanders Moss include so many of the species already discussed as bryophyte inhabitants (Swain & Usher 2004). But, as seen in Table 1, There are some new ones as well.

Table 1. Harvestmen collected in pitfall traps, October 2002 - October 2003, on Flanders Moss, United Kingdom (Swain & Usher 2004).

	Bog	Restor.	Wood	Total	Figure
Nemastoma bimaculatum	20	43	188	251	Figure 30
Mitostoma chrysomelas	29	32	11	72	Figure 38
Oligolophus tridens	2	30	1911	1943	Figure 14
Oligolophus hanseni	0	0	88	88	Figure 28
Paroligolophus agrestis	152	162	817	1131	Figure 39
Lacinius ephippiatus	0	1	355	356	Figure 16
Mitopus morio	5	12	295	312	Figure 11
Rilaena triangularis	56	4	41	101	Figure 1
Lophopilio palpinalis	0	0	44	44	Figure 29
Unidentified juveniles	20	70	429	519	
Total	284	354	4179	4817	

Figure 38. ***Mitostoma chrysomelas*** (**Nemastomatidae**). Photos by Barbara Thaler-Knoflach, with permission.

Paroligolophus agrestis (**Phalangiidae**; Figure 39-Figure 41) is an ubiquitous European endemic and is the only member of its genus. It is listed as one of the species in the bog at Flanders Moss (Table 1). The legs are somewhat short for a harvestman and the body is only 3-5

mm (TrekNatur 2007). The short legs could be an advantage in navigating mosses, particularly if it were to duck into the mat to avoid a predator or escape the sun.

Figure 39. ***Paroligolophus agrestis*** (formerly *Oligolophus agrestis*). Photo by Trevor & Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 40. ***Paroligolophus agrestis*** on ***Sphagnum***. Photo by J. Paul Richards <www.invertebrate -images.co.uk>, with permission.

Figure 41. Female ***Paroligolophus agrestis*** on a moss, possibly ***Pleurozium schreberi***. Photo by Morten D. D. Hansen, with permission.

Peatland harvestmen tend to be generalists (Swain & Usher 2004), occurring in a wide range of habitats. Swain and Usher suggest that the high exposure and rapid temperature fluctuations of mires creates a harsh environment that requires adaptations to a wide range of microclimatic conditions, thus explaining the preponderance of generalists.

Order Pseudoscorpionida – Pseudoscorpions

These tiny creatures with claws look a bit like miniature flattened crabs. They were once called book scorpions because they often appeared in books, where they preyed on book lice (Wikipedia 2012). They typically live among leaf litter and mosses above the soil (epedaphic), and one pseudoscorpion website states that they might more accurately be called moss scorpions (Project Noah 2012; Pseudoscorpions 2012). Their diet of Collembola (springtails), mites, and other small, soil-dwelling animals (BugLife 2012) is usually readily available among the soil-dwelling mosses.

Although pseudoscorpions are rare among bryophytes, some make the bryophytes home (Thydsen Meinertz 1962). Nevertheless, one of the most common of British pseudoscorpion species, ***Neobisium carcinoides*** (Neobisiidae; formerly *N. muscorum*) (Figure 42-Figure 45), can occur among them (Kinchin 1992) and is known as a moss scorpion. This species is particularly interesting because it gets transported to new habitats by hitching a ride on flying insects! (Natural England). It should be happy among mosses because its diet is especially rich in mites and springtails, both fairly common moss inhabitants.

Figure 42. ***Neobisium carcinoides***, known from mosses in boggy areas of Finland and also called moss scorpions. Photo by Hanne Farnæs, with permission.

Figure 43. Pseudoscorpion ***Neobisium carcinoides*** feeding on the springtail ***Orchesella cincta***. Photo by Ab H. Baas.

Figure 44. Pseudoscorpion ***Neobisium carcinoides*** feeding on the springtail ***Orchesella cincta***. Photos by Ab H. Baas, with permission.

Figure 45. Pseudoscorpion ***Neobisium carcinoides*** feeding on the springtail ***Orchesella cincta***. Photos by Ab H. Baas, with permission.

In Finland forested and boggy sites, Biström and Pajunen (1989) reported ***Neobisium carcinoides*** among mosses at all five main sites. These sites were dominated by ***Sphagnum girgensohnii*** (Figure 20), ***S. squarrosum*** (Figure 46), and ***Polytrichum commune*** (Figure 19). This pseudoscorpion was a generalist, occurring with a density of 0.7 to 2.0 individuals per square meter. It seemed to have little preference for wet vs dry habitat.

Figure 46. ***Sphagnum squarrosum***. Photo by Janice Glime.

Whereas ***Neobisium carcinoides*** is somewhat of a generalist, the bog chelifer ***Microbisium brevifemoratum*** (**Neobisiidae**; Figure 47) seems to be restricted to ***Sphagnum*** bogs and fens (Jørgen Lissner, pers. comm. 3 February 2011). ***Microbisium brevifemoratum*** (Figure 47) ranges 1.6-2.4 mm in length. It is a rare pseudoscorpion and a true **tyrphobiont** found only in ***Sphagnum*** mires (Jørgen Lissner, pers. comm. March 2011). It can be sifted from coarse ***Sphagnum*** species such as ***Sphagnum papillosum*** (Figure 48) and ***Sphagnum magellanicum*** (Figure 49), and seems to prefer microhabitats found on hummocks. ***Neobisium carcinoides*** is much more widespread and abundant in ***Sphagnum*** fens as well as in many other European types of bogs and fens. However, this widely distributed species thrives in a wide range of environments (**eurytopic**) and is not dependent on mosses for habitat.

Figure 47. ***Microbisium brevifemoratum*** (Bog Chelifer), a pseudoscorpion that seems to be restricted to ***Sphagnum*** bogs and fens. Photos by Jørgen Lissner, with permission.

Figure 48. ***Sphagnum papillosum*** with sundews. Photo by Michael Lüth, with permission.

Graves and Graves (1969) likewise found specificity lacking among pseudoscorpions in their study. They seemed to have a wide niche ranging among fungi, mosses, *Rhododendron* leaf litter, and other microhabitats in a North Carolina, USA, highland forest floor.

Figure 49. ***Sphagnum magellanicum***, a species that typically develops red coloration in the sun. Photo by Michael Lüth, with permission.

Apochthonius minimus (Chthoniidae; see Figure 50) is a small pseudoscorpion that inhabits bark, mosses, and leaf litter in the northwestern USA and British Columbia, Canada (Johnson & Wellington 1980). The Collembola that share its bryophyte habitat provide food. The larger ***Neobisium carcinoides*** appears to account for significant mortality of these springtails, most likely competing with the smaller ***Apochthonius minimus***.

Figure 50. ***Apochthonius diabolus***. Photo by Steve Taylor and Mike Slay, with permission.

Another species of ***Apochthonius***, ***A. forbesi***, occurs in lava tube sinks in central Oregon (Benedict 1979). The warm thermal caves house relict species. Cold air is trapped deeper in the cave and permanent ice forms at the end where a mossy-litter layer houses pseudoscorpions such as ***A. forbesi*** and ***Syarinus*** sp. (Syarinidae).

Order Scorpiones

Be careful what you grab! Although this order is not usually represented among the bryophyte fauna, Tamás Pócs (Bryonet 1 April 2016) found one crawling from his moss packet after a collecting trip in Batumi (Georgia, Abkhazia). The moss was an epiphyte. It continued to live among wet mosses for weeks afterwards.

Summary

Most harvestmen on or near bryophytes are casual visitors whose long legs make navigation within the bryophyte clump more than a challenge. Their use of bryophytes seems to be that of gaining moisture by moving across them. Some, however are adapted by having short legs and overall smaller size and often resemble a seed or other forest floor element. Some of these harvestmen prefer peatlands, where they associate with such mosses as ***Polytrichum commune***, ***Sphagnum girgensohnii***, and ***Sphagnum squarrosum***. Distinct differences were present among the communities of these three mosses at some sites, suggesting a moisture relationship. This moisture may be why some harvestmen mate on moss-covered rocks. Some species lay their eggs on bryophytes. Bryophytes may also serve as overwintering sites for some species, but evidence is lacking. In peatlands harvestmen tend to be generalists, permitting them to survive the wide range of microhabitats found there.

Some harvestmen (***Nemastoma***, ***Neosadocus***) actually can have leafy liverworts (**Lejeuneaceae**) growing on their backs. The liverworts have adhesive cells on their propagules that help in their establishment, and the harvestmen have long lives to accommodate them.

Pseudoscorpions often live among mosses, where they find suitable food in springtails, mites, and other small soil invertebrates. Some species are specific to ***Sphagnum***, but most seem to lack specificity in their habitats.

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CHAPTER 9-1
ARTHROPODS: MITES (ACARI)

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CHAPTER 9-1
ARTHROPODS: MITES (ACARI)

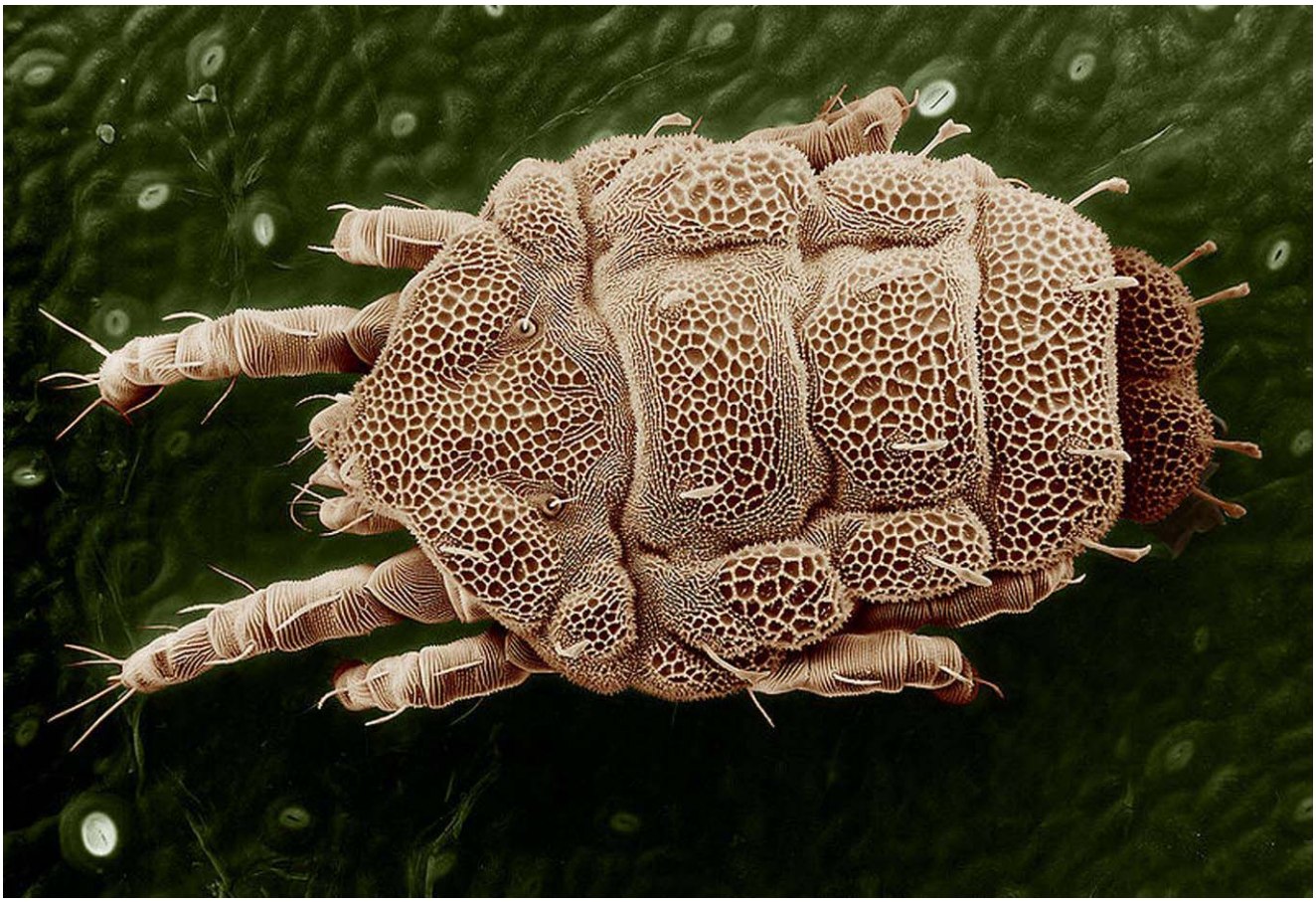


Figure 1. SEM of ***Lorryia formosa*** (yellow mite; **Tydeidae**) on leaf. This citrus dweller (<250 µm) also lives on a variety of other plant species. Its habit of eating fungi actually reduces fungal infections on citrus crops (Mendel & Gerson 1982). Its commonness is at least partly due to the ability to produce young through unfertilized embryos. Some mites that infect crops use bryophytes during seasons when crop plants are unavailable. Photo Eric Erbè, through public domain.

Order Acari – Mites

Mites are similar to spiders, but differ in having no separation between the thorax and abdomen (and available at <http://digitalcommons.mtu.edu/bryophyte-ecology2/>.). Like the spiders, the adults have eight legs, but the larval stage has only six.

I still remember my first experience with a mite among mosses. I was working late at night rehydrating and identifying mosses collected the previous summer for my M.S. research. No one else was around, and I was getting tired. Then I looked through my dissecting microscope and there was an apparition – a tiny, pink, roundish creature with six legs and red eyes! Despite its six legs, I knew by its shape it was no insect. A bit of exploring in my books revealed that this tiny creature was the larval stage of a mite (Figure 2). The extra pair of legs is a nymphal and adult characteristic. Mite life cycles include larval, several nymphal, and the adult stages.

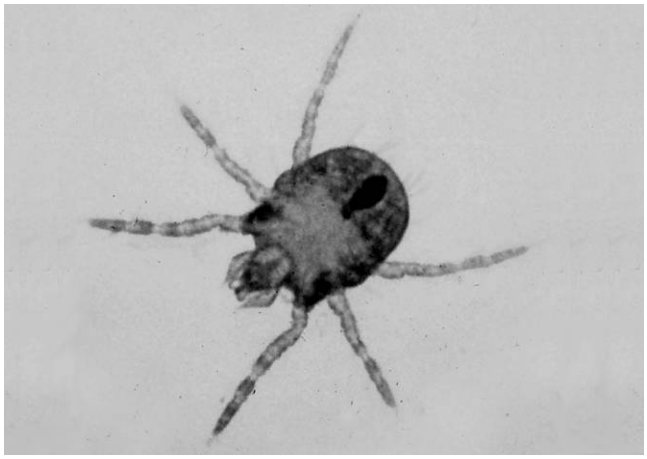


Figure 2. Larval mite (chigger), showing its six legs. Photo by Hansell F. Cross, through Creative Commons.

Habitat Relations

Mites have been associated with bryophytes from their mutual beginnings. Fossil records from 470 million years ago (Ordovician period) provide evidence of fungi in fecal pellets of mites. McNamara and Selden (1993) suggest that these mites fed on the decomposing remains of bryophytes.

Although many mites traverse the cushions and mats of bryophytes at some time during their lives (Figure 3), a smaller number actually live there. And of those, we must ask how many require the bryophytes in any part of their life cycle. Temporary ponds, floodplains, and tidally influenced coastal regions are amphibious habitats that alternate between wet and dry conditions. Changes in these phases often open up new nutrient loads that are favorable to many of their inhabitants (Wiggins *et al*. 1980). In such amphibious habitats, an organism must be adapted for both very wet and quite dry conditions, or move elsewhere when conditions change. But being able to survive these changes in amphibious habitats can also make the organism suited for other habitats within that range of conditions. Wohltmann (2005) asked the question, "No place for generalists?" To answer the question, he compared members of the Parasitengonina, which seems an appropriate group for asking the question. Wohltmann found that the temporary pools of forests and the rocky shores of estuaries had a large percentage of habitat-specific mites, but that floodplains had mostly opportunistic colonizers. Can we use the literature to answer this question for any mossy habitats?

Figure 3. ***Eutrombidium*** sp., a mite that is parasitic on grasshoppers, sits here on a bed of mosses, most likely just travelling through. Photo by Jenilee, through Creative Commons.

Habitat is tied to food choice, locomotion, and respiration as a driver of evolution in many mites (Wohltmann 1991). For those mites that are able to swim in open water, respiration is greater, as one might expect. And for those in open water, catching swimming prey provides additional food choices, but a short survival period without food (about 2 weeks), and again requires a higher respiratory rate. For those mites that live in amphibious habitats such as temporary pools, being able to survive long periods without food is important, and the respiratory rate is lower. Mites survived up to 400 days with no food (***Thyas barbigera*** and ***Limnochares aquatica***), but these were species that ate only immobile food and **crawled** on their substrate to eat. Both of these species are able to use bryophytes as substrates (Smith in Smith *et al*. 2011; Andreas Wohltmann, pers. comm. 17 September 2011). Smith and Cook (2005) noted that the sclerotized plates on the backs of ***Limnochares*** species provided substrate for muscle attachment, hence facilitating their ability to crawl.

Lawrey (1987) cautioned that what may appear to be a preference of certain species may instead be a preference for the substrate of that species. Andre (1979) determined that what appeared to be an association with certain bark-inhabiting lichens was instead an association with the tree species where these lichens grew – *i.e.*, the mites and lichens preferred the same species of trees. Similar relationships are likely for mites inhabiting bryophytes.

Mite Adaptations to Bryophyte-Dwelling

Many of the mites are brilliant red or orange (Hingley 1993; Figure 4). This coloration is due to carotenoids and is thought to protect the mites from UV light (David E. Walter, pers. comm. 6 June 2011). However, David Walter finds that even in ***Sphagnum***, most of the mites are duller colors, with brown to beige predominating (Figure 5). This cryptic coloration makes them less conspicuous against the soil and among the bryophytes. Oribatid (moss mites), usually the most abundant mites in mosses, are almost uniformly dull. These are slow-moving creatures (Kinchin 1990) and some feed on contents of moss leaf cells or on capsules (Figure 6; Gerson 1969). The prostigmatids, on the other hand, are often bright red (Figure 4) and may be very fast-moving (Kinchin 1990). It is likely that the bright red color serves as a warning coloration against some predators.

Figure 4. Velvet mite, probably ***Austrothrombium*** (**Parasitengonina**: **Trombidiidae**), among liverworts and lichens on a tree trunk. This mite has a parasitic larval stage. Photo by Michael Whitehead, through Creative Commons.

Figure 5. ***Atropacarus*** sp. mite, showing the subdued colors typical of many peatland-dwelling and moss mites. Photo by Scott Justis, with permission.

Figure 6. **Erythraeidae** mite on a moss capsule. Lipid sources in the spores may serve as a rich food source, but these spores are still young and the capsule most likely presents an impenetrable barrier to the mite. Photo by Aniruddha Dhamorikar, through Creative Commons.

Figure 7. ***Leptus beroni*** larva on the harvestman ***Mitopus***. Both are moss dwellers. Photo by Andreas Wohltmann, with permission.

Mites are tiny creatures, mostly less than 1 mm in length (Wikipedia: Acari 2011), sometimes appearing as specks on the legs and other body parts of insects and other arachnids (Figure 8-Figure 9). This small size makes it easy for them to maneuver among the stems and leaves of bryophytes. And their sucking mouth parts permit some of them to use the bryophytes as a food source.

Figure 8. ***Mitopus morio*** (harvestman) with a red mite larva in the genus ***Leptus*** (**Parasitengonina**: **Erythraeidae**) attached to its leg. Photo by Ed Nieuwenhuys, with permission.

Figure 9. ***Leptus trimaculatus*** adult, a known moss dweller. Photo by Andreas Wohltmann, with permission.

Since many of the moss mites are bright colored, camouflage is not going to work for them. This seems to be the case for some of the bright red moss mites such as ***Trombidium***. Instead of hiding or running (many mites are not very good at this), they roll onto their backs and play dead (**thanatosis**). Figure 10 shows one of these moss mites doing just that. Aside from being motionless, and thus attracting less attention, I have never figured out how that helps, but opossums seem to think so, and so do some salamanders, snakes, and insects, and so do humans facing grizzly bears!

Miyatake *et al.* (2004) asked that same question about potential advantage. And to our good fortune, they asked it using an arthropod, the beetle *Tribolium castaneum*. First, they showed that there was heritable variability in the duration of the death-feigning behavior. Using ten

generations of this species, they showed that the strain that had the greatest inheritance of the behavior (longest duration of death feigning) had the greatest frequency of thanatosis. Next they showed that there was greater fitness (greater survival) of those with the long-duration thanatosis trait when they were presented with a predator, a female Adanson jumper spider (***Hasarius adansoni***, Salticidae). Finally, they showed that the frequency of predation was lower on those mites in the strain with long-duration death feigning than from those with short-duration feigning. These experiments met the three criteria proposed by Endler (1986) to demonstrate the evolution of an adaptive trait by natural selection: variation of the trait among individuals; differences in fitness as related to the trait; inheritance of the trait.

Figure 10. ***Trombidium holosericeum*** in a state of **thanatosis** (playing dead). In this case, the mite was touched with a brush. Photo by Andreas Wohltmann, with permission.

The behavior of the spider, when encountering her prey, may help us to understand how this trait is adaptive. The Adanson's jumper spider had rather different behavior when provided with a live fly, *Drosophila hydei*. She never set the fly free and immediately ate it. But when the spider was presented with the *Tribolium castaneum*, she always let go again. The researchers suggested that this was due to the hard cuticle and/or a chemical released as anti-predator defense (Happ 1968). Only if the beetle moved after the attack did the spider once again attack, and in several cases, eat the beetle.

There might be a nutritional reason as well. If the fly has evolved along with its prey organisms, dead organisms, at least arthropods, could mean a waste of energy when attempting to eat them. Enzymes released from the cells of the insect quickly digest the interior of the insect, leaving mostly chitin, which presumably supplies little energy and may take more energy to penetrate than will be obtained. It is likely that some of the same powerful enzymes that help the mites digest their food are also released when they die, potentially digesting the interior of the mite as well.

Having a number of species with the same adaptive defense behavior of playing dead is considered a form of **aggressive mimicry**. According to the World of Darkness Wiki (2010), the appearance of death is supposed to conjure up the sense of rot and decay and all that goes along with death. But I would think that would require the attendant odors as well. Could it be that these beasts elicit the odor of rotting bodies that we humans have not yet detected, but that these animals have? In fact, that may be the case for the beetle *Tribolium costatum* and others (Miyatake *et al*. 2004).

Symbioribates papuensis has an unusual adaptations to mosses. It lives on mosses that grow in the backs of Papuan weevils, hence getting a free ride that provides dispersal (Aoki 1966).

The Inhabitants

Mites are abundant in bryophytic habitats (Sellnick 1908; Willmann 1931, 1932; Rajski 1958; Aoki 1959; Higgins & Woollery 1963; Wood 1966; Popp 1970; Seniczak 1974; Bonnet *et al*. 1975; von der Dunk & von der Dunk 1979; Harada 1980; Seyd 1988; Seyd & Colloff 1991; Smith & Cook 1991; Hoffmann & Riverón 1992; Kinchin 1992; Seniczak *et al*. 1995; Seyd *et al*. 1996; Winchester *et al*. 1999; Fischer 2005; Bettis 2008), so much so that oribatid mites have been termed moss mites. Aoki (2000) reported on oribatid mites in moss cushions on Japanese city constructions. Their abundance is illustrated by a study by Yanoviak *et al.* (2006), who reported that 65% of the arthropod fauna among epiphytes in a Costa Rica cloud forest were mites.

Weiss (1916) reported ***Bdella cardinalis*** in mosses as well as under leaves and rotten wood in New Jersey, USA. Jacot (1938) later concluded that this species was a synonym of ***Bdella oblonga***, which is common on decayed fallen trunks and among their mosses. Members of the family **Bdellidae** (snout mites; Figure 11-Figure 13) occupy mosses in Mexico (Baker & Balock 1944) where they feed on other arthropods, including mites. These include ***Biscirus lapidarius*** (only a single specimen) and ***Bdella oblonga*** from mosses at Deseirto de los Leones. The type specimen of ***Bdella rio-lermensis*** was collected from mosses in Rio Lerma. ***Bdella mexicana*** is known from mosses in Valle del Bravo. Likewise, the type specimen for both the genus and the species of ***Opserythraeus hoffmannae*** were collected as larvae from mosses in Rugege Forest, Rwanda (Fain 1996).

Figure 11. **Bdellidae**, a family that inhabits mosses on rotten logs and elsewhere. Photo by S. E. Thorpe, through Wikimedia Commons.

Even in habitats where numbers of mites are few, greater numbers are likely to be found among bryophytes (Covarrubias & Mellado 1998). Oribatid mites were recorded from mosses and lichens in the Krkonose Mts. (Czech Republic) along an altitudinal gradient reaching from submontane to the alpine belt (Materna 2000). In 197 stands, 104 oribatid species were present. On the other hand, Materna found rather poor oribatid mite communities

among saxicolous mosses in the Krkonose Mountains, Czech Republic. Among these the predominant taxa were ***Oribatula cf. pallida*** (see Figure 14), ***Mycobates tridactylus*** (see Figure 15), and ***Trichoribates monticola*** (see Figure 16). Despite the poor representation in some rock communities, Shure and Ragsdale (1977) found that mites contribute to the fauna during primary succession on granite outcrops.

Figure 12. **Bdellidae** species, a moss-dweller family. Photo by Walter Pfliegler, with permission.

Figure 13. **Bdellidae** species on rotting wood with mosses. Photo by John Davis, with permission.

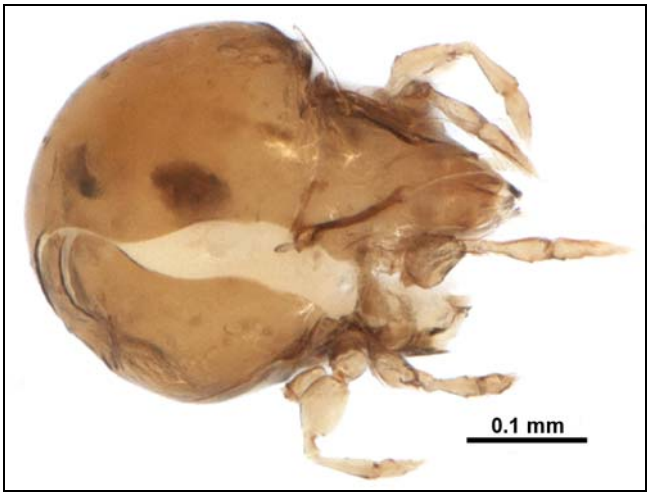


Figure 14. Ventral side of ***Oribatula tibialis***, member of a genus in which some members are among the few moss-dwelling mites on rocks. Photo from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

Even in habitats where numbers of mites are few, greater numbers are likely to be found among bryophytes (Covarrubias & Mellado 1998). Oribatid mites were recorded from mosses and lichens in the Krkonose Mts. (Czech Republic) along an altitudinal gradient reaching from submontane to the alpine belt (Materna 2000). In 197 stands, 104 oribatid species were present. On the other hand, Materna found rather poor oribatid mite communities among saxicolous mosses in the Krkonose Mountains, Czech Republic. Among these the predominant taxa were ***Oribatula cf. pallida*** (see Figure 14), ***Mycobates tridactylus*** (see Figure 15), and ***Trichoribates monticola*** (see Figure 16). Despite the poor representation in some rock communities, Shure and Ragsdale (1977) found that mites contribute to the fauna during primary succession on granite outcrops.

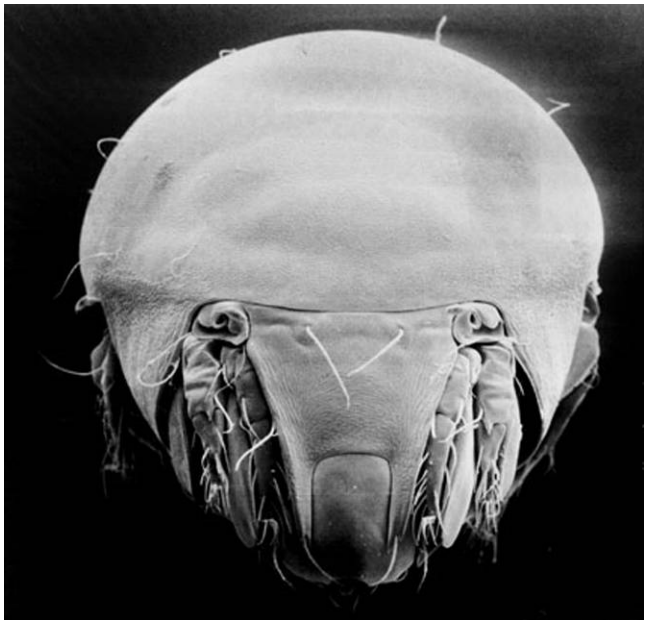


Figure 15. SEM of ***Mycobates dryas***, a member of a genus with moss-dwellers on rocks. Photo by Valerie Behan-Pelletier & Barb Eamer, with permission.

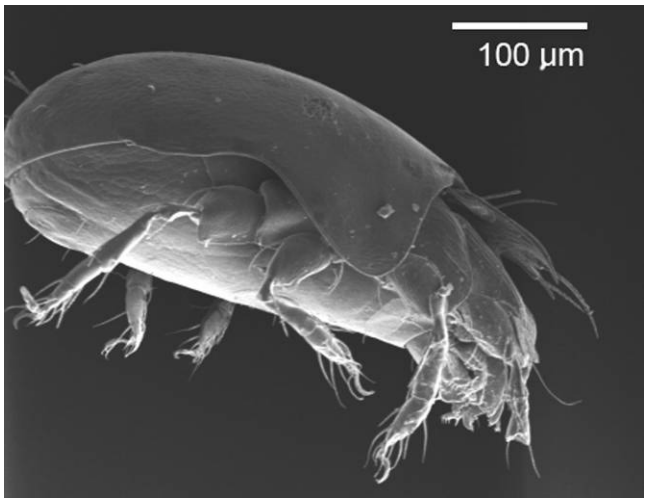


Figure 16. SEM image of ***Trichoribates***, a contributor to primary succession of mosses on rocks. Photo courtesy of Birgit Balkenhol, Samantha Kühnel, and the Senckenberg Museum of Natural History, Görlitz.

In wet litter and mosses near bodies of water in the mixed forest plains of Canada, one can find adults of the **Trombellidae** and **Johnstonianidae** (Figure 17; Smith *et al*. 2011). The mite ***Rostrozetes ovulum*** (Figure 22) occurs in bogs. ***Johnstoniana errans*** (Figure 18-Figure 20) lives in forests and at the edge of ponds where its **deutonymph** stage and adult, the two active stages in the life cycle, live primarily in damp mosses on rotting wood (Wohltmann 1996). These mites are nocturnal and use the mosses as hunting grounds for larvae and pupae of the cranefly ***Tipula* spp.** (Diptera; Figure 18). The mite larvae search for the pupae (Figure 19) of the craneflies, where they aggregate and await the transformation from the ***Tipula*** pupa into the emergence of the adult. The larval mites are parasites on ***Tipula*** adults, beginning just after emergence, once the larvae have moved onto the adult body from the surface of the pupa (Figure 18).

Figure 17. ***Johnstoniana parva*** (Parasitengonina) mite larvae parasitic on the mite ***Microtrombidium pusillum*** (**Parasitengonina**); both can live among mosses near water. Photo by Andreas Wohltmann, with permission.

Figure 18. ***Johnstoniana errans*** larva on the cranefly ***Tipula*** sp. Both are known moss dwellers. Photo by Andreas Wohltmann, with permission.

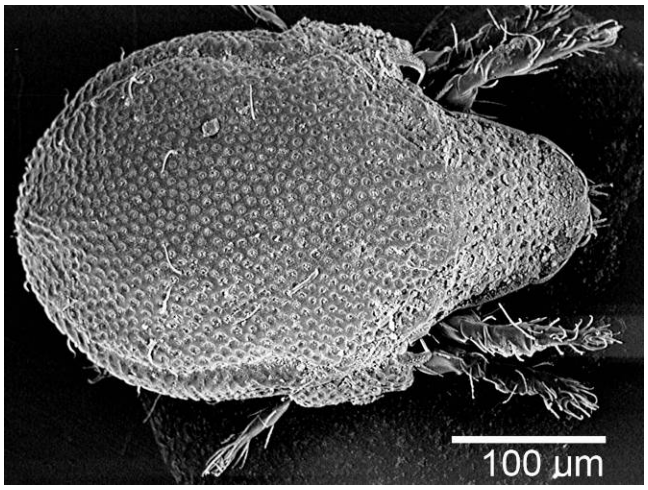
Figure 19. Pupa of the cranefly ***Tipula***, a moss dweller that is often host to mite larvae. Photo by Ted Kropiewnicki through Creative Commons.

Figure 20. ***Johnstonaina errans*** adult on moss litter. Photo by Andreas Wohltmann, with permission.

Figure 21. ***Johnstoniana errans*** deutonymph on moss. Photo by Andreas Wohltmann, with permission.

Some genera seem to show up on mosses fairly often, as indicated by the number of pictures with a mossy substrate. For example, George (1908) found ***Trombidium bicolor*** (Figure 23) in damp mosses, especially in ditches.

Michael Whitehead shared his picture of a species of ***Austrothrombium*** (Figure 24) on a leafy liverwort.



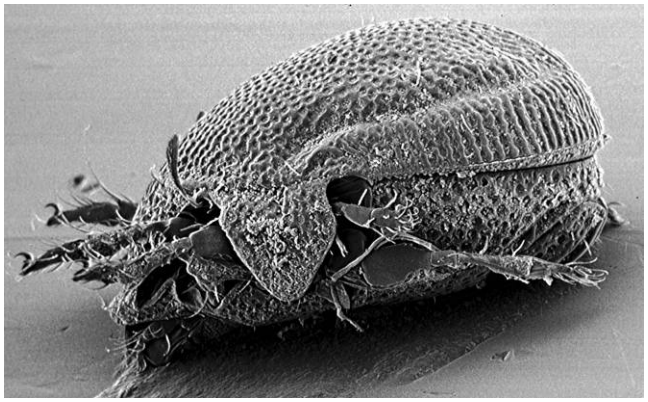


Figure 22. SEM of ***Rostrozetes ovulum***, a bog dweller. Photos by Barb Eamer, with permission.

Figure 23. ***Trombidium holosericeum***. Photo by Ruth Ahlburg, with permission.

Some of the moss dwellers seem to be somewhat specialized. The genera ***Damaeus*** (Figure 25), ***Belba***, and ***Metabelba*** (Figure 28) are fungal eaters and live in habitats that make close contact with the soil, such as mosses (Smrž 2010). They rarely occur among mosses on trees. ***Belba minuta*** in parts of eastern central USA, less than 0.5 mm in length, occurs among mosses, although it occurs mostly on animal substances (Banks 1895).

Figure 24. Trombidioid mite, probably ***Austrothrombium***, on a bed of leafy liverworts. Photo by Michael Whitehead, through Creative Commons.

Figure 25. ***Damaeus onustus***. Photo by Mick E Talbot, through Creative Commons.

Figure 26. ***Belba*** sp. Photo by Barbara Thaler-Knoflach, with permission.

Figure 27. ***Metabelba*** sp., a fungal eater that can find its food sources among mosses. Photo by Walter Pfliegler, with permission.

Figure 28. ***Metabelba*** sp., a moss-dwelling fungal eater. Photo by Walter Pfliegler, with permission.

Armed with names like **Bryobiinae** (Figure 29) and ***Bryobia*** (Figure 30), I searched with anticipation for information on their habits. My first find was that the common name was **clover mite**, somewhat dashing my hopes for a bryophyte dweller. But when I keyed in moss with its name, I found it did legitimately use *bryo* in its name, using mosses as habitat.

Figure 29. Member of **Bryobiinae**, a family with moss-dwellers. This green one suggests that it is a plant eater, but do they eat bryophytes? Photo by Walter Pfliegler, with permission.

Figure 30. ***Bryobia*** sp., member of a genus that uses mosses when larger hosts are not available. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

Bryobia praetiosa (as *B. humeralis*; Figure 31) was first described by Halbert (1923) from mosses and a wall. Later, Flechtmann and Baker (1970) listed bryophytes among its hosts, and Tuttle and Baker (1976) reported it from mosses in Utah. Nevertheless, it seems to live predominantly on tracheophyte hosts. From there, the records seemed scarce until Hatzinikolis and Panou (1996) discovered ***Bryobia emmanoueli*** and ***B. meteoritica*** as new species among mosses in Greece. I suspect that more moss dwellers have been described in the older literature that has not yet found its way to the internet. As you will see, mosses can act as alternate "hosts" when tracheophytes are seasonally absent.

Figure 31. ***Bryobia praetosa***. Photo by Jarmo Holopainen, with permission.

Figure 32. ***Erythraeus*** (**Parasitengonina**) on bark with a moss branch nearby. Photo by James K. Lindsey, through Creative Commons.

Some mites that live on bark and other substrates traverse mosses and obtain moisture from them. Such is likely the case for some members of the **Erythraeoidea** (Figure 32).

Wood (1967) documented the presence among mosses of the mite ***Eustigmaeus*** (as ***Ledermuelleria***; Figure 33), a genus of red species. In 1972 Wood described new species of ***Eustigmaeus***, from mosses in Canada. With publication in the same year, Gerson (1972) sampled 160 mosses in eastern Canada and the USA and found that nearly half of them housed mites. Of these, eleven species were in the genus ***Eustigmaeus***. Furthermore, among the 55 species of mosses, 38 housed ***Eustigmaeus*** species. The species ***E. arcticus***, ***E. gersoni***, and ***E. rhodomela*** occurred primarily on mosses that colonize open soil. On the other hand, ***E. frigida*** preferred mosses in shaded, humid places.

Figure 33. ***Eustigmaeus*** sp., a genus that is common on mosses and uses some of them for food. Photo by David E. Walter and Anthony O'Toole, with permission.

The Role of Bryophytes

Bryophytes can offer an important physical component that provides a habitat for mites. Dewez and Wauthy (1981) used sponges as artificial substrata and found that mites did colonize the sponges in areas where bryophytes had been removed.

This suggests that the ability to provide a moist environment permits mosses to provide suitable mite habitat even on rocks (Materna 2000). In the Krkonose Mountains of The Czech Republic, mosses in areas approaching the treeline and protected by tracheophytes housed a rich community of ubiquitous mite species with high moisture requirements. Where the rocks lacked tracheophytes, the soil was less developed and few soil mites occurred. The moss mite community had few frequent species. The most common mite was ***Oribatula cf. pallida*** (Figure 14). Two of the species [***Mycobates tridactylus*** (see Figure 15) & ***Trichoribates monticola*** (see Figure 34)] were specialists that lived only on mosses and lichens.

Leafy liverworts such as species of ***Frullania*** with lobules (Figure 37) provide a protected habitat that maintains moisture when most other places are dry and house such mites as ***Birobates hepaticolus*** (Figure 37), as both immature and adult individuals (Colloff & Cairns 2011). And for food? It eats liverwort tissue!

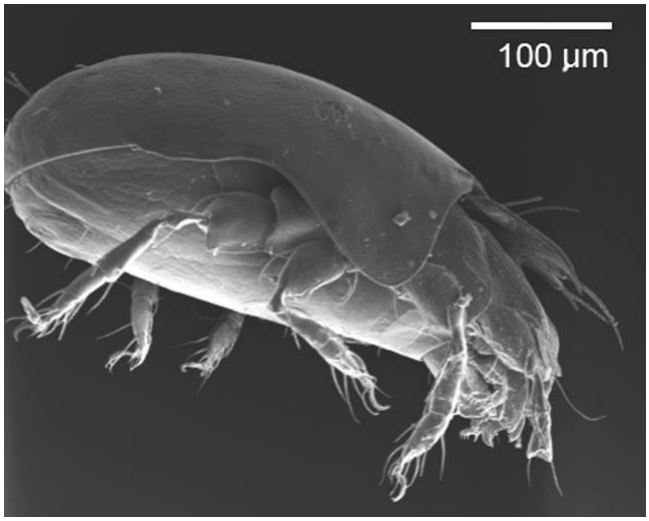


Figure 34. SEM of ***Trichoribates*** sp., member of a genus where some members specialize on moss and lichen habitats. Photo by Birgit Balkenhol and Samantha Kühnel, the Senckenberg Museum of Natural History, Görlitz, with permission.

Experimental work with moss mites can provide us with information to help explain their presence in a given habitat. Smrž (2006) studied the saprophagous mites living among mosses on a roof to determine their biology. Two species of oribatid mites [***Scutovertex minutus*** (see Figure 35-Figure 36), ***Trichoribates trimaculatus*** (see Figure 34)] comprised the moss mite community. They used these mites in laboratory experiments to determine their nutritional needs, moisture relations, mobility, and food selection. Such factors as digestive processes, vertical and horizontal distribution, and ability to disperse defined different niches within the moss community for these two species.

Figure 35. ***Scutovertex sculptus***, in a genus where some members live among mosses. Photo by Matthew Shepherd, through Creative Commons.

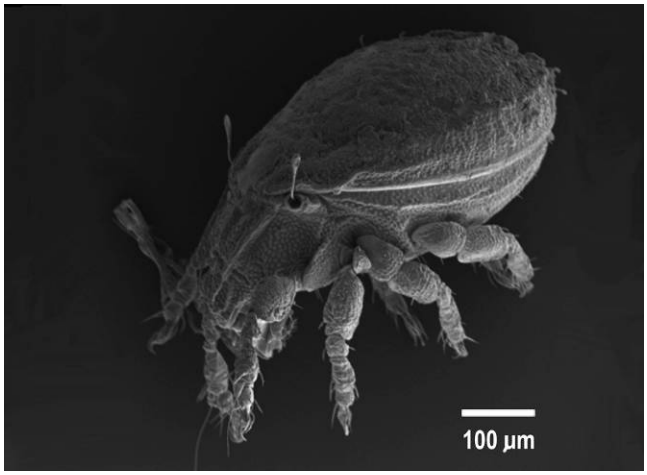


Figure 36. SEM of ***Scutovertex sculptus***, a species in a moss-dwelling genus. Photo by Jürgen Schulz, Birgit Balkenhol, and Samantha Kühnel, the Senckenberg Museum of Natural History Görlitz, with permission.

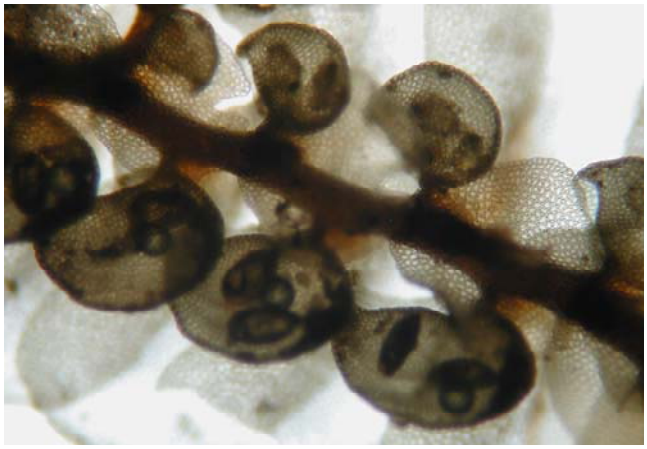


Figure 37. ***Frullania ferdinandi-muelleri*** with ***Birobates hepaticolus*** in its lobules. Photo courtesy of Andi Cairns.

Bryophytes as Food

The oribatid mites eat fungi, algae, and dead organic matter (Bhaduri & Raychaudhuri 1981). With about 10,000 described species (David E. Walter, pers. comm. 15 September 2011), their habitats are varied, including leaf litter, lichens, bryophytes, humus, and compost heaps. Ponge (1991) found all these foods in feces of the phthiracarid mites living among Scots pine litter. Within the bryophyte communities, mites can often find all of their favorite food sources.

Lawrey (1987) contends that "there is only the scantest evidence that mosses are actually eaten" by mites. Nevertheless, Gerson (1969) states that mites are among the few animals known to eat bryophytes regularly. Woodring (1963) reported that he had been able to rear several mites [***Euphthiracarus flavum*** (see Figure 38), ***Galumna nervosa*** (see Figure 39-Figure 41), ***Oribotria*** spp., ***Pseudotrita*** spp.] on mosses as food, indicating that at least some mosses are nutritionally adequate for at least some mites.

Gerson (1969) provided us with his personal observation of oribatid mites "gnawing" on various moss capsules and eating the spores. The fact that mites can be sustained on mosses under laboratory conditions suggests that either the mosses or the microflora and fauna of the mosses provide sustenance (Sengbusch 1954; Woodring 1963; Lawrey 1987). Schuster (1956) found moss remains in the guts of four out of 40 oribatid species. In Brazil, Flechtmann (1984) described the species ***Eustigmaeus bryonemus*** (see Figure 33) for the first time, noting that it feeds on mosses. When the mite is cleared of its red color, the green moss in the gut becomes visible. But is it the moss that serves the nutritional needs, or micro-organisms and detritus on and among the leaves?

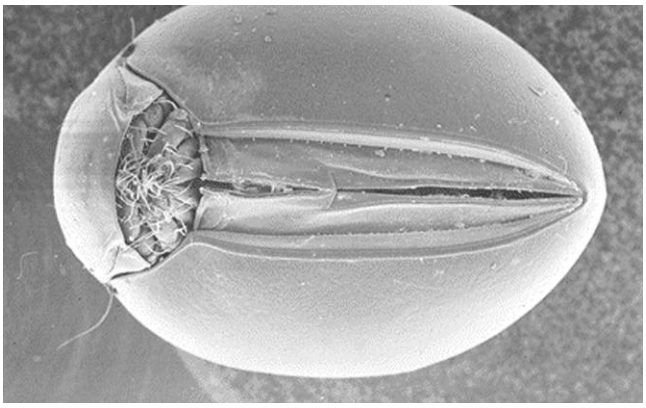


Figure 38. SEM of **Euphthiracaroid** mite from peatlands. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

Figure 39. **Galumnidae**, a mite group that is able to subsist in mosses. Photo by Scott Justis, with permission.

Figure 40. ***Galumna*** sp. (shield-sided fungus mite) that can subsist on mosses. Photo from Flickr through Creative Commons.

The genus ***Eustigmaeus*** (Figure 33) is one of the common moss mites to feed on the bryophytes, and evidence suggests that the moss is indeed the intended food item. Gerson (1972) reported, based on laboratory

experiments, that ***Eustigmaeus frigida*** mites (Figure 42) pierce stem and leaf tissues of mosses with their needlelike chelicerae, enabling them to suck the contents from the cells (David Walter, pers. comm. 6 June 2011), leaving behind skeletons of cell walls (Gerson 1972). Such feeding can cause the young moss shoots to discolor to a silvery grey and shrivel (Gerson (1972). David E. Walter (pers. comm. 15 September 2011) describe this as using "spike-like movable digits to puncture the leaves of the mosses on which they feed." Experiments by Gerson (1972) indicate that they will eat many moss species and survive on the diet. However, they only reproduced following a diet of a restricted few species. In addition to ***Eustigmaeus frigida***, ***E. rhodomela***, ***E. clavata***, and ***E. schusteri*** also feed on various mosses and have similar life cycles to those of ***E. frigida***.

Figure 41. ***Galumna*** representatives, members of a genus where some species are known to be able to subsist on mosses as food. Photo by Walter Pfliegler, with permission.

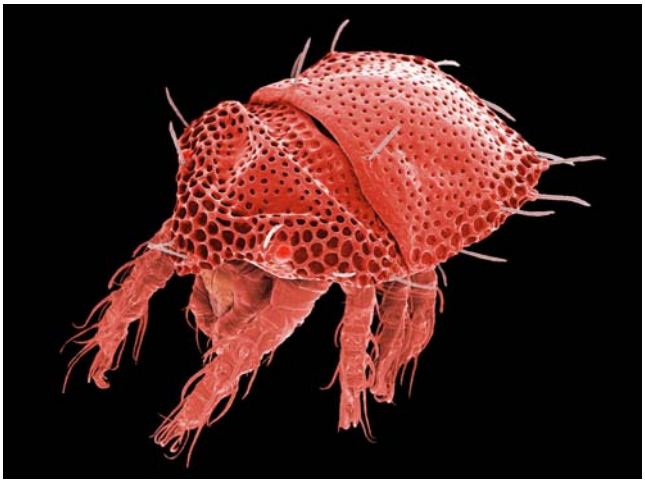


Figure 42. ***Eustigmaeus frigida***, a common moss inhabitant that has specialized mouth parts for piercing mosses, but not those with thick leaves. Photo by David E. Walter, with permission.

Length of stylet plays a role in species of mosses that can be eaten by mites. Of five species Gerson observed on ***Polytrichum*** clumps (Figure 43), ***E. frigida*** has the shortest (23 µm) and narrowest (1 µm) stylet, compared to 32-58 µm long and 2-4 µm wide stylets among other residents (Gerson 1972). There was no survival of ***E. frigida*** on relatively large mosses: ***Pogonatum urnigerum*** (Figure 44), ***Polytrichum commune*** (Figure 43), ***Polytrichum piliferum*** (Figure 45), ***Leucobryum glaucum*** (Figure 46), or ***Atrichum altecristatum*** (Figure 47-Figure 49).

Eustigmaeus (Figure 33) species, in particular, have special stylets that pierce stems and leaves and suck out cell contents (Gerson 1969). Like that of ***E. frigida***, part of the specialization to feeding on certain mosses seems to be related to length of stylet (Gerson 1969). ***Eustigmaeus clavata*** and ***E. microsegnis*** have long (40 & 32 µm respectively), thick (3-4 µm) stylets and can survive on ***Polytrichum*** mats. ***Eustigmaeus frigida*** in Gerson's experiments has short (23 µm), thin (1 µm) stylets and are unable to survive on ***Polytrichum*** species with their thick dorsal cell walls and covering ventral lamellae.

Figure 43. ***Polytrichum commune*** in a peatland, a moss that is home for some mites but unsuitable for others. Photo by Michael Lüth, with permission.

Figure 44. ***Pogonatum urnigerum***, a mite habitat. Photo by Michael Lüth, with permission.

Figure 45. ***Polytrichum piliferum***, a mite habitat. Photo from bryology website at University of British Columbia, with permission.

Figure 46. ***Leucobryum glaucum*** cushion on forest floor, a habitat that is not suitable food for some mites. Photo by Janice Glime.

Figure 47. ***Atrichum altecristatum***. Hydrated mosses showing lamellae in middle of leaf along costa. This large moss is inedible for many species of ***Eustigmaeus.*** Photo by Eric Schneider, with permission.

Figure 48. ***Atrichum altecristatum*** leaf cross section showing lamellae along the costa. Photo by John Hribljan, with permission.

Gerson (1987) reported mites from 38 species of bryophytes. Among these, all the active stages of ***Eustigmaeus*** fed on both leaves and stems of mosses, showing no preference for acrocarpous vs pleurocarpous taxa. However, as in earlier experiments, mites with short mouth parts were unable to feed on mosses with thick cell walls.

Woodring (1963) reared four species of mites through their 50- to 70-day life cycle on a diet exclusively of mosses. Josephine Milne (Bryonet 18 March 1996) found ca 18 species of mites, among other invertebrates, to be abundant on her cultures of the moss ***Dicranoloma*** (Figure 50) from a cool temperate rainforest in Australia. The mites fed especially on new leaves at the tips of the plants, frequently chewing out the young buds.

Figure 49. ***Atrichum altecristatum***. Dehydrated mosses showing the contortion of the leaves. Photo by Eric Schneider, with permission.

Figure 50. ***Dicranoloma billardierei***, potential home for many mite species. Photo by Michael Lüth, with permission.

Penthaleus species (Figure 51) are large, brightly colored mites that feed on plants and are frequent plant pests (Umina 2004). Russell (1979) discovered that at least some of them also eat bryophytes. By keeping one species in the lab, he was able to observe both adults and juveniles feeding on the moss ***Orthotrichum*** (Figure 91)from Oregon, USA. They subsisted on this food source for up to two weeks.

The Penthaleidae (Earth Mites; Figure 51) have needle-like mouthparts that permit them to puncture leaf cells or fungal hyphae and suck out the contents. These mites spend their early stages in the soil where they feed on fungi, algae, and bryophytes. In contrast, the older stages clamber onto the low-growing vascular plants where they feed on the leaves. The red-legged earth mites look black because of dense concentrations of chlorophyll from their food. The red legs gain their color from carotenoids deposited in the cuticle – a possible adaptation to protect them from UV-light.

Early stages of the Earth mites, Penthaleidae (Figure 51-Figure 52), feed in the soil on fungi, algae, and bryophytes, whereas the older stages move to low-growing tracheophytes where they feed on the leaves (David Walter, pers. comm.). They use their needle-like mouthparts to puncture leaf cells (or hyphae of fungi when they are in the

soil) and drain the cell contents. The red-legged earth mite is a well-known pest that looks nearly black due to dense accumulations of chlorophyll. Their legs are red, presumably protecting them from UV radiation.

Figure 51. ***Penthaleus major***. Note the drop of liquid where the anus is. This anal position adapts the mite to its upside-down feeding position. Photo by Scott Justis, with permission.

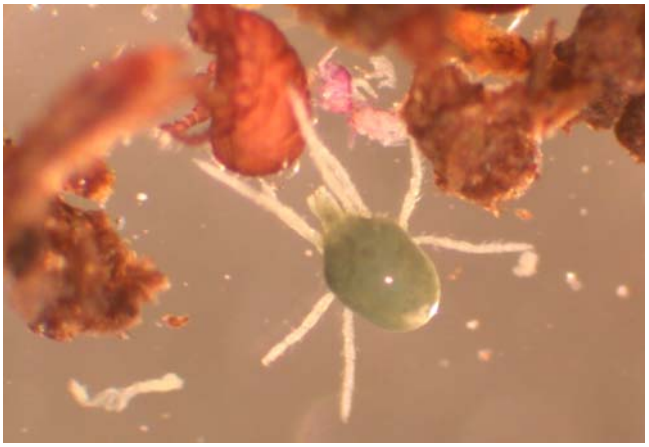


Figure 52. This mite from an epiphytic leafy liverwort is most likely a member of the **Penthaleidae**. Its green color reveals a recent diet of chlorophyll, possibly the liverwort, or algae/Cyanobacteria growing on it. The brown mite just above it is a nymphal oribatid mite (**Achipteridae**?). Photo by Jessica Nelson and Duncan Hauser, permission status unknown.

When we know so little about organisms that eat bryophytes, it is a rare treat to find a report where the observers were able to watch the bryophyte herbivore closely. But Cronberg and coworkers (2008) did just that – they observed mites feeding on the protonemata of mosses (Figure 53). Whereas it appeared that the springtails lacked the apparatus necessary for protonemal dinners, the mites used their jaws to cut the protonemata into two pieces. They then consistently fed on only the distal (tip) piece. These mites also carried gemmae of ***Bryum argenteum*** (Figure 54-Figure 55), but the researchers were not so fortunate as to watch any banquet on these. Too bad for the springtails – they also form part of the diet of the mites! (Figure 56).

Figure 53. ***Bryum argenteum*** protonemata with ***Scutovertex*** sp. feeding on it. Photo by Nils Cronberg, Hans Berggren, & Rayna Natcheva, with permission.

Figure 54. ***Bryum argenteum***, showing the compact nature of this bryophyte. Mites can carry gemmae of this species. Photo by George Shepherd, through Creative Commons.

Figure 55. ***Bryum argenteum*** with gemmae; these gemmae can be dispersed by mites. Photo by Rui-Liang Zhu, with permission.

Most of the experiments and observations on mites that feed on bryophytes involve mosses, not liverworts. It would be an interesting experiment to give them choices of a range of mosses **and** liverworts to see if both are eaten. Liverworts are known to house a number of secondary compounds that serve as antiherbivore compounds, but then, many (perhaps most) mosses contain phenolic compounds that discourage herbivory as well (Mues 2000).

Other reports of bryophyte-feeding mites include those in laboratory enclosures where mosses were provided for cover and sources of moisture. Wallwork (1958) reported that adult ***Achipteria coleoptrata*** (Figure 57) ate living young stem tissue of mosses and survived on that diet for more than a month. It appears that bacteria in the gut are necessary to digest at least some cell types in tracheophytes, particularly those with lots of lignin (Haq & Konikkara 1989). It would be interesting to see if a gut flora is equally important in digesting non-lignified bryophytes.

Figure 56. Mite eating a springtail in the mountains of West Virginia, USA. Both can be found among mosses. Photo by Roy A. Norton, permission unknown.

The oribatid mites, known as moss mites, live among bryophytes, but rarely eat them (David walter, pers. comm.). Rather, the bryophytes provide a habitat where the mites can feed on fungi that live among the bryophytes, and at the same time they enjoy the protection of the bryophytes against large predators, UV light, and desiccation.

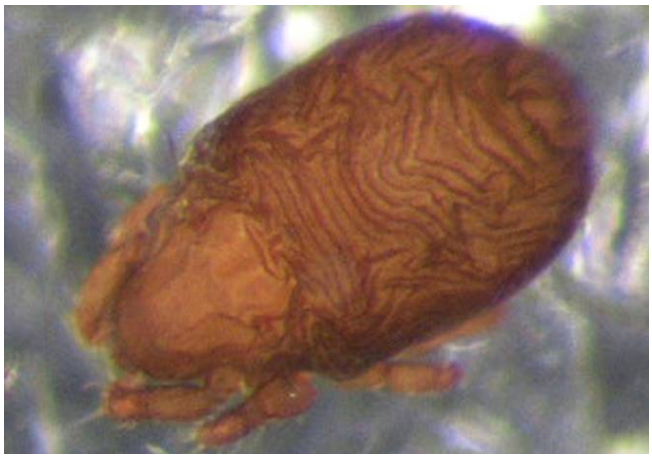


Figure 57. ***Achipteria coleoptrata***, a mite that eats young moss stem tissue. Photo by the CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

Community Food Sources

Bryophytes seem more likely to provide food for the mites indirectly by housing suitable food organisms, as can be seen for a number of moss-dwellers listed in Table 1. Smrž (2010) reported that ***Achipteria coleoptrata*** (Figure 57) ate fungi and other food types within the moss mats on soil and on trees, as did ***Hermannia gibba*** (Figure 58). Other mites likewise used the moss habitat on tree trunks as a food source, with ***Oribatula tibialis*** (Figure 14) feeding on fungi, ***Phthiracarus*** sp. (Figure 60-Figure 61) feeding on litter, and others [***Achipteria coleoptrata***, ***Chamobates cuspidatus*** (see Figure 62-Figure 63), ***Chamobates subglobus***, ***Liacarus coracinus*** (Figure 64), ***Tectocepheus velatus*** (Figure 105) finding a variety of suitable foods there. ***Melanozetes mollicomus*** fed on the epiphytic mosses themselves. Among mosses on tree roots, ***Melanozetes mollicomus*** again fed on mosses, ***Phthiracarus*** on plant litter, ***Achipteria coleoptrata*** and ***Damaeus auritus*** (Figure 25) on fungi, and the remaining species used a variety of foods [***Hermannia gibba*** (see Figure 58), ***Hermanniella granulata***, ***Hafenrefferia gilvipes*** (see Figure 65), ***Hypochthonius rufulus*** (Figure 66-Figure 69), ***Tectocepheus velatus*** (Figure 105)].

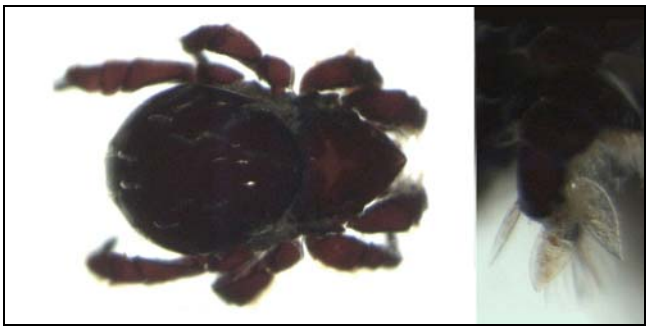


Figure 58. ***Hermannia phyllophora***, a fungal mite that finds its fungal food within moss mats. Image on right shows leg scales. Photo by S. E. Thorpe, through Creative Commons.

Figure 59. ***Hermanniella*** sp., a mite that lives among mosses on tree roots. Photos by Walter Pfliegler, with permission.

Table 1. Oribatid mites found on mosses of mixed wood plains in Canada and their food habits. From Smith *et al*. 2011.

Family	Habitat	Food	Family	Habitat	Food
Cosmochthoniidae	moss, lichen, litter	algivorous	Licnodamaeidae	moss, litter	unknown
Arborichthoniidae	moss, litter	unknown	Damaeidae	moss, litter	fungivorous
Brachychthoniidae	moss, soil, litter, lichens	fungivorous, algivorous	Cepheidae	moss, litter	saprophagous
			Eremaeidae	litter, moss, lichen	fungivorous
Epilohmanniidae	litter, moss	unknown	Megeremaeidae	litter, moss	fungivorous
Nothridae	moss, litter	saprophagous	Zetorchestidae	moss	fungivorous
Camisiidae	semiaquatic, moss, litter, canopy,	saprophagous	Tenuialidae	moss	unknown
			Liacaridae	moss, litter	saprophagous
Trhypochthoniidae	semiaquatic, moss, litter, aquatic	fungivorous, algivorous	Astegistidae	moss, litter	fungivorous
			Pelppiidae	moss, litter	fungivorous
Malaconothridae	semiaquatic, moss, litter	fungivorous, algivorous	Gustavioidea	moss, litter	unknown
			Kodiakellidae	moss, litter	unknown
Nanhermanniidae	moss	fungivorous	Thyrisomidae	soil, litter, moss	fungivorous
Hermanniidae	moss	fungivorous	Chamobatidae	semiaquatic, moss	saprophagous
Hermanniellidae	moss, litter	fungivorous, saprophagous	Mycobatidae	moss, litter	fungivorous, saprophagous
			Oribatellidae	litter, moss	saprophagous
Plasmobatidae	moss, litter	unknown	Achipteriidae	litter, moss	saprophagous
Liodidae	moss, canopy	saprophagous	Tegoribatidae	litter, moss	saprophagous
Plateremaeidae	moss, dry litter	unknown	Galumnatidae	litter, moss	saprophagous, predaceous

Figure 60. ***Phthiracarus*** sp.; members of this genus live among mosses on tree trunks and eat litter. Photo by Walter Pfliegler, with permission.

Figure 61. ***Phthiracarus*** sp. This mite looks like a tiny seed and members of the genus live among mosses on tree trunks. Photo by Walter Pfliegler, with permission.

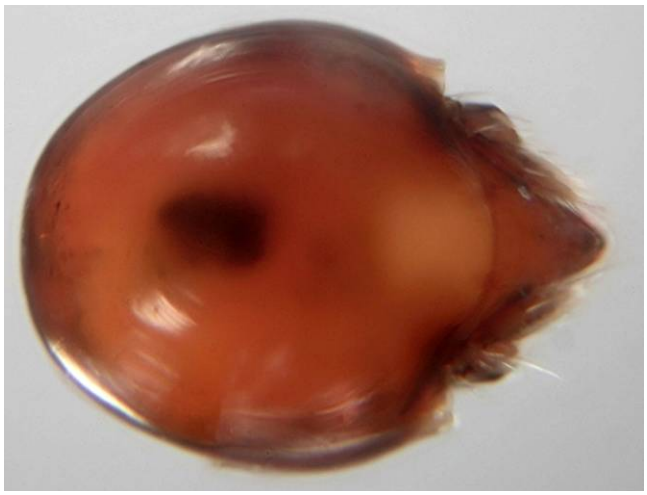


Figure 62. ***Chamobates*** sp., a mite that feeds on fungi among mosses on tree trunks. Photo by Walter Pfliegler, with permission.

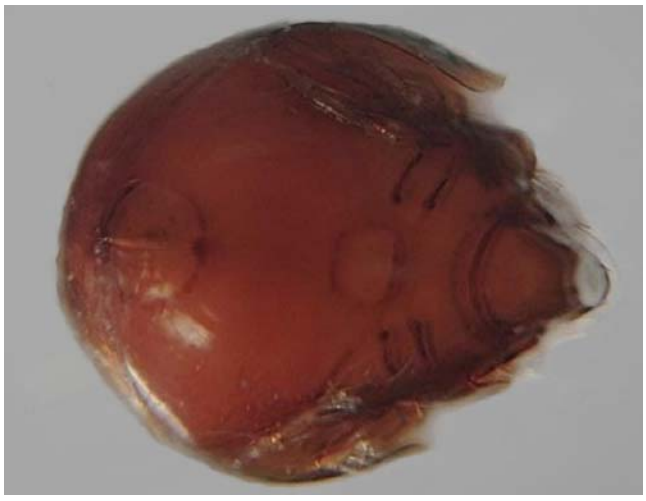


Figure 63. Ventral surface of ***Chamobates*** sp., a fungal mite from mosses. Photo by Walter Pfliegler, with permission.

Figure 64. **Liacaridae** on moss, a family that can be found among mosses on tree trunks. Photos by Walter Pfliegler, with permission.

Figure 65. ***Hafenrefferia*** sp., mite that lives among mosses on tree roots and eats a variety of foods. Photo by Walter Pfliegler, with permission.

Figure 66. ***Hypochthonius rufulus*** from Virginia Beach, USA, a mite that lives among mosses on tree roots. Photo by Scott Justis, with permission.

Figure 67. ***Hypochthonius rufulus***, a mite that lives among mosses on tree roots. Photo by Walter Pfliegler, with permission.

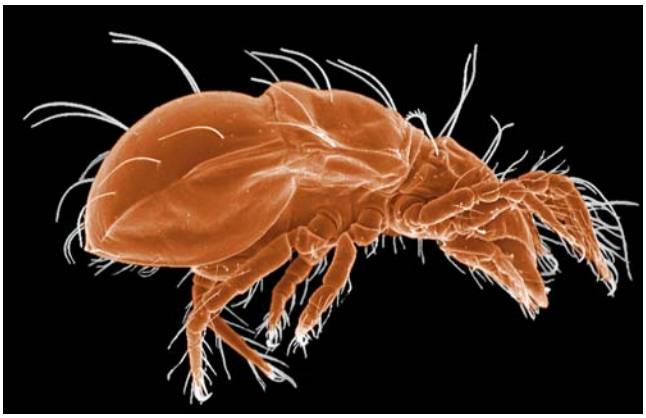


Figure 68. SEM of ***Hypochthonoius rufulus*** from a lateral view. Photo by David E. Walter, with permission.

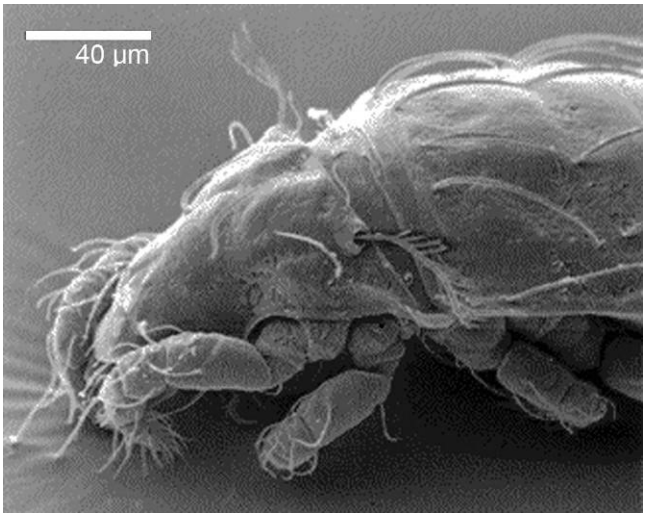


Figure 69. SEM image showing details of head region of ***Hypochthonius*** sp., a moss-dweller on tree roots Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

Some bryophytes may even provide a food source underground. The primitive leafy liverwort ***Haplomitrium*** (Figure 70) extends its stem below ground, where it is inhabited by endophytic fungi (Carafa *et al.* 2003). Whether these are available as food for mites remains a question, but many bryophytes have fungal associates that could provide food sources.

Figure 70. ***Haplomitrium gibbsiae***, a leafy liverwort that has underground endophytic fungi – an unevaluated potential food source for mites. Photo by Jan-Peter Frahm, with permission.

Wolf and Rockett (1984) experimented with the diet of ***Rhysotritia*** (Figure 71). They found that those mites taken from their natural habitat contained significantly fewer bacteria in their guts than those maintained in the lab in a soil-moss habitat. This suggests that bryophytes can provide significant bacterial food sources to the mite inhabitants.

Figure 71. ***Rhysotritia*** sp. from Norfolk, VA, USA; this mite can subsist on bacteria among mosses. Photo by Scott Justis, with permission.

At least some aquatic mites use mosses for food. Gerson (1982) reported that some use the moss ***Cratoneuron filicinum*** (Figure 72) for food.

Spider mites at Kadoorie Farm & Botanic Garden in Hong Kong also use bryophytes as food. The mites, reported as ***Tetranychus*** sp. (Figure 74) [but not spider mites, and probably ***Halotydeus*** (Figure 73-Figure 74) according to David Walter, pers. comm. 6 June 2011], actually eat the gemmae of the epiphytic moss ***Octoblepharum albidum*** (Figure 75), leaving only the basal cells where the gemmae attach to the leaf margins (Zhang *et al*. 2002, 2003). ***Halotydeus signiensis*** in the South Orkney Islands and ***H. bakerae*** in Australia are described from mosses (Walter 2006; David Walter, pers. comm. 7 June 2011). Their food relationships are not described.

Figure 72. ***Cratoneuron filicinum***, a moss that serves as food for some mites. Photo by Michael Lüth, with permission.

Determining the diet of such small animal by gut analysis has long been a challenge. However, modern techniques using DNA matching may permit the identification of food eaten by mites collected from the field (see Remén *et al*. 2010), at least to the phylum level, and eventually to much lower levels as our bank of DNA fingerprints increases.

Figure 73. ***Halotydeus*** sp., member of a genus with moss-dwelling members. Photo by Walter Pfliegler, with permission.

Importance of Bryophytes for Food

David Walter (pers. comm. 6 June 2011) suggests that mosses may be most important as food for earth mites [species of ***Halotydeus*** (Figure 73-Figure 74, Figure 76, Figure 81), ***Penthaleus*** (Figure 51)] in early spring before tracheophytes emerge from the ground or produce their leaves. Bryophytes are often the only green plants around, aside from tough conifers, when the snow melts and mites become active. He suggests that bryophytes might also be more important for the early instars – those 6-legged ones like I saw late at night when I was trying to identify the moss. This seems like a fertile topic for experimentation, looking for changes in diet between early and late life cycle stages. It would be interesting to see if older instars or adults might have a wider array of mosses in their diets, or abandon them altogether for tracheophytes.

Figure 74. ***Halotydeus*** sp. on leaves of the moss ***Octoblepharum albidum***. Note its resemblance to ***Penthaleus*** (Figure 51), but its absence of a dorsal anus. The arrow indicates the location of gemmae. Photo by Li Zhang from Zhang *et al*. 2002, with permission.

Figure 75. Gemmae of ***Octoblepharum albidum***. These can be dispersed by bryophytes. Photo by Li Zhang from Zhang *et al.* 2002, with permission.

Ridsdill-Smith and Pavri (2000) demonstrated that the diet of the mite ***Halotydeus destructor*** (known to feed on mosses; Figure 76) does not depend on a specific plant species. Rather, a diversified diet can provide nutrients for these mites as the seasons and weather change. Its ability to use plants with different nutrient suitability not only permits it to live through the changing seasons, but permits it to take advantage of the differing microclimates from soil to plant leaves. This feeding strategy contributes to its being very abundant, and unfortunately, enables it to be an agricultural pest.

Bryophytes may serve indirectly in providing food in at least some cases. For the mite ***Ameronothrus*** sp. (Figure 77), algae growing in association with the moss ***Schistidium maritimum*** (Figure 78) in a coastal splash zone at Yachats, Oregon, USA, provided a food source (Merrifield 1994). These mites emerged from perichaetia, mature capsules, and spent capsules, as well as from samples extracted with a Baermann funnel. A student of Stefan Schneckenburger (Bryonet 7 July 2015) likewise found eggs and adults of small mites in the capsules of ***Schistidium*** and other **lithophytic** (rock-dwelling) mosses. These capsules had no spores and the opercula were secured.

Figure 76. ***Halotydeus destructor***, a mite that eats a diversified diet that includes mosses. Photo © Victorian Government of Australia, permission for educational use only.

Figure 77. ***Ameronothrus lineatus***. Some members of this genus eat algae associated with the moss ***Schistidium maritimum***. Photo by Steve J. Coulson, with permission.

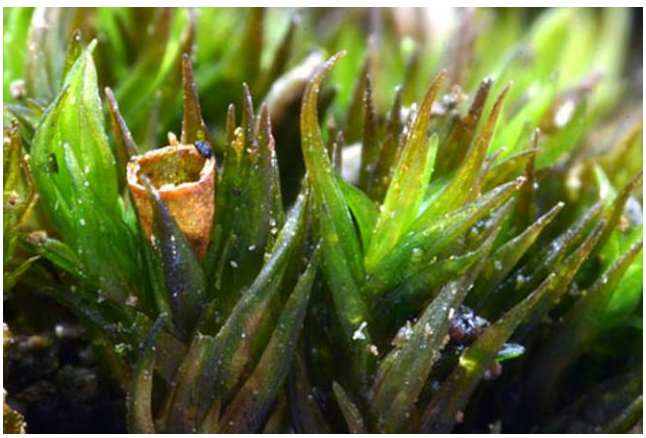


Figure 78. ***Schistidium maritimum*** with sporophyte. Algae on this moss provide food for some species of mites. Photo by Des Callaghan, with permission.

Lawrey (1987) suggests that mosses are not that different from tracheophytes in their nutritional value. The sugars seem to be the same, although ***Sphagnum*** has some that are different (Maass & Craigie 1964), and there are lots of mosses that have not been analyzed. Caloric content likewise is similar to that of tracheophytes. Lipids seem to be highest in the spores (Lawrey 1987), perhaps accounting for reports of mites in capsules (Merrifield 1994). The essential elements may be lower in bryophytes – not surprising because of the low nutrient conditions in which many mosses live, with N being quite variable and K and Mg somewhat lower than in tracheophytes (Prins 1981). But mosses seem to have lower concentrations of those soluble carbohydrates and hemicelluloses that are easily digested, exhibiting instead higher concentrations of structural components such as cellulose and polyphenolic lignin-like compounds – compounds that are harder to digest. Tracheophytes, by contrast, have lots of leaf parenchyma cells that lack lignin. While bryophytes all lack lignin, their polyphenolic compounds with lignin-like structure and properties, often serve as chemical deterrents to herbivory. The highly structured ***Polytrichastrum*** (=*Polytrichum*) ***ohioense*** has less "desirable" structural compounds than those found in the lichen ***Cladonia cristatella*** (Figure 112), ***Pinus resinosa*** (red pine), or angiosperm tree leaves (Table 2), but I must question if the highly evolved structure of this moss with known cuticle and conducting cells is really a reliable representative of the mosses. This chemical structure could explain why mites in the study by Gerson (1972, 1987) did not survive when provided with only ***Polytrichum*** as food.

Presence of mites among bryophytes may be more a function of the substrate than of the food source. As Lawrey (1987) concluded, the habitat may be more important than the nutrition. But given a choice among otherwise suitable habitats, it appears that nutrition does play a role (Young & Block (1980). In an experimental study on the Antarctic mite ***Alaskozetes antarcticus*** (Figure 79), the mites maintained on lichens had the highest respiration rate and metabolism compared to those on the green alga ***Prasiola crispa*** or on **guano** (bird droppings). The mites also selected the lichens as food among these three choices.

Table 2. Comparison of structural components of a bryophyte (***Polytrichum ohioense***) with two trees and a lichen (*Cladonia cristatella*). Values represent percent of oven-dry weight; n=5. From Lawrey 1977.

Pinus resinosa leaves	35.41	13.44	19.37	23.56
Angiosperm tree leaves	43.89	11.59	20.43	11.04
Polytrichastrum ohioense leafy plant	16.51	14.07	24.37*	12.90
Cladonia cristatella thalli	19.93	66.54^{+}	2.98^{+}	0.78^{+}

*Mosses don't have a true lignin.
$^{+}$Lichens have chitin and lichenin as cell wall components and do not have true hemicellulose, cellulose, or lignin.

Figure 79. ***Alaskozetes antarcticus***, a common Antarctic moss-dweller. Photo by Richard E. Lee, Jr., permission pending.

Krantz and Lindquist (1979) consider the **Penthalodidae** and **Eupodidae** to survive in moss substrates, whereas other species are fungivores. Later, McDonald *et al*. (1995) stated that the early life stages of ***Penthaleus*** (Figure 51) species were "likely to feed on lower plants and microflora found on the soil surface."

The observations of mites feeding on associated algae and fungi were followed by studies on the suitability and use of microflora as food for moss-feeding mites. Maclennan *et al*. (1998) compared the success of development for the plant pest ***Halotydeus destructor*** (**red-legged earth mite**; Figure 81) when reared on sand, bare soil, microflora from two locations, wheat, vetch, and combinations of microflora with wheat or vetch. This species is a pest in Australia, New Zealand, and southern Africa (Ridsdill-Smith 1997; Umina 2004). Maclennan *et al*. (1998) found that the microflora (including mosses, algae, and detrital matter) was an important supplement to the plant diet (Figure 80). When overgrazing caused the tracheophyte canopy to decline (Grimm *et al*. 1995), the loss of cover caused the microflora to decline. Maclennan *et al*. suggest that the mite densities dropped in response to the declining microflora.

As mentioned by David E. Walter (pers. comm. 6 June 2011), feeding by the immature stages on the microflora avoided competition with the adults. But when tracheophyte food is unavailable, ***Halotydeus destructor*** (Figure 76) is able to feed for 26 days (duration of the experiment and well into adulthood) on microflora alone in some sites (Bundoora) (Maclennan *et al*. 1998). And even the tracheophyte wheat was not sufficient to sustain them when eaten without microflora as a supplement (Figure 80).

The additional advantage of the mosses and microflora is their ability to provide a suitable microhabitat at times when the tracheophytes are inhospitable. In this study, the microflora crust at Dookie was dominated by the alga *Vaucheria*, but the moss ***Bryum dichotomum*** (Figure 82) and liverwort ***Riccia crystallina*** (Figure 83) were also present. At Bundoora, ***Tortula truncata*** (Figure 84; formerly *Pottia truncata*), ***Fissidens vittatus***, ***Ceratodon purpureus*** (Figure 85-Figure 86), ***Barbula unguiculata*** (Figure 87), ***Zygodon hookeri***, and ***Bryum*** sp. (see Figure 82) were present, as well as Cyanobacteria.

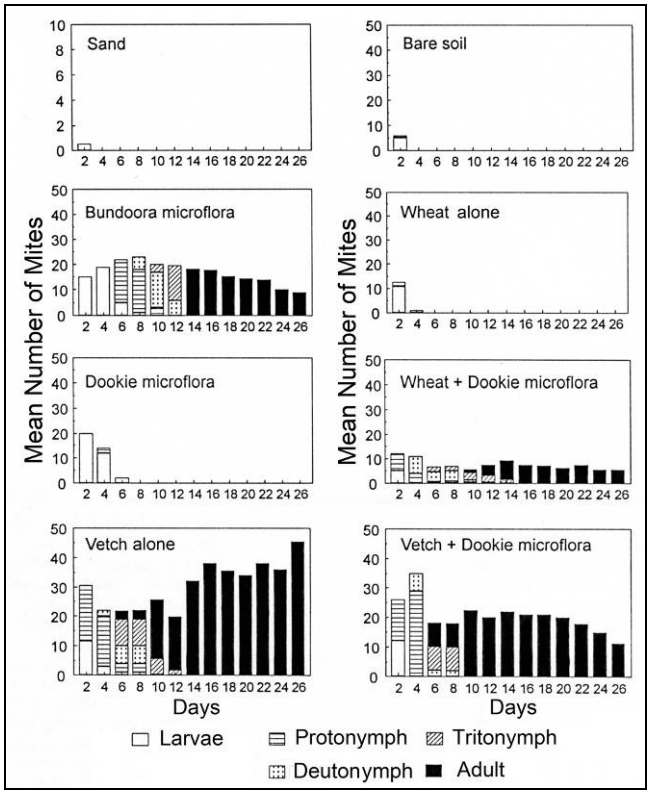


Figure 80. Mean density estimates and development of the red-legged mite ***Halotydeus destructor*** on sand and soil substrates compared to plants along and with microflora at two sites. Redrawn from Maclennan *et al*. 1998.

Figure 81. ***Halotydeus destructor***, the tiny black mite with red legs, includes mosses in its diet. The larger, red mite is ***Anystis*** (Prostigmata), a predator of ***Halotydeus*** species! Photo from <agspsrv34.agric.wa.gov.au>, for educational use only.

Figure 82. ***Bryum dichotomum***, a moss that is a likely mite habitat. Photo by Barry Stewart, with permission.

Figure 83. ***Riccia crystallina***, a thallose liverwort that provides cover for mites. Photo by Des Callaghan, with permission.

It appears that the microflora, including mosses, is important for the early life stages. Maclennan *et al*. (1998) found that the larvae and protonymphs spent almost no time on the wheat or vetch, but rather developed in the moss layer (Figure 80). Even adults would retreat there under unfavorable microclimate conditions on their tracheophyte food plants.

Figure 84. ***Tortula truncata*** (formerly *Pottia truncata*), a tiny moss that houses mites. Photo by Michael Lüth, with permission.

Figure 85. ***Ceratodon purpureus*** in its hydrated condition, making it desirable to keep mites hydrated. Photo by Andrew Spink <http://www.andrewspink.nl/mosses/>, with permission.

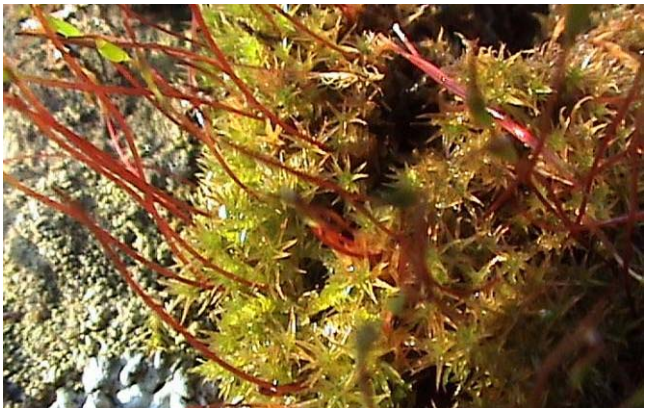


Figure 86. ***Ceratodon purpureus***, a widespread species that hosts mites. Photo by Christian Hummert, through Creative Commons.

Figure 87. ***Barbula unguiculata***, a common open habitat species that provides moist cover for mites. Photo by Michael Lüth, with permission.

In prairie, desert, and other dry habitats where cryptogamic crusts develop, the bryophytes may be particularly important to serve as sources of food for the mites. They are almost a necessity because the bryophytes provide the only locations with sufficient moisture for most species. The co-habitants of fungi, algae, and some Cyanobacteria provide potential food for some mite inhabitants (Lukešová & Frouz 2007). On the other hand, all oribatid mites tested rejected the Cyanobacterium *Nostoc.*

Reproductive Site

Gerson (1969) brought mites, collected from mosses in Quebec, Canada, into the laboratory and allowed them to breed and lay eggs. Among the available mosses, they laid eggs on ***Brachythecium*** (Figure 88), ***Hypnum*** (Figure 89), ***Didymodon*** (Figure 90), and ***Ceratodon purpureus*** (Figure 85-Figure 86).

One tiny mite even lays its eggs in the tiny capsules of ***Orthotrichum pusillum*** (Keeley 1913; Figure 91). The eggs are sticky, so the spores adhere, giving the appearance of an oval mass of tiny beads of spores. The eggs are so glutinous that even boiling fails to dislodge the adhering spores. But is this a common occurrence, or just a lucky one-time find? And what is the fate of the spores when the young mites hatch? Do the mite children eat the spores, or do the mites become unwitting dispersal agents?

Figure 88. ***Brachythecium rutabulum***, a substrate that has been used by mites in the laboratory as an egg-laying site. Photo by Janice Glime.

Figure 89. ***Hypnum pratense***, a potential egg-laying site for mites. Photo by Michael Lüth, with permission.

Figure 90. ***Didymodon fallax*** (formerly in *Barbula*), a moss where mites are known to lay eggs. Photo by Michael Lüth, with permission.

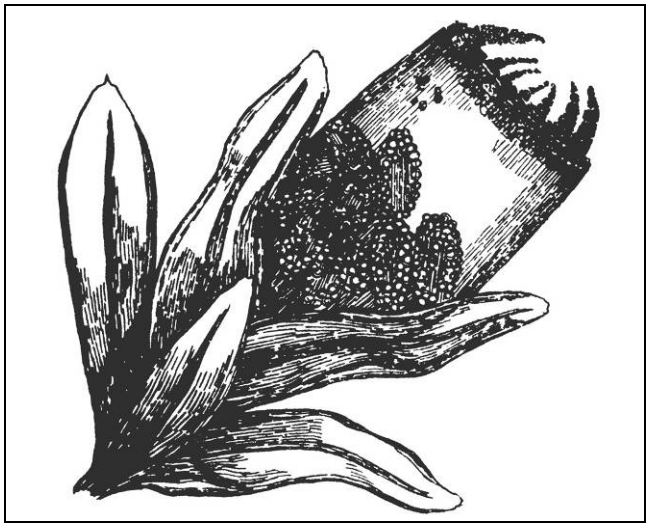


Figure 91. This capsule of ***Orthotrichum pusillum*** houses the eggs of a tiny mite. Spores of the moss adhere to the eggs, forming clusters. Drawing modified from Keeley 1913.

Figure 92. ***Orthotrichum pusillum***, a moss known to house mite eggs in its capsules. Photo by Robert Klips, with permission.

Eustigmaeus (formerly ***Ledermuelleria***; Figure 33) lays eggs on a variety of mosses, but it also seems to avoid some, and there is evidence that eggs or young will not survive on some species (Table 3; Gerson 1987). These mites have a life cycle of 30 days with isolated females producing only male offspring (Gerson 1972). The female lays about 21 eggs, and reproduction seems unrelated to day length.

Johnstoniana exima (formerly *J. tuberculata*) is one of the mites with a parasitic larval stage. This small species lives in moist areas near lakes, where it is completely hidden just below the litter surface (Wohltmann *et al*. 1994). This litter could include mosses, but specific documentation seems to be lacking. The female lays her eggs in autumn and both sexes die shortly afterwards. The eggs overwinter, with larvae emerging in May and June. This emergence synchronizes perfectly with that of the host for the larvae, the cranefly ***Limonia*** sp. (see Figure 93). This synchronization suggests that the same factors control the development and hatching in both the mite and the adult cranefly. Since ***Limonia*** often lives among bryophytes [*e.g.* ***L. sexocellata***, ***L. capicola*** in South Africa (Harrison & Barnard 1972); species in Colorado (Ward & Dufford 1979)], it is likely that the bryophyte habitat may play an important role when the mite attempts to locate a host.

But this overwintering pattern is not true for all ***Johnstoniana*** species. ***Johnstoniana parva*** requires a humid habitat, which they are able to find in the litter, and presumably mosses (Wendt *et al*. 1994). It has two egg-laying periods. After insemination in the autumn, overwintering eggs enter diapause in the bedrock. Other females are inseminated in the fall, then these adults hibernate for the winter and lay their eggs in late spring.

At least some of the aquatic mites use pheromones to find their mates (Smith & Hagman 2002). ***Arrenurus manubriator*** males respond to water in which females of the species have been kept previously. When put into water with these pheromones, the male assumes a readiness posture in readiness for coupling.

Figure 93. ***Limonia nubeculosa***, member of a genus of common moss-dwelling craneflies (Diptera) and hosts to mite larvae. Photo by James K. Lindsey, with permission.

Table 3. Survival and oviposition of ***Eustigmaeus frigida*** on various moss species. + = presence of ***E. frigida*** on that species in the field. From Gerson 1987.

Survival and Oviposition	Survival but no Oviposition	No Survival
Amblystegium serpens	*Bryum argenteum*	*Atrichum altecristatum*
Barbula unguiculata	*Bryum pseudotriquetrum*	*Leucobryum glaucum*
Brachythecium salebrosum (+)	*Dicranum scoparium*	*Pogonatum urnigerum*
Brachythecium sp.	*Ditrichum pusillum*	*Polytrichum commune*
Ceratodon purpureus	*Fissidens taxifolius*	*Polytrichum piliferum*
Didymodon tophaceus	*Funaria hygrometrica*	
Drepanocladus aduncus	*Hedwigia ciliata*	
Callicladium haldanianum (+)	*Plagiomnium cuspidatum*	
Calliergonella lindbergii (+)	*Plagiomnium ellipticum*	
Hypnum reptile (+)	*Pleurozium schreberi*	
Leptodictyum riparium (+)	*Pohlia wahlenbergii*	
Thuidium delicatulum (+)	*Racomitrium heterostichum*	
	Rhodobryum roseum	
	Sphagnum magellanicum	
	Sphagnum recurvum	

But mites are not the only things reproducing. West (1984) found mites and Collembola to be particularly important in ***Polytrichum*** clumps on South Georgia in the sub Antarctic. He found that different species of ***Polytrichum*** had different species of mites, using it as food, shelter, or both. Cronberg *et al*. (2006) found that the relationship between mosses and mites (***Scutovertex minutus***; Figure 94) or Collembola (***Isotoma caerulea***) can be even more intimate. In their experiments, these arthropods served as sperm vectors for the moss (Figure 95). This breakthrough discovery helps to explain how sperm may reach females 10 cm, even 1 m, away (Milius 2006). Mosses as close as 2-4 cm failed to reproduce unless cultures were in the company of these arthropods. In fact, it appears that the mites and springtails actually move to the fertile males and females more often than to "sterile" (non-fertile) shoots (Figure 96). The springtails seem to be more effective than the mites.

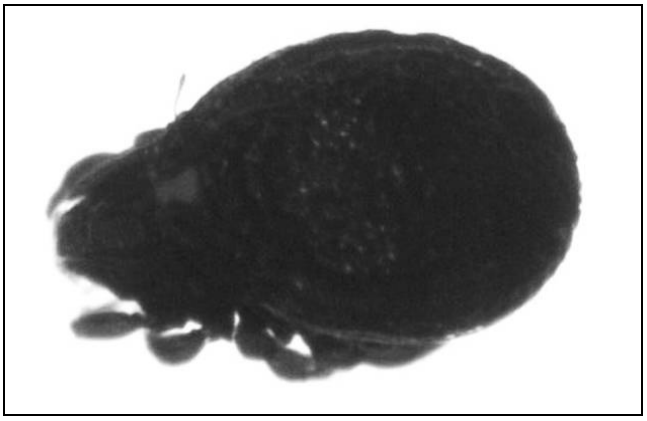


Figure 94. ***Scutovertex sculptus***, member of a genus known to disperse the sperm of the moss ***Polytrichum***. Photo by S. E. Thorpe, through Creative Commons.

The mite ***Eustigmaeus bryonemus*** (see Figure 33) in Brazil not only feeds on mosses, but it lays its eggs there as well (Flechtmann 1984). Its bright red eggs are laid mostly on the middle and lower leaves of fresh moss shoots. These are placed on the surface and not glued.

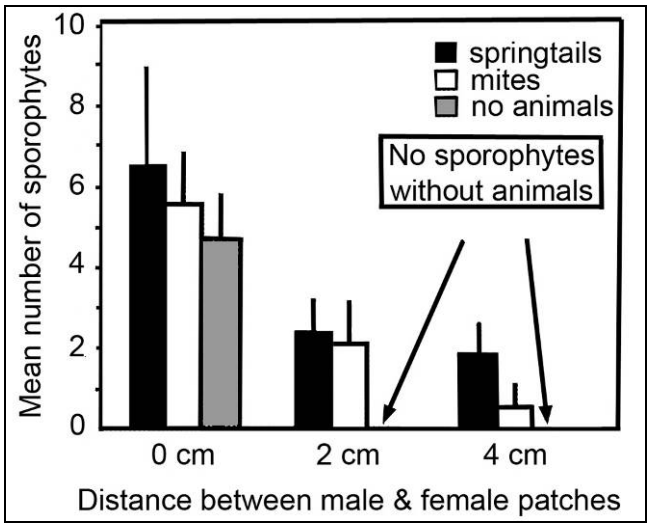


Figure 95. Comparison of sporophytes produced, indicating fertilizations, with male and female moss patches (***Bryum argenteum***) at 3 distances apart. Bars are mean number of sporophytes produced by 7 replicates. Vertical lines represent standard errors. Redrawn from Cronberg *et al*. 2006.

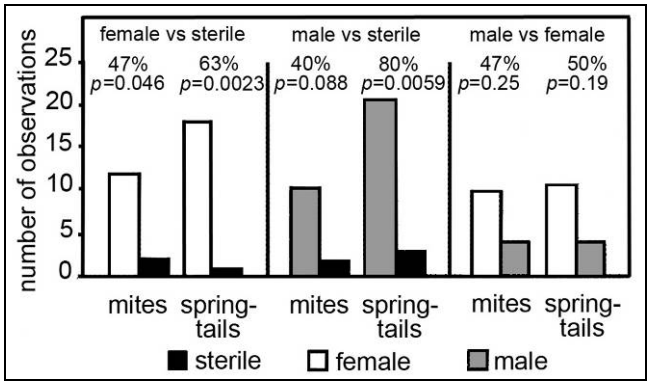


Figure 96. Preferences of mites (***Scutovertex minutus*** & ***S. sculptus***) and springtails (***Isotoma caerulea***) for fertile male, fertile female, and sterile plants of ***Bryum argenteum***. Percentages are proportion of 30 replicate moss shoots on which animals were present. Bars represent numbers of animals present on fertile or sterile shoots. Probability is based on G test. Redrawn from Cronberg *et al*. 2006

Tydeus tilbrooki, the smallest arthropod in the Antarctic, lays its eggs among mosses, especially ***Polytrichum*** species that are encrusted with lichens (Gressitt 1967). It eats fungal hyphae and lichens there. ***Rhagidia gerlachei*** (see Figure 97) and ***Rhombognathus gressitti*** (an intertidal species) likewise use mosses for egg-laying sites in the Antarctic, as do ***Stereotydeus***, ***Protereunetes***, ***Oppia*** (Figure 98), and ***Halozetes***.

Figure 97. ***Rhagidia*** sp. The tiny mites are most likely larvae of the same species. In the Antarctic, members of this genus lay eggs among mosses. Photo by Andrew Lewington @ <http://www.cavelife.org.uk/>, with permission.

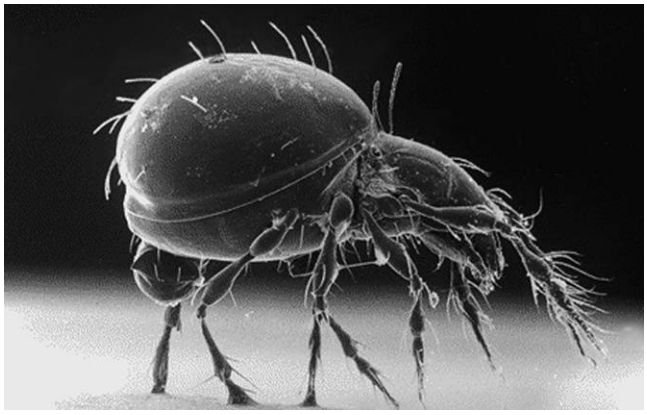


Figure 98. ***Oppia*** sp. is a member of a genus that lays its eggs in mosses in the Antarctic. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

Parasitic Mites

Many of the mites have larval stages that are parasites on other organisms. This group, known as the **Parasitengonina**, belong to the **Prostigmata** (Krantz & Walter 2009). Compared to the oribatids (moss mites), they are large mites, often display a bright reddish coloration (Figure 99), and are characterized by their particular life cycle, beginning with a parasitic larva. Although most of these larvae parasitize other arthropods (primarily flying insects), humans are familiar with the chiggers that parasitize humans and other vertebrates. The life cycle of this mite group is in an interesting one that makes them both parasites and predators. The parasitic larva matures into a **protonymph**, an immobile stage within the larval skin. This is followed by a predatory stage, the **deutonymph**, that feeds on other arthropods. The third and final nymphal stage is the **tritonymph**, once more an immobile stage within the deutonymphal skin. This emerges from its "skin" prison as an **adult** that once again preys on other arthropods). Only a few Parasitengonina have a life cycle that varies from this pattern by having free-living larvae or additional moults (Wohltmann 2000).

Figure 99. A water scorpion (**Heteroptera: Nepidae**) infected by parasitic mites, larvae of a species of ***Hydrachna***. Photo by Walter Pfliegler, with permission.

Andreas Wohltmann (pers. comm. 17 September 2011) considers that "mosses (and lichens) constitute part of the microhabitat of almost all Parasitengonina except a few species (e.g. desert-dwelling species such as ***Dinothrombium*** spp. and possibly some subterranean watermites) and thus Parasitengonina mites can be sampled in these substrates during mating, oviposition or searching for prey (or suitable hosts in the case of larvae)." Nevertheless, no evidence exists to suggest that any of the Parasitengonina feed on mosses or that any life cycle is dependent on them for mating or oviposition. Based on his field sampling, Wohltmann has concluded that there seems to be a greater correlation between bryophytes and Parasitengonina among the species in semiaquatic habitats than elsewhere.

Stur *et al*. (2005) examined non-biting midges (Chironomidae) in spring habitats in Luxembourg in search of parasitic water mite larvae. There were several species of midges what were not parasitized, and they suggested that general unavailability of the host or life cycle incompatibility could account for the abasnce of parasites. But they also suggested that two species of ***Chaetocladius*** among the mosses, along with their moss-dwelling life style, might also account for the lack of parasites on the sampled ***Chaetocladius***. They suggested that the semiterrestrial moss-dwelling life style of these two ***Chaetocladius*** species made them less available to these aquatic parasitic mite larvae.

Adaptations of Parasitengonina

One of the major subgroups of **Parasitengonina** is the **Hydrachnidae** (formerly Hydracarina; Figure 100). As its

name suggests, this is a group that lives in a broad range of aquatic habitats, many of which have bryophytic substrates (Andreas Wohltmann, pers. comm. 17 September 2011).

Figure 100. ***Hydrachna cruenta*** amid ***Elodea canadensis*** leaves. This large mite is 3 mm in diameter. Photo by Andreas Wohltmann, with permission.

The terrestrial subgroups include the **Erythraiae** and the **Trombidiae**, both of which include a few terrestrial species. Among the **Trombidiae**, the members of the family **Johnstonianidae** are all amphibious. In contrast to the aquatic mites, terrestrial **Parasitengonina** have dense body hairs (**hypertrichy**) that prevent the cuticle from getting wet (Andreas Wohltmann, pers. comm. 17 September 2011). This causes an air bubble to form around the body when it gets wet. Water mites have few hairs and the body makes direct contact with the water. This lowers the **hemolymph osmolality** and reduces osmotic pressure, permitting them to live in fresh water without exploding.

The **Erythraeoidea** have a higher drought resistance than members of the **Trombidioidea** (Wohltmann 1998). This greater resistance results from differences in the body plan much like some of the characteristics that protect bryophytes. These include a reduction of body openings (bryophytes have none in their gametophytes, except in thallose liverworts) and lipids that help to seal others. This combination reduces water loss. But also like most bryophytes, the **Trombidioidea** are able to gain moisture from the atmosphere, although this has not been observed for erythraeoid eggs or protonymphs. In the **Trombidioidea**, this vapor uptake can increase fresh body mass by about 50% prior to the protonymph stage. Wohltmann suggests that this increase in body mass may serve to stretch the cuticle and provide more space for the next developing instar. Hence, it might not have any relationship to drought resistance. In fact, one might speculate that stretching the cuticle could even reduce its resistance to losing water.

Bryophytes or Lichens?

Both bryophytes and lichens are small turfs that provide spaces and protection. Hence we should expect many species to live among both. But it appears that we do not really know very much about why they choose one or the other, or both.

Some species occur predominantly on lichens, and others on bryophytes. ***Halozetes crozetensis*** is predominately among mosses, but occurs in lichens as well, with the choice apparently depending on the location and its climatic factors (Seyd & Seaward 1984). Some seem to be facultative moss dwellers, using them only when the lichens are unavailable. ***Scutovertex minutus*** (see Figure 35-Figure 36) and ***Zygoribatula frisiae*** (see Figure 101) live among mosses when lichens are absent, but are common lichen inhabitants. ***Lepidozetes singularis*** occurs among mosses in the Black Forest, but lives among lichens elsewhere (Seyd & Seaward 1984).

Figure 101. ***Zygoribatula bulanovae***. Some members of this genus prefer lichens but use mosses when no lichens are available. Photo from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

General

Carabodes labyrinthicus (Figure 102) is widespread on mosses as well as lichens (Seyd & Seaward 1984). ***Ommatocepheus ocellatus*** likewise is known from mosses and liverworts as well as lichens, and is known to feed on saturated lichens. ***Tricheremaeus serratus*** occurs with both lichens and bryophytes. ***Adoribatella punctata*** occurs in both, as does ***Alaskozetes antarcticus***, a detritivore. ***Ameronothrus lineatus*** (Figure 77) occurs in both, although it seems to be more common among lichens. ***Centroribates uropygium*** occurs in both. ***Chamobates cuspidatus*** (see Figure 62-Figure 63) is primarily a moss dweller, but occurs also on lichens. ***Leiosoma palmicincta*** occurs on both and survived from egg to adult on lichens alone. ***Eremaeus oblongus*** (see Figure 103) and ***Tectocepheus sarekensis*** (see Figure 105) occur in a wide range of habitats that include mosses and lichens. In Sierra de Cazorla, ***Ghilarovus hispanicus*** lives among mosses and lichens on rocks. ***Tegoribates bryophilus*** in Colorado, USA, and ***Metrioppia helvetica*** are known from mosses and lichens. ***Parachipteria petiti*** was taken from the lichen ***Parmelia*** (Figure 104) as well as from mosses and liverworts. ***Micreremus brevipes*** seems especially fond of pine forests, where it can be found among litter, but also among corticolous lichens, and mosses.

Figure 102. ***Carabodes labyrinthicus***, a mite that lives on both mosses and lichens. Photo by Monica Young, through Creative Commons.

Figure 103. ***Eremaeus*** female, a genus that can be found on both lichens and mosses. Photo by Walter Pfliegler, with permission.

Figure 104. ***Parmelia saxatilis*** growing over a moss and often sharing mite fauna. Photo by Rick Demmer, USDA Forest Service, through public domain.

As food sources, it appears that there are at least preferences between bryophytes and lichens. That is not surprising because the lichen provides primarily fungal food that is relatively easy to eat once the outer covering of the lichen has been penetrated. But in bryophytes, the thick cellulose walls provide a somewhat different challenge for the tiny mites. Some overcome this with a stylet type of apparatus that is able to penetrate the bryophyte cells. Nevertheless, some mites are associated with both mosses and lichens (Travé 1963, 1969), but their food preferences may still be similar, relying more on the associated organisms than on the bryophyte itself.

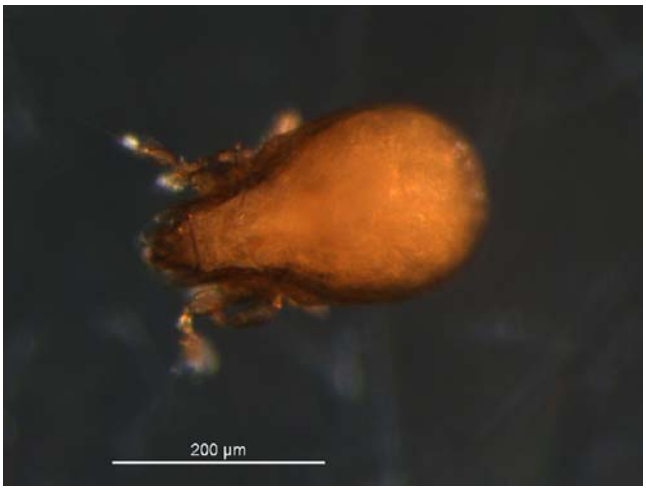


Figure 105. ***Tectocepheus velatus***, a member of a genus that lives on both mosses and lichens. Photo by Monica Young, through Creative Commons.

Cool Sites

In the cold climate of Spitsbergen, numerous mites occupy lichens, but some at least are also found on mosses (Seyd & Seaward 1984). These include ***Calyptozetes sarekensis***, but this species is more abundant among lichens. ***Camisia invenusta***, a mite of mountain summits and other cool areas, inhabits both, but is more common among lichens and mosses on rocks than in the canopy. ***Carabodes willmanni*** (see Figure 102), on the other hand, prefers mosses. ***Hydrozetes capensis*** (see Figure 106) was found in dripping mosses and lichens in a canal.

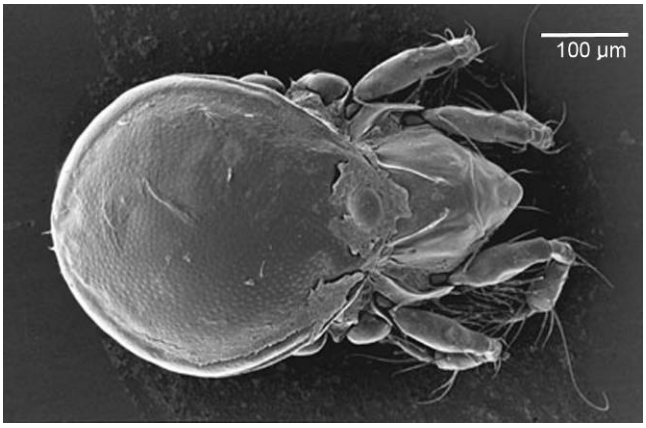


Figure 106. SEM of ***Hydrozetes***, a lichen and moss-dwelling genus common in peatlands. Photos by Valerie Behan-Pelletier and Barb Eamer, with permission.

The Arctic ***Diapterobates notatus*** (Figure 107-Figure 109) can occur in large numbers in moss and lichen litter. ***Halozetes belgicae***, an Antarctic species, lives among both lichens and mosses. ***Hermannia reticulata*** (Figure 110) occurs on both in areas with cool climates. ***Lamellovertex caelatus*** occurs among mosses in the Swiss Alps. ***Sphaerozetes arcticus*** dwells among mosses and lichens in northern Canada and Alaska.

Figure 107. Dorsal view of ***Diapterobates*** sp., member of a genus that inhabits Arctic moss litter. Photo by Walter Pfliegler, with permission.

Figure 108. ***Diapterobates*** sp., ventral view. Photo by Walter Pfliegler, with permission.

Figure 109. ***Diapterobates notatus***, inhabitant of Arctic moss litter. Photo by Steve Coulson using multifocus stacking, with permission.

Sphagnum

Camisia segnis likewise occurs in cooler areas and inhabits both lichens and mosses, including ***Sphagnum*** (Seyd & Seaward 1984). It is known to eat lichens, but I don't know if it eats mosses. ***Carabodes areolatus*** and ***C. marginatus*** live among both lichens and mosses, including ***Sphagnum***. ***Carabodes minusculus*** seems to prefer lichens, but nonetheless, it does occupy mosses, including ***Sphagnum***. Immature ***Mycobates parmeliae***, as its name implies, lives most commonly among lichens such as *Parmelia* (Figure 104), but as adults it is most frequently in mosses and liverworts (Travé 1963), including ***Sphagnum***. This suggests a change in resource needs, but we don't know which one(s). ***Trhypochthonius cladonicola***, named for the lichen genus *Cladonia*, also occurs among mosses, including ***Sphagnum***.

Figure 110. ***Hermannia reticulata***, a moss and lichen inhabitant in cool climates. Photo from Bold Systems, Biodiversity Institute of Ontario, through Creative Commons.

Arboreal

Many of the mites that occur in arboreal habitats also occur on rocks and some can be found in association with both bryophytes and lichens. ***Phauloppia coineaui*** occurs among both mosses and lichens on rocks and in trees, but they seem to prefer lichens (Seyd & Seaward 1984). ***Pseudachipteria magnus*** is predominately a moss dweller, but it also can occur in saxicolous and arboreal lichens. ***Liodes theleproctus*** lives among lichens, mosses, and liverworts on rocks and in trees in the Pyrénées. ***Strenzkea depilata*** occurs among lichens, mosses, and liverworts on rocks and trees. Others seem to be predominately arboreal. ***Humerobates rostrolamellatus*** is arboreal and feeds on fungi and lichens, but it also occurs among mosses. ***Lucoppia nemoralis*** prefers to live among mosses and lichens on trees, including the trunk. The arboreal ***Phauloppia lucorum*** can be extremely abundant in lichens, but is known from mosses; it feeds on lichens. ***Cymbaeremaeus cymba*** lives predominately among arboreal lichens and mosses. ***Licneremaeus discoidalis*** lives among arboricolous mosses and lichens in Guatemala. ***Phereliodes wehnckei*** occurs among arboreal mosses and lichens in Guatemala. ***Poroliodes farinosus*** occurs among lichens, especially ***Parmelia*** (Figure 104), but also among arboreal mosses and liverworts.

Coastal

Hermannia scabra (see Figure 58) lives among mosses and lichens in coastal as well as inland sites (Seyd & Seaward 1984). ***Oribatella calcarata*** is common among lichens in the intertidal zone, but are also known from mosses, including ***Sphagnum***, in coastal areas. ***Oribatula***

venusta (see Figure 111) has been taken from mosses as well as lichens on the sea shore as well as inland.

From this somewhat extensive list, it would appear that lichens and bryophytes may offer a number of common features suitable for mites. Lichens can offer cover, except for the crustose forms, and food, possibly from the fungal component (Seyd & Seaward 1984). The difference in food, with lichens providing fungi, may be a major factor dividing the species. For example, although ***Oribatula exsudans*** (see Figure 111) was collected from mosses, its fecal pellets contained no mosses – only pollen grains, fungal spores, fungal mycelia, and portions of lichen thallus (Seyd & Seaward 1984).

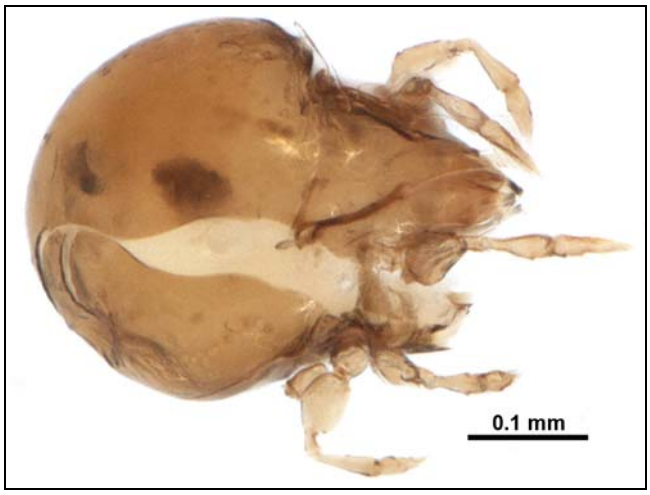


Figure 111. ***Oribatula tibialis,*** member of a genus that includes mites that live on both lichens and mosses. Photo by CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

Interestingly, for oribatids that occupy both bryophytes and lichens, the lichen is primarily species of ***Cladonia*** (Figure 112; Seyd & Seaward 1984) and presumably also ***Cladina***. This group of lichens has a 3-d structure somewhat like that of a moss, providing a labyrinth of internal spaces that serve as a refuge.

Figure 112. ***Cladonia cristatella***, a fruticose lichen that often occurs with mosses and shares many species of mite fauna. Photo by Charles Peirce, USDA Forest Service, through public domain.

Camouflage does not seem to be highly selected. For example, larvae of ***Mycobates parmeliae*** (see Figure 113) are bright orange and blend with their lichen habitat of ***Xanthoria parietina*** (Figure 114), but the adults apparently move to bryophytes, where bright orange does not match the color pattern (Seyd & Seaward 1984). This seeming contradiction may be explained, however, by the better covering ability of the bryophytes.

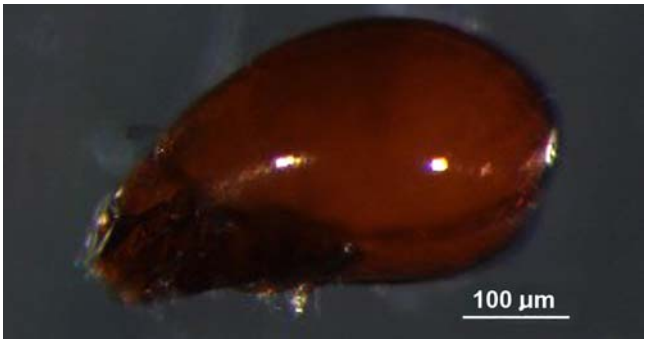


Figure 113. ***Mycobates perates***, member of a genus containing bright orange lichen dwelling larvae (***M. parmeliae***), but that then switch to mosses as adults. Photo by Monica Young, through Creative Commons.

Figure 114. ***Xanthoria parietina***, host of the larvae of ***Mycobates parmeliae***, a mite that lives among bryophytes as adults. James K. Lindsey, with permission.

Gall Formers?

Galls are unknown on extant thalloid liverworts or hornworts (Aller Hernick *et al*. 2008). But researchers have also reported that some thallose liverworts (***Metzgeriothallus sharona***) from the Middle Devonian had minute galls that might have been created by mites (Aller Hernick *et al*. 2008; Labandeira 2014). These liverworts are only revealed by projecting polarized light on the shale and siltstone surfaces.

Summary

Mites (**Acari** = Acarina) are common bryophyte inhabitants, especially the oribatids, resembling tiny spiders (mostly less than 1 mm) with 8 legs but no separation between the thorax and abdomen. Bryophytes provide a moist environment where movement up and down permits the mites to find the microclimate that best fulfills their needs and avoids damaging UV-B radiation. The bryophytes provide protective conditions suitable for many species to use for egg-laying.

Some mites use sucking mouth parts to extract food from bryophyte cells. Stylet size in ***Eustigmaeus***, a common genus among bryophytes, determines which bryophytes are edible. Some eat protonemata and others both eat and disperse gemmae. Some available bryophytes are avoided and on some, there is no survival for mites that do survive on other bryophyte taxa when the bryophytes are the sole source of food. Other mites are fungal eaters that take advantage of the soil-bryophyte interface where conditions are good for fungal growth, and others feed on organisms living among the bryophytes. On the other hand, the mites often serve as food for other inhabitants of the bryophytes. The bryophytes may be most important as a food source in early spring when herbaceous tracheophytes have not yet developed. Some mites live in liverwort lobules, taking advantage of the moisture, protection from predators, and liverwort food source.

During their travels among the bryophytes, mites can disperse sperm (and other propagules), and it seems that the reproductive structures of some bryophytes may actually attract them. Hairs protect the terrestrial members by providing trapped air spaces when they get wet. Aquatic members have few hairs.

Members of the Parasitengonina generally occur in habitats where mosses may provide substrate during their life cycle. These mites have a **parasitic larva**, an immobile **protonymph,** a free-living predatory **deutonymph**, another immobile stage – the **tritonymph**, and finally a free-living predatory **adult**.

Lichens provide some of the same advantages as bryophytes, offering small spaces where the mites can escape UV radiation, desiccation, and predation, but lichens offer different food choices, including the lichens themselves, contributing to a degree of specificity in the choice of bryophyte vs lichen.

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David Walter provided invaluable insights into the mites and provided a critical review of an earlier version of this sub-chapter. Andreas Wohltmann checked identifications on the images I obtained from the internet and provided me with replacements and additional images as well as reference material and his own observations of bryophyte-dwelling mites. Many people have provided images, permission to use images, and free access and permission to use pictures in the public domain.

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CHAPTER 9-2
ARTHROPODS: MITE HABITATS, MINOR ARACHNIDS, AND MYRIAPODS

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CHAPTER 9-2
ARTHROPODS: MITE HABITATS AND MINOR ARACHNIDS

Figure 1. Red mite (**Stigmaeidae**) on ***Riccia ciliata***. Photo by Michael Lüth, with permission.

Mites occur among bryophytes in a variety of habitats (Figure 1). These can be grouped into forests, aquatic, peatlands, polar/alpine, and tropics to define the major differences in community structure. Within those categories, communities are divided both vertically and seasonally, as well as divisions into niches that differ in light, moisture, and sometimes temperature. This defines those that are generalists and those that are specialists in food or cover type.

Forest Bryophytes

Forests offer a variety of microhabitats for both bryophytes and mites. Monson (1998) found more than 100 species of mites among mosses in Slapton Wood and nearby in the United Kingdom. And the dominant mite species can exhibit considerable variability. For example, ***Minunthozetes pseudofusiger*** (**Punctoribatidae**) can be very common among mosses in one site and nearly absent in another (Monson 1998). In his study of oribatid mites in mosses at Slapton Wood, UK, Monson found a number of species new for the UK, including ***Minunthozetes pseudofusiger*** (**Punctoribatidae**), ***Cepheus tuberculosus*** (**Cepheidae**; see Figure 2), ***Microzetes petrocoriensis*** (**Microzetidae**), ***Liochthonius perfusorius*** (**Brachychthoniidae**; see Figure 3), and ***Quadroppia pseudocircumita*** (**Quadroppiidae**).

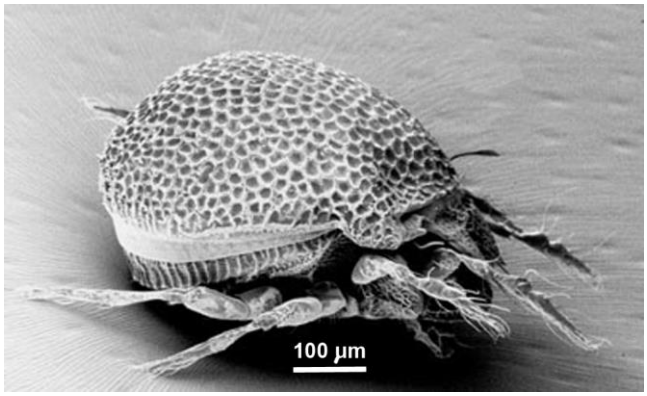

Figure 2. ***Cepheus corae*** SEM. ***Cepheus tuberculosus*** is a moss dweller in the UK. Photo by Christopher Taylor. PERMISSION PENDING

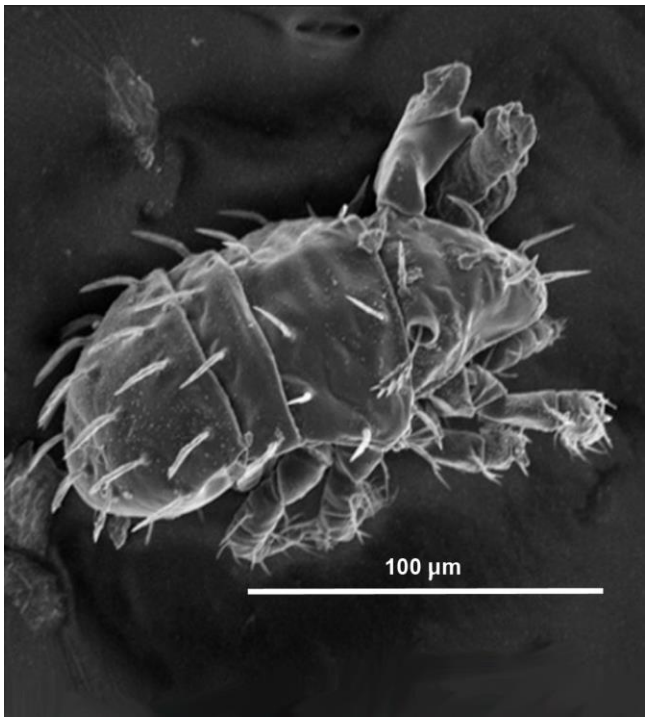

Figure 3. ***Liochthonius propinquus***. ***Liochthonius perfusorius*** is a moss dweller in the UK. Photo by Christopher Taylor. PERMISSION PENDING

Eremaeus stiktos (**Eremaeidae**; see Figure 5-Figure 4) was described from moss-covered logs and other forest habitats in Washington state, USA (Higgins 1962). Other members of this genus and segregates of the genus also occur on mossy logs and among bryophytes on the forest floor (Figure 6-Figure 4). Woolley (1968) reported ***Liacarus bidentatus*** (**Liacaridae**; see Figure 7) on the forest floor among mosses in Washington state, USA, and in mosses in Wyoming. ***Liacarus spiniger*** (see Figure 7) also occurs among mosses. In Illinois, USA, ***Platynothrus peltifer*** (**Camisiidae**; Figure 9; formerly *Hermannia bistriata*) lives among mosses and under logs (Ewing 1909).

Figure 4. SEM of ***Eueremaeus tetrosus***, member of a forest bryophyte-dwelling genus. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

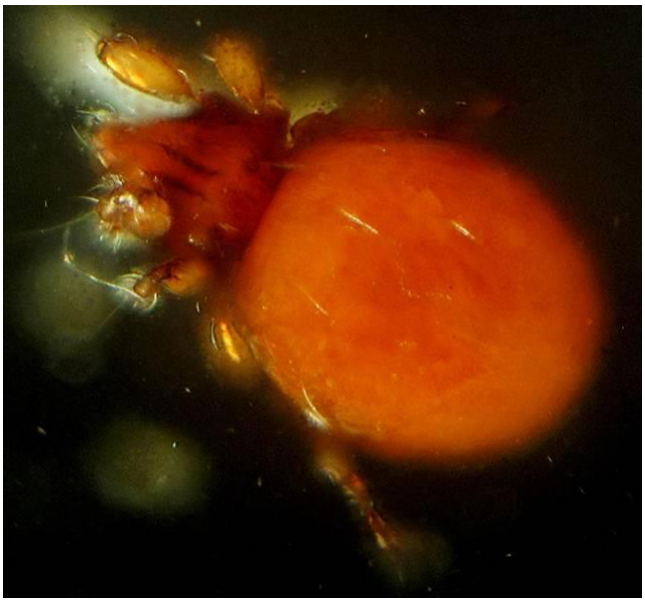

Figure 5. ***Eremaeus*** sp., member of a forest bryophyte-dwelling genus Photo by Walter Pfliegler, with permission.

Figure 6. SEM of ***Eueremaeus foveolatus***, member of a moss-dwelling genus on logs and the forest floor. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

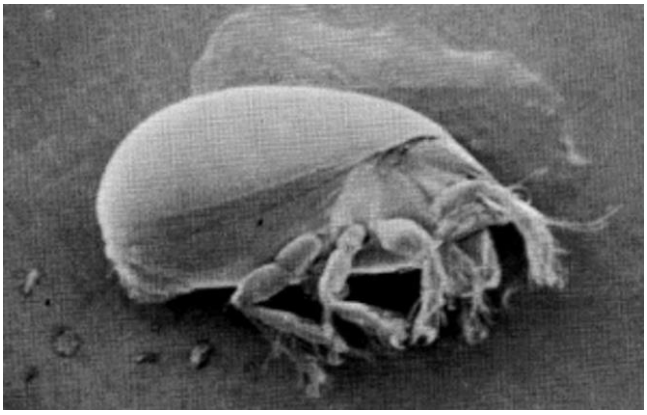

Figure 7. ***Liacarus*** nr. ***robustus***. ***Liacarus bidentatus*** and ***L. springeri*** are moss dwellers. Photo from <www.fs.fed.us> through public domain.

Figure 8. ***Platynothrus peltifer*** (**Camisiidae**) dorsal view, a moss dweller. Photos from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

Figure 9. ***Platynothrus peltifer***, a moss dweller. Photos from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

Forest Floor

Mites are a common component on the forest floor, where they may inhabit soil, leaf litter, logs, or moss (Sywestrowicz-Maliszewska *et al*. 1993; Proctor *et al.* 2002). ***Epicriopsis rivus*** (**Ameroseiidae**) lives among mosses and litter in pine forests in northern Latvia (Salmane 2011). Members of ***Epicrius*** (**Epicriidae**; Figure 10) live among mosses (David E. Walter, pers. comm. 1 September 2011). Some members of the genus ***Epidamaeus*** (**Damaeidae**; Figure 11) occur among leaf litter and mosses on soil. (Ermilov & Łochyska 2009). **Labidostommatidae** live on and in the soil, as well as in overlying vegetation and litter, including mosses (Krantz & Walter 2009). From this vantage point, they prey on smaller invertebrates (Figure 12). This soil/moss interface provides a moist environment where fungi and other micro-organisms can provide food sources.

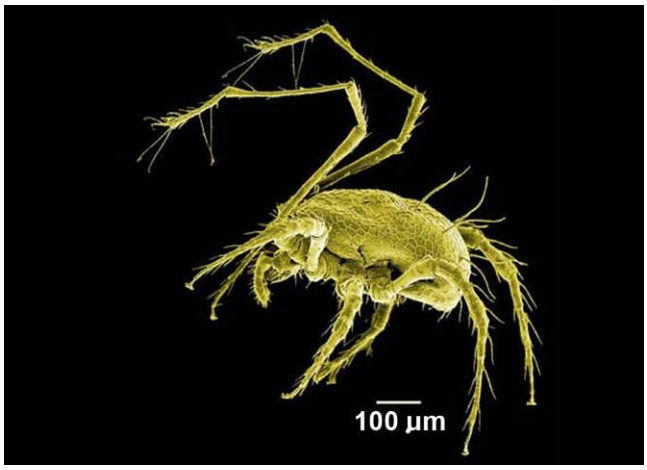

Figure 10. ***Epicrius*** sp., member of a mite genus that can live among forest bryophytes. Photo by David E. Walter, with permission.

Figure 11. ***Epidamaeus*** sp., a forest floor bryophyte dweller, on leaf litter. Photo by Walter Pfliegler, with permission.

Figure 12. ***Labidostomma mamillata*** eating a springtail amid dead moss. Photo by Roy A. Norton, in Smith *et al*. 2011, with permission.

Salmane and Brumelis (2008) demonstrated the importance of the moss layer to the diversity of the predatory mites in the **Gamasina** group (an infraorder within the **Mesostigmata**; Figure 13) in the coniferous forest. In coniferous forests, bryophytes are able to establish on the forest floor because the narrow conifer leaves permit them to gain sufficient light to grow through the litter. In these forests, bryophytes are often the predominant forest floor vegetation and provide a moist haven for invertebrates. And, as seen in the previous sub-chapter, the bryophytes can serve as food.

Feather mosses [***Hylocomium splendens*** (Figure 14), ***Pleurozium schreberi*** (Figure 15), ***Ptilium crista-castrensis*** (Figure 16)], common boreal forest mosses, harbor a diversity of predatory **Gamasina** mites (Figure 13; Salmane & Brumelis 2008). Salmane and Brumelis removed the feather mosses, then compared species richness, **Shannon diversity**, and equitability. In the spring, these all decreased where the moss layer was removed, but not in the autumn. Moss plots housed 31 mote species, plots with mosses turned over housed 24, and removal plots housed only 16 species. The mosses buffer the temperature (Skre & Oechel 1979; Startsev *et al*. 2007), a possible reason for those mites that lived only among the mosses. It is also likely that the **Collembola**, nematodes, and enchytraeids (annelid worms) among the mosses provided food (Karg 1983; Moore *et al*. 1988; Koehler 1999). The **Collembola** move down into the soil to avoid drought stress (Huhta *et al*. 1986; Pflug & Wolters 2001; Juceviča & Melecis 2002), and mites can easily follow them.

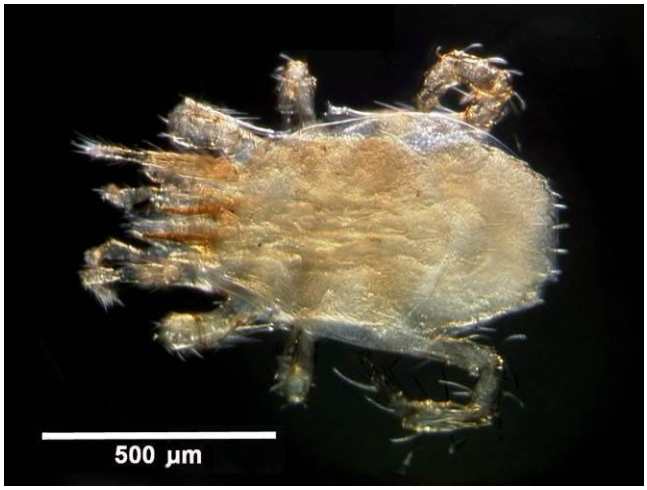

Figure 13. ***Veigaia nemorensis*** (**Veigaiidae**), a **Gamasina** (**Mesostigmata**) mite that depends on mosses for its habitat. Photo by Derek Tan from Diane Srivastava's online Mite Classification Guide at <http://www.zoology.ubc.ca/~srivast/mites/>, with permission.

Although many species of mites occupy both leaf litter and bryophytes on the forest floor, bryophytes can provide unique habitats unlike those of the forest floor leaf litter. Womersley (1961) reported a new species of trachytid mite, ***Acroseius tuberculatus*** (as ***Polyaspinus tuberculatus***; **Ascidae**; see Figure 17; see Bloszyk *et al*. 2005) from Queensland, Australia, noting that it occurred only in the leaf litter and not among the mosses, indicating the uniqueness of the two habitats. David Walter later found another member of the genus in litter (including mosses) in Queensland (pers. comm. 15 September 2011; Figure 17).

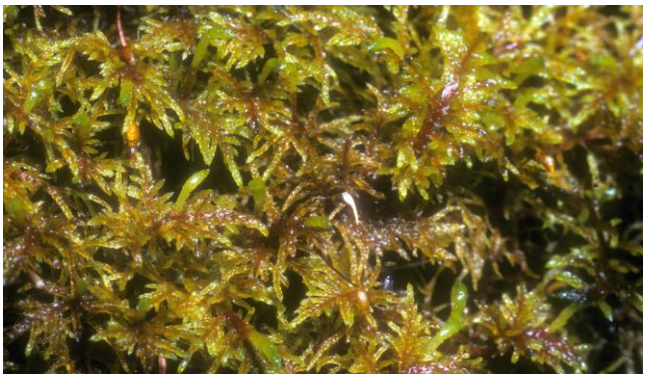

Figure 14. ***Hylocomium splendens***, a feather moss known to harbor a number of predatory **Gamasina** mites. Photo by Janice Glime.

Figure 15. ***Pleurozium schreberi***, a feather moss known to harbor a number of predatory **Gamasina** mites. Photo by Janice Glime.

Figure 16. ***Ptilium crista-castrensis***, a feather moss known to harbor a number of predatory **Gamasina** mites. Photo by Janice Glime.

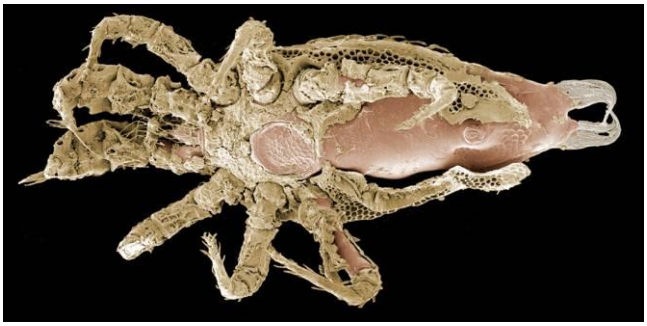

Figure 17. ***Acroseius***, new species from litter (including mosses), from Queensland, Australia. Photo by David E. Walter, with permission.

Arboreal Habitats

Canopy communities of mites are distinct from those of the forest floor (Arroya *et al*. 2010). In an old-growth Sitka spruce (*Picea sitchensis*) forest on Vancouver Island, Canada, Behan-Pelletier and Winchester (1998) found 36 oribatid mite species in the canopy and forest floor. In Ireland, 22 species occupied the Sitka spruce forest in the canopy or moss growing on the tree or on the soil.

The canopy community is more homogeneous than that on the soil surface. Five of these species occurred exclusively in the canopy. Three members of **Zerconidae** lived only in the canopy and in moss mats on tree branches. Among these moss-dwelling bryophytes is ***Trachytes aegrota*** (Figure 18), recorded by Arroya *et al*. (2010) for the first time in Ireland, despite being known since 1841.

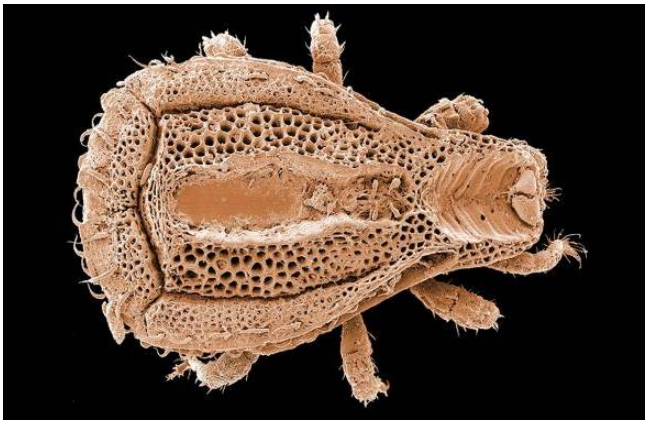

Figure 18. ***Trachytes*** sp., member of an arboreal genus with bryophyte-dwelling members. Photo by David E. Walter, with permission.

Epiphytes

Epiphytic bryophytes serve as habitat for a number of oribatid mites (Travé 1963; Walter & Behan-Pelletier 1999). In arboreal habitats, bryophytes can provide both 3-dimensional structure and a safe haven that protects against desiccation and predation. In these habitats, one can find a variety of arboreal oribatid mites, with differences occurring among habitat types within the forests (Seniczak 1974). Even within the same Sitka spruce (*Picea sitchensis*) forest, those species occurring in canopy moss mats can differ significantly from those located elsewhere in the canopy (Behan-Pelletier & Winchester 1998).

Figure 19. Red mite on moss ***Dicranum montanum*** on bark near tree base. Photo by Michael Lüth, with permission.

André (1984) found that 34% of the arthropod epiphyte dwellers in the Belgian Lorraine were oribatid mites, represented by 19,000 individuals in 36 species. The typical ***Zygoribatula exilis*** (**Oribatulidae**; see Figure 20) association (Pschorn-Walcher & Gunhold 1957; Travé 1963; Lebrun 1971; Gjelstrup 1979) was not present. This mite association is most typical among mosses, liverworts, and foliose lichens in the shade and requires a continuous high humidity (Travé 1963). Thus, it did not find suitable habitat here.

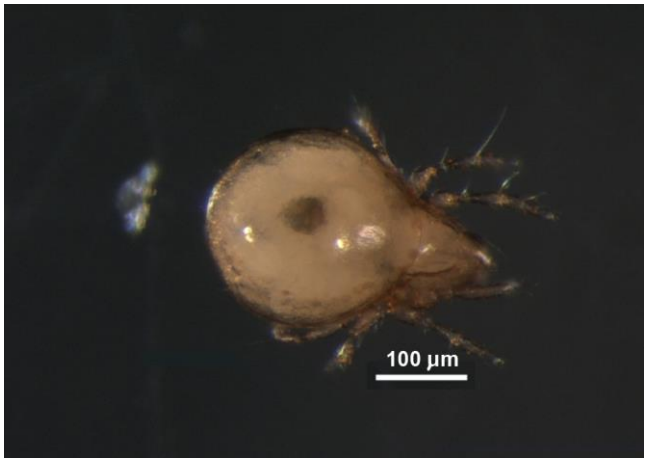

Figure 20. ***Zygoribatula*** *bulanovae*. ***Zygoribatula exilis*** is a typical moss dweller among mosses, liverworts, and lichens in shaded, moist areas. Photo from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

The activities of mites on the bole of forest trees (which are often covered by bryophytes) raised the question of the role of the tree bore and its bark. As asked by Proctor *et al.* (2002), "Are tree trunks habitats or highways?" In their Australian study of oribatid mites on the hoop pine (*Araucaria cunninghamii*), they found that indeed the bark of the bole harbors a unique community compared to the forest floor. Using insecticides to immobilize the communities, they collected from leaf litter and tree bole. Not only did they find unique communities, but they were nearly 100% distinct! Only ***Pseudotocepheus*** sp. (**Tetracondylidae**) occurred in both litter and bark habitats. The richness of litter was greater,

but on the bark the oribatid mites comprised the greater percentage of total mites. The researchers were surprised that, contrary to their expectations, the more consistent physical nature of bark as a substrate did not result in greater similarity of oribatid faunas among trunks compared to litter. Rather, greater similarity occurred among litter faunas. They suggested that tree trunks act as islands and that faunal differences represent dispersal challenges that result from traversing across different habitats to reach a new "island." The conclusion: tree boles are not highways from the ground layer to the canopy, at least in this Australian system.

Trapping experiments by Behan-Pelletier and Winchester (1998) in the Sitka spruce canopy on Vancouver Island, Canada, support the hypothesis that dispersal of mites among canopy habitats is due to random movement. Nevertheless, single unidentified species in the genera ***Eporibatula*** (**Oribatulidae**), ***Sphaerozetes*** (**Ceratozetidae**), and ***Dendrozetes*** (**Ceratoppiidae**; Figure 21) had a frequency greater than 50% in canopy traps, suggesting that random dispersal is a successful means for these taxa. One might conclude that the same random dispersal is likely for the bole, but the boles of the individual trees are not touching, whereas the canopies are. Furthermore, bryophytes often provide the dispersal unit, and they are more likely to become attached on a horizontal surface than on a vertical one.

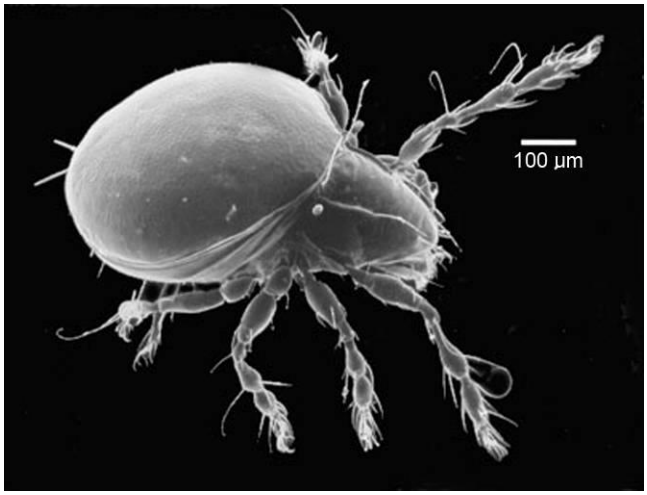

Figure 21. SEM of ***Dendrozetes*** sp., member of a genus known from Sitka spruce canopy bryophytes. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

Peck and Moldenke (2010) became concerned with the role of moss harvesting on the movement of invertebrate communities, including many mites, to new locations. They used Berlese funnels to assess the fauna of bryophyte mats on two shrub species [vine maple (*Acer circinatum*; Figure 22) and huckleberry (*Vaccinium parvifolium*; Figure 23)] in the Pacific Northwest, USA. This method revealed 205 morphospecies of arthropods, and it is likely that there was a portion of the fauna that did not respond to the Berlese funnel arrangement, hence were not counted. The communities between the tree species did not differ, but there seemed to be differences in communities that related to the location of the moss mats.

Figure 22. ***Acer circinatum***, understory home for moss-dwelling mites. Photo from <www.nwplants.com> through Creative Commons.

Figure 23. ***Vaccinium parvifolium*** with fruit, home for moss-dwelling mites. Photo by Walter Siegmund, through Creative Commons.

Lobule Mites

Leafy liverworts are common on the boles and canopy branches of forest trees. Among these, ***Radula*** (Figure 24-Figure 25), ***Porella*** (Figure 26-Figure 27), ***Frullania*** (Figure 28-Figure 29), and others have lobes. In ***Frullania***, these lobes are modified into **lobules** (Figure 28-Figure 29) that trap and hold water through capillarity.

Figure 24. ***Radula buccinifera*** on tree, showing growth habit. Photo by David Tng <www.davidtng.com>, with permission.

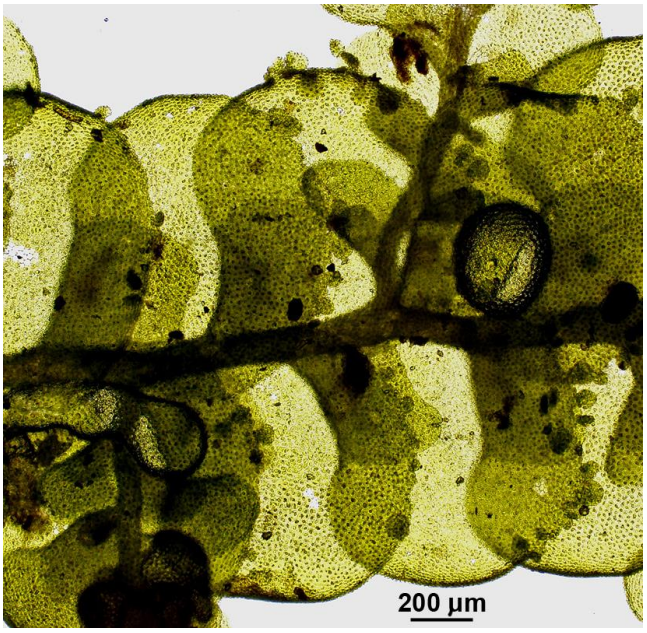

Figure 25. ***Radula complanata*** ventral view showing folded lobes where mites hide. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 26. ***Porella platyphylla*** showing growth habit on tree. Photo by Tigerente, through Creative Commons.

Figure 27. ***Radula complanata*** ventral side showing lobes where mites may hide. Photo by Hermann Schachner, through Creative Commons.

Figure 28. Leafy liverwort ***Frullania rostrata*** ventral view showing dark brown lobules where some mites are able to live in members of the genus. Photo by Matt von Konrat, with permission.

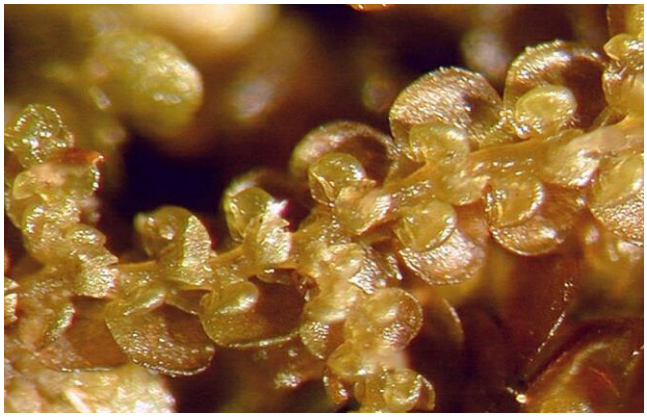

Figure 29. ***Frullania dilatata***, showing the arrangement of leaves, underleaves, and **lobules** that provide a nearly continuous route of moisture to help mites move about. Photo by Michael Lüth, with permission.

Andi Cairns, Tamás Pócs, Saci Pócs, Chris Cargill, and Elizabeth Brown discovered tiny oribatid mites moving about in the lobules of ***Frullania ferdinandi-muelleri*** (Figure 30-Figure 31) in the Australian Wet Tropics (Andi Cairns, pers. comm.). Andi later found similar mites in other specimens of ***F. ferdinandi-muelleri*** they had collected. Matt Colloff determined these to belong to the genus ***Birobates*** (Figure 31-Figure 33), the first record for the genus in Australia. Because of its association with liverwort lobules, Colloff and Cairns (2011) named this mite ***Birobates hepaticolus*** (**Oripodidae**; Figure 31-Figure 33). The lobules of the ***Frullania*** (Figure 31-Figure 32) buffer the mite against moisture loss. The lobules have an opening, giving mites free access, and generally are close to each other and the underleaves, providing a nearly continuous moist enironment. Hence, the liverwort provides a moist habitat that permits these mites to live in otherwise dry habitats. Colloff and Cairns (2011) point out that even if the mites die during periods of liverwort desiccation, the population is likely to survive through its eggs.

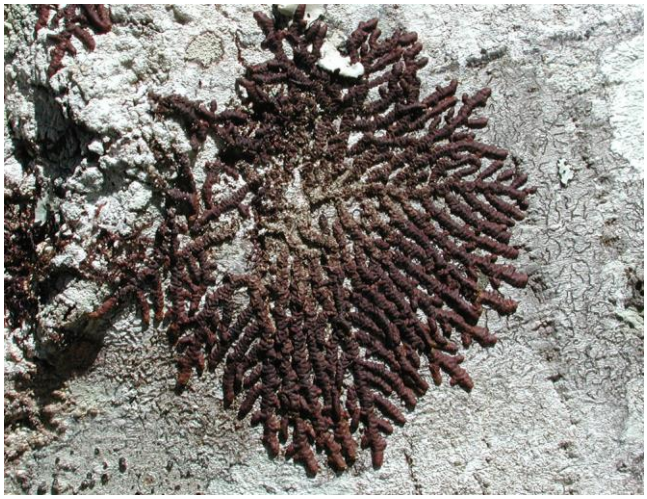

Figure 30. ***Frullania ferdinandi-muelleri*** in Ingham, North Queensland, Australia, a leafy liverwort that serves as home to the newly described ***Birobates hepaticolus***. Photo courtesy of Andi Cairns.

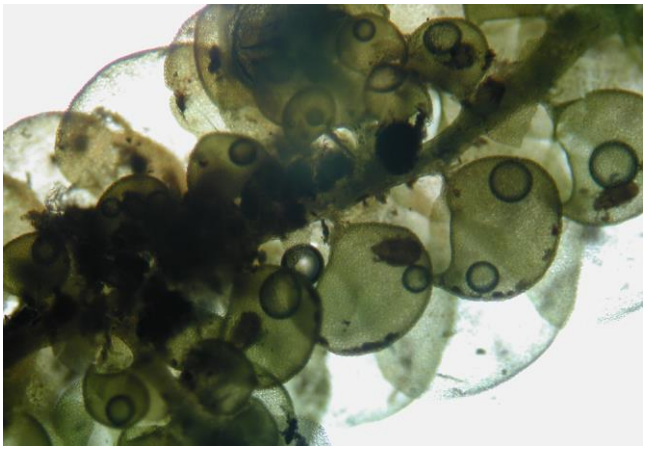

Figure 31. ***Frullania ferdinandi-muelleri***. Note the many ***Birobates hepaticolus*** in lobules, but frequently only one per lobule. Photo courtesy of Tamás Pócs.

Figure 32. ***Birobates hepaticolus*** mite in the lobule of the liverwort ***Frullania ferdinandi-muelleri***. Photo courtesy of Tamás Pócs.

Figure 33. ***Birobates hepaticolus*** taken from a lobule of the leafy liverworts ***Frullania ferdinandi-muelleri*****.** Photo courtesy of Andi Cairns.

Colloff and Cairns (2011) found that lobules that had mites generally had one to four individuals. The frequency of occupied lobules ranged from contiguous occupation to one in thirty. Every one of the many locality samples had mites in this species of liverwort, although abundance varied widely. It is interesting that only two nymphs were found, whereas there were well over 100 adults.

Furthermore, the liverwort apparently serves as a food source (Colloff & Cairns 2011). Presence of fecal pellets indicated that the mites had been in the lobules for an extended period of time. Consumption of liverworts by mites was not known previously. ***Frullania*** (Figure 28-

Error! Reference source not found.) is known to have volatile compounds that would discourage eating (Asakawa *et al.* 2003). Dense material in the pellets had the same spectral qualities as the liverworts and appeared to be cells of the same (Colloff & Cairns 2011). In addition to being food itself, the lobules house bacteria, protozoa, rotifers and other small invertebrates that can serve as food.

Figure 34. ***Frullania ferdinandi-muelleri*** grazed, probably by ***Birobates hepaticolus***. Photo courtesy of Andi Cairns.

Semiaquatic Habitats

Terrestrial members of **Parasitengonina** (parasitic mites) may be found among mosses in semiaquatic niches. In particular, members of **Johnstonianidae** all can occur in mosses (Wohltmann 2004). Among these, Wohltmann and co-workers have specifically found ***Centrotrombidium*** (Figure 35; Wohltmann & Wendt 1996), ***Diplothrombium*** spp. (Wohltmann 2004), and ***Johnstoniana*** spp. (Figure 36). Sevsay and Özkan (2005) reported the new species ***Johnstoniana hakani*** from mosses in Turkey.

Figure 35. ***Centrotrombidium schneideri***, a mite whose larva is a parasite on the biting midge ***Culicoides***. Photo by Andreas Wohltmann, with permission.

Centrotrombidium schneideri (**Johnstonianidae**; Figure 35) larvae recognize the pupae of the biting midge ***Culicoides*** sp. (Figure 37) and attach to it to await the emergence of the adult (Wohltmann & Wendt 1996). By attaching to this immobile stage, the larva is guaranteed that its host won't move to an unfavorable location. As an adult, the ***Culicoides*** remains in a moist environment that provides the humidity needs of the mite. As the host emerges, the larvae become parasitic on the adult stage.

Figure 36. ***Johnstoniana*** sp. Photo by Walter Pfliegler, with permission.

Figure 37. ***Culicoides*** (biting midges) adults, host (as a larva) of the mite ***Centrotrombidium schneideri***. Photo by A. J. Cann through Creative Commons.

All developmental stages of these **Johnstonianidae** genera desiccate easily when the air is less than saturated. Mosses, as well as litter, provide the necessary humidity for mating, oviposition, and resting. Other members of **Trombidiae** (**Trombiculidae**, **Trombidiidae**, **Microtrombidiidae**) can burrow into the soil as **deutonymphs** and adults – the mobile stages, but the **Johnstonianidae** are unable to do that. Active stages of all of these **Trombidiae** search among the mosses as well as other locations for prey and for hosts for the next life stage.

Unlike the **Johnstonianidae**, which are confined to amphibious habitats, other mites can occur in such habitats as well as other locations (Andreas Wohltmann, pers. comm. 17 September 2011). These mites that sometimes occur in semiaquatic habitats can be frequent in mosses:

Erythraiae: ***Calyptostoma*** (Figure 38) in the **Calyptostomatidae**, ***Abrolophus*** (Figure 39), ***Leptus*** (Figure 40-Figure 41), ***Erythraeus*** (Figure 42), and ***Charletonia*** (Figure 43) in the **Erythraeidae**; **Trombidiae**: ***Trombidium*** (Figure 44) and ***Allothrombium*** (Figure 45) in the **Trombidiidae**, ***Podothrombium*** (Figure 46-Figure 47) in the **Podothrombiidae**, ***Microtrombidium*** (Figure 48), ***Atractothrombium***, ***Camerotrombidium*** (Figure 49), ***Enemothrombium*** (Figure 50), ***Valgothrombium***, ***Echinothrombium rhodinum***, and ***Platytrombidium*** (Figure 51) in the **Microtrombidiidae**.

Figure 38. ***Calyptostoma velutinus*** adult, a free-living stage that can occur among mosses in semi-aquatic habitats. Photo by Andreas Wohltmann, with permission.

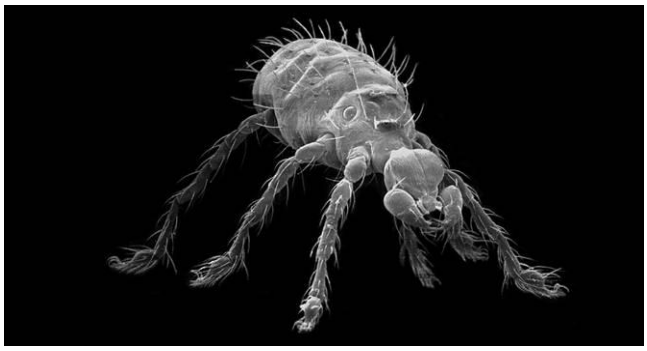

Figure 39. ***Abrolophus*** larva, a mite that can occur frequently among mosses when it ventures into semi-aquatic habitats. Photo by Andreas Wohltmann, with permission.

Figure 40. ***Leptus trimaculatus*** adult. Note the three spots that give it its name. This mite can occur in wet habitats where it becomes frequent among mosses. Photo by Andreas Wohltmann, with permission.

Figure 41. ***Leptus beroni***, parasitic larva on the harvestman ***Mitopus*** sp. Both species can occur among bryophytes. Photo by Andreas Wohltmann, with permission.

Figure 42. ***Erythraeus*** sp. Some members of this genus are frequent among mosses in semiaquatic habitats. Photo by Tom Murray, through Creative Commons.

Figure 43. ***Charletonia*** sp. adult feeding on fly (Diptera) eggs. This genus sometimes occurs in semi-aquatic habitats where it can be frequent among bryophytes. Photo by Andreas Wohltmann, with permission.

Figure 44. ***Trombidium holosericeum***, velvet mite on soil, where its bright red color makes it easy to see. Photo by Ruth Ahlburg, with permission.

Figure 45. ***Allothrombium*** sp., a mite shown here on grass, but that can also inhabit bryophytes. Photo by Sankax on Flickr through Creative Commons.

Figure 46. ***Podothrombium*** sp., a mite of amphibious and other habitats and that can be frequent among bryophytes. Photo by Walter Pfliegler, with permission.

Figure 47. Female ***Podothrombium filipes*** with eggs visible in her body. However, the eggs in the upper part of the picture are not hers, but eggs of a centipede (***Geophilomorpha***), a source of food for this mite. Photo by Andreas Wohltmann, with permission.

Figure 48. ***Microtrombidium pusillum***, a species that maintains its moisture among mosses. Photo by Walter Pfleigler, with permission.

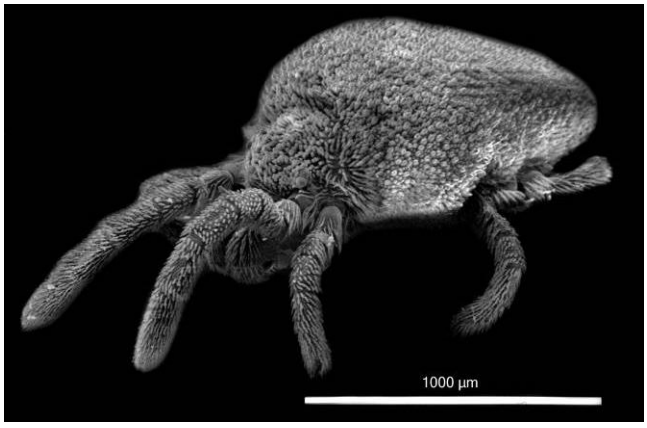

Figure 49. ***Camerotrombidium pexatum*** adult, a free-living stage that can occur among bryophytes in a variety of habitats. Photo by Andreas Wohltmann, with permission.

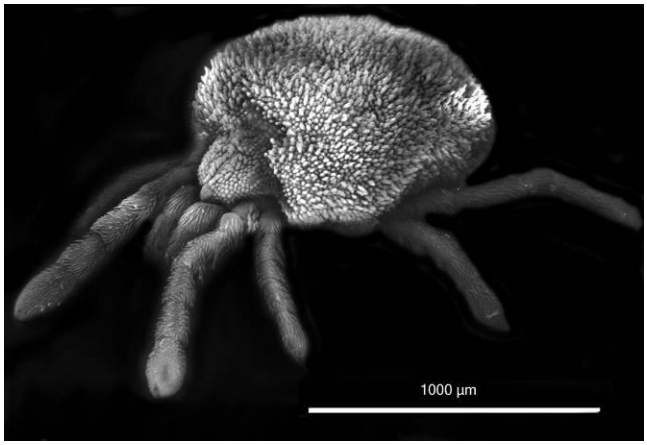

Figure 50. ***Enemothrombium bifoliosum*** adult, a free-living stage that can occur among bryophytes in a variety of habitats. Photo by Andreas Wohltmann, with permission.

Figure 51. ***Platytrombidium fasciatum*** adult, a free-living stage that occurs among bryophytes in a variety of habitats, including semi-aquatic ones. Photo by Andreas Wohltmann, with permission.

Hosts of parasitic stages of these mites are typically arthropods, and new ones are still being discovered. Stur *et al*. (2005) suggested that the moss-dwelling habit of the midge ***Chaetocladius perennis*** (Figure 52) may be the reason for absence of mites in their collections. Aquatic mite larvae typically find hosts in the water, not among mosses. This same absence of mites held true for other moss-dwelling midges in these Luxembourg springs. On the other hand, moss dwellers like ***Tvetenia calvescens*** (**Chironomidae**; Figure 53) and ***T. bavarica*** (Figure 54-Figure 55) were parasitized in the two springs. Their mossy habitat meant they rarely encountered mites. But Stur and coworkers offered three additional explanations: 1) no water mites parasitize these potential hosts; 2) those water mites that could use these hosts are absent in these springs; 3) the midges are efficient in avoiding colonization by mites.

Figure 52. ***Chaetocladius perennis*** adult. Members of this species seem able to avoid being parasitized by aquatic mites by living among mosses. Photo by James K. Lindsey, with permission.

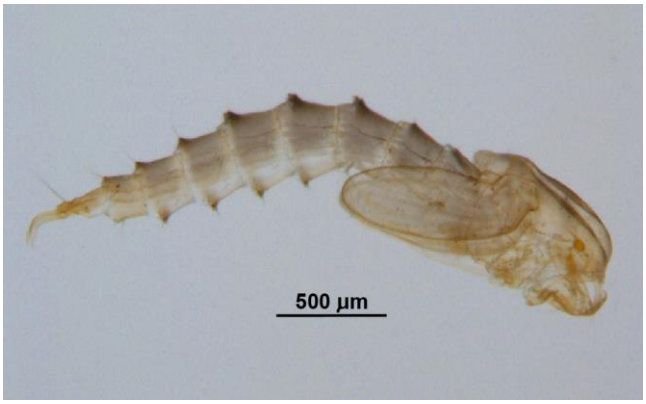

Figure 53. ***Tvetenia calvescens*** pupa, host for parasitic mites. Photo by P. Kranzfelder, NTNU University Museum, through Creative Commons.

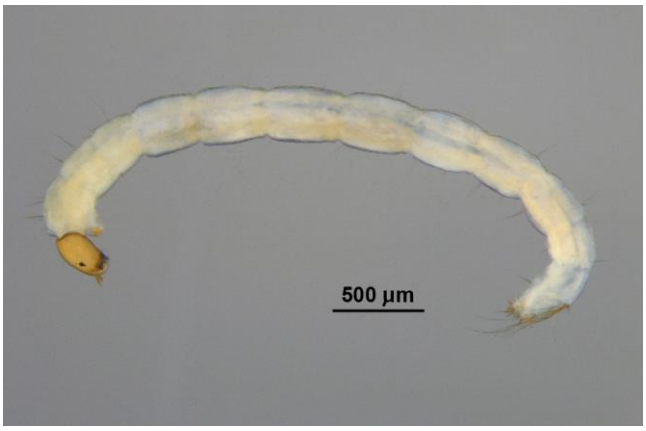

Figure 54. ***Tvetenia bavarica*** (**Chironomidae**) larva, host for parasitic mites. Photo by Aina Maerk Aspaas, NTNU University Museum, through Creative Commons.

Figure 55. ***Tvetenia bavarica*** pupa, host for parasitic mites. Sondre Dahle, NTNU University Museum, through Creative Commons.

Calyptostoma velutinus (**Calyptostomatidae**; Figure 38) is a mite that lives on the cranefly ***Tipula*** (Andreas Wohltmann, pers. comm. 17 September 2011) and probably others. The larvae live on the pupae of ***Tipula*** (Figure 56), a genus in which the pupal stage often occurs among mosses. This species of mite can also be found on the thorax of the cranefly ***Limonia*** (Figure 57). Similarly, ***Johnstoniana eximia*** (Figure 57) lives on the abdomen of ***Limonia***. Both of these mites take advantage of the aquatic stages of craneflies for their early development, then emerge when the adult craneflies emerge (Figure 58).

Figure 56. ***Tipula*** sp. pupa, the stage in the cranefly life cycle that is sought by larvae of the mite ***Calyptostoma velutinus***. Several members of ***Tipula*** pupate among mosses. Photo by Ted Kropiewnicki, through Creative Commons.

Figure 57. Mites ***Calyptostoma velutinus*** on the thorax and ***Johnstoniana eximia*** on the abdomen of ***Limonia*** (cranefly). This genus of cranefly is known to pupate among mosses, permitting the mites to develop there and emerge with the adult craneflies. Photo by Andreas Wohltmann, with permission.

Figure 58. Larva of mite ***Calyptostoma velutinus*** on thorax of the cranefly ***Tipula***. ***Tipula*** is a common inhabitant of mosses in both its larval and pupal stages. Hence, it is available to moss-dwelling mites as it emerges into the terrestrial habitat. Photo by Andreas Wohltmann, with permission.

Even in the juvenile stage, mites can be subjected to decreased water availability. Although eggs and protonymphs of members of the **Trombidioidea** can take in water vapor from the atmosphere, Wohltmann (1998) demonstrated that this does not occur in **Erythroidea**, including ***Calyptostoma velutinus*** (**Calyptostomatidae**; Figure 38). Rather, the **Parasitengona** (including ***Calyptostoma velutinus***) may have had this character early in their evolution, but have subsequently lost it. Nevertheless, ***Calyptostoma velutinus*** and others in the **Erythraeoidea** have a higher drought resistance in both instars than do the **Trombidioidea**. Although water uptake seems to be absent in eggs and protonymphs, water uptake prior to the protonymph stage has been observed in post-parasitic larvae of **Trombidioidea** as well as in ***C. velutinus***.

Wohltmann (1998) suggests that instead of preventing desiccation by this mechanism of water uptake, drought protection is achieved by a greater sealing of body openings with lipids, as well as reduction in body openings. Together, these result in reduced water loss. This apparently facilitates the consequent increase in body fresh mass by 50% before the protonymph stage begins by increasing the size of the cuticle. For ***Calyptostoma velutinus*** (**Calyptostomatidae**; Figure 38), this results in "a considerable increase in fresh mass at the end of the post-parasitic larval phase." This may be important in explaining the longer (several days long) post-parasitic stage in this species.

Larval mortality is a high selection pressure among the **Parasitengona**. Two evolutionary traits – larger eggs or more eggs – can help to give the species an advantage against this selection pressure. In the case of **Parasitengona**, evolutionary constraints apparently have kept the egg numbers low (100-300) (Wohltmann 1999). These constraints include difficulty of finding a suitable host in time and restriction to only three growth periods during development that limits adult size. However, some

of the terrestrial and aquatic subgroups have indeed adapted by producing 1000 or more eggs per female.

But reproductive problems do not stop there. Finding a mate can be problematic due to the small numbers of individuals in a single bryophyte clump. Witte (1991) examines the indirect sperm transfer in prostigmatic mites. Important considerations include adaptation of **spermatophores** (protein capsule containing mass of **spermatozoa** (motile sperm, transferred during mating in several invertebrate groups) to low or changing humidities. Like the eggs of some mites, the spermatophores may also exhibit passive uptake of atmospheric water vapor. A second consideration is osmotic protection of sperm cells. Other important factors include spermatophore viability, types of signals used to guide individuals to spermatophores or to a partner, and deposition of spermatophores in absence of a female.

Aquatic Habitats

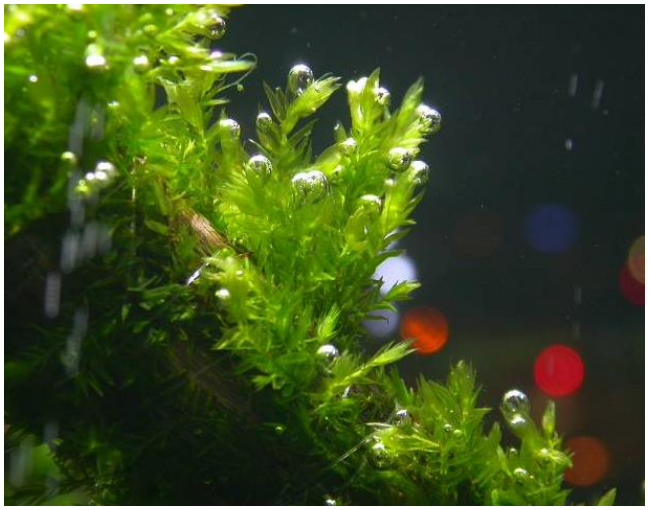

Figure 59. Pearling (air bubbles) on the brook moss ***Fontinalis*** sp. Photo by Loh Kwek Leong, with permission.

Aquatic mosses have their own mite fauna, the most common being **Hydrachnidia** (Vlčková 2001/2002) [=**Hydracarina** (Clifford 2012)]. These don't look like aquatic organisms with their chubby morphology, suggesting they often need plants for clinging to avoid being swept away. Furthermore, special adaptations may be needed to permit life in this low-oxygen environment. Smith *et al*. (2011) described the mite ***Tegeocranellus muscorum*** (**Tegeocranellidae**; Figure 60) in eastern North America as having special structures above the middle two pairs of legs for holding an air bubble when submerging (Figure 61). These bubbles, formed in a condition known as **pearling** (Figure 59) when they come from underwater plants (Benito Tan, pers. comm. 6 June 2011), work like a diving bell into which the mite can exchange CO_2 for O_2 gases. When the bubble gets too small, the mite must return to the surface or the plant for another bubble. Oxygen bubbles produced during plant photosynthesis can provide this source of oxygen, and submersed mosses are often so covered with bubbles that their own structure cannot be discerned (Figure 62).

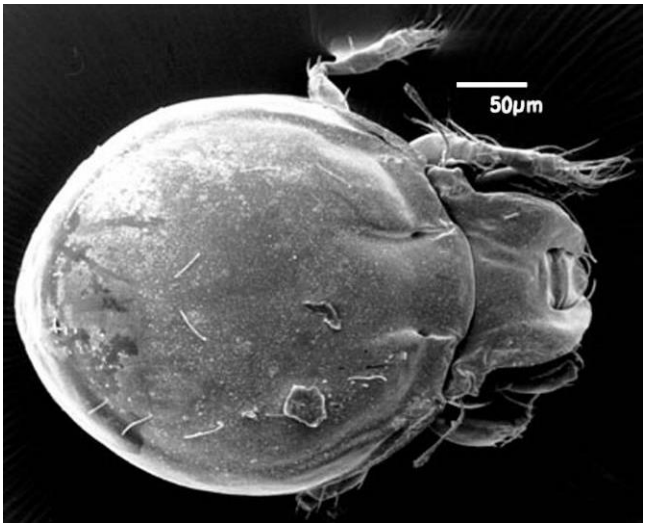

Figure 60. SEM of ***Tegeocranellus muscorum***, an aquatic bryophyte-dwelling mite. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

Figure 61. SEM of ventral surface of aquatic bryophyte-dwelling ***Tegeocranellus muscorum***, where air bubble is held for gas exchange. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

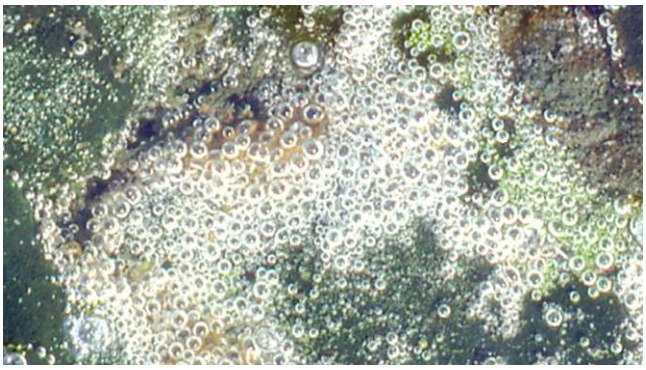

Figure 62. **Pearling** on submerged ***Ceratodon purpureus*** (Figure 141) from Casey Station, Antarctica, demonstrating complete coverage of the moss. Photo courtesy of Rod Seppelt.

Suren (1991) found that **Hydracarina** were poor indicators of bryophytes compared to gravel in two New Zealand alpine streams, but that they were moderate indicators of shaded conditions. They represented 3.3% of the fauna among gravels in unshaded streams, but only 1.1% among bryophytes there. In the shaded stream, they represented 11.4% of the gravel fauna, but only 5.9% among the bryophytes.

Hynes (1961) found somewhat higher percentages of **Hydracarina** (Figure 63) on bryophytes than on artificial silk mosses in a Welsh mountain stream. This might be the result of better places for these clumsy balls with legs to escape the current among the moss branches, but it could also be related to food availability.

Compared to other arthropods, the **Hydracarina** (Figure 63) on bryophytes are not very abundant. Stern and Stern (1969) found only 1-2 per 0.1 m^2 of moss/algae in a springbrook in Tennessee, USA. Similarly, Frost (1942) found only ca 1% of the fauna to be **Hydracarina** in her study of moss inhabitants in the River Liffey, Ireland. Nevertheless, these averaged 147 individuals per 200 g wet weight of bryophyte sample in the acid stream and 114 in the alkaline stream and comprised 29 species.

Figure 63. **Hydracarina**, a group of bryophytes that occasionally live among aquatic bryophytes. Photo by BioPix, through Creative Commons.

In a "rip-rapped" channel, Linhart *et al*. (2002) found a strong correlation between the size fractions and quantity of organic matter and mineral matter and the number of hydrachnid mites living within the sediments collected by the moss ***Fontinalis*** sp. (Figure 64). They contended that ***Fontinalis*** increased the biodiversity because of the number of organisms supported by that habitat. Needham and Christenson had already noted this phenomenon in 1927.

Cowie and Winterbourn (1979) compared the fauna of three mosses [***Achrophyllum quadrifarium*** (=***Pterygophyllum quadrifarium***; Figure 67), ***Fissidens rigidulus*** (Figure 65), ***Cratoneuropsis relaxa***] in the Southern Alps in New Zealand. They found the mites ***Notopanisus*** sp. (**Hydryphantidae**) on all three mosses and ***Platymamersopsis*** sp. (**Anisitsiellidae**) on ***Achrophyllum quadrifarium*** (=***Pterygophyllum quadrifarium***; Figure 67) and ***Cratoneuropsis relaxa***. Nevertheless, knowledge of the bryophyte fauna is poor (Suren 1992). Suren found four new species of mites in his study of bryophyte communities in alpine streams of New Zealand.

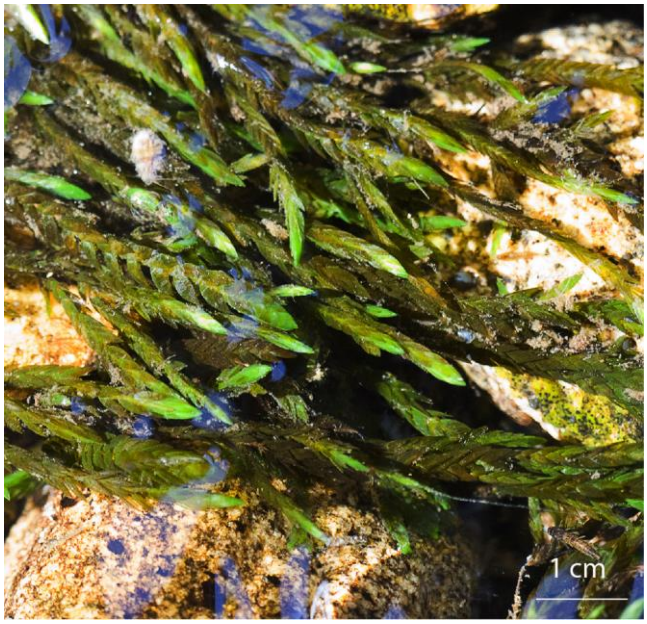

Figure 64. ***Fontinalis antipyretica***, home for hydrachnid mites. Photo by Projecto Musgo through Creative Commons.

Figure 65. ***Fissidens rigidulus***, home for mites in New Zealand. Photo from Museum of New Zealand, Te Papa Tongerewa, through Creative Commons.

Andreas Wohltmann (pers. comm. 17 September 2011) has found that in temporary pools, ***Sphagnum*** (Figure 66), and probably other mosses, can house species of **Hydryphantoidea** [***Euthyas*** (Figure 68), ***Parathyas*** (syn. ***Thyas***; Figure 69), ***Hydryphantes*** (Figure 70)]. During their terrestrial phase, these mites sit in the water film around the mosses. Unlike other water mites, **deutonymphs** and **adults** of this group can crawl in these terrestrial conditions and thus can move to more humid areas as the moisture conditions change. On the other hand, the superfamilies **Stygothrombioidea**, **Hydrovolzioidea**, **Hydryphantoidea**, and **Eylaoidea** all have terrestrial larvae, whereas only the **Hydryphantoidea** are able to crawl as deutonymphs and adults in that terrestrial environment. The eggs of all four of these superfamilies are deposited in the water, but larvae climb/crawl to the water surface and seek a host at the surface or in the surrounding terrestrial area. In at least some locations, the terrestrial surroundings as they emerge from the water are likely to be covered with bryophytes that help to conserve water.

Figure 66. ***Sphagnum*** pools, home for a variety of mites. Photo by Boréal, through Creative Commons.

Figure 67. ***Achrophyllum quadrifarium***, a bryophyte habitat for mites in streams in the Southern Alps in New Zealand. Photo by Jan-Peter Frahm, with permission.

Figure 68. ***Euthyas*** sp. This is a preserved specimen that is normally red when alive. Photo CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

Figure 69. ***Parathyas barbigera*** adult, a phase that sits in the water film of mosses near temporary pools. Photo by Andreas Wohltmann, with permission.

Figure 70. ***Hydryphantes*** sp., lacking normal color due to preservation. Photo courtesy of BOLD Systems Biodiversity Institute of Ontario.

On the other hand, the larvae of **Hydrachnoidea**, **Sperchontoidea**, **Arrenuroidea**, **Lebertioidea**, and **Hygrobatoidea** lack the musculature needed for crawling and must seek their larval hosts in the water column. Likewise, the adults of other water mite genera [*e.g.* ***Arrenurus*** (**Arrenuridae**; Figure 83-Figure 86), ***Limnochares*** (**Limnocharidae**; Figure 71), ***Piona*** (**Pionidae**; Figure 72), ***Tiphys*** (**Pionidae**; Figure 73)] lack this ability to crawl under terrestrial conditions. Most of them find hosts among the **Diptera**, especially the **Chironomidae** (midges; Figure 54), which are often abundant among aquatic mosses. The mite larvae locate larvae or pupae of these potential hosts and aggregate there, awaiting the emergence of the adult, which they will

parasitize. This method of finding a host (**preparasitic attendance**) is absent among those mites having terrestrial larvae and even among most of the terrestrial **Parasitengonina**.

Figure 71. ***Limnochares appalachiana***, decolored due to preservation. The sclerotized plates on the back of this eastern North American species provide additional structure for muscle attachment to support its crawling ability (Smith & Cook 2005). Photo courtesy of BOLD Systems Biodiversity Institute of Ontario.

Figure 72. ***Piona coccinea***, an aquatic moss that is unable to crawl on land. Photo by Roger S. Key, with permission.

Figure 73. ***Tiphys*** *cf.* ***ornatus*** swimming among moss leaves. Photo by Gerard Visser <www.microcosmos.nl>.

Larvae of ***Panisellus thienemanni*** (**Hydryphantoidea**; Figure 74) parasitize the springtail ***Arthropleona*** (**Collembola**; Figure 74) in the spring. Andreas Wohltmann (pers. comm. 17 September 2011) has found these mites exclusively in wet mosses of amphibious biotopes. Larvae are also known to parasitize both young and adults of the springtails ***Pogonognathellus flavescens*** (Figure 75) and ***Tomocerus minor*** (Figure 76) (Boehle 1996).

Figure 74. ***Panisellus thienemanni*** larva on the springtail ***Arthropleona*** sp. (Collembola). Photo by Andreas Wohltmann, with permission.

Figure 75. ***Pogonognathellus flavescens***, a species whose larvae parasitize springtails. Photo by Ab H Baas, with permission.

Figure 76. ***Tomocerus minor***, a species whose larvae parasitize springtails. Photo by Andy Murray, through Creative Commons.

Some species of **Eylaoidea** [*e.g.* ***Eylais*** (**Eylaidae**; Figure 77), ***Piersigia*** (**Piersigiidae**; Figure 78), but not ***Limnochares*** (**Limnocharidae**; Figure 81-Figure 82)], and of the so-called 'higher water mites' such as ***Tiphys*** (**Pionidae**; Figure 73) and some ***Arrenurus*** (**Arrenuridae**; Figure 83-Figure 86) and ***Piona*** (**Pionidae**; Figure 72) species inhabit temporary waters where they are likely to interact with bryophytes (Andreas Wohltmann, pers. comm. 17 September 2011). The larvae of the genus ***Eylais*** commonly parasitize **Coleoptera** (beetles), but Smith (1986) found six species that parasitize water boatmen (**Heteroptera**: **Corixidae**). This is a genus of large species, typically 5-6 mm (Halbert 1903). ***Eylais hamata*** (see also Figure 77) is heavily endowed with carotenoid pigments that can protect it from UV light and make it less conspicuous in its habitat (Czeczuga & Czerpak 1968). For most of these, data are needed to support just how the bryophytes are used.

Figure 77. ***Eylais discreta***, an inhabitant of temporary ponds and pools where bryophytes most likely help them to maintain moisture as water levels decrease. Note the deep golden color due to carotenoid pigments. Photo by Andreas Wohltmann, with permission.

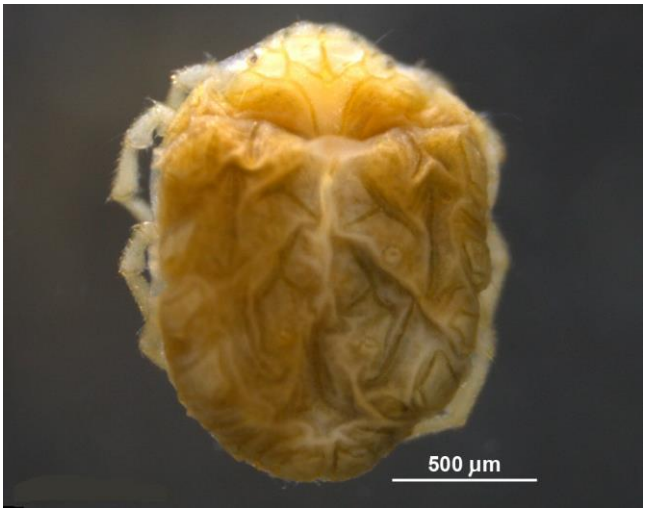

Figure 78. ***Piersigia***, preserved – a genus that inhabits temporary waters where bryophytes occur. Photo by Centre for Biodiversity Genomics, through Creative Commons.

In the genus ***Eylais*** (**Eylaidae**; Figure 79), as many as twenty species may occur in the same area in central New York, USA, *i.e.*, they are **sympatric** (Lanciani 1970). Their larvae are parasitic on **Heteroptera** (true bugs) and **Coleoptera** (beetles) in shallow ponds. They venture to the surface of the water as larvae and await the host when it goes to the surface to renew its oxygen supply. At that time they are able to hitch a ride and attach to the host. According to the Gaussian principle, such species overlap of closely related mites should not occur unless they use their common resources differently. In this case, they partition the resources. Some separation occurs by having different host species, but for those that occupy the same host, separation can occur by season, location on the host, or **biotope** within the habitat. Once attached to the host, they begin feeding and become immobile (Lanciani 1971). Those that have the largest space available grow the most, and larger species tend to occupy larger hosts.

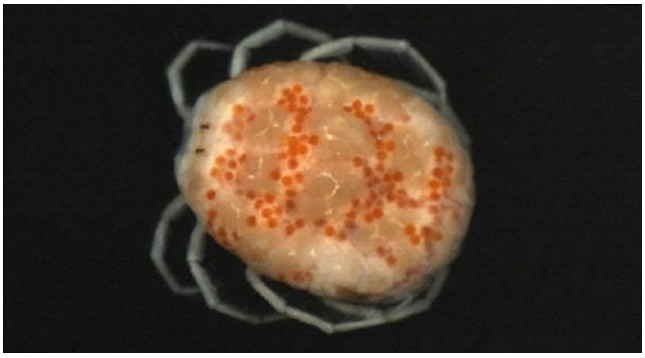

Figure 79. ***Eylais*** sp., member of a genus with moss-dwelling species. This decolorized preserved specimen reveals the red spots that are most likely internal eggs. Photo courtesy of BOLD Systems, Biodiversity Institute of Ontario.

In eastern Canada, there are at least ten species of the genus ***Tiphys*** (**Pionidae**; Figure 73) (Smith 1976, 1987). ***Tiphys diversus*** (**Pionidae**) lives in stream pools and lakes in the southeastern part of the country (Wiggins *et al.* 1980). Eight of the species live in vernal pools. These ten species of mites survive the drying of the temporary pools as

deutonymphs (non-feeding stage that moults into adult), embedding their mouthparts in the leaf axils of mosses. Here they remain at rest until the following spring when the pool again has water.

Moss crawling seems to be common for moss-inhabiting mites, perhaps as a means to maintain moisture. ***Chelomideopsis besselingi*** (**Athienemanniidae**; Figure 80) is one northeastern North American mite that is common crawling in moss mats and in detritus in springs in the mixed wood plains (Smith 1991, 1992). In ***Sphagnum*** mats of bog pools (Figure 66), one can find the crawling species ***Limnochares aquatica*** (**Limnocharidae**; Figure 81; Smith in Smith *et al*. 2011), whose larvae may be attached to the bodies of other arthropods (Figure 82).

The mite ***Trichothyas muscicola*** (**Hydryphantidae**) in the eastern USA lives in mats of mosses and algae kept moist by seepage areas and splash (Smith 1991). Its northern limit is the Niagara Gorge of the Lake Erie Lowland Ecoregion.

Another Canadian species is ***Arrenurus dinotoformis*** (**Arrenuridae**; see Figure 83-Figure 86), a taxon known exclusively from moss mats at margins of boggy pools where the mites are in and out of the water (Smith in Smith *et al*. 2011). *Arrenurus siegasianus*, a predaceous species (Smith *et al*. 2004) with a boreal distribution, is common in sluggish streams from Newfoundland to Alberta, thus occupying a different niche.

Figure 80. ***Chelomideopsis besselingi***, a dweller of moss mats in springs. Photo by Ian M. Smith, Evert E. Lindquist, and Valerie Behan-Pelletier, with permission.

Figure 81. ***Limnochares aquatica***, a mite that lives in moss mats of ***Sphagnum*** pools, shown here in front view displaying two red eyes. Photo by Andreas Wohltmann.

Figure 82. ***Limnochares aquatica*** **larvae** attached to the legs of a water strider (Heteroptera). Adults can live among mosses in bog pools. Photo by Walter Pfliegler, with permission.

Figure 83. ***Arrenurus*** sp.; some species of this genus live exclusively among ***Sphagnum***. Photo by Ian M. Smith, Val Behan-Pelletier, and Barb Eamer, with permission.

Figure 84. ***Arrenurus*** **(*Megaluracarus*)** ***globator*** female; some members of this genus live exclusively among ***Sphagnum***. Photo by Walter Pfliegler, with permission.

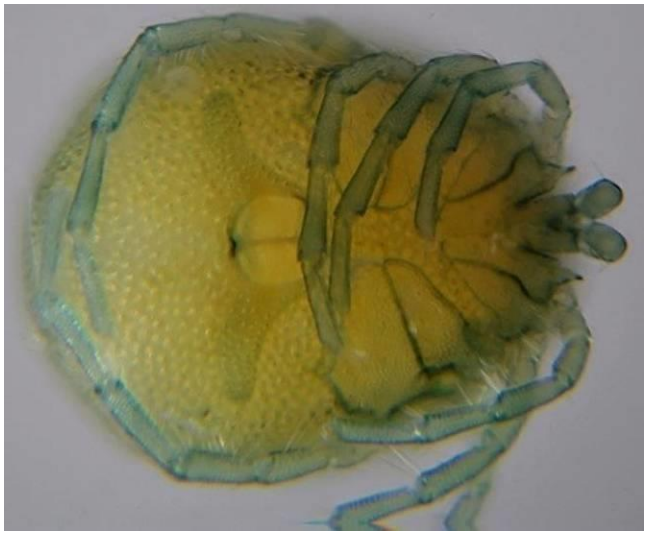

Figure 85. ***Arrenurus* (*Megaluracarus*) *globator*** female; some members of this genus live exclusively among ***Sphagnum***. Photo by Walter Pfliegler, with permission.

Figure 86. ***Arrenurus*** sp. larva; some members of this genus live exclusively among ***Sphagnum***. Photo by Walter Pfliegler, with permission.

Some mites, such as ***Malaconothrus*** (**Malaconothridae**; Figure 87), can appear in large numbers among the aquatic mosses (Krantz & Lindquist 1979). Behan-Pelletier (1993) reports that deutonymphs and adults of aquatic mites are often specialized for their habit of crawling among mosses and detritus. Most of them are also cold-adapted. Others, such as ***Laversia berulophila*** (**Laversiidae**), are more generalized and are able to live in the **profundal** zone (deep zone of inland body of free-standing water, located below range of effective light penetration) of **oligotrophic lakes** (lake relatively low in plant nutrients, containing abundant oxygen in deeper parts) as well (Smith in Smith *et al.* 2011). In bog/fen pools there are nearly 50 species in Canada in the mixed forest plains. These are adapted for clinging to ***Sphagnum*** (Figure 95) and other mosses (Figure 88), but also for swimming. They are adapted for cool water in the northeastern and boreal peatland pools, mostly in relict habitats.

Figure 87. ***Malaconothrus*** sp., member of a genus that can be found among aquatic mosses. Photo courtesy of BOLD Systems, Biodiversity Institute of Ontario.

Figure 88. These water mites (probably **Hydryphantoidea**) are inhabiting the moss ***Palustriella falcata*,** a species common in moderate to highly mineral-rich pools and ponds. Photo by Dan Spitale, with permission.

In **streams**, Badcock (1949) found that mites were most abundant where moss or other substrate provided shelter. In my own collections of stream mosses, I did occasionally find tiny red mites. However, these were never abundant and were infrequent. Stream edge and streamside habitats, on the other hand, provide a moist habitat where these non-streamlined mites are out of the danger of current. Red seems to be a common color for water mites, possibly serving as warning coloration – or not (Figure 1, Figure 88).

In an attempt to determine the role of bryophytes that had been lost from a stream suffering from sewage effluents, Dewez and Wauthy (1981) used sponges to simulate the bryophyte habitat and capture water mites. These sponge colonizations suggested that loss of bryophytes had impacted both numbers and diversity of mites negatively. They also found that the mite ***Hygrobates fluviatilis*** (**Hygrobatidae**; Figure 89) played a major role in determining the numbers and organization of the communities. Since sponges served as a suitable habitat, one might conclude that the bryophyte served primarily as a substrate and safe site, not as a direct source of food.

Angelier *et al.* (1985) found that both the presence and type of moss, compared to gravel, were important in determining the mite community. One factor that seemed to play a role in this relationship was stability of the rock substrate. Mosses only developed colonies on rocks that stayed put.

The species ***Hydrovolzia mitchelli*** (**Hydrovolziidae**; Figure 90), a species from the mixed wood plains, prefers cold **springs** and seepage areas (below 10°C) (Smith in Smith *et al.* 2011). The deutonymphs and adults spend

time crawling through detritus and moss mats, a slow feat for them. The larvae are parasites on adult **Empididae** (Figure 91), a small dipteran whose larvae sometimes live among mosses. Members of the **Unionicolidae** (Figure 92) can be found in streams, where they inhabit mosses like ***Hygroamblystegium*** (Figure 93) (Paul Davison, pers. comm. 27 September 2011). ***Fissidens fontanus*** (Figure 94) also serves as a suitable habitat for water mites. These mites avoid open water and seem to need to be in contact with a substrate.

Figure 89. ***Hygrobates fluviatilis***, a species that depends on aquatic mosses. Note the brown patches – they are body parts visible through the transparent soft body integument. Photo by Nigrico, through Creative Commons.

Figure 90. ***Hydrovolzia mitchelli***, a mite of cold springs where it crawls among detritus and moss mats. Photo by Ian M. Smith, Evert E. Lindquist, and Valerie Behan-Pelletier, with permission.

Figure 91. ***Empis bistortae***, host of larval mites (***Hydrovolzia mitchelli***) that crawl among mosses as adults. Photo by James K. Lindsey, with permission.

Figure 92. Water mite (probably **Unionicolidae**), a common group among aquatic mosses. This one was in a spring-fed stream on mosses like ***Hygroamblystegium*****.** Photo by Paul Davison, with permission.

Figure 93. ***Hygroamblystegium fluviatile***, home for members of **Unionicolidae**. Photo by Michael Lüth, with permission.

Figure 94. ***Fissidens fontanus***, home for aquatic mites that avoid open water. Photo by Michael Lüth, with permission.

Sphagnum Peatlands

Peatlands present unique challenges to their inhabitants (Behan-Pelletier & Bissett 1994). Not only do they experience highly fluctuating temperatures at the surface, seasonal water-logging, and low nutrients, but they also have a low *p*H resulting from the activities of the ***Sphagnum*** (Figure 95) itself (see below). Furthermore, the low conductivity of the moss results in a shorter frost-free season than that of the surrounding habitats. Relative humidity among the moss stalks generally remains at 100%, but at the surface it may drop to 40% during the day. For those mites able to migrate up and down (see below), finding a suitable temperature and humidity combination should not be difficult.

Figure 95. ***Sphagnum capillifolium*** lawn. Photo by Bernd Haynold, through Creative Commons.

Among the microarthropods, the mites are the most abundant and diverse group of organisms on the peatland bryophytes (Behan-Pelletier & Bissett 1994), but not in the open water. These peatland mites include water mites, oribatids, and **Mesostigmata** (Hingley 1993). The **Oribatida** (moss mites) are predominant among these (Behan-Pelletier & Bissett 1994). Behan-Pelletier and Bissett (1994) reported 71 species of oribatids in the peatlands of Canada. These are species of widespread distributions, either Holarctic or worldwide. The aquatic species, on the other hand, seem to be restricted to the Nearctic.

Peatland mosses typically offer a compact cover that is generally moist, hence providing both protection from predators and from desiccation. For mites, this habitat is therefore often an inviting one (Seyd 1988). This habitat is, nevertheless, quite variable in water availability. Silvan *et al*. (2000) demonstrated that "soil" mites increased in numbers with drainage and draw-down of peat soils, suggesting that in many areas the peatlands are simply too wet for many species. In fact, older drained sites typically had mite populations ten times as large as those on undrained sites. Re-wetting caused an abrupt drop in numbers. Among those invertebrates found, the oribatid mites were the most frequent, comprising nearly 60% of the fauna on undrained sites.

Many mite families found elsewhere in the general area, including those on mosses (*e.g.* some **Eremaeidae**, **Oppiidae**, **Galumnidae**), are absent or poorly represented in peatlands. Both wet and dry extremes in peatlands have few mite species but a high number of individuals. Thus, it is the intermediate levels of moisture that provide the best locations for most of the oribatid mite species (Tarras-Wahlberg 1961; Belanger 1976; Borcard 1988, 1991c, e; Behan-Pelletier & Bissett 1994).

Within the peatlands, one can find multiple niches with considerable differences in microclimate. Belanger (1976) found 44 species of oribatids in a North American poor fen peatland, 26 of which were also known from European peatlands. Among the microarthropods there, oribatids comprised 84% of the species within the peat, 70% of that on ***Sphagnum*** (Figure 95) stalks, and 39% of that on ***Sphagnum*** tops. But from the perspective of the mites, the ***Sphagnum*** stalks seemed to be the "optimum microhabitat" in the ***Sphagnum*** because of its species richness and density. This was the habitat where the oribatid assemblage was the most stable.

In Europe, the mite fauna of ***Sphagnum*** (Figure 95) peatlands is well known (*e.g.* Scandinavia: Tarras-Wahlberg 1954, 1961; Dalenius 1960, 1962; Solhøy 1979; Markkula 1986a, 1986b; Russia: Laskova 1980; Druk 1982; Lithuania: Eitminavichyute *et al*. 1972; Germany: Beier 1928; Willmann 1928, 1931a, b, 1933; Peus 1932; Sellnick 1929; Popp 1962; Switzerland: Borcard 1988, 1991a, b, c, d, e). These studies indicate that the peatland oribatid species are seldom restricted to peatlands. North American studies seem to have lagged behind, with notable ones scattered broadly in time (Banks 1895; Jacot 1930; Belanger 1976; Behan-Pelletier 1989; Larson & House 1990; Palmer 1990; Hingley 1993; Behan-Pelletier & Bissett 1994).

The Fauna

Peatlands generally have low numbers of mite species. Smith (in Smith *et al*. 2011) reported that ***Hydrozetes*** (**Hydrozetidae**; Figure 96) are the most numerous of the oribatids in peatland pools, where they move about by clinging to the surface film of the water. In eastern Canada, the most species-rich genus within the moss mat is ***Limnozetes*** (**Limnozetidae**; Figure 97), often being the only genus in the dripping ***Sphagnum*** (Figure 95) and layers of peat (Behan-Pelletier & Bissett 1994; Smith in

Smith *et al*. 2011). Borcard (1991c) reported up to 100,000 specimens of oribatid mites from just one cubic meter of wet ***Sphagnum*** in Canada. Popp (1962) reported ***Limnozetes ciliata*** and ***L. rugosus*** (see Figure 107-Figure 112) in the ***Sphagnum fuscum*** (Figure 98) association in Germany; in the same bog, ***Pilogalumna tenuiclavus*** (**Galumnidae**) occurred in the ***Sphagnum magellanicum*** association (Figure 99).

Figure 96. ***Hydrozetes*** sp., member of a genus that is common in peatland mills. Photo by Walter Pfliegler, with permission.

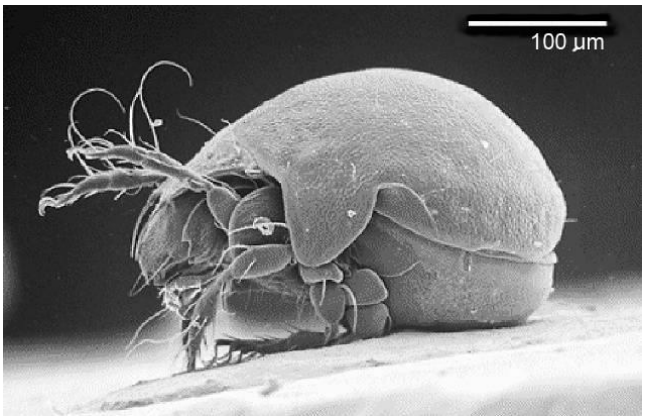

Figure 97. ***Limnozetes***, a common genus in dripping ***Sphagnum*** and peat layers. Photo by Valerie Behan-Pelletier & Barb Eamer, with permission.

Figure 98. ***Sphagnum fuscum*** in Alaska. Photo by Andres Baron Lopez, with permission.

Figure 99. ***Sphagnum magellanicum*** (red) mixed with other species of ***Sphagnum*** at Cape Hope. Photo from NY Botanical Garden, through public domain.

Donaldson (1996) demonstrated the richness of oribatid mites in a moat bog in New Hampshire, USA. Among the 220 adult oribatids collected, 44 species were represented from three ***Sphagnum*** species. These three species formed a moisture gradient with increasing height above the water surface, from ***S. cuspidatum*** (Figure 100) in the water, to ***S. recurvum*** (Figure 101), to ***S. magellanicum*** (Figure 99) on top. This same gradient also represented increasing light levels. The oribatid mite species diversity increased from water level to hummock top. The genus ***Limnozetes*** (**Limnozetidae**; Figure 107-Figure 112) was well represented by four species associated with ***Sphagnum*** in this bog.

Figure 100. ***Sphagnum cuspidatum***, a moss that is typically mostly submersed. Photo by Jutta Kapfer, with permission.

Figure 101. ***Sphagnum recurvum*** var ***mucronatum***, a moss that is typically mostly submersed. Photo by Jan-Peter Frahm, with permission.

This study was surpassed in breadth by that of Mumladze *et al*. (2013). They reviewed studies on the oribatid mites throughout the Holarctic region by examining data from 46 peat bog localities and found reports of 410 species. They found a non-random metacommunity structure for all the ecological guilds studied. Although they found no latitudinal gradients in species composition, they did find a non-linear decay with distance between communities. They found that at the community level, structure of the species is determined primarily by interspecific interactions and common biogeographical history. At the metacommunity level, on the other hand, the postglacial colonization processes are the most important factors in determining patterns.

Among the oribatids, the community composition varies among peatlands, with many of the species also found in other types of wetlands. Nevertheless, two genera have a high fidelity to Canadian peatlands: ***Malaconothrus*** (**Malaconothridae**; Figure 87) and ***Limnozetes*** (**Limnozetidae**; Figure 107-Figure 112) (Behan-Pelletier & Bissett 1994). But even these may be absent in some dry, oligotrophic bogs (Solhøy 1979). ***Limnozetes***, a fungal grazer on the surface of the ***Sphagnum*** (Figure 95) plants, is so important in describing the community that Behan-Pelletier and Bissett (1994) suggested that the species composition could be useful to characterize peatlands. The adults of ***Limnozetes*** species graze all surfaces of the moss, whereas the immatures graze only the inner, cupped surfaces. ***Ceratozetes parvulus*** (**Ceratozetidae**; see Figure 102), a "constant component" of the peatland fauna, seems to have some subtle restrictions; in one virgin bog in Finland it was restricted to the hollows (Markkula 1986a).

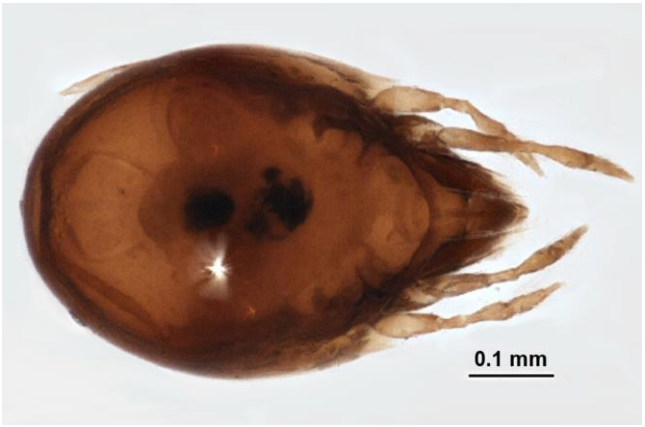

Figure 102. ***Ceratozetes*** sp. ***Ceratozetes parvulus*** is a predictable bog dweller. Photo from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

In some areas of Europe, the bog mite fauna seems to lack study. The family **Cunaxidae** (Figure 103) lives in saturated mosses such at those at the edge of bog pools (Hughes 1959). Krogerus (1960) found records of three species of **Erythraeoidea** from Finnish bogs, but there were no preserved specimens available for species verification (Gabryś *et al*. 2009).

In Great Britain, over 60 species have been recorded in peatlands (Hingley 1993). Many species of oribatids (seed mites) occur. In addition, there are several species of **Hydracarina** (water mites) and **Mesostigmata**. The characteristic genera include ***Malaconothrus*** (***Trimalaconothrus***; **Malaconothridae**; Figure 87), ***Hydrozetes*** (**Hydrozetidae**; Figure 104-Figure 106), and ***Limnozetes*** (**Limnozetidae**; Figure 107-Figure 112). ***Hydrozetes lacustris***, and probably also ***Limnozetes ciliatus*** (see Figure 107-Figure 112), live among the stems and leaves. ***Trimalaconothrus maior*** (**Malaconothridae**) lives in the leaf axils. Seeming to defy the Gaussian principle, up to five species of ***Limnozetes*** (see Figure 107-Figure 112) can occur on a single ***Sphagnum*** (Figure 98-Figure 99) sample, but perhaps no resource, especially space, is limiting. None of these species is limited to ***Sphagnum***. Fewer species but more individuals occur in the drier parts of the peatlands.

Figure 103. Member of **Cunaxidae**, a peatland family. Photo by Scott Justis, with permission.

Figure 104. ***Hydrozetes*** sp. on the leaf of an aquatic plant. This genus is common in peatlands. Photo by Walter Pfliegler, with permission.

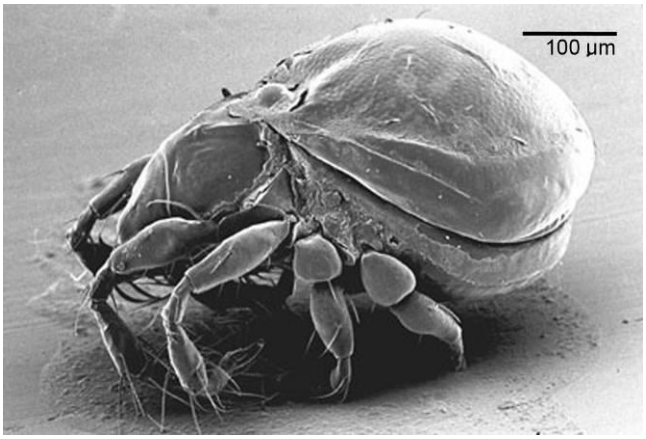

Figure 105. SEM of ***Hydrozetes***, a genus common in peatlands. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

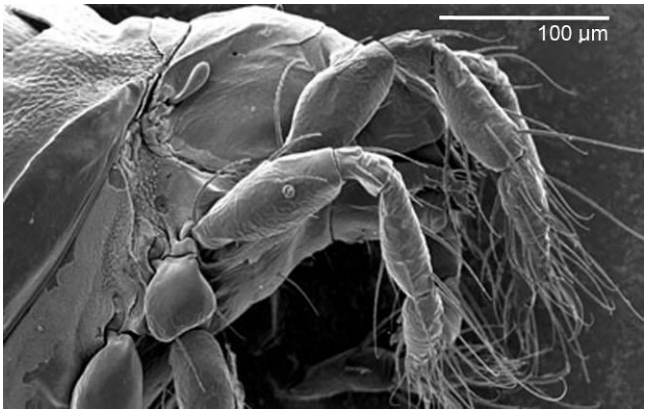

Figure 106. SEM of head region of ***Hydrozetes***, a genus common in peatlands. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

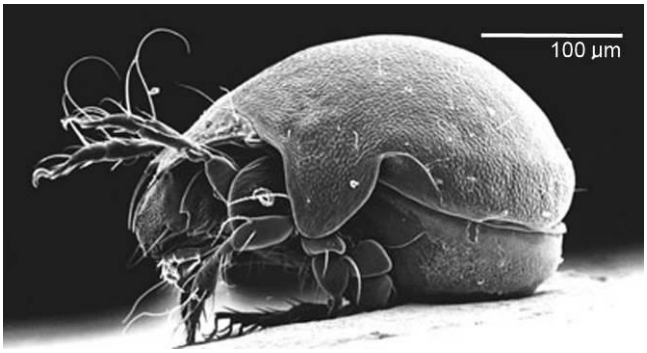

Figure 107. SEM of ***Limnozetes borealis*.** Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

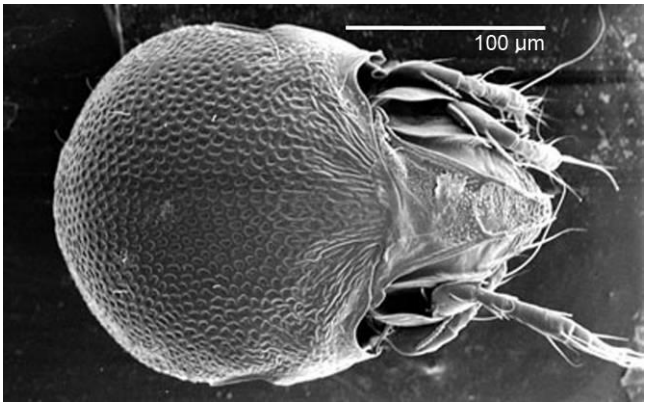

Figure 108. SEM of ***Limnozetes guyi***. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

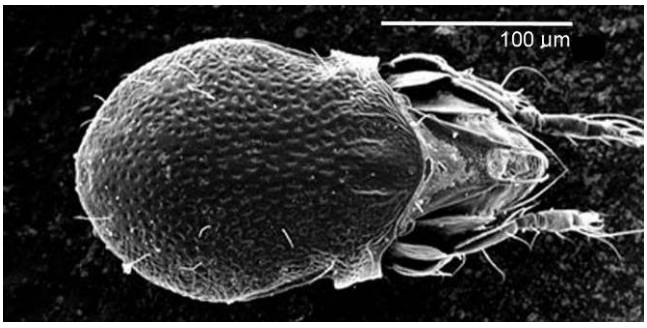

Figure 109. SEM of dorsal view of ***Limnozetes palmerae***, member of a genus that is common on peatland mosses. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

Figure 110. SEM of head region of ***Limnozetes latilamellatus***, member of a genus that can have high diversity on peatland mosses. Photos by Valerie Behan-Pelletier and Barb Eamer, with permission.

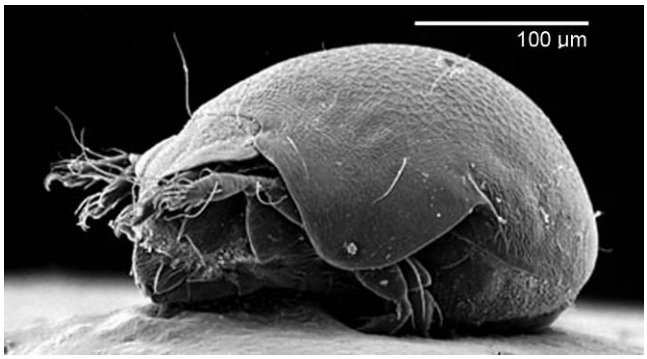

Figure 111. SEM of ***Limnozetes latilamellatus***, member of a genus that can have high diversity on peatland mosses. Photos by Valerie Behan-Pelletier and Barb Eamer, with permission.

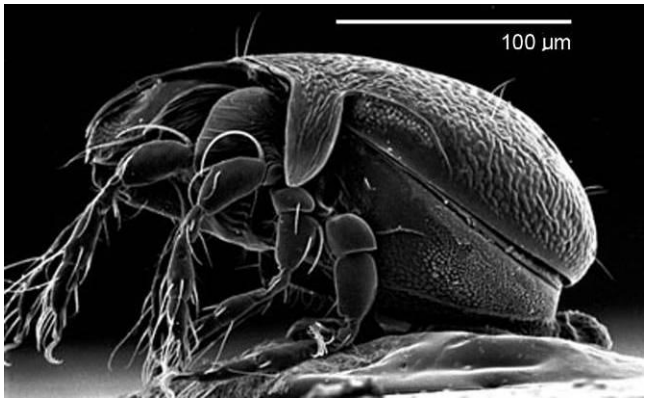

Figure 112. SEM of side view of ***Limnozetes palmerae***, member of a genus that is common on peatland mosses. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

In Canada, the genera are somewhat different from those in Europe, with mites such as ***Parhypochthonius*** (**Parhypochthoniidae**; Figure 113) and ***Nanhermannia*** (**Nanhermanniidae**; Figure 114) occurring in peatlands (Smith *et al*. 2011). The latter is one of the most common and most abundant of the oribatid mites in northeastern North American peatlands (Behan-Pelletier & Bissett 1994). By contrast, the poorly represented families **Oppiidae** and **Suctobelbidae** in Canada are dominant in some bogs in Europe (Sweden: Tarras-Wahlberg 1961; Finland: Markkula 1986a; Switzerland: Borcard 1992), with

Oppiella nova (**Oppiidae**; Figure 115) being among the most abundant (Behan-Pelletier & Bissett 1994).

Figure 113. SEM of ***Parhypochthonius*** sp., member of a Canadian peatland mite genus. Valerie Behan-Pelletier and Barb Eamer, with permission.

Figure 114. ***Nanhermannia*** from peatlands in Canada. Valerie Behan-Pelletier and Barb Eamer, with permission.

Figure 115. ***Oppiella nova***, an abundant mite in bogs. Photo from SNSB, Zoologische Staatssammlung Muenchen, through Creative Commons.

Trampling

I know of no other study on the effects of trampling in bogs and poor fens, but the study by Borcard and Matthey (1995) is quite interesting. Not only does it demonstrate differences between species of ***Sphagnum*** (Figure 95, Figure 98-Figure 99) in their response to this abuse, but its primary objective was to determine the effects on the oribatid mite community.

During cranberry season, and in some bogs and poor fens, during blueberry season, the mosses can be subjected to considerable trampling by berry pickers. I have been to these habitats just after picking season and could see the destruction. I have also seen it following a class field trip, causing me to keep the students off the mat in later trips. But I had given little thought to the effects on the organisms within the mat.

In experiments involving 1 m^2 plots, Borcard and Matthey (1995) compared mite communities associated with hollow (wet) species ***Sphagnum recurvum*** (Figure 101) with that of hummock (drier) species ***Sphagnum fuscum*** (Figure 98) in a raised bog in Switzerland. Two plots of each species were trampled for ten minutes each, three times per year for four years, and compared with control plots. The plot with ***S. recurvum*** became a "muddy depression." The oribatid mites fared no better, dropping from 20 species to 4. ***Limnozetes ciliatus*** (**Limnozetidae**; see Figure 97), a common peatland mite, had a 96% relative frequency and was the overwhelming dominant following trampling.

The ***Sphagnum fuscum*** (Figure 98) hummock had a quite different response. The moss died, but the hummock retained its shape. The mite community, as in ***S. recurvum*** (Figure 101), had a reduction in species, but in this case was only reduced to 10 compared to its former 23. The surprise was that one species, ***Ceratozetes parvulus*** (**Ceratozetidae**; see Figure 102), that had been nearly absent before the trampling actually benefitted from the trampling.

Several factors account for the decrease in mite diversity and abundance. In both cases, the mosses were strongly compacted. The density of the top 3.5 cm increased more than 2-fold in both species. The entire vertical expanse became very homogeneous, lacking the vertical stratification of space and moisture available in the controls. Water content increased on a per volume basis. This compaction and increased water content made a habitat unsuitable for the original moss mite inhabitants.

The sampling itself made changes to both control and experimental plots. Removal of three cores (5 cm diameter, 13 cm deep) created a less dense habitat that permitted greater drying. This resulted in species shifts, even in control plots. In ***Sphagnum recurvum*** (Figure 101) control plots, ***Oppiella nova*** (**Oppiidae**; Figure 115) increased in numbers, possibly benefitting from drying around sampler holes. More hygrophilous species [***Limnozetes ciliatus*** (**Limnozetidae**; see Figure 97), ***Hoplophthiracarus pavidus*** (**Phthiracaridae**)] tended to decrease for the same reasons. On the other hand, fungi invaded sample holes, providing a potential food source for fungivorous mites.

Loss of abundance followed different patterns in the two moss species (Figure 116). Those in ***Sphagnum recurvum*** (Figure 101) exhibited a "saw-tooth" pattern that indicates partial recovery between autumn and spring or summer sampling/trampling dates. Furthermore, the evenness dropped precipitously, with the semi-aquatic ***Limnozetes ciliatus*** (**Limnozetidae**) see Figure 97) having extreme dominance. By contrast, the decrease in number of species in ***S. fuscum*** (Figure 98) was less dramatic, and evenness did not change significantly. The latter greater constancy is attributable to a greater retention of non-inundated spaces within the hummock.

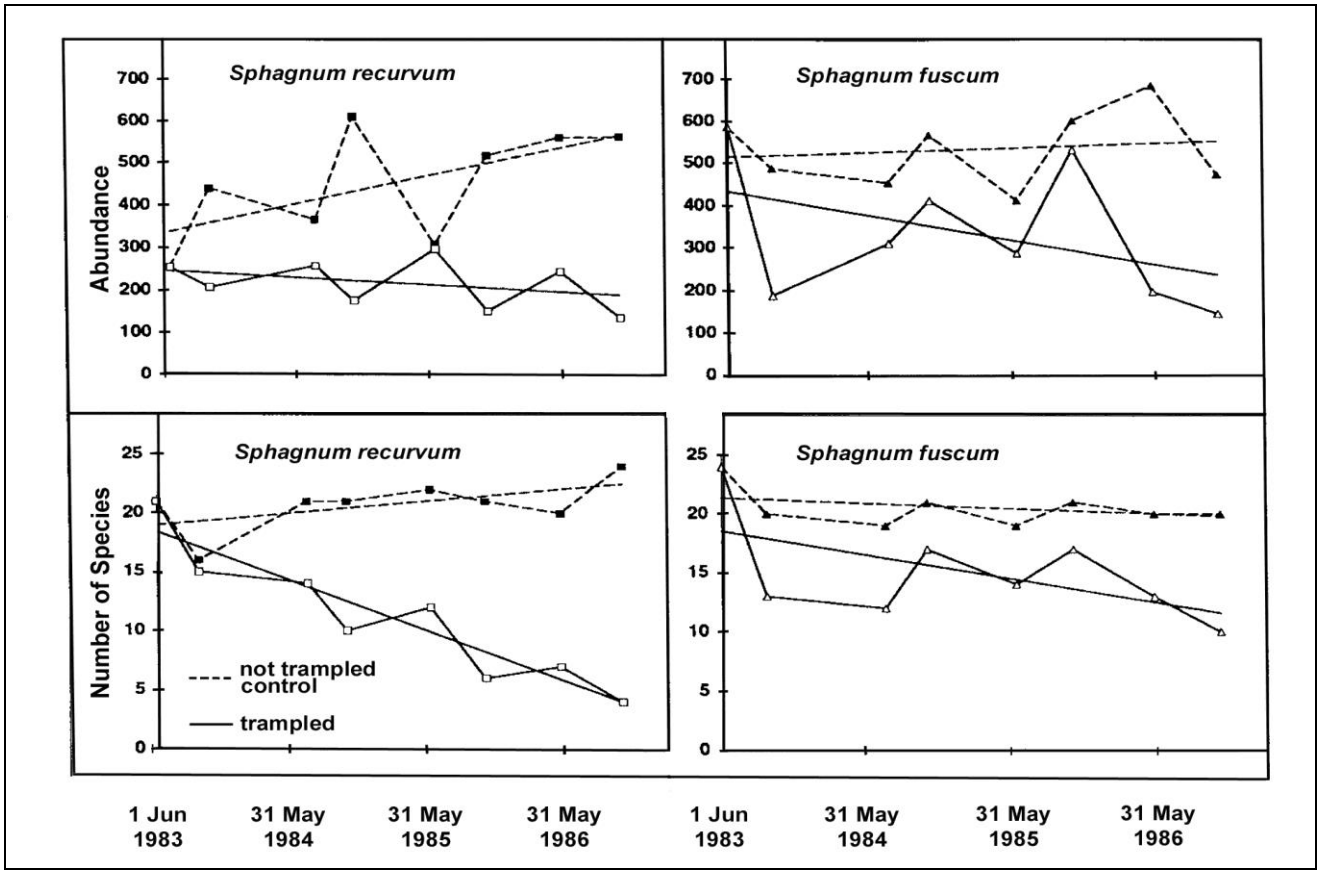

Figure 116. Changes in number of oribatid mite species and abundance in sample ***Sphagnum*** cores (5 cm diameter, 13 cm deep) through four successive years of trampling. Redrawn from Borcard & Matthey 1995.

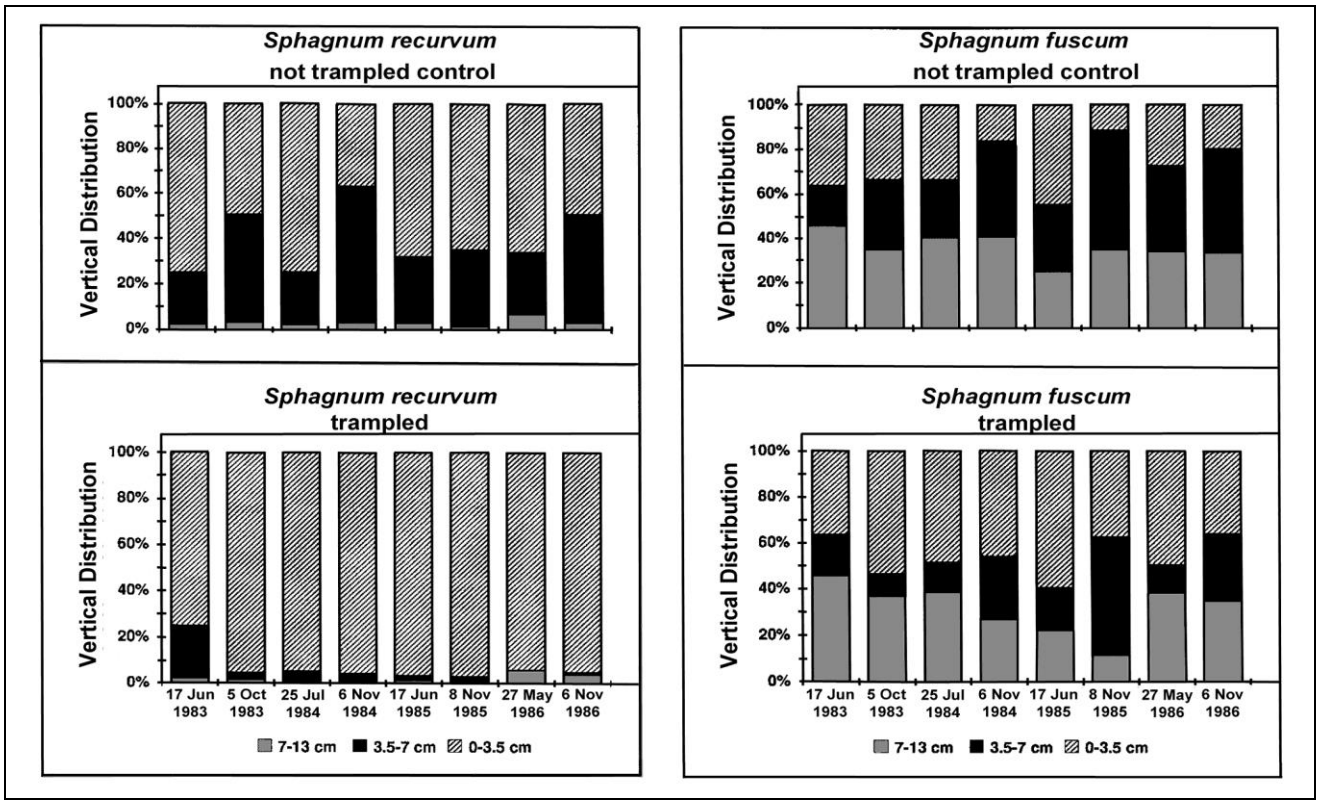

Figure 117. Vertical distribution of oribatid mites in two ***Sphagnum*** species in trampled and non-trampled control plots in a bog in Switzerland. Redrawn from Borcard & Matthey 1995.

As one might expect, the vertical distribution of the mites changed as the structure of the moss strata changed (Figure 117). In ***Sphagnum recurvum*** (Figure 101), there was a severe loss of mites from lower strata, with remaining individuals located predominately in the upper 3.5 cm. Such dramatic change was not evident in ***Sphagnum fuscum*** (Figure 98), where original structure changed little following trampling, despite death of the moss.

One interesting result is a dramatic increase of the tiny ***Ceratozetes parvulus*** (see Figure 102) in the ***Sphagnum fuscum*** (Figure 98) hummock. This species is rare throughout the bog, so its increase to 13-30% under disturbance is a surprise. Could this flattened species have benefitted from compaction that permitted it to maneuver out of reach of larger predators?

Predation

Hiding oneself deep in the ***Sphagnum*** (Figure 98) peat may prevent at least some predation on the mite fauna. This would seem to be likely for those known to be prey of the newt ***Notophthalmus viridescens*** (Figure 118), also a peatland dweller. At least 45 species of oribatids are known food items for this species (Norton & MacNamara 1976). The compact peat is often impenetrable for this newt. But known oribatid predators such as the smaller beetles and ants (Riha 1951; Schuster 1966; Schmid 1988; Norton & Behan-Pelletier 1991) that co-inhabit the mosses should be able to penetrate many of the same small spaces as the mites. For those living in the pools and channels of the peatlands, the naiads of dragon- and damselflies (**Odonata**) can be major predators. Behan-Pelletier and Bissett (1994) found that 63% of the 60 ***Aeshna sitchensis*** guts they examined had oribatid mites in them, with a mean of 7 per gut. Presence in the other four species examined ranged from 10% frequency upward. Adult mites were more common than immatures, a phenomenon that Behan-Pelletier and Bissett suggested might relate to the habit of the immatures to graze only on the inner surfaces of the leaves where they were much more protected. The **Odonata** were apparently better collectors than the researchers – several species in the gut had not been located previously in the bog pools! The **Odonata** guts also contained predators of the mites, suggesting that these insect naiads were both friend and foe.

Figure 118. ***Notophthalmus viridescens*** adult, a predator on mites. Photo © Gary Nafis at <CaliforniaHerps.com>, with permission.

Acidity Problems

One problem that organisms always face in ***Sphagnum*** peatlands (Figure 66) is the low *p*H. Although ***Sphagnum*** is usually too acid for most mites, ***Hydrovolzia placophora*** (**Hydrovolziidae**; see Figure 90) seems to be tolerant of the low *p*H and occurs in the axils of leaves that protect it from open water (Gledhill 1960). This mite is not able to swim.

For mites, the acidity could present itself as difficulty in hardening of the cuticle due to the need for calcium. Although a common form of calcium is calcium carbonate, it appears that calcium oxalate (whewellite) can also serve this purpose, at least for the mites ***Eniochthonius minutissimus*** (**Eniochthoniidae**; Figure 119), ***Archoplophora rostralis*** (**Mesoplophoridae**), and ***Prototritia major*** (**Protoplophoridae**), and is deposited even in ***Sphagnum*** peatlands (Figure 66) (Norton & Behan-Pelletier 1991). Norton and Behan-Pelletier (1991) suggested that the calcium oxalate is probably obtained from crystals precipitated by fungi and used as food by the mites. This discovery was the first to demonstrate the role of minerals in hardening of the cuticle of arachnids.

Figure 119. ***Eniochthonius minutissimus*** ventral composite. Photo by Matthew Shepherd, through Creative Commons.

Jarmo Holopainen (pers. comm. 16 September 2011) considers the biochemistry of peatlands to have a negative impact on mites. Volatile organic compounds are released from the ***Sphagnum*** (Figure 95) and many of the compounds produced by this genus have antibiotic effects against microbes – important food organisms for many mites. The peat has a high content of **Actinobacteria** (=**Actinomycetes** – formerly thought to be fungi; Figure 120), a group that produces antibiotics that might also have an effect on mite abundance. On the other hand, oribatid mites are known to have **Actinobacteria** in their digestive systems (Cromack *et al*. 1977), suggesting that at least some might benefit from the fungi.

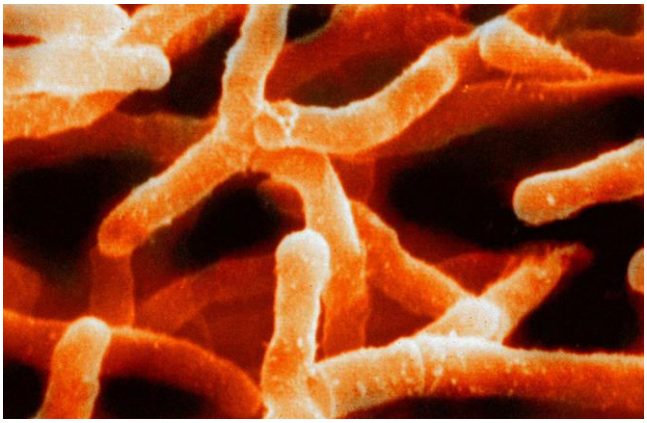

Figure 120. ***Actinomyces israelii*** with false color, a member of **Actinobacteria**. Photo by Graham Colm through Creative Commons.

Mites have a role in this scenario in another way. Spores of the Actinomycetes, and other **propagules** (dispersal units), are transported by the mites (Ruddick & Williams 1972) and in some cases undoubtedly introduce them to peatlands and other bryophytic habitats.

Historical Indicators

Like the testate amoebae, mites have been used to reconstruct the long-term history of peatlands and lakes (Erickson 1988; Markkula 1986a; Behan-Pelletier & Bissett 1994; Luoto 2009). Birks *et al*. (2000) used community structure of subfossil vegetation including mosses and invertebrates including mites to reconstruct past history (late-glacial and early-Holocene) of Kraekenes Lake, western Norway. ***Hydrozetes oryktosis*** (**Hydrozetidae**; see Figure 104-Figure 106) and ***Limnozetes*** *cf.* ***rugosis*** (**Limnozetidae**; see Figure 107-Figure 112) can be used to infer lake levels (Erickson 1988; Solhøy 2001). In the Antarctic, Hodgson and Convey (2007) found ***Alaskozetes antarcticus*** (**Ameronothridae;** Figure 130) and ***Halozetes belgicae*** (**Ameronothridae**), both known moss dwellers, in a sediment core. The expansion of their numbers indicated a temperate period. In Finland, Markkula (1986a) found that ***Limnozetes ciliatis*** (see Figure 97) indicated presence of hollows, being absent in the hummocks. For the genus ***Limnozetes***, acidity is important in defining which species occur (Behan-Pelletier & Bissett 1994).

Antarctic and Arctic

The Antarctic usually provides a good source of information on moss-dwelling invertebrates, and mites are no exception (Goddard 1979; West 1984; Schenker & Block 1986; Mitra 1999). In the Antarctic, bryophytes are an especially important habitat for mites (Booth & Usher 1986). Barendse *et al*. (2002) suggest that bryophytes and lichens may have served as glacial refugia during the Neogene (23.03 ± 0.05 million years ago), had their own fauna, and still provide a source from which tracheophytes can be colonized.

Ino (1992) found that moss colonies at Langhovde, East Antarctica, housed mites, among other invertebrates. Barman (2000) examined the mites inhabiting mosses on the Schirmacher Oasis in East Antarctica. He found the family **Haplochthoniidae** (Figure 121), the first report from the Antarctic, and reported three new species [***Haplochthonius antarcticus*** (**Haplochthoniidae**), ***H. maitri***, and ***H. longisetosus***]. ***Tyrophagus antarcticus*** (**Acaridae**; see) was likewise recorded for the first time in the Antarctic. He considered the prostigmatid mites to be some of the toughest terrestrial animals in the world, occupying nunataks on the Antarctic continent. The Antarctic ***Nanorchestes antarcticus*** (see Figure 123) is only 0.3 mm long.

Figure 121. **Hypochthoniidae** mite, probably ***Eohypochthonius***. Photo by David E. Walter, with permission.

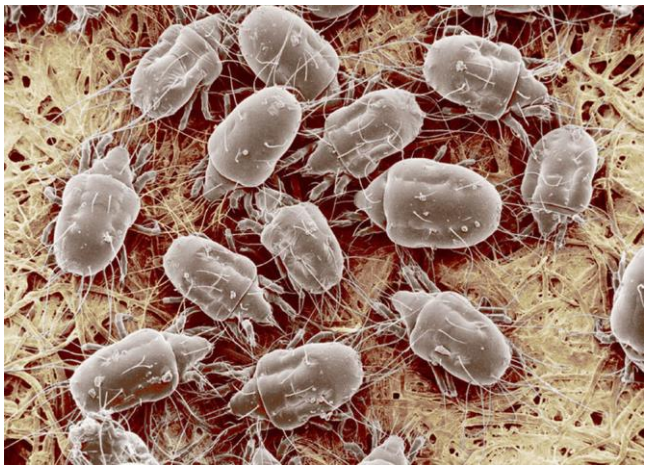

Figure 122. ***Tyrophagus putrescentiae***. Some members of this genus are present in Antarctic mosses. Photo from USDA, through public domain.

Figure 123. ***Nanorchestes*** sp., member of an Antarctic bryophyte-dwelling genus. Photo by David E Walter, with permission.

One might expect bryophytes to be a safe site in the Antarctic, with edible moss tissue and cover to protect from larger predators. But not all bryophytes are equally protective. Usher and Booth (1986) found that the predatory ***Cyrtolaelaps*** (*Gamasellus*; **Ologamasidae**) lacked any pattern of distribution related to scale of sampling, exhibiting random distribution, whereas the prostigmatic ***Ereynetes*** (**Ereynetidae**), ***Eupodes*** (**Eupodidae**; Figure 124), and ***Nanorchestes*** (**Nanorchestidae**; Figure 123) had distinct patterns at a scale less than 30-40 cm. A small scale pattern was present at 10-20 cm in ***Polytrichum*** (Figure 125), with slightly larger scales (up to 30 cm) in ***Chorisodontium*** (Figure 126) as well as in lichens. For other species, large scale (40-50 cm or more) differences were related to environmental variables. By contrast, relationships between species were more important at smaller scales (5-10 cm). Perhaps the ***Cyrtolaelaps*** (*Gamasellus*) lacks a pattern of scale because it goes where the food is, crossing "zones."

Figure 124. ***Eupodes longisetatus***. The genus ***Eupodes*** is a moss dweller in the Antarctic. Photo from Museum of New Zealand, Te Papa Tongarewa, with online permission.

Among these same mosses, Davis (1981) found the turf communities [***Polytrichum strictum*** (formerly ***P. alpestre***; Figure 125) and ***Chorisodontium aciphyllum*** (Figure 126)] and the carpet communities [***Calliergidium austrostramineum*** (Figure 126), ***Warnstorfia sarmentosa*** (Figure 127), and ***Sanionia uncinata*** (Figure 128)] had similar levels of productivity, trophic structure, and organic matter transfer efficiency, but the standing crops of Collembola and mites differed. Concurrent with these standing crop differences were differences in moss turnover and accumulation of dead organic matter. There was no bryophyte consumption in these two communities.

Figure 125. ***Polytrichum strictum***, a mite habitat in the Antarctic. Photo by Michael Lüth, with permission.

Figure 126. ***Chorisodontium aciphyllum***, a common Antarctic moss that serves as habitat for mites. This picture was taken in Tierra del Fuego with *Nothofagus* in the background. Photo by Juan Larraín, with permission.

Figure 127. ***Warnstorfia sarmentosa***, a common mite habitat in the Antarctic. Photo by Michael Lüth, with permission.

Figure 128. ***Sanionia uncinata***, a common Antarctic moss with mite inhabitants. Photo by Michael Lüth, with permission.

But in the Stillwell Hills region of Kemp Land, East Antarctica, Kennedy (1999) found that microalgae supported more of the microarthropods than did the sites with a mix of mosses, lichens, and macroalgae. Kennedy suggested that the mites were able to avoid the extremes of temperature, but that they were limited by heat stress and desiccation. Furthermore, they found only three taxa, all under rocks.

Schwarz *et al*. (1993) found the greatest abundance of mites and other invertebrate groups in the top 5 cm of mosses in post-melt conditions. Usher and Booth (1984; Booth & Usher 1986) found a distinct vertical distribution among the mites and **Collembola** living among mosses in an Antarctic turf. The distribution of a species varied with its developmental stage. The populations were aggregated, but again, that aggregation within the mite species depended on the developmental stage. A major factor in the vertical distribution was the state of the moss tissue. The green moss community (living; 0-1.5 cm layer at surface) differed from the dead moss community (below 3 cm). The same six species of mites and Collembola occurred in both communities, but the relative proportions differed considerably. An interesting aside to this story is the fact that Booth and Usher (1984) found that the chemical characteristics (sodium, potassium, calcium, phosphorus) of the environment most influenced the distribution of the arthropods in the green moss communities, with physical characteristics being of less importance. The percentage of the various mite species in the green moss zone ranged from 24% (**Ereynetidae**: ***Ereynetes macquariensis***) to 63% (**Ologamasidae**: ***Gamasellus racovitzai***). In the ***Polytrichum*** (Figure 125) cover, only a weak relationship existed between moss cover and arthropods, including mites, in the green moss zone, whereas none existed in the dead moss zone.

At the Canada Glacier, mites were less abundant than protozoa, rotifers, nematodes, and tardigrades (Schwarz *et al*. 1993). On the other hand, Strong (1967) found mites to have the greatest species richness at Palmer Station, with at least 11 species representing the suborders **Prostigmata**, **Mesostigmata**, and **Cryptostigmata**. The **Collembola** comprised 4 species and **Diptera** 1. The two predatory mites feed mostly on the **Collembola**. Three of the oribatid species form aggregations to survive the winter. The others spend the winter in the same locations as their summer homes.

Antarctic Lakes likewise have an important mite fauna. In Priyadarshani, an oligotrophic lake, mosses and algae cover the bottom sediments. There one can find a microfauna that includes mites (Ingole & Parulekar 1990).

Temperature and Humidity Protection

Bryophytes may afford a protection from the Antarctic temperature that is not present elsewhere. Gressitt (1967) measured temperatures among mosses and found that some could create thermal conditions quite different from those in the atmosphere. ***Polytrichum*** (Figure 125) could reach January temperatures up to 13°C above atmospheric temperature, but ***Drepanocladus*** (*sensu lato*; Figure 127-Figure 128) maintained temperatures that differed little from ambient. (Note that the actual bryophyte species of these two genera may now be in different genera.)

As suggested for the two lycosid spiders earlier in this volume, other arthropods may also benefit from the ameliorating effects that bryophytes have on temperature. For example, the mites and **Collembola** have no known tolerance to freezing and survive winter by supercooling (Sømme 1981). This seems to involve both use of such cryoprotective compounds as glycerol and the elimination of nucleating proteins from the gut.

Block *et al*. (1978) noted that the mite ***Alaskozetes antarcticus*** (**Ameronothridae**; Figure 130) in the Antarctic has the ability to supercool to -30°C, but to realize this ability it depends on starvation, and possibly desiccation. They reported that about 1% of its fresh weight is glycerol. Cannon (1986b) found that for this species, those cold-hardy mites provided with distilled water and glucose lost about 20-25°C in supercooling ability. When no liquid was provided, they lost only about 4°C. In both cases, the glycerol concentrations in the mites decreased. In the Antarctic, even the summer temperatures can be quite cool. Block (1985) found that these could reach -8.4°C within the moss mats.

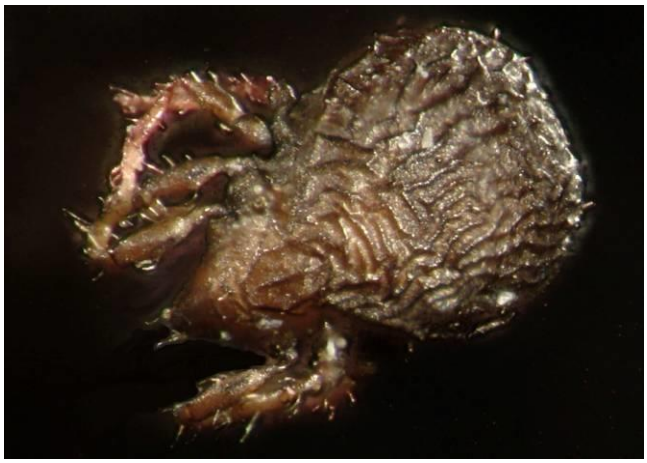

Figure 129. ***Ameronothrus lineatus***, a moss-dweller from the high Arctic of Svalbard. Photo by Steve J. Coulson, with permission.

Figure 130. ***Alaskozetes antarcticus***, an Antarctic moss-dweller that is capable of supercooling. Photo by Richard E. Lee, Jr., permission unknown.

Cannon (1986a) experimented with the humidity relations of ***Alaskozetes antarcticus*** (**Ameronothridae**; Figure 130) at 0, 26, 42, 55, 86, and 100% relative humidity at 4°C. He found that under saturated conditions the winter mites gradually lost cold hardiness while losing glycerol and increasing the temperature to which they could supercool. When they were maintained in dry conditions (r.h. <55%), their glycerol levels were relatively high (accumulation of glycerol was directly related to rate of water loss) and their supercooling temperature remained relatively constant. Even in summer conditions, the loss of water stimulated the accumulation of glycerol and the depression of the supercooling temperature.

Ice nucleation is always a danger at sub-freezing temperatures. Most invertebrates evacuate the gut in preparation for low temperatures (Sømme 1982), and this may relate to the problems seen when glucose was made available.

On the other hand, **tritonymphs** (third developmental stage) and adults of the mite ***Alaskozetes antarcticus*** (**Ameronothridae**; Figure 130) collected from mosses (or soil) in the Antarctic summer exhibited poor supercooling ability (-3 to -4°C) compared to those collected from beneath rocks (-20 to -30.8°C for tritonymphs, -2 to -29°C for adults) (Shimada *et al*. 1993). They were able to survive at temperatures below 0°C until they were frozen. This supports the notion that desiccation may be important to their cryoprotection mechanisms. Active mites survived lower temperatures than did the resting mites, and Shimada and coworkers suggested that items in their diet might contribute ice nucleating proteins that permit them to survive. It also appears that these mites are able to make antifreeze proteins that protect them from freezing in the fluctuating temperatures of summer (Block & Duman 1989). They are aided in their survival of low temperatures by having a very dark color that makes them into a "black body" that absorbs heat from the sun. Their slow development (5-7 years) is most likely a result of the low temperatures, but it could also mean they require less resources to continue their development.

Like most things, not all cryoprotection depends on the same conditions. Block (1979) found that the cryptostigmatid mites of the Alaskan taiga had supercooling ability that increased with the cold of autumn and early winter. But for these mites, there was no correlation with water content. Freezing was generally lethal, but supercooling prevented death until a frozen condition was reached.

One can only speculate on the role of the bryophytes in maintaining survival of ***Alaskozetes antarcticus*** (**Ameronothridae**; Figure 130). Since the bryophytes are likely to be frozen during a large portion of the year in the Antarctic, it is possible that ice crystals on their surfaces could contribute to desiccation of the mites by drawing the nearby water to the ice crystals of the bryophytes. Removal of water in this way from the mites would reduce the danger of crystal formation within the mites. Evacuation of the gut would further support the inability to form internal ice crystals. This could potentially protect the mites within the mats from episodes of fog and other moisture sources during cold weather, wherein small objects tend to collect the moisture and hold it, be they mites or mosses. Certainly research is needed to support my hypothesis on the role of the bryophytes.

A major problem for such small organisms in the Antarctic climate is the great variability in climatic conditions. Not only does the mite experience extremes through time, but it has great variability among its niches at the same time. Hence, having plasticity in one's response to this environmental heterogeneity is an asset for organisms such as mites. ***Halozetes belgicae*** (**Ameronothridae**) has **superplasticity** in its acclimation potential, as shown by the cold acclimation of an Antarctic population (Hawes *et al*. 2007). This species can cold harden very rapidly in the range of 0 to -10°C. In just two hours at 0°C, mites that had been acclimated at 10°C adjusted their supercooling points by 15°C. This is the most efficient ability to lower the lethal temperature known for any terrestrial arthropod. They seem to achieve this supercooling ability by evacuation of the gut, thus ridding themselves of potential nucleation sites in the gut. This could be a difference in physiological races or microspecies because the ability varies latitudinally, but it also varies with seasons.

Nielsen and Wall (2013) predicted that climate change responses will differ between Arctic and Antarctic invertebrate communities. They consider the changes in the Arctic to be driven by changes in the vegetation, whereas the Antarctic will respond to changes in the microbial community as well as changes in the plant communities. Both areas will most likely have a greater arrival of non-native species. In the species-rich Arctic, this may have a locally negative impact, with invaders reducing the diversity of native species by competition. These changes could cause the Arctic to become a carbon source, whereas the Antarctic could become a carbon sink.

The moss-dwelling ***Ameronothrus lineatus*** (**Ameronothridae**; Figure 129) lives in the high Arctic heath of the Svalbard, West Spitsbergen (Coulson & Birkemoe 2000). Collections of soil demonstrated that at least some individuals can survive temperatures of -22°C. But how tolerant will these high Arctic species be to greater maximum temperatures? Deep ***Sphagnum*** may be a refuge, but dark colors in the sun, including red ***Sphagnum*** species, will actually become warmer than the atmosphere on sunny days.

On the other hand, warming alone might not harm the mites. In the Arctic, Coulson *et al*. (1996) found no change in mite populations and species composition between controls and soil heated by having small polythene tents covering them. At the same time, numbers of **Collembola** declined significantly. The number of juveniles of mites increased significantly in the polar semi-desert regions of the Arctic, suggesting that this life stage might survive better at warmer temperatures, ultimately increasing the population size overall.

Tropics

In the cloud forest of Costa Rica, Yanoviak *et al*. (2006) found abundant arthropods among the epiphytes (including but not limited to bryophytes). There seemed to be little difference in faunal frequency and abundance between the **secondary forest** (forests regenerating largely through natural processes after significant human and/or natural disturbance) and **primary forest** (forest with native

species and no indication of human intervention) except for the significantly greater abundance of ants (11.4% with more than 10 per sample) in the secondary forest compared to 1.7% in the primary forest. Wet versus dry season seemed to make little difference in abundance. There was a slight tendency toward more morphospecies (10%) of arthropods in the wet season compared to the dry season. Yanoviak and coworkers warned that arthropods might be undercollected during the dry season because they become dormant and therefore do not fall into the Tullgren funnel due to lack of movement.

Nadkarni and Longino (1990) found in montane forests of Costa Rica that relative abundances of the major arthropod taxa were "the same" in the canopy and on the forest floor. They interpreted this to mean that the organic matter was similar in these two habitats, resulting in similar invertebrate communities. On the other hand, densities were 2.6 times as high on the ground as in the canopy. The highly mobile ants seemed to have equal densities in both places. Mites were among the dominant taxa in both canopy and ground detritus, but were less abundant in the canopy. They considered more wind, more frequent mist, higher maximum air temperatures, and more frequent wetting/drying cycles as contributing to a high biomass (4730 kg ha^{-1}) of organic matter in the canopy. These same factors seemed to contribute to reduced densities of arthropods. Tree species seem to make little difference in contributions by the thick epiphytic mats (Lawton & Dryer 1980).

These invertebrates are major fragmenters of the organic matter in tropical montane forests, although in most sites oligochaetes (worms such as earthworms) are also major contributors (Collins 1980, Pearson & Derr 1986, Leakey & Proctor 1987). Reported differences in abundance of oligochaetes in other studies, accompanied by lower relative abundances of arthropods, may reflect the different sampling techniques, where this study used sifting methods and others used hand sorting (Nadkarni & Longino 1990).

Epizootic

Even in the miniature community of bryophytes, there are animals that get a free ride on other animals. Among these is the oribatid mite, ***Symbioribates papuensis*** (**Symbioribatidae**; Figure 133), that is epizoic on backs of Papuan weevils (Aoki 1966). The beetle genus ***Gymnopholus*** (subfamily **Leptopiinae**; Figure 131) is inhabited by both lichens and liverworts, and liverworts in turn house the oribatid mite (Gressitt & Sedlacek 1967). Gressitt and Sedlacek (1967) reported a new species of weevil from New Guinea (***Gymnopholus carolynae***) that had abundant algae, fungi, and mosses growing on its back.

Vertical Distribution

Various types of gradients exist in habitats, and the responses of mites is to have different communities in different areas of these gradients (Popp 1970; Behan-Pelletier & Winchester 1998; Proctor *et al*. 2002; Smrž 2006). Bryophytes can provide amelioration of some of the critical differences among habitats due to their ability to absorb water rapidly, reduce substrate evaporation, and reduce extremes of both moisture and temperature (Gerson 1982; Smrž 1992). Oribatid mites commonly are abundant where there is decaying plant material and high moisture, both of which are present in bryophyte communities (Bonnet *et al*. 1975; Seyd & Seward 1984).

Figure 131. ***Gymnopholus reticulatus*** with the moss ***Daltonia angustifolia*** living epizootically on the weevil. Mites are known to live in this association. Photo courtesy of Rob Gradstein.

Lindo *et al*. (2008) found that within one year, 90 artificial canopy habitats of soil and mosses attached to planks were colonized by 59 oribatid mite species. These artificial habitats were distributed at three heights on 10 western red cedar (*Thuja plicata*; Figure 132) trees and represented three patch sizes. The established communities exhibited a typical species-area relationship. Richness increased with moisture content and size of habitat patch. Hence, species richness and abundance decreased with increased height in the canopy. The community composition and species richness patterns exhibited a non-random distribution and were significantly nested. Non-randomness could be explained in part by individual species tolerances and dispersal abilities. Previously known canopy-specific species [***Eupterotegaeus rhamphosus*** (**Cepheidae**), ***Epidamaeus*** nr ***floccosus*** (**Damaeidae**; see Figure 11), ***Scheloribates*** (**Scheloribatidae**; Figure 133)] from the area were all present on the artificial substrata. These species were even found in the small, desiccated patches located highest in the canopy and exhibited drought tolerance and adaptations to living in a patchy environment. The earliest colonists were generally strongly desiccation tolerant. These canopy specialists seemed to lack dispersal limitation.

Figure 132. ***Thuja plicata*** showing vertical structure where mite communities differ by height in canopy. Photo by Abdallahh, through Creative Commons.

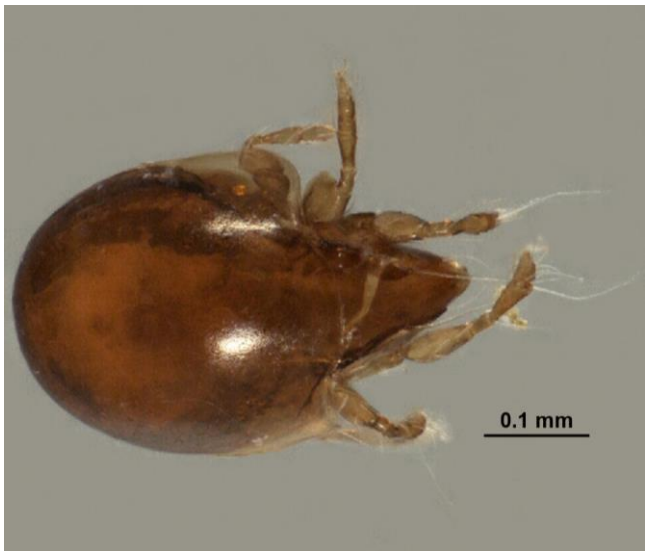

Figure 133. ***Scheloribates clavilanceolatus***. Some members of the genus are high-canopy bryophyte dwellers. Photo from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

Forest Habitat Strata

Vertical differences exist within the forest. In the canopy, bryophytes are often a primary habitat (Winchester *et al*. 1999). Proctor *et al*. (2002) found distinct communities among the base, trunk, and canopy habitats in Australia. Bonnet *et al*. (1975) examined the vertical gradient of mites at Tarn, France, from soil to arboreal mosses. There were 63 species of mites, although only 58 could be identified. The importance of temperature and humidity were clear, with invertebrate communities following the same transitions as the habitat. These communities can differ in both abundance and species composition. In the tropical montane forest of Costa Rica, where mites represented one of the numerically dominant groups, Nadkarni and Longino (1990) found that the forest floor fauna had a mean density 2.6 X that of the canopy.

In attempts to determine the impact of moss harvesting on invertebrate faunas, Peck and Moldenke (1999) compared the fauna at the stem base and at the tips of shrubs in the Eugene District, Oregon, USA. They found that presence of hardwood trees and greater abundance of mosses increased the mite fauna. At the bases of the shrubs, typical moss fauna were ***Ceratoppia*** sp. (**Ceratoppiidae**; Figure 134), ***Hermannia*** spp. (**Hermanniidae**; Figure 135), and ***Phthiracarus*** sp. (**Hermanniidae**; Figure 136) (all turtle mites). Samples at the tips were characterized by **microspiders** and **springtails**. Based on these community structures, they recommended that moss harvesting be prohibited in mixed or hardwood-dominated stands and from the lower 0.5 m of any shrubs.

Figure 134. ***Ceratoppia*** sp. Photo by Walter Pfliegler, with permission.

Figure 135. ***Hermannia reticulata***. Photo by Bold Systems Biodiversity Institute of Ontario, with permission.

Figure 136. ***Phthiracarus*** sp. Photo by Walter Pfliegler, with permission.

Wagner *et al*. (2007) examined the distribution of epiphytes and invertebrates on the bole of red maple trees (*Acer rubrum*; Figure 137) in Maine, USA. They found that mites were among the predominant fauna at the base and **Diptera** (flies) above 2 m. Gap harvesting reduced the cover of epiphytes and the arthropod fauna, suggesting that the epiphytic bryophytes could play a role in the distribution of these invertebrates.

Figure 137. ***Acer rubrum*** bark with epiphytes, home for mites and diptera. Photo by Wanda Rice, with permission.

Within Bryophyte Clumps

Because of moisture differences, and possible UV damage, vertical differences exist among mite communities within bryophyte clones (Dalenius 1962; Harada 1980). The importance of humidity differences (Smrž 1994) is reflected in the vertical positioning of the mites within the moss clone.

In Canada, nearly 50% of the 100 moss samples collected by Richardson (1981) had mites living among them. The distribution of mite species can differ within the vertical strata of the mosses, indicating differences in conditions at these depths (Harada & Aoki 1984; Usher & Booth 1984). Borcard (1993) found that the 38 species of oribatid mites in ***Sphagnum*** (Figure 95) differed between two vertical layers of moss. Evidence for these differences is further supported by the daily migrations of mites that have been observed in some mosses (Rajski 1958).

In a cloud forest in Costa Rica, Yanoviak *et al*. (2004) found a vertical distribution of mites within epiphytic mats of bryophytes, with a greater mass of oribatid mites occurring in the brown portions than in the upper green portions. The brown tissue was more dense and its grain was finer than that of the green portion. On the other hand, the green portions had a greater density and richness of arthropods than did the brown parts. Mites were the most abundant arthropod group in this habitat. As expected, Booth and Usher (1984) found an increase in arthropod abundance with an increase in moss dry mass.

Vertical Migration

Vertical migration permits some species to escape the heat and desiccating events of the day by escaping to deeper layers of the mosses. Among the moss habitats, this may be most prevalent in ***Sphagnum*** (Figure 95) habitats, where the surface is exposed to full sun and can become quite hot and dry while lower depths remain cool and moist. Popp (1962) observed such vertical migration behavior for ***Limnozetes ciliatus*** (see Figure 107-Figure 112) and ***Hypochthonius rufulus*** (Figure 138) in response to hummock temperature changes.

Figure 138. ***Hypochthonius rufulus*** on ***Sphagnum***. Photo by Walter Pfliegler, with permission.

Ceratozetes (**Ceratozetidae**; Figure 102) and ***Eremaeus*** (**Eremaeidae**; Figure 5-Figure 4) species migrate in the soil to optimize moisture and temperature conditions (Mitchell 1978). They also segregate by ages, with younger members occupying lower depths that have a more ameliorated climate. These migrate upward as adults. These two genera are also known among bryophytes, so it is likely that at least some of these bryophyte dwellers also exhibit vertical migrations.

Magalhães *et al*. (2002) showed that some mites respond to species-specific predator odors that stimulate their migration upward or downward in response. In tracheophytes, this behavior combination can actually benefit the plants. Mite predators sit in the rapidly growing

tender tips, causing the herbivorous mites to migrate downward, thus protecting these sensitive plant areas (Magalhães *et al*. 2002; Onzo *et al.* 2003) from mite herbivory. I can find no study to indicate whether bryophyte-dwelling mites respond to similar chemical stimuli of predators among the bryophytes. If they do, would this likewise protect growing tips from mite damage, or is their often fungivorous diet sufficient protection for the bryophytes? Might the chemical odors of the bryophytes override predator odors, or nullify them, or in some other manner ameliorate their effectiveness?

Elevational Differences

Elevational differences exist as well. Andrew *et al.* (2003) examined the elevational relationships of mites among bryophytes in New Zealand (Table 1-Table 2). Taxa on Mt. Field and Mt. Rufus represented the **Mixonomatides** and the families **Oribatellidae**, **Galumnidae**, **Oppiidae**, **Microzetidae**, **Cepheidae**, **Adelphacaridae**, **Mycobatidae**, **Phthiracaridae**, **Carabodidae** (Figure 139-Figure 140), and **Cymbaeremaeidae**. All but **Adelphacaridae** and **Cymbaeremaeidae** were collected in more than one location. On Mt. Otira, New Zealand, the researchers found **Oribatulidae**, **Eutieidae**, **Epilohmanniidae** (only at higher elevations of 1000-1500 m), **Oribotritiidae**, **Nanhermanniidae** (Figure 114), **Pedrocortesellidae** (the latter three only from lower elevations of 250 m), **Microzetidae** (1 location at 750 m), and **Tectocepheidae** (in 10 out of 12 locations at 1500 m only).

Elevational patterns for mite species richness were not in evidence in this study (Andrew *et al.* 2003), and those that did exist differed widely between mountains. Nevertheless, for some families, as mentioned above, distinct elevational ranges are suggested. Evidence is needed to tie these elevational differences to differences in bryophyte species. Nigel Andrew (Bryonet) suggested that moss species and growth form were important factors in determining arthropod abundance and diversity in the New Zealand mountains; these are likely to differ with elevation.

Table 1. Elevational distribution of mite families living among bryophytes on Kaikoura, New Zealand. Each location is represented by six samples. Elevations are in meters. Data are presence out of six locations at that elevation. From Andrew *et al.* 2003.

	m asl					
	1130	1225	1325	1425	1520	2000
Oribatellidae	4	5	1		6	1
Oribatulidae		4	1			5
Oppiidae		1	1			
Crotonidae						

Table 2. Family presence of mites among bryophytes at 250-m elevation intervals on three mountains in Tasmania and New Zealand. For Mt. Field and Mt. Rufus in Tasmania, two locations were included at each elevation; the numbers represent the number of locations. For Mt. Otira in New Zealand, 12 samples were included at each elevation. Locations are **Mt Field first line, Mt. Rufus second line, Mt. Otira third line.** From Andrew *et al*. 2003.

	m asl					
	250	500	750	1000	1250	1500
Mixonomatides	2	2	1	1	1	
	1					
Oribatellidae	1	2	2			
	2	2	1		1	
	7	1		5	3	
Galumnidae	1	1		1		
			1	1		
Oppiidae	1	1	2		2	
	2					
	7	1	1		2	10
Microzetidae	1		1	1	2	
	2	1		2	1	
			1			
Cephidae		1	1			
			1		1	
Adelphacaridae	1			1		
Mycobatidae	1	1	1	1		
Phthiracaridae		1	1		1	
	3	1		1	3	
Carabodidae		2	2	1		
Cymbaeremaeidae						
			1			
Mt Otira only						
Oribatulidae	5	3		2	2	
Euieidae	3	4			1	
Epilohmanniidae				1	2	6
Oribotritiidae	1					
Nanhermanniidae	3					
Pedrocortesellidae		2				
Tectocepheidae						10

Figure 139. Mite species in the family **Carabodidae**, sitting on a moss. Photo by Walter Pfliegler, with permission.

Figure 140. Mite species in the family **Carabodidae**, sitting on a moss. Photo by Walter Pfliegler, with permission.

Seasons

Sampling season will influence the abundance of mites in the soil (Popp (1970), and presumably among the bryophytes. Merrifield and Ingham (1998) found that the abundance of aquatic mites (and tardigrades) among mosses varied significantly between sampling dates in the Oregon Coastal Range, USA. Gerson (1969) reported oribatids that live on mosses under the snow. Block (1966) found that mites were most abundant in May and December, and least abundant in August in Westmorland, UK, but this can be modified by the weather.

Just as vertical differences exist within the moss mat on any given day, they likewise exist seasonally. Moss depths provide a safe overwintering habitat for mites, protecting them from extreme temperatures and desiccation. Popp (1962) found that the peatland oribatids ***Limnozetes ciliatus*** (**Limnozetidae**; see Figure 107-Figure 112), ***Ceratozetes parvulus*** (**Ceratozetidae**; see Figure 102), and ***Trimalaconothrus novus*** (**Malaconothridae**; see Figure 87) migrate to the deeper layers of the peat hummocks to spend the winter.

Gerson (1969) dug the mosses ***Ceratodon purpureus*** (Figure 141) and ***Bryum*** (Figure 142) out from 1.6 m of snow on Montreal Island, Quebec, Canada, and found many live ***Eustigmaeus*** (**Stigmaeidae**; Figure 143) present. These began to oviposit when warmed on a suitable substrate in the lab. It is likely that bryophytes are important overwintering sites for a number of mites. The ability of at least some members of this genus to eat mosses (Walter & Latonas 2011) may help them to survive there.

Figure 141. ***Ceratodon purpureus***, home for ***Eustigmaeus***. Photo by Bob Klips, with permission.

Figure 142. ***Bryum caespiticium***. ***Bryum*** serves as home for ***Eustigmaeus***. Photo by Bob Klips, with permission.

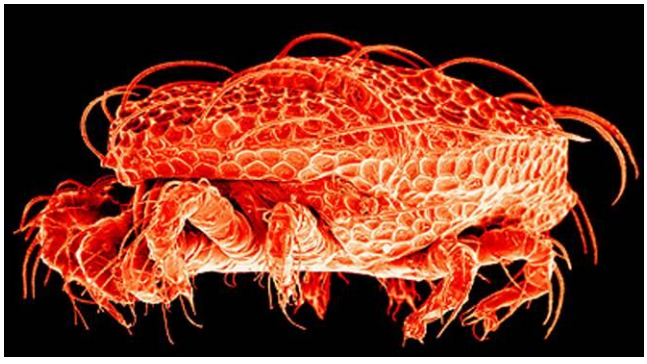

Figure 143. ***Eustigmaeus*** sp., a mite that can overwinter on mosses in Canada. Photo by David E. Walter and A. O'Toole, with permission.

Salmane (2000) investigated the seasonal activity of **Gamasina** (an infraorder of the **Mesostigmata**) mites (Figure 13) in soil under mosses in a pine forest in Latvia. She determined that the abundance and diversity of this predatory mite group was seasonally dynamic. These

changes in abundance and diversity related first to relative humidity and secondarily to temperature. The greatest diversity was in August (17 species), but some species (**Rhodacaridae**: ***Rhodacarus reconditus***) did not appear until October. In her April to October study, the greatest numbers of **oribatid** and **Gamasina** mites were in April and August.

Disturbance Effects

Starzomski and Srivastava (2007) conducted one of the few experimental studies on terrestrial arthropod communities, where mites (**Acari**) and springtails (**Collembola**) comprised part of the fauna. These were tiny animals, mostly less than 1 mm in length, that inhabited patches of the mosses ***Polytrichum*** (Figure 125) and ***Bryum*** spp. (Figure 142) on granitic outcrops in Vancouver, British Columbia, Canada. In their experiments, they simulated drought frequencies as a form of disturbance. Effects of humidity on ***Scutovertex minutus*** (**Oribatida**; see Figure 144) were already known from studies by Smrž (1994). The oribatid microarthropods may reach 200 or more morphospecies in an area of less than 20 m^2 (Starzomski & Srivastava 2007). In their BC study, 163 species were found, comprising 26,274 individuals.

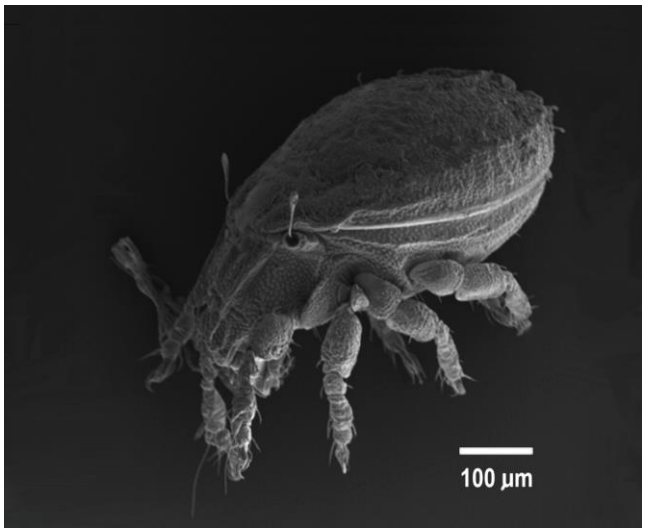

Figure 144. SEM of ***Scutovertex sculptus***, members of a genus that lives on ***Polytrichum*** and ***Bryum.*** Photo by Jürgen Schulz, with permission.

Connectedness between patches is important in determining number of species, although microarthropods may migrate across bare rock to other moss patches (Starzomski & Srivastava 2007). Increases in drought disturbances decreased the number of species, but not the number of individuals. On the other hand, fragmentation caused an increase in species abundance. In unconnected plots with no disturbance, the mean number of individuals was 620, whereas in the undisturbed connected patches, mean abundance was only 372. However, disturbance in the fragmented sites caused a drop in abundance below that of the other treatments. The smallest regions experienced the greatest rate of drop in both species richness and abundance (2.5X faster for species richness, 4X faster for number of individuals). In connected regions, oribatid mites exhibited a dampened response to disturbance compared to other species, perhaps due to protection from desiccation by their hard exoskeleton. For all the other taxa, abundance, body size, and trophic position had no effect on their responses to disturbance.

Although corridors are undoubtedly important in providing safe sites for migration between patches of bryophytes, they do not always provide the same benefits. Starzomski and Srivastava (2007) found that the microarthropods offer increased community resilience to disturbance and enhanced species richness in small patches. Corridors facilitate movement (Schmiegelow *et al*. 1997), maintain ecosystem processes (Gonzalez & Chaneton 2002; Levey *et al*. 2005), and prevent local extinctions (Gonzalez *et al*. 1998). However, Hoyle and Gilbert (2004) found that different connectivity treatments did not contribute to species richness, a finding supported by Starzomski and Srivastava (2007). Both of these studies did suggest that corridors are important under disturbance (in this case drought) conditions, supporting the contention of Honnay *et al*. (2002) that they may be very important in the presence of climate change.

Cryptogamic crusts are subject to disturbance by grazing animals. Within these crusts of lichens, mosses, and algae/Cyanobacteria, many invertebrate types dwell, including mites (Brantley & Shepherd 2004). In a piñon-juniper woodland in central New Mexico, 29 of 38 taxa of invertebrates occurred on mossy patches and 27 on mixed lichen and moss patches. Mosses had the highest abundance, suggesting that their ability to hold moisture might benefit these organisms. Furthermore, abundance was greater in winter than in summer.

Pollution Indicators

Watermites (**Prostigmata**) can serve as bioindicators of pollution in streams, in part because they are affected by the changes in moss growth caused by the pollution (Bolle *et al*. 1977). Most moss mites (Oribatida) decline in numbers when exposed to industrial pollution. On the other hand, the pollution-tolerant mite ***Hygrobates fluviatilis*** (**Hygrobatidae**Figure 145) increases with industrial effluent additions (Bolle *et al*. 1977).

Figure 145. ***Hygrobates fluviatilis,*** a pollution-tolerant moss mite. Photo by Nigrico through Creative Commons

Terrestrial mites can be used as well; in a Scots pine forest in Poland, bryophyte mite fauna responded to nitrogen fertilizer pollution (Seniczak *et al*. 1995).

Recent evidence of increasing levels of UV-B suggest that bryophytes could provide refugia for invertebrates such as mites, blocking the dangerous radiation from reaching their inhabitants (Robson *et al.* 2001). To my surprise, Robson and coworkers found that biodiversity of **microfauna** among ***Sphagnum*** (Figure 95) species increased in plots exposed to higher UV-B levels. Nevertheless, mites responded negatively to the increase in near UV-B by having reduced numbers (Robson *et al*. 2005). Robson and coworkers suggested that under UV-B radiation at near-ambient levels, leaching of nutrients from the mosses may result and possibly changes occur in the morphology of the ***Sphagnum*** capitulum.

Steiner (1995a) found that air pollution can alter the species composition and abundance of the mites among mosses. Richness decreases and the mite communities become more uniform. The species ***Zygoribatula exilis*** (**Oribatulidae**; see Figure 20) proved to be the most useful as an air quality indicator. Not only does air pollution have direct effects on the mites, but it also can alter relative humidity, substrate availability, and *p*H of the mosses, which in turn influence the mite species able to live there. Even so, the mites are less sensitive to pollution than nematodes and tardigrades (Steiner 1995b). Exceeding tolerance demonstrated by tardigrades is quite a feat.

Dispersal of Mites and Bryophytes

It is likely that dispersal works both ways in the moss-mite relationship. Several studies have indicated the role of mites in bryophyte dispersal. Both mites and bryophytes can be dispersed aerially (Mandrioli & Ariatti 2001).

Risse (1987) pointed to studies that indicate the bryophyte gemmae do not develop below the ground surface, and this includes rhizoidal gemmae and tubers. But the attachment of gemmae of ***Schistostega pennata*** (Figure 146-Figure 149) to the legs of mites indicates that these bryophytes have a means of dispersal that is likely to drop off at least some of the propagules at the surface (Ignatov & Ignatova 2001). Such a form of dispersal is likely to remove them from the territory of the parent, where the gemmae may be inhibited, presumably by chemicals from the parent.

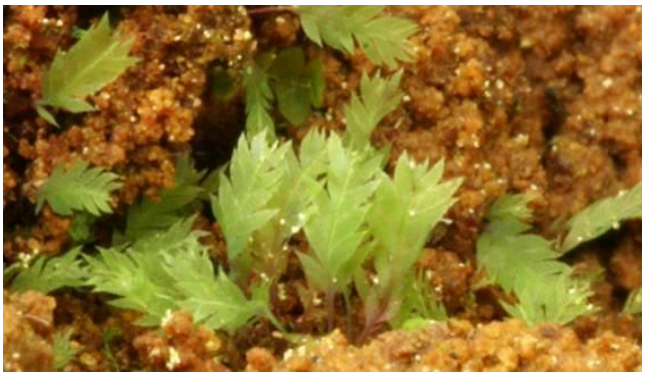

Figure 146. ***Schistostega pennata*** mature leafy gametophyte plants. This species has gemmae that are dispersed by attaching to the legs of mites. Photo courtesy of Martine Lapointe.

Figure 147. ***Schistostega pennata***. Reflective protonemata with a few leafy plants. The protonemata produce gemmae that can be dispersed by mites. Photo courtesy of Martine Lapointe.

Figure 148. ***Schistostega pennata***. Young leafy plants developing from the protonemata. Photo courtesy of Misha Ignatov.

Figure 149. ***Schistostega pennata***. Microscopic view of the protonemata, showing the loosely connected cells that can develop into new leafy plants. The long, fusiform branch is a protonemal gemma that can be carried to the surface by mites. Photo courtesy of Misha Ignatov.

Zhang and coworkers (2002) provide further evidence of possible transport of gemmae in the moss ***Octoblepharum albidum*** (Figure 150-Figure 151). In this species, mites consume the gemmae, and in the process could manage to transport some of those gemmae to new locations. At the very least, they are likely to dislodge some gemmae that drop before they get eaten. One must wonder if gemmae cells survive the digestive system, providing yet another mechanism for transport. More experiments waiting to be done!

Figure 150. ***Octoblepharum albidum***, a moss whose gemmae are dispersed by mites. Photo by Janice Glime.

But mites themselves can have some difficulties getting dispersed. Sudzuki (1972) did wind tunnel experiments with mosses, using various wind speeds. During the two months of experiments, mites were apparently never dispersed, and the Crustacea and Arachnomorpha were rarely dispersed at wind velocities under 2 m s^{-1}. They concluded that mites are not transported by wind. On the other hand, this does not preclude the passive dispersal of mites along with mosses that are moved by the wind, especially in such vulnerable locations as the canopy or among the terrestrial moss balls.

Lindo (2011) suggested mosses might serve as "magic carpets" for the mites. She reported 57 species of oribatid mites among litterfall, including mosses, in her study of canopy and ground level litter. She found a high species richness in litterfall in canopy habitats and suggested that the mosses not only served as transportation vessels, but that they also increased survivorship during the journey.

Figure 151. Gemmae of ***Octoblepharum albidum***, potentially distributed by mites that also eat some of them. Photo by Li Zhang, with permission.

No Place for Generalists?

At the beginning of the first subchapter on mites, I introduced the question "Can we use the literature to answer this question for [mites in] any mossy habitats?" My first response to this is that I would have to change my professional path from bryology to acarology to attempt to answer it. My second response is almost as wishy-washy. Certainly many examples in this chapter have included mites that go to bryophytes to replenish moisture, and probably to hide. These might be called generalists because they use a variety of habitats. But we know that many mites that are plant pests seem to be specialists. The mosses, on the other hand, often seem to be only a refuge habitat when the primary habitat becomes unavailable or unsuitable. But the bryophytes where they seek refuge may in some cases be the only suitably moist habitat. It's a good thing that some of these plant specialists can go for a long time without eating.

I am inclined to think that those mites that live on bacteria and fungi are generalists, able to live wherever there is sufficient moisture and a fungal or bacterial food source. For many, this means soil, leaf litter, and mosses.

At the other end of the spectrum are those mites that eat mosses and lay their eggs there, but how many of these can survive as well in other locations? To answer that question we must await more research, experimentation, and publication of older literature on the web. And before that can provide us with definitive answers, DNA-based identification of species will be necessary to separate the cryptic species that may indeed represent specialists.

Limitations of Methods

The high abundance of mites among bryophytes often requires special extraction techniques (Borcard 1986; see discussion in Chapter 6-1 of this volume). When general surveys are done, they typically have a bias against some groups of organisms and favor others. Furthermore, most require that the organisms are mobile, so dormant organisms are missed. Yanoviak *et al*. (2003) reminded us of the limitations of fogging, a common canopy method, for invertebrates such as mites because they would typically remain within the moss mat.

Likewise, information on bryophyte-dwelling mites requires special and extensive searching techniques. Most of the information is hiding in species descriptions, or not mentioned at all. As I am finishing this chapter, I have the feeling I have only scratched the surface on the available information of bryophyte-dwelling mites.

Nelson and Hauser (2012), students at Lewis and Clark College working on an undergraduate report, tested two methods of surveying invertebrate communities of epiphytic bryophytes in the Tryon Creek State Natural Area, Oregon, USA. They compared arthropod extraction using a Berlese funnel to a simple water technique. In the latter, they examined ten drops of water from each wet bryophyte sample. Acari were the most abundant and most frequent. They could find no differences in communities between mosses and liverworts. But a comparison of the two extraction techniques demonstrated almost no overlap in taxa! Rather, the two techniques complemented each other. The Berlese funnel sampling provided the greatest numbers of different species of Acari.

Order Acari – Ticks

Ticks are not organisms we normally think of as moss fauna, but Slowik and Lane (2001) showed that the western black-legged tick ***Ixodes pacificus*** (**Ixodidae**; Figure 152) was more common on moss-covered oak trees than on trees without mosses. They found that the moss reduced the

surface temperature by ~1.9ºC and increased the relative humidity 2.5%, perhaps contributing to the greater abundance of these ticks as bryophyte associates. Slowik and Lane suggested that the bark provided refugia and that the western fence lizard could be responsible for presence of these ticks on the bark. Mites, on the other hand, are quite common as bryophyte fauna (Kinchin 1990; Seyd & Colloff 1991; Seyd *et al.* 1996).

Figure 152. ***Ixodes pacificus***, an inhabitant of moss-covered oak trees. Photo by CDC/ Amanda Loftis, William Nicholson, Will Reeves, Chris Paddock/ James Gathany, through Creative Commons.

In the Antarctic, the tick ***Ixodes uriae*** (**Ixodidae**; Figure 153) likewise makes use of mosses. It lays its eggs under mosses or grasses (Gressitt 1967).

Figure 153. ***Ixodes uriae***, an Antarctic that lays its eggs under mosses. Photo from Tromso University Museum, through Creative Commons.

SUBPHYLUM MYRIAPODA

The myriapods represent a much smaller subphylum (~13,000) than that of the **Arachnida** (Wikipedia: Myriapoda 2010). The name myriad literally refers to 10,000 (legs). Although this is not literally true, these arthropods can have from fewer than 10 up to 750 legs. Three classes are represented among bryophytes: **Chilopoda** (centipedes), **Diplopoda** (millipedes), and **Symphyla** (garden centipedes). The eggs hatch into miniature myriapods with fewer segments and legs. Secretions from many of the members can cause one's skin to blister.

Class Chilopoda (Centipedes)

Centipedes are mostly carnivorous and are distinguished by one pair of legs per segment (Wikipedia: Chilopoda 2010). They lack a waxy covering and lose water easily, hence preferring high humidity and low light (Mitić & Tomić 2002). It is likely this dependence on water that makes mosses such as ***Sphagnum*** suitable habitat for some species. ***Lithobius curtipes*** (**Lithobiidae**; Figure 154) lives among the mosses [***Polytrichum commune*** (Figure 156), ***Sphagnum girgensohnii*** (Figure 157), ***S. squarrosum*** (Figure 155)] on the forest floor in Finland (Biström & Pajunen 1989). In Great Britain, Eason (2009) found it in great numbers in moss, under stones, and on bark. In the Ural Mountains, this is the only centipede species that extends into the tundra (Farzalieva & Esyunin 2008). ***Geophilus proximus*** (**Geophilidae**; see Figure 158) also occurs on ***Polytrichum commune*** (Biström & Pajunen 1989).

Figure 154. ***Lithobius curtipes***, a centipede inhabitant of ***Sphagnum girgensohnii***, ***S. squarrosum***, and ***Polytrichum commune***. Photo by Stefan Schmidt through Creative Commons.

Figure 155. ***Sphagnum squarrosum***, a forest floor species that is home to some species of centipedes. Photo by Michael Lüth, with permission.

Figure 156. ***Polytrichum commune***, home to some centipedes, but unfit for many other bryophyte dwellers. Photo by Michael Lüth, with permission.

Figure 157. ***Sphagnum girgensohnii***, a forest floor moss that is home to some species of centipedes. Photo by Michael Lüth, with permission.

Figure 158. ***Geophilus carpophagus***, a centipede member of a genus that is present among bryophytes, shown here on leaf litter. Photo by Walter Pfliegler, with permission.

In their study of invertebrate communities among bryophytes [predominantly ***Atrichum undulatum*** (Figure 159), ***Brachythecium rutabulum*** (Figure 160), and ***Hypnum cupressiforme*** (Figure 161-Figure 162)] in the Czech Republic, Božanić *et al*. (2013) found that the **Chilopoda** chose habitats on the ground or close to it. They, like the **Diplopoda** and **Isopoda**, were numerous in small cushions, whereas the **Enchytraeidae** (**Annelida**) were abundant in larger moss carpets. The larger centipedes, including adults of somewhat smaller species, feed on smaller chilopods such as ***Lithobius*** (**Lithobiidae**; Figure 154) species that inhabit the soil surface (Rawcliffe 1988). This causes some of the ***Lithobius*** species to escape into the mosses at the lower parts of living trees (Biström & Pajunen 1989). Others such as ***Lithobius mutabilis*** (Figure 163) and juveniles of other species of ***Lithobius*** occur among mosses on larger trees (Božanić *et al*. 2013).

Figure 159. ***Atrichum undulatum***, home for ground-dwelling **Chilopoda**. Photo by Michael Lüth, with permission.

Figure 160. ***Brachythecium rutabulum***, one of the ground mosses chosen by **Chilopoda** as a home. Photo by Michael Lüth.

Figure 161. ***Hypnum cupressiforme*** habitat, housing species of **Chilopoda** that live near the ground. Photo by Dick Haaksma, with permission.

Figure 162. ***Hypnum cupressiforme*** var ***cupressiforme***, home for centipedes near the ground. Photo by David T. Holyoak.

Figure 163. ***Lithobius mutabilis*** female, a species that lives among mosses on larger trees. Photo by Walter Pfliegler, with permission.

Class Diplopoda (Millipedes)

The millipedes are unusual in having each pair of segments fused, hence having two pairs of legs per fused segment (Wikipedia: Diplopoda 2010; Figure 164). They are not common among mosses, or at least there are few reports. Biström and Pajunen (1989) found ***Polyzonium germanicum*** (**Polyzoniidae**; Figure 165), ***Proteroiulus fuscus*** (**Figure** 166), ***Polydesmus complanatus*** (**Polydesmidae**; Figure 167), and ***Leptoiulus proximus*** (**Julidae**; Figure 170), on the ***Polytrichum commune*** (Figure 156) in Finnish forests. ***Polydesmus complanatus*** occurred not only on ***Polytrichum commune***, but also on ***Sphagnum girgensohnii*** (Figure 157) and ***S. squarrosum*** (Figure 155).

Figure 164. Millipede on moss. Photo courtesy of Josh Jones.

Figure 165. ***Polyzonium germanicum***, a millipede that lives among bryophytes, shown here on leaf litter. Photo by Ruth Ahlburg, with permission.

Figure 166. ***Proteroiulus fuscus***, one of the few millipedes that lives among bryophytes, shown here on a bed of leafy liverworts. Photo by E. C. Schou, with permission.

Figure 167. ***Polydesmus complanatus***, a millipede known from both ***Sphagnum*** and ***Polytrichum***, shown here on a mat of mosses. Photo by Joerg Spelda, SNSB, Zoologische Staatssammlung Muenchen, through Creative Commons.

Božanić *et al*. (2013) found that type of substrate and height above ground are often the most important factors in determining the invertebrate fauna of the bryophytes in the Litovelské luhy National Nature Reserve, Czech Republic. The mosses here are mostly ***Atrichum undulatum*** (Figure 159), ***Brachythecium oedipodium*** (Figure 168), ***B.***

rutabulum (Figure 160, and ***Hypnum cupressiforme*** (Figure 161-Figure 162). As a whole, these house the highest numbers of invertebrate species. In contrast to the **Chilopoda**, the **Diplopoda** live among mosses high in the trees, sometimes as high as 160 cm above the ground. They prefer small cushions to larger carpets.

Figure 168. ***Brachythecium oedipodium***, a moss that houses **Chilopoda**. Photo by Michael Lüth, with permission.

Polydesmus angustus (**Polydesmidae**; Figure 169) commonly make nests on moss cushions in London, UK, especially during April to July (Banerjee 1973). The nests are constructed from "worked-up" soil from the gut of the female. As the millipedes develop, different instars construct their own molting chambers using bits of soil and humus.

Figure 169. ***Polydesmus angustus*** at Crowle Moors, UK. Photo by Brian Eversham, with permission.

Figure 170. ***Leptoiulus proximus***, a millipede known from *Polytrichum commune*. Photo by Stefan Schmidt through Creative Commons.

In the UK, Stenhouse (2007) reported ***Ommatoiulus sabulosus*** (striped millipede; **Julidae**; Figure 171) in moss and the daddy-long-legs ***Nemastoma bimaculatum*** (**Nemastomatidae**; Figure 172) under moss.

Figure 171. ***Ommatoiulus sabulosus*** on mosses. Photo by Roger S. Key, with permission.

Figure 172. ***Nemastoma bimaculatum***, a daddy-long-legs that lives under mosses. Photo by Tom Murray, through Creative Commons.

Tachypodoiulus niger (black snake millipede; **Julidae**; Figure 173), a millipede of chalky and limestone soils, is very common in the UK and occurs among mosses and similar habitats (Stenhouse 2007). Haacker (1968) considers it to be a dry-resistant or xerophilous species that prefers cool temperatures, but has only limited freezing tolerance (David & Vannier 1997). ***Tachypodoiulus niger*** is active mostly from one hour after sunset to one hour before sunrise, but can become active in the afternoon during summer (Banerjee 1967). When disturbed, it will coil itself into a spiral with its legs on the inside and its head in the center (Figure 174; Wikipedia 2012), but it also has the option to flee with side-winding movements like some snakes. These millipedes feed on algae, detritus, and some fruits such as raspberries (Wikipedia 2012).

Figure 173. ***Tachypodoiulus niger*** on a mat of moss. Photo from Wikimedia Commons.

Figure 174. ***Tachypodoiulus niger*** curled in its defensive position. Note legs on inner side of spiral and head in the middle. Photo from Wikimedia Commons.

Josh Jones (pers. comm.) found ***Cylindroiulus punctatus*** (**Julidae**; Figure 175) on a species of the moss ***Thuidium*** (Figure 175). It has a diurnal cycle with a major activity period from one hour before sunrise to one hour after in April, May, and July, but also one hour before sunset to one hour after throughout March-August except July (Banerjee 1967).

Figure 175. The moss ***Thuidium*** sp. with the millipede ***Cylindroiulus punctatus.*** Photo courtesy of Josh Jones.

In January 2012, Erin Shortlidge queried Bryonet about an unusual invertebrate she found among the bryophytes. This, Bryonetters identified as the millipede ***Polyxenus*** (**Polyxenidae**; Figure 176-Figure 177), differing somewhat from the European ***P. lagurus*** (Figure 178) (Edi Urmi, Bryonet 8 January 2012). The bristles serve as defense against ants (Paul G. Davison, Bryonet 8 January 2012). Jean Faubert offered the identification of ***P. fasciculatus*** (Figure 176-Figure 177).

Figure 176. Ventral view of ***Polyxenus lagurus*** or ***P. fasciculatus*** from ***Ceratodon purpureus*** (Figure 141). Photo courtesy of Erin Shortlidge.

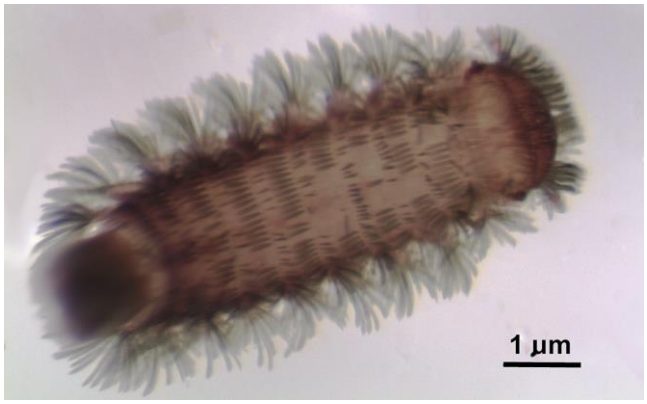

Figure 177. Dorsal view of ***Polyxenus lagurus*** or ***P. fasciculatus*** from ***Ceratodon purpureus***. Photo courtesy of Erin Shortlidge.

Figure 178. ***Polyxenus lagurus***. Photo by Mick E. Talbot, through Creative Commons.

Božanić (2008) found that the most abundant taxa of invertebrates among mosses were **Isopoda** (439 individuals among 66 moss samples) and **Diplopoda** (240 individuals). The most important factors in determining taxa were type of substrate, height above ground, and size of moss sample. For epiphytic bryophyte dwellers, the tree diameter was important. One should exercise some caution in interpreting these results because researchers used a Tullgren funnel with heat extraction, a method that works against less-mobile organisms that are unable to escape the moss clump before dying from heat or desiccation.

Epizootic Bryophytes

Rob Gradstein (14 November 2011) sent me a note that I might be interested in a Colombian millipede with ten bryophyte species (Figure 179) growing on it! Of course I was interested. These ten species represented five families (**Fissidentaceae**, **Lejeuneaceae**, **Metzgeriaceae**, **Leucomiaceae**, **Pilotrichaceae**) that comprised both mosses and liverworts (Martínez-Torres *et al*. 2011), a record Gradstein suggested might be suitable for the Guinness Book of World Records. The millipede of interest is ***Psammodesmus***, ultimately named ***Psammodesmus bryophorus*** (**Platyrhacidae**; Figure 180), from a transitional Andean-Pacific montane rainforest in Colombia (Hoffmann *et al*. 2011).

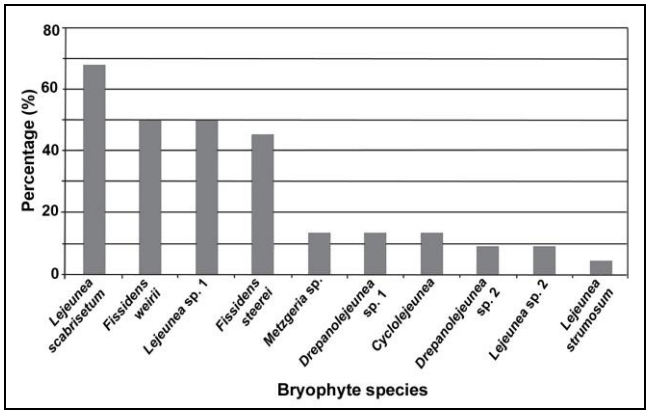

Figure 179. Percentage of bryophyte species on the exoskeletons of ***Psammodesmus bryophorus***. Redrawn from Martínez-Torres *et al.* 2011.

Figure 180. ***Psammodesmus bryophorus*** male with bryophytes in numerous positions on the dorsal exoskeleton. Photo by Shirley Daniella Martínez-Torres, with permission.

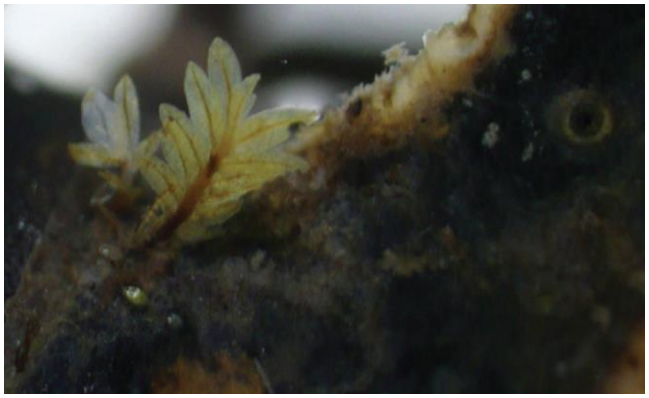

Figure 181. The moss ***Fissidens*** sp. on ***Psammodesmus bryophorus.*** Photo by Shirley Daniella Martínez-Torres, with permission.

Out of 18 individuals of ***Psammodesmus bryophorus*** (**Platyrhacidae**; Figure 180), 11 had more than 400 individuals of bryophytes, mostly on the dorsal side. In all, 22 individuals were inspected, and 15 of these had a species mosaic, primarily of ***Lepidopilum scabrisetum*** (Figure 182), ***Lejeunea*** sp. 1 (Figure 183-Figure 184), and ***Fissidens weirii*** (Figure 181) (Martínez-Torres *et al.* 2011). All species were epiphylls except for the two **Fissidentaceae** species, which are typical of soil. The bryophytes were especially located on the keels (Figure 181-Figure 185).

Figure 182. ***Lepidopilum scabrisetum***, a species that can live on the millipede ***Psammodesmus bryophorus***. Photo by Claudio Delgadillo, with permission.

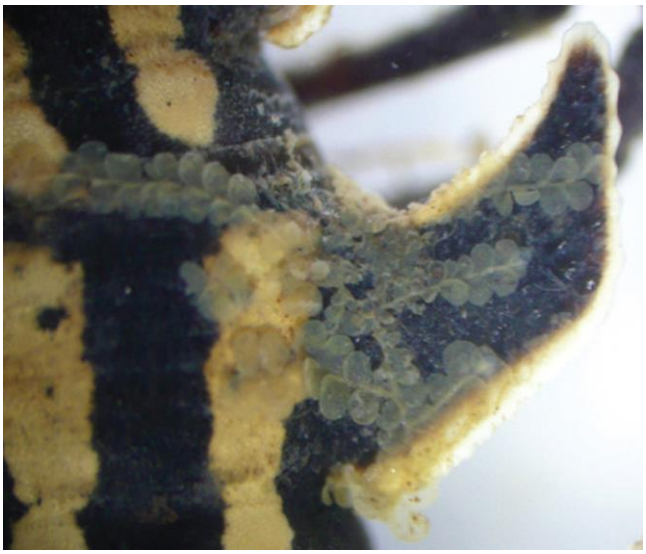

Figure 183. A leafy liverwort in the family **Lejeuneaceae** on ***Psammodesmus bryophorus.*** Photo by Shirley Daniella Martínez-Torres, with permission.

Figure 184. ***Lejeunea*** *cf* ***aphanella***, member of a genus that inhabits the millipede ***Psammodesmus bryophorus***. Photo by Michaela Sonnleitner.

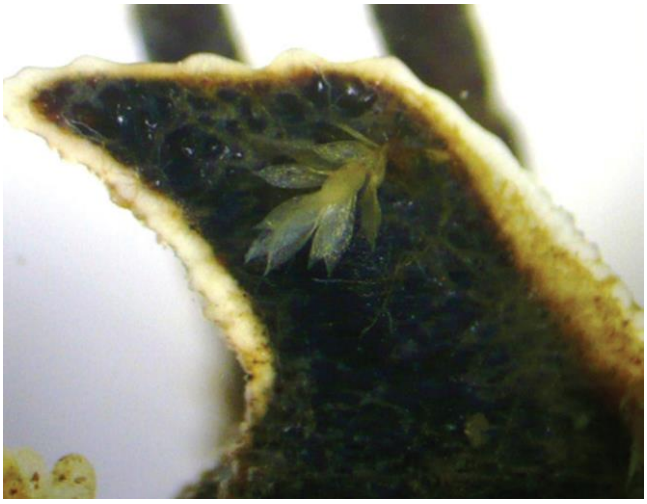

Figure 185. **Pilotrichaceae** on the exoskeleton of ***Psammodesmus bryophorus***. Photo by Shirley Daniella Martínez-Torres, with permission.

Class Pauropoda

Pauropods (Figure 186) are small, light-colored arthropods that resemble centipedes but are more closely related to millipedes. They live mostly in the soil and leaf litter, but some find mosses to be a suitable habitat (Greenslade 2008). In the temperate rainforests of Tasmania the mosses typically have a higher moisture content than their usual habitats elsewhere, and here one can find numerous **Pauropoda**. Greenslade found fifteen species among mosses in 79 collection records. These species were not common in other habitats of the collections areas, attesting to the importance of the mosses as a habitat.

Figure 186. Typical member of Pauropoda. Photo by David R. Maddison through Tree of Life Creative Commons.

Class Symphyla

This small class includes the common house-hold centipede with the long legs. Symphylans lack eyes, so their long antennae serve as sensory organs. The female lays her eggs and attaches them in crevices or to moss or lichen with her mouth (Barnes 1982). In the Finnish forests, Biström and Pajunen (1989) found an unidentified member of the **Scutigerellidae** (Figure 187) in two samples of ***Polytrichum*** (Figure 125).

Figure 187. ***Scutigerella*** sp., member of a family of symphytans know to inhabit bryophytes. Photo by Walter Pfliegler, with permission.

Summary

Bryophytes on the forest floor can provide unique habitats that have moss mite faunas different from that of the leaf litter. However, it is often the interface between the bryophytes and the soil where mites find food and suitable moisture environments.

Epiphytic leafy liverworts with lobules seem to be especially good at providing both a safe site and moisture, and fecal pellet volatile compounds suggest they are also a food source. This lobule niche is especially important in the tropical canopy.

Aquatic bryophytes provide safe sites not only against some predators, but against the rapid current in streams. In peatlands, the need for calcium carbonate, unavailable in the low *p*H, can be avoided by using calcium oxalate in the hardening of the cuticle.

Peatland genera differ between Europe and North America, with ***Limnozetes*** and ***Malaconothrus*** dominating in Canadian peatlands. ***Limnozetes*** is also the most species-rich and its communities may be useful in characterizing peatlands. Oribatids are the predominant mite group in both European and North American peatlands.

Peatland pools may have ***Hydrozetes***. Predation by **Odonata** causes some mites to hide in the concavity of the upper surfaces of ***Sphagnum*** leaves.

In the Antarctic, bryophytes can have temperatures up to 13°C above the ambient air temperature; some mites are able to supercool. Tropical bryophytes, especially epiphytes, are often rich habitats for invertebrates, including mites. The mites can contribute to the breakdown of canopy litter and thus have a role in nutrient cycling.

Vertical zonations exist among both the bryophytes and the mites, with the canopy increasing stresses due to UV-B light and desiccation. Within a bryophyte mat, zonation can separate communities of the older, brown portions and the young growing tips. The lower brown

portion of these two habitats differs in providing more decaying material, greater moisture, and less exposure to UV-B radiation. The temperature at that depth may be greater or lower than near the surface and is usually buffered compared to apical portions. The apical green portions (growing tips) provide greater ease of movement and fresh moss material for those able to use it as food.

Vertical migrations permit mites to seek suitable combinations of moisture and temperature within the moss mat. Some may migrate in response to predators, and some may migrate as a response to entering a new life cycle stage.

Communities of bryophyte-dwelling mites differ as elevation increases, with both numbers and kinds of species changing. Seasons affect numbers, with most mites becoming dormant during cold seasons. Some mites will migrate lower into the ground or lower portions of the moss to escape cold of winter or heat of summer.

When bryophyte patches are disturbed, corridors help mites to reach other patches, although some will traverse bare rocks and soil to reach a new patch. Dispersal is passive in most cases and does not seem to be facilitated by wind, but mites can be dispersed with their mossy shelter. On the other hand, mobile mites can carry sperm and gemmae to new locations.

Mites can serve as pollution indicators and monitors. Most will decline in numbers under stress of industrial pollution. However, ***Hygrobates fluviatilis*** will actually increase in numbers. Most species are sensitive to UV-B light and will respond negatively.

It is likely that moss mites provide a significant role in recycling nutrients from moss communities back to the ecosystem. This miniature ecosystem and the role of its fauna is poorly known and may yield fascinating relationships as we explore the interrelationships.

Ticks, centipedes, and millipedes occur among bryophytes, but both diversity and numbers are low.

Acknowledgments

David Walter provided invaluable insights into the mites and provided a critical review of that portion of this sub-chapter. Andreas Wohltmann checked identifications on the images I obtained from the internet and provided me with replacements and additional images as well as reference material and his own observations of bryophyte-dwelling mites. Benito Tan helped me to obtain the picture of pearling, provided by Loh Kwek Leong. Andi Cairns provided invaluable help in telling the story of the lobule mites and providing images. Thank you to Rob Gradstein and Pina Milne for alerting me to the publications on ***Psammodesmus bryophorus.*** Many people have contributed to the images; I especially thank all those generous people who have placed their wonderful images in the public domain.

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CHAPTER 10-1
ARTHROPODS: CRUSTACEA – COPEPODA AND CLADOCERA

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CHAPTER 10-1
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Figure 1. ***Simocephalus*** sp. with eggs in the carapace. Note the white ***Vorticella*** on the lower left edge of the carapace and near the base of the antennae. Photo by Jasper Nance through Creative Commons.

SUBPHYLUM CRUSTACEA

Crustaceans (Figure 1) are those tiny arthropods that most of us have never noticed on the bryophytes. But in some habitats, and some parts of the world, the bryophytes – invaders of land – are home for such terrestrialized arthropods.

This large subphylum is mostly marine or aquatic, including such familiar animals as barnacles, crabs, crayfish, krill, lobsters, and shrimp (Wikipedia: Crustacean 2011). But it is mostly the smaller animals, the microcrustacea, that inhabit the bryophytes. The Crustacea are distinguished from other arthropods by their two-parted limbs (**biramous**; *e.g.* the pincers on the end of a crab claw or divided antenna of ***Daphnia*** or ***Simocephalus*** – Figure 13) and a life cycle that includes a **nauplius** larva stage (first larval stage of many crustaceans, having an unsegmented body and usually a single eye, Figure 2), although most have additional larval stages after that. Almost all of them have a chitinous exoskeleton.

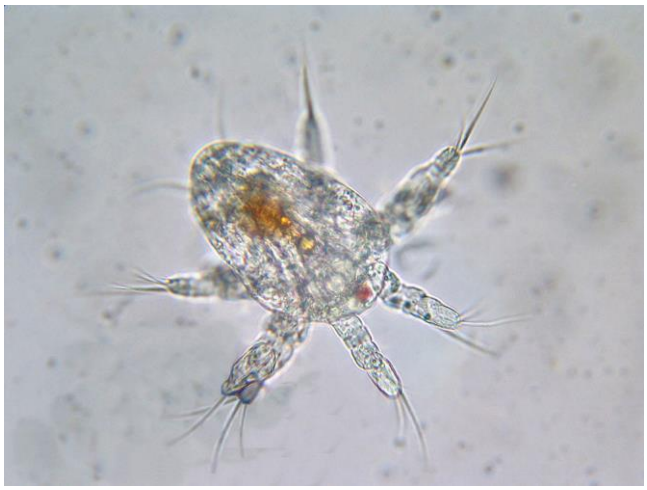

Figure 2. Nauplius of copepod. Photo from Wikipedia Creative Commons.

Reproduction

Most crustaceans have separate sexes, but some change sex and many are **parthenogenetic**, with females producing viable eggs that develop into new organisms in the absence of fertilization (Wikipedia: Crustacean 2011). Eggs are generally released into the water column, but some **isopods** form a brood pouch and carry their eggs and young around with them. Many **copepods** form egg sacs that hang from the body until the young hatch. **Decapods** typically carry their eggs attached to their swimmerets. The **meiofauna** [small metazoans that pass through 500µm or greater sieves, but are retained on 40 or 62 or 40 µm sieves (Dražina *et al*. 2011)] of springs typically have shorter life cycles, permitting such groups as cyclopoid copepods to have a rapid recruitment ability (Robertson 2002) and other copepods and ostracods to develop rapidly compared to insects, completing their development in only a few months (Dole-Olivier *et al*. 2000).

Dispersal

As with mites and other bryophyte dwellers, microcrustacea might be dispersed on a "magic carpet" – bryophyte fragments on which they are living. Sudzuki (1972) tested this hypothesis by exposing moss-soil samples to wind velocities of 2.9 m s^{-1}. Sampling at distances of 100-400 cm from the "wind" source, they determined that even after 2 months, wind velocities up to 2 m s^{-1} failed to disperse the Crustacea. Those animals dispersed were primarily protozoa. Nevertheless, encysted animals could get dispersed with bryophyte fragments or even with moss clumps that get carried by small mammals or wind.

Habitat Fragmentation

Microarthropods must move from one leaf patch to another, or from hiding places to food sources. During this time, especially if disturbed during the daytime, they are vulnerable to desiccation. Gonzalez *et al*. (1998) experimented with such fragmented microcosms to determine parameters that led to success of the inhabitants. They found that when microecosystems were fragmented, species declines occurred. But when the patches were connected by habitat corridors, much as has been shown for large mammals, both abundance and distribution of the fauna experienced a rescue effect through immigration. Bryophytes can often serve as such corridors, providing places to replenish lost moisture and to hide from predators.

Gonzalez and Chaneton (2002) used bryophyte habitats for experimentation. They fragmented the bryophyte communities and found that this system likewise experienced loss of both faunal species richness and community biomass. Rare species were more likely to become extinct. Moss habitat corridors that connected fragments to a larger "mainland" of bryophytes permitted immigration and maintained microarthropod richness, abundance, and biomass in the fragments.

While we tend to view corridors as continuous suitable habitats, such continuity is probably not necessary for the larger arthropods like isopods. They can use the bryophyte clumps as islands of safety between larger suitable habitats such as leaf litter.

Habitat Importance

Krebs (2001) reminded us that habitat heterogeneity is related to the creation of more ecological niches. Bryophytes can create many niches, providing protected space for the small microcrustaceans. Srivastava *et al*. (2004) contend that moss-arthropod ecosystems form natural microcosms that are useful for testing such concepts as fragmentation, metacommunity theory, and connections between biodiversity and ecosystem processes. Their small size, short generation times, hierarchical spatial structure, and contained, definable systems provide advantages in conducting field experiments that are subject to natural conditions and interactions with neighboring communities. The authors argue that "natural microcosms are as versatile as artificial microcosms, but as complex and biologically realistic as other [larger] natural systems."

Terrestrial

Acosta-Mercado *et al*. (2012) found strong support for the hypothesis that abiotic factors (especially water chemistry of the bryophytes and *p*H) are important determinants of terrestrial microcrustacean diversity. They added that water-holding capacity is correlated with the morphology and canopy structure of the bryophytes. Roughness of the bryophyte canopy in the Bahoruco Cloud Forest, Cachote, Dominican Republic, was important in determining differences in species composition. For amoebae, the lowest species richness was on ***Acroporium pungens*** (Figure 3), a species with low roughness and faunal density, whereas ***Thuidium urceolatum*** had the highest roughness index, highest faunal richness, and highest species density. But for the 26 microcrustacean morphospecies among 11 bryophyte species, there was no detectable canopy effect on faunal richness or density. The lowest density of 1 individual per 50 cm^2 was on the cushions of ***Leucobryum*** (Figure 4) with a maximum of 6±3.37 on the same area of the thallose liverwort ***Monoclea*** (Figure 5), suggesting that openness of the community might play a role in diversity.

Figure 3. ***Acroporium pungens*** in the Neotropics, a species with low roughness and low faunal density. Photo by Michael Lüth, with permission.

Figure 4. ***Leucobryum glaucum*** cushion, a species with low faunal density. Photo by Janice Glime.

Figure 5. ***Monoclea forsteri***, a liverwort that harbors a relatively high microcrustacean diversity. Photo by Jan-Peter Frahm, with permission.

Peatlands

Peatlands, for our purposes those habitats dominated by ***Sphagnum*** and not including other types of peatlands (Figure 6), provide a mix of moist and dry mosses and pools influenced by those mosses. The "terrestrial plankton" are often sensitive to high CO_2 concentrations and low O_2 tensions such as those found among rotting leaves and other areas with high rates of decomposition (Stout 1963). For these organisms with good tolerance for low *p*H (sometimes below 4.0), ***Sphagnum*** provides a suitable habitat. Krebs (2001) found that the center of the ***Sphagnum*** moss mat had a higher species diversity than the edges, perhaps due to additional niches (habitat heterogeneity) resulting from the plant-associated species dwelling there.

On the other hand, the low *p*H created through cation exchange and organic acids produced by mosses in the genus ***Sphagnum*** (Figure 6) is detrimental to many organisms. Hillbricht-Ilkowska *et al*. (1998) examined the role of *p*H on **Crustacea** and other organisms by providing powdered lime to the system. Measurements after 1-4 years and 20-23 years indicated that both the water Ca and that of the sediment were permanently raised. This change coincided with a significantly increased rate of decomposition and an increase in species richness and diversity of **crustaceans**, among others. Overall diversity was doubled. The treatment eliminated peatmosses from encroaching on the lake but had no effect on those of the surrounding area.

Figure 6. Bohemia bog with ***Sphagnum cuspidatum***, ***S. denticulatum***, and others, showing the varied habitats of hummocks, hollows, and small pools available to bog fauna. Photo by Jonathan Sleath, with permission.

To add to this image of ***Sphagnum*** (Figure 6) as an unfriendly substrate, Smirnov (1961) stated that few animals were specialized to gain their nutrition by consuming emersed ***Sphagnum***. He cited only one species of flies whose larvae are known to feed directly on ***Sphagnum***. On the other hand, in such ***Sphagnum*** lakes the bladderwort, an insectivorous plant, traps and digests **Crustacea** such as ***Daphnia*** (Cladocera) – a not so friendly place for many.

But ***Sphagnum*** (Figure 6) may play a more positive role in the lives of these fauna. ***Sphagnum*** has long been known for its antibiotic properties; it was used as a wound dressing in WWI. Could it protect the crustaceans from fungal or bacterial attacks? Furthermore, for these invertebrates it may serve as a refugium – a place to escape predators (Kuczyńska-Kippen 2008), possibly due to its antifeedant properties as well as small hiding places.

Springs

Among the favored habitats of **limnoterrestrial** (living in wet films on land) Crustacea are mosses of springs, *i.e.* these Crustacea are **crenophilous**, where temperature and *p*H were important determinants of community composition in four Northern Apennine springs (Bottazzi *et al*. 2011). Mosses in these springs usually had harpacticoid copepods and ostracods representing the Crustacea. The moss inhabitants had a seasonality, whereas drift assemblages did not. Bottazzi *et al*. suggest that the mosses were important in increasing the species diversity in these springs.

Springs are often a transitional habitat between aquatic and terrestrial systems. Even within the spring habitat, such a transition is typical, and moisture zones within the habitat can change as the seasons and weather change. Thus, the bryophytes of this habitat provide not only a refuge, but an avenue (more like a labyrinth) where macroinvertebrates can travel to escape the receding preferred moisture level.

Crustacea are not usually seen among bryophytes, but in some areas they can be quite abundant. For example, Michaelis (1977) reported that at Pupu Springs in New Zealand, there were ten species of bryophytes. The fauna included Crustacea among the most abundant groups. Suren (1993) suggests that the abundance of crustaceans in the New Zealand bryofauna may be due to the absence of some of the bryophyte dwellers found elsewhere, *i.e.* some families of Trichoptera (caddisflies), Plecoptera (stoneflies), and Ephemeroptera (mayflies).

Bottazzi *et al*. (2011) reported the **ostracods** and **Harpacticoida** (an order of copepods) among the three most abundant taxon groups among mosses in northern Apennine **rheocrene springs** (springs that become streams immediately upon emerging from the ground). Like Michaelis (1977) and Suren (1993), they suggested that favorable habitats, including mosses, accounted for the high diversity and the large numbers of these two crustacean groups.

Bottazzi *et al*. (2011) concluded that emergent mosses were important in increasing species diversity of these springs (see also Barquín & Death 2009; Ilmonen & Paasivirta 2005). Bryophytes act as an ecotone between the aquatic and terrestrial habitat by creating a range of microhabitats that vary both horizontally and vertically (Lindegaard et al. 1975; Thorup & Lindegaard 1977), including the **madicolous** zone (having thin sheets of water flowing over rock surfaces). These provide a range of moisture conditions that permit the meiofauna to migrate to a more suitable location as moisture conditions change. While providing a refuge from rapid flow (Madaliński 1961; Elliot 1967; Gurtz & Wallace 1984; Suren 1992; Glime 1994), bryophytes provide a variety of food sizes in trapped particulate matter (Habdija *et al*. 2004). Linhart *et al*. (2002c) demonstrated a direct association between harpacticoid copepods, including nauplii, and trapped organic and mineral matter among the mosses.

Lindegaard *et al*. (1975) found that in the Danish spring at Ravnkilde these vertical and horizontal differences among the bryophytes provided a source of diversity among the macroinvertebrates. They found that whereas the horizontal zonation sported different assemblages of species, the fauna of the neighboring stones had little influence on the moss fauna. More importantly, the flow rate and available detritus as a food source could account for the horizontal differences.

Lindegaard *et al*. (1975) found that the numbers of individuals fluctuated throughout the year, corresponding with changes in the life cycle stages of the dominate species. Bryophyte habitation is also seasonal in Northern Apennine springs, with a maximum in the spring and minimum in winter, whereas seasonal habitation is nearly constant in non-bryophyte areas sampled by the traps Bottazzi *et al*. (2011). On the other hand, permanent meiofauna had its minimum in autumn; temporary meiofauna of the mosses peaked in spring, then decreased thereafter.

Streams

Bryophytes in streams create a rich source of invertebrate fauna, so much so that the aquatic moss ***Fontinalis antipyretica*** (Figure 7) was transplanted to streams in South Africa to increase the food source for trout (Richards 1947). The bryophytes are able to provide a refuge from fast-flowing water and to increase stream heterogeneity (Tada & Satake 1994; Wulfhorst 1994; Dražina *et al*. 2011).

Figure 7. ***Fontinalis antipyretica***. Photo by Jan-Peter Frahm, with permission.

Despite their seeming rarity among bryophytes, Amos (1999) included ostracods, cladocerans, copepods, and amphipods as "life in the torrent" in the UK – a description of the inhabitants of ***Fontinalis*** (Figure 7). His point was that "all was quiet" at the bottom of the moss clump despite the torrent occurring at the surface.

Linhart *et al*. (2002a), in Europe, found that regulated channels had a much greater meiofauna, including **Cladocera** and **Harpacticoida** (copepods), when the channel was overgrown by aquatic bryophytes, in this case ***Fontinalis antipyretica*** (Figure 7). In a different stream, the meiofauna of mosses was an order of magnitude higher than that in the surrounding mineral substrate (Linhart *et al*. 2000), but the crustaceans were not a significant part of this fauna. Rather, the density of the **Harpacticoida** was the second most abundant group in the gravel, where the fine particulate matter was also highest compared to that among the mosses. They further determined that high flow rates approaching the mosses had a negative impact on the crustaceans [**Cladocera**, **Ostracoda**, and **Cyclopoida** (an order of copepods)], although the velocity seemed to have no effect on the **Harpacticoida** (Linhart *et al*. 2002b, c). They suggested that fine detritus trapped by the ***F. antipyretica*** provided food for the **harpacticoid copepods**. It is interesting that in their 2000 study Linhart *et al*. suggested that it is "questionable whether ***F. antipyretica*** can serve as a refuge from the current for stream meiobenthos," a seeming contradiction to their conclusions in a different stream. It appears that food is the primary factor in distribution of the microcrustacea, but that does not rule out the role of the mosses as a refuge when sufficient food is present.

Collection Methods

Methods of collection can have a biasing effect on the relative numbers of taxa collected. Copepods and other **Crustacea** in aquatic habitats can be collected by squeezing mosses into a collection bottle or squeezing the mosses in place and collecting the crustaceans downstream from the mosses with a plankton net (Gerecke *et al*. 1998; Reid 2001; Stoch 2007). Copepods, ostracods, and

amphipods may all be extracted from forest litter by the Berlese funnel, but as the litter dries out many will perish before they can escape (Stout 1963). Heat extraction can present the same problem. Chapman (1960) was successful in extracting terrestrial ostracods alive by slowly drying out the leaf litter (but it would work for bryophytes as well) in a Berlese funnel, using a water-jacket at 40° C to avoid overheating, in which case the ostracods close their valves and stop moving. The end of the funnel led to water rather than alcohol.

CLASS BRANCHIOPODA, ORDER CLADOCERA

The class name of **Branchiopoda** literally means gill feet and refers to the **pereiopods** by which the aquatic species can swim. The order name **Cladocera** derives from the Ancient Greek κλάδος (kládos, "branch") and κέρας (kéras, "horn").

Adaptations

Structural

Cladocera are a predominately aquatic group of small individuals known as water fleas (no relationship to the insect group of fleas). They swim using their antennae, using a series of jerks similar to the hops of a flea. Some have adapted to terrestrial habitats with free water, such as bromeliad basins. Others are able to use the film of water from the capillary spaces and leaf surfaces of bryophytes. Not only are the antennae important for swimming, but they are also powerful chemical sensory organs (Ecomare 2014). They can use these not only to find food, but also to detect the presence of enemies. The body of a cladoceran is a valve-like carapace that covers an unsegmented thorax and abdomen. Adults have a single compound eye.

Life Cycle Strategies

Cladocerans spend most of their lives as a female population that reproduces multiple times asexually by **cyclical parthenogenesis**. When conditions become unfavorable, they produce male offspring and subsequently reproduce sexually, producing resting eggs that remain within the carapace (***Daphnia***; Figure 8). In this state, they can dry out and travel long distances on wind currents or as hitch hikers on other travelling animals or even moss fragments. In fact, some of these dormant eggs are known to remain viable for 70-80 years in Lake Superior sediments (Kerfoot & Weider 2004) and can even survive the digestive tracts of birds (Figuerola & Green 2002).

Habitats

Cladocera are primarily aquatic and marine, but a few are adapted to terrestrial living, taking advantage of films of water, pools in bromeliads, and other surfaces where they have easy access to water when they are active.

Terrestrial

Since Cladocera live primarily in fresh or marine water, living on land requires special adaptations for both water conservation and locomotion. It seems that few cladoceran species have accomplished this, or we simply haven't found them yet. There are indications that appendage reduction is a terrestrial adaptation in this group. After all, why waste energy to make appendages that are not useful. Frey (1980) describes the non-swimming chydorid ***Bryospilus*** (Figure 9) from wet cloud forests as lacking a compound eye, a change that still requires explanation. The genus resembles the limnoterrestrial genus ***Monospilus***, possibly through convergence. They exhibit reduced setation on their antennae and trunk limb, perhaps facilitating their slow crawl among wet bryophytes as high as 3-5 m above the forest floor.

Figure 8. ***Daphnia pulex*** with three eggs shown here to the right of the digestive tract. Photo by Paul Hebert, through Wikimedia Commons.

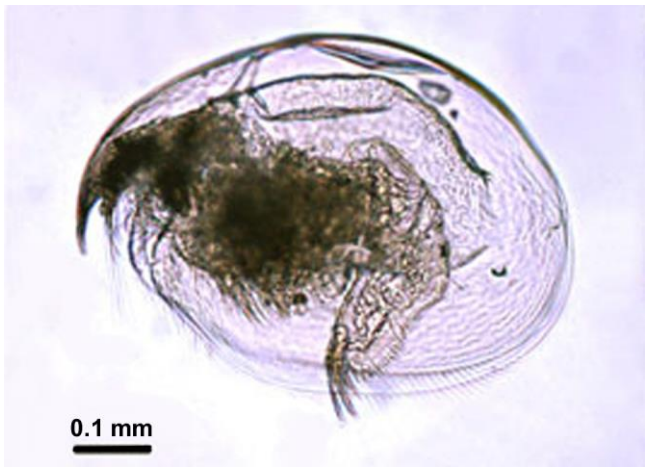

Figure 9. ***Bryospilus repens***, a chydorid cladoceran that lives mostly in wet moss.. Photo by Francisco D. R. Sousa <Cladocera.wordpress.com>, with permission.

Existing 3-5 meters above the rainforest floor are Cladocera that crawl from place to place, unable to swim. Frey (1980) reported the cladoceran ***Bryospilus repens*** (Figure 9), a semiterrestrial species known from wet mosses in Puerto Rico, Venezuela, and New Zealand, and

Bryospilus bifidus from New Zealand, both in the same subfamily of Chydoridae as ***Alona*** (Figure 10-Figure 11), a common cladoceran from springs. Resting eggs are often buried in deep masses of vegetation (Powers & Bliss 1983) where they are protected from water loss. Dispersal of fragments of mosses they inhabit can aid in dispersal of both eggs and adults to new sites. Frey suggested that the mossy habitat in the rainforest exhibited the same continuity through time as ancient lakes, thus being a likely site for even more endemic species. Van Damme *et al*. (2011) consider ***B. repens*** (Figure 9) to be a "well known" species that lives in wet moss. They consider its occasional presence in river samples to be the result of individuals that got washed into the river from these mossy homes.

There may be more species of these tiny cladocerans hiding among bryophytes in terrestrial habitats. These organisms are typically studied by aquatic biologists who spend their time looking at plankton. Terrestrial bryophyte habitats are rarely studied with the aim of locating **Cladocera**. I have to wonder if somewhere there might be some Cladoceran species living in liverwort lobules.

Peat Bogs

Living among ***Sphagnum*** (Figure 6) or in the bog pools requires a tolerance of low *p*H. Nevertheless, ***Sphagnum*** can increase the abundance of **Cladocera** by as much as tenfold in Swedish peatlands (Henrickson 1993). The heterogeneity of the ***Sphagnum*** habitat illustrated in Figure 6 provides shelter and refuge against predation while being a suitable foraging site. The bryophytes further contribute to this habitat through their production of antibiotics, organic acids, and cation exchange.

Bog lakes can support a number of species of Cladocera. Minelli (2004) listed ***Alona quadrangularis*** (Figure 10), ***Alona affinis*** (Figure 11), ***Simocephalus exspinosus*** (Figure 12), ***S. vetulus*** (Figure 13), and ***Ceriodaphnia pulchella*** as being among the common species in bog lakes in Italy. Hingley (1993) reported ***Streblocerus serricaudatus*** (Figure 14) and ***Acantholeberis curvirostris*** (Figure 15) swimming in UK peat pools. Macan (1974) likewise reported the latter species in ***Sphagnum*** (Figure 6). ***Chydorus piger*** (Figure 16) is typical of bare substrates such as rock or sand, but including ***Sphagnum***, and is known from acidic pools in peatlands in Europe (Duigan & Birks 2000).

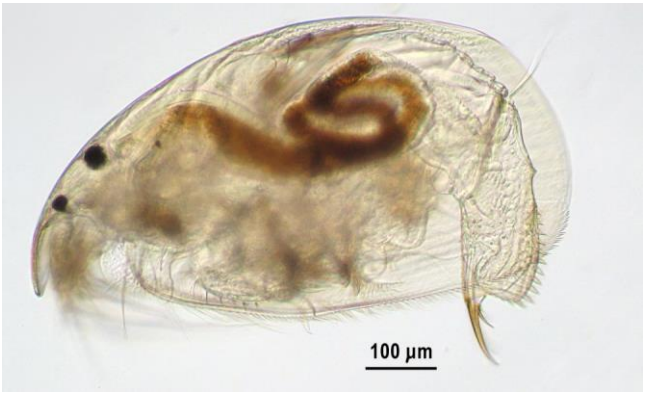

Figure 10. ***Alona quadrangularis***, a common species in bog lakes. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 11. ***Alona*** cf ***affinis***, a common species in bog lakes. Photo by Yuuji Tsukii, with permission.

Figure 12. ***Simocephalus exspinosus***, a common species in bog lakes. Photo by Malcolm Storey through <http://www.discoverlife.org/>, through online license.

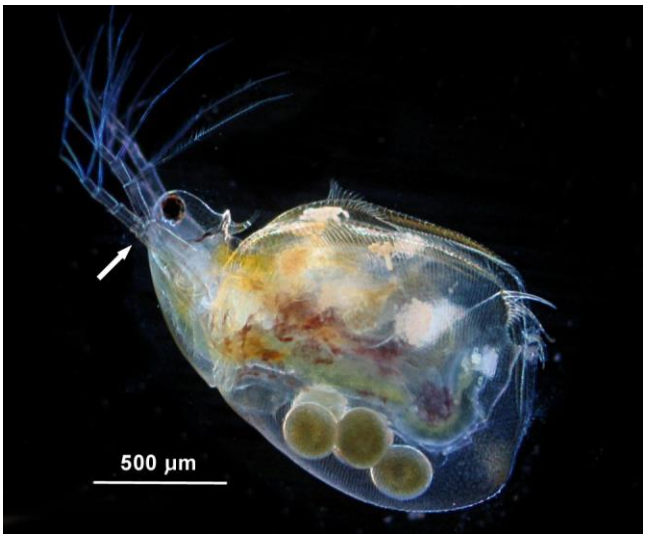

Figure 13. ***Simocephalus vetulus***, a common species in bog lakes. Note the divided (biramous) antenna (**arrow**). Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

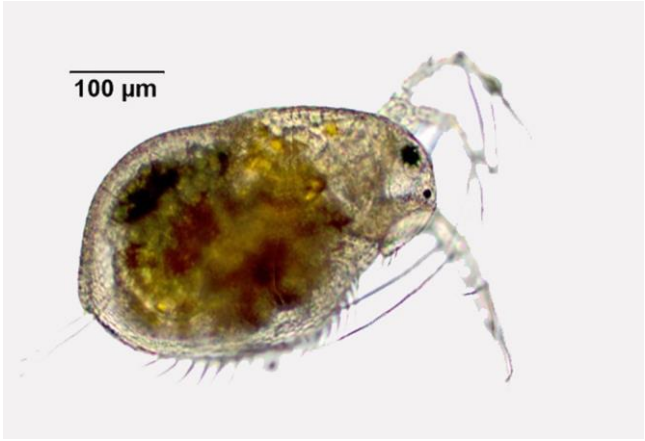

Figure 14. ***Streblocerus serricaudatus***, a cladoceran that inhabits peatland pools. Photo from Haney, J. F. *et al.* 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.

Figure 15. ***Acantholeberis curvirostris***, a cladoceran of peatland pools. Photo from Haney, J. F. *et al.* 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.

Figure 16. ***Chydorus piger***, a cladoceran from peatland pools. Photo by Angie Opitz, through online permission.

Kairesalo *et al*. (1992) considers the peatland habitat to be unsuitable for ***Daphnia*** (Figure 17) because the available food is "recalcitrant." In a lake in southern Finland that was bordered by the mosses ***Warnstorfia*** (Figure 18) and ***Sphagnum*** (Figure 6), the organic carbon excreted by ***Warnstorfia*** suppressed the growth of planktonic algae and provided little contribution to bacterial productivity. This meant that bacterial productivity was necessarily dependent on humic acids for their carbon source, resulting in decreased availability of this food source for the ***Daphnia***. The predominantly particulate matter in the water was largely useless for the ***Daphnia*** as a food source.

Figure 17. ***Daphnia***. Photo by Gerard Visser through Creative Commons.

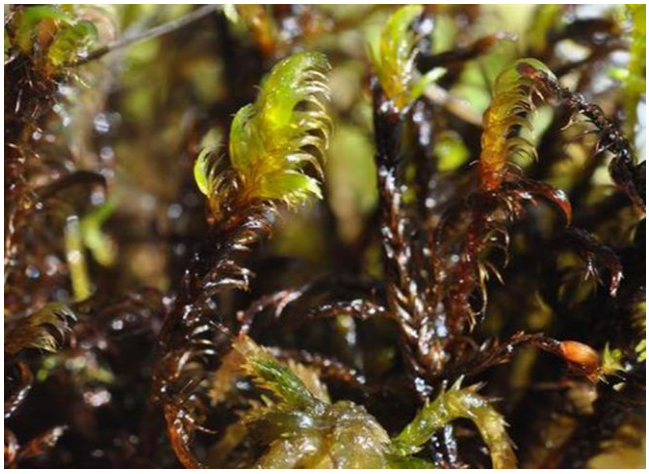

Figure 18. ***Warnstorfia exannulata***, a peatland moss that seems to be "recalcitrant," unable to provide food for the Cladocera living there. Photo from Biopix through Creative Commons.

Cladocera have played a role in reconstructing the history of some peatlands. Duigan and Birks (2000) report on ***Sphagnum*** (Figure 6) and other bryophytes from 9200 BP microfossils in western Norway with ***Alonella nana*** (Figure 19), ***Alonella excisa*** (Figure 20), and ***Alona rustica*** (Figure 21). ***Alona rustica*** is also known in peat bogs among mosses in Italy (Minelli 2004).

Figure 19. ***Alonella nana***, a cladoceran from peat deposits in ~9200 BP. Photo from Great Lakes Research Laboratory, through public domain.

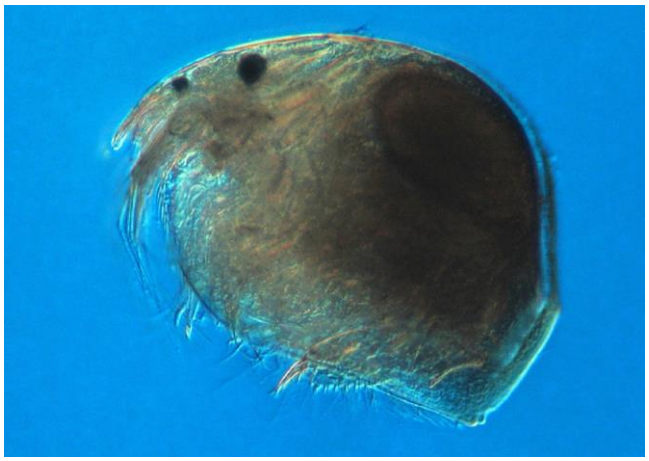

Figure 20. ***Alonella excisa***, a cladoceran that occurs in peat deposits in ~9200 BP. Photo by Manuel Elias, ECOSUR, through Creative Commons.

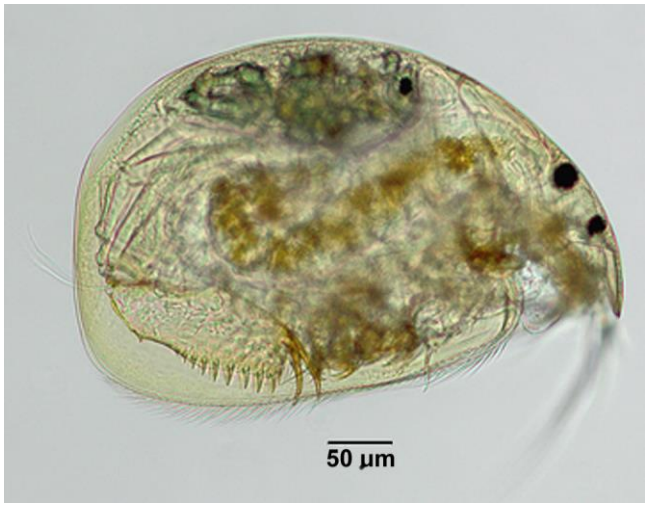

Figure 21. ***Alona rustica***, a cladoceran that lives among bryophytes on stream banks. Photo from Haney, J. F. *et al.* 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.

Aquatic

Lakes

Typically, cladocerans are rare among aquatic mosses, being adapted for planktonic life. However, in the subAntarctic lakes of South Georgia, the most common invertebrate was the cladoceran genus ***Alona*** (Figure 22), with 2544 individuals in a liter of water (Hansson *et al*. 1996). Several species in this genus were present, with the greatest numbers among mosses that extended into shallow lakes. In fact, the littoral mosses had the highest number of invertebrate species (20) and abundance (1539 individuals) of invertebrates in those lakes. With increasing UV levels reaching the shallow Antarctic lakes, mosses may provide refugia that protect these invertebrates from UV damage.

Figure 22. ***Alona*** sp., a genus with a number of terrestrial bryophyte-dwelling species. Photo by Yuuji Tsukii, with permission.

Van Damme *et al*. (2011) explain the absence of ***Alona karelica*** in littoral samples of European lakes by suggesting that it may actually be a terrestrial cladoceran that is normally associated with moss. This species has been reported twice from ***Sphagnum*** (Figure 6) in Europe (Flößner 2000; Kuczyńska-Kippen 2008) and its European distribution coincides with that of regions of high ***Sphagnum*** diversity (see Séneca & Söderström 2008; Van Damme *et al*. 2011). Another species of ***Alona***, ***A. bromelicola***, is from Nicaragua and lives in the basins of bromeliads (Van Damme *et al*. 2011). Yet another species, ***Alona rustica*** (Figure 21), is present in collections of bryophytes from stream banks in Italy (Margaritora *et al*. 2002), another transitional habitat. Such transitional habitats often have both higher diversity and density of organisms, a phenomenon known as the **edge effect** (Leopold 1933; Lay 1938; Good & Dambach 1943; Bider 1968; Wiens 1976).

Kuczyńska-Kippen (2008) examined the role of ***Sphagnum*** (Figure 6) compared to open water for zooplankton in a lake in Poland. The highest species diversity values occurred in the peat mat (mean = 0.67 for crustaceans compared to 1.76 for rotifers), whereas the

lowest values occurred in open water (0.36 and 0.99 respectively). The cladocerans present in the transition zone between the peat mat and the open water seem to relate to the presence of both invertebrate and vertebrate predators, and competition between the large cladocerans and smaller rotifers. For the cladocerans, ***Sphagnum*** (Figure 23) can serve as a refugium to protect them from other invertebrate predators.

Figure 23. ***Sphagnum cuspidatum*** mat (**foreground**) and nearby hummock (**upper left**), habitats where one can find more Cladocera than in the open water (**upper left**). Photo by Michael Lüth, with permission.

Cammaerts and Mertens (1999) discovered ***Bryospilus repens*** (Figure 9) in the **Palaeotropics** (tropical areas of Africa, Asia, and Oceania, excluding Australia) of western Africa, where it occurred in vernal pools of forests. This dispels the notion that this genus is strictly a moss dweller.

One problem in sorting out the Cladocera-bryophyte relationship is that species descriptions frequently fail to include the substrate, reporting only the general habitat, if even that.

Streams

Stream drift, a popular topic in the 60's and 70's, is generally a phenomenon we relate to the insects and other macroinvertebrates. But microcrustacea can be part of this as well. For moss-dwelling Cladocera, this is a means to get from one moss clump to another in an unfriendly moving environment. Peric *et al*. (2014) found that of 60 invertebrate taxa in a moss-rich karst system in Croatia, six were annelids and arthropods from the meiofauna, representing 35% of the total drift, but among the most abundant drift organisms were several species of ***Alona*** (26.7%) (Figure 22), a cladoceran known for being a moss-dweller (Hansson *et al*. 1996; Van Damme *et al*. 2011). The drift was lowest in winter and highest in autumn and late spring to early summer.

CLASS MAXILLOPODA, SUBCLASS COPEPODA

The name **Copepoda** comes from the Greek word κωπηποδ, which literally means oar-feet (Wikipedia: Copepod 2014). Copepods are microcrustacea, mostly 0.5-2 mm (Encyclopaedia Britannica 2012), usually occurring as planktonic or benthic organisms and not ones we would expect to be frequent in moss communities. The entire group comprises about 13,000 species with three of its ten orders being the most common (**Harpacticoida**, **Cyclopoida**, **Calanoida**) and containing the ones known from bryophytes (Wikipedia: Copepod 2014). Copepods have two pairs of antennae and a single red compound eye (in most). They are perhaps the fastest organisms alive, swimming in irregular spurts (Kiørboe *et al*. 2010). Some of the meiofauna taxa have switched to **direct development** (lacking the larval stage) and care of their young (Dahms & Qian 2004), traits that are absent in most copepods but that are beneficial in a terrestrial environment.

The **Harpacticoida** (Figure 24) have a short pair of first antennae (Figure 25), often a somewhat wormlike body, and are mostly benthic (living on the bottom) (Wikipedia: Harpacticoida 2013). Nevertheless, Dumont and Maas (1988) consider the harpacticoid copepods to be widespread in wet habitats such as wet mosses. The harpacticoid copepods include crawlers, walkers, and burrowers (Dole-Olivier *et al*. 2000), pre-adapting the crawlers and walkers to mobility in the water film of bryophytes.

Figure 24. Terrestrial **Canthocamptidae** male, a harpacticoid copepod. Photo by Walter Pfliegler, with permission.

Figure 25. ***Canthocamptus***, a harpacticoid copepod showing antennae. Photo by Yuuji Tsukii, with permission.

The **Cyclopoida** (Figure 26) are mostly **planktonic** (live in water column and float or drift – can't swim against a current) (Wikipedia: Cyclopoida 2013). Their antennae are longer than those of Harpacticoida but shorter than those of Calanoida, reaching no farther than the thorax. They are capable of rapid movement.

Figure 26. ***Cyclops vicinus***, a cyclopoid copepod carrying egg sacs. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

The **Calanoida** (Figure 27) are also mostly planktonic species (Wikipedia: Calanoida 2013). Unlike the short antennae of the Harpacticoida, the first antennae of the Calanoida extend about half the length of the body or more.

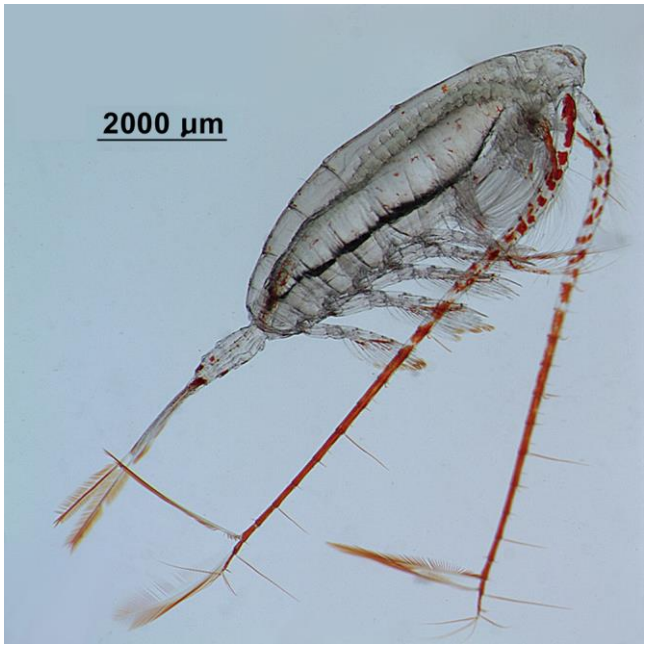

Figure 27. ***Neocalanus cristatus***, a calanoid copepod showing the long antennae. Photo by Seward Line <www.sfos.uaf.edu>, with online permission for educational use.

Copepods are known for their egg longevity, with some surviving as much as 322 years (Hairston *et al*. 1995).

Adaptations

Copepods, like several other crustacean groups, have evolved to a terrestrial life style, but still live where water is generally available (Stout 1963). Bryophytes provide such a habitat. Stout suggests that through evolutionary time both copepods and ostracods moved from streams to adjoining moss carpets and currently are able to live among ***Sphagnum*** (Figure 23) as well as forest litter (Harding 1953, 1955).

Bryophyte-dwelling copepods are not very numerous, which probably explains, in part, the absence of descriptions of adaptations to the bryophytic habitat. Nevertheless, one might consider the adaptations to a terrestrial life style as exemplary of bryophytic adaptations. One such adaptation is the absence of hemoglobin (Green 1959). This is a stretch, because it appears that this pigment has evolved primarily in those species with a parasitic life style and a limited number of mud-dwelling taxa. Nevertheless, it suggests that oxygen is in adequate supply in the bryophytic habitat, so energy-requiring pigment development is not necessary.

Structure

The moss-dwelling **nauplius** (larval stage; Figure 28) of the copepod uses its antennae for swimming and possesses a single eye that can disappear in some species in later developmental stages. The copepod eye, in at least some species, senses the direction of light and permits the copepod, by moving its tail, to keep its back oriented toward the light (Land 1988). This behavior furthermore permits the copepod to distinguish its own species from other species by the movement patterns. Directed movement in response to light seems to be useful in minimizing exposure to UV light in tidal areas (Martin *et al*. 2000). These light avoidance behaviors are probably less useful among bryophytes.

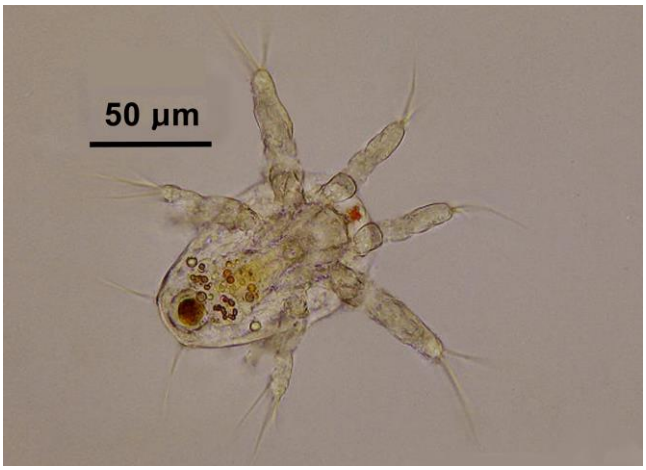

Figure 28. Copepoda nauplius, the immature state. Photo by Graham Matthews <http://www.micromagus.net/microscopes/pondlife_copepoda.html>, with permission.

Life Cycle Strategies

Whether living in water that freezes, pools that dry up, or among mosses and other terrestrial habitats, life cycle strategies are important in enduring unfavorable seasons

(Santer 1998). Terrestrial habitats are all unstable. Evolution favors traits that help the copepods sense and prepare for these potentially deadly periods. These strategies include dormancy and migration as escape mechanisms, but also include synchronizing growth and reproduction with favorable periods.

Dormancy is a common trait among copepods, particularly in higher and temperate latitudes (Dahms 1995; Williams-Howze 1997). It permits them to survive periods of desiccation and other unfavorable conditions. The timing of dormancy varies with the species and can occur in different forms in multiple life cycle stages, including desiccation-resistant resting eggs, arrested larval development, **encystment** of juveniles and adults (Deevey 1941; Dahms 1995), and arrested development of adults (Dahms 1995; Williams-Howze 1997). Dormancy saves energy during a time when living conditions are unfavorable. In addition to facilitating copepod survival during desiccation, dormancy helps copepods escape unfavorable temperatures, insufficient oxygen availability, limited food availability, and predation.

Among these dormancy strategies, one potential adaptation is encystment. ***Canthocamptus staphylinoides*** (Figure 29) is a harpacticoid copepod that encysts (Deevey 1941). Some members of this genus are known from mosses in the aquatic environment and peat bogs, where encystment can permit them to survive not only desiccation but also unfavorable temperatures.

Figure 29. ***Canthocamptus staphylinoides***. Photo from US Geological Survey, through public domain.

Diapause can be defined as a delay in development in response to regular and recurring periods of adverse environmental conditions. In its narrow sense, it is initiated and terminated by triggers such as photoperiod, temperature, chemical cues, population density, and physiological factors (Dahms 1995).

Feeding

Fryer (1957a, b) considered chance encounter to be a primary mechanism in finding food for the mostly planktonic copepods. Nevertheless, chemoreceptors help them to distinguish edible from inedible food particles and thus may help somewhat in locating food. The carnivorous diet appears to be the primitive condition, with the change to an algal diet facilitating adaptive radiation.

Habitats

Reid (1986, 1987, 1999, 2011) has contributed considerably to our knowledge of bryophyte-dwelling copepods. She reported them from such overlooked habitats as mosses (including ***Sphagnum*** – Figure 23) and liverworts, as well as from tree holes (Reid 1986). She described the new species ***Muscocyclops therasiae*** from Brazil, primarily from soils, but also from mosses. Reid (2001) considered the publications on the harpacticoids and small cyclopoids from mosses in humid climates to be so numerous that they were almost impossible to review. She found that such "aquatic" mosses as ***Sphagnum*** (Figure 23) and ***Hypnum*** (Figure 30) as well as those bryophytes from more humid habitats provide homes for their own unique communities of copepods. Stoch (2007) attributes the copepod abundance to the complex spatial structure and high availability of food resources among bryophytes. In their study on ***Fontinalis antipyretica*** (Figure 7) meiofauna in Central Europe, Vlčková *et al*. (2002) found that harpacticoid copepods were able to feed on organic matter in the size range of 30-100 µm trapped within the moss clumps.

Figure 30. ***Calliergonella lindbergii*** (=***Hypnum lindbergii***), a moss genus where copepods are known to live. Photo by Jan-Peter Frahm, with permission.

Terrestrial

One would not expect a plankton organism like the copepods to occur on mosses on land, but a few have managed to venture into that habitat. Paul Davison (pers. comm. 9 November 2011) reported to me that harpacticoid copepods are well known from terrestrial mosses, but finding documentation of that has been challenging. Menzel (1921, 1925) reported both cyclopoid and harpacticoid copepods as moss dwellers. Bryophytes do not harbor a rich fauna, so they have not attracted much attention from the copepodologists. Nevertheless, those copepods that live among mosses can, at times, be important to ecosystem functioning. For example, the harpacticoid copepods are a first food source for the young salamanders living near and among the mosses (Paul Davison, pers. comm. 9 November 2011) (See Epiphytes below).

Scattered reports of terrestrial bryophyte-dwelling copepods, especially harpacticoids, occur in the literature (*e.g*. Olofsson 1918; Lang 1931), including mosses

(including ***Sphagnum*** – Figure 23) and liverworts as habitat.

The genus ***Bryocamptus*** seems to be among the more common taxa in the Eastern Hemisphere. ***Bryocamptus pygmaeus*** and ***B. zschokkei*** (Figure 31) occur primarily among mosses in Central Europe (Illies 1952). Harding (1958) reported ***Bryocamptus stouti*** from mosses in New Zealand.

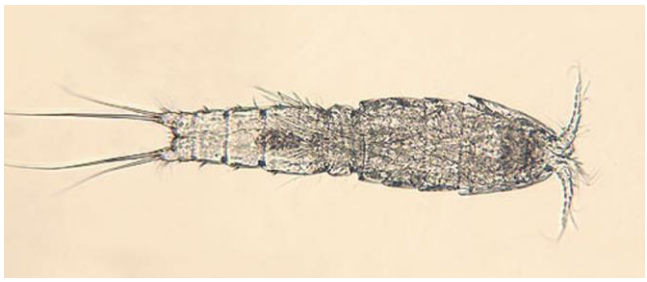

Figure 31. ***Bryocamptus zschokkei*** female, a moss dweller. Photo from US Geological Survey, through public domain.

Lewis (1984) reported twelve species of harpacticoid copepods from terrestrial mosses in forests and open areas in New Zealand. Lewis (1972a) found copepods in New Zealand among forest mosses that remained moist most of the year. These included ***Elaphoidella silvestris*** (see Figure 32), a copepod among damp mosses on the forest floor or nearby, but this species is limited to the damp conditions of higher altitude bush areas of North Island and dripping wet forests of the West Coast of South Island.

Figure 32. ***Elaphoidella bidens***. Members of this genus live among damp mosses on the forest floor of New Zealand. Photo through Creative Commons.

Mrázek (1893) found the harpacticoid copepod ***Maraenobiotus vejdovski*** among mosses in Bohemia, and Harding (1953) reported them from woodland mosses in Scotland. These copepods are small and slender, permitting them to live an aquatic life in the water film among mosses (Harding 1953).

Scourfield (1939) reported ***Bryocyclops*** and ***Muscocyclops*** as living among mosses in Wales. With a name like ***Bryocyclops muscicola***, one expects to find a moss-dweller. Reid (1999) reported this species, originally described from Indonesia, from a plant nursery in Florida, USA, apparently introduced with some of the plants, perhaps mosses. This is the only species of ***Bryocyclops*** known from continental US, although ***Bryocyclops caroli*** is known from Puerto Rico. In the Eastern Hemisphere the genus seems to be more common than in the Western Hemisphere, or perhaps just better known.

Menzel (1926) described the new species ***Bryocyclops anninae*** from moist mosses in Java and reported ***Bryocyclops bogoriensis*** from the Fiji Islands among mosses and in tree holes. More recently, Watiroyram *et al*. (2012) listed ten additional wet moss dwellers in the genus ***Bryocyclops*** in Thailand, mostly near springs and waterfalls.

Harding (1953) reported that ***Epactophanes*** (Figure 54) and ***Maraenobiotus*** live in damp mosses in Europe. ***Epactophanes muscicola*** (in UK) avoids mosses that are very wet. Michailova-Neikova (1973) found that of the nine harpacticoid copepods living among wet mosses near water bodies on a mountain in Bulgaria, eight also lived among leaf litter.

In an apparently rare Western Hemisphere record of bryophyte dwellers, Rocha (1994) described ***Metacyclops oraemaris*** as a new species from moist moss in São Paulo, Brazil. In neighboring Suriname, Menzel (1916) found ***Parastenocaris staheli*** (see Figure 33) among mosses in the old leaf axils of the palm *Livingstonia*.

Figure 33. ***Parastenocaris lacustris*** female, member of a genus with species that live among epiphytic mosses. Photo from US Geological Survey, through public domain.

North American records seem to be almost non-existent. Nevertheless, Margaret (Maggie) Ray (pers. comm. 9 November 2011) told me that she found copepods in many of her bryophyte samples across North Carolina, USA. Paul Davison (pers. comm. 9 November 2011) likewise has often found them among bryophytic epiphytes in Alabama. Others have reported on them as a group (Camann 2011; Camann *et al*. 2011).

Seepage Areas – Seepage areas, typically with bryophytes, seem like a logical place to look for limnoterrestrial copepods. Scourfield (1932) found ***Bryocyclops pygmaeus***, a common species, and ***Speocyclops dimentiensis*** among mosses of seeps on rock outcrops at Tenby in Wales. In New Caledonia, Hamond (1987) found ***Fibulacamptus*** among wet mosses as well as other wet terrestrial substrata.

Fiers and Ghenne (2000) suggested an interesting role for mosses in forests. They provide epigean highways, especially for the tiny (~0.5 mm long) species, that help to connect the various patches of leaf litter and moist soils while also serving as a temporary or permanent habitat.

Epiphytes – It is interesting that one can see canopy food webs similar to those in the water, with bryophytes forming the habitat structure. In a (regrettably) rare North American study, Camann and coworkers (Camann 2011; Camann *et al*. 2011) report communities at 84 m above the forest floor in the redwood forest of California, USA. In these humus moss patches harpacticoid copepods dwell, encysting when conditions get dry. And further up the food web are Wandering Salamanders (***Aneides vagrans***; Figure 34), likewise bryophyte dwellers, that use the copepods as food. Most likely there are birds or other vertebrates that prey on the salamanders.

Figure 34. ***Aneides vagrans***, a salamander whose larvae feed on terrestrial copepods. Photo by John P. Clare, through Creative Commons..

Antarctic

Pesta (1928) described the harpacticoid copepod ***Attheyella koenigi*** (**Harpacticoida**: **Canthocamptidae**; see Figure 35) from mosses in a stream on the island of South Georgia in the Antarctic. Also on the island of South Georgia, it is likewise the family **Canthocamptidae** that has the only known copepod species living among mosses at the edges of shallow lakes (Hansson *et al*. 1996). Although only three larval forms were found, the mosses were the only location where these copepods appeared in that study of Antarctic lakes. Also among these Antarctic dwellers is the harpacticoid copepod ***Marionobiotus jeanneli*** (family **Thalestridae**) living among wet mosses (Pugh *et al*. 2002).

Figure 35. ***Attheyella americana*** immature. This genus has several bryophyte-dwelling species. Photo by US Geological Survey, through public domain.

Peat Bogs and *Sphagnum*

Bog lakes and pools in peat bogs are often rich in copepod species (Minelli 2004). In the Italian bog pools and lakes (and likely throughout most of Europe as well), the copepods are represented by the orders **Cyclopoida** and **Harpacticoida**. The most abundant species are typically widespread predators, including ***Megacyclops viridis*** (Figure 36), ***Macrocyclops albidus*** (Figure 37-Figure 38), and ***Diacyclops bicuspidatus*** (Figure 39), and algal or detritus feeders including ***Paracyclops fimbratus*** (see Figure 48), ***Eucyclops serrulatus*** (Figure 55), ***Thermocyclops dybowskii*** (see Figure 40), and ***Tropocyclops prasinus*** (Figure 41). ***Megacyclops viridis*** seems to have been introduced to the Great Lakes of North America; in Austria it is commonly associated with salt pools (Kipp *et al*. 2012). The most common species in high-altitude peat bogs of Europe is ***Acanthocyclops vernalis*** (Figure 42), reaching an altitude of 2800 m in the Alps.

Figure 36. ***Megacyclops viridis***, a widespread species whose habitats include peatlands. Photo by R. M. Kipp *et al.* at USGS, with permission.

Figure 37. ***Macrocyclops albidus*** female with egg sacs. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

Figure 38. ***Macrocyclops albidus*** nauplius. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

Figure 39. ***Diacyclops bicuspidatus*** with egg sacs, a widespread predator that can be found on Antarctic bryophytes**.** Photo from Haney, J. F. *et al.* 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.

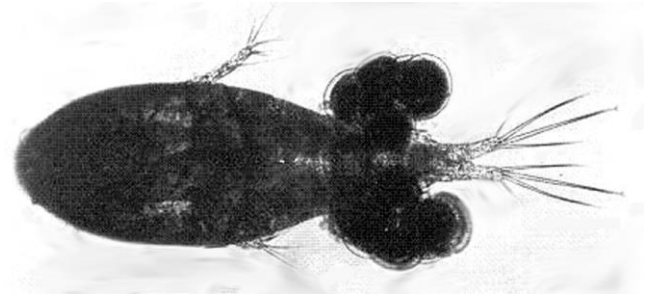

Figure 40. ***Thermocyclops*** sp. with egg sacs. Photo through Creative Commons.

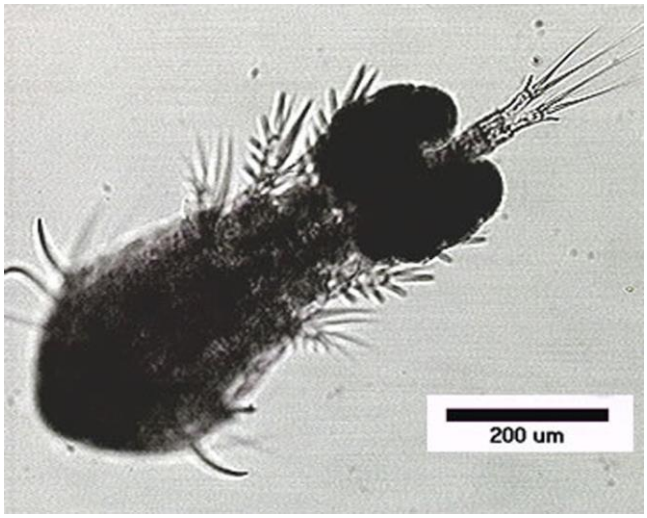

Figure 41. ***Tropocyclops prasinus*** with egg sacs. Photo from Haney, J. F. *et al.* 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.

Figure 42. ***Acanthocyclops vernalis*** female with egg sacs. Photo from Haney, J. F. *et al.* 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.

Peat bogs, with a ground cover of ***Sphagnum*** species (Figure 43), provide the film of water needed by limnoterrestrial copepods. ***Diacyclops languidus*** and ***D. hypnicola*** (see Figure 44) are small species adapted to living in the water film on the mosses and characteristic of peat bogs in the Alps, Apennines, and central and northern Europe (Minelli 2004). Among European alpine ***Sphagnum*** and other moss cushions one can find ***Bryocamptus pygmaeus***, ***Epactophanes richardi*** (Figure 54), and ***Phyllognathopus viguieri***. Barclay (1969) found the latter species in New Zealand among mosses at the base of gravel piles in the winter when the mosses become quite soggy. A species of ***Bryocyclops*** is common in this same habitat.

Figure 43. ***Sphagnum*** blanket bog. Photo through Creative Commons.

Figure 44. ***Diacyclops*** sp., a genus of small copepods with some species adapted for living in the water film of bog mosses. Photo from USGS, through public domain.

Stoch (1998b) originally described the new species ***Moraria alpina*** and re-described ***M. radovnae*** (see Figure 45) from the Alps of Italy and Slovenia, where they occurred among mosses, in bogs, and in interstitial spaces in brooks. Additional European alpine species, for example ***Bryocamptus veidovskji***, ***Elaphoidella gracilis***, ***Moraria mrazeki***, ***M. alpina***, ***Maraenobiotus veidovskji***, and ***Hypocamptus brehmi***, live only in peat bogs and interstitial mountain habitats (Minelli 2004). In Britain, one can find ***Moraria arboricola*** among ***Sphagnum*** (Figure 43), as well as in leaf litter and tree hole pools (Fryer 1993). It seems none of these are strict **tyrphobionts** (living only in peat bogs and mires).

Figure 45. ***Moraria laurentica*** female, member of a genus including moss dwellers in the Antarctic South Georgia Island and known from mossy swamps and wet mosses on stream banks in the Great Lakes area, USA. Photo from US Geological Survey, through public domain.

Herbst (1959) reported ***Metacyclops paludicola*** and ***Ectocyclops herbsti*** (see Figure 46) from a ***Sphagnum*** bog in São Paulo, Brazil. Hingley (1993) reported ***Moraria sphagnicola*** (see Figure 45) and ***Canthocamptus weberi*** (see Figure 47) as associated with ***Sphagnum*** (Figure 43) in Europe. In addition to living in mossy tarns, ***Attheyella*** (***Delachauxiella***) ***brehmi*** and ***Attheyella*** (***Chappuisiella***) ***maorica*** (see Figure 35) occur among ***Sphagnum*** in New Zealand (Lewis 1972a).

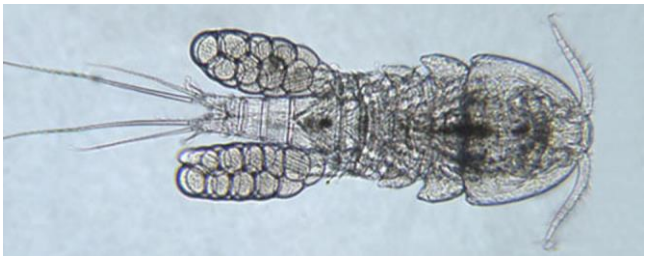

Figure 46. ***Ectocyclops phaleratus*** with egg sacs, member of a genus in which some species occur in peat bogs. Photo from Haney *et al.* 2013, with permission

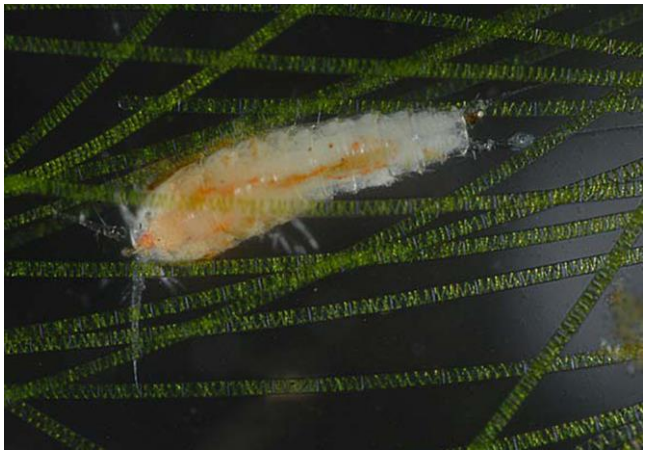

Figure 47. ***Canthocamptus*** sp. on the alga *Spirogyra*. Photo by Gerard Visser through Creative Commons.

In peatlands, the mosses can have an indirect influence on the fauna due to the tracheophytes they support. The rare North American copepod ***Paracyclops canadensis*** (Figure 48) is common in the pool of water in the leaves of the pitcher plant (***Sarracenia purpurea***, Figure 49) (Hamilton *et al.* 2000). In ***Sphagnum*** (Figure 43) peatlands, the mosses are a necessary habitat element to support the growth of pitcher plants.

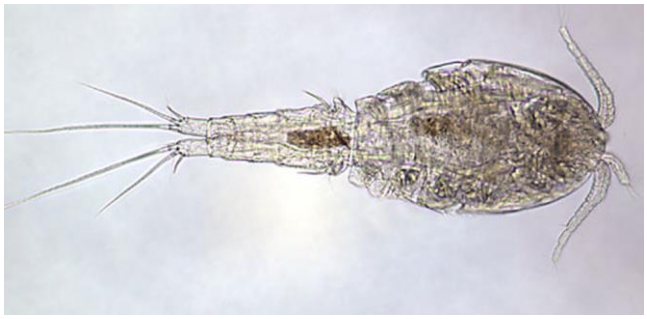

Figure 48. ***Paracyclops canadensis***, an inhabitant of pitcher plants. Photo from US Geological Survey, through public domain.

Figure 49. ***Sarracenia purpurea*** leaf amid ***Sphagnum*** where copepods can live in the pool formed within the leaf. Photo by Janice Glime.

Aquatic

Reid (2001) reported that squeezing aquatic mosses would reveal small copepods such as members of ***Acanthocyclops*** (Figure 50-Figure 51), ***Diacyclops*** (Figure 52), and other small cyclopoid genera (Gurney 1932; Scourfield 1932, 1939). Aquatic bryophytes can provide cyclopoid genera with safe sites from strong flow, hide them from predators, and trap particulate matter that serves as food.

Figure 50. ***Acanthocyclops venustoides***, genus of the small copepods that live among aquatic mosses. Photo by US Geological Survey, through public domain.

Figure 51. ***Acanthocyclops robustus***, member of a genus of small copepods that live among bryophytes. Photo from Haney, J. F. *et al.* 2013. An Image-Based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.

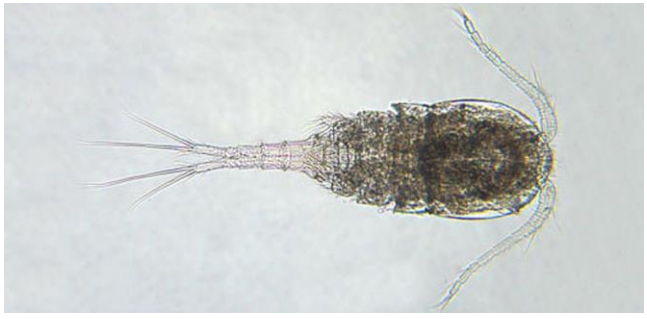

Figure 52. ***Diacyclops navus***, genus of the small copepods that live among aquatic mosses. Photo from US Geological Survey, through public domain.

Mossy Tarns

Tarns (Figure 53) are small mountain lakes. For the crustaceans, the mossy tarn habitat is similar in many ways to peatland pools, but it may differ in its *p*H and does not necessarily have ***Sphagnum*** (Figure 43) or may have different ***Sphagnum*** species. Several copepod species seem to prefer mossy tarns in New Zealand (Lewis 1972a). Among these are ***Attheyella*** (***Delachauxiella***) ***brehmi*** and ***Attheyella*** (***Chappuisiella***) ***maorica*** (species known to occur among ***Sphagnum***; see Figure 35) and ***Attheyella*** (***Delachauxiella***) ***bennetti***, genera known also from peatlands.

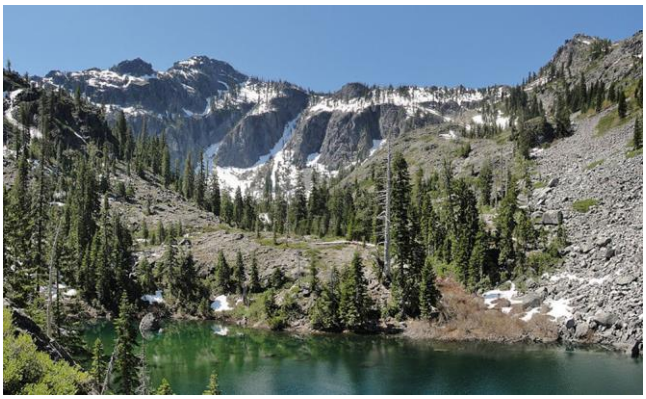

Figure 53. Tarn in Siskiyou Wilderness, CA, USA. Photo by Miguel Vieira, through Creative Commons.

Springs

Stoch (2007) found that mosses in springs in Italy were particularly good habitats for copepods, supporting large numbers. This may be due to their complex structure and highly available food sources. At the same time, the spring-dwelling species are often not true **crenobionts** (occurring only in springs and spring brooks) (Stoch 1998a), also occurring in other damp or aquatic habitats such as the littoral zone of lakes, moist mosses elsewhere, in groundwater, and in the epirithral region (upstream stream region suitable for trout) (Gerecke *et al.* 1998; Jersabek *et al.* 2001; Galassi *et al.* 2002; Stoch 1998a, 2003, 2006, 2007). Within the springs, species often segregate into microhabitats that supply their needs, including hygropetric rivulets, mosses, and patches of sediments with different characteristics (Stoch 2003; Fiasca *et al.* 2005). Bottazzi *et al.* (2011) reported **crenophilous** ("loving" springs and spring brooks) crustaceans from mosses in the Northern Apennine **rheocrene** springs (springs that flow to surface from underground), with *p*H and temperature best explaining their distribution and diversity pattern. In fact, the harpacticoid copepods and ostracods dominated the moss fauna, along with stoneflies and Chironomidae. The mosses were important contributors to the biodiversity.

We know that the copepod genera ***Moraria*** (Figure 45) and ***Bryocamptus*** are associated with wet or submerged mosses in Europe, including springs (Harding 1953). In their Italian study, Bottazzi *et al.* (2008) used traps, tubes, and moss samples to determine the copepod fauna of **rheocrene springs** (those that exhibit flow immediately after emerging from the substrate). They found 63% of the copepod taxa in these springs were represented among the

mosses, including a species of ***Moraria***, in this case, ***M. poppei***. Some of the copepod taxa occurred only in the moss habitat (i.e., were not collected in traps). These were the harpacticoid copepods ***Bryocamptus tatrensis***, ***B. alpestris*** (see Figure 31), ***Moraria vejdovski***, ***M. vejdovski truncatus***, ***M. poppei***, ***Epactophanes richardi*** (Figure 54), ***Attheyella crassa*** (see Figure 35), and the cyclopoid ***Eucyclops serrulatus*** (Figure 55). ***Bryocamptus*** species were evenly recorded from both moss and trap samples.

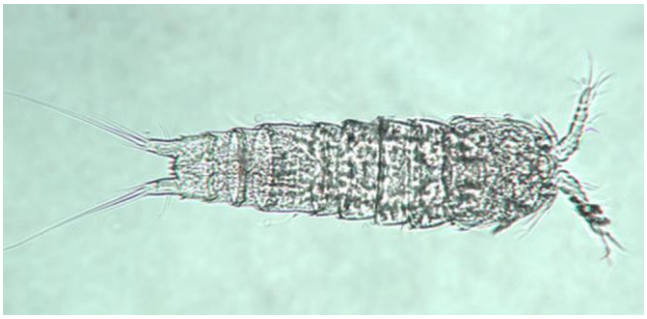

Figure 54. ***Epactophanes richardi*** female, a harpacticoid copepod of rheocrene springs that seems to prefer mosses. Photo from US Geological Survey, through public domain.

Figure 55. ***Eucyclops serrulatus***, a harpacticoid copepod that lives among mosses of rheocrene springs. Photo by Fausto at <microscopio.it.gg>, with permission.

Bottazzi *et al*. (2011) also reported that the taxa most represented in the Northern Apennine rheocrene springs were the harpacticoid copepods: ***Bryocamptus zschokkei*** (Figure 31) (mean number of individuals per sample = 2 for traps, 14 for mosses) and ***B. pygmaeus*** (1 individual/sample for traps, 5 for mosses). Out of their total of 3,284 invertebrates collected, **Ostracoda**, **harpacticoid Copepoda**, and **Diptera** were the most abundant among the 54 taxa. Bottazzi and coworkers considered the mosses to be a favorable habitat that contributed to the high species diversity.

Rivulets

Rivulets, often as outflow from springs, often have mosses that serve as copepod habitats. Stoch (2003, 2007) reported copepods from mosses in **hygropetric** rivulets (having water forming a surface film on rocks). Genera such as ***Moraria*** (Figure 45), ***Epactophanes*** (Figure 54), ***Arcticocamptus***, ***Nitocrella***, ***Parastenocaris*** (see Figure 33), ***Speocyclops***, and ***Diacyclops*** (Figure 52) occur among hygropetric rivulet mosses (Fiasca *et al.* 2005).

Streams

It appears that copepods are important bryophyte inhabitants in mountain streams of New Zealand. In unshaded areas of the streams, Suren (1992) found ***Canthocamptus howardorum***, ***C. maoricus*** (see Figure 56), ***Attheyella stillicidarum***, ***A.*** cf. ***brehmi*** (see Figure 35), ***Antarctobiotus elongatus***, and ***A.*** cf. ***diversus***, all in the **Harpacticoida** (Figure 57). In 1992, Suren suggested that the large numbers of Copepoda found in association with bryophytes there may relate to the high food value of abundant periphyton that grow on the surfaces and the ability of the bryophytes to serve as safe sites against fast water currents. But in 1993, he refined his assessment to suggest that the copepods are especially important on bryophytes that are covered with detritus rather than periphyton (Suren 1993).

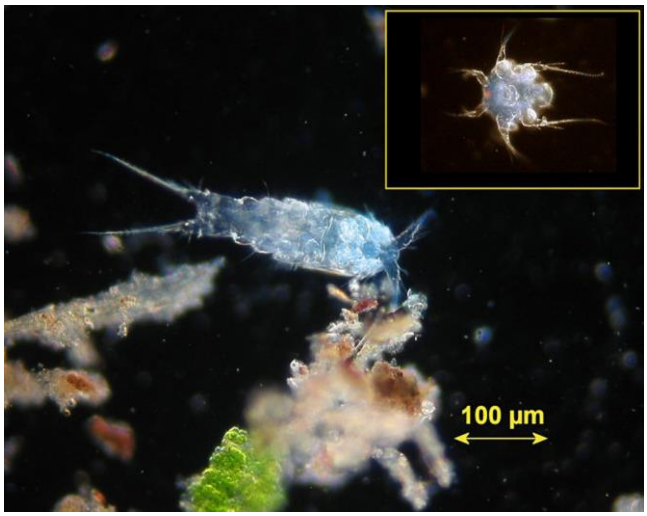

Figure 56. ***Canthocamptus*** from moss; note nauplius in insert. Photo by Graham Matthews <http://www.micromagus.net/microscopes/pondlife_copepoda.html>, with permission.

Figure 57. Harpacticoid copepod on leaf of ***Fontinalis antipyretica***, demonstrating how tiny it is. Photo by Dan Spitale, with permission.

Leaf axils of bryophytes can be particularly protective against the current, but they also serve as collection sites for detritus. The differences in periphyton vs organic detritus may relate to location in sun vs shade. Cox (1988) found that bryophytes from an unshaded location had predominantly periphyton associated with them, whereas

those from the shaded site had predominately fine amorphous detritus associated with them. This is reasonable, as more light would promote greater algal growth. But flow rates will play into this as well, and oxygen content will differ with both flow rate and periphyton vs detrital matter.

Chironomidae (midges) are typically the dominant group on stream bryophytes [see, for example Williams (1989) in southern Ontario, Canada, and Nolte (1991) in Germany, who found that chironomids dominated on the submerged moss ***Hygroamblystegium tenax*** (Figure 58)]. In New Zealand alpine streams, Suren (1992) found that harpacticoid copepods and ostracods were among the most abundant groups of non-chironomids. Suren found that there was a "strong positive relationship" between copepod density and high water velocity, with densities among the bryophytes there reaching twice that of macroinvertebrates. At first, this seems like a contradiction because meiofauna are intolerant of high water velocity (Winner 1975) and avoid it by burrowing into the hyporheic zone (sediment). Suren (1992) pointed out that the copepods ***Bryocamptus vejdovskyi*** and ***B. zschokkei*** (Figure 31) in Minnesota, USA, can only be found in the hyporheos in fast-flowing streams. He suggests that the bryophytes provide a "biotic hyporheic zone." The studies by Suren (1992) in New Zealand are in sharp contrast to those of Cox (1988) who found that in streams in Tennessee, USA, it was rotifers that dominated the bryophytic "hyporheic zone" in the mosses ***Fontinalis novae-angliae*** (Figure 59) and ***Platyhypnidium riparioides*** (Figure 60).

Figure 58. ***Hygroamblystegium tenax***, a submerged moss dominated by Chironomidae (midges - Diptera) rather than copepods in Germany. Photo by Barry Stewart, with permission.

Figure 59. ***Fontinalis novae-angliae*** at edge of stream, a moss that supports dominant rotifer fauna, not copepod fauna, in the hyporheic zone in Tennessee, USA. Photo by Janice Glime.

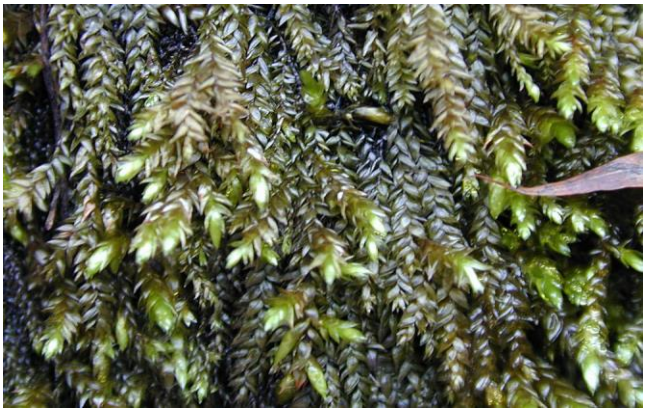

Figure 60. ***Platyhypnidium riparioides***, a moss that supports a dominant rotifer fauna rather than a copepod fauna in the hyporheic zone in Tennessee, USA. Photo by Michael Lüth, with permission.

Splash Zones

Stream edges and waterfall splash zones provide a suitable habitat for some limnoterrestrial copepods (Lewis 1972a. In New Zealand one can find such taxa as ***Attheyella stillicidarum*** (see Figure 35) among the mosses and liverworts, preferring either permanently dripping mossy banks or areas in the splash zones of streams, apparently requiring moving (fresh, not stagnant) water. ***Attheyella humidarum*** and ***Attheyella fluviatalis*** likewise prefer dripping mossy banks and damp "bush" moss. In addition to these ***Attheyella*** species, Lewis (1972b) also described six new species in the genus ***Antarctobiotus*** (***A. ignobilis***, ***A. diversus***, ***A. elongatus***, ***A. australis***, ***A. exiguus***, ***A. triplex***) from damp mosses in New Zealand.

Cave Pool

Galas *et al*. (1996) examined the decomposition of litter in a cave pool in Poland. These pools included copepods, among other fauna. Respiration released more energy by activity of microorganisms on mosses (***Polytrichum***, Figure 61) than on the litter of *Sorbus* and *Alnus* in the pool. This higher rate among the bryophytes suggests that they may have provided a better food source of fine particulates and microorganisms for small organisms such as copepods than that associated with the submersed leaf litter.

Figure 61. ***Polytrichum commune*** in a geothermal spring, Yellowstone, WY, USA. Photo by Janice Glime.

Summary

Microcrustacea are primarily aquatic and marine, but some, including Copepoda and Cladocera, have developed characteristics that permit them to live on land in such habitats as wet bryophytes. Moisture, water chemistry, *p*H, and roughness of the moss habitat can be important determinants of microcrustacean diversity.

Adaptations to land may include separate sexes, ability to change sex, and parthenogenesis. Cyclopoid copepods have short life cycles that permits them to increase recruitment. They can sometimes disperse with their bryophyte substrate.

Truly terrestrial Cladocera are few, with ***Bryospilus*** being best represented among this group. Springs seem to be a transitional habitat between aquatic and terrestrial systems, with bryophytes serving as a refuge vertically and horizontally as moisture levels change. In streams, bryophytes can serve as a safety net to catch drifting organisms. The bottom of the moss clump provides a safe haven from the torrential waters above while being a collection site for food. Food is often fine detritus trapped by the bryophytes In these aquatic and wet habitats, the bryophytes can contribute significantly to increasing the faunal diversity. Peatlands/***Sphagnum*** bogs increase diversity by offering multiple niches both in the mosses and among the tracheophyte vegetation. ***Alona*** and ***Alonella*** are among the most common there; ***Alona*** is also the most common drift cladoceran in streams.

Cladoceran adaptations can include appendage reduction, shorter life cycle, eggs placed in dense masses of vegetation, and ability to swim in a thin film of water.

Copepods on land use their antennae to swim in the larval stage. Dormancy permits them to survive dry periods, including resting eggs, arrested development, and encystment of both juveniles and adults.

The ability of land-dwelling copepods to live among bryophytes is reflected in such names as ***Muscocyclops, Bryocyclops***, and ***Epactophanes muscicola***. Bryophytes can provide moist islands when copepods move from one location to another. Other species live among canopy epiphytes. Some even live among bryophytes in the Antarctic. ***Attheyella*** and ***Moraria*** are among the genera known from peat bogs, with genera such as ***Paracyclops*** found in pitcher plants there. Small copepods hide among the aquatic bryophytes. Harpacticoid copepods can dominate the moss fauna in springs, where temperature and *p*H are important factors in diversity. ***Canthocamptus*** and ***Attheyella*** are well represented in streams in New Zealand. Like the Cladocera, copepods often feed on periphyton or detritus among the bryophytes.

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CHAPTER 10-2
ARTHROPODS: CRUSTACEA – OSTRACODA AND AMPHPODA

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CHAPTER 10-2
ARTHROPODS: CRUSTACEA – OSTRACODA AND AMPHPODA

Figure 1. Terrestrial amphipod on leafy liverworts from New Zealand. Photo by Paddy Ryan, with permission.

The amphipods (Figure 1) and ostracods (Figure 2) might be considered as mimics that live in the bryophyte world. The amphipods look like miniature shrimp and the ostracods look like miniature mussel shells with a shrimp inside instead of a mussel.

CLASS OSTRACODA

Mark Papp (pers. comm. 19 November 2011) reported to me that he had a very sore neck and shoulders, but no ostracods to report. He had been looking at roof mosses where he had originally taken many ostracods at Chalfont St. Peter, UK. Their identity as ostracods was confirmed by a marine ecologist. He did find the remains of a copepod. The ostracods are evasive, making it that much more delightful when you find them. Those on the roof had apparently moved on.

The name **Ostracoda** comes from the Greek *óstrakon*, meaning shell. Ostracods (sometimes known as seed shrimp) look like miniature clams (or seeds) with a tiny shrimp-like animal living inside the shell. They typically are marine and freshwater organisms, but some have become terrestrialized. They are not common among bryophytes, but they do sometimes occur there.

Figure 2. Ostracod, showing internal digestive system through the shell. Photo by Anna Syme through Wikipedia Commons.

Adaptations

Harding (1953) claimed the first find of a terrestrial ostracod (***Mesocypris terrestris***) as a new species occurring among mosses at the source of a small stream on Mt. Elgon in Kenya. Another occurred among mosses in a waterfall. But this ostracod is too large and globular for close alliance to the aquatic environment, so Harding (1953) reasoned that it must be more truly terrestrial. This ostracod is blind, presumably surviving loss of eyes because eyes are of little use among the mosses, and their swimming setae are very reduced as well. Instead, the second pair of antennae is especially powerful and Harding suggested that it might aid in movement in the water film among the mosses, a movement typically accomplished on mosses and liverworts by crawling (Powers & Bliss 1983). Excretion seems to be poorly understood, but some form of nitrogenous waste is excreted through glands on the maxillae, antennae, or both (Barnes 1982). Their food includes diatoms, bacteria, and detritus (Miracle 2014), items found not only in aquatic habitats, but also among terrestrial bryophytes.

Swimming to Crawling

A loss of ability to swim seems to be the result of an evolutionary loss of setae on antennae and reduction of setae on antennules (Harding 1953; De Deckker 1983; Martens *et al*. 2004). Instead, the terrestrial ostracods use their antennae to move along solid surfaces, much as benthic ostracods move along the bottom surface (Harding 1953; De Deckker 1983). On a moss, the ostracod is surrounded by a film of water at the bottom of the carapace (shell). This water is trapped by numerous hairs, especially ventrally and laterally, to about mid-height. This mechanism seems to work only on moist substrates. When ***Austromesocypris australiensis*** (=*Mesocypris australiensis*) was placed on a dry Petri plate, it was unable to retain all of the water when it moved (De Deckker 1983). Whereas most ostracods lie on their sides when at rest, this moss-dweller remains upright. As members of this species dry, they migrate to wetter conditions, but when it is too dry they close their shells (compare Figure 3 to Figure 9) to curtail water loss.

Figure 3. Dead **ostracod** with its shell open, revealing the exoskeleton. When taken out of water, this shell immediately closes. Photo by Paul Davison, with permission.

Reproduction

About half the non-marine ostracod species belong to the family **Cyprididae** (Wikipedia 2014). Many of these occur in temporary water bodies, requiring a degree of terrestrialization, and have drought-resistant eggs, mixed sexual and parthenogenetic reproduction, preadapting them to terrestrialization, and to living among bryophytes (Powers & Bliss 1983). There seems to be a prevalence of asexual reproduction among terrestrial ostracods compared to their aquatic counterparts (Pinto *et al*. 2005a). Nevertheless, terrestrialization of some may include retention of the fertilized eggs, protecting them from desiccation. Observations by Chapman (1961) suggest that the developing embryos of the moss-dweller ***Scottia audax*** (=*Mesocypris audax*) may be retained within the shell of the mother until they become free-living juveniles.

Habitats

Terrestrial

Although most ostracods are marine or aquatic, some, such as ***Mesocypris*** spp., live in wet terrestrial habitats, including mosses (Introduction to the Ostracoda 2002). This genus seems to be widespread among bryophytes in the Eastern Hemisphere from the Russian Far East (I'm unable to confirm this record) to Australia (Martens *et al*. 2004). Terrestrial species also occur in South America (Pinto *et al*. 2005a, b).

Although Harding (1953) claimed the first record of terrestrial ostracods in Africa with his finding of ***Mesocypris terrestris***, this one was still in the wet habitats of a waterfall and source waters of a stream among mosses. De Deckker (1983) collected ***Austromesocypris australiensis*** from Cammoo Caves in Queensland, Australia, from wet moss. De Deckker points out that although most ostracods are aquatic or marine, several species are able to live among leaf litter and mosses that are able to provide a moist environment. Among these, the type specimen of ***Austromesocypris australiensis*** was found among mosses, and others were living among ***Sphagnum*** (Figure 4) on the side of a road near a small creek in New South Wales, Australia. In fact, these individuals were unable to swim freely even in free water.

Figure 4. ***Sphagnum cristatum*** from a soil bank in New Zealand. Photo by Janice Glime.

In Queensland, the terrestrial ostracod ***Scottia audax*** (also known from mosses in New Zealand; Chapman 1961) occurred along with ***Austromesocypris australiensis*** in mosses (De Deckker 1983). ***Scottia birigida*** (Figure 5)

occurs among mosses in Japan (Robin James Smith, pers. comm. 31 March 2014). In Tasmania, ***Mesocypris tasmaniensis*** likewise occurs among mosses as well as litter (De Deckker 1983). Røen (1956) named ***Bryocypris grandipes*** from Africa (GBIF 2013), but I have only its name to suggest it dwells among bryophytes. De Deckker stated that terrestrial ostracods are known only from Gondwanaland: Africa, Madagascar, Australia, and New Zealand, but they have since been found in Europe (Pieri *et al*. 2009; Mark Papp, pers. comm. 19 November 2011) and South America, where ***Caaporacandona iguassuensis*** occurs among moist Brazilian forest mosses (Pinto *et al*. 2005a). Although members of the **Cyprididae** occur in North America, thus far terrestrial representatives seem to be undocumented. Nevertheless, Paul Davison (pers. comm. 31 May 2014) reports them from dripping cliffs (Figure 6) among algae and suspects they could inhabit bryophytes under similar conditions. Bryologists should watch for them!

Figure 5. ***Scottia birigida***, a moss dweller in Japan. Photo by Robin James Smith, with permission.

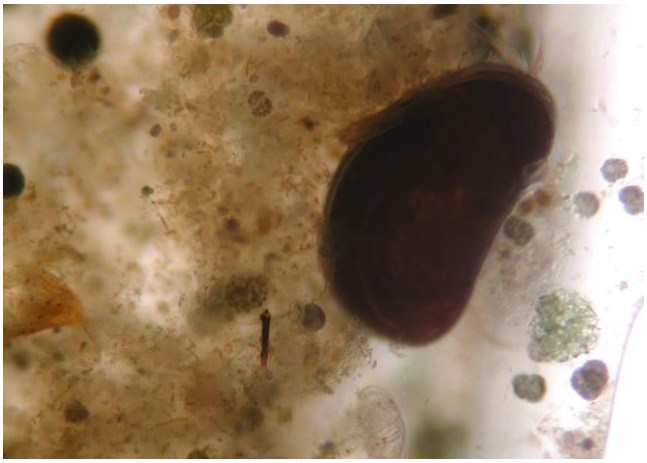

Figure 6. Ostracod from wet wall, a potential bryophyte dweller. Photo by Paul Davison, with permission.

Pieri *et al*. (2009), reporting on ostracods from Friuli Venezia Giulia, Italy, found three species distributed on mosses: ***Cypria ophthalmica*** (Figure 7), ***Cyclocypris laevis*** (Figure 8), ***Cyclocypris ovum*** (Figure 9). It is not clear what the habitat was for these mosses. ***Cypria ophthalmica*** is known as a widespread species from the karst region of Italy (Wagenleitner 1990). All three species occur at the margins of lakes in the reed belt among the vegetation and on the sediment surface (Kiss 2007). The mosses were only examined from one site. One should note that these three species are also among the three most common taxa in the study (Figure 10), which included all the likely habitats for ostracods in the study area.

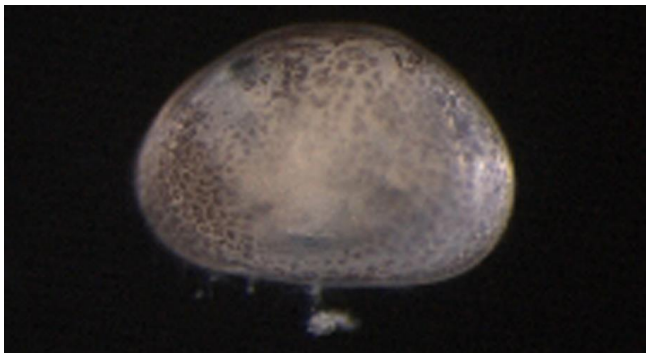

Figure 7. ***Cypria ophthalmica***, a moss-dweller in Italy. Photo from Bold Systems through Creative Commons.

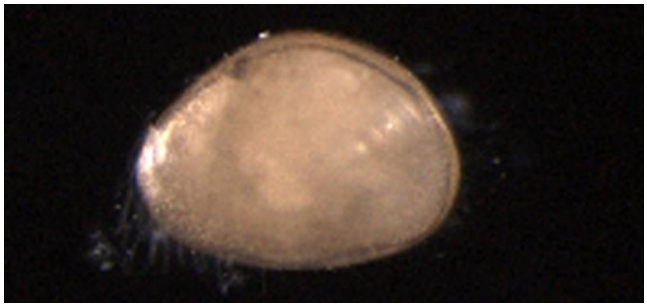

Figure 8. ***Cyclocypris laevis***, a moss-dweller in Italy. Photo from Bold Systems through Creative Commons.

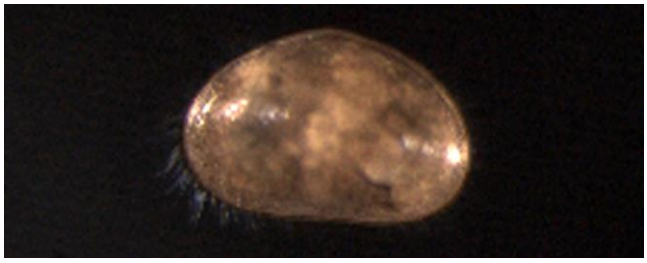

Figure 9. ***Cyclocypris ovum***, a moss-dweller in Italy, with its shell closed. Photo by Bold Systems Creative Commons.

Peat Bogs

Peat bogs seem to be a rich site for ostracod species. Harding (1953, 1955) states that ostracods tend to occur in ***Sphagnum*** (Figure 11) as well as in forest litter. Bryophytes influence the species composition by creating a diversity of niches, from pools to dry hummock tops, and many microniches among the stems and leaves. Likewise, a gradation of *p*H can sometimes be found vertically and horizontally, providing more niche choices. Temperature differs between the surface and deeper portions of peat. Figure 10 shows the relationships of four environmental parameters with the five most common ostracod species in 200 sites in the sampling of surface, interstitial, and ground waters of Friuli Venezia Giulia, Italy (Pieri *et al*. 2009).

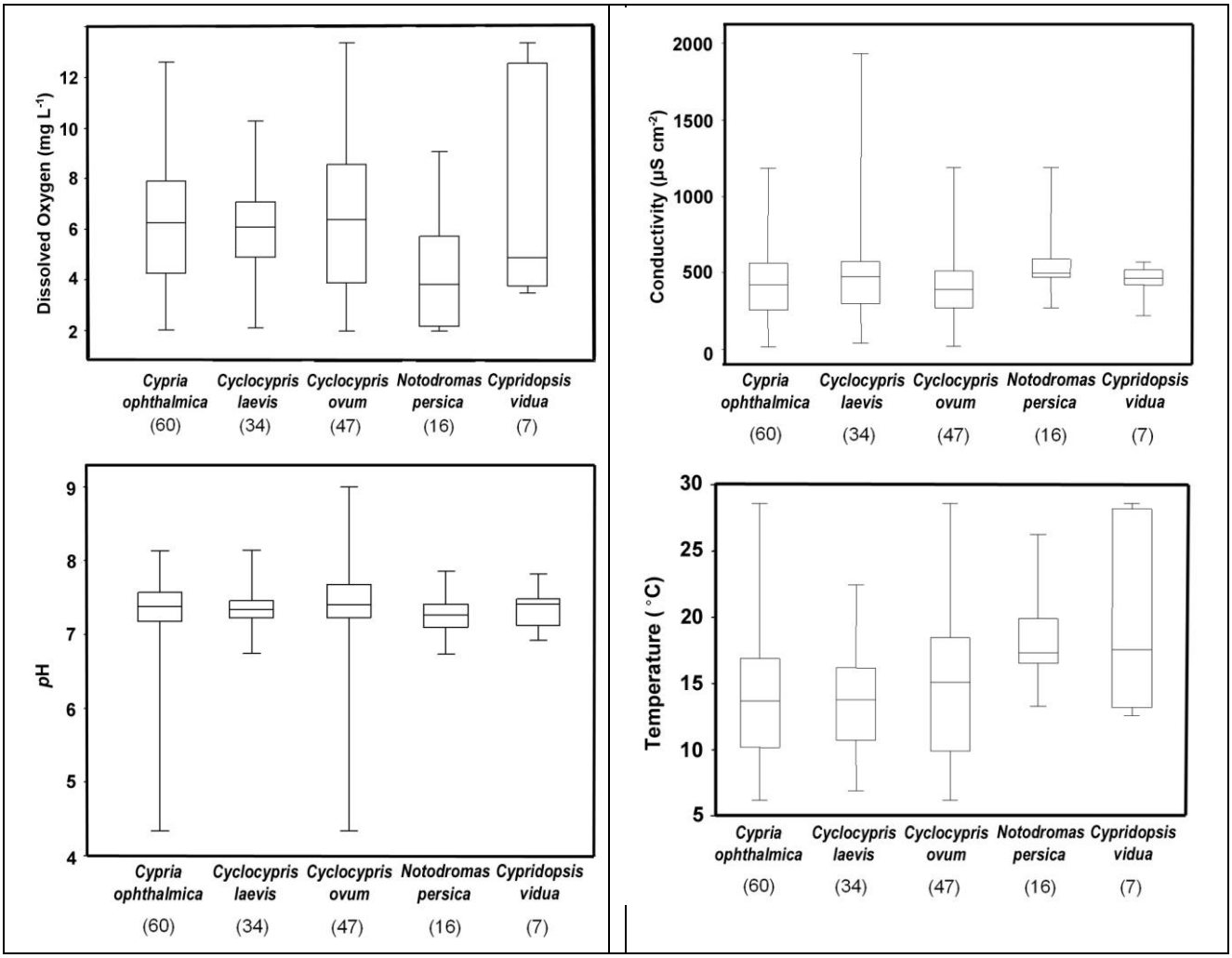

Figure 10. Comparison of environmental parameters for the five most common species in Friuli Venezia Giulia, Italy that also occur in peat bogs. The boxes show 25-75% quartiles. The horizontal line is the median, and vertical bars (whiskers) show the maximum and minimum values. The numbers of analyzed samples appear in parentheses below the species names. Redrawn from Pieri *et al*. 2009.

Figure 11. ***Sphagnum capillifolium*** representing a genus that houses several species of terrestrial ostracods. Photo by Blanka Shaw, with permission.

At Friuli Venezia Giulia, Italy, the five most widespread and common species of ostracods also occurred in peatlands (Pieri *et al*. 2009). Pieri and coworkers reported 24 species in 16 genera from peat bogs (Table 1).

Table 1. Ostracod species among those at Friuli Venezia Giulia, Italy, that occurred in peat bogs. From Pieri *et al*. 2009.

Darwinula stevensoni Figure 12	*Cyclocypris ovum* Figure 9
Penthesilenula brasiliensis	*Ilyocypris bradyi* Figure 29
Microdarwinula zimmeri Figure 13	*Ilyocypris inermis* Figure 19
Pseudocandona lobipes	*Notodromas persica* Figure 20
Pseudocandona compressa Figure 14	*Eucypris pigra* Figure 21
Pseudocandona pratensis Figure 15	*Herpetocypris* sp. Figure 22
Pseudocandona cf. *sucki*	*Herpetocypris reptans* Figure 22
Cryptocandona vavrai	*Scottia pseudobrowniana*
Candonopsis scourfieldi see Figure 16	*Cypridopsis elongata* Figure 23
Cypria ophthalmica Figure 7	*Cypridopsis vidua* Figure 24
Cyclocypris globosa Figure 17	*Cavernocypris subterranea*
Cyclocypris laevis Figure 18	*Metacypris cordata* Figure 25

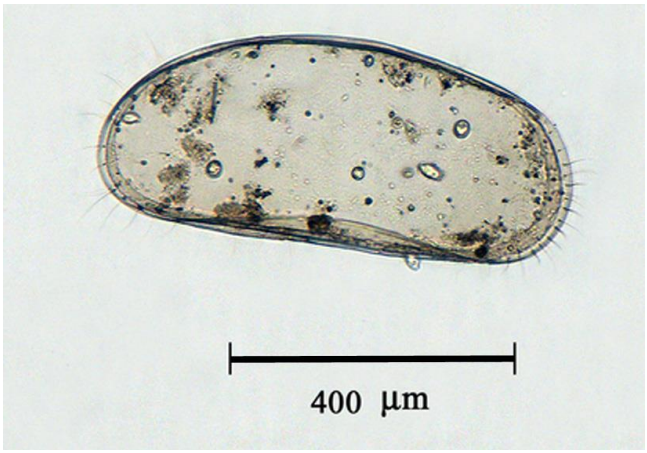

Figure 12. ***Darwinula stevensoni***, an ostracod from mosses in peatlands in Italy. William Dembrowski through Creative Commons.

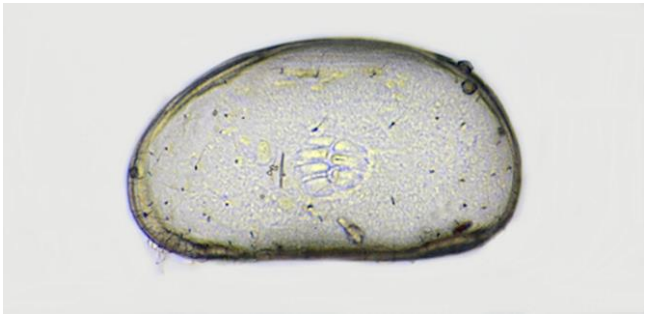

Figure 13. ***Microdarwinula zimmeri***, a peat moss ostracod. Photo by Robin J. Smith, with permission.

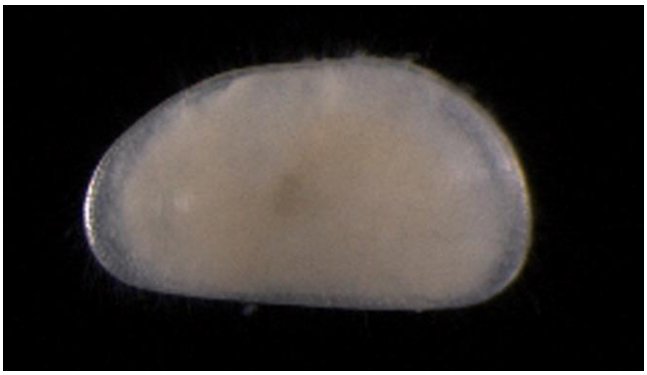

Figure 14. ***Pseudocandona compressa***, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

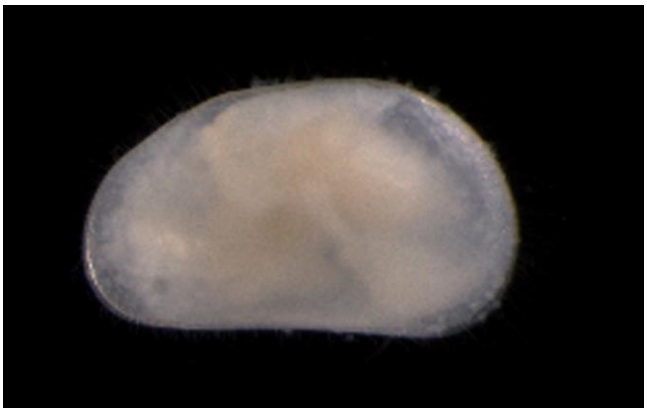

Figure 15. ***Pseudocandona pratensis***, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

Figure 16. ***Candonopsis kingsleii***, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

Figure 17. ***Cyclocypris globosa***, a peat bog species in Italy. Those white ovals near its surface are attached protozoa. Photo from Bold Systems through Creative Commons.

Figure 18. ***Cyclocypris laevis***, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

Figure 19. ***Ilyocypris inermis***, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

Figure 20. ***Notodromus*** sp., a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

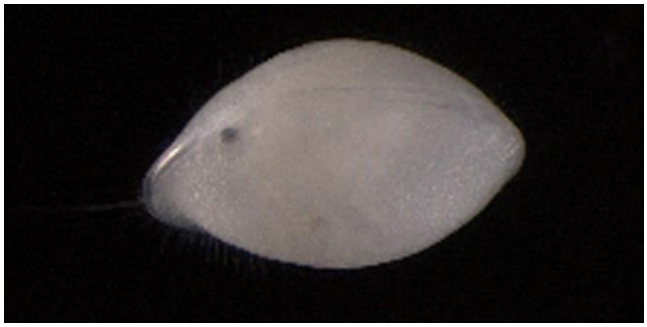

Figure 21. ***Eucypris pigra***, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

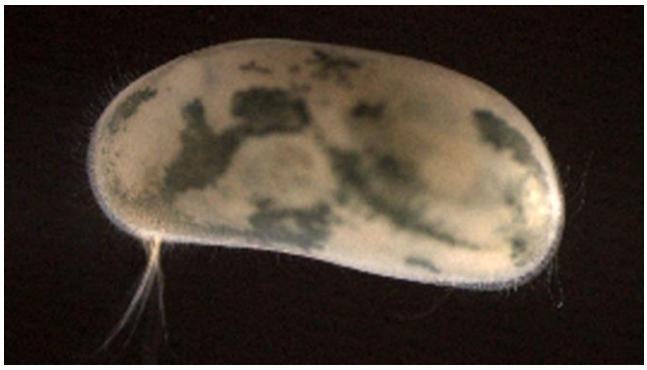

Figure 22. ***Herpetocypris reptans***, a genus with members living in peat bogs in Italy. Photo from Bold Systems through Creative Commons.

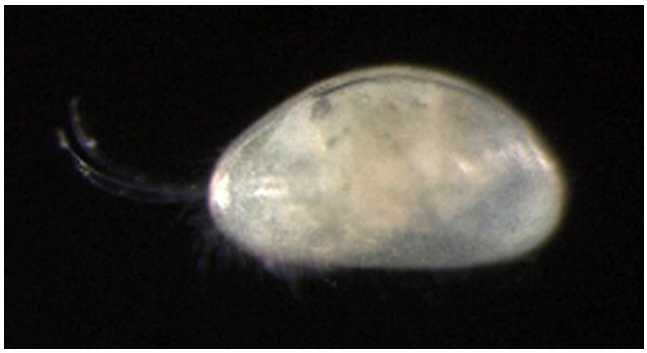

Figure 23. ***Cypridopsis elongata***, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

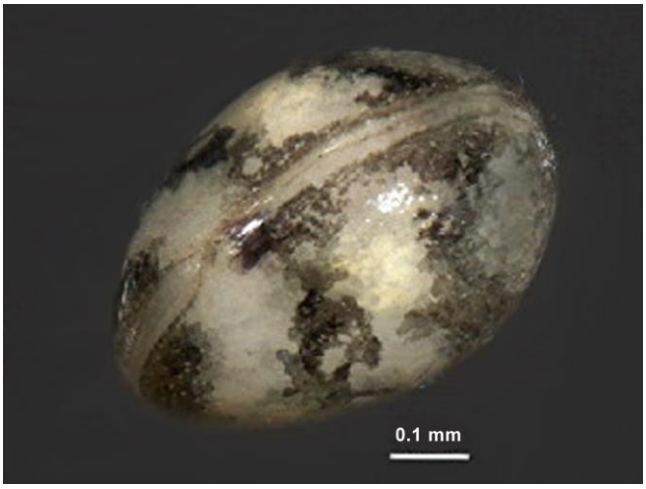

Figure 24. ***Cypridopsis vidua***, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

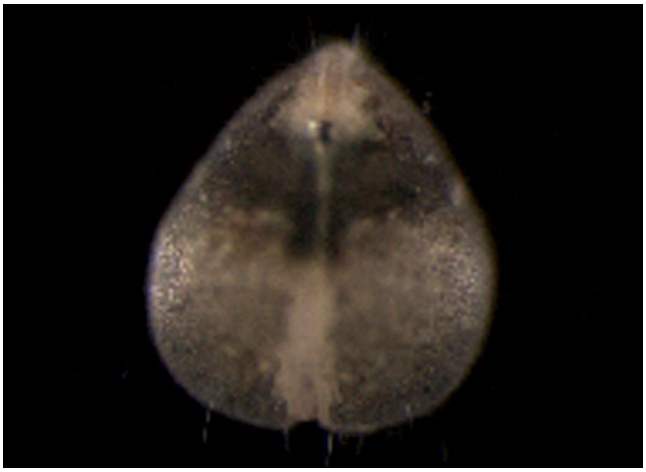

Figure 25. ***Metacypris cordata***, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

It is interesting that some of these Italian bog-dwelling species are so widespread. For example, ***Penthesilenula brasiliensis*** is known on all the continents except Antarctica and North America (Pieri *et al.* 2009). Its wide range of habitats (rivers, streams, interstitial water, bromeliad basins, rain forest leaf litter, and bog mosses) may permit this widespread geographic distribution. Furthermore, three of the most common species in this part of Italy have a wide altitudinal distribution (Figure 26). Surely they occur among bryophytes in other European countries as well.

Some species seem to be restricted to bogs, making them **tyrphobionts**. In their study of Friuli Venezia Giulia, Italy, ***Cavernocypris subterranea*** and ***Cryptocandona vavrai*** were apparently restricted to peat bogs at high altitudes (Pieri *et al*. 2009). Barclay (1968) reported the new species ***Penthesilenula sphagna*** (=*Darwinula sphagna*) from New Zealand, living above the water among ***Sphagnum*** (Figure 4). Similar relationships of ostracods to ***Sphagnum*** are known from eastern Africa (Menzel 1916).

The importance of mosses in bogs can be indirect. In ***Sphagnum*** (Figure 11) peatlands, mosses are a necessary habitat element to support the growth of pitcher plants (***Sarracenia purpurea***; Figure 27). The leaves of these plants form pitchers of water that provide a suitable habitat

for some ostracods in North America (Hamilton *et al*. 2000), including those in Florida, USA (Harvey & Miller 1996).

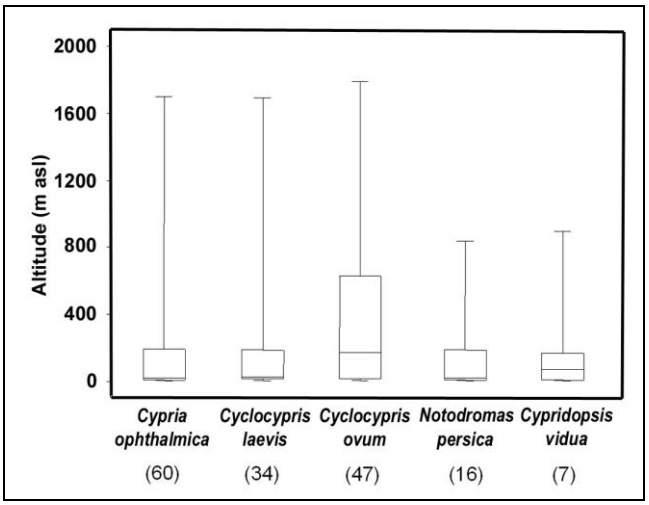

Figure 26. Comparison of altitudinal ranges of the five most common ostracods in Friuli Venezia Giulia, Italy, all five of which also occur in peat bogs. The boxes show the 25-75% quartiles. The horizontal line is the median, and the vertical bars (whiskers) show the maximum and minimum values. The numbers of analyzed samples appear in parentheses below the species names. Redrawn from Pieri *et al*. (2009).

Figure 27. ***Sarracenia purpurea*** in a ***Sphagnum*** bog. Photo from Wikimedia Creative Commons.

Aquatic

Streams

Potamocypris pallida (Figure 28) in Macedonia occurs in moss cushions on the sandy and rocky bottoms of mountain springs and brooks (Petrovski & Meisch 1995). In my own stream bryophyte collections in Appalachian Mountain, USA, streams, I rarely encountered ostracods and considered them to be accidental or temporary residents since they more commonly occur in quiet water.

Springs

Spring habitats have a number of features in common with peat bogs. They typically have a dominant bryophyte flora, and they can be dry during part of the year. But their *p*H range can reach into basic values, creating conditions that favor different communities.

Bottazzi *et al*. (2011) compared ostracods collected in traps with those collected from mosses in **rheocrene** springs (where aquifer water reaches the surface) of the Northern Apennines. Ostracods were among the most abundant taxa, particularly among the permanent meiofauna. Such common inhabitants of springs can be called **crenophiles** (literally, spring-lovers). Only ***Psychrodromus bertharrami*** was collected in both traps and mosses, with similar numbers (20 individuals per sample in traps, 17 for mosses). ***Ilyocypris bradyi*** (Figure 29) was only recovered from mosses. All other taxa (except one of questionable identity) were collected in traps. Fryer (1955) described ***Potamocypris thienemanni*** (see Figure 28) as new to Britain, inhabiting bryophytes, including ***Sphagnum*** (Figure 11), in a spring. This species was also known from three springs in Germany.

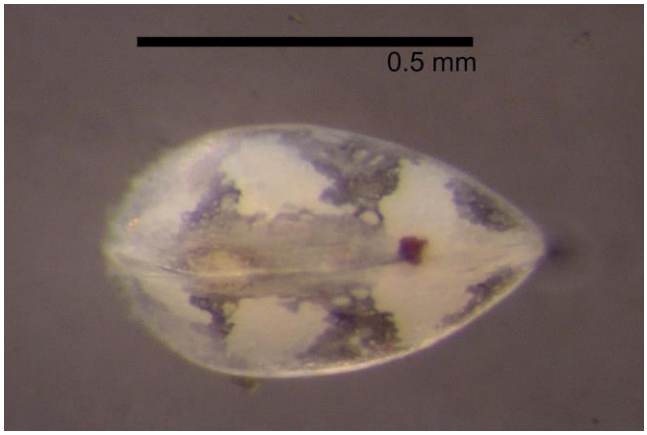

Figure 28. ***Potamocypris pallida***, moss-dweller on sandy and rocky bottoms of Macedonian mountain springs and streams.. Photo by Elissa Dey, Zooplankton Project. Accessed 13 May 2014 at <http://www.biology.missouristate.edu/ostracods/Default.htm>.

Figure 29. ***Ilyocypris bradyi***, an ostracod that in the northern Apennine springs seems to be limited to living among mosses. Note the hairy carapace that is typical of terrestrial ostracods. Photo from Bold Systems through Creative Commons.

CLASS MALACOSTRACA, ORDER AMPHIPODA

I have occasionally found amphipods in my collections of stream mosses, but they are more typically in quiet water

of larger streams. Nevertheless, it appears that in some cases they can be an important part of the aquatic moss faunal community (Minckley 1963; Minckley & Cole 1963; Matonickin & Pavletic 1964; Willoughby & Sutcliffe 1976). Badcock (1949) found ***Gammarus*** (Figure 30) to be most numerous in mosses and other protected niches, reporting an estimated fifty in a single tuft of moss (Cheney 1895). They are even known from terrestrial mosses (Merrifield & Ingham 1998).

Figure 30. ***Gammarus pulex*** showing the massive numbers in shallow pools. Photo through Creative Commons.

In some systems, amphipods can be quite abundant among the bryophytes. Wulfhorst (1994) found this to be true in two acid streams in the Harz Mountains, Germany, where they far exceeded those in the interstitial spaces (Figure 31).

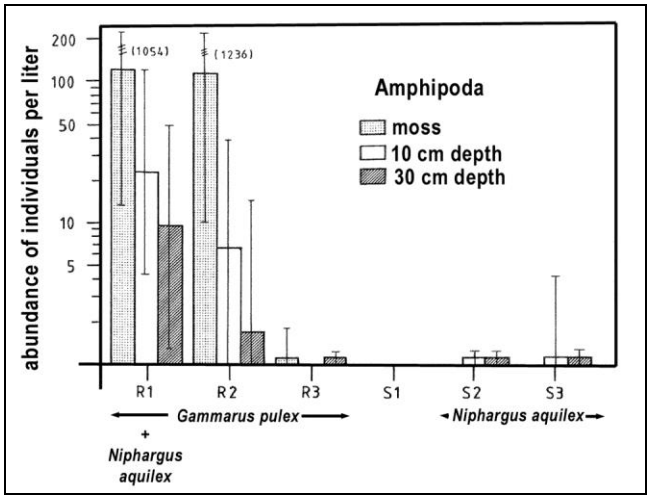

Figure 31. Abundance (number of individuals per liter) of the amphipods ***Gammarus pulex*** and ***Niphargus aquilex*** (Figure 32) among mosses and the interstitial spaces at 10 and 30 cm depth at six stations in two Harz Mountain streams. Bars indicate 95% confidence interval; n = 14 for mosses and 28-36 for interstitial spaces. Redrawn from Wulfhorst 1994.

Figure 32. ***Niphargus aquilex***, a moss dweller. Photo by Grabow-Universität Koblenz-Landau, permission pending.

Adaptations to Land – and Bryophytes

Stout (1963) summarized three evolutionary pathways for terrestrial plankton. Among these, Hurley (1959) proposed that amphipods moved from the **supralittoral** (splash zone) fauna directly to the forest floor. Another suggestion is that fauna such as amphipods may have originated in freshwater streams, extended to the wet mossy banks and ***Sphagnum*** (Figure 11) bogs to the forest floor and ultimately to mineral soil. Stout considers the latter route to be the most convincing.

Hurley (1959, 1968) reported that all the terrestrial species of amphipods are in the family **Talitridae**, occurring in damp habitats. To survive in these terrestrial habitats required several morphological and behavioral changes, not to mention the physiological changes needed. They needed to become air breathers, jump instead of swim (accomplished by reduced **pleopods**, *i.e.* swimmerets, – to stumps in some species), adapt their life cycle to the changes in the seasons (Hurley 1959), and excrete uric acid instead of ammonia (Dresel & Moyle 1950). But they can have more than 50% ammonia excretion (Hurley 1959), perhaps releasing their ammonia as a gas like the isopods (O'Donnell & Wright 1995). It appears that they may have evolved different solutions to some of these problems from those of some of the other crustacean groups.

We can understand the small number of terrestrial amphipod species by comparing them to the isopods, where both aquatic and terrestrial species likewise exist. Terrestrial amphipods are less adapted to their terrestrial life than the isopods, being restricted to more narrow niches (Hurley 1968). The amphipods lack the isopod advantages of evaporative cooling at high temperatures and have exoskeletons with greater permeability, leading to greater risk of desiccation (Hurley 1959). Terrestrial isopods have lost their antennae, whereas in amphipods they are merely simplified. Both groups have modified their behavior to stay where it is cool and moist.

In wet leaf litter, the amphipods may move upward, a behavior we should look for among mosses (Hurley 1968). It is interesting that in the Fiordland of New Zealand the high level of rainfall and saturated ground has driven the amphipods to living among mosses or under bark of trees rather than their usual habitat of leaf litter. Avoidance of leaf litter there seems to be especially true for ***Arcitalitrus sylvaticus*** (=*Talitrus sylvaticus*; Figure 33). Its relative

Arcitalitrus dorrieni (Figure 34) also occurs with mosses on bark in Australia.

Figure 33. ***Arcitalitrus sylvaticus***, an amphipod that avoids leaf litter and lives among mosses in the New Zealand Fiordland. Photo by Arthur Scott Macmillan through Creative Commons.

Figure 34. ***Arcitalitrus dorrieni*** on bark among mosses. Photo by Dluogs through Creative Commons.

Obtaining water, no problem for aquatic species, requires special behavioral techniques for the land dwellers. It is interesting that the water-obtaining behavior is similar to that of the terrestrial oniscid isopods. The terrestrial amphipods both gain and eliminate water by dabbing the uropod tips (tails) onto wet or dry substrata, respectively (Moore & Richardson 1992). The water is exchanged rapidly in or out of the central channel through the capillary spaces between the body parts. Beating **pleopods** (abdominal appendages also known as swimmerets) transfer water from the abdomen to the thorax in most terrestrial taxa. Water that pools beneath the tail is taken in by anal drinking.

Reproduction and Early Development

Among amphipods, the male is typically larger than the female and mounts her dorsally when she is ready to molt (Sutcliffe 1992). This behavior of having the male carry the female beneath him, known as **mate guarding**, helps to protect her during the crucial mating molt while she is more vulnerable to predation, and on land to desiccation. The eggs are deposited in the external brood pouch when she molts, followed by deposition of the sperm by the male. Following fertilization, embryos are carried by the female, but hatchlings, resembling miniature adults, are on their own. The terrestrial ***Talitrus saltator*** (a sandhopper; Figure 35) lays its eggs four days after molting, compared to laying them immediately after copulation (Figure 36) in the aquatic ***Gammarus*** (Hurley 1959). The latter species can hold the spermatozoa in a brood pouch for up to four days. The aquatic male ***Gammarus*** carries the female under him for several days (Figure 36), whereas the terrestrial male of ***Talitrus saltator*** does not carry the female, a behavior difference that seems backwards until you realize he is jumping around on the sand and the female would get in the way. The 1-10 terrestrial eggs are much larger than the small and numerous aquatic eggs. The eggs of the terrestrial species furthermore remain in the brood pouch longer, affording them greater protection from desiccation.

Figure 35. ***Talitrus saltator***, a sand hopper that holds its eggs four days after molting. Photo by Arnold Paul through Wikimedia Commons.

Figure 36. ***Gammarus pulex*** copulating, with the larger male on top. Photo by J. C. Schou, with permission.

A further means to conserve both energy and water is **neoteny**. ***Orchestia*** (Figure 37) reaches sexual maturity at an earlier growth stage and smaller size (Powers & Bliss 1983). This results in fewer offspring. They have a female bias, somewhat compensating for the smaller number of offspring, and females are larger than males, which is atypical for amphipods. Stephensen (1935) reported ***Orchestia floresiana*** from moss in Java, where it grows in waterfalls, rivulets, and fountains.

Figure 37. ***Orchestia cavimana*** at Colwick Park, Notts, UK This terrestrial genus has females larger than males. Photo by Roger S. Key, with permission.

Food among the Bryophytes

Felten *et al*. (2008) found that some aquatic amphipods, or at least ***Gammarus fossarum*** (Figure 38), eat mosses, and that the relative proportion in the diet increases as they grow from 2 mm to 4 mm, increasing only slightly after that (Figure 39). Conversely, the proportion of fine amorphous detritus steadily decreases as the amphipods grow. Felten *et al*. suggest that the younger (smaller) amphipods do not have mouth parts that are developed well enough to eat the larger food items like bryophytes. The proportion of bryophytes in the diet also depends on where they are living, with those living among bryophytes eating a greater proportion of bryophytes (Figure 40). It is interesting that those in the detrital pools have a greater proportion of minerals, suggesting that they are unable to sort out the nutritious items from the non-nutritious items that surround them. It was unclear if the detrital pool populations were actually nibbling on the bryophytes or just eating fragments that had collected where they were.

Figure 38. ***Gammarus fossarum***, an aquatic amphipod that eats mosses when its mouth parts are developed well enough to do so. Photo from BioLib.cz through public domain.

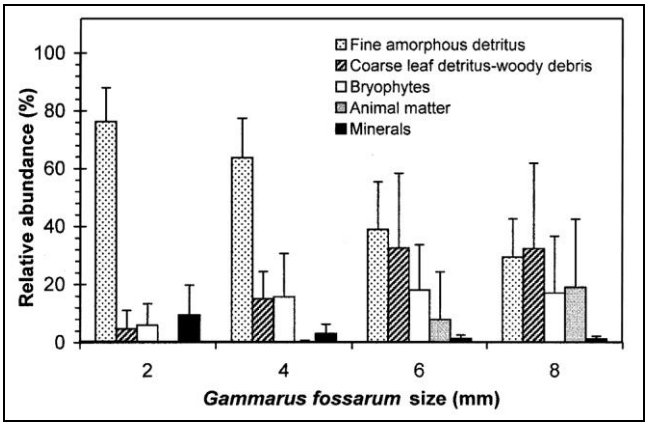

Figure 39. Comparison of mean percentage food types ±SD. of ***Gammarus fossarum*** as it relates to size. Modified from Felten *et al*. 2008.

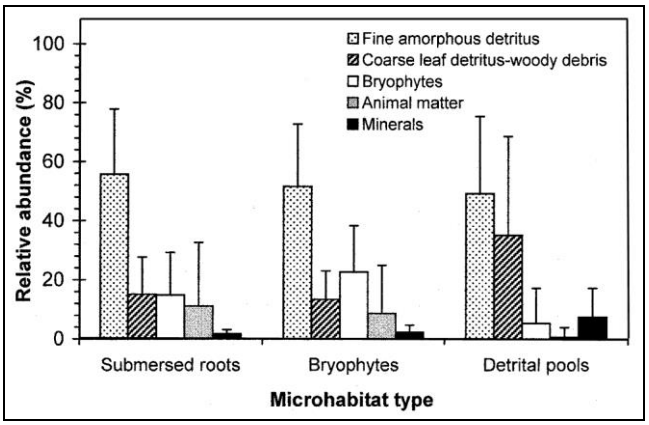

Figure 40. Comparison of mean proportion (±SD) of bryophytes vs other food items eaten by ***Gammarus fossarum*** in three habitat types. Modified from Felten *et al*. 2008.

Gladyshev *et al*. (2000) examined the gut contents of ***Gammarus lacustris*** (Figure 41) and found that they ingested mostly seston, obtaining omega 3 fatty acids from bottom sediment particles. They also consumed cells of the green alga *Botryococcus*. This alga not only survived the digestive tract, but its photosynthetic activity increased. They considered this activity to contribute to the dispersal of the alga, causing blooms in the littoral zone. Could this also be true of bryophytes they consume?

Figure 41. ***Gammarus lacustris***, an amphipod that consumes mostly seston. Photo by Bold Systems Creative Commons.

Food particle size can determine which species are able to survive in a habitat. Graca *et al*. (1994) found that ***Gammarus pulex*** (Figure 30-Figure 36) occupies different zones in rivers from those of the isopod ***Asellus aquaticus*** (Figure 42). The researchers found that the selection of substrate by ***G. pulex*** was based on size, with larger individuals choosing larger-sized substratum particles; juveniles were mostly associated with plants, including mosses. The substrate choices were most likely food choices. For the aquatic amphipods, it is likely that the detritus collected by the mosses serves as a food source. It would be interesting to determine the role of food sources in the choices of terrestrial amphipods for particular bryophytes.

Figure 42. ***Asellus aquaticus***, an aquatic isopod shown here on leaf litter. Photo by Malcolm Storey through Discover Life.

Acosta and Prat (2011) partially supported the idea of mosses as food collectors for the amphipod ***Hyalella*** sp. (Figure 43) in the headwaters of a High Andes river. Those living among layers of travertine had 69.5% fine particulate organic matter (FPOM), but even the bryophyte-dwellers had 56.8% FPOM. Those from leaf litter, on the other hand, had 68% of their gut contents from coarse particulate organic matter, suggesting a high level of flexibility in the diet.

Figure 43. ***Hyalella azteca***, a common bryophyte dweller in streams and rivers. Photo by Barbara Albrecht at <http://www.ipm.ucdavis.edu/WATER/U/hyalella.html>, with permission.

One hypothesis is that increased density of bryophytes would increase available organic detritus and thereby increase invertebrate abundance. However, Suren and Winterbourn (1992) found that reducing stem density of mosses had little effect on periphyton biomass, but that the detrital biomass was reduced on low-density artificial mosses. In any case, stem density had little effect on invertebrate abundance. Nevertheless, detrital and periphyton availability seemed to be the determining factor for invertebrate density.

Gladyshev *et al*. (2012) examined the gut contents of gammarids as part of a food chain study including ***Fontinalis antipyretica*** (Figure 44). Following Kalachova *et al*. (2011), they used acetylenic acids, considered as biomarkers for ***Fontinalis antipyretica***, to trace the food through the mosses, periphyton, Trichoptera, gammarids, and Siberian grayling (Gladyshev *et al*. 2012). Gladyshev *et al*. (2012) found small amounts of consumption of the mosses among both the Trichoptera (caddisflies) and the gammarid ***Eulimnogammarus*** (*Philolimnogammarus*) ***viridis***. The latter species had the highest concentrations of acetylenic acids in the winter and the lowest in summer (Kalachova *et al*. 2011), suggesting a shift to mosses in winter. It is likely that both the caddisflies and gammarids ate the moss to gain the periphyton and detritus accumulated there. The moss and associated periphyton and detritus are especially important in winter when other food sources are scarce (Gladyshev *et al*. 2012).

Figure 44. ***Fontinalis antipyretica*** var ***gracilis***, home for the amphipod ***Eulimnogammarus*** (***Philolimnogammarus***) ***viridis***. Photo by Des Callaghan, with permission.

But Parker *et al*. (2007) found that even when the moss ***Fontinalis novae-angliae*** (Figure 52) was cleaned of particulate matter, the amphipods still ate significant quantities of it. Earlier studies by Minckley and Cole (1963) likewise indicated that amphipods ate mosses. On the other hand, Mulholland *et al.* (2000) found that the amphipod ***Gammarus minus*** (Figure 45) depended on fine benthic (bottom) organic matter, despite the presence of bryophytes.

One feeding possibility in nature that might not be evident in laboratory studies is the role of fungi. Barlocher and Porter (1986) demonstrated that ***Gammarus tigrinus*** (Figure 46) was able to digest plant polysaccharides and release sugars from maple leaves. They also had the right enzymes to break down glycosidic linkages in small molecules, much as that done in microbial decomposition.

Furthermore, fungal carbohydrases ingested with the food of the ***Gammarus*** remained active in the gut. The implication seems to be that ***Gammarus*** could benefit from fungi associated with bryophytes in the field. Similarly, Sarah Lloyd (pers. comm.) has documented that terrestrial amphipods eat slime molds that live on mosses (Figure 47).

It appears that at least some bryophytes are not suitable food for ***Gammarus*** (Figure 30-Figure 36). Willoughby and Sutcliffe (1976) conducted feeding experiments on ***Gammarus pulex*** (Figure 30) from the River Dutton. They found that those provided with only the liverwort ***Nardia*** sp. (Figure 48) were unable to grow or survive.

Figure 45. ***Gammarus minus***, an amphipod that seems to prefer fine benthic organic matter over bryophytes. Photo through Creative Commons.

Figure 46. ***Gammarus tigrinus***, an amphipod that can digest fungi from leaves. Photo by Hugh MacIsaac, with permission.

Figure 47. Amphipod, probably ***Keratroides***, possibly ***K. vulgaris***, eating a slime mold (probably ***Diderma*** sp.) on moss. Photo by Sarah Lloyd, with permission.

Figure 48. ***Nardia scalaris***, a leafy liverwort genus in which a European species failed to sustain ***Gammarus pulex*** as a food source. Photo from Europe by Michael Lüth, with permission.

Habitats

Terrestrial

Terrestrial amphipods are rare, but bryophytes can provide the kind of moist habitat needed for them to survive. Merrifield and Ingham (1998) found amphipods in their Oregon Coast Range, USA, study of the fauna of ***Eurhynchium oreganum*** (Figure 49). In most months they were not evident, but in the December collection their numbers rose to 1 per gram of moss in 10 5-cm samples. The second "peak" was in April, with 0.6 per gram. Sarah Lloyd (pers. comm.) found what appears to be ***Keratroides***, possibly ***K. vulgaris***, among mosses in a wet eucalypt forest in northern Tasmania.

Figure 49. ***Eurhynchium oreganum***, a moss that is known to house amphipods in North America. Photo by Adolf Ceska, with permission.

Figure 50. Terrestrial amphipod, probably ***Keratroides***, possibly ***K. vulgaris***, on mosses in wet sclerophyll (eucalypt) forest at Birralee in Northern Tasmania, Australia. Photo courtesy of Sarah Lloyd.

Friend (1987) described the new species ***Orchestiella neambulans*** from litter that accumulated between mosses in Tasmania.

The Antarctic seems to be the most likely place to find limnoterrestrial Crustacea among mosses, but the amphipods are poorly represented. Pugh *et al*. (2002) found only one (***Makawe insularis***) in their study, a species with a broad niche of wood, leaf litter, lichens, tussock grass, under stones, penguin nests, and...among mosses.

Aquatic

Rocky streams are often dominated by mosses and liverworts in extensive mats over the rocks. These provide a foothold that protects their inhabitants from being swept away. Macan and Worthington (1951) found that amphipods such as ***Gammarus*** (Figure 30-Figure 36) were more likely on mosses that were not so thick, whereas thicker mosses were dominated by Chironomidae. They found that fish food organisms increased in number when the streams had rooted plants or mosses. One problem faced by the inhabitants of tracheophytes is that the plants begin die-off in late summer and the amphipods must find a new substrate with sufficient periphyton and detritus to provide food. ***Gammarus*** is among the slow colonizers (Fontaine & Nigh 1983), so it might benefit from the stable year-round habitat of bryophytes as a source of shelter and detrital and periphytic food.

Elliott (2005) found that ***Gammarus pulex*** had significant day-night differences in its habitat distribution. These were explained by dry weights of bryophytes, leaf material, organic detritus, distance from bank, water depth, water velocity, and particle size class. The bryophyte weight correlated positively with larger particle sizes and negatively with smaller particle sizes, perhaps explaining some of the choices by ***G. pulex*** for bryophytes. But this correlation may have been due to the preference of bryophytes for larger stones. Juvenile densities in the daytime correlated positively with smaller particles and negatively to larger particles, also correlating with the weight of bryophytes. However, at night the densities were unrelated to particle sizes or bryophyte weight.

Parker *et al*. (2007) found that the amphipod ***Crangonyx gracilis*** (see Figure 51) was a common inhabitant of the brook moss ***Fontinalis novae-angliae*** (Figure 52), where it used the moss shelter as a food source. Badcock (1949) found that ***Gammarus*** (Figure 30-Figure 36) species were more numerous in sheltered sites such as mosses. Minckley (1963) found ***Gammarus*** among the moss ***Fissidens*** sp. (Figure 53) in a Kentucky, USA, stream. It not only lived there, but ate the moss that served as its home (Minckley & Cole 1963).

Figure 51. ***Crangonyx pseudogracilis***, relative of ***C. gracilis*** that lives among ***Fontinalis novae-angliae*** and also eats it. Photo from Discover Life - Creative Commons.

Figure 52. ***Fontinalis novae-angliae***, shelter for ***Crangonyx gracilis***. Photo by Janice Glime.

In an unlikely place, the depths of Yellowstone Lake, associated with active geothermal vents, ***Fontinalis*** abounds (Lovalvo *et al*. 2010). Associated with this unusual inhabitant are, among other invertebrates, the amphipods ***Hyalella*** (Figure 43) and ***Gammarus*** (Figure 30-Figure 36, Figure 41, Figure 45).

Figure 53. ***Fissidens fontanus***, both a home and food for some species of ***Gammarus***. Photo by Michael Lüth, with permission.

Summary

Both Ostracoda and Amphipoda are primarily marine, with fewer species in freshwater and much fewer in terrestrial habitats. Nevertheless, ostracods are known from roof mosses, and the genus ***Mesocypris*** is a common terrestrial moss dweller, especially in the Southern Hemisphere.

Their adaptations to living among bryophytes (and other terrestrial locations) include swimming instead of crawling, small size, loss of eyes in some, reduced setae (used for swimming), excretion of nitrogenous waste from maxillae, antennae, or possibly through the carapace (perhaps as gaseous ammonia), drought-resistant eggs, and parthenogenesis. Food often consists of detritus, algae, and bacteria, but some amphipods eat bryophytes as well.

Bogs offer habitats where ostracods can migrate vertically or horizontally to find suitable conditions as the temperature and moisture change. Some are even true **tyrphobionts**. But there appear to be few, if any, records for amphipods. Some ostracods live among the pitcher plants in the bogs.

Few ostracods are known from among mosses in streams, but several amphipods can be found there. However springs seem to be suitable habitats for several species in both groups.

The microcrustacea may have advanced onto land through wet mosses of springs and stream banks. They are represented by few families, the **Cypridae** among the ostracods and the **Talitridae** among the amphipods.

Terrestrial amphipods are not well known, and thus far their presence among ***Sphagnum*** does not seem to be documented.

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CHAPTER 10-3
ARTHROPODS: CRUSTACEA – ISOPODA, MYSIDA, AND DECAPODA

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CHAPTER 10-3
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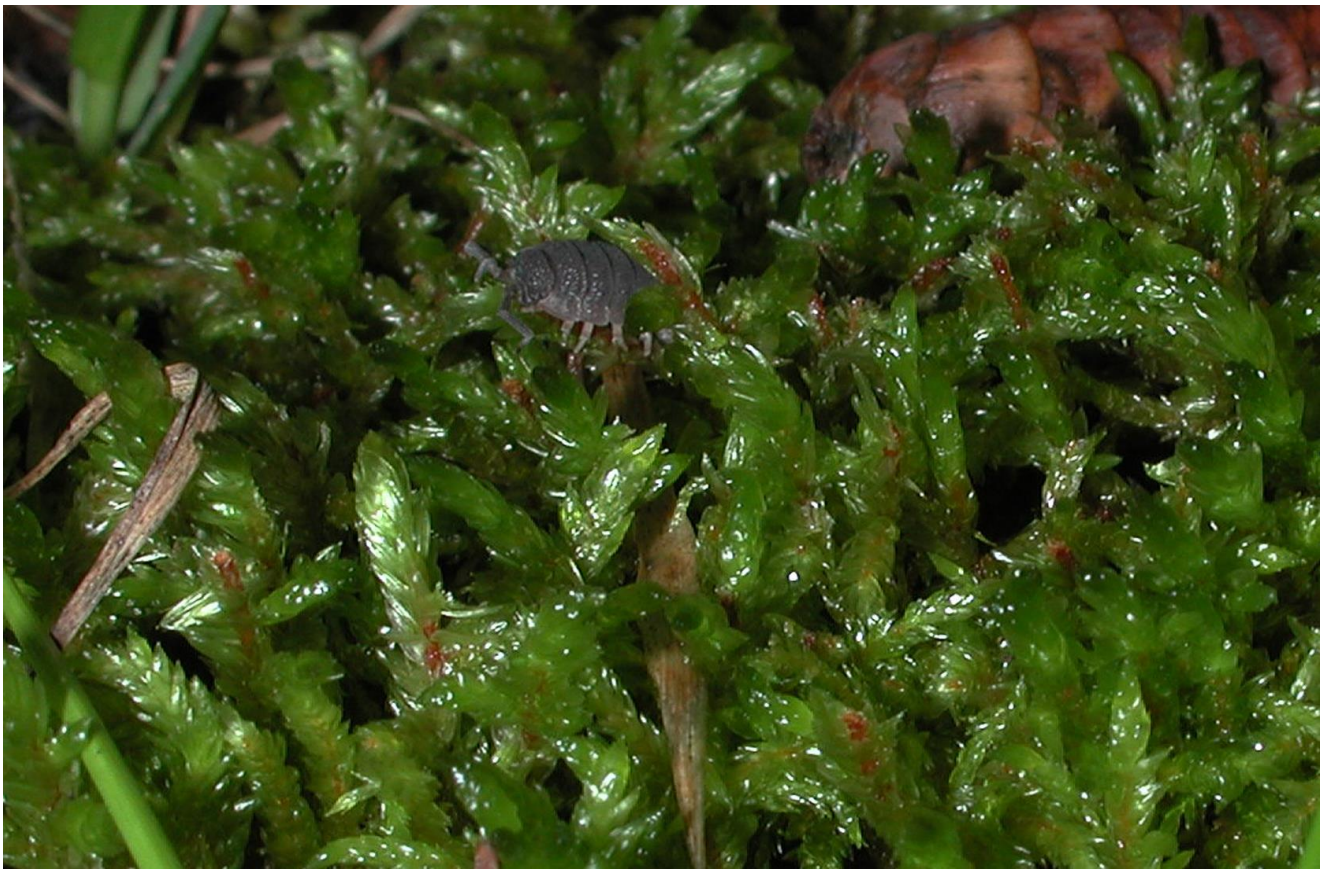

Figure 1. ***Porcellio scaber*** eating ***Pleurozium schreberi*** at midnight in Houghton, Michigan, USA. Photo by John Hribljan, with permission.

CLASS MALACOSTRACA, ORDER ISOPODA

Then there are the Isopoda (Figure 1), the well-known pillbugs, woodlice, roly polies, potato bugs, or sowbugs (but they aren't bugs!). These aren't insects at all, but are arthropods with legs on each segment, sometimes included among the **multipedes**, which is an unofficial classification referring to arthropods with many legs. And at least some of them seem to love mosses.

As a teacher, these were my favorite creatures. They have wonderful behavior responses to all sorts of things, especially light, moisture, and contact. Hence, they were excellent experimental organisms for behavior experiments for beginning students. They were easy to collect (just put out potatoes, with holes drilled through them, in a deciduous forest and give them 2-3 days to colonize). And they responded quickly and predictably.

But for research on herbivory on bryophytes, these organisms are unparalleled. Both aquatic and terrestrial species eat mosses, are abundant, and can be used to test for preferences. Nevertheless, they should not be considered as models for the feeding preferences of other invertebrates, as you will see when we discuss digestion.

I have a small moss garden, and it is occasionally the site of my experiments, planned or otherwise! I had inherited a mat of mosses that had made themselves unwelcome on an asphalt parking lot. Some of these I had draped over a large rock in hopes that they would find it similar to their past home. In an attempt to keep them in place, I had used a mix of raw egg to act as glue. All seemed well for 2-3 weeks. Then one day when I went to look at them the mat looked like Swiss cheese! This carpet of a half-meter diameter had numerous relatively large holes in it! I found the carpet was loose, so I lifted it from the rock. As I did that, woodlice (mostly ***Porcellio scaber***, Figure 2) fell to the ground and scrambled for cover. There were at least 20 of them! And many still remained on or within the mat.

Figure 2. ***Porcellio scaber***, a common moss inhabitant. Photo from <www.aphotofauna.com>, with permission.

Compared to other arthropods, the isopods, at least on land, probably have the most interaction with the bryophyte community. Božanić (2008) sampled 66 mosses and extracted their inhabitants using heat with a Tullgren apparatus. She recorded multiple factors to determine the niche requirements of the faunal species. The mosses represented 15 species. The **Isopoda** were the most abundant taxa (439 individuals); others included **Chilopoda** (centipedes), **Diplopoda** (millipedes), **Araneae** (spiders), **Pseudoscorpionida** (pseudoscorpions), **Opilionida** (daddy-long-legs), **Lumbricidae** (earthworms), and **Formicidae** (ants). The diplopods (another multipede) were second in abundance (240 individuals). The most important environmental factors in determining the faunal higher taxa were type of substrate, height above ground, and moss/sample area. The species factors, like those of the higher taxa, were substrate type and height above the ground, but in addition to these the tree diameter was important, possibly indicating colonization time. Farkas (2007) likewise found tree diameter to be important for the isopods ***Porcellium collicola*** (Figure 3), ***P. conspersum***, and ***Trachelipus rathkii*** (Figure 4), all rather common among epiphytic mosses in Hungary.

Figure 3. ***Porcellium collicola***, an isopod that lives among epiphytic mosses. Photo by Dragiša Savić, with permission.

Figure 4. ***Trachelipus rathkii***, an isopod that lives among epiphytic mosses in Hungary. Photo by Dragiša Savić, with permission.

External Anatomy

Isopods have two compound eyes (Figure 5) that permit them to detect motion easily. They have a very small head, long thorax, and short abdomen (Figure 6). There are two pairs of antennae, but the first is short and not always visible (Figure 5). That pair may have a chemosensory function to detect odors and tastes (Massey University 2014). The second pair of antennae is large and easily seen; the function is **tactile** (touch sensation).

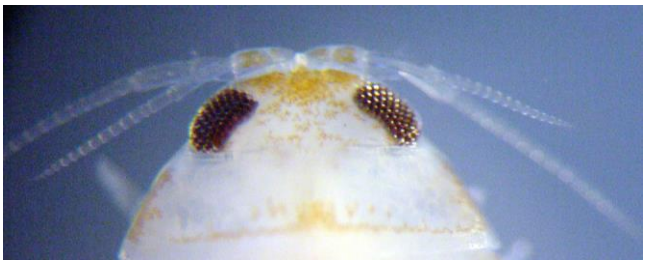

Figure 5. Isopod head showing compound eyes. Note the multiple small sections in each eye. Photo from NOAA, through public domain.

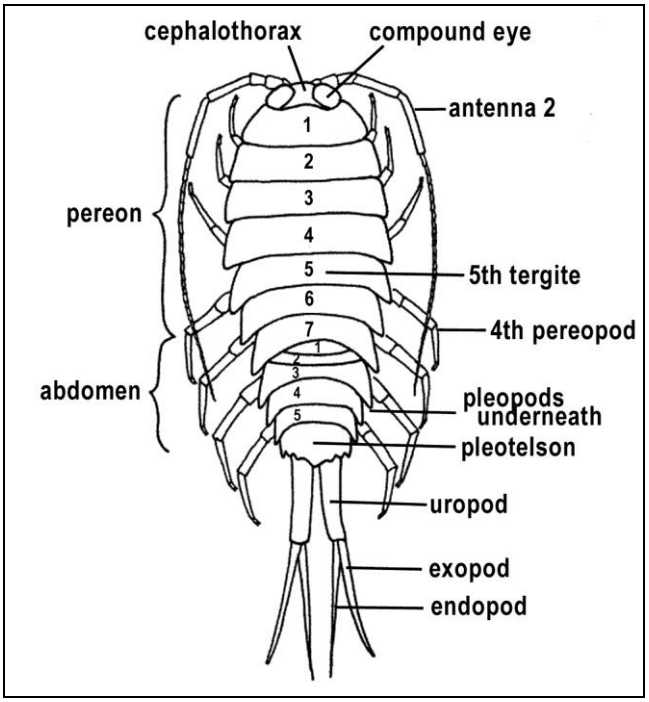

Figure 6. ***Ligia***, a genus that sometimes inhabits bryophytes, showing typical isopod external anatomy. Redrawn from Richard Fox.

Adaptations to Terrestrial Life and to Bryophytes

Isopods are predominately aquatic and marine. Life on land requires special adaptations. Even so, some isopod taxa have rather broad niches. ***Porcellio laevis*** (Figure 7), a cosmopolitan species and largest member of the genus, at least in the UK (Harding & Sutton 1985), is known for its plasticity in response to the environment (Lardies & Bozinovic 2008), and this plasticity may be the most important adaptation of all. There seem to be few morphological adaptations specific to land dwelling, although one could argue there are no really large species like some of the marine species.

Figure 7. ***Porcellio laevis***, an isopod from which we have learned many terrestrial adaptations. Photo by Roger S. Key, with permission.

Bryophytes make good homes for isopods. These organisms hide from light and require a moist environment, conditions which can be provided by bryophytes. There are probably many species still to be discovered on land, especially among bryophytes, because of the sheltering behavior of isopods in daylight.

Water Relations

For any organisms evolving from water to land, maintenance of hydration is a critical adaptation. Dias *et al*. (2013) experimented with 22 species of terrestrial northwestern European isopods to determine the importance of three traits related to desiccation resistance. They found that 90% of the interspecific variation could be explained by water loss rate and fatal water loss. Body surface area affects desiccation resistance through modification of water loss rate. Soil moisture affects species distributions, and by extension, it is likely that bryophyte moisture does as well.

Edney (1951a) examined the evaporation of water from woodland isopods and found that in ***Armadillidium*** (Figure 8-Figure 9) and ***Porcellio*** (Figure 7) it was the **pleopods** (abdominal appendages also known as swimmerets, Figure 6, Figure 10) that lost water most rapidly, ranging 10-20 times as fast per unit area as the dorsal or ventral surfaces. However, the most water was actually lost from the dorsal and ventral surfaces because of the much greater area. Water loss rates differed among the terrestrial genera tested, in the order from greatest loss to least as ***Ligia*** (Figure 11), ***Philoscia*** (Figure 12), [***Oniscus*** (Figure 13), ***Porcellio*** (Figure 7), *Cylisticus*], and ***Armadillidium nasatum*** (Figure 9) to ***A. vulgare*** (Figure 8). This order also reflects the progression from most moist to least moist habitat preferences. ***Armadillidium*** species further conserve water by curling (Figure 9), a behavioral adaptation that earned it the name of roly poly.

Figure 8. ***Armadillidium vulgare***, the common roly poly that rolls into a ball. Photo from <www.aphotofauna.com>, with permission.

Figure 9. ***Armadillidium nasatum*** curled into a ball, permitting it to reduce water loss. Photo by Lynette Schimming, through Creative Commons.

Figure 10. ***Oniscus asellus*** lying on its back and exposing its **pereopods** (see Figure 6). The **pleopods** are on the white abdomen behind these 7 pairs of legs and cannot be discerned in this picture. Note that the head is to the right where you can see two of the antennae. Photo by Brian Eversham, with permission.

Figure 11. ***Ligia oceanica***, member of a coastal genus that readily loses water. Photo by Gilles San Martin, through Wikimedia Commons.

Figure 12. ***Philoscia muscorum*** in bark crevice in the forest. Photo by Brian Eversham, with permission.

Figure 13. ***Oniscus asellus***, a frequent moss-dweller in western and northern Europe. Photo by Brian Eversham, with permission.

When terrestrial isopods become desiccated, they can restore their original weight by absorption of moisture through the mouth and anus by contact with free water surfaces, and by mouth from moist surfaces (Edney 1954). This suggests a possible role for the bryophytes as pillbugs traverse such dry habitats as tree bark, rocks, or even soil. They could run from clump to clump of moss, rehydrating when they visit the mosses (or liverworts). Edney (1954) suggests that they are most susceptible to mortality during their wandering rather than while in their selected permanent shelter habitat. Interestingly, living isopods could rehydrate by absorption of water vapor or liquid water, but dead ones could not (Edney 1951a).

Waste Elimination

Even the elimination of waste products must be modified to conserve water on land. Digestive and bodily processes accumulate nitrogenous wastes, and these are toxic, requiring a means of efficient elimination. In aquatic animals, these are usually eliminated as toxic ammonia that is diluted in water (Dresel & Moyle 1950). But terrestrial animals cannot afford the large quantity of water needed to dilute ammonia to safe levels. Nevertheless, like aquatic isopods, most terrestrial isopods still excrete ammonia, but with a twist. They lack any organ homologous to the kidney or liver to detoxify or facilitate excretion of ammonia (Hartenstein 1968). Hartenstein studied this ammonia elimination mystery in ***Oniscus asellus*** (Figure 13) and concluded that rather than excreting liquid ammonia like most aquatic animals, the terrestrial isopods eliminate their ammonia as a gas. In addition, some of the nitrogen waste is stored in the body wall as uric acid and is eliminated during molting. Wieser and Schweizer (1970) likewise found that the terrestrial isopods ***Oniscus asellus*** and ***Porcellio scaber*** (Figure 1-Figure 2) eliminate their ammonia as gas. Their data refute earlier ideas that nitrogen metabolism is suppressed; instead, they accounted for loss of all the excess nitrogen intake through body wall storage and mostly through the body wall as ammonia gas, thus eliminating the need for large water losses – or kidneys.

Osmotic Balance

The osmotic pressure of the blood of terrestrial species is somewhat lower than that of sea water and adaptation to land seems to be achieved by osmotic tolerance rather than regulation (Edney 1954). Nevertheless, ***Porcellio scaber*** does not change its body fluid concentration as rapidly as it loses weight during desiccation (Horowitz 1970), implying it could have a limited balancing mechanism. Lindqvist and Fitzgerald (1976) explored this further and determined that initially the blood osmotic concentration remains essentially unchanged until about a 10% loss of body weight. Meanwhile, the oral fluid increases its osmotic concentration rapidly during about 90 minutes of drying. When severe desiccation occurs, these two compartments progress to an osmotic equilibrium, presumably due mostly to withdrawal of water from the gut lumen into the blood.

Molting has the potential to affect the osmotic balance. Calcium is an important element in the exoskeleton. Before the animal molts, the calcium is resorbed and stored in the body of terrestrial isopods and little is lost, whereas in aquatic taxa, little is resorbed and most of the exoskeleton calcium is lost (Greenaway 1985). When needed, additional calcium is gained from food and **exuviae** (shed exoskeleton). Despite this resorption of high amounts of calcium in terrestrial species, most of it is not stored in ionic form and thus has little effect on the osmotic balance.

Respiration

Terrestrial isopods have **pseudotracheae**, assisting them with respiration in dry air (Edney 1954), whereas the importance of integumental oxygen absorption decreases in terrestrial species compared to aquatic species. The inner

branch of each **pleopod** (Figure 6, Figure 10) is modified into a gill-like structure (Figure 14) with a thin, permeable cuticle where gas exchange occurs (Schotte *et al*. 2008-2014). These even somewhat resemble lungs in the terrestrial isopods.

Figure 14. *Porcellio siculoccidentalis* pleopods modified to function in gas exchange and resembling lungs. Photo by Giuseppi Montesanto, with permission.

Temperature Tolerance

The temperature tolerance follows the same sequence of genera as for water loss rates above [least in ***Ligia*** - Figure 11 < ***Philoscia*** - Figure 12 < (***Oniscus*** - Figure 13, ***Porcellio*** - Figure 7, *Cylisticus*) < ***Armadillidium*** (Figure 8)], with ***Armadillidium*** having the highest temperature tolerance (Edney 1951b). There was no difference in body temperature between living and dead woodlice, and once the animals reached equilibrium their temperatures differed from that of the air by no more than 0.1°C in moist air. However, in dry air the isopod temperatures were depressed relative to air temperature, apparently due to evaporative cooling.

Moisture and Temperature Interaction

Temperature and moisture rarely act alone in ecosystems, and responses by isopods to one of these typically depends on the other. In experiments with the isopods discussed above, Edney (1951b) found that after 30 minutes in dry air at 20° and 37°C, mean temperature depressions were for ***Ligia*** (Figure 11), 2.6°C and 6.8°C; ***Oniscus*** (Figure 13), 1.5 and 2.7°C; ***Porcellio*** (Figure 7), 0.4 and 1.3°C; ***Armadillidium*** (Figure 8), 0.5 and 1.8°C, respectively. ***Ligia*** differed from the others, with its body temperature rising for at least 2 hours, whereas the others reached equilibrium at a temperature lower than ambient air temperature after 25 minutes. It is the ability to evaporate water rapidly that permits these isopods to maintain a safe temperature for short intervals, and this at least partly explains their need for moist environments. On the other hand, if the air is saturated, they are unable to use evaporative cooling, and higher temperatures become lethal. Both temperature and moisture needs explain the migration of the isopods to deeper moss layers or even into the soil in the daytime, returning to the surface for feeding at night.

Behavior

The best adaptations of this group seem to be behavioral (Edney 1954), and these behaviors are what make them so interesting to watch. Pick up a rock and pillbugs scramble in all directions, soon disappearing under leaves or into the soil. They run from light, which might be an indicator of drying conditions. They seem to lack a well-developed cuticle, although both endocuticular and epicuticular layers are known from some species (Edney 1968), and thus they are able to use evaporative cooling, but this only works for a short time, hence making a behavioral solution essential.

Edney (1968) suggests that the nightly activity of ***Porcellio scaber*** (Figure 1-Figure 2) on trees may permit them to transpire excess water. ***Armadillidium vulgare*** (Figure 8) also has greater activity at night when the air is more moist. It appears that males of ***Porcellio scaber*** and ***Armadillidium vulgare*** use surface shelters, including bryophytes, between foraging events (Dangerfield & Hassall 1994), sometimes providing them with a location to gain or reduce water content.

Congregating Behavior

Aggregating or congregating (Figure 15) in large numbers in a suitable habitat, as is easily observed under a log, board, or small rock, is generally accepted as a means to reduce their water loss to the atmosphere (Broly *et al*. 2013). This behavior is mostly **thigmotactic** (a contact response), and possibly **olfactic** (an odor response) (Edney 1968). Olfaction seems to play a role in seeking shelter. But the role of aggregation in preventing water loss may be misleading. Broly and coworkers suggest other potential benefits, including reduction of oxygen consumption, increase in body growth, stimuli for reproduction, better access to mates, shared predator defense, promotion of coprophagy, sheltering, and acquisition of internal symbionts. They suggest that congregating behavior provides terrestrial isopods with a non-physiological alternative to coping with climate constraints.

Figure 15. Isopod congregation. Photo by William Leonard, with permission.

But crowding does not seem to have the same benefit for all terrestrial isopods. ***Armadillidium nasatum*** (Figure 16) and ***A. vulgare*** (Figure 8), members of the most xeric genus, had reduced growth rate, survivorship, and size at first reproduction as density increased in laboratory experiments (Ganter 1984). Since limited food reduced both growth rate and mortality in these experiments, these same detrimental factors might not exist in nature where foraging might be unlimited.

Figure 16. ***Armadillidium nasatum*** showing two color variants. Photo by Stan Gilliam, through Creative Commons.

To put this in perspective, Hassall *et al*. (2010) experimented with aggregation behavior in ***Philoscia muscorum*** (Figure 17), ***Oniscus asellus*** (Figure 13), ***Porcellio scaber*** (Figure 1-Figure 2), and ***Armadillidium vulgare*** (Figure 8) from Norwich, UK. The first three are isopods known from terrestrial bryophytes, whereas ***Armadillidium vulgare*** tends to occur in drier habitats. The first three species clump more at lower levels of relative humidity and at higher temperature, whereas changing the humidity has little effect on clumping in ***A. vulgare***.

Figure 17. ***Philoscia muscorum*** on moss. Photo by Dick Jones, with permission.

Sheltering

Sheltering (staying in one place that is protected) is common among some isopods, but not others (Hassall & Tuck 2007). ***Porcellio scaber*** (Figure 1-Figure 2), a common moss dweller, sheltered significantly more than either ***Platyarthrus hoffmannseggi*** (Figure 18) or ***Armadillidium vulgare*** (Figure 8), and ***Philoscia muscorum*** (Figure 17) sheltered the least, despite some individuals spending at least winter under mosses. Sheltering declined in all four species after the breeding season, continuing through winter. ***Porcellio scaber*** sheltered more where the soil was more **calcareous** (occurring on chalk or limestone), ***Philoscia muscorum*** more under the shade of trees, and both ***P. muscorum*** and ***Armadillidium vulgare*** more in grazed than in ungrazed areas. For ***A. vulgare*** sheltering was positively correlated with both rainfall and temperature of the day before sampling, whereas for ***Philoscia muscorum*** it was negatively correlated with rainfall.

Figure 18. ***Platyarthrus hoffmannseggi***, an isopod that shelters under mosses. Photo by Jan van Duinen <http://www.janvanduinen.nl/>, with permission.

Dias *et al*. (2012) examined the influence of microclimate on sheltering in three terrestrial isopods: ***Porcellio scaber*** (Figure 1-Figure 2), ***Oniscus asellus*** (Figure 13), and ***Armadillidium vulgare*** (Figure 8, Figure 23). The first two are common among mosses, whereas ***A. vulgare*** typically lives in drier habitats. All three species spent more time sheltering and less in activities when the environment was drier (50% relative humidity) compared to more moist conditions (90% relative humidity). ***Oniscus asellus*** is the least terrestrialized of these three and thus the most susceptible to desiccation. Sheltering can also reduce the quality of food consumed because less time is spent on foraging.

Reproduction

Reproduction among terrestrial invertebrates usually requires modifications from that of aquatic taxa. Terrestrial isopods carry their young in a **marsupium** (brood pouch, Figure 19). The marsupium is filled with fluid and the eggs and embryos are surrounded by mucous. Warburg (1987) considers this to be one of the most important innovations for successful living on land. The mucous may contribute to nourishment of the young, possibly explaining their ability to survive when the mother doesn't eat.

Figure 19. ***Armadillidium vulgare*** lying on its back, showing young (cream-colored) isopods in a brood pouch on the ventral side. Photo by Malcolm Storey, through Creative Commons.

In the isopods, gonadal development is stimulated by a long photoperiod and high temperatures (Edney 1968). Temperature seems to play a role in controlling reproductive output and consequent water loss.

Females are dominant throughout most of the year in ***Porcellio scaber*** (Figure 1-Figure 2) (Nair 1998), and this is likely true in other species as well, sometimes indicating **parthenogenesis** (reproduction from an egg without fertilization). Some species that exhibit parthenogenesis do not necessarily do so in their populations everywhere (Christensen 1979; Fussey & Sutton 1981; Fussey 1984). For example, in the British Isles some populations of an isopod that often lives among bryophytes, ***Trichoniscus pusillus*** (Figure 25), are parthenogenetic and others are not. Christensen (1979) demonstrated that the parthenogenetic populations represented different genotypes in this species. Fussey (1984) was unable to find a relationship between this parthenogenetic expression and latitude, longitude, altitude, or seven climatic variables, but it did correspond with calcareous habitats.

But genes are not the only causes of alteration in the reproductive type. The bacterium *Wolbachia pipientis* is able to infect the isopods ***Hyloniscus riparius*** (Figure 20), ***Trachelipus rathkii*** (Figure 26), and ***Trachelipus ratzeburgii*** (Figure 21) (Nyirő *et al*. 2002), all species known to inhabit mosses (Božanić 2011). The bacterium lives in the ovaries and can cause such changes as loss of maleness and shift to parthenogenesis in these isopods. The bacterium also infects the eggs and thus is transferred from mother to offspring. Could the antibiotic properties of bryophytes protect the isopods from this population-altering bacterium?

Figure 20. ***Hyloniscus riparius***, whose gender is altered by the bacterium *Wolbachia pipientis*. Photo by Dragiša Savić, with permission.

Figure 21. ***Trachelipus ratzeburgii***, an isopod whose gender is altered by the bacterium *Wolbachia pipientis*. Photo by Dragiša Savić, with permission.

Food quality can have a strong effect on the success of both reproduction and survival of the offspring. For example, Kautz *et al*. (2000) were only able to maintain a stable population of ***Trichoniscus pusillus*** (Figure 25) on a diet of *Alnus* litter with high microbial activity. Such needs may explain changes in the diet of isopods throughout the year. It would be interesting to test the effect of a bryophyte diet on reproductive success.

On the other hand, Lavy *et al*. (2001) found that in ***Porcellio scaber*** (Figure 1-Figure 2) and ***Oniscus asellus*** (Figure 13) diet had no effect on the number of juveniles or their weight. Rather, the weight of the offspring was correlated with the weight of the female. Nair (1998) found that for ***Porcellio scaber*** in Benghazi, Libya, the total number of eggs correlated with body length of the female.

High temperatures can be lethal or detrimental to developing isopods. In the terrestrial *Porcellio ficulneus*, at 25°C, oocytes matured sooner, and many were resorbed (Hornung & Warburg 1993). The Mediterranean population compensated for these losses by breeding earlier. Females must balance the advantages of faster brood development in higher temperatures with the risk of excessive water loss (Dangerfield & Hassall 1994).

Incubation periods for ***Porcellio scaber*** (Figure 1-Figure 2) in Benghazi were 18 days in summer and autumn but extended to 32 in late winter and spring (Nair 1998). Spring embryo production was higher in spring compared to summer and autumn. In ***Armadillidium vulgare*** (Figure 8), if females are dehydrated, they reproduce instead of growing (Warburg 1987).

Terrestrial isopods care for their young, an uncommon feature in the aquatic habitat (Lardies *et al*. 2004). Such care can be costly energetically, but it increases the survival of the young in the terrestrial environment, and it might even reduce water loss of the adult, much like the congregating behavior. But there is a downside. Lardies and coworkers found that in ***Porcellio laevis*** (Figure 7) not only was the carrying of developing eggs energetically costly, the females carrying them had a lower ingestion rate and lower ability to digest food than non-carrying females. The net result was that egg-carrying females stored only about 20% as much energy as females with no eggs.

Carrying eggs and young creates other problems for these woodlice. Females carrying broods were slower and moved shorter distances to avoid light than non-brooding females of ***Porcellio laevis*** (Figure 7) (Kight & Nevo 2004). Physical stress causes a reduction in both distance travelled and velocity in brooding females. Many eggs and embryos die before reaching their swimming stage. These are typically eaten by their siblings in the marsupium and larger larvae often eat the smaller ones (Warburg 1987). Once the young leave the marsupium they begin a life free of their mother.

Predators

Bryophytes can serve as a refuge for hiding from large predators like birds, but they may not be so safe from insect predators. Ants such as ***Tetramorium caespitum*** (Figure 22) influence the behavior of the isopods ***Armadillidium vulgare*** (Figure 8) and ***Porcellio laevis*** (Figure 7) (Castillo & Kight 2005). ***Armadillidium vulgare*** females were hidden better than those of ***P. laevis*** whether ants were present or not. But some of their behavior was rather strange. Isopods that had no experience with ants remained further from them than those with previous exposure, with ***P. laevis*** keeping a significantly greater distance than that of ***A. vulgare***. This difference in behavior of the two species may be explained by the ability of ***A. vulgare*** to roll into a ball (Figure 23), whereas ***P. laevis*** is endowed with the ability of rapid locomotion.

Figure 22. Ant ***Tetramorium caespitum*** eating larva, most likely of an insect. This ant causes soil isopods to stay hidden. Photo from Antwiki, through Creative Commons.

Figure 23. ***Armadillidium vulgare*** in a ball, a protection against predators. Photo from <www.aphotofauna.com>, with permission.

The brooding period of ***Armadillidium vulgare*** (Figure 8) was shortened when it was exposed to ants, whereas such exposure had no effect on brood time for ***Porcellio laevis*** (Figure 7) (Castillo & Kight 2005). This is a greater advantage for ***A. vulgare*** because it is unable to roll into a sealed ball when it is carrying its brood. Nevertheless, ***P. laevis*** is slowed down when carrying a brood (Kight & Ozga 2001; Kight & Nevo 2004).

Overwintering

It is difficult to find information on the use of bryophytes for overwintering of crustaceans. Samouelle (1819) reported that one could find ***Philoscia muscorum*** (Figure 17) under mosses in January in Great Britain. Le Gay Brereton (1957) reported that the isopod ***Porcellio scaber*** (Figure 1-Figure 2, Figure 24) overwintered "in large numbers" in the moss layers at the bases of oaks (*Quercus*) and ash (*Fraxinus*). These same aggregations did not occur at eye level, suggesting that the larger moss clumps at the tree bases were more suitable than the small clumps or shallow mats of the bole. One would presume that the tree base had both warmer and less desiccating conditions than any position on the bole.

Figure 24. ***Porcellio scaber***, a common moss dweller and consumer that eats its own feces to assimilate more nutrients. Photo by Eric Schneider, with permission.

Terrestrial isopods are not well adapted to cold temperatures and must seek locations where they are insulated from the cold. ***Porcellio scaber*** (Figure 1-Figure 2, Figure 24), a common species that is known from bryophytes and under many other objects, is able to adjust somewhat by acclimation, but is nevertheless susceptible to both freezing and chilling (Tanaka & Udagawa 1993). The temperature causing 50% mortality was -1.37°C in August but dropped to -4.58°C in December. At -7°C, the animal was unable to avoid freezing of its tissues, a temperature limit that was the same throughout the year.

The winterization in ***Porcellio scaber*** (Figure 1-Figure 2, Figure 24) corresponded to the presence of low molecular weight carbohydrates that may have protected it against chilling injury (Tanaka & Udagawa 1993). The supercooling temperature of -7°C seemed to be associated with the year-round gut content. We know that at least in the autumn this species can live among mosses and deciduous and conifer leaf litter where it prefers mosses as food (Hribljan 2009; Hribljan & Glime in prep). Could the mosses help to prepare it for winter by contributing arachidonic acids that have lower freezing points (see Prins 1982)? Hansen and Rossi (1991) showed that ***Rhytidiadelphus triquetrus*** (Figure 49), a food of ***Porcellio scaber*** in autumn (Figure 53; Hribljan 2009; Hribljan &

Glime in prep), contains 30% arachidonic acid at 20°C, which slightly decreases at lower temperatures. Tanaka and Udagawa (1993) also suggest that food derivatives could serve as ice nucleation centers that could reduce freezing of tissues.

Bryophytes as Food

In the other crustaceans, we have seen that bryophytes serve mostly as trapping devices, collecting detritus and growing periphyton that can serve as food for the crustaceans. The crustaceans have carried their aquatic habit of eating detritus into the terrestrial environment. Isopods are also litter-dwelling organisms that eat litter, but they eat bryophytes too.

Digestion

Generally bryologists might not care much about the digestive process of a bryophyte dweller, but understanding isopod digestion helps us explain bryophyte herbivory and why isopods can be such good bryovores whereas other invertebrates generally are not. As organisms derived from aquatic ancestry, isopods required adaptations to digest terrestrial food. They are among the few organisms known to readily eat bryophytes. Food sources on land can differ somewhat for isopods, although leaf litter, a common food for them, is available in streams and lakes as well as on land.

Hames and Hopkin (1989) observed the digestive tracts of two terrestrial isopods known from mosses, ***Oniscus asellus*** (Figure 13) and ***Porcellio scaber*** (Figure 1-Figure 2, Figure 24), and determined that their digestive tracts are divided into five regions: foregut, anterior chamber, papillate region, rectum, and hepatopancreas. The latter opens into the foregut. There is a powerful muscular sphincter between the papillate region and the rectum.

As food passes from the foregut to the hindgut it is mixed with secretions from the hepatopancreas (Hames & Hopkin 1989). When the hindgut is full, muscles contract to force the liquids and fine food particles back to the foregut through special channels. This re-entry can occur several times, each time being subject to further degradation by the microbial gut flora. Material left in the hindgut passes to the rectum where the fecal pellets are compacted for expulsion. And like a rabbit, ***Armadillidium vulgare*** (Figure 8) and ***Porcellio scaber*** (Figure 1-Figure 2, Figure 24) eat their own fecal pellets, preferring fresh ones to decaying ones (Hassall & Rushton 1982). Hames and Hopkin (1989) suggest that the ability to recycle the food, each time extracting more liquid, may be one of the major changes making their life on land successful.

Isopods are good at digesting their food but poor at assimilating it. This may also help explain their ingestion of feces, to gain more nutrients from it (Warburg 1987). Food quality is important for growth (Merriam 1971), and fresh leaves are better for growth than decayed leaves (Beck & Bretowsky 1980).

But we are left with the question of circumventing the high **phenolic** content of bryophytes and some types of leaf litter. **Phenolic** compounds are known for their production as a stress response in bryophytes (Graham *et al.* 2004). There is ample evidence that they deter herbivory in both terrestrial and aquatic bryophytes, as discussed below. But it appears that not all isopods are created equal in their tolerance of phenolic compounds. And not all bryophytes are equal in making them.

Zimmer (1997) showed that the common moss dweller ***Porcellio scaber*** (Figure 1-Figure 2, Figure 24) has significant ability to reduce gut surface tension. Phenolic compounds, well known to prevent digestion in other invertebrates due to the ability of the phenolics to increase the surface tension, seem to have a less negative effect on this species. These surfactants may be the key to the ability of ***Porcellio scaber*** to eat mosses without suffering from the typical binding of proteins suffered by many other kinds of organisms that eat phenolics. In insects, the phenolics precipitate proteins in the diet, preventing the insects from assimilating these essential nutrients, but in the isopods the surfactants bind the phenolics, leaving the proteins free for assimilation by the isopods. The concentration of surfactants in ***Porcellio scaber*** was 80 times as high as the "critical micelle concentration" needed to permit binding of the phenolics.

Further research on ***Porcellio scaber*** (Figure 1-Figure 2, Figure 24) indicated that endosymbiotic bacteria residing in the hepatopancreas were able to oxidize the phenolics, disabling their adverse properties (Zimmer 1999). When the gut flora of ***Porcellio scaber*** was reduced, Zimmer demonstrated that bacteria in the gut apparently had an important role in hydrolyzing gallotannins. When galloylglucose esters were ingested, they greatly reduced the microbial component of the hindgut. Ingestion of gallic acid reduced both palatable fungi and bacteria, but not as strongly, and increased the gut microflora. Zimmer's study suggests that the ingestion of hydrolyzable tannins, as found in some mosses, can inhibit the digestion of other foods in the diet of this species. The gut differences among the isopod species can account for their preferences among bryophytes, and possibly account for those taxa that don't eat bryophytes at all. Similarly, differences in hydrolyzable tannin concentrations among bryophyte species can account for preferences for some bryophytes over others.

Zimmer and Brune (2005) examined the physiological properties of the gut of four species of terrestrial isopods [***Oniscus asellus*** (Figure 13), ***Porcellio scaber*** (Figure 1-Figure 2, Figure 24), ***Trichoniscus pusillus*** (Figure 25), and ***Trachelipus rathkii*** (Figure 26)]. These adaptations were manifest as a steep gradient of oxygen, high at the periphery and low at the center of the gut transection. This gradient provides suitable habitat for both aerobic and anaerobic symbionts that can contribute to digestion. The *p*H gradient ran from acidic in the anterior hindgut to neutral in the posterior hindgut of ***O. asellus***, ***P. scaber***, and ***T. rathkii***. In ***Trichoniscus pusillus***, the *p*H in the hindgut lumen was nearly constant. Zimmer and Brune (2005) suggested that the *p*H gradient differences may be adaptive in providing differences in the digestion of lignocellulose from their food sources. Bryophytes lack true lignin, so the expenditure of resources to create the conditions suitable for digesting lignin could be spared in those isopods that eat mosses. These differences in gut physiology could also account for some of the differences in food preferences and survival of isopods on bryophytes vs other foods.

Figure 25. ***Trichoniscus pusillus***, a terrestrial isopod. From <www.aphotofauna.com>, with permission.

Figure 26. ***Trachelipus rathkii***, a terrestrial isopod. Photo by R. E. Jones, with permission.

Terrestrial Consumers

Terrestrial isopods seem to prefer a varied diet and exhibit food preferences (Dudgeon *et al*. 1990). Dudgeon and coworkers found that four species of isopods from a Hong Kong forest ate more food when given a mixture of leaves than when only one type was available. Their preferences did not seem to relate to ash, calcium, copper, soluble tannin, or energy content. Dudgeon and coworkers suggested that the isopods satisfied their nutrient requirements by consuming certain foods, then switching to others to avoid excessive tannins or other allelochemicals.

Rushton and Hassall (1983a, b) examined the feeding preferences and rates of ***Armadillidium vulgare*** (Figure 8) among dicotyledonous and monocotyledonous plants and bryophytes (***Calliergonella cuspidata***, Figure 27). This pillbug, known as a roly poly due to its ability to roll into a ball, can live in drier habitats than ***Porcellio*** and is much less likely to be associated with mosses. These isopods initially preferred the dicotyledonous plants to the other two choices. But after the monocotyledonous plants began to decay, these were preferred. Nevertheless, eating monocots increased mortality and drastically reduced growth rates and reproductive output, even when it was in a later decay state. Defenses in the food become more concentrated as the food decays and carbon sources are removed. Chemical defenses in mosses may play a role in the isopod choice of leaf litter over mosses in ***Armadillidium vulgare***.

Figure 27. ***Calliergonella cuspidata***, a moss that seems to deter feeding by ***Armadillidium vulgare***. Photo by J. C. Schou, through Creative Commons.

Rushton and Hassall (1983a) suggested that ***Armadillidium vulgare*** (Figure 8) compensates for low quality food by eating more, but that plant defenses can interfere with this compensation. Even though the moss is likely to provide a suitable moist habitat, and ***Armadillidium vulgare*** may be able to absorb at a high rate on low quality food by increasing its rate of consumption, it appears that plant defenses of ***Calliergonella cuspidata*** (Figure 27) might outweigh its habitat desirability (Rushton & Hassall 1983a).

Dead mosses may be less desirable than dead tree leaves or even monocot leaves, particularly after the tracheophyte leaves begin to decay. It is likely that very little nutritional material is available relative to cell wall material in dead mosses (see Pakarinen & Vitt 1974 for lower N content), especially if nutrients are moved from dead portions to living portions, but that relationship requires further testing.

Figure 28. ***Hypopterygium didictyon*** from Chile, a moss in the same genus as one grazed in Costa Rica. Photo by Juan Larrain, with permission.

Nevertheless, at times isopods can be voracious consumers of bryophytes. Angela Newton (Bryonet, 20 November 2006) reported seeing extensive grazing on ***Hypopterygium*** sp. (Figure 28) in the montane rainforest of Costa Rica. The isopods sheared off the green lamina and left the branches and costa, much like the feeding behavior

of insects on tracheophyte leaves. However, grazing of isopods and silverfish on damp herbarium labels and plants in packets made her question whether they were simply feeding on the associated fungi and consumed the mosses in the process.

Isopods can be downright pests on garden mosses. Henk Greven, in a communication to Bryonet (23 October 2003) writes: "Apart from mammals, birds and slugs, sow-bugs (***Oniscus asellus*** L.; Figure 13) are fervent bryophyte eaters. In my garden, I keep several ***Grimmia*** species on pieces of rock. When I put these on the ground, sow-bugs are hiding during the day under these rocks. In the evening they climb above and start eating my ***Grimmias***. They have a special preference for ***Grimmias*** growing on limestone, basic sandstone, and basic basalt. In no time, they have eaten all my ***Grimmia plagiopoda*** (Figure 29), ***G. crinita*** (Figure 30), and ***G. orbicularis*** (Figure 31). Species on acidic rock, however, are not safe either. The only species they don't like is ***Ptychomitrium polyphyllum*** (Figure 32). I had this species nearly ten years on a piece of rock on my garden floor. I learnt my lesson and now I keep pieces of rock on a table where they are safe from sow-bugs."

Figure 29. ***Grimmia plagiopoda***, a species that seems to be preferred food for ***Oniscus asellus*** on limestone rocks. Photo by Michael Lüth, with permission.

Figure 30. ***Grimmia crinita***, a species that seems to be preferred food for ***Oniscus asellus***. Photo by Michael Lüth, with permission.

Figure 31. ***Grimmia orbicularis*** with capsules, growing on rock. This seems to be a preferred food for ***Oniscus asellus*** in limestone habitats. Photo by Michael Lüth, with permission.

Figure 32. ***Ptychomitrium polyphyllum***, a moss that is not eaten by ***Oniscus asellus***. Photo by David T. Holyoak, with permission.

Likewise, I have already reported above on my own sad experience with ***Porcellio scaber*** (Figure 24) eating my carpet of mosses so that it looked like Swiss cheese. And Daniel Marsh (Bryonet, 18 November 2006) reported that wood lice (isopods) have usually consumed any liverwort he tried to cultivate in his garden or greenhouse. "The attraction seems to be immediate." In contrast, he reports that he has not noticed such consumption of liverworts by isopods in wild communities.

We (Weston 1995; Liao & Glime unpubl) attempted to find out what sorts of things might deter pillbugs (***Porcellio scaber*** (Figure 24). Using ***Polytrichum juniperinum*** (Figure 33) and ***P. commune*** (Figure 34) from Houghton, MI, USA, we compared consumption of stems and leaves. ***Polytrichum juniperinum*** leaves were consumed 3:1 over stems; ***P. commune*** leaves were consumed 5.5:1 over stems (Figure 35). It made no difference whether the leaves were still connected to the stems or not.

Figure 33. ***Polytrichum juniperinum***, a species in which ***Porcellio scaber*** prefers eating leaves over stems. Photo by Li Zhang, with permission.

Figure 34. ***Polytrichum commune***, a species in which ***Porcellio scaber*** prefers eating leaves over stems. Photo by David T. Holyoak, with permission.

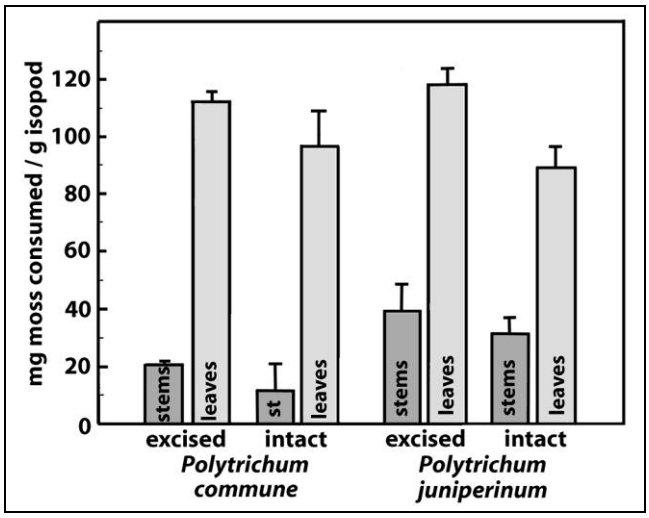

Figure 35. Comparison of mean isopod (***Porcellio***) consumption ± 95% CI of excised leaves and stems vs intact leaves and stems in two species of moss. Data based on unpublished laboratory data of Weston 1995; Liao & Glime unpublished data; n = 3.

In both ***Polytrichum juniperinum*** (Figure 33) and ***P. commune*** (Figure 34), the leaves had roughly double the protein content per dry weight compared to the stems (Figure 36) (Weston 1995; Liao & Glime unpubl), suggesting that the isopod ***Porcellio scaber*** (Figure 24) could gain more protein nutrition from eating leaves. And structurally leaves would seem to be easier to chew than the tough stems endowed with thickened walls and coloration suggesting phenolic compounds. But it is surprising to find that the leaves of at least ***P. commune*** seem to have a higher concentration of phenolic compounds than do their stems (Figure 37), yet that species had the higher consumption ratio of leaves to stems. Perhaps the presence of folded-over leaf edges in ***Polytrichum juniperinum*** (Figure 38), absent in ***P. commune*** (Figure 39), makes it easier to obtain the nutritious photosynthetic lamellae in ***P. commune*** (Figure 39).

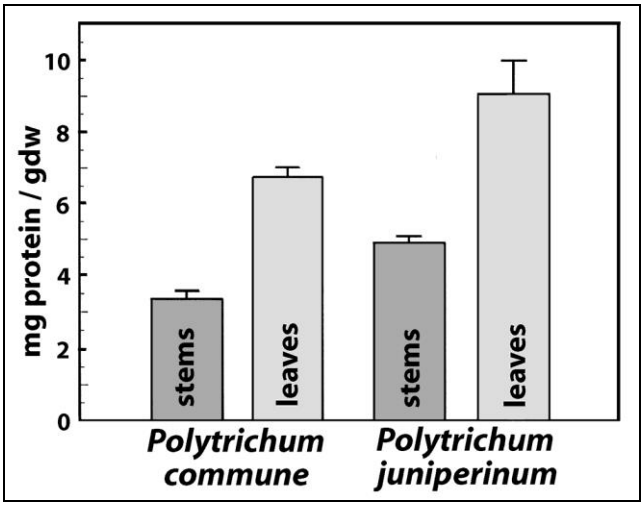

Figure 36. Comparison of mean protein ± 95% CI in stems and leaves of two ***Polytrichum*** species. Based on Weston 1995; Liao & Glime unpublished data; Bradford's (1976) test, n = 3.

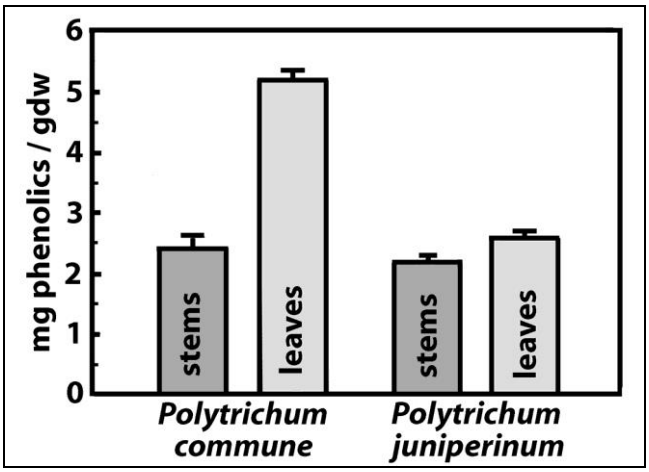

Figure 37. Comparison of mean phenolic content ± 95% CI in stems and leaves of two ***Polytrichum*** species. Based on Weston 1995; Liao & Glime unpublished data; Folin-Denis test (Swain & Hillis 1959) and Prussian Blue test for tannin; n = 3.

Figure 38. ***Polytrichum juniperinum*** leaf cross section showing margin of leaf rolled over the lamellae, partially covering them. Photo by John Hribljan, with permission.

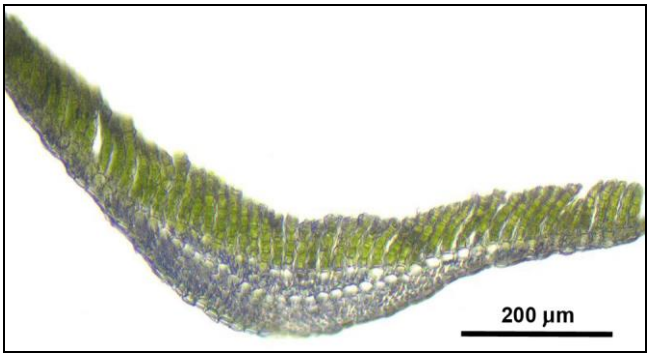

Figure 39. ***Polytrichum commune*** leaf cross section showing absence of rolled over leaf margin, thus giving exposure to all the lamellae. Photo by Kristian Peters, through Creative Commons.

Isopods can be a major inhabitant of bryophytes, becoming especially obvious at night when they migrate to the surface to feed (Hribljan & Glime in prep.). But even the isopods are fussy about which bryophytes they eat. Phenolic content seems to deter isopod consumption of various leaves (Warburg 1987). But deterrents may not be the only answer to these food preferences. ***Porcellio scaber*** (Figure 24) will eat ***Thuidium delicatulum*** (Figure 40-Figure 41) ravenously, but ignore ***Dicranum polysetum*** (Figure 42) and sometimes ignore ***Pleurozium schreberi*** (Figure 43) (Liao 1993; Glime 2006). When faced with ***Polytrichum*** (Figure 33), they eat the leaves, but little of the stems (Liao 1993, unpublished data; Hribljan 2009). This suggests that chemistry might be more important than structure, as ***Thuidium delicatulum*** is a crunchy moss with papillae (but small leaves, Figure 41) whereas ***P. schreberi*** and ***D. polysetum*** are softer and more flexible, lacking papillae (but with large leaves). But it appears that we may not have examined enough potential deterrents in ***Thuidium***. And we need to beware of differences between populations and seasons. Fatoba *et al*. (2003) found that whereas ***Thuidium gratum*** from the Nigerian tropics lacked detectable phenolics, it had tannins, alkaloids, and cardiac glycosides. In a different location in tropical Nigeria (and a different date), Adebiyi *et al*. (2012) found that this same species had a high content of saponins (absent in the Fatoba *et al*. 2003 study) and flavonoids, but also had a very low content of phenolics. Perhaps isopods, like many humans, just prefer a crunchy snack.

Figure 40. ***Thuidium delicatulum***, a moss readily eaten by ***Porcellio scaber***. Photo by Bob Klips, with permission.

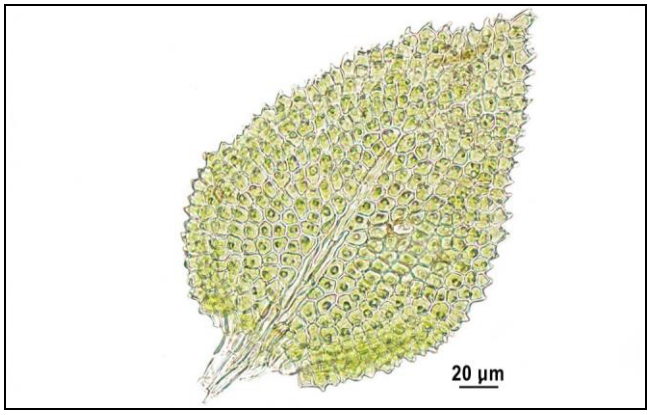

Figure 41. ***Thuidium delicatulum*** branch leaf showing small cells and papillae (note bumps on cells). Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 42. ***Dicranum polysetum***, a moss that is ignored, not eaten, by ***Porcellio scaber***. Photo by Bob Klips, with permission.

Figure 43. ***Pleurozium schreberi***, a moss that is sometimes eaten and sometimes ignored by the wood louse ***Porcellio scaber***. Photo by Janice Glime.

Hribljan and Glime (in prep) explored the food preferences of populations of ***Porcellio scaber*** (Figure 24) in the Keweenaw Peninsula of Michigan, USA. In food preference experiments, these isopods preferred the moss ***Pleurozium schreberi*** (Figure 44) over leaf litter from ***Acer saccharum*** (Figure 45) and ***Pinus strobus*** (Figure 46) in each of three study months of September – November (Figure 47). They compared the carbohydrates, proteins, and phenolics in these three species for the three months of the feeding trials and found that ***Pleurozium schreberi*** had the lowest levels of phenolics and highest levels of carbohydrates of the three choices of food (Figure 48). This is interesting because some studies (*e.g.* Pakarinen & Vitt 1974) have suggested that mosses were unable to provide enough energy for herbivores, but it appears that compared to leaf litter the mosses may, at least at times, have more carbohydrates than litter and be preferred food for isopods. Furthermore, all five mosses tested [***Pleurozium schreberi***, ***Thuidium delicatulum*** (Figure 40-Figure 41), ***Polytrichum juniperinum*** (Figure 33), ***Rhytidiadelphus triquetrus*** (Figure 49), and ***Dicranum polysetum*** (Figure 42)] had higher carbohydrate contents than the leaf litter of the trees tested (Figure 50-Figure 51). However, protein was higher in both types of tree leaf litter tested compared to that of ***Pleurozium schreberi*** (Figure 48).

Figure 44. ***Pleurozium schreberi*** showing damage from ***Porcellio scaber*** that feeds on it at night. Note the less green plants on left that have suffered considerable damage. On the right you can see naked red stem tips where leaves and buds have been eaten. Photo by John Hribljan, with permission.

Figure 45. Freshly fallen *Acer saccharum* (sugar maple) leaves, a food source less preferred by ***Porcellio scaber*** than the moss ***Pleurozium schreberi*** in September to November. Photo by Janice Glime.

Figure 46. A common sight of needles of *Pinus strobus* (white pine) mixed with the moss ***Pleurozium schreberi***. The needles are a food less preferred in September to November by ***Porcellio scaber*** than the moss ***Pleurozium schreberi***. Photo by Janice Glime.

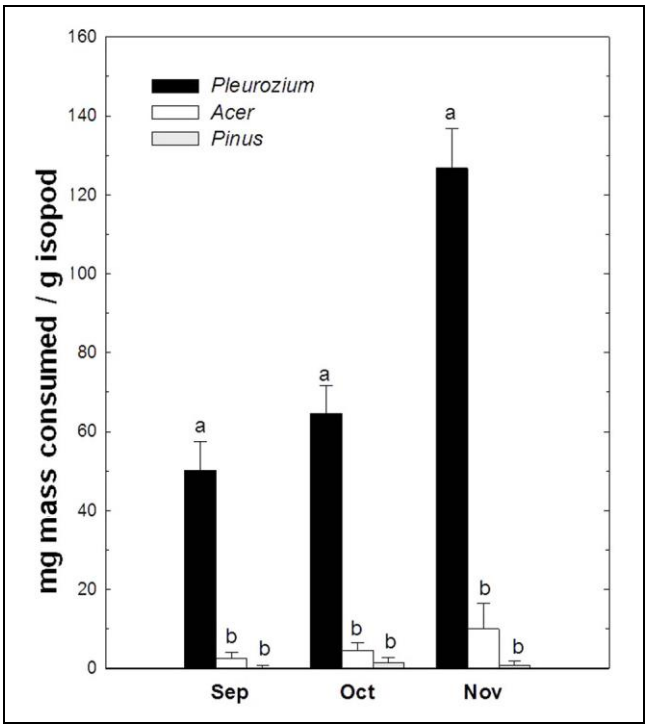

Figure 47. Comparison of mean air-dried mass (±95% CI) consumed by isopods in 24 hours when given the choice of the moss ***Pleurozium schreberi*** and the tree leaves of ***Acer saccharum*** and ***Pinus strobus***. The same letters signify means that are not significantly different from each other ($\alpha = 0.05$ post two-way ANOVA & Tukey test, n = 10). Hribljan 2009; Hribljan & Glime in prep.

Based on these experiments, Hribljan and Glime (in prep) compared the preferences among five species of mosses that occurred within the foraging distance of the isopods. ***Porcellio scaber*** (Figure 24) significantly preferred the moss ***Pleurozium schreberi*** (Figure 44) to the mosses ***Rhytidiadelphus triquetrus*** (Figure 49), ***Thuidium delicatulum*** (Figure 40), ***Dicranum polysetum*** (Figure 42), and ***Polytrichum juniperinum*** (Figure 50), with ***Pleurozium schreberi*** and ***Rhytidiadelphus triquetrus*** having lower phenolic concentrations than ***Dicranum polysetum*** and ***Polytrichum juniperinum*** (Figure 51). The

Thuidium delicatulum, preferred in earlier experiments over ***Pleurozium schreberi*** (Liao 1993; Glime 2006), was not among the top preferences, perhaps due to its lower carbohydrate content at a time of year when the isopods were preparing for winter.

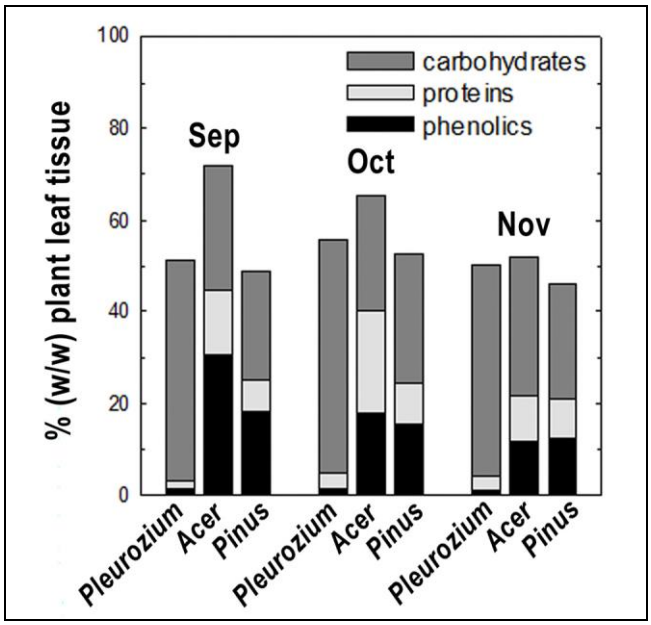

Figure 48. Comparison of percent of carbohydrates, proteins, and phenolics in freeze-dried leaves of the moss ***Pleurozium schreberi***, sugar maple tree ***Acer saccharum***, and white pine ***Pinus strobus***. Samples were taken once each month during to compare stages of decay in the tree leaves. Values are means of 10 samples. Redrawn from Hribljan & Glime (in prep).

Chemical analysis revealed that ***P. schreberi*** contains a high protein:phenolic ratio (Figure 55) (Hribljan & Glime in prep). Despite the high phenolic content and low protein content of ***Rhytidiadelphus triquetrus*** (Figure 49), these isopods would still consume it (Figure 52-Figure 53), perhaps for its high carbohydrate content, but it was not a preferred food (Figure 50-Figure 51). On the other hand, the feces indicated that this moss had not been well digested (Figure 54). As a terrestrial moss, it collects only minimal detritus, suggesting that it could have limited food value. ***Dicranum polysetum*** was least preferred despite a relatively high carbohydrate content (Figure 50-Figure 51).

Figure 49. ***Rhytidiadelphus triquetrus***, a less preferred bryophyte as autumn food for ***Porcellio scaber***, growing as it typically does amid leaf litter. Photo by Michael Lüth, with permission.

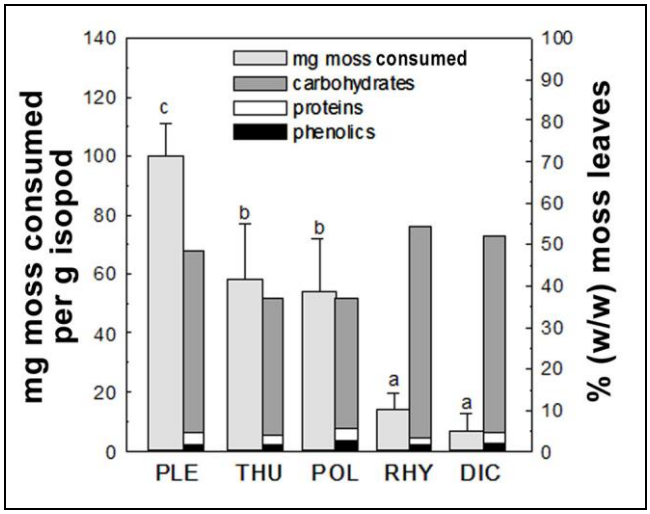

Figure 50. Comparison of moss consumed (mean ±95% CI) with mean percent by weight of phenolics, proteins, and carbohydrates in leaves of the mosses ***Pleurozium schreberi*** (PLE), ***Thuidium delicatulum*** (THU), ***Polytrichum juniperinum*** (POL), ***Rhytidiadelphus triquetrus*** (RHY), and ***Dicranum polysetum*** (DIC). n = 10. Hribljan 2009; Hribljan & Glime in prep.

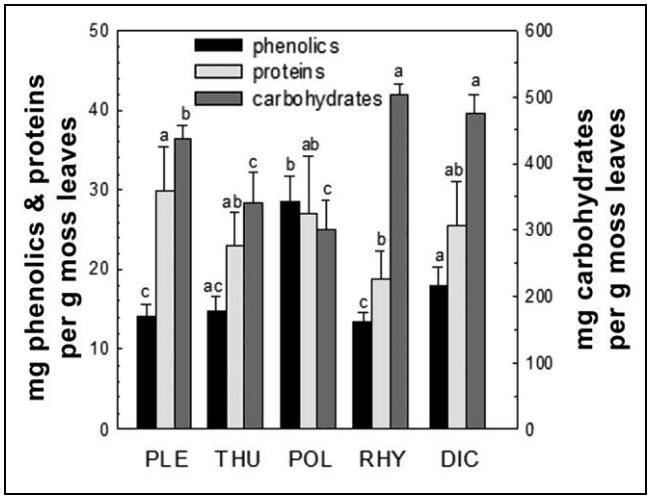

Figure 51. Comparison of means ±95% CI of phenolics, proteins, and carbohydrates in leaves of the mosses (arranged from most to least eaten) ***Pleurozium schreberi*** (PLE), ***Thuidium delicatulum*** (THU), ***Polytrichum juniperinum*** (POL), ***Rhytidiadelphus triquetrus*** (RHY), and ***Dicranum polysetum*** (DIC). n = 10. Bars with the same letters are not significantly different (α=0.05, n=10).

Figure 52. Branches of ***Rhytidiadelphus triquetrus*** that have been nibbled by ***Porcellio scaber***. Photo by John Hribljan, with permission.

Figure 53. Moss branches of ***Rhytidiadelphus triquetrus*** being eaten by ***Porcellio scaber***. Photos by John Hribljan, with permission.

Figure 54. Moss leaf fragments extracted from feces of ***Porcellio scaber*** fed only ***Rhytidiadelphus triquetrus***. Photo by John Hribljan, with permission.

Hribljan (2009) suggested that the protein:phenolic ratio might be more important in determining isopod herbivory than concentration of phenolic compounds alone. In this case, ***Pleurozium schreberi*** (Figure 44) had the highest ratio of proteins:phenolics (Figure 55), but it was not significantly different from that of ***Dicranum polysetum*** (Figure 42), which had the lowest mass eaten, suggesting that this ratio alone did not account for the preference (Hribljan & Glime in prep). With their unusual digestive tracts (see Digestion above), the terrestrial isopods may be able to gain sufficient nutrition from mosses despite phenolics, whereas other arthropods like the cranefly ***Tipula montana***, a moss-food-avoider, cannot (Smith *et al*. 2001).

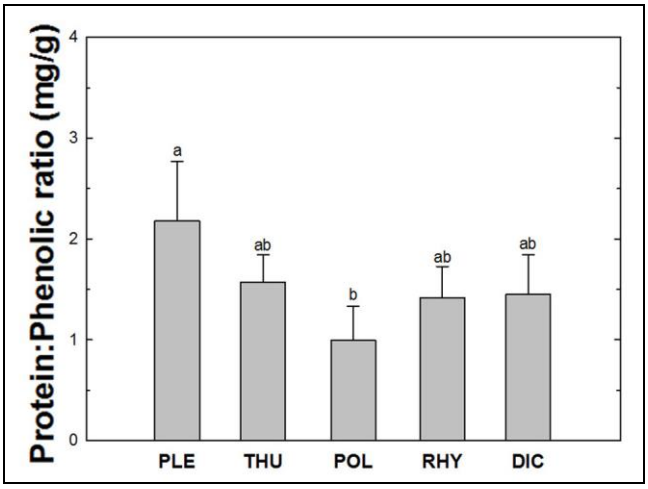

Figure 55. The mean protein:phenolic ratio of leaves (± 95% CI), arranged in order from most to least consumption, of freeze-dried mosses ***Pleurozium schreberi*** (PLE), ***Thuidium delicatulum*** (THU), ***Polytrichum juniperinum*** (POL), ***Rhytidiadelphus triquetrus*** (RHY), and ***Dicranum polysetum*** (DIC). n = 10; bars with the same letter are not significantly different, post ANOVA Tukey test, $\alpha = 0.05$).

We cannot rule out the possible importance of carbohydrates, and Forman (1968) provides evidence that caloric content is highest in two of the mosses that seem to be preferred in our experiments (Hribljan & Glime in prep). Forman showed that ***Thuidium delicatulum*** (Figure 40) had the highest caloric value (4305 cal/gdw) among the ten mosses he tested; ***Pleurozium schreberi*** (Figure 43) had the second highest caloric content (4240 cal/gdw), fitting with our data on carbohydrates. On the other hand, the lowest content was that of ***Dicranella heteromalla*** (Figure 56) (3749 cal/gdw), a moss in the same family as ***Dicranum polysetum*** (Figure 42), the latter being least preferred in our experiments. Furthermore, Sveinbjörnsson and Oechel (1991) found that the carbohydrate concentration varied with season in ***Polytrichum commune*** (Figure 34), but not in ***Polytrichastrum alpinum*** (Figure 57). Could it be that some bryophytes become more desirable in autumn due to higher carbohydrate concentrations?

Figure 56. ***Dicranella heteromalla*** in its typical soil bank habitat. This moss has a relatively low caloric content. Photo by Janice Glime.

Figure 57. ***Polytrichastrum alpinum*** with capsules. Photo by Michael Lüth, with permission.

Several other factors could account for the preferences. First, we know that other deterrents such as saponins, alkaloids, and steroids are present in some mosses and were not tested here (Adebiyi *et al*. 2012). Leaf structure could make it difficult to obtain energy from the leaves or they might be harder to chew and break off (**toughness**). We have no measures of such toughness differences for these species, so we must keep an open mind about that possibility. The structure of the cell wall might make it difficult to obtain the cell contents easily (Figure 58-Figure 59). As seen in Figure 58, ***Pleurozium schreberi*** has much thinner cell walls than the much less preferred ***Dicranum polysetum*** (Figure 42, Figure 59). But does this really translate to toughness? Or edibility? And the leaves might differ from the stems in their phenolic content, making measurements of whole plants meaningless if only leaves are eaten. However, Hribljan and Glime (in prep) used only leaves for their analyses of proteins, carbohydrates, and phenolics. They did compare the chemistry of stems and leaves in ***Pleurozium schreberi***; for all three chemical groups (phenolics, protein, carbohydrates), leaves had the higher content (Figure 60).

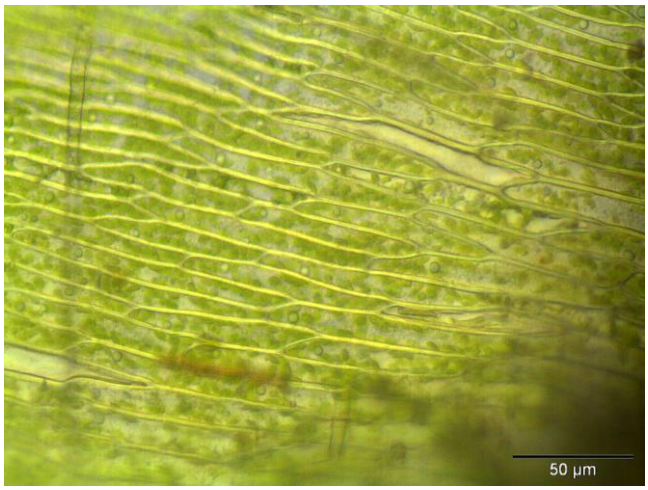

Figure 58. Leaf cell structure of ***Pleurozium schreberi*** showing thin cell wall and high ratio of cell contents to cell wall. This species was most consumed among the five moss species in the study by Hribljan and Glime (in prep.). Photo from Wikimedia Commons.

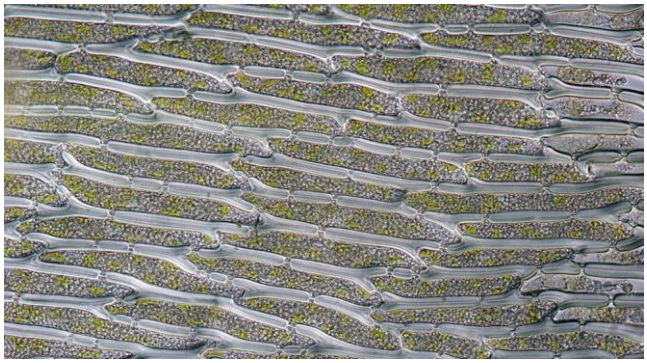

Figure 59. Leaf cell structure of ***Dicranum polysetum*** showing thick cell wall and low ratio of cell contents to cell wall. This species was least consumed among the five moss species in the study by Hribljan and Glime (in prep.). Photo by Walter Obermayer, with permission.

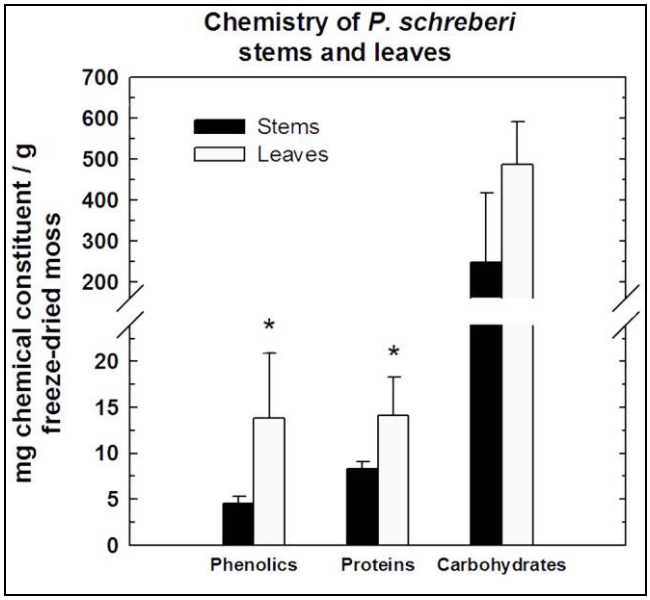

Figure 60. Comparison of mean phenolic, protein, and carbohydrate content (± 95% CI) of ***Pleurozium schreberi*** between freeze-dried leaves and stems (paired t-test, an asterisk indicates a significant difference between the two bars, $\alpha = 0.05$, n = 3).

These studies leave many questions unanswered, especially regarding season. Do the concentrations in the bryophytes change with season? Do the isopod needs change with season? Does the tree litter change in such a way that bryophytes are preferable at some times and not others without requiring any change in the bryophytes? And are the relationships the same if liverworts are presented instead of mosses? Finally, what evolutionary patterns can we observe and how do they relate to habitat and dominant herbivores?

Defenses and Apparency Theory

Plant defenses can be grouped into **physical** and **chemical defenses**. **Physical defenses** include structural modifications into such deterrents as thorns and spines or tissue modifications that include hard cell walls (Cooper & Owen-Smith 1986). The small bryophyte structure does not permit the large thorns found in some tracheophytes, but hard cell walls and hard papillae as extensions of the cell wall do fall into this category.

Chemical defenses can be divided into **quantitative** and **qualitative defenses** (Feeney 1975, 1976; Rhoades & Cates 1976; Yamamura & Tsuji 1995). **Qualitative defenses** include toxic substances like the milky juices of milkweed plants. Few bryophytes have been tested for such substances as those found in the milkweed, but as mentioned above, similar compounds do exist in the few that were tested (Fatoba *et al*. 2003; Adebiyi *et al*. 2012). **Quantitative defenses**, on the other hand, are quite common in bryophytes and typically interfere with digestion (Yamamura & Tsuji 1995), creating malnutrition in the herbivore. Phenolics typically fall in this category.

The **apparency theory** (Feeney 1976) was developed to explain the production of secondary compounds such as **phenolics** among some plants and not others (Coley *et al*. 1985). Coley and coworkers contended that resource availability in the environment was a primary determinant of both the amount and type of plant defense. Under resource limitation, slow-growing plants are favored by the environment over fast-growing plants because the former use lower levels of resources. At the same time, slow growth rates favor larger investments in **antiherbivore** defenses because growth is not fast enough to replace effects of herbivory. Since bryophytes are slow-growing, they are often able to inhabit locations with low levels of resources, including sunlight, where few other plants grow robustly, making the bryophytes one of the obvious, or **apparent**, plants in the area. Hence, bryophytes could benefit in these situations by the production of antiherbivore compounds. In fact, development of such compounds may have been essential to their success on land as the arthropods likewise became terrestrialized (Graham *et al*. 2004). Phenolic compounds, occurring in varying concentrations from the bryophytes tested, are useful as antiherbivore compounds. And it appears that bryophytes are not eaten by many kinds of organisms. Isopods are a notable exception to that avoidance. But even they have preferences.

We have seen above that for the isopod ***Porcellio scaber*** (Figure 1-Figure 2), ***Dicranum polysetum*** (Figure 42, Figure 59) is a less-preferred moss compared to ***Thuidium delicatulum*** (Figure 50) (Hribljan & Glime in prep). The former is an **apparent** moss (one with high visibility in its habitat) with high concentrations of secondary compounds (phenolic compounds), whereas ***Thuidium delicatulum*** is **unapparent** (grows with other potential food plants) and is low in secondary compounds (Liao 1993). Furthermore, ***Thuidium delicatulum*** tends to grow where there is more sun and often more nutrients, thus supporting the concept that production of phenolic compounds may be related to resource limitation (see Coley *et al*. 1985).

But it is not so simple. ***Pleurozium schreberi*** (Figure 43) is a very apparent moss, sometimes covering hectares with 100% cover, yet had the highest consumption. The study by Liao (unpublished) and the discussion here related to the study by Hribljan and Glime (in prep) seem to be the only studies that have tested the apparency theory in bryophytes. This should be an interesting topic for study.

Aquatic Consumers

Among the aquatic isopods, some consume bryophytes, but others apparently do not. Torres-Ruiz *et al*. (2007) traced food and fatty acids in macroinvertebrates and determined that the isopods in a stream food web fed on terrestrial food sources and on algae. ***Asellus*** species consume a variety of aquatic vegetation. Marcus *et al*. (1978) experimented with a sometimes moss dweller, ***Asellus aquaticus*** (Figure 61), and demonstrated that it ate both *Elodea canadensis* and **periphyton** (adhering algae), being able to survive on either. They found fragments of *Elodea* leaves and pieces of oak (*Quercus*), as well as the alga *Oedogonium* in the guts of some individuals of this species from Lake Windermere, England.

Figure 61. ***Asellus aquaticus***, an aquatic isopod that dines on ***Fontinalis novae-angliae***. Photo from Wikimedia Commons.

Parker *et al.* (2007) found that ***Asellus aquaticus*** (Figure 61) consumed large quantities of the brook moss ***Fontinalis novae-angliae*** (Figure 62) but rejected the riverweed *Podostemum ceratophyllum* (Figure 63), despite having similar protein content in both. The isopods continued to eat the ***F. novae-angliae*** even when the organic matter was removed from the plants, demonstrating that the moss itself was most likely a food source. They suggested that the mosses served as a refuge against larger predators that could eat the ***A. aquaticus***, largely because such predators as crayfish (*Procambarus spiculifer*, Figure 64; Figure 95) and Canada geese (*Branta canadensis*; Figure 65) avoided the mosses despite its comprising 89% of the plant cover in the stream. It seems that the chemical deterrents to the geese and crayfish served to protect the many macroinvertebrates living there. And to the advantage of the ***A. aquaticus***, these isopods rejected the riverweed. On the other hand, this species was not deterred by the chemical defenses of the mosses.

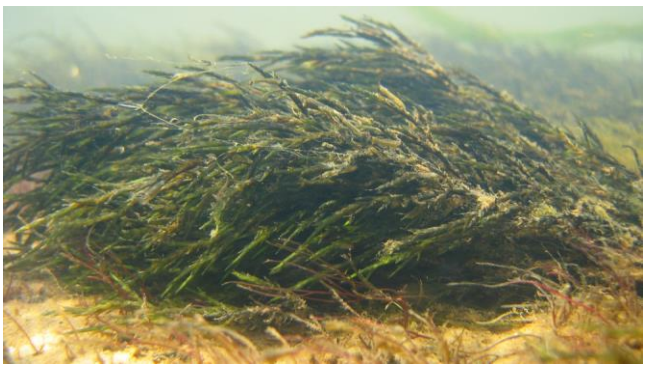

Figure 62. ***Fontinalis novae-angliae***, a habitat and a food source for species of ***Asellus***. Photo by John Parker, with permission.

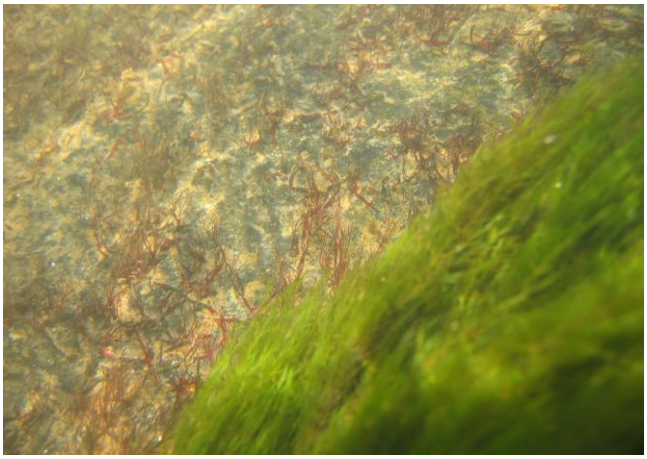

Figure 63. *Podostemum ceratophyllum* (riverweed) in upper left, appearing as fine red threads here. This plant has been heavily grazed, whereas the ***Fontinalis novae-angliae*** on the right has not. Photo by John Parker, with permission.

Figure 64. *Procambarus spiculifer*, a crayfish that avoids mosses, thus making the mosses a protected site for the isopods dwelling there. Photo by Chris Lukhaup, with permission.

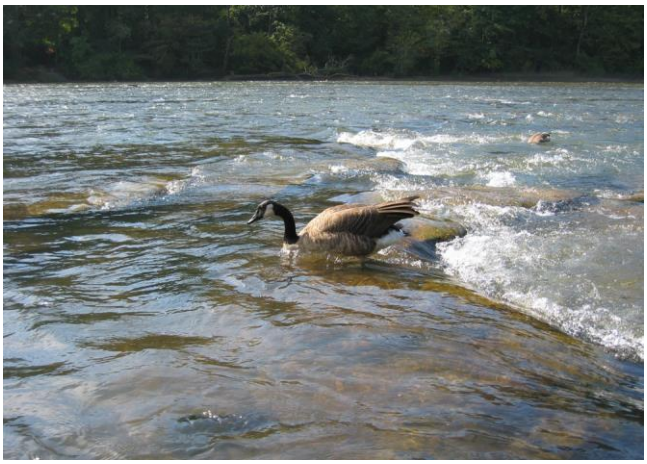

Figure 65. ***Branta canadensis*** (Canada Goose), a large bird that avoids mosses, thus permitting the mosses to protect would-be food items that hide there. This one is feeding on riverweed (*Podostemum ceratophyllum*). Photo by John Parker, with permission.

Asellus *cf.* ***militaris*** (Figure 66) eats ***Fontinalis antipyretica*** (Figure 66) in lab experiments and in the field (LaCroix 1996a). Likewise, ***A.*** cf. ***militaris*** feeds on ***Fontinalis novae-angliae*** (Figure 62) in its native aquatic habitat (LaCroix 1996a; Parker *et al*. 2007). Fragments of ***F. antipyretica*** were found in the feces of freshly collected ***A.*** *cf.* ***militaris*** (Figure 67), and when ***A.*** *cf.* ***militaris*** was cultured in the lab with the moss as a substrate it produced fecal pellets containing the moss. Gut analysis revealed diatoms and detrital matter along with small fragments of ***Fontinalis*** (Figure 68). LaCroix found that even terrestrial isopods would eat ***F. antipyretica***.

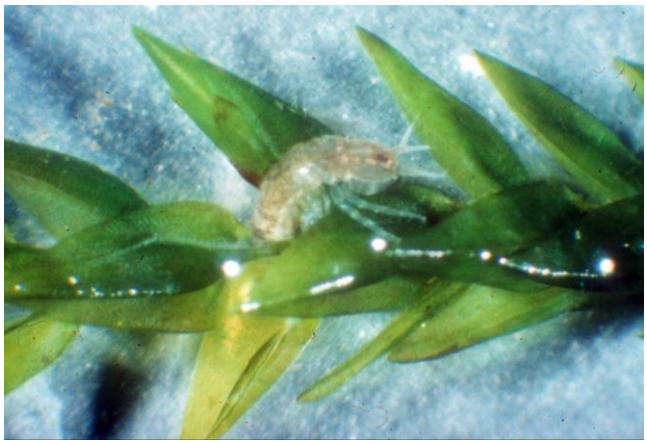

Figure 66. ***Asellus*** *cf.* ***militaris*** on a branch of ***Fontinalis antipyretica***, where it lives in slow-moving streams and uses the moss as a food source. Photo by Jacob LaCroix, with permission.

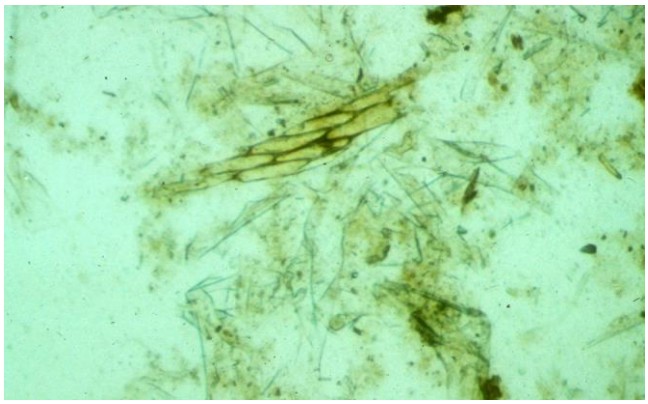

Figure 67. ***Asellus*** *cf.* ***militaris*** feces containing ***Fontinalis antipyretica*** and detrital matter. Photo by Jacob LaCroix, with permission.

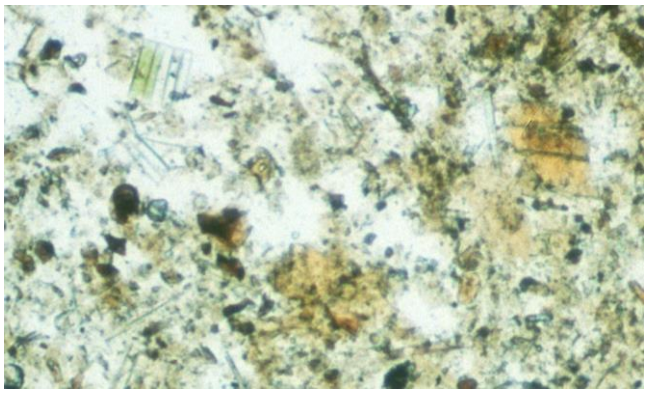

Figure 68. ***Fontinalis antipyretica*** and diatoms in gut of ***Asellus*** *cf.* ***militaris***. Photo by Jacob LaCroix, with permission.

Stern and Stern (1969) determined the greatest abundance in February and the lowest in July in a cold springbrook in Putnam County, Tennessee, USA. ***Asellus***

militaris occurs on ***Fontinalis antipyretica*** for the first few instars, then moves to the leaf litter.

Observations by LaCroix and Glime (unpublished) suggest that this species can live among the mosses for a much greater part of the life cycle in northern Michigan, USA. Like terrestrial isopods, ***Asellus cf. militaris*** (Figure 66) avoids the light. Hence, more of these isopods were on the mosses in the shade in the stream than in the sun (LaCroix 1996a; Glime 2006). When both sun and shade mosses were brought to the lab and placed under the same light conditions, the isopods preferred those that had grown in the sun. Furthermore, the isopods chose to go to the mosses collected from the sunny location under both light and dark conditions (LaCroix 1996a). Surprisingly, the shade populations had higher concentrations of phenolic compounds (LaCroix 1996a), a phenomenon contrary to the use of phenolic compounds as light protectants in tracheophytes (Swain & Hillis 1959; Martin & Martin 1982; Mole *et al.* 1988; Vergeer *et al*. 1995), but consistent with the preference for those grown in the sun when light was no longer a factor. Bryophytes often take advantage of phenolic compounds as protection against UV radiation (Jorgensen 1994; Clarke & Robinson 2008; Wolf *et al*. 2010), suggesting that herbivory was a stronger factor in this case than light. This combination of circumstances raises several questions.

First, how can we explain isopod preference for high phenolic shade bryophytes in the field but preference for lower phenolic sun bryophytes in the lab (Figure 69)? Parker *et al*. (2007) showed ***Asellus aquaticus*** (Figure 61) was not deterred by extracts from ***Fontinalis novae-angliae*** (Figure 62). Parker *et al*. suggested these isopods have some means to render the deterrent compounds ineffective, as suggested above in the discussion of the digestive system. LaCroix (1996a, b) concluded that food quality of the moss determined what isopods ate, but that shade was a more important determining factor controlling their location (and hence available food) in the field. This combination can structure communities in which small invertebrates live among unpalatable hosts that provide enemy-free space, and isopods have the benefit of avoiding their own predators while being able to eat the substrate.

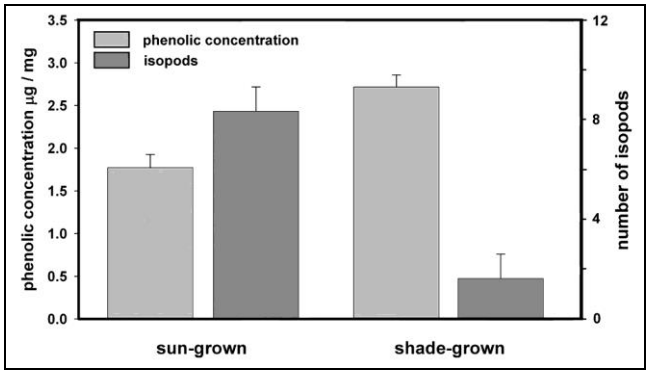

Figure 69. Comparison of moss ***Fontinalis antipyretica*** mean phenolic content (± 95% CI) and number of moss-dwelling isopods ***Asellus cf. militaris*** (± 95% CI) choosing to inhabit it. Most of the isopods in the lab chose to go to the sun-grown ***Fontinalis antipyretica*** that had a lower phenolic content than that in the shade plants. Based on LaCroix 1996b.

Apparency or UV Protection?

Having suggested an explanation for the behavior of the isopods, we are left with the question of the higher production of phenolic compounds by the bryophytes in the shade compared to those in the sun. As suggested above for terrestrial bryophytes, it is possible that the production of phenolic compounds by mosses in the shade is an evolutionary response to **apparency**. In shady locations of streams, mosses are likely to be the dominant macrophyte vegetation, with aquatic tracheophytes preferring sun LaCroix 1996a). As the dominant (most apparent) organism, probability would make the bryophytes the most likely to be eaten. Furthermore, the ***Fontinalis*** had phenolic compounds in both locations, so it is likely that they had sufficient levels in the sun to provide the needed protection against UV radiation.

Could it be that the ***Fontinalis*** produces phenolic compounds in response to herbivory? If so, are they able to signal (chemically) to the nearby mosses to do likewise? Or might this moss have evolved to produce more phenolic compounds in the shade under the selective pressure of one of its primary herbivores, aquatic isopods, that spends most of its time in the shade?

Habitat

You know where isopods hang out. Look under anything with a tiny bit of space to give access and you will find them. They go scurrying away in seek of shelter when you lift their cover. But look out at night. They come out in force to eat your vegetables – and your mosses.

Bryophytes seem to play multiple roles in the niches of isopods. For terrestrial species, bryophytes provide refuge against some predators, but even for litter-dwelling species they may represent islands for rehydration amid a dry food area. But the bryophytes can also serve as food, especially at night when desiccation is less of a problem. Aquatic bryophytes likewise serve as a refuge against predators and can also serve as food or a food substrate for periphyton and detritus. Zimmer and Topp (1997) found that ***Porcellio scaber*** (Figure 1-Figure 2) populations decreased in response to acidification, and that microorganisms, often reduced by acid conditions, were important in the maintenance of juveniles.

It seems logical that the first consideration for a habitat for isopods is a moist place with good aeration that provides shelter and darkness, but that also has a food source. In the water, detritus and periphyton can serve as the food source, but on land periphyton is too minor and detritus is more likely to be in the soil. Hence, bryophytes that provide these physical characteristics and are also palatable and chewable become a food source and provide a suitable habitat.

Terrestrial

Terrestrial habitats require special adaptations for these groups, as discussed above. Edney (1954) found that terrestrialization increased in the order of **Ligiidae**, **Trichoniscidae**, **Oniscidae**, **Porcellionidae**, to **Armadillidiidae**. This order can be interpreted as their order for tolerating drought. And each of these families has members known from bryophytes.

Božanić (2011) sampled the moss invertebrate fauna in a forest in the Vrapač National Nature Reserve, Czech Republic. The most abundant groups were **Acarina** (mites – 2946 individuals), **Collembola** (springtails – 1341 individuals), and **Isopoda** (320 individuals). Within moss colonies on the forest floor and tree trunks they found the isopods ***Androniscus roseus***, ***Hyloniscus riparius*** (Figure 86), ***Hyloniscus*** spp., ***Lepidoniscus minutus***, ***Ligidium hypnorum***, ***Porcellium collicola*** (Figure 3), ***Porcellium conspersum***, ***Trachelipus rathkii*** (Figure 26), ***Trachelipus ratzeburgii*** (Figure 85), ***Trachelipus*** spp., and ***Trichoniscus pusillus*** (Figure 25). In the adjoining forest floor, the isopods were not among the most numerous groups sampled. Sample size was important in determining abundance, with more isopods occurring in larger sample sizes of ~400 sq cm. ***Trichoniscus pusillus*** and ***Hyloniscus riparius*** in particular preferred thicker mosses, especially in ***Plagiomnium undulatum*** (Figure 70) with a 50-mm thickness. These two species are known to be **hygrophilous** (water-loving) (Tajovský 2000), perhaps explaining their preference for thicker mats that could retain moisture longer. This preference could create danger as this thicker moss was also in the range of preference of a predator ant, ***Myrmica ruginodis*** (Figure 71), that occurred primarily in mosses having 40-50 mm thickness (Božanić 2011). In poplar forests of Hungary, ***Hyloniscus riparius*** (Figure 86) occurs primarily in wet, decaying trees that are covered with mosses (Farkas 1998).

Figure 70. ***Plagiomnium undulatum***, a moss that forms 50 mm deep mats where the isopods ***Trichoniscus pusillus*** (Figure 25) and ***Hyloniscus riparius*** (Figure 86) take shelter. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Philoscia muscorum (Figure 17), an isopod with a mossy name, is common and widespread in the UK among mosses and other substrata (Stenhouse 2007). ***Porcellio*** is perhaps the most common genus in the Northern Hemisphere, occurring with mosses in Europe and North America. ***Porcellio scaber*** (Figure 1-Figure 2) is often found among mosses and is one of the commonest of the woodlice in the UK (Stenhouse 2007). Its ability to feed on bryophytes is discussed above.

Diver (1938) examined the common woodlouse (***Porcellio scaber***, Figure 24) in five coastal animal successional zones in the British Isles where the plant carpet played a major role in characterizing the habitat. In the *Calluna-Psamma* zone, there was a well-developed lichen-moss carpet that replaced the grass turf. Nevertheless, only one species of isopod occurred there, whereas two more were added in the *Calluna* zone where the ground cover was nearly 100% *Calluna*. In a separate study that compiled many records, Harding and Sutton (1985) reported ***Trichoniscus pusillus*** (Figure 25) from all five dune zones, but primarily in dune slacks, where it was associated with mossy areas as well as damp hollows, large pieces of concrete, or decaying wood.

Figure 71. ***Myrmica ruginodis***, an ant that lives among the same mosses as the isopods ***Trichoniscus pusillus*** and ***Hyloniscus riparius***, and is a known arthropod predator. Photo by Boris Ginestet and Nicolas Calmejane, through Creative Commons.

Božanić and coworkers (Božanić 2008; Božanić *et al*. 2013) used heat to extract invertebrates from 61 terrestrial bryophyte samples from forests of the Czech Republic. They found 45 invertebrate species (13 higher taxonomic groups) from among 15 bryophyte species. The moss ***Brachythecium oedipodium*** (Figure 72) seems to be a preferred habitat, exhibiting the highest invertebrate diversity on decaying wood, where **Isopoda** were the most abundant (439 specimens), but diversity was also high in ***B. salebrosum*** (Figure 73) (mean 4 spp. per sample) and ***B. rutabulum*** (Figure 74) (mean 5.5 spp. per sample).

Atrichum undulatum (Figure 75), ***B. rutabulum***, and ***Hypnum cupressiforme*** (Figure 76) were the most frequent mosses and presented a high number of invertebrate taxa. This abundance is despite the content of hydroxycinnamic and phenolic acids present in ***B. rutabulum*** (Davidson *et al*. 1989).

Figure 72. ***Brachythecium oedipodium***, a preferred habitat for invertebrates, including **Isopoda**. Photo by Michael Lüth, with permission.

Figure 73. ***Brachythecium salebrosum***, a bryophyte with a high diversity of invertebrates. Isopods were most abundant in small cushions. Photo by Michael Lüth, with permission.

Figure 74. ***Brachythecium rutabulum*** capsules, a moss with high invertebrate diversity, including isopods. Photo by Martin Cooper, through Creative Commons.

Figure 75. ***Atrichum undulatum***, mosses where clump size is important in determining isopods (smaller clumps) vs annelids (larger clumps). Photo by Michael Lüth, with permission.

Figure 76. ***Hypnum cupressiforme***, a bryophyte with a high diversity of invertebrates. Isopods were most abundant in small cushions. Photo by Michael Lüth, with permission.

Type of substrate, size of cushion, and height above the ground were important determinants of the invertebrate species in these Czech forests (Božanić 2008; Božanić *et al*. 2013). **Isopoda** were numerous in small cushions, in contrast to the **Enchytraeidae** (Annelida) that were abundant in larger moss carpets. The woodlice (isopods) were most abundant among the moss ***Plagiomnium*** (Figure 77) on the ground. Tree size also played a role, with isopods ***Trichoniscus pusillus*** (Figure 78) and ***Porcellium collicola*** (Figure 3) living among mosses on smaller trees, whereas the isopod ***Trachelipus rathkii*** (Figure 26) occurred among mosses growing on larger trees. It is possible that correlation with tree diameter resulted from colonization rates and succession of the community. Nevertheless, ***T. pusillus*** also occurred among mosses on volcanic rock in the Azores (Vandel 1968). Because the bryophyte habitat was one of the earliest ones available to invasion of land, Božanić and coworkers (2013) suggest that the bryophytes may serve as refugia in expected future climate change.

Figure 77. ***Plagiomnium drummondii*** on rocks in forest, a moss where isopods are abundant. Photo by Janice Glime.

Figure 78. ***Trichoniscus pusillus***, an isopod that lives among mosses on small trees and among mosses on exposed lava rocks. Photo by Graham Montgomery, with permission.

While pillbugs require moisture, a boggy habitat can be too moist. Although ***Armadillidium*** is among the best adapted of isopods to terrestrial life, surviving in relatively dry habitats, some species do use mosses as a habitat. Dale and Dale (1986) report ***Armadillidium pulchellum*** (Figure 79) in moss mats of the coastal cliff slopes in the UK. They were surprised to find this species also inland in abundance under mosses on a wall. Harding and Sutton (1985) likewise report them under mats of mosses as well as under stones and mats of the flowering plants *Thymus* spp. and *Sedum anglicum* in the UK. In the daytime, one can also find ***Armadillidium pictum*** (Figure 80) under stones and among mosses in the UK (Harding & Sutton 1985).

Figure 79. ***Armadillidium pulchellum***, a coastal isopod found among coastal mosses in the UK. Photo by Jan van Duinen <http://www.janvanduinen.nl/>, with permission.

Figure 80. ***Armadillidium pictum***, an isopod that lives under stones and among mosses in the UK. Photo by Jan van Duinen <http://www.janvanduinen.nl/>, with permission.

The genus ***Ligia*** (Figure 81) is one of the less terrestrialized isopods, requiring more moisture than other terrestrial genera that have been studied, often living in tidal zone cliffs and rocky beaches. But on the Hawaiian Island of Kauai, ***L. perkinsi*** commonly occurs among wet mosses of indigenous trees in the montane rainforests above 600 m, whereas on Oahu it is known instead from a windward wet rocky cliff at only 300 m (Taiti *et al*. 2003).

Figure 81. ***Ligia*** sp., related to the moss dweller ***Ligia perkinsi*** that occurs among wet mosses on trees in Hawaiian rainforests. Photo by Steve Nanz, through Creative Commons.

Isopods even live in the exposed higher parts of trees. In the neotropical montane forests of Costa Rica, isopods dwell in both the ground litter and canopy litter, which includes bryophytes (Nadkarni & Longino 1990). But in the montane forests, the isopods had higher densities on the ground.

In the Polynesian islands, ***Philoscia truncata*** occurs both under stones and among mosses at 500 m on the Society Islands (Jackson 1938). On the Mangareva Islands ***Spherillo marquesarum*** occurs under mosses and rocks. In the Tasmanian temperate rainforests, isopods and other invertebrates often occur among mosses in places where they are not common on other substrates (Greenslade 2008). The higher moisture content of the mosses most likely accounts for the higher species richness, with 28 species of isopods among the mosses there. ***Styloniscus nichollsi*** is common in Tasmania and can occur among ***Sphagnum*** (Figure 83) at 1600 m at Point Lookout (Green

1974). In the Antarctic, several species of ***Styloniscus*** occur among mosses: ***S. otakensis*** (Figure 88), ***S. pallidus***, ***S. thompsoni***, ***S. verrucosus*** (Pugh *et al*. 2002).

Working in the Azores and Madeira, Vandel (1968) found a number of bryophyte-dwelling species not mentioned in other locations cited here, including ***Trichoniscus pygmaeus*** among mosses, ***Miktoniscus chavesi*** among mosses in a lava field and the bottom of a crater, but also among liverworts in *Erica* bush, ***Chaetophiloscia guernei*** among mosses in the *Erica* forest and other indigenous vegetation, and ***Eluma purpurascens*** among mosses at snowline, under mosses at the roadside of an old lava field, and among mosses in the *Erica* forest and heath. ***Androniscus dentiger*** (Figure 82) occurred on exposed lava rocks covered with mosses and lichens

Figure 82. ***Androniscus dentiger***, an inhabitant of mosses and lichens on lava rock in the Azores. Photo by Gilles San Martin, through Creative Commons.

Peatlands

Sphagnum (Figure 83) in peatlands often has its own unique fauna, in part due to the unique assemblage of plants. The *p*H can influence some species. The surface can get quite hot, thus being inhospitable to isopods. But within the peat mats, the gradient of temperature and moisture often provides suitable habitat with the possibility for vertical migration as conditions fluctuate.

Figure 83. ***Sphagnum cristatum***, a moss from boggy habitats where the isopod ***Trachelipus rathkii*** (Figure 26) lives in New Zealand. Photo by Jan-Peter Frahm, with permission.

Antonović *et al*. (2012) used pitfall traps to study the isopods living in the Dubravica peat bog and surrounding forest in Croatia. They found eight species of isopods, comprising 389 individuals, during their two-year study, with little difference in species richness between the bog and forest. They considered the small size of the bog peatland, progressive succession of plant life, and interactions among species to account for the high species richness there. Where the grass *Molinia* spread into the bog, the ***Sphagnum*** (Figure 83) was less humid and provided habitats for forest isopod species. The edge (**ecotone**) had the highest diversity, probably due to multiple factors: greater variety of niches, seasonal immigration, and less predator abundance relative to the open bog. Within the bog, cohabiting lycosid spiders (see Chapter 7-4 on Peatland Spiders) and ***Myrmica*** ants (Figure 84) were a threat to the isopods. In the bog ***Trachelipus rathkii*** (Figure 26), a known bryophyte dweller, was the most common isopod, whereas in the forest it was ***Protracheoniscus politus*** (Figure 85). Bog-specific species were absent. Instead the isopod fauna was dominated by widespread species with wide niche requirements, which Antonović *et al*. attributed to the degradation process on the bog. Antonović and coworkers considered one bog inhabitant here, ***Hyloniscus adonis*** (see Figure 86), to be **tyrphoxenous**, *i.e.*, a vagrant not reproducing in the bog.

Figure 84. ***Myrmica*** sp, an ant predator genus to isopods in bogs. Photo by Alex Wild <www.alexanderwild.com>, with permission.

Figure 85. ***Protracheoniscus politus*** (top) and ***Trachelipus ratzeburgii*** (bottom), the upper being the most common moss dweller in a forest surrounding a bog in Croatia. Photo by Walter Pfliegler, with permission.

Figure 86. ***Hyloniscus riparius***, relative of the vagrant isopod ***Hyloniscus adonis*** in bogs. Photo by Tom Murray, through Creative Commons.

Springs

I expected to find a number of records of isopods among mosses in springs and was surprised to find relatively few. In some of these, although mosses were abundant, the isopods were in the open water and bottom sediments, but not among the mosses (Gooch & Glazier 1991; Erman 2002). Erman (2002) could find no relationship between moss mats and invertebrate diversity, including that of isopods. The only relationship he found was that the mosses indicated that the spring had constancy and persistence.

In his study of isopods in habitats of the Azores and Madeira, Vandel (1968) found ***Trichoniscus pusillus*** (Figure 25) among mosses in a spring on the mountain slope and among ***Sphagnum*** at another spring. But the other spring species were less familiar among moss dwellers, including ***Miktoniscus chavesi***, ***Chaetophiloscia guernei***, and ***Eluma purpurascens*** among mosses. ***Oniscus asellus*** occurred among mosses in sheltered ravines and under wet moss in the ravine.

Waterfalls

Waterfalls provide a variety of niches from very aquatic to damp terrestrial. These microhabitat niches change as water levels recede and may be quite dry in summer when the waterfall recedes or disappears altogether. Stephensen (1935) found terrestrial Talitridae in such habitats in Java in the Marquesas where ***Orchestia floresiana*** occurred among mosses of rivulets, fountains, and waterfalls.

Aquatic

Aquatic isopods can also be moss inhabitants. Fontaine and Nigh (1983) suggest that aquatic isopods like ***Asellus*** (Figure 61) may be limited by their slow colonization rate. When such host plants as ***Nitellopsis*** (Figure 87) die off, the isopods need an alternative substrate with sufficient food available (Hargeby 1990). In habitats where bryophytes occur, these bryophytes could provide the permanence needed by the slow isopod colonizers.

Figure 87. ***Nitellopsis obtusa***, an alga that provides habitat for isopods like ***Asellus*** but that can disappear in some habitats for part of the year, causing the isopods to seek other shelter. Photo through Public Domain.

Although ***Asellus aquaticus*** (Figure 61) is well known from bryophytes, it is the juveniles that are most abundant in algal and bryophyte mats, whereas the larger adults are typically associated with large-sized substratum particles (Graca *et al*. 1994). As already noted in discussing bryophytes as food, ***Asellus cf. militaris*** (Figure 66) occurs in mats of ***Fontinalis*** spp. in streams where it feeds on both the mosses and associated detritus and periphyton.

On Macquarie Island in the sub-Antarctic, ***Styloniscus otakensis*** (Figure 88) lives among mosses on margins of streams, among other places (Greenslade 2008). Cowie and Winterbourn (1979) found that the isopod ***Styloniscus otakensis*** was the only common invertebrate on the moss ***Cratoneuropsis relaxa*** (Figure 89) in the outer spray zone of a spring brook in the Southern Alps of New Zealand. They attributed differences in fauna among the moss species to differences in flow rates, availability of detritus, and differences in water saturation.

Figure 88. ***Styloniscus otakensis***, an aquatic species in a genus with a number of terrestrial moss-dwelling members in forests and bogs of Tasmania, New Zealand, and nearby islands. Photo by Mark Stevens. PERMISSION PENDING.

Figure 89. ***Cratoneuropsis relaxa***, genus of mosses that occur in springbrooks in the Southern Alps of New Zealand and home to ***Styloniscus otakensis***. Photo by Tom Thekathyil, with permission.

South Africa may have species unfamiliar to most of us in the Northern Hemisphere. Enckell (1970) found ***Protojanira prenticei*** among mosses in the upper part of a streamlet there.

Pollution

Pollution in the form of heavy metals can quickly move up the food chain in streams. Detrital feeders like ***Asellus*** species can concentrate the metals from the detritus on the streambed or among mosses, then get eaten by larger invertebrates or fish, further concentrating the pollutants (Eimers *et al*. 2001). However, Eimers and coworkers found that when the sediment organic content was increased (20% peatmoss), the cadmium concentration in ***Asellus racovitzai*** decreased compared to that of mineral sediment treatments, indicating that bryophytes, especially ***Sphagnum*** (Figure 83), might be able to protect the isopods and organisms higher up the food chain by sequestering the heavy metals and keeping them out of the water column. Other mosses, for example ***Fontinalis antipyretica*** (Figure 66), occurring in the same waters with ***Asellus aquaticus*** (Figure 61), also accumulate heavy metals. Lithner *et al*. (1995) found that when the *p*H decreased, the bioconcentration factors decreased in the bryophytes while several of the metals simultaneously increased in fish. Hence, using aquatic bryophytes as bioaccumulators to protect the organisms is complicated, but they could be a useful tool to predict imminent fish die-off.

CLASS MALACOSTRACA, ORDER MYSIDA

The **Mysida** are known as oppossum shrimps because of the brood pouch where females carry their larvae. Mysids are not common on bryophytes, but they can use them as a restaurant in aquatic habitats. ***Mysis relicta*** (Figure 90) in Char Lake, Northwest Territories, Canada, feeds primarily on diatoms and inorganic particles on moss substrata (Lasenby & Langford 1973). It is known as an opportunistic feeder, permitting it to survive on a variety of resources (Grossnickle 1982).

Figure 90. ***Mysis relicta***, a species that feeds on diatoms and detritus among mosses in some habitats. Photo by Perhols, through Creative Commons.

CLASS MALACOSTRACA, ORDER DECAPODA

Decapods include such animals as crayfish, lobsters, crabs, and hermit crabs. For such large invertebrates to succeed on land they have developed morphological, physiological, biochemical, and behavioral adaptations (Bliss & Mantel 1968). Adult land crabs maintain water balance through the coordinated action of gills, pericardial sacs, and the gut, taking up, storing, and redistributing both salts and water to maintain an osmotic and water balance. In larvae, on the other hand, this suite of responses is not practiced. As is known for the isopods, there is evidence that at least some decapods excrete some of their ammonia as a gas (Weihrauch *et al*. 2004). Adult land crabs use both gills and the highly vascularized lining of the branchial chambers for gas exchange (Bliss & Mantel 1968). They generally cannot survive low temperatures, but their cytochrome C seems to help in their survival of high temperatures. Finding a mate is typically accomplished by both visual and acoustic signals, coupled with ritualistic behavior.

Decapods generally are too large to live among most bryophytes, but they are not without interesting bryological interactions. The decapod ***Thalassina anomala*** (Figure 91-Figure 93), a mud lobster, forms soil mounds (Figure 92-Figure 93) when it builds its nest (Yamaguchi *et al*. 1987). It is on these soil mounds in the mangrove forests of Japan that ***Fissidens microcladus*** dwells. By living on the soil mounds, the moss is never submerged at high tide and most likely benefits from the moist air.

Figure 91. ***Thalassina anomala***, a mud lobster that makes mounds in mangrove forests – mounds that have somewhat unique flora including ***Fissidens microcladus***. Photo by Ariff Aziz, through Creative Commons.

Figure 92. Mound of the mud lobster, ***Thalassina anomala***, in a mangrove forest. Photo by Ariff Aziz, through Creative Commons.

Figure 93. Close view of a mound of the mud lobster, ***Thalassina anomala***, showing greenish patches that could be protonemata of the moss ***Fissidens microcladus***. Photo by Ariff Aziz, through Creative Commons.

Coffey and Clayton (1988) have suggested that deep water bryophytes in New Zealand lakes do not occur in the presence of freshwater crayfish. It appears that in the presence of the crayfish ***Paranephrops*** spp. (Figure 94), the bryophytes suffer both mechanical damage and browsing. In Lake Wanaka, there is a deep water (down to 50 m) community of bryophytes (Coffey & Clayton 1988). But in other New Zealand lakes the mosses were absent. This absence correlated with the presence of large crayfish (***Paranephrops*** spp.) populations. Coffey and Clayton suggest that the mosses are absent not due to different habitat needs from the crayfish, but from the browsing and mechanical damage caused by the crayfish.

Figure 94. ***Paranephrops planifrons***, member of a genus of crayfish that inflicts mechanical damage on bryophytes. Photo by David Wilson, through Creative Commons.

The relationship of the ***Parenephrops*** species with stream mosses contrasts with the avoidance of mosses by the crayfish ***Procambarus spiculifer*** (Figure 64, Figure 95; see also discussion under Isopoda – Aquatic Consumers) reported by Parker *et al*. (2007). The latter crayfish is selective in its plant habitat, choosing the flowering plant *Podostemum ceratophyllum* (riverweed; Figure 96) over ***Fontinalis novae-angliae*** (Figure 62; Figure 96), despite the greater abundance of the moss (89% of total biomass) (Parker *et al*. 2007). Furthermore, the mosses supported twice as many macroinvertebrates as did the riverweed. This revelation suggests that the mosses might provide a safe refuge for macroinvertebrates, allowing them to escape from larger predators, perhaps due to their chemical defenses. This hypothesis is supported by the presence in the moss of C_{18} acetylenic acid, octadeca-9,12-dien-6-ynoic acid, a defense compound that inhibits crayfish feeding. A similar avoidance was absent in the amphipods and isopods in the stream, permitting them to find safe refuge there. This discriminatory behavior of the antifeedant against crayfish but not microcrustacea permits these small arthropods to live where they can avoid the predation of larger arthropods.

Figure 95. ***Procambarus spiculifer*** eating *Egeria densa*. This crayfish avoids eating the moss ***Fontinalis novae-angliae***, thus protecting its invertebrates as well. Photo by John Parker, with permission.

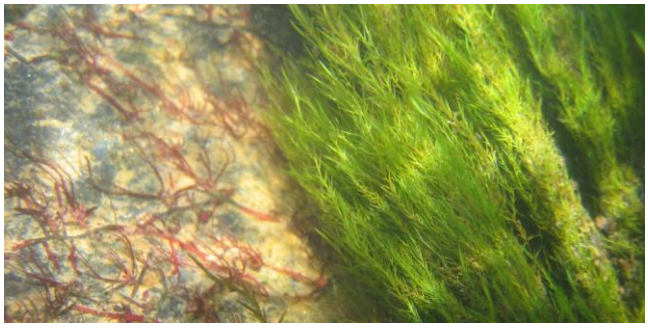

Figure 96. ***Podostemum ceratophyllum*** (**left**) and ***Fontinalis novae-angliae*** (**right**) showing effects of grazing by the crayfish ***Procambarus spiculifer*** on the ***P. ceratophyllum***. The moss remains untouched. Photo by John Parker, with permission.

Summary

Isopods include a number of terrestrial genera, many of which include bryophyte dwellers, including the families **Ligiidae**, **Trichoniscidae**, **Oniscidae**, **Porcellionidae**, and **Armadillidiidae**. ***Asellus*** seems to be the most common genus in streams. Springs seem to have few isopods inhabiting mosses. Other taxa benefit from the moisture of bogs, migrating vertically to achieve optimum moisture and temperature.

As descendents of aquatic and marine organisms, isopods benefit from the moisture and protection of bryophytes, finding food among them as detritus, periphyton, and the bryophytes themselves. Their digestive system is modified by reducing gut surface tension and culturing gut flora to render the phenolic compounds safe in their diet. They are known to eat a wide range of bryophytes, but they do have preferences, and some taxa are ignored.

In addition to sheltering, the isopods use the bryophytes as a place to remove excess water or gain needed water. They conserve water by releasing their nitrogenous waste as ammonia gas. Isopods are sensitive to temperature, and bryophytes can provide shade and evaporative cooling.

Isopods often go into the soil in the daytime, emerging and climbing to the tips of the bryophytes to dine at night. They congregate under bryophytes, as well as rocks, logs, and boards, reducing water loss and oxygen consumption, stimulating reproduction, increasing predator defense, promoting coprophagy, and acquiring internal symbionts. Reproduction is typically sexual, but parthenogenesis is possible in some taxa. The eggs and young are carried by the mother.

Some isopods overwinter under bryophytes or in the soil under bryophytes. They generally cannot survive temperatures below -7°C.

At least some bryophytes exemplify the **apparency theory**. The bryophytes are small and slow-growing. They contain a wide range of antiherbivore compounds that deter most herbivores. Isopods, on the other hand, circumvent the antiherbivore compounds through their digestive system, permitting them to gain a food source (bryophytes) where they are protected from a number of would-be predators. However, ants are a predatory threat even among the bryophytes.

Members of the order **Mysida** are rarely reported from bryophytes, but in Char Lake they feed on diatoms and inorganic particles among mosses.

The Decapoda (crayfish) generally do not live among mosses, in some cases actually avoiding them, apparently due to the presence of C_{18} acetylenic acid, octadeca-9,12-dien-6-ynoic acid in the mosses (and possibly other compounds). Others damage the bryophytes by moving their heavy bodies across them. Invertebrates are able to avoid predation by crayfish by living among the mosses.

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CHAPTER 11-1
AQUATIC INSECTS: BIOLOGY

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CHAPTER 11-1
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Figure 1. ***Rhyacophila carolina*** larva, a free-living caddisfly that occurs commonly on bryophytes. Photo by Bob Henricks, with permission.

Aquatic Insects

Cascading waterfalls, silt-laden torrents, lurking predators, limited oxygen, unpredictable water levels, icy winters – all these dangers face the insects (Figure 1) that call lakes, and especially streams, their homes. So why do the insects choose to live there, and how do bryophytes help to make life in such unfriendly conditions possible?

The relationship between aquatic insects and bryophytes is a topic dear to my heart. When I was working on my M.S. project on the bryophytes, my roommate was working on aquatic insects. Never passing up an opportunity for a field trip, I accompanied her on all her collecting trips. We both soon realized that in her rocky mountain streams of northern West Virginia, USA, there were typically more insects among the bryophytes than in any other microhabitat in these streams. It was this discovery that led me to my Ph. D. research topic on the insects associated with Appalachian stream bryophytes and the many studies I have done on ecology of aquatic mosses since then.

These wonderful bryophyte-insect communities are not a new discovery. Stream ecologists in particular have observed the importance of mosses as cover for aquatic insects and other aquatic invertebrates and even fish (Thienemann 1912; Carpenter 1927; Percival & Whitehead 1929, 1930; Humphries & Frost 1937; Jones 1941, 1948, 1951; Frost 1942; Badcock 1949; Illies 1952; Hynes 1961; Minckley 1963; Egglishaw 1969; Arnold & Macan 1969; Lindgaard *et al*. 1975; Hawkins 1984; McKenzie-Smith 1987; Suren & Winterbourn 1992a, b; Gislason *et al*. 2001; Linhart *et al*. 2002; Paavola 2003).

In Idaho, USA, Maurer and Brusven (1983) found that ***Fontinalis neomexicana*** (Figure 2) housed 5-30x the densities of insects found associated with the mineral substrates; biomass, however, was only 2x as great. The moss did not alter insect densities in the underlying **hyporheic** zone (saturated zone beneath the bed of a river or stream that can support invertebrate fauna). The diversity of functional groups was greater among mosses, but the species richness was similar to that of the mineral substrate.

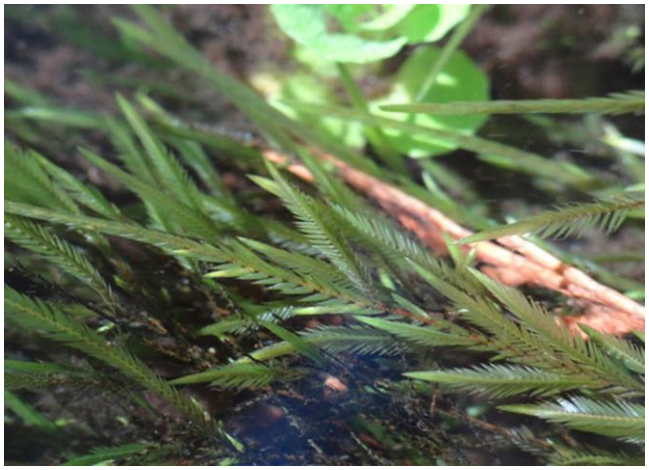

Figure 2. ***Fontinalis neomexicana***, a moss that greatly increases the density of stream insects. Photo by Belinda Lo, through Creative Commons.

The numbers of insects among bryophytes can be extensive (Figure 3). Minckley (1963) found that mosses had the highest densities of insects compared to sand, stones, and tracheophytes in a Kentucky, USA, stream. Lillehammer (1966) found that moss-covered stones had 606 individuals m^{-2} compared to 471 m^{-2} on stones with no mosses.

Figure 3. This branch of ***Palustriella commutata*** demonstrates the variety and density of aquatic insects that can occur on aquatic mosses. Photo by Dan Spitale.

When more sophisticated statistical methods became available, bryophyte biomass emerged as one of the factors accounting for the variation in insect fauna among streams, and as we might expect, it has a positive influence on the insect fauna (Gislason *et al*. 2001). Furthermore, bryophytes can occupy deeper waters, forming a zone that is lower than that of tracheophytes, and this zone is able to support fauna that could not otherwise live at those depths (Blackstock *et al*. 1993).

Minshall (1984) considered bryophytes to be a major factor in increasing insect numbers because of the increased surface area offered by them. Egglishaw (1969) found that most species of invertebrates, including insects, were less aggregated in clumps among the mosses than they were under stones. One might interpret that this is due to the complex nature of the mosses and the large space in which they can be distributed. On the other hand, it would seem that the stone habitat would be more homogeneous and thus one might expect less clumping. Another mystery.

Table 1. Orders of insects and their abundances among bryophytes in various locations around the world. NR refers to not recorded, which may mean the researcher(s) didn't look at the group.

		Collembola	Odonata	Diptera	Coleoptera			
	sample size	Ephemeroptera	Plecoptera	Trichoptera				Reference
Straffan, River Liffey, Ireland	200 g	NR	533	NR	22	11446	492	262	Frost 1942
Ballysmuttan, River Liffey, Ireland	200 g	NR	16	NR	310	10482	148	1095	Frost 1942
Cold Springbrook, TN, USA	0.1 m^2	NR	7.1	NR	8	215	24.6	0.4	Stern & Stern 1969
Bystřice, Czech Republic	10 g dry	NR	1103	NR	18	44762	359	184	Vlčková *et al*. 2001-2002
Mlýnský náhon, Czech Republic	10 g dry	NR	176	NR	0	11035	13	5	Vlčková *et al*. 2001-2002
Welsh Dee Tributary, Wales	~300 cm^2	NR	9.7	NR	513	82.8	0.4	7.4	Hynes 1961
Mouse Stream, Alpine, NZ	1 m^2	NR	NR	NR	540	61270	730	0	Suren 1991a
Tim's Creek, Alpine, NZ	1 m^2	NR	NR	NR	270	24580	260	90	Suren 1991a
West Riding, Yorkshire, UK – loose moss	%	NR	13.42	NR	154	65.3	3.1	6.7	Percival & Whitehead 1929
West Riding, Yorkshire, UK – thick moss	%	NR	8.03	NR	0.65	42	8	4.4	Percival & Whitehead 1929
alpine unshaded stream, NZ	%	NR	NR	NR	2.1	58l.8	NR	NR	Suren 1991b
alpine shaded stream, NZ	%	NR	NR	NR	2.5	69.9	NR	NR	Suren 1991b
River Sawdde, Wales		rare	NR	NR	very rare	NR	NR	very rare	Jones 1949

Life Cycle Stages

Life cycle stages play a major role in the occupancy of water habitats by insects. Most of these orders of insects have poor ability to survive freezing, so escape into water can maintain their temperatures above freezing. The flowing part of water generally remains at ~1°C throughout the winter, and lakes and ponds that don't freeze to the bottom have water just above 0 up to 4°C.

Because of the importance of water in the life cycle of the major groups of aquatic insects, we must understand the types of life cycles among them before we can begin a discussion of the biology and ecology of these groups. There are two major groups of classification among the insects, based on life cycles and their developmental stages.

Collembola

The **Collembola** (Figure 4), or springtails, long considered to be insects, have been kicked out of the **Insecta** by cladistics, due to linkages shown by their DNA and supported by their morphology. Because they have much of their ecology in common with insects, and their earlier inclusion among Insecta, they will be discussed among these aquatic insect subchapters.

The **Collembola** have the simplest life cycle, one in which the hatchling is a miniature of the adult. The immature stage is known as a **nymph**. Their life cycle consists of **egg/embryo**, **nymph**, and **adult**. The **Collembola** hatch from their egg casing and look like the adults, perhaps in somewhat different proportions; they

continue to increase in size without changing their basic form as they become adults.

Figure 4. **Collembola *Arthropleona oruarangi***, a group of "pre-insects" that are born looking like little adults. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Hemimetabolous Insects (Hemimetabola)

Nymphs

Among the aquatic insects, this group includes the true bugs (order **Hemiptera**), a group that lacks gills in all stages. The **Hemiptera** are **hemimetabolous** insects and thus lack the pupal stage (familiar to most people as the chrysalis of butterflies). Instead, they have only the **egg**/**embryo** (Figure 8), **nymph** (including **naiads** in the other hemimetabolous orders), and **adult**. [The **holometabolous** insects, on the other hand, have an **egg**/**embryo**, **larva**, **pupa**, and **adult** (**imago**).]

Naiads

Those orders with obligate aquatic immature stages that do not resemble the adults, but that do not pass through a second stage as a pupa before becoming an adult, have an aquatic stage known as a **naiad**. The **naiad** is a specialized nymph stage known only among aquatic insects and occurs in the orders **Plecoptera** (Figure 5, Figure 73, Figure 74, Figure 77), **Ephemeroptera** (Figure 6), and **Odonata** (Figure 7). The naiad usually differs from the adult in having some form of gills to aid in gaining oxygen in the aquatic environment. When it is time for the adult to emerge, these insects climb to the surface or out of the water, often on an emergent plant, and often hang vertically while they climb out of their naiad **exoskeleton** (Figure 5). The shed exoskeleton is the **exuvia** (pl. **exuviae**; Figure 5). In the **Ephemeroptera**, the emergent stage is a subadult known as a **subimago** (Figure 6). This subimago goes through one additional moult to become the adult (**imago**).

Holometabolous Insects (Holometabola)

The remaining orders of aquatic insects are **holometabolous** and have what is known as **complete metamorphosis**. These insects have four life cycle stages: **egg**/**embryo** (Figure 8), **larva** (Figure 1), **pupa** (Figure 9), **adult** (**imago**; Figure 10). The larva stage looks nothing like the adult. It is familiar to most people in the moths and butterflies as the caterpillar. The larva is a worm-like creature, with or without legs, or in some cases with prolegs that are of soft tissues. The aquatic larvae have gills in many taxa, but not in others. Some have fleshy legs with hooks at the posterior end.

Figure 5. **Plecoptera** exuvia. Photo by Jason Neuswanger at <Troutnut.com>, with permission.

Figure 6. ***Baetis*** male subimago emerging to adult. Photo by Jason Neuswanger at <Troutnut.com>, with permission.

Figure 7. ***Enallagma*** damselfly naiad. Photo by Tom Murray, through Creative Commons.

The **pupa** is usually a stationary phase (known as a chrysalis in butterflies). As the pupa develops, the larva develops a chitinous outer covering that has the imprint of parts like wings and antennae. The insect is likely to be dormant or in **diapause** (in insects, period of suspended development, especially during unfavorable environmental

conditions) during its pupal stage, providing it reprieve from winter's cold or tropical drought. But during this time the insect goes through a number of changes in both form and physiology. When the insect has matured into an adult and conditions are right for its emergence, it breaks out of the pupa. In most cases, those that spend their larval lives in the water emerge into the atmosphere, spending their adult lives as terrestrial organisms (except in most of the beetles).

Figure 8. Emerald dragonfly with eggs. Photo by Bob Armstrong, with permission.

Figure 9. **Chironomidae** (midge) pupa. Photo by Bob Henricks, with permission.

Figure 10. **Chironomidae** adult male. Photo by Roger S. Key, with permission.

The holometabolous insect orders that live among bryophytes include **Coleoptera**, **Trichoptera**, **Megaloptera**, **Neuroptera**, and **Diptera**.

Adaptations to Aquatic Bryophyte Life

Bryophyte dwellers might benefit from several behavioral and structural adaptations to make life among the bryophytes easier. They need to be able to gain sufficient oxygen (Hynes 1970), to move about freely, to avoid being pulled out if a predator catches a tail or leg, to avoid being swept away by the current, and to eat the available food. In streams where the water level varies a lot or dries up, they need to have a means to avoid desiccation.

Life Cycle Strategies

Although I would normally discuss structural adaptations first, the life cycle adaptations appear to be the most important ones among the insects. Differing requirements among life cycle stages permit insects to survive from year to year in changing environmental conditions.

Blackstock *et al*. (1993) found the insects in a clear sequence of bryophyte to herbaceous swamp to woody plant community occupying different depth zones in the basin of Pant-y-llyn, Wales. These changes, on a large scale, require a degree of mobility on the part of the insect inhabitants as the habitat changes from aquatic to terrestrial seasonally. But even more permanent aquatic habitats have their down times. Success for an aquatic insect means having a strategy to survive during stages when the habitat is dry (Blackstock *et al*. 1993), too cold, or too hot.

To understand the role of bryophytes in the life of their insect inhabitants, one must understand these life cycles. Only twelve orders of insects plus the **Collembola** (Figure 4) are generally considered to have aquatic members, but even these aquatic members typically live out of the water during part of their lives (Thorp & Covich 1991; Ward 1992). Since most of the aquatic insects live in the water in immature stages, an understanding of these stages is necessary to understand fully how bryophytes are so important for them.

Danks (1991) points out that we can understand insect life cycle adaptations best by understanding the options. These include the choices (evolutionarily) to develop or to enter **diapause** (period of suspended development) and to grow rapidly or grow slowly. These developmental options respond to photoperiod and temperature, among other things (Danks 1991; Zwick 1996). Because of dependency on these cues, eggs of some stoneflies are able to remain in the sediments for years, providing a "seed bank" (Zwick 1996). The choices that have been programmed into the life cycle impact the life span of the insect.

Eggs (Figure 8) are an important stage for insects with a terrestrial adult stage and aquatic immature stage(s). The term egg is used somewhat loosely, referring to both the unfertilized egg and the embryonic stage that remains within the egg "shell," indicated herein as **egg/embryo**. Most of these insects lay their eggs in the water, so a substrate that anchors and protects them from both flowing water and predation is important. Even such free-swimming insects as the dragonfly ***Sympetrum*** (Figure 11) in the **Odonata** sometimes lay their eggs in plates on moss

growths, securing the eggs and hatchlings (Figure 12) (Wesenberg-Lund 1943).

Figure 11. ***Sympetrum sanguineum*** mating. Photo by Qartl through Creative Commons.

Figure 12. ***Sympetrum striolatum*** egg-laying among grasses and mosses. Photo by Hugh Venables through Creative Commons.

Some of the aquatic insects live in immature stages in the water for more than one year (Danks 1992; Ulfstrand 1968b). These extended lives may result from slow development, long or repeated dormancy, or adults that live a long time (Danks 1991, 1992). Others, in particular the mayflies (**Ephemeroptera**), may live for only one day as adults (Figure 13), just long enough to mate and lay eggs, but can spend about one year in the naiad stage in the water. The long life cycles are usually coupled with several factors, including cold, unpredictable temperatures, unreliable or low quality food supplies, natural enemies, and large adult size. Life cycle traits relate strongly to the predictability of the environment where the insect lives and the environmental signals that are provided (Danks 2006). But Danks cautions that much more detail is needed to understand these life cycle patterns in insects.

Figure 13. ***Callibaetis ferrugineus*** subimago. Photo by Jason Neuswanger, with permission.

Radford and Hartland-Rowe (1971) examined the life cycles of stream insects from Alberta, Canada. Several of these represent genera [***Nemoura***/***Zapada***/***Prostoia*** (Figure 14), ***Ephemerella***/***Drunella*** (Figure 15)] that are common among bryophytes. Of these, ***Prostoia*** (=*Nemoura*) ***besametsa*** (see Figure 16) and ***Drunella*** (=*Ephemerella*) ***coloradensis*** (Figure 17) are characterized as fast seasonal types. But in the same family, ***Zapada*** (=*Nemoura*) ***cinctipes*** (Figure 18), ***Z. columbiana*** (Figure 19), ***Z. oregonensis*** (Figure 20-Figure 21), and ***Drunella doddsii*** (Figure 22) are slow seasonal types. None of these species has more than one brood per year except ***Zapada cinctipes***, which has two. Temperature is important in determining growth rate in these species.

Figure 14. ***Nemoura*** sp. naiad, a genus with both fast and slow development. Photo by Bob Henricks, with permission.

Figure 15. ***Ephemerella invaria*** naiad, a genus with both fast and slow development. Photo by Bob Henricks, with permission.

Figure 16. ***Prostoia*** naiad, a common bryophyte dweller. Photo by Jason Neuswanger, with permission.

Figure 17. ***Drunella coloradensis*** naiad, having a fast seasonal type of development. Photo by Bob Henricks, with permission.

Figure 18. ***Zapada cinctipes*** naiad. Photo by Bob Armstrong, with permission.

Figure 19. ***Zapada columbiana*** adult on snow, emerging in winter. Photo by Jason Neuswanger, with permission.

Figure 20. ***Zapada oregonensis*** naiad showing gills. Photo by Jim Moore, through Creative Commons.

Figure 21. ***Zapada oregonensis*** adult. Photo by Jim Moore, through Creative Commons.

Figure 22. ***Drunella doddsii*** naiad, having a slow seasonal type of development. Photo by Bob Henricks, with permission.

Since insects have little tolerance for low temperatures (Dunman *et al*. 1991; Moore & Lee 1991), they must spend winter in a way that avoids the dangers of freezing (Ramløv 2000), as will be discussed in more detail below. It is this need to avoid freezing that forces some insects to spend part of their lives in the water. Bryophytes provide a habitat that helps them to cope with this watery habitat.

As Danks (1991) points out, the life cycle strategies provide options that facilitate survival: develop or enter diapause; grow rapidly or grow slowly. These are typically under the control of such environmental parameters as temperature and photoperiod.

Life Cycle Cues

As already stressed, changes in life cycle phases are often necessary to survive changing weather conditions as the seasons change. Danks (1999) pointed out that life cycles are influenced by climate severity, seasonality, unpredictability, and variability. Some insects solve the unpredictability and variability problems by having flexible life cycles. These modifications can be determined by factors such as food availability and temperature. Danks (1991) points out that various stages in the life cycle are used in combination to adapt the insects to the changes of the seasons in nature.

In cold environments, some of the **Chironomidae** (***Diamesa incallida***; Figure 23) may produce 8-10 generations in a single year, with egg-laying occurring throughout the year (Nolte & Hoffmann 1992). ***Diamesa incallida*** is a hot-spring-dwelling midge that lives in water at 76-80°C, a community where we are not likely to find bryophytes, but it demonstrates the role of temperature and the wide range of capabilities in a family that is common among bryophytes. Some Arctic **Chironomidae** solve the problem of finding a sexually mature mate by negating the need for mating and being **parthenogenetic** (producing offspring without fertilization) (Langton 1998).

Figure 23. ***Diamesa*** (**Diptera**) pupal exuvium, a genus that may produce 8-10 generations in a single year. Photo by Will Bouchard, with permission.

Shama and Robinson (2009) demonstrated that an alpine caddisfly (***Allogamus uncatus***, a bryophyte dweller) in Switzerland responded to late season photoperiod cues by accelerating development, but the species showed adaptive plasticity in response to season length, making responses different among populations with only small geographic differences. Furthermore, the responses of the two sexes can differ (Shama & Robinson 2006).

On the other hand, the bryophyte-dwelling caddisfly ***Limnephilus externus*** (Figure 24-Figure 26) did not make developmental adjustments in response to diet supplementation, although it did grow to a larger size (Jannot *et al*. 2008). Furthermore, this caddisfly was unable to adjust to pond drying, responding by reduced growth rates and delayed development. This indicates the danger of an unpredictable environment for the aquatic insects.

Figure 24. ***Limnephilus externus*** larva in case. Photo by Wendy Brown <Gunnison Insects>, with permission.

Figure 25. ***Limnephilus externus*** adult, a caddisfly that does not adjust its development in response to food supplements. Photo by Jason Neuswanger, with permission.

Figure 26. ***Limnephilus externus*** larva showing abdominal gills. Photo by Wendy Brown <Gunnison Insects>, with permission.

In unpredictable or unstable environments, flexibility in the life cycle is important (Brittain & Saltveit 1989). Knispel *et al*. (2006) found that the bryophyte-dwelling mayfly ***Baetis alpinus*** (Figure 27) in the Swiss floodplains has synchronous egg development with high hatching success. By developing faster in warmer habitats it is able to hatch when conditions are favorable in the autumn. Long development time and delayed hatching permit success in unpredictable habitats in the cold glacial conditions. The mayfly ***Rhithrogena*** *nivata* (see Figure 28) has a long incubation period; the timing of hatching and glacial discharge conditions determine the success of development. This plasticity permits it to live in the very unstable, cold habitats that are limiting to other species.

Figure 27. ***Baetis alpinus*** naiad, a mayfly with synchronous egg development that promotes high hatching success. Photo by Andrea Mogliotti, with permission.

Many insects have developmental cues similar to those of plants. These include degree-days (calculated by taking the average of the daily maximum and minimum temperatures compared to a base temperature necessary for growth by the species). As in many plants, degree days may be important in determining the rate of development. For example, the mayfly ***Leptophlebia cupida*** (Figure 29) in the Bigoray River, Alberta, Canada, has only one reproductive period each year (Clifford *et al*. 1979). Clifford *et al*. (1979) found that degree days of water temperature was more important than number of days for development, with 34 instars being produced in the laboratory at 20°C. That number is most likely plastic in response to environmental conditions.

Figure 28. ***Rhithrogena impersonata*** naiad, a genus in which some species have life cycle plasticity that depends on local weather. Photo by Donald S. Chandler, with permission.

Figure 29. ***Leptophlebia cupida*** naiad, a species with only one reproductive cycle per year. Photo by Jason Neuswanger, with permission.

For aquatic insects, the temperatures are much more tempered than in the terrestrial environment. In a study of 95 aquatic species, Pritchard *et al*. (1996) found that only 4 of 92 possible comparisons among **congenerics** (members of same genus) demonstrated significant differences in degree of cold adaptation. All **Odonata** (damselflies and dragonflies), 71% of **Diptera** (true flies), and 81% of **Ephemeroptera** (mayflies) had significant slopes indicating that they were warm adapted. They suggested that the **Plecoptera** are cold-adapted species that may use the egg stage to survive when the temperatures are too high.

In the stonefly family **Leuctridae**, commonly represented among bryophytes, the length of the naiad stage depends on the temperature. In ***Leuctra ferruginea*** (Figure 30) those individuals living in the coolest streams required two years for their life cycle, whereas those in the warmest waters were able to complete the life cycle in one

year (Harper 1973). The **Leuctridae** (Figure 30) and **Nemouridae** (Figure 14) are both common at the cooler upstream stations in Southern Ontario. Six species of the stonefly ***Isogenoides*** (Figure 31) from Colorado, USA, a genus also known from mosses, varied in hatching time both among the species and within some species (Sandberg & Stewart 2004). In one species the eggs hatched over an extended period of time, stopped hatching for the winter, then resumed hatching in May-June the following year. Some eggs even survived and hatched two years later. In one species, a summer diapause was needed before the eggs would hatch. Members of the genus required three months to four years before hatching.

Figure 30. ***Leuctra ferruginea*** naiad, a stonefly that has modified its life cycle to suit the climatic conditions. Photo by Tom Murray at BugGuide.

Figure 31. ***Isogenoides hansoni*** naiad, in a genus with moss-dwelling members in which life cycles vary both between and within species. Photo by Bob Henricks, with permission.

Temperature Relations

As already noted, temperature plays an important role in determining when life cycle stages occur. Freezing, desiccation, and anoxia are all lethal among aquatic insects, from egg to adult (Lencioni 2004). When in the aquatic habitat, these three factors are related, with ice preventing the renewal of oxygen, and ice crystals drawing water from the cells, causing desiccation. Some of the aquatic insects enter **diapause** during winter. This usually requires storage of food as glycogen and lipids, hormonal control, and depression or suppression of oxidative metabolism with mitochondrial degradation.

But the mosses themselves seem to present a relatively constant temperature. Thorup (1963) considered the temperature among mosses in springs to be so constant that it would not provide the developmental temperature point needed to trigger changes in stages. Correlated with the moss habitats in springs was an insect life cycle with only one generation per year.

Overwintering

Duman *et al*. (1991) defined two physiological mechanisms by which insects survive winter: freeze tolerance and freeze avoidance or freeze resistance (see also Ramløv 2000). Aquatic insects have only limited ability to survive at temperatures below freezing (Moore & Lee 1991). They can supercool to only -3 to -7°C and only some members in the order **Diptera** are known to be freeze tolerant. The adults seem to be somewhat more cold tolerant. Thus this is a group of insects for which aquatic habitats that do not freeze provide them with an escape to suitable temperatures for the winter. What is fascinating is the plasticity of their responses. Duman *et al*. (1991) found that not only do different populations of the same species exhibit different overwintering mechanisms, but that even the same population may change its overwintering mechanism from year to year.

Because of their need for warmer temperatures in immature stages than that needed by terrestrial insects, most of the aquatic insects spend their egg and immature stages in the water. In fact, warm-water insects avoid the freezing dangers of winter by surviving as eggs. This is particularly true for the blackflies (**Simuliidae**; Figure 51-Figure 53) (Hynes 1970).

Insects rarely spend their entire lives in the water, but some spend larval stages there, pupal stages on land, then return to the water as adults, as in many **Coleoptera** (beetles). Others, particularly some of the **Trichoptera** (caddisflies) overwinter as adults. In fact, some even emerge mid-winter in cold climates. And the adult stonefly ***Zapada cinctipes*** (**Nemouridae**; Figure 18) re-enters the water when air temperatures drop below freezing (Tozer 1979). However, the stream chironomid ***Diamesa mendotae*** (Diptera; Figure 32-Figure 33) does things quite differently – its freeze tolerance is actually greater in the larval (stream) stage (Figure 33). Although it has a larval super-cooling-point (SCP) temperature of -7.4°C and pupal SCP of -9.1°C, compared to -19.7°C for the adults (Bouchard *et al*. 2006), the larvae of ***D. mendotae*** are freeze tolerant, with a lower lethal temperature (99% dead) of -25.4°C, ~10°C lower than their minimum super cooling point (-15.6°C). They change from freeze tolerant as larvae to freeze intolerant as adults! Nevertheless, the adults are able to tolerate cold temperatures sufficiently to mate on the snow (Ferrington *et al*. 2010). Furthermore, they can survive under the snow for extended periods of time (Anderson *et al*. 2013).

The often moss-dwelling ***Serratella ignita*** (Figure 60) overwinters from late summer until late the next spring as an egg (Arnold & Macan 1969). On the other hand, the mayfly ***Ameletus inopinatus*** (Figure 34) and stonefly ***Leuctra hippopus*** (Figure 35), a stony bottom dweller, do the most developing in the naiad stage while their stream is iced over, at least in northern Sweden (Ulfstrand 1968b). The low temperatures slow, but usually do not stop, development and growth.

Figure 32. ***Diamesa mendotae*** adult on snow. Permission to reproduce given by Leonard Ferrington on behalf of the Chironomidae Research Group at the University of Minnesota.

Figure 33. ***Diamesa mendotae*** larvae alive in Petri dish after freezing. Permission to reproduce given by Leonard Ferrington on behalf of the Chironomidae Research Group at the University of Minnesota.

Figure 34. ***Ameletus ludens*** naiad, member of a genus where some species develop under the ice in streams. Photo by André Wagner, with permission.

It is interesting that in alpine streams that have snow cover for 6-9 months of the year, taxa richness and abundance of the insects seems to have no seasonal pattern. Nevertheless, the species composition differs significantly from summer to winter. Schütz *et al*. (2001) found two strategies for larval survival. The insects either had to be adapted to the extreme conditions of summer or avoid these by developing during the winter (typical of **Ephemeroptera** and **Plecoptera**).

Figure 35. ***Leuctra hippopus***, a stonefly that develops in Sweden while the stream is iced over. Photo by Niels Sloth, with permission.

But ice is also a good insulator, so those insects living on the bottom of lakes and ponds are usually able to avoid lethal low temperatures there. Such insects as the **Chironomidae** (Figure 90) typically live in sediments where oxygen content is low. Cold water holds more oxygen, and since these organisms are adapted to low oxygen conditions, there is sufficient oxygen in the cold water. Some **Chironomidae** and **Trichoptera** (Figure 83) actually occur in ice and frozen sediment, as noted in a north Swedish river (Olsson 1981). Olsson found that 80-100% of these frozen insects survived thawing. **Chironomidae** survived exposure to -4°C for five months. Danks and Oliver (1972a) found that in the Arctic **Chironomidae** that overwinter are mature larvae and are ready to emerge as soon as the winter season is over. They take advantage of the warm sun by emerging in the middle of the day when the water temperature is highest (Danks & Oliver 1972b).

It is interesting that **Plecoptera**, **Ephemeroptera**, **Trichoptera**, **Diptera**, and **Coleoptera** have all been recovered alive from **anchor ice** (submerged ice anchored to the bottom; Figure 36). Anchor ice can encase bryophytes as well, and when it breaks loose, it can take the entire patch of bryophytes with it. Hence, it would likewise take all the insect inhabitants as well, moving them downstream to a new location.

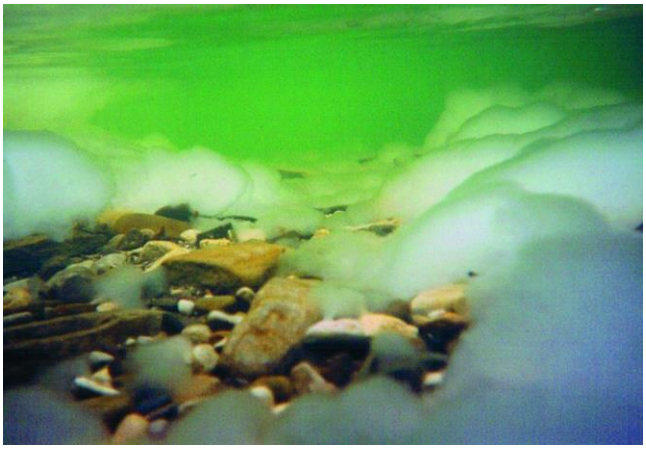

Figure 36. Anchor ice, Alberta, Canada, visible here as cloud-like mounds of ice attached to the rocks under water. Courtesy of Pacific Northwest National Laboratory.

Structural

Hynes (1970) summarized the adaptations of stream insects to include flattening, streamlining, friction discs, close application to the surface of stones, and in some the presence of hydraulic suckers. But many of these adaptations pertain to a life on rocks or other relatively smooth substrate. Such characters as flattening, friction discs, close application to the surface, and hydraulic suckers are of little value among the chambers of a bryophyte mat. This leaves us with only one adaptation from his list, that of streamlining (Figure 37), present in the stoneflies [**Plecoptera: Leuctridae** (Figure 37), **Capniidae** (Figure 38), **Chloroperlidae** (Figure 39), and some **Gripopterygidae** (Figure 40)], and mayflies [**Ephemeroptera: Leptophlebiidae** (Figure 41) and **Baetidae** (Figure 45)] – all known from bryophytes. Others have retained the dorsi-ventral flattening, but it is better described as compressing (Figure 42) since these insects do not quite fit the definition of flat. And compression is useful among bryophytes. Other bryophyte adaptations include small size, attachment hooks, and gill covers or gills absent (Glime 1968).

Figure 39. **Chloroperlidae** naiad. Photo by Bob Henricks, with permission.

Figure 37. ***Leuctra laura*** naiad showing streamlining. Photo by Tom Murray at BugGuide, through Creative Commons.

Figure 40. ***Zelandobius illiesi***, a stonefly naiad with streamlining. Photo by Stephen Moore, Landcare Research NZ, with permission.

Figure 38. ***Allocapnia*** sp. naiad showing streamlining. Photo by Bob Henricks, with permission.

Figure 41. ***Paraleptophlebia mollis*** naiad, a mayfly illustrating streamlining. Photo by Tom Murray through Creative Commons.

Figure 42. ***Ephemerella*** naiad showing dorsi-ventral compression. Photo by Bob Henricks, with permission.

Bryophyte-dwelling insects therefore do not necessarily have the same adaptations as stream insects in general. Streamlining helps, but does not need to be as severe. Steinmann (1907, in Muttkowski 1929) found that about 30% of the bryophyte-dwelling taxa were streamlined. But in the streams of the Appalachian Mountains, streamlining was not common (Glime 1994). For example, the common bryophyte-dwelling mayfly ***Ephemerella*** (Figure 42) is neither flattened nor streamlined (Arnold & Macan 1969), but has a shape more like a terrestrial insect – it is dorsiventrally compressed.

Small size is also an advantage and seems to be the most important characteristic of bryophyte dwellers. Bryophytes provide small spaces where invertebrates can hide, but these same small spaces limit the sizes of the organisms that can occur there. This explains why bryophytes tend to harbor small species and hatchling insects (Figure 43).

Figure 43. ***Taeniopteryx*** naiad on the edge of a Syracuse watch glass, demonstrating the small size of this bryophyte dweller. Photo by Bob Henricks, with permission.

Dudley (1988) suggested that while the complex structure of bryophytes might interfere with attachment by larger larvae, it reduces frequency of encounter between such predators and the small insect inhabitants. In the Appalachian, USA, streams 70% of the bryophyte dwellers were less than 6 mm long (Glime 1994). Egglishaw (1969) found that a higher proportion of smaller animals occurred on mosses than on stones of riffles. In ***Leuctra inermis*** (see Figure 37, Figure 44), ***Baetis rhodani*** (Figure 45), and ***Isoperla grammatica*** (Figure 46) it was the young (small) stages that occurred among the bryophytes.

Figure 44. ***Leuctra inermis*** adult, a species whose early naiad instars live among mosses in riffles. Photo by James K. Lindsey, with permission.

Frost (1942) remarked that because of the very young and thus small specimens, identification was both difficult and questionable, forcing identification to genus or subfamily only. Glime (1994) found that ***Baetis*** sp. was present among mosses (10 per gram) in summer, but were absent in later stages when the larger naiads were present among rocks in the stream bed. Others that moved out of the bryophytes when they got larger were the cranefly ***Limonia*** (Figure 47), stonefly ***Taeniopteryx*** (Figure 48), and caddisflies ***Lepidostoma*** (Figure 49) and ***Neophylax*** (Figure 50). Similar migration of older stages occurs in Europe (Thienemann 1912; Carpenter 1927; Egglishaw 1969).

Figure 45. ***Baetis rhodani***, a mayfly that starts its life among bryophytes, but moves out as it grows larger. Photo by J. C. Schou through Creative Commons.

Figure 46. ***Isoperla grammatica*** naiad showing dorsiventral compression. Photo by Dragiša Savić, with permission.

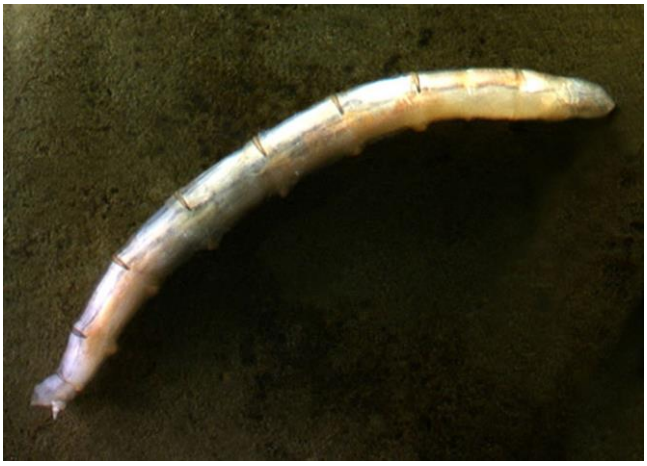

Figure 47. ***Limonia*** sp., an insect that lives among bryophytes until it gets too large; then it moves out. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 48. ***Taeniopteryx*** sp. naiad, a moss-dwelling stonefly that moves to substrates with more space when it gets larger. Photo by Bob Henricks, with permission.

Figure 49. ***Lepidostoma*** larva and case, a caddisfly that moves out of the bryophytes as it grows. Photo by Bob Henricks, with permission.

Figure 50. ***Neophylax atlanta*** larva and case, a caddisfly that moves from bryophytes to other substrates as it grows. Photo by Bob Henricks, with permission.

Attachment

While torrents bring much-needed oxygen, they also are treacherous, dislodging the insects and sweeping them downstream. Black flies (**Simuliidae**; Figure 51-Figure 53) are among the best adapted of the aquatic insects for surviving this torrential onslaught, living on the upper surface of the bryophyte mats (Niesiolowski 1979). On both rocks and mosses, they are able to anchor themselves with a circle of hooks on the rear of the abdomen (Figure 51) (Arnold & Macan 1969). Furthermore, they manufacture a silken thread that they lay down on their substrate surface as an anchor. When they do become dislodged by chance or choice, they have a tether that prevents them from travelling too far and helps them to gain a "foothold" on their new downstream substrate. Those hooks, on both the abdomen and the single proleg foot (Figure 52), enable blackfly larvae to grab onto the silken mat (Figure 53) they have made. They are able to use these same two sets of hooks to move along their silken mat like inch worms.

Figure 51. **Simuliidae** larva showing anal hooks. Photo by Bob Henricks, with permission.

Figure 52. ***Prosimulium mixtum*** larva showing single proleg. Photo by Tom Murray at BugGuide, through Creative Commons.

Figure 53. Simuliidae larvae on leaf where silken threads form a mat, aiding in attachment. Photo by Bob Henricks, with permission.

The net-spinning caddisflies (**Hydropsychidae**) accomplish anchorage by a pair of hooks on the posterior end (Figure 54), a modification of many caddisflies for pulling themselves into their cases. But among the free-living caddisflies like the **Hydropsychidae** and **Rhyacophilidae** [*e.g.* ***Rhyacophila dorsalis*** (Badcock 1949)], these hooks (Figure 55) serve as anchors among the bryophytes. Other insects have hooked claws that help them to clamber among the bryophytes, including the beetles (*e.g.* **Elmidae**, Figure 56) and some mayflies (e.g. **Ephemerellidae,** Figure 60) and stoneflies [*e.g.* ***Nemoura*** (Figure 57) and ***Acroneuria*** (Figure 58)]. Others, like the **Chironomidae**, achieve anchorage by nestling at the leaf bases (Figure 59) where little flow occurs.

Figure 54. ***Hydropsyche*** larva showing posterior prolegs with hooks that provide anchorage. Photo by Bob Henricks, with permission.

Figure 55. ***Rhyacophila fuscula*** larva showing anal hooks that serve as anchors. Photo by Jason Neuswanger, with permission.

Figure 56. **Elmidae** adult showing clawed feet that help it climb among mosses. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 57. ***Nemoura*** sp. naiad showing hooked claws. Photo by Bob Henricks, with permission.

Figure 58. ***Acroneuria abnormis*** naiad showing hooked claws. Photo by Tom Murray, through Creative Commons.

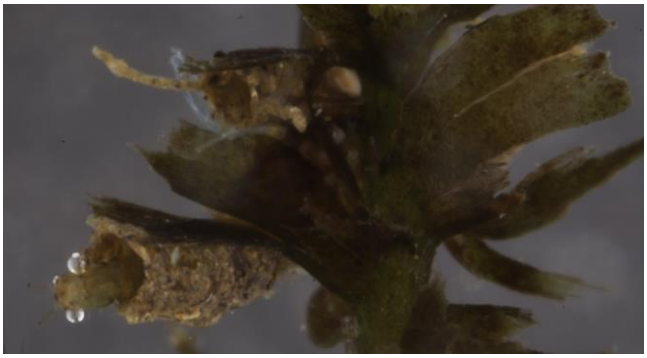

Figure 59. ***Rheotanytarsus exiguus*** (**Chironomidae**) group nestled in leaf bases. This species makes a tube where it lives. Photo by D. N. Bennett, with permission.

Hora (1930) and Ward (1992) suggested that backward pointing dorsal spines (Figure 60-Figure 64) of some moss dwellers, *e.g.* the **Gripopterygidae** (Figure 61), are adaptations to reduce chances of being swept downstream. Illies (1961) reported large dorsal spines on a moss-dwelling stonefly from Chile. Similar (but smaller) spines are known on the common moss-dwelling mayfly ***Ephemerella ignita*** (Figure 60; Hynes 1970). Even **Diptera** larvae [*e.g.* **Psychodidae** (Figure 62), **Tipulidae** (Figure 63-Figure 64)] can have backward-directed spines. But the tipulid larvae of ***Phalacrocera*** (Figure 63) and ***Triogma*** (Figure 64-Figure 65) have such projections and live mostly among semiaquatic mosses where there is no flow to dislodge them. This suggests the spines may serve either as camouflage or as trapping devices to prevent would-be predators from pulling them out of the moss mat.

Figure 60. ***Serratella ignita*** naiad showing spinelike structures on the dorsal side of the abdomen. Photo by J. C. Schou through Creative Commons.

Figure 61. ***Zelandobius illiesi*** (**Gripopterygidae**) showing backward-pointing dorsal spines. Photo by Stephen Moore at Landcare Research, NZ, with permission.

Figure 62. ***Clogmia albipunctata*** (Psychodidae) larva with backward pointing spines. Photo by Ashley Bradford through Creative Commons.

Figure 63. ***Phalacrocera replicata*** larva showing green color and projections that help to camouflage it among mosses. Photo from Wikimedia Commons.

Figure 64. ***Triogma*** larva showing backward pointing spines. This larva also has cryptic coloration that makes it difficult to detect among the bryophytes. Photo by Janice Glime.

Figure 65. ***Triogma trisulcata*** larva among ***Sphagnum*** showing appendages that mimic moss leaves. Photo by Walter Pfliegler, with permission.

Gill covers help to keep silt from accumulating among the gills, since the mosses often reside where they collect large amounts of silt. The gill covers can also be used to fan the fills, hence moving the water and facilitating oxygen exchange. Gill covers are common among the **Ephemeroptera**, especially in the **Ephemerellidae** (Figure 66-Figure 67) and **Caenidae** (Figure 68).

Figure 66. ***Drunella grandis*** naiad showing raised gill covers and fimbrillate gills. Photo by Bob Newell, with permission.

Figure 67. ***Serratella*** gills showing gill covers and fibrillate gills on successive abdominal segments. Photo by Bob Henricks, with permission.

Figure 68. ***Caenis latipennis*** naiad showing large gill covers over the dorsal abdomen. Photo by Donald S. Chandler, with permission.

Behavioral

Behavior often permits organisms to change their locations, providing the best location available to them as the season changes and required resources are in new locations. Behavioral adaptations can help them capture prey, avoid being prey themselves, gain sufficient oxygen, avoid being swept away by the current, and escape cool or freezing temperatures.

Bryophytes provide a series of zones (Figure 69) that permit insects to live in the flow regime they require. As will be seen, oxygen can be a limiting factor, requiring some insects to live near the surface of the bryophyte where torrential waters trap oxygen from the air. Hence, these insects require a means of anchorage lest they themselves become part of the torrent. Others are well adapted to the low oxygen levels and live at the base where detritus accumulates and predators seldom venture. But it is advantageous that they can move about and seek the zone within the stream or lake and within the bryophyte community that best meets their needs.

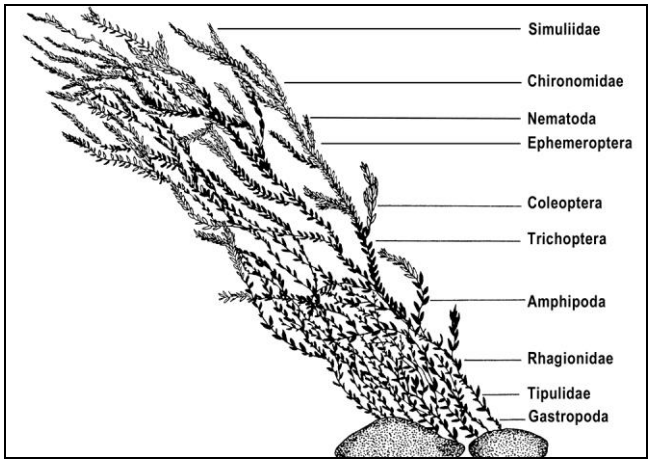

Figure 69. ***Fontinalis*** zonation of insects. Redrawn from Niesiolowski 1979.

Aquatic insects tend to avoid light, exhibiting negative phototaxis (Moon 1940; Shelford 1945). Mayflies, in particular, demonstrate a negative phototaxis, preferring darker locations (Wodsedalek 1911; Gros 1923; Percival & Whitehead 1926). This may account for the presence of some taxa among the darker spaces of mosses, particularly in rapid water where rock surfaces may be highly exposed to light. Others may avoid light to be less conspicuous to their prey. On the other hand, ***Baetis harrisoni*** (Figure 70) chose illuminated stones 112 times compared to 14 for shaded stones, exhibiting strong positive phototaxis (Hughs 1966).

Figure 70. ***Baetis harrisoni*** naiad, a mayfly that prefers illuminated stones. Photo by Helen James through Creative Commons.

Insects often escape adverse conditions in their environments by modifying the environments themselves. Such modifications may include making shelters (Figure 71), excavating, aggregating (Figure 53), forming colonies, and parental actions (Danks 2002). Although all of these actions may be found among aquatic insects, not all of these occur among those living among bryophytes. The bryophyte itself sometimes makes such actions as excavating and making shelters unnecessary. For example, several families of caseless caddisflies live among bryophytes. But the very tiny **Hydroptilidae** may take advantage of the bryophytes for case-building materials.

Figure 71. ***Helicopsyche*** case, made by the caddisfly as a shelter. Photo by Mike Quinn, through Creative Commons.

Oxygen Conditions

Ponds can become quite anoxic in winter when the surface is frozen (Nagell & Brittain 1977). Streams are less likely to become anoxic, but within the bryophyte mat water can be quite quiet and oxygen can be used up quickly by decaying organisms. However, insects have a wide array of adaptations to help them through places and times of anoxia (Hoback & Stanley 2001). For example, 10 Arctic species of **Collembola** (springtails) are known to survive anoxia at 5°C for up to 36 days (Hodkinson & Bird 2004). The mayfly *Cloeon dipterum* (Figure 72) is able to survive 3-4 months in anoxic ponds, and naiads survived up to 155 days at 0°C in the lab (Nagell 1977).

Figure 72. ***Cloeon dipterum***, a mayfly that can survive 3-4 months in anoxic pond water. Photo by Malcolm Storey, through Creative Commons.

As is obvious from previous studies, oxygen relations in the insects are dependent on temperature (Jacob & Walther 1981). More oxygen can dissolve at low temperatures. In fact, oxygen limitations due to temperature are so important that they set the thermal limits in at least some species of aquatic insects (Verberk & Bilton 2011). Furthermore, since smaller insects use less oxygen, large insects may have been an adaptation to excess oxygen in the Carboniferous Era (Verberk & Bilton 2011). Oxygen limitations may explain in part the presence of small insects among the bryophytes, whereas

the larger stages move to rock faces where flow is uninterrupted and able to replenish the oxygen more easily.

Knight and Gaufin (1966) measured oxygen consumption as a function of temperature in two stonefly naiads that associate with bryophytes: ***Hesperoperla pacifica*** (Figure 73) and ***Pteronarcys californica*** (Figure 74). These insects followed the general trend of consuming more oxygen at higher temperatures. This relationship is problematic because gasses are lost from the water at higher temperatures, thus limiting the most available oxygen to winter.

Figure 73. ***Hesperoperla pacifica*** with its pompom-like gills peeking out from the ventral thorax. Photo by Arlen Thomason, with permission.

Figure 74. ***Pteronarcys californica***, probably the largest insect inhabitant of bryophytes. Photo by Bob Henricks, with permission.

Among the common bryophyte dwellers, the mayflies (**Ephemeroptera**) are the least tolerant of low oxygen (Gaufin *et al*. 1974), making them good indicator organisms. These are followed by stoneflies (**Plecoptera**), then caddisflies (**Trichoptera**), flies (**Diptera**), and damselflies (**Odonata**) in that order. Of course there are exceptions within the orders.

Insects living in low oxygen conditions may be adapted by developing enlarged respiratory organs (Figure 75) (Dodds & Hisaw 1924), including enlargement of tracheal gills (Figure 76) (Golubkov *et al*. 1992). Behavior can play an important role, with most species moving away from the anoxic sediments when oxygen becomes limiting (Kolar & Rahel 1993). But moving is not always a good choice because it can result in being swept into the current and usually means becoming more visible, hence being more obvious to predators. The movement itself attracts attention through the excellent vision in the well developed eyes of other arthropods and fish.

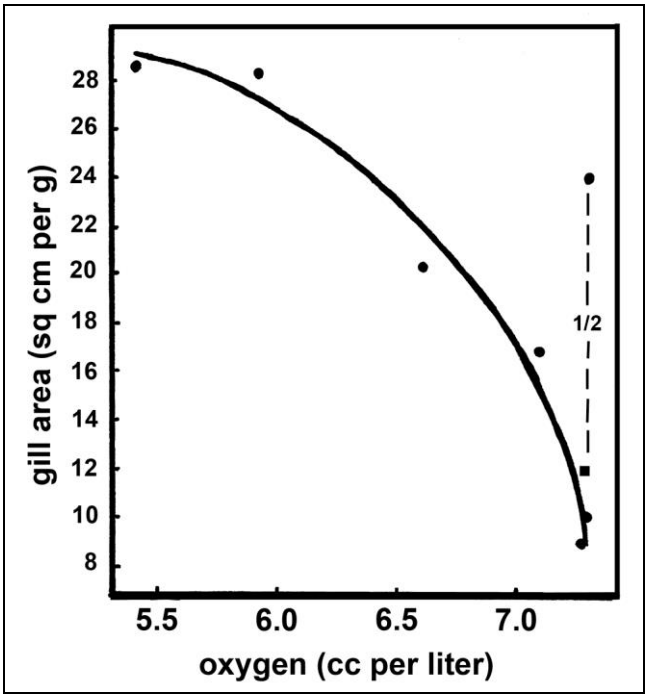

Figure 75. Relationship of gill size in seven species of **Ephemeroptera** to oxygen availability in aquatic systems. The outlier species on the right is the genus ***Iron***, a genus for which the gills form a suction cup, preventing one side of the gills from functioning in oxygen uptake. Its position when only half the area is used is shown by the square at the base of the dotted line on the right. Redrawn from Dodds & Hisaw 1924.

Gills are a common adaptation to low oxygen, especially in **Ephemeroptera** (Figure 76), **Plecoptera** (Figure 77-Figure 79), and **Trichoptera** (Figure 80). These are placed in almost every position (*e.g*. Figure 78), depending on the genus or family, and are useful taxonomic characters in some groups. But they also tend to be protected, between legs or under gill covers. Others have cutaneous breathing – providing the expanse of the insect's surface and avoiding the danger of collecting sediments.

Figure 76. ***Leptophlebia nebulosa*** showing abdominal (tracheal) gills. Photo by Don S. Chandler, with permission.

Figure 77. ***Nemoura*** sp. naiad showing clusters of white thoracic gills at the "neck." Photo by Bob Henricks, with permission.

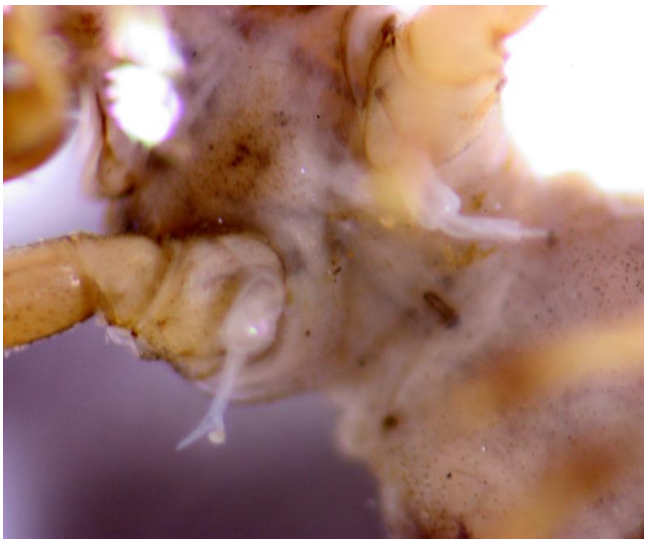

Figure 78. Coxal gills on a winter stonefly. Photo by Bob Henricks, with permission.

Figure 79. ***Acroneuria carolinensis*** naiad showing gills on the ventral thorax. Photo by Tom Murray, through Creative Commons.

Figure 80. ***Hydropsyche*** sp. larva showing gills on ventral side. Photo by Bob Henricks, with permission.

As early as 1907, Babak and Foustka concluded that as the oxygen concentration in the water decreased, movement of the gills of mayflies increased. Dodds and Hisaw (1924) showed a relationship between gill area and oxygen concentration in mayflies. But in the mayfly ***Baetis*** (Figure 45, Figure 70) used for testing, the gills never beat and it seems that they do not use their gills for oxygen consumption in the range of 5.0 to 8.0 cc L^{-1} (Wingfield 1939). Rather, these mayflies live in rapid streams where oxygen concentrations are usually above 4 cc L^{-1} and rapid flow keeps fresh, oxygenated water flowing over the gills. Under these conditions their cuticular respiration is sufficient. Macan (1962) reported on the work of Ambühl (1959). He found that ***Baetis vernus*** was scarce when the current speed was below 10 cm sec^{-1} and increased in relative numbers up to 40 cm sec^{-1}. ***Ephemerella ignita*** (Figure 60) was most common at current speeds of 10-30 cm sec^{-1}.

Movements of another type – undulating the body (Figure 81) or fanning the gills (Figure 82) – can increase the rate of oxygen movement across the gills. Undulations typically begin as oxygen levels are low and are also used for swimming, a second way to gain more oxygen. These undulations are easily seen when high-oxygen-requiring mayflies are brought to the lab and put in quiet water. **Ephemerellidae** species accomplish water movement over their gills by moving the gill covers (Figure 82) up and down, fanning the gills. **Trichoptera** (caddisflies) are able to pump water through their cases (Figure 83) to renew oxygen. Humps and projections maintain space between the larva and its case, permitting water (and oxygen)

movement through the case. But these activities require energy and the insects cannot sustain prolonged use of these behaviors (Hynes 1970).

Figure 81. ***Baetis tricaudatus*** naiad showing the tail and abdomen flipped up in an undulation. Photo by Bob Henricks, with permission.

Figure 82. ***Ephemerella subvaria*** naiad showing four gill covers on each side. Photo by Tom Murray, through Creative Commons.

Figure 83. ***Limnephilus*** sp. showing spacer hump just behind the thorax. Photo by Jason Neuswanger, with permission.

Most of the bryophyte dwellers do not carry oxygen in the air bubble of a **plastron** (Figure 84) or other form of bubble (Figure 85), as done by a number of free-swimming species. However, the plastron mechanism is useful to some of the **Elmidae** (Figure 84), tiny beetles that clamber among the bryophytes (Arnold & Macan 1969). The plastron is much like a diving bell. The insect traps a bubble of air and carries it beneath the water surface. As the insect breathes, it exchanges its CO_2 for the O_2 in the plastron. Oxygen in the water will diffuse into the bubble as the oxygen is depleted, but as the nitrogen leaves the bubble, the bubble shrinks. The same mechanism applies to other types of bubbles such as the one in Figure 85. Eventually the concentration of oxygen in the bubble is too low and the insect must resurface to grab another bubble, or grab one from a photosynthesizing plant, including bryophytes. The collection of bubbles on plants under water is known as **pearling** (Figure 86).

Figure 84. ***Stenelmis crenata*** showing plastron (white area under ventral side). Photo by M. J. Hatfield through Creative Commons.

Figure 85. ***Lancetes angusticollis*** adult from South Georgia clinging to moss. Note the anal air bubble used like a diving bell. Photo by Roger S. Key, through Creative Commons.

Obtaining Food

Feeding strategies include shredders, gatherers, scrapers, and detritus feeders. Venturing away from the protective bryophyte substrate is dangerous because the insects can easily be swept away by the current in streams. Thus, it is not any surprise that many of the insects have adapted strategies that permit them to obtain food without venturing away from their safe site. Many are detritus

feeders, and if they have adaptations to get enough oxygen, they can live in the silt or sand. Others such as the net-spinning caddisflies (Figure 87) and the blackflies (Figure 88-Figure 89) trap their food as it flows by them. The very effective anchorage permits the **Simuliidae** (blackflies) to hang from the rear and expose the head fans (Figure 89) into the current to trap organic particles, including diatoms, for food. Some eat their surrounding homes – the bryophytes.

Figure 86. ***Riccia fluitans*** with pearling. Photo through Creative Commons.

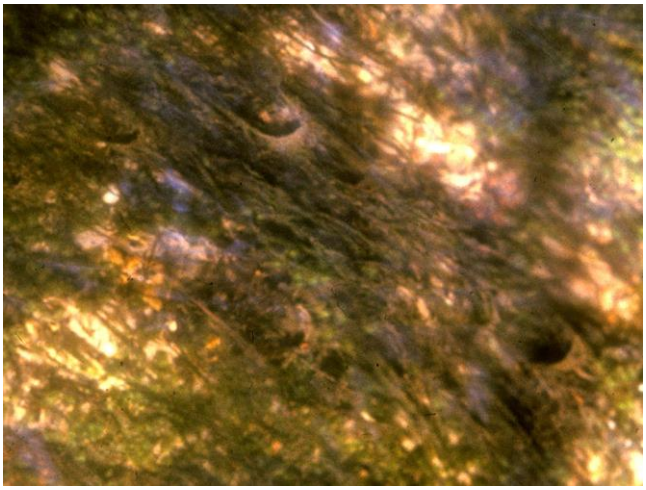

Figure 87. ***Cheumatopsyche*** nets on ***Fontinalis***, trapping detritus and algae that flow by. Photo by Janice Glime.

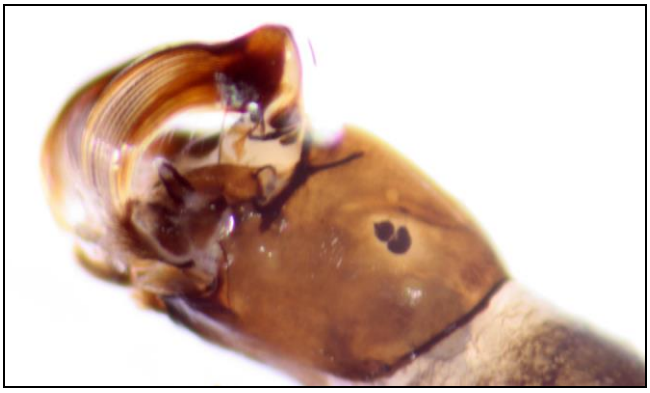

Figure 88. Simuliidae larva head fans closed. Photo by Bob Henricks, with permission.

Figure 89. **Simuliidae** larva showing head fans that are used to capture food. Photo by Bob Henricks.

Others, including some of the net-spinning **Hydropsychidae** (Figure 87), let the bryophytes do the trapping and eat the periphyton and detritus within the bryophyte mat. I base this assumption on finding many more larvae than nets among the mosses. The **Chironomidae** (Figure 90) live in leaf bases where detrital matter accumulates, obtaining both protection and food. In any case, the diet of the aquatic stage is usually quite different from that of the adult.

Figure 90. ***Coryneura*** sp. (**Chironomidae**). Photo by Stephen Moore, Landcare Research, NZ, with permission.

Who Lives There?

Aquatic bryophytes in mountain streams typically are replete with insects, crawling about and dining on the detritus and algae in the milieu. They find themselves safely out of the torrent above and tucked away from the view of fish and other predators. It seems like they should have a pretty cushy life.

When I began my studies on insects living among bryophytes in Appalachian Mountain, USA, streams, few studies were available for comparison, and most of those

were from Europe. Like the development of keys for bryophytes, the development of keys for aquatic insects lagged way behind what was needed. To further complicate the problem, many of the insects had been described from adults, but studies to link the immature aquatic stages to their adults were lacking for many. It was the insect version of the early ***Takakia*** classification problem.

As I delved into the many more recent papers to prepare this chapter, I found many unfamiliar names of genera, only to discover that those familiar genera from nearly 50 years ago had gone through reclassification and were now represented under multiple new names, especially at the generic level. To further complicate these changes in generic concepts, the insects, like the bryophytes, comprise many microspecies. Limited dispersal distances for short-lived adult stages, mountain and land barriers, and disconnected stream or lake systems all contributed to the isolation needed for development of differences in physiology, behavior, phenology, and morphology (see for example Hughes *et al.* 1999; Monaghan *et al*. 2002). As bryologists we are well aware of these problems in classifying things separated by great distances, but for these insects the microspecies differences can be manifest over much shorter distances, a phenomenon that has been recognized in some aquatic bryophytes as well (Glime 1987; Shaw & Allen 2000). Nevertheless, there are lessons to learn from the orders, families, and even the genera as we examine who lives among the bryophytes – and why.

Drozd *et al*. (2009) used pitfall traps to compare invertebrate inhabitants related to bryophytes in the mountain areas (384-1200 m asl) of the Czech Republic. In most cases, the **Collembola** were the most abundant group except for the high number of ants at Podolánky. The numbers differed by bryophyte and moisture level (Figure 92). Insects were highest in the dry litter control (within 2 m of moss area). The lowest numbers were in wet ***Sphagnum fallax*** (Figure 91).

Figure 91. ***Sphagnum fallax*** with capsules, the species with the lowest number of **Collembola** among bryophytes in the mountainous areas of the Czech Republic. David T. Holyoak, with permission.

Drozd and coworkers (2009) considered several caveats in interpreting their results. Some of the invertebrates move about little and would therefore be poorly represented in the pitfall traps. Others that do move about would move easily between the bryophytes and litter, possibly only passing over the bryophytes in their search for food. Others may reside among the bryophytes as transient visitors, seeking escape from a predator or avoiding the desiccation common in more open areas, but returning to the litter habitat when that environment was safe. In any case, insects that met all their needs within the bryophyte mat would be under-represented in the pitfall traps.

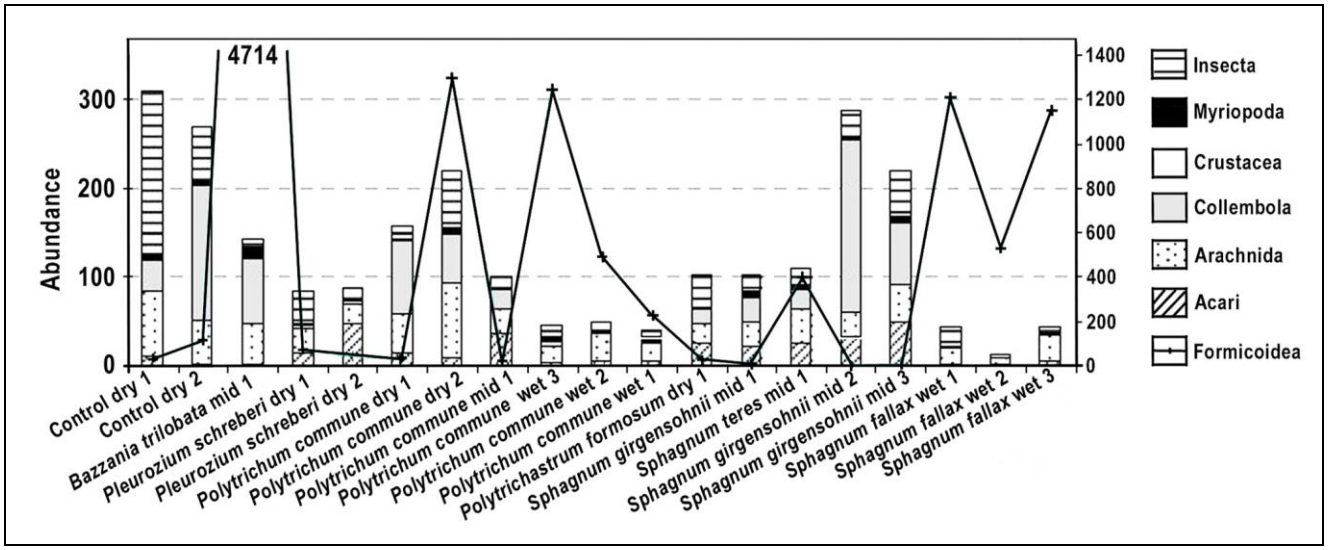

Figure 92. Abundance of taxonomical groups in pitfall traps associated with several species of bryophytes in dry, moist, and wet conditions at five locations in mountains of the Czech Republic. The scale at right is for ant data (**Formicoidea**) from Podolánky. Redrawn from Drozd *et al*. 2009. Controls are litter areas

The insects found among the mosses in streams are mostly **Ephemeroptera** (mayflies), **Plecoptera** (stoneflies), **Trichoptera** (caddisflies), **Diptera** (flies), and **Coleoptera** (beetles) (Needham & Christenson 1927; Wesenberg-Lund 1943; Cowie & Winterbourn 1979; Glime 1994; Gislason *et al*. 2001). But moving about

among stems and leaves of mosses is not easy for the weak-legged or swimming insects in the small spaces. Hence, as already noted, most of the inhabitants are small (Thienemann 1912; Glime 1994; Amos 1999; Drazina *et al*. 2011). This also means that young, immature naiads of **Ephemeroptera** and **Plecoptera** are common (Stern & Stern 1969).

Many species overwinter as eggs on the mosses, then begin their immature lives there. Among the **Diptera**, ***Dicranota*** (Figure 93), ***Atherix*** (Figure 94), and ***Simulium*** (Figure 51-Figure 53) are common at this time; likewise, young **Elmidae** (larvae; Figure 95) are common among the mosses (Thienemann 1912).

Figure 93. ***Dicranota*** larva, a common stream moss inhabitant. Photo by Tom Murray, through Creative Commons.

Figure 94. ***Atherix*** sp. larva, a common dweller among stream bryophytes. Photo by Jason Neuswanger, with permission.

Figure 95. **Elmidae** larva, a common beetle larva among stream bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

In a New Zealand stream, Cowie and Winterbourn (1979) found 44 species of invertebrates, mainly immature stages of insects. The moss ***Acrophyllum*** sp. (Figure 96) hosted the stonefly ***Austroperla cyrene*** (Figure 97), a species of beetle in the **Helodidae** (Figure 98), and a triclad, ***Neppia montana*** (Figure 99); the moss ***Fissidens*** sp. (Figure 100) hosted the stonefly ***Zelandoperla fenestrata*** (see Figure 101), the caddisfly ***Zelolessica cheira*** (Figure 102), a fly in the family **Empididae** (Figure 103), and several species of midges (**Chironomidae;** Figure 90); . The moss ***Cratoneuropsis*** (Figure 104) had only one common taxon, a terrestrial isopod, ***Styloniscus otakensis***, suggesting that the streamside ***Cratoneuropsis*** habitat is more terrestrial than aquatic. In addition to water saturation and flow rates, the ability of mosses to trap detritus was important in determining invertebrate inhabitants.

Figure 96. ***Achrophyllum quadrifarium*** from New Zealand, home to beetles in **Helodidae**. Photo by Bill & Nancy Malcolm, with permission.

Figure 97. ***Austroperla cyrene*** from NZ. Photo by Steve Pawson, permission pending.

Figure 98. **Helodidae** adult, member of a family that lives among leaves of the moss ***Acrophyllum*** sp. Photo from <www.pybio.org>, with permission.

Figure 99. ***Neppia***, an inhabitant of the moss ***Acrophyllum*** sp. Photo by Stephen Moore, Landcare Research, NZ., with permission

Figure 100. ***Fissidens fontanus*** with Amano shrimp in an aquarium. Photo through Creative Commons.

Figure 101. ***Zelandoperla*** sp., an inhabitant of ***Fissidens*** in New Zealand. Photo by Stephen Moore, Landcare Research NZ, with permission.

Figure 102. ***Zelolessica*** sp., an inhabitant of aquatic ***Fissidens*** in New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.

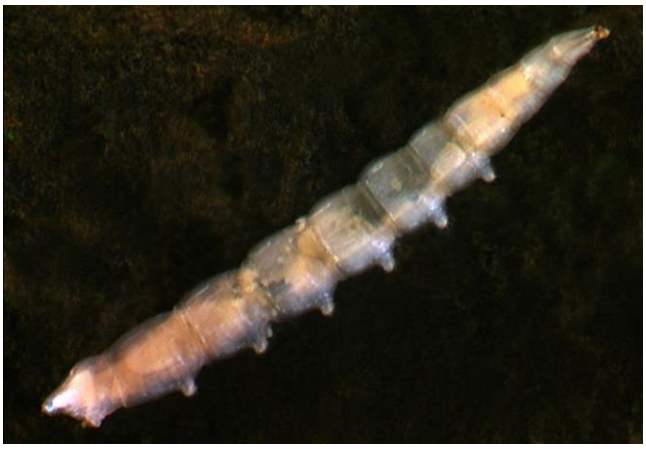

Figure 103. **Empididae** larva, an inhabitant of aquatic ***Fissidens*** in New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 104. ***Cratoneuropsis relaxa***, in a genus that commonly houses isopods but few insects in New Zealand. Photo by Tom Thekathyil, with permission.

Suren (1988) examined faunal assemblages in New Zealand alpine streams, with the stoneflies (**Plecoptera**) ***Zelandoperla*** (Figure 101) and ***Zelandobius*** (Figure 105) and midge larvae (**Chironomidae**; Figure 90) being dominant. The mosses supported 5-15 times as many invertebrates as did the rocky habitats. In addition to these dominant insects, several non-insect invertebrates were dominant.

Figure 105. ***Zelandobius illiesi***, a stonefly genus that is common among alpine stream mosses in New Zealand. Photo by Stephen Moore, Landcare Research NZ, with permission.

One of the interesting questions about bryophyte fauna is whether any species has a unique fauna. So far we have seen little specificity among the other invertebrates. Nevertheless, differences may exist dependent upon the niches of the bryophytes themselves. Some bryophytes occupy fast flow, some occupy areas where they spend part of the year above water, some are deep, and certainly differences exist among growth forms that create differences in the protection they afford. And some **Trichoptera** use liverworts or mosses to construct their cases, forcing them to live with certain species. Coinciding with these differences are the kinds of food the bryophyte habitats provide, again affecting who can survive there.

Paavola (2003) examined the concordance among the macroinvertebrates, bryophytes, and fish to look for possible **surrogates** to describe the system and its state of health. **Surrogates** are groups of organisms that can be used to assess suitability of a habitat for another group of organisms such as fish. When considered across drainage systems, there was strong concordance, but within a single river system that concordance was weak.

Bryophyte locations in the Paavola (2003) study were mainly related to nutrient levels and in-stream complexity, whereas macroinvertebrates correlated with stream size and fish correlated with oxygen levels, depth, and substrate size. But macroinvertebrates also relate to in-stream complexity (Allan 1975; Hart 1978; Trush 1979; Wise & Molles 1979; Williams 1980; Vinson & Hawkins 1998) and to substrate texture (Glime & Clemons 1972). And bryophytes add to that complexity. Some of the genera that inhabit bryophytes are also common in leaf packs – a substrate that provides cover and detritus for food. These include ***Baetis*** (Figure 45), ***Leuctra*** (Figure 30), and **Chironomidae** (Figure 90) (Robinson *et al*. 1998).

Due to differences in growing season, ice-free season, winter severity, available food, and flow regime changes from year to year, the fauna assemblage can also change from year to year. This can result in the temporary disappearance of an entire species, or even an entire order (Milner *et al*. 2006). This disappearance is particularly true for **Plecoptera**. Channel stability is important in determining faunal stability, but a normally stable channel can suffer from heavy rains or flooding during snow melt. And channel stability likewise determines the stability of bryophytes, hence playing a role in the bryophyte fauna.

In my study of the insects inhabiting the bryophytes of mid-Appalachian Mountain streams, I identified 141 species occurring among 10 species of bryophytes in 28 streams, and that does not include the species of the **Chironomidae** (Figure 90), which were identified only to family (Glime 1994). The smallest of the insects occurred on the leafy liverwort ***Scapania undulata*** (Figure 106) and the largest could be found on various species of ***Fontinalis*** (Figure 107). As in many other studies, the most abundant insects were midges (**Chironomidae)**, the stoneflies ***Leuctra*** (Figure 30) and ***Isoperla bilineata*** (Figure 108), and the blackflies (***Simulium tuberosum***; Figure 109).

Figure 106. ***Scapania undulata***, home for the smallest aquatic insects. Photo by Michael Lüth, with permission.

Figure 107. ***Fontinalis antipyretica***, a large moss that houses the largest moss dwellers. Photo by Bernd Haynold Wikimedia Commons.

Figure 108. ***Isoperla bilineata***, a common stream moss dweller in the Appalachian Mountains, USA. Photo by Bob Henricks, with permission.

Figure 109. ***Simulium tuberosum***, a common inhabitant of bryophytes in Appalachian Mountain streams. Photo by Tom Murray, through Creative Commons.

Heino and Korsu (2008) questioned the species-area concept in aquatic systems, examining rocks and bryophyte cover in two river sites. They found only a weak species-area relationship on stream stones. On the other hand, bryophyte biomass was important both in supporting species richness and in increasing number of individuals of stream macroinvertebrates. They suggested that cover was important in increasing number of individuals and that the species richness was a subsequent passive response. The bryophyte biomass can be expected to increase with time, whereas the area of stones will not. The mechanisms that promote these species-area relationships need to be demonstrated experimentally. These could involve food relationships, sampling methods, niche space, flood disturbance, predation refugia, or flow regime.

Specificity

Many streams have only one dominant bryophyte, and others have the species intermingled. These conditions complicate any attempts to determine insect preference. Nevertheless, some specificity seems to exist, but keep in mind that it might be a preference of both insect and bryophyte for the same stream conditions. The caddisfly ***Rhyacophila*** cf. ***invaria*** (Figure 110) was present in 36% of the collections (Figure 118) of ***Platyhypnidium riparioides*** (Figure 111) in mid-Appalachian Mountain, USA, streams, but totally absent among ***Hygroamblystegium fluviatile*** (Figure 112), despite the frequent occurrence of these two mosses in the same streams, often on the same rocks (Glime 1994). ***Rhyacophila carolina*** (Figure 1) reached its greatest abundance in clumps of the leafy liverwort ***Scapania undulata*** (Figure 106; Figure 118).

Less distinct preferences occurred in the elmid beetle larva ***Optioservus*** sp. (Figure 113; Figure 118) [36% of ***Hygroamblystegium fluviatile*** (Figure 112), 7% of ***Platyhypnidium riparioides*** (Figure 111)] (Glime 1994). The stonefly ***Pteronarcys proteus*** (Figure 114) occurred in 24% of the ***H. fluviatile***, 7% of the ***P. riparioides***, and never in any of the other species, including ***Scapania undulata*** (Figure 106), ***Fontinalis dalecarlica*** (Figure 115), and ***Hygrohypnum*** spp. (Figure 116) (Figure 118).

Figure 110. ***Rhyacophila invaria*** larva, a common free-living caddisfly among ***Platyhypnidium riparioides*** in Appalachian Mountain, USA, streams. Photo by Donald S. Chandler, with permission.

Figure 111. ***Platyhypnidium riparioides***, a common moss in Appalachian Mountain, USA streams. Photo by David T. Holyoak, with permission.

Figure 112. ***Hygroamblystegium fluviatile***, a common moss for insect fauna in Appalachian Mountain, USA, streams. Photo by Michael Lüth, with permission.

Figure 113. ***Optioservus*** sp., a common beetle larva among ***Hygroamblystegium fluviatile*** and ***Platyhypnidium riparioides*** in Appalachian Mountain, USA, streams. Photo by Arlo Pelegrin, with permission.

Figure 114. ***Pteronarcys proteus***, a stonefly that seems to have some selection in bryophytes it will inhabit. Photo by Jason Neuswanger, with permission.

Figure 115. ***Fontinalis dalecarlica***, a large moss but that did not house ***Pteronarcys proteus*** in Appalachian Mountain, USA, streams. Photo by Kristoffer Hylander, with permission.

The liverwort ***Scapania undulata*** (Figure 106) has a different form from that of any of the mosses. This flattened habit seems to favor the fast-water members of **Simuliidae**, with ***Prosimulium hirtipes*** (Figure 117) in 58% of the collections and ***Simulium tuberosum*** (Figure 109) in 75% of the collections (Figure 118) of this liverwort in mid-Appalachian Mountain, USA, streams (Glime 1994). But ***S. tuberosum*** also occurred in 78% of the ***Fontinalis dalecarlica*** (Figure 115) collections (Figure 118).

Figure 116. ***Hygrohypnum luridum***, a moss that is not suitable habitat for the large ***Pteronarcys*** in the streams of the Appalachian Mountains, USA. Photo by Michael Lüth, with permission.

Figure 117. ***Prosimulium hirtipes***, a common blackfly on the liverwort ***Scapania undulata***. Photo by Janice Glime.

Diversity differs little among bryophyte species (Figure 119), although richness can be higher in the larger ***Fontinalis*** (Figure 115) species (Glime 1968, 1994). ***Fontinalis*** species are also the only ones that typically house larger insects. ***Scapania*** (Figure 106), on the other hand, housed the smallest insects in the Appalachian Mountains, USA, streams.

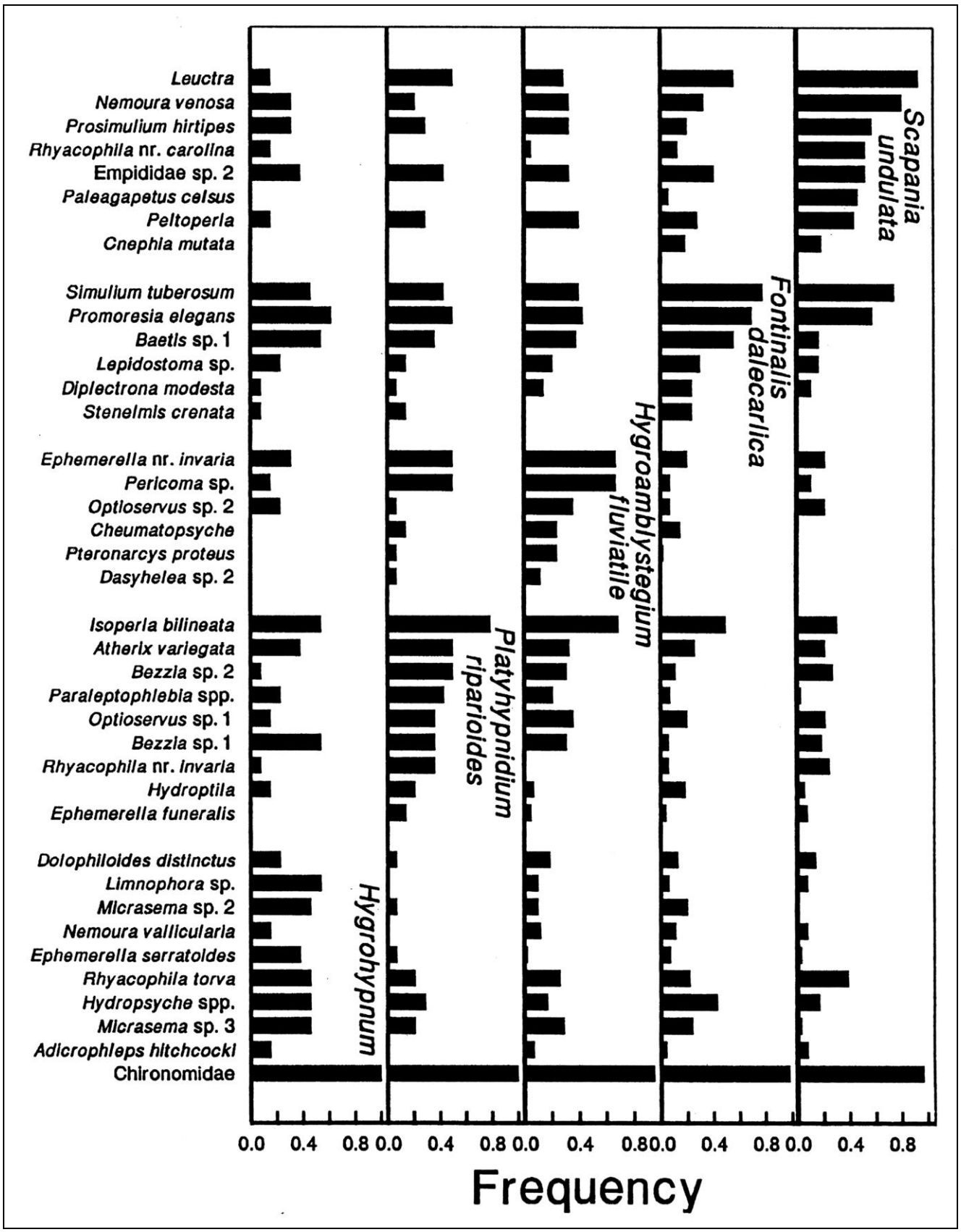

Figure 118. Frequencies of insects on five bryophyte species sampled in 28 streams in the middle Appalachian Mountains, USA. Only insects with at least 10% frequency on at least one species of bryophyte are included. The bryophyte name appears by the group of species that was most abundant on that bryophyte; the name applies to all groups in that frame. From Glime 1994.

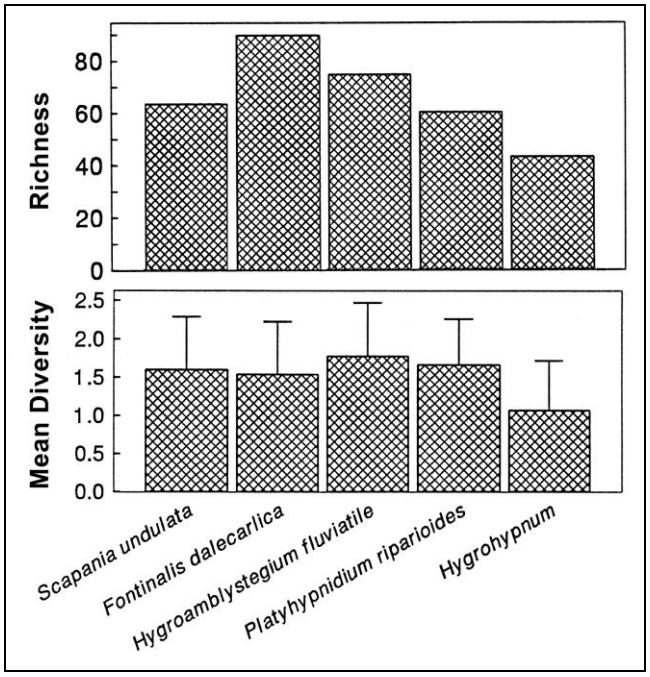

Figure 119. Comparison of mean insect richness and Shannon diversity on a leafy liverwort (***Scapania undulata***) and four species of mosses in 28 mid Appalachian Mountain streams, USA. Redrawn from Glime 1994.

Perhaps the greatest specificity is among some of the case-making caddisflies (**Trichoptera**). Several species in the **Hydroptilidae** make their cases exclusively from bryophytes, including ***Palaeagapetus celsus*** from leafy liverworts (Flint 1962; Glime 1978, 1994). The flat leaves of ***Scapania undulata*** seem to be ideal for their method of cutting nearly circular pieces that they cement together for the cases, apparently causing these larvae to live almost exclusively among leafy liverworts (Glime 1978, 1994). Likewise, in the **Brachycentridae** ***Adicrophleps hitchcocki*** (Figure 120) uses bits of ***Fontinalis*** (Figure 107) leaves or other mosses to construct its cases (Flint 1965; Glime 1994). When it uses ***Hygroamblystegium fluviatile*** (Figure 112) it may use only costae to make the case, sometimes leaving the ends of the costae dangling from the case (Glime 1994). The **Chironomidae** (Figure 90), as a family, was present in 98-100% of the collections of all species (Figure 118), but these comprised multiple species that could have differed among bryophytes and streams.

The acidity may affect the inhabitants, causing an appearance of bryophyte specificity. Frost (1942) found that the **Plecoptera** and **Coleoptera** were less important in the calcareous stream than in the acid stream, whereas the **Ephemeroptera** and **Trichoptera** reached their greatest density in the more calcareous stream.

Seasons

One reason for insects to live among bryophytes is to escape the cold of winter. To this end, some insects are more abundant in streams in the winter, but many spend the winter as pupae or eggs.

Thienemann (1912) found that young fauna were especially common among mosses in summer. Seasons can partition niches, with different sizes of insects occupying different niches. This means that larger members of a genus or family can occupy the same moss clump as younger members of other species in that family feeding group because they have different feeding niches. In some cases this niche partitioning is done by a seasonal migration to a different substrate. Hildrew and Edington (1979; see also Muotka 1990) found that early instars of ***Hydropsyche siltalai*** (Figure 121) and ***H. pellucidula*** (Figure 122) occupied the same rocks. However, in spring ***H. siltalai*** migrates to moss beds, but ***H. pellucidula*** was totally absent among the mosses at that time.

Figure 120. ***Adicrophleps hitchcocki*** showing case made with ***Hygroamblystegium***. Note costae protruding near opening. Photo by Bob Henricks, with permission.

Figure 121. ***Hydropsyche siltalai***, a caddisfly larva that moves to moss beds as it gets older, avoiding competition with ***H. pellucidula***. Photo by Urmas Kruus, with permission.

Figure 122. ***Hydropsyche pellucidula***, a net-spinning caddisfly that avoids niche competition with ***H. siltalai*** by avoiding moss beds when the latter migrates there. Photo by Niels Sloth, with permission.

In the Appalachian Mountain streams, the total numbers diminish in the winter (Glime 1968), but some insects, like the blackfly ***Prosimulium hirtipes*** (Figure 51-Figure 53; Figure 123), hatch in late fall and spend the winter in the water, emerging as adults in spring.

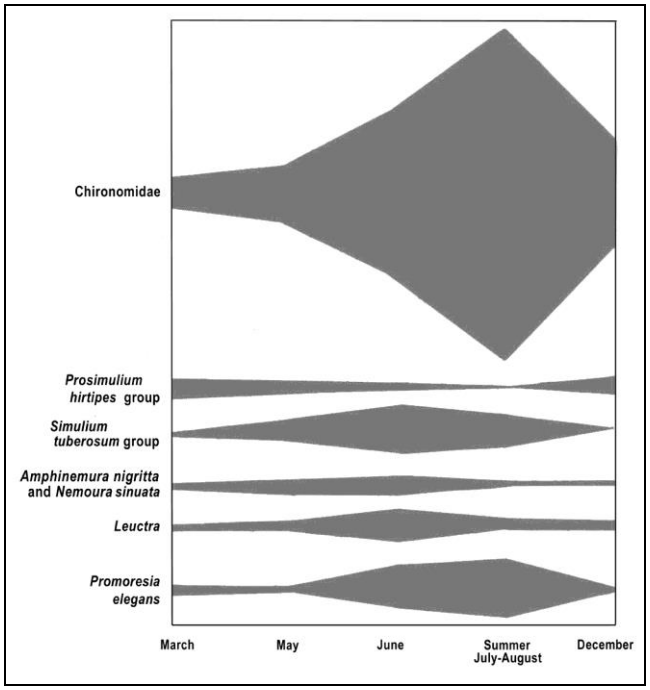

Figure 123. Relative abundance of the six most common insects among bryophytes in five collecting seasons in Appalachian Mountain, USA, streams. Based on Glime 1968.

In these Appalachian streams, counts do not always track diversity and richness (Figure 127; Glime 1994). What is more interesting is that **Shannon diversity** (following Patten 1962) and species richness do not always agree. This may be the result of the differences in counts, which are reflected in the **Shannon diversity:**

$$H' = -\sum_{i=1}^{R} p_i \log_2 p_i$$

where p_i = the proportion of individuals belonging to the ith type, or count of the species divided by total count of all species

R = richness, or total number of species

Richness, on the other hand, is simply the number of species present. In these streams, Shannon diversity was highest in March, but richness was highest in July. It is also interesting that these seasonal differences can be different among bryophyte species (Figure 124-Figure 127).

The ever-present **Chironomidae** (Figure 90) often peak among the mosses in winter (Frost 1942), but in the Appalachian Mountain, USA, streams the peak is mid-summer (Figure 123) (Glime 1968). Whitehead (1935) suggested that this might be a behavioral attribute in which the insects seek shelter among the mosses to avoid or respond to the ravages of flooding. But clearly the insects differ among orders, families, and seasons, as seen in these Appalachian Mountain streams (Figure 125-Figure 126).

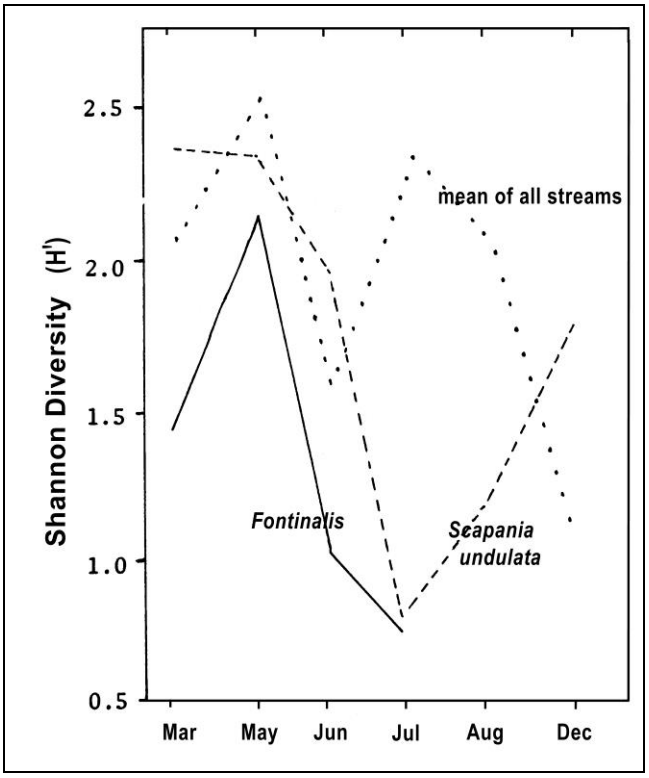

Figure 124. Seasonal changes in species diversity (H') among mosses (***Fontinalis*** spp. ▬) and liverworts (***Scapania undulata*** --) in Appalachian Mountain, USA, streams.

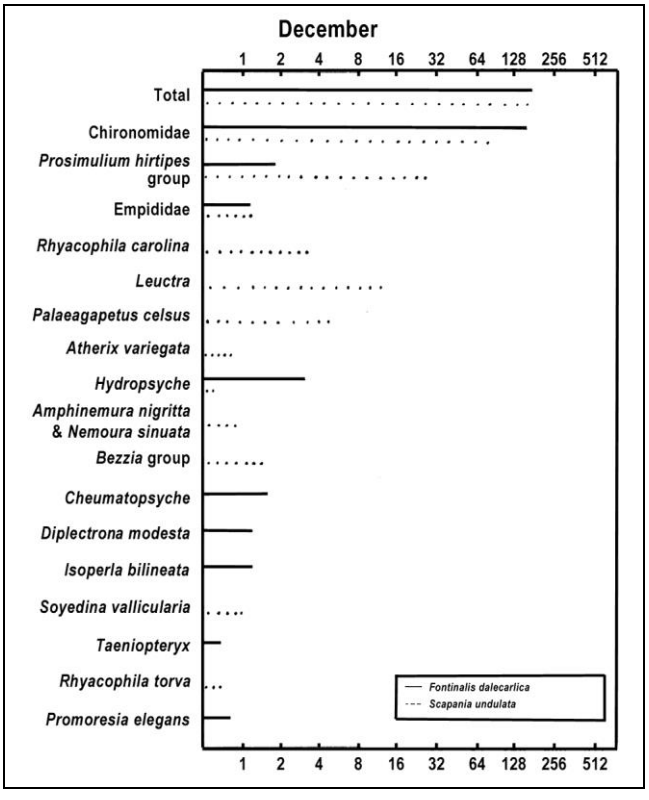

Figure 125. Relative numbers of the most abundant species (>3 occurrences) of insects per gram dry weight of bryophyte in December in Appalachian Mountain, USA, streams. Frequencies appear at right end of each bar. Based on Glime 1968.

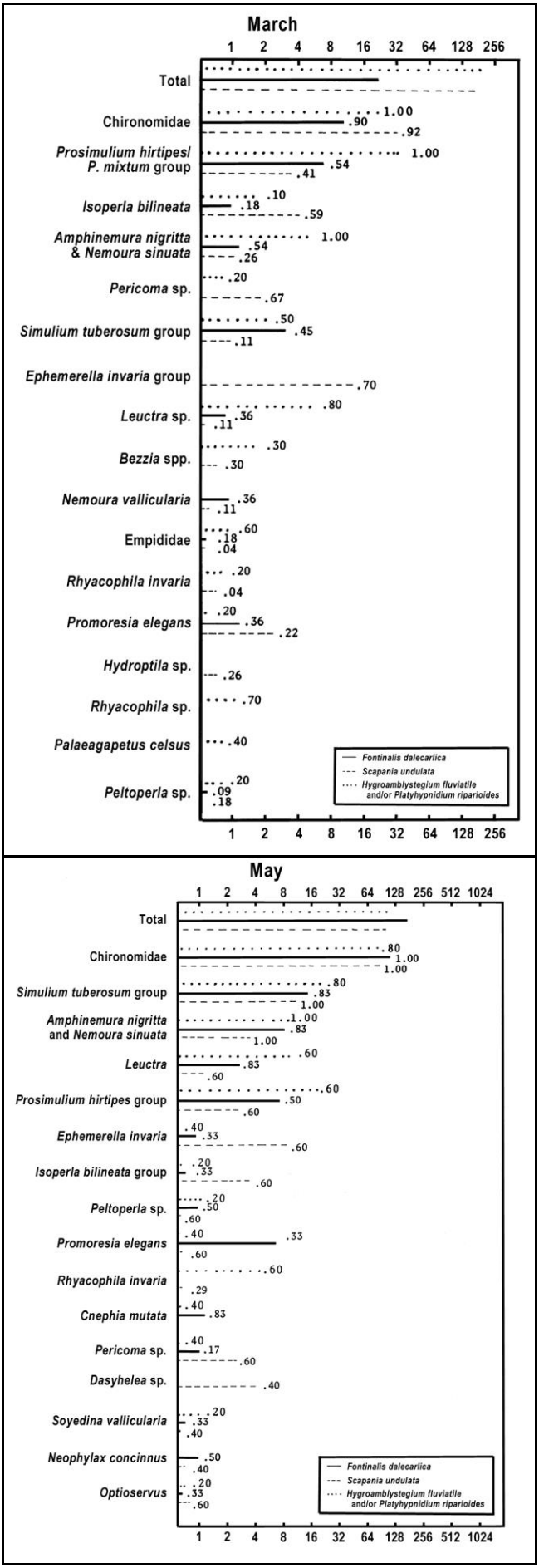

Figure 126. Seasonal relative numbers of the most abundant species (>3 occurrences) of insects per gram dry weight of bryophyte in Appalachian Mountain, USA, streams. Frequencies appear at right end of each bar. Based on Glime 1968.

Table 2. Common genera of bryophyte-dwelling aquatic insects. Numbers refer to references: (**1**) Percival & Whitehead 1930 (UK); (**2**) Glime 1994 (Appalachian Mountains, USA); (**3**) Thienemann 1912 (North Rhine-Westphalia); (**4**) Suren 1988 (alpine NZ); (**5**) Muttkowski & Smith 1929 (Yellowstone USA); (**6**) Frost 1942 (UK); (**7**) Tada & Satake 1994 (Japan); (**8**) Krno 1990 (Slavakia). Only studies that included all insect groups are included; note that most studies did not identify genera of the Chironomidae.

COLLEMBOLA	2
Isotomidae – *Isotoma*	2
EPHEMEROPTERA	1,2,3,5,6,7,8
Baetidae	1,2,3,6,7,8
Baetis	1,2,3,6,7,8
Baetiscidae – *Baetisca*	2
Caenidae – *Caenis*	6,8
Ephemerellidae	1,2,5,6,7,8
Drunella	5,7
Ephemerella	1,2,6,7,8
Torleya	8
Heptageniidae	1,5,7,8
Cinygmula	7
Heptagenia	1,5
Rhithrogena	8
Stenacron	2
Leptophlebiidae	2,6,8
Habroleptoides	8
Leptophlebia	6
Paraleptophlebia	2,6
ODONATA	2
Gomphidae – *Gomphus*	2
PLECOPTERA	1,2,4,5,6,7,8
Chloroperlidae – *Chloroperla*	6,7
Chloroperla	6
Gripopterygidae	4
Zelandobius	4
Zelandoperla	4
Leuctridae – *Leuctra*	1,2,6,8
Nemouridae	1,2,4,5,6,7,8
Amphinemura	6,7,8
Nemoura	2,8
Protonemura	6,7,8
Perlidae	5
Acroneuria	5
Perlodidae	2,6,7,8
Megarcys	7
Isoperla	2,6,7,8
Peltoperlidae – *Peltoperla*	2
Pteronarcidae – *Pteronarcys*	2,5
Taeniopterygidae – *Taeniopteryx*	2,6
HEMIPTERA	2
Veliidae – *Microvelia*	2
DIPTERA	1,2,3,4,6,7,8
Athericidae – ***Atherix***	2,3
Ceratopogonidae	2,8
Bezzia	2
Dasyhelea	2
Chironomidae	1,2,3,4,6,7
Corynoneura	3
Cricotopus	3
Dactylocladius	3
Diamesa	3
Orthocladius	3,7
Tanytarsus	3
Thienemanniella	3
Empididae	2
Clinocera	6
Hemerodromia	6
Limoniidae – *Antocha*	7
Muscidae – *Limnophora*	1,3,6
Pediciidae – *Dicranota*	3,6
Psychodidae – *Pericoma*	2,3,6,8
Simuliidae	2,6,7,8
Cnephia	2
Odagmia	8
Prosimulium	2,8
Simulium	2,6
Tipulidae	1,2,6,7
Hexatoma	1,2
Limnobiinae	6
Limnophora	2
Tipula	2,6
COLEOPTERA	1,2,3,6,8
Dytiscidae – *Ilybius*	2
Elmidae	1,2,3,6,8
Dubiraphia	2
Elmis	1,8
Esolus	3,6
Limnius	3,6
Optioservus	2
Promoresia elegans	2
Stenelmis crenata	2
Gyrinidae – *Gyrinus*	6
Hydraenidae	3
Hydraena	3
Limnebius	3
TRICHOPTERA	1,2,3,5,6,7,8
Brachycentridae	2,3,7,8
Adicrophleps	2
Brachycentrus	5,8
Micrasema	2,3,7
Hydropsychidae	1,2,3,8
Arctopsyche	7
Cheumatopsyche	2
Diplectrona	2
Hydropsyche	1,2,3,6,8
Parapsyche	2
Hydroptilidae	1,2
Agapetus	1,6
Agraylea	2
Hydroptila	1,2,3,6
Ithytrichia	1,2,3,6
Oxyethira	2,3,6
Paleagapetus	2
Leptoceridae – *Leptocerus*	1,6
Lepidostomatidae – *Lepidostoma*	1,2,6
Limnephilidae	7,8
Allogamus	8
Drusus	8
Parachiona	8
Pseudostenophylax	7
Philopotamidae	1,2,3
Chimarra	2,6
Dolophiloides	2
Philopotamus	1,3
Polycentropodidae – *Polycentropus*	1,2,6
Psychomyiidae – *Psychomyia*	1,6
Rhyacophilidae – *Rhyacophila*	1,2,3,6,7,8
Uenoidae	2,5
Neophylax	2
Thremma	5

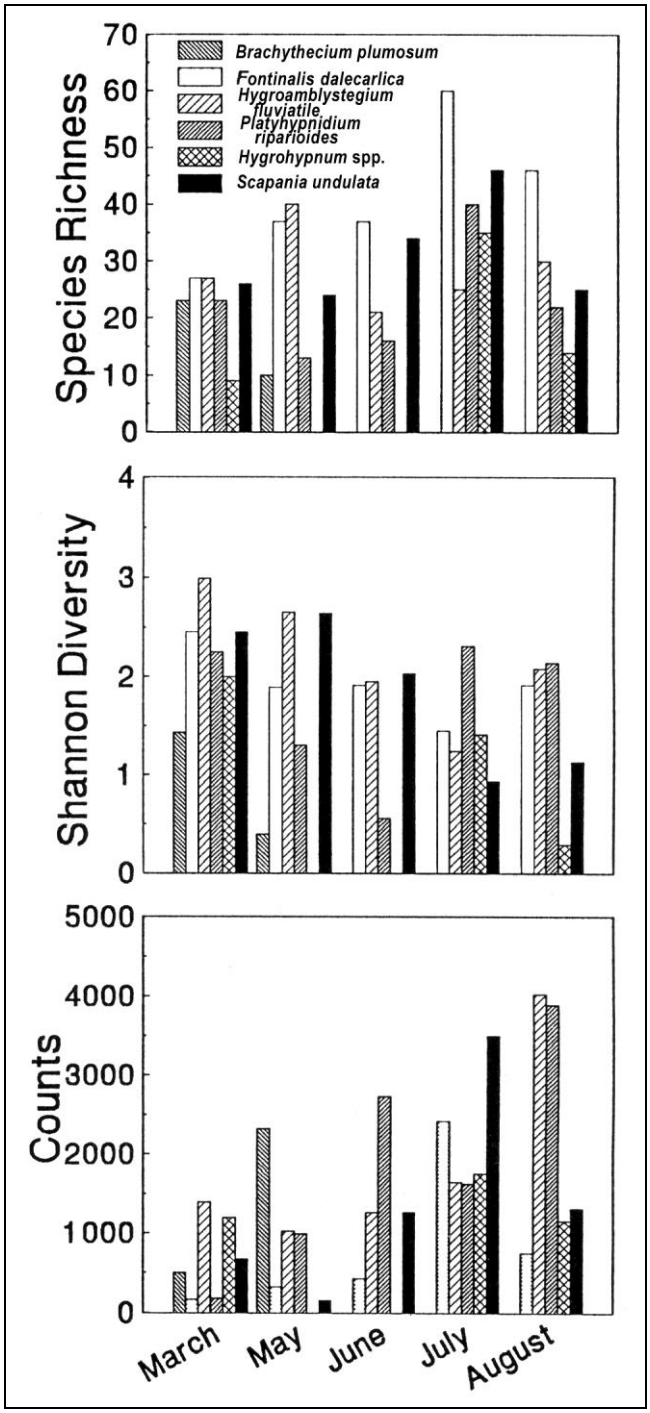

Figure 127. Bryophyte-dwelling insect seasonal richness, species diversity, and counts from handful samples. Redrawn from Glime 1994.

Sampling

Sampling of the fauna of aquatic bryophytes can be a time-consuming process. And sampling used for most terrestrial or stream habitats can introduce strong biases for these sheltered species.

My own methods were to use hand grabs, then determine the dry weight of the bryophytes after the fauna had been removed. This sampling kept the internal fauna intact, and to test for surface losses, I initially placed a net just downstream from my collections. Very few invertebrates landed in the net, so I proceeded with my hand collections. These were placed in baby food jars with 95% alcohol and a few drops of glycerine added to prevent predation and decay until the jars reached the lab. I removed the insects with microforceps while systematically searching through a dissecting microscope at 10 X.

Frost (1942) was one the early surveyors of bryophyte fauna. Her sample size was 200 g of wet moss. Kamler (1967) cut 10x10 cm samples under water. Maurer and Brusven (1983) were particularly careful. They surrounded the moss with a nylon organdy net of 250 µm mesh while removing the moss from the stream, then used several washes and hand picking to extract the insects.

Armitage (1961) used the modified square foot sampler, similar to the Surber sampler (Figure 128) used by Gurtz and Wallace (1984), to catch insects from rocks, mosses, sticks, and under rubble in streams. However, most bryophyte dwellers are adapted to clinging to the bryophyte and require more than a little disturbance to free them. This leads to underestimates of the bryophyte fauna relative to those among the rubble of the stream bottom and also to species bias. Wulfhorst (1994) modified this method slightly, using a box sampler to cut a square of 14 cm^2 to sample mosses in an acid stream. The moss samples were quantified by volume using displacement of water in a graduated cylinder.

In his New Zealand studies, Suren (1988) likewise used a Surber sampler (Figure 128) with 100 µm mesh to sample 0.01 sq m. Rocky areas were sampled with a 0.02 sq m sampler that had a thick foam flange around the bottom to provide a seal with the substrate. Mosses were scraped into the sampler with a razor blade. This method permitted the same area to be sampled in both rock and moss areas.

Figure 128. Surber sampler being used as drift net for winter stream drift sampling. Photo by Janice Glime.

Preservative

It is important to understand the role of the preservative. Not only does it keep the organisms from decaying and being eaten by cohabitants during the period until the sample can be examined, but it increases the extraction efficiency for flotation techniques (discussed below), at least in a sucrose solution of 1.12 specific gravity (Pask & Costa 1971). In samples preserved for 14 days in 10% formalin compared to those not preserved but examined the same day, the preserved insects had a recovery of 91% whereas those with no preservation had only an 83% recovery rate.

Since any collection of bryophytes will bring significant water with it, it is necessary to use a higher concentration than that used when preserving just insects. I added 95% alcohol to my bryophyte collections (with insects), hoping to achieve a concentration of around 70%.

Extraction

The least bias in extraction can be achieved by careful hand picking while observing through a dissecting microscope. When I first tried to publish my Ph. D. work, the reviewer wanted to know what method I had used to "estimate" the numbers of **Chironomidae**, which could reach thousands in a single handful of moss. But I had removed and counted every single one of them at 10X magnification! Gurtz and Wallace (1984) also hand-picked invertebrates from the mosses at 7X under a dissecting microscope, using a count per dry weight of moss.

There are simpler and less time-consuming methods for those who don't want to spend three years searching among the bryophytes with a microscope. But, these each have their biases. The Tullgren funnel (Andrew & Rodgerson 1999) creates a temperature gradient over the sample, typically with a tungsten light bulb above it. Mobile organisms will move away from the higher temperatures and fall into a collecting vessel with alcohol or mixed preservative. But not all insects move quickly, and some may die from the heat and desiccation before falling to their death in the alcohol below. Furthermore, some will die before reaching the lab due to the reduced oxygen.

Fairchild *et al*. (1987) developed a behavioral method for extracting invertebrates from ***Sphagnum*** (Figure 91). The method includes a vertical temperature gradient coupled with dissolved oxygen gradients in a column of water containing the ***Sphagnum*** sample. They determined the overall extraction to be 85% efficient (n=4). I do have concerns about bias in the species extracted.

Teskey (1969) developed a method especially for sampling the small flies of the family **Tabanidae**. He used a combination of a specially designed sieve with a multiple Berlese funnel (similar to the Baermann funnel in Figure 129) or by using hand searching to sample these larvae. But to identify the larvae, as in many of the aquatic taxa, they had to be reared to adults. Cochrane (1913) used sieves to collect larvae of ***Culicoides furensoides*** (**Diptera**: **Ceratopogonidae**) from ***Sphagnum*** (Figure 91).

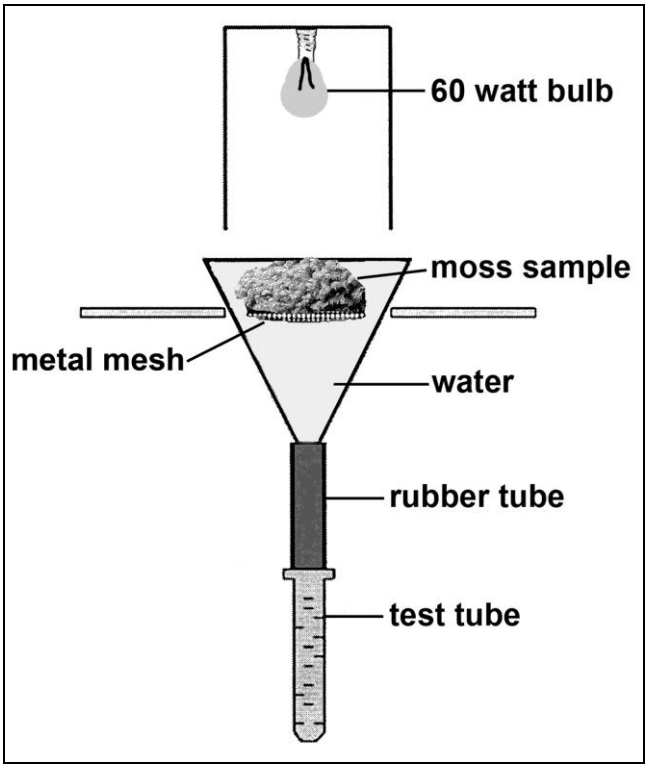

Figure 129. Baermann funnel using moss sample and modified from the Berlese funnel setup, using water instead of air. Modified from Briones 2006.

Flotation

Any flotation technique requires that the density of the flotation liquid be greater than that of the insects but less than that of the debris (Lackey & May 1971). The 1.12 specific gravity sucrose solution of Pask and Costa (1971) works well in this regard. The kerosene phase separation extracts more total individuals than those extracted by sugar flotation or the Tullgren funnel, particularly more **Acari** (mites) and **Collembola** (springtails) (Andrew & Rodgerson 1999).

Fast (1970) pointed out that calling the flotation techniques "flotation" was a misnomer. While the sugar solution is important, many of the organisms remain lodged at leaf bases or caught among the leaves and stems. He preserved samples with 10% formalin. To separate the organisms, he used 360 g sucrose per liter of water and gave the samples only one immersion in the sugar solution. He then sorted at 3.5X magnification. One problem I found with the flotation method was that tiny creatures like the Chironomidae got trapped in the surface tension. They were almost impossible to pick up, so they needed to be trapped on a filter. By the time you have then picked them off the filter, you might as well sort them directly from the moss and learn about their hideouts and spatial relationships at the same time.

Hribar (1990) reviewed ten methods for sampling biting midge larvae. Some of these will work for aquatic bryophytes. Hribar was successful in extracting larvae of **Ceratopogonidae** (***Alluaudomyia***, ***Atrichopogon***, ***Bezzia***, ***Culicoides***, ***Dasyhelea***, and ***Forcipomyia***) from ***Fontinalis***

(Figure 107) and aquatic liverworts by using a Berlese funnel (see Figure 129). He found that sugar flotation and salt flotation provided similar results, but the sugar flotation caused less mortality. Magnesium sulfate is a slower process but results in fewer deaths than salt solutions. Nevertheless, he considered agar extraction and salt flotation to be the most effective for collecting larvae. Sieving, sieving plus salt flotation, and Berlese funnels worked well for mosses.

In short, unbiased sampling to determine numbers of insects living among bryophytes requires time and patience.

Artificial Mosses

Several researchers have attempted to explain the role of aquatic bryophytes by using artificial mosses. Glime and Clemons (1972) used strips of plastic and bundles of string (Figure 130) as artificial mosses. The plastic permitted colonization by **periphyton** (attached organisms) but lacked the chambering found among mosses; only 13 species occurred on the 33 samples. The string offered a soft substrate with limited chambers; 23 species of aquatic insects occurred on the 35 samples, some of which were not present on the real mosses. The real mosses [***Fontinalis novae-angliae*** (Figure 131) & ***F. dalecarlica*** (Figure 115) had 25 species among the 46 samples, differing little in overall richness from that of the string mosses. It appeared that density of insects was higher among real mosses, but there was no common base upon which to compare them. It is interesting that the Shannon diversity differed little among the three substrata (1.8 on moss, 1.9 on string, and 1.7 on plastic). Nevertheless, the Shannon diversity (d) on plastic was significantly different from that on mosses or strings. The lack of complexity and smaller surface area of the plastic may have accounted for the limited diversity.

Figure 130. Artificial mosses made of cotton string. Photo by Janice Glime; see Glime & Clemons 1972.

Suren (1988) used nylon twine (5 cm long, 1 mm thick) to weave squares 0.01 m^2 thick with a pore size of 4 mm. He found no differences in the fauna between artificial and real mosses in a New Zealand stream. The artificial mosses even had abundant periphyton growth [especially ***Epithemia*** (Figure 132) in winter and spring], but their accumulation of detritus and silt was sparse. This perhaps explains the significantly lower numbers of detritus feeders such as **Acarina** (mites), **Collembola** (springtails), **Tardigrada** (water bears), **Dorylaimoidea** (nematodes), and **Ostracoda** (seed shrimp) on the artificial mosses.

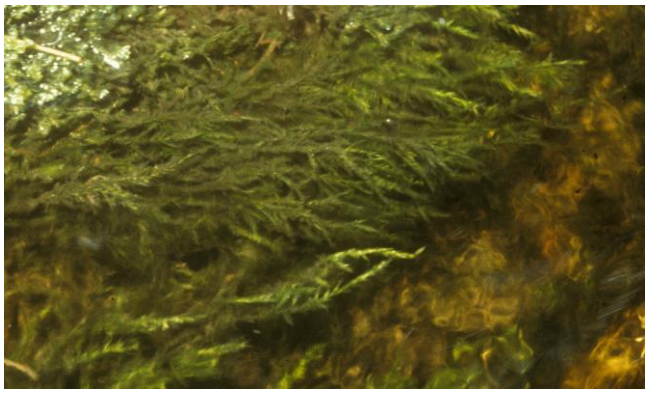

Figure 131. ***Fontinalis novae-angliae***, a moss with around 25 species of insects in a New Hampshire, USA, stream. Photo by Janice Glime.

Figure 132. ***Epithemia*** sp., a common diatom genus on mosses, on a filamentous alga. Photo by Jason Oyadomari, with permission.

Summary

Aquatic insects are those insects that spend part of their life cycles in the water, usually as a means of escaping the harsher environment on land during one or more seasonal conditions. For most, the immature stages are those requiring such an escape.

Aquatic bryophyte dwellers include the **Collembola** (no longer considered to be insects) that look like miniature adults when born. The **hemimetabolous** insects include the **nymphs** of **Hemiptera** that look like their parents from birth and simply grow larger. The **naiads** of **Ephemeroptera**, **Odonata**, and **Plecoptera** are likewise hemimetabolous, but the naiads often differ from the adults in having gills, different mouth parts, and wing

pads instead of wings. Their life cycle goes from egg/embryo to naiad to adult. The **holometabolous** insects have four distinct stages in the life cycle – **egg/embryo**, **larva**, **pupa**, and **adult**. These orders, among bryophytes, include **Coleoptera**, **Neuroptera**, **Megaloptera**, **Trichoptera**, and **Diptera**. Some have gills as larvae but not as adults.

As an escape from unfavorable conditions, the life cycle stages often respond to environmental cues, including photoperiod, temperature, or available food. Aquatic insects are especially sensitive to temperature, and many of them are in the water for winter to escape the below-freezing temperatures in the terrestrial environment. Some overwinter as dormant eggs or pupae, others as active larvae, naiads, or adults.

Structural adaptations include streamlining, small size, gills, hooks or silk for anchoring, gill covers, and cases or tubes. They move about in the bryophyte clumps to achieve the best oxygen and flow conditions, often leaving as they grow larger. Oxygen may be obtained through gills, cuticle, or a **plastron** that carries an air bubble from the surface or from photosynthesizing plants or algae. Bryophyte dwellers include shredders, gatherers, scrapers, and detritus feeders that prey upon smaller organisms, including periphyton, or eat the detritus gathered by the bryophytes. Some eat the bryophytes. Some make nets to trap food. A few species have a specific requirement for bryophytes for case building, but most simply need a refuge with adequate oxygen, food, and cover.

Sampling is often done with nets, but is best by hand grabs and hand sorting. The faster methods such as nets are commonly used, but they have biases against interior and clinging organisms. Sorting by flotation or Berlese funnels has similar biases. Artificial mosses can sample colonizers but they may not provide the food sources needed and require somewhat lengthy colonization times.

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CHAPTER 11-2
AQUATIC INSECTS: BRYOPHYTE ROLES AS HABITATS

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CHAPTER 11-2
AQUATIC INSECTS: BRYOPHYTE ROLES AS HABITATS

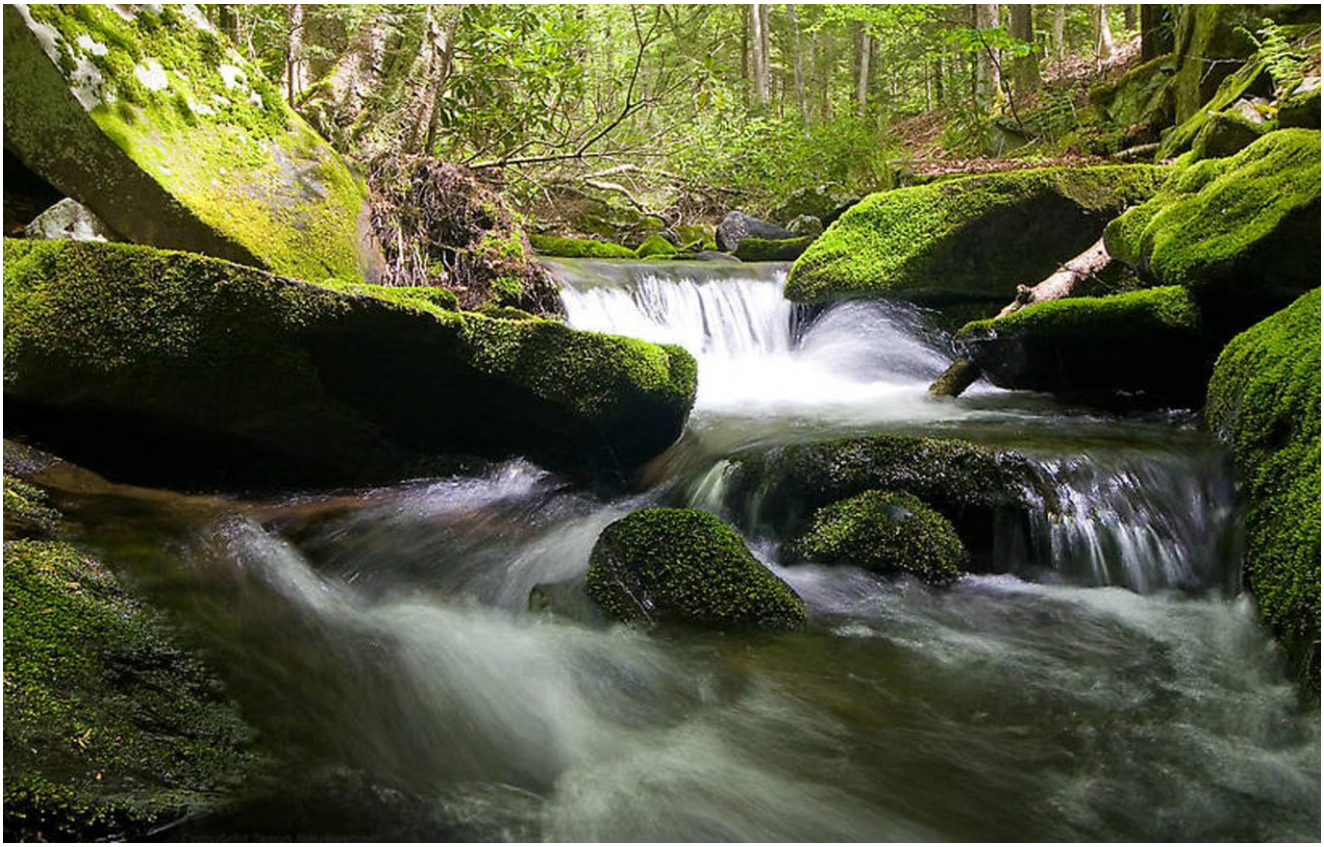

Figure 1. Habitat for stream bryophyte dwellers, Wolf Brook, NY, USA. Photo by Jason Neuswanger, with permission.

Potential Roles

Ulfstrand (1967) astutely stated that aquatic insects select their habitats on the basis of factor combinations. While some minimal levels of factors are important – oxygen, temperature, space, stability – the most important factor determining location within this medley of minimums is usually food. And that food works in two directions: enough food to maintain nutrition and avoidance of becoming food themselves. To satisfy both food factors, Ulfstrand found that substrate is especially important; bryophytes are often important choices among those substrates.

Bryophytes are major components in several types of ecosystems, including peatlands, mountain streams (Figure 1), high latitudes, and boreal forest floor. Many researchers have found that bryophytes are important substrata for insects (Percival & Whitehead 1929). Arnold and Macan (1969) found the greatest species richness and number of individuals among mosses, citing their role as cover and source of food by trapping particles.

Bryophytes, both mosses and liverworts, often form extensive cover in rocky and stony reaches of streams (Macan & Worthington 1951). These can have profound effects on the fauna by providing footholds against the current. Mosses with moderate thickness are suitable for the mayflies ***Baetis*** (Figure 2) and ***Ephemerella*** (Figure 3) and **Plecoptera** (stoneflies; Figure 20). Fish benefit as well, with the greatest production of fish-food organisms where there are either rooted plants or mosses. For example, **Chironomidae** (Figure 9) are in greatest numbers among thick mosses. And fish certainly eat **Chironomidae** (Mousavi *et al*. 2002). Based on gut contents, Frost (1939) considered moss-dwelling insects to be an important constituent of the diet of trout (Frost 1939) and young salmon (Frost & Went 1940) in the River Liffey, Ireland. Likewise, Minnows appear to crop the moss fauna (Frost 1942). On the other hand, Brusven *et al*. (1990) found that at least in the daytime when salmonid fish feed, the insects drifting in the moss-covered channel (***Fontinalis neomexicana*** – Figure 4) did not provide any greater biomass for fish food than in channels where mosses were absent and insect faunal density was much less. Bowden *et*

al. (1999) likewise questioned whether fish actually benefit from the increased abundance of insects in streams where bryophytes are present, citing a lack of evidence.

Figure 2. ***Baetis rhodani*** on sand, a mayfly that also lives among mosses. Photo by J. C. Schou, with permission.

Figure 3. ***Ephemerella dorothea*** on moss (***Platyhypnidium riparioides***) in Virginia, USA. Photo by D. N. Bennett, with permission.

Figure 4. ***Fontinalis neomexicana***, a slightly amphibious species that provides shelter for moss dwellers. Photo by Belinda Lo, through Creative Commons.

I am aware of no study that demonstrates quantitatively that the increase in number of insects in moss mats benefits fish. It appears that insects may have evolved to drift at night precisely to avoid predation by day-feeding fish. Bryophytes are a difficult place for fish to locate and catch the insects, perhaps reducing the catchable food from what might have been available if rock-dwelling insects were present instead. The hypothesis that bryophyte dwellers increase available fish food needs to be tested.

Corona (2010) suggested that immature insects in streams stayed together because that behavior would increase survival, a concept already suggested for vertebrates by Elgar (1986), Robinette *et al*. (1995), and Brown and Brown (2004). Bryophytes that provide a stable, protected habitat would facilitate such behavior.

Nearly fifty years after Macan and Worthington (1951) expressed the profound contribution of bryophyte-dwelling insects, Bowden *et al*. (1999) summarized that bryophytes "can profoundly influence both the abundance and community structure of stream invertebrates." But they further stated that "the number of fundamentally important roles of bryophytes in stream ecosystems remain unexamined." I will attempt to pull together what various scattered studies around the world have revealed about the roles of stream bryophytes.

Paddling a Kayak to gain first-hand information, Yamamura (2009) observed the adaptations of aquatic insects to various flow regimes in the rivers of Idaho, following up on studies by Rosentreter (1984). In their studies, Yamamura and Rosentreter found that aquatic insects benefit by having aquatic bryophytes because:

1. Bryophytes **decrease stream velocity** on the rock's surface layer.
2. Bryophytes **trap more detritus** (Figure 5; product of disintegration, especially organic matter produced by the decomposition of organisms) than smooth rock (food for shredder insects).
3. Bryophytes provide hiding cover (**refuges**) from predators.
4. Bryophytes provide better background coloration for **camouflage**.
5. Bryophytes provide **greater surface area**, providing a greater amount of habitat area.
6. Bryophytes provide **more food** since algae can grow upon the greater surface area created by the three dimensions of the moss surface.
7. Bryophytes provide greater **algae retention** and protection when stream flow regimes are low enough to create dry surfaces. The bryophytes **retain water longer** than other substrata in the stream, permitting the algae to dry slowly and acclimate to the encroaching desiccation.
8. Perennial bryophytes such as ***Scouleria aquatica*** (Figure 6) can provide **long-term stability** to an ephemerally dry rock surface, permitting survival of algae, insect larvae, and eggs.

Yamamura (2009) concluded that insect larval data support the interpretation that larvae in spring-fed streams (streams containing aquatic moss) are larger compared to those in runoff-dominated streams (streams that lacked mosses). He concurred with Rosentreter (1984) that spring-fed (mossy) streams have three cohorts present while most run-off (non-mossy) streams have two cohorts. This raises the question, do mosses in runoff-dominated streams benefit insects enough to produce larger larvae and another generation (cohort) per year? Perhaps the insects benefit

from the added cover of bryophytes – insect predators in Idaho streams include other insects, fish, shore birds, and the American dipper. Mosses provide cover in which to hide from all these predators.

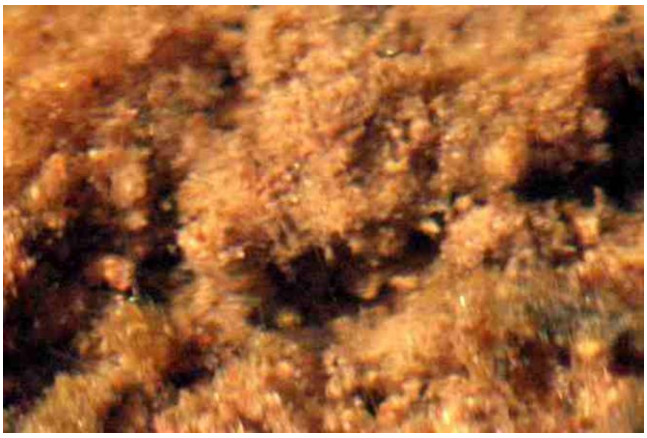

Figure 5. **Detritus**, a common food for aquatic insects and typically accumulated at plant and leaf bases among bryophytes. Photo by James K. Lindsey, with permission.

Figure 6. ***Scouleria aquatica*** on rock near stream water. Photo by Matt Goff, with permission.

Refuge

Bryophytes serve as refuges in both moving water and lentic systems such as lakes and ponds. In streams, they provide a refuge against the torrents of rapidly flowing water, permitting insects to live where they can take advantage of the higher oxygen and suspended food sources available in flowing water while remaining safely anchored within the moss or clinging to its surface. In both habitats, the bryophyte provides a hiding place from predators, especially fish, but also larger insects, crayfish, and birds.

The importance of bryophyte-dwelling insects as fish food is a subject for speculation. While the bryophytes provide homes for numerous insects, there is no direct evidence that these insects are available as increased fish food. Greig and McIntosh (2008) examined the effect of brown trout (***Salmo trutta***) predation on the caddisfly ***Zelandopsyche ingens***, a bryophyte dweller in New Zealand. They determined that these trout can have positive effects on the size and fecundity of the adult caddisflies by reducing competition among the larvae through predation. The striking revelation of this study was that despite the detritus-based diet of these caddisflies, reduction in the number of larvae still had a positive effect on the adults of the species when compared to those in fishless streams. The adults were larger and the females had 33% more eggs, but the egg size was unchanged. Nevertheless, the increase in number of eggs did not compensate for the loss of larvae.

The study by Greig and McIntosh (2008) suggests that fish have an impact on insects that typically live among the bryophytes, many of whom are detritus feeders. Thus, the bryophyte cover potentially increases the number of insects surviving and the number of adults reproducing, but we are left with the question of whether the bryophytes ultimately produce more available fish food.

Habitat Diversity and Substrate Variability

Habitat diversity offers more niches, hence making the area suitable for more species. Clenaghan *et al*. (1998) identified ecological factors that contribute to macroinvertebrate community composition. Local ecological factors include acidic water, moss, shading, agricultural runoff, longitudinal trends in stream physico-chemistry (distance from headwaters, geology, land use) and season (related to life history patterns of the invertebrates). In their study of a conifer-afforested catchment in Ireland, macroinvertebrate density and richness increased with the distance from the headwaters and the concomitant increases in *p*H, water hardness, and available nutrients.

Douglas and Lake (1994) demonstrated that habitat diversity was important in increasing species richness in streams. Bryophytes not only add to that diversity, but increase available surface area. Based on a review of the literature, Smith-Cuffney (1987) reported that stream mosses in low order, high elevation streams have a structurally unique community. Measured as respiration rates, the communities among ***Fontinalis*** (Figure 4) had three times the rates found in the stone community and five times that of the **hyporheic** community. Arnold and Macan (1969) found the largest number of species and individuals of insects inhabited mosses in a Shropshire Hill stream in the UK, where the mosses provided both shelter and trapped food.

Pardo and Armitage (1997) demonstrated the importance of environmental variables in the spatial distribution of aquatic insects based on eight mesohabitats. They found that water velocity and flow dynamics, together with the nature of the substrate were the major determinants of **benthic** (bottom) communities. Heino (2009) looked at the environmental variables somewhat differently, attempting to explain why such things as the influence of altitude varied with geography. He found *p*H, stream size, and moss cover were the most important variables, with functional diversity increasing with moss cover. These two approaches are not that different, with *p*H and water velocity both influencing moss cover and moss cover providing safe sites in areas of high flow rates.

Špoljar *et al*. (2012) likewise found that flow velocity and *p*H had the greatest effect on community structure. In two springs in Papuk Nature Park, Croatia, the

macroinvertebrate taxa numbered only 25. Where the bryophyte cover was dense (90% cover), the community structure was most affected by flow velocity and *p*H; macroinvertebrate diversity and abundance were higher than in the stream with only 50% bryophyte cover. In the latter stream, algae, protozoa, and **meiofauna** (minute inimals living in small spaces in soil or aquatic sediments) reached higher abundance, apparently resulting from suspended organic matter and epiphytes.

Bryophyte communities exemplify the species-area relationship (Gleason 1922). Increased bryophyte cover means an increase in available substrate due to its three-dimensional structure. Heino and Korsu (2008) found a strong relationship between species richness and number of individuals, and both of these were significantly related to the bryophyte biomass. They attributed the relationship to the increased cover provided by greater bryophyte coverage. Heino *et al.* (2005) found that despite the highest congruence between bryophytes and macroinvertebrates among the stream biological groups, that congruence was nevertheless weak. This seems to relate to differences in the stream factors that determine bryophyte locations. Bryophyte diversity followed water color, habitat stability, and stream size, in that order. Macroinvertebrate diversity instead was determined in the order of stream size, water color, and acidity.

Nutrients

Nutrients can affect moss growth in some cases and limit it due to competition for light by encrusting algae in others. In their study of the Kuparuk River, Alaska, USA, Lee and Hershey (2000) found that fertilization with phosphorus increased the growth of mosses (***Hygrohypnum*** – Figure 7), but that insects did not respond as extensively as one might expect. Invasion by mosses resulted in an increased density of the mayfly ***Ephemerella aurivillii*** (Figure 8) and **Chironomidae** (midges; Figure 9), but had no effect on densities of the mayfly ***Baetis*** spp. (Figure 2) or **Simuliidae** (blackflies; Figure 22). Both ***Baetis*** and ***Ephemerella*** grew larger in fertilized areas, but Lee and Hershey suggested that this was most likely due to the increase in epiphytic diatoms. Only ***Ephemerella*** seemed to be affected by substrate type (bare rock, natural moss, artificial moss), with the greatest densities among the mosses, presumably due to increased habitat complexity. Clenaghan *et al*. 1998) compared several factors and found that mosses were one of the factors explaining the diversity of insects in a catchment stream in Ireland, and that both density and richness increased with moss weight. Voelz and McArthur (2000) likewise concluded that habitat complexity was one of the most important factors in determining species richness in streams.

In my own culturing studies, I have found that enrichment was often detrimental to the mosses. These mosses lost their green color and were covered by algae that presumably intercepted the light – and CO_2. While the bryophytes remained intact, even if dead, this enrichment could benefit the insects by increasing food sources, but such enrichment most likely would make establishment of new mosses or increased coverage by existing ones less likely.

Figure 7. ***Hygrohypnum alpinum***, home of many aquatic insects. Photo by Michael Lüth, with permission.

Figure 8. ***Ephemerella aurivillii*** naiad, a species whose density increases when there are mosses. Photo by Tom Murray, through Creative Commons.

Figure 9. **Chironomidae** larva, an insect that increases in abundance when greater moss growth occurs. Photo by Bob Henricks, with permission.

Substrate Size

The biodiversity of macroinvertebrates typically increases linearly with the substrate suitability index [suitability of sediment, **periphyton** (freshwater organisms attached to or clinging to plants, but also used to include other objects projecting above the bottom sediments; *Aufwuchs*), and benthic organic materials] (Duan *et al*. 2009). In large rivers in China (Yangtze River, Yellow River, East River, Juma River), Duan *et al*. found that the macroinvertebrate community was not dependent upon macroclimatic conditions or latitude, but rather responded to the commonality of instream habitat conditions of substrate composition and flow conditions in these rivers.

They found that taxa richness was highest on cobble covered with hydrophytes, high on moss-covered bedrock, and low on clay or cobble where there were no plants. Sandy beds were unstable and thus devoid of benthic macroinvertebrates. As in many stream studies, the EPT insects [**Ephemeroptera** (Figure 8, **Plecoptera** (Figure 20), **Trichoptera** (Figure 13)] dominated the cobble, gravel, and moss-covered bedrock. But contrasting with most stream studies (see Chapter 11-9, Holometabolous Insects – **Diptera**), the **Chironomidae** larvae (Figure 9) reached greatest dominance in the clay beds.

But substrate size apparently does not act alone and importance differs among types of insects (see for example Ulfstrand 1967). Contrasting with other studies, Wise and Molles (1979) found that small substrates supported more insect individuals than did the larger stones. And mixed sizes supported numbers between the small and large sizes.

Stability

I love the expression "A rolling stone gathers no moss," because it so perfectly describes the situation of stability. This expression can be traced to Erasmus' Adagia, first published around 1500, and has since taken on wide usage with somewhat conflicting interpretations. Nevertheless, in the context of a stream, its meaning is clear.

Bryophytes themselves indicate a stable substrate (Yamamura 2009). Such stable areas are present due to stream channel geometry. Rapids can focus the ice scraping at the center of the river, away from the sides where bryophyte populations are able to grow. Hence, some invertebrates may live in those mossy areas simply because they, too, only survive where the substrate is stable and the water has a reduced shearing effect.

Stability is most important for eggs and many pupae that cannot move to a more favorable location when the need arises. Bryophytes will only become well established on stable rocks and boulders, so they signal a stable habitat. Furthermore, as water levels recede, bryophytes maintain water content well beyond the time that a rock can do so, creating a moisture stability. And when the young insects hatch from the eggs, these tiny animals are not only easy prey for larger animals, but they are poor swimmers unable to navigate in the flowing water. The bryophytes provide cover and protection in their small-chambered labyrinth that prevents entry to predators such as fish and large insects and that reduces the flow to near-pool conditions (Glime 1978).

*p*H Relationships

The **depauperate** (lacking in numbers or variety of species) fauna of some bryophytes may relate more to the preferred habitats of the bryophytes than to the bryophytes themselves. For example, in Wales, Ormerod *et al*. (1987) found that in streams with low *p*H the bryophytes [liverworts ***Scapania undulata*** (Figure 10) and ***Nardia compressa*** (Figure 11)] had few insects; 60% of the ***S. undulata*** sites had fewer than 20 macroinvertebrate taxa. The *p*H where Ormerod *et al*. found these liverworts growing was 5.2-5.8. On the other hand, less than 5% of the sites with the red alga ***Lemanea*** (Figure 12) (*p*H 5.5-8.5) were so impoverished. In particular, ***Hydropsyche*** (Figure 13) was absent at sites with ***S. undulata*** and ***N. compressa***, but present in streams with ***Fontinalis squamosa*** (Figure 14).

Figure 10. ***Scapania undulata***, a leafy liverwort that can serve as food for the mayfly ***Ecdyonurus***. Photo by Michael Lüth, with permission.

Figure 11. ***Nardia compressa***, a leafy liverwort that can be eaten in some streams by the mayfly ***Ecdyonurus*** sp. Photo by Des Callaghan, with permission.

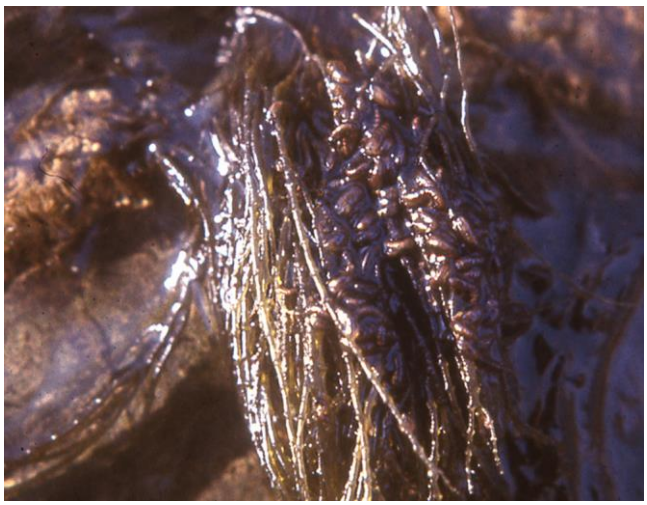

Figure 12. ***Lemanea*** sp. covered with blackflies. Photo by Janice Glime.

Figure 13. ***Hydropsyche*** larva, a net-spinning caddisfly that frequents ***Fontinalis antipyretica*** (Figure 18) and ***Platyhypnidium riparioides***. Photo by Guillaume Doucet <http://guillaume.doucet.free.fr/>, with permission.

Figure 14. ***Fontinalis squamosa*** above and below water on rocks, home to several stonefly genera. Photo by Janice Glime.

Research by Willoughby and Mappin (1988) suggests that the insect avoidance of the two leafy liverworts that Ormerod *et al*. (1987) observed may not have been a response to *p*H, but rather the result of the liverwort terpenes and terpene alcohols in the oil bodies. On the other hand, some insects such as the mayfly ***Ecdyonurus*** (Figure 15) feed on such acid-tolerant bryophytes as ***S. undulata*** (Figure 10), but are unable to live in the acid streams at the lower end of the *p*H tolerance range of this liverwort. Ormerod and coworkers (1987) considered that these mayflies are therefore physiologically restricted from acid streams.

Figure 15. ***Ecdyonurus venosus*** naiad, a mayfly genus in which some members feed on ***Scapania undulata*** (Figure 10) when the *p*H is not too low. Photo by Guillaume Doucet <http://guillaume.doucet.free.fr/>, with permission.

Other factors may affect the choices of many insects to avoid colonizing these acid-tolerant bryophytes. For example, one possibility that Ormerod *et al*. (1987) considered was that the diatom ***Eunotia*** (Figure 16) that grows in the leaf axils of leafy liverworts (acid-loving) is inaccessible to grazing ***Baetis*** (Figure 2), whereas the diatom ***Cocconeis*** (Figure 17) grows on the leaf lamina of the moss ***Hygrohypnum*** (Figure 7; growing at a higher *p*H) where it is easily grazed (Sutcliffe *et al*. 1986).

Figure 16. ***Eunotia*** sp., a diatom that grows in leaf axils of leafy liverworts where ***Baetis*** is unable to reach it. Photo by Janice Glime.

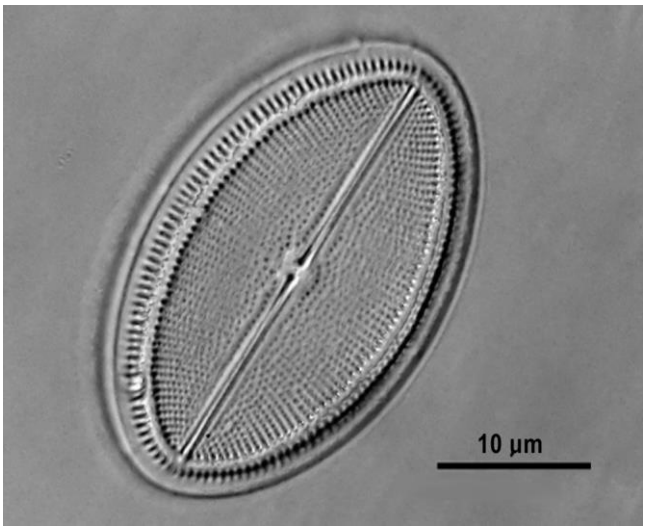

Figure 17. ***Cocconeis placentula***, an epiphytic diatom that cements itself to aquatic bryophyte leaves. Photo by Ralf Wagner at <http://www.dr-ralf-wagner.de/>, with permission.

Heino (2005) likewise found that functional richness of macroinvertebrates increased with increased *p*H, with total nitrogen, water color, and substrate particle size also varying with moss cover in 111 boreal headwater streams in Finland. The functional structure depended on these same variables with its dominant pattern being related to increase of shredder-sprawlers and decrease of scraper-swimmers in acidic conditions.

Frost (1942) compared the fauna on the mosses in acid and alkaline streams in her survey of River Liffey, Ireland. **Chironomidae** (Figure 9) constituted 40-54% of the fauna in these streams. In the carboniferous limestone sites,

Fontinalis antipyretica (Figure 18) and ***Platyhypnidium riparioides*** (Figure 19) dominated in a *p*H range of 7.4 to 8.4. The stonefly fauna of these mosses was comprised of predominantly ***Isoperla*** (Figure 20). The dominant caddisfly genus was ***Hydropsyche*** (Figure 13). Mayflies included **Ephemerellidae** (Figure 8) (mean 533 per sample of 200 g wet weight), ***Baetis*** (Figure 2), and ***Caenis*** (Figure 21). The blackfly ***Simulium*** (Figure 22) was common. In the acid streams (peat bog drainage), the *p*H ranged 4.4-6.8, and the bryophytes were dominated by ***Fontinalis squamosa*** (Figure 14) with a small coverage by the leafy liverwort ***Scapania undulata*** (Figure 10). The stonefly fauna was comprised of ***Protonemura*** (Figure 104), ***Amphinemura*** (Figure 105), ***Leuctra*** (Figure 49), and ***Chloroperla*** (Figure 23). ***Polycentropus*** (Figure 24) was the predominant caddisfly.

Figure 18. ***Fontinalis antipyretica***, home to the stonefly ***Isoperla*** and net-spinning caddisfly ***Hydropsyche***. Photo by Andrew Spink, with permission.

Figure 19. ***Platyhypnidium riparioides***, home to the stonefly ***Isoperla*** and net-spinning caddisfly ***Hydropsyche***. Photo by Andrew Spink, with permission.

Figure 20. ***Isoperla similis*** naiad, member of a genus that inhabits ***Fontinalis antipyretica*** (Figure 18) and ***Platyhypnidium riparioides***. Photo by Donald S. Chandler, with permission.

Figure 21. ***Caenis youngi*** naiad, member of a genus that sometimes inhabits ***Fontinalis antipyretica*** (Figure 18) and ***Platyhypnidium riparioides***. Photo by Bob Newell, with permission.

Figure 22. ***Simulium*** (blackfly) larvae showing the large numbers that can occupy one rock – or moss. Photo by F. Christian Thompson, through USDA public domain.

Figure 23. **Chloroperlidae** naiad, a detritus inhabitant, including mosses. Photo by Bob Henricks, with permission.

Figure 24. ***Polycentropus*** larva, a dominant caddisfly among ***Fontinalis*** in acid streams. Photo by Jason Neuswanger, with permission.

In a similar study, Willoughby and Mappin (1988) found that growth of the mayfly ***Serratella ignita*** (Figure 25) was similar when fed on food from acid or alkaline streams. In acid streams they fed on the leafy liverwort ***Nardia compressa*** (Figure 11) with the filamentous alga ***Klebsormidium subtile*** (**Chlorophyta**; see Figure 26), whereas in the alkaline streams they ate the moss ***Platyhypnidium riparioides*** (Figure 19) with the epiphytic diatom ***Cocconeis placentula*** (Figure 17). But if the alga ***Klebsormidium subtile*** was absent in the acid streams, they were unable to subsist on the liverworts alone.

Figure 25. ***Serratella ignita*** naiad, a mayfly species that can subsist in both acid and alkaline streams, feeding on bryophytes and associated algae. Photo by J. C. Schou, with permission.

Figure 26. ***Klebsormidium flaccidum***, a green alga associated with ***Nardia compressa*** in acid streams, providing food for ***Serratella ignita***. Photo by Sarah Kiemle, with permission.

Bryophyte Structure

Not all bryophytes are created equal, despite their frequent treatment as one entity in ecological studies. Their structures can differ greatly, and this has a strong influence on which organisms can live there. This structure is seldom considered in describing the habitat and the influences of the bryophytes on the inhabitants. Let's consider a few and the differences they offer.

Scapania undulata

This is a leafy liverwort whose chemical components of terpenoids have already been mentioned. Its growth form is somewhat layered (Figure 27), and its leaves are **conduplicate** (Figure 28). That is, the leaf is folded over so that the smaller portion is on top. This fold provides a protected area where several small insects such as the stoneflies ***Leuctra*** (Figure 49) and ***Nemoura*** (Figure 40) like to hide (Glime 1968). Its layered effect makes it somewhat more open to the water, permitting predators to penetrate more deeply in search of prey, a problem that is avoided by the small insects that can hide within the folds of the leaves.

Figure 27. ***Scapania undulata*** showing layered effect. Photo by Hermann Schachner, through Creative Commons.

Figure 28. ***Scapania undulata*** showing folded leaves with smaller lobes on top. Photo by Florent Beck, through Creative Commons.

Hygroamblystegium spp.

This genus, including ***Hygroamblystegium fluviatile*** and ***H. tenax***, forms thick mats on rocks (Figure 29). Its extensive branching provides an array of spaces within the mat, affording protection from both the current and most larger insects and fish. The leaf has a strong costa (Figure 30) that is used by some caddisflies in the construction of their cases (to be discussed later in the **Trichoptera** subchapter). Its small leaves and branches afford small spaces unavailable to larger insects, thus limiting the species and life stages that can live there.

Figure 29. ***Hygroamblystegium tenax*** in a dry stream bed. Photo by Janice Glime.

Figure 31. ***Platyhypnidium riparioides***, home to many kinds of aquatic insects. Photo by Michael Lüth, with permission.

Figure 30. ***Hygroamblystegium fluviatile*** showing cupped leaves and strong costa used by some caddisflies in construction of their cases. Photo by Hermann Schachner, with permission.

Figure 32. ***Platyhypnidium riparioides***, showing leaves where many kinds of insects are able to hide. Photo by John Hribljan, with permission.

Platyhypnidium riparioides

This species occurs in many of the same streams as those of ***Hygroamblystegium fluviatile*** (Figure 30). It is a widespread species that forms a chambered mat. It has somewhat larger leaves than ***H. fluviatile*** but creates a similar habitat with many species in common. It is not unusual to find these two species on the same rock, often intermixed. ***Platyhypnidium riparioides*** (Figure 31-Figure 32) affords somewhat larger spaces within the mat. Its costa is reduced and much thinner than that of ***Hygroamblystegium*** species and does not seem to be particularly useful for case building.

Fissidens grandifrons

Fissidens grandifrons (Figure 33) tends to prefer alkaline streams. It is a large moss with flat branches that are layered somewhat like those of ***Scapania undulata*** (Figure 27-Figure 28), an inhabitant of acid streams. It occurs in very cold water and waterfalls, both conditions that provide it access to more CO_2 than would be available in un-aerated warmer water. I never searched this moss for insects, but my collections of it did not reveal any conspicuous fauna. It is a stiff moss and its preference for torrential water may discourage them.

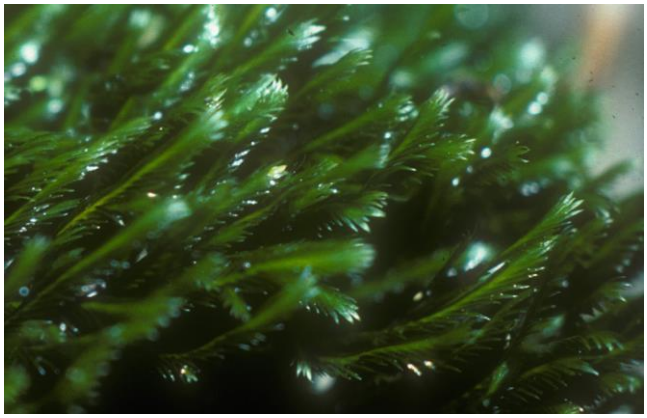

Figure 33. ***Fissidens grandifrons*** showing the flat branches and accessible spaces between them. Photo by Janice Glime.

Fontinalis spp.

Fontinalis species are large mosses (Figure 34). They have a **streamer** growth form in which all stems dangle in the same direction as the flow of water, at least where there is a distinct flow. The end portions of the stems are

exposed, harboring **Simuliidae**. The leaf structure varies among species, thus providing differing suitability for the insects. ***Fontinalis antipyretica*** (Figure 35) has large, keeled leaves that form a 3-sided branch with well protected interior space. However, this space may be somewhat difficult for many insects to enter due to the close **appression** (state of being pressed close to) of leaves. ***Fontinalis hypnoides*** (Figure 36) has narrow, more or less flat leaves that do not provide much enclosed space. In between these two extremes are various degrees of enclosure and access to that enclosure. The flat surface of the branch of ***F. antipyretica*** would be ideal for blackfly larvae, but this ***Fontinalis*** species is often not successful in the very fast flow needed by these larvae. If the moss is in fast flow, the keel is easily worn away and the leaves become tattered. However, in cool streams there is usually sufficient oxygen for both the moss and blackflies to survive.

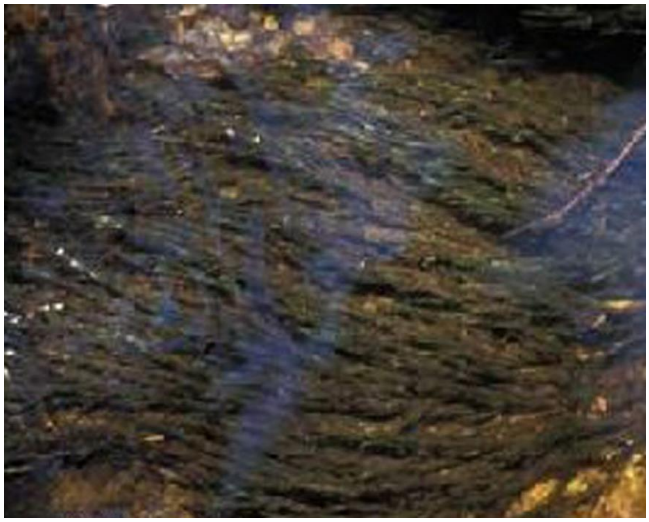

Figure 34. ***Fontinalis dalecarlica***, a refuge for invertebrates during low water levels. Photo by Kristoffer Hylander, with permission.

Figure 35. ***Fontinalis antipyretica*** demonstrating the folded, overlapping leaves that give little accessibility to the interior leaf space. Photo by David T. Holyoak, with permission.

Figure 36. ***Fontinalis hypnoides*** showing flattened, narrow leaf. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Fontinalis squamosa (Figure 37), a European species, is one of the several intermediate species. Its leaves are concave and provide hiding places within the concavities. Like all ***Fontinalis*** species, it lacks a costa. This species has been indicated as home to numerous insects in many European stream studies.

Figure 37. ***Fontinalis squamosa*** showing concave leaves. Photo by Michael Lüth, with permission.

Flow Regimes

Flow regimes provide another limitation for bryophyte inhabitants. Many bryophytes live in areas of high flow that is too abrasive for the establishment of **tracheophytes** (plants with lignified vascular tissue, *i.e.*, all plants that are not bryophytes). At the same time, many insects require protection from the rapid flow. Furthermore, insects drift in streams for various reasons – searching for food, making a false move that puts them in the current, overpopulation, finding a site for pupation, and dislodgment due to changes in flow.

Baker *et al*. (1996) found that the hydraulic stability of streams over multiple years determined whether a site was dominated by periphyton, bryophytes, or tracheophytes. Variations within the year can control periphyton biomass, with low velocities favoring both periphyton and tracheophytes that serve as additional substrate for them. Bryophytes, on the other hand, are often restricted to areas of high velocity; these same high velocities restrict colonization and accumulation of detritus.

Bryophytes modify the internal flow of water. The arrangement of sedimentary deposits and fauna below the leaves of submerged stream bryophytes supports this concept of internal current modification (Devantery 1995). Using ***Platyhypnidium riparioides*** (Figure 19) and colored liquid, Devantery was able to demonstrate that a single leaf of this moss caused symmetrical twirling behind it. Between the leaves he observed a retrocurrent in the direction of the leaf. This current was slowed progressively and directed the water toward the leaf insertion, explaining the accumulation of detritus there. The same hydrodynamics also occurred in a second species of bryophyte that had a different leaf morphology.

Certain insects take advantage of refugia, especially during periods of high flow (Lancaster & Hildrew 1993). Bryophytes are able to provide such refugia and are likely to be especially important for such species as ***Nemurella pictetii*** (Figure 38) and larger naiads of ***Leuctra nigra*** (Figure 39), both stoneflies known from bryophytes. Lancaster and Hildrew found that seasonal flow conditions affected the distribution of these two species in streams after high-flow events, but that these seasonal differences in flow seemed to have little effect on the **Chironomidae** or the young **instars** (instar is developmental stage between molts of an insect) of ***Leuctra nigra***.

Figure 38. ***Nemurella pictetii*** naiad, a species that uses bryophytes as refugia. Photo by Urmas Kruus, with permission.

Figure 39 ***Leuctra nigra*** naiad, a species that uses bryophytes as refugia. Photo by J. C. Schou, with permission.

Flow Rates

One possible role of bryophytes as a habitat for insects and other invertebrates is their ability to provide a refuge with multiple current velocities (Madaliński 1961; Elliott 1967a; Gurtz & Wallace 1984; Suren 1992a, b; Glime 1994). Hence, organisms can migrate within the bryophyte mass to locate the current velocity that meets their needs. Macan and Worthington (1951) suggested that mosses can "profoundly influence the fauna by providing a foothold for animals which otherwise could be swept away by the current."

Devantery (1987) reminds us of the importance of flow in contributing to the accumulation of food resources in the bryophyte mat. With regard to the moss ***Platyhypnidium riparioides*** (Figure 19), Devantery considers that the moss increases the spatial uniformity, a perspective that seems to be in contrast with those who consider the moss to increase the complexity of the habitat (Dražina *et al*. 2011). The flow serves as an antagonist with the danger that it can dislodge the bryophytes.

Flow rates approaching the bryophytes influence the insects that make those bryophytes home. The **Chironomidae** (Figure 9) are reduced by higher flow velocities associated with ***Fontinalis antipyretica*** (Figure 18), whereas the smallest of the **Simuliidae** larvae (Figure 22) are positively influenced (Linhart *et al*. 2002a, b). This may relate to available food, with the Simuliidae trapping fine particles with their head fans and **Chironomidae** living among the detritus that has been trapped by the moss.

Overturned Rocks

The famous statement, "a rolling stone gathers no moss," applies in its literal sense as well as the figurative. Bryophytes cannot grow under an overturned rock, and rolling is abrasive, damaging new stems and knocking off older clumps. For stream ecosystems, these dangers prevail. Englund (1991) found that 16.7% of the moss-covered stones in North Swedish woodland streams had been overturned in the last few years. Small stones rarely had mosses (See also Slack & Glime 1985), a factor most likely related to their instability. But when stone size exceeded more than 12 cm, mosses were abundant even on rocks that were not embedded into the substrate.

Englund (1991) experimented on the effects of overturning not only on the mosses, but also on their invertebrate fauna. Overturning, as expected, reduced both diversity and abundance of fauna as well as reducing the dry weight of mosses. Nevertheless, 3 out of 16 invertebrate taxa increased, predominantly on the moss-covered underside. For the remaining taxa, peak densities occurred on the upper moss-covered sides of control stones, and these densities decreased on the overturned stones. Despite the introduction of insects through stream drift (see below), recovery was still weak 14 months later, probably because of the slow recovery of the mosses.

Life History and Flow

For insects living in streams, the habitat is likely to be too fast at times and too dry at others. Yamamura (2009) concluded that the variability of the flow regime can limit the distribution and the life history traits of aquatic insects.

Some have solved this transient habitat problem by life cycle stages that either are dormant or that do not require water. Among these, the egg stage is a suitable stage for surviving drought in some stoneflies, mayflies, and dipterans (Ward 1992). In the case of the stonefly ***Nemoura*** (*s.l.*) (Figure 40), a common moss dweller, in a Welsh stream, the adults emerge at the end of the drought (Hynes 1958; Ward 1992). In their short adult life stage,

they may take advantage of newly formed pools in the stream for oviposition before the stream returns to normal flow.

Figure 40. ***Nemoura*** naiad, a common bryophyte dweller. Photo by Bob Henricks, with permission.

Mosses may often play an important role in providing moist sites for the aquatic insects during fluctuating conditions, but their role at such times has scarcely been investigated. In a Welsh mountain stream, severe flooding transported large quantities of gravel (Hynes 1968). Gravel-dwelling insects were greatly reduced, and the moss cover was reduced by 80%. But the fauna living among the remaining mosses was not significantly decreased. The stoneflies, caddisflies, and **Elmidae** (riffle beetles; Figure 41) recolonized the area before any reproduction could have contributed to their recovery. Hynes hypothesized that these insects migrated to deep within the benthic zone (away from abrasion) during the flood and then reappeared after the water level returned to normal.

Figure 41. **Elmidae** adult, a rapid colonizer of bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Water Level

Water level changes bring problems of not only hydration but also food availability for aquatic insects. Open-water carnivores can easily move and will most likely still have access to smaller insects and other invertebrates for food. But those that feed on periphyton, and most likely on high quality detritus, may depend on the chambered bryophyte clumps for their dinner. Fortunately, these bryophytes help to provide both hydration and food for herbivores and detritus feeders. As the water level decreases, bryophytes can act like a filter to trap detrital matter from the slow water. In a Québec, Canada, stream, Cattaneo *et al*. (2004) found that many of the invertebrates moved to or remained among mosses (***Fontinalis dalecarlica***; Figure 34) at low water levels. Water depth explained 50-80% of the variation in the invertebrate biomass among the mosses and the biomass was lower on shallow mosses that had more frequent exposure. Grazers were more common in the moss habitat than in the gravel, but carnivores such as **Plecoptera** and **Odonata** were in the gravel.

Stream Drift

Stream drift is a natural occurrence among stream fauna, especially insects (Anderson & Lehmkuhl 1968). Waters (1972) emphasized that this is an episodic event and not a continuous phenomenon. The drift organisms are bottom and vegetation organisms. When stream discharge is reduced by seasonal events, **catatrostrophic drift** can occur. Two primary organisms in such drift in Oregon, USA, are ***Simulium*** sp. and ***Baetis tricaudatus***, both bryophyte dwellers (Corrarino & Brusven 1983).

Catastrophic drift (Minckley 1964) occurs from a physical disturbance such as flooding, **anchor ice** (ice anchored to bottom) (O'Donnell & Churchill 1954), pollution (Coutant 1964), drought, and high temperatures (Wojtalik & Waters 1970; Reisen & Prins 1972 for ***Simulium*** - Figure 22). **Behavioral drift** occurs at a particular time of day or night; it may result from crowding, competition, need for food, predation, making a new case, or attempting to reach land at emergence time (Waters 1972). **Constant drift** is comprised of small numbers that are always present as organisms move about and become dislodged from their substrates (Waters 1972).

Most drift occurs at night (Bishop 1969; Elliott 1965, 1968; Holt & Waters 1967), and it always moves the drifters downstream, at least initially. This night-time drift typically has two peaks: one just after darkness begins and one just before dawn (Waters 1972). But in some species, younger individuals may drift in the daytime and older, larger individuals at night (Anderson & Lehmkuhl 1968). Light often suppresses drifting in night drifters (Holt & Waters 1967); a full moon on a clear night can suppress it (Anderson 1966; Bishop & Hynes 1969).

Brusven (1970) found that the riffle beetle ***Optioservus seriatus*** (Figure 42) was much more likely to drift as an adult compared to its larval form. This species demonstrated the complexity of the drift phenomenon, with drift relating closely to density in one stream but not in the other in this study.

Larimore (1974) studied a very different kind of stream in the Salt Fork Basin, Illinois, USA. This stream ran through farmland where farm runoff was common and rooted macrophytes and bryophytes were absent. Only **Chironomidae** (Figure 9) among the drift organisms matched those found in cooler streams with rocky bottoms discussed above.

Figure 42. ***Optioservus seriatus*** adult, an insect more likely to drift as an adult than as a larva. Photo from ISUInsects.org, through Creative Commons.

Drift distances are usually not far. McLay (1970) found that the maximum drift in a New Zealand stream was 45.7 m, with a mean of only 10.7 m. Waters (1965) found that ***Baetis tricaudatus*** (Figure 43) travelled 50-60 m, but Elliott (1971a) showed that this strong swimmer was also capable of dropping out of the drift rapidly. Elliott (1967a) found that when dense macrophyte vegetation was present the maximum drift distance was only about 10 m. Nevertheless, this is sufficient to redistribute the insects and reduce local population competition.

Figure 43. ***Baetis tricaudatus*** naiad, a drifter that can travel 50-60 m in the drift, or drop out rapidly. Photo by Bob Henricks, with permission.

Many of the species enter the drift as young naiads and larvae, permitting them to disperse and to reduce population competition (Anderson 1967; Elliott 1967a, b; Waters 1969). But more frequently it is the larger stages later in the life cycle that enter the drift (Anderson 1967; Elliott 1967a; Müller 1966; Ulfstrand 1968). While drifting permits macroinvertebrates in streams to seek a more favorable location and to colonize new habitats, it poses its own set of threats (Brittain & Eikeland 1988). The insects may fall prey to predatory fish or fail to stop at a favorable habitat before reaching a quiet area of the stream where drift can no longer help them to relocate.

Some insects enter the drift to avoid or escape from predators. In experiments the net-spinning caddisfly ***Ceratopsyche*** *bronta* (Figure 44) moved from one area to another in an artificial stream when the predator stonefly ***Acroneuria*** *lycorias* (Figure 45) was present (Michael & Culver 1987). However, it did not exhibit the same drift response to the predator megalopteran *Corydalus cornutus* (Figure 46). Michael and Culver suggested that the caddisfly might have been unable to detect the megalopteran.

Figure 44. ***Ceratopsyche bronta*** larva, an insect that drifts in response to the presence of the predator stonefly ***Acroneuria lycorias***. Photo by Bob Henricks, with permission.

Figure 45. ***Acroneuria lycorias*** naiad, predator on the caddisfly ***Ceratopsyche bronta*** larvae. Photo by Tom Murray, through Creative Commons.

Figure 46. ***Corydalus cornutus*** larva, a stream predator. Photo by Alan Cressler, with permission.

Researchers were curious about how the upstream positions got repopulated. Elliott (1971b) marked insects and found that some immature insects were able to move upstream on the stream bottom, especially small naiads of stoneflies and mayflies, small larvae of true flies, and beetle larvae. In winter, upstream movement was about 30% of downstream drift; in spring and summer it fell to only 7-10%. Madsen *et al*. (1973) examined upstream movement in adult mayflies and stoneflies and found that the representative of the common moss-dwelling stonefly genus ***Nemoura*** (Figure 40) did not move upstream, whereas the mayflies ***Caenis rivulorum*** (Figure 47), ***Baetis rhodani*** (Figure 2), ***B. vernus*** (Figure 48), and ***Serratella ignita*** (Figure 25) all moved upstream; all three of these mayfly genera are known from bryophytes. Furthermore, females migrated upstream more than males.

Figure 47. ***Caenis rivulorum*** naiad, a mayfly whose adults move upstream to lay eggs. Photo by Urmas Kruus, with permission.

Figure 48. ***Baetis vernus*** adult, a species in which females fly upstream to lay eggs. Photo by Walter Pfliegler, with permission.

Elliott (1971a) divided the drift invertebrates into three groups based on their ability to return to a substrate. The first group apparently had no control over their return to a substrate and did so at the same rate as dead organisms. This group included the **Chironomidae** (Figure 9). The second group includes several bryophyte dwellers, including ***Leuctra*** (Figure 49) and ***Simulium*** (Figure 22). These insects travelled shorter distances and were able to return to the substrate more quickly than dead ones at low velocities (10-12 cm sec^{-1}) but not at faster velocities (≥19 cm sec^{-1}). The third group, which included bryophyte dwellers such as ***Serratella ignita*** (Figure 25), ***Hydropsyche*** spp. (Figure 13), and ***Baetis rhodani*** (Figure 2), returned to the substrate significantly faster and drifted significantly shorter distances at all velocities tested; ***Baetis*** and ***Simulium*** are usually the insects with the highest numbers in the drift (Waters 1972). Caddisflies with cases fall out of the drift very quickly.

Figure 49. ***Leuctra*** sp naiad. Photo by Guillaume Doucet <http://guillaume.doucet.free.fr/>, with permission.

Elliott (2003) examined dispersal in nine genera of aquatic invertebrates, most of which occur among bryophytes. He found that dispersal of invertebrates in the streams was not density dependent. Rather, it was a constant percentage of the initial number of each species. The most rapid dispersers, with 70-91% dispersing within 24 hours, were the carnivores ***Perlodes*** (Figure 50), ***Rhyacophila*** (Figure 116), and ***Isoperla*** (Figure 20), travelling up to 13.5 m per day. ***Protonemura*** (Figure 104) and ***Rithrogena*** (Figure 51) exhibited about 50% dispersal within 24 hours and travelled only about 8 m per day. The third group, ***Ecdyonurus*** (Figure 15), ***Hydropsyche*** (Figure 13), ***Gammarus*** (Figure 52), and ***Baetis*** (Figure 2, Figure 48), only had about 33-40% dispersal in 24 hours and travelled only 5.5-7 m per day. All of these genera dispersed upstream. These examples do not answer the question of why drift, but they suggest that some of that downstream drift is compensated by upstream movement.

Figure 50. ***Perlodes microcephala*** naiad, a genus in the high dispersing insects of Elliott 2003. Photo by Niels Sloth, with permission.

Figure 51. ***Rhithrogena impersonata*** naiad, a genus with 50% dispersal in 24 hours. Photo by Donald S. Chandler, with permission.

Figure 52. ***Gammarus pulex***, a genus in the dispersing invertebrates of Elliott 2003. Photo by Niels Sloth, with permission.

Lehmkuhl (1969) found that the six mayfly species in his study, including the sometimes moss-dweller ***Baetis tricaudatus*** (Figure 43), were displaced by winter flooding. He found that in these species drift was not related to habitat. Two of the species that were abundant in the riffle areas were scarce in the drift. In the lab, drift rate did not correlate with ability of a species to hold to its substrate.

Lehmkuhl and Anderson (1972) demonstrated that drift of individual species is seasonal. Within the four species of **Ephemeroptera** studied, some species had peak drift in October and others in May. Winter floods accounted for lesser peaks in drift. Periods of low drifting occur when a species is in its egg state, suggesting that life cycle stages are among the determinants of who is drifting.

Some insects enter the drift at the time of emergence, not by choice, but because they must at that time break through the water-air interface and penetrate the surface tension. If there is no suitable emergent rock or vegetation, this becomes a nearly impossible task. Bryophyte-covered rocks can afford a better place to climb out than a smooth rock. However, there is thus far no study to determine if any insect group might seek out bryophytes as opposed to just rocks for this dangerous endeavor.

The behaviors of the ***Hydropsyche*** spp. (Figure 13) are worthy of note. This net-spinning caddisfly must live near the water surface where it can trap food in its nets (Edington 1968). When released into the water, larvae would swim with side-to-side movements toward the surface (Edington 1965; Elliott 1971a). When the velocity was slow, they returned to the bottom (Elliott 1971a). When they encountered mosses in swift-flowing areas they made "firm contact." It appears that bryophytes may have a role in catching these drifters.

Elliott (1967a) suggested that aquatic plants served as a natural net for drifting insects. Previously Elliott (1965) examined invertebrate drift in a Norwegian mountain stream where bryophytes formed a dense bottom cover. He did not show a direct link between the bryophyte fauna and drift, but did list the dominant insects in both. Using 400 cm^2 samples, he found ***Baetis*** sp. (Figure 2), ***Simulium*** spp. (Figure 22), ***Rhyacophila*** sp. (Figure 79), **Polycentropidae** (Figure 24), and **Plecoptera** (Figure 49). When he calculated those insects in the water column above a square meter of bottom at any time, he found that the values were extremely low, although all the insects among the top taxa in the mosses except **Polycentropidae** were also in the drift.

At least some of the bryophyte dwellers are drift organisms, including ***Simulium*** (Figure 22), ***Isoperla*** (Figure 20), and ***Ephemerella*** (*s.l.*) (Figure 8) (Minshall & Winger 1968). In these three genera, the drift is suppressed by light, including that of a full moon on a clear night. Density may play a role in the number of individuals entering the drift, as in **Capniidae** (Figure 109), ***Ephemerella*** sp., and ***Hydropsyche*** sp. (Figure 13) in a South Carolina, USA, stream (Reisen & Prins 1972; see also Waters 1962, 1966). And, to my surprise, Minshall and Winger (1968) found that reductions in flow cause an increase in drift. The latter may relate to the need for a new location to gain suspended food or oxygen. To this end, ***Simulium*** larvae may drift at least 100 m (Carlsson 1967). Elliott (2002) calculated the rate of drift and found that most of the organisms had a very constant amount of time spent in a drifting event. For ***Serratella ignita*** (Figure 25) the mean drift time was 28.8 s, whereas for ***Baetis rhodani*** (Figure 2) it was 9.4 s, the same drift time as for the amphipod ***Gammarus pulex*** (Figure 52). For the blackfly ***Simulium*** it was only 6.4 s, with their choice of rapid water accounting for the 100 m drifting they can accomplish.

In Oregon, USA, Anderson and Lehmkuhl (1968) likewise found known moss dwellers in the drift: the mayflies ***Paraleptophlebia*** (Figure 53) and ***Baetis*** (Figure 2), the stoneflies ***Nemoura*** (Figure 40), ***Capnia*** (Figure 109), and possibly ***Leuctra*** (Figure 49) (small ***Capnia*** and ***Leuctra*** are difficult to distinguish), dipterans **Chironomidae** (Figure 9) and **Simuliidae** (Figure 22). Dendy (1944) likewise found ***Baetis***, ***Nemoura***, **Simuliidae**, **Chironomidae**, and **Hydropsychidae** (Figure 13) in the drift in a stream in Michigan, USA, but added significant numbers of the mayfly ***Ephemerella*** (*s.l.*) (Figure 8) and caddisfly ***Brachycentrus americanus*** (Figure 54) to those found by Anderson and Lehmkuhl. To these, Reisen and Prins (1972) added the stoneflies ***Isogenus*** (probably now ***Isogenoides***; Figure 55) and ***Isoperla*** (Figure 20).

Figure 53. ***Paraleptophlebia bicornuta*** naiad, a moss-dweller genus that enters the drift. Photo by Bob Newell, with permission.

Figure 54. ***Brachycentrus americanus*** larva, moss dweller that enters the drift. Photo by Donald S. Chandler, with permission.

Figure 55. ***Isogenoides frontalis*** larva, a moss-dweller that enters the drift. Photo by Donald S. Chandler, with permission.

Bryophytes may provide safe sites for drifting organisms, primarily insects. There is a periodicity in stream drift, with light, even strong moonlight, suppressing activity (Albrecht 1968). Numerous organisms, particularly stoneflies, mayflies, and caddisflies, become detached from their substrate and join the water current (Bishop & Hynes 1969). Diptera are day-active and contribute significant numbers to daytime drift. Lest they travel ultimately to a lake or even the distant sea, these drifting organisms must find a suitable substrate where they can cling against a sometimes raging current. Furthermore, it is during these excursions that they are most visible and vulnerable to predation by birds and especially fish.

Bryophytes would seem to provide an ideal location for regaining their composure and taking a more leisurely approach to locating a suitable settling place. The 3-d surface of the bryophyte provides numerous "handles" for hanging on in the current and gives the insects either an instant home or one that can be traversed while maintaining a safe hold to something permanent. On the other hand, one theory for the cause of drift is to decrease population numbers (Müller 1954; Waters 1961, 1962; Pearson & Franklin 1968; Bishop & Hynes 1969). If such is the case, a rock with both smooth surface area and bryophyte cover would support such loss by forcing at least some individuals to the smooth rock as the bryophyte itself becomes overpopulated. This would seem to eventually provide a selection factor against those organisms that did not do their nightly foraging among the mossy safe site. Is there really a selection factor involved in moss-seeking behavior?

Glime and Clemons (1972) set out to determine the relative importance of bryophytes in catching such insects and constructed artificial mosses to determine how the new colonizers compared to the organisms in the drift. Clemons (unpubl data; Glime & Clemons 1972) used string mosses to determine the use of substrata similar to mosses as a catching net for drifting organisms and compared this substrate to that of real mosses and Visqueen (polyethylene plastic sheeting) strips. In the 24 hours following the placement of 7 of these artificial mosses, insects were found on the strings. These included the mayfly ***Baetis*** sp. (Figure 2), stoneflies ***Amphinemura nigritta*** (=*Nemoura venosa*) (Figure 56) and ***Leuctra*** sp. (Figure 49), blackflies ***Cnephia*** sp. (Figure 57) and ***Prosimulium mixtum*** (Figure 58), midges **Chironomidae** (Figure 9), and the caddisfly ***Lepidostoma*** sp. (Figure 59) occurring in more than one of the string habitats. The Visqueen strips had a smaller and less diverse fauna. While this experiment provides evidence that insects can settle on such substrates rather quickly from the drift, much more study is needed to determine the importance of bryophytes in providing safety nets for drifting insects. Gurtz and Wallace (1984) found that following a major disturbance that dislodged many of the insects, it was moss-covered rock faces that increased in insect density more than any other substrate. Furthermore, they considered that the mosses may enhance the stability of the substrate on which they reside.

Figure 56. ***Amphinemura nigritta*** naiad, a rapid bryophyte colonizer. Photo by Donald S. Chandler, with permission.

Figure 57. ***Cnephia*** adult, a genus that sometimes lives among bryophytes and enters the drift. Photo by Sam Houston, with permission.

Figure 58. ***Prosimulium mixtum*** larva, a blackfly that lives among bryophytes and enters the drift. Photo by Tom Murray, through Creative Commons.

Figure 59. ***Lepidostoma*** larva, a drifting caddisfly that sometimes lives among bryophytes. Photo by Jason Neuswanger, with permission.

In alpine streams the drift pattern may differ. Hieber *et al*. 2003) found no night-day differences in these streams. They found that **Chironomidae** (Figure 9) were the dominant drifting organisms, so one might look at this group in alpine streams as creating more food for fish in streams with mosses than in those without.

The complex structure of bryophytes may not only catch drift, but it may also deter stream drift. Holomuzki *et al*. (1999) found that resettlement choices after drifting by hydropsychid caddisfly larvae depended on the complexity of the algal community. Drift entry of hydropsychids due to stonefly predation increased on rocks with a biofilm, but not on rocks with a thick periphyton mat or macroalgae such as *Cladophora* (Figure 60), with drift inversely related to the amount of *Cladophora* on the rocks. Since bryophytes are even more complex in structure, it is reasonable to assume that they reduce drift.

Figure 60. ***Cladophora crispata***, a filamentous alga that keeps ***Hydropsychidae*** from entering the drift in the presence of predatory stoneflies. Photo by Yuuji Tsukii, with permission.

It is interesting that when Perić *et al*. (2014) sampled the invertebrate drift in a moss-rich **karst** (landscape underlain by limestone that has been eroded by dissolution, producing characteristic landforms) stream system, they did not find the **Chironomidae** (Figure 9) (3.9%) to be the most abundant. Rather, the most abundant insects were the beetles in **Elmidae** (Figure 41) (13.2%) and blackflies **Simuliidae** (Figure 58) (12.2%).

So let's revisit the possibility that other bryophyte dwellers besides **Chironomidae** do not enter the drift as readily as insects on other substrates. Brusven *et al*. (1990) found that in a channel of the South Fork Salmon River, Idaho, USA, the 20% moss-covered portion (***Fontinalis neomexicana***, Figure 4) had 1.6-7.2 times the diversity of the moss-free channel and 1.4-6.1 times the biomass. But the mossy portion did not have any greater numbers in the drift than did the moss-free channel. This, however, does not offer us much on which to base a conclusion because the study only included daytime drift. Their drift organisms were more than 50% **Chironomidae** (Figure 9), a group that drifts equally in day and night (Anderson & Lehmkuhl 1968). The implications for fish are that the bryophytes do not benefit them because the food organisms they house do not increase the daytime drift, at least in this one example.

Safe Sites

For many insects, the mosses offer a safe site, a pool-like environment in which they can forage for food without danger of being swept away by rapidly flowing water. Beetles (**Coleoptera**), scuds (***Gammarus***; Figure 52) and mites occupy only sheltered niches and mosses in the Welsh Dee (Badcock 1949). On vertical faces of waterfalls, the dipteran ***Limnophora*** (Figure 61) can be found only in moss (Badcock 1949).

Figure 61. ***Limnophora*** larva, sometimes a bryophyte dweller. Photo by Stephen Moore, Landcare Research, NZ, with permission.

In aquatic habitats, fish are a major predator on insects. The result is that fishless lakes have a higher insect species richness and diversity than lakes inhabited by fish, as demonstrated for chironomids (midge larvae) (Mousavi *et al*. 2002). Bryophytes are typically inhabited by many **Chironomidae** (Figure 9) and when present in lakes or streams they can provide safe sites with loads of detrital food.

Several studies have alluded to the possibilities of bryophytes in providing a **refuge**, a location in the stream where the small organisms can escape predation by larger ones. For example, Parker *et al*. (2007) found twice as many insects on ***Fontinalis novae-angliae*** (Figure 62) as on *Podostemum ceratophyllum* (Figure 62). One possibility is that the insects are avoided because the moss provides an unpalatable location – an **enemy-free space**. Parker *et al*. (2007) remind us that a number of studies have shown that small herbivores that use plants as both a habitat and a food source may be protected by living on hosts that are chemically defended against wood-be insect consumers. Aquatic mosses may be just such safe sites. To test this hypothesis, Parker and coworkers observed the feeding habits of the Canada goose (*Branta canadensis*, Figure 63-Figure 64) and a crayfish (*Procambarus spiculifer*, Figure 65). In a riverine system where both the riverweed *Podostemum ceratophyllum* (Figure 62) and the moss ***Fontinalis novae-angliae*** (Figure 62) occurred, both animals consumed riverweed in preference to the moss. This was despite the fact that the moss comprised 89% of the plant biomass. At the same time, there were twice as many macroinvertebrates among the mosses as associated with the riverweed. Examination of the moss chemistry revealed the presence of C_{18} acetylenic acid, octadeca-9,12-dien-6-ynoic acid, a compound that deterred the crayfish from eating it. Some invertebrates, on the other hand, had different connoisseurial preferences; the amphipod ***Crangonyx gracilis*** (Figure 66) and the isopod ***Asellus aquaticus*** (Figure 67) rejected the riverweed, but consumed significant quantities of ***Fontinalis novae-angliae***. For periphyton-consuming insects, the same chemical deterrents could protect them without affecting their food source.

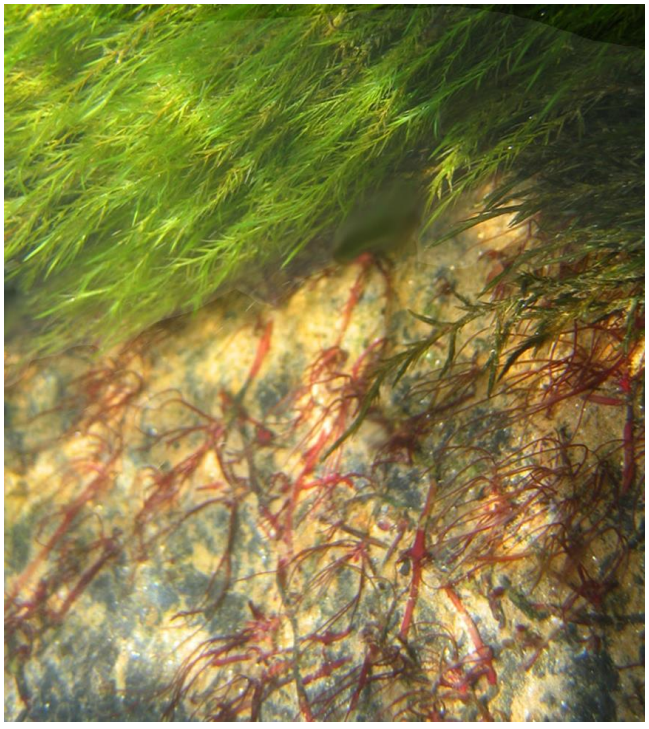

Figure 62. *Podostemum ceratophyllum* (red) and ***Fontinalis novae-angliae***, the latter protecting invertebrates from grazing by geese. Photo by John Parker, with permission.

Figure 63. Canada Goose (***Branta canadensis***) searching for food. Photo by Eileen Dumire, with permission.

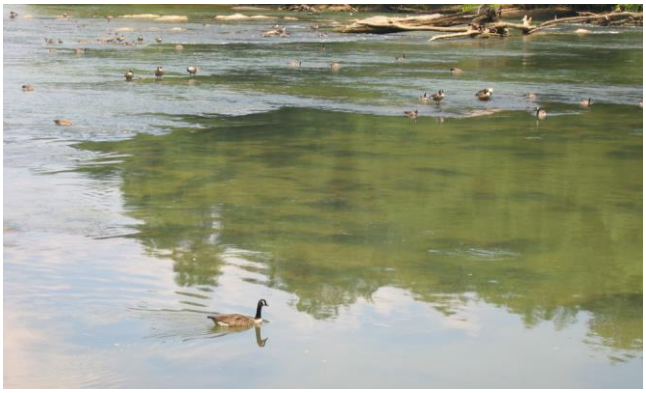

Figure 64. Canada Geese (***Branta canadensis***) grazing on *Podostemum ceratophyllum*. Photo by John Parker, with permission.

Figure 65. ***Procambarus spiculifer*** eating *Egeria*. Photo by John Parker, with permission.

Figure 66. ***Crangonyx*** sp., an amphipod ***Fontinalis*** consumer. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 67. ***Asellus aquaticus***, an isopod ***Podostemum*** avoider and ***Fontinalis*** consumer. Photo by Niels Sloth, with permission.

But bryophytes are not always selected for their provision of shelter. Using experimental reduction of bryophyte stem density in New Zealand alpine streams, Suren and Winterbourn (1991b) found that only two out of 22 taxa of invertebrates selected the bryophytic home based on shelter as the primary factor in the shaded site; none of them selected it based primarily on its offer of shelter in the sunny site. Rather, periphyton or detrital biomass were the primary influencing factors.

Winterbottom *et al*. (1997) cleverly tested the importance of refugia against the effect of reduction of shear stress during periods of peak flow by creating artificial refugia using cages of different mesh sizes to restrict the flow within cages. They compared a 1.1 mm mesh size that created a reduced flow within the cage with that of a 15 mm mesh size that did not restrict flow. They found that during periods of high flow the invertebrates accumulated more in the flow-restricted refugia than they did there during low-flow periods or in the unrestricted cages. By contrast, in a second stream with lower flow rates generally and during the experimental period, the number of invertebrates did not increase in the refugia during natural spates of increased flow (but less flow than in the first stream), suggesting that the reduced flow in the 1.1 mm mesh cages enabled them to serve as refugia in the first stream during periods of rapid flow. However, the researchers were unable to determine if the accumulation of invertebrates was by active movement to the refugia or by passive collection. Nevertheless, this experiment demonstrates that bryophytes with different mesh sizes could provide differential refugia for insects during periods of high flow rates.

Biomass and Richness

Many insects hang out among the riffles, taking advantage of the flowing water that brings food and oxygen. Dodd (2011) found that in a river community 516 out of 521 individuals collected occurred among riffles and mosses. These are the sites where biomass and richness usually reach their peaks.

Clenaghan *et al*. (1998) concluded that macroinvertebrate density and richness increased with moss weight. Wulfhorst (1994) compared the biomass of insects among mosses with those in the interstitial spaces of the substrate (Figure 68). In general, they were orders of magnitude higher (100's of times) in biomass among the mosses. These included **Ephemeroptera**, **Plecoptera**, **Trichoptera** and **Coleoptera** (EPTC).

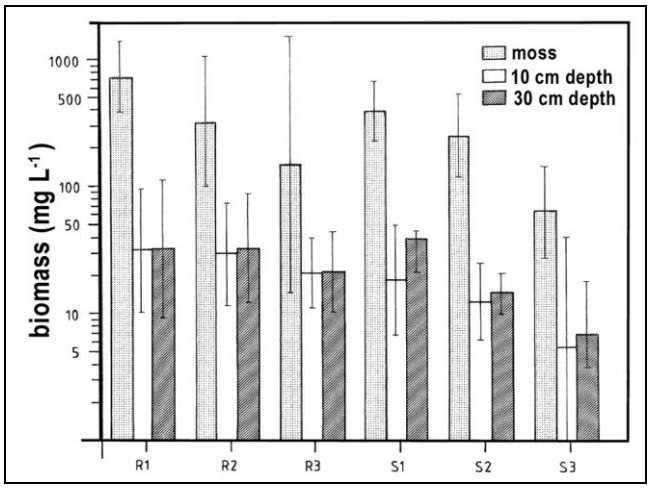

Figure 68. Combined biomass (mg L^{-1}) of **Ephemeroptera**, **Plecoptera**, **Trichoptera**, and **Coleoptera** at six stations of two brooks in the Harz Mountains in mosses and interstitial spaces of the hyporheic zone at 10 and 20 cm depth. Bars show 95% CI. N = 14 for mosses, 28-36 for interstitial spaces. Redrawn from Wulfhorst 1994.

Linhart *et al*. (2002a, b) examined the **meiobenthos** (meiofauna; between .1 mm and 1 mm in size) of two low-order streams (*i.e.*, small feeder streams) and found that these bryophytes harbored ten times as many organisms as the surrounding mineral bed. In this case, the **Chironomidae** (midge larvae, Figure 9) were the dominant organisms, but a number of other aquatic insects and other invertebrates call this location home, at least in the early stages of their lives.

Brusven *et al*. (1990) studied the effect of bryophyte biomass on macroinvertebrate density in the South Fork of the Salmon River, Idaho, USA. They compared the insect densities on sand, pebbles, cobbles, and the moss ***Fontinalis neomexicana*** (Figure 4). Insect densities in moss clumps were 4-18 times as great as those in adjacent mineral substrata. Although mosses occupied only 20% of the channel, insect density was 1.6 to 7.2 times as great, with 1.4 to 6.1 times as much insect biomass as the moss-free channel, thus accounting for nearly 50% of the insects in the stream. Midges (**Chironomidae,** Figure 9) typically comprised over 50% of the insect community, whereas

annelids were the primary non-insect invertebrates. The moss seemed to provide a safe site, at least during the day, because despite the greater number of insects present, daytime drift was not greater. Hence, the salmonid fish that feed primarily on drifting invertebrates during the day derive little benefit from the increased numbers in the bryophytes.

On the other hand, Tada and Satake (1994) found that in a cool mountain stream in Japan macroinvertebrates from ***Platyhypnidium riparioides*** (Figure 19) had 11-13 **taxa** (species), whereas bare rock bottoms had 13-14. Nevertheless, the caddisfly ***Micrasema*** sp. (Figure 69) exceeded 100,000 individuals per m^2 of mosses in November, a level that ranged 2.8-16.3 times as high as that on the bare rock bottom.

Figure 69. ***Micrasema charonis*** larva, a common genus on bryophytes. Photo by Robert G. Henricks, with permission.

Chantha *et al*. (2000) found that the invertebrate communities of bryophytes and algae in a Quebec, Canada, stream were dominated by **Chironomidae** (especially **Orthocladiinae**; Figure 9). The algae and invertebrates formed stable communities during the summer, even sustaining during strong mid-summer flooding. Like many other northern streams, the **Ephemeroptera** and **Coleoptera** were important components. The relative importance of the various taxa changed with the seasons as sizes and life cycle stages changed. Moss biomass explained 43% of the algal spatial variation, but surprisingly the periphyton did not increase proportionally with increase in moss biomass. The epiphytes were less dense per unit of bryophyte biomass as the bryophyte biomass increased in density. Insects in this system became more abundant, but smaller, as the moss biomass increased, with a net result of little change in insect biomass per moss biomass. This may be a function of decreased light for algal growth and decreased oxygen for insects in deeper parts of the moss mat.

Matthaei *et al*. (2006) found that runoff from land use could reduce both aquatic mosses and invertebrate density. The greatest decrease in richness occurred in **Ephemeroptera**, **Plecoptera**, and **Trichoptera**, the three most abundant moss-dwelling orders that move among the open spaces of the bryophyte mats.

Food Sources

Bryophytes harbor a wide variety of invertebrates that can serve as food for the larger members of the bryophyte fauna. Dražina *et al*. (2011) reported 100 taxa of meiofauna among bryophytes in a European study. For example, rotifers averaged 219 individuals per cm^3.

Bryophytes are usually predominate in the upper reaches of streams where the flow rate is greater and the stream is shaded. Shredders likewise predominate among the bryophytes in these reaches. Hawkins and Sedell (1981) found that functional groups characterized different stretches of the river continuum. Upstream in shaded reaches the shredders were dominant. Scrapers were most important in the intermediate sections. Collectors increased in importance progressively downstream. Predators were represented equally throughout the stream.

Mosses seem to afford ideal feeding locations for some kinds of insects. In particular, filterers and scrapers can be more common there than elsewhere in streams, showing a positive correlation with such habitats, whereas shredders are negatively correlated, *i.e.*, are moss avoiders (Ely 2005). On the other hand, Zalewski *et al*. (2001) found a significant correlation between **CPOM** (coarse particulate organic matter), bryophytes, and shredders. Smith-Cuffney (1987) found that mosses in streams of a clearcut community supported collector-gatherers, whereas in the forested streams the shredders formed a much larger proportion of the moss fauna.

Cattaneo *et al*. (2004) found that in a Québec stream grazers were more abundant in mosses than among gravel, suggesting that they used the periphyton. The reduction of periphyton when shallow water mosses are exposed may explain why deeper mosses might house more invertebrates.

Wallace *et al*. (1988) found that the mosses retained large amounts of detritus, providing abundant food for collector-gatherers. Like Ely, they found that scrapers reached greatest abundance on cobbles and pebbles that were free of mosses. Smith-Cuffney (1987) found that in a southern Appalachian Mountain stream, mosses in a clearcut community of a forested watershed supported predominantly collector-gatherers with shredders as a minor component. Shredders were a much larger component in the stream that drained the clearcut. Scrapers were more common in the clearcut system where periphyton were abundant. Collector-filterers such as ***Parapsyche cardis*** (see Figure 70) benefited from the physical environment provided by the mosses.

Although aquatic mosses are seldom eaten by their inhabitants (Haefner & Wallace 1981), they can provide a rich food source through the other inhabitants. Fontaine and Nigh (1983) considered the periphyton (Figure 71) on bryophytes to be an important food source. In New Zealand, periphyton and detritus were primary food sources (Suren 1993). Unfortunately, bryophytes tend to be shade plants and periphyton tends to prefer the sun, so the periphyton is not at its max. Nevertheless, invertebrate densities were higher among mosses containing periphyton than among those with detritus, most likely reflecting the higher food quality of periphyton. Ogbugu and Akinya (2001) likewise found that mosses in Nigeria provided a suitable substrate for periphytic algae, especially diatoms.

Figure 70. ***Parapsyche apicalis*** larva, member of a genus known to seek shelter in bryophytes. Photo by Donald S. Chandler, with permission.

Figure 71. Stream mosses in Tucquan Creek, Lancaster County, Pennsylvania, USA, laden with a detrital-periphyton complex. It is likely that the schist bedrock is contributing to the light color. Photo by Keith Williams, with permission.

McWilliam-Hughes *et al*. (2009) found ***Fontinalis*** sp. (Figure 4) abundant in headwater streams and ***Drepanocladus*** (*s.l.*) sp. (Figure 72) abundant in low-order streams. The scrapers living in low-order streams seemed to depend more on ***Fontinalis*** as a food source than did scrapers in high-order streams depend on ***Drepanocladus*** (*s.l.*). They suggested that in low-productivity, nutrient-limited rivers primary consumers might switch to marginal food sources such as bryophytes when more preferred food is limited or unavailable.

The feeding guilds change with the seasons. Habdija *et al*. (2004) found that current velocity and food supply affected the composition of insects inhabiting bryophytes in karst streams. Those inhabiting the bryophytes were predominantly small forms of oligochaetes, **Diptera** (Figure 58), and **Coleoptera** (Figure 41), comprising 64.1-98.7% of the total macroinvertebrate individuals. **Collector-gathers** dominated in spring and summer, whereas in autumn it was **collector-filterers**, and in winter **scrapers** reached their maximum. Gregg and Rose (Gregg 1981; Gregg & Rose 1985) found that among the **tracheophytes** (plants with lignified vascular tissue, *i.e.*, all plants that are not bryophytes), shredders, scrapers, and predators were the primary guilds in the autumn and that all guilds had their highest abundances in spring. Bryophytes offer the advantage of being present year-round, and their extensive periphyton growths provide a good winter food source for those insects that remain active in the winter. It is interesting that Gregg found that ***Hydropsyche*** (Figure 13), ***Simulium*** (Figure 22), ***Baetis tricaudatus*** (Figure 43), ***Glossosoma velona*** (Figure 73), and ***Helicopsyche borealis*** (Figure 74) avoided macrophytes, whereas all of these genera are known from bryophytes (though ***Helicopsyche*** is rare there). One problem for these insects was that the tracheophytes reduced the velocity, creating problems for these high-oxygen taxa. The advantage in the presence of tracheophytes seemed to be that of increasing heterogeneity, an advantage also offered by bryophytes.

Figure 72. ***Drepanocladus exannulatus***, a less desirable food source than ***Fontinalis*** for insect scrapers. Photo by Michael Lüth, with permission.

Figure 73. ***Glossosoma*** sp. larvae, a tracheophyte avoider that lives among bryophytes. Photo by Jason Neuswanger, with permission.

Figure 74. ***Helicopsyche*** sp. larva & case. ***Helicopsyche borealis*** avoids tracheophytes, but the genus is known from bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Thus, we have seen that the reduced water velocity within a bryophyte mat (Devantery 1987; Suren 1991) makes the bryophytes suitable safe sites not only for insects, but also for the periphyton and detrital food components, as shown in New Zealand (Suren 1991), as well as for the insect prey species, as shown in the North Temperate Zone (Elliott 2005).

Bryophytes as Food

Early reports indicated that bryophytes were ingested, but the food value remained in question. Nevertheless, ***Fontinalis*** (Figure 4) was found in gut contents (Gaevskaya 1969). Jones (1949, 1950) found ***Fontinalis*** in the guts of the stoneflies ***Amphinemura*** (Figure 105), ***Chloroperla*** (Figure 23), ***Dinocras*** (Figure 75), ***Leuctra*** (Figure 49), and ***Protonemura*** (Figure 104), the mayflies ***Ecdyonurus*** (Figure 15) and ***Ephemerella*** (*s.l.*) (Figure 8), as well as in the caddisflies ***Hydropsyche*** (Figure 13) and ***Philopotamus*** and the beetle ***Oreodytes*** (Figure 76).

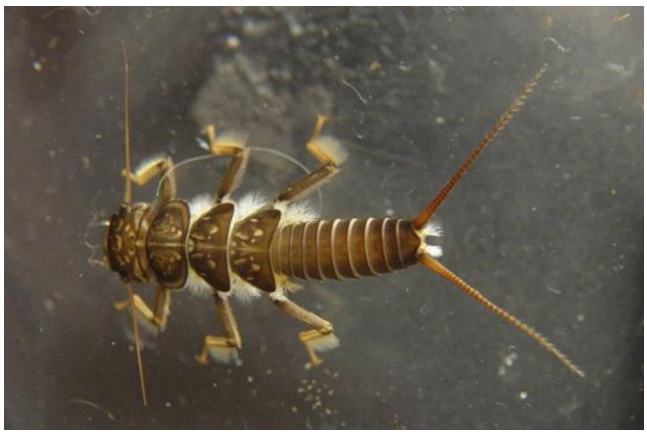

Figure 75. ***Dinocras cephalotes*** naiad, a stonefly genus that eats mosses. Photo by Guillaume Doucet <www.guillaume.doucet@yahoo.fr>, with permission.

Jones (1951) considered ***Fontinalis antipyretica*** (Figure 18) to be one of the main foods for herbivorous insects in his study of the River Towy, Wales. But Dangles (2002) cautions us against categorizing food habits by generic or higher levels. In his study of four streams in northeastern France he found that two species in the same genus with very similar mouthparts had different diets, one feeding on bryophytes and the other on detritus, including leaf litter.

Figure 76. ***Oreodytes septentrionalis***, a genus including bryophyte consumers. Photo by Brian Eversham, with permission.

Caddisflies ***Pycnopsyche guttifera*** (Figure 77) and ***Philocasca alba*** both feed on mosses. In an interesting study, Mutch and Pritchard (1984) found that the late-instar larvae of ***Philocasca alba*** had significantly higher growth rates if their diet of detritus or leaf litter was supplemented with mosses.

Figure 77. ***Pycnopsyche guttifera*** larva, a consumer of mosses. Photo by Donald S. Chandler, with permission.

Tada and Satake (1994), working with insects on mats of the moss ***Platyhypnidium riparioides*** (Figure 19) in a cool mountain stream in Japan, found the mayflies ***Baetis*** (Figure 43) and ***Ephemerella*** (*s.l.*) (Figure 8), the stoneflies ***Acroneuria*** (Figure 45) and ***Isoperla*** (Figure 20), and the caddisflies ***Micrasema*** (Figure 69), ***Rhyacophila*** (Figure 79), and ***Palaeagapetus rotundatus*** not only live among the bryophytes, but also feed on the leaves of the leafy liverwort ***Chiloscyphus polyanthos*** (Figure 78) and ***Scapania undulata*** (Figure 10). Interestingly, they do not feed on leaves of the moss ***Platyhypnidium riparioides***, suggesting the possibility of antifeedant compounds in that species.

Figure 78. ***Chiloscyphus polyanthos*** in the fluctuating water level zone where several kinds of insects eat the leaves. Photo from <www.aphotofauna.com>, with permission.

Even the free-living carnivore caddisfly ***Rhyacophila dorsalis*** (Figure 79) apparently eats mosses (Slack 1936). One out of nine had ***Fontinalis antipyretica*** (Figure 18) leaves in the gut. For the mayfly ***Ephemerella*** (*s.l.*) (Figure 8), ***Fontinalis*** is a common food (Jones 1949). ***Ephemerella*** (*s.l.*) feeds on the green alga *Ulothrix* when it is available, but feeds on the ever-present moss when the alga is scarce or absent (Jones 1949). On the other hand, in a different study, Jones (1950) found that beetles and mayflies did not eat ***Fontinalis*** (Figure 18), but the moss was in the gut of ***Chloroperla*** (Figure 23), ***Leuctra*** (Figure 49), ***Protonemura*** (Figure 104), and ***Amphinemura*** (Figure 105), all stoneflies, and in the gut of the net-spinning caddisfly ***Hydropsyche*** (Figure 13) – a genus that traps its food with a net. In addition to using the moss for housing, the caddisfly ***Micrasema*** (Figure 69) eats mosses and associated periphyton (Chapman & Demory 1963; Decamps & Lafont 1974). Chapman and Demory (1963) found that in its preferred food was ***Platyhypnidium riparioides*** (Figure 19). It is possible that many insects eat the mosses primarily for their associated periphyton, but for ***Micrasema*** it appears that the primary target is the mosses themselves. Even the filter-feeding blackflies such as ***Simulium tuberosum*** (Figure 80) will feed on aquatic mosses (Jones 1949), but we need to check to see if they are really digested.

Figure 79. ***Rhyacophila dorsalis*** larva, a moss consumer. Photo by Walter Pfliegler, with permission.

Figure 80. ***Simulium tuberosum*** larva, known to have mosses in its gut. Photo by Tom Murray, through Creative Commons.

Most members of the caddisfly genus ***Rhyacophila*** (Figure 79) are carnivores, although some of these bryophyte dwellers eat bryophytes. Perhaps more importantly is their ability to hide among the mosses to ambush their prey at dusk and dawn [*e.g.* ***Baetis*** (Figure 43), ***Gammarus*** (Figure 52)]. Elliott (2005) found most of the ***Rhyacophila dorsalis*** (Figure 79) among clumps of the leafy liverwort ***Scapania*** (Figure 10) and the mosses ***Platyhypnidium riparioides*** (Figure 19) and ***Fontinalis antipyretica*** (Figure 18). Although most of the ***Rhyacophila*** species are carnivores, most of their guts had fragments of bryophytes, but these appeared to be undigested, exhibiting chlorophyll. Older individuals fed primarily at night and diatoms occurred in 29% of the guts of 4th instars; bryophytes occurred in 25%. However, in the 5th instar, only 9% contained diatoms and 7% contained bryophytes. The ***Rhyacophila*** larvae would disappear into the moss colony to search for food, then return to the bryophyte surface to eat it. These observations suggest that the bryophytes may have been eaten inadvertently when capturing prey.

The inadvertent consumption of bryophytes by carnivores is a likely occurrence in a number of insects. For example, Jones (1950) found ***Fontinalis*** (Figure 14) in the guts of **Plecoptera** [***Chloroperla*** (Figure 23), ***Leuctra*** (Figure 49), ***Protonemura*** (Figure 104), ***Amphinemura*** (Figure 105)] and **Trichoptera** (***Hydropsyche***, Figure 13), but these could have resulted from bits of the moss mixed in with their typical food. ***Hydropsyche*** is a filter feeder, spinning its own nets to trap food, but bits of drifting moss may get trapped in the net. Nevertheless, Jones did not find any ***Fontinalis*** in guts of either **Coleoptera** (beetles) or **Ephemeroptera** (mayflies) in these same collections.

Nutritional and Antifeedant Properties

Few protein values are published for aquatic mosses, so we cannot judge if any relationship to protein content is typical. However, it has been a common view among biologists that mosses are avoided as food because of their low food value, among other reasons. Nevertheless, Winterbourn and co-workers (1986), using C^{13} ratios, found bryophytes to be important sources of carbon for the benthic fauna in two British rivers.

Suren and Winterbourn (1991a) examined the gut contents of 23 invertebrate taxa that dwell among bryophytes in two New Zealand alpine streams. Fourteen of these taxa had bryophytes in the guts, but the researchers found that only the tipulid larvae of ***Limonia hudsoni*** (Figure 81) and caddisfly larvae ***Zelandopsyche ingens*** (Figure 82) and ***Oeconesus similis*** (Figure 83) regularly consumed the bryophytes. They found that the bryophytes contained more refractory and indigestible compounds than other riparian plants and were thus less nutritious for the animals. They suggested that the bryophytes might also contain **antifeedant** compounds (compounds that discourage herbivory). Such compounds do exist in aquatic bryophytes, including ***Fontinalis*** (Liao 1993; LaCroix 1996). But we must keep in mind that modifications of digestive systems and their *p*H and enzymes make these "indigestible" foods digestible to some specialists (see discussion in Chapter 10-3 on ***Asellus***).

Figure 81. ***Limonia*** larva; some species are regular consumers of bryophytes. Photo courtesy of State Hygienic Laboratory, University of Iowa, with permission.

Figure 82. ***Zelandopsyche*** larva & case; some species include bryophytes in their regular diet. Photo by Stephen Moore, Landcare Research, NZ, with permission.

But sometimes the consumed mosses carry with them associated periphyton that might be the real food source, as in ***Micrasema*** (Figure 69) of the Pyrénées (Decamps & Lafont 1974). Dudley (1988) likewise considered that the real food might be the associated periphyton. Suren (1988) similarly concluded that the mosses were not an important food source, citing the similarity of faunal communities on artificial mosses that became colonized with periphyton. But separating assimilation of moss tissue vs periphyton is a challenging endeavor.

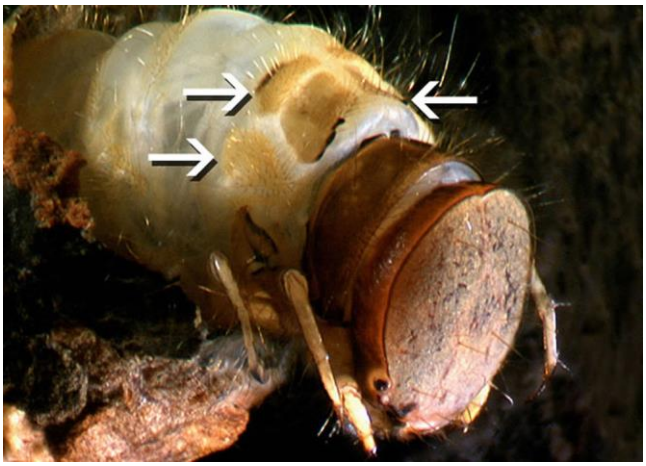

Figure 83. ***Oeconesus*** larva head; ***O. similis*** frequently eats bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Modern methods have made it somewhat easier to determine the diets of aquatic insects. Using Δ13C, Winterbourn *et al*. (1986) demonstrated the importance of bryophytes as important food sources. It is surprising that so many invertebrates eat aquatic mosses. Pritchard and Berté (1987) found that the aquatic moss ***Leptodictyum*** (Figure 84) had the lowest protein content of the five foods tested (wheat flakes, alder, burreed, willow leaves, ***Leptodictyum***. Wheat flakes and alder had the most, burreed and willow leaves were next. Nevertheless, Pritchard and Berté (1987) found that despite the low nutritional value in ***Leptodictyum***, the caddisfly ***Limnephilus externus*** (Figure 85) chose mosses second out of the five choices, and the caddisfly ***Nemotaulius hostilis*** (Figure 86) chose mosses third among these choices. As the larvae grew, they increased their intake of moss, preferring it over alder or willow. Their preference for burreed over moss varied and was sometimes equal. Nevertheless, ***N. hostilis*** grew more slowly on mosses than on alder or burreed.

Figure 84. ***Leptodictyum riparium***, an aquatic moss with lower protein content than several tracheophytes, but still eaten by the caddisfly ***Limnephilus externus***. Photo by David T. Holyoak, with permission.

Figure 85. ***Limnephilus externus*** larvae, consumers of the moss ***Leptodictyum***. Photo by Bob Newell, with permission.

Figure 86. ***Nemotaulius hostilis*** larva in case. This species chooses mosses third compared to tracheophyte choices. Photo by Donald S. Chandler, with permission.

Tracing Bryophytes in the Food Chain

If identification of assimilated bryophytes is a challenge, the identification of the role of bryophytes in the food chain is an even greater challenge. To what degree is the assimilated carbon from bryophytes passed upward to predators and top carnivores? Or is it simply stored in the insect tissues and unavailable to them? Or is it mostly lost through **egestion** (process of ridding the body of undigested or waste material; defecation; not to be confused with elimination of nitrogenous waste such as that in urination)?

Identification of unique acetylenic fatty acids in bryophytes, including ***Fontinalis antipyretica*** (Figure 18) (Anderson & Gellermann 1975; Dembitsky & Rezanka 1995; Sushchik *et al*. 2007), has enabled us to use these fatty acids as markers. These unique acetylenic fatty acid markers are absent in tracheophytes, algae (*e.g.* Sushchik *et al*. 2007), and bacteria, providing us with a tool to trace bryophytes in their consumers (Dembitsky & Rezanka 1995). When testing five aquatic bryophytes, Dembitsky and Rezanka determined that acetylenic fatty acids occurring in the triacylglycerols of bryophytes comprised from 6.6% of the fatty acids in the moss ***Calliergon cordifolium*** (Figure 87) to 80.2% in the thallose liverwort ***Riccia fluitans*** (Figure 88). Identification of these unique acetylenic fatty acids opened the possibility of determining if the bryophytes were actually assimilated into tissues of their consumers (Kalachova *et al*. 2011).

Figure 87. ***Calliergon cordifolium***, a moss in which acetylenic fatty acids comprise 6.6% of the triacylglycerols. Photo by Michael Lüth, with permission.

Figure 88. ***Riccia fluitans***, a thallose aquatic liverwort that contains 80.2% acetylenic fatty acids in its triacylglycerols. Photo by Jan-Peter Frahm, with permission.

Torres-Ruiz *et al*. (2007) used fatty acid content to identify the food groups eaten by several aquatic invertebrates. They found the aquatic primary producers had a higher EFA content for 18:2ω6 and 18:3ω3 in green algae, 20:5ω3 in diatoms, and 20:4ω6 in bryophytes. Furthermore, they identified specific markers for diatoms (20:5ω3 [eicosapentaenoic acid], 16:1ω7, 16:ω4s, 16C-polyunsaturated FAa [PUFAa]), green algae (18:3ω3 [α-linolenic acid], 18:2ω6 [linoleic acid], 16C-PUFAb), and bryophytes (20:4ω6, 20:3ω3), permitting them to identify aquatic primary producers as the primary food source for the moss-dwelling mayfly ***Ephemerella*** (*s.l.*) (Figure 3, Figure 8) and caddisfly ***Hydropsyche*** (Figure 13). Gladyshev *et al*. (2012) used stable isotope composition of fatty acids to trace a food web from periphyton and mosses, to consumers, including **Trichoptera**, and finally to the secondary consumer fish, the grayling, in the Yenisei River in Siberia.

Kalacheva *et al*. (2009) and Kalachova *et al*. (2011) used similar logic to determine the use of ***Fontinalis antipyretica*** (Figure 18) as a food source in the Yenisei River. In addition to the differences among fatty acids listed above by Torres-Ruiz *et al*. (2007), green algae and Cyanobacteria synthesize high amounts of α-linolenic acid

(18:3ω3); bacteria synthesize odd-numbered, branched fatty acids (Kalacheva *et al*. 2009; Kalachova *et al*. 2011). Bryophytes differ from these and from tracheophytes not only by having highly specific acetylenic fatty acids, but also the levels in the bryophytes maintain a high level of these fatty acids throughout the year (Kalacheva *et al*. 2009).

Kalacheva *et al*. (2009) used fatty acid and stable isotope analyses in a 4-year study on the food sources of macroinvertebrates in the Yenisei River. Using the highly specific biomarkers of acetylenic acids in ***Fontinalis antipyretica*** (Figure 18), they determined that the lipids of gammarids, **Ephemeroptera**, **Trichoptera**, and **Chironomidae** (Figure 9) all demonstrated the presence of these acetylenic acids in their fatty acids. In some cases, these were seasonal. For example, the amphipod ***Eulimnogammarus viridis*** exhibited maximum levels of the ***F. antipyretica*** biomarker in winter and minimum levels in summer. In particular, ***Serratella ignita*** (Figure 25) and ***S. setigera*** had the highest level of acetylenic acids A18 and A20 when analyzed. On the other hand, the **Chironomidae** ***Prodiamesa olivacea*** (Figure 89) and ***Pseudodiamesa branickii*** (Figure 90) and **Trichoptera** ***Apatania crymophila*** (Figure 91) had the lowest. The researchers concluded that for most of the aquatic insects the ***Fontinalis antipyretica*** in the Yenisei River played only a minor role in assimilation. On the other hand, the aquatic insects seemed to have a more depleted ^{13}C content than the biofilms, an indication that the consumption of ***F. antipyretica***, which likewise has a lower δ13C value than biofilms, contributed to their assimilation. Although the moss was consumed as a minor supplement year-round, consumption in general increased in winter when food sources such as epilithic biofilms were greatly reduced.

Figure 89. ***Prodiamesa*** sp. larva. ***Prodiamesa olivacea*** had low levels of bryophyte-derived acetylenic fatty acids, indicating little or no consumption of bryophytes. Photo by Peter Cranston, with permission.

Kalachova and coworkers (2011) raised the question of whether the moss was consumed directly or transferred up the food pyramid by consumption of invertebrates that had eaten it. They concluded that it was direct consumption because of lack of the marker fatty acids in the invertebrates lower in the food pyramid. Perhaps the most important conclusion is that these mosses were assimilated into the tissues of the mayfly ***Serratella*** (Figure 25) species and others, a conclusion that cannot be supported by gut analysis alone. This line of research is worth pursuing further in other systems to determine the importance of bryophytes in the food web.

Figure 90. ***Pseudodiamesa branickii***, a species that had low levels of bryophyte-derived acetylenic fatty acids, indicating little or no consumption of bryophytes. Photo from <Benthos.narod.ru>, with online permission.

Figure 91. ***Apatania crymophila*** larva, a caddisfly with low levels of acetylenic acid. Photo from Omnilexicon, through Creative Commons.

Macroinvertebrates can be flexible in their choices of food. In four acid streams of northeastern France, only 24-36% of the biomass consumed by shredders was comprised of leaf fragments; 44% of their diet was benthic algae and bryophytes (Dangles 2002). Some taxa such as the stonefly ***Brachyptera seticornis*** (Figure 92) and caddisfly ***Chaetopterygopsis maclachlani*** (Figure 93), specialized on benthic algae and bryophytes. Even though the caddisfly ***Pycnopsyche guttifera*** (Figure 77) is a classical shredder, it eats algae and is known to eat even terrestrial mosses (Williams & Williams 1982).

Figure 92. ***Brachyptera seticornis*** naiad, stonefly that specializes in eating algae and bryophytes. Photo from <http://www.nebudbaiduzhym.com>.

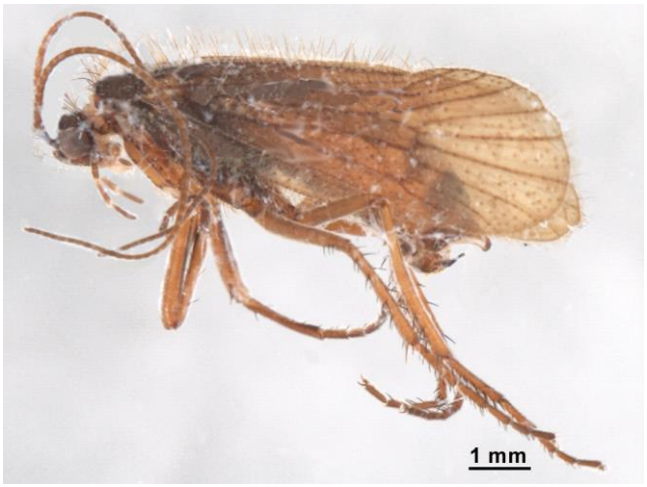

Figure 93. ***Chaetopterygopsis maclachlani*** adult. The larvae specialize on bryophytes as food. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Few preference experiments have been done with aquatic mosses as a choice. Leberfinger and Bohman (2010) gave detritivores ***Limnephilus bipunctatus*** (caddisfly, Figure 94) and ***Nemoura*** sp. (stonefly; Figure 40) the choice of shrubby cinquefoil, birch, Swedish whitebeam, dead and fresh grass, aquatic moss, and algae. Both insects preferred leaves of shrubby cinquefoil; ***Nemoura*** sp. also ate algae. The dead grass was the least preferred food. The shrubby cinquefoil had the highest nutritional value among the detritus choices. Leberfinger and Bohman considered the high carbon to nitrogen content of the fresh foods to be a contributing factor in their choice.

Figure 94. ***Limnephilus bipunctatus*** larva in case, a species that preferred aquatic mosses over grass, but less than shrubby cinquefoil.. James K. Lindsey, with permission.

The **Tipulidae** (craneflies) are known from both terrestrial and aquatic habitats. In the terrestrial realm they typically live in wet habitats such as cedar swamps. ***Tipula oropezoides*** (Figure 95) is one such species. And it feeds on both mosses and liverworts. Wyatt and Stoneburner (1989) observed the larvae feeding on the moss ***Rhizomnium punctatum*** (Figure 96). It would strip the one-cell-thick lamina from the thick costa and leaf borders.

Figure 95. ***Tipula*** larva, a genus that is common among bryophytes and leaf litter and is known to feed on both mosses and liverworts. Photo by J. C. Jones, through Creative Commons.

Figure 96. ***Rhizomnium punctatum***, food for ***Tipula opezoides***. Photo by Jan-Peter Frahm, with permission.

Food when Food Is Scarce

Bryophytes are often considered to be emergency foods for aquatic insects (Dangles 2002; McWilliam-Hughes *et al*. 2009; Kalachova *et al*. 2011). They can be particularly important as a winter food source when other foods become scarce (Kalachova *et al*. 2011). Even within the growing season, the abundance of insects changes and this changes their impact on the bryophytes they consume (Figure 97) (Dangles 2002).

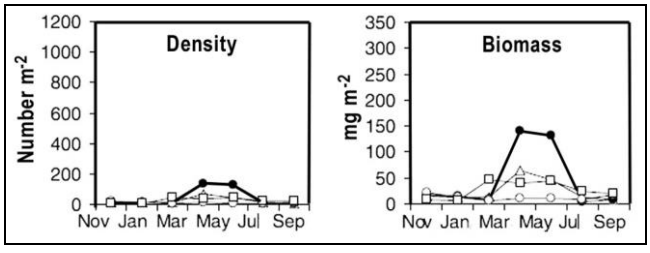

Figure 97. Density and biomass of insect shredders feeding on bryophytes in four streams in four replicate study streams (shown by 4 different symbols and lines) in Vosges Mountains (northeastern France). Modified from Dangles 2002.

Bryophytes can also serve as food in areas of a stream where other food sources are scarce (McWilliam-Hughes *et al*. 2009). Based on δ13C values, McWilliam-Hughes and coworkers determined that scrapers in low-order streams were more dependent on ***Fontinalis*** sp. (Figure 23) than scrapers in high-order streams depended on the ***Drepanocladus*** sp. (Figure 72) that was dominant there. In fact, 98% of the scraper δ13C values were enriched relative to bryophyte δ13C values and those two measures correlated well (r=0.53). When the values from pool habitats were removed, the correlation increased to r=0.76. McWilliam-Hughes and coworkers suggested that in low-productivity rivers, primary consumers might switch to alternative marginal food sources such as ***Fontinalis*** sp.

Epiphytes and Meiofauna of Bryophytes

In aquatic habitats, bryophytes are typically covered with periphyton. This periphyton coating can serve as food for many kinds of insects. The most common of these are diatoms (Ward 1994; pers. obs.). Amos (1999) found diatoms, desmids, and filamentous algae associated with ***Fontinalis*** (Figure 62). In New Zealand, Suren (1988) found that as day length increased the mosses were covered with flocculent masses of the diatom ***Diatoma*** sp. (Figure 98) and the filamentous green alga ***Ulothrix*** sp. (Figure 99) **Cyanobacteria** included ***Placoma*** (Figure 100), ***Tolypothrix*** (Figure 101), and ***Chamaesiphon*** (Figure 102). Suren (1992b) found that the bryophytes provided an abundant and persistent food source for invertebrates, one that was more stable than that on plain tiles. The bryophytes grew a high biomass of the filamentous diatom ***Diatoma hiemale*** (Figure 98) in the unshaded site and the crustose diatom ***Epithemia sorex*** (Figure 103) at the shaded site. The masses of filamentous diatoms were of short duration because they were easily washed away.

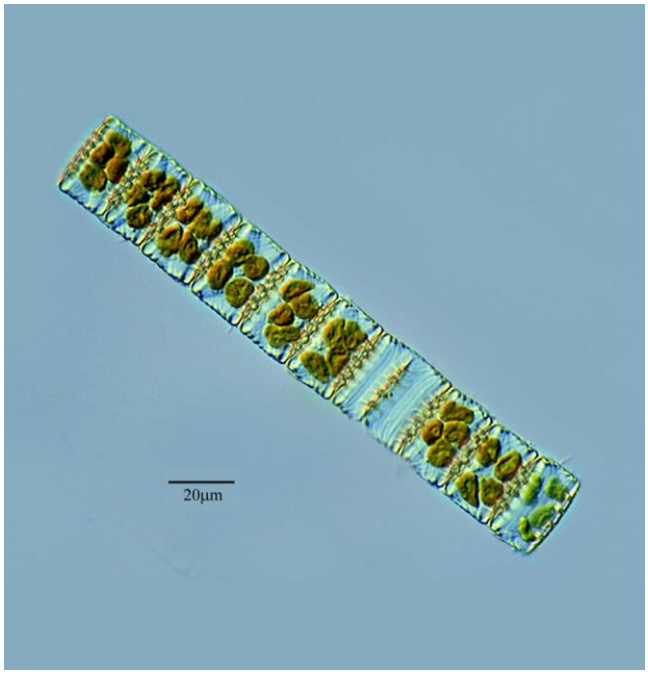

Figure 98. ***Diatoma hiemale***, a common diatom on bryophytes at unshaded sites in New Zealand. Photo from Proyecto Agua, with permission.

Figure 99. ***Ulothrix***, a filamentous green alga that covers stream mosses as days grow longer in spring. Photo by Yuuji Tsukii, with permission.

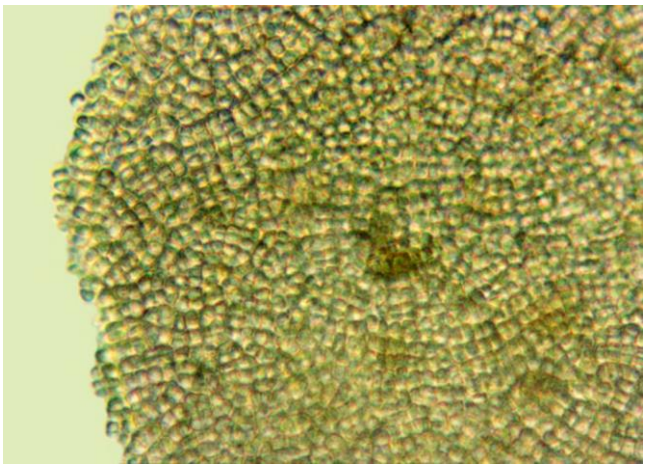

Figure 100. ***Placoma*** sp., a member of **Cyanobacteria** that covers stream mosses as days grow longer in spring. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 101. ***Tolypothrix tenuis***, a member of **Cyanobacteria** that covers stream mosses as days grow longer in spring. Photo by Yuuji Tsukii, with permission.

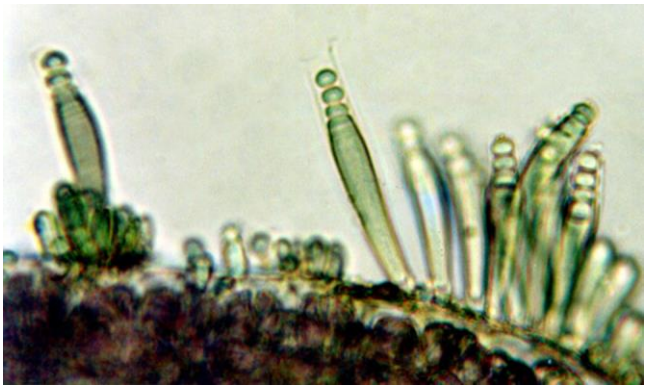

Figure 102. ***Chamaesiphon*** sp., member of **Cyanobacteria** that covers stream mosses as days grow longer in spring. Photo by Stephen Moore, Landcare Research, NZ, with permission.

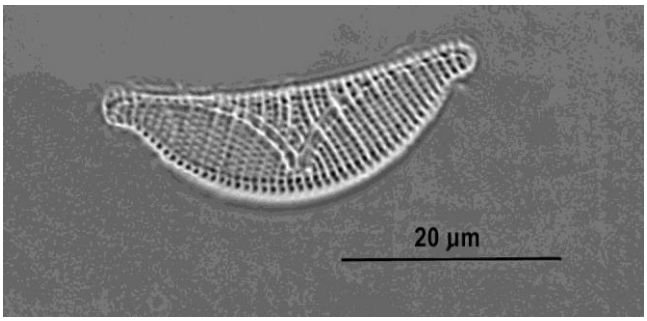

Figure 103. ***Epithemia sorex***, a common inhabitant on bryophytes in shaded streams of New Zealand. Note the **puncta** (holes) in the cell wall. Photo by Ralf Wagner, with permission.

Diatoms (**Bacillariophyta**) at first appear to be indigestible boxes with glass shells of SiO_2. However, Ogilvie and Clifford (1986) reported that insects can digest the cytoplasm of diatoms through the tiny holes (**puncta**; Figure 103) in the cell wall. Diatoms and detritus are important foods for the tiny insect inhabitants of bryophytes. But meiofauna, intolerant of high water velocity (Winner 1975), can also reside there, seeking refuge from the high velocity of water on rocks and other substrata in the area.

As already noted, Chantha *et al*. (2000) found that as the moss biomass increased in a Quebec, Canada, stream, the invertebrates became more abundant but smaller. Clumps of moss with greater depth provided more spaces for invertebrates, but the algae did not increase proportionally, presumably due to diminishing light deeper into the mat. Both the algal biomass (5-fold) and invertebrate density (10-fold) was much greater on mosses compared to the nearby rocks, but the overall invertebrate biomass was similar on these two substrates because of the much greater area of bare rock.

Trapping Detritus

The ability of bryophytes to trap detritus (Butcher 1933; Cowie & Winterbourn 1979; Gurtz & Wallace 1984; Suren & Winterbourn 1992a, b) as well as other food resources (Devantery 1987) undoubtedly plays an important role in feeding many kinds of inhabitants. Bryophytes trap **CPOM** (coarse particulate organic matter), **FPOM** (fine particulate matter), and **UFPOM** (ultra fine particulate organic matter) (Habdija *et al*. 2004). The fine particulate matter may to be particularly important for the meiofauna, including such small insects as the **Chironomidae** (Figure 9) (Aguila-S. 1998). Trapping is possible due to the reduced flow within the bryophyte mat, and this same slower flow provides a refuge from flow for stream insects (Madaliński 1961; Elliott 1967a, b; Gurtz & Wallace 1984; Suren 1992a, b; Glime 1994).

Huryn and Wallace (1987) found that in mountain stream areas where bedrock outcrops are covered with mosses, collector-gatherers consume the FPOM (fine particulate organic matter) collected by the moss colony. Some probably also eat the dung that accumulates there from the many inhabitants (Fisher & Gray 1983).

Cherchesova *et al*. (2012) suggested that small and medium stoneflies living among mosses and other locations where **detritus** (Figure 5) is common probably eat detritus. These include ***Protonemura aculeata*** (see Figure 104), ***Amphinemura trialetica*** (Figure 105), ***Taeniopteryx nebulosa*** (Figure 106), ***Taeniopteryx caucasica***, ***Brachyptera transcaucasica*** (see Figure 107), ***Chloroperla*** sp. (Figure 23), ***Nemoura cinerea*** (Figure 108), ***Capnia nigra*** (Figure 109), ***Leuctra fusca*** (Figure 110), and ***Leuctra hippopus*** (Figure 111), all in genera that commonly live among mosses.

Figure 104. ***Protonemura meyeri*** naiad, seen here amid a bed of detritus. Photo by James K. Lindsey, with permission.

Figure 105. ***Amphinemura*** naiad, a stonefly that blends well with detritus. Photo by Bob Henricks, with permission.

Figure 106. ***Taeniopteryx nebulosa*** naiad, a detritus dweller. Photo by Niels Sloth, through Creative Commons.

Figure 107. ***Brachyptera risi*** naiad. Photo by Guillaume Doucet <www.guillaume.doucet.free.fr>, with permission.

Figure 108. ***Nemoura cinerea*** naiad, a moss and detritus dweller. Photo by James K. Lindsey, with permission.

Figure 109. ***Capnia*** sp. naiad, a detritus dweller. Photo by Jason Neuswanger, with permission.

Figure 110. ***Leuctra fusca***, a probably detritus feeder. Photo by Louis Boumans, through Creative Commons.

Figure 111. ***Leuctra hippopus*** naiad, a probably detritus feeder. Photo by Niels Sloth, with permission.

Suren (1992b) found that bryophytes increase the periphyton and detritus through increased habitat stability, acting much like debris jams in forested North American streams, but on a micro scale. The variation of periphyton among the bryophytes was much lower than that of plain tiles, suggesting that this food source is more stable than that on rocks. Thus the bryophyte periphyton and detritus provide persistent food sources for the bryophyte inhabitants.

Linhart *et al*. (2002a, b) found that **Chironomidae** (Figure 9) and rotifers responded negatively to flow velocity, but correlated positively with the fine detrital matter trapped within the moss clump. Within ***Fontinalis antipyretica*** (Figure 18), the amount of trapped fine matter was dependent on the local flow velocity. Egglishaw (1969) found that detritus was the most important factor determining the structure of the community.

The moving waters provide a continuous renewal of organic particles that serve as food items. This permits the filter feeders among the Trichoptera and the Simuliidae to form large populations there (Galdean *et al*. 2001).

Macan and Worthington (1951) found that the fauna on different bryophyte growth forms differed. The not-so-thick moss housed the mayflies ***Baetis*** (Figure 43) and ***Ephemerella*** (*s.l.*) (Figure 8), stoneflies, and the scud ***Gammarus*** (Figure 52). Thick mosses supported great numbers of **Chironomidae** (Figure 9) (75% of the individuals). These mosses support some of the greatest productivity of the fish food organisms.

In Appalachian headwater streams, Wallace *et al*. (1988) found that thick mats of moss on the bedrock were important in retaining large amounts of organic matter. This seemed to account for the 48% collector-gatherers (insects) in the stream with dense mosses compared to 31% in the one with mostly cobbles and pebbles that were free of mosses. Habdija *et al*. (2000) found a positive correlation between flow velocity and the deposition rate of CPOM in moss mats, the location where most of the CPOM was deposited in an alkaline stream. Miliša *et al*. (2006) found similar relationships in the Plitvice Lakes of Croatia.

It is interesting that some folks in the UK have proposed that the increase of aquatic bryophytes downstream of sheep-dip (insecticide & fungicide mix) or heavy metal mines may be evidence that invertebrates are a major factor controlling aquatic bryophyte abundance (Richard Lansdown, Bryonet 13 January 2008). I wonder if the metals, at least, reduce the growth of periphyton, reducing competition and permitting higher productivity among the bryophytes. On the other hand, it is possible that sheep feces provide a food source, as suggested by Fisher and Gray (1983) in regard to macroinvertebrates living in a moss matrix in a desert stream.

Seasonal fluctuations in water level can present a challenge to stream macroinvertebrates. Wood *et al*. (2016) examined the role of trapped organic matter among the inundated clumps of the leafy liverwort ***Porella pinnata*** in the Middle Oconee River, GA, USA. This liverwort is generally above the water level, but during periods of high flow it becomes inundated. They found a significant increas in macroinvertebrate biomass, insect density, and organic matter among the ***P. pinnata*** than on adjoining bare rock. Thus, the presence of bryophytes explained the additional organic matter, insect biomass, and density. Among these opportunistic insects were the **Diptera** and **Plecoptera** as the most abundant. I would suggest that additionally, the liverworts may have provided "landing sites" for insect that were caught up in the high-water flow.

Detrimental Effects?

But the encroachment of bryophytes is not good for all members of the stream community. Bryophytes displace epilithic algae that would otherwise occupy the rocks. These diatoms and other algae serve as food for the scrapers, some of whom cannot carry out the same feeding strategy on the bryophytes. The soft structure and irregular surface of bryophytes sometimes requires a different scraping apparatus from that used on a rock. Slavik *et al*. (2004) found that added phosphorus in an Alaskan stream increased epilithic algae initially, but that after eight years of fertilization the bryophytes replaced the diatoms as primary producers. This increased moss growth altered ammonia uptake rates, benthic gross primary productivity, habitat structure, insect abundance, and faunal species composition.

The detrimental effects of bryophyte encroachment was apparent in a South African stream when managers chose to transplant ***Fontinalis*** (Figure 18) into the stream to increase habitat for insects and ultimately increase fish production (Richards 1947). While the idea sounded good, the mosses took over the rock surfaces that had been inhabited by scrapers and insects adapted to clinging to smooth rock surfaces and displaced the native fauna. Unfortunately, I don't know the long-term outcome, which may indeed have increased the number of insects once the bryophyte-adapted species were able to colonize.

Bryophytes vs Tracheophytes

It is clear that bryophytes house numerous aquatic insects. And we know that aquatic insects serve as fish food. But do the insects that live among the bryophytes achieve that role? Bowden *et al*. (1999) found that such a role was unclear. As will soon be seen, bryophytes serve as safe sites for the insects. On the other hand, tracheophytes usually provide a more open habitat than the small chambers of bryophytes. And the tracheophytes can house larger individuals, sheltering fish that seek food there.

Macroinvertebrate biomass, insect density, and organic-matter content were significantly greater in patches of P. pinnata than on adjacent bare rock. Bryophyte biomass explained additional variation in organic matter, insect biomass, and density. The most abundant insects in P. pinnata patches were Dipterans and Plecopterans.

A legitimate comparison between the bryophyte fauna and that of tracheophytes is difficult because these two plant groups tend to occupy different habitats. In lakes the bryophytes are able to extend into deeper water where there is less light than that needed to support the more rapidly growing tracheophytes. The greater depth furthermore coincides with lower temperatures and less temperature fluctuation. Nutrients and dissolved O_2 also differ. And the meshlike nature of the bryophyte more easily traps detritus that can serve as a food source.

In streams, most tracheophytes are unable to tolerate the rapid flow regime that bryophytes can withstand. Since bryophytes occupy greater flow, their surface interface can have a higher oxygen concentration. And since the bryophytes tend to occupy upstream reaches that are steeper and more rocky, they coincide with a different group of insects adapted to faster water, sometimes lower temperatures, some drying in summer, and different species of predators, especially fish. With such limitations on the comparisons, it should be no surprise that studies designed to compare the inhabitants between bryophytes and tracheophytes are rare.

Harrod (1964) found that in a UK chalk stream four aquatic tracheophytes [*Ranunculus fluitans* (Figure 112), *Callitriche platycarpa* (Figure 113), *Veronica beccabunga* (Figure 114), and *Carex* sp. (Figure 115) had some inhabitants, present on all four species, that are also known bryophyte inhabitants: ***Baetis rhodani*** (mayflies; Figure 2) (Frost 1942), ***Rhyacophila dorsalis*** (free-living caddisflies; Figure 116) (Slack 1936), and **Chironomidae** (midges; Figure 9) (Hynes 1961). ***Hydropsyche*** sp. (net-spinning caddisflies; Figure 13) and ***Ephemerella*** (*s.l.*) spp. (mayflies; Figure 3, Figure 8, Figure 25) preferred *C. platycarpa*. ***Simulium ornatum*** (blackflies; Figure 117) dominated both *Carex* sp. and *R. fluitans* (Harrod 1964).

Figure 112. ***Ranunculus fluitans*** with flower, a species where ***Simulium ornatum*** is dominant. Photo by Rasbak, through Creative Commons.

Figure 113. ***Callitriche platycarpa***, a preferred substrate for ***Hydropsyche*** and ***Ephemerella***. Photo by J. C. Schou, with permission.

Figure 114. ***Veronica beccabunga*** with flowers. Photo by Jacopo Werther, through Creative Commons.

Figure 115. ***Carex hystricina*** with flowers, a species where ***Simulium ornatum*** is dominant. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 116. ***Rhyacophila dorsalis*** larva, a bryophyte inhabitant that also occurs on aquatic tracheophytes. Photo by Walter Pfliegler, with permission.

Krecker's (1939) model contends that invertebrate abundance varies with macrophyte biomass, but also with plant species. Those plants with finely dissected leaves have more inhabitants than do plants with broad leaves. Cyr and Downing (1988) tested this assumption with macrophytes and found that the dissected *Myriophyllum* spp. (Figure 118) harbored significantly ($p<0.01$) more epiphytic invertebrates than did the broad-leaved taxa of *Potamogeton amplifolius* (Figure 119), *P. robbinsii* (Figure 120), or *Vallisneria americana* (Figure 121). But they also

found more invertebrates on the large *P. amplifolius* than on the other two broad-leaved species. The numbers of **Trichoptera** (caddisflies; Figure 91) and **Chironomidae** (midges; Figure 90) varied based on plant species. Interestingly, they found that plants with dissected leaves (*Ceratophyllum demersum* (Figure 122) and *Myriophyllum* spp.) did not usually support more invertebrates than did species with large leaves, attesting to the importance of surface area.

Figure 117. *Simulium ornatum* / *intermedium* / *trifasciatum* adult, a blackfly species complex whose larvae are common on both *Ranunculus fluitans* and *Carex*. Photo by Malcolm Storey, through Discover Life online permission.

Figure 118. *Myriophyllum* sp., a tracheophyte with intermediate densities of insects, inferior to that of mosses. Photo by Alison Fox through USDA, with permission.

Figure 119. *Potamogeton amplifolius*, a broad-leaved aquatic plant that harbors fewer insects than those found among dissected leaves. Photo by Jean Pawek, with online permission.

Figure 120. *Potamogeton robbinsii*, a broad-leaved aquatic plant that harbors fewer insects than those found among dissected leaves. Photo by Barre Hellquist, through Creative Commons.

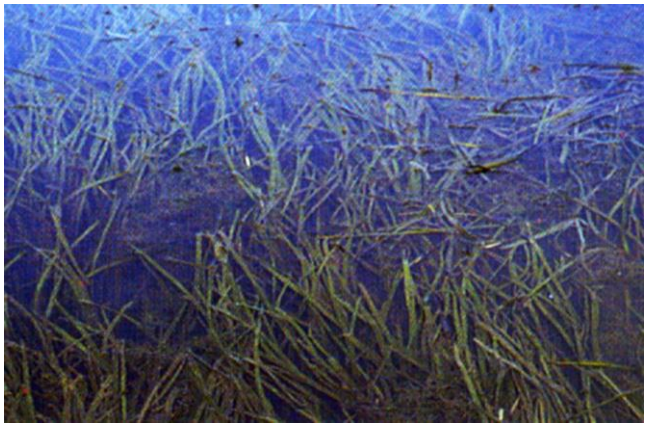

Figure 121. *Vallisneria americana* showing its dense habit of growth. Photo by William & Wilma Follette, through Creative Commons.

Figure 122. *Ceratophyllum demersum*, an aquatic plant with dissected leaves that does not support as many invertebrates as macrophytes with large leaves. Photo from DoralBio5 website, through Creative Commons.

Epele *et al*. (2012) conducted a similar study on **Chironomidae** (midge) assemblages in Patagonia. They recorded 35 taxa of **Chironomidae**. The most abundant subfamilies were **Orthocladiinae** (20), **Chironominae** (7), and **Podonominae** (4). The five most abundant species represented five genera: ***Parametriocnemus*** (Figure 123), ***Parapsectrocladius***, ***Paratrichocladius*** (Figure 124), ***Pseudochironomus***, and ***Rheotanytarsus*** (Figure 125) most abundant taxa. *Myriophyllum quitense* (Figure 126) is structurally complex and was inhabited by 11 taxa. ***Isoetes savatieri***, a structurally simple plant, hosted only 5 taxa. Among the bryophytes in areas of rapid flow they found **Podonominae**, ***Eukiefferiella*** spp., ***Parapsectrocladius*** sp. They found that stability of the substrate was important, with boulders, cobbles, and rooted plants supporting more **Chironomidae** abundance, richness, and diversity than did sand/gravel. They concluded that more complex substrates supported greater diversity.

Figure 123. *Parametriocnemus* sp., a common genus on aquatic plants in Patagonia. Photo by Gillian Martin, Biodiversity Institute of Ontario, through Creative Commons.

Figure 124. *Paratrichocladius skirwithensis* pupa, a genus that is common on macrophytes in Patagonia. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.

Boerger *et al*. (1982) compared the **Chironomidae** (midge larvae; Figure 9) fauna on several aquatic plants and the moss ***Drepanocladus revolvens*** (Figure 127) in the North Fork of the Bigoray River, Alberta, Canada, on several sampling dates. When compared to *Sparganium* (Figure 128), *Potamogeton* (Figure 129), *Hippuris* (Figure 130), sponge, filamentous algae, and wood, the moss generally had the highest density of **Chironomidae** (larvae per sq cm on wood or per gram dry weight on all others). On 11 June the density among mosses was more than double that among filamentous algae, with the others having only 1/6 or less density than that among the mosses. But on 21 June, *Hippuris* had 457 midge larvae compared to 268 on mosses; the algae had none, and the other plants had much lower densities than the mosses. By 11 July, the density among the mosses was nearly double that on *Hippuris* with all others trailing behind. Similar results persisted on 31 July, but on 20 August no insects were reported for the mosses! On 1 October the moss inhabitants reached their highest density (1817 per gram), nearly twice that on *Hippuris*. Differences in surface area are likely to account for the generally higher habitation among mosses (Table 1). Could the low numbers on 20 August have been movement of larvae from mosses to a better food source during low flow?

Figure 125. *Rheotanytarsus*, a genus that is common on macrophytes in Patagonia. Photo by Jason Neuswanger <Troutnut.com>, with permission.

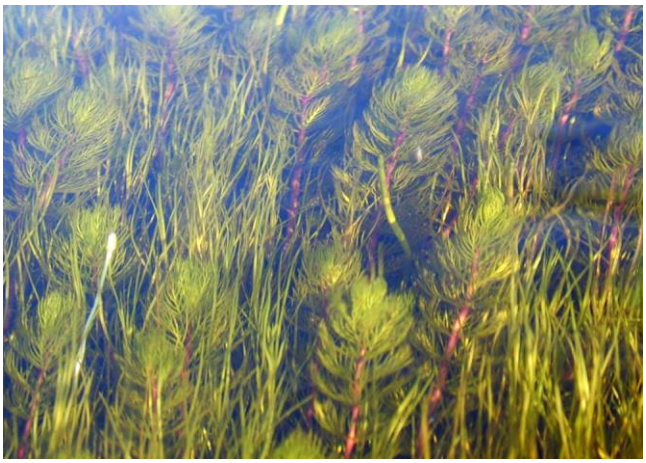

Figure 126. *Myriophyllum quitense*, home to 11 taxa of Chironomidae in Patagonia. Photo from Jardín Botánico Nacional, through Creative Commons.

Figure 127. ***Drepanocladus revolvens***, a moss with higher density of **Chironomidae** when compared with nearby aquatic tracheophytes. Photo by Kristian Peters, with permission.

Figure 128. *Sparganium angustifolium* with flowers, a tracheophyte with fewer **Chironomidae** than that on mosses. Photo by Barbara Studer, through Creative Commons.

Figure 129. *Potamogeton perfoliatus*, a plant with fewer fauna than found on nearby mosses. Photo by Donald Cameron, through public domain.

Table 1. Comparison of surface area and volume per weight of three tracheophytes, ***Drepanocladus revolvens*** (Figure 127), filamentous algae, and willow leaves. From Boerger *et al*. 1982.

Plant type	n	area/wt $cm^2\ g^{-1}$	vol/wt $cm^2\ g^{-1}$	area/vol $cm^2\ g^{-1}$
Sparganium	8	707±13	19.7±1.2	37.6±2.4
Potamogeton	10	1028±116	14.0±0.9	73.6±7.2
Drepanocladus revolvens	10	1526±136	15.2±1.5	103±9.4
Hippurus	9	2549±638	20.9±2.2	122±9.6
Filamentous algae	5	–	23.5±5.6	–
Willow leaves	9	250±9		

In UK lakes and rivers, Macan and Worthington (1951) found that thick mosses on stones and boulders had a mean of 431,941 animals per square meter, whereas *Potamogeton perfoliatus* (pondweed; Figure 129) had only 243,972 and bare rocks had only 4600. Both rooted plants and mosses increased the food used by fish. Percival and Whitehead (1929) likewise found that bryophytes in UK streams had greater insect densities, with intermediate densities on the alga *Cladophora* (Figure 131) and loose mosses, but with the highest densities on thick moss and river weed (Podostemaceae?).

Figure 130. *Hippuris vulgaris*, a tracheophyte with only half the insect density found on mosses. Photo through Creative Commons.

Figure 131. *Cladophora crispata*, member of a genus that is home to aquatic insects. Photo by Yuuji Tsukii, Protist Information Server, with permission.

In Doe Run, Kentucky, USA, Minckley (1963) found intermediate densities on the vascular plants *Nasturtium* (Figure 132), *Myriophyllum* (Figure 118), and *Myosotis* (Figure 133), with the highest densities on mosses. Gregg (1981) found that when the insects were counted on available surface area (3-d, not stream bed), the bare substrate had significantly more insects than did the tracheophytes *Ranunculus* (Figure 134) or *Rorippa* (Figure 135). It seems that the most important role of these tracheophytes was to increase available substrate. It is likely that bryophytes have that role as well.

Figure 132. ***Nasturtium officinale*** with flowers, an emergent plant with lower insect densities than that found on mosses. Photo by Matt Lavin, through Creative Commons.

Figure 133. ***Myosotis scorpioides***, an emergent tracheophyte that had fewer insect inhabitants than mosses. Photo by Les Mehrhoff, through DiscoverLife <http://www.discoverlife.org>.

Figure 134. ***Ranunculus aquatilis***, a tracheophyte genus that had even fewer insects than bare substrate in a Kentucky, USA, stream. Photo by Teun Spaans, through Wikimedia Commons.

Figure 135. ***Rorippa palustris***, an emergent tracheophyte genus that has fewer insects than the bare substrate in a Kentucky, USA, stream. Photo by Mel Harte, through DiscoverLife <www.discoverlife.org)>.

Unlike the bryophytes that trap large quantities of detritus, the tracheophytes tend to be somewhat cleaner because they have fewer pockets in which to trap things. Soszka (1975) used both laboratory and field experiments to examine how insects in a Polish lake used the tracheophytes. He found that only the larvae of Lepidoptera depended on the tracheophytes for food. Rather, most of the insects ate the epiphytic algae and detritus.

Nearly 60% of the invertebrate taxa associated with macrophytes studied by Krull (1970) occurred on only three or fewer species of macrophytes and 33 invertebrate taxa were associated with only one species. **Odonata** (Figure 136) are relatively common among macrophytes (Corbet 1962) but nearly totally absent among bryophytes (see Chapter 11-4 of this volume). The reasons remain to be explored, but the **Odonata** are large and tend to occur in quiet water where they can lie in wait for prey, whereas bryophytes are more common in rapid water.

Figure 136. A head-on view of the dragonfly ***Tanypteryx hageni*** naiad lying in wait for its prey. Photo by Greg Courtney, with permission.

The morphology of the plant appears to be of a major importance. Krecker (1939) found that the lowest number of insects occurred on *Vallisneria* (Figure 121), a plant with smooth, linear leaves. On the other hand, *Myriophyllum* (Figure 118) species (Figure 118) are divided and provide a large surface area. *Potamogeton crispus* (Figure 137) has very wavy leaves and had high faunal densities. Harrod (1964) considered the colonization of aquatic macrophytes to depend on four factors: morphology, position in stream, epiphytes present, and chemical nature. Habitat permanence may be important in lakes (Hargeby 1990). (Hutchinson 1975) suggested that chemical defenses were not well developed in aquatic macrophytes compared to terrestrial plants. Presumably they are also less well developed than in bryophytes.

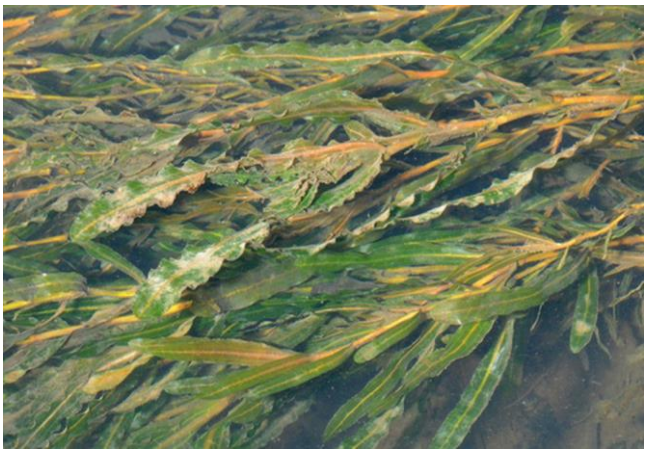

Figure 137. ***Potamogeton crispus*** showing dense growth. Photo by J. C. Schou, with permission.

Despite the open nature of most macrophytes, Tarzwell (1936) found more organisms on the tracheophytes than on the mosses in Michigan, USA, streams. Using a relative scale in which 1.0 represented the numbers on sand, he reported individuals on the tracheophytes *Ranunculus* (Figure 134) (194), *Rorippa* (Figure 135) (301), and *Elodea* (Figure 138) (452) to be greater than those on mosses on gravel (111) or mosses on gravel and rubble (140). Similarly, Percival and Whitehead (1929) found that fauna on a square decimeter of the tracheophyte *Potamogeton* (Figure 129) (2405) exceeded that of both loose moss (709) and thick moss (2140).

Figure 138. ***Elodea canadensis*** flowering. Note detrital accumulation on substrate but little at leaf bases. Photo by Christian Fischer, through Creative Commons.

The ability to colonize tracheophytes vs bryophytes often depends on the suitability of the morphology. Although bryophytes have a large surface area, most of it is below the interface with flowing water, hence creating surfaces that may be lacking in sufficient oxygen as well as being unsuitable for filter feeders that depend on the flow. This appears to be the case for blackflies. Niesiołowski (1980) found a greater number of blackflies on *Potamogeton* (Figure 137) than on ***Fontinalis*** (Figure 62). He attributed this to the differences in leaf size and setting. *Potamogeton* leaves are all exposed to the current whereas only tips of bryophyte branches that interface with the water flow are available for these filter-feeding larvae.

Clearly the relationships between aquatic insects and bryophytes are complex and may be indirect. They serve as refuges and food sources, but these roles may change as the seasons change. Their importance in increased diversity is certain, but their role in overall productivity of the habitat is still elusive.

Summary

Bryophytes provide a stable habitat with lots of surface area, a variety of internal spaces with oxygen and flow gradients, a place to hide from predators or escape from flow (enemy-free space/refuges/safe sites), a trap for algae and detritus to serve as food, and a place to hunt for smaller organisms while hiding from larger predators. Bryophytes can also serve as a moist refuge and a place to find food during times of low water. Hence, a rich bryophyte fauna exists to take advantage of these benefits, increasing the functional diversity. The bryophytes provide habitats for insects in streams, rivers, lake margins, deep waters of lakes, ponds, bogs, and fens.

Two strong determinants of the bryophyte faunal composition are velocity and *p*H. Nutrients can change the dynamic, in some cases increasing moss cover and fauna, but in others increasing algal dominance and reducing bryophyte cover due to competition for light and CO_2.

Some insects specialize on parts of the mosses, with some in leaf axils, some in liverworts, some on the leaf lamina. Morphology of the bryophyte may help to define the faunal community. Other insects specialize on the food types that grow on the mosses – diatoms, Cyanobacteria, filamentous green algae. Some preferences for bryophyte species may relate to the preference of the bryophyte for a particular *p*H range, flow, or other conditions. Bryophytes can also serve as a trap for drifting insects while helping others to avoid the drift altogether. The bryophytes seem to keep at least some species from joining the drift at emergence by providing a substrate where they can climb out of the water.

Artificial string mosses are colonized by the same dominant insects as are mosses, but Visqueen strips have a smaller, more selective fauna.

New methods using fatty acids have supported the gut analyses that reveal bryophytes in the diets of a number of insects. These fatty acids have been used as tracers to implicate the movement of bryophyte carbon upward in the food pyramid. Antiherbivore compounds may keep some insects from eating the bryophytes; in other cases they keep predators from attacking the insects because they prefer eating among plants that lack these compounds. But it appears that trapped detritus and adhering periphyton may play the most important role in determining bryophyte insect inhabitants.

Although macroinvertebrate density and richness increase with moss weight, lower reaches within the mat may be unacceptable habitats for many, so that area covered is more important. And in some cases, encroachment by bryophytes can eliminate insects adapted to smooth rocks.

Bryophytes offer different advantages compared to those of tracheophytes. They occur in rapid water of streams where tracheophytes are unable to survive, they provide enclosed, protective spaces, they trap more detritus, and they persist year-round. But large-leaved tracheophytes provide better habitats for such taxa as **Simuliidae** because more of their surface area is in direct flow where these blackflies can filter out their food.

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Throughout this chapter I must thank my sister, Eileen Dumire, for her devoted time to accompany me in the field, to sort insects from the mosses, to make entries in my bibliography, and to review these subchapters. And I thank my parents for taxiing me to my field sites. I thank my advisor, William B. Drew, for his willingness to advise such an interdisciplinary project. Many others have helped in the formation of my perspectives, in providing images, and in general encouragement.

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CHAPTER 11-3
AQUATIC INSECTS: BRYOPHYTE HABITATS AND FAUNA

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Figure 1. ***Sphagnum*** blanket bog. Photo through Creative Commons.

Aquatic Bryophyte Habitat and Fauna

Insect distribution and abundance depend on freedom from predation, interspecific competition, and physical disturbance (McAuliffe 1983). Bryophytes offer a refuge from all three of these dangers. Aquatic insect biodiversity depends on gradients in habitat size and acidity (Harrison & Agnew 1962; Heino 2009). Bryophytes can contribute to the acidity, particularly in ***Sphagnum*** (Figure 1) habitats, and add to both habitat size diversity and complexity. Thus, bryophytes can increase the diversity of insects in streams, lakes, bogs, and springs by creating more niches for occupation.

Moon (1939) summarized his study of aquatic insects as evidence that the substrate provides mechanical support for the fauna and is the surface on which food grows or is deposited. Bryophytes can contribute greatly to the available substrate, growing periphyton, and trapping detritus. For carnivorous insects, the bryophytes also harbor animal food organisms. Others have reported similar advantages of the moss substrate: increased substrate area (Glime & Clemons 1972), increased algal cell counts (Gurtz & Wallace 1984), replacing scour or sediment-buried algal cover (Hains 1981), protection from scour (Gurtz & Wallace 1984), filtering and trapping detritus (Gurtz & Wallace 1984), providing high prey density (Gurtz & Wallace 1984). The mosses also permit the insects to gain a hold in areas of high velocity where the insects may be able to reduce ventilation needed to gain oxygen, thus saving energy (Johnson 1978; Gurtz & Wallace 1984).

Gurtz and Wallace (1984) found that after a clearcut in the southern Appalachians, USA, the insect fauna increased in density more on the moss-covered (mostly ***Hygroamblystegium tenax*** – Figure 2) rock faces than on other stream substrates. It was primarily the collector-gatherers and scrapers that increased, whereas shredders declined. They considered that the mosses contributed to the biological stability of their substrates. They were most important in areas of rapid, shallow, turbulent flow. These habitats not only replenished the CO_2 and nutrient supply for the mosses, but provided the flow needed for the net-spinning caddisfly ***Parapsyche*** (Figure 3).

Figure 2. ***Hygroamblystegium tenax***, where insect fauna increased after a forest clearcut in the southern Appalachians, USA. Photo by Barry Stewart, with permission.

Figure 3. ***Parapsyche apicalis*** larva, a net-spinning caddisfly that lives on mosses. Photo by Donald S. Chandler, with permission.

By experimenting on colonization of ***Fontinalis neomexicana*** (Figure 4), Maurer and Brusven (1983) found that collector-gatherers were the most numerous (74% of the density), with shredders, collector-filterers, engulfers, and scrapers making up the remainder. Arrival of ***Brachycentrus*** sp. (Figure 5), a collector-filterer, and ***Hydroptila*** sp. (Figure 6), a scraper, both caddisflies, changed these percentages after three weeks. Maurer and Brusven believed that fine particulate matter and epiphytic algae may have facilitated the rapid recolonization.

Figure 4. ***Fontinalis neomexicana***, home to many collector-gatherers. Photo by Belinda Lo, through Creative Commons.

Figure 5. ***Brachycentrus appalachia*** (larger), a common bryophyte dweller that colonized after three weeks. Photo by Bob Henricks, with permission.

Figure 6. ***Hydroptila*** in case, one of the smallest caddisflies, and a colonizer on ***Fontinalis neomexicana*** (Figure 4). Photo by Bob Henricks, with permission.

In a Nepalese river system, altitude was an important determinant of the bryophytes and associated fauna (Ormerod *et al*. 1994). Not only did the substrate change, with bryophytes being more common at higher altitudes, but attached diatoms were more common among higher altitude streams. The high altitude springs supported dense

cover of bryophytes, but bryophytes were not well supported by the cold streams of ice and glacial melt.

Ward (1986) studied altitudinal relationships in the Rocky Mountains, USA. As in the Nepalese system, aquatic tracheophytes were absent in the high mountain sites. Rather, bryophytes dominated in the headwaters. The **zoobenthos** (animals that live on the bottom) density experienced a 3-fold to 6-fold increase from the tundra to the plains at lower elevations. Vinson and Hawkins (2003) likewise found that diversity of genera decreased as elevation increased, with only **Plecoptera** (stoneflies; Figure 25) being an exception.

Like altitude, latitude affects stream insect richness. Vinson and Hawkins (2003) examined data on **Ephemeroptera** (mayflies; Figure 8-Figure 9), **Plecoptera** (stoneflies; Figure 25), and **Trichoptera** (caddisflies; Figure 6) from 495 published studies on richness. **Ephemeroptera** showed three richness peaks (~30°S, 10°N, 40°N) with the highest near 5-10°N and 40°N latitude. **Plecoptera** richness was distinctly highest at ~40°N latitude and similarly at 40°S latitude. **Trichoptera** richness showed less latitudinal variation than the other two orders, although it was slightly higher near the equator and at 40°N and S latitude than at other latitudes.

In a study of mosses growing on filter beds, Hussey (1982) found that growth of mosses [***Leptodictyum riparium*** (Figure 7) was most common] changed the macroinvertebrate community. Even the thickness of the moss will cause differences among communities (Macan & Worthington 1951). The mayflies ***Baetis*** (Figure 8) and ***Ephemerella*** (Figure 9), **Plecoptera** (Figure 25), and the scud ***Gammarus*** prefer not-so-thick moss, whereas thick moss harbors abundant **Chironomidae** (Figure 15). Macan and Worthington found that of the 431,941 animals per sq m of thick moss, 75% were **Chironomidae**. Despite the small size of the moss inhabitants, they found that rooted plants and attached mosses provide the greatest productivity of fish food organisms. That probably refers to the kinds of organisms that fish eat, not to organisms among the mosses that are actually eaten as these may be unavailable unless they enter the drift. (See Chapter 11-2, Bryophyte Roles as Insect Habitats – Food.)

Figure 7. ***Leptodictyum riparium***, a moss whose growth changed the macroinvertebrate community. Photo by Jan-Peter Frahm, with permission.

Figure 8. ***Baetis rhodani***, a common bryophyte inhabitant. Photo by J. C. Schou, with permission.

Figure 9. ***Ephemerella dorothea*** on moss (***Platyhypnidium riparioides*** or ***Hygrohypnum*** sp.). Photo by Donna Bennett, with permission.

Streams

Streams can be rich habitats for aquatic fauna. In the Åland Islands of Finland, Autio and Salmela (2010) collected 104 **Diptera** species from 19 sites, using Malaise traps. These sites included open mires, wooded mires, rich fens, Baltic shore meadows, ditches, and a grove. These **Diptera** included the semiaquatic families **Limoniidae**, **Tipulidae**, **Pediciidae**, **Cylindrotomidae**, **Ptychopteridae**, **Psychodidae**, and **Dixidae**. But the species richness was less than that in other parts of Finland, a phenomenon that Autio and Salmela attributed to the absence of brooks and springs.

In a Victorian Australia upland stream the habitats included mossy stones and the tracheophyte *Ranunculus fluitans*, with number of species reaching 19 among mosses compared to 5 in stony riffles (McKenzie-Smith 1987). The densities among the bryophytes were greater than that McKenzie-Smith could explain on the basis of greater surface area, so he concluded that they offered more than just space.

In Appalachian Mountain streams, I found that the insect communities on the leafy liverwort ***Scapania undulata*** were most similar to those on ***Fontinalis dalecarlica*** (Figure 16) (Glime 1968). These seem like strange similarities because these two bryophyte species

were the most different from each other structurally. However, they did tend to occur in the same streams, suggesting that conditions of flow, nutrients, and temperature may have been more important for the insects. ***Scapania undulata*** provided a unique habitat where insects were able to hide within the folded leaves. The large, streaming moss ***Fontinalis dalecarlica*** may have offered a similar advantage by having a leaf that was somewhat rolled, making it tubular and providing good shelter for the very small.

In many northern streams the bryophytes remain throughout the year, providing a habitat for insects when the tracheophytes disappear. But in English rivers, ***Fontinalis antipyretica*** (Figure 10), ***Fissidens crassipes*** (Figure 11), and ***Leptodictyum riparium*** (Figure 7) decline considerably during winter (Wehr & Whitton 1983; Kelly & Whitton 1987).

Figure 10. ***Fontinalis antipyretica***, a species that declines in English winters. Photo by Bernd Haynold, through Wikimedia Commons.

Figure 11. ***Fissidens crassipes***, a moss that diminishes in English rivers in the winter. Photo by Michael Lüth, with permission.

As noted earlier, bryophytes in streams increase the heterogeneity of the habitat, increasing the available niches for insects (Allan 1975; Williams 1980). And size matters – sometimes (Bourassa & Morin 1995). Although the taxonomic composition differs among streams, the size distribution is quite similar. But substrate composition in nine Canadian streams did affect overall abundance – more than it did their size. Eutrophic sites favored higher abundance, but only for organisms larger than 1 mm (approximately 1 µg dry mass). These small organisms contribute to less than 3% of the respiration of the stream ecosystem, contrasting with the results of Smith-Cuffney (1987 – see above). Does this mean that bryophytes, with their fauna of the smallest organisms, contribute little to the stream ecosystem? I think not, because it is these small organisms that become big ones, and without the shelter of bryophytes they are more likely to be food for predators.

In a Tennessee, USA, springbrook, Stern and Stern (1969) found that the highest number of insects on bryophytes and algae occurred in winter. In February they found 768 individuals per 0.1 m^2, whereas in July they found only 43 per 0.1 m^2 (Figure 12). **Diptera** comprised 84.4% of the fauna, Trichoptera 9.6%, **Plecoptera** 3.1%, and **Ephemeroptera** 2.8%. **Coleoptera** comprised only 0.1%.

Following logging in a southern Appalachian, USA, stream, Gurtz and Wallace (1984) found that the stonefly ***Amphinemura wui*** (Figure 13) increased in numbers, a response they attributed to the particulate accumulation by bryophytes. Baetid mayflies and the spiny crawler mayfly ***Ephemerella*** (*s.l.*) (Figure 9) increased most among mosses, correlating with a similarly high increase in diatoms among mosses. And as one might expect, the **Orthocladiinae** (**Chironomidae** – midges, Figure 15) increased in response to the increased sediment among the mosses.

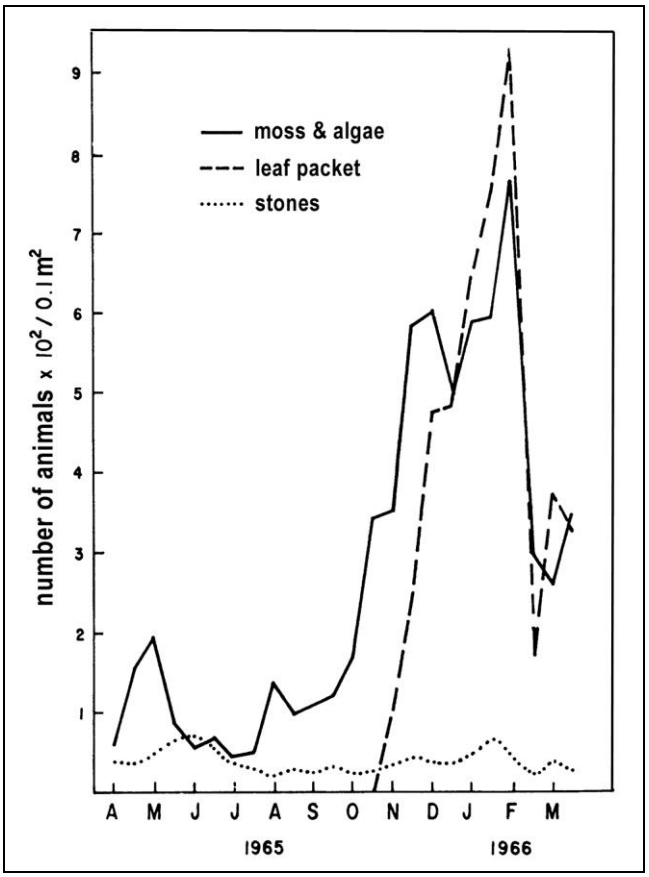

Figure 12. Seasonal distribution of invertebrates on three substrate types in a springbrook in Tennessee, USA. Redrawn from Stern & Stern 1969.

Figure 13. ***Amphinemura wui*** adult, a species that lives among mosses in its naiad state and feeds on detritus. Photo by Donald S. Chandler, with permission.

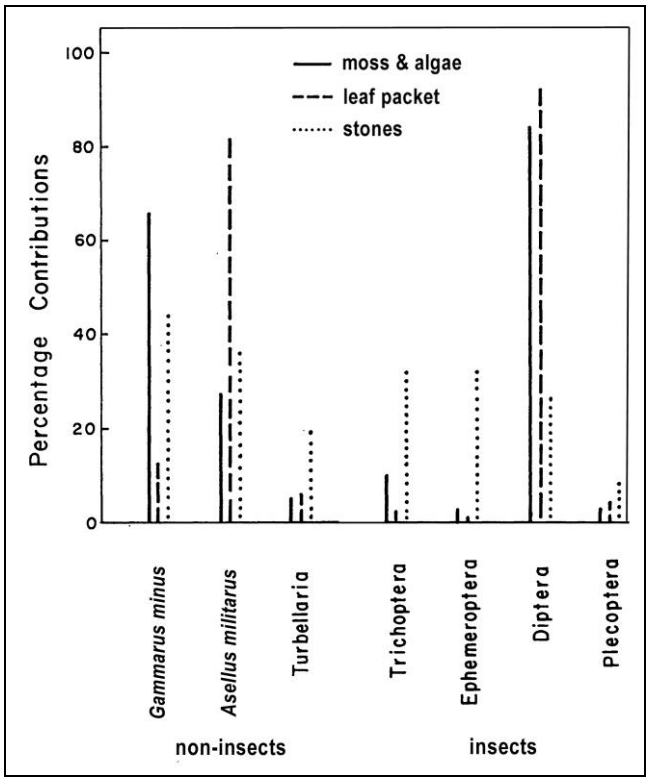

Figure 14. Comparison of insects and other invertebrates among mosses and algae, leaf packets, and stones in a Tennessee springbrook. Redrawn from Stern & Stern 1969.

One of the uses of bryophytes in stream studies could be to serve as **surrogates** – indicators of the habitat and the organisms one might expect to find there. But it seems that bryophytes do not make very reliable surrogates (Paavola 2003; Paavola *et al*. 2003, 2006). Paavola and coworkers, using 101 boreal stream sites, found that within stream areas, the insect communities correlate primarily with stream size, *p*H, and water color. Bryophytes, on the other hand, correlate with nutrient levels and habitat heterogeneity, whereas fish correlate with oxygen levels, depth, and substrate size. But the surrogate role is not as dismal as it may seem. At the level of ecoregions, all three respond to acidity and depth as well as spatial coordinates and the community concordance is much smaller than it is on the level of a single stream or stretch of stream. Nevertheless, these three taxonomic groups had low predictive value. When Virtanen *et al*. (2009) examined bryophyte correlations in 138 boreal springs, temperature was a major driver of communities. The **EPTC** insects [**Ephemeroptera** (Figure 8-Figure 9), **Plecoptera** (Figure 25), **Trichoptera** (Figure 6), and **Coleoptera** (Figure 41-Figure 43), *i.e.* major orders on bryophytes and in fast streams] were not good surrogates for the bryophytes, nor were the **Chironomidae** (Figure 15). Concordance between bryophytes and **Chironomidae** was a little better than with the EPTC group.

Figure 15. **Chironomidae** larva, a common bryophyte inhabitant that is not a good surrogate for bryophytes. Photo by Jason Neuswanger, with permission.

In their study of ***Fontinalis dalecarlica*** (Figure 16) communities, Catteneo *et al*. (2004) found that depth was an important contributor to differences in invertebrate biomass. Shallow mosses supported lower invertebrate biomass than did the deeper ones, possibly due to frequent exposure of the shallow mosses.

Figure 16. ***Fontinalis dalecarlica***, a moss able to occupy a wide range of depths that affect the composition of the insect communities. Photo by Kristoffer Hylander, with permission.

Streamside

The streamside habitat is one of changing water levels, providing a moisture gradient and a place to leave behind the naiad or pupal stage and crawl to the terrestrial environment for adulthood. Lindegaard *et al*. (1975) examined four zones related to the fauna on the moss ***Cratoneuron*** (Figure 17). Underlying the moss they found a detritus zone, with numerous flies and earthworms. Above it was a zone of water-covered mosses. The **madicolous** zone occurred just above the water surface and the moss remained constantly wet by splash and capillary water. This madicolous zone and the water zone were suitable for caddisflies, flies, and molluscs. Above that the moss was dry, occupied by springtails, beetles, spiders, and predaceous mites.

Figure 17. ***Cratoneuron filicinum***, member of a genus that creates faunal zones. Photo by Barry Stewart, with permission.

Artificial Bryophytes

Artificial substrata provide important information on the role of the moss in the association with invertebrates (Cox 1988). Suren (1988) used mosses constructed from nylon twine woven into squares. These artificial mosses were colonized by the stoneflies ***Zelandoperla*** (Figure 18) and ***Zelandobius*** (Figure 19), midges, nematodes, mites, copepods, and ostracods.

Figure 18. ***Zelandoperla pennulata*** adult from the Takitimu Mountains, N Z. Photo by Brian Patrick, with permission.

Figure 19. ***Zelandobius illiesi***, a stonefly that colonized artificial mosses in New Zealand. Photo by Stephen Moore, Landcare Research NZ, with permission.

Glime and Clemons (1972) found that aquatic insects may only colonize mosses as a place to live. In their experiments, insects on artificial string mosses (Figure 20) formed similar communities to those on ***Fontinalis*** (Figure 16), but the number of species on mosses made of polyethylene strips was more limited.

Figure 20. Artificial string moss used in study by Glime & Clemons (1972). Photo by Janice Glime.

Suren (1987, 1988) found that artificial mosses in high alpine streams of New Zealand provided habitat similar to that of mosses, but some taxa, for example **Collembola**, were not restored due to lack of suitable food. Others can be absent due to lack of suitable materials for building their "houses." Suren did find that these surrogate mosses did develop abundant periphyton in one stream, but in another they collected primarily detritus and silt. For substitute mosses, the right kind of artificial structure must be found to also house the needed food. This most likely would require longer for the dependent organisms to colonize.

Suren (1991b) also found that colonization of artificial bryophytes was rapid, reaching a peak in abundance after only 4 weeks. After two months, the density and richness resembled that of the natural bryophytes. Nevertheless, some taxa did not reach normal levels, with larvae of **Empididae** (**Diptera**; Figure 21) and the cranefly ***Limonia hudsoni*** (see Figure 22) having lower numbers. Taxa that were characteristic of riffles, *e.g.*, the mayflies ***Deleatidium*** sp. (Figure 23) and ***Nesameletus*** sp. (Figure 24), or stoneflies ***Stenoperla prasina*** (Figure 25) and ***Zelandobius*** sp. (Figure 19), did not colonize the "stems" of artificial

bryophytes very well but did colonize the bases of these and the bedrock beneath. TWINSPAN identified a strong similarity between the artificial mosses and the real mosses, but the fauna of the artificial substrates were different from that of the riffles.

Figure 21. **Empididae** larva, a dipteran group that did not reach normal numbers on artificial mosses. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 22. ***Limonia*** larva, a genus with lower numbers on artificial mosses than on the real ones. Photo from State Hygienic Laboratory, University of Iowa, with permission.

Figure 23. ***Deleatidium*** sp., a riffle stonefly that colonized the bases, but not the stems, of artificial mosses. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 24. ***Nesameletus*** naiad, a riffle mayfly that colonized the bases, but not the stems, of artificial mosses. Photo by Stephen Moore, Landcare Research, NZ, with permission.

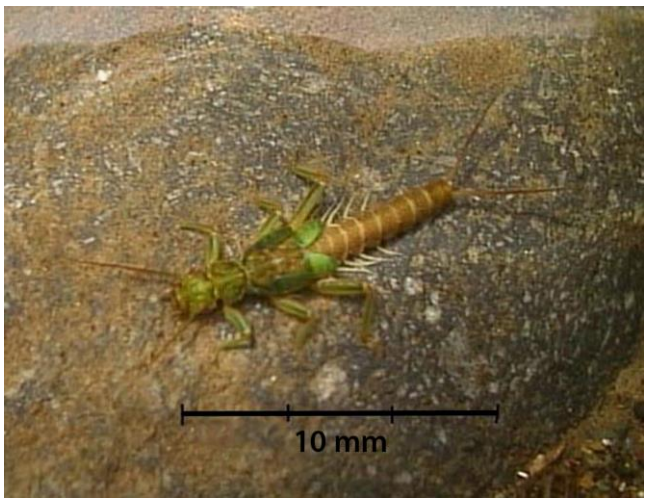

Figure 25. ***Stenoperla prasina*** naiad, a stonefly that colonized the bases, but not the stems, of artificial mosses in New Zealand. Photo by Kanji Saito, with permission.

Suren and Winterbourn (1992) experimented with artificial bryophytes in shaded and unshaded New Zealand portions of an alpine stream. The artificial mosses consisted of pieces of nylon twine woven into 4 mm pores of nylon mesh cut into 0.01 m^2 squares. They found that at the unshaded site seven taxa preferred substrata with high detrital and periphytic biomass. Of the 22 taxa there, 8 were influenced by periphyton biomass, three by detrital biomass, and two by exposure time. At the shaded site, only two taxa had a relationship with these food groups. Exposure time was the most important variable for four of these taxa.

Preference Experiment

Corona (2010) experimented with substrate choice of wood, cobble, sand, and moss to help explain the distributions of **Ephemeroptera** (Figure 8-Figure 9), **Plecoptera** (Figure 25), and **Trichoptera** (Figure 6) in streams in the San Bernardino National Forest (SBNF) in Southern California. She placed three of these preference samplers (615 cm^2 Plexiglass trays) in each of the three streams to determine where the insects chose to live. The actual stream had the leafy liverwort ***Porella*** sp. (Figure 26), but moss with a similar 3-d structure was chosen

because it was available commercially. Of the possible combinations of substrata, only two pairs were significantly different: large gravel vs sand and sand vs moss. The majority of species had greater species abundance in the liverwort and experimental moss compared to other microhabitats. Species diversity was greater in the experimental moss habitat compared to the sand habitat (Table 1). Corona suggested this could be a response to the greater food source that accumulated in the more complex structure of the mosses. In the stream, ***Drunella grandis*** (Figure 27) characterized the ***Porella*** habitat. Other species seemed to be influenced by habitat availability, with **Plecoptera** sp. 1 characterizing sand in the natural habitat, but characterizing the moss in the experimental preference habitat.

Figure 26. ***Porella pinnata***. This genus provides a suitable habitat for ***Drunella grandis*** in California, USA, streams. Photo by Jan-Peter Frahm, with permission.

Figure 27. ***Drunella grandis***, a stonefly naiad that inhabits ***Porella pinnata***. Photo by Bob Newell, with permission.

Torrents and Waterfalls

The precipice nears and the clump of mosses soon finds itself in a freefall, wet, and being carried by the pounding water and convection currents. Soon it will rejoin the stream below, bumping along until it gets pinned behind a log or rock.

In that same freefall are insects, dwellers of the water, giving in to the strong movement of the water, then drifting with the stream. Like the moss, they await a place where they can lodge. But for them, that lodging place might be the moss itself, a haven out of the torrent that takes them to unknown destinations. A haven where they can lay their eggs and find algae, bacteria, fungi, or smaller insects to eat. A haven where they can rest safe from larger hungry predators. A place to be until that day when they must climb to the water's surface and take their maiden flight, free from the rushing torrent that made their life so tenuous.

Table 1. Field Tray Results for species contributors with a cut-off at 90% contribution characterizing microhabitats across all depths.

	Moss	Large Gravel	Sand	Wood
Lower Barton Creek				
Baetis tricaudatus	8.24	59.89	100	24.85
Diphetor hageni	28.15	34.76		45.08
Micrasema	8.01			
Nemouridae immature	9.30			
Plecoptera sp. 1	8.01			
Zapada cinctipes	9.61			
Santa Ana				
Baetis tricaudatus	51.87	18.45	74.47	31.99
Ephemerella dorothea	6.51	27.95	12.77	12.52
Lepidostoma errigenum	23.92	25.69	12.77	15.99
Paraleptophlebia	12.12	27.91		35.49
Upper Barton Creek				
Baetis tricaudatus				57.14
Psychoglypha	100			42.86

Thomas (1980) successfully reared the torrential dweller ***Porricondyla ramadei*** (**Diptera: Cecidomyiidae**), taken from submerged bryophytes in the turbulent water of a mountain stream in the Pyrénées. There were also hundreds of other strictly torrential invertebrates in the sample. Wallace and Ross (1971) described a new species of caddisfly, ***Pseudogoera singularis*** (**Odontoceridae**) from mosses in waterfalls of the Southern Appalachians, USA.

Springs

Virtanen *et al*. (2009) investigated bryophyte inhabitants in 138 boreal springs. They found that water chemistry and temperature determined bryophyte assemblages. By contrast, Ilmonen (2009) found that the macroinvertebrate assemblages correlated with physical habitat but not with changes in chemistry.

Chironomids likewise responded to temperature, but water chemistry had little effect on them in 138 springs in Finland; physical habitat was somewhat important in their distribution (Virtanen *et al*. 2009). The **Chironomidae** (Figure 15) had a closer correspondence with **Ephemeroptera** (Figure 27), **Plecoptera** (Figure 25), **Trichoptera** (Figure 6), and **Coleoptera** (Figure 41-Figure 43) than with the bryophytes. Hence, as in stream habitats, spring bryophytes and insects are relatively poor surrogates for each other. Even when the insect assemblages were similar, the environmental characters differed. As in streams, better concordance occurred when larger geographic areas were included.

Huryn *et al*. (2005) found that springs in the Arctic separated from other stream types based on nutrient concentrations and likelihood of freezing. Glacier and

mountain streams separated from both springs and tundra streams on substrate instability and likelihood of freezing.

Lindegaard *et al*. (1998) concluded that the high variability of substrate within a spring accounted for the low variation among Danish streams. This same variability also made it impossible for Lindegaard and coworkers to correlate environmental variables with fauna. They classified the macroinvertebrates associated with springs and springbrooks into seven groups: (1) **cryobiotic** species restricted to the spring area, (2) **crenophilous** species with maximum abundances in springs, (3) **lotic** species also living in the spring area, (4) **lentic** species found in **limnocrenes**, (5) **ubiquitous** species, (6) **madicolous** species, and (7) **terrestrial** species.

Thorup (1963) described insects from Danish springs. Although I don't know how they correlated with the bryophytes, the genera and some of the species mentioned are known from bryophytes: ***Baetis rhodani*** (Figure 8), ***Brachyptera risi*** (Figure 28), ***Nemurella picteti*** (Figure 29, ***Leuctra hippopus*** (Figure 30), ***Leuctra fusca*** (Figure 31), ***Agapetus*** *fuscipes* (Figure 32), ***Crunoecia irrorata*** (Figure 33), ***Pericoma*** cf. *blandula* (Figure 34), and ***Simulium ornatum*** (Figure 35).

Figure 28. ***Brachyptera risi*** naiad, a bryophyte inhabitant in Danish springs. Photo by Guillaume Doucet <www.guillaume.doucet.free.fr>, with permission.

Figure 29. ***Nemurella picteti*** adult, a stonefly whose naiads live in Danish springs. Photo by Pete Hillman, with online permission.

Figure 30. ***Leuctra hippopus*** naiad, a stonefly that lives in Danish springs. Photo by Niels Sloth, with permission.

Figure 31. ***Leuctra fusca*** naiad, a stonefly that lives in Danish springs. Photo by James K. Lindsey, with permission.

Figure 32. ***Agapetus fuscipes*** larva in its case, an insect that inhabits Danish springs. Photo by J. C. Schou, with permission.

Figure 33. ***Crunoecia irrorata*** larva in its case, an insect inhabiting Danish springs. Photo by Niels Sloth, with permission.

Figure 34. ***Pericoma blandula*** adult, a species whose larvae live in Danish springs. Photo Copyright by Nick Upton <www.naturepl.com>, with permission.

Figure 35. ***Simulium ornatum / intermedium / trifasciatum*** complex adult, a species group the lives in Danish springs as larvae. Photo by Malcolm Storey, through Discover Life online permission.

Unlike other studies on surrogates, Ilmonen (2009) found that a rare spring-dwelling caddisfly (***Crunoecia irrorata***) was a good surrogate for springs that had a high conservation value. These springs had high overall species diversity, including other rare (red-listed) species. But as in other studies cited herein, these relationships held on a regional, but not within-spring system basis. Ilmonen and Paasivirta (2005) found that while there were differences in relative abundances among types of springs, the most common taxa were the same in all of them. The insects were somewhat more abundant in moss carpets and less abundant in sites that were pools. The strongest separators related to water flow and minerogenic substrate, a relationship supported by studies in Spain (Barquin & Death 2009).

Depth is an important factor for some insects. At the Pupu Springs, NZ, the invertebrates on the moss ***Cratoneuropsis relaxa*** (Figure 36) were 20 times more abundant at 0.6 m depth than at 4.3 m depth (Michaelis 1977). Such depth differences can relate to temperature, oxygen availability, and photosynthetic organisms (algae) for food. Boulders with bryophytes had more invertebrates than those at similar depths with no bryophytes.

Figure 36. ***Cratoneuropsis relaxa***, a moss where depth matters to the insects. Photo by Tom Thekathyil, with permission.

Bottazzi *et al*. (2011) found that springs with mosses served as home for predominately **Chironomidae** (Figure 15) and **Plecoptera (**Figure 29-Figure 31**)**, as well as the crenophilic microcrustaceans in **Harpacticoida** and **Ostracoda**. Only *p*H and temperature explained the diversity pattern, factors demonstrated as important by (Virtanen *et al*. 2009). Nevertheless, the presence of mosses increased the species diversity of the springs.

Seepage areas differ from other springs by having small flow rates in which the source water has filtered into permeable earth. These are often suitable habitats for bryophytes. In England, these seepage areas provide habitat for the cranefly ***Tipula cheethami*** (Figure 37) larvae living among the moss ***Platyhypnidium riparioides*** (Figure 38) and the snipefly ***Spania nigra*** (Figure 39) larvae on the liverwort ***Pellia neesiana*** (Figure 40) (Boyce 2002). On cliff seepages, one might find the tiny beetle ***Sphaerius acaroides*** (Figure 41-Figure 42) among the mosses. ***Ochthebius poweri*** (Figure 43) (**Coleoptera: Hydraenidae**) live in these seeps, eating the algae there. Some caddisflies occur there as well.

Figure 37. ***Tipula abdominalis*** larva, member of a genus that is found among ***Platyhypnidium riparioides*** in seepage areas of England. Photo by Tom Murray, through Creative Commons.

Figure 38. ***Platyhypnidium riparioides***, a moss home for insects in seepage areas in England. Photo by David T. Holyoak, with permission.

Figure 39. ***Spania nigra*** adult, a snipefly whose larvae are known from the liverwort ***Pellia neesiana*** in seepages. Photo by Marko Mutagen, through Creative Commons.

Figure 40. ***Pellia neesiana***, home for the snipefly ***Spania nigra*** in seepages. Photo by Jan-Peter Frahm, with permission.

Figure 41. ***Sphaerius acaroides*** adult, an inhabitant of mosses on cliff seepages. Photo by David Maddison, through Creative Commons.

Figure 42. ***Sphaerius acaroides*** larva, an inhabitant of mosses on cliff seepages. Photo by David Maddison through Creative Commons.

Figure 43. ***Ochthebius exaratus*** adult, an inhabitant of mosses in seepage cliffs, where it eats algae. Photo by Udo Schmidt through Creative Commons.

Ward and Dufford (1979) found that mosses and water cress (tracheophyte) had similar macroinvertebrate biomass in a Colorado springbrook-pond system. The tiny caddisfly ***Hydroptila*** (Figure 6) developed its largest populations on the moss. The cranefly ***Limonia*** (Figure 22) was present in large numbers and was restricted to mosses; ***Euparyphus*** (**Stratomyiidae**; Figure 44), another dipteran, was the second most abundant organism. Surprisingly, the **Coleoptera** (Figure 41) were the most diverse on mosses.

Figure 44. ***Euparyphus*** sp. larva, a genus that was restricted to mosses in a Colorado springbrook-pond system. Photo from EPA, through public domain.

Bryophytes in springs provide a continuous gradient from land to water, both vertically and horizontally (Lindegaard *et al.* 1975; Thorup & Lindegaard 1977; Bottazzi *et al.* 2011). Thus they provide a wide range of niches that promote a high invertebrate diversity. This transition furthermore makes an easy transition area for insects emerging from their aquatic stage into adults.

Bogs and Fens

Bogs and fens are dominated by bryophytes at the ground level, creating unique and generally favorable habitats for invertebrates. Bogs have a wide temperature range within a single day (Gerson 1969). At the surface, the temperature can have a 30°C span in a single day while the stem layer experiences only a 5°C temperature span. Similarly, the surface humidity can range 40-100% while the stem layer remains at 100%. The *p*H ranges widely from acid bogs to rich fens, having a strong influence on some members of the insect assemblages.

Bogs have been widely studied for their unusual plant assemblages, but invertebrates have received much less attention, an omission known for a long time (Jewell & Brown 1929). Muttkowski (1912) summarized the insects in trout bogs in Yellowstone National Park, USA. These included **Ephemeroptera** (rare), **Odonata** (rare), **Hemiptera** (few), **Trichoptera** (rare), **Chironomidae** (Figure 15) (common), **Psychodidae** (common), and **Tipulidae** (frequent).

Many insects live in peatlands because of the diversity of habitats present there. For example, Bordoni (1972) found 179 species of beetles (Coleoptera) in a Tuscan fen, but only a few were actually bryophilous. Members of the **Staphylinidae** are known to feed on mosses (Mani 1962) and were well represented in that Tuscan fen. The **Sphaeriidae** (minute bog beetles) live among mosses (Arnett 1971).

A member of the insect order **Grylloblattodea** (crickets and grasshoppers) lays its eggs among mosses (Gerson 1969; Richards & Davies 1977). Crickets and grasshoppers in peatlands even feed on ***Sphagnum*** (Figure 1) (Vickery 1969). Uvarov (1977) suggested that these insects may eat the mosses to obtain water. Paasivirta *et al.* (1988) found that aquatic sites had greater insect emergence than semi-terrestrial sites in a boreal raised bog of central Finland.

As the hummocks and hollows build, the ***Sphagnum*** species change. ***Sphagnum*** (Figure 1) bogs undergo succession and their fauna changes as the ***Sphagnum*** species change (Murphy 1955). This succession of species is true for oribatid mites (Tarras-Wahlberg 1952-53) and pselaphid beetles (Reichle 1966). The fauna often occupy a specific position relative to the water table, presumably due to a preferred moisture level. Murphy (1955) found that the springtail ***Sminthurides malmgreni*** (Figure 45) became associated with the most humid hollow and pool species, ***Sphagnum cuspidatum*** (Figure 46) and ***S. subsecundum*** (Figure 47). When the mosses ***S. papillosum*** (Figure 48) and ***S. magellanicum*** (Figure 49), typical hummock mosses, become available, the springtails ***Folsomia brevicauda*** (see Figure 50) and ***Isotoma sensibilis*** (see Figure 51) are likely. Still others are present in the dry ***Calluna*** (Figure 52) and ***Cladonia*** (probably *Cladina*) habitat.

Figure 45. ***Sminthurides malmgreni***, a bog dweller in hollows and pools. Photo by Jan van Duinen, with permission.

Figure 46. ***Sphagnum cuspidatum***, a hollow and pool species where one can find ***Sminthurides malmgreni***. Photo by Jonathan Sleath, with permission.

Figure 47. ***Sphagnum subsecundum***, a bog hollow and pool species where one can find ***Sminthurides malmgreni***. Photo by Michael Lüth, with permission.

Figure 48. ***Sphagnum papillosum***, a hummock species that is home to ***Folsomia brevicauda*** and ***Isotoma sensibilis***, with sundew. Photo by Michael Lüth, with permission.

Figure 49. ***Sphagnum magellanicum***, a hummock species that is home to the springtails ***Folsomia brevicauda*** and ***Isotoma sensibilis***. Photo by Michael Lüth, with permission.

Figure 50. ***Folsomia fimetaria***, a springtail that lives in hummocks of bogs. Photo by Andy Murray, through Creative Commons.

Figure 51. ***Isotoma*** sp., a genus found in hummocks of ***Sphagnum papillosum*** and ***S. magellanicum***. Photo by Anki Engström at <www.krypinaturen.se>, with permission.

Figure 52. *Calluna vulgaris* heath on drier hummocks in the Outer Hebrides. Photo by Alan Silverside, with permission.

Bryophytes play a major role in the fauna of bogs. That fauna is often shared with fauna of surrounding habitats, but some unique organisms prefer that habitat, and others use it seasonally.

Collembola - Springtails

Whereas **Collembola** are not common among submerged bryophytes, a number of species occur among bryophytes, especially ***Sphagnum*** (Figure 1, Figure 46-Figure 49), in bogs. Usinger (1974) suggests collecting these bog taxa by submersing the moss in water until the **Collembola** float.

Bright (2002) reported 15 springtail species in Michigan bogs. These included ***Bourletiella arvalis***

(Figure 53), ***Folsomia prima*** (Figure 54), ***Heteraphorura subtenuis***, ***Hydroisotoma schaefferi*** (Figure 55), ***Hypogastrura nivicola*** (Figure 56), ***Isotoma viridis*** (Figure 57), ***Neelus minutus*** (see Figure 58), ***Orchesella albosa*** (Figure 59), ***Sminthurides aquatica*** (Figure 60-Figure 61), ***Sminthurides malmgreni*** (Figure 62), ***Sminthurides occultus***, ***Sminthurides penicillifer*** (Figure 63), ***Sminthurinus aureus*** (Figure 64), ***Sminthurinus bimaculatus*** (Figure 65), and ***Tomocerus flavescens*** (Figure 66).

Figure 53. ***Bourletiella arvalis***, a tiny bog-dwelling springtail. Photo by Jan van Duinen, with permission.

Figure 54. ***Folsomia*** sp.; ***F. prima*** is a bog dweller. Photo by Jan van Duinen, with permission.

Figure 55. ***Hydroisotoma schaefferi*** male, a species that can be found with ***Sphagnum*** (Figure 1, Figure 46-Figure 49) in bogs. Photo by Tom Murray, through Creative Commons.

Figure 56. ***Hypogastrura nivicola***, a bog inhabitant. Photo by Scott Justis, with permission.

Figure 57. ***Isotoma viridis***, a species that occurs in bogs. Photo by Jan van Duinen, with permission.

Figure 58. ***Neelus murinus*** with eggs – a bog inhabitant. Photo by Frans Janssens, with permission.

Figure 59. ***Orchesella cincta***, member of a genus with bog inhabitants. Photo by Malcolm Storey, through Creative Commons.

Figure 60. ***Sminthurides aquatica***, a bog-dweller. Photo by Andy Murray, through Creative Commons.

Figure 61. ***Sminthurides aquatica*** on frog's eye, demonstrating its small size. Photo by Kim Fleming, through Creative Commons.

Figure 62. ***Sminthurides malmgreni***, a bog dweller. Photo by Jan van Duinen, with permission.

Figure 63. ***Sminthurides*** cf. ***penicillifer*** female. Photo by Andy Murray, through Creative Commons.

Figure 64. ***Sminthurinus aureus***. Photo by Andy Murray, through Creative Commons.

Figure 65. ***Sminthurinus bimaculatus***. Photo by Andy Murray, through Creative Commons.

Figure 66. ***Tomocerus flavescens***, a bog dweller. Photo by Royce Bitzer, with permission.

Coleoptera - Beetles

Crenitis punctatostriata (**Hydrophilidae**; Figure 67) is a true **bryobiont** (animal exclusively associated with bryophytes) that lives its entire life among ***Sphagnum*** (Figure 1) and is known from the Jura Mountains (Matthey 1977). This species lays its eggs among the mosses and the larvae remain there. The pupa lives in a cell formed from the bryophytes.

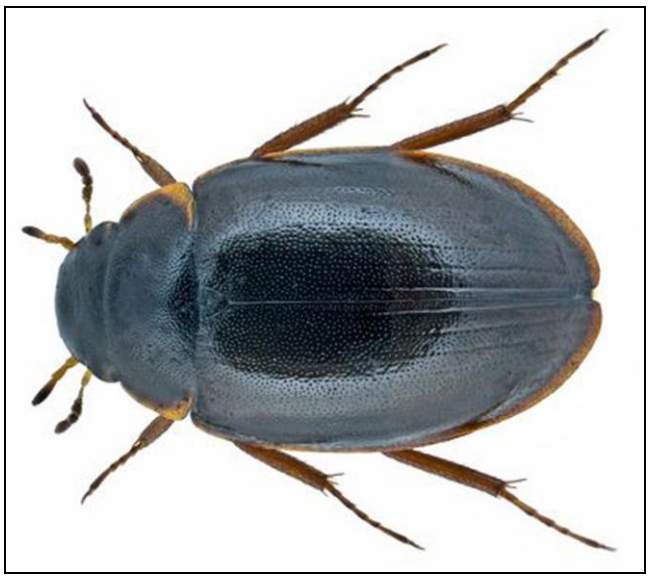

Figure 67. ***Crenitis punctatostriata*** adult, a species that lays its eggs among mosses and the larva develop there. Photo by Udo Schmidt, through Creative Commons.

For some ***Sphagnum*** (Figure 1)-associated insects, this moss provides a safe haven during unfavorable seasons. One of the more unusual of these is the tiny water beetle ***Hydroporus morio*** (quick silver diver; Figure 68) (Jackson 1956 in Gerson 1982). This beetle lives in ***Sphagnum*** pools in Europe and is sensitive to heat. When these pools dry out in summer, the exposure to heat on a sunny ***Sphagnum*** mat can be dangerous for ***H. morio***. To survive, the beetle bores small round holes into the damp ***Sphagnum*** in the "dried" pool and **aestivates** (summer equivalent of hibernates) in that protected (and insulated) location until the rains return. In the southern parts of its range, it is disappearing, apparently due to climate warming (Anderson 2015).

Figure 68. ***Hydroporus morio*** adult, an insect that lives in ***Sphagnum*** pools, then bores holes into the mat to aestivate when the pools dry. Photo by Niels Sloth, with permission.

Others find bryophytes a suitable place to survive the winter (Reichle 1966). More than 20 species of beetles in the **Pselaphidae** live in ***Sphagnum*** (Figure 1) bogs, where they can find a microclimate similar to that of their early postglacial ancestors. Among these are beetles that overwinter as adults in the interstitial spaces of frozen moss mats.

Larson and House (1990) found that small pools were dominated by oligochaetes, beetles, and mosquitoes. Hebauer (1994) listed **Coleoptera** (Figure 68) species he considered to be **tyrphophils**, *i.e.*, living among ***Sphagnum*** (Figure 1), in middle Europe. These included ***Ilybius erichsoni*** (Figure 69), ***Agabus congener*** (Figure 70), ***I. wasastjernai*** (Figure 71), ***Bidessus grossepunctatus*** (Figure 72), ***Hygrotus novemlineatus*** (Figure 73), ***Colymbetes paykulli*** (Figure 74), ***C. striatus***, ***Enochrus affinis***, ***E. coarctatus***, ***E. ochropterus*** (Figure 75), ***Hydrochus brevis*** (Figure 76), ***H. megaphallus***, ***Hydroporus brevis*** (Figure 77), ***H. melanarius*** (Figure 78), ***H. memnonius*** (Figure 79), ***H. scalesianus*** (Figure 80), ***H. tristis*** (Figure 81). Underground springs with ***Sphagnum*** housed ***Hydroporus ferrugineus*** (Figure 82), ***H. obsoletus***, and ***H. longicornis*** (Figure 83). Leng (1913) reported **Parnidae** and **Elmidae** (Figure 84) in ***Sphagnum*** (Figure 1) bogs.

Figure 69. ***Ilybius erichsoni*** adult, a tyrphophil, on ***Sphagnum***. Photo by Niels Sloth, with permission.

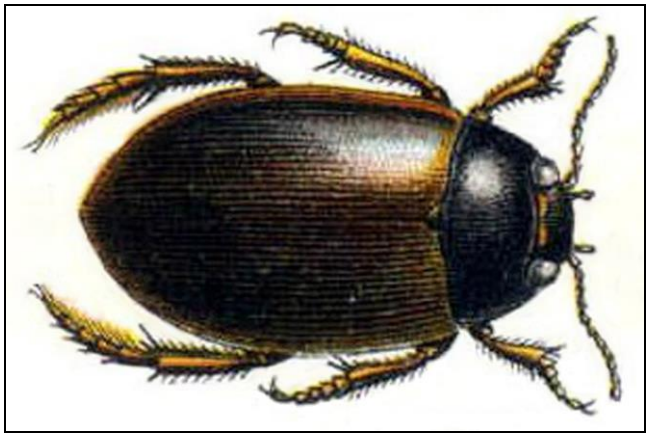

Figure 70. ***Agabus congener*** adult, a ***Sphagnum*** dweller. Image through Creative Commons.

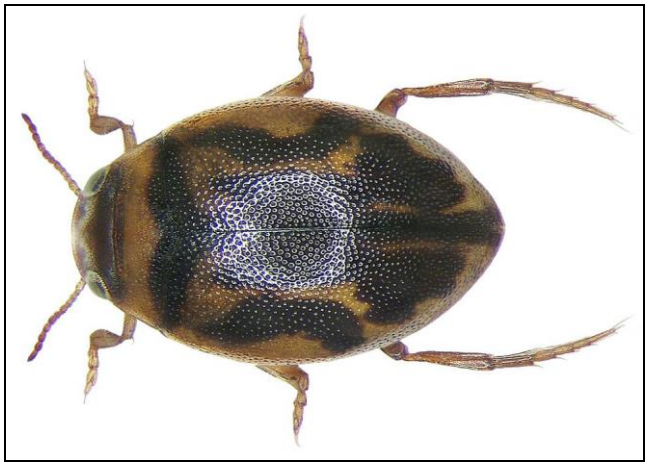

Figure 73. ***Hygrotus inaequalis*** adult, a ***Sphagnum*** dweller. Photo by Udo Schmidt, with permission.

Figure 71. ***Ilybius wasastjernai*** adult, a ***Sphagnum*** dweller. Photo by Niels Sloth, with permission.

Figure 74. ***Colymbetes paykulli*** adult, a ***Sphagnum*** dweller. Photo by Niels Sloth, with permission.

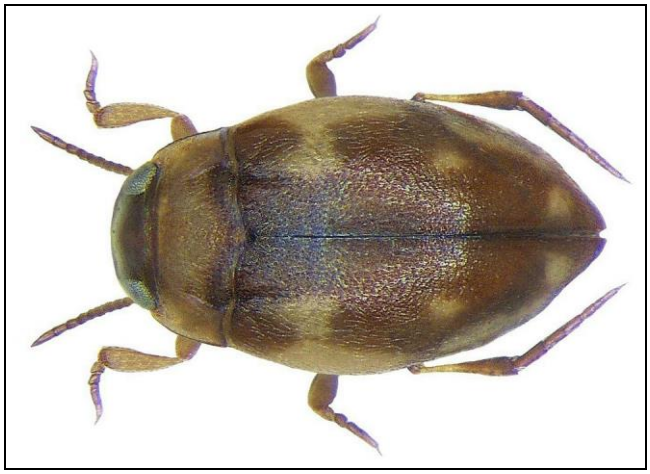

Figure 72. ***Bidessus unistriatus*** adult, a ***Sphagnum*** dweller. Photo by Udo Schmidt, through Creative Commons.

Figure 75. ***Enochrus ochropterus*** adult, a ***Sphagnum*** inhabitant. Photo by Niels Sloth, with permission.

Figure 76. ***Hydrochus brevis*** adult, a ***Sphagnum*** inhabitant. Photo by Christoph Benisch <kerbtier.de>, with permission.

Figure 77. ***Hydroporus brevis*** adult, a ***Sphagnum*** inhabitant. Photo by Niels Sloth, with permission.

Figure 78. ***Hydroporus melanarius***, a bog dweller, on moss. Photo by Niels Sloth, with permission.

Figure 79. ***Hydroporus memnonius*** adult, a bog dweller, on moss. Photo by Niels Sloth, with permission.

Figure 80. ***Hydroporus scalesianus*** adult on leaf litter. Photo by Niels Sloth, with permission.

Figure 81. ***Hydroporus tristis*** adult on moss. Photo by Wolfram Sondermann, through Creative Commons.

Figure 82. ***Hydroporus ferrugineus***, an inhabitant of underground springs with ***Sphagnum***. Photo by Roger S. Key, with permission.

Figure 83. ***Hydroporus longicornis*** adult on moss, an inhabitant of underground springs with ***Sphagnum***. Photo by Niels Sloth, with permission.

Figure 84. **Elmidae** larva, a ***Sphagnum*** bog dweller. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Reichle (1967) considered temperature and humidity to be the most important variables influencing the pselaphid beetles in bogs. These beetles respond to saturated humidities of 95-100%, and these match the conditions found among the interstices created by the mosses. The temperature stratification created by the mosses could explain the differences in species at different **seral stages** (stages in succession).

For the five species of pselaphids Reichle (1967) studied, these preferences were ***Bythinopsis tychoides***, mean 21.5±0.81, range 25.9-15.3°C; ***Decarthron defectum***, 28.5±0.55, 31.4-24.0; ***Pselaphus bellax*** (Figure 85), 19.5±0.86, 24.7-13.0; ***Reichenbachia borealis*** (Figure 86), 21.±0.99, 26.2-14.4; and ***Rybaxis clavata*** (Figure 87), 28.3±0.41, 29.9-25.1. These preferences correlated well with the natural conditions of the microhabitats where they resided in the New York bog.

To these species, a report from the New York Entomological Society (Anonymous 1925) added the pselaphid ***Pselaphus erichsoni*** and the staphylinid ***Boreaphilus henningianus***, cohabiting in a New York, USA, bog with ***Bythinopsis tychoides***. Mr. Nicholay, at that same meeting, recommended using sifting to locate the **Coleoptera** in such habitats.

Figure 85. ***Pselaphus bellax*** adult, a ***Sphagnum*** bog dweller. Photo by Yann Gobeil, through Creative Commons.

Figure 86. ***Reichenbachia borealis*** adult, a ***Sphagnum*** bog dweller. Photo by Tom Murray, through Creative Commons.

Figure 87. ***Rybaxis*** female adult, a ***Sphagnum*** bog dweller. Photo by Tom Murray, through Creative Commons.

Odonata – Dragonflies and Damselflies

The **Odonata** are commonly seen flying about bogs. These strong fliers can easily migrate there. Boudot and Jacquemin (2002) identified 20 species of **Odonata** as tyrphobionts in France. Larson and House (1990) found that **Odonata** dominated, along with **Chironomidae** (**Diptera**; Figure 15), in the large, stable, vegetated pools. With two or more years in their naiad stage, the **Odonata** are important consumers in this habitat and may be a major factor in the insects that survive there. These dragonflies included ***Aeshna subarctica*** (Figure 88), ***Somatochlora arctica*** (Figure 89), ***Leucorrhinia dubia*** (Figure 90), and ***Somatochlora alpestris*** (Figure 91). The bog habitat influences these dragonflies by its strong *p*H fluctuations, low secondary productivity, few vertical plant structures (needed for emergence), and the isolation of bogs from each other (Dreyer 1988). Goffart and Fichefet (2003) observed female ***Aeshna subarctica*** laying eggs (Figure 88) by inserting them into ***Sphagnum*** (Figure 1) at the water surface. Sahlén *et al*. (2004) found that ***Aeshna subarctica elisabethae*** from central and eastern Europe was "strictly" related to ***Sphagnum*** habitats.

Figure 88. ***Aeshna subarctica*** laying eggs in ***Sphagnum***. Photo by Guillaume Doucet <www.guillaume.doucet.free.fr>, with permission.

Figure 89. ***Somatochlora arctica*** adult male; females lay eggs in ***Sphagnum***. Photo by Piet Spaans, through Creative Commons.

Figure 90. ***Leucorrhinia dubia***, a prominent predator in bogs. Photo by L. B. Tettenborn through Creative Commons.

Michiels and Dhondt (1990) observed dragonflies (***Sympetrum danae*** – Figure 92) during their egg-laying activities in bogs. This species typically oviposits in flight while still paired in copulation. This behavior seems to make them subject to frog predation – those that were post-tandem were attacked less frequently by the frogs. The females seemed to prefer ***Sphagnum*** (Figure 1) as a substrate for their eggs. They avoided warmer sites and often chose sites that already had ovipositing females on them. Michiels and Dhondt reported several threatened and potentially threatened **Odonata** species living in these diminishing habitats. These included ***Nehalennia speciosa*** (Figure 94), ***Coenagrion johanssoni*** (see Figure 93), ***Aeshna caerulea*** (Figure 95), ***A. crenata***, ***A. subarctica elisabethae*** (Figure 88), ***Somatochlora arctica*** (Figure 89), and ***S. alpestris*** (Figure 91). In northern Europe where the habitat is common, these species, except ***N. speciosa*** and ***A. crenata***, are likewise common.

Figure 91. ***Somatochlora alpestris*** adult, a prominent predator in bogs. Photo by Gilles San Martin, through Creative Commons.

Figure 92. ***Sympetrum danae*** female adult, a species that lays her eggs in bogs. Photo by L. B. Tettenborn, through Creative Commons.

Figure 93. ***Coenagrion hastulatum*** adult. Photo by L. B. Tettenborn, through Creative Commons.

Figure 94. ***Nehalennia speciosa*** mating damselfly adults. These bog dwellers lay their eggs in bogs. Photo by Guillaume Doucet <http://guillaume.doucet.free.fr/>, with permission.

Figure 95. ***Aeshna caerulea*** adult emerging. Photo by Guillaume Doucet <guillaume.doucet.free.fr>, with permission.

The ground cricket ***Pteronemobius*** sp. (Figure 96) not only eats bryophytes, but also punctures ***Sphagnum*** leaves with its ovipositor to place its eggs in the resulting cavity (Vickery 1969).

Figure 96. ***Pteronemobius heydenii***, a genus of cricket that eats bryophytes and punctures ***Sphagnum*** leaves to lay its eggs. Photo through Flickr Creative Commons.

Diptera – Flies

If you have ever walked through a forest surrounding a bog on a humid summer evening, you probably have not forgotten the experience of blood-giving. Mosquitoes are not typical bryophyte fauna, but in bogs ***Aedes excrucians*** (Figure 97) occurs in bog pools and occasionally among the ***Sphagnum*** (Figure 1) mosses there (Elgmork & Sæther 1970).

Figure 97. ***Aedes excrucians*** larvae, bog pool dwellers. Photo by Donald S. Chandler, with permission.

The **Tipulidae** (Figure 98) often deposit eggs and live as larvae and pupae among the peat mosses. ***Tipula*** (Coulson 1962; Freeman 1968) and ***Dolichopeza*** (Byers 1961) also feed on the mosses. The moss-mimicking tipulid ***Phalacrocera replicata*** feeds on *Sphagnum* spp. (Clymo & Hayward 1982). Other tipulid species burrow into ***Sphagnum*** (Figure 1) spp.

But bogs often attract human traffic for berry picking and other interests. This traffic can be detrimental to these developing **Diptera**. ***Molophilus ater*** (Figure 99) (**Limoniidae**) numbers are lower among the peat along a path than in adjacent areas (Duffey 1979). These limoniid cranefly adults seem to spend more time where there is vegetation than on bare ground, although they seem to prefer the bare ground for laying eggs. This same preference for egg laying is not true for large bare areas. Unfortunately, larvae are often crushed along the paths, especially those near the surface.

Figure 98. **Tipulidae** adult, a common family in bogs. Photo by Bob Armstrong, with permission.

Figure 99. ***Molophilus ater*** adult, a species negatively affected by bog traffic. Photo by James K. Lindsey, with permission.

As in most aquatic moss habitats, **Chironomidae** (Figure 15) are important contributors to the fauna (Muttkowski 1912; Larson & House 1990). Smirnov (1961) did not find any abundant species in ***Sphagnum*** (Figure 1) bogs to specialize on a food group, but one chironomid, ***Psectrocladius psilopterus***, was the only species to eat submerged ***Sphagnum***; even so, it ate primarily algae.

Other Insects

The moisture available within a ***Sphagnum*** habitat, perhaps made safer by the antibiotic properties of the moss, provides a suitable habitat for nests of ***Myrmica ruginodis*** (Figure 100-Figure 101) and ***Formica picea*** (Figure 102) (Matthey 1971). These ants also feed on the mosses (Plitt 1907) and become major predators when the bog dries up (Grdović & Sabovljević 2008).

Figure 100. ***Myrmica ruginodis*** pupa among mosses. Photo by James K. Lindsey, with permission.

Figure 101. ***Myrmica ruginodis*** adult amid mosses. This species makes it nest of ***Sphagnum*** fragments. Photo by James K. Lindsey, with permission.

Figure 102. ***Formica picea*** adult, a species that makes nests of ***Sphagnum***. Photo by April Nobile <www.antweb.org>.

On one fortunate adventure into a Michigan, USA, fen I had the privilege of watching ants on one of their nests on a windy day (Figure 103). The light-weight ***Sphagnum*** pieces were flying off the nest faster than they could grab new ones and repair the nest. This of course created great activity among the ants (Figure 104).

Figure 103. Ant nest in ***Sphagnum*** in a Michigan fen. Photo by Janice Glime.

Figure 104. Close view of ants repairing nest of ***Sphagnum*** in a Michigan fen as its bits of ***Sphagnum*** are being scattered by wind. Photo by Janice Glime.

A number of terrestrial insect types can be found in bogs and fens as well, including crickets and grasshoppers (Vickery 1969), caterpillars of moths (Chapman 1894), and aphids in the genera ***Myzodium*** (Figure 105) and ***Muscaphis*** (Figure 106) (Gerson 1969). But aquatic and semi-aquatic types occur there as well, including the biting midge ***Forcipomyia*** (Figure 107) (Oldroyd 1964) and mayfly naiads (Richardson 1981).

Figure 105. ***Myzodium mimulicola***, aphids that live in bogs. Photo by Andrew Jensen, through Creative Commons.

Figure 106. ***Muscaphis utahensis***, a bog-dwelling aphid. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 107. ***Forcipomyia*** sp. larvae, a biting midge that lives among mosses in bogs. Photo by Tom Murray, through Creative Commons.

Although some of the insects eat ***Sphagnum***, Danks and Rosenberg (1987) report that most species in Canadian bogs are generalists. Flannagan and Macdonald (1987) likewise found the **Ephemeroptera** and **Trichoptera** of Canadian peatlands to be generalists. They suggested that the ability for some insects to survive in temporary pools provided adaptations that also permitted them to live in other wet habitats such as peatlands. Mayfly naiads even use ***Sphagnum*** species for "nests" (Richardson 1981).

Lakes and Ponds

Floating bryophytes can be abundant in small lakes and ponds. The thallose liverwort ***Riccia fluitans*** (Figure 108) can form dense 3-d mats that provide a protective network. The spaces formed house numerous invertebrates in these floating habitats (Armstrong 2014).

Needham (1901) found layers of shed exuviae of the dragonfly ***Gomphus exilis*** (Figure 109), with ***G. spicatus*** mixed in, among mosses on logs at the edge of Little Clear Pond, suggesting the mosses created a preferred site for emergence.

Figure 108. ***Riccia fluitans***, home for numerous insects in the floating mats. Photo by Jan-Peter Frahm, with permission.

Figure 109. ***Gomphus exilis*** female, a species that uses mosses for emergence. Photo by Sheryl Pollock, with permission.

One of the unusual habitats at the edge of lakes is the **moss ball**. Moss balls generally begin on a small pebble that gets moved back and forth across the shoreline as the water gets blown onto the shore and recedes. These are able to develop a special fauna of ***Asellus aquaticus*** oligochaetes, and leeches on balls formed by ***Fontinalis antipyretica*** (Figure 10) and ***Drepanocladus sendtneri*** (Figure 110), but insects were not mentioned (Luther 1979 in Gerson 1982).

Figure 110. ***Drepanocladus sendtneri***, a moss-ball former that is inhabited by invertebrates. Photo by Michael Lüth, with permission.

Floating plants provide a habitat that is constantly wet, yet does not require breathing under water. Plants such as those in the flowering plant family Lemnaceae (duckweeds) have their own fauna of insects. And in some lakes and ponds, the floating thallose liverwort ***Ricciocarpos natans*** (Figure 111) may occur with the duckweeds. In these habitats one might find the springtail ***Sminthurides aquaticus*** (Figure 112) that eats from the surface, the beetle ***Tanysphyrus lemnae*** (Figure 113) that completes its entire life cycle in only two weeks on *Lemna* (Figure 113), but it is not yet known from ***Ricciocarpos***, and ***Mesovelia mulsanti*** (Figure 114), a bug known as the water treader, crawling on the surface and in depressions on the surface of this floating habitat (Scotland 1934). The liverwort ***Ricciocarpos natans*** is also capable of rearing the dipteran ***Phytoliriomyza mesnili*** (**Agromyzidae**) (Spencer 1990), but it can pupate on more occasionally inundated species such as ***Riccia beyrichiana*** (Figure 115) and feed on this and other terrestrial bryophytes (Hering 1966).

Figure 111. ***Ricciocarpos natans***, home for springtails and other surface dwellers. Photo by Jan-Peter Frahm, with permission.

Figure 112. ***Sminthurides aquaticus***, a springtail that lives on ***Ricciocarpos natans***. Photo by Andy Murray, through Creative Commons.

Figure 113. ***Tanysphyrus lemnae*** on ***Lemna***. Note the holes chewed in the leaves by these weevils. Photo by Aydin Örstan through, Creative Commons.

Figure 114. ***Mesovelia mulsanti***, a surface dweller. Photo by Matt Bertone, through Creative Commons.

Figure 115. ***Riccia beyrichiana***, site for pupation of ***Phytoliriomyza mesnili*** when the thallus is inundated. Photo by Jan-Peter Frahm, with permission.

Arctic and Alpine

In investigating alpine streams of New Zealand, Suren (1993) found that streambed stability strongly influenced the bryophyte distribution. These communities are dominated by **Nematoda**, **Oligochaeta**, **Copepoda**, and **Chironomidae** (Figure 15). These differed in fauna from bryophytes outside New Zealand, particularly certain families of **Ephemeroptera**, **Plecoptera**, and **Trichoptera** (EPT) that are also present elsewhere in New Zealand. Nevertheless, the invertebrate densities within the bryophytes are higher above treeline than below. The invertebrate densities are higher among bryophytes that have a high periphyton component compared to those with a higher detrital component.

In the alpine area of the South Island of New Zealand, Suren (1988) found that the dominant bryophyte dwellers are the stoneflies ***Zelandoperla*** (Figure 18) and ***Zelandobius*** (Figure 19) and the midges (**Chironomidae**, Figure 15). The mosses had 5-15 times as many invertebrates as the rocky areas, but these moss-dwelling invertebrates also include nematodes, mites, copepods, ostracods, and other non-insect invertebrates. The most common mayflies are restricted to rocky areas.

In the Southern Alps of New Zealand, Cowie and Winterbourn (1979) found 44 species of invertebrates among the mosses. These are mainly immature stages of insects, with the fauna varying by moss; the moss species reflects differences in habitat. ***Fissidens rigidulus*** (Figure 116) grows in the torrential middle channel of the stream and supports ***Zelandoperla fenestrata*** (**Plecoptera**; see Figure 18), ***Zelolessica cheira*** (**Trichoptera**; see Figure 117-Figure 118), **Empididae** (**Diptera**; Figure 21) and the ever-present **Chironomidae** (Figure 15). Among the clumps of ***Pterygophyllum quadrifarium*** (Figure 119) in the saturated inner spray zone Cowie and Winterbourn found ***Austroperla cyrene*** (**Plecoptera**), and **Helodidae** (**Coleoptera**) as the most abundant species, along with the flatworm ***Neppia montana***. ***Cratoneuropsis relaxa*** (Figure 36), in the outer spray zone, was not a good insect habitat, housing primarily the isopod ***Styloniscus otakensis***. water Saturation, flow rates, and available detritus as a food source seem to have the greatest influence on the locations of these insects.

Figure 116. ***Fissidens rigidulus***, a moss that grows in the torrential mid-channel where **Plecoptera** and **Diptera** are common. Photo by Bill & Nancy Malcolm, with permission.

Figure 117. ***Zelolessica*** sp., prevalent among ***Fissidens rigidulus*** midstream in Southern Alps of New Zealand. Photo by Stephen Moore, Landcare Research NZ, with permission.

Figure 118. ***Zelolessica*** sp., prevalent among ***Fissidens rigidulus*** midstream in the Southern Alps of New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 119. ***Pterygophyllum quadrifarium***, a moss that houses insects in the spray zone of torrential channels in New Zealand. Photo by Bill and Nancy Malcolm, with permission.

Robinson *et al*. (2001) studied the glacial streams of the Swiss Alps. These streams experience strong seasonal changes in water chemistry resulting from the seasonal changes in glacial melt, especially in water turbidity, particulate phosphorus, and conductivity. The macroinvertebrates likewise vary seasonally, with winter macroinvertebrate taxon richness being 2-3 times as high as that in summer. These same differences are also reflected in higher numbers and biomass in winter. Although taxa are not delimited by substrate in this study, many of the dominant taxa are species known as common bryophyte inhabitants.

Diptera, common among temperate streams, are even more common in Alaskan streams (Oswood 1989). **Plecoptera** and **Ephemeroptera** are next in abundance, but **Trichoptera** are somewhat rare. The **Hemiptera**, **Odonata**, **Megaloptera**, **Coleoptera**, net-spinning caddisflies, burrowing mayflies, and the stoneflies **Pteronarcyidae**, **Peltoperlidae**, and **Perlidae** are rare or absent. On the other hand, the ever present **Chironomidae** (**Diptera**; Figure 15) and **Nemouridae** (**Plecoptera**) actually increase from south to north in the northern hemisphere.

A similar predominance of **Chironomidae** (Figure 15) is seen in the European Central Alps – comprising 90-95% of the emergence (Füreder *et al*. 2005). As in Oswood's (1989) Alaskan study, **Ephemeroptera**, **Plecoptera**, and **Trichoptera** comprised much fewer numbers. Füreder *et al*. (2001) considered seasonal shifts from harsh summers to less severe autumn and winter conditions in the Tyrolean Alps, Austria, to affect the insect life history patterns and maintain a relatively high insect diversity and productivity in glacier-fed streams. As in glacial streams, the individual alpine streams of the French Pyrénées seem to differ greatly in diversity, displaying distinct benthic macroinvertebrate communities. Within a stream, the 15 most abundant taxa were consistently more stable and persistent from one year to the next than was the entire stream community (Brown *et al*. 2006).

Miller and Stout (1989), working in Alaska, suggested that to be so successful the dipterans that compose the most numerous and variable taxa in the Arctic must have variable **diapause** (period of suspended development; state of physiological dormancy), ability to grow in cold waters, and good dispersal powers.

Disturbance

Disturbance greatly reduces the number of invertebrates, and in some cases the bryophytes, on stones in streams (Englund 1991; Parker & Huryn 2006). Small stones rarely have bryophytes (Slack & Glime), except when they are embedded in the substrate (Englund 1991). Rock size likewise affects the diversity of stream insects (Hart 1978). In Englund's study, following disturbance, several invertebrate taxa increased their density on moss-covered undersides of over-turned stones. The undisturbed moss-covered rocks acquired increased density of invertebrates as a result of the disturbance. On the other hand, on disturbed rocks recovery of lost mosses [***Fontinalis dalecarlica*** (Figure 16), ***Hygrohypnum*** (Figure 120-Figure 121], and hence invertebrate inhabitants, was poor even 14 months after the stones were overturned.

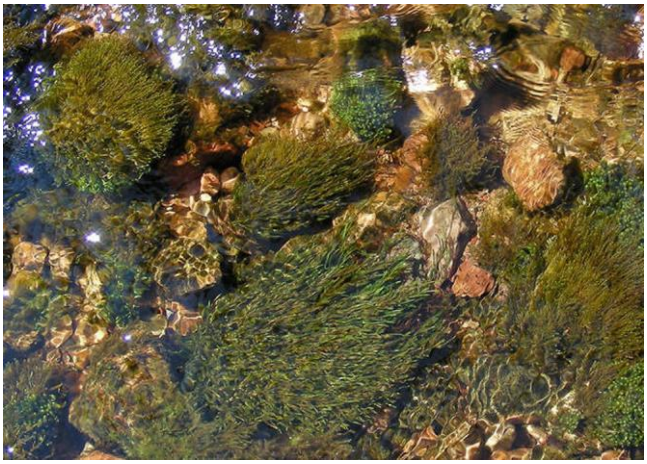

Figure 120. ***Hygrohypnum ochraceum*** habitat, a genus that can have poor recovery after disturbance, resulting in loss of insects. Photo by Dick Haaksma, with permission.

Figure 121. ***Hygrohypnum ochraceum***, home to many insects. Photo by Michael Lüth, with permission.

In an Alaskan stream, Parker and Huryn (2006) attributed the high macroinvertebrate density in a spring stream to the density of bryophytes there. That biomass was more than 1000 times the density of the mountain stream where disturbance among the loose rocks was great during spring melt.

Disturbance can take the opposite form as well. During the dry season, aquatic insects must find a place of refuge that provides sufficient moisture, or go dormant. In a first-order stream in the Atlantic Forest, Brazil, Rosa *et al*. (2011) found that Chironomidae dominate in both the rainy and dry seasons, but that in the rainy season the Ceratopogonidae are second, whereas in the dry season it is the annelid family Naididae that is second. Rosa and coworkers concluded that the bryophyte habitat provides refuge during spates, minimizing downstream movement of the invertebrate fauna. The density of the fauna is much greater during the rainy season, but the diversity is similar.

Retention

Restoration is not always friendly to mosses. In a headwater stream, the moss cover declined dramatically following restoration (Muotka & Laasonen 2002). This resulted in increases of insects only among the algae-eating scrapers. The mosses were an important retentive feature for macroinvertebrates, but the restoration techniques knocked them loose from numerous locations, favoring the growth of algae.

Colonization

The rapidity of invertebrate recolonization of mosses can be amazing. Maurer and Brusven (1983) found that insects colonized insect-free ***Fontinalis neomexicana*** (Figure 4) to capacity within one week. The moss substrate had 5-30 times the densities of insects compared to the mineral substrate. As in many streams, larvae of midges (**Chironomidae**, Figure 15) were most abundant. Thienemann (1936), in his enumeration of alpine **Chironomidae**, commented on the importance of mosses as a habitat.

Korsu (2004) found that the restoration procedure in one Finnish stream destroyed almost half of the bryophytes and invertebrate densities plummetted. But recolonization was rapid. The disturbed area was recolonized within two weeks and peak numbers were reached within one month. Korsu found that recovery was especially fast in winter, with bryophytes playing a major role. It is interesting that the density of insects on bryophytes was higher after the restoration than before. The mayfly ***Baetis*** (Figure 8) had a negative correlation with the bryophytes before restoration, but afterwards (within 1 day!) it had a positive correlation. A similar response occurred for ***Hydropsyche siltalai*** (Figure 122). Korsu concluded that bryophytes provided refugia during the disturbance and remained a shelter long afterwards.

Figure 122. ***Hydropsyche siltalai*** larva, a species that increased in numbers after restoration of a stream in Finland. Photo by Urmas Kruus, with permission.

Experimental studies on colonization of mosses are relatively rare. Some of these have been discussed earlier under Artificial Mosses (Chapter 11-1). Maurer and Brusven (1983), however, designed a study using live ***Fontinalis neomexicana*** (Figure 4) in an Idaho, USA, river. After removing all the insects, they trimmed the moss clumps into 40 X 15 cm plots and arranged them in a natural streambed in five staggered rows with three clumps per row, as well as two comparative samplings. After three weeks of colonization, moss clumps were collected in nylon organdy net (250 µm mesh) to keep insects intact. Insects were removed by washing and hand picking. It

took only one week for insects to reach carrying capacity of the mosses (compared to controls)! The caddisfly ***Micrasema*** sp. (Figure 123) and mayfly ***Diphetor hageni*** (=*Baetis parvus*; Figure 124) were especially prevalent among moss clumps during the study. At the same time, the moss cover did not change the insect densities in the underlying hyporheic zone.

Figure 123. ***Micrasema charonis*** larva with a case made from moss parts. Photo by Bob Henricks, with permission.

Figure 124. ***Diphetor hageni*** naiad, common among ***Fontinalis neomexicana*** in Idaho. Photo by Donald S. Chandler, with permission.

Maurer and Brusven (1983) found that the **Ephemeroptera** were the most abundant in both test and control clumps, with **Diptera**, **Trichoptera**, **Coleoptera**, and **Plecoptera** following in that order. The **Chironomidae** (Figure 15) made up ~94% of the **Diptera**. The riffle beetle ***Cleptelmis ornata*** (Figure 125) was a slow colonizer, reaching carrying capacity only after 4-6 weeks.

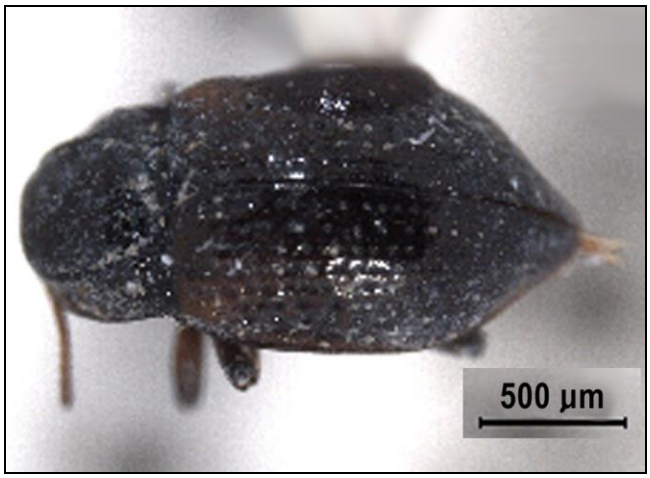

Figure 125. ***Cleptelmis ornata*** adult, a slow colonizer of bryophytes. Image modified from Biodiversity Institute of Ontario, through Creative Commons.

Mackay and Waters (1986) found that mosses provided suitable sites for the **Hydropsychidae** (net-spinning caddisflies; Figure 3) downstream of impoundments. They suggested that the mosses and algae provided suitable sites for attachment of their nets and the location benefitted from the settling effect of the impoundment on abrasive sand.

Streams suffer natural disturbance. In two North Swedish woodland streams nearly 17% of the moss-covered stones were overturned in just a few years (Englund 1991). In experiments, overturning rocks with mosses resulted in a reduction of both ash-free dry weight and diversity. On the other hand, three out of 16 taxa actually increased density on the underside of the overturned stones, living among the buried mosses. All the other taxa decreased in density. Even after 14 months the mosses and invertebrate populations had not recovered.

As already noted, Gurtz and Wallace (1984) found that presence of mosses increased the density of taxa following clear cutting surrounding a southern Appalachian Mountain stream. But disturbance resulting from the insecticide fenitrothion on bogs did not have as favorable a result (Fairchild & Eidt 1993). The poison caused a reduction in insect emergence for the next 6-12 weeks, with the **Chironomidae** (Figure 15) and **Ceratopogonidae** (Figure 126) experiencing more that 50% reduction for at least 1 month after the treatment. Since bog pool insects carry the nutrients to land, this nutrient transfer diminished and more nutrients accumulated in the bog pools.

Figure 126. ***Bezzia*** larva, in a family (**Ceratopogonidae**) that is quickly reduced by fenitrothion in bogs. Photo from <www.dfg.ca.gov>, through public domain.

It is interesting that in a study of Swedish streams, Malmqvist and Hoffsten (2000) found a negative correlation between macroinvertebrate richness and moss (***Fontinalis*** – Figure 10) coverage. In a glacial river in Iceland, Gislason *et al*. (2001) found that distance from glacier, altitude, bryophyte biomass, and Pfankuch Index of channel stability explaining 31% of the variability in the macroinvertebrate data. The **Chironomidae** (Figure 15) predominated, but **Simuliidae** (Figure 35), **Plecoptera** (Figure 28-Figure 31), and **Trichoptera** (Figure 123) were present in low numbers.

In New Zealand alpine streams, bryophytes were confined to stable substrates (Suren 1991a). Suren (1988) found a negative effect on **Collembola** (Figure 45) when real mosses were replaced by artificial mosses in the high

alpine streams of the South Island of New Zealand. Among those moss-inhabited substrates, ***Limonia hudsoni*** (see Figure 22) and ***Zelandoperla*** sp. (Figure 18) were typically associated with bryophytes (Suren 1991a).

Not all bryophyte growths bring a positive recovery of the insect fauna. In the Kuparuk River, Alaska, USA, fertilization by phosphorus encouraged the growth of mosses after eight years of increased phosphorus. Persistence of the mosses had both positive and negative effects on the insect populations. It prevented the recovery of ***Ephemerella*** (Figure 9) (Slavik *et al*. 2004) and midge (**Chironomidae**, Figure 15) taxa, including the tube-building ***Orthocladius rivulorum*** (Figure 127-Figure 128) that had been affected by the shifts in primary producers. This shift included the loss of epilithic algae due to human activity, but they subsequently returned within 2-3 years. Once the bryophytes became established, they persisted, changing the morphology of the stream bottom.

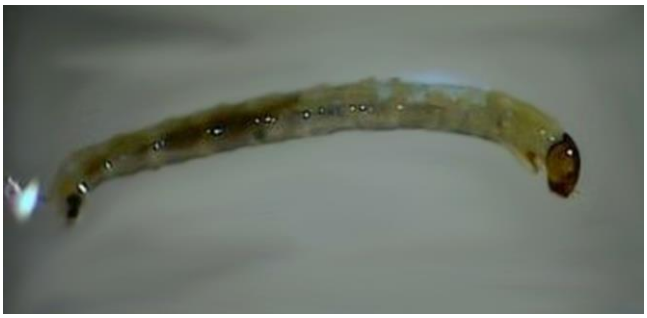

Figure 127. ***Orthocladius rivicola*** larva, an insect that did not recover from phosphorus fertilization that caused an increase in moss growth in an Alaskan river. Photo from Stroud Water Research Center, through Creative Commons.

Figure 128. Orthoclad in silt tube. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Disturbances that remove mosses can greatly affect the invertebrate fauna. Gurtz and Wallace (1984) found that moss (***Hygroamblystegium tenax*** – Figure 2) density and leaf detritus were the most important characters determining abundance of aquatic insects following a disturbance. Following clearcutting, the greatest increase in taxon density in the stream that drained the clear-cut watershed occurred in the moss-covered rock face compared to any other substrate. Moss habitats experienced increases of the shredder stonefly ***Amphinemura wui*** (Figure 13), a response that Gurtz and Wallace attributed to the accumulation of particulate matter by the moss. The **Baetidae** mayflies likewise increased, experiencing their greatest increase among mosses where there was also the greatest increase in number of diatoms. But the chironomid ***Eukiefferiella*** spp. (Figure 129) showed the sharpest increase among the insects, occupying mosses on the rock face.

Figure 129. ***Eukiefferiella*** (**arrow**) on ***Nesameletus ebop-ohaupapa***. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Forestry practices for logging and drainage often have considerable impact on the bryophytes and their inhabitants. In a small headwater stream where ***Fontinalis dalecarlica*** (Figure 16) formed the dominant habitat in riffles, forestry disturbances by ditch construction changed these mossy habitats to sand riffles (Vuori & Joensuu 1996). Transplanted mosses in the disturbed sites accumulated considerably more inorganic matter than did undisturbed controls. Subsequently, the invertebrate richness was significantly lower as well. The mosses at the control site supported a dominance of shredder stoneflies whereas the disturbed site was dominated by blackflies (**Simuliidae**; Figure 35).

Pollution Effects

In addition to physical disturbances of flooding and human activities, pollution affects both the bryophytes and their fauna. Winterbourn *et al*. (2000) looked for effects on the food chain in New Zealand streams where mosses were a significant component. Despite the lowering of *p*H and increases in aluminium and iron in the water, there was not a biomagnification effect in the food web. The metal concentrations in the invertebrates was considerably lower than that in the mosses. It is possible that the bryophytes were able to sequester the metals, thus protecting the invertebrates from those that might have increased in their algal and detrital food.

Geographic Differences

If one were to examine bryophytes in New Zealand streams, the fauna would be significantly different from that of bryophytes in the North Temperature Zone. In New Zealand, instead of the typical mayflies, stoneflies, and caddisflies, the fauna is dominated by nematodes, oligochaetes, and copepods, with the only abundant insect being **Chironomidae** (Figure 15) (Suren 1993). In fact, other types of insects comprise less than 2% of the

invertebrate fauna. This is not due to a difference in bryophytes, but rather the absence of families that typically inhabit the North Temperate bryophyte habitat.

By contrast, Egglishaw (1969) found that mayflies occupied up to 16% of the invertebrate fauna of Scottish streams. Suren (1993 – updated in Table 2) reviewed studies from other parts of the world and found that the most important bryophyte insects were **Plecoptera** (**Nemouridae**, **Perlodidae**, **Leuctridae**, **Chloroperlidae**), **Ephemeroptera** (**Baetidae**, **Heptageniidae**, **Ephemerellidae**), and **Trichoptera** (**Brachycentridae**, **Glossosomatidae**, **Lepidostomatidae**, **Limnephilidae**, and **Sericostomatidae**). These families mesh well with my own studies in bryophytes of Appalachian Mountain streams, eastern USA, except for **Perlodidae**, **Heptageniidae**, and **Sericostomatidae**. Others (**Baetidae**, **Lepidostomatidae**, **Limnephilidae**) were uncommon in the Appalachian streams.

Table 2. Percentages of the contributions by invertebrate taxa > 0.1% of the total invertebrate density in ten studies on invertebrate fauna of stream bryophytes: 1) Percival & Whitehead 1929 from a) thin moss & b) thick moss; 2) Percival & Whitehead 1930; 3) Frost 1942; 4) Egglishaw 1969; 5) Stern & Stern 1969); 6) Glime & Clemons 1972; 7) Lindegaard *et al*. 1975; 8) Cowie & Winterbourn 1979; 9) McKenzie-Smith 1987; 10) Smith-Cuffney 1987 from a) unshaded and b) shaded streams; 11) Suren 1991a from a) unshaded and b) shaded streams; 12) Vlčková *et al*. 2002; - = not reported with abundances > 0.1% total density. (from Suren 1993). The last two columns indicate the number of studies presented here in which the taxon was represented by >0.1% and the average percent of the community the taxon represented.

	References														No.	Av %
	1a	1b	2	3	4	5	6	7	8	9	10a	10b	11a	11b	12 Studies	Comp
Turbellaria	-	-	-	0.4	-	0.3	-	-	-	-	1.6	-	-	-	0.26 3	0.2
Nematoda	-	-	-	-	-	-	-	-	-	-	1.8	2.8	22.1	12.5	14.65 4	2.8
Oligochaeta	3.6	3.3	24.1	0.4	-	-	-	10.3	-	2.9	6.0	1.4	-	-	0.57 8	5.8
Tardigrada	-	-	-	-	-	-	-	-	-	-	-	-	2.4	-	0.59 1	0.2
Amphipoda	1.2	1.1	0.1	-	-	4.8	-	6.9	-	42.5	-	-	-	-	6	4.0
Copepoda	-	-	57.8	2.5	-	-	-	-	-	-	-	4.0	9.0	1.5	0.47 5	5.3
Ostracoda	-	-	-	-	-	-	-	-	-	-	-	-	-2.8	0.7	0.13 2	0.3
Isopoda	-	-	-	-	-	1.9	-	-	-	-	-	-	-	-	1	0.2
Hydracarina	3.3	3.0	3.6	1.0	-	0.1	-	6.3	-	-	2.7	7.0	1.1	5.9	0.73 10	2.4
Collembola	-	-	-	-	-	-	-	4.2	-	-	1.2	-	-	-	2	0.9
Ephemeroptera	15.9	6.5	-	4.0	4.2	2.6	2.0	-	-	5.46	15.2	1.8	-	-	0.88 9	4.1
Plecoptera	-	-	-	-	44.6	2.9	5.7	16.7	22.5	5.4	3.1	8.2	2.1	2.5	0.01 10	11.4
Diptera	1.3	1.5	0.1	2.3	2.3	-	12.6	-	21.2	-	1.1	6.1	1.5	7.7	1.96 11	5.2
Chironomidae	54.3	40.9	9.2	83.0	34.1	77.9	71.7	33.2	33.7	21.6	54.0	53.0	57.7	63.4	33.81 14	49.1
Coleoptera	6.2	4.2	3.6	2.0	-	0.1	2.9	0.7	-	2.3	-	-	-	-	0.15 8	1.5
Trichoptera	4.0	0.3	0.1	3.7	1.4	9.1	3.4	-	23.6	13.4	6.2	7.9	-	-	0.29 11	5.2

Summary

Bryophytes increase the number of niches for occupancy by aquatic insects. They increase surface area, culture algae, collect detritus, provide high prey density, and provide a refugium against the current. At the same time they permit the insects to live in the greater oxygen provided by the rapid flow, saving them ventilation energy. Feeding groups of these insects include collector-gatherers, scrapers, shredders, collector-filterers, and engulfers, with collector-gatherers typically being most abundant.

Altitude and latitude are important determinants of both the bryophytes and the associated fauna. Thickness of the moss mat also is important in determining the fauna, with thicker mats creating more niches.

The most common orders of moss dwellers in streams are **Ephemeroptera** (mayflies), **Plecoptera** (stoneflies), **Trichoptera** (caddisflies), and **Diptera** (flies). Streams in the Arctic and alpine habitats lack most of the **Trichoptera** (caddisflies), but otherwise have similar order representation among stream bryophytes, with even more **Chironomidae**. The associations of insects with the species of bryophytes may be a consequence of both needing similar conditions, as exemplified by the similarities of insect communities on the moss ***Fontinalis dalecarlica*** and the liverwort ***Scapania undulata***, two species that often occur side-by-side. Nevertheless, bryophytes do not make good surrogates for the stream inhabitants, correlating primarily with nutrient levels and habitat heterogeneity, whereas insects correlate more with stream size, *p*H, and water color. In fact, clumps of string and other artificial mosses seem to attract communities similar to those on real mosses. On the other hand, the presence of bryophytes will usually indicate a high density of insects.

The bryophytes may serve as a refuge for insects in winter when non-bryophyte plants are absent and the bryophytes are common in fast water where freezing is less common. The bryophytes furthermore serve as a location of collected detritus and a site for winter diatoms.

Within the clump of bryophytes of a stream one can find a detritus zone with little or no flow, a water zone within the moss clump, and a **madicolous** zone just above the water surface but where the bryophytes are still wet. And at the surface of the moss, but submerged, the highest water velocity and therefore the most oxygen exist.

Waterfalls may have specialists that live among the wet mosses, avoiding the torrent itself. Springs often have dense bryophyte cover. **Chironomidae** here

respond to temperature; many insects also respond to nutrient concentrations or *p*H. Depth of streams, pools, and springs can influence insect community composition, in part because of temperature and oxygen gradients. Bogs and fens have both pool and dry hummock conditions, contributing a wide range of niches that differ in moisture, temperature, and light. Consequently, there is a wide variety of insects, and even flying adults make use of the mosses for egg deposition, mating, and resting. More **Collembola** (springtails) are found in bogs and fens than in most aquatic habitats. **Coleoptera** (beetles) and **Odonata** (dragonflies and damselflies) likewise are common in these habitats. **Hymenoptera** (ants, bees) are absent from streams and lakes, but in bogs and fens ants build nests from the ***Sphagnum***. Little seems to be published about insects associated with lake bryophytes. Some of the beetles are associated with floating ***Riccia fluitans*** and ***Ricciocarpos natans*** in shallow lakes. In one case, the latter is inhabited by the leaf miner ***Phytoliriomyza mesnili***.

Disturbance immediately reduces the number of invertebrates, but if mosses remain or are replaced, they are quickly recolonized by remaining drifting organisms or from egg-laying. Attempts at restoration can cause the bryophytes to break loose and reduce the insect fauna.

If one compares the bryophyte fauna around the world, differences in relative abundance of the orders are apparent. These differences are often the result of evolutionary and distributional differences. For example, the families of the insects are different in Australia and New Zealand from those in North America.

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CHAPTER 11-4
AQUATIC INSECTS: HEMIMETABOLA – COLLEMBOLA AND EPHEMEROPTERA

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CHAPTER 11-4
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Figure 1. ***Serratella ignita***, a common moss dweller. Photo by J. C. Schou, with permission.

COLLEMBOLA – Springtails

This group was traditionally considered to be one of the insect orders, but more recently they have been classified in the class **Entognatha**. **Collembola** are quite small and lack wings. They have three pairs of legs, like insects, but have only six abdominal segments (Thorp & Covich 1991). The young (**nymphs**) resemble the adults, changing to adults by breaking their outer covering (**exoskeleton**) and discarding it, then expanding while the new exoskeleton is still soft.. They are unique in having a **furcula** (Figure 3-Figure 5) that forms the spring and a **collophore** (cylindrical ventral tube; Figure 3, Figure 6). When at rest, the furcula bends forward under the abdomen and is held in place by the **tenaculum (**Figure 3), a midventral structure that clasps the furcula. The springtail accomplishes rapid distance movement by releasing the furcula, which springs backward, propelling the springtail forward several centimeters. This can be used even on the water surface. Some can be seen bouncing around on the snow in winter.

Figure 2. ***Podura aquatica*** moulting; note split in outer skeleton. Photo by Jan van Duinen, with permission.

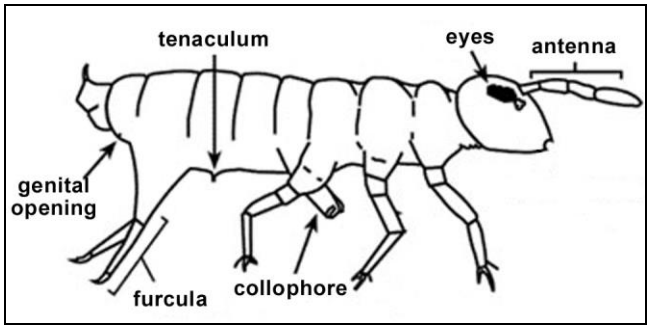

Figure 3. **Collembola** external anatomy. Modified from Cooperative Extension illustration, University of Missouri.

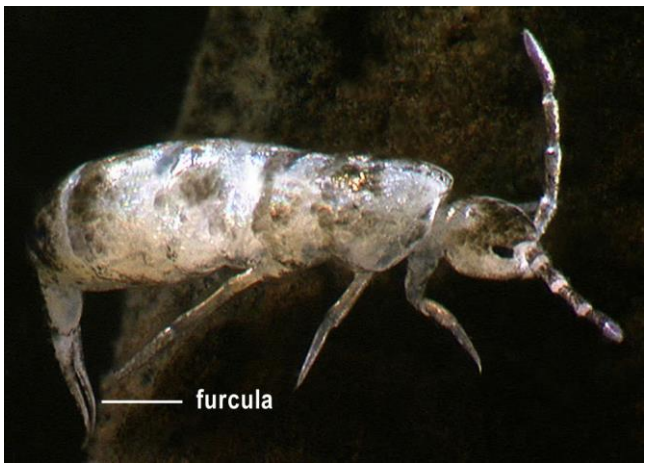

Figure 4. ***Arthropleona oruarangi*** showing furcula. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 5. ***Dicyrtomina ornata*** ventral side showing **furcula**. Photo by Jan van Duinen, with permission.

Collembola can be sexual or parthenogenetic. Sexual males deposit **spermatophores** in clusters or individually. Females stimulate this deposition by producing pheromones (Waldorf 1974). But among many of the soil **Collembola**, presumably including bryophyte dwellers, females lay eggs (Figure 7-Figure 8) that have not been fertilized, *i.e.*, are produed **parthenogenetically**. Since few reproductive studies exist, I cannot generalize of aquatic bryophyte dwellers. What makes this reproduction so interesting is the role of symbiotic bacteria in the genus ***Wolbachia*** (Werren *et al*. 1995). These bacteria live in and reproduce in the female reproductive organs and eggs of the springtail. It is these bacteria that control the parthenogenesis in the colonized species. That is, they feminize the springtails.

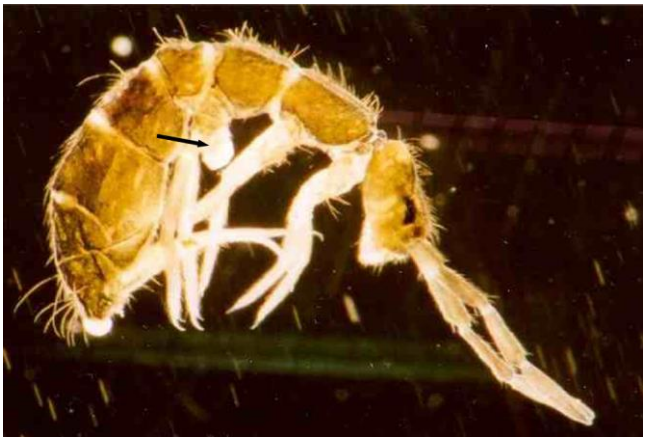

Figure 6. ***Isotoma*** (springtail) showing **collophore** (**arrow**). Photo by U. Burkhardt, through Creative Commons.

Figure 7. **Collembola** eggs. Photo by Jan van Duinen, with permission.

Figure 8. ***Sminthurides*** eggs in duckweed. Photo by Jan van Duinen, with permission.

The **Collembola** are predominately moist terrestrial organisms, but some can hop on the water surface (Figure 9) or live among wet mosses. Waltz and McCafferty (1979) considered only 10 species as semiaquatic and five as **riparian** (relating to bank of river or other moving water). The waxy cuticle (Chang 1966), coupled with small size, permits them to float on water. The **collophore** (ventral tube) serves a double function: absorption of water and respiration.

The **Collembola** seem to be particularly responsive to drawdown and drainage (Silvan *et al.* 2000). On older drained sites their numbers were up to 100 times as high compared to pre-drawdown. Other invertebrates were typically about ten times as high. The **Collembola** occurred mostly in the top 4 cm of the drained land.

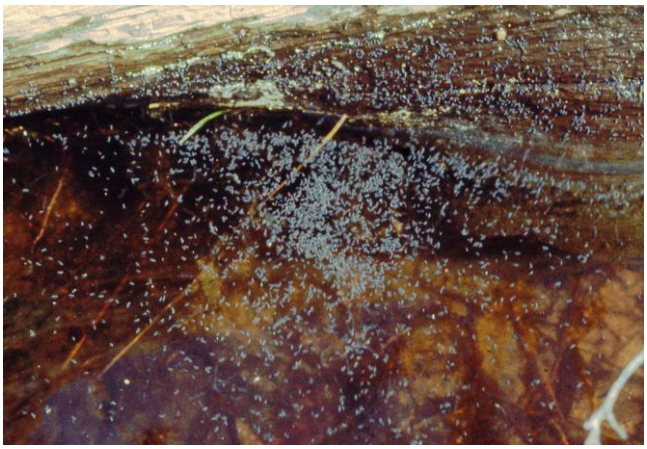

Figure 9. **Collembola** (springtails) on water where they can jump about on the surface tension. Photo by Janice Glime.

In my search for information on the bryophyte-dwelling springtails, I was surprised to find so little that related to aquatic habitats. In my own studies in the Appalachian Mountain, USA, streams, I found representatives of eight families, albeit not frequently. The species in these collections were ***Odontella lamellifera*** (Figure 10) (**Brachystomellidae**), ***Entomobrya griseoolivata*** (Figure 11) and ***Orchesella quinquefasciata*** (Figure 12) (**Entomobryidae**), ***Hypogastrura armatus*** (see Figure 13), and ***Schotella glasgowi*** (**Hypogastruridae**), ***Hydroisotoma schaefferi*** (Figure 14)**,** ***Isotoma violacea***, ***Isotoma viridis*** (Figure 15), and ***Isotomurus palustris*** (Figure 16) (**Isotomidae**), ***Pseudachorutes lunatus*** (**Neanuridae**; see Figure 17), ***Onychiurus subtenius*** (**Onychiuridae**), ***Sminthurides aquaticus*** (Figure 18) (**Sminthuridae**), and ***Tomocerus flavescens*** (Figure 19) (**Tomoceridae**). Of these taxa, only ***Isotomurus palustris*** was present in more than two collections. Nevertheless, I recorded ***Orchesella quinquefasciata*** in North America for the first time (Toliver Run, Garrett County, MD) (Richard Snider, pers. comm.). The ***Hydroisotoma schaefferi*** was an atypical blind form from Little Bennett Creek,. Montgomery Co., MD. Snider also found this species (not blind) in ponds surrounded with mosses in Michigan, USA (Snider 1967). It is likely that some of these springtails were living at the surface of emergent mosses. But the tiny size of these insects suggests they may have been missed in collections using insect nets. Others may have "sprung" away from surface locations as the collector approached.

Figure 10. ***Odontella*** cf. ***incerta***; ***O. lamellifera*** is a springtail that occasionally occurs among stream bryophytes in the Appalachian Mountains, USA. Photo by Andy Murray, through Creative Commons.

Figure 11. ***Entomobrya griseoolivata***, a springtail that sometimes occurs among Appalachian Mountain stream bryophytes. Photo by Domingo Zungri, through Creative Commons.

Figure 12. ***Orchesella quinquefasciata***, a springtail that sometimes occurs among Appalachian Mountain stream bryophytes. Photo by Malcolm Storey, through DiscoverLife Creative Commons.

Figure 13. ***Hypogastrura nivicola***; ***H. armatus*** is a springtail that sometimes occurs among Appalachian Mountain stream bryophytes in eastern USA. Photo by Scott Justis, with permission.

Figure 14. ***Hydroisotoma schaefferi***, a springtail that sometimes occurs among Appalachian Mountain stream bryophytes. Photo by Tom Murray, through Creative Commons.

Figure 15. ***Isotoma viridis***, a springtail that sometimes occurs among Appalachian Mountain stream bryophytes. Photo by Kyron Basu, through Creative Commons.

Figure 16. ***Isotomurus palustris***, an aquatic springtail that keeps its offspring together for two days after birth. Photo by Scott Justis, with permission.

Figure 17. ***Pseudachorutes*** sp.; ***Pseudachorutes lunatus*** lives among mosses in mountain streams. Photo by Jan van Duinen, with permission.

Figure 18. ***Sminthurides aquaticus***, a springtail that sometimes occurs among Appalachian Mountain stream bryophytes. Photo by Andy Murray, through Creative Commons.

Figure 19. ***Tomocerus flavescens***, a springtail that sometimes occurs among Appalachian Mountain stream bryophytes. Photo by Royce Bitzer, through Creative Commons.

Isotomidae

The family **Isotomidae** was most frequently (almost exclusively among springtails) represented in the publications I found regarding bryophyte fauna. Among these, ***Isotomurus palustris*** (Figure 16) is most typically considered to be aquatic, although a few other species, including ***Sminthurus aquaticus*** (Figure 18), have names that suggest they are aquatic.

Isotomurus palustris (Figure 16) is able to float on the water because of their non-wetting waxy epicuticle composed of a lipid monolayer that is extremely impermeable to water (Beament 1960). But Noble-Nesbitt (1963) provided evidence that the presence of wax gives it **hydrofuge** (shedding water) properties. A cementing substance contributes to this hydrofuge ability. The cuticle, combined with surface hairs, provides this springtail with a protective air layer that both makes these springtails **unwettable** (repelling water) and makes them float. Springtails also are very sensitive to desiccation, so the protection by the cuticle is important.

The **collophore** is **wettable** (doesn't repel water) and doubles as both a respiratory and water-taking organ (Noble-Nesbitt 1963). The air layer on the surface also behaves as a **plastron** (breast plate breathing apparatus). These springtails also take water by mouth and this may additionally supply dissolved oxygen. I wonder if they ever get hiccups! This tubule, combined with their small size, would permit them to drink water from the leaves of emergent mosses.

But it appears that the cuticle may also play an important role in their locomotion on the water surface (Noble-Nesbitt 1963). In the water, the furcula is used as a spring, much as it is on land. On the water surface the insect actually walks, using only its limbs.

Isotomurus palustris (Figure 16) is **viviparous**, producing one egg at a time (Chang 1966). These eggs are carried internally and hatched inside the female with the nymph emerging from the genital pore. The female arches its body to permit the emerging nymph to reach the water surface. In observations on newborns of ***Isotomurus palustris*** (Figure 16) and *Folsomia fimetaria* (Figure 20), Chang found that the newborns stayed close to the mothers for the first two days. The young are able to float, walking on the surface tension with their **non-wetting** (repelling water) claws, but if they are forced to submerge they will sink. The cuticle does not develop until they spend time above water.

Figure 20. *Folsomia fimetaria*, a springtail whose newborns stay close to the mother for two days. Photo by Andy Murray, through Creative Commons.

Antennae are important in assessing the environment in both ***Isotomurus palustris*** (Figure 16) and *Folsomia fimetaria* (Figure 20). They are the sensory organ, often in consort with the post-antennal organ, that recognizes light intensity, wind direction, and heat. When one or the other of these organs is removed or cauterized, the springtails move about aimlessly or not at all, whereas those with both organs intact wiggle their antennae and exhibit a directional movement in response to the stimulus.

Some **Collembola** like it cold – ***Anurida frigida*** (**Neanuridae**) occurs under mosses on stones and on stones by melt-water brooks in the high alpine of Swedish Lapland (Fjellberg 1973). The greatest numbers of these were located under mosses that were wet by ice-cold meltwater. In the Nordic countries, ***Agrenia riparia*** prefers wet mosses, especially on lowland stream banks (Fjellberg 2007b)

Bog Springtails

These tiny creatures seem often to be overlooked, but a treatment of **Collembola** in Michigan, USA, indicates that many species can occur in bogs (Snider 1967):

Hypogastrura nivicola (**Onychiuridae**; Figure 21)
Isotoma viridis (**Isotomidae**; Figure 15)
Lepidocyrtus cyaneus (**Entomobryidae**; Figure 32)
Lepidocyrtus lignorum (**Entomobryidae**; Figure 22)
Lepidocyrtus unifasciatus (**Entomobryidae**)
Lepidocyrtus violaceous (**Entomobryidae**; Figure 23) – in ***Sphagnum***
Neelus minutus (Neelidae; see Figure 24)
Orchesella ainsliei (**Entomobryidae**)
Orchesella albosa (**Entomobryidae**)
Pseudobourletiella spinata (**Sminthuridae**; Figure 25)
Sminthurides aquaticus (**Sminthuridae**; Figure 18) – in ***Sphagnum***
Sminthurides lepus (**Sminthuridae**)
Sminthurides malmgreni (**Sminthuridae**; Figure 26) – semi-aquatic habitats
Sminthurides occultus (**Sminthuridae**)
Sminthurides penicillifer (**Sminthuridae**; Figure 27)
Sminthurinus aureus (**Sminthuridae**; Figure 28)
Sminthurinus bimaculatus (**Sminthuridae**; Figure 29)
Tomocerus flavescens (**Tomoceridae**; Figure 19) – in ***Sphagnum***

Figure 21. ***Hypogastrura nivicola*** on snow. Photo by Charley Eiseman, through Creative Commons.

Figure 22. ***Lepidocyrtus lignorum***, a bog inhabitant. Photo by Jan van Duinen, with permission.

Figure 23. ***Lepidocyrtus violaceus***, a bog ***Sphagnum*** dweller. Photo by Jan van Duinen, with permission.

Figure 24. ***Neelus murinus*** carrying eggs; ***Neelus minutus*** is a bog dweller. Photo by Frans Janssens, with permission.

Figure 25. ***Pseudobourletiella spinata***, a bog inhabitant. Photo by Tom Murray, through Creative Commons.

Figure 26. ***Sminthurides malmgreni***, a bog inhabitant. Photo by Andy Murray, through Creative Commons.

Figure 27. ***Sminthurides*** nr. ***penicillifer*** female, a bog inhabitant. Photo by Andy Murray, through Creative Commons.

Figure 28. ***Sminthurinus aureus***, a bog dweller. Photo by Andy Murray, through Creative Commons.

Figure 29. ***Sminthurinus bimaculatus***, a bog dweller. Photo by Andy Murray, through Creative Commons.

In his treatment of the **Collembola** of Fennoscandia and Denmark, Fjellberg (2007a) included ***Maristoma canaliculata*** as a species usually found in ***Sphagnum*** and ***Maristoma tenuicornis*** in ***Sphagnum*** bogs. The treatment for Nordic Collembola (Fjellberg 2007b) includes ***Marisotoma canaliculata*** in ***Sphagnum*** ponds; ***Marisotoma tenuicornis*** in boreal ***Sphagnum*** bogs; ***Desoria olivacea*** (**Isotomidae**; Figure 30) common in acidic forest bogs; ***Desoria blufusata*** (Figure 31) in bogs and wet meadows; ***Lepidocyrtus cyaneus*** (**Entomobryidae**; Figure 32) common in humid habitats including ***Sphagnum***/*Salix* bogs; ***Sminthurides schoetti*** common in bogs and damp meadows; ***Sminthurides pseudassimilis*** in boreal ***Sphagnum*** bogs and smaller lakes, boreal; ***Sminthurides parvulus*** uncommon in bogs, wet meadows, and shores of lakes; ***Neelides minutus*** uncommon in bogs; ***Arrhopalites cochlearifer*** and ***Arrhopalites principalis*** (common) in bogs; ***Isotomurus unifasciatus*** (Figure 33) in forest bogs; ***Isotomurus balteatus*** in boreal bogs and wetlands; ***Dicyrtomina minuta*** and ***Dicyrtoma fusca*** (Figure 34) common in bogs; ***Heterosminthurus insignis*** in wet meadows and bogs.

Figure 30. ***Desoria olivacea***, a species of acidic forest bogs. Photo by Jan van Duinen, with permission.

Figure 31. ***Desoria blufusata***, a common species in bogs and wet meadows. Photo by Arne Fjellberg, through Creative Commons.

Figure 32. ***Lepidocyrtus cyaneus***, a species of ***Sphagnum*** bogs. Photo by Steve Hopkin, with permission.

Figure 33. ***Isotomurus unifaciatus***, a species of boreal bogs and wetlands. Photo by Jan van Duinen, with permission.

Figure 34. ***Dicyrtoma fusca***, a species common in bogs. Photo by Jan van Duinen, with permission.

Greenslade *et al*. (2006) suggests that ***Mesaphorura macrochaeta*** may have been introduced to the Southern Hemisphere by human importations of soil and moss peat.

HEMIMETABOLA

The **hemimetabolous** insects are those with **incomplete metamorphosis**. Instead of a larva, they have a **nymph** or **naiad** stage that resembles the adult except for having reduced wings or only wing pads. They lack a pupa stage and pass directly from the nymph or naiad stage to the adult stage. Most of the aquatic Hemimetabola have a stage with gills and wing pads and are distinguished as **naiads**.

EPHEMEROPTERA – Mayflies

As in most of the names of insect orders, *optera* refers to wings. In the **Ephemeroptera**, *ephemera* refers to short-lived. Hence, these are insects that are short-lived in the winged, or adult, stage.

The immature mayflies, known as **naiads**, are all aquatic (Thorp & Covich 1991). They can be distinguished by their three (two in some) long caudal filaments that are also present in the adults. They are most similar to the stoneflies (**Plecoptera –** see subchapter on Plecoptera in this chapter), but differ in having abdominal gills (lacking in middle abdominal segments of stoneflies) and typically three tails (caudal filaments), which always number two in stoneflies. Most of the naiads are herbivores and some eat bryophytes.

The mayfly naiads are largely night-active and appear most often in the night-time drift (Elliott 1967). Adult mayflies emerge from the naiad first as a **sub-imago** (also known as a **dun**; Figure 35-Figure 40), a stage that often becomes a nuisance to motorists (Figure 36) in the area because of the large numbers that meet their demise (Figure 37) on the windshields. To complete emergence they must climb so they can pump fluids into their new wings (Figure 41). The adult does not eat – in fact lacking mouthparts – and typically lives for only a few days.

Figure 35. ***Baetis*** male subimago emerging to adult. Photo by Jason Neuswanger at <Troutnut.com>, with permission.

Figure 36. Adult mayflies on emergence day. Photo by Jeff Reutter, through Ohio Sea Grant public domain.

In my own studies in the Appalachian Mountain streams, USA (Glime 1968, 1994), the **Ephemerellidae** was by far the most abundant of the mayflies. Frost (1942) reported the importance of the mayflies ***Ephemerella*** (*s.l.*) (Figure 45) and ***Baetis*** (**Baetidae**; Figure 35-Figure 40) among aquatic mosses, where they feed mostly on algae, but occasionally on bryophytes (Hynes 1961; Chapman & Demory 1963). Frost (1942) found about 530 mayfly nymphs per 200 g of mosses in Ireland. In a cool mountain stream of central Japan, Tada and Satake (1994) found that ***Baetis thermicus*** (Figure 38) and ***Ephemerella*** (*s.l.*) sp.

were more abundant among the moss ***Platyhypnidium riparioides*** (Figure 39) than in bare rock areas.

Figure 37. Mayflies that met their end on a travelling car during an emergence in August in Michigan, USA. Photo by Eileen Dumire, with permission.

Figure 38. ***Baetis thermicus*** naiad, a common moss dweller of the moss ***Platyhypnidium riparioides*** in Japan. Photo from Shiiba Research Forest. Permission requested.

Figure 39. ***Platyhypnidium riparioides*** partially submersed at the edge of a waterfall. Photo by Michael Lüth, with permission.

Figure 40. ***Baetis*** sub-imago showing huge eyes. Photo by Jason Neuswanger at <Troutnut.com>, with permission.

Figure 41. Emerging **Ephemeroptera**. Mayflies live their immature lives as naiads in the water of streams and lakes. When they emerge as adults, they must climb, like these naiads, so they can pump up their wings once they have exited the naiad exuvia. Photo by Jason Neuswanger at <Troutnut.com>, with permission.

With such a dwarfed lifespan, finding a mate quickly is paramount. This is accomplished by flying in giant swarms, facilitated by coordinated emergence time. At this time, they are a nuisance for motorists and a feast for birds (Figure 42). Those females that survive deposit their eggs, often among mosses.

Figure 42. Hermit thrush (*Catharus guttatus*) with mayfly subimago in its beak, enjoying the brief period of emergence. Photo by Bob Armstrong, with permission.

Increased biomass of bryophytes may increase some insects while having no effect on others. Lee and Hershey (2000) found that a dense growth of the moss ***Hygrohypnum*** (Figure 43-Figure 44) following stream fertilization in Alaska increased the density of the mayfly ***Ephemerella aurivillii*** (Figure 45) but not ***Baetis*** (Figure 46). In the fertilized zone, these mayflies both grew larger, a fact Lee and Hershey attributed to the greater growths of epiphytic diatoms. Furthermore, although the density of ***Ephemerella*** increased with increased moss density, the highest drift ratios were in the unfertilized zone with lower moss density. In enclosure experiments, they found that bare rock, mosses, and artificial mosses had no effect on any taxa except ***Ephemerella***. They considered that the ***Ephemerella*** benefitted from the increased complexity of the moss habitat.

Figure 43. ***Hygrohypnum ochraceum***, home for a variety of stream insects. Photo by Michael Lüth, with permission.

Figure 44. Close view of ***Hygrohypnum ochraceum***, home for a variety of insects. Photo by Michael Lüth, with permission.

Figure 45. ***Ephemerella aurivillii*** naiad, a mayfly that increased with increased coverage of ***Hygrohypnum*** in Alaska. Photo by Tom Murray, through Creative Commons.

Figure 46. ***Baetis*** naiad, a bryophyte inhabitant in many streams. Photo by Bob Henricks, with permission.

Jones (1950) did extensive gut analysis of insects from the River Rheidol. Among the **Ephemeroptera**, none of the five species examined had fragments of the common moss ***Fontinalis antipyretica*** (Figure 47) in the gut. Detritus was the most common food. Gilpin and Brusven (1970) found six mayfly species with ***Fontinalis*** sp. in their guts, but these all amounted to less than 1% of the gut contents.

Figure 47. ***Fontinalis antipyretica***, a moss found in the guts of some mayflies in the River Rheidol. Photo by Kristian Peters, with permission.

It is surprising to find such flattened, rock-adapted genera as ***Heptagenia*** (Figure 48) among mosses, but Muttkowski and Smith (1929) did find it several times among mosses in trout streams of Yellowstone National Park, USA.

Figure 48. ***Heptagenia dalecarlica*** naiad, a flattened species adapted for smooth rocks, but that occasionally visits mosses. Photo by Urmas Kruus, with permission.

Suborder Furcatergalia

Leptophlebiidae – Prong-gilled Mayflies

This is a family that lives in freshwater streams and lakes where the naiads eat detritus and algae (Leptophlebiidae 2013). Their length is up to 20 mm; they are **nocturnal** (active at night) and are poor swimmers, generally clinging to rocks. Only a few seem to live among bryophytes.

Paraleptophlebia (Figure 49) was a minor component of the bryophyte communities in my own Appalachian, USA, stream studies (Glime 1968). Maurer & Brusven (1983) found ***Paraleptophlebia heteronea*** (Figure 49) frequently in the clumps of ***Fontinalis neomexicana*** (Figure 79) in an Idaho stream. In their study of four Appalachian streams, Woodall and Wallace (1972) found this genus where there was moderate or slow current among decaying leaves, bark, and wood. Its food is predominately detritus (Chapman & Demory 1963).

Figure 49. ***Paraleptophlebia*** sp. naiad, a frequent dweller among ***Fontinalis neomexicana***. Photo by Jason Neuswanger, with permission.

Macan (1957) found ***Leptophlebia*** (Figure 50) among mosses in Ford Wood Beck, UK. Berner (1959) described this genus as one that would live in submerged mossy banks and other quiet areas. The genus is negatively **phototactic** (movement of organism toward or away from source of light), explaining their presence in the secluded shade of streambank mosses. When it is time for the naiads to emerge into adults, they become positively phototactic and crawl upward onto sticks, logs, or other protruding structure, probably including emergent bryophytes.

Vuori *et al*. (1999) considered ***Leptophlebia marginata*** (Figure 50) to be among the dominant moss dwellers in the Tolvajärvi region of the Russian Karelia. Bengtsson (1981) found that ***L. marginata*** demonstrated a steady growth rate throughout winter, permitting it to thrive in such northern regions.

Figure 50. ***Leptophlebia marginata*** naiad on waterweed. Photo by Niels Sloth, with permission.

One advantage enjoyed by some members of this family is tolerance of somewhat low *p*H. Mayflies in general are indicators of fresh, unpolluted water. They do not generally tolerate extremes, low *p*H included (Raddum & Fjellheim 1988; Raddum *et al*. 1988; Braukmann 1992; Lingdell & Engblom 1995). Thus the streams that drain ***Sphagnum*** fens and bogs (Figure 51) are generally **depauperate** (lacking in numbers or kinds of species) of mayflies. However, this habitat is suitable for a few, including ***Leptophlebia vespertina*** (Figure 52) (Bauernfeind & Moog 2000). This intolerance of low *p*H may explain its relative rarity among bryophytes in the mid-Appalachian Mountain streams (Glime 1968).

Figure 51. ***Sphagnum affine***, member of a genus that contributes H^+ ions, lowering the *p*H of bogs and their outflow waters. Photo by Michael Lüth, with permission.

Figure 52. ***Leptophlebia vespertina*** adult, a species whose naiads can inhabit the acid outflows of acid bog lakes. Photo by Niels Sloth, with permission.

In New Zealand ***Austroclima sepia*** (see Figure 53) frequently lives among mosses in small waterfalls (Winterbourn & Gregson 1981). Similarly, Towns (1987) reported this species along with ***A. jollyae*** and ***Mauiulus luma*** (Figure 54) as 72%, 13%, and 9%, respectively, of the fauna from mosses in rapid flow (where only 4 insect species lived!) on the Great Barrier Island, New Zealand.

Figure 53. ***Austroclima*** naiad, a genus with moss dwellers in New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 54. ***Mauiulus luma*** naiad, a mayfly that lives among mosses in small waterfalls in New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.

In his study of the River Rajcianka, Krno (1990) found a genus I have not encountered elsewhere – ***Habroleptoides***. ***Habroleptoides modesta*** (Figure 55) is a bryophyte dweller in the river, but like many of the mayfly genera, it is unable to live among the wet mosses above the water level.

Figure 55. ***Habroleptoides modesta*** naiad, a mayfly that sometimes lives among bryophytes in rivers. Photo by Alfeo Busilacchio, with permission.

Caenidae - Small Squaregill Mayflies

The **Caenidae** are small sprawlers in quiet and sometimes stagnant water as well as streams (Caenidae 2014). They are adapted to the relatively low oxygen of silt.

Caenis (Figure 56) seems to prefer loose mosses (Percival & Whitehead 1929). Frost (1942) found that it was most likely to occur among mosses that had accumulated considerable silt. In the River Rajcianka in Slovakia, ***Caenis beskidensis*** (Figure 56) lives among submerged bryophytes but is not found, like some mayflies, among the wet emergent bryophytes (Krno 1990). In the Appalachian Mountain, USA, streams naiads of ***Caenis*** were among the lesser of the moss inhabitants, appearing mostly among ***Fontinalis dalecarlica*** (Figure 69).

Figure 56. ***Caenis lactea*** naiad, a mayfly that prefers loose mosses. Photo by Niels Sloth, with permission.

Neoephemeridae

The rare genus ***Neoephemera*** (Figure 57) sometimes lives deep within submerged moss mats in rapid water in eastern North America (Berner 1959), including

Neoephemera compressa (Figure 57) among mosses on submersed parts of trees (Berner 1956). The naiad moves slowly, but when it bends its 3 tails over its abdomen, then suddenly lashes them back, this action propels it forward (see Figure 60).

Figure 57. ***Neoephemera compressa***, an inhabitant of mosses on submersed parts of trees. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

In Australia, ***Neoephemera*** (Figure 57) naiads live in protected parts of streams with slow to moderate flow where they hide among debris, plant roots, and mosses (Edmunds *et al*. 1976). These naiads are difficult to dislodge from the mosses, partly because they grip the mosses. The membranous respiratory gills are fragile and they need the protection that is provided by the fused, sclerotized **opercula** (gill covers) (Notestine 1994). This genus relies heavily on these gills for respiration.

Ephemerellidae – Spiny Crawlers

This family occurs throughout North America as well as the United Kingdom (Ephemerellidae 2014). These collector-gatherers occur where there is moving water, including lake shores subject to wave action, but seem to require reduced flow. They are able to live in fast water by accepting the protection of bryophytes.

When these mayfly naiads are threatened by a predator, they raise their three tails like a scorpion, arching them up and over their backs, making them appear larger (Ephemerellidae 2014). They will then project the tails forward to poke the enemy. Spines on the back of the abdomen (Figure 58) may contribute to their protection. One suggestion is that the spines help the mayflies hold their positions when attacked from behind by a predator.

This family takes advantage of the protection of the bryophyte habitat while modulating the oxygen and keeping its tuft of gills clean with its gill covers. When oxygen concentrations become too low, the **Ephemerellidae** move the gill covers (Figure 58) up and down to keep fresh water circulating across the gills (Figure 59) (Ephemerellidae 2014). Their bodies are somewhat flattened dorsiventrally and are adapted to crawling among the chambers of their mossy habitat. When they are in open water and need to move quickly, mayflies in this family flip their tails upward over their backs and down to act like a paddle (Figure 60), thrusting them forward.

Figure 58. ***Ephemerella subvaria*** naiad gill covers, closed over gills. Photo by Tom Murray, through Creative Commons.

Figure 59. ***Drunella*** sp. naiad with gill covers up to expose the tufts of gills. Photo by Bob Henricks, with permission.

Figure 60. ***Ephemerella subvaria*** naiad in a swimming position with its tails flipped upward. Photo by Bob Henricks, with permission.

Berner (1959) described some members of this family as living on the tops of rocks, deep within the moss. Arnold and Macan (1969) found that **Ephemerellidae** (Figure 58-Figure 64) were common among mosses in a

Shropshire Hill stream in the UK. In a study of the McKenzie River, Oregon, USA, Hawkins (1984) reported that 5 species [***Serratella teresa***, ***C. hystrix*** (Figure 61), ***Caudatella cascadia*** (now a synonym of ***C. hystrix***), ***C. edmundsi*** (Figure 62), and ***Drunella spinifera*** (Figure 63)] out of 12 **Ephemerellidae** species were common among mosses, including ***Fontinalis*** sp. (Figure 79) and others. Gilpin and Brusven (1970) likewise found ***C. edmundsi*** among clumps of ***Fontinalis***. Hawkins (1984) found those restricted to mosses were usually at upstream locations where the mosses were abundant. However, two moss dwellers [***Caudatella edmundsi*** (100% moss usage - found only on ***Fontinalis***), ***Drunella spinifera*** (54%)] were most abundant downstream, living among mats of the moss ***Fontinalis*** sp. For other species with more than 5% use of bryophyte habitats he found ***Serratella teresa*** (85%), ***Caudatella cascadia*** (46%), and ***Caudatella hystrix*** (22%).

Brittain and Saltveit (1989) found that river impoundments had "profound" effects on the **Ephemerellidae** (Figure 58-Figure 64) living there. Changes in temperature, discharge, flow patterns, food availability, and predator density all contribute to changes in living conditions for the mayflies. Increased growth of mosses and additional available substrata for periphyton below the dams often favor some of the **Ephemerellidae** while reducing suitable habitat for **Heptageniidae** (Figure 48). The mayflies living under these changeable regimes often have flexible life cycles or shorter periods of rapid growth with a long period of egg development that permit them to survive unsuitable periods.

Figure 61. ***Caudatella hystrix*** naiad, a common moss dweller in the McKenzie River, Oregon, USA. Photo by Bob Newell, with permission.

Figure 62. ***Caudatella edmundsi*** naiad, a common moss dweller. Photo by Bob Newell at <Troutnut.com>, with permission.

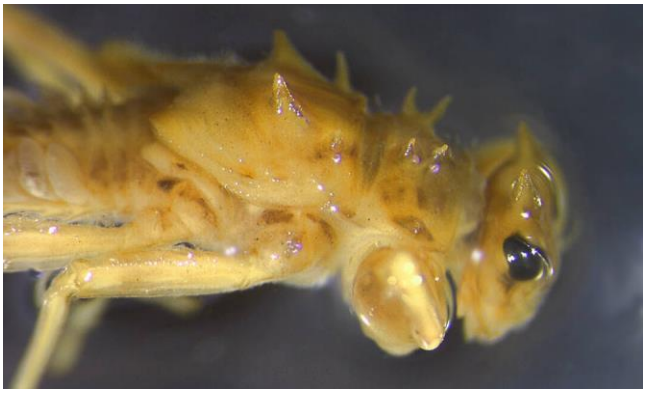

Figure 63. ***Drunella spinifera*** naiad. Photo by Bob Newell at <Troutnut.com>, with permission.

Percival and Whitehead (1929) considered mosses and algae to be the main food of the **Ephemerellidae** (Figure 58-Figure 64). Woodall and Wallace (1972) found ***Eurylophella funeralis*** (=***Ephemerella funeralis***, Figure 64) to be the most abundant ***Ephemerella*** species among mosses in the southern Appalachian Mountains, USA, and I found a similar relationship for ***E. funeralis*** and ***E. temporalis*** in the middle Appalachian Mountain streams (Glime 1968). The members of ***Ephemerella*** tended to avoid the heavily shaded hardwood stream where mosses and algae were scarce.

Figure 64. ***Eurylophella funeralis***, a common mayfly among mosses in the southern Appalachian Mountain, USA, streams. Photo by Donald S. Chandler, with permission.

Brittain and Saltveit (1989) found that growth of mosses and associated periphyton below dams favored presence of **Ephemerellidae** (Figure 58-Figure 64). They reasoned that flexible life cycles permitted them to survive adverse conditions, including rapid nymphal growth and long period of egg development. Eggs typically form a ball (Figure 65).

Percival and Whitehead (1929) found ***Eurylophella funeralis*** (=***Ephemerella funeralis***) (Figure 64) to be the most abundant species of the ***Ephemerella*** genus group in their study of UK streams. The main foods of ***Ephemerella*** species are algae and mosses (Percival & Whitehead 1929; Jones 1949, 1950; Gerson 1969). This is convenient because this genus is common among mosses, but it also occurs on the pebbles on the bottom. Jones (1949, 1950) found that ***Ephemerella*** *s.l.* fed primarily on ***Fontinalis*** (Figure 47) and the alga *Ulothrix* (Figure 66) in **calcareous** (having dissolved chalk or limestone) streams of South

Wales. Among 14 specimens examined on 14 July the moss was the primary food, but they concluded that ***Ephemerella*** feeds on *Ulothrix* when it is abundant but switches to ***Fontinalis antipyretica*** (Figure 47) when the *Ulothrix* becomes scarce.

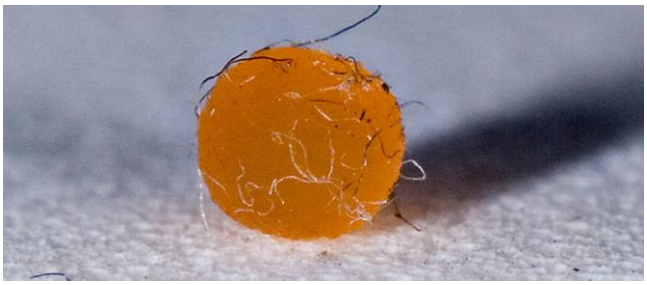

Figure 65. ***Ephemerella*** egg mass with debris stuck to it. Photo by Jason Neuswanger at <Troutnut.com>, with permission.

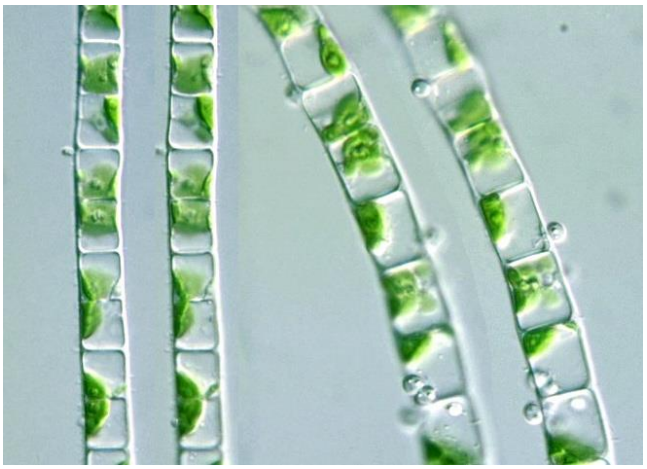

Figure 66. ***Ulothrix***, food for ***Eurylophella funeralis***. Photo by Yuuji Tsukii, with permission.

Reproduction in the mayflies involves swarming, a behavior that maximizes contact of males and females that typically live for only one day as adults. In ***Serratella ignita*** (Figure 67) this swarming occurs in the late afternoon and evening (Elliott & Humpesch 1980). The egg mass is a greenish ball. Once fertilized, eggs are laid in turbulent water, usually where there are mosses. The female flies upstream to deposit the eggs on the water surface. She then usually falls on the surface and is vulnerable to fish predation. The egg mass separates when it enters the water and each egg attaches to the substrate with its polar anchoring cap.

Figure 67. ***Serratella ignita*** naiad. Photo by J. C. Schou, through Creative Commons.

The family **Ephemerellidae** (Figure 58-Figure 64) seems to have bryological preferences, or preferences that match those of the bryophytes. They reach extremely high numbers among ***Hygroamblystegium fluviatile*** (Figure 68) in mid-Appalachian streams, but are nearly absent in ***Fontinalis dalecarlica*** (Figure 69) and ***Scapania undulata*** (Figure 70) in different streams (Glime 1968).

Figure 68. ***Hygroamblystegium fluviatile***, home to large numbers of **Ephemerellidae**. Photo by Michael Lüth, with permission.

Figure 69. ***Fontinalis dalecarlica***, a stream moss that houses some of the larger insects. Photo by Jan-Peter Frahm, with permission.

Figure 70. ***Scapania undulata***, a leafy liverwort that has few of the typical moss-dwelling **Ephemerellidae**. Hermann Schachner, through Creative Commons.

D. N. Bennett (pers. comm. 19 April 2011) described her field experience with an aquatic entomologist, Bob Henricks. Henricks was attempting to distinguish between mosses and grasses, so she began looking at the inhabitants of the mosses. When the moss-covered rocks were removed from the stream, the insects began moving about and became more noticeable. There were often 40-50 **Ephemerellidae** naiads on a single moss-covered rock – determined to be ***Hygroamblystegium***, probably ***H. tenax*** (Figure 71-Figure 72). The moss grew on and "under" the rock, and it was the submersed "under" portion that housed the many mayflies. She observed the naiads rolling up the algae from the moss leaf surface, starting at the leaf tip and moving to the stem.

Figure 71. ***Hygroamblystegium tenax*** in a dry stream bed. Photo by Janice Glime.

Figure 72. ***Hygroamblystegium tenax***, home to many kinds of stream insects, including **Ephemerellidae**. Photo by Jan-Peter Frahm, with permission.

Seasons

Seasonal differences in the life cycle stages spent in the water are often the key to success for these species. Timing differences in emergence times and hatching times can separate realized niches in closely related species. In the **Ephemerellidae** (Figure 58-Figure 64), the life cycle is typically one year with one brood per year (**univoltine**). For example, ***Serratella ignita*** (Figure 1) has an annual cycle with the eggs spanning the winter in a dormant state, hatching in April and May in the River Endrick in Scotland (Maitland 1955). The naiads develop quickly, emerging in July and August, and adults typically lay eggs within 24 hours of emergence. These eggs are often laid among mosses in abundance (Percival & Whitehead 1928). The eggs are laid in evening light and are caught by ***Platyhypnidium riparioides*** (Figure 39) and ***Fontinalis*** species (Figure 47) where they adhere as a greenish gelatinous mass.

In a Shropshire Hill stream in the UK, Arnold and Macan (1969) found that the longest stage in ***Serratella ignita*** (Figure 1) was the egg, a stage that remained from late summer one year to late spring the next year, hence overwintering as an egg (Elliott 1967). Rosillon (1988) found that completion of naiad development on a diatom diet required about 950 **degree-days** above a temperature of 3.5°C (range 9.5-18°C). [Degree days for insect development can be calculated by adding the minimum and maximum temperature of the day and dividing by 2. The minimum required for development is subtracted from that number to determine how many degree-days have been added that day. (Townsend *et al*. 2010)]. Those reared on detritus rarely achieved adult stage. Rosillon suggested that poor food quality would reduce **fecundity** (reproductive rate) of females. Furthermore, it appears that under ideal conditions ***Serratella ignita*** could have a **bivoltine** (2 broods per year) life cycle.

Emergence patterns can be gleaned from the stages of the naiad development of mayflies in samples. Based on such sampling, Gurtz & Wallace (1984) estimated that in a stream in the southern Appalachian Mountains, USA, the moss inhabitants ***Ephemerella catawba*** (Figure 73) probably emerged from May to July, ***E. hispida*** from April to June, ***E. excrucians*** (Figure 81) in May and June, and ***Drunella tuberculata*** (Figure 74) from June to September. Both ***Ephemerella catawba*** and ***Ephemerella invaria*** occurred among mosses in the acidic mid Appalachian streams in my own studies (Glime 1968). ***Ephemerella invaria*** (Figure 75) increased in Big Hurricane Branch following a clearcut, but no specimens with fully developed wing pads were ever collected, suggesting that nymphs of this species might complete their development farther downstream in Shope Creek (Gurtz & Wallace 1984).

Figure 73. ***Ephemerella catawba***, a moss inhabitant as a naiad that emerges May to July in the southern Appalachian Mountains, USA. Photo by Biodiversity Institute of Ontario, through Creative Commons.

Figure 74. ***Drunella tuberculata***, a summer emerger. Photo by Bob Henricks, with permission.

Figure 75. ***Ephemerella invaria*** naiad. Photo by Bob Henricks, with permission.

Ephemerella invaria (Figure 75) occurred both above and below a hydroelectric plant on the Sturgeon River in northern Michigan, USA, with similar abundance and growth (Mundahl & Kraft 1988). ***Ephemerella subvaria*** (Figure 76) naiads were 4x as abundant below the plant (136 m^{-2} below vs. 33 m^{-2} above), but grew more slowly there. Nevertheless, the growth rate increased with distance downstream from the power plant for nearly 10 km. Extensive beds of ***Fontinalis*** (pers. obs.) may have contributed to the improved growth rates, with the mosses serving as traps for **seston** (swimming or floating living organisms and non-living matter) being released from the reservoir. Both of these species occur among bryophytes in streams of the mid Appalachian Mountains, USA (Glime 1968).

Figure 76. ***Ephemerella subvaria*** naiad. Photo by Donald S. Chandler, through Creative Commons.

Food

The **Ephemerellidae** (Figure 58-Figure 64) are the most commonly reported mayflies among the bryophyte consumers (Table 1). ***Caudatella hystrix*** (as ***C. cascadia***; Figure 61) varies its diet depending on the site (Coffman *et al*. 1971; Hawkins 1985). Detritus is important in its diet, but the proportion decreases when that of moss increases (Hawkins 1985). The naiads of ***Caudatella edmundsi*** (Figure 62, Figure 101) feed primarily on diatoms, but also include detritus and mosses in their diet. Hawkins found that as size increased in the **Ephemerellidae**, especially in ***Caudatella edmundsi*** and ***Ephemerella dorothea infrequens*** (Figure 80), the consumption of both animal matter and mosses increased. Hawkins found that eight species demonstrated a correlation between moss consumption and size. López-Rodríguez *et al*. (2008) likewise found that the proportion of mosses in the diet increases in **Ephemerellidae** as naiads age. Several researchers (Hynes 1941; Chapman & Demory 1963; Gaevskaya 1969) found that mosses are eaten by members of this family more often than other aquatic macrophytes (not including algae). But it is not clear if the moss is eaten for its own food value or for the attached periphyton. Percival and Whitehead (1929) found that two species in this family ingested large amounts of moss, suggesting that the moss itself was an important food source. Among the members of **Ephemerellidae** studied by Hawkins (1985), ***Caudatella edmundsi***, ***C. heterocaudata***, ***C. hystrix***, and ***Serratella teresa*** were moss shredders. Others living among the mosses and ingesting them were detritus shredders, including ***Attenella margarita*** (Figure 77), ***Ephemerella dorothea infrequens***, ***E. excrucians*** (Figure 81), ***E. velmae***, ***Serratella tibialis*** (Figure 84), and ***Timpanoga hecuba*** (Figure 78). ***Drunella pelosa*** is a diatom scraper, permitting it to eat the many diatoms adhering to the moss leaves.

Table 1. Correlations between size (mm) and percent composition of major food items in the gut. Values are correlation coefficients (*r*). * = *P*<0.05; ** = *P* < 0.01. Percentages arcsine-transformed prior to analysis. From Hawkins 1985.

Species	n	diatoms	detritus	animal	moss	wood	fungus
Caudatella cascadia (=*C hystrix*)	18	0.191	0.149	–	-0.369	0.027	-0.518*
Caudatella hystrix	23	-0.550**	0.166	0.203	0.398	-0.213	-0.117
Caudatella edmundsi	17	-0.115	-0.609**	0.313	0.573*	–	–
Serratella teresa	21	0.660**	-0.550**	-0.183	0.001	–	-0.412
Serratella tibialis	13	-0.095	-0.199	0.160	0.424	–	–
Ephemerella dorothea infrequens	60	-0.129	-0.177	0.109	0.295*	0	0.080
Drunella spinifera	33	0.037	0.050	-0.016	-0.057	-0.035	-0.128
Drunella doddsi	36	-0.067	-0.324	0.211	-0.255	–	-0.165
Drunella coloradensis	65	-0.313**	-0.138	0.433**	0.144	-0.168	-0.142
Drunella pelosa	29	-0.463*	0.256	0.179	0.330	–	–
Drunella grandis	5	-0.863	-0.371	0.394	0.245	–	0.158
All species	359	-0.115*	-0.099	0.257**	0.008	-0.034	-0.067

Figure 77. ***Attenella margarita*** naiad, a moss shredder. Photo by Donald S. Chandler, with permission.

Figure 78. ***Timpanoga hecuba*** naiad, a detritus shredder. Photo by Bob Newell, with permission.

Ephemerella

Ephemerella and its segregates are usually the most common mayflies among mosses. Needham & Christenson (1927) reported ***Ephemerella*** s.l. from moss-covered boulders in streams of northern Utah, USA. In their study of colonization of ***Fontinalis neomexicana*** (Figure 79) in Idaho, USA, Maurer and Brusven (1983) found ***E. dorothea infrequens*** (Figure 80) to be common among these mosses. In the St. Maries River of Idaho, USA, Gilpin and Brusven (1970) occasionally found ***E. excrucians*** (Figure 81) and ***E. dorothea infrequens*** clinging to ***Fontinalis*** and other vegetation, but mostly they were on submerged logs and rocks. Nevertheless, mosses comprised 8% of the diet of this variety (Hawkins 1985).

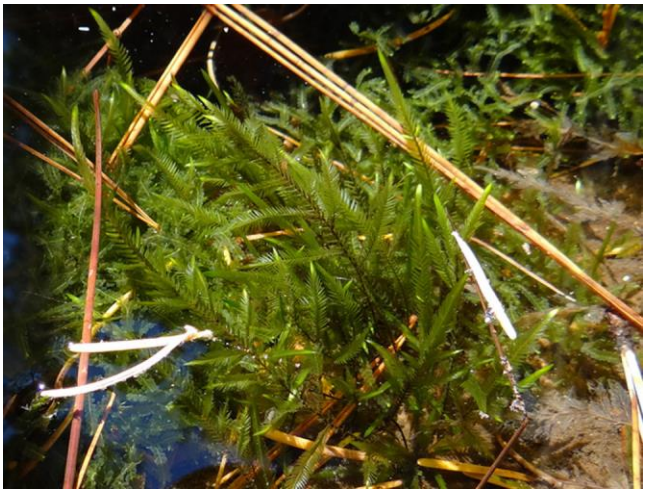

Figure 79. ***Fontinalis neomexicana***, home to several species of ***Ephemerella*** naiads. Photo by Belinda Lo, through Creative Commons.

Figure 80. ***Ephemerella dorothea infrequens*** naiad. Photo by Bob Henricks, with permission.

Figure 81. ***Ephemerella excrucians***, a common inhabitant of ***Fontinalis neomexicana*** in streams of Idaho, USA. Photo by Jason Neuswanger, with permission.

In Straffan, UK, ***Ephemerella notata***, a species once considered close to ***Serratella ignita***, lived among mosses (Frost 1942; Kimmins & Frost 1943), including ***Fontinalis*** (Figure 47) (Kimmins & Frost 1943). Although ***Ephemerella*** sometimes eats a considerable diet of bryophytes, Jones (1950) did not find moss tissue in the guts of any of the five species of mayflies, including ***Ephemerella notata***, in the River Rheidol, UK.

Bob Henricks reported 40-50 spiny crawlers (***Ephemerella***) on a mossy rock in a stream. He noted that in this stream the mosses held tiny sand grains and minute rocks instead of fine silt. In the mountain streams the mosses held fine silt and organic matter with many fewer of these mayflies. They avoid the mosses that grow on the tops of rocks and that float on the surface where the moss reaches the air. Rather, they tend to be on the under-surface of the mosses that wrap around the rocks in the water (Figure 82).

Figure 82. ***Ephemerella*** on rock with mosses. The mayflies blend with the algal-detrital mat on the mosses. Photo by D. N. Bennett, with permission.

Bengtsson (1981) found that ***Ephemerella mucronata*** (Figure 83) demonstrated a steady growth rate throughout winter in Sweden. This species has an interesting niche in the River Rajcianka, Slovakia, where it occurs among the wet emergent bryophytes but not among the submerged ones (Krno 1990).

Figure 83. ***Ephemerella mucronata***, a mayfly that continues to grow throughout winter in Sweden. Photo by Biodiversity Institute of Ontario, through Creative Commons.

Serratella

Serratella tibialis (Figure 84) is a collector-gatherer, feeding on detritus (Aquatic Insects 2008). Both early instars and mature naiads are common among mosses, including ***Platyhypnidium riparioides*** (Figure 39) and ***Fontinalis antipyretica*** (Figure 47) (Langford & Bray 1969). ***Serratella teresa*** occurs on mosses and other vegetation in swiftly-flowing streams (Allen & Edmunds 1963). In the McKenzie River, Oregon, USA, Hawkins (1984) found that 85% of the individuals of this species sampled were in clumps of ***Fontinalis*** sp. (Figure 79). Furthermore, 17% of the food for ***S. teresa*** in Oregon was mosses (Hawkins 1985).

Figure 84. ***Serratella tibialis***, a naiad common among mosses in both its young and older stages. Photo by Bob Henricks, with permission.

In Straffan, UK, Frost (1942) found that ***Serratella ignita*** (Figure 67) lived among mosses. Percival and Whitehead (1929) found that mosses form the primary habitat for ***S. ignita***, and that the moss also is its dominant food, an observation consistent with that of López-Rodríguez *et al*. (2008). Langford and Bray (1969) found this species among ***Fontinalis antipyretica*** (Figure 47) and ***Platyhypnidium riparioides*** (Figure 39) as well as on bare sand and tracheophytes in Britain.

Macan (1957) found that among the streams he studied in Ford Wood Beck, UK, the abundance of ***Serratella ignita*** (Figure 1, Figure 67) increased as the flow became more sluggish and the vegetation became thicker. In all

streams, this species was more common when either tracheophytes or mosses were present. In faster streams, this relationship with mosses might explain the presence of this species. Furthermore, this species is able to move about in the wet moss mats above the water level (Krno 1990). ***Serratella ignita*** is among the species that not only live among mosses, but it also eats them (Percival & Whitehead 1929).

Serratella ignita (Figure 1, Figure 67) usually lays its eggs where moss is present in fast-flowing water (Elliott 1978). The development time for the eggs depends on the temperature, with hatching time decreasing with increasing water temperature in the range of 5.9-14.2°C. However, at higher temperatures the hatching time increases with temperature. Correlations of naiad numbers with moss coverage may be a correlation with temperature.

Serratella ignita (Figure 67) prefers a flow of 10-30 cm sec^{-1} (Macan 1962). Willoughby and Mappin (1988) were unable to find it in upland streams of the River Duddon where the *p*H was low (4.8-5.2), but it did occur in lowland streams with *p*H values of 6.6 and higher. But it appears that the *p*H was not the direct cause of its absence. In the lab, it was very tolerant of low *p*H and low ion content, and growth rates were equally good whether food supplied was that available in low *p*H streams (liverwort ***Nardia compressa*** (Figure 85) plus the filamentous alga ***Klebsormidium subtile*** (**Charophyta**; see Figure 86) or that available in high *p*H streams [moss ***Platyhypnidium riparioides*** (Figure 39) with the epiphytic diatom ***Cocconeis placentula*** (**Bacillariophyta**; Figure 87). Nevertheless the absence of ***K. subtile*** as a food at the higher *p*H seems to account for the absence of ***S. ignita*** there. Percival and Whitehead (1929) found mosses in the guts of ***Serratella ignita*** in Great Britain. But are the mosses really a preferred food? In preference experiments, Rosillon (1988) found that ***S. ignita*** preferred diatoms over detritus. In these experiments, the growth rate was significantly higher on the diatom diet than that on the detritus diet, no matter what the temperature. In fact, larvae reared on the detritus diet had slower development and usually failed to reach the adult stage. If diatoms are the preferred food, eating the moss may simply be the most efficient means of obtaining them.

Figure 85. ***Nardia compressa***, a leafy liverwort in low *p*H streams where ***Serratella ignita*** feeds. Photo by David T. Holyoak, with permission.

Figure 86. ***Klebsormidium flaccidum***, a congener of ***K. subtile*** that is an important food for ***Serratella ignita*** in the bryophyte habitat. Photo by Sarah Kiemle, with permission.

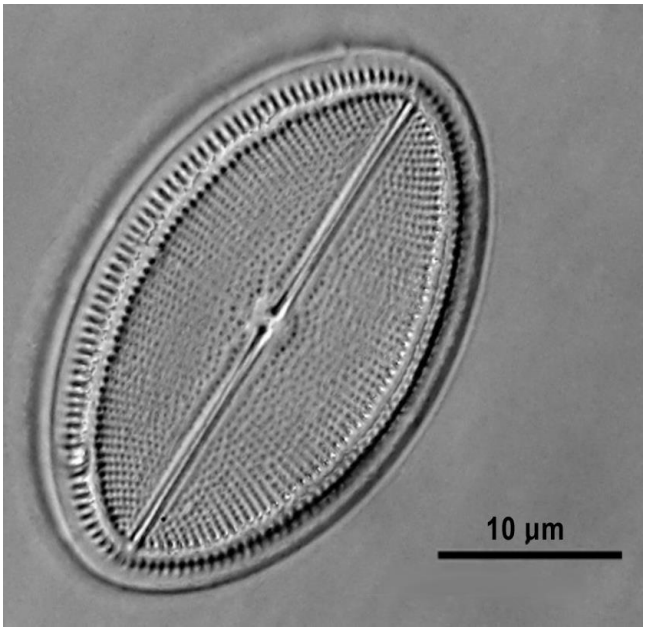

Figure 87. ***Cocconeis placentula***, a common epiphyte on aquatic bryophytes and important food for ***Serratella ignita***. Photo by Ralf Wagner, with permission.

Rosillon (1988) demonstrated that temperature was an important factor in determining mortality for ***Serratella ignita*** (Figure 67). Furthermore, as the temperature increased, mortality was higher on the detritus diet than on the diatom diet. The bryophytes are more likely to be abundant in the cooler habitats, often being overtaken by algal and microbial growth where it is warmer.

Serratella serratoides (Figure 88) occurs primarily among ***Hygroamblystegium fluviatile*** (Figure 68) – ***Platyhypnidium riparioides*** (Figure 39) mats in Appalachian Mountain, USA, streams (Glime 1968). In the southeastern USA it burrows into the moss mats a few cm below the surface (Berner & Allen 1961).

Figure 88. ***Serratella serratoides*** naiad. Photo by Bob Henricks, with permission.

Even for this common moss-dwelling genus, other substrata are often acceptable as well. ***Serratella spinosa nevadensis*** (as *Ephemerella ikonomovi nevadensis*) only occurred in soft water in Spain, living at margins or midstream where roots, moss, algae, or other form of vegetation, along with detritus, was present (Alba-Tercedor 1990; López-Rodríguez *et al*. 2008). Unlike most of the **Ephemerellidae** that increase moss consumption with size, the naiads of ***S. spinosa nevadensis*** increase the percentage of detritus in the diet as they grow larger.

Some **Ephemerellidae** take advantage of ecosystem engineering by other insects. They are poor swimmers that need to cling to vegetation or other objects for support in the current (DEP 2014). ***Serratella setigera*** prefers slow flow (Nakano *et al*. 2005). In field experiments on artificial substrata, this species took advantage of the flow reduction in retreats of the net-spinning caddisfly ***Hydropsyche orientalis*** (Figure 89). In the experiments, those living on experimental plates with no caddisflies were mostly lost during high flow events, whereas none of the naiads in the caddisfly retreats were lost. It is likely that bryophytes provide similar retreats on rocks for some members of this genus. The researchers suggested that in the complex habitat created by mosses, the advantages provided by the ***Hydropsyche*** retreats would weaken. ***Hydropsyche orientalis*** occurs in moss mats of ***Platyhypnidium riparioides*** (Figure 39) in Japan (Takemon & Tanida 1992), but I could find no documentation that ***Serratella setigera*** likewise occurs there.

Figure 89. ***Hydropsyche orientalis*** larva, provider of retreats for ***Serratella setigera***. Photo by Takao Nozaki, with permission.

Teloganopsis

Teloganopsis (=*Serratella*) ***deficiens*** (Figure 90-Figure 91) is known from bryophytes in eastern North America (Allen & Edmunds 1963; Glime 1968). In the southeastern states it lives primarily among mosses and other plants in rocky, swift streams, but in Michigan it also occurs among detritus (Allen & Edmunds 1963). Among the mosses they are protected from the current and find a sufficient food supply.

Figure 90. ***Telogonopsis deficiens*** naiad, a ***Fontinalis*** inhabitant. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

Figure 91. ***Teloganopsis deficiens*** naiad, a ***Fontinalis*** inhabitant. Photo by Bob Henricks, with permission.

Cincticostella

In Japan, the narrowly distributed ***Cincticostella nigra*** (Figure 92) occurs in mats of ***Platyhypnidium riparioides*** (Figure 39) (Takemon & Tanida 1992). This species is restricted to Honshu, Japan (Allen 1971).

Figure 92. ***Cincticostella nigra*** naiad. Photo from Shiiba Research Forest. Permission pending.

Drunella

Allen and Edmunds (1962) did not report any bryophyte dwellers among the North American species of ***Drunella*** they examined. But Muttkowski and Smith (1929) did find ***Drunella*** twice among the mosses of strong rapids in Yellowstone National Park, USA. Hawkins (1984) found only 2% of two ***Drunella*** (Figure 93) species [***D. pelosa***, ***D. coloradensis*** (Figure 93)] among mosses in western Oregon, USA. But ***D. spinifera*** (Figure 94) was collected primarily (54%) in mats of ***Fontinalis*** (Figure 79). ***Drunella allegheniensis*** (see Figure 95) occurs among bryophytes in the Appalachian Mountain, USA, streams (Glime 1968). Gilpin and Brusven (1970) found ***D. grandis*** (Figure 96) among ***Fontinalis*** clumps in Idaho, USA, as well as in other habitats with protective cover. ***Drunella spinifera*** was common on ***Fontinalis***. And Barton (1980) found the latter species to be abundant on moss-covered stones in riffles and rapids of a stream in northeastern Alberta, Canada.

Figure 93. ***Drunella coloradensis*** naiad, a genus sometimes found among bryophytes. Photo by Bob Henricks, with permission.

Figure 94. ***Drunella spinifer*** naiad, a ***Fontinalis*** dweller. Photo by Joseph Fortier, through Creative Commons.

Figure 95. ***Drunella tuberculata***, a species very similar to ***Drunella allegheniensis***. Photo by Bob Henricks, with permission.

Figure 96. ***Drunella grandis*** naiad, a ***Fontinalis*** dweller. Photo by Bob Newell, with permission.

Drunella grandis (Figure 97) was a characteristic species among clumps of the leafy liverwort ***Porella*** (Figure 98) in California, USA (Corona 2010). This species seems to be adapted to its bryological habitat by large dorsal projections on the head, thorax, and abdomen. These projections reduce the chance of being swept away by rapid current in the locations of the liverwort, hooking the mayfly on the branches (Hora 1930).

Figure 97. ***Drunella grandis*** naiad, a leafy liverwort dweller in California, USA. Photo by Bob Newell, with permission.

Figure 98. ***Porella pinnata***. This genus provides a home for ***Drunella grandis*** in California, USA. Photo by Des Callaghan, with permission.

Caudatella

Although the records of the members of this genus inhabiting bryophytes are limited, Hawkins (1985) reported that four species of ***Caudatella*** had three of the four highest percentages of bryophytes in the gut among all the **Ephemerellidae** in Oregon, USA. The moss percentage in the diet of these species, which we must presume were associated with mosses, were ***C. histrix*** (Figure 99-Figure 100) (15% + 20% listed as ***C. cascadia***), ***C. edmundsi*** (Figure 101) (19%), and ***C. heterocaudata*** (15%).

Figure 99. ***Caudatella hystrix*** naiad, a mayfly for which mosses comprise 35% of the diet in Oregon, USA, streams and rivers. Photo by Bob Newell, with permission.

Figure 100. ***Caudatella hystrix*** adult. Naiads live in fast riffles in Idaho, USA, clinging to ***Fontinalis***. Photo by Bob Newell, with permission.

Figure 101. ***Caudatella edmundsi***, a naiad that sometimes occurs exclusively on ***Fontinalis***. Photo by Bob Newell, with permission.

In the St. Maries River of Idaho, USA, ***Caudatella hystrix*** (Figure 99-Figure 100) typically occurred in fast riffles where it would cling to ***Fontinalis*** (Figure 79) or the alga *Prasiola* (Maurer & Brusven 1983). These substrata did an effective job of concealing the naiads. ***Caudatella edmundsi*** (Figure 62, Figure 101) occurs in streams with lower mean summer temperatures at higher elevations and coincides with higher moss coverage (Jacobus *et al*. 2006; Hogue & Hawkins 2008). Hawkins (1984) found ***Caudatella edmundsi*** exclusively among ***Fontinalis*** in western Oregon, USA.

Attenella

I am only aware of two species in this genus that live among the bryophytes. ***Attenella margarita*** (Figure 77) is a detritus shredder that also eats bryophytes and lives among them. In Appalachian Mountain streams, ***A. attenuata*** lives among the bryophytes, particularly ***Fontinalis dalecarlica*** (Figure 69), but its use of bryophytes for food is unknown (Glime 1968).

Torleya

This is one of the many genera that have been split off from ***Ephemerella***. ***Torleya major*** is a bryophyte dweller in the River Rajcianka in Slovakia, where it lives below the surface but is not found among the emergent wet bryophytes (Krno 1990).

Leptohyphidae – Little Stout Crawler Mayflies

This is a family of small mayflies (3-10 mm) that are clingers and sprawlers (Leptohyphidae 2015). They are widespread in North America, but most are not common among bryophytes. They do crawl about on plants.

Tricorythodes (Figure 102) burrows among the stems and rhizoids of mosses (Armitage 1961). In North America Berner (1959) found it in streams with a perceptible current where it lived among mosses or other plant growth on large stones or amid fine sand and gravel. They eat mostly plants (Leptohyphidae 2015). These naiads rarely swim, but rather move by crawling (Berner 1959). Their gill covers protect the gills, keep them clean, and move water across them when the current is insufficient to provide the needed oxygen.

Figure 102. ***Tricorythodes*** sp. naiad, a genus that burrows among moss stems and rhizoids. Photo by Bob Henricks, with permission.

Suborder Pisciforma

Ameletidae – Combmouthed Minnow Mayflies

Unlike the **Leptophlebiidae**, the **Ameletidae** are fast swimmers. They are mostly limited to clean, cold water (Henricks 2011) of North America and Europe (Ameletidae 2015) where they feed by scraping algae (Zuellig *et al*. 2006). Some members of this univoltine family may be **parthenogenetic** (reproducing with an unfertilized egg). They range 7-21 mm in length (Zloty & Pritchard 1997).

Ameletus (Figure 103) is not generally a moss dweller, preferring more open waters with a stream substrate free of silt (Schwiebert 2007). Nevertheless, mosses can play a role in its location. It is among the few mayflies able to tolerate acid water, permitting it to live downstream from a lake acidified by ***Sphagnum*** (Figure 51) (Bauernfeind & Moog 2000). ***Ameletus inopinatus*** (Figure 104) lives in such a habitat at higher altitudes. In my Appalachian Mountain streams it was an infrequent occupant of the bryophytes (Glime 1968).

Figure 103. ***Ameletus ludens*** naiad. Some members of this genus are able to tolerate the acidified outflow from ***Sphagnum*** lakes. Photo by Jason Neuswanger, with permission.

Figure 104. ***Ameletus inopinatus*** naiad, a species that is able to live in the *p*H extremes of outflow from ***Sphagnum*** fens and bogs at higher elevations. Photo by André Wagner, with permission.

Baetidae – Blue-winged Olives

The **Baetidae** are distributed throughout the cooler (but not polar) parts of both the Northern and Southern Hemispheres (Hebert 2012). They are among the smallest mayflies, usually <10 mm, and mostly members of the open water column, hanging out on the stream bottom or darting into the flow (Baetidae 2013). They are strong swimmers, but feed mostly on algae. Nevertheless, the youngest naiads can be found sheltered among the bryophytes, out of the flow that is beyond their ability for controlled swimming at that early stage (Hynes 1961; Glime 1968). They leave the bryophytes when their swimming skills develop, but when it is time to emerge, the **Baetidae** may once again use the bryophytes to facilitate their break through the surface tension safely. And once above water, they may cling to bryophytes to escape their naiad skin (Figure 105).

Figure 105. **Baetidae** newly emerged adults on wet moss. Photo by Jason Neuswanger, with permission.

Despite their open water nature, ***Baetis*** species are common among bryophytes in the River Rajcianka in Slavakia (Krno 1990). Those on submerged bryophytes include ***Baetis alpinus*** (Figure 106), ***B. fuscatus*** (Figure 107), ***B. lutheri***, ***B. muticus*** (Figure 108), ***B. rhodani*** (Figure 111), ***B. scambus***, ***B. vardarensis*** (Figure 109), and ***B. vernus*** (Figure 110). Among these, naiads of ***Baetis lutheri***, ***B. muticus***, ***B. rhodani***, and ***B. scambus*** are also able to move about among the wet emergent bryophytes.

Figure 106. ***Baetis alpinus*** naiad. Photo by Andrea Mogliotti <www.euroflyangler.com>, with permission.

Figure 107. ***Baetis fuscatus*** adult. Photo by Andrea Mogliotti <www.euroflyangler.com>, with permission.

Figure 108. ***Baetis muticus*** naiad, a species sensitive to low water *p*H. Photo by Andrea Mogliotti <www.euroflyangler.com>, with permission.

Figure 109. ***Baetis vardarensis*** naiad, a dweller of submerged bryophytes. Photo from Zoologische Staatssammlung Muenchen through Creative Commons.

Figure 110. ***Baetis vernus*** adult. Photo by Walter Pfliegler, with permission.

In a Welsh mountain stream Hynes (1961) found the very small (under 3 mm) members of ***Baetis*** (Figure 105-Figure 112) among mosses. I found a similar relationship of early instars among the mosses in Appalachian Mountain, USA, streams (Glime1968). Macan (1980) found that naiads of ***Baetis rhodani*** (Figure 111) in the River Lune, England, were common and abundant in the moss-covered area of the stream in winter. Naiads of four species of mayflies lived there spring to autumn, then overwintered in the egg. Hence, in the summer these other species appeared to displace ***Baetis rhodani*** from the mossy area. Wallace and Gurtz (1986) found that the biomass and production of ***Baetis*** were more than twice that of the weighted stream biomass and production. They suggested that part of this surge in biomass might be due to the large diatom count on mosses. Galdean (1994) further supported the importance of food among the mosses. On boulders where the velocity had increased in a stream, and the mosses on these boulders formed a felt that lacked detritus, ***Baetis rhodani*** was rare.

The mayfly ***Baetis*** (Figure 105-Figure 112) is well adapted to living where water levels fluctuate in streams. It can crawl to deeper water as the water level recedes, and it can relocate by entering the drift (Corrarino & Brusven 1983). When ***Baetis*** is in the drift, it swims to the surface, does a somersault, and hopefully is able to establish a hold on a substrate (Hughes 1966). Its streamlining makes it a good swimmer, and it is among the few insects that can swim against a current. It is positively phototactic and exits from its dark enclosures when there is the light.

In their experiments on effects of *p*H on mayflies, Willoughby and Mappin (1988) found that ***Baetis muticus*** (Figure 108) and ***Baetis rhodani*** (Figure 111) are directly sensitive to the low *p*H of the water, whereas ***Serratella ignita*** (Figure 1) was tolerant but absent in low *p*H water due to an inadequate food supply. Water acidity accounted for the absence of these ***Baetis*** species in the Upper Duddon, UK.

Figure 111. ***Baetis rhodani***, a species that is sensitive to low *p*H. Photo by J. C. Schou, with permission.

Figure 112. ***Baetis tricaudatus*** naiad, a common mayfly among ***Fontinalis neomexicana*** in Idaho, USA. Photo by Tom Murray, through Creative Commons.

Frost (1942) found that ***Baetis***, including the common ***B. rhodani*** (Figure 111), often makes its naiad home among mosses. In their study of colonization of ***Fontinalis neomexicana*** (Figure 79) in an Idaho stream, Maurer and Brusven (1983) found ***Baetis tricaudatus*** (Figure 112) to be common among the mosses.

The food of ***Baetis*** is typically diatoms, desmids, and filamentous algae (Butcher 1933; Percival & Whitehead 1929). But Brown (1961) found that detritus was the primary food of ***B. rhodani*** (Figure 111), a sometimes moss-dweller. Food of ***B. rhodani*** varied somewhat with habitat and season, also including algae. On the other hand, ***Baetis*** is frequent prey for fish. Frost (1942) found that 71% of the fish examined at Ballysmuttan and 59% at Straffan had ***Baetis*** in their guts. Such consumption is likely because of their frequent ventures into the open water.

Lee and Hershey (2000) found that ***Baetis*** (Figure 105-Figure 112) did not increase in numbers in fertilized reaches of the Kuparuk River in Alaska when the moss ***Hygrohypnum*** (Figure 43-Figure 44) increased in density. However, they grew larger in the fertilized zone, a fact Lee and Hershey attributed to greater abundance of epiphytic diatoms.

Wulfhorst (1994) compared naiads of ***Baetis*** (Figure 105-Figure 112) on mosses and in the **interstitial** spaces (spaces between individual sand grains in the soil or aquatic sediments) in the **hyporheic** zone (region beneath and alongside a stream bed) of two streams in the Harz Mountains, West Germany. There the mosses were home to many more of these mayflies than the interstitial spaces of the stream bed (Figure 113). On the other hand, Arnold and Macan (1969) found that ***Baetis***, in addition to inhabiting mosses, occurred on unstable bare stones on the stream bottom.

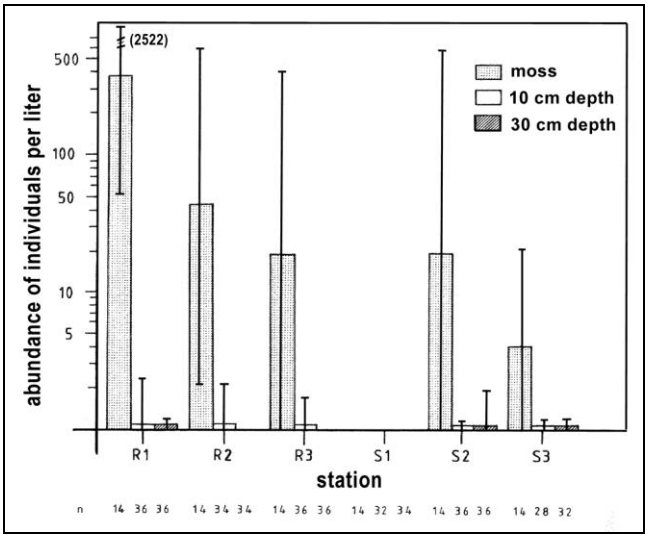

Figure 113. Mean abundance ± 95% CI of ***Baetis*** naiads in moss clumps in two streams in the Harz Mountains, West Germany. Redrawn from Wulfhorst 1994.

In the Arctic, conditions that favor mosses do not always favor the insects. Cold temperatures require life cycles that protect them in the winter. Among those species known to occupy mosses elsewhere, Giberson *et al*. (2007) found ***Ephemerella aurivillii*** (Figure 45) and ***Baetis tricaudatus*** (Figure 112) in the Arctic streams of Nunavut, Canada. The **Baetidae** was the most common family there. ***Baetis bundyae*** (Figure 114) naiads hatched within 2-3 weeks of ice-out and completed their development in 2.5-4 weeks. Giberson *et al*. considered the female-biased sex ratio to be an indication they might experience parthenogenesis. The Arctic **Baetidae** species are able to survive by having freeze-tolerant eggs, good dispersal, and a female-biased sex ratio that promotes greater reproduction.

Figure 114. ***Baetis bundyae*** naiad, a species with a female-biased sex ratio that is possibly parthenogenetic. Photo by Donna Giberson, with permission.

When we enter the Southern Hemisphere, the fauna changes, but major groups tend to remain the same. In Africa, baetid ***Acanthiops elgonensis*** (=*Afroptilum erepenscan*) attaches to mosses, barely covered by water, in the spray of water falls (Gillies 1990).

Siphlonuridae - Primitive Minnow Mayfly

This family generally occurs in slow water. In St. Maries River in Idaho, USA, Gilpin and Brusven (1970) found ***Siphlonurus occidentalis*** (Figure 115) typically clinging to ***Fontinalis*** (Figure 47) growing at the stream margins.

Figure 115. ***Siphlonurus occidentalis*** naiad. Photo by Bob Newell, with permission.

Heptageniidae – Clinger Mayflies

This family is widespread in the Holarctic, Oriental, and Afrotropical regions, as well as Central American Tropics and extreme northern South America (Heptageniidae 2014). Most of them occur in very fast flow where they anchor themselves on rocks by using their collective gills as a suction cup.

Because of this suction cup arrangement, bryophytes are not friends to the **Heptageniidae**. For example, when mosses increased in growth downstream from impoundments, the **Heptageniidae** diminished or were eliminated completely (Brittain & Saltveit 1989). Bottová and Derka (2013) reported that ***Rithrogena semicolorata*** avoided mosses in a karstic spring in the West Carpathians, despite its high coverage of mosses. But in the moderately eutrophic River Rajcianka in Slovakia ***Rithrogena ferruginea*** did occur among the bryophytes, despite the family's adaptations for smooth rock surfaces.

This is a family of flattened mayflies adapted to living on rock surfaces, typically with gills arranged along the abdominal segments to form a suction cup. Nevertheless, Jones (1949, 1950) found all of the guts with identifiable contents from 22 ***Ecdyonurus venosus*** naiads (Figure 116) contained the moss ***Fontinalis antipyretica*** (Figure 47). Winterbourn *et al*. (1986) likewise found that this species ate mosses in two British river systems. In the St. Maries River of Idaho, USA, ***Cinygmula*** sp. (Figure 117) occasionally occurred in clusters among ***Fontinalis*** (Gilpin & Brusven 1970). Among bryophytes in mid-Appalachian Mountain, USA, streams, I only found ***Epeorus*** (Figure 118-Figure 119) representing this family (Glime 1968).

Figure 116. ***Ecdyonurus venosus*** naiad, a mayfly that eats ***Fontinalis antipyretica***. Photo by Guillaume Doucet <http://guillaume.doucet.free.fr/>, with permission.

Figure 117. ***Cinygmula subaequalis*** naiad, member of a genus with moss-dwelling members. Photo by Donald S. Chandler, with permission.

Figure 118. ***Epeorus*** sp. naiad showing flattened body and legs. Photo by Tom Murray, through Creative Commons.

Figure 119. ***Epeorus*** sp. naiad showing ventral arrangement of gills into a suction cup. Photo from NABS through NSF funding public domain.

Isonychiidae

The **Isonychiidae** are mostly North American, with scattered records in Asia (Isonychiidae 2015). These active swimmers are 8-17 mm long and occupy rapid currents (Waterbugkey 2015). They filter algae and diatoms from the water by using the long hairs on their forelegs, but they also eat smaller insects.

In the Appalachian Mountain streams I (Glime 1968) found ***Isonychia*** (Figure 120-Figure 121) occasionally among the bryophytes.

Figure 120. ***Isonychia bicolor*** naiad, member of a genus that sometimes occurs among bryophytes. Photo by Jason Neuswanger, with permission.

Figure 121. ***Isonychia bicolor*** naiad, showing fibrillate gills with gill covers. Photo by Jason Neuswanger, with permission.

Oligoneuriidae – Brushleg Mayflies

This is mostly a river family, but occasionally they are associated with bryophytes. In the Sierra Nevada Mountains in southern Spain, young naiads of ***Oligoneuriella marichuae*** (Figure 122) require physical support and a way to capture food in the absence of a well developed filtering device (Alba-Tercedor 1990). For this they use roots, filamentous algae, and mosses. After they grow, they are able to move into the current.

Figure 122. ***Oligoneuriella rhenana*** naiad, a congener of ***O. marichuae*** that lives among mosses. Photo by Guillaume Doucet <www.guillaume.doucet.free.fr>, with permission.

Suborder Carapacea

Baetiscidae – Armored Mayflies

This small family of North American mayflies has a distinctive morphology (Figure 123) – the **notum** (Figure 124) covers the thorax and part of the abdomen (Edmunds 1960). These mayflies are medium sized (4-14 mm long) and live in pools or flowing water of sandy streams (Baetiscidae 2015b). Hence their occurrences among bryophytes are rare. Their feeding strategies are gatherers and scrapers (Baetiscidae 2015a). When they swim, they tuck their legs under the body and move by undulating the abdomen and caudal filaments (Baetiscidae 2015b).

I am delighted to report this unusual-looking family as having at least occasional moss dwellers. In fact, both ***Baetisca obesa*** (Figure 123) and ***B. rogersi*** (Figure 124) are moss dwellers. Berner (1955, 1956) found ***B. obesa*** among mosses that grew on submersed parts of trees in slow streams in North America. Later, Pescador (1973) found ***B. rogersi*** early instars in thick mats of the moss ***Leptodictyum riparium*** (Figure 125), likewise in slow water. In Appalachian Mountain, USA, streams, I found ***B. callosa*** and ***B. carolina*** among bryophytes, but infrequently (Glime 1968).

Figure 123. ***Baetisca obesa*** naiad, a species that lives on mosses in slow water. Photo by Jason Neuswanger, with permission.

Figure 124. ***Baetisca rogersi*** naiad, whose early instars occur in thick mats of the moss ***Leptodictyum riparium***. Note the large **notum** that covers the thorax and part of the abdomen. This one has a large spine on each side. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

Figure 125. ***Leptodictyum riparium*** in shallow root pit. Photo by Betsy St. Pierre, with permission.

Summary

The **Collembola** are no longer considered insects and are now placed in the class **Entognatha**. Few live in the water and small numbers may mean they have fallen in. But some can occur in large numbers on the water surface, wet bryophytes of bogs, fens, and streambanks, and emergent bryophytes. They possess a **furcula** that propels them forward like a spring. The **collophore** facilitates respiration and absorption of water. Antennae recognize light intensity, wind direction, and heat.

The **Isotomidae** is the most frequent aquatic family, especially ***isotomurus palustris***. This species is **viviparous**.

The **Hemimetabola** have **incomplete metamorphosis** with egg, nymph or naiad, and adult. Naiads typically have gills.

Ephemeroptera (mayflies) live only about one day as adults, emerging, mating, and dying, but not eating. Mating is accomplished in swarms. All the immatures (***naiads***) are aquatic. Some are **univoltine** (one brood per year) and some are **bivoltine** (two broods per year).

Most mayflies have high oxygen requirements. Mayfly naiads have gills, and those with gill covers are able to increase movement of water and oxygen across the gills by beating the gill covers. Some use body undulations to increase contact with oxygenated water.

The most common mayfly family among bryophytes is the **Ephemerellidae**. This is the family that most commonly eats bryophytes, and consumption of mosses increases as the naiads age. However it is not clear if they eat the mosses to assimilate them or if they only assimilate the attached algae and bacteria. ***Baetis*** (**Baetidae**) seems to use bryophytes as a nursery and a stopping point when they enter the drift, a usage common among a number of other families.

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Juan Carlos Villarreal helped me obtain the information on the oviposition of ***Epiophlebia superstes***. D. N. Bennett shared her fauna stories and passed on to me the information from Bob Henricks on ecology of some of the insects, especially ***Ephemerella***. Richard J. Snider verified identifications of the **Collembola** from my mid-Appalachian Mountain study and Lewis Berner verified the species of **Ephemerellidae**. My sister Eileen Dumire helped me make this more layperson friendly and caught many proof-reading errors.

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CHAPTER 11-5
AQUATIC INSECTS: HEMIMETABOLA – ODONATA

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AQUATIC INSECTS: HEMIMETABOLA – ODONATA

Figure 1. ***Lanthus vernalis*** (**Gomphidae**) exuviae on the terrestrial moss ***Thuidium*** sp. Photo by Richard Orr, with permission.

ODONATA – Dragonflies and Damselflies

This order contains both dragonflies (**Anisoptera**; Figure 2-Figure 4) and damselflies (**Zygoptera**). You can recognize adult dragonflies by their wings at rest (Figure 2) – they are spread horizontally; the term *anisoptera* means uneven wings. The damselflies, by contrast, usually fold the wings together above the body at rest (Figure 5); their wings are of equal size (**Zygoptera**). Both dragonflies and damselflies have an aquatic stage, the **naiad** (gilled nymph). Dragonflies can be recognized in the naiad stage by having internal anal gills and relatively stout bodies (Figure 3). Damselflies have three blade-like external anal gills and slender bodies (Figure 6).

Both groups are predators (Thorp & Covich 1991) and the naiads have a large, scooplike **labium** (mouth part; Figure 4 & Figure 8, Figure 7) that extends to capture the prey. These giant jaws are formidable and the **Odonata** are efficient in catching prey.

The naiads climb out of the water and must climb up rocks or vegetation before they split their exoskeleton and emerge (Figure 1). They must then pump fluids into their wings before they fly away. Unlike the mayflies, the dragonfly naiads live as long as 5-6 years and adults for 5-6 months (Dragonfly 2015). Dragonflies are among the strongest fliers in the insect world – just try to catch one!

Figure 2. Dragonfly adult with spread wings. Photo by Eileen Dumire, with permission.

Figure 3. ***Anax junius*** (dragonfly; **Aeshnidae**) naiad showing stout body and anal opening that surrounds internal gills. Photo by Tom Murray, through Creative Commons.

Figure 4. ***Diplacodes*** (dragonfly; **Libellulidae**) young naiad showing extended labium. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 5. ***Enallagma cyathigerum*** (**Coenagrionidae**) Blue Damselfly adult illustrating the wings folded above the abdomen. Photo by Umberto Salvagnin, through Creative Commons.

Figure 6. ***Argia*** (**Coenagrionidae**) naiad showing three external anal gills typical of damselfly naiads. Photo by Bob Henricks, with permission.

Figure 7. ***Lestes*** (damselfly; **Lestidae**) showing extended labium. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

Figure 8. ***Cordulegaster boltonii*** (dragonfly; **Cordulegasteridae**) jaws on exuvia. Photo by Tim Faasen, with permission.

Bryophytes are not the usual homes of **Odonata** naiads in lakes, ponds, and streams. In a Québec, Canada stream, **Odonata** preferred gravel to the moss ***Fontinalis dalecarlica*** (Figure 9) (Cattaneo *et al*. 2004). These carnivores preferred places where they could remain hydrated as the water level decreased and were not tied to the bryophytes for obtaining the periphyton required by many other orders.

Figure 9. ***Fontinalis dalecarlica***, a moss often less preferred than sand, at least in Quebec streams. Photo by J. C. Schou, with permission.

But bryophytes do seem to hold importance for some **Odonata**. In my studies of Appalachian Mountain, USA, streams, the dragonfly genus ***Cordulegaster*** (**Cordulegastridae** – spiketail dragonflies; Figure 10) was occasionally present among bryophytes (Glime 1968). The gomphids ***Gomphus*** (**Gomphidae** – clubtail dragonflies; Figure 11) and ***Octogomphus*** (**Gomphidae**; Figure 12) also occurred among the bryophytes, both rarely, representing the dragonfly naiads (Glime 1968).

The presence of exuviae provides indirect evidence that the **Odonata** use bryophytes for emergence (Needham *et al*. 1901). Both ***Gomphus exilis*** (dragonfly; **Gomphidae**) (Figure 13) and ***G. spicatus*** (Figure 14) exuviae (Figure 15) appeared in layers among mosses at the edge of a pond in the Adirondack Mountains of New York, USA.

Figure 10. ***Cordulegaster erronea*** (dragonfly; **Cordulegastridae**) naiad, an occasional dragonfly genus among bryophytes in mid-Appalachian Mountain streams. Photo by Richard Orr, with permission.

Figure 11. ***Gomphus lividus*** (dragonfly; **Gomphidae**) naiad, a genus that is a rare bryophyte inhabitant in the mid-Appalachian Mountain streams. Photo by Richard Orr, with permission.

Figure 12. ***Octogomphus specularis*** (dragonfly; **Gomphidae**) naiad, a genus that is a rare bryophyte inhabitant in the mid-Appalachian Mountain streams. Photo by Mark Melton, with permission.

Figure 13. ***Gomphus exilis*** (dragonfly; **Gomphidae**) female adult, a species that uses mosses for emergence. Photo by Sheryl Pollock through Discover Life, with permission.

Figure 14. ***Gomphus spicatus*** (dragonfly; **Gomphidae**) adult, a species that uses mosses for emergence. Photo through Creative Commons

Figure 15. ***Somatochlora tenebrosa*** (dragonfly; **Corduliidae**) exuvia. Photo by Richard Orr, with permission.

Suborder Zygoptera – Damselflies

Specific records of damselfly naiads living among bryophytes outside of bogs and fens are few, partly because they do not tend to inhabit the types of habitats where many of the aquatic bryophytes grow. But it seems more likely that the bryophytes do not afford a suitable habitat for their elongate labium to catch prey.

In the Red Cedar River, East Lansing, MI, I found a number of damselfly naiads early in the spring in large clumps of ***Fontinalis*** (Figure 16). ***Teinobasis ponapensis*** (see Figure 17), in the **Coenagrionidae** – narrow-winged damselflies, a damselfly from the eastern Caroline Islands of Micronesia, occurred as adults only near mosses (Paulson & Buden 2003).

Figure 16. ***Fontinalis antipyretica***, home for damselfly naiads in early spring. Photo by Michael Lüth, with permission.

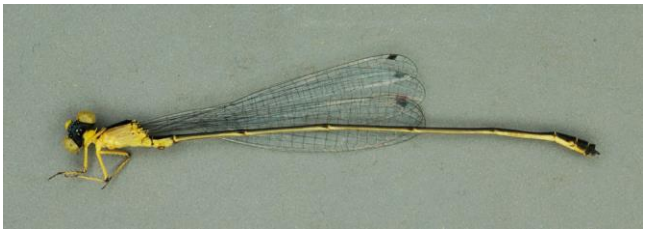

Figure 17. ***Teinobasis sjupp*** (damselfly; **Coenagrionidae**) adult, relative of ***T. ponapensis*** that is known as adults only near mosses in the Caroline Islands of Micronesia. Photo by V. J. Kalkman, through Creative Commons.

But there appear to be interesting relationships still waiting for us. Two new species of the genus ***Argiolestes*** (**Argiolestidae** or **Megapodagrionidae**; damselflies; Figure 18) in Papua New Guinea are known only from shaded areas of water courses; ***Argiolestes fornicatus*** avoids sunny areas of the watercourses and occurs primarily in areas with high moss cover (Michalski & Oppel 2010). ***Argiolestes tuberculiferus*** (Figure 19) and ***A. verrucatus*** were discovered only recently in Papua New Guinea. Other bryophyte relationships most likely remain for discovery in less studied parts of the world.

Figure 18. ***Argiolestes ornatus*** (damselflies; **Megapodagrionidae**) male adult from Papua, Indonesia. Note that the wing position at rest is spreading, unlike other members of **Zygoptera**. (**Lestidae** hold them at 45° angles.) Photo by Vincent J. Kalkman.

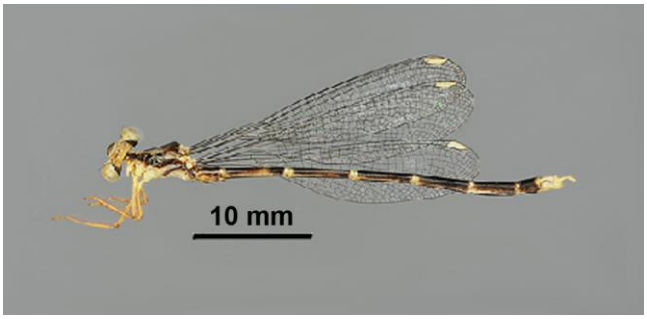

Figure 19. ***Argiolestes tuberculiferus*** adult. Photo by Naturalis Biodiversity Centre through Creative Commons.

Suborder Anisoptera – Dragonflies

Direct usage of bryophytes by **Odonata** naiads is not well documented, but there seems to be more usage for the dragonflies than for the damselflies. It appears that mosses, as well as other protective pond locations, can protect some species when their ponds dry up. ***Somatochlora semicircularis*** (**Corduliidae** – emerald dragonflies; Figure 20-Figure 21) uses mosses, as well as rocks, logs, and deep in the bases of sedge clumps, to escape the drying conditions of exposure when their Colorado, USA, ponds dry up in late August and September (Willey & Eiler 1972). This species has the further advantage that it loses water more slowly than other dragonflies such as ***Aeshna interrupta interna*** (Figure 79-Figure 80) and ***Libellula quadrimaculata*** (Figure 22), neither of which seems to live among bryophytes.

Figure 20. ***Somatochlora semicircularis*** (dragonfly; **Corduliidae**) adult whose survival could depend on naiads seeking shelter in mosses when their ponds dry up. Photo by Belinda Lo through Creative Commons.

Even if **Odonata** are unable to live among bryophytes where their large size would make movement and prey capture more difficult, they may still take advantage of them for cover. ***Somatochlora provocans*** (dragonfly; **Corduliidae**) (Figure 23) occurred in a small lake inlet in southeastern USA, where ***Sphagnum*** (*e.g.* Figure 24) provided a border (Tennessen 1975). The naiads were common in the flowing water, but were hanging out near that ***Sphagnum*** cover.

Figure 21. ***Somatochlora linearis*** (dragonfly; **Corduliidae**) naiad. Some species in this genus retreat to bryophytes when their water body dries up. Photo by Richard Orr.

Figure 22. ***Libellula quadrimaculata*** (dragonfly; **Libellulidae**) naiad, a species that loses water rapidly and cannot survive when its aquatic habitat dries up. Photo by Tim Faasen.

Figure 23. ***Somatochlora provocans*** (dragonfly; **Corduliidae**) adult. Naiads of this species stay near the ***Sphagnum*** cover in pools. Photo by Mike Ostrowski through Creative Commons.

Figure 24. ***Sphagnum*** peatland in Alaska, USA. Photo by Vita Plasek.

Oplonaeschna armata (Figure 25), a member of the **Aeshnidae** – hawkers or darners, may not live among mosses, but the species still finds them useful. Some individuals of this dragonfly left traces of their behavior behind as exuviae clinging to mosses 0.8-1.25 m above the water on vertical rocky walls of a canyon (González Soriano & Novelo Gutiérrez 1998).

Figure 25. ***Oplonaeschna armata*** (dragonfly; **Aeshnidae**) adult, a species that climbs to mosses a meter above water to emerge from the naiad state. Photo by Greg Lasley through Creative Commons.

Life Cycle Considerations

Bryophytes can actually provide several functions for **Odonata**, from wet habitats in waterfalls to safe sites or cover at the margins of streams, ponds, and lakes. The most important of these uses seems to be for egg depositories.

Mating and Egg-Laying

Mosses may not house naiads in many habitats, but they are a preferred site for egg deposition in many bogs and fens. ***Aeshna subarctica*** (dragonfly; **Aeshnidae**) (Figure 27) in northwestern Wisconsin flies along the northwest shoreline, the sunny side, where there is a mat of floating mosses and sedges (DuBois *et al*. 1999). While they submerge the ends of their abdomens into the moist ***Sphagnum*** (Figure 27) they are not ready for a quick getaway. Naiads of this species require submerged mosses in their habitat. ***Aeshna sitchensis*** (Figure 61) does not distinguish between ***Sphagnum*** bog pools and pools of fens with ***Drepanocladus*** (Figure 59) (Cannings *et al*. 2004). In the muskeg, ***Aeshna coerulea septentrionalis*** (dragonfly; **Aeshnidae**) (Figure 62) uses wet moss patches between tufts of scant grass as well as the muskeg "slime" as deposition sites in small pools, or in the creamy-pink muskeg slime bordering small pools (Whitehouse & Walker 1941). During mating and oviposition is a good time to catch the **Odonata** because they are occupied in laying eggs and not in flying.

The female of ***Argia moesta*** (damselfly; **Coenagrionidae**; Figure 26), in Ohio, USA, deposits her eggs on submerged mosses, logs, and algae-covered stones (Kellicott 1899). ***Tanypteryx hageni*** was once thought to insert eggs into plant tissues, but in a closer examination Svihla (1959) found that these were deposited below the water among mosses, liverworts, and other bog plants.

Figure 26. ***Argia moesta*** adult, a species that lays its eggs on submerged mosses. Photo by Richard Murphy through Creative Commons.

Corbet (1999) specifically reports naiads of ***Thaumatoneura inopinata*** (**Megapodagrionidae**), the giant water damselfly, as moss dwellers. This species oviposits among mosses that grow adjacent to, but not within, the main current.

Leucorrhinia hudsonica (dragonfly; **Libellulidae** – skimmers; Figure 29) at a black spruce ***Sphagnum*** bog (Figure 30) in Québec, Canada, uses that habitat for egg deposition (Hilton 1984). The males first establish territories, then perch there except for short attack flights against intruders. Females visit those sites to deposit eggs and are intercepted by the males who enter into tandem formation and copulate with them. Unlike many of the other **Odonata**, they perch near the egg-laying sites during copulation. Once copulation is completed, the females dip their abdominal tips in rapid succession into the small pools of water associated with the saturated ***Sphagnum*** (Figure 51). Males hover nearby to guard the females during this process, chasing off competing males. In Illinois, USA, when females of ***Leucorrhinia*** are pursued by too many males, they land on the mosses and deposit their eggs (Needham & Hart 1901).

Figure 27. ***Aeshna subarctica*** (dragonfly; **Aeshnidae**) female laying eggs in ***Sphagnum***. Photo by Guillaume Doucet <guillaume.doucet.free.fr>, with permission.

Some species use terrestrial mosses for egg deposition. For example, one female ***Tetracanthagyna plagiata*** (**Aeshnidae**; Figure 28), the heaviest of all extant **Odonata**, deposited eggs on a moss-covered log adjacent to a stream, arching its abdomen to insert its ovipositor into the soft substrate (Leong & Tay 2009).

Figure 28. ***Tetracanthagyna plagiata*** (dragonfly; **Aeshnidae**) adult in Malaysia. Photo by Keith Wilson, through Creative Commons.

Figure 29. ***Leucorrhinia hudsonica*** (dragonfly; **Libellulidae**) female adult. Photo by Richard Orr, with permission.

Figure 30. Spruce bog in Pennsylvania, USA. Photo by Nicholas A. Tonelli, through Creative Commons.

One smart dragonfly in Oregon, USA, used mosses to make egg-laying a safer venture. Using her legs to cling to streambank mosses, ***Octogomphus specularis*** (dragonfly; **Gomphidae**) (Figure 31) dipped her ovipositor into the stream water, avoiding the danger of being washed away and helpless against the current (Opler 2013).

Figure 31. ***Octogomphus specularis*** (dragonfly; **Gomphidae**) clinging to moss while ovipositing in the water. Photo by Jim Johnson, with permission.

Temperature plays a major role in the timing and coordination of emergence in ***Somatochlora alpestris*** (dragonfly; **Corduliidae**) (Figure 34) and ***S. arctica*** (Figure 35-Figure 36) (Sternberg 1995). Eggs can hatch the same season or go into diapause and remain in their aquatic habitat throughout the winter. This is a facultative response that causes eggs deposited late in the season to increase from 0 diapausal eggs early in the season to 37% later in the season in ***S. alpestris*** and from 0 to 18% in ***S. arctica***. Depending on the temperature during development, egg development requires 17 to 38 days. Dark mosses and dark bog water help to increase the ambient temperature and hasten development.

Few studies have identified egg-laying locations in streams. Bryophytes would seem to be ideal, even if the naiads leave soon after hatching to chase food items in open water. Askew (1988) did in fact observe ***Caliaeschna microstigma*** (**Aeshnidae**; Figure 32-Figure 33) depositing eggs in mosses on boulders of a stream in Europe.

Figure 32. ***Caliaeschna microstigma*** adult. Photo by Cosmin O. Manci, with permission.

Figure 33. ***Caliaeschna microstigma*** exuvia. Photo by Cosmin O. Manci, with permission.

Emergence

Donnelly (1990) reported with implied amazement a finding of naiads of a species of the damselfly ***Nesobasis*** (**Coenagrionidae**; Figure 37) crawling over wet mosses near a stream in the Fijian Islands, but it was not clear if they lived there or were seeking an emergence site to climb. It appears that mosses are among the sites used for emergence (Walker 1923). Exuviae from several species of the dragonfly ***Ophiogomphus*** (**Gomphidae**; Figure 38-Figure 40) were present on mosses under underhanging foliage at Godbout, Quebec, Canada, where they were a meter or more from the present waterline.

Figure 34. ***Somatochlora alpestris*** (dragonfly; **Corduliidae**) adult, a dragonfly whose egg maturation time depends on the temperature. Photo by Gilles San Martin, through Creative Commons.

Figure 35. ***Somatochlora arctica*** (dragonfly; **Corduliidae**) adult male, a species whose egg maturation time depends on temperature, permitting it to keep its niche separate from that of ***S. alpestris***. Photo by Piet Spaans, through Creative Commons.

Figure 36. ***Somatochlora artica*** (dragonfly; **Corduliidae**) naiad exuvia. Photo by Guillaume Doucet <guillaume.doucet.free.fr>, with permission.

Figure 37. ***Nesobasis erythrops*** (damselfly; **Coenagrionidae**) adult, a genus whose naiads climb across wet mosses in the Fijian Islands. Photo by Mark O'Brien, through Creative Commons.

Figure 38. Adult ***Ophiogomphus cecilia*** (dragonfly; **Gomphidae**) that has just emerged from its exuvia, a genus that sometimes emerges on overhanging mosses by streams. Photo by Tim Faasen, with permission.

Figure 39. ***Ophiogomphus cecilia*** (dragonfly; **Gomphidae**) exuvia, a genus with some members that crawl onto overhanging mosses to emerge. Photo by Tim Faasen, with permission.

Figure 40. ***Ophiogomphus cecilia*** (dragonfly; **Gomphidae**) adult, a genus that apparently uses mosses for emergence. Photo by Varel, through Creative Commons.

Somatochlora elongata (dragonfly; **Corduliidae**) (Figure 41) sometimes sheds its exuvia on mosses at the edge of ponds (Needham *et al*. 1901). ***Somatochlora semicircularis*** (Figure 20) faces imminent danger as it emerges. First, it must find a suitable site for climbing out of the water, and if these sites are scarce, they may all be occupied (Willey 1974). Then, it is vulnerable while it is emerging because it can neither fly nor return to the safety of cover. At this time it is especially vulnerable to birds, and its relatively large size can make a hearty meal. Once free of its nymphal skin, its maiden flight easily draws the attention of hungry predators. At this time, it gains the advantage of safety in numbers. Emergence is highly synchronized, and although many die, the emergence of 50% of the adults within the first three to six days prevents birds from capturing all of them. Considerable space is needed for catching these strong fliers in the air, limiting the number of predators. Life cycle processes from naiad to adult to egg laying can be seen in Figure 42-Figure 48.

Figure 41. ***Somatochlora elongata*** (dragonfly; **Corduliidae**) male adult, a species that may shed its naiad exuvia on mosses bordering ponds. Photo by Denis A. Doucet, with permission.

Life Cycle Stages of the Damselfly *Coenagrion scitulum*

Figure 42. ***Coenagrion scitulum*** naiad, illustrating the three anal gills of the **Zygoptera**. Photo by Tim Faasen, with permission.

Figure 43. Naiad climbing up a plant to emerge to adulthood. Photo by Tim Faasen, with permission.

Figure 44. Adult emerging from exuvia. Photo by Tim Faasen, with permission.

Figure 45. Exuvia of emerged adult. Photo by Tim Faasen, with permission.

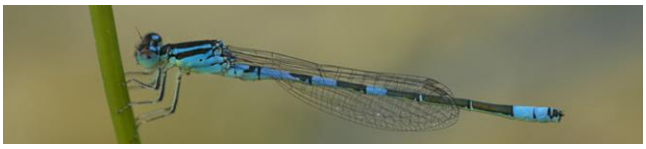

Figure 46. Adult ***Coenagrion scitulum*** ready to mate. Photo by Tim Faasen, with permission.

Figure 47. Mating ***Coenagrion scitulum*** pair, male on top, female below. Photo by Tim Faasen, with permission.

Figure 48. Male (left) and female (right) ***Coenagrion scitulum*** in tandem following copulation. They are most likely looking for a suitable site to lay eggs. Photo by Tim Faasen, with permission.

Safety in Numbers

The dragonfly ***Sympetrum vicinum*** (**Libellulidae** – skimmers; Figure 49) typically uses wet mosses at the edge of a lake for depositing eggs (Whitehouse & Walker 1941). Mating and egg laying can be particularly dangerous for the **Odonata**. These able fliers are at a disadvantage when coupled during mating and when dipping into the water to lay eggs. One strategy for reducing chances of becoming frog dinner is for the mating pair to join other mating pairs, with up to seven pairs of ***Sympetrum vicinum*** (Figure 49) grouping together in a single 1 m^2 plot (McMillan 2000). Interestingly, frogs attacked lone pairs more frequently than they attacked pairs in aggregations. On the other hand, the presence of multiple pairs may have signalled a safe site against the predation.

Figure 49. ***Sympetrum vicinum*** (dragonfly; **Corduliidae**) adults mating. Photo by Phil Myers, through Creative Commons.

Sympetrum danae (dragonfly; **Corduliidae**) (Figure 50-Figure 52) does not remain in tandem pairs (compare to Figure 48) like ***S. vicinum*** (Figure 49). In the field, 14% of females that started oviposition while still in tandem and 10% of those that had separated from the males were killed by frogs (Michiels & Dhondt 1990). A curious observation is that separated ovipositing females were attacked less often by the frogs than were those females that were not observed mating previously. Females of this species preferred sites with ***Sphagnum*** (Figure 24), but when non-aquatic mosses with a similar structure were substituted, they were selected equally, suggesting that selection was based on surface characteristics of the mosses. Within the bog, temperature played a role in oviposition location. In the cooler part of the season the females selected the south-facing side of a hummock, whereas in the warmer part of the season they selected the cooler north-facing side of the hummock.

Figure 50. ***Sympetrum danae*** (dragonfly; **Corduliidae**) naiad. Photo by Tim Faasen, with permission.

Figure 51. The male dragonfly ***Sympetrum danae*** (dragonfly; **Corduliidae**) resting on ***Sphagnum*** in the habitat it prefers for mating. Photo copyright by David Kitching <http://www.brocross.com/dfly/dfly.htm>, with permission.

Figure 52. ***Sympetrum danae*** (dragonfly; **Corduliidae**) mating. Once mating is completed, this species separates and does not fly in tandem. Photo by Tim Faasen, with permission.

Bogs and Fens

Bogs and fens in many ways offer ideal conditions for adult **Odonata**. These strong fliers prefer bright sunshine and become quiet when the weather is cloudy. Sunny, open bogs are thus best suited for them, compared to other kinds of habitats. As discussed earlier regarding bog habitats (Chapter 11-2), the adults are easily seen flying about in bogs (Boudot *et al*. 1990).

Some **Odonata** seem to prefer bogs as adults, using them as a place to forage and for "sport" (Needham *et al*. 1901). One such dragonfly is ***Cordulia shurtleffi*** (American emerald – **Corduliidae**; Figure 53) in the Adirondack Mountains of eastern North America.

Figure 53. ***Cordulia shurtleffi*** (American emerald dragonfly) adult, a species that forages and plays around bog pools. Photo by Richard Orr, with permission.

But is this habitat equally suitable for the naiads? As Krebs (2001) reminded us, habitat heterogeneity provides more ecological niches, and bogs fit that heterogeneity of moisture and temperature as well as differences in microtopography. Some of these may use the mosses as occasional cover in the naiad stage (Figure 54).

Figure 54. ***Cordulia aenea*** (downy emerald dragonfly) naiad with mosses. This species is a relative of ***C. shurtleffi***, a bog species. Photo by Tim Faasen, with permission.

In Ontario, Canada, naiads of ***Williamsonia fletcheri*** (**Corduliidae;** Figure 55) live among the dead ***Sphagnum*** stems (Charlton & Cannings 1993). They matched the ***Sphagnum*** and rarely moved, giving them excellent camouflage. In Maine, USA, the males perch on ***Sphagnum*** hummocks in spruce bogs.

Figure 55. ***Williamsonia fletcheri***, a species whose naiads live among dead ***Sphagnum*** stems. Photo by Diana-Terry Hibbitts, through Creative Commons.

Odonata can have a strong impact on the communities where they live. The naiads are efficient carnivores with highly specialized scoops for capturing prey. Larson and House (1990) concluded that they may be the principal organism determining abundance and distribution of potential prey organisms in the bog pool system.

Normally bogs and fens have rather different flora and fauna from each other. But Cannings and Cannings (1994) concluded that there were no clear differences between the **Odonata** in these two habitat categories. Rather than responding to acidity or nutrient levels, they seem to respond to the form and structure that is similar in these two habitats.

In a study of the northern Cordilleran peatlands, Cannings and Cannings (1994) found that of 40 species there, 8 are obligate peatland inhabitants and another 4 almost always occur there. The most common genera there are ***Aeshna*** (**Aeshnidae**; Figure 56-Figure 62) – 11 species) and ***Somatochlora*** (**Corduliidae**; Figure 20-Figure 21) – 10 species, both dragonflies. The peatlands serve as **refugial** habitats (having isolated populations of once more widespread species, *i.e.* **relict populations**), with 25

species that are restricted to boreal regions and six that are **Holarctic** (majority of habitats found throughout the northern continents of the world).

Figure 56. ***Aeshna juncea*** (dragonfly; **Aeshnidae**) depositing eggs among the ***Polytrichum*** plants. It is common in small acid pools of bogs. Photo copyright by David Kitching <http://www.brocross.com/dfly/dfly.htm>, with permission.

Aeshna juncea (dragonfly; **Aeshnidae**) (Figure 56-Figure 57) prefers the acid water of bog pools and lays its eggs among the bog bryophytes (Figure 56). ***Aeshna subarctica*** (Figure 27) likewise lays its eggs among ***Sphagnum*** (Figure 24), but in the northern Cordilleran peatlands, ***A. subarctica*** (Figure 58) is more commonly associated with ***Drepanocladus*** (*s.l.*) (Figure 59) and ***Scorpidium*** (Figure 60) (Cannings & Cannings 1997). Its males patrol only the floating mats in search of females; the females lay their eggs directly on these mats. ***Aeshna sitchensis*** (Figure 61) lives where the peatlands have filled-in depressions. The mossy fen ponds of the Yukon include ***Aeshna septentrionalis*** (Figure 62) and ***A. subarctica*** among their fauna. ***Aeshna septentrionalis*** females use the sedge-moss habitat for oviposition.

Figure 57. ***Aeshna juncea*** (dragonfly; **Aeshnidae**) naiad, a species of acid bog pools, with mosses. Photo by Tim Faasen, with permission.

Figure 58. ***Aeshna subarctica*** (dragonfly; **Aeshnidae**) adult, a bog dweller. Photo by Arnold Sennhauser, through Creative Commons.

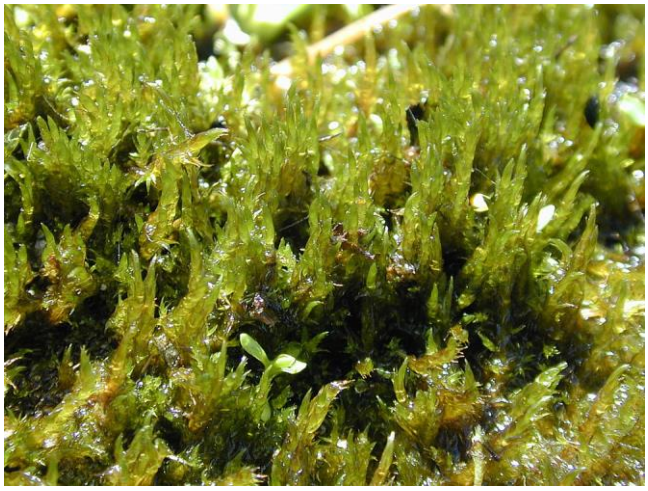

Figure 59. ***Drepanocladus aduncus*** var. ***polycarpon***, home for species of ***Aeshna***, ***Somatochlora***, and ***Leucorrhinia*** in the Yukon. Photo by Michael Lüth, with permission.

Figure 60. ***Scorpidium scorpioides***, home for species of ***Aeshna***, ***Somatochlora***, and ***Leucorrhinia*** in the Yukon. Photo by Michael Lüth, with permission.

Figure 61. ***Aeshna sitchensis*** (dragonfly; **Aeshnidae**) adult, a bog dweller. Photo by Five Acre Geographic, through Creative Commons.

Figure 62. ***Aeshna caerulea*** (dragonfly; **Aeshnidae**) male adult. Photo by Guillaume Doucet <guillaume.doucet.free.fr>., with permission.

In the Czech Republic, ***Aeshna caerulea*** (Figure 62) is a relict, living in bogs that are drying up, suffering from nitrogen deposition, suffering from global warming – all factors contributing to the disappearance of the bogs that serve as its habitat (Dolný 2013).

Mossy fen ponds in the Yukon, Canada, provide us with some idea of the dominant **Odonata** in northern habitats (Cannings & Cannings 1997). In addition to ***Aeshna*** species, their distinctive fauna includes the damselfly ***Coenagrion interrogatum*** (**Coenagrionidae**; Figure 63-Figure 64) and dragonfly ***Somatochlora sahlbergi*** (**Corduliidae**; Figure 65; see Figure 66 for ***Somatochlora*** naiad). ***Coenagrion interrogatum*** is only common where the aquatic mosses are abundant. Where the peatlands have filled in depressions the habitat is characterized by ***Aeshna sitchensis*** (Figure 61), ***Somatochlora franklini*** (Figure 67), ***S. kennedyi*** (Figure 82), ***S. whitehousei*** (Figure 83), and ***Leucorrhinia patricia*** (**Libellulidae**; Figure 84). These dragonfly males patrol the floating mats of mosses that include ***Drepanocladus*** (*s.l.*) (Figure 59) and ***Scorpidium*** (Figure 60). ***Leucorrhinia patricia*** (Figure 84) is restricted to water bodies that have aquatic mosses either floating or near the surface. In Sweden, ***Leucorrhinia rubicunda*** (Figure 85-Figure 86) hunts for its food in bogs as adults (Scholl 2002). In the boreal ecosystems this species occurs only in transitional mires, but in the Netherlands it is the most abundant species of **Odonata** in the spring in degraded and rewetted mires (Desrochers & van Duinen 2006).

Figure 63. ***Coenagrion interrogatum*** (dragonfly; **Coenagrionidae**) adult, an inhabitant of mossy fen ponds in the Yukon, Canada. Photo by Jim Johnson, with permission.

Figure 64. ***Coenagrion*** (damselfly; **Coenagrionidae**) naiad, genus that sometimes lives in mossy fen ponds. Photo by Gerard H. Visser <www.microcosmos.nl>, with permission.

Figure 65. ***Somatochlora sahlbergi*** (dragonfly; **Corduliidae**) adult, a bog dweller. Photo by Mark Zekhuis, with online permission.

Figure 66. ***Somatochlora metallica*** (dragonfly; **Corduliidae**) naiad. Several species in this genus live in bogs. Photo by Tim Faasen, with permission.

Figure 67. ***Somatochlora franklini*** (dragonfly; **Corduliidae**) adult, a bog dweller. Photo by Larry deMarch, through Creative Commons.

In northern British Columbia, Canada, species are similar to those of the Yukon. In standing open water with submerged mosses provides a suitable naiad home for many species with wide ecological tolerances: ***Coenagrion interrogatum*** (Figure 63-Figure 64), ***Aeshna septentrionalis*** (Figure 62), ***A. subarctica*** (Figure 27), ***Somatochlora kennedyi*** (Figure 82), ***S. septentrionalis***, ***Leucorrhinia patricia*** (Figure 84). In slender sedge fens with ***Drepanocladus*** (Figure 59), one can find ***Lestes disjunctus*** (Figure 101), ***Coenagrion interrogatum***, ***C. resolutum*** (Figure 68), ***Nehalennia irene*** (Figure 69), ***Aeshna juncea*** (Figure 56-Figure 57), ***Aeshna subarctica***, ***Leucorrhinia hudsonica*** (Figure 29), ***L. proxima*** (Figure 70), and ***Sympetrum obtrusum*** (Figure 71-Figure 72) (Cannings *et al*. 2004). In shallow sedge-moss fens, typical of patterned fens with ***Drepanocladus***, ***Lestes disjunctus***, ***L. congener*** (Figure 73), ***L. forcipatus*** (Figure 102), ***Enallagma boreale*** (Figure 74), ***Coenagrion resolutum***, ***Nehalennia irene***, ***Aeshna septentrionalis***, ***A. sitchensis*** (Figure 61), ***A. tuberculifera*** (Figure 75), ***Somatochlora brevicincta***, ***S. franklini*** (Figure 76), ***S. kennedyi***, ***S. semicircularis*** (Figure 87), ***S. whitehousei*** (Figure 83), ***Leucorrhinia hudsonica***, and ***Sympetrum danae*** (Figure 50-Figure 52) occur. The outer coastal bogs have a communities of *Pinus contorta* – *Empetrum nigrum* – ***Sphagnum austinii*** (Figure 77) and *Juniperus communis* – *Trichoporum cespitosum* – ***Racomitrium lanuginosum*** (Figure 78). These are suitable habitats for ***Lestes disjunctus***, ***Enallagma boreale***, ***Aeshna interrupta*** (Figure 79-Figure 80), ***Aeshna sitchensis***, ***Cordulia shurtleffii*** (Figure 53), ***Somatochlora albicincta*** (Figure 88), ***Leucorrhinia hudsonica***, ***Libellula quadrimaculata*** (Figure 22), and ***Sympetrum danae***. The seepages and springs of coastal fen associations with *Eriophorum angustifolium* and ***Sphagnum*** are typical habitats for ***Tanypteryx hageni*** (Figure 81), which burrows into the seepage.

Figure 68. ***Coenagrion resolutum*** laying eggs. Photo by D. Gordon E. Robertson, through Creative Commons.

Figure 69. ***Nehalennia irene*** male adult. Photo by Rsbernard, through Creative Commons.

Figure 70. ***Leucorrhinia proxima*** adult, a fen species. Photo by Ed McAskill, through Creative Commons.

Figure 71. ***Sympetrum obtrusum*** female in central Connecticut. Photo by Sage Ross, through Wikimedia Commons.

Figure 72. ***Sympetrum obtrusum*** male, a species that occurs in sedge fens with ***Drepanocladus***. Photo by D. Gordon E. Robertson, through Creative Commons.

Figure 73. ***Lestes congener*** adult. Photo by Richard Orr, with permission.

Figure 74. ***Enallagma boreale*** adult, a species of patterned fens with ***Drepanocladus***. Photo by Mike Ostrowski, through Creative Commons.

Figure 75. ***Aeshna tuberculifera*** adult flying, a species of patterned fens with ***Drepanocladus***. Photo by Mike Ostrowski, through Creative Commons.

Figure 76. ***Somatochlora franklini*** male adult. Photo by Denis A. Doucet, with permission.

Figure 77. ***Sphagnum austinii***, outer coastal species that is home to a number of **Odonata** species. Photo by Michael Lüth, with permission.

Figure 78. ***Racomitrium lanuginosum***, outer coastal species that is home to a number of **Odonata** species. Photo by Juan Larrain, with permission.

Figure 79. ***Aeshna interrupta*** naiad, a species that lives in habitats with ***Sphagnum austinii*** and ***Racomitrium lanuginosum***. Photo by Donald S. Chandler, with permission.

Figure 80. ***Aeshna interrupta*** adult, a species that lives in habitats with ***Sphagnum austinii*** and ***Racomitrium lanuginosum***. Photo by Kam's World, through Creative Commons.

Figure 81. ***Tanypteryx hageni*** adults mating. Photo by Roy J. Beckemeyer, with permission.

Somatochlora franklini (Figure 76) patrols over ***Sphagnum*** (Figure 24) in bogs and over water-soaked mosses in fens, preferring spring-fed ***Sphagnum*** fens. ***Somatochlora sahlbergi*** (Figure 65) naiads (see Figure 66) live where the water is underlain with mosses. As adults they drop their eggs into the water, but again in sites underlain with mosses. Both ***S. semicircularis*** (Figure 87) and ***S. albicincta*** (Figure 88) prefer mossy substrata, the former in a sedge-moss marsh and the latter in mud-bottomed, mossy fen ponds. ***Somatochlora semicircularis*** (Figure 89) flies low over bogs in search of egg-laying sites among the pools; naiads develop in the spring pools and swamps (Usinger 1974).

Figure 82. ***Somatochlora kennedyi*** (dragonfly; **Corduliidae**) male adult, a species that patrols the ***Sphagnum*** mats to find a female. Photo by Denis A. Doucet, with permission.

Figure 83. ***Somatochlora whitehousei*** (dragonfly; **Corduliidae**) adult, a species that patrols the ***Sphagnum*** mats to find a female. Photo by Jim Johnson, with permission.

Figure 84. ***Leucorrhinia patricia*** (dragonfly; **Libellulidae**) adult male, a species restricted to water bodies with mosses near the surface. Photo by Denis A Doucet, with permission.

Figure 85. ***Leucorrhinia rubicunda*** (dragonfly; **Libellulidae**) male, a species that hunts in bogs. Photo by Guido Gerding, through GNU Free Documentation.

Figure 86. ***Leucorrhinia rubicunda*** (dragonfly; **Libellulidae**) naiad on ***Sphagnum***. Photo by Tim Faasen, with permission.

Figure 87. ***Somatochlora semicircularis*** (dragonfly; **Corduliidae**) adult, a species that prefers a mossy fen-marsh. Photo by Leslie Flint, through Creative Commons.

Figure 88. ***Somatochlora albicincta*** (dragonfly; **Corduliidae**) adult, an inhabitant of mud-bottomed, mossy fen ponds. Photo by Chuunen Baka, through Creative Commons.

Figure 89. ***Somatochlora artica*** (dragonfly; **Corduliidae**) adult; the female flies low over bogs to find a suitable place to lay eggs. Naiads develop in pools there. Photo by Guillaume Doucet <guillaume.doucet.free.fr>, with permission.

Dragonflies often deposit their eggs among bryophytes (Macan 1963), with the naiads subsequently living there (Gerson 1982). These bryophyte dwellers include ***Leucorrhinia dubia*** (**Libellulidae** – skimmers; Figure 90-Figure 93) from Europe (Matthey 1971) and ***Calicnemia miles*** (**Platycnemididae –** white-legged damselflies; Figure 94) from the Himalayan Mountains (Kumar & Prasad 1977).

Macan (1962) attempted to explain why (and how) ***Leucorrhinia dubia*** (Figure 90-Figure 93), a **Libellulidae** dragonfly, chose bog pools for laying eggs. He found that this genus was attracted to a white surface on the ground, but that hardly explained anything since ***Leucorrhinia*** species lay eggs by flying and dipping to deposit the eggs in the water during flight. Schiemenz (1954) found that it preferred a ***Sphagnum*** (Figure 51) pool (68%) to tap water, but considered this to be inconclusive. It is likely that water chemistry plays a role.

Figure 90. ***Leucorrhinia dubia*** (**Libellulidae**) naiad, a dragonfly species that changes color in late naiad stages to blend with the surrounding ***Sphagnum*** (Figure 51). Photo by Tim Faasen, with permission.

Figure 91. ***Leucorrhinia dubia*** (**Libellulidae**) emergent adult dragonfly and exuvia. Photo by Tim Faasen, with permission.

Figure 92. Female white-faced darter, ***Leucorrhinia dubia*** (dragonfly; **Libellulidae**). Photo copyright by David Kitching <http://www.brocross.com/dfly/dfly.htm>, with permission.

Figure 93. Male white-faced darter, ***Leucorrhinia dubia*** (**Libellulidae**), a bog-dwelling dragonfly. Photo copyright by David Kitching <http://www.brocross.com/dfly/dfly.htm>, with permission.

Figure 94. ***Calicnemia miles*** (**Platycnemididae**) adult female damselfly who often lays eggs among wet mosses in the Himalayas. Photo by Davidvraju, through Creative Commons.

The dragonfly ***Leucorrhinia dubia*** (white-faced darter; dragonfly; **Libellulidae**) (Figure 90-Figure 93) is so well adapted to the ***Sphagnum*** (Figure 24) habitat that the late instar naiads (immature stages) actually change color to blend with the brown and green color of ***Sphagnum*** (Figure 95) (Henrikson 1993). These naiads show preference for the ***Sphagnum*** substrate over debris in laboratory tests, a behavior that seems to permit them to be more successful in preying on aquatic pillbugs, ***Asellus aquaticus*** (Figure 96). Henrikson suggested that the complex habitat of ***Sphagnum*** serves both as shelter and as a foraging site; the ***Sphagnum*** apparently provides a safe habitat against predators – where large mats of this moss exist, ***Leucorrhinia dubia*** is able to coexist with the fish without becoming dinner.

Figure 95. ***Sphagnum angustifolium*** showing brown and green colors that ***Leucorrhinia dubia*** dragonfly naiads can mimic. Photo by Michael Lüth, with permission.

Figure 96. ***Asellus aquaticus***, food of ***Leucorrhinia dubia***. Photo by Niels Sloth, with permission.

Tanypteryx hageni (Figure 97-Figure 99) (dragonfly; **Petaluridae –** petaltails) adults are most common in alpine bogs. Naiads have been found in mosses in seepage along the west coast of USA (Usinger 1974).

Figure 97. ***Tanypteryx hageni*** (dragonfly; **Petaluridae**) naiad clinging to mosses. Photo by Greg Courtney, with permission.

Figure 98. ***Tanypteryx hageni*** (**Petaluridae**) adult, a dragonfly that lives in alpine bogs; naiads can be found among mosses in seepage. Photo by Dana Kenneth Johnson, through Creative Commons.

Figure 99. ***Tanypteryx*** (dragonfly; **Petaluridae**) burrows amid mosses and swamp litter. Note the holes. Photo by Greg Courtney, with permission.

Damselflies (**Zygoptera**) seem less common among the bog fauna than dragonflies. The common genus ***Lestes*** (**Lestidae** – spreadwings; Figure 100-Figure 102), a damselfly, includes bogs among its many habitats. In British Columbia, Canada, ***Lestes disjunctus*** (Figure 101) is common in several bog types whereas ***L. forcipatus*** (Figure 102) is uncommon in one type and absent in the others (Cannings & Simaika 2005). ***Lestes forcipatus*** is most common in the cold sedge and moss fens and is relatively rare in warmer habitats.

Figure 100. ***Lestes viridis*** (damselfly; **Lestidae**) naiad, a bog inhabitant, among ***Sphagnum*** mosses. Photo by Tim Faasen, with permission.

Figure 101. ***Lestes disjunctus*** (damselfly; **Lestidae**) adult, a species common in several types of bogs in British Columbia, Canada. Photo by Phil Myers, through Creative Commons.

Figure 102. ***Lestes foricpatus*** (damselfly; **Lestidae**) pair mating; the upper male clasps the female at the neck. Note the posterior ovipositor on the female. Photo by Richard Orr, with permission.

Summary

The **Odonata** are **hemimetabolous**, having egg, naiad, and adult stages. They are comprised of dragonflies (**Anisoptera**) and damselflies (**Zygoptera**). Neither is common among bryophytes, most likely due to their large labium used for catching prey and to their large size. Nevertheless, some occur among the bryophytes as naiads, some lay their eggs there, and some gather on bryophytes to emerge to the adult stage.

The **Odonata** are common in bogs and fens, with naiads living among the many pools, sometimes darting into the dangling mosses for cover. The form and structure of the bryophytes may be important determinants in where they live. At mating time, some of the **Odonata** increase the safety of the species by forming aggregations – safety in numbers. ***Aeshna*** and ***Somatochlora*** are the most common genera in the bogs. In both the naiad and adult stages the **Odonata** are voracious carnivores and thus have a major impact, especially in the bog ecosystem.

The typical bog inhabitants include members of **Aeshnidae**, **Coenagrionidae**, **Corduliidae**, **Lestidae**, **Libellulidae**, **Platycnemididae**, and **Petaluridae**. Other families that may be found among bryophytes include **Argiolestidae**, **Cordulegastridae**, and **Gomphidae.**

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CHAPTER 11-6
AQUATIC INSECTS: HEMIMETABOLA – PLECOPTERA

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CHAPTER 11-6
AQUATIC INSECTS: HEMIMETABOLOUS INSECTS – PLECOPTERA

Figure 1. ***Taeniopteryx*** sp. naiad, a common inhabitant of stream bryophytes, especially in early stages. Photo by Bob Henricks, with permission.

PLECOPTERA – Stoneflies

Like the other **hemimetabolous** (incomplete metamorphosis with egg, naiad, and adult) aquatic orders, the **Plecoptera** (Figure 1) have an aquatic immature stage known as a **naiad**. They differ from the **Ephemeroptera** (Chapter 11-4) in that they consistently have only two tails (**caudal filaments**). Their gills occur in various locations but are not found in the middle of the abdomen. The gills are usually not extensive and are absent in many (Dodds & Hisaw 1924; Pennak 1953), so **Plecoptera** naiads require water with high oxygen levels (Needham 1901; Dodds & Hisaw 1924; Macan & Worthington 1951; Pennak 1953; Ward & Whipple 1959), making them good indicators of relatively clean water.

The naiads reach their greatest numbers in fast, cold mountain streams (Thorp & Covich 1991). Although most occur in streams, a few occur in cold, **oligotrophic** (low nutrient) lakes. The naiads must climb out of the water to emerge from their exoskeleton and become adults. The adults are short-lived, but live longer than mayflies, usually several days to two weeks (Thorp & Covich 1991). The naiads are largely night active and appear most often in the night-time drift (Elliott 1967).

Krno and Žiak (2012) found that the number of stoneflies in West Carpathian calcareous **submontane** (ecological zone pertaining to lower slopes of mountains) rivers increased with an increase in mosses, with several genera maintaining their highest density on mosses. **Plecoptera** can use bryophytes in a number of ways. The most obvious is their use as a substrate and shelter from the flowing water. They are especially common there as young instars when the bryophytes can protect these less able swimmers from the flowing water. Many are able to obtain food there, either by preying on smaller invertebrates, by using the collected **detritus** (dead organic matter and debris) and **periphyton** (attached algae and other microorganisms), or less often by eating the mosses themselves. When it is time to emerge, they can use the bryophytes to help them climb through the surface tension and sometimes even provide a surface on which to emerge from naiad to adult, spread their wings, and fly away (Figure 2). Finally, these adults may return to the mosses to lay their eggs (Figure 3).

Figure 2. ***Isoperla*** sp. emerging, using emergent vegetation for support and to pump fluids into its wings. Photo by Richard Bartz, through Creative Commons.

Figure 3. **Plecoptera** eggs, laid here on a rock. Photo by Wendy Brown <www.gunnisoninsects.org>, with permission.

But the presence of some stoneflies as major inhabitants among bryophytes may be the preference of both the stonefly and the bryophyte for the same habitat. Two of the most common families, **Leuctridae** and **Nemouridae**, prefer cooler upstream stations in a southern Ontario, Canada, stream (Harper 1973), a habitat type also very suitable for bryophytes. Both benefit from clean, cool water with rapid flow and a rocky substrate.

Predation Retreat or Restaurant?

Many of the stoneflies are carnivores on a microscale. Since they are small, living in water torrents, they need a food source that is close by. For many, bryophytes can provide that habitat, a place where they can move about, safe from the current, and find an abundance of yet smaller prey items. For them, it is a restaurant with an impressive menu, but it is also a retreat from larger predators. For the yet smaller insects – well, it might be easier to escape predators, but it might also be a trap where they are eaten.

Elliott (2003) used ***Baetis*** naiads as experimental prey items to determine the effect on stonefly interactions, including three known bryophyte dwellers [***Perlodes microcephalus*** (Figure 80), ***Isoperla grammatica*** (Figure 75), ***Dinocras cephalotes*** (Figure 42)]. They found that feeding was density dependent, with the number of ***Baetis*** being eaten dependent on the number provided (between 20 and 200). Handling time was not affected by predator density or presence of other predators. However, attack rate decreased as predator density decreased. As expected, prey consumption also decreased as predator density decreased, with the severity of competition with a paired species being similar to that with the same species.

Food Relationships

Gerson (1982) suggested that **Plecoptera** may feed on aquatic bryophytes, but Stern and Stern (1969) found that detritus was the most common food for stoneflies, and detritus is common among the mosses. Jones (1950) examined the gut contents of **Plecoptera** naiads in the River Rheidol. Four of the six species studied had mosses (***Fontinalis antipyretica***, Figure 4) in the gut: ***Chloroperla tripunctata*** (see Figure 15-Figure 16), ***Leuctra hippopus*** (Figure 5), ***Protonemura meyeri*** (Figure 20), ***Amphinemura sulcicollis*** (= *A. cinerea*; Figure 19). The highest number with mosses in the gut was 12 out of 100 for the species ***Protonemura meyeri***. But the question remains, were the mosses digested or just eaten for their adhering periphyton and detritus?

Figure 4. ***Fontinalis antipyretica***, food for a number of ***Plecoptera*** naiads. Photo by Kristian Peters, with permission.

Figure 5. ***Leuctra hippopus***, member of a genus that is common among stream bryophytes. Photo by Niels Sloth, with permission.

Small streams in the Tolvajärvi region of the Russian Karelia are characterized by higher nutrient and iron concentrations as well as a large amount of organic matter compared to the lake outlet. These small streams are dominated by the mosses ***Fontinalis*** (Figure 4) and ***Hygrohypnum*** (Figure 6) like the lake outlet habitats, but also the leafy liverworts ***Scapania*** sp. (Figure 7), ***Marsupella*** spp. (Figure 8), and ***Jungermannia*** sp. (Figure 9). The dominant moss inhabitants are stonefly **shredders** in the genera ***Nemurella*** (Figure 10-Figure 11), ***Nemoura*** (Figure 12-Figure 13), and ***Leuctra*** (Figure 5). Shredders typically eat leaf litter. Unfortunately, we have no data to indicate what they were shredding among the bryophytes.

Figure 6. ***Hygrohypnum alpinum***, habitat for stonefly shredders in the Russian Karelia. Photo by Michael Lüth, with permission.

Figure 7. ***Scapania undulata***, a common emergent liverwort in streams and home for a number of insects. Photo by David T. Holyoak, with permission.

Figure 8. ***Marsupella aquatica***, a stream insect habitat. Photo by Michael Lüth, with permission.

Figure 9. ***Jungermannia exertifolia*** ssp. ***cordifolia***, home for stream insects. Photo by Michael Lüth, with permission.

Figure 10. ***Nemurella pictetii*** naiad, a bryophyte inhabitant. Photo by Urmas Kruus, with permission.

Figure 11. ***Nemurella pictetii*** adult, a stonefly whose naiads live among bryophytes. Photo by Tim Faasen, with permission.

Typical Fauna

When I examined the bryophytes from the Appalachian Mountain streams in Pennsylvania, Maryland, and West Virginia, USA, I found that the stoneflies were mostly small members in the genera ***Nemoura*** (Figure 12-Figure 13), ***Allocapnia*** (Figure 14), and ***Leuctra*** (Figure 5). Berthélemy (1966) found the moss-dwelling species generally to be smaller than those living among stones. Stern and Stern (1969) likewise found that the bryophytes

served the smaller stoneflies, especially ***Nemoura*** (Figure 12), and acted as a nursery for the young of other Plecoptera.

Figure 12. ***Nemoura*** sp. naiad, a common bryophyte inhabitant in streams. Photo by Bob Henricks, with permission.

Figure 13. ***Nemoura*** cervical gills that enable the species to live in somewhat low oxygen. Photo by Bob Henricks, with permission.

Figure 14. ***Allocapnia*** naiad, common among stream bryophytes in its early (small) stages. Photo by Bob Henricks, with permission.

Frost (1942) found that the moss fauna differed between acid and alkaline waters of the River Liffey, Ireland. In the acid areas, ***Protonemura*** (Figure 20), ***Amphinemura*** (Figure 19), ***Leuctra*** (Figure 5), and ***Chloroperla*** (Figure 15-Figure 16) dominated the mosses, whereas in the alkaline waters only ***Isoperla*** (Figure 17) was common. This is consistent with my finding of **Nemouridae** and ***Leuctra*** among bryophytes in the acidic Appalachian Mountain, USA, streams (Glime 1968).

Figure 15. ***Chloroperla*** adult, a genus whose naiads are common in acid stream water. Photo by G. Bohne, through Creative Commons.

Figure 16. **Chloroperlidae** naiad, a group dominant among mosses in acid water. Photo by Bob Henricks, with permission.

Figure 17. ***Isoperla*** naiad, the only genus common among mosses in alkaline streams. Photo by Bob Henricks, with permission.

In a study of a cool mountain stream of central Japan, Tada and Satake (1994) found that the density of many **Plecoptera** was greater among bryophytes than in bare rock areas. These included ***Scopura*** sp. (**Scopuridae**; Figure 18) (also known from glaciers), ***Amphinemura*** (Figure 19), ***Protonemura*** (Figure 20), ***Isoperla towadensis*** (see Figure 21), and ***I. nipponica***.

Figure 18. ***Scopura longa***, a species whose naiads live on bryophytes in cold mountain streams in Japan. Photo by Shiro Kohshima, with permission.

Figure 19. ***Amphinemura sulcicollis*** adult; naiads of this genus are common among bryophytes in cool mountain streams of Japan. Photo by James K. Lindsey, with permission.

Figure 20. ***Protonemura meyeri*** naiad, member of a genus that is common among bryophytes in cool mountain streams in Japan. Photo by James K. Lindsey, with permission.

Figure 21. ***Isoperla carbonaria*** adult, member of a genus that occurs among stream mosses in Japan. Photo through Creative Commons.

Reproductive Use

Stoneflies can use bryophytes for emergence and egg laying. But in some cases the bryophytes are used in mating behavior. Some stoneflies have an interesting way to attract females. They wait on the shoreline of streams or lakes for the females to emerge from the water and escape their naiad skins. Then they drum their abdomens on such available objects as rocks, dry leaves, and mosses, presumably to attract females (Erman 1984). Mating takes place on the ground (Brinck 1949).

Life cycles are typically attuned to the climate, permitting the insects to overwinter or survive dry spells. These life cycle needs thus dictate part of the required niche. Hynes and Hynes (1975) reported that the life cycle of Australian species were less rigid than those of stoneflies in the Northern Hemisphere. Hence, they tend to have broader ecological niches.

Capniidae – Small Winter Stoneflies

This family of medium-sized stoneflies (usually 5-10 mm) is poorly represented among bryophytes, despite being one of the largest families with about 300 species (Capniidae 2014). In the mid-Appalachian Mountains I found only ***Allocapnia*** (Figure 22) represented among the stream bryophytes (Glime 1968). ***Allocapnia*** adults (Figure 23-Figure 24) emerge in winter (Ross & Ricker 1971). The males are wingless, and these stoneflies often can be seen on the snow (Figure 23), wandering as much as 100 m from their naiad stream. Even the females have reduced wings, poorly developed wing venation, and reduced **thoracic sclerites** (plates forming the outer cover of an arthropod thorax) associated with the flight muscles, so their dispersal ability may be more limited than in other genera. Nevertheless, they do have the ability to disperse downstream, with **gravid females** (females carrying eggs) occurring in the drift and riding on floating ice. And adults may disperse upstream by **planing** – climbing up trees and structures, then gliding to a new location.

Figure 22. ***Allocapnia pygmaea*** male naiad, member of a genus that spends young instars among mosses. Photo by Donald S. Chandler, with permission.

Figure 23. ***Allocapnia pygmaea*** male adult, a winter emerger. Photo by Donald S. Chandler, with permission.

Figure 24. ***Allocapnia pygmaea*** female adult, a winter emerger that can ride the ice downstream. Photo by Donald S. Chandler, with permission.

Bryophytes can be an important location for finding food for some members of the **Capniidae**. Production of ***Capnia vidua*** (Figure 25) naiads in the High Tatra of Slovakia is dependent on the detritus collected by the mosses, making the mosses a suitable habitat for them (Krno & Sporka 2003). This genus also contains members that emerge and flit about on the snow (Figure 26).

Figure 25. ***Capnia*** naiad, a frequent bryophyte dweller. Photo by Jason Neuswanger, with permission.

Figure 26. **Capniidae** adult on snow. Photo by Bob Armstrong, with permission.

Leuctridae - Rolled-winged Stoneflies

This is likewise a family of medium size (5-13 mm). They are long, narrow stoneflies of streams. Berthélemy (1966) suggested that ***Leuctra*** (Figure 5, Figure 30-Figure 31) might be a **muscicole** (living in association with mosses). The genus is known as the rolled-wing stoneflies because of the manner in which the wings curve around the adult body (Figure 27). However, a number of species are **apterous** (without wings) as adults.

Figure 27. ***Leuctra fusca*** adult showing rolled wings. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

The genus ***Leuctra***, along with the **Nemouridae**, are among the most common naiads among the European bryophytes (Carpenter 1927; Frost 1942; Illies 1952).

In the mid-Appalachian Mountain, USA, streams, ***Leuctra*** was a fairly common bryophyte inhabitant, occurring among ***Fontinalis dalecarlica*** (Figure 78), ***Hygroamblystegium fluviatile*** (Figure 89) – ***Platyhypnidium riparioides*** (Figure 62), and most abundant on the leafy liverwort ***Scapania undulata*** (Figure 7) (Glime 1968). These naiads are relatively small, and those on bryophytes tend to be the youngest, *i.e.* smallest, making species identification nearly impossible. In Toliver Run, Garrett Co., MD, USA, this genus reaches a peak in June, but reaches a secondary peak in December, suggesting the presence of two different species. Mackereth (1957) likewise reported seasonal peaks that differed among species in this genus. I also found one adult in my collections, suggesting that they may emerge among the bryophytes (Glime 1968).

Wulfhorst (1994) examined the relative abundance of **Leuctridae** in mosses and in **interstitial** (spaces between individual sand grains in the soil or aquatic sediments) spaces in the **hyporheic** zone (beneath the bed of a river or stream) of two streams in the Harz Mountains of West Germany. She found that the **Leuctridae** were more abundant among the mosses at most collection stations, but that they were also abundant in the interstitial spaces of the **hyporheic** zone at 10 and 20 cm depths (Figure 28).

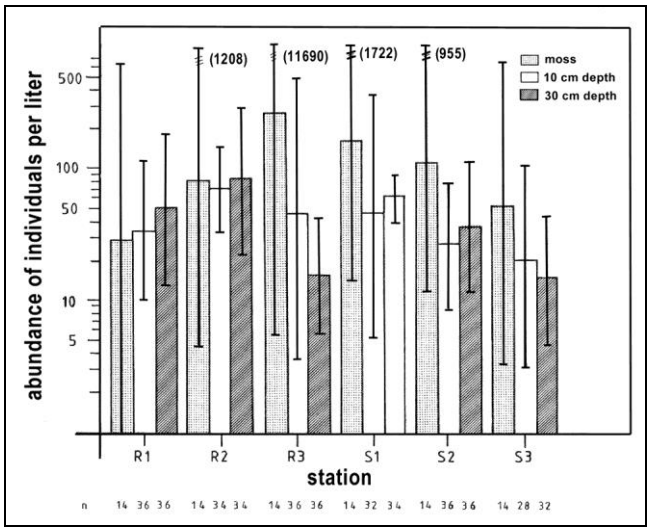

Figure 28. Mean abundance ± 95% CI of **Leuctridae** in moss clumps compared to depths of the hyporheic zone in two streams in the Harz Mountains, West Germany. Redrawn from Wulfhorst 1994.

Several species of ***Leuctra*** [***L. armata*** (Figure 29), ***L. autumnalis***, ***L. pusilla***] contribute to the production of Hincov Brook, High Tatra, Slovakia (Krno & Sporka 2003). Krno and Sporka concluded that these detritivorous stoneflies depend on the mosses to trap the coarse **benthic** (bottom) organic matter needed for their diet. The cold period produces higher productivity, attributable to reduction in feeding by brown trout.

In Radíkovský Brook in the Czech Republic, Jezberová (2003) found that substrate explains a large fraction of the data variability for **Ephemeroptera** and **Plecoptera**. Bryophytes play an important role for several species of ***Leuctra*** in that stream. Among these ***Leuctra albida*** and ***L. teriolensis*** highly prefer a bryophyte substratum.

Figure 29. ***Leuctra armata*** adult, a species whose naiads depend on mosses to trap detritus for their food. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Leuctra is herbivorous (Frison 1929). Jones (1949) found that ***Leuctra fusca*** (=*L. fusciventris*; Figure 30) and ***L. geniculata*** (Figure 31) had ***Fontinalis antipyretica*** (Figure 4) leaf fragments in about half the gut analyses from calcareous streams in South Wales. In the River Rheidol, UK, Jones (1950) found ***Fontinalis*** fragments in 8 of the 20 guts in which contents could be identified. Percival and Whitehead (1929) reported that several species of UK ***Leuctra*** had mosses in their guts. Dangles (2002) considered members of this genus to be generalist feeders, including bryophytes among their food choices.

Figure 30. ***Leuctra fusca***, a consumer of ***Fontinalis antipyretica*** in South Wales. Photo by Louis Boumans, through Creative Commons.

Figure 31. ***Leuctra geniculata*** naiad, a consumer of ***Fontinalis***. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

In the River Rajcianka, Slovakia, submerged bryophytes are home to ***Leuctra hippopus*** (Figure 5), ***L. inermis*** (Figure 32), and ***L. rauscheri*** (Krno 1990). Most are restricted to the submerged portions, but ***L. rauscheri*** is able to live above the water surface among emergent bryophytes.

Figure 32. ***Leuctra inermis*** adult, a species whose naiads live among bryophytes in River Rajcianka, Slovakia. Photo by James K. Lindsey, with permission.

Nemouridae – Spring Stoneflies

This is a family of small to medium stoneflies (5-20 mm). Wulfhorst (1994) examined the relative abundance of **Nemouridae** in mosses and in interstitial spaces in the hyporheic zone of two streams in the Harz Mountains of West Germany. She found that the **Nemouridae** were much more abundant among the mosses at all collection stations (Figure 33) than on other substrata. Furthermore, she found that most of them avoided 10 and 30 cm depths.

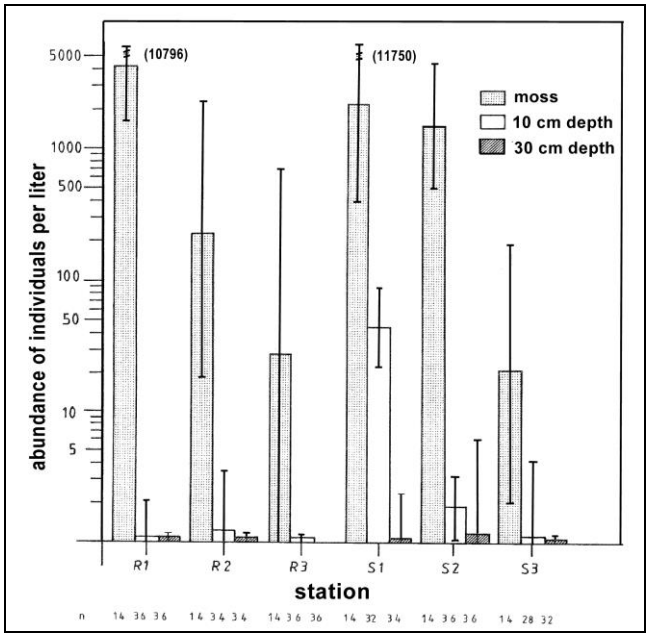

Figure 33. Mean abundance ± 95% CI of **Nemouridae** (***Amphinemura***/***Protonemura***) in moss clumps in two streams in the Harz Mountains, West Germany. Redrawn from Wulfhorst 1994.

In the Appalachian Mountain streams I studied, **Nemouridae** (Figure 34-Figure 37) were the most frequent and abundant of the Plecoptera, reaching their greatest numbers on turfs of ***Scapania undulata*** (Glime 1968, 1994). The species included ***Nemoura sinuata*** (Figure 34), ***Soyedina vallicularia***(?) (Figure 35-Figure 36), and ***Amphinemura nigritta*** (Figure 37). These occurred at all instar stages and most likely emerged to adulthood from the bryophyte mat.

Figure 34. ***Nemoura sinuata*** adult, a species that lives among bryophytes as naiads in Appalachian Mountain, USA, streams. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 35. ***Soyedina vallicularia*** naiad, a common inhabitant (or a similar species) among bryophytes in Appalachian Mountain, USA, streams. Photo courtesy of the State Hygienic Laboratory at the University of Iowa, with permission.

Figure 36. ***Soyedina vallicularia*** adults. Photo by R. E. DeWalt, through Creative Commons.

Figure 37. ***Amphinemura nigritta*** naiad, a common nemourid among Appalachian Mountain stream mosses. Photo by Tom Murray, through Creative Commons.

In subarctic Fennoscandia, some members of ***Nemoura***, such as ***N. viki***, deposit their eggs on damp mosses, although most are deposited in the water (Lillehammer 1986, 1988). ***Nemoura viki*** and ***N. arctica*** differ in their life cycles and in their preferred biotopes, effectively separating their niches. The temperature tolerance range of the eggs of ***N. arctica*** is wider. For the latter, temperature nevertheless has a profound effect on naiad development time. After 700 days at 4°C, the naiads still are not ready for emergence. On the other hand, at 16°C, the naiads can reach maturity in 120 days.

Wu (1923) reported that ***Nemoura*** (Figure 12) was a herbivore, eating mostly desmids and diatoms; he never found animal tissue in the diet. On the other hand, Chapman and Demory (1963) found that ***Nemoura*** in two Oregon, USA, streams consumed mostly detritus. Leberfinger and Bohman (2010) found that ***Nemoura*** sp. chose algae and shrubby cinquefoil when offered leaves of birch, Swedish whitebeam, shrubby cinquefoil, dead and fresh grass, moss, and algae. The least consumed food was dead grass, despite its being the most abundant food in the stream. Even though the fresh food had the highest carbon to nitrogen content, it was the dead leaves of the shrubby cinquefoil that was the food of choice, suggesting that perhaps fungal or bacterial decomposer organisms might have been important in the diet. A word of caution – the genus ***Nemoura*** has since been divided into multiple genera, so these generic designations may be misleading; The designation by Leberfinger and Bohman (2010) is recent and is most likely reflective of modern nomenclature.

Nemoura flexuosa (Figure 38), ***N. marginata***, and ***N. monticola*** all live among bryophytes in the River Rajcianka, Slovakia (Krno 1990). ***Nemoura monticola*** seems to be restricted to submerged bryophytes, whereas the other two species are able to move about within the wet bryophyte clumps above that water line.

Figure 38. ***Nemoura flexuosa*** naiad, a bryophyte dweller in Europe. Photo by Niels Sloth, with permission.

Nemoura cinerea (Figure 39-Figure 40) survives low oxygen levels better than ***Diura bicaudata*** (**Perlodidae**; Figure 41) and ***Dinocras cephalotes*** (**Perlidae**; Figure 42) (Benedetto 1970), perhaps explaining the ability of ***N. cinerea*** to live among mosses with heavy sedimentation. Furthermore, ***N. cinerea*** was the only species among the four tested that did not display undulations as oxygen levels became low (Benedetto 1970). ***Amphinemura*** has a cluster of pompon-like gills in each side of the neck (Figure 43). But ***N. cinerea***, like all ***Nemoura*** species, lacks this group of gills and does not have the ability to acclimate and change its low oxygen response to temperature (Nagell & Fagerstrom 1978).

Figure 39. ***Nemoura cinerea*** mating, a species whose naiads are unable to acclimate to low oxygen but that is a better survivor in these conditions than ***Diura bicaudata*** and ***Dinocras cephalotes***. Photo by James K. Lindsey, with permission.

Figure 40. ***Nemoura cinerea*** naiad, lacking cervical gills. Photo by James K. Lindsey, with permission.

Figure 41. ***Diura bicaudata*** adult, a species that is not able to survive well in low oxygen. Photo by Pentti Ketola, through free usage.

Figure 42. ***Dinocras cephalotes*** naiad, a species that does not survive low oxygen levels, a factor that may keep it out of some bryophyte clumps. Photo by Guillaume Doucet <guillaume.doucet.free.fr>, with permission.

Figure 43. ***Amphinemura*** cervical gills, adapting it to low oxygen levels. Photo by Bob Henricks, with permission.

Nemouridae (Figure 39-Figure 43) are very tolerant of low temperatures, achieving a growth rate of 1.6% per day at a mean water temperature of only 0.6°C in a subalpine lake in the Jotunheimen Mountains of southern Norway (Brittain 1983). This is also a typical stream temperature in northern Appalachian Mountain streams of New Hampshire in winter (Glime, unpubl data).

Krno (1990) reported several species of ***Protonemura*** on submerged bryophytes in the River Rajcianka, Slavakia: ***Protonemura auberti***, ***P. autumnalis***, ***P. hrabei*** (Figure 44), ***P. intricata*** (Figure 45), ***P. praecox*** (Figure 46-Figure 48). Of these, ***Protonemura auberti***, ***P. autumnalis***, ***P. hrabei***, and ***P. intricata*** also occurred on emergent wet bryophytes. Krno and Žiak (2012) reported that ***Protonemura*** was one of the taxa that was greatest on bryophytes in calcareous submontane rivers of the West Carpathians. ***Protonemura*** is likewise abundant among mosses in the Pyrénées (Berthélemy 1966), causing Berthélemy to consider ***P. pyrenaica*** to be a **muscicole** (living in association with mosses).

Figure 44. ***Protonemura hrabei*** naiad, a Slovakian moss dweller. Photo by J. C. Schou, with permission.

Figure 45. ***Protonemura intricata*** adult, a species whose naiads live among bryophytes. Photo by Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 46. ***Protonemura praecox*** emergent female adult before wings are inflated. Photo by Walter Pfliegler, with permission.

Figure 47. ***Protonemura praecox*** emergent female adult attempting to inflate her wings. Photo by Walter Pfliegler, with permission.

Figure 48. ***Protonemura praecox*** female adult with fully inflated wings. Photo by Walter Pfliegler, with permission.

Protonemura meyeri (Figure 20) is common on ***Fontinalis*** (Figure 4) and other mosses in Europe (Hynes 1941; Costello 1988). This is a species that not only lives among bryophytes below the water surface, but also is able to go above the water level in the protective moisture of the bryophytes (Krno 1990). Frost (1942) concluded that ***P. meyeri*** lives among mosses throughout its entire naiad life. Not only did Hynes (1941) find that moss is the primary habitat for ***P. meyeri***, but Frost (1942) found that in the River Liffey it feeds almost entirely on mosses. However, Jones (1950) found ***Fontinalis*** in the guts of only 12 out of 32 ***Protonemura meyeri*** and in 2 out of 43 ***Amphinemura sulcicollis*** (Figure 19) in the River Rheidol, UK. Availability of moss vs other food choices influence which the stoneflies will eat.

On the other hand, Dangle (2002) considered ***Protonemura*** to be a generalist, including mosses among its food selections. But Dangle also cautioned against making generalizations from one species to another within a genus, even when the mouth parts were essentially the same. Krno and Sporka (2003) found that mosses were important for ***P. montana*** and ***P. nimborum*** because of the coarse benthic organic matter that accumulated there, providing both a stable habitat and a detrital food source.

Kamler (1967) found large numbers of ***Protonemura nitida*** among mosses in the early naiad stages. Bottová and Derka (2013) found that ***P. nitida*** was a significant contributor to the biomass in a **karstic** (limestone terrain characterized by sinks, ravines, and underground streams) spring in the West Carpathians. Its numbers reached 13,585 per m^2 in moss there, making them the most abundant stonefly. Steiner (1991) was surprised to find that when the surface film in ***Fontinalis antipyretica*** (Figure 4) was removed, small ***P. nitida*** fed on the leaf interior, but larger naiads tore the leaves, becoming moss shredders.

In the calcareous submontane rivers of the West Carpathians, ***Amphinemura*** was in its greatest abundance on mosses (Krno & Žiak 2012). Percival and Whitehead (1929) found ***Amphinemura sulcicollis*** (Figure 19) would occupy both thick and loose mosses, but it is much more abundant in the tracheophyte *Potamogeton* (Figure 49). Butcher *et al*. (1937) commented that it is probable that all the naiads belonged to this species, alluding to the difficulty in identifying the young instars. Frost (1942) found only two individuals of this species among the mosses in the alkaline station, but over 2000 at the acid water station. In their experiments, Willoughby and Mappin (1988) found that the tolerance of low *p*H by ***Amphinemura sulcicollis*** from acidic streams in the watershed of the River Duddon was similar to that of the mayfly ***Serratella ignita*** (Figure 1). It is interesting that ***A. sulcicollis*** slightly increases the percentage of detritus in its diet as it grows rather than increasing the moss component, as is common among other stoneflies and mayflies (López-Rodríguez *et al*. 2008). Nevertheless, mosses appear to be important components of the habitat for ***A. sulcicollis*** as evidenced by its presence in thirteen localities on the Isle of Man where mosses or overhanging grass were present (Hynes 1952). In North America, ***A. nigritta*** (Figure 50) occurs among bryophytes in the mid-Appalachian Mountain streams, inhabiting all the major bryophytes there: ***Fontinalis dalecarlica*** (Figure 78), ***Hygroamblystegium fluviatile*** (Figure 89) – ***Platyhypnidium riparioides*** (Figure 62), and ***Scapania undulata*** (Figure 7) (Glime 1968).

Figure 49. ***Potamogeton gramineus***, a genus that is a common home for ***Amphinemura sulcicollis***, also a moss dweller. Photo by Kristian Peters, with permission.

Figure 50. ***Amphinemura nigritta*** naiad, a common bryophyte inhabitant in Appalachian Mountain streams. Photo by Tom Murray, through Creative Commons.

In streamside mosses like ***Cratoneuron*** (Figure 51), the stonefly ***Nemurella pictetii*** (Figure 10-Figure 11) may reach 16,500 individuals per square meter in a Danish spring (Lindegaard *et al*. 1975), and Thorup (1963) considered it to prefer mosses as a substrate. This species not only occurs in springs, but is among the few moss dwellers that are also common in lakes (Kamler 1967). Its adaptability to climate changes and habitat differences is seen in its ability to have both **bi**- and **trimodal** emergence patterns (having 2 and 3 peaks, respectively), coupled with partial **bivoltinism** (two broods per year), in Central Europe (Wolf & Zwick 1989), representing the only confirmed multivoltinism in a stonefly. Its emergence threshold temperature of 8°C prevents it from emerging when freezing danger is still likely. Rather than relying on seasonal life cycle cues, this species seems to be regulated by temperature, registered as accumulated degree days and an emergence temperature threshold.

Figure 51. ***Cratoneuron filicinum*** where ***Nemurella pictetii*** lives on springs and streamside. Photo by Michael Lüth, with permission.

Zapada cinctipes (=*Nemoura cinctipes*; Figure 52) was most abundant in the upper reaches of Trout Creek, Utah, USA, where the substrate was densely covered with the moss ***Hygrohypnum bestii*** (Figure 53) (Hales & Gaufin 1971). ***Zapada columbiana*** (Figure 54), a native of subalpine streams in Calgary, Canada, has a three-year life cycle (Mutch & Pritchard 1984, 1986). The naiads live primarily on boulders and cobble among mosses (Clifford 2014). Despite their long life cycle, they only grow during the ice-free season (Mutch & Pritchard 1986). The females do not move upstream to lay eggs (Mutch & Pritchard 1984). Of the six females examined, their egg production ranged 800-1200 eggs each (Mutch & Pritchard 1986). These eggs hatch before winter so that the young naiads spend the first winter living among the mosses. Nevertheless, the eggs of these stoneflies develop best at lower temperatures.

Figure 52. ***Zapada cinctipes*** naiad, a species common where ***Hygrohypnum bestii*** is present in Trout Creek, Utah, USA. Photo by Bob Armstrong, with permission.

Figure 53. ***Hygrohypnum bestii***, home of the stonefly ***Zapada cinctipes***. Photo by Robin Bovey, with permission through Dale Vitt.

Figure 54. ***Zapada columbiana*** adult on snow. Photo by Bob Newell, with permission.

Although ***Zapada columbiana*** (Figure 54) lives for three years in the rocky streams of the Alberta, Canada, Rocky Mountains, some naiads may complete their life cycle in two years (Mutch & Pritchard 1984). Important to these naiads is the food available to them. Mutch and Pritchard found that at any time during their growth season (June to November) at least 50% of them were living among the mosses covering the boulders or cobble in riffles. Furthermore, mosses are the predominant food in the gut for these shredders, but during winter highly conditioned conifer detritus becomes the predominant component. In experiments these naiads grow better on a moss diet than on the leaves of the willow *Salix glauca.*

Notonemouridae

This New Zealand/southern Africa family is another stonefly addition to the moss fauna and is not known from the Northern Hemisphere. All the genera are endemic to New Zealand except ***Notonemoura*** (McLellan 1991). They are typical of cool, high elevation lakes and rivers (Notonemouridae 2015), but some have terrestrial naiads and others have naiads that spend their early instars in the water and later instars on land, and some live in lowlands (McLellan 1991). They are herbivores and detritivores. Their enlarged hind femora helps them to climb vertical surfaces against flowing water (Notonemouridae 2015). The females lay their sticky eggs in the crevices of logs and rocks. These are small stoneflies (5-8 mm) and are mostly leaf shredders (Picker *et al*. 2004).

Notonemoura latipennis occurs in bog pools and bog outlet streams (McLellan 1991). ***Spaniocercoides hudsoni*** (see Figure 55) naiads live in ***Sphagnum*** bogs (Figure 56-Figure 57) (McLellan 2005). ***Spaniocerca zelandica*** naiads live in streams under stones or fallen logs or hidden among mosses or leaf litter (Winterbourn 1968).

Figure 55. ***Spaniocercoides philpotti*** naiad, member of a genus that lives in bogs and in streams among mosses. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Chloroperlidae – Green Stoneflies

Members of this family are medium in size (10-20 mm) and typically green as adults (Figure 58). ***Chloroperla tripunctata*** (see Figure 59) occasionally eats fragments of ***Fontinalis*** (Figure 4), but Jones (1950) reported only 3 specimens out of 113 with this moss in their guts in the River Rheidol, UK.

Figure 56. Bog in Fiordland, NZ. Photo through Creative Commons.

Figure 57. ***Sphagnum crispum***, a common ***Sphagnum*** species in New Zealand. Photo by Janice Glime.

Figure 58. **Chloroperlidae** exuviae (shed exoskeletons) and adults showing the green color of the adults. Photo by Jason Neuswanger, with permission.

Figure 59. **Chloroperlidae** naiad, a family where some members occasionally eat ***Fontinalis***. Photo by Bob Henricks, with permission.

In the High Tatra of Slovakia, ***Siphonoperla neglecta*** (Figure 60) depends on mosses that trap the coarse benthic detritus that serves as their food (Krno & Sporka 2003). The moss helps them to avoid predation by the brown trout until the cold season when the trout cease feeding actively.

Figure 60. ***Siphonoperla torrentium*** mating; ***Siphonoperla neglecta*** escapes brown trout predation by hiding among mosses. Photo by James K. Lindsey, with permission.

Taeniopterygidae – Winter Stoneflies

The Taeniopterygidae are among the small to medium (10-20 mm) bryophyte-dwelling stoneflies. These shredders and detritivores prefer cold, clear running water of large streams and rivers (Entz 2006). They emerge in winter and are not among the bryophytes year-round because they are very sensitive to warm temperatures and require high oxygen levels.

The genus ***Taeniopteryx*** (Figure 61) commonly develops among mosses (Berthélemy 1966). It is common in some mid-Appalachian Mountain streams among ***Hygroamblystegium fluviatile*** (Figure 89) – ***Platyhypnidium riparioides*** (Figure 62) clumps, seemingly either abundant or absent. (Glime 1968). This species disappears from the bryophytes as it grows and is never present in older stages. Krno and Žiak (2012) reported that ***Taeniopteryx auberti*** is one of the taxa that reaches its greatest abundance on mosses in calcareous submontane rivers of the West Carpathians. Tiny naiads of ***Taeniopteryx nebulosa*** (Figure 61) are common among ***Platyhypnidium riparioides*** in Britain (Langford & Bray 1969). Hubault (1927) considered ***Taeniopteryx hubaulti*** to be a strong muscicole.

Figure 61. ***Taeniopteryx nebulosa*** naiad, member of a genus that is common among ***Platyhypnidium riparioides*** in the UK. Photo by Niels Sloth, with permission.

Figure 62. ***Platyhypnidium riparioides***, home of ***Taeniopteryx nebulosa***. Photo by Michael Lüth, with permission.

Brachyptera risi (Figure 63) in a Dartmoor stream was confined to mosses on the sides of boulders in the stream (Elliott 1967). Costello (1988) found it both widespread and abundant among mosses in Irish streams. Langford and Bray (1969) found larger nymphs of this species throughout the year on the mosses ***Platyhypnidium riparioides*** (Figure 62) and ***Fontinalis antipyretica*** (Figure 4), two species that usually did not occur together, in British lowland streams. Dangles (2002) reported ***Brachyptera seticornis*** as specializing on algae and bryophytes for its food.

Figure 63. ***Brachyptera risi*** naiad, a species confined to mosses in a Dartmoor stream. Photo by Guillaume Doucet <guillaume.doucet.free.fr>, with permission.

Perlidae – Common Stoneflies

The **Perlidae** are larger than members of the previous families, reaching 20-50 mm as adults. Although their distribution is nearly worldwide, they are most abundant in eastern North America (Perlidae 2013). Although they typically occur in cool, clear medium-sized to large streams, they can occur in quiet waters. When water is not moving over their bodies, they undulate the body to increase oxygen exchange. They are predators that engulf their prey.

Krno and Žiak (2012) reported that the perlid genus ***Dinocras*** reached its greatest abundance among mosses, compared to other substrata, in calcareous submontane rivers of the West Carpathians. Berthélemy (1966) considered ***Dinocras*** to be a muscicole, suggesting that the mosses help to stabilize the habitat for ***Dinocras cephalotes*** (=*Perla cephalotes*) (Figure 42). ***Dinocras cephalotes*** is one of the largest stoneflies in the Shropshire Hill Stream, UK, and is found mostly in streams and rivers where mosses cover stable stones (Arnold & Macan 1969). Hynes (1941) similarly found that it was much more common where the substrate was stable and moss-covered. And ***Dinocras cephalotes*** occasionally ingests mosses, including ***Fontinalis antipyretica*** (Figure 4) (Percival & Whitehead 1929; Jones 1949). But more importantly, at least in North Wales, the ***D. cephalotes*** hung out near where the triclads (flatworms) were abundant, forcing the triclads to live exclusively in dense patches of moss (Wright 1975).

In trout streams of Yellowstone National Park, USA, one could find ***Hesperoperla pacifica*** (Figure 64) among mosses and the green alga *Cladophora* (Figure 65) (Muttkowski & Smith 1929). This medium-sized species is a carnivore, but Muttkowski and Smith did find mosses in many of the guts, perhaps taken along with a grab for an insect prey.

Figure 64. ***Hesperoperla pacifica*** naiad, a moss inhabitant in trout streams in Yellowstone. Photo by Arlen Thomason, with permission.

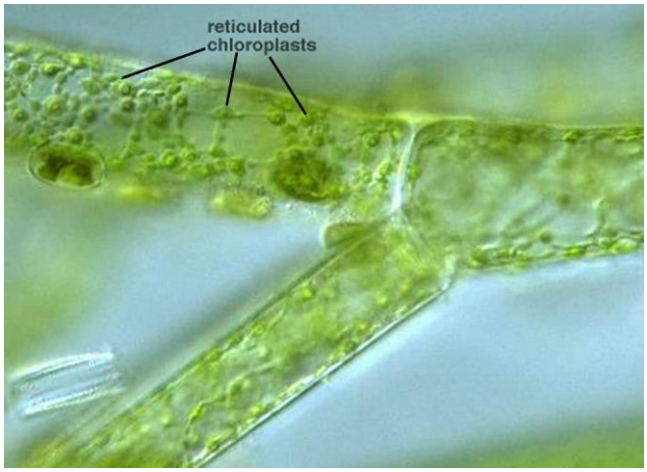

Figure 65. *Cladophora*, habitat, along with mosses, for ***Hesperoperla pacifica***. Photo by Yuuji Tsukii, with permission.

In the eastern USA, one can find a different array of **Perlidae** among the stream bryophytes. In the Appalachian Mountains, I found ***Acroneuria*** (Figure 66), ***Agnetina capitata*** (Figure 67), ***Perlesta placida*** (Figure 68-Figure 69), and ***Paragnetina*** (Figure 70) (Glime 1968). ***Acroneuria carolinensis*** (Figure 66) in Panther Creek, West Virginia, USA, clings to mosses, sand, rocks, and stems of *Rhododendron* (Schmidt & Tarter 1985). I often found this genus among the bryophytes in Appalachian Mountain streams (Glime 1968).

Figure 66. ***Acroneuria carolinensis*** naiad, a species that clings to mosses and other things in its native streams. Photo by Bob Henricks, with permission.

Figure 67. ***Agnetina capitata*** naiad, a species that sometimes occurs among ***Fontinalis*** species. Photo by Donald S. Chandler, with permission.

Figure 68. ***Perlesta placida*** adult, a species whose naiads sometimes occur among bryophytes in the Appalachian Mountains. Photo by Jason Neuswanger, with permission.

Figure 69. ***Perlesta nelsoni*** naiad, a New Hampshire, USA, species in a genus that sometimes occurs among stream bryophytes. Photo by Donald S. Chandler, with permission.

Figure 70. ***Paragnetina immarginata*** naiad, member of a genus that sometimes occurs among bryophytes in Appalachian Mountain streams. Photo by Donald S. Chandler, with permission.

Perlodidae – Springflies & Yellow Stones

Like the **Perlidae**, the **Perlodidae** tend to be somewhat larger than the previous families (10-50 mm). The adults hatch in April to June and the eggs provide **diapause** (period of suspended development; physiological dormancy) during the warmer months, making the naiads absent from their native streams at that time because they have only one generation per year (Perlodidae 2014). Like the **Perlidae**, they are mostly engulfing predators, but some are scrapers and collector-gatherers. In addition to their diet of small invertebrates, at least some eat plant material, especially when they are young.

This is not a common family among moss dwellers, but in their study of an Idaho, USA, stream, Maurer and Brusven (1983) found a species of ***Cultus*** (Figure 71) to be common in clumps of ***Fontinalis neomexicana*** (Figure 72) as well as on the mineral substrate. Naiads climb out of the water and emerge on nearby rocks and vegetation (Figure 73).

Figure 71. ***Cultus verticalis*** naiad, from a genus that is common among ***Fontinalis neomexicana*** in Idaho, USA, streams. Bryophytes may also provide emergence sites. Photo by Tom Murray, through Creative Commons.

Figure 72. ***Fontinalis neomexicana*** in a dry streambed; home of ***Cultus verticalis*** naiads. Photo by Janice Glime.

Figure 73. **Perlodidae** emerged on rock at edge of stream. Photo by Janice Glime.

Krno and Žiak (2012) reported that ***Isoperla*** is one of the taxa that is at its greatest abundance on mosses in calcareous submontane rivers of the West Carpathians. ***Isoperla petersoni*** is abundant in the upper 100 m of a Utah stream where the moss ***Hygrohypnum bestii*** (Figure 74) provides heavy cover on the substrate (Hales & Gaufin 1971). ***Isoperla grammatica*** (Figure 75) seems to be more common elsewhere than among mosses, but in her study of the River Liffey, Ireland, Frost (1942) found it to be the dominant moss-dwelling stonefly in the alkaline station of her study. Percival and Whitehead (1929) likewise found it to form denser populations among mosses than among stones. Langford and Bray (1969) reported it to have its largest numbers among the moss ***Platyhypnidium riparioides*** (Figure 62) in Britain, citing Brinck's (1949) comment that it has the widest ecological amplitude of all Swedish **Plecoptera**. This is a species that is common among submerged bryophytes in the River Rajcianka, Slovakia, but unlike some stoneflies, it is absent among the wet emergent mosses (Krno 1990). The same relationship of confinement to submersed bryophytes is true for ***Isoperla oxylepis*** and ***I. sudetica***. Krno and Sporka (2003) found that ***Isoperla sudetica*** in the High Tatra of Slovakia depends on the detritus collected by mosses. This stonefly is most productive in winter when the brown trout is not actively feeding.

Figure 74. ***Hygrohypnum bestii***, home to ***Isoperla petersoni*** in a Utah, USA, stream. Photo by Robin Bovey, with permission.

Figure 75. ***Isoperla grammatica*** naiad, a stonefly whose preference for mosses varies among streams. Photo by Urmas Kruus, with permission.

In the Nearctic, Nelson and Kondratieff (1983) found ***Isoperla major*** only at the source of a stream where naiads hid under large, moss-covered cobble. In Appalachian Mountain streams, ***Diploperla duplicata*** (Figure 76) and ***Isoperla bilineata*** (Figure 77) both occur among mosses (Glime 1968). The former is the most common, occurring among all the major bryophytes [***Fontinalis dalecarlica*** (Figure 78), ***Hygroamblystegium fluviatile*** (Figure 89) – ***Platyhypnidium riparioides*** (Figure 62), ***Scapania undulata*** (Figure 7)]. What is surprising here is that these are mature naiads, not the tiny young ones.

Figure 76. ***Diploperla duplicata*** naiad, a common bryophyte inhabitant in Appalachian Mountain streams. Photo by Bob Henricks, with permission.

Figure 77. ***Isoperla bilineata*** naiad, a common bryophyte inhabitant in Appalachian Mountain streams. Photo by Royce Bitzer (<Iowa State Entomology Image Gallery>, with permission.

Figure 78. ***Fontinalis dalecarlica*** habitat Highlands, NC. Photo by Janice Glime.

In the Sturgeon River, northern Michigan, USA, ***Isoperla signata*** (Figure 79) had similar growth above and below a hydroelectric power plant, but the naiads were six times as abundant below the power plant (46 m^{-2} vs 7 m^{-2}) (Mundahl & Kraft 1988). Mundahl and Kraft suggested that the greater abundance below the dam may be from the rich growth of ***Fontinalis*** below the dam. These mosses were able to trap the detritus released from the dam and thus provide both cover and food for the stoneflies.

Figure 79. ***Isoperla signata*** naiad, a species that thrives on detritus collected by ***Fontinalis***. Photo by Royce Bitzer <Iowa State Entomology Image Gallery>, with permission.

In the High Tatra, Slovakia, ***Diura bicaudata*** (Figure 41) is dependent on detritus that collects among mosses (Krno & Sporka 2003). This species is common in both stream mosses and in lakes (Kamlet 1967).

In Estonia ***Perlodes microcephalus*** (Figure 80) occurs in stony and gravelly bottoms where ***Fontinalis*** (Figure 4) grows (Timm 2000). ***Perlodes intricatus*** in the High Tatra of Slovakia depends on the detritus that accumulates among mosses in streams (Krno & Sporka 2003). The mosses also provide them with shelter from the predatory brown trout.

Figure 80. ***Perlodes microcephalus*** naiad, a species that hangs out near ***Fontinalis*** in stony streams of Estonia. Photo by Niels Sloth, with permission.

Susulus venustus from California, USA, is one of the species that drums on mosses and other substrates to attract females (Bottorff *et al*. 1989). The male drumming call is 1-3 groups of bi-beats and is a unique pattern among the **Perlodidae**. After mating, the females fly to the dark detritus and moss substrate, then walk into the shallow water where they release their eggs.

Peltoperlidae – Roachflies

This family (~8-20 mm) did not appear in any of the published studies I found. This is understandable because their preferred habitat is flowing streams characterized by sediments, vascular plants, and detritus (Peltoperlidae 2014). However, I did find ***Peltoperla*** (Figure 81) occasionally among all the major bryophytes [***Fontinalis dalecarlica*** (Figure 78), ***Hygroamblystegium fluviatile*** (Figure 89) – ***Platyhypnidium riparioides*** (Figure 62), and ***Scapania undulata*** (Figure 7)] I studied in the Appalachian Mountain, USA, streams (Glime 1968). It typically preferred the mat habit.

Figure 81. ***Peltoperla*** naiad, an occasional dweller among bryophytes in streams in the Appalachian Mountains, USA. Photo by Bob Henricks, with permission.

Gripopterygidae

This family has become terrestrialized to the degree that the naiads usually live among damp substrata on land (McLellan 1977). But the naiads of ***Zelandoperla fenestrata*** (10-14 mm; see Figure 82) are widely distributed, especially among mosses, in stony streams in the mountains of New Zealand (Winterbourn & Gregson 1981). This species is most abundant among the ***Fissidens rigidulus*** (Figure 83) in the torrential water mid stream (Cowie & Winterbourn 1979). These naiads feed on the diatoms and detritus collected there.

Figure 82. ***Zelandoperla pennulata*** from the Takitimu Mountains, N. Z. Photo by Brian Patrick, with permission.

Figure 83. ***Fissidens rigidulus***, home to ***Zelandoperla fenestrata*** in New Zealand. Photo by Bill & Nancy Malcolm, with permission.

Cardioperla nigrifrons occurs in large numbers among surface mosses in a fast waterfall (45° angle) in Tasmania (Dean & Cartwright 1992).

South American Plecoptera, like those from New Zealand and Tasmania, are often different from the ones found in the Northern Hemisphere. ***Alfonsoperla flinti*** occurs among mosses in high waterfalls in Chile (McLellan & Zwick 2007). Illies (1963) found this species among mosses on the stream beds.

Zelandobius (Figure 84-Figure 85) is one of the common small stoneflies in New Zealand, starting its life at about 0.6 mm length, with adults 7-11 mm (Death 1990). It is amphibious and is able to climb out of the water and move about among the emergent wet mosses of streams (Auckland Council 2011).

Figure 84. ***Zelandobius*** sp. naiad, a genus that can climb out of the water to explore among emergent mosses. Photo from Landcare Research, through Creative Commons.

Figure 85. ***Zelandobius illiesi*** naiad, a genus that can climb out of the water to explore among emergent mosses. Photo from Landcare Research, through Creative Commons.

Pteronarcyidae – Giant Stoneflies

This family has the largest members (15-70 mm) among the **Plecoptera**, hence the common name. The largest stonefly I have encountered among mosses is ***Pteronarcys biloba*** (Figure 86) (Glime 1968, 1994). The large size of older individuals seems to preclude their habitation among smaller mosses like ***Platyhypnidium riparioides*** (Figure 62) and ***Hygroamblystegium fluviatile*** (Figure 89). But within the larger spaces among branches of ***Fontinalis*** species (Figure 4) the genus is able to move about more freely. One feature that may contribute to its ability to hide deep within the streaming ***Fontinalis*** away from the rapid current is its possession of numerous thoracic tufts of gills that resemble pompoms (Figure 88). These gill tufts facilitate obtaining oxygen and permit the stoneflies to live deep within the clump, out of the rapid flow that brings oxygen to surface dwellers. On the other hand, small individuals (early instars) of ***Pteronarcys proteus*** (Figure 87-Figure 88) are able to live among the smaller spaces of ***Hygroamblystegium fluviatile*** (Figure 89).

Figure 86. ***Pteronarcys biloba*** naiad, a ***Fontinalis*** dweller in the Appalachian Mountain streams. Photo by Donald S. Chandler, with permission.

Figure 87. ***Pteronarcys proteus*** naiad, an occasional occupant of ***Hygroamblystegium fluviatile*** in the Appalachian Mountains. Photo by Jason Neuswanger, with permission.

Figure 88. ***Pteronarcys proteus*** naiad, an occasional moss dweller, showing well-developed thoracic gills. Photo by Jason Neuswanger, with permission.

Muttkowski and Smith (1929) found mosses, along with diatoms (especially ***Epithemia***, Figure 90) in the guts of five out of six ***Pteronarcys californica*** (Figure 91) examined from among mosses in strong rapids of trout streams in Yellowstone National Park, USA. The researchers were surprised that this large stonefly was a vegetarian, with only 4% of its diet consisting of animals; instead the guts contained over 50% detritus.

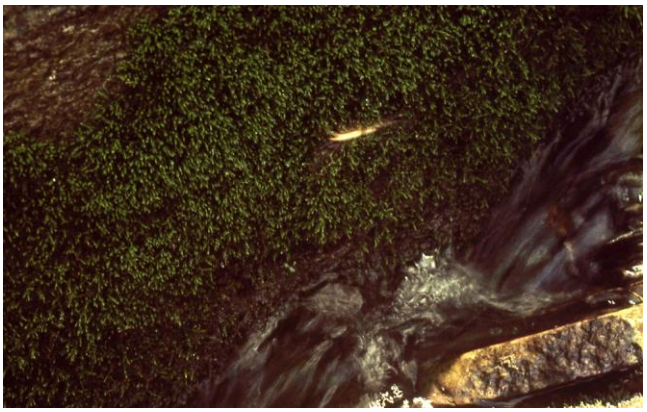

Figure 89. ***Hygroamblystegium fluviatile*** in the Appalachian Mountains, USA, a moss that provides spaces too small for ***Pteronarcys biloba***, but houses smaller individuals of ***P. proteus***. Photo by Janice Glime.

Figure 90. ***Epithemia*** on a filamentous alga. Photo by Jason Oyadomari, with permission.

Figure 91. ***Pteronarcys californica*** naiad, a bryophyte consumer. Photo by Bob Henricks, with permission.

Several researchers have attempted to explain these diet preferences. ***Pteronarcys pictetii*** (Figure 92) and ***P. californica*** (Figure 91) have a diet that is 50-80% detritus during most of the year (Martin *et al*. 1981). Lechleitner and Kondratieff (1983) found that ***P. californica*** naiads switch from a diet of 40% algae in October to one with more mosses and blackflies in December. However they increase their moss intake when their normal food is insufficient. Martin and coworkers (1981) found that the midgut **proteolytic** (breaking down of proteins into simpler compounds) activity of the naiads is very high, similar to that in other aquatic detritivores. But the conditions differ from those of detritus-feeding **Diptera** and lack the digestive systems that are adapted for digesting proteins that are bound to **polyphenols** (compounds such as tannic acid composed of multiple phenol structures and that have toxic, metabolic, and other biological properties). They furthermore are poorly adapted for digesting the major **polysaccharides** (carbohydrate such as starch, cellulose, or glycogen whose molecules consist of a number of sugar molecules bonded together) present in detritus. Polysaccharide digestion is presumed to be restricted to α-1,4-glucans, the primary storage polysaccharide of higher plants, algae, and presumably bryophytes. But there seemed to be little enzymatic activity on the major structural polysaccharides of higher plants, suggesting that organisms that accompany the food items may help in the digestion.

Figure 92. ***Pteronarcys pictetii*** naiad, a detritus feeder. Photo from <Plecoptera.SpeciesFile.org> through Creative Commons.

Pteronarcella badia (Figure 93) is generally a detritus feeder in its early stages, but in later instars the naiads make mosses a substantial portion of their diet (Fuller & Stewart 1979). The other eight stonefly species examined from several Colorado, USA, rivers ate predominantly animals – **Chironomidae** (Figure 94), **Simuliidae** (Figure 95), and **Ephemeroptera** (see Chapter 11-4). Even though diets shifted for these other species as they developed, only ***Pteronarcella badia*** shifted to mosses (Fuller & Stewart 1977).

Figure 93. ***Pteronarcella badia*** naiad, a species that switches to feeding on mosses as it gets older. Photo by Arlo Pelegrin, with permission.

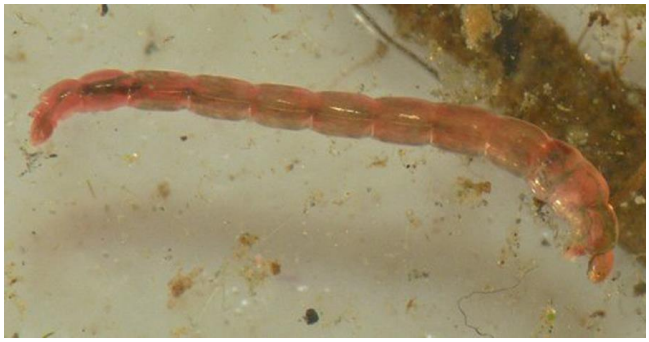

Figure 94. **Chironomidae** larva, a typical part of stonefly diet. Photo by Bob Armstrong.

Figure 95. **Simuliidae** larvae on rock, common food for stoneflies. Photo by Jason Neuswanger, with permission.

Hassage *et al*. (1988) examined feeding behavior in the shredder species ***Pteronarcella badia*** and found that in small groups (1-4) the naiads distributed themselves in proportion to the available surface area. However, when the group was increased to 14, they formed aggregations that often involved body contact. Addition of the predator ***Claassenia sabulosa*** (Figure 96) cause them to exhibit a random distribution. It would be interesting to see if this behavior differs on rocks vs bryophytes.

Figure 96. ***Claassenia sabulosa*** naiad, a predator on ***Pteronarcys badia***. Photo by Bob Henricks, with permission.

Summary

The **Plecoptera** (stoneflies) are **hemimetabolous**, having eggs, naiads, and adults. Some have gills and others are gill-less, requiring high oxygen concentrations. This requirement for oxygen makes them more common in cold, rapid streams. The naiads are mostly night active. Many of the smaller **Plecoptera** are moss dwellers, especially in young stages, where they eat mostly **detritus** and **periphyton**, but some eat bryophytes.

The stoneflies use the bryophytes for depositing eggs, escaping the drift, protection and food source during early instars, and emergence. Adults of some use the bryophytes as a substrate for attracting females – the males drum their abdomens on the mosses. Some stoneflies, however, emerge in the winter, often climbing out of the water on emergent bryophytes, and can be seen on the snow.

The **Nemouridae** and **Leuctridae** are the most common families among bryophytes, although in some locations the **Taeniopterygidae** are abundant. The **Notonemouridae** is a somewhat terrestrialized moss-dwelling family restricted to the Southern Hemisphere. In New Zealand one can find **Gripopterygidae** among stream mosses, although this stonefly family is mostly terrestrialized. Large stoneflies like the **Pteronarcyidae** are usually absent in the small spaces of most bryophytes, but they are able to maneuver among the larger branches of ***Fontinalis***. Other families that include regular moss dwellers are **Capniidae**, **Chloroperlidae**, **Perlidae**, **Perlodidae**, and **Peltoperlidae**.

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CHAPTER 11-7
AQUATIC INSECTS: HEMIMETABOLA – HEMIPTERA

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CHAPTER 11-7
AQUATIC INSECTS:
HEMIMETABOLA – HEMIPTERA

Figure 1. ***Pachybrachius luridus***, a species of bogs and fens. Photo by Tristan Bantock, with permission.

HEMIPTERA – True Bugs, Cicadas, Hoppers, Aphids, and Allies

Aquatic bryophyte dwellers are rare in this insect order. Most members are either free swimming or skate on the top of the surface tension. However, bogs and bog pools do provide a suitable habitat for some species. Rédei *et al*. (2003) found no specificity for species among ***Sphagnum*** (Figure 2) or any species that was characteristic for that moss. ***Ceratocombus coleoptratus*** (Figure 6-Figure 7) and ***Hebrus ruficeps*** (Figure 13) had the highest dominance in that habitat, with ***Cryptostemma pusillimum*** (Figure 3), **Saldidae** (Figure 27-Figure 31), and **Miridae** (Figure 4) also occurring here. They considered the similarity of the bog community to that of the soil moss community to be due to the low relative dominance of larvae from the large family **Lygaeidae** (Figure 32-Figure 37) in both habitats.

Members of this family lack gills and their immature stages are nymphs, placing them in the **Hemimetabola**. Some breathe by a **plastron** (mechanism for carrying an air layer next to the body).

Figure 2. ***Sphagnum fuscum***, a genus that is home for a few members of the **Hemiptera**. Photo by Michael Lüth, with permission.

Figure 3. ***Cryptostemma*** sp. ***Cryptostemma pusillimum*** is among the **Hemiptera** with the highest dominance in bogs. Photo by Michael F. Schönitzer, through Creative Commons.

Figure 4. ***Campyloneura virgula*** (**Miridae**), a dominant species in bogs. Photo by Valter Jacinto, through Creative Commons.

Cicadellidae – Leafhoppers

This family was previously placed in the Homoptera, but is now included in the order **Hemiptera**. It is not, however, a true bug.

This is the second largest hemipteran family. The members live primarily on land (Leafhopper 2015). They use the hairs on their legs to facilitate a secretion over their bodies that acts as a water repellent and carrier of pheromones. They obtain their food by sucking sap from a variety of plants.

Megophthalmus scanicus (Figure 5; 3-4 mm) is a widespread species in the UK where it overwinters among mosses (Edwards 1874-1879). This is a species of wide habitat variety, including both wet and dry habitats.

Figure 5. ***Megophthalmus scanicus*** nymph, a species that overwinters among mosses. Photo from <www.biolib.cz>, through public domain.

Ceratocombidae

The **Ceratocombidae** is mostly tropical and lives primarily in leaf litter along water margins. This is a group of small bugs, 1.5-3.0 mm, mostly dull-colored, from yellowish to dark brown (Livermore & Rider 2015). These insects require permanently damp conditions such as those provided by the wet mosses close to running water. Members of this family overwinter as adults, requiring the permanent wetness of habitats like wet mosses near running water (Howe 2004). ***Ceratocombus brevipennis*** (see Figure 6) is one of these moss dwellers in central and southern Europe (Michael Münch personal communication 30 October 2014).

Figure 6. ***Ceratocombus coleoptratus***, an inhabitant of wet mosses in Europe. Michael Münch <www.insekten-sachsen.de>, with permission.

Ceratocombus coleoptratus (Figure 7) was rare in the UK even as early as the 1870's (Edwards 1874-1879). It lives among mosses, perhaps being under-collected and accounting for its presumed rarity. Fortunately it still

exists, living in moss cushions, needle litter, and dead plant material at the edges of forests (Münch 2012). It also occasionally lives in moss beds in swampy meadows.

Figure 7. ***Ceratocombus coleoptratus*** wending its way through its moss home. Photo by Michael Münch, with permission.

Dipsocoridae – Jumping Ground Bugs

This family (Figure 3) of tiny bugs (2-3 mm) is found mostly among wet mosses by running water in Wales (Howe 2004). These bugs, despite their small size, are predators with rapid movements that typically live near streams and rivers.

In particular, some species of the genus ***Pachycoleus*** are closely associated with bryophytes in central and southern Europe (Michael Münch pers. comm. 30 October 2014). In Wales, it is ***Pachycoleus waltli*** that is common among the wet mosses (Howe 2004). Kment *et al*. (2013) found ***P. waltli*** among wet mosses that covered dead branches along a stream. This species is typical of permanently wet to very wet moss [***Sphagnum*** (Figure 2), ***Hypnum*** (Figure 8), ***Brachythecium*** (Figure 9), ***Cratoneuron*** (Figure 10)] and may stay fully submerged.

Figure 8. ***Hypnum cupressiforme***, a home for ***Pachycoleus waltli***. Photo by Li Zhang, with permission.

Figure 9. ***Brachythecium plumosum***, a home for ***Pachycoleus waltli***. Photo by Janice Glime.

Figure 10. ***Cratoneuron commutatum***, a wet habitat where one might find members of the genus ***Pachycoleus***. Photo by Michael Lüth, with permission.

Using Berlese funnels to sample in Hungarian bogs, Rédei *et al*. (2003) found ***Cryptostemma pusillimum*** (Figure 3) among the common **Hemiptera**.

Gerridae – Water Striders

The most distinctive feature of the **Gerridae** is their ability to skate about on the water surface. They are larger (~4-18 mm) than the other surface bugs described here. Their skating ability is possible due to hydrofuge (water-repelling) hairs, retractable claws, and long legs (Ward 1992). The hairs are arranged in hair piles with more than 1000 microhairs per mm. They cover the entire body, repelling water drops that could otherwise weigh them down.

Gerris is not a genus that finds mosses important in the water, instead skating on its surface. To my surprise, I read an old report of ***Gerris lacustris*** (Figure 11) hibernating under a terrestrial moss nearly a km from water! (Butler 1886). This species is a water strider – the spider-like insect that skates on the surface tension of quiet pools of ponds and streams. Furthermore, ***Gerris argentatus*** (Figure 12) occurs among wet mosses (Edwards 1874-1879).

Figure 11. ***Gerris lacustris*** on pond, a species that hibernates under terrestrial mosses. Photo by Jakub Rom through public domain.

Figure 12. ***Gerris argentatus***, a species that can be found among wet mosses. Photo by Niels Sloth, with permission.

Hebridae – Sphagnum Bugs, Velvet Water Bugs

The **Hebridae** are small insects (1.3-3.7 mm) of semiaquatic habitats, living mostly in moist detritus or among floating plants, wet moss, or margins of still waters (McClarin 2006). The **Hebridae** are most common among wet mosses (Howe 2004) and the genus ***Hebrus*** lays its eggs among mosses, hiding them in leaf axils, or between closely spaced leaves, where it uses a gelatinous glue to adhere them (Polhemus & Chapman 1979a). In the bogs and fens of Hungary the diversity of **Hemiptera** is very low when a large spatial area is considered (Rédei *et al.* 2003). This is because one wet moss species, ***Hebrus ruficeps*** (Figure 13), dominates, comprising 90% of the **Hemiptera** fauna!

Figure 13. ***Hebrus ruficeps***, a moss dweller in ***Sphagnum*** bogs that is able to survive the winter frozen in ice at the water surface. Photo by Ruth Ahlburg, with permission.

Members of ***Hebrus*** are small bugs, only 1.3-3.7 mm long (Ramel 2014). Their preferred habitat is ponds with ***Sphagnum*** (Figure 14) or along margins of streams. Although the genus has about 150 species worldwide, mostly in tropical environments of Southeast Asia, the UK has only two species, both moss dwellers.

Figure 14. ***Sphagnum cuspidatum***, in a genus that is home to ***Hebrus*** in ponds. Photo by Blanka Shaw, with permission.

Hebrus concinnus was observed laying its eggs between the leaves of mosses where the eggs were partially concealed (Hungerford 1920). Edwards (1874-1879) reported ***Hebrus pusillus*** (Figure 15) from wet moss. Münch (2013) likewise considered ***H. pusillus*** a moss dweller, but that it also lives on the water surface and at the edge of the water where it reproduces. Howe (2004) reported that it is associated with ***Sphagnum*** (Figure 2, Figure 14) and other mosses.

Figure 15. ***Hebrus pusillus*** on a moss. Photo by Michael Münch, with permission.

But not all members of ***Hebrus*** live along streams. ***Hebrus pusillus*** (Figure 15) and ***H. ruficeps*** (Figure 13) both occur among ***Sphagnum*** (Figure 2) in bogs (Butler 1886). ***Hebrus ruficeps*** is able to survive the winter frozen in ice at the water surface (Ramel 2014). Butler (1886) recommended tearing a handful of the moss into small pieces and examining each carefully to find these tiny bugs.

The genus ***Merragata*** (Figure 16), like ***Hebrus***, lays its eggs on moss leaves, or under algae, where they incubate for 8-12 days (Polhemus & Chapman 1979a).

Figure 16. ***Merragata hebroides***, a genus that lays its eggs on moss leaves or under algae. Photo by Don Loarie, through Creative Commons.

Mesoveliidae – Water Treaders

These are small usually greenish or yellowish surface bugs of about 2-5 mm length. ***Mesovelia mulsanti*** (Figure 17) prefers lakes and bogs with lots of surface vegetation where they live on mosses and other floating plants (Figure 18; Menke 1979). They feed on lily pads and easily run on the surface of the water. ***Mesovelia amoena*** (Figure 19), on the other hand, occurs on mosses in hot spring caves of Death Valley and avoids the water unless disturbed (Hungerford 1917; Polhemus & Chapman 1979b). At least some populations must be **parthenogenetic** (giving birth without fertilization) because only the female of ***Mesovelia amoena*** occurs in Hawaii.

Figure 17. ***Mesovelia mulsanti***, a bog dweller. Photo by Matt Bertone, through Creative Commons.

Figure 18. ***Mesovelia*** sp. blending with several floating duckweed species. Photo by Steve Nanz, through Creative Commons.

Figure 19. ***Mesovelia amoena***, a moss dweller, including those in a hot spring cave. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

Veliidae – Small Water Striders, Riffle Bugs

The family **Veliidae** (1-12 mm) is best adapted for surface activity, walking easily on the surface tension. The surface tension facilitates their detection of food items (small arthropods) by vibrating as the prey organisms move about (McLeod 2005).

In my studies of Appalachian Mountain, USA, stream bryophyte inhabitants, ***Microvelia*** (Figure 20-Figure 22) was the only member of **Hemiptera** that I found (Glime 1968). The genus ***Microvelia*** has a unique means of locomotion. Instead of clambering about on the water surface by paddling with its middle legs like other **Hemiptera**, it exudes a fluid that reduces the surface tension in the water behind it. This causes the surface there to expand and push it forward.

Microvelia and ***Paravelia*** species lay their eggs on such floating objects as moss, duckweed, and living or dead leaves just above or below the water surface (Polhemus & Chapman 1979d). ***Microvelia reticulata*** (Figure 20) overwinters as an adult (Ramel 2014). It lays eggs in mosses and feeds on tiny invertebrates, including mosquito eggs.

Figure 20. ***Microvelia reticulata***, a species that lays its eggs among mosses. Photo by Niels Sloth, with permission.

Microvelia buenoi (Figure 21) lives among mosses at the edge of a pond in Indiana, USA (Bamd 2007), where it was sampled using a Berlese funnel. In Florida, Herring (1950) found ***Microvelia hinei*** (Figure 22) in mats of ***Sphagnum*** (Figure 14) in acid swamps and bog streams. This species illustrates a short incubation time of only 6.41 days (mean) (Taylor & McPherson 2003). Nymphal development requires only 25 days for its 5 **instars** (developmental stages).

Figure 21. ***Microvelia buenoi***, a species that occurs among mosses at the edge of a pond. Photo by Tim Faasen, with permission.

Figure 22. ***Microvelia hinei***, an inhabitant of ***Sphagnum*** mats in bogs. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Macroveliidae – Macroveliid Shore Bugs

This new world family never exceeds 5 mm in length. ***Macrovelia hornii*** (Figure 23; ~4.2 mm) nymphs and adults live among mosses and other floating vegetation at the water's edge in protected niches behind rocks or logs or among debris (Usinger 1956; Menke 1979). Polhemus and Chapman (1979c) consider this species to be common among the mosses of California springs and seeps. They lay their eggs glued to wet mosses (Menke 1979).

Figure 23. ***Macrovelia*** sp. Some species live among mosses in crevices at the water's edge Photo by Paul A. Rude, through Creative Commons.

Corixidae – Water Boatmen

This family ranges 2-14 mm and is free-swimming in ponds and slow-moving streams (Corixidae 2014). Thus, they are not typically among the bryophyte dwellers. Unlike most aquatic **Hemiptera**, they are predominantly herbivores, feeding on algae and aquatic plants. And, Macan and Maudsley (1968) report ***Micronecta poweri*** (Figure 24) to be associated with vegetation, including ***Fontinalis*** (Figure 25). The **Corixidae** inject enzymes into the plants (or animals) through the strawlike mouthparts (Figure 26), then suck the cell contents back through that same straw (Corixidae 2014).

Figure 24. ***Micronecta poweri***, a water boatman that sometimes lives among ***Fontinalis***. Photo by Urmas Kruus, with permission.

Figure 25. ***Fontinalis antipyretica***, a genus that is home to ***Micronecta poweri***. Photo by Bas Kers, through Creative Commons.

Figure 26. **Corixidae** eating mosquito pupa. Photo by Bob Armstrong, with permission.

Saldidae – Shore Bugs

The **Saldidae** are small to medium in size (2-8 mm) (Saldidae 2013). ***Salda*** (Figure 27) is known as a bog-moss dweller at pond margins (Butler 1886). ***Salda morio*** and ***S. muelleri*** live in bog pond margins (Spuņģis 2009) among mosses (Michael Münch pers. comm. 30 October 2014). ***Salda littoralis*** occurs in salt marshes and tidal zones, where it hides under marine algae at low tide and migrates to the edge of the water in high tide, but it also lives in freshwater habitats (Spuņģis 2009) where it often associates with bryophytes, including living among ***Sphagnum*** (Figure 14) in a mountain lake in the Italian Alps (Michael Münch pers. comm. 30 October 2014). It will occasionally submerse into the water (Polhemus 1976).

Figure 27. ***Salda lugubris***, member of a genus that has bog moss dwellers. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

Saldula pallipes (Figure 28) lays its eggs at the bases of mosses or in between their leaves at the edges of ponds (Usinger 1956).

Figure 28. ***Saldula pallipes*** lays its eggs at the bases or between leaves of mosses at the edges of ponds. Photo by Charlie Eiseman, through Creative Commons.

Chartoscirta cocksii (=*Salda cocksii*; Figure 29) lives in ponds, mossy areas, and wetlands. Michael Münch (pers. comm. 30 October 2014) found it in a swamp among a taller moss (not ***Sphagnum***). In early surveys, ***Chartoscirta cocksii*** was the primary hemipteran among ***Sphagnum*** (Figure 2, Figure 29) in the UK (Butler 1886). This tiny black bug has huge eyes and stout antennae, making a striking find. Butler recommends putting mud, mosses, and dead leaves in a box to watch how many saldids will hatch out. This species will also take an occasional dip in the pools of the bog (Polhemus 1976).

Figure 29. ***Chartoscirta cocksii*** on ***Sphagnum papillosum***. Photo by Barry Stewart, with permission.

Chartoscirta elegantula (Figure 30) occurs between tide marks, but it also can be common among ***Sphagnum*** (Figure 2) (Michael Münch pers. comm. 30 October 2014). Like ***Gerris lacustris***, it migrates to overwinter in dry moss or leaves on land far from its summer habitat.

Figure 30. ***Chartoscirta elegantula elegantula***, a species that often migrates from the intertidal zone to overwinter among dry mosses. Photo by Sanjo, through Creative Commons.

Ioscytus nasti (Figure 31) occurs in bogs in North America (Usinger 1956). This is a poorly known genus and may provide some surprises in the bogs.

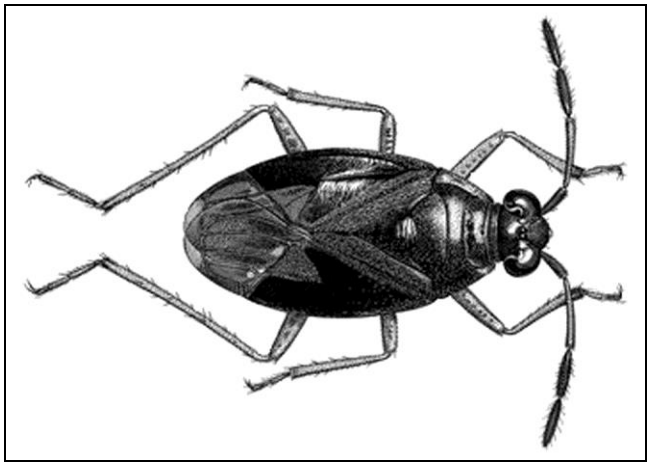

Figure 31. ***Ioscytus nasti***, a bog inhabitant. Image from Smithsonian Institution, through Creative Commons.

Lygaeidae – Seed Bugs, Cinch Bugs

This family of bugs, ranging 4-20 mm (Lygaeidae 2015), feeds primarily on seeds. Hence, bryophytes do not provide an ideal habitat. Nevertheless, the family has several bog and fen dwellers (Michael Münch pers. comm. 30 October 2014). Among these are ***Scolopostethus pilosus*** (Figure 32) in calcareous fens, ***Cymus glandicolor*** (Figure 33) in fens, ***Ligyrocoris sylvestris*** (Figure 34) in hill moors, ***Pachybrachius luridus*** (Figure 35) in bogs and fens, ***P. fracticollis*** (Figure 36) rare in bogs, fens, and wet meadows (Spuņģis 2009), all among mosses (Michael Münch pers. comm. 30 October 2014). ***Scolopostethus puberulus*** (Figure 37), on the other hand, lives primarily in deciduous forests, but also in **mesic** meadows (environment with moderate amount of moisture) (Spuņģis 2009), as a moss dweller (Michael Münch pers. comm. 30 October 2014).

Figure 32. ***Scolopostethus pilosus***, a moss dweller in calcareous fens. Photo by Boris Loboda, with permission.

Figure 33. ***Cymus glandicolor***, a moss dweller in fens. Photo by Tristan Bantock, with permission.

Figure 34. ***Ligyrocoris sylvestris***, a moss dweller in hill moors. Photo by Tom Murray, through Creative Commons.

Figure 35. ***Pachybrachius luridus***, a moss dweller in bogs and fens. Photo by Tristan Bantock, with permission.

Figure 36. ***Pachybrachius fracticollis***, a rare moss dweller in bogs, fens, and wet meadows. Photo by Barry Stewart, with permission.

Figure 37. ***Scolopostethus puberulus***. Photo by Michael Münch <www.insekten-sachsen.de>, with permission.

Rhyparochromidae – Dirt-colored Seed Bugs

Like the Lygaeidae, the **Rhyparochromidae** feed primarily on seeds, making bryophytes less than ideal habitats. ***Rhyparochromus pini*** (Figure 38) has adults 7-8 mm in length (British Bugs 2015). Most in Great Britain live in heathland, often under the heath; others live on sand dunes. However, Spuņģis (2009) found that this species also lives in bogs and fens.

Figure 38. ***Rhyparochromus pini*** nymph, an inhabitant of bogs and fens. Photo by Tristan Bantock, with permission.

Summary

The Homoptera have been moved into the order **Hemiptera** and the family **Cicadellidae** has a few members that use wet mosses to overwinter.

The true bugs have more aquatic members, but few are true bryophyte dwellers. The families **Ceratocombidae** and **Dipsocoridae** require permanently damp conditions and therefore many live in wet mosses. The surface-dwelling **Gerridae** sometimes spend the winter far from water among bryophytes. The **Hebridae** are frequent bryophyte dwellers among wet mosses and some lay their eggs there; others live in bogs. **Mesoveliidae** occur in lakes, bogs, and among mosses of hot spring caves. Some **Veliidae** lay their eggs on mosses and live among them in pools, acid swamps, and bog streams. Macroveliidae are more terrestrial but may live among mosses as nymphs. The **Saldidae** have some species that prefer bog pond margins among the mosses; others live among the taller bog bryophytes. Even the **Lygaeidae** and **Rhyparochromidae** occur among mosses in bogs. The larger, free-swimming **Corixidae** can occur among ***Fontinalis*** in slow-moving water.

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CHAPTER 11-8
AQUATIC INSECTS: HOLOMETABOLA – NEUROPTERA AND MEGALOPTERA

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CHAPTER 11-8
AQUATIC INSECTS: HOLOMETABOLA – NEUROPTERA AND MEGALOPTERA

Figure 1. ***Nigronia serricornis*** larva (**Megaloptera**), a species that sometimes pupates in mosses. Photo by Jason Neuswanger, with permission.

HOLOMETABOLA

The **holometabolous** insects are those with a complete life cycle – egg/embryo > larva > pupa > adult. These insects typically spend only part of the life cycle in the water. Some lay their eggs near water and larvae develop in the water. Some have eggs, larvae, and pupae in the water, but their emerging adults break through the water surface and climb onto land to emerge. For most, adult life and mating occur on land.

NEUROPTERA – Net-winged Insects

Neuroptera literally means nerve wings, so-named because of the prominent wing veins of the adults. This order is not well represented among bryophytes, and only the larvae are associated with aquatic habitats.

Osmylidae

On continents other than North America a small family, the **Osmylidae** (Figure 2-Figure 6), occurs among mosses and organic matter in and near streams (Flint 1977). ***Osmylus fulvicephalus*** (Figure 2) is the only species known in the UK, likewise living among mosses of streambanks (Elliott *et al*. 1996) and seeking food there (NatureSpot 2015). The adults (Figure 3; 25 mm long including wings) don't stray far from water but are not aquatic. The females lay their eggs on overhanging plants, tree trunks, or stones (Osmylidae 2014), and especially on mosses (Elliott *et al.* 1996) near water, laying about 30 eggs either singly or in pairs. Larvae leave the egg site within 1-3 days to burrow into mosses. Larvae may live in or out of water, but pupation is on land, lasting 7-18 days. If the larvae are submersed, they crawl out of the water (Ward 1965). If the moss is submersed, they burrow deeply into it, but within 8-28 days of submersion they die. Adults live two weeks to three months, depending on species and location.

Figure 2. ***Osmylus fulvicephalus*** larva, a species that lives among mosses on streambanks and feeds there. Photo by Walter Pfliegler, with permission.

Figure 3. ***Osmylus fulvicephalus*** adult that lays its eggs on overhanging vegetation. Larvae live among streambank mosses. Photo through Creative Commons.

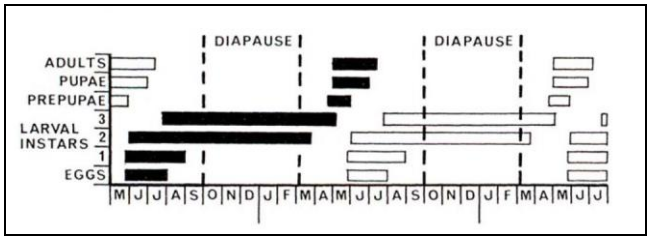

Figure 4. Phenological events (cyclic and seasonal natural phenomena, especially in relation to climate) of the life cycle of ***Osmylus fulvicephalus***. From Elliott *et al*. 1996.

Osmylus fulvicephalus (Figure 3) is controversial in that its larvae live in wet mosses, but drown in 8-28 days of submersion (Elliott *et al.* 1996). Nevertheless, they do enter the water in search of food. It seems safe to say, however, that their relationship with mosses is damp, but not aquatic. The larva feeds among these mosses. When movement is detected, it jabs at it with the long proboscis, then injects it with a salivary secretion that paralyzes it. A chironomid larva is paralyzed within 10 seconds. The ***O. fulvicephalus*** then sucks out the interior of the prey. The larvae stop eating during mid autumn and burrow down to the moss rhizoids to hibernate for the winter. Fortunately, in this state they can survive occasional submersion in water, thus surviving **spates** (sudden flood in a river, especially one caused by heavy rains or melting snow). In spring they spin a silken cocoon, sometimes incorporating bits of moss in the cocoon. Just before pupation the long jaws break off (Figure 5). The pupa becomes immobile during pupation. It grows a pair of mandibles that it uses to cut its way out of the cocoon.

Figure 5. ***Osmylus fulvicephalus*** larva showing large jaws. Photo by Walter Pfliegler, with permission.

Like ***Osmylus fulvicephalus*** (Figure 2-Figure 5), ***Kempynus*** sp. (Figure 6) in the Southern Alps of New Zealand is somewhat amphibious, living at the edge between water and land (Cowie & Winterbourn 1979). In springbrooks it lives in clumps of the mosses ***Acrophyllum quadrifarium*** (=*Pterygophyllum quadrifarium*; Figure 7) and ***Cratoneuropsis relaxa*** (Figure 8).

Figure 6. ***Kempynus*** sp larva, member of the small family **Osmylidae** that inhabits mosses near streams. Photo by Stephen Moore, Landcare Research NZ, with permission.

Figure 7. ***Pterygophyllum quadrifarium***, a moss habitat for ***Kempynus*** sp. at stream borders and in springbrooks in New Zealand. Photo by Bill and Nancy Malcolm, with permission.

Figure 8. ***Cratoneuropsis relaxa***, a moss habitat for ***Kempynus*** sp. at stream borders and in springbrooks in New Zealand. Photo by Tom Thekathyil, with permission.

Chrysopidae

There are a number of reports of the larvae of the green lacewing ***Leucochrysa pavida*** (Figure 9-Figure 12) using bits of lichen as camouflage (Tauber *et al.* 2009; Moskowitz & Golden 2012). In fact, Wilson and Methven (1997) found that the larvae at their Illinois, USA, site were somewhat specific in the species of lichens they chose. But Slocum and Lawrey (1976) found that this insect was not totally specific. In addition to the lichens, it also includes pieces of bark, angiosperm pollen, fungal spores, insect debris, and (of course) bryophyte gametophytes. Slocum and Lawrey demonstrated that the lichens, at least, are still alive and that they have photosynthetic rates equal or greater than those same lichen species still growing on a bark substrate. Furthermore, these lichen propagules are still viable when the cocoons are attached to the bark, giving the lichens the opportunity and establish in this new location. Unfortunately, there are no similar studies on the bryophytes in this camouflage arrangement, but it at least provides the possibility for a means of dispersal.

Figure 9. ***Leucochrysa pavida*** larva with lichen back pack, showing its camouflage against tree bark lichens. Photo by Jim McCormac, with permission.

Figure 10. ***Leucochrysa pavida*** larva with lichen back pack, showing the legs and mandibles of the larva. Photo by Jim McCormac, with permission.

Figure 11. ***Leucochrysa pavida*** larva showing ventral side. Photo by Jim McCormac, with permission.

Figure 12. ***Leucochrysa pavida*** larva showing head and large mandibles of this carnivore. Photo by Jim McCormac, with permission.

MEGALOPTERA – Dobsonflies and Alderflies

Megaloptera means large wing; one adult is known with a wingspan of 21 cm, the largest of any aquatic insect in the world (Megaloptera 2014). The order is relatively small, and is close to the **Neuroptera**. Its members have

aquatic larvae, but they pupate on land in damp soil or under logs. The pupae are fully mobile and can defend themselves against predators with their large mandibles. Female adults lay 1000's of eggs on overhanging vegetation where larvae can drop into the water (Figure 13). The adults often live only a few hours and usually don't eat.

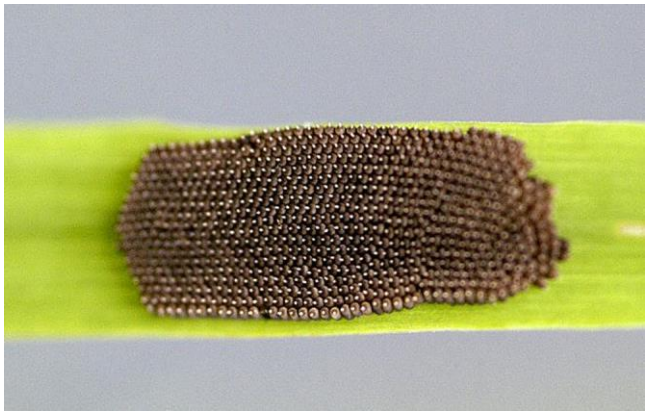

Figure 13. ***Sialis fuliginosa*** eggs. Photo by James K. Lindsey, with permission.

Sialidae – Alderflies

This is a small family that can be up to 25 mm long (Alderfly 2014). They occur sparsely worldwide with a concentration of known species in Europe (Sialidae 2015).

I have only found reference to one genus of bryophyte dwellers, ***Sialis*** (Figure 13-Figure 17) (Lithner *et al*. 1995). I likewise found this genus occasionally among bryophytes in Appalachian Mountain, USA, streams (Glime 1968). It has aquatic larvae, but adults are terrestrial and lay eggs near water (Alderfly 2014). Fully grown larvae of ***Sialis*** pupate in soil, mosses, under stones, and other locations, usually near water. In Canada, after about one month the adults appear. ***Sialis nigripes*** prefers mosses for egg laying (Elliott *et al*. 1996). ***Sialis lutaria*** (Figure 15-Figure 17) was used in a study comparing heavy metal accumulation in mosses (***Fontinalis*** spp.; Figure 18), insects, and fish (Lithner *et al*. 1995).

Figure 14. ***Sialis*** adult, a genus that sometimes pupates and lays eggs among streamside bryophytes. Photo by Patrick Coin, through Wikimedia Commons.

Figure 15. ***Sialis lutaria*** larva, the aquatic stage that migrates into the water, sometimes from streamside bryophytes. Photo by André Karwath, through Creative Commons.

Figure 16. ***Sialis lutaria*** adult. Photo ©entomart, through Creative Commons.

Figure 17. ***Sialis lutaria*** adults mating. Photo by James K. Lindsey, with permission.

On the South African Cape, pupae of **Sialidae** along streams or waterfalls live in ***Sphagnum*** (Figure 19) and other mosses (Barnard 1931). These pupae require a wet, but not submersed, habitat, so the mosses must be soaking wet.

Figure 18. ***Fontinalis antipyretica***, home to numerous kinds of insects and useful for comparing heavy metal accumulation. Photo by Malcolm Storey, through Creative Commons.

Figure 19. ***Sphagnum fimbriatum***, a genus that lives in Africa and is a potential home for pupae of **Sialidae**. Photo by Blanka Shaw, with permission.

Corydalidae- Dobsonflies and Fishflies

This family occurs mostly in the Northern Hemisphere and in South America, including both temperate and tropics (Corydalidae 2014). Their body size is usually greater than 25 mm and ranges up to 80 mm (Penny *et al*. 1997; Bartlett 2004). The larvae are aquatic, are called hellgrammites, and are predators.

Nigronia, an aquatic member of the **Corydalidae**, is not typically a moss inhabitant, although I did occasionally find larvae of this genus among Appalachian Mountain stream bryophytes (Glime 1968). But like many other aquatic insects, ***Nigronia serricornis*** (Figure 20-Figure 21) pupates among mosses as well as under stones and logs (Needham *et al*. 1901). Likewise, ***Chauliodes pectinocornis*** (Figure 22) and ***C. rastricornis*** (Figure 24-Figure 24) pupate in these habitats. Pupation lasts about 2 weeks in these **Corydalidae**.

Figure 20. ***Nigronia serricornis*** larva showing powerful jaws. The aquatic larva often crawls into mosses to pupate. Photo by Jason Neuswanger, with permission.

Figure 21. ***Nigronia serricornis*** adult. Pupae of this insect often reside in mosses. Photo by Phil Myers, through Creative Commons.

Figure 22. ***Chauliodes pectinicornis*** adult, a species that lives in the water as larvae and pupates among mosses. Photo by Stephen Cresswell, with permission.

Figure 23. ***Chauliodes rastricornis*** larva, a species that may move to mosses to pupate. Photo by Tom Murray, through Creative Commons.

Figure 24. ***Chauliodes rastricornis*** adult, a species that lives in the water as larvae and pupates among mosses. Photo by Stephen Cresswell, with permission.

Summary

The **Holometabola** have a complete life cycle with egg, larva, pupa, and adult.

The **Neuroptera** are represented among aquatic bryophytes by only one family, the **Osmylidae**. The larvae of ***Osmylus*** may live among bryophytes in streams or on streambanks and obtain food there. Some species lay their eggs on mosses that overhang streams. Larvae bore into mosses in or out of the water. ***Kempynus*** species often live among mosses in springbrooks.

The **Megaloptera**, like the **Neuroptera**, have few aquatic bryophyte dwellers. ***Sialis*** (**Sialidae**) larvae occasionally occur among stream bryophytes; the pupae are often among terrestrial mosses. Some species lay eggs among mosses. Wet ***Sphagnum*** along streams or near waterfalls serves as a home for some **Sialidae**. Some members of ***Nigronia*** and ***Chauliodes***, both in the **Corydalidae**, pupate among mosses.

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CHAPTER 11-9
AQUATIC INSECTS: HOLOMETABOLA – COLEOPTERA, SUBORDER ADEPHAGA

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CHAPTER 11-9
AQUATIC INSECTS: HOLOMETABOLA – COLEOPTERA, SUBORDER ADEPHAGA

Figure 1. ***Lancetes angusticollis*** adults on moss, South Georgia in the Antarctic. ***Lancetes angusticollis*** has a two-year life cycle, with overwintering possible in three life stages – aquatic larvae, terrestrial pupae (not proven), and aquatic adults. Note the air supply at the tip of the abdomen. This external air supply makes it necessary for these beetles to cling to vegetation, when they are not swimming, to avoid floating to the surface, hence their use of mosses. Photo by Roger S. Key, with permission.

COLEOPTERA BACKGROUND

The Coleoptera seem to have a somewhat closer relationship to terrestrial life than other aquatic bryophyte dwellers. First of all, they get their air from the atmosphere or underwater plants where they grab an air bubble (Figure 2). They can accumulate air as bubbles under the **elytra** (hardened forewings; wing covers), through the **plastron** (breast plate breathing apparatus; Figure 3) (Oliveira de Sousa *et al*. 2012), or an anal bubble. The **plastron** is a ventral structure that acts as a physical gill by using various combinations of hairs, scales, and undulations projecting from the cuticle. This apparatus holds a thin layer of air along the outer surface of the body (Figure 3). In all three of these mechanisms, the nitrogen in the air bubble diffuses into the water slowly while the replacement oxygen diffuses into it 2-3 times as fast (Rich Merritt, pers. comm. 28 January 2015). Thus, as the insect uses up the oxygen from the bubble, the water replaces it by oxygen diffusion for a reasonable period of time. The CO_2 from respiration enters the bubble and rapidly diffuses into the water, having little effect on bubble size. Many beetles attach an anal gas bubble (Figure 1, Figure 18-Figure 19) that uses this diffusion mechanism. They may have hairs that help hold the bubble in place. (See **Elmidae** in Coleoptera, Suborder Polyphaga, for details of the plastron functioning in that family.)

Figure 2. ***Berosus luridus*** adult on moss where air bubbles from photosynthesis can be used to replenish the air supply. Photo by Tim Faasen, with permission.

Figure 3. ***Chaetarthria siminulum*** adult with plastron. When the plastron is full of air, the beetle must cling to vegetation in order to descend into the water column. Photo by Gerard Visser <www.microcosmos.nl>, with permission.

Nearly all aquatic **Coleoptera** go to land to pupate (Leech & Chandler 1956; Pennak 1978; Erman 1984), then return to the water as adults. Others clamber about on the surface of the plants. Some of these are associated with floating plants, including ***Ricciocarpos natans*** (Figure 4) (Scotland 1934). To get below the surface requires muscle action to break the surface tension (Leng 1913).

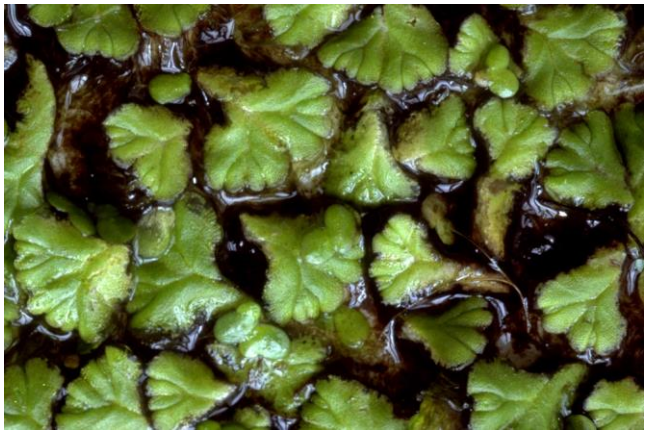

Figure 4. ***Ricciocarpos natans***, a floating liverwort. Photo by Jan-Peter Frahm, with permission.

Percival and Whitehead (1930) noted that the mosses in streams in the UK were very important to both larvae and adults of the small Coleoptera. In 1949, Badcock indicated that beetles were more common among mosses than associated with stones, especially loose stones. Ogbogu (2000) found **Coleoptera** among the insects associated with ***Fontinalis*** (Figure 5) in an intermittent reservoir spillway in Ile-Ife, Nigeria. Many of the **Coleoptera** in rivers of northwest Spain prefer moss as a substrate, as indicated by both species richness and abundance (Fernández-Diaz 2003; Sarr *et al*. 2013). They attributed this to the abundance of food available for the herbivores (Passos *et al*. 2003; Sarr *et al*. 2013). This applied particularly to the **Elmidae** and **Hydraenidae**.

Figure 5. ***Fontinalis antipyretica*** on rocks of a stream bed. Photo by Betsy St. Pierre, with permission.

Among the most common of these bryophyte dwellers are the **Elmidae** (Figure 6), small beetles only a few mm in length (Percival & Whitehead 1930; Glime 1994). But many studies miss the small **Coleoptera** that live among the bryophytes, necessitating special collecting techniques for such habitats as submerged roots, wood, and mosses (Zaťovičová *et al*. 2004). Zaťovičová and coworkers found 13-61% more species when they used qualitative sampling that included these habitats.

Figure 6. **Elmidae** adult, one of the most common of beetle families among bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Whereas mosses in streams and lakes are not especially important for beetles, bogs and fens have greater

species numbers. Some live in the acidic pools, some burrow into the moss mats, and some run about the surface. The **Dytiscidae** (Figure 18-Figure 55) are particularly important in the pools. These bog dwellers, although often not adapted to a submerged aquatic habitat, will be included here.

Jones (1950) did extensive gut analysis of insects from the River Rheidol and found that none of the **Coleoptera** had mosses (***Fontinalis antipyretica***, Figure 5) in their guts, although **Plecoptera** and **Trichoptera** did. Rather, these **Coleoptera** were all carnivores.

Suborder Adephaga

This suborder is comprised of a group of highly specialized beetles.

Carabidae – Ground Beetles

The **Carabidae** forms a large family (>40,000 species) (Ground Beetle 2015), ranging 0.7-66 mm long (Bartlett 2004a). Despite this large number of species, they are mostly either shiny black or metallic and have ridged elytra (Ground Beetle 2015). Their distribution is worldwide, but records from Africa and Asia are scant. Typical homes are under tree bark, under logs, and among rocks or sand by the edge of ponds and rivers. Many expel an especially noxious and painful liquid for their defense. They are predators, often rapidly chasing their prey, usually at night (Bartlett 2004a).

These are not aquatic beetles, but they do live in bogs (Boyce 2011). In Dartmoor, UK, ***Agonum ericeti*** (Figure 7) prefers mires that have both ***Sphagnum*** (Figure 7) hummocks and warm, bare peat. Here they run around on the bog surface and are one of the most "important" species in the bog. They occur only where there are abundant bog mosses.

Figure 7. ***Agonum ericeti*** adult, a mire dweller, on ***Sphagnum.*** Photo by Niels Sloth, with permission.

Pterostichus rhaeticus (Figure 8) prefers to live among ***Sphagnum*** (Figure 7) of a blanket bog (Boyce 2011). ***Pterostichus diligens*** (Figure 9) likewise lives in blanket bogs, but lives in litter as well as among mosses. ***Acupalpus dubius*** is sometimes restricted to the moss ***Drepanocladus aduncus*** (Kopecky 2001).

Figure 8. ***Pterostichus rhaeticus*** adult, a blanket-bog dweller. Photo by Niels Sloth, with permission.

Figure 9. ***Pterostichus diligens*** adult, an inhabitant of mosses and leaves in blanket bogs. Photo by Niels Sloth, with permission.

Figure 10. ***Acupalpus dubius*** on leafy liverworts and mosses. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 11. ***Drepanocladus aduncus***, home for ***Acupalpus dubius***. Photo by Bob Klips, with permission.

Gyrinidae – Whirligig Beetles

This family is aptly named for its behavior of skating in whirling patterns on the water surface. The most unusual feature of this family is the eyes. They are divided so that two eyes are above the water and two are below, protecting the beetles from predators above and permitting them to see what is beneath them (Gyrinidae 2015). Their size ranges 3 to 18 mm long (Whirligig Beetles 2014). They eat insects that fall into the water, sensing the vibrations of their struggles by using their antennae. They are worldwide, with a heavy concentration in Europe.

But even these insects sometimes use mosses. At least some members of the **Gyrinidae** (Figure 12-Figure 14) use mosses as hiding places during the day (Leng 1913). And in the Appalachian Mountain, USA, streams, the mosses may provide a refuge for ***Dineutus*** (Figure 12-Figure 14) during times of high flow (Glime 1968).

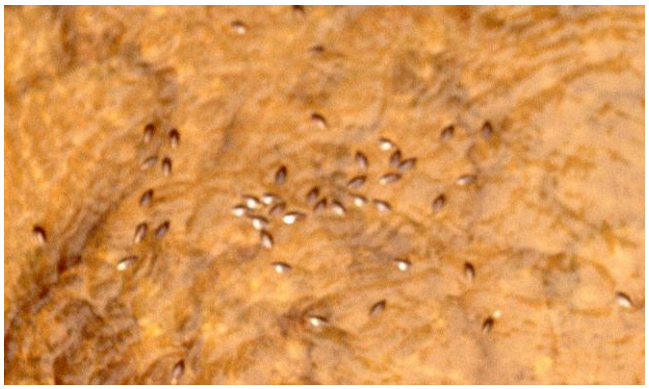

Figure 12. ***Dineutus discolor*** (whirligig beetles) on the water surface. Photo by Janice Glime.

Figure 13. ***Dineutus assimilis*** adult showing split eyes. Photo by Joyce Gross, with permission.

Figure 14. ***Dineutus*** larva, a genus that sometimes occurs among bryophytes when it is resting. Photo by Bob Henricks, with permission.

Haliplidae – Crawling Water Beetles

The **Haliplidae** are clumsy swimmers, alternating the motion of their legs (Haliplidae 2014). Hence, they move about mostly by crawling. The adults are convex on the dorsal side and range 1.5-5.0 mm long. The hind legs have large coxal plates and are immobile. The primary function of these legs seems to be that of storing air, supplementing the air stored under the elytra. The larvae eat only algae, but the adults are omnivorous. They live among aquatic vegetation around the borders of small ponds, lakes, and quiet streams. Their worldwide distribution is similar to that of the **Scirtidae**, with the greatest diversity known in Europe (Haliplidae 2015).

These are mostly not bryophyte dwellers, but the genus ***Haliplus*** (Figure 15) still benefits from the presence of ***Sphagnum*** (Figure 7). ***Haliplus variegatus*** (Figure 16) in Poland lives in canals that are created by beavers in floating ***Sphagnum*** mats (Buczyński *et al.* 2014).

Figure 15. ***Haliplus*** larva. Some members of this genus live in bogs and ***H. variegatus*** lives in beaver canals in floating ***Sphagnum*** mats. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

Figure 16. ***Haliplus variegatus*** adults, inhabitants of beaver canals in floating ***Sphagnum*** mats of Poland. These color phases and the spots can help to camouflage the beetles among the mosses. Photo by Stefan Schmidt, through Creative Commons.

In my own studies (Glime 1968) in the Appalachian Mountain, USA, streams, I found the genus ***Brychius*** (Figure 17). The generic name suggests a possible moss habitat, but I was unable to find additional information on the habitat.

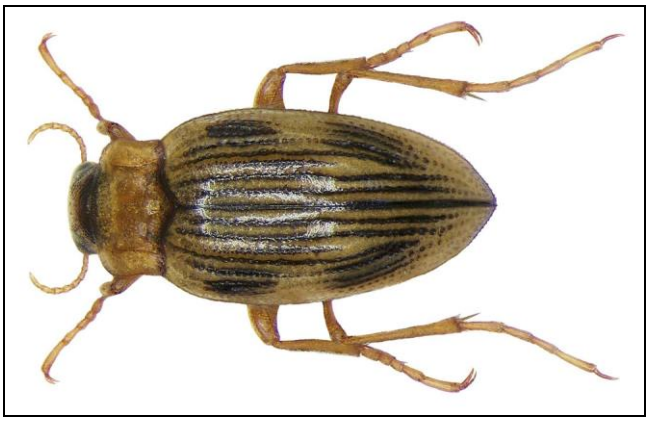

Figure 17. ***Brychius elevatus*** adult, a genus with moss inhabitants in Appalachian Mountain, USA, streams. Photo by Udo Schmidt, through Creative Commons.

Hygrobiidae – Squeak Beetles

This small family has only one genus, ***Hygrobia***, with six species, and is distributed in Europe, North Africa, China, and Australia (Hygrobia 2014). ***Hygrobia*** adults make a grating noise, earning them their name of squeak beetles (Pendleton & Pendleton 2014). Their size is moderate (8.5-10 mm). They are most common in stagnant water, where they walk or swim; they do not dive (Watson & Dallwitz 2003a). They obtain their oxygen from the air collected and stored under the elytra. ***Hygrobia hermanni*** (Figure 18) reaches large populations at pond margins where it lives among the submerged ***Sphagnum*** (Figure 39) (Denton 2013).

Figure 18. ***Hygrobia hermanni*** adult, an inhabitant of submerged ***Sphagnum***. Note the anal air bubble. Photo by Trevor and Dilys Pendleton, with permission.

Dytiscidae – Predaceous Diving Beetles and Noteridae – Burrowing Water Beetles

The **Noteridae** are often included with the **Dytiscidae** and I will do so here because it makes the discussion easier. The larvae of **Dytiscidae** are known as water tigers. They are passive predators, waiting quietly until a prey organism passes nearby (Dytiscidae 2014). On the other hand, several members of the family are eaten by humans in China, Japan, and Mexico, as well as other places in the world. This worldwide family has a large range of sizes (1.2-40 mm long) (Bartlett 2004b). They are distributed throughout the world, but with the best known concentrations in North America, Europe, and Australia (Dytiscidae 2015). The larvae live in the water, but they climb to land and bury themselves in the mud for pupation, returning to the water as adults.

The adult **Dytiscidae**, like other beetles, lack true gills. Instead, they carry a bubble of air with them as they descend down the water column. This bubble is either held against the body or stored under the **elytra** (outer hardened wings) (Figure 1). As oxygen is used up, nitrogen maintains the size of the bubble so that oxygen can diffuse into the bubble. When the bubble becomes too small, they must obtain another bubble from plant surfaces or the water surface by exposing the tip of the abdomen (Figure 19).

Figure 19. ***Rhantus suturellus*** adult replenishing air supply at surface. Photo by Niels Sloth, with permission.

Based in my own studies on moss-dwelling aquatic insects in the Appalachian Mountains, USA, it seemed that the predaceous diving beetles (**Dytiscidae**) do not typically hang out among the bryophytes. But many of the species occur in mossy wet areas, especially associated with bogs and fens. Usinger (1974) describes three types of ovipositors in the **Dytiscidae**. Those with a long ovipositor are able to inject their eggs into moss mats growing in the water. And some species even ingest mosses occasionally (Jones 1949).

Roger Key (pers. com. 31 October 2014) considers the primary role of bryophytes in the life of the predaceous aquatic beetles to be that of a structural component, a place for cover to escape predators. But these beetles are mostly predators themselves (Figure 20). In some cases the mosses are important as a place to hang or climb to avoid being carried to the surface by their air supply – the plastron apparatus or air layer under the elytra. For example, ***Lancetes*** in South Georgia may make use of mosses, among other anchored substrata, to get back under the surface or to stay there when it is not actively swimming. In places like South Georgia, mosses are the predominant, if not the only, vegetation at the margins of streams, hence providing these roles for aquatic beetles there.

Figure 20. ***Dytiscus*** larva eating young fish. Photo by Roger S. Key, with permission.

Graphoderus zonatus (spangled diving beetle; Figure 21) occurs where ***Fontinalis*** (Figure 5) provides the major vegetation in a heathland mire in Hampshire, UK (Roger S. Key, pers. comm. 31 October 2014). This diving beetle is frequently found associated with the mosses and can be collected by shaking the mosses over a container. The bryophyte role, as suggested above, is one of cover.

Oreodytes davisii (Figure 22) and ***O. sanmarkii*** (Figure 23) both live among aquatic bryophytes in a stream in Yorkshire, UK (Gilbert *et al*. 2005). ***Oreodytes rivalis*** may occasionally even ingest mosses such as ***Fontinalis antipyretica*** (Figure 5) (Jones 1949), perhaps in their attempts to capture one of the other invertebrates dwelling there.

Figure 21. ***Graphoderus zonatus*** adult in a heathland mire in Hampshire, UK. Photo by Roger S. Key, with permission.

Foster (1992) found ***Hydroporus umbrosus*** (Figure 24) among mosses at the edge of a pond in Inner Hordaland, Norway. Usinger (1974) describes the small members of the genus ***Hydroporus*** as able to occupy moss-covered seepages no bigger than a hand. Buczyński *et al.* (2014) reported ***H. incognitus*** (Figure 25) from ***Sphagnum*** bogs (Figure 26) in Poland. In spring-fed boggy areas one can find ***Hydroporus longulus*** (Figure 27) among mosses and leaves (Denton 2013).

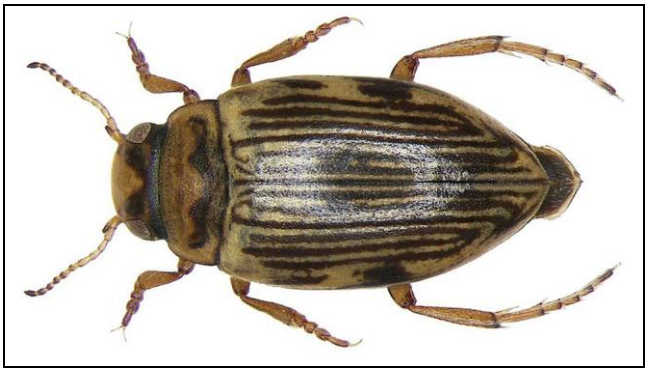

Figure 22. ***Oreodytes davisii*** adult, a bryophyte dweller in UK streams. Photo by Udo Schmidt, with permission.

Figure 23. ***Oreodytes sanmarkii*** adult, a stream bryophyte dweller in the UK. Photo by Christoph Benisch <www.kerbtier.de>, with permission.

Figure 24. ***Hydroporus umbrosus*** adult, a moss dweller at the edge of ponds in Norway. Photo by Niels Sloth, with permission.

Figure 25. ***Hydroporus incognitus*** adult, an inhabitant of ***Sphagnum*** bogs in Poland. Photo by Niels Sloth, with permission.

Figure 26. ***Sphagnum*** blanket bog, home to many kinds of beetles. Photo through Creative Commons.

Figure 27. ***Hydroporus longulus*** adult, a beetle one can find among mosses in spring-fed boggy areas. Photo by Tim Faasen, with permission.

Graphoderus zonatus (Figure 28) in North Hampshire, UK, lives in a variety of habitats, particularly in ***Sphagnum***-dominated (Figure 39) lake margins (Denton 2013).

Figure 28. ***Graphoderus zonatus*** adult with ***Sphagnum***. Photo by Niels Sloth, with permission.

Moors, Bogs, and Fens

These three habitats are partially aquatic, providing wet or damp bryophytes and pools where there may be submerged bryophytes. **Moors**, a term used more commonly in Europe, are upland habitats including heathlands and fens and characterized by low vegetation and acidic soils (Moorland 2014). The term **bog** has a mixed history, with North Americans using a much broader definition than that of the northern Europeans. Until relatively recently, North Americans tended to include any wetland with ***Sphagnum*** as a bog. English language dictionaries go even further to define a bog as any muddy or spongy wetland. The more restrictive European definition is a habitat that is dominated by ***Sphagnum*** and receives only precipitation as a source of new nutrients. By contrast, a **fen** may have ***Sphagnum*** or other dominant bryophytes, but it receives nutrients through surface or ground water in addition to precipitation. Most of the habitats that North Americans have called bogs (including most current definitions and websites on the internet) are actually **poor fens**, *i.e.*, wetland habitats with low nutrients, ground or surface water, and ***Sphagnum*** species similar to those of true bogs.

Fens and bogs provide habitats for a number of **Dytiscidae** and provide the most common associations with bryophytes. The genus ***Agabus*** is among these common inhabitants (Nelson 1996). ***Agabus affinis*** (Figure 29) can be considered a characteristic species, a **tyrphobiont** (species living only in peat-bogs and mires) in high moors (Hebauer 1974), often accompanied by ***A. unguicularis*** (Figure 30), in the moss lawns of lowland fens and bogs of Ireland (Nelson 1996) and flooded ***Sphagnum*** (Figure 39) (Denton 2013). In Scotland ***A. unguicularis*** occurs in peaty water with mosses or other dense vegetation (Knight 2014). ***Agabus melanocornis*** is less common and occurs in mossy drains, fens, and bogs (Nelson 1996). ***Agabus melanarius*** (Figure 31) is easily overlooked in North Hampshire, UK, where it lives in shallow water with mosses.

Figure 29. ***Agabus affinis*** adult with ***Sphagnum***. Photo by Tim Faasen, with permission.

Figure 30. ***Agabus unguicularis*** adult, a common inhabitant of bogs and fens, carrying an anal air bubble. Photo by Niels Sloth, with permission.

Figure 31. ***Agabus melanarius*** adult, a species from shallow water among mosses. Photo by James K. Lindsey, with permission.

In contrast to other bryophyte habitats, bogs are a mix of terrestrial and aquatic microhabitats that provide homes for a number of **Dytiscidae**. Brink and Terlutter (1983) found ***Dytiscus lapponicus*** (Figure 32-Figure 34), ***Hydroporus tristis*** (Figure 35), ***H. erythrocephalus*** (Figure 36), and ***Acilius canaliculatus*** (Figure 37), as well as **Noteridae** (burrowing water beetles, sometimes included in the **Dytiscidae**) – ***Noterus crassicornis*** (Figure 38), to be acid **tyrphophiles** (characteristic of bogs but not confined to them) associated with ***Sphagnum cuspidatum*** (Figure 39). ***Acilius*** is one of the genera with a long ovipositor that permits egg-laying among mosses and other substrata (Usinger 1956). These eggs are laid in the water and sometimes out of water. From Dartmoor, UK, Boyce (2011) also reported ***Hydroporus tristis*** in small, peaty pools that had ***Sphagnum*** (Figure 39). Boyce also found ***Hydroporus gyllenhalii*** (Figure 40) among ***Sphagnum*** in bogs and in small peat pools that likewise had at least some ***Sphagnum*** in both undisturbed and eroded blanket mires. ***Hydroporus obscurus*** (Figure 42-Figure 43) was more restricted, living only in relatively pristine blanket bogs where it lived in small ***Sphagnum***-dominated peat pools.

Figure 32. ***Dytiscus lapponicus*** larva, a species associated with ***Sphagnum cuspidatum***. Photo by James K. Lindsey, with permission.

Figure 33. ***Dytiscus lapponicus*** adult with mosses and aquatic plants. Photo by Niels Sloth, with permission.

Figure 34. ***Dytiscus lapponicus*** adult with mosses and aquatic plants. Photo by Niels Sloth, with permission.

Figure 35. ***Hydroporus tristis*** adult amid aquatic mosses. Photo by Tim Faasen, with permission.

Figure 36. ***Hydroporus erythrocephalus*** adult with leaf and ***Sphagnum***. Photo by Tim Faasen, with permission.

Figure 37. ***Acilius canaliculatus*** adult, a species associated with ***Sphagnum cuspidatum*** (Figure 39). Photo by Niels Sloth, with permission.

Figure 38. ***Noterus crassicornis*** adult on leaf litter in stream. Photo by Niels Sloth, with permission.

Figure 39. ***Sphagnum cuspidatum***, home for some **Dytiscidae** and **Noteridae**. Photo by Jan-Peter Frahm, with permission.

Figure 40. ***Hydroporus gyllenhalii*** adult, a species that lives among ***Sphagnum*** in bogs and bog pools. Photo by Niels Sloth, with permission.

In his studies in Central Europe, Hebauer (1974) similarly found ***Hydroporus pubescens*** (Figure 41) to be a tyrphobiont, as well as such tyrphobionts as ***Hydroporus obscurus*** (Figure 42-Figure 43) and ***H. melanocephalus*** in the high moors (Hebauer 1994).

The smallest member of Irish ***Hydroporus*** is ***H. scalesianus*** (Figure 44) (Nelson 1996). In the Appalachian Mountain, USA, streams, this genus lives among stream mosses (Glime 1968), whereas in Ireland it lives exclusively among mossy carpets of undisturbed fens, mires, and lake basins.

Figure 41. ***Hydroporus pubescens*** adult among ***Sphagnum***. Photo by Tim Faasen, with permission.

Figure 42. ***Hydroporus obscurus*** adult on ***Sphagnum***. Photo by Tim Faasen, with permission.

Figure 43. ***Hydroporus obscurus*** adult climbing on a moss. Photo by Niels Sloth, with permission.

Figure 44. ***Hydroporus scalesianus*** adult, the smallest ***Hydroporus***, on ***Sphagnum,*** from the high moors of Europe. Photo by Tim Faasen, with permission.

Other tyrphobionts in the high moors included ***Rhantus suturellus*** (Figure 19, Figure 45) (Hebauer 1974), a species also found in Poland in peaty pools (Boyce 2011). In Ireland, ***Graptodytes granularis*** (Figure 46) lives in mossy carpets of undisturbed fens, mires, and lake basins, but requires permanently wet mosses (Nelson 1996).

Ilybius crassus and ***I. aenescens*** (Figure 47-Figure 48) are tyrphobionts in European high moors (Hebauer 2994). ***Ilybius aenescens*** also occurs in flooded ***Sphagnum*** (Figure 39) of heathlands of North Hampshire, UK, but it is rare (Denton 2013). Boyce (2011) found that ***Ilybius montanus*** usually occur in shallow bog pools where there are dense growths of ***Sphagnum***. ***Ilybius fuliginosus*** (Figure 49) is quite ubiquitous and thus might be found hiding among the mosses (Tim Faasen, pers. comm. 20 October 2014). But ***Ilybius*** is not restricted to bogs and moors, appearing among mosses in Appalachian Mountain, USA, streams (Glime 1968).

Figure 45. ***Rhantus*** larva. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

Figure 46. ***Graptodytes granularis*** adult, dwelling in the high moors of Europe. Photo by Tim Faasen, with permission.

Figure 47. ***Ilybius aenescens*** adult among mosses. Photo by Tim Faasen, with permission.

Figure 48. ***Ilybius aenescens*** adult, a bog dweller. Photo by Niels Sloth, with permission.

Figure 49. ***Ilybius fuliginosus*** adult, a ubiquitous species that hides among vegetation, shown here on mosses. Photo by Tim Faasen, with permission.

Laccornis oblongus (Figure 50) is a flightless beetle that lives in Irish fens that lack open water (Nelson 1996). It occurs among wet moss carpets, especially those associated with clumps of sedges. ***Hydaticus seminger*** (Figure 51) is a dweller of typical mossy fens. This species is not frequent in North Hampshire, UK, but it does occur among flooded ***Sphagnum*** and in detritus pools (Denton 2013).

Figure 50. ***Laccornis oblongus*** adult, a flightless beetle known from moss carpets in Irish fens. Photo by Niels Sloth, with permission.

Figure 51. ***Hydaticus seminiger*** adult, a mossy fen dweller. Photo by Tim Faasen, with permission.

Floating moss carpets are often associated with bogs and fens. ***Bidessus grossepunctatus*** (Figure 52) is one of the inhabitants of these moss carpets in small lakes, ponds, fen pools, and mires (Nilsson & Holmen 1995).

Figure 52. ***Bidessus grossepunctatus*** adult, an inhabitant of floating moss carpets, on ***Sphagnum***. Photo by Tim Faasen, with permission.

Special techniques can facilitate collecting bog and fen species. Since bryophytes in these habitats are typically underlain by water, these semi-terrestrial beetles can be collected by depressing the mosses, creating a depression until they are covered by water (Nilsson & Holmen 1995; Knight 2014). The beetles can then be swept from the water with a tea strainer. Knight (2014) considers this technique especially useful for sampling **Hydraenidae** and small **Hydrophilidae**.

In the Japanese rice fields, many invertebrates find refuge. Some of these fields even have peat mosses. Such communities include ***Cybister japonicus*** (Figure 53-Figure 54) (Ohba 2009), a species eaten by humans in Japan (Dytiscidae 2014). These carnivores feed on insects such as Odonata in early instars, but starting in the third instar they feed on small vertebrates such as amphibia as well. In the last larval stage, they burrow into the peat moss and enter the pupation period.

Figure 53. ***Cybister japonicus*** adult, a species that hides among peat mosses in Japanese rice fields. Photo through Creative Commons.

Figure 54. ***Cybister japonicus*** larva, a species that hides among peat mosses in Japanese rice fields. Photo through Creative Commons.

Liodessus cantralli (Figure 55) lives in small pools in North America, but also lives in moss mats of fens (less often in bogs) (Larson & Roughley 1990). They are particularly associated with ***Drepanocladus*** *s.l.* (Figure 56) in depressions in the moss mats.

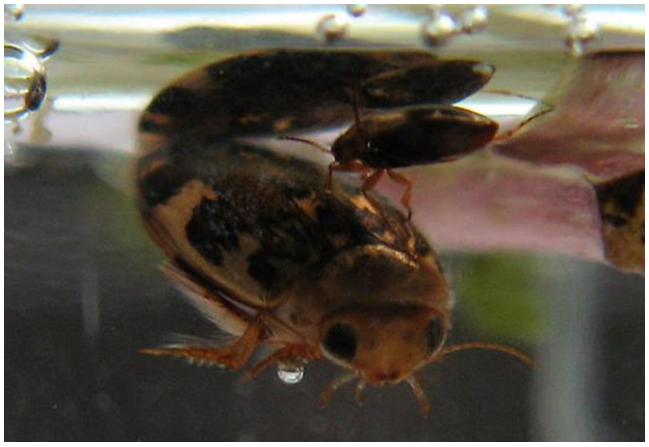

Figure 55. ***Liodessus*** adult; ***L. cantralli*** lives in moss mats of fens. Photo © Stephen Luk through BugGuide non-commercial use, with permission.

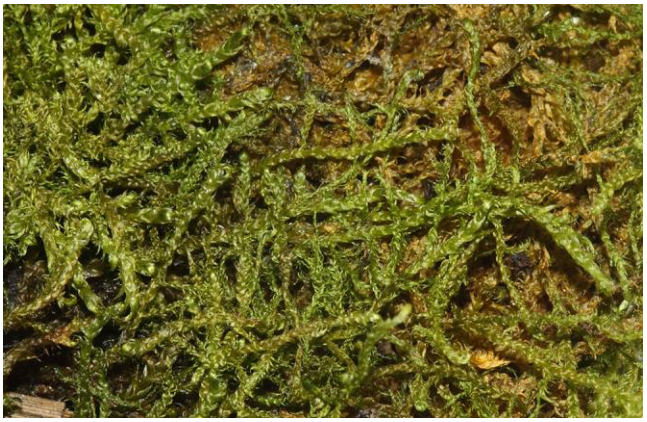

Figure 56. ***Drepanocladus aduncus***, home of ***Liodessus cantralli*** in North America. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University.

Summary

Coleoptera can live in the water as larvae and as adults, but the pupae are generally on land. The aquatic adults gain oxygen by using a **plastron**, accumulating air under the forewings, or from an anal bubble. Some live on the surface and may crawl over plants such as ***Ricciocarpos natans***. Smaller beetles live among mosses in streams. But the greatest number of aquatic bryophyte associations for beetles occurs in bogs and fens.

The order **Coleoptera** (beetles) has two sub orders: **Adephaga** and **Polyphaga**. In the **Adephaga** the families **Carabidae**, **Gyrinidae**, **Haliplidae**, **Hygrobiidae**, and **Dytiscidae**. The **Dytiscidae** are especially common and diverse in bog pools and this is the only family of **Adephaga** frequently associated with bryophytes.

Acknowledgments

Tim Faasen not only gave me permission to use his wide collection of insect images, he also helped me to understand the ecology of some of the species and provided me with additional images I needed. Thank you to Roger S. Key not only for his permission to use his images but for sharing his experiences with me regarding beetle use of bryophytes. Ronald Willson verified my beetle identifications for the mid-Appalachian Mountain study. And thank you to Amy Marcarelli, Wayne Minshall, and especially Rich Merritt for helping me with my query about the anal air bubble in aquatic beetles. Eileen Dumire proofread the chapter and suggested changes to provide more clarity.

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CHAPTER 11-10
AQUATIC INSECTS: HOLOMETABOLA – COLEOPTERA, SUBORDER POLYPHAGA

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CHAPTER 11-10
AQUATIC INSECTS: HOLOMETABOLA – COLEOPTERA, SUBORDER POLYPHAGA

Figure 1. ***Ilybius erichsoni*** adult on ***Sphagnum.*** Photo by Niels Sloth, with permission.

Suborder Polyphaga

This suborder includes more than 90% of the **Coleoptera** species. As its name suggests, it eats a tremendous variety of foods.

Helophoridae

This is a family of North America and Europe and has only one genus, ***Helophorus*** (Helophoridae 2014). They are relatively small (2-9 mm) (Helophoridae 2014) and live primarily in wetlands (Helophoridae 2015). Most adults live in shallow standing water where they are **saprophagous** (Fikáček 2009) (organism that feeds on decaying organic matter). Larvae, on the other hand, live in terrestrial, but moist, habitats near water and are predators on small invertebrates.

Helophorus grandis (Figure 2) occurs among the aquatic mosses in a stream in Yorkshire, UK (Gilbert *et al*. 2005). In Canada, ***Helophorus orientalis*** (Figure 3) occurs in wet mosses beside small streams (Majka 2008). ***Helophorus strigifrons*** (Figure 4) lives in bogs in North Hampshire, UK, among moss and litter (Denton 2013).

Figure 2. ***Helophorus grandis***, an inhabitant of stream mosses in the UK. Photo by Tim Faasen, with permission.

Figure 3. ***Helophorus orientalis*** adult, a species that lives among wet mosses along streams in Ontario, Canada. Photo by Tom Murray, through Creative Commons.

Figure 4. ***Helophorus strigifrons*** adult, a bog dweller in North Hampshire, UK, among moss and litter. Photo by Zoologische Staatssammlung Muenchen, through Creative Commons.

Hydrochidae

Although this family is worldwide, it has only one genus, and most of the records are from Europe (Hydrochidae 2015a). Adults and larvae live in both quiet and flowing water where they are herbivores – shredders (Hydrochidae 2015b). The adults range 4-60 mm long. Some of these are associated with bryophytes.

Hydrochus ignicollis (Figure 5), a very rare species in Ireland, appeared in collections only twice between 1988 and 1996 (Nelson 1996). Both finds were from mossy calcareous fens adjacent to **marl lakes** (calcium carbonate or lime-rich lakes. These are alkaline lakes with unconsolidated calcium carbonate or lime-rich mud or mudstone which contains variable amounts of clays and silt (Figure 6-Figure 7).

Figure 5. ***Hydrochus ignicollis*** adult, a rare inhabitant of mossy calcareous fens in Ireland. Photo by Tim Faasen, with permission.

Figure 6. Marl lake in Jasper National Park, Canada. Photo by Janice Glime.

Figure 7. Marl at margin of marl lake in Jasper National Park, Canada. Photo by Janice Glime.

Hydrophilidae – Water Scavenger Beetles

This is a worldwide, mostly aquatic family, typically in open water (Cotinus 2005). The larvae often emerge from the water to pupate, usually hanging from moss at the edge of the water (Water Beetles 2014). The final larval skin is found beneath the pupa. The adults (1-40 mm) are mostly scavengers, but some are predators; larvae are often predators (Cotinus 2005).

Some **Hydrophilidae** join the **Dytiscidae** as common beetles swimming in bog waters. ***Enochrus*** (Figure 8-Figure 9) is a common genus there (Denton 2013). ***Enochrus affinis*** (Figure 10) is often abundant in ***Sphagnum***-dominated (Figure 51) areas of acidic heathland pools (Figure 11) of North Hampshire, UK ***Enochrus coarctatus*** (Figure 12) is a mire dweller, preferring older detritus pools but also living in ***Sphagnum***-filled large bog pools. ***Enochrus ochropterus*** (Figure 13) does not occur in areas of pure ***Sphagnum*** where the ***Enochrus*** is exclusively ***E. affinis***. However, it does occur in richer areas with ***E. coarctatus***. The importance of the ***Sphagnum*** in its habitats may be due to its role in acidification. ***Enochrus fuscipennis*** (Figure 14) lives in the ***Sphagnum***-choked shallow pools of undisturbed blanket bogs in Dartmoor, UK (Boyce 2011). ***Enochrus hamiltoni*** (Figure 15), on the other hand, lives in wet mosses next to small streams on Prince Edward Island, Canada (Majka 2008). In the Appalachian Mountain streams, eastern USA, the genus ***Enochrus*** can occasionally be found among mosses, as well as the genus ***Tropisternus*** (Figure 16-Figure 17) (Glime 1968).

Figure 8. ***Enochrus*** larva, common among bog bryophytes. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

Figure 9. ***Enochrus*** larval head. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

Figure 10. ***Enochrus affinis*** adult, an abundant species in ***Sphagnum***-dominated heathland pools in North Hampshire, UK. Photo by Christoph Benisch <kerbtier.de>, with permission.

Figure 11. Heathland with a pool. Photo by Jim Champion, through Creative Commons.

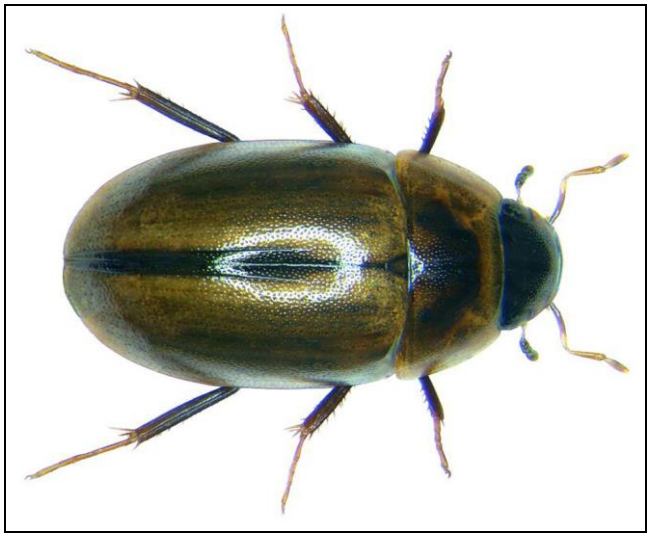

Figure 12. ***Enochrus coarctatus*** adult, an inhabitant of mire pools, often among ***Sphagnum***. Photo by Udo Schmidt, with permission.

Figure 13. ***Enochrus ochropterus*** adult, a species of rich mires, often associated with ***Sphagnum***. Photo by Niels Sloth, with permission.

Figure 14. ***Enochrus fuscipennis*** adult, a species that lives in ***Sphagnum***-filled shallow pools in blanket bogs. Photo by James K. Lindsey, with permission.

Figure 15. ***Enochrus hamiltoni*** adult, a dweller of wet mosses next to small streams on Prince Edward Island, Canada. Photo by Tom Murray, through Creative Commons.

Figure 16. ***Tropisternus*** sp. larva, an occasional moss inhabitant in Appalachian Mountain, USA, streams. Photo by Tom Murray, through Creative Commons.

Figure 17. ***Tropisternus natator*** adult, an occasional moss inhabitant in Appalachian Mountain, USA, streams. Photo by Donald S. Chandler, with permission.

The genus ***Laccobius*** (Figure 18-Figure 19) associates with mosses in both stream and mire habitats. ***Laccobius reflexipennis*** (see Figure 18) live in wet mosses next to small streams on Prince Edward Island, Canada (Majka 2008). ***Laccobius atratus*** in Ireland and Great Britain occurs in ***Sphagnum*** (Figure 51) bogs and other peatlands (Friday 1987; Nelson 1996; Denton 2013). ***Laccobius ytenensis*** adults live among mosses around the tiny pools that occur in the seepage lines of UK bogs (Denton 2013).

Figure 18. ***Laccobius*** sp. adult, a genus with several species that live in water or bog mosses. Photo by Gerard Visser <www.microcosmos.nl>, with permission.

Figure 19. ***Laccobius*** adult with open wings showing the membranous wings under the hardened elytra. Photo by Michael Schmidt, through Creative Commons.

Chaetarthria siminulum (Figure 20) can be present in "huge" numbers among mosses at the edges of ponds (Denton 2013). It also lives among mosses in fens and in fen litter.

Figure 20. ***Chaetarthria siminulum*** adult with plastron. When the plastron is full of air, the beetle must cling to vegetation in order to descend into the water column. Photo by Gerard Visser, with permission.

Hebauer (1994) found ***Crenitis punctatostriata*** (Figure 21) in the high moors, living as a tyrphobiont. ***Hydrobius fuscipes*** (Figure 22-Figure 23) on Prince Edward Island (Majka 2008) occurs in ***Sphagnum*** (Figure 51) bogs and other peatlands.

Figure 21. ***Crenitis punctatostriata*** adult, a beetle that lives in bogs of the high moors. Photo by Udo Schmidt, with permission.

Figure 22. ***Hydrobius fuscipes*** adult, a species of ***Sphagnum*** bogs. Photo by Tim Faasen, with permission.

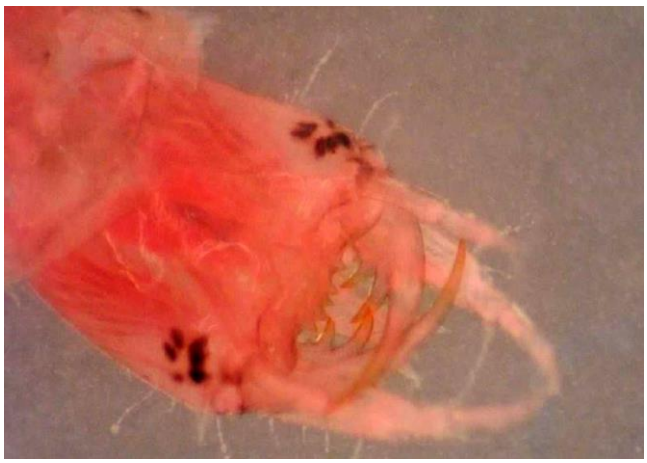

Figure 23. ***Hydrobius*** larval head showing large mandibles. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

Friends are wonderful, and I recently received this story and all the images from Andrea Ares. She found an "amazing place" covered with the leafy liverwort Jungermannia vulcanicola (Figure 24-Figure 25) in Chatubomigoke Park, Gunma Prefecture, Japan. Soon she also discovered a small (6-7 mm) black beetle wending its way upon and within the "big, robust carpet" of the liverwort in this acid stream. This beetle was identified by Itouga san as ***Hydrobius pauper*** (Figure 26-Figure 28), the only member of the genus in Japan. There was not just one, but the bases of the liverworts were "full" of them.

Figure 24. Cushions of ***Jungermannia vulcanicola*** (chartreuse-colored cushions) in Chatubomigoke Park in Japan. Photo courtesy of Angela Ares.

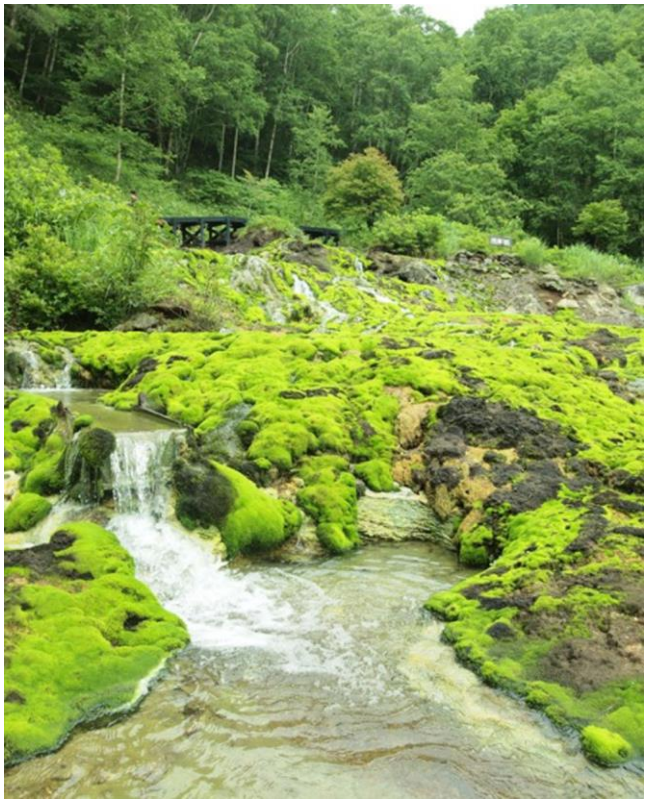

Figure 25. Habitat of ***Jungermannia vulcanicola*** (chartreuse-colored cushions) in Chatubomigoke Park in Japan. Photo courtesy of Angela Ares.

Figure 26. Cushion of ***Jungermannia vulcanicola*** with its inhabitants, ***Hydrobius pauper***. Photo courtesy of Angela Ares.

Figure 27. Disturbed cushion of ***Jungermannia vulcanicola*** showing bases of plants with its inhabitants, ***Hydrobius pauper***. Photo courtesy of Angela Ares.

Figure 28. ***Hydrobius pauper*** adult. Photo by Itago san.

Berosus luridus (Figure 29, Figure 30) is tyrphophilic, living among ***Sphagnum*** (Figure 51), but can also be found in other places (Tim Faasen, pers. comm.). I have found no other records of it living among ***Sphagnum***, but it is rare in the Netherlands and may be rare elsewhere. Perhaps the ***Sphagnum*** provides a relict habitat, a safe site where conditions are still tolerable.

Figure 29. ***Berosus luridus*** adult on moss, a rare beetle in the Netherlands, but present in bogs among ***Sphagnum*** there. Note the air bubbles on the moss; these can be used to replenish the air supply. Photo by Tim Faasen, with permission.

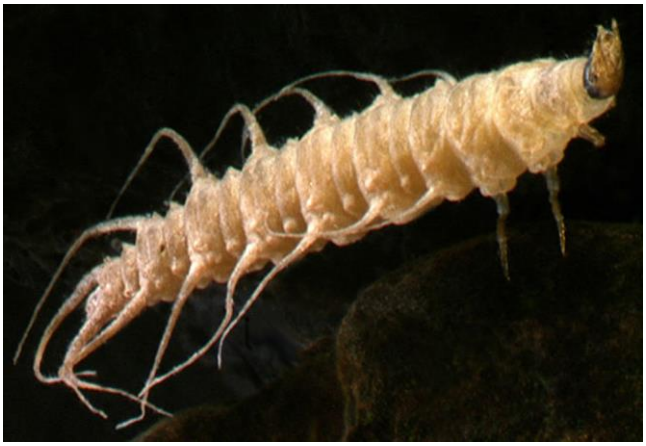

Figure 30. ***Berosus*** larva, a moss dweller in bogs of New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.

In tropical Africa, the genus ***Anacaena*** is probably more common than is recognized. Komarek (2004) described nine new species. Among these, four were from mosses. ***Anacaena capensis*** occurs among the mosses and leaf litter of mountain rivulets in South Africa. ***Anacaena glabriventris*** lives among mosses in small streams; ***A. reducta*** likewise lives among mosses in small streams, but with steep channels. ***Anacaena tenella*** lives among **hygropetric** mosses (mosses growing on vertical rock faces where a thin film of water flows) in mountain streams. ***Anacaena limbata*** (Figure 31) lives in wet mosses next to small streams on Prince Edward Island, Canada (Majka 2008).

Figure 31. ***Anacaena limbata*** adult, an inhabitant of wet mosses adjacent to streams. Photo by Tim Faasen, with permission.

Anacaena globulus (Figure 32) lives among ***Sphagnum*** (Figure 32) in bogs in Europe and can be collected by squeezing the moss (Buczyński *et al*. 2014). However, Faasen (personal communication) does not find them typically in ***Sphagnum*** bogs in the Netherlands, but considers them widespread, occasionally occurring in bogs.

Also in Dartmoor, UK, ***Helochares punctatus*** (Figure 33) is an obligate mire species, living among saturated ***Sphagnum***, particularly ***S. cuspidatum*** (Figure 34), of pools and acid flushes.

Figure 32. ***Anacaena globulus*** adult on ***Sphagnum***, one of its many habitats. Photo by Tim Faasen, with permission.

Figure 33. ***Helochares punctatus*** adult on moss. Photo by Niels Sloth, with permission.

Figure 34. ***Sphagnum cuspidatum***, home for ***Helochares punctatus***. Photo by David T. Holyoak, with permission.

Nelson (1996) found several additional species of **Hydrophilidae** in Irish mossy fens. These included ***Cercyon convexiusculus*** (Figure 35-Figure 36) in mossy fens. In North Hampshire, UK, Denton (2013) found this species to be abundant in detritus and rotting leaf litter, but also among mosses that bordered richly vegetated sites. ***Cercyon marinus*** similarly occupied mosses or decaying organic matter at the water's edge in Ireland (Nelson 1996). ***Cercyon ustulatus*** (Figure 37) occurs in mossy areas of ponds and also occurs among mosses growing on sewage filter beds (Denton 2013).

Figure 35. ***Cercyon convexiusculus*** adult, an inhabitant of mossy fens. Photo by Tim Faasen, with permission.

Figure 36. ***Cercyon convexiusculus*** adult, an inhabitant of mossy fens. Photo by Christoph Benisch <kerbtier.de>, with permission.

Figure 37. ***Cercyon ustulatus*** adult, an inhabitant of mossy areas of ponds and filter beds. Photo by Tom Murray, through Creative Commons.

Paracymus scutellaris (Figure 38) occurs among peat mosses in Ireland (Nelson 1996).

Figure 38. ***Paracymus scutellaris*** adult, a peat moss dweller in Ireland. Photo by Udo Schmidt, with permission.

Hydraenidae – Minute Moss Beetles

Adults of **Hydraenidae** (Figure 39), known as minute moss beetles (1-3 mm length), are aquatic, but the larvae drown if completely submersed (Watson & Dallwitz 2012). Even adults are poor swimmers (EOL 2014); most eat plants, but a few are carnivorous or **saprophagous** (feeding on decaying organic matter) (Hydraenidae 2014). They are sparsely distributed worldwide with a concentration in Europe (EOL 2014).

Sarr *et al*. (2013) found that ***Hydraena*** was correlated with a moss substrate in Northwest Spain. Berthélemy (1966) found this family commonly among mosses in the Pyrénées, including ***Hydraena gracilis*** (Figure 40), ***H. minutissima***, and ***H. pygmaea*** (Figure 41), with the latter two being considered **muscicoles** (thriving among mosses). He also considered ***Hydraena pulchella*** (Figure 42) and ***Hadrenya*** to be **muscicoles**. Nelson (1996) reported ***Hydraena gracilis*** as a common and widespread species in Britain where it lives on mossy rocks in fast-flowing streams and rivers.

Figure 39. **Hydraenidae** adult, an aquatic minute moss beetle that commonly lives among mosses in the Pyrénéenes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 40. ***Hydraena gracilis*** adult, a common aquatic moss inhabitant in the Pyrénées. Photo by Tim Faasen, with permission.

Figure 41. ***Hydraena pygmaea*** adult, a muscicole in the Pyrénées. Photo by Tim Faasen, with permission.

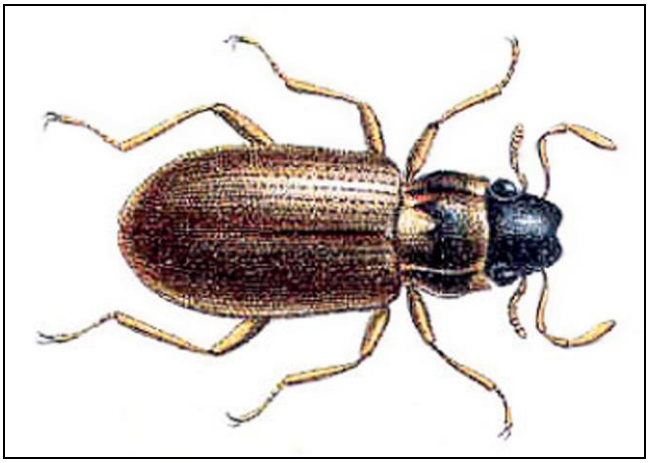

Figure 42. ***Hydraena pulchella*** adult, a tiny beetle that lives among stream mosses in Europe. Image through Creative Commons.

Hydraena nigrita is a tiny beetle that lives among mosses at the edges of streams, but it will climb out if the moss is placed under water (Anderson 2014). It is considered vulnerable because of siltation and loss of habitat (Foster *et al*. 2009). ***Hydraena rufipes*** (Figure 43) lives among mosses (Nelson 1996; Knight 2014) and fine **shingle** (mass of small rounded pebbles) along rivers (Nelson 1996).

Figure 43. ***Hydraena rufipes*** adult, a species that lives among mosses along rivers. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Hebauer (1994) found similar species representation from this family in middle Europe. Among the stream mosses he found ***Hydraena minutissima***, ***H. pygmaea*** (Figure 41), and ***H. pulchella*** (Figure 42). Several more used mosses or algae as a substrate: ***Ochthebius granulatus*** (Figure 44), ***O. metallescens*** (Figure 45), ***O. exsculptus*** (Figure 46), ***O. melanescens***, ***O. colveranus***, and ***O. halbherri***. Eggs of ***Ochthebius*** are either naked or somewhat covered by loosely applied silk provided by the mother; the eggs hatch in 7-10 days. In rivers in Northwest Spain, Sarr *et al*. (2013) found that ***Ochthebius heydeni*** was likewise correlated with a moss substrate.

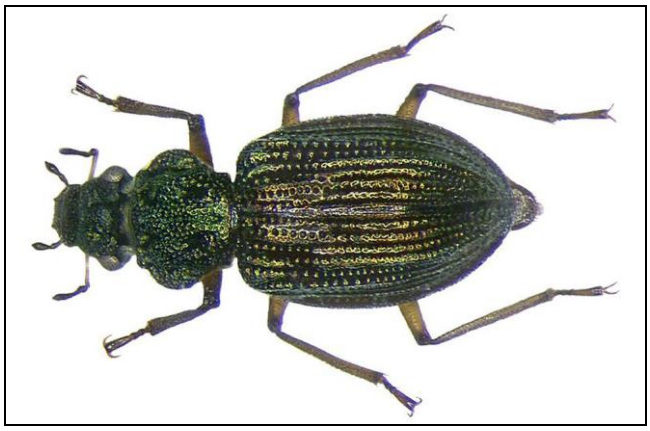

Figure 44. ***Ochthebius granulatus*** adult, a stream moss dweller in middle Europe. Photo by Magnus Manske.

Figure 45. ***Ochthebius metallescens*** adult, a beetle that uses mosses and algae as substrates. Photo by Tim Faasen, with permission.

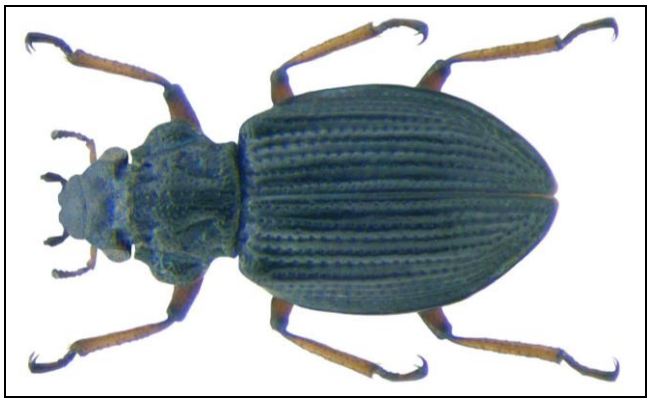

Figure 46. ***Ochthebius exsculptus*** adult, a European stream moss dweller. Photo by Udo Schmidt, with permission.

Limnebius nitidus (Figure 47) is among the smallest of the water beetles and in addition to wet mud, it makes mosses in swamps and at the edges of pools and streams its home (Nelson 1996). Adults are a mere mm long, so these scavengers of dead plants and animals are easily overlooked (Hilsenhoff 1975). Eggs of this genus are either naked or somewhat covered with loosely applied silk and hatch in 7-10 days (Usinger 1956). In my studies in the Appalachian Mountain streams of the eastern US, this genus likewise occurred among submerged mosses (Glime 1968).

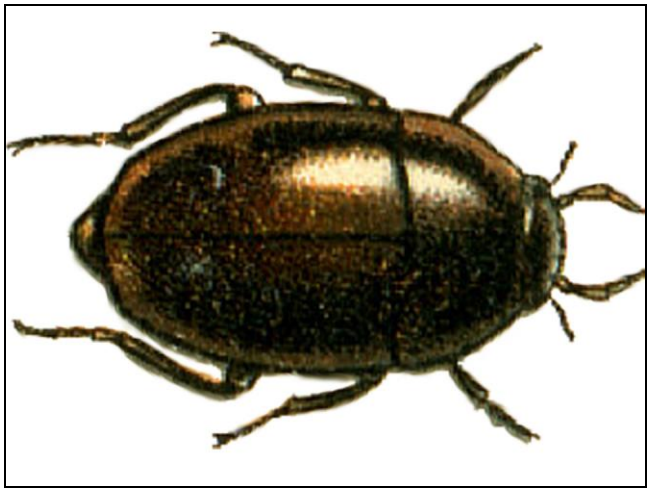

Figure 47. ***Limnebius nitidus*** adult, one of the smallest of all water beetles and a moss dweller in swamps. Photo through United States public domain.

Hygrotus decoratus (Figure 48) lives in shallow, mossy fens in North Hampshire, UK, where mosses may provide safe sites for larvae and adults (Denton 2013). ***Hygrotus novemlineatus*** was reared with **Chironomidae** larvae as a food source (Nilsson 1983). Mosses were provided in the culture chamber. After a few days, the beetles laid eggs, attaching them to branches of mosses. But is this a normal substrate for egg-laying in nature? The habitat seems suitable, providing lots of **Chironomidae** larvae as food. This genus should be sought among bryophytes in other fens.

Figure 48. ***Hygrotus decoratus*** adult, a species of shallow mossy fens, at surface getting air. Photo by Niels Sloth, with permission.

Ptiliidae – Featherwing Beetles

This is a large, worldwide family of minute (0.3-2 mm long) beetles (Ptiliidae 2015). The egg size is half the length of the body and only one is developed at a time, permitting the female to store a large energy supply in the egg. Their wide-ranging habitats include moist leaf litter, under bark of dead trees, along sand and gravel banks of rivers and streams, beneath seaweed on beaches, in mammal nests, on dung, rotting cacti, ant and termite colonies, and other habitats containing rotting or damp organic material. And some seem to live their entire lives in bogs.

The small size of several **Ptiliidae** beetles – ***Tychobythinus bythinioides*** (**Staphylinidae or Ptiliidae;** Figure 65), ***Ptiliopycna moerens*** (Figure 49), ***Acrotrichis*** (Figure 50) – and other small beetles in bogs seems to correlate with a high incidence of **parthenogenesis** (reproduction from an unfertilized egg) in **relict** (habitat that survived from an earlier period) bogs (Dybas 1978), most likely having poor dispersal as an additional selection factor.

Figure 49. ***Ptiliopycna moerens*** adult, a parthenogenetic inhabitant of relict bogs. Photo © Stephen Luk for non-commercial use, with permission.

Figure 50. ***Acrotrichis*** sp. adult, a parthenogenetic inhabitant of relict bogs. Photo by Joyce Gross, with permission.

Ptiliopycna moerens is minute, less than 1.0 mm long, and lives in the northeastern United States and adjacent Canada (Dybas 1978). It lives in ***Sphagnum*** in bogs and swamp forests, confined within the limits of Wisconsinian glaciation. Males are seemingly restricted to the northern part of the range. More southern locations have parthenogenetic females, a common character of small beetles in relict bogs. (See the chapter on Terrestrial Insects – Coleoptera for further discussion of beetles in bogs.)

Silphidae – Large Carrion Beetles

This family is predominantly in the Northern Hemisphere, although scattered records exist in the Southern Hemisphere (Silphidae 2015a). Ranging in size from 7-45 mm, the family is rare in the tropics where ants might out-compete them (Silphidae 2015b). As the common name implies, the family feeds on decaying organic matter. Because of this feeding behavior, forensic scientists use their stage of development to determine how long a body has been dead.

Despite the need to find new carcasses as their carcass home ages, the **Silphidae** use walking as their primary means of locomotion (Silphidae 2015b). Most of their activity occurs at night.

The **Silphidae** have a variety of defenses (Silphidae 2015b). These include color warnings from **aposematism** (use of bright colors to advertise danger or unpalatability) to **Batesian mimicry** (mimicking coloration or behavior of poisonous or unpalatable species), chemical defenses, and parental care. And many of them use camouflage, having dark colors with a mix of gold, black, and brown to blend with their environment.

Some carrion beetles (**Silphidae**) occur in bogs. Beninger and Peck (1992) described the resource use by ***Nicrophorus*** species (carrion beetles, **Silphidae**) in a ***Sphagnum*** (Figure 51) bog near Ottawa, Canada, and found that resource use differed little from resource use in forested habitats. However, ***Nicrophorus vespilloides*** (Figure 52) used only small carrion (Figure 53) in the bog for reproduction, whereas the closely related ***N. defodiens*** (Figure 54) went to the nearby forest for reproduction. Likewise, ***N. sayi*** (Figure 55), ***N. orbicolis*** (Figure 56), and ***N. tomentosus*** (Figure 57), also bog inhabitants, were rarely associated with the small carrion of the bog, but rather reproduced mostly in the forest.

Figure 51. ***Sphagnum*** blanket bog. Photo through Creative Commons.

Figure 52. ***Nicrophorus vespilloides*** adult, a common carrion beetle that occurs in bogs. Photo by Tim Faasen, with permission.

Figure 53. ***Nicrophorus vespilloides*** with small carrion, a preferred substrate for its reproduction in bogs. Photo by Niels Sloth, with permission.

Figure 54. ***Nicrophorus defodiens*** adult, a bog dweller that goes to the forest to reproduce. Photo by Derek Sikes, through Creative Commons.

Figure 55. ***Nicrophorus sayi*** adult, a bog dweller that goes to the forest to reproduce. Photo by Tom Murray, through Creative Commons.

Figure 56. ***Nicrophorus orbicolis*** adult, a bog dweller that goes to the forest to reproduce. Photo by Tom Murray, through Creative Commons.

Figure 57. ***Nicrophorus tomentosus*** adult, a bog dweller that goes to the forest to reproduce. Photo by Tom Murray, through Creative Commons.

Staphylinidae – Rove Beetles

These beetles are distinctive in having short wings that cover less than half the abdomen (Bartlett 2004). This large family has about 58,000 species, ranging in size from 1 to 35 mm, but mostly 2-8 mm (Rove Beetle 2014). Distribution is worldwide, but records are lacking in vast areas of Asia and Africa. They live in every imaginable type of habitat and likewise eat everything – except living plants! There is now one exception to that – a recent discovery of a herbivore.

Like the **Carabidae**, the **Staphylinidae** are not aquatic, but likewise inhabit bogs (Boyce 2011). In Dartmoor, UK, ***Gymnusa brevicollis*** (Figure 58) is **stenotopic** (able to tolerate only a restricted range of habitats or ecological conditions). Its preferred habitat is saturated ***Sphagnum*** (Figure 51) in extremely wet acid mires where they can be found at the edge of bog pools.

Figure 58. ***Gymnusa brevicollis*** adult, a beetle that lives among saturated ***Sphagnum*** at the edge of bog pools of wet acid mires. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Myllaena kraatzi (Figure 59), a nationally (UK) rare species, is restricted to very high quality acid mires with abundant bog mosses (Boyce 2011). It is collected by shaking the ***Sphagnum*** (Figure 51) and litter, suggesting close ties with these two substrates. ***Oxypoda procerula*** (Figure 60) is likewise sampled by shaking the litter and ***Sphagnum***, indicating that it is directly a moss dweller.

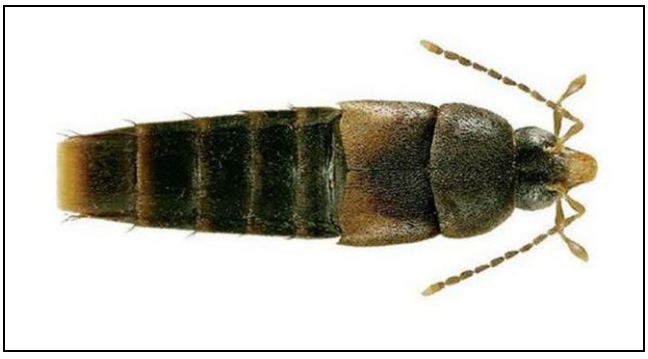

Figure 59. ***Myllaena vulpina*** adult. ***Myllaena kraatzi*** is a rare species of high quality acid mires in the UK. Photo by Reginald Webster, Jan Klimaszewski, Georges Pelletier, and Karine Savard through Creative Commons.

Figure 60. ***Oxypoda procerula*** adult, a ***Sphagnum*** and litter dweller. Photo by Udo Schmidt, through Creative Commons.

Philonothus nigrita (Figure 61) is a characteristic species in ***Sphagnum***-dominated (Figure 51) acid mires (Boyce 2011). It can be found by treading on the moss cushions, causing it to float out of the saturated ***Sphagnum***. ***Stenus brevipennis*** (see Figure 62) lives among ***Sphagnum*** in blanket bogs. ***Stenus kiesenwetteri*** (Figure 63) is rare in the UK, occurring in very wet ***Sphagnum*** (Butler 1886).

Figure 61. ***Philonothus nigrita*** adult, a species that characterizes ***Sphagnum***-dominated acid mires. Photo by Marko Mutanen, through Creative Commons.

Figure 62. ***Stenus biguttatus*** adult. ***Stenus brevipennis*** lives among ***Sphagnum*** of blanket bogs. Photo through Creative Commons.

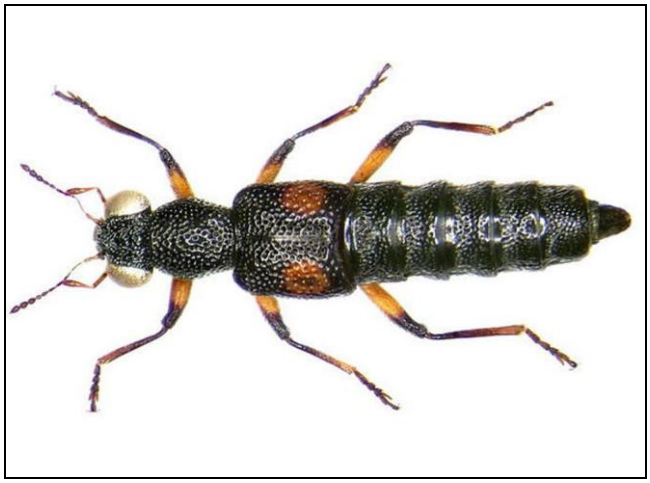

Figure 63. ***Stenus kiesenwetteri*** adult, a rare beetle inhabiting very wet ***Sphagnum***. Photo by Udo Schmidt, through Creative Commons.

Unlike the other **Staphylinidae** discussed here, ***Dianous coerulescens*** (Figure 64) lives where water trickles over mosses and liverworts (Butler 1886).

Figure 64. ***Dianous coerulescens*** adult on leafy liverwort. Photo by Malcolm Storey, through Creative Commons.

The **Pselaphinae** beetles are represented along the postglacial fringe in the central and eastern United States where they inhabit ***Sphagnum*** (Figure 51) bogs (Reichle 1966). More than 20 species of pselaphids characterize these bogs. They are relict species with specific habitat requirements and poor dispersal ability. Some have very specific temperature range requirements: ***Tychobythinus bythinioides*** (=***Bythinopsis tychoides***; Figure 65), 21.5±0.81, 25.9-15.3°C; ***Decarthron defectum***, 28.5±0.55, 31.4-24.0; ***Pselaphus ulkei***, 19.5±0.86, 24.7-13.0; ***Reichenbachia borealis*** (a short-winged mold beetle; Figure 66), 21.±0.99, 26.2-14.4; ***Rybaxis clavata*** (Figure 67), 28.3±0.41, 29.9-25.1 (Reichle 1967). The moss microhabitats provide them with both the required near-saturation humidities and the multiple temperature ranges they require. Changes in temperature stratification regimes result in different species occurring at different seral stages in the bogs.

Figure 65. ***Tychobythinus bythinioides*** adult, a minute beetle that takes advantage of the temperature and moisture stratification in a ***Sphagnum*** bed to meet its needs. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 66. ***Reichenbachia borealis*** adult, a minute beetle that takes advantage of the temperature stratification in a ***Sphagnum*** bed to meet its temperature needs. Photo by Tom Murray, through Creative Commons.

Figure 67. ***Rybaxis clavata*** adult, a minute beetle that takes advantage of the temperature stratification in a ***Sphagnum*** bed to meet its temperature needs. Photo by Tom Murray, through Creative Commons.

Scirtidae (=Helodidae) – Marsh Beetles

This is a worldwide family, but is most diverse in the temperate region (Murray 2005). The larvae live in both stagnant and flowing water where abundant decomposing plant material is present. Adults live on vegetation and on rotting vegetation. The **Scirtidae** are soft-bodied relative to other beetles and are slightly flattened to nearly **subglobular** (almost globe-shaped) (TOL 2011). Their sizes range 1-15 mm long. Some females secrete substances that may be pheromones used to stimulate males into courtship (Ruta 2008).

This is typically a beetle of open water, but in a subalpine springbrook in the southern Alps of New Zealand, **Scirtidae** (Figure 68) are most abundant in the moss ***Acrophyllum quadrifarium*** (=*Pterygophyllum quadrifarium*; Figure 69) at the edge of the inner spray zone where the mosses are saturated (Cowie & Winterbourn 1979).

Figure 68. **Helodidae** adult, a beetle that is abundant among ***Acrophyllum quadrifarium*** in the subalpine springbrooks of the southern Alps of New Zealand. Photo from Pybio at <www.pybio.org.>, with permission.

Figure 69. ***Achrophyllum quadrifarium***, a bryophyte habitat for **Helodidae** in streams in the Southern Alps of Australia. Photo by Jan-Peter Frahm, with permission.

Cyphon (Scirtidae; Figure 70-Figure 72) has been collected from wet mosses at the edge of a cold spring (Usinger 1974). ***Cyphon hilaris*** (Figure 71) in Dartmoor, UK, prefers bog pools that have ***Sphagnum*** (Figure 51) (Boyce 2011). In North Hampshire, UK, ***C. hilaris*** occurs infrequently in wetlands with peaty soils, acidic bogs, and fens (Denton 2013). ***Cyphon padi*** (Figure 72), also in North Hampshire, prefers peaty areas in wooded sites where the ***Sphagnum*** is flooded.

Figure 70. ***Cyphon*** pupa. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

Figure 71. ***Cyphon hilaris*** adult, a species that occurs among wet mosses at the edge of a spring Photo by Stefan Schmidt, through Creative Commons.

Figure 72. ***Cyphon padi*** adult, a species of flooded ***Sphagnum*** in peaty forested areas. Photo by Miroslav Deml, through Creative Commons.

Elmidae – Riffle Beetles

These are small beetles (1-8 mm) (Gordon & Post 1965). The **Elmidae** have a distribution similar to that of the **Silphidae**, but there are more known locations, including southern Africa (Harrison 2009). As the common name describes, these beetles usually live in the riffles of cool, rapid streams (Arnett *et al*. 2002; Harpootlian 2005). They feed mostly on decaying plants and algae (Epler 2010).

Only three species of **Elmidae** are considered to be frequent aquatic bryophyte dwellers: ***Promoresia tardella*** (Figure 73), ***Atractelmis wawona*** (Figure 74), and ***Cleptelmis addenda*** (Figure 75) (Brown 1972; Shepard & Barr 1991; Bowles *et al*. 2003; Elliott 2008a), all from North America where the family has many more species (80 species) than in Europe (46 species) (Elliott 2008a). But if one looks among the liverworts in the Pacific states of USA, a fourth genus, ***Bryelmis*** (Figure 108-Figure 110) is lurking (Bowles *et al*. 2003 – see below); further searching among submerged leafy liverworts may expand this ***Bryelmis*** distribution. Nevertheless, a number of species use bryophytes at some stage in their lives. Both larvae and adults of some **Elmidae** are able to feed on mosses (Usinger 1974). When disturbed, **Elmidae** may play dead for a number of hours before attempting to relocate (Usinger 1956). ***Cleptelmis*** (Figure 75) may wait for 12-15 hours before moving. Such patience!

Figure 73. ***Promoresia tardella*** adult, one of the few frequent bryophyte dwellers in the **Elmidae**. Photo through Creative Commons.

Figure 74. ***Atractelmis wawona*** adult, a frequent bryophyte inhabitant. Photo through Creative Commons.

Figure 75. ***Cleptelmis addenda*** adult, one of the few frequent **Elmidae** bryophyte dwellers. Photo by Crystal Maier, through Creative Commons.

Elmidae colonize mosses when insect-free mosses are introduced, but some of the elmids may be slow to colonize. This is no surprise since they creep and don't swim. For example, Maurer and Brusven (1983) found that the elmid ***Cleptelmis ornata*** (Figure 76) was the only insect that was slow to colonize insect-free test clumps of ***Fontinalis neomexicana*** (Figure 77) during a field experiment in Idaho, USA.

Elliott (2008a) summed up some of the characters that define the bryophyte dwellers. Their larvae have a triangular cross section. Among this group he included ***Elmis*** (Figure 87-Figure 86), ***Esolus*** (Figure 84-Figure 85), and ***Oulimnius*** (Figure 88-Figure 89), none of which were considered by earlier researchers mentioned above to be the frequent bryophyte dwellers. All members of the family have aquatic larvae and most have aquatic adults. The pupae are terrestrial. This means that the newly emerged adults must re-enter the water – no small feat for such a small insect. They must break through the surface tension – easy for us, but nearly impossible for them unless they have something to cling to and provide leverage for them to break through (see Figure 78). Bryophytes, plants, and rocks can help here.

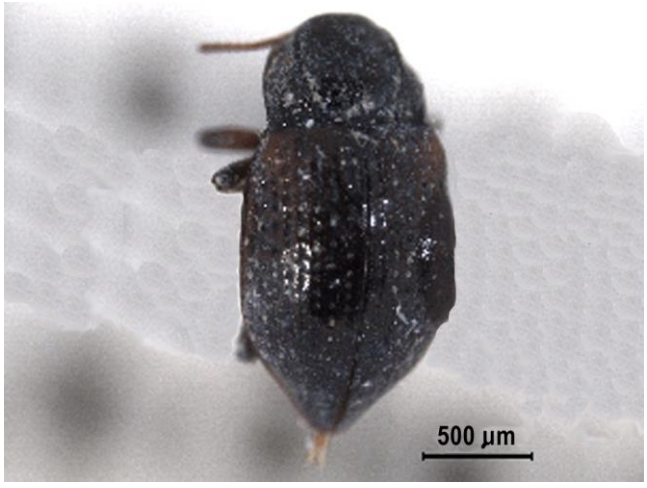

Figure 76. ***Cleptelmis ornata*** adult, a slow colonizer of ***Fontinalis neomexicana***. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 77. ***Fontinalis neomexicana***, a moss that is avoided as home for liverwort-dwelling ***Bryelmis***. Photo by Belinda Lo, through Creative Commons.

Figure 78. ***Dryops auriculatus*** (**Dryopidae)** adult entering water by clinging to a plant. Note the rings in the water and depression of the surface by the beetle body. Photo by Tim Faasen, with permission.

The aquatic adults use the **plastron** for oxygen availability (Thorpe & Crisp 1949) – they are air breathers. The plastron apparatus is seen as a silvery layer (Figure 79) on the ventral side of the beetle. Some members include the antennae as part of the apparatus that holds the air bubble. They groom the plastron with brushes on the femur of the leg and also use these brushes to add air bubbles to the plastron apparatus by smearing bubbles over the plastron. Most do not need to return to the surface, using the mouthparts to capture oxygen bubbles emitted by plants. If the plastron air layer is thick, it has a silvery sheen and is called a **macroplastron** (Figure 116). When air diminishes from the macroplastron to the normal, smaller plastron, air exchange with the water is generally adequate to maintain the duller-looking air bubble and meet their needs. This low need for fresh air is likely possible because these beetles do not swim, requiring less oxygen for their clambering movements.

In a tributary of the Danube, ***Elmis maugetii*** and ***Riolus subviolaceus*** (Figure 80) were abundant in high flow areas among coarse mosses, whereas ***Esolus parallelepipedus*** (Figure 81) and ***Limnius volckmari*** (Figure 82-Figure 83) were among algae in moderately flowing water (Dietrich & Waringer 1999). ***Esolus***

angustatus (Figure 84-Figure 85) and ***Oulimnius tuberculatus*** (Figure 88-Figure 89) were more common in moderate flow with abundant moss-covered pebbles.

Figure 79. ***Riolus subviolaceus*** adult with thin plastron showing as a silver line where the elytra meets the ventral plastron. Photo by Tim Faasen, with permission.

Figure 80. ***Riolus subviolaceus*** adult, inhabitants of high flow areas among coarse mosses. Photo by Tim Faasen, with permission.

Figure 81. ***Esolus parallelepipedus*** adult, a species with a high drift rate. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 82. ***Limnius volckmari*** larva, an elmid that seems to prefer algae to mosses as a substrate. Photo by Urmas Kruus, with permission.

Figure 83. ***Limnius volckmari*** adult, an elmid that seems to prefer algae to mosses as a substrate. Photo by Urmas Kruus, with permission.

Figure 84. ***Esolus angustatus*** larva, member of a genus that has the triangular cross section that characterizes many bryophyte dwellers. Photo by Tim Faasen, with permission.

Figure 85. ***Esolus angustatus*** adult, member of a genus that is common among bryophytes. Photo by Tim Faasen, with permission.

In British streams and rivers, ***Elmis aenea*** (Figure 86-Figure 87), a moss dweller in rapid streams and rivers (both above and below water), occurred among bryophytes as both adults and larvae, but larvae were more abundant among small stones or under larger ones (Elliott 2008a). In these rivers and streams, ***Oulimnius tuberculatus*** (Figure 88-Figure 89) preferred tracheophytes.

Figure 86. ***Elmis aenea*** larva, a species whose distribution is related to elevation. Photo by Niels Sloth, with permission.

Figure 87. ***Elmis aenea*** adult, a moss dweller in rapid streams and rivers. Photo by Tim Faasen, with permission.

In a 39-month study, Elliott (2008b) examined the effect of density on drift rate. Most of the larvae and adults of **Elmidae** drift at night with very few drifting in daytime. Elliott found that the **Elmidae** in the study, including the bryophyte dwellers, did not drift on the basis of density. Drift losses accounted for only about 0.07% of total losses in the benthos. The exception to this was the high drift, during a heavy rainfall, of early stages of immature adults of ***Elmis aenea*** (Figure 87), ***Oulimnius tuberculatus*** (Figure 88-Figure 89), and ***Esolus parallelepipedus*** (Figure 81), all species known from bryophytes. For ***Elmis aenea***, the highest drift density was in the earliest life stage soon after egg hatching; for ***O. tuberculatus*** it was the start of the larval overwintering period. Frost (1942) found that ***Oulimnius tuberculatus*** lives among mosses (and other habitats); moving to land for pupation most likely subjects this insect to the drift.

Figure 88. ***Oulimnius tuberculatus*** adult, a European moss dweller. Photo by J. C. Schou, with permission.

Figure 89. ***Oulimnius tuberculatus*** larva, an aquatic moss dweller. Photo by J. C. Schou, with permission.

Nelson (1996) described ***Elmis aenea*** (Figure 86-Figure 87) as a species from moss-covered rocks in rapid rivers and streams. Berthélemy (1966) found larvae (Figure 86) and adults (Figure 87) of ***E. aenea*** and ***E. maugetii*** were often abundant among mosses and liverworts in the Pyrénées. The moss-dwelling species were generally smaller than those among stones. Nelson found that the proportion of ***E. aenea*** vs ***E. rioloides*** (Figure 90) among mosses was related to elevation.

Figure 90. ***Elmis rioloides*** adult, a moss dweller whose distribution is affected by elevation. Photo through Creative Commons.

Gurtz and Wallace (1984) found larvae of the elmid ***Promoresia*** in only one sample in Big Hurricane Branch.

They had learned from J. Haefner (personal communication) that these larvae in Sawmill Branch occurred almost exclusively among aquatic mosses (Haefner & Wallace 1981). I found ***Promoresia elegans*** (Figure 91-Figure 92) frequently among the bryophytes [***Fontinalis dalecarlica*** (Figure 93-Figure 94), ***Hygroamblystegium fluviatile*** (Figure 95), ***Scapania undulata*** (Figure 112)] of Appalachian Mountain, USA, streams. This is a genus that exhibits the triangular cross section that Elliott (2008a) suggested to be characteristic of bryophyte dwellers.

Figure 91. ***Promoresia elegans*** adult, a common stream moss inhabitant. Photo through Creative Commons.

Figure 92. ***Promoresia elegans***, a larva that is common among bryophytes**.** Photo by Erin Hayes-Pontius, through Wikimedia Commons.

Figure 93. Riffles with ***Fontinalis dalecarlica***, home for ***Promoresia elegans***. Photo by Janice Glime.

Figure 94. ***Fontinalis dalecarlica*** showing the dangling streamers. Photo by Jan-Peter Frahm, with permission.

Figure 95. ***Hygroamblystegium fluviatile***, home to several species of **Elmidae**. Photo by Janice Glime.

In addition to ***Elmis***, Berthélemy (1966) found ***Riolus cupreus*** (Figure 96-Figure 97), ***Esolus parallelepipedus*** (Figure 81), and ***Oulimnius tuberculatus*** (Figure 88-Figure 89) among mosses in streams in the Pyrénées. ***Elmis*** and ***Oulimnius*** were strong **muscicoles** (living among or in association with mosses). Hebauer (1994) found ***Elmis obscura***, ***E. rioloides*** (Figure 90), and ***Oulimnius tuberculatus*** among mosses in streams in Central Europe.

Figure 96. ***Riolus cupreus*** larva, an inhabitant of Pyrénées stream mosses. Photo by Urmas Kruus, with permission.

Figure 97. ***Riolus cupreus*** adult, an inhabitant of Pyrénées stream mosses. Photo by Urmas Kruus, with permission.

The **Elmidae** spend their larval life in the water, pupate on land, then after their initial dispersal flight they return to the water. The interesting note here is that once they return to the water, they lose their ability to fly (Ward 1992). This locks them into their habitat no matter what the water conditions. For those inhabiting stream mosses, this means that if the water level drops, they must remain in the habitat of the mosses, unable to disperse for any significant distance. But for them it seems to be no problem because they have a high drought tolerance (Larimore *et al*. 1959; Iverson *et al*. 1978).

Steffan (1961) suggested that the mosses such as ***Fontinalis*** (Figure 94) were necessary for some **Elmidae** and **Dryopidae** to make the transition from water to land (and back to the water) during their amphibious life. Bryophytes would permit them to gain a firm hold while breaking through the surface tension in either direction.

In Louisiana, USA, the endangered riffle beetle ***Heterelmis comalensis*** (Figure 98-Figure 99) lives on submerged roots and aquatic mosses (Barr & Chapin 1988). In this same habitat, ***Microcylloepus pusillus*** (Figure 100-Figure 101) likewise uses these substrata. In the Appalachian Mountain streams, USA, I found a species of ***Microcylloepus*** among the submerged mosses (Glime 1968).

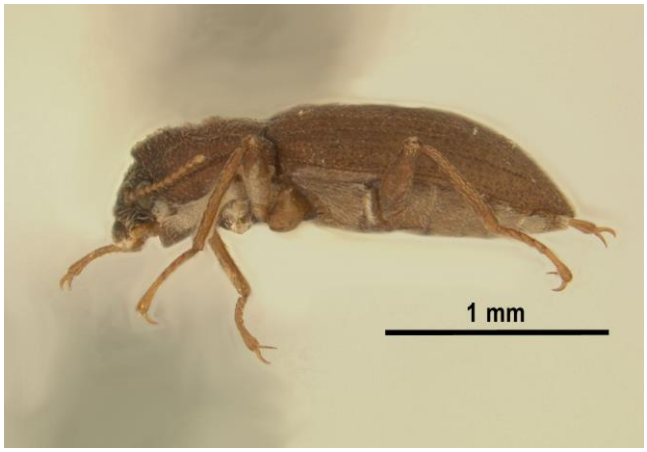

Figure 98. ***Heterelmis comalensis*** adult, a moss dweller, as well as living on submerged roots. Photo through Creative Commons.

Figure 99. ***Heterelmis comalensis*** larva, a moss inhabitant. Photo by Mike Quinn, through Creative Commons.

Figure 100. ***Microcylloepus pusillus*** larva, an inhabitant of submerged roots and mosses. Photo by Mike Quinn, through Creative Commons.

Figure 101. ***Microcylloepus pusillus*** adult, an inhabitant of submerged roots and mosses. Photo by Mike Quinn, through Creative Commons.

My experience with **Elmidae** among the stream bryophytes in the Appalachian Mountains, USA, differs from that in many of the reports cited here (Glime 1968). I found six species, and among these only ***Microcylloepus*** (Figure 100-Figure 101) and ***Promoresia elegans*** (Figure 91-Figure 92) (both larvae and adults) have been reported in the other studies cited herein. The numbers of ***Promoresia elegans*** actually exceeded the numbers of **Chironomidae** among bryophytes in one stream in March; in winter I found only two adults. In addition I found two species of ***Optioservus*** (Figure 102-Figure 103) on ***Hygroamblystegium fluviatile*** (Figure 95); on ***Fontinalis dalecarlica*** (Figure 93-Figure 94), I found ***Stenelmis crenata*** (Figure 105-Figure 104) and one species of ***Dubiraphia*** (Figure 106-Figure 107).

Figure 102. ***Optioservus fastiditus*** adult, member of a genus that lives among mosses in Appalachian Mountain, USA, streams. Photo by Sarah McManus, through Creative Commons.

Figure 103. ***Optioservus*** larva, member of a genus that lives among mosses in Appalachian Mountain, USA, streams. Photo by Joseph C. Fortier, through Creative Commons.

Figure 104. ***Stenelmis*** larvae, an inhabitant of bryophytes in Appalachian Mountain, USA, streams. Photo by Erin Hayes-Pontius, through Creative Commons.

Figure 105. ***Stenelmis crenata*** adult, a moss dweller in Appalachian Mountain, USA, streams. Photo by Tom Murray, through Creative Commons.

Figure 106. ***Dubiraphia*** larva. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

Figure 107. ***Dubiraphia vittata*** adult. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

It is no surprise that new species remain to be discovered among the bryophytes. But one such recent discovery in the western states of the USA was not just a new species, but a new genus, widespread, and with multiple species! And these were among aquatic bryophytes, particularly leafy liverworts (Barr 2011). These three species were ***Bryelmis idahoensis*** (Figure 108), ***B. rivularis*** (Figure 109), and ***B. siskiyou*** (Figure 110) from streams and springs in the states of Washington,

Oregon, California, and Idaho. Once Barr alerted her colleagues in neighboring states of her find, they began searching this new habitat, the leafy liverwort ***Chiloscyphus polyanthos rivularis*** (Figure 111). After searching through 652 adult and over 200 larval specimens from museum and new collections, she distinguished three species, all previously unknown. And now all these people know the difference between a moss and a liverwort – the latter houses ***Bryelmis***.

Figure 108. ***Bryelmis idahoensis*** adult male, a species that seems to be restricted to leafy liverworts. Photo by Traci Grzymala, with permission.

Figure 109. ***Bryelmis rivularis*** adult male, a species that seems to be restricted to leafy liverworts. Photo by Traci Grzymala, with permission.

Figure 110. ***Bryelmis siskiyou*** adult male, a species that seems to be restricted to leafy liverworts. Photo by Traci Grzymala, with permission.

Figure 111. ***Chiloscyphus polyanthos***, primary home to the recently discovered genus ***Bryelmis***. Photo by Jan-Peter Frahm, with permission.

Barr had found ***Bryelmis idahoensis*** in association with aquatic bryophytes on rocks, but some also occurred on water-soaked wood. ***Bryelmis rivularis*** preferred ***Chiloscyphus polyanthus rivularis*** (Figure 111) and ***Scapania undulata*** (Figure 112) and tended to avoid both of the mosses ***Fontinalis neomexicana*** (Figure 77) and ***Platyhypnidium riparioides*** (Figure 113). By targetting aquatic liverworts she discovered another new species, ***B. siskiyou***.

Figure 112. ***Scapania undulata***, home for some members of ***Bryelmis***. Photo by Hermann Schachner, through Creative Commons.

Figure 113. ***Platyhypnidium riparioides***, a habitat rejected by ***Bryelmis***, a leafy liverwort inhabitant. Photo by Hermann Schachner, through Creative Commons.

In Mexico, Central America, and the West Indies, ***Lara avara*** (Figure 114-Figure 115) spends 4-6 years as larvae, going through seven instars (Spangler & Santiago-Fragoso 1992). The larvae leave the stream water in spring and move to mosses at the stream bank in their last instar. In their last instar they burrow into small "cells" under mosses at water's edge (Spangler & Santiago-Fragoso 1992) or under mosses on the upper surface of emergent logs (Elliott 2008a). When the moss dries in early summer the larvae begin pupation (Spangler & Santiago-Fragoso 1992). This pupation lasts only two or more weeks.

Figure 114. ***Lara avara*** adult, a species that pupates among mosses. Photo through Creative Commons.

Figure 115. ***Lara avara*** larva, a species that crawls out of the water to pupate among mosses at the water's edge. Photo by Arlo Pelegrin, with permission.

Dryopidae – Long-toed Water Beetles

The **Dryopidae** are mostly Northern Hemisphere (Dryopidae 2015), but the scant records in the Southern Hemisphere may reflect limited collecting rather than absence of beetles. This is an interesting family in that the larvae are mostly terrestrial, living in decaying plant material, rotting wood, and soil, whereas the adults (3.5-5.5 mm long) return to running water to lay eggs (Watson & Dallwitz 2003). They are unable to swim and clamber about by clinging to plants. They eat plants as adults, but larvae may also prey on small animals. The **Dryopidae** occur on every continent except Antarctica and Australia, but they are most common in the tropics (Dryopidae 2015). They use hairs to create a **plastron** apparatus (see introductory information), enabling them to breathe under water.

The **Dryopidae** (Figure 116) seem seldom to be reported among the bryophytes of aquatic habitats. Nevertheless, Percival and Whitehead (1930) found that the **Helminae** (**Dryopidae**) reached 1244 per dm^2 in the mossy area of streams in the UK, whereas among stones with no mosses they reached only 10-15 per dm^2. Buczyński *et al*. (2014) reported that in Poland ***Dryops anglicanus*** (Figure 117) lives in canals created by beavers in floating ***Sphagnum*** (Figure 51) mats. In rivers of Northwest Spain, ***Dryops luridus*** preferred moss substrata (Sarr *et al*. 2013). In the Appalachian Mountain, USA, streams, I found a species of ***Helichus*** (Figure 118) (Glime 1968).

Figure 116. ***Dryops luridus*** adult with plastron surrounding entire body, a **macroplastron**. Photo by Tim Faasen, with permission.

Figure 117. ***Dryops anglicanus*** adult, an inhabitant of beaver-made canals in floating ***Sphagnum*** mats. Photo by Stefan Schmidt, through Creative Commons.

Figure 118. ***Helichus lithophilus*** adult, member of a genus with bryophyte dwellers in Appalachian Mountain, USA, streams. Photo by Mike Quinn, through Creative Commons.

Chelonariidae – Turtle Beetles

These are relatively small beetles (adults 2.5-10 mm long) and somewhat resemble turtles in that their heads are hidden and their legs can be tucked into depressions in the abdomen made for them (Harpootlian 2006). They are best known from eastern North America, western South America, and Central America, but there are some records from eastern Asia (Chelonariidae 2015). They reach their greatest diversity in the Neotropics.

Sometimes it is hard to determine if the insects are aquatic or terrestrial. Perhaps it is just a wide niche with a wide water tolerance. In other cases, entrance into the aquatic world may be accidental. Such seems to be the case with ***Chelonarium*** (Figure 119), a genus that inhabits damp moss (Spangler 1980). From these damp mosses, they may occasionally get washed into the nearby stream by rain or high water (Brown 1972). The larvae, once considered aquatic, lack gills (Spangler 1980). Members of the genus are often associated with the roots of terrestrial **epiphytes** (plants that grow on other plants but are not parasitic) and often feed on ants and termites.

Figure 119. ***Chelonarium lecontei*** adult, a species once thought to have aquatic larvae. Note how the legs fit into the exoskeleton. Photo through Creative Commons.

Lampyridae – Lightning Bugs

"When night closes in, fireflies flicker with an ethereal and haunting light" (WWF 2011). This is the family of fireflies (Figure 120) that delighted us as children. And one of them, ***Luciola ficta*** (see Figure 121), lives in the water as a larva and uses mosses (Ho *et al*. 2010)! The adults court, mate, and females oviposit on mosses (or under leaf litter, in root gaps, or in soil clefts), but on land. The young hatchlings must make their way to the water. This unique Asian beetle is in danger of extinction because its habitat is disappearing. However, the Chinese are attempting to save it by learning its development (Ho *et al*. 2006) and creating small pools for it (WWF 2011).

Figure 120. **Lampyridae** adult showing the portion that lights up. Photo by Andy Deans, through Creative Commons.

Figure 121. ***Luciola lusitanica*** adult. ***Luciola ficta*** is a species with aquatic larvae and adults that oviposit on terrestrial mosses. Photo by Tim Faasen, with permission.

Latridiidae – Minute Brown Scavenger Beetles

Minute it is, with sizes up to 3 mm (McClarin 2005). The family mostly eats fungi and slime molds, frequenting decaying vegetation (Latridiidae 2015). Records of this family are concentrated in Europe, with scattered records in North America, South America, Africa, and Australia. But this family is even present in the Antarctic region.

In South Georgia (southern Atlantic Ocean) bryophytes often play an important role as habitats for insects. One such inhabitant is ***Aridius malouinensis*** (Figure 122) (Arnold & Convey 1998).

Figure 122. ***Aridius malouinensis*** adult, a moss dweller on the island of South Georgia. Photo by Roger S. Key, with permission.

Curculionidae – Weevils

Despite the fact that **Curculionidae** (Figure 123) is the third largest animal family (Curculionidae 2014), its presence is missing among aquatic mosses. Its distribution is worldwide, although records are lacking in vast areas of Asia and Africa (Curculionidae 2015). Adults range 1-40 mm long and are plant feeders.

Figure 123. ***Cionus hortulanus*** adult, showing one of many thousands of bizarre forms present in this family. Photo by Lukas Jonaitis, through Creative Commons.

This terrestrial family has limited associations with the water. The marine weevil ***Palirhoeus eatoni***, on the Prince Edward Islands south of Africa, lives among tufts of algae as larvae (Doyen 1976). When it pupates it goes above the high water level among clumps of the shoreline moss ***Grimmia amblyophylla*** (Jeannel 1940, 1953).

Lagriidae

Our records of bryophyte dwellers from Africa seem to be rare, so it is pleasing to see a study on bryophagy in South Africa (Chown 1993). Chown found that members of the **Lagriidae** in the Afromontane forest fed on both green and brown parts of the moss ***Braunia secunda***. This is a family with poorly known feeding habits, and the species discovered here was unnamed.

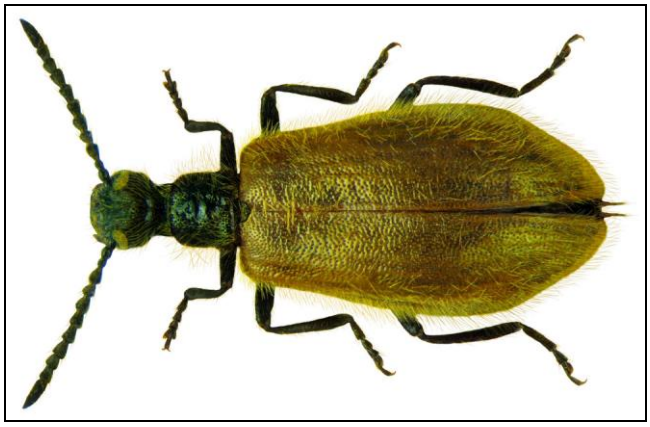

Figure 124. ***Lagria hirta*** adult, a beetle that eats the moss ***Braunia secunda***. Photo by Udo Schmidt, with permission.

Figure 125. ***Braunia secunda***, home for some members of the Lagriidae. Photo by Efrain De Luna, with permission.

Summary

The suborder **polyphaga** includes a number of families of beetles that live among bryophytes, especially the small members.

These include **Helophoridae** that live in both bogs and streams among bryophytes. **Hydrochidae** live among bog mosses. **Hydrophilidae** are common in bog pools, where diversity is high, but some also occur among stream bryophytes. The **Hydraenidae** are tiny beetles that live primarily among bryophytes in streams and fast rivers. Some small members of the **Ptiliidae** are **parthenogenetic** and live in **relict** bogs. The **Silphidae** are carrion feeders and those in bogs breed on small carrion such as frogs. The **Staphylinidae** are not typical bryophyte dwellers, and are not aquatic, but they live in bogs. The **Scirtidae** find suitable habitat in the saturated mosses of the spray zone of the springbrooks in the Alps of New Zealand.

The best adapted family of the beetle bryophyte dwellers is the **Elmidae**. They use a **plastron** to breathe and are small enough to clamber about among the bryophyte stems and leaves. The **Dryopidae** are similarly adapted and both families can be found among stream bryophytes.

Some species of the **Chelonariidae** live among wet mosses of stream banks and seem to occasionally fall in. The species ***Luciola ficta*** is a firefly in the family **Lampyridae**. Its larvae live in the water and the adults deposit their eggs on mosses and other substrata near water. The **Latridiidae** are among the insects in South Georgia where one species lives among the bryophytes. The **Curculionidae** are weevils and few are associated with aquatic habitats. Some live on floating plants and one species leaves its water home to pupate among shoreline mosses.

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Tim Faasen not only gave me permission to use his wide collection of insect images, he also helped me to understand the ecology of some of the species and provided me with additional images I needed. Thank you to Roger S. Key not only for his permission to use his images but for sharing his experiences with me regarding beetle use of bryophytes. Ronald Willson verified my beetle identifications for the mid-Appalachian Mountain study. Eileen Dumire proofread the chapter and offered suggestions to improve clarity.

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CHAPTER 11-11
AQUATIC INSECTS: HOLOMETABOLA – TRICHOPTERA, SUBORDER ANNULIPALPIA

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Figure 1. ***Fontinalis antipyretica*** in a small stream. This moss is often home to many kinds of insects, including even larger Trichoptera. Photo by Betsy St. Pierre, with permission.

LEPIDOPTERA – Moths and Butterflies

This predominantly terrestrial order has a number of aquatic members whose larvae live on tracheophytes. These include such families as the **Pyralidae** (Figure 2) and **Noctuidae**. Larvae of some aquatic species possess gills (Bouchard *et al*. 2004). The aquatic **Pyralidae** are the only **Lepidpotera** with aquatic pupae.

I have not been able to find any records of this order on bryophytes. However, on one occasion I found a caterpillar of the **Nymphalidae** in a bed of ***Fontinalis*** in the Red Cedar River, East Lansing, MI. Unfortunately, I was there for a different purpose and don't have any further details.

Figure 2. ***Petrophila*** larva (ventral view), a common aquatic moth that lives among aquatic plants. Photo by Bob Henricks, with permission.

TRICHOPTERA – Caddisflies

The **Trichoptera** are distinguished as adults by the hairs on their wings (Figure 3) and the resting position that looks like a pup tent (Figure 4). Their distribution is worldwide and size varies greatly. Most build cases that serve as retreats for both larvae and **pupae** (immature stages, often immobile) between larvae and adults).

Figure 3. ***Brachycentrus appalachia*** adult wings showing hairs. Photo by Jason Neuswanger, with permission.

Figure 4. ***Limnephilus frijole*** adult showing wings folded like a pup tent. Photo by Bob Newell, with permission.

Caddisflies are common inhabitants among mosses (Oswood 1979; Glime 1994; Ogbogu 2000; Ogbogu & Akinya 2001). Berg and Petersen (in Macan 1963) found a mean of 260 Trichoptera in just 1 sq meter of ***Fontinalis*** (Figure 1) in Lake Gribso. And Frost (1942) found 492,200 individuals per gram of mosses in Ireland. Several families of caddisfly larvae have members that use bryophytes in the construction of their homes (Glime 1978).

In North America, caddisfly larvae are closely associated with mosses such as ***Fontinalis*** (Figure 1) (Ogbogu 2001a). As the density of these mosses increases, so does the density of the caddisfly larvae. Ogbogu suggested that use of the mosses as part of their life cycle strategy permits these larvae to survive in the unstable habitats of streams.

Krno (1990) found that some **Trichoptera** were able to climb out of the water to move about among the wet emergent mosses. However, the fauna there was not as rich as that among submerged mosses. Galdean (1994) found that some caddisflies were common on the mosses lining the walls of the Somequl Cald Gorges. These mosses were clean, lacking **detritus** (organic matter produced by the decomposition of organisms), and formed a felt on the walls.

Some insect assemblages even partition the moss into several habitats. The caddisfly ***Brachycentrus*** (**Brachycentridae**; Figure 5) uses mosses (as well as rocks and sticks) for attachment; ***Tricorythodes*** (**Ephemeroptera**: **Leptohyphidae**) burrows among the stems and rhizoids; and the caddisfly ***Chimarra*** (**Philopotamidae**; Figure 6) lives in the gravel and sand at the base of the mosses, all in the riffles of one Wyoming river (Armitage 1961).

Figure 5. ***Brachycentrus occidentalis*** larvae. Photo by Arlen Thomason, with permission.

Figure 6. ***Chimarra tsudai*** larva, member of a genus that lives in gravel and sand at the bases of mosses in riffles. Photo by Takao Nozaki, with permission.

In the case of ***Helicopsyche sperata*** (**Helicopsychidae**; Figure 7), the aquatic surroundings are achieved by living on mossy rocks out of the stream but in the sun in locations kept wet by constantly dropping water (McLachlan 1880).

Figure 7. ***Helicopsyche*** sp. larva and case, a genus that lives on wet mosses in the splash of streams. Photo by Stephen Moore, Landcare Research, with permission, NZ.

Drift

Unlike most of the drifting aquatic insect species, many species of Trichoptera are day-active and do most of their drifting during the day (Waters 1972). This makes this group more vulnerable to predation by fish (White 1967), and this would particularly apply to the caseless caddisflies that are the most common caddisflies among bryophytes. However, Brusven (1970) found that among the caseless net-spinning caddisflies, ***Arctopsyche*** (Figure 8) drifted mostly at night and ***Hydropsyche*** (Figure 9) was rare in the drift. It is reasonable to assume that the bryophyte habitat may help to keep these caddisflies anchored as they move about, hence offering a safe refuge.

Figure 8. ***Arctopsyche ladogensis*** (**Hydropsychidae**) larva, a night drifter. Photo by Donald S. Chandler, with permission.

Figure 9. ***Hydropsyche pellucidula*** larva (**Hydropsychidae**), a rare drifter that can be found among bryophytes. Photo by Niels Sloth, with permission.

Food

Slack (1936) compared the food of twelve species of caddisflies. Among these, all but three had bryophyte leaf fragments in the gut. Those with more than half the larvae having bryophyte fragments were **Limnephilidae**: ***Glyphotaelius*** sp. (Figure 10), ***Limnephilus rhombicus*** – an opportunist in using a variety of materials to build its case (Figure 11), ***Stenophylax*** sp. (Figure 12), and ***Halesus*** sp. (Figure 13) and **Sericostomatidae**: ***Sericostoma personatum*** (Figure 14). Among common bryophyte dwellers, ***Hydropsyche*** sp. (Figure 9) had none and ***Rhyacophila dorsalis*** (Figure 15) had bryophyte fragments in only one out of nine larvae. An image on Garden World Images by Dave Bevan (Bevan 2014) suggests that some ***Stenophylax*** species eat mosses. (The image looks like either protonemata or a filamentous alga.)

Figure 10. ***Glyphotaelius pellucidus*** larva in its case, a genus known to eat bryophytes. Photo by Niels Sloth, with permission.

Figure 11. ***Limnephilus rhombicus*** larva showing two very different cases for the same species. This species eats bryophytes. Photo by Niels Sloth, with permission.

Figure 12. ***Stenophylax permistus*** adult, a genus known to eat bryophytes. Photo by Wouter Bosgra, through Creative Commons.

Figure 13. ***Halesus radiatus*** larva, a genus which has bryophyte consumers. Photo by Malcolm Storey, through Creative Commons.

Figure 14. ***Sericostoma personatum*** larva, a genus known to eat mosses. Photo by J. C. Schou, with permission.

Figure 15. ***Rhyacophila dorsalis*** larva, a common bryophyte dweller that had no moss in the gut of 8 out of 9 individuals. Photo by Walter Pfliegler, with permission.

Trichoptera is a large order, surpassing Ephemeroptera, Odonata, and Plecoptera in the number of genera (Wiggins & Mackay 1978). Most of the filter-feeders are in eastern North America in the deciduous forest biome. In addition to filter feeders, they are represented by grazers, especially upstream in the mountains where waters are cool. Shredders, especially in the **Limnephilidae**, can be found in lakes, ponds, streams, and even terrestrial habitats. Shredder-collectors are more common upstream and grazer-collectors are more common downstream. Some are predators.

Cairns (2005) reported that some caddisfly larvae consumed stream mosses. Kalachova *et al*. (2011) used acetylenic acids as biomarkers of ***Fontinalis antipyretica*** (Figure 1) to demonstrate consumption of this moss by Trichoptera in the Yenisei River.

Case Building

Case building provides most species of Trichoptera with a mobile home that protects them from predation. Some of these case-builders use bryophytes in their construction, including the New Zealand genus ***Zelolessica*** (**Helicophidae**; Figure 16) that sometimes uses bryophytes exclusively (Suren 1988). Frost (1942) found that a rather dominant caddisfly in her acid site on the River Liffey, Ireland, made cases from fragments of ***Fontinalis*** (Figure 1), but the larvae were too small for identification.

Figure 16. ***Zelolessica***, a caddisfly that sometimes uses bryophytes in case construction. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Elliot and Spribille found that in a northwest Montana fen caddisfly larvae use living ***Scorpidium scorpioides*** (Figure 17) to build cases. The larvae harvest small tips of branches (*ca*. 2 cm) of the ***S. scorpioides*** from plants that grow submerged in shallow water and attach them to their cases. Elliot and Spribille suggested that the moss provides a "buoyant platform" from which the caddisfly can emerge, prey on the invertebrate fauna, and then fly off without being trapped by the surface tension.

Figure 17. ***Scorpidium scorpioides***, a moss used for building caddisfly cases. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

SUBORDER ANNULIPALPIA

Hydropsychoidea

Ecnomidae

This is a relatively small family with worldwide distribution (Holzenthal *et al*. 2007). Although records of this family are worldwide, their main distribution is Gondwanan (Ecnomidae 2014). The larvae are of moderate size (5-10 mm) and live in retreats that they construct of silk in slow-water streams or lakes. They are predators, but some eat algae and detritus.

From Ceylon, Schmid (1958) reported ***Ecnomus ceylanicus*** (see Figure 18) and a new species, ***Ecnomus vaharika***, from large, mossy rocks in the torrent.

Figure 18. ***Ecnomus tenellus*** adult, member of a genus in which some species live in mossy torrents in Ceylon. Photo by Dick Belgers, through Creative Commons.

Hydropsychidae – Net-spinning Caddisflies

This worldwide family occupies a wide range of rivers and streams, always requiring flowing water to obtain its food (Hydropsychidae 2014). For example, in Ceylon Schmid (1958) reported ***Pseudoleptonema ceylanicum*** (see Figure 19) from a small, mossy creek in the jungle.

Figure 19. ***Pseudoleptonema supalak*** adult. In Ceylon, larvae of ***P. ceylanicum*** live in a mossy creek. Photo from Biodiversity Institute of Ontario, through Creative Commons.

The larvae can be relatively large, ranging 5-25 mm (Hydropsychidae 2015). The larvae of this family build retreats from plant and mineral fragments. These retreats open into the nets used to catch their food, including algae, detritus, and small animals. When another caddisfly attempts to occupy the retreat, the current occupant uses its hind legs, rubbing them under the head, to produce stridulations that warn the intruder to vacate (Jansson & Vuoristo 1979).

Larvae of ***Hydropsyche angustipennis***, ***H. siltalai***, ***H. nevae***, and ***H. pellucidula*** will enter any suitable retreat when forced to leave their own, and it need not be their own species or unoccupied. When it is already occupied, a vigorous fight will ensue. Larger defenders lost more fights as the size of the intruder increased. Stridulation increased the likelihood of a defender winning the fight.

Several researchers have supported the importance of mosses in the habitats of net-spinning caddisflies (Sprules 1947; Tanaka 1968). Oswood (1979) found that in a lake outlet stream in Montana, USA, larvae of **Hydropsychidae** had greater densities on moss-covered substrata (up to >1400 0.2 m^{-2}) than elsewhere. In a gorge of the Some River, Galdean (1994) considered the mosses on the walls of the gorge to create the conditions needed for the **Hydropsychidae** to develop. The boulders were cleaned by the river velocity on the concave bank, permitting the mosses, hence the **Hydropsychidae**, to develop there.

Parapsyche cardis preferred substrata in the order of mossy rock face > cobble riffle > pebble riffle > sandy reach (Gurtz & Wallace 1986). This relationship held true for all instars (larval stages) in both studied streams. Thus, mossy rock faces accounted for 94.8% of the total production of ***Parapsyche*** (Figure 20) in Hugh White Creek (with 36.5% rocky channel) and 87.3% in Big Hurricane Branch (with 16.8% rocky channel) in the southern Appalachian Mountains, USA. Haefner and Wallace (1981a, b) likewise found that the distribution of ***P. cardis*** was highly correlated with the distribution of moss in Sawmill Branch. In several Maryland, USA, streams, ***Parapsyche apicalis*** occurred among bryophytes, mostly ***Fontinalis dalecarlica***, and at the time were new records for Maryland, but it was not one of the more common **Hydropsychidae** represented among the mid-Appalachian bryophytes (Glime 1968).

Figure 20. ***Parapsyche apicalis*** larva, a species I collected among bryophytes in several Maryland streams. ***Parapsyche carda*** distribution is correlated with moss cover. Photo by Donald S. Chandler, with permission.

Wulfhorst (1994) examined the relative abundance of the caddisfly larva ***Diplectrona*** (Figure 29) in mosses and in **interstitial spaces** (spaces between individual sand grains in soil or aquatic sediments) in the **hyporheic** zone (region beneath and alongside a stream bed, where mixing of shallow groundwater and surface water occurs) of two streams in the Harz Mountains of West Germany. She found that ***Diplectrona*** was more abundant among the mosses at most collection stations, but that they were also abundant in the interstitial spaces of the hyporheic zone at 10 and 30 cm depths (Figure 21).

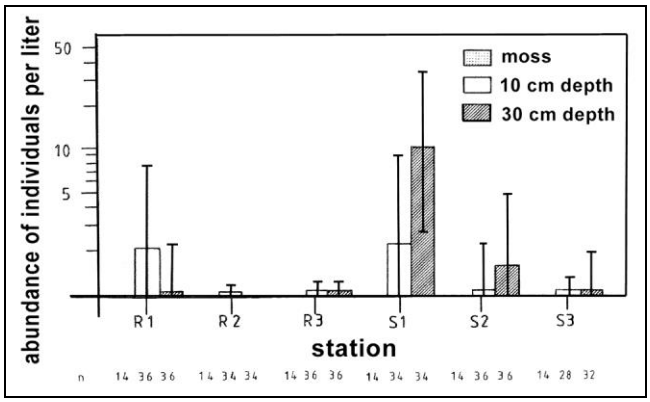

Figure 21. Mean abundance ± 95% CI of ***Diplectrona*** spp. in moss clumps in two streams in the Harz Mountains, West Germany. Numbers of samples are shown at the bottom. Redrawn from Wulfhorst 1994.

The high density of **Hydropsychidae** among stream mosses is supported by their ability to colonize that habitat rapidly. Smith-Cuffney (1987) found that artificial mosses reached their capacity of these net-spinning colonizers in only 7 days; Georgian and Thorp (1992) found that 6-9 days provided enough time for them to reach their constant colonization density among the artificial mosses. Mosses provide a particularly easy place to colonize relative to other stream habitats because their rough surface makes it easy to gain a hold that rescues them from the speeding water.

The **Hydropsychidae** can be considered ecosystem engineers (Nakano *et al*. 2005). In Japan, ***Hydropsyche orientalis*** (Figure 22, Figure 23) make their larval retreats on the upper surfaces of stones. These retreats provide a safe site for naiads of the mayfly ***Serratella setigera***, providing them with the slower flow that they prefer. It is likely that in the absence of these caddisflies and their nets that mosses could play a similar role in creating a suitable refuge. And in some cases it appears that the hydropsychids use the mosses in place of some, but not all, nets (Figure 24).

Ogbogu (2000) found **Hydropsychidae** associated with ***Fontinalis*** (Figure 1) in Nigeria and reported that the density of larvae increased when the moss grew. Both ***Cheumatopsyche*** (Figure 45) and ***Amphipsyche*** formed close associations and Ogbogu (2001a, b) suggested that the moss served as a **refugium** (area in which population of organisms can survive through period of unfavorable conditions, even glaciation) during vulnerable life cycle stages.

Figure 22. ***Hydropsyche orientalis***, a species that provides shelter used by the mayfly ***Serratella setigera***. Photo by Takao Nozaki, with permission.

Figure 23. ***Hydropsyche orientalis*** net where ***Ephemerella setigera*** takes refuge. Photo by Takao Nozaki, with permission.

Figure 24. **Hydropsychidae** nets among mosses. Photo by Janice Glime.

Pupal Sites

Frost, in her 1942 study of the River Liffey, Ireland, found that few Trichoptera pupae were present among the mosses. She considered this an expected absence because the caddisfly larvae usually seek another type of environment instead of mosses for **pupation** (period of development of pupa). For example, ***Ceratopsyche morosa*** (Figure 25) lives among moss and algae in young larval stages (Stern & Stern 1969), but just prior to pupation it moves to stones.

Temperature can signal that it is time to pupate. At least some ***Hydropsyche*** species cannot live below 8°C (Kaiser 1965). Instead, they build loose cases and go into the pupa state in autumn. Sleight (1913) found ***Hydropsyche*** pupae (Figure 26-Figure 28) among mosses in strong currents in the eastern USA. At maturity, these pupae moved to the surface where the pupal case would split and adults would emerge. The larval hooks made it possible for these caddis larvae to climb over the vegetation to find a suitable place for the pupa.

Figure 25. ***Ceratopsyche morosa*** larva, a moss dweller that leaves the mosses to pupate among stones. Photo by Bob Henricks, with permission.

Figure 26. ***Hydropsyche*** pupae, a genus that pupates among the protective mosses in strong currents. Photo by Mark Melton, with permission.

Crowding and Niche Separation

It appears that mosses might separate the niches of co-habiting net spinners. Late instar ***Diplectrona modesta*** (Figure 29) has a somewhat uniform occupancy among substrata in Big Hurricane Branch (Gurtz & Wallace 1986). The first three instars are most abundant on the (mossy) rock face and the fourth and fifth are more evenly distributed. But in Hugh White Creek, the rocks have a lower density of moss, and ***D. modesta*** is less common than in Big Hurricane Branch, where the moss is thicker. In fact, in Hugh White Creek, ***D. modesta*** is most abundant in the cobble riffle and least abundant in the rock face samples, while first instars are most common on sand. Gurtz and Wallace suggested that the lower density of moss in the Hugh White Creek may not provide enough microhabitats and that differences in available substrata could account for the differences in productivity. Mosses provide a suitable substrate for attaching the nets (Figure 30) and retreats of these caddisflies while providing a range of current velocities. The nets themselves do not, however, appear to contribute directly to their food; none were found in the gut analysis (Haefner & Wallace 1981a). The larvae are also relatively common among ***Hygroamblystegium fluviatile*** (Figure 31), ***Platyhypnidium riparioides*** (Figure 32), and ***Fontinalis dalecarlica*** (Figure 33) in Appalachian Mountain streams (Glime 1968).

Figure 27. ***Hydropsyche*** pupae removed from their pebble cases. Photo by Mark Melton, with permission.

Figure 28. ***Hydropsyche*** pupa, common among mosses in strong currents. Photo by Jason Neuswanger, with permission.

Figure 29. ***Diplectrona modesta*** larva, a species that is more common among mosses in early instars but is more evenly distributed between mosses and other substrata in later instars. Photo by Bob Henricks, with permission.

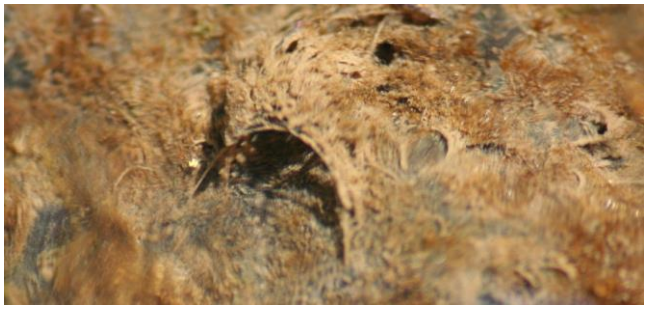

Figure 30. ***Cheumatopsyche*** larval net. These are often attached to bryophytes and are able to trap detritus and algae. Photo by Justin Montem, through Creative Commons.

Figure 31. ***Hygroamblystegium fluviatile***, a home for smaller insects. Photo by Michael Lüth, with permission.

Figure 32. ***Platyhypnidium riparioides***, a home for smaller insects, sometimes serving as food and case-building materials. Photo by David Holyoak, with permission.

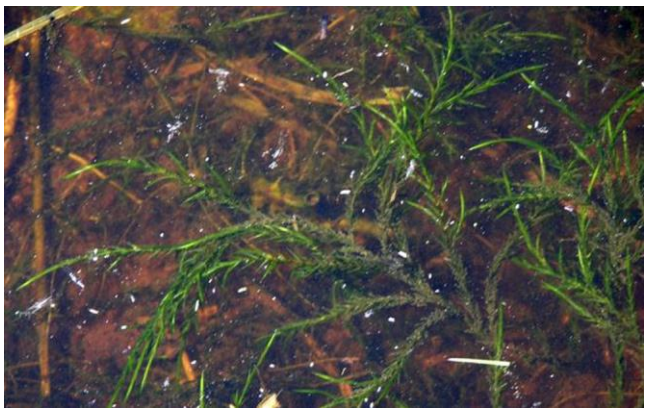

Figure 33. ***Fontinalis dalecarlica***, home to some larvae of ***Cheumatopsyche***. Photo by J. C. Schou, with permission.

When ***Cheumatopsyche*** sp. (Figure 34) reaches high densities it becomes more aggressive (Glass & Bovbjerg 1969). This aggressiveness dictates a pattern of **dispersion** (pattern of distribution of individuals within a habitat) that is a function of density. Hildrew and Edington (1979) found that larvae are able to make ultrasonic sounds to discourage intruders when they approach. Fortunately, for overlapping generations of the same species larval sizes differ at a given point in time, permitting them to use different net sizes (Figure 35-Figure 36) and avoid competition for food.

Figure 34. ***Cheumatopsyche*** larva, a caddisfly that becomes less aggressive when it has shelter. Photo by Bob Henricks, with permission.

Figure 35. ***Hydropsyche*** net showing mesh size that can differ in size with species. Photo by Michael Wiesner <www.waldzeit.ch>, with permission.

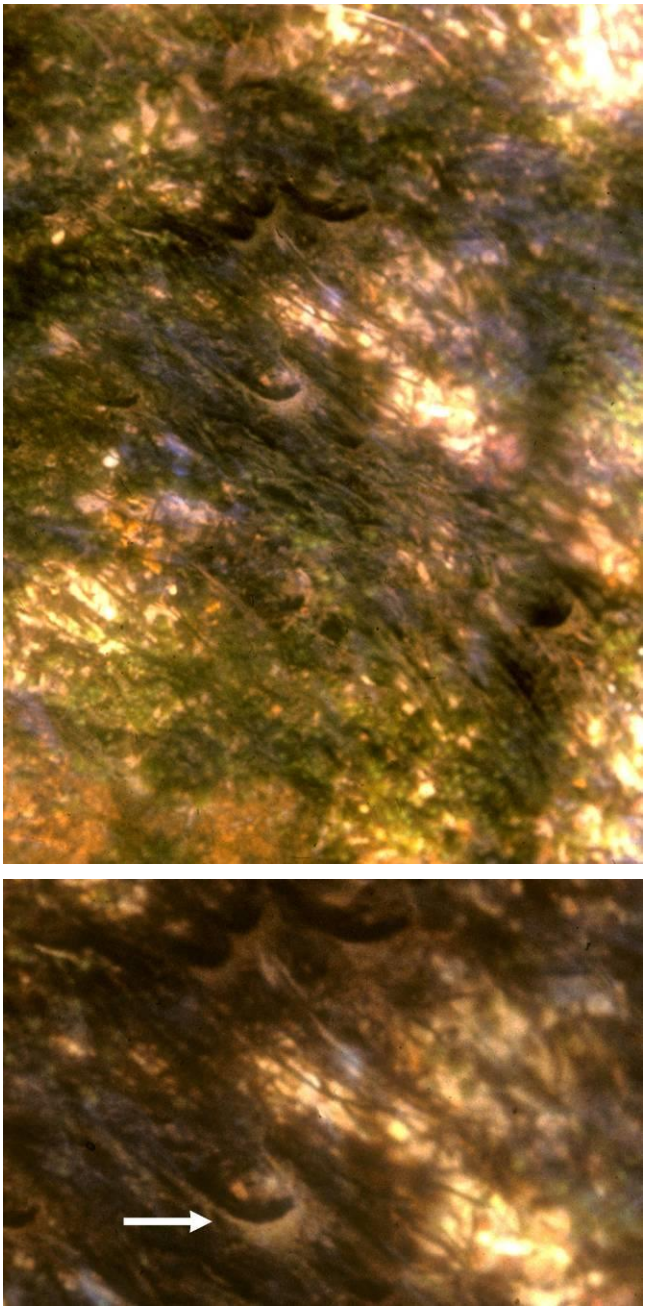

Figure 36. Nets of the net-spinning caddisfly, ***Cheumatopsyche***, on ***Fontinalis***. The number of larvae usually greatly exceeds the number of nets on the ***Fontinalis***, suggesting that they may be using the mosses as nets to gather detritus and diatoms. Photos by Janice Glime.

Williams and Hynes (1973) suggested that mossy habitats provide the greatest number of protected sites. Furthermore, the rapid flow typical of locations where mosses grow will bring more food per unit of time. ***Cheumatopsyche*** (Figure 37) larvae are common among the mosses ***Hygroamblystegium fluviatile*** (Figure 31), ***Platyhypnidium riparioides*** (Figure 32), and ***Fontinalis dalecarlica*** (Figure 33) in the mid-Appalachian Mountain streams (Glime 1968). And ***Cheumatopsyche*** (Figure 34) larvae seem to be less aggressive when shelter is readily available (Glass & Bovbjerg 1969). Williams and Hynes (1973) found that the hydropsychids ***Cheumatopsyche oxa*** (Figure 37) and ***Ceratopsyche sparna*** (Figure 38) occupied the mossy areas of boulders, whereas the philopotamid ***Chimarra aterrima*** (Figure 39), a potential competitor, occupied the spaces under large stones. The two hydropsychid species share the same sites, eat the same foods, and have similar life cycles. In contrast to ***Chimarra aterrima***, these net-spinning caddisflies have mechanisms in their gut for crushing diatoms, important constituents of the diet and one that separates their niche from that of ***C. aterrima***.

Figure 37. ***Cheumatopsyche oxa*** larva, an occupant of mossy areas on boulders. Photo by Trevor Bringloe, Biodiversity Institute of Ontario, through Creative Commons.

Figure 38. ***Ceratopsyche sparna*** larva, a species that prefers mossy areas to those under stones. Photo by Bob Henricks, with permission.

Figure 39. ***Chimarra aterrima*** larva, a species that occupies spaces under rocks in preference to that of mosses. Photo by Stroud Water Research Center, Stroud Water Research Center, through Creative Commons.

Hydropsyche pellucidula (Figure 40-Figure 41) occurs among submerged mosses in the River Rajcianka (Krno 1990). Elsewhere, when ***Hydropsyche pellucidula*** and ***H. siltalai*** (Figure 42) occur together, the moss cover is important in permitting these two caddisflies to partition the rocks into two functional feeding (net-spinning) niches and co-exist throughout their larval lives (Hildrew & Edington 1979). In late winter and early spring, there is rapid growth of moss (particularly ***Fontinalis antipyretica***, Figure 43) on boulders and bedrock in rapids. ***Hydropsyche siltalai*** (but not ***H. pellucidula***) migrates onto the moss in spring. Although large numbers of ***H. siltalai*** occupied the moss, not a single ***H. pellucidula*** could be found there. Plastic artificial grass, similar to moss mats, proved to be a suitable surface for net-spinning.

Figure 40. ***Hydropsyche pellucidula*** larva, a species that occurs among mosses in the River Rajcianka of Slovakia. Photo by Niels Sloth, with permission.

Figure 41. ***Hydropsyche pellucidula*** larva showing the large jaws. Photo by Niels Sloth, with permission.

Figure 42. ***Hydropsyche siltalai*** larva, a species that migrates to mosses to avoid competition from ***H. pellucidula.*** Photo by Urmas Kruus, with permission.

Figure 43. ***Fontinalis antipyretica***. Photo by Bernd Haynold, through Wikimedia Commons.

Hydropsyche siltalai (Figure 42) filters its food with a fine-meshed net (mean 100x70 µm) while ***H. pellucidula*** (Figure 40-Figure 41) is larger and uses nets with a mean mesh of 370x240 µm (Hildrew & Edington 1979). Migration of ***H. siltalai*** onto mosses (***Fontinalis antipyretica***; Figure 43) in spring further separates their niches. Englund (1993) observed that whereas small IV instar larvae were able to construct nets on the mosses, the physical structure seemed unsuitable for the larger V instar larvae to do so.

Food

Although Frost (1942) reported several studies in which ***Hydropsyche instabilis*** ate primarily **Chironomidae**, and Slack (1936) found that it ate diatoms, it also ingests mosses. In Great Britain (Percival & Whitehead 1929) and in calcareous streams in South Wales, ***Hydropsyche instabilis*** (Figure 44) ingested ***Fontinalis antipyretica*** (Figure 43) (Percival & Whitehead 1929; Jones 1949). Frost (1942) found that ***Hydropsyche instabilis*** (Figure 44) lived primarily among mosses in an acid stream, but in the alkaline stream it was ***Cheumatopsyche lepida*** (Figure 45) that was dominant among the mosses, in this case where there was more silt. Jones (1950) did extensive gut analysis of insects from the River Rheidol; among the **Trichoptera**, only ***Hydropsyche instabilis*** of the six species examined had fragments of ***Fontinalis antipyretica*** (Figure 43) in the gut (7 out of 27). Fragments of this moss were present in nine of the 23 analyses with identifiable gut contents (Jones 1949). Algae and detritus were the most common foods.

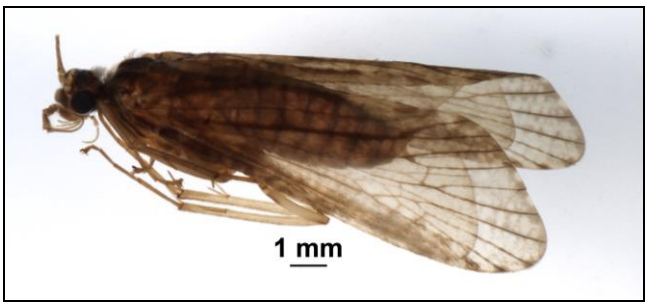

Figure 44. ***Hydropsyche instabilis*** adult, a species whose larvae sometimes eat mosses. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 45. ***Cheumatopsyche lepida*** larva, a dominant caddisfly among mosses with lots of silt in an alkaline stream. Photo through Creative Commons.

On the other hand, occurrence of net-spinning caddisflies among mosses may offer the advantage of a greater number of prey organisms. Although these insects trap their food on finely constructed nets, they are also carnivores. Haefner (1980) found a significantly higher (2x) density of prey organisms (***Baetis*** spp., ***Ephemerella*** spp., ***Nemoura*** spp., ***Hydroptila*** sp., and **Chironomidae**) in rock face samples, where mosses were typically dense. These organisms are common among stream mosses – ***Hydroptila*** less so (Glime 1994), thus the abundance of prey invertebrates may account for the greater productivity of ***Parapsyche cardis*** (see Figure 20) there.

Although ***Diplectrona modesta*** (Figure 29) had little correlation with mossy rocks in one of two Appalachian Mountain streams, and few such rocks existed in the other (Haefner & Wallace 1981a,b), this and other studies (Gurtz & Wallace 1986) suggest that the mosses provide a variety of niches that benefit both the potential prey organisms and the net-spinning caddisflies.

In a study to determine the source of foods for aquatic invertebrates, Torres-Ruiz *et al*. (2007) used the distinctive fatty acids for green algae, diatoms, and bryophytes, each of which also differed from fatty acids of terrestrial food sources. They determined that ***Hydropsyche*** spp. (Figure 40-Figure 42) consumed primarily **autochthonous** (originating from within the stream system) food sources, not the terrestrial **allochthonous** (originating from elsewhere) food such as leaf litter. In Appalachian Mountain streams the **Hydropsychidae**, including species of ***Hydropsyche***, seemed to use the mosses instead of constructing nets to capture their food (Glime 1968). There always seemed to be many more larvae than nets.

Gut *p*H is often important in determining the digestible food sources. ***Hydropsyche betteni*** (Figure 46-Figure 47) had a gut *p*H close to neutral but somewhat alkaline (Barlocher & Porter 1986). Hence, this species was unable to **hydrolyze** (break down a compound by chemical reaction with water) proteins of maple leaves that were not yet conditioned by decomposer organisms. They could, however, digest starch and laminarin (storage product in many seaweeds). Unlike those in the cranefly ***Tipula***, the fungal **carbohydrases** (enzymes that break down carbohydrates) ingested with decomposing leaves remained active in the guts of this species.

Figure 46. ***Hydropsyche betteni*** larva, with a gut *p*H that is alkaline. Photo by Bob Henricks, with permission.

Figure 47. ***Hydropsyche betteni*** larva showing ventral gills. Photo by Donald S. Chandler, with permission.

Role of Water Velocity

The larvae of the **Hydropsychidae** are able to partition the niches of the most immature from those of the nearly mature (Osborne & Herricks 1987; Muotka 1990). Osborne and Herricks (1987) found that ***Hydropsyche*** (Figure 40-Figure 42) species in their study separated the larger larvae into communities at higher velocities, whereas the smaller, less mature larvae sought areas of diminished flow. The same size distribution occurs between species. These larvae seek out depressions where they can gather passing detritus but where sedimentation is minimal. Turbulence seems to play a role in determining distribution, perhaps contributing to food availability and preventing

sedimentation. Larger larvae are apparently able to occupy greater velocities; this is coupled with the construction of a larger mesh size, hence dividing the feeding niche from that of smaller larvae.

The net-spinning caddisflies prefer a habitat with a stable substrate and high water velocity. Georgian and Thorp (1992) showed that 96% of the **Hydropsychidae** larvae selected artificial moss substrates that had high velocity water flowing over them. They estimated that a prey item would be consumed within 5.5 m of travel in the drift. It appears that one advantage afforded these moss dwellers is that they can take advantage of high-flow rates while themselves finding a flow-rate suitable for their own safety.

Current speed also influences net-spinning activity, with a greater percentage of larvae spinning nets at 20 cm sec^{-1} (73%) than at 10 cm sec^{-1} (10%) (Edington 1965). Edington found that hydropsychid larvae formed tunnels into the moss mats with nets at the moss surface. When the nets were removed (and when they were not) and the flow was artificially reduced, the larvae moved to a different area. When something restricts the flow, the larvae move to a new location and construct new nets (Edington 1965, 1968).

Muotka (1990) considered that it was the flow pattern, rather than the flow velocity itself, that determined the pattern of occupancy by filter-feeding caddisfly larvae. He based this on the ability of multiple sizes of caddisflies, including ***Hydropsyche*** (Figure 40-Figure 42) to coexist at the same flow rates. Nevertheless, he concluded that species were often ecologically closer to other species than to other instars of their own species. In their study, many of the sites were covered with bryophytes [mosses ***Fontinalis antipyretica*** (Figure 43), ***Cratoneuron commutatum*** (Figure 48), leafy liverwort ***Jungermannia exsertifolia*** (Figure 49)] and the uneven surface of this substrate would create multiple flow patterns. It is noteworthy that in the stream that lacked bryophytes only one filter-feeding caddisfly was present – ***Hydropsyche saxonica*** (Figure 50) – whereas seven species occurred in the two streams with heavy bryophyte cover.

Figure 48. ***Cratoneuron commutatum***, a moss that alters flow patterns, as it is doing here. Photo through Creative Commons.

Figure 49. ***Jungermannia exsertifolia*** ssp ***cordifolia***, contributor to flow patterns that allow niche partitioning for **Hydropsychidae**. Photo by Michael Lüth, with permission.

Figure 50. ***Hydropsyche saxonica*** larva, the only filter-feeding caddisfly in a stream with no mosses. Photo by Niels Sloth, with permission.

Food capture is important in the location of nets, and water velocity helps to determine the food available. Mosses on the rocks actually prevent some insects from living there. The caddisfly ***Leucotrichia*** (**Hydroptilidae**; Figure 51) is unable to live on a substrate dominated by heavy moss growth and instead the net spinner ***Hydropsyche*** (Figure 40-Figure 42) occupies those locations (McAuliffe 1983). The larvae arrange their nets very evenly downstream but are often crowded across the substrate, preventing the water from being filtered by a net above them.

Figure 51. ***Leucotrichia pictipes*** larva, a genus that cannot live on a substrate with heavy moss cover. Photo by Stroud Water Research Center, through Creative Commons.

As I already noted in the Appalachian Mountain streams, some caddisflies actually use the mosses to help them gather food. Hildrew and Edington (1979) found that favorable situations for net-spinning caddis larvae (**Hydropsychidae**), such as moss covered rocks, often seem to be occupied to capacity. I have observed the same relationship, but it appeared that the caddisflies in some cases took advantage of the collecting ability of the moss and did not make nets. This would be useful for those species that eat primarily small invertebrates living among the bryophytes (Ross & Wallace 1983), but it could also take advantage of the bryophytes as filter traps.

Role Below Impoundments

Mosses are important habitats at impoundments. In Valley Creek in Minnesota, USA, **Hydropsychidae** caddisflies use mosses and filamentous algae as sites for attachment and building materials for retreats, with the mosses providing an environment that protects the larvae from the abrasive sand deposited by the impoundment (Mackay & Waters 1986).

Ogbogu (2000; Ogbogu & Akinya 2001) likewise found that ***Fontinalis*** (Figure 1) was important to the **Hydropsychidae** in an impoundment at Ile-Ife, Nigeria. They occupied the spillway, among the ***Fontinalis***, in large numbers when sampled in August (1233 m^{-2}), September (900 m^{-2}), and November (1178 m^{-2}). The moss provided refuge from the rapid water of the spillway, protection from predators, and food (epiphytic diatoms and other algae) trapped among the mosses.

Polycentropodidae – Tube Maker Caddisflies

Members of this worldwide family are relatively small to moderate in size, with the forewing reaching 6-13 mm (Hickin 1967). Larvae live in both quiet and flowing waters and trap their food in a tube (Murray 2006).

Polycentropus (Figure 52) is not a caddisfly one thinks of as a moss dweller because of its long, tubular net. But in both Ballysmuttan and Straffan, UK, it does occur among mosses, as well as other locations (Frost 1942). Percival and Whitehead (1929) found that ***Polycentropus flavomaculatus*** (Figure 52) was most abundant in thick mosses compared to other types of substrate. In mid-Appalachian Mountain streams, larvae of this genus are occasional inhabitants of bryophytes (Glime 1968).

Figure 52. ***Polycentropus flavomaculatus*** larva, a species that is more abundant in thick mosses than elsewhere. Photo by Dragiša Savić, with permission.

In one location in the Pyrénées Décamps (1967) found that ***Plectrocnemia scruposa*** (see Figure 53) comprised 4.5% of the **Trichoptera** fauna among mosses. Edington (1965) found that ***Plectrocnemia*** *conspersa* (see Figure 53) spun more nets at a flow rate of 10 cm sec^{-1} (80% of the larvae) than at 20 cm sec^{-1} (4%), a relationship just the opposite of that of ***Hydropsyche instabilis***. Furthermore, in both species, those few making nets at the less favorable flow rate had a tendency to construct abberrant nets.

Figure 53. ***Plectrocnemia geniculata*** larva, member of a genus in which some larvae live among mosses Photo from Biodiversity Institute of Ontario, through Creative Commons.

From Ceylon, Schmid (1958) reported ***Nyctiophylax devanampriya*** (Figure 54), ***Pseudoneureclipsis watagoda*** (Figure 55), and ***P. thuparama*** from large, mossy rocks in the torrent.

Figure 54. ***Nyctiophylax*** sp larva; ***N. devanampriya*** occurs among mosses in torrents in Ceylon. Photo by Dana R. Denson Florida Association of Benthologists, with permission.

Figure 55. ***Pseudoneureclipsis*** adult, a genus whose naiads can live on mossy rocks in torrents. Photo by Biodiversity Institute of Ontario, through Creative Commons.

But this family relies primarily on food trapped in its funnel-shaped net. Ross and Wallace (1983) demonstrated that 80% of the food for this family in a southern Appalachian Mountain, USA, stream was fine detritus. Another 15% was diatoms. So why do we find them among bryophytes at all?

Psychomyiidae – Net Tube Caddisflies

The **Psychomyiidae** are widespread, but are concentrated in the Oriental Region and absent in the Neotropical Region (Kjer 2010a). The adults are of moderate size (5-8 mm long forewings) (Watson & Dallwitz 2003). This family traps its food in a silken tube (Figure 56), with the diet consisting of algae, leaves, and animal matter (Neuswanger 2015). Grazing may occur both on the tubes and nearby, therefore consisting mostly of diatoms and other algae (Holzenthal *et al*. 2007; Kjer 2010a). Females dive to the bottom of the stream to lay their eggs (Neuswanger 2015).

Figure 56. **Psychomyiidae** net. Photo by Janice Glime.

Mosses occurred in the guts of ***Psychomyia pusilla*** (see Figure 57) and ***Tinodes waeneri*** (Figure 58-Figure 59) in UK streams (Percival & Whitehead 1929), attesting to their residence among bryophytes.

Figure 57. ***Psychomyia flavida*** larva. ***Psychomyia pusilla*** eats mosses. Photo from Stroud Water Research Center through Creative Commons, with permission.

Figure 58. ***Tinodes waeneri*** larva, a species that consumes mosses. Photo by Niels Sloth, with permission.

Figure 59. ***Tinodes waeneri*** larval tube. Photo by Niels Sloth, with permission.

Philopotamoidea

Philopotamidae – Finger-net Caddisflies

The larvae of this worldwide family build nets that can require more than 1 km of silk (Wallace & Malas 1976); these are used to trap small particles for food (McLeod 2005). To use them, the larvae are restricted to fast-flowing water of rivers and streams. The adult body is 5-9 mm long.

The net-building behavior would seem to preclude mosses as a substrate, but exceptions occur. ***Philopotamus montanus*** is not typically a bryophyte inhabitant and captures its food with a tube net. But this net can trap bits of mosses travelling downstream, and of the 15 guts with identifiable contents, two had ***Fontinalis antipyretica*** (Figure 43) (Jones 1949).

Chimarra (Figure 39; Figure 60-Figure 65) lives among mosses but prefers the gravel and sand at their bases (Armitage 1961). Williams and Hynes (1973) suggested that the affinity of ***C. aterrima*** (Figure 39) for moss-covered rocks may have been more related to the large size of those rocks rather than the presence of the moss. For example, in a wooded Ontario, Canada, stream, ***Wormaldia moesta*** (Figure 66) preferred bare stones, whereas ***Rhyacophila minor*** (**Rhyacophilidae**) preferred moss-covered stones in the same area (Singh *et al*. 1984). ***Wormaldia moesta*** grazed on diatoms when its primary food supply, detritus/**seston** (living organisms and non-living matter swimming or floating in a water body), became scarce. In my own studies of the fauna of bryophytes in the Appalachian Mountain streams, ***C. aterrima*** was occasionally present, but in small numbers, among ***Fontinalis dalecarlica*** (Figure 33) in larger streams (Glime 1968). It was absent in the other bryophytes.

Figure 60. ***Chimarra tsudai*** tubes with thallose liverworts at the funnel opening. Photo by Takao Nozaki, with permission.

Figure 61. ***Chimarra*** pupal case. Photo by Mark Melton, with permission.

Figure 62. ***Chimarra*** pupa showing on underside of sand case. Photo by Mark Melton, with permission.

Figure 63 ***Chimarra*** pupa removed from sand case, showing shed sclerotized parts from larva inside the pupal covering. Photo by Mark Melton, with permission.

Figure 64. ***Chimarra*** pupa removed from case. Photo by Mark Melton, with permission.

Figure 65. ***Chimarra tsudai*** adult. Takao Nozaki, with permission.

Figure 66. ***Wormaldia moesta*** larva, a species that prefers bare stones even when mosses are present. Photo by Donald S. Chandler, with permission.

Another occasional visitor to bryophytes in Appalachian Mountain, USA, streams was ***Dolophilodes distinctus*** (Figure 67) (Glime 1968**).** In this case, it occurred among all four of the primary bryophytes in the study: ***Hygroamblystegium fluviatile*** (Figure 31), ***Platyhypnidium riparioides*** (Figure 32), ***Fontinalis dalecarlica*** (Figure 33), and ***Scapania undulata*** (Figure 68), preferring the mats and turfs over ***Fontinalis*** streamers.

Figure 67. ***Dolophilodes distinctus*** larva, an occasional visitor to Appalachian Mountain stream bryophytes. Photo by Donald S. Chandler, with permission.

Figure 68. ***Scapania undulata***, a leafy liverwort that can modify flow patterns and house insects. Photo by Michael Lüth, with permission.

Summary

Lepidoptera apparently do not use aquatic bryophytes.

Trichoptera, on the other hand, are among the common inhabitants. Those that enter the drift may use bryophytes as a means to get out of the drift. Some larvae use the bryophytes for food and many use them as a safe site for capturing food, using both filtering strategies and predation of smaller inhabitants. The mosses themselves may serve as filter traps for caddisfly food, including drifting algae, bacteria, decomposing organic matter, and detritus. For some caddisflies the bryophytes themselves serve as food and may be a seasonal staple when other foods are unavailable. Some build their cases from bryophytes and liver among the bryophytes to capture food.

Larvae of most **Trichoptera** are aquatic, and many may also use the bryophytes as a site for pupation and emergence. The most common families among bryophytes are The **Hydropsychidae** and **Rhyacophilidae**. These are both caseless caddisflies, and the bryophytes may provide some of the protection otherwise afforded by cases.

Hydropsychidae take advantage of the bryophytes to partition their niches and avoid competition for food. In some cases this is the result of changing diets at later instar stages. Others use differences in flow within the bryophyte mat. They seem to be able to use the bryophytes to trap food, and the bryophytes create locations with a variety of flow regimes. Still other caddisflies are selective about which species of bryophytes they use, with a few selecting leafy liverworts only and others avoiding them.

The importance of the bryophytes as food remains a mystery. It is possible they are ingested along with adhering periphyton and detritus without being digested.

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CHAPTER 11-12
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CHAPTER 11-12
AQUATIC INSECTS: HOLOMETABOLA – TRICHOPTERA, SUBORDERS INTEGRIPALPIA AND SPICIPALPIA

Figure 1. ***Adicrophleps hitchcocki*** (**Brachycentridae**), a larva that makes its case from mosses. Note the "furry" portion near the opening. Photo by D. N. Bennett, with permission.

SUBORDER INTEGRIPALPIA

Leptoceroidea

Odontoceridae – Mortarjoint Casemakers

This worldwide family lives in springs and small to medium streams and rivers, typically with slow flow; some are associated with waterfalls (Holzenthal *et al*. 2010c). Also known as the strong case-maker caddis, the larvae make very strong cases from bits of rock with more than usual amounts of the silk glue (Henricks 2011).

Although I never found ***Pseudogoera*** in my studies of stream insects among bryophytes in the mid Appalachians, ***P. singularis*** (Figure 2) is associated with mosses in waterfalls in the southern Appalachians, USA (Wallace & Ross 1971).

Figure 2. ***Pseudogoera singularis*** larva, a species that lives in mosses of waterfalls in the southern Appalachian Mountains. Photo by BIO Photography Group, through Creative Commons.

In the mid-Appalachian Mountain streams, I found two species of ***Psilotreta*** (Figure 3) among ***Hygroamblystegium fluviatile*** (Glime 1968). This genus has forewings of 6-17 mm (Parker & Wiggins 1987), representing one of the larger of the bryophyte dwellers.

Figure 3. ***Psilotreta*** larva, an inhabitant of ***Hygroamblystegium fluviatile*** in the Appalachian Mountains. Photo by Bob Henricks, with permission.

Figure 4. ***Hygroamblystegium fluviatile***, home of ***Adicrophleps hitchcockii***. Photo by Michael Lüth, with permission.

Figure 5. ***Hygroamblystegium fluviatile*** leaf showing strong costa that seems to be used in making the cases of ***Adicrophleps hitchcockii***. Photo by Michael Lüth, with permission.

Limnephiloidea

Goeridae

This family occurs on all continents except Australia and South America (Holzenthal *et al*. 2007). Adults have a forewing length of 6-9 mm and are typically light brown (Figure 6) (Houghton 2012). The larvae (Figure 7) live in cool, flowing water and graze on **periphyton**. Their larval cases consist entirely of rock fragments, sometimes with larger rocks on each side of the case (Figure 8).

Figure 6. *Goera pilosa* adult, demonstrating the light brown wings typical of the family **Goeridae**. Photo from Biopix, through Creative Commons.

Figure 7. *Pseudogoera singularis* larva. Photo by BIO Photography Group, through Creative Commons.

Figure 8. *Goera calcarata* larva showing large rock fragments on sides of case. Photo by Bob Henricks, with permission.

Goerita is a small genus with only three species and is restricted to the Appalachian Mountains and Allegheny Plateau in eastern North America (Parker 1998). The larvae are **bryobionts**, in this case living on rocks covered with mosses and liverworts where the rocks can be dry or covered by a film of water. The larvae do not eat the bryophytes, but instead feed on detritus and diatoms growing there.

Goerita semata lives on the undersides of rocks (Flint 1960), but in western North Carolina, Huryn and Wallace (1985) found the larvae among liverworts and mosses on vertical rock faces; fewer than 2% were found on other substrata. ***Goerita betteni*** lives in a similar habitat (Wiggins 1973). Huryn and Wallace (1985) suggested that the bryophytes may offer the larvae some protection from desiccation. Pupae typically occur on these same rocks with mosses and a thin film of water. Ultimately, females lay their eggs away from water on bare rock, mosses, and liverworts. Food of the larvae consists primarily of fine amorphous detritus (65%), and diatoms (32%), but diatom composition increases to an average of 64% in spring. Bryophyte clumps are typically good sources of both. Although the mechanisms of desiccation resistance are unknown in larvae of this species, it is likely that they are adapted behaviorally by living among the bryophytes.

In the River Rajcianka in Slovakia, ***Lithax niger*** (Figure 9) is a bryophyte dweller, living under water, but not in the wet emergent bryophytes (Krno 1990). This is a mountain species, occurring in the Alps and Balkans.

Figure 9. ***Lithax niger*** adult, a species whose larvae live among mosses in the River Rajcianka. Photo by Paul Frandsen, through public domain.

The larvae of ***Archithremma ulachensis*** move to a layer of ***Sphagnum*** (Figure 10) on the bank of a spring to pupate (Levanidova & Vshivkova 1984). These pupae are morphologically reduced, lacking long **setae** (hairs) and projections used to clean the silk disks that close the case. They also lack swimming legs. The larvae live in streams that have low water temperatures (3-5°C) in summer.

In a cool mountain stream of central Japan Tada and Satake (1994) found that ***Pseudostenophylax ondakensis*** (Figure 12) was significantly more abundant on mats of the moss ***Platyhypnidium riparioides*** (Figure 13) than in bare rock areas. Décamps (1967, 1968) found ***Rhadicoleptus spinifer*** (see Figure 14) to be abundant among mosses in the Pyrénées; at one station it comprised ~15% of the moss **Trichoptera** fauna (Décamps 1967).

Figure 10. ***Sphagnum cuspidatum***, a pupation site for ***Limnephilus peltus*** and ***Architremma ulachensis***. Photo by Bernd Haynold, through Creative Commons.

Limnephilidae – Northern Caddisflies

The **Limnephilidae** encompasses a wide variety of case-making caddisflies in a wide range of habitats. Their ingenuity in making these homes could challenge some of our most creative artists. This is one of the largest caddisfly families, with recent segregate families diminishing its numbers. Although it occurs worldwide, its records are concentrated in Europe and North America (Limnephilidae 2015). In North America it is often the dominant group in higher elevation streams. But these are mostly large caddisflies (15-35 mm) (Houghton 2012), making navigation difficult among bryophytes. ***Fontinalis*** (Figure 11), on the other hand, is a large enough moss with a streamer habit that permits these larger larvae to navigate (Glime 1968, 1994). Their dependence on terrestrial litter makes the larvae vulnerable to deforestation (Houghton 2012).

Figure 11. ***Fontinalis antipyretica***, home to many kinds of insects. Photo by Kristian Peters, with permission.

Figure 12. ***Pseudostenophylax ondakensis*** larva, a species that is significantly more abundant on the moss ***Platyhypnidium riparioides*** than on bare rock. Photo by Takao Nozaki, with permission.

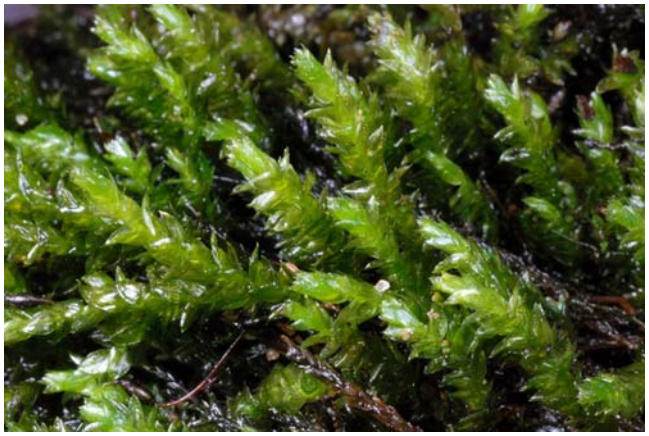

Figure 13. ***Platyhypnidium riparioides***, home to ***Pseudostenophylax ondakensis*** in Japan. Photo by J. C. Schou, with permission.

Figure 14. ***Rhadicoleptus alpestris*** adult. ***Rhadicoleptus spinifer*** larvae are abundant among mosses in the Pyrénées. Photo by Niels Sloth, with permission.

The larvae of ***Chaetopterygopsis maclachlani*** (Figure 15) typically occur among clumps of ***Fontinalis*** (Figure 11) in the Vosges Mountains, eastern France, mostly in areas with slower or laminar flow (Lehrian *et al*. 2010). The mosses constitute ~65% of their diet, with the remainder being coarse leaf detritus (Dangles 2002). Dangles warned that some species, including this one, are able to shift their diet based on availability, causing misinterpretations based on the general feeding guild classification of these insects. Dangles (2002) considered ***Chaetopterygopsis maclachlani*** (Figure 15) to be a specialist on bryophytes; they furthermore build their cases from ***Fontinalis*** (Figure 62) (Malicky 1994). As adults they typically crawl, not fly, among the **riparian** (streambank) vegetation.

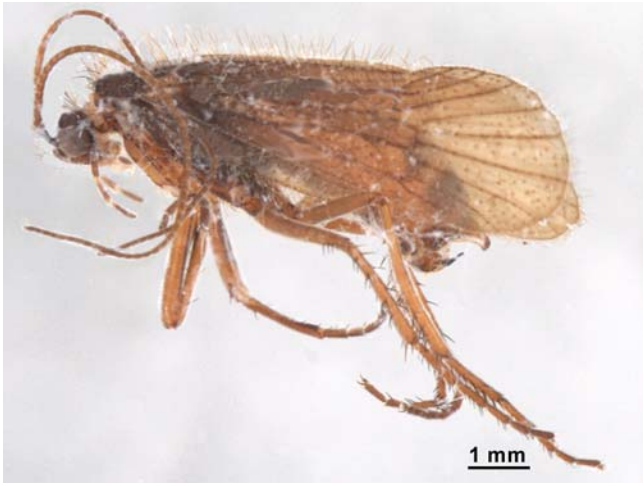

Figure 15. ***Chaetopterygopsis maclachlani*** adult, a species whose larvae live among ***Fontinalis*** and eat mosses as 65% of their diet. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Chaetopterygosis machlachlani is widespread in the Pyrenees to Baikal, specializing in ***Fontinalis*** and other streambed mosses (Báilint *et al*. 2011).

In the mid-Appalachian Mountain, USA, streams, the **Limnephilidae** are poorly represented among bryophytes (Glime 1968). Furthermore, those few that are present differ from any of the species I found in the literature as moss dwellers. Two species of ***Pycnopsyche*** [***P. luculenta***, ***P.*** cf. ***scabripennis*** (Figure 16)] were the most common, appearing in clumps of ***Fontinalis*** (Figure 62) (Glime 1968). This restriction is most likely due to the large size of the **Limnephilidae** larvae, especially when their bulky case is considered. They would have real difficulty moving about in ***Hygroamblystegium fluviatile*** (Figure 4-Figure 5) or ***Platyhypnidium riparioides*** (Figure 13).

Figure 16. ***Pycnopsyche scabripennis*** larva, a ***Fontinalis*** dweller. Photo by Tom Murray, through Creative Commons.

In an experimental study on ***Limnephilus rhombicus*** (Figure 17), Higler (1975) was able to keep the larvae alive on a diet of ***Fontinalis antipyretica*** (Figure 11) with dead birch and oak leaves. However, it appears that its natural diet is mostly living plants (Slack 1936), dead leaves (Slack 1936; Lepneva 1966) and sometimes Naididae (aquatic segmented worms). It is not typically a moss dweller, so the moss diet was most likely unnatural. But Slack (1936) did find that it ate ***Fontinalis*** in the field. On the other hand, when ***Potamophylax rotundipennis*** (Figure 18-Figure 19) was provided choices of birch, oak, and beech leaves and ***Fontinalis antipyretica***, it avoided the moss and beech leaves.

Figure 17. ***Limnephilus rhombicus*** larva, showing yet a third very different case, one using snail shells. Photo by Dragiša Savić, with permission.

Figure 18. ***Potamophylax*** larva and case. ***Potamophylax rotundipennis*** rejects ***Fontinalis antipyretica*** as a food choice. Photo by Michael Wiesner <www.waldzeit.ch>, with permission.

Although most of the **Limnephilidae** make large cases with large components of twigs and leaf fragments, some use bryophytes. ***Limnephilus externus*** (Figure 20-Figure 21) larvae are known to use the moss ***Leptodictyum riparium*** (Figure 22) to construct their barrel-shaped cases (Pritchard & Berté 1987). In experiments, this species was able to use wheat flakes, but not alder leaves, to make its case. In the same experiment, ***Nemotaulius hostilis*** (Figure 23) used alder, willow, and burreed but did not use wheat flakes or mosses. These same two insects are shredders that consume tracheophyte detritus, but the proportion of mosses in the diet increases as the larvae become older.

Figure 19. ***Potamophylax*** adult. Photo through Creative Commons.

Figure 20. Two ***Limnephilus externus*** larvae with the second grabbing the rear of the first. The two cases appear to be made of bits of grass and this camouflage most likely fools their predators because it confused my non-biologist reviewer! Photo by Wendy Brown <www.gunnisoninsects.org>, with permission.

Figure 21. ***Limnephilus externus*** larva. Photo by Wendy Brown <www.gunnisoninsects.org>, with permission.

Limnephilus peltus (Figure 24) doesn't spend much time among mosses as a larva, but when it is time to pupate, it burrows into mosses along fen streams where it spends its pupal life (Erman 1984). Unfortunately, if the stream dries out, the pupa is likely to die.

Figure 22. ***Leptodictyum riparium***, home of larvae of ***Limnephilus externus***. Photo by Jan-Peter Frahm, with permission.

Figure 23. ***Nemotaulius hostilis*** larva showing case made of leaf litter. Photo by Donald S. Chandler, with permission.

Figure 24. ***Limnephilus*** sp. larva, a genus that sometimes pupates in mosses of fens. Photo by Jason Neuswanger, with permission.

The habitat of larvae of the high altitude ***Drusus discolor*** (Figure 25) in the Pyrénées consisted of filamentous algae and the moss ***Bryum*** (Figure 26) (Décamps 1968). This caddisfly is one of the two most abundant caddisflies among mosses (Décamps 1967). In the River Rajcianka in Slovakia, ***Drusus annulatus*** (Figure 27) occurs not only among submerged bryophytes but also moving about among the wet bryophytes that emerge above the water level (Krno 1990).

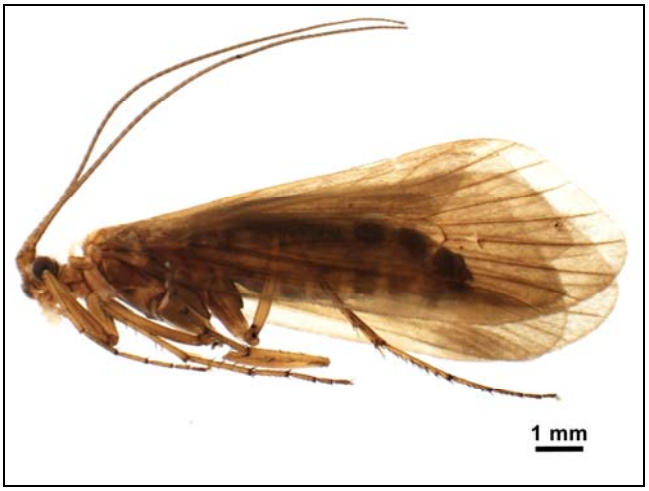

Figure 25. ***Drusus discolor*** adult, a species that lives among the moss ***Bryum*** in the Pyrénées. Photo from Biodiversity Institute of Ontario, through Creative Commons.

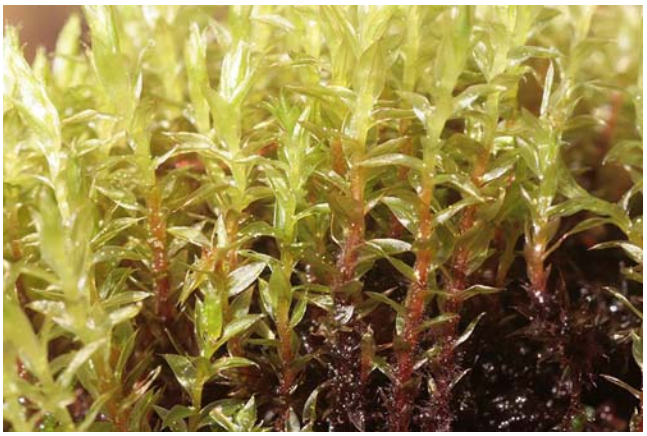

Figure 26. ***Bryum pseudotriquetrum***, home to several species of ***Drusus*** in Europe. Photo by Hermann Schachner, through Creative Commons.

Figure 27. ***Drusus annulatus*** adult, a species whose larvae can live above or below the water surface among bryophytes. Photo by James K. Lindsey, with permission.

Frenesia difficilis (Figure 28) lays its eggs out of the water, sometimes on mosses that overhang the water (Flint 1956). In this terrestrial location the eggs may freeze in winter. In the Massachusetts, USA, fish hatchery, Flint found no other relationship with mosses during the life cycle.

Figure 28. ***Fresnia difficilis*** male, a species that sometimes lays its eggs on mosses that overhang the water. Photo by Tom Murray, through Creative Commons.

The Arctic caddisfly ***Sphagnophylax meiops*** lives in Arctic pools in the tundra in the Northwest Territories of Canada (Wiggins & Winchester 1984) where the larvae take advantage of the surface water in the pool (Winchester *et al*. 1993). When the water recedes the larvae move to the organic materials accumulated above the permafrost to feed, grow, and metamorphose into pupae and adults. This caddisfly is flightless and has long bristles on its short wings.

Most **Trichoptera** spend their larval life in the water, but in the genus ***Enoicyla*** (**Limnephilidae**; Figure 29), the larvae are terrestrial and the adult female has only vestigial wings, limiting her travel and agility. Males, however, are capable fliers. Larvae may live far from water among the mosses around tree roots (Watson & Dallwitz 2003). Green (2012) noted at least 50 of these larvae climbing up logs, with several browsing a black slime mold. One can observe many larvae together on the surface of mosses and liverworts growing on a stream bank following rain.

Enoicyla pusilla (Figure 29) uses fine sand grains and other vegetable matter to make cases where it lives among the mosses (Watson & Dallwitz 2003). The larvae of ***Enoicyla***, despite being terrestrial, require 100% humidity (Green 2012). But when they become saturated, they climb upwards to dry, then drop back down when they need to get wet again (at 7% relative humidity). Their respiration is through the cuticle; they lack gills.

Figure 29. ***Enoicyla pusilla*** larvae, a terrestrial species that requires 100% humidity – a condition often found among mosses. Photo by Ernest van Asseldonk, through Creative Commons.

In his arguments to support that the **Trichoptera** (with hairs on wings) and **Lepidoptera** (with scales on wings) were closely related, Crampton (1920) used the common ability to use mosses in the caddisfly ***Enoicyla*** (**Limnephilidae**; Figure 29) and the larvae of moths in **Micropterygidae**.

The caddisflies living in peatlands are typically generalist taxa with wide habitat requirements (Flannagan & Macdonald 1987). But a few are **tyrphobionts** (living only in peat bogs and mires). The larvae of ***Phanocelia canadensis*** (Figure 30-Figure 31) are elusive. The second report of the larvae by Colburn and Clapp in 2006 was from kettle hole wetlands in Massachusetts, USA. Colburn and Clapp attribute the limited reports of larvae of this species to its limited habitat requirements. It lives in ***Sphagnum*** (Figure 10) habitats with low *p*H and makes its case from ***Sphagnum*** (Figure 30) [The picture below (Figure 31) indicates other mosses are used as well.] Larvae remain closely associated with the moss during development. They become dormant in summer, remaining in unsealed cases that are firmly attached to the moss. In autumn they seal the ends of the case and develop into pupae. Even fossil records support their preference for ***Sphagnum*** (Figure 10) bogs. The larva was originally described from floating ***Sphagnum*** at the edge of acidic ponds in a spruce-***Sphagnum*** bog in New Brunswick, Canada (Fairchild & Wiggins 1989). It appears that adult habitats are much broader, perhaps misleading its collectors (Colburn & Clapp 2006).

Figure 30. ***Phanocelia canadensis*** larva showing its case made with ***Sphagnum***. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 31. ***Phanocelia canadensis*** larva showing case made with at least some non-***Sphagnum*** mosses. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Leberfinger and Bohman (2010) gave larvae of ***Limnephilus bipunctatus*** (Figure 32) choices of food that included grasses, mosses, algae, and leaves. The larvae preferred leaves of the shrubby cinquefoil. Although they ate little of the mosses, grass was the least preferred food.

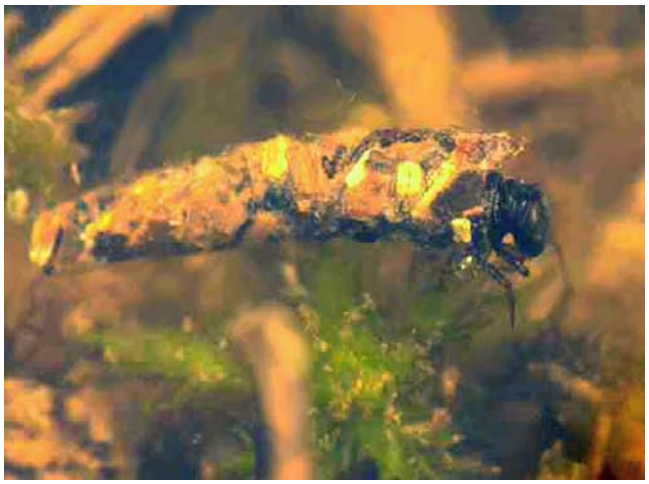

Figure 32. ***Limnephilus bipunctatus*** larva in case, a species that includes mosses in its diet. Photo by James K. Lindsey, with permission.

Philocasca is not a genus one often reads about in moss habitats. Nevertheless, mosses appear to be suitable sites for pupation. In describing the new species ***Philocasca rivularis*** (see Figure 33) Wiggins and Anderson (1968) state that pupae attach to the undersides of moss clumps along stream banks. Mutch and Pritchard (1984) found that instar V larvae of ***P. alba*** (Figure 34) in a Rocky Mountain stream had mostly moss (***Hygrohypnum luridum*** – Figure 35) in the gut in spring and summer, but had leaf fragments in the gut in autumn. Furthermore, when fed detritus supplemented with moss these larvae grew significantly better than when fed detritus alone, suggesting that the moss was an important nutrient source.

Figure 33. ***Philocasca thor*** adult. ***Philocasca rivularis*** pupates on undersides of moss clumps on streambanks. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 34. ***Philocasca alba*** adult, a species whose larvae feed on the moss ***Hygrohypnum luridum*** in a Rocky Mountain, USA, stream in spring and summer. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 35. ***Hygrohypnum luridum***, a species that typically occurs both in the water and above it. Photo by Dale Vitt, with permission.

Onocosmoecus unicolor (Figure 36-Figure 37) is a large shredder that includes mosses in its varied diet (National Park Service 2014).

Figure 36. ***Onocosmoecus unicolor*** larva, a moss consumer. Photo by Jason Neuswanger, with permission.

Figure 37. ***Onocosmoecus unicolor*** adult. Photo by Bob Newell, with permission.

Chyranda centralis (Figure 38) is a caddisfly of small spring streams among leaf accumulations. Its food includes leaves, bark, and may even include mosses (National Park Service 2014).

Figure 38 ***Chyranda*** larva of small spring streams; it may sometimes eat mosses. Photo from California Department of Fish and Wildlife, through public domain.

Mosses provide vertical zonation possibilities for the caddisflies. Krno (1990) addressed these vertical zones in the River Rajcianka in Slovakia. There, the limnephilids ***Allogamus auricollis*** (Figure 39-Figure 40) (a shredder), ***A. uncatus***, and ***Drusus annulatus*** (Figure 41) occurred among the submerged mosses, but above water only ***Allogamus auricollis*** and ***Drusus annulatus*** occurred among emergent wet mosses. On the other hand ***Parachiona picicornis*** (Figure 42) was only found above water among the wet mosses.

Figure 39. ***Allogamus auricollis*** larva, a species that traverses among mosses both below and above the water surface. The larva is seen here breaking the surface tension. Photo through Creative Commons.

Figure 40. ***Allogamus auricollis*** larvae. Photo by Wolfram Graf, with permission.

Figure 41. ***Drusus annulatus*** adult, a species whose larvae live among submerged mosses and will venture above the water among wet mosses. Photo by James K. Lindsey, with permission.

Figure 42. ***Parachiona picicornis*** adult, a species whose larvae live among submerged mosses but will not venture above the water among wet mosses. Photo by James K. Lindsey, with permission.

Chaetopterygopsis maclachlani larvae in the Carpathians are "specialized" on the aquatic moss ***Fontinalis*** (Figure 62) in mountain streams (Bálint *et al.* 2011).

Figure 43. ***Chaetopterygopsis machlachlani*** larva, a ***Fontinalis*** dweller. Photo by Michael Balke, through Creative Commons.

Lepidostomatidae – Bizarre Caddisflies

This family is widespread in the Northern Hemisphere, extending southward to Panama, New Guinea, and the Afrotropical region (Holzenthal *et al*. 2010a). Hilsenhoff (1975), in reporting on Wisconsin, USA, **Lepidostomatidae**, considered the larvae of this family to inhabit a wide range of clean streams. The larvae live among rocks, debris, and mosses on rocks and eat mostly detritus (BugGuide 2005). In North America the larvae inhabit springs, streams, and large slow-moving rivers where they eat detritus. They build a log cabin style of case from stem and leaf pieces or sand grains.

I did find ***Lepidostoma americana*** in clumps of ***Hygroamblystegium fluviatile*** (Figure 4-Figure 5) in the Appalachian Mountain streams (Glime 1968). Some older cases of ***Lepidostoma*** sp. contained fragments of the liverwort ***Scapania undulata*** (Figure 74) in them near the opening. ***Lepidostoma hirtum*** (Figure 44-Figure 45) is common among mosses at both Ballysmuttan and Straffan in the UK (Frost 1942). Its diet consists of algae, mosses, and tracheophytes (Rousseau *et al*. (1921). The moss not only provides a suitable location to find its food, but provides it protection from trout and other fish that are its predators.

Figure 44. ***Lepidostoma hirtum*** larva, an inhabitant of bryophytes that also eats them. Photo by Urmas Kruus, with permission.

Figure 45. ***Lepidostoma hirtum*** larva head. Photo by Urmas Kruus, with permission.

Crunoecia irrorata (Figure 46) prefers moss cushions and fallen leaves (Köcherfliegen 2015). In UK streams, this species had mosses in the gut (Percival & Whitehead 1929).

Oeconesidae

This is a small family from Tasmania (1 species) and New Zealand (Holzenthal *et al*. 2007), but of a relatively large size (adults 30-38 mm) (Oeconesidae 2013). Larvae live in small, forested streams, make cases from plant and rock material, and feed on plant debris (Holzenthal *et al*. 2007).

Figure 46. ***Crunoecia irrorata*** larva, a moss consumer. Photo by Niels Sloth, with permission.

In New Zealand, both ***Oeconesus maori*** (see Figure 47) and ***Zelandopsyche ingens*** (Figure 48) occasionally ingest bryophytes (Suren 1988). Suren and Winterbourn (1991) determined that of the 14 taxa that had bryophyte fragments in their guts, only ***Zelandopsyche ingens*** and ***Oeconesus similis*** consumed them regularly.

Figure 47. ***Oeconesus*** larva, a bryophyte dweller and bryophyte consumer in New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 48. ***Zelandopsyche*** larva and case, a bryophyte dweller and regular bryophyte consumer. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Uenoidae

This family lives mostly in cool, fast-flowing headwaters and is distributed in North America, southern Europe, and eastern Asia (Holzenthal *et al*. 2007). Their cases may be constructed either of coarse pebbles, as in ***Neophylax*** (Figure 53-Figure 55), or of fine sand, flattened, and shaped like the shell of a limpet, as in ***Thremma*** (Figure 49). Larvae eat diatoms and fine particulate matter that they scrape from rocks. These larvae are among the smaller caddisflies, being up to 15 mm (Wiggins 2004), although for moss dwellers they would be in the medium to large category.

Figure 49. ***Thremma gallicum*** larva showing limpet type of case. Photo from Guillaume Doucet, with permission.

Thremma sp. (Figure 49) in the trout streams of Yellowstone National Park, USA, occurs among mosses and the alga *Cladophora* in strong rapids (Muttkowski & Smith 1929). Each of these caddisflies collected from the mosses had mosses in the gut, averaging 70% of the contents. The alga ***Epithemia*** (Figure 50), most likely living among the mosses, comprised the remaining 30%. Brown (2007) found significant numbers of ***Neothremma alicia*** (Figure 51-Figure 52) in small, mossy streams in the headwaters of the East River, Colorado, USA.

Figure 50. ***Epithemia***, a diatom genus that is a common food source for the caddisfly ***Thremma***. Photo by Kristian Peters, with permission.

Figure 51. ***Neothremma alicia*** larva with case, a moss dweller in small, headwater streams. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 52. ***Neothremma alicia*** larva outside its case. Photo from Biodiversity Institute of Ontario, through Creative Commons.

In the Appalachian Mountain stream bryophytes, the **Uenoidae** were represented by a completely different genus from the ones I found in publications, the only one being ***Neophylax*** (Figure 53-Figure 55), a genus that sometimes reached large numbers among the **Trichoptera**, but usually was absent (Glime 1968). Nevertheless, three species were represented: ***N. concinnus*** (Figure 53), ***N. consimilis*** (Figure 54), ***N. oligius*** (Figure 55). These were usually in the mat-forming bryophytes, a location permitted by their smaller size.

Figure 53. ***Neophylax concinnus*** larva, a moss dweller in mid-Appalachian Mountain streams. Photo by Bob Henricks, with permission.

Figure 54. ***Neophylax consimilis*** larva, a moss dweller in mid-Appalachian Mountain streams. Photo by Bob Henricks, with permission.

Figure 55. ***Neophylax oligius*** larva, a moss dweller in mid-Appalachian Mountain streams. Photo by Tom Murray, through Creative Commons.

Phryganeoidea

Brachycentridae – Humpless Casemaker Caddisflies

The **Brachycentridae** are a Northern Hemisphere family (Holzenthal *et al*. 2010b). They eat algae and plankton (Neuswanger 2015b), but some also ingest bryophytes (Muttkowski & Smith 1929). These caddisflies build cases that resemble log cabins or cylinders made of tiny plant fragments (Holzenthal *et al*. 2010b), including bryophytes in some genera (Glime 1968). Often they are found among mosses (Bouchard 2004). When they emerge, they do so on the surface, which sometimes subjects them to 3-7 m of drifting (Neuswanger 2015b). Females may dive to lay eggs or land with spread wings on the surface to accomplish the task.

Brachycentrus

Larvae of ***Brachycentrus*** (Figure 56-Figure 59) species actually attach to the mosses (Armitage 1961; Glime 1968). ***Brachycentrus*** was one of only two genera of caddisflies that Muttkowski and Smith (1929) found among mosses in the trout streams of Yellowstone National Park, USA. Needham and Christenson (1927) reported ***Brachycentrus*** from mosses in streams of northern Utah, USA. In Europe, Krno (1990) found ***Brachycentrus montanus*** (Figure 56) among mosses in the River Rajcianka, Slavakia. In the Appalachian Mountains, ***B.*** cf. ***numerosus*** (Figure 56) occurred in clumps of the moss ***Hygroamblystegium fluviatile*** (Figure 4-Figure 5) (Glime 1968).

Figure 56. ***Brachycentrus numerosus*** larva, a species like one that is common among ***Hygroamblystegium fluviatile*** in the Appalachian Mountain streams. Photo by Tom Murray, through Creative Commons.

Figure 57. ***Brachycentrus montanus*** adult, a species that lives among stream mosses. Photo by James K. Lindsey, with permission.

Gallepp (1977) considered ***Brachycentrus*** – ***B. americanus*** (Figure 58), ***B. occidentalis*** (Figure 59) – to be filter feeders, but Muttkowski and Smith (1929) found that mosses were among the food items in the gut, with one individual having 90% moss. Others had only algae and a few had aquatic insects.

Figure 58. ***Brachycentrus americanus*** larva, a moss consumer. Photo by Donald S. Chandler, with permission.

Figure 59. ***Brachycentrus occidentalis*** larvae, a moss consumer species. Photo by Arlen Thomason, with permission.

Gallepp (1977) found that two species of ***Brachycentrus*** were more responsive to temperature and food availability than to the flow rate. Although case-building decreased with increasing temperature over the range of 4-17°C, ***B. occidentalis*** (Figure 59) grew faster as the temperature increased in the range of 4-27°C.

Micrasema

The larvae of the grazer genus ***Micrasema*** (Figure 60) (Gallepp 1977) are common among mosses (Glime 1968, 1994; Tada & Satake 1994). In the mid-Appalachian Mountain streams I was able to distinguish three different morphotypes (species?) among the bryophytes (Glime 1968). In fact, this genus seems to be almost restricted to that habitat (Hilsenhoff 1975). Tada and Satake (1994) found a species in this genus to be the most abundant insect taxon on mats of ***Platyhypnidium riparioides*** (Figure 13) in a cool mountain stream in central Japan. Among the bryophyte mats its density exceeded 100,000 individuals per square meter in November, an abundance that was 2.8-16.3 times as high as that on the bare rock bottom. At least one species of ***Micrasema*** (Figure 60) constructs a "log cabin" out of moss stems and leaves (Glime 1968).

Figure 60. ***Micrasema charonis*** larva, a common moss-dweller that often makes its case from mosses. Photo by Bob Henricks, with permission.

Chapman and Demory (1963) found that in two streams in Oregon, USA, this genus occurred only among mosses and liverworts where there was little detritus. They graze on periphytic algae during the first instar, but in later instars they are likely to be herbivore-chewers (shredders) on mosses and other small photosynthetic material (Chapman & Demory 1963; Aquatic Insects). In fact, Chapman and Demory (1963) found that ***Platyhypnidium riparioides*** (Figure 13) was the most frequent food, but both mosses and liverworts were eaten. Diatoms were also present in the gut, but they might have been eaten inadvertently along with the bryophytes. And in the Pyrénées ***Micrasema morosum*** behaves as a shredder and eats mosses (and periphyton) as well (Décamps & Lafont 1974).

In the Pyrénées Décamps (1968) found that ***Micrasema morosum*** was abundant in the mosses ***Cratoneuron commutatum*** (Figure 61) and ***Bryum*** (Figure 26) and was the most abundant bryophyte-inhabiting caddisfly. At one station ***M. morosum*** comprised 56% of the Trichoptera fauna among mosses and at another it comprised 87.8% (Décamps 1967). ***Micrasema vestitum*** was abundant in ***Fontinalis squamosa*** (Figure 62) and in one location it comprised 69% of the **Trichoptera** fauna among the mosses**.**

Figure 61. ***Cratoneuron commutatum***, home to several species of ***Micrasema***. Photo through Creative Commons.

Figure 62. ***Fontinalis squamosa***, home to several species of *Micrasema* larvae. Photo by David T. Holyoak, with permission.

Décamps and Lafont (1974) demonstrated the change in moss substrate for ***Micrasema morosum*** as altitude changes in the Pyrénées. At 1940 m asl the dominant bryophytes were ***Brachythecium rivulare*** (Figure 63), ***Cratoneuron commutatum*** (Figure 61), and ***Hygrohypnum molle*** (Figure 64). At 1590 m asl dominance shifted to ***Fontinalis squamosa*** (Figure 62), ***Fissidens polyphyllus*** (Figure 65), and ***Platyhypnidium riparioides*** (Figure 13). At 1360 m asl ***Fissidens grandifrons*** (Figure 66) appeared and ***Platyhypnidium riparioides*** (Figure 13) remained in the stream flora. At

550 m asl the dominant mosses were ***Brachythecium rivulare***, ***Fissidens grandifrons***, ***Platyhypnidium riparioides***, and ***Chiloscyphus polyanthos*** (Figure 67), with a change in the ***Micrasema*** species to ***M. morosum***, ***M. longulum***, ***M. moestum***, ***M. difficile***, and ***M. minimum***. At the lowest location of 430 m, asl ***Brachythecium rivulare***, ***Cinclidotus fontinaloides*** (Figure 68), ***Fontinalis antipyretica*** (Figure 11), ***Platyhypnidium riparioides***, and ***Cratoneuron filicinum*** (Figure 69) with ***Micrasema morosum*** once again the predominant species. The food of these ***Micrasema*** species consisted of fragments of mosses and periphytic algae, with some food unidentifiable.

Figure 63. ***Brachythecium rivulare***, home to several species of ***Micrasema*** larvae. Photo by David T. Holyoak, with permission.

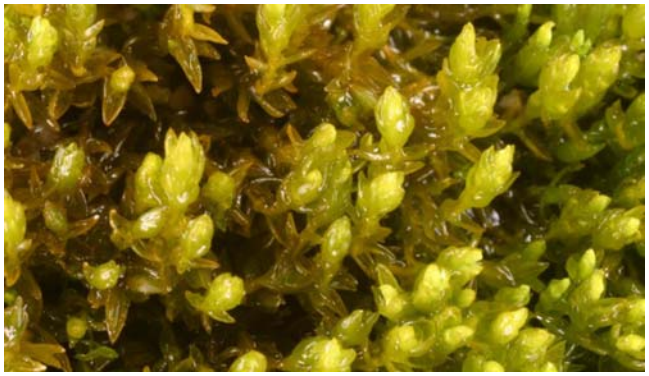

Figure 64. ***Hygrohypnum molle***, home to several species of ***Micrasema*** larvae. Photo by Jan-Peter Frahm, with permission.

Figure 65. ***Fissidens polyphyllus***, home for several species of ***Micrasema***. Photo by David T. Holyoak, with permission.

Figure 66. ***Fissidens grandifrons***, home to larvae of several ***Micrasema*** species. Photo by Scot Loring, through Creative Commons.

Figure 67. ***Chiloscyphus polyanthos***, home to lower elevation species of ***Micrasema*** larvae in the Pyrénées. Photo by Barry Stewart., with permission

Figure 68. ***Cinclidotus fontinaloides***, home to lower elevation species of ***Micrasema*** larvae in the Pyrénées. Photo by David T. Holyoak, with permission.

Figure 69. ***Cratoneuron filicinum*** in Europe, home for many immature insects. Photo by Michael Lüth, with permission.

In Japan, ***Micrasema uenoi*** (Figure 70) feeds on the leaves of ***Platyhypnidium riparioides*** (Figure 13) and the first instar larvae make their cases of its leaves (Kato 1995). The first two instars live in greater numbers among mosses than on cobble, but by third to fifth instars the numbers are about equal. When artificial mosses (glass wool) and cleaned mosses were introduced, these larvae reached normal densities in 15-30 days. Surprisingly, the density on the glass wool was 2-3 times that among the mosses, but it subsequently decreased quickly. Gut contents of those third to fifth instars on bryophytes was 80% moss; those on the glass wool contained litter and detritus instead. The larvae move about a lot between the pebbles and the mosses. Eggs were apparently absent on the mosses, suggesting that the hatchlings move there.

Figure 70. ***Micrasema uenoi*** adult, a species whose larvae feed on leaves of ***Platyhypnidium riparioides*** in Japan. Photo by Takao Nozaki, with permission.

D. N. Bennett (pers. comm. 6 August 2013, 12 August 2014) observed ***Micrasema wataga*** (Figure 71-Figure 72) larvae eating moss (possibly ***Hygrohypnum montanum***) leaves (Figure 71) in the Blue Ridge Mountains of Virginia, USA. They made their cases of the same moss, starting with a tiny cone of minute sand grains. The mosses closest to this cone part, hence the oldest, were no longer green, but those near the opening were still green. This can be a possible source of dispersal of fragments that break away from the unfinished cases. But a later observation showed that the mosses in the case actually sprouted there (Figure 72)! This case was apparently occupied by a pupa, ceasing the activity that could break off these sprouts before they attained sufficient size to exist on their own.

Figure 71. ***Micrasema wataga*** eating moss (***Hygrohypnum montanum***?). Photo by D. N. Bennett, with permission.

Figure 72. ***Micrasema wataga*** case with moss sprouts. A pupa is hiding inside. Photo by D. N. Bennett, with permission.

Adicrophleps hitchcockii

This interesting larva makes its case from bryophytes. It was relatively common among ***Hygroamblystegium fluviatile*** (Figure 4-Figure 5) in Appalachian Mountain streams (Glime 1968). It appeared to have used costae from this moss in the construction of its cases.

D. N. Bennett likewise collected larvae of the somewhat rare ***Adicrophleps hitchcockii*** (Figure 1, Figure 73) in several cold, rapid streams (1-10 m wide) from the aquatic leafy liverwort ***Scapania*** (Figure 74) growing in riffle areas (Henricks 2013; D. N. Bennett, pers. comm. September 2014). But the case is not made of liverworts, but rather it displays mosses. Wiggins (1977) described these as "4-sided, tapered, and constructed of pieces of moss arranged transversely; trailing ends frequently left attached to the moss pieces give the case a furry appearance."

Figure 73. ***Adicrophleps hitchcocki***, a species that lives among bryophytes and makes its case from mosses. Photo by D. N. Bennett, with permission.

Figure 74. ***Scapania undulata***, home for ***Adicrophleps hitchcocki*** but not used for case building. Photo by Hermann Schachner, through Creative Commons.

Phryganeidae – Giant Casemakers

This family with relatively large larvae lives mostly in lakes and rivers (Neuswanger 2015a). The pupae crawl from their watery location to shore to emerge. Females run across the water surface to lay their eggs. The larvae are most common among aquatic plants in ponds and marshes, but some occur in streams and others in temporary pools and deep in lakes (Holzenthal *et al*. 2007). Larvae are typically either predators or herbivores.

This family is not common among the bryophytes. But, ***Yphria californica*** (Figure 75), a species restricted to the west coast states of USA, lays its eggs (Figure 76) underwater among mosses that dangle over the stream in the Sierra Nevada, North America (Erman 1984). To do that, the adult must swim underwater.

Figure 75. ***Yphria californica*** adult, a USA west coast species that lays its eggs among mosses. Biodiversity Institute of Ontario, through Creative Commons.

Figure 76. **Trichoptera** eggs, often laid on bryophytes. Photo by Bob Armstrong, with permission.

The larvae of ***Eubasilissa regina*** (Figure 77) in Japan begin their construction days by making cases of liverworts, but as they develop they change to terrestrial leaf litter and move their abode from the liverworts to pools (Ito 1988).

Figure 77. ***Eubasilissa regina*** adult, a large Japanese caddisfly for which the larvae begin their case construction using liverworts. Photo through Creative Commons.

Oligostomis ocelligera (Figure 78) lives in moist places such as under mosses where it is protected (Redell *et al*. 2009). It usually occupies positions with a mean distance of 6.1 cm below the surface.

Figure 78. ***Oligostomis ocelligera*** larva, a species that lives under mosses. Photo by Tom Murray, through Creative Commons.

Hagenella clathrata is a rare caddisfly in Europe, inhabiting the disappearing bog habitat (Buczyńska *et al*. 2012). In particular, the species often occurs in bog pools that occur only in rapidly disappearing floating bogs, hence being dependent on the particular habitat created by ***Sphagnum*** (Figure 10) (Kleef et al. 2012).

Sericostomatoidea

Beraeidae

This family is scattered about the globe, being concentrated in the western **Palaearctic Region** (Eurasia from western Europe to the Bering Sea), but also occurs in Tanzania, Japan, and eastern North America (Hamilton 1985; Holzenthal *et al*. 2007). Adults have forewings that are only 4-6 mm long (Watson & Dallwitz 2003). Larvae live in springs, seeps, and small streams where they utilize a variety of substrates, including bryophytes (Hamilton 1985; Holzenthal *et al*. 2007). They eat plant and fungal material, but there seem to be no records of eating bryophytes.

Beraea maura (Figure 79) represents this family in the River Rajcianka, Slovakia, where it inhabits the submerged bryophytes (Krno 1990). Unlike several members of the **Limnephilidae** and **Rhyacophilidae**, this species is not found above the water level in the wet mosses there. In the Pyrénées, Décamps (1968) found larvae of this family among mosses, but this family had a wide range of habitats in addition to the mosses.

Figure 79. ***Beraea maura*** adult, a species that lives among submerged bryophytes as larvae. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Conoesucidae

Among the unfamiliar **Trichoptera** names (to those of us in the northern hemisphere), the **Conoesucidae** (Figure 80) is another of bryophyte-dwelling families from down under (Winterbourn & Gregson 1981). The family is endemic to Australia, New Zealand, and Tasmania (Johanson *et al*. 2009). Among the bryophyte dwellers is ***Confluens hamiltoni***, an endemic on the North Island, New Zealand, where it is associated with mosses, liverworts, and algae in rapid-flow streams (Winterbourn & Gregson 1981). On the South Island, this species is replaced by ***C. olingoides***, occupying conditions like those of ***C. hamiltoni***.

Figure 80. ***Pycnocentrodes aureolus*** adult, member of a family (**Conoesucidae**) with bryophyte dwellers in the Australian region. Photo by Maurice, through Creative Commons.

Helicophidae

This family of 6-14 mm length (Helicophidae 2015b) is mostly known from Australia, New Zealand, and New Caledonia, but also from southern South America and scattered locations in North America (Helicophidae 2015a). The larvae live in slow streams and are mostly detritivores (Helicophidae 2015b).

Trichoptera are not as common in New Zealand as in other parts of the planet, but the **Helicophidae** are represented there, sometimes associated with mosses (Winterbourn & Gregson 1981). ***Zelolessica cheira*** (Figure 81) occurs among ***Fissidens rigidulus*** (Figure 82) in the torrential waters near the middle of stream channels in the Southern Alps (Cowie & Winterbourn 1979). ***Zelolessica cheira*** is usually associated with mosses and liverworts in rapid streams with a stable, rocky substrate (Winterbourn & Gregson 1981; Eward *et al*. 1994). The cases are curved, comprised variously of sand grains, liverworts, and mosses.

Figure 81. ***Zelolessica*** larvae. Some members make their cases from bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 82. ***Fissidens rigidulus***, home for ***Zelolessica cheira*** in torrential New Zealand waters. Photo by Bill & Nancy Malcolm, with permission.

Alloecentrella (Figure 83) is known from China, Australia, New Zealand, and the Antarctic. In New Zealand, ***Alloecentrella magnicornis*** and an unnamed species occur among mosses and liverworts in rocky streams where they build their cases using bryophytes (Eward *et al*. 1994).

Figure 83. ***Alloecentrella*** sp. larva, a species that covers its case with mosses and liverworts. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Sericostomatidae – Bushtailed Caddisflies

These caddisflies are of moderate size, with wings 8-15 mm long (Watson & Dallwitz 2011). This family is cosmopolitan except for the Australian region (Sericostomatidae 2015). Nevertheless, many of the genera are endemic to small areas of their continents. At least some larval members of the family move little. For example, more than 120,000 larvae of ***Gumaga nigricula*** (Figure 84-Figure 85) were released in pools of a California mountain stream and 87-93% of them remained within 4 m of the pools (Jackson *et al*. 1999). In this clever experiment, the larvae were provided with bright gold or magenta sand grains to complete their cases so that they could easily be tracked.

Figure 84. ***Gumaga*** sp. larva, a relatively immobile caddisfly. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 85. ***Gumaga nigricula*** adult, a relatively immobile caddisfly in the larval stage. Photo from Biodiversity Institute of Ontario, through Creative Commons.

The **Sericostomatidae** live in both streams and lakes and mostly feed on leaf litter (Family Sericostomatidae 2015). They build slightly to strongly curved tubular cases from sand grains or just silk. Because of their interesting designs and strength, the Tupi-Guarani Indians in Brazil used the cases of ***Grumicha*** as adornment.

Some of the moss dwellers are quite rare. Stern and Stern (1969) found the larvae of ***Sericostoma*** sp. (Figure 86) only among algae and mosses in a Tennessee, USA, springbrook.

Sericostoma pedemontanum (Figure 86), a caddisfly of fast-running streams, refused ***Fontinalis antipyretica*** (Figure 11) when provided a diet of birch, beech, and oak leaves with it (Higler 1975). Birch was the preferred food.

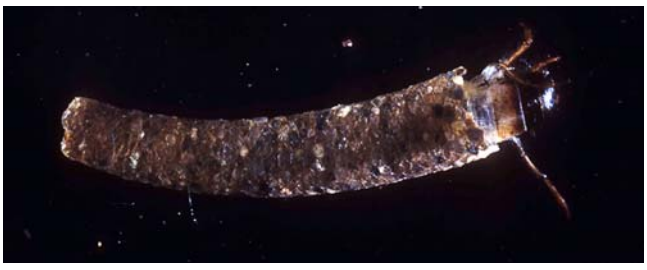

Figure 86. ***Sericostoma pedemontanum*** larva, a species that refused ***Fontinalis*** and chose various species of leaf litter in a feeding experiment. Photo by Massimo Del Guasta, with permission.

SUBORDER SPICIPALPIA

Glossosomatoidea

Glossosomatidae – Tortoise or Saddle-case Makers

This worldwide family makes its larval cases from pebbles in the shape of a turtle shell (Glossosomatidae 2014). It is probably this structure that forces them to build a new case in each new instar, rather than adding to the old one as most caddisfly families do. These small to medium-sized larvae usually occur in cool mountain streams where they scrape algae from the rocks as their food. The female adults lay their eggs in gelatinous masses under rocks at the water surface or on floating objects, probably including mosses. The gelatinous material protects the eggs from desiccation.

From Ceylon, Schmid (1958) reported ***Agapetus rawana*** (see Figure 87-Figure 90) from large, mossy rocks in the torrent. In the Appalachian Mountains, ***Glossosoma*** (Figure 91) larvae and pupae were often present among the bryophytes (Glime 1968).

Figure 87. ***Agapetus fuscipes*** larva and case, a genus known from large, mossy rocks of torrents in Ceylon. Photo by J. C. Schou, with permission.

Figure 88. ***Agapetus fuscipes*** larvae showing the unusual shape of the case. Photo by Dragiša Savić, with permission.

Figure 89. ***Agapetus*** prepupa in larval case. Photo by Mark Melton, with permission.

Figure 90. ***Agapetus*** pupa removed from case. Photo by Mark Melton, with permission.

Figure 91. ***Glossosoma*** sp. larvae, showing its "turtle shell" case. Photo by Jason Neuswanger, with permission.

Hydroptiloidea

Hydroptilidae – Microcaddisflies, Purse-case Caddisflies

This is a worldwide family, less than 5 mm long, that builds flattened cases often resembling an eyeglass case (Hydroptilidae 2015). The members of the family solve the problem of locating food by depositing their eggs near a suitable food source (Leader 1970). They typically feed on algae by sucking out the cell contents or by feeding on diatoms.

In the Appalachian Mountain streams where I worked, this tiny caddisfly is usually not very common, but Percival and Whitehead (1929) found them more commonly among mosses on stones than on other substrates in the UK. Hughes (1966) found them to be more abundant in open areas than in shaded ones, a factor that usually contrasts with bryophyte preferences. Percival and Whitehead (1929) found that the hydroptilids from mosses feed on algae and diatoms. The larvae of this family have mouthparts that are able to pierce and suck, enabling them to suck the contents from filamentous algae or to scoop up diatoms (Nielsen 1948).

It is perhaps telling that at least in Denmark, the genera ***Agraylea*** (Figure 92), ***Hydroptila*** (Figure 93), ***Oxyethira*** (Figure 94-Figure 95), and ***Orthotrichia*** (Figure 96) are very common in eutrophic lakes (Nielsen 1948). This suggests that in streams we should look for the bryophyte dwellers deep within the mat where there is reduced flow. But even in the lakes these genera occupy vegetation near the surface. ***Agraylea*** and ***Orthotrichia*** occur in slowly flowing water, and this is where mosses can add possible niches. ***Orthotrichia*** often becomes coated in detritus and will pass one of its hind legs down the dorsal side of its abdomen to clean the tracheal gills there.

Figure 92. ***Agraylea sexmaculata*** larva, a genus that lives among bryophytes in slowly flowing water. Photo by Massino Del Guasta, with permission.

Figure 93. ***Hydroptila sparsa*** larvae, member of a genus that occurs among bryophytes in lakes and streams. Photo by Massimo Del Guasta, with permission.

Figure 94. ***Oxyethira*** larva, a moss dweller in Danish lakes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 95. ***Oxyethira*** pupa. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 96. ***Orthotrichia*** sp larva and case, a species that lives among mosses in lakes. Photo by Urmas Kruus, with permission.

Hydroptila (Figure 93) can build a case of detrital matter and sand grains in about four hours (Nielsen 1948). To increase the size of the case, the larva splits it open along the ventral edge, adding sand grains to the edge. The completed case, as in most members of the family, looks like a case for eye glasses (Figure 93) – the one with an

open end – which is where the head protrudes in the caddisfly version. Some cases are built with algal filaments, especially in ***Agraylea*** (Figure 92), and I have observed cases made almost entirely of diatoms. In both ***Hydroptila*** and ***Agraylea*** the outer coating of sand or algae will wear off as the larva nears maturity, leaving only the smooth inner wall made of silk spun by the larva as it cements the case together. ***Orthotrichia*** (Figure 96) and ***Ithytrichia*** (Figure 97) species use only silk in the construction of their cases. These genera feed by sucking the contents out of algal cells.

Figure 97. ***Ithytrichia lamellaris*** larva & case, a genus that uses only silk in its case. Photo by Urmas Kruus, with permission.

When these four genera (***Agraylea***, ***Hydroptila, Orthotrichia***, ***Ithytrichia***) emerge, they split the pupal case, then move about until they find a protruding object to climb up and out of the water (Nielsen 1948). Once out they can flit about on the water surface and in the air.

The moss-dwelling genus ***Oxyethira*** (Figure 94-Figure 95), including more than one species, comprised 44.5% of the Trichoptera fauna at the acid site in Frost's (1942) moss fauna study of the River Liffey, Ireland. It was absent at the alkaline site. ***Oxyethira frici*** lives in the angle between the leaf and the stem of the moss and pupates among the mosses, a behavior that is uncommon among caddisflies. By contrast, ***Ithytrichia lamellaris*** (Figure 97), a species almost restricted to mosses, was common at the alkaline site and absent from the acid site. It likewise lives in the angle between the leaf and the stem of the moss and pupates among the mosses. Both of these genera were present, but rarely, among the bryophytes of Appalachian Mountain mostly acid streams, USA (Glime 1968). They were more common on ***Fontinalis***, where larvae of ***Oxyethira*** and ***Hydroptila*** sometimes decorated the branches of ***Fontinalis dalecarlica*** (Figure 98).

From Ceylon, Schmid (1958) reported ***Chrysotrichia hapitigola***, and ***Hydroptila kirilawela*** from large, mossy rocks in the torrent.

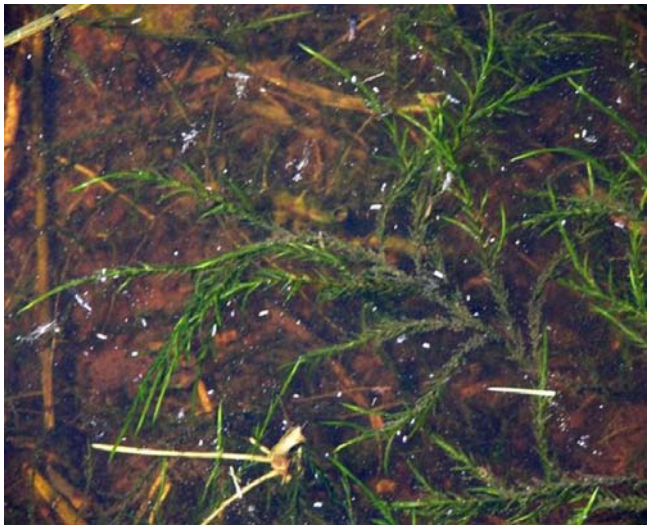

Figure 98. ***Fontinalis dalecarlica***, home to many insects. Photo by J. C. Schou, with permission.

Woodall and Wallace (1972) found ***Ochrotrichia*** sp (Figure 99) on moss-covered granite outcrops in the Appalachian, USA, streams that they studied. They considered the moss-covered rock outcrops to be the central factor influencing the distribution of this species in the area. In my own studies of the mid-Appalachian Mountain streams, this genus was not present, but I did occasionally find ***Mayatrichia***, ***Neotrichia***, and ***Stactobiella*** in addition to the more common ones discussed above under this family (Glime 1968).

Figure 99. ***Ochrotrichia eliaga*** larva and case, a genus found on moss-covered granite outcrops in Appalachian streams. Photo by Trevor Bringloe, Biodiversity Institute of Ontario, through Creative Commons.

In a Tennessee, USA, springbrook, ***Ochrotrichia unio*** (see Figure 100) live among algae and mosses as larvae, then move to bare rocks to pupate (Stern & Stern 1969). In Great Britain, the larvae of this species feed on diatoms and other algae (Percival & Whitehead 1929).

Figure 100. ***Ochrotrichia*** larva, a genus in which some larvae live among mosses, then migrate to bare rocks to pupate Photo from California Department of Wildlife, through public domain.

Ptilocolepus

Ptilocolepus granulatus is **crenophilic** (describing organism preferring spring environments but may also occupy similar habitats), living in montane to subalpine regions of central Europe (Waringer & Graf 2002). Wesenberg-Lund (1943) reported that ***Ptilocolepus granulatus*** lives in moss cushions and makes its case from moss fragments. Similarly, González *et al.* (2000) reported that ***P. extensus***, an endemic on the Iberian Peninsula and a close relative, uses leaf pieces of several moss and liverwort species to make its final instar case. Unlike most of the **Hydroptilidae**, this case is flattened dorsiventrally, but still has the typical elongate-oval shape.

In the Pyrénées, Thienemann (1950) and Décamps (1968) found ***Ptilocolepus granulatus*** among mosses and liverworts. These bryophytes also formed a significant portion of their food as well as construction material for their cases. Ito (1998) reported that this genus lives among, eats, and builds its cases from the leafy liverworts ***Chiloscyphus polyanthos*** (Figure 67) and ***Scapania undulata*** (Figure 74). Depisch (1999) and Ito and Higler (1993) all found that the species commonly lives among and feeds on the liverwort ***Scapania undulata***. In Belgium ***Ptilocolepus granulatus*** uses ***Jungermannia riparia*** for food, but surprisingly, it also sometimes builds its case from the moss ***Fontinalis*** (Figure 11) (Ito & Higler 1993). Thus it is not surprising that Dittmar (1955) found it associated with ***Fontinalis***. Ito and Higler found that it does not seem to feed on the moss, but later Ito (1998) states that it is the only species in the subfamily **Ptilocolepinae** that is able to feed on ***Fontinalis*** (and other mosses), attributing this ability to its large mandibles.

Palaeagapetus

Microcaddisflies such as ***Hydroptila*** (Figure 93) often attach their tiny homes to the moss leaves and stems, but ***Palaeagapetus*** in the same family constructs its home strictly out of leafy liverworts (Flint 1962; Glime 1978; Ito & Hattori 1986; Ito 1991), even when these are growing side by side with mosses such as ***Fontinalis*** (Figure 11). The species of liverwort depends on availability, with cases of ***Paleagapetus celsus*** from the eastern USA known from ***Scapania nemorea*** (Flint 1962; Glime 1978) (Figure 101), ***S. undulata*** (Glime 1978) (Figure 74), ***Plagiochila porelloides*** (Glime 1978) (Figure 102), ***Frullania*** sp. (Glime 1978) (Figure 103). In those I observed, the pieces of liverwort were cut into nearly circular pieces and cemented together along their margins, forming a case typical of many hydroptilids – the shape of an eyeglass case. Ito and Vshivkova (1999) described the pieces of liverworts comprising the cases of ***Palaeagapetus finisorientis*** from the Russian Far East similarly as being roughly rounded fragments.

Figure 101. ***Scapania nemorea***, one of the species used for making cases of ***Palaeapetus celsus***. Photo by Bernd Haynold, through Creative Commons.

Figure 102. ***Plagiochila porelloides***, a species used by ***Palaeagapetus celsus*** for making its case. Photo by Hermann Schachner, through Creative Commons.

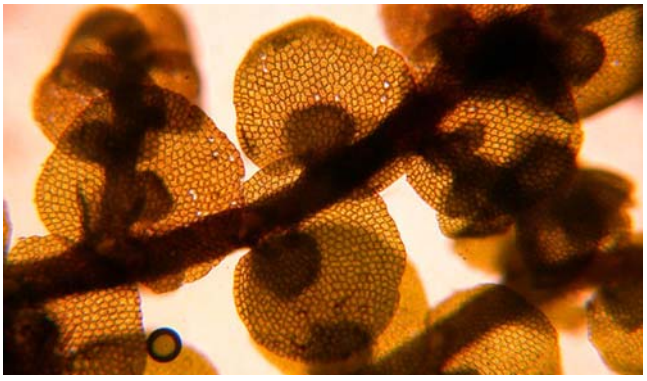

Figure 103. ***Frullania eboracensis***, a terrestrial epiphytic species that may fall into the water and be used in the case of ***Palaeagapetus celsus***. Photo by Bob Klips, with permission.

Not only do members of this genus use liverworts in the construction of their cases, but the liverworts are also a primary food source (Botosaneanu & Levanidova 1987). In his review of four species of ***Palaeagapetus***, Ito (1998) found that all of them used the liverworts ***Chiloscyphus polyanthos*** (Figure 67) and ***Scapania undulata*** (Figure 74) for food, housing, and case construction. It appears that all known members of the genus have this same strong dependence on leafy liverworts, including those in the eastern part of the former Soviet Union (Botosaneanu & Levanidova 1987), Japan (Ito & Hattori 1986; Ito 1988, 1991), and North America (Flint 1962; Glime 1978). In the western USA, ***Palaeagapetus nearcticus*** uses ***Scapania uliginosa*** for its case and food (Ito *et al*. 2014). The larvae pierce the cells and consume the liverwort one cell at a time. Ito and Vshivkova (1999) found that in the ***Palaeagapetus*** species they observed, the early instars fed on the contents of the liverwort cells, whereas the final instar cut off the leaves and apparently ingested them, reminiscent of human babies who also shift from sucking to chewing. Ito (1991) found that ***Palaeagapetus rotundatus*** feeds on the leaves of leafy liverworts ***Chiloscyphus polyanthos*** and ***Scapania undulata*** (Figure 74), but will not feed on the moss ***Platyhypnidium riparioides*** (Figure 13).

Ito (1988) followed the life history of ***Palaeagapetus ovatus*** in a spring stream in Japan. He found that the density changed with season, reaching the highest in winter and being low in summer. Living with it was a predatory **Trichoptera**, ***Eubasilissa regina*** (**Phryganeidae**; Figure 77), that preyed upon it among the liverworts.

We know more about this genus and its liverwort relationship through the description of a new species, ***Palaeagapetus ovatus***, in Japan (Ito & Hattori 1986). This liverwort dweller fed exclusively on the leaves of the leafy liverwort ***Chiloscyphus polyanthos*** (Figure 67). Its fifth and final instar made the typical oval case from the leaves of this liverwort. And the females, within two days of emergence, laid 50-85 eggs on the leaves of this liverwort. The eggs do not form a mass and at 10.5-12°C they hatch in 21-23 days. ***Palaeagapetus nearcticus*** also deposits its orange eggs on liverwort leaves (Ito *et al*. 2014).

More recently, Woods (2002) was surprised to find the thallose liverwort ***Riccardia chamedryfolia*** (Figure 104) moving in a slow, jerky motion on the sandy bottom of a pool in Wales. Investigation revealed that two matching pieces of the thallus had been cemented together by a caddisfly larva that was using it for a home (case). The larva was not identified but could have been a member of **Hydroptilidae**.

Scelotrichia

My email makes Christmas come all year-round. One of these nice surprises came when Andi Cairns sent me pictures of a caddisfly that was a bryological surprise. This new species, actually in a genus new to Australia, was ***Scelotrichia willcairnsi*** (Figure 105) living among the mosses in a waterfall (Figure 106). It was feeding on ***Rhynchostegium brevinerve*** (Figure 107), a new species previously thought to be ***Platyhypnidium muelleri*** and renamed by Huttunen and Ignatov (2010), in north-eastern Queensland, Australia. This microcosm was full of surprises!

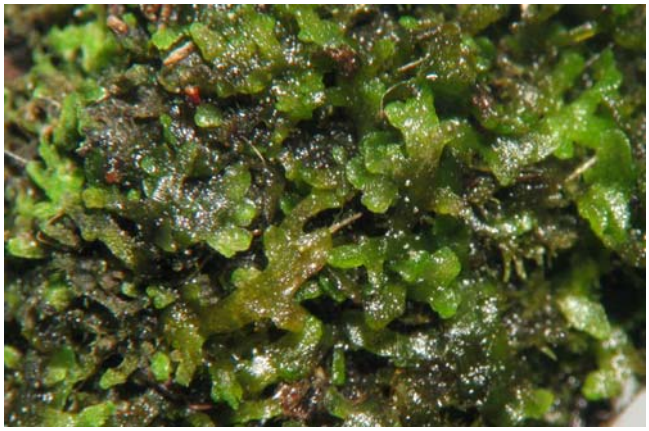

Figure 104. ***Riccardia chamedryfolia***, a liverwort that some caddisflies use to make a case. Photo by Kristian Peters, with permission.

Figure 105. The caddisfly ***Scelotrichia willcairnsi*** (**Hydroptilidae**) with a case made of pieces of the moss ***Rhynchostegium brevinerve***. Note the way pieces fit together as parallel rings. Photo courtesy of Andi Cairns.

Figure 106. ***Rhynchostegium brevinerve*** in Fishery Falls, Australia, home to ***Scelotrichia willcairnsi***. Photo courtesy of Andi Cairns.

Figure 107. ***Rhynchostegium brevinerve***, home to the caddisfly ***Scelotrichia willcairnsi***. Photo courtesy of Andi Cairns.

The ***Scelotrichia willcairnsi*** larva had a case (Figure 105) it had built by cementing moss leaf fragments together (Figure 108) – the same species of moss it was eating (Cairns & Wells 2008). It remained in this case to pupate, cementing it to the moss stems (Figure 109). When making a case, the larvae cut the leaves longitudinally, in parallel with the long axis of the leaf and its cells, giving them long pieces (Figure 108). Cairns and Wells described these: "neatly, the fragments fitted together, almost in rings." Ohkawa and Ito (2002) had already distinguished the types of cuts for leaves and for food in ***Scelotrichia ishiharai***. This microcaddis uses the moss ***Rhynchostegium*** sp. (Figure 107-Figure 109) for food (Figure 110-Figure 111) and case building (Figure 105-Figure 109), likewise using different orientations for the two kinds of cuts.

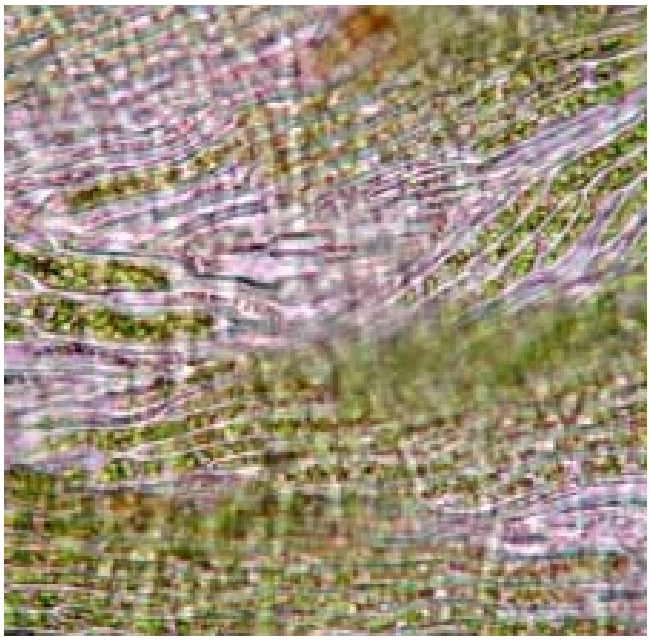

Figure 108. Pieces of the moss ***Rhynchostegium brevinerve*** from the case of the caddisfly ***Scelotrichia willcairnsi*** (**Hydroptilidae**). Photo courtesy of Andi Cairns.

Figure 109. Pieces of the moss ***Rhynchostegium brevinerve*** with numerous cases of the caddisfly ***Scelotrichia willcairnsi*** (Trichoptera: Hydroptilidae). Photo courtesy of Andi Cairns.

When Cairns and Wells (2008) examined the gut contents, they discovered that these tiny caddisfly engineers cut the pieces of moss very differently for food than they did for cases. For food, they cut the leaves perpendicular to the long axis and across the cells (Figure 110-Figure 111). Such a cut would give the gut enzymes more access to the contents of the cells.

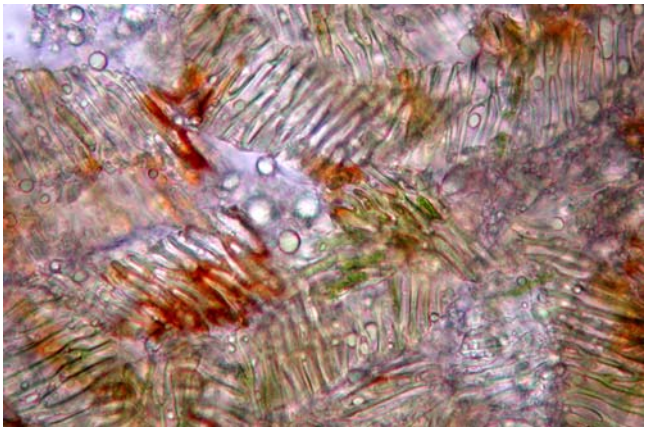

Figure 110. Pieces of the moss ***Rhynchostegium brevinerve*** from the gut of the caddisfly ***Scelotrichia willcairnsi*** (**Hydroptilidae**). Photo courtesy of Andi Cairns.

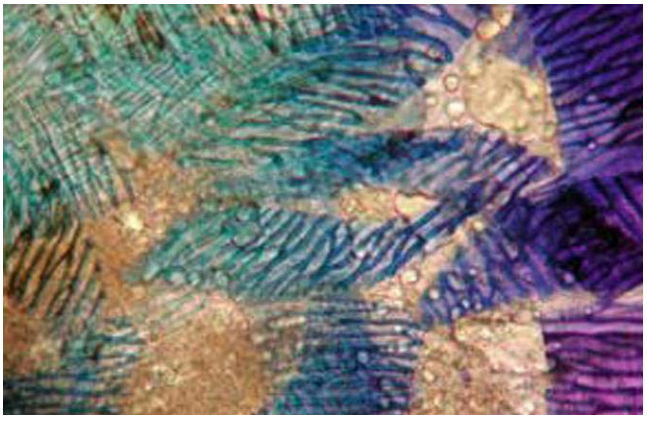

Figure 111. Pieces of the moss ***Rhynchostegium brevinerve*** from the gut of ***Scelotrichia willcairnsi***. The moss fragments are stained with Toluidine blue to make cell walls more evident. Note that cell contents appear to be gone in nearly all fragments, suggesting digestion. Photo courtesy of Andi Cairns.

Elsewhere, in Papua New Guinea, ***Scelotrichia*** was similarly collected from mosses in the strong currents at the crest of a short waterfall (Wells 1990). They likewise made their cases of the moss leaves and later attached their pupal cases to the stems of the same species of moss. Wells found adults of two other species of ***Scelotrichia*** near waterfalls or soaked mosses. As in ***S. willcairnsi*** (Figure 105), the caddisfly larvae from Papua New Guinea had cut slivers of the moss down the long axis of the leaf, making the cells parallel to the length of the fragment. These differed from the pieces cut by ***Paleagapetus*** and ***Ptilocolepus***, which were cut from leafy liverworts and glued together to resemble a patchwork quilt (Ito 1998; Ito & Higler 1993). It appears that cutting behavior can determine the type of bryophyte that is suitable for making the case.

Rhyacophiloidea

Rhyacophilidae – Free-living Caddisflies

This is a Northern Hemisphere family from the temperate parts of North America, Europe, and Asia, extending into India and the tropical areas of southeastern Asia (Kjer 2010). The larvae are 9-16 mm long and are green or brown, blending easily with the bryophytes (Bumble.org 2013). Don't be misled by the pink color they assume in preservative.

Larvae of this family do not build cases (Figure 112), so they do not attach themselves to the substrate by gluing their cases like some caddisflies do. Their life cycle is one year, with two generations overlapping. The larvae prefer rapid, cold streams where they are able to stay themselves in the current by clinging to mosses or debris (Hilsenhoff 1975). Most are carnivorous, but a few are herbivorous. And some can live above the water level among wet emergent mosses: ***Rhyacophila nubila*** (Figure 113), ***R. polonica***, and ***R. tristis***, whereas in the same River Rajcianka, Slavakia, these three species plus ***R. obliterata*** (Figure 117), ***R. philopotamoides***, and ***R. vulgaris*** occur among the mosses under water (Krno 1990).

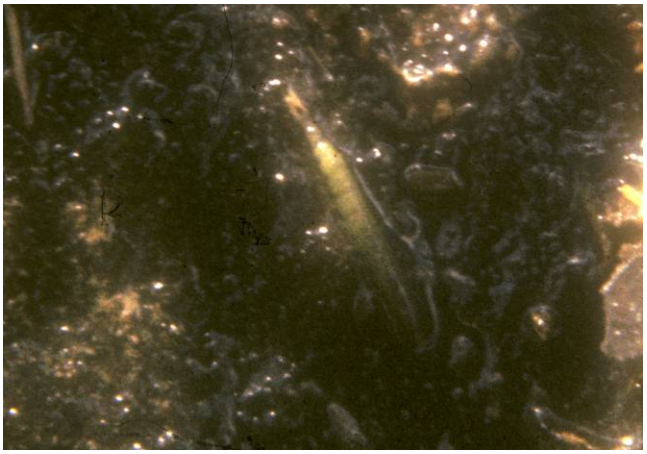

Figure 112. The free-living caddisfly, ***Rhyacophila***, is a common member of the stream moss community. Its color is typically green, and it has large hooks that permit it to cling to mosses and other substrata to avoid being washed away by the fast-flowing water it inhabits. Its lack of a case permits it to traverse the internal chambers of the moss without getting caught by the branches. Photo by Janice Glime.

Figure 113. ***Rhyacophila nubila*** larva, a species that can live among mosses above or below the water surface. Photo by Niels Sloth, with permission.

In my studies of Appalachian Mountain stream mosses in Maryland and Pennsylvania, USA, the genus ***Rhyacophila*** was among the most common and constant of the caddisfly larvae among the bryophytes. Décamps (1967, 1968) found ***Rhyacophila laevis*** to be abundant among mosses in the Pyrénées. In a cool mountain stream of central Japan, Tada and Satake (1994) found that ***R. towadensis*** was significantly more abundant among the moss ***Platyhypnidium riparioides*** (Figure 13) than in bare rock areas.

Many members of **Rhyacophilidae** most likely benefit both from the protection afforded by the bryophytes, but also from the resident fauna that serves as food, especially the numerous **Chironomidae.** In their study of four small Appalachian, USA, streams, Woodall and Wallace (1972) found larvae of ***Rhyacophila torva*** (Figure 124) (see also Roback 1975), ***R. nigrita*** (Figure 114), ***R. carolina*** (Figure 121), ***R. minora*** (Figure 115) (see also Glime 1968), ***R. glaberrima*** (Figure 116), and ***R. fuscula*** (Figure 122-Figure 123) among mats of mosses on rock outcrops. They fed on the **Chironomidae** larvae (Ross 1944) that shared the bryophyte habitat. In one of my collections from the mid-Appalachian Mountains I caught ***R. carolina*** in the act – it was preserved with a chironomid larva in its mouth. Although ***R. minora*** in a wooded Ontario, Canada, stream is typically carnivorous, early instars feed on plant material (Singh *et al*. 1984). This strategy works well until they gain the size and skill to be predators.

Figure 114. ***Rhyacophila nigrita*** larva, a moss dweller in Appalachian Mountain streams. Photo by Donald S. Chandler, with permission.

Figure 115. ***Rhyacophila minora*** larva, an Appalachian Mountain stream bryophyte dweller. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 116. ***Rhyacophila glaberrima*** larva, a common species among mosses in the Appalachian Mountain streams. Photo by Donald S. Chandler, with permission.

Figure 117. ***Rhyacophila obliterata*** adult, a species whose larvae are common among bryophytes. Photo by James K Lindsey, with permission.

Food

Most ***Rhyacophila*** species are carnivores that do not make cases, but the ***Verrula*** group eat photosynthetic organisms with their **hypognathous** heads (oriented downwards), feeding on algae, diatoms, and particularly bryophytes (Smith 1968; Thut 1969). Cummins (1973) likewise reported that ***R. verrula*** in western North America is a herbivore and especially eats aquatic mosses (Slack 1936; Gerson 1982; Smith 1968). In his study of diets of the ***Rhyacophila*** species in constructed streams in western USA, Thut (1969) found that ***R. verrula*** feeds predominantly on aquatic mosses. This effect is intensified in winter when several mosses are dominant and diatoms are abundant. Interestingly, diatoms become more important in the fourth and fifth instars than they are in earlier instars.

In a Tennessee cold springbrook, ***Rhyacophila lobifera*** larvae fed among the moss and algae, eating smaller caddisfly larvae, midge larvae, naiads of mayflies and stoneflies, detritus, and diatoms (Stern & Stern 1969). Slack (1936) also reported that one out of nine ***Rhyacophila dorsalis*** (Figure 118) had leaves of ***Fontinalis antipyretica*** (Figure 11) in the gut, but that it is primarily carnivorous. Nevertheless, one specimen contained only diatoms in the gut and the one with ***Fontinalis*** had only plant material. In a study in the English Lake District, Elliott (2005) found that early instars ate primarily diatoms (mostly ***Achnanthes*** spp., Figure 119), with bryophyte fragments also present in nearly all gut samples, but the bryophytes appeared to be undigested, displaying their chlorophyll. These bryophytes may have been eaten to obtain adhering diatoms. Both second and third instars would disappear into the bryophyte clumps to search for prey, but they returned to the surface of those clumps to consume their finds. Fourth and fifth instars fed only at night and used an ambush strategy to capture prey, which includes ***Baetis*** and ***Gammarus***.

Figure 118. ***Rhyacophila dorsalis*** larva, a carnivorous species that sometimes has leaves of ***Fontinalis antipyretica*** in its gut. Photo by Walter Pfliegler, with permission.

Larvae of most of the predominantly carnivorous ***Rhyacophila dorsalis*** (Figure 118) occur among bryophytes [leafy liverwort ***Scapania*** sp. (Figure 74) and mosses ***Platyhypnidium riparioides*** (Figure 13) and ***Fontinalis antipyretica*** (Figure 11)] (Slack 1936). For less active prey they use a searching strategy (**Chironomidae**, **Simuliidae**). The percentage of larvae with bryophytes in the gut was much smaller than that of prey. It appears that this species changes its diet as it grows, but it may also be

an opportunist regarding its diet. But if one considers that both the diatoms and bryophytes still had chlorophyll in their cells, it appears that even the first and second instar larvae may have been carnivores, eating these photosynthetic organisms by chance while attempting to capture prey. Instead, the first and second instar larvae eat copepods, rotifers, and tardigrades, common bryophyte inhabitants, but these require special preservation techniques in order to recognize them in gut samples. Instead of a shift from apparent herbivore to carnivore, Elliott (2005) demonstrated a shift in size of prey.

Figure 119. ***Achnanthes longipes***. Photo by Victor Chepurnov, through non-commercial license.

The caddis larvae of ***Rhyacophila dorsalis*** (Figure 118) begin their early instars by feeding equally day and night, but by the 4th to 5th instar they shift to feeding almost totally at night (Elliott 2005). They can feed on other insects inhabiting their moss habitat, such as **Ephemeroptera** (mayflies), **Simuliidae** (blackflies), and **Chironomidae** (midges). As they grow older, instars 4 and 5, they adopt an ambush strategy at dusk and dawn, catching such active prey as the mayfly ***Baetis*** and the scud ***Gammarus***. During the night they used a searching strategy to capture the more sedentary prey, for example **Chironomidae** (midges) and **Simuliidae** (blackflies).

Thut (1969) suggested that the high proportion of moss fragments in the diets of the herbivorous ***Rhyacophila*** was at least in part the result of seasonal changes in the available primary producers in streams. Bryophytes are available in winter when most of the algae are dormant in a resting stage.

Substrate Preference

Rhyacophila species typically make their larval homes under rocks or among mosses (Bouchard 2004). They are able to use their claws (Figure 120) to anchor themselves or cling to the mosses, but also use them as they creep along in the stony stream bed (Badcock 1949). Percival and Whitehead (1929) found that ***Rhyacophila dorsalis*** (Figure 118) preferred thick mosses and *Potamogeton* on stones. Elliott (2005) found some larvae found under large stones, but most were among bryophytes growing on the upper surfaces of large stones [***Scapania*** (Figure 74), ***Platyhypnidium riparioides*** (Figure 13), ***Fontinalis antipyretica*** (Figure 11)].

Figure 120. ***Rhyacophila fuscula*** larva showing anal hooks that cling to its substrate. Photo by Jason Neuswanger, with permission.

In the Great Smoky Mountains National Park, ***R. montana*** lives in the films of water that flow over vertical rock faces, crevices, or among wet mosses (Parker *et al*. 2007). ***Rhyacophila evoluta*** and ***R. intermedia*** are characteristic of mosses in torrents in the Pyrénées (Décamps 1967). ***Rhyacophila evoluta*** has the ability to go into a cold-induced diapause at any stage in its development. This permits it to complete its development in one, two, or three years, depending on the temperatures.

Some species seem to prefer liverworts and some to prefer mosses for their homes (locations, not cases). In the mid-Appalachian Mountain streams I found ***Rhyacophila*** cf. ***carolina*** (Figure 121) primarily among liverworts (***Scapania undulata***; Figure 74), whereas ***R. fuscula*** (Figure 120, Figure 122-Figure 123) predominated in ***Fontinalis dalecarlica*** (Figure 98) and ***R. torva*** (Figure 124) in ***Hygroamblystegium fluviatile*** (Figure 4-Figure 5) and ***Platyhypnidium riparioides*** (Figure 13). ***Rhyacophila invaria*** (Figure 125) occurred frequently among clumps of the moss ***Platyhypnidium riparioides*** (36% frequency) but was absent among ***Hygroamblystegium fluviatile*** clumps despite the frequent intermingling of these two mosses. It reached its greatest numbers in ***Scapania undulata***.

Figure 121. ***Rhyacophila carolina*** larva, species that is common among clumps of the leafy liverwort ***Scapania undulata*** in Appalachian Mountain, USA, streams. Photo by Bob Henricks, with permission.

Figure 122. ***Rhyacophila fuscula*** larva, a moss dweller on boulders in the Appalachian Mountain streams. Photo by Donald S. Chandler, with permission.

Figure 123. ***Rhyacophila fuscula*** pupa. Photo by Bob Henricks, with permission.

Figure 124. ***Rhyacophila torva*** larva, a moss dweller in Appalachian Mountain streams. Photo by Trevor Bringloe, Biodiversity Institute of Ontario, through Creative Commons.

Figure 125. ***Rhyacophila invaria*** larva, a species that occupies both mosses and liverworts in Appalachian Mountain streams. Photo by Donald S. Chandler, with permission.

Unknown Caddisfly Cases

One caddisfly larva included moss leaves, liverwort leaves, and even hornwort thallus, all in one case (Chris Cargill, pers. comm. 30 March 2016). And all these pieces were still alive! (Figure 126-Figure 129).

Figure 126. ***Megaceros flagellaris*** fragments used in caddisfly case. Photo courtesy of Andi Cairns.

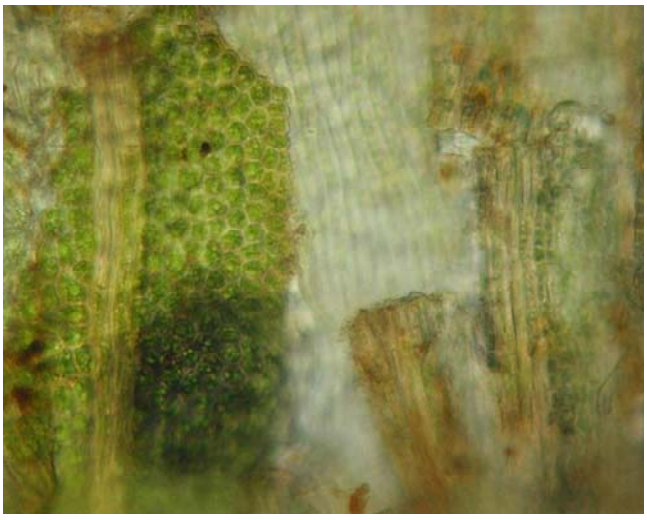

Figure 127. ***Megaceros flagellaris*** fragments used in caddisfly case. Photo courtesy of Andi Cairns.

Figure 128. ***Megaceros flagellaris*** fragments used in caddisfly case. Photo courtesy of Andi Cairns.

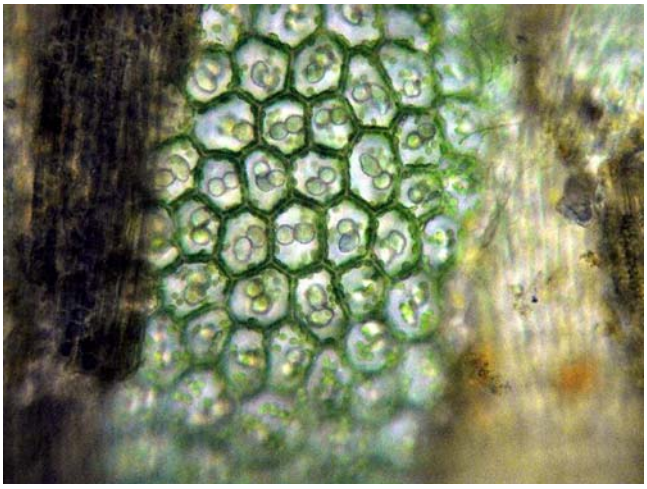

Figure 129. ***Megaceros flagellaris*** fragment used in caddisfly case. Photo courtesy of Andi Cairns.

Chris Cargill told me she later found discarded cases made of thalli from liverworts or hornworts and new thalli had started to grow from the case (Figure 130). I think we have just added a new means of bryophyte dispersal!

Figure 130. Caddisfly case with old thalli and new growth of living liverworts. Photo courtesy of Chris Cargill.

Helicophidae

Andi Cairns brings me many interesting interactions of animals with bryophytes. This one is a member of the **Helicophidae** (Figure 131Figure 132that has made a case from ***Solenostoma*** sp. (Figure 133) leaves where it lives in a stream in Australia.

Figure 131. **Helicophidae** sp with **Solenostoma** sp case, C Cloudy Ck, Australia. Photo courtesy of Andi Cairns.

Figure 132. **Helicophidae** larva. Photo courtesy of Andi Cairns.

Figure 133. ***Hypnodendron vitiense*** ssp ***australe*** (**dark green**) and ***Solenostoma*** sp (**medium green)** underwater at Cloudy Creek Paluma, Australia, home of **Helicophidae** larva that uses the liverwort leaves to make its case. Photo courtesy of Andi Cairns.

Summary

The **Limnephilidae** are mostly large and therefore are usually absent from the smaller mosses. However, sometimes several may occur within a clump of ***Fontinalis***.

The **Brachycentridae** are common among bryophytes. Some (***Micrasema***, ***Adicrophleps hitchcockii***) use mosses in their cases and some also eat them.

The genera ***Palaeagapetus*** and ***Scelotrichia***, both in the **Hydroptilidae**, use bryophytes (exclusively?) for food and case construction, the former using leafy liverworts and the latter using mosses. In the same family, ***Ptilocolepus*** uses both mosses and liverworts for food and in case construction.

The family **Rhyacophilidae** is a free-living caddisfly and is mostly carnivorous. However, some of the bryophyte dwellers eat bryophytes, whereas others use them as a place to capture prey.

Other families that can be found among bryophytes less commonly include **Odontoceridae**, **Goeridae**, **Limnephilidae**, **Lepidostomatidae**, **Oeconesidae** (especially in New Zealand), **Uenoidae**, **Phryganeidae**, **Beraeidae**, **Conoesucidae**, **Helicophidae**, **Sericostomatidae**, and **Glossosomatidae**. Among these, the **Limnephilidae** and **Phryganeidae** have mostly large larvae that are unable to move about in most of the bryophytes but that can live among the large branches of ***Fontinalis*** species. Unlike the **Coleoptera**, this order is poorly represented in bogs and fens, but they are common in streams and less so in lakes.

Acknowledgments

As a graduate student I relied heavily on the expertise of Oliver Flint, Glenn Wiggins, Tom Waters, and Ken Cummins for both encouragement and identification help in my novice years. Thank you so much to D. N. Bennett for making a special trip to photograph live *Micrasema wataga* eating and showing the mosses sprouting on the case, just for this chapter! She also made additional trips to the field to determine the identity of the moss. David Tempelman helped me to obtain some of the images and permission for use and provided me with references on *Ptilocolepus*. Eileen Dumire proofread the chapter and helped me improve the clarity and readability.

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CHAPTER 11-13a
AQUATIC INSECTS: HOLOMETABOLA – DIPTERA, SUBORDER NEMATOCERA

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CHAPTER 11-13a
AQUATIC INSECTS: HOLOMETABOLA – DIPTERA, SUBORDER NEMATOCERA

Figure 1. ***Triogma trisulcata*** among mosses. This species makes its home among wet mosses of bogs and swamps and is effectively a moss mimic. Photo by J. C. Schou, with permission.

DIPTERA – FLIES

Gerson (1969) suggested that the ancestral fly groups originated among mosses where it is always damp. Because the systematics of the fly groups are still poorly understood, I have divided the treatments into the two suborders, **Nematocera** and **Brachycera**. From there they are alphabetical within superfamilies, but the superfamilies are not delineated by name.

Diptera adults are distinguished by having only two wings, as reflected in the name of **Diptera** (*di* = 2; *pteron* = wing). In place of the second pair of wings the flies have a pair of **halteres** (Figure 2), thoracic projections that resemble lollipops, one on each side of the thorax. In the larval stage, they are distinguished by having only fleshy **prolegs** (Figure 9) or no legs. They lack the chitinized, jointed thoracic legs found in most larval insects (Johannsen 1969).

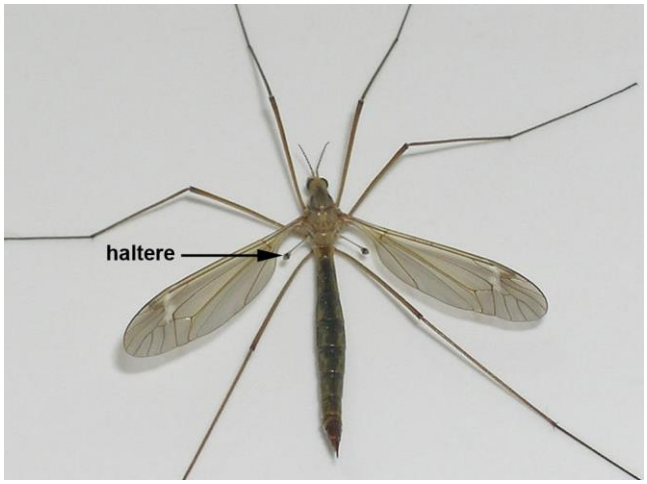

Figure 2. **Tipulidae** showing two wings and halteres. Photo by Pinza, through Creative Commons.

Gerson (1982) reported a number of bryophyte-dwelling **Diptera** of medical and veterinary importance because they bite. Among these are the sand flies [**Psychodidae** (see Chapter 13b; Quate 1955)], mosquitoes [**Culicidae** (see Chapter 13b; Fantham & Porter 1945)], black flies [**Simuliidae** (Figure 3); Snow *et al*. 1958)], biting midges [**Ceratopogonidae** (Figure 84-Figure 88; Séguy 1950)], and horse flies [**Tabanidae** (Figure 4; Teskey 1969)]. All of these are discussed in this chapter except **Tabanidae**. I found it only occasionally among bryophytes in Appalachian Mountain, USA, streams; the other studies I reviewed did not mention it.

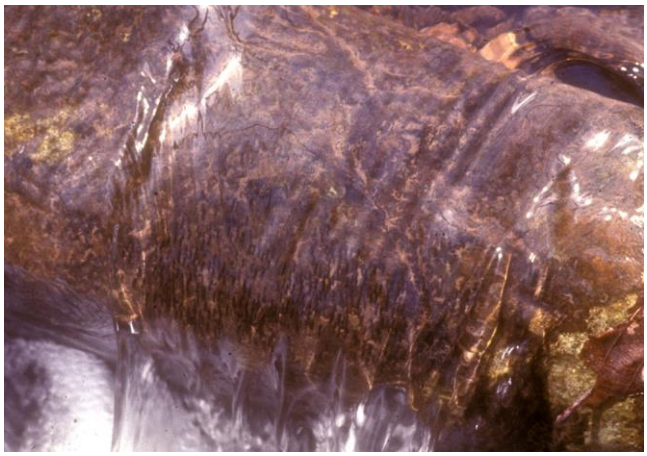

Figure 3. **Simuliidae** larvae in the rapid flow of a stream. Photo by Janice Glime.

Figure 4. ***Chrysops divaricatus*** (**Tabanidae**) adult, an adult pest (horse fly) whose larvae sometimes live among the bryophytes. Photo by Kallema, through Creative Commons.

In streams, bryophytes are often important contributors to biodiversity. Flow rates are important in determining the type of **Diptera** able to live there. The abundance of **Chironomidae** (see Chapter 13b) is negatively correlated with flow rate as it approaches clumps of mosses (***Fontinalis antipyretica***; Figure 5), whereas the abundance of the smallest **Simuliidae** (Figure 3) is positively correlated (Linhart *et al*. 2002a). In the Plitvice Lakes National Park in the Dinaric karst region of Croatia, Čmrlec (2013) found that the Diptera families were least abundant in silt and that mosses were the preferred substrate. These correlations with speed and silt do not prevent both groups of species from living in the same bryophyte clump – the slow-water silt lovers live near the bottom while the fast-water silt avoiders live near the surface of the bryophyte clump.

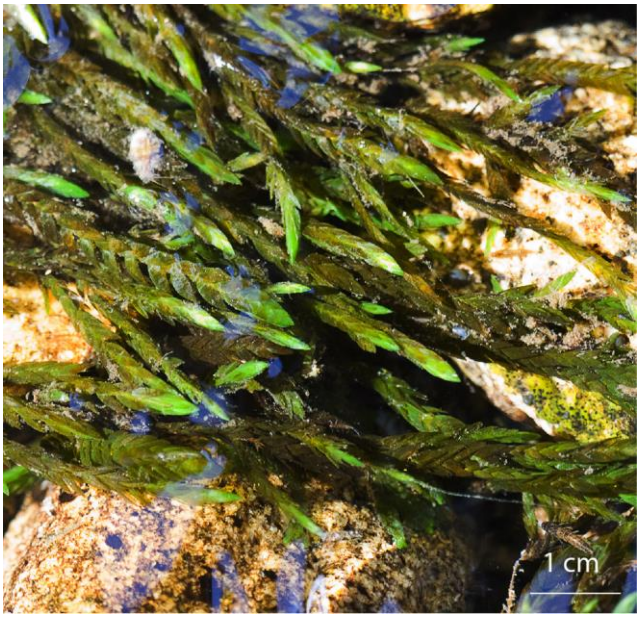

Figure 5. ***Fontinalis antipyretica***, home for numerous aquatic insects and suitable for larger ones. Photo from Projecto Musgo, through Creative Commons.

Bryophytes accumulate coarse (CPOM), fine (FPOM), and ultrafine (UPOM) particulate organic matter that serves as a food source for their inhabitants (Habdija *et al*. 2004). These conditions favor small forms of oligochaetes, **Diptera**, and **Coleoptera** that comprise 64-99% of the **macrophyte** (plant – especially aquatic – large enough to be seen without a lens) individuals. Collector gatherers dominate in spring and summer, collector-filterers in autumn, and scrapers in winter.

In a cool mountain stream in central Japan, five of the six taxa of Diptera identified (mostly at the level of family or subfamily) were significantly more abundant in clumps of the moss ***Platyhypnidium riparioides*** (Figure 6) than in areas of bare stones (Kato 1992). These included **Limoniidae** (***Antocha*** spp.; Figure 7), **Simuliidae** (Figure 3), and **Chironomidae** [Figure 8; **Tanypodinae, Diamesinae**, ***Orthocladius*** spp.].

Figure 6. Emergent but wet ***Platyhypnidium riparioides*** in Europe, a common home for **Diptera**. Photo by Michael Lüth, with permission.

Figure 7. ***Antocha***, a larva that inhabits the moss ***Platyhypnidium riparioides*** (Figure 6) in cool mountain streams in Japan. Photo by Bob Henricks, with permission.

In Alaska, **Diptera** dominate by an even larger proportion than in streams of temperate North America (Oswood 1989). The **Chironomidae** (Figure 8) exhibit a significant increase from south to north, whereas most other taxa (excluding **Nemouridae**) decrease.

Figure 8. **Chironomidae** larva, a common bryophyte-dwelling family whose numbers increase from south to north. Photo by Jason Neuswanger, with permission.

The **Diptera** have a variety of adaptations to their aquatic domicile of choice. For example, Bass and Cooling (1983) reported that **Muscidae** (**Brachycera**), **Ichneumonidae** (**Hymenoptera**), and **Simuliidae** (Figure 3) were associated with mosses below a reservoir in southern England. Both the larvae and pupae had posterior projections to anchor them to the mosses. Amos (1999) describes the role of the brook moss ***Fontinalis*** (Figure 5) in providing a safe habitat in the torrent, and this moss likes cold water (Glime 1987) where few tracheophytes persist. Here one can find many small invertebrates, but it seems still to be a challenge to stay put. The mountain midge larva (**Deuterophlebiidae,** Figure 9) survives the torrent by the use of strong suction to hold the rock. The suction cups of ***Deuterophlebia*** (Figure 9) are of little use among bryophytes, but are fantastic for adhering to "bare" rocks. Respiratory adaptations are numerous and will be discussed for the various families.

The floating community includes only a few species of bryophytes, notably ***Ricciocarpos natans*** (Figure 10) and ***Riccia fluitans*** (Figure 11). In some cases, the **Diptera** associated with the thallose floating liverwort ***Ricciocarpos natans*** are the same ones found among floating tracheophytes such as *Spirodela*, *Lemna minor* (Figure 10), and *Wolffia* (Scotland 1934).

Figure 9. ***Deuterophlebia*** ventral side showing suction cups. Photo from Aquatic Bioassessment Laboratory <www.dfg.ca.gov>, with permission.

Figure 10. ***Ricciocarpos natans*** and *Lemna minor*, floating plants that can harbor surface-dwellers. Photo by Jan-Peter Frahm, with permission.

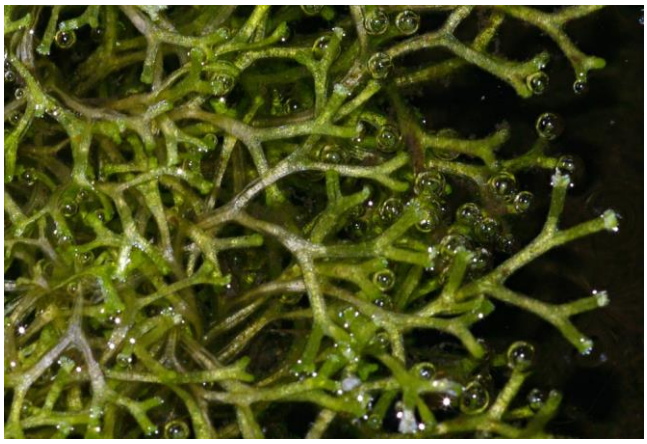

Figure 11. ***Riccia fluitans*** with pearling (oxygen bubbles produced by the plants), a floating community that provides cover and oxygen for aquatic insects. Photo by Christian Fischer, through Creative Commons.

Despite the number of families of **Diptera** among the bryophytes, and the presence of such mixed terrestrial/aquatic families as the **Tipulidae** (Figure 46-

Figure 73, Figure 75, Figure 77-Figure 76), it is interesting that this order is poorly represented among the wet emergent mosses in the River Rajcianka in Slovakia (Krno 1990). Only the **Psychodidae** (see Chapter 13b) were able to take advantage of the safety of the emergent bryophytes there. On the other hand, fauna of the submerged mosses were represented by not only the **Psychodidae**, but also the **Ceratopogonidae** (Figure 84-Figure 88) and **Simuliidae** (Figure 3). Conspicuously absent in these **eutrophic** (referring to lake or other body of water rich in nutrients and thus supporting dense plant/algal populations) waters were the **Tipulidae** and **Chironomidae** (Figure 8).

Occasionally, or perhaps frequently, the insects do something beneficial for the bryophytes they visit. In a study to determine the role of adult **Diptera** in dispersing algae and **Protozoa**, Revill *et al*. (1967) found that in addition to 21 species of viable algae and 5 of **Protozoa**, the washings from the four species of **Diptera** produced viable moss spores/protonemata as well. These transporting insects included ***Tipula triplex*** (**Tipulidae**; Figure 12), ***Bittacomorpha clavipes*** (**Ptychopteridae,** Figure 13), ***Chaoborus punctipennis*** (**Chaoboridae**, Figure 14-Figure 15), and ***Chironomus*** (**Chironomidae**; Figure 16).

Figure 12. ***Tipula triplex*** adult, a cranefly known to disperse bryophyte spores or protonemata. Photo by Paul Rhine <www.discoverlife.org>, through Creative Commons.

Figure 13. ***Bittacomorpha clavipes*** adult, a phantom cranefly that carries bryophyte spores or protonemata. Photo by Matt Muir, through Creative Commons.

Figure 14. ***Chaoborus punctipennis*** adult, a species known to carry bryophyte spores/protonemata. Photo by Tom Murray, through Creative Commons.

Figure 15. ***Chaoborus*** sp., larva of one of the **Diptera** known to carry bryophyte spores/protonemata. Photo by Viridiflavus, through Creative Commons.

Figure 16. ***Chironomus dorsalis*** adult, an insect known to transport bryophyte spores or protonemata. Photo by James K. Lindsey, with permission.

Suborder Nematocera

The name **Nematocera** means "thread horns" and refers to the long, threadlike antennae. These are elongated flies with thin, segmented antennae. The larvae are mostly aquatic and the family includes craneflies, gnats, midges, mosquitoes, and blackflies.

Nymphomyiidae

This is a family of tiny (2 mm) flies in the northern parts of the Northern Hemisphere, especially eastern North America and eastern and central Asia (Nymphomyiidae 2013). The adults are **neotenic** (retaining larval or immature characters in adulthood), with straplike wings having **poor venation** (few wing veins). They live in running waters, where they often are found on moss-covered rocks, and **pupation** (development process between larva and adult) usually occurs in the same place (Courtney 1994). Adults have aborted mouth parts and live only a short time, some dying while still in the copulatory (mating) position.

Nymphomyia is the only genus currently listed in this family (Myers *et al*. 2014). It lives among aquatic mosses in small, rapid streams (Courtney 1994; Courtney *et al*. 1996). Not only larvae, but also often pupae and adults of ***Nymphomyia***, live on rocky substrates covered with aquatic mosses such as ***Platyhypnidium riparioides*** (Figure 6), ***Fontinalis*** (Figure 5), and ***Hygroamblystegium*** (Figure 91) (Cutten & Kevan 1970; Adler *et al.* 1985).

Cylindrotomidae – Long-bodied Craneflies

The family **Cylindrotomidae** is often separated from the **Tipulidae** (Figure 46-Figure 73, Figure 75, Figure 77-Figure 76), which I have chosen to do to make it easy to discuss its unique characters relative to bryophytes. These are of moderate size (11-16 mm) and yellowish to pale brownish as adults (Cylindrotominae 2014). Most larvae live among mosses – terrestrial, semiaquatic, and aquatic mosses (Cylindrotominae 2014), and feed on mosses and **tracheophytes** (plants with lignified vascular tissue) (Gelhous *et al*. 2007). The family occurs mostly in the Holarctic and Oriental Regions, but there are scattered records in southern South America, New Guinea, and Australia.

The aquatic insects don't seem to have the elaborate camouflage known in some terrestrial insects, but some still do an excellent job at blending. The **Cylindrotomidae** in particular are bryophyte dwellers and are world-class mimics of that habitat – bryocamouflage!

The larvae of ***Triogma trisulcata*** (Figure 1, Figure 17) are known for their mimicry in a ***Sphagnum*** (Figure 69) habitat, but they also occur in streams where the larvae attach to ***Fontinalis antipyretica*** (Figure 5) (Gerson 1969). The leaflike appendages most likely are equally useful in that habitat as camouflage.

Figure 17. ***Triogma trisulcata*** larva posterior showing flanges that make it almost invisible among ***Sphagnum***. Photo by Walter Pfliegler, with permission.

Triogma trisulcata (Figure 17) larvae are inhabitants of semiaquatic mosses, especially in stagnant water in bogs (Brinkmann 1997). In contrast to the tracheal gill respiration of ***Phalacrocera replicata*** (Figure 18), another bryophyte dweller in this family, the larvae lie on the leaves of the moss in a position that places the **spiracular disk** (apparatus that contains the breathing openings called spiracles) at the level of the water surface. Like ***P. replicata***, these larvae have appendages that match the color and mimic the morphology of the surrounding mosses. These have been variously interpreted as mimetic camouflage to protect them against enemies and as respiratory organs. It seems reasonable that both interpretations may be correct. The pupae remain in these same positions until a short time before the adults emerge (**ecdysis**). Just before ecdysis, they search for drier mosses. Eggs are laid singly on mosses just below the surface by females dipping the tip of the abdomen into the water to touch the leaves. The eggs are attached by an adhesive.

Figure 18. ***Phalacrocera replicata*** larva, an effective moss mimic that develops among mosses. Photo through Wikimedia Commons.

Phalacrocera replicata (Figure 18) lives among ***Sphagnum*** (Figure 69), ***Fontinalis antipyretica*** (Figure 5), and ***Warnstorfia fluitans*** (Figure 19) (Brinkmann 1997). Larvae in this species find tufts of mosses, then attach themselves to the leaves and stalks by affixing the anterior part of the body using the **mandibles** (crushing organs in an arthropod's mouthparts) to grab onto the edge of a leaf. They then crawl by crooking the body and securing the dorsal hooks. They have backward-pointing appendages that presumably help prevent them from being swept away by the current. At this stage they have functional spiracles that they do not use. Instead, the long, filiform appendages along the body function as tracheal gills, supplemented by **cutaneous** (referring to outer cuticle of insect body) gas exchange. But when it is time for pupation, the larvae move to the water surface to expose their **spiracles** (external openings through which insects breathe) to the atmospheric air. To maintain this contact with surface air, the pupae hang beneath the surface film, using their

respiratory horns, and cling to the stems of mosses or other plants with the appendages on the last of the abdominal segments, positioning their bodies horizontally.

Figure 19. ***Warnstorfia fluitans***, one of the homes of larvae of ***Phalacrocera replicata***. Photo by Michael Lüth, with permission.

Clymo and Hayward (1982) reported that ***Phalacrocera replicata*** feeds on ***Sphagnum*** (Figure 69). Miall and Shelford (1897) found that ***P. replicata*** (Figure 18) larvae eat ***Warnstorfia exannulata*** (Figure 20). They described pupae that attach to the moss leaves by dorsal appendages on posterior segments. The females lay about 60 eggs in **axils** (upper angle between leaf stalk or branch and stem from which it grows) of the moss leaves.

Figure 20. ***Warnstorfia exannulata***, food for ***Phalacrocera replicata*** (Figure 18). Photo by Michael Lüth, with permission.

Byers (1961) reported that the larvae of ***Liogma*** (Figure 21) use bryophytes for their larval habitats. Larvae of the genera ***Liogma*** and ***Triogma*** (Figure 17) have a green color with markings that make them look like leafy mosses (Gerson 1969). These two genera live among and eat the mosses ***Rhytidiadelphus squarrosus*** (Figure 22) and ***Hypnum cupressiforme*** (Figure 23). Larvae of ***Triogma trisulcata*** (Figure 17) inhabit the brook moss ***Fontinalis antipyretica*** (Figure 5) in mountain streams (Alexander 1920). These larvae have appendages that resemble leaves on a branch, and the color is typically green and black.

Figure 21. ***Liogma nodicornis*** adult, a species whose green larvae have markings that make them look like the leafy mosses where they live. Photo by Ilona L., through Creative Commons.

Figure 22. ***Rhytidiadelphus squarrosus***, home and food for ***Liogma*** (Figure 21) and ***Triogma*** (Figure 17) larvae. Photo by Michael Lüth, with permission.

Figure 23. ***Hypnum cupressiforme***, home and food for ***Liogma*** (Figure 21) and ***Triogma*** (Figure 17) larvae. Photo by Li Zhang, with permission.

Limoniidae – Limoniid Craneflies

The **Limoniidae** (Figure 24) family is an offshoot of the **Tipulidae** and thus many of the taxa discussed here were originally reported as members of **Tipulidae**. They are a worldwide family, mostly aquatic, and of moderate size (Limoniidae 2015). Their feeding groups vary considerably, including **phytophagous** (eating plants), **saprophagous** (eating dead organisms), **mycetophagous** (eating fungi), and **carnivorous** (eating animals) species.

Figure 24. **Limoniidae** adults mating, a family with larvae that often live among mosses, some consuming them. Photo by Anki Engström at <www.krypinaturen.se>, with permission.

From Cape Town, South Africa, we have a report of the **Limoniidae** occupying mosses in the stream of an isolated mountain (Harrison & Barnard 1972). The genus ***Geranomyia rostrata*** (see Figure 25) lives among algae, wet mosses, and thallose liverworts in the eastern part of North and South America (Rogers 1927; Johannsen 1969). These larvae are greenish and **translucent** (allowing light but not clear images to pass through), slow movers, and herbivores on algae and moss (Johannsen 1969). ***Geranomyia sexocellata*** (see Figure 25) larvae live in a gelatinous tube made with minute sand grains and attached to mosses in waterways that are only trickles.

By contrast, ***Dicranomyia capicola*** (syn. of ***Limonia capicola***?; see Figure 26) larvae live among mosses at the edge of a rapidly flowing streamlet (Harrison & Barnard 1972) and larvae of ***Limonia*** sp. and ***Ormosia*** sp. (Figure 28) live among bryophytes in Appalachian Mountain streams (Glime 1968). Harrison and Barnard (1972) also found ***Elephantomyia aurantiaca*** (see Figure 29) larvae among the damp mosses and liverworts.

Several researchers have reported ***Limonia*** species from bryophytes (Byers 1961; Hilsenhoff 1975; Suren 1991). Suren (1991) found that ***Limonia hudsoni*** (see Figure 27) apparently required more from the bryophytes than just a substrate. It failed to colonize the artificial bryophytes in his New Zealand stream studies. Instead, Suren and Winterbourn (1991) reported that it actually commonly consumes bryophytes. Apparently artificial ones couldn't fill the bill.

Figure 25. ***Geranomyia*** sp adult. ***Geranomyia rostrata*** larvae live among mosses and thallose liverworts in North and South America. Photo by Ted Kropiewnicki, through Creative Commons.

Figure 26. ***Dicranomyia modesta*** adult, member of a genus with some larvae that live among mosses at streambanks. Photo by James K. Lindsey, with permission.

Figure 27. ***Limonia wellingtonia***, member of a genus with some moss-dwelling members. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 28. ***Ormosia*** adult, a genus whose larvae sometimes live among mosses. Photo by Malcolm Storey, through Creative Commons.

Figure 29. ***Elephantomyia westwoodii*** adult female; larvae live among damp mosses and liverworts. Photo by Robert Lord Zimlich, through Creative Commons.

An important use of bryophytes can be that of providing a place for them to emerge. ***Rhipidia maculata*** emerges from the stream bed and also from thin moss layers on exposed rocks (Needham 1908; Johannsen 1969).

In my studies of Appalachian Mountain stream moss communities, both ***Hexatoma*** cf. ***longicornis*** and ***H.*** cf. ***spinosa*** occurred among the leafy liverworts ***Scapania undulata*** (Figure 30) (Glime 1968). ***Hexatoma*** (Figure 31-Figure 32) is known to ingest mosses (Percival & Whitehead 1929), so perhaps it is looking for food.

Figure 30. ***Scapania undulata***, home for several species of ***Hexatoma***. Photo by Michael Lüth, with permission.

Figure 31. ***Hexatoma*** larva; some members of this genus eat mosses. Photo by Jason Neuswanger, with permission.

Figure 32. ***Hexatoma*** (***Eriocera***) ***gravelyi*** male adult. Photo by Muhabbet Kemal, with permission.

Limnophila occurs among bryophytes in several locations (Alexander 1919; Hilsenhoff 1975). In the Appalachian Mountain streams several species occur among the bryophytes, including ***L.*** cf. ***macrocera*** (Glime 1968). ***Limnophila alleni*** (see Figure 33) lays its eggs

among mosses (Alexander 1919). Lauga and Thomas (1978) found that **Limoniidae** in France were more likely to be found among bryophytes when it was time for pupation and molting. The same relationship was seen for members of **Athericidae** and **Rhagionidae** (**Brachycera**).

Figure 33. ***Limnophila*** larva, member of a genus known to lay eggs in mosses. Photo by Tom Murray, through Creative Commons.

Erioptera (Figure 34), ***Pseudolimnophila*** (Figure 35), and ***Pilaria*** (Figure 36) in Wisconsin, USA, use mosses among their larval substrata (Hilsenhoff 1975). Byers (1961) reported that the larvae of ***Erioptera*** and ***Gonomyia*** (Figure 37) use bryophytes as larval habitats. In the Appalachian Mountain streams (USA), one can find the genus ***Antocha*** (Figure 7) (Glime 1968), a genus found in similar habitats in Japan.

Figure 34. ***Erioptera*** sp. larva, a moss inhabitant. Photo courtesy of the State Hygienic Laboratory at the University of Iowa, with permission.

Figure 35. ***Pseudolimnophila*** sp. larva breathing apparatus, a genus that lives among Wisconsin mosses. Photo by Urmas Kruus, with permission.

Figure 36. ***Pilaria*** sp. larva breathing apparatus, a genus that lives among Wisconsin mosses. Photo by Urmas Kruus, with permission.

Figure 37. ***Gonomyia*** adult, a genus whose larvae live among bryophytes. Photo by Joe Zito, through Creative Commons.

Blanket bogs have their own fauna, some of which is unique. Larvae that live in these habitats in Dartmoor, UK, include ***Molophilus occultus*** (Figure 38) whose larvae seem to require areas of bare, wet peat where they live in litter and among mosses (Boyce 2011). But this genus can also be found among bryophytes in Appalachian Mountain, USA, streams (Glime 1968). ***Phylidorea squalens*** (Figure 39) larvae in the Dartmoor blanket bogs live in the bog pools.

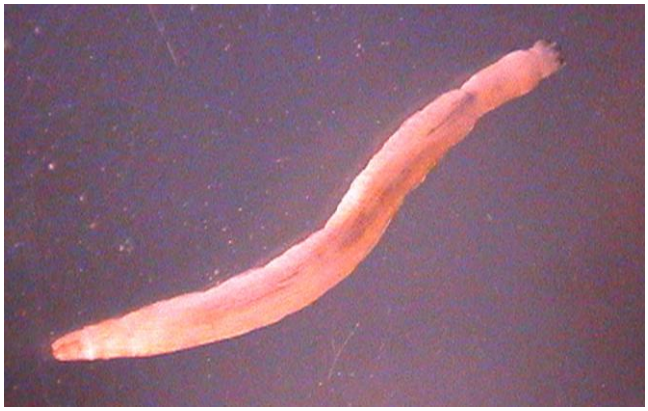

Figure 38. ***Molophilus*** sp. larva, a larva that seems to require bare, wet peat. Photo by Erin Hayes-Pontius, through Creative Commons.

Figure 39. ***Phylidorea squalens*** adult male, a species whose larvae live in bog pools. Photo by James K. Lindsey, with permission.

Pediciidae – Hairy-eyed Craneflies

The **Pediciidae** occur in the temperate zones of both hemispheres (Kits 2005b). These are medium to large (20-35 mm) flies (Pediciidae 2014) that resemble craneflies.

Pedicia (Figure 40) (now placed in **Pediciidae**) is one of the craneflies found among mosses as larvae (Figure 41) in some streams in the Appalachian Mountains, USA (Glime 1968). Hilsenhoff (1975) reported the genus in Wisconsin, USA, where it includes mosses among its substrata.

Figure 40. ***Pedicia rivosa*** adult on *Equisetum*. Larvae of some species live among mosses in Appalachian Mountain streams. Photo by Niels Sloth, with permission.

Figure 41. ***Pedicia albivitta*** larva, member of a genus of moss dwellers. Photo by Jason Neuswanger, with permission.

Tipulidae – Craneflies

This is a worldwide family that occupies a wide range of habitats as larvae, from water to mosses to dry logs (Hofsvang 1997). As adults they live only a few days and may not eat. That's right, they are not giant mosquitoes and won't bite you! But they do look like giant mosquitoes, with long legs and bodies 7-35 mm long (Tipulidae 2014), but narrow. Unlike the **Limoniidae**, the **Tipulidae** (Figure 42) are mostly terrestrial. Their larval food choices include algae, microflora, and both living and decomposing plant matter, including wood.

Figure 42. The cranefly ***Tipula*** occurs frequently among leaf litter that it helps to shred by eating it, but it can also occur among submerged and moist moss clones where its ecological role is unknown. Photo by Janice Glime.

The **Tipulidae** accomplish most of their respiration by using a posterior respiratory apparatus (Figure 43-Figure 44) (Pritchard 1983). They have a single pair of spiracles located there. The spiracles can't be closed, but there are tiny hairs on the walls of the spiracle opening that reduces water loss. There also seems to be cuticular respiration.

Figure 43. Larva of ***Tipula*** showing respiratory apparatus at right. Photo from Beentree, through Creative Commons.

Figure 44. Respiratory apparatus with spiracles of ***Tipula*** sp. Photo from Beentree, through Creative Commons.

Egg-laying (Figure 45) of tipulids on bryophytes has been known for a long time. For example, Alexander (1919) reported that ***Tipula nobilis*** laid her eggs in moss. Females already have mature eggs when they emerge from the pupa and after copulation they deposit them on wet soil or algae, or drop them (Tipulidae 2014). These eggs are usually black and may have a thin thread that could help to attach them in the water.

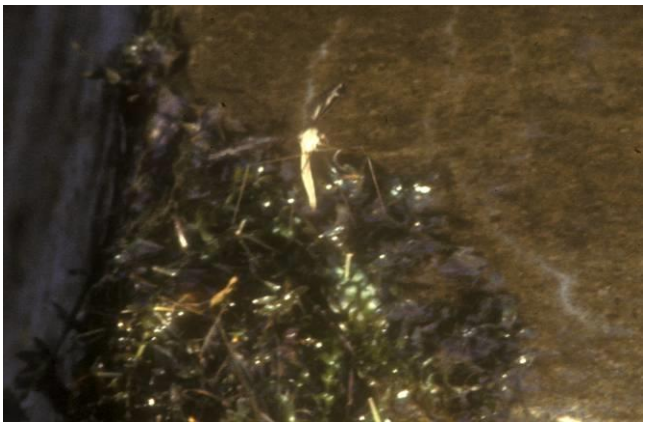

Figure 45. Cranefly laying eggs in submerged mosses. Photo by Janice Glime.

Tipulidae adults look like giant mosquitoes because of their long legs (Figure 46). In some regions they are known as daddy-long-legs for the same reason, but these are not to be confused with the 8-legged daddy-long-legs that are arachnids. Many **Tipulidae** live among aquatic leaf litter and mosses as larvae. Likewise, most of them pupate in soil near water, in mosses, or in litter (Byers 1978, 1996; Erman 1984).

Figure 46. ***Tipula*** adult. Photo by Micka 972, through Creative Commons in <Omnilexica.com>.

Larvae of craneflies are highly susceptible to desiccation (Pritchard 1983) and bryophytes seem to be an important habitat for maintaining moisture in bog species and terrestrial species. ***Tipula montana*** burrows into mosses when it is disturbed (Smith *et al*. 2001). ***Dolichopeza*** (Figure 77) species select their moss habitat for its suitability for making burrows (Byers 1961). The cranefly larvae seem to prefer compact mosses rather than loose ones in the same species (Todd 1993).

Tipula ignobilis occurs throughout the year among mosses on boulders in a Tennessee, USA, springbrook (Stern & Stern 1969). Slightly farther north in the Appalachian Mountains, I found what appeared to be seven different species of ***Tipula*** among bryophytes in the 28 streams I studied, including ***Tipula collaris*** (Figure 47) (Glime 1968). At Barrow, Alaska, USA, ***Tipula carinifrons*** (Figure 48) is common in the dry moss hummocks (MacLean 1980).

Figure 47. ***Tipula collaris*** adult, a species whose larvae live among bryophytes in Appalachian Mountain streams. Photo through Carnegie Museum of Natural History, through Creative Commons.

Figure 48. ***Tipula carnifrons*** adult male, a common species in dry moss hummocks of Alaska. Photo by Ashley Bradford, through Creative Commons.

Byers (1961) listed bryophytes as the larval habitat of many ***Tipula*** species. The genus ***Tipula*** is typically a consumer of leaf litter. But mosses can be a major part of the diet in some species. Dangles (2002) found that in the four study streams of Vosges Mountains in northeastern France bryophytes comprised 96% of the diet of ***Tipula*** (***Savtshenkia***) (Figure 49).

Figure 49. ***Tipula*** (***Savtshenkia***) adult, a genus in which the larvae can eat considerable amounts of bryophytes. Photo by James K. Lindsey, with permission.

Tipulidae larvae commonly feed on mosses (Coulson 1962; Freeman 1967; MacLean 1980; Richardson 1981; Todd 1993), and these mosses often form a significant portion of the diet (Coulson 1962). Larvae of ***Tipula signata*** (Figure 50) feed on aquatic mosses (Hemmingsen 1965).

Figure 50. ***Tipula signata*** adult male, a species whose larvae eat aquatic mosses. Photo by James K. Lindsey, with permission.

Tipula montana is a bog dweller and is surrounded by bryophytes as a larva. Smith *et al*. (2001) experimented with food preference in larvae of this species. The research team gave the larvae trials with five individual species of mosses, then with two-species pairs, to determine their growth responses and preferences. Larvae grew on diets of each of the five species of mosses [***Racomitrium lanuginosum*** (Figure 51), ***Dicranum fuscescens*** (Figure 52), ***Sphagnum girgensohnii*** (Figure 53), ***Pleurozium schreberi*** (Figure 54), and ***Polytrichum commune*** (Figure 55)], but there was a wide range in which mean weights differed by a factor of two. The highest development rate, by far, was for larvae fed ***Pleurozium schreberi***, with nearly 50% reaching the fourth instar, whereas fewer than 5% of those fed on the other moss species reached that stage (Figure 56). ***Pleurozium schreberi*** also was the best moss for promoting growth, with weight gain double that of larvae fed on ***Sphagnum girgensohnii*** (Figure 57). Nevertheless, there was little difference among the survivorships of the larvae fed on each on the five mosses (Figure 58). But the larvae preferred ***Racomitrium lanuginosum*** to the other mosses and often avoided ***Pleurozium schreberi*** when given a choice (***Sphagnum girgensohnii*** was the least preferred). This avoidance of ***Pleurozium schreberi*** is likely because of the high **phenolic** content (compounds that taste bad, including tannic acid) of ***P. schreberi*** (Liao 1993; Glime 2006; Hribljan 2009; see chapter 10-3 on Isopoda in this volume).

Figure 51. ***Racomitrium lanuginosum***, a preferred food for ***Tipula montana***. Photo by Michael Lüth, with permission.

Figure 52. ***Dicranum fuscescens***, a moss with a high relative percentage of observations of being eaten by ***Tipula montana***. Photo by Michael Lüth, with permission.

Figure 53. ***Sphagnum girgensohnii***, the least preferred moss among choices given to ***Tipula montana***. Photo by Michael Lüth, with permission.

Figure 54. ***Pleurozium schreberi*** a moss that gives ***Tipula montana*** good growth performance but that is not preferred. Photo by Janice Glime.

Figure 55. ***Polytrichum commune***, a potential food avoided by ***Tipula montana***. Photo by Michael Lüth, with permission.

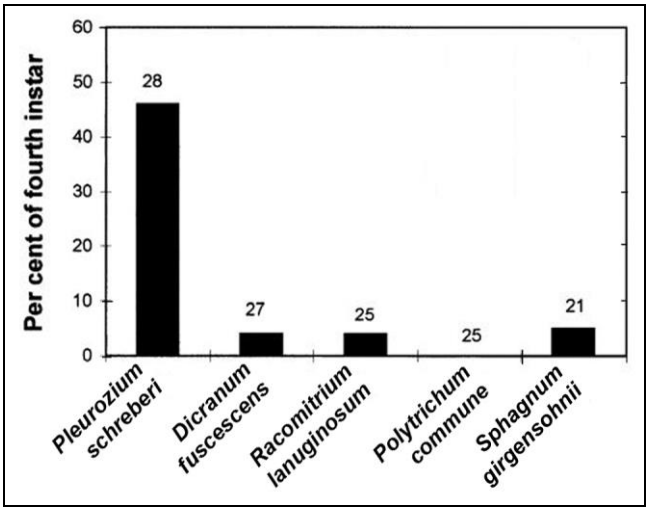

Figure 56. Survival percentages of ***Tipula montana*** larvae, starting with second-instar larvae, entering fourth instar after 52 days of feeding on diets of five moss species. Sample sizes appear above bars. Redrawn from Smith *et al*. 2001.

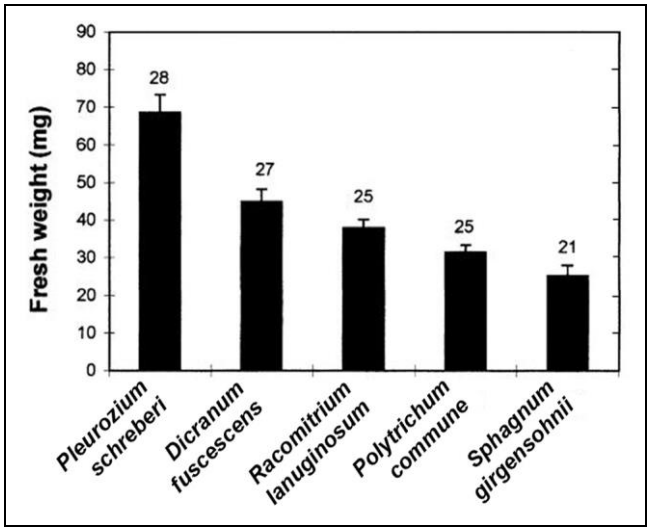

Figure 57. Mean fresh weight (+ standard error) of larvae of ***Tipula montana***, starting with second-instars, after 52 days on each of five moss species. Sample sizes appear above bars. Redrawn from Smith *et al*. 2001.

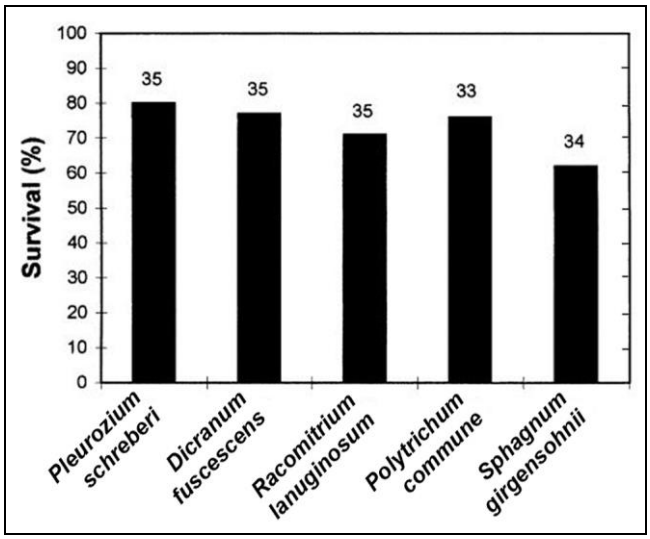

Figure 58. Percent survival of ***Tipula montana*** larvae fed on each of five moss species for 52 days. Sample sizes appear above bars. Redrawn from Smith *et al*. 2001.

Smith *et al*. (2001) issued a note of caution: The fecal indications of moss herbivory did not match the observational data. They suggested this may have been due to behavior differences between the larvae and the observers. The observers noted feeding behavior between 8:30 hours and 19:30 hours, but the larvae may have been feeding actively above ground at night, with daylight causing them to avoid the greater exposure on the sedge *Carex bigelowii*. This could explain the estimated lower percentage of *Carex bigelowii* in the observed diet in the field when using observations, and accounting for the higher percentage of ***Dicranum fuscescens*** (Figure 52) in the observations when compared to the ratio in the feces. Ratios of other mosses were similar using both methods. In the field, when *Carex bigelowii* was readily available, it was the clear choice compared to the mosses. The researchers also concluded that the bryophytes may be more important as a refuge than as a food source in nature. As pointed out by the researchers, experiments in which

development and growth on the sedge compared to those of the mosses would be instructive. It may be that the best growth is on a combination of these, with reduced growth or development resulting when no mosses are eaten. On the other hand, avoidance of predators may force the larvae to remain among the mosses and to eat them in the daytime. Several birds are primary predators on these larvae (Galbraith *et al*. 1993; Nethersole-Thompson 1966).

Tipula subnodicornis (Figure 59) feeds on liverworts in British moorland blanket bogs and consumes large quantities of ***Sphagnum*** (Figure 53, Figure 69) leaves (Coulson 1962; MacLean 1980). MacLean estimates that more than 25% of the energy consumption may be derived from the living plants of ***Sphagnum***.

Figure 59. ***Tipula subnodicornis*** adult, a cranefly whose larvae feed on liverworts in British blanket bogs but seem to have little preference in experiments with moss species. Photo by James K. Lindsey, with permission.

In the genus ***Tipula***, later instars ingest only slightly more vegetable matter as they grow to larger and larger instars. Rather, the early and late instars ingest similar-sized particles. In feeding experiments, Todd (1993) found that ***Tipula confusa*** (Figure 60) preferred woodland moss species, whereas ***T. subnodicornis*** (Figure 59) showed no preference between woodland and moorland mosses. ***Tipula confusa*** had a hierarchical preference among the 10 moss species offered, whereas ***T. subnodicornis*** showed much less hierarchy in food choices. Brindle (1960) noted that ***T. subnodicornis*** (Figure 59) typically associates with wet species such as those of ***Sphagnum*** (Figure 69) and ***Hypnum*** (Figure 23) in moorlands. Among 11 species Todd (1993) studied, 8 were moss consumers, with 7 of these in the same subgenus ***Savtshenkia*** (***Tipula rufina*** (Figure 61), ***T. confusa***, ***T. pagana*** (Figure 62), ***T. staegeri***, ***T. limbata*** (Figure 63), ***T. alpium*** (Figure 64), and ***T. subnodicornis***). Brindle (1960) had earlier observed that all the moss feeders known to him had four pairs of short anal papillae, whereas in wetter environments these papillae were longer. The eighth, ***T. montana*** is in the subgenus ***Vestiplex***. In Great Britain, approximately one-fourth of the 59 (Freeman 1967) members of ***Tipula*** feed on mosses. Even the invasive species ***Campylopus introflexus*** (Figure 65) is ***Tipula*** food in the recently burned *Calluna* heath. ***Tipula montana*** in the upland moors feeds exclusively on mosses.

Figure 60. ***Tipula confusa*** adult; larvae eat mosses, preferring woodland species. Photo by Malcolm Storey, through Creative Commons <www.discoverlife.org>.

Figure 61. ***Tipula rufina*** adult, a species whose larvae eat small particle sizes of bryophytes. Photo by Malcolm Storey, through Creative Commons <www.discoverlife.org>.

Figure 62. ***Tipula pagana*** male adult, a species whose larvae eat small bites of bryophytes. Photo by James K. Lindsey, with permission.

Figure 63. ***Tipula limbata*** adult, a species whose larvae eat bryophytes in small bites. Photo by Derek Sikes, University of Alaska Museum, through Creative Commons.

Figure 64. ***Tipula alpium*** adult, a species whose larvae eat bryophytes in small bites. Photo by Malcolm Storey, through Creative Commons.

Figure 65. ***Campylopus introflexus***, an invasive species that has become a food source for ***Tipula*** larvae in the ***Calluna*** heath. Photo by Michael Lüth, with permission.

The insect **feces** (excrement; waste material discharged from gut) reveal a great deal about the use of mosses as food (Todd 1993). The particle size remains the same in the feces as it was in the cut ingested portion (Pritchard 1983). Interior cells of the pieces are significantly less damaged (Todd 1993). Instead, digestion appears to be limited to the broken cells on the edges, with little or no damage caused by passage through the gut. This inability to obtain nutrients from the interior cells accounts for the consistency in small-sized particles from early to late instars. The particle sizes are significantly smaller for ***Tipula rufina*** (Figure 61), ***T. lateralis*** (Figure 66), and ***T. subnodicornis*** (Figure 59); ***T. paludosa*** (Figure 67) and ***T. oleracea*** (Figure 68) ingest significantly larger particles than any other species. These differences are at least partly explained by mandible size. ***Tipula paludosa*** has significantly larger mandibles and ***T. rufina*** has significantly smaller ones than any other species. In short, those species feeding on grass are generally larger and have longer mandibles than those species feeding on mosses.

Figure 66. ***Tipula lateralis*** adult, a species whose larvae ingest small particle sizes. Photo by James K. Lindsey, with permission.

Figure 67. ***Tipula paludosa*** larva, a bryophyte consumer. Photo by Roger S. Key, with permission.

Figure 68. ***Tipula oleracea***, a bryophyte consumer that ingests large particles. Photo by Malcolm Storey, through Creative Commons <www.discoverlife.org>.

Tipula has both terrestrial and aquatic members. Some of these in both habitats consume bryophytes. But ***Tipula subnodicornis*** (Figure 59) prefers the cottongrass *Eriophorum vaginatum* to the terrestrial moss ***Campylopus paradoxus*** and bog moss ***Sphagnum papillosum*** (Figure 69) (Todd 1993). However, in early winter (10 December to 9 January) the preference changes significantly from cottongrass to ***Sphagnum papillosum***. It is interesting, however, that during the growing season there is a mix of *Eriophorum vaginatum* with ***S. papillosum*** where the larvae spend the most time.

Figure 69. ***Sphagnum papillosum***, a moss that becomes a preferred food in winter for ***Tipula subnodicornis***. Photo by Michael Lüth, with permission.

Bisang (1996) reports a rather bizarre experience in The Bryological Times. She had several cultures of ***Anthoceros agrestis*** (Figure 70) and ***Phaeoceros carolinianus*** (Figure 71), both hornworts. Using the same techniques as she had used previously, she cultured these in jars, keeping two in Switzerland and taking one to Sweden. To her surprise, one of the cultures in Switzerland and the one taken to Sweden virtually disappeared from the jar. They had not dried and sabotage seemed absurd. Careful examination revealed larvae 1.5 cm long with a breathing apparatus at the posterior end. The cultures were supporting a healthy colony of larvae of ***Tipula*** (Figure 42), craneflies. The hornworts seemed to be a preferred food, as ***Bryum*** (Figure 72) sp. and several seedlings were untouched.

Figure 70. ***Anthoceros agrestis***, food source for ***Tipula*** larvae. Photo by Jan-Peter Frahm, with permission.

Figure 71. ***Phaeoceros carolinianus***, food source for ***Tipula*** larvae. Photo by Michael Lüth, with permission.

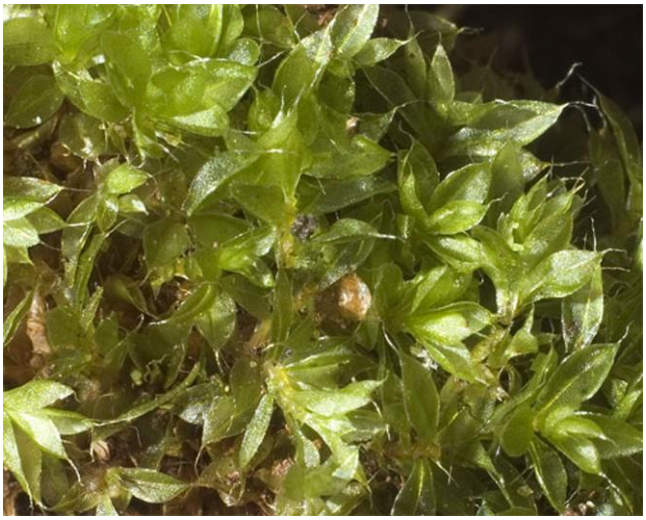

Figure 72. ***Bryum capillare***. A species of ***Bryum*** was refused as food by larvae of a species of ***Tipula***. Photo by Aimon Niklasson, with permission.

The members of ***Tipula*** are among the few documented moss consumers, although there is much more consumption than is generally recognized. Todd (1993) suggested that the presence of cell wall bioflavonoids in bryophytes might function not only to resist fungal invasion (Geiger 1990), but also to discourage insect

browsers. It is also possible that in some cases the fungi are needed to facilitate digestion, making mosses that lack them indigestible. Furthermore, lignin-like compounds in the bryophyte cell walls protect the cell wall compounds (cellulose, hemicellulose, and other kinds of polysaccharides) from **hydrolytic attack** (using a chemical reaction where something reacts with water and is changed into a new substance), preventing the consumers from using hydrolytic attack to extract cell contents, as demonstrated in ***Tipula abdominalis*** (Figure 75) (Martin *et al*. 1980). Nevertheless, in North America the genus ***Tipula*** (Figure 75) is able to hydrolyze proteins from unconditioned maple (*Acer*) leaves (Barlocher & Porter 1986).

Suitable food sources often depend on *p*H of the gut (Martin *et al*. 1980). Very high and very low *p*H levels seem to work best. But Barlocher and Porter (1986) found that the larvae of ***Tipula caloptera*** (Figure 73) have a gut *p*H that is somewhat alkaline. Fungal carbohydrases ingested with the leaves do not remain active in the ***T. caloptera*** gut, but do in the nearly neutral *p*H of the amphipod ***Gammarus tigrinus*** and net-spinning caddis larva ***Hydropsyche betteni*** (Figure 74).

Figure 73. ***Tipula caloptera*** adult female. Larvae of this species have an alkaline gut that may help it digest plant material. Photo by Tom Murray, through Creative Commons.

Figure 74. ***Hydropsyche betteni*** larva, a species with a slightly alkaline gut and ability to keep fungal enzymes alive. Photo by Donald S. Chandler, with permission.

In ***Tipula abdominalis*** (Figure 75) the midgut has a *p*H near 11.5 in a narrow section where there is extremely high proteolytic activity (Martin *et al*. 1980). In addition to low *p*H created by ***Sphagnum*** (Figure 69) and other mosses, mosses are well known for their antibiotics (McCleary *et al*. 1960; McCleary & Walkington 1966), additional factors that might interfere with gut digestion.

Figure 75. ***Tipula abdominalis*** larva. Larvae have a high *p*H in the midgut. Photo by Tom Murray, through Creative Commons.

Dolichopeza (Figure 77) is a genus known from mosses in various parts of the world. ***Dolichopeza americana*** is generally considered to be a terrestrial larva (Byers pers. comm.), but in the Appalachian Mountain streams it occurs among the leafy liverworts (***Scapania undulata***; Figure 30) in small waterfalls in March and December (Glime 1968). ***Dolichopeza albipes*** (see Figure 77) is a white-footed ghost cranefly whose larvae live among the mosses and liverworts of the Ghyll woodlands in Sussex, UK (Roper 2001). But this genus also chooses mosses for home in South Africa (Harrison & Barnard 1972). Members of this genus are known to lay their eggs among bryophytes, giving these larvae their start in life among the bryophytes.

Dolichopeza barnardi, ***D. hirtipennis***, and ***D. peringueyi*** larvae live beneath and within cushions of wet mosses and liverworts at the sides of waterfalls in South Africa (Harrison & Barnard 1972). And in North America, the genus feeds on terrestrial mosses (Byers 1961). In the coastal tundra near Barrow, Alaska, ***Prionocera recta*** (Figure 76) is restricted to mossy depressions.

Figure 76. ***Prionocera turcica*** adult, relative of ***P. recta*** restricted to mossy depressions in the Alaskan tundra. Photo by Andre Vrigens, through Creative Commons.

Figure 77. ***Dolichopeza carolus*** adult. Larvae of several species in this genus live among mosses, including at the sides of waterfalls. Photo by Tom Murray, through Creative Commons.

Many of the **Tipulidae** that inhabit mosses as larvae do so among terrestrial bryophytes and will be discussed in a separate chapter on Terrestrial Insects.

Anisopodidae – Wood Gnats, Window Gnats

This family is worldwide, but bryophytes are not a usual habitat. Most are small (4-12 mm) (Anisopodidae 2014). Fungi are typical foods, but it appears that at least some feed on micro-organisms, as I have observed.

While looking for mosses one day, I found some (***Philonotis fontana***?; Figure 78) in a seepage area on a cliffside. There on one of its branches was a small larva eating away at the wet moss. But as I watched for awhile, I realized that the mosses were going into one end of the larva covered with detritus and coming out the other end clean and still bright green. I was unable to identify this single larva beyond family.

The larvae of ***Sylvicola cinctus*** (Figure 79) was reported from mosses in Norway (Søli 1992). Perhaps there are other members of this small family hiding among the bryophytes.

Axymyiidae

This is a small family of six known species (Axymyiidae 2014). Its limited distribution is Holarctic and Oriental (Hauser 2008). The larvae live in decomposing wood (Axymyiidae 2014).

Figure 78. ***Philonotis fontana*** similar to seepage area where a member of **Anisopodidae** was eating and defecating bits of moss. Photo by Michael Lüth, with permission.

Figure 79. ***Silvicola cinctus*** male adult, a species whose larvae live among bryophytes in Norway. Photo by Walter Pfliegler, with permission.

I have seen only one record from this little-known family. ***Axymyia furcata*** (Figure 80) is a semi-aquatic fly in its larval stage and is typically a wood inhabitant. However, Wihlm and Courtney (2011) found that the larvae often choose logs that are covered with mosses.

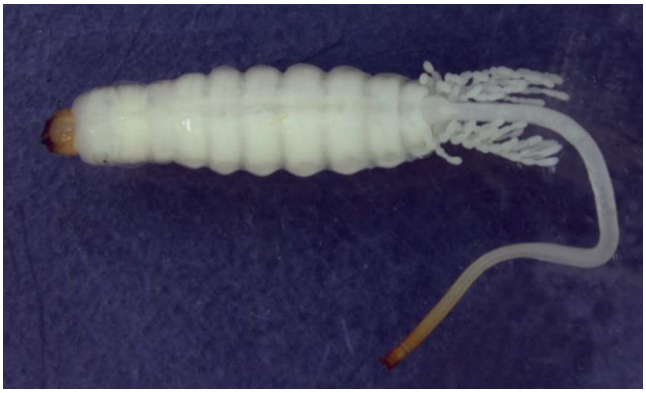

Figure 80. ***Axymyia furcata***, a semi-aquatic larva that lives among mosses on logs. Photo by M. J. Hatfield, through Creative Commons.

Cecidomyiidae – Gall Midges, Gall Gnats

This family is worldwide with most records in the Northern Hemisphere. They are small flies, mostly 1-5 mm (Balaban & Balaban 2004). Most of these are gall makers, with their larvae living on the gall material, but some feed on plants and some on decaying matter. Hence, as one might expect, they are predominantly terrestrial, but there are aquatic exceptions.

Although the **Cecidomyiidae** (Figure 81) are not typical bryophyte inhabitants, some do prefer mosses in torrents (Thomas 1980). ***Porricondyla ramadei*** was described as a new species from tufts of mosses in the turbulent waters of high Pyrénées streams. This is a poorly known fauna, and it is likely more insects may be discovered among the bryophytes there.

Figure 81. **Cecidomyiidae** larva; some members of this family live among mosses in torrents. Photo by M. J. Hatfield, through Creative Commons.

Mycetophilidae – Fungus Gnats

As the name implies, these flies live among fungi, hence making them most common in damp or sometimes wet habitats (Mycetophilidae 2014). They are worldwide, especially in forested areas (Kits 2005a). Although they are worldwide, most records are in the Northern Hemisphere (Mycetophilidae 2015). They typically feed on the fruiting bodies of the fungi (Mycetophilidae 2014). But some live among mosses and liverworts.

Fungi are often moist, so it may not be so surprising that some of these fungus gnats have found bryophytes to be suitable habitats. ***Gnoriste apicalis*** (Figure 82) is a semi-aquatic species. The larvae are able to live in saturated moss clumps on lake shores (Lenz 1927; Johannsen 1969). The pale green coloring may help it to be inconspicuous as it feeds on detritus. It may also make a dense but delicate white web in which it lives in such habitats, with the web offering further camouflage.

Sciaridae – Dark-winged Fungus Gnats

As you might expect of a fungus gnat, these flies prefer moist sites and eat the fruiting bodies of mushrooms and various parts of other fungi (Sciaridae 2014). They are worldwide in distribution, including such extremes as deserts, sub-Antarctic islands, and altitudes over 4000 m. Because they live among litter and fungi, they are frequent in flower pots. They are small, up to 7 mm long.

Figure 82. ***Gnoriste*** sp. adult; larvae of ***Gnoriste apicalis*** live in saturated mosses. Photo from Biodiversity Institute of Ontario, through Creative Commons.

In Korea, Japan, China, and other parts of Asia, the shiitake mushroom business is important. To this end, studies on the pests of this delicacy are common. And sometimes we find that mosses are involved. Shin *et al*. (2012) found that one of the mushroom pests, ***Bradysia difformis*** (Figure 83), also occurs in moorland on peat moss.

Figure 83. ***Bradysia difformis***, a shiitake mushroom pest whose larvae sometimes live on peat mosses of moorlands. Photo by David Pilling, with permission.

Ceratopogonidae – Biting Midges, No-see-ums, Sand Flies, Punkies

Their small size (<3 mm) has earned the **Ceratopogonidae** such names as no-see-ums and the adults can be quite a nuisance along lakes in June and July (Moisset 2005). Their distribution is worldwide in salt and freshwater marshes, forests, edges of ponds, and streams.

Usinger (1974) lists mosses among the usual habitats for larvae in the **Ceratopogonidae** and Krno (1990) found them to be representative of bryophyte habitats in the River Rajcianka in Slovakia. In addition to those aquatic

members, ***Forcipomyia*** (Figure 84) species live among damp mosses, including building nests in ***Sphagnum*** species (Figure 69) (Oldroyd 1964). The larvae in this family are elongate, wider in the middle, and most of them lack legs (Usinger 1974).

Figure 84. ***Forcipomyia*** sp larvae – inhabitants of damp mosses. Photo by Tom Murray, through Creative Commons.

In Germany, ***Kolenohelea calcarata*** occurs among mosses in a spring and ***Serromyia femorata*** (Figure 85) occurs among damp mosses (Strenzke 1950).

Figure 85. ***Serromyia femorata*** adult, a damp moss dweller. Photo by James K. Lindsey, with permission.

In the Atlantic Forest of the coastal area of South America, **Ceratopogonidae** were second in dominance during the rainy season among mosses in a first-order stream (Rosa *et al*. 2011). Living among the bryophytes minimizes the downstream loss in fast-moving water.

In European alpine areas, ***Dasyhelea modesta*** (see Figure 86-Figure 87) and ***Bezzia xanthocephala*** (see Figure 88) use mosses for their pupal site (Thienemann 1936). ***Dasyhelea*** (Figure 87) larvae likewise can spend their lives among mosses. The species known to Thienemann as ***Culicoides neglectus*** (*nom. dub*. – a name without valid publication) lived as pupae among mosses in small alpine waterfalls. (This name is now excluded, so I can't be sure what species he found.) Species in ***Culicoides*** as it is currently known are the ones that bite humans (Moisset 2005).

Figure 86. ***Dasyhelea flavifrons*** adult, member of a genus that is frequent among stream bryophytes. Photo by Walter Pfliegler, with permission.

Figure 87. ***Dasyhelea lithotelmatica*** larvae, member of a genus that frequents stream bryophytes. Photo by Roger S. Key, with permission.

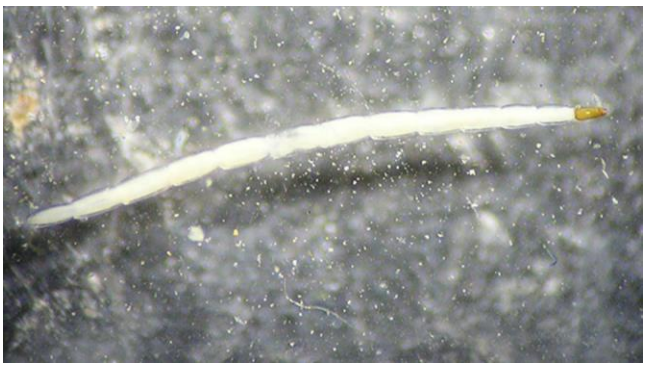

Figure 88. ***Bezzia*** larva, a frequent inhabitant of stream bryophytes. Photo from California Department of Wildlife, through public domain.

In my Appalachian Mountain, USA, streams, I found at least two species of ***Bezzia*** (Figure 88), two of ***Dasyhelea*** (Figure 86-Figure 87), and one each of ***Alluaudomyia*** (Figure 89) and ***Atrichopogon*** (Figure 90)

among the bryophytes. These were mostly among ***Hygroamblystegium fluviatile*** (Figure 91) – ***Platyhypnidium riparioides*** (Figure 6), but also occurred among ***Fontinalis dalecarlica*** (Figure 92) and ***Scapania undulata*** (Figure 30).

Figure 89. ***Alluaudomyia paraspina*** adult female, a genus with some species whose larvae live among bryophytes in Appalachian Mountain streams. Photo by Tom Murray, through Creative Commons.

Figure 90. ***Atrichopogon*** larva, a genus with some species whose larvae live among bryophytes in Appalachian Mountain streams. Photo courtesy of the State Hygienic Laboratory at the University of Iowa, with permission.

Figure 91. ***Hygroamblystegium fluviatile***, home for multiple species of **Ceratopogonidae**. Photo by Michael Lüth, with permission.

Figure 92. ***Fontinalis dalecarlica***, home for a number of genera of **Ceratopogonidae**. Photo by Kristoffer Hylander, with permission.

Summary

The **Nematocera** are primarily aquatic as larvae and a number of species and genera live among bryophytes. Adaptations to the bryophyte habitat, differing little from those needed for aquatic living, include claws and hooks to hold them in place, cutaneous breathing and/or gills, small size, often slender, and a detritus feeding habit. In return for the hospitality of the bryophyte, they may disperse bits of the plants or their spores to other suitable locations.

The dominant **Diptera** among bryophytes are **Chironomidae** and **Simuliidae**, with **Tipulidae**, **Limoniidae**, and **Ceratopogonidae** being less abundant. The **Chironomidae** can reach 1000's in a single handful of moss.

The **Cylindrotomidae** are among the few bryophyte mimics. They live among mosses in wet areas and bogs and the projections from their bodies resemble moss leaves.

In the genus ***Tipula*** (**Tipulidae**), a high gut *p*H may facilitate digestion of bryophytes.

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George W. Byers verified my identifications of Tipulidae and Julian P. Donahue verified some of the remaining Diptera from my mid-Appalachian Mountain study.

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CHAPTER 11-13b
AQUATIC INSECTS: HOLOMETABOLA – DIPTERA, SUBORDER NEMATOCERA

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CHAPTER 11-13b
AQUATIC INSECTS: HOLOMETABOLA – DIPTERA, SUBORDER NEMATOCERA

Figure 1. **Chironomidae** larvae, the most common and abundant family of insects among mosses. Photo by Simon Carmichael, through Creative Commons.

Suborder Nematocera, continued

Chironomidae – Midges

These small flies are 1-10 mm long and are everywhere (Cotinis 2004)! Only some areas of the desert seem to lack them. They are the flies that seem to follow you as clouds (swarms). The larvae are mostly aquatic and use filter feeding.

If you haven't met the **Chironomidae**, you haven't looked at the bases of aquatic moss leaves. Hynes (1961) considered the **Chironomidae** (Figure 1) to be the "key industry" organisms among mosses. Such a concept is supported by their role as food for fish. Johannsen (1969) contended that in some locales they may constitute almost the entire diet of brook trout (*Salvelinus fontinalis*). But the mosses provide excellent hiding places for these larvae, so the bryophytes may be a detriment rather than a source of fish food.

Thienemann (1936) reported many **Chironomidae** from mosses in the alpine areas of Europe. These occurred in springs, waterfalls, bogs, and streams. The **Chironomidae** are by far the most numerous organisms in most stream bryophyte habitats (Arnold & Macan 1969; Gerson 1982; Maurer & Brusven 1983; Brusven *et al.* 1990; Glime 1994; Chantha *et al.* 2000; Linhart *et al.* 2002a), typically comprising more than 50% of the insects living there (Brusven *et al.* 1990). Needham and Christenson (1927) reported ***Chironomus*** (Figure 1) and

Tanytarsus (Figure 2) from moss-covered boulders in streams of northern Utah, USA. Frost (1942) found that among submerged mosses she studied in Ireland, about five-sixths of the almost 600,000 organisms in those streams were **Chironomidae**. Lindegaard *et al*. (1975) found that more than 40% of the invertebrates living among the moss ***Cratoneuron*** (Figure 3) were **Chironomidae**.

Figure 2. ***Tanytarsus*** larva and tube. Photo from Cobb County, GA, government, Cobb County Water System website, through public domain.

Figure 3. ***Cratoneuron commutatum*** var ***falcatum*** in Europe, a habitat where many **Chironomidae** live among the mosses. Photo by Michael Lüth, with permission.

Chironomidae (Figure 1) can reach 100,000 in a collection of ***Cratoneuron*** (Figure 3) (Gerson 1969). Frost (1942) found that in an acid stream the **Chironomidae** comprised 84% of the moss fauna; in the alkaline stream they comprised 83%. Haefner and Wallace (1981) found that this family had mean annual densities of 23,000 m^2 among the thick mosses of rockface habitats in a southern Appalachian, USA, stream. Brusven *et al*. (1990) reported that moss clumps had insect communities in which 50% of the organisms were **Chironomidae**. These did not seem to contribute to increased daytime drift.

Boerger *et al*. (1982) found that densities of **Chironomidae** (Figure 1) on mosses in a brown-water stream of Alberta, Canada, were high (978) compared to a range of 32-466 on tracheophytes, sponge colonies, and algae. But diversity was only 3 species on mosses, compared to 13 for sediment, 2 for *Sparganium*, and 1 for the other tracheophytes, algae, wood, and none for sponges and leaf litter.

Nolte (1991) found that the **Chironomidae** (Figure 1) in the mosses of a small upland stream in central Germany were small, with 98% being <5 mm. There were more than 65 species in 26 genera! The greatest diversity was near the source and the species changed downward in the stream. The fully submersed mosses had approximately five times as many larvae as those that were semi-submersed. The highest density reached 830 larvae per 10 square cm. Nolte found that the location of the moss in the stream had the greatest effect on the diversity, but the biomass and abundance were most influenced by the constancy of flow and factors such as temperature and detritus deposition that related to flow.

In most locations, species of bryophyte doesn't seem to matter much. In the Appalachian Mountain streams of eastern USA, they were abundant in all three dominant species: ***Fontinalis dalecarlica*** (Figure 4), ***Hygroamblystegium fluviatile*** (Figure 5) – ***Platyhypnidium riparioides*** (Figure 6), and ***Scapania undulata*** (Figure 7).

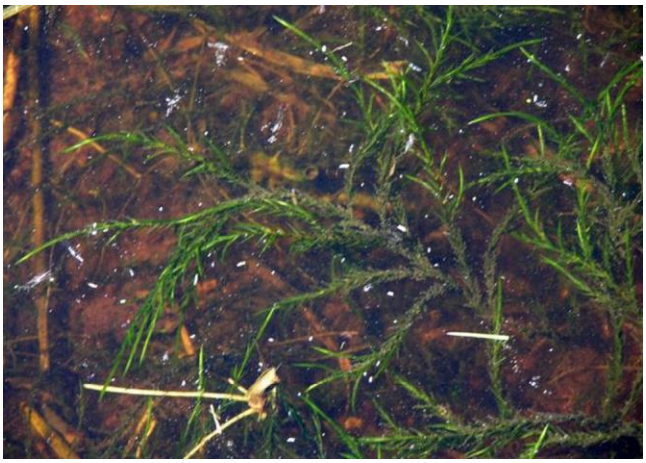

Figure 4. ***Fontinalis dalecarlica***, moss that is home to large numbers of **Chironomidae**. Photo by J. C. Schou, with permission.

Figure 5. ***Hygroamblystegium fluviatile***, a moss that is home to large numbers of **Chironomidae**. Photo by Hermann Schachner, through Creative Commons.

Figure 6. ***Platyhypnidium riparioides***, home to many **Chironomidae**. Photo by Michael Lüth, with permission.

Figure 7. ***Scapania undulata***, a leafy liverwort that is home to large numbers of **Chironomidae**. Photo by Hermann Schachner, through Creative Commons.

Emergence

Some **Chironomidae** (Figure 1) use the mosses for emergence. Adults of ***Microtendipes pedellus*** (Figure 8) emerged from both mossy and muddy substrates in a Quebec highland stream (Harper & Cloutier 1979). The researchers suggested that some typically lentic (non-moving water) chironomid species were able to live in the protection of mosses in streams. The huge numbers found there and in other habitats result in clouds of adults during emergence time (Figure 9).

Figure 8. ***Microtendipes pedellus*** adult, a midge that often uses mosses for emergence. Photo through Wikimedia Commons.

Figure 9. **Chironomidae** adult swarm. Photo by Robert Janke, with permission.

Usinger (1974) reared ***Boreochlus*** sp. (Figure 10) from mosses in a bog near Washington, D.C., USA. Becker and Wagner (2004) compared the emergence of **Chironomidae** (Figure 1) from sand and moss-covered rocks in a stream in Germany. They recorded 99 species from the sand traps and 85 from the traps over the moss-covered stones! The **Tanytarsini** (Figure 2) dominated in the traps on the moss-covered stones, whereas the **Prodiamesinae** and **Chironomini** predominated in traps above sand. They suggested that the smaller number of species above the moss-covered rocks may have been due to escapes from the nets on the irregular surfaces with lower flow rates trapping more pupae over the sand.

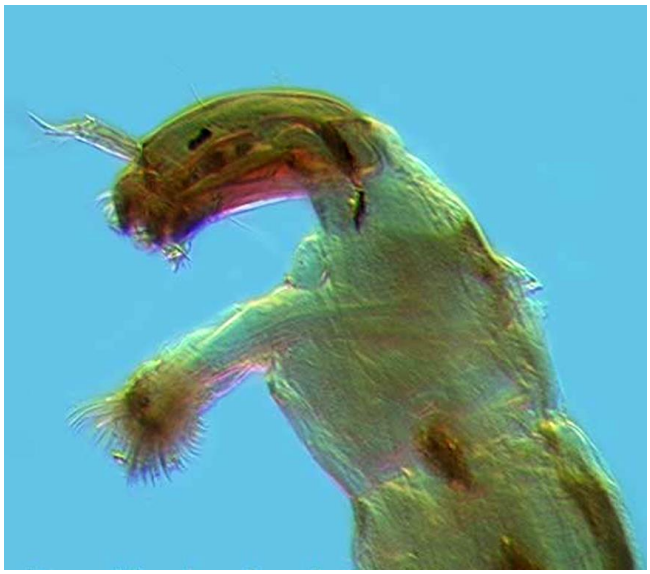

Figure 10. ***Boreochlus sinuaticornis*** larva, member of a genus that lives among bryophytes in bogs. Photo by Pete Cranston, with permission.

In Appalachian Mountain, USA, streams, the Chironomidae make thin cases for their pupae between the upper and lower leaves of the leafy liverwort ***Scapania undulata*** (Figure 7) (Glime 1968). One larva even crawled into an empty case of the caddisfly ***Paleagapetus celsus*** to pupate, a case made from ***Scapania undulata***. The leaves of this liverwort also provide a location where one can find larvae and eggs of the midges.

Seasons

The **Chironomidae** (Figure 1) are present year-round, but the taxa change. For example, among bryophytes in an Atlantic Forest stream (biome along the Atlantic coast of Brazil from Rio Grande do Norte in the north to Rio Grande do Sul in the south), Rosa *et al*. (2011) found that **Chironomidae** were dominant in both periods of study (3months each of dry season and rainy season). In the dry season, the **Naididae** (annelid worms) were second in number.

Pseudodiamesa branickii (Figure 11) demonstrates the variability in life cycles of some **Chironomidae**. This species produces three generations in one year in a German stream, but the generation time varies based on photoperiod effects on eggs and larvae (Nolte & Hoffmann 1992). In this stream there are two strains, one that is **bivoltine** (producing two broods per season) and one that is **trivoltine** (producing three broods per season).

Figure 11. ***Pseudodiamesa branickii*** larva, a species with at least two strains that differ in the length of the life cycle. Photo by Erik Bostrom, NTNU Museum of Natural History and Archaeology, through Creative Commons.

Temperature differences can cause differences in emergence times. For example, in the high Arctic, **Chironomidae** (Figure 1) from deeper water emerge as much as three weeks later than those in warmer shallow water (Danks & Oliver 1972). Among the 112 species of **Chironomidae** in a muskeg stream in Alberta, Canada, emergence extends over 140 days. In New South Wales, emergence (Figure 12) is governed by flooding, with ***Chironomus tepperi*** (Figure 13) emerging first and ***Procladius paludicola*** (see Figure 14) emerging as the former declines (Stevens 1994).

Figure 12. ***Chironomus dorsalis*** emerging to an adult. Photo by James K. Lindsey, with permission.

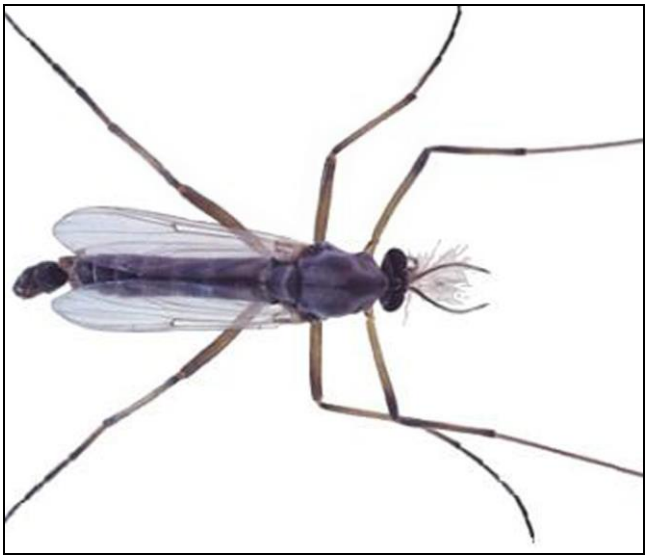

Figure 13. ***Chironomus tepperi*** adult male, an earlier emerger than ***Procladius paludicola***, thus separating their niches. Photo through Creative Commons.

Figure 14. ***Procladius*** *lugens* adult. ***Procladius paludicola*** is a later emerger than ***Chironomus tepperi***, thus separating their niches. Photo by James K. Lindsey, with permission.

Differences in emergence times can maintain the isolating mechanism that keeps species distinct, as in two sibling species of ***Chironomus*** (Figure 15) in Arctic ponds (Butler 1982). Although the two species are morphologically indistinct as larvae, they maintain strict, but different, emergence times, despite 7-year developmental periods.

Figure 15. ***Chironomus***, a genus known from among bryophytes. Photo by Gerard Visser, with permission.

Cold-water Species

Cold temperatures seem to favor some of the **Chironomidae** (Figure 1). Welch (1976) found that ***Orthocladius*** (Figure 16), ***Pseudodiamesa arctica*** (see Figure 11), ***Paracladius quadrinodosus*** (see Figure 17), and ***Micropsectra***(?) sp. (Figure 18) occur primarily in the rocky and moss zones. They are able to withstand temperatures down to 0°C, which is important for their life cycle of 2-3 years. The genus ***Diamesa*** (Figure 19-Figure 20) is common among mosses of European glacier-fed streams where the temperature is constantly less than 2°C (Lods-Crozet *et al*. 2001). Elgmork and Sæther (1970) found it among mosses in creeks and springs in the Colorado Rocky Mountains, USA. It is able to overwinter under the snow (Anderson *et al*. 2013).

Figure 16. ***Orthocladius*** *rubicundus*, a genus with larvae among bryophytes in cold water. Photo by J. K. Lindsey, with permission.

Figure 17. ***Paracladius conversus*** female adult. Some members of this genus live among mosses in rocky zones of cold streams. Photo by James K. Lindsey, with permission.

Figure 18. ***Micropsectra*** larva, member of a genus with moss-dwelling species. Photo by NTNU University Museum, Department of Natural History, through Creative Commons.

Figure 19. ***Diamesa mendotae*** larvae, member of a genus that is common among mosses in cold-water streams. Permission to reproduce given by Leonard Ferrington on behalf of the Chironomidae Research Group at the University of Minnesota.

Figure 20. ***Diamesa mendotae*** female on snow. Permission to reproduce given by Leonard Ferrington on behalf of the Chironomidae Research Group at the University of Minnesota.

Macropelopia notata (Figure 21) and ***M. adaucta*** are cold-water species that are c**renobionts** (living in springs) (Fittkau 1962). They prefer mosses in soft water. ***Macropelopia notata*** occurs in **rheo-hygropetric** springs (flowing film of water on rocks in springs) and **helocrenes** (springs originating from marshes or bogs) with abundant mosses (Lencioni *et al*. 2011). In the Danish spring

Ravnkilde, Lindegaard *et al*. (1975) found large numbers of ***Macropelopia notata*** in the moss carpets. These carpets exhibit both vertical and horizontal zonation patterns that do not seem to be influenced by the fauna of the neighboring stone. Rather, horizontal distribution seems to result from differences in current velocity and detritus capture.

Figure 21. ***Macropelopia notata*** adult, a species whose larvae live among mosses in springs. Photo by James K. Lindsey, with permission.

In the Antarctic, mosses often play a role in protecting invertebrates from the harsh and changeable environment. The **Chironomidae** (Figure 1) are no exception, living among bryophytes in a first-order stream of the Atlantic Forest (Tilbrook 1967; Rosa *et al*. 2013). The mosses are able to provide protection from the rushing waters during periods of higher rainfall, and the high retention of food particles support both species richness and density during the high rainfall periods.

Parochlus steinenii (Figure 22) is a chironomid of lakes in the central plateau of the Byers Peninsula, Antarctica (Rico & Quesada 2013). It lives among the mosses on the bottoms of lakes and streams. The second of the two chironomids in that part of Antarctica is ***Belgica antarctica*** (Figure 23) that lives in streams that run through moss beds. Both species feed on a variety of foods associated with the biofilm and microbial material among the mosses.

Figure 22. ***Parochlus steinenii*** adults, a chironomid that lives among mosses in the Antarctic. Photo by Roger S. Key, with permission.

Figure 23. ***Belgica antarctica*** larvae, a chironomid that is common in streams running through moss beds of Antarctica. Photo by Juanita Constible, through Creative Commons.

Overwintering

Some **Chironomidae** larvae become encased in ice in winter, yet survive, an ability that is rare among the insects (Moore & Lee 1991). Although this seems only to be known where they can live in sediments of pools and ponds, it is possible that they likewise do this among sediments collected by bryophytes. Irons *et al*. (1993) found that **Chironomidae** (Figure 1) in Alaska, USA, are able to overwinter in a frozen habitat.

Frost (1942) found that the chironomid larvae in her River Liffey, Ireland, survey reached their peak in winter in the moss samples.

Current Velocity

Many of the **Chironomidae** (Figure 1) live in areas of high water velocity, but are protected from it by the bryophytes. They are able to nestle at leaf bases where they benefit not only through protection from the current, but also from the collection of detritus there. Oliver and Bode (1985) described a new species of ***Cardiocladius*** (Figure 24) that resembles ***Cardiocladius albiplumus*** among bryophytes where the current velocities are 20-100 cm s^{-1}.

Figure 24. ***Cardiocladius*** adult, a genus that has larvae that sometimes live among bryophytes. Photo by M. J. Hatfield, through Creative Commons.

Diversity

The **Chironomidae** do not lack species diversity among bryophytes (see Table 1). In a mountain river in the Western Tatra Mountains, Ertlova (1984) found 56 species. The most varied species composition occurred among mosses on large stones. The dominant species was ***Orthocladius rivicola*** (Figure 25).

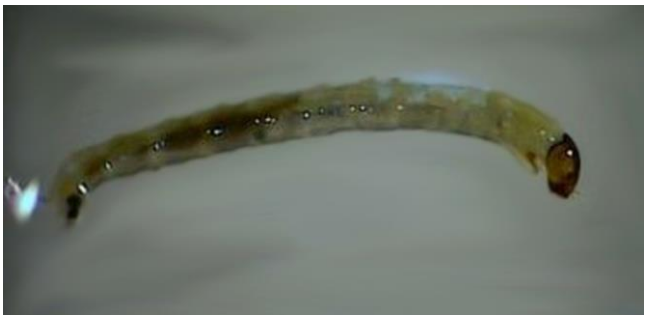

Figure 25. ***Orthocladius rivicola*** larva, a moss inhabitant. Photo from Stroud Water Research Center, through Creative Commons.

The **Chironomidae** is a large family and its species are difficult to identify. Few people attempt the identification of larvae (Figure 1). Most ecologists simply indicate **Chironomidae**. This results from the difficulty of finding distinguishing characters between related species and the need to rear them before a name can be applied and the larva described. For example, ***Krenosmittia*** (Figure 26) larvae are known in Europe from springs and moss-filled seeps (Ferrington 1984). The habitat of North American larvae is unknown, although adults are known, but the habitat is likely to be similar, or they might occur in the **hyporheic** zone (area or ecosystem beneath bed of river or stream, saturated with water and supporting invertebrate fauna) of streams. Creating a list of bryophyte taxa is further complicated by changing views of the classification. For many of the taxa in Table 1 I was unable to verify the name or find the name currently in use.

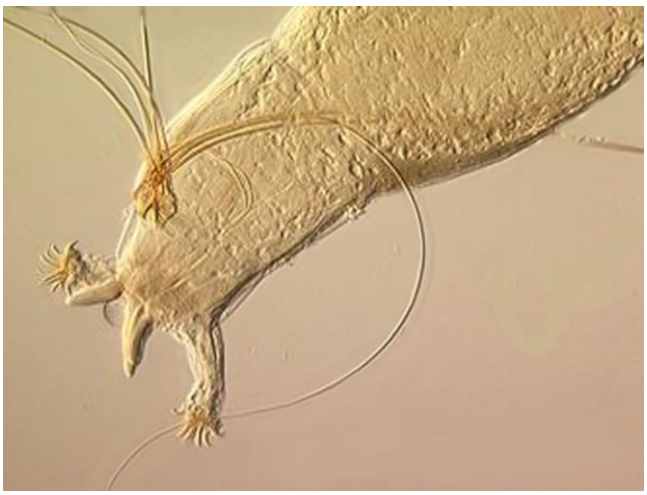

Figure 26. ***Krenosmittia*** larva posterior, an inhabitant of moss-filled seeps in Europe. Photo by Peter Cranston, with permission.

A few brave souls have done the tedious work to provide species lists of **Chironomidae**. In their study of the Colorado Rocky Mountain, USA, streams, Elgmork and Sæther (1970) identified a number of **Chironomidae** (Figure 1) species among mosses. These included ***Pseudokiefferiella parva*** (Figure 27) in creeks and springs, and occasionally ***Orthocladius*** (Figure 16)**.** Among the mosses of high mountain brooks they found ***Metriocnemus*** (Figure 28), ***Parakiefferiella***, and ***Rheocricotopus effusus*** (see Figure 29). ***Paraphaenocladius*** (Figure 30), a primarily terrestrial genus, can also occur in bogs and among mosses of mountain creeks, particularly cold springs. They found species of ***Nanocladius*** (Figure 31) in their streams, but did not mention mosses; ***Nanocladius bicolor*** lives among mosses in high mountain creeks in Europe (Thienemann 1954; Freeman 1956). Likewise, ***Thienemannia*** cf. ***gracils*** (see Figure 32), present in their study, is known among mosses in mountain creeks (Thienemann 1954; Brundin 1956a, b) and among perennial mosses in a river in Romania (Gardenfors 2001). Frost (1942) was also among the brave who identified the **Chironomidae** among the mosses in the River Liffey, Ireland. Including both an acid and an alkaline area, she found 24 genera, many different from those of Elgmork and Sæther (1970) in the Rocky Mountain, USA, streams, as seen in Table 1.

Figure 27. ***Pseudokiefferiella parva*** larva, an inhabitant of mosses in the Rocky Mountains, USA, streams and springs. Photo from <Benthos.narod.ru>.

Figure 28. ***Metriocnemus edwardsii*** from ***Darlingtonia californica*** (western pitcher plant). Photo by Barry Rice, through Creative Commons.

Figure 29. ***Rheocricotopus atripes*** female adult, member of a genus known from mosses in high mountain brooks in the Colorado Rocky Mountains. Photo by James K. Lindsey, with permission.

Figure 31. ***Nanocladius*** larva amid the legs of a larger invertebrate. ***Nanocladius bicolor*** lives among mosses in high mountain creeks of Europe. Photo by Pete Cranston, with permission.

Figure 30. ***Paraphaenocladius*** sp. adult; larvae of this genus can occur in bogs and among mosses of mountain creeks. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.

Figure 32. ***Thienemannia gracei*** adult, member of a genus whose larvae often live among mosses in mountain streams and rivers. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.

Table 1. Chironomidae known to include bryophytes among their choices of shelter in streams. Taxa preceded by * indicate taxa I was unable to verify on current nomenclature lists. Available images follow the table.

Taxon	Habitat	References
****Ablabesmyia costalis***	River Liffey, Ireland European alpine	Humphries & Frost 1937; Frost 1942; Thienemann 1936
Ablabesmyia mallochi	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
****Ablabesmyia minima***	European alpine streams; River Liffey, Ireland	Thienemann 1936; Humphries & Frost 1937; Frost 1942
Ablabesmyia nigropunctata	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Ablabesmyia sexannulata	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Belgica antarctica	Antarctic streams in moss beds	Rico & Quesada 2013
****Brillia alulata***	European alpine springs	Thienemann 1936
Brillia modesta	European alpine	Thienemann 1936
Camptocladius sp.	River Liffey, Ireland	Frost 1942
Cardiocladius albiplumus	fast water	Oliver & Bode 1985
Chaetocladius perennis	pupae in European alpine	Thienemann 1936
****Chironomus genuines***	River Liffey, Ireland	Frost 1942

Cladotanytarsus	River Liffey, Ireland	Frost 1942
Conchapelopia flavifrons	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Conchapelopia puncticollis	European alpine	Thienemann 1936
Corynoneura sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942;
	larvae & pupae in European alpine	Thienemann 1936
Corynoneura lobata	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Cricotopus sp.	***Drepanocladus revolvens***, Alberta, Canada;	Boerger *et al*. 1982
	Fontinalis & ***Hygrohypnum*** in Russian lake outlets	Vuori *et al*. 1999
Cricotopus bicinctus	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Cricotopus miricornis	European alpine	Thienemann 1936
Cricotopus prolongatus	European alpine	Thienemann 1936
Cricotopus trifasciatus	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Cryptochironomus sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Culicoides rivicola	European alpine	Thienemann 1936
Culicoides neglectus (*nom dub*)	European alpine	Thienemann 1936
Diamesa sp.	River Liffey, Ireland	Humphries & Frost 1937
Diamesa fissipes gr.	European alpine	Thienemann 1936
Diamesa prolongata	pupae in European alpine	Thienemann 1936
Diamesa steinboecki	European alpine	Thienemann 1936
Diamesa tonsa	pupae among mosses in European alpine	Thienemann 1936
Diplocladius cultriger	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Endochironomus sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
****Eukiefferiella alpestris***	European alpine streams	Thienemann 1936
Eukiefferiella brevicalcar	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Eukiefferiella caerulescens	larvae among ***Fontinalis***; pupae among mosses	Thienemann 1936
Eukiefferiella endobryonia	larvae & pupae in tubes made of ***Fontinalis*** spp.	Imada 2020
****Eukiefferiella longicalcar*** (nomen dubium)	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Eukiefferiella lobifera	European alpine	Thienemann 1936
Eukiefferiella minor	European alpine streams	Thienemann 1936
Eukiefferiella subalpina	European alpine streams	Thienemann 1936
****Eutanytarsus inmermepes***	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Heterotrissocladius sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Heterotrissocladius changi	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Krenosmittia	European springs & seeps	Ferrington 1984
****Labrudinia pilosella***	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Limnophyes borealis	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Limnophyes globifer	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Limnophyes prolongatus	European alpine	Thienemann 1936
Macropelopia sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Macropelopia adaucta	mosses in coldwater springs	Fittkau 1962; Lindegaard *et al*. 1975
Macropelopia notata	mosses in coldwater springs	Fittkau 1962; Lindegaard *et al*. 1975
Metriocnemus	in high mosses of high mountain brooks of Europe	Thienemann 1954
	Colorado Rocky Mountain, USA, streams	Elgmork & Sæther 1970
****Metriocnemus cuneatus***	European alpine springs	Thienemann 1936
Metriocnemus fuscipes	European alpine springs	Thienemann 1936
Metriocnemus hygropetricus	European alpine	Thienemann 1936
Micropsectra sp.	European alpine streams	Thienemann 1936
Microtendipes sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Microtendipes pedellus	emergences in mossy areas, Quebec, Canada	Harper & Cloutier 1979
Nanocladius sp.	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Nanocladius bicolor	high mountain streams in Europe	Thienemann 1954; Freeman 1956
Neostempellina thienemanni	exclusively alkaline springs & streams	Reiss 1984
Orthocladius luteus	European alpine streams	Thienemann 1936
Orthocladius oblidens	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Orthocladius rivicola	European alpine streams	Thienemann 1936
Orthocladius rivulorum	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Orthocladius saxicola	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Orthocladius thienemanni	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Paraboreochlus minutissimus	European alpine springs	Thienemann 1936
Paracladius quadrinodosus	moss & rock zones	Welch 1976
Paracricotopus sp.	larvae & pupae in alpine streams & waterfalls	Thienemann 1936
Parakiefferiella sp.	Holarctic mountain brooks	Thienemann 1944; Oliver 1963; Elgmork
	Drepanocladus revolvens, Alberta, Canada;	& Sæther 1970; Boerger *et al*. 1982
Parakiefferiella bathophila	River Liffey, Ireland	Frost 1942
Paramerina fragilis	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Paraphaenocladius	bog mosses, mountain streams, cold springs	Elgmork & Sæther 1970
Parapsectrocladius	mountain streams, Argentina	Epele *et al*. 2012
Paratanytarsus sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Parochlus steinenii	mosses on Antarctic lake bottoms	Rico & Quesada 2013

Polypedilum	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Polypedilum scalaenum	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Psectrocladius dilatatus	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Psectrocladius psilopterus	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Psectrocladius simulans	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Pseudodiamesa arctica	moss & rock zones	Welch 1976
Pseudodiamesa branickii	mid-mtn creeks,Colorado Rocky Mountain, USA	Elgmork & Sæther 1970
Pseudodiamesa nivosa?	European alpine	Thienemann 1936
Pseudokiefferiella parva	Colorado Rocky Mountain, USA, creeks and springs	Elgmork & Sæther 1970
Rheocricotopus effusus	pupae in alpine areas	Thienemann 1936;
	larvae in streams in high mountain areas	Elgmork & Sæther 1970
Rheocricotopus fuscipes	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
	European alpine	Thienemann 1936
Rheotanytarsus sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Rheotanytarsus distinctissimus	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Stempellina bausei	European alpine streams	Thienemann 1936
****Syndiamesa macronyx***	European alpine	Thienemann 1936
Synorthocladius semivirens	European alpine	Thienemann 1936
****Synorthocladius tipulatus***	River Liffey, Ireland, European alpine springs	Thienemann 1936; Humphries & Frost 1937; Frost 1942
Tanytarsus curticornis	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Tanytarsus dispar	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Tanytarsus gregarius	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Thienemannia gracilis	mountain streams in Europe & Iceland	Thienemann 1936,1954; Brundin
	streams, Colorado Rocky Mountain, USA	1956a, b; Elgmork & Sæther 1970
Thienemanniella fusca	European alpine	Thienemann 1936
Thienemannimyia	Russian streams	Vuori *et al.* 1999
****Trichocladius*** sp. (invalid genus)	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Trissopelopia longimana	European alpine streams	Thienemann 1936
Trissopelopia ogemawi	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Tvetenia bavarica	European alpine waterfalls	Thienemann 1936
Tvetenia calvescens	semiterrestrial mosses in springs, Europe	Stur *et al*. 2005; Thienemann 1936;
	European alpine streams; River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Tvetenia discoloripes	European streams	Thienemann 1936, 1954
	Colorado Rocky Mountain, USA, streams	Elgmork & Sæther 1970
	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Xenochironomus xenolabis	Quebec highland stream	Harper & Cloutier 1979

Figure 33. ***Ablabesmyia*** larva, a common genus among bryophytes in Europe. Photo by Walter Pfliegler, with permission.

Figure 34. ***Ablabesmyia*** egg sack, a common genus among bryophytes in Europe. Photo by Walter Pfliegler, with permission.

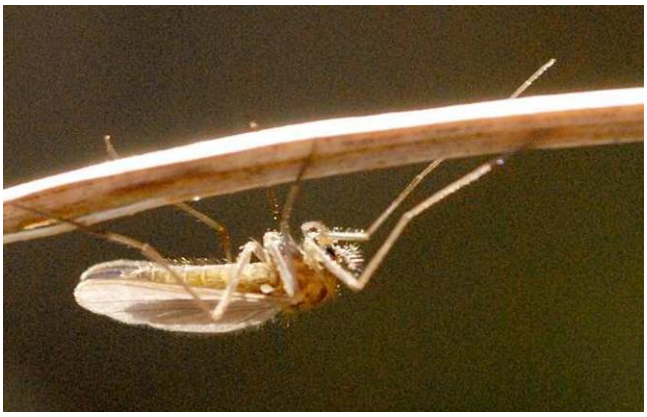

Figure 35. ***Brillia bifida*** adult, member of a genus that inhabits aquatic mosses in Europe. Photo by James K. Lindsey, with permission.

Figure 36. ***Chaetocladius perennis*** adult, a species whose larvae are known from bryophytes. Photo by James K. Lindsey, with permission.

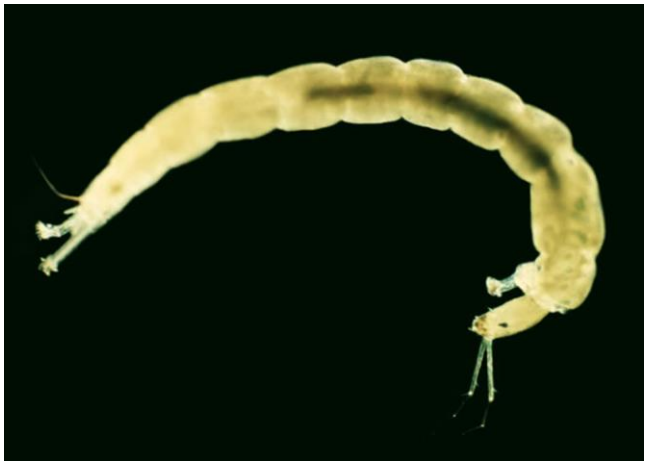

Figure 37. ***Corynoneura taranaki*** larva, member of a genus with bryophyte dwellers. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 38. ***Cricotopus lebetis*** larva, member of a genus known from the mosses ***Fontinalis*** and ***Hygrohypnum*** in Russia. Photo by Jerry F. Butler, with permission.

Figure 39. ***Cryptochironomus obreptans*** female adult, member of a genus with larvae that can inhabit stream mosses. Photo by James K. Lindsey, with permission.

Figure 40. ***Culicoides imicola*** adult, member of a genus whose larvae can live among bryophytes. Photo by Alan R. Walker, through Creative Commons.

Figure 41. ***Diplocladius cultriger***, a species whose larvae sometimes live among mosses. Photo by Tom Murray, through Creative Commons.

Figure 42. ***Endochironomus*** larva, a genus whose larvae sometimes live among mosses. Photo by J. C. Schou, with permission.

Figure 43. ***Endochironomus*** male adult, genus with larvae that sometimes live among bryophytes. Photo by Don Loarie, through Creative Commons.

Figure 44. ***Eukiefferiella*** (arrow) on *Nesameletus ebopohaupapa*. Several species of ***Eukiefferiella*** live among stream bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 45. ***Limnophyes habilis*** adult, member of a genus with several species that live among bryophytes. Photo by James K. Lindsey, with permission.

Figure 46. ***Macropelopia nebulosa*** pupa, member of a genus with larvae of some species occurring among aquatic mosses. Photo by J. C. Schou, with permission.

Figure 47. ***Macropelopia nebulosa*** adult, member of a genus that sometimes lives among mosses as larvae. Photo by James K. Lindsey, with permission.

Figure 48. ***Metriocnemus fusipes*** male adult, a species whose larvae can occur among stream bryophytes. Photo by James K. Lindsey, with permission.

Figure 49. ***Paracladius conversus*** female adult, member of a genus that is represented among the bryophyte fauna of streams in Europe. Photo by James K. Lindsey, with permission.

Figure 50. ***Paramerina fragilis*** adult, a species whose larvae occur with the moss ***Drepanocladus revolvens*** in Canada. Photo by Ilona L, through Creative Commons.

Figure 51. ***Paratanytarsus tenuis*** male adult, member of a genus whose larvae inhabit stream bryophytes. Photo by James K. Lindsey, with permission.

Figure 52. ***Polypedilum*** larva in plant litter. ***Polypedilum scalaenum*** occurs among ***Drepanocladus revolvens***. Photo by Stephen Moore, Landcare Research NZ, with permission.

Figure 53. ***Psectrocladius sordidellus*** emerging female adult, member of a genus that sometimes occurs among stream bryophytes. Photo by James K. Lindsey, with permission.

Figure 54. ***Stempellina bausei*** adult, a species whose larvae live among bryophytes in European alpine streams. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.

Figure 55. ***Trissopelopia longimana*** adults mating, a species whose larvae live in European alpine streams. Photo by James K. Lindsey, with permission.

Suren (1993) considered that the dominance of **Chironomidae** (Figure 1) among New Zealand mosses may reflect the absence in New Zealand of some of the important moss families of **Ephemeroptera**, **Plecoptera**, and **Trichoptera** in other parts of the world.

Bryophyte Preferences?

Like the **Chironomidae** (Figure 1), the mosses are difficult for non-bryologists to identify and few studies actually name both the mosses and the **Chironomidae** associated with them. In the pristine streams of the Russian Karelia, Vuori *et al*. (1999) found that algae-eating **Chironomidae** larvae dominated the insect fauna in stable lake outlets where mosses formed abundant vegetation. The mosses were predominantly ***Fontinalis*** (Figure 4) and ***Hygrohypnum*** (Figure 56). ***Cricotopus*** sp. (Figure 38) and ***Thienemannimyia*** sp. (Figure 57) were the dominant **Chironomidae**.

Figure 56. ***Hygrohypnum ochraceum***, home of **Chironomidae**. Photo by Michael Lüth, with permission.

Figure 57. ***Thienemannimyia*** larva posterior, a moss dweller. Photo by Pete Cranston, with permission.

In their study of an Arctic stream (Alaska, USA), Lee and Hershey (2000) found that **Chironomidae** increased in density when the mosses (***Hygrohypnum***, Figure 56) increased to dense growths. They suggested that it was the increase in habitat complexity that caused the increase in the **Chironomidae**.

In New Zealand, the **Chironomidae** (Figure 1) were most abundant in ***Fissidens rigidulus*** (Figure 58) in the midstream torrential water, whereas other taxa dominated in mosses of the spray zones (Cowie & Winterbourn 1979).

What's for Dinner?

Aside from nematodes and rotifers, the **Chironomidae** were the dominant fauna in beds of ***Fontinalis antipyretica*** (Figure 59) in the Czech Republic, making them the most abundant insect group (Linhart *et al*. 2000, 2002a,c). Those among mosses had a positive density correlation with organic particles of 30-100 µm. Some **Chironomidae** larvae build tubes to trap detritus (Figure 60). In one rip-rapped channel (used to stabilize the stream banks) in the Czech Republic, Linhart *et al*. (2002b) found the fine particulate matter trapped by the moss provided a food source for the moss dwellers. Unlike those in many mossy habitats, the **Chironomidae** comprised only 4.08% of the fauna, outnumbered by rotifers and nematodes. They concluded that the rip-rap rocks, covered with mosses, increased both stability and diversity of the streams.

Figure 58. ***Fissidens rigidulus***, a moss that houses abundant **Chironomidae** midstream in New Zealand. Photo by Bill & Nancy Malcolm, with permission.

Figure 59. ***Fontinalis antipyretica***, a moss where **Chironomidae** are dominant in the Czech Republic. Photo by Michael Lüth, with permission.

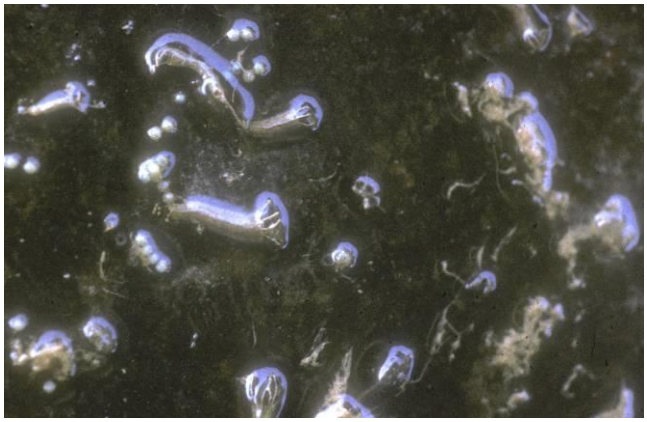

Figure 60. These tubes of **Chironomidae** are often present among mosses. The larvae live near the bottom of the moss clump and trap detritus in the net or use the moss as a trap, using the detrital matter for food. Photo by Janice Glime.

Smirnov (1961) concluded that no abundant insects fed on mosses in bogs, but ***Psectrocladius psilopterus*** (Figure 61) – a chironomid larva, ate the ***Sphagnum*** (Figure 62). There is some evidence that bryophytes may serve insects as emergency foods or provide an important part of the diet, albeit in small proportions.

Figure 61. ***Psectrocladius sordidellus*** emerging female adult. Larvae of ***Psectrocladius psilopterus*** eat ***Sphagnum***. Photo by James K. Lindsey, with permission.

Figure 62. ***Sphagnum capillifolium***, member of a genus that is eaten by ***Psectrocladius psilopterus*** in bogs. Photo by Blanka Shaw, with permission.

Although **Chironomidae** (Figure 1) feed predominately on the detritus among the mosses, they consume mosses as well (Kalachova *et al*. 2011). This consumption may actually be moss components of the detritus. Using acetylenic acids as biomarkers from the moss ***Fontinalis antipyretica*** (Figure 59), Kalachova *et al*. (2011) demonstrated this chemical group in the **Chironomidae**, especially in winter when other food sources, especially zoobenthos and biofilms, become scarce.

Parasite Protection?

Mosses might offer an advantage unknown in most habitats. They protect their guests from parasitic mites. In Luxembourg, two species of ***Chaetocladius*** (Figure 63) were free of water mite parasites (Stur *et al*. 2005). Stur *et al*. suggested that the semiterrestrial lifestyle of these insects among the mosses made them less available to the

mite larvae. On the other hand, moss dwellers like ***Tvetenia calvescens*** and ***T. bavarica*** (see Figure 64-Figure 65) did have mite parasites in the springs where they lived. Of the **Chironomidae** species examined, those free of mites lived in bryophyte habitats where the numerous generalist parasitic mites *Sperchon thienemanni* (see Figure 66) and *Atractides fonticolus* were not likely to occur.

Figure 63. ***Chaetocladius piger***, a member of a chironomid genus that seems to be protected from mites when it lives in wet, semiterrestrial mosses. Photo by J. K. Lindsey, with permission.

Figure 64. ***Tvetenia discoloripes*** larva, a bryophyte inhabitant. Photo by Walter Pfliegler, with permission.

Figure 65. ***Tvetenia discoloripes*** larva, a bryophyte inhabitant. Photo by Walter Pfliegler, with permission.

Figure 66. ***Sperchon*** cf. ***setiger***, member of a genus with parasites on **Chironomidae**. Photo by Yann, through Creative Commons.

Refuge in Bryophytes

Not only do the bryophytes provide a refuge among their leaves, but some Chironomidae use bryophytes to make a case and others **pupate** (Figure 67) among the leaves (Suren 1988). But Humphries and Frost (1937) found few pupae of **Chironomidae** (Figure 1) among the mosses in the River Liffey in any season, despite the huge numbers of larvae. Rather, most pupae are free-living in the open water (Armitage *et al*. 1995).

Figure 67. **Chironomidae** pupa, a rare find among bryophytes. Photo by Jason Neuswanger, with permission.

Tube Makers

It is not unusual for **Chironomidae** larvae to make tubes. However, ***Eukiefferiella endobryonia*** (Figure 68) is unusual (Imada 2020). It lives in streams among the leaves of ***Fontinalis dalecarlica*** (Figure 69) and ***Fontinalis novae-angliae*** (Figure 70) and feeds on the leaves (Figure 71). It makes its "tubes" (more like a case) for pupation by

binding together a case from the leaves of ***Fontinalis*** (Figure 72), a truly aquatic moss. The third instar larva may use feces of mature larvae to build its case (Figure 73), but the fourth instar larva uses ***Fontinalis*** spp. leaves exclusively and it remains attached to the apical shoot of the moss (Figure 74-Figure 75). The larvae pupate in this moss case. Debris and other materials are deposited at one end of the case as the larva changes into a pupa (Figure 76-Figure 77). There are few other chironomids that make tubes exclusively of plant materials.

Figure 68. ***Eukiefferiella endobryonia*** 4th instar larva. Photo by Yume Imada, with permission.

Figure 69. ***Eukiefferiella endobryonia*** habitat in a colony of ***Fontinalis dalecarlica*** growing on the sides of pebbles in a gently flowing inlet. Photo by Yume Imada, with permission.

Figure 70. ***Eukiefferiella endobryonia*** habitat among ***Fontinalis novae-angliae*** occurring in a rapidly flowing stream at Sparks Lane, Tennessee, USA. Photo by Yume Imada, with permission.

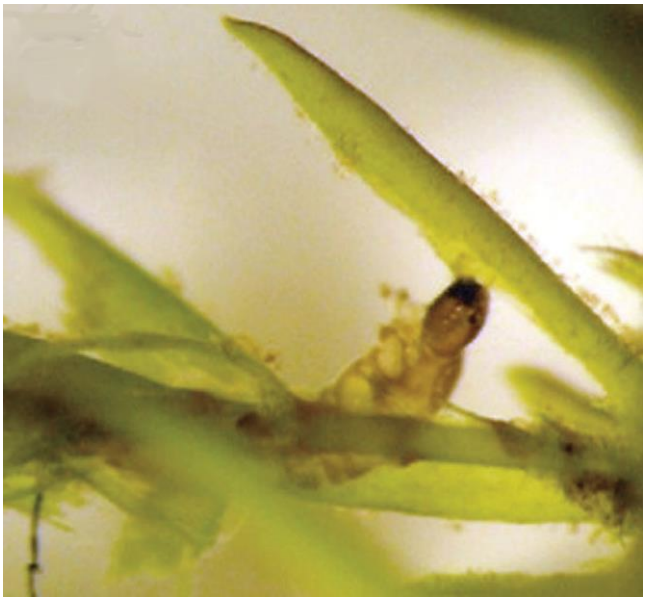

Figure 71. ***Eukiefferiella endobryonia*** fourth-instar larva feeding on leaf margin of ***Fontinalis dalecarlica***. Photo by Yume Imada, with permission.

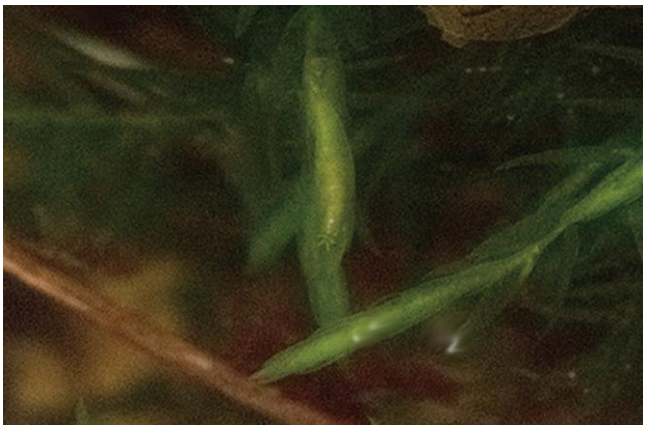

Figure 72. ***Eukiefferiella endobryonia*** early fourth instar larva with undulating body in tube. Photo by Yume Amada, with permission.

Figure 73. ***Eukiefferiella endobryonia*** tube of third-instar larva, mostly built from feces of mature larvae. Photo by Yume Imada, with permission.

Figure 74. ***Eukiefferiella endobryonia*** case of ***Fontinalis dalecarlica.*** Photo courtesy of Yume Imada.

Figure 75. ***Eukiefferiella endobryonia*** pupa in its case. Photo by Yuma Imada, with permission.

Figure 76. ***Eukiefferiella endobryonia*** dissected leaf-rolling cases. Photo by Yume Imada, with permission.

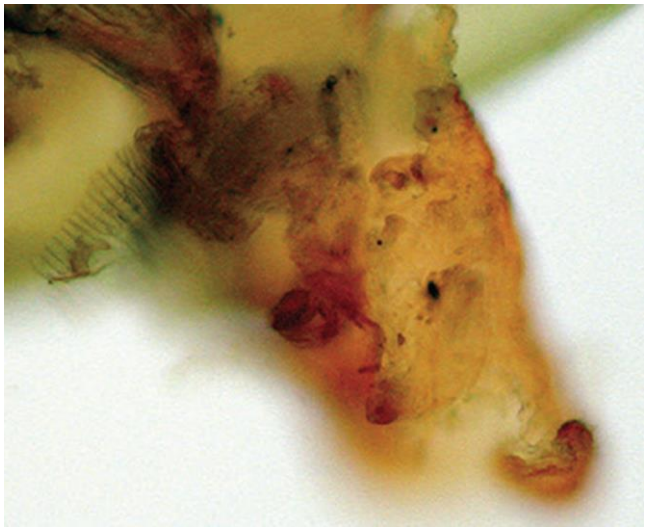

Figure 77. ***Eukiefferiella endobryonia*** amorphous, jelly-like silk mass spotted with detritus and diatoms, ripped off inner wall of end of pupal case. Photo by Yume Imada, with permission

Culicidae – Mosquitoes

Although most mosquitoes are small, they can range 3-15 mm long (Bartlett 2004a). They are distributed worldwide and the larvae live almost anywhere there is quiet water. These larvae are able to feed on algae, Protozoa, and organic debris that is filtered from the water. Only a few are predaceous.

Bryophytes are not typical habitats for the mosquitoes. Nevertheless, Elgmork and Sæther (1970) found that ***Aedes excrucians*** (Figure 78; a woodland mosquito that bites humans) occurred in bog pools and occasionally among ***Sphagnum*** mosses (Figure 79).

Figure 78. ***Aedes excrucians*** larvae, inhabitants among ***Sphagnum*** and bog pools. Note the posterior breathing tube that often hangs from the water surface. Photo by Donald S. Chandler, through Discover Life.

Figure 79. ***Sphagnum cuspidatum*** and bog pool, suitable habitat for larvae of ***Aedes excrucians***. Photo by Michael Lüth, with permission.

Simuliidae – Blackflies

These are small flies, 1-5.5 mm (Kits 2005). They are best known for their nasty bite that leaves the wound bleeding due to an injection of an anticoagulant, although most species get their blood meal from birds. Although they are more abundant at higher latitudes, their distribution is worldwide in rapid, cold water. They are filter feeders and must therefore live on the surface of the substrate.

In the right habitat, blackfly larvae occur in large numbers (Figure 80). Blackfly larvae require fast flowing water where they can get sufficient oxygen and trap their food with their large head fans. Carlson (1967) suggested that at depths within 10 cm of the surface, the bryophytes offer a preferred habitat for the **Simuliidae**. In suitable sites, they can be quite dense; *e.g.*, one blade of grass 1 cm wide and 15 cm long can hold 300-800 ***Simulium vittatum*** (Figure 81) larvae (Anderson & Dicke 1960).

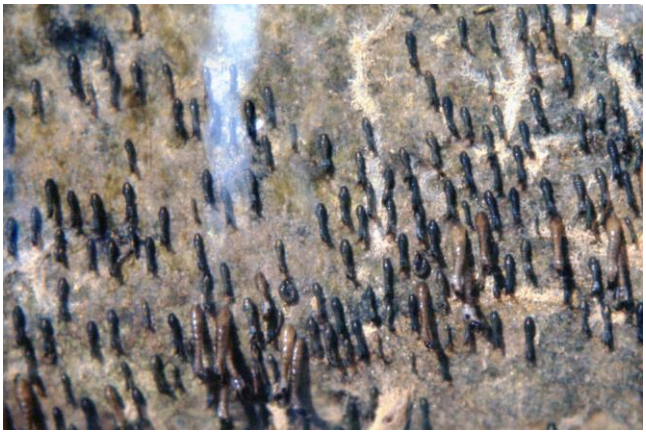

Figure 80. **Simuliidae** larvae on rock, showing how dense they can be. Photo by Janice Glime.

Figure 81. ***Simulium vittatum tribulatum*** complex larva, an abundant species on some bryophytes. Photo by D. S. Chandler <www.discoverlife.org>, through Creative Commons.

They are adapted to such sites by a circle of hooks on the abdominal posterior and on the prolegs, facilitating their anchorage (Arnold & Macan 1969). They furthermore produce silken threads that serve as anchors and that they use to cover the surfaces of stones to make a small mat to anchor themselves (Arnold & Macan 1969; Tarshis & Neil 1970). When water flow is stopped in a stream, larvae form both single silken threads and cables. The latter, supporting the greatest numbers of blackflies, reveal 25-50 threads with the larvae attached in concentric rings around the threads and cables (Tarshis & Neil 1970). The threads can be more than 1 m long and facilitate regaining the original position when falling from it or travelling to a new one (Rubtsov 1962). Tarshis and Neil (1970) observed a spectacular display of threads ranging 1-8 m long!

Many blackflies overwinter in the egg stage (*e.g.* ***Simulium venustum*** (Figure 82), ***S. vittatum*** (Figure 81) , but others hatch as early as December. Hatching of the eggs is apparently dependent on temperature, as noted in this family in Wisconsin, USA (Anderson & Dicke 1960). Larval development takes several weeks, 4-5 at temperatures of ~15-20°C, but the pupal stage is brief, lasting only 5-7 days. Wolfe and Peterson (1959) reported a unique use of stems of dead mosses to form the stalk on the pupal cocoon of ***Ectemnia invenusta*** (Figure 83). Depending on the local species, late summer and autumn often lack blackflies in bryophyte collections; at this time

some species are either in egg or adult stages (Anderson & Dicke 1960).

Figure 82. ***Simulium venustum verecundum*** complex, blackflies that overwinter as eggs. Photo by David S. Chandler, with permission.

Figure 83. ***Ectemnia invenusta*** larva, a blackfly that uses dead mosses to form its pupal stalk. Photo by Tom Murray, through Creative Commons.

Needham and Christenson (1927) reported **Simuliidae** from mosses in streams in northern Utah. In the Plitvice Lakes National Park in the Dinaric **karst** (landscape underlain by limestone eroded by dissolution, producing ridges, towers, fissures, sinkholes, *etc*.) region of Croatia, the **Simuliidae** showed a statistically significant preference for moss on **tufa** [porous limestone formed from calcium carbonate ($CaCO_3$) deposited by springs etc.] and pebbles (Čmrlec 2013). This family is known from every continent but Antarctica (Clifford 2014).

In their experiments on the effects of phosphorus on Arctic streams, Lee and Hershey (2000) found that the moss ***Hygrohypnum*** (Figure 56) increased, forming dense growths. As one might expect, this changed the structure of the insect communities. Whereas some may have benefitted from an increase in periphyton abundance as a food source, the **Simuliidae** were apparently not affected by these changes. Since these larvae live at the surface and collect food from the passing water, the increased habitat complexity of the mosses did not change the available habitat for them.

In a Polish river, blackflies were in greater numbers on the tracheophyte *Potamogeton* than on the brook moss ***Fontinalis*** (Figure 59) (Niesiołowski 1980). Niesiołowski attributed this to the differences in leaf size and position that permitted the blackflies to live both at the water surface and on any of the lower leaves of *Potamogeton*. Blackflies are restricted to the surface region of the substrate where they can use their head fans to filter algae from the passing water, and in mosses this prevents them from living in the interior of the moss clumps.

Crosskey (1990) describes larvae in this family, stating that they use mosses as larval food as well as a substrate. As adults they use the mosses for mating.

The blackflies do not seem to be able to sort the food flowing by them. Anderson and Dicke (1960) found that all the food available in the flowing water was also present in the gut. In addition to these, the guts contained the diatoms ***Rhoicosphenia*** spp. (Figure 84) and ***Cocconeis*** spp. (Figure 85). The latter is a common diatom adhering to moss leaves (pers. obs.).

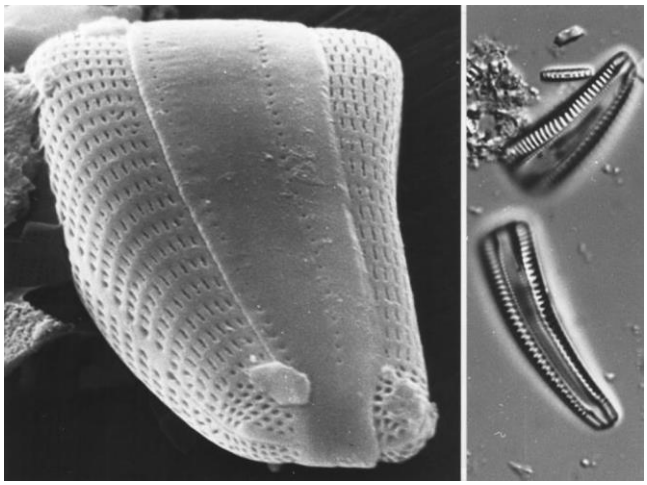

Figure 84. ***Rhoicosphenia abbreviata***, member of a genus that is food for moss-dwelling blackflies. Photo by Pauli Snoeijs, through Creative Commons <www.nordicmicroalgae.org>.

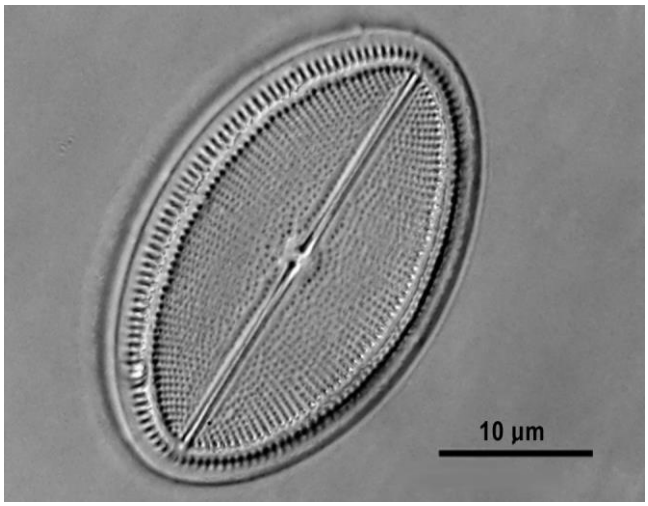

Figure 85. ***Cocconeis placentula***, a diatom that embeds itself in the surface of bryophyte leaves and also serves as food for blackflies in streams. Photo by Ralf Wagner at <http://www.dr-ralf-wagner.de/> (Mikroscopie).

Simulium

These larvae can be quite dense on their substrate. For example, ***Simulium pictipes*** is common in the eastern USA where larvae attach to bedrock of swift-flowing streams, especially below waterfalls (Kurtak 1974) where the water is well oxygenated. These larvae congregate, forming dense patches with as many as 50 individuals per cm^2. Members of this species, and most blackflies, overwinter as larvae and are among the most abundant insects in winter. Reisen and Prins (1972) found that ***Simulium*** increased in the drift as the temperature increased. This genus has a low tolerance for temperatures above 16°C.

Butcher *et al*. (1937) suggested that ***Simulium equinum*** (Figure 86) apparently does not occur among mosses because it was absent in the River Tees above Croft. But Frost (1942) found it among mosses in the River Liffey, Ireland, in alkaline waters, along with ***S. ornatum*** (Figure 87). In acid waters of the same river she found ***S. venustum*** (Figure 82) and ***S. latipes*** (Figure 88) on bryophytes. Pentelow (1935) likewise found ***S. equinum*** in alkaline waters. But in a different river he found ***S. ornatum***, likewise in alkaline water.

Figure 86. ***Simulium equinum*** *s.l.* adult, a blackfly whose larvae occur on mosses in some streams and not others in the same area. Photo by Malcolm Storey, Discover Life through Creative Commons.

Figure 87. ***Simulium ornatum*** / ***intermedium*** / ***trifasciatum*** adult, a blackfly complex whose larvae are common on bryophytes. Photo by Malcolm Storey through Discover Life.

Figure 88. ***Simulium latipes*** adult, a blackfly of mosses in acid waters. Photo by James K. Lindsey, with permission.

Simulium cataractarum (Figure 89), as its name implies, lives in waterfalls. It seems to play it safe, living primarily on the wet mosses on the rock wall beside the main waterfall Schroeder 1988).

Figure 89. ***Simulium cataractarum*** devouring an **Ephydridae** larva. Photo by Simon Pollard, Department of Biological Sciences, University of Alberta, Canada.

In studying blackflies in Utah, USA, Peterson (1956) found that **Simuliidae** avoid algae-covered rocks and sticks. Rather, the dominant ***Simulium*** species occur primarily on rocks that are covered with mosses and the alga *Vaucheria*. Peterson found that these larvae would scrape algae and other food items from the surrounding substrate. But when only slimy algal films cover the rock, they are unable to attach. In his study of New York, USA, blackflies, Jamnback and Stone (1955) found several bryological associates. ***Simulium fibrinflatum*** (Figure 90) occurred on mosses at several locations, but also occurred on twigs and other types of vegetation.

Figure 90. ***Simulium fibrinflatum*** larva, a moss-dweller in streams in New York, USA. Photo by Donald S. Chandler, with permission.

In the Appalachian Mountain streams this family is common among the bryophytes, repeating many of the species reported by other studies in North America and Europe. These include ***Simulium*** cf. ***gouldingi***, ***S. impar***, ***S. parnassum***, ***S. tuberosum*** (Figure 91), ***S. venustum-S. verecundum*** complex (Figure 82), and ***S. vittatum*** (Figure 81). The most widespread of these is ***S. tuberosum***, appearing among all the common bryophytes: ***Fontinalis dalecarlica*** (Figure 4), ***Hygroamblystegium fluviatile*** (Figure 5) **–** ***Platyhypnidium riparioides*** (Figure 6), and ***Scapania undulata*** (Figure 7).

Figure 91. ***Simulium tuberosum***, the most common blackfly on mosses and liverworts in Appalachian Mountain, USA, streams. Photo by Tom Murray, through Creative Commons.

The **Simuliidae** require a relatively rapid flow rate. For ***Simulium ornatum*** (Figure 87) this is a rate of at least 20 cm/sec in order to filter enough food items from the water using their head fans (Figure 92) (Harrod 1965). For ***Simulium***, these head fans catch algal cells, especially diatoms, but also trap fragments of mosses and leaves [Puri 1925; Percival & Whitehead 1929 (***S. reptans***); Jones 1949, 1950]. Fredeen (1960, 1964) fed several members of ***Simulium*** [***S. venustum*** (Figure 82), ***S. verecundum*** (Figure 82), ***S. vittatum*** (Figure 81), ***S. arcticum***] on three species of bacteria as food and concluded that bacteria form an important food base for these blackflies in some streams. In these experiments, ***Simulium arcticum*** did not develop past the last larval instar, but all the others reached the adult stage. ***Simulium venustum***, ***S. verecundum***, and ***S. vittatum*** are widespread and commonly abundant species (O'Kane 1926; Anderson & Dicke 1960); bryophytes are not a unique habitat for them.

Hynes (1970) noted that members of the genus ***Simulium*** are able to coexist due to developmental timing. ***Simulium reptans*** and ***S. variegatum*** exemplify such timing differences with large larvae of one coexisting with small larvae of the other. In this way they don't compete for the same food sizes.

Peterson (1956) observed the emergence of ***Simulium vittatum*** (Figure 81). These newly emerged adults took flight almost immediately when they broke through the surface tension of the water, but they soon alighted to dry their wings. Others [***S. vittatum***, ***S. decorum*** (Figure 93-Figure 94)] crawled out of the water onto various substrata to dry their wings before their first flight.

Figure 92. **Simuliidae** larva head showing head fans that are used to trap food. Photo by Bob Henricks, with permission.

Figure 93. ***Simulium decorum*** larvae, blackflies that crawl out of the water to dry their wings before flight. Photo by Whitney Cranshaw, through Creative Commons.

Figure 94. ***Simulium decorum*** pupa with thin cocoon. Photo by Whitney Cranshaw, through Creative Commons.

As one might expect for a fly whose larvae live on mosses, the adults use them for egg-laying sites (Baba &

Takaoka 1989). ***Simulium japonicum*** and ***S. rufibasis*** both laid eggs on bryophytes on a water-splashed boulder. These were laid individually in the upper 5 cm of water.

Females seem to have some difficulty in laying their eggs where there is sufficient oxygen because these locations have high water velocity. Peterson (1956) observed several that dived into the water and reappeared 70 cm downstream. Several were washed downstream. Some of these flies seem to have two options – dropping eggs into the water while in flight and letting them settle to the bottom or climbing/diving into the water and depositing the eggs on a substrate. Surely these flies fare better when they choose bryophytes for their egg-laying.

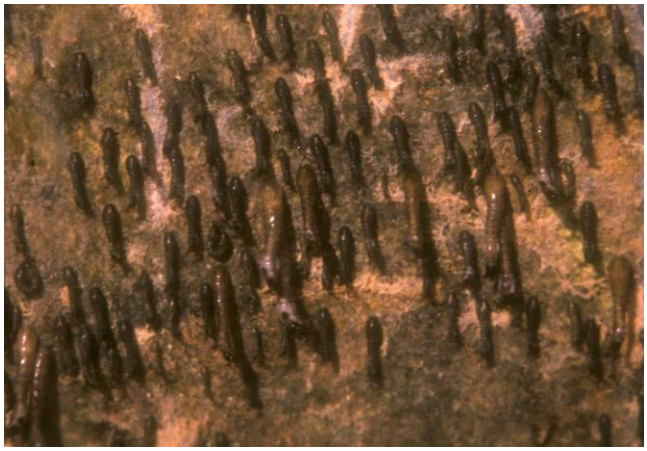

Figure 95. Blackfly (**Simuliidae**) larvae attach by tiny posterior hooks in fast current. Their heads with head fans point downstream and trap small particles of detritus, bacteria, algae, and even mosses for food. Photo by Janice Glime.

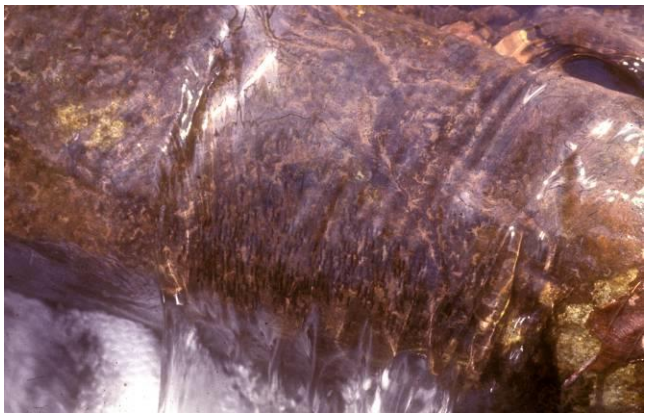

Figure 96. These blackfly larvae (**Simuliidae**) are just as common on these mosses as they often are on rocks in fast water. Larvae of the blackflies, **Simuliidae**, can use leaves of ***Fontinalis*** (Figure 59) in place of the usual net-like cocoon used to house the pupa. Photo by Janice Glime.

Prosimulium

Prosimulium was a common genus among the bryophytes in my Appalachian Mountain stream study. Krno (1990) likewise found it among bryophytes in the River Rajcianka in Slavakia.

Prosimulium fontanum lives in forest and bog-fed streams (Davies & Syme 1958) where ***Sphagnum*** (Figure 62) influences the *p*H in the latter and may be an important determinant of habitat suitability. This species commonly pupates in ***Fontinalis*** (Figure 59). Its cocoon is the least developed of all the ***Prosimulium*** species in three Ontario, Canada, streams.

It appears that this genus builds its cocoons based on flow rate and abrasive potential (Davies & Syme 1958). ***Prosimulium fuscum*** (Figure 97) lives in the fastest, most abrasive water of the three species studied and builds the strongest cocoon. The second in line is that of ***P. mixtum*** (Figure 98), an inhabitant of slower streams, that builds a somewhat weaker cocoon. Of these three, ***P. fontanum*** makes the weakest cocoon.

Figure 97. ***Prosimulium fuscum***, a species that lives on bryophytes in very fast water. Photo by Donald S. Chandler, with permission.

Figure 98. ***Prosimulium mixtum*** larva lives on bryophytes in slower streams than those of ***Prosimulium fuscum***. Photo by Donald S. Chandler, with permission.

The genus ***Prosimulium*** was common among bryophytes in Appalachian Mountain, USA, streams (Glime 1968). The most common was ***Prosimulium hirtipes*** (Figure 99-Figure 100, appearing among all the common mosses: ***Fontinalis dalecarlica*** (Figure 4), ***Hygroamblystegium fluviatile*** (Figure 5) – ***Platyhypnidium riparioides*** (Figure 6), and ***Scapania undulata*** (Figure 7). Others included ***P. magnum*** (mostly on ***Hygroamblystegium fluviatile***), ***P. mixtum*** (Figure 98), and ***P. rhizophorum***.

Figure 99. ***Prosimulium hirtipes*** among leafy liverworts. Photos by Janice Glime.

Figure 100. ***Prosimulium hirtipes*** is a common blackfly on stream mosses. Photos by Janice Glime.

Prosimulium hirtipes (Figure 99-Figure 100) avoids rocks with algal layers in a Utah, USA, stream, instead occupying those with mosses or the filamentous alga *Vaucheria*. In the mid-Appalachian Mountain streams, this species reaches its greatest abundance on the leafy liverwort ***Scapania undulata*** (Figure 7) (Glime 1968). In May one could find numerous pupae attached to the curled tips of the liverwort on both upper and lower surfaces. In June it was ***Simulium tuberosum*** that pupated there. This is a highly seasonal family, disappearing from June until the eggs hatch again in the cold water of late autumn (Davies *et al*. 1962).

Although some insects empty the gut rapidly, ***Prosimulium hirtipes*** (Figure 99-Figure 100) requires more than a week to empty its gut at 49-50°C (Davies 1949). Peterson (1956) found that at a lower temperature (4.4-10°C) it likewise takes more than a week for them to empty the gut. They can fill their guts in 20-26 hours (Davies 1949). This may permit them to digest intransigent materials that drift into their head fans.

Prosimulium hirtipes (Figure 99-Figure 100), ***P. tomosvaryi***, and ***P. subrufipes*** use moist terrestrial mosses, mostly ***Brachythecium rivulare*** (Figure 101), for egg deposition, laying them about 20 cm above the streams (Davies 1949). Unlike those of many of the **Simuliidae**, the eggs are deposited in batches, sometimes quite large ones with as many as 56 x 10^6 eggs. These eggs cannot survive complete desiccation, hence the need for mosses. Many eggs hatch in response to the diminishing temperatures and rainfall that saturates the mosses. But others actually stay in the mosses and hatch in spring. The first instar larvae lack the distinctive head fans needed for filter feeding. Instead, the first instar feeds as a scraper in a stage that lasts 5-11 days at 10°C.

Figure 101. ***Brachythecium rivulare*** at the edge of a stream where some species of blackflies lay eggs. Photo by Janice Glime.

Prosimulium kiotoense in a stream on Kyushu Island, Japan, likewise oviposits among mosses on riverbank rock surfaces (Baba & Takaoka 1991). Although the eggs are laid singly, so many females select the same site that the eggs soon form large, irregular masses. These blackflies select dense bryophyte cover 0-15 cm above the water instead of depositing eggs in the water. Eggs are laid in late April when the air temperature rises to approximately 15°C. It appears that this above water position is sufficient to keep the eggs moist while they develop, permitting the larvae to take advantage of the June rainy season (and perhaps warmer temperatures for development).

Cnephia/*Metacnephia*

I found larvae of ***Cnephia mutata*** (Figure 102) among mosses in my Appalachian stream study, but they were not as abundant as ***Prosimulium*** (Figure 97-Figure 100) or ***Simulium*** (Figure 86-Figure 95) (Glime 1968). Other aquatic bryophyte habitat studies I have found do not mention them.

Figure 102. ***Cnephia*** adult; larvae of ***C. mutata*** occasionally occur among mosses in mid-Appalachian, USA, streams. Photo by Sam Houston, with permission.

Meissner *et al*. (2009) conducted a fascinating experiment that explains the interesting relationship of the blackfly larvae of ***Metacnephia pallipes*** with the predator caddisfly ***Rhyacophila nubila*** (Figure 103) in Europe. In the absence of the predator, these blackflies show no preference between rocks and mosses. ***Rhyacophila nubila*** prefers stones only when the flow is slow. But, when ***R. nubila*** is present, the blackflies prefer mosses – the preferred habitat of the caddisfly! This seeming lapse in judgment by the blackflies must be examined in 3-d. The ***M. pallipes*** occupies the tips of branches, placing them at the surface of the moss clump, whereas ***R. nubila*** occupies the bases where they are protected from the rapid flow. When they attack the blackflies, the latter typically let go and enter the drift. If they are fast enough, they escape predation. They fully colonize artificial bryophytes (Finnturf) in only one day. The caddisflies are most successful in prey capture at intermediate velocities. For the blackflies to be safe from predation, they require velocities of 100 cm sec^{-1}. The blackflies are a preferred food because they have high fat reserves (Wotton 1982; Crosskey 1990) and in this case seem to be the only food (Meissner *et al*. 2009).

Figure 103. ***Rhyacophila nubila*** larva, a predator that cohabits with the blackfly ***Metacnephia pallipes*** on mosses. Photo by Niels Sloth, with permission.

Stegopterna

Pupae of the ***Stegopterna mutata*** complex (Figure 104-Figure 105) are often concealed among mosses in streams in Pennsylvania, USA (Adler & Kim 1986). Moving to mosses to pupate makes it easier for the adult to break through the surface tension to emerge.

Figure 104. ***Stegopterna***, a genus that often moves to mosses to pupate. Photo courtesy of the State Hygienic Laboratory, University of Iowa, with permission.

Figure 105. ***Stegopterna mutata-diplomutata*** complex, with larvae that move to mosses to emerge from streams in Pennsylvania, USA. Photo by Donald S. Chandler, with permission.

In Slovakia, in the River Rajcianka, Krno (1990) found the genus ***Odagmia***, a genus I have not found elsewhere in preparing for this chapter.

Thaumaleidae – Trickle Midges

These are little fellows, 2-4.5 mm long (Carr 2013). They live mostly in the temperate areas of both hemispheres where their larval habitats are predominantly in vertical, thin water films alongside waterfalls and torrents where they are able to graze on diatoms.

Curran (1927) described ***Thaumalea*** adults (Figure 106) as occurring along streams, particularly those bordered by mosses. In the Appalachian Mountains, USA, I occasionally found larvae of this genus (Figure 107) among the stream mosses (Glime 1968). They may be more abundant among bryophytes elsewhere – typical stream sampling methods are likely to miss them in this habitat.

Figure 106. ***Thaumalea*** adult, an occupant along streams bordered by mosses. Photo by Kirk C. Tonkel, through Creative Commons.

Figure 107. ***Thaumalea*** larva, an occasional bryophyte dweller. Photo by J. C. Schou, with permission.

Psychodidae – Moth Flies and Sand Flies

Larvae of this species are 3-10 mm long, but adults are smaller (1.5-4 mm) (Bartlett 2004b). They are worldwide,

but they are most common in the tropics. The larvae live mostly in organic sludge where they feed on algae, fungi, and bacteria, but a few wander into clean water where bryophytes may provide a habitat.

Usinger (1974) included mosses of quiet or slow-moving streams and splash areas among the typical habitats for members of this family in California, USA.

In Britain, the moss ***Leptodictyum riparium*** (Figure 108) has gotten the reputation of being a nuisance moss because of the **Psychodidae** and **Chironomidae** (Kelly & Huntley 1987). These insects breed in the organic and other particulate matter trapped by this moss in the brewery channels, causing swarms of insects.

Figure 108. ***Leptodictyum riparium***, a stream and lake moss that is home for such nuisance **Diptera** as **Psychodidae** and **Chironomidae**. Photo by Michael Lüth, with permission.

Thorup (1963) found ***Pericoma blandula*** (Figure 109), a detritus feeder, living among mosses in a Danish springs. Satchell (1949) reported breeding of ***Pericoma*** among damp mosses. It, like other moss dwellers, has only one generation per year (**univoltine**) (Thorup 1963). The temperature among the mosses in the springs has almost no annual variation. Omelkova and Ježek (2012) likewise found this widespread European species among mosses in the Czech Republic in both shaded and unshaded habitats.

Figure 109. ***Pericoma blandula*** adult female; larvae live among mosses. Photo by Walter Pfliegler, with permission.

Pericoma fallax is a moss dweller that occurs in Europe and western Siberia where it is common in both shaded and unshaded habitats of ponds, swampy meadows, bottomlands of brooks, and reservoirs. In the streams of the Appalachian Mountains, USA, its larvae are fairly frequent among ***Hygroamblystegium fluviatile*** (Figure 5) and ***Platyhypnidium riparioides*** (Figure 6) colonies but not among those of the leafy liverwort ***Scapania undulata*** (Figure 7) or the large moss ***Fontinalis dalecarlica*** (Figure 4) (Glime 1968).

Both larvae and pupae of ***Pericoma*** (Figure 110) live in damp sites at the banks of streams in the UK, with mosses being a common habitat, sometimes with several species in a small (several meters) area (Satchell 1949; Roper 2001). ***Pericoma albitarsis*** lives among mosses in streams and among wet mosses near waterfalls (Johannsen 1969). In a Tennessee, USA, springbrook, this species lives among mosses and algae (Stern & Stern 1969; Stern & Stern 1969). The larvae of this genus are substrate feeders that eat the path in front of them (Vaillant 1959). They are able to do this even on a moss substrate. Vaillant found larvae of ***Pericoma marginalis*** and ***Telmatoscopus*** sp. (Figure 111) on a dripping rock cliff among mosses where diatoms were abundant. Egglishaw (1969) reported a species of ***Pericoma*** as being restricted to moss. In the southern Appalachian Mountains, Haefner and Wallace (1981) found that densities of ***Pericoma*** were five times as high in moss-covered outcrops compared to non-moss areas of a first-order stream.

Figure 110. ***Pericoma*** larva, a frequent bryophyte dweller. Photo from <www.dfg.ca.govpng> through public domain.

Figure 111. ***Telmatoscopus*** (***Clogmia***) larva. Some members live on dripping cliffs among mosses. Photo by Ashley Bradford, through Creative Commons.

In the Ghyll woodlands of Sussex, UK, several other members of this family are moss dwellers (Roper 2001). These include ***Bazarella neglecta*** larvae among mosses around mill races and waterfalls. ***Bazarella subneglecta*** is an uncommon Eurasian species from hygropetric (water on a vertical surface) ones with moss cushions, spring areas, and brooks (Omelkova & Ježek 2012). Ježek *et al*. (2012) reported ***Peripsychoda fusca*** from Czech Republic and Slovakia wetland habitats that have moss cushions and leaf packs.

Larvae of the moth fly ***Sycorax silacea*** (see Figure 112) live on wet stones and mosses near cascades, springs, and "trickles" (Jung 1958; Andersen 1992). Omelkova and Ježek (2012) reported this species from European spring areas and from mosses in running water habitats and their "neighborhoods." The ornate larvae in this genus are protected from would-be predators by mimicking mosses (Roper 2001).

Figure 112. **Psychodidae** larva, a family that occurs among bryophytes in small numbers. Photo by Erin Hayes-Pontius, through Creative Commons.

Jungiella longicornis is widely distributed in Europe and western Siberia, living in both unshaded and shaded stream banks among moss cushions, as well as in ponds and forest seepages (Omelkova & Ježek 2012). ***Satchelliella crispi*** inhabits decaying organic matter in Europe, typically in leaf packs or moss cushions near springs and streams. ***Satchelliella pilularia*** is widespread in Europe, but is nevertheless relatively rare; its larvae live among mosses in running water of springs and streams from lowlands to mountains.

Ulomyia fuliginosa (Figure 113) is among the most common of European **Psychodidae** (Omelkova & Ježek 2012). It lives among mosses in running water where it associates with detritus and in springs, streambanks, marshes, swampy meadows, and forest pools.

Figure 113. ***Ulomyia fuliginosa*** adult, a species whose larvae live among mosses in running water. Photo by James K. Lindsey, with permission.

Berdeniella (Figure 114) larvae are also known to live among mosses (Troiano 1981) and are particularly abundant in alpine streams (Withers 2005). Wagner *et al*. (2011) contend that this genus lives exclusively among partly or totally inundated mosses at the shoreline of cold mountain streams in Central Europe, based on their study of the Breitenbach. In these habitats they found ***B. illiesi***, ***B. manicata***, and ***B. unispinosa***.

Figure 114. ***Berdeniella*** sp., as genus whose larvae live among alpine stream bryophytes, showing the posterior of the larva. Photo by Urma S. Kruus, with permission.

Summary

The two most common dipteran bryophyte dwellers are the **Chironomidae** and **Simuliidae**. The **Chironomidae** in particular can have many species within a single stream. **Chironomidae** have a wide range of habitats and temperatures and are tolerant of low oxygen and slow flow. **Simuliidae**, on the other hand, require cold temperatures and rapid flow with high oxygen content. **Chironomidae** eat mostly detritus that they can scavenge from that trapped by the bryophytes or available in the sediments, whereas the **Simuliidae** filter the detritus and microalgae from the water using their head fans.

Both families can overwinter among the bryophytes as larvae and emerge in spring or early summer. Both use the bryophytes for emergence, but the **Simuliidae** commonly pupate there whereas the **Chironomidae** are more common in open water as pupae.

Bryophytes can serve as a refuge from predators for both families. And in some cases, it appears that the bryophytes may protect the **Chironomidae** larvae from parasites, although the mechanism is unclear.

Other **Nematocera** of families of much less importance include the **Culicidae** (quiet water), **Thaumaleidae** (beside waterfalls), and **Psychodidae** (quiet or slow-moving water).

Acknowledgments

Douglas M. Davies verified the Simuliidae and Julian P. Donahue verified some of the remaining Diptera from my mid-Appalachian Mountain study. Eileen Dumire helped me pull the numerous **Chironomidae** from the bryophytes. She proofread the chapter and offered suggestions to make it clearer.

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CHAPTER 11-14
AQUATIC INSECTS: HOLOMETABOLA – DIPTERA, SUBORDER BRACHYCERA

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CHAPTER 11-14
AQUATIC INSECTS: HOLOMETABOLA – DIPTERA, SUBORDER BRACHYCERA

Figure 1. ***Limnophora*** sp. larva (**lower**) and pupa (**upper**) (**Muscidae**), occasional bryophyte inhabitants. Photo by Stephen Moore, Landcare Research, NZ, with permission.

DIPTERA – FLIES

Suborder Brachycera

This suborder is less aquatic than the **Nematocera**. Furthermore, few of its members use aquatic bryophytes. Nevertheless, it is a convenient way to break up the chapter into shorter segments.

Athericidae/Rhagionidae – Watersnipe Flies

The larvae of these flies occur in pristine streams with the adults nearby (Kits 2005). They include predaceous members that eat other invertebrates, including caddisflies, and saprophagous members on wooden debris (Athericidae 2014). The larvae are distinguished by **crochets** on their abdominal prolegs (Figure 2), permitting them to live in rapid montane streams and torrents without being washed away.

Figure 2. ***Atherix ibis*** larva showing crochets in two rows in each proleg. Photo by Urmas Kruus, with permission.

This family is not well represented among bryophytes. ***Atherix ibis*** (Figure 3) includes bryophytes among its substrates in streams (Neveu 1976). The larvae eat small invertebrates (McLeod 2005), most likely finding the bryophytes to serve as an adequate dinner table. In Carpathian streams, this species is positively correlated with stream order and warmer water temperatures (Bulánková & Duricková 2009). Its eggs are laid on overhanging leaves and hatched larvae slide into the water; the larvae are henceforth very sensitive to desiccation. They are, however, quite tolerant of human activity and pollution.

Figure 3. ***Atherix ibis*** larva, a stream-dweller that can be found among bryophytes. Photo by Niels Sloth, with permission.

In the acid streams in the Appalachian Mountains, USA, ***Atherix variegata*** occurred in all of the common moss habitats [***Fontinalis dalecarlica*** (Figure 4), ***Hygroamblystegium fluviatile*** (Figure 5), ***Platyhypnidium riparioides*** (Figure 6), and ***Scapania undulata*** (Figure 7)] (Glime 1968).

Figure 4. ***Fontinalis dalecarlica*** with capsules, home to ***Atherix variegata*** in Appalachian Mountain, USA, streams. Photo by Janice Glime.

Figure 5. ***Hygroamblystegium fluviatile***, home to ***Atherix variegata*** in Appalachian Mountain streams. Photo by Janice Glime.

Figure 6. ***Platyhypnidium riparioides***, home to ***Atherix variegata*** in Appalachian Mountain streams. Photo by Andrew Spink, with permission.

Figure 7. ***Scapania undulata***, home to ***Atherix variegata*** in Appalachian Mountain streams. Photo by Michael Lüth, with permission.

In the Plitvice Lakes National Park in the Dinaric karst region of Croatia, the **Athericidae** preferred moss on tufa (P <0.05, n = 12) (Čmrlec *et al*. 2013). These flies pupate on mosses, and that substrate is the preferred substrate for emergence of the adults (Thomas 1997; Čmrlec *et al*. 2013).

Spaniidae/Rhagionidae

This family, well known from records in amber, exhibits only scattered records throughout the world today (Arillo *et al*. 2009). Roper (2001) reported the bryophyte dweller ***Spania nigra*** (Figure 8), a snipe fly, from **ghyll** (deep ravine) woodlands in Sussex, UK (Roper 2001).

Dolichopodidae – Long-legged Flies

These are small (1-9 mm) flies with a worldwide distribution (Dolichopodidae 2015). The larvae are predominantly terrestrial, but there are also many semi-aquatic taxa that live in or near water margins. Some can even walk on the water surface. Larvae are typically predatory, although a few live in the stems of reeds and other monocots near water.

Figure 8. ***Spania nigra*** adult, a species with a larval bryophyte dweller in Sussex. Photo by Marko Mutanen through Creative Commons.

This family does not seem to be reported as a moss dweller, but it does occasionally live among mosses in the Appalachian Mountain, USA, streams (Glime 1968). I was able to identify ***Hydrophorus*** larvae (Figure 9-Figure 10) in these collections. But it is also possible that they fell in or got swept in by flooding.

Figure 9. ***Hydrophorus oceanus*** larvae, member of a genus that sometimes occurs among stream bryophytes. Photo by Hans Hillewaert, through Creative Commons.

Empididae – Dance Flies

These are small flies with a worldwide distribution and that can be aquatic, but can also live in semiaquatic habitats, in dung, in bird nests, among roots, and associated with fungi (Cresswell 2004). Larvae mostly feed on decaying matter, but also can be predatory.

Figure 10. ***Hydrophorus praecox*** adult, member of a genus that can be found among Appalachian Mountain stream bryophytes. Photo by James K. Lindsey, with permission.

The **Empididae** (Figure 11) are little flies, so it is not any surprise to find them among mosses as larvae. In fact, larvae and pupae of many species occur among mosses in streams (Ivković *et al*. 2007).

Figure 11. **Empididae**, a frequent larva on bryophytes in streams. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Because of their small size and the tedious process of sorting through moss samples, this family is not well known among the mosses and more species are likely to be found on close observation. Pusch and Wagner (1993) found and described the new species ***Bergenstammia aurinae*** in the eastern Alps where it lived among wet mosses in two small brooks with a steep elevation gradient but no glacial melt water.

In the Plitvice Lakes National Park in the Dinaric karst region of Croatia, the **Empididae** preferred moss on tufa and macrovegetation where they have shelter and food (Watson & Rose 1985; Nolte 1991; Linhart *et al*. 1998, 2002a, b, c; Ivković *et al*. 2007). Emergence was almost equal above substrates of moss on tufa, pebbles, and tufa with detritus (Ivković *et al.* 2012).

Suren (1991) experimented with artificial bryophytes in two New Zealand alpine streams. He found that whereas most insects had densities similar to that on natural bryophytes, the **Empididae** had lower densities on the artificial ones, suggesting that the bryophytes themselves have an important role for these larvae.

Fast-water Refuge

Those larvae that are truly aquatic stream-dwellers usually live among the mosses in fast water. Ivković *et al*. (2012) recorded the highest abundance of dance flies from Plitvice Lakes National Park, Croatia, in stream habitats that had moss, gravel, and particulate tufa with detritus and fast current. In Malaysia, larvae of ***Hemerodromia*** (Figure 12-Figure 13) live at least 10 cm beneath the water surface in the **hyporheic** zone (Grootaert 2004). They are sensitive to light and disappear from streams when the forest is gone. Light plays an important role in their mating – a behavior that earns them the name of dancing flies. Unlike many Diptera that rely on gills or spiracles, the aquatic larvae of ***Hemerodromia*** exchange oxygen directly from the water, whereas many other members of the family use spiracles positioned to be in direct contact with the air. Larvae are predacious and often feed on their cohabitants such as blackflies or **Chironomidae** (Vaillant 1951, 1967; Vaillant & Gagneur 1998; Grootaert 2004). The adults are small (3-5 mm) are mostly yellow or black and prefer boulders covered with moss or a splash zone where moisture loss is not a problem (Grootaert 2004). In Europe, ***H. praecatoria*** (syn. of ***Chelifera precatoria***?) live among mosses in nearly stagnant water (Bischoff 1924b; Johannsen 1969). In Belgium this species occurs in pools of ***Sphagnum*** bogs (Dipterainfo 2014). This same genus occurred among ***Fontinalis dalecarlica*** (Figure 4) in Appalachian Mountain, USA, streams (Glime 1968). The species resembled ***H. rogatoris*** and ***H. seguyi***.

Figure 12. ***Hemerodromia*** larva, a frequent bryophyte inhabitant. Photo courtesy of the State Hygienic Laboratory, University of Iowa, with permission.

Bischoff (1924a) reported that the genus ***Clinocera*** occurred (Figure 14-Figure 15) among mosses in swift streams. In Malaysia, the larvae, like those of ***Hemerodromia***, live at least 10 cm below the water surface in the hyporheic zone and exchange oxygen directly through the cuticle (Grootaert 2004). Sinclair (2000) described a new species, ***Clinocera gressitti*** (Figure 14), from mosses on submerged stones in New Zealand. Adrian Plant (pers. comm. 27 August 2014) observed that members of this genus often pupate (Figure 15) among the mosses.

Figure 13. ***Hemerodromia superstitiosa*** female adult, member of a genus with moss-dwelling larvae. Photo by Seth Burgess, through Creative Commons.

Figure 14. ***Clinocera*** larva, an inhabitant of mosses in swift streams. Photo from <www.dfg.ca.gov>, through public domain.

Figure 15. ***Clinocera nigra*** pupal exuvia. Photo by Adrian Plant, with permission.

In a springbrook in the Southern Alps of New Zealand, Cowie and Winterbourn (1979) found three zones of bryophytes. In the torrential waters near the middle of the channel, **Empididae** (Figure 11) were among the most abundant species living among ***Fissidens rigidulus*** (Figure 16). Not surprisingly, these were accompanied by several abundant species of **Chironomidae** (see Chapter 11-13b).

Figure 16. ***Fissidens rigidulus***, home for **Empididae** in torrents. Photo by Bill and Nancy Malcolm, with permission.

In a German stream, larvae of ***Wiedemannia bohemani*** (see Figure 17) were abundant in the middle reach, with many occurring in partly submerged mosses on stones, both at and below the water lever (Wagner & Gathmann 1996). Vaillant (1967) likewise found both larvae and pupae of ***Wiedemannia*** in streams and rivers of France, with adults remaining nearby on stones that were partially submersed. The larvae feast on the **Chironomidae** that are so abundant among mosses.

Figure 17. ***Wiedemannia bistigma*** emerging on stones. Photo by Adrian Plant, with permission.

Harper (1980) found that ***Hemerodromia*** (Figure 12-Figure 13), ***Neoplasta*** (Figure 18-Figure 19), and ***Roederiodes*** (Figure 20) in the Laurentian watershed, Quebec, Canada, typically inhabit the mainstream and the larger tributaries. These species usually prefer fast water with a substrate of moss and rubble.

Figure 18. ***Neoplasta*** larva, a bryophyte inhabitant. Photo from <dfg.ca.gov>, through public domain.

Figure 19. ***Neoplasta*** adult, a genus with larval bryophyte inhabitants. Photo by Adrian Plant, with permission.

Figure 20. ***Roederiodes recurvatus*** adult, a genus whose larvae are associated with mosses in fast water in the Laurentian watershed of Canada. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Hemerodromia (Figure 12-Figure 13) larvae occur primarily in lotic habitats and among mosses on stream

cobble (Merritt & Cummins 1996), but also live in mosses at or just above the water level (Brammer *et al*. 2009). Larvae of ***Hemerodromia*** consume blackfly larvae that are living on the mosses (Vaillant 1953). Some of these **Empididae**, especially ***Hemerodromia***, larvae have an interesting habitat choice, living in cases and nets of other insects. Larvae of the ***Hemerodromia empiformis*** complex have been found inside the tubes of the midge ***Rheotanytarsus*** (Figure 21-Figure 22) in southern California, USA. The last instar larvae and pupae of ***H. brevifrons*** have been found inside cocoons of **Simuliidae** (Figure 23) in a stream in Los Angeles County, California, USA. Pupae of a South American ***Neoplasta*** (Figure 18) can occur inside cocoons of caddisflies (Brammer *et al*. 2009). Thus their habitation of mosses may be indirect.

Figure 21. ***Rheotanytarsus exiguus*** larval tubes made by the moss inhabitant larvae, but these tubes also house the larvae of ***Hemerodromia empiformis***. Photo by D. N. Bennett, with permission.

Figure 22. ***Rheotanytarsus*** sp. larva from the above tubes. This genus inhabits mosses and other sites. Photo by Jason Neuswanger, with permission.

Figure 23. ***Simulium aureum*** pupa with cocoon where the empidid ***Hemerodromia brevifrons*** sometimes lives. Photo by Malcolm Storey, Discover Life, through Creative Commons.

Where Shall We Go for Dinner?

Some adult members of the family devour their food from invertebrates trapped by the surface film. ***Wiedemannia bistigma*** (Figure 24) adults climb about on floating algae for just this purpose (Laurence 1953). Like maggots on a road kill, the empidids gather in numbers on the carcass of a dead insect. This adult behavior may not be as effective for most larval bryophyte-dwellers because the bryophyte habitats are often in fast water.

Figure 24. ***Wiedemannia bistigma*** adult, a species whose larvae can live among stream mosses. Photo by Adrian Plant, with permission.

Empididae larvae include both predaceous and non-predaceous larvae (and adults) (Oldroyd 1964). Many species of the subfamily **Hemerodromiinae** live in streams where their predatory larvae live among mosses and on wet rocks (Gerson 1969; Roper 2001). Some members are predators on larval blackflies (Vaillant 1951, 1953; Sommerman 1962; Wirth 1983; Werner & Pont 2003).

Empididae in the Cold

The **Empididae** are particularly adept at surviving cold conditions, whereas most insects lack cold resistance (Irons *et al*. 1993). Nevertheless, they cannot survive temperatures even 1°C below zero. In Alaska many insects survive by moving away from a freezing front or living in one that will not freeze. The **Empididae**, like the **Chironomidae**, will spend the winter in a frozen habitat. The **Empididae** have a high survival rate under freezing and thawing conditions. The ice serves as insulation

against sub-zero temperatures, with flowing water remaining typically at about 0.8°C.

Oreogetonidae

The **Oreogetonidae** is a small family, a segregate from the **Empididae** (Bayless 2011). The larvae are freshwater carnivores (Cresswell 2004). The family is widespread, with a concentration in South America, but also occurring in North America, Europe (one species), Asia, Australia, and New Zealand (Oreogetonidae 2014).

The genus ***Oreogeton*** (Figure 25) associates with mosses, but they are sprawlers-burrowers that engulf their prey, including blackflies and caddisflies (Aquatic Insects 2008; National Park Service 2014). These prey insects may be the reasons they enter the moss realm.

Figure 25. ***Oreogeton*** sp. adult. Larvae in this genus are sprawler-burrowers among mosses, feeding on blackflies and caddisflies. Photo by Tom Murray, through Creative Commons.

Syrphidae – Hoverflies

These worldwide flies are mostly 10-20 mm long, but can range up to 35 mm (Bartlett 2004). Many of the terrestrial larvae live in ant nests, but some occur in bogs. The larvae are mostly predators, although the family include a wide range of food sources. Some aquatic members have a long breathing tube, earning them the name of rat-tailed maggots. ***Sericomyia borealis*** (Figure 26) larvae occur in pools of peat bogs (Bloomfield 1897).

Figure 26. ***Sericomyia silentis*** adult, member of a genus in which some larvae live in bog pools. This one, like many syrphids, is a bee mimic. Photo by Richard Bartz, through Creative Commons.

Ephydridae – Shore-flies

The name **Ephydridae** literally means "living on the water" (Moisset 2004). The larvae filter microorganisms, including bacteria, one-celled algae, and yeasts, but some are predators on **Chironomidae** larvae. They are small to medium in size (2.5-9 mm) and have a worldwide distribution.

This is not typically a bryophyte family. ***Discocerina*** (Figure 27) burrows into moss mats or lives among algae at the borders of streams, ponds, and lakes (Merritt *et al*. 1996). ***Gymnoclasiopa plumosa*** (see Figure 28) breeds in algae and mosses in the forest (Grünberg 1910).

Figure 27. ***Discocerina obscurella*** adult, a genus that burrows into moss mats at water's edge. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 28. ***Gymnoclasiopa taxoma*** adult. ***Gymnoclasiopa plumosa*** breeds in forest mosses. Photo from USFWS, through public domain.

Sciomyzidae – Marsh Flies

The **Sciomyzidae** family (Figure 29-Figure 30) has worldwide distribution. The adults are 5-10 mm long and

live around marshes, lakes, ponds, and wooded areas, but the larvae are aquatic (Leung 2004). These larvae feed on snails, either as predators or parasites. ***Poecilographa decora*** is the only American species in this genus (Usinger 1974). Its pupae are known from woodland mosses.

Figure 29. **Sciomyzidae** larva indicating spiracular disc. Photo by Stephen Moore, Landcare Research, NZ.

Figure 30. **Sciomyzidae** pupa; some species pupate among mosses. Photo by Stephen Moore, Landcare Research, NZ.

Agromyzidae – Leaf-miner Flies

The **Agromyzidae** are 1-5 mm long and are leaf miners (Murray 2005). Although these are mostly miners on tracheophytes, the **Agromyzidae** are known from liverworts from scattered locations around the world in such distant locales as the West Indies, Mexico, Peru, the Juan Fernandez Islands, New Zealand, and France (Spencer 1990).

The leaf miner ***Phytoliriomyza mesnili*** (see Figure 31) develops successfully on the floating liverwort ***Ricciocarpos natans*** (Figure 32) (d'Aguilar 1945). It also occurs on ***Riccia beyrichiana*** (Figure 33) where the larva feeds within the thallus, then pupates there. This miner is known exclusively from liverwort and hornwort thalli.

Figure 31. ***Phytoliriomyza melampyga*** larva showing leaf mine trail in a tracheophyte leaf. Photo by Malcolm Storey.

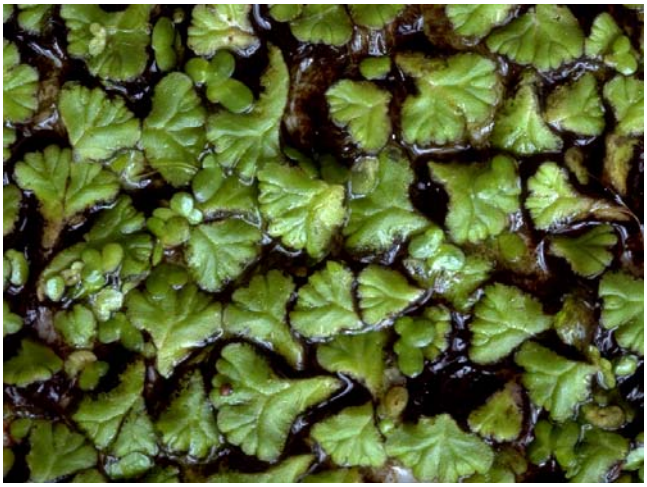

Figure 32. ***Ricciocarpos natans***, a suitable thallus for development of ***Phytoliriomyza mesnili***. Photo by Jan-Peter Frahm.

Figure 33. ***Riccia beyrichiana*** with eggs deposited in a cavity made on the left thallus. This liverwort species serves as home for larvae of the agromyzid fly ***Phytoliriomyza mesnili***. Photo by Malcolm Storey, DiscoverLife, Creative Commons.

Muscidae – House Flies and Kin

This is a worldwide family whose larvae live in dung, carrion, soil, nests, decaying vegetation, and less commonly among bryophytes in running water (Balaban & Balaban 2004). Adults range 2-14 mm in length (Muscidae 2015).

Many species of ***Limnophora*** (Figure 1, Figure 34-Figure 35) carry out their larval development among mosses and liverworts in running water where they are able to prey on **oligochaetes** (segmented worms such as earthworms) and small insect larvae (Glime 1968; Skidmore 1985; Roper 2001). In the Appalachian Mountain, USA, streams these occur most abundantly among clumps of ***Hygrohypnum luridum*** (Figure 36), especially in small waterfalls (Glime 1968). Axelrod and Vorderwinkler (1983) found that the European muscid fly ***Limnophora riparia*** (Figure 35) prefers mosses as a substrate; it is a good place to eat chironomid, blackfly, and other larvae (Wotton & Merritt 1988). This species typically lives among bryophytes in waterfalls, splash zones, and lake outlets. When the larvae were placed under water in enamel trays, all of them drowned within 24 hours. They burrow into any possible substrate to avoid light.

Figure 34. ***Limnophora*** adult, a genus where some members use mosses for egg-laying, larvae, and pupae. Photo by Luis Miguel Bugallo Sánchez, through Wikipedia Commons.

Figure 35. ***Limnophora riparia*** larva, a species that lays its eggs, develops, and pupates in mosses as a preferred site. Photo by Niels Sloth, through Creative Commons.

Figure 36. ***Hygrohypnum luridum***, home to ***Limnophora*** larvae in mid-Appalachian waterfalls. Photo by Hermann Schachner, through Creative Commons.

The larvae of ***Limnophora riparia*** (Figure 35) hatch from the egg as a third instar larva and are immediately ready to prey upon living invertebrates (Merritt & Wotton 1988). One of their peculiar adaptations is to attach the anterior of their prey and to remove and digest the contents of the head and body, leaving the cuticle and guts behind. The life cycle is synchronized with the main prey item, larvae of the blackfly ***Simulium noelleri***, and other invertebrate prey items so that there is always plenty of food for the developing larva. When the larva matures, it continues to select mosses for its site to pupate.

Badcock (1949) found that the muscid ***Calliophrys*** only occurs in mosses on the vertical face of a waterfall in the Welsh Dee.

Summary

The **Brachycera** are mostly terrestrial, but a few have associations with the aquatic bryophytes. Among these, the **Empididae** are probably the most common. Bryophytes seem to be important to them as they colonize bryophytes more readily than they colonize artificial bryophytes. Both larvae and pupae live among the bryophytes. And like the bryophytes, they are often in stream openings that don't freeze.

The most interesting family to a bryologist includes those few members of the leaf miners (**Agromyzidae**) that live exclusively in the tissues of thallose bryophytes – liverworts and hornworts. As such, the thalli provide both protection and food.

Some members of the **Ephydridae** burrow into the mosses at the borders of streams and ponds. **Sciomyzidae** larvae live in the water, but the pupae occur among woodland mosses. Even some **Muscidae** complete their larval development among aquatic bryophytes. Other families with a few members living in association with aquatic or predominantly wet bryophytes are **Athericidae**, **Spaniidae**, **Dolichopodidae**, **Oreogetonidae**, **Syrphidae**, and **Sciomyzidae**.

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CHAPTER 12-1
TERRESTRIAL INSECTS: HABITAT AND ADAPTATIONS

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CHAPTER 12-1
TERRESTRIAL INSECTS: HABITAT AND ADAPTATIONS

Figure 1. This tiny moving moss on the back of an insect is among the many unknown wonders awaiting us among the bryophyte-insect interactions. Photo courtesy of Aline Horvath.

Mosses are useful to the insect tribe, countless numbers of which find homes among their branches, and roam about in their shades as in mighty forests, looking with their thousand eyes upon the wonders of their leaves, and sunning their wings of purple and of gold, and burnishing their shining armour upon the polished columns of their urns. Frances Tripp, British Mosses, 1888.

Bryophytes can be so unique as to be the source of as yet undescribed species (Figure 1) and even genera of insects, as will be seen in the many orders of insects discussed in the following subchapters. They harbor numerous kinds of insects as well as other arthropods (*e.g.* Takaki 1957). And they provide habitat to protect insects all over the world (Schwarz *et al*. 1993) and in all kinds of habitats (Merrifield 1994).

Bryophytes as Habitat

Bryophytes not only provide a direct habitat for insects, but they alter the soil habitat beneath them. Gerson (1969) suggested that abundance of arthropods in the Antarctic is dependent on this soil alteration. Presence of moss can moderate the soil temperature and moisture and may in some cases discourage digging by would-be predators on soil organisms.

The bryophyte habitat is subject to the climatic and microclimatic differences dictated by elevation, distance from sea, topography, and latitude, resulting in arthropod community differences (Andrew *et al*. 2003). These differences extend to such limited habitats as that of epiphyllous liverworts (Lücking & Lücking 1998). Andrew and Rodgerson (1999) found that in the Tasmanian Mountains, site scale variation (2 km or less) is the major contributor to the bryophyte faunal diversity, seemingly more important than altitude.

Drozd *et al*. (2008, 2009) found that even higher taxonomic levels formed associations that indicate interactions between the presence of bryophytes and other microhabitat features. Sampling only seven bryophyte species in the Czech Republic, they obtained more than 55,000 specimens of arthropods. They show that the presence of bryophytes, the species of bryophytes, and the moisture levels are very important determinants of arthropod abundance. Nevertheless, abundance of arthropods was greater in the litter than in the moss cushions. Since many of the arthropods are searching for prey, the density of the moss cushions limits the size and requires agility to permit the arthropods to navigate to capture prey. Instead, the bryophytes serve as a refuge for prey organisms that can find their food there. These require only limited movement, making them relatively invisible to predators. This limited movement also leads to trap bias in the pitfall traps as these insects typically do not leave the safety of the bryophyte cushions. Weikel and Hayes (1999) pointed out that while the abundance of arthropods as potential food for birds may correlate positively with bryophyte cover, the bryophytes may act as hiding places, thus rendering most of them unavailable to the birds.

Drozd *et al*. (2007) found that about 25% of the insect species in forest floor communities (litter and mosses) are present only among the mosses. Moisture was the primary factor accounting for their distribution.

But, as Drozd *et al*. (2007) pointed out, our knowledge of the mosses as a food source is all but unknown. One of the means of identifying whether bryophytes are eaten is to recognize bryophyte fragments in the faeces or frass. Matthaias Nuss (pers. comm. 16 January 2008) provided me with an image of ***Tortula truncata*** with chewed leaves and what appeared to be frass on the plant (Figure 2). But then, how often can we identify the producer of the frass?

Figure 2. Possible insect frass on ***Tortula truncata***. Matthaias Nuss of the Museum für Tierkunde / Museum of Zoology, Dresden, Germany (pers. comm. 16 January 2008) suggests that these may be sclerified head or mandible parts that have an interesting attachment to the sporophytes of these mosses. There appear to be no silk threads, ruling out moth larvae, but **Byrrhidae** (**Coleoptera**) or some **Mecoptera** are good candidates. Photo courtesy of Robin Stevenson.

Drozdová *et al*. (2009) considered mosses to be unique habitats that could provide safe sites against predators. To test this hypothesis, they used living bait in a vertical gradient (surface level, moss cushions, bushes, tree trunks). The bait was living larvae of the blowfly ***Calliphora vicina***, a common prey item. The locations included leaves of blueberries (*Vaccinium myrtillus*), mosses [***Polytrichastrum formosum*** (Figure 3), ***Polytrichum commune*** (Figure 4), and ***Dicranella*** sp. (Figure 4)], and spruce (*Picea abies*) trunks. After 30 minutes of exposure the researchers counted the attacked and missing larvae and noted the presence of predators. The dominant predators were ants and spiders, the same as the forest floor in general (Drozdová *et al*. 2009). The predation rate inside the moss cushions was about the same as that in the litter, but the taxonomic groupings of the predators differed. Millipedes were the dominant predators in cushions of ***Dicranella*** sp and ***Polytrichum commune***, with spiders and beetles (**Carabidae** and **Staphylinidae**) following. Centipedes also occurred on the ground in areas of moss cushions under the *Vaccinium myrtilloides*. The highest predation occurred inside the ***Polytrichum*** cushions, with the same rate on the terminal parts of the plants as on the tree trunks. It appears that the structure of the moss cushion – the growth form – might be an important determinant of predation risk.

Figure 3. ***Polytrichastrum formosum***, a forest moss that houses a moderate number of insects. Photo by David T. Holyoak, with permission.

Figure 4. ***Polytrichum commune***. ***Polytrichum*** cushions can be home to numerous beetle species. Photo by A. J. Silverside, with permission.

Figure 5, ***Dicranella heteromalla*** with capsules, a species that is home to millipede predators. Photo by Michael Becker, through Creative Commons.

We aren't always sure why or how bryophytes contribute to the habitat needs of insects, but there is certainly evidence that they make a difference. Pavel *et al*. (2007) used pitfall traps in the Czech Republic to compare the beetles (**Coleoptera**) in forest communities with and without a moss layer. With the caveat that there is not necessarily a cause and effect relationship, an accumulation of such studies do indicate that it is worth exploring the role of the bryophytes. In this case, two traps were placed in ***Polytrichum*** (Figure 4) cushions and two were at least 10 m away from the nearest cushions at each of three sites. In their collections, beetles reached the highest numbers among the insects, with 56 species and the greatest abundance. Overall, they found a higher insect species richness in the moss communities, with ~25% of the insect species only occurring among the mosses. Not surprisingly, moisture was the most important environmental character affecting habitat preference, but presence of a moss layer was not significant. Only one of the species was **bryophagous** (bryophyte consuming), a member of the beetle family **Byrrhidae** (Figure 6). Especially in drier regions, the insects tended to inhabit the moss cushions, behaving as **bryobionts**.

In the Spitsbergen coastal tundra, Bengston *et al*. (1974) found 268,000 insects on the wet moss tundra, compared to 518,000 on grassland. The abundance of major insect groups were similar between the Spitsbergen tundra and high alpine areas of southern Norway.

In the Czech Republic, Božanić *et al*. (2013) used heat extraction from bryophytes to determine the effects of species of bryophytes and environmental factors on the animals present. In these samples they found 45 species of invertebrates among the 15 bryophyte species examined. Surprisingly, few were insects, all in the **Formicidae** (4 species of ants). Rather, there were 9 species of centipedes, 7 of millipedes, 4 of pseudoscorpions, 6 of isopods, 4 of harvestmen, 6 of earthworms, and 5 of spiders. ***Brachythecium oedipodium*** (Figure 7) had the richest assemblages of invertebrates. These numbers are probably minimal as some bryophyte dwellers do little moving and may die before escaping the heat within the bryophyte clump in the funnel and heat separation apparatus. The ones found are all able to move rather quickly, so this may explain the absence of bugs, beetles, and other insect groups. The type of substrate and height above ground proved to be the most important factors affecting the invertebrate distribution.

Figure 6. ***Cytilus sericeus*** (**Byrrhidae**) adult on mosses. Photo by S. Rae, through Creative Commons.

Figure 7. ***Brachythecium oedipodium***, home to a rich assemblage of invertebrates. Photo by Michael Lüth, with permission.

At McKenzie Table Mountain Preserve in California, USA, Bettis (2008) found that the moss fauna on two species of **Grimmia** (Figure 8) were mostly tardigrades, mites, springtails, and midge larvae. Studies of bryophyte fauna commonly indicate that spiders (**Araneae**), springtails (**Collembola**), and mites (**Acari**) are the most common fauna (von der Dunk & von der Dunk 1979; Kinchin 1990). Even on Signy Island in the maritime

Antarctic, the mites and springtails predominate (Usher & Booth 1984). The upper, green moss communities differed from the lower, dead moss communities. The same species tended to occur in both layers, but the proportions differed.

Figure 8. ***Grimmia pulvinata*** with capsules, home to tardigrades, mites, springtails, and midge larvae in California, USA and elsewhere. Photo by Javier Martin, through Creative Commons.

Von der Dunk and von der Dunk (1979) listed the arthropods in clumps of five species of mosses in March to May, including counts (Table 1). In addition to unidentified larvae, they listed the **Collembola *Sminthurinus*** (Figure 9), ***Xenylla*** (Figure 10), and ***Tomocerus*** (Figure 11-Figure 12) as well as thrips.

Figure 9. ***Sminthurinus aureus*** f. ***ochropus*** on mosses, member of a springtail genus that is common among mosses in spring. Photo by Andy Murray, through Creative Commons.

Figure 10. ***Xenylla*** sp. among mosses. Photo by Andy Murray, through Creative Commons.

Figure 11. ***Tomocerus*** sp. juvenile on mosses. Photo by Andy Murray, through Creative Commons.

Figure 12. ***Tomocerus minor*** , member of a genus that is common among mosses. Photo by Andy Murray, through Creative Commons.

Table 1. Number of insects found in moss polsters in Germany in March to May. From von der Dunk & von der Dunk 1979.

	Rhytidiadelphus	***Scleropodium***	***Hypnum***	***Plagiothecium***	***Brachythecium***
Sminthurinus	46	52	-	-	-
Xenylla	4	2	7	106	-
Tomocerus	-	-	1	-	4
thrips	+	+	+		+

Nutrients in the ecosystem affect the types of plants that will grow there, and bryophytes seem to have an aversion to high nutrients. Richardson *et al*. (2002) experimented with nutrients and their effects on plant communities and their insect herbivores in a Scandinavian sub-Arctic dwarf shrub heath. After nine years of nutrient enrichment, the subordinate plant functional groups (grasses and mosses) experienced greater effects than did the dominant dwarf shrubs. The insect herbivores showed evident changes in abundance. The biomass changes in the

grasses and mosses contributed more to these insect changes in biomass and species composition than did the shrubs. One moss-eating species of **Heteroptera** in the fertilized plots dropped to as little as 6% that of the control plots. The abundance of grass specialists in **Homoptera** in fertilized plots, on the other hand, reached 400% that of controls. This study emphasized the importance of the subdominant plant species in driving the insect species composition of the habitat.

Temperature Relations

Because of their construction with lots of air spaces, bryophytes can act like a fluffy winter quilt. They are able to buffer temperatures with these trapped air spaces (Soudzilovskaia *et al*. 2013). In some instances, they may remain warmer from reradiated heat from rocks or soil. In other cases their capillary water may cool them by evaporative cooling. Differences between bryophyte species comply with physical laws and can be explained by differences in mat thickness and moisture content. There are, however, few data sets to evaluate the extent of this role in a variety of ecosystems. Some of these differences are provided in Chapter 10-1 on Temperature in Volume 1.

Of course food is a problem in winter, but some insects are able to feed on alternate food sources. ***Diamesa*** sp. (**Diptera: Chironomidae**; Figure 13) is a cold-tolerant insect that lives on a glacier in the Nepal Himalayas (Kohshima 1984). This flightless insect is able to walk on the surface and in small cavities beneath the glacier. The larvae feed on Cyanobacteria and other bacteria, permitting this species to spend its entire live in the glacier. And it is still active at -16°C. While this is not a bryophyte dweller, it illustrates the ability of insects to survive in cold habitats, such as those in the Arctic and Antarctic, and to subsist on foods like bacteria and Cyanobacteria that are available among the bryophytes.

Figure 13. ***Diamesa bohemani*** larva, member of a genus in which at least one species is able to survive on glaciers and feed on Cyanobacteria and bacteria. Photo from NTNU Museum of Natural History & Archaeology, through Creative Commons.

Preparation for Winter

As we noted in the aquatic insect chapter, insects can avoid freezing damage in two ways (Duman *et al*. 1991). The most flexible means is to obtain freeze tolerance, permitting the insect to survive formation of ice on the outside of the body. The second mechanism is to avoid freezing. The latter can be subdivided into physiological mechanisms that prevent the insect from freezing by altering the freezing point of the organism or preventing ice nucleation through manufacture of antifreeze proteins (Duman *et al*. 2004). The other is a behavioral adaptation that places the insect in a place where it is protected from freezing (Duman *et al*. 1991).

Bryophytes are often a winter refuge or site of hibernation for insects. The bryophyte offers insulation against the wind and cold. Under the snow, the dark color of most bryophytes absorbs heat from the light that is able to penetrate the snow. Nevertheless, bryophytes may be exposed to severe cold before the snow arrives or after it melts in spring. Hence, their inhabitants still require some sort of protection from the cold.

Storey and Storey (1992) listed two stresses that can prevent winter survival in terrestrial insects. The obvious one in many places is lack of food, but some insect larvae are able to feed on the bryophytes. Others may survive as eggs or pupae, stages in which there is no feeding. Some insects compensate for the lack of food by accumulating large lipid and carbohydrate reserves in the body fat in preparation for winter (Storey & Storey 1992). Others enter into a state of reduced metabolic rate (**quiescence**) or arrested development (**diapause**) in which they can rely on limited food reserves.

The second winter stress is tissue damage at low temperatures, especially freezing (Storey & Storey 1992). Insects have two options to survive in areas that attain sub-freezing temperatures: **freeze avoidance** and **freeze tolerance** (Bale 2002). Freeze avoidance includes life cycle adaptations that do not require the insect to be present during the cold period. For some, this is through migration. For others, it is finding warmer locations such as deep soil, in the water, or even among deep mosses. But insects also can have physiological means of freeze avoidance while existing in locations with sub-zero temperatures.

Protein ice nucleators (PINs) limit supercooling and induce freezing (Duman 2001). When the nucleating proteins are internal, a small size can help to prevent the formation of large crystals. In insects, freeze-tolerant species produce PINs in the hemolymph. These allow freezing in the hemolymph at temperatures just below freezing and inhibit freezing within the cells. In some cases, these PINs are "removed" in the winter, promoting supercooling. **Antifreeze proteins** (AFPs) prevent freezing. One beetle has AFPs in the hemolymph and gut that inhibit the ice nucleators in winter.

One theory of freeze avoidance in insects is that of **heterogeneous nucleation**. However Zachariassen *et al*. (2004) provide evidence that it is water volume that determines the nucleation temperatures in freeze-avoiding insects. The relationship between the aqueous solutions and the particular freeze avoidance displayed behaves more like that of homogeneous nucleated samples.

One of the strategies to survive winter is the ability to **supercool** (Holmstrup *et al*. 2002). This ability seems to have evolved at the same time as the ability for insects to retain body water in dry environments. But soil invertebrates are far less resistant to desiccation than the above ground insects. It is likely that bryophyte dwellers are more like the soil invertebrates but in some cases may find greater moisture among bryophytes. Soil invertebrates

dehydrate in frozen soil; only a few degrees of supercooling causes substantial water loss which continues until the vapor pressure of body fluids equals the vapor pressure of the surrounding ice. At this point, tissue ice formation is eliminated and the invertebrate can survive subzero temperatures. But the Arctic soil invertebrates do not base their winter survival on this method of supercooling. Rather, they dehydrate to equilibrate their body-fluid melting point to that of the ambient temperature. This method works even in the extreme cooling rates of the polar soils.

For those insects that are sensitive to freezing, but still exhibit cold hardiness, their survival is typically achieved through **supercooling**, with some exhibiting supercooling points to below -25°C (Zachariassen & Husby 1982). These low non-freezing temperatures are accomplished through polyols and proteinaceous thermal hysteresis antifreeze agents that reputedly prevent the growth of ice crystals down to approximately -10°C. This prevention is increased dramatically when the crystal size is diminished. This added ability to prevent crystal formation permits them to live through temperatures as low as -30°C. In such cases, the insects can survive even in exposed areas where the snow does not accumulate.

Freeze tolerance in terrestrial insects occurs primarily among the **Coleoptera** (beetles), **Lepidoptera** (moths & butterflies), **Diptera** (flies), and **Hymenoptera** (bees & ants) (Storey & Storey 1992), whereas only the **Diptera** seem to have any tolerance to freezing in the aquatic stage (Moore & Lee 1991). Freeze tolerance may require preparation or it may be present year-round.

Freeze tolerance is energetically expensive and carries risks of ice crystal damage or other physical damage. The insect furthermore must survive osmotic stresses when water and solutes are rapidly redistributed across cell membranes during freezing and thawing periods. And part of this strategy is extracellular freezing that can damage membranes, not to mention the obstruction of oxygen flow to the body.

Freeze avoidance is the less expensive strategy and permits insects to be active under the snow where the snow provides suitable insulation (Storey & Storey 1992). Insects in cold environments further avoid freezing by the presence of hairs and dark body colors (Danks 2004), the former to insulate and the latter to absorb heat on sunny days. The insects complement these physical adaptations by behavioral adaptations – being active on sunny days and going to protected locations when it is getting cold (Danks 2004, 2005). Danks (2007) discusses their responses, including dispersal, habitat selection, habitat modification, resistance to cold, dryness, and food limitation, recognition of environmental signals, diapause, modifications to developmental rate, life cycle patterns that include multiple alternatives within the species, variation in phenology and development, and tradeoffs among these.

The behavioral escape of freezing could be to burrow into the ground below the frost line, go into decomposing material that generates heat, or find some other protected location locally. But for a few insects, this escape is a migration to a warmer climate, as is well known for the Monarch butterfly.

Bryophytes may come into the picture for some of the insects that are able to eat them. Cold induces changes in membranes and protein structure in insects due to phase changes in the molecules, changes in electrolyte concentrations and other solutes in body fluids, and changes in metabolism (Ramløv 2000). In some cases, animals switch diets prior to winter, some of which may include bryophytes (Prins 1982). This usefulness of such a behavior among insects remains unknown.

We know that bryophytes are rich in **arachidonic acids** that help to keep membranes pliable (Hansen & Rossi 1991). Insects produce little or no arachidonic acid (McPartland *et al*. 2001). Nevertheless, ladybird beetles (*Coleomegilla maculata*; Figure 14-Figure 15) have their highest proportion of arachidonic acid in the coldest part of winter (Zar 1968). Thus, a winter switch to bryophytes by some insects seems to be a reasonable hypothesis, and a potential source of arachidonic acid.

Figure 14. ***Coleomegilla maculata*** larva, a species with its highest concentrations of arachidonic acid in the coldest part of winter. Photo by Tom Murray, through Creative Commons.

Figure 15. ***Coleomegilla maculata*** adult, a species with its highest concentrations of arachidonic acid in the coldest part of winter. Photo by Tom Murray, through Creative Commons.

Whether arachidonic acids help in cold resistance for insects or not, they may help to keep membranes pliable for movement. Although Prins (1982) demonstrated a relationship with bryophytes in the diet of vertebrates, arachidonic acid, and winter survival, and we know that insects typically have quantities of the acid in their tissues (Dadd & Kleinjan 1979; Stanley-Samuelson & Dadd 1983), there does not yet seem to be research to demonstrate this relationship between arachidonic acid, winter tolerance, and insects. The closest evidence is that arachidonic acid enables the mosquito *Culex pipiens* to fly when it emerges as an adult (Dadd & Kleinjan 1979).

Arachidonic acid may not be the only chemical change in preparation for winter. Low temperatures not only affect the insects and cause different cell and membrane chemicals to initiate, the bryophytes also produce different chemicals or different concentrations when the temperatures drop. In ***Rhytidiadelphus squarrosus*** (Figure 16) and ***Eurhynchium striatum*** (Figure 17) there is a switch from 30% **arachidonic acid** (AA) and 5% **eicosapentaenoic acid** (EPA) to higher percentages of EPA, **α-linolenic acid**, and **dihomo y-linolenic acid**, accompanied by a slight decrease in AA and **linoleic acid** (Hansen & Rossi 1991). This particular study does not support the hypothesis that AA increases in bryophytes in preparation for winter, but it is likely that the bryophytes still have higher concentrations of arachidonic acids than tracheophytes at those temperatures or any time (Herbert & Prins 1982; Hartmann *et al*. 1986; Groenewald & Van der Westhuizen 1997; Kajikawa *et al*. 2008).

Figure 16. ***Rhytidiadelphus squarrosus***, a species that decreases in arachidonic acid in winter. Photo by Michael Lüth, with permission.

Figure 17. ***Eurhynchium striatum*** with a capsule, a species that decreases in arachidonic acid in winter. Photo by J. C. Schou, with permission.

Field biologists often consider winter to be a "down" season when insects are inactive, and therefore it is not a useful season for field work. But insects must find some way to survive winter and pass their genes to the next generation. Many do this as eggs or pupae. And bryophytes seem to be an ideal place for both, at least for some insects. They provide protection against easily damaged tissues of pupae when larger animals walk or climb about, they hide them from predators, they decrease the threat of desiccation, and they provide insulation. And for active insects, they may provide food directly or through other organisms that live among the bryophytes. Surely many species spend their winters there in this bryophytic safe site.

But little literature exists on the bryophyte as an overwintering home. Not only is this season less conducive to field study, but even those who do collect are faced with a daunting task of identification. Pupae and eggs must be matched with adults to avoid the danger of creating new species for what is simply a different life cycle stage. That requires rearing to maturity, a special challenge for eggs. And someone needs to have done that already if there are to be any keys or descriptions to aid identification. Hence, even those collections that are made rarely see publication due to the lengthy process of putting names to the organisms.

Most taxonomic treatments on insects give only general habitats for the insects, and often I wonder if there wasn't a moss involved, as food or shelter, but unnoticed, or at least unreported, by the collector. Treatments of forest floor insects often compare soil and litter organisms, and even those on rocks, but no mention is made of mosses, although they are often lumped with litter.

The use of bryophytes on a phenological calendar is demonstrated by The Entomologist's Calendar (Samouelle 1819). Those arthropods living on or under mosses in January were ***Philosia muscorum*** (**Isopoda**; Figure 18), ***Cylindroiulus londinensis*** (**Diplopoda**), ***Cylindroiulus punctatus*** (Figure 19), ***Geophilus acuminatus*** (**Chilopoda**; see Figure 20), ***Siro rubens*** (**Opiliones**; see Figure 21), ***Neobisium carcinoides*** (**Pseudoscorpiones**; Figure 22), ***Cychrus caraboides*** (**Coleoptera**; Figure 23), ***Acropagus glabricollis*** (name no longer in use); in February ***Bryaxis haematica*** (**Coleoptera**; species name no longer in use; see Figure 24), ***Staphylinus morio*** (**Coleoptera**; see Figure 25); in March ***Gyrohypnus punctulatus*** (**Coleoptera**; Figure 26), ***Chlaenius prasinus*** (Figure 27), ***Tachinus analis*** (**Coleoptera**), ***Tachyporus analis*** (**Coleoptera**), ***Choleva oblonga*** (**Coleoptera**), ***Catops sericeus*** (**Coleoptera**; species name no longer in use; see Figure 28); in April ***Staphylinus aenoecephalus*** (**Coleoptera**; species name no longer in use), ***Staphylinus decorus***; species name no longer in use; in May ***Dasytes ater*** (**Coleoptera**; species name no longer in use; see Figure 29); in June – November no moss records; in December ***Tachyporus chrysomelinus*** (**Coleoptera**; Figure 30). This change from winter to summer suggests that the bryophytes offer these insects something in winter, whether it is only shelter, or there is also a food source.

Figure 18. ***Philoscia muscorum***, an isopod that can be found under mosses in January in Europe. Photo by Africa Gomez <abugblog.blogspot.com>, through Creative Commons.

Figure 19. ***Cylindroiulus punctatus***, a millipede that can be found under mosses in January in Europe. Photo by G. Drange <Biopix>, through Creative Commons.

Figure 20. ***Geophilus flavus*** (centipede) on moss protonemata. ***Geophilus acuminatus*** can be found under mosses in Europe in January. Photo by Anthony Barber, through Creative Commons.

Figure 21. ***Siro*** sp. on moss; ***Siro rubens*** occurs under mosses in January in Europe. Photo by Marshal Hedin, through Creative Commons.

Figure 22. ***Neobisium carcinoides***, a pseudoscorpion species that spends January under mosses in Europe. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 23. ***Cychrus caraboides*** adult, a species that occurs under mosses in January in Europe. Photo by Siga, through Creative Commons.

Figure 24. ***Bryaxis bulbifer*** adult; ***Bryaxis haematica*** occurs under mosses in February in Europe. Photo by Christoph Benisch <kerbtier.de>, with permission.

Figure 25. ***Staphylinus*** sp. adult; ***Staphylinus morio*** occurs under mosses in February in Europe. Photo by Alvesgaspar, through Creative Commons.

Figure 26. ***Gyrohypnus punctulatus*** adult, a species that occurs among mosses in March in Europe. Photo from Naturalis, Biodiversity Centre, through Creative Commons.

Figure 27. ***Chlaenius prasinus*** adult, a species that occurs among mosses in March. Photo by Mike Quinn, through Creative Commons.

Figure 28. ***Catops tristis*** adult; ***Catops sericeus*** occurs under mosses in March in Europe. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 29. ***Dasytes plumbeus*** adult. "***Dasytes ater***" is associated with mosses in May. Photo by Sarefo, through Creative Commons.

Figure 30. ***Tachyporus chrysomelinus*** adult on bryophytes. Photo by Malcolm Storey, through Creative Commons.

Water Relations

Water is often the limiting factor for terrestrial insects (Tauber *et al*. 1998; Hayward *et al*. 2004). It can account for the importance of other variables such as elevation (Lee & La Roi 1979). Tauber *et al*. (1998) suggested that moisture was important in determining insect seasonality, stimulating diapause, modulating development and reproductive rates, and providing a cue for seasonal events. Bryophyte species are also limited by moisture, thus creating different moisture regimes available to the ground-dwelling and arboreal insects (Whittaker & Niering 1975; Slack 1977; Lee & La Roi 1979; Vitt 1991; During 1992; Wolf 1994; Li & Vitt 1995; Vitt & Belland 1997).

Fragmentation and Corridors

One of the causes of declines in species is the inability to disperse due to unfavorable habitat between suitable locations. Gonzalez *et al*. (1998) found that when patches of suitable habitat were connected by habitat corridors, they provided a rescue effect. Both abundance and distribution improved when habitats were connected. For many kinds of insects, bryophytes can provide such corridors, providing moisture and shelter even when they are unsuitable as food.

Starzomski and Srivastava (2007) experimented with landscape geometry and found that reducing the size of patches had little effect on community resilience. However, habitat loss caused complete loss of connectivity between patches. In their experiments with the microarthropod community (mostly mites and springtails) of mosses (***Polytrichum*** and ***Bryum***) on a granitic outcrop in BC, Canada, repeated disturbance caused rapid declines in species richness and abundance, altering community structure. These two arthropod groups were highly abundant, reaching 200 or more morphospecies in areas of only 20 m^2.

Insect Adaptations to Bryophytes

Insects often modify their environment to make it suitable for their homes. These include excavations in soil and other substrates, construction of feeding or resting shelters, inducing plant responses such as galls, forming aggregations, building colonial nests, and using parental care (Danks 2002). These alterations can buffer temperatures, increase moisture, and avoid flooding. Moisture needs (Danks 2004) may drive them to bryophytes, especially during summer dry spells. The excavations and shelters protect primarily against physical factors (Danks 2002). On the other hand, aggregations, colonies, and parental actions usually influence the ability to acquire resources.

Perhaps the most important characteristic of a bryophyte inhabitant is the ability to navigate within the small spaces available. This means the insects must be small, and it means their appendages must not get in the way. Hence, large insects like butterflies and moths cannot navigate as adults, and many are likewise too large as larvae to move within the mat.

Another adaptation is the ability to utilize the moss. If it is unable to use the bryophyte as a food source, it might not be worth the energy to enter the moss community.

But food is not the only reason to enter a bryophyte clump. As seen in other invertebrates, insects can seek out the moss as a safe site from the dangers of desiccation. However, they lack the ability to encyst that is beneficial to several invertebrate groups. Instead, their life cycles permit them to be inactive during the winter season, and their mobility permits them to leave when the going gets rough. Thus, pupae of insects with a **holometabolic** (having eggs, larvae, pupae, and adults) life cycle and eggs of all insects provide life cycle options to permit residency during dry or cold periods. And most likely they, like many other invertebrates, migrate vertically as moisture or temperature within the bryophyte community changes (Markkula 1981).

The bryophyte can provide camouflage. In addition to having the bryophyte create a plethora of light and dark areas with small spaces and overlying leaves and branches, the insect may itself exhibit camouflage (Lacrampe 2003), permitting it even greater protection against predators. For example, the cranefly ***Triogma*** (Figure 31) has a green and black pattern that makes it resemble a moss branch, sporting projections that resemble leaves (Figure 31). Species in this genus exist in both aquatic and terrestrial habitats, exhibiting a camouflage that suggests it evolved to survive in its mossy habitat (Alexander 1920).

Figure 31. This larva of the cranefly ***Triogma*** has green and black patterns that make it resemble the moss branches where it lives. Photo by Janice Glime.

Abundance

Invertebrates, and particularly arthropods, can be especially abundant among mosses. Peck and Moldenke (1999) found 125 morphospecies, comprising 18 orders and

5 functional groups, in their study of vine-maple (*Acer circinatum*; Figure 32) in the Willamette National Forest (Oregon, USA). The bases of shrubs exhibited the highest species richness and abundance. The composition likewise differed between the bases and tips of the shrubs. The most abundant insect was ***Sminthurus*** (Figure 33), a springtail (**Collembola**). Such abundance raises serious concerns about the harvest and export of mosses, especially in the first half meter above the ground.

Figure 32. ***Acer circinatum*** (vine maple), a species with a rich bryophyte fauna. Photo by El Grafo, through Creative Commons.

Figure 33. ***Sminthurus*** sp. with spermatophore, the most abundant species among bryophytes on the vine maple. Photo by Petter Bøckman, through Creative Commons.

The high abundance of insects in some moss communities requires special extraction techniques. Andrew and Rodgerson (1999) suggest using kerosene to float the insects because it attaches to the cuticle of the insects. The moss-insect community must first be preserved in 95% ethanol for two weeks. This preserved mix is shaken vigorously after topping off with kerosene. The insects settle to the bottom, then float at the interface between the ethanol and kerosene. The kerosene can be pipetted off and insects collected from the interface layer. I have not actually tried this method, but it would appear to work only on relatively small insects and things without legs to get caught. Further discussion of sampling methods appears later in this chapter.

Food Sources

Many researchers have considered bryophytes to be inedible for insects and other invertebrates (Haines & Renwick 2009). Others have commented on how rare bryophagy seems to be (Longton 1984). Even on Bryonet, people familiar with bryophytes marvelled at how little we know about bryophyte herbivory. Nevertheless, Paul Johnson reported studying several groups of insects that feed on mosses or liverworts, many of which are strict **bryophages** (organisms that feed on bryophytes). Kathy Merrifield reported finding much evidence of grazing on mosses that grow in the cracks of tree bark. Several members have provided images that evidence the bryophage damage, as will be seen in succeeding subchapters of terrestrial insect interactions. It is likely that the presence of bryophagy has been largely overlooked.

Nevertheless, some of the oddities among growth forms seem to be the result of **bryophagy** (see Ghullam & Stevenson 2013; Figure 35). Since a dense cluster of apical filaments is an oddity among members of ***Zygodon rupestris*** (Figure 34), those clusters (Figure 35) observed by Robin Stevenson (pers. comm. 2 June 2016) seem to be produced in response to herbivory. The herbivore is unknown. Normal gemmae (Figure 36) of this species were present along the stem, but these terminal filaments (Figure 37-Figure 38) seemed to be the result of damage to the terminal bud (pers. comm., Robin Stevenson 2 June 2016). ***Fontinalis*** produces similar filaments (protonemata) when the apex of the stem is removed (Figure 39). And could it be that the herbivore deposits a hormone such as that used to produce galls in tracheophytes? Stevenson suggested that the normal axillary gemmae may be dispersed by hares and deer that brush against the tree trunks where the moss lives. It is possible that these terminal filaments might likewise be dispersed and serve as propagules. Anomalies such as these should provide an interesting area for research on development and evolution.

Figure 34. ***Zygodon rupestris*** growing normally with no terminal clusters of filaments. Photo by David T. Holyoak, with permission..

Figure 35. Chewed ***Zygodon rupestris***. Note that several of the apices lack the gemmae clusters. Photo courtesy of Robin Stevenson.

Figure 36. ***Zygodon rupestris*** normal axillary gemmae. Photo courtesy of Robin Stevenson.

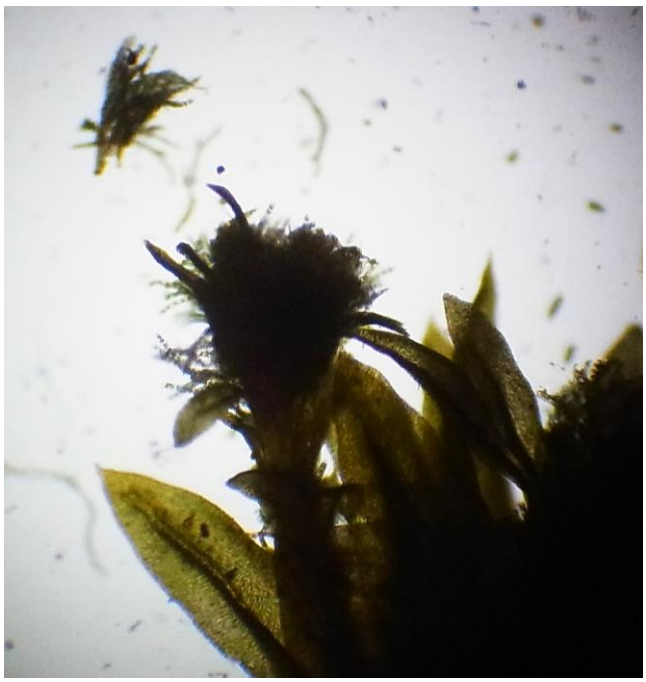

Figure 37. ***Zygodon rupestris*** with apical threads produced after herbivory. Photo courtesy of Robin Stevenson.

Figure 38. ***Zygodon rupestris*** apical threads produced after herbivory. Photo courtesy of Robin Stevenson.

Figure 39. ***Fontinalis hypnoides*** filaments (protonemata) produced after the stem apex was broken. Photo by Janice Glime.

Biologists have considered three classes of mechanisms to provide barriers to bryophagy: chemical defenses, low digestibility, and low nutrient content. But just as in tracheophytes, not all bryophytes are the same. Some are eaten while others just beside them are not, suggesting chemical defenses (Swain 1977). Haines and Renwick (2009) compared four bryophyte species by examining pre- and post-ingestive defenses by the bryophytes, all of which were mosses. Using the generalist caterpillar ***Trichoplusia ni*** (Figure 40-Figure 41), a generalist caterpillar, they found that mosses were consumed much less than lettuce or wheat germ. Of the four mosses tested [(***Bryum argenteum*** (Figure 42), ***Climacium americanum*** (Figure 43), ***Leucobryum glaucum*** (Figure 44), and ***Sphagnum warnstorfii*** (Figure 45)], only ***Climacium americanum*** was consumed in sufficient quantity to evaluate post-ingestive responses by the caterpillars. Extracts of ***Leucobryum glaucum*** placed on discs showed that this moss, the least eaten, contained a deterrent. Haines and Renwick suggested that preingestive mechanisms are more important than post-ingestive mechanisms, but much more study is needed before such a generalization is well supported.

Figure 40. ***Trichoplusia ni*** caterpillar, a species that prefers lettuce over mosses, and avoids mosses even when only mosses are offered as food. Photo by Phil Bendle, with permission.

Figure 41. ***Trichoplusia ni*** adult, a species whose larvae prefer lettuce over mosses, and avoids mosses even when only mosses are offered as food. Photo by Kurt Kulac, through Creative Commons.

Figure 42. ***Bryum argenteum***, a food source that is less preferred by ***Trichoplusia ni*** than is lettuce. Photo by Michael Becker, through Creative Commons.

Figure 43. ***Climacium americanum***, a food source that is less preferred by ***Trichoplusia ni*** than is lettuce, but it is eaten. Photo by Alan S. Heilman, through Creative Commons.

Figure 44. ***Leucobryum glaucum***, a food source that is less preferred by ***Trichoplusia ni*** than is lettuce. Photo by James K. Lindsey, with permission.

Figure 45. ***Sphagnum warnstorfii***, a food source that is less preferred by ***Trichoplusia ni*** than is lettuce. Photo by Jouko Rikkinen, through Creative Commons.

Longton (1984) reviewed the literature on the role of bryophytes and concluded that the energy content of bryophytes is generally slightly lower than that of

associated plants. Wielgolaski and Kjelvik (1975) demonstrated this for Scandinavian tundra Communities. Lewis Smith and Walton (1973) demonstrated it for a sub-Antarctic island and Bliss (1962) for an alpine tundra. But is this true in warmer habitats? Gorham and Sanger (1967) found it likewise to be true in Minnesota, USA, but that is still a relatively cold climate, at least in winter.

There does seem to be an increase in caloric content with latitude (Forman 1968, 1969; Rastorfer 1976), as there is for flowering plants, with a range of 3.7-4.8 Kcal g^{-1} for bryophytes. Longton (1984) suggests that the lower energy content in bryophytes results from lower concentrations of carbohydrates, proteins, and lipids. This was true at least for proteins and readily soluble carbohydrates in a Norwegian alpine tundra (Skre *et al*. 1975).

Lawrey (1987) challenged the notion that bryophytes had little nutritional value. Some researchers have argued that they are lower in calories than tracheophytes (Forman 1968; Pakarinen & Vitt 1974), but others consider them to fall into the same range as those of tracheophytes (Bliss 1962; Forman 1968; Pakarinen & Vitt 1974; Rastorfer 1976). Davidson *et al*. (1990) compared uneaten gametophytes to edible sporophytes and found that the ash-free caloric values did not differ, further suggesting that caloric values are not a limiting factor. On the other hand, Skre *et al*. (1975) found that both their protein and carbohydrate content is typically low in alpine bryophytes compared to tracheophytes. And levels of potassium and magnesium tend to be lower in mosses than in tracheophytes (Prins 1982).

The sugars in bryophytes are the same as in tracheophytes, although some additional ones occur. Spores are especially high in lipids and may account for consumption by ants (Plitt 1907). Pelser *et al.* (2002) even reported that some mosses [***Catharomnion ciliatum*** (Figure 46), ***Canalohypopterygium tamariscinum*** (Figure 47)] produce oils. They considered that the oil may have an energy storage function, but rather than considering it to be a food source for invertebrates, they suggested that it could serve to repel invertebrates, fungi, or bacteria.

Figure 46. ***Catharomnion ciliatum***, a species that produces oils that may be a deterrent to herbivory. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Figure 47. ***Canalohypopterygium tamariscinum***, a species that produces oils that may be a deterrent to herbivory. Photo by Pieter B. Pelser, with educational permission.

Sveinbörnsson and Oechel (1991) questioned the carbohydrate and lipid changes in tundra mosses as the seasons changed. Using ***Polytrichum commune*** (Figure 4) and ***Polytrichastrum alpinum*** (Figure 48), they samples three times per year. On the raised polygon rims, both lipid and carbohydrate concentrations were higher in ***Polytrichum commune*** than in ***Polytrichastrum alpinum***. The green parts of the plants had significantly higher concentrations of lipids than did rhizomes in ***Polytrichum alpinum***, but this relationship was not true in ***Polytrichastrum alpinum***. Sugar concentrations were higher in green parts in both species, whereas starch concentrations were highest in the rhizomes.

Only ***Polytrichum commune*** demonstrated seasonal variation in starch and sugar concentrations (Sveinbörnsson & Oechel 1991). There was a significantly strong negative relationship between sugars and starches. On the other hand, there was a significant positive relationship between lipids and starch+sugar. The seasonal relationship of these two **Polytrichaceae** mosses is like that of evergreen tracheophytes.

Figure 48. ***Polytrichastrum alpinum***, a polygon rim species in the Arctic. This species has high sugar content in green parts and high starch content in the rhizomes. Photo by David T. Holyoak, with permission.

Chapin *et al*. (1986) found that seasonal fluctuations in carbohydrate concentration varied between moss species in

the Alaskan tundra. Brown parts of ***Aulacomnium*** spp. exhibited greater seasonal differences than did species of ***Polytrichum*** and ***Pogonatum***. Lipids increased in autumn in brown tissues of mosses and declined in summer. Surprisingly, mosses had the greatest levels of lignin-like substances when compared with tussock graminoids (grasses & sedges), deciduous shrubs, evergreen shrubs, deciduous forbs (non-graminoid herbs), and lichens; *Eriophorum* (cottongrass) and lichens had the least. The preferences of the eight generalist herbivores in the study responded to nutrient levels, preferring higher levels of nitrogen, phosphorus, and potassium but lower levels of lipid and cellulose in the plants.

Russell (1979) found that the liverworts preferred by ***Caurinus dectes*** actually had a low nutrient content (Table 2), particularly for nitrogen, an important component of protein. But he pointed out that the ***Caurinus*** was able to extract the nutrients from the cells without having to eat and digest the cellulose that is so abundant in some bryophyte leaves, thus making the concentrations higher than that indicated in the table.

Table 2. Macronutrient concentrations (% dry weight) in the gametophytes of some bryophytes collected in ***Caurinus dectes*** habitat at Marys Peak, Oregon, USA. From Russell 1979.

		P	N	Na	K	Ca	Mg
Mosses							
Dicranum fucescens	Figure 49	.142	.932	.038	.546	.418	.145
Rhizomnium glabrescens	Figure 50	.251	2.083	.043	1.125	.972	.261
Eurhynchium oreganum	Figure 51	.146	.829	.056	.741	.518	.190
Isothecium spiculiferum	Figure 52	.142	.949	.034	.512	.516	.177
Antitrichia curtipendula	Figure 53	.151	.686	.028	.631	.430	.170
Rhytidiadelphus loreus	Figure 54	.164	.727	.072	.770	.440	.171
mean		**.166**	**1.034**	**.045**	**.721**	**.551**	**.186**
Liverworts							
Scapania bolanderi	Figure 55	.072	.748	.035	.659	.275	.111
Porella navicularis	Figure 56	.155	.890	.026	1.040	.426	.156
Frullania tamarisci ssp. *nisquallensis*	Figure 57	.107	.874	.030	.904	.515	.134
mean		**.111**	**.834**	**.030**	**.868**	**.405**	**.134**

Figure 49. ***Dicranum fuscescens***, the species with the lowest concentrations of several macronutrients among the nine bryophytes tested (Table 2). Photo by Michael Lüth, with permission.

Figure 50. ***Rhizomnium glabrescens***, the species with the highest concentrations of P, N, K, Ca, and Mg among the nine bryophytes tested (Table 2). Photo by Matt Goff <www.sitkanature.org>, with permission.

Figure 51. ***Eurhynchium oreganum***, the species with the highest concentration of Mg of the nine species tested (Table 2). Photo by Matt Goff <www.sitkanature.org>, with permission.

Figure 54. ***Rhytidiadelphus loreus***, the species with the highest concentration of Na among the nine species of bryophytes tested (Table 2). Photo by Malcolm Storey <www.discoverlife.org>, with online permission.

Figure 52. ***Isothecium spiculiferum***, the species with the lowest concentrations of P and K among the nine bryophytes tested (Table 2). Photo by Ben Carter, through Creative Commons.

Figure 55. ***Scapania bolanderi*** with capsules, a species with the lowest concentrations of P, Ca, and Mg among the nine species tested (Table 2). Photo by Chris Wagner, with permission.

Figure 53. ***Antitrichia curtipendula***, the species with the lowest concentrations of N and Na among the nine bryophytes tested (Table 2). Photo by Hermann Schachner, through Creative Commons.

Figure 56. ***Porella navicularis***, the species with the highest concentration of P and N among the liverworts tested (Table 2). Photo by Rosemary Taylor, with permission.

Figure 57. ***Frullania tamarisci***, the species with the highest concentration of Ca among the liverworts tested (Table 2). Photo by Tim Waters, through Creative Commons.

Rather than low nutrients, it seems likely that antiherbivore compounds may contribute to the avoidance of bryophytes by herbivores (Clymo & Hayward 1982; Davidson 1988; Davidson *et al*. 1989; Liao 1993). Lawry (1987) suggests that the same compounds already known for their antibiotic activity (Madsen & Pates 1952; Pates & Madsen 1955; Ramaut 1959; McCleary *et al*. 1960; Wolters 1964a,b; McCleary & Walkington 1966; Gupta & Singh 1971; Banerjee & Sen 1979) may serve also as antiherbivore compounds. For example, phenolic compounds and other related bio-active compounds have been demonstrated multiple times (Markham & Porter 1978, 1983; Asakawa 1981, 1982, 1984, 1990; Wilschke & Rudolph 1988; Harborne 1988; Zinsmeister & Mues 1988; Davidson *et al*. 1989; Xie & Lou 2009).

Ferulic acid in shoots (but not young capsules) of ***Mnium hornum*** (Figure 58) may account for avoidance of the shoots; ferulic acid, one of the hydroxycinnamic acids, is considered a primitive defense against herbivores in flowering plants (Swain 1977; Fry 1983). These cell wall components would be likely to discourage organisms that chew and grind, but may have no effect on those that pierce and suck, explaining the high incidence of such invertebrates (Longton 1992). In liverworts, it seems that the oil bodies store terpenoids and lipophilic aromatic compounds that have strong antifeedant activity, as shown against the African army worm ***Spodoptera exempta*** (**Lepidoptera**; Figure 59-Figure 60) (Asakawa 1990).

Thus far there is no evidence that insects take an **offensive approach** to bryophyte herbivory (Karban & Agrawal 2002). Karban and Agrawal suggest that offensive behavior includes choices for feeding and oviposition, enzymes that make it possible to digest or assimilate certain foods, sequestration of toxins, *etc*., morphological adaptations, symbionts, induction of plant galls, and induced plant susceptibility. Isopods seem to have such offensive tactics that enable them to eat and assimilate bryophytes (see Chapter 10-3 in this volume). However, special enzymes, bacteria, or other mechanisms permitting insects to digest and assimilate bryophytes seemingly remain to be discovered.

Figure 58. ***Mnium hornum***, a species that produces ferulic acid, a known antiherbivore compound. Photo by Tim Waters, through Creative Commons.

Figure 59. ***Spodoptera exempta*** larva, a species that avoids liverworts with oil bodies that store terpenoids and lipophilic aromatic compounds that have strong antifeedant properties. Photo from the University of Arkansas, through Creative Commons.

Figure 60. ***Spodoptera exempta*** adult, a species whose larvae avoid liverworts as food. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Both algae (Ceh *et al*. 2005) and tracheophytes have inducible antiherbivore compounds (*e.g.* Fowler & Lawton 1985; Kruidhof *et al*. 2012). The brown alga ***Sargassum asperifolium*** (Figure 61) and red alga ***Hypnea pannosa***

(Figure 62-Figure 63) both exhibited lower grazing levels on individuals that had been grazed previously than on those with no previous grazing, suggesting that these algae produced antiherbivore compounds in response to grazing.

Figure 61. ***Sargassum*** sp., a brown alga that seems to have inducible antiherbivore compounds. Photo through Creative Commons.

Figure 62. ***Hypnea pannosa***, a red alga that seems to have inducible antiherbivore compounds. Photo by Ria Tan, through Creative Commons.

No one has attempted to show whether these secondary compounds are ever induced in bryophytes. Karban and coworkers considered the advantages of inducible antiherbivore compounds (Karban & Baldwin 1997; Karban *et al*. 1997). Whereas most ecologists had argued that the inducible compounds saved costs, empirical data failed to support this argument (Karban *et al*. 1997). Karban and coworkers suggested that instead it was the variability that was important – "maximal levels of defense are constrained, variability will increase the effectiveness of a given level of investment in defense."

Gerson (1969, 1982) reports that some members of **Collembola**, **Diptera**, **Hemiptera**, **Hymenoptera**, **Orthoptera**, **Cryptostigmata**, and **Prostigmata** (**Acarina**) feed on mosses. But it is likely that the number is far greater than we suppose. Certainly **Lepidoptera** must be added to the list (Chapman 1894; Tillyard 1926). We have found that Isopods can do considerable damage to mosses, but their feeding occurs at night. A number of insects are night active, hence avoiding visibility to birds that feed on them.

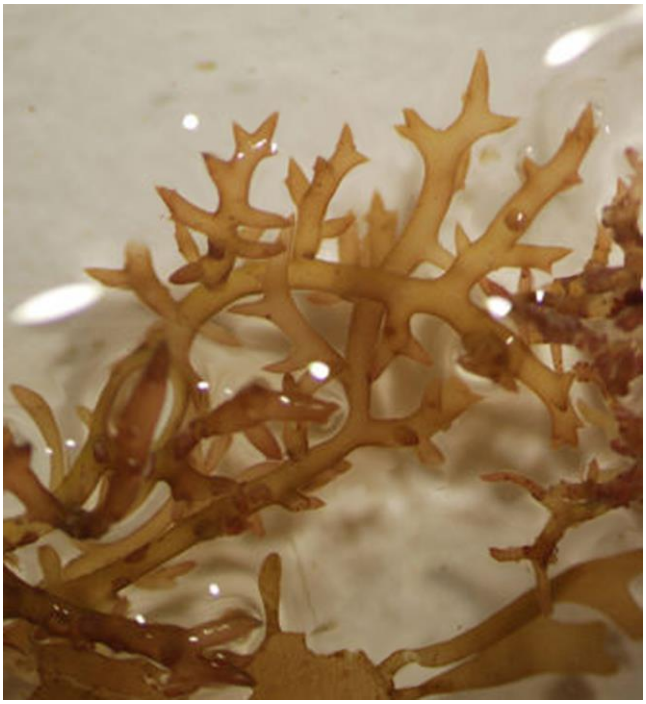

Figure 63. ***Hypnea pannosa***, a red alga that seems to have inducible antiherbivore compounds. Photo by Cal Photos, through Creative Commons.

Antiherbivore compounds in liverworts have been greatly elaborated by Asakawa (1981, 1982, 1984, 1990). Despite the widespread presence of these compounds, some liverworts are still eaten. For example, Robin Stevenson sent me an image of ***Marchantia polymorpha*** (Figure 64) with evidence of herbivory on the gemmae cups.

Figure 64. ***Marchantia polymorpha*** showing gemmae cups where the gemmae have apparently been eaten; the bottom of the cup is eaten through to the soil. Photo courtesy of Robin Stevenson.

A common pattern of bryophyte consumption is for the insect to strip the leaf lamina cells while avoiding the costa and border cells (Wyatt & Stoneburner 1989; Davidson *et al*. 1990). Other insects avoid the cell wall problem by using a straw-like stylet, such as those of aphids and mites, sucking out the contents without the necessity of digesting cell walls.

Loren Russell (pers. comm.) observed the locations and food habits of insects in western Oregon and Washington, USA, and researched their food habits through

published feeding observations and gut analyses. He found at least 26 species of **bryophagous** insects (those eating bryophytes). Among these, only three species were reported as associated with liverworts. To the list of liverwort consumers, he added **Tipulidae** larvae and ***Lioligus striolatus*** (a member of the bryophyte-dwelling beetle family **Byrrhidae**; Figure 65).

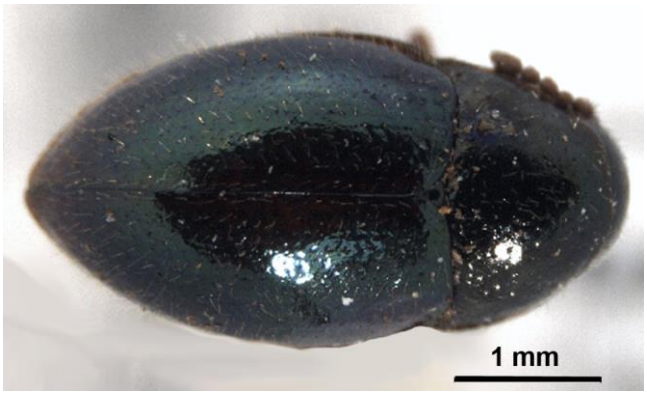

Figure 65. ***Lioligus nitidus*** adult, a bryophyte dweller and liverwort consumer. Photo by CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Bryophyte herbivory may have been more extensive among early bryological evolution. As insects and other herbivores became more abundant and diverse, those that survived were more likely to be those protected by antiherbivore compounds, tough tissues, lack of nutrients, or inconspicuous locations. To shed light on early herbivory, Labandeira *et al*. (2014) examined fossil evidence from the late Middle Devonian liverwort ***Metzgeriothallus sharonae*** (Figure 66) from eastern New York state shale fragments. Using microscopic analysis, they detected an "extensive repertoire" of arthropod herbivory. This represented three functional feeding groups and nine types of damage by arthropods. They considered the oil bodies were similar to those of modern liverworts and probably provided chemical defense against the arthropod herbivory on this species. The evidence suggested that these early herbivores were significantly smaller than those of the later Palaeozoic and that they had an important role in early terrestrial ecosystems.

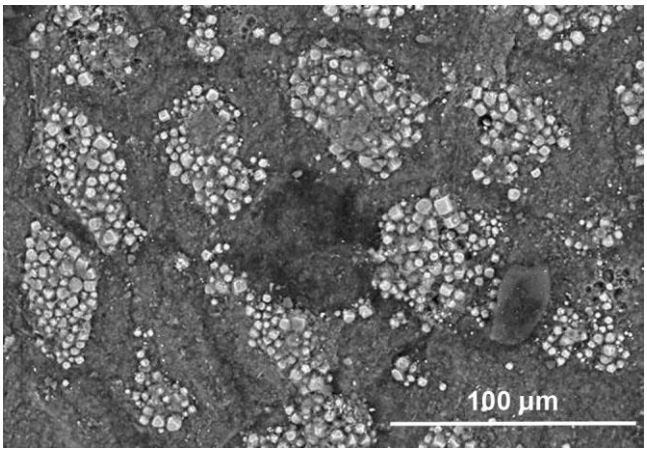

Figure 66. ***Metzgeriothallus sharonae*** fossil showing cells. This fossil species is known to have provided food for at least three feeding groups. Photo by Susan Tremblay, with permission.

It is now clear that bryophytes are eaten, but that this is not widespread among the members of the animal kingdom. Claudio Delgadillo (pers. comm. 30 March 2016) was surprised when a student discovered bryophyte tissue in a sea urchin gut. One had a liverwort and one had a moss! And most of us have probably seen capsules with holes in their sides, indicating something had been nibbling. Sometimes only the stems remain, and in the image of ***Orthotrichum affine*** (Figure 67) sent to me by Robin Stevenson. It remains a challenge to match the identity of the bryophages with their food organisms.

Figure 67. ***Orthotrichum affine*** eaten by some sort of terrestrial invertebrate, most likely an insect or isopod. Photo courtesy of C. Robin Stevenson.

Bryophytes as Pesticides

Since many bryophytes have been refused in feeding trials, and many bryologists consider their secondary compounds with antifeedant properties to be important in deterring potential feeders, it should be no surprise that some enterprising bryologists and their colleagues have attempted to use these compounds in pesticides (Singh *et al*. 2015). Singh and coworkers found the enzyme thiaminase from ferns and mosses exhibited insect resistance activity. They were able to patent crude protein extracts of several ferns and mosses that caused 70-100% mortality and reduced growth in caterpillars of the Noctuidae *Spodoptera frugiperda* (fall army worm) and *Helicoverpa zea* (corn earworm), neither of which is known to eat mosses. Such pesticides may be a boon to agriculture by decreasing destruction. Since they are natural compounds, they are probably already avoided by birds. Nevertheless, their safety as a pesticide must be evaluated, particularly in regard to pollinators.

Sampling Methods

Field Collection

A common method of field collection for soil and bryophyte invertebrates is the use of **pitfall traps**. Drozd *et al*. (2009) were surprised to find that the total abundance for arthropods was higher in the litter samples than from the moss cushions. As they point out, conclusions of this sort should be evaluated carefully based on the methods. Bryophyte dwellers may seek refuge there and may be relatively immobile. They also may be species that tend to desiccate easily, hence their retreat into the more moist

bryophyte cushions. Their nighttime movements may be vertical rather than horizontal, hence never going near the pitfall traps. In the daytime they retreat into the protective cushion of bryophytes where it is harder for predators to see them and they are more protected from desiccation. This same protection in a dense moss cushion prevents rapid movement. The arthropod surface activity may be mostly that of predators in search of dinner. Those within the bryophyte clump may be species that feed on bryophytes or the collected detritus and microorganisms, hence having no need to move from the clump at all.

If these problems concern you, then the best method of collection is to sample bryophyte clumps. Andrew and Rodgerson (1999) recommend 2.5 x 2.5 cm clumps. Unfortunately, this method is destructive and should never be done with rare bryophyte species or fragile ecosystems.

One method I have not tried is to use a **sugar flotation** technique with live bryophyte cushions (see Pask & Costa 1971 below). After floating off the insects, clean the cushion well in rainwater or stream water and return it to its original position. If the clump is kept intact, it may survive. But I don't know if it will survive the sugar solution, and the effectiveness of extracting the insects without disturbing the integrity of the moss clump needs to be tested.

Extraction

Heat gradients are common methods for extracting invertebrates from soil and bryophytes. Tuf and Tvardik (2005) used a Tullgren funnel with a heat source (lamp) above the mosses in the funnel. Invertebrates are then captured in a jar of alcohol or other preservative below the funnel. This is biased against slow-moving organisms that desiccate easily.

In mosses as dense as some ***Sphagnum*** (Figure 45) mats, behavioral extraction (also a heat technique) may be beneficial (Fairchild *et al*. 1987). But Fairchild and coworkers added another gradient – dissolved oxygen. Both the heat and oxygen form a vertical gradient in a column of water with the ***Sphagnum*** immersed at the top. Mean sorting time was reduced from >16 hr to <2 hr per sample. This method was effective for insects and other invertebrates, but was intended for aquatic invertebrates. Its usefulness for emergent bog species remains to be tested. The method takes advantage of the need for oxygen and the avoidance of warmer temperatures among the aquatic organisms.

Temperature gradients have their problems for extracting insects. Some are slow-moving or might burrow deeper into the bryophytes to avoid the heat. Others may become desiccated by the heat and no longer be able to move.

Preserved samples permit the researchers to do the extractions at their convenience. This is sometimes a necessity for extended field work. Pask and Costa (1971) recommend preserving the samples in 10% formalin, but this is highly carcinogenic and should be avoided. Using 70% ethanol (or 95% for aquatic samples) works well. A few drops of glycerine can protect the organisms if too much alcohol evaporates (pers. experience). Pask and Costa compared preserved vs unpreserved samples using extraction with a sucrose solution of 1.12 sp. gr. They found a mean recovery of 90.8% for persevered samples compared to 83% from unpreserved samples. Furthermore, the unpreserved samples yielded much greater variability in efficiency of recovery than did the preserved samples. And some groups seemed to be easier to recover in the preserved samples (**Zygoptera**, **Hemiptera**, **Trichoptera**, and **Chironomidae**). No group was under-represented in the preserved samples.

Andrew and Rodgerson (1999) tested two common insect extraction methods: **Tullgren funnels** (*e.g.* Tuf & Tvardik 2005) and **sugar flotation** (Pask & Costa 1971), and compared these to a new technique using kerosene phase separation. They found that the kerosene extraction recovered significantly more invertebrate individuals than did the sugar extraction and represented similar numbers of orders.

Kerosene phase separation (Andrew & Rodgerson 1999; Andrew *et al*. 2003)**:** Upon collection in the field (2.5 x 2.5 cm samples), the bryophyte-invertebrate samples should be placed in 95% ethanol for 2 weeks before extraction. For densely tufted bryophytes, pre-washing samples in 95% ethanol may be useful because there is more interference by the bryophytes. In the **kerosene phase separation**, the kerosene attaches to the insect cuticle to facilitate flotation:

1. First put the bryophyte-insect mix into 2 large test tubes (2 cm wide X 17 cm long).
2. Then fill the test tube 3/4 full of sample with ethanol and top it off with 1 cm of kerosene.
3. Shake this mix vigorously to fully mix the solutions.
4. After 10-15 minutes of settling, roll each tube to release trapped bubbles from the sides and bottom.
5. When the tubes are then kept upright, a distinct interface will form between the ethanol and kerosene; insects will collect onto the interface layer. Pipette off the kerosene to within 1 mm of the interface layer.
6. Then pipette off remaining kerosene plus interface.
7. Wash the sides of the tube with 95% ethanol to dislodge the kerosene stuck to the sides and repipette and collect.
8. Repeat the whole process to get remaining invertebrates (increases total number by about 16%).
9. Push the invertebrates in the kerosene layer into the ethanol, using a fine brush, to dislodge the kerosene from the cuticle.
10. Examine the interface mix in a Petri dish with a binocular microscope under a fume hood for your own safety. Collect and sort the invertebrates.

Habitats

Many practices of humans threaten the bryophytes on the planet Earth. Perhaps the greatest of these in purely terrestrial ecosystems is the management practices of forests. Management for timber threatens the forest floor bryophytes, not to mention those that live on the trees themselves. A major problem is the imposed dispersal limitation to recolonize cut forests, and the larger the cut and isolation, the greater the problem for recolonization (Fenton & Frego 2005). Islands of trees provide refugia where at least some bryophytes may survive long enough to recolonize. Temperature, total daily photosynthetically active radiation, and vapor pressure deficit were significantly different between areas with remnant canopy and those without. If bryophytes are unable to colonize or

survive, the insects that depend on them for moisture, food, and refuge from predators are vulnerable and their mortality increases, often to their local extinction.

Bogs and Wetlands

Data would suggest that bogs and wetlands have the highest populations of insects living among bryophytes. This is at least in part due to the greater biomass of mosses, a ratio of 1.6:1 in a Stordalen mire when compared to tracheophytes (Rosswall *et al*. 1975). Since they are also the habitats with the greatest cover of bryophytes, this high population of insects should probably be expected. Nevertheless, there seems to be little evidence that the bryophytes are used as food. Of nine species of **Nematocera** (midge) larvae, Smirnov (1961) found that only ***Psectrocladius*** from the ***psilopterus*** group (Figure 68-Figure 69) had eaten ***Sphagnum***, and then it constituted only 16% of the food volume. Rather, algae and detritus among the bryophytes formed the main food for the herbivorous members of the group. The **Collembola** (springtails) eat the fungi that grow on decomposing ***Sphagnum***. Thus, the ***Sphagnum*** provides the substrate needed to make the food available.

Figure 68. ***Psectrocladius*** sp. larva, a genus that includes one species that eats ***Sphagnum***. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

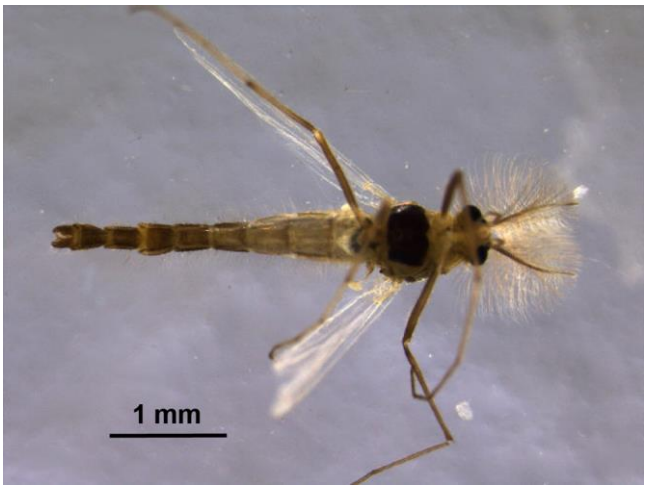

Figure 69. ***Psectrocladius psilopterus*** adult, species group where some larvae eat ***Sphagnum***. Photo by NTNU Museum of Natural History and Archaeology, through Creative Commons.

Insects in boreal peat bogs may be more distinctive. Spitzer and Danks (2006) found that these bogs have not only the generalists that seem to be common in many bogs, but also distinct **tyrphobionts** (species restricted to bogs) and **tyrphophiles** (species frequenting bogs but not restricted to them). One reason for the great diversity in some bogs is the topographic diversity of bogs, including hummocks that can become dry and hollows that are underwater, with the opportunity to migrate short distances vertically to find suitable moisture levels. Especially in boreal regions, many bogs may be hundreds and some thousands of years old, preserving relict communities that are well established. The isolation of bogs from each other has permitted them to develop unique insect communities.

Brink and Wingstrand (1949) found that the four species considered typical for bogs (Krogerus 1939, 1947) were also present in the Virihaure area of Swedish Lapland. These were the beetles (**Coleoptera**) ***Agonum consimile*** (**Carabidae**) and ***Elaphrus lapponicus*** (**Carabidae**) and the flies (**Diptera)** ***Dolichopus fraterculus*** (**Dolichopodidae**) and ***Delia lineariventris*** (**Anthomyiidae**). They also considered **Staphylinidae** beetles ***Anthobium lapponicum***, ***Stenus hyperboreus***, ***S. umbratilis***, the **Linyphiidae** spiders ***Erigone capra*** and ***Bathyphantes setiger***. On the other hand, Agrell (1941) was unable to find any **Collembola** that were characteristic bog species.

Forests

Biomass production of bryophytes in forests can be high. In oak woodlands, Rieley *et al*. (1979) reported that bryophytes contributed 90% of the ground vegetation green biomass compared with only 60% of the annual production, providing a standing crop (green + brown) of 200-640 g m^{-2} in pine forests and mires.

Garry Oak trees sport a variety of bryophytes, providing habitat for various invertebrates (pers. comm. Wynne Miles 12 January 2008). Miles found tufts of ***Orthotrichum*** (Figure 70) that were missing their sporophytes and only the broken setae remained. In another case, a collection of epiphytes, including ***Tortula*** (Figure 71), was grazed while in its collecting bag.

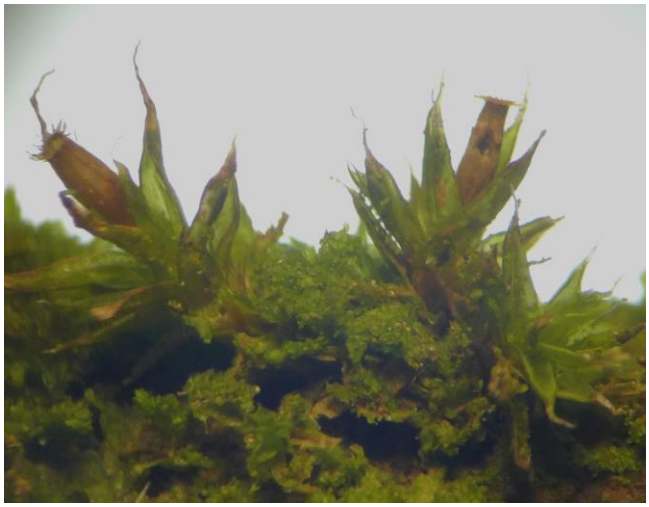

Figure 70. ***Orthotrichum diaphanum*** with a chewed capsule (on right) similar to that observed by Wynne Miles. Photo courtesy of Robin Stevenson.

Figure 71. Larva (**Lepidoptera**) on ***Tortula*** sp. This inadvertently collected larva grazed a collection of epiphytic mosses that had been growing on a large Garry Oak. Photo courtesy of Wynne Miles.

Figure 72. ***Sphagnum teres***, a forest moss that houses a moderate number of arthropods. Photo by A. Neumann <www.biopix.org>, with online permission.

Forest ecosystems offer a diversity of habitats to insects. Because of their ability to fly as adults, the adult habitat can differ significantly from that of the larvae. The habitats of eggs and pupae – immobile stages – are typically the same as those of the larvae. But once the adult emerges, it is able to move from the food habitat of the larva to the feeding habitat of the adult, or in some cases, the adult does not feed. For many of the adults mating is the first and only priority.

In boreal forests, the bryophytes can often form 100% cover (Oechel & Van Cleve 1986). Although they are a minor part of the biomass, they perform a major portion of the primary productivity and ground cover. Hence, they also provide a major function in determining the invertebrate communities.

Drozd *et al*. (2009) used pitfall traps in a submountain and mountain forest ecosystem of the Czech Republic amid ***Polytrichum commune*** (Figure 4), ***Polytrichastrum formosum*** (Figure 3), ***Sphagnum teres*** (Figure 72), ***Sphagnum girgensohnii*** (Figure 73), ***Sphagnum fallax*** (Figure 74), ***Bazzania trilobata*** (Figure 75), ***Pleurozium schreberi*** (Figure 76), ***Eurhynchium angustirete*** (Figure 77), and ***Oligotrichum hercynicum*** (Figure 78). The traps followed a moisture gradient in moss cushions and in litter with no moss (controls). Drozd and coworkers suggested that the relationship with the mosses seemed to have broader implications than just that of a substrate, *i.e.*, the data indicate interaction between moss presence and other microhabitat features. The great number of insects in these forest floor habitats was indicated by the 55,000 specimens collected (66 traps, 5 locations), averaging 850 individuals per trap. Drozd and coworkers found that moss species, as well as moss presence, was important in determining both total abundance and taxon diversity (Figure 79). But moisture was important as well, perhaps contributing to moss species preference. Nevertheless, trapped arthropod abundance was greater in the litter samples.

Figure 73. ***Sphagnum girgensohnii***, a forest moss that houses large numbers of arthropods, including insects. Photo by Mark Melton (Noah Project), with permission.

Figure 74. ***Sphagnum fallax***, a forest moss that houses a small number of arthropods. Photo by Michael Lüth, with permission.

Figure 75. ***Bazzania trilobata***, a forest liverwort that houses a moderate number of arthropods with few being insects. Photo by Bernd Haynold, through Creative Commons.

Figure 77. ***Eurhynchium angustirete***, a forest moss species that houses insects. Photo by Marko Vainu, through Creative Commons.

Figure 76. ***Pleurozium schreberi***, a forest moss species with a moderate number of insects. Photo by Sture Hermansson, with online permission.

Figure 78. ***Oligotrichum hercynicum***, a forest moss species that houses insects. Photo by Hermann Schachner, through Creative Commons.

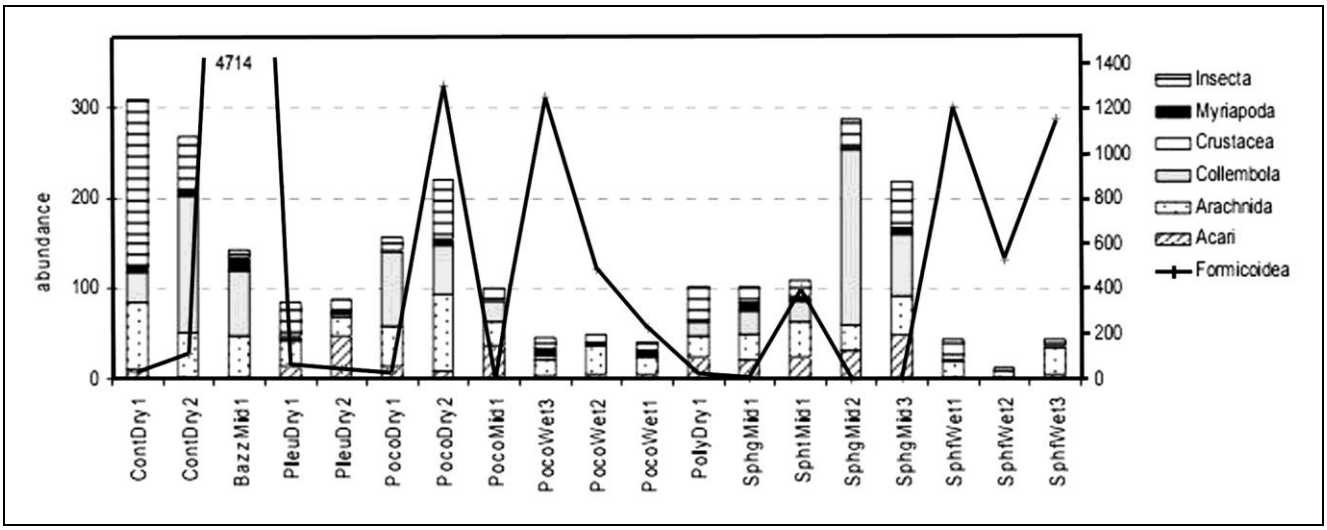

Figure 79. Arthropods from mosses in the Podolánky area of the Czech Republic. Poco = ***Polytrichum commune***, Poly = ***Polytrichastrum formosum***, Spht = ***Sphagnum teres***, Sphg = ***Sphagnum girgensohnii***, Sphf = ***Sphagnum fallax***, Bazz = ***Bazzania trilobata***, Pleu = ***Pleurozium schreberi***, Eurh = ***Eurhynchium angustirete***, Olig + ***Oligotrichum hercynicum***, Spha = ***Sphagnum*** spp., Cont = litter; moisture Wet = high, Mid = middle, Dry = low. Modified from Drozd *et al.* 2009.

As Drozd and coworkers (2009) pointed out, bryophages and detritivorous arthropods "have no reason to move about," potentially causing a low capture rate in traps that require movement. But these researchers also suggested that bryophytes may serve only as shelter and a temporary place to prevent desiccation, referring to the oft held view that the bryophytes are low in nutrients. This latter assumption, however, has been contested, as you will seen earlier in this chapter.

Few studies have attempted to find the uses made by the bryophyte inhabitants (Drozd *et al*. 2009). Rather, most have simply enumerated species, perhaps correlating them with other physical factors such as temperature and moisture.

One of the few studies that elaborates on the relationship between bryophyte species and the invertebrate inhabitants is that of Božanić *et al*. (2013). In this case, ***Brachythecium curtum*** on a decaying tree housed the greatest number of species. The layers of the forest were important, with type of substrate and height above ground proving to be the most important factors to determine the invertebrate distribution.

Figure 80. ***Brachythecium curtum***, a species with a rich fauna of arthropods. Photo by Janice Glime.

Montane Tropical Rainforests

In the Atlantic Forest of Brazil, Maciel-Silva and dos Santos (2011) found a number of insects associated with the mosses ***Hypopterygium tamarisci*** (Figure 81) and ***Lopidium concinnum*** (Figure 82). These include **Lepidoptera** larvae, leafhoppers, aphids, and **Psocoptera**, as well as isopods, snails, mites, and spiders.

Figure 81. ***Hypopterygium tamarisci***, home to several orders of insects. Photo by Peter Woodward, through Creative Commons.

Figure 82. ***Lopidium concinnum***, a habitat for several orders of insects. Photo by Juan Larrain, through Creative Commons.

Epiphytes

A number of species of arthropods are associated with the epiphytes, including several groups of insects. Miller *et al*. (2008) compared the epiphyte arthropod fauna at three heights on red maple (*Acer rubrum*; Figure 83) trees in the Acadian forest of Maine, USA. They found that there was a close association between springtails and spiders and suggested that the spiders were there because of the abundance of springtail prey. When the bryophytes diminished following gap harvesting, the spiders and springtails did as well. One surprise was the abundance of **Diptera** associated with the epiphytes. Fifteen families of these flies were represented. Overall, the numbers of morphospecies was positively correlated with bryophyte abundance except for the springtail family **Isotomidae**. Abundance of the other springtail morphospecies were correlated with dense bryophyte cover at the bases of trees.

Figure 83. ***Acer rubrum***, a species that supports arthropods living in epiphytic bryophytes. Photo by Jean-Pol Grandmont, through Creative Commons.

In the Pacific Northwest of North America, the epiphytic bryophyte mats in the subcanopy likewise house numerous insects. In collections of over 143,000 individuals, Peck and Moldenke (2011) recovered 205 morphospecies from 337 moss mats (less than 25 kg of mosses, fresh weight). These mosses were collected to determine the impact of moss harvesting on the insect community, but they also provide us with information on community structure. The faunal morphospecies composition between moss mats from the two shrubs, vine maple (***Acer circinatum***; Figure 84) and huckleberry (***Vaccinium parvifolium***; Figure 85) did not differ. Likewise, the fauna of the vine maple did not differ between the bases and branch tips of these shrubs, differing from their results in the Willamette National Forest (Peck & Moldenke 1999). Instead, the invertebrate fauna composition correlated with elevation, stand age, and vertical distance to water.

Figure 84. ***Acer circinatum***, a shrub that supports growths of mosses that are often commercially harvested, with their accompanying invertebrate fauna. Photo by El Grafo, through Creative Commons.

Figure 85. ***Vaccinium parvifolium***, a species with moss mats that hold arthropods. Photo by Walter Siegmund, through Creative Commons.

In the tropics, canopy bryophytes may be especially important for some of the invertebrates. Pócs (1982) estimated an excess of 1000 g m^{-2} of bryophytes in the elfin forests. Trees in Costa Rican montane forests build canopy soils (including bryophytes) that house mites, amphipods, isopods, beetles, springtails, ants, and insect larvae as the dominant invertebrate groups (Nadkarni & Longino 1990). The ground fauna had a mean density of 2.6 times that of the canopy. Only ants did not fit this pattern. However, it is difficult to assess these tropical mats because the mosses are typically only a minor component. Instead, the mats are primarily leafy liverworts and filmy ferns (Yanoviak *et al*. 2007). Yanoviak and coworkers found that these insect assemblages resembled the fauna of the soil mosses and accompanying humus layer. These are dominated by mites, springtails, ants, and minute beetles (Yanoviak *et al.* 2003, 2004). Unfortunately, the fauna of mosses in the canopy may be under-sampled because the fogging method used in many studies of canopy invertebrates is ineffective for sampling the tiny insects that inhabit the canopy bryophytes (Yanoviak *et al*. 2003).

Even within a mat of epiphytic bryophytes and other plants, vertical differences exist (Yanoviak *et al*. 2004). In a Costa Rican lower montane forest, the green portion of the mat housed twice as many individuals and species per gram dry mass compared to the brown portion. Morphospecies composition was similar, but some taxa differed significantly in relative abundance. Predators were randomly distributed in the larger patch sizes (up to 50 cm^2). They found that interspecific interactions were more important than the environmental variables in determining the distribution of the mat fauna in small patch size (20 cm^2).

Cryptogamic Crusts

The cryptogamic crusts are those habitats in arid ecosystems that are comprised of algae, bacteria, fungi, lichens, and bryophytes. These crusts are of major importance in these ecosystems, covering as much as 70% of the soil (Brantley & Shepherd 2004).

The arthropod fauna make use of the crusts for retreats and homes. In piñon-juniper woodland in central New Mexico, the crusts differ little in major groups from bryophyte habitats in other ecosystems, with tardigrades, nematodes, springtails, small insects, mites, and spiders predominating (Brantley & Shepherd 2004). Of the 38 taxa identified in the study, 27 occurred on mixed lichen and moss patches and 29 on moss patches. Only 21 were found on pure lichen patches. Of the three types of crusts, 15 arthropod taxa occurred on all three. Not only did the mosses have the highest number of arthropod species, but they also had the greatest abundance of arthropods. In this very dry climate, the greatest arthropod richness and abundance occurred in winter.

Altitude

Altitudinal gradients are complicated. Although the temperature tends to decrease and winds increase, moisture may be greater or less, and microhabitats abound. Vegetation changes and can increase or decrease shade. UV light may come into play.

Differences between elevations may be more due to microclimate differences than to those differences caused by elevations (Andrew *et al*. 2003). For example, Andrew and coworkers found that whereas altitude had a significant effect on diversity of insects in Tasmania and New Zealand, there was no general trend present along the altitudinal gradient. Mt. Field in Tasmania had the highest invertebrate and bryophyte diversity at 750 m. But Mt.

Rufus had low bryophyte and insect diversity throughout the altitudinal gradient. In Tasmania Mt. Otira had the highest diversity of both invertebrates and bryophytes at low altitudes, whereas Mt. Kaikoura had the highest invertebrate and lowest bryophyte diversity at the highest altitude. Clearly different factors are important for the bryophytes compared to those important for the invertebrates. Andrew and coworkers stressed the importance of scale and the need to sample both broad scale and microscale community patterns.

Tundra

Bryophytes are important ground cover in the tundra. In Spitsbergen, Bengston *et al*. (1974) found a total arthropod abundance of 268,000 individuals m^{-2} on wet moss tundra, compared to 42-63,000 on lichen tundra and 518,000 on grassland. The mites and springtails comprised 96-99% of the arthropod fauna, with small numbers of spiders, flies, and **Hymenoptera**. These major groups were similar in abundance to those of the high alpine in southern Norway.

Boreus in Norway takes advantage of mosses to provide protective space. This is a safe space in which they lay their eggs (Håvar 2001). And it appears that it might be a site of copulation, an event rarely observed on the snow. The chambered air spaces most likely also provide space for this winter-active scorpionfly. Adults of ***Boreus elegans*** (Figure 86) and ***B. californicus*** (Figure 87-Figure 88) feed on ***Racomitrium heterostichum*** (Figure 89-Figure 90); larvae and pupae of ***B. elegans*** can be found under ***Brachythecium*** (Figure 91) and other mosses (Russell 1979).

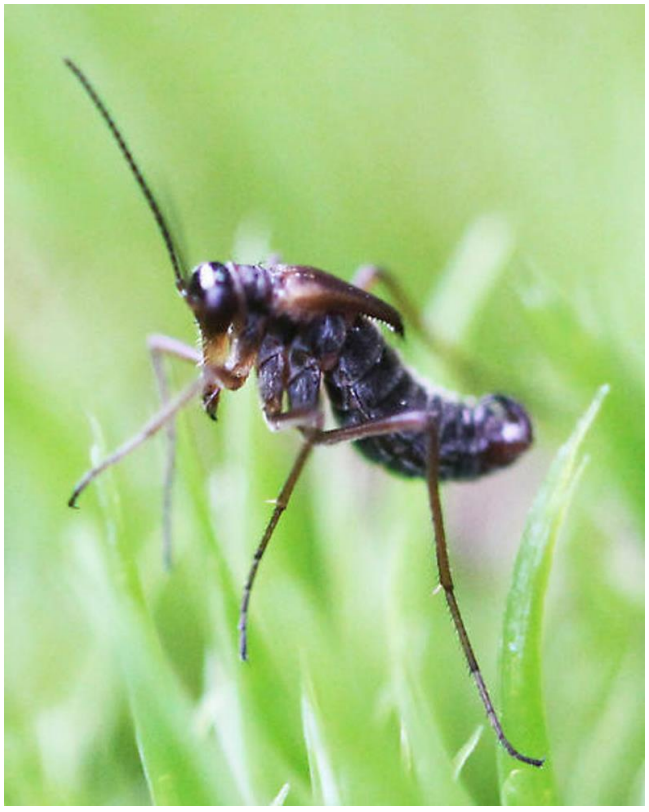

Figure 86. ***Boreus elegans*** adult, a winter-active scorpionfly that lays eggs among mosses. Photo by Megan Asche, with permission.

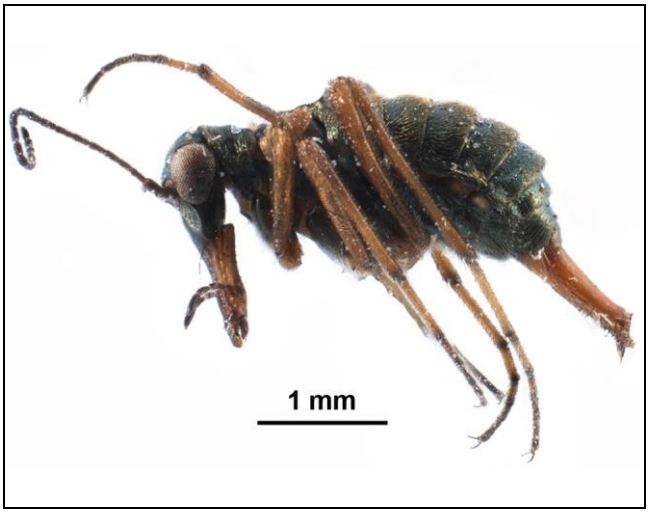

Figure 87. ***Boreus californicus*** adult female, a species that feeds on ***Racomitrium heterostichum***. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

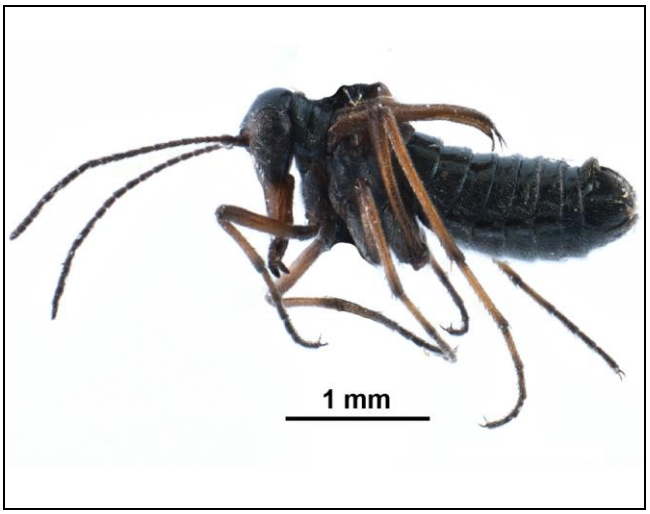

Figure 88. ***Boreus californicus*** adult male, a species that feeds on ***Racomitrium heterostichum***. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 89. ***Racomitrium heterostichum*** habitat and home for ***Boreus californicus*** and ***B. elegans***. Photo by Andrew Spink, with permission.

Figure 90. ***Racomitrium heterostichum***, food for ***Boreus californicus*** and ***B. elegans***. Photo by J. C. Schou <www.biopix.com>, with permission.

Figure 91. ***Brachythecium rutabulum***, home for larvae and pupae of ***Boreus elegans***, with capsules. Photo by Tim Waters, through Creative Commons.

The family **Apteropanorpidae** has a single genus, ***Apteropanorpa*** (Figure 92), with only four species (Wikipedia 2011). These are the Tasmanian snow scorpionflies, and they live among mosses in Tasmania and southern Australia. The adults are predators, but the larvae live among the mosses.

Figure 92. ***Apteropanorpa tasmanica***, a moss dweller that is often infested with one or two species of parasitic mites. Photo by Simon Grove ©, Tasmanian Museum and Art Gallery, with permission.

The best-known species, ***Apteropanorpa tasmanica*** (Figure 92), is known to carry two species of parasitic mites (Seeman & Palmer, 2011). These are ***Leptus agrotis*** (**Erythraeidae**) and ***Willungella rufusanus*** (**Microtrombidiidae**).

Antarctic

In the Antarctic, bryophytes form the dominant vegetation and house the most arthropods (mites, springtails, insects) (Gerson 1969). Gerson reported that the ***Polytrichum-Dicranum*** (Figure 93) mats housed more arthropods than did ***Pohlia*** (Figure 94-Figure 95). The former was less wet and cold in the summer and its open texture made it easier for movement, especially of larger arthropods.

Figure 93. ***Polytrichum juniperinum*** in ***Dicranum scoparium*** mat, a species combination that is home for many arthropods. Photo by Kirill Ignatyev, through Creative Commons.

Figure 94. ***Pohlia nutans*** with capsules, a common sight in the Arctic and Antarctic. ***Pohlia*** species house arthropods there. Photo by Michael Lüth, with permission.

Figure 95. ***Pohlia nutans*** with capsules, a genus that is home to arthropods. Photo by Michael Lüth, with permission.

The Antarctic is dominated by small organisms. In that regard, bryophytes are an important habitat for invertebrates. Davis (1981) compared the invertebrates on two kinds of moss communities on Signy Island: a moss turf dominated by ***Polytrichum alpestre*** (=***P. juniperinum***; Figure 96) and ***Chorisodontium aciphyllum*** (Figure 97-Figure 98) and a moss carpet composed of ***Warnstorfia sarmentosa*** (Figure 99), ***Sanionia uncinata*** (Figure 100), and ***Calliergidium austrostramineum*** (Figure 101), with the liverwort ***Cephaloziella varians*** (Figure 102). The trophic structure, organic matter transfer, and production of primary producers (which included lichens and algae in addition to the bryophytes) were similar in these two community types, but the standing crops of **Collembola** (springtails; Figure 33) and **Acari** (mites) differed. These differences may have related to the differences observed in turnover of mosses and accumulation of dead organic matter.

Figure 96. ***Polytrichum juniperinum***, a common moss on Signy Island and home to **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola**. Photo by Juni, through Creative Commons.

Figure 97. ***Chorisodontium aciphyllum*** in Antarctica, home to a variety of invertebrates. Photo from Polar Institute, through Creative Commons.

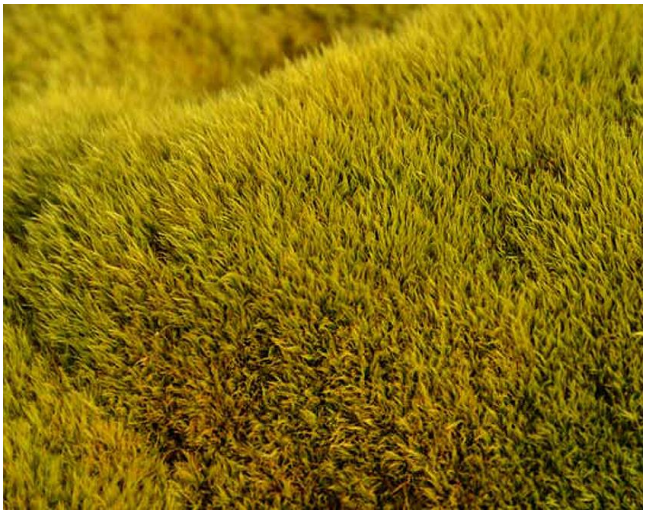

Figure 98. ***Chorisodontium aciphyllum*** in the Antarctic, a primary producer and home for the same groups of organisms as ***Polytrichum juniperinum***, but with different proportions. Photo by Zicheng Yu, through Public Domain.

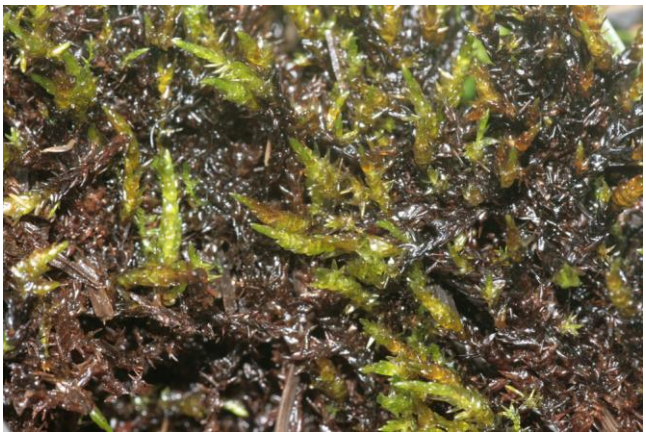

Figure 99. ***Warnstorfia sarmentosa***, home for a variety of invertebrates, including **Collembola**, on Signy Island. Hermann Schachner, through Creative Commons.

Figure 100. ***Sanionia uncinata***, home for invertebrates in the Antarctic. Photo by Hermann Schachner, through Creative Commons.

Figure 101. ***Calliergidium austro-stramineum***, home for invertebrates in the Antarctic. Photo by Bill Malcolm, with permission.

Figure 102. ***Cephaloziella varians*** with ***Polytrichum*** sp., home for invertebrates in the Antarctic. Photo by Christian Peters, with permission.

The maritime Antarctic has a flora that is predominately bryophytic (Tilbrook 1967). The invertebrate fauna has few species with any great abundance. This area produced a number of indigenous insects: only seven species of **Collembola** (springtails) and one of **Diptera** (flies), but 20 species of mites. The dominant arthropod is ***Cryptopygus antarcticus*** (**Collembola**). The highest densities of insects are among the vegetation, but some occur in areas free of permanent ice. Habitat specificity is uncommon. It is likely that the ability of bryophytes to absorb radiation and affect the microhabitat temperature, coupled with the insulation of snow, makes the bryophyte habitat a suitable habitat for the arthropods. Geothermal areas, as discussed below, further provide a bryophytic habitat that is suitable for arthropods.

Strong (1967) considered the Antarctic mosses to serve primarily as shelter and concluded that they do not provide a significant source of nourishment. Humidity seems to be the major controlling factor, with temperature playing a secondary role. Wind is an important feature that modifies temperature and humidity. The primary consumers include springtails and the midge ***Belgica*** (Figure 103). Adaptations to the climate seem to be primarily physiological rather than developmental or behavioral.

Figure 103. ***Belgica antarctica***, a moss consumer, mating. Photo, through Creative Commons.

Usher and Booth (1984) cut five sets of 96 contiguous samples from moss turf on Signy Island in the maritime Antarctic. They found only 10 taxa of arthropods, comprised of mites and springtails. Of the six species with enough abundance to analyze, they found a vertical separation of the species, with three occurring near the surface, two in an intermediate position, and one deep in the mat, resulting in many negative correlations arthropod between species at any given depth. However, when the depths were combined, there were no negative correlations, and many positive correlations were present. Even within a species the vertical distribution differed with life cycle stage. Overall, two distinct communities were present – the green moss community (0-1.5 cm) and the dead moss community (below 3 cm). Nevertheless, the two communities were composed of the same six species, but the proportions differed.

Geothermal

Cold climates are harsh and many organisms do not have the life cycle and physiological adaptations needed to survive in them. However, one habitat provides the year-round warmth for survival of more temperate organisms that are able to arrive there. These are the geothermal areas that are in polar regions of both the Antarctic and Arctic landscapes.

Bryophytes serve as buffers in these habitats. Their own depth insulates the tips of the plants from the heat beneath, and the "steam" emanating from the vents keeps the habitat moist (Glime & Iwatsuki 1990). Lichens seem

unable to survive these hot but moist environments, but the bryophytes protect their own growing tips and survive at higher moist temperatures than those suitable for lichens.

Elmarsdottir *et al*. (2003) address the paucity of knowledge about the geothermal ecosystems. Most studies have been descriptive, with little attention to the interactions of this unique ecosystem. Soil temperatures dominate the limiting factors, with soil *p*H and carbon content also influencing species composition. Nevertheless, a number of bryophytes have been able to tolerate the heat or escape it by providing their own insulation through decaying lower parts. These bryophytes provide homes for invertebrates.

Historically, geothermal areas most likely served as refugia from glaciers, and once glaciers receded, these heated areas permitted recolonization of nearby non-geothermal regions. Fraser *et al*. (2014) tested this hypothesis, based on the expectation that the greatest diversity would occur closest to the geothermal areas. Using Antarctica as a test, they did indeed find the greatest diversity closest to the geothermal areas.

Convey and Lewis Smith (2006) reported that the bryophytes on South Sandwich Islands in the Antarctic had the greatest richness in geothermally influenced ground. In fact, only four of the mosses on the islands were never associated with geothermal areas; 35 moss species and 9 liverwort species were present in all. On the other hand, 8 liverwort and 50% of the mosses occurred only on heated or recently heated geothermal areas. ***Campylopus introflexus*** was the only bryophyte to tolerate the maximum temperatures (40-47°C) of the upper 0.5 cm of the bryophyte layer. The flora of the unheated ground is similar to that of the maritime Antarctic (Convey *et al*. 2000). The heated ground contains species common to both the maritime and sub-Antarctic areas, supporting the importance of the geothermal areas for successful colonization elsewhere

Given the success of bryophytes in geothermal areas, it is easy to imagine that the ubiquitous insects would likewise be represented there, likewise taking advantage of the extra warmth. Even in Hawaii, geothermal areas permit ants to extend to higher elevations than would otherwise be possible (Wetterer 1998).

Boothroyd and Browne (2006) found that the invertebrate species occupying geothermal areas of New Zealand tended to be common species. Willoughby *et al*. (2015) found that the bryophytic fauna in the Waikato Region of New Zealand did not correlate with the soil temperature.

Some studies are focussing on the impact of human activity, especially for harvesting geothermal heat and power, on the flora and fauna (Miller *et al*. 1995). Human activity poses a threat to these fragile systems. Connectivity between suitable sites is important to maintain these communities and their fauna.

Pollution Effects

Bryophytes are well known for their ability to collect air pollutants, especially heavy metals. As a result, we might expect that the bryophagous insects would also have higher concentrations than those feeding on plants that are less efficient collectors (Steiner 1994).

We might also predict that these high concentrations could be lethal for some of the inhabitants. Varga (1992) tested ***Plagiobryum zierii*** (Figure 104) and ***Saelania glaucescens*** (Figure 105) from a polluted roadside in Hungary and found higher lead concentrations in them. Concomitantly, the invertebrate fauna, including insects, was lower than that found in mosses from an unpolluted control site. Furthermore, the invertebrates from the polluted mosses exhibited high concentrations of lead.

Figure 104. ***Plagiobryum zierii*** from Europe, a moss that accumulates lead that can then accumulate in bryophagous insects. Photo by Michael Lüth, with permission.

Figure 105. ***Saelania glaucescens***, a moss that accumulates lead that can then accumulate in bryophagous insects. Photo by Michael Lüth, with permission.

Pollution can have positive or negative effects on insects. When mosses in an area polluted with heavy metals were analyzed, those from less polluted areas had more molybdenum, whereas those from the polluted areas had increased levels of cadmium and chromium (Soltes 1996). These increased Cd and Cr contents corresponded with the areas of spruce bark beetle outbreak.

Climate Change

Pollution with CO_2 is generally blamed for global climate changes. It not only means that some areas will be hotter, some will be colder, more severe storms will occur, water levels will rise, and seasons will have different periodicities, but nutrient levels will change as well.

Richardson *et al*. (2002) examined the impact of changes in nutrients and warming in a sub-Arctic heath on vegetation and insect herbivores. The bryophagous **Heteroptera** in fertilized plots was reduced to as little as 6% that of the unfertilized controls. **Homoptera** that fed on grasses became 400% more abundant. The changes in the insect community was driven primarily by the subordinate plant groups (grasses and mosses), emphasizing the importance of the mosses in this tundra habitat. Nutrients had a greater impact than the rise in temperature.

Summary

Bryophytes serve as habitat for numerous kinds of insects. They provide moisture (an important limiting factor for insects), food, shelter, refuge from predators, and a buffer against the climate. The insects that live there are limited in their adaptations, but some are wingless, have cryptic coloration, are able to eat bryophytes, and are small and flexible enough to maneuver among the bryophytes.

Those that live in northern regions often use mosses as a winter home. They may eat bryophytes to survive in winter and it is possible these bryophytes may help to adapt them to the winter cold, possibly through providing **arachidonic acids**.

Because bryophyte dwellers typically have limited mobility, their dispersal is limited. Fragmented landscapes and separated microhabitats often require corridors that connect the habitats with suitable microhabitats to permit recolonization of disturbed sites.

Although most of the bryophyte inhabitants seem to use the associated invertebrates, algae, bacteria, and fungi as food, some do eat the bryophytes and some are even liverwort specialists. Bryophytes often have secondary compounds that prevent herbivory and those insects that eat bryophytes do have preferences. Some bryophytes are so effective at deterring herbivores that they are being developed as pesticides.

Again because bryophytes have limited mobility, typical insect sampling methods are often inappropriate and biased. Using heat to cause the insects to fall into traps or using pitfall traps may miss whole taxonomic groups that fail to move away from the bryophytes. Hand sorting of bryophyte clumps is the only (nearly) unbiased method, but it is destructive and therefore limits the number of samples.

The most common bryophyte-dwelling arthropods worldwide are spiders, springtails, and mites. The typical orders of insects present include **Collembola**, **Odonata**, **Notoptera**, **Psocoptera**, **Hemiptera**, **Megaloptera**, **Neuroptera**, **Coleoptera**, **Hymenoptera**, **Trichoptera**, **Lepidoptera**, **Mecoptera**, and **Diptera**.

In bogs and wetlands, ants are common ***Sphagnum*** inhabitants making nests of the ***Sphagnum***. **Lepidoptera** are common and depend on plants that depend on the environment created by the bryophytes. Several families of beetles, especially **Carabidae**, live among the bryophytes.

Forest bryophytes have fewer species and the bryophyte fauna there seems to be less well known. In the tropical rain forests, epiphytes provide important habitats, especially for ants and springtails. In cryptogamic crusts of the desert, bryophytes provide a refuge from the hot sun and a place where moist periods last longer, but the life cycle needs to be attuned to the short moist periods or the insects must be able to burrow deep into the soil.

At high altitudes, in the tundra, and in the Antarctic, the bryophytes are the most hospitable habitat for terrestrial insects, providing a buffer against the extreme temperatures, maintaining moisture, and harboring smaller food organisms. It is also likely that they protect against UV light. Geothermal areas in these cold regions provide a haven for species normally found in warmer habitats, and the bryophytes are usually the dominant vegetation.

Bryophytes are known accumulators of air pollutants, so insects that eat them or eat other invertebrates that eat them may be seriously affected by the accumulated heavy metals. A warming climate is likely to decrease the bryophytes in northern climates and thus affect the insect herbivores. Furthermore, increases in nutrients resulting from climate warming cause decreases in bryophagous **Heteroptera** and increases in **Homoptera** that feed on grasses.

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CHAPTER 12-2
TERRESTRIAL INSECTS: HEMIMETABOLA – COLLEMBOLA

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CHAPTER 12-2
TERRESTRIAL INSECTS: HEMIMETABOLA – COLLEMBOLA

Figure 1. ***Hypogastrura*** sp. on ***Schistidium apocarpum***. Photo by Christophe Quintin, through Creative Commons.

Meet the Collembola

These tiny creatures, the springtails, are easily overlooked until they start popping about before your eyes. Previously considered to be insects, they are currently placed in the class **Entognatha**, where the name **Collembola** has been elevated from an order to a subclass. Among the bryophytes, they blend with the dark crevices between the leaves. Numerous studies attest to their frequency among bryophytes (*e.g.* Bonnet *et al*. 1975; Acon & Simon 1977; Skarzynski 1994). The bryological habitat is likely to yield some surprises, even new species (Acon & Simon 1977; Skarzynski 1994).

Their diversity includes the tiny non-jumping ones to the larger ones equipped with a **furcula** (Figure 2) that permits them to spring like those metal cricket toys some of us remember (Kinchin 1992). A **collophore** (Figure 3) holds the furcula in place and ready to spring. The collophore may be used in osmoregulation, water intake, and excretion (Wikipedia 2016). By comparative body size, these 15-cm jumps are equivalent to a human jumping over the Eiffel Tower (Shockley 2011). Like other insects, they shed their outer covering (**exuvia**; Figure 4-Figure 5) in order to grow.

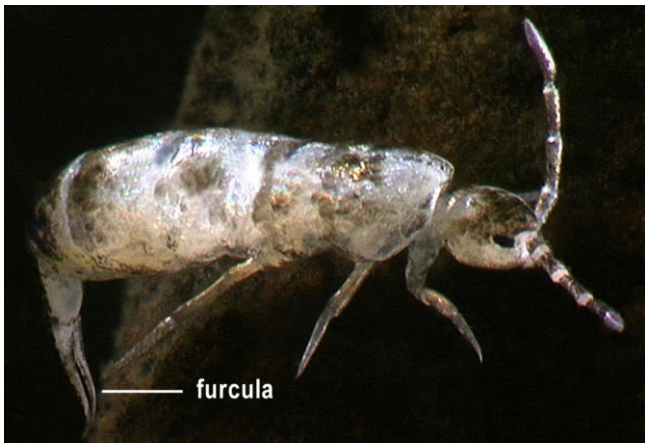

Figure 2. ***Arthropleona oruarangi*** showing **furcula**. Photo by Stephen Moore, Landcare Research, NZ, with permission.

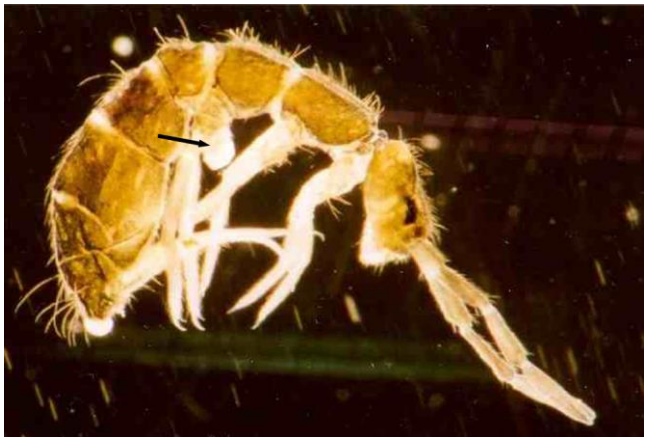

Figure 3. ***Isotoma*** (springtail) showing **collophore** (**arrow**). Photo by U. Burkhardt, through Creative Commons.

Figure 4. ***Kalaphorura burmeisteri*** molting. Note the clean new covering exposed on the thorax as the old one splits to become the **exuvia**. Photo by Andy Murray, with permission.

Figure 5. ***Dicyrtoma fusca*** with **exuvia**. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.

Swan (1992) suggests that "insects" such as the primitive **Collembola** may have invaded land even before the early bryophytic land plants. Mosses are often present as a photosynthetic band at the edge of **Aeolian** (wind erosion) zones, benefitting from nutrients delivered by the winds. But these windborne nutrients were available even before mosses arrived, with organic compounds collecting along the Aeolian zone. It is not hard to imagine, then, that when mosses appeared, **Collembola** colonized them.

Moisture Needs

It is easy to imagine that bryophytes can help to maintain moisture for **Collembola** in many habitats. But in many habitats both bryophytes and **Collembola** are susceptible to desiccation stress (Verhoef & Witteveen 1980). Some **Collembola** produce a special grooming fluid (Figure 6) that keeps their heads moist (Shockley 2011). They have two inflatable tubes (Figure 6) that help them to distribute the fluid. These tubes double as "arms" if the springtail lands on its back – the tubes are used to stick to the substrate and pull the springtail over to its proper position or to attach it to the substrate to prevent it from tumbling on an incline.

Figure 6. ***Sminthurus*** cf ***wahlgreni*** with its inflatable **adhesion tube** attached to its abdomen. Note drops of grooming fluid on the head and abdomen. Photo by Jan van Duinen, with permission.

Reproduction

Mating is a bit unusual in the springtails. Rather than depositing sperm into the female, the male produces a small packet (**spermatophore**; Figure 7-Figure 8) that he attaches on a short stalk onto a substrate (Shockley 2011). The female must then take the spermatophore into her reproductive tract. The mating itself can take many forms in an attempt to insure that a female will attain the sperm. These include

1. random deposition of spermatophores across the landscape.
2. deposition of a spermatophore followed by the male using antennae to drag the female across it.
3. locating a female and depositing multiple spermatophores; male then tries to lure the female through this "garden" of spermatophores.
4. locating a female and surrounding her with spermatophores so she must contact one or more to escape.
5. holding a male-female courtship dance [*e.g.* ***Deuterosminthurus pallipes*** (Figure 9) – a species found among mosses in the floodplain meadow of the Kargy River in Russia (Bretfeld 2010)], doing a face-to-face push and retreat ritual to establish a rhythm. As the female tries to get away, the male continues to woo her. If the female accepts, the male deposits the spermatophore directly in front of her; she picks it up

and either deposits it in her reproductive tract or – eats it.

Figure 7. ***Lepidocyrtus*** sp. with a spermatophore at the lower far right. Photo by Andy Murray, with permission.

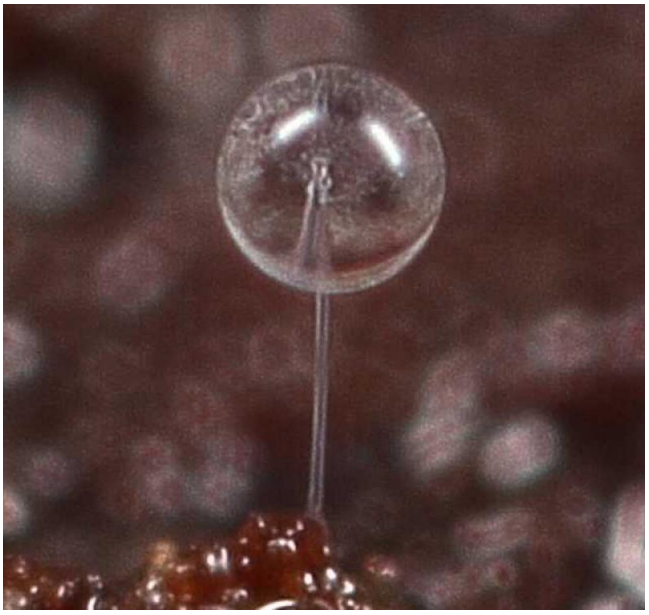

Figure 8. **Isotominae** spermatophore. Photo by Jan van Duinen, with permission.

Figure 9. ***Deuterosminthurus pallipes*** courting; the female is the larger one. Photo by Jan van Duinen, with permission.

Some species, *e.g.* ***Folsomia candida*** (Figure 10-Figure 11) (**Isotomidae**), are **parthenogenetic** (giving birth without fertilization). This is helpful in the disconnected bryophyte patches where contact is limited.

Figure 10. ***Folsomia candida*** with eggs. Photo by Steve Hopkin, with permission.

Figure 11. ***Folsomia candida*** with young. Photo by Steve Hopkin, with permission.

Christiansen *et al.* (1992) reported a generation time of about one month for most laboratory-reared **Collembola** species. But some species are **univoltine** (one generation per year) and others are **multivoltine** (more than one generation per year) (Hopkin 1997). Mitchell (1977) provided evidence that **Collembola** communities have seasonal fluctuations in composition and numbers.

Dispersal

Data for dispersal rates for **Collembola** dwelling among the bryophytes seem to be lacking. But those living in soil and those living within the bryophyte clumps may be similar. Ojala and Huhta (2001) determined the rate for soil **Collembola** to be 0.5-1 cm per week, compared to 1-2 cm per week for cryptostigmatic mites. This of course is likely to be different if they must migrate between patches where they can hop much longer distances than the

distances travelled within the confines of the moss mat itself.

For the moisture-requiring **Collembola**, winter is often the time for dispersal, a feat often accomplished across the snow (Figure 12) (Leinaas 1981a, b, c; Hågvar 1995; Zettel 1984, 1985; Zettel & Zettel 1994).

Figure 12. **Collembola –** snow flea on snow. Photo by Bob Armstrong, with permission.

It might be useful to consider the possibility of springtails being dispersed along with the bryophytes, a phenomenon already considered for tardigrades (Janiec 1996). Although this may be a rare occurrence for larger adults, might small species or the eggs get dispersed on bryophyte fragments in the winter when bits can travel long distances across the snow and even glaciers (Miller & Howe Ambrose 1976)?

Collembola appear early in succession of new moss colonies. The first organisms to appear are rotifers and protozoa (Mukerji *et al*. 2000). These are followed by nematodes, mites, and **Collembola** once the moss has formed a detrital layer. In high altitudes, the **Collembola** abound among colonizing mosses, which also serve as their food (Mani 1962).

On the other hand, Sinclair *et al*. (2003) found that **Collembola** not only graze on bryophytes, but that mosses may be essential to their temperature maintenance in the Antarctic. When the springtail ***Desoria klovstadi*** (**Isotomidae**; see Figure 105) was collected while foraging on moss, it had a high **supercooling point** (point of crystallization), but when the animals were starved for 2-8 hours, the supercooling point shifted towards the low group. But acclimating them with lichen or algae for five days resulted in even higher supercooling points than if supplied with moss, while those starved (with free water or 100% relative humidity) displayed a trimodal supercooling point distribution. On the other hand, the supercooling point of this springtail was lower when they were acclimated for five days and provided with moss than when supplied with algae or lichens. Sinclair and coworkers found that other pretreatments, including cold, heat, desiccation, and slow cooling, did not induce any supercooling point shifts, suggesting that their diet of mosses, algae, and lichens may have been the controlling factors. They suggested that vertical migration might permit the springtails to escape the cooler temperatures of night. In other Antarctic locations, vertical distributions indicate distinct communities (Usher & Booth 1984).

Bryophytes as a Habitat for Springtails

Kinchin (1990) considered the **Collembola** to be one of the two most abundant groups among bryophytes, the other being the mites. Studies from wide-ranging locations have demonstrated the importance of the bryophytes as habitats (*e.g.* Mexico: Varga 1989, 1991; Varga & Vargha 1992; Brazil: Abrantes *et al*. 2010; Hungary: Traser *et al*. 2006; Antarctica: Seppelt & Ochyra 2008). In Brazil, ***Brachystomella agrosa*** (see Figure 13), ***B. contorta*** (**Brachystomellidae**), ***Seira melloi*** (see Figure 14), ***S. subannulata*** (**Entomobryidae**), and ***Ballistura fitchi*** (**Isotomidae**) inhabit mosses (Abrantes *et al*. 2010).

Figure 13. ***Brachystomella parvula*** juvenile, a moss dweller. Pigment protects it from UV light. Photo by Andy Murray, with permission.

Figure 14. ***Seira dollfusi***, from a genus that inhabits mosses in Brazil. Photo by Andy Murray, with permission.

Božanić (2011) considered the bryophytes to be important habitats for hiding from predators and unfavorable weather, for feeding, and for laying eggs. Bryophytes absorb water rapidly, reduce substrate evaporation, and insulate against temperature and wind (Gerson 1982; Smrz 1992; Andrew *et al*. 2003). By ameliorating the habitat conditions, they permit **Collembola** to aggregate (Figure 190), thus avoiding dry conditions (Joose & Verhoef 1974; Leinaas & Sømme 1984; Usher & Booth 1984).

For those who are eager to find new species, bryophytes are a good habitat for finding such treasures. Skarzynski (1994) found two species new to the Polish flora by looking at ***Sphagnum*** (Figure 15) inhabitants. Their small size makes these springtails easy to overlook, and sorting through samples with a microscope is time-consuming and destructive. Because of the chambered structure of the mosses, most extraction techniques are not as effective as in other kinds of samples. (See Sampling below.)

Figure 15. ***Sphagnum angustifolium***, a moss where one might find new springtail species by careful sorting. Photo by Michael Lüth, with permission.

Species and Abundance

Species numbers, abundance, and dominance in bryophyte **Collembola** communities can vary widely between locations, as can be seen in Figure 17 (Traser *et al*. 2006). Traser and coworkers collected 60 species (3,451) of **Collembola** in 18 moss species in three habitats in Hungary. The highest diversity was in the reed bed (Tómalom), accompanied by very low abundance and more evenness than the other two sites: Fertőrákos is a dry grass habitat and Sopron is a Botanic Garden, both with lower diversity and higher richness. Interestingly, the **bryobiont** (animal that occurs exclusively associated with bryophytes) ***Hymaphorura dentifera*** was absent, but several **bryophilic** (bryophyte-loving) species (*e.g.* ***Xenylla boerneri***; Figure 144) were present. None of the dominant species is restricted to bryophytes. The two most abundant species were ***Cryptopygus bipunctatus*** (Figure 28) and ***Folsomia manolachei*** (Figure 29). ***Sphaeridia pumilis*** (Figure 53) and ***Parisotoma notabilis*** (Figure 187) occurred on ***Calliergonella cuspidata*** (Figure 16) in two locations. ***Brachythecium rutabulum*** (Figure 161) housed four species whereas ***Hypnum cupressiforme*** (Figure 18) housed 14. ***Entomobrya nivalis*** (Figure 86) occurred on ***H. cupressiforme*** in two locations. The most abundant species were different for each location (Figure 17). The dominant species primarily belong to the families **Isotomidae** and **Hypogastruridae** [followed by **Entomobryidae** and **Symphypleona** (spherical springtails)]. Moss-dwelling species included:

Hypogastruridae (Figure 1): ***Hypogastrura socialis***, ***Hypogastrura vernalis*** (Figure 19), ***Xenylla boerneri*** (Figure 144), ***Xenylla maritima*** (Figure 82), ***Xenylla brevicauda***, ***Willemia virae*** (see Figure 20)

Brachystomellidae: ***Brachystomella parvula*** (Figure 13)

Neanuridae: ***Friesea truncata*** (see Figure 157), ***Anurida pygmaea*** (Figure 21), ***Neanura muscorum*** (Figure 166)

Onychiuridae: ***Supraphorura furcifera*** (Figure 22), ***Protaphorura armata*** (Figure 23)

Tullbergiidae: ***Doutnacia xerophila*** (see Figure 24), ***Mesaphorura critica***, ***Mesaphorura hylophila*** (Figure 25), ***Tullbergia krausbaueri***, ***Tullbergia macrochaeta*** (Figure 26), ***Metaphorura affinis*** (Figure 27)

Isotomidae: ***Pachyotoma crassicauda***, ***Cryptopygus bipunctatus*** (Figure 28), ***Folsomia manolachei*** (Figure 29), ***Folsomia penicula*** (Figure 30), ***Folsomia quadrioculata*** (Figure 88), ***Isotomiella minor*** (Figure 31), ***Parisotoma notabilis*** (Figure 187), ***Isotoma viridis*** (Figure 32), ***Isotoma riparia*** (Figure 33), ***Isotomurus*** cf. ***palustris*** (Figure 34), ***Isotomurus prasinus*** (Figure 35)

Entomobryidae: ***Entomobrya corticalis*** (Figure 36), ***Entomobrya handschini*** (Figure 37), ***Entomobrya multifasciata*** (Figure 38), ***Entomobrya nigriventris***, ***Entomobrya nivalis*** (Figure 86), ***Lepidocyrtus cyaneus*** (Figure 120), ***Lepidocyrtus lanuginosus*** (Figure 39), ***Lepidocyrtus lignorum*** (Figure 40), ***Lepidocyrtus paradoxus*** (Figure 41), ***Lepidocyrtus peisonis***, ***Lepidocyrtus violaceus*** (Figure 42), ***Pseudosinella alba*** (Figure 43), ***Pseudosinella octopunctata*** (Figure 44)

Orchesellidae: ***Orchesella cincta*** (Figure 68), ***Orchesella bifasciata*** (Figure 150), ***Orchesella xerothermica*** (Figure 45), ***Heteromurus major*** (Figure 46), ***Heteromurus nitidus*** (Figure 47)

Tomoceridae: ***Tomocerus*** cf. ***baudoti*** (Figure 48), ***Tomocerus minor*** (Figure 164-Figure 165)

Cyphoderidae: ***Cyphoderus albinus*** (Figure 49)

Oncopoduridae: ***Oncopodura crassicornis*** (Figure 50)

Neelidae: ***Megalothorax minimus*** (Figure 51), ***Neelides minutus*** (Figure 52)

Sminthuridae: ***Sphaeridia pumilis*** (Figure 53)

Katiannidae: ***Sminthurinus elegans*** (Figure 54), ***Sminthurinus aureus*** (Figure 55)

Dicyrtomidae: ***Dicyrtoma fusca*** (Figure 5)

Bourletiellidae: ***Deuterosminthurus bicinctus*** (Figure 56), ***Fasciosminthurus strigatus***, ***Heterosminthurus bilineatus*** (Figure 57)

Figure 16. ***Calliergonella cuspidata***, home to the springtails ***Sphaeridia pumilis*** (Figure 53) and ***Parisotoma notabilis*** (Figure 187) in Hungary. Photo by Michael Lüth, with permission.

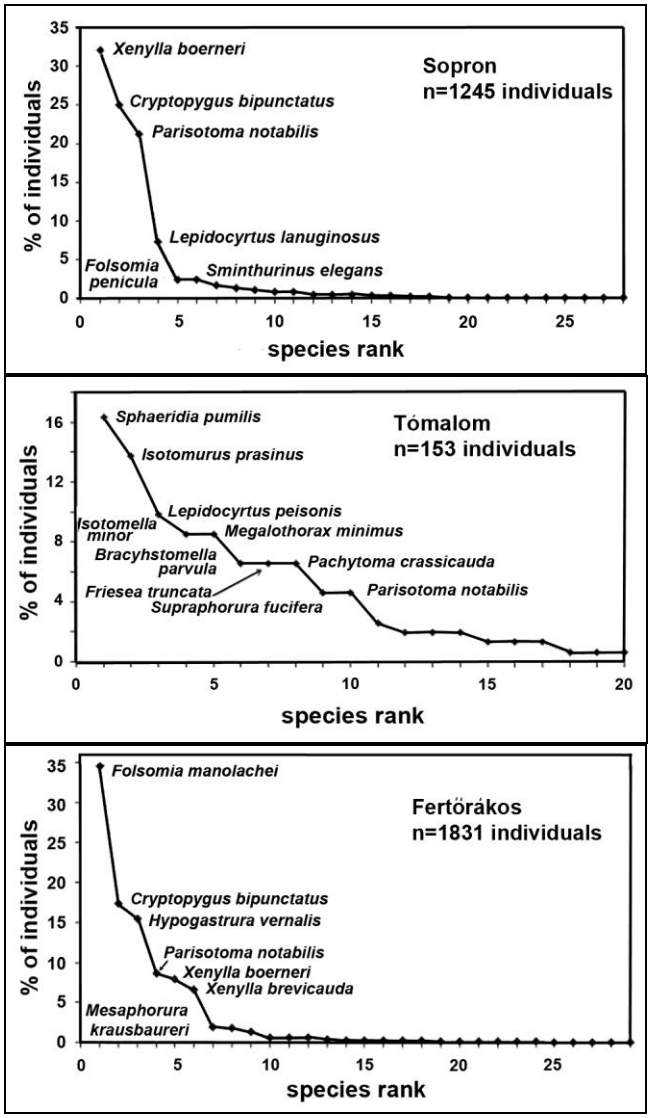

Figure 17. Comparison of dominant species and percent of individuals at three locations in Hungary. Redrawn from Traser *et al*. 2006.

Figure 18. ***Hypnum cupressiforme***, home for at least 14 species of springtails in Hungary. Photo by Michael Lüth, with permission.

Figure 19. ***Hypogastrura vernalis***, a moss dweller in Hungary. Photo by Arne Fjellberg, through Creative Commons.

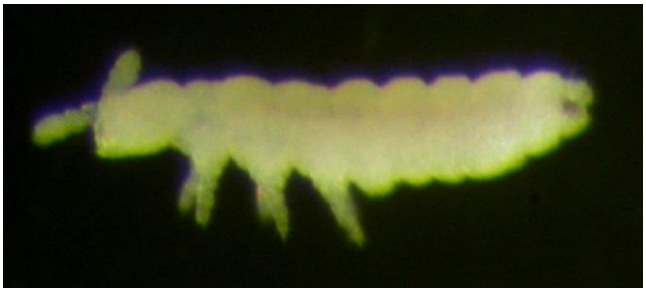

Figure 20. ***Willemia similis***, a moss dweller in Hungary. Photo by Arne Fjellberg, through Creative Commons.

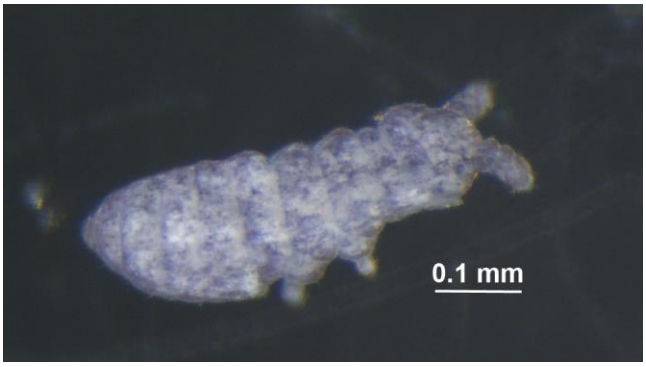

Figure 21. ***Anurida pygmaea***, one of the tiny moss-dwelling **Collembola**. Photo by David Porco, through Creative Commons.

Figure 22. ***Supraphorura furcifera***, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.

Figure 23. ***Protaphorura armata***, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.

Figure 24. **Tullbergiidae**; several members, including ***Doutnacia xerophila***, occur among mosses in Hungary. Photo by Andy Murray, through Creative Commons.

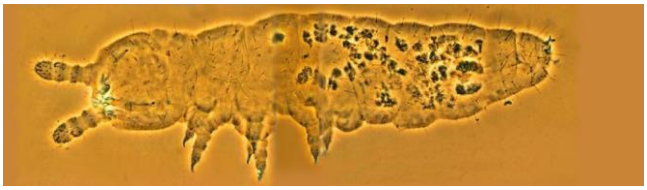

Figure 25. ***Mesaphorura hylophila***, a moss dweller in Hungary. Photo by Steve Hopkin, with permission.

Figure 26. ***Tullbergia macrochaeta***, a moss dweller in Hungary. Note the absence of eyes. Photo by Andy Murray, through Creative Commons.

Figure 27. ***Metaphorura affinis***, a blind moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.

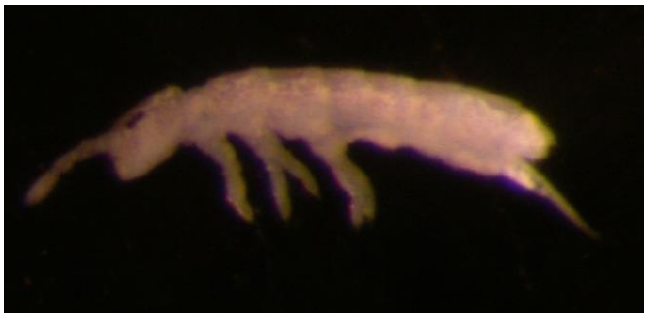

Figure 28. ***Cryptopygus bipunctatus***, a common species among mosses in Hungary. Photo by Arne Fjellberg, through Creative Commons.

Figure 29. ***Folsomia manolachei***, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.

Figure 30. ***Folsomia penicula***, a moss dweller in Hungary. Photo by Galina Bushmakiu, through Creative Commons.

Figure 31. ***Isotomiella minor***, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.

Figure 32. ***Isotoma viridis*** var. ***violacea.*** This species lives among mosses in Hungary. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.

Figure 33. ***Isotoma riparia***, a moss dweller in Hungary. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.

Figure 34. ***Isotomurus palustris***, a species associated with both aquatic and terrestrial bryophytes. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.

Figure 35. ***Isotomurus prasinus*** or ***I. gramineus***, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.

Figure 36. ***Entomobrya corticalis***, a bryophyte dweller in Hungary. Photo by Miroslav Deml, through Creative Commons.

Figure 37. ***Entomobrya handschini***, a moss dweller in Hungary. Photo by Steve Hopkin, with permission.

Figure 38. ***Entomobrya multifasciata***, a moss dweller in Hungary. Photo by Valter Jacinto, through Creative Commons.

Figure 39. ***Lepidocyrtus lanuginosus***, a moss dweller in Hungary. Photo by Andy Murray, with permission.

Figure 40. ***Lepidocyrtus lignorum***, a moss dweller in Hungary. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.

Figure 41. ***Lepidocyrtus paradoxus***, a moss dweller in Hungary. Photo by Christophe Quintin, through Creative Commons.

Figure 42. ***Lepidocyrtus violaceus***, a moss dweller. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.

Figure 43. ***Pseudosinella alba***, an inhabitant of mosses in Hungary. Photo by Andy Murray, through Creative Commons.

Figure 44. ***Pseudosinella octopunctata***, a moss dweller in Hungary. Photo by Galina Bushmakiu, through Creative Commons.

Figure 45. ***Orchesella xerothermica***, a moss dweller in Hungary. Photo by Galina Bushmakiu, through Creative Commons.

Figure 46. ***Heteromurus major***, a moss dweller in Hungary. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.

Figure 47. ***Heteromurus nitidus***, a moss dweller in Hungary. Photo by Steve Hopkin, with permission.

Figure 48. ***Tomocerus baudoti***, a moss dweller in Hungary. Photo by Louis Deharveng, through Creative Commons.

Figure 49. ***Cyphoderus albinus***, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.

Figure 50. ***Oncopodura crassicornis***, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.

Figure 51. ***Megalothorax minimus***, a tiny moss dweller. Photo by Andy Murray, through Creative Commons.

Figure 52. ***Neelides minutus***, a tiny moss dweller. Photo by Andy Murray, through Creative Commons.

Figure 53. ***Sphaeridia pumilis*** on mosses. Photo by Andy Murray, through Creative Commons.

Figure 54. ***Sminthurinus elegans***, a springtail with markings that could hide it among mosses. Photo by Scott Justis, with permission.

Figure 55. ***Sminthurinus aureus*** forma ***maculata***, a moss dweller shown here with **Cyanobacteria**. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.

Figure 56. ***Deuterosminthurus bicinctus***, a springtail that lives among mosses in Hungary. Photo by Andy Murray, through Creative Commons.

Figure 57. ***Heterosminthurus bilineatus*** female, a moss dweller. Photo by Jan van Duinen, with permission.

The greatest numbers of bryophyte-dwelling **Collembola** seem to be those in the Antarctic. But abundance numbers seem to be rare in the literature. Matveyeva (1972) found that moss carpets in the tundra sedge-moss community of Taimyr, USSR, supported 4000 **Collembola** per square meter. That moss carpet area accumulates more snow than areas with turf and the mosses may provide a protected habitat in which the **Collembola** can move and find sufficient food without being detected.

At Spitsbergen, mites and springtails comprised 96-99% of the total arthropods, numbering 268,000 individuals m^{-2} in the wet moss tundra compared to 42,000-63,000 on lichen tundra and 518,000 on grassland there (Bengtson *et al*. 1974).

Božanić (2011) reported 1341 Collembola in individual samples from the Litovelské luhy National Nature Reserve, Czech Republic, compared to only 137 in the control samples (soil, wood, *etc*.). These numbers compared to 2946 mites and 320 isopods. Other groups exhibited lesser numbers.

In the Antarctic, mites and springtails typically dominate the bryophyte habitat. **Collembola** [especially ***Parisotoma octooculata*** (Figure 58) and ***Cryptopygus antarcticus*** (Figure 78)] ranged up to 20,540 individuals per 100 cm^2 of ***Polytrichastrum alpinum*** (Figure 64) (Schenker & Block 1986).

Figure 58. ***Parisotoma octooculata***, a common bryophyte inhabitant in the Antarctic. Photo by Te Papa, through Creative Commons.

Food

Collembola are opportunists, feeding on fungi, detritus, and mosses (Gerson 1969; Peterson & Luxton 1982; Hodkinson *et al*. 1994; Chen *et al*. 1995; Varga *et al*. 2002a, b). Ponge (2000) demonstrated that **Collembola** living in soil of 13 Belgian beech forests had gut contents that corresponded with the available food in their immediate proximity. Nevertheless, the **Onychiuridae** (Figure 59) exhibited plasticity of food items based on depth.

Figure 59. ***Onychiurus*** sp., a species with adaptable food preferences. Photo by Andy Murray, through Creative Commons.

At least some **Collembola** eat bryophytes. And they have actually been seen eating mosses in Antarctica (Pryor 1962; Janetschek 1967). In addition, Pryor (1962) successfully reared them on mosses in the lab. ***Gomphiocephalus*** (Figure 60 - Figure 61) (**Hypogastruridae**) prefers mosses over **Cyanobacteria**, red lichens, and the mold ***Penicillium*** (in Gerson 1969). Gerson (1969) reported that ***Isotoma*** feeds extensively on mosses. ***Desoria klovstadi*** (see Figure 105) prefers mosses over fungi and feeds extensively on them (Pryor 1962). Nevertheless, Davis (1981) found no evidence of **Collembola** feeding on bryophytes in two Antarctic terrestrial moss communities. Despite the dominance of bryophytes in the flora of Antarctica, Block (1985) similarly found that arthropods feed on epiphytic algae, micro-flora, and detritus.

Figure 60. ***Gomphiocephalus*** feeding on algae that are growing on ***Bryum argenteum*** on the continent of Antarctica. Photo courtesy of Catherine Beard.

Figure 61. ***Gomphiocephalus*** feeding on the lichen ***Caloplaca setrina*** growing on dead ***Bryum argenteum*** in the Antarctic. Photo courtesy of Rod Seppelt.

Merrifield (2000) suggested that **Collembola** may graze on some bryophytes, possibly causing the increased dependence on gemmae for reproduction. A search of the moss ***Syntrichia laevipila*** (Figure 62) revealed considerable grazing, but this could also have been the activity of slugs.

Figure 62. ***Syntrichia laevipila*** with capsules, a species that is grazed, possibly by **Collembola**. Photo by Michael Lüth, with permission.

Megaphorura arctica (Figure 63) (**Onychiuridae**) in West Spitsbergen feeds mostly on living and dead bryophytes, detritus, and sometimes algal cells (Hodkinson *et al*. 1994). The bryophytes include ***Sanionia uncinata*** (Figure 184-Figure 185), ***Polytrichastrum alpinum*** (Figure 64), and ***Racomitrium lanuginosum*** (Figure 65-Figure 66).

Figure 63. ***Megaphorura arctica***, a species that feeds on living and dead bryophytes in Spitsbergen. Photo by Arne Fjellberg, through Creative Commons.

Figure 64. ***Polytrichastrum alpinum***, a springtail habitat and food in cold places. Photo by John Hribljan, with permission.

Figure 65. ***Racomitrium lanuginosum*** hummocks, common **Collembola** habitat in the Arctic. Photo by Janice Glime.

Figure 66. ***Racomitrium lanuginosum***, a source of food and shelter for **Collembola**, as snow is melting. Photo by Michael Lüth, with permission.

The fungi within bryophyte mats can serve as a food source for bryophyte dwellers (Varga *et al*. 2002b). McMillan and Healey (1971) found mosses in guts of the genus ***Tomocerus***. But even the fungi they eat might be moss inhabitants. The springtails ***Tomocerus longicornis*** (Figure 67) (**Entomobryidae**) and ***Orchesella cincta*** (Figure 68) (**Entomobryidae**) feed on fungi living on the moss ***Tortella tortuosa*** (Figure 69) preferentially over other fungi (Varga *et al*. 2002b). One can recognize ***T. longicornis*** because when it is disturbed, it curls the ends of its antennae (Figure 67). Gut contents of these two species consisted of detritus (55 & 63%), moss particles (20 & 33%), and fungal propagules (10 & 24%), respectively. The fungal gut contents were not in the same proportion as those on the moss, indicating that the springtails were selective in their choice of fungi.

Figure 67. ***Tomocerus longicornis*** showing coiled antennae in response to disturbance. Photo by Steve Hopkin, with permission.

Figure 68. ***Orchesella cincta***, a moss dweller that feeds on the fungi living there**.** Photo by G. Drange, through Creative Commons.

Figure 69. ***Tortella tortuosa***, home of fungi that serve as food for springtails. Photo by Michael Lüth, with permission.

Many springtails that live among mosses are treated to choices of fungi that grow in the association. At least some springtails are able to use olfactory cues – scents provided by the fungi – to both locate the fungi and to distinguish those that are poisonous (Staaden *et al*. 2011).

Bengtsson *et al*. (1988) further supported this discriminatory ability in the springtail ***Onychiurus armatus*** (**Onychiuridae**; see Figure 59). This species locates **hyphomycetous** fungi (fungi in Hyphomycetes; molds) by volatile compounds released by the **mycelium** (fungal threads). However, their choice of species differs depending on whether the fungus was grown on agar or on soil.

Sarah Lloyd sent me images of a Tasmanian endemic springtail species of ***Acanthanura*** (Figure 70) apparently dining on the plasmodium of the slime mold ***Diderma*** sp. (Figure 70-Figure 71) which is growing on a moss.

Predators

Bryophytes can be safe sites for the smaller creatures such as springtails. They make movement and even striking difficult for larger predators. But when the springtails are in the open spaces (Figure 72), their best protection is their powerful spring.

Figure 70. ***Acanthanura*** sp. (springtail genus endemic in Tasmania) on slime mold plasmodium (probably ***Diderma*** sp) on a moss. Photo courtesy of Sarah Lloyd.

Figure 71. ***Diderma*** fruiting bodies on moss. Photo courtesy of Sarah Lloyd.

Figure 72. The ant *Lasius flavus* with springtails (***Cyphoderus albinus***) and no immediate place for the springtails to hide. Photo by Andy Murray, through Creative Commons.

Miller *et al*. (2008) found a positive correlation among the bryophytes, springtails, and spiders in the Acadian Forest of Maine, USA. However, they found no correlation between number of **Collembola** and adult spiders (Miller *et al*. 2008). They considered spiders to be potential predators on bryophyte-inhabiting **Collembola**, thus confounding the correlations. The relationship between spiders and **Collembola** was sensitive to a decline in bryophyte abundance. This relationship with spiders might influence the abundance of the Brown Creeper (***Certhia americana***; Figure 73) (Miller *et al*. 2008), a bird that feeds on spiders that feed on springtails that live among bryophytes at the bases of trees (Mariani & Manuwal 1990; Weikel & Hayes 1999).

Figure 73. ***Certhia americana*** (Brown Creeper), part of the food web of bryophytes, springtails, and spiders at tree bases in Maine, USA. Photo by B. J. Stacey, through Creative Commons.

In the coastal grey dunes of France, Bonte and Mertens (2003) found that dwarf spiders considered springtails to be dinner there as well. They found a positive relationship between the phenology of the preferred springtails and the **stenotopic** (tolerating a narrow range of habitats) dwarf spiders. This was especially true for the female spiders because of their dependence on their prey, usually springtails, for reproduction. The spiders and springtails likewise have similar spatial aggregations. And the springtail aggregations typically occur among mosses.

The distribution of the spider ***Coelotes terrestris*** (Figure 74-Figure 75) was positively related to the cover of mosses and negatively related to litter cover in a beech-dominated (*Fagus sylvatica*; Figure 76) forest floor habitat in Europe (Sereda *et al*. 2012). But Sereda and coworkers did not find an association of spiders to prey-rich areas (**Collembola**) at the scale of 100 m, based on pitfall traps. It could be that the moss dwellers were within the moss clumps and not active near the traps, but these **Collembola** did have a positive relationship to medium deadwood pieces (**Entomobryidae** except ***Lepidocyrtus*** spp., Figure 77).

Figure 74. ***Coelotes terrestris***, a predator spider that hangs out in mossy areas to catch **Collembola**. Photo by James K. Lindsey, with permission.

Figure 75. ***Coelotes terrestris*** nest among mosses and needles. Photo by James K. Lindsey, with permission.

Figure 76. ***Fagus sylvatica*** forest floor, habitat where the spider ***Coelotes terrestris*** (Figure 74-Figure 75) is positively related to the cover of mosses. Photo by Nikanos, through Creative Commons.

Figure 77. ***Lepidocyrtus*** sp., a genus that has no relationship to medium deadwood pieces but does have moss dwellers. Photo by Andy Murray, through Creative Commons.

The Antarctic herbivore ***Cryptopygus antarcticus*** (Figure 78) is abundant in areas with bryophytes (Block 1985). The single arthropod predator, the mite ***Gamasellus racovitzai*** (see Figure 79) (**Ologamasidae**), feeds primarily on ***C. antarcticus***, the most abundant of the available prey. In the summer this predator is non-selective and in the winter it does little feeding. Block considers it unlikely that such a predator ever has a shortage of food in bryophyte habitats. This aggregation has a strong relationship to moss cover. However, Usher and Booth (1986) considered ***Gamasellus*** (Figure 79-Figure 80) to have a random distribution. It is probably more accurate to say that the aggregations are random.

Figure 78. ***Cryptopygus antarcticus***, the most abundant moss-dweller in Antarctica. Photo by Richard E Lee Jr., with permission.

Figure 79. ***Gamasellus***; ***G. racovitzai*** is a common predator on **Collembola** in the Antarctic. Photo by Monica Young, Biodiversity Institute of Ontario, through Creative Commons.

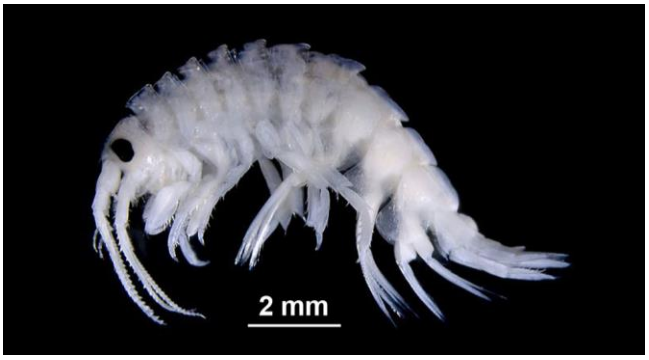

Figure 80. ***Gammarellus angulosus***, member of a genus that is a **Collembola** predator among mosses. Photo by Hans Hillewaert, through Creative Commons.

Wandering Salamanders (***Aneides vagrans***, Figure 81) prey on **Collembola** in the old-growth redwood forest of western USA (Camann 2011). In the canopy the springtails and mites are the most abundant arthropods, with springtails being by far the more abundant group. The salamanders hide in humus moss mats and other more moist locations in the crown of the tree and dine on these abundant springtails.

Figure 81. ***Aneides vagrans***, a predator on **Collembola** that dwell in bryophyte refuges. Photo by Todd Pierson, with permission.

Adaptations

So how does a primitive, tiny, land-invader springtail survive among the bryophytes? First, being tiny is an advantage, making it possible for it to crawl about easily amid bryophyte leaves and stems and hide from predators. Some are blind (Figure 26), but that may be an adaptation to living in soil, with bryophytes also being a suitable habitat. Salmon and Ponge (2012) suggest that blind species may have better developed chemical senses. The ability to survive winter helps too. And its need for water is coupled with the ability to survive desiccation (Leinaas & Sømme 1984), making it well attuned to the wet-dry cycling in bryophytes.

Little has been written about adaptations to living among bryophytes, but Leinaas and Sømme (1984) described adaptations for **Collembola** that live among lichens on alpine rocks. Those should apply for many bryophytes as well, although the species of **Collembola**

may be different. The springtails ***Xenylla maritima*** (Figure 82) (**Hypogastruridae**) and ***Anurophorus laricis*** (Figure 83) (**Isotomidae**) in South Norway have seasonal cold hardiness. They prevent formation of ice crystals by gut evacuation in preparation for winter and accumulate cryoprotective substances during autumn in preparation for winter cold. These activities permit them to supercool below normal expected winter temperatures. However, those springtails in unprotected areas of the rocks were killed by an exceptionally cold period, suggesting the importance of lichens (or bryophytes) as a refuge. These two species are able to survive **anaerobic** (no free oxygen) conditions, permitting them to survive when their habitat is encased in ice. Both are able to survive drought stress. Reproduction later in the season than other **Collembola** species permits the hatchlings to emerge after the driest periods of summer.

Figure 82. ***Xenylla maritima***, a lichen-dwelling species with seasonal cold hardiness in Norway. Photo by Jan van Duinen < www.janvanduinen.nl>, with permission.

Figure 83. ***Anurophorus laricis***, a lichen-dwelling species with seasonal cold hardiness in Norway. Photo by Jan van Duinen < www.janvanduinen.nl>, with permission.

Salmon and Ponge (2012) speculated on adaptations for living among bryophytes and other communities associated with tree bark. They considered a short furcula, dark color, stocky body, and limited number of eyes (Figure 84) to be adaptations to living in concealed environments. These are accompanied by small size and limited movement. Pigmentation provides protection from UV light.

Figure 84. ***Neelus murinus*** showing few eyes and spherical body typical of epiphyte dwellers. Photo by Andy Murray, through Creative Commons.

Collembola commonly form aggregations (Figure 190). Benoit *et al*. (2009) suggest that in the Antarctic, where exposure is more dangerous, the **Collembola** ***Cryptopygus antarcticus*** (Figure 78) and ***Friesea grisea*** (see Figure 157) emit chemical cues (**pheromones**) that help them to locate each other, particularly for mating.

Sampling Methods

Pitfall traps are often used for trapping insects in the soil and have also been used to trap those inhabiting bryophytes (Drozd *et al*. 2009; Sereda *et al*. 2012). Drozd and coworkers express concern that the moss clumps are too dense for ease of movement by most invertebrates. Furthermore, the patchy, random distribution of aggregations of springtails necessitates a large number of samples.

Predators are active on the surface, but they are unable to navigate the "bushy obstacle" created by the mosses. On the other hand, **bryophagous** (eating bryophytes) and **detritivorous** (eating dead organic matter – detritus) arthropods such as **Collembola** have no reason to leave the moss clump, again avoiding traps. Similar problems are encountered when using **fogging** techniques (pesticides) to collect arthropods from canopy bryophytes (Yanoviak *et al*. 2003). The bryophyte dwellers fail to drop from the moss clumps.

Shaw (2013) suggested the use of "inert" pads to collect small arthropods as a nondestructive method in areas with sensitive cover of bryophytes. Standard scouring pads are ideal because of their relatively large pore spaces that somewhat resemble moss clumps. The accumulated arthropods can then be extracted using a Tullgren funnel (see below). He found that the percent of total species of sampled **Collembola** communities were between those of soil and those of bark (Figure 85). The numbers were slightly less than those of soil. I have to wonder if the paucity of food would not greatly decrease the number potential.

Heat gradients are common methods for extracting invertebrates from soil and bryophytes (Tuf & Tvardik 2005; Božanić *et al*. 2013). Nadkarni and Longino (1990)

used a Winkler sifting apparatus to extract insects, including **Collembola**, from tropical canopy samples. Hoyle and Gilbert (2004) used a similar method with the Tullgren funnel. The Berlese funnel is a similar method (Briones 2006). Block (1982) used a gradient of temperature and moisture for six days to extract **Collembola** from bryophytes and soil, based on a method used for lichens (Goddard 1979). Brantley and Shepherd (2004) used heptane flotation to extract springtails and other invertebrates from lichens and mosses in cryptogamic crusts in the piñon-juniper woodland in New Mexico, USA. See Chapter 4-1 of this volume for more information and an illustration on heat gradients.

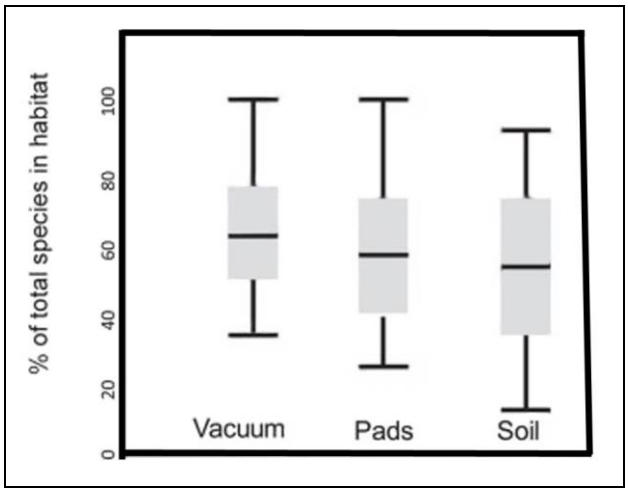

Figure 85. The proportion of **Collembola** collected by three different sampling techniques. Modified from Shaw 2013.

Andrew and Rodgerson (1999) found that the kerosene phase separation was especially more effective in extracting larger numbers of mites and springtails when compared to heat separation with the Tullgren funnel or sucrose flotation (Pask & Costa 1971; see Chapter 12-1 in this volume). Especially for **Collembola**, they concluded that two samples should be used and extracted as replicates, rather than a bulk sample, because of the important effect that spatial scales have on the distribution of these invertebrates.

Temperature Survival

Zettel (1999) examined the cold hardiness of alpine **Collembola**. He found that the winter-inactive hibernator ***Entomobrya nivalis*** (Figure 86) (**Entomobryidae**), an inhabitant of mosses on boulders, builds up cold hardiness in an anticipatory fashion, using photoperiod and temperature as cues, whereas the winter-active ***Isotoma hiemalis*** (**Isotomidae**) only responds to sub-zero (<0°C) temperatures. Alpine populations of ***E. nivalis*** living among the lichens on trees hibernate through the winter in crevices under bark flakes. This was the only alpine species Zettel found to increase its low-molecular-weight antifreeze in the winter, making it more sluggish compared to its behavior at the same temperatures in summer. But when this species overwinters in Norway where the temperatures are even colder, it hibernates under the snow (Leinass 1983).

Figure 86. ***Entomobrya nivalis***, a moss-dwelling species that anticipates oncoming cold based on photoperiod and temperature. Photo by Steve Hopkin, with permission.

Some alpine **Collembola** survive winter by going deeper into the soil (Zettel (1999). Soil surfaces under the snow are typically above 0°C, despite subzero air temperatures. And deeper in the soil the temperature is typically even warmer. Spaces in the soil make such migrations to deeper locations possible.

Pigmentation provides a mechanism for absorbing heat, even at low temperatures. Zettel (1999) reported that only one snow-dwelling, winter-active collembolan in the European alpine area had a light color. All others were dark in color. This dark color simultaneously protects them from the high UV radiation present in the alpine zone.

Since **Collembola** are common among bryophytes in the Antarctic, it is easy to understand that the **Collembola** there must have special means to tolerate the low temperatures. These can include physiological adaptations that protect them against the formation of internal ice crystals, the ability to supercool, and life cycle adaptations in which they are dormant during the long, cold winters. Coulson and Birkenmoe (2000) found that the springtails ***Hypogastrura tullbergi*** (Figure 87) (**Hypogastruridae**) and ***Folsomia quadrioculata*** (Figure 88) (**Isotomidae**) survived for four years at temperatures below -22°C in soil samples in the lab.

Figure 87. ***Hypogastrura tullbergi***, a species that can survive for four years at -22°C. Photo by Arne Fjellberg, through Creative Commons.

Figure 88. ***Folsomia quadrioculata***, a species that can survive for four years at -22°C. Photo by Andy Murray, through Creative Commons.

One mechanism in two common Antarctic **Collembola** species is the ability to **supercool** (Block *et al*. 1978). ***Cryptopygus antarcticus*** (Figure 78) can supercool to -30°C. To do this, they must evacuate the gut by starvation prior to winter cold. This can protect them against internal ice crystal formation by removing water. Such behavior seems to be common among **Collembola** that must endure low temperatures. They lack freeze tolerance, so supercooling is their only physiological survival mechanism (Sømme 1981). For this to work, the gut must be empty to avoid the danger of **ice nucleation** (formation of crystals around proteins and other nucleators). Accumulation of **glycerol** or other **cryoprotectant** (substance that protects against damage by low temperatures) further helps them to survive. Glycerol is used to keep insects from drying out completely in museum collections. Could it serve a similar function for the live animal?

Cannon (1986) likewise demonstrated the importance of evacuation of the gut in preparation for cold weather. He investigated the common ***Cryptopygus antarcticus*** (Figure 78) (**Isotomidae**) from Signy Island in the Antarctic. If the animal has a diet of moist algae and distilled water at 5°C, it loses most of its ability to supercool. The guts of field-collected animals contain unicellular green algae, dead mosses, fungi, and mineral particles, but living mosses are absent in the gut. As winter approaches, these springtails exhibit a decline in feeding activity. Those foods containing potential **ice nucleators** (small particles such as proteins that serve as the centers for ice crystal formation; such crystals damage cell membranes) are eliminated and replaced by alcohols such as **glycerol**. The glycerol renders a **cryoprotective** (protection against cold) role and is produced in response to low temperatures.

Some Antarctic **Collembola** survive because they live among bryophytes in geothermal areas where temperatures remain warm year-round. In the heat-tolerant ***Campylopus introflexus*** (Figure 89), the upper 0.5 cm of the moss remains at 40-47°C (Convey & Lewis Smith 2006). More **Collembola**-friendly temperatures occur in slightly cooler geothermal sites. The mosses ***Anisothecium hookeri***, ***Sanionia georgico-uncinata***, ***Pohlia nutans*** (Figure 90-Figure 91), and ***Notoligotrichum trichodon*** (Figure 92), and the liverworts ***Cryptochila grandiflora*** (Figure 93) and ***Marchantia berteroana*** (Figure 94) live where temperatures are 25-35°C and subsurface temperatures are 50-60°C.

Figure 89. ***Campylopus introflexus***, a common springtail habitat in geothermal areas. Photo by Michael Lüth, with permission.

Figure 90. ***Pohlia nutans***, showing extensive bed of the ubiquitous moss that houses springtails in geothermal areas of Antarctica. Photo by Michael Lüth, with permission.

Figure 91. ***Pohlia nutans***, a ubiquitous moss that houses springtails in geothermal areas of Antarctica. Photo by Michael Lüth, with permission.

Figure 92. ***Notoligotrichum trichodon***, a moss that provides suitable temperatures for **Collembola** in geothermal areas of Antarctica. Photo by Jan-Peter Frahm, with permission.

Figure 93. ***Cryptochila grandiflora***, a leafy liverwort that provides a suitable habitat for **Collembola** in geothermal areas of the Antarctic. Photo by Juan Larrain, with permission.

Fertilizing Mosses

The most exciting bryological discovery this century, at least for me, has been that of arthropod fertilization of mosses. This was presented to us in a video at the biennial meeting of the International Association of Bryologists in Kuala Lumpur, Malaysia. Cronberg *et al*. (2006) found that the relationship between mosses and mites (***Scutovertex minutus***, **Scutoverticidae**) or **Collembola** (***Isotoma caerulea***, **Isotomidae,** Figure 95) can be **mutualistic** (both benefitting). In their experiments, these arthropods served as sperm vectors for the moss. This relationship permits sperm to reach females 10 cm, even 1 m, away (Milius 2006). In experiments, if the mosses were even as close as 2-4 cm, they did not reproduce unless they had one of these arthropod vectors to transfer the sperm. The springtails are more effective than the mites in making the transfer. Both seem to be attracted by something in the female moss because they visit it more often than they do the males (Figure 96 (see also Chapter 6-3 in this volume). That's good, because one visit to a male could potentially carry many sperm and thus fertilize a number of females.

Figure 94. ***Marchantia berteroana*** female, a thallose liverwort that provides a suitable habitat for **Collembola** in geothermal areas of the Antarctic. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 95. ***Isotoma caerulea*** on mosses, a species that fertilizes some moss species. Photo by Andy Murray, through Creative Commons.

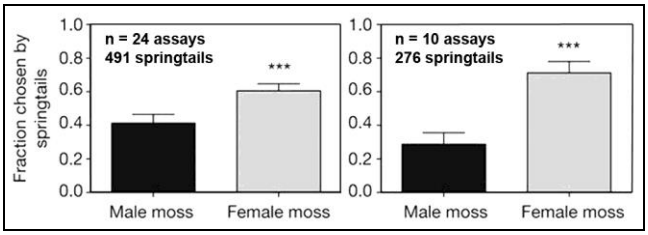

Figure 96. Gender preference of ***Ceratodon purpureus*** by springtails in Petri dishes (**left**) and olfactometer (**right**). Bars are means with error bars. ****P*<0.0001. From Milius 2006.

Both of the mosses ***Ceratodon purpureus*** (Figure 97) and ***Bryum argenteum*** (Figure 98-Figure 99) use springtails (***Folsomia candida***, Figure 10-Figure 11,

Figure 97) to transfer their sperm (Cronberg *et al*. 2008; Rosenstiel *et al*. 2012). It is ironic that this species that lacks sexual reproduction itself helps to accomplish it in mosses. Rosenstiel *et al.* demonstrated that springtails are attracted by volatile substances emitted from the moss ***Ceratodon purpureus***. Furthermore, these volatile chemicals are sex-specific. Much as in flowering plant pollination, the springtails significantly increase moss fertilization rates (Figure 100). But unlike in pollination, water is important in springtail transfer of sperm. Rosenstiel and coworkers found that water alone and springtails alone were equally effective at fertilizing mosses, but when the two were present together, moss reproduction was more than twice as successful (Figure 100).

Figure 98. ***Bryum argenteum*** males with perigonia. Photo by George J. Shepherd, through Creative Commons.

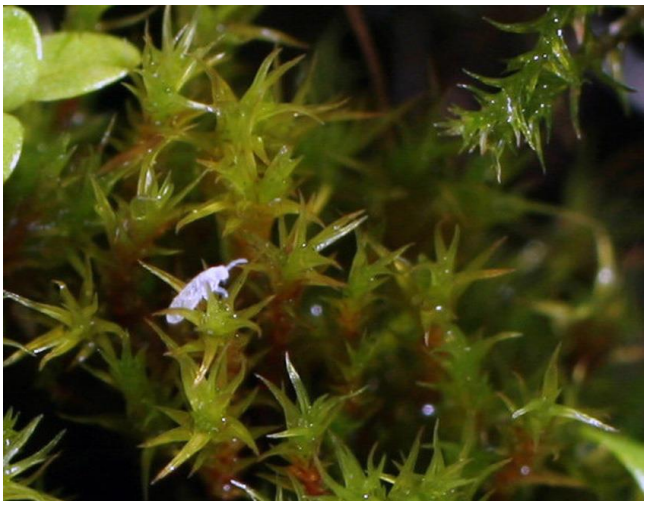

Figure 97. ***Folsomia candida*** on ***Ceratodon purpureus***, a springtail that fertilizes this moss. Photo courtesy of Erin Shortlidge.

Figure 99. ***Bryum argenteum*** male with perigonia. Photo by George J. Shepherd, through Creative Commons.

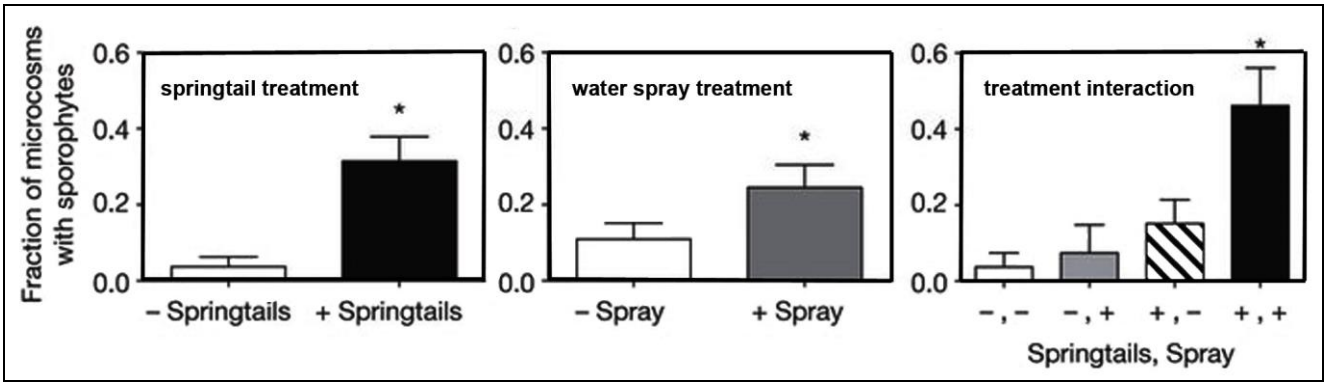

Figure 100. Fertilization success in ***Ceratodon purpureus*** and ***Bryum argenteum***, measured as the fraction of microcosms that developed sporophytes. Bars are means ± standard error. Plus and minus symbols represent the presence and absence of springtails and water spray. n = 108 microcosms. *P<0.05. Modified from Rosenstiel *et al*. 2012.

Bisang and Hedenäs (2015) suggest that springtails, and perhaps other organisms, may be more widespread among bryophytes as agents of fertilization than we have realized. They found ***Xenylla humicola*** (Figure 101) in great numbers on ***Tortula cernua*** (Figure 101). Further examination revealed a mix of immature and mature antheridia and mature archegonia. They postulated that the mosses produce a volatile substance at this stage that attracts the springtails. The springtails, in return, increase the fertilization success. This moss, unlike the previous examples in dioicous mosses, is **autoicous** (antheridia & archegonia in different clusters on the same plant). Hence, we have three examples in three different moss families (**Bryaceae**, **Ditrichaceae**, **Pottiaceae**) to demonstrate moss fertilization by **Collembola**. Thus far no examples are known for pleurocarpous mosses or liverworts.

Figure 101. ***Xenylla humicola*** on ***Tortula cernua*** during fertilization season for the moss. Photo courtesy of Lars Hedenäs & Irene Bisang.

There is yet another case of a member of ***Xenylla*** that can live in the spent antheridial cup of ***Polytrichum piliferum*** (Fjellberg *et al*. 2017). This species, ***Xenylla maritima*** (Figure 102), presents a puzzle because two individuals were curled up there when the splash cup was already producing new growth from the center, indicating that the sperm had already been dispersed much earlier. Hence, we are left to wonder what attracted them to this location, and in the right season do they acilitate dispersal of the sperm.

Figure 102. ***Xenylla maritima***, an isopod, in the male splash cup of the moss ***Polytrichum piliferum***. Note the new, green growth in the center of the cup. Photo by Arne Fjellberg, with permission.

Habitat Differences

Bryophytes in different habitats house different species of **Collembola**. These differences seem to be primarily the result of the habitat differences, not the bryophyte differences. In either case, moisture is an important determinant (Lek-Ang *et al*. 2007).

Bogs and Wetlands

Blackith (1974) pulled together the known literature on **Collembola** from blanket bogs in Ireland and assessed their ecological needs. He found that they are sensitive to waterlogging, being driven from the peat in spring when the water level rises. This is time of high mortality for them, in part because they have lost their shelter. They benefit from the heat sink provided by the bog mosses, and only a small number of them have a dark color as would be typical of tundra species. This lack of dark color is more typical of tropical species. The **Collembola** are very specific in their choice of host (food) plants, essentially eliminating competition between **Collembola** species.

Many bog **Collembola** are also associated with a particular layer/depth of the peat. Krab *et al*. (2010) experimented with the parameters that determine that depth by literally turning the bog layers upside down with their **Collembola** inhabitants still in them. The responses were of two sorts. The **stayers** remained with the stratum they were in, thus remaining with the substrate of choice. The **movers** left the original position and returned to the vertical position corresponding to their original position. Presumably, the latter group sought a suitable moisture and temperature level. These **Collembola** are important in making the peat suitable for decomposers, and the behavior of the mover group suggests that if the bogs were to undergo warming, this would affect the faunal composition and decomposition rate of the bog.

In a further study of this decomposition relationship, Krab *et al*. (2013) found that in a high-latitude ecosystem, increased litter from birch (*Betula pubescens*), a predictable event from global warming, changed the feeding habits of the resident **Collembola**. Instead of their normal levels of the peat moss ***Sphagnum fuscum*** (Figure 103) in the diet, all species switched to a strong dietary preference (67%) for *Betula*-associated food sources instead of ***Sphagnum***. This resulted in slower decomposition of the ***Sphagnum*** litter while the **Collembola** species composition remained the same.

Figure 103. ***Sphagnum fuscum***, home of **Collembola** with non-specific feeding habits. Photo by Jutta Kapfer, with permission.

In 13 mire habitats of Norway, Fjellberg (1976) found 35 species of surface-active species of **Collembola**. He even found three species new to Norway: ***Isotoma tenuicornis*** (see Figure 104), ***Arrhopalites cochlearifer***, and ***Sminthurides pseudassimilis***. Typical mire inhabitants included ***Desoria olivacea*** (Figure 105), ***Isotoma neglecta***, ***I. tenuicornis***, ***Isotomurus plumosus*** (Figure 106),

Sminthurides aquaticus (Figure 107), ***Arrhopalites principalis*** (Figure 108), and ***Heterosminthurus novemlineata*** (Figure 109). As is typical with other insects, the highest species richness occurred in the transition zone between the mires and the forest.

Figure 104. ***Isotoma anglicana***; ***I. tenuicornis*** and ***I. neglecta*** are typical mire inhabitants in Europe. Photo by Arne Fjellberg, through Creative Commons.

Figure 105. ***Desoria olivacea***, a bog moss dweller in Norway. Photo by Andy Murray, through Creative Commons.

Figure 106. ***Isotomurus plumosus***, a bog moss dweller in Norway. Photo by Arne Fjellberg, through Creative Commons.

Figure 107. ***Sminthurides aquaticus*** on a moss. This is a common bog species. Photo by Andy Murray, through Creative Commons.

Figure 108. ***Arrhopalites principalis***, a typical mire inhabitant in Norway. Photo by Andy Murray, through Creative Commons.

Figure 109. ***Heterosminthurus novemlineata***, a typical species in Norwegian mires. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Sławska (2000) found that even the small basin bogs of pine forests have **stenotypic** (able to live in only a narrow range of environmental conditions) species of **Collembola**. These included many typical mire species: ***Ceratophysella mosquensis*** (see Figure 110), ***C. scotica***, ***Isotomurus plumosus*** (Figure 106), ***Ballistura crassicauda***, ***Arrhopalites principalis*** (Figure 108), ***Sminthurides schoetti*** (Figure 111), ***S. malmgreni*** (Figure 112), ***S. parvulus*** (Figure 113), and ***S. pseudassimilis***. Rare species included ***Isotoma neglecta***, ***I. tenuicornis***, ***Desoria fennica*** (Figure 114), ***Folsomia bisetosa*** (Figure

115), ***Pseudanurophorus binoculatus*** (Figure 116), ***Arrhopalites spinosus***, and ***Stachorutes sphagnophilus***. Seven of these species are the same as those found by Fjellberg (1976) as typical of the Norwegian mires. Sławska found that the species composition and diversity varied with the size of the peatland, mire type, water conditions, plant communities, and topography, but that the boreal-alpine species in basin bogs did not seem to relate to these parameters. Instead, geography seemed to be an important determinant of the boreal-alpine communities.

Figure 110. ***Ceratophysella denticulata***; ***Ceratophysella mosquensis*** and ***C. scotica*** are typical mire species in Europe. Photo through Creative Commons.

Figure 111. ***Sminthurides schoetti*** on moss, a typical bog species in Europe. Photo by Andy Murray, through Creative Commons.

Figure 112. ***Sminthurides malmgreni***, a typical bog species in Europe. Photo by Jan van Duinen, with permission.

Figure 113. ***Sminthurides parvulus***, a typical bog species in Europe. Photo by Andy Murray, through Creative Commons.

Figure 114. ***Desoria fennica***, a rare bog species. Photo by Arne Fjellberg, through Creative Commons.

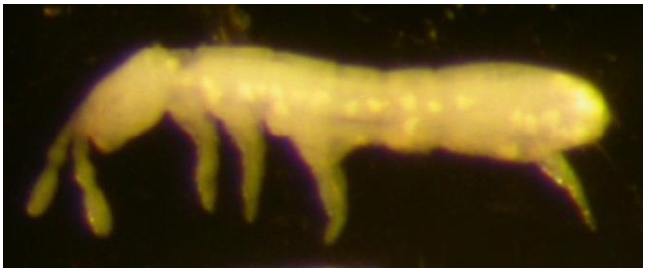

Figure 115. ***Folsomia bisetosa***, a common bog species in Europe. Photo by Arne Fjellberg, through Creative Commons.

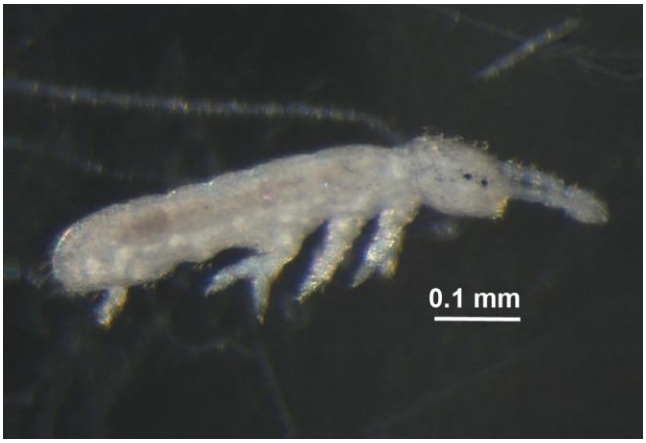

Figure 116. ***Pseudanurophorus binoculatus***, a typical bog species in Europe. Photo by David Porco, through Creative Commons.

Kuznetsova (2002) found that *Vaccinium myrtillus* and green mosses serve as indicators of mesic conditions where one can find **mesophilous** (loving mid-moisture conditions) **Collembola**. The ***Sphagnum*** communities

typify wet sites and house **hygrophilous** (water-loving) **Collembola** communities. Saraeva *et al*. (2015) identified **continuous** and **spotty distributions** of **Collembola** in ***Sphagnum*** pine forests of Karelia, Russia. But these patterns are influenced little by relative humidity, mass of moss cover, and litter thickness.

Predators are important in reducing springtail numbers. Bardwell and Averill (1997) found 24 spider genera that possessed prey items in cranberry bogs in Massachusetts, USA. Among 7009 spiders, 2.7% of them possessed prey. The prey items represented 11 orders of insects; 18.6% of these were **Collembola**.

Forests

Moisture seems to be a primary driving factor in delineating differences among collembolan communities. Lek-Ang *et al*. (2007) examined the gradient from forest to peat bog in the French Pyrenees and found a total of 63 species using 48 samples in the bog and 20 in the forest. They found that the peat bog communities were always distinct from those of the forest. Variations were strongly correlated with substrate water content, ***Sphagnum*** (Figure 117), and grass cover. In this case, the **ecotone** (transition zone between two biological community types) between the forest and bog did not display a greater **species richness** (number of species). (Generally an ecotone has species of both communities, resulting in greater species richness).

Figure 117. ***Sphagnum squarrosum***, a collembolan home in forest transition habitats. Photo by J. C. Schou, through Creative Commons.

Snider (1967) reports collecting ***Bourletiella arvalis*** (**Bourletiellidae,** Figure 118) from ***Sphagnum*** (Figure 117) in Michigan, USA, forests. ***Sminthurinus quadrimaculatus*** (**Katiannidae;** Figure 119) occurred in forest moss scrapings and ***Lepidocyrtus cyaneus*** (Figure 120) and ***L. helenae*** among mosses.

Figure 118. ***Bourletiella arvalis*** a species that lives among ***Sphagnum*** in Michigan forests. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.

Figure 119. ***Sminthurinus quadrimaculatus***, a species from forest mosses in Michigan, USA. Photo by Tom Murray, with permission.

Figure 120. ***Lepidocyrtus cyaneus***, a species from forest mosses in Michigan, USA. Photo by Steve Hopkin, with permission.

Miller *et al*. (2007) found that the abundance of most of the **Collembola** species in the Acadia Forest in Maine, USA, were correlated with the dense bryophyte cover at the base of sampled trees. Only the family **Isotomidae** (Figure

10-Figure 11) seemed to decrease in abundance as bryophyte cover increased. Instead, this family was primarily associated with the epiphytic lichen ***Usnea subfloridana*** (Figure 121) higher up the trees. Nevertheless, Snider (1967) listed few **Collembola** from bryophytes outside of bogs in his treatment of Michigan, USA, **Collembola**. Could it be that the human collectors have the same problem as the predators – the **Collembola** are too difficult to see or capture when they live among the bryophytes?

Figure 121. ***Usnea subfloridana***, preferred home for **Isotomidae** compared to mosses. Photo by Jerzy Opioła, through Creative Commons.

Majzlan and Fedor (2003) found that springtails may "crawl" up trees, observing this activity on the trunks of *Aesculus hippocastanum* (horse chestnut) in Slovakia (but they were unable to observe downward movement). They determined that this activity might relate to their trophic preference (bryophytes, lichens, algae) or to their tolerance of soil humidity. [Davies (1928) found that the optimum humidity for **Collembola**, except ***Entomobrya***, at 25°C was a saturated atmosphere.] Majzlan and Fedor (2003) documented that there were four times as many springtails in the lower (1 m) tree samples compared to the upper ones (5 m), but in autumn, this number increased to ten times as many in the lower samples.

Rodgers and Kitching (1998) examined the vertical stratification of **Collembola** in the subtropical rainforest site at Lamington National Park in southeast Queensland, Australia. They found that the vertical stratification was complex for the arthropods. The greatest homogeneity existed among samples on the forest floor and the greatest dissimilarity in the upper canopy. They considered that dispersal barriers might account for some of the observed differences, accompanied by a greater risk of extinction in the upper canopy. These two limiting factors could account for the greater heterogeneity of canopy **Collembola** species. Since Rodgers and Kitching used leaf litter as a substrate to sample the **Collembola**, suspending the samplers in canopy epiphytes, it is unclear how these differences relate to stratification of bryophyte-**Collembola** communities.

Forest Floor

Deciduous forests and conifer forests have very different ground flora. Bryophytes in deciduous forests are restricted to emergent structures such as logs, stumps, tree bases, vertical inclines, and rocks. This is because the leaf litter buries them elsewhere. These bryophytes serve as important habitats for **Collembola**.

In a boreal forest in northern Sweden, removal of mosses, such as that following fire, strongly negatively impacted both abundance and diversity of the **Collembola** (Bokhorst *et al*. 2014). On the other hand, the species diversity of the **Collembola** community gradually increased with forest decline in Tam Dao National Park, Vietnam (Vu & Nguyen 2000). A major reason for the correlation of **Collembola** with bryophytes is the need of these springtails for moisture, whether it be in the bryophyte mat or is the soil beneath them (Jucevica & Melecis 2005).

For some species, mosses are a seasonal habitat. In a spruce forest of the High Tatra Mountains, Slovakia, there is a mosaic cover of the mosses ***Dicranum scoparium*** (Figure 122) and ***Hylocomium splendens*** (Figure 123) (Čuchta *et al*. 2012). ***Vertagopus cinereus*** (Figure 124) lives in that moss layer in winter and in early spring, but it migrates into the soil during summer (Prat & Massoud 1982). On the other hand, Čuchta *et al*. (2012) found that in this same spruce forest, ***Orchesella cincta*** (Figure 68) and ***Xenylla tullbergi*** are far more common among bark pieces and tree mosses and lichens than in the litter layer.

Ponge *et al*. (1993) experimented with litter perturbations to see the effects on the **Collembola** community. They found that the bog species ***Sminthurides schoetti*** (Figure 111) and ***S. parvulus*** (Figure 113) increased in abundance following litter disappearance in the forest. These two species are typical of ***Sphagnum*** bogs (Stach 1956; Gisin 1960; Sławska 2000). Ponge (1993) concluded that vegetation does not itself directly influence the **Collembola**, but that it may affect them indirectly by humus formation.

Figure 122. ***Dicranum scoparium***, a dominant moss in the spruce forests where one can find several **Collembola** species in the moss layer. Photo by Janice Glime.

Figure 123. ***Hylocomium splendens***, a dominant moss in the spruce forests where one can find several **Collembola** species in the moss layer. Photo by Andrew Spink <www.andrewspink.nl>, with permission.

Figure 124. ***Vertagopus cinereus*** juvenile on bryophytes, a species that migrates into the soil in summer. Photo by Jan van Duinen, with permission.

In ***Picea sitchensis*** (Figure 125) plantations, succession after cutting starts with unvegetated needle litter and progresses to well-developed herb or shrub layers that then become suppressed by shade during canopy closure about 15-20 years after clear-cutting (Butterfield 1999). Depending on thinning, little ground vegetation may remain, but sparse moss cover may be present. **Collembola** densities were high in spring when the canopy was open, decreasing in summer. Under closed canopy, the opposite relationship occurred, with drying most likely accounting for the low summer densities in the open. The closed canopy also supported higher **Collembola** densities in the upper soil layer than in the drier ones under the open canopy.

Figure 125. ***Picea sitchensis*** with storm damage, showing areas of open canopy. Photo by Max East, through Creative Commons.

The Checklist of Nordic **Collembola** notes mosses among the habitats for many **Collembola** species (Fjellberg 2007b). These include ***Micranurida anophthalmica*** (**Neanuridae**), a rare species among mosses on rotten wood; ***Appendisotoma abiskoensis*** (**Isotomidae**) among boreal forest mosses; ***Pseudisotoma sensibilis*** (Figure 141, common) (**Isotomidae**), ***Orchesella spectabilis*** (**Entomobryidae**; Figure 126), ***Pogonognathellus flavescens*** (**Tomoceridae**; Figure 127), and ***Lipothrix lubbocki*** (**Sminthuridae**; Figure 128-Figure 129) in moss and forest litter; ***Orchesella cincta*** (Figure 68) common in moss and dry forest litter; ***Orchesella flavescens*** (Figure 130) in moss and litter in damp forests, mainly conifers; ***Pogonognathellus longicornis*** (Figure 131) among mosses and forest litter, mainly hardwoods; ***Sminthurinus aureus signatus*** (**Katiannidae**; Figure 132) in moss and litter of damp habitats in forests; and ***Gisinianus flammeolus*** (**Katiannidae**; Figure 133) in moss and litter of rich, moist hardwood forests.

Figure 126. ***Orchesella spectabilis*** male among mosses. Photo by Gábor Keresztes <xespok.net>, with permission.

Figure 127. ***Pogonognathellus flavescens***, a species of Nordic forest mosses and litter. Photo by Anki Engström at <www.krypinaturen.se>, with permission.

Figure 128. ***Lipothrix lubbocki*** adult, a species of forest mosses and litter in Nordic countries. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.

Figure 129. ***Lipothrix lubbocki*** juvenile, a species of forest moss and litter. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.

Figure 130. ***Orchesella flavescens***, a species living among mosses and litter in damp conifer forests of Nordic countries, shown here on a species of ***Polytrichum***. Photo by Jan van Duinen, with permission.

Figure 131. ***Pogonognathellus longicornis***, a species that lives among Nordic hardwood forest mosses and litter. Photo by S. D. Lund, through Creative Commons.

Figure 132. ***Sminthurinus aureus*** orange form on moss, a species from mosses and litter in damp Nordic forest habitats. Photo by Andy Murray, through Creative Commons.

Figure 133. ***Gisinianus flammeolus***, a species that lives among Nordic hardwood forest mosses and litter. Photo by Arne Fjellberg, through Creative Commons.

Tetrodontophora bielanensis (**Onychiuridae**; Figure 134) is common on the forest floor of the Bielany Hills near Kraków, Poland, where it lives among dead leaves, mushrooms, and on mosses (Klag 1982). In Hungary, ***Xenylla brevisimilis*** and ***Tetracanthella franzi*** (**Isotomidae**) occur in mosses and litter (Dány & Traser 2008). ***Tetracanthella wahlgreni*** (Figure 135) lives among **xerophilous** (dry-loving) mosses and lichens.

Figure 134. ***Tetrodontophora bielanensis*** on mosses, a forest dweller on dead leaves, mushrooms, and mosses in Poland. Photo by Steve Hopkin, with permission.

Figure 135. ***Tetracanthella wahlgreni***, a species that lives among xerophilous mosses and lichens. Photo by Andy Murray, through Creative Commons.

Andy Murray (2015) describes chasing ***Sminthurides schoetti*** (**Sminthuridae**; Figure 136) through a "forest of moss" in order to get its picture. It at least appears to use mosses to escape as well as being a common bog dweller. Murray describes finding ***Stenacidia violacea*** (**Sminthuridae**; Figure 137-Figure 139) among mosses. This forest species is relatively common and may even use bryophytes for mating sites (Figure 137).

Figure 136. ***Sminthurides schoetti*** on moss. Photo by Andy Murray, through Creative Commons.

Figure 137. ***Stenacidia violacea*** courtship ritual. Photo by Andy Murray, through Creative Commons.

Figure 138. ***Stenacidia violacea*** juvenile checking out the mosses. Photo by Andy Murray, through Creative Commons.

Figure 139. ***Stenacidia violacea*** juvenile on moss. Photo by Andy Murray, through Creative Commons.

Some species that live on rotten wood also take advantage of the mosses occurring there. Such is the case for ***Sminthurinus bimaculatus*** (Figure 140) as seen in this picture by Andy Murray. ***Pseudisotoma sensibilus*** (**Isotomidae**; Figure 141) prefers cushions on logs not far above the ground (Bauer & Christian 1993).

Figure 140. ***Sminthurinus bimaculatus*** on moss. Photo by Andy Murray, through Creative Commons.

Figure 141. ***Pseudisotoma sensibilis***, a common species among mosses on logs in Nordic countries. Photo by Arne Fjellberg, through Creative Commons.

Entomobrya muscorum (Figure 142) has been a puzzle for me. This species has a name that suggests that it should live among mosses. But instead, I was able to verify it as living on soil. Finally, as I was preparing the final formatting of this sub-chapter, I made one more search. A study on nematode predators on other invertebrates verified that it does indeed live among mosses as well, and it eats nematodes there (Heidemann *et al*. 2014).

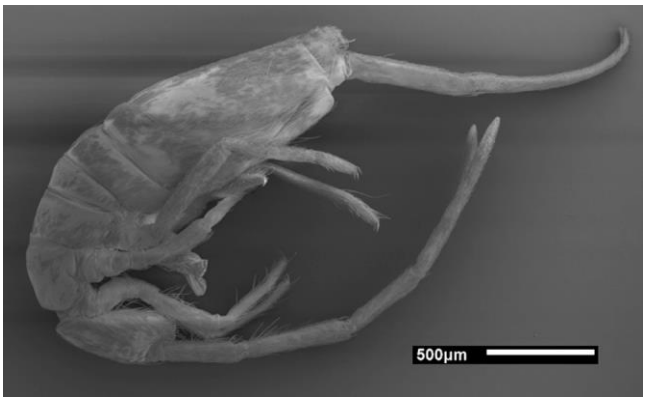

Figure 142. ***Entomobrya muscorum***, a soil dweller and sometimes a moss dweller. Photo by Jürgen Schulz, with permission.

Epiphytes

The epiphytic bryophytes seem like an unlikely habitat for an insect with a spring on it. But not all "springtails" have springs. Hence, they may be small and round, lack a furcula, be small, and produce a glue that helps to hold them to the tree or catch them like a tether when they fall.

Dicyrtoma fusca (Figure 5) is well adapted to living among epiphytic bryophytes by its small, globular shape (Figure 143) (Traser *et al*. 2006; Nature Spot 2015). It feeds on mold and other fungi. Dány and Traser (2008) found that ***Xenylla boerneri*** (Figure 144) is **corticophilous** (bark-loving), living among epiphytic mosses in Hungary; its furcula is reduced to two small warts. Fjellberg (2007b) reported ***Entomobrya albocincta*** (Figure 145) (**Entomobryidae**) and ***Pseudachorutes boerneri*** (Figure 146) (**Neanuridae**) in mosses and lichens on trees in the Nordic countries. These two genera do have well-developed furculas.

Figure 143. ***Dicyrtoma*** (**left**) and ***Sminthurinus*** (**right**) showing differences in size among collembolans. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.

Figure 144. ***Xenylla boerneri***, a springtail that inhabits epiphytic mosses in Hungary. Photo by Arne Fjellberg, through Creative Commons.

Figure 145. ***Entomobrya albocincta***, a springtail of Nordic mosses and lichens on trees. Photo by Andy Murray, through Creative Commons.

Figure 146. ***Pseudachorutes*** sp.; ***P. boerneri*** lives among mosses on boulders and tree trunks in Nordic Countries. Photo by Andy Murray, through Creative Commons.

Both epiphytic bryophytes and **Collembola** are affected by gap harvesting. Wagner *et al*. (2007) found that springtails, mites, and spiders were most abundant near the tree bases in the Acadian forest of central Maine, USA. Gap harvesting reduced the abundance of all three of these groups on the bark of red maple (***Acer rubrum***; Figure 147). There was a positive correlation among these three groups. It is likely that the spiders preyed on the **Collembola** and that gap harvesting affected the spiders by affecting their prey. Miller *et al*. (2008) found that spiders tended to be where the **Collembola** were, but they also found indications of an association between six families of **Diptera** (flies) and members of the **Collembola** family **Entomobryidae**.

Figure 147. ***Acer rubrum*** in autumn, home of springtails, mites, and spiders among epiphytic bryophytes. Photo by Anderson & Ryser (2015), through Creative Commons.

Cutz-Pool *et al*. (2010) examined **Collembola** communities at three different heights among epiphytic mosses on trees in Mexico, where they collected 12 **Collembola** species. Both species richness and density decreased with increasing height on the tree. Height on the tree had a significantly negative effect on the densities of ***Pseudachorutes subcrassus*** (**Hypogastruridae**; see Figure 146), ***Entomobrya*** cf. ***triangularis*** (**Entomobryidae)**, ***Americabrya arida*** (**Entomobryidae**; Figure 148), and ***Ptenothrix marmorata*** (**Dicyrtomidae**; Figure 149).

Figure 148. ***Americabrya arida***, an epiphytic moss dweller. Photo by Jesse Christopherson, through Creative Commons.

Figure 149. ***Ptenothrix marmorata***, an epiphytic moss dweller. Photo by Tom Murray, with permission.

The epiphyte mats of tropical cloud forests provide important niches for a diverse microarthropod community, including the **Collembola** among the most abundant (Yanoviak & Nadkarni 2001). The bryophytes buffer the environment against the wind, retain moisture, provide foraging sites, provide shelter for egg deposition, and provide safe sites against predators (Gerson 1982; André 1983; Nadkarni 1994; Kitching *et al*. 1997; Yanoviak *et al*. 2004). Yanoviak *et al*. (2004) investigated the differences in arthropod communities in the green vegetative portion and brown humic portions of these epiphytic mats, a portion of which was comprised of bryophyte species. The dominant arthropods were mites, ants, and springtails. The green portion of the mats housed twice as many arthropod individuals and species per gram compared to the brown portion and **Collembola** were more abundant in the green portion.

In a neotropical montane forest in Costa Rica, Nadkarni and Longino (1990) found that while the relative abundance of arthropods, including **Collembola**, are essentially the same on the forest floor and in the canopy. The densities of all groups except ants are significantly higher on the ground by a factor of 2.6. Among these, mites, beetles, ants, and springtails are consistently the most abundant arthropod taxa in the mats of epiphytes and humus (Longino & Nadkarni 1990; Nadkarni & Longino 1990; Paoletti *et al*. 1991; Yanoviak & Nadkarni 2001; Yanoviak *et al*. 2003).

A number of additional species of **Collembola** live among bryophytes on both tree trunks and boulders, as discussed below.

Boulders and Rock Canyons

As in trees, some bryophytes can provide the necessary moisture for collembolans in the harsh environment of boulders and rock walls. Hence, bryophytes on boulders share many of the same **Collembola** species that live among bryophytes on tree trunks. Fjellberg (2007a) included ***Vertagopus arboreus*** (Figure 151) (**Isotomidae**), ***Vertagopus westerlundi*** (Figure 152), ***Vertagopus pseudocinereus*** (Figure 153), and ***Pseudisotoma sensibilis*** (Figure 141) (**Isotomidae**) among boulder and tree trunk mosses in Fennoscandia and Denmark. Likewise, the Nordic **Collembola** include many species common to mosses of both boulders and tree trunks (Fjellberg 2007b): ***Orchesella bifasciata*** (**Entomobryidae**; Figure 150), ***Xenylla boerneri*** (**Hypogastruridae**; Figure 144), ***Tetracanthella strenzkei*** (**Isotomidae**; see Figure 158**)**, ***Vertagopus arboreus*** (**Isotomidae**; Figure 151), ***Vertagopus westerlundi*** (northern; Figure 152).

Figure 150. ***Orchesella bifasciata***, a Nordic species of mosses on boulders and tree trunks. Photo by Anki Engström <www.krypinaturen.se>, with permission.

Figure 151. ***Vertagopus arboreus***, a species that lives among mosses on boulders and tree trunks. Photo by Andy Murray, through Creative Commons.

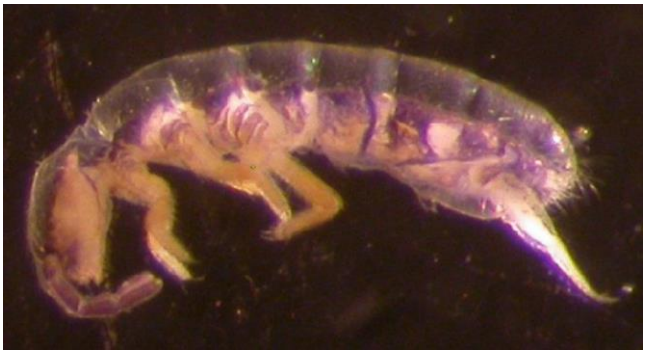

Figure 152. ***Vertagopus westerlundi***, a species that lives among mosses on boulders and tree trunks. Photo by Arne Fjellberg, through Creative Commons.

Figure 153. ***Vertagopus pseudocinereus***, a species that lives among mosses on boulders and tree trunks. Photo by Jan van Duinen, with permission.

But boulders can also have unique assemblages of bryophyte-dwelling **Collembola**. In beech and spruce forests in Bohemia, Rusek (2001) found that the **Collembola** communities among mosses on boulders differed significantly from other forest communities. Forest age and microhabitat characteristics were important in determining the forest collembolan inhabitants, and some species were restricted to only one or two microhabitats. As in a number of other studies, Rusek demonstrated the importance of examining both local patch variation and broader ecosystem differences.

Onychiurus armatus (**Onychiuridae**; see Figure 59) lives exclusively in moss cushions on granite boulders in Australia where the microclimate is stable, taking advantage of the supercooling ability and avoiding the need to cross bare rock (Bauer & Christian 1993). ***Xenylla boerneri*** (Figure 144) is the dominant species when the microclimate is unstable in cushions on boulders and does not share any aversion to bare rock. The mosses may help these collembolans to survive the winter.

Wood (1967) found it difficult to categorize communities associated with moorland soils in Yorkshire, England, based on the species assemblages of 200 species of mites and springtails. However, on limestone boulders one indicator emerged – the springtail ***Anurophorus laricis*** (**Isotomidae**; Figure 83) seemed to be characteristic of the moss genus ***Grimmia*** (Figure 154) and lichens on these boulders.

Figure 154. ***Grimmia pulvinata*** on a wall where **Collembola** live among them. Photo from Botany Department Website, University of British Columbia, Canada, with permission.

In Fennoscandia and Denmark, Fjellberg (2007a) adds the rock/boulder-dwelling ***Isotomurus antennalis*** (**Entomobryidae**; Figure 155) in damp moss of rocky habitats and ***Vertagopus sarekensis*** (**Isotomidae**; Figure 156) among mosses and lichens on alpine rocks. Among the Nordic **Collembola** (Fjellberg 2007b), rock and boulder dwellers include ***Friesea claviseta*** (**Neanuridae**; Figure 157), ***Anurophorus fulvus*** (**Isotomidae**) and ***Anurophorus laricis*** (**Isotomidae**; Figure 83) (common) in moss/lichen patches on rocks, ***Vertagopus sarekensis*** and ***Vertagopus arcticus*** among alpine mosses on rocks, ***Megaphorura arctica*** (**Onychiuridae**; Figure 63) common in the Arctic on rocks with moss/algae growth, ***Tetracanthella arctica*** (**Isotomidae**; Figure 158) in the Arctic among mosses and lichens on seashore rocks, and ***Isotomurus antennalis*** among wet mosses on rocks of seashores. In Michigan, USA, Snider (1967) reports ***Isotoma nigrifrons*** (**Isotomidae**) from mosses on a rocky bluff.

Figure 155. ***Isotomurus antennalis***, a species of damp mosses on rocks and boulders. Photo by G. Drange, through Creative Commons.

Figure 156. ***Vertagopus sarekensis***, a species that lives among mosses and lichens on alpine rocks. Photo by Arne Fjellberg, through Creative Commons.

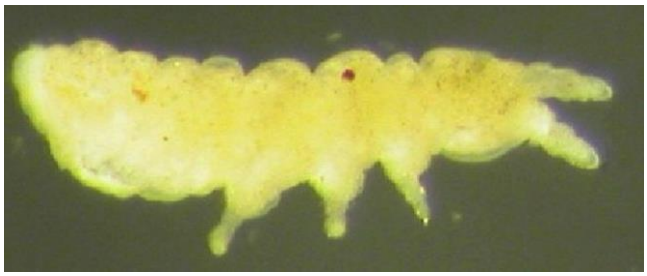

Figure 157. ***Friesea claviseta***, a moss-lichen dweller on boulders in Nordic countries. Photo by Arne Fjellberg, through Creative Commons.

Figure 158. ***Tetracanthella arctica***, a species that lives in the Arctic among mosses and lichens on seashore rocks. Photo by Arne Fjellberg, through Creative Commons.

Some boulder-dwelling **Collembola** are more specific in their locations. ***Mackenziella psocoides*** (**Mackenziellidae**) occurs in rock fissures and among mosses on sand (Fjellberg 2007b). ***Folsomia***

coeruleogrisea (**Isotomidae**; Figure 159) lives among mosses on **bird cliffs** (steep cliffs with numerous small shelves that serve as nesting locations for bird colonies).

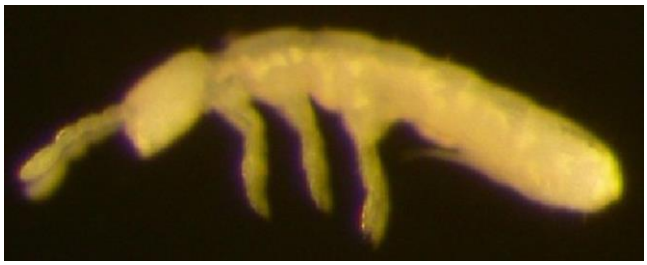

Figure 159. ***Folsomia coeruleogrisea***, a species among mosses on bird cliffs. Photo by Arne Fjellberg, through Creative Commons.

Boulders can present harsh conditions for **Collembola**, particularly on a hot summer day. And some boulders are subject to frequent disturbance. Inhospitable conditions make it difficult for the tiny springtails to navigate from one moss patch to another. Hoyle and Gilbert (2004) studied the role of bryophyte corridors in movement of **Collembola** and other arthropods among bryophyte [***Homalothecium sericeum*** (Figure 160), ***Brachythecium rutabulum*** (Figure 161), ***Hypnum lacunosum*** var. ***lacunosum*** (Figure 162)] patches on a wall habitat, a good model for boulders as well. They found 12 morphospecies of **Collembola**, including ***Entomobrya nivalis*** (**Entomobryidae**; Figure 86), ***Orchesella villosa*** (**Entomobryidae**; Figure 163), ***Tomocerus minor*** (**Entomobryidae**; Figure 164-Figure 165), ***Neanura muscorum*** (**Neanuridae**; Figure 166), ***Pseudisotoma sensibilis*** (**Isotomidae**; Figure 141), ***Dicyrtomina minuta*** (**Dicyrtomidae**; Figure 167-Figure 168), and ***Lepidocyrtus curvicollis*** (**Entomobryidae**; Figure 169). These were represented by 314 individuals per moss patch, on average. Numbers were positively correlated with patch weight. They found no evidence that populations of predators were more affected by fragmentation than non-predators. Hoyle and Gilbert suggested that corridors of mosses might be more important during extreme conditions.

Figure 160. ***Homalothecium sericeum*** on a stone wall where **Collembola** are able to live among them. Photo by Michael Lüth, with permission.

Figure 161. ***Brachythecium rutabulum***, a species that provides shelter for **Collembola** on stone walls. Photo by Michael Lüth, with permission.

Figure 162. ***Hypnum lacunosum***, a species that provides shelter for **Collembola** on stone walls. Photo by Michael Lüth, with permission.

Figure 163. ***Orchesella villosa***, a species that lives among mosses on stone walls, shown here on a thallose liverwort. Photo by Steve Hopkin, with permission.

Figure 164. ***Tomocerus minor*** juvenile, a species among mosses on stone walls. Photo by Steve Hopkin, with permission.

Figure 165. ***Tomocerus minor*** adult, a species among mosses on stone walls. Photo by Andy Murray, through Creative Commons.

Figure 166. ***Neanura muscorum***, a species among mosses on stone walls. Photo by Andy Murray, through Creative Commons.

Figure 167. ***Dicyrtomina minuta*** eating algae. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.

Figure 168. ***Dicyrtomina minuta***, a species that lives on mosses on rock walls. Photo by Tom Murray, with permission.

Figure 169. ***Lepidocyrtus curvicollis***, a springtail that lives among mosses on stonewalls. Photo by Steve Hopkin, with permission.

Limestone outcrops are absent in many parts of the world. Some **Collembola** prefer living among mosses in such habitats. In Moldova, several species of ***Orchesella*** (Figure 150) and ***Entomobrya*** (Figure 86) occurred in these habitats, with ***Orchesella maculosa*** occurring in most of the canyons in the Moldova study, but not in other ecological conditions (Buşmachiu *et al*. 2015).

Considering this problem of migrating from one patch to another, Starzomski and Srivastava (2007) examined the effect of fragmentation of moss patches and the importance of disturbance on mites and springtails – two taxa comprising more than 200 morphospecies in <20 m^2. The moss community covered a granite outcrop in British Columbia, Canada, and was comprised of ***Polytrichum*** (Figure 170) and ***Bryum*** (Figure 171) moss species. Starzomski and Srivastava determined that the disturbance

rate, size, and connectivity were the most important factors affecting species richness and abundance in local patches. Reductions in patch size had little effect unless there was also an absence of connectivity between patches. Repeated disturbance also caused rapid declines in both richness and abundance and caused considerable change in the community composition.

Figure 170. ***Polytrichum piliferum***, a moss that can grow on rocks and house **Collembola** there. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 171. ***Bryum capillare*** with capsules, a moss that can grow on rocks and house **Collembola** there. Photo by Lairich Rig, through Creative Commons.

Vertical Gradients

The transition from soil to soil bryophytes to boulder bryophytes creates a gradient of moisture, light, and food sources. Bonnet *et al*. (1975) considered this gradient for 26 species of **Collembola**, but restricted the observations to the soil and aerial mosses and ignored the soil mosses. On the south faces of rocks, the habitat is dry with highly drained mosses. On the north sides of the rock the soil is deep. The gradients of **Collembola** in these locations emphasize the importance of humidity and temperature in determining the distribution of these moss-inhabiting springtails.

Mountains, Alpine, and Arctic

Fjellberg (2007b) has contributed much to our knowledge of **Collembola** among the bryophytes in alpine and Arctic areas. These records include ***Folsomia binoculata*** (**Isotomidae**; Figure 172) in wet mossy habitats, Arctic Islands only; ***Folsomia agrelli*** (**Isotomidae**; Figure 173), rare in high alpine wet moss communities; ***Desoria tolya*** (**Isotomidae** Figure 174) in moss and forest litter, more common in alpine rocky habitats; ***Sminthurinus concolor*** (**Katiannidae**; Figure 175) in damp moss on rocks of the Arctic tundra.

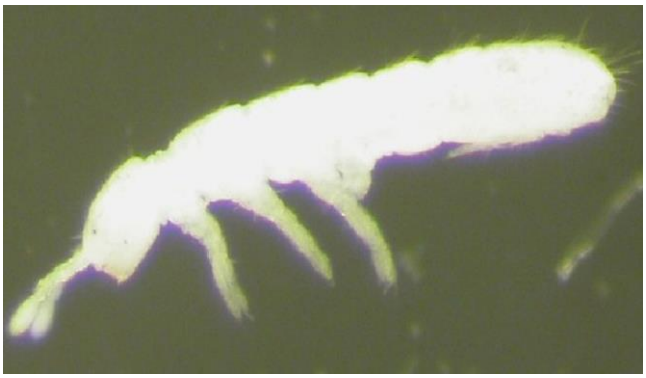

Figure 172. ***Folsomia binoculata***, a species of wet, mossy Arctic habitats. Photo by Arne Fjellberg, through Creative Commons.

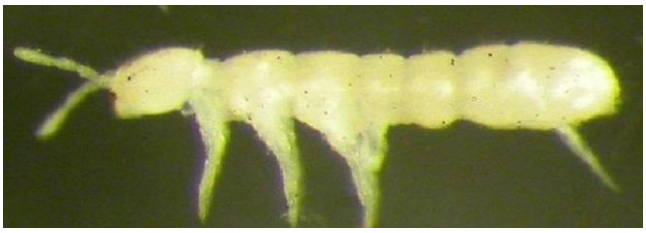

Figure 173. ***Folsomia agrelli***, a rare species among high alpine wet mosses. Photo by Arne Fjellberg, through Creative Commons.

In the poor high mountain areas of the North Swedish Mountains, Agrell (1941) found the **Collembola** to be well represented by **stenotopic** species (able to tolerate only a restricted range of habitats or ecological conditions) with few stenotopic **Coleoptera** (beetles), but he found no characteristic bog species there.

Figure 174. ***Desoria tolya***, a species of mosses and forest litter, especially in alpine rocky habitats. Photo by Arne Fjellberg, through Creative Commons.

Figure 175. ***Sminthurinus concolor***, a species of damp moss on rocks of the Arctic tundra. Photo by Arne Fjellberg, through Creative Commons.

In the Russian tundra, Bretfeld (2010) reported ***Arrhopalites principalis*** (**Arrhopalitidae**; Figure 176) in moss, ***Sminthurinus alpinus*** (**Katiannidae**; Figure 177) in moss-lichen tundra, ***S. oiskiyensis*** in moss on rocks along a river in a small forest with *Abies sibirica* at 1300 m altitude, and ***Sminthurus cogsonzavi*** (**Sminthuridae**) in an alpine moss-lichen tundra at 1500-1800 m altitude.

Figure 176. ***Arrhopalites principalis***, a species of moss-lichen tundra in Russia. Photo by Andy Murray, through Creative Commons.

Figure 177. ***Sminthurinus alpinus***, a species of moss-lichen tundra in Russia. Photo by Arne Fjellberg, through Creative Commons.

Altitudinal Gradients

Cutz-Pool *et al*. (2008) examined altitudinal gradient effects on the structure of the collembolan community among **epiphytic** (bark) mosses in a sub-humid forest in Mexico. Density was greatest at the highest altitude (3250 m asl), but species richness was highest at the lowest altitude in the study (2750 m asl). Density had a significant positive relationship with altitude. ***Americabrya arida*** (Figure 148) and ***Willowsia mexicana*** (Figure 178) (both **Entomobryidae**) were the dominant species among these epiphytic mosses.

Figure 178. *Willowsia platani*; ***Willowsia mexicana*** is among the dominant springtails among epiphytic mosses in Mexico. Photo by Andy Murray, through Creative Commons.

Antarctic Bryophyte Communities

The Antarctic continent is covered with ice except for about 2% of the surface (Seppelt & Ochyra 2008). The vegetation is comprised of lichens, bryophytes, algae, Cyanobacteria, and fungi. **Collembola**, **Diptera**, and mites are the predominant arthropod fauna (Strong 1967; Tilbrook 1967), and the lichens and bryophytes provide a suitable cover (Tilbrook 1973 – Signy Island; Lewis Smith 1996). In the drier areas, the bryophytes are covered with algae and Cyanobacteria (Green & Broady 2001).

Even bryophytes with very different species can have similar trophic levels. Davis (1981) examined two moss communities on Signy Island in the Antarctic. One was a moss turf dominated by ***Polytrichum juniperinum*** (Figure 179) and ***Chorisodontium aciphyllum*** (Figure 180-Figure 181). The second was a moss carpet of ***Calliergon sarmentosum*** (Figure 182), ***Calliergidium austro-stramineum*** (Figure 183), and ***Sanionia uncinata*** (Figure 184-Figure 185) along with the leafy liverwort ***Cephaloziella varians*** (Figure 186). The two communities had similar productivity levels, trophic structure, and organic matter transfer efficiencies, but the standing crops of **Collembola** and mites, turnover of mosses, and accumulation of dead matter differed.

Figure 179. ***Polytrichum juniperinum***, a turf-former in the Antarctic and home for **Collembola**. Photo by Janice Glime.

Figure 180. ***Chorisodontium aciphyllum*** in Antarctica, a **Collembola** home. Photo from Polar Institute, through Creative Commons.

Figure 181. ***Chorisodontium aciphyllum***, home for **Collembola** in the Antarctic. Photo by Jan-Peter Frahm, with permission.

Figure 182. ***Calliergon sarmentosum***, home for **Collembola** in the Antarctic. Photo by Michael Lüth, with permission.

Figure 183. ***Calliergidium austro-stramineum***, home for **Collembola** in the Antarctic. Photo by Bill Malcolm, with permission.

Figure 184. ***Sanionia uncinata*** with grass in Antarctica. ***Sanionia uncinata*** is a suitable **Collembola** habitat. Photo from Polar Institute, through Creative Commons.

Figure 185. ***Sanionia uncinata***, Antarctic home for **Collembola**. Photo by Michael Lüth, with permission.

Figure 186. ***Cephaloziella varians*** with ***Polytrichum***, a **Collembola** habitat in the Antarctic. Photo by Kristian Peters, with permission.

Who Dares to Live Here?

With temperatures reaching extremes within a single day, a long, harsh winter, and elevated UV radiation, it is little wonder that the flora and fauna of the Antarctic are limited. But some **Collembola** (as well as mites and **Diptera**) are relatively common here. Bryophytes serve as important habitats for many of these arthropods, providing cover and protection and ameliorating the microclimate.

On the Schirmacher Oasis, a 25 km long and up to 3 km wide ice-free plateau with more than 100 freshwater lakes on the Antarctic continent, Mitra (1999) reported two families of **Collembola** inhabiting mosses. The springtail ***Cryptopygus antarcticus*** (Figure 78) is the dominant arthropod in the maritime Antarctic (Tilbrook 1967). Gressitt (1967) reports ***Gomphiocephalus hodgsoni*** (**Hypogastruridae**; see Figure 60), ***Friesea*** (**Neanuridae**; Figure 157), and ***Parisotoma*** (**Isotomidae;** see Figure 187) as common in moss clumps. Block (1982) reported ***Friesea grisea***, ***Parisotoma octooculata*** (see Figure 187), and ***Cryptopygus antarcticus*** in the ***Polytrichum-Chorisodontium*** moss turf (Figure 179-Figure 181) of Signy Island, where they had a density of 49,928 individuals per m^{-2}. In the ***Calliergon-Calliergidium-Drepanocladus*** moss carpet (Figure 182-Figure 185) **Collembola** averaged 9913 individuals m^{-2}. ***Cryptopygus antarcticus*** was present in 99% of the moss turf samples and 100% of the moss carpet samples. This species was significantly more abundant in ***Polytrichum*** (Figure 179) than in dead moss or bare peat. But this is not a bryophage – it feeds on unicellular green algae that grow on the mosses (see also Green & Broady 2001).

Figure 187. ***Parisotoma notabilis***, a common species among mosses in the maritime Antarctic. Photo by Andy Murray, through Creative Commons.

On Anvers Island of the Antarctic Peninsula, ***Cryptopygus antarcticus*** (Figure 78) is again abundant in the moss ***Dicranum*** (***Chorisodontium aciphyllum***?; Figure 180-Figure 181) (Lippert 1971). These live mostly at about 5 cm depth in the moss mat, with few in the first cm. ***Polytrichum*** (Figure 179) had this same species, but also provided home to ***Parisotoma*** (**Isotomidae**; Figure 187), ***Friesea*** (**Neanuridae**; Figure 157), as well as several mite species. And as usual, ***C. antarcticus*** was the most abundant. This dominant species also occurred in wet ***Sanionia uncinata*** (Figure 184-Figure 185).

Species are often arranged vertically by temperature and moisture preference (Sømme 1995). These behavioral adaptations permit them to move up or down as the moisture and temperature conditions change on daily and seasonal regimes. For example, ***Cryptopygus antarcticus*** (Figure 78) occurs mostly in the upper 1.5 cm of moss, preferring the moisture content there. ***Friesea woyciechowskii*** (**Neanuridae**) is absent in that zone, but is distributed below it down to 9 cm or more. For ***F. woyciechowskii***, water content of the moss seems to be of little importance.

Geothermal Areas

For several arthropods in polar regions, the **geothermal** (steam vent) areas provide cozy homes with suitable temperatures. The higher temperatures support a richer vegetation with a longer growing season (Convey & Lewis Smith 2006). These plants, largely bryophytes, support a more diverse and abundant fauna than other areas of Antarctica, including species that are non-native and unknown elsewhere on the continent (Greenslade *et al*. 2012). The bryophytes are restricted by moisture (Kennedy 1993; Convey 2001), and geothermal areas provide them with moisture coming from the warmer air arising from the soil in heated areas. This same moisture is favorable for the **Collembola** (Hogg *et al*. 2006). Greenslade *et al*. (2012) found ***Proisotoma minuta*** (Figure 188) and ***Hypogastrura viatica*** (Figure 189-Figure 190), both non-indigenous species, on heated ground where bryophytes dominate. They suggest that the moisture there may be more important than the temperature.

Figure 188. ***Proisotoma minuta***, a non-native species that is able to survive among mosses in geothermal areas of Antarctica. Photo by Andy Murray, through Creative Commons.

Figure 189. ***Hypogastrura viatica***, an invasive species among mosses in geothermal areas of Antarctica. Photo by Andy Murray, through Creative Commons.

Figure 190. ***Hypogastrura viatica*** showing its common habit of forming aggregations. Photo by Mick Talbot, through Creative Commons.

Habitat Suitability and Collembolan Adaptations

Water is one of the most important factors in determining the species composition of Antarctic moss-turf communities (Booth & Usher 1984). For example, ***Cryptopygus antarcticus*** (Figure 78) has an optimum water content, but this species has a relatively wide acceptable moisture range.

Most of the arthropods in the maritime Antarctic are concentrated in the upper layers among vegetation (Tilbrook 1967), including mostly mosses and grasses. The soil and mosses absorb the solar radiation and winter snow insulates, creating temperature regimes that are more suitable for the **Collembola** than elsewhere in the area. Gressitt (1967) found that temperatures in clumps of the moss ***Polytrichum*** (Figure 179) could exceed the air temperatures by as much as 13°C. Temperatures in mat-forming ***Drepanocladus*** s.l. (most likely ***Sanionia uncinata***; Figure 184-Figure 185) had temperatures closer to ambient air temperatures.

Like so many other invertebrates, the **Collembola** exhibit differences in vertical distribution (Usher & Booth 1984). And it appears that the Collembolans use the mosses to survive winter in the Antarctic. But it is not the protection of the bryophyte cushion cover that saves them from the cold. Rather, they may eat the mosses and gain the ability to survive lower temperatures (Sømme & Block 1982). When fed moss turf homogenate, ***Cryptopygus antarcticus*** (**Isotomidae**; Figure 78) from Signy Island, Antarctica, exhibited evidence of efficient nucleators in their moss substrate. When fed purified green algae, a high proportion of low group supercooling points were retained, *i.e.* it required a lower temperature for tissue freezing to occur, suggesting a lack of nucleators in the algae. In ***C. antarcticus*** the concentrations of cryoprotective substances increase at -5°C, concurrent with lowering of the mean supercooling point. The primary substances of this cryoprotectant system were **trehalose**, **mannitol**, and **glycerol**.

Collembola can migrate vertically to achieve the best combination of conditions within the mosses. The relationship between the green zone of ***Polytrichum*** (Figure 179) and the **Collembola** is weak; chemical characteristics seem to be the most important influence on the distribution of the arthropods in the green zone (Booth & Usher 1984). There seems to be no relationship of the arthropod communities with the dead moss zone.

On Signy Island, 78-88% of the **Collembola** were in the top 6 cm of ***Polytrichum-Chorisodontium*** (Figure 179-Figure 181) turf and 96-99% were in the top 6 cm of the ***Calliergon-Calliergidium-Drepanocladus*** carpet (Figure 182-Figure 185) (Block 1982). ***Cryptopygus antarcticus*** (Figure 78) responded to seasonal changes by migrating vertically. In summer it reached as many as 94% of its individuals in the top 3 cm, but in winter this percentage dropped to as low as 48%. Some were as deep as 21 cm, but they rarely went below 6 cm in the moss carpets. The carpets have less extreme temperatures and accumulate more snow than does the turf, ranging 25 to -20°C. The **Collembola** need temperatures of -5 to +5°C to be able to move, and hence to feed. But the moss carpet presents a different problem – it periodically floods, a condition intolerable for the **Collembola** (Kühnelt *et al.* 1976).

Usher and Booth (1986) looked at the relationship of scale in the bryophyte faunal communities. The common ***Cryptopygus antarcticus*** (Figure 78) demonstrates different patterns at scales of 10 and 60 cm depth in the surface layer of the moss turf. ***Friesea grisea*** (see Figure

157), on the other hand, occurs deeper – at 5 cm – and has only a single scale of pattern. Their predator, the mite ***Gamasellus*** (**Ologamasidae**; Figure 79), is distributed randomly. The moss ***Polytrichum*** (Figure 179) exhibits moisture trends along transects and at smaller scales, perhaps accounting for the patterns seen in at least some of the **Collembola**.

In contrast to its abundance among mosses, ***Cryptopygus antarcticus*** (Figure 78) is not desiccation tolerant and is thus absent from the drier rock platform habitat (Hayward *et al*. 2004). Instead, ***Friesea grisea*** (**Neanuridae**; see Figure 157) is the only collembolan able to survive there. Nevertheless, ***F. grisea*** has a stronger preference for 98% relative humidity conditions than does ***C. antarcticus***, suggesting that the former species can take advantage of such refuges when available.

Temperatures in the Antarctic summer can vary considerably between day and night. Some of the Antarctic **Collembola** exhibit a bimodal supercooling point (**SCP**) distribution (Sinclair *et al*. 2003). Mosses may play a slight role in setting the supercooling point. ***Desoria klovstadi*** (**Isotomidae**) that was foraging on mosses had high SCPs (froze at higher temperatures), but these shifted to the low group when the springtails were starved for 2-8 hours. They developed even higher SCPs when fed with lichen or algae for five days, compared to those supplied with mosses. ***Friesea grisea*** (**Neanuridae**; see Figure 157), on the other hand, had unimodal distribution of SCPs that did not vary between day and night.

Eat and Be Eaten

Suitable food is always a requirement in any habitat. In some cases, food preferences may determine where organisms live. In the Antarctic, food sources can be limiting as few organisms can survive the harsh climate. Furthermore, provision of cryoprotectants can play a role in determining suitable food sources, providing the springtails with cryoprotectants in preparation for winter or for cold events during the growing season.

Gressitt (1967) found that many **Collembola** eat fungal hyphae and lichens in the Antarctic. ***Friesea*** (Figure 157) lays eggs among the mosses, suggesting that the young probably find their food among the mosses, most likely eating fungal mycelia.

But larger organisms among the bryophytes also need to eat, and for the carnivores, these springtail aggregations (Figure 190) may be an ideal food source. On the Antarctic Peninsula of Antarctica, predators on **Collembola** include the mites ***Rhagidia*** (**Rhagidiidae**) and ***Cyrtolaelaps*** (**Ologamasidae**) (Strong 1967). Strong considers the live mosses to provide little nourishment for insects and mites, serving mostly as a site of shelter. Nevertheless, the mosses provide a suitable environment for other sources of food, including fungi and algae, for the **Collembola (**Figure 191**)**. These springtails typically spend the winter in the same habitat, probably enjoying at least some insulation among the moss cushions while having adequate moisture.

Figure 191. These Antarctic **Collembola** are common on this ***Bryum subrotundifolium***. Photo courtesy of Catherine Beard.

Glacier Mice – Moss Balls

One unusual habitat for arthropods is among "glacier mice." These are actually unattached moss balls that form from wind-blown mosses on the glaciers. Coulson and Midgley (2012) explored this unusual habitat on glaciers in Iceland. In this case, the moss was a species of ***Racomitrium*** (Figure 65-Figure 66), a common genus in Iceland. The 8-10 cm balls always contained invertebrates and housed two species of **Collembola.** ***Pseudisotoma sensibilis*** (**Isotomidae**; Figure 141) numbered 12-73 individuals per ball, with ***Desoria olivacea*** (**Isotomidae**; Figure 192) comprising far fewer inhabitants. Tardigrades numbered approximately 200 while nematodes numbered near 1000. Surprisingly, there were no mites or arachnids and no annelids.

Figure 192. ***Desoria olivacea***, a springtail that can be found in glacial moss balls. Photo by Andy Murray, through Creative Commons.

Pollution

Air pollution can be harmful not only to bryophytes, but also to the fauna within, including **Collembola** (Steiner 1995). Species richness decreases as a function of increased pollution. This is especially true for mites, possibly giving the springtails a small advantage if their predators diminish in numbers. Alterations in relative humidity, substrate type, and *p*H can have further influence on the species richness. Nevertheless, the arthropods are less sensitive than are nematodes and tardigrades.

The subalpine mosses ***Plagiobryum zierii*** (Figure 193) and ***Saelania glaucescens*** (Figure 194) near a busy road in the Bükk Mountains of Hungary are protected species there, but they are subject to pollution from the traffic on the road (Varga 1992). They exhibit a higher lead level and poorer fauna, including **Collembola**, than mosses from an unpolluted site.

Figure 193. ***Plagiobryum zierii***, a moss that houses **Collembola** in the subalpine. Photo by Michael Lüth, with permission.

Figure 194. ***Saelania glaucescens***, a moss that houses **Collembola** in the subalpine zone. Photo by Michael Lüth, with permission.

Summary

Collembola were once considered insects but are now considered a subclass instead of an order. Most species spring by a **furcula**, a structure that is absent among some of the epiphyte dwellers. These springtails most likely existed before bryophytes did and moved to inhabit them later. They are sensitive to moisture and use bryophytes to maintain it. They eat algae, detritus, fungi, and slime molds among the bryophytes, and occasionally the bryophytes themselves, depending on the springtail species. Some are parthenogenetic and others deposit the sperm in a spermatophore that the female places into her reproductive tract. Their dispersal is slow and traversing bare rock or other non-vegetated areas brings the risk of desiccation. Bryophytes can provide safe channels for migration; **Collembola** are among the first arthropods to colonize mosses.

Bryophytes provide cover, feeding sites, and egg-laying sites. Some **Collembola** are important in transferring sperm from male to female mosses. The bryophytes are moist and may help in lowering the supercooling point and protect the **Collembola** from freezing damage when the gut is empty. Vertical migration in the bryophyte mat can also help them find the best temperature and moisture where they can aggregate, further reducing water loss. Bryophytes provide safe sites against predators, especially spiders and mites, but also some salamanders. Few true **bryobionts** exist, one being ***Hymaphorura dentifera***. The dominant families seem to be **Isotomidae**, **Hypogastruridae**, and **Entomobryidae** as well as the spherical springtails (**Symphypleona**).

The **Collembola** are adapted by small size and pigmentation where they live exposed to light. Those living among bryophytes on tree bark often have short furculas, dark color, stocky body, few eyes, small size, and limited movement. Sampling is usually done by pit traps or collecting the bryophytes. Bryophytes can be placed in funnels with a heat gradient that causes the **Collembola** to drop into a preservative or by using a flotation technique. But many won't leave the bryophytes to be sampled by these techniques. The springtails may number hundreds of thousands in a square meter, especially in Arctic and Antarctic regions.

Bogs seem to be important for some species, with water content being a controlling factor. Species living among epiphytic bryophytes are often the same as those among bryophytes on boulders. In forests they are usually in moist sites such as log or soil mosses, especially in wetter areas. In the Antarctic, ***Cryptopygus antarcticus*** is by far the most abundant, often reaching 95-100% of the springtail community among bryophytes. Some live in mobile homes known as glacier mice – moss balls on glaciers.

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CHAPTER 12-3
TERRESTRIAL INSECTS: HEMIMETABOLA – ODONATA

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CHAPTER 12-3
TERRESTRIAL INSECTS:
HEMIMETABOLA – ODONATA

Figure 1. ***Uropetala chiltoni*** naiad emerging from burrow hidden among leafy liverworts. Photo by Rod Morris, with permission.

ODONATA – DRAGONFLIES AND DAMSELFLIES

Most of the **Odonata** are discussed in Chapter 11-5 with the aquatic insects, but some are terrestrial even as naiads and are appropriately discussed here. The **Odonata** are **hemimetabolous**. That is, they have an incomplete life cycle, one in which the immature animal resembles the adult and has no **larval** or **pupal** stage. Rather, the **naiad** (Figure 2), or **nymph**, develops directly into the adult. Naiads are the aquatic nymphs and thus the term doesn't apply in the strict sense to the terrestrial species. The large eyes (Figure 3) and scoop mouth enable these to be formidable carnivores. The odonate wings develop within the wingpads of the nymphs/naiads and expand when the last nymphal skin is shed. These adults must climb upward and pump fluids into the wing veins to expand them. They are vulnerable at this time because they are not yet ready to fly. Refer to Chapter 11-5 for more detailed discussion of this order of insects.

Figure 2. ***Aeshna interrupta*** naiad, a species whose naiads are not tolerant to drying. Photo by Donald S. Chandler <www.discoverlife.org>, with permission.

Figure 3. ***Sympetrum striolatum*** head showing large eyes. Photo by Anki Engström <www.krypinaturen.se>, with permission.

Both dragonflies (**Anisoptera**) and damselflies (**Zygoptera**) have members that spend their nymphal life among bryophytes on land. These habitats provide cover and help the **Odonata** retain moisture. Others deposit eggs among mosses near water bodies where it is easy for nymphs to reach water through flooding, crawling, and or dropping into the water.

Biology

The **Odonata** are voracious carnivores and are preyed upon as naiads primarily by fish in their aquatic habitat. On land, this larger predator is absent and birds and amphibians are the most likely predators for both nymphs and adults. But their larger danger as nymphs on land is drying out. Hence, enter the bryophytes.

Paulson and Buden (2003) collected **Odonata** on the Eastern Caroline Islands of Micronesia, bagging 448 specimens. These comprised 15 species, six of which were damselflies in the genus ***Teinobasis*** (**Coenagrionidae**), a genus with known bryophyte dwellers. ***Teinobasis ponapensis*** (see Figure 4) was taken only in areas with moss and fern cover, suggesting that even adults can find some advantage in association with bryophytes. On that island they found that body size increases with an increase in altitude.

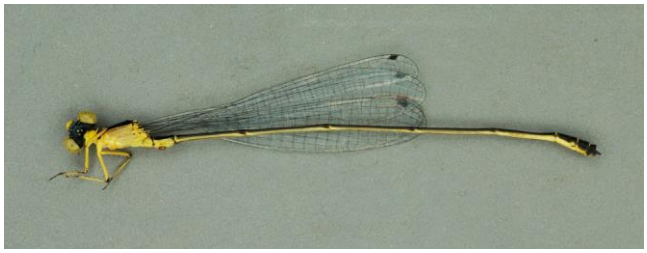

Figure 4. ***Teinobasis sjupp*** adult. ***Teinobasis ponapensis*** is a species whose adults live only in areas with mosses and ferns. Photo by V. J. Kalkman, through Creative Commons.

Terrestrial Naiads

Terrestrial nymphs are known for some families of **Odonata**, and moist forests, especially montane rainforests, seem especially suited for the moisture needs of this "aquatic" insect. Oppel (2005) reported on the **Odonata** of Papua New Guinea, where its 61 species were predominately among the **Zygoptera** (damselflies). Most were associated with moving or standing water, but one group was associated with temporary water sources or forest sites with high non-seasonal rainfall and high humidity. No **Anisoptera** (dragonflies) were among these terrestrial associations. Surprisingly to me, there was a negative correlation between the **Odonata** and mosses among this group.

Nevertheless, bryophytes can play an important role for some species. In Australia, the nymphs of ***Pseudocordulia*** (**Corduliidae** or **Pseudocorduliidae** – dragonflies) occur among leaf litter in the rain forests and moss forests of northern Queensland far from water (Watson 1982). Thus it should be no surprise to find **Odonata** nymphs among mosses as well, and many records of **Odonata** in litter may include mosses – soil biologists typically include mosses as part of the litter layer. ***Austropetalia patricia*** and ***A. tonyana*** (Figure 5-Figure 6) (**Austropetaliidae** – dragonflies) nymphs live on logs or among mosses in waterfalls and on streambanks (Theischinger & Hawking 2006). These alpine species are often rare due to limited habitat.

Figure 5. ***Austropetalia tonyana*** adult, a species whose nymphs can live among terrestrial mosses. Photo by Reiner Richter, with permission.

Figure 6. ***Austropetalia tonyana*** habitat where nymphs live above water among mosses. Photo by Reiner Richter, with permission.

Some **Odonata** use water-filled tree holes for their naiads. It is interesting that the rare damselfly naiads of ***Podopteryx selysi*** (**Megapodagrionidae** – damselflies; Figure 7) occur in such tree holes in the rainforest of north Queensland, Australia, but Watson and Dyce (1978) surmise that this species must lay its eggs on moss-covered stones or bushes. They apparently base this on finding the adults clinging to shrubs along paths and to the use of mosses for egg laying by other rainforest **Odonata**.

Figure 7. ***Podopteryx selysi*** adult, a species that may lay its eggs among mosses near tree holes in the rainforest. Photo by Reiner Richter, with permission.

In the Northern Sierra Madre Natural Park, Philippines, ***Risiocnemis elegans*** (**Cordulegasteridae** – dragonflies; Figure 8) nymphs occur in shaded seepages and on the moist forest floor several meters from water (Villanueva *et al*. 2009). In these locations, the females lay eggs on moist mosses.

Figure 8. ***Risiocnemis*** cf ***elegans***, a species that lays its eggs on moist mosses. Photo through Project Noah, with permission.

The genus ***Gomphomacromia*** (**Corduliidae** – dragonflies) also has at least semi-terrestrial nymphs. Von Ellenrieder and Garrison (2005) found nymphs under stones about 3 m from a moist, rocky area in Chile. Louten *et al*. (1996) found ***G.*** cf. ***fallax*** (Figure 9) on a moist, moss-covered slope along a dirt trail in Pakitza, Peru. That Beckemeyer (2002) found ***Gomphomacromia fallax*** laying eggs in dripping mosses on a cliffside suggests that nymphs of this species live there as well.

Figure 9. ***Gomphomacromia*** cf. ***fallax*** adult, s species that sometimes lays eggs in dripping mosses. Photo by Roy J. Beckemeyer, with permission.

Bryophytes can be a refuge for aquatic **Odonata** naiads when their habitat dries up. Willey and Eiler (1972) observed this in ***Somatochlora semicircularis*** (**Corduliidae**; Figure 10) from subalpine pools in Colorado, USA. When their pond dried up, they could be found under rocks, in moss mats, under logs, and at the bases of sedge clumps. This species dries more slowly than the dragonflies ***Aeshna interrupta interna*** (Figure 2, Figure 11) and ***Libellula quadrimaculata*** (Figure 12). It takes ***S. semicircularis*** twice as long to reach the same lethal state of dryness as that experienced by these two less tolerant species. This advantage seems to be incurred by a lower transpiration rate, and further protection is afforded by the early formation of snow pack over the dry pond. The mosses and other substrata are sufficient to protect the naiads from drought until the snow arrives.

Figure 10. ***Somatochlora semicircularis*** adult; this species has naiads that use wet mosses when its pond dries up. Photo by Belinda Lo through Creative Commons.

Figure 11. ***Aeshna interrupta*** adult. Photo by Kam's World, through Creative Commons.

Figure 12. ***Libellula quadrimaculata*** adult, a species with poor desiccation tolerance as a naiad. Photo by Böhringer Friedrich, through Creative Commons.

Donnelly (1990) found damselfly naiads of the dominant Fijian genus ***Nesobasis*** (**Coenagrionidae**; Figure 13) near a stream, crawling over wet mosses. As Donnelly cautiously pointed out, these may not be truly terrestrial. Rather, normally aquatic insects often climb above the water level in search of food, or perhaps to avoid excessive flow – or just because they can. In other cases, receding water levels after a rainstorm may leave them above the water surface. There is sufficient moisture for them to maintain hydration until they return to the water. But naiads must leave the water to shed their naiadal skin and emerge as adults, perhaps also explaining this above-water observation.

Figure 13. ***Nesobasis*** sp., a species whose naiads are known to crawl over wet mosses occasionally. Photo through Creative Commons.

Mosses may aid in the selection of burrowing sites of terrestrial dragonflies. Rod Morris (2010) shows the giant mountain dragonfly (***Uropetala chiltoni***; Figure 1, Figure 14) nymph poking its head out of its burrow in the soil and into a bed of mosses in a small wetland in New Zealand.

Figure 14. ***Uropetala chiltoni*** nymph emerging from burrow to a bed of mosses. Photo by Rod Morris, with permission.

Emergence

Terrestrial bryophytes can serve as emergence sites where the naiads shed their exoskeleton, leaving it behind as an **exuvia** (Figure 15-Figure 16), to become adults (Needham *et al*. 1901). These researchers found layers of shed exuviae of both ***Gomphus exilis*** (Figure 17) and ***G. spicatus*** (**Gomphidae** – dragonflies; Figure 18-Figure 19) among the mosses on logs at the edge of a pond. Similarly, ***Somatochlora elongata*** (**Corduliidae** – dragonflies; Figure 20; see also Figure 21-Figure 22) left exuviae on mosses at the edge of a pond. Sorianol and Gutiérrez (1998) found the exuviae of ***Oplonaeschna magna*** (**Aeshnidae** – dragonflies; see Figure 23-Figure 24), a new species at the time, clinging to mosses on the vertical rock walls of a canyon in Mexico. These exuviae were 0.80-1.25 m above the water, reaching as much as 3 m on tree trunks and shrubs. Bryophytes are easy to climb, provide moisture, and permit at times a refuge or limited camouflage.

Figure 15. ***Lestes*** sp. emerging on a reed, leaving behind its shed **exuvia**. Photo by Richard Orr, with permission.

Figure 16. ***Tetragoneuria cynosura*** emerging. Photo by Richard Orr, with permission.

Figure 17. ***Gomphus exilis*** adult, a species that uses mosses as emergence sites. Photo by Richard Orr, with permission.

Figure 18. ***Gomphus spicatus*** naiad, a species known to emerge among mosses on logs near water. Photo by Donald S. Chandler, with permission.

Figure 19. ***Gomphus spicatus*** male adult. Photo by Richard Orr, with permission.

Figure 20. ***Somatochlora elongata*** male, a species that emerges on mosses. Photo by Denis A. Doucet, with permission.

Figure 21. ***Somatochlora tenebrosa*** exuvia, shed here on a moss-covered surface. Photo by Richard Orr, with permission.

Figure 22. ***Somatochlora tenebrosa*** male adult. Photo by Richard Orr, with permission.

Figure 23. ***Oplonaeschna armata*** adult, a species that uses mosses for emergence. Photo by Jerry Oldenettel, through Creative Commons.

Figure 24. ***Oplonaeschna armata*** adult ovipositing in mud. Photo by Jerry Oldenettel, through Creative Commons.

Once the dragonflies shed their naiad exoskeleton, the newly emerged adults must climb or hang in place to spread their wings and pump fluids into those veins (Figure 25). I have watched them climb *Eleocharis* to the top, then climb down and climb another, apparently in search of a minimum height where they finally stayed to emerge. In the Huron Mountains of the Upper Peninsula of Michigan, USA, Kielb *et al*. (1996) observed emergent adults of ***Stylogomphus albistylus*** (**Gomphidae** – dragonflies; Figure 26) resting on vertical moss-covered rock faces below waterfalls and on nearby trees.

But not all naiads must assume a vertical position to emerge. ***Aeshna juncea*** (Figure 28-Figure 29) is able to emerge in a horizontal position on ***Sphagnum*** (Figure 33) (Maitland 1967).

Figure 25. ***Anax junius*** on *Eleocharis*, where it is has emerged and is preparing to pump fluids into its wings. Photo by Richard Orr, with permission.

Figure 26. ***Stylogomphus albistylus*** adult, a species that can emerge on vertical rocks covered by mosses. Photo by Richard Orr, with permission.

Perching and Mating

Although the adults are strong fliers, even they must rest at times. For some, mosses seem to be suitable sites (Figure 27), especially in bogs.

Figure 27. ***Celtithemis martha tenera*** adult resting on male ***Polytrichum***. Photo by Richard Orr, with permission.

Figure 28. ***Aeshna juncea*** naiad with mosses. Photo by Tim Faasen, with permission.

Figure 29. ***Aeshna juncea*** in flight. Photo by Jens Nielsen Buurgaard, through Creative Commons.

Adults no longer must live in the water and these strong fliers (Figure 29) can often stray far from their naiadal home. For example, members of ***Enallagma*** (Figure 30) occasionally travel up to 1 km to a different lake to lay eggs (McPeek 1989). But some exhibit mass annual migrations of a much greater distance, a phenomenon noted as early as 1494 in Europe! (Calvert 1893; May 2013). Matthews (2007) used a hydrogen isotope ratio to track migrations of *Anax junius* from Ontario, Canada, to Veracruz, Mexico in late August to

October. Matthews found that about 90% of the individuals moved southward for a mean distance of ca. 900 km, but exhibited a maximum of nearly 3,000 km. During these migrations they often stop to feed, mate, or lay eggs (Russell *et al*. 1998; Wikelski *et al.* 2006; Matthews 2007). Distance travelled depends on species, sex, age, size, and weather (Angelibert & Giani 2003). They may seek a particular habitat as adults that differs from that adjacent to the water, at least in part to avoid predators such as frogs while mating.

Figure 30. ***Enallagma divagans*** mating pair. Photo by Richard Orr, with permission.

In New Guinea, the genus ***Lanthanusa*** (**Libellulidae** – dragonflies) is restricted to high elevations above 1350 m (Lieftinck 1955). ***Lanthanusa lamberti*** occurs in the moss forests at 2800-2850 m, the highest known elevation of any **Libellulidae** in New Guinea. The mosses there may simply like the same atmospheric conditions and habitat as the odonates, but the presence of the moss could also provide some aspect of the habitat that makes it more suitable for these dragonflies. One such possibility could be as sites for egg deposition and nymphal development.

Beckemeyer (2002) found ***Gomphomacromia fallax*** (Figure 9) adult males perching on mosses beneath cliff sides where there was dripping water. Females were flitting about nearby and flicking their abdomens to deposit eggs toward the mosses. A discussion of perching and mating in bogs (Figure 31) is in Chapter 11-5 of this volume.

Figure 31. The dragonfly ***Sympetrum danae*** rests here on the moss ***Polytrichum***. It prefers ***Sphagnum*** peatlands for mating. Photo copyright by David Kitching <http://www.brocross.com/dfly/dfly.htm>, with permission.

Oviposition

If a nymph is terrestrial, then the eggs must also be laid in a terrestrial habitat, although the converse is not necessarily true. (Hatched naiads could drop into the water from overhanging plants or crawl to the water.) Most aquatic **Odonata** are not moss inhabitants, but the female may nevertheless lay her eggs among mosses, providing them with a secure and hidden location for development. Such is the case for ***Austroargiolestes chrysoides*** (Figure 32) in Australian rainforest streams (Theischinger & Hawking 2006).

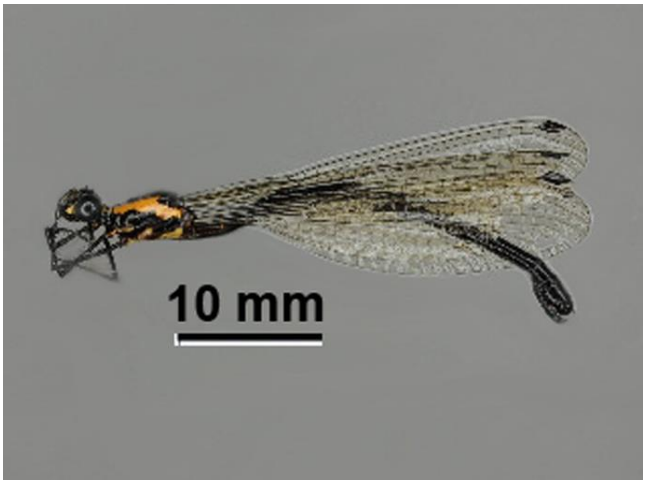

Figure 32. ***Austroargiolestes chrysoides*** adult, a species that lays its eggs among mosses in Australian rainforest streams. Photo from Biodiversity Centre, through Creative Commons.

Michiels and Dhondt (1990) described the selection of the oviposition site by the dragonfly ***Sympetrum danae*** (**Libellulidae**; Figure 33). This species deposits its eggs among ***Sphagnum*** (Figure 33), but given the choice of ***Sphagnum*** and ***Mnium hornum*** (Figure 34-Figure 35), some females will deposit eggs in the latter as well. Michiels and Dhondt attempt to explain the choice of these mosses, considering them to have similar form but distinctly different odors, at least to humans. They thus eliminate odors as determining the choice and consider moss form to be a more likely determining factor. They derived a list of advantages for depositing eggs among ***Sphagnum***, based on a number of literature references:

1. Wet ***Sphagnum*** prevents summer drying of eggs and is likely to be submerged in the spring when eggs hatch and naiads develop.
2. Acid water associated with ***Sphagnum*** has fewer fish and other predator species.
3. Conditions are optimal for mycobacteria that feed **Cladocera** that in turn feed naiad **Odonata**.
4. ***Sympetrum danae*** (Figure 33) naiads are sprawling and need support and shelter found among ***Sphagnum*** (Figure 33).

Figure 33. ***Sympetrum danae*** male on ***Sphagnum***, a suitable egg deposition site. Photo copyright by David Kitching <http://www.brocross.com/dfly/dfly.htm>, with permission.

Figure 34. ***Mnium hornum*** hummock, giving a superficial similarity to ***Sphagnum***. Photo by Michael Lüth, with permission.

Figure 35. ***Mnium hornum*** up close, showing that it is quite different from ***Sphagnum***. Photo by Bob Klips, with permission.

These advantages would not be present in the terrestrial moss ***Mnium hornum*** (Figure 34-Figure 35), so the choice of ***Sphagnum*** for egg deposition is also dependent on its availability in the proximal habitat to that of the naiads. Nevertheless, mosses near water bodies and in rain forests do afford more limited protection from drying. One must wonder how the terrestrial nymphs are adapted for obtaining prey. The large jaws and watch and wait behavior should still work on land, but the prey items will be different.

Egg-laying among bryophytes has been observed for a long time. Lucas (1900) noted that ***Aeshna caerulea*** (**Aeshnidae** – dragonfly) occurred on "moss-hags" around peaty tarns and laid its eggs in wet, mossy ground. A female ***Aeshna juncea*** (Figure 36) on the Brooks Peninsula of Vancouver Island, Canada, oviposited into the wet mosses clinging to a vertical rock surface at the edge of a drying pool (Cannings & Cannings 1983).

Wang (2000, in Reels & Dow 2006) found that ***Bayadera brevicauda brevicauda*** (**Euphaeidae** – damselflies; Figure 37) from Taiwan uses moss-covered stones or fallen leaves, often at some distance from water, as oviposition sites.

In Hawaii, the seepage damselfly ***Megalagrion hawaiiense*** (**Coenagrionidae**; Figure 38) deposits her eggs in dripping moss banks (Williams 1936). These damselflies are territorial (Moore 1983) and males guard the females while they lay eggs (Williams 1936; Polhemus 1994). The eggs hatch in about ten days.

Figure 36. ***Aeshna juncea*** ovipositing in ***Polytrichum***. Photo copyright by David Kitching <http://www.brocross.com/dfly/dfly.htm>, with permission.

Figure 37. ***Bayadera brevicauda***, a species that uses moss-covered stones away from water for oviposition. Photo by Cao Heihua, through Creative Commons.

Figure 38. ***Megalagrion hawaiiense***, a species that lays its eggs in dripping moss banks. Photo by Karl Magnacca, with permission.

The heaviest of all dragonflies, females of ***Tetracanthagyna plagiata*** (**Aeshnidae**; Figure 39-Figure 40), seem to prefer soft substrates (Leong & Tay 2009). One such substrate is decaying logs kept moist and soft by moss cover. Leong and Tay observed this behavior on a log next to a stream in Singapore.

Figure 39. ***Tetracanthagyna plagiata*** (dragonfly; **Aeshnidae**) adult in Malaysia. This is the heaviest of the dragonflies. Photo by Keith Wilson, through Creative Commons.

Matushkina and Klass (2011) suggest that the ovipositor of female ***Phenes raptor*** (**Petaluridae**; Figure 41) is particularly adapted for the substrate where the eggs are to be laid. This ovipositor (Figure 42) has numerous sensilla of different shapes and Matushkina and Klass suggest these may be able to detect suitable places for depositing eggs. These females choose loose substrata, including mosses, grass roots, and decaying plant matter. The ovipositor also lacks serration and the interlocking mechanism that connects the first two valves medially is reduced, both adaptations they suggest to relate to depositing eggs within soft substrata, including mosses.

Figure 40. ***Tetracanthagyna plagiata*** showing oviposition into soft wood. Photo by Marcus Ng, with permission.

Figure 41. ***Phenes raptor*** ovipositing into the soft end tissue of log. Mosses help to keep logs moist so they become soft. Photo by Eric LoPresti, with permission.

Figure 42. ***Phenes raptor*** female showing ovipositor. Photo by Eric LoPresti, with permission.

It would be interesting to see if the **Odonata** have preferences for growth forms of mosses. Dense cushions would seem appropriate for those adapted to a soft but solid substrate. Others that drop or "throw" the eggs to the substrate may prefer loose, thick mats, or at least be able to use them. If such correlations exist, the structure of the ovipositor may tell us the kinds of mosses or liverworts they would prefer.

Sampling

These nymphs are worth bringing home live for a closer look, but bring some smaller food items for observations of the interesting feeding. Keep them separate until you are ready to watch! Lucas (1900) suggests carrying the live specimens home in wet moss to avoid the jostling they would get in a jar. They can live this way for several hours to several days. Winstanley *et al*. (1981) were able to keep nymphs of ***Uropetala carovei carovei*** (**Petaluridae**; Figure 43) from New Zealand alive and rear them through emergence to adults by filling 2-liter containers with leaf mold, moss, and water.

Figure 43. ***Uropetala carovei***, a species that can be reared using mosses, leaf mold, and water. Photo by Geoff Tutty, through Creative Commons.

Collection of terrestrial nymphs that live among bryophytes is a matter of collecting the bryophytes. Some may be collected by using traps, but small ones may not leave the bryophyte. Adults are usually collected with insect nets.

Life in a Thallus

Some of the **Odonata** use bryophytes as food for larvae and pupae, providing a safe, moist habitat for their survival in semiterrestrial habitats. For the dragonfly ***Epiophlebia superstes*** (**Epiophlebiidae**; Figure 44), an **endemic** (restricted to certain area or country) in Japan (Asahina & Eda 1982; Inoue 1983; Tabaru 1984), it appears that bryophytes also provide egg-laying substrata. This dragonfly is often confused with damselflies because its hind wings are nearly equal to the forewings and it folds its wings over its back at rest like damselflies do. Furthermore, it lacks the jet propulsion typical of dragonflies but absent in damselflies (Tabaru 1984). But it has apparently branched from a dragonfly, then become separated from them when the Himalayas uplifted. Normally the adult lays her eggs in vegetation alongside a waterfall (Asahina & Sugimura 1981). However, in the absence of any nearby tracheophytes, females in locations in Nakamura, Kochi Prefecture, Japan, used bryophytes on the nearby rocks. The eggs were injected into the thallose tissues of the thallose liverworts ***Dumortiera hirsuta*** (Figure 45), ***Conocephalum*** (Figure 46), and ***Pellia*** (Figure 48). In China, ***Epiophlebia diana*** selects tracheophytes, and Carle (2012) considers the preferred plants of ***E. superstes*** there to be tracheophytes as well as the liverworts ***Dumortiera***, ***Conocephalum***, and ***Pellia*** (Asahina 1934, 1950; Asahina & Eda 1958, 1982; Asahina & Sugimura 1981; Tamiya & Miyakawa 1984; Tokunaga & Odagaki 1939).

In fact, it appears that the dragonfly ***Epiophlebia superstes*** (Figure 44) actually prefers the liverworts (Asahina & Eda 1958, 1982) for oviposition. Males stake out a "territory" over a patch of ***Conocephalum conicum*** (Figure 46), despite the presence of the usual tracheophyte egg depositories of *Petasites japonica* and *Eutrema wasabi*. Subsequently the female deposits her eggs in the tissues of this thallose liverwort (Figure 47). Upon dissection Asahina and Eda discovered that the eggs were precisely deposited in the air chambers of the thallus. Further egg deposits are also made into another thallose liverwort, ***Pellia endiviifolia*** (Figure 48). Because the liverwort thallus has an irregular shape compared to the symmetry of the tracheophyte leaves, the female has to keep changing her position relative to the surface, resulting in some of the eggs being laid in nearby tracheophytes.

Figure 44. ***Epiophlebia superstes*** (**Epiophlebiidae**) adult, a dragonfly that lays its eggs in thallose liverworts. Photo through Creative Commons.

Figure 45. ***Dumortiera hirsuta***, a thallose liverwort that houses eggs injected into it by the dragonfly ***Epiophlebia superstes***. Photo by Li Zhang, with permission.

Figure 46. ***Conocephalum conicum*** thallus, species where ***Epiophlebia superstes*** deposits its eggs. Photo by Li Zhang, with permission.

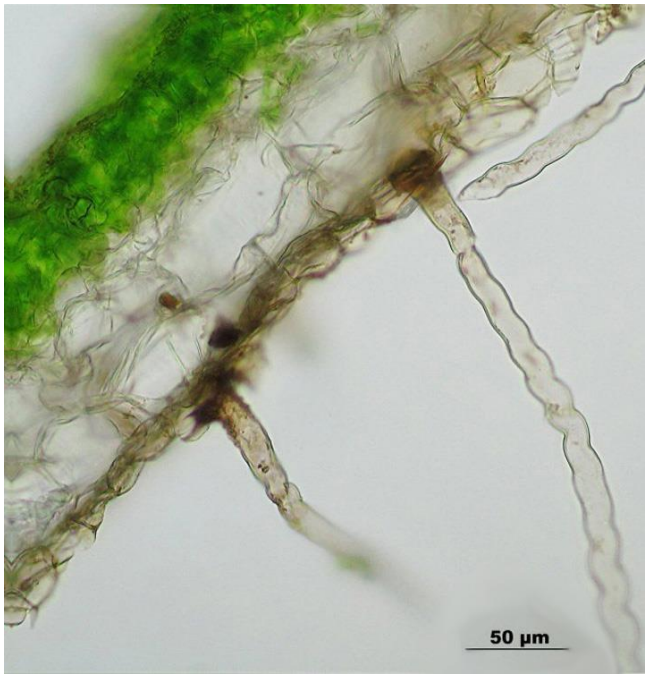

Figure 47. ***Conocephalum conicum*** thallus cross section showing chambering where nymphs of ***Epiophlebia superstes*** are able to live. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

Figure 48. ***Pellia endiviifolia***, site of egg deposition for the dragonfly ***Epiophlebia superstes.*** Photo by Michael Lüth, with permission.

The ovipositor leaves a small "scar" on the liverwort thallus and the young nymphs later hatch through this hole. These holes permitted the researcher to identify thalli containing eggs and to count them. One thallus had 175 eggs! Others had lesser numbers of 24, 51, and 100. Development of the nymphs to become adults requires 5-8 years, perhaps setting the record for **Odonata** (Tabaru 1984). Use of the liverworts seems to vary between locations, with females in some areas seemingly avoiding the liverworts despite their suitable availability.

Asahina and Eda (1982) suggest that the related ***Epiophlebia laidlawi*** (**Epiophlebiidae**; Figure 49), a relict species from the Himalayas, might also use bryophytes for egg-laying. Now one can find in Wikipedia the statement that bryophytes are the preferred egg-laying substrate for that species, citing information from Silby (2001). At these high altitudes, mostly above 2000 m, the nymphs can take up to six years to develop before they emerge as adults.

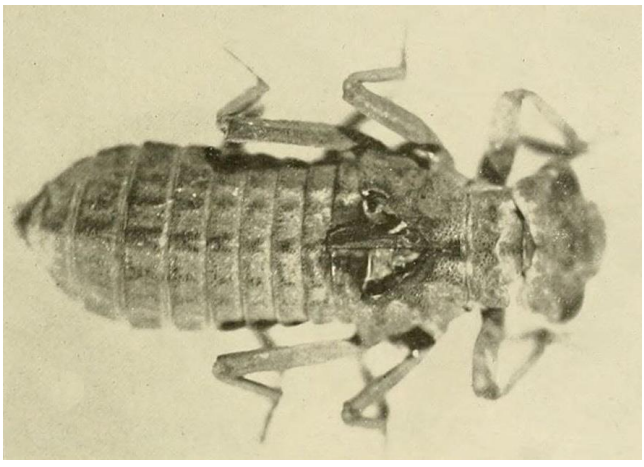

Figure 49. ***Epiophlebia laidlawi***, dragonfly nymph that hatches from eggs laid in thallose liverworts. Photo by Shyamal, through Creative Commons.

It appears that ***Epiophlebia*** (Figure 44, Figure 49), which has only four species (Wikipedia 2007) and these are restricted to Asia, may not be the only odonate that uses a bryophyte thallus for oviposition (Villareal 2009). It's not

water, but it offers similar protection from desiccation – what better place than within the tissues of a plant that is seldom eaten? In this case, the nymphs were damselflies (**Zygoptera;** Figure 50-Figure 55), but their identity remains unknown. Although ***Nothoceros aenigmaticus*** (Figure 53) is not a true liverwort, but rather is a hornwort, its thalloid structure is similar to that of liverworts. This species is endemic to the southern Appalachian Mountains, USA, where, sadly, it is threatened to extinction resulting from a plague of hemlock woolly adelgids (*Adelges tsugae* – Hemiptera) on the hemlocks (*Tsuga canadensis*) that make its environment suitable for the hornworts (Jacobs 2005; Hyatt 2006).

Figure 52. Young damselfly from within the thallus of a hornwort. Photo courtesy of Juan Carlos Villareal.

Figure 50. Young damselfly from within the thallus of a hornwort. Photo courtesy of Juan Carlos Villareal.

Figure 53. ***Nothoceros aenigmaticus*** thallus, a hornwort, with eggs that are probably those of a dragonfly or damselfly. Note that the small dark-green patches are ***Nostoc*** **symbionts** (blue-green bacteria that live in partnership with the hornwort, contributing converted atmospheric nitrogen). Dragonfly identification is by K. Tennessen. Photo courtesy of Juan Carlos Villareal.

Figure 51. Anal gills and abdomen of a young damselfly from within the thallus of a hornwort. Photo courtesy of Juan Carlos Villareal.

Figure 54. Damselfly egg cases in ***Nothoceros aenigmaticus***. Photo courtesy of Chris Cargill.

Figure 55. Damselfly egg case from ***Nothoceros aenigmaticus***. Photo courtesy of Chris Cargill.

Juan Carlos Villareal (pers. comm. 23 December 2008) made a similar find in Mexican populations where the developing larvae were leaf miners on the thallus. The damselflies, identified by Ken Tennessen, were in the **Coenagrionidae**, possibly the genus ***Argia*** (Figure 56).

Figure 56. ***Argia tibialis*** adult, member of a genus whose nymphs may be one of those that live in hornwort thalli. Photo by Richard Orr, with permission.

I could find no observations on feeding by these thallus dwellers. How long do they remain in the thallus? What do they eat while they are there? This order of insects is highly adapted to be carnivorous. The chances that they find animal food items within the thallus seem slim.

Summary

The **Odonata** are predominately aquatic in the immature stage, but some nymphs are terrestrial, and some of these use bryophytes to protect themselves and to maintain moisture. These carnivores can find food among the bryophytes, including spiders, while hiding from their own predators – mostly amphibians and birds.

Bryophytes provide a good site for egg laying, and even aquatic species may lay eggs on streamside or poolside bryophytes. Some naiads may seek bryophytes as their water body dries up. Many more species climb to the banks of streams and lakes to emerge from their nymphal skins, leaving behind evidence as numerous **exuviae** on the bryophytes. Others use moss hummocks as perching sites.

Live **Odonata** nymphs, including aquatic species, may be kept alive by placing wet moss in the container with them. Adults can be collected with insect nets.

A few **Odonata** actually live within the thalli of liverworts and hornworts. In particular, ***Epiophlebia superstes*** in Asia lays its eggs in several liverwort species and nymphs develop there. An unidentified damselfly develops within hornwort thalli; others appear to be in the genus ***Argia***.

Acknowledgments

Thank you to Bob Marr for reviewing the chapter and providing me with an additional reference. And thank you to the many photographers who made their images available through Creative Commons or gave me permission to use their images.

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CHAPTER 12-4
TERRESTRIAL INSECTS: HEMIMETABOLA – ORTHOPTEROIDEA

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CHAPTER 12-4
TERRESTRIAL INSECTS: HEMIMETABOLA - ORTHOPTEROIDEA

Figure 1. **Orthopteran** moss mimic, blending with surrounding bryophytes. Photo courtesy of Matt von Konrat.

The **Orthopteroidea** (Figure 1) comprise a group of insects that used to be in the order **Orthoptera**. The group has recently been split into multiple orders, one of which is still called **Orthoptera**.

ORTHOPTERA – Grasshoppers and Crickets

Most grasshoppers are big, and in fields of tall grasses and **forbs** (non-grass herbaceous plants) they seem to be everywhere (Paranjape *et al*. 1988). But do they inhabit or use bryophytes? And what can bryophytes offer them?

At least some grasshoppers eat mosses (Appelqvist 1997). Uvarov (1977) suggested that the grasshoppers might eat mosses for their water content. But some seem to subsist primarily on mosses (Hochkirch *et al*. 2007). And some have color patterns that hide them well against the patterned moss surface (Figure 2-Figure 3) (Forsman & Appelqvist 1998). Others choose bryophytes for laying eggs (Langmaack 1997), presumably providing them with some protection (concealment) from predators and decreasing the danger of desiccation.

Figure 2. Forest grasshopper of Ecuador with liverwort color patterns on its sides and a moss hanging from its head. It appears that this hopper can help in dispersal. Photo by Arthur Anker, with permission.

Figure 3. Juvenile grasshopper in Ecuador with markings that look like leafy liverworts that are so common on tropical leaves. Photo by Arthur Anker, with permission.

Any increase in niches is likely to increase insect diversity, and bryophytes can play this role for some of the **Orthoptera**. Noting that the grasshopper family **Tetrigidae** (pygmy grasshoppers) included mosses in their diet (Hochkirch *et al*. 2000), Hochkirch *et al*. (2007) experimented with members of this family to determine how **sympatric** (having overlapping geographic distribution) species might co-exist. They used the mosses ***Rhytidiadelphus squarrosus*** (Figure 4) and soil algae as food sources. ***Tetrix ceperoi*** (Figure 5) and ***T. subulata*** (Figure 6), both sometimes moss inhabitants, were cultured together in the lab experiments. ***Tetrix ceperoi*** exhibited substantial decrease in copulations with its own species when in the presence of ***T. subulata***. The males attempted more mating events with females of ***T. subulata***, but the females rejected them. Although none of these two-species matings was successful in the lab, they substantially reduced the success of ***T. ceperoi*** in field experiments. It required much denser populations to have similar depression effects on ***T. subulata***. Hochkirch *et al*. (2007) surmised that to prevent such reproductive interference the species may evolve different mating signals or different habitat preferences, spatial patterns, or temporal segregation. Having bryophytes in the habitat provides differences in available niches, including moisture and food item differences (Figure 7).

Figure 4. ***Rhytidiadelphus squarrosus***, an acceptable food source for ***Tetrix*** species. Photo by Michael Lüth, with permission.

Figure 5. Mating grasshoppers, ***Tetrix ceperoi***, on the moss ***Atrichum subulatum*** in the Czech Republic. Holes appear in the leaves where they have been eaten. Research continues on feeding preferences of these insects. Photo by Petr Kočárek, with permission.

Figure 6. ***Tetrix subulata*** female, a species that eats bryophytes and uses them for perching sites during mating. Photo by Joy Markgraf, with permission.

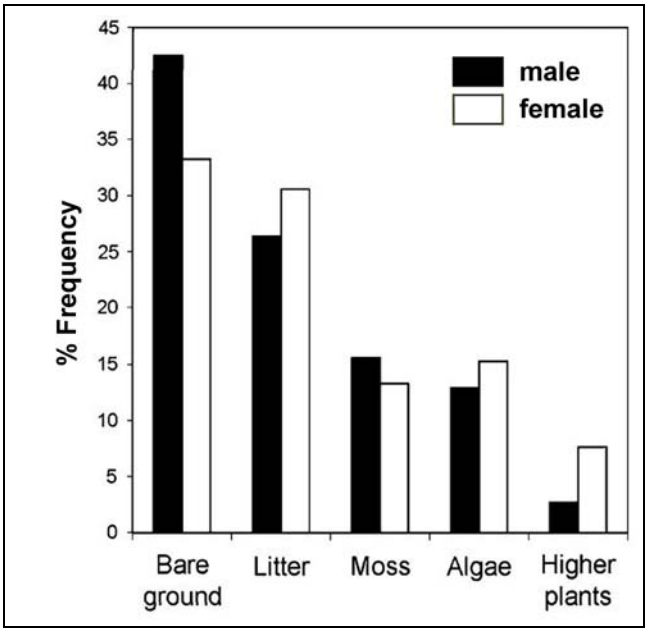


Figure 7. ***Tetrix ceperoi*** (Figure 5) frequency of perching on moss compared to other perching sites in its habitat. Modified from Hochkirch *et al*. 2007.

Tetrigidae – Pygmy Grasshoppers

The pigmy grasshoppers (Figure 8) are common moss dwellers and moss consumers (Hancock 1902; Chopard 1951; Bastow *et al*. 2002).

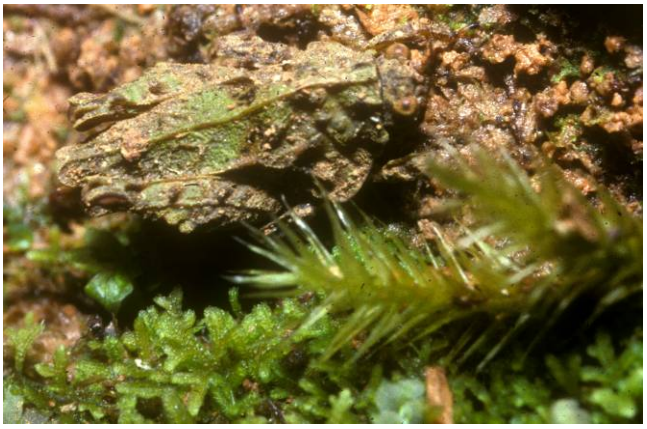


Figure 8. This grasshopper appeared to have protonemata cultured on its back. At the very least, it has cryptic coloration that makes it nearly invisible among these mosses – until it jumps! Photo by Janice Glime.

Tetrix

Tetrix granulata in Oregon, USA, lives in shaded meadows with damp mossy ground and short grass (Fulton 1930). Buckell (1921) noted that ***Tetrix brunneri*** (Figure 9) in the Chilcotin District of British Columbia, Canada, was present only in a small area where it lived among leaf litter and mosses under birch (*Betula*) and willow (*Salix*) surrounding an upland spring. This species occurs as high as 3,300 m among boulders in Colorado, USA (Alexander 1964). But the most widespread of these moss dwellers in North America is ***Tetrix subulata*** (Figure 6) (Rehn & Grant 1955).

Figure 9. ***Tetrix brunneri***, a species that seems to prefer mossy areas. Photo by Lynette Schimming, through Creative Commons.

Tetrix subulata (Figure 6) has the somewhat unusual character of having both **brachypterous** (short-winged) and **macropterous** (large-winged) forms (Lock *et al*. 2006). There is a tradeoff in these insects between dispersal and reproduction, with the short-winged forms reproducing faster and the long-winged ones travelling farther and colonizing new habitats. The long-winged form consumes significantly more energy and exhibits a significantly higher protein content compared to the short-winged form. Carbohydrate and lipid content do not differ. The males have higher protein content and consume more energy than females, providing males with the energy needed to search for females.

Color Morphs – Thermoregulation or Camouflage?

Many grasshoppers exhibit color morphs (Nabours 1929; Rowell 1971; Holst 1986; Forsman 1999, 2000). ***Tetrix subulata*** is able to exhibit a variety of morphs (Figure 6, Figure 10-Figure 11) even within a single clutch (Forsman 2000). ***Tetrix subulata*** occurs in damp places on the soil surface where it eats mosses, algae, and humus (Forsman 1999) and is widespread in Europe (Holst 1986). This species exhibits discontinuous color morphs that could affect body temperature or protection from predation (Forsman 1997). Forsman (1997) found that black morphs had up to 49% higher **temperature excess** (difference between ambient and body temperature) compared to white morphs in the same external conditions. Forsman (2000) found that females preferred higher body temperatures than did males. Dark morphs both attain higher temperatures and prefer higher temperatures compared to paler morphs.

Figure 10. ***Tetrix subulata*** as a dark variant. with somewhat shortened wings. Photo from Biopix, through Creative Commons.

Figure 11. ***Tetrix subulata*** as a grey variant. with long wings. Photo from Biopix, through Creative Commons.

Gause's Law and Bryophyte Dwellers

When multiple species in the same genus occupy the same area, one must ask what keeps the species from competing – and out-competing (**Gause's Law**)? Gause (1934) described this "law" and experiments to support it in his "Struggle for Existence." This "law" has become known as the **competitive exclusion principle**. Based on many plant experiments, Gause put forth the principle that competition begins due to the reaction when plants are spaced in such a way that the reaction of one affects the response of the other by **limiting** it. He used this base to suggest that animal experiments are needed, demonstrating that when there is growth a number of individuals of a first and a second species will compete for common food. "At a certain moment food will have been consumed, or toxic waste products will have accumulated, and as a result growth of the population will cease. Competition will take place for utilization of a certain **limited** amount of energy." I have emphasized "limited" because this part of Gause's argument is often ignored. If food and space are unlimited or in excess, competitive exclusion need not apply.

Gause built his famous law upon the work of many other ecologists. In his comprehensive treatment of competitive exclusion (Gause's Law), Gause again emphasized the importance of experiment, providing guidance on the types of experiments needed. Levin (1970) presented it somewhat differently: "No stable equilibrium can be attained in an ecological community in which some *r* of the components are limited by less than *r* limiting factors. The limiting factors are thus put forward as those aspects of the niche crucial in the determination of whether species can coexist." If each species is limited by an independent combination of predation and resource limitation, it is possible for them to coexist. "If the two have comparable threshold values, which is certainly possible, any equilibrium reached between the two will be highly variable, and no stable equilibrium situation will result."

Here is where proving the competitive exclusion principle gets messy. Two species may co-exist because the environment is constant and advantages for survival may shift as the weather shifts. As a result of this and other problems with the complex relationship, Gause's law has come under close scrutiny, with many researchers providing examples that appear to disprove it. For example, Simberloff (1982) stated that it "has not helped us to understand how nature works. It has generated predictions that are either practically untestable, by virtue of immeasurable parameters or unrealizable assumptions, or trivially true."

Simberloff (1982) recognized the inherent problems with our use of Gause's law and offered an explanation. "When species do compete with one another, effects are usually moderated by other factors (*e.g.*, weather, predators, pathogens) that keep populations below levels at which exclusion would occur, or else each competitor is favored in a different set of times and/or places and this fact combined with normal individual movements keep all species in the system."..."Chance plays a major role in many potentially competitive interactions, and there is good evidence that many species that do compete with one another do so rarely or intermittently, and at most times their population dynamics are governed by other forces." While this explains why closely related species are able to co-exist, it does not disprove Gause's law.

But in many of the examples that seem to refute Gause's law, the requirement of competition for a limiting resource or being preyed upon by a common predator is often missing because neither population has reached a limiting state for the needed resource. Levin (1970) attempted to improve upon our understanding of the "law" by suggesting three considerations:

1. Eliminate the restriction that all species are resource-limited, a restriction persistent in the literature.
2. The results relate in general to periodic equilibria rather than to constant equilibria.
3. The nature of the proof relates to the crucial question of the behavior of trajectories near the proposed equilibrium, and provides insight into the behavior of the system when there is an insufficient number of limiting factors.

Vance (1978) added further to the explanation of seeming exceptions. He took the position that one means by which two closely related species can co-exist is by having "suitable differences in spatial refuges from the predator, differences in appearance and/or location which induce frequency-dependent predation, and a difference in energy allocation between competitive and predatory defense." Vance concluded that "Gause's Law is just as true when predators are common and important as when they are absent. Most of those prey in nature whose coexistence is known to depend on predation differ in resource use; *i.e.*, these prey appear to partition environmental resources just as is expected of coexisting species in predator-free systems. A large proportion of cases of coexistence of similar species in nature probably results not from resource partitioning alone or from predation alone but from both mechanisms operating simultaneously."

Hanski (1983) carries this argument somewhat farther to include the role of a patchy environment. He concludes that two possible outcomes of regional competition are (1) a decrease in the fraction of habitat patches occupied by the competing species and (2) an increase in the proportion of regionally rare species, some of which may ultimately go extinct. This study has implications for bryophytes as a habitat because of the often patchy nature of their distribution within a habitat. This patchiness can especially affect invertebrate species that have limited dispersal ability.

Caesar *et al*. (2010) examined the application of Gause's Law within the moss-dwelling pygmy grasshopper genus ***Tetrix***. According to Gause's Law, if two species are in the same genus, then their niches are likely to be similar, but one might be expected to be better in that niche, out-competing the other. An often overlooked part of this law is the part "if any factor is limiting."

Tetrix subulata (Figure 6) not only differs within the species by differences in color pattern, but also in form, behavior, and physiology (Caesar *et al*. 2010). Caesar and coworkers tested the interactions of these factors, using the moss ***Polytrichum*** sp. (Figure 12) as food. Individuals climbed the moss to feed and to find the best combination of moisture, light, and temperature. Survival is higher in low density of mothers than in high density. In high

density, the intermediate color morphs survived best, but survival was independent of color diversity at low densities, presumably due to less intense competition. Mixed siblings had higher survival than mixes of non-siblings, suggesting some competitive advantage. The mosses in their natural habitat therefore provided not only food, but permitted the various morphs to find locations suitable to their temperature, moisture, and light needs as well as being the safest place for particular morphs.

Figure 12. ***Polytrichum juniperinum***, an acceptable food source for ***Tetrix subulata*** (Figure 4). Photo by Janice Glime.

To demonstrate the advantages of certain color patterns against predators in grasshoppers, Forsman and Appelqvist (1998) likewise experimented with ***Tetrix subulata*** (Figure 6). By manipulating color patterns and exposing these pygmy grasshoppers to predation from domestic chickens they could determine prey advantages (Figure 13). They painted some black and others striped. The striped individuals experienced enhanced survival when reaction distance was short and jumping performance was poor, but when the reaction required a long distance jump with high performance, their survival decreased compared to those individuals painted black. The advantage to the multiple color patterns seems to differ with circumstances, resulting in each morph surviving at different times and circumstances. The differences in form, behavior, and physiology make their specific habitat needs differ, hence defining different niches.

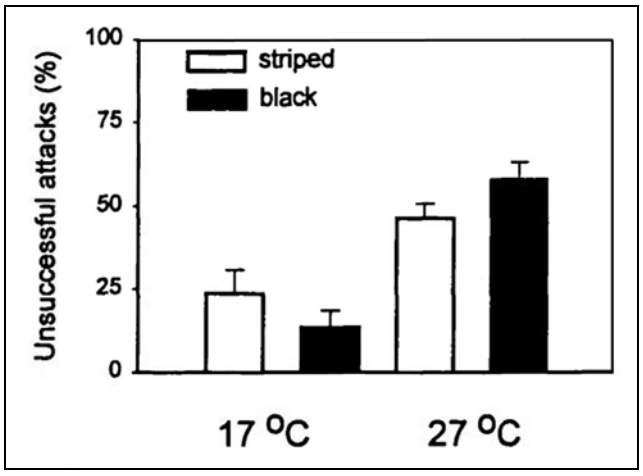


Figure 13. Comparison of ***Tetrix subulata*** (Figure 6) painted solid black and with stripes to determine the success of chickens preying upon them. Modified from Forsman & Appelqvist 1998.

Discotettix

One species, ***Discotettix belzebuth*** (=*Tetrix belzebuth*; Figure 14), occurs on mossy tree trunks in the orient (Gen & Rahman n.d.). Rather than having its own cryptic coloration, this species is sometimes bedecked with small plants of bryophytes or algae (I was unable to independently verify this). This enables them to move about undetected while they eat the epiphytic mosses, plants, and detritus on the tree trunks. However, when I searched for a picture to demonstrate this, all representatives were clean. Nevertheless, as you can see in Figure 14, the species is well suited for culturing bryophytes and algae. Its surface has pits where they can cling and become established, and the "thorns" could even help to hold larger bryophytes in place. These same pits and thorns provide disruptive coloration that helps to camouflage the uninhabited ones.

Figure 14. ***Discotettix belzebuth*** showing the pits in the exoskeleton and the thorns, both of which could aid in establishment of mosses. Photo by Bernard Dupont, through Creative Commons.

Vibration Sites

It seems a bit odd that females rest on mosses, but males do not call from mosses. But there is a very sound reason for that (pun intended!). Males attract females for mating by using vibrations (Kočárek 2010). But for vibrations to be effective, the hopper must be sitting on a suitable substrate, and that is not a moss. Moss, instead, can effectively absorb sounds. Rather, the males sit on bare ground, especially when exhibiting mating behavior. Sand is especially good at transmitting the sound, especially in the hearing range of frequencies between 300 and 400 Hz. And this is a choice mating substrate for males of ***Tetrix ceperoi*** (Figure 5), despite the increased risk of predation compared to resting on mosses or other vegetation. These vibrations are important in mate recognition in this species (Kočárek 2010).

Elias *et al*. (2004) examined the effectiveness of sound transmission from several substrates in their study of a jumping spider, ***Habronattus dossenus***. They found that both rocks and sand quickly attenuated the sound, and that leaf litter was the most effective of the three for sound transmission. Furthermore, there is great variability among rock types. But mosses are more like a sponge, whereas

leaf litter has a large, nearly flat surface that can reflect and direct sound. I would hypothesize that at least some mosses would make effective sound-proofing. And different organisms make sounds with different tones and frequencies, so more study is needed to determine if mosses are good or bad for carrying mating sounds to females of any particular species. (See ***Troglophilus neglectus*** below.)

Reproduction

Competition isn't the only problem for closely related species living together. Reproductive barriers are likewise needed to maintain species differences. These are especially important for **sympatric** (having overlapping distributions) species such as members of ***Tetrix***. To be an effective barrier, there must be an isolating mechanism such as behavior, timing, habitat, morphology, or genetics.

Reproduction is energetically costly. It typically carries a cost in future ability to reproduce, growth, or survival (Forsman 2001). Age is important in determining **clutch** size [number of eggs deposited in single reproductive bout (Godfray 1994)], with **clutch** size decreasing progressively from the first to the third clutch (Forsman 2001). Furthermore, larger first clutches correlate with greater reduction in the size of the next clutch and increase the time to the next clutch.

Reproduction in **ectothermic** (temperature controlled by external environment) animals, including insects, can be modified by body temperature. Temperature in grasshoppers affects both activity levels and physiological performance. Forsman (2001) compared four different color morphs under two different temperatures in ***Tetrix subulata*** (Figure 6). Different colors absorb different amounts of heat, whereas white reflects it. Warmer females were more likely to oviposit, had earlier first clutches, produced more clutches, and had decreased intervals between clutches compared to females kept at cooler temperatures. Some color morphs produced larger clutches with fewer clutches per unit time. No differences in relative fat content existed between dark and pale individuals in either sun or shade exposures. The data suggest that the differences in color morphs were advantageous in camouflage against predators rather than providing any reproductive advantage.

Forsman (1999) examined reproductive performance in five of these morphs, noting variation in body size and reproductive life-history characteristics. These lived in an area characterized by bare rocks and boulders, with bryophytes [***Ceratodon purpureus*** (Figure 15), ***Pohlia nutans*** (Figure 16-Figure 17), ***Polytrichum commune*** (Figure 18), ***P. juniperinum*** (Figure 12)] and some tussock sedges (*Carex* spp.) dominating the vegetation. Season played a major role, with number of females with eggs declining significantly as the season progressed from mid-May (100%) to mid-June (40%). However, seasons had no effect on body size, clutch size, or egg size. On the other hand, morphs differed from each other in body size, and these size differences accounted for differences in clutch and egg size.

Figure 15. ***Ceratodon purpureus*** on bare rock, home for ***Tetrix subulata*** in Norway. Photo by Michael Lüth, with permission.

Figure 16. ***Pohlia nutans*** on expanse of rocks, forming a suitable habitat for ***Tetrix subulata***. Photo by Michael Lüth, with permission.

Figure 17. ***Pohlia nutans*** bare rocks, a suitable habitat for ***Tetrix subulata***. Photo by Michael Lüth, with permission.

Figure 18. ***Polytrichum commune***, home and probably food for ***Tetrix subulata*** on rocks. Photo by David T. Holyoak, with permission.

The ratio of egg size to clutch size also differed among the morphs (Forsman 1999). These factors suggest that different color morphs may have different reproductive strategies. The color differences may be responsible for variation in thermoregulation, but they also most likely affect the ability to avoid predation due to cryptic coloration. This implies that predation would differ among the morphs.

Food Consumption

Most grasshoppers are not moss consumers. In Bavaria, all tested grasshoppers except ***Tetrix*** (Figure 1, Figure 11, Figure 30-Figure 31, Figure 34) rejected mosses, but in 80% of the fecal pellets of ***Tetrix*** there were leaves of the moss ***Hypnum*** (Figure 19) and rhizoids and protonemata of a variety of mosses (Verdcourt 1947). Kaufman (1965) likewise found that ***Tetrix*** sp. fed on mosses, whereas other grasshopper genera in that study fed on **forbs** (non-grass herbaceous flowering plants).

Figure 19. ***Hypnum cupressiforme*** with young sporophytes. Fecal pellets of ***Tetrix*** contained leaves from this genus. Photo by Dick Haaksma, with permission.

Tetrix ceperoi (Figure 5) is among the moss consumers in the **Tetrigidae** (Kočárek *et al*. 2008a, b). Kočárek and coworkers examined the gut of 21 males and 18 females of this species. Of the nine mosses [***Amblystegium serpens*** (Figure 20), ***Barbula convoluta*** (Figure 21), ***Brachythecium albicans*** (Figure 22), ***B. velutinum*** (Figure 23), ***Bryum argenteum*** (Figure 24), ***B. caespiticium*** (Figure 25), ***Ceratodon purpureus*** (Figure 15), ***Funaria hygrometrica*** (Figure 26), ***Plagiomnium undulatum*** (Figure 27)] in their sandy habitat, all nine appeared in at least one gut. The most frequent species was ***Bryum argenteum*** (in 81% of specimens). At least one fragment of moss occurred in 92% of the specimens, *i.e.* only 8% had not consumed mosses. **Tracheophytes** (in this case grasses) were in 20%, all females, and algae were in 25%. The average number of species of mosses per gut was three, but some contained as many as six. Hence, mosses appeared to be the preferred food, but there seemed to be only limited preference for any particular moss.

Figure 20. ***Amblystegium serpens***, a species found in the guts of ***Tetrix ceperoi*** (Figure 5). Photo by David T. Holyoak, with permission.

Figure 21. ***Barbula convoluta***, a moss found in the guts of ***Tetrix ceperoi*** (Figure 5). Photo by Janice Glime.

Figure 22. ***Brachythecium albicans***, food for ***Tetrix ceperoi*** (Figure 5) in Europe. Photo by Michael Lüth, with permission.

Figure 23. ***Brachythecium velutinum***, a species eaten by ***Tetrix ceperoi*** (Figure 5) in Europe. Photo by Michael Lüth, with permission.

Figure 24. ***Bryum argenteum***, a species eaten by ***Tetrix ceperoi*** (Figure 5) in Europe. Photo by Dick Haaksma, with permission.

Figure 25. ***Bryum caespiticium*** males, a species eaten by ***Tetrix ceperoi*** (Figure 5) in Europe. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 26. ***Funaria hygrometrica*** young female plants, a species eaten by ***Tetrix ceperoi*** (Figure 5). Photo by Janice Glime.

Figure 27. ***Plagiomnium undulatum***, a species eaten by ***Tetrix ceperoi*** (Figure 5). Photo by Michael Lüth, with permission.

Based on the gut analysis of ***Tetrix ceperoi*** (Figure 5), Kočárek *et al*. (2008c) found its "favorite" to be ***Bryum caespiticium*** (Figure 25), but this was also the most common moss in the area with a 70% cover (Table 1). Other commonly consumed mosses included ***Bryum argenteum*** (Figure 24), ***Ceratodon purpureus*** (Figure 15), and ***Barbula convoluta*** (Figure 21) and/or ***B. unguiculata*** (Figure 28). Only the females had grasses in their diet, whereas 94% of females and 86% of males had at least one fragment of moss in the gut. Males had an average of 1.5 moss species and females had an average of 2, whereas the maximum number of species in any gut was 4 (Figure 29). It was not unusual to find three species in the crop at one time. Kočárek and coworkers offer three explanations for this behavior:

1. A mixed diet promotes better health, development, and survival for grasshoppers than a single-food diet (Chapman & Sword 1997).
2. Mosses often contain toxic secondary compounds (Zinsmeister *et al.* 1991; Becker 1994; Markham *et al.* 2006) and must thus be consumed only in small quantities.
3. The multiple species indicate that the grasshoppers move around a lot and are able to sample the high diversity of mosses present in the area.

Table 1. Frequency of moss species in guts of 39 specimens of ***Tetrix ceperoi*** (Figure 5). From Kočárek *et al*. 2008c.

Moss species	*T. ceperoi* specimens					
	♂(ind.)	♂(%)	♀(ind.)	♀(%)	Σ(ind.)	Σ(%)
Barbula sp. (B. convoluta or/and B. unguiculata)	6	31.6	6	35.3	12	33.3
Bryum argenteum	4	21.1	6	35.3	10	27.8
Bryum caespiticium	15	78.9	17	100	32	88.9
Ceratodon purpureus	6	31.6	7	41.2	13	36.1

Figure 28. ***Barbula unguiculata***, a moss present in the gut of ***Tetrix ceperoi*** (Figure 5). Photo by Michael Lüth, with permission.

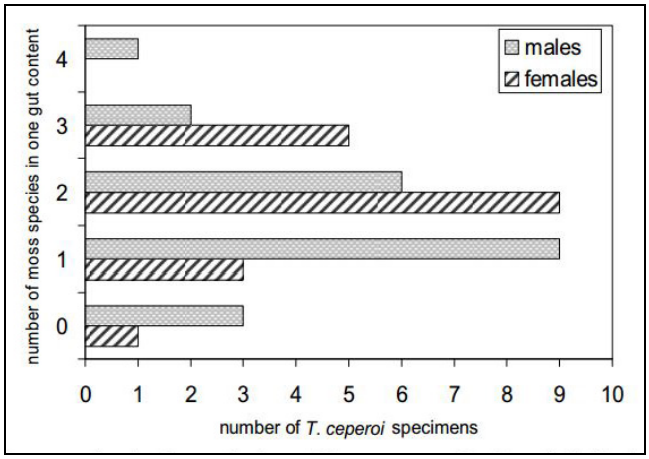


Figure 29. Comparison of mosses in guts of one individual in males and females of ***Tetrix ceperoi*** (Figure 5). Modified from Kočárek *et al*. 2008c.

Like the aforementioned species of ***Tetrix***, ***T. bolivari*** (Figure 30) eats primarily detritus and mosses (Kočárek 2011). The main mosses consumed in this European study were ***Bryum caespiticium*** (Figure 25) and ***B. argenteum*** (Figure 24), but at least eight different species were consumed. Like the other species, these were sensitive to temperature and were most active at warmer temperatures. However, their activities were negatively correlated with humidity, suggesting that mosses were most likely not important in maintaining a humid environment for them.

Figure 30. ***Tetrix bolivari***, a moss eater. Photo by Petr Kočárek, with permission.

The moss eater ***Tetrix undulata*** (Figure 31) eats mosses throughout its life (Hodgson 1963). As it gets older, it is able to eat coarser food. Both young and old eat mosses, humus, lichens, and algae, but adults add **tracheophytes** (lignified vascular plants) such as grass to their diet.

Figure 31. ***Tetrix undulata***, a moss eater on moss. Photo by Gilles San Martin, through Creative Commons.

Paranjape (1985) compared the diets of three subfamilies of the **Tetrigidae** and found that not only mosses, but also liverworts and hornworts are consumed (Figure 32).

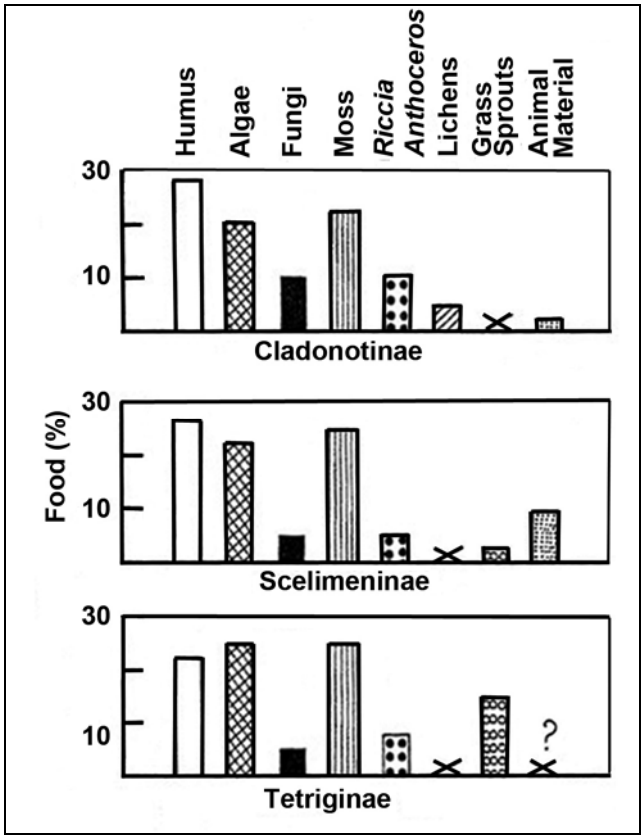


Figure 32. Diet of three subfamilies of **Tetrigidae**. Note that in addition to mosses, they consume the liverwort ***Riccia*** and the hornwort ***Anthoceros***. Modified from Paranjape 1985.

Age and Seasonal Differences

Tough foods require strong mandibles and teeth to break through the lignin in vascular tissue. The strength can change as the nymphs age, so diets can change or expand as the organism matures. Similarly, moss tissues can change with the seasons, becoming tough when dry and soft when wet. These factors can affect the diet of the consumers.

Tetrix tenuicornis specializes on mosses and detritus (Kuřavová & Kočárek 2015). This species maintains its moss diet throughout the growing/feeding season. But the moss species change. More moss species occur in the alimentary tract in spring and summer compared to autumn. Females eat more food than males, and the diet changes with developmental stage. Furthermore, the rate of consuming detritus is affected by ambient temperature (most at 19-21°C), whereas the rate of moss consumption is primarily affected by relative humidity (lowest at 67-72%, highest at 90% or higher). Detrital consumption increases as body size increases.

These groundhoppers do not seem to specialize on any part of the mosses, consuming leaves, gemmae, and rhizoids (but apparently not stems) (Kuřavová & Kočárek 2015). Furthermore, they show little preference for moss species, consuming all of those present except ***Pohlia nutans*** (Figure 16-Figure 17) and ***Bryoerythrophyllum recurvirostrum*** (Figure 33). Nevertheless, an individual never contained more than 3 moss species, with the average being 1.9. Moss consumption was considerably less than that of detritus, with one population having 12% moss in the gut and the other only 3%. The amount of moss consumption is linearly related to the amount of moss available. Kuřavová and Kočárek suggest that keeping the moss consumption low prevents poisoning by secondary compounds produced by mosses. A reduction in moss consumption near the end of the growing season supports this hypothesis. Mosses increase their production of secondary compounds in autumn in preparation for the freezing conditions of winter (Cornelissen *et al*. 2007).

Figure 33. ***Bryoerythrophyllum recurvirostrum***, a moss that seems to be avoided as food by ***Tetrix***. Photo by Hermann Schachner, through Creative Commons.

It is also possible (probable?) that the choice of food is more a choice of habitat as the environmental conditions change. Low or high temperatures could drive the groundhoppers to the more stable conditions of the moss cushions. Furthermore, unfavorable conditions most likely reduce activity, resulting in lower consumption.

Mandibular Abrasion

Tetrix tenuicornis (Figure 34) avoids eating grasses, instead eating mosses [16.3%; ***Barbula convoluta*** (Figure 21), ***Brachythecium albicans*** (Figure 22), ***Bryum caespiticium*** (Figure 25), ***Campylopus introflexus*** (Figure 54), and ***Ceratodon purpureus*** (Figure 15)] and detritus (83.7%) (Kuřavová *et al*. 2014). But it still exhibits

increased mandible abrasion with age, with females showing more age-related abrasion than males, perhaps due to greater frequency of feeding. On the other hand, Hence, even detritus and bryophytes cause wear on groundhopper mandibles.

Figure 34. ***Tetrix tenuicornis***, a species whose mandibles show wear from eating bryophytes. Photo by B. J. Schoenmakers, through Creative Commons.

It is interesting that the diet of males and females may differ. Hochkirch *et al*. (2000) found that ***Tetrix subulata*** (Figure 6) males fed exclusively on algae and mosses, but females consumed grasses and forbs as well, perhaps accounting for the greater mandibular abrasion in females of ***T. tenuicornis*** observed by Kuřavová *et al*. (2014). Temperature also plays a major role in feeding, with only 1% feeding on a cool day but 24.7% feeding on the warmest day of the study (Hochkirch *et al*. 2000). When not feeding, the grasshoppers preferred sitting on the more open, warmer locations. These resting locations differed significantly from the feeding locations, which included mosses, suggesting that a color morph might be at a disadvantage in one of those locations.

Potua sabulosa

This pygmy grasshopper (Figure 35) is also a moss consumer, having mosses, especially ***Funaria*** (Figure 26), as its preferred food (Bhalerao *et al*. 1987). It lacks the molar dentes that are used for eating tracheophyte leaves, making it difficult to eat these foods as an alternative food source. For example, female adults fed on only "paddy" sprouts died within 5-6 days. The species overwinters as an adult. During the cold winters and hot, dry periods in summer it does not eat.

Figure 35. ***Potua sabulosa***, a moss consumer that lacks polar dentes. Its roughened body helps it to blend with its surroundings. Photo by Jason Weintraub, through Creative Commons.

These tiny grasshoppers can jump 25-35 cm (Paranjape & Bhalerao 1985). In southwest India they hang out among mosses, being protected by their cryptic coloration. They also eat the mosses, as well as humus, and are capable of making an entire clump of moss disappear (Paranjape 1985). In the summer they survive the heat and drought by burrowing into soil, where they can remain for at least two months without food (Paranjape & Bhalerao 1985). When it is time for egg laying, the females dig a small burrow (~2 mm) in the soil or between the dense moss tufts, using their ovipositors. Their 23-25 eggs are laid in a loose cluster, hatching 10-12 days later at 23-25°C.

Acrididae – Grasshoppers

Akris is the Greek word for locust and is the basis for the name of the family that contains them (Acrididae 2015). More than 10,000 species comprise this family. The species are medium to large, as grasshoppers go. They are **diurnal** (day-active) and typically travel by jumping in their preferred open habitats. They often have cryptic coloration, but some are brightly colored. And many prefer "mossy" habitats.

"Three years ago there was a grasshopper 'explosion' in some central British Columbia grassland sites" (Terry McIntosh, pers. comm. 6 September 2013). "In the Gilpin Grasslands, they completely cleaned up most of the broad-leaved herbaceous plants (and ignored the grasses by the way), then started browsing on some shrubs, including, at one site, poison ivy! Later that day, I noticed a peculiar ***Grimmia*** on an outcrop. On closer inspection, the reason it look odd was because the whole moss face (mainly G. ovalis) had been grazed by the 'hoppers.' Not one plant in some 10 square meters had any leaf tips left." And the capsules were eaten too. (See discussion of other moss eaters under Food below.)

Figure 36. ***Grimmia ovalis*** growing on a rock outcrop where it may serve as food for grasshoppers during outbreaks. Photo by Michael Lüth, with permission.

Figure 37. ***Grimmia ovalis*** grazed by grasshoppers. Note the absence of white tips on the leaves. Photo courtesy of Terry McIntosh.

Melanoplus

Although this genus (Figure 38-Figure 44) does not exhibit the close food association exhibited by the **Tetrigidae**, at least several members prefer mossy habitats. ***Melanoplus lovetti*** lives in damp mossy ground, avoiding taller grasses (Fulton 1930). ***Melanoplus islandicus*** (Figure 38) in Michigan, USA, occurs along damp shorelines of pools where vegetation includes short grasses and sedges as well as mosses and organic debris (Bland 1989).

Figure 38. ***Melanoplus islandicus*** male, a shoreline inhabitant where there are short grasses and mosses. Photo by David Kleiman, through Creative Commons.

Melanoplus borealis (Figure 39) is well camouflaged among the mosses near Fairbanks, Alaska, USA. Kaufmann (1971) recounts seeing an adult that jumped/flew away from the approaching human. Once it landed, it became invisible among the moss-covered field where its color pattern blended with both the colors and spongy texture of the mosses. This species, like others in the genus, avoided areas of tall grass, apparently requiring areas where they could rest in the sun.

Figure 39. ***Melanoplus borealis*** male, a species well camouflaged among the Arctic mosses. Photo by Denis Doucet, with permission.

This genus has a variety of feeding strategies. Kaufmann (1968) found that ***Melanoplus differentialis*** (Figure 40) in Maryland, USA, prefers *Taraxacum officinale* (dandelion), but will also feed on grasses. They also eat dried plants, even when fresh ones are present. Kaufman found that the habitat was more important in the

choice of food (light, temperature, plant orientation) than the foods themselves. The mandibles are typical of grasshoppers that eat forbs, but the maxillae are similar to the moss feeders in the genus ***Tetrix***.

Figure 40. ***Melanoplus differentialis***, a grasshopper that eats mostly forbs but has maxillae similar to those of moss feeders. Photo by Rob Curtis, through Creative Commons.

Melanoplus femurrubrum (Figure 41-Figure 43), like many of the grasshoppers, has many color forms (Figure 41-Figure 43). This species has been studied to determine the effect of food absence on survival. As you may know, grasshoppers will eat their own appendages when starved for days. Bland (1981) found that nymphs survived up to 113 hours with no food. But hatchlings required food within 48 hours to insure their continued survival and growth. This species tends to eat the first suitable food it encounters, using olfactory senses to find it.

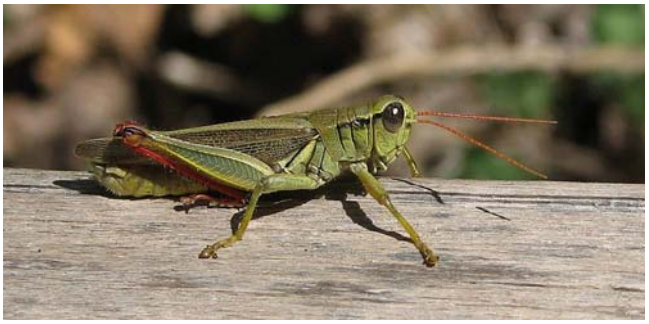


Figure 41. ***Melanoplus femurrubrum*** in Zion National Park, showing an olive-green form. Photo by Leyo, through Creative Commons.

Figure 42. ***Melanoplus femurrubrum*** grayish green color form. Photo by Sheryl Pollock <www.discoverlife.org>, with permission.

Figure 43. ***Melanoplus femurrubrum*** reddish form. Photo by Sheryl Pollock <www.discoverlife.org>, with permission.

It appears that members of this genus have not been tested for sensitivity to secondary compounds in mosses. In tests of compounds in tracheophytes on nymphs of *Melanoplus sanguinipes* (Figure 44), a species that does not typically eat mosses, many elicited no response, but several compounds caused a reduction in mean weight (Westcott *et al*. 1992). Saponin decreased survival and seven compounds significantly decreased both survival and mean weight. Vanillic acid significantly increased mean weight. This leaves the intriguing question of the effects of secondary compounds of bryophytes. Investigations into the chewing apparatus and digestive response to bryophytes compared to preferred foods may help us to understand why some insects choose bryophytes while others avoid them.

Figure 44. *Melanoplus sanguinipes* female, a forb feeder that benefits from vanillic acid in forbs. Photo by Lynette Schimming, through Creative Commons.

Not only do populations of ***Melanoplus*** (Figure 40-Figure 44) differ in coloration, but their physiology can differ as well. Fielding (2006) demonstrated **facultative diapause** (resting period that can change based on conditions) in the widely distributed *Melanoplus sanguinipes.* In an Idaho population, diapause in this species was facultative, with pre-diapause embryos averting diapause when held at 5°C for 90 days. On the other hand, this same population entered diapause in the late stage of development if held at 22°C for 30 days or more (Figure 45). The subarctic Alaskan populations had obligate diapause and entered diapause in a late stage of development. Chilling in the pre-diapause stages had no effect on diapause. These differences in life cycle strategies permit this species to occupy its wide distribution and are likely to be important for some of the moss-dwelling species as well.

Chorthippus

Langmaack (1997) found that mosses were important in the reproduction of some grasshoppers. ***Chorthippus montanus*** (Water-meadow Grasshopper; Figure 46) and ***C. parallelus*** (Figure 47) (**Acrididae**), both flightless, clearly selected moist mosses for depositing their egg pods.

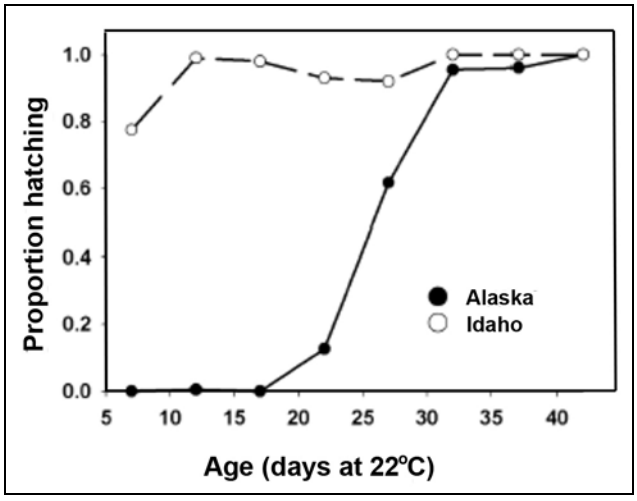


Figure 45. Comparison of proportion of eggs from Alaska and Idaho populations of *Melanoplus sanguinipes* that hatched after exposure to 5°C for 90-100 days following incubation at 22°C for different times. n > 200 observations at each point. Modified from Fielding 2006.

Figure 46. ***Chorthippus montanus***, a flightless grasshopper that selects moist mosses for egg deposition. Photo by Gilles San Martin, through Wikimedia Commons.

Figure 47. ***Chorthippus parallelus*** male, a flightless grasshopper that selects moist mosses for egg deposition. Photo by Atlasroutier, through Wikimedia Commons

Chorthippus montanus (Figure 46) is a flightless wetland species and therefore it is likely to become rarer because its habitat is disappearing. Using a mark-recapture technique, Weyer *et al*. (2012) found that this species travels on average only 23.5 m, with a maximum of 104 m. This is not sufficient to permit its dispersal among widely fragmented wetland landscapes, and even the requirement to replace a drained wetland with another (somewhere else) will not solve this dispersal problem. Even if it could travel farther, it has restricted habitat requirements and is unable to traverse unsuitable habitats.

Based on fecal analyses, ***Chorthippus pullus*** (Figure 48) has a varied diet that includes dicotyledons, monocotyledons, and bryophytes (Steiner & Zettel 2006). The bean *Astragalus onobrychis* was the most consumed food in the Steiner and Zettel study. Moss consumption, including the moss ***Dicranoweisia crispula*** (Figure 49), formed a greater part of the diet in seasons and locations when other herbs were less abundant, despite having mandibles adapted for eating grasses. At one location ***D. crispula*** comprised 45% of the diet. Contrary to the suggestion of Uvarov (1977) that grasshoppers eat mosses for their water content, the water content of this moss was the lowest among the top four foods consumed, suggesting that the grasshoppers derived some other value from eating it.

Figure 48. ***Chorthippus pullus***, a species that lays its eggs in moss **polsters** (cushions) in Austria. Photo by Gabriele Kothe-Heinrich, through Creative Commons.

Figure 49. ***Dicranoweisia crispula***, a species that can form as much as 45% of the diet of ***Chorthippus pullus*** (Figure 48). Photo by Michael Lüth, with permission.

In the Lake Salzburg area of Austria, ***Chorthippus pullus*** (Figure 48) lays its eggs in June and July as an **ootheca** (egg case; Figure 50) in sand or moss polsters (Schwarz-Waubke 2001). This species deposits an average of 75 eggs during its lifetime. Each ootheca contains an average of 6.1 eggs. These moss polsters are especially important in rocky areas where they supply protection in an otherwise hostile environment.

Figure 50. Insect **ootheca**. Photo by Gilles San Martin, through Creative Commons.

Nicarchus

The genus ***Nicarchus*** (Figure 51) is flightless and lives on tree trunks (Rowell 2009). These grasshoppers are adapted to their habitat by having a wider thorax with reduced sternal lobes, the latter correlating with the reduced wings and flightless condition. This reduction in wing muscle provides additional space for a larger than typical **crop** (part of digestive system in which food is stored before digestion). Like other members of this group of tree trunk orthopterans (**Ommatolampinae**), their adaptations include cryptic coloration that mimics mosses, lichens, or bark; roughened cuticle or spines, again mimicking their substrate; strongly protuberant eyes; pronotum with bumpy projections; widely separated metasternal lobes; nodular antennae; 7 external spines on hind tibia; all but ***Sciaphilacris*** (Figure 52) flightless. They live on the trunks and major branches of tropical forest trees in the Amazon basin and in Central America. Among this group, only ***Nicarchus*** is known to feed on mosses, a habit that is probably favored by the enlarged crop.

Figure 51. ***Nicarchus erinaceus***, a species that lives among mosses on tree trunks and branches in the tropical forest and feeds on mosses. Photo by Frank through What's that Bug <http://www.whatsthatbug.com/2014/01/19/orthopteran-costa-rica/>.

Sciaphilacris – Moss and Lichen Mimics

Sciaphilacris (Figure 52) lacks many of the modifications noted for ***Nicarchus*** and is the only member of **Ommatolampinae** that is not flightless (Rowell 2009). Nevertheless, despite having somewhat reduced wings, it rarely flies. Little seems to be known about it – it lives in South and Central America and most likely spends part of its time among the mosses, blending well.

Figure 52. ***Sciaphilacris alata***, a good moss mimic. Photo by Arthur Anker, with permission.

Myrmeleotettix maculatus

Interactions with mosses is not always positive, and ***Myrmeleotettix maculatus*** (Figure 53) would most likely agree. In Europe it is a species of acidic coastal dunes. However, these dunes are being invaded by the exotic moss ***Campylopus introflexus*** (Figure 54). In a comparison of invaded dunes vs non-invaded dunes, Schirmel (2010) found that the mean number of captures of this species in non-invaded (native) plots was significantly higher than that in the invaded plots. Schirmel suggested that this difference may have been due to the higher proportion of grasses as food, more appropriate shelter, or more favorable microclimate in the native plots, leading to a higher mortality in the invaded plots. On the other hand, the mean number of young and older nymphs did not differ between the two habitats, suggesting that the invaded sites were suitable for oviposition but in some way detrimental to adults.

Figure 53. ***Myrmeleotettix maculatus*** female, a species that is disappearing in European coastal dunes due to the invasion of the moss ***Campylopus introflexus*** (Figure 54). Photo by Brian Eversham, with permission.

Figure 54. ***Campylopus introflexus***, an invasive moss that may destroy grasshopper habitat in Europe. Photo by Michael Lüth, with permission.

Food

Kaufman (1965) found that the feeding rate of **Acrididae** grasshoppers in Bolivia increased greatly with temperature. Feeding habits seem to correspond with mandibles and maxillary laciniae. These mouth parts can be divided into the graminivorous (grass) type, the forb-feeding type, and the moss-feeding type. Even the gastric caeca can be divided into four types based on diet preference. Nevertheless, experiments with *Euthystira brachyptera* (Figure 55) suggest that feeding on several different species, in this case of grasses, improves mortality, longevity, fecundity, and body weight.

Figure 55. ***Euthystira brachyptera*** female, a species that feeds on grasses but thrives best on mixed species. Photo by Gilles San Martin, through Creative Commons.

Position of the food can be important (Kaufman 1965). ***Chorthippus parallelus*** (Figure 47) prefers to feed on vertical grass blades. Passage time for the food in the alimentary tract differs not only in different species, but also depends on food plant, individual differences, and developmental stage. And males seem to assimilate more of the food they eat than do females.

Patterson (1984) demonstrated differences in shape and arrangement of dentes resulting in different mandibular ratios among members of the **Acrididae** with different feeding choices. Patterson (1984) and Kaufman (1965) pointed out the need for comparative studies among the moss-feeding species. Some of the species in this family are **stenophagous** (having narrow range of suitable foods) (Philippe 1991). For example, whereas ***Trimerotropis saxatilis*** (Figure 56-Figure 57) is specialized on eating mosses, *Bootettix punctatus* (Figure 58) specializes on *Larrea tridentata*, an evergreen shrub.

Figure 56. ***Trimerotropis saxatilis*** nymph well camouflaged among the grey lichens. Photo by Ted C. MacRae <beetlesinthebush.wordpress.com>, with permission.

Figure 57. ***Trimerotropis saxatilis***, a specialist for eating mosses, is conspicuous here on mosses. Photo by Ted C. MacRae <beetlesinthebush.wordpress.com>, with permission.

Figure 58. ***Bootettix argentatus***, a specialist on the shrub *Larrea tridentata*. Photo by Margarethe Brummermann, through Creative Commons.

In the southeastern United States lichen grasshoppers, also known as rock grasshoppers (***Trimerotropis saxatilis***; Figure 56-Figure 57), are important consumers in desert-like rock outcrops (Duke & Crossley 1975). This small species consumes 27.25 mg of the moss ***Grimmia laevigata*** (Figure 59), an **apparent** (conspicuous) moss, per day, totalling 391 mg m^{-2} per year in this harsh habitat. This grasshopper species has a variety of color patterns that help it blend with its lichen and moss environment (Morse 1907). Although Morse says that ***T. saxatilis*** is restricted to bare rock surfaces, as its name implies, it has to eat somewhere, and it is a vegetarian. Do the math!

Figure 59. ***Grimmia laevigata*** on a rock outcrop, common habitat for ***Trimerotropis saxatilis*** (Figure 56-Figure 57). Photo by Michael Lüth, with permission.

Oviposition

Knowing that some grasshoppers eat mosses, it is not hard to imagine that they also lay their eggs among mosses. ***Chorthippus pullus*** (Figure 48), in Salzburg, Austria, is endangered in Europe (Schwarz-Waubke 2001). Despite this rarity, in the proper habitat of wild river landscape near Taugl it is a **eudominant** [>10% (Bick 1989)] among 12 other members of the **Saltatoria** (suborder of **Orthoptera** including grasshoppers, crickets, and related forms). This species lays its eggs as an ootheca (Figure 50) in sand or moss clumps during June and July.

Some species of ***Chorthippus*** seem to have an inexplicable combination of oviposition habitats. For example, ***C. albomarginatus*** (Figure 60), ***C. montanus*** (Figure 46), and ***C. parallelus*** (Figure 47) prefer vertical plant surfaces for oviposition (Langmaack 1997). But ***C. parallelus*** and ***C. montanus*** also use moist mosses for egg deposition, a quite different type of structure. Rather than structure, it seems that height is important, with ***C. albomarginatus*** preferring 2-6 cm, ***C. montanus*** 0.5-2 cm, and ***C. parallelus*** 0-0.5 cm. Langmaack suggested that these preferences may indicate different requirements for moisture and temperature during development. ***Chorthippus albomarginatus***, the species ovipositing at the greatest height, has the greatest desiccation resistance and highest temperature requirement for its eggs. Eggs of both ***C. parallelus*** and ***C. montanus*** have low desiccation resistance and a low temperature requirement.

Figure 60. ***Chorthippus albomarginatus*** female, a species that prefers higher positions of 2-6 cm above the ground for its egg deposition, including moss locations. Photo by Gilles San Martin, through Creative Commons.

Gryllidae – Crickets

The common names of the families of "crickets" have been hopelessly confused among the continents (Alexander *et al*. 1972), and me, so I will stay with only scientific names for most of these. The males are the callers in these groups, but in some the female may also call. The crickets make their well known chirps by rubbing together the leathery forewings. These chirps increase in frequency as the temperature increases. Overlapping species may have "songs" that we cannot distinguish, but they can be distinguished by instrumentation – and other crickets. Females are attracted to the calls and go to the males for mating. We know that frogs use mosses to modulate their calls, so it is appropriate to ask how grasshoppers might use them.

Alexander *et al*. (1972) report ***Eunemobius melodius*** singing in a ***Sphagnum*** bog (Figure 61) in Michigan, USA. Strang (2015) states that the sphagnum ground cricket (***Neonemobius palustris***; Figure 62-Figure 64) is not found outside of ***Sphagnum*** bogs. Some crickets make nests in ***Sphagnum*** (Vickery 1969). Crickets don't seem to be commonly known from mosses, but in captivity with

predators like frogs and lizards they will typically hide among the mosses. Does that happen in nature as well?

Figure 61. ***Sphagnum*** blanket bog where one might hear the song of ***Eunemobius melodius***. Photo through Creative Commons.

Figure 62. ***Neonemobius palustris*** male (sphagnum ground cricket) on ***Sphagnum***, its only known home. Photo by Brandon Woo, with permission.

Figure 63. ***Neonemobius palustris*** female on ***Sphagnum***, its only known home. Photo by Brandon Woo, with permission.

Figure 64. ***Neonemobius palustris*** nestled among ***Sphagnum*** of bog. Photo by Carl Strang, with permission.

Rhaphidophoridae – Camel Crickets, Wetas

These **Rhaphidophoridae** like it dark, living in forests, caves, animal burrows, under stones, in wood, and in cellars (Rhaphidophoridae 2015). They occur on all seven continents, where they are usually active at night and rely on their sense of touch to identify things in their environment. Wetas are characterized by lack of wings, lack of auditory organs, long, compressed tarsi with no pads, small bodies, and long hind legs and antennae (Richards 1961). They are primarily scavengers, often eating plant debris that is washed into the cave and left stranded on the cave walls, but they also eat bryophytes.

Johns and Cook (2014) found the new genus and species ***Maotoweta virescens*** (Figure 65-Figure 66) hidden in a moss forest in New Zealand. This mottled green weta is inconspicuous among the mosses; *maoto* is the Maori word for fresh green. Johns and Cook reported the difficulty of finding this weta on the mossy tree trunks during their night-time activity; it required 16 person hours for them to locate only 5 individuals. The only female collected was in copulation – on a moss.

Figure 65. ***Maotoweta virescens*** on bryophytes, a recently described weta that is well camouflaged among bryophytes. Photo by Tony Jewell, with permission.

Figure 66. Green weta (cf. ***Maotoweta virescens***) in its mossy habitat. Photo by George Gibbs, with permission.

In the caves of New Zealand, one might find ***Pallidoplectron turneri*** feeding on the thallose liverwort ***Marchantia*** that grows near the electric lights, but I cannot verify the reference and my new Zealand colleagues and I suspect it was really fern prothalli being eaten.

Troglophilus (Figure 67-Figure 69) species exhibit cryptic coloring with shades of marble brown, green, or grey (Karaman *et al*. 2011). These color patterns blend well with the forest background and the lichen and moss-covered rocks where they hide during the day.

One consideration for crickets of all kinds is the need to call in order to connect with a mate. But all calls are not equal (Stritih & Čokl 2012). The surroundings modify the calls, and mosses have a different resonance than that of grasses or bushes. The **sympatric** (occupying overlapping distributions) ***Troglophilus neglectus*** (Figure 67-Figure 68) and ***T. cavicola*** (Figure 69-Figure 70) use vibratory signalling to distinguish the opposite sex of their own species. ***Troglophilus neglectus*** uses abdominal vibrations, whereas this behavior is absent in ***T. cavicola***. Both species use whole-body vibrations after copulation. Although they most frequently use bark for both signalling and mating, mosses are often used as well. The signalling frequency depended on the substrate. On rocks, the intensity of ***T. neglectus*** is below the detection range for this species and therefore could not be heard if they signal from within a cave. The frequency extends up to 600 Hz on mosses, whereas its highest frequency on stone was below 250-300 Hz. This difference explains the movement from the caves to bark, or less often moss, for mating calls, with mosses and litter providing suitable vibratory substrate (Magal *et al*. 2000; Elias *et al*. 2004).

Figure 67. ***Troglophilus neglectus*** female in cave. Photo by Florin Rutschmanni, through Creative Commons at <www.orthoptera.ch>.

Figure 68. ***Troglophilus neglectus*** female with green and brown cryptic coloration. Photo by František Chládek, with permission.

Figure 69. ***Troglophilus cavicola*** male with marbled brown coloration that blends with mosses and litter. Photo by Walter P. Pfliegler, with permission.

Figure 70. ***Troglophilus cavicola*** on moss. Photo by Stefan Pluess, through Creative Commons.

Tettigoniidae – Katydids

Katydids can be abundant and diverse. At only three collecting sites in Loreto Province, Peru, Nickle and Castner (1995) found more than 370 species of **Tettigoniidae**.

Many katydid males offer a large gelatinous spermatophore to the female during mating (Del Castillo & Gwynne 2007). This is energy expensive and the larger the

reward offered, the less calling is done, another energy expensive activity. Size of the spermatophore and of the male do not seem to play any role in mate selection, but larger females seem to be favored over smaller ones.

Bogs seem to be the most common place for moss-associated katydids. The bog bush cricket ***Metrioptera brachyptera*** (Figure 71-Figure 72) is frequent in southern England heaths and bogs, but in northern England it is rare and in Scotland it has been found only once (Aucheninnes 2011). ***Neonemobius palustris*** (Figure 62-Figure 64) in Canada is rare, confined to ***Sphagnum*** (Figure 61) bogs (Johnstone & Vickery 1970; Kevan 1979), and feeds on the ***Sphagnum*** (Kevan 1979). Not only are the various ***N. palustris*** populations distinct genetically, but their **phenotypes** (sets of observable characteristics of individuals resulting from interaction of genes with environment) differ as well because interbreeding is rare if not non-existent between populations in different locations. Both ***Neonemobius palustris*** and ***Allonemobius fasciatus*** (Figure 73) lay their eggs on ***Sphagnum*** (Gerson 1969). Only these two species are considered to be characteristic peatland species in Canada (Marshall & Finnamore 1999).

Figure 71. ***Metrioptera brachyptera***, a green bog bush cricket. Photo by Gilles San Martin, through Creative Commons.

Figure 72. ***Metrioptera brachyptera*** female, a black bog bush cricket. Photo by Robert Vlk, through Creative Commons.

Figure 73. ***Allonemobius fasciatus***, a cricket that lays its eggs on ***Sphagnum***. Photo through Creative Commons.

Camouflage

Like the previous **Orthoptera**, katydids exhibit cryptic coloration. ***Haemodiasma tessellata*** (Figure 74-Figure 75), known as a moss mimic katydid, exhibits a mix of brown and green with a roughened light and dark surface (Thorman 2008) that helps it blend not only with mosses but also with leaf litter. But ***Steiroxys strepens*** (Figure 76), with a nearly solid green coloration, was sitting on damp mossy ground where it most likely blended better with the short grasses there (Fulton 1930).

Figure 74. This katydid (***Haemodiasma tessellata***) from Costa Rica was billed as a moss mimic katydid (Thorman 2008), but it seems to resemble a tracheophyte leaf more than it does a moss. It does have markings that would blend with epiphyllous bryophytes. Photos by Mary Thorman, permission pending.

Figure 75. ***Haemodiasma tessellata*** showing its cryptic coloration that could blend with leaves or bryophytes. Photo by Bernard Dupont, through Creative Commons.

Figure 76. ***Steiroxys strepens*** male, illustrating the solid colors typical of most katydids. Photo by Jim Johnson, with permission.

Nickle and Castner (1995) summarized the strategies used by katydids in the rainforests of northeastern Peru to protect themselves against daytime predators. These included primary defenses – camouflage, concealment within leaf parts or litter, territoriality by defending roosting sites against other katydids; secondary defenses used when making contact with predators – colorful displays by distasteful species (Figure 77), aggressive counterattacks, **aposematic** (serving to warn or repel) wasp mimicry, visual or acoustical alarm displays. They seem to return to the same daytime locations, suggesting they may be aware of their camouflage in those surroundings. Of the 378 species, 71.4% had general color patterns of green (208 spp.), brown (46 spp.), and both green and brown (19 spp.). Another 13.8% were more specific, mimicking wasps, bark, twigs, leaves, or lichens. Another 4.8% hid from view within vegetation or litter. Nickle and Castner did not distinguish any as having bryophyte camouflage, but some patterns that work well among leaf litter also work well among bryophytes (Figure 75).

Figure 77. ***Acanthodis*** sp. female showing startle display in Campana Highlands, Panama. Photo by Arthur Anker, with permission.

In Columbia, ***Championica bicuspidata*** (Figure 79) feeds on mosses and mimics them (Cardona Granda 2012). This genus has a number of moss mimics, including ***C. pallida*** (Figure 78-Figure 80). ***Acanthodis curvidens*** (see Figure 77) is also a moss mimic and rests prostrate to avoid detection (Robinson 1991). In addition to its camouflage, on Barro Colorado Island, Panama, this katydid avoids predation by bats when it is calling by maintaining a low frequency of calls (Belwood 1988). Bats locate katydids that produce frequent calls in about 26 seconds, immediately flying directly from their perch to the singing insect. In contrast, bats require nearly 34 minutes to locate the katydids (***Acanthodis curvidens***) that call less often (about once per minute), typically flying about seemingly randomly.

Figure 78. ***Championica pilata*** blending with a leaf and its epiphylls. Photo by Arthur Anker, with permission.

Figure 79. ***Championica*** sp. in Ecuadorian Amazon, illustrating its cryptic coloration that hides it on mosses. Photo by Geoff Gallice, through Creative Commons.

Figure 80. ***Championica pilata*** blending with a dead leaf. Photo by Arthur Anker, with permission.

Paraphidnia

Paraphidnia (Figure 81-Figure 85) is known as the moss katydid. Its markings look like leafy liverworts and lichens, making it blend well with its rainforest habitat, where it lives among and eats mosses and lichens (Ferrari 2015).

Figure 81. ***Paraphidnia*** sp. (lichen katydid) with markings that resemble leafy liverworts. Photo by Andreas Kay, through Creative Commons.

Figure 82. ***Paraphidnia*** sp. (lichen katydid) mimicking a stick that has bryophytes and lichens. Photo by Andreas Kay, through Creative Commons.

Figure 83. ***Paraphidnia*** sp (mossy katydid) mimicking a stick with leafy liverworts. Photo by Arthur Anker, with permission.

Figure 84. ***Paraphidnia*** sp (mossy katydid) on bryophytes, mimicking a stick with leafy liverworts. Photo by Arthur Anker, with permission.

Figure 86. ***Balboana tibialis*** male with mosses on a branch covered with lichens. Photo by Arthur Anker, with permission.

Figure 85. ***Paraphidnia*** sp. from Ecuador, mimicking a stick with leafy liverworts. Photo by Arthur Anker, with permission.

Balboana tibialis

Like many tropical species, little seems to be known about ***Balboana tibialis*** (Figure 86-Figure 87). And like many katydids, it most likely benefits from its cryptic coloration.

Figure 87. ***Balboana tibialis*** in Gamboa, showing camouflage markings suitable for living on bryophytes. Photo by Arthur Anker, with permission.

Arachnacris tenuipes – Emperor Bush Cricket

A big thank you to Nick Garbutt for allowing me to use his image to show ***Arachnacris tenuipes*** (Figure 88) eating a moss. This is a species that may reach 12 cm (Hincks 1956), and it has the largest wingspan (27.4 cm) in the **Orthoptera** *s.s.* (Cowardine 2008). Its size is limited by temperature (Makarieva *et al*. 2005). Because of increases in metabolism with increasing temperature, the maximum length increases approximately twofold for each 10°C increase in ambient temperature. Hence, larger **poikilotherms** (those with temperature controlled by the environment) occur farther north, with smaller individuals in the tropics. ***Arachnacris tenuipes*** (syn. *Macrolyristes imperator*) is known from Malaysia and Indonesia, but its distribution may be wider. This may be the first report that it eats mosses.

Figure 88. ***Arachnacris tenuipes***, an emperor bush cricket (katydid) eating moss. Photo by Nick Garbutt, with permission.

"Endless forms most hidden." Thus is the title of an article by Kikuchi *et al*. (2017) in *Ecology* regarding katydids that mimic mosses. A katydid, ***Adeclus*** cf. ***trispinosus*** (Cadena-Castaneda 2011), was discovered as a short-winged adult male, presenting a wing pattern and coloration with legs and other parts that made it resemble a moss (Kikuchi *et al*. 2017). The katydid that became famous in *Ecology* uses three strategies of concealment: background matching, disruptive coloration, and masquerade. A member of the **Pleminiini**, it joins many other species that resemble mosses. Other moss mimics in the **Tettigoniidae** include ***Panacanthus varius*** (Figure 89) and ***P. intensus*** (Montealegre-Z & Morris 2004). This type of mimicry seems to have evolved multiple times in the **Orthoptera** (Mugleston *et al*. 2013).

Figure 89. ***Panacanthus varius***, a moss mimic. Photo by Andreas Kay, through Creative Commons.

PHASMIDA – Walking Sticks

The common name of walking stick indicates that the **Phasmida** is a group of mimics. While looking like a stick is cool, looking like a hanging moss is awesome! And some members in the rainforests do just that (Figure 90), resembling pendent mosses in both color and appearance (Robinson 1969). The genus ***Acanthoclonia*** (**Pseudophasmatidae**) exhibits this moss-mimicking appearance (Gutiérrez & Bacca 2014).

Figure 90. Moss mimic walking stick. This one moves with a swaying, vibrating motion that mimics the movement of moss branches in the wind. Photo by Neil Bell, permission pending.

This kind of camouflage has been named in different ways, including **Batesian mimicry** and **crypsis**. But these terms may both be misleading conceptually (Skelhorn *et al*. 2010). Rather, the term **masquerade** has been applied to them (Figure 91). One problem in naming and understanding this phenomenon is the paucity of evolutionary studies on it, perhaps because its greatest representation is in the tropics where our level of understanding the systematics is much less than in other parts of the world. The term **masquerade** was introduced to describe those organisms that cause misidentification by other organisms.

Figure 91. A walking stick in Peru that looks like a twig with mosses growing on it. Photo by Arthur Anker, with permission.

Trychopeplus laciniatus

An incredible insect, ***Trychopeplus laciniatus*** (**Diapheromeridae**; Figure 92-Figure 98), is a montane Neotropical rainforest walking stick that looks like strands of mosses and leafy liverworts. Its range includes the mountainous forests of Costa Rica, Nicaragua, Panama, and Colombia. It "sways" its way through its mossy habitat, a behavior scientists have suggested resembles the moving of mosses in the wind. Regarding its presence in Monte Verde, Costa Rica, Ryan Burrows (Bryonet 14 April 2010) states that it "would be a perfect match to the habitat there." This phenomenal insect bears such resemblance to the mosses on the cloud forest tree trunks that it is virtually

undetectable to an untrained eye. It is flightless and slow moving, and has no means of defense (Simon 2015). Hence, this invisibility is its only means of protection.

Figure 92. An immature walking stick, ***Trychopeplus laciniatus***, from Nectandra Cloud Forest Garden in Balsa, Costa Rica. Photo by Diane Lucas, with permission.

Figure 93. ***Trychopeplus laciniatus*** in Costa Rica. Photo by Dorothy Allard, with permission.

Figure 94. Bryophytes in Monte Verde, Costa Rica, Nectandra cloud forest where ***Trychopeplus laciniatus*** lives. Photo by Diane Lucas, with permission.

Figure 95. ***Trychopeplus laciniatus***, a walking stick that mimics bryophytes, on twig in Costa Rica. Photo by David Meagher.

Figure 96. Bryophytes in Monte Verde, Costa Rica, Nectandra cloud forest where ***Trychopeplus laciniatus*** lives. Photo by Diane Lucas, with permission.

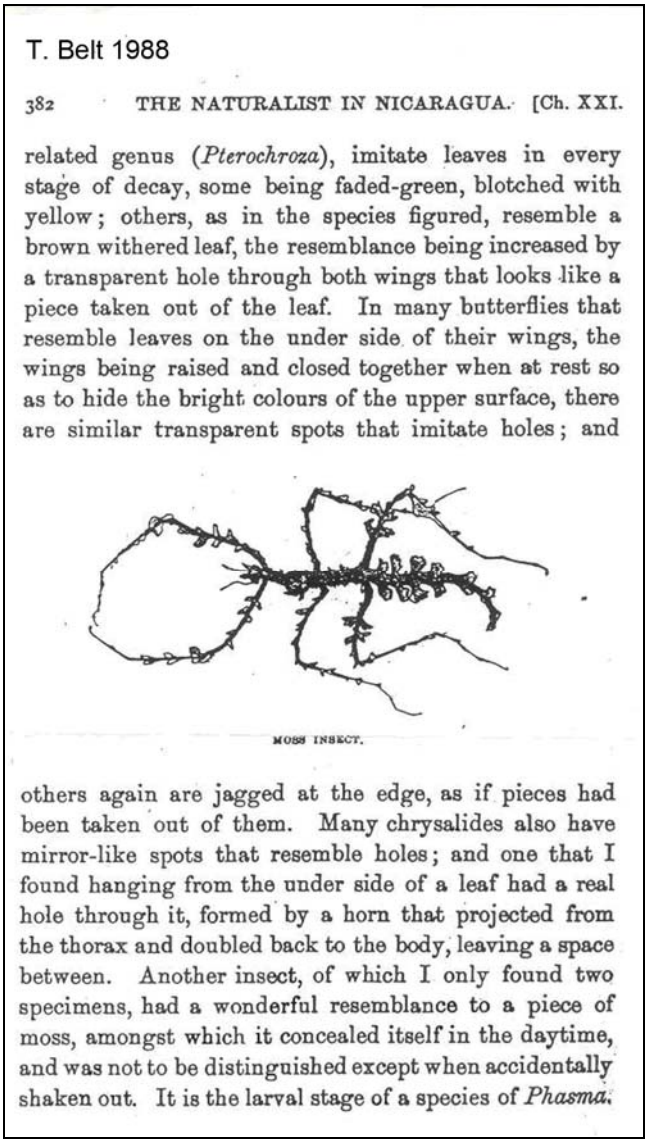
Figure 97. ***Trychopeplus laciniatus*** on bark. Photo by Dan Doucette through Project Noah, with permission.

Figure 98. ***Trychopeplus laciniatus***, clearly masquerading as a bryophyte. Photo by Dan Doucette through Project Noah, with permission.

Another observer (Anonymous 2015) describes the mating in more detail. ***Trychopeplus laciniatus*** is a herbivore and uses its mossy appearance to hide among the mosses while it feeds. Instead of laying its eggs in a cluster like most mantids, it lays them singly and loosely on the trees. The eggs subsequently fall to the forest floor where the nymphs hatch and develop.

Ng (2015) reports a moss mimic stick insect that laid eggs among mosses in the Botanical Garden of the Kinabalu Park, Malaysia (film is available on website). In China, ***Pericentrus*** (**Phasmatidae**; possibly synonym of ***Trychopeplus laciniatus***, **Error! Reference source not found.**-Figure 98) has coloration of green and brown that makes it look like mosses and lichens (Hennemann *et al*. 2008). It moved its body back and forth from side to side as it laid the eggs, occasionally releasing the ovipositor and re-inserting. It is likely that variants of these mimics exist in many locations in the tropics. Some may have been transported along with mosses, but their lack of wings would limit their distribution once they arrived. This kind of isolation promotes the formation of new species through the **founder principle** and **genetic drift**. For example, Belt figured one of these masqueraders in 1988 (Figure 99). But Tilgner (2002) disagrees with this explanation, suggesting instead that the multiple locations of such masquerading phasmids is the result of **convergent evolution**.

In Puerto Rico, ***Lamponius nebulosus*** (**Pseudophasmatidae;** Figure 100), a spiny green and brown mantid, represents the mimics (Nico Franz & Ines Sastre-de Jesus, Bryonet 15 April 2010). Those moss "leaves" you see are the spiny cuticle projections. This species is endemic to the cloud forest in the Luquillo Experimental Forest (Tilgner *et al*. 2000; Tilgner 2002) and has only been known for a short time. Its host plants include *Miconia* sp. and *Guzmania*, both likely to have associated mosses where it can rest undetected. In this group, activity is typically restricted to only certain times of day; when they are resting they are well camouflaged (Willig *et al*. 1993; Basset 2000; Berger 2004). But this species has two backup plans if it is discovered – it can exhibit **catalepsy** (trance state) or regurgitate fluid from its mouth.



T. Belt 1988

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related genus (*Pterochroza*), imitate leaves in every stage of decay, some being faded-green, blotched with yellow; others, as in the species figured, resemble a brown withered leaf, the resemblance being increased by a transparent hole through both wings that looks like a piece taken out of the leaf. In many butterflies that resemble leaves on the under side of their wings, the wings being raised and closed together when at rest so as to hide the bright colours of the upper surface, there are similar transparent spots that imitate holes; and

MOSS INSECT.

others again are jagged at the edge, as if pieces had been taken out of them. Many chrysalides also have mirror-like spots that resemble holes; and one that I found hanging from the under side of a leaf had a real hole through it, formed by a horn that projected from the thorax and doubled back to the body, leaving a space between. Another insect, of which I only found two specimens, had a wonderful resemblance to a piece of moss, amongst which it concealed itself in the daytime, and was not to be distinguished except when accidentally shaken out. It is the larval stage of a species of *Phasma*.

Figure 99. "Moss insect" from Nicaragua as illustrated in "The Naturalist in Nicaragua" by Thomas Belt 1888. Photo by Rob Gradstein, with permission.

Figure 100. ***Lamponius nebulosus***, a moss mimic. Photo courtesy of Alfredo D. Colon Archilla <alfredocolon.zenfolio.com>.

Even egg shape may contribute to adaptations for living among bryophytes (see Hennemann 2008). ***Parastheneboea foliculata*** (**Diapheromeridae**) has many

irregular pale green, straw, or brown markings and speckles that give it good camouflage among lichens and mosses. ***Parastheneboea exotica*** (Figure 101) and ***P. imponens*** (Figure 102-Figure 103) have elongate, cylindrical, bullet-shaped eggs with conical polar ends. The **operculum** (lid) is surrounded by a collar of **setae** (hairs). This egg shape is usually associated with taxa having an appendicular ovipositor that is suitable for laying eggs into soil, moss, and bark crevices.

Figure 101. ***Parastheneboea exotica***, a species with good camouflage among lichens and mosses. Photo by Albert Kang through Project Noah, permission pending.

Figure 102. ***Parastheneboea imponens***, a moss and lichen mimic. Photo by Albert Kang through Project Noah, permission pending.

Figure 103. ***Parastheneboea imponens*** is blending here among the mosses. Photo by Albert Kang through Project Noah, permission pending.

In ***Cnipsus rachis*** (**Phasmatidae**; Figure 104) the thorn pads consist of a single pair (Buckley *et al*. 2010). Projections along the body resemble moss leaves. Some of the New Caledonian species prefer ferns for food, but it seems that New Zealand species do not feed on ferns.

Figure 104. Mantid ***Cnipsus rachis*** from Costa Rica – and New Caledonia. Photo by Louis Thouvenot, with permission.

Neoclides laceratus

Neoclides laceratus is a stick insect from Sumatra, Kalimantan, and Sarawak (Meagher 2022). In the swampy forests of Borneo it resembles creeping moss or the liverwort ***Jungermannia*** (Figure 106) with the insect's olive-green color and leaf-like projections.

Figure 105. ***Neoclides laceratus*** camouflaged perfectly among bryophytes on wood in Costa Rica. Photo by David Meagher.

Figure 106. ***Jungermannia atrovirens***, in a liverwort genus that is mimicked by the stick insect ***Neoclides laceratus***. Hermann Schachner, through Creative Commons.

Antongilia laciniata (Bacillidae)

The moss mimic stick insect ***Antongilia laciniata*** (Figure 107) blends well with mosses in its aerial habitat. Although there are several images of this mimic online, there seems to be little information about its life.

Figure 107. ***Antongilia laciniata*** showing its moss-like camouflage in Madagascar. Photo by Frank Vassen, through Creative Commons.

Phanocles (Diapheromeridae)

The genus ***Phanocles*** (Figure 108) is distributed in Central and South America (Gutiérrez & Bacca 2014) where it blends in with the epiphytic and epiphyllous bryophytes due to its markings and its shape like a twig.

Figure 108. ***Phanocles*** sp. nymph resembling a twin with adnate mosses, liverworts, and lichens in Panama. Photo by Arthur Anker, with permission.

MANTODEA – Preying Mantids

This group of mantids are predators, hence the name preying mantis, but they also look like they are praying, so you will see the name spelled both ways. I still recall seeing my first mantid as a child. I thought at first someone had dropped a pocket knife, then realized it was the largest insect I had ever seen. These insects usually are safely camouflaged while at rest (Figure 109), but when they are searching for food or attacking prey they become more visible (Figure 110). Some are able to secrete a nasty spray that can blind the predators ("Steve" on Fellowship of the Minds 6 May 2013).

Figure 109. Mantid moss mimic among mosses on tree trunk. Photo by Nick Garbutt <www.nickgarbutt.com>, with permission.

Figure 110. ***Polytrichum strictum*** capsules with a mantid. Photo by Michael Lüth, with permission.

But they are not all so large – Zborowski (1993), in Animals in Disguise, illustrates mantids from Borneo that are no more than a cm long. Coyne (2013) discusses ***Pogonogaster tristani*** (**Thespidae**; Figure 111-Figure 112), described in 1918 but reported only a few times since. Others in this genus are present in Colombia (Gutiérrez & Bacca 2014). This is one of the minute preying mantids that mimics mosses.

Figure 111. ***Pogonogaster tristani***, one of the many moss mimics in this genus. Photo by Oscar Blanco, through Creative Commons.

Figure 112. Mantid that resembles mosses. Photo by Evelyne Lennette.

Not all camouflage involves morphology of the insect. Some mantids carry their own flora around with them. Two species of the shield mantis, ***Choeradodis rhombicollis*** (Figure 113) and ***C. rhomboidea*** (Figure 114-Figure 115) (**Mantidae**) in Costa Rica have **epizoic** (growing on animals) leafy liverworts and lichens growing on them (Lücking *et al*. 2010). Of the 84 individuals Lücking and coworkers examined in the lowland rainforests, 60 of them had epizoites, comprised of five liverwort species, 23 lichen species, and several unidentified fungi (Figure 116). These epizoites grew mainly on the enlarged pronotum, but some also grew on the forewings. The liverworts were all in the family ***Lejeuneaceae*** and were all species typical as **epiphylls** on leaves, especially ***Leptolejeunea elliptica*** (Figure 117). These pronotal inhabitants were more pronounced in ***C. rhombicollis*** than in ***C. rhomboidea***, and more in females than in males (Figure 116). One female of ***C. rhombicollis*** also had the leafy liverworts ***Diplasiolejeunea brunnea*** (Figure 118), ***Cololejeunea gracilis*** (Figure 119), ***C. camillii*** (Figure 121), and ***Colura tortifolia*** (Figure 120). The researchers suggested that the longer life span of females may account for the greater development of liverworts there. This camouflage permits these large mantids to rest undetected among the leaves with their own flora of "epiphylls."

Figure 113. ***Choeradodis rhombicollis*** showing the large hood that resembles a leaf. Photo by Andreas Kay, through Wikipedia Commons.

Figure 114. ***Choeradodis rhomboidea*** carrying a flora on its back like the leaves it inhabits. Photo by Andreas Kay, through Creative Commons.

Figure 115. ***Choeradodis rhomboidea*** showing its hood thorax (=enlarged pronotum) that resembles a leaf – in this case a damaged one. Photo by Andreas Kay, through Creative Commons.

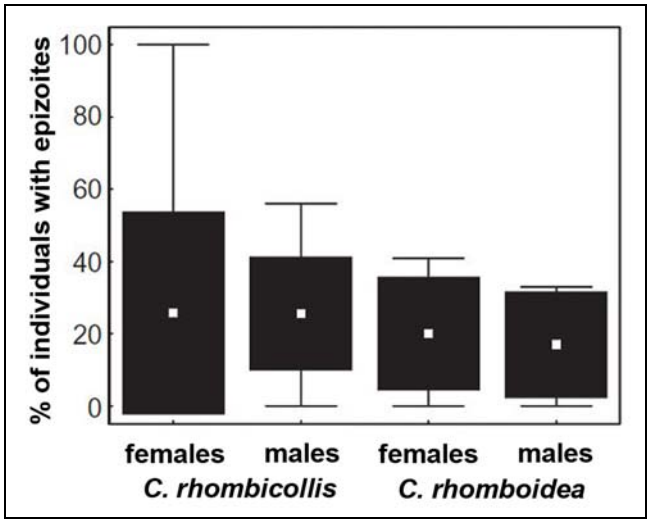

Figure 116. Comparison of males and females of two ***Choeradodis*** species showing percentage with liverwort, lichen, and fungus epizoites. Modified from Lücking *et al*. 2010.

Figure 117. ***Leptolejeunea elliptica*** epiphylls. Photo by Yan Jia-dang, through Creative Commons.

Figure 118. ***Diplasiolejeunea brunnea*** on leaf in Ecuador. Photo courtesy of Tamás Pócs.

Figure 119. ***Cololejeunea gracilis*** var. ***linearifolia***, a tiny liverwort that can grow on larger liverworts as well as leaves of evergreen plants. Photo courtesy of Tamás Pócs.

Figure 120. ***Colura tortifolia***, an occasional epizoite on ***Choeradodis rhombicollis***. Photo by Michaela Sonnleitner, with permission.

Figure 121. ***Cololejeunea camillii*** on leaf in Panama. Photo courtesy of Tamás Pócs.

Liturgusidae

Members of the genus ***Majangella*** can even resemble liverworts – a common group of bryophytes in the tropics. ***Majangella moultoni*** (Figure 122) has a green and brown patterned coloration with various protuberances that give it good camouflage when it is among mosses and liverworts. This species is tropical southeast Asian from Borneo, Indonesia, Malaysia, and Sumatra where it is inconspicuous in its rainforest habitat (Svenson & Vollmer 2014).

Figure 122. ***Majangella moultoni*** closely resembling the bryophytes beneath it. Photo by Hee Jenn Wei, with permission.

Mating

The mantids are well known for their mating behavior (Figure 123). The male is smaller than the female, and the female needs to be well fed before producing her egg case with eggs (Figure 124). Perhaps this is why the katydid males have evolved to offer a gelatinous spermatophore before mating. In short, it isn't safe to be the male mantid – you might get eaten! The predatory females see the smaller males as food (Figure 125), so males must make their moves carefully.

Figure 123. ***Mantis religiosa*** couple mating. Note that the smaller, brown mantid is the male. Photo by Zwentibold, through Creative Commons.

Figure 124. ***Mantis religiosa*** egg case. Photo by Hans Hillewaert, through Creative Commons.

Figure 125. ***Polyspilota*** sp female chewing on the head of the male while mating with him. Photo by Arthur Anker, with permission.

BLATTODEA – Cockroaches and Termites

You would most likely prefer not to think of cockroaches and termites as moss dwellers. If so, it may please you to know that the Australian wood-boring cockroach ***Panesthia australis*** (**Blaberidae**; Figure 126) prefers odors of individual tracheophyte species over the odor-neutral ***Sphagnum*** (Figure 61) (Billingham *et al*. 2009).

Figure 126. ***Panesthia australis***, a cockroach that avoids mosses as a food item. Photo by Toby Hudson, through Creative Commons.

But the tables can be turned. Bernard Dupont photographed the **ootheca** (Figure 127) of a cockroach that was deposited on bryophytes and that had leafy liverworts growing up onto the ootheca. And Chatervedi sent me a picture of a cockroach that was hiding under the thallose liverwort ***Dumortiera hirsuta*** (Figure 129).

Figure 127. Cockroach ootheca with leafy liverworts growing on it. Photo by Bernard Dupont, through Creative Commons.

Figure 128. Cockroach on ventral surface of ***Dumortiera hirsuta***. Photo courtesy of Chatervedi.

Figure 129. ***Dumortiera hirsuta***, a hiding place for cockroaches. Photo by David T. Holyoak, with permission.

ISOPTERA – Termites

Termites have lost their status as an order and are now included as an infraorder within the **Blattodea**. Termites have a division of labor much like that of the ants.

There are some bizarre habitats occupied by bryophytes, and these include termite mounds (Figure 131-Figure 133). One of these is the preferential occurrence of four species of ***Fissidens*** (***F. gymnostomus***, ***F. hornschuchii***, ***F. scariosus***, and ***F. subulatus*** on termite structures in the Amazon (Reese & Pursell 2002). In one case, ***F. allionii*** co-occurred with ***F. subulatus*** on mounds in Amazonian Brazil. In another ***F. pellucidus*** var. ***pellucidus*** (Figure 130) and ***F. prionodes*** both occurred on one mound.

Figure 130. ***Fissidens pellucidus*** var ***pellucidus***, a termite mound colonizer. Photo by Scott Zona, with permission.

Figure 131. Termite mounds in the Bungle Bungle Range in Western Australia. Photo by Ouderkraal, through Creative Commons.

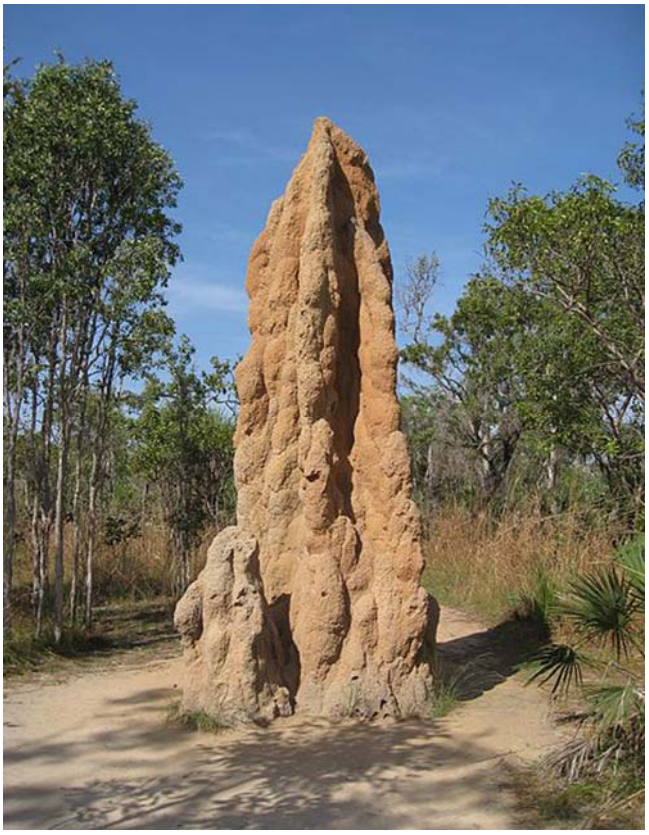

Figure 132. *Nasutitermes triodiae* in Northern Territory, Australia. Photo by J. Brew, through Creative Commons.

These organically enriched structures may benefit from the mosses through erosion control, while the mosses benefit from enrichment by feces, saliva, and other substances (Reese & Pursell 2002). The raised mounds serve in the same way as tree roots and soil banks by elevating the substrate above the leaf litter accumulation. Nevertheless, few other mosses and liverworts seem able to live in this habitat.

It appears that ***Fissidens*** may actually help the termites (Reese & Pursell 2002). One can observe fishbone-like patterns on some kinds of termite nests, and ***Fissidens*** provides such a pattern on nests it occupies. This pattern most likely facilitates drainage of rainfall. Furthermore, the mosses can serve to bind the particles that comprise the nest as well as softening the blow as raindrops strike.

Fissidens termitarum in Bolivia and Brazil occurs almost exclusively on termite structures (Reese & Pursell 2002). In the Amazon Churchill (1998) recorded 13 of the 38 ***Fissidens*** taxa on termite structures, but none were found there exclusively. In Rondônia, Brazil, Lisboa (1993) found 7 of the 15 ***Fissidens*** taxa associated with termite nests.

Figure 133. Termite mound with mosses at base. Photo by Izuchukwu Ezukanma, with permission.

Fissidens is also known from termite mounds in Africa (Potier de la Varde 1928, 1936; Bizot & Pócs 1979; Bizot *et al.* 1990; Bruggeman-Nannenga 1993). Likewise, Catcheside and Stone (1988) reported this genus from termite mounds in northern Australia. Even Mitten (1869) referred to ***Fissidens pellucidus*** (Figure 130) on "ant mounds," but Reese and Pursell (2002) considered that these were most likely termite mounds.

Other species of mosses are rare on the termite structures. Reese (2001) reported several species of **Calymperaceae** on termite structures. Churchill (1998) has the largest number of collections noted, including **Calymperaceae**: ***Syrrhopodon cryptocarpus*** (Figure 138), ***S. ligulatus***, ***S. xanthophyllus***; **Pilotrichaceae**: ***Brymela parkeriana***; **Stereophyllaceae**: ***Pilosium chlorophylum***. Reese and Pursell (2002) found ***Phyllodrepanium falcifolium*** (**Phyllodrepaniaceae**) with ***Fissidens*** on one termite structure in the Amazon. Nevertheless, none of these non-***Fissidens*** species seems to frequent the nests. Ezukanma (in prep) found 5 species (none included above) on termite nests in the Eastern Nigeria highlands: ***Campylopus savannarum*** (Figure 134), ***Daltonia angustifolia*** var. ***angustifolia*** (Figure 135), ***Philonotis hastata*** (Figure 136), ***Rhachitheciopsis tisserantii***, and ***Sematophyllum brachytheciiforme***.

Figure 134. ***Campylopus savannarum***, a species that occurs on termite nests in the Eastern Nigeria highlands. Photo by A. J. Ramalho, through Creative Commons.

Figure 135. ***Daltonia angustifolia***, a species known from Nigerian termite mounds, shown here growing on the weevil ***Gymnopholus reticulatus***. Photo courtesy of Rob Gradstein.

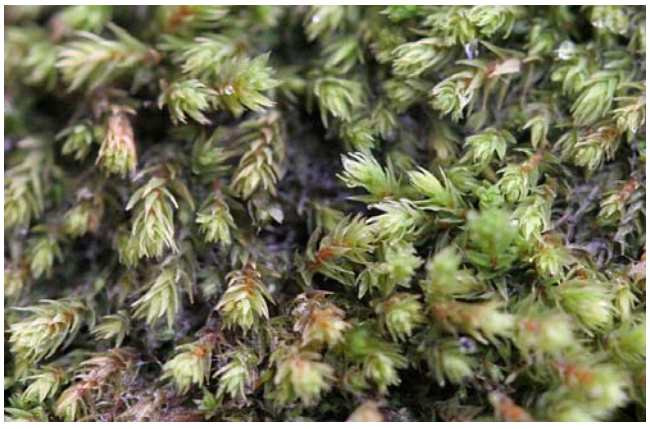

Figure 136. ***Philonotis hastata***, a species known from Nigerian termite mounds. Photo by Michael Lüth, with permission.

Termites are generally unable to digest mosses (Bush 2015). Their guts have protozoa that facilitate their digestion of cellulose and lignin, hence their ability to eat wooden houses. Some people have considered termites to actually be a deterrent to mosses. Bush (2015) refers to a study in Ontario, Canada, that compared various types of mulch on termite mortality. When used as the only source of food, peat moss starved the termites to death. Another study showed that subterranean termites tended to avoid travelling through peat, but only if the peat was moist. Dry peat seemed to have no effect.

Nevertheless, ***Hospitalitermes umbrinus*** (**Termitidae**; Figure 137) has "food balls" that contain bryophytes, but it prefers lichens (Collins 1979). This species forms foraging parties of roughly 500,000 soldiers and workers that leave the nest in the evening and return in the morning carrying these food balls.

Figure 137. ***Hospitalitermes umbrinus***, a species that makes food balls containing bryophytes. Photo by Budak, through Creative Commons.

Termite mounds are an interesting ecosystem engineering feat. The termites actually benefit the ecosystem. The structure of these mounds cause more water to be absorbed into the soil and thus provide oases where green plants are able to subsist, preventing desertification (Bonachela *et al*. 2015; Hance 2015).

Figure 138. ***Syrrhopodon*** sp. Several species in this genus are known from termite mounds. Photo by Blanka Shaw, with permission.

EMBIOPTERA - Webspinners

This is a little-known order of tropical and subtropical net spinners. The name *embio* refers to the fluttery wings (*ptera*) of the first one described (Meyer 2009). One must wonder why one net spinner was collected from a moss cushion in Israel (Gerson 1982), but the image (Figure 139) below from Brazil supports it.

Figure 139. **Embioptera** from Brazil with net on mosses. Photo by Arthur Anker, with permission.

Summary

The **Orthopteroidea** include grasshoppers, pygmy grasshoppers, crickets, wetas, katydids, walking sticks, preying mantids, cockroaches, ice crawlers, and **Embioptera**. Among this group are many forms of camouflage and mimicry, and some of these are adaptations to living among bryophytes.

The pygmy grasshoppers (**Tetrigidae**) include may species that live among bryophytes and eat them. Some species have multiple morphs, permitting the species to occupy a variety of habitats. Many in this family also lay eggs there, as do many members of the **Acrididae**, a family that also includes bryophyte feeders. ***Discotettix belzebuth*** has bryophytes growing on it, providing camouflage.

Mosses contribute a variety of patchy habitats that enable grasshoppers to remain separated spatially, supporting **Gause's** law by coexisting in the same environment but failing to compete due to the spatial separation.

Gryllidae (crickets) are rare among bryophytes, with bogs being the primary bryophyte habitat for them. Wetas are often found with bryophytes in caves or among them on tree trunks.

Rhaphidophoridae (camel crickets and wetas) include cave dwellers and other species that have color patterns blending with bryophytes. Some of the cave crickets also eat bryophytes.

Tettigoniidae (katydids) are good leaf mimics and some blend well with bryophytes by having a more broken color pattern. Some feed on ***Sphagnum*** and some lay their eggs there.

Walking sticks (**Phasmida**) are the master of disguise, mimicking pendent mosses in their rainforest homes. This type of mimicry, in which the insect can be mistaken for a hanging moss, may more appropriately be termed **masquerading**. This type of mimicry has recently been termed masquerading. Some of these seem to have egg shapes adapted for oviposition among bryophytes.

The mantids (**Mantodea**) can have bryophyte camouflage and blend well, but their broad bodies prevent them from being mimics of pendent bryophytes. However, some do an excellent job of mimicking leaves with epiphylls living on them, including liverwort epiphylls, by having their own garden of bryophytic epizoites.

Cockroaches (**Blattodea**) seem to avoid mossy habitats, but one image shows the **ootheca** on bryophytes with liverworts growing onto the ootheca. Termites, formerly **Isoptera**, are members of the **Blattodea**. They often build mounds, especially in Australia, Africa, and the Amazon. These mounds are suitable habitats for a number of species of ***Fissidens***, some of which seem to prefer that habitat. Few other bryophyte species occupy the mounds.

The **Embioptera** are probably not moss dwellers, although they were reported among mosses once.

Acknowledgments

Pavel Drozd helped me obtain some of the grasshopper photos. Heino Lepp and Judith Curnow introduced me to the tiny moss-mimicking mantids from Borneo. Jessica Beever, Thomas Buckley, and Sven Bradler helped me to get the identity of *Trychopeplus laciniatus.* Ryan Burrows helped me find web sites with information and the scientific name of the walking stick, *Trychopeplus laciniatus.* Louis Thouvenot sent me the image of another mantid mimic, *Cnipsus rachis*. Rob Gradstein provided me with the story of liverworts on *Choeradodis* (Mantidae). Matt Renner provided the reference on using the term masquerade. Thank you to all the photographers who gave me permission to use their images or placed them in Creative Commons. Three professional photographers game me permission to use their images in this chapter – thank you to Nick Garbutt for the mantis moss mimic, Tony Jewell for his picture of *Maotoweta virescens*, and Alfredo D. Colon Archilla for his picture of *Lamponius nebulosus*. Tomás Pócs took pictures of Lejeuneaceae just for use in this chapter. Allan Fife helped me make contacts to try to understand the role of bryophytes for cave wetas. Petr Kočárek kindly sent me images of *Tetrix* spp. and *Discotettix beelzebuth* on mosses. Izuchukwu Ezukanma showed me an advance copy of his manuscript that documented termites on Eastern Nigerian highlands mosses on termite mounds.

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CHAPTER 12-5
TERRESTRIAL INSECTS: HEMIMETABOLA – NOTOPTERA AND PSOCOPTERA

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CHAPTER 12-5
TERRESTRIAL INSECTS: HEMIMETABOLA – NOTOPTERA AND PSOCOPTERA

Figure 1. Example of **Mantophasmatodea**, a subgroup of the **Notoptera**. Photo by Michael F. Schönitzer through Creative Commons.

NOTOPTERA

The order **Notoptera** perhaps deserves its own chapter simply because the smallest chapter is appropriate for the smallest order (<30 species) of insects (Ando & Machida 1987). But alas, for practical reasons, I have included the **Psocoptera** here as well, a much larger order but rare among bryophytes. The order **Notoptera** is poorly known and has limited, but widespread, distribution. Nevertheless, it is important in our understanding of insect evolution (Vrsansky *et al*. 2001). And mosses seem to play a role for at least some of their lives.

The order **Notoptera** is **relict** (survived from an earlier time period) (Vrsansky *et al*. 2001; Schoville & Kim 2011) and in addition to the two living families, it is known from fossils in middle Eocene (Lutetian) Baltic amber (Arillo & Engel 2006) and the Lower Permian (Aristov 2004), suggesting that it has been widespread in time and space. The living **Notoptera** are known only from Canada (Walker 1914), western United States (Caudell & King 1924; Kamp 1963, 1970), Russia (Bey-Bienko 1951; Kevan 1979), Korea (Storozhenko & Park 2002; Kim & Lee 2007), China (Wang 1987), and northern Japan (Schoville 2010). Genetic isolation in parts of Asia may have resulted from geologic events in which islands fragmented and collided, causing mountain uplifts in Japan (Schoville *et al*. 2013). The remaining taxa appear to be a "poorly dispersing, cold-adapted terrestrial insect lineage" that occupies Japan, Korea, and Russia. The island fragmentation events have created a number of endemic species. In the western US, several Grylloblattidae and **Gryllacrididae** returned to the devastated Mt. St. Helens within three years after its eruption in 1980 (Sugg & Edwards 1998), suggestion that it has some means of dispersal.

The order **Notoptera** was named in 1915 but was largely overlooked (Wikipedia 2016a). More recently, it was somewhat resurrected and joined with the Grylloblattodea, placing both of them in the order **Notoptera**.

These insects resemble mantids, but never have wings (Ando & Machida 1987). They live under stones and in

caves in the alpine areas (Schoville & Kim 2011). They are well adapted to cold conditions (Pritchard & Scholefield 1978; Kevan 1979; Jarvis & Whiting 2006). Many retreat deep below the surface to escape surface temperatures ranging -35 to +45°C (Kevan 1979).

Grylloblattodea – Ice Crawlers

The **Grylloblattodea** are predominately nocturnal and feed on detritus (Wikipedia 2015). They are wingless and have either reduced eyes or no eyes (Figure 2). There is only one family and it is comprised of only 5 genera and 34 species that live mostly in leaf litter and under stones of extremely cold environments of higher elevations.

Figure 2. Member of **Grylloblattidae** on snow, a small family that may lay eggs in mosses. Photo by Alex Wild through Creative Commons.

When temperatures are cold enough for ice crystals to form in the body, the **Grylloblattidae** retreat under the snow pack near the soil (Grimaldi & Engel 2005). They feed mostly on arthropod carcasses, but if these are insufficient they rely on plant material (Wikipedia 2015). At least one member deposits its eggs among mosses (Richards & Davies 1977).

Grylloblattidae – Ice Crawlers

The North American ice crawlers are known for their adaptations to cold, whereas the Asian members are the most diverse (Jarvis 2005; Jarvis & Whiting 2006). They are rarely encountered, but this may be due to their seclusive habit of going underground or hiding among mosses. Bai *et al*. (2010) suggested that they lost their wings and became adapted to living under rocks or hidden in mosses in cold areas.

Most members of this family are carrion feeders, but they will also eat plant material, fungi, and detritus (Bai *et al*. 2010).

The modern (extant) members of this family are 14-34 mm long, pale, wingless, and avoid light (nocturnal or living in caves) (Bai *et al*. 2010).

Galloisiana

Galloisiana nipponensis (Figure 3) was first described by Caudell and King in 1924 from Japan. This was the introduction of a new genus and new family, the **Grylloblattidae**. This species occurs on the ground under stones and in moss (Memim Encyclopedia 2015). To date, no eggs have been found among mosses in ***G. nipponensis*** (Rentz & Ingrisch 2009).

Figure 3. ***Galloisiana nipponensis***, an extant member of the **Notoptera** in northern Japan. Photo by Obsidian Soul through Creative Commons, with modified background.

Three quarters of a century later, ***Galloisiana olgae*** is a recently described species occurring in a small area on the banks of the Vasilkovka River in southeastern Russia (Vrsansky *et al*. 2001). The genus has also spread to Korea (Schoville & Kim 2011) and China (Wang 1987). It inhabits wet soil and is found under rocks that are covered with mosses. This raises an interesting question. What is the importance of the mosses on those rocks. I venture a guess. This and all members of the order are omnivores, often feeding on carcasses of other arthropods (Wikipedia 2015). Rocks with mosses provide easy access for these wingless insects to hunt for food among the mosses at night (or whenever they feed).

Grylloblatta

In North America, 13 species of ***Grylloblatta*** (Figure 4) have been described, but Schoville and Graening (2013) considered that another 16 are awaiting description and publication. Its known distribution in western North America (Caudell & King 1924) includes California, USA (Caudell 1923; Schoville & Roderick 2010; Schoville 2012), to British Columbia, Canada (Gregson 1938; Kamp 1979; Huggard & Klenner 2003). This is a genus with high endemism and small species ranges.

Bai *et al*. (2010) considered temperature to be the primary limiting factors in their distributions. This does not bode well for them in the face of global warming. A species of ***Grylloblatta*** (Figure 4) on Mt. Rainier, Washington, USA, is active on the snow in summer, where it forages at night (Edwards 1982). But they have behavioral strategies that enable them to avoid freezing, as seen in this ***Grylloblatta***. This species lacks the usual means to survive freezing (cryoprotectants, supercooling) and dies at a mere -6.5°C (Edwards 1987). On the other hand, it experiences heat convulsions at temperatures of 14°C. Morrissey and Edwards (1979) similarly found that the Mt. Rainier species suffers lethal heat convulsions at 15-20°C and speculated that unsaturated fatty acids might be important in their low-temperature adaptations. Could it

be that arachidonic acid, a polyunsaturated fatty acid in mosses, might contribute to this cold tolerance? Nevertheless, it migrates downward to overwinter among the rocks under deep snow where it is assured of temperatures above its -6.5°C lethal temperature (Edwards 1987). Henson (1957) was able to maintain nymphs of ***Grylloblatta campodeiformis*** (Figure 4) at 4.5°C for six months.

Figure 4. ***Grylloblatta campodeiformis***, a cold climate species that lays eggs on mosses. Photo through NSF public domain.

Huggard and Klenner (2003) collected 147 specimens of ***Grylloblatta campodeiformis*** (Figure 4) in British Columbia, Canada, in pitfall traps in the subalpine spruce-fir forest and lower elevation cedar-hemlock forest. Many were associated with mossy old-growth forests. They suggested that the moss layer was important for this species and that forest management practices might be reducing suitable habitat by affecting microclimate and snow accumulation – and moss cover.

When the female is about one year old, she will deposit black eggs singly among mosses or in soil (Kamp 1963, 1970; Ramel 2015). These eggs require another year to incubate, and the nymphal instars require about 5 years (8 instars) to become adults.

Grylloblatta campodeiformis (Figure 4) is a predaceous species that feeds on other arthropods (Pritchard & Scholefield 1978). Pritchard and Scholefield collected this species in the Rocky Mountains in Alberta, Canada at 1300 asl. Beamer (1933) found ***G. campodeiformis*** var. ***occidentalis*** in Mt. Baker in Washington.

The gut contents contained arthropods and little else, with a cranefly in the Tipulidae being the most common food. Both the ***Grylloblatta campodeiformis*** (Figure 4) and the tipulid are typical of cold, montane habitats. The ***G. campodeiformis*** eat only live or recently killed animal prey and both larvae and adults fail to develop or grow without animal food. To detect their prey, they use their antennae. Both the antennae and palpi (mouth parts) have sensitive hairs that most likely help in prey identification. The prey are seized by the mandibles.

I would expect to find some of them living among mosses or going there to feed because there are several species of cranefly larvae that live among the mosses. It could explain their association with the moss layer in old-growth forests. One cannot expect a wingless species to travel very far for food.

Members of ***Grylloblatta*** (Figure 4) possess **sensilla** (McIver & Sutcliffe 1982), a series of branched hairs protected by cuticle near the tip of the mandibles. Baker (1982) suggests they may be used to sense the pressure being exerted on the mandible tips, perhaps avoiding damage to the muscles.

Grylloblattella

Grylloblattella cheni was described as the second species in this genus, occurring in China (Bai *et al*. 2010). It is known from only one specimen, collected in the primary boreal coniferous forest near a lake. It was under the bark of a log near the summer snow line. This and other extant species have a shorter meso- and metathorax than prothorax, the opposite of the fossil species where the prothorax is shorter. They suggest this may be due to the loss of wings in the extant species.

PSOCOPTERA – Booklice, Barklice, Barkflies

This order is considered the most primitive of hemipteroids (Wikipedia 2016b). These are small insects(1-10 mm long). The barklice are harmless to the trees where they live, eating mostly algae and lichens. Their small size apparently makes scraping their food somewhat hazardous; their chewing mandibles are accompanied by a slender rod modified from the central lobe of the maxilla. This modified rod is used to brace them while they scrape their food with their mandibles. Some can spin silk, covering large areas of the bark (Hoell *et al*. 1998).

Most of the **Psocoptera** feed on detritus, epiphytes, fungi, and some on leaves (Baz 2008). They have a thin cuticle and thus are susceptible to desiccation. They are able to take up moisture from the atmosphere and obtain some of their water from food, but rarely by drinking.

Bryopsocus (**Bryopsocidae**) is associated with trees and mosses in wet forests (New & Lienhard 2007). This genus is endemic to New Zealand. Only two species occur there, both associated with mosses: ***Bryopsocus angulatus*** and ***B. townsendi***, ranging 2-3 mm long (Bess & Johnson 2009). Likewise in New Zealand, ***Echmepteryx madagascariensis*** (**Lepidopsocidae**; Figure 5) lives on mosses that grow on the horizontal trunks of ***Metrosideros*** (Figure 6) (Smithers 1973). Smithers (1974) also collected ***Spilopsocus avius*** (**Elipsocidae**) from mosses in the subAntarctic islands of New Zealand.

Figure 5. ***Echmepteryx madagascariensis***, a species that lives among mosses on horizontal trunks of ***Metrosideros***. Photo by Sean McCann through Creative Commons.

Figure 6. ***Metrosideros umbellata*** (rata) showing horizontal trunks with mosses where one might find ***Echmepteryx madagascariensis***. Photo by John Barkla, with permission.

Evidence of members of **Psocoptera** eating bryophytes is limited. Valle *et al*. (1977) reported one that feeds on mosses and lichens growing on citrus in Cuba.

Lucking (2000) pointed out that the **Psocoptera** are among the insects that feed on epiphyllous bryophytes, as well as other organisms (algae, fungi, lichens) that grow on the leaves. Unlike the **Lepidoptera** feeding there, the **Psocoptera** are generalists, eating whatever is available on the leaf. They typically lay their eggs on the lower leaf surfaces. The young juveniles are protected by their mothers. Lucking concluded that although they did considerable damage to the leaf habitat, they positively influenced the diversity of the lichen and bryophyte community.

Schmidt and New (2008) recorded other **Psocoptera** in association with mosses in Tasmania. ***Lepinotus patruelis*** (**Trogiidae**; Figure 7) was among mosses on a log; ***Liposcelis*** (**Liposcelidae**; Figure 8) occurs among mosses on logs and living trees.

Figure 7. ***Lepinotus patruelis***, a moss dweller on logs and trees in Tasmania. Photo from <www.aphotofauna.com>, with permission.

Figure 8. ***Liposcelis*** sp. hiding under bark. Photo by Peter J. Bryant, with permission.

Some members of this order are known from mossy forests, but the role of the mosses is unclear. García Aldrete (2009) reported several species from this habitat in Argentina: ***Polypsocus jujuyensis***, ***Polypsocus selenius*** (**Amphisocidae**), ***Lachesilla dividiproctus***, ***Lachesilla peckorum***, and ***Lachesilla cuala*** (**Lachesillidae**). On the other hand, Thornton (1985) found that the numbers and diversity of **Psocoptera** decreased on mountain tops with wet conditions and epiphytic mosses in many areas of the Pacific.

Some **Psocoptera** are restricted to caves. The **neotenous** (retaining juvenile characteristics in adults) ***Cyptophania pakaratii*** (Figure 9) seems to be limited to the fern-moss "gardens" in the cave entrances (Figure 10) in the Pacific basin (Mockford & Wynne 2013). These habitats serve as relict habitats of the last glacial maximum, supporting species that are restricted to the conditions they offer (Benedict 1979; Northup & Welbourn 1997; Wynne 2013; Wynne *et al*. 2014).

Figure 9. ***Cyptophania pakaratii***, a species apparently restricted to the fern-moss patches in cave entrances. Photo by Jut Wynne, with permission.

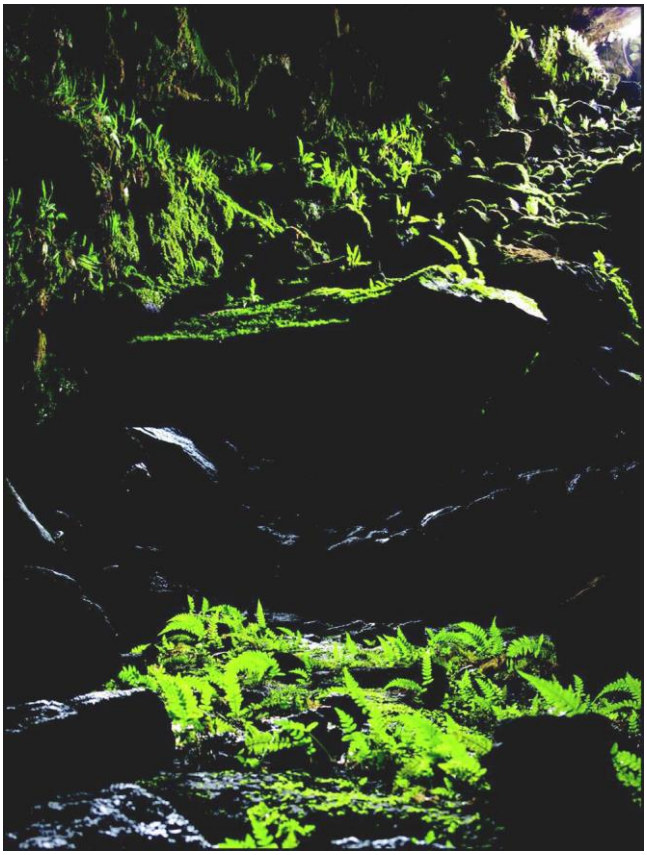

Figure 10. Relict fern-moss garden in cave at Rapa Nui National Park, Easter Island, Chile. Photo by Jut Wynne, with permission.

Summary

The **Notoptera** is a small order of relict insects, due in part to absence of wings and dispersal limitations. The **Grylloblattodea** (ice crawlers) are mostly nocturnal detritus feeders. Some can use mosses for oviposition. Members of **Grylloblattidae** may live under mosses in cold regions. ***Grylloblatta campodeiformis*** is often associated with mossy old-growth forests and deposits her eggs on the mosses.

Few species of **Psocoptera** are moss inhabitants, but their small size permits some of them to live there. The genus ***Bryopsocus*** is known only from mossy habitats in New Zealand. Some may feed on bryophytes, including epiphyllous bryophytes. Some are restricted to cave entrances where they live among mosses and ferns.

Acknowledgments

Thank you to Wikipedia as a free source of basic information on so many taxa. Those who have placed their images in the public domain or given me permission have made this chapter more interesting for the readers.

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CHAPTER 12-6
TERRESTRIAL INSECTS: HEMIMETABOLA – HEMIPTERA (HETEROPTERA)

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CHAPTER 12-6
TERRESTRIAL INSECTS: HEMIMETABOLA – HEMIPTERA (HETEROPTERA)

Figure 1. Lacebug (**Tingidae**) with moss ***Tortula papillosa*** and lichen *Candelaria concolor*. Photo by Robert Klips, with permission.

HEMIPTERA – True Bugs

While many people call all insects bugs, there is only one order that officially carries that name. Their scientific name of **Hemiptera** revealed their most unique character, wings that are "half" membranous and "half" chitinized. But recent classification has added other groups to the **Hemiptera** that do not have this character, and some have no wings at all. The order is now divided, including the traditional "bugs" in the suborder **Heteroptera**. The **Hemiptera** are **hemimetabolous**, having a life cycle of eggs, nymphs, and adults. The overwintering stage depends on the species and may be spent among mosses.

Although most bugs feed on tracheophyte (mostly flowering plant) leaves, often specializing on one species, for many the bryophytes are important alternate hosts when the tracheophyte leaves are no longer available or no longer hospitable. But Rédei *et al*. (2003) considered the ground fauna to be under-sampled relative to the pest species that occurred above ground on plants. Using Berlese funnels for extraction (without specifying sample size) they found that the assemblages of **Hemiptera** from mosses were similar to those from soil and could occur "in great numbers" (Table 1). In fact, moss samples had higher numbers per sample than soil samples, although it is hard to know the appropriate base (weight, area, volume, *etc*.) on which to compare them. To sample **Hemiptera** among bryophytes, Marie-Claude Larivière uses a sieve technique (Figure 2).

As an example of moss hemipteran diversity, the communities among various moss species in Hungary differ little from each other, with the exception of those on ***Sphagnum*** (Figure 3; Table 1) (Rédei *et al*. 2003). On the other hand, the **Hemiptera** communities on bryophytes differ significantly ($p<0.05$) from those of tussocks and those of soil, leaf litter, and debris (Figure 4). An important factor among the bryophyte habitats is the moisture level. Mosses on the ground retain water longer

than those on tree trunks, with those on rocks retaining the least water and providing the driest habitats. Consequently, **Hemiptera** species preferring humid conditions are common among bryophytes on the ground and some tree trunk conditions but do not occur among the drier rock dwellers.

Table 1. Comparison of Hemiptera in bryological samples and non-bryological samples on the ground. From Rédei *et al*. 2003.

substrate	number of samples	numb specimens	numb per sample
mosses on tree trunks	225	725	3.2
mosses on stones and rocks	292	1240	4.2
mosses on ground	259	520	2.0
other mosses	117	221	1.9
Sphagnum	94	107	1.1
soil	390	159	0.4
leaf litter, debris	795	586	0.7
tussocks, tufts of sedges	287	209	0.7

Figure 2. Marie-Claude Larivière sifting moss and leaf litter in NZ to find **Hemiptera**. Photo by André Larochelle, with permission.

Figure 3. ***Sphagnum*** becoming established on *Potentilla fruticosa* as a fen becomes more moist and acidified. The fen and bog locations typically have both flowering plants and mosses, providing the two alternative hosts needed by many **Hemiptera** species. Photo by Janice Glime.

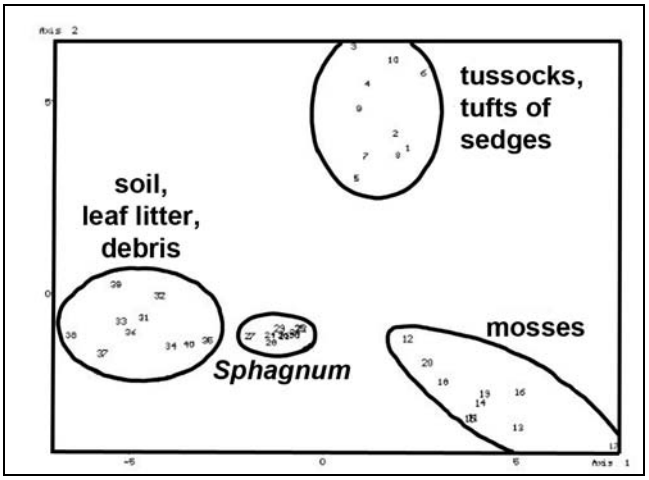

Figure 4. Similarity pattern of communities associated with the four major substrata groupings of Hungarian hemipteran ground fauna. Redrawn from Rédei *et al*. 2003.

True bugs are affected by the nutrients available to mosses. Richardson *et al*. (2002) found that moss-feeding true bugs in fertilized plots in Scandinavia diminished in number to as little as 6% of those in the unfertilized controls. The **Homoptera** on grasses, on the other hand, were more than 400% more abundant, indicating that fertilization was detrimental to the moss communities. Such a reduction could be the result of nutritional changes in the mosses or a reduction in mosses, reducing both food and cover for bryophyte-adapted bugs.

Adaptations

Most of the bugs that live among bryophytes are tiny, often only 1-2 mm in length. Their biggest adaptation is that many of the moss dwellers are able to eat mosses. This ability not only may involve differences in mouthparts, but at least sometimes requires the presence of **endosymbiotic** bacteria to help in digestion (Kuechler *et al*. 2013). But it seems that few other adaptations exist. Their coloration is often brown, and I find that the common moss-dwelling lace bugs often resemble seeds, not mosses. That's not a bad appearance if you are hiding from carnivores, but it doesn't make you invisible. Instead, the coloration of most species is adaptive for the primary host. On the other hand, mosses provide a habitat where behavior is important. Many species are able to migrate vertically within the moss mat to find suitable temperature and humidity (Marie-Claude Larivière, pers. comm. 1 September 2015).

Nutrients

Among the factors that limit **Hemiptera**, nutrients in the plants can play an important role. This can be especially important for some adapted to Arctic and sub-Arctic habitats where nutrient turnover is slow. In a dwarf shrub heath community, Richardson *et al*. (2002) manipulated nutrients and temperatures to determine responses. Nutrient addition had a strong effect on the subordinate mosses and resulting changes in the abundance of the insect herbivores. These changes had a greater impact on the insect herbivore community than those of the shrub layer. Those **Hemiptera** (**Heteroptera**) on the fertilized plots reached an abundance only 6% that of the unfertilized controls. **Homoptera** (former classification),

on the other hand, were more than 400% more abundant. The grass-eating **Delphacidae** (plant hoppers) were only present in fertilized plots.

Habitats

Forests

Forests offer a variety of habitats for bryophyte-dwelling **Hemiptera** (Lattin & Moldenke 1990). In the woodland habitats of Hungary, Rédei *et al*. (2004) found ***Acalypta carinata*** (2.5 mm; **Tingidae**; Figure 5) among the ***Sphagnum*** (Figure 3) and the moss ***Abietinella abietina*** (Figure 6), living on tree trunks or the ground. This lace bug prefers humid, shady woodland habitats. ***Acalypta musci*** (2.5-2.8 mm; Figure 7) is typically a moss dweller, but it also occurs on fungi on tree trunks and among mosses at tree bases.

Figure 5. ***Acalypta carinata*** female on moss in Germany. Photo by Michael Münch <www.insekten-sachsen.de> through GBIF, with permission

Figure 6. ***Abietinella abietina***, a woodland home for ***Acalypta carinata.*** Photo by Janice Glime.

Figure 7. ***Acalypta musci***, a species named for its association with mosses. Photo by Boris Loboda, with permission.

The mossy forests of the temperate and Antarctic rainforests of New Zealand (Figure 8) are home to the tiny **Peloridiidae** (2-4 mm) (Burckhardt 2010; Burckhardt *et al*. 2011; Harris 2011, 2014). The **Peloridiidae** also occur in temperate forests in Australia (Grozeva *et al*. 2014). The genus ***Xenophyes*** (2.18-3.23 mm; Figure 9), a member of **Peloridiidae**, is common in the rainforests throughout the southern hemisphere, including Chile, Argentina, New Zealand, New Caledonia, and Australia (Burckhardt *et al*. 2011). ***Peloridium hammoniorum*** (3.9-4.3 mm), the only member of the family with both winged and flightless forms, was recently described as a new species from Chilean secondary forests, living among mosses, primarily on ***Polytrichadelphus magellanicus*** (Figure 10) (Shcherbakov 2014).

Figure 8. Wet Rimu (***Dacrydium***) forest in New Zealand where **Heteroptera** live among mosses. Photo by Marie-Claude Larivière, with permission.

Figure 9. ***Xenophyes rhachilophus***, member of a genus that is common among mosses in rainforests of the Southern Hemisphere. Photo by S.E. Thorpe, through Creative Commons.

Figure 10. ***Polytrichadelphus magellanicus***, home of ***Peloridium hammoniorum***. Photo by Juan Larrain, with permission.

Dikraneura aridella (5.6-6 mm; **Cicadellidae**; Figure 11) lives in moss-covered coniferous European forests, where it feeds on grasses (Söderman 2007). ***Aguriahana pictilis*** (~5 mm; **Cicadellidae**; Figure 12) likewise lives in moss-covered forests, but it feeds on blueberry (*Vaccinium myrtillus*) leaves. The importance of the mosses for these two species is unclear. Elsewhere, ***Macrocixius emeljanovi*** (0.51-0.64 mm; **Cixiidae**) and ***M. oropilus*** (0.69-0.70mm) live in high mountain mossy forests in Taiwan and Nepal (Orosz 2013). ***Melanocoryphus albomaculatus*** (~9 mm; **Lygaeidae**; Figure 13-Figure 14), a critically endangered species in the Czech Republic, lives under lichens, moss, dry leaves, stones, etc. (Kment *et al*. 2013a). Its bright orange and black color patterns seem left over from some prior host of its relatives because they do not seem adaptive to mosses or to some of its host plants like *Senecio* (Chateau Moorhen 2015). And, oddly for a moss dweller, in France it likes hot, dry places!

Figure 11. ***Dikraneura aridella***, a species that prefers moss-covered coniferous forests in Europe. Photo by Marko Mutanen, through Creative Commons.

Figure 12. ***Aguriahana pictilis***, an inhabitant of moss-covered forests. Photo by Gernot Kunz, with permission.

Figure 13. ***Melanocoryphus albomaculatus***, a critically endangered species in the Czech Republic, often living under mosses. Photo by Valter Jacinto, through Creative Commons.

Figure 14. ***Melanocoryphus albomaculatus***, a moss dweller that does not have cryptic coloration for moss dwelling. Photo by Didier Descouens, through Creative Commons.

Larivière *et al*. (2011) reported ***Oiophysa ablusa*** (**Peloridiidae**; Figure 15) from montane ***Nothofagus*** forests in New Zealand where they lived among wet mosses and leaf litter. ***Oiophysa cumberi*** (Figure 16) is a more lowland species, living in broadleaf-podocarp and ***Nothofagus*** forests among both mosses and liverworts on the ground and on trees. ***Oiophysa distincta*** is likewise in the lowland to montane podocarp and ***Nothofagus*** forests where it lives among mosses on the ground and on trees as well as in litter. This species also occurs on the pendulous moss ***Weymouthia*** sp. (Figure 17).

Figure 15. ***Oiophysa ablusa*** on leafy liverwort. Photo by E. Wachmann through M.-C. Larivière, with permission.

Epiphytes

Tree-trunk bryophytes are typically drier than those growing on the ground and some species of **Lygaeidae** prefer to live among mosses in this habitat (Rédei *et al*. 2003). Members of **Peloridiidae** (Bechly & Szwedo 2007) and **Rhyparochromidae** (Rédei *et al*. 2003) are common on tree trunk mosses in Europe. Furthermore, the genus ***Acalypta*** (**Tingidae**) is represented there by a number of species, and ***Piesma maculatum*** (2-3 mm.; **Peismatidae**; Figure 18), ***Myrmedobia exilis*** (1.3-2.2 mm; **Microphysidae**; Figure 19), ***Cryptostemma*** (2.5-2.8 mm; **Dipsocoridae**; Figure 20), and ***Ceratocombus coleoptratus*** (1.5-2.0 mm; **Ceratocombidae**; Figure 21) also prefer this tree trunk habitat, as well as ground and other substrata. Rédei *et al*. consider many terrestrial ***Hebrus*** (**Hebridae**; Figure 36-Figure 38) species, including young nymphal stages, to prefer moss on tree trunks, ground, and other surfaces. In Tasmania, ***Xenophyes cascus*** (2.48-3.10; **Peloridiidae**; Figure 22) occurs among bark mosses (Burckhardt *et al*. 2011).

Figure 16. ***Oiophysa cumberi***, a moss inhabitant. Photo by George Gibbs, with permission.

Figure 17. ***Weymouthia mollis***, home for some members of ***Oiophysa distincta***. Photo by Phil Bendle, through Creative Commons.

Figure 18. ***Piesma maculatum***, a hemipteran living among mosses on tree trunks. Photo by Joe Botting, with permission.

Figure 19. ***Myrmedobia exilis***, a tree-trunk bryophyte dweller. Photo by Mardon Erbland, through Creative Commons.

Figure 20. ***Cryptostemma*** sp.; ***Cryptostemma waltli*** lives among mosses in shaded habitats. Photo by Michael F. Schönitzer, through Creative Commons.

Figure 21. ***Ceratocombus coleoptratus***, a tree-trunk and ground moss dweller. Photo by Michael Münch <www.insekten-sachsen.de> through GBIF, with permission

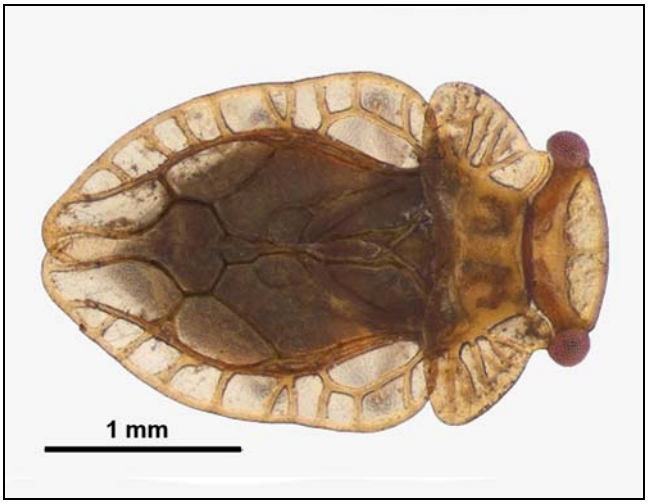

Figure 22. ***Xenophyes cascus***, a species that lives among epiphytic mosses in epiphytes. Photo by Marie-Claude Larivière, with permission.

The **Saldidae** (shore bugs; Figure 24-Figure 23) include a range of habitats from the intertidal zone to terrestrial habitats. Among these habitats is the moss on the trunks of rainforest trees (Polhemus & Chapman (1979). ***Lampracanthia crassicornis*** (1 mm; Figure 23) and ***Salda anthracina*** (Figure 24) lay their eggs between the leaves of mosses (Hungerford 1918). ***Salda anthracina*** is much like the preying mantis in its mating behavior. But unlike the preying mantis, the male initially follows the female around, keeping a safe distance (Hungerford 1919). When he decides to mate (or the opportunity is right), he pounces upon her. He exits quickly at completion lest he too, like the preying mantis male, be eaten by his mate. And sometimes he is eaten.

Figure 23. ***Lampracanthia crassicornis***, a species that lays its eggs on mosses. Photo from CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons

Figure 24. ***Salda anthracina***, a species that lays her eggs among moss leaves and will eat her mate if he doesn't leave fast enough. Photo by Tom Murray, through Creative Commons.

Sand Dunes

In dunes, bryophytes can offer respite from the dry sand. Spungis (2005) found that **Hemiptera** density was limited by available cover of mosses and lichens. Sand dunes are dry and inhospitable for insects that do not have desiccation protection. For some, that protection comes in surface waxes, hard chitin, and a reduced physiological need for water. For others, behavior is the most important adaptation, allowing the hemipterans to move to mosses when host plants become inhospitable. Spungis (2005) found that mosses provided a refuge for bugs in the coastal grey dunes (Figure 25) of Latvia. The number of species of **epigeic** (active at the soil surface) **Hemiptera** correlated with the moss-lichen cover in the dunes (p<0.01). The density of ground-dwelling species was low and both population density and species diversity were limited by available cover of lichens and mosses. ***Nysius thymi*** (3.5-4.5 mm; **Lygaeidae**; Figure 26) and members of **Miridae** (jumping tree bugs; Figure 118-Figure 123) had high population densities and were dominant compared to the grass-dwelling hemipterans. ***Sciocoris cursitans*** (4.5-6.0 mm; Figure 27) in the **Pentatomidae** dominated the soil dwellers (41%), with a high correlation (r=0.81; p<0.01) with moss and lichen cover.

Figure 25. Coastal grey dunes in The Netherlands. Similar sites in Latvia have limited **Hemiptera-**moss associations, including mostly **Miridae**. Photo by Bas Kers, through Creative Commons.

Figure 26. ***Nysius thymi*** on thyme flower. This species is dominant in sandy areas of Latvia with dense moss and lichen cover. Photo by Tristan Bantock, with permission.

Figure 27. ***Sciocoris cursitans*** adult, a soil dweller with a high correlation with mosses and lichens. Photo by Tristan Bantock, with permission.

In Hungary, Rédei *et al.* (2004) found that ***Acalypta gracilis*** (2-2.8 mm; **Tingidae**; Figure 28) preferred the Pannonic dune open grassland patches (Figure 29) over the dune-slack (Figure 30) purple moor grass meadow. ***Acalypta marginata*** (2.0-3.0 mm; Figure 31-Figure 32) was present equally in the Pannonic dune open grassland and the Pannonic sand puszta patches (Figure 33), but likewise avoided the dune-slack purple moor grass meadow. Both species are moss dwellers.

Figure 28. ***Acalypta gracilis***, a moss dweller that prefers dune open grassland in Hungary. Photo by Michael Münch <www.insekten-sachsen.de> through GBIF, with permission.

Figure 29. Pannonic sand steppe, Hungary. Photo by Daniel Dítě in Šefferová Stanová *et al*. 2008, with authorized reproduction.

Figure 30. Dune slack and meadow in UK, a habitat that seems to be avoided by moss dwelling ***Acalypta*** species in Hungary. Photo by David Hawgood, through Creative Commons.

Figure 31. ***Acalypta marginata*** with moss, a dweller among mosses in sandy areas, including dunes. Photo by Boris Loboda, with permission.

Figure 32. ***Acalypta marginata*** disappearing into the depths of a moss. Photo by Boris Loboda, with permission.

Figure 33. Pannonic sand puszta with draw well in Hungary. Photo by Andreas Poeschek, through Creative Commons.

Streamside and Wet Habitats

This habitat group includes bugs with high moisture requirements, but that are not truly aquatic. For example, ***Macrovelia hornii*** (4.2 mm; **Macroveliidae**; Figure 34) nymphs and adults live among mosses at the water's edge but are unable to live in the water or on its surface (Usinger 1974).

Figure 34. ***Macrovelia hornii***, a moss inhabitant at water's edge. Photo by Jerry Wilson, with permission.

Hebrus concinnus (2.25-2.5 mm; **Hebridae**; Figure 35), from a genus that is dominant among **Hemiptera** in bogs and fens (see Chapter on aquatic Hemiptera in this volume), lays its eggs where they are partially concealed between moss leaves (Usinger 1974). Schuh and Slater (1995) described them as living deep in moss mats, with ***Hebrus ruficeps*** (1.3-3.7 mm; Figure 36) overwintering frozen in ice among ***Sphagnum*** (Figure 37). ***Hebrus pusillus*** (1.6-2.1 mm; Figure 38) is associated with ***Sphagnum*** and other mosses (Howe 2004) and also reproduces among mosses at the edge of water (Münch 2013). Hebrids also often lay their eggs among mosses, suggesting that early instars may develop there.

Figure 35. ***Hebrus concinnus***, a species that lays its eggs among mosses. Photo through Creative Commons.

Figure 36. ***Hebrus ruficeps*** on ***Sphagnum***, a common bog dweller that overwinters in ice among ***Sphagnum***. Photo by Ruth Ahlburg, with permission.

Figure 37. Frozen ***Sphagnum fimbriatum*** and ice habitat where ***Hebrus ruficeps*** is able to spend its winter in ice among the moss plants. Photo by Dick Haaksma, with permission.

Figure 38. ***Hebrus pusillus***, among the dominant ***Hebrus*** species in bogs and fens. Photo by Joseph Botting, with permission.

Micracanthia schuhi (2.64-3.35; **Saldidae**; see Figure 39) is a moss dweller in Oregon, USA, where it lives beside a small stream on Mt. Hood among moist mosses (Lattin 1968, 1997). It moves up and down within the moss mat to achieve the best temperature level (Lattin 1968).

Figure 39. *Micracanthia marginalis*. ***Micracanthia schuhi*** lives among mosses on Mt. Hood, Oregon, USA. Photo by Jürgen Deckert, with permission.

Cryptostemma waltli (1.2-1.5 mm; **Dipsocoridae;** Figure 20) lives in shaded wet habitats where it inhabits the mosses ***Sphagnum*** (Figure 37), ***Hypnum*** (Figure 40), ***Brachythecium*** (Figure 41), and ***Cratoneuron*** (Figure 42) (Kment *et al.* 2013b).

Figure 40. ***Hypnum lindbergii***, potential home for ***Cryptostemma waltli*** in wet, shaded habitats. Photo by Michael Lüth, with permission.

Figure 41. ***Brachythecium rutabulum*** with capsules, a genus that could be home to ***Cryptostemma waltli*** in shaded, wet habitats. Photo by Malcolm Storey through DiscoverLife.

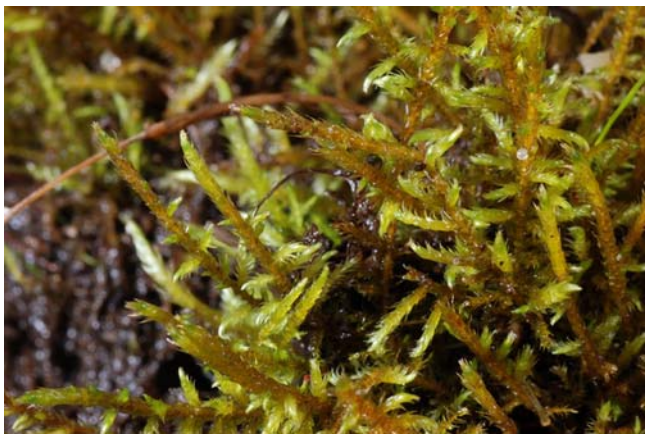

Figure 42. ***Cratoneuron filicinum***, one of the mosses that may house ***Cryptostemma waltli*** in shaded, wet habitats. Photo by J. C. Schou, with permission.

Peatlands

Peatlands are borderline between aquatic and terrestrial habitats. I have already discussed the more aquatic-leaning taxa in the chapter on Aquatic Insects, especially those living in bog pools. Here I will treat the species that use other (non-bryophyte) plants that live in the bogs, perhaps also using the mosses, but that require or benefit from the peatland habitat.

Rédei *et al*. (2003) found that the **Hemiptera** tussock community and species living among ***Sphagnum*** (Figure 3) species were comprised primarily of ubiquitous species that were able to occupy most kinds of mossy substrata. Like many other invertebrates, many of the species of **Hemiptera** are not restricted to bogs and tend to be widespread (Holzinger & Schlosser 2013).

Holzinger and Schlosser (2013) conducted a survey of the **Hemiptera** fauna of Austrian peat bogs in the Bohemian Forest. They found that the **Auchenorrhyncha** formed a considerable fauna, with 93 species among 7465 specimens in these bogs, making them one of the most abundant animal groups in peatlands (see also Holzinger 1995, 2000; Holzinger & Novotny 1998). Eleven of these species were either **tyrphobiontic** (peat bog specialist; restricted to bogs) or **tyrphophilous** (common in bogs but not restricted to them). Tyrphobiontic species in these bogs include ***Sorhoanus xanthoneurus*** (3.1-3.4 mm; **Cicadellidae**; Figure 43) and ***Stroggylocephalus livens*** (5-6.5 mm; **Cicadellidae**; Figure 44), ***Kelisia vittipennis*** (3-3.6 mm; **Delphacidae;** Figure 45), and ***Cixius similis*** (5 mm; **Cixiidae**; Figure 46) (see also Trivellone 2010). ***Cixius similis*** migrates from mosses to shrubs to feed and mate, then returns to the moss-covered ground to oviposit (Söderman 2007). Tyrphophilous species include the **Cicadellidae** ***Sorhoanus assimilis*** (often the most frequent hemipteran; 2-2.9 mm; Figure 47), ***Cicadula saturata*** (4-5.5 mm; Figure 48), and ***Macrosteles ossiannilssoni*** (Figure 49), and the **Delphacidae** ***Paradelphacodes paludosa*** (2.8-3 mm; Figure 50), ***Kelisia ribauti*** (3-4.5 mm; Figure 51), and ***Oncodelphax pullula*** (2-4 mm; Figure 52) (Holzinger & Schlosser 2013).

Figure 43. ***Sorhoanus xanthoneurus***, a restricted bog dweller. Photo by Joe Botting, with permission.

Figure 44. ***Stroggylocephalus livens***, a restricted bog species in Europe. Photo by Gernot Kunz, with permission.

Figure 45. ***Kelisia vittipennis***, a species restricted to bogs. Photo by Joe Botting, with permission.

Figure 46. ***Cixius similis***, a bog-restricted species that moves from mosses to shrubs to feed and back to mosses to oviposit. Photo by Joe Botting, with permission.

Figure 47. ***Sorhoanus assimilis*** adult, a bog-loving moss dweller. Photo by Gernot Kunz, with permission.

Figure 48. ***Cicadula*** sp. adult, a tyrphophilous species. Photo by Tristan Bantock, with permission.

Figure 49. ***Macrosteles ossiannilssoni***, a tyrphophilous bog dweller. Photo by Marko Mutanen, through Creative Commons.

Figure 50. ***Paradelphacodes paludosa*** adult, a bog-loving moss dweller. Photo by Gernot Kunz, with permission.

Figure 51. ***Kelisia ribauti***, a species that is common in bogs but that is not restricted to them. Photo by Gernot Kunz, with permission.

Figure 52. ***Oncodelphax pullula*** on Cyanobacteria, a species that is common in bogs but not restricted to them. Photo by Joe Botting, with permission.

Conomelus lorifer (**Delphacidae**; Figure 53-Figure 54) occurs in ***Sphagnum***-*Carex* associations in Switzerland (Trivellone 2010) at higher altitudes (Ökteam 2012). ***Conomelus anceps*** (4 mm; Figure 55-Figure 56) is a lower altitude species and comprised 17% of the individuals in the Austrian peat bogs and was the most common species there (Holzinger & Schlosser 2013). This species was followed by ***Muellerianella extrusa*** (3.6-4.2 mm; **Delphacidae**; Figure 57) (9.2%), ***Sorhoanus xanthoneurus*** (**Cicadellidae;** Figure 43) (7.6%), ***Jassargus pseudocellaris*** (**Cicadellidae**; Figure 58) (5.5%), and ***Macustus grisescens*** (5-6 mm; **Cicadellidae**; Figure 59) (5.2%). Most of these species are **stenoecious** (having a narrow habitat range) and specialize not only on the habitat, but also on their host plants (Nickel *et al*. 2002; Nickel 2003). The bogs have more **univoltine** (having one brood of offspring per year) **Auchenorrhyncha** species compared to other habitats in Austria and likewise more of their species in the bogs hibernate during their nymphal stage (Holzinger & Schlosser 2013). Densities of adults are low in spring (10-60 individuals per m^2), rising to a high of 180 individuals per m^2 in July.

Figure 53. ***Conomelus lorifer***, a bog dweller in Europe. Photo by Gernot Kunz, with permission.

Figure 54. ***Conomelus lorifer*** adult, a bog dweller. Photo by Gernot Kunz, with permission.

Figure 55. ***Conomelus anceps*** nymph, a bog dweller. Photo by James K. Lindsey, with permission.

Figure 56. ***Conomelus anceps*** adult, a bog dweller, with moss. Photo by Tim Faasen, with permission.

Figure 57. ***Muellerianella extrusa***, a species associated with ***Sphagnum*** in Europe. Photo by Gernot Kunz, with permission.

Figure 58. ***Jassargus pseudocellaris*** adult, a species associated with ***Sphagnum***. Photo by Tristan Bantock, with permission.

Figure 59. ***Macustus grisescens***, a ***Sphagnum*** associate in Europe. Photo by Tristan Bantock, with permission.

In Austrian peatlands, life cycle stages of the **Auchorrhyncha** represent different proportions than in the whole of the Austrian fauna (Figure 60) (Holzinger & Schlosser 2013). The number of generations tends to be fewer in peatlands than in the general fauna (Figure 60).

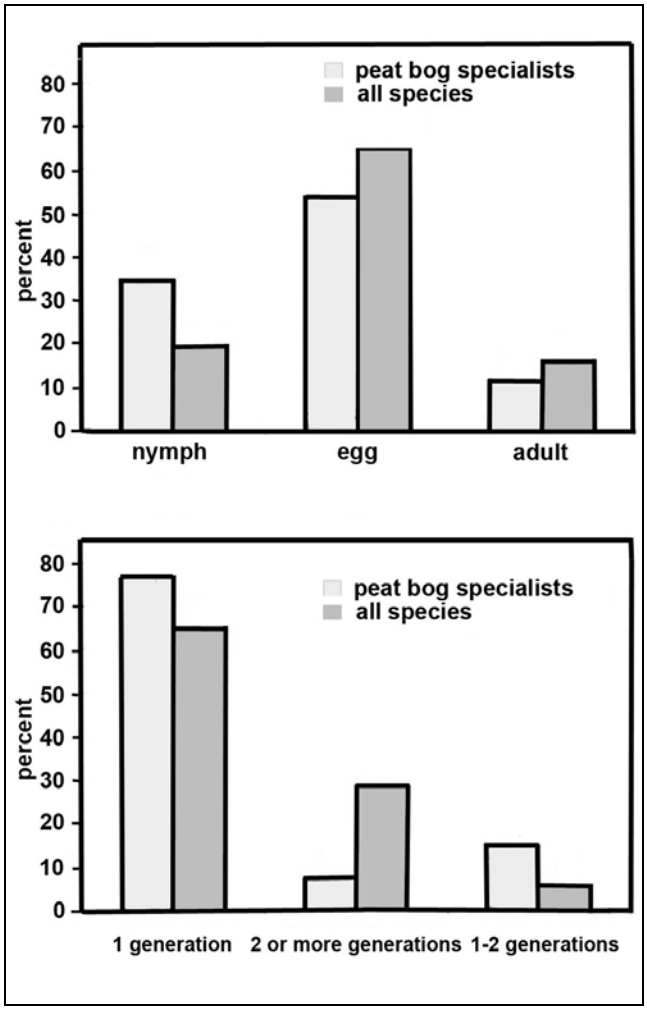

Figure 60. Comparison of generation stages and numbers of generations per year for species of **Auchenorrhyncha** in Bohemian forest peat bogs compared to those of the whole Austrian **Auchenorrhyncha** fauna. Redrawn from Holzinger & Schlosser 2013.

SUBORDER HETEROPTERA (true, typical bugs)

PENTATOMOMORPHA – STINK BUGS, FLAT BUGS, AND SEED BUGS

Thyreocoridae – Ebony Bugs

One member of this family was collected among mosses of the Cheviot Hills, UK – ***Corimelaena scaraboeoides*** was common among mosses (Champion 1871). ***Thyreocoris scarabaeoides*** (Figure 61-Figure 63) is a common moss inhabitant, measuring only 3-4 mm (British Bugs 2015a). Its black color as an adult makes it difficult to notice in the depths of the moss. (I can't find confirmation of the nomenclature for ***Corimeleana scaraboeoides***, so it may be a synonym of ***Thyreocoris scarabaeoides***.)

Figure 61. ***Thyreocoris scarabaeoides*** mid-instar nymph, a common moss inhabitant in the UK. Photo by Tristan Bantock, with permission.

Figure 62. ***Thyreocoris scarabaeoides*** late-instar nymph. Photo by Tristan Bantock, with permission.

Figure 63. ***Thyreocoris scarabaeoides*** adult. Photo by Tristan Bantock, with permission.

Cydnidae – Burrowing Bugs, Shield Bugs

Burrowing bugs don't normally inhabit bryophytes, but there are some exceptions. These include the somewhat larger ***Canthophorus impressus*** (6-7 mm; Figure 64), a rare species (British Bugs 2015b) that hibernates in groups under mosses and leaves in winter (eImageSite.net 2013). Records for ***Canthophorus dubius*** (7mm; Figure 65) are often actually ***C. impressus***, requiring dissection for certain identification (British Bugs 2015b).

Figure 64. ***Canthophorus impressus***, a species that hibernates in groups under mosses. Photo by Tristan Bantock, with permission.

Figure 65. ***Canthophorus dubius***, a winter moss inhabitant in the chalk downs of the UK. Photo by Dragiša Savić, with permission.

The shield bug ***Adomerus biguttatus*** (Figure 66-Figure 67) overwinters among bryophytes (Southwood & Leston 1959).

Figure 66. ***Adomerus biguttatus*** nymph on moss, its overwintering site. Photo by Tristan Bantok, with permission.

Figure 67. ***Adomerus biguttatus*** adult on moss, its overwintering site. Photo by Tristan Bantok, with permission.

Pentatomidae – Stink Bugs and Shield Bugs

In Hungary this family is represented in great numbers in moss mats (Rédei *et al*. 2003). In the UK Champion (1871) reported ***Rhacognathus punctatus*** (7-9 mm; Figure 68-Figure 69) among mosses in heath (Figure 70) and ***Zicrona caerulea*** (5-7 mm; Figure 71-Figure 72) as a common bug among mosses on the chalk downs (Figure 73). ***Sciocoris cursitans*** (4.5-6 mm; Figure 27) dominated the epigeic **Hemiptera** at the coastal gray dunes in Latvia (Spungis 2005) and demonstrated a significant positive correlation with the amount of moss-lichen cover. This family seems to prefer mosses for cover in relatively exposed and dry habitats. Despite the statement by Rédei *et al*. (2003) that they occur in great numbers in moss mats, there seems to be little published about the role of these relationships.

Figure 68. ***Rhacognathus punctatus*** nymph, a species that lives among mosses in heath in the UK. Photo by Tristan Bantock, with permission.

Figure 69. ***Rhacognathus punctatus*** adult, a moss dweller. Photo by James K. Lindsey, with permission.

Figure 70. Heathland where one might find ***Rhacognathus punctatus*** among mosses. Photo by James K. Lindsey, with permission.

Figure 71. ***Zicrona caerulea*** early instar, a moss inhabitant. Photo by Tristan Bantock, with permission.

Figure 72. ***Zicrona caerulea*** adult, a common bug among mosses in UK chalk grasslands. Photo from <www.entomart.be>, through Creative Commons.

Figure 73. Chalk downs at Chanctonbury Hill Chalk Pits, UK, hone to ***Zicrona caerulea*** among mosses. Photo by Malcolm Oakley, with permission.

Berytidae – Stilt Bugs

The **Berytidae** are comprised of about 100 species (Encyclopædia Britannica 2015). They are delicate looking, with slender bodies, and despite their long legs they are slow moving. They are somewhat larger (5-9 mm) than most moss dwellers, but their brown color helps them to blend somewhat with at least some mosses. All members of the family are plant feeders and they sometimes damage crop plants. A few are known moss dwellers.

Berytinus signoreti (4.5-6 mm; Figure 74-Figure 75), ***Berytinus minor*** (Figure 76), and ***Neides tipularius*** (10-11.5 mm; Figure 77) are all moss dwellers in the UK (Champion 1871). Woodroffe (1959) reported ***Berytinus signoreti*** occurring under the flower *Lotus corniculatus*, but also noted "scattered individuals" among mosses. ***Berytinus minor*** is common among mosses and grass roots in the UK (Douglas & Scott 1865). In Dorset, England, members of ***Cymus*** (2.5-5 mm; Figure 78-Figure 79) live in meadows and heathlands on rushes, but in winter this genus overwinters under moss or bark (Recording Dorset 2011).

Figure 74. ***Berytinus signoreti***, a moss dweller in the UK. Photo by Tristan Bantock, with permission.

Figure 75. ***Berytinus signoreti*** adult, a moss dweller. Photo by Tristan Bantock, with permission.

Figure 76. ***Berytinus minor***, a moss dweller in the UK. Photo by Miroslav Deml, through Creative Commons.

Figure 77. ***Neides tipularius***, a moss dweller in the UK. Note the long legs. Photo by Tristan Bantock, with permission.

Figure 78. ***Cymus glandicolor*** nymph, a moss dweller. Photo by Tristan Bantock, with permission.

Figure 79. ***Cymus glandicolor***, a species that overwinters under mosses or bark. Photo by Tristan Bantock, with permission.

Lygaeidae – Seed Bugs and Milkweed Bugs

Most of the members of this family are ill-suited for living among bryophytes. They typically feed on seeds, but some are predatory, some feed on sap, and some feed on blood (TrekNature 2011). They often exhibit bright colors (Figure 80) and are too large to move easily among most kinds of mosses.

Figure 80. ***Lygaeus creticus*** on ***Atrichum***, exhibiting a size and sharp color contrast that does not make this a safe environment. Photo by Dragiša Savić, with permission.

In Eastern Europe, Kment *et al*. (2013a) found ***Melanocoryphus albomaculatus*** (7-9.5 mm; Figure 13-Figure 14), a colorful bug, under lichens, mosses, dry leaves, and stones. They preferred sunny rocky hillsides and clearings. Perhaps its red and black warning colors are enough to scare away would-be predators, or it simply isn't seen when under the moss. ***Taphropeltus hamulatus*** (2.9-3.4 mm; Figure 81) lives in well-drained base-rich sites, particularly among the mosses in areas with loose rocks (Alexander 2008). At least its colors are less conspicuous. ***Lamproplax picea*** (4.0-5.0 mm; Figure 82) is a moss dweller in the UK and has similar dark coloration (Hallett 1916).

Figure 81. ***Taphropeltus hamulatus***, a moss dweller in well-drained, base-rich sites. Photo by Tristan Bantock, with permission.

Figure 82. ***Lamproplax picea***, a moss dweller in the UK. Photo by Joe Botting, with permission.

Piesmatidae – Ash-Grey Leaf Bugs

This is a small family of plant-eating bugs. Using the Berlese funnel to extract bugs from various substrata, Rédei *et al*. (2003) found that ***Piesma maculatum*** (2-3 mm; Figure 83) preferred to live among mosses on tree trunks, ground, and other substrata. Alexander (2008) likewise found it in moss litter in the UK. I have not found any other records for this family among bryophytes.

Figure 83. ***Piesma maculatum***, a species that "prefers" living among mosses. Photo by Joe Botting, with permission.

Rhyparochromidae – Seed Bugs

I discovered a record of this family by accident as I was searching for harvestman pictures. Naturalist Graeme Lyons (2011) of Sussex, UK, reported "beating" a clump of ***Thuidium tamariscinum*** (Figure 84) to find invertebrates. With this activity, he was able to add a new species of **Hemiptera** to his list of finds: ***Peritrechus nubilus*** (5-6 mm; Figure 85). In New Zealand, this family occurs among mosses in the forest (Figure 86).

Figure 84. ***Thuidium tamariscinum*** with capsules, home to ***Peritrechus nubilus***. Photo by Michael Lüth, with permission.

Figure 85. ***Peritrechus nubilus***, a species found in the moss ***Thuidium tamariscinum***. Photo by Tristan Bantock, with permission.

Figure 86. **Rhyparochromidae** habitat under moss in Arthur's Pass, NZ. Photo by Marie-Claude Lariviére, with permission.

Early reports of bryophyte dwellers in this family date as far back as 1871 (Champion 1871). A species of ***Peritrechus lundii*** (4-5 mm; Figure 87) along with two ***Drymus*** (Figure 97-Figure 98) species, ***Trapezonotus arenarius*** (4-4.5 mm; Figure 88-Figure 89), and ***Stygnocoris sabulosus*** (2.5-3 mm; Figure 90-Figure 91), were most common among mosses in alder (*Alnus*) woods.

Figure 87. ***Peritrechus lundii***, a moss dweller. Photo by Tristan Bantock, with permission.

Figure 88. ***Trapezonotus arenarius*** nymph, a common species among UK mosses in alder woods. Photo by Tristan Bantock, with permission.

Figure 89. ***Trapezonotus arenarius*** adult, a common species among alder woods in the UK. Photo by Tristan Bantock, with permission.

Figure 90. ***Stygnocoris sabulosus***, a moss dweller. Photo by Tristan Bantock, with permission.

Figure 91. ***Stygnocoris sabulosus*** adult at Crowle Moors, UK. Photo by Brian Eversham, with permission.

Alexander (2008) reported that ***Trapezonotus desertus*** (4-5 mm; Figure 92) nymphs occurred among dry mosses and lichens. ***Peritrechus geniculatus*** (5-6 mm; Figure 93-Figure 94) is also known from mosses and leaves on light sandy and chalky soils in Dorset, England (Alexander 2008; Recording Dorset 2011). This species overwinters as an adult, protected by the mosses. ***Eremocoris abietus*** (6-7.5 mm; Figure 95) and ***Stygnocoris rusticus*** (3-4 mm; Figure 96) likewise occur among mosses elsewhere in the UK (Champion 1871).

Figure 92. ***Trapezonotus desertus***, a species whose nymphs live among dry mosses and lichens. Photo by Tristan Bantock, with permission.

Figure 93. ***Peritrechus geniculatus*** nymph, an inhabitant of mosses and leaves on light sandy and chalky soils in the UK. Photo by Tristan Bantock, with permission.

Figure 94. ***Peritrechus geniculatus*** adult, a species that spends time among mosses in the UK. Photo by Tristan Bantock, with permission.

Figure 95. ***Eremocoris abietis***, a moss dweller in Europe. Photo by R. Altenkamp, Berlin, through Creative Commons.

Figure 96. ***Stygnocoris rusticus***, a species that lives among mosses in the UK. Photo by Tristan Bantock, with permission.

Drymus sylvaticus (Figure 97), ***D. brunneus*** (Figure 98), ***Stygnocoris sabulosus*** in a UK study occurred primarily among mosses in the alder woods. ***Canthophorus dubius*** (**Cynidae**; Figure 65) was more rare, overwintering among mosses under junipers of the chalk downs, a habitat where ***Zicrona coerulea*** (**Pentatomidae**; Figure 71-Figure 72) was common. ***Drymus brunneus*** (4-5 mm) occurs among mosses in damp, shady places; it is widespread and common (Stenhouse 2007) despite preferring damper soils than other species of ***Drymus*** (Alexander 2008). ***Drymus sylvaticus*** (4-5 mm) is one of the most common of the British ground bugs, often occurring among mosses on dry soil (Alexander 2008; Bury Wildlife 2014). This species becomes active at night, feeding on mosses and fungal hyphae (Southwood & Leston 1959; Alexander 2008). Champion (1871) reported both of these species from mosses near Cheviot Hills, UK. *Recording Dorset* (2011) reports ***D. sylvaticus*** as common, occurring in most dry habitats that have mosses. In the UK, the rare ***Drymus pilicornis*** (3.9 mm) lives mostly in moss clumps among grasses on calcareous or base-rich grassland (Alexander (2008). In France, the rare ***Drymus pilipes*** (~2 mm) lives among mosses and litter (Péricart 1999).

Figure 97. ***Drymus sylvaticus*** adult, a moss dweller on dry soil in the UK. Photo by Tristan Bantock, with permission.

Figure 98. ***Drymus brunneus***, a moss dweller in damp, shady places in Europe. Photo by Tristan Bantock, with permission.

Pterotmetus staphyliniformis (5-5.5 mm; Figure 99) is a rare species in the UK, living on moss-covered boulders on cliffs (Alexander 2008). Both ***Megalonotus praetextatus*** (4-5 mm; Figure 100) and ***M. sabulicola*** (4.5-5.5 mm; Figure 101) live in dry areas, the former where it is warm and sunny, especially in dunes and quarries, but it also lives on cliffs with mosses on partly vegetated ledges and gentle slopes. ***Megalonotus sabulicola*** is mainly coastal and is a ground-dwelling species that is most easily found among mosses. ***Megalonotus chiragra*** attaches its eggs to moss stems (Southwood & Leston 1959; Gerson 1982).

Figure 99. ***Pterotmetus staphyliniformis***, a rare species that lives on moss-covered boulders on cliffs. Photo by Gernot Kunz, with permission.

Figure 100. ***Megalonotus praetextatus***, a species that lives on cliffs with mosses on partly vegetated ledges and gentle slopes. Photo by Tristan Bantock, with permission.

Figure 101. ***Megalonotus sabulicola***, a coastal species found most easily among mosses. Photo by Tristan Bantock, with permission.

The *Recording Dorset* (2011) website notes that the tiny ***Tropistethus holosericus*** (2mm) (Figure 102) lives among the low vegetation and mosses over sand and chalk, overwintering there as adults.

Figure 102. ***Tropistethus holosericus***, a species of low vegetation and mosses. Photo by Michael Münch <www.insekten-sachsen.de> through GBIF, with permission.

Rédei *et al*. (2003) found this family "in great numbers" in moss mats in Hungary. Abundant species included ***Plinthisus pusillus*** (1.8 mm; Figure 103) and ***Rhyparochromus vulgaris*** (7-8 mm; Figure 104). Adult members of **Rhyparochromidae** preferred mosses on tree trunks, ground, and other substrata. The seed eaters in this family search mostly on the ground, where they live among the mosses. In Hungary Rédei *et al*. (2003) found that **Stygnocorini** young nymphs (a tribe in the **Rhyparochromidae**) preferred moss mats on rocks. Other members of the family **Rhyparochromidae** seemed to prefer mosses on tree trunks, ground, and other surfaces. Within these, humidity conditions typically determined the preference.

Figure 103. ***Plinthisus pusillus***, an abundant species in moss mats in Hungary. Photo from Zoologische Staatssammlung Muenchen, SNSB, through Creative Commons.

Figure 104. ***Rhyparochromus vulgaris*** on moss, an abundant species there in Hungary. Photo by Tristan Bantock, with permission.

In Dorset, England, one can find ***Scolopostethus puberulus*** (4 mm; Figure 105) among mosses that reside with taller vegetation, especially at cliff bases and in marshy places (Champion 1871; Recording Dorset 2011). Alexander (2008) likewise found this species in damp, mossy places. The adults hibernate in mosses (Champion 1871). Other moss-dwelling members of this genus include overwintering ***S. thomsoni*** (3.5-4 mm; Figure 106) and commonly ***S. affinis*** (3.5-4.5 mm; Figure 107) (Torre-Bueon 1917).

Figure 105. ***Scolopostethus puberulus***, an inhabitant of mosses at cliff bases and other mossy places. Photo by Michael Münch <www.insekten-sachsen.de> through GBIF, with permission.

Figure 106. ***Scolopostethus thomsoni***, a species that overwinters among mosses. Photo by Tom Murray, through Creative Commons.

Figure 107. ***Scolopostethus affinis***, a common species among mosses. Photo by Tristan Bantock, with permission.

Englund (2003) found several new species of **Rhyparochromidae** in the Austral Islands. These were mostly located by fogging mosses in the rata (*Metrosideros*) forest (Figure 108). Englund commented that his habitat had been largely overlooked.

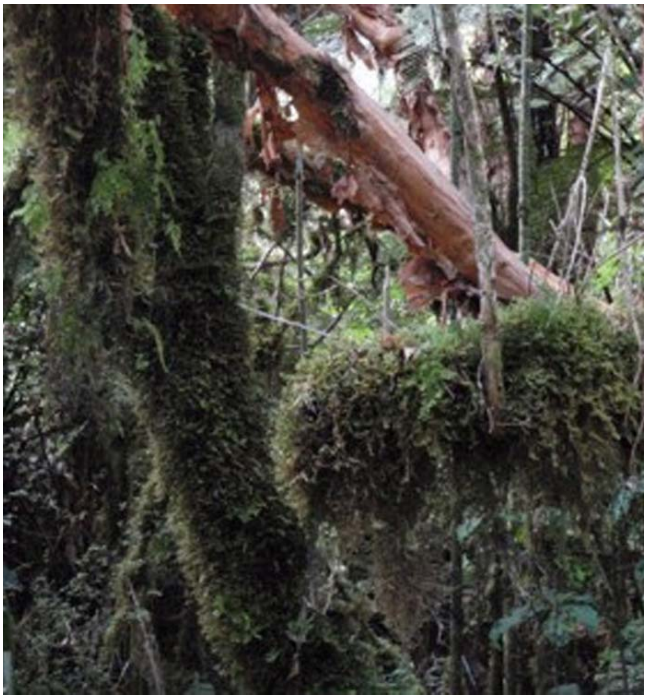

Figure 108. Rata (*Metrosideros*) forest near stream, home for Austral **Rhyparochromidae** in mosses. Photo by Marie-Claude Larivière, with permission.

Scutelleridae – Jewel Bugs

The **Scutelleridae** are rarely reported from mosses. Alexander (2008) reported the coastal species ***Odontoscelis lineola*** (4-5 mm; Figure 109), a warmth-loving species, on fairly stable sandy substrates, often with growth of mosses. This species is an active burrower. But the mosses may simply have been indicative of the habitat.

Figure 109. ***Odontoscelis lineola***, a burrowing species that often occurs with mosses in coastal regions. Photo by Tristan Bantock, with permission.

CIMICOMORPHA – BED BUGS, BAT BUGS, ASSASSIN BUGS, AND PIRATE BUGS

Anthocoridae – Minute Pirate Bugs or Flower Bugs

These are predaceous bugs that suck fluids from their prey by cutting a hole in the prey, injecting enzymes, and drinking the contents (Wikipedia 2016). In Hungary Rédei *et al*. (2003) found the **Anthocoridae** (among others) represented in great numbers in moss mats by using Berlese funnel extraction, but it is possible he was referring to those previous members of the family treated herein as **Microphysidae**.

Nevertheless, ***Anthocoris nemorum*** (3-4 mm; Figure 110) builds a **hibernaculum** (winter shelter for dormant animal) in sheltered places under bark, in leaf litter, or among mosses (Hill 1957). ***Temnostethus pusillus*** (2.5-3.1 mm; Figure 111) often occurs on branches and trunks that are overgrown with mosses (Graff 2015). Fauvel (1999) suggests that mosses and lichens on trees may help members of the **Anthocoridae** to colonize that habitat.

Figure 110. ***Anthocoris nemorum***, a species that uses mosses for its winter hibernaculum. Photo by Joe Botting, with permission.

Figure 111. ***Temnostethus pusillus***, a species that lives on branches and tree trunks overgrown with mosses. Photo by Tuomo Vainio, through Creative Commons.

Microphysidae – Minute Bladder Bugs

This is a family of tiny insects (0.5-2.4 mm long) that emit a repugnant liquid to defend themselves (Watson & Dallwitz 2003). The family **Microphysidae** (Figure 112-Figure 113) finds its food among the bryophytes (Howe 2004). They feed on booklice, aphids, and other small creatures under bark and among those lichens and mosses growing on trees.

Figure 112. ***Loricula*** sp. female, member of the family **Microphysidae**. This predominately terrestrial family feeds on organisms living among mosses. Photo by Sarefo, through Creative Commons.

Figure 113. ***Loricula*** sp. male, a predator on moss-dwelling organisms. Photo by Sarefo, through Creative Commons.

Loricula ruficeps (lichen bugs) (1.5-1.6 mm; see Figure 112-Figure 113) in Hungary is numerous in moss mats (Rédei *et al*. 2003). ***Myrmedobia exilis*** (3 mm; Figure 19) lives among mosses on tree trunks, ground, and other substrata. It is often associated with ***Polytrichum commune*** (Figure 138) or ***Rhytidiadelphus triquetrus*** (Figure 114) (EOL 2015). The good news is that it is a predator on ***Adelges*** (see **Adelgidae** in next sub-chapter on Hemiptera). Nymphs of ***Myrmedobia exilis*** live among mosses in open clearings on acid or sandy soils, but the adult females move to conifers to feed on aphids (Alexander 2008). ***Myrmedobia coleoptrata*** (0.5 mm; Figure 115) usually grows beneath the bark of various trees, especially *Picea*, but it occasionally occurs in tufts of mosses at the tree base (Alexander 2008), as well as being associated with ***Rhytidiadelphus triquetrus*** and ***Polytrichum commune*** (EOL 2015). Douglas (1861) considered it a rare species that lives with ants. Moisture is important in determining which species occur in which locations (Rédei *et al*. 2003).

Figure 114. ***Rhytidiadelphus triquetrus***, one of the homes of ***Myrmedobia exilis*** and ***M. coleoptrata***. Photo by Janice Glime.

Figure 115. ***Myrmedobia coleoptrata*** with moss, a species that occasionally lives among mosses at tree bases. Photo by Rob Ryan, with permission.

Nabidae – Damsel Bugs

In Hungary Rédei *et al*. (2003) found the **Nabidae** (among others) represented in great numbers in moss mats by using Berlese funnel extraction. The **Nabidae** were mostly 5-10 mm long. ***Nabis ferus*** (8-8.5 mm; Figure 116) lives on mossy outcrops in the relict dry acid grassland of the UK (Alexander 2008).

Figure 116. ***Nabis ferus***, a species living on mossy outcrops in dry acid grasslands in Europe. Photo by Joe Botting, with permission.

Miridae – Jumping Tree Bugs

Wheeler (2001) stated that mosses have been undocumented hosts for **Miridae** until recently. Using the Berlese funnel method, Rédei *et al*. (2003) found the **Miridae** (among others) represented in great numbers in moss mats. Humidity was important in determining locations and substrata.

Spungis (2005) found this family to have high population densities in the coastal grey dunes (Figure 25) of Latvia, dominating over grass-dwelling **Hemiptera**. These habitats suggest that these hemipterans may do best in somewhat dry habitats, but that they require the protective cover of mosses to survive there.

The predominantly North American genus ***Bothynotus*** (Figure 117) is relatively small (2.4-4.7 mm), typically brown, and densely pilose (Henry 1979), making it somewhat inconspicuous on soil or among mosses. Mosses may serve as the main habitat for the predatory ***Bothynotus pilosus*** (Figure 117) in Great Britain (Southwood & Leston 1959; Wheeler 2001). Bedwell (1930) found this species among ***Sphagnum*** and other mosses in Scotland. Later, Scudder (1995) found that it has a Nearctic distribution as well, occurring on the ground (probably among mosses) in the Yukon and British Columbia, Canada, and now it is known in China (Qi & Huo 2007). Henry (1979) considered that its association with conifers may actually be an association with the mosses that grow there, with few collectors actually finding them on the conifers. Nevertheless, the importance of bryophytes to this genus remains unknown, but ground level trapping records suggest that mosses may be an important habitat for it.

Figure 117. ***Bothynotus pilosus***, a ground dweller that might live among mosses. Photo by Petri Parkko, through Creative Commons.

In another study in Great Britain, ***Plagiognathus chrysanthemi*** (Figure 118-Figure 120) and ***Amblytylus delicatus*** (see Figure 121) occurred among mosses (Woodroffe 1959).

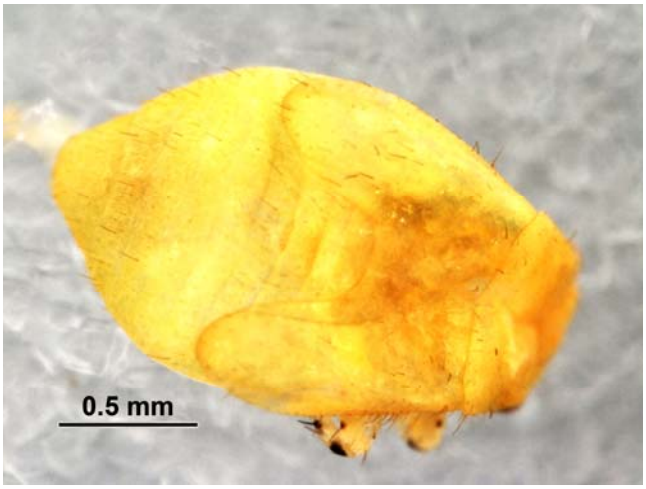

Figure 118. ***Plagiognathus chrysanthemi*** nymph, a moss dweller. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 119. ***Plagiognathus chrysanthemi*** adult, a moss dweller in Great Britain. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

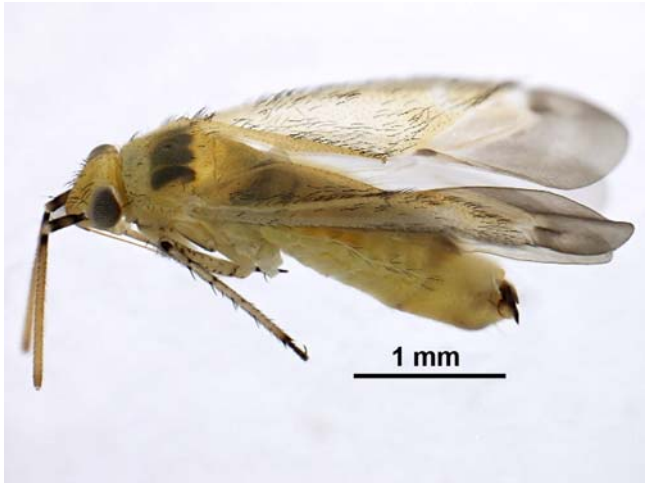

Figure 120. ***Plagiognathus chrysanthemi*** adult, a moss dweller in Great Britain. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 121. *Amblytylus nasutus* adult; ***A. delicatus*** is a moss dweller in Great Britain. Photo by Ruth Ahlburg, with permission.

In Hawaii, the endemic species ***Kamehameha lunalilo*** (Figure 122) occurs on the mosses and ferns that cover trunks and branches of a number of tree species (Zimmerman 1948). Few of the moss dwellers have long legs and antennae like this species.

Figure 122. ***Kamehameha lunalilo***, a moss dweller in Hawaii. Photo from American Museum of Natural History, through Public Domain.

Pseudoclerada (Figure 123), an endemic genus with only two species currently, is another Hawaiian **Miridae** (Asquith 1997). This genus lives in mid-elevation wet gulches and mid- to high-elevation mesic to wet forests. The species are usually solitary and live among the mosses covering tree branches.

Figure 123. ***Pseudoclerada kilaueae***, a moss dweller on tree branches. Photo from American Museum of Natural History, through Public Domain.

Tingidae – Lace Bugs

This is a family of small to mid-sized bugs (2-10 mm) with lacy wings. The **Tingidae** are primarily associated with flowering plants, but ***Acalypta*** (Figure 124-Figure 125, Figure 133-Figure 136, Figure 139, Figure 146, Figure 149) is most frequently collected from mosses (Froeschner 1976). In fact, it appears that mosses offer an alternative habitat housing a number of species.

The evolutionary history of ***Acalypta*** (Figure 124-Figure 125, Figure 133-Figure 136, Figure 139, Figure 146, Figure 149) is reflected in its occasional use of seed plants (Froeschner 1976). This seems to occur most commonly when the mosses are not in a favorable condition for lace bug development. Predictably, the genus is absent in the dry desert and plains states of the United States, but its absence along the Mississippi River is more difficult to explain. Its **brachypterous** (short) wings and recent geological history of the Mississippi flood plain may account for its continued absence there – it is dispersal limited.

Many species in ***Acalypta*** (Figure 124-Figure 125, Figure 133-Figure 136, Figure 139, Figure 146, Figure 149) live among the bryophytes (Michael Münch pers. comm. 30 October 2014). The bryophyte-dwelling members of the genus are tiny (~2 mm long) and have short (brachypterous) wings (British Bugs 2011). Some species, such as the widespread ***Acalypta parvula*** (~2 mm; Figure 124-Figure 125) (Hallett 1916), also have frequent macropterous (large or normal winged) forms. This species, the smallest of the ***Acalypta*** species, is common in the UK among short mosses, especially where soils are dry. It overwinters as an adult.

Figure 124. ***Acalypta parvula*** on moss in Germany. Photo by Michael Münch <www.insekten-sachsen.de> through GBIF, with permission.

Figure 125. ***Acalypta parvula*** amid mosses and soil. Photo by Tristan Bantock, with permission.

In the United Kingdom, five species of ***Acalypta*** feed on both capsules and vegetative parts of mosses (Howe 2004). Bailey (1951) likewise observed members of ***Acalypta*** feeding on the capsules of ***Climacium*** (Figure 126-Figure 128) after the calyptra had fallen.

Figure 126. ***Climacium dendroides*** individuals, a species whose capsules and leaves are eaten by ***Acalypta***. Photo by Michael Lüth, with permission.

Figure 127. ***Climacium dendroides***; the capsules and leaves serve as food for ***Acalypta***. Photo by Janice Glime.

Figure 128. Capsules of ***Climacium americanum*** that have shed their calyptrae and are suitable food for species of ***Acalypta***. Photo by Janice Glime.

The substrate under the moss helps to determine which ***Acalypta*** species will occur there (Rédei *et al*. 2003). ***Acalypta musci*** (2.5-2.8 mm; Figure 7) prefers mosses on stones and rocks, along with most nymphs in the ***Acalypta*** genus. In addition to living among ***Abietinella abietina*** (Figure 6), often a rock dweller, ***A. musci*** also lives on typical soil moss species such as ***Plagiomnium cuspidatum*** (Figure 129) and ***P. undulatum*** (Figure 130) (Roshko 1969; Putshkov 1974; Rédei *et al*. 2004), and frequently occurs among mosses growing at the bases of trees (Singer 1952; Jordan 1963; Wagner 1967; Rédei *et al*. 2004). In the Bükk Mountains of Hungary, Varga (1992) found ***Acalypta musci*** and ***A. gracilis*** (Figure 28) living among the protected subalpine moss species ***Plagiobryum zieri*** (Figure 131) and ***Saelania glaucescens*** (Figure 132). Nearby road traffic polluted these mosses with lead, causing a poor bryofauna, and those invertebrates living there, including the two ***Acalypta*** species, contained high concentrations of lead. ***Acalypta gracilis flaventis*** occurs in the eastern and central Palaearctic among mosses under *Ephedra* (Golub 1998). ***Acalypta susanae*** has been observed feeding on mosses (Allen *et al*. 1988). Whereas its typical habitat is among mosses, ***Acalypta*** can also occur on fungi growing on tree trunks (Rédei *et al*. 2004).

Figure 129. ***Plagiomnium cuspidatum***, home for ***Acalypta musci***. Photo by Michael Lüth, with permission.

Figure 130. ***Plagiomnium undulatum***, home for ***Acalypta musci***. Photo by Michael Lüth, with permission.

Figure 131. ***Plagiobryum zierii***, mountain home for ***Acalypta musci*** and ***A. gracilis***. Photo by Michael Lüth, with permission.

Figure 132. ***Saelania glaucescens***, mountain home for ***Acalypta musci*** and ***A. gracilis***. Photo by Michael Lüth, with permission.

Tree trunk mosses, ground, and other surfaces are preferred by ***Acalypta carinata*** (2.5 mm; Figure 5) and ***A. platycheila*** (Figure 133). ***Acalypta carinata*** occurs among ***Sphagnum*** (Figure 37), but also can be found in the drier habitat of the moss ***Abietinella abietina*** (Figure 6) in Hungary (Rédei *et al.* 2004). In southeast England, Kondorosy *et al*. (2010) found ***Acalypta platycheila*** feeding on mosses in apple orchards (Figure 134). The typical habitat of this species is humid, shady woodland.

Figure 133. ***Acalypta platycheila***, a tree-trunk moss dweller. Photo by Boris Loboda, with permission.

Figure 134. Apple orchards at Leavenheath, UK. Photo by Jonathan Billinger, through Creative Commons.

Moss mats house numerous ***Acalypta marginata*** (Figure 31) in Eurosiberia and ***A. platycheila*** (Figure 133) in Hungary (Rédei *et al*. 2003). ***Acalypta marginata*** occurs in mosses such as ***Rhytidiadelphus*** sp. (Figure 135) as well as among tracheophytes (Roshko 1969; Rédei *et al.* 2004). In these habitats it occurs throughout the year, oviposits in the mosses and litter, and overwinters as adults or older larvae (Putshkov 1974; Rédei *et al.* 2004). ***Acalypta platycheila*** and ***A. carinata*** (Figure 5) also live among mosses in the *Dryopteridi-Alnetum* (ferns and alders) (Rédei *et al.* 2004), but Alexander (2008) considered them to have a preference for mosses on rotting logs in the UK. ***Acalypta brunnea*** is most likely to occur among mosses at tree bases or on decaying stumps (Alexander 2008). These substrate preferences of both the mosses and the species of ***Acalypta*** can be explained by differences in humidity.

Figure 135. ***Rhytidiadelphus loreus***, home to ***Acalypta marginata***. Photo by David T. Holyoak, with permission.

In Scotland, Corbet (2006) reported ***Acalypta nigrina*** (Figure 136) among mosses. Moss form may play a role in the choice of habitat by some hemipterans, but for ***Acalypta nigrina*** the selected mosses have diverse forms, including the horizontal-growing (**pleurocarpous**) ***Hylocomium splendens*** (Figure 137) and upright (**acrocarpous**)

Polytrichum sp. (Figure 138) among its Hungarian habitats (Rédei *et al*. 2004). However, both moss species form deep "mats" that provide a relatively wide moisture and light range that would permit the lace bug to seek the most suitable humidity level and temperature.

Figure 136. ***Acalypta nigrina***, a moss dweller in Scotland. Photo by Johannes Skaftason, with permission.

Figure 137. ***Hylocomium splendens***, one of the diverse forms of mosses inhabited by ***Acalypta nigrina***. Photo by Michael Lüth, with permission.

Figure 138. ***Polytrichum commune***, showing upright growth form, one of the forms occupied by ***Acalypta nigrina*** (Figure 136). Photo by Bob Klips, with permission.

Acalypta saundersi (Figure 139) does seem to have a moss form preference, selecting loose-growing bryophyte forms on fallen logs (Lattin 1997). It lives only in old-growth western USA coniferous forests and its flightlessness, like that of other members of the genus, seems to correlate with its requirement for old growth (Lattin & Moldenke 1990), probably due to limited dispersal that causes a long colonization time. To find the lace bugs in this habitat, Lattin (1997) suggests gathering quantities of mosses and using a Tullgren funnel with heat and light to drive the bugs out of the moss. Sadly, this method is highly destructive if one wants to make a quantitative study and some slow-moving taxa simply die in place.

Figure 139. ***Acalypta saundersi***, a species among loose-growing mosses on logs. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

In Hungary, Rédei *et al*. (2004) found only ***A. marginata*** (Figure 31) and ***A. gracilis*** (Figure 28) among the mosses of Kiskunság National Park, both in great numbers. ***Acalypta gracilis*** occurs in typical boreal forest mosses such as ***Pleurozium schreberi*** (Figure 140) and ***Ptilium crista-castrensis*** (Figure 141), as well as in the dry habitat of exposed sites among ***Syntrichia ruralis*** (Figure 142-Figure 143) (Péricart & Golub 1996).

Figure 140. ***Pleurozium schreberi*** on sand, home in the boreal forest for ***Acalypta gracilis***. Photo by Janice Glime.

Figure 141. ***Ptilium crista-castrensis***, home for ***Acalypta gracilis*** in the boreal forest. Photo by Li Zhang, with permission.

Figure 142. ***Syntrichia ruralis*** dry, home for ***Acalypta gracilis***. Photo by Janice Glime.

Figure 143. ***Syntrichia ruralis*** wet, home for ***Acalypta gracilis***. Photo by Janice Glime.

Although most of the species of ***Acalypta*** occur in relatively moist habitats, in the Upper Columbia River Basin, western North America, ***Acalypta cooleyi*** (Figure 144) lives at the bases of sagebrush (Figure 145) and other shrubs (Lattin 1995). There it finds refuge among the mosses, which it also eats.

Figure 144. ***Acalypta cooleyi***, a species that finds refuge among mosses and eats them in sagebrush habitats. Photo by Bio Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 145. Sagebrush and moss, home for ***Acalypta cooleyi*** in western North America. Photo courtesy of Roger Rosentreter.

Acalypta barberi (1-2 mm; Figure 146) and ***A. saundersi*** (Figure 139) both feed and breed among the mosses (Drake & Lattin 1963). Interestingly, ***A. barberi*** feeds on mosses until they dry up. Then it shifts to hops (*Humulus lupulus*). Both adults and nymphs of ***A. barberi*** occurred on ***Eurhynchium oreganum*** (Figure 147) in Oregon and Washington, USA (Russell 1979). In the lab it subsisted for several weeks on this species. This widespread lace bug caused a shipment of nursery stock from Japan to be halted at quarantine in New York because of the danger of importing it among the mosses and introducing it where it can damage crops (Drake & Lattin 1963). In Arkansas, ***A. susanae*** (1.9 mm) was described as a new species from a log where it lived with mosses and slime molds (Allen *et al*. 1988). This species also eats mosses.

Figure 146. ***Acalypta barberi***, a species that feeds on and breeds among mosses. Photo by Gary Griswold, with permission.

Figure 147. ***Eurhynchium oreganum***, home and food for ***Acalypta barberi***. Photo by Matt Goff, with permission.

Bryophytes are often used as packing material for house plants and garden plants. Froeschner (1991) suggested that the new species ***Acalypta laurae*** (2 mm) was almost introduced to the United States from Mexico in the mosses used for packing the house plant *Tillandsia inoantha* (Figure 148).

Figure 148. *Tillandsia ionantha*, a species that is packed in mosses for shipment. These mosses could introduce ***Acalypta laurae*** from Mexico to the US. Photo by Cliff, through Creative Commons.

Wheeler and Reeves (2004) searched for members of ***Acalypta*** in the southeastern United States. In North Carolina they found one nymph and one adult of ***Acalypta duryi*** (Figure 149) associated with the moss ***Dicranum scoparium*** (an acrocarpous moss; Figure 150). In Tennessee they found both nymphs and one adult of this species associated with ***Hylocomiastrum umbratum*** (a pleurocarpous moss; Figure 151) and adults from ***Anomodon rostratus*** (a pleurocarpous moss; Figure 152). ***Acalypta lillianis*** (~2.2 mm; Figure 153) occurred with ***Polytrichum commune*** (acrocarpous; Figure 138) and ***P. juniperinum*** (Figure 154) in the southeastern states, including new records for Alabama and South Carolina. Bailey (1951) observed ***A. lillianis*** feeding on mosses. These tiny insects are hard to find and require destructive collecting techniques to be thorough. Both ***Acalypta lillianis*** and ***A. mera*** are bryophagous in northwestern USA.

Figure 149. ***Acalypta duryi***, a species that has been found among several moss species in the southeastern United States. Photo by Nancy Lowe, through Discover Life.

Figure 150. ***Dicranum scoparium*** (acrocarpous), one of the several moss species where ***Acalypta duryi*** lives. Photo by Janice Glime.

Figure 151. ***Hylocomiastrum umbratum*** (pleurocarpous), one of the several moss species where ***Acalypta duryi*** lives. Photo by Michael Lüth, with permission.

Figure 152. ***Anomodon rostratus***, one of the several moss species where ***Acalypta duryi*** lives. Photo by Bob Klips, with permission.

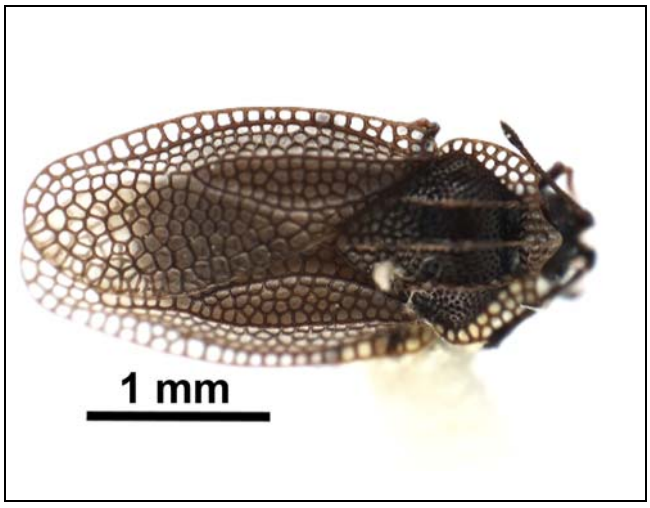

Figure 153. ***Acalypta lillianis***, a moss-eating species in northern North America. Photo by Bio Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 154. ***Polytrichum juniperinum***, one of the several moss species where ***Acalypta lillianis*** lives. Photo by Janice Glime.

But other genera of **Tingidae** do occur among mosses. Alexander (2008) described the habitat of ***Campylosteira verna*** (Figure 155) in the UK as one among mosses on hot, dry slopes, usually in calcareous grassland. ***Campylosteira*** and ***Acalypta*** (Figure 124-Figure 125, Figure 133-Figure 136, Figure 139, Figure 146, Figure 149) are **phytophagous** (plant-eating) bugs and subsist mostly on moss mats or stems of various herbaceous plants (Rédei *et al*. 2003). In their Hungarian study, Rédei *et al*. (2003) found more ***Acalypta*** species on mosses than on any other substrate. But for ***Campylosteira verna***, only 16.2% were collected on moss, whereas 61.6% were collected among leaf litter. Based on their studies in Hungary, Redei *et al.* considered members of ***Acalypta*** to be **muscicolous** (growing best among mosses). The other **Tingidae** genera found among mosses seem to have wider preferences.

Figure 155. ***Campylosteira verna***, a species that lives among mosses and elsewhere in hot, dry, calcareous grassland in the UK, often eating the mosses. Photo by Boris Loboda, with permission.

In West Virginia, USA, Torres-Miller (1995) found a different representative of this family. She was able to extract ***Leptoypha mutica*** (2.7-3.0 mm; Figure 156-Figure 157) from mosses with a Berlese funnel. ***Derephysia foliacea*** (foliaceous lace bug) (3-3.5 mm; Figure 158) hibernates as adults among mosses in the Ukraine

(Putshkov 1974; Lattin 2009). Thomas (1938) found that the uncommon species ***Catoplatus fabricii*** (3.8-4.5 mm; Figure 159) was located more easily among mosses, where it could even be abundant; Woodroffe (1959) reaffirmed that it was most frequently collected among mosses.

Figure 156. ***Leptoypha mutica*** nymph, a moss dweller in West Virginia, USA. Photo by Claude Pilon, with permission.

Figure 157. ***Leptoypha mutica*** adult, a moss dweller in West Virginia, USA. Photo by Tom Murray, through Creative Commons.

Figure 158. ***Derephysia foliacea***, a foliaceous lace bug that hibernates among mosses in winter in the Ukraine. Photo by Tristan Bantock, with permission.

Drake and Buhoff (1959) reported a moss-feeding member of the **Tingidae** from Mexico. Lis (2000b) recently described ***Paraphatnomella tamasi*** (2.35 mm) as a new genus and species from India, likewise a moss dweller.

Figure 159. ***Catoplatus fabricii*** adult, a species found mostly among mosses in Great Britain. Photo by Boris Loboda, with permission.

Cantacaderidae

This family is a segregate of the **Tingidae**. And like some **Tingidae**, some members of **Cantacaderidae** are bryophyte eaters. Moir and Brennan (2007) point out that the more primitive bug families like these two feed on fungi, lichens, mosses, and underground roots. In Australia, ***Carldrakeana tingalei*** feeds on mosses and lichens (Hacker 1928). More recently, Lis (2000a) described a new Australian species, ***C. pallida*** (2.04-2.52 mm), also a moss feeder.

Reduviidae

There's always one! A beetle, a lizard, a mantid, and now a bug! These are all animals that cultivate bryophytes on their exterior. These are not just idle passengers using free transportation. The bryophytes actually grow on these animals. But unlike the other bryophyte gardeners, nymphs of ***Reduvius personatus*** (masked bug; Figure 160) actually place soil and various objects, sometimes including bryophytes (Figure 160), on their bodies as camouflage (Harz 1952; Weirauch 2006). Members of the genus ***Reduvius*** are only 9-14 mm in length (Wygodzinsky & Usinger 1964), so the kinds of plants that can grow on them are limited to those no bigger than bryophytes – small bryophytes.

Figure 160. ***Reduvius personatus*** with liverwort and insect camouflage. Photo compliments of Kurt (Hock Ping Guek) <orionmystery.blogspot.com>.

Reduvius personatus (Figure 160) builds two layers of camouflage. The first layer is made from soil, often called a **dust coat** (Brandt & Mahsberg 2002) or **natural camouflaging** (Figure 161) (Ambrose 1999). This was originally thought to be a product of dust in the habitat, but instead it is accumulated by an active process of kicking it there with the hind legs (Weber 1930; Immel 1955), using the **tarsal fan** (Weirauch 2006). This dust layer is present in all the reduviids that use this form of camouflage.

Figure 161. ***Reduvius personatus*** nymph with only the first layer of cover, the dust coat. Note the flatness typical of the nymph in spring. Photo by Whitney Cranshaw, through Creative Commons.

The second layer is more variable among the individuals. It typically contains coarser particles, including such objects as corpses of insects the reduviid nymph has eaten (Figure 161). This habit has earned this layer the name of **corpse camouflaging** (Ambrose 1999) or **backpack** (Brandt & Mahsberg 2002). It is this layer that sometimes has bryophytes in it (Figure 161). The question remains whether these bryophytes were placed there deliberately, or if they arrived as spores or fragments and grew there. I have seen pictures with protonemata growing on the soil layer. This entire camouflage apparatus must be replaced each time the insect molts. Nevertheless, I have seen pictures of liverworts with branches fully developed. Javahery (2013) reported that third instars were dormant during the first winter and the fifth instar was dormant during the second winter, with the life cycle being completed in two years. With the right climate and timing, this could permit the observed growth from a spore.

Reduvius personatus has multiple means of holding the soil particles there. Short setae help trap the dust and hold the first layer in place (Weirauch 2006). There are short-projection trichomes and long-projection trichomes that help to hold the outer layer. At least in some species, short-projection trichomes appear to be responsible for the fastening of the camouflaging layer close to the integument, whereas long-projection trichomes may hold the outer layer of camouflaging material in place. Both short-projection trichomes and long-projection trichomes, as well as grouped trichomes, secrete a sticky substance that helps to affix such items as smooth-bodied insect carcasses (Weirauch 2006; Javahery 2013).

The nymph becomes engorged before entering winter dormancy and does not eat during the entire winter (Readio 1931). By the time warm weather returns, the body is thin and flat (Figure 161). Nevertheless, it has enough energy remaining to once again eat and be active. This dormancy behavior appears to be due to a biological clock and is not altered when the insect is maintained over winter in a warm environment with a supply of its normal food.

Other members of the **Reduviidae** in West Africa likewise adorn themselves with soil and the "backpack" materials. ***Paredocla*** and ***Acanthaspis*** (Figure 162) species add larger objects to the second layer, including prey corpses and plant parts (Brandt & Mahsberg 2002). In these species, the dust covering masks the chemical and tactile cues that are recognized by the worker ants that they often eat, making it easier for the reduviid nymphs to hunt. On the other hand, the second layer, the backpack, seems to play only a minor role in deterring the ants from approaching and being caught.

The predators on West African ***Paredocla*** and ***Acanthaspis*** (Figure 162) species include spiders, geckos, and centipedes (Brandt & Mahsberg 2002). In experiments using these three predators, the bug nymphs were more likely to survive with full camouflage than were the ones denuded of their covering. Not only did the backpack layer confuse the visually oriented predators, it also could be shed to distract the enemy while the reduviid nymph ran away, working much like the detached lizard's tail. In a different set of experiments in East Africa, Jackson and Pollard (2007) demonstrated that three species of the spider family **Salticidae** (*Hyllus* sp., *Plexippus* sp., and *Thyene* sp.) responded as predators to the naked ***Acanthaspis petax*** (Figure 162) (back packs removed) significantly more often than they responded to the masked bugs.

Figure 162. ***Acanthaspis petax*** nymph with ant carcass camouflage. This one is also eating an ant. Photo by Orionmystery, through Wikimedia Creative Commons.

DIPSOCOMORPHA

Dipsocoridae

Cryptostemma (Figure 20) in Hungary seems to prefer living among mosses on tree trunks, ground, and other surfaces (Rédei *et al*. 2003).

Ceratocombidae

Rédei *et al*. (2003) used Berlese funnels to assess the **epigeic** (ground-living) Hemiptera in Hungary. The

Ceratocombidae are not common among mosses, with only one species represented. ***Ceratocombus coleoptratus*** (1.5-2 mm; Figure 21) prefers mosses on tree trunks, ground, and other substrata as well as mosses in swampy meadows (Alexander 2008; Münch 2012). Edwards (1874) considered it to be rare in Norfolk, UK.

Ceratocombus vagans (3.8-4.5; Figure 163) is predaceous, eating such small arthropods as oribatid mites and springtails that frequently occur among bryophytes (Lattin 1997). In northern Michigan, USA, it lays its eggs at the end of the summer, inserting them into the tissues of ***Sphagnum*** (Figure 37) with its well-developed ovipositor.

Figure 163. ***Ceratocombus vagans*** nymph, a species that preys on small organisms among bryophytes and lays its eggs among ***Sphagnum***. Photo by Jim McClarin, with permission.

Schizopteridae – Jumping Soil Bugs

This is a relatively small, mostly tropical family, but it has bryophyte dwellers among its species. Members of the family are suitable for moss-dwelling by their small size (0.5-2 mm). They eat small invertebrates, so bryophytes should provide suitable hunting grounds.

In New Zealand, ***Hypselosoma acantheen*** (Figure 164) lives mostly in forests among litter and mosses (Hill 1999). In New Caledonia, one can find ***Hypselosoma rembaiensis***, another recently described species, among mosses (Hill 2013). In Australia, new species of ***Kaimon*** were described from mosses (***K. polysperes***, ***K. thorntonensis***, ***K. webbensis***) (Hill 2004).

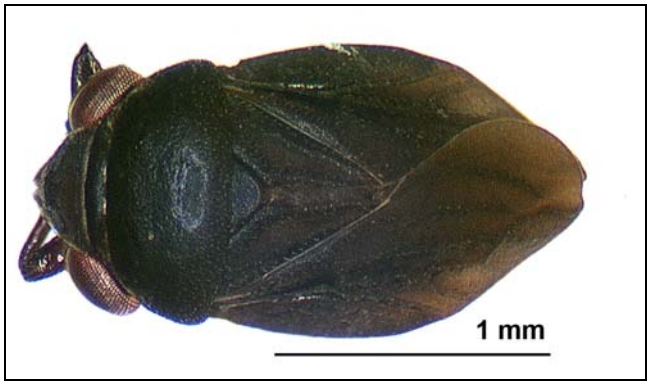

Figure 164. ***Hypselosoma acantheen***, an inhabitant of forest mosses and litter. Photo by Marie-Claude Lariviere, through Landare Research, with permission.

India likewise has newly discovered moss dwellers in this family. Rédei (2008) described ***Kikeshia stysi*** from sifted mosses in West Bengal.

GERROMORPHA – SEMIAQUATIC BUGS OR SHORE-INHABITING BUGS

Hydrometridae

A few weeks ago I received an email from Eugenia Ron with an image of a strange object attached to the capsule of one (Figure 165) and seta of another (Figure 166) ***Funaria hygrometrica*** (Figure 167). This alien was unknown to both of us and was clearly not of bryophyte origin. We considered fungi, slime molds, and insects, so Eugenia sent the images to specialists in these groups. The fungal and slime mold experts said it wasn't one of theirs. Today Eugenia sent me an answer to the mystery.

Figure 165. ***Hydrometra stagnorum*** eggs on ***Funaria hygrometrica*** capsule courtesy of Tomas Sobota and Eugenia Ron.

Figure 166. ***Hydrometra stagnorum*** eggs on ***Funaria hygrometrica*** seta. Photo courtesy of Tomas Sobota and Eugenia Ron.

Figure 167. ***Funaria hygrometrica*** with maturing capsules. Photo by Jiří Kameníček (BioLib, Obázek), with permission.

Dr. Hernández de Miguel (Universidad Complutense, Madrid, Spain) identified it as the eggs of ***Hydrometra stagnorum*** (Figure 168), (**Hemiptera**, family **Hydrometridae**). Eugenia Ron has found additional eggs on both acrocarpous and pleurocarpous mosses and on leafy liverworts. The environments are always very humid near a river. This species uses its body like a kayak, rowing over the water surface of quiet streams or ponds to find food.

Figure 168. ***Hydrometra stagnorum***, a species that often lays its eggs on bryophytes. Photo by alderash, through Creative Commons.

Mesoveliidae – Water Treaders

Although most of these species live on floating plants, some live in forest leaf litter and damp moss (DiTerlizzi 2004).

Gerridae

"Aquatic insects" are only aquatic for part of their lives, so many of the species discussed earlier as aquatic insects may also appear here as terrestrial insects. Among the amphibious species is ***Gerris lacustris*** (Figure 169). It skates on the water and does not live among mosses in the water, but when it hibernates it may seek out the protection and moisture of terrestrial mosses near its pond (Butler 1886).

Figure 169. ***Gerris lacustris*** adult in its aquatic, surface-dwelling stage. It may seek mosses on land to spend the winter. Photo by Jakub Rom, through EOL Public Domain.

NEPOMORPHA

Aphelocheiridae

I found only one record of this family associated with mosses. Alexander (2008) reported ***Aphelocheirus aestivalis*** (8.5-10.5 mm; Figure 170) among the UK fauna, living where there is overhanging vegetation or on moss-covered rocks.

Figure 170. ***Aphelocheirus aestivalis***, a species one can find on moss-covered rocks. Photo by Niels Sloth, with permission.

Summary

Several orders of insects have been lumped into the current order **Hemiptera**. The suborder **Heteroptera** contains those members that were traditionally **Hemiptera**. Among these are a number of moss dwellers. The Hemiptera have a life cycle of egg – nymph – adult.

Some members of **Hemiptera** use bryophytes as a habitat, an egg-laying site, a food source, an overwintering site, and a hunting site. Most of the faithful species are tiny but seem to lack any special resemblance to bryophytes. They benefit from the moisture and protection while often finding food there among algae, slime molds, fungi, bryophyte leaves, and invertebrate fauna.

The most common habitats of moss dwellers include forest floor and epiphytic bryophytes, sand dunes, streamside and other wet mosses, and peatlands. Some aquatic bugs leave the water to spend the winter under mosses.

The most primitive **Hemiptera** are typically moss dwellers, especially the **Tingidae** and closely related families. Members of the genus ***Acalypta*** are typically moss dwellers, eat mosses, and have many species among mosses. Many of the species have limited distribution.

The **Miridae** most likely have bryophyte dwellers that are yet to be discovered, with evidence suggested by ground traps. In some parts of the world, **Rhyparochromidae** are common among mosses. A number of families have lesser representation than those just mentioned.

Some members of the **Reduviidae** include bryophytes among the camouflage items they carry on their backs. Such "back packs" are known to discourage would-be predators.

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CHAPTER 12-7
TERRESTRIAL INSECTS: HEMIMETABOLA – HEMIPTERA (NON-HETEROPTERA) AND THYSANOPTERA

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CHAPTER 12-7
TERRESTRIAL INSECTS: HEMIMETABOLA – HEMIPTERA (NON-HETEROPTERA) AND THYSANOPTERA

Figure 1. ***Brachythecium buchananii*** with capsules, overwintering home of ***Schlechtendalia chinensis***, a gall aphid. Photo by Ivanov, with permission.

SUBORDER AUCHENORRHYNCHA

(Cicadas, Leafhoppers, Treehoppers, Planthoppers, and Spittlebugs)

Holzinger and Schlosser (2013) identified 93 species of **Auchenorrhyncha** fauna in Austrian peat bogs in the Bohemian Forest, indicating how common this group of **Hemiptera** is in bogs. Disturbance increases the number of species and densities in this group, but the number of species and densities of peatland specialists (**tyrphobionts**) decreases with disturbance.

CICADOMORPHA

Cicadellidae – Leaf Hoppers

Megophthalmus scanicus (3-4 mm; Figure 2) is among the few European **Cicadellidae** with a bryophyte association (Edwards 1874). This species overwinters among mosses. ***Sorhoanus xanthoneurus*** (3.1-3.4 mm; Figure 3), ***Sorhoanus assimilis*** (often the most frequent hemipteran; 2-2.9 mm; Figure 4), and ***Stroggylocephalus livens*** (5-6.5 mm; Figure 5) associate with ***Sphagnum*** (Figure 6) in bogs in Austria and seem to be true **tyrphobionts** (Holzinger & Schlosser 2013). Another

moderately common member of the family associated with ***Sphagnum*** is ***Macustus grisescens*** (5-6 mm; Figure 7).

Figure 2. ***Megophthalmus scanicus***, a leaf hopper that overwinters among mosses in Europe. Photo by Tristan Bantock, with permission.

Figure 3. ***Sorhoanus xanthoneurus***, a tyrphobiont associated with ***Sphagnum*** in Austria. Photo by Joe Botting, with permission.

Figure 4. ***Sorhoanus assimilis*** adult, a species commonly associated with ***Sphagnum*** in Austria. Photo by Gernot Kunz, with permission.

Figure 5. ***Stroggylocephalus livens***, a tyrphobiont associated with ***Sphagnum*** in Austria. Photo by Gernot Kunz in Gallery, with permission.

Figure 6. ***Sphagnum*** blanket bog where several tyrphobionts in the **Cicadellidae** live. Photo through Creative Commons.

Figure 7. ***Macustus grisescens***, a ***Sphagnum*** associate. Photo by Joe Botting, with permission.

Jassargus dentatus (Figure 8) occurs in association with ***Sphagnum*** in Slovenia and the Piedmont of Italy (Trivellone 2010). ***Jassargus pseudocellaris*** (Figure 9) is among the abundant hemipterans in Austrian bogs (Holzinger & Schlosser 2013).

Figure 8. ***Jassargus dentatus***, a ***Sphagnum*** associate in parts of Europe. Photo by Gernot Kunz, with permission.

Figure 9. ***Jassargus pseudocellaris***, a bog inhabitant in Austria. Photo by Tristan Bantock, with permission.

Paracephaleus curtus (Figure 10) lives on grass tufts of *Chionochloa rubra* (Figure 11) and mats of short plants, including mosses (Larivière *et al*. 2010).

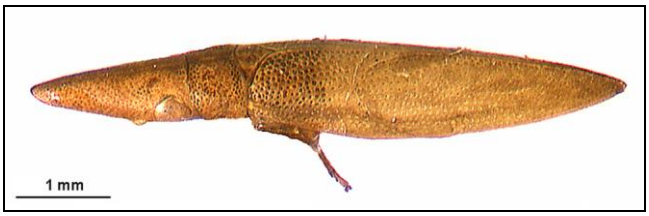

Figure 10. ***Paracephaleus curtus***, a species that sometimes lives among mosses. Photo by Marie-Claude Lariviere, with permission.

Figure 11. ***Chionochloa rubra*** in New Zealand, home for ***Paracephaleus curtus***. Photo by Ulrich Lange, through Creative Commons.

Spittlebugs are so-named for their production of a frothy medium that resembles human spit. This "spittle" provides them a place to hide from would-be predators, but it not only hides them, it has an acrid taste that deters the predators (Wikipedia 2015). It is good insulation against heat and cold, much like hiding in water, but with air spaces that make it an even better insulator. And it provides moisture, protecting the soft-bodied nymphs from dehydration. The nymphs are plant suckers, and it appears that bryophytes, at least ***Polytrichum juniperinum***, are on the menu (Figure 12-Figure 13), as well as many tracheophyte species.

Figure 12. Spittlebug on ***Polytrichum juniperinum***. Photo courtesy of Timea Deakova, with permission.

Figure 13. Spittlebug nymph. Photo by Diliff, through Creative Commons.

FULGOROMORPHA - PLANTHOPPERS

Delphacidae – Delphacid Planthoppers

The **Delphacidae** is a family of herbivores with a worldwide distribution. A sweep net revealed ***Euconomelus lepidus*** (1.8-3 mm; Figure 14) from mosses beside a lake in Scotland (Bratton 2012). This is one of the few species that seems to be associated with bryophytes.

Figure 14. ***Euconomelus lepidus*** lives in association with mosses near a lake in Scotland. Photo by Tristan Bantock, with permission.

Javesella opaca (see Figure 15, Figure 16) is a planthopper that feeds on mosses in the eastern United States (Wheeler 2003). Nymphs live on the upright leafy gametophytes of ***Polytrichum commune*** (Figure 17) and ***Polytrichastrum alpinum*** (Figure 18) where these mosses grow over flatrock areas. In South Carolina, USA, the late instars overwinter among ***Polytrichum commune***, with adults developing by mid- to late March. Most of the adults are **brachypterous** (having short wings). It is interesting that these insects feed on the thick stems of the mosses, whereas in our experiments with pillbugs the stems were avoided in ***Polytrichum*** and only leaves were eaten. In Russia, ***Javesella discolor*** (Figure 19) lives in moss bogs, moist forests, and swamp meadows (Emeljanov 1988), where mosses play an important role in creating a suitable microclimate.

Figure 15. ***Javesella pellucida***; ***J. opaca*** feeds on mosses in the eastern US. Photo by Tom Murray, through Creative Commons.

Figure 16. ***Javesella opaca***, a moss feeder. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 17. ***Polytrichum commune***, home for ***Javesella opaca*** in the eastern United States. Photo by Christopher Tracey, through Creative Commons.

Figure 18. ***Polytrichastrum alpinum***, home and food for ***Javesella opaca*** in Europe. This species also overwinters here. Photo by Michael Lüth, with permission.

Figure 19. ***Javesella discolor***, a species that lives in mossy bogs and other mossy habitats. Photo by Joe Botting, with permission.

Muellerianella extrusa (2.1-3.1 mm; Figure 20) occurs in association with ***Sphagnum*** in Austria (Holzinger & Schlosser 2013).

Figure 20. ***Muellerianella extrusa***, a ***Sphagnum*** associate in Austria. Photo by Gernot Kunz, with permission.

Richardson *et al*. (2002) found that changes in subordinate plant species had a greater impact on the herbivorous insect community than on those living on the dominant dwarf shrubs. Moss-feeding bugs were reduced to as little as 65% of the controls when their plots were fertilized, whereas grass-feeding insect species showed a 400% increase. This benefitted the **Delphacidae**, a **graminivorous** (grass-eating) family, suggesting that for most of the species the mosses were not important.

Derbidae – Planthoppers

Wilson and Wheeler (2015) attempted to learn more about the life history of this little known family. They were able to rear ***Cedusa hedusa*** (Figure 21) successfully from fifth instars to adults. These were collected from populations of the moss ***Polytrichum commune*** (Figure 17) in Alabama, USA. Nevertheless, food of the nymphs remains unknown, as well as oviposition sites and food preferences of the adults.

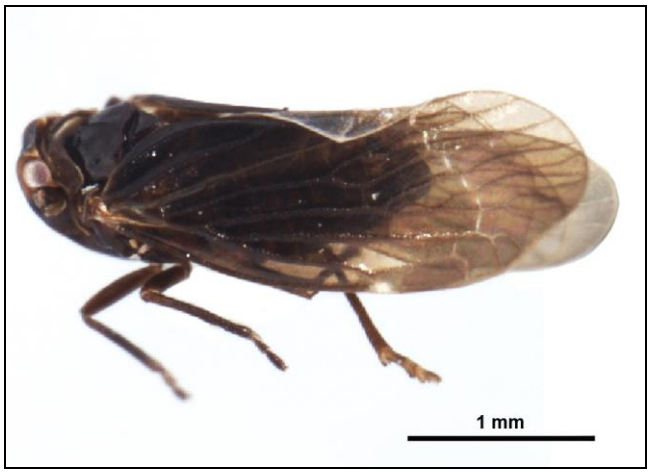

Figure 21. ***Cedusa hedusa***, a species that lives on the moss ***Polytrichum commune*** in Alabama, USA. Photo from CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Issidae – Planthoppers

Issus coleoptratus (3-4 mm; Figure 22-Figure 23) seems to spend most of its nymphal time among mosses (undocumented comment from Flickr). ***Issus muscaeformis*** (1.9-3.6 mm; Figure 24) has a name that suggests it has some relationship with mosses, but I can find no reference that places it in such a habitat. Consulted references include those that describe mosses as habitats for other insects.

Figure 22. ***Issus coleoptratus*** nymphal instar, a stage that lives among mosses. Photo through Creative Commons.

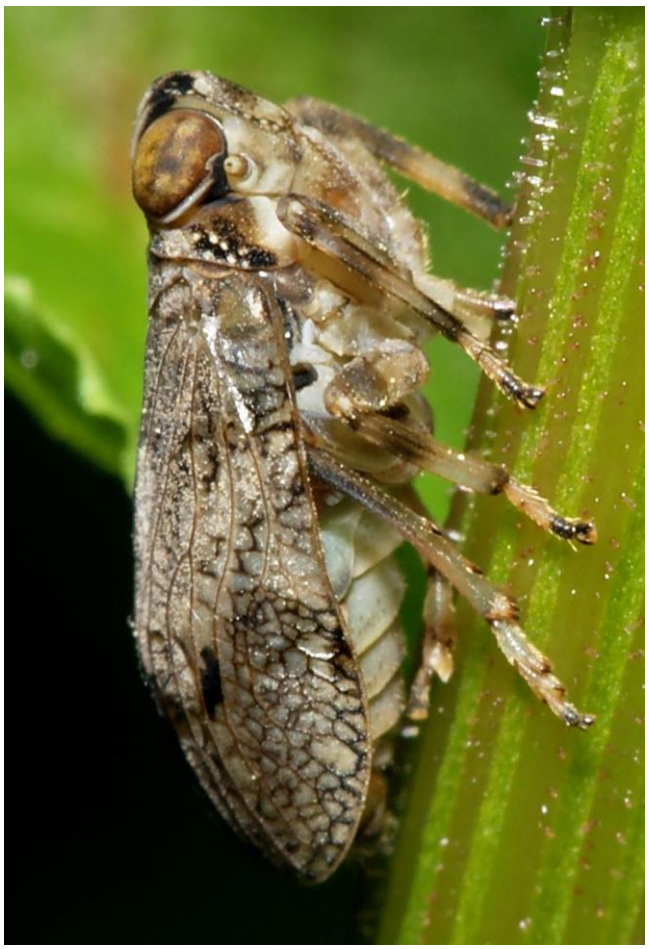

Figure 23. ***Issus coleoptratus*** adult, a moss-dwelling species. Photo by Sarefo, through Creative Commons.

Figure 24. ***Issus muscaeformis*** adult, a likely moss dweller. Photo by Roger S. Key, with permission.

The genus ***Issus*** (Figure 22-Figure 25) has an unusual means of locomotion (Burrows & Sutton 2013). It uses gears that intermesh, rotating like mechanical gears (Figure 25). These are located on the hind legs at the trochanter and rub together to propel the insect when it jumps. They insure that both legs have the same velocities and are synchronized. But as strange and unique as these are, they exist only in the nymphs, disappearing at the last molt. The adults must move like other insects.

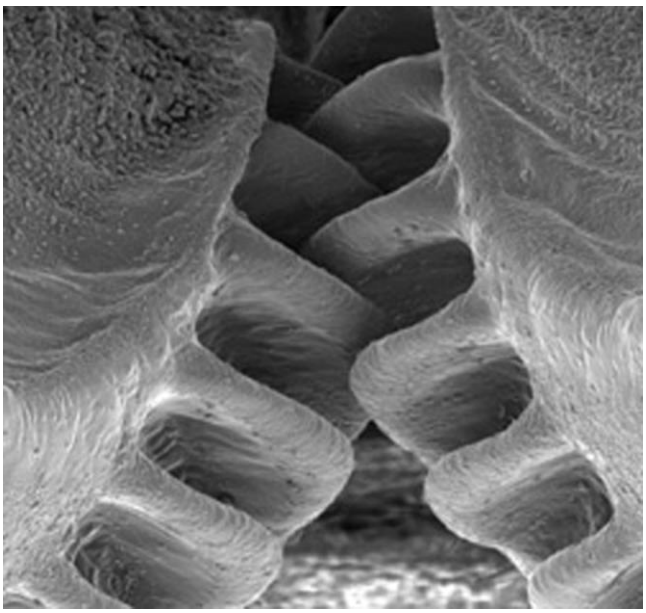

Figure 25. ***Issus coleoptratus*** interactive gears in the hind legs. Photo by Malcolm Burrows & Gregory Sutton, through Creative Commons.

SUBORDER STERNORRHYNCHA

(aphids, whiteflies, and scale insects)

Anyone who has kept a greenhouse will probably cringe at the mention of these insects. All are pests in that environment. And you might just introduce some of them with mosses you bring in.

Eriococcidae – Scale Insects

One of these greenhouse horrors is the scale insect (Figure 26). These seem like unlikely moss inhabitants, but Henderson (2007) considered mosses and ferns to be the most likely candidates as host plants for ***Affeldococcus kathrinae*** (0.4-0.65 mm). This very tiny species lacks a specific host tree, but lives in the high canopy epiphyte mat of the rata (*Metrosideros* spp.; Figure 27) in New Zealand. This led Henderson to conclude the epiphytic bryophytes and/or ferns might be the hosts.

Figure 26. ***Eriococcus coriaceus*** on *Eucalyptus* in Australia, representing a family with one known species of moss dwellers (***Affeldococcus kathrinae***). Photo by Arthur Chapman, through Creative Commons.

Figure 27. Rata forest (*Metrosideros umbellata*), Enderby Island, New Zealand. These forests have mostly mosses and ferns as ground cover and provide a suitable home for ***Affeldococcus kathrinae***. Photo by John Barkla, with permission.

Aphididae (including Pemphigidae) - Aphids

Although incidences of **bryophagy** (eating bryophytes) are not well known among aphids, there are actually species that specialize on bryophytes, and others that eat them for special purposes (Hille Ris Lambers 1954; Müller 1973; Smith & Knowlton 1975; Stekol'Shchikov & Shaposhnikov 1994). Moss aphids pierce the cells, then suck the contents from the cells (Thomas & Lombard 1991; Longton 1992). Aphids are common enough among mosses that there is a whole group known as the moss aphids (Müller 1973; Smith & Knowlton 1975).

Aphids are not common moss inhabitants, with the exception of the gall aphids, but perhaps we aren't looking in the right places. Recently Robin Stevenson found ***Sphagnum*** forming sleeves around young saplings of *Pinus sylvestris* and *Betula* spp. (Stevenson & Masson 2015). He pursued these strange sleeves, determining that they were formed by ants (***Lasius platythorax***). But why? Upon tearing them apart, he found lots of aphids (***Symydobius oblongus***; Figure 28-Figure 29) were running about. Ants are well known for tending aphids, using the "honey dew" excreted from two tubercles at the ends of the alimentary (digestive) canals (Figure 28). See Chapter 12-10 on Hymenoptera for more details on this relationship.

Figure 28. ***Symydobius oblongus*** nymph, a species that lives in ***Sphagnum*** sleeves created by ants on young birch and pine saplings in bogs. Note the two tiny white tubercles near the end of the abdomen where ants are able to harvest honey dew. Photo from <www.influentialpoints.com>, through Creative Commons.

Figure 29. ***Symydobius oblongus*** adult, a species that lives in ***Sphagnum*** sleeves created by ants on young birch and pine saplings in bogs. Photo from <www.aphotofauna.com>, with permission.

Gall Aphids

Some moss aphids form galls (Figure 85-Figure 86), but not on the mosses. Instead, the mosses act as alternate hosts (Chiuh 1976). One of the few remaining agricultural uses of mosses is the culturing of mosses as the winter host for Chinese gall aphids (Li *et al*. 1988, 1999; Liu & Li 1992, 1993; Liu *et al*. 1994). This has led to studies on the effects of temperature and water content on the vitality of these host mosses in winter (Liu *et al*. 1994) and on the physioecology of these mosses (Liu 2000).

Liu and coworkers (Liu 2000; Liu *et al*. 2000) studied the hosts ***Plagiomnium acutum*** (Figure 30), ***P. maximoviczii*** (Figure 41), ***Thuidium cymbifolium*** (Figure 31), and ***Chrysocladium retrorsum*** (Figure 32), hoping to cultivate them at optimal conditions. These mosses are able to maintain a net photosynthetic gain at temperatures as low as -15 to -10°C. The optimum temperatures for ***T. cymbifolium*** and ***C. retrorsum*** were in the range of 25-36°C in spring, dropping to 20-30°C in winter.

Figure 30. ***Plagiomnium acutum***, overwintering host for gall aphids in China. Photo through Creative Commons.

Figure 31. ***Thuidium cymbifolium*** with capsules, a host plant for gall aphids, including ***Schlechtendalia elongallis***. Photo by Li Zhang, with permission.

Figure 32. ***Chrysocladium retrorsum***, a host plant for gall aphids. Photo by Yao Kuiyu, through Creative Commons.

Li *et al*. (1999) compared photosynthetic capacity in the two gall aphid hosts ***Plagiomnium acutum*** and ***Herpetineuron toccoae***. ***Plagiomnium acutum*** had lower photosynthesis on sunny days and higher on cloudy and rainy days compared to that of ***H. toccoae***. Consistent with its preferred bright days, ***H. toccoae*** also had lower transpiration rates than did ***P. acutum***, permitting the former to tolerate high temperatures and dry environments.

There are at least 24 known species of moss hosts in China, and their cultivation is critical to the production of the gall nuts (Li 1990). In China, the gall aphid species are generally highly specialized on only a few winter moss hosts (Chiuh 1976; Li *et al*. 1988). Among those used are ***Mnium lycopodioides*** (Figure 33), ***M. thomsonii*** (Figure 34), ***Orthomnion dilatatum***, ***Plagiomnium rhynchophorum***, ***Brachythecium albicans*** (Figure 35), ***B. buchananii*** (Figure 1), ***B. velutinum*** (Figure 36), ***B. rutabulum*** (Figure 37), ***Homalothecium leucodonticaule*** (Figure 38), ***Hypnum callichroum*** (Figure 39), and ***Erythrodontium julaceum*** (Figure 40). The first four of these are winter hosts of the Chinese gall aphid ***Schlechtendalia chinensis*** (**Aphididae**; Figure 42). The virus-carrying **Melaphidini** (**Pemphigidae**, a segregate from **Aphididae**) species shift their habitat between ***Rhus*** (sumac; Figure 85) and bryophytes (Eastop 1977).

Figure 33. ***Mnium lycopodioides***, a winter host of the Chinese gall aphid ***Schlechtendalia chinensis***. Photo by Michael Lüth, with permission.

Figure 34. ***Mnium thomsonii***, a winter host of the Chinese gall aphid ***Schlechtendalia chinensis*** (Figure 42). Photo by Hermann Schachner, through Creative Commons.

Figure 35. ***Brachythecium albicans***, an alternate host for gall aphids in China. Photo by Janice Glime.

Figure 36. ***Brachythecium velutinum*** with capsules, an alternate host for gall aphids in China. Photo by Michael Lüth, with permission.

Figure 37. ***Brachythecium rutabulum*** with capsules, an alternate host for gall aphids in China. Photo by Malcolm Storey from DiscoverLife, through Creative Commons.

Figure 38. ***Homalothecium leucodonticaule*** (= ***Homalothecium laevisetum***), a species used by Chinese gall aphids. Photo through Creative Commons.

Figure 39. ***Hypnum callichroum***, an alternate host for gall aphids in China. Photo by Michael Lüth, with permission.

Figure 40. ***Erythrodontium julaceum***, an alternate host for gall aphids in China. Photo by Michael Lüth, with permission.

Plagiomnium maximoviczii (Figure 41) is also a common species that serves as the winter host for the Chinese gall aphids (Horikawa 1947; Tang 1976; Lao *et al*. 1984; Li *et al*. 1988). The aphids ***Schlechtendalia chinensis*** (**Pemphigidae**; Figure 42), ***Nurudea shiraii***, and ***Nurudea yanoniella*** (**Pemphigidae**) are important commercially in China because of the galls they make on the sumac (***Rhus***) tree (Tang 1976; Min & Longton 1993). These galls are highly prized for medicines (expectorant; treatment of cankers and wounds) and the chemical industry (black dyes for dyers and tanners; ink) (Fagan 1918). The aphids migrate to the mosses for the winter, using them for both shelter and food (Chiuh 1976; Tang 1976; Lai *et al.* 1990).

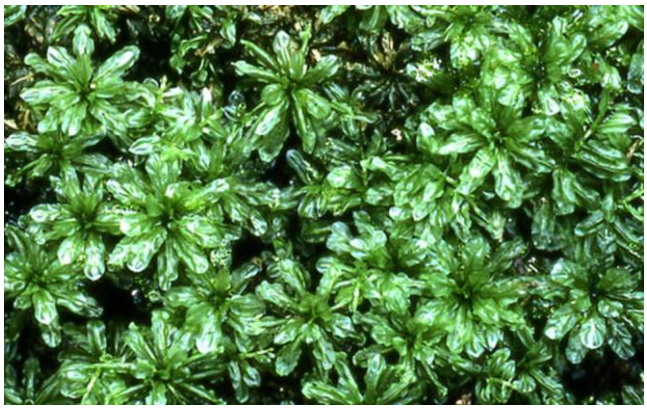

Figure 41. ***Plagiomnium maximoviczii***, a winter host for Chinese gall aphids. Photo from Hiroshima University Digital Museum of Natural History, with permission.

Schlechtendalia

Schlechtendalia chinensis (Figure 42) makes its galls on *Rhus chinensis.* It uses ***Plagiomnium maximoviczii*** (Figure 41), ***P. cuspidatum*** (Figure 43), and ***P. vesicatum*** (Figure 44) for its winter shelter (Chiuh 1976). When the galls burst open at maturity, the aphids emerge and migrate to their moss hosts. There they produce 20-30 nymphs that will develop into spring migrants. The newly emerged nymphs move to the moss stalks near the ground and cover their bodies with a waxy secretion in preparation for winter. In early spring they develop into the winged females that give live birth. These females are spring migrants that move to the ***Rhus chinensis*** (sumac; Figure 45) where they will feed. Their offspring will be wingless. These become wingless adults and will be ready to mate in 4-8 days.

Figure 42. ***Schlechtendalia chinensis*** gall, a species that uses mosses as overwintering hosts. Photo from SanHerb, with permission.

Figure 43. ***Plagiomnium cuspidatum***, one of the winter hosts of the Chinese gall aphid ***Schlechtendalia chinensis*** (Figure 42). Photo by Michael Lüth, with permission.

Figure 44. ***Plagiomnium vesicatum*** (formerly included in ***Mnium***), a winter host for the Chinese gallnut ***Schlechtendalia chinensis*** (Figure 42). Photo from the Digital Museum, University of Hiroshima, with permission.

Figure 45. ***Rhus chinensis***, host of the Chinese gall aphid ***Schlechtendalia chinensis*** (Figure 42). Photo from Kinmen National Park Digital Archives, through Creative Commons.

The females lay their eggs on the mosses (Lai *et al*. 1990). Because the host tree, the sumac, grows on dry slopes and the mosses tend to grow on more humid stream banks, there are few places where the mosses are sufficiently close to the trees for the relationship to work for the aphids (Zhang, pers. comm.). Hence, it is desirable to create more suitable habitats, possibly by cultivating mosses, placing them near the sumac at the appropriate season, then culturing the mosses through the winter in a favorable environment.

In addition to the ***Plagiomnium*** species, ***Schlechtendalia*** (Figure 42) also uses ***Homomallium*** (Figure 46), ***Palamocladium*** (Figure 47) (Liu & Li 1994), and ***Herpetineuron toccoae*** (Figure 48) (Li *et al*. 1999).

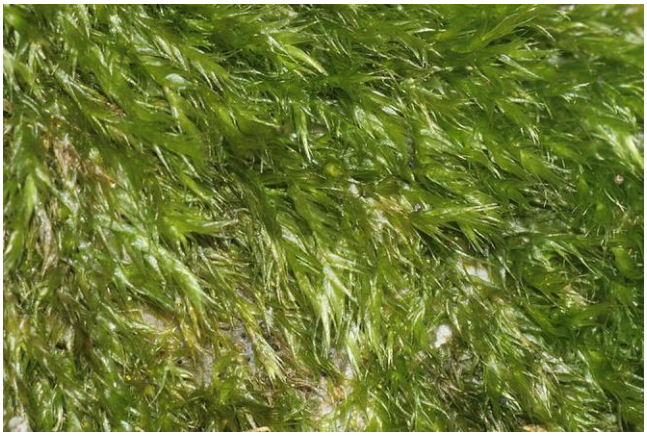

Figure 46. ***Homomallium incurvatum***, member of a genus that provides a winter host for ***Schlechtendalia chinensis*** (Figure 42) in China. Photo by Hermann Schachner, through Creative Commons.

Kaburagia

Another gall-making aphid, ***Kaburagia rhusicola*** (1.3-1.5 mm), likewise uses mosses for winter hosts in China (Lai & Zhang 1994). These mosses include ***Brachythecium*** spp. (Figure 35-Figure 37), ***Entodon*** (Figure 49), and ***Oxyrrhynchus*** (=***Eurhynchium***?; Figure 94). In northern China, this aphid species moves from galls in late summer, and hibernates in an immature stage on the secondary host, the moss ***Eurohypnum leptothallum*** (Figure 50) (Chinese Academy of Forestry Science Institute of Resource Insects 2014; The Aphids 2015). This institution has patented the procedure for growing the aphids on ***E. leptothallum***. ***Kaburagia ensigallis*** (perhaps the same species as ***K. rhusicola***) uses ***Brachythecium buchananii*** (Figure 1) as a host plant (Lou & Chen 2000).

Figure 47. ***Palamocladium leskeoides***, member of a genus that provides a winter host for ***Schlechtendalia chinensis*** (Figure 42) in China. Photo courtesy of Claudio Delgadillo Moya.

Figure 48. ***Herpetineuron toccoae***, a species that provides a winter host for ***Schlechtendalia chinensis*** (Figure 42) in China. Photo by Michael Lüth, with permission.

Figure 49. ***Entodon*** cf ***myurus*** with capsules, member of a genus that provides a winter host for ***Kaburagia rhusicola*** in China. Photo by Michael Lüth, with permission.

Figure 50. ***Eurohypnum leptothallum***, where ***Kaburagia rhusicola*** migrates in late summer in China and hibernates for the winter. Photo from <prologue.blog.naver.com>, through Creative Commons.

Muscaphis

But China does not have a corner on the gall aphid/moss association. Among the moss inhabitants is ***Muscaphis escherichi*** (1.7-2.7 mm; Figure 51), a bryophagous species on *Sorbus*, but when it is seasonally unavailable as a suitable habitat, they live primarily on the moss ***Rhytidiadelphus loreus*** (Figure 52) in the state of Washington, USA (Russell 1979). In Europe ***M. escherichi*** is common on many species of mosses, but researchers have had poor success in rearing it on any species but ***Plagiothecium laetum*** (Figure 53) and males have never been found on mosses (Stekolshchikov & Shaposhnikov 1993). ***Muscaphis cuspidata*** (0.9-1.3 mm) lives on ***Calliergonella cuspidata*** (Figure 54) and ***Drepanocladus aduncus*** (Figure 55), either close to the water or just below the water level. ***Muscaphis mexicana*** (1.7-2.1 mm) migrates to unidentified mosses, where wingless yellow or yellowish green aphids (0.6-0.8 mm) are produced (The Aphids 2015). The species ***Muscaphis musci*** (1.1-1.5 mm; Figure 56) occurs on many species of mosses, including those in ***Amblystegium*** (Figure 57), ***Atrichum*** (Figure 58), ***Barbula*** (s.l.; Figure 59), ***Brachythecium*** (Figure 37), ***Bryum*** (Figure 60), ***Calliergonella***, ***Eurhynchium*** (Figure 94), ***Hylocomium*** (Figure 61), ***Mnium*** (probably ***Plagiomnium***) (Figure 33-Figure 44), ***Polytrichum*** (s.l.) (Figure 17), ***Pseudoscleropodium*** (Figure 62), and ***Tortula*** (s.l.; Figure 63). In Denmark, Wilkaniec & Borowiak-Sobkowiak (2009) report ***Muscaphis musci*** from ***Calliergonella cuspidata***, ***Brachythecium rutabulum*** (Figure 37), ***Atrichum undulatum*** (Figure 58), and ***Plagiomnium undulatum*** (Figure 64). ***Muscaphis utahensis*** (0.7-1.1 mm; Figure 65) occurs on mosses in the western USA and is thus far known only from the moss ***Cratoneuron filicinum*** (Figure 66) (Stekolshchikov & Shaposhnikov 1993). In most of the ***Muscaphis*** species, the bryophytes serve as alternate hosts and oviposition sites.

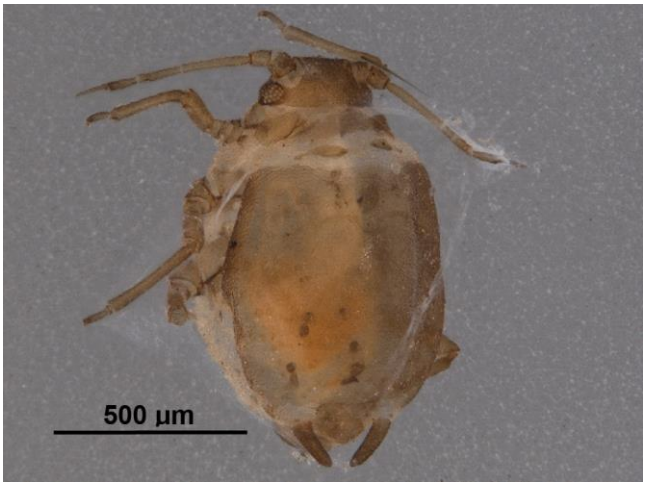

Figure 51. ***Muscaphis escherichi***, a bryophagous species that lives on ***Rhytidiadelphus loreus*** in the western USA. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 52. ***Rhytidiadelphus loreus***, the primary home for ***Muscaphis escherichi*** (Figure 51) in Washington, USA. Photo by Michael Lüth, with permission.

Figure 53. ***Plagiothecium laetum***, the only species that seems to result in successful rearing of ***Muscaphis escherichi***. Photo by Kristian Peters, with permission.

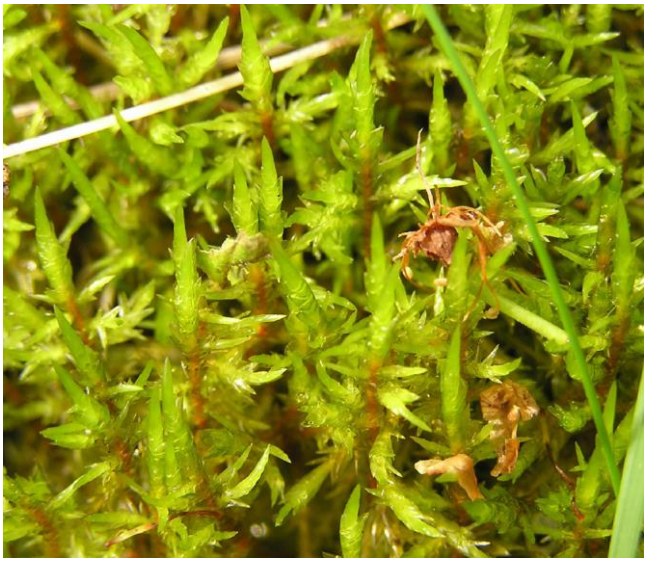

Figure 54. ***Calliergonella cuspidata***, home to ***Muscaphis cuspidata***. Photo by Michael Becker, through Creative Commons.

Figure 55. ***Drepanocladus aduncus***, home to ***Muscaphis cuspidata***. Photo by Michael Lüth, with permission.

Figure 56. ***Muscaphis musci***, an aphid that occurs on many bryophyte species. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 57. ***Amblystegium serpens***, a genus that is home for ***Muscaphis musci*** (Figure 56). Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

Figure 58. ***Atrichum undulatum***, home to ***Muscaphis musci*** (Figure 56). Photo by Janice Glime.

Figure 59. ***Barbula convoluta***, home for ***Muscaphis musci*** (Figure 56). Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 60. ***Bryum capillare***, home for ***Muscaphis musci*** (Figure 56). Photo by James K. Lindsey, with permission.

Figure 61. ***Hylocomium splendens*** where you might find ***Muscaphis musci*** (Figure 56). Photo by Janice Glime.

Figure 62. ***Pseudoscleropodium purum***, a species inhabited by ***Muscaphis musci*** (Figure 56). Photo by Michael Lüth, with permission.

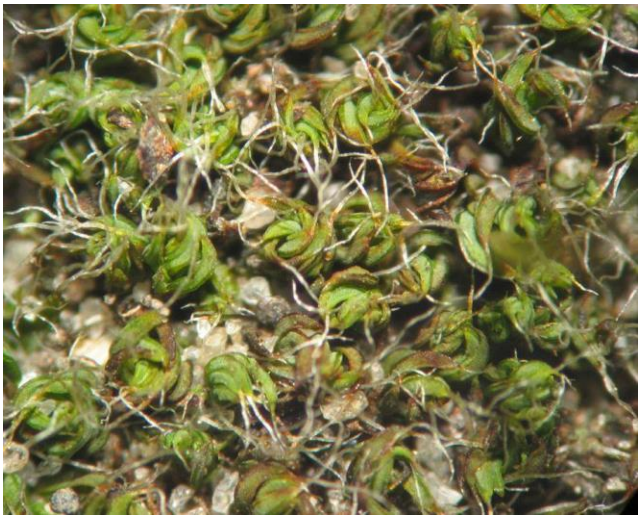

Figure 63. ***Tortula muralis*** dry. This species is in a genus that provides a home for ***Muscaphis musci*** (Figure 56). Photo by Kristian Peters, through Creative Commons.

Figure 64. ***Plagiomnium undulatum***, a home for ***Muscaphis musci*** (Figure 56). Photo by Michael Lüth, with permission.

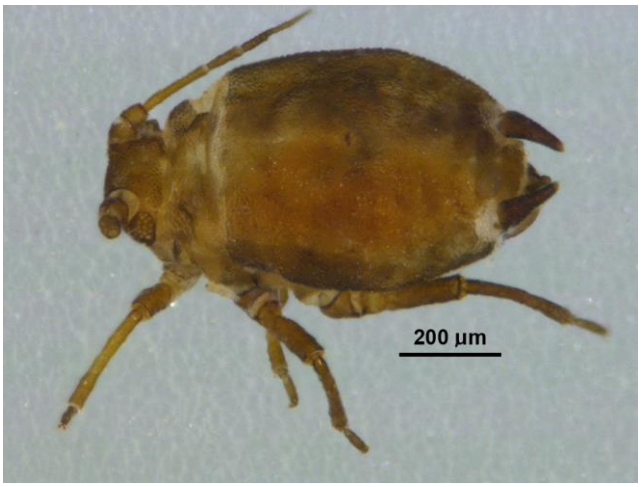

Figure 65. ***Muscaphis utahensis***, a species lives on the moss ***Cratoneuron filicinum***. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 66. ***Cratoneuron filicinum***, home for ***Muscaphis utahensis*** (Figure 65). Photo by David Holyoak, with permission.

Myzodium

Another moss-dwelling aphid is the genus ***Myzodium*** (0.9-1.9 mm; Figure 67), one of the few genera of aphids that builds nests among ***Sphagnum*** (Figure 6) (Gerson 1969), and at least some of them eat mosses.

Aphids tap into the phloem of vascular plants to obtain nutrients. Clever researchers have used this behavior as a means to determine what substances are travelling in the phloem. Thomas and Lombard (1991; Thomas 1993) have used these tiny moss-dwelling aphids on ***Polytrichum commune*** (Figure 17) to obtain similar information on this moss. Their impact is sufficient to reduce the flow of labelled materials to other individuals that share rhizomes with the infested individuals. ***Myzodium*** sp. (~1.5-1.9 mm; Figure 67-Figure 68) not only diverts the nutrients from the **leptoids** (moss food-conducting cells) but also alters the normal source-to-sink flow within the moss turf.

Russell (pers. comm.) found many nymphs of ***Myzodium modestum*** (1.2-1.9 mm; Figure 67-Figure 68), a **bryophagous** species (eats bryophytes) (Müller 1973), overwintering on ***Polytrichum*** sp. (Figure 17) in early September at Waldo Lake, Oregon, USA. This species lives on other mosses as well, including ***Dicranella crispa*** (Figure 69), ***Dicranum*** sp. (Figure 113), ***Oligotrichum aligerum*** (Figure 70), ***Pleurozium schreberi*** (Figure 114), ***Pogonatum dentatum*** (Figure 71), ***Polytrichastrum alpinum*** (Figure 72, ***Polytrichastrum formosum*** (Figure 73), ***Polytrichastrum longisetum*** (Figure 74), ***Polytrichum commune*** (Figure 17), ***Polytrichum juniperinum*** (Figure 75), ***Racomitrium*** sp. (Figure 76), ***Roellia roellii*** (Figure 77), ***Sanionia uncinata*** (Figure 78), and ***Sphagnum rubellum*** (Figure 79) (Pike *et al*. 2010). This list attests to a wide variety of habitats including bogs, alpine, forest, boreal, and others as well as a wide range of bryophyte families from primitive to advanced, and it includes both acrocarpous and pleurocarpous mosses. ***Polytrichum juniperinum*** seems to have the most collection records. Unlike many species on tracheophytes, ***Myzodium modestum*** is not attended by ants.

Figure 67. ***Myzodium*** sp. nymphs, often born among ***Sphagnum*** (Figure 6). Photo by Andrew Jensen through Creative Commons.

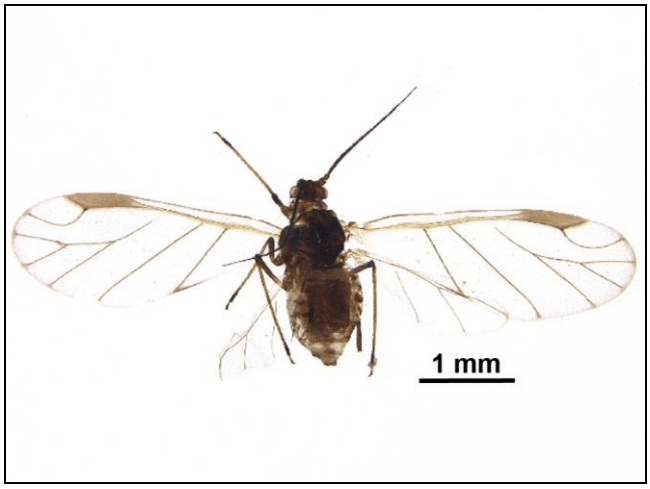

Figure 68. ***Myzodium modestum*** adult; nymphs spend the winter among mosses and feed on them by injecting a stylet into the leptoids. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 69. ***Dicranella crispa***, home for ***Myzodium modestum*** (Figure 68). Photo by Ivanov, with permission.

Figure 70. ***Oligotrichum aligerum***, a species inhabited by ***Myzodium modestum*** (Figure 68). Photo by Martin Hutten, with permission.

Figure 71. ***Pogonatum dentatum***, a northern moss species that hosts ***Myzodium modestum*** (Figure 68). Photo by Michael Lüth, with permission.

Figure 72. ***Polytrichastrum alpinum***, a species inhabited by ***Myzodium modestum*** (Figure 68). Photo by Andrew Hodgson, with permission.

Figure 73. ***Polytrichastrum formosum***, a species inhabited by ***Myzodium modestum*** (Figure 68). Photo by David T. Holyoak, with permission.

Figure 74. ***Polytrichastrum longisetum***, a species inhabited by ***Myzodium modestum*** (Figure 68). Photo by Hermann Schachner, through Creative Commons.

Figure 75. ***Polytrichum juniperinum*** male with new growth from antheridial splash cups. This species is home to ***Myzodium modestum*** (Figure 68). Photo by Janice Glime.

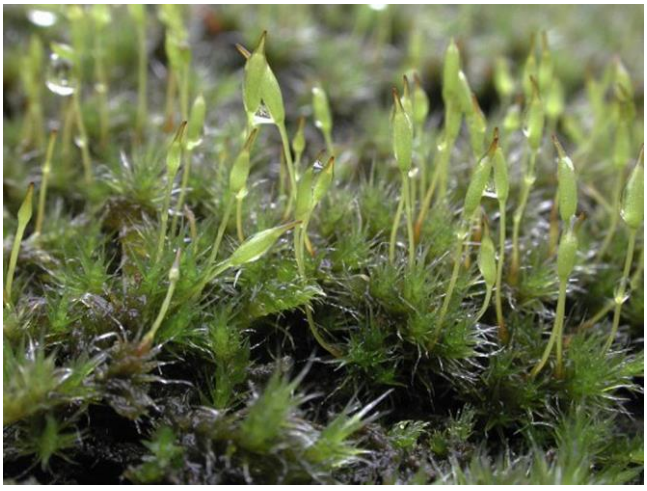

Figure 76. ***Racomitrium heterostichum***, home to ***Myzodium modestum*** (Figure 68). Photo by Jan-Peter Frahm, with permission.

Figure 77. ***Roellia roellii***, home to ***Myzodium modestum*** (Figure 68). Photo by Martin Hutten, with permission.

Figure 78. ***Sanionia uncinata***, home to ***Myzodium modestum*** (Figure 68). Photo by Janice Glime.

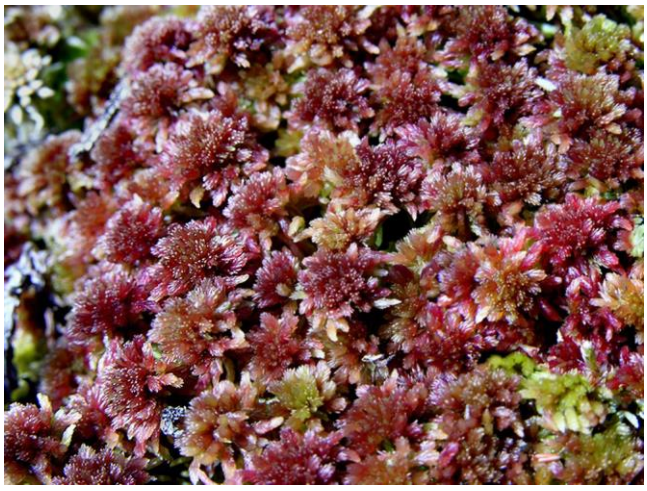

Figure 79. ***Sphagnum rubellum***, home to ***Myzodium modestum*** (Figure 68). Photo by J. C. Schou <http://www.biopix.com/>, with permission.

Myzodium mimulicola (0.9-1.9 mm; Figure 80) occurs on ***Aulacomnium palustre*** (Figure 81), ***Brachythecium frigidum*** (Figure 82), ***Straminergon stramineum*** (Figure 83), ***Philonotis fontana*** (Figure 84), and ***Sanionia uncinata*** (Figure 78), another mixture of acrocarpous and pleurocarpous mosses, in western North America (Pike *et al*. 2010).

Figure 80. ***Myzodium mimulicola*** adult, a species that occurs on several moss species in western North America. Photo by Andrew Jensen, through Creative Commons.

Figure 81. ***Aulacomnium palustre*** with gemmae, a species that is home to ***Myzodium mimulicola*** (Figure 80). Photo by Bob Klips, with permission.

Figure 82. ***Brachythecium frigidum***, a species that is home to ***Myzodium mimulicola*** (Figure 80). Photo by David Wagner, with permission.

Figure 83. ***Straminergon stramineum***, a species that is home to ***Myzodium mimulicola*** (Figure 80). Photo by David T. Holyoak, with permission.

Figure 84. ***Philonotis fontana***, a species that is home to ***Myzodium mimulicola*** (Figure 80). Photo by Michael Lüth, with permission.

Melaphis

The sumac gall aphid ***Melaphis rhois*** (**Pemphigidae**; Figure 85-Figure 89) is one of these moss aphids in the USA, alternating between mosses and sumac [***Rhus glabra*** (Figure 90) and ***R. typhina*** (Figure 91)] (Moran 1989; Hebert *et al*. 1991; Pike *et al*. 2012).

Figure 85. ***Melaphis rhois*** galls on sumac (***Rhus***) in the US. This species shifts its habitat to bryophytes when conditions on the leaves are not favorable. Photo from Department Agriculture, Conservation, and Forestry, Augusta, Maine, through Public Domain.

Figure 86. ***Melaphis rhois*** nymphs in gall, a stage that exists on the sumac host. Photo by Claude Pilon, with permission.

Figure 87. ***Melaphis rhois*** young nymph, a stage that may be found among mosses. Photo by Claude Pilon, with permission.

Figure 88. ***Melaphis rhois*** adult, a moss and sumac inhabitant. Photo by Claude Pilon, with permission.

Figure 89. ***Melaphis rhois*** adult, a species that lives on sumac and uses mosses as alternate hosts for winter and egg laying. Photo by Claude Pilon, with permission.

Figure 90. ***Rhus glabra*** with flowers, primary host of ***Melaphis rhois***. Photo from Superior National Forest, through Creative Commons.

Figure 91. ***Rhus typhina***, primary host of ***Melaphis rhois***. Photo through Creative Commons.

Moran (1992), an avid aphidologist, was walking in the Santa Catalina Mountains, Arizona, USA, when she discovered 5-cm galls (Figure 85-Figure 86) on a stand of smooth sumac (***Rhus glabra***; Figure 90). Further inspection revealed the sumac gall aphid, ***Melaphis rhois*** (0.8-1.2 mm; Figure 85-Figure 89). Upon further research, she discovered that this aphid was known from New York and that A. C. Baker had suspected that the tiny aphids he found among mosses in West Virginia, USA, might be the unknown spring migrant stage of ***Melaphis rhois***. A return trip to the mountains enabled Moran to gather mosses and find that they indeed were inhabited by tiny aphids. She also transferred aphids from the sumac to the mosses and these produced morphs exactly matching those identified by Baker in West Virginia. After spending the summer inside the gall, where the single female reproduces asexually to make daughters, and they in turn her granddaughters, the granddaughters leave the gall in autumn as the sumac leaves begin dying and winter approaches. The granddaughters must find appropriate mosses where they deposit tiny aphid offspring. There the tiny daughters (great grandchildren of the original gall-maker) feed, develop, and reproduce. Their own waxy secretions protect them from desiccation. In spring of the first – or the second – year these females produce not only females but also males. Within a week they mate, females

deposit their eggs once more on the sumac, and the mating generation dies.

This species depends on the mosses for food (Baker 1919; Heie 1980; Moran 1989; Hebert *et al*. 1991). Pike *et al*. (2012) list a number of mosses that serve as hosts for ***M. rhois***: ***Rhytidiadelphus loreus*** (Figure 52), ***Leucolepis acanthoneura*** (Figure 92), ***Claopodium crispifolium*** (Figure 93), ***Eurhynchium praelongum*** (Figure 94), and ***Dicranum scoparium*** (Figure 113).

Figure 92. ***Leucolepis acanthoneura***, home of ***Melaphis rhois***. Photo by Matt Goff <http://www.sitkanature.org/>, with permission.

Figure 93. ***Claopodium crispifolium***, winter home of ***Melaphis rhois***. Photo by Matt Goff <www.sitkanature.org>, with permission.

Figure 94. ***Eurhynchium praelongum***, home for ***Melaphis rhois*** when sumac leaves are unsuitable. Photo by Blanka Shaw, with permission.

Clydesmithia (Pemphigidae)

Clydesmithia canadensis (1.5-2.7 mm; Figure 95) includes a number of species among its moss hosts and is associated with mosses in Alaska (Pike *et al*. 2012). These moss alternate hosts are summarized in a table in Pike *et al*. (2012) and include such species as ***Climacium dendroides*** (Figure 96) and ***Rhizomnium magnifolium*** (Figure 97) that have not been mentioned here for other aphids.

Figure 95. ***Clydesmithia canadensis*** nymph, a species that is associated with a number of moss species. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 96. ***Climacium dendroides***, one of the bryophyte hosts for ***Clydesmithia canadensis*** (Figure 95). Photo by Michael Lüth, with permission.

Figure 97. ***Rhizomnium magnifolium***, an alternate host for ***Clydesmithia canadensis*** (Figure 95). Photo by Janice Glime.

Pemphigus (Pemphigidae)

There seem to be few reports of European gall makers that use mosses as alternate hosts. In the UK, ***Pemphigus trehernei*** (1.3-2.4; see Figure 98-Figure 100) reproduces only by **parthenogenesis** (reproduction from an unfertilized egg), using roots of grasses and moss mats for oviposition (Alexander 2008). Norzikulov (1964) reported ***Pemphigus hydrophilus*** (1.9-2.2 mm) from ***Cratoneuron filicinum*** (Figure 101) and possibly also ***Hygrohypnum luridum*** (Figure 102) in Russia.

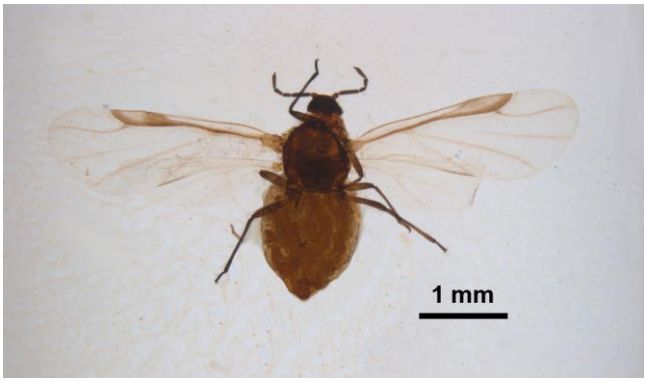

Figure 98. ***Pemphigus bursarius***, a gall maker in a genus that uses mosses as alternate hosts. Photo from Pest and Diseases Image Library, through Creative Commons.

Figure 99. ***Pemphigus bursarius*** showing detail of antenna. Photo from Pest and Diseases Image Library, Bugwood.org, through Creative Commons.

Figure 100. ***Pemphigus spirothecae*** gall, member of a genus that uses mosses as alternate hosts. Photo by Georg Slickers, through Creative Commons.

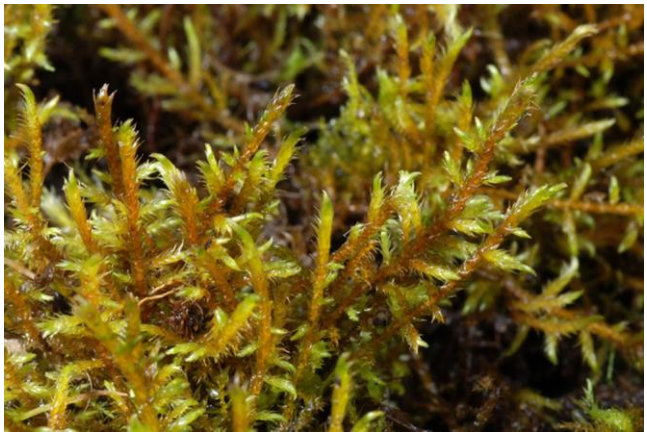

Figure 101. ***Cratoneuron filicinum***, home for ***Pemphigus hydrophilus***. Photo by J. C. Schou, with permission.

Figure 102. ***Hygrohypnum luridum*** home for ***Pemphigus hydrophilus*** in Europe. Photo by Michael Lüth, with permission.

Other Aphididae that Live Among Mosses

Decorosiphon corynothrix (1.4-1.9 mm; **Aphididae**; Figure 103) lives on basal parts of ***Polytrichum*** spp. (Figure 17) growing in damp, shady situations and on ***Atrichum undulatum*** (Figure 104) (The Aphids 2015).

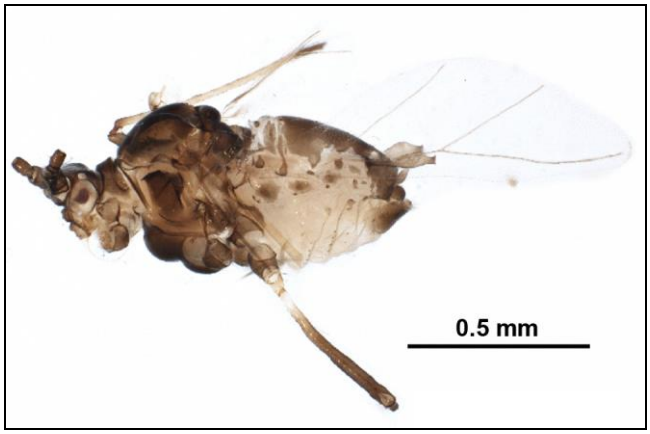

Figure 103. ***Decorosiphon corynothrix***, a species that lives on the basal parts of ***Polytrichum*** spp. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 104. ***Atrichum undulatum***, home to ***Decorosiphon corynothrix***. Photo by Janice Glime.

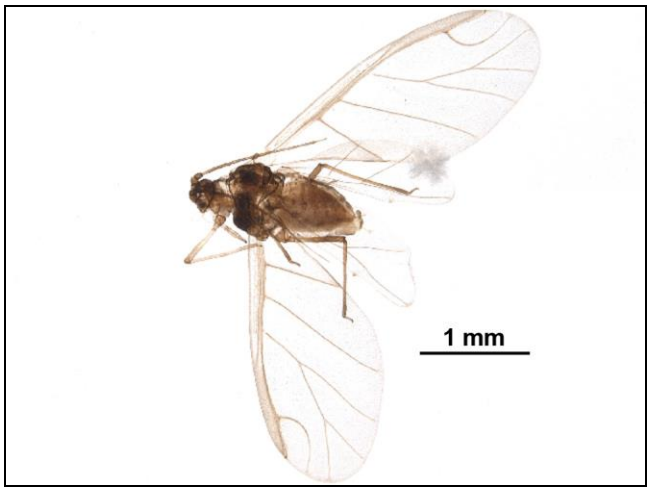

Figure 105. ***Jacksonia papillata***, an aphid that often spends time among mosses. Photo through BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Jacksonia papillata (**Aphididae**; Figure 105) often occurs among mosses (Müller 1973). This is consistent with the mossy habitats of its primary hosts. Müller suspects that it sometimes feeds on mosses. ***Pachypappa rosettei*** (0.84-1.41 mm; **Aphididae** or **Pemphigidae**; Figure 106), ***Pachypappa sacculi*** (Figure 107), ***Prociphilus xylostei*** (~3 mm; **Aphididae**; Figure 108-Figure 109), and ***Thecabius populimonilis*** (only once; **Aphididae**; Figure 110-Figure 111) also occur on mosses (Pike *et al.* 2012). ***Prociphilus xylostei*** is a strange-looking insect that secretes copious wax to cover and camouflage itself, making it look more like a fungus than an insect.

Figure 106. ***Pachypappa rosettei***, a moss inhabitant. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

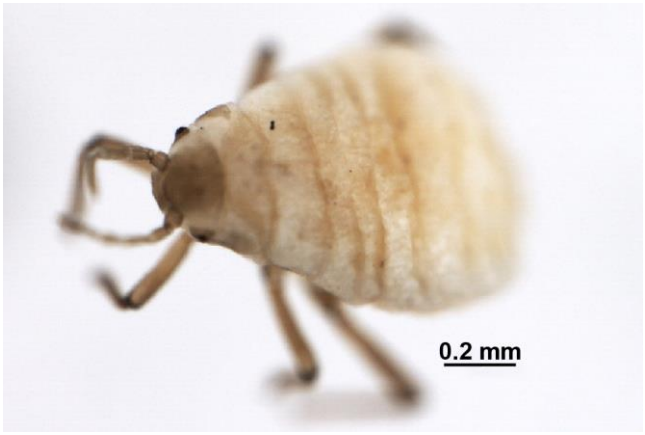

Figure 107. ***Pachypappa sacculi***, a moss inhabitant. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

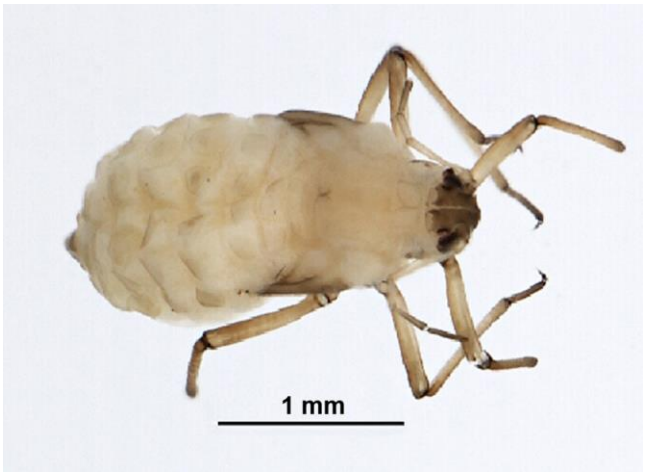

Figure 108. ***Prociphilus xylostei*** nymph, a moss dweller. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

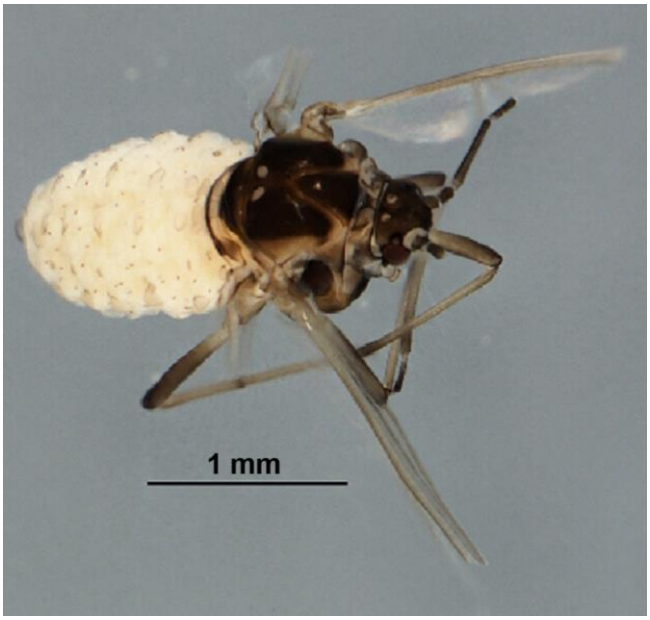

Figure 109. ***Prociphilus xylostei*** adult, a moss dweller that secretes wax that serves to camouflage it. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 110. ***Thecabius populimonilis***, a moss inhabitant. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Pseudacaudella rubida (0.7-1.0 mm; Figure 111-Figure 112) lives on the moss genera ***Calliergonella*** (Figure 54), ***Climacium*** (Figure 96), ***Dicranum*** (Figure 113), ***Hylocomium*** (Figure 61), ***Mnium*** (probably ***Plagiomnium***; Figure 33-Figure 34, Figure 43-Figure 44), ***Pleurozium*** (Figure 114), ***Polytrichum*** (Figure 17), ***Pseudoscleropodium*** (Figure 62), and ***Thuidium*** (Figure 31) (The Aphids 2015).

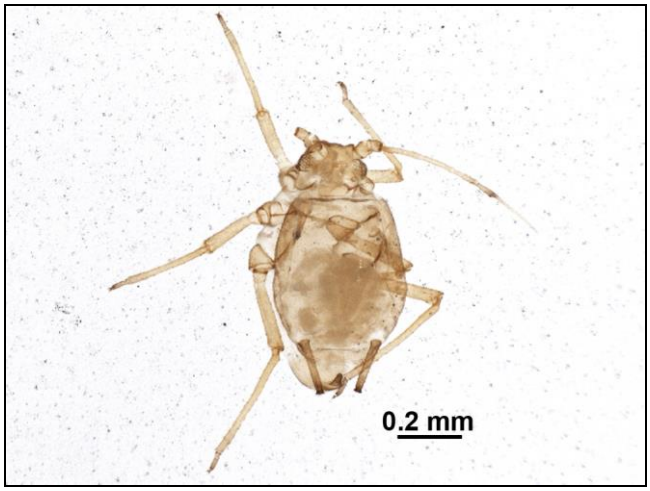

Figure 111. ***Pseudacaudella rubida*** nymph, a species that lives in a variety of mosses. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

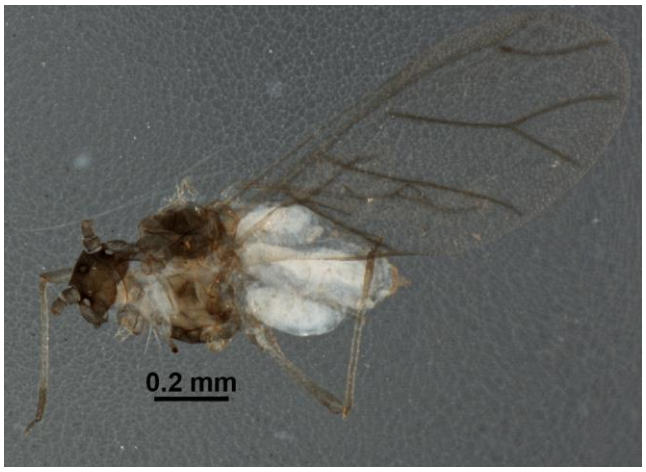

Figure 112. ***Pseudacaudella rubida*** adult. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 113. ***Dicranum scoparium*** with developing capsules, a moss that hosts ***Pseudacaudella rubida***. Photo by Janice Glime.

Figure 114. ***Pleurozium schreberi***, secondary host for ***Pseudacaudella rubida***. Photo by Michael Lüth, with permission.

Attractants?

Do aphids help mosses attract more aphids? ***Nurudea shiraii*** (**Aphididae**) uses ***Hypnum plumaeforme*** (Figure 115) as a food plant (Lou & Chen 2000). ***Thuidium cymbifolium*** (Figure 31) is the host plant of ***Schlechtendalia elongallis*** (**Pemphigidae**). Lou and Chen found that these two mosses and the host moss ***Brachythecium buchananii*** (Figure 1) produce such aliphatic compounds as alcohols, aldehydes, ketones, and esters. They suggested that production of these compounds might be induced by the damage caused by their inhabiting aphids. They further suggested that these compounds might help the aphids locate their host plants. This sounds like an interesting hypothesis in need of testing.

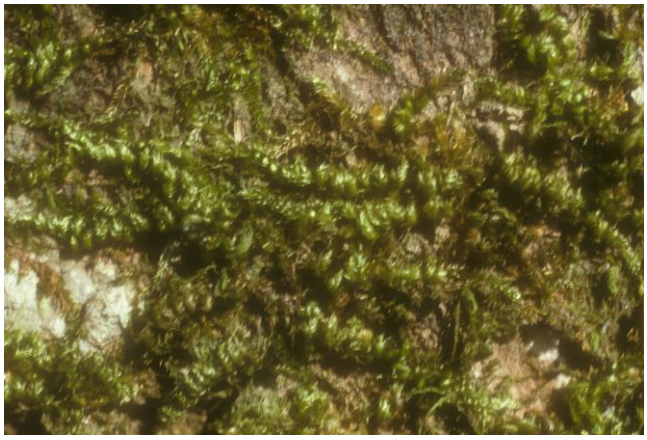

Figure 115. ***Hypnum plumaeforme***, food for ***Nurudea shiraii***, produces aliphatic compounds that might help aphids to locate these mosses. Photo by Janice Glime.

Why Alternate Hosts?

Moran (1989) speculated on the evolutionary pressures that would cause such a host alternation as mosses and woody plants to evolve. Since this strategy is present in both the Chinese species and the North American ones, she postulated that both had their origins in Alaska and were separated when forced southward before the land bridge across the Bering Strait separated. Moran (1989) had already found fossil evidence of a 48-million-year-old aphid (***Melaphis rhois***; Figure 85-Figure 88) – host plant association with a similar moss/sumac alternation in Alaska, apparently established prior to the southward retreat of sumac. Unlike the alternation seen in China and North America, in England and Scandinavia the aphid has lost its alternate host behavior and lives entirely on mosses, but has sacrificed all sexual behavior. This type of response is also known in the whitefly parasitoid *Encarsia formosa* (**Hymenoptera**) (Birkett *et al*. 2003), but both the production of aliphatic compounds by the moss and the insect response to these need to be verified as a consequence of moss herbivory.

Adelgidae – Woolly Conifer Aphids

The **Adelgidae** made their claim to fame by destroying forests, especially in the Appalachian Mountains, USA. Their connection with bryophytes is indirect, but can be strong. The wooly adelgids (***Adelges tsugae***; 1.5-mm; Figure 116-Figure 118) have had a major impact on the eastern hemlock (***Tsuga canadensis***; Figure 119-Figure 120) in the Appalachian Mountains, as far south as the Smoky Mountains (Jackson & Bellemare 2014). This disturbance has caused a decline in the leafy liverwort ***Bazzania trilobata*** (Figure 121) because the dying hemlocks open the canopy and the habitat becomes drier. This is accompanied by more deciduous litter (resulting from invasion of black birch – *Betula lenta*), greater light exposure, and higher temperatures.

Figure 116. ***Adelges tsugae*** on host eastern hemlock (***Tsuga canadensis***). Photo from Connecticut Agricultural Experiment Station Archive, USA, through Creative Commons.

Figure 117. ***Adelges tsugae***, a destroyer of eastern hemlock forests. Photo by Shimat Joseph, University of Georgia, through Creative Commons.

Figure 118. ***Adelges tsugae*** eggs. Photo by Shimat Joseph, University of Georgia, through Creative Commons.

Figure 119. Dead hemlocks (***Tsuga canadensis***) in South Carolina resulting from ***Adelges tsugae*** infestations. Photo by Steve Norman, U.S. Forest Service, through Public Domain.

Figure 120. ***Tsuga canadensis*** showing open canopy after attack by ***Adelges tsugae***. Photo by Matthew Willis, through Creative Commons.

Figure 121. ***Bazzania trilobata***, a leafy liverwort that is disappearing where hemlocks have been killed by ***Adelges tsugae***. Photo by Janice Glime.

Quite the opposite story can be told about one moss in the southern Appalachian Mountains of North Carolina. There, in high elevation locations, the moss ***Leptodontium viticulosoides*** (Figure 122-Figure 123) had become rather rare (Zander 1980). But prior to 1980 it began spreading. This spread is attributed to ***Adelges piceae bouvieri*** (Figure 124, Figure 125, Figure 128). In this case, the adelgid aphid causes the bark of the **endemic** (growing in a limited area) Fraser fir (***Abies fraseri***; Figure 126-Figure 128) tree to peel, creating habitat suitable for the moss.

Figure 122. ***Leptodontium viticulosoides***, a moss that is spreading in areas where bark of Fraser fir (***Abies fraseri***) is peeling due to infestations of ***Adelges piceae***. Photo courtesy of Claudio Delgadillo Moya.

Figure 123. Close view of ***Leptodontium viticulosoides***. Photo by Li Zhang, with permission.

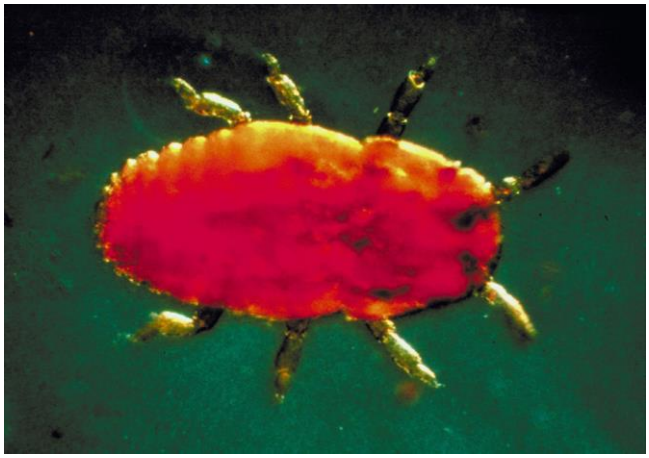

Figure 124. ***Adelges piceae***, a species that causes the bark of the Fraser fir to peel, permitting the moss ***Leptodontium viticulosoides*** to become established. Photo by USDA Forest Service - Ashville Archive, through Creative Commons.

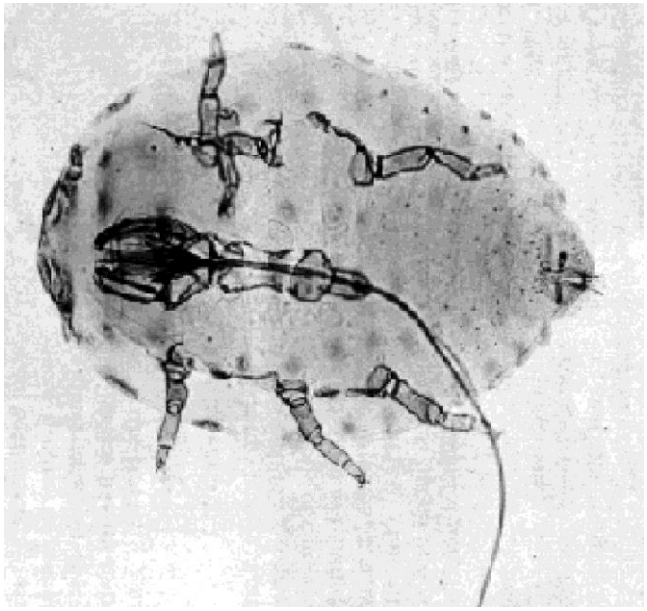

Figure 125. ***Adelges piceae***, a species that damages Fraser Fir and opens habitat for the moss ***Leptodontium viticulosoides***. Note the long proboscis. Photo from USDA, in Public Domain.

Figure 126. ***Abies fraseri*** in the Blue Ridge Mountains, USA. Photo by Gene, through Creative Commons.

Figure 127. ***Abies fraseri***, home for ***Adelges piceae*** in the southern Appalachian Mountains, USA. Photo by Steve Baskouf <www.bioimages.vanderbilt.edu>, through Creative Commons.

Figure 128. ***Adelges piceae*** on ***Abies fraseri***. Photo by William M. Ciesla, Forest Health Management International, <Bugwood.org>, through Creative Commons.

In the Southern Appalachian Mountains, the hornwort ***Megaceros aenigmaticus*** suffered a decrease in sexual reproduction. Although this was partly due to its rarity and lack of contact between males and females, Villareal (2009) suggested that its survival is further threatened by habitat degradation due to the adelgid plague on the hemlocks that created its habitat.

SUBORDER COLEORRHYNCHA (moss bugs or beetle bugs)

The **Coleorrhyncha**, with only one exception, are flightless. They have an extremely reduced **pharyngeal ring** muscle layer (muscles surrounding the pharynx, which is the first part of the foregut) (Spangenberg *et al.* 2013). Spangenberg and coworkers suggest that this reduction prevented any secondary shift in diet (these are bryophyte eaters), preventing them from using a broad range of food sources and consequently preventing radiation of the species into new locations and new species.

Peloridiidae – Moss Bugs

The **Peloridiidae** are cryptic species that frequent wet mosses, liverworts, and leaf litter (Spangenberg *et al*. 2013). They are small (2-4 mm), flattened, and cryptically-colored relict **Hemiptera** in the Southern Hemisphere (Evans 1982; Burckhardt 2009), resulting in their remaining undiscovered in Australia until 1932, although they were known elsewhere in the area (Monteith 2015). Cranston (2010) cites this family as one living among ***Sphagnum*** and liverworts (Austin *et al*. 2004; Cranston 2009). Evans (1941) considered the presence of moss in a habitat that is moist all year round to be a necessity.

One adaptation of bryophyte fauna that is often forgotten is vibration frequency of the "call." Hoch *et al.* (2006) considered the small size of the **Peloridiidae** to necessitate vibrational signals for mates to locate each other. The low frequency of the signals suggests that they may be adapted to calling from their host of soft mosses. This signal is effective at short range and would therefore be effective to initiate courtship or signal disturbance.

The history of the **Peloridiidae** is an interesting one. ***Peloridium*** (Figure 129) had been collected from Tierra del Fuego in 1892, ***Xenophyes*** (Figure 131) from New Zealand in 1920, and ***Hemiodoecus*** (Figure 135) from Tasmania in 1904 (Monteith 2015). But in total, only six specimens had been collected to represent these three genera! All came from dripping wet *Nothofagus* forests (Figure 130). In 1932, Hacker described ***Hemiodoecus veitchi*** from the Antarctic Beech forest of Lamington National Park, Queensland, Australia. This name was later changed to honor both Hacker and his mentor – ***Hackeriella veitchi***. In 1971, a further discovery by Bob Taylor resulted in the description of ***Rhacophysa taylori*** (Burkhardt 2009) from dripping mosses near Cairns, Queensland, a wet area receiving 8 m of rainfall per year.

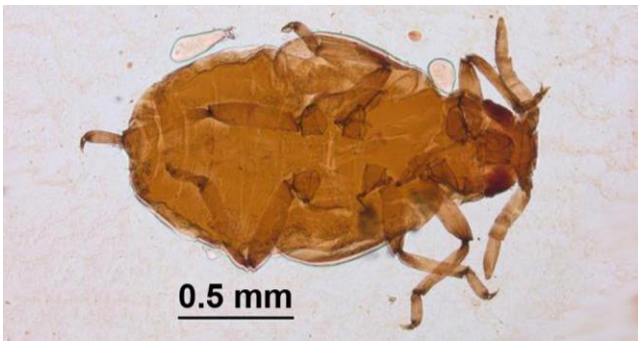

Figure 129. ***Pemphigus bursarius***, member of a moss-dwelling genus. Photo from Pest and Diseases Image Library, Bugwood.org, through Creative Commons.

Despite having only 21 species known in 1982 (Evans 1982), the **Peloridiidae** have been reported from bryophytes many times compared to other **Hemiptera**. These frequent reports, nevertheless, most likely grossly under-represent their presence because of their cryptic habits and small size (Burckhardt *et al*. 2011). Adequate sampling requires sifting of the mosses and forest litter with a sieve. They also tend to occur in remote locations that are hard to reach.

Moss bugs are known from fossils, occurring on mosses in the wet, cool ***Nothofagus*** (beech) forests (Figure 130) in the Southern Hemisphere (Bechly & Szwedo 2007). Today they are most common in the ***Nothofagus*** forests of southern South America, Australia, Tasmania, New Caledonia, Lord Howe Island, and New Zealand, where they live in damp mosses on decaying mossy trunks and twigs of the ***Nothofagus***. In addition to eating the leafy mosses, they may feed on moss rhizoids, wood-decaying fungi, or lichens.

Figure 130. ***Nothofagus*** beech forest with a dense bryophyte ground cover, Eglinton Valley, NZ. Photo from Department of Conservation of NZ, through Creative Commons.

Drake and Salmon (1948) first reported ***Xenophyes cascus*** (2.48-3.10 mm; Figure 131) from New Zealand in 1948, identifying it from damp moss. ***Xenophyes cascus*** is currently distributed in temperate forests and fens in the Southern Hemisphere (Australia, New Zealand, New Caledonia, Chile, Argentina) (Grozeva *et al*. 2014). They also occur on the moss ***Notoligotrichum crispulum*** (Figure 132) in heavily forested areas where *Weinmannia racemosa* (Figure 133) is dominant (Carter 1950). These are both moss dwellers and moss feeders. Burckhardt *et al*. (2011) reported New Zealand moss dwellers to include ***Xenophyes cascus*** from moss on an old log, the broadleaf-taraire dominant ***Xenophyes adelphus*** (2.35-2.63 mm) by sifting mosses from cloud forests and the mosses and liverworts on tree trunks and branches, ***Xenophyes goniomus*** (2.68-3.10 mm) and ***Xenophyes kinlochensis*** (2.80-3.23 mm) from mosses, ***Xenophyes metoponcus*** (2.35-2.55 mm) from mosses in mixed podocarp/broadleaf forest, and ***Xenophyes rhachilophus*** (2.18-2.95 mm; Figure 134) from mosses under beech trees, sifted mosses, and mosses on a wet bank.

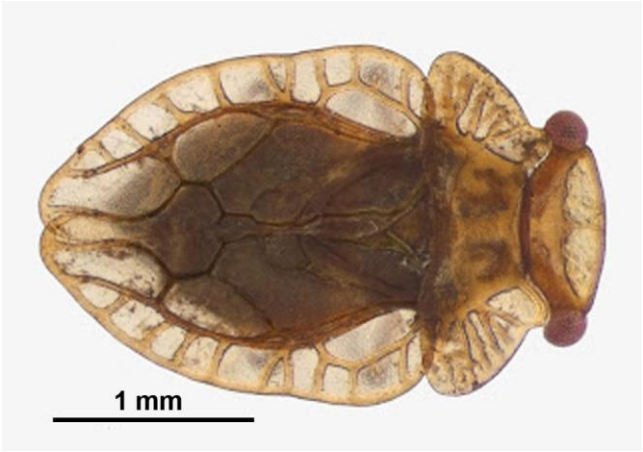

Figure 131. ***Xenophyes cascus***, an inhabitant of ***Notoligotrichum crispulum*** in New Zealand. Photo by Birgit E. Rhodes in Larivière *et al*. 2011, with permission.

Figure 132. ***Notoligotrichum crispulum*** with capsules, home of ***Xenophyes cascus*** (Figure 131) in New Zealand and elsewhere. Photo by David Tng <http://www.davidtng.com/>, with permission.

Figure 133. ***Weinmannia racemosa***, home for the moss ***Notoligotrichum crispulum*** and inhabiting ***Xenophyes cascus***. Phil Bendle, through Creative Commons.

Figure 134. ***Xenophyes rhachilophus***, a species that occurs among mosses under beech trees in New Zealand. Photo by S. E. Thorpe, through Creative Commons.

It was a recent surprise to find the moss dweller ***Hemiodoecus leai*** (2.95-3.63 mm; Figure 135) on the South Island of New Zealand (Wakelin & Larivière 2014; Harris 2014). It was known from Queensland, Australia and elsewhere (China 1932), but not from New Zealand. Wakelin and Larivière considered that it may have been introduced with fish eggs that were frozen in mosses from Tasmania. In captivity, ***Hemiodoecus leai*** ate both pendent mosses ***Ptychomnion aciculare*** (Figure 136), ***Weymouthia cochlearifolia*** (Figure 137), and ***W. mollis*** (Figure 138), and upright mosses ***Bartramia*** sp. (Figure 139) and ***Polytrichadelphus magellanicus*** (Figure 154). These bugs spend most of their time at the bases of the mosses and rarely move between moss clumps through open spaces (Wakelin & Larivière 2014).

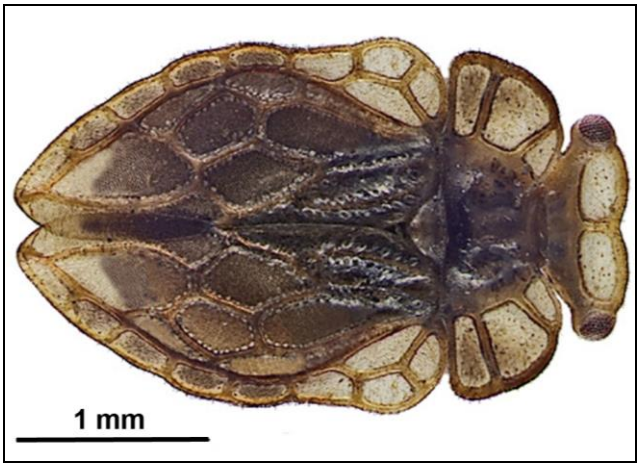

Figure 135. ***Hemiodoecus leai***, a species most likely introduced into New Zealand with frozen fish eggs packed in mosses. Photo by Marie-Claude Larivière <www.nzhemiptera.com>, with permission.

Figure 136. ***Ptychomnion aciculare***, home for ***Hemiodoecus leai*** (Figure 135). Photo by Andy Hodgson, with permission.

Figure 137. ***Weymouthia cochlearifolia***, home for ***Hemiodoecus leai*** (Figure 135). Photo by Juan Larrain, with permission.

Figure 138. ***Weymouthia mollis***, home for ***Hemiodoecus leai*** (Figure 135). Photo by Juan Larrain, with permission.

Figure 139. ***Bartramia*** sp., home and food for ***Hemiodoecus leai*** (Figure 135). Photo by Andy Hodgson, with permission.

The genera ***Oiophysa*** (2.19-2.98 mm; Figure 140) and ***Xenophysella*** (2.34-3.00 mm) are among the moss dwellers in New Zealand (Larivière *et al.* 2011). These include ***Oiophysa ablusa*** (3 mm; Figure 140), ***O. cumberi*** (2.5 mm; Figure 141), ***O. distincta*** (2.6 mm), ***O. pendergrasti*** (2.5 mm), ***Xenophysella greensladeae*** (2.48-3.0 mm), and ***X. stewartensis*** (2.34-2.63 mm; Figure 142). ***Xenophysella greensladeae*** has two 3-lobed **bacteriomes** where bacteria are maintained. Larivière and coworkers presumed that as environmental conditions become drier the **Peloridiidae** would move deeper into the moss layers where there is greater humidity, remaining there until the surface becomes more suitable.

Figure 140. ***Oiophysa ablusa***, a New Zealand bryophyte dweller on a leafy liverwort. Photo by E. Wachmann through M.-C. Lariviére, with permission.

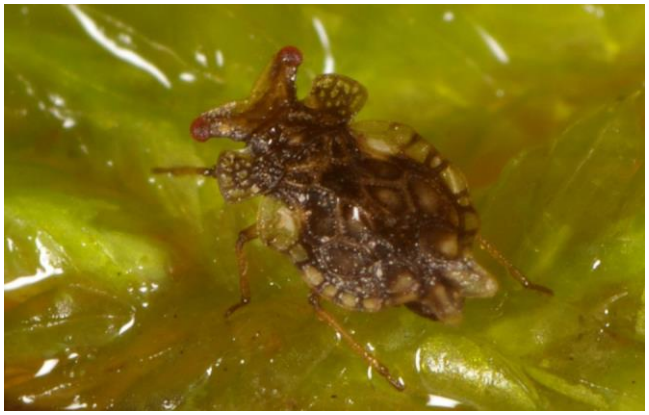

Figure 141. ***Oiophysa cumberi***, a New Zealand bryophyte dweller on a moss. Photo by George Gibbs, with permission.

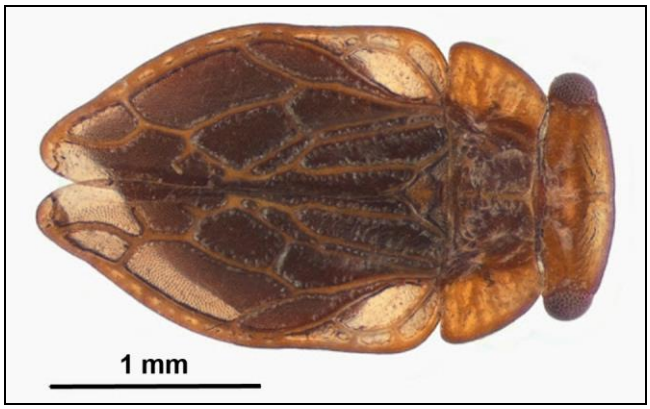

Figure 142. ***Xenophysella stewartensis***, a New Zealand moss dweller. Photo by Birgit E. Rhodes in Larivière *et al*. 2011, with permission.

Oiophysa distincta (2.44-2.98 mm) is considered a living fossil relict in native New Zealand forests, where it lives among wet mosses in the temperate and Antarctic rainforests (Figure 143) (Harris 2011; Grozeva *et al*. 2014). Today other **Peloridiidae** likewise occur in damp mosses, frequenting the decaying mossy trunks and branches of ***Nothofagus*** (Figure 130), where they feed on wood-decaying fungi, lichens, and moss rhizoids (Bechly & Szwedo 2007).

Figure 143. Rainforest, Fiordland National Park, New Zealand, mossy home for ***Oiophysa distincta***. Photo by Christiaan Briggs, through Creative Commons.

On Lord Howe Island, ***Howeria kingsmilli*** (3.0-3.1 mm) occurs on the long pendent moss ***Spiridens vieillardii*** (Figure 144) and on the leafy liverwort ***Porella elegantula*** (Figure 145-Figure 146) (Evans 1967).

Figure 144. ***Spiridens vieillardii*** with capsules, a pendent moss that houses ***Howeria kingsmilli***. Photo by Louis Thouvenot, with permission.

Figure 145. ***Porella elegantula***, a leafy liverwort that is home to ***Howeria kingsmilli***. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Figure 146. ***Porella elegantula*** showing its underside. This pendent leafy liverwort is home to ***Howeria kingsmilli***. Photo by Jan-Peter Frahm, with permission.

In Australia, ***Hemiodoecellus fidelis***, like ***Hemiodoecus leai*** (Figure 135) in New Zealand, lives in

damp moss where its movement is limited by its short legs and limited space for movement (Robinson 2003).

In Australia, ***Hackeriella veitchi*** (3.0-3.3 mm; Figure 147) inhabits the pendent moss ***Papillaria crocea*** (Figure 148) (Helmsing & China 1937; Carter 1950; Spangenberg *et al*. 2013). On the other hand, a much later visit to the area failed to reveal any individuals of this species on the ***P. crocea*** (Spangenberg *et al*. 2013). Nevertheless, new locations hae been found, making this the most readiy available member of the family. ***Hackeriella veitchi*** is unique among the **Peloridiidae** in being able to jump. This is accomplished without any apparent morphological adaptation, but rather by suddenly rotating the hind **femora** (third segments of legs) on the **coxae** (bases of legs) (Burrows *et al*. 2007).

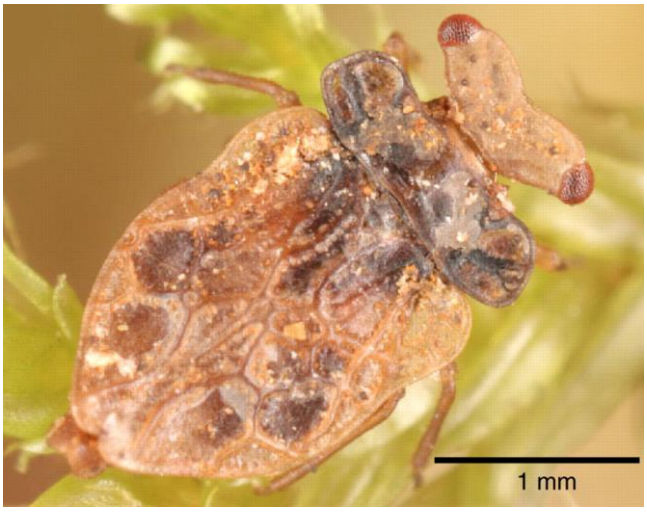

Figure 147. ***Hackeriella veitchi***, an inhabitant of a pendent moss in Australia. Photo by J. Deckert, with permission.

Figure 148. ***Papillaria crocea*** in cloud forest where it can provide a home for ***Hackeriella veitchi***. Photo by Peter Woodard, through Creative Commons.

Burckhardt and Agosti (1991) reported ***Peloridora kuscheli*** (2.8-3.3 mm; Figure 149), ***P. minuta*** (~2.6 mm), and ***P. holdgatei*** (~2.6 mm) from mosses in the ***Nothofagus*** forests (Figure 130) in Chile. Other Chilean moss dwellers include ***Pantinia darwini*** (3.2-3.9 mm; Figure 150) and ***Pantinia*** sp. and several unidentified early instar nymphs.

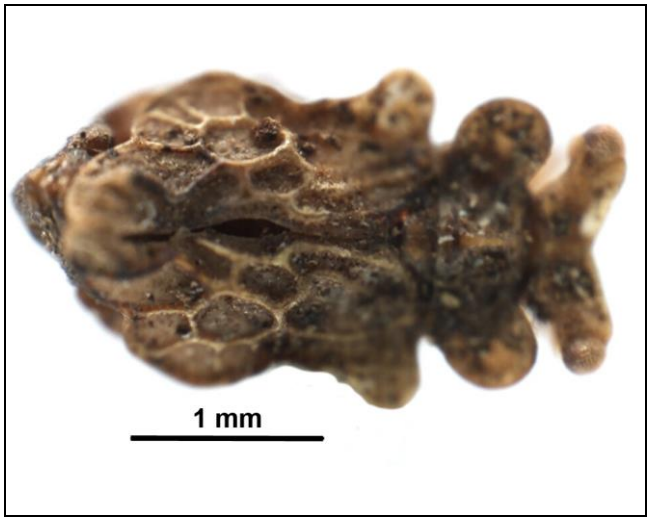

Figure 149. ***Peloridora kuschelli***, an inhabitant of mosses in the ***Nothofagus*** forests of Chile. Photo from CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 150. ***Pantinia darwinii***, a moss dweller in ***Nothofagus*** forests (Figure 130) in Chile. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Shcherbakov (2014) found that some of the **Peloridiidae** are restricted to one or only a few bryophyte species (**mono-** or **oligophagous**). For example, ***Peloridium hammoniorum*** (3.8-5.2 mm; Figure 151) in Fuegia in Southern Patagonia was found only on ***Pohlia cruda*** (Figure 152) (China 1962; Cekalovic 1986), ***Polytrichum strictum*** (Figure 153) (Estévez & Remes Lenicov 1990), and ***Polytrichadelphus magellanicus*** (Figure 154) (Shcherbakov 2014), and it is known to eat mosses (Larivière *et al*. 2011; Shcherbakov 2014). [The host ***Polytrichum strictum*** was not reported previously from that region (Larrain 2007) and may be a misidentification.] The recently described species ***Peloridium pomponorum*** (3.4-4.1 mm) is only known from ***Sphagnum magellanicum*** (Figure 156) and ***S. cf. recurvum*** (Figure 157), both in open areas (Shcherbakov 2014).

Figure 151. ***Peloridium hammoniorus*** on ***Polytrichadelphus magellanicus***. Photo by Roman Rakitov, with permission.

Figure 152. ***Pohlia cruda***, a moss where ***Peloridium hammoniorum*** lives in Southern Patagonia. Photo by Martin Hutten, with permission.

Figure 153. ***Polytrichum strictum***, a peatland species where ***Peloridium hammoniorum*** might live in Southern Patagonia. Photo by Janice Glime.

Figure 154. ***Polytrichadelphus magellanicus***, home of ***Peloridium hammoniorum*** in Fuegia in Southern Patagonia. Photo by David Tng <www.davidtng.com>, with permission.

Figure 155. ***Peloridium pomponorum*** on ***Sphagnum magellanicum***. Photo by Roman Rakitov, with permission.

Figure 156. ***Sphagnum magellanicum***, a home for ***Peloridium pomponorum***. Photo by Janice Glime.

Figure 157. ***Sphagnum recurvum***, a home for ***Peloridium pomponorum***. Photo by Jan-Peter Frahm, with permission.

Symbiotic Bacteria

One of the factors that may permit the **Peloridiidae** to eat mosses is their associated symbiotic bacteria. The **Coleorrhyncha**, including the **Peloridiidae**, is one of the oldest lineages of **Hemiptera.** Kuechler *et al*. (2013) analyzed **Peloridiidae** bacterial symbionts from 15 representatives from South America, Australia, Tasmania, and New Zealand. These proved to be an unknown group of **Gammaproteobacteria**, which they named ***Candidatus Evansia muelleri***. These bacteria develop at the posterior pole of a developing oocyte and thus are transmitted from parent to offspring before birth. A second bacterium was usually associated with the Malpighian tubules, an endosymbiont in the genus ***Rickettsia*** (Figure 158).

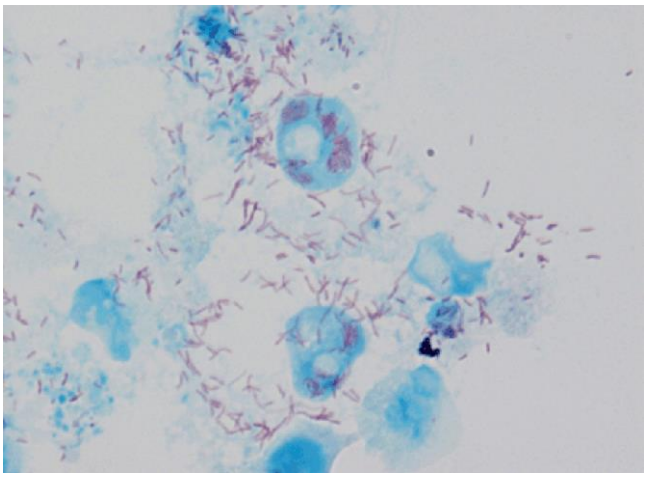

Figure 158. ***Rickettsia conorii***, a possible symbiont of **Peloridiidae** that permits it to digest mosses. Photo by Clarisse Rovery, Philippe Brouqui, & Didier Raoult, through Creative Commons.

ORDER THYSANOPTERA – Thrips

The thrips are tiny, slender insects with fringed wings (Greek *thysanos* = fringe) (Thrips 2015). They feed by sucking cell contents of plants or animals. Their tiny size (<1mm) gives them an ideal fit among bryophytes, but only one sub-tribe among the 6,000 species lives there (Mound 1989). Curiously, the word "thrips" is both singular and plural.

Although an insect most people do not often notice, these insects (**Thysanoptera**) can be associated with mosses (Mound 1989). Bhatti (1979) found two new species in a new genus of thrips (**Thripidae**) living among mosses in West Africa. Mound (1970) reported ***Nesothrips lativentris*** from this family among mosses on the Solomon Islands.

The Old World genera of ***Bournierothrips*** and ***Muscithrips*** are bryophyte dwellers. In fact, ***Bournierothrips*** seems to be restricted to mosses (Bournier 1979). A recent new genus, ***Solanithrips***, was described from Mexico as an inhabitant of *Solanum* (Johansen 1997). This genus is closely related to the two Old World bryophyte-dwelling genera, so it is possible that it too may just use bryophytes when the *Solanum* is seasonally unavailable. Other members of **Thysanoptera** are known from bryophytes (and lichens) in Mexico (Mojica Guzman & Johansen 1990).

In their study of New Zealand **Thysanoptera**, Mound and Walker (1982) found records of a number of species of **Thripidae** in association with mosses: ***Anaphothrips obscurus*** (1.5 mm), ***Anaphothrips woodi***, ***Aptinothrips rufus*** (1.5mm; Figure 159-Figure 160), ***Aptinothrips stylifer*** (~1.5 mm; Figure 161), ***Ceratothrips frici*** (Figure 162), ***Lomatothrips paryphis***, ***Pseudanaphothrips achaetus***, ***Thrips australis***, ***T. nigropilosus***, ***T. obscuratus***, ***T. tabaci*** (Figure 163). At least some species, including ***Ceratothrips frici***, are attracted to their primary hosts by colors (Teulon & Penman 1992). ***Ceratothrips frici*** is attracted to white and yellow traps. The associations of all these thrips with a number of flowering plants suggest that the mosses were most likely a refuge and not a food source (Mound & Walker 1982).

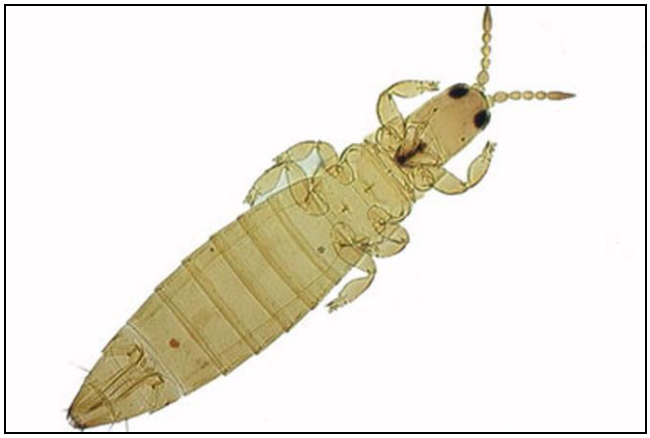

Figure 159. ***Aptinothrips rufus***, a moss associate in New Zealand. Photo by John W. Dooley, through Creative Commons.

Figure 160. ***Aptinothrips rufus***, a moss associate and flowering plant eater in New Zealand. Photo through Creative Commons.

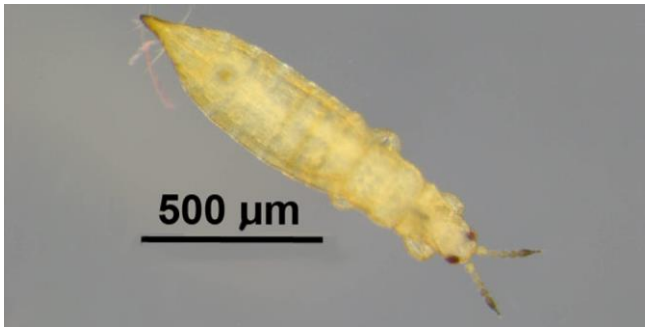

Figure 161. ***Aptinothrips stylifer***, a moss associate in New Zealand. Photo through Creative Commons.

Figure 162. ***Ceratothrips frici***, a New Zealand moss dweller. Photo by John W. Dooley, USDA APHIS PPQ, through Public Domain.

Figure 163. ***Thrips tabaci***, a flowering plant associate that also spends time among mosses. Photo by Alton N. Sparks, through Creative Commons.

Johansen *et al*. (1983) discussed the New World (Eastern Mexico and Costa Rica) ***Wegenerithrips*** (0.738–1.16 mm; **Thripidae**), a genus with nine species at the time, as a bryophyte feeder. This is a genus thus far known only from females (Taylor 2013). Most likely more of these bryophyte feeders remain unknown.

Mound (1989) reported that only one sub-tribe within **Thysanoptera** feeds on mosses, the **Williamsiellina** (family **Phlaeothripidae**). This sub-tribe is comprised of two genera, ***Lissothrips*** and ***Williamsiella***. These are mostly New World species. In addition to their small size, these genera seem further adapted to moss dwelling by being wingless. And their ability to feed on mosses seems to be a highly derived character. One even bears the name ***Lissothrips muscorum*** (1.17 mm), a wingless female found among mosses in Illinois, USA, and only known from mosses (Rhode 1955). Chiasson (1986) reported it from ***Sphagnum*** and moss litter, and it feeds on mosses. An early record of **Phlaeothripidae** among mosses is that of ***Liothrips ocellatus*** (Figure 164) in Illinois, USA (Hood 1908).

Figure 164. ***Liothrips ocellatus***, one of the early known moss dwellers among the thrips. Photo through Creative Commons of Snipeview.

But it may not always be the moss that gives them their nutrition. In Australia and New Zealand species of these two genera have a blue-green gut, suggesting they may eat the associated **Cyanobacteria** (Mound & Tree 2015). The fact that these genera are understudied is indicated by the new finds: two species of ***Lissothrips*** were recorded from Australia for the first time in 2015, as well as six new species; ***Williamsiella*** was recorded from Australia for the first time with a new species.

Bryophytes may actually play an important role for leaf-inhabiting thrips. When the weather becomes cool and wet, these leaf dwellers seem to disappear from the landscape (Mound & Walker 1982). But if one uses a Berlese funnel to extract them from leaf litter and ground mosses, many will appear. The mosses serve as a refuge when leaves become inhospitable. Further evidence of bryophytes as a refuge comes from ***Iridothrips mariae*** (**Thripidae**). In Hungary, this species seeks mosses in the fall as a place to spend the winter (Jenser 2013).

Peck and Moldenke (1999) have been concerned with the invertebrates, especially insects, that are collected with harvestable mosses. Not only does this disturb the communities of origin, in some cases depriving birds, lizards, and other predators of a food source, but also it introduces these creatures to a new ecosystem where they may have no or few natural predators. They could easily become crop pests in some receiving ecosystems. Peck and Moldenke reported that the number of individuals of **Thysanoptera** per gram were greater in those moss samples collected at the bases of shrubs than in those from the tips of branches. They recommended prohibiting the harvesting of mosses from the shrub bases due to their importance in housing insect diversity.

Summary

Several previous orders have been combined into the **Hemiptera**, including leaf hoppers, plant hoppers, aphids, and moss bugs.

Some of the **Cicadellidae** are true **tyrphobionts** (bog dwellers). The **Delphacidae** includes moss eaters, especially on **Polytrichaceae**; few seem to be bog dwellers.

Other important moss-dwelling aphids include members of ***Myzodium*** and ***Muscaphis***, both of which typically use mosses for overwintering and seasonal food. **Derbidae** and **Issidae** have moss dwellers, but little seems to be known about their habits. The latter uses a pair of gears to aid jumping in nymphs. Even less is known about **Eriococcidae** that live among mosses.

This classification includes several kinds of gall makers in the **Aphididae** that depend on bryophytes, especially **Mniaceae**, for part of the life cycle and winter food. For the Chinese gall maker ***Schlechtendalia chinensis*** and others, and even some North American gall makers, the bryophytes serve as an essential winter host, serving for both food and shelter and often oviposition sites. In the **Aphididae**, a family with a stylet for sucking plant juices, moss specialists have been used to trace the movement of fluids in the leptoids of mosses in the **Polytrichaceae**. Some of these moss inhabitants may respond to aliphatic compounds in the moss, but direct relationships remain to be tested.

Members of the genus ***Adelges*** (**Adelgidae**) have destroyed habitat for the leafy liverwort ***Bazzania trilobata*** and in other cases have opened new habitat for the moss ***Leptodontium viticulosoides***.

The family **Peloridiidae** is so common among mosses that the common name of "moss bugs" is applied. They seem to require that constantly moist environment, probably burrowing deeper as the moss dries. At least some members of the family may have bacteria that help in their digestion of the mosses.

Information on thrips (**Thysanoptera**) is limited, but several genera are represented among bryophytes, with the sub-tribe **Williamsiellina** feeding on mosses.

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CHAPTER 12-8
TERRESTRIAL INSECTS: HOLOMETABOLA – MEGALOPTERA AND NEUROPTERA

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Figure 1. ***Chauliodes pectinicornis*** adult, a species that spends its pupal stage among mosses. Dorothy Pugh <www.dpughphoto.com>, with permission.

MEGALOPTERA – Alderflies, Dobsonflies and Fishflies

This is a small order and most are aquatic as larvae. Nevertheless, some members of the **Corydalidae** (dobsonflies) pupate under mosses, a stage lasting about two weeks (Needham *et al*. 1901). These species include ***Chauliodes pectinicornis*** (Figure 1-Figure 2), ***C. rastricornis*** (Figure 3-Figure 4), and ***Nigronia serricornis*** (Figure 5-Figure 6).

Figure 2. ***Chauliodes pectinicornis*** pupa, a stage that often develops among mosses. Photo by Patrick Coin, through Creative Commons.

Figure 3. ***Chauliodes rastricornis*** adult, a species that pupates under mosses. Photo by Seabrooke Leckie, through Creative Commons.

Figure 4. ***Chauliodes rastricornis*** adult male head showing large eyes and comb-like antennae. Photo by Seabrooke Leckie, through Creative Commons.

Figure 5. ***Nigronia serricornis*** larva, a species that pupates under mosses. Photo by Donald S. Chandler at <www.Discoverlife.org>, with permission.

Figure 6. ***Nigronia serricornis*** adult, a species that pupates under mosses. Photo by Richard Orr <www.marylandinsects.com>, with permission.

Barnard (1931) reported pupae of alderflies (**Sialidae**) from ***Sphagnum*** and other wet or aquatic mosses that grew near or in streams and waterfalls in South Africa. These alderflies required that the mosses be wet.

NEUROPTERA – Lacewings

Not many members of Neuroptera use bryophytes, but Richards and Davies (1977) reported that lacewing larvae search for prey in mosses.

Osmylidae

The larvae of ***Osmylus*** (Figure 7) live in the mosses on the banks of woodland streams (Elliott 1996). Even the adults are typically found near these small streams that have mossy banks suitable for larval development. In Great Britain, the larvae can be found in these mosses throughout the year. In the winter they migrate deep into the moss rhizoids where they hibernate.

The female ***Osmylus fulvicephalus*** (Figure 7) lays about 30 eggs 2-3 days after mating (Elliott 1996). These often are laid in small groups. When deposited on mosses they are laid singly or in pairs on the undersides of leaves and near the water (Lestage 1920; David 1936; Ward 1965). The eggs are cylindrical and slightly flattened. These white eggs darken to brown within a few days, making them less obvious than the white version. Eggs hatch in 4-22 days, depending on the temperature (Withycombe 1923; David 1936; Ward 1965).

Figure 7. ***Osmylus fulvicephalus*** larva, a moss dweller near woodland streams. Photo by Walter Pfliegler, with permission.

When the larvae of the giant lacewing, ***Osmylus fulvicephalus*** (Figure 7), emerge, they burrow into the mosses (Elliott *et al*. 1996) and live among damp mosses in the splash zones of river banks and streams (Plant 1994; Roper 2001). These larvae are only 5 mm when they hatch, but reach 15 mm by the third (final) instar from which they develop into pupae (Elliott 1996).

In this moss habitat ***Osmylus fulvicephalus*** (Figure 7) larvae are able to eat small arthropods (Elliott *et al*. 1996). They strike at movement and inject enzymes that paralyze the prey. When they hatch, the first instar larvae eat mites and **Collembola**, but second and third instars switch to

eating larvae of small **Diptera**. The common **Chironomidae** (midges) are paralyzed in 10 seconds by the enzymes. They then suck the contents out of the prey. The larvae may dive into the water to find prey, but if they are forced to remain submersed they die within 8-28 days (Ward 1965).

The third (and final) larval instar overwinters in **diapause** and is able to withstand total immersion during flooding (Elliott *et al*. 1996). When spring arrives, the larvae make a cocoon, incorporating some of the moss in the cocoon, then pupate for 10-14 days before cutting their way out with their mandibles. They then emerge as adults (Figure 8) without further feeding. The adults fly about over the water surfaces in their woodland homes in the evening (**crepuscular**) (Elliott 1996).

Figure 8. ***Osmylus fulvicephalus*** adult, a species that lays its eggs on moss leaves. Photo from <www.invertebradosdehuesca.com>, through Creative Commons.

Chrysopidae

The modern **Chrysopidae** are not known to live among bryophytes, but they sometimes wear them. The larvae attach various pieces of debris, including bits of mosses and lichens, on their backs (Figure 9) (Skorepa & Sharp 1971; Slocum & Lawrey 1976; Eisner *et al.* 2002; Pérez-de la Fuente *et al*. 2012; Anonymous 2015; Newman *et al*. 2015). This cloak provides camouflage that hides them from both predators and prey.

Figure 9. **Chrysopidae** larva with cloak of debris and lichens. Note the head and large jaws at right. Photo by David Illig, through Creative Commons.

Larvae of the green lacewing ***Leucochrysa pavida*** (Figure 10-Figure 13) (Slocum & Lawrey 1976) and the brown lacewing (Anonymous 2015) take their camouflage with them. They make packets of lichen fragments, bark, pollen grains, fungal spores, and moss fragments that they attach to spines on their backs (Slocum & Lawrey 1976). Likewise, immature brown lacewings use lichen and moss coverings to camouflage and protect them from predators and to disguise themselves from their prey (Insects 2014).

Figure 10. ***Leucochrysa pavida*** larva with lichen back pack. This species also uses mosses. Photo by Jim McCormac, with permission.

Figure 11. ***Leucochrysa pavida*** larva with lichen back pack, ventral view. Photo by Jim McCormac, with permission.

Figure 12. ***Leucochrysa pavida*** larva with lichen back pack showing its camouflage against lichen-covered substrate. Photo by Jim McCormac, with permission.

Figure 13. ***Leucochrysa pavida*** larva with lichen back pack, mandibles ready. Photo by Jim McCormac, with permission.

Hallucinochrysa diogenesi (Figure 14) is a fossil lacewing that attached plant fibers, bark, leaves, algae, mosses, snail shells, and corpses of its food prey on its back (Pérez-de la Fuente *et al.* 2012). These were held in place by the bristles on the backs of the larvae.

Figure 14. ***Hallucinochrysa diogenesi***, representation of the fossil that attached mosses and other substances to its back. Photo by Jose Antanio Penas, through Creative Commons.

Fossil evidence suggests that some larvae of the **Chrysopidae** have been associated with liverworts (Liu *et al*. 2018). ***Phyllochrysa huangi*** larvae (Figure 15, Figure 16) from Burmese amber (Upper Cretaceous ~100 million years old) exhibit "distinctive foliate lobes" on the thorax and abdomen. This mimicry permits individuals to hide from prey (Figure 16) or to be ambush predators because the larvae are hard to distinguish from their background vegetation.

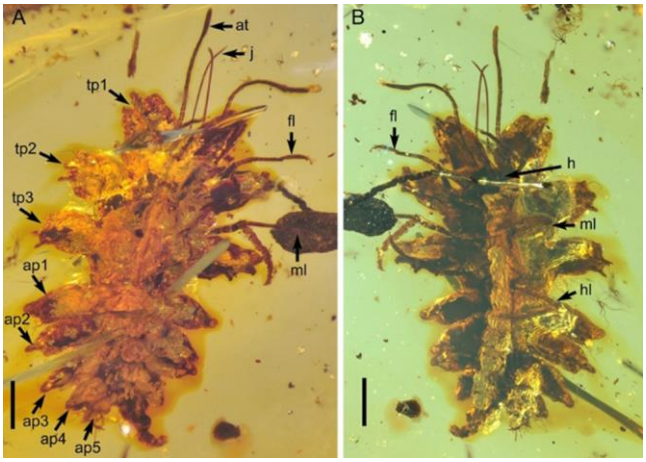

Figure 15. Chrysopid larvae, ***Phyllochrysa huangi***, in Burmese amber. Image from Liu *et al*. 2018, with permission.

The shape of this larva is similar to that of bryophytes (Figure 16, Figure 17). Furthermore, its head is small and concealed under the anterior thoracic lobe (Figure 16) (PPI 2018). Antennae are extremely long with enlarged ends. The researchers found several amber fossil bryophyte species with similar morphologies (Figure 17), including size, leaf shape and arrangement, leaf folds, and lines.

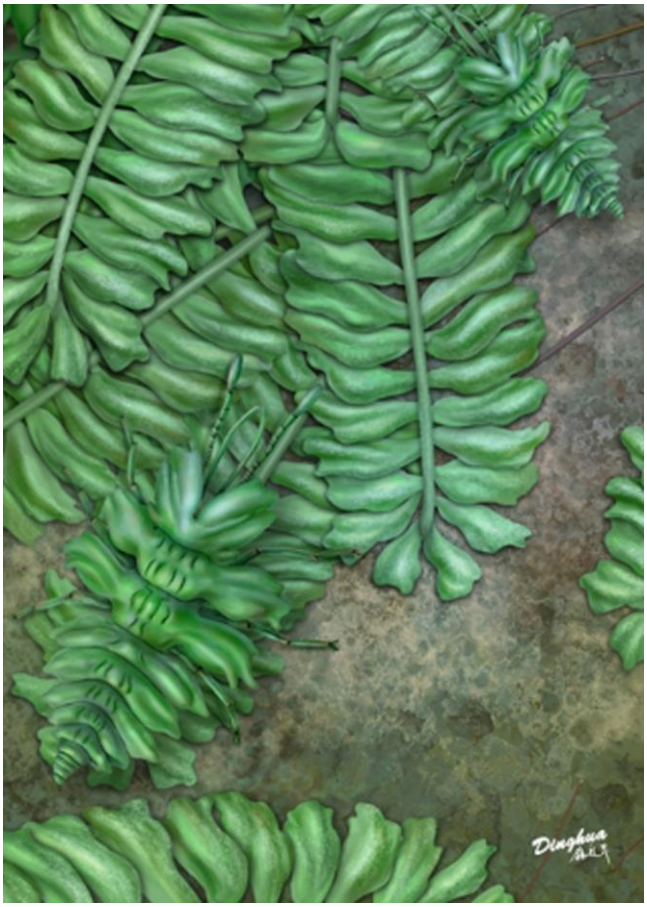

Figure 16. Models of ***Phyllochrysa huangi*** larvae and hypothetical liverworts. Image from Liu *et al*. 2018, with permission.

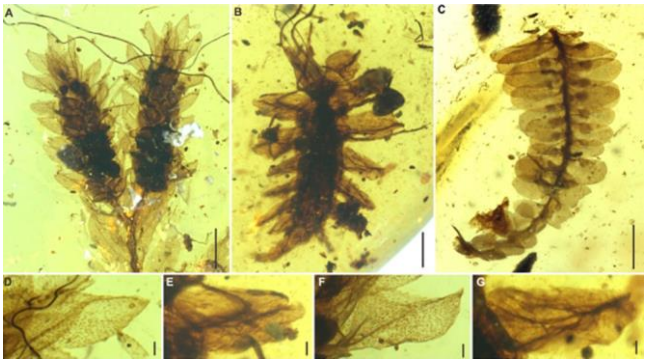

Figure 17. Burmese mosses (B, E, & G) and liverworts in amber – potential hosts for ***Phyllochrysa huangi*** larvae. Image from Liu *et al*. 2018 and PPI 2018, with permission.

Summary

The **Megaloptera** and **Neuroptera** are small orders. Hence there are few bryophyte dwellers. Some members of **Megaloptera** pupate under mosses. In the **Neuroptera**, the best known bryophyte-dwelling genus is ***Osmylus***. ***Leucochrysa pavida*** makes packets of camouflage that include moss fragments among other objects.

Acknowledgments

Bernard Goffinet alerted me to the story on fossil ***Phyllochrysa huangi*** larvae that mimicked liverworts. Thank you to all the photographers who placed their images online with Creative Commons permission and to those who gave me permission to use their images.

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CHAPTER 12-9a
TERRESTRIAL INSECTS: HOLOMETABOLA – COLEOPTERA BIOLOGY AND ECOLOGY

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CHAPTER 12-9a
TERRESTRIAL INSECTS: HOLOMETABOLA – COLEOPTERA BIOLOGY AND ECOLOGY

Figure 1. ***Ptychomitrium*** in the Neotropics with beetle navigating within the mat. Photo by Michael Lüth, with permission.

COLEOPTERA – BEETLES

I opened my email one morning to see one subject labelled "Catching Beetles." Upon investigation, I found this was an advertisement for a new book, 320 pages, all directed toward the various methods for catching beetles in the myriad of habitats they occupy and the families you might encounter (Julio 2011). This large book attests to the huge number of species, sizes, and wide range of habitats of beetles. The picture of a car with large fine-mesh funnel nets on the top and sides struck me as a symbol of their **ubiquitous** (found everywhere) nature.

It seemed like every time I looked up information on a beetle species, I found three more beetle species that inhabited mosses during part of the life cycle. At some point I had to stop and ignore or this volume would never get past the beetle chapter. Hence, I know there are more records that are out there, but these are adequate to show the wide range of families, uses, habitats, and adaptations.

Among the insects, the **Coleoptera**, those hard-winged insects known as beetles, are the largest group of organisms on the planet, and are likewise abundant within the shelter of bryophytes. A renowned biochemist and friend of the entomologist E. O. Wilson, J. B. S. Haldane, when asked by a theologian what the natural world had taught him about the Creator, replied that he has "an inordinate fondness for beetles." It is unclear whether Haldane is the one who coined the phrase because many variants of it appear in the literature (Farrell 1998).

With such large numbers, it is not surprising that we find some of them among mosses. For example, **Parnidae** and **Elmidae** are common in ***Sphagnum*** peatlands (Figure 2) (Leng 1913). That means that they can become unwitting passengers on harvested mosses, travelling around the world with them (Reich 1974; Peck & Moldenke 1999).

Figure 2. ***Sphagnum*** lawn, home for some members of **Parnidae** and **Elmidae**. Photo from Creative Commons.

Moss-dwelling beetles have been known for a long time (for example, Douglas 1871; Waterhouse 1871). Ferguson (1901) enumerated many species of beetles among mosses in the Clyde area of the British Isles, listing the most in the families **Curculionidae** (weevils) and **Staphylinidae** (rove beetles). Day (1907) reported several species from mosses in Cumberland, England. Brown (1972) considered that some seek mosses to maintain their moisture.

Des Callaghan (pers. comm. 3 February 2012) relayed to me his experience with grubs he thought might be beetle larvae. He had saved a sample of ***Micromitrium tenerum*** (Figure 3) for photography, but when he was ready for the photography all he found was soil covered by capsules! He later observed the grubs eating the leaves of the moss.

Figure 3. ***Macromitrium tenerum***, a species for which clumps can be completely devoured by beetle grubs. Photo by Jan-Peter Frahm, with permission.

Bryophagids – Eating and Being Eaten

As seen above, a surprising number of beetles feed on mosses. A variety of small beetles eat mosses and use them as their homes (Drozd *et al*. 2007).

A number of genera in the **Byrrhidae** occur among mosses, use them for egg laying, or eat them. ***Exomella pleuralis*** (Figure 4) can be found in ***Racomitrium heterostichum*** (Figure 5), and adults both feed and oviposit on ***Eurhynchium oreganum*** (Figure 6) (Russell 1979). ***Curimopsis albonotata*** (Figure 7) and ***C. brevicollis*** are limited to higher elevations in the Pacific Northwest; ***C. brevicollis*** from northern Idaho had moss in its gut. ***Lioligus nitidus*** (Figure 8) and ***L. striolatus*** feed on a variety of mosses in the lab: ***Eurhynchium oreganum***, ***Hylocomium splendens*** (Figure 9), ***Hypnum circinale*** (Figure 10), ***Plagiothecium undulatum*** (Figure 11), ***Racomitrium heterostichum***, ***Rhytidiadelphus loreus*** (Figure 12), and ***R. triquetrus*** (Figure 13). One specimen was reared from an egg to an adult on the leafy liverworts ***Diplophyllum plicatum*** (Figure 14) and ***Scapania bolanderi*** (Figure 15). On the other hand, adults refused to eat ***S. bolanderi*** and other liverworts or ***Metaneckera menziesii*** (Figure 16).

Figure 4. ***Exomella pleuralis*** adult, a species that feeds on ***Eurhynchium heterostichum*** and oviposits there. Photo from CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 5. ***Racomitrium heterostichum*** with capsules, home for ***Exomella pleuralis***. Photo by Kristian Peters, with pernission.

Figure 6. ***Eurhynchium oreganum***, home, food, and site for oviposition for ***Exomella pleuralis***. Photo by Matt Goff <http://www.sitkanature.org/>, with permission.

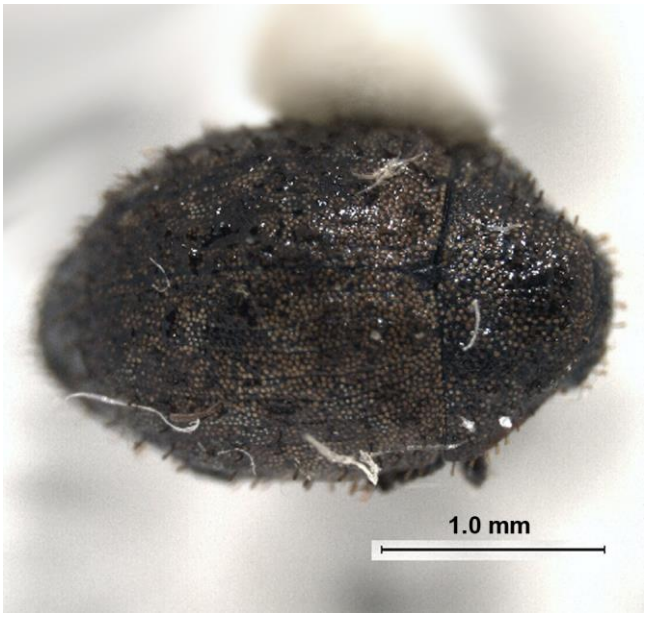

Figure 7. ***Curimopsis albonotata*** adult, a moss consumer at higher elevations. Photo by CNB-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 8. ***Lioligus nitidus***, a species that eats a variety of mosses. Photo by Matt Goff <http://www.sitkanature.org/>, with permission.

Figure 9. ***Hylocomium splendens***, food for ***Lioligus striolatus***. Photo by Chmee2, through Creative Commons.

Figure 10. ***Hypnum circinale***, food for ***Lioligus striolatus***. Photo by Matt Goff <www.sitkanature.org>, with permission.

Figure 11. ***Plagiothecium undulatum***, food for ***Lioligus striolatus***. Photo by David T. Holyoak, with permission.

Figure 12. ***Rhytidiadelphus loreus***, food for ***Lioligus striolatus***. Photo by Hermann Schachner, through Creative Commons.

Figure 13. ***Rhytidiadelphus triquetrus***, food for ***Lioligus striolatus***. Photo by Eric Schneider, with permission.

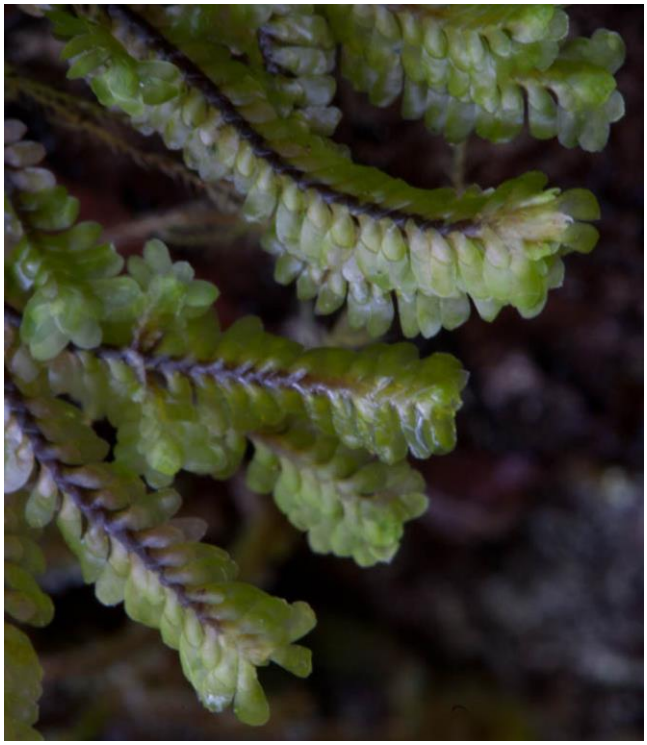

Figure 14. ***Diplophyllum plicatum***, food for larvae of ***Lioligus striolatus***. Photo by Martin Hutten, with permission.

Figure 15. ***Scapania bolanderi***, food for larvae of ***Lioligus striolatus***. Photo by Matt Goff <www.sitkanature.org>, with permission.

Figure 16. ***Metaneckera menziesii***, a moss the adults of ***Lioligus striolatus*** refuse to eat. Photo by Dale Vitt, with permission.

Adults of ***Lioon puncticeps*** and ***L. simplicipes*** (Figure 17) live among many kinds of mosses (Russell 1979). In the laboratory, ***Lioon puncticeps*** adults and larvae both feed on ***Dicranum fuscescens*** (Figure 18), ***Rhytidiadelphus loreus*** (Figure 12), ***Antitrichia curtipendula*** (Figure 19), ***Eurhynchium oreganum*** (Figure 6), and ***Plagiothecium undulatum*** (Figure 11). On ***Polytrichum commune*** (Figure 20), they eat only lamellae and leaf tips while avoiding the tougher parts.

Figure 17. ***Lioon simplicipes*** adult, a species that lives among many kinds of moss. Photo by Joyce Gross, with permission.

Figure 18. ***Dicranum fuscescens***, food for ***Lioon puncticeps***. Photo by Michael Lüth, with permission.

Figure 19. ***Antitrichia curtipendula***, food for ***Lioon puncticeps***. Photo by Dale Vitt, with permission.

Figure 20. ***Polytrichum commune***, food for ***Lioon puncticeps***. Photo by Michael Lüth, with permission.

Listemus acuminatus (Figure 21) and ***L. formosus*** grow among mosses on soil, rocks, and logs, but not among epiphytes (Russell 1979). In the lab they feed on ***Eurhynchium oreganum*** (Figure 6), ***Hypnum circinale*** (Figure 10), and ***Plagiothecium undulatum*** (Figure 11). Larvae occur in mats of the leafy liverworts ***Gyrothyra underwoodiana*** (Figure 22) and ***Nardia scalaris*** (Figure 23), but they may only feed on associated mosses.

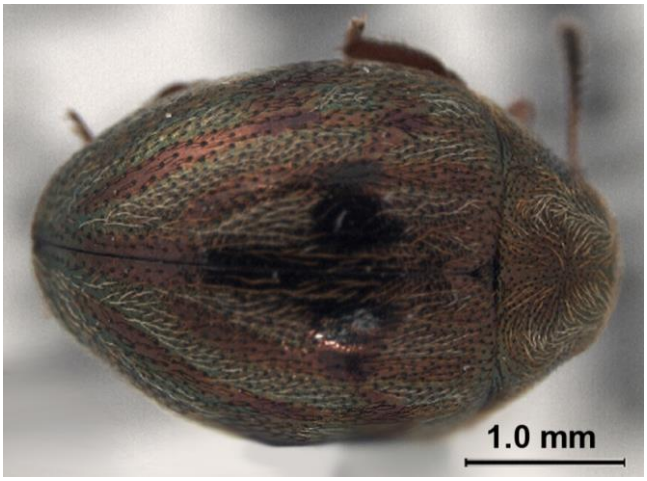

Figure 21. ***Listemus acuminatus***, a species that lives among mosses on soil, rocks, and logs, but does not venture up the boles of trees. Photo from CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

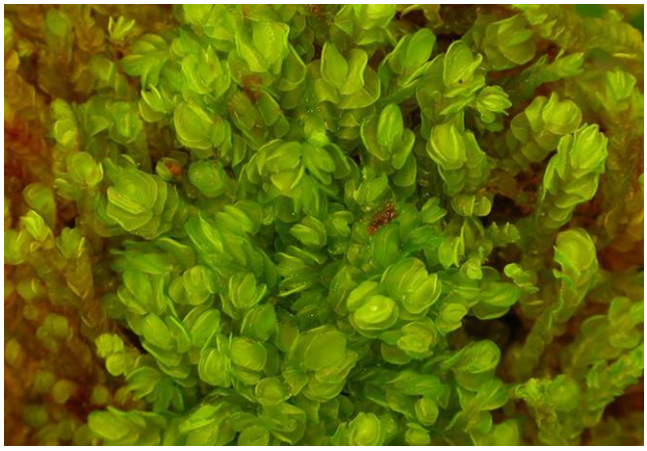

Figure 22. ***Gyrothyra underwoodiana***, a home that doesn't seem to be eaten by ***Listemus acuminatus***. Photo by Li Zhang, with permission.

Figure 23. ***Nardia scalaris*** with capsules, a home but not food for ***Listemus acuminatus***. Photo by J. C. Schou <http://www.biopix.com/>, with permission.

Byrrhus americanus (Figure 24), ***B. concolor*** (Figure 25), and ***B. kirbyi*** (Figure 26) have been found with mosses in their guts (Russell 1979). Hradílek and Boukal (2003) reported **Polytrichaceae** cells from the gut of ***Byrrhus luniger***. These were lamellae with papillae on the terminal cells (Figure 28, Figure 30), suggesting either ***Pogonatum urnigerum*** (Figure 27-Figure 28) or ***Polytrichastrum alpinum*** (Figure 29-Figure 30).

Figure 24. ***Byrrhus americanus*** adult, a moss feeder. Photo by Tom Murray, through Creative Commons.

Figure 25. ***Byrrhus concolor***, a moss feeder. Photo by Tom Murray, through Creative Commons.

Figure 26. ***Byrrhus kirbyi*** adult, a moss consumer. Photo by Tim Loh, with permission.

Figure 27. ***Pogonatum urnigerum***, probable food for ***Byrrhus luniger***. Photo by David T. Holyoak, with permission.

Figure 28. ***Pogonatum urnigerum*** lamellae showing papillae on the terminal cells like those in the gut of ***Byrrhus luniger***. Photo by Kristian Peters, with permission.

Figure 29. ***Polytrichastrum alpinum***, probable food for ***Byrrhus luniger***. Photo by Andrew Hodgson, with permission.

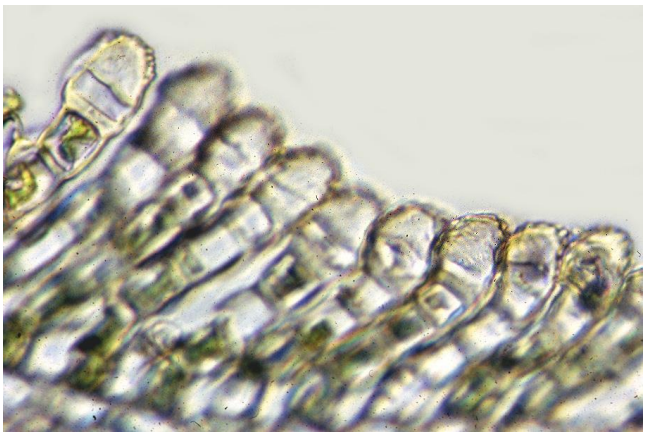

Figure 30. ***Polytrichastrum alpinum*** lamellae showing papillae on the terminal cells like those in the gut of ***Byrrhus luniger***. Photo by Janice Glime.

It appears that all North American species of the **Artematopodidae** might be bryophagids (Russell 1979). Adults of ***Macropogon*** (Figure 31) and larvae of ***Eurypogon*** (Figure 32) in western Washington and Oregon usually occur on trees or shrubs near moss-covered rocks, but some larvae have been collected under the moss ***Ceratodon purpureus*** (Figure 33).

Figure 31. ***Macropogon testaceipennis*** adult, a North American bryophagid. Photo by Joyce Gross, with permission.

Figure 32. ***Eurypogon niger*** adult, a North American bryophagid. Photo by Tom Murray, through Creative Commons.

Figure 33. ***Ceratodon purpureus***, habitat for larvae of ***Eurypogon***. Photo by Jiří Kameníček <BioLib, Obázek>, with permission.

A beetle in the family **Lagriidae** in the Afromontane forest of South Africa feeds on both living and dead parts of the moss ***Braunia secunda*** (**Hedwigiaceae**; Figure 34-Figure 35), as evidenced by gut analysis (Chown 1993), but whether it is specific to this food is not known. Among the weevils (**Curculionidae**) in the sub-Antarctic Prince Edward Islands, ***Antarctonesiotes elongatus***, ***Bothrometopus randi***, ***Ectomnorrhinus marioni***, ***Mesembriorrhinus brevis***, and ***Palirhoeus eatoni*** (**Brachyceridae**) all feed on cryptogams, including bryophytes (Chown & Scholtz 1989a). Similar relationships are known from Marion Island in the Antarctic (Smith 1977), where ***Mesembriorrhinus brevis*** and ***Ectomnorrhinus marioni*** prefer bryophytes over flowering plants (Chown & Scholtz 1989a). ***Ectomnorrhinus similis***, a weevil (**Curculionidae**), consumed 1.67 mg per day of ***Brachythecium rutabulum*** (Figure 36) on an Antarctic island. On the other hand, mosses and lichens consumed by microfauna in two other Antarctic moss communities were less than 0.2 g m^{-2} yr^{-1}.

Figure 34. ***Braunia secunda*** wet, food and home for a member of the **Lagriidae**. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 35. ***Braunia secunda*** dry, food and home for a member of the **Lagriidae**. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 36. ***Brachythecium rutabulum***, food and home for a member of the **Lagriidae**. Photo by Michael Lüth, with permission.

Lazarenko *et al*. (1960) reported the use of mosses as food for flax flea beetles (**Chrysomelidae**). Wallin *et al*. (1999) examined the food habits of beetles inhabiting ***Sphagnum*** (Figure 2) mosses as a possible cause of mandibular wear. The species that exhibited the greatest mandibular wear was not the one with the highest consumption of mosses. Rather, they found that mandibular wear in the carabid beetles ***Chlaenius costulatus*** (Figure 37) and ***C. sulcicollis*** (Figure 38) appeared to be caused by their activities in biting and burrowing into ***Sphagnum***-hummocks.

Figure 37. ***Chlaenius costulatus*** adult, an inhabitant of a protected bog in Sweden. Photo by Tim Faasen, with permission.

Figure 38. ***Chlaenius sulcicollis*** adult, a species that suffers mandibular wear from biting and burrowing into ***Sphagnum***. Photo by Zoologische Staatssammlung Muenchen, through Creative Commons.

Chown (1990) found that even in the presence of the abundant grass *Agrostis magellanica* (see Figure 39), some larvae of the weevil ***Ectemnorhinus*** (see Figure 40) in the sub-Antarctic feed on bryophytes, primarily the leafy liverwort ***Blepharidophyllum densifolium***. The smaller of the two species found by Chown and Scholtz (1989b), ***E. marioni***, lives among the mosses, feeding on them at all stages and having a generation time of one year or less. By contrast, the larger species, ***E. similis***, feeds on detritus as larvae and flowering plants as adults. It has a generation time of more than one year and has more instars. The advantage to ***E. marioni*** of a bryophyte diet appears to be that the bryophytes are both abundant and available year-round. Furthermore, they contrast with the flowering plants in their seasonal N distribution. The seed plants have the highest concentrations in spring, whereas the mire bryophytes have the highest concentrations in autumn. It is interesting that the bryophytes have high concentrations of polyphenolic lignin-like compounds that interfere with digestion, whereas the flowering plants lack these.

On Heard Island, Chown and Klok (2001) found that the weevil species complex of ***Ectemnorhinus viridis*** feed on both tracheophytes and bryophytes. Cryptogams, including both lichens and bryophytes, serve as a primary source of energy and nutrients for 5 of the 6 species of weevils on the sub-Antarctic Marion Island (Crafford & Chown 1991).

Figure 39. *Agrostis curtisii*, a relative of *Agrostis magellanica*, which is ignored as food by ***Ectemnorhinus*** that eats bryophytes in the same habitat of the sub-Antarctic. Photo by Malcolm Storey through <www.discoverlife.org>, through Creative Commons.

Figure 40. ***Ectemnorhinus vanhoeffenianus***; several members of this genus in the sub-Antarctic feed on bryophytes, primarily on the leafy liverwort ***Blepharidophyllum densifolium***. Photo by Alex Puzyr, with permission.

Carabid beetles also seem to find bryophytes, particularly in peat bogs, to be suitable habitats. Främbs (1994) found that the Swedish ***Agonum ericeti*** (Figure 41) and ***Pterostichus rhaeticus*** (Figure 42) use the damp lawns in the summer and migrate to drier hummocks for overwintering. Therefore, larger populations were restricted to areas with distinct hummock-hollow complexes (Figure 43).

Figure 41. ***Agonum ericeti*** in its summer habitat among moist ***Sphagnum*** leaves. Photo by Walter P. Pfliegler, with permission.

Figure 42. ***Pterostichus rhaeticus***, a species that requires a hummock-hollow complex in Swedish bogs. Photo by Niels Sloth <www.biopix.com/>, with permission.

Figure 43. Bohemian bog with ***Sphagnum cuspidatum***, ***S. denticulatum***, and other species creating a hummock-hollow complex. Photo by Jonathan Sleath, with permission.

Beetles in geothermal areas seek refuge from the heat of the soil by inhabiting the cooler bryophytes (Elmarsdottir *et al*. 2003). In turn, bears may eat the beetles, as suggested by their piles of feces (Figure 44) in the area (personal observation).

Figure 44. Bear dung at Ponponyama, Japan. Many beetles are present in this dung. The moss in the foreground is ***Campylopus japonicus***. Photo by Janice Glime.

Epichorius longulus and ***E. aucklandiae*** (**Byrrhidae**) live in the coastal rata (***Metrosideros***) forest (Figure 45) of Auckland Island, New Zealand (Farrell 1974). ***Epichorius longulus*** lives in the ground layer, whereas ***E. aucklandiae*** lives in the canopy. The former species was abundant in the liverwort ***Riccardia*** spp., but rarely occurred among ***Bazzania adnexa*** (Figure 46). When larvae were reared on the ***Riccardia*** (Figure 47), they gained more weight than on ***Bazzania adnexa***. The adults of ***E. longulus*** sought shelter under the leaf litter in the daytime but moved about to feed on bryophytes at night.

Figure 45. Coastal rata forest where ***Epichorius*** lives among liverworts. Photo by James Russell <islandconservation.auckland.ac.nz>, with permission.

Figure 46. ***Bazzania adnexa***, rarely a home for ***Epichorius aucklandiae*** in the rata canopy in New Zealand. Photo by Andy Hodgson, with permission.

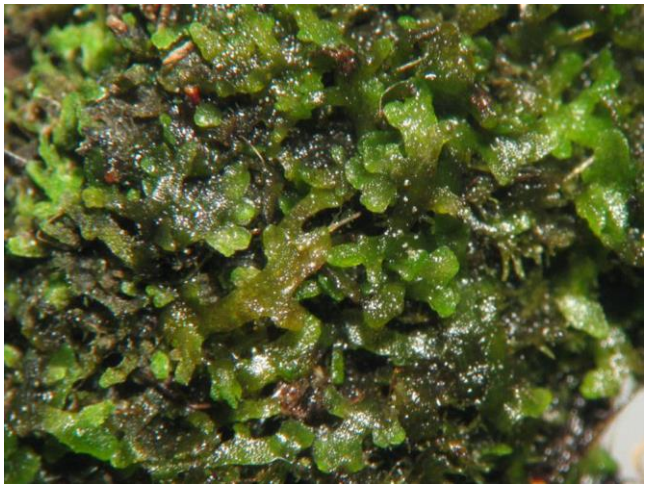

Figure 47. ***Riccardia chamedryfolia***, a genus that is home and food for ***Epichorius aucklandiae*** in the New Zealand. Photo by Kristian Peters, with permission.

Some bryophytes apparently are eaten unintentionally by animals searching for food, including the beetle fauna. The carnivorous salamander ***Phaeognathus hubrichti*** (Red Hills Salamander; Figure 48) typically has a diet that is nearly 70% arthropods, including beetles (Gunzburger 1999). But also in the gut and feces one can find moss fragments, most likely consumed as the salamanders forage for arthropods among the mosses.

Figure 48. ***Phaeognathus hubrichti***, a salamander that eats insects among mosses. Photo by Danté B. Fenolio, with permission.

Sampling

Most researchers have used the same sampling methods for bryophytes as they use for leaf litter. But bryophytes provide small spaces, and some insects never leave those small spaces. This behavior impacts the suitability of trapping methods.

Nelson and Hauser (2012) used both Berlese funnels and water sampling for bryophyte fauna, accounting for many small invertebrates that are usually not found in these associations. Nevertheless, small insects, including tiny beetles, might not have crawled out of the moist moss and into the funnels. The bias of sampling methods is demonstrated by the near absence of overlap between the two sampling methods.

Beetles (Coleoptera) are so common among the ***Sphagnum*** plants (Figure 2) (Brink 1983; Runtz & Peck 1994) that sifting through squeezed mosses can be the best method of collecting (Leiler 1983). Boháč and Bezděk (2004) once again emphasized the role of sampling method in determining the bryophyte fauna. This may be especially true for beetles, where a number of species are wingless and do little moving around. In the Mrtvy Luh peat bog they found that of 38 species in their traps, only 3 were found in both pitfall and light traps.

Boháč and Bezděk (2004) found that the light traps in the Czech Republic peat bog had more species, but many were accidental species that were not typical bog inhabitants. Among these the dominant species were species that are good fliers. Based on these findings, Boháč and Bezděk (2004) recommended that sifting and **trampling** (pressing the moss down to create a pool of water and causing the beetles to float) be included in the sampling strategies. But be aware that sifting and hand grabs are destructive and should be avoided in fragile systems or where repeated sampling is planned.

Leiler (1983) was particularly successful in finding beetle fauna by sifting squeezed wet ***Sphagnum***. Wallin *et al*. (1999) used pitfall traps that were connected with a gutter and embedded into large ***Sphagnum*** hummocks. Lindroth (1974) considered the ordinary insect sieve to be indespensible for sampling in leaf litter and "not too wet" moss, especially for hibernating insects. He suggested that litter samples could also be put under water to force the insects to the surface. For pitfall traps, he suggested adding a few drops of detergent to the formalin to break the surface tension.

Based on the differences seen among these methods, I once again recommend hand picking using a dissecting microscope if an unbiased, quantitative sampling is desired. Some insects move too slowly to get away from a heat source before they die. Some may burrow deep into the mat without vacating it. In any case, not all insects will enter traps equally.

Habitat Relations

The bryophytes are different in different habitats, and so are the beetles. But the correlations are likely to be secondary, with both of them correlating with moisture and bryophytes also with light and suitable substrate availability.

Forests

Pavel *et al*. (2007) found the **Coleoptera** to be the most abundant of the insect taxa in a forest study in the Czech Republic. Pitfall traps were used in three sites to compare those in ***Polytrichum*** cushions (Figure 49) with those at least 10 m away with no moss. Of the 56 species found, ~25% were found only among the mosses. These, combined with those also found in other parts of the forest floor, demonstrated a higher species richness among the mosses. Nevertheless, only one of these species (***Symplocaria*** sp., **Byrrhidae**) was a **bryophage** (one that eats bryophytes). Monte-Carlo permutation tests suggest that the beetles are correlated with moisture and the mosses just happen to provide the right moisture conditions. Those beetle species in dry habitats tend to be restricted to moss cushions, making them strict **bryobionts** (living only on bryophytes).

Figure 49. ***Polytrichum*** cushions that form habitat islands for ***Cytilus sericeus*** and other beetles, providing moisture in exposed areas. Photo by James K. Lindsey, with permission.

Nelson and Hauser (2012) surveyed the epiphytic bryophyte communities at the Tryon Creek State Natural Area in Oregon, USA. Among the five phyla represented, insects were among the top five taxonomic sub-groups (except for the recently ousted **Collembola**). In addition to the five more dominant insect taxa, **Diptera** and **Coleoptera** were present. Hence, beetles were not represented in proportion to their prominence among species numbers on Earth.

Hitch-hikers

Peck and Moldenke (1999) were concerned about the export of potential pest insects in commercial harvests of bryophytes in Oregon, USA. They likewise used the Berlese funnel extraction for arthropods on 200 samples of harvestable mosses. They compared the invertebrate populations at the bases and tips of shrubs of the vine maple (*Acer circinatum*; Figure 50). The base mosses had substantially higher species richness and total abundance overall. For **Coleoptera**, the bases had greater numbers of individuals than did the tips of the shrubs. Mites were the most common arthropods at the base, whereas spiders (**Micryphantidae**) and ***Sminthurus*** (**Collembola**) were the predominant taxa in mosses at the tips.

Figure 50. ***Acer circinatum***, home for **Coleoptera** in mosses at base and on branches. Photo by Ken Gilliland, through Creative Commons.

Forest Disturbance and Recovery

The carabid beetle ***Agonum fuliginosum*** (Figure 51) in Europe seems to have a generalist approach to canopy closure, but it does depend on the presence of ***Sphagnum*** (Figure 2) mires in the forest (Koivula 2002a, b; Koivula & Niemela 2002; Koivula *et al.* 2002). Even small islands of ***Sphagnum*** within a clear-cut forest will permit it to remain, presumably providing needed moisture. ***Patrobus assimilis*** (**Carabidae**; Figure 52) likewise requires the presence of ***Sphagnum*** to survive in forests (Koivula 2002b). On the other hand, ***Agonum mannerheimii***, despite being a mire specialist, is unable to survive in remaining mires if the forest is clearcut (Niemelä *et al.* 1993a, b). It can take 50-60 years for a spruce mire (Figure 53) to recover its forest cover after clearcutting, but it takes longer if there is serious disturbance of the ground layer (Koivula *et al.* 2002).

Figure 51. ***Agonum fuliginosum***, a species that seems to depend on ***Sphagnum*** for moisture in exposed or disturbed forest sites. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 52. ***Patrobus assimilis***, a species that requires mosses to survive in forests. Photo by Roy Anderson ©Roy Anderson <www.habitas.org.uk>, with permission.

Figure 53. ***Picea mariana*** forest in Northern Alberta, Canada, with ***Pleurozium schreberi*** and ***Hylocomium splendens***. Photo by Richard Caners, with permission.

Species of beetles in old-growth forests (Figure 54) are especially affected by logging (Figure 55) (Niemelä 1997). Microhabitats such as coarse woody debris, large deciduous trees, and patches of wet swamp forest and mires may disappear or be greatly reduced. These disturbances tend to cause the old-growth specialists to disappear, including those of beetles. Instead, species richness may increase as generalists remain and numerous open-habitat species invade. This trend is especially true for the ground beetles, which include moss dwellers.

Figure 54. Old Growth in Cathedral Grove, British Columbia, Canada, showing moss-covered logs (dead wood) and low-light plants. Photo by Sang Trinh, through Creative Commons.

Figure 55. Clearcut forest patches at Lewis and Clark River, Oregon, USA. Photo by Walter Siegmund, through Creative Commons.

Niemelä *et al*. (1993b) concluded that retaining habitat diversification on a regional scale was the best management strategy for retaining diversity of ground-dwelling arthropods, including beetles. Hence, retaining moss corridors for those species like the flightless ***Agonum mannerheimii*** may be necessary to permit these species to disperse and to retain the original species richness in the stand (Hoyle & Gilbert 2004). On the other hand, Jonsson and Jonsell (1999) showed that the occurrences of bryophytes are not good predictors for the species richness of beetles. Djupström *et al*. (2010) found only a weak positive correlation between beetles and bryophytes in Swedish boreal forests, and none between beetles and lichens. Like Jonsson and Jonsell, they found that the tested taxa did not provide reliable surrogates. On the other hand, dead wood diversity (Figure 54) represented both **saproxylic** (those that eat dead wood) beetles and bryophytes better than did random samples.

Effects of Beetles on Forest Bryophytes

Clear cutting (Figure 55) removes shade, changes the temperature, and eliminates many kinds of microhabitats. But bark beetles can also have an impact on the forest, removing cover and permitting the sun to raise the temperature. Nevertheless, a bark beetle outbreak in the Central European mountain spruce forests did not have the devastating effect on bryophytes that was experienced under clear cutting (Jonášová & Prach 2008). The latter causes a loss of forest floor bryophytes and the invasion of open habitat pioneers. The beetle outbreak left standing dead (Figure 56) that permitted the bryophytes to remain. Instead of promoting pioneer invasions, the beetle attack left the forest in a state that was more likely to avoid the pioneer stage and to promote a direct forest recovery, including the bryophytes.

Figure 56. Spruce bark beetle damage to the spruce forest in Rio Grande National Forest, USA. Standing dead spruce trees still provide shade, permitting bryophytes to survive. Photo from US Forest Service, through Public Domain.

Dunes

Following habitat restoration of dry dunes (Figure 57) on the Belgian coast, several dune-living ground beetles increased in population size (Maelfait *et al*. 2007). The researchers concluded that the rapid development of the ground vegetation, including both bare sand and moss patches, contributed to the rapid improvement of the insect fauna.

Figure 57. Sand dune in Belgium, where the invasive ***Campylopus introflexus*** is becoming a problem. Photo through Creative Commons.

Heathland

Beetles seem to prefer some mosses and to avoid others. In the *Empetrum* heathlands (Figure 58), beetles avoid the moss ***Pleurozium schreberi*** (Figure 59), but in the *Calluna* heath (Figure 60), with different bryophytes, the beetles were much more common (Barkman 1979, p. 138, in van Tooren 1990).

Figure 58. Dune heath with ***Calluna*** and ***Empetrum***. In ***Empetrum*** heaths, beetles avoid the ***Pleurozium schreberi***. In the ***Calluna*** heaths, beetles live among the different moss species there. Photo by Pat Doody, National Coastal Consultants, UK, with permission.

Figure 59. ***Pleurozium schreberi***, a moss that is avoided by beetles in *Empetrum* heathlands. Photo by J. C. Schou <www.biopix.com/>, with permission.

Figure 60. Heath with *Calluna vulgaris* (pink flowers) and *Ulex europaea* (yellow flowers), where bryophytes seem to be an important part of the habitat for beetles. Photo by Magnus Manske, through Creative Commons.

In a wet heathland in Scotland, the heather beetle ***Lochmaea suturalis*** (**Chrysomelidae**; Figure 61) is a herbivore on ***Calluna*** (Figure 62) (Scandrett & Gimingham 1991). The result of this herbivory is that cover decreases and the mosses ***Sphagnum plumulosum*** (Figure 63) and ***Hypnum jutlandicum*** (Figure 64) increase. The increases in these mosses is concurrent with the decline of ***Sphagnum compactum*** (Figure 65) and ***Pleurozium schreberi*** (Figure 59), thus improving the habitat for bryophyte-dwelling beetles. The ***Calluna*** regenerates mostly by layering, with only limited restoration through seedlings that germinate in the moist ***Sphagnum***.

Figure 61. ***Lochmaea suturalis*** adult, a herbivore on ***Calluna***, causing an increase in ***Sphagnum plumulosum*** (Figure 63) and ***Hypnum jutlandicum*** (Figure 64) as light increases. Photo by James K. Lindsey, with permission.

Figure 62. ***Calluna vulgaris*** – food source for ***Lochmaea suturalis***. Photo by Janice Glime.

Figure 63. ***Sphagnum plumulosum*** (= ***S. subnitens***), a species that increases when cover decreases. Photo by J. C. Schou <www.biopix.com/>, with permission.

Figure 64. ***Hypnum jutlandicum***, a species of mosses that increases in dunes following herbivory by ***Lochmaea suturalis***. Photo by Andrew Spink, with permission.

Figure 65. ***Sphagnum compactum***, a species that declines when ***Sphagnum plumulosum*** and ***Hypnum jutlandicum*** increase following loss of cover due to herbivory by ***Lochmaea suturalis***. Photo by Andrew Hodgson, with permission.

In the ***Racomitrium lanuginosum*** heaths (Figure 66), the Dotterel ***Charadrius morinellus*** (Figure 67) adults eat a large number of beetles (Galbraith *et al*. 1993). Both chicks and adults prefer habitats where both montane bogs and ***Racomitrium lanuginosum*** heaths are available to meet the feeding requirements of both adults and chicks. Overgrazing by sheep has endangered these suitable habitats.

Figure 66. ***Racomitrium lanuginosum*** hummocks in the UK. Photo by Alan Silverside, with permission.

Figure 67. ***Charadrius morinellus*** male, a forager for beetles in ***Racomitrium lanuginosum***. Photo by Helwig Brunner, through Creative Commons.

Bogs and Wetlands

Boháč and Bezděk (2004) found that in the Mrtvy Luh, Czech Republic, peat bog the species of **Staphylinidae** differed significantly between the bog margin and the center. Only 1 **tyrphophilous** (bog affiliate) species occurred in the marginal peat, whereas there were no **tyrphobionts** (species living only in bogs) or **tyrphophiles** (bog affiliates, breeding in bogs and elsewhere) in the center. Rather, the center of the bog was home to ***Drusilla canaliculata*** (Figure 68), a staphylinid that eats ants.

Figure 68. ***Drusilla canaliculata*** adult male, a bog dweller that eats ants. Photo by Christoph Benisch <www.kerbtier.de>, with permission.

Likewise, Bordoni (1972) found 179 species of Coleoptera, representing 25 families) in a Tuscan fen. Many were generalists and few were bryophilous. On the other hand, the Staphylinidae were the best represented and are moss feeders (Mani 1962). And ***Cretinis punctatostriata*** (**Hydrophilidae**) spends its entire life cycle in ***Sphagnum***, making it a true **bryobiont** (Matthey 1977). Its eggs are deposited in the ***Sphagnum*** and its pupation cell is constructed from bryophytes. On the other hand, many of the **bryophilous** mosses do not feed on the mosses, but rather feed on the epiphytic algae (LeSage & Harper 1976).

Using yellow pan traps and emergence traps, Runtz and Peck (1994) found 5734 beetles, representing 30 families, in a mature spruce-***Sphagnum*** bog (fen?) (Figure 69) in Algonquin Park, Ontario, Canada. Among these, members of the **Ptiliidae** were the most abundant and **Staphylinidae** was the most taxonomically diverse family. The **Carabidae** were also important, ranking second in diversity and third in abundance. But, as in many other studies, there are few beetle species specific to the bog. Most of the species in the bog are from adjacent habitats.

Figure 69. Boreal forest fen with spruce (***Picea mariana***) and ***Sphagnum fuscum***, home for many **Ptiliidae** and **Staphylinidae**. Photo by Richard Caners, with permission.

Kvamme (1976) found similar relationships to these in mires at Eidskog, Norway. He trapped (pitfall) 18 species of **Carabidae** and 4 of **Curculionidae** in thirteen mire habitats there. Only ***Agonum ericeti*** (Figure 41) seemed to be a true **tyrphobiont** (restricted to bog and mire habitats). Six species if **Carabidae** were **tyrphophiles** (typical in bogs and mires but not restricted to them). The greatest number of species occurred in the transition zone between the mire and the forest.

On the other hand, bogs are habitats where rare species occur. Wallin *et al*. (1999) found the rare carabid ***Chlaenius costulatus*** (Figure 37) in a protected bog in central Sweden. Wallin *et al.* (2000) likewise found the rare ***Chlaenius sulcicollis*** (Figure 38). ***Chlaenius costulatus*** overwinters in the bog; larvae (Figure 70) and newly emerged adult beetles appeared in pitfall traps, suggesting that they have surface activity during all developmental stages.

Figure 70. ***Chlaenius*** sp. larva, a rare bog dweller. Photo by Tom Murray, through Creative Commons.

Carabid beetles have specific requirements within the bog that determine their distribution. The development of that fauna is closely related to the presence of a mosaic of hummocks and hollows (Främbs 1994). On the Swedish Ryggmossen ***Agonum ericeti*** (Figure 41) and ***Pterostichus rhaeticus*** (Figure 42) use damp ***Sphagnum*** lawns (Figure 2) for summer activities but migrate to drier hummocks for overwintering, accounting for the need for the mosaic. The rare carabid ***Chlaenius sulcicollis*** (Figure 38) was discovered in Sweden in a bog dominated by large ***Sphagnum*** hummocks (Wallin *et al*. 1999, 2000). Severe mandible wear in this beetle could be caused by intensive biting and burrowing needed to navigate the ***Sphagnum*** hummocks.

Hydroporus morio (Figure 71) has a similar topography requirement (Jackson 1956). This member of the **Dytiscidae** lives in bog pools, but when the pools dry out in summer it bores small, round holes in the deep ***Sphagnum***. There it **aestivates** (spends hot or dry period in prolonged state of torpor or dormancy) until the rain returns.

Figure 71. ***Hydroporus morio*** adult, a species that bores into ***Sphagnum*** when the bog pools dry out. Photo by Niels Sloth <www.biopix.dk>, with permission.

The genus ***Sphaerius***, a member of the family **Sphaeriusidae**, has members that live among mosses in bogs (Wikipedia 2015). The bog dwellers are able to store air under the **elytra** (hardened outer wings). ***Sphaerius acaroides*** is a minute scavenger beetle that occurs in moss and plant litter at the edge of slumping cliff seepages (Boyce 2002). Other scattered records exist from sites throughout England, including other wetland habitats such as fens.

It appears that some carrion beetles may be specific to peatlands (Beninger & Peck 1992). ***Nicrophorus*** carrion beetles (Coleoptera: Silphidae; Figure 72-Figure 73) utilize small mammal carcasses; some are able to spend their entire lives in the bog, using the bog carrion for reproduction, whereas others migrate to the nearby forest to reproduce (Beninger & Peck 1992). In the genus ***Nicrophorus*** (Coleoptera: **Silphidae**), the proportion of dead mice (***Mus musculus*** – house mouse; Figure 74) utilized in the peatland as a resource did not differ from that of the nearby forest. ***Nicrophorus*** buries its carrion under mosses and leaf litter (Eggert & Müller 1997). However, ***N. vespilloides*** (Figure 72) reproduced exclusively in the ***Sphagnum***, whereas ***N. defodiens*** (Figure 73) reproduced exclusively in the nearby mixed forest. Furthermore, three other species in the genus rarely occurred on bog carrion but were common on forest carrion. In other cases, it is the larvae of the beetles that live among the mosses (LeSage 1983).

Figure 72. ***Nicrophorus vespilloides*** adult, a species that reproduces in ***Sphagnum***. Photo by Holger Gröschl, through Creative Commons.

Figure 73. ***Nicrophorus defodiens*** adult, a species that leaves the ***Sphagnum*** to reproduce in the forest. Photo by John and Jane Balaban, through Creative Commons.

Figure 74. ***Mus musculus***, a mouse that provides small carrion for reproduction of some species of ***Nicrophorus***. Photo by Ozwildlife, through Creative Commons.

Parthenogenesis (reproduction from an egg without fertilization) is common in bogs, and ***Ptiliopycna moerens*** is one such species in the beetle family **Ptiliidae** (Dybas 1978). These featherwing beetles live mostly in ***Sphagnum*** bogs and similar habitats in swamp forests in eastern North America. In addition, ***Acrotrichis*** (Figure 75), ***Bythinopsis tychoides***, and ***Ptinella mekura*** are all small beetles in these bogs and all are parthenogenetic there.

Figure 75. ***Acrotrichis discolorides*** adult, member of a genus of small, parthenogenetic beetles of ***Sphagnum*** bogs. Photo through Creative Commons.

Antarctica and Antarctic Islands

Beetles are one of the groups of organisms that are able to survive in the harsh conditions of the Antarctic (Figure 76). On this icy continent, the **Curculionidae** exhibit two feeding groups – those that feed on flowering plants and those that feed on cryptogams (algae, lichens, and bryophytes). These feeding constraints result in habitat constraints. For example, on Heard Island, ***Ectemnorhinus viridis*** lives from sea level to 600 m, where it feeds on tracheophytes and bryophytes (Chown & Klok 2001). ***Candonopsis sericeus*** likewise feeds on these two plant groups, but in a narrower altitudinal range. Further details of Antarctic feeding habits in this family are discussed in the sub-chapter on Coleoptera Families.

Figure 76. Mosses in Antarctica, a safe refuge for beetles. Photo by Sharon Robinson, through Creative Commons.

Home for Rare Species

Bryophytes can often hold surprises, species that have been considered rare or were previously unknown. Such was the case when a group of British entomologists were forced to abandon collecting due to very cold, wet weather on the Isle of Wight (Appleton 1986). In a last furtive effort to make the trip worthwhile, the entomologists grabbed handfuls of moss to sample at home. As they sieved through them, they found three individuals of ***Baris analis*** (**Curculionidae**; Figure 77), unknown for a century, from mosses that had grown on low cliffs. Shepard and Barr (1991) were able to describe the larva of ***Atractelmis*** (**Elmidae**; Figure 78) from a bryophyte habitat. In Sweden, several red-listed ***Chlaenius*** (**Carabidae**; Figure 38) species inhabited the mosses (Wallin *et al.* 2000).

Figure 77. ***Baris analis*** adults mating, a rare species known from mosses. Photo by Roger Key, with permission.

Some moss beetles have been even more elusive. Duckett *et al.* (2006) described ***Ivalia korakundah*** (**Chrysomelidae**) as a new species from the Doddabetta Valley, India, where it inhabits mosses. On rocks, adults of this species occur among the branches of the moss ***Isopterygium*** sp. (Figure 79). Both adults and larvae were found by sifting mosses from large pine tree trunks.

Figure 78. ***Atractelmis*** larva, a bryophyte inhabitant. Photo by Joseph Fortier, through Creative Commons

Figure 79. ***Isopterygium elegans***, home for ***Ivalia korakundah*** on rocks. Photo by Kristian Peters, with permission.

In addition to rare species, new species are likely to be lurking among the mosses, and until more collecting is done in these habitats, these will seem rare. For example, Konstantinov and Duckett (2005) found a new member of **Chrysomelidae** – ***Clavicornaltica dali*** (Figure 80) – in Asia. Its type locality is in Yunnan, China, where it was found under a moss. This is a tiny, rounded beetle (1.13-1.24 mm) and the only known species of ***Clavicornaltica*** that has wingless males – a possible adaptation for moss-dwelling that can reserve more space and energy for developing the gut or other structure. In the same collection in China they found a new species of ***Benedictus*** together with ***Clavicornaltica dali*** (Konstantinov & Lourdes Chamorro-Lacayo 2006). No moss-inhabiting weevils were known from the New World until 2006 when these same researchers found the new genus ***Kiskeya*** (**Chrysomelidae**; Figure 81) and named two new species in the Dominican Republic.

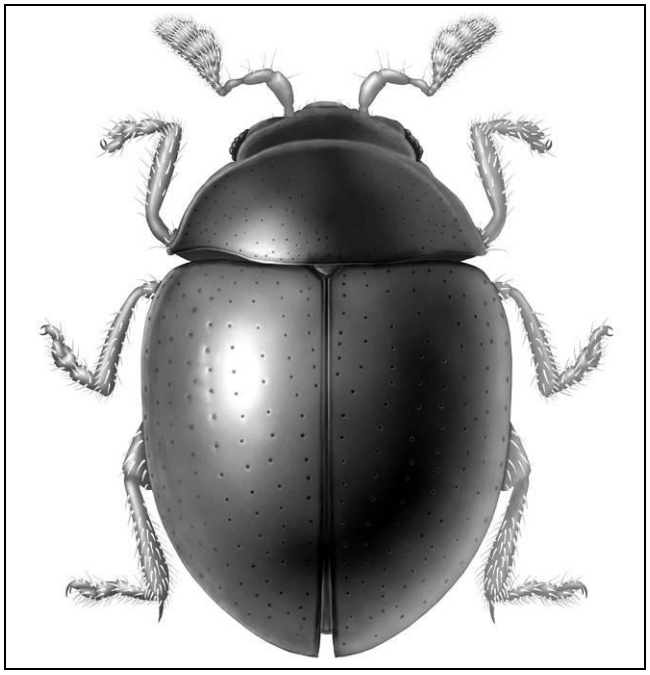

Figure 80. ***Clavicornaltica dali***, a moss-inhabiting flea beetle. Photo by Alexander Konstantinov; permission pending.

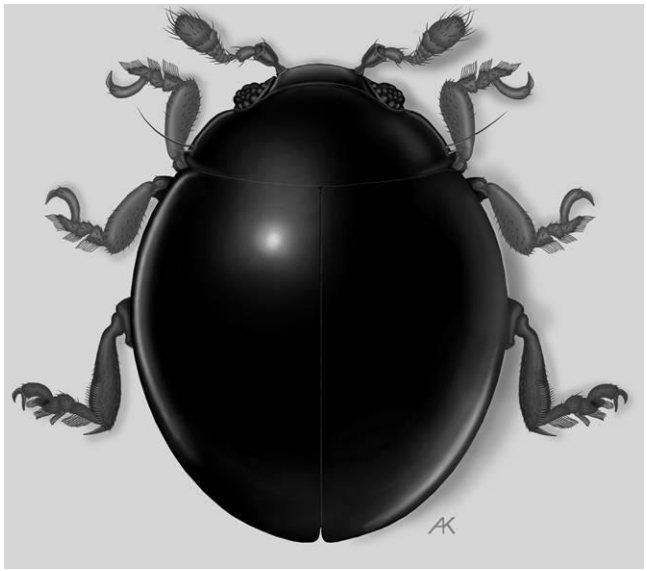

Figure 81. ***Kiskeya baorucae***, a moss-inhabiting flea beetle. Photo by Alexander Konstantinov; permission pending.

Invasive Bryophytes

We know that ***Curimopsis*** (**Byrrhidae**; Figure 7) eats the invasive moss ***Campylopus introflexus*** (Figure 82) (Brian Eversham, pers. comm.). On the other hand, Schirmel *et al*. (2011) found that the invasion of ***Campylopus introflexus*** into acidic coastal dunes (grey dunes; Figure 83) at the southern Baltic Sea shore coincided with a reduction among plant-eating beetles in **Carabidae** compared to those in native dune habitat. They considered this reduction to be the result of reduced food supply of arthropod food items in areas with dense carpets of this invasive moss. This is concerning because the dunes are home to many endangered species of arthropods.

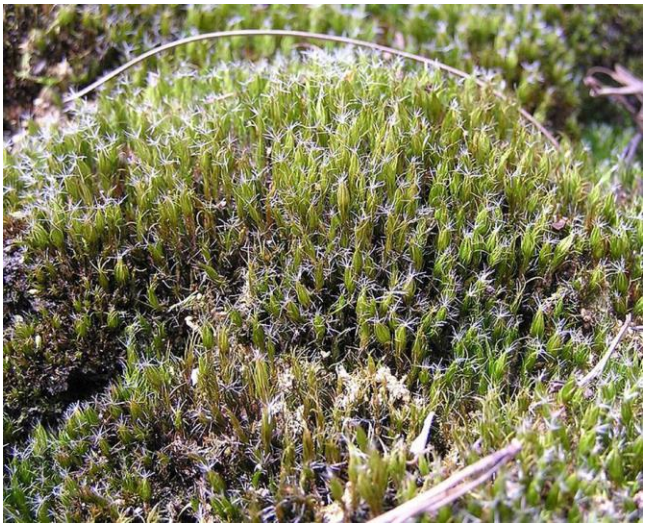

Figure 82. ***Campylopus introflexus***, an invasive moss in Europe that is food for ***Curimopsis***. Photo by Michael Becker, through Creative Commons.

Figure 83. ***Campylopus introflexus*** invading sand dunes. Photo from BIOSOS, permission pending.

Campylopus introflexus (Figure 82) forms dense carpets in these acidic coastal dunes, replacing native vegetation. Using pitfall traps, Schirmel and Buchholz (2013) compared trait composition of beetles and spiders. They found that this invasive moss caused body size and feeding preference of the **Carabidae** to shift. The species examined were smaller in the native habitats, perhaps because percentages of web-building spiders decreased in the sites of moss invasion. But the plant-eating beetles were reduced as well. Hence, the functional diversity of the **Carabidae** was likewise reduced. The functional diversity of spiders increased in the invaded dunes, but that of the carabid beetles decreased.

On South Georgia Island, introduced reindeer reduced the native grass vegetation of ***Poa flabellata*** (Christie 2010). This grass, home of ***Hydromedion sparsatum*** (**Perimylopidae;** Figure 84-Figure 87), was replaced by short grass ***Poa annua***, moss carpets, bare soil, and other unsuitable substrata for ***Hydromedion sparsatum***. As a result, this abundant beetle was reduced from more than 33% of the invertebrate fauna to 7-9%.

Figure 84. ***Hydromedion sparsatum*** larva, a species whose abundance is reduced by invasion of mosses on South Georgia. Photo by Roger Key, with permission.

Figure 85. ***Hydromedion sparsatum*** pupa, a species whose abundance is reduced by invasion of mosses on South Georgia. Photo by Roger Key, with permission.

Figure 86. ***Hydromedion sparsatum*** adult, a species whose abundance is reduced by invasion of mosses on South Georgia. Photo by Roger Key, with permission.

Figure 87. ***Hydromedion sparsatum*** adult, a species whose abundance is reduced by invasion of mosses on South Georgia. Photo by Roger Key, with permission.

Summary

Beetles comprise the largest order of insects and live in almost every imaginable habitat. Their membranous wings are protected by the outer hardened **elytra**, but many of the bryophyte dwellers are flightless. The greatest numbers among bryophytes are **Curculionidae** and **Staphylinidae**, both very large families, but some, like the **Byrrhidae**, are moss specialists, living mostly in bryophytes and eating them.

The moss-dwelling beetles are typically tiny and rounded. Some are able to play dead (**Byrrhidae**) and can retract their legs into grooves on the lower surface. This family, and others, lay their eggs among the mosses. Some live in water as larvae and adults, but come to land to pupate among the mosses. Some migrate up and down in ***Sphagnum*** hummocks to adjust to changing moisture conditions or to overwinter.

Many beetles not only live among mosses, but also eat them. A wide range of mosses seem to be suitable for food, but some are refused. Few beetles, however, seem to eat liverworts. In geothermal areas, the mosses provide a moist and warm refuge in these polar climates.

In forests, bryophytes provide a more moist refuge following a disturbance that opens the canopy. In other cases, the beetles may attack the forest canopy, exposing the bryophytes and causing species changes. Many forest species are likely to be transported around the world as hitch-hikers among horticultural mosses.

In dunes, the invasion of the moss ***Campylopus introflexus*** is changing the kinds of species of beetles occurring there, reducing the beetle functional diversity. Different kinds of heathlands differ in kinds of bryophytes and their beetle fauna.

Bogs are often home to rare beetle species, and some are tiny, wingless, and parthenogenetic, hence poorly dispersed. Here, and elsewhere, sampling bias can miss these tiny, immobile beetles. Hand sorting is the only reliable, albeit time-consuming, method for finding all the species.

On one hand, bryophytes often harbor rare or unknown species. On the other hand, invasive bryophytes can cause reductions in the number of beetle species or their abundance due to replacing food plants.

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CHAPTER 12-9b
TERRESTRIAL INSECTS: HOLOMETABOLA – COLEOPTERA FAMILIES

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CHAPTER 12-9b
TERRESTRIAL INSECTS: HOLOMETABOLA – COLEOPTERA FAMILIES

Figure 1. ***Elaphrus*** sp. on moss, a genus known to live on and among bryophytes. Photo by Bob Armstrong, with permission.

The **Coleoptera** are divided into the **Adephaga** and **Polyphaga**. This chapter has used this division and within the larger group **Polyphaga**, superfamily groupings are used. However, the order if these superfamilies and the families within them is alphabetical.

ADEPHAGA

Whereas five families of **Adephaga** are among the aquatic bryophyte-dwelling beetles, I know of only one family (**Carabidae**) with bryophyte dwellers among the terrestrial beetles. Nevertheless, there are a number of species among the terrestrial members of this family that live among bryophytes.

Carabidae – Ground Beetles

The **Carabidae** have many genera and species represented among bryophytes and were among the early reported bryophyte dwellers. For example, Westwood (1839) reported ***Carabus coriaceus*** (Figure 2) larvae living under mosses. Several species of ***Carabus*** have been photographed on mosses, perhaps only traversing them or getting a bit of remoistening (Figure 3-Figure 5).

Figure 2. ***Carabus coriaceus*** adult, a species that seeks refuge among mosses. Photo by Rotatebot, through Creative Commons.

Figure 3. ***Carabus cancellatus*** adult on moss. Photo by Ladislav Tábi, with permission.

Figure 4. ***Carabus glabratus*** adult on moss. Photo by Ladislav Tábi, with permission.

Figure 5. ***Carabus nemoralis*** adult on moss. Photo by Ladislav Tábi, with permission.

Waterhouse (1871) reported ***Bradycellus collaris*** (Figure 6) from mosses. Later, Lindroth (1974) reported that ***Bradycellus sharpi*** (Figure 7) lives under leaves and mosses in shady places, usually near water. Luff (1998) noted that ***Bradycellus csikii*** (Figure 8) occurs on mosses and other substrata in Central Europe.

Figure 6. ***Bradycellus collaris*** adult on ***Sphagnum***. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 7. ***Bradycellus sharpi*** adult with moss where it dwells near water. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 8. ***Bradycellus csikii*** adult, a moss dweller in Central Europe. Photo through Creative Commons.

In Japan, Bates (1883) reported ***Leistus subaeneus*** living under forest mosses at high elevations and ***Leistus obtusicollis*** occurs in mosses on the trunks of ***Cryptomeria***. In Europe, ***Leistus rufomarginatus*** (Figure 9) and ***L. ferrugineus*** (Figure 10) occur among mosses (Lindroth 1974).

Figure 9. ***Leistus rufomarginatus***, a moss dweller in Europe. Photo by Niels Sloth <www.biopix.com>, with permission.

Figure 10. ***Leistus ferrugineus***, a moss dweller in Europe. Photo by František Šaržík, through Public Domain.

This family has 40,000 species worldwide and are among the 10 largest families of animals worldwide (Wikipedia 2015a). Common habitats are under the bark of trees, under logs, or among rocks or sand by the edge of ponds and rivers. Most species are active nocturnal carnivores. Some are able to run swiftly to catch prey, up to 9 km h^{-1} (Friedlander 1998). They are larger than most moss-dwelling beetles and most don't seem to have any camouflage adaptations. Rather, these most likely visit the mosses to find food organisms and to replenish moisture.

Many members of the family overwinter under mosses (Anonymous 1879). This habit of overwintering under mosses serves for ***Elaphrus fuliginosus*** (Figure 11) and ***E. clairvillei*** (Figure 12) in low woodlands (Kilman 1889).

Figure 11. ***Elaphrus fuliginosus***, a species that overwinters under mosses. Photo by Yves Bousquet, through Creative Commons.

Figure 12. ***Elaphrus clairvillei*** adult, a species that hibernates under mosses in winter. Photo by Gimenez de Cordoba, Beatriz through Creative Commons.

Unlike the many tiny beetles with limited distribution, many of these species are widespread. ***Pterostichus diligens*** (5-7 mm; Figure 13) is numerous among mosses, widespread (Eurasian Boreo-temperate), and common in wet heath, mire, and grass tussocks (Stenhouse 2007). ***Pterostichus strenuus*** (Figure 14) stays in shady places, especially damp deciduous forests on clayish soil, where it lives among mosses and leaf litter (Lindroth 1974). ***Ocys harpaloides*** (4-6 mm; Figure 15) is widespread among mosses in the UK (Stenhouse 2007) and along the European and African Atlantic coast (Anderson *et al*. 2000).

Figure 13. ***Pterostichus diligens*** adult, a species that is numerous among mosses in mires in the UK. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 14. ***Pterostichus strenuus*** adult, a species of shady places, especially damp deciduous forests on clayish soil, where it lives among mosses and leaf litter. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 15. ***Ocys harpaloides*** adult on moss, a widespread moss-dweller in the UK. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

One of the more comprehensive treatments of the **Carabidae** is that of Lindroth (1974). He cited many species that live among mosses in the British Isles. These include ***Notiophilus germinyi*** (Figure 16) among mosses in the open; ***Blethisa multipunctata*** (Figure 17) with mosses and *Carex*; ***Elaphrus lapponicus*** (Figure 18) on wet mosses near wells and streams and in bogs; ***Asaphidion pallipes*** (Figure 19) on fine, slightly moist sand with patches of "tiny moss;" ***Miscodera arctica*** (Figure 20) on fine, dry sand with fine mosses; ***Platyderus depressus*** (Figure 21) in open country among leaves and mosses; ***Amara communis*** (Figure 22) under mosses and dry leaves in a wide range of open habitats and forests with light shade; ***Amara lunicollis*** (Figure 23) in similar shade situations on peaty soil and under moss carpets of rocks; ***Harpalus pimalicus*** (see Figure 24) among mosses and leaves under bushes and trees on gravel moraines; ***Badister unipustulatus*** (Figure 25) among leaves and mosses on moist, shaded places, typically near pools; and ***Syntomus obscuroguttatus*** (Figure 26) in moist habitats on heavy soil among mosses.

Figure 16. ***Notiophilus germinyi*** adult on ***Sphagnum***. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 17. ***Blethisa multipunctata*** adult, a moss inhabitant. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 18. ***Elaphrus lapponicus***, a species of bogs and wet mosses. Photo by Gimenez de Cordoba, Beatriz through Creative Commons.

Figure 19. ***Asaphidion pallipes*** adult on mosses; this species occurs on sand with patches of tiny mosses, as shown here. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 20. ***Miscodera arctica*** adult on leafy liverwort. This species lives on fine, dry sand with fine mosses. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 21. ***Platyderus depressus***, a litter and moss inhabitant. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 22. ***Amara communis*** adult, a species that lives under mosses and dry leaves. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 23. ***Amara lunicollis*** adult, a species of peaty soil or under moss carpets of rocks. Photo by Tom Murray, through Creative Commons.

Figure 24. *Harpalus rufipes* adult. ***Harpalus pimalicus*** lives among mosses and leaves under bushes and trees on gravel moraines. Photo by Rasbak, through Creative Commons.

Figure 25. ***Badister unipustulatus*** adult, a species that lives among leaves and mosses near pools. Photo by Gábor Keresztes (xespok.net), with permission.

Figure 26. ***Syntomus obscuroguttatus*** adult, a species that lives among mosses in moist habitats. Photo by Brian Eversham, with permission.

Such widespread species as ***Notiophilus biguttatus*** (Figure 27) will traverse mosses in some of their habitats as they travel across the terrain. They may find cover there from the sun, search for food, gain moisture, or even take a drink, but they do not necessarily live there.

Figure 27. ***Notiophilus biguttatus*** adult on moss. Photo by Ladislav Tábi, with permission.

Trechus rivularis (Figure 28) occurs among mosses in lowland fens and upland mires of northern and eastern Europe (Luff 1998). ***Patrobus septentrionis*** (Figure 29) lives near water as well, living among mosses in the UK, but at lower elevations in other parts of its circumpolar distribution. Its widespread distribution is most likely facilitated by its ability to fly.

Figure 28. ***Trechus rivularis*** adult, an inhabitant of lowland fen mosses and upland mires. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 29. ***Patrobus septentrionis***, a species that lives among mosses near water. Photo ©Roy Anderson <habitas.org.uk>, with permission.

The genus ***Agonum*** has a number of bryophyte-dwelling species (Lindroth 1974), occurring in the Holarctic and Mediterranean regions to a southern limit in Central Asia (Wikipedia 2015b). These beetles are small to mid-sized and often have a metallic sheen. ***Agonum obscurum*** (Figure 30) lives among leaves and mosses in

damp deciduous forests and densely vegetated marshes (Lindroth 1974). The very **hygrophilous** (water-loving) ***A. livens*** (Figure 31) lives in marshy deciduous forests among leaves and ***Sphagnum***. ***Agonum versutum*** (Figure 32) lives at the margin of fresh water where it keeps sufficiently moist among mounds of the sedge *Carex* and mosses. ***Agonum fuliginosum*** (Figure 51) lives among mosses and leaves in moist, shady places under bushes and forest trees. ***Agonum gracile*** (Figure 33) likewise lives in very damp, shady places such as quagmires with ***Sphagnum*** (Figure 35-Figure 36) and mossy lake shores. ***Agonum sexpunctatum*** (Figure 34) lives in wet peatlands in Europe (Wikipedia 2015c). It also occurs on moist, mossy ground near water where low, mossy vegetation occurs, including damp patches in otherwise sandy heathland in Europe (Luff 1998).

Figure 30. ***Agonum obscurum*** adult, a species typical of leaves and mosses in damp deciduous forests and densely vegetated marshes. Photo by Brian Eversham, with permission.

Figure 31. ***Agonum livens*** adult, a species of marshy deciduous forests among leaves and ***Sphagnum***. Photo by Brian Eversham, with permission.

Figure 32. ***Agonum versutum*** adult, a species at the margin of fresh water among the sedge *Carex* and mosses. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 33. ***Agonum gracile*** adult, a species of quagmires with ***Sphagnum*** and mossy lake shores. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 34. ***Agonum sexpunctatum*** adult on mosses, a species that seems to be tied to bryophytes in its habitat. Photo by Christoph Benisch <www.kerbtier.de>, with permission.

In comparing ***Sphagnum*** bog habitats (Figure 35) on several continents, Främbs (1994) considers the open ***Sphagnum*** mat to be an extreme habitat with only a few carabid species. Furthermore, the behavior of ***Agonum ericeti*** (Figure 36) and ***Pterostichus rhaeticus*** (Figure 37) indicates that the carabids may only use the damp ***Sphagnum*** lawn habitats in the summer, moving to drier hummocks (Figure 38) to overwinter. In fact, these two species of ground beetles are scarce in bog areas in which there is no clear pattern of hummocks and hollows to allow them to escape the water.

Figure 35. ***Sphagnum*** in Turbal in Valle de Andorra in the east Pyrenees. Photo through Creative Commons.

Figure 36. ***Agonum ericeti*** adult on ***Sphagnum***, its summer habitat. Photo by Niels Sloth <www.biopix.dk>, with permission.

Figure 37. ***Pterostichus rhaeticus*** on wet mosses. Photo by Christoph Benisch <www.kerbtier.de>, with permission.

Figure 38. ***Sphagnum papillosum*** and ***Sphagnum capillifolium*** forming a hummock where Carabidae can spend the winter. Photo by Janice Glime.

The carabid species ***Carabus menetriesi*** (**Carabidae**) is associated with ***Sphagnum*** (Figure 35) in northern Europe and northern Russia (Barbara Knoflach-Thaler, pers. comm. 9 June 2011). It is an **FFH-species** (endangered all over Europe) and needs ***Sphagnum*** for overwintering; otherwise it would disappear. ***Carabus arvensis*** (Figure 39) hibernates under mosses as well as tree stumps (Lindroth 1985). ***Carabus glabratus*** (Figure 40), a widespread species of central and northern Europe, is day active and prefers damp areas such as peat hummocks (Figure 38) and other mosses (Weiss-Roessler 2015).

Figure 39. ***Carabus arvensis***, a species that hibernates under mosses. Photo by Christoph Benisch <www.kerbtier.de>, with permission.

Figure 40. ***Carabus glabratus*** adult on moss, a species that prefers damp areas such as peat hummocks and other mosses. Photo by Stanislav Krejčík, through Creative Commons.

Carabus clathratus (23-24 mm; Figure 41), a widespread Palaearctic species, is day active and lives an amphibious life style, including under mosses (Obydov 2006), diving under water to search for food. Its larvae develop in the summer and it overwinters as an adult to breed in early to late summer (Wallin *et al*. 1999). This overwintering can be far from water where it hibernates on drier land.

Figure 41. ***Carabus clathratus*** adult on ***Sphagnum***. Photo ©Roy Anderson <habitas.org.uk>, with permission.

In Finland, several species of **Carabidae** live in ***Sphagnum*** habitats (Figure 41) (Ljungberg 1999; Wallin *et al*. 1999). Among these is ***Chlaenius costulatus*** (striped velvet runner, hairy ground beetle; Figure 42; Figure 43). This species is a 13-14 mm predator. In other European mires, with mosses like ***Drepanocladus*** (Figure 44), one can find ***Chlaenius sulcicollis*** (swamp velvet runner; Figure 45). In Sweden, ***Chlaenius sulcicollis***, a species of Europe and Asia north to the Arctic Circle, is a critically endangered species that lives among ***Sphagnum*** in bogs (Wallin *et al*. 2000). ***Chlaenius nigricornis*** (Figure 46) lives in sheets of mosses in damp places (Bates 1843). ***Chlaenius nitidulus*** (Figure 47) lives among grasses and mosses in silty and damp places along the coast (Lindroth 1974).

Figure 42. ***Chlaenius*** sp. larva, frequently a moss dweller. Photo by Tom Murray, through Creative Commons.

Figure 43. ***Chlaenius costulatus*** adult, a ***Sphagnum*** inhabitant. Photo by Tim Faasen, with permission.

Figure 44. ***Drepanocladus aduncus***, home for several beetle species in the Czech Republic. Photo by Heike Hofmann ©swissbryophytes <swissbryophytes.ch>, with permission.

Figure 45. ***Chlaenius sulcicollis*** adult, a species found in ***Drepanocladus*** in mires. Photo by Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 46. ***Chlaenius nigricornis*** adult on moss like the sheet mosses where it lives. Photo by Niels Sloth <www.biopix.dk>, with permission.

Figure 47. ***Chlaenius nitidulus*** adult, a coastal species that lives among grasses and mosses in silty and damp places. Photo by Gernot Kunz, with permission.

In other European mires with mosses like ***Drepanocladus*** (Figure 44), one can find ***Panagaeus cruxmajor*** (great cross runner; 8-10 mm; Figure 48). The Wikipedia author for this family recounted this from Charles Darwin (1846), regarding his attempted capture of ***Panagaeus cruxmajor***:

> "I must tell you what happened to me on the banks of the Cam in my early entomological days; under a piece of bark I found two carabi (I forget which) and caught one in each hand, when lo and behold I saw a sacred ***Panagæus crux major***; I could not bear to give up either of my carabi, and to lose ***Panagæus*** was out of the question, so that in despair I gently seized one of the carabi between my teeth, when to my unspeakable disgust and pain the little inconsiderate beast squirted his acid down my throat and I lost both carabi and ***Panagæus***!"

In European mires with mosses like ***Drepanocladus*** (Figure 44), one can find ***Agonum hypocrita*** (lacquer runner; Figure 49). In Finnish boreal forests, ***Sphagnum*** (Figure 41) is a refuge for some carabids following cutting of the forests (Figure 50) (Koivula 2001). ***Agonum fuliginosum*** (Figure 51), ***Amara brunnea*** (Figure 52), ***Carabus glabratus*** (Figure 53), ***Carabus hortensis*** (Figure 54), ***Cychrus caraboides*** (Figure 55), and ***Pterostichus niger*** (Figure 56) were almost exclusively in the ***Sphagnum*** mires after cutting. On the other hand, ***Calathus micropterus*** (Figure 57) did not inhabit the mires and diminished in numbers after cutting, presumably due to increased exposure. ***Platynus mannerheimii*** (Figure 58) likewise disappeared after clearcutting, but distribution of ***Agonum fuliginosum*** is not affected by canopy cover, permitting it to survive in the more open ***Sphagnum*** mires. Hence, the ***Sphagnum*** provides a refugium that can permit at least some of the **Carabidae** to re-inhabit the forest when it regrows.

Figure 48. ***Panagaeus cruxmajor*** adult, a species found in ***Drepanocladus*** in mires. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 49. ***Agonum hypocrita*** adult, a bog dweller. Photo by Marko Mutanen, through Creative Commons.

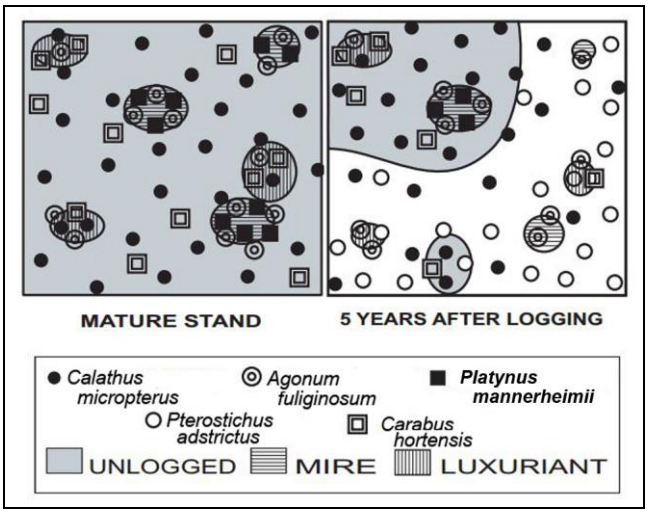

Figure 50. Response in abundance of major **Carabidae** species following clearcut logging in a mature spruce forest with three mires and three "luxuriant" sites. Modified from Koivula 2001.

Figure 51. ***Agonum fuliginosum*** adult, a species that associates with ***Sphagnum*** in boreal forests. Photo by Niels Sloth <www.biopix.dk>, with permission.

Figure 52. ***Amara brunnea*** adult, a species that associates with ***Sphagnum*** in boreal forests. Photo by Niels Sloth <www.biopix.dk>, with permission.

Figure 53. ***Carabus glabratus*** adult on moss. Photo by Dodoni, through Creative Commons.

Figure 54. ***Carabus hortensis*** adult, a moss dweller shown here on moss. Photo from <brouci.fotobarvinek.cz>, for non-commercial use.

Figure 55. ***Cychrus caraboides*** adult on moss, a species that uses ***Sphagnum*** as a refuge following forest disturbance. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 56. ***Pterostichus niger*** adult, a moss dweller shown here on moss. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 57. ***Calathus micropterus*** adult on moss in forest. Photo ©Roy Anderson <habitas.org.uk>, with permission.

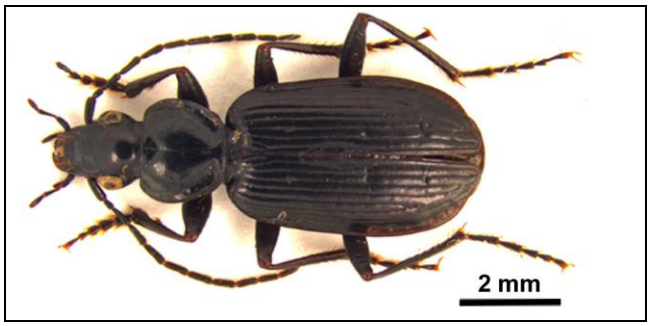

Figure 58. ***Platynus mannerheimii*** adult, a species that is unable to live in mires and thus disappears after clearcutting. Photo by Derek Sikes, through Public Domain.

It is unusual for any invertebrate to show host specificity among the bryophytes, although some bryophytes are certainly avoided by many bryophagous species. However, the carabid beetle ***Acupalpus dubius*** (Figure 59) seems to be restricted to the wetland moss ***Drepanocladus aduncus*** (Figure 44), at least in one study in the Czech Republic (Kopecký 2001). On the other hand, ***A. brunnipes*** (Figure 60) and ***A. flavicollis*** (Figure 61) seem to lack such specificity (Luff 1998). ***Acupalpus brunnipes*** occurs in both mosses and litter on mud near water in northern and western Europe, Greece, and North Africa. ***Acupalpus flavicollis*** sometimes occurs in bogs, but it is more common on river banks and in gravel pits in fine silt-covered sand where there is sparse vegetation and some mosses.

Cold temperatures seem to preclude most **Carabidae**. In the geothermal areas of Iceland, some of the geothermal areas are covered by the mosses ***Archidium alternifolium*** (Figure 62) and ***Campylopus introflexus*** (Figure 94) and the leafy liverwort ***Gymnocolea inflata*** (Figure 63) (Elmarsdottir *et al.* 2003). In some of these hotter areas, the carabids ***Bembidion bipunctatum*** (Figure 64) and ***Nebria rufescens*** (Figure 65) could survive, whereas they were not present in the colder, non-geothermal areas. Lindroth (1974) reported ***Nebria brevicollis*** (Figure 66) among mosses in UK forests and Barry (2014) found it under moss in a flower bed.

Figure 59. ***Acupalpus dubius*** adult on liverwort, a beetle that lives among ***Drepanocladus aduncus*** in the Czech Republic. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 60. ***Acupalpus brunnipes*** adult, a species that lives among mosses and litter on mud near water. Photo by Wim Rubers, through Creative Commons.

Figure 61. ***Acupalpus flavicollis*** adult, a species that sometimes occurs in bogs as well as river banks and in gravel pits where there are some mosses. Photo by Tim Faasen, with permission.

Figure 62. ***Archidium alternifolium***, a geothermal moss that supports several species of **Carabidae**. Photo by Michael Lüth, with permission.

Figure 63. ***Gymnocolea inflata*** with perianths, a geothermal leafy liverwort that supports several species of **Carabidae**. Photo by Malcolm Storey, through Creative Commons.

Figure 64. ***Bembidion bipunctatum***, moss inhabitants in geothermal areas of Iceland. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 65. ***Nebria rufescens*** adult, a species that takes advantage of geothermal mosses in cold regions. Photo ©Roy Anderson <habitas.org.uk>, with permission.

Figure 66. ***Nebria brevicollis*** adult with moss, a species known to occur under mosses. Photo by Fritz Geller-Grimm, through Creative Commons.

Elsewhere, in the UK, ***Bembidion gilvipes, B. biguttatum***, and ***B. mannerheimii*** live among mosses (Lindroth 1974). The first two of these live in forests. ***Bembidion mannerheimii*** lives in forests and fens. All three species also live among leaf litter and other substrata as well. Darwin even reported the genus from a nest of mosses (Smith & Freeman 1987).

The **Carabidae** are generalist feeders, suggesting they should be able to find food among any of the bryophytes, including fungi, bacteria, detritus, and various invertebrates (König *et al*. 2011). Thus far there seems to be no evidence that they eat the bryophytes.

POLYPHAGA

Artemotopoidea

Artematopidae – Soft-bodied Plant Beetles

Larvae and adults of beetles often live in different places. And if they are both in the same aquatic habitat, the pupae are typically on land. Even among the terrestrial bryophytes, the physiology and morphology differ sufficiently that many prefer different habitats. On the other hand, many are flightless, restricting their ability to move around.

Such habitat difference seems to be the case for members of ***Macropogon***. Adults of ***Macropogon testaceipennis*** (Figure 67) and ***M. piceus*** (Figure 68) in western Washington and Oregon, USA, usually live on trees and shrubs near moss-covered boulders or rock outcrops (Loren Russell, pers. comm.). ***Macropogon*** larvae, on the other hand, can be found under mosses such as ***Ceratodon purpureus*** (Figure 69) and others growing on sandy loam of a stream bank in Viento State Park, Oregon.

Figure 67. ***Macropogon testaceipennis*** adult, a species that seems to prefer trees and shrubs with moss-covered rocks nearby. Photo by Joyce Gross, with permission.

Figure 68. ***Macropogon piceus***, a species whose adults seem to prefer trees and shrubs with moss-covered rocks nearby. Photo by Jim McClarin, with permission.

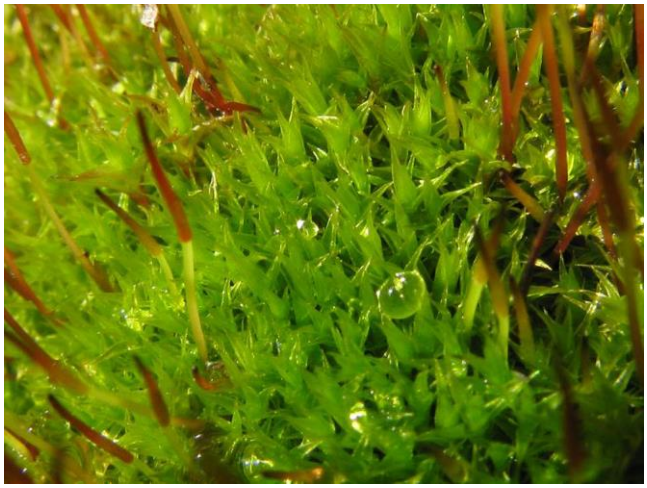

Figure 69. ***Ceratodon purpureus***, home for larvae of ***Macropogon*** species. Photo by Jiří Kameníček (BioLib, Obázek), with permission.

Larvae of another member of this family, ***Eurypogon*** cf. ***californicus*** (Figure 70), occur under mosses growing on exposed rocks of road cuts at Mary's Peak, Oregon, and near the Alsea River (Loren Russell, pers. comm.).

Figure 70. ***Eurypogon californicus***, species that lives under mosses on exposed rocks. Photo from Museum of Comparative Zoology, Harvard, through Creative Commons.

Byrrhoidea

Byrrhidae – Pill Beetles

The **Byrrhidae** are known for their habit of living among mosses. Not only do they live there, but the mosses serve as their food source in most cases (pers. comm. Loren Russell & Paul Johnson, 21 March 2012). A few actually feed on liverworts, and some on **tracheophytes** (lignified vascular plants, including flowering plants). In the Pacific Northwest, USA, the genus ***Amphicyrta*** (Figure 71) is the only member of the family known to feed on tracheophytes and no bryophytes, becoming a pest in lily fields. But generally, members of this family are adapted to living in transitional **ruderal** (wasteland) microhabitats where mosses dominate (Majka & Langor 2011), including such open habitat mosses as ***Ceratodon purpureus*** (Figure 69), ***Polytrichum juniperinum*** (Figure 72), and ***P. piliferum*** (Figure 73) growing on moist, thin or scarified soil (Johnson 2002).

Figure 71. ***Amphicyrta*** sp. adult, an unusual member of **Byrrhidae** not known to eat bryophytes. Photo by Joyce Gross, with permission.

Figure 72. ***Polytrichum juniperinum*** with males, common home for **Byrrhidae**. Photo by Dale Vitt, with permission.

Figure 73. ***Polytrichum piliferum***, common home for **Byrrhidae**. Photo by Thomas Brown, through Creative Commons.

Several of the byrrhid characteristics suit them for the moss habitat. Their small size (1-10 mm) (Johnson 2002) and convex, compact shape, and retractile appendages (Johnson 2013) permit ease of movement among the moss maze and make them inconspicuous to most predators. When detected, they have the ability to play dead by retracting their legs and antennae into grooves on the lower surface (Figure 74-Figure 75), remaining motionless (Lindquist & Ingram 1968). This motionless behavior along with their shape has earned them the common name of pill beetles. Their ability to subsist on mosses suggests that they may have special digestive adaptations as well.

The **Byrrhidae** are common farther north and at higher altitudes than most of the insects. Majka and Langor (2011) suggest that this may be possible due to their ability to eat bryophytes. The bryophyte species diversity changes little with latitude (Shaw *et al*. 2005), whereas tracheophyte diversity diminishes. Furthermore, most bryophytes have longer growing seasons than most tracheophytes and are available immediately upon snow melt as a source of food. We know that bryophytes produce **arachidonic acid** (a fatty acid) (Shinmen *et al*. 1991; Kajikawa *et al*. 2008) and it would be interesting to explore whether the arachidonic acid in bryophytes may help to keep membranes of bryophyte consumers more fluid at cold temperatures. Furthermore, it may be helpful in promoting larval growth (Fraenkel & Blewett 1947), permitting these beetles to complete their life cycles in the short growing season of cold ecosystems.

Figure 74. ***Byrrhus*** sp playing dead in Scotland. Photo by Roger S. Key, with permission.

Figure 75. **Byrrhidae** feigning death. Note how the legs fit into grooves on the underside. Photo by Barbara Thaler-Knoflach, with permission.

Members of the **Byrrhidae** (***Cytilus sericeus***, ***Byrrhus fasciatus***, ***Byrrhus pilula***, ***Byrrhus glabratus***) often travel some distances from the mosses where they sleep, preferring acrocarpous mosses to pleurocarpous ones (Pyszko *et al*. in prep). Their guts contain considerably higher moss species richness than that in their immediate microhabitats.

Although several authors have considered that the direct evidence for associations of Byrrhidae with mosses is still rare (Reichenbach 1844; Watt 1971; LeSage 1983; Johnson 1986; Hradílek & Boukal 2003), that family is better known among terrestrial bryophyte inhabitants than other groups. ***Cytilus sericeus*** has been reported from ***Sphagnum*** spp. (Mateleshko, 2009), ***Tortula muralis*** (Reichenbach 1844) and ***Amblystegium varium*** (Pristinskaya 2003). ***Byrrhus fasciatus*** is known from ***Aulacomnium*** spp. (Böcher 1988), ***Andreaea*** spp., ***Brachythecium velutinum***, ***Bryum*** spp., ***Myurella*** spp. (Pristinkaya 2003), ***Philonotis tomentella*** (Lindroth 1931), and ***Racomitrium*** spp. (Janetschek 1949); ***Byrrhus pilula*** occurs with ***Sphagnum*** spp. and ***Polytrichum*** spp. (Pristinskaya 2003; Sushko 2007); and ***Byrrhus glabratus*** with ***Plagiomnium cuspidatum*** and ***Rhizomnium punctatum*** (Reichenbach 1844).

The slow or incomplete digestion of bryophytes permits identification from the guts of bryophagous insects (Haines & Renwick 2009; Kočárek *et al*. 2008).

Amphicyrta

This genus (Figure 71), restricted to California and Oregon, USA, is the exception among the **Byrrhidae**. Larvae and adults of this genus are not bryophyte feeders (Johnson 2013). Rather, they feed on succulent leaves and stems of forest and meadow herbs and on deciduous shrubs.

Byrrhus

Byrrhus (Figure 76) ranges from tiny to small (1-10 mm) (Johnson 2013). All the adults in this genus that feed on bryophytes are surface grazers. In addition to bryophytes they may occasionally feed on conifer seedlings, grasses, and clover in the moist areas that have abundant mosses. The larvae, on the other hand, burrow through the bryophyte layers and feed at the tunnel entrance by extending part of the body out to graze on bryophyte leaves and shoots.

Figure 76. ***Byrrhus fasciatus*** on moss in UK, showing underside with legs tucked into grooves while it plays dead. Photo by Roger S. Key, with permission.

Byrrhus luniger eats its own home. In Štramberk, a small town in the Moravian-Silesian Region of the Czech Republic, these beetles spend at least part of their lives among **Polytrichaceae**. Gut analysis reveals cells of these mosses in the gut (Hradílek & Boukal 2003). Papillae on the terminal lamina cells suggest that the mosses were either ***Pogonatum urnigerum*** (Figure 77) or ***Polytrichastrum alpinum*** (Figure 78).

In northwestern United States, Loren Russell and Paul Johnson (pers. comm. 21 March 2012) found different species of ***Byrrhus*** as moss dwellers: ***Byrrhus americanus*** (Figure 80), ***B. concolor*** (Figure 81), and ***Byrrhus kirbyi*** (~6.5 mm; Figure 82). Gut analysis of museum specimens of all three species revealed that mosses had served as food items. Not surprisingly, these beetles have seldom been collected, perhaps because the tiny creatures seldom venture out of their cozy cushions to fall into pitfall traps.

Figure 77. ***Pogonatum urnigerum***, a likely food of ***Byrrhus luniger***. Photo by James K. Lindsey, with permission.

Figure 78. ***Polytrichastrum alpinum***, likely food for ***Byrrhus luniger***. Photo by David T. Holyoak, with permission.

Some records of this genus among mosses are old. Ferguson (1901) reported ***Byrrhus pilula*** (Figure 79) from mosses in the Clyde Area of the British Isles.

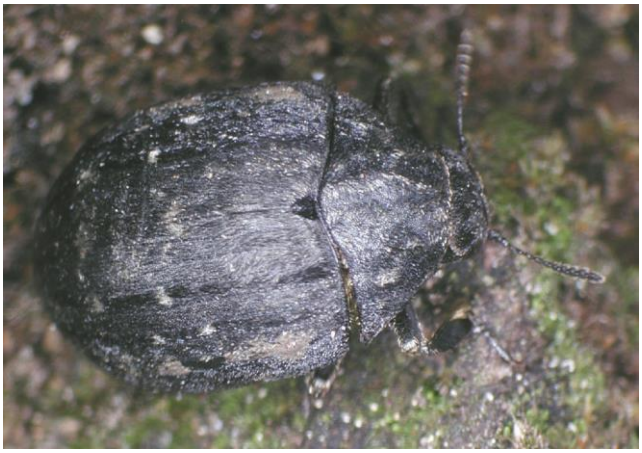

Figure 79. ***Byrrhus pilula***, a moss dweller in the British Isles. Photo by Petr Kočárek and Pavel Drozd, with permission.

Figure 80. ***Byrrhus americanus*** adult, a moss dweller and consumer in northwestern United States. Photo by Tom Murray, through Creative Commons.

Figure 81. ***Byrrhus concolor***, moss feeder in northwestern USA. Photo by Tom Murray, through Creative Commons.

Figure 82. ***Byrrhus kirbyi*** adult, a moss dweller in northwestern USA. Photo by Tim Loh, with permission.

Chaetophora

Yes, ***Chaetophora*** is also a genus of green algae. Neither group of nomenclatural taxonomists has created a rule to prevent using the same name in another kingdom. The byrrhid ***Chaetophora*** is a native of Eurasia, but it is adventive in northeastern USA (McLeod 2006). It lives in areas with sparse vegetation, but with mosses.

Chaetophora spinosa (Figure 83) appears to be invasive in North America as a European immigrant (Johnson 1990). On Prince Edward Island, Canada, ***Chaetophora spinosa*** occurs on the moss ***Mnium hornum*** (Figure 84) and the nearby bare mud. In Idaho, USA, adults can be found in large numbers with the mosses ***Pohlia atropurpurea***, ***Dicranella varia*** (Figure 85), and ***Aloina brevirostris*** (Figure 86), but ***A. brevirostris*** has not been confirmed as a host for food (Johnson 1990). The beetles also consume the Cyanobacterium ***Nostoc*** (Figure 87) and it would be interesting to know if the occurrence of ***Nostoc*** on mosses might serve as an attractant and food source there.

Figure 83. ***Chaetophora spinosa*** adult, an invasive moss dweller in North America. Photo by Tom Murray, through Creative Commons.

Figure 84. ***Mnium hornum***, home for ***Chaetophora spinosa***. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

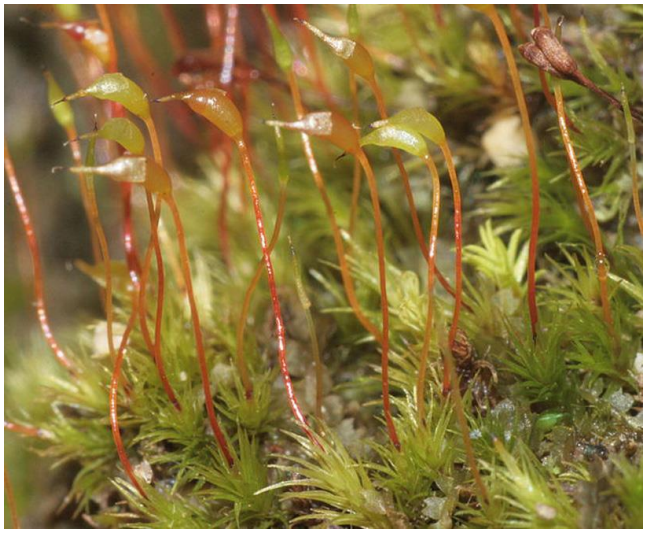

Figure 85. ***Dicranella varia*** with capsules, home for ***Chaetophora spinosa***. Photo by Hermann Schachner, through Creative Commons.

Figure 86. ***Aloina brevirostris***, home for ***Chaetophora spinosa***. Photo by Michael Lüth, with permission.

Figure 87. ***Nostoc*** cf ***commune*** on bryophytes. Photo by Jiří Kameníček (BioLib, Obázek), with permission.

Chalciosphaerium

This moss-dwelling genus (Figure 88-Figure 90) was not known from South Georgia until 2009 when Roger S. Key (2009) found it with larvae (Figure 88) and pupae (Figure 89) that might be the same species. The species was later determined to be ***Chalciosphaerium solox*** (Figure 90), a species known from the Falklands (Roger S. Key, pers. comm. 4 December 2015). DNA confirmation is pending. If it is indeed that species, it is likely that it arrived with human traffic. Its apparent absence in other relatively nearby locations (indicated by searches for it) further support this interpretation. The location was a few hundred meters from the dis-embarkation site for many tourists and other visitors. Its small size would make it easy to be a hitchhiker on boots or other clothing or backpacks.

This species occurred with ***Polytrichum*** that was mixed with grasses (Roger S. Key, pers. comm. 4 December 2015). The researchers were unable to find it among nearby grasses that had no moss associates. More were, however, among other patches of the nearby mosses.

Figure 88. Larva, probably ***Chalciosphaerium*** sp., among mosses and liverworts at Grytviken, South Georgia. Photo by Roger S. Key, with permission.

Figure 89. Pupa, probably ***Chalciosphaerium*** sp., among mosses and leafy liverworts at Grytviken, South Georgia. Photo by Roger S. Key, with permission.

Figure 90. ***Chalciosphaerium*** sp. adult on leafy liverworts from Grytviken, South Georgia. Photo by Roger S. Key, with permission.

Figure 92. ***Dicranella cerviculata*** with capsules, home and food for ***Curimopsis***. Photo by David T. Holyoak, with permission.

Curimopsis

Some of our photographers make great observations! Both my sister and I have been surprised on occasion to find an insect in our pictures when we enlarge them on the computer screen, but we never saw it when we were taking the picture. So I admire and envy these astute photographers who note the interesting behavior of these tiny inhabitants.

One such photographer is Brian Eversham. He shared with me his observations on ***Curimopsis*** (Figure 95-Figure 98) in Great Britain (Brian Eversham, pers. comm. 21 March 2012). He studied this genus for several years and found that it seems to prefer ***Dicranella*** [***D. heteromalla*** (Figure 91) and ***D. cerviculata*** (Figure 92)] for shelter and food among the mosses in its habitat. It also eats ***Pohlia nutans*** (which is common there too; Figure 93) and even the invasive ***Campylopus introflexus*** (Figure 94).

Figure 93. ***Pohlia nutans*** with capsules, home and food for ***Curimopsis***. Photo by J. C. Schou <www.biopix.com>, with permission.

Figure 91. ***Dicranella heteromalla***, home and food for ***Curimopsis***. Photo by Janice Glime.

Figure 94. ***Campylopus introflexus***, home and food for ***Curimopsis***. Photo by Michael Lüth, with permission.

In peat areas, the peat dries out in the summer in Thorne and Hatfield Moors, UK, due to the low rainfall (Brian Eversham, pers. comm. 21 March 2012). When this occurs, the females construct burrows down to 4 cm deep in the peat. These are usually close to the ***Dicranella*** (Figure 91-Figure 92) species. To build their burrows they collect moss leaves, one at a time, and like ants they carry them in their jaws. These are carried underground to line the burrows in a spiral arrangement around the walls. This "wallpaper" serves to feed the young larvae.

Johnson (1986) found ***Curimopsis moosilauke*** (Figure 95) to be a characteristic species above the **krummholz ecotone** (transition to stunted windblown trees growing near the tree line on mountains). These beetles often occurred between rocks and boulders where fine, moist, matted mosses grew on the sandy soils.

Figure 95. ***Curimopsis moosilauke*** adult, a moss associate above the krummholz. Photo by Kirill V. Makarov <www.zin.ru>, through public domain.

Curimopsis nigrita (mire pill beetle, bog-hog; Figure 96-Figure 97) is a tiny beetle only about 1.2 mm long. It burrows in peat and under mosses, lining these burrows with moss leaves (Roger S. Key, pers. comm. 31 October 2014). Perhaps this is the species seen by Brian Eversham, both in the UK.

Figure 96. ***Curimopsis nigrita***, on Hatfield Moors, South Yorkshire. Photo by Brian Eversham, with permission.

Figure 97. ***Curimopsis nigrita*** (mire pill beetle), uncovered from its burrow under mosses. Note how well it blends with its surroundings. Photo by Roger S. Key, with permission.

On Mt. Hood, Oregon, USA, ***Curimopsis albonotata*** (Figure 98) lives at higher elevations (Loren Russell & Paul Johnson, pers. comm. 21 March 2012). Similarly, ***C. brevicollis*** lives at high elevations on Mt. Rainier, Washington, USA. The latter, collected in northern Idaho, had mosses in its gut. Both of these species seem to be limited to higher elevations.

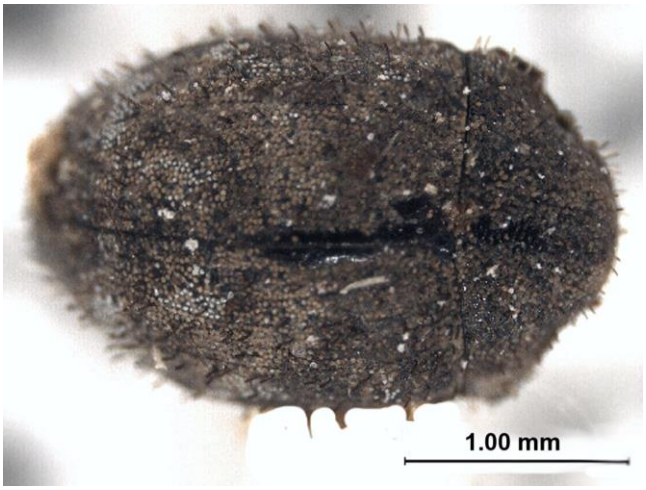

Figure 98. ***Curimopsis albonotata*** adult, a moss-dwelling, high-elevation species on Mt. Rainier, Washington, USA. Photo by CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Cytilus

In the Atlantic region of Canada, larvae of the boreal ***Cytilus alternatus*** (Figure 99-Figure 100) live in thick layers of ***Sphagnum*** (Figure 35) (LeSage 1983; Majka & Langor 2011). ***Cytilus*** species, unlike those of most **Byrrhidae**, do not burrow and instead feed at the surface as larvae (Johnson 2013). And unlike most of the **Byrrhidae**, members of ***Cytilus*** are active in open mossy areas in sunlight (Figure 103) (Johnson 2002). The guts of these larvae contain dead leaves, dead wood of Ericaceae (heaths), mosses, liverworts, and other vegetable matter, suggesting that this species is a detritivore. Both adults and larvae include mosses in their diet.

Figure 99. ***Cytilus alternatus*** larva, a stage that eats mosses, among other things. Photo by Tom Murray, through Creative Commons.

Figure 100. ***Cytilus alternatus*** eating moss. Note that the tip of the larger ***Plagiomnium*** at the right has been eaten. Photo by Alex Wild, free for educational use.

In the northwestern United States, ***Cytilus alternatus*** (Figure 99-Figure 100) is a widely distributed boreal insect of open rocky sites, often near seepages or waterfalls (Loren Russell & Paul Johnson, pers. comm. 21 March 2012). ***Cytilus sericeus*** (Figure 101-Figure 102) lives among the **Polytrichaceae** (Figure 103), where it feeds on mosses. These are in the typical open habitats known for this genus (Figure 50).

Figure 101. ***Cytilus sericeus***, a bryophagid in peatland. Photo by James K. Lindsey, with permission.

Figure 102. ***Cytilus*** larva, a peatland inhabitant. Photo by Don Loarie, through Creative Commons.

Figure 103. ***Cytilus sericeus*** habitat with clumps of **Polytrichaceae**. Photo by James K. Lindsey, with permission.

Epichorius

Epichorius hails from the other end of the Earth from Auckland Island, New Zealand (Wahedi *et al*. 1974). Here one can find larvae of ***E. longulus*** and ***E. aucklandiae*** among bryophytes in the coastal rata forest (Figure 104-Figure 105). ***Epichorius longulus*** larvae can be found among bryophytes on the ground, abundantly occupying species of the thallose liverwort ***Riccardia*** (Figure 106) and rarely in mats of the leafy liverwort ***Bazzania adnexa*** (Figure 107). This difference may be one of nutrition. Larvae that fed on ***Riccardia*** thalli gained more weight that those fed on the leafy liverwort ***Bazzania adnexa***. The larvae were absent on bare ground and among tree roots. But the larvae were not immobile. They sought shelter under leaf litter during the day and appeared on the liverworts at night to feed.

Figure 104. Rata forest, Auckland Island, where ***Epichorius*** lives among liverworts. Photo by James Russell <islandconservation.auckland.ac.nz>, with permission.

Figure 105. Rata forest (*Metrosideros umbellata*), Enderby Island in sub-Antarctic New Zealand. This forest is home for ***Epichorius*** among the liverworts. Photo courtesy of John Barkla.

Figure 106. ***Riccardia latifrons***, a genus that is home for ***Epichorius longulus*** larvae. Photo by David T. Holyoak, with permission.

Figure 107. ***Bazzania adnexa***, home for ***Epichorius longulus*** larvae. Photo by Niels Klazenga, with permission.

Exomella

This genus is restricted to mesic coniferous forests in the Pacific Northwest, USA. ***Exomella pleuralis*** (Figure 108) inhabits ***Racomitrium heterostichum*** (Figure 109) (Johnson & Russell 1978). In the lab they both ate and oviposited on ***Eurhynchium oreganum*** (Figure 110).

Figure 108. ***Exomella pleuralis*** adult, an inhabitant of ***Racomitrium heterostichum*** in the Pacific Northwest, USA. Photo by CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 109. ***Racomitrium heterostichum***, home for ***Exomella pleuralis***. Photo by Michael Lüth, with permission.

Figure 110. ***Eurhynchium oreganum***, suitable food for ***Exomella pleuralis***. Photo by Matt Goff <www.sitkanature.org/>, with permission.

Lioligus

Both ***Lioligus nitidus*** (Figure 111) and ***L. striolatus*** occur in mossy sites of the coastal mesic coniferous forests in the Pacific Northwest, USA (Loren Russell & Paul Johnson, pers. comm. 21 March 2012). ***Lioligus striolatus*** is more northern, living in northwest Washington, whereas ***L. nitidus*** is more common in western Oregon. Russell and Johnson suggest that they may be two forms of the same species. Laboratory experiments indicate that both have broad food choices in both larval and adult stages. In the lab, their foods included the mosses ***Eurhynchium oreganum*** (Figure 110), ***Hylocomium splendens*** (Figure 112), ***Hypnum circinale*** (Figure 113), ***Plagiothecium undulatum*** (Figure 114), ***Racomitrium heterostichum*** (Figure 109), ***Rhytidiadelphus loreus*** (Figure 115), and ***R. triquetris*** (Figure 116). The moss ***Metaneckera menziesii*** (Figure 117) was refused. In the lab, Russell and Johnson found that one specimen of ***L. striolatus*** survived from egg to adult with only leafy liverworts [***Diplophyllum plicatum*** (Figure 118) and ***Scapania bolanderi*** (Figure 119)] to eat. However, this was an isolated success – other adult members of ***Lioligus*** would not feed on ***Scapania*** or other liverworts in cultures.

Figure 111. ***Lioligus nitidus*** adult female, a species that eats both mosses and liverworts. Photo by Louisiana State Arthropod Museum, through Creative Commons.

Figure 112. ***Hylocomium splendens***, a suitable food for species of ***Lioligus***. Photo by Andrew Spink, with permission.

Figure 113. ***Hypnum circinale*** with capsules, a suitable food for species of ***Lioligus***. Photo by Tab Tannery, through Creative Commons.

Figure 114. ***Plagiothecium undulatum***, a suitable food for species of ***Lioligus***. Photo by Kristian Peters, with permission.

Figure 115. ***Rhytidiadelphus loreus***, a suitable food for species of ***Lioligus***. Photo by Andrew Spink, with permission.

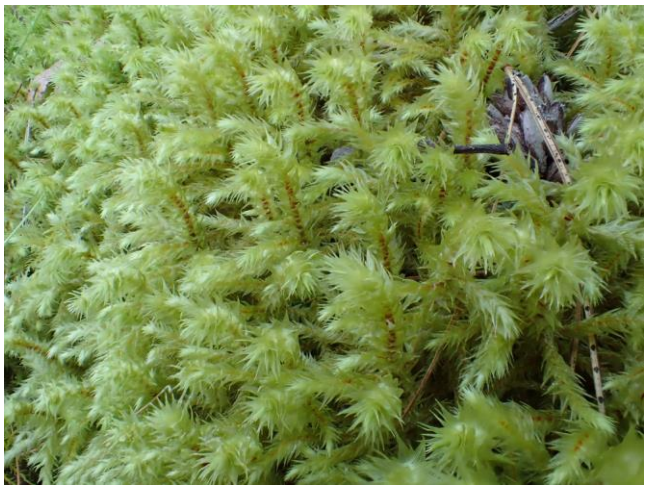

Figure 116. ***Rhytidiadelphus triquetrus***, a suitable food for species of ***Lioligus***. Photo by Janice Glime.

Figure 117. ***Metaneckera menziesii***, a potential food that was refused by species of ***Lioligus***. Photo by Michael Lüth, with permission.

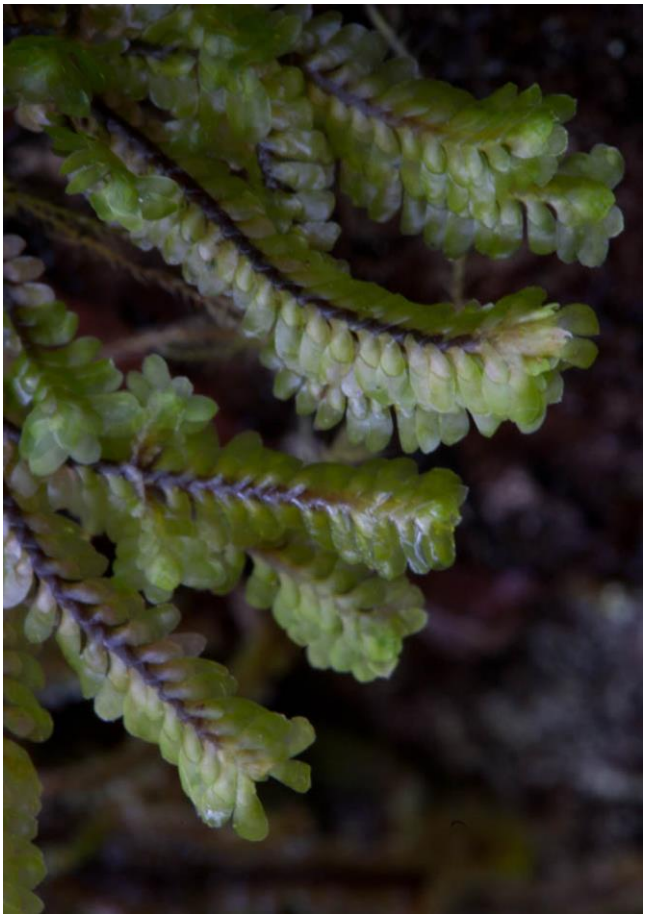

Figure 118. ***Diplophyllum plicatum***, a suitable food for ***Lioligus striolatus***. Photo by Martin Hutten, with permission.

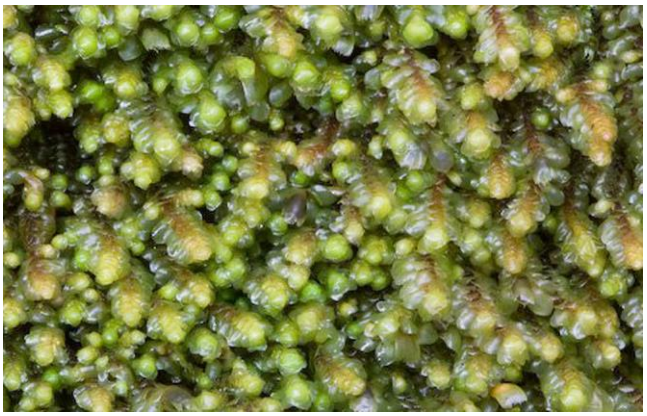

Figure 119. ***Scapania bolanderi***, a suitable food for ***Lioligus striolatus*** in the lab, but not for other members of the genus. Photo by Matt Goff <www.sitkanature.org>, with permission.

Lioon

Lioon puncticeps and ***L. simplicipes*** (Figure 120) are closely related species in the coastal coniferous forests of western USA (Loren Russell & Paul Johnson, pers. comm. 21 March 2012). Larvae and adults have a wide range of mossy habitats, ranging from wet, boggy soil to dry epiphytes. Like ***Lioligus*** (Figure 111), they accept a wide range of host mosses, including ***Antitrichia curtipendula*** (Figure 121), ***Dicranum fuscescens*** (Figure 122), ***Eurhynchium oreganum*** (Figure 110), ***Plagiothecium***

undulatum (Figure 114), and ***Rhytidiadelphus loreus*** (Figure 115) for ***L. puncticeps***. They also eat leaf tips and leaf lamellae of ***Polytrichum commune*** (Figure 123), but they leave the tougher parts such as the stems.

Figure 120. ***Lioon simplicipes*** adult, a species that lives among mosses in a wide range of habitats in western USA. Photo by Joyce Gross, with permission.

Figure 121. ***Antitrichia curtipendula***, a host species for ***Lioon puncticeps***. Photo by James K. Lindsey, with permission.

Figure 122. ***Dicranum fuscescens***, a host species for ***Lioon puncticeps***. Photo by Michael Lüth, with permission.

Figure 123. ***Polytrichum commune*** habit, common home and food for beetles, including ***Lioon puncticeps***. Photo by Sten Porse, through Creative Commons.

Listemus

Listemus is a small genus with three species in northwestern North America. These include ***L. acuminatus*** (Figure 124) and ***L. formosus*** (Russell 1979; Loren Russell & Paul Johnson, pers. comm. 21 March 2012). They are restricted to mesic coniferous forests of the Pacific Northwest, USA, but differ from ***Lioligus*** (Figure 111) and ***Lioon*** (Figure 120) in being restricted to mosses on soil, rocks, or logs and are not known from epiphytic bryophytes. In the lab both adults and larvae of ***Listemus acuminatus*** can survive on ***Eurhynchium oreganum*** (Figure 110), ***Hypnum circinale*** (Figure 113), and ***Plagiothecium undulatum*** (Figure 114). In the field one can find larvae of ***L. acuminatus*** in nearly pure mats of the leafy liverworts ***Gyrothyra underwoodiana*** (Figure 125) and ***Nardia scalaris*** (Figure 126), but there is no evidence that these beetles feed on them. It is possible that they feed on the occasional mosses that grow with the liverworts.

Figure 124. ***Listemus acuminatus*** adult, a species among mosses on the ground, rocks, or logs. Photo by Joyce Gross, with permission.

Figure 125. ***Gyrothyra underwoodiana***, home for larvae of ***Listemus acuminatus***, but apparently not suitable food. Photo by Tab Tannery, through Creative Commons.

Figure 126. ***Nardia scalaris*** with capsules, home for larvae of ***L. acuminatus***, but apparently not suitable food. Note the accompanying mosses. Photo by J. C. Schou <www.biopix.com>, with permission.

Nothochaetes

Nothochaetes howensis (see Figure 127), a new genus and species, lives among mosses on trees in Australia (Lawrence *et al*. 2013).

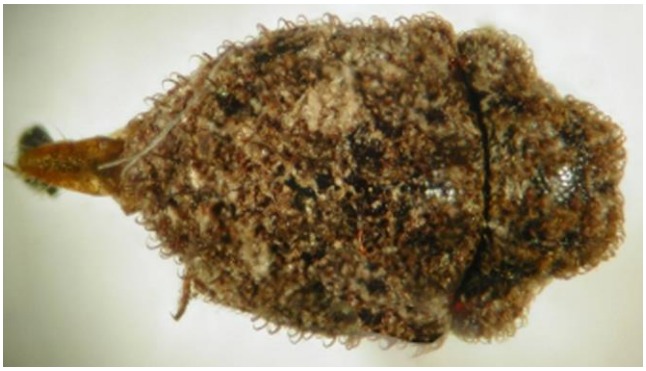

Figure 127. ***Nothochaetes fasciculatus*** adult. ***Nothochaetes howensis*** lives among mosses on Australian trees. Photo by Lynne Forster, with permission.

Notolioon

Lawrence *et al*. (2013) described six new genera from the **Byrrhidae** in Australia (Figure 128-Figure 129) and made nomenclatural changes in how some of the existing species are classified. This study suggests that many more **Byrrhidae** might be found around the world if more bryophytes are searched.

Notolioon nodipennis (Figure 128-Figure 129), a member of the most water-loving of the Australian **Byrrhinae**, occurs in the wet forests of southeastern Australia and Tasmania (Lawrence *et al*. (2013). Both adults and larvae appear to be adapted to feeding on mosses and liverworts, based on their lack of digging legs in the adult and the occurrence in the larvae of a well-sclerotized dorsal cuticle that has defensive glands.

Figure 128. ***Notolioon nodipennis*** among mosses, a species newly described in 2013. Photo by Kristi Ellingsen, Insects of Tasmania, with permission.

Figure 129. ***Notolioon nodipennis*** among mosses, demonstrating its ability to play dead by pulling its legs against its body. Photo by Kristi Ellingsen, Insects of Tasmania, with permission.

Simplocaria

In western Europe one can find ***Simplocaria metallica*** (Figure 130) in the lower part of the alpine zone. In this alpine area it lives among mosses in sandy places, often close to water courses or lakes, attesting to the importance of water in its habitat. It also occurs in the sub-alpine region, but it is rarely found in conifer forests (Böcher 1988). In Greenland, it is typically associated with the mosses ***Polytrichum commune*** (Figure 123) and ***Aulacomnium*** sp. (Figure 131), but also with the lichen *Peltigera* sp. (Figure 132) and the flowering plant *Cerastium alpinum* (Figure 133). Johnson (1990) found it with different mosses (***Bryum***?; Figure 134) on sandy gravel in boulder fields. These larvae, like those of ***Byrrhus*** (Figure 74, Figure 76-Figure 81), burrow into the moss mats (Böcher 1988).

Figure 130. ***Simplocaria metallica*** adult, a moss dweller in alpine and subalpine zones in Europe. Photo from Louisiana State Arthropod Museum, through Creative Commons.

Figure 131. ***Aulacomnium palustre***, home for ***Simplocaria metallica***. Photo by Janice Glime.

Figure 132. ***Peltigera canina***, a lichen genus that is one of the habitat choices for ***Simplocaria***. Photo by J. C. Schou <www.biopix.com>, with permission.

Figure 133. ***Cerastium alpinum***, alternate host of ***Simplocaria metallica***. Photo by Meneerke Bloem, through Creative Commons.

Figure 134. ***Bryum algovicum***, in a genus that can serve as host for ***Simplocaria metallica***. Photo by David T. Holyoak, with permission.

Simplocaria semistriata (Figure 135) is a native of Europe, but it has become widespread in North America (McClarin 2006). It grazes on the pioneer moss ***Dicranella heteromalla*** (Figure 85) and in Scotland on ***Mnium hornum*** (Figure 84) (Johnson 1990). Like ***Chaetophora spinosa*** (Figure 83), ***Simplocaria semistriata*** appears to be an invasive species in North America (Johnson 1990). Here it feeds, mates, and oviposits on mats of ***Dicranella heteromalla***. At the same time, both larvae and adults avoid feeding on intermixed ***Atrichum angustatum*** (Figure 136) in both the field and laboratory. Since ***Mnium hornum*** is abundant in North America, but in more moist sites than those of ***D. heteromalla***, it is likely that ***Simplocaria semistriata*** will be found on that host in North America as well. Nate Schoonover (BugGuide 2015) reports that this species plays dead when disturbed. His 3 mm adults appeared in his terrarium among "cushion mosses" collected in Dover, New Hampshire, USA.

Figure 135. ***Simplocaria semistriata*** (Coleoptera: Byrrhidae), a North American invasive moss dweller shown here on mosses. Photo by Vítězslav Plášek, with permission.

Figure 136. ***Atrichum angustatum***, a moss that is avoided as food by ***Symplocaria semistriata***. Photo by Michael Lüth, with permission.

Chelonariidae – Turtle Beetles

This family, mostly tropical (Harpootlian 2006), was presumed to be aquatic, but Spangler (1980) discovered that it included a number of terrestrial larvae in ***Chelonarium*** (Figure 137). The adults are larger than most moss dwelling beetles (2.5-10 mm) and have the oval shape and somewhat flattened body typical of swimming beetles. But these lack gills and in the tropics they are associated with roots of a number of species of orchids and a few other epiphytes. Although the larvae have been reported from aquatic habitats, Brown (1972) suggested that these larvae might have been living on damp mosses near the streams and occasionally were washed into streams.

Figure 137. ***Chelonarium lecontei*** adult. Some members of this genus that have terrestrial larvae associated with mosses near water. Photo by Mike Quinn, through Creative Commons.

Limnichidae – Minute Marsh-loving Beetles

This is a relatively small family (~400 spp.), as beetles go, but it nevertheless has worldwide distribution (Harpootlian 2005). It is small (~2 mm) and rounded and, in the word of Harpootlian, otherwise "unremarkable" (Figure 138). This family is primarily riparian, living streamside, on emergent plants, on wood, or in windrows of debris. The larvae live in damp soil near water. Little is known about their food – they are presumed to be herbivorous.

Figure 138. ***Eulimnichus*** adult showing the nondescript appearance of the **Limnichidae**. Photo by Tom Murray, through Creative Commons.

Although little is known about the biology of the **Limnichidae**, some are known to feed on algae and mosses (Pütz 1998). Jim McClarin (pers. comm. 30 August 2014) finds **Limnichidae** with bryophytes in the cloud forest zone of eastern Ecuador.

Pütz (1998) reported on members of this family in China. There one can find ***Cephalobyrrhus sichuanensis*** on algae and mosses of sandy river banks. Champion (1925) earlier reported ***Cephalobyrrhus gibbicollis*** running over wet mosses on river banks in India.

Summary

The **Carabidae** are the only members of **Adephaga** I have found to associate with bryophytes. The **Carabidae** among bryophytes lack any special adaptations for that habitat. Some are there to feed, including fungi, bacteria, detritus, and various invertebrates. Bryophytes themselves do not seem to serve as a food source for them. Nevertheless, the diversity of **Carabidae** among bryophytes is large. Some use the mosses as a summer refuge where they can find moisture or a place to spend the winter. Some, often rare species, inhabit bogs. ***Sphagnum*** mires in forests serve as a refuge for carabid species following cutting.

Some members of **Artematopidae** live among bryophytes as larvae.

The **Byrrhidae** are well known as moss-dwelling beetles. They are typically tiny and rounded. Some are able to play dead when disturbed and can retract their legs into grooves on the lower surface. Most of them also eat bryophytes, including a wide range of species, and some are known to eat liverworts. Some burrow into ***Sphagnum***. The ability of these beetles to survive at high altitudes and latitudes may be due to the **arachidonic acid** from their bryophyte diet. The family is ancient and worldwide. Because of the difficulty of sampling these tiny moss inhabitants, and their inability to disperse far, one is likely to encounter new species if venturing into an unexplored region. Other species are invasive as passengers with their moss habitat when it is used commercially.

Other moss-dwelling members of **Byrrhoidea** include some species in the **Chelonariidae** and **Limnichidae**.

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CHAPTER 12-9c
TERRESTRIAL INSECTS: HOLOMETABOLA – COLEOPTERA FAMILIES

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CHAPTER 12-9c TERRESTRIAL INSECTS: HOLOMETABOLA – COLEOPTERA FAMILY

Figure 1. **Curculionidae** on moss and litter in Ecuador. Photo by Andreas Kay, through Creative Commons.

POLYPHAGA cont.

Chrysomeloidea

Chrysomelidae – Flea Beetles, Leaf Beetles

This family of 35,000 species ranges 1-18 mm in length (Wikipedia 2015c). They are distributed everywhere except the high Arctic and the Antarctic (Benisch 2015a). All the species have wings, although some are slightly shortened so that the tip of the abdomen is visible (Wikipedia 2015c). And most are serious agricultural pests. But some are moss dwellers.

Among the earliest records of the **Chrysomelidae** from mosses is ***Plateumaris sericea*** (**Donaciinae**; Figure 2). Beare (1899) found several of these in his collecting in Surrey, UK.

Figure 2. ***Plateumaris sericea*** mating, a species that lives among mosses in the UK. Photo by Hedwig Storch, through Creative Commons.

One of the most frequently reported bryobionts is ***Mniophila muscorum*** (Figure 3), the moss flea beetle (Champion 1871; Kühnelt 1976; Cox 1997; Konstantinov & Lourdes Chamorro-Lacayo 2006). Its name says it all – a moss-loving moss dweller. It is a true **bryobiont**, living among the "litter" and feeding on mosses (Kühnelt 1976). And it has the typical small size of a moss dweller (1.1-1.6 mm for the genus), is globose, and has reduced hind wings (Nadein 2009). A shiny black elytra is common among small moss-dwelling beetles and is likewise characteristic of these. These characters are shared by ***Mniophilosoma***, ***Apteropeda*** (Figure 4), ***Minota*** (Figure 5), ***Clavicornaltica*** (Figure 6), and ***Kiskeya*** (Figure 40).

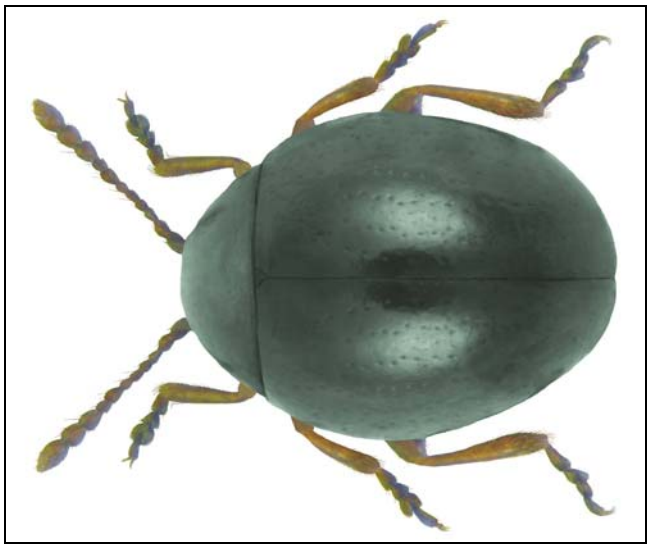

Figure 3. ***Mniophila muscorum***, the common moss dweller known as the moss flea beetle. Photo by Udo Schmidt, with permission.

Figure 4. ***Apteropeda globosa*** adult with moss. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

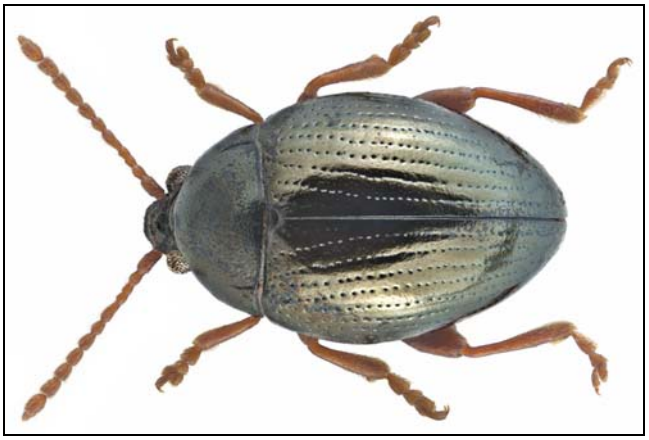

Figure 5. ***Minota obesa***, a shiny black and minute moss dweller. Photo by Udo Schmidt, with permission.

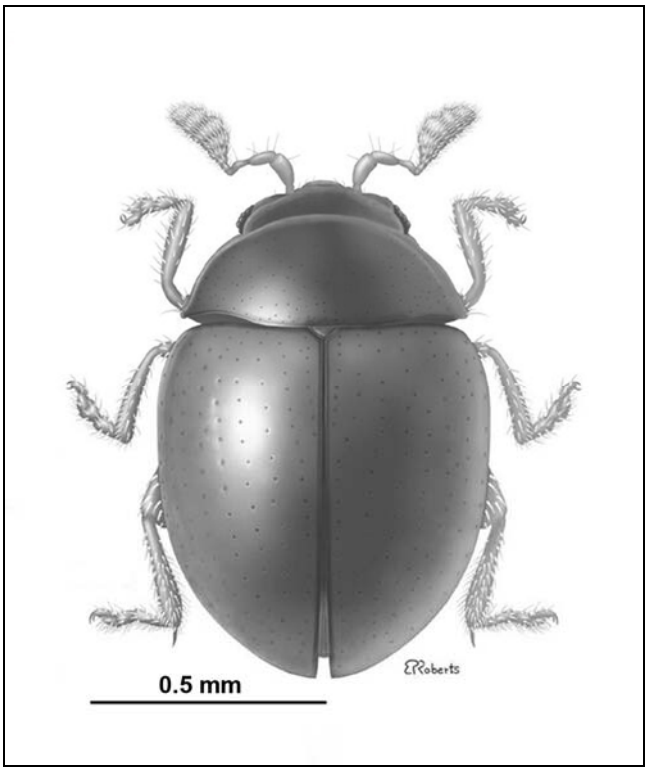

Figure 6. ***Clavicornaltica dali***, a common moss dweller. Image by Sasha Konstantinov, with permission.

Unlike many members of the family, ***Mniophila muscorum*** (Figure 3) is not a leaf miner (Cox 1997). Instead, both larvae and adults occur on mosses, the latter including ***Rhytidiadelphus loreus*** (Figure 7), ***R. triquetrus*** (Figure 8), and ***Eurhynchium striatum*** (Figure 9), all of which grow in a variety of habitats and on a variety of substrates (log stumps, fallen trees, tree branches, rocks, walls, and chalky slopes). They are also known from a number of other bryophyte species of both ground, boulders, and tree boles, including liverworts (Nadein 2009). Their substrate preference seems to depend on elevation. Those on vertical surfaces are usually restricted to thicker mats and cushions. And at least the first instar larvae are surface feeders on mosses. Nadein (2009) described the new species ***Mniophila taurica***, ***M. transcaucasica***, and ***M. caucasica*** from mosses in the Crimean Mountains. ***Mniophila taurica*** is known from the

mosses ***Brachythecium glareosum*** (Figure 10), ***Homalothecium philippeanum*** (Figure 11), and ***Plagiomnium rostratum*** (Figure 12). The genus ***Mniophila*** seems to prefer fresh mosses – not dry or sopping wet. The beetles may be on the surface or within the moss colony.

Figure 7. ***Rhytidiadelphus loreus***, home for larvae and adults of ***Mniophila muscorum***. Photo by Hermann Schachner, through Creative Commons.

Figure 8. ***Rhytidiadelphus triquetrus*** Canyon Falls, MI, home for larvae and adults of ***Mniophila muscorum***. Photo by Janice Glime.

Figure 9. ***Eurhynchium striatum*** with capsules, a species of a wide variety of habitats, serving as a home for ***Mniophila muscorum***. Photo by J. C. Schou <www.biopix.com/>, with permission.

Figure 10. ***Brachythecium glareosum***, home to some ***Mniophila taurica***. Photo by Michael Lüth, with permission.

Figure 11. ***Homalothecium philippeanum***, home to some ***Mniophila taurica***. Photo by Michael Lüth, with permission.

Figure 12. ***Plagiomnium rostratum***, home to some ***Mniophila taurica***. Photo by Michael Lüth, with permission.

Let's return to those look-alikes for ***Mniophila*** (Figure 3). Gillerfors (1986) described ***Mniophilosoma obscurum*** from ***Sphagnum*** (Figure 13) and other substrata in the Azores. ***Mniophilosoma laeve*** occurs among mosses and other substrata in Europe (Wollaston 1857). Despite the generic name, which translates to moss-loving body, this

genus often lives under bark. ***Apteropeda orbiculata*** (Figure 14-Figure 15) and ***A. globosa*** (Figure 4) both occur on mosses (Tomlin 1913). Tomlin also described ***Phaedon tumidulus*** (Figure 16-Figure 17), which occurs among mosses in Great Britain (Tomlin 1913). ***Cassida viridis*** (Figure 18-Figure 19) occasionally overwinters among mosses.

Figure 13. ***Sphagnum russowii***, a potential home for many species of beetles. Photo by Andrew Hodgson, with permission.

Figure 14. ***Apteropeda orbiculata*** larva, a moss dweller. Photo by Willem Ellis, with permission.

Figure 15. ***Apteropeda orbiculata*** adult, a moss dweller. Photo through Creative Commons.

Figure 16. ***Phaedon tumidulus*** larva, a resident among mosses at times. Photo by Keith Edkins, through Creative Commons.

Figure 17. ***Phaedon tumidulus*** adult, a sometimes moss resident. Photo by Keith Edkins, through Creative Commons.

Figure 18. ***Cassida viridis*** larva, a species that occasionally overwinters among mosses. Note the shed exuvia that the larva is carrying on its back. This is an unusual habit that may have a role in avoiding predation. Photo by James K. Lindsey, with permission.

Figure 19. ***Cassida viridis*** adult, a species that occasionally overwinters among mosses. Photo by Roger S. Key, with permission.

The adult of ***Minota*** (Figure 5) occurs among mosses or litter in northern Eurasia (Medvedev 1997). But ***Minota nigropicea*** feeds on the ferns *Dryopteris erythrosora* (Figure 20), *Pteridium aquilinum* (Figure 21), and *Cyrtomium fortunei* (Figure 22) (Kimoto 1984; Kato 1991). Thus, being tiny, globose, shiny black, and having reduced hind wings adapts these flea beetles for not only mosses, but also for life on ferns and under bark.

Figure 20. ***Dryopteris erythrosora***, food for ***Minota nigropicea***. Photo by Megan Hansen, through Creative Commons.

Figure 21. ***Pteridium aquilinum*** habitat at edge of forest, food for ***Minota nigropicea***. Photo by Rasback, through Creative Commons.

Figure 22. ***Cyrtomium fortunei***, food for ***Minota nigropicea***. Photo by Harum.Koh, through Creative Commons.

In a Cornish *Calluna* heath (Figure 23), Brown (1991) noted that the young larval stages of the heather beetle, ***Lochmaea suturalis*** (Figure 24), are dependent on the moisture of the moss layer. They are only found in older *Calluna* heaths, where ***Pleurozium schreberi*** (Figure 25) has had time to develop. When there is no moss layer present, these larvae have a density of about 0.4 per sample compared to 25 per sample when a moss layer is present. The mosses are essential to the larvae (Garvey 2011). Adults are destructive of the *Calluna*. This destruction initiates a complex series of events (Scandrett & Gimmingham 1991). The ***Sphagnum plumulosum*** (Figure 26) and ***Hypnum jutlandicum*** (Figure 27) increase, while ***Sphagnum compactum*** (Figure 28) and ***Pleurozium schreberi*** decrease. The *Calluna* is able to regenerate through layering, no doubt facilitated by the moisture-holding mosses, and by seedling development, especially in the ***Sphagnum***.

Figure 23. Heathland, home of the heather beetle, ***Lochmaea suturalis***, where the beetle larva lives among the moss ***Pleurozium schreberi***. Photo by Willow, through Creative Commons.

Figure 24. ***Lochmaea suturalis*** adult, a species whose larvae require the moisture of moss mats. Photo by Niels Sloth <www.biopix.dk>, through Creative Commons.

Figure 25. ***Pleurozium schreberi***, home for ***Lochmaea suturalis*** in heathlands. Photo by J. C. Schou <www.biopix.com/>, with permission.

Figure 26. ***Sphagnum subnitens***, a species that increases when ***Lochmaea suturalis*** damages the *Calluna* and increases light penetration. Photo by Michael Lüth, with permission.

Figure 27. ***Hypnum jutlandicum***, a species that increases when ***Lochmaea suturalis*** damages the *Calluna* and increases light penetration. Photo by Janice Glime.

Figure 28. ***Sphagnum compactum***, a species that decreases when ***Lochmaea suturalis*** damages the *Calluna* and increases light penetration. Photo by Michael Lüth, with permission.

In the heathland, ***Lochmaea suturalis*** (Figure 24) oviposits at the base of the *Calluna* (Figure 23), usually among ***Sphagnum*** (Beagan 2015). The larvae crawl up the *Calluna* to eat the leaves, developing to as much as 2 cm in length. The mature larvae return to the mosses, where they spend 4 weeks to pupate. Then adults return to eat the *Calluna* leaves again, but once more return to ground level to spend the winter.

Recently, Sasha Konstantinov and associates have entered the picture, specializing in the tiny tribe of **Alticini**, among which are many previously ignored moss dwellers. The tiny size and time-consuming process of separating these beetles from their moss cushions seems to have discouraged most coleopterists. After all, this is the largest order of insects, and there were many much easier beetles to study.

The elusive ***Phaelota*** beetles living among mosses are typically small, with lengths about 2-3 mm, and are flightless (Prathapan & Konstantinov 2009). Among collections of six new species in the genus ***Phaelota*** from India, three were from mosses and a fourth moss dweller (***P. semifasciata***) was not new but was longer (up to 5 mm). The new moss-dwelling species include ***Phaelota saluki*** (Figure 29) from the moss ***Forsstroemia thomsonii***, ***P. maculipennis*** (Figure 30), and ***P. viridipennis*** (Figure 31) from moss on tree trunks and rocks. The two groups of species are separated by their ability to fly – those living on ferns are capable of flight, but the moss-dwelling species are flightless. This flight restriction may be an adaptation to protect them from the windy mountain habitat (> 1470 m) where they reside in Southern India. In India they occur in the humid tropical evergreen forests of the Western Gats at 1000-2600 m asl (Konstantinov *et al*. 2013). ***Phaelota kerzhneri*** (Figure 32) from Borneo, like other flightless members of ***Phaelota***, is probably also an inhabitant of moss (Prathapan & Konstantinov 2008).

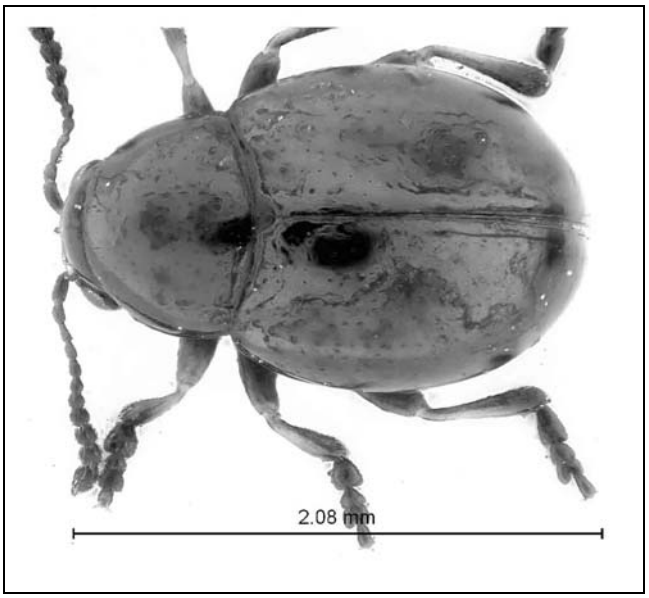

Figure 29. ***Phaelota sakuli*** adult, a moss dweller in India. Photo courtesy of Sasha Konstantinov.

Figure 30. ***Phaelota maculipennis*** adult, a moss dweller in India. Photo courtesy of Sasha Konstantinov.

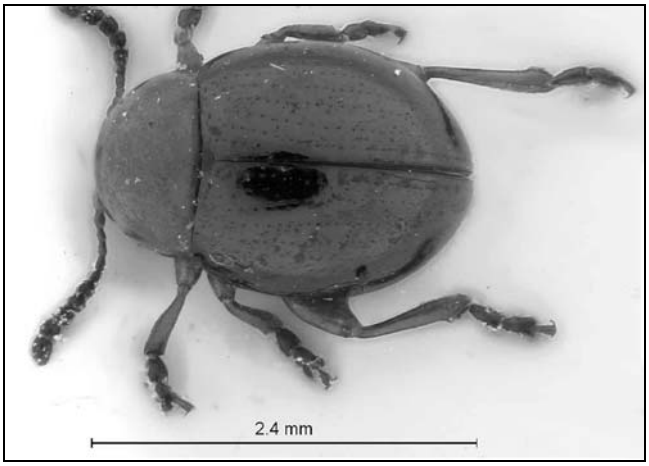

Figure 31. ***Phaelota viridipennis*** adult, a moss dweller in India. Photo courtesy of Sasha Konstantinov.

Figure 32. ***Phaelota kerzhneri*** adult, a probable moss dweller from Borneo. Image by Sasha Konstantinov, with permission.

Both Indian species in the genus ***Ivalia*** are moss dwelling, but their selection of host plants is not related to a loss of flight – their flightlessness apparently evolved before their choice of mosses for food (Prathapan & Konstantinov 2009). Recently, Duckett *et al*. (2006) found both adults and larvae of the new species ***Ivalia korakundah*** (Figure 33) on mosses in southern India by sifting mosses from the trunks of large pine trees. ***Ivalia korakundah*** also feeds on mosses. In one case, adults were found on the moss ***Isopterygium*** sp. (Figure 34). This genus seems to prefer more humid environments of the tropical evergreen forests, especially at altitudes of 1000 to 2600 m asl in the Western Ghats (Konstantinov *et al*. (2013).

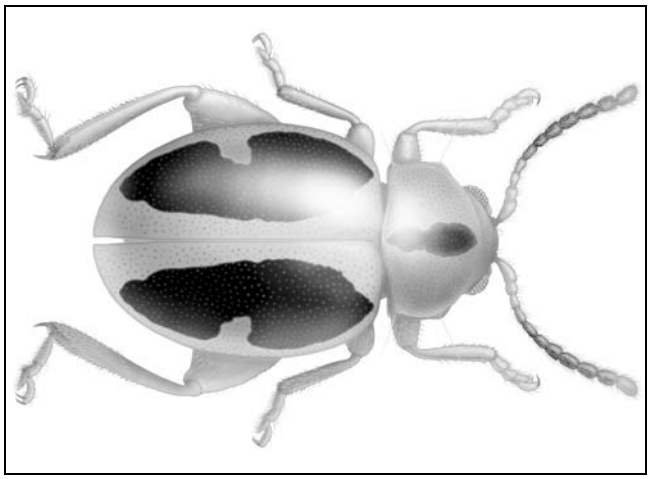

Figure 33. ***Ivalia korakundah***, a moss dweller from pine trees in India. Image by Sasha Konstantinov, with permission.

Figure 34. ***Isopterygium elegans***, potential home, and probably food, for ***Ivalia korakundah***. Photo by Robin Bovey, with permission from Dale Vitt.

In China, Konstantinov *et al*. (2013) described the new genus and species ***Cangshanaltica nigra*** (Figure 35-Figure 36) from the moss cushions of ***Hypnum*** (Figure 27). Unlike findings in most of the studies on such tiny beetles, Konstantinov and coworkers were able to find ***Hypnum*** in the guts of these beetles. These likewise are among the smallest leaf beetles; they have round bodies with robust appendages, reduced hind wings, highly simplified and shortened meso- and metathorax, and their antennae have "more or less" enlarged apical antennomeres.

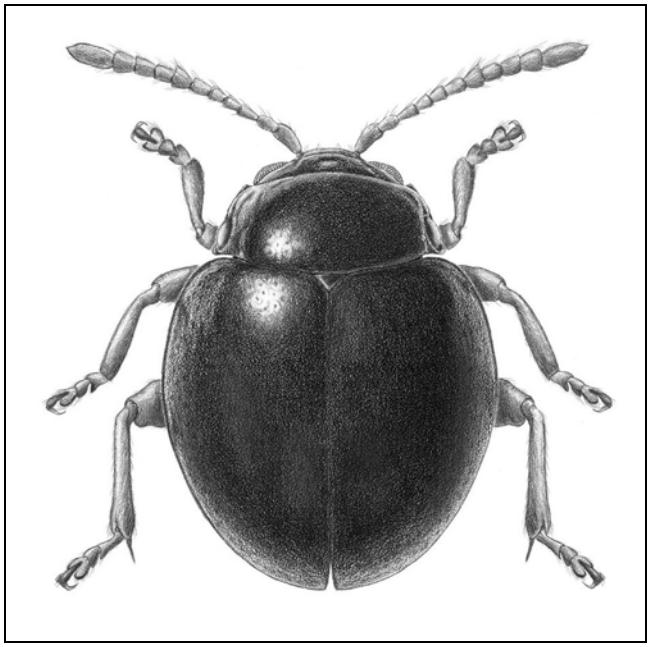

Figure 35. ***Cangshanaltica nigra*** adult, a species that lives among ***Hypnum*** in China. Image courtesy of Sasha Konstantinov.

Figure 36. ***Cangshanaltica nigra*** habitat. Photo courtesy of Sasha Konstantinov.

Figure 37. ***Hypnum cupressiforme***, a genus that provides homes for ***Cangshanaltica nigra*** in China. Photo by Michael Becker, through Creative Commons.

The members of ***Cangshanaltica*** (Figure 35) are small (0.8.-.2 mm) and rounded (Konstantinov & Duckett 2005). The elytra covers the abdomen, but the bodies are fragile and easily broken. The genus is distinctive in having **clavate** antennae (thicker at apex, like a club).

The additions of moss-dwelling species continue. Damaška and Konstantinov (2016) added another species of ***Cangshanaltica siamensis*** (Figure 38) from Thailand. In this case, the beetles are able to survive the dry season in the moss cushions.

Figure 38. ***Cangshanaltica siamensis***, a moss dweller from Thailand. Photo by Sasha Konstantinov, with permission

Konstantinov and Duckett (2005) found ***Clavicornaltica dali*** (Figure 39) at 3300 m in China under mosses. The tiny ***Clavicornaltica*** are distributed in Sri Lanka, Vietnam, and Thailand, despite their wingless males and mostly wingless females. This new species is among the first known for the genus in China and raises the question of dispersal mechanisms. Could they be distributed with the mosses they inhabit?

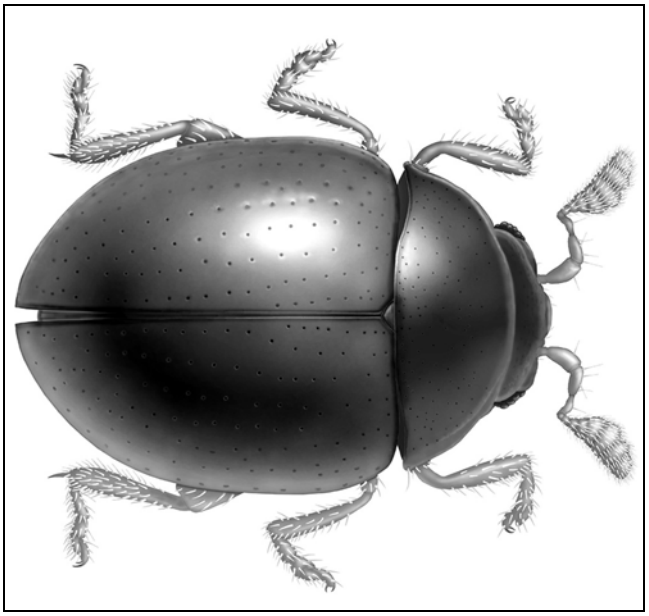

Figure 39. ***Clavicornaltica dali***, an Asian species that lives under mosses. Image by Alexander Konstantinov, with permission.

Benedictus (Figure 53), a moss inhabitant in Asia, is not present (or hasn't been discovered) in the New World (Sprecher-Uebersax *et al*. 2009). In fact, it seems that the Eastern and Western Hemispheres have distinct genera.

As is common for the **Alticini** bryophyte dwellers, new species and even genera are lurking in these neglected habitats, and this seems especially true for the Western Hemisphere. Konstantinov and Lourdes Chamorro-Lacayo (2006) sieved moss samples in forests of the Dominican Republic and were able to describe the new genus ***Kiskeya*** (Figure 40), small, rounded beetles at 1.06-1.10 mm long, with two species, ***K. baorucae*** (Figure 40) and ***K. neibae***. ***Kiskeya baorucae*** was collected from mosses in forests where they were growing on rocks, dangling as pendent mosses, and growing on the boles of trees. ***Kiskeya neibae*** was collected in forests from mosses growing on rocks, tree stumps, boles, and branches (Figure 41). Using a Berlese funnel, the researchers also extracted ***Aedmon*** sp. (**Alticini**; Figure 42) from the mosses.

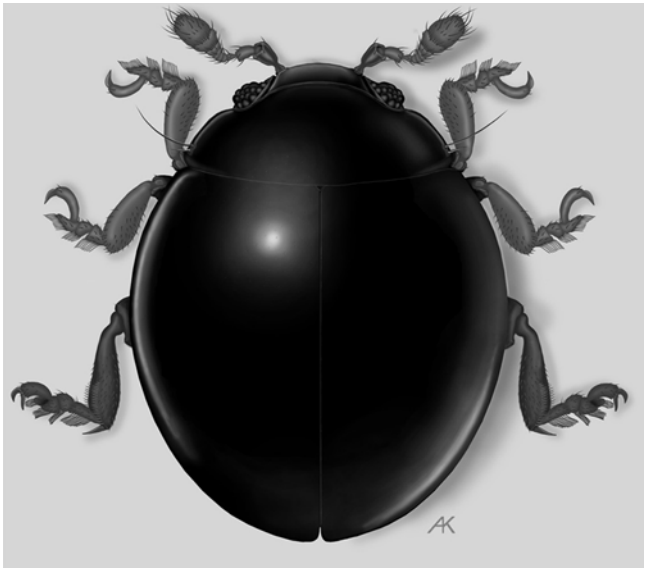

Figure 40. ***Kiskeya baorucae***, a species that lives on mosses in forests – on rocks, tree boles, and pendent mosses. Photo by Alexander Konstantinov, with permission.

Figure 41. ***Kiskeya neibae*** habitat. Photo courtesy of Sasha Konstantinov.

Figure 42. ***Aedmon ferruginea*** adult, a moss dweller in the Dominican Republic. Photo by Celeigher Piñango, through Creative Commons.

Again in 2011, Konstantinov and Konstantinova found a new genus (***Borinken***) and three new species of moss dwellers in Puerto Rico by sifting mosses. ***Borinken elyunque*** (Figure 43) is a tiny (1.08-1.18 mm) beetle from the forest, living in mosses on rocks, tree stumps, tree boles, and branches. ***Kiskeya elyunque*** (Figure 44), an even smaller species (0.81-0.92 mm), lives in similar habitats. By comparison, ***Ulrica eltoro*** (Figure 45) is much larger (1.94-2.16 mm) and likewise lives among mosses in similar locations, whereas ***Ulrica iviei*** (Figure 46), also a new species, is thus far known only from leaf litter.

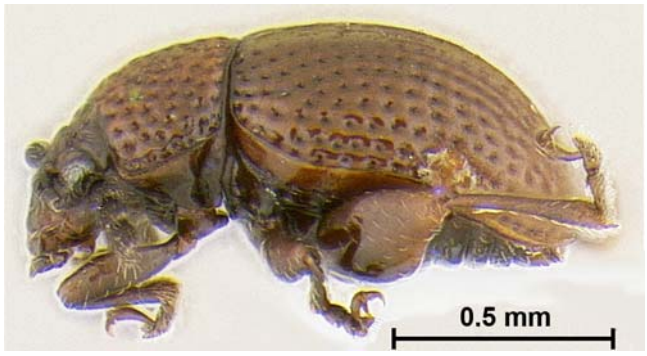

Figure 43. ***Borinken elyunque***, a moss dweller in Puerto Rico. Photo courtesy of Sasha Konstantinov.

Figure 44. ***Kiskeya elyunque*** adult, a moss dweller in Puerto Rico. Photo courtesy of Sasha Konstantinov.

Figure 45. ***Ulrica eltoro*** adult, a moss dweller in Puerto Rico. Photo courtesy of Sasha Konstantinov.

Figure 46. ***Ulrica iviei*** adult, a litter species in the Dominican Republic. Photo by Sasha Konstantinov, with permission.

The moss-inhabiting ***Kiskeya*** (Figure 40, Figure 44) is known elsewhere in the Neotropics. There are three species in the West Indies, two in the Dominican Republic, and one in Puerto Rico (Konstantinov & Konstantinova 2011).

Konstantinov *et al*. (2013) described ***Cangshanaltica nigra*** from Yunnan Province in China.

Konstantinov *et al*. (2015) have recently added five new species of ***Monotalla*** in the West Indies. Of these, ***Monotalla maierae*** is a new species that occurs in mosses and litter and ***M. viridis*** is a new species from epiphytic mosses.

Figure 47. ***Monotalla maierae*** adult, a moss dweller in the West Indies. Photo by Sasha Konstantinov, with permission.

Figure 48. ***Monotalla viridis*** adult, a species from epiphytic mosses in the West Indies. Photo by Sasha Konstantinov, with perission.

As is clear by these examples, the Western Hemisphere moss inhabitants have remained almost unexplored. Konstantinov *et al*. (2009) found another new genus in Nicaragua. ***Nicaltica selvanegra*** (Figure 49), a species similar to ***Kiskeya***, likewise lives among mosses there. In Bolivia, Konstantinov *et al*. (2014) discovered another new genus of moss and litter dwellers; ***Stevenaltica normi*** (Figure 50) and ***S. erronis*** (Figure 51) both include mosses as well as leaf litter as their habitats.

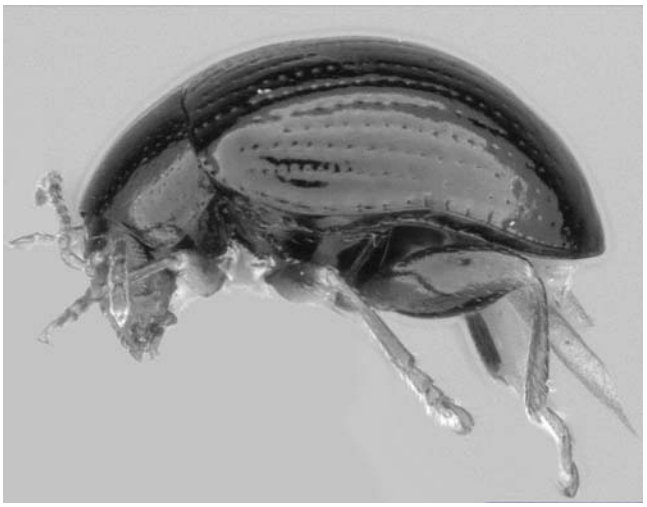

Figure 49. ***Nicaltica selvanegra*** male, a moss dweller in Nicaragua. Photo courtesy of Sasha Konstantinov.

Figure 50. ***Stevenaltica normi*** adult. a moss and leaf litter dweller in Bolivia. Photo courtesy of Sasha Konstantinov.

Figure 51. ***Stevenaltica erronis***. a moss and leaf litter dweller in Bolivia. Photo courtesy of Sasha Konstantinova.

Distigmoptera borealis (Figure 52) eats mosses in North America (Konstantinov, pers. comm. 26 June 2016). And that's it! Other records for North America are lacking. This species is known from North Dakota (Fauske 2014) and Oklahoma (Palmer 2016).

Figure 52. ***Distigmoptera borealis***, the only moss-dwelling genus known in North America. Photo from BIO Photography group, Biodiversity Institute of Ontario, through Creative Commons.

As of 2013, of the 14 known genera of moss-dwelling **Alticini**, only six were true **bryobionts** [***Kiskeya*** (Figure 40), ***Borinken*** (Figure 43), ***Cangshanaltica*** (Figure 35), ***Mniophila*** (Figure 3), ***Nicaltica*** (Figure 49), and ***Ulrica*** (Figure 45)] (Konstantinov *et al*. 2013). The remaining eight are **bryophiles** [***Benedictus*** (Figure 53), ***Clavicornaltica*** (Figure 39), ***Ivalia*** (Figure 33), ***Monotalla*** (Figure 47-Figure 48), ***Minota*** (Figure 5), ***Paraminota*** (Figure 54), ***Paraminotella*** (Figure 55), and ***Phaelota*** (Figure 29-Figure 32)]. By 2016, the number of known moss-inhabiting **Alticini** genera in the world grew to 15 and the number of species to 30 (Damaška & Konstantinov 2016).

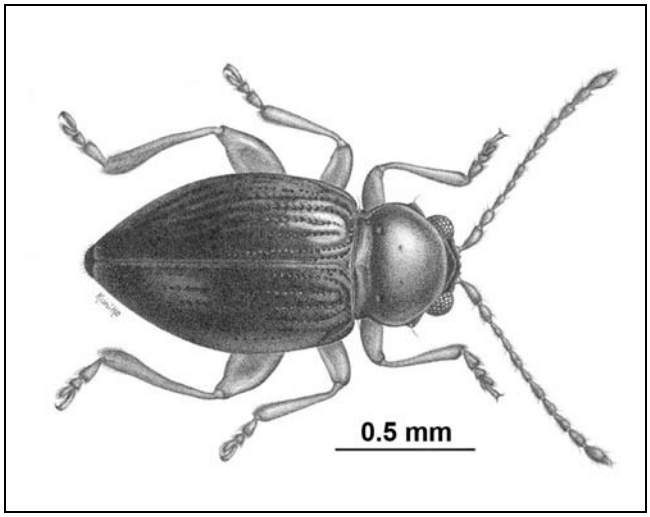

Figure 53. ***Benedictus shivalayanicus*** adult, Sasha Konstantinov.

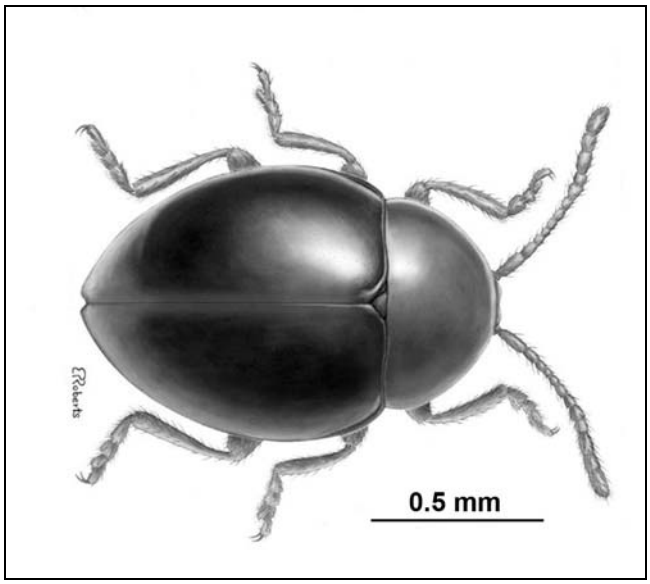

Figure 54. ***Paraminota lauribina***, member of a moss-dwelling genus. Image permission from Sasha Konstantinov.

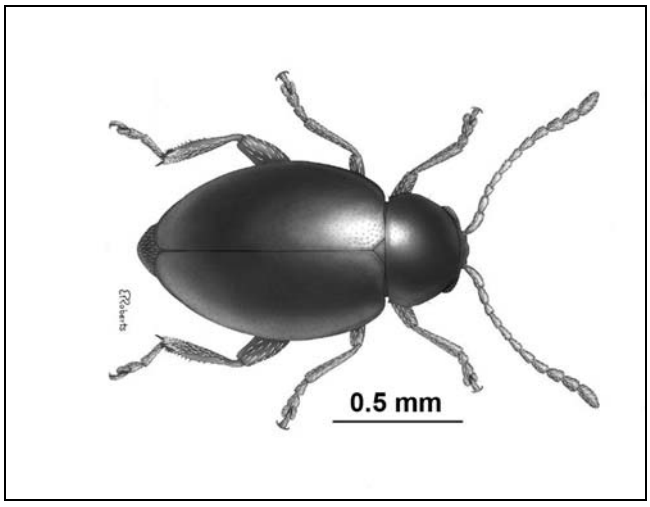

Figure 55. ***Paraminotella nigrita*** adult, member of a moss-dwelling genus. Image permission from Sasha Konstantinov.

There is good reason why so many new beetle species remain to be found among bryophytes. Many of these bryophyte dwellers are flightless. Furthermore, their moisture requirements are somewhat specific. Many are mountain-dwellers, living only above certain elevations. This combination makes it difficult for the beetles on one mountain to mix with those on another. When one or a few do disperse to a new mountain, both the **founder principle** (small population arrives in a new area and does not represent the genetic frequencies of its parent population) and **genetic drift** (random changes in gene frequencies that are common in small populations) are likely to play a role. As time passes, original and new populations diverge genetically, and over geologic time – or less – they can become separate species. When a single individual arrives in a new location, perhaps carrying fertilized eggs or for some beetles being **parthenogenetic** (reproducing from an unfertilized egg), this individual does not represent the middle of the curve of variation and produces offspring that are recognizably different from most of the individuals at the source. Do they pass the test of reproductive isolation? As long as they are separated by a valley, yes. Could they interbreed if they were joined? That remains to be tested.

Figure 56. ***Physarum cinereum*** plasmodium, a bryophyte-inhabiting slime mold that feeds slime-mold-eating **Latridiidae**. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Cucujoidea

Latridiidae – Minute Brown Scavenger Beetles

These small (0.8-3 mm) beetles number 1000 species (McClarin 2005). Most are associated with leaf litter, but around habitation they associate with other rotting vegetable matter. They are elongate with sculptured thorax and outer wings. Aside from their small size, they are not well adapted for bryophytes, although their coloration is usually dull and may be mottled. The sculpturing may also help to disguise them.

Some **Latridiidae** (Figure 58) take advantage of moss inhabitants for food. This family of beetles feeds on **Myxomycetes** (slime molds; Figure 56-Figure 57) (Dudka & Romanenko 2006), and these are often found among bryophytes. Decaying logs provide good habitats for slime molds and for mosses. And the slime molds often invade the space of the bryophytes. The mosses may also improve the habitat for the slime molds by increasing the moisture retention. Hence, the bryophytes on these logs provide protected sites where the **Latridiidae** can feed on the slime molds.

Dudka and Romanenko (2006) found 13 species of slime molds on 9 species of mosses and 3 of liverworts at the Crimean Nature Reserve. Most of these slime molds occur on non-bryophyte substrates as well, but some, like ***Physarum cinereum*** (Figure 56-Figure 57), occur predominantly on bryophyte substrates. Dudka and Romanenko (2006) found that ***Enicmus*** (Figure 58) and ***Dienerella*** (Figure 59) were the most common **Latridiidae** on moss-dwelling slime molds. The beetles not only use the slime molds for food, but also for oviposition and cover.

Figure 57. ***Physarum cinereum*** with fruiting bodies, a bryophyte-inhabiting slime mold that feeds slime-mold-eating **Latridiidae**. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

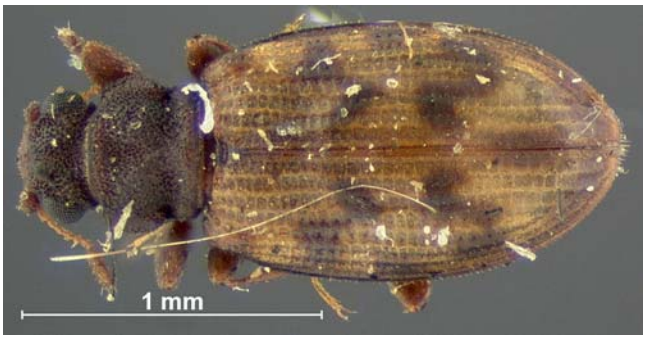

Figure 58. ***Enicmus maculatus*** adult, one of the most common **Latridiidae** genera that lives on moss-dwelling slime molds. Photo from Museum of Comparative Zoology Harvard, through Creative Commons.

Figure 59. ***Dienerella ruficollis*** adult, one of the most common **Latridiidae** genera on moss-dwelling slime molds. Photo by Tom Murray, through Creative Commons.

Curculionoidea

Atelabidae – Leaf-rolling Weevils

This family got its name because the female lays her eggs in leaves, then rolls the leaf around them. It is unlikely that these are regular moss dwellers. It is more likely that these are one of many of the beetles that traverse mosses simply because they are there. Although the mosses can provide moisture and a home for prey items, many species of beetles may arrive there without actually choosing to be in a mossy habitat. Such may be the case for the atelabid ***Eugnamptus angustatus*** (Figure 60), a 4.8 mm beetle Stephen Cresswell found walking on a moss in West Virginia, USA. Or it may have been searching there for food or replenishing body moisture. Behavioral studies on beetles associated with bryophytes are greatly needed.

Figure 60. ***Eugnamptus angustatus*** on moss – does it live there, or is it just visiting? Photo by Stephen Cresswell, with permission.

Curculionidae – Weevils

These are the cute little beetles with long "snouts" (Figure 61), somewhat resembling a miniature aardvark. A number of species have been discovered on bryophytes, eat them [Chown (1993) reported records of 35 species eating bryophytes], and some weevils even carry mosses around as camouflage.

Figure 61. ***Cionus hortulanus*** adult showing long snout with antennae on it. Photo by Lukas Jonaitis, through Creative Commons.

It seems that most beetles treat mosses as if they were litter, much like many soil biologists do. ***Ceutorhynchus erysimi*** (Figure 62), a species of Europe and invasive in the US, lives among mosses and forest litter around rhododendrons (in The Netherlands) (USDA 1950). ***Cryptorhynchus lapathi*** (Figure 63) lays its 1 mm long eggs mostly at stem bases, but also high in the crowns of large trees, under soil, or in the moss layer (Broberg 1997).

Figure 62. ***Ceutorhynchus erysimi*** adult among mosses, a species that lives among mosses and forest litter. Photo by Mick E. Talbot, through Creative Commons.

Figure 63. ***Cryptorhynchus lapathi*** adult, a species that sometimes lays eggs on mosses. Photo by Gyorgy Csoka, through Creative Commons.

I have been finding the best records of bryophyte-dwelling insects among those of the UK, especially the old records. For example, Moncreaff (1871) reported ***Baridius lepidii***, ***Phytobius waltoni*** (=*Pelonomus waltoni*; Figure 64), and ***Litodactylus leucogaster*** (=*Phytobius leucogaster*) from mosses in Portsea, British Isles. ***Bagous laticollis*** was abundant in mosses. Tomlin (1913) was able to find ***Liosoma ovatulum*** among mosses in Glamorgan, Wales, year round.

Figure 64. ***Phytobius waltoni*** adult, a moss dweller in the British Isles. Photo by Stefan Schmidt, through Creative Commons.

Dyer and Nijholt (2016) reported finding adults of ***Pseudohylesinus sericeus*** (Figure 65) and ***P. grandis*** (Figure 66), both pests on conifers in the western part of North America (USDA 2016), hibernating in thick mosses that grew on the trunks of oak trees in Oregon, USA. But in British Columbia, ***P. granulatus*** (Figure 67) instead penetrated the mosses on the amabilis fir and once there bored into the bark.

Figure 65. ***Pseudohylesinus sericeus*** adult, a conifer pest that hibernates among mosses. Photo by Javier Marcado, USDA APHIS ITP, Bugwood.org, through Creative Commons.

Figure 66. ***Pseudohylesinus grandis*** adult, a conifer pest that hibernates among mosses. Photo by Tim Loh, with permission.

Figure 67. ***Pseudohylesinus granulatus*** adult, a species that enters mosses to bore into the amabilis fir bark. Photo by Steven Valley, USDA APHIS ITP, Bugwood.org, through Creative Commons.

Some beetles only use bryophytes in part of their life cycle. Larvae of the weevil ***Palirhoeus eatoni*** (syn. =***Mesembriorrhinus eatoni***) develop in tufts of algae (Doyen 1976). But when it is time for pupation, the larvae in Antarctic waters move above the high water line to pupate in clumps of the moss ***Grimmia amblyophylla***. Mosses are often a safe haven for Antarctic arthropods in winter.

On the Austral Islands of the South Pacific, a number of new, hence **endemic**, species of ***Miocalles*** (Figure 68) were located by fogging mosses in the rata forest (Englund 2003). These included ***M. albolineatus***, ***M. akao***, ***M. carinatus***, ***M. hemata***, ***M.*** cf ***irregularis***, ***M. perau***/***maii***, ***M. pusillus***, ***M. setifer***, ***M.*** cf ***silvestris***, ***M.*** nr ***varians***, ***M.*** nr ***sanctijohni***.

The weevils are among the unique fauna of the Antarctic region. The genus ***Bothrometopus*** has several members that live among rocks on Marion Island, including ***B. randi***, ***B. parvulus***, and ***B. elongatus*** (Van der Merwe *et al*. 1997). All three of these species occur on rock surfaces, in crevices, and within the rock-dwelling bryophytes. On Heard Island, ***Bothrometopus brevis*** and ***B. gracilipes*** both feed on cryptogams (Chown & Klok 2001).

Figure 68. ***Miocalles*** adult, a genus with a number of new endemic bryophyte-dwelling species on the Austral Islands. Photo by April Yang, through Creative Commons.

Bryophagy and Evolution

Bryophagy is known in at least 35 species of **Curculionidae** from the sub-Antarctic (Kuschel 1964, 1971; Chown & Scholtz 1989a). Chown and Scholtz (1989a) suggest that a specialized moss herbivory, rare among **Curculionidae**, may have evolved in response to the adverse conditions during Pleistocene glaciations when bryophyte species were more likely to survive than their tracheophyte counterparts. Let's examine a few examples and then return to the evolution of this bryophyte-curculionid herbivory relationship.

Dichotrachelus stierlini (Figure 69) is a moss-eating weevil, known from 3350 m in the Alps (Thaler 1999). It is easily collected in alpine regions by sieving mosses (Barbara Thaler-Knoflach, pers. comm. 9 June 2011). As seen in Figure 69, this weevil has numerous protuberances that give it texture similar to that of a moss. A shiny weevil would be much more obvious among the mosses.

Figure 69. ***Dichotrachelus stierlini***, a curculionid beetle (weevil). Note how this highly textured beetle would blend with the similarly highly textured bryophytes. Photo by Barbara Thaler-Knoflach, with permission.

Smith (1977) examined the consumption of ***Ectemnorrhinus similis*** (formerly ***Dusmoecetes similis***) adults on sub-Antarctic Marion Island. These weevils reached densities up to 220 m^{-2}, representing a biomass of about 1 g m^{-2}. Their diet included 14% of their body weight per day of *Acaena magellanica* (flowering plant in Rosaceae; Figure 70) and 37% per day of the moss ***Brachythecium rutabulum*** (Figure 71). In fact, it appears that nearly all members of the tribe **Ectemnorhinini** are cryptogam feeders, especially on bryophytes (Chown & Scholtz 1989a). This is unusual in the **Curculionidae**, a family that predominantly feeds on tracheophytes.

Figure 70. *Acaena magellanica*, part of the diet of ***Ectemnorrhinus similis***. Photo by El Grafo, through Creative Commons.

Figure 71. ***Brachythecium rutabulum***, home and food for ***Ectemnorrhinus similis***. Photo by J. C. Schou <www.biopix.com>, with permission.

Chown (1989) suggests that the near absence of flowering-plant feeders in the **Ectemnorhinini** is due to the previous climatic conditions, claiming that they would preclude flowering plant herbivory. What we know about the habitat use, diet, and species morphology supports this view (Table 1; see also Chown & Klok 2001). Using ***Ectemnorhinus*** (see Figure 72) in the sub-Antarctic as an example (Chown & Scholtz 1989b; Chown 1990), Chown and Scholtz showed feeding and morphological differences between the larger species, ***E. similis***, that feeds on angiosperms [but also on bryophytes (Grobler *et al*. 2006)], as adults and detritus as larvae, and the smaller species, ***E. marioni***, that feeds on bryophytes in all its life cycle stages. Both of these species are found on ***Azorella selago*** (see Figure 74), but ***E. marioni*** feeds exclusively on the epiphytic bryophytes, whereas ***E. similis*** only eats bryophytes when the quality of the tracheophytes deteriorates (Chown & Scholtz 1989b).

Table 1. Feeding strategies of the tribe **Ectemnorhinini** of **Curculionidae** from sub-Antarctic Marion and Prince Edward Islands. % of cryptogams (**crypt**) and bryophytes (**bryo**) represent the percentage of individuals examined that fed on each of these groups. Note that bryophytes are included in cryptogams. Data were gathered from field observations and gut analyses. The bryophyte associations are defined by Gerson (1982) with **bryobionts** occurring exclusively in association with bryophytes, **bryophiles** usually living on bryophytes but also occurring elsewhere, **bryoxenes** regularly spending part of their life cycle on bryophytes, and **occasionals** spending part of their time on bryophytes but not dependent on them. n = number in sample. Modified from Chown and Scholtz 1989a.

			food		
Species	**Stage**	**n**	**% crypt**	**% bryo**	**bryo assn**
Palirhoeus eatoni	larvae	17	100	6	bryoxene
	adults	40	100	0	occasional
Bothrometopus randi	larvae	38	100	16	bryoxene
	adults	46	100	2	occasional
Antarctonesiotes elongatus	larvae	28	100	18	bryoxene
	adults	62	100	7	occasional
Mesembriorrhinus brevis	larvae	50	100	61	bryophile
	adults	116	98	21	bryoxene
Ectemnorhinus marioni	larvae	67	97	97	bryobiont
	adults	1314	88	88	bryobiont
Ectemnorhinus similis	larvae	82	9	9	occasional
	adults	1037	38	38	bryoxene

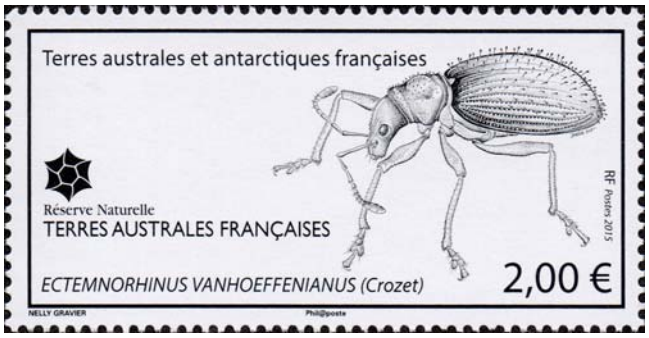

Figure 72. ***Ectemnorhinus vanhoeffenianus*** on French stamp. Photo by Alex Pozyr, with permission.

Figure 73. ***Ectemnorhinus vanhoeffianus***. Photo by Alex Pozyr, with permission.

In a later publication, Crafford and Chown (1991) cast doubt on the thesis that a colder climate would preclude these weevils from feeding on flowering plants due to energy constraints. Although five of the six species of weevils in the **Ectemnorhinini** on the sub-Antarctic Marion Island feed on cryptogams, temperature does not seem to be involved. They tested the consumption rate and approximate digestibility for the two native species of ***Ectemnorhinus*** (Figure 72) and found that the digestibility of the leafy liverwort ***Blepharidophyllum densifolium*** and dry mass differed little between 5°C and 10°C. Similar results were present for ***E. similis*** adults fed *Azorella selago* (see Figure 74). On the other hand, the performance ratios for ***E. similis*** feeding on *Azorella selago* was greater at 5°C than that for ***E. marioni*** feeding on bryophytes at either temperature. Crafford and Chown (1991) modified their interpretation to suggest that moss feeding more likely evolved in response to an absence of angiosperms during glacial periods, rather than because of a nutritional advantage associated with bryophagy at low temperatures. This is supported by studies on these beetles on islands. These feeding habits constrain species in their habitat distributions in the South Indian Ocean Province Islands where they seem to have been a result of climatic forcing (Chown 1994).

Figure 74. ***Azorella compacta*** from Tierra del Fuego, a flowering pant that resembles a moss. ***Azorella selago*** serves as food for ***Ectemnorhinus similis*** and ***E. marioni***. Photo by Heretiq, through Creative Commons.

In *Agrostis* (Figure 75) mires the genus ***Ectemnorhinus*** (Figure 72) feeds exclusively on bryophytes, mostly the leafy liverwort ***Blepharidophyllum densifolium***, even in the presence of the grass *Agrostis magellanica*. Chown (1990) considers the bryophytes to be a relatively poor food source, but they have the advantage of being available year-round. Another factor is that flowering plants have their highest nitrogen concentrations in the spring, whereas the bryophytes have their highest in autumn. Only the bryophytes have secondary compounds that serve as dietary inhibitors, resulting in the bryophyte feeders being smaller than the flowering-plant feeders. In fact, Chown suggests that the differences in feeding strategies lead to both size differences in the beetles and spatial separations between the two feeding groups. These differences keep the species groups from interbreeding.

Figure 75. *Agrostis*, a common genus in mires, but ***Ectemnorhinus*** species there feed mostly on leafy liverworts. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

Bryophytes are well known for their insecticidal properties. Abay *et al*. (2012) demonstrated that extractions of the cosmopolitan moss ***Hypnum cupressiforme*** (Figure 76) had high levels of contact activity against the granary weevil *Sitophilus granarius*. This research was expanded to include the mosses ***Dicranum scoparium*** (Figure 77), ***Polytrichastrum formosum*** (Figure 78), ***Homalothecium lutescens*** (Figure 79), and the thallose liverwort ***Conocephalum conicum*** (Figure 80) (Abay *et al*. 2013). Using *Sitophilus granarius* in their bioassays, Abay and coworkers determined that hexane extracts of ***Polytrichastrum formosum*** exhibited the highest insecticidal activity (70.3%). Mortality was highest (53.34%) from the fatty acid **myristic acid**. **Palmitic acid** resulted in 17.75% mortality and **lauric acid** 4.32%. Abay and coworkers consider liverworts to be preferred foods nutritionally because of the presence of oil bodies (Kang *et al*. 2007; Abay *et al*. 2013). Yet there seem to be few reports of insects feeding on liverworts.

Figure 76. ***Hypnum cupressiforme***, a species known to have contact insecticidal properties against some beetles. Photo by J. C. Schou <www.discoverlife.org>, with permission.

Figure 77. ***Dicranum scoparium***, a species known to have contact insecticidal properties against some beetles. Photo by Janice Glime.

Figure 78. ***Polytrichastrum formosum***, a species known to have contact insecticidal properties against some beetles. Photo by Alexander Klink, through Creative Commons.

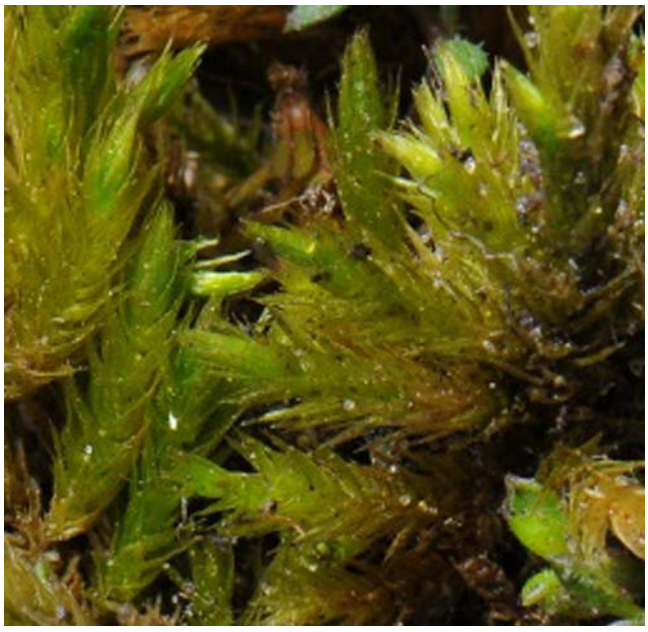

Figure 79. ***Homalothecium lutescens***, a species known to have contact insecticidal properties against some beetles. Photo by J. C. Schou <www.biopix.com>, with permission.

Figure 80. ***Conocephalum conicum***, a species known to have contact insecticidal properties against some beetles. Photo by Li Zhang, with permission.

Wahedi *et al.* (2013) expanded on the research on the effects of bryophyte compounds with *Sitophilus zeamais*. They tested powders from ***Calymperes afzelli*** (Figure 81), ***Thuidium gratum***, ***Bryum coronatum*** (Figure 82), and ***Semibarbula lambarenensis***. All four species were effective in reducing oviposition and F_1 progeny emergence rate, prolongation of pre-adult duration, and having toxicity. The order of efficacy in toxic effects was ***B. coronatum*** > ***T. gratum*** > ***C. afzelli*** > ***S. lambarenensis***, although the symptomatic effects were different among these. The bryophyte powders were so effective that the authors suggested using them as insecticides against the weevils in maize.

New compounds are constantly being discovered in the bryophytes (You *et al*. 2007; Jockovic *et al*. 2008). Many of these are phenolic acids, often unique with the bryophytes. Others are flavonoids or unique or scarce fatty acids. The research on the effects of these compounds on herbivory are limited, especially for mosses. And we don't know if any of these are inducible or if they are always present at similar levels. Likewise, we don't know how they are affected by seasons. Understanding these phenomena could help to explain some of the seasonal food choices of part-time bryophages.

Figure 81. ***Calymperes afzelli***, a species that can reduce oviposition and cause other toxic reactions in powder from on at least some beetles. Photo by Scott Zona, with permission.

Figure 82. ***Bryum coronatum***, a species with antibiotic properties against at least some beetles. Photo by Michael Lüth, with permission.

Impacts on Ecosystems

The weevils can play important roles in ***Sphagnum*** (Figure 13, Figure 83, Figure 128) habitats. For example, warming trends have an interesting way of increasing spruce bark beetles in ***Sphagnum*** fens (Figure 84), ultimately resulting in more frequent fires. Beetles in the Kenai Peninsula of Alaska typically take two years to develop in their ***Sphagnum*** habitat, but during recent warming the fen increased in temperature (Berg 2008). These longer, warmer summers reduced the life cycle to one year and caused exponential growth in the spruce bark beetle. The beetles declined ultimately as a result of destruction of their food source. At the same time, the warmer summers dried the fens and reduced their role as firebreaks, causing invasion of woody shrubs and white spruce. Instead of being fire breaks, the spruce and woody shrubs became fuel bridges. A 400-600-year fire interval was reduced by the beetles to one of 50 years. The warming and beetle invasion makes the lowland areas more vulnerable to fire, whereas the upland areas are likely to change toward grasslands and hardwoods with lower fire potential.

Figure 83. Spruce, Denali National Park, showing an advancing front of bark beetle damage (**right** and **distance**). Photo from National Park Service, through public domain.

Figure 84. Spruce beetle damage, Denali National Forest, Alaska. Photo by Davyd Betchkal, NPS, through public domain.

Another example of the role of these beetles, albeit indirect, is the role of bark beetles following logging (Jonásová & Prach 2008). In the Central European mountain spruce forests (*Picea abies*; Figure 85), logging had a greater impact on the bryophyte cover than did forest damage by bark beetles. Rather, the mountain spruce forests will recover from a bark beetle outbreak without intervention.

Figure 85. ***Picea abies*** forest, trees that provide cover for bryophytes even when damaged by bark beetles, but not when logging occurs. Photo by Crusier, through Creative Commons.

Camouflage

What better way to look like a bryophyte than to grow them on your back! Weevils of the moss forests of New Guinea "cultivate" the mosses (Gressitt *et al*. 1965, 1968; Gerson & Seaward 1977) and one liverwort species (Gerson 1969) as camouflage. The large moss forest weevils may even have special secretions that encourage the growth of the mosses on their backs (Gressitt *et al.* 1965).

Gressitt *et al*. (1968) reported mosses growing on a ***Gymnopholus*** weevil (Figure 86). These moss garden weevils seem to be restricted to high moss forest ridges and moist summits of New Guinea. Two of the involved genera are endemic there. These garden transporters include not only ***Gymnopholus***, but ***Pantorhytes*** (Figure 87) and some of the cryptorhynchine weevils. The weevils provide a favorable environment for the mosses and the mosses provide a protective cover and possibly a chemical predator deterrent for the weevils.

Figure 86. The moss ***Daltonia angustifolia*** living epizootically on the weevil ***Gymnopholus reticulatus***. Photo courtesy of Rob Gradstein.

Figure 87. ***Pantorhytes*** adult with epizootic lichens. Photo by Alex Riedel, with permission.

The leaf-eating weevils ***Gymnopholus*** (Figure 86) and ***Pantorhytes*** (Figure 87) have pits in their carapaces and these pits are colonized by algae, lichens, liverworts, and mosses (Gressitt *et al.* 1965, 1968; Gressitt & Sedlacek 1967). Some weevil species (*e.g.* ***Gymnopholus reticulatus***, Figure 86) seem to be moss specialists, especially the moss ***Daltonia angustifolia*** (Figure 86) (Gradstein *et al*. 1984), and others are lichen specialists. Tiny mites live among these epizootic mosses and may serve as moss dispersal agents to new hosts. The epizootic mosses take advantage of the soft substrate of the beetle. The small branches of montane rainforest trees seem to provide the sources for the mosses and the humidity keeps the garden growing. ***Daltonia angustifolia*** (see Figure 88) matures quickly, further supporting its suitability for its mobile, short-lived habitat.

Figure 88. ***Daltonia*** cf ***longifolia*** from the Neotropics. Photo by Michael Lüth, with permission.

It appears that the weevils have gained sufficient benefit from their gardens that their evolution has preserved characters that encourage the camouflage growth. In addition to secretions mentioned earlier (Gressitt *et al*. 1965), the genus ***Gymnopholus*** (Figure 86) provides depressions and grooves on its outer wings, along with specialized scales and hairs (Gressitt 1966). The bryophytes grow on the fused **elytra**, but often also grow on the pronotum. ***Symbiopholus*** likewise is modified to encourage cryptogamic growth. It has depressions, pits, and grooves. The dorsal surface is rough and may have specially modified hairs or scales. It likewise has secretions that seem to encourage growth of its garden. It appears that the hairs and scales are modified in ways that encourage growth of the flora, and these are the locations where the bryophytes and lichens begin their growth (Gressitt & Sedlacek 1970). The species of ***Gymnopholus*** that do not have plant associations have normal, flat scales or have a smooth, hairless body surface.

The latest member of this family to be described with attached bryophytes is ***Lithinus rufopenicillatus*** (Figure 89) from Madagascar. Paul Bertner and his associates are studying this unusual weevil, so look for more information in the future.

Figure 89. ***Lithinus rufopenicillatus*** with liverworts and mosses in its "backpack." Photo by Paul Bertner, with permission.

But do these gardens help the beetles? Using a reduviid bug, Jackson and Pollard (2007) demonstrated that carrying natural objects such as moss bits or dead ants does indeed reduce predation on the camouflaged bugs. However, such experiments remain to be performed on the camouflaged weevils.

Travelling Ecosystems

Some of these elytral moss gardens are moving microecosystems. Aoki (1966) found an epizootic symbiosis in which the oribatid mite ***Symbioribates papuensis*** lived on lichens on the backs of weevils in Papua, New Guinea. Gressitt (1970) likewise found epizootic mites in the plant growth on three members of the weevil genus ***Gymnopholus*** (Figure 86), a genus that lives on leaves of woody plants in moss forests and on alpine shrubs (Gressitt 1966).

Not only were mites part of this travelling ecosystem, but also lichens, fungi, rotifers, nematodes, diatoms, and other microorganisms (Gressitt 1966; Gressitt & Sedlacek 1967). Psocopterans even feed on the plants growing on the weevils. One individual of ***Gymnopholus acarifer*** had 60 oribatid mites among the resident fungi. The absence of flight in ***Gymnopholus*** (Figure 86) has resulted in different species evolving on different ridges in New Guinea. This mountain-valley system of geographic separation has resulted in 47 such specialists recognized in ***Gymnopholus*** in New Guinea (Gressitt & Sedlacek 1967).

Of the 850 ***Symbiopholus*** specimens examined, 675 had plant growth on their backs (Gressitt 1966). These included the liverworts ***Metzgeria*** (Figure 90) and members of the epiphytic/epiphyllous family **Lejeuneaceae** (Figure 91). Mites, only 0.2 mm long, were abundant among the fungal growth on the ***Symbiopholus***. The mites are able to spread to other weevils when the weevils mate, and the spores of the fungi may likewise spread that way as well as being carried on the bodies of the mites. The mites are absent from three of the weevil species that have hairy-sided, flat-bottomed pits.

Elateroidea

Lampyridae – Fireflies

This family was one of those nice surprises one can find while browsing the internet. I was searching for images on insects on mosses when I found one of eggs of the Japanese firefly on mosses. The eggs of ***Luciola cruciata*** (Figure 92) were nestled among the apical portions of mosses, and one video image shows a tiny larva crawling about. Another short video shows the emerging larva getting its first view of its larval moss home <http://www.gettyimages.com/detail/video/closeup-shot-moment-of-firefly-hatch-stock-video-footage/505766040>. But does the larva stay there and eat the mosses?

Figure 90. ***Metzgeria conjugata***, in a genus that is eaten by ***Symbiopholus***. Photo by David T. Holyoak, with permission.

Figure 91. ***Colura vitiensis*** growing on a leaf in the Fiji Islands. Species in this family can colonize members of **Curculionidae**. Photo courtesy of Tamás Pócs.

Figure 92. ***Luciola cruciata*** larva, a species that can lay eggs on mosses in Japan. Photo by Keisotyo, through Creative Commons.

This species flashes, using luciferase to activate the light (Tatsumi *et al*. 1989). The frequency of the light is dependent on temperature, with more frequent flashes at lower temperatures (Iguchi 2010).

Lycidae – Net-winged Beetles

The **Lycidae** are larger beetles, 10-15 mm long (Wikipedia 2015d). They are protected from predators by their toxicity. The larvae live under bark or in leaf litter and are predaceous.

This family is unusual in that the females are **neotenous**, whereas the males go through full metamorphosis of larvae, pupae, and adults (Masek & Bocak 2014). **Neotenous** refers to reaching sexual maturity at an immature morphological stage. In this case, the females are sexually mature as mature larvae and never change into pupae and adults.

Platerodrilus paradoxus (syn. = *Duliticola paradoxa*) (trilobite beetle; Figure 93) seems to be an exception to the carnivorous habit, but perhaps it is just hunting for prey. Nevertheless, the prey must be small.

Figure 93. ***Platerodrilus paradoxus*** (larval trilobite beetle) foraging on moss from Borneo. Note the tiny head protruding from the triangular prothorax at the bottom of the picture. Photo by Nick Garbutt, with permission.

Platerodrilus paradoxus (Figure 93) has only been observed in copulation twice, but that proves that mating does occur. Crew (2014) described the mating process of *Platerodrilus ruficollis* (syn. = *Platerodrilus hoiseni*), based on research by Wong (1998). One can only guess if it is similar in ***P. paradoxus***. The female of *Platerodrilus ruficollis* arches her abdomen upward to expose her gonopore. The male, which is much smaller (about 10% the size of the female) climbs onto the female and attaches to the gonopore. About three hours after copulation is completed, the male drops dead. The female incubates the eggs for about three days, then places them among leaf litter. Then she too dies a few weeks later.

Bupestroidea

Bupestridae – Jewel Beetles

Trachys troglodytes (Figure 94-Figure 95) is a species that likes high humidity. It is widespread and lives in damp, grassy places and ***Sphagnum*** bogs (Smith & Freeman 1987). As an adult, it hibernates among ***Sphagnum***.

Figure 94. ***Trachys troglodytes*** larva, a species that occurs in ***Sphagnum*** bogs. Photo by Steve Wullaert, through Creative Commons.

Figure 95. ***Trachys troglodytes*** adult, a hibernator in ***Sphagnum*** bogs. Photo by Boris Loboda, through Creative Commons.

Hydrophiloidea

Helophoridae – Water Scavenger Beetles

This is a family of small insects (2-9 mm) with only one genus. They are mostly **Holarctic** (zoogeographical region comprising Nearctic and Palaearctic regions combined), but a few occur in the tropics. ***Helophorus brevipalpis*** (2-3.5 mm; Figure 96) is ubiquitous and common, often occurring far from water in mosses (Stenhouse 2007).

Figure 96. ***Helophorus brevipalpis*** adult, a member of an aquatic family, but it can live far from water among mosses. Photo by James K. Lindsey, with permission.

Some members of the genus are flightless, but ***Helophorus brevipalpis*** (Figure 96) always has functioning flight "apparatus" (Landin 1980). This flight ability permits this mostly aquatic species to travel great distances. It is interesting that it rarely has food in its gut when it is flying, suggesting that mosses may provide it with moisture but probably do not provide food.

Hydrophilidae – Water Scavenger Beetles

This family, widespread in Europe, is generally considered to be aquatic. Some of these beetles are amphibious, but require a very moist environment. For example, ***Chaetarthria simillima*** (Figure 97) is a tiny water beetle, but it has been found among mosses growing beside a lake in the Outer Hebrides (Bratton 2012).

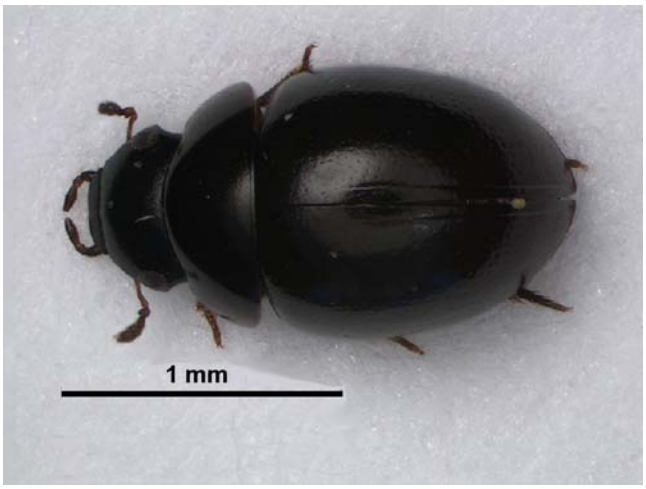

Figure 97. ***Chaetarthria seminulum*** adult, an aquatic beetle that can live among mosses near water on land. Photo from Naturalis, Biodiversity Centre, through Creative Commons.

Crenitis punctatostriatus (Figure 98) is a true bryobiont. It spends its entire life among ***Sphagnum*** (Matthey 1977).

Figure 98. ***Crenitis punctatostriatus*** adult, a ***Sphagnum*** dweller. Photo from SNSB, Zoologische Staatssammlung Muenchen, through Creative Commons.

Scaraboidea

Scarabaeidae

Darwin reported ***Pinotus torulosa*** from mosses (Smith & Freeman 1987). This name has apparently been superseded and I can't find its current name or any further information.

Staphylinoidea

Leiodidae – Round Fungus Beetles

This worldwide family (1.2-7 mm long) seems to have dropped off the radar in recent studies. However, Sharp (1865) found ***Agathidium varians*** (Figure 99) to be abundant among mosses in Great Britain. Most are fungal

feeders (Wikipedia 2015b), a food frequently available among mosses. Most of the members of this genus are known as slime mold beetles (Miller & Wheeler 2005) and their association with slime molds may explain the association of this species with mosses, often the substrate for slime molds.

Figure 99. ***Agathidium varians*** adult on moss, a once-abundant moss dweller in Great Britain. Photo by Tim Faasen, with permission.

Darwin reported several members of this family from mosses, including ***Nargus anisotomoides*** (Figure 100), ***N. wilkini*** (Figure 101), ***Ptomaphagus medius*** (Figure 102), and ***Choleva angustata*** (Figure 103), but none of these were bryobionts, having not only mosses but also dead leaves and other substrata among their choices (Smith & Freeman 1987).

Figure 100. ***Nargus anisotomoides*** adult, a species that includes mosses among its substrata. Photo by NSB, Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 101. ***Nargus wilkinii*** adult, a species that includes mosses among its substrata. Photo by SNSB, Zoologische Staatssammlung Muenchen, through Creative Commons.

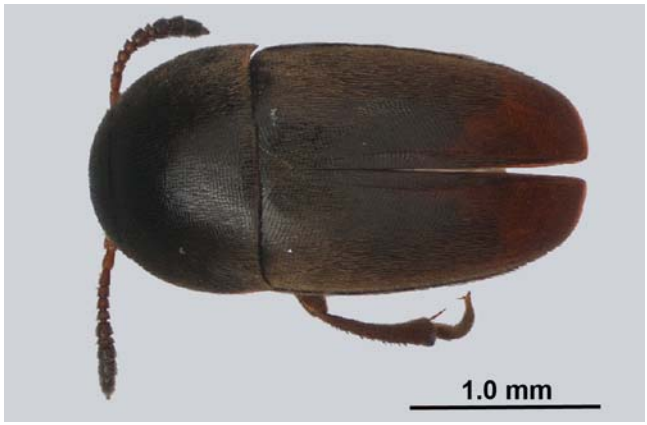

Figure 102. ***Ptomaphagus medius*** adult, a species that includes mosses among its substrata. Photo from Naturalis, Biodiversity Centre, through Creative Commons.

Figure 103. ***Choleva angustata*** adult, a species that includes mosses among its substrata. Photo by Stefan Schmidt, SNSB, through Creative Commons.

Pselaphidae – Short-winged Mold Beetles

This is a worldwide family, but it reaches its greatest diversity in the tropics (Benisch 2015b). More than 9000 species are known. Most prefer moist habitats such as the edges of bogs and marshes, under bark of dead trees, and especially in leaf litter and rotten wood. Like the **Staphylinidae**, they have a short elytra, leaving most of the abdomen exposed (Figure 104-Figure 105).

Ferguson (1901) reported three genera in this family living among mosses in the Clyde area of the British Isles: ***Bythinus*** (Figure 104), ***Bryaxis*** (Figure 105), and ***Pselaphus*** (Figure 106).

Figure 104. ***Bythinus macropalpus*** adult, member of a genus with moss dwellers. Photo by Christoph Benisch <kerbtier.de>, with permission.

Figure 105. ***Bryaxis collaris*** adult, member of a genus with moss dwellers. Photo by Christoph Benisch <kerbtier.de>, with permission.

Figure 106. ***Pselaphus heisei*** adult, a British moss dweller. Photo by Rudolf Macek, with permission.

Ptiliidae – Featherwing Beetles

Bogs provide another set of isolated habitats, and they seem to have more than their share of parthenogenetic females. For example, ***Ptiliopycna moerens*** is a minute (<1.0 mm) featherwing beetle in the northeastern USA and adjacent Canada (Dybas 1978). This moss dweller lives primarily in ***Sphagnum*** (Figure 84) bogs/poor fens and swamp forests. In most of its range, only females are known, thus making these populations parthenogenetic. Males are known only from the northern part of the range. Other parthenogenetic small beetles in bogs include species of ***Pteryx*** (Figure 107), ***Acrotrichis*** (Figure 108), and ***Ptinella*** (Figure 109) – all in **Ptiliidae**. Dybas surmised that the incidence of parthenogenesis in small beetles in relict bogs is unusually high. This is advantageous because it means they can remain in the safety of the mosses without having to venture farther and expend a lot of energy to find a mate, often unsuccessfully.

Figure 107. ***Pteryx suturalis*** adult, a moss dweller in bogs. Photo by Udo Schmidt, through Creative Commons.

Figure 108. ***Acrotrichis sitkaensis*** adult among mosses. Photo by Tim Faasen, with permission.

Figure 109. ***Ptinella pustulata*** adult, a parthenogenetic beetle in bogs. Photo by S.E. Thorpe, through Creative Commons.

Figure 111. ***Syntomium aeneum*** adult, one of the earliest species to be reported among bryophytes. Photo by Tim Faasen, with permission.

Staphylinidae – Rove Beetles

This is a family of 58,000 species and thousands of genera, a family even larger than the **Carabidae**. They don't look like most of the other beetles because their hard, outer wings do not cover the abdomen, leaving more than half the abdomen exposed (Figure 110-Figure 111). Their size range is large (<1-35 mm). Even on mosses, the range is large. Like the **Carabidae**, these beetles are elongate and seem to lack morphological adaptations to a bryophyte habitat. They live in every imaginable habitat, including submersion at high tide (Frank & Ahn 2011), and eat almost anything, depending on the species.

The earliest records of occurrences of the **Staphylinidae** among mosses seem to be those of Champion (1871) and Waterhouse (1871). Waterhouse reported ***Anthophagus alpinus*** (Figure 110) from mosses in Scotland. Champion reported ***Syntomium aeneum*** (Figure 111) and ***Atheta tibialis*** (Figure 113) from mosses and ***Corticaria fuscula*** (see Figure 112) in peat mosses. Klimaszewski *et al*. (2015) found ***Atheta graminicola*** (Figure 114) in Saskatchewan and Newfoundland, Canada, where mosses near water provided a home for some adults.

Figure 112. ***Corticaria foveola*** adult; ***C. fuscula*** lives among peat mosses. Photo by Marko Mutanen, University of Oulu, through Creative Commons.

Figure 110. ***Anthophagus alpinus*** adult, one of the early-reported moss dwellers from Scotland. Photo by Udo Schmidt, with permission.

Figure 113. ***Atheta tibialis*** adult, one of the earliest species to be reported among bryophytes. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 114. ***Atheta graminicola*** adult with mosses. Photo by Tim Faasen, with permission.

Early records from the UK show that ***Gymnusa brevicollis*** (Figure 115) was a moss inhabitant (Beare 1899). Widespread and common species ***Atrecus affinis*** (Figure 116), ***Phloeocharis subtilissima*** (Figure 117), and ***Tachyporus obtusus*** (Figure 118) occur in mosses in the UK (Stenhouse 2007). ***Bythinus burrelli*** (Figure 119) occurs in mosses on the ground and on tree stumps (Stenhouse 2007). Others that have been found in mosses at least once include ***Aleochara funebris*** (female), ***Aleochara verna*** (female; Figure 120), ***Geostiba circellaris*** (female; Figure 121), ***Gyrohypnus fracticornis*** (Figure 122), ***Othius subuliformis*** (Figure 123), ***Oxypoda elongatula*** (female; Figure 124), ***Quedius nitipennis*** (female; Figure 125), and ***Stenus impressus*** (Figure 126).

Figure 115. ***Gymnusa brevicollis*** adult on moss. Photo by Tim Faasen, with permission.

Figure 116. ***Atrecus affinis***, a widespread species that lives among mosses in the UK. Photo by Udo Schmidt, with permission.

Figure 117. ***Phloeocharis subtilissima***, a widespread species that lives among mosses in the UK. Photo by Stefan Schmidt, through Creative Commons.

Figure 118. ***Tachyporus obtusus***, a widespread species that lives among mosses in the UK. Photo by Entomart, through Creative Commons.

Figure 119. ***Bythinus burrelli***, a widespread species that lives among mosses in the UK. Photo by Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 120. ***Aleochara verna***, a species that at least occasionally visits mosses. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 121. ***Geostiba circellaris***, a species that is at least an occasional visitor to mosses. Photo by Tim Faasen, with permission.

Figure 122. ***Gyrohypnus fracticornis***, a species that is at least an occasional visitor to mosses. Photo by Trevor and Dilys Pendleton <eakringbirds.com>, with permission.

Figure 123. ***Othius subuliformis***, a species that is at least an occasional visitor to mosses. Photo by Trevor and Dilys Pendleton <eakringbirds.com>, with permission.

Figure 124. ***Oxypoda elongatula***, a species that is at least an occasional visitor to mosses. Photo by Tim Faasen, with permission.

Figure 125. ***Quedius nitipennis***, a species that is at least an occasional visitor to mosses. Photo by Trevor and Dilys Pendleton <eakringbirds.com>, with permission.

Figure 126. ***Stenus impressus***, a species that is at least an occasional visitor to mosses. Photo by Trevor and Dilys Pendleton <eakringbirds.com>, with permission.

Stenus (Figure 126-Figure 127), a moss visitor, has an unusual adult behavior. These species are predators on small invertebrates, including **Collembola** (Piper 2007). To catch their prey, they shoot out the **labium** using blood pressure. This narrow structure ends in a pad of bristles and hooks. Between the bristles are small pores that exude an adhesive that sticks to the prey.

Like some **Carabidae**, some of the **Staphylinidae** obtain their moisture from wet mosses. For example, ***Stenus kiesenwetteri*** (Figure 127) is a rare species living among very wet ***Sphagnum*** (Figure 128); ***Dianous coerulescens*** (Figure 129) lives where water trickles over mosses and liverworts (Butler 1886). And some are aquatic, as discussed in the **Coleoptera** subchapter on Aquatic Insect interactions.

Figure 127. ***Stenus kiesenwetteri***, a species that uses terrestrial mosses to create an aquatic habitat (**limnoterrestrial**). Photo by Udo Schmidt, with permission.

Figure 128. ***Sphagnum*** in flush, a potential home for the rare ***Stenus kiesenwetteri*** that prefers very wet ***Sphagnum***. Photo by Andrew Hodgson, with permission.

Figure 129. ***Dianous coerulescens*** adult on leafy liverworts. This is a species that uses terrestrial bryophytes to create an aquatic habitat. Photo by Malcolm Storey, through Creative Commons.

In Great Britain, ***Achenium humile*** (Figure 130) is widespread. This species is predatory and lives in broad-leaved woodlands, fields, sand dunes, coastal marshes, and alluvial flats (Hyman & Parsons 1994). It takes advantage of habitats under bark on dead wood, under stones, among mosses, at roots of grasses, muddy dykes, and clay banks. ***Bryophacis crassicornis*** (Figure 131) is more restricted, living in dry mixed woodlands among leaves, moss, and rotting fungi, but also in heathlands among the *Calluna* litter (Lindgren & Palm 2011).

Figure 130. ***Achenium humile*** adult on mosses, a widespread species with a wide range of habitats, including mosses. Photo by Tim Faasen, with permission.

Figure 131. ***Bryophacis crassicornis*** adult male, a species that includes mosses among its homes. Photo by Christoph Benisch <kerbtier.de>, with permission.

Philonthus nigrita (Figure 132) lives in high and transitional moors. It is most common in the ecotone between water bodies and peat "bogs," living in the partly submerged ***Sphagnum*** layer (Figure 133) (Burakowski *et al*. 1980; Koch 1989; Staniec & Pietrykowska-Tudruj 2008).

Figure 132. ***Philonthus nigrita*** adult on ***Sphagnum***. Photo by Christoph Benisch <kerbtier.de>, with permission.

Figure 133. Peatland in Alaska showing the wet ***Sphagnum*** that borders peatland pools, a potential habitat for ***Philonthus nigrita***. Photo by Vita Plasek, with permission.

There is little information regarding the specific eating habits of the moss dwellers among the **Staphylinidae**, but Mani (1962) reported that some staphylinids are moss feeders in high alpine areas.

In Canada, ***Trichiusa*** (Figure 134) species live in forest leaf litter and mosses, especially at the edges of streams and pools (Klimaszewski *et al*. 2015).

Figure 134. ***Trichiusa immigrata*** adult, member of a genus that sometimes lives among mosses. Photo by Veli-Matti Mukkala, in Public Domain.

Scydmaenidae – Ant-like Stone Beetles

This worldwide family (Figure 135) lives in moist forests where they often take advantage of the moisture they can find among mosses (O'keefe 2001, 2005). They feed primarily on mites (Wikipedia 2015a), perhaps contributing to their presence on bryophytes, where mites are common. They are closely related to the **Staphylinidae** and Grebennikov and Newton (2009) have proposed their inclusion in that family.

Figure 135. ***Microscydmus nanus*** (**Scydmaenidae**) adult among mosses. Photo by Tim Faasen, with permission.

The **Scydmaenidae** are frequently associated with ants. And they even resemble ants by having constrictions between the head and thorax and between the thorax and abdomen. O'Keefe (2000) reviewed all the published relationships between ants and these beetles. He suggested that they may occur in the same locations because of a common preferred food. If so, then we should expect some of these associations to be among mosses. Ants are common among a number of kinds of mossy locations, as will be seen in the chapter on **Hymenoptera**. It would be interesting to know just why there are so many members of this family associated with ants and what they gain from the relationship.

Tenebrionoidea

Perimylopidae (=Promecheilidae)

The Antarctic has beetle species that take advantage of the insulation and moisture available when living within the moss clumps. The **Perimylopidae** contribute some of these species. ***Perimylops antarcticus*** (Figure 136-Figure 137) seems to be well adapted by eating bryophytes (Worland *et al*. 1993) and has cold-adapted low-temperature respiration activation rates (Sømme *et al*. 1989). It lives among the moss ***Polytrichastrum alpinum*** (Figure 138) and lichens. Worland and coworkers tested **ice nucleation** in these insects – a process that causes ice crystals to form, expand, and ultimately damage cell membranes. They found that the gut freezes at 1°C lower than does the adult insect. The fecal material experiences ice nucleation at temperatures as high as -2°C and the insects themselves nucleate -3°C. The mosses nucleate at -4 to -5°C. They suggest that bacteria may be responsible for the nucleation proteins, since this food has a lower nucleation temperature than does the beetle.

Figure 136. ***Perimylops antarcticus*** larva on **Polytrichaceae**, South Georgia. Photo by Roger S. Key, with permission.

Figure 137. ***Perimylops antarcticus*** adult on South Georgia, a species that eats mosses. Photo by Roger S. Key, with permission.

Figure 138. ***Polytrichastrum alpinum***, home for ***Perimylops antarcticus***. Photo by Michael Lüth, with permission.

Lagriidae – Long-jointed Beetles

The **Lagriidae** (Figure 139) are medium-sized (Benisch 2015c). They are worldwide, but are concentrated in the tropics. Typical habitats are trees, shrubs, and herbaceous plants, with larvae in decaying wood or leaf litter. Chown (1993) found that **Lagriidae** from the Afromontane forest in South Africa fed on both live and dead parts of the moss ***Braunia secunda*** (Figure 140), based on both field observations and gut analysis. This unknown species is the only record of bryophagy in the family.

Figure 139. ***Lagria*** from a West Java mountain rainforest; at least one member of this family eats mosses. Photo by gbohne, through Creative Commons.

Figure 140. ***Braunia secunda***, food for an unidentified member of the **Lagriidae**. Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Nevertheless, ***Adelium alpicola*** (see Figure 141larvae are known from damp forest moss in Australia (Watt 1974). But there is no evidence that they eat the mosses – or that they don't.

Figure 141. ***Adelium pustulosum*** adult; ***Adelium alpicola*** larvae occur among damp forest mosses in Australia. Photo by Tamara Leitch, through Creative Commons.

Tetratomidae – Polypore Fungus Beetles

The **Tetratomidae** is a small Palaearctic and Nearctic family (~30 species) that is typically associated with fungi, especially wood-decay fungi and those on tree boles (Lawrence 1991; Pollock 2008, 2012). They are poorly known, both taxonomically and biologically.

Tetratoma fungorum (Figure 142) is not generally a moss dweller, as implied by its name. Nevertheless, it finds mosses to be suitable hiding places to survive the winter (Curtis 1823-1840).

Figure 142. ***Tetratoma fungorum*** adult with mosses, a species that overwinters under mosses. Photo by Tim Faasen, with permission.

Summary

There are probably more families of beetles among bryophytes than the ones represented here. Some of these are full-time bryophyte dwellers, some go to the bryophytes at specific times in the life cycle or for specific purposes, and others may simply traverse them while going from one point to another.

One of the largest families, **Staphylinidae**, has bryophyte dwellers among them. They range in size from tiny to large, even on mosses, and seem to have little specialization among the bryophyte dwellers. These include both casual visitors and those that spend part of their lives among mosses. Their lack of well-developed wings suggests they don't travel far. Some of these are bog dwellers. For many of them, mosses appear to be just more litter on the forest floor. The best and most common adaptations to living among bryophytes seems to be those of being small, roundish, smooth, and perhaps shiny and black, as seen in many of the **Chrysomelidae**.

There is some suggestion that bryophytes as food may provide a means to survive the cold, providing gut contents that have lower nucleation temperatures than the surrounding beetle.

Families like **Latridiidae** find suitable food among mosses, particularly slime molds.

The weevils (**Curculionidae**) are among the most abundant species among bryophytes. Their sizes vary; some seem to have camouflage. A few unique taxa have depressions in the elytra and bryophytes and lichens grow there, anchoring among hairs or spikes and being facilitated by a type of glue secreted by the beetle. A number of weevil species also eat bryophytes, sometimes on a seasonal basis when tracheophyte food becomes unavailable or unpalatable.

For those that eat bryophytes, suitable food includes a wide range of bryophyte species. Nevertheless, some bryophytes seem to be avoided. Liverworts may be eaten because of the rich food source in their oil bodies. Some beetles may take advantage of the fatty acids that remain fluid at low temperatures.

Sphagnum habitats often have rare species. They also provide places to survive forest disturbance or to survive the dry season (for those that can fly). Beetles can change the form of the habitat in ways that affect the mosses. In bogs, they can destroy the cover, causing the mosses to dry and more tolerant species to replace them. Bark beetles damage the spruce forests, but recovery of the forest, mosses, and moss-dwelling beetles is faster than it is from clear cutting.

Some terrestrial beetles in aquatic families use mosses as a limnoterrestrial habitat, maintaining their moisture because the moss remains damp.

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CHAPTER 12-10
TERRESTRIAL INSECTS: HOLOMETABOLA – HYMENOPTERA

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CHAPTER 12-10
TERRESTRIAL INSECTS: HOLOMETABOLA – HYMENOPTERA

Figure 1. Ant hill in Finland with leafy liverworts (***Barbilophozia hatcheri***, ***B. floerkei***, ***Tritomaria quinquedentata***, ***Lophozia ventricosa***) and the moss ***Pohlia nutans***. Photo by Des Callaghan, with permission.

HYMENOPTERA – Sawflies, Wasps, Bees, and Ants

Andrew *et al*. (2003) examined the variation in bryophyte fauna in Tasmania and New Zealand using different spatial scales along altitudinal gradients. Among these collections, they found six families of **Hymenoptera**. Although 77% of the faunal families were represented by 44 families, these 44 contributed only 10% of the total abundance.

This order is absent among bryophytes in the aquatic habitat, but in the terrestrial habitat, bees and ants find them useful in a variety of ways. As stated by Gerson (1969), some **Hymenoptera** feed on mosses. But others use them for nest materials, to house eggs, to provide water, and to provide cover. And of course some, including the sawflies, use them for pupation (Nägeli 1936).

Ants

Bryophytes, along with ants and grass, had a unique role for one Marine (Anonymous 1983). Trapped in a ravine in California for weeks, this marine subsisted on ants, moss, and grass! No wonder he lost 75 pounds before he found a way out!

The Phenomenal Ants

Ants are perhaps the most ordered insects on the planet. They work together to hunt and to build their trails and nests. In fact, they have been described as superorganisms because of their ability to work together as a unit (Oster & Wilson 1978). Ants are well endowed with defense, and depending on the species, they can bite, sting, or spray chemicals (Figure 2) such as formic acid (Wikipedia 2016). Their well-developed mandibles (Figure

3) serve for protection and prey capture. When an ant is killed, it emits a chemical that attracts ants from some distance, bringing an army to attack the intruder. Ants can also use chemical senses to identify dead colony members and remove them, and the workers are diligent in keeping the nest clean and free of bacteria. Their chemical signals, along with sounds and contact, permit them to communicate with each other. They also recognize their nest mates through the scent of hydrocarbon-laced secretions from their exoskeletons.

Figure 2. ***Formica aquilonia***, preparing to spray and adjusting the position of the abdomen with its legs. Photo by Brian Eversham, with permission.

Figure 3. ***Myrmica*** sp. mandibles, a genus with a number of bryophyte dwellers. Photo from <fir0002/flagstaffotos.com.au>, through Creative Commons.

Ants are common among bryophytes, especially in bogs. Those that frequent the bryophytes don't seem to have any special adaptations, but this has not really been explored systematically. Their body constrictions give them considerable flexibility compared to most other insects, permitting even large species to maneuver among the bryophytes. The bryophytes provide a temperature-buffered environment where many food organisms can be found. They also provide a suitable underground habitat for growing fungi, cultivated by the ants, and kept moist by the bryophytes that reduce moisture loss at the soil surface.

Where Ants Are Absent

Acacia ants, on the other hand, may actually avoid mosses. In Costa Rica, Angela Newton (Bryonet, 20 November 2006) found that ants under ant-acacias left the bryophytes mostly undisturbed, except for some obvious nibbling around the edges. The green patches of moss in the otherwise clear ant-acacia circles were quite healthy and more numerous than in the surrounding forest. The mosses seemed to benefit from the ants' gardening activities, whereby the ants removed the larger plants that could pose a competition threat.

Food Source?

We generally think of the ants with their large jaws and sharp bite as carnivores. But Plitt (1907) found moss capsules that were gnawed and spores removed. A patch of "***Webera sessilis***" (probably ***Diphyscium foliosum***, Figure 4) occurred immediately over an ant's nest. Both ***Myrmica ruginodis*** (Figure 39) and ***Formica picea*** (Figure 5) fed on the mosses and managed to gnaw a hole in nearly every capsule to obtain the spores. And beware – they were on the mosses in the collector's vasculum.

Figure 4. ***Diphyscium foliosum*** with capsules. Spores in these capsules serve as food for ***Myrmica ruginodis*** (Figure 39) and ***Formica picea*** (Figure 5). Photo by David T. Holyoak, with permission.

Figure 5. ***Formica picea*** on ***Sphagnum***. This ant species feeds on the spores of ***Diphyscium foliosum***. Photo by Barbara Thaler-Knoflach, with permission.

Loria and Herrnstadt (1980) found that in the Negev desert the harvester ant (***Messor***, Figure 6) ate capsules of ***Aloina aloides*** (Figure 7-Figure 8), ***Crossidium crassinerve*** (Figure 9), and ***Bryum bicolor*** (Figure 10) in winter when other food was not available. The ants climbed the seta of ***C. crassinerve***, chewed off the capsules, and carried them to their nests, forming a parade 15 m long. An average of 30 capsules per minute arrived at the nest! Longton (1984) considered this behavior to be opportunistic because capsules are not available every year in the desert climate. It is possible that this behavior is advantageous for the mosses as well – the ants are likely to place the capsules in places more suitable for spore maturation in this environment where such sites are rare. However, Loria and Herrnstadt (1980) emphasized that mosses do not seem to derive any advantage from this harvesting process.

Figure 6. ***Messor barbarus***, member of the genus that eats moss capsules in the Negev Desert. Photo by Valter Jacinto, through Creative Commons.

Figure 7. ***Messor*** on capsules of ***Bryum bicolor*** in Negev desert. Photo courtesy of Ilana Herrnstadt.

Figure 8. ***Aloina aloides*** with capsules. Capsules of this species serve as food for ***Messor*** in the Negev Desert. Photo by David Holyoak, with permission.

Figure 9. ***Crossidium crassinerve*** with capsules. Capsules of this species serve as food for ***Messor*** in the Negev Desert. Photo by Michael Lüth, with permission.

Figure 10. ***Bryum bicolor*** with capsules. Capsules of this species serve as food for ***Messor*** in the Negev Desert. Photo by Jonathan Sleath, with permission.

Bear feces are known to contain mosses, with one study reporting 50-90% mosses, primarily ***Pleurozium schreberi*** (Figure 30) (Dalen *et al*. 1996). But when the

feces contained 15% ***Brachythecium reflexum*** (Figure 11), Dalen and coworkers concluded that it was unlikely that the mosses were eaten by choice. Rather, they probably came along with its inhabiting food organisms – the ants.

Figure 11. ***Brachythecium reflexum***, a moss where ants can dwell and the moss seems to be eaten by bears along with the ants. Photo by Michael Lüth, with permission.

The Green Salamander, ***Aneides aeneus*** (Figure 12), is a well-known moss-dwelling insectivore. At Cooper's Rock in West Virginia, USA, the gut consisted of 53% ants, but also included moss fragments (Lee & Norden 1973). It is likely that this is another case of a moss inhabitant getting mosses along with its intended prey. Gunzburger (1999) likewise concluded that mosses in the gut of the Red Hills Salamander ***Phaeognathus hubrichti*** (Figure 13) got there in the process of eating moss inhabitants, including ants.

Figure 12. ***Aneides aeneus***, a moss-dwelling salamander that eats of lot of ants. Photo by Mike Graziano, with permission.

Figure 13. ***Phaeognathus hubrichti***, another moss dweller that eats ants among mosses and consumes part of the moss along with them. Photo by Danté B. Fenolio, with permission.

Anthills

Anthills range in size from those tiny volcanoes in the cracks in the sidewalk to massive structures that rival termite mounds (Figure 1). And some are simple entrances to a series of underground tunnels. In British chalk grasslands, King (1977) found that anthills have shorter vegetation, more rabbit dung, drier soil, smaller structural aggregates, lower bulk density, and more temperature extremes than the surrounding pasture. Several of these factors also lead to less moisture.

Eiseman and Charney (2010) report mosses on the abandoned anthill mounds of ***Formica exsectoides*** (Figure 14). Des Callaghan (Bryonet 3 August 2014) recently visited Finland and photographed a giant ant nest. The ants had cleared the nest of its tracheophytes, but, as he put it, they appear to have a fondness of leafy liverworts. Several species of liverworts [***Barbilophozia hatcheri*** (Figure 15), ***B. floerkei*** (Figure 16), ***Tritomaria quinquedentata*** (Figure 17), ***Lophozia ventricosa*** (Figure 18)] cover one of the mounds. In addition the mound served as substrate for the ubiquitous ***Pohlia nutans*** (Figure 19).

Figure 14. ***Formica exsectoides*** mound. Photo by Greg Schechter, through Creative Commons.

Figure 15. ***Barbilophozia hatcheri***, a colonizer on anthills of ***Formica exsectoides***. Photo by Michael Lüth, with permission.

Figure 16. ***Barbilophozia floerkei***, a colonizer on anthills of ***Formica exsectoides***. Photo by Hermann Schachner, through Creative Commons.

Figure 17. ***Tritomaria quinquedentata***, a colonizer on anthills of ***Formica exsectoides***. Photo by Malcolm Storey, through DiscoverLife.

Figure 18. ***Lophozia ventricosa***, a colonizer on anthills of ***Formica exsectoides***. Photo by Michael Lüth, with permission.

Figure 19. ***Pohlia nutans***, a colonizer on anthills of ***Formica exsectoides***. Photo by Michael Lüth, with permission.

Pekka Punttila (pers. comm.) explained the mound nests of the two species that may be inhabiting the mounds photographed by Des Callaghan (Figure 1). ***Formica lugubris*** (Figure 20) is **monogynous** (has only one queen in a mound). The longevity of this queen and her colony lasts typically only about 20 years. This loss opens the mound to invasion by other species or simply to die off if something happens to the queen. ***Formica aquilonia*** (Figure 21-Figure 23), on the other hand, is **polygynous**, meaning it has more than one queen in a mound. That strategy permits the species to maintain its nest for a long time. Furthermore, if many mounds are present, it is likely to be that of ***F. aquilonia***, a **polydomous** species. These mounds may reach dozens or even hundreds in an area. ***Formica lugubris*** typically builds single mounds.

Figure 20. ***Formica*** cf ***lugubris***, a monogynous species that builds single mounds. Photo by Richard Bartz, through Creative Commons.

Figure 21. ***Formica aquilonia*** mound. Photo by Villak, through Creative Commons.

Figure 22. ***Formica aquilonia*** on moss. Photo by Brian Eversham, with permission.

Figure 23. ***Formica aquilonia***, attacking its prey. Photo by Brian Eversham, with permission.

The monogynous species such as ***Formica lugubris*** (Figure 20) are able to disperse during their nuptial flight, temporarily parasitize other nests, and establish in young forests or older forest fragments (Punttila 1996). The polygynous species, including ***F. aquilonia*** (Figure 21-Figure 23), disperse primarily by "nest budding," permitting them to form large colonies of cooperative nests. These are found in older forests and larger old forest fragments.

Anthills create microhabitats of their own. This is evidenced by the moss ***Pseudoscleropodium purum*** (Figure 24). This species predominates on the north-facing sides of anthills constructed by ***Lasius flavus*** (Figure 25-Figure 26) (King 2003). King experimented with survivorship of the moss by rotating the anthills either 360° or 180°. Hence, half the anthills were now facing south. For those mosses facing south, over half the shoots turned white at the tips and up to 20 mm from the apex. Those rotated 360°, thus still facing north, remained green and healthy. Nevertheless, most of the mosses on the south side survived. Those on the north side grew faster and King concluded that it may be more difficult for the fragments to establish on the south side due to the longer periods that were dry and unfavorable for growth. Carl Farmer found anthills of this species in Scotland completely covered by mosses while the ants thrived inside.

Figure 24. ***Pseudoscleropodium purum***, a moss that lives on the north sides of anthills of ***Lasius flavus***. Photo by Michael Lüth, with permission.

Figure 25. ***Lasius flavus***, an ant that makes mounds where one can find ***Pseudoscleropodium purum*** on the north side of the mound. Photo by Anki Engström <www.krypinaturen.se>, with permission.

Figure 26. ***Lasius flavus*** tending aphids. Photo by Anki Engström <www.krypinaturen.se>, with permission.

In acidic grasslands, bryophytes may be confined to anthills. King (1981) found that the acrocarpous mosses ***Dicranum scoparium*** (Figure 27), ***Polytrichum juniperinum*** (Figure 28), and ***Polytrichum piliferum*** (Figure 29), all colonizers, were almost confined to the anthills in the Gower Peninsula of South Wales. King considered dispersal ability and ability to withstand burial to be primary factors to favor these mosses over surrounding tracheophyte plants, downplaying the importance of soil chemical and physical factors. ***Lasius flavus*** (Figure 25-Figure 26) builds mounds that are 15-20 cm high and 50-70 cm in diameter. In these acidic habitats, King found that ***Pleurozium schreberi*** (Figure 30), like ***Pseudoscleropodium purum***, is abundant on the north-facing sides of the mounds. On the other hand, ***Polytrichum juniperinum*** and ***Polytrichum piliferum*** are more frequent at the summit of the mound than at the periphery, but ***P. piliferum*** is more frequently on the south side, a location consistent with its habitation of more exposed, xeric habitats. ***Polytrichum juniperinum*** has its base 15 cm below the soil, suggesting that it grew up through the anthill as the anthill increased in size.

Figure 27. ***Dicranum scoparium***, a species that is common on anthills in South Wales. Photo by Janice Glime.

Figure 28. ***Polytrichum juniperinum***, a species that is common at the summit of anthills. Photo by Janice Glime.

Figure 29. ***Polytrichum piliferum***, a species that is frequent at the summit of anthills, but mostly on the south side. Photo by David Holyoak, with permission.

Figure 30. ***Pleurozium schreberi***, a moss that grows on north-facing slopes of anthills made by ***Lasius flavus***. Photo by Michael Lüth, with permission.

Des Callaghan (Bryonet 10 May 2017) has seen ***Buxbaumia viridis*** (Figure 31) living on the ant hills of the wood ant, ***Formica rufa*** (Figure 53-Figure 55). Many Bryonetters have reported what appears to be herbivory on this species of ***Buxbaumia***, but thus far there is no direct evidence that these are consumed by ants.

Figure 31. ***Buxbaumia viridis*** capsules, a species that can inhabit wood ant (***Formica rufa***) nests. Photo by Hermann Schachner, through Creative Commons.

For mosses in deciduous forests, anthills provide a substrate that rises above the forest floor. This permits the leaf litter to fall downward, keeping the anthill exposed and preventing burial of the bryophytes by leaf litter.

Ants as Gardeners

In several tropical areas, ants make ant gardens (Ule 1901; Blüthgen *et al*. 2001). These aerial gardens usually consist of plants, started as seeds by the ants, and used as a matrix in which soil is placed to construct a nest. But Ule reported only flowering plants in these ant gardens. In 1985, Frahm reported risk of life to collect a nest 15 cm in diameter with a yellow-green center surely of moss. The escapade began when he and Rob Gradstein chopped down the tree holding the nest, using machetes. But alas, the tree fell, only to land within the arms of another tree, with the nest still out of reach. Again, the second tree was cut in like manner, but it fell 10 meters deep into the river, thus drowning the ants in their nest! Not to be discouraged from their quest, the two bryologists then had to cross the river, as the tree was accessible only down a steep and rocky slope and to the other side of the valley. Attempts to raise the nest to the bridge with a rope destroyed most of it, but they were able to rescue the moss, determined as ***Brachymenium columbicum*** (Figure 32), a moss known also from Colombia and Ecuador, and now, for the first time, from Peru.

Figure 32. Ant garden, primarily of ***Brachymenium columbicum*** (and seedlings), from a tree in Peru. Photo by Jan-Peter Frahm, with permission.

Blüthgen *et al*. (2001) suggested the importance of these aerial ant gardens. Nutrients are scarce in the canopy. Some plants are adapted by producing **adventitious** roots (roots that arise from stems and other non-root axis points) that are able to grow and penetrate animal debris, bromeliad tanks, bryophytes, and plant cavities. But some lack the ability to take advantage of these nutrient sources. Among these some are able to form commensalistic associations. The association between ants and epiphytes is one such association. The ants carry seeds that they imbed in the garden. The ants then care for the garden by protecting it and providing a stable germination and establishment state. As noted by Frahm (1985), some of these gardens, as already noted, have bryophytes that can further help by maintaining moisture and trapping airborne dust and nutrients.

The leafy liverwort ***Nardia*** sp. (Figure 33) is a pioneer on volcanic ash, forming layered deposits up to 15 cm thick (Jongmans *et al*. 2001). These growths are able to adhere to vertical cliffs and to form bridges between volcanic boulders, facilitating the establishment of vascular plants. These carpets sometimes are invaded by ants and other insects that help to keep the liverworts clean and bring seeds and spores to continue the garden. In Costa Rica ants took up residence among the fronds of the hanging garden liverwort ***Nardia succulenta*** on the ash of volcano Arenal (Jongmans *et al*. 2001).

Figure 33. ***Nardia scalaris***. ***Nardia*** is a genus that forms bridges between volcanic boulders and is maintained by ants. Photo by Hermann Schachner, through Creative Commons.

Gibson (1993a, b) found that ants placed seeds of the cow wheat (***Melampyrum lineare***, Figure 34-Figure 36) more frequently under ***Polytrichum*** (Figure 28-Figure 29) than expected by chance, based on its relative cover (Figure 37). In the oak-pine forest of the New Jersey Pinelands, Gibson and Good (1987) found that the seeds of ***Melampyrum lineare*** were restricted to mossy patches. Ants gather these seeds and store them, later using the oily and nutrient-rich eliasome (Figure 36) as a food source without damaging the seed to which it is attached (Gibson 1993a, b). Litter and lichens were also used, but ***Polytrichum*** seemed to be highly selected. ***Dicranum*** (Figure 27) and ***Pleurozium*** (Figure 30), although more abundant than the ***Polytrichum***, attracted far fewer ants to store seeds. This behavior afforded the seeds a safe place where mice did not eat them and they retained sufficient moisture to survive. These seeds have low survival if they dry out and will die if they fall to the soil and remain exposed. If they remain in the capsules until evening, the mice will eat them.

Figure 34. ***Melampyrum lineare***, a hemiparasite whose seeds are dispersed by ants. These seeds are often deposited under mosses and lichens. Photo by Janice Glime.

Figure 35. ***Melampyrum lineare*** fruits. Photo by Keir Morse at <gobotany.newenglandwild.org>, with permission.

Figure 36. ***Melampyrum lineare*** moist seeds. Note the white eliasome. If the seeds drop to the ground they will dry out and turn black. Photo by Keir Morse at <gobotany.newenglandwild.org>, with permission.

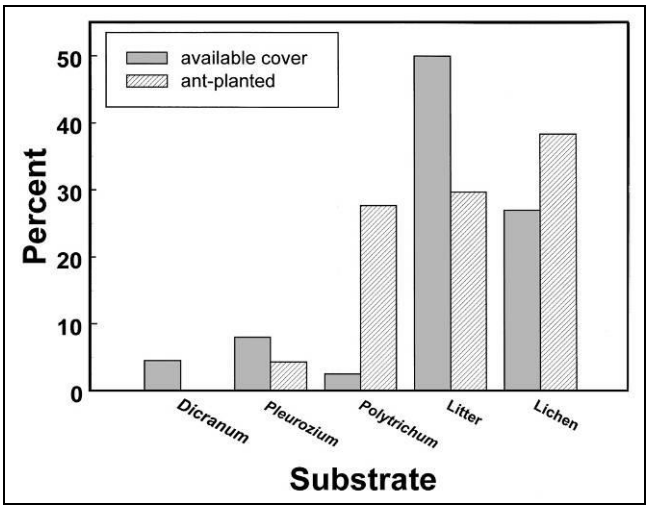

Figure 37. Percent frequency of ***Melampyrum lineare*** seeds stored by ants under various available substrates near Houghton, Michigan, USA. Modified from Gibson 1993a.

Forest Ants

I have found little literature on forest floor bryophytes and their ant inhabitants. Ward (2000) reviewed some of these from leaf litter communities. Wilson and Hölldobler (2005) included bryophytes among the sites offering the desirable small spaces to ponerine ants on the forest floor. While these species are relatively abundant in the tropical and warm-temperate forests, they are scarce in the cool-temperate forests, deserts, and arid grasslands.

Myrmica rubra (Figure 38), ***M. ruginodis*** (Figure 39), and ***Formica lemani*** (Figure 40-Figure 41) are widespread among forest mosses (Stenhouse 2007). The latter nests in stumps. ***Myrmica rubra*** is the most moisture-loving of the ***Myrmica*** species, preferring moist, shady forests (Kupianskaya *et al.* 2000). It builds its nests in decaying stumps and logs, under mosses, and other moist locations. ***Myrmica ruginodis*** is the most abundant of the red ants in the North Vidzeme Biosphere Reserve, Latvia (Gluhovs 2013). Gluhovs determined that soil *p*H, bryophyte cover, and coarse woody debris did not have a significant effect on the ant communities in the forest.

Figure 38. ***Myrmica rubra*** workers drinking from a water droplet on a leaf. Photo by Richard Becker at <www.bwars.com>, through open source permission.

Figure 39. ***Myrmica ruginodis*** worker carrying pupa. This species is common among forest mosses in Europe. Photo by Brian Eversham, with permission.

Figure 40. ***Formica lemani*** queen on moss. Photo by Brian Eversham, with permission.

Figure 41. ***Formica lemani*** worker carrying pupa across moss. Photo by Brian Eversham, with permission.

In addition to ***Myrmica rubra***, it is likely that moisture is important to other species and may account for vertical distribution of species and location of nesting sites. Billings and Drew (1938) demonstrated that bryophytes created a microhabitat that held six times as much water as the bare bark of old-growth tulip trees (*Liriodendron tulipifera*) in Tennessee.

Myrmica lobifrons and ***Dolichoderus pustulatus*** are the dominant ants in bogs in New England, USA (Gotelli & Ellison 2002). In fact, ***M. lobifrons*** seems to specialize in bogs and other humid habitats.

In forest sites in the Czech Republic, the **Formicidae** were among the most abundant taxa in the biggest bryophyte samples (400 cm^2) (Božanić 2011). ***Lasius brunneus*** (Figure 42) was abundant among epiphytic mosses on trees with a diameter of 60-110 cm, especially on old oak trees.

Figure 42. ***Lasius brunneus*** adult, an inhabitant of old oak trees where it lives among epiphytic mosses. Photo by Stanislav Krejčík, through Creative Commons.

Božanić (2008) examined the aspects of forest mosses that made them suitable environments for invertebrates. He suggested that ants may live there or go to mosses to search for food or shelter or to lay eggs. The microclimate, especially in retaining moisture, provides a haven for forest dwellers. On the other hand, the invertebrates help the bryophytes by spreading spores. Using heat extraction with a Tullgren funnel, Božanić extracted invertebrates from 66 moss samples. The richest fauna of invertebrates, including **Formicidae**, occurred with the moss ***Brachythecium curtum*** (Figure 43). The most important factors for number of taxa were type of substrate, height above ground, and moss sample area. The species were affected by the type of substrate, height above ground, and tree diameter.

Figure 43. ***Brachythecium curtum***, a preferred moss for habitation by members of **Formicidae**. Photo by Janice Glime.

Božanić *et al*. (2013) investigated the factors that affected invertebrate communities among bryophytes in forests of the Czech Republic. The dominant bryophyte was ***Hypnum cupressiforme*** (Figure 44) and Božanić and coworkers reported on 13 invertebrate groups, encompassing 45 species. Of these classes, orders, and families, 4 species of **Formicidae** (ants) were present. Height above ground was an important parameter in describing the **Formicidae** communities. But unlike the epiphyte communities in Costa Rica described by Longino and Nadkarni (1990) discussed below, Božanić *et al*. found that the **Formicidae** preferred habitats on the ground or

close to it. It is likely that the epiphyte cover in the Czech Republic is much less developed and protective compared to that in the cloud forests of Costa Rica.

Figure 44. ***Hypnum cupressiforme***, a dominant bryophyte in forests of the Czech Republic and home to ants there. Photo by Michael Lüth, with permission.

Epiphyte Communities

As seen above, Blüthgen *et al*. (2001) have demonstrated one importance of ants as epiphyte gardeners. Yanoviak *et al*. (2007) likewise considered the epiphytic mats as important habitats. In Costa Rica, these mats were thinner and exhibited less structural diversity in secondary forests compared to undisturbed forests. But for ants, the diversity was significantly greater in the secondary forests, especially *Solenopsis* spp. (subterranean fire ants). During the dry season, arthropod diversity declined among the epiphytes.

Nadkarni and Longino (1990) used the Winkler sifting apparatus to extract arthropods from Costa Rican canopy soils. They found that ants were among the dominant invertebrate groups in these habitats. In fact, the ants were the only group that did not have higher densities on the ground than in the canopy.

Longino and Nadkarni (1990) demonstrated a vertical zonation of ants in these Costa Rican cloud forests. The genera were similar in the canopy (litter and humus that include mosses) to those among the ground litter, but represented a subset of those genera. But at the species level, the two habitats were distinct with rare overlap in species between the two. Surprisingly, their new find was on the ground, where ***Stenamma*** JTL-3 (see Figure 62) was nesting under moss mats.

Ant activity in the tropical forests seems to be greater in the canopy than on the ground. Yanoviak and Kaspari (2000) used bait defense to determine these differences. The bait indicated more defense in the canopy (60%) than in the litter (32%), independent of tree species and bait type. It also indicated higher activity in defending protein baits than carbohydrate baits. Furthermore, the litter and canopy had no species in common.

Epiphylls as Defenders

Not all bryophytes favor the ants. The leafcutter ant ***Atta cephalotes*** (Figure 45) is repelled by epiphylls, including bryophytes, on citrus leaves. Mueller and Wolf-Mueller (1991) removed the epiphylls from citrus leaves and found 2-3 times as much herbivore damage from ants comparee to leaves with epiphylls intact. These epiphylls consisted of leafy liverworts and crustose lichens. They suggested that the epiphylls increased the cutting effort, or that secondary compounds in the liverworts might have been major contributors to the antiherbivory (see Swain 1977). A further possibility is that the epiphylls inhibited the growth of the fungi that served as food for these ants.

Coley *et al*. (1993) looked at the relationship from a different perspective. They found that long-lived tracheophyte leaves have better defenses against herbivores and pathogens than those with deciduous leaves. They suggested that liverworts may provide protection of the leaves, citing the rich concentration of terpenoids in liverworts. It takes only two years to cover leaves with species that have rapid colonization rates.

Figure 45. ***Atta cephalotes***, a leaf cutter ant that is repelled by epiphylls such as leafy liverworts. Photo by Scott Bauer, through public domain.

Dispersal

The busy ants run all over their habitats and the tiny, widely spaced hairs on their bodies would seem to provide ideal locations for some sizes of dispersal units. Rudolphi (2009) set out to discover if such a hypothesis was indeed viable. He reasoned that both ants (***Lasius platythorax***, Figure 82) and mosses, ***Aulacomnium androgynum*** (Figure 46) in particular, occurred on the same dead wood in Swedish forests. Therefore, it is reasonable that the gemmae (Figure 47) of this moss might be transported by the ants. First he tested whether the gemmae would adhere to the ants. He put one tuft of moss in each of eight Petri dishes and released eight ants into each dish, repeating the experiment 8 times. Once the ants ran across the moss (at least 30 seconds), they were removed by letting them crawl into a bottle. Ants were frozen and examined for adherence of gemmae. As many as six gemmae did, in fact, adhere, with 1/3 of the ants having gemmae within less than two minutes of exposure. He found that while moisture on the moss did not influence time the ant spent on the moss (42 sec wet vs 48 sec dry), the adherence was five times as great on the dry mosses (mean 0.94) vs wet (mean 0.19).

Figure 46. ***Aulacomnium androgynum*** showing gemmae that adhere to ants that share the same dead wood. Photo by Michael Lüth, with permission.

Figure 47. ***Aulacomnium androgynum*** gemmae. Photo by Des Callaghan, with permission.

Rudolphi (2009) followed this with a second experiment to determine residence time of the gemmae on the ants. Using nine ants in each of five time periods (0, 1, 2, 4, 8 hours), he attached two gemmae to the dorsal abdomen and let the ants run around. Ants were then frozen and examined for gemmae. Each time interval experiment was again repeated 8 times. After two hours, ants averaged retention of one gemma. After eight hours, 24% of the ants still had at least one gemma attached, suggesting that ants could be an effective dispersal agent of these gemmae.

But why more dry propagules? Wet gemmae tend to stick together, making the dispersal unit larger and heavier, thus easier to dislodge. This greater success of dry gemmae is actually advantageous because the ants are more active when the weather is dry (Elchuk & Wiebe 2003). Now we just need to watch the ants to see if they traverse the mosses on the logs and if they drop the propagules in suitable sites for successful establishment. Surely both of these conditions are met at least some of the time.

Ants are able to make trails – trails that we can see and follow. They do this by cutting vegetation that slows them down, and that includes cutting bryophytes. This activity provides an opportunity for dispersal. Korpelainen *et al*. (2011) explored the importance of this role in the leafy liverwort ***Barbilophozia attenuata*** (Figure 48). Using microsatellite markers, they showed significant kinship relationships up to 8 m. After that the relationship coefficients approached 0, then decreased to negative correlations. At more than 25 m they again approached 0, indicating random distribution. They suggested that the large gemmae permit effective establishment more easily than do spores. Gemmae were favored over spores along the ant trails (and are more likely in other areas of disturbance). Nevertheless, the researchers concluded that ants do not have a large role as dispersal agents, and the physical structure of the ant trails likewise does not lead to greater dispersal. Rather, the trails provide colonization sites available to this liverwort.

Figure 48. ***Barbilophozia attenuata***, a liverwort with gemmae that are distributed by ants. Photo by Andrew Spink, with permission.

Spain (2012a) puzzled over a section of moss lawn where the mosses exhibited a trail (Figure 49). It ended at the base of a tree, ruling out a watering hose as the causal factor. Finally he observed the trail long enough to see carpenter ants (***Camponotus*** sp.; Figure 50) following the trail (Figure 49) in both directions, one after the other. The ants had apparently removed thousands of moss plants to make the trail, hence making travelling easier (Figure 52). They no longer needed to climb up and down across the stems (Figure 51). Although the trail was only 10 m long, by ant lengths it was equivalent of the length of more than 7 football fields traversed by a human. This trail had actually been cut to remove the obstructing branches. Spain suggests if you want to get rid of the ants, give the nests frequent disturbance, such as hosing them, or fill the entrance with disturbing powders such as cinnamon, diatomaceous earth, or cloves (Spain 2012b).

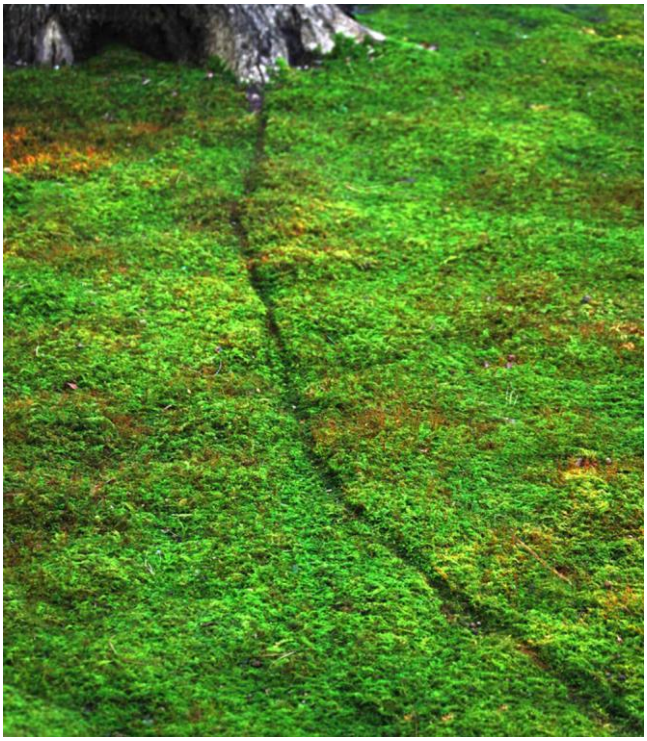

Figure 49. Moss-trail by made by carpenter ant. Photo from Moss and Stones Garden, with permission.

Figure 50. Carpenter ant (***Camponotus*** sp.) that made the moss trail. Photo from Moss and Stones Garden, with permission.

Figure 51. Here the busy ants appear to be dancing on a mound of moss, but its rough nature slows them down on their trail. Photo from Moss and Stones Garden, with permission.

Figure 52. Ant trail showing cut through mosses. Photo from Moss and Stones Garden, with permission.

Recognizing the importance of bryophyte fragments, Heiken *et al*. (2007) sampled nesting material from 25 ***Formica rufa*** (Figure 53-Figure 55) group nest mounds in five different forest types in Germany. In these nests they found numerous fragments of 20 bryophyte species occurring on almost all sampled mounds. Although both lichens and bryophytes occurred in the nests, 20 species represented bryophytes, whereas only 10 were lichens. The choices indicated some specificity. Those used were the abundant ones – no surprise there, but life form seemed to matter. Weft bryophytes accumulated on the mounds, but tall turfs seemed to be ignored. ***Hypnum cupressiforme*** (Figure 44) was the most abundant on the nests, appearing in 16 of the 25 samples and comprising 67.5% of the fragments detected. Other common flora were ***Pleurozium schreberi*** (Figure 30) and species of ***Brachythecium*** (Figure 63-Figure 64, Figure 43). Certain life forms (weft bryophytes, reindeer lichens) accumulate on mounds, while others (tall turfs, cup-type *Cladonia* spp.) discriminate, reflecting fragmentation features of the species.

Figure 53. ***Formica rufa*** nest in which bryophyte fragments are incorporated. Photo through public domain.

Figure 54. ***Formica rufa***, an ant that is known to use at least 20 species of mosses in its nests. Photo by Brian Eversham, with permission.

Figure 55. ***Formica rufa***, ready to bite or fire chemical weapons in its defense. Photo by Brian Eversham, with permission.

Some bryophytic nest contents were restricted by forest type (Heiken *et al*. 2007). ***Pohlia nutans*** (Figure 19) and ***Polytrichum piliferum*** (Figure 29) occurred in *Cladonio-Pinetum* nests; ***Pleurozium schreberi*** (Figure 30) in *Leucobryo-Pinetum*; ***Polytrichastrum formosum*** (Figure 56) and ***Rhytidiadelphus squarrosus*** (Figure 57) in spruce forests; ***Campylopus pyriformis*** (Figure 58) in low-mountain ranges; ***Plagiothecium*** spp. (Figure 59) in *Calamagrostio-Piceetum*.

Figure 56. ***Polytrichastrum formosum*** with frost. This species is found in ant nests in spruce forests. Photo by Aimon Niklasson, with permission.

Figure 57. ***Rhytidiadelphus squarrosus***, a species found in ant nests in spruce forests. Photo by Michael Lüth, with permission.

Figure 58. ***Campylopus pyriformis***, a moss used in ant nests in low mountain ranges. Photo by Michael Lüth, with permission.

Figure 59. ***Plagiothecium laetum***. Several species of this genus are ant nest components in the *Calamagrostio-Piceetum.* Photo by Michael Lüth, with permission.

Heiken *et al*. (2007) concluded that the ants were important dispersal agents by dropping fragments during transport and providing a colonization site on the mounds, especially those that were abandoned.

Anthills are not friendly bryophyte sites. The outer part of the nest dries faster than the forest floor (Heiken *et al*. (2007). Nests are frequently disturbed by ants, birds, and wild boar, suppressing the growth of the bryophytes. Heiken and coworkers determined that at least 25,000 fragments of bryophytes and lichens were carried to ant nests in one year. That is no guarantee they will grow.

Nesting

Ants build elaborate nests in trees or underground (Figure 60-Figure 61) (Wikipedia 2016). They typically maintain the nest at a temperature that is ideal for development of the larvae. They do this by choosing the location, materials, ventilation, and solar radiation. The worker and activity and metabolism help to contribute to heat control. In moist nests, microbial activity helps to control the temperature.

Figure 60. Ant nest under ***Dicranum scoparium***. Photo courtesy of Serhat Ursavas.

Figure 61. Ant nest under ***Dicranum scoparium*** showing closer view of the ants. Photo courtesy of Serhat Ursavas.

Longino (2005) examined nesting behavior of two species of the neotropical ***Stenamma*** (**Formicidae**; Figure 62). By comparing ants on soil banks, he found that they are absent from new (unvegetated) banks. They are very abundant on the banks at the intermediate stage that has only a sparse covering of small bryophytes. But when the mosses become abundant, the abundance of ants decreases greatly.

Ants use bryophytes to varying degrees to construct nests (Figure 63-Figure 65). Some nest under them (Figure 66). Some incorporate small bits of bryophytes in nest construction. And some use bryophytes almost exclusively. General collecting by Longino and Nadkarni (1990) in Monteverde and other highland sites in Costa Rica has revealed that ***Stenamma*** (Figure 62) makes nests under moss mats in the forest understory.

Figure 62. ***Stenamma brevicorne***, a species that lives under mosses, litter and similar protected sites, in this case carrying a grub. Photo by Galpert, through Creative Commons.

Figure 63. These ants have included ***Brachythecium*** (Figure 64) and ***Hypnum*** (Figure 65), among other things, in their nest. Photo by Janice Glime.

Figure 64. ***Brachythecium*** sp., a genus incorporated into ant nests. Photo by Janice Glime.

Figure 65. ***Hypnum imponens*** and ***H. jutlandicum***, mosses than can be incorporated into ant nests. Photo by Michael Lüth, with permission.

Figure 66. ***Polydesmus angustus*** nest under moss, Crowle Moors, UK. Photo by Brian Eversham, with permission.

The Neotropical frog ***Agalychnis saltator*** (**Hylidae**) makes nests and lays its eggs among mosses on lianas (vines) (Roberts 1994). Among the dangers to these eggs are cohabiting ants. As adults these frogs are able to escape quickly by parachuting.

My own experience is watching ants repair an ant nest mound made of ***Sphagnum*** during heavy winds (Figure 67-Figure 68). Bits were flying off the mound as fast as the ants could repair it. Ants are fairly common in bogs, and grabbing a handful of ***Sphagnum*** can result in an arm full of ants.

Figure 67. ***Formica*** on ***Sphagnum*** nest that makes this hummock in Michigan, USA. Photo by Janice Glime.

Figure 68. ***Formica*** on ***Sphagnum*** nest in Michigan, USA. These ants are busy repairing the nest as it is being blown apart by wind. Photo by Janice Glime.

Abandoned nests can become the site of moss invasions, as seen in Figure 69.

Figure 69. Ant hill with moss. Photo by Annette Schimming, with permission.

If you have ever trudged through a peatland with hummocks and hollows, you know how difficult walking can be. It is easy to twist your ankle on the uneven substrate. What you may not know is that ants can be

responsible for some of that rough terrain. They are clever engineers and in the peatlands they build elaborate nests, as you have just seen. But in natural hummocks formed by ***Sphagnum*** growth, ants can play a role in the changes in microtopography (Luken & Billings 1986). Due to their tunneling behavior, it appears that when the mosses die, hummock retrogression is accelerated by the tunnelling of the ants. In fact, some of these collapsed hummocks can eventually form hollows.

Ants, *Sphagnum* Collars, and Aphids

Robin Stevenson (Bryonet 17 June 2015) reported moss collars around the bases of pine (Figure 70-Figure 73) and birch (Figure 74) trees. "The lower part of the 'trunk' was covered in little bits of dried ***Sphagnum*** (Figure 78), and the whole plant was swarming with lots of ants. We didn't see the ants actually moving any of the ***Sphagnum***, but they did look as if they were coming up from *underneath* it. We got the impression that it was the ants who were responsible."

Figure 70. Ants, aphids, and ***Sphagnum*** sleeves on sapling in bog. Photo courtesy of Robin Stevenson.

Figure 71. Ants and basal sleeve of ***Lasius platythorax*** in bog. Photo courtesy of Robin Stevenson.

Figure 72. Ant (***Lasius platythorax***) ***Sphagnum*** sleeves on pine. Photo courtesy of Robin Stevenson.

Figure 73. Partial sleeve made by ***Lasius platythorax*** around branching point in Durham Bog. Photo courtesy of Robin Stevenson.

Figure 74. Birch sleeve of ***Sphagnum*** built by ***Lasius platythorax***. Photo courtesy of Robin Stevenson.

I have several hypotheses for the ***Sphagnum*** ant nests:

1. The ants are just beginning a nest and the pine serves as a central support column.
2. The nest has been mostly destroyed and the ants are repairing it.
3. The ***Sphagnum*** is tucked into the pine to maintain higher moisture for laying eggs. (I doubt that is the case.).
4. There is some commensal/symbiotic relationship going on, probably aphids, and the ants are improving conditions for aphids or other insects that will serve as food.

Stevenson returned to the site and found three more of these constructions (pers. comm. 22 June 2015). Not all were at the bases, but rather formed collars farther up the sampling trunk (Figure 75). The ants were scurrying about, on, and through, the moss collars (Figure 76). These collars were made of a variety of the materials available (Figure 77), but mostly of ***Sphagnum fallax*** (Figure 78) and ***Aulacomnium palustre*** (Figure 79-Figure 80), but also included leaves of ***Polytrichum commune*** (Figure 81), *Erica tetralix*, and *Calluna vulgaris*. Much of the composition was ***A. palustre*** tomentum (Figure 80). ***Sphagnum*** was tucked in among the leaves of the pine, well above the substrate (Figure 75).

Figure 75. Partial sleeve by ***Lasius platythorax*** at branching point on pine. This nest is at some distance from the tree base. Photo courtesy of Robin Stevenson.

Figure 76. ***Lasius platythorax*** in nest where they are running about. Photo courtesy of Robin Stevenson.

Figure 77. Sleeve material of ***Lasius platythorax*** collars that house aphids. Photo courtesy of Robin Stevenson.

Figure 78. ***Sphagnum fallax***, a moss used by ants to make collars housing aphids on saplings of pines and birches. Photo by Michael Lüth, with permission.

Figure 79. ***Aulacomnium palustre***, a common moss in ant-made moss collars in UK bogs. Photo courtesy of Robin Stevenson.

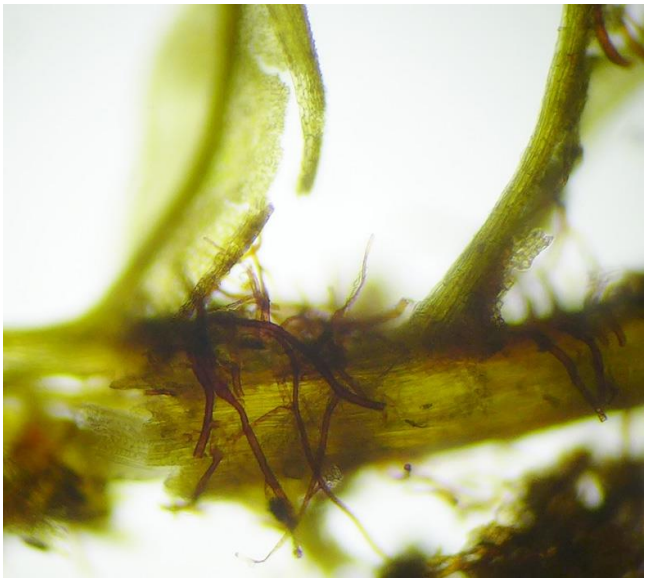

Figure 80. ***Aulacomnium palustre*** showing tomentum from ant nest at Durham Bog. Photo courtesy of Robin Stevenson.

Figure 81. ***Polytrichum commune*** fragments from nest of ***Lasius platythorax***. Photo courtesy of Robin Stevenson.

So let's return to the moss collars to shed more light on these hypotheses. On another return visit, Stevenson had a "good look to see what the ants were up to: lots of scurrying about, and a few interactions with aphids – of which there didn't seem to be too many. However... when I broke a bit of sleeve off, there were a lot of aphids all huddled together underneath. So, it looks as if the ants are herding them under the cover of the sleeve – or might they shelter there of their own volition? Herding sounds more likely – but how does that work? I'd have thought that pine bark was a bit tough, even for an aphid's mouth parts, and they would have been better off up among the leaves?"

The ants were ultimately identified as ***Lasius platythorax*** (Figure 82-Figure 83) (Wells 2015). The aphids provide **honeydew** (Figure 84-Figure 85) for the ants, and the ants, in turn, police the stems with the nests (Figure 83, Figure 86), warding off a number of kinds of predators. Interestingly, the aphids are species-specific. That is, the birch aphids are ***Symydobius oblongus***, whereas those on the pine are ***Cinara pini*** (Figure 84-Figure 86).

Figure 82. ***Lasius platythorax***, an ant that makes moss sleeves around saplings in bogs to cultivate aphids. Photo by April Nobile, through Creative Commons.

Figure 83. Ants (***Lasius platythorax***) and free aphids (***Cinara pini***) on pine stem at Durham Bog, UK. Photo courtesy of Robin Stevenson.

Figure 84. ***Cinara pini*** with honeydew drop at anus. This one is on ***Pinus sylvestris***. Photo from <Influentialpoints.com>, through Creative Commons.

Figure 85. Ant feeding on aphid honeydew. Photo by Jmalik, through Wikipedia Commons.

Bauer-Dubau (2000) found that ***Cinara pini*** (Figure 84-Figure 86) produces more offspring when attended by ants. In Germany, the aphids on several pine species are heavily attended by the ant ***Lasius fuliginosus*** (Figure 87). The density of ants increased from 10-20 to 26-48 ants per colony in one generation. Without the ants, the aphid anus becomes covered with honeydew and the colony disperses.

Beattie (1985) reviewed ant service to aphids. That review demonstrated that the ants provide not only protection, but also sanitation and transportation, decrease their development time, and increase the colony growth rate, survivorship, and fecundity (Kennedy & Stroyan 1959; El-Ziady 1960; Banks 1962; Way 1963; Banks & Macauley 1967; Bristow 1982). Furthermore, the ants reduce parasitism by wasps (27.4-98.4% reduction) by preventing the egg-bearing female parasites from landing on the aphids and ovipositing there (Bartlett 1961). Disturbance by ants resulted in 27.4% to 98.4% reduction in parasitism, depending on the parasite species. Ants even place aphids in areas that give them better access to the phloem that provides their food source (Banks 1962; Way 1963). The ants build shelters that protect them from rain and enemies, using soil, vegetation, and other materials (Andrews 1929; Levieux 1967; Duviard 1969; Duviard & Segeren 1974.

Figure 86. The aphid ***Cinara pini*** being attended by the wood ant ***Formica rufa*** on ***Pinus sylvestris*** at Flatropers Wood. Photo from <influentialpoints.com>, through Creative Commons.

Figure 87. ***Lasius fuliginosus***, a species that attends the aphid ***Cinara pini*** on pines in Germany. Photo by Ab H Baas, with permission for non-commercial use.

Ants are known for feats of strength and strong societal behavior. In one recent study in Israel, Gelblum *et al*. (2015) describe their seemingly undirected behavior while carrying a Cheerio. The ants doing the carrying can't see what is ahead and often get off course. But navigator ants (scouts) occasionally enter the scene and direct the Cheerio carriers back on course. The communication between the scout and the carrier ants seems to be through the changed direction felt through the Cheerio. It would be interesting to observe whether similar carriers and scout leaders exist in the movements of mosses to make the mounds observed in bogs and fens or the collars around birch trees.

Bogs and Fens

One must be careful when reaching deep into a moss hummock to collect the moss because a swarm of ants may soon be on its way up one's arm! I have experienced this in several locations in North America. Rosengren (1969) and Collingwood (1979) relate the commonness of ants among ***Sphagnum*** turfs in Central Europe, where such ants as ***Formica uralensis*** (Figure 88) likewise carve nests (Figure 89) out of the peat (Stankiewicz *et al*. 2005) and hibernate under mosses in winter (Collingwood 1979) . This species is restricted mostly to ***Sphagnum*** habitats. Matthey (1971) reported that both ***Myrmica ruginodis*** (Figure 39) and ***Formica picea*** (Figure 5) make nests in ***Sphagnum***. As mentioned above, I have observed nests made of ***Sphagnum*** (Figure 90), but I was unable to identify the species. Blank Shaw found a similar nest in Maine (Figure 91).

Figure 88. ***Formica uralensis***, an ant that nests in ***Sphagnum*** in Europe. Photo by Ruth Ahlburg, with permission.

Figure 89. Nest of ***Formica uralensis***, made of ***Sphagnum***. Photo by Ruth Ahlburg, with permission.

Figure 90. These ants are busy repairing their nest in this ***Sphagnum*** hummock on a windy day in Michigan's Upper Peninsula. Photo by Janice Glime.

Figure 91. Ant nest made of ***Sphagnum rubellum*** in Maine. Photo by Blanka Shaw, with permission.

Šteffek and Wiezik (2008) reported 11 species of ants in a peat bog at Hrabušice, N Slovakia. ***Myrmica scabrinodis*** (Figure 92) is dominant there in patches with the highest humidity. They build their colonies among the thick mosses. In Switzerland, the inhabiting ***Myrmica ruginodis*** (Figure 39) and ***Formica picea*** (Figure 5) form nests among the ***Sphagnum*** (Matthey 1971).

Figure 92. ***Myrmica scabrinodis***, a dominant ant in peat bogs of northern Slovakia. Photo by Tim Faasen, with permission.

Certainly many insects are housed in mosses, but one of the most distinctive nests is the smooth dome built by ants in a fen. I watched these industrious creatures groom

their mound of ***Sphagnum*** continuously on a windy day, weaving each loose fragment of moss back into the construction (Glime, personal observation). They could barely move against the wind and often were moved backward by its force.

Lesica and Kannowski (1998) reported that the ants ***Formica podzolica*** (Figure 93), ***Myrmica fracticornis*** (Figure 94), and ***M. incompleta*** (Figure 95) are common in large rich fen complexes of Montana, USA. All three of these species build nests there. ***Formica podzolica*** nests are much larger than nests of the two species of ***Myrmica*** and occur in the hummock-hollow complex. The nests are about the size of a hummock, and likewise have elevated levels of K, PO_4^-, Mg, and Na similar to those of hummocks. Lesica and Kannowski (1998) suggested that the hummocks were actually abandoned ant mounds. Even here, the ***Formica podzolica*** gains most of its nutrition by tending the aphids that feed on the shrubs. And the shrubs are provided a rich habitat for establishment when they germinate in the mounds. Because of this germination relationship, the ants become ecosystem engineers that permanently change the structure and composition of the rich fen vegetation. But there is a feedback mechanism in which the ants benefit from the increase in host plants for the aphids.

Figure 93. ***Formica podzolica*** adult, a species that nests in large, rich fen complexes in Montana, USA. Photo by Tracy Barbaro, through Creative Commons.

Figure 94. ***Myrmica fracticornis*** adult, a species that nests in large, rich fen complexes in Montana, USA. Photo by Dan Kjar <www.discoverlife.org>, through Creative Commons.

Figure 95. ***Myrmica incompleta*** adult, a species that nests in large, rich fen complexes in Montana, USA. Photo by Tom Murray, through Creative Commons.

In a Norway mire, Collingwood (1976) found even greater diversity. Using pit-fall traps, Collingwood recorded 18 species in 13 mires habitats at Eidskog. Among these, ***Formica forsslundi*** and ***F. transkaucasica*** are ture mire species. Among the most abundant species were ***Myrmica scabrinodis***, ***M. ruginodis***, ***F. transkaucasica***, and ***Leptothorax acervorum***.

Ants can influence the distribution of other invertebrates in peatlands. Antonovic *et al.* (2012) suggested that the higher diversity of terrestrial isopods could in part be the result of predator pressure by ***Myrmica*** ants (and lycosid spiders).

Bees

Bees are disappearing in alarming numbers, so anything new we can learn about them may be important in saving them. It may surprise you to learn that a number of bees use mosses for various purposes.

Guy Brassard (Bryonet 31 March 2016) reported that bees on Ellesmere Island in the Canadian High Arctic use bryophytes in their nests! He identified more than 50 species of mosses and about 8 species of liverworts among the 47 nests, with an average of 6-7 species per nest. Some of the moss species were present in more than 25 nests and some in very few nests, suggesting that the bees are selective about the bryophytes chosen.

Annie Martin (Bryonet 31 March 2016) reported observations of honey bees, wasps, and butterflies gathering on mosses at her Mossery. They would sit for up to half an hour instead of just a quick stop. A beekeeper explained that worker bees gather water and take it back to the hive or nest. Given the choice between a puddle or larger water body compared to moss colonies, the bees seem to prefer the moss option! There didn't seem to be any species preference.

And if you are a moss gardener, beware. Martin also has found yellow jackets, carpenter bees, wasps, ants, and termites making their homes in giant ***Polytrichum commune*** (Figure 81) colonies.

Apidae – Honey Bees, Bumblebees, Carder Bees, *etc.*

Honey Bee

The small red dwarf honey bee, ***Apis*** (***Micrapis***) ***florea*** (**Apidae**; Figure 96-Figure 98) has a mysterious habit of collecting "something" from mosses. Sunil Chaturvedi observed this species probing the pots with mosses, whereas they were not doing this in nearby pots of similar moisture but no mosses (Bryonet 26 February 2011). Daniel McConnell, a US Forest Service botanist, reported seeing this behavior for many years (probably with a different honey bee species), and observed that it seemed to be much more common on calcareous mosses (Bryonet 27 February 2011). Wolfgang Hofbauer (Bryonet 28 February 2011) stated that "bees love to take in water at open moist places. For this purpose moss cushions seem to be very suitable. In spring beekeepers even offer them moistened moss cushions near their beehives."

Figure 96. ***Apis florea*** adult, a species that collects something, probably water, from bryophytes. Photo by John Ascher <www.discoverlife.org>, through Creative Commons.

Figure 97. ***Apis*** (***Micrapis***) ***florea*** on moss, apparently getting water, but perhaps not. Photo by Sunil Chaturvedi, with permission.

In their blogspot, the Hive Honey Shop recommends providing bees with water in summer (Beekeeping 2013). They warn not to use fresh water because the bees will not touch it. Rather, they prefer mature mineral-rich water. Provide them with a number of places where they can land to get water without drowning. They suggest putting moss around the edges or in the water dish not only for safe footing, but also to filter the water and prepare it for drinking (Figure 98).

Figure 98. Close-up of ***Apis*** (***Micrapis***) ***florea*** on ***Pohlia***, apparently getting water, or is it simply attracted by UV reflectance by the bulbils of the ***Pohlia***? Photo by Sunil Chaturvedi, with permission.

But what draws the bees to the mosses? Sunil Chaturvedi suggested that the mosses may bring more bees to the area because of UV reflectance, hence increasing pollination of crop plants. These observations recalled to my mind the interesting observations of Gisela Nordhorn-Richter that demonstrated UV reflectance of ***Pohlia*** **bulbils** (Figure 99). Could it be that the bees are attracted to some bryophytes by UV waves, seen by bees but not by humans? Jon Shaw (pers. comm.) noted that the mosses observed by Sunil Chaturvedi appeared to be ***Pohlia*** with abundant **bulbils** (Figure 99). In any case, the mosses seem to be important sources of seasoned water for the bees.

Figure 99. ***Pohlia bulbifera*** bulbils. These fluoresce under ultraviolet light and could possibly attract bees. Photo by Des Callaghan, with permission.

Annie Martin (2015) reports that honey bees rest on the mosses in her moss garden, simply sitting quietly for a period of time. These bees drink the water on the leaves of the mosses. Beekeepers have suggested that the bees prefer moss water, possibly because of antibiotics in the water (Adventures in Natural Beekeeping 2017). This needs to be verified.

Grdović and Sabovljević (2008) also observed bees visiting bryophytes in beehive yards. They suggested that the bryophytes influence the humidity, maintaining a milder microclimate for the flowering plants and enabling those plants to remain moist longer and grow better. The same moisture provides a water source for the bees.

Figure 100. Honey bee (***Apis*** so.) on ***Sphagnum*** cf. ***palustre***, where it is able to get a drink of water and rehydrate. Photo courtesy of J. Paul Moore.

One could pose several hypotheses for this bee activity on mosses. Tom Thekathyil stated that bees and wasps often "imbibe water" from the surfaces of mosses and suggested that the mosses may have tiny pools of free water that are not available on the bare soil. This is a reasonable hypothesis, given the tiny capillary spaces on mosses that typically hold water longer than the soil surface. The straw-like mouth parts (Figure 101) of the honey bees would permit them to extract water from these tiny droplets.

Figure 101. Honey bee proboscis. Photo from <www.MzePhotos.com>, through Creative Commons.

Another hypothesis is that the water quality might be different on the mosses. On calcareous soil, high concentrations of carbonates might deter the bees, whereas the capillary water of the mosses could be altered by the cation exchange on the moss surface, or by the addition of oxygen from photosynthesis. This suggestion is supported by the observations at the Hive Honey Shop (Beekeeping 2013).

Water certainly seems to be a likely motivator. Bashir Yusuf Abubakar, Bryonet 28 February 2011, pointed out that water is a prime requirement of bees in culture such that they are always available in moistened areas. One can even find them surrounding a dripping tap. The water retention capacity of mosses varies between mosses and could account for differences in visitation frequencies.

The bee mouthparts facilitate the use of tiny drops of water such as those on bryophytes. The proboscis (Figure 101) uses capillary action and suction to draw a fine stream of liquid to the mouth (Krenn *et al*. 2005).

Bumblebees

Guy Brassard (Bryonet 1 June 2010) identified bryophytes from 47 bumblebee nests, primarily ***Bombus polaris*** (Figure 102) and ***Bombus hyperboreus*** (Figure 103) on northern Ellesmere Island, in the Canadian High Arctic (Richards 1973). The use of mosses helps to insulate the nests, permitting these two bees to survive farther north than other bumble bees (Heinrich 2004). But then, ***B. hyperboreus*** is a parasite on ***B. polaris***. Hence, the behavior of ***B. polaris*** determines the temperature control for both species.

Bombus polaris sometimes takes advantage of the activities of rodents, building their own nests in lemming and other burrows, but these locations are too cold. Instead, most build their nests in meadows and marginal pools on flat areas, in depressions, and beside small hummocks of mosses or other vegetation. Entrances typically faced the sun during the daily temperature peak. and rearranging the mosses to suit their needs (Richards 1973). The female pulls the moss with her mandibles and forelegs, pushing it under her body with her mid- and hind legs to the desired position. The queens and assisting workers continue to rearrange the bryophytes as the colony expands. Guy Brassard (pers comm. 1 April 2016) reported to me that an individual nest typically had 2-14 species of bryophytes and an average of about 6 or 7 species per nest. These comprised at least 56 species of mosses and 6 species of liverworts overall (see Richards 1970). Only one of the nests lacked any bryophytes. Bryophytes were typically intermixed with dried sedge leaves to cover the nest and create a thick, tight surface of insulation. The most frequent bryophyte species were all common in the region. The following were the most often found (with total number of nests out of 47): ***Campylium arcticum*** (33) (Figure 107); ***Orthothecium chryseum*** (29) (Figure 109); ***Drepanocladus revolvens*** (28) (Figure 108); ***Distichium capillaceum*** (21) (Figure 105); ***Ditrichum flexicaule*** (19) (Figure 106); also *Bryum* sp. (38 – tiny unidentifiable scraps) (Figure 10). The three pleurocarpous species were usually dominant or abundant; the others were often very minor components.

Figure 102. ***Bombus polaris***, a species that uses mosses in its nest. Photo by J. C. Schou, with permission.

Figure 103. ***Bombus hyperboreus*** adult, a species that uses mosses in its nest. Photo by Marko Mutanen, through Creative Commons.

Figure 104. **Apoidea** nest uncovered from mosses, showing bees in the nest. Photo by Panoramedia, through Creative Commons.

Figure 105. ***Distichium capillaceum***, one of the species used in bee nests. Photo by Michael Lüth, with permission.

Figure 106. ***Ditrichum flexicaule***, one of the species used in bee nests. Photo by Michael Lüth, with permission.

Figure 107. ***Campylium arcticum***, one of the species used in bee nests. Photo by Michael Lüth, with permission.

Figure 108. ***Drepanocladus revolvens***, one of the species used in bee nests. Photo by Kristian Peters, with permission.

Figure 109. ***Orthothecium chryseum***, nesting material for bees. Photo by Michael Lüth, with perission.

Bumblebees (***Bombus***; Figure 110) can use abandoned mouse nests in areas with tussock grass or moss (Saunders 2015). Goulson (2010) found that suitable sites for nesting provided insulating materials for the nest. Such materials include mosses, feathers, hair, and grass. Harvey (2015) echoed this advice for rearing bees, including the need for attracting mice and voles to create nesting sites. In fact, Sladen (2014) reported that a carder bee may build its own nest when moss is abundant instead of occupying abandoned nests of small animals.

Figure 110. ***Bombus*** sp. adult, a genus that uses abandoned mouse nests that often contain mosses. Photo by Yann, through Creative Commons.

Fussell and Corbet (1992) found that nesting sites differed significantly among color groups of British bumblebees. These involved position of the nest relative to ground level, time of day at which direct sunlight reached the nest, and nature of the immediate environment of the nest.

Bumblebee visits to bryophytes may be facultative (Grdović & Sabovljević 2008). These researchers did find that a relationship of the bees with the bryophytes was supported statistically, suggesting that humidity and a milder microclimate supported the relationship.

Even bumblebees that do not build nests of mosses may find them useful for overwintering. ***Bombus lucorum*** (white-tailed bumblebee; Figure 111), ***B. lapidarius*** (Figure 112), and ***B. hortorum*** (garden bumblebee; Figure 113) spend their winter in mosses (Alford 1969). ***Bombus pratorum*** (early bumblebee; Figure 114) uses mosses facultatively – overwintering sometimes in moss, sometimes underground.

Figure 111. ***Bombus lucorum*** adult, a bee that overwinters among mosses. Photo by James K. Lindsey, with permission.

Figure 112. ***Bombus lapidarius*** adult, a bee that overwinters among mosses. Photo by Beate & Heinz Beyerlein, through Creative Commons.

Figure 113. ***Bombus hortorum*** adult on protonemata on soil. Photo by Trevor & Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 114. ***Bombus pratorum*** adult sometimes overwinters in mosses and sometime underground. Photo by Aiwok, through Creative Commons.

Carder Bees

Carder bees include the moss carder bee, ***Bombus muscorum*** (Figure 115). These bees are so-named because they cleanse/comb the mosses before inserting them into the nest construction (Smith 1876). They typically build the nest entirely of moss, working it with their feet into a compact mass that resists the weather (Cuthbert 1895). If mosses are abundant, the nest may be made entirely of mosses, but if mosses are scarce, they may build nests with no mosses. The nest is comprised of a series of cells connected by coarse brown wax (Cuthbert 1895).

Figure 115. ***Bombus muscorum*** adult, a species that uses mosses to build its nest. Photo by J. C. Schou <www.biopix.com>, through Creative Commons.

Rennie (1857) describes the nest-building of ***Bombus muscorum*** (Figure 115) as a series of backward pushes. The bees establish a line of up to 6 bees to transport the moss from the source to the nest. The last bee in the file grabs some moss with her mandibles, disentangling it and carding it with her forelegs into a small bundle. She pushes this bundle under her body to the next bee, who passes it to the next with the same under body move, and so forth.

The nest has a long, arched passageway that is formed by a variety of mosses, wide enough to permit free passage for the bees (Smith 1876). The final nest has a dome of 10-15 cm above the ground (Rennie 1857). Wax from the bees forms the ceiling, repelling rain and preventing high winds from carrying away the nest. During the day, the top of the dome may be opened more than 2.5 cm, apparently to ventilate the nest. It is not used for entry, and it is closed again at night. Instead, there is an entrance passage at the bottom of the nest that is about 30 cm long and 1.2 cm wide. The larvae spin cells. When the grubs are ready to emerge, it is the older bees that chew off the cover to free them. One of these spheres may house 3-30 eggs. Rennie found that the adults were of a color similar to the moss they used.

Bombus muscorum (Figure 115) carders collect mosses and dry grass, constructing the nests on or just under the ground (Wikipedia 2015a). The mosses and grass are used to cover the nest. Once the nest is completed, the bee aggressively protects it, attacking intruders by biting and stinging them simultaneously.

The carder bees differ from other members of ***Bombus*** that nest underground (Carvell 2002). The partially above ground nesting by carder bees seems to necessitate the grass-moss habitat to maintain warmth. Nevertheless, there is a negative relationship between number of carder bees and depth of moss. On the other hand, Jukes (2008) reported that ***Bombus muscorum*** (Figure 115) in Sussex made its nest in deep moss in exposed places.

Iles (2010) listed the carder bees ***Bombus humilis*** (Figure 116), ***B. sylvarum*** (Figure 117), and ***B. muscorum*** (Figure 115) as species that require tall grassland with "plenty of leaf litter or moss" to use as nesting material. ***Bombus pascuorum*** (Figure 118) appears to be more flexible, as indicated by its many habitats. Similarly, ***Bombus ruderarius*** (Figure 119) builds its nest at the surface or just below, using grass and mosses, and likewise often utilizing an abandoned mouse or vole nest (Benton 2008).

Figure 116. ***Bombus humilis*** adult, a species that uses mosses to build its nest. Photo by Tim Faasen, with permission.

Figure 117. ***Bombus sylvarum*** adult, a species that uses mosses to build its nest. Photo by James K. Lindsey, with permission.

Figure 118. ***Bombus pascuorum*** adult, a species that uses mosses in its nests, but that occupies a variety of habitats. Photo through Creative Commons.

Figure 119. ***Bombus ruderarius*** adult, a species that nests under mosses and grasses. Photo by James K. Lindsey, with permission.

The common carder bee, ***Bombus pascuorum*** (Figure 118), is widespread in Europe, living in meadows, waste ground, ditches, embankments, roads, gardens, parks, and forests (Wikipedia 2015b). Like the moss carder bee ***B. muscorum***, this species also collects mosses and grasses, constructing a small, hollow sphere. Walls of this sphere are bonded with wax and sealed off. Inside they form a large bowl (5 mm diameter) of brown wax filled with pollen. They deposit 5-15 eggs, then close the cell. They fill a second chamber (20 mm high) with nectar to provide a food reserve for days when weather is not suitable for foraging. Larvae hatch in 3-5 days, then spend only a week to mature as they feed on the food reserves.

Braconidae – Parasitic Wasps

In New Zealand, a new genus, ***Shireplitis***, was described as mostly in moss, litter, or tussock grasslands (Fernández-Triana *et al*. 2013). ***Parolitis wesmaeli***, also **Braconidae**, from Europe, is a parasitic wasp that uses larvae of ***Scoparia basistrigalis*** (**Pyralidae**) and ***Bryotropha umbrosella*** (**Gelechiidae**) (both **Lepidoptera**) as hosts. Larvae of both of these hosts feed from their silken tube or tent, grazing on mosses and grasses. Four of the ***Shireplitis*** species (*e.g.* Figure 120) were themselves collected from mosses and may likewise live on moss-eating **Lepidoptera**. Fernández-Triana *et al*. considered the robust body and legs with shortened antennae of these **Braconidae** to be adaptive for moving among "litter" while searching for hosts. See Chapter 12-14 for further discussion of the Lepidoptera hosts.

Figure 120. ***Shireplitis bilboi*** adult, an inhabitant of ***Sphagnum*** and grasses. Photo through Creative Commons.

Cynipidae and Mimicry

Some members of the **Cynipidae** take advantage of mosses in a different way. ***Diplolepis rosae*** (Figure 121) causes a gall formation that resembles a moss to house its eggs and larvae (Callan 1940).

Figure 121. ***Diplolepis rosae*** gall, a mimic of real mosses. Photo by Björn Appel, through Creative Commons.

Diprionidae – Conifer Sawflies

Jarmo Holopainen (pers. comm. 16 September 2011) found that in experiments pupae of pine sawflies (***Neodiprion sertifer*** – **Diprionidae**; Figure 122-Figure 125) had a higher emergence rate when kept in ***Sphagnum*** peat. He suggested that the antibiotic properties of peat helped to increase wasp survivorship.

Figure 122. ***Neodiprion sertifer*** female and male adults, a species that has a higher emergence rate when kept among ***Sphagnum***. Photo by Jarmo Holopainen, with permission.

Figure 123. ***Neodiprion sertifer*** larva and eggs, a species that survives better when cultured in ***Sphagnum***. Photo by Jarmo Holopainen, with permission.

Figure 124. ***Neodiprion sertifer*** larvae, a species that survives better when cultured in ***Sphagnum***. Photo by Jarmo Holopainen, with permission.

Ichneumonidae

Among the **Ichneumonidae**, twelve genera are able to overwinter as adults (Duffield & Nordin 1970). These take advantage of the insulating properties of logs, rocks, and mosses to endure the extreme conditions of winter. Those that overwinter accumulate glycerol and sorbitol when subjected to cold temperatures of winter. Dana <Abundantnature.com> tells of lifting a clump of moss from a rock and discovering not one, but two, species of ***Ichneumon*** hibernating there as adults (Figure 126-Figure 128).

Figure 125. ***Neodiprion sertifer*** pupa, a species that has higher emergence rates when cultured in ***Sphagnum***. Photo by Jarmo Holopainen, with permission.

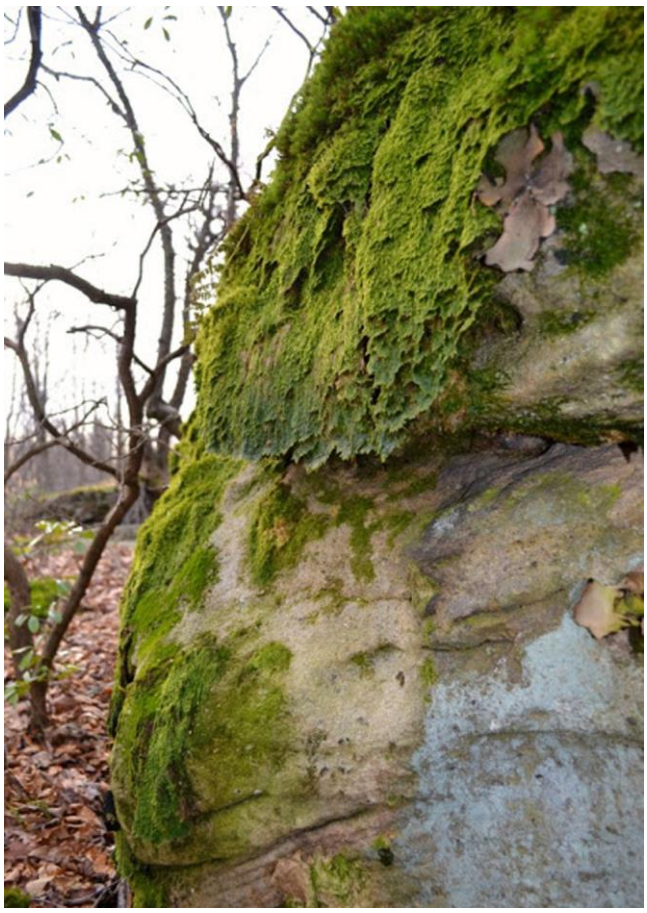

Figure 126. Habitat of ***Ichneumon*** *cf* ***mendax*** hibernating adults. Photo by Dana <Abundantnature.com>, with permission.

Figure 127. ***Ichneumon*** *cf* ***mendax*** and a second species, hibernating adults under mosses. Photo by Dana <Abundantnature.com>, with permission.

Figure 128. ***Ichneumon*** *cf* ***mendax*** hibernating adult that has been disturbed. Photo by Dana <Abundantnature.com>, with permission.

Lungu-Constantineanu and Constantineau (2014) found the importance of mosses as hibernation sites for at least 10 species of **Ichneumonidae** in the Bârnova Forest Massif, Romania. They found six types of hibernation sites, two of which required mosses. Ten of these sites were between the cracks of bark covered by moss. Others were in dense carpets of mosses on stones. They found that pollution reduced the moss cover, resulting in the disappearance of large ichneumonid clumps with dozens of hibernating individuals. Instead, the hibernating ichneumonids were mostly isolated individuals. The mosses that contributed to the large number of habitats for ichneumonid hibernation between cracks of bark of old but living trees were ***Anomodon attenuatus*** (Figure 130-Figure 131), ***A. viticulosus*** (Figure 132-Figure 133), ***Brachythecium salebrosum*** (Figure 134), ***Hypnum cupressiforme*** (Figure 44), ***Platygyrium repens*** (Figure 135), and ***Porella platyphylla*** (Figure 136). These ichneumonids under mosses in the cracks in tree bark were ***Apaeleticus mesostictus***, ***Deloglyptus pictus***, ***Diadromus troglodites*** (Figure 137), ***Herpestomus brunnicornis*** (Figure 138), ***Heterischnus truncator***, (Figure 139), ***Ichneumon balteatus*** (Figure 140), ***Ichneumon simulans*** (Figure 141), ***Rhadinodonta flaviger*** (Figure 142), and ***Tycherus cephalotes*** (=***Phaeogenes cephalotes***). Only one species of ichneumonid (***Cinxaelotus erythrogaster***) hibernated on the rocks, where ***Mnium stellare*** (Figure 143) covered them.

Figure 129. ***Ichneumon stramentor*** adult on moss, a species that hibernates as an adult under mosses. Photo by Ladislav Tábi, with permission.

Figure 130. ***Anomodon attenuatus*** on tree base, covering cracks in the bark where ichneumonid adults overwinter. Photo by Bob Klips, with permission.

Figure 131. ***Anomodon attenuatus***, a moss that provides insulation for ichneumonids overwintering in cracks and under bark. Photo by Michael Lüth, with permission.

Figure 132. ***Anomodon viticulosus*** covering cracks in bark where ichneumonids overwinter. Photo by Michael Lüth, with permission.

Figure 133. ***Anomodon viticulosus***, overwintering home for adult ichneumonids in cracks in bark. Photo by Michael Lüth, with permission.

Figure 134. ***Brachythecium salebrosum*** covering broken bark where ichneumonids overwinter. Photo by Michael Lüth, with permission.

Figure 135. ***Platygyrium repens*** on bark, covering cracks where ichneumonid adults overwinter. Photo by Dick Haaksma, with permission.

Figure 136. ***Porella platyphylla*** on bark, overwintering home for adult ichneumonids in cracks in bark. Photo by Michael Lüth, with permission.

Figure 137. ***Diadromus troglodytes*** adult, a species that hibernates in cracks in bark under mosses. Photo by James K. Lindsey, with permission.

Figure 138. ***Herpestomus brunnicornis*** adult, a species that hibernates in cracks in bark under mosses. Photo by Marko Mutanen, through Creative Commons.

Figure 139. ***Heterischnus truncator*** adult, a species that lives in cracks in tree bark under mosses. Photo by Jonas Lutz, through Creative Commons.

Figure 140. ***Ichneumon balteatus*** adult, a species that hibernates in cracks in bark under mosses. Photo by Stefan Schmidt, through Creative Commons.

Figure 141. ***Ichneumon simulans*** adult, a species that hibernates under mosses in cracks in bark. Photo by James K. Lindsey, with permission.

Figure 142. ***Rhadinodonta flaviger*** adult, a species that hibernates in cracks in bark under mosses. Photo by Stefan Schmidt, through Creative Commons.

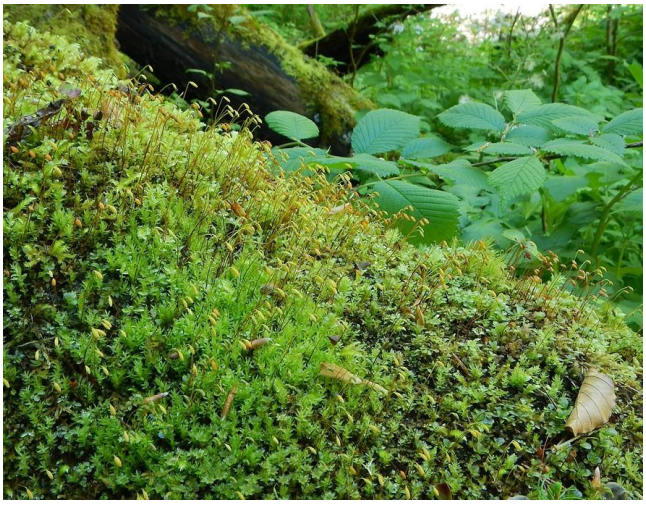

Figure 143. ***Mnium stellare*** on rock outcrop, providing an overwintering habitat for ***Cinxaelotus erythrogaster***. Photo by Michael Lüth, with permission.

But overwintering is not the only use they make of mosses. Sarah Lloyd caught one in the act of ovipositing among mosses (Figure 144).

Figure 144. Ichneumonid wasp ovipositing on moss. Photo courtesy of Sarah Lloyd.

Pompilidae

Bees and wasps do not seem to be usual active inhabitants of bryophytes, but the rare spider wasp, ***Anoplius caviventris*** (**Pompilidae**; Figure 145) in Sweden lives in a ***Sphagnum*** habitat (Berglind 1993). In Sweden, this species was found in 1991 and 1993 in a reed swamp (*Phragmites communis*) where it was living on mosses, primarily ***Sphagnum*** in three different mires.

Figure 145. ***Anoplius caviventris*** adult, a ***Sphagnum*** dweller in Sweden. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Scelionidae

It appears that among the **Hymenoptera**, the ants are the only ones with well-developed relationships in peatlands. However, Austin (1988) did find a new genus of wasps in the **Scelionidae** to be associated with mosses in New Zealand. Austin (1988) described this new genus, based on ***Neobaeus novazealandensis***. Austin found that collection data indicate this species lives on moss-covered ground, with 80% of the specimens collected by putting mosses in Berlese funnels. This species differs from ***Baeus*** in having a micropterous (short-winged) male. Austin suggested that wings would hinder movement in this mossy habitat.

Sphecidae

O'Brien (1987) observed ***Tachysphex aethiops*** (**Sphecidae**; Figure 146) digging at the bases of clumps of moss on sand. They inspected the burrow entrances throughout the day at various times. Females of this species typically nest in mossy sand slopes where they use pre-existing burrows made by other kinds of insects. One female intermittently removed sand from a burrow, raking the sand onto the nest mound after carrying several loads out of the nest.

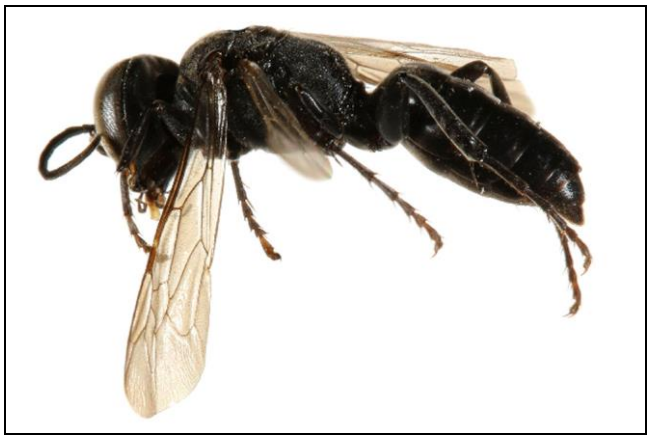

Figure 146. ***Tachysphex aethiops*** adult, a species that nests in mossy sand slopes. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Vespidae – Wasps

The yellow jackets [***Vespula*** (Figure 147) and ***Dolichovespula*** (Figure 148); **Vespidae**] are best known for their papery aerial nests (Figure 149). But they also can inhabit mosses such as ***Polytrichum*** (Figure 28-Figure 29) with at least 15-20 cm of soil attached, where they constantly go in and out (Annie Martin, pers. comm. 6 October 2013).

Figure 147. ***Vespula germanica*** worker, a species that sometimes lives under mosses. Photo by James K. Lindsey, with permission.

Figure 148. ***Dolichovespula arenaria*** adult, member of a genus that sometimes lives under mosses. Photo by Gilles Gonthie,r through Creative Commons.

Figure 149. ***Vespula vulgaris*** nest showing the interior intricacies of this papery nest. Photo by Richerman, through Creative Commons.

A Calyptra Mimic

This story lacks a critical detail – the name of the wasp. But it is too interesting to omit, and perhaps someone can shed light on the wasp involved.

Györffy (1952) tells of checking out the twin capsules on the seta of ***Polytrichum strictum*** (Figure 150). Upon closer examination, he found that these were not Siamese twins, but rather a capsule with its calyptra and a wasp cocoon, both perched on a single seta. In one of his favorite haunts in Austria, Györffy had seen these "twin capsules" among the "billions" of plants of this moss species in the harvested peat bogs. In this exploration, what he found was that the second twin was a lemon yellow cocoon closely adjacent to the calyptra, and from these cocoons deep black larvae hatched. Mimicry of a calyptra by Hymenoptera – or any other invertebrate – seems to be reported only here. Györffy concluded that such mimicry protected the larvae from cocoon-eating birds as they would prefer to do their "gymnastics" on tree branches.

Figure 150. ***Polytrichum strictum*** capsules with calyptrae – a structure mimicked by the egg cocoon of a wasp. The insect shown here appears to be an orthopteran – also somewhat resembling the covered capsules. Photo by Michael Lüth, with permission.

Summary

Ants have flexible bodies that permit the to maneuver among the bryophytes. The ants are able to chew and move the bryophytes, permitting them to build trails through the bryophytes, making their foraging easier. They defend themselves with strong mandibles, stings, and chemical sprays. They keep their nests clean. Some remove the tracheophytes around their nests, thus creating space where bryophytes can grow.

Bryophytes provide insulation that maintains a buffered temperature and moisture. For some ants such as ***Messor***, bryophytes also provide food, especially the capsules, but some are also known to eat the leafy plants. bryophytes also provide a suitable habitat for some of their predators such as salamanders. Even bears may forage in the bryophytes for ants. As the ants move about, spores, fragments, and gemmae may be trapped between the body hairs and get transported to a new location.

Some bryophytes are prone to growing on ant hills, possibly taking advantage of the higher concentration of nutrients or being raised above the forest floor where

they can avoid burial by leaf litter. They also avoid competition. Some take advantage of the north-facing slope to reduce desiccation.

A number of ant species use bryophytes in building nests. ***Sphagnum*** in particular is used, in some cases to make a nest for aphids that provide honeydew for the ants. Ants may be responsible for the hummocks in some peatlands. Some ants create arboreal gardens, using mosses and planting seeds among them. Others place seeds under mosses on the ground, providing them with a suitable protected germination site.

Bryophytes in the environment provide sites for finding drops of water and seeking cover. Others use them for finding food or laying eggs. Epiphylls on leaves, especially in tropical forests, may produce compounds that discourage herbivory on the leaves.

Honeybees appear to use bryophytes for obtaining water from that resting on the bryophytes. Beekeepers often place bryophytes near hives to provide watering sites, but species such as ***Pohlia*** spp. may attract more bees by reflecting UV light.

Bumblebees use bryophytes in their nests. Some species overwinter under the bryophytes. Carder bees build elaborate nests, partly above ground, lined with bryophytes.

Some species of the parasitic wasps in **Braconidae** are consistently associated with mosses because their lepidopteran hosts live there. One member of the **Cynipidae** mimics mosses with the galls it makes. For some **Hymenoptera**, the peat helps survival, possibly through antibiotic properties. A number of **Ichneumonidae** overwinter in and under mosses and some may oviposit there. Some members of **Pompilidae** live in ***Sphagnum*** habitats. The scelionid ***Neobaeus novazealandensis*** lives on moss-covered ground. Even the wasps sometimes nest under mosses such as ***Polytrichum***.

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CHAPTER 12-11
TERRESTRIAL INSECTS: HOLOMETABOLA – TRICHOPTERA

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CHAPTER 12-11
TERRESTRIAL INSECTS: HOLOMETABOLA – TRICHOPTERA

Figure 1. ***Eniocyla pusilla*** larva, the most common terrestrial caddisfly and often a moss dweller. Photo by John Bingham, with permission.

The adults of caddisflies are terrestrial, but most caddisflies have aquatic larvae. Nevertheless, a few have adapted to living in wet places on land. And mosses can provide those wet places. For example, Sleight (1913) described one member of **Limnephilidae** in mosses at tree roots, but not in the water.

Some aquatic larvae are able to feed near the surface of water. The aquatic ***Pycnopsyche guttifera*** (Figure 2) will sometimes eat terrestrial mosses, but this occurs when the mosses are just below the water line (Williams & Williams 1982).

Figure 2. ***Pycnopsyche guttifera*** larva, a larva that eats terrestrial mosses when they become submersed. Photos by Tom Murray, through Creative Commons.

Larvae

We now know that there are three species of terrestrial ***Enoicyla*** (**Limnephilidae**; Figure 1) in Europe, and that larvae of these live in the humid and temperate mosses of deciduous forests and rock crevices (Crampton 1920; Meidl & Molenda 2000), often far from water (Crampton 1920). Perhaps the best known of these terrestrial larvae are those of ***Enoicyla pusilla*** (Figure 3-Figure 5). These larvae build cases from fine grains of sand and vegetable matter among mosses (Butler 1886). In Britain, ***Enoicyla pusilla*** is restricted to woodlands, and Harding (1998) suggested that it may have been accidentally introduced from the European continent. This species has five larval instars, becoming more scarce by late summer. Eggs hatch in October and November, and larval success may depend on rainfall during those months. The larvae of this species typically occur among mosses and leaf litter.

Figure 3. ***Enoicyla pusilla*** larvae, a species that inhabits mosses and leaf litter. Photo by Ernest van Asseldonk, through Creative Commons.

Figure 4. ***Enoicyla pusilla*** larva feeding on a slime mold. Photo by John Bingham, with permission.

Figure 5. ***Enoicyla pusilla*** adult, a species whose larvae live among terrestrial mosses. Photo by James K. Lindsey, with permission.

Green (1997) reported that in the UK the larvae of ***Enoicyla pusilla*** (Figure 3) feed on the soft tissues of dead leaves, mosses, and algae. In one observation, 50 or more individuals were actively climbing up logs and apparently browsing on black slime molds (Green 2012). Their requirement for nearly 100% humidity limits their terrestrial habitats. They have no gills and must rely on cutaneous respiration. If they get too wet, they climb upward and "hang themselves out to dry." When the humidity decreases to 70%, they drop again to the ground. Sometimes many larvae occur together on the surfaces of mosses and liverworts on stream banks after a rain (Green & Westwood 2005; Green 2012).

Flint (1958) considered that *Ironoquia pusilla* in northeastern United States closely resembled ***Enoicyla pusilla*** in its pupal stage. He reported that the larvae of *I. parvula* left the water and climbed to land where they spent their pupal stage among the leaf litter.

Another genus of caddisfly that lives on land as larvae is ***Manophylax*** (**Apataniidae**) (Chuluunbat *et al*. 2010). ***Manophylax futabae*** larvae can be found on the vertical sides of large rocks 10-30 m from mountain streams, as well as on vertical rocky outcrops. Chuluunbat and coworkers found that these larvae were often covered with mosses and lichens, but assumed that their only water usually came from precipitation. ***Manophylax alascensis*** and ***M. annulatus*** both construct their cases (4.0-9.8 mm) from fine rock fragments with attached moss and algal fragments dorso-laterally.

It may be that the movement of Trichoptera to land began with species that moved there to feed. *Desmona bethula* (**Limnephilidae**) is one such species (Erman 1981). When it reaches its fifth instar, it adventures from the water to feed on semiaquatic plants. But for this species, inclusion of bryophytes is not known.

Oviposition

If there are larvae on land, then there must be oviposition on land, at least for species that are not adjacent to water. It is interesting that the information I have found on the terrestrial caddisflies is not well linked. We know about the larvae of ***Enoicyla*** (Figure 3-Figure 5) feeding on bryophytes, but I have found no discussion of their oviposition. On the other hand, I have found information on egg-laying in the **Leptoceridae**.

Leptorussa darlingtoni (**Leptoceridae**) females become active in late afternoon in oviposition (Towns 1983). In Australia, most had congregated in damp mosses near the water surface, with 30 adults along an 80-cm line at 10-20 cm above the water. ***Leptorussa darlingtoni*** deposits its egg masses in communities above the water, whereas ***Lectrides varians*** (Figure 6), also in the **Leptoceridae**, deposits a single egg mass at 65-95 cm above the water. For ***Leptorussa darlingtoni***, the egg masses are placed in small crevices, but they are always near extensive moss cover. Nevertheless, the moss moisture does not seem to be important as the eggs survive in these same locations when the mosses are dry in years with little rainfall. Towns suggested that the terrestrial deposition may be an avoidance of the fluctuating oxygen levels in the water. In fact, when Towns attempted to rear the eggs on damp mosses in the laboratory, fungal infections caused death of the eggs. Towns asserted that ***Leptorussa darlingtoni*** is the only species of caddisfly that has communal oviposition and hatching without water.

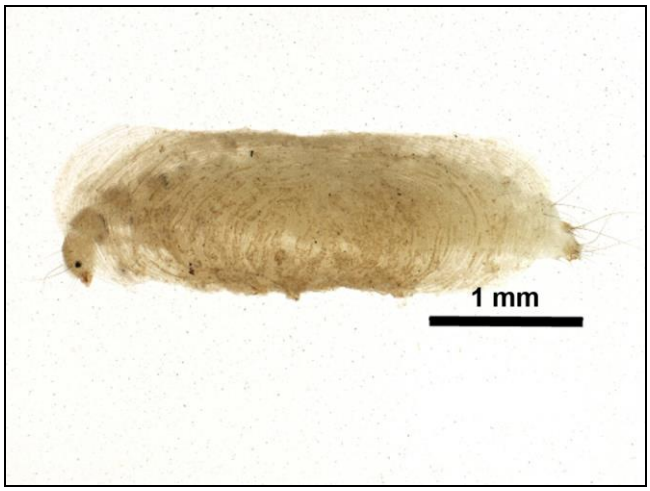

Figure 6. ***Lectrides varians*** larva, a species that deposits its eggs where there are lots of mosses. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Pupation

Most of the aquatic larvae of **Trichoptera** remain in the water to pupate, emerging onto vegetation or rocks to climb out of the water as adults. But if larvae can live on land, we can assume that their pupae, and perhaps pupae of others, may survive terrestrial life. Erman (1984) suggested that terrestrial pupation in this group evolved as an adaptation to living in intermittent streams. Some larval members of **Limnephilidae** leave the water in the final instar to pupate on land. ***Limnephilus peltus*** (see Figure 7) leaves spring streams shortly after the snow melts in the Sagehen Creek basin, California, USA, to burrow into the mosses at the edges of fen streams. If the spring flow ends too early and the mosses dry, some pupae may die without any adult emergence.

Another caddisfly, in the **Goeridae**, ***Archithremma ulachensis***, spends its larval days in a layer of ***Sphagnum*** (Figure 8) on a springbank (Levanidova & Vshivkova 1984). Its pupa seems to be adapted to this dense terrain. It lacks long setae and projections used by other pupae in the family to clean the silk disks that close the case. The first abdominal segment lacks posterior rugosity, and there are no swimming legs. The larvae, however, live in water courses that have cold summer temperatures (3-5°C). The authors consider these cold brooks to have less food competition, thus favoring the larvae of this species.

Figure 7. ***Limnephilus*** sp. larva; ***L. peltus*** burrows into mosses to pupate. Photo by Jason Neuswanger, with permission.

Figure 8. ***Sphagnum capillifolium***; ***Sphagnum*** is home for the larvae of ***Archithremma ulachensis***. Photo by Bernd Haynold, through Creative Commons.

Hayashi *et al*. (2008) cite the terrestrial habits of the limnephilid ***Nothopsyche***. This genus has species in which both pre-pupae and pupae are entirely terrestrial. Their mitochondrial data indicate that this genus was originally aquatic and that just one lineage became terrestrial in the pre-pupal and pupal stages. In this terrestrial lineage, ***Nothopsyche montivaga*** became completely terrestrial. The terrestrial line also exhibit a switch in case materials from plant matter to sand.

Bogs

For an order of insects evolving from water to land, bogs would seem to be the ideal place to begin. The mosses wick water upward, remaining moist most of the year. Furthermore, water can often be reached by moving downward.

Buczyńska *et al*. (2012) searched for the rare ***Hagenella clathrata*** (**Phryganeidae**; Figure 9-Figure 10) in Poland. This species is associated with bogs, making it even more threatened due to habitat destruction. This research team was able to collect larvae in the mountain area using Barber pitfall traps, indicating their mobility in terrestrial habitats.

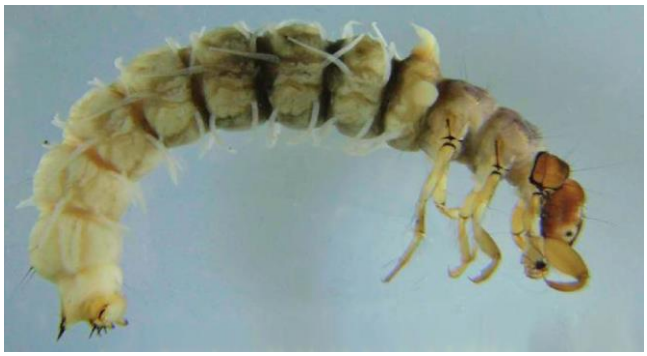

Figure 9. ***Hagenella clathrata*** larva, a species that lives in bogs. Photo by Marko Mutanen, through Creative Commons.

Figure 10. ***Hagenella clathrata*** adult, a bog dweller. Photo by Rob Felix, through Creative Commons.

Summary

Few of the caddisfly larvae have adapted to terrestrial living, and even fewer use bryophytes for their terrestrial adventures. Several of the bryophyte associates are in the **Limnephilidae.** ***Pycnopsyche guttifera*** sometimes eats terrestrial mosses that extend below water. ***Limnephilus peltus*** burrows into mosses to pupate. But the best known example is that of ***Enoicyla pusilla***, larvae that live terrestrially and include mosses in their varied diet.

Larvae of ***Manophylax*** (**Apataniidae**) may include mosses in their cases. ***Leptorussa darlingtoni*** (**Leptoceridae**) lays eggs near water in damp mosses, but the eggs can dry safely and thus may not require mosses. Larvae and pupae of ***Archithremma ulachensis*** (**Goeridae**) live among ***Sphagnum***. ***Hagenella clathrata*** (**Phryganeidae**) likewise live in bogs.

Acknowledgments

Thank you to those photographers who gave me permission or placed their images in Creative Commons. For this chapter, I would welcome additional images!

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CHAPTER 12-12
TERRESTRIAL INSECTS: HOLOMETABOLA – LEPIDOPTERA BIOLOGY AND ECOLOGY

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CHAPTER 12-12
TERRESTRIAL INSECTS: HOLOMETABOLA – LEPIDOPTERA BIOLOGY AND ECOLOGY

Figure 1. These **Lepidoptera** seem to be on these epiphytic bryophytes for a reason, but often we don't know why. Photo by Janice Glime.

Lepidoptera

I was surprised to find that in one study in Romania Dincă (2005) found that 1.8% of the approximately 1000 Macrolepidoptera taxa were "moss" consumers. Pierce (1995) stated that larvae that live in mosses have an environment that is close to aquatic. But few **Lepidoptera** live in the water, so we can expect that these terrestrial insects may have other reasons for visiting or living in bryophytes. On the other hand, the **Trichoptera** and **Lepidoptera** are closely related (Crampton 1920; Shields 1988; Britannica 2008), and most **Trichoptera** larvae are aquatic. Shields contends that the **Lepidoptera** evolved from aquatic **Trichoptera**, so it is therefore predictable that some have strong needs for moisture. This divergence most likely occurred in the late Triassic at a time when many streams were dry and water was scarce, eliminating many insects that were dependent on water.

Klok and Chown (1997) report that water balance is important for the sub-Antarctic caterpillar, ***Pringleophaga marioni*** (**Tineidae**; Figure 2). But these moths seem to have no mechanisms for preserving or regulating their water, hence requiring moist habitats. One of these habitats for the larvae is in the mire moss ***Sanionia uncinata*** (Figure 3) (Burger 1978). These moths are wingless as adults and thus have a limited distribution on Marion Island.

Figure 2. ***Pringleophaga marioni*** adult, a sub-Antarctic moth with no known mechanism to regulate water. Photo by S. L. Chown, B. J. Sinclair, H. P. Leinaas, and K. J. Gaston, with permission.

Figure 3. ***Sanionia uncinata*** with capsules. This species is home for ***Pringleophaga marioni*** on Marion Island in the sub-Antarctic. Photo by Andrew Hodgson, with permission.

Like all creatures, adult **Lepidoptera** need water. Bryophytes collect water and it often stays at leaf bases and other capillary spaces where cohesion keeps it from rolling away. These water droplets are suitable for the tube-feeding adult **Lepidoptera** to get a drink of water (Figure 4). Martin (2015) has observed butterflies and moths pausing for a drink of water from the moss leaves in her moss garden.

Figure 4. Butterfly on ***Palustriella commutata***, a place where one can often find water droplets. Photo by Serhat Ursavas, with permission.

Life Cycle

All stages of **Lepidoptera** (egg-larva-pupa-adult) are known from bryophytes. The adult females of bryophyte-feeding larvae often lay eggs there. Several families include members whose larvae live in and feed on bryophytes, a number of which specialize on liverworts. These bryophyte-feeding larvae are often in primitive families that originated before flowering plants.

Eggs

For those **Lepidoptera** that use the bryophytes for egg-laying, the bryophytes provide a safe haven for emerging larvae. This is the case for the hemlock looper (***Lambdina fiscellaria***; Figure 5) (an inchworm; **Geometridae** – see Chapter 12-13), which is a serious conifer pest (Shepherd & Gray 1972).

Figure 5. The hemlock looper (***Lambdina fiscellaria***) larva hiding in moss in autumn. Photo from USFS, through public domain.

Some females create cocoons in which they lay eggs (Figure 6-Figure 7). Timea Deakova sent me images of a cocoon of eggs from the moss ***Climacium dendroides*** in Oregon, USA. The larvae eat moss and grass.

Figure 6. Moth cocoon on ***Climacium dendroides***. Photo courtesy of Timea Deakova.

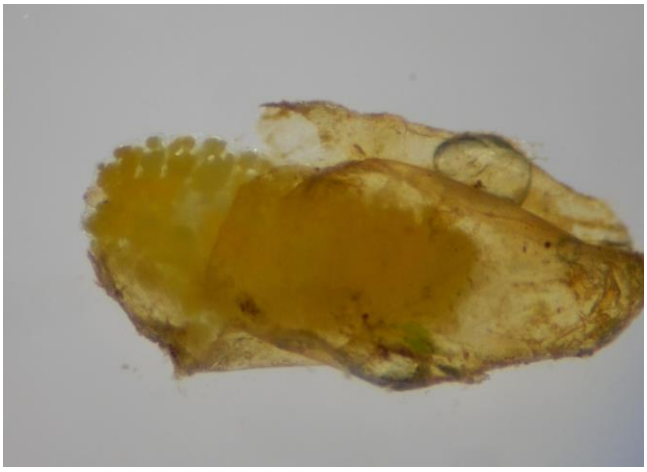

Figure 7. Cocoon from ***Climacium dendroides***, with eggs emerging. Photo courtesy of Timea Deakova.

Figure 8. Moth caterpillar on moss in ***Polytrichum juniperinum*** in Oregon, USA. This larva developed and hatched into the adult in Figure 9. Photo courtesy of Timea Deakova.

Figure 9. Adult that hatched from the above larva on mosses. The ragged wings are due to hungry larvae feeding on them in captivity. Photo courtesy of Timea Deakova.

Figure 10. Moth hatched from larva on moss. Photo courtesy of Timea Deakova.

Larvae

Larvae of **Lepidoptera** can be recognized by the presence of **crochets** (hooks; Figure 11) on their **prolegs** (fleshy short legs on the abdomen) Some **Lepidoptera** spin their cocoons in mosses or use bits of mosses or liverworts as part of the cocoon (Figure 12-Figure 13). Buchanan (1971) reported this behavior for ***Pyrausta cingulata*** (**Crambidae**; Figure 13-Figure 14), ***Phycis subornatella*** (**Pyralidae**), and ***Eana penziana*** (**Tortricidae**; Figure 15) near Perth, Australia. Buckler (1871) reported silken cocoons of larvae of ***Acronicta myricae*** (**Noctuidae**; see Figure 16-Figure 17) covered with moss.

Figure 11. ***Cossus cossus*** larval prolegs showing crochets. Photo by Anki Engström <www.krypinaturen.se>, with permission.

Figure 12. **Lepidoptera** larval cocoon of the liverwort ***Riccardia filicina***. Although the larva has left its cocoon, the liverwort fragments are still alive. Photo courtesy of David Glenny.

Figure 13. ***Pyrausta cingulata*** larva with bits of its cocoon. Photo by Bob Heckford, with permission.

Figure 14. ***Pyrausta cingulata*** adult, a species that spins its cocoon on mosses. Photo by Olaf Leillinger, through Creative Commons.

Figure 15. ***Eana penziana*** adult. Larvae of this species build cocoons on mosses. Photo by Kurt Kulac, through Creative Commons.

Figure 16. ***Acronicta euphorbiae*** larva, a species related to the moss user ***Acronicta myricae***. Photo by Harald Süpfle, through Creative Commons.

Figure 17. ***Acronicta*** sp. adult. ***Acronicta myricae*** builds cocoons on mosses. Photo by Olaf Leillinger, through Creative Commons.

Pupation

Bryophytes offer a safe site for pupation of **Lepidoptera** (Figure 18-Figure 20). It is likely that a number of **Lepidoptera** pupate among the bryophytes, but this stage is difficult to identify and is easily overlooked. Hence the records of this stage may not be truly representative of the usage of mosses for overwintering and escape from desiccation. Nevertheless, I have been pleasantly surprised not only by the number of records, but by the identification of the bryophytes involved for both larvae and pupae.

Figure 18. **Lepidoptera** pupal shell in moss. Photo courtesy of Sarah Lloyd.

Figure 19. **Lepidoptera** pupal shell in moss. Photo courtesy of Sarah Lloyd.

Figure 20. **Lepidoptera** pupa on moss. Photo by Vinicius Santana Orsini Brazil.

Some **Lepidoptera** pupae, for example the privet hawk moth ***Sphinx ligustri*** (**Sphingidae**; Figure 21-Figure 24), survive winter in rotting logs covered with mosses, but the necessity for the moss has not been assessed (Brackenbury 1994).

Figure 21. ***Sphinx ligustri*** adult, a species that survives winter as pupae in logs covered with mosses. Photo by Olaf Leillinger, through Creative Commons.

Figure 22. ***Sphinx ligustri*** larva. Photo by Georg Slickers, through Creative Commons.

Figure 23. ***Sphinx ligustri*** pupating, an activity it commonly does in moss-covered logs. Photo ©entomart, through Creative Commons

Figure 24. ***Sphinx ligustri*** mature pupa, the overwintering stage in logs covered with mosses. Photo from ©entomart, through Creative Commons.

Food Sources

Gerson (1982) reviewed what could be found regarding bryophytes as food sources for **Lepidoptera**. He reported that the larvae of **Meessiinae** feed on both lichens and mosses, but they also incorporate the fragments of these two groups of organisms in their cases. ***Nudaria mundana*** eats both saxicolous lichens and liverworts (Forster & Wohlfahrt 1960). Some larvae have a safe haven while they feed on the bryophytes. The ***Sabatinca*** larva is a liverwort mimic with its greenish color and large setae (Tillyard 1922; Yasuda 1962; Gerson 1982; Holloway 1993).

Feeding on Leafy Gametophytes

As I worked on this chapter, I became amazed at the number of **Lepidoptera** that feed on bryophytes. Most feed on the leafy plants (Figure 25). Some of them feed on mosses and others feed exclusively on liverworts.

Figure 25. Caterpillar feeding on the moss ***Fabronia leikipiae***. The caterpillar has an ideal color and pattern to blend in with the bryophyte branches. Photo by Min Petiot.

As early as 1894, Chapman noted that some **Lepidoptera** larvae feed on mosses, especially in the primitive families. We now know that some are bryophyte specialists. Robin Stevenson shared his image with me to demonstrate feeding on mosses (***Tortula truncata***) by **Lepidoptera** larvae (Figure 26).

Figure 26. ***Tortula truncata*** showing feeding damage by larval **Lepidoptera**. Photo courtesy of C. Robin Stevenson.

A number of **Lepidoptera** larvae feed on the leafy gametophytes of bryophytes. Members of the primitive lepidopteran suborder **Zeugloptera** are moss feeders (Chapman 1894; Tillyard 1926), suggesting that the advent of flowering plants opened new food sources for them. Among these bryophyte feeders is ***Micropterix calthella*** (**Micropterigidae**; Figure 27-Figure 28) (Chapman 1894).

Figure 27. ***Micropterix calthella*** adult, a bryophyte feeder in its larval stage**.** Photo by Wouter Bosgra, through Creative Commons.

Figure 28. ***Micropterix calthella*** adult of a larval bryophyte feeder. Photo by Tom Deroover, through Creative Commons.

Feeding on Capsules

Fang and Zhu (2012) reviewed accounts of **Lepidoptera** feeding on bryophyte capsules. They found that the known feeding habits of lepidopteran larvae included capsules in only four families: **Micropterygidae** (Gerson 1969), **Mnesarchaeidae** (Grehan 1984), **Arctiidae** (as **Lithosiidae**) (Liu 1989), and **Geometridae** (Maciel-Silva & dos Santos 2011). Thus, theirs is the first record of **Noctuidae** larvae that feed on mosses. ***Agrotis*** sp. (**Noctuidae**; Figure 29) larvae commonly feed on capsules of ***Haplocladium microphyllum*** (Figure 30) in Shanghai in the spring (Fang & Zhu 2012).

Figure 29. ***Agrotis*** feeding on capsules of ***Physcomitrium sphaericum***. Photo by Rui-Liang Zhu, with permission.

Figure 30. ***Haplocladium microphyllum*** capsules and setae where capsules have been completely eaten by a species of ***Agrotis***. Photo by Rui-Liang Zhu, with permission.

Butterflies

"Among those groups of butterflies that feed on plants, none is known to feed on bryophytes or on Psilopsida, Lycopsida, or Sphenopsida, nor is any known from ferns" (Ehrlich & Raven 1964). This statement surprised me because I had already found a number of **Lepidoptera** that feed on bryophytes. But I soon realized these are almost entirely moths. However, there are exceptions (see PAPILIONOIDEA in Chapter 12-14) in the **Lycaenidae** (Callaghan 1992), **Nymphalidae** (Singer & Mallet 1986; Hamm 2015), and **Rionidae** (DeVries 1988). It is interesting that two of these exceptions are butterfly larvae that feed on the epiphylls that live on tracheophyte leaves.

It is not unusual for **Lepidoptera** to eat plants, but it is unusual among the butterflies. While bryophytes are not a main fare, some satyrid butterflies do consume bryophytes (Singer & Mallet 1986). In Japan, the primitive ***Sabatinca*** (Figure 31) and ***Neomicropteryx nipponensis*** (both in **Micropterigidae**; Figure 32) feed on liverworts (Figure 33) (Yasuda 1962).

Figure 31. ***Sabatinca congruella*** larva on a leafy liverwort, demonstrating its cryptic form and color. Photo by George Gibbs, with permission.

Figure 32. ***Neomicropteryx nipponensis*** larva feeding on ***Conocephalum conicum***. Photo by Yume Imada, with permission.

Figure 33. ***Conocephalum conicum***, food for ***Sabatinca*** and ***Neomicropteryx nipponensis*** in Japan. Photo by Hermann Schachner, through Creative Commons.

Epiphylls as Food

Bodner *et al*. (2015) found that in southern Ecuador the caterpillar assemblages often did not feed on their expected hosts. Rather, they chose foliose lichens, dead leaves, and the epiphylls, including bryophytes.

Invertebrates on the Menu

One normally thinks of caterpillars, the larvae of the **Lepidoptera**, as plant eaters. But Murawski (2003) describes "killer" moths that are carnivores, usually on soft-bodied insects and spiders. They use camouflage, seductive odors, and armor shields to enable them to sneak up on their prey. Some (***Maculinea alcon*** – **Lycaenidae**; Figure 34) visit flowers to obtain a waxy cover of hydrocarbons that smell like ***Myrmica*** (Figure 35-Figure 36) ant larvae, enabling them to enter the ant nest. They then trick the ants into accepting them and feeding them while they attack the ant larvae! The ants whose nests are invaded include ***Myrmica scabrinodis*** (Figure 35), ***Myrmica ruginodis*** (Figure 36), and ***Myrmica rubra*** (Figure 37). All three of these ant species are associated with mosses, often nesting under them, hence the **Lepidoptera** live under mosses as well.

Figure 34. ***Maculinea alcon*** adult; larvae of this species trick ants into accepting them and feeding them. These ants typically associate with mosses, hence, so does the ***Maculinea alcon***. Photo by Joris Egger, through Creative Commons.

Figure 35. ***Myrmica scabrinodis***, an ant that is mimicked in smell by the larvae of ***Maculinea alcon***. Photo by Tim Faasen, with permission.

Figure 36. ***Myrmica ruginodis*** adult on moss, an ant species that is fooled by the odors of ***Maculinea alcon*** and takes care of their larvae. Photo by James K. Lindsey, with permission.

Figure 37. ***Myrmica rubra*** workers, a species whose nests are invaded by ***Maculinea alcon***. Photo by Gary Alpert, through Creative Commons.

Some **Lepidoptera** that are indeed carnivorous caterpillars take advantage of the mosses to gain their food in a quite different way. In Hawaii, these carnivores are camouflaged as leaf litter, lichens, twigs, or mosses (Figure 38), permitting them to stalk their invertebrate prey (Murawski 2003).

Figure 38. ***Adelpha serpa celerio***, a moss-mimicking caterpillar from Panama, but in this case, not a carnivore. Photo by Arthur Anker, with permission.

Antiherbivory

The limitation of **Lepidoptera** larvae primarily to leaves of seed plants may be due to antiherbivore compounds. Wada and Manakata (1971) demonstrated that some liverwort terpenoids inhibit feeding by **Lepidoptera** larvae. Ottosson and Anderson (1983) showed that fewer species were associated with ferns than with other tracheophytes and providd evidence that the wide range of chemical defenses in the ferns discouraged many insects from eating them. Nevertheless, the **Lepidoptera** seemed able to exhibit spatiotemporal adaptations that permitted them to avoid the unfavorable biochemistry of the ferns.

Krishnan and Murugan (2013) investigated feeding by **Lepidoptera** on bryophytes, using 20 species. They chose two species [corn earworm, *Helicoverpa zea* (Figure 39) – Noctuidae, and armyworm, *Spodoptera litura* (Figure 40) – Noctuidae)] that do not eat bryophytes. They compared the effects of protein extracts from bryophyte species with those from the normal food plant *Glycine max* (Figure 41) cultivar using bioassays. In these experiments, protein extracts from four species [***Octoblepharum albidum*** (Figure 42), ***Fissidens virens*** (see Figure 43), ***Bryum argenteum*** (Figure 44), and ***Marchantia linearis*** (Figure 45)] caused the greatest decrease in damage in leaf-disk assays and in insect larval growth. They also caused a reduction in efficiency of digestion and food conversion. Further discussion of antiherbivory in **Lepidoptera** is in the following subchapters.

Figure 39. ***Helicoverpa zea*** larva, a species that does not eat bryophytes and avoids extracts of them. Photo by R. L. Croissant, through Creative Commons.

Figure 40. ***Spodoptera litura*** adult, a species whose larvae do not eat bryophytes and avoid extracts of them. Photo by Merle Shepard, Gerald R. Carner, and P. A. C. Ooi, through Creative Commons.

Figure 41. ***Glycine max***, a normal food plant of larvae of ***Helicoverpa zea*** and ***Spodoptera litura***. When bryophyte extracts were applied to these leaves, the larvae of these two species reduced feeding on it. Photo by Pancrat, through Creative Commons.

Figure 42. ***Octoblepharum albidum***, a species that deters at least some **Lepidoptera** larvae from eating it. Photo by Niels Klazenga, with permission.

Figure 43. ***Fissidens dubius***; ***F. virens*** deters at least some **Lepidoptera** larvae from eating it. Photo by Kurt Stüber, through Creative Commons.

Figure 44. ***Bryum argenteum***, a species that deters at least some **Lepidoptera** larvae from eating it. Photo by Martin Hutten, with permission.

Figure 45. ***Marchantia linearis***, a species that deters at least some **Lepidoptera** larvae from eating it. Photo by Manju C. Nair, through Creative Commons.

Adaptations

Bryophytes can provide a number of characteristics that are favorable for small invertebrates. They absorb water rapidly, reduce evaporation, and provide insulation against extremes of temperature and wind (Gerson 1982).

Most adult **Lepidoptera** associated with bryophytes do not have morphological adaptations for the bryophytic habitat, but rather blend with the flowers they visit. Others, however, are dull grays and browns that permit them to blend with the bark where they rest.

Larvae, on the other hand, are usually colored with browns, grays, and greens, and have tubercles or spines. Some have behaviors that cause them to include bryophytes in the construction of cocoons or cases. Their biggest adaptation, however, seems to be the ability to eat and digest the bryophytes. On the other hand, for at least some families, this is a primitive trait (Powell *et al*. 1999; Hashimoto 2006).

Some of the larvae, but few of the adults, have color patterns that would camouflage them among the bryophytes (Figure 46-Figure 47). Intermixed greens, browns, and black would make it easy for the larvae to hide among bryophytes, but these colors do not always coincide with known uses. Is this just our lack of sufficient observations, or are they adapted to walking among the mosses on their way from one location to another?

Figure 46. Caterpillar on moss, showing greens, black, and a brown head capsule. But does it live there? Photo by Carrie Andrew, with permission.

Figure 47. Moth adult on bryophytes, showing cryptic coloration. Photo courtesy of Sarah Lloyd.

One type of mimicry that seems not to be reported elsewhere is that reported by Györffy (1952). He relays his adventures in checking out twin capsules, only to discover that one was not a capsule at all. On the setae of ***Atrichum undulatum*** (Figure 48) he found not only a capsule, but also a cocoon. He reared the cocoon successfully to its maturity, from which emerged a moth. He did not describe it in this case, so it is not clear if it truly resembled a capsule of the moss, but especially noticeable as the animal it was.

Figure 48. ***Atrichum undulatum*** with capsules, home for some **Lepidoptera** pupae on the setae. It is easy to see how a pupa might be inconspicuous among these capsules. Photo by Michael Lüth, with permission.

Habitats

In their altitudinal study in Australia and New Zealand, Andrew *et al*. (2003) collected bryophytes and extracted invertebrates using the kerosene phase separation method. They identified these to family and found only one family of **Lepidoptera**. Nevertheless, bryophyte-dwelling **Lepidoptera** are more common than most of us might suspect in the forests and peatlands.

Forests

Diversity of **Lepidoptera** in forests is related to, but not limited to, the layers of the forest, disturbance, and management (Thorn *et al*. 2015). These researchers found that abundance of moth larvae of the **saproxylic** (pertaining to decaying wood) and detritus-feeding guilds was higher under a regime of natural disturbance and in multi-layered stands. Larvae of moss-feeding moths, on the other hand, was lower in multi-layered stands.

Some of the relationships may be indirect, but nevertheless, important. ***Liphyra brassolis*** (**Lycaenidae**; Figure 49-Figure 51) is a rarely found species, protected as larvae from ant bites by a leathery "hide." Larvae of this species enter green tree ant (***Oecophylla smaragdina*** – **Formicidae**; Figure 52) nests (Figure 53) to feast on larvae. These don't involve bryophytes, but similar behavior in aerial moss nests of ants is possible (See Chapter 12-10). It is certainly worth looking for them.

Figure 49. Ventral view of ***Liphyra brassolis*** larva, an insect that invades ant nests and is protected from attack by its leathery covering. Photo by Martin Lagerwey, with permission.

Figure 50. ***Liphyra brassolis*** larva showing head view, an insect that invades ant nests and is protected from attack by its leathery covering. Photo by Martin Lagerwey, with permission.

Figure 51. Dorsal view of ***Liphyra brassolis*** larva, showing its thick, leathery covering that protects it from ant attacks. Photo by Martin Lagerwey, with permission.

Figure 52. Tree-dwelling ***Oecophylla smaragdina*** carrying a grub. Photo by Zloulemark, through Creative Commons.

Figure 53. Aerial nest of ***Oecophylla smaragdina*** where caterpillars of ***Liphyra brassolis*** go to feed. Photo by J. M. Garg, through GNU Free License.

Epiphytes

In the tropical tree canopy, bryophyte and other epiphyte assemblages can be important food sources. Yanoviak *et al*. (2004). observed that larvae of the **Lepidoptera** on bryophytes occurred exclusively in the green fraction. The distribution of small epiphytes is influenced by the gross epiphyte morphology and location (Martin 1938; Gerson 1982).

Events such as hurricanes can have a severe impact on the epiphytic flora, including bryophytes, and the fauna living among them (Loope *et al*. 1994). Loss of bryophytes may not only be a loss of food and cover, but the **Lepidoptera** that live among them may be dispersed during the hurricane, but not necessarily to a suitable habitat.

But not all leaf dwellers feed on the leaves they inhabit. Some species of **Lepidoptera** occur regularly in the canopy leaf habitat and feed on the epiphylls, including bryophytes, algae, lichens, and fungi (Lucking 2000). Some are broad spectrum feeders, but the larvae of **Lepidoptera** seem to specialize on either the lichens or bryophytes.

Pettersson *et al*. (1995) found that larger invertebrates (>2.5 mm) served as food for foraging perching birds. These food invertebrates are higher in number in natural forests and include **Lepidoptera** among the dominant species. Their number and biomass relate to the abundance of lichens. This suggests that it would be worthwhile to look for similar relationships with bryophytes.

Bogs and Wetlands

Peatlands can be ideal habitats for many butterflies and moths. Spitzer and Jaroš (1993) found 569 **Lepidoptera** species in a single peat bog in Central Europe! Jaroš *et al*. (2014) found 1040 species of moths and butterflies in just five peat bogs in the Třeboň Basin up to the montane/subalpine zone of the Bohemian Forest. These included 33 relict species of cold-adapted **tyrphobionts** [species living only in peat bogs and mires (Peus 1928)] and 74 **tyrphophilous** species that prefer peatlands. Spitzer and Jaroš (2014) contend that the bogs are refugia for northern **Lepidoptera** species by creating a climate that is suitable. The ***Sphagnum*** (Figure 54) is responsible for temperature-buffered microclimates that are suitable for these northern relict species of **Lepidoptera**.

Väisänen (1992) used a belt transect to sample butterflies and day-active moths in a raised bog in southeastern Finland. The species richness was higher in the adjacent mineral land, with the highest number of both species and individuals on the **lagg** [nutrient-enriched zone that grades to land (Paradis *et al*. 2015)] and marginal slope. The Lepidoptera communities were related primarily to the structural characteristics of the bog, including tree height and undergrowth floristic characteristics (Väisänen 1992).

Figure 54. ***Sphagnum magellanicum***, dominant ***Sphagnum*** in a raised bog that has 11 tyrphobiontic and 14 tyrphophilous **Lepidoptera**. Photo by James K. Lindsey, with permission.

A number of butterflies (**Lepidoptera**: especially **Lycaenidae**, **Nymphalidae**, and **Satyridae**) complete their entire life cycle within peatland habitats of the Lake Superior drainage basin in northwestern Wisconsin (Nekola 1998). Nekola surveyed 70 peatlands in the drainage basin. The highest number of taxa occur in the muskeg sites, including five species that do not occur in other peatlands. In both the muskegs and kettlehole peatlands, butterfly species richness correlates highly with habitat size. These sites provide the southernmost locations for these northern species.

Chapman (1894) noted that some moth caterpillars in bogs use ***Sphagnum*** (Figure 54) for nests. And some eat the ***Sphagnum***. But more commonly, the ***Sphagnum***

provides a suitable habitat for the host plant. For example, one species, ***Nola aerugula*** (**Nolidae**; Figure 55), seems to be present as a dominant in a number of bogs, at least in Lithuania (Dapkus 2004a, b). It occurs throughout most of Europe, east to Japan. The larvae feed on *Trifolium* (Figure 56) and *Lotus corniculatus* (Figure 57), but also on *Betula* (Figure 58), *Salix* (Figure 59), and *Populus* (Figure 60) species, indicating its wide habitat distribution, but not indicating any direct use of the bryophytes.

Figure 55. ***Nola aerugula*** adult, a species that is often dominant in Lithuanian bogs. Photo by André den Ouden, through Creative Commons.

Figure 56. ***Trifolium repens***, a genus that is food for ***Nola aerugula***. Photo by Forest and Kim Starr, through Creative Commons.

Figure 57. ***Lotus corniculatus***, food for ***Nola aerugula***. Photo by David G. Smith <www.delawarewildflowers.org>, with online permission.

Figure 58. ***Betula populifolia*** leaves, in a genus that is food for ***Nola aerugula***. Photo by Richtid, through Creative Commons.

Figure 59. ***Salix cinerea*** leaves, in a genus that is food for ***Nola aerugula***. Photo by Sten Porse, through Creative Commons.

Figure 60. ***Populus tremula*** leaf, in a genus that is food for ***Nola aerugula***. Photo by Treetime, through Creative Commons.

Dapkus (2000) compared **Lepidoptera** in two peatlands and a raised bog in Lithuania. The raised bog was dominated by ***Sphagnum magellanicum*** (Figure 54) and exhibited true tyrphophilic and tyrphobiontic species, but none was present in the two peatlands that had been affected by disturbance due to peat extraction. In all, the raised bog had 11 tyrphobiontic and 14 tyrphophilous **Lepidoptera**, whereas the Baloða peatland had 4 tyrphobiontic and 9 tyrphophilous **Lepidoptera** species. The Palios peatland fared even worse with only 3 tyrphophilous and no tyrphobiontic **Lepidoptera** species.

Spitzer and Jaroš (1993) conducted an extensive survey of the **Lepidoptera** of a bog in southern Bohemia. They noted that all the tyrphobionts feed on peat bog plants. But for some of the tyrphophilous species, mosses are on the dinner table. These include ***Bryotropha boreella*** (**Gelechiidae**; Figure 61-Figure 63), ***Phiaris micana*** (**Tortricidae**; Figure 64-Figure 65), and ***Phiaris palustrana*** (**Tortricidae**; Figure 66-Figure 67). In addition, ***Thumatha senex*** (**Erebidae**; Figure 68) feeds on both mosses and lichens.

Figure 61. ***Bryotropha boreella*** adult on ***Sphagnum***, a food source for its larvae. Photo by Stephen Palmer, with permission.

Figure 62. ***Bryotropha boreella*** larva on its food source, a moss. Note the net surrounding the larva. Photo © Bob Heckford, with permission.

Figure 63. ***Bryotropha boreella*** pupa on moss. Photo © Bob Heckford, with permission.

Figure 64. ***Phiaris micana*** larva, a moss eater in bogs. Photo by James K. Lindsey, with permission.

Figure 65. ***Phiaris micana*** adult, a bog species with larvae that eat mosses. Photo by James K. Lindsey, with permission.

Figure 66. ***Phiaris palustrana*** adult, a bog species with larvae that eat mosses. Photo by Donald Hobern, through Creative Commons.

Figure 67. ***Phiaris palustrana*** larva, a moss eater in bogs. Photo by Bob Heckford, with permission.

Figure 68. ***Thumatha senex*** adult, a species whose larvae feed on mosses and lichens. Photo by James K. Lindsey, with permission.

The question remains, why are bogs important to these tyrphobiontic and tyrphophilous species? What is the role of the bryophytes? Do they simply provide the habitat needed by tracheophyte food plants, or are they necessary to survive in some stage of the life cycle?

So far, it appears that few studies indicate that any bog species feed on the bryophytes. In New Zealand Grehan and Patrick (1984) found that the larvae of ***Cladoxycanus minos*** (**Hepialidae**; Figure 69) build feeding tunnels in the moss, extending to 300 mm deep and under the water. This species eats ***Sphagnum cristatum*** (Figure 70). Two other unidentified species of **Hepialidae** likewise make tunnels into the moss mat. In the same bog ***Wiseana umbraculata*** (**Hepialidae**; Figure 71) occurs on saturated mosses that are in close contact with the soil surface.

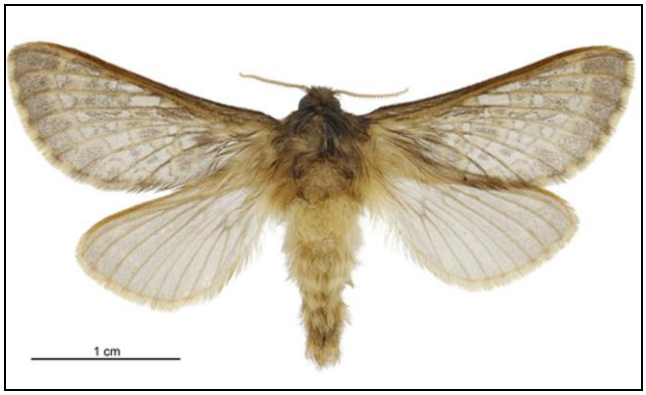

Figure 69. ***Cladoxycanus minos*** male adult; this species builds larval feeding tunnels in mosses. Photo from Landcare Research, Manaaki Whenua, with online permission.

Figure 70. ***Sphagnum cristatum***, food for ***Cladoxycanus minos*** in New Zealand. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

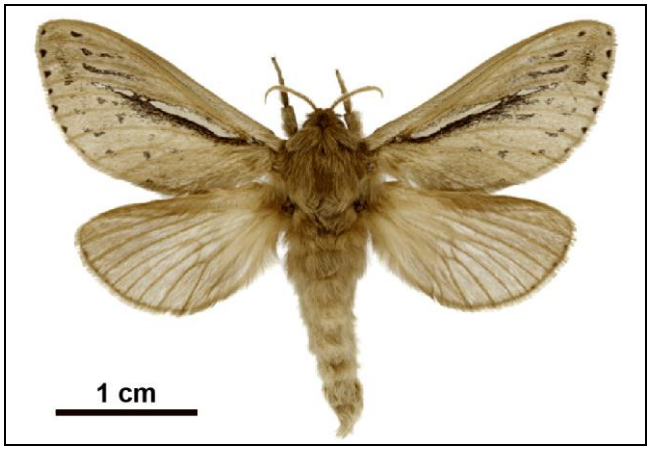

Figure 71. ***Wiseana umbraculata*** male adult, a species that occurs on saturated mosses. Photo from Landcare Research, Manaaki Whenua, with permission.

Sunny peatlands seem to be suitable for the mustard white butterfly, ***Pieris oleracea*** (**Pieridae**; Figure 72). But where ***Sphagnum*** (Figure 54) grows, danger often lurks. Chew (1978) observed one of these butterflies stuck to the sticky hairs of sundew leaves (Figure 73) in Vermont, USA, quite dead. And this species is not alone in being snared by bog-dwelling sundews (Figure 73). As these butterflies and moths struggle to get free, they only get further entangled in the sticky hairs.

Figure 72. ***Pieris oleracea*** adult, a bog resident that gets trapped by sundews. Photo by D. Gordon E. Robertson, through Creative Commons.

Figure 73. ***Drosera rotundifolia*** that has caught a bog butterfly. Photo by Noah Elhardt, through Creative Commons.

Disappearing Species

Local species extinctions have been occurring at a high rate, and members of **Lepidoptera** are no exception (Franco *et al*. 2006). Both climate change and habitat loss account for these losses. Typically, the species retract northward. Franco and coworkers concluded that mountain and northern species may be in jeopardy due to climate warming.

By contrast, Nöske *et al*. (2008) compared moths in **Geometridae** and **Arctiidae** (**Erebidae**?) in mature and recovering forest and in open vegetation of the montane belt in Andes of Ecuador. There was no uniform pattern of change in species richness with increasing disturbance. Rather, species richness of geometrid moths was significantly higher in the recovering forest than in the mature forest or the open habitats. The **Arctiidae** were also most species-rich in the recovering forest, but also in the open vegetation compared to the mature forest.

Any recovery of species following logging depends on the availability of colonists (Niemelä 1997). Butterflies, in particular, suffer from logging of old-growth forests, as do bryophytes (Hydén & Sjökvist 1993), and sometimes the **Lepidoptera** may suffer because of loss of bryophytes.

Maelfait *et al*. (2007) reported the loss of the butterflies ***Aricia agestis*** (**Lycaenidae**; Figure 74-Figure 77) and ***Issoria lathonia*** (**Nymphalidae**; Figure 78-Figure 79) from Dutch coastal dunes. This loss was attributed to loss of the varied vegetation structure that included patches of mosses and bare sand, both of which disappear when tall grasses expand coverage (Brouwer *et al*. 2005).

Figure 74. ***Aricia agestis*** adult, a species that lives where there are bryophytes in the habitat. Photo by Hectonichus, through Creative Commons.

Figure 75. ***Aricia agestis*** adult, a species that lives where there are bryophytes in the habitat. Photo by Jérôme Albre, with permission.

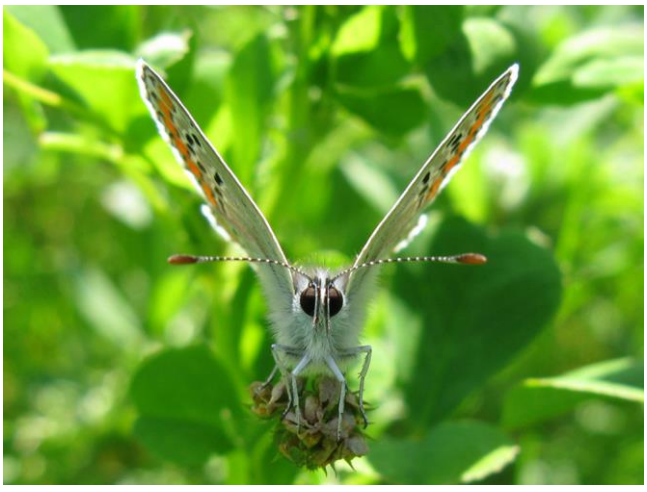

Figure 76. ***Aricia agestis*** adult showing its antennae and eyes. Photo by Jérôme Albre, with permission.

Figure 77. ***Aricia agestis*** larva, a species that disappears when bryophytes disappear from its habitat. Photo by Jérôme Albre, with permission.

Figure 78. ***Issoria lathonia*** larva, a species that seems to depend on mosses in the dunes. Photo by Wolfgang Wagner, with permission.

Figure 79. ***Issoria lathonia*** adult, a species that disappears when dune mosses are replaced by grasses. Photo by Korall, through Creative Commons.

Schtickzelle and Baguette (2004) expressed the importance of demographic parameters in fragmented landscapes. For the bog fritillary butterfly (***Proclossiana eunomia*** – **Nymphalidae**; Figure 80), a specialist glacial relict, density dependence seemed to be related to parasitism of the larvae. Dispersal was dependent on the ability to move between patches of suitable bog habitat.

Hence, destruction of bogs can easily lead to the demise of this species, in part due to crowding and increased parasitism.

Figure 80. ***Proclossiana eunomia***, a bog dweller. Photo by Gilles San Martin, through Creative Commons.

Because of their vulnerability due to changes in drainage, bogs are disappearing habitats. Murdock (1994) claims that one-third of the threatened and endangered species in the USA live in wetlands. In the Southern Appalachian Mountains, USA, bogs and fens house many rare and unique species that occur in no other habitats. Among these is the rare Baltimore butterfly, ***Euphydryas phaeton*** (**Nymphalidae**; Figure 81-Figure 83).

Figure 81. ***Euphydryas phaeton*** (Baltimore butterfly) larva, a rare bog inhabitant in the Southern Appalachian Mountains, USA. Photo by Pennsylvania Department of Conservation and Natural Resources, through Creative Commons.

Figure 82. ***Euphydryas phaeton*** adult, a rare bog species in the Southern Appalachian Mountains, USA. Photo by Alison Hunter, through Creative Commons.

Figure 83. ***Euphydryas phaeton*** adult, a rare bog species. Photo by D. Gordon E. Robertson, through Creative Commons.

Many examples, such as those reported by Pescott *et al*. (2015), attest to the effect of changing air quality in causing the disappearance of bryophytes. They provided the first evidence for the indirect association between returning air quality and the increase of lichenivorous moths.

Changing climate can put life cycle stages out of sync. Food plants may mature at the wrong time for developing larvae. Males and females may respond to different stimuli, causing them to be ready for mating at different times. The Earth's mean global temperature has increased by about 0.6°C in the past century (Walther *et al*. 2002). Migrant butterflies are arriving at their spring destinations earlier and breeding earlier than times recorded before the 20th century. Bryophytes may play a role in retaining moisture as the climate dries.

Summary

The **Lepidoptera** are primarily plant eaters as larvae, and for some this includes bryophytes. This appears to be a relict trait from the early **Lepidoptera** that appeared at about the same time as bryophytes became abundant. Many of these bryophyte dwellers have similarities to their sister group, the **Trichoptera**, including case making, wings that rest like a pup tent, and hairs on the wings. Larvae often have appendages and coloration that help them to blend with the bryophytes. They are holometabolous, having eggs, larvae, pupae, and adults in their life cycle.

Pupae develop in bryophytes in some taxa. Adults use the bryophytes for resting sites, in some cases having coloration that camouflages them. Some lay their eggs among bryophytes. Butterflies are less represented than moths and few feed on them.

Although most of the lepidopteran bryophages eat the leaves, some are specialists on capsules. And some eat only liverworts, especially the thallose liverwort ***Conocephalum conicum***. Others specialize on epiphyllous bryophytes and some eat the periphyton on the bryophytes. But some bryophytes seem to be inedible, presenting terpenoids and other compounds that serve as chemical defense. A few larvae are carnivorous and ambush prey by resembling bryophytes and hiding there to attack.

Many of the bryophyte dwellers have poor or no flying ability and therefore have limited dispersal ability and distribution. This makes them susceptible to extinction as forests and bogs are destroyed. While peatlands can have a huge number of species, some of these are very rare and easily extirpated as these relict habitats disappear. Bog drainage, climate change, peat harvesting, pollution, and logging all contribute to the losses of these rare species.

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CHAPTER 12-13
TERRESTRIAL INSECTS: HOLOMETABOLA – LEPIDOPTERA: MICROPTERIGOIDEA – GELECHIOIDEA

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CHAPTER 12-13
TERRESTRIAL INSECTS: HOLOMETABOLA – LEPIDOPTERA: MICROPTERIGOIDEA – GELECHIOIDEA

Figure 1. Upper altitude limit of ***Sabatinca chrysargyra*** (**Micropterigidae**). Photo by George Gibbs, with permission.

MICROPTERIGOIDEA

Micropterigidae – Mandibulate Archaic Moths

As flowers rapidly expanded into numerous colors, sizes, and shapes, so did the **Lepidoptera** (see Powell *et al*. 1999). But these new flowers fed the adults, not the larvae.

This family is an ancient group, so it is not surprising that there are bryophyte specialists among them. Among these is the rarely collected ***Epimartyria*** sp. in the moth family **Micropterigidae** (Loren Russell pers. comm. Jan. 2008). The ***Epimartyria*** (Figure 11-Figure 16) larvae feed on ***Conocephalum conicum*** (Figure 2) and other liverworts in mountain springs, as well as on ***Pellia neesiana*** (Figure 3-Figure 4), the leafy liverworts ***Scapania bolanderi*** (Figure 5), and the ***Calypogeia-Riccardia*** association on logs, and once on ***Porella navicularis*** (Figure 6), an epiphyte.

Figure 2. ***Conocephalum conicum***, home and food source for members of ***Epimartyria***. Photo by Janice Glime.

Figure 3. ***Pellia neesiana*** showing the habitat that is home and food for ***Epimartyria*** larvae. Photo by C. & C. Johnson, with permission.

Figure 4. ***Pellia neesiana*** with antheridia, home and food for ***Epimartyria*** larvae. Photo by C. & C. Johnson, with permission.

Figure 5. ***Scapania bolanderi***, home and food for species of ***Epimartyria***. Photo by Matt Goff, with permission.

Figure 6. ***Porella navicularis***, home and food for species of ***Epimartyria***. Photo by Tonya Yoder, through Creative Commons.

In the lab, ***Epimartyria*** sp. survived feeding on ***Riccardia latifrons*** (Figure 7) and the leafy liverworts ***Calypogeia fissa*** (Figure 8), ***Jungermannia obovata*** (Figure 9), and ***J. rubra*** (Figure 10) (Loren Russell pers. comm. Jan. 2008). Russell found them to be most abundant in wet seepage zones with abundant ***Pellia neesiana*** and ***Conocephalum conicum***.

Figure 7. ***Riccardia latifrons***, food for species of ***Epimartyria***. Photo by Kristian Peters (Korseby Online), with permission.

Figure 8. ***Calypogeia fissa***, food for species of ***Epimartyria***. Photo by David T. Holyoak, with permission.

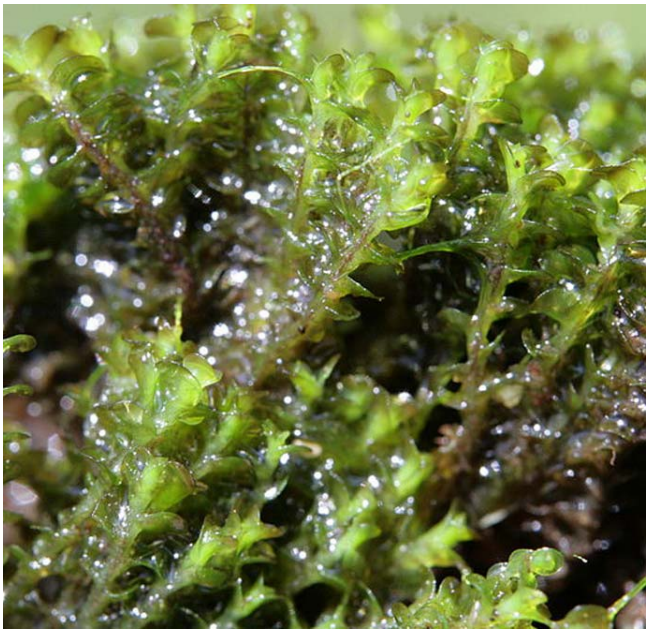

Figure 9. ***Jungermannia obovata***, food for species of ***Epimartyria***. Photo by Hermann Schachner, through Creative Commons.

Figure 10. ***Jungermannia rubra*** with perianth, food for species of ***Epimartyria***. Photo by Ken-Ichi Ueda, through Creative Commons.

In northeastern USA and Canada, ***Epimartyria auricrinella*** (Figure 11) lives in shaded locations of wet, swampy woods, boggy ditches, and streamsides where leafy liverworts are abundant (Gibbs 2010). One of its food plants is the leafy liverwort ***Bazzania trilobata*** (Figure 12-Figure 13) (Davis & Landry 2012). ***Epimartyria bimaculella*** (Figure 14), in the northwestern USA and Canada (Gibbs 2010), likewise feeds on leafy liverworts, including ***Lepidozia*** (Figure 15) (Davis & Landry 2012). Davis and Landry (2012) successfully reared them in the lab from larvae that were provided with only the leafy liverwort ***Jungermannia obovata*** (Figure 9). The larvae have a plastron mechanism (see Chapter 11-10) that permits them to survive short periods of flooding.

Figure 11. ***Epimartyria auricrinella*** adult, a species whose larvae live among and eat moist leafy liverworts. Photo by Jim Vargo, through Creative Commons.

Figure 12. ***Bazzania trilobata*** on a log where ***Epimartyria auricrinella*** was found. Photo by D. R. Davis and J.-F. Landry, through Creative Commons.

Figure 13. ***Bazzania trilobata***, home and food of ***Epimartyria auricrinella***. Photo by Michael Lüth, with permission.

Figure 14. ***Epimartyria bimaculella*** adult, a species whose larvae feed on leafy liverworts. Photo by Donald R. Davis and Jean-Francois Landry, through Creative Commons.

Figure 15. ***Lepidozia reptans***, home for ***Epimartyria bimaculella***. Photo by David T. Holyoak, with permission.

In 1989, Gibbs considered the **Micropterigidae** and **Mnesarchaeidae** to be similar in their habitats and seasonal requirements, often occurring together in New Zealand. But the **Micropterigidae** have a distribution around the Pacific rim, whereas the **Mnesarchaeidae** are endemic to New Zealand. Gibbs also considered the larvae of both families to live in the "periphyton layer" of their bryophytic habitat. In this often moist layer the larvae can find algae, bacteria, and fungi that provide suitable food.

The basal lineage of **Lepidoptera –** many as members of the **Micropterigidae –** continued their habit of feeding on cryptogams as larvae (Powell *et al*. 1999; Hashimoto 2006). Powell and coworkers pointed out that in East Asia there are about 25 endemic species that exclusively eat the thallose liverwort ***Conocephalum conicum*** (Figure 2). Nevertheless, the worldwide distribution of this family is patchy (Imada *et al*. 2011a). Its greatest species diversity is in Japan and Taiwan (greater than 25 spp.), New Caledonia (greater than 20 spp.), New Zealand (20 spp.), and Madagascar (ca 15 spp.) (Gibbs 2010). The **Micropterigidae** of Japan represent the largest radiation of herbivorous insects known from a single host taxon (Imada *et al*. 2011a).

Epimartyria pardella (Figure 16) is one such example of the dispersal limitations. This species lives in northern California to northern Oregon, USA (Tuskes & Smith 1984). Its flight is very sporadic, and on those occasions when it does fly, it fails to go more than 21 cm! These moths are day-active as adults and associate closely with liverworts [***Conocephalum*** (Figure 2) and ***Pellia*** (Figure 3-Figure 4)]. They frequent canyon walls and streamsides. When they are protected from the wind, they often perch on the upper surfaces of fern fronds, but always near liverworts. When it is windy or dry, they remain among the moist bryophytes such as ***Hookeria lucens*** (Figure 17), ***Atrichum undulatum*** (Figure 18), and ***Conocephalum conicum*** (Figure 2). But unlike the Japanese members of this family, larvae of this species prefer the thallose ***Pellia*** for food. Young larvae are active both day and night, but older larvae become night active. They typically do not damage the margin of the thallus. Instead, they feed on the underside of the thallus, removing it but not chewing through the upper surface.

Figure 16. ***Epimartyria pardella***, a dweller among moist bryophytes and liverwort feeder with limited dispersal ability. Photo by Donald R. Davis and Jean-Francois Landry, through Creative Commons.

Figure 17. ***Hookeria lucens*** with capsules, habitat for ***Epimartyria pardella***. Photo by Matt Goff <www.sitkanature.org>, with permission.

Figure 18. ***Atrichum undulatum*** with capsules, habitat for ***Epimartyria pardella***. Photo by Mejdlowiki, through Creative Commons.

The poor dispersal ability of this group with its limited flying ability has created localized populations where the liverwort is available, creating geographic isolation that has resulted in this high diversity of endemic ***Conocephalum*** (Figure 2, Figure 19) specialists. In fact, larvae of the modern species in this family feed on either detritus or bryophytes (Kristensen 1999; Powell & Opler 2009).

The **Micropterigidae** in Japan illustrate the species radiation of this family, and it goes beyond ***Epimartyria***. In the Japanese archipelago, 17 species of **Micropterigidae** are present (Hashimoto 2006). These species are typical of moist riverine environments, a habitat suitable for lush growths of bryophytes and ferns. Kobayashi and Ando (1981) demonstrated that both larvae and eggs of ***Neomicropteryx nipponensis*** (Figure 19-Figure 21) are easily harmed by drought stress. Four [***Palaeomicroides*** (Figure 21), ***Neomicropteryx***, ***Kurokopteryx*** (Figure 22), ***Issikiomartyria*** (Figure 23)] of these five genera feed exclusively on ***Conocephalum conicum*** (Figure 2) (Yasuda 1962; Imada *et al*. 2011a). This is in habitats where as many as 14 other bryophyte species commonly co-occur. It is interesting that despite their specificity on this species, these larvae do not discriminate (Imada *et al.* 2011b) among the three cryptospecies (Akiyama & Hiraoka 1994; Miwa *et al*. 2009) of ***C. conicum***. Only ***Paramartyria*** (Figure 24) uses several liverworts as food: ***Makinoa crispata*** (Figure 25), ***Heteroscyphus coalitus*** (Figure 26), and ***Conocephalum conicum***.

Figure 19. ***Neomicropteryx nipponensis*** larva feeding on ***Conocephalum conicum***. Note the darkened necrotic areas where the outer cells have been removed. Photo by Yume Imada, with permission.

Figure 20. ***Neomicropteryx nipponens*** adult, a species whose larvae eat ***Conocephalum conicum***. Photo by Yume Imada, with permission.

Figure 21. ***Palaeomicroides obscurella*** adult, a species whose larvae feed exclusively on ***Conocephalum conicum***. Photo from BIO Photography Group, Biodiversity Institute, Ontario, through Creative Commons.

Figure 22. ***Kurokopteryx dolichocerata*** adult, a genus whose larvae feed exclusively on ***Conocephalum conicum***. Here the adult is resting on that liverwort. Photo by Yume Imada, with permission.

Figure 23. ***Issikiomartyria*** sp. adult, a genus whose larvae feed exclusively on ***Conocephalum conicum***. Photo by Yume Imada, through Creative Commons.

Figure 24. ***Paramartyria semifasciella*** adult, in a genus that feeds on several species of thallose liverworts. Photo by Yume Imada, through Creative Commons.

Figure 25. ***Makinoa crispata***, food for larvae of ***Paramartyria***. Photo through Creative Commons.

These genera are spatially separated (**allopatric**) (Imada *et al*. 2011a; Imada & Kato 2018). Among these, ***Issikiomartyria*** (Figure 23) occurs only in the snow-rich area facing the Sea of Japan. ***Kurokopteryx*** (Figure 22) occurs only in south central Japan, facing the northwest Pacific Ocean. Yet their diets are the same, representing the "largest radiation of herbivorous insects that does not accompany any apparent niche differentiation" (Powell *et al*. 1999). These five genera [***Palaeomicroides*** (Figure 21), ***Neomicropteryx*** (Figure 19-Figure 20), ***Kurokopteryx*** (Figure 22), ***Issikiomartyria*** (Figure 23)**,** ***Paramartyria*** (Figure 24)] of larvae feed on the thalli of ***Conocephalum conicum*** (Figure 2) by grazing the surface, with no apparent differences in feeding mode among these micropterigid species (Imada *et al*. 2011a).

Figure 26. ***Heteroscyphus coalitus***, food for larvae of ***Paramartyria***. Photo by Jiadong Yang, through Creative Commons.

In Japan and New Caledonia, the larvae of the endemic ***Sabatinca*** live (Harris 2012) and feed on bryophytes (Figure 1) (Yasuda 1962; Holloway 1993). ***Sabatinca*** larvae have cryptic coloration that is greenish with large setae that help to camouflage them among the liverworts (Tillyard 1922). On Mt. Cargill, N. Z., ***Sabatinca quadrijuga*** (Figure 27-Figure 28) lives on leafy liverworts as larvae (Harris 2015). Most of the adults of ***Sabatinca*** are day-active and feed mostly on fern spores, but they also eat club moss (Lycopodiaceae) spores or pollen from sedges and other flowers (Gibbs & Lees 2014). The adult still has an affinity for bryophytes, however. It "hops" around on the mosses on rocks (flying close to the ground), but only when the sun is shining (Harris 2015).

Figure 27. ***Sabatinca quadrijuga*** eggs. This species is a leafy liverwort inhabitant and feeder. Photo by George Gibbs, with permission.

Figure 28. ***Sabatinca quadrijuga*** adult, a species that lives among and eats liverworts as larvae and hops around on mosses as an adult. Photo by George Gibbs, with permission.

Sabatinca caustica (Figure 29-Figure 31) illustrates the bryophytic adaptations of this genus. The hunch-backed caterpillars (Figure 29) are camouflaged by their pigments (Gibbs & Lees 2014). Like all members of ***Sabatinca***, they feed on leafy liverworts and are known as **exposed feeders** because they feed on the surface.

Figure 29. ***Sabatinca caustica*** larva, illustrating bryophytic adaptations. Note the hunched back, bryophytic coloring, and projections that resemble bryophyte leaves. Photo by George Gibbs, with permission.

Figure 30. ***Sabatinca caustica*** adult, a species whose larvae eat leafy liverworts. Photo by George Gibbs, with permission.

Figure 31. Habitat with mosses and liverworts where one can find ***Sabatinca caustica***. Photo by George Gibbs, with permission.

Gibbs (2014) described four new species of ***Sabatinca*** in New Zealand. All 19 of the New Zealand species are confirmed liverwort feeders. The life cycle of this genus is typically annual. Larvae grow throughout the winter and the pupal stage is short. The larvae exhibit cryptic coloration (Figure 32), but the adults instead often have brilliant iridescent colors (Figure 33, Figure 36, Figure 38). Nevertheless, the adult coloration helps to conceal these small moths in the spotty light of their wooded and streamside habitats. ***Sabatinca calliarcha*** (Figure 32-Figure 33) and ***S. doroxena*** (Figure 35-Figure 36), and a number of other ***Sabatinca*** species, exhibit on the upper forewing (at rest) a black patch with several brilliant white spots in it (Figure 33, Figure 36). Gibbs speculated that these might serve as mimics of one of their main predators, a jumping spider in the **Salticidae** (Figure 34).

Figure 32. ***Sabatinca calliarcha*** larva showing adaptations to the bryophyte habitat, shown here on a leafy liverwort. Photo by George Gibbs, with permission.

Figure 33. ***Sabatinca calliarcha*** adult showing black area with white spots on wings. Photo by George Gibbs, with permission.

Figure 34. ***Maratus volans*** (**Salticidae**) showing color patterns and black spots (eyes) that seem to be mimicked by some species of ***Sabatinca***. Photo by Jurgen Otto, with permission.

Gibbs (2014) was able to name specific larval hosts, mostly leafy liverworts, for a number of the New Zealand ***Sabatinca*** (Table 1). Larvae of ***Sabatinca*** on ***Plagiochila*** not only feed there, but they roll the leaves or otherwise use them to form a cocoon (David Glenny, pers. comm.; Figure 45).

Figure 35. ***Sabatinca doroxena*** larva, a recently described liverwort feeder from streamsides in New Zealand. Photo by George Gibbs, with permission.

Figure 36. ***Sabatinca doroxena*** adults copulating, a recently described liverwort dweller from streamsides in New Zealand. Photo by George Gibbs, with permission.

Table 1. Larval hosts for some of the New Zealand members of ***Sabatinca***, based on Gibbs (2014).

S. aurella	Figure 37-Figure 38	*Heteroscyphus normalis* possibly *Plagiochila intertexta*	Figure 39
S. bimacula	Figure 40	*Bazzania involuta*	
S. chalcophanes	Figure 41	*Hymenophyton flabellatum*	Figure 42-Figure 43
		variety of foliose liverworts	Figure 43
S. doroxena	Figure 35-Figure 36	*Heteroscyphus normalis*	Figure 39
S. heighwayi	Figure 45-Figure 47	*Plagiochila circumcincta*	Figure 48
S. weheka	Figure 49-Figure 50	*Plagiochila deltoidea*	Figure 51-Figure 53

Figure 37. ***Sabatinca aurella*** larva on a leafy liverwort. Photo by George Gibbs, with permission.

Figure 38. ***Sabatinca aurella*** adult, a species whose larvae feed on ***Heteroscyphus normalis***. Photo by George Gibbs, with permission.

Figure 39. ***Heteroscyphus*** cf. ***normalis***, a leafy liverwort eaten by ***Sabatinca aurella*** larvae. Photo by Andrew Hodgson, with permission.

Figure 40. ***Sabatinca bimacula*** larva, a species that lives on ***Bazzania involuta***. Photo by George Gibbs, with permission.

Figure 41. ***Sabatinca chalcophanes*** adult, a liverwort feeder as larvae. Photo by Neville Hudson, through Public Domain.

Figure 42. ***Hymenophyton flabellatum***, home and food for ***Sabatinca chalcophanes***. Photo by Niels Klazenga, with permission.

Figure 43. ***Sabatinca*** habitat where one can find ***S. aurantissima*** (Figure 44), ***S. aurella***, ***S. aemula***, ***S. chalcophanes***. Photo by George Gibbs, with permission.

Figure 44. ***Sabatinca aurantissima*** larva, an inhabitant of bryophytes. Photo by George Gibbs, with permission.

Figure 45. Pupa of ***Sabatinca heighwayi*** showing leaves of ***Plagiochila*** cf. ***fasciculata***. Photo by George Gibbs, with permission.

Figure 46. Pupa of ***Sabatinca heighwayi*** removed from its cocoon. Photo by George Gibbs, with permission.

Figure 47. ***Sabatinca heighwayi*** male adult, a species whose larvae feed on ***Plagiochila circumcincta***. Photo by George Gibbs, with permission.

Figure 48. ***Sabatinca*** habitat with ***Plagiochila circumcincta***, host of ***S. heighwei***. Photo by George Gibbs, with permission.

Figure 49. ***Sabatinca weheka*** larva, a species that feeds on ***Plagiochila deltoidea***. Photo by George Gibbs, with permission.

Figure 50. ***Sabatinca weheka*** male adult, a species whose larvae feed on ***Plagiochila deltoidea***. Photo by George Gibbs, with permission.

Figure 51. ***Plagiochila deltoidea***, host of ***Sabatinca weheka***. Photo by George Gibbs, with permission.

Figure 52. ***Plagiochila deltoidea***, food and home for ***Sabatinca weheka***. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Figure 53. ***Sabatinca*** habitat where one can find ***S. weheka***, ***S. aurella, S. chrysargyra*** (Figure 54), and ***S. chalcophanes*** in New Zealand. Photo by George Gibbs, with permission.

Figure 54. ***Sabatinca chrysargyra*** larva on ***Plagiochila***. Photo by George Gibbs, with permission.

But not all members of the **Micropterigidae** are bryophyte feeders. Some are not able to eat bryophytes and choose other food sources (Lorenz 1961; Luff 1964). Instead, these larvae eat fungi, detritus, and flowering plant green leaves (Kristensen 1998). For example, ***Micropterix calthella*** (Figure 55) and ***M. aruncella*** (Figure 56-Figure 57) ate the flowering plant *Stellaria* spp. in the lab and refused both mosses and liverworts (Carter & Dugdale 1982). But Shield (1856) recorded them from mosses and Meyrick (1895) found that both live on wet mosses in the British Isles, claiming that the genus feeds on mosses. Likewise, Chapman (1894) found that they eat mosses. Later, Coutin (2004b) stated that the larvae of ***M. calthella*** feed on mosses and liverworts. Perhaps they are choosy about the mosses they eat.

Figure 55. ***Micropterix calthella*** adult, a member of **Micropterigidae** whose larvae bryophytes sometimes, but refuse them at other times. Photo by Tom Deroover, through Creative Commons.

Figure 56. ***Micropterix aruncella*** adult, a species of ***Micropterix*** that sometimes refuses to feed on bryophytes. Photo by Marko Mutanen, no rights reserved.

Figure 57. ***Micropterix aruncella*** adult, a species of ***Micropterix*** may eat bryophytes but at other times refuses to feed on them. Photo by Marko Mutanen, no rights reserved.

Gibbs (1983) noted that in Australia the evolution of the **Micropterigidae** is paralleled by the evolution of the eastern Australian rainforests. In other locations, particularly in New Caledonia, the developing lineages seem to mirror the development or disappearance of different land masses.

Recently, Imada and Kato (2018) discovered four new species of ***Issikiomartyria*** [***I. catapasta*** (Figure 58), ***I. hyperborea***, ***I. leptobelos***, ***I. trochos*** (Figure 59-Figure 60)], and a new genus (***Melinopteryx***) in the subalpine zone in Japan. These species of ***Issikiomartyria*** and the new ***Melinopteryx bilobata*** (Figure 61) are all associated with ***Conocephalum conicum***, which serves as the food source for larvae. How many more undescribed species and genera are hiding inside liverwort thalli?

Figure 58. ***Issikiomartyria catapasta*** adult; larvae feed on ***Conocephalum conicum***, Tachimata-keikoku, Akita Pref., Japan. Photo by Yume Imada, with permission.

Figure 59. ***Issikiomartyria trochos*** adult, a new species whose larvae feed on ***Conocephalum conicum*** at Mahirudake-rindo, Iwate Pref., Japan. Photo by Yume Imada, with permission.

Figure 60. ***Issikiomartyria trochos***, a new species whose larvae feed on ***Conocephalum conicum*** at Jintsu-kyo, Yamagata Pref., Japan. Photo by Yume Imada, with permission.

Figure 61. ***Melinopteryx bilobata*** adult, a new species whose larvae feed on ***Conocephalum conicum*** at Ushikubi-touge, Shizuoka Pref., Japan. Photo by Yume Imada, with permission.

MNESARCHAEOIDEA

Mnesarchaeidae – New Zealand Primitive Moths

When the **Micropterigidae** emerged, the New Zealand endemic **Mnesarchaeidae** likewise was becoming established. ***Mnesarchaea acuta*** (Figure 62) can occur in large numbers on the damp moss-covered banks of streams in a variety of New Zealand forests and at a wide range of altitudes (Gibbs 1979). But it is the **periphyton** (algae and **Cyanobacteria** – Figure 63) layer on the mosses and liverworts that serves as their food. Their fecal matter indicates that they ingest pieces of both live and dead moss leaves, liverwort leaves and rhizoids, fern sporangia, fungal spores and hyphae, and filamentous algae. This is an unusually diverse diet for any lepidopteran. When the females are placed in vials with sufficient periphyton on mosses and liverworts, ***M. loxoscia*** (Figure 64) and ***M. acuta*** lay their eggs on the bryophytes. The suitable bryophytes live on rotting logs, tree trunks, and soil in the damp portions of the forests.

Figure 62. ***Mnesarchaea acuta***, a species with larvae that eat the algae and **Cyanobacteria** on the bryophytes and adults lay their eggs there. Photo by George Gibbs, with permission.

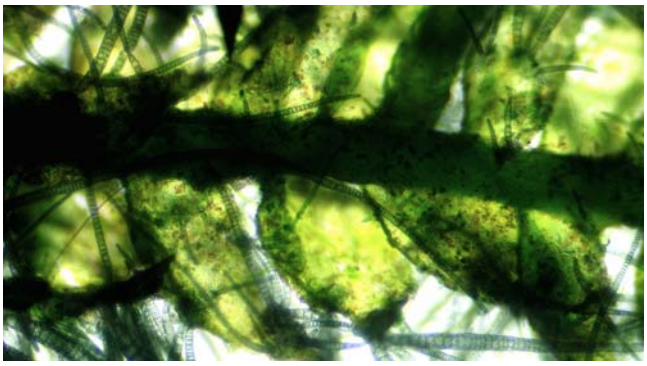

Figure 63. **Cyanobacteria** on moss, food for ***Mnesarchaea acuta***. Photo by Nat Tarbox, through Creative Commons.

Figure 64. ***Mnesarchaea loxoscia***, a species whose larvae eat the algae and **Cyanobacteria** on the bryophytes and females lay their eggs there. Photo by George Gibbs, with permission.

HEPIALOIDEA

Hepialidae – Ghost Moths

The **Hepialidae** can be considered indicators of the ancient fauna of New Zealand (Patrick 1988). Their larvae are common in bogs among the mosses. They have poor dispersal ability because the females generally either have short wings or are reluctant to fly. Even with mobile males, reproduction in a distant location is not possible.

Grehan (1989) considered the mosses to be among the food sources for the **Hepialidae** larvae. Grehan suggested that this family was originally fungivorous (feeding on fungi) and that its change to primarily tracheophytes resulted from suppression of mycophagy. But in pastures and grassland species mosses may be important food sources, whereas liverworts seem to be ignored. Among these moss feeders is ***Korscheltellus gracilis*** (Figure 65-Figure 67) (Brower 1984). Larvae of this species feed above ground in thick mosses.

Figure 65. ***Korscheltellus gracilis*** larva, a species where larvae feed above ground under mosses. Photo by Johnathan Leonard, with permission.

Figure 66. ***Korscheltellus gracilis*** host tree where larvae live under mosses. Photo by John Grehan, with permission.

Larvae of ***Korscheltellus gracilis*** (Figure 65) typically take two years to mature, following an egg development of 16-19 days at 22°C. Pupation occurs on the forest floor in the second year. These require another month to develop before the adult (Figure 67) emerges. It is the larval stage that is of interest to us. These larvae are **polyphagous** – that is, they eat a variety of foods, including leaf litter, fungi, mosses, and below ground tissues of ferns and seed plants.

Figure 67. ***Korscheltellus gracilis*** adult, a species that emerges from pupae on the forest floor. Photo by Matthew Priebe, with permission for educational purposes.

Korscheltellus gracilis (Figure 65-Figure 67) has an interesting mating behavior that may give insight into other members of the family. Using wind tunnel experiments, Kuenen *et al*. (1994) found that when light intensity was reduced to 11-25 lux after a 16-hour photophase of 450 lux, females initiated wing fanning. Males downwind of them began wing fanning, rapid walking, or both, and flew upwind toward the female soon afterwards. If the hind wings of the females were removed, the fanning activity of the females failed to evoke a male response. Hence, Kuenen and coworkers concluded that the hind wings emit a pheromone that elicits the male's mating behavior.

Bogs seem to be the best site for bryophyte-feeding members of this family. ***Cladoxycanus*** (Figure 68) and ***Heloxycanus*** (Figure 78-Figure 79) both feed on cushion plants in bogs, including both mosses and tracheophytes (Dugdale 1994). ***Heloxycanus*** larvae eat other mosses as well as ***Sphagnum*** (Figure 69) by cutting the stems to create fragments. It would be interesting to see if this results in dispersal and establishment. ***Cladoxycanus*** larvae live at the margins of moss-covered bogs and seepages and feed by cropping the mosses. ***Cladoxycanus minos*** (Figure 68) larvae live in the bogs but also probably occupy mosses in adjoining forests. These two **Hepialidae** genera are restricted to bogs where they live deep in the ***Sphagnum*** and keep warm because the ***Sphagnum*** absorbs heat.

Figure 68. ***Cladoxycanus minos*** male adult, a bog inhabitant that lives in and feeds on cushion plants, including mosses. Photo by Landcare Research, Manaaki Whenua, with online permission.

For ***Cladoxycanus*** (Figure 68) and ***Heloxycanus*** (Figure 78-Figure 79) in New Zealand, growth form seems to be important in food choice. These two genera browse on both mosses and higher plants that have a cushion growth form in moss-bog communities (Dugdale 1994).

Figure 69. ***Sphagnum*** habitat of ***Heloxycanus patricki***. Photo by Hamish Patrick, with permission.

Larvae and pupae of ***Cladoxycanus*** (Figure 68) live in areas where the ***Sphagnum*** (Figure 69) is harvested and the larvae contribute to cropping the moss, as do ***Heloxycanus*** (Figure 78-Figure 79) species (Patrick *et al*. 1987; Barratt *et al*. 1990). Both cut the stems and fragment the ***Sphagnum*** in a way that could reduce its commercial value.

Larvae of soil and moss-inhabiting larvae in bogs in this family excavate a silk-lined shaft (Figure 71). Typically this shaft has side chambers where fecal pellets are stored, but in ***Wiseana*** (Figure 73-Figure 75) (Barratt *et al*. 1990), ***Aoraia*** (Figure 70-Figure 71) (Grehan 1989), ***Oncopera brachyphylla*** (Figure 72) (in Australia; Elder 1970), and ***Eudalaca rufescens*** (in South Africa; Joubert 1975), another chamber may be used as a storage room for cut plant material. For those living in bogs [***Cladoxycanus*** (Figure 68) and ***Heloxycanus*** (Figure 78-Figure 79)] the ***Sphagnum*** (Figure 69) surface absorbs radiant heat and larvae spend the daytime up in that warm chamber. These bog dwellers have larval shafts that reach or even penetrate the water surface (Grehan & Patrick 1984). ***Cladoxycanus minos*** (Figure 68) occurs in water as deep as 300 mm and eats ***Sphagnum cristatum*** (Figure 76) (Grehan & Patrick 1984). A similar construction is present for ***Wiseana umbraculata*** (Figure 74-Figure 75) (Dugdale 1994). This permits it to avoid submersion during high water levels; this species is only known from saturated mosses where it is in relatively close contact with the soil surface (Grehan & Patrick 1984).

Figure 70. ***Aoraia enysii*** female adult, member of a genus that makes side chambers in its tunnels in bogs. Photo by Birgit E. Rhode, Landcare Research, with permission for non-commercial educational use.

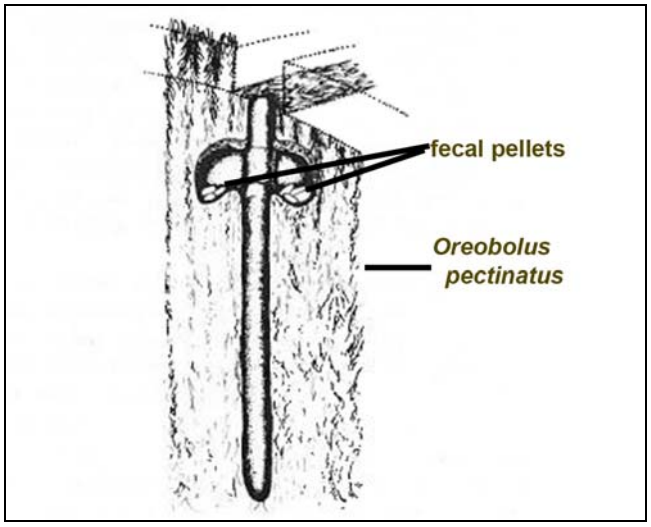

Figure 71. ***Aoraia*** sp. tunnel under ***Oreobolus pectinatus*** in bog showing chambers where fecal pellets are deposited. Modified from Grehan 1989.

Figure 72. ***Oncopera brachyphylla*** female adult, a species whose larvae excavate tunnels in the sedges (*Oreobolus pectinatus*) of bogs. Photo by John Grehan, with permission.

Figure 73. ***Wiseana*** larva, a genus that lives among mosses. Photo by Phil Bendle, with permission from John Grehan.

Figure 74. ***Wiseana umbraculata*** female adult; larvae often live among mosses. Photo from Landcare Research, Manaaki Whenua, with online permission.

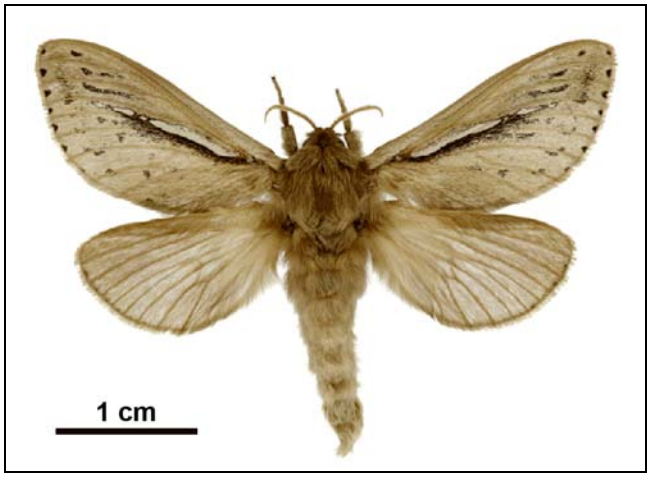

Figure 75. ***Wiseana umbraculata*** male adult; larvae often live among mosses. Photo from Landcare Research, Manaaki Whenua, with permission.

Figure 76. ***Sphagnum cristatum***, a species consumed by ***Cladoxycanus minos*** in New Zealand. Photo by Jan-Peter Frahm, with permission.

Wiseana (Figure 73-Figure 75) lives among litter and mosses and has a predator in the beetle family **Staphylinidae** (Eyles 1966). This beetle, ***Thyreocephalus chloropterus*** (Figure 77), attacks the ***Wiseana*** and sucks out its fluids. Some of the ***Wiseana*** larvae may be killed to protect the beetle eggs. Both live in a habitat with plant litter and mosses and are often associated with ants.

Figure 77. ***Thyreocephalus chloropterus***, a beetle that attacks ***Wiseana*** larvae to suck out its fluids. Photo by Ken Walker, Living Atlas of Australia, through Creative Commons.

Heloxycanus patricki (Figure 78-Figure 79) is a New Zealand ghost moth that feeds on ***Sphagnum*** (Figure 78-Figure 79) (Hamish 2011). It is an endemic and is in danger of extinction as its habitat has become severely fragmented and further suffers from collection for horticulture. Its adults disappear in even-numbered years, presumably indicating that the larvae require two years to develop.

Figure 78. ***Heloxycanus patricki*** adult on ***Sphagnum***, its larval food source. Photo by Hamish Patrick, with permission.

Figure 79. ***Heloxycanus patricki*** adult on ***Sphagnum***. Photo by Hamish Patrick, with permission.

Many of the bryophyte-dwelling larvae in **Hepialidae** spin a web in which they feed or pupate, or both (Figure 80). The larvae of the borer ***Aenetus virescens*** (Figure 81-Figure 85) live on trees (Grehan 1983). The larva enters its host by positioning itself axially with its head uppermost. It then places silk threads over itself, fastening them to the bark to form a roughly oval web that covers the larva. The larva is still visible through the cover at this stage. Sometimes the larva does this from within a depression so that the cover is nearly flat with the substrate surface. Once this cover is completed, the larva removes the mosses and lichens growing on the surface and places these particles inside the web. This task completed, the larva begins construction of the feeding tunnel by excavating the bark and wood tissue under the top part of the web. These fragments likewise are placed within the net cover, creating a cover that completely hides the larva inside. This chamber becomes filled with wood chips, causing the larva to make an inner silk lining to form a bag-like cavity extending from the entrance to the tunnel. Fecal pellets are placed in the lower third of the cover. ***Aenetus virescens*** larvae (Figure 81, Figure 83) feed primarily on the fruiting bodies of eight species of wood-inhabiting fungi (Grehan 1984).

Figure 80. Insect pupa inside its web, Kyushu, Japan. Photo by Janice Glime.

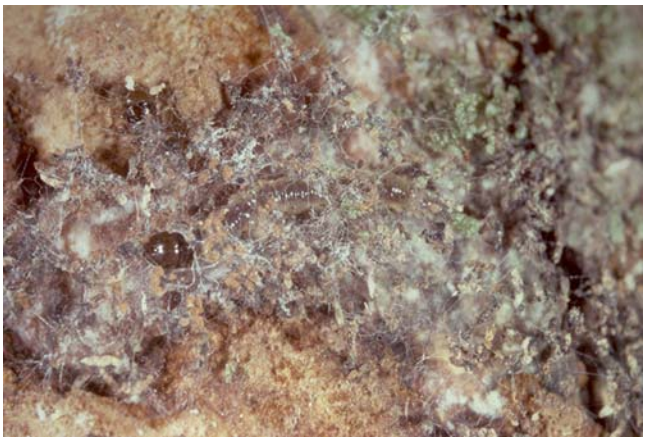

Figure 81. ***Aenetus virescens*** first instar feeding on fungus. Photo by John Grehan, with permission.

Figure 82. ***Aenetus virescens*** new tunnel under moss. Photo by John Grehan, with permission.

Figure 83. ***Aenetus virescens*** tunnel in ***Nothofagus***. Photo by John Grehan, with permission.

Figure 84. ***Aenetus virescens*** litter of frass pellets. Photo by John Grehan, with permission.

Figure 85. ***Aenetus virescens*** adult emerging. Photo by Nga Manu Images NZ, through Creative Commons.

Aoraia macropis (Figure 86) has been collected from mosses (Dugdale 1994), including those larvae that build shafts in ***Sphagnum*** (Figure 68) peat (Grehan 1989). Females of this species are **brachypterous** (short-winged), but males are able to fly. This arrangement suggests limited dispersal and brachyptery seems to be a common characteristic for bryophyte-dwelling insects. The genus is endemic to New Zealand.

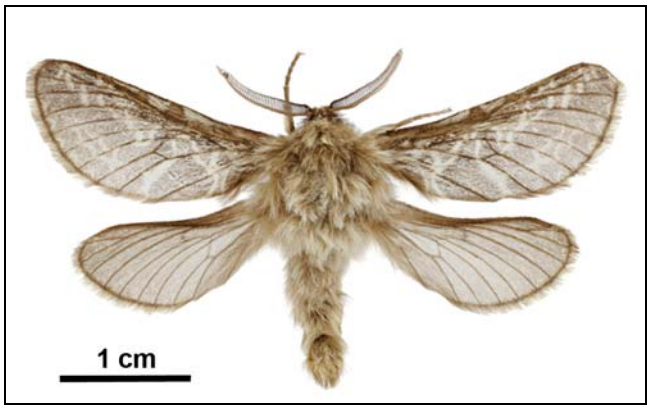

Figure 86. ***Aoraia macropis*** male adult, a moss dweller that builds shafts in ***Sphagnum***. Photo by Birgit E. Rhode, Landcare Research, for non-commercial educational use.

Phymatopus hecta (Figure 87) was originally reported as a feeder on dandelion (*Taraxacum*) (Stainton 1857). But Sterling and Heckford (2005) found the final three larval instars feed on the moss ***Mnium hornum*** (Figure 89-Figure 90) at the bases of oak trees. Later, Heckford and Stella Beavan found a larva that had spun its silken web over ***Mnium hornum*** in an open woodland (Grehan 2016). The larva lived in a tunnel in the soil, but it fed on the moss. They also succeeded in rearing the third instar larvae to adulthood with only ***Mnium hornum*** as a food source. Nevertheless, multiple records indicate that it is also a root feeder.

Figure 87. ***Phymatopus hecta*** larva amid mosses and litter in Ashurst Wood, Hampshire, U.K. This species feeds on ***Mnium hornum*** in the final larval instars. Photo © Stella Beavan and Bob Heckford, with permission.

Figure 88. ***Phymatopus hecta*** adult, a larval moss feeder. Photo by Stanislav Krejčík, through Creative Commons.

Figure 89. ***Mnium hornum*** on tree base, home for ***Phymatopus hecta*** larvae. Photo by Ján Jad'ud'. PERMISSION PENDING.

Figure 90. ***Mnium hornum***, home for ***Phymatopus hecta*** larvae. Photo by Tim Waters, through Creative Commons.

Palaeosetidae – Miniature Ghost Moths

Although their small size would suggest that bryophytes could make a suitable home for these ghost moths, few actually are known to live there. Heppner *et al*. (1995) has collected both males and females of ***Ogygioses caliginosa*** (Figure 91) that were congregating on mossy banks of streams where the mosses were kept wet. The larvae in the lab were provided a variety of food plants, but only the mosses appeared to be eaten. Surely there are other bryophyte associates in this family awaiting our discovery.

Figure 91. ***Ogygioses caliginosa*** adult, a species in which adults congregate on mosses and the larvae eat them. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

TINEOIDEA

Psychidae – Bagworm Moths, Case Moths

These moths construct cases or bags as larvae (Figure 92-Figure 93). These larvae are mobile, although they may attach when at rest. The bag is later used for pupation and at that time is attached to its substrate.

Figure 92. **Psychidae** case moth on moss. Photo courtesy of Sarah Lloyd.

Figure 93. **Psychidae** case moth on bryophytes, with lichen decorations on case. Photo courtesy of Sarah Lloyd.

Although the case moths usually occur with lichens and algal films, some feed on grass and a few feed on mosses. For example, Dugdale (1987) recommends beating low shrubs and branches covered by bryophytes in order to collect more larvae of ***Grypothec***a (Figure 94). Sapphire McFish (Bryonet 31 March 2016) reports accidentally collecting some of the case moth larvae in Tasmania. These were on mossy buttresses and logs in a wet forest gully. The larvae stuck 2-3 mosses in their cases in about the same proportions as the mosses appeared in the area. Among these was ***Thuidiopsis sparsa***.

Figure 94. ***Grypotheca triangularis***, a genus whose larvae live among bryophytes on low shrubs and branches. Picture from America Pink, with online permission for educational use.

Dincă (2005) surveyed the **Macrolepidoptera** at Istriţa Hill in Romania and found that ***Canephora hirsuta*** (Figure 95-Figure 97, a bryophyte feeder, occurs there.

Figure 95. ***Canephora hirsuta*** larva in case. This species eats bryophytes. Photo through Creative Commons.

Figure 96. ***Canephora hirsuta*** larva head, the head of a moss eater. Photo by Donald Hobern, through Creative Commons.

Figure 97. ***Canephora hirsuta*** adult, a species with larvae that feed on mosses. Photo by Jeroen Voogd <info @ butterflies-moths.com>, with permission.

Dr. Peter B. McQuillan of the University of Tasmania described a larva that may be a species of ***Narycia*** (Figure 98-Figure 99). This larva makes an "untidy case" near the ground. This seems to be an advantage in providing camouflage. The larvae include grasses and mosses and other small plants in their diet.

Figure 98. ***Narycia duplicella*** larva with a case adorned with lichens. Photo by Patrick Clement, with permission.

Figure 99. ***Narycia duplicella*** larva with grey lichens adorning its case, blending with the grey lichens on the substrate. Photo by Jeroen Voogd <info@butterflies-moths.com>, with permission.

Tineidae – Fungus Moths

Tinea (Figure 100-Figure 101) is a stone mason caterpillar. The larvae cement together grains of stone, including small fragments of mosses and lichens (Rennie 1857; Zagulyayev 1970). This encasement is carried around much like the cases of the caddisflies.

Figure 100. ***Tinea pellionella*** larva in case that earned it the name of stone mason. Photo from ©entomart, through Creative Commons.

Figure 101. ***Tinea pellionella*** adult; larvae sometimes incorporate bryophytes in their cases. Photo from ©entomart, through Creative Commons.

Klok and Chown (1997) looked at temperature tolerance in a member of this family. Using ***Pringleophaga marioni*** (Figure 102), they found that this moth had a tolerance range from -0.6°C to 38.7°C, a range it might encounter on any day in its larval life in the sub-Antarctic Marion Island. These larvae are able to supercool to -5.0°C, with 100% of the caterpillars surviving freezing to -6.5°C. Their high temperature survival, however, was poor at 35°C and above. Larvae of this species have no osmoregulatory ability. Klok and Chown suggest that they are able to survive by living in damp situations.

Figure 102. ***Pringleophaga marioni*** adult, a sub-Antarctic species that tolerates temperatures to -6.5°C as larvae. Note reduced wings that seem to characterize many moss dwellers. Photo by Steven L. Chown, through Creative Commons.

Pringleophaga marioni (Figure 102) is a decomposer (Sinclair *et al*. 2004). It often nests in old albatross nests (Haupt *et al*. 2014). Haupt *et al*. suggested that the moths might select habitats that meet their thermal requirements. They choose newly abandoned nests of the Wandering Albatross (*Diomedea exulans*) more frequently than other habitats. But nests are short-lived, so other resources seem to be important. The researchers looked for possible chemosensory and thermal cues among choices in the laboratory, but they found no significant difference in larval preferences for newly abandoned nest material over old nests, the common mire moss ***Sanionia uncinata*** (Figure 104-Figure 103), or no choice. Larvae commonly occur in this mire moss species (Burger 1978). Although the larvae preferred lower temperatures (5°C) over higher ones (15°C), the researchers concluded that temperature and chemical cues were not the basis for the choice of substrate materials. Furthermore, the caterpillars apparently do not seek the materials that compose the nests, but rather avoid high temperatures.

Figure 103. ***Sanionia uncinata*** with capsules, nest material for ***Pringleophaga marioni***. Photo by David T. Holyoak, with permission.

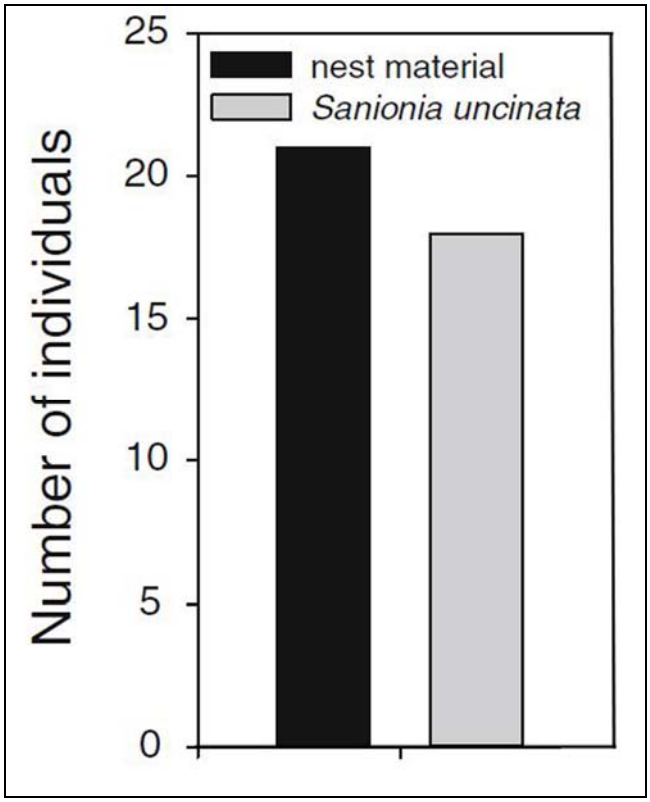

Figure 104. ***Pringleophaga marioni*** (Figure 102) choice of bird nest material vs the moss ***Sanionia uncinata*** (Figure 103) for their nests. Adapted from Haupt *et al.* 2014.

GELECHIOIDEA

Gelechiidae – Twirler Moths

This is one of the largest families of **Microlepidoptera** (Powell 1980). They are common in north temperate zones and use mosses and liverworts as their larval food. However, the family includes leaf and needle miners, gall makers, and scavengers. Of these 2% of the records of food are from mosses (18 records). Fewer than 2% of the larvae have multiple host plant species.

The **Gelechiidae** are characterized by being concealed while feeding. Some accomplish this by feeding within tracheophyte leaf tissue. The bryophyte feeders seem to accomplish this by hiding under bark or bryophytes, or by creating their own cover (*e.g.* ***Bryotropha umbrosella*** – Figure 105) by making silken tubes or tents (Fernández-Triana *et al*. 2013). Unfortunately, these do not protect them from the parasite ***Shireplitis*** spp. (**Hymenoptera: Braconidae**; Figure 106) that uses this caterpillar as a host (Fernández-Triana *et al*. 2013).

Kullberg *et al*. (2013) lamented that we know little about the role of mosses for the many **Lepidoptera** species living in the Arctic tundra of European Russia. Yet ***Bryotropha*** (*e.g.* Figure 105-Figure 107; originally considered part of ***Gelechia***) is one of the most common **Gelechiidae** in the Holarctic (Rutten & Karsholt 2004). The genus ***Bryotropha*** is among the relatively few **Lepidoptera** known to feed on bryophytes, especially mosses (Heckford & Sterling 2002, 2003; Rutten & Karsholt 2004).

Figure 105. ***Bryotropha umbrosella*** adult, a larval moss dweller that is subject to parasitism by **Braconidae**. Photo by Janet Graham, through Creative Commons.

Figure 106. ***Shireplitis bilboi*** adult, member of a genus that is parasitic on ***Bryotropha umbrosella***. Photo through Creative Commons.

Kullberg and coworkers (2013) were able to report that ***Bryotropha galbanella*** (Figure 107) lives on mosses. In Europe, this species lives on the mosses ***Dicranum scoparium*** (Figure 108) and ***Homalothecium lutescens*** (Figure 109) as its food source (Rutten & Karsholt 2004). In 1856, Shield reported ***Bryotropha desertella*** (Figure 110-Figure 111) and ***B. umbrosella*** (=***B. mundella***; Figure 105) from among bryophytes on sandhills in Europe.

Figure 107. ***Bryotropha galbanella*** adult, a species whose larvae live among mosses and eat them. Photo by Roy Leverton, with permission.

Figure 108. ***Dicranum scoparium***, home and food for ***Bryotropha galbanella***. Photo by Dale Vitt, with permission.

Figure 109. ***Homalothecium lutescens***, home and food for ***Bryotropha galbanella***. Photo by Michael Lüth, with permission.

Figure 110. ***Bryotropha desertella*** larva on moss, a common substrate for it. Photo by R. J. Heckford, with permission.

In the Netherlands, one can often collect large numbers of adults of these drab ***Bryotropha*** moths (*e.g.* Figure 112, Figure 115-Figure 117, Figure 119-Figure 120) (Rutten 1999). Most of them occur in open heaths and dunes, some in forests or urban areas. But all are thought to feed on mosses as larvae. ***Bryotropha basaltinella*** (Figure 112)

feeds on mosses, especially ***Syntrichia ruralis*** (Figure 113), on walls and thatched roofs (Britain – Meyrick 1895; Netherlands – Rutten 1999).

Figure 111. ***Bryotropha desertella*** adult on moss. Photo by Phil Boggis, with permission.

Figure 112. ***Bryotropha basaltinella*** adult, a species that lives among and eats mosses, including ***Syntrichia ruralis***, on roofs as a larva. Photo by Dick Belgers, through Creative Commons.

Figure 113. ***Syntrichia ruralis***, home and food for ***Bryotropha basaltinella***. Photo by Hermann Schachner, through Creative Commons.

Bryotropha affinis (Figure 114-Figure 115), ***B. senectella*** (Figure 116-Figure 117), and ***B. domestica*** (Figure 118-Figure 119) larvae feed on mosses on walls, but they make a silken gallery in which to live and move about, affording them cover and camouflage (Meyrick 1928; Rutten 1999). But for the Netherlands, Rutten was only able to list "possible" food plants for ***B. similis*** (Figure 120): ***Hypnum cupressiforme*** (Figure 121), ***Brachythecium rutabulum*** (Figure 122), ***Syntrichia ruralis*** (Figure 113), ***S. montana*** (Figure 123), ***Grimmia pulvinata*** (Figure 124), ***Rosulabryum capillare*** (Figure 125), and ***Bryum caespititium*** (Figure 126) (see also Stainton 1871). Only ***Bryotropha basaltinella*** has a preference for urban areas, the location of most of the walls covered with mosses. Rutten reminds us that it is easier to locate the larvae on wall mosses and that in non-urban areas the adults are abundant in dry areas with no mosses.

Figure 114. ***Bryotropha affinis*** larva, a species that makes its silken feeding tunnels on mosses on walls. Photo through Public Domain.

Figure 115. ***Bryotropha affinis*** adult, a moss dweller in its larval state. Photo by Patrick Clement, with permission.

Figure 116. ***Bryotropha senectella*** adult, gray form, a species whose larvae make their silken feeding tunnels on mosses on walls. Photo by Patrick Clement, with permission.

Figure 117. ***Bryotropha senectella*** adult, brown form, a species whose larvae make their silken feeding tunnels on mosses on walls. Photo by Patrick Clement, with permission.

Figure 118. ***Bryotropha domestica*** larva, a species whose larvae make their silken feeding tunnels on mosses on walls. Photo through Public Domain.

Figure 119. ***Bryotropha domestica*** adult, a species whose larvae make their silken feeding tunnels on mosses on walls. Photo by Patrick Clement, with permission.

Figure 120. ***Bryotropha similis*** adult, a species whose larvae make their silken feeding tunnels on mosses on walls. Photo by Janet Graham, through Creative Commons.

Figure 121. ***Hypnum cupressiforme***, home and food for ***Bryotropha similis***. Photo by J. C. Schou, Biopix, with permission.

Figure 122. ***Brachythecium rutabulum*** with capsules, home and food for ***Bryotropha similis***. Photo by J. C. Schou <www.biopix.com>, with permission.

Figure 123. ***Syntrichia montana***, home and food for ***Bryotropha similis***. Photo by Michael Lüth, with permission.

Figure 124. ***Grimmia pulvinata*** on wall, home and food for ***Bryotropha similis***. Photo by J. C. Schou, Biopix, through Creative Commons.

Figure 125. ***Rosulabryum capillare*** with capsules, home and food for ***Bryotropha similis***. Photo through Creative Commons.

Figure 126. ***Bryum caespiticium***, home and food for ***Bryotropha similis***, with capsules. Photo by Michael Lüth, with permission.

In Europe, the silken feeding tubes of ***Bryotropha boreella*** (Figure 127-Figure 129) occur on species such as ***Hypnum jutlandicum*** (Figure 130), ***Rhytidiadelphus squarrosus*** (Figure 131), and ***Aulacomnium palustre*** (Figure 132) (Palmer 2016). All of these species are also suitable for breeding ***B. boreella***.

Figure 127. ***Bryotropha boreella*** larva in its silken feeding tube on ***Rhytidiadelphus squarrosus***. Photo by R. J. Heckford, with permission.

Figure 128. ***Bryotropha boreella*** pupa among mosses. Photo by R. J. Heckford, with permission.

Figure 129. ***Bryotropha boreella*** adult on ***Sphagnum***. Photo by Stephen Palmer, with permission.

Figure 130. ***Hypnum jutlandicum*** with capsules, a moss where ***Bryotropha boreella*** builds silken feeding tubes. Photo by J. C. Schou, with permission.

Figure 131. ***Rhytidiadelphus squarrosus***, a moss where ***Bryotropha boreella*** builds silken feeding tubes. Photo by Michael Lüth, with permission.

Figure 132. ***Aulacomnium palustre***, a moss where ***Bryotropha boreella*** builds silken feeding tubes. Photo by Kristian Peters, with permission.

Bryotropha terrella (Figure 133-Figure 134) in the British Isles feeds on the moss ***Rhytidiadelphus squarrosus*** (Figure 131) and the grass *Agrostis capillaris* (Palmer & Palmer 2016b). But elsewhere in Europe it is also known from the mosses ***Syntrichia ruralis*** (=***S. ruraliformis***; Figure 113), ***Hypnum jutlandicum*** (Figure 130), and ***Calliergonella cuspidata*** (Figure 135). Early instars construct a tough, opaque silken tube low among moss or grass, the upper end reaching near the moss surface. The tube is covered with chewed moss fragments and bits of grass. But in the final instar, the larva makes a flimsy, transparent gallery with no attached plant material.

Figure 133. ***Bryotropha terrella*** larva, a species that includes mosses in its feeding tube until its last instar, shown here on ***Rhytidiadelphus squarrosus***. Photo by R. J. Heckford, with permission.

Figure 134. ***Bryotropha terrella*** adult, a species whose larvae live among mosses or at the base of grasses. Photo by Steve Palmer, with permission.

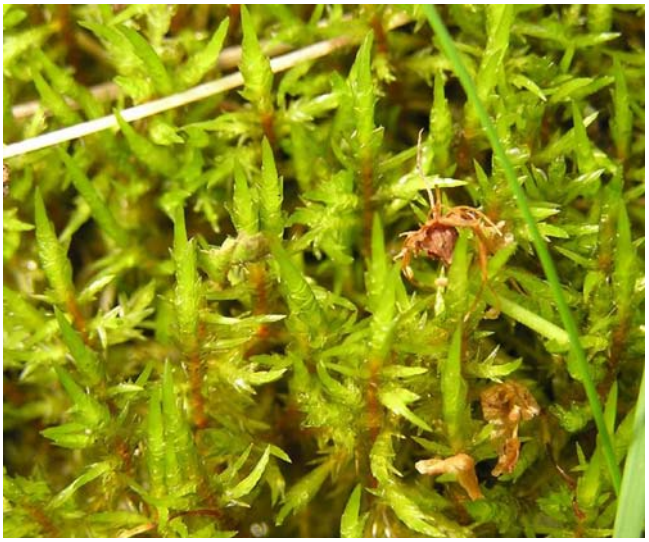

Figure 135. ***Calliergonella cuspidata***, larval home of ***Bryotropha terrella***. Photo by Michael Becker, through Creative Commons.

Larvae of ***Bryotropha politella*** (Figure 136), also from the British Isles, feeds on ***Rhytidiadelphus squarrosus*** (Figure 131) (Palmer & Palmer 2016a). But these larvae also can occur under the moss ***Schistidium*** (Figure 137), although its food relationship to that species is not known (Heckford & Sterling 2003).

Figure 136. ***Bryotropha politella*** larva on moss. Photo © Bob Heckford, with permission.

Figure 137. ***Schistidium apocarpum*** with capsules, a moss genus that sometimes provides cover for ***Bryotropha politella*** larvae. Photo by Hermann Schachner, through Creative Commons.

In the USA and Canada, the genus ***Bryotropha*** is less common. ***Bryotropha gemella*** (Figure 138) sometimes occurs on mosses (Rutten & Karsholt 2004). The bryophage ***Bryotropha galbanella*** is also known from Alaska.

Figure 138. ***Bryotropha gemella*** adult, a North American species that sometimes lives among mosses as larvae. Photo by Jeremy deWaard, through Creative Commons.

In Russia, Bidzilya and Li (2010) reported that ***Agnippe echinuloides*** (Figure 139) lives in moss bogs.

Figure 139. ***Agnippe echinuloides*** adult, a bog species in Russia. Photo by Marko Mutanen, through Creative Commons.

Monochroa tenebrella (Figure 140) lives among mosses in Europe (Shield 1856). ***Pseudotelphusa scalella*** (Figure 141) larvae feed on mosses, lichens, and *Quercus robur* in Europe (Wikipedia 2015b).

Hoare (2011) found a new species of ***Kiwaia*** in northern New Zealand. Two specimens were found on the dominant moss ***Campylopus introflexus*** (Figure 142). Laboratory experiments verified that these larvae could grow to adulthood when only this moss was available as food. On the other hand, ***K. jeanae*** live on *Raoulia* (Asteraceae; Figure 143-Figure 144) mats, cushions that somewhat resembles a cushion of ***Campylopus introflexus***, suggesting that the growth form may be important for moisture conservation.

Figure 140. ***Monochroa tenebrella*** adult, a species whose larvae live among mosses. Photo by Patrick Clement, Gelechiid Recording Scheme, with permission.

Figure 141. ***Pseudotelphusa scalella*** adult, a species whose larvae live among mosses. Photo by Donald Hobern, through Creative Commons.

Figure 142. ***Campylopus introflexus***, probably home for a species of ***Kiwaia***. Photo by J. C. Schou, through Creative Commons.

Figure 143. ***Raoulia*** sp. in full flower, home for ***Kiwaia jeanae***. Photo by Nicola Tilley, through Creative Commons.

Figure 144. ***Raoulia*** sp. cushion with a few flowers, home for ***Kiwaia jeanae***. The cushion suggests a similarity to a moss cushion. Photo from the University of Basel, through Creative Commons.

But food is not the only use this family makes of mosses. The pupal stage of ***Teleiodes luculella*** (Figure 145-Figure 147) in the Maltese Islands overwinters (Patocka 1987). Sorhagen (1996) found that this stage can occur under mosses or bark (Zerafa 2009).

Figure 145. ***Teleiodes luculella*** larva, a species that overwinter as pupae under mosses on bark. Photo © Bob Heckford, with permission.

Figure 146. ***Teleiodes luculella*** adult, a species that overwinters as pupae under mosses and bark. Photo by Peter Clement, with permission.

Figure 147. ***Teleiodes luculella*** adult, a species that overwinters as pupae under mosses and bark. Photo by Trevor & Dilys Pendleton <www.eakringbirds.com>, with permission.

Oecophoridae – Concealer Moths

At least some of the **Oecophoridae** (concealer moths) prefer mossy habitats (Coutin 2004a). The larva of the rare ***Aplota palpella*** (Figure 148-Figure 149) lives among mosses on tree trunks; this species was recorded in England by Phil Sterling and Derek Hallett in Dorsett County for the first time since the 19th century! (Butterfly Conservation 2001). ***Crassa tinctella*** (Figure 150) develops from September to May among the arboreal plant bodies of mosses and lichens, which also serve as its food (Coutin 2004b).

Figure 148. ***Aplota palpella*** adult, a species whose larvae live among mosses on tree trunks. Photo by Peter Huemer, through Creative Commons.

Figure 149. ***Aplota palpella*** adult, a species whose larvae live among mosses on tree trunks. Photo by Graham Wenman, with permission.

Figure 150. ***Crassa tinctella*** adult, a species whose larvae develop among epiphytic bryophytes and lichens and use them for food. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Summary

The Microlepidoptera include the **Micropterigidae** and the **Mnesarchaeidae**, but it is really a group of small Lepidoptera without close phylogenetic ties. The **Micropterigidae** is a primitive family that specializes on liverworts, although some (*e.g.* ***Epimartyria pardella***) eat mosses. The **Mnesarchaeidae** seem to prefer the periphyton living on the moss leaves and stems. The **Hepialidae** seem to ignore liverworts and feed mostly on mosses, but they are less likely to be specialists. Some include both bryophytes and tracheophytes or fungi in their diets. Bryophyte feeders seem to prefer bogs. ***Heloxycanus*** prefers cushion plants – mosses or otherwise. Many of the bryophyte dwellers spin a web on the bryophytes for feeding or pupation.

In the **Palaeosetidae**, only one species is known as a moss dweller and moss feeder. The **Psychidae** construct "bags" and cases that sometimes include bryophytes. The **Tineidae** make stone cases and these may include small moss fragments. The **Gelechiidae** hide, while feeding in such places as interiors of tracheophyte leaves, under bark or bryophytes, or in silken tubes of their own making, and some eat mosses. In the **Oecophoridae**, mosses are eaten by at least a few members, typically epiphytes on trees.

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CHAPTER 12-14
TERRESTRIAL INSECTS: HOLOMETABOLA – LEPIDOPTERA: TORTRICOIDEA – PAPILIONOIDEA

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CHAPTER 12-14
TERRESTRIAL INSECTS: HOLOMETABOLA – LEPIDOPTERA: TORTRICOIDEA – PAPILIONOIDEA

Figure 1. Larva of **Lepidoptera (Crambidae?)** on the moss ***Syntrichia***. Photo courtesy of Wynne Miles.

TORTRICOIDEA

Tortricidae – Tortrix Moths, Leaf-roller Moths

This family has larvae that live among bryophytes on tree trunks. A male ***Pammene albuginana*** (Figure 2) was reared from mosses collected from decaying beechwood in Ireland (Bond & O'Connor 2012). Buchanan White (1971) reported ***Eana penziana*** (Figure 3) from among mosses near Perth, Australia, where it spins its feeding web (Buchanan White 1971). It is also known from Europe and the Near East where it apparently feeds on tracheophyte roots (Wall 2016).

Figure 2. ***Pammene albuginana*** adult, a species that can survive on mosses in its larval stage. Photo by Patrick Clement, with permission.

Figure 3. ***Eana penziana*** adult. Larvae of this species spin feeding webs on mosses in Australia. Photo by Kurt Kulac, through Creative Commons.

Another sometimes bryophyte user is ***Cnephasia pasiuana*** (Figure 4) – a cereal leafroller in Europe. The young, 1 mm long larvae of this species crawl about on the bark for about 2 days, then hide in bark crevices or among mosses (Ulenberg 2015). They then weave a small white cocoon (**hibernaculum**). They spend the summer there and continue there into a winter dormancy.

Figure 4. ***Cnephasia pasiuana*** adult, a species whose larvae hide in bark crevices and among mosses. Photo by James K. Lindsey, with permission.

Celypha aurofasciana (Figure 5) lives in galleries on trunk-dwelling mosses and liverworts, but is also suspected of eating rotting wood in the UK (Meyrick 1895; Cryer 2016).

Figure 5. ***Celypha aurofasciana*** adult; larvae make galleries on mosses and liverworts on tree trunks. Photo by Phil Boggis, with permission.

Mosses may contribute to providing suitable breeding grounds for ***Merophylas*** sp., in Danseys Pass, New Zealand (Patrick 1982). These moths fly from March to May, but the females have short wings. Two females were found on mosses in wet locations, suggesting that the mosses may be suitable egg-laying sites, or that both the moths and bryophytes like the same habitats.

PYRALOIDEA

Crambidae – Grass Moth; Sod Worms

Members of this family are often included in the **Pyralidae**. I have separated them here because the crambids seem to have a relationship with bryophytes that is seldom seen in the remaining **Pyralidae**.

Members of this family construct silken tunnels on their food plants (grasses and mosses) and reside there in relative safety as they feed (Shield 1856). The subfamily **Scopariinae** is listed in The Peterson Field Guide to Moths of Northeastern North America (Beadle & Leckie 2012) as the moss-eating Crambidae. These include ***Scoparia*** and ***Eudonia***. Munroe (1972) has found species of ***Eudonia*** (*e.g.* Figure 8-Figure 12), ***Scoparia*** (*e.g.* Figure 25-Figure 28), and ***Cosipara*** (Figure 6) adults among the mosses in forests of Vancouver, Canada.

Figure 6. ***Cosipara*** adult, a genus whose adults frequent forest mosses in Vancouver, Canada. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

I was introduced to this family when Will Haines (pers. comm. 17 February 2012) sent me a picture of ***Eudonia*** (Figure 7) from Hawaii. Over 60 species of this genus occur in Hawaii, many of which feed on mosses. This one came along with some mossy rocks that Haines collected for his terrarium. Loren Russell (pers. comm.) likewise suggested that this genus feeds on mosses in the forests of Vancouver. This suggestions is based on reports of the genus in the area (Munroe 1972) and Russell's own observations of adults in the genus in mossy habitats there.

Figure 7. ***Eudonia*** sp. caterpillar eating moss in Hawaii. Photo courtesy of Will Haines, with permission.

Eudonia meristis (Figure 8), an endemic in Hawaii, feeds on mosses (Wikipedia 2015a). In Europe, northwest Africa, and Asia, larvae such as ***Eudonia lacustrata*** (Figure 9-Figure 10) feed on mosses, usually on walls or tree trunks (Doremi 2016b). In eastern North America, ***Eudonia strigalis*** (Figure 11) larvae are moss eaters (Beadle & Leckie 2012).

Figure 8. ***Eudonia meristis*** adult, a Hawaiian species whose larvae feed on mosses. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 9. ***Eudonia lacustrata*** larva on moss, where it feeds on walls and trees. Photo © Bob Heckford, with permission.

Figure 10. ***Eudonia lacustrata*** adult, a species whose larvae feed on mosses. Photo by James K. Lindsey, with permission.

Figure 11. ***Eudonia strigalis*** adult, a moth species whose larvae feed on mosses in eastern North America. Photo by Elizabeth, through Creative Commons.

Hoare (2011) suggested that ***Eudonia steropaea*** (Figure 12) feeds on the moss ***Campylopus*** (Figure 13) in New Zealand. To these ***Eudonia*** species, Patrick *et al.* (2011) added larvae of ***Eudonia aspidota*** (Figure 14), ***E. dinodes*** (Figure 15), and ***E. minualis*** (Figure 16) as having moss hosts in New Zealand; ***Eudonia philerga*** (Figure 17) lives in and presumably eats moss on wood. These researchers even added a new species of ***Eudonia*** feeding on mosses on coastal rocks.

Figure 12. ***Eudonia steropaea*** adult, a species whose larvae most likely feed on the moss ***Campylopus***. Photo by Donald Hobern, through Creative Commons.

Figure 13. ***Campylopus introflexus***, home and likely food for ***Eudonia steropaea***. Photo by J. C. Schou, through Creative Commons.

Figure 14. ***Eudonia aspidota*** adult, a species whose larvae live on mosses in New Zealand. Photo by Jon Sullivan, through Creative Commons.

Figure 15. ***Eudonia dinodes*** adult, a species whose larvae feed on mosses in New Zealand. Photo by Steve Kerr, through Creative Commons.

Figure 16. ***Eudonia minualis*** adult, a species that lives among and eats mosses in New Zealand. Photo by Phil Bendle, through Creative Commons.

Figure 17. ***Eudonia philerga*** adult, a species whose larvae eat mosses on logs in New Zealand. Photo by Donald Hobern, through Creative Commons.

Shield (1856) described ***Eudonia murana*** (Figure 18-Figure 19) as a species that occupies mosses on walls in the British Isles, spinning their webs among these plants.

Figure 18. ***Eudonia murana*** larva on moss. Photo © Bob Heckford, with permission.

Figure 19. ***Eudonia murana*** adult, a species whose larvae live among mosses on walls in the British Isles. Photo by Chris Johnson, with permission.

Heckford (2009) found one larva of ***Eudonia pallida*** (Figure 20-Figure 22) on the moss ***Calliergonella cuspidata*** (Figure 23) in Cornwall, England. It had spun a small silken ball covered in **frass** (insect feces). In captivity, the larva constructed a silken gallery along the moss stems and was reluctant to leave it. Wegner and Kayser (2006) reported four larvae of the species with similar silken tunnels on the moss ***Pleurozium schreberi*** (Figure 24). These were enclosed in a strong cocoon made of moss fragments; their frass was usually attached. These larvae laid eggs on the mosses in the lab.

Figure 20. ***Eudonia pallida*** early instar larva on moss. Photo by Heckford, with permission.

Figure 21. ***Eudonia pallida*** last instar larva on moss. Photo by Bob Heckford, with permission.

Figure 22. ***Eudonia pallida*** larva in cocoon on moss. Photo by Bob Heckford, with permission.

Figure 23. ***Calliergonella cuspidata***, home for ***Eudonia pallida*** larvae. Photo by David T. Holyoak, with permission.

Figure 24. ***Pleurozium schreberi***, home for ***Eudonia pallida*** larvae. Photo by Malcolm Storey, Discover Life, through Creative Commons.

Included among the moss eaters in eastern North America are larvae of ***Scoparia biplagialis*** (Figure 25) and ***S. basalis*** (Figure 26) (Beadle & Leckie 2012).

Figure 25. ***Scoparia biplagialis*** adult, a species of larval moss eaters in eastern North America. Photo by Andy Reago and Chrissy McClarren, through Creative Commons.

Figure 26. ***Scoparia basalis*** adult, a species whose larvae eat mosses in eastern North America. Photo by Andy Reago and Chrissy McClarren, through Creative Commons.

Stainton (1871) likewise considered ***Scoparia*** larvae to be moss eaters, citing a number of species that live among mosses in Europe. Larvae of ***Scoparia basistrigalis*** (Figure 27) feed on moss (Heckford & Sterling 2005). Heckford (2011) made it clear that not all members of ***Scoparia*** are moss eaters. Rather, based on experiments by Thurnall (1907, 1908) we know that at least ***S. pyralella*** (= *S. dubitalis*; Figure 28) feeds on roots of ***Rumex acetosella*** (Figure 29), and possibly other roots.

Figure 27. ***Scoparia basistrigalis*** adult, a moth whose larvae are parasitized by **Braconidae** and that feeds on mosses. Photo by J. C. Schou through Biopix.com, with permission.

Figure 28. ***Scoparia pyralella*** adult, a species of ***Scoparia*** whose larvae do not feed on mosses. Photo by Hectonichus, through Creative Commons.

Figure 29. ***Rumex acetosella***, host for ***Scoparia pyralella*** larvae in Europe. Photo by Forest and Kim Starr, through Creative Commons.

Paroplitis wesmaeli is a European species of **Braconidae**, a parasitic wasp that has larval **Lepidoptera** as hosts (Yu *et al*. 2012). Two of the **Lepidoptera** host larvae, ***Scoparia basistrigalis*** (**Crambidae**; Figure 27) and ***Bryotropha umbrosella*** (**Gelechiidae**; see Figure 30), feed on mosses (Heckford & Sterling 2005; Hantmoth 2012), the latter while living in a silken tube.

Figure 30. ***Bryotropha boreella*** larva on moss ***Rhytidiadelphus squarrosus***. Photo © Bob Heckford, with permission.

In New Zealand, ***Scoparia minusculalis*** (Figure 31) uses mosses as host plants (Patrick *et al*. 2011). But mosses are not the only food for the Crambidae. Cowley (1988) found that in Waikato hill country (New Zealand) the **Scopariinae** larvae were abundant in mossy regions but consumed most of the pasture grasses. When they laid their eggs, they chose both grasses and moss stems, laying to depths of 10 mm just below the ground level. The larvae that hatched constructed silk **hibernacula** (cocoons). To these they attached fine soil particles and mosses. If mosses were prolific, the larvae constructed their retreats at the bases of moss plants. The large larvae cut whole blades of grass or stems of mosses and dragged them into their burrows for food. These mosses and grasses were clipped near the burrow so that eventually the burrows were surrounded by an area that was entirely clipped. This clearing resulted in weed invasion, hence affecting the vegetation. Cowley found that all the Waikato hill country species of the **Scopariinae** were able to survive on mosses alone in the lab.

Figure 31. ***Scoparia minusculalis*** adult with epiphylls on a leaf. Photo by Maurice, through Creative Commons.

Heckford (2009) provides us with a rare view of the details of moss use by the **Lepidoptera**. When ***Scoparia ambigualis*** (Figure 32-Figure 33) larvae were reared in the lab with only the moss ***Polytrichum commune*** (Figure 34) for food and home, these first instar larvae spun fine silken strands in the leaf axils. Heckford interpreted these silken nets as cushions because the larvae curled up on them when they were not feeding. These are not very hairy larvae, but nevertheless, Heckford suggested that this net cushion may permit the larvae to get support for their bodies without crushing their hairs.

Figure 32. ***Scoparia ambigualis*** larva on moss. Note the spun cushion under it and the frass around it. Photo © Bob Heckford, with permission.

Figure 33. ***Scoparia ambigualis*** adult, a species whose larvae spin "cushions" in the leaf axils of ***Polytrichum commune***. Photo by James K. Lindsey, with permission.

Figure 34. ***Polytrichum commune***, home and food for ***Scoparia ambigualis*** larvae. Photo by Michael Lüth, with permission.

These ***Scoparia ambigualis*** (Figure 32-Figure 33) larvae ate only moss leaves in this lab observation (Heckford 2009). Their feces (**frass**) were pale greenish or yellowish for young larvae. In later instars these became reddish brown. Then Heckford added the mosses ***Rhytidiadelphus loreus*** (Figure 35) and ***Dicranum scoparium*** (Figure 36), as well as fragments of fern fronds of ***Pteridium aquilinum*** (Figure 37), to the choices for the larvae. Larvae occur on all three of these species in Devon, England. The larvae fed on all the mosses, but none ate the fern fragments.

Figure 35. ***Rhytidiadelphus squarrosus***, a food choice of ***Scoparia ambigualis*** larvae. Photo by Michael Lüth, with permission.

Figure 36. ***Dicranum scoparium***, one of the food choices of ***Scoparia ambigualis*** larvae. Photo by Michael Lüth, with permission.

Figure 37. ***Pteridium aquilinum***, a food choice that was refused by ***Scoparia ambigualis*** larvae. Photo by Sanja, through Creative Commons.

Patrick *et al*. (2011) reports ***Gadira acerella*** (Figure 38) and ***Glaucocharis elaina*** (Figure 39) in moss on rocks in New Zealand, whereas ***Helastia corcularia*** (**Geometridae**; Figure 40-Figure 41) lives on moss and herbs there – an unusual non-specialist strategy. Gaskin (1971) also reported ***Glaucocharis elaina*** on mosses, including ***Funaria*** (Figure 42). Hudson (1928) reared ***G. microdora*** (Figure 43) and ***G. metallifera*** (Figure 44-Figure 45) on bryophytes.

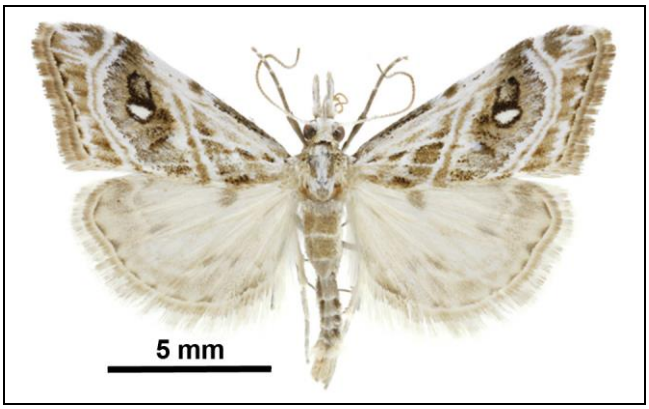

Figure 38. ***Gadira acerella*** adult. Larvae of this species live among mosses on rocks in New Zealand. Photo from Landcare Research, Manaaki Whenua, with online permission.

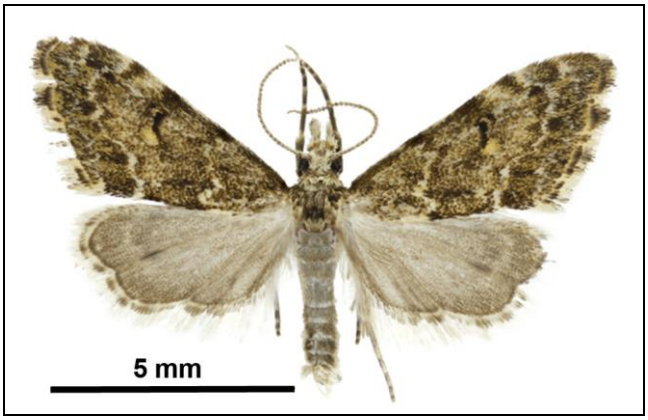

Figure 39. ***Glaucocharis elaina*** adult. Larvae of this species live among mosses on rocks in New Zealand. Photo from Landcare Research, Manaaki Whenua, with online permission.

Figure 40. ***Helastia corcularia*** female adult, a species whose larvae eat both mosses and herbs. Photo by Phil Bendle, with permission through John Grehan.

Figure 41. ***Helastia corcularia*** male adult, a species whose larvae eat both mosses and herbs. Photo by Phil Bendle, with permission through John Grehan.

Figure 42. ***Funaria hygrometrica*** leaves, food for larvae of ***Helastia corcularia***. Photo through Creative Commons.

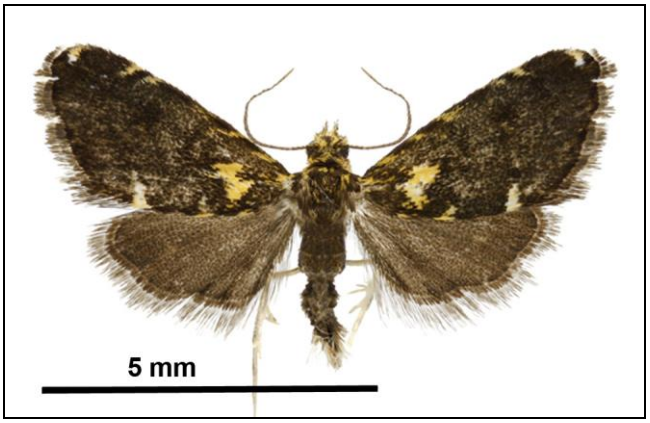

Figure 43. ***Glaucocharis microdora*** adult male, a species that has been reared on bryophytes. Photo from Landcare Research, NZ, with online permission for non-commercial educational use.

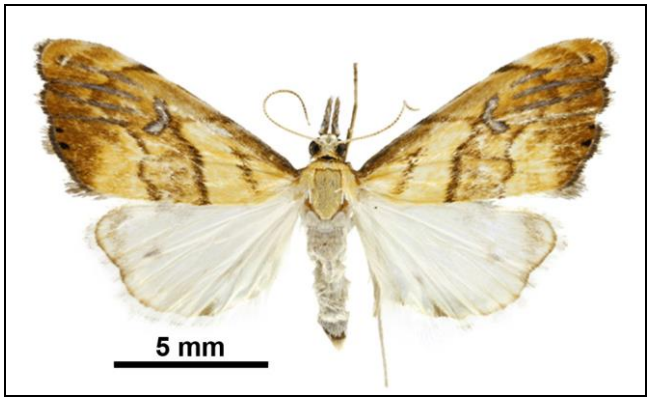

Figure 44. ***Glaucocharis metallifera*** adult female, a species that has been reared on bryophytes. Photo from Landcare Research, NZ, with permission for non-commercial educational use.

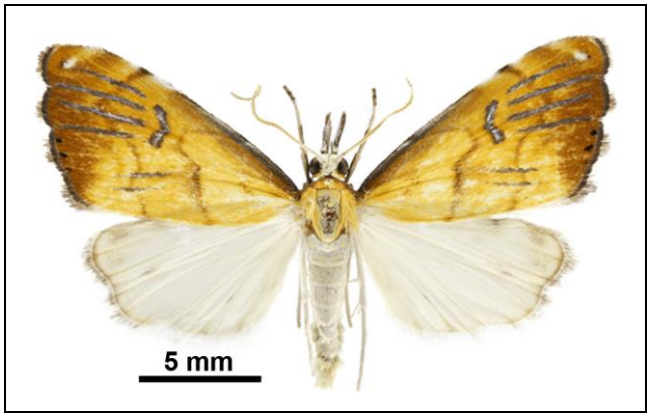

Figure 45. ***Glaucocharis metallifera*** adult male, a species that has been reared on bryophytes. Photo from Landcare Research, NZ, with online permission for non-commercial educational use.

Beever and Dugdale (1994) observed severe damage to a colony of the moss ***Dawsonia superba*** (Figure 46) on a stream bank on the southern slopes of Mt Ruapehu, North Island, NZ. This damage was later determined to be the work of the moth larva ***Glaucocharis epiphaea*** (Figure 47). Its feeding resulted in chewing off terminal portions of many leaves. They left the shoots with heavy encrustations of refuge tunnels made with silk, leaf fragments, and frass from the larvae. Leaves were severely chewed, with only 1-5 mm of green lamina remaining and the shoot apex completely destroyed. Beever (Beever & Dugdale 1994) also reared ***G. bipunctella*** (Figure 48) on liverwort cushions from a forest remnant.

Figure 46. ***Dawsonia superba***, home for larvae of ***Glaucocharis epiphaea*** (Figure 47). Photo by Phil Bendle, with permission from John Grehan.

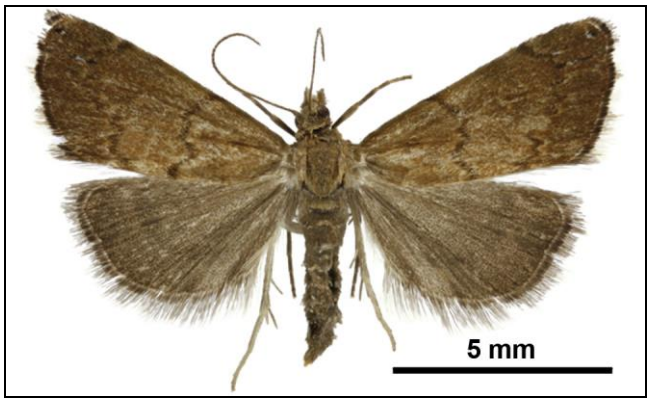

Figure 47. ***Glaucocharis epiphaea*** adult female, a species whose larvae consume ***Dawsonia superba*** in New Zealand. Photo from Landcare Research, NZ, with online permission for non-commercial educational use.

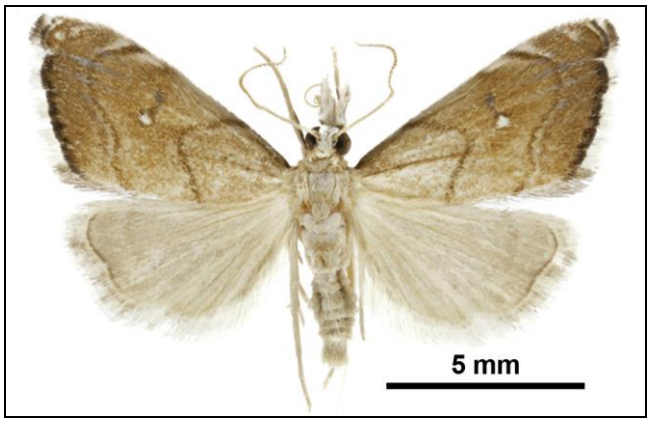

Figure 48. ***Glaucocharis bipunctella*** adult male. Larvae of this species develop successfully on liverworts. Photo from Landcare Research, NZ, with online permission for non-commercial educational use.

Beever and Dugdale (1994) followed these observations by collecting larvae of ***Glaucocharis epiphaea*** (Figure 47) in September and rearing them to adults on shoots of ***Polytrichadelphus magellanicus*** (Figure 49). ***Glaucocharis epiphaea*** is an endemic that lives in the montane rainforests and alpine seepage areas in New Zealand.

Figure 49. ***Polytrichadelpus magellanicus***, food for ***Glaucocharis epiphaea***, with capsules. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Members of the **Acentropinae** make cases or tunnels (Yen 2016). Many are aquatic and feed on aquatic plants, including mosses. However terrestrial larvae live in portable cases or make tunnels under mosses or lichens. The pupa of the ***Paracymoriza nigra*** (Figure 50) group rests in a chamber-like cocoon under mosses. Larvae of ***Nymphicula morimotoi*** (Figure 51) in the Philippines occur along streams on stones and rocks with rich growths of liverworts in the **Jungermanniaceae** (Yoshiyasu 1997). Females of ***Nymphicula morimotoi*** in the laboratory laid eggs one by one between the leaves of the liverwort. The hatchlings spin fine soil particles around themselves to construct small cases.

Figure 50. ***Paracymoriza nigra*** adult, a species that pupates in a cocoon under mosses. Photo through Creative Commons.

Figure 51. ***Nymphicula queenslandica*** adult. ***Nymphicula morimotoi*** larvae in the Philippines live among liverworts in the **Jungermanniaceae** on rocks along streams. Photo from Photography Group, BIO-CSIRO, through Creative Commons.

In Australia, ***Pyrausta cingulata*** (syn=***Ennychia cingulalis***; Figure 52-Figure 53) lives among mosses and spins its web in them (Buchanan White 1971). This behavior was known more than a century ago in Europe, where its retreat is among mosses and dead leaves (Heyden 1861). It can be located by the large heaps of frass nearby.

Figure 52. ***Pyrausta cingulata*** larva, a species that lives among mosses and spins its web there. Photo by Bob Heckford, with permission.

Figure 53. ***Pyrausta cingulata*** adult, a species that lives among mosses and spins its web there. Photo by Tiroler Landesmuseen, through Creative Commons.

Crambus tristellus (see Figure 54) occurs in damp locations along ditches where it makes silken galleries on mosses (Shield 1856). Other former members of ***Crambus*** (Figure 54) that dwell among mosses have been reclassified into a variety of genera. Buckler (1901) reported that members of ***Crambus*** feed among stems and roots of grasses or on moss (Stainton 1852), but these bryophages may now belong to other genera.

Figure 54. ***Crambus pascuella*** male adult. ***Crambus tristellus*** makes silken galleries on mosses in damp locations. Photo by Jérôme Albre, with permission.

Catoptria falsella (syn=*Crambus falsellus*; Figure 55) is a wall dweller (Doremi 2016a). The larva builds a silk tube that helps to hide it while it is feeding, typically on mosses, and especially on the moss ***Tortula muralis*** (Figure 56). This is the ultimate site for its pupation. Shield (1856) found larvae of ***Catoptria falsella*** in the unique habitat of mosses on thatch of a barn. This species primarily hides among mosses on walls, stones, and rocks in the daytime, feeding at night on mosses, including ***Tortula muralis***, ***Syntrichia ruralis*** (Figure 57), ***Barbula*** (Figure 58), and ***Brachythecium rutabulum*** (Figure 59) (Wikipedia 2014). South (1890) reported ***Catoptria verellus*** (syn=*Crambus verellus*; Figure 60) among mosses on tree trunks, particularly older plum, apple, and poplar trees. The species also occurs in fir woods with moss-covered ground.

Figure 55. ***Catoptria falsella*** adults – wall dwellers, showing two color phases. Larvae typically feed on mosses, including ***Tortula muralis***. Photos by Donald Hobern, through Creative Commons.

Figure 56. ***Tortula muralis*** with capsules on wall, food for ***Catoptria falsella***. Photo by Mike, through Creative Commons.

Figure 57. ***Syntrichia ruralis***, food for the nighttime feeder ***Catoptria falsella***. Photo by Hermann Schachner, through Creative Commons.

Figure 58. ***Barbula unguiculata***. Some members of this genus provide food for the nighttime feeder, ***Catoptria falsella***. Photo by James K. Lindsey, with permission.

Figure 59. ***Brachythecium rutabulum***, nighttime food for ***Catoptria falsella***, with capsules. Photo by J. C. Schou <www.biopix.com>, with permission.

Figure 60. ***Catoptria verellus*** adult, a species whose larvae live on moss-covered tree trunks and moss-covered ground. Photo by Donald Hobern, with permission.

Chrysoteuchia culmella (=*Crambus hortuellus*; Figure 61) larvae build silken galleries on the ground under mosses (Shield 1856). Where it is damp along ditches, one can also find larvae of ***Agriphila straminella*** (syn=*Crambus culmellus*; Figure 62) with their silken galleries. The larvae mature there and spend their pupation there.

Figure 61. ***Chrysoteuchia culmella*** adult. Their larvae build their silken galleries under ground mosses. Photo through Wikimedia Commons.

Figure 62. ***Agriphila straminella*** adult; the larvae occur along damp ditches, including among mosses. Photo by André Karwath, through Creative Commons.

Huggins (2011) listed ***Oxyelophila callista*** (Figure 63) as a species of moss shredders, but these are aquatic mosses.

Figure 63. ***Oxyelophila callista*** adult; larvae are shredders of aquatic mosses. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Some evidence that **Crambidae** live among mosses is indirect (Russell 1979). Their head capsules have been found numerous times in mosses on logs and deciduous tree trunks. Webbing and fecal pellets occur among damaged mosses. Based on this evidence, it appears that ***Hypnum circinale*** (Figure 64) and ***Tetraphis pellucida*** (Figure 65) are most likely eaten by larvae of **Crambidae** (formerly placed in **Pyralidae**).

Figure 64. ***Hypnum circinale***, food for larvae of the **Crambidae**, with capsules. Photo by Matt Goff, with permission.

Figure 65. ***Tetraphis pellucida*** with gemmae, a species most likely eaten by members of the **Crambidae**. Photo by Hermann Schachner, through Creative Commons.

Pyralidae – Snout Moths

There are few known bryophages remaining in this family in its more restricted definition. Fraenkel and Blewett (1947) suggested that some of this snubbery of the bryophytes may be due to the chemical composition. However, they failed to show that bryophytic linoleic acid was detrimental, and bryophyte arachidonic acid actually promotes growth of the larvae of ***Ephestia kuehniella*** (Figure 66-Figure 67).

Figure 66. ***Ephestia kuehniella*** larva, a species whose growth is promoted by arachidonic acid from bryophytes. Photo by Simon Hinkley and Ken Walker, Museum Victoria, through Creative Commons.

Figure 67. ***Ephestia kuehniella*** mating adults. Photo by Magne Flåten, through Creative Commons.

Synaphe punctalis (Figure 68) and ***S. angustalis*** (Figure 69) builds its scant webs among damp mosses on the ground (Meyrick 1895). In addition to these, in

Australia, ***Phycis subornatella*** lives among mosses and spins its web in it (Buchanan White 1971).

Figure 68. ***Synaphe punctalis*** adult, a species whose larvae build webs among damp ground mosses. Photo by Thorsten Denhard, through Creative Commons.

Figure 69. ***Synaphe angustalis*** adult, a species whose larvae build scant webs on damp mosses. Photo from ©entomart, through Creative Commons.

HESPERIOIDEA

Hesperiidae – Skippers

These lepidopteran differ from both moths and butterflies. They have short, fat bodies like moths, hooked antennae unlike the club antennae of butterflies or the feathery antennae of moths, and a unique rapid, skipping flight (Bartlett 2004; Wikipedia 2015c).

The skippers are generally not associated with mosses. However, ***Polites mardon*** (Figure 70-Figure 73) builds a larval shelter of silk with mosses, dry grass blades, litter, and dry frass serving to camouflage it (Henry & Beyer 2013). These are located at the bases of grasses near the soil surface.

Figure 70. ***Polites mardon*** larva, a species that incorporates pieces of mosses in its silk shelter. Photo by Jim P. Brock, with permission.

Figure 71. ***Polites mardon*** pupa, a species that incorporates pieces of mosses in its silk shelter. Photo by Jim P. Brock, with permission.

Figure 72. ***Polites mardon*** adult, a species whose larvae include mosses in their net. Photo by Lauren Sobkoviak, through Creative Commons.

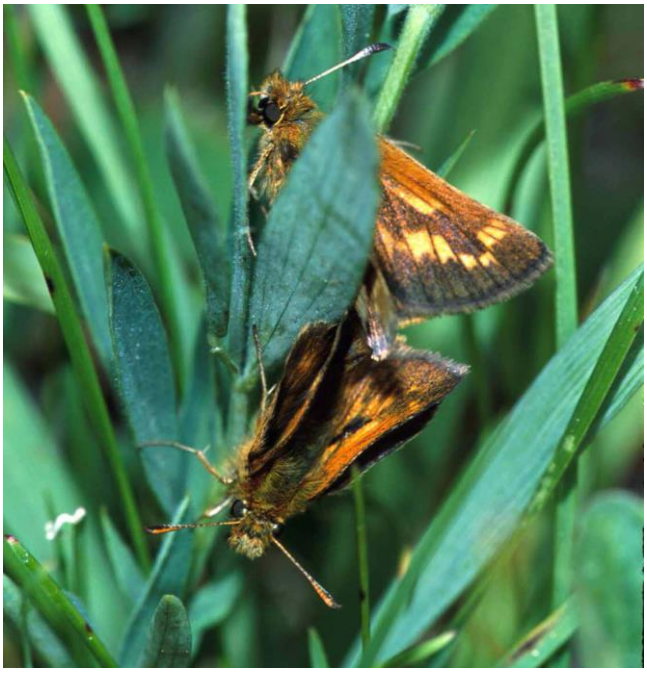

Figure 73. ***Polites mardon*** adult, a species that incorporates pieces of mosses in its silk shelter. Photo by William Leonard, with permission.

PAPILIONOIDEA

Lycaenidae – Blues, Coppers, Hairstreaks, Harvesters (Butterflies)

Some Lepidoptera seem to have switched from feeding on leaves to feeding on the **epiphylls** (Figure 74) on the leaves (Callaghan 1992). It appears that in this case, the bryophytes, mostly the leafy liverworts in **Lejeuneaceae**, were an important food source. In a Nigerian cola forest, ***Pentila picena cydaria*** (Figure 75) lays its eggs singly on live trees. Its substrate includes not only the woody stems, but also green lichens and mosses. These eggs are initially white, but within a day they become dark brown, making them less conspicuous.

Figure 74. **Lejeuneaceae** epiphylls on leaf, food for several **Lepidoptera**, including ***Pentila piceana cydaria***. Photo by Claudine Ah-Peng, with permission.

Figure 75. ***Pentila picena*** adult, a species whose larvae feed on epiphylls, including bryophytes. Adults include mosses among their oviposition sites. Photo by Sáfián Szabolcs, with permission.

Nymphalidae – Brush-footed Butterflies

Singer and Mallet (1986) expressed excitement at finding ***Euptychia insolata*** (Figure 76) alighting on "green" tree trunks in Costa Rica. As they continued observations, they found six green spherical eggs, then observed the female ovipositing on the epiphytic moss ***Neckeropsis undulata*** (Figure 77). This species landed on tree trunks with green bryophytes, searching for oviposition sites. The larvae of this butterfly are well camouflaged on the moss. They are "moss-shaped" and moss-colored. This appears to be the first record for butterfly larvae that feed on a moss (Singer *et al.* 1983; Singer & Mallet 1986), but they were unable to determine if they were restricted to this moss species. Singer and Mallet (1986) were able to raise 5 adults from 6 eggs by using ***Neckeropsis undulata*** as the only food source. The larvae of this species are "moss-shaped" and have cryptic coloration, rendering them safe on this moss.

Figure 76. ***Euptychia insolata*** adult, a butterfly that oviposits on epiphytic mosses on tree trunks and its larvae eat there. Photo by Will & Gill Carter, with permission.

Figure 77. ***Neckeropsis undulata***, oviposition site for ***Euptychia insolata***. Photo by Bobby Hattaway, from <www.discoverlife.org>, through Creative Commons.

Hamm (2015) expressed surprise that members of ***Euptychia*** have switched from feeding on grasses to feeding on low-nutrient plants like ***Selaginella*** (a fern ally; Figure 78) and mosses (Scriber & Slansky 1981). On the other hand, Egorov (2007) concluded that the epiphytic mosses had sufficient nitrogen due to contributions from epiphytic **Cyanobacteria** (Figure 79) and the slow growth of the mosses. Furthermore, in experiments with ***E. westwoodi*** (Figure 80), Hamm (2015) found that the larvae would not eat grasses (*Lasiacis ruscifolia*, a preferred food of close relatives) when those were the only choice, losing weight and ultimately dying. Those fed with ***Selaginella*** ate and developed normally.

Figure 78. ***Selaginella***, a fern ally that ressembles a moss, has low nutrients, and serves as food for some species of ***Eutypchia***. Photo by Tim Waters, through Creative Commons.

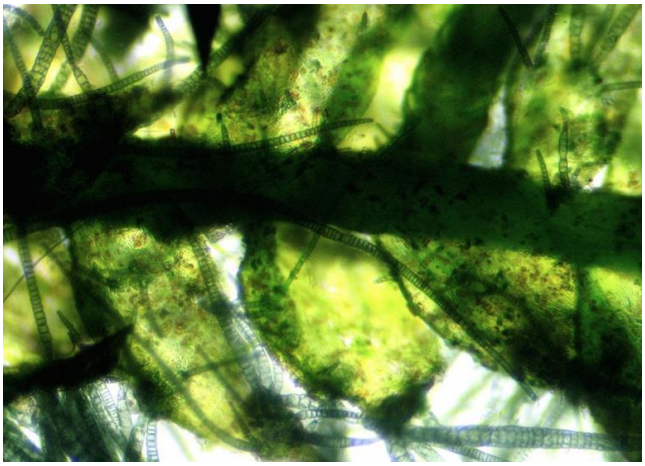

Figure 79. **Cyanobacteria** on a moss, a source of nitrogen for feeders on epiphytic bryophytes. Photo by Nat Tarbox, through Creative Commons.

Figure 80. ***Euptychia westwoodi*** adult, a species that will not eat grasses as larvae. Photo by Daniel H. Janzen, through Creative Commons.

The genus ***Euptychia*** occurs elsewhere in South America. Pulido *et al*. (2011) describe it as living in the mountain foothills and montane forests of the Andes in Colombia and Peru. Neild *et al*. (2014) described a new species from the Amazon Basin and the Guianas, describing the genus as occurring throughout the Neotropical region. This is a small butterfly and seems to generally have singular hosts among fern allies and mosses. Singer and Mallet (1986) predicted that we will eventually find that many South American **Euptychiines** feed on "lower" plants.

But not all members of ***Euptychia*** are bryophages. Beccaloni *et al*. (2008) reported that ***Euptychia hilara*** feeds on a member of **Poaceae** (grasses).

Bryophytes are often among a group of convenient locations for pupation. This is the case for the White Mountain Arctic butterfly (***Oeneis melissa semidea***; Figure 81) (Lucking 2000). Its larvae are night-active feeders, spending their day between or under rocks (Scudder 1874, 1889; Gradish & Otis 2015). Pupation, however, uses safe sites under rocks, moss, or soil. Male adults perch in areas with considerable Bigelow's sedge, the probable substrate for oviposition and food plant for the larvae (Scudder 1891, 1901).

Figure 81. ***Oeneis melissa semidea*** (White Mountain Arctic) adult, a species whose pupae often occur under mosses. Photo by Kent McFarland, through Creative Commons.

Some adult **Lepidoptera** provide very interesting mimics. The moth in Figure 82 resembles a leaf with epiphyllous liverworts (Figure 74). Is there some advantage to adding the liverworts? The leaf itself is brown, suggesting it may be high in tannins and not very palatable. Do the liverworts further discourage carnivory? Might the Lejeuneaceae they seem to mimic have secondary compounds that discourage "herbivory" (in this case on a fake)? Or do they just blend with leaves, hence avoiding larger carnivores such as birds?

Figure 82. Moth mimicking a leaf with epiphyllous bryophytes, especially liverworts, in Malaysia. Photo courtesy of Tamás Pócs.

The bog fritillary, ***Boloria eunomia*** (Figure 83-Figure 87), is of special concern in Wisconsin, USA (WDNR 2009). Its habitat is in classical acid bogs (Wikipedia 2011), a habitat that is diminishing. Schtickzelle and Baguette (2004) warn that glacial relict species such as this one are increasingly more vulnerable as their fragmented habitat becomes more and more rare. Typically, the ***Sphagnum*** (Figure 88) mosses provide the right conditions for the host plants. Natives of Scotland have been concerned about the conversion of the classic bog at Aucheninnes Moss to a landfill (Buglife 2011). This is the location of the small pearl-bordered fritillary ***Boloria selene*** (Figure 89-Figure 92), a species of conservation concern, and the only site in Scotland for the sorrel pigmy moth ***Enteucha acetosae*** (Figure 93). A third species there, ***Coenonympha tullia*** (Figure 94-Figure 97), is listed as vulnerable in Europe. These moss-dominated bog habitats house many insects that are in danger of disappearing as these bogs disappear.

Figure 83. ***Boloria eunomia*** first instar caterpillar, a bog species. Photo by Gilles San Martin, through Creative Commons.

Figure 84. ***Boloria eunomia*** last instar, a bog species. Photo by James K. Lindsey, with permission.

Figure 85. ***Boloria eunomia*** adult, a bog dweller. Photo by Gilles San Martin, through Creative Commons.

Figure 86. ***Boloria eunomia***, a bog dweller. Photo by Gilles San Martin, through Creative Commons.

Figure 89. ***Boloria selene tollandensis*** 5th instar larva, a bog dweller. Photo by Todd Stout, with permission.

Figure 87. ***Boloria eunomia*** egg, a bog species. Photo by Gilles San Martin, through Creative Commons.

Figure 90. ***Boloria selene tollandensis*** pupa, a bog species. Photo by Todd Stout, with permission.

Figure 88. ***Sphagnum capillifolium***, one of the bog mosses that provide suitable homes for ***Boloria eunomia***. Photo by Michael Lüth, with permission.

Figure 91. ***Boloria selene*** adult, a bog dweller. Photo by Kristian Peters, through Creative Commons.

Figure 92. ***Boloria selene*** adult, a bog dweller. Photo by James K. Lindsey, with permission.

Figure 93. ***Enteucha acetosae*** adult, a rare bog dweller. Photo by Patrick Clement, with permission.

Figure 94. ***Coenonympha tullia*** egg, a vulnerable bog species. Photo by Wolfgang Wagner, with permission.

Figure 95. ***Coenonympha tullia*** larva on moss. Its colors permit it to blend with mosses in bogs. Photo by Wolfgang Wagner, with permission.

Figure 96. ***Coenonympha tullia*** pupa, a bog species. Photo by Wolfgang Wagner, with permission.

Figure 97. ***Coenonympha tullia*** adult, a bog species. Photo by Ryan Hodnett, through Creative Commons.

Some members of this family are so well adapted to living among mosses that their cryptic form and coloration has earned them the name of moss caterpillars. At least some of these unusual caterpillars are in the Western Hemisphere genus ***Adelpha*** (Figure 98-Figure 103). The earliest record of these seems to be that of Moss (1933) for ***Adelpha melona leucocoma*** larvae that resemble a moss. In Costa Rica, ***Adelpha serpa celerio*** resembles mosses on a twig (DeVries 1987). Wilmott (2003) cited several species in ***Adlepha*** that mimicked mosses, including ***Adelpha leucophthalma leucophthalma*** larvae that resemble moss-covered twigs. There seem to be multiple forms of these mimics, and those forms may contribute to their occurrences in different habitats, potentially leading to separation as species.

Figure 98. ***Adelpha serpa celerio***, moss-mimicking caterpillar in Panama, blending with its habitat. Photo by Arthur Anker, with permission

Figure 99. ***Adelpha serpa celerio***, showing the byrophyte-like appendages of this moss-mimicking caterpillar in Panama. Photo by Arthur Anker, with permission.

Figure 100. ***Adelpha serpa celerio*** spinning its web on a leaf. Photo by Arthur Anker, with permission.

Figure 101. ***Adelpha*** (?) larva from Brazil, showing head and appendages. Photo by Troy Bartlett, through Creative Commons.

Figure 102. ***Adelpha*** (?) larva looking like moss on a twig. Photo by Troy Bartlett, through Creative Commons.

Figure 103. ***Adelpha fessonia*** adult, a member of the moss caterpillar genus showing the differences in coloration from its cryptic larva. Photo by Thomas Bresson, through Creative Commons.

Rionidae – Tropical Butterflies

This small family of butterflies does not seem to have a common name.

The species ***Sarota gyas*** (Figure 104) in the tropics can be found on leaves of tracheophytes, but Mota *et al*. (2014) pointed out that these are not the real hosts. Instead, the larvae are there to feed on the **epiphylls** (Figure 74) – the non-nitrogen-fixing epiphylls (DeVries 1988). In one case, larvae on a member of the Urticaceae fed on leafy liverwort epiphylls in the **Lejeuneaceae** (Figure 74). Apparently the host tree is unimportant for either oviposition or larval feeding. These larvae have long setae that provide defense and they are camouflaged among the epiphylls.

Figure 104. ***Sarota gyas*** adult, a species whose larvae live on leaves of tracheophytes where they feed on epiphylls (Figure 74). Photo by Harold Greeney, through Creative Commons.

Summary

The **Tortricidae** include a few bryophyte associates, particularly those on tree trunks. The **Crambidae**, on the other hand, construct silken tunnels on mosses and grasses where they feed in safety. The subfamily **Scopariinae** is known as the moss-eating **Crambidae**. This family has been separated from the **Pyralidae** and few bryophyte associates remain in the **Pyralidae**. The **Hesperiidae** are skippers and seem to have only one member (***Polites mardon***) that associates with mosses. The **Lycaenidae** feed on the **epiphylls** on leaves, particularly the leafy liverworts in the **Lejeuneaceae**. In the **Nymphalidae**, ***Euptychia insolata*** adults are cryptically colored to be able to alight on moss-covered tree trunks without being obvious. These are butterflies and among the ones that feed on mosses. They may use the mosses as a source of nitrogen derived from their epiphytic **Cyanobacteria**. ***Adelpha***, in the **Nymphalidae** also exhibits moss mimicry. Members of this family are common bog dwellers. The **Rionidae** has one member, ***Sarota gyas***, that feeds on epiphylls such as members of the **Lejeuneaceae**, in particular to obtain nitrogen from the associated nitrogen fixers.

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CHAPTER 12-15
TERRESTRIAL INSECTS: HOLOMETABOLA – LEPIDOPTERA: GEOMETROIDEA – NOCTUOIDEA

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CHAPTER 12-15
TERRESTRIAL INSECTS: HOLOMETABOLA – LEPIDOPTERA: GEOMETROIDEA – NOCTUOIDEA

Figure 1. **Geometridae** larva eating ***Hypopterygium tamarisci***. Photo by Adaises Maciel da Silva, with permission.

GEOMETROIDEA

Geometridae – Geometrid Moths (Inch Worms)

The **Geometridae** get their name from their larvae, popularly known as inch worms (Figure 2). The method of movement has suggested that the larvae are measuring the earth. This family has cryptic coloration as larvae (Figure 2) (Bodner *et al*. 2010). In the montane rainforest of southern Ecuador, the brown, green, and gray tones help them to blend with the montane rainforest. For example, ***Phyllodonta semicava*** (see Figure 3) and ***Cargolia arana*** (Figure 4-Figure 5) resemble the mossy bark where they live.

Figure 2. **Geometridae** larva "inching" along the stem. Photo by Jérôme Albre, with permission.

Figure 3. ***Phyllodonta*** sp. adult; some species resemble the mossy bark where they rest. Photo by Daniel H. Janzen, through Creative Commons.

Figure 4. ***Cargolia arana*** larva, resembling mossy banks where it lives. Photo by Wilmer Simbaña and Luis Salgaje, through Creative Commons.

Figure 5. ***Cargolia arana*** adult with cryptic coloration. Photo by James Sullivan, with online permission.

In tropical montane rainforests of Brazil, larvae in the **Geometridae** are the culprits that feed on the mosses ***Hypopterygium tamarisci*** (Figure 7-Figure 14) and ***Lopidium concinnum*** (Figure 15), especially at the beginning of the rainy season (September to December) (Maciel-Silva & dos Santos 2011). Using an index of damage (ID) in 2007 and 2008, Maciel-Silva and dos Santos found that ***H. tamarisci*** had higher damage (68%, 35%) than ***L. concinnum*** (38%, 23%) in these two years (Figure 6), but they were unable to separate that of the geometrid from that of a cohabiting snail. Furthermore, these rates were lower than those for tracheophytes. They found no correlation of herbivory with phenols, proteins, or the ratio between these (Figure 6).

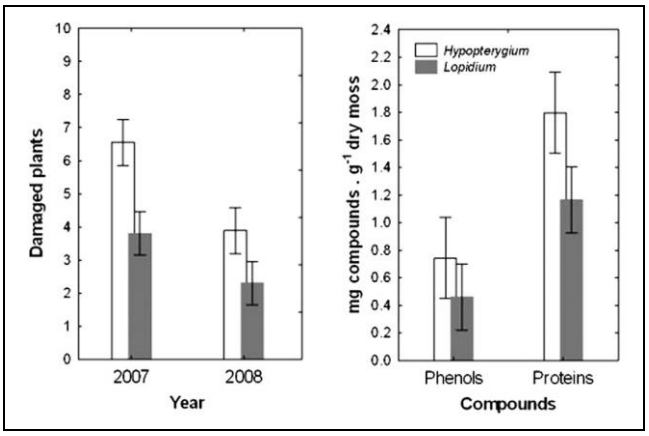

Figure 6. **Charopidae** (snail) and **Geometridae** damage to mosses in 10 colonies of plants. Modified from Adaises Maciel-Silva and Nivea Dias dos Santos.

Figure 7. Field damage to ***Hypopterygium tamarisci*** by larvae of the **Geometridae**. Photo by Adaises Maciel-Silva and Nivea Dias dos Santos, with permission.

Figure 8. Field damage to ***Hypopterygium tamarisci*** by larvae of the **Geometridae**. Photo courtesy of Adaises Maciel-Silva and Nivea Dias dos Santos, with permission.

Figure 9. Damage to leaves (circled) of ***Hypopterygium tamarisci*** by a **Geometridae** larva in the laboratory over about 50 days. Photo courtesy of Adaises Maciel da Silva.

Figure 10. **Geometridae** on its host plant, ***Hypopterygium tamarisci***. Photo courtesy of Adaises Maciel da Silva.

Figure 11. **Geometridae** on the host plant ***Hypopterygium tamarisci***. Photo courtesy of Adaises Maciel da Silva.

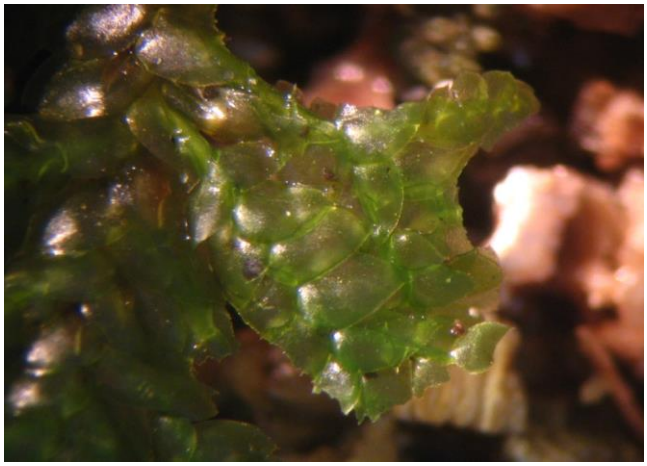

Figure 12. ***Hypopterygium tamarisci*** herbivory by **Geometridae** larvae. Photo courtesy of Adaises Maciel da Silva.

Figure 13. ***Hypopterygium tamarisci*** herbivory by **Geometridae**. Photo courtesy of Adaises Maciel da Silva.

Figure 14. Larva of **Geometridae** feeding on ***Hypopterygium tamarisci***. Photo by Adaises Maciel-Silva and Nivea Dias dos Santos, with permission.

Figure 15. ***Lopidium concinnum***, food for some larvae of **Geometridae**. Photo by Leon Perrie, through Creative Commons.

Orthonama obstipata (=*Camptogramma fluviata*; Figure 16) is not a moss feeder as far as I can tell, but it does "retire" among mosses or just below the soil surface (Hellins 1871). One must wonder if the mosses are an important component of its niche. It constructs a cocoon that is weak, thin, and made of silk. Mosses may help to buffer the temperature and maintain moisture.

Figure 16. ***Orthonama obstipata*** adult, a species that "retires" among mosses, or in the soil just below them. Photo by Ben Sale, through Creative Commons.

Helastia mutabilis (Figure 17) larvae feed on mosses in eastern Otago, New Zealand (Patrick 2016). The larva of ***Helastia mutabilis*** feeds on the moss ***Racomitrium*** (Figure 18) in the local area of Otago, thus far the only known host plant for it.

Figure 17. ***Helastia mutabilis*** adult, a species whose larvae feed on mosses in New Zealand. Photo by Donald Hobern, through Creative Commons.

Figure 18. ***Racomitrium lanuginosum***. ***Helastia mutabilis*** larvae feed on members of this genus. Photo by Juan Larrain, through Creative Commons.

Perizoma taeniatum (=*Martania taeniata*; Figure 19) is one of the macro-moths that most likely feeds on mosses as larvae (Pescott *et al*. 2015). Pescott and coworkers expressed concern that air pollution is harming the lichens and bryophytes and may lead to the demise of those that feed on them.

Figure 19. ***Perizoma taeniatum*** adult, a species whose larvae apparently feed on mosses and may be harmed by loss of mosses and lichens due to air pollution. Photo by M. Virtala, through Creative Commons.

Eupithecia austeraria (Figure 20) pupae occur among mosses on stumps, close to the moisture of the rotting wood (Shield 1856). ***Eupithecia irriguata*** (Figure 21) spends its pupal winters under bark and mosses (Dietz 1871). Krampl (1994) reported ***Eupithecia thalictrata*** (Figure 22) pupation in cocoons, usually in dry mosses near the base of its host plants. The pupae overwinter and adults emerge that spring.

Figure 20. ***Eupithecia austeraria*** adult, a species that pupates among mosses on stumps. Photo from Wikiwand.

Figure 21. ***Eupithecia irriguata*** adult, a species that overwinters as a pupa under bark and mosses. Photo by Marko Mutanen, through Creative Commons.

Figure 22. ***Eupithecia thalictrata*** adult, a species that pupates in dry mosses. Photo by Püngeler, through Public Domain.

Scotorythra paludicola (Figure 23) larvae don't eat mosses – they eat leaves and phyllodes of *Acacia koa* (Haines *et al.* 2013) and other members of the Fabaceae (Barton & Haines 2013). But the adults do use the mosses. The females lay their eggs in bark crevices and in mosses on the trunks of host trees, providing them with cover during development while keeping them close to their host leaves.

Figure 23. ***Scotorythra paludicola*** larva, a species that begins its life among mosses on *Acacia koa* where females lay eggs on tree trunks. The larvae then move to the leaves and phyllodes to feed. Photo by Forest Starr and Kim Starr, through Creative Commons.

Hyposidra talaca (Figure 24-Figure 25) lives in the tea plantations of northeastern India (Sinu *et al*. 2013). The species is a pest there, and the tree bark and its moss cover offer protection for the eggs of this species. This is one of the moths that oviposits in different places from the ones where it feeds (Wiklund 1977; Tammaru *et al*. 1995). Similarly, the Bruce spanworm (***Operophtera bruceata***; Figure 26-Figure 27) infests tree leaves, but the eggs are often laid among mosses growing at the bases of these trees (Ives 1984).

Figure 24. ***Hyposidra talaca*** larva, a pest in tea plantations. The female deposits eggs where they are hidden by mosses. Photo by Vaikoovery, through Creative Commons.

Figure 25. ***Hyposidra talaca*** adult, a pest in tea plantations. It deposits eggs where they are hidden by mosses. Photo by Sterling Sheehy, through Creative Commons.

Figure 26. ***Operophtera bruceata*** larva (Bruce spanworm) that begins it life among mosses at the base of host trees. Photo by E. Bradford Walker, through Creative Commons.

Figure 27. ***Operophtera bruceata*** adult. Females lay their eggs among mosses at the base of trees. Photo by Cody Hough, through Creative Commons.

Not all bryophyte associates are drab browns and grays. ***Milionia isodoxa***, although not a bryophyte dweller, does make use of them and is quite colorful. The adults of ***Milionia isodoxa*** (Figure 28) in Papua New Guinea illustrate the method that seems typical for obtaining water among many **Lepidoptera** (Wylie 1982). These moths probe and feed at moist sand and mud and in soil of puddle margins. Occasionally they obtain their water from mosses on rocks or on stream debris, but they do not drink from the free water itself.

Figure 28. ***Milionia isodoxa*** adult, a species that drinks from the moist mosses on rocks or along streams. Photo by David Polluck, through Creative Commons.

Camouflage is important, and even adults may rest where they are not easily seen. In New Zealand, ***Declana griseata*** (Figure 29) larvae feed on mistletoe that grows as a parasite in the trees, but as adults these moths rest on the mossy trunks of trees in the vicinity, blending with the color patterns there (Patrick & Dugdale 1997).

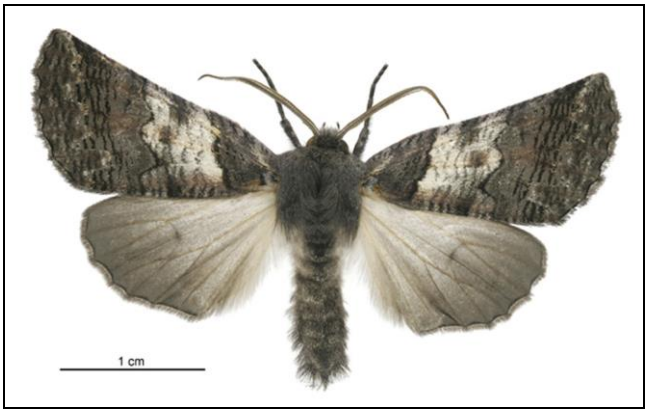

Figure 29. ***Declana griseata*** male adult, a species that rests on mossy tree trunks. Photo by Landcare Research, Manaaki Whenua, with permission.

Shaking a carefully removed clump of epiphytic moss may reveal the cocoon of ***Odontopera bidentata*** (Figure 30) attached to the tree trunk and looking like "dark whitey-brown paper with a few pieces of moss attached to it" (Shield 1856). The larvae are good mimics of lichens on a twig (Figure 31).

Figure 30. ***Odontopera bidentata*** adult showing its cryptic coloration for resting on bark. Photo by Donald Hobern, through Creative Commons.

Figure 31. ***Odontopera bidentata*** larva, a species that builds a cocoon on tree trunks, attaching mosses to it. This one is a lichen mimic. Photo by Kimmo Silvonen, with permission.

Hydriomena impluviata (syn=*Ypsipetes impluviaria*; Figure 32) pupates in mosses and Shield (1856) describes the method to look for them. He warns that one must remove the moss carefully from its bark substrate, starting at the moss tips and holding it on both sides. A sample the size of one's hand should be removed, then shaken to dislodge the black pupae. The moss should be kept intact as a sheet. Unfortunately, this method is quite destructive of the mosses.

Figure 32. ***Hydriomena impluviata*** adult, a species that pupates among mosses. Photo by Fvlamoen, through Creative Commons.

Erannis jacobsoni (Figure 33) larvae defoliate the trees in the spruce-fir forests of Russia (Турова & Юрченко 1996). Outbreaks of this species are primarily in the "green-moss" types of these forests, suggesting that the mosses may be important in their life cycle, perhaps as a place for laying eggs. For example, Kinghorn (1952) found that the western hemlock looper lays eggs among mosses and that oviposition increases when the density of the mosses is greater. On the trees, having mosses grow to higher positions increases the correlation between egg density and height on tree. Kinghorn suggested that moss density might be the strongest single factor influencing the place where eggs were deposited.

Figure 33. ***Erannis jacobsoni*** larva, a species that defoliates trees in spruce-fir forests with abundant moss ground cover. Photo by Vladimir Petko, through Creative Commons.

The western hemlock looper, ***Lambdina fiscellaria lugubrosa*** (Figure 34), along the western coast of North America lays most of its eggs in mosses on tree trunks, branches, and logs (Hopping 1934; Carolin *et al*. 1864; Shore 1990). But in the forests of the interior, their preferred oviposition sites are on the pendant lichen ***Alectoria*** spp. (Figure 35) (Thomson 1958). ***Lambdina fiscellaria fiscellaria*** (Figure 36) usually lays its eggs singly, but sometimes these are in groups of 2 or 3 (Carroll 1956). These are typically placed on mosses and lichens on the tree trunk or under old bark scales, but also on mosses covering stumps and logs.

Figure 34. ***Lambdina fiscellaria lugubrosa*** (western hemlock looper) larva, a species that often lays its eggs in mosses. Photo by Jerald E. Dewey, through Creative Commons.

Figure 35. ***Alectoria sarmentosa***, one of the preferred oviposition sites for ***Lambdina fiscellaria lugubrosa*** (Figure 34). Photo by Jason Hollinger, through Creative Commons.

Figure 36. ***Lambdina fiscellaria fiscellaria*** larva. Photo from Pennsylvania Department of Conservation and Natural Resources, through Creative Commons.

Shepherd and Gray (1972) bemoaned the difficulty of counting the eggs (Figure 37) of the hemlock looper (***Lambdina fiscellaria lugubrosa***; Figure 34) that were attached to mosses. Finding it both tedious and inaccurate, they devised a more consistent method for this process. They treated moss samples with 0.5% NaOH for 1 minute to release the eggs. These were then washed and filtered out of the moss sample. A solution of 15% NaCl helps to separate other debris from the sample by flotation. Using this method, they were able to obtain density estimates with two standard errors.

Figure 37. ***Lambdina fiscellaria*** eggs on fir. Photo from Natural Resources Canada, Canadian Forest Service, with online permission.

Otvos and Bryant (1972) likewise tested methods for assessing the eggs present on mosses and bark. They tried a range of bleach solutions and found that a 2% bleach solution bath for 45 minutes would release eggs of ***Lambdina fiscellaria*** (Figure 38) eggs without deleterious effects.

Figure 38. ***Lambdina fiscellaria*** adult, the hemlock looper. Photo by D. Gordon E. Robertson, through Creative Commons.

Dobesberger (1989) developed a management plan for ***Lambdina fiscellaria fiscellaria*** (Figure 36). Dobesberger determined that only six midcrown branches were adequate to obtain an average sample number. More eggs were present on the midcrown area of the balsam fir, ***Abies balsamea*** (Figure 39), than on other substrates including ground mosses – mostly ***Hylocomium splendens*** (Figure 40), ***Pleurozium schreberi*** (Figure 41), and ***Ptilium crista-castrensis*** (Figure 42), as well as loose bark of paper birch and lichens in the crown (mostly *Usnea longissima*; Figure 43).

Figure 39. ***Abies balsamea***, most common egg-laying site for ***Lambdina fiscellaria fiscellaria*** (Figure 36). Photo by DVS, through Creative Commons.

Figure 42. ***Ptilium crista-castrensis***, lesser egg-laying site for ***Lambdina fiscellaria fiscellaria*** (Figure 36). Photo by Li Zhang, with permission.

Figure 40. ***Hylocomium splendens***, lesser egg-laying site for ***Lambdina fiscellaria fiscellaria*** (Figure 36). Photo by Andrew Spink, with permission.

Figure 41. ***Pleurozium schreberi*** occasional egg-laying site for ***Lambdina fiscellaria fiscellaria*** (Figure 36). Photo by Michael Lüth, with permission.

Figure 43. ***Usnea*** sp., one of the substrates for egg laying of ***Lambdina fiscellaria fiscellaria***. Photo by T.cegy, through Creative Commons.

Eggs of ***Lambdina fiscellaria lugubrosa*** (Figure 34) in coastal forests of British Columbia, Canada, could be sampled at 6-7 m intervals from the ground level to the top of tree trunks by sampling the mosses (Richmond 1947). When defoliation averaged 82%, the egg count was 226 healthy eggs per 30 cm square of moss from ground level

to the top of the tree at 27 m elevation. But at 427 m, the mean defoliation dropped to 10% and the egg count to 0.3 eggs per 30 cm square of moss.

But why are the entomologists so interested in counting eggs of this species on mosses? Feeding on the leaves by the hemlock looper can devastate a hemlock forest in only one year, fir trees in 2-3 (USDA 2016). Hébert *et al.* (2003) found that the outbreaks of ***Lambdina fiscellaria*** (Figure 38) have a sudden rapid increase and patchy distribution across wide areas. This means that predicting where control is needed can be difficult. To be prepared, it is necessary to conduct egg surveys, a tedious and expensive process. But Hébert and coworkers found a simpler means. They used white polyurethane foam substrates with the Luminoc insect trap and a portable light trap. These oviposition traps were highly efficient for sampling eggs and the results were highly correlated with those of extracting eggs from mosses on 1-m branches.

Otvos and Bryant (1972) pointed out the importance of assessing ***Lambdina fiscellaria*** eggs (Figure 37), present September to June, as a means to help them prepare for potentially devastating years. The larvae that cause the damage are present for only two weeks before the damage becomes serious. By counting eggs, managers can assess and prepare for the upcoming year. These larvae are able to cause great damage not by fully consuming leaves, but by nibbling the ends of leaves, causing rapid and permanent desiccation (USDA 2016).

But all is not well for the eggs of the eastern hemlock looper (***Lambdina fiscellaria fiscellaria***; Figure 36). A pest on the balsam fir, ***Abies balsamea*** (Figure 39), the eggs (Figure 37) of this species are subject to parasitism (Otvos 1977). Otvos experimented with these in the lab using eggs collected on the peat moss ***Sphagnum*** spp. (Figure 44), the lichen (*Usnea* sp.; Figure 43) and on birch bark (*Betula* spp.; Figure 45). Otvos found that the percentage of mortality for overwintering eggs is inversely related to the difference between the mean winter temperature and normal winter temperature. Mortality from parasites was about the same for eggs collected in autumn and spring.

Figure 44. ***Sphagnum magellanicum*** and ***Sphagnum fimbriatum***, egg laying sites for ***Lambdina fiscellaria fiscellaria***. Photo from NY Botanical Garden, through Public Domain.

Figure 45. Birch (*Betula*) bark where ***Lambdina fiscellaria fiscellaria*** deposits eggs. Photo by Sue Sweeney, through Creative Commons.

The hemlock looper also uses mosses for pupation. ***Lambdina fiscellaria somniaria*** (Figure 46-Figure 48) uses both mosses and bark crevices on the lower branches and tree trunks as well as debris on the ground near the host trees, providing them with protection during this stage (Willhite 2013). In Alaska, when it is time for pupation, the full-fed larvae of ***Lambdina fiscellaria*** extend a silken thread and descend from the conifer needles to the ground where they pupate under mosses or bark scales or in crevices of rotting tree stumps (Torgersen & Baker). In 14-20 days the adult emerges.

Figure 46. ***Lambdina fiscellaria somniaria*** (hemlock looper) larva, a species that uses mosses for pupation. Photo from USFS, through Public Domain.

Figure 47. ***Lambdina fiscellaria somniaria*** larva in moss. Photo from USFS, through Public Domain.

Figure 48. ***Lambdina fiscellaria somniaria*** pupa in moss. Photo from USFS, through Public Domain.

LASIOCAMPOIDEA

Lasiocampidae – Snout Moths

Norman (1871) noted that ***Macrothylacia rubi*** (as ***Lasiocampa rubi***; Figure 49-Figure 50) larvae swarm on mosses in autumn in Morayshire, Scotland. These larvae are known to the ophthalmologists because their hairs cause conjunctivitis of the eye.

Figure 49. ***Macrothylacia rubi*** female adult. In Scotland, larvae of this species swarm on mosses in autumn. Photo by Jérôme Albre, with permission.

Figure 50. ***Macrothylacia rubi*** female adult. Larvae of this species swarm on mosses in autumn in Scotland. Photo by Jérôme Albre, with permission.

Some of the interactions get complicated. ***Bracca*** sp. occurs on the ground where moss and leaf litter are common in their habitat between tree buttresses (Brown 2006). What makes this interesting is that the ***Bracca*** sp. mimics the coral snake (*Hemibungarus calligaster*) in the Philippines. These two species share this habitat.

NOCTUOIDEA

Arctiidae – Tiger Moths *etc*.

You may be familiar with this family through the woolly bear caterpillar. Few members of the family seem to be bryophyte dwellers. Nevertheless, I have already noted that the subfamily **Lithosiinae** eat bryophyte capsules (Liu 1989 in Fang & Zhu 2012). Yuanfu (1989) concluded that the large number of species and individuals in this family that occur in the tropical mountain rainforest of Hainan Island can "be explained" by the large number of mosses and lichens here.

The larvae of ***Cybosia mesomella*** (Figure 51-Figure 52) (sometimes placed in **Erebidae**) consume liverwort leaves, particularly the genus ***Jungermannia*** (Figure 53), as well as lichens (Coutin 2004). Some of the larvae of the lichen moths (**Lithosiinae**) (*e.g.* ***Hypoprepia miniata***; Figure 54-Figure 55) feed on mosses as well as algae and lichens (Rawlins 1984; Anonymous 2011). Members of this subfamily normally feed on cryptogams such as algae, lichens, and bryophytes, eating only the photosynthetic partner in the lichens (Simonson 2016).

Figure 51. ***Cybosia mesomella*** larva, a species that eats the leafy liverwort ***Jungermannia***. Photo by Wolfgang Wagner, with permission.

Figure 52. ***Cybosia mesomella*** adult, a species that eats leafy liverworts as larvae. Photo by Stanislav Krejčik, through Creative Commons.

Figure 53. ***Jungermannia leiantha*** with perianths, a genus that is a food source for ***Cybosia mesomella***. Photo by Hermann Schachner, through Creative Commons.

Figure 54. ***Hypoprepia miniata*** larva, a species that feeds on both mosses and lichens. Its coloration hides it well among mosses. Photo by M. J. Hatfield, through Creative Commons.

Figure 55. ***Hypoprepia miniata*** adult. Photo by Tom Peterson, Fermilab, through Public Domain.

In northern Europe ***Nudaria mundana*** (Figure 56) larvae feed on both lichens and liverworts growing on rocks (Forster & Wohlfahrt 1960).

Figure 56. ***Nudaria mundana*** adult; larvae feed on lichens and liverworts on rocks. Photo by James K. Lindsey, with permission.

Erebidae

Many of the bryophyte-feeding species have been removed from **Arctiidae** and placed in **Erebidae**, whereas other systematists keep them in **Arctiidae**. I have chosen to list them under **Erebidae** because the majority of bryophyte feeders are grouped here. My usual source for nomenclature, Encyclopedia Online, is inconsistent in its placement of them.

Atolmis rubricollis (Figure 57-Figure 59) is one of these species. Its larvae feed on mosses and lichens growing on the trunks of trees (epiphytes) (Shield 1856; Dincă 2005). Hence, it is not surprising that the pupae occur under moss, but on decaying trees. ***Atolmis rubricollis*** is a tiny, inconspicuous moth that makes its winter cocoon in mosses and litter (Coutin 2004).

Figure 57. ***Atolmis rubricollis*** larva, a stage that eats mosses and makes cocoons there on trees. Photo by Harald Süpfle, through Creative Commons.

Figure 58. ***Atolmis rubricollis*** pupa on moss where it spends its winter. Photo by Harald Süpfle, through Creative Commons.

Figure 59. ***Atolmis rubricollis*** adult, emergent from a pupa that overwinters in mosses and litter. Photo by Sanja565658, through Creative Commons.

Larvae of both ***Miltochrista miniata*** (Figure 60-Figure 62) and ***Lithosia quadra*** (Figure 63-Figure 64) are bryophyte and lichen feeders in Romania (Dincă 2005). Likewise, ***Dysauxes ancilla*** (Figure 65-Figure 67) and the genus ***Eilema*** include bryophytes in their larval diet there, including ***E. lurideola*** (Figure 68-Figure 70), ***E. complana*** (Figure 71-Figure 72), ***E. pseudocomplana*** (Figure 73), and ***Eilema sororcula*** (Figure 74-Figure 76). In addition to these, Wagner (2016b) adds ***E. morosina*** (Figure 77-Figure 80) as a species that includes mosses in its diet in Europe.

Figure 60. ***Miltochrista miniata*** eggs on rotting wood, a species whose larvae include mosses among their food. Photo by Wolfgang Wagner, with permission.

Figure 61. ***Miltochrista miniata*** larva on moss, one of its food sources. Photo by Wolfgang Wagner, with permission.

Figure 62. ***Miltochrista miniata*** adult, a species whose larvae feed on bryophytes. Photo by Stanislav Krejčík, through Creative Commons.

Figure 63. ***Lithosia quadra*** larva, a species that includes mosses and lichens in its diet. Photo by Wolfgang Wagner, with permission.

Figure 64. ***Lithosia quadra*** adult, a species whose larvae feed on bryophytes. Photo by František Šaržík, through Creative Commons.

Figure 65. ***Dysauxes ancilla*** larva, a species that includes mosses in its diet. Photo by Wolfgang Wagner, with permission.

Figure 66. ***Dysauxes ancilla*** habitat. Photo by Wolfgang Wagner, with permission.

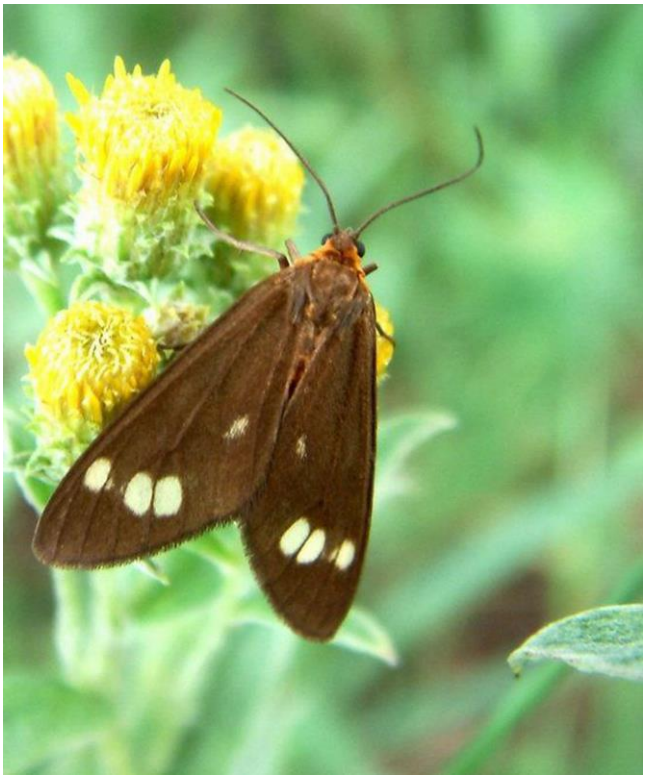

Figure 67. ***Dysauxes ancilla*** adult, a species whose larvae include mosses in their diet. Photo by Ondřej Zicha, through Creative Commons.

Figure 68. ***Eilema lurideola*** larva, a moss and lichen feeder. Photo by Wolfgang Wagner, with permission.

Figure 69. ***Eilema lurideola*** pupa, a species that includes bryophytes in its larval diet. Photo by Wolfgang Wagner, with permission.

Figure 70. ***Eilema lurideola***, a species whose larvae feed on a variety of plants, including mosses. Photo by Kurt Kulac, through Creative Commons.

Figure 71. ***Eilema complana*** larva on moss, one of its food items. Photo by Tristan Bantok, with permission.

Figure 72. ***Eilema complana*** adult, a species with a broad larval diet that includes mosses. Photo by Ondřej Zicha, through Creative Commons.

Figure 73. ***Eilema pseudocomplana*** adult, a species whose larvae include mosses in the diet. Photo by Matthew Gandy, with permission.

Figure 74. ***Eilema sororcula*** larva, a species with a broad diet that includes mosses and lichens. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 75. ***Eilema sororcula*** larval head, a species having a broad diet that includes mosses and lichens. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 76. ***Eilema sororcula*** adult, a species whose larvae include mosses in their diet. Photo by Miroslav Fiala, through Creative Commons.

Figure 77. ***Eilema morosina*** larva, a moss eater. Photo by Wolfgang Wagner, with permission.

Figure 78. ***Eilema morosina*** larval habitat. Photo by Wolfgang Wagner, with permission.

Figure 79. ***Eilema morosina*** pupa. Photo by Wolfgang Wagner, with permission.

Figure 80. ***Eilema morosina*** adult, a species whose broad larval diet includes mosses. Photo by Wolfgang Wagner, with permission.

Hypercompe scribonia (syn. = *Ecpantheria deflorata*; Figure 81-Figure 82) actually eats the thallose liverwort, ***Conocephalum conicum*** in western Indiana, USA (Figure 83) (Spencer *et al*. 1984). It normally feeds on two species of *Plantago* (Figure 84), a seed plant, and Spencer and coworkers suggest that the surface is similar to that of the liverwort and the two plants grow intermixed, possibly causing the shift despite major differences in chemistry. They noted this liverwort feeding behavior in the autumn, which suggests the possibility that the chemical shift may be a means of preparing for winter. Nevertheless, they raised several larvae to adults in the lab, using ***C. conicum*** as the only food source.

Figure 81. ***Hypercompe scribonia*** larva, a herbivore on ***Conocephalum conicum***. Photo by Micha L. Rieser, through Creative Commons.

Figure 82. ***Hypercompe scribonia*** adult, a species whose larvae consume the liverwort ***Conocephalum conicum***. Photo by R. A. Nonenmacher, through Creative Commons.

Figure 83. ***Conocephalum conicum***, a food source for ***Hypercompe scribonia***. Photo by Hermann Schachner, through Creative Commons.

Figure 84. ***Plantago major***, a genus that is normal food for ***Hypercompe scribonia***. Photo by Olivier Pichard, through Creative Commons.

The secondary compounds of ***Conocephalum conicum*** (Figure 83) are well known. This liverwort is rich in mono- and sesquiterpenoids (Asakawa *et al.* 1976; Markham & Porter 1978; Spencer 1979). We also know that some terpenoids from liverworts inhibit Lepidoptera feeding (Wada & Munakata 1971). *Plantago* (Figure 84), on the other hand, is rich in iridoid glycosides (Jensen *et al*. 1975). It is possible that whatever permits the larvae to feed on the toxic glycosides also permits them to feed on the terpenoids in liverworts.

The **Lithosiini** have been known from several studies as bryophyte feeders (Forbes 1960; Holloway 1988; Aba 2013). Moreno *et al*. (2014) summarized feeding in the family by stating that the members of the tribe **Arctiini** feed on a wide range of plant species whereas the **Lithosiini** specialize on lichens, algae, and bryophytes (Wagner 2009).

Several species of Tribe **Lithosiini** resemble **Microlepidoptera** as adults (Coutin 2004). Furthermore, the larvae consume liverworts. Larvae of ***Thumatha senex*** (Figure 85) likewise consume liverwort leaves, particularly the genus ***Jungermannia*** (Figure 53), as well as lichens. Manley (2009) treated ***Thumatha senex*** as a nighttime cryptogam feeder that includes mosses in its diet (Macek *et al*. 2007; Manley 2009).

Figure 85. ***Thumatha senex*** adult, a liverwort and lichen consumer. Photo by James K. Lindsey, with permission

Lymantriidae – Tussock Moths

Lymantria dispar (Figure 86-Figure 87), the gypsy moth, spins threads over its retreat in a crack in the bark (Rennie 1857). Occasionally they may use a curtain of moss such as ***Hypnum*** (Figure 88) growing there instead of spinning these threads.

Figure 86. ***Lymantria dispar*** (gypsy moth) male adult. Larvae of this species sometimes use mosses instead of spinning threads over their retreat on bark. Photo by Jérôme Albre, with permission.

Figure 87. **Lymantridae** larva. ***Lymantria dispar*** sometimes uses mosses instead of spinning a cocoon. Photo by Jérôme Albre, with permission.

Figure 88. ***Hypnum cupressiforme*** with young sporophytes on bark. ***Hypnum*** is sometimes used to cover larvae of ***Lymantria dispar***. Photo by Dick Haaksma, with permission.

Noctuidae – Owlet Moths

Haines and Renwick (2009) summed up the paucity of bryophagous insects. They considered that three deterrents were responsible for their limited consumption: chemical defenses, low digestibility, and low nutrient content. They examined this phenomenon by testing pre and post-ingestive defenses of four species of mosses [***Bryum argenteum*** (Figure 89), ***Climacium americanum*** (Figure 90), ***Leucobryum glaucum*** (Figure 91), ***Sphagnum warnstorfii*** (Figure 92)]. Even when they had no other choice, larvae of ***Trichoplusia ni*** (cabbage looper; Figure 93-Figure 94) ate considerably more lettuce or wheat germ than they did any of the moss species. Post ingestive responses could only be evaluated in ***C. americanum*** because the larvae ate too little of the other species for evaluation. Digestibility, assimilation, and overall utilization efficiency did not differ between lettuce and ***C. americanum***. In disk choice experiments, ethanol extracts of ***Leucobryum glaucum*** were deterrent, explaining why this was the least consumed moss in the experiment and providing evidence of pre-ingestive mechanisms. The hypotheses of poor nutrient content and low digestibility were not supported in these experiments.

Figure 89. ***Bryum argenteum***, a moss avoided by ***Trichoplusia ni*** in feeding trials. Photo by Michael Becker, through Creative Commons.

Figure 90. ***Climacium americanum***, a moss avoided by ***Trichoplusia ni*** in feeding trials. Photo by Li Zhang, with permission.

Figure 91. ***Leucobryum glaucum***, a moss avoided by ***Trichoplusia ni*** in feeding trials. Photo by James K. Lindsey, with permission.

Figure 92. ***Sphagnum warnstorfii***, a moss avoided by ***Trichoplusia ni*** in feeding trials. Photo by Michael Lüth, with permission.

Figure 93. ***Trichoplusia ni*** larva, a species that avoids eating bryophytes. Photo by M. J. Hatfield, through Creative Commons.

Figure 94. ***Trichoplusia ni*** adult, a species whose larvae do not choose mosses even with no other choice. Photo by Barry Stewart, with permission.

Several species in Romania feed on mosses (Dincă 2005). These include ***Parascotia fuliginaria*** (Figure 95), ***Calymma communimacula*** (Figure 96)**,** ***Cryphia receptricula*** (Figure 97), and ***Cryphia raptricula*** (Figure 98). Wagner (2016a) also includes ***Cryphia muralis*** (Figure 99) and ***C. algae*** (Figure 100-Figure 102) among the moss feeders in Europe.

Figure 95. ***Parascotia fuliginaria*** adult, a species whose larvae include mosses in their diet. Photo by Biopix, through Creative Commons.

Figure 96. ***Calymma communimacula*** adult, a species whose larvae include mosses in their diet. Photo by Dumi, through Creative Commons.

Figure 97. ***Cryphia receptricula*** adult, a species whose larvae feed on mosses. Photo by Peter Huemer, through Creative Commons.

Figure 98. ***Cryphia raptricula*** adult, a species whose larvae eat mosses. Photo by Biopix, through Creative Commons.

Figure 99. ***Cryphia muralis*** larva, a species that includes mosses and lichens in its diet. Photo by Wolfgang Wagner, with permission.

Figure 100. ***Cryphia algae*** larva, a species that eats mosses, algae, and lichens. Photo by Wolfgang Wagner, need permission.

Figure 101. ***Cryphia algae*** larval habitat. Photo by Wolfgang Wagner, with permission.

Figure 102. ***Cryphia algae*** adult, a species whose larvae include mosses in their diet. Photo by Jérôme Albre, with permission.

Kimmo Silvonen (pers. comm. 1 March 2016) told me about ***Caradrina montana*** (Figure 103) in Europe. He found this larva on a rocky hill on a moss. It accepted the moss as food during rearing, but it may be a polyphagous species that eats a variety of plants. Among these, it feeds on alfalfa leaves in northwestern North America (McLeod 2005).

Figure 103. ***Caradrina montana*** larva, a species that can be reared on moss. Photo courtesy of Kimmo Silvonen.

The feeding of ***Agrotis*** sp. (Figure 104) on moss capsules (Figure 105-Figure 106) of ***Haplocladium microphyllum*** (Figure 107) is well documented. Fang and Zhu (2012) experimented to see what else they would eat and found they would feed to various degrees on capsules of ***Ditrichum pallidum*** (Figure 108), ***Funaria hygrometrica*** (Figure 109), ***Physcomitrium sphaericum*** (Figure 110), ***Pogonatum inflexum*** (Figure 111), and ***Trematodon longicollis*** (Figure 112). The latter two species were only sparsely grazed and caused a high mortality rate. Fang and Zhu suggested that the lipid content may be important in their selection.

Figure 104. ***Agrotis puta*** adult male, member of a genus in which larvae of at least some species feed on moss capsules. Photo by Jérôme Albre, with permission.

Figure 105. ***Agrotis*** eating capsules of ***Haplocladium microphyllum***. Photo by Rui-Liang Zhu, with permission.

Figure 106. ***Haplocladium microphyllum*** capsules missing due to feeding by ***Agrotis***. Photo by Rui-Liang Zhu, with permission.

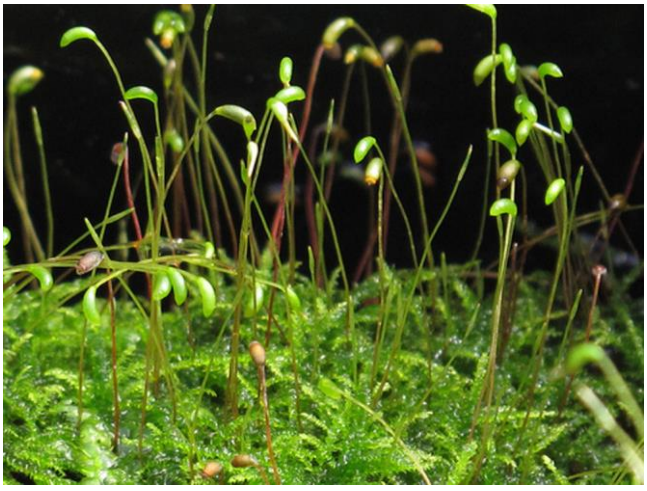

Figure 107. ***Haplocladium microphyllum*** with capsules. Species of ***Agrotis*** feed on these capsules. Photo by Scott Zona, through Creative Commons.

Figure 108. ***Ditrichum pallidum*** with capsules that serve as food for ***Agrotis***. Photo by Bob Klips, with permission.

Figure 109. ***Funaria hygrometrica*** with capsules that serve as food for ***Agrotis***. Photo by Li Zhang, with permission.

Figure 110. ***Agrotis*** sp. eating a capsule of ***Physcomitrium sphaericum***. Photo by Rui-Liang Zhu, with permission.

Figure 111. ***Pogonatum inflexum*** with capsules that serve as food for ***Agrotis***. Photo through Creative Commons.

Figure 112. ***Trematodon longicollis*** capsules that serve as food for ***Agrotis***. Photo by Bobby Hattaway, through Creative Commons.

Agrotis sp. avoids the capsules of ***Pogonatum inflexum*** (Table 1; Fang & Zhu 2012). On the other hand, when only ***Haplocladium microphyllum*** was available as food, a late-instar larva consumed 190 capsules (Figure 113). Similar herbivory occurred on ***Physcomitrium sphaericum*** and ***Funaria hygrometrica*** (Figure 113) Fang and Zhu compared the phenolic content (Figure 114) and nutrient content (Figure 115) among several mosses. They found that These capsules contained significantly more lipids that the tracheophyte leaves from the same environment (Figure 115).

Table 1. 24-hour consumption of moss capsules in three samples of 30 capsules each by an individual ***Agrotis*** sp. in early, mid, and late instar stages. Based on Fang & Zhu 2012.

	instars		
	early	**mid**	**late**
Haplocladium microphyllum	30 –	30 –	30
Funaria hygrometrica	30 –	30 –	30
Physcomitrium sphaericum	30 –	30 –	30
Trematodon longicollis	30 –	30 –	28
Ditrichum pallidum	30 –	2 –	3
Pogonatum inflexum	5 –	4 –	7

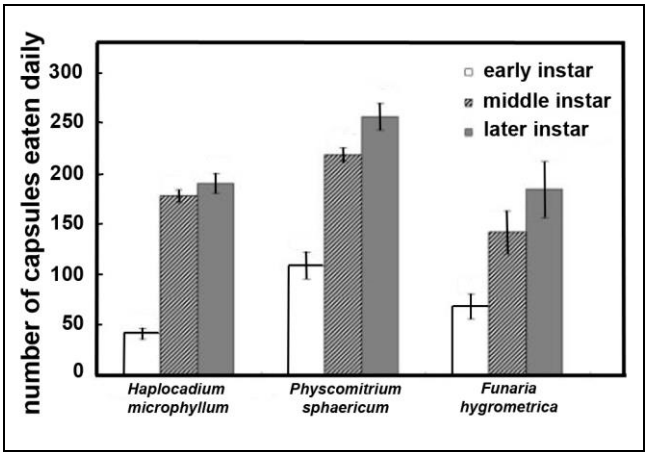

Figure 113. Number of moss capsules consumed in 24 hours by individuals of ***Agrotis*** sp. Based on Fang & Zhu 2012.

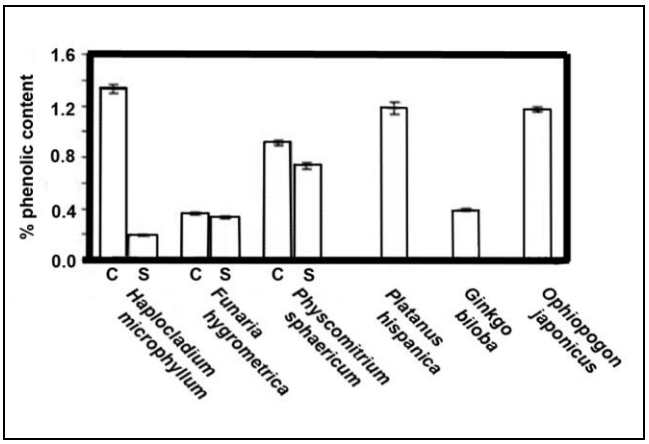

Figure 114. Phenolic content of capsules of three mosses compared to that of three tracheophytes. Based on Fang & Zhu 2012.

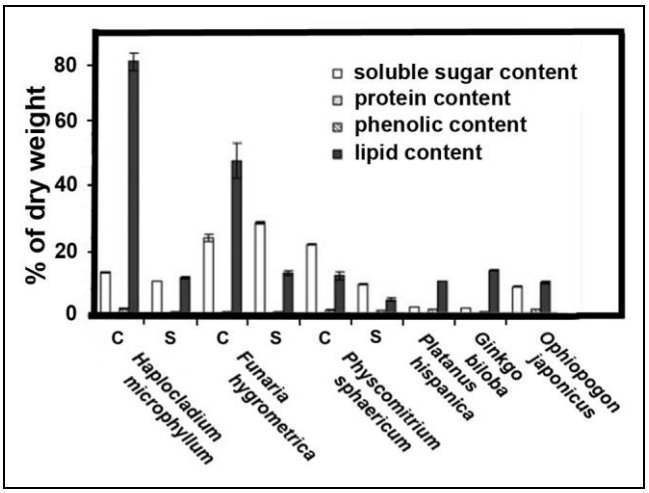

Figure 115. Percentage nutrient content of moss capsules (C) and setae (S) by weight, compared to that of three tracheophytes. Leaves of *Ophiopogon japonicus* (flowering plant) were fresh; the other two seed plant leaves were fallen. Redrawn from Fang & Zhu 2012.

In Europe under mosses on the spreading beech roots, one can find the brown pupae (Figure 116) of ***Herminia grisealis*** (**Noctuidae**; Figure 117-Figure 119) (Shield 1856).

Figure 116. ***Herminia grisealis*** pupa; these can be found under mosses on beech roots. Photo by Wolfgang Wagner, with permission.

Figure 117. ***Herminia grisealis*** larva, a species that pupates under mosses. Photo by Wolfgang Wagner, with permission.

Figure 118. ***Herminia grisealis*** adult, gray color variant, a species that pupates under mosses among beech roots. Photo by ©entomart, through Creative Commons.

Figure 119. ***Herminia grisealis*** brown color variant, a species that pupates under mosses among beech roots. Photo by Donald Hobern, through Creative Commons.

Larvae of the green mahoe moth (***Feredayia graminosa***; Figure 120-Figure 123) in New Zealand feeds on mahoe (*Melicytus ramiflorus*; Figure 124), a woody member of the violet family (Harris 2015). But when it becomes an adult, it rests on tree trunks, where its 18 mm length makes it very obvious on white bark. Fortunately for these moths, they are able to seek out epiphytic mosses on these trees, resting on them during the day undetected because their cryptic coloration hides them from the casual view of avian predators. They feed at night when their predators are sleeping. The males smell like vanilla and use their enlarged hind wings to fan this odor over females during mating.

Figure 120. ***Feredayia graminosa*** adult on moss, showing its ability to blend with mosses. Photo by Donald Hobern, through Creative Commons.

Figure 121. ***Feredayia graminosa*** adult looking like a patch of moss on bark. Photo by Jon Sullivan, with permission.

Figure 122. ***Feredayia graminosa*** blending with mosses and lichens on bark as it rests during the day. Photo by Pete McGregor, with permission.

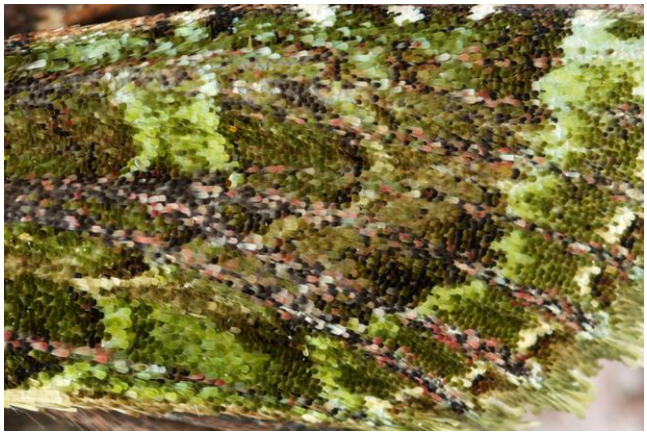

Figure 123. ***Feredayia graminosa*** wing scales showing cryptic coloration that blends with lichens and mosses on bark. Photo by Jon Sullivan, with permission.

Figure 124. ***Melicytus ramiflorus***, food plant of ***Feredayia graminosa***. Photo by Jon Sullivan, through Creative Commons.

Rennie (1857) discovered interesting behavior of a species of the moth in the genus ***Bryophila*** (Figure 125-Figure 126). This caterpillar is small and feeds on minute mosses and lichens on old walls. It builds its cocoons from moss branchlets cut into suitable lengths, including a portion of earth with these detached pieces (Figure 126). In making its cocoon, it arranges the earth on the inside and moss on the outside to make a vault. If this species is deprived of soil in the lab, but provided with moss, it will build a hollow ball by interweaving the moss.

Shield (1856) reported that larvae of ***Bryophila domestica*** (=*Cryphia domestica*; Figure 125) include bits of mosses in their webbing (Figure 126). They bite their way out of these cocoons when the weather is warm, returning to them and resealing them when it is again too cold. The included mosses and other bits help to conceal them while they are in hiding. Shield observed them biting off bits of moss and weaving them between the threads of silk, completely hiding the larva inside.

Figure 125. ***Bryophila domestica*** adult, a species whose larvae include mosses in their webbing. Photo by Ian Kimber, with permission.

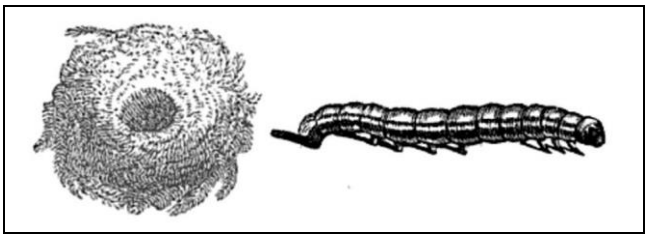

Figure 126. ***Bryophila domestica*** (maybe) nest with mosses and caterpillar. Image by James Rennie (book from 1800's), through public domain.

Acronicta myricae (see Figure 127) is also among the moths that spin silken cocoons, in this case covered with mosses (Buckler 1871).

Figure 127. ***Acronicta euphorbiae*** larva; ***Acronicta myricae*** builds its cocoons on mosses. Photo by Harald Süpfle, through Creative Commons.

We don't always know the role of the mosses, and they may only be indicators of a suitable environment. For example, in areas with boreal forest, ***Xestia rhaetica*** (Figure 128) is distributed in the old, moist spruce forests where mosses form a thick layer (Mönkkönen & Mutanen 2003). But what is the role of these mosses, if any?

Figure 128. ***Xestia rhaetica*** adult, an occupant of old, moist spruce forests with a thick layer of mosses. Photo by Dumi, through Creative Commons.

Now there appears to be a new noctuid added to the bryophages. Timea Deakova has sent me images that appear to be those of ***Noctua pronuba*** (Figure 129-Figure 130). A hoard of these hungry larvae devoured a large portion of her experiments on nitrogen. Could it be the nitrogen in the experiment or do these larvae just like mosses?

Figure 129. ***Noctua pronuba*** larva eating ***Bryum capillare*** and surrounded by frass. Photo courtesy of Timea Deakova.

Figure 130. ***Noctua pronuba*** larva on ***Polytrichum juniperinum***. Photo courtesy of Timea Deakova.

Summary

In the **Geometridae**, larvae are often colored to blend with their surroundings (including bryophytes), having patterns of brown, green, and gray. Some of these larvae can do considerable damage to the bryophytes, particularly mosses, through herbivory. Some overwinter among mosses as pupae. Others lay eggs on mosses, close to the tree leaves that are eaten by the larvae. And some use the water associated with the bryophytes. The hemlock looper often lays eggs among mosses, then becomes a nuisance when its larvae migrate to conifer leaves and consume the leaf tips, killing the leaves.

One member of the **Lasiocampidae** swarm on mosses in autumn – for whatever reason. Few of the **Arctiidae** are bryophyte associates, but some members of the subfamily **Lithosiinae** eat bryophyte capsules. Other members feed on liverwort leaves or moss leaves. The **Erebidae**, sometimes included in the **Arctiidae**, includes most of the bryophyte dwellers that were once **Arctiidae**. **Lymantridae** sometimes use mosses in place of making a web to hide themselves.

Some **Noctuidae** find bryophytes distasteful; in ***Climacium americanum***, digestibility, assimilation, and overall use efficiency did not differ from that of lettuce, but there was far more consumption of lettuce. However, some species do feed on mosses. And a species of ***Agrotis*** feeds on moss capsules, but avoids those of ***Pogonatum inflexum***. In fact, the other moss capsules contained more lipids than the local tracheophytes. Some species also use mosses for pupation sites. And some adults have coloration that permits them to rest on tree-trunk bryophytes without being seen easily. Some species incorporate bryophytes in their cocoons.

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Thank you to John Steel for his continued support and for sending me articles from the Otago Daily Times about

Lepidoptera associated with mosses. Timea Deakova has generously shared ongoing research and images with me. Thank you to Rui-Liang Zhu for sharing research and images from his lab with me. Adaises Maciel-Silva provided me with images from research in his lab. Once again, I appreciate all the photographers who have placed their images in Creative Commons or given me permission for use. Scott Zona alerted me to the wonderful image of the lampet moth caterpillar.

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CHAPTER 12-16
TERRESTRIAL INSECTS:
HOLOMETABOLA – MECOPTERA

Figure 1. ***Boreus hyemalis***, female, among ***Polytrichum piliferum***, Thetford Warren Lodge, Norfolk, UK. Photo by Brian Eversham, with permission.

MECOPTERA – SCORPIONFLIES

The **Mecoptera** comprise a small order of about 550 known species (Wikipedia 2016), 9 families, and 32 genera (Byers & Thornhill 1983). They were more abundant in the Permian, Mesozoic, and Tertiary periods, with 348 species in 87 genera and 34 families known. They are known as scorpionflies because of the position of the

Scorpionfly larvae (Figure 2) are among those that live in mosses (as well as damp soil) (Miall 1902). It is interesting that many of the relatively few **bryophagous** animals (including arthropods) often show unusually high levels of winter activity. Larvae of snow scorpionflies (**Mecoptera**: **Boreidae**) are active ONLY in the winter in temperate regions, hopping about and even mating on the snow (Figure 3). Some insects, including gall aphids, move from a summer angiosperm host to a winter moss host. Could these snow scorpionflies and gall aphids, and probably other insects, be sequestering compounds from mosses that allow them to remain active at sub-freezing temperatures? Aside from chemistry, the correlation between bryophagy and cold weather could be explained by the simple fact that mosses remain green throughout the winter, and therefore might become a more attractive host plant during this period. Or do the winter-active fauna simply have the right enzymes or gut *p*H to permit them to gain nutrients from mosses and survive by being active at a time of year when predators are limited in their activity?

Figure 2. ***Panorpa*** sp. larva, genus that lives among bryophytes. Photo by Pierre-Marc Brousseau, with permission.

Figure 3. ***Boreus westwoodi*** mating on snow. Photo by hrasiranta, with online permission.

Choristidae

Tillyard (1926) was among the early reporters on the relationship of the **Mecoptera** with bryophytes. He considered the Australian *Choristes* to be both a bryophyte resident and a **bryophage** (eats bryophytes). However, this genus name has been pre-empted by other phyla (the genus *Choristes* is a sea snail in the Gastropoda) and was changed to ***Chorista*** (Figure 4) in the **Mecoptera** (see <http://direct.biostor.org/reference/80557.text>).

Figure 4. ***Chorista australis*** adult, a bryophyte dweller and bryophage. Photo by John Tann, through Creative Commons.

Chorista is a small genus of only two apparent species. Its family, the **Choristidae**, lives among mosses as larvae (Wikipedia 2015). The larvae are unusual among holometabolous insects in having **compound eyes** with ommatidia, a trait shared by the scorpionflies ***Neopanorpa*** (Figure 93) and ***Panorpa*** (Figure 94), both in the **Panorpidae** and also bryophyte dwellers (Ramel 2016). Compound eyes are best at detecting motion. Could it be that living among bryophytes selects for these compound eyes in an environment where there is limited light and many of the inhabitants tend to blend in until they move?

The food of ***Chorista*** (Figure 4) seems to be contested, or perhaps just wide ranging. Tillyard (1926) considered them to eat mosses. On the other hand, in the lab both larvae and adults fed on dead insects, fresh fruit, strained carrots, and beef (Bush 1967; Byers & Thornhill 1983).

Members of ***Chorista*** (Figure 4) oviposit loose clusters of eggs, using pre-existing cavities in moist soil (Miyake 1912; Tillyard 1926; Byers 1963; Riek 1970). We need to look for the eggs among or under the bryophytes as well. If the larvae feed on bryophytes, surely the eggs must be near the host plants.

Boreidae

The family **Boreidae** has only three genera (Cannings & Scudder 2005). ***Boreus*** (Figure 1, Figure 3, Figure 5-Figure 14, Figure 18-Figure 20, Figure 24, Figure 27) has 14 known species in Eurasia and 12 in North America; only two of these are in the eastern USA. ***Hesperoboreus*** (Figure 89) has only two species, confined to western North America from Washington to California. ***Caurinus*** (Figure 28-Figure 30, Figure 38-Figure 39) has two species, one occurring only in Oregon and Washington, USA, and another in Alaska. Both larvae and adults of the **Boreidae** feed exclusively on bryophytes (Russell 1979a, b). Because of their small size and clandestine habitat, it is likely that more species await our discovery.

The **Boreidae** are small (2-5 mm), dark-colored mecopterans and are most easily seen when they are on the snow (Figure 5) (Byers 2002). They resemble fleas, but use their legs to propel them. When they land, they tuck their legs against their bodies (Figure 6) and resemble a bit of dirt on the surface of the snow. The dark body color (Figure 5-Figure 13) may help them to maintain sufficient temperature when they are bouncing around on snow (Cannings & Scudder 2005).

Figure 5. ***Boreus brumalis*** on snow. Photo by J. Mihuc, through Creative Commons.

Figure 6. ***Boreus brumalis*** adult, showing the legs tucked against the body as they are when the adults land after a hop. Photo by Tom Murray, through Creative Commons.

The **Boreidae** are boreal, with the adults appearing in winter or at high elevations. They are sufficiently different from other **Mecoptera** that some systematists consider them to be a separate order, the **Neomecoptera** (Cannings & Scudder 2005). The larvae lack both abdominal prolegs and conspicuous dorsal setae. They have lateral eyes and usually have three **ommatidia** (units of the compound eye) per eye.

Several researchers have provided lists of moss species from which boreids have been collected or on which they have been reared (*e.g.* Svensson 1972; Cooper 1974; Penny 1977). Both larvae and adults in the **Boreidae** feed on mosses (Svensson 1972; Cooper 1974; Penny 1977; Byers & Thornhill 1983). But Brauer (1863 in Carpenter 1931) found that they also feed on other small animals that live among the moss rhizoids. And Penny (2006) stated that they feed on leaves of mosses, club mosses (*Selaginella*?), and liverworts as adults, but feed on the rhizoids of these same plants as larvae. They seem to require little food (Withycombe 1926), but need "a great deal of moisture" (Penny 2006). Penny (1977) concluded that **Boreidae** prefer mosses that form low, compact cushions with their rhizoids tightly matted. The loose mats, which had fewer **Boreidae**, may have more predator **Carabidae** beetles. Or they may lose moisture too quickly.

In contrast to ***Chorista*** (Figure 4), the **Boreidae** oviposit single eggs or small clusters in the soil surrounding moss rhizoids (Cooper 1974; Penny 1977; Byers & Thornhill 1983). Some deposit eggs among epiphytic bryophytes (Russell 1979a; Byers & Thornhill 1983).

As one might guess for a boreal species that hops about on the snow, temperature is an important parameter in the niche of **Boreidae** (Byers & Thornhill 1983), even more important than light (Cooper 1974). Nevertheless, the minimum temperature for adult activity is close to 0°C (Sauer 1966; Svensson 1966; Penny 1977; Byers & Thornhill 1983). When their mossy habitat becomes dry, the boreid larvae may go as much as 20 cm down into the soil below the mosses to attain suitable humidity (Strübing 1950).

Scorpionfly larvae [***Boreus*** (Figure 1, Figure 3, Figure 5-Figure 14, Figure 18-Figure 20, Figure 24, Figure 27), ***Caurinus*** (Figure 28-Figure 30, Figure 38-Figure 39)] feed on moss cushions on trees in damp woodlands (Penny 1977; Russell 1979a, b; Shorthouse 1979), making mosses their principal food. Adults of the family **Boreidae** are well known for their moss diet (Cooper 1974; Penny 1977).

Boreus

Although ***Boreus*** (Figure 1, Figure 3, Figure 5-Figure 14, Figure 18-Figure 20, Figure 24, Figure 27) seems always to be associated with mosses, its distribution is clearly not limited by its host mosses, but rather by some other parameter of its environment that is more restrictive (Cooper 1974). I suggest that limitation is moisture, combined with bryophytes that are suitable food. Both larvae and adults of ***Boreus*** eat mosses (Withycombe 1922; Fraser 1943; Strübing 1950; Svensson, 1966; Hågvar 2010).

Boreus brumalis (Figure 7, Figure 13) includes the mosses ***Dicranella heteromalla*** (Figure 8-Figure 9) and ***Atrichum angustatum*** (Figure 10-Figure 11) in its diet in Illinois, USA (Webb et al. 1975) and New England, USA (Maier 1984).

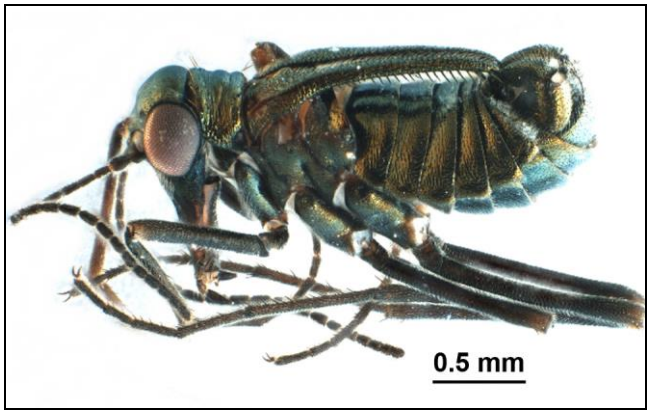

Figure 7. ***Boreus brumalis*** male showing modified wings that are used to clasp the female. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 8. ***Dicranella heteromalla*** on soil bank – food for ***Boreus brumalis***. Photo by Janice Glime.

Figure 9. ***Dicranella heteromalla*** with capsules – food and home for **Boreus brumalis**. Photo by Michael Lüth, with permission.

Figure 10. ***Atrichum angustatum***, home and food for ***Boreus brumalis***. Photo by Michael Lüth, with permission.

Figure 11. ***Atrichum angustatum***, home and food for ***Boreus brumalis***. Photo by Michael Lüth, with permission.

Desiccation can be a problem, and the moss habitat would seem to be ideal for these organisms. It typically stays moist longer than other kinds of plants, it provides cover against not only desiccation but also many kinds of predators, and it is a food source. Furthermore, being flightless, it is an advantage to have your food and cover in the same place.

This genus has a somewhat different mating behavior from that of other **Mecoptera** (Byers 2002). The male has slender, hardened wings that he uses to grasp the female (Figure 7). He manipulates her to a position above his back (Figure 12) with the lower part of her ovipositor inserted into his ninth (genital) segment (Figure 12) (Cockle 1908).

Figure 12. Mating pair of the snow scorpionfly, ***Boreus westwoodi***. Note the female is on top of the male, held by two wings of male. Photo by Barbara Thaler-Knoflach, with permission.

Boreus brumalis (Figure 7, Figure 13) feeds primarily on bryophytes (Gerson 1982). Shorthouse (1979) determined that both larvae and adults of ***Boreus brumalis*** (Figure 13) in Ontario, Canada, eat the bryophytes in the winter under the snow.

Figure 13. ***Boreus brumalis*** female adult on snow. Photo by Tom Murray, through Creative Commons.

Boreus hyemalis (Figure 1, Figure 14), an inhabitant of heaths and moors, is well known for its habitation of mosses (Plant 1994; Winnall 2009). Nevertheless, because of this seclusion, it is often overlooked (Whitehead 2010). This insect is flightless (Hågvar 2010) and can be seen moving about on the snow in exposed locations. Carpenter

(1931) reported that adults could be seen in spring and early summer among moss rhizoids and under stones, but that their activity is confined to winter. On sunny winter days they hop on the snow, as far as 15 cm in a single leap.

Figure 14. ***Boreus hyemalis*** in moss at Ellerburn Beck, UK. Photo by Roger S. Key, with permission.

Bingham (2012) found that the typical habitat for ***Boreus hyemalis*** (Figure 1, Figure 14) in Wyre Forest (UK) seemed to be oak woodlands or other open woodlands with sparse ground flora to compete with the mosses, mostly ***Polytrichastrum formosum*** (Figure 15) and ***Dicranum scoparium*** (Figure 16). He also perceived a possible connection between acid woodland and the presence of ***B. hyemalis***.

Figure 15. ***Polytrichastrum formosum***, home of ***Boreus hyemalis***. Photo by David T. Holyoak, with permission.

Figure 16. ***Dicranum scoparium***, home for ***Boreus hyemale***. Photos from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Boreus hyemalis (Figure 1, Figure 14) lays its eggs among mosses and the larvae make tunnels between the moss and the substrate – soil, logs, walls (Russell 1979a). Although many entomologists have reported this species from the mosses, only Fraser (1959) has identified the moss used for oviposition as ***Polytrichum commune*** (Figure 17). Most likely other species of bryophytes are also used. Carpenter (1931) observed that the larvae eat both moss "roots" and liverworts.

Figure 17. ***Polytrichum commune***, home and oviposition site for ***Boreus hyemale***. Photo by Michael Lüth, with permission.

Boreus in Norway takes advantage of mosses to provide protective space. This is a safe space in which they lay their eggs (Hågvar 2001). And it appears that mosses might be a site of copulation (Figure 12), an event rarely observed on the snow (Figure 3). The chambered air spaces most likely also provide space for this winter-active scorpionfly to move about in safety. Adults of ***B. elegans*** (Figure 18) and ***B. californicus*** (Figure 19-Figure 20) feed on ***Racomitrium heterostichum*** (Figure 21); larvae and pupae of ***B. elegans*** can be found under ***Brachythecium*** (Figure 22) and other mosses (Russell 1979a). Russell (1979a) has found ***B. elegans*** on mosses on a north-facing roadcut, in mosses near a hillside spring, and among mosses on logs in a coastal forest in the Pacific coastal states, USA. Both larvae and pupae were present under a mat of ***Brachythecium*** sp. and other mosses.

Figure 18. ***Boreus elegans*** adult, a species that feeds on ***Racomitrium heterostichum***. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 19. ***Boreus californicus*** male, a species that lives in compact mosses such as ***Grimmia***. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 20. ***Boreus californicus*** on one of the compact mosses it calls home. Photo by Baldo Villegas <www.discoverlife.com>, through Creative Commons.

Figure 21. ***Racomitrium heterostichum***, food for ***Boreus californicus*** and ***B. elegans***. Photo by Michael Lüth, with permission.

Figure 22. ***Brachythecium rutabulum***, home for ***Boreus elegans***. Photo by Michael Lüth, with permission.

Boreus californicus (Figure 19-Figure 20) occurs primarily east of Cascade Mountain (Russell 1979a). In western Oregon, it seems to occur in more open, rocky sites than ***B. elegans*** (Figure 18), but in some sites both species occur. Larvae of ***B. californicus*** also occur in soil under mosses in crevices of jointed basalt and under moss among grasses in deep sandy loam on a stream bank. In California, Penny (2006) found ***B. californicus*** on the tightly compacted ***Grimmia*** (Figure 23).

Figure 23. ***Grimmia longirostris***, exhibiting the compact cushion character of many **Grimmiales**. Photo by Hermann Schachner, through Creative Commons.

Boreus reductus (Figure 24) is likewise east of the Cascades, but in semi-arid regions of the Northwest (Russell 1979a, b). Although the larvae usually inhabit mosses (Russell 1979a, b), they can also occur in mats of ***Selaginella*** (Figure 25-Figure 26), a moss look-alike that is related to club mosses (tracheophytes) (Penny 1977).

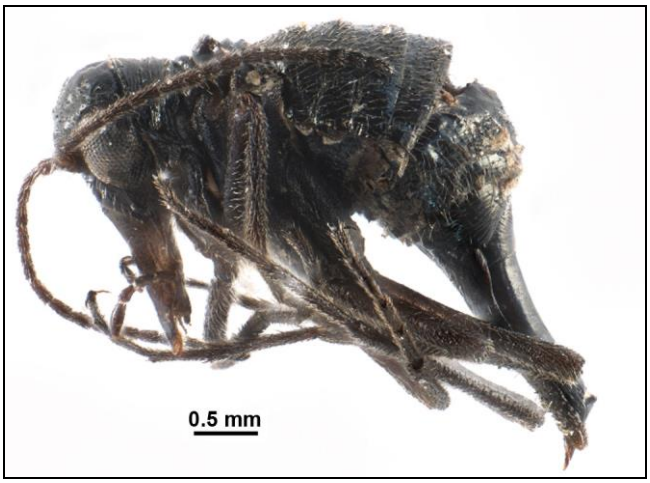

Figure 24. ***Boreus reductus*** female, a species east of the Cascades that eats mosses and ***Selaginella***. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 25. ***Selaginella wallacei*** in its epiphytic habitat where one might find ***Caurinus dectes***. Photo by Paul Slichter, with permission.

Figure 26. ***Selaginella wallacei***, home for ***Caurinus dectes***. Photo by Paul Slichter, with permission.

In Fennoscandia, ***Boreus westwoodi*** (Figure 3, Figure 12, Figure 27) and ***B. hyemalis*** (Figure 14) larvae develop in the soil that occurs among the mosses (Hågvar 2010). The adults hatch in autumn before the new snow becomes established. Each adult migrates in its own separate and fixed direction by continuous jumping, achieving 1.2 m per minute (Hågvar 2001). The adults spend most of winter below the snow, among the mosses. On warmer days when the temperature is just above freezing, they climb tree trunks to reach the snow surface where they hop about. Jumping about on sunny, cloudless days may be risky because the temperature is likely to drop rapidly as the sun sets.

Figure 27. ***Boreus westwoodi*** adult female on one of the mosses where it lives. Photo by Petr Kočárek, with permission.

These adults lay eggs throughout the winter (Hågvar 2001) and ***Boreus hyemalis*** (Figure 14) is able to produce a maximum of 320 eggs per female (Steiner 1937). They oviposit in mosses in the **subnivean** (beneath snow) air spaces (Hågvar 2001), laying 1-2 eggs at a time (Withycombe 1922; Strübing 1950; Svensson 1966; Cooper 1974). Larvae develop there, feeding on the mosses, and continue to feed on them as adults.

Caurinus

I was delighted when, in January of 2008, David Wagner sent me a note about his former student who had studied a small boreid, ***Caurinus dectes*** (Figure 28-Figure 30) (Russell 1979a, b, 1982). Unlike ***Boreus*** (Figure 1, Figure 3, Figure 5-Figure 14, Figure 18-Figure 20, Figure 24, Figure 27), this insect feeds primarily on liverworts! Wagner helped me contact his former student, Loren Russell, who has been very helpful in providing me with further information. Russell learned how to find his study insect by a change in the branching pattern of the leafy liverwort, ***Scapania bolanderi*** (Figure 31), the preferred food of the boreid (David Wagner, pers. comm. January 2008). It chewed the tender tips, which caused the liverwort to branch, causing a fluffy appearance that is in evidence even from a distance! The larvae feed on the liverwort in mines or galleries constructed there (Penny 2012).

Figure 28. ***Caurinus dectes*** female, a liverwort dweller. Photo courtesy of Loren Russell.

Figure 29. ***Caurinus dectes*** male. Photo courtesy of Loren Russell.

Figure 30. ***Caurinus dectes*** larva on a species of the leafy liverwort ***Scapania***. Photo courtesy of Loren Russell.

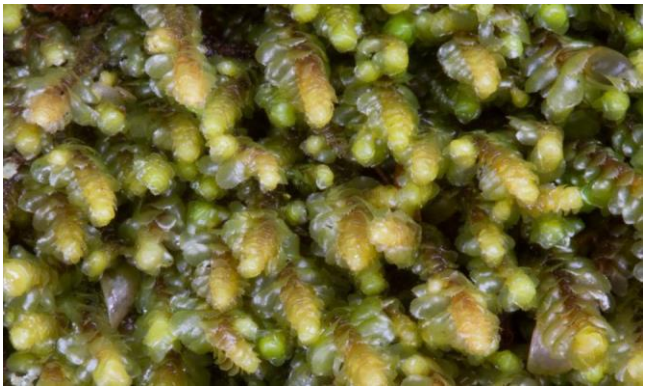

Figure 31. ***Scapania bolanderi***, a common home for ***Caurinus dectes***. Photo by Matt Goff, with permission.

Fabian *et al*. (2015) took advantage of this knowledge of food choice to locate larvae of ***Caurinus dectes*** (Figure 28-Figure 30) for their study on larval morphology. Penny (2012) used heat to cause adults of this species to drop from the epiphytic liverworts (***Porella navicularis***; Figure 32) on vine maple (*Acer circinatum*). Penny noted that the most common mosses associated with these vine maple stems are ***Rhytidiadelphus loreus*** (Figure 33), ***Metaneckera menziesii*** (Figure 34-Figure 35), and ***Neckera douglasii*** (Figure 36-Figure 37). Nevertheless, its favorite food is ***Porella navicularis***. Penny contends that ***C. dectes*** breeds in these epiphytes.

Figure 32. ***Porella navicularis***, an epiphytic liverwort where one can find ***Caurinus dectes*** larvae feeding on the liverwort. Photo by John Davis, with permission.

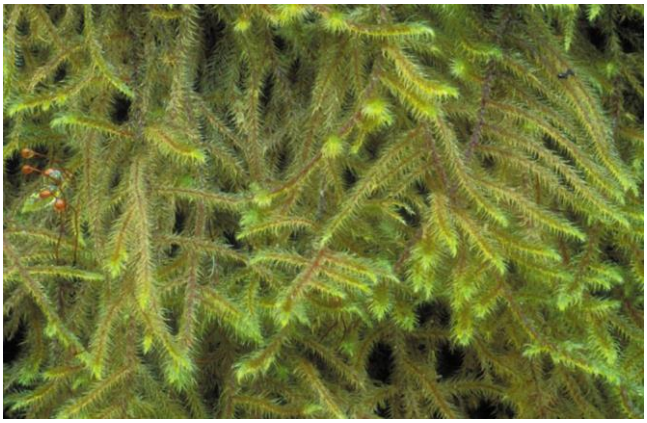

Figure 33. ***Rhytidiadelphus loreus***, potential home for ***Caurinus dectes***. Photo by Martin Hutten, with permission.

Figure 34. ***Metaneckera menziesii***, potential home for ***Caurinus dectes***. Photo by Dale Vitt, with permission.

Figure 35. ***Metaneckera menziesii***, potential home for ***Caurinus dectes***. Photo by Michael Lüth, with permission.

Figure 36. ***Neckera douglasii***, one of the epiphytic mosses in areas where one can find ***Caurinus dectes***. Photo by Kirill Ignatyev, through Creative Commons.

Figure 37. ***Neckera douglasii***, potential home for ***Caurinus dectes***, but refused as a food source. Photo by Dale Vitt, with permission.

Caurinus dectes (Figure 28-Figure 30) survives in a warmer climate than other members of the **Boreidae**. Its distribution is in Washington and Oregon, USA (Russell 1979a, b; Rood *et al*. 2015). It occurs in moist forests where mosses are abundant both on trees and on the ground. Knowing where to look often adds new species. In 2013, Sikes and Stockbridge described a new species, ***Caurinus tlagu*** (Figure 38) from Prince of Wales Island, Alaska, USA. Its habitat is different from the primary forested habitat of ***C. dectes*** (Figure 28-Figure 30), but ***C. dectes***, like ***C. tlagu***, also occurs in open rocky sites with the moss ***Rhytidiadelphus loreus*** (Figure 33). This moss species provides 20% of the cover at the Alaskan alpine tundra site where ***C. tlagu*** occurs.

Figure 38. ***Caurinus tlagu***, a moss dweller in Alaska, USA. Photo by Derek Sikes, through Creative Commons.

Byers and Thornhill (1983) conjectured that ***Caurinus*** (Figure 28-Figure 30) probably pupates in damp mosses without making a cell (Russell 1979a). Russell (1982) pointed out that its larvae, unlike other **Mecoptera**, make a silk-lined cell or cocoon where pupation occurs. Pupation occurs in July to August in northwestern USA. The life cycle is **univoltine** (one generation per year), but two generations may overlap for a period.

Penny (2006) pointed out that in ***Caurinus dectes*** (Figure 28-Figure 30), the larvae (Figure 30) are almost legless. Furthermore, the adults lack hind wings (Figure 28-Figure 29). Hence, this small (1.4-1.9 mm) insect is not going to travel very far to escape unfavorable conditions of weather or other environmental change. It lives in moist forests where both epiphytic and terrestrial bryophytes are abundant. The adults feed on the epiphytic leafy liverwort ***Porella navicularis*** (Figure 32), but also occur on mosses (Russell 1979a). When females lay their eggs, the eggs are coated with black cement and they are attached to the bryophytes (Figure 39) (Russell 1982).

Figure 39. ***Caurinus dectes*** eggs on a leafy liverwort. Photo courtesy of Loren Russell.

Because other boreids are known to feed on mosses, Russell (1979a, b) provided his ***Caurinus*** (Figure 28-Figure 30) with several epiphytic moss choices: ***Antitrichia curtipendula*** (Figure 40-Figure 41), ***Isothecium spiculiferum*** (Figure 43), ***Metaneckera menziesii*** (Figure 34-Figure 35), and ***Rhytidiadelphus loreus*** (Figure 33), all common on the trees in forests where ***C. dectes*** occurs. Although most of the larvae survived for three weeks, there was no evidence of feeding. He broadened their choices, providing ***Rhizomnium glabrescens*** (Figure 44), the foliose lichen *Peltigera canina*, the common mushroom *Agaricus campestris*, apple slices, and springtails. Again, nothing was eaten. Finally, when the leafy liverwort ***Porella navicularis*** (Figure 32) was presented, the boreids had dinner.

Figure 40. ***Antitrichia curtipendula*** growing epiphytically and providing a potential home, but not food, for ***Caurinus dectes***. Photo by Michael Lüth, with permission.

Figure 41. ***Antitrichia curtipendula*** with snow, a potential refuge for ***Caurinus dectes*** under snow, but not eaten by them. Photo by Michael Lüth, with permission.

Figure 42. ***Antitrichia curtipendula***, a species in the range of ***Caurinus dectes***, but not eaten even when there is no other food choice. Photo by James K. Lindsey, with permission.

Figure 43. ***Isothecium spiculiferum***, potential home of ***Caurinus dectes***, but not eaten by them. Photo by Ben Carter, through Creative Commons.

The boreid ***Caurinus dectes*** (Figure 28-Figure 30) apparently feeds only on leafy liverworts and completes its life cycle on ***Scapania*** (Figure 45), and several other liverwort epiphytes (Loren Russell, pers. comm. Jan. 2008). Among 11 liverwort taxa tested, the adults accepted about two-thirds of the species. ***Scapania*** serves as both food and home for depositing eggs. Russell studied three other local species of boreids, but these three are all moss specialists, never feeding on liverworts.

Figure 44. ***Rhizomnium glabrescens***, a moss not eaten by ***Caurinus dectes*** even when there is no other food choice. Photo by Paul Slichter, with permission.

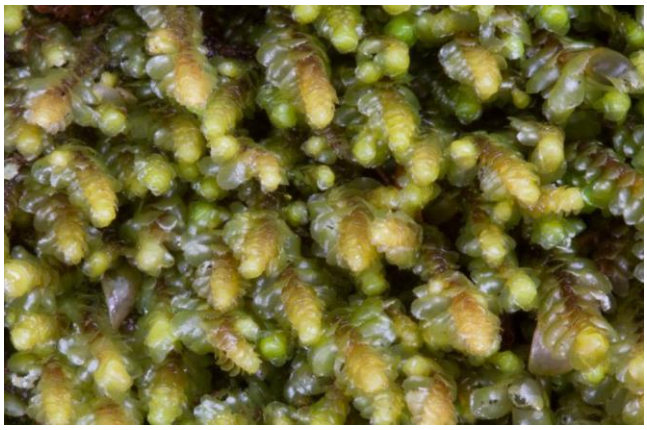

Figure 45. ***Scapania bolanderi***, food of ***Caurinus dectes***. Matt Goff, with permission.

Russell (1979a) learned that ***Caurinus dectes*** (Figure 28-Figure 30) is an excellent liverwort taxonomist. In its various habitats, it recognized certain species to eat or to avoid, both as larvae and adults. On deciduous trees and shrubs, it readily accepted (as host and food) ***Porella navicularis*** (Figure 32) and ***Frullania tamarsci*** (Figure 46) (less so, and only if primary hosts were not available), but would not accept ***Radula bolanderi*** (Figure 47) or ***Metzgeria conjugata*** (Figure 48). On decaying logs and stumps with bark, it recognized a new array of species, accepting ***Scapania bolanderi*** (Figure 31) and ***Bazzania tricrenata*** (Figure 49) and less preferentially (when given no choice) ***Ptilidium californicum*** (Figure 50), ***Bazzania ambigua***, and ***Lophocolea cuspidata***. Here ***Lepidozia***

reptans (Figure 51) was not accepted, even under starvation conditions. On older logs and stumps that had lost their bark, it found ***Calypogeia fissa*** (Figure 52), ***C. muelleriana*** (Figure 53), ***Kantius trichomanis***, ***Scapania bolanderi***, ***S. umbrosa*** (Figure 54-Figure 55), and ***Lophocolea heterophylla*** (Figure 56) to be highly acceptable, whereas ***Geocalyx graveolens*** (Figure 57), ***Lophozia incisa*** (Figure 58), ***Cephalozia bicuspidata*** (Figure 59) (larvae only), ***C. lunulifolia*** (Figure 60) (adults only), ***Calypogeja fissa***, ***Jamesoniella autumnalis*** (Figure 61), ***Jungermannia atrovirens*** (Figure 62), and ***Riccardia latifrons*** (Figure 63) were only secondary hosts, used when preferred choices were unavailable. ***Cephalozia bicuspidata*** (adults only), ***C. lunulifolia*** (larvae only), ***Blepharostoma trichophyllum*** (Figure 64), ***Chiloscyphus pallescens*** (Figure 65), and ***Lepidozia reptans*** were not accepted. Although refusing some members, ***Caurinus dectes*** is apparently mostly a **Jungermanniales** specialist.

Figure 46. ***Frullania tamarisci***, an epiphytic liverwort that is eaten by ***Caurinus dectes*** when the primary food (***Porella navicularis***) is not available. Photo by Bernd Haynold, through Creative Commons.

Figure 47. ***Radula bolanderi*** growing epiphytically, a species that ***Caurinus dectes*** would not eat.. Photo by Ken-ichi Ueda, through Creative Commons.

Figure 48. ***Metzgeria conjugata***, a species that is not accepted as food by ***Caurinus dectes***. Photo by Michael Lüth, with permission.

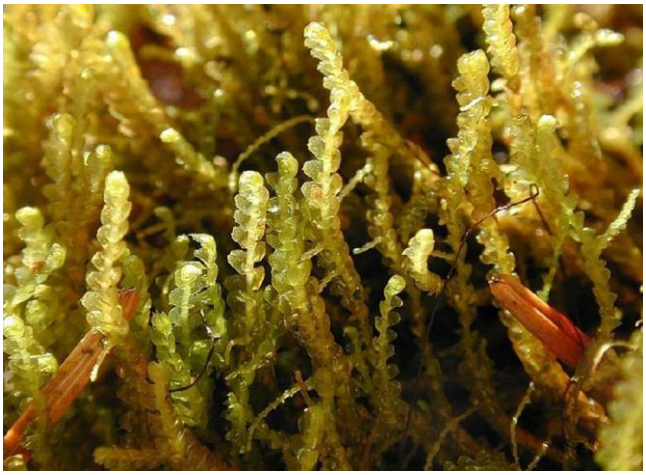

Figure 49. ***Bazzania tricrenata***, food for ***Caurinus dectes*** on logs. Photo by Michael Lüth, with permission.

Figure 50. ***Ptilidium californicum***, a secondary choice for food by ***Caurinus dectes*** on logs. Photo by Scot Loring, through Creative Commons.

Figure 51. ***Lepidozia reptans***, a food choice refused by ***Caurinus dectes*** on logs, even when no other choice was available. Photo by David T. Holyoak, with permission.

Figure 52. ***Calypogeia fissa***, an acceptable food for ***Caurinus dectes*** on older logs. Photo by Bernd Haynold, through Creative Commons.

Figure 53. ***Calypogeia muelleriana***, an acceptable food for ***Caurinus dectes*** on older logs. Photo by Hermann Schachner, through Creative Commons.

Figure 54. ***Scapania umbrosa*** on an old log where it is an acceptable food for ***Caurinus dectes***. Photo by Hermann Schachner, through Creative Commons.

Figure 55. ***Scapania umbrosa***, an acceptable food for ***Caurinus dectes*** on older logs. Photo by Hermann Schachner, through Creative Commons.

Figure 56. ***Lophocolea heterophylla*** on a log that has lost its bark where it is an acceptable food for ***Caurinus dectes***. Photo by Sture Hermansson, with online permission.

Figure 57. ***Geocalyx graveolens***, a species on old logs that ***Caurinus dectes*** larvae eat when their primary host liverworts are not available. Photo by Michael Lüth, with permission.

Figure 58. ***Lophozia incisa*** with perianth, a species on older logs and that ***Caurinus dectes*** larvae eat when their primary host liverworts are not available. Photo by J. C. Schou, with permission.

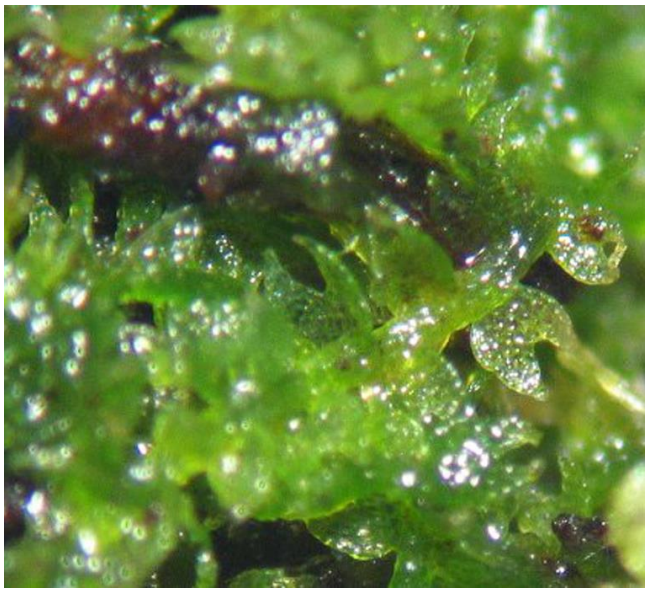

Figure 59. ***Cephalozia bicuspidata***, a species on older logs and that ***Caurinus dectes*** larvae (but not adults) eat when their primary host liverworts are not available. Photo by Christian Peters, with permission.

Figure 60. ***Cephalozia lunulifolia***, a species on older logs and that ***Caurinus dectes*** adults (but not larvae) eat when their primary host liverworts are not available. Photo by Michael Lüth, with permission.

Figure 61. ***Jamesoniella autumnalis***, a species on older logs and that ***Caurinus dectes*** eats when its primary host liverworts are not available. Photo by Michael Lüth, with permission.

Figure 62. ***Jungermannia atrovirens***, a species on older logs and that ***Caurinus dectes*** eats when its primary host liverworts are not available. Photo by Hermann Schachner, through Creative Commons.

Figure 63. ***Riccardia latifrons***, a species on older logs and that ***Caurinus dectes*** eats when its primary host liverworts are not available. Photo by Julita Klusa <daba.dziedava.lv>, with online permission.

Figure 64. ***Blepharostoma trichophyllum***, although common on logs where ***Caurinus dectes*** lives, is an unacceptable food. Photo by Hermann Schachner, through public domain.

Figure 65. ***Chiloscyphus pallescens***, although common on logs where ***Caurinus dectes*** lives, is an unacceptable food. Photo by Michael Lüth, with permission.

On compacted soil, highly accepted food species for ***Caurinus dectes*** (Figure 28-Figure 30) included ***Gyrothyra underwoodiana*** (Figure 66), ***Nardia scalaris*** (Figure 67), ***Diplophyllum albicans*** (Figure 68), and ***D. obtusifolium*** (Figure 69), with secondary hosts of ***Gyrothyra underwoodiana*** (adults only), ***Jungermannia rubra*** (Figure 70), and ***Blasia pusilla*** (Figure 71) (Russell 1979a). They did not accept ***Pellia neesiana*** (Figure 72), ***Athalamia hyalina*** (Figure 73), ***Conocephalum conicum*** (Figure 74), or ***Anthoceros punctatus*** (Figure 75), all thallose species. On boulders and outcrops they preferred ***Plagiochila porelloides*** (Figure 76), with ***Porella cordaeana*** (Figure 77) and ***Scapania americana*** (Figure 78) serving as alternatives when their preferred foods were unavailable. Even forest litter provided a suitable host in the form of ***Plagiochila porelloides***.

Figure 66. ***Gyrothyra underwoodiana***, a highly accepted food for larvae and secondary food for adults of ***Caurinus dectes*** on compacted soil. Photo by Tab Tannery, through Creative Commons.

Figure 67. ***Nardia scalaris***, a highly accepted food for ***Caurinus dectes*** on compacted soil. Photo by Hermann Schachner, through Creative Commons.

Figure 68. ***Diplophyllum albicans***, a highly accepted food for ***Caurinus dectes*** on compacted soil. Photo by Hermann Schachner, through Creative Commons.

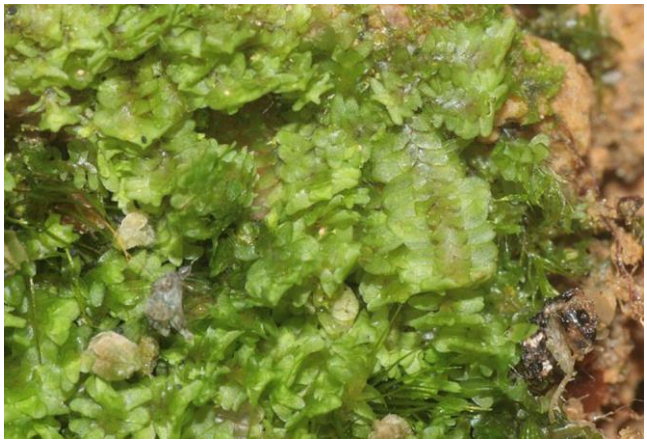

Figure 69. ***Diplophyllum obtusifolium***, a highly accepted food for ***Caurinus dectes*** on compacted soil. Photo by Hermann Schachner, through Creative Commons.

Figure 70. ***Jungermannia rubra***, a secondary food for ***Caurinus dectes*** on compacted soil. Photo by Ken-Ichi Ueda, through Creative Commons.

Figure 71. ***Blasia pusilla***, a secondary food for ***Caurinus dectes*** on compacted soil. Photo by Tim Faasen, with permission.

Figure 72. ***Pellia neesiana***, a potential food on highly compacted soil, but that is refused by ***Caurinus dectes***. Photo by Bernd Haynold, through Creative Commons.

Figure 73. ***Athalamia hyalina***, a potential food on highly compacted soil, but that is refused by ***Caurinus dectes***. Photo by Jason Hollinger, through Creative Commons.

Figure 74. ***Conocephalum conicum***, a potential food on highly compacted soil, but that is refused by ***Caurinus dectes***. Photo by Hermann Schachner, through Creative Commons.

Figure 75. ***Anthoceros punctatus***, a potential food on highly compacted soil and seepages, but that is refused by ***Caurinus dectes***. Photo by Proyecto Musgo, through Creative Commons.

Figure 76. ***Plagiochila porelloides***, a preferred food for ***Caurinus dectes*** on boulders. Photo by Bernd Haywold, through Creative Commons.

Figure 77. ***Porella cordaeana***, a secondary food for ***Caurinus dectes*** on rocks where the preferred foods are unavailable. Photo by Michael Lüth, with permission.

Figure 78. ***Scapania americana***, a secondary food for ***Caurinus dectes*** on rocks where the preferred foods are unavailable. Photo by Chris Wagner, with permission.

Russell (1979a, b) was not able to locate any highly acceptable hosts for ***Caurinus dectes*** among liverworts from streams and seepages, but ***Chiloscyphus polyanthos*** (Figure 79), ***Riccardia multifida*** (Figure 80), and ***Blasia pusilla*** (Figure 71) served as "emergency" foods when others were not available. ***Scapania undulata*** (Figure 81) and ***Anthoceros punctatus*** (Figure 75) were rejected.

Figure 79. ***Chiloscyphus polyanthos***, an emergency food for ***Caurinus polyanthos*** from streams and seepages. Photo by Kristian Peters, with permission.

Figure 80. ***Riccardia multifida***, an emergency food for ***Caurinus polyanthos*** from streams and seepages. Photo by Hermann Schachner, through Creative Commons.

Figure 81. ***Scapania undulata***, a rejected food for ***Caurinus polyanthos*** from streams and seepages. Note that some species of ***Scapania*** are eaten. Photo by Hermann Schachner, through Creative Commons.

One of the most interesting observations by Russell (1979a, b) was that although these boreids had accepted ***Porella navicularis*** (Figure 32) as food, and readily tasted ***Porella roellii*** (Figure 82), they soon showed a distinct distaste for ***P. roellii***. Evidence included regurgitation, signs of distress, and repeated grooming of their mouthparts. This behavior commenced within 30 seconds of tasting the ***P. roellii***. Once eating this species, they subsequently would no longer eat ***P. navicularis***, a previously staple food source for them in the lab. ***Porella roellii*** is known for its "violent, burning taste" which is evidenced after a few seconds of delay.

Figure 82. ***Porella roellii***, a leafy liverwort that appears to be repugnant to ***Caurinus dectes***. Photo by Paul Wilson, with permission.

Russell (1979a, b) rejected the hypothesis that liverworts provided better nutrient quality than the less preferred mosses. In fact, the liverworts seemed to have less nitrogen, an essential component of protein, and rarely exceeded the content of mosses for any of the nutrients tested (Table 1). The switch in some cases from larval to adult preferences is interesting. Also of interest is that this insect specializes on Jungermanniales, with 18 species accepted in laboratory tests.

Table 1. Macronutrient concentrations in the gametophytes of some bryophytes collected in ***Caurinus dectes*** habitat at Marys Peak, Oregon, USA. From Russell 1979a.

		P	N	Na	K	Ca	Mg
Mosses							
Dicranum fuscescens	Figure 83	.142	.932	.038	.546	.418	.145
Rhizomnium glabrescens	Figure 44	.251	2.083	.043	1.125	.972	.261
Eurhynchium oreganum	Figure 84-Figure 85	.146	.829	.056	.741	.518	.190
Isothecium spiculiferum	Figure 43	.142	.949	.034	.512	.516	.177
Antitrichia curtipendula	Figure 40-Figure 41	.151	.686	.028	.631	.430	.170
Rhytidiadelphus loreus	Figure 33	.164	.727	.072	.770	.440	.171
mean		**.166**	**1.034**	**.045**	**.721**	**.551**	**.186**
Liverworts							
Scapania bolanderi	Figure 31	.072	.748	.035	.659	.275	.111
Porella navicularis	Figure 32	.155	.890	.026	1.040	.426	.156
Frullania tamarisci ssp. *nisquallensis*	Figure 46	.107	.874	.030	.904	.515	.134
mean		**.111**	**.834**	**.030**	**.868**	**.405**	**.134**

Figure 83. ***Dicranum fuscescens***, a food species for adults of ***Hesperoboreus brevicaudus***. Photo by Michael Lüth, with permission.

Figure 84. ***Eurhynchium oreganum*** habitat in area where ***Caurinus dectes*** lives. Photo by Matt Goff, with permission.

Figure 85. ***Eurhynchium oreganum*** in habitat where ***Caurinus dectes*** lives. Photo by Matt Goff, with permission.

Hesperoboreus

In Oregon, USA, ***Hesperoboreus brevicaudus*** (see Figure 89) larvae are inhabitants of epiphytic mosses, whereas adults may also occur among thick, matted mosses on rocks (Russell 1979a, b). Penny (2006) reported them from vertical moss banks and epiphytic mosses in California, USA. In the lab, adults feed on ***Polytrichum*** (Figure 1, Figure 17) leaf lamellae (Figure 86), ***Rhizomnium glabrescens*** (Figure 44), and ***Dicranum fuscescens*** (Figure 83) (Russell 1979a). Larvae feed extensively on ***Funaria hygrometrica*** (Figure 87), ***Rhytidiadelphus loreus*** (Figure 33), ***Antitrichia curtipendula*** (Figure 40-Figure 41), and ***Plagiothecium undulatum*** (Figure 88) in the lab.

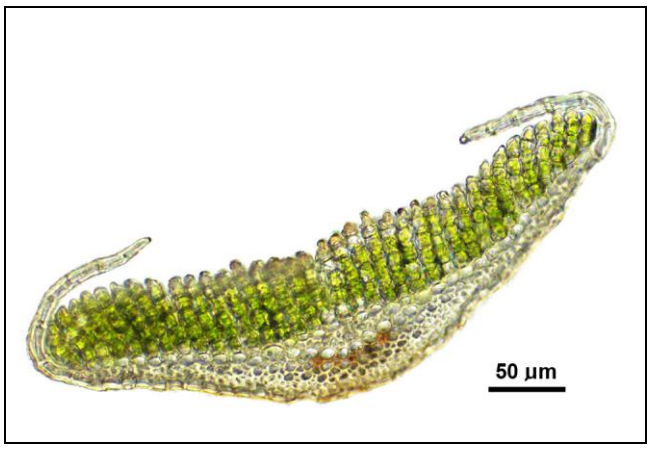

Figure 86. ***Polytrichum juniperinum*** leaf cs, showing lamellae that are eaten by adults of ***Hesperoboreus brevicaudus***. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 87. ***Funaria hygrometrica***, food of ***Hesperoboreus brevicaudus***. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

Figure 88. ***Plagiothecium undulatum***, food of ***Hesperoboreus brevicaudus***. Photo by Walter Obermayer, with permission.

These mossy habitats, especially among epiphytic mosses, dry out in seasons with little rainfall (Gerson 1982). To accommodate for this unwelcome dryness, the larvae of ***Hesperoboreus notoperates*** (Figure 89) make hardened cells, using salivary secretions, among the moss rhizoids (Cooper 1974). These cells apparently conserve water until moisture returns. After sufficient rainfall, the larvae break out of the cells and begin feeding again.

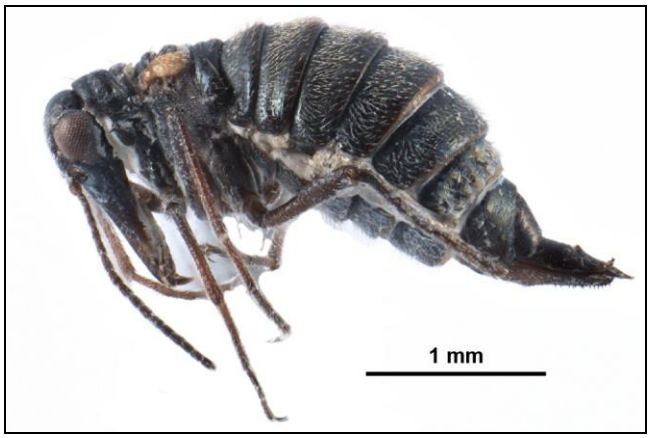

Figure 89. ***Hesperoboreus notoperates***, a species that prefers compact cushion mosses. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Cooper (1974) noted parasites, especially on ***Hesperoboreus notoperates*** (Figure 89) in Southern California. Living in such confined quarters may be dangerous for the young boreids because it most likely makes transfer of the parasites from one to another easy. Nevertheless, tight cushions of **Grimmiales** (Figure 23) and **Isobryales** (Figure 90) (Cooper 1974) seem preferable to open mats (Penny 1977), perhaps for greater conservation of moisture.

Figure 90. ***Fontinalis antipyretica***, a member of **Isobryales**. Photo by Tab Tannery, through Creative Commons.

Nannochoristidae

Nannochorista (Figure 91) has carnivorous aquatic larvae that feed on larvae of **Chironomidae** (midges) (Tillyard 1917; Byers & Thornhill 1983; Byers 1989; Palmer 2009). The adult diet is unknown. But during pupation, ***Nannochorista*** sometimes uses damp mosses as a substrate, avoiding the need to make a special cell for that purpose (Pilgrim 1972; Byers & Thornhill 1983). Those larvae that migrate to soil or bark for pupation create a cell by excavating the soil or wet wood. They pupate above the water, but within 10-20 cm of it (Pilgrim 1972). ***Nannochorista philpotti*** (Figure 91) is a predatory species that sometimes spends part of its life among bryophytes.

Figure 91. ***Nannochorista philpotti*** adult, a predatory species that sometimes spends part of its life among bryophytes. Photo by Steve Kerr, with permission.

Panorpidae

It is the **Panorpidae** that have earned the name of scorpionflies for the order **Mecoptera** (Wikipedia 2016). The genitalia of the males are enlarged and curved upward, arching over the back, much like the stinger of a scorpion (Figure 92).

Figure 92. ***Panorpa nuptialis*** male adult. Note the resemblance to a scorpion. Photo by Karen Perez, through Creative Commons.

The larvae of **Panorpidae** are unusual among holometabolous insects in having compound eyes with ommatidia, a trait shown by ***Neopanorpa*** (Figure 93) and ***Panorpa*** (Figure 94) (Ramel 2016). As Farkač *et al.* (2005) have reminded us, ***Panorpa hybrida*** (Figure 94) is an endangered species in the Czech Republic. And this species lives mostly among mosses.

Figure 93. ***Neopanorpa*** sp. adult, a species whose larval eyes are compound. Photo by E. S. Ross <www.discoverlife.com>, with online permission.

Figure 94. ***Panorpa hybrida*** adult, a moss dwelling species in Europe. Photo by Ivelina Assyova, with permission.

But the members of the genus ***Panorpa*** (Figure 94) are not all associated with bryophytes. Some are carnivores, eating freshly killed katydids, grasshoppers, and caterpillars in the lab (Cai & Hua 2009).

Panorpa (Figure 94) has three types of mating (Ramel 2016). In all cases, the male emits a **pheromone** that attracts females, and unfortunately, also other males. In one strategy, the male offers the female a gift, food of course (Figure 95), that she devours during copulation (perhaps helping to prevent her from eating her mate as is known in other carnivores such as the preying mantis). In fact, Cockle (1908) observed the female of ***Boreus californicus*** (Figure 19-Figure 20) drag the male around on his back until he died. The second strategy is similar – the male finds a dead arthropod, which he partially consumes (Ramel 2016). Then the male stands beside it and emits the pheromone attractant or secretes a salivary mass on a nearby leaf or other substrate, again resting beside it and secreting a pheromone. Copulation occurs while the female feeds, either on the arthropod or the salivary mass. In the third strategy, the male offers nothing – no food and no pheromones. Rather, he rushes at the female and attempts to mate with her, a strategy known as **forced copulation**, and often he succeeds. This latter strategy is most used by those males who lose to other males in their attempt to gain food for a gift. Not surprisingly, females prefer the males with gifts, and those that do receive gifts lay more eggs than females that have had forced copulation.

Figure 95. Male ***Panorpa communis*** with prey item (***Diogma glabrata glabrata***) such as that offered to females before mating. Photo by Richard Bartz, through Creative Commons.

Kullmann and Sauer (2005) investigated other species of ***Panorpa*** and learned that other strategies are present as well. They found that the males of both ***Panorpa similis*** and ***Panorpa connexa*** carry out their copulations with one salivary mass as a nuptial gift or have copulations without any nuptial gift, but always without the use of force.

Earlier researchers reported that ***Panorpa*** oviposits loose clusters of eggs, using pre-existing cavities in moist soil (Miyake 1912; Tillyard 1926; Byers 1963; Riek 1970; Byers & Thornhill 1983). But ***Panorpa communis*** (Figure 95-Figure 96), the common scorpionfly that was named by Linnaeus, oviposits beneath mosses (Malyshev 1968). Byers (1963) found that in ***P. nuptialis*** (Figure 92, Figure 97) size increase is rapid in the young larvae, but the prepupal stage is prolonged. Adults emerge from pupae in about 20 days.

Figure 96. ***Panorpa communis*** male adult, a species that oviposits under mosses. Photo by Gail Hampshire, through Creative Commons.

Figure 97. ***Panorpa nuptialis*** adult. Photo by Robby Deans, through Creative Commons.

Apteropanorpidae

This tiny family has only one genus (***Apteropanorpa***; Figure 99) with four species known as Tasmanian snow scorpionflies (Palmer *et al*. 2007; Wikipedia 2011). The larvae live among mosses in Tasmania and southern Australia (Byers & Yeates 1999; Wikipedia 2011). Adults are wingless predators, but likewise live among mosses (Kaltenbach 1978; Byers & Yeates 1999).

Like the **Boreidae**, the **Apteropanorpidae** are active in the cold of winter (Byers & Thornhill 1983). Both larvae and adults live among mosses (Kaltenbach 1978; Ferrington 2008) where conditions remain moist most of the time (Russell 1979a). Although Ferrington (2008) considered this family to be aquatic, Palmer (2009) argues that they are not, stating "There is no evidence suggesting that adults of any species of ***Apteropanorpa*** predictably occupy riparian or aquatic vegetation." Further, Evans (1942) collected two **Mecoptera** larvae from mosses at 600-900 m on Mt. Wellington and these have now been determined to be ***Apteropanorpa*** (Palmer 2009). Balian *et al*. (2008) noted the ability of mosses to retain a film of water that permits limnoterrestrial invertebrates to live there. But Palmer cautions that larval stages of this genus are poorly known and mosses may not be their only habitat.

But danger lurks among the bryophytes. Like several other mecopteran families, this one is plagued by parasitism. Adults of ***Apteropanorpa tasmanica*** (Figure 99-Figure 99) are parasitized by larvae of the mites ***Leptus agrotis*** and ***Willungella rufusanus*** (Seeman & Palmer 2011).

Figure 98. ***Apteropanorpa tasmanica***, a species whose larvae live among mosses. Photo © Simon Grove, Tasmanian Museum and Art Gallery, with permission.

Figure 99. ***Apteropanorpa tasmanica***, a species whose larvae live among mosses. Photo © Simon Grove, Tasmanian Museum and Art Gallery, with permission.

Meropeidae

This tiny family has only two members, one in eastern USA – ***Merope tuber*** (Figure 100-Figure 101) and one in Australia – ***Austromerope poultoni*** (Byers 1973, 1988; Kaltenbach 1978). It appears to be an ancient family that was once more widespread.

Merope tuber (Figure 100-Figure 101) adults live among aquatic or riparian vegetation or bryophytes (Ferrington 2008). Presumably the bryophytes provide sufficient moisture for these terrestrial living sites.

Figure 100. ***Merope tuber*** adult, a species that includes bryophytes among its substrates. Photo by Tom Murray, through Creative Commons.

Figure 101. ***Merope tuber*** adult male showing claspers. Photo by R. Machado, R. Kawada, and J. Rafael, through Creative Commons.

Merope tuber is a poorly known species (Dunford *et al*. 2007). Its larvae have never been described and its habits are largely unknown. We do know that the adults are nocturnal, and flight traps have revealed that the species is more common than we had imagined (Byers 2005). Its range is from southeastern Canada to Florida and west to Kansas, Minnesota, and eastern Iowa Byers (1973, 1993; Dunford *et al*. 2007). The Appalachian Mountain range and eastern mesic forests provide it with suitable habitat (Dunford *et al*. 2007). Its presence in the more western and southern parts of its range suggest that these disjunct locations may be relict habitats where it found refuge during glacial advances (Byers 1969, 1993; Schiefer & Dunford 2005). The two species are able to survive in these two distant geographic locations on opposite sides of the Earth along streams in ravines (Killington 1933; Byers 1988) that provide temperatures that vary little from 20°C (Means 1985).

Bittacidae

The **Bittacidae** are not true bryophyte associates, but they do occasionally feed on mosses (Setty 1931). More commonly they are **saprophagous** and feed on things like dead earthworms or dead insects (Setty 1931, 1940; Byers & Thornhill 1983). Like the **Nannochoristidae**, ***Harpobittacus australis*** (Figure 102) uses pheromones for mating attraction (Crossley & Waterhouse 1969). Most of the bittacids hang on vegetation by their legs to drop their eggs to the ground (Ramel 2016). Hence, any association of eggs with bryophytes is probably coincidental.

Figure 102. ***Harpobittacus australis*** adult, a species that uses pheromones to attract his mate. Photo by John Tann, through Creative Commons.

Currie (1932) relates fascinating observations of the larval behavior of ***Harpobittacus tillyardi*** in the lab. In preparation for molting, the larvae move to a higher location on a soil mound or on a liverwort leaf. When the larvae molt, they move their body fluids forward, causing the anterior to swell. Eventually the head capsule splits and the larva crawls out, then eats its former skin. After a 10-minute rest, the larvae moved the posterior end up above the head capsule. They then proceeded to expell sand and soil from the anus and to cover the larval skin with it as they moved the anus backward. After about 20 minutes, this process was repeated. This covering rendered the larvae nearly invisible on its substrate. During feeding, which was almost entirely on dead matter, the larva occasionally took a bit of liverwort in the lab. Maintenance of moisture was important, and larvae would expel fluids from the mouth to spread over the body to keep it moist. If it ran out of this fluid, it would die in the dryness.

Summary

The **Mecoptera** include the snow scorpionflies, and these typically feed on mosses or algae associated with them. ***Chorista*** (**Choristidae**) is among the bryophages. The **Boreidae** has three genera, all of which feed almost exclusively on bryophytes as both larvae and adults. In addition to food, the mosses may be important as a moist refuge. Many lay their eggs on mosses under the snow. For ***Boreus***, mosses seem to be important, whereas for ***Caurinus***, liverworts are important. ***Hesperoboreus brevicaudus*** species occur among epiphytic mosses as larvae but migrate to mosses on rocks as adults.

In the **Nannochoristidae**, has aquatic larvae that are carnivorous, but the larvae may move to damp mosses for pupation. The **Panorpidae** have compound eyes, unusual in this order, that may help them to detect motion in their dark bryophyte habitat. However, not all **Panorpidae** are bryophyte associates. Both larvae and adults of **Apteropanorpidae** live among mosses and are winter-active. ***Merope*** (**Meropeidae**) adults can live among aquatic vegetation or among bryophytes. The **Bittacidae** only occasionally associate with bryophytes and feed on them.

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CHAPTER 12-17
TERRESTRIAL INSECTS: HOLOMETABOLA – DIPTERA BIOLOGY AND HABITATS

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CHAPTER 12-17
TERRESTRIAL INSECTS:
HOLOMETABOLA – DIPTERA OVERVIEW

Figure 1. Adult **Diptera** resting on mosses in a canyon in Ohio, USA. Insects this large are unlikely to move within the moss mat, but the mat can still be important in keeping them alive. Such rest stops may be for getting from one place to another, rehydrating the body, drinking, or ovipositing. Photo by Janice Glime.

Diptera Overview

Diptera derive their name from having only two wings (Figure 1). In place of the second pair of wings, they have a pair of **halteres** (Figure 2), structures that resemble a knob on a stalk, like the dumbbells of the same name. The halteres instead serve as a guidance system (Wikipedia 2016). They record both vertical and horizontal changes in direction, permitting the flies to maintain balance and stabilize the head and to perform their acrobatic maneuvers quickly.

Wagner (1980) concluded that in the Breitenbach of Germany, changes in fly populations are linked with changes in the bryophyte cover. When Andrew and Rodgerson (1999) developed a kerosene extraction technique for removing invertebrates from bryophytes, they found that **Acari**, **Collembola**, and **Diptera** were the most abundant arthropods. This chapter will explore the many ways in which the **Diptera** are associated with bryophytes and often depend on them. Bryophytes play an important role in the life cycles of a number of dipteran taxonomic groups (Kinchin 1992).

The **Diptera** are part of the panorpid complex (Britannica 2008). This group includes the **Mecoptera**, **Trichoptera**, **Lepidoptera**, **Siphonaptera**, and **Diptera**. It is a current belief that all these orders evolved from a moss-dwelling ancestor. They are all 4-winged insects (except the halteres of **Diptera**) that resemble craneflies, some making cases as larvae.

Most bryologists are probably unaware that some **Diptera** larvae behave as parasites in the thalli of liverworts. Pettet (1967) reported such an interaction in

thalli of ***Riccia frostii***. The rosettes of thalli each had 5-25 small, yellow-orange larvae. The thallus loses its turgidity and becomes flabby. In the last larval stage, the upper surface of the thallus disintegrates. Pupation follows inside the thallus.

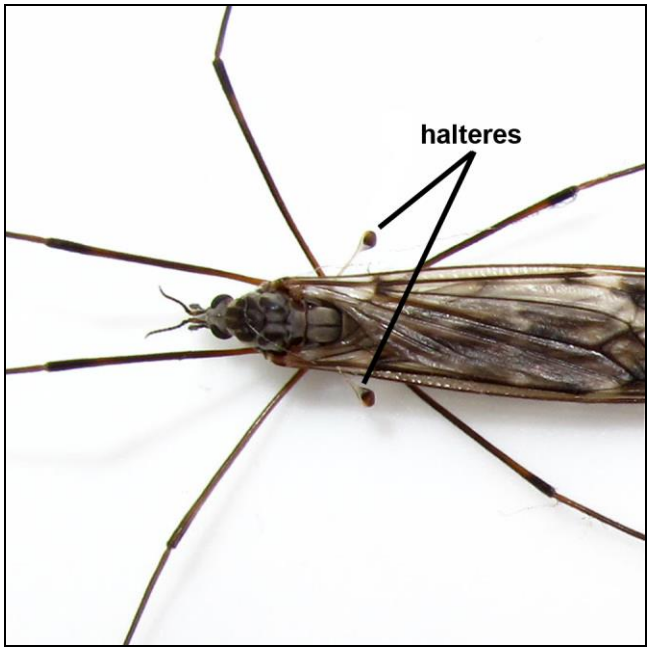

Figure 2. Cranefly (***Tipula*** cf. ***scripta***) halteres. Photo from BugBlog, through Creative Commons.

Role of Bryophytes

As with other insects, bryophytes provide a safe haven for small dipterans to hide from predators. They likewise provide a moist haven from the sun and drying winds. And they are a source for food. For some dipterans, the bryophytes themselves are eaten. For others, microorganisms, fungi, and other arthropods that live among the bryophytes provide food sources. Galas *et al* (1996) reported that in the cave water they tested the amount of energy released by the bryophyte microorganisms was greater than that for the litter species they tested.

Andrew *et al*. (2003) summed up the advantage of bryophytes – they are able to absorb water rapidly, reduce evaporation, and provide insulation against extreme environmental conditions of cold and wind (see also Gerson 1982; Smrz 1992). Several researchers suggest that by modifying the environment, bryophytes permit aggregations of **Diptera** to live where they would not otherwise be able to tolerate the dry conditions (Joosse & Verhoef 1974; Leinaas & Somme 1984; Usher & Booth 1984).

Clément and Touffet (1981) examined the role of bryophytes in the big picture of heathlands in Brittany. The larvae of ***Tipula*** (**Diptera**; Figure 3) were responsible for the death of many bryophytes following fire. Bryophytes were destroyed by the scraping of rabbits and roe-deer. Once bryophytes returned, led by ***Funaria hygrometrica*** (Figure 4) and ***Ceratodon purpureus*** (Figure 5) following fire, organic matter built up quickly, permitting the invertebrate fauna to flourish.

Figure 3. ***Tipula abdominalis*** larva, a genus responsible for destroying bryophytes in burned areas. Photo by Tom Murray, through Creative Commons.

Figure 4. ***Funaria hygrometrica*** with capsules, bryophytes that colonize after a fire, permitting invertebrates such as **Diptera** to begin colonization. Photo by Janice Glime.

Figure 5. ***Ceratodon purpureus***, bryophytes that colonize after a fire, permitting invertebrates such as **Diptera** to begin colonization. Photo by Janice Glime.

Substrate type is important in the establishment and emergence of **Diptera** from lakes (Čmrlec *et al*. 2013). In lake outlets in Poland, mosses were the most preferred substrate for emergence, especially on tufa and pebbles. Mosses provide a place to climb to the surface without being carried away by the current, then extending above ground to give a solid surface from which to escape the aquatic realm. In particular, the **Athericidae** (Figure 6) select mosses for emergence, but then, they also select mosses for their pupation, making this a readily available emergence site (Thomas 1997). The **Chironomidae** (Figure 7-Figure 10) and **Dixidae** (Figure 11-Figure 12)

(Poepperl 1999) have no substrate preference, but **Empididae** (Figure 13-Figure 15) not only use the mosses for emergence, but also use them for food and shelter (Watson & Rose 1985; Nolte 1991; Ivković *et al*. 2007).

Figure 6. ***Ibisia marginata***, a member of the family **Athericidae**, many of which select mosses for emergence. Photo by Hectonicus, through Creative Commons.

Figure 7. **Chironomidae** larva, a stage often found in aquatic mosses and also occurring in terrestrial ones. Photo by Jason Neuswanger, with permission.

Figure 8. **Chironomidae** pupa, a stage that is sometimes spent among mosses. Photo by Jason Neuswanger, with permission.

Figure 9. **Chironomidae** adults emerging from pupae in moss at Helfdi, Myvatn, Iceland. Photo by Janice Glime.

Figure 10. ***Chironomus plumosus*** (**Chironomidae**), one of the many midges that emerge in large numbers from mosses. Photo ©entomart, through Creative Commons.

Figure 11. **Dixidae** larva, a stage that sometimes occurs in mosses but has no preference for them. Photo by Aina Maerk Aspass, NTNU, through Creative Commons.

Figure 12. ***Paradixa*** pupa, a stage that sometimes occurs in mosses. Photo from Landcare Research, Manaaka Whenua, NZ, with online permission.

Figure 13. **Empididae** larva, a moss inhabitant and feeder. Photo through Manaaka Whenua, NZ, with online permission.

Like many other orders discussed earlier, the **Diptera** have their parasites. The cranefly ***Limonia*** (**Limoniidae**; Figure 16) is one of these (Wohltmann *et al*. 1994), as is ***Paradixa*** (**Dixidae**; Figure 17). Larvae of ***Limonia*** are subject to the parasitic mite, ***Johnstoniana tuberculata*** (Figure 18) (Wohltmann *et al*. 1994). It appears that the moss provides suitable conditions for both the cranefly and the parasite. This mite overwinters in its egg stage and the larvae emerge in May-June – the same time their hosts become available.

Figure 14. **Empididae** pupa, a stage often found in mosses. Photo from Landcare Research, Manaaka Whenua, NZ, with online permission.

Figure 15. ***Empis stercorea*** adult, member of the **Empididae**, a family that often pupates in mosses and that also eats them as larvae. Photo from ©entomart, through Creative Commons.

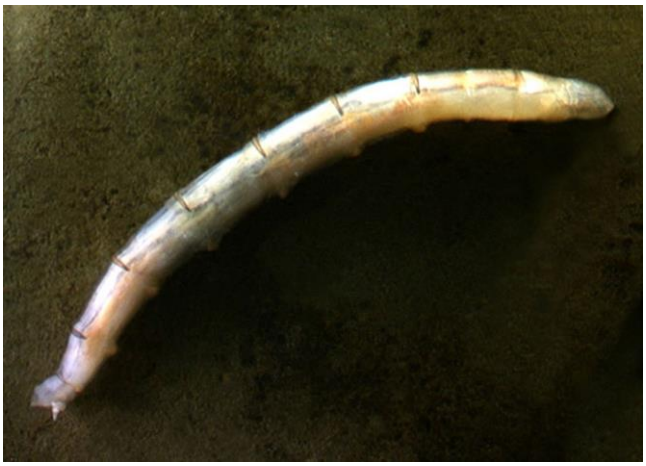

Figure 16. ***Limonia*** (**Limoniidae**) larva, a genus that lives among mosses and has mite parasites. Photo from Manaaka Whenua, Landcare Research, NZ, with online permission.

Figure 17. ***Paradixa*** (**Dixidae**) larva with parasitic mites. Photo from Landcare Research, Manaaka Whenua, NZ, with online permission.

Figure 18. ***Johnstoniana*** sp., a parasitic mite such as those found on moss-dwelling **Diptera**. Photo by Walter Pfliegler, with permission.

Collection and Extraction Methods

Several methods of collection are usually necessary to assess the **Diptera** fauna. Most larvae are difficult to identify and often must be reared to adults for certain identification. This need can sometimes be eliminated by a thorough sampling of the adult fauna during their active seasons. The most common method I encountered for adult surveys was the use of the **Malaise traps** (*e.g.* Salmela 2001; Salmela & Ilmonen 2005; Figure 19). These are large, tent-like structures used for trapping flying insects, especially **Hymenoptera** and **Diptera**. Insects are directed to the top of a slanted pyramid where they encounter a vial of preservative. Other methods for flying insects include **window traps** (Figure 20) and **sweep netting** (Figure 21) (Salmela 2001).

Figure 19. Malaise trap for emergent and flying insects. Photo by Ceuthophilus, through Creative Commons.

Figure 20. Window-pane trap used to capture adult insects including **Diptera**. Photo from North Dakota State University, with online permission.

Figure 21. Sweep net used to catch adult insects, including **Diptera**. Picture from Peter Oboyski, with permission.

Window-pane traps (Figure 20) are made with clear plexiglass to serve as a barrier over a container of ethylene glycol (anti-freeze). The window is mounted on a wooden frame that is suspended between two pipes anchored in the ground. The frame height should be at the top of the

growing vegetation, or at least above the peak of the bryophyte clumps.

Ground dwelling **Diptera**, including larvae and pupae, are often sampled by **pan traps** (Figure 22) (Taillefer & Wheeler 2010) or **pitfall traps** (Figure 23-Figure 24) (Galbraith *et al*. 1993; Horsfield & MacGowan 1997; Miller *et al*. 2008). These are placed among the vegetation, and for our purposes this would be among mosses. The rim should be below the moss surface so that insects don't have to climb up to enter the trap. **Pan traps** (Figure 22) are simple small pans with soapy water in them (MacGown 2015). One drop of detergent in the pan or bowl is sufficient to break the surface tension and cause the insects to drown. The pans can be in colors chosen to suit the insect group you are interested in, with meat red being a suitable color for catching **Diptera**. On the other hand, a neutral color may give a more representative sample, avoiding the bias of attracting a particular group. The traps should be checked at least once a day to prevent mold. When removing the insects, pour the soap-water solution through a fine aquarium mesh net. Then rinse the net with water into a jar of 95% ethanol. The water will dilute the solution to the approximately 70% ethanol needed for preservation.

Figure 22. Pan trap used for ground insects. These are usually positioned so the rim is at the same height as the tops of the ground vegetation such as mosses. Photo by Peter Oboyski, with permission.

Figure 23. Pitfall trap to capture ground-dwelling insects. Photo from Stephen F. Austin State University, through Creative Commons.

Figure 24. Barber pitfall trap. The cover helps keep out rain and debris. Photo by Mnolf, through Creative Commons.

A **pitfall trap** (Figure 23) is similar to a pan trap. It is used for small animals, including insects, especially for ecological studies. Two types of traps can be used: dry and wet. The **dry pitfall trap** is simply a container buried in the ground with its rim at the soil surface. The **wet pitfall trap** differs only in containing a preserving liquid such as 10% formaldehyde, methyl alcohol, ethanol, ethylene glycol (anti-freeze), trisodium phosphate, or picric acid. A drop of detergent will remove the surface tension, making it easier for insects to fall to the bottom and be preserved. Water (plus soap) can be used if traps are checked within a day. Both wet and dry traps usually have a raised cover to reduce entry of rainfall and debris. If the insect is one that can climb or fly out, then the wet trap is preferable.

Extracting invertebrates from bryophytes is always challenging, and sorting the **Diptera** from the bryophytes is no exception. This separation is further complicated by the small size of some of the members. Andrew and Rodgerson (1999) tested several methods for extracting the invertebrates. They used **Tullgren funnels** with sugar flotation and a new technique using **kerosene phase separation**. Bryophyte samples were placed in 95% ethanol when they were collected to preserve the insects, some of which would die in the changed conditions of their habitat and others would be eaten if their predators were not immobilized. In the kerosene method, the bryophyte samples are placed in two large test tubes and 95% ethanol added to make the tube ~3/4 full. Kerosene is added to within 1 cm of the top. The tubes are shaken vigorously to ensure thorough mixing of the kerosene and ethanol. After

10-15 minutes the tubes should be rolled to eliminate any trapped bubbles of kerosene, causing them to rise from the bottom and sides. Once the ethanol and kerosene separate (kerosene on top), the invertebrates settle onto the interface layer. When this separation is complete, the kerosene should be pipetted off to within 5 mm of the interface and discarded. Then the remaining interface plus kerosene is collected. A second ethanol wash should be used to dislodge kerosene from the sides of the tube and the new interface pipetted and collected. This whole procedure should then be repeated, a part of the technique that Andrew and Rodgerson found increased the number of invertebrates collected by 16%. The collected interface material should then be examined in a Petri dish under the binocular microscope in a fume hood. Any invertebrates trapped in the kerosene should be pushed into the alcohol with a fine brush to remove the kerosene. This method retrieved significantly more invertebrates than the sugar extraction.

Identification of larvae often requires rearing to adulthood. Ferreira and Rafael (2006) developed a method for rearing immature horseflies by using bryophytes and sand. They considered this method advantageous for rearing species with long development periods.

Fly Dispersal of Spores

Revill *et al*. (1967) experimented with ability of **Diptera** to carry viable propagules, including moss spores. Using ***Tipula triplex*** (**Tipulidae**; Figure 25), ***Chaoborus punctipennis*** (**Chaoboridae**; Figure 26-Figure 27), ***Chironomus*** sp. (**Chironomidae**; Figure 10), and ***Bittacomorpha clavipes*** (**Ptychopteridae**; Figure 28), these researchers demonstrated that moss protonemata could be transported and subsequently germinate. Moss protonemata were among the least frequent, but at least five of them germinated in 51 cultured washings, demonstrating that diptera adults are possible dispersal vectors.

Figure 25. ***Tipula triplex***, a cranefly that is able to disperse moss spores. Photo by Paul Rhine <www.discoverlife.org>, through Creative Commons.

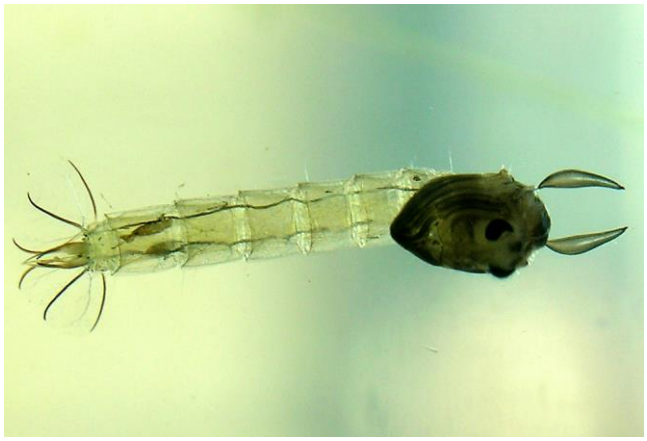

Figure 26. ***Chaoborus*** sp. pupa. Photo by Piet Spaans, through Creative Commons.

Figure 27. ***Chaoborus punctipennis*** adult, a species that is able to disperse moss spores. Photo by Tom Murray, through Creative Commons.

Figure 28. ***Bittacomorpha clavipes*** adult, a species that is able to serve as a vector for moss spores. Photo by Phil Myers, through Creative Commons.

Perhaps the best-known of the dipteran associations with bryophytes is that of flies that help in the dispersal of spores of the bryophyte family **Splachnaceae** (Bequaert 1921; Erlanson 1930; Walsh 1951; von der Dunk 1971; Koponen & Koponen 1978; Troilo & Cameron 1981 Marino 1988, 1991a, b; Koponen 1990; Eriksson 1992; Marino *et al*. 2009). This family of mosses lives exclusively on organic matter, including dung, bone, owl pellets, corpses, and enriched gravel (Koponen 1990). Among the frequent visitors to ***Splachnum ampullaceum*** (Figure 29) in the Great Lakes area is the muscid dipteran ***Eudasyphora cyanicolor*** (Figure 30) (Troilo & Cameron 1981).

Figure 29. ***Splachnum ampullaceum*** capsules showing expanded hypophysis that produces chemicals and a reddish color that attract flies. Photo by Michael Lüth, with permission.

Figure 30. ***Eudasyphora cyanicolor***, one of the visitors to capsules of ***Splachnum ampullaceum***. Photo by Tristram Brelstaff, through Creative Commons.

The **Splachnaceae** that attract flies are adapted for that attraction by their substrate, capsule shape, and chemical attractants that typically mimic the odor of dung (Koponen 1990; Koponen *et al.* 1990). These odors are produced only in the capsule and its **hypophysis** (enlarged portion at base of spore-bearing part of capsule). The odors are created by volatile compounds – octane derivatives and organic acids including acetic, propionic, and butyric acids.

It is of evolutionary significance that four families of flies are known to visit the aromatic **Splachnaceae** (Cameron & Wyatt 1986). About half the members of the **Splachnaceae** use wind dispersal, and insect dispersal arose more than once in the family, with dispersal mechanisms going back and forth between wind and insects (Goffinet *et al*. 2004; Marino *et al*. 2009). Evidence suggests that the moss capsule diversification may have followed the transition to **coprophily** (loving dung and dead animal matter) and **entomochory** (insect dispersal) (Marino *et al*. 2009).

There also appear to be differences in attraction ability. There are a number of cases in which the sporophyte colors and odors differ and the fly visitors differ accordingly (Marino *et al*. 2009). For example, ***Splachnum ampullaceum*** (Figure 30) associated with dung had more spores carried by the flies than did ***S. luteum*** (Figure 31-Figure 32) (Marino 1991b). There was also a greater proportion of flies associated with ***S. ampullaceum*** than with ***S. luteum***.

Figure 31. ***Splachnum luteum*** capsules among peat mosses. Note the broad umbrella-like hypophysis. Photo by Dick Haaksma, with permission.

Figure 32. ***Splachnum luteum*** capsules. Photo courtesy of Bernard Goffinet.

Members of **Scatophagidae** – ***Scatophaga furcata*** (Figure 33), **Anthomyiidae** – ***Delia platura*** (Figure 34), ***Phorbia*** (Figure 35), and **Muscidae** – ***Myospila metidabunda*** (Figure 36), ***Eudasyphora cyanicolor*** (Figure

30) are all known as North American and European visitors to the **Splachnaceae** that effect spore dispersal (Bequaert 1921; Cameron & Wyatt 1986; Koponen 1990). Cameron and Wyatt found the **Scatophagidae** to be both the most frequent and the most effective visitors to the capsules in Isle Royale National Park, Michigan, and Alaska, USA. They were able to demonstrate that wind is not an effective mechanism of dispersal for ***Splachnum rubrum*** (Figure 37-Figure 38) and that the visitation to dung by the **Scatophagidae** was an important component of the restriction of this moss species to dung.

Figure 33. ***Scathophaga furcata*** adult, a species that visits Northern Hemisphere **Splachnaceae** capsules. Photo by Aiwok, through Creative Commons.

Figure 34. ***Delia platura***, a Northern Hemisphere visitor to **Splachnaceae** capsules. Photo by Janet Graham, through Wikimedia Commons.

Figure 35. ***Phorbia longipilis***, a Northern Hemisphere visitor to **Splachnaceae** capsules. Photo by James K. Lindsey, with permission.

Figure 36. ***Myospila meditabunda*** female, member of a genus in which some flies visit **Splachnaceae** capsules. Photo by James. K. Lindsey, with permission.

Figure 37. ***Splachnum rubrum*** capsules showing the umbrella-shaped hypothesis that is the color of red meat and slightly iridescent. Photo by Janice Glime.

Figure 38. ***Splachnum rubrum*** with fly. Photo courtesy of Bernard Goffinet.

The common **Splachnaceae** visitor ***Eudasyphora cyanicolor*** (**Muscidae**; Figure 30) prefers carrion, but

when it is not available, the adults choose dung and thus are able to interact with ***Splachnum ampullaceum*** (Figure 29) capsules (Troilo & Cameron 1981). Nevertheless, they leave the capsules when they discover no food is present. Troilo and Cameron found that the capsules of ***S. ampullaceum*** were more attractive to these flies than either carbohydrates or fly medium.

Tayloria dubyi (**Splachnaceae**; Figure 39) is unusual in that it lives exclusively on bird dung (Figure 40) in the sub-Antarctic Magallanes (Jofre *et al.* 2011). Furthermore, this dung is predominately, and perhaps only, that of the Upland Goose ***Chloephaga picta*** (Figure 41-Figure 42). Jofre and coworkers set up traps (Figure 43) above the capsules of the moss and above the adjacent ***Sphagnum*** (Figure 39) to see if this species also attracted flies. In traps above the ***T. dubyi*** capsules they captured 64 flies comprised of **Muscidae** – ***Palpibracus chilensis***, **Tachinidae** – ***Dasyuromyia*** sp., and **Sarcophagidae** (Figure 44). No flies were captured above the adjoining ***Sphagnum***.

Figure 39. ***Tayloria dubyi*** with capsules growing on Upland Goose dung amid ***Sphagnum***. Photo by Jocelyn Jofre, through Creative Commons.

Figure 40. Goose dung, home for some **Splachnaceae**. Photo courtesy of Kim Barton.

Figure 41. Upland Goose (***Chloephaga picta***) male, the one that deposits dung that is colonized by ***Tayloria dubyi***. Photo by Bernard Dupont, through Creative Commons.

Figure 42. Goose dung. Although this is not the Upland Goose, it illustrates the large size and nature of the dung of that species. Photo by Janice Glime.

Figure 43. ***Splachnum luteum*** with fly trap. Photo courtesy of Bernard Goffinet.

Figure 44. **Sarcophagidae** adult; some members of this family visit ***Tayloria dubyi*** capsules. Photo by Toby Hudson, through Creative Commons.

Marino (1988) found that few **Splachnaceae** species ever co-existed on the same set of dung droppings. There seemed to be few mechanisms that would promote the co-existence of the mosses. Differences in timing of capsule maturation kept ***Tetraplodon angustatus*** (Figure 45) and ***Tetraplodon mnioides*** (Figure 46) from being on the same dung at the same time. Surprisingly, each species of **Splachnaceae** attracted 10-17 spore vector flies (Marino 1991b). The fly species attracted to each moss species had 77-99% different species composition from each other. Furthermore, the competition between species of **Splachnaceae** is strong. When grown together from spores there were fewer individuals of each species than when the species were grown separately (Marino 1991a). The competitive abilities between species grown in the lab related to differences in growth rates. Differences between lab and field growth suggest that habitat differences may keep species separate. Marino (1991b) demonstrated that in wet habitats ***Splachnum*** (Figure 29, Figure 31, Figure 37) is the primary **Splachnaceae** genus, whereas in dry habitats the dung mosses are primarily ***Tetraplodon*** (Figure 45-Figure 46).

Figure 45. ***Tetraplodon angustatus*** with capsules that attract flies. Photo by Des Callaghan, with permission.

Figure 46. ***Tetraplodon mnioides*** with mosquito on capsules. Photo courtesy of Lynden B. Gerdes.

Bequaert (1921) described details of the behavior of ***Phorbia*** (**Anthomyiidae**; Figure 35) flies visiting ***Tetraplodon mnioides*** (Figure 46). They landed on the upper end of the capsules and moved downward to reach the hypophysis, travelling from one capsule to another. They would pass the soft part of the proboscis over the upper part of the hypophysis, licking up its secretions. If they were disturbed, they flew away but returned quickly, apparently unwilling to pass up the treat. As these flies leave the capsules where they alight, they inevitably carry away some of the sticky spores on their hairs, legs, and other parts. The upper half of the hypophysis has exceptionally large, crowded stomata. Bequaert suggested that these stomata may exude the substance that seems so important to the visiting ***Phorbia***.

In Chile, ***Tayloria mirabilis*** (Figure 47-Figure 48) is endemic to temperate rainforests. Mighell (2011) used pitfall traps to trap flies over this species, then germinated the spores collected from these flies. Of the 218 flies collected (Figure 48), 63 were carrying spores of ***T. mirabilis***. These included seven species from **Muscidae** (4 species of ***Palpibracus***) and **Calliphoridae**. The dung represented multiple types, indicating that the mosses, and perhaps the flies were not specific in their dung substrate. Furthermore, the forest mammals providing the dung are introduced species, but the moss is endemic to Chile.

Figure 47. ***Tayloria mirabilis*** with capsules, a **Splachnaceae** member that is endemic to Chile and for which flies aid in dispersal of spores. Photo from NYBG, through public domain.

Figure 48. ***Tayloria mirabilis*** capsules with fly, near Cape Horn, Chile. Photo by Adam Wilson, NYBG, through public domain.

The fascinating dispersal relationships are described in detail in Volume 1 in the chapter on Adaptive Strategies: Spore Dispersal.

Habitats

Wetlands

Peat mosses, as might be expected, have a significant fauna of flies, particularly larvae and pupae. Warner and Asada (2006) concluded that bryophytes contribute the most to species richness in bogs. This richness includes the animals that inhabit them. Holarctic peatlands typically have both diverse and abundant dipteran fauna (Rohácek 1982; Blades & Marshall 1994; Taillefer & Wheeler 2010).

In reference to Canadian peatlands, Warner and Asada (2006) reported for mosquitoes (**Culicidae**; Figure 49-Figure 51) 10 species in bogs and 11 species in fens, for horse flies and deer flies (**Tabanidae**; Figure 52-Figure 56) 32 in bogs and 11 in fens, and for the no-see-ums (**Ceratopogonidae**; Figure 57-Figure 59) 3 in bogs. But none of these species seems to be restricted to bogs – *i.e.*, there are no true **bryobionts** among these **Diptera**.

Figure 49. ***Anopheles*** sp. larva, a member of **Culicidae** that is commonly found in wetlands. Photo by Steve Marshall, through Creative Commons.

Figure 50. ***Culex*** larvae getting oxygen while hanging from surface water. These larvae can occur in pools and in pitcher plants in wetlands, including bogs. Photo by James Gathany, through Creative Commons.

Figure 51. **Culicidae** adult, a well-known pest in wetlands. Photo by Mathias Krumbholz, through Creative Commons.

Figure 52. ***Chrysops vittatus*** larva. Deerflies in this genus inhabit wetlands, bogs, and forests. Photo by Sturgis McKeever, through Creative Commons.

Figure 53. ***Tabanus americanus*** pupa, a wetland inhabitant. Photo by Sturgis McKeever, though Creative Commons.

Figure 54. ***Chrysops caecutiens*** (**Tabanidae**) adult. Deerflies in this genus live in wetlands, bogs, and forests. Photo by Hectonichus, through Creative Commons.

Figure 55. **Tabanidae** female laying eggs, a site one might see in a wetland. Photo by Bernard Dupont, through Creative Commons.

Figure 56. ***Tabanus imitans*** eggs. Look for these in wetlands. Photo by Sturgis McKeever, through Creative Commons.

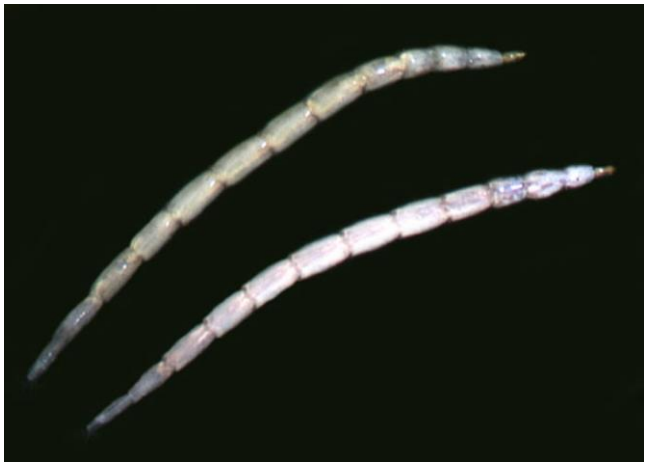

Figure 57. **Ceratopogonidae** larvae, a family that lives in wetlands and bogs. Photo by Landcare Research, Manaaka Whenua, with online permission.

Figure 58. **Ceratopogonidae** pupa, a family one can find in wetlands and bogs. Photo by Tom Murray, through Creative Commons.

Figure 59. **Ceratopogonidae** female, a family that lives in wetlands and bogs. Photo by Walter Pfliegler, with permission.

But these numbers seem modest compared to other studies. Salmela *et al*. (2007) reported 156 species of nematoceran **Diptera** in southern Finnish wetlands. Among their 8,606 specimens, they identified **Limoniidae** (80 species; Figure 16), **Psychodidae** (26; Figure 60-Figure 62), **Tipulidae** (20; Figure 3, Figure 25; Figure 80-Figure

82), **Pediciidae** (10; Figure 63-Figure 64), **Dixidae** (9; Figure 11-Figure 12; Figure 17), **Cylindrotomidae** (4; Figure 65-Figure 67), **Ptychopteridae** (4; Figure 68), **Thaumaleidae** (1; Figure 69-Figure 70), **Pleciidae** (1; Figure 71), and **Pachyneuridae** (1; Figure 72). One reason for the high diversity of **Diptera** is the high diversity of microhabitats in bogs and fens. But this also makes it difficult to assess the number of terrestrial species in these sites that live among mosses. In these studies, the microhabitat is often not described. Furthermore, the habitat changes with seasons (Blackstock *et al*. 1993). During the summer, the wetlands, both bogs and fens, become dry. Hence the life cycles of the invertebrates must be synchronized between their moisture needs and availability. And it means that the organisms moving about in the wet season are likely to be different from those that are active when it is dry.

Figure 60. ***Clogmia albipunctata*** larvae, representing the **Psychodidae** in wetlands. Photo by Ashley Bradford, through Creative Commons.

Figure 61. ***Clogmia albipunctata*** pupae, representing the **Psychodidae** of wetlands. Photo by Ashley Bradford, through Creative Commons.

Figure 62. **Psychodidae** adult, a family common in wetlands. Photo by Fritz Geller-Grimm, through Creative Commons.

Figure 63. ***Pedicia albivitta*** larva, representing a family that is common in Finnish Wetlands. Photo by Jason Neuswanger, with permission.

Figure 64. ***Pedicia albivitta*** adult, representing a family that is common in Finnish wetlands. Photo by M. J. Hatfield, through Creative Commons.

Figure 65. ***Phalacrocera replicata*** (**Cylindrotomidae**) pupa among mosses in a wetland. Photo by Janice Glime.

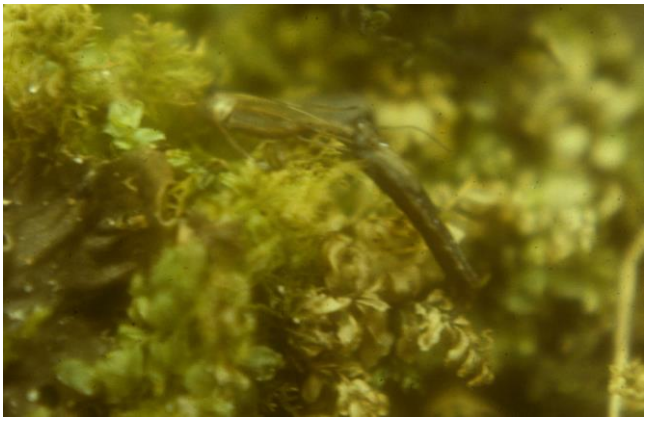

Figure 66. ***Phalacrocera replicata*** (**Cylindrotomidae**) adult emerging from its pupal enclosure among mosses. Photo by Janice Glime.

Figure 67. ***Cylindrotoma distinctissima*** adult female, a wetland inhabitant. Photo by James K. Lindsey, with permission.

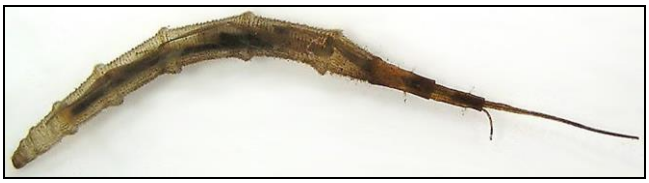

Figure 68. **Ptychopteridae** larva, a wetland inhabitant. Photo by Jason Neuswanger, with permission.

Figure 69. **Thaumaleidae** larva, a wetland inhabitant. Photo from Landcare Research, Manaaka Whenua, with permission.

Figure 70. **Thaumaleidae** adult, an inhabitant of wetlands. Photo by Walter Pfliegler, with permission.

Figure 71. ***Plecia nearctica*** adult, representing a family that occurs in wetlands. Photo by Alexpb, through Creative Commons.

Figure 72. ***Cramptonomyia spenceri*** (**Pachyneuridae**) adult, representing a family from wetland habitats. Photo by Lynette Elliott, through Creative Commons.

In the examination of the effects of drainage ditches on peatlands, Taillefer and Wheeler (2010) likewise found much greater numbers in southern Quebec, Canada, peatlands. Their study focused on the predominately terrestrial peat remaining near drainage ditches. They examined the **Brachycera** at the Johnville Bog and Forest Park in Quebec. They found 1453 individuals of **Brachycera**, comprising 24 families and 166 species. Simpson's species diversity index indicated a higher diversity at 6 and 11 m than at 1 m from the ditch. Taillefer and Wheeler suggested that this difference may be due to the homogeneous moss cover and moister conditions at greater distance from the ditch. On the other hand, raw species richness was greater at 1 m and the numbers of specimens per sample were 177.5 at 1 m, decreasing to 92 at 11 m, based on pan trap sampling.

Blades and Marshall (1994) identified a range of 62-106 species of acalyptrate **Diptera** in four peatlands in southern Ontario, Canada. Diversity in individual localities ranged from 12 in an **oligotrophic** (low nutrient) fen to 69 in a rich fen. One reason for this high diversity is the wide range of habitats, including both aquatic and terrestrial.

Other select taxa groups studied in peatlands include **Chironomidae** (Figure 7-Figure 10) (Wrubleski 1987), biting flies (Lewis 1987), **Empididae** (Figure 13-Figure 15; Figure 73) (Barták & Roháček 1999), **Dolichopodidae** (Figure 74-Figure 75) (Rampazzi 2002), **Sphaeroceridae** (Figure 76-Figure 77) (Marshall 1994), and multiple other acalyptrate families (Roháček & Máca 1982; Roháček *et al*. 1998).

Figure 73. **Empididae** adult on leafy liverwort. Photo courtesy of Sarah Lloyd.

Figure 74. **Dolichopodidae** larva, one of the wetland inhabitants. Photo from Landcare Research, Manaaka Whenua, NZ, with online permission.

Figure 75. **Dolichopodidae** adult, a wetland inhabitant. Photo by Matt Reinbold, through Creative Commons.

Figure 76. Dung inhabited by **Sphaeroceridae**, a family that occurs in wetlands. Photo by James K. Lindsey, with permission.

Figure 77. ***Lotophila atra*** (**Sphaeroceridae**) adult, representing a family that is present in peatlands. Photo by James K. Lindsey, with permission.

Autio and Salmela (2010) found 104 species of **Diptera** [**Limoniidae** (Figure 16), **Tipulidae** (Figure 3, Figure 25; Figure 80-Figure 82), **Pediciidae** (Figure 63-Figure 64), **Cylindrotomidae** (Figure 65-Figure 67), **Ptychopteridae** (4; Figure 68-**Error! Reference source not found.**), **Psychodidae** (Figure 60-Figure 62), and **Dixidae** (9; Figure 11-Figure 12; Figure 17)] in the open mires, wooded mires, rich fens, Baltic shore meadows, ditches, and groves of Åland Islands in Finland. The Baltic shore meadows had the greatest richness, with 44 species. The **Nematocera** of the islands comprised fewer species than did mainland regions of southern Finland, and Autio and Salmela suggested that the theory of island biogeography might explain this lower species number. The island is ~40 km from the nearest continental sites. But they countered this with the fact that some of the most species-rich habitats (*e.g.* brooks and springs) are lacking on the islands.

Savage *et al*. (2011) found 381 species of **Schizophora** (section of true flies containing 78 families) in temperate Nearctic bogs. Species richness ranged 96-192 per site. The dominant species were usually not peatland specialists. Bog size had no effect on species richness, but vegetation cover at the sampling sites was important. In summary, perhaps referring to the **Diptera** of wetlands is best described as semi-aquatic (Autio & Salmela 2010).

One reason for these seeming contradictions regarding diversity is the paucity of faunal studies in these bog, fen, and mire habitats (Rosenberg & Danks 1987). Salmela and Ilmonen (2005) reiterated this lack of knowledge, specifically for the **Tipuloidea** – the craneflies. They bemoaned the disappearance of many natural mires in Finland. They recorded 29 cranefly species in the Kauhaneva mire system, including some that were regionally threatened. Mesotrophic sites had the highest species richness; **oligotrophic** (having low nutrients) and **ombrotrophic** (dependent on atmosphere for its nutrients) sites had equally low richness.

Loss of peatlands bodes poorly for the invertebrate inhabitants. But this loss is not the only human problem faced by these invertebrates. Peatland crops such as cranberries and other fruits can put them in danger as well. Bayfield (1979) showed that the cranefly ***Molophilus ater*** (**Limoniidae**) suffers from the compaction of the peat, especially where trails are developed. Physical crushing in experiments killed large numbers of larvae. It is also possible that eggs were damaged on the foot paths.

Forests

Forest floor bryophytes often harbor **Diptera**. Logs covered with bryophytes are among the important sites. Mosses help to keep them moist and provide safe sites for the **Diptera** (Schuck *et al*. 2005). Others **Diptera** live on roots covered with drier mosses such as ***Brachythecium velutinum*** (Figure 78) and feed there on the moss (Sevchenko 1966). But these damp logs may have their dangers lurking. It is the site where the parasitic mite ***Johnstoniana errans*** (Figure 79) larvae and adults actively hunt for **Diptera** larvae and pupae among the damp mosses (Wohltmann 1996). These larvae exclusively parasitize species of ***Tipula*** (**Tipulidae**) during the pupa (Figure 80-Figure 81) and adult (Figure 82) stages.

Figure 78. ***Brachythecium velutinum***, home for **Tipulidae** in forests. Photo by Michael Lüth, with permission.

Figure 79. ***Johnstoniana*** sp. ***Johnstoniana errans*** is a parasite on ***Tipula*** species in forests. Photo by Walter Pfliegler, with permission.

Figure 80. ***Tipula*** pupa, a stage vulnerable to being parasitized by ***Johnstonia errans***. Photo by Ted Kropiewnicki, through Creative Commons.

Figure 81. **Tipulidae** adult emerging from pupal stage among forest mosses. Photo by Janice Glime.

Figure 82. ***Tipula*** cf. ***varipennis*** adult, a stage vulnerable to parasites in forests. Photo by Anki Engström at <www.krypinaturen.se>, with permission.

Recently, researchers have attempted to find **surrogates** – species or groups that can serve as predictors for the presence or status of other groups. Smith *et al*. (2008) found that no one of the species groups in their forest survey could serve as a surrogate for the other species groups. However, they did find that forest bryophytes and saproxylic hoverflies (**Syrphidae**; Figure 83) could possibly serve as surrogates for each other. That is, these groups can indicate the biodiversity of each other.

Figure 83. **Syrphidae** adult, a family one can find among the epiphytes. These flies are bee mimics, but they don't sting. Photo by VladimirZh, through Creative Commons.

Epiphytes

Bar-Ness *et al*. (2006) surmised that *Eucalyptus obliqua* forests have strong age effects in the range of 0-80 years on species composition of bryophytes and tracheophytes. Thus they concluded that the same may be true for canopy invertebrates. The **Diptera** fauna on epiphytes is poorly known. In the Northwest, USA, Nelson and Hauser (1021) used Berlese funnels to extract arthropods. They compared the fauna of mosses and liverworts as pairs from the same tree. **Diptera** were only minor contributors to these communities.

Miller and coworkers (Miller 2006; Wagner *et al*. 2007; Miller *et al*. 2008) found a different picture in the Acadian forest of central Maine, USA. Whereas the **Collembola** and spiders were most abundant at the base of red maple (***Acer rubrum***) of the Acadian forest, correlating with the abundance of bryophytes there, the **Diptera** reached their highest abundance above 2 m on the tree. Miller (2006) found fifteen **Diptera** families, but only eight of these were common. These eight common families used the tree habitats differently, depending on the height above ground. For the **Diptera**, lichens were important. Furthermore, they responded differently to forest gaps. When gaps were created, the bryophytes became less abundant, but the other guilds did not seem to be affected by the loss of canopy. At higher positions on the trees, small foliose lichens were more abundant, whereas in the lower positions the bryophytes and cyanolichens were more abundant. In the first 6 m on the bole of ***Acer rubrum*** on the south-facing side, they found percent frequencies of

Ceratopogonidae (18; Figure 57-Figure 59), **Chironomidae** (22.5; Figure 7-Figure 10), **Dolichopodidae** (8; Figure 74-Figure 75), **Empididae** (4; Figure 13-Figure 15), **Psychodidae** (9; Figure 60-Figure 62), **Sciaridae** (12; Figure 84), **Phoridae** (35; Figure 85), **Cecidomyiidae** (80; Figure 86), **Chaoboridae** (2; Figure 27), **Culicidae** (7.5; Figure 49-Figure 51), **Drosophilidae** (0.8; Figure 87), **Simuliidae** (7; Figure 88), **Syrphidae** (0.8; Figure 83), and **Tabanidae** (0.8; Figure 52-Figure 54). Only the **Chironomidae** occurred in pitfall traps, suggesting that these taxa were true arboreal dwellers. The suborder **Nematocera** was the most abundant of the **Diptera** in the arboreal habitat above 2 m (Miller *et al*. 2007). These flies may use bryophytes for a drink of water, egg laying, pupation, cover, or escape from wind. And some most likely find food there among the smaller invertebrates. These relationships remain to be elucidated.

Figure 86. **Cecidomyiidae** (**Lestremiinae**) male feeding. This is a family with some members that live among epiphytes. Photo by Richard Orr, with permission.

Figure 84. ***Bradysia praecox*** (**Sciaridae**) adult, representing a family in which some members live among epiphytes. Photo by James K. Lindsey, with permission.

Figure 87. ***Drosophila melanogaster*** adult, representing the **Drosophilidae**, a family often found among epiphytes. Photo by André Karwath, through Creative Commons.

Figure 85. **Phoridae** mating in Rock Creek Park, MD, USA. This family can be found among epiphytes. Photo by Katja Schulz, through Creative Commons.

Figure 88. **Simuliidae** larvae. Some members of this family occur among epiphytic mosses. Photo by Steve Marshall, through Creative Commons.

Forest gaps make the terrestrial environment even less inviting for the moisture lovers. Using the red maple tree

(*Acer rubrum*) in the Acadian forest of central Maine, USA, Wagner *et al*. (2007) compared undisturbed red maple forest and forest areas with gaps. Gap harvesting reduced the major groups of arthropods on the trees.

The tree bark habitat with bryophyte mats can provide an ideal habitat for moisture-requiring larvae. Old-growth ***Liriodendron tulipifera*** in Tennessee exhibited nearly six times as much water in bark under bryophyte mats at the tree base as that in bare bark at about 2 m (Billings & Drew 1938; Ulyshen 2011). We should expect to find **Diptera** taking advantage of these moisture sources.

Harvesting Stowaways

Epiphytes, and especially bryophytes on logs in old-growth forests, are often harvested for use in floral arrangements and other uses. JeriLynn Peck became concerned at the massive amounts of bryophytes being removed, and was furthermore concerned about the invertebrates that were being shipped with the bryophytes to their place of sale. Peck and Moldenke (2011) reported that more than 3.7 million kg yr^{-1} of fresh epiphytic bryophytes are harvested from the Coast and Cascade Mountain ranges in the Pacific Northwest of North America.

Peck and Moldenke (2010) researched the processing methods used in the moss trade. Most of the material from the Pacific Northwest is shipped dry, but that is little comfort because many of the invertebrates have means to survive this dry state. One processor tumbles the moss in large cylindrical tumblers with a sieve to remove needles, twigs, and other debris from the mosses. This method seems to have a high degree of success in removing the invertebrates as well. Only a few adult **Sciaridae** (dark-winged fungus gnats; Figure 89-Figure 90), an isopod, and a few oribatid mites were present in the tumbled mosses, whereas the non-tumbled fresh mosses had both high diversity and high abundance.

Figure 89. Fungus gnat (**Sciaridae**) herbivory on ***Buxbaumia aphylla*** capsules. Photo by Jörg Müller, through Creative Commons.

Altitude

Andrew *et al*. (2003) assessed the invertebrate-bryophyte community on four Australasian mountain ranges. The invertebrates were identified only to family, but the bryophytes were identified to species. In total, they collected six families of **Diptera** [**Ceratopogonidae** (Figure 57-Figure 59), **Chironomidae (**Figure 7-Figure 10), **Cecidomyiidae** (Figure 86), **Tipulidae** (Figure 3, Figure 25; Figure 80-Figure 82), **Psychodidae** (Figure 60-Figure 62), **Phoridae** (Figure 85)], and these were usually among the top five in number of families among the represented groups. **Diptera** comprised 9% of the fauna in both Tasmania and New Zealand.

Figure 90. Fungus gnat (**Sciaridae**) herbivory on ***Buxbaumia aphylla***. Photo by Jörg Müller, with permission.

Summary

Diptera differ from other insect orders in having only one pair of wings and a pair of **halteres**. Larvae of various families (especially **Chironomidae** and **Tipulidae**) often develop among bryophytes, and the same is typically true of the pupae. Some larvae even live in the thalli of liverworts.

The bryophytes provide a safe haven from predators and dry air. They serve as an insulating layer against cold. And in some cases they serve as food.

Collecting bryophyte-dwelling **Diptera** in the larval stage can be done with pan traps and pitfall traps, whereas in the adult stage sweep nets, Malaise traps, and windowpane traps are useful. They can be separated from the mosses with Tullgren funnels with sugar flotation, kerosene phase separation, or hand picking. The bryophytes with their inhabitants can be preserved in 95% ethanol, but rearing is often needed to identify the larvae.

The moss family **Splachnaceae** is adapted for spore dispersal by several families of flies, attracting them with odors in the capsules, colors, and having sticky spores. The mosses themselves grow on dung and other organic substrates, hence reaching there via the flies.

Peatlands and other wetlands typically have high diversity of **Diptera**, with many benefitting from the high moisture content. Forests also harbor a number of species among the bryophytes, especially in the larval and pupal stages, but adults may use the bryophytes for regaining moisture, avoiding predators, and oviposition. Even epiphytic bryophytes often house **Diptera**, and harvesting these epiphytes and other forest bryophytes for commercial purposes is a means of introducing invasive species where they are sold. Food may be available among the bacteria, fungi, protozoa, algae, and small invertebrates. Altitudinal differences of bryophyte dwellers seem to be poorly known in most of the world.

Acknowledgments

Thank you to Sara Altenfelder for alerting me to the mine flies that live on mosses and liverworts and supplying me with copies of old papers. Sarah Lloyd sent me images as she progressed with her research on moss inhabitants. Thank you to Sarah Lloyd who has shared her stories and images. I appreciate the many photographers who gave me permission or made their photographs available through Creative Commons license.

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CHAPTER 12-18
TERRESTRIAL INSECTS: HOLOMETABOLA – DIPTERA NEMATOCERA: TIPULOIDEA

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CHAPTER 12-18
TERRESTRIAL INSECTS: HOLOMETABOLA – DIPTERA NEMATOCERA: TIPULOIDEA

Figure 1. ***Triogma trisulcata*** larva among mosses, demonstrating mimicry of mosses with its many leaflike appendages protruding. The moss is probably ***Calliergonella cuspidata***. Photo by J. C. Schou <www.biopix.com>, with permission.

NEMATOCERA

The **Nematocera** are elongated flies that have thin, segmented antennae. Their larvae are mostly aquatic, but some are able to live on land, often using the limnoterrestrial habitat of mosses to maintain their hydration.

Using transplant experiments at the Moor House National Nature Reserve, UK, Briones *et al*. (1997) noted that **Diptera** larvae responded to changes in climate. The larvae depended on the moisture in the upper soil layers and populations diminished at higher temperatures and lower moisture levels.

Using Malaise and window traps as well as sweep netting, Salmela (2001) surveyed the **Nematocera** associated with 27 springs and springbrooks in Southern Finland. Among the 2714 individuals collected, Salmela found 95 species, comprised of 24 **Tipulidae**, 2 **Cylindrotomidae**, 54 **Limoniidae**, 12 **Pediciidae**, and 3 **Ptychopteridae**. This is a habitat that typically has extensive bryophyte cover.

Cylindrotomidae

The **Cylindrotomidae** is one of the families of the **Tipulomorpha**, an infraorder whose families were once included in the family **Tipulidae**; then the family **Cylindrotomidae** and others were separated. But the trend today is that most researchers include these 115 species in the **Cylindrotominae**, back in the family **Tipulidae**. I have maintained the separation here for ease of discussion.

The flies are yellowish to pale brown, 11-16 mm long. Most of the larvae are herbivores, and some are adapted for living among and eating bryophytes (Figure 2-Figure 3).

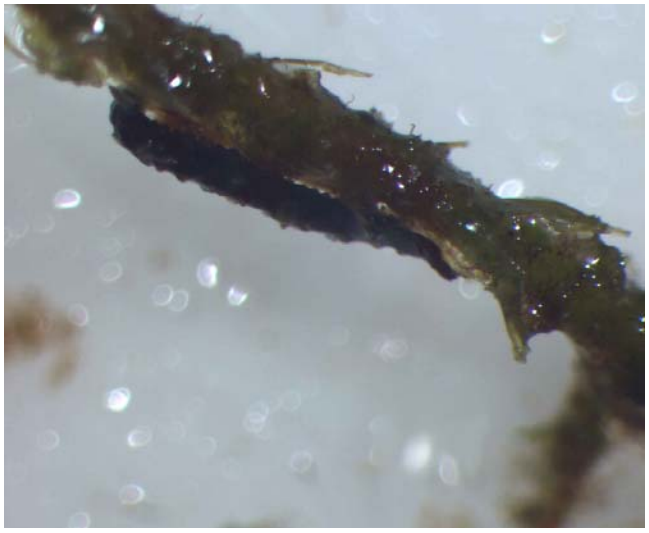

Figure 2. **Cylindrotomidae** eating ***Cratoneuron filicinum***. Photo courtesy of Misha Ignatov.

Figure 3. ***Cratoneuron filicinum*** eaten by Tipulidae. Photo courtesy of Misha Ignatov.

Adaptations

The **Cylindrotomidae** larvae often occur among bryophytes and appear to exhibit camouflage to that habitat by their coloration and numerous horizontal, elongated, cuticular lobes on the integument. Imada (2021) explored the selective pressures and functions that might be responsible for the retention of these characters. He challenged the notion that this apparent camouflage protected the larvae from predators because of the apparent absence of visual predators such as birds. Could it be that the camouflage is so good that the birds never find these larvae?

So of what importance, if any, are the lobes? Imada (2021) noted that these moss dwellers tended to crawl among the mosses, with movement starting at the posterior end and shifting to the anterior end. Imada then considered that these lobes might contribute to that movement on the soft moss beds. He found that the musculature of the larvae seems to support this movement, but he has not yet been able to demonstrate whether or not this is the case. The coloration of greens and browns, while adaptive as camouflage among the mosses, is common among plant-eating larvae in general and therefore may represent an evolutionary leftover from related families of Diptera.

Triogma

Triogma trisulcata (Figure 1, Figure 5-Figure 4) is one such mimic from upland seepage bogs and streams (Falk 1991), mosses of springs (Hemmingsen 1968), and eutrophic fens (Mannheims 1965; Salmela 2002). In streams the larvae hook themselves onto mosses such as ***Fontinalis antipyretica*** (Figure 6) or ***Calliergonella cuspidata*** (Figure 7). This species lives among the mosses and feeds on them, resembling the mosses where they live (Alexander 1920).

Figure 4. Posterior end of ***Triogma trisulcata*** showing the structures that resemble moss leaves. Photo by Walter Pfliegler, with permission.

Figure 5. ***Triogma trisulcata*** on ***Plagiomnium*** sp. Photo by Janice Glime.

Figure 6. ***Fontinalis antipyretica***, aquatic home for ***Triogma trisulcata***. Photo by Chris Wagner, with permission.

Figure 7. ***Calliergonella cuspidata***, home for ***Triogma trisulcata***. Photo by Michael Becker, through Creative Commons.

Diogma

The genus ***Diogma*** (**Cylindrotomidae**) is a terrestrial version resembling the more aquatic ***Triogma trisulcata*** (Figure 5-Figure 4) (Brinkmann 1997). It often lives near the water in humid terrestrial mosses and like ***T. trisulcata*** has dorsal processes that help to camouflage it, along with its green color (Müggenburg 1902). The larvae remain small throughout winter, reaching 2 cm at maturity. The pupae likewise live among the mosses. Müggenburg reported that ***Diogma glabrata*** (Figure 8) not only lived among leaves of the moss ***Rhytidiadelphus squarrosus*** (Figure 9) as larvae and pupae, but also that it ate them and laid its eggs there in the leaf axils. Adults emerge from the pupae in only a few days.

Figure 8. ***Diogma glabrata*** adult. Green larvae and pupae live among mosses and eat ***Rhytidiadelphus squarrosus***. Photo by Louis Boumans, with permission.

Figure 9. ***Rhytidiadelphus squarrosus***, home, food, and oviposition site for ***Diogma glabrata***. Photo by Johan N, through Creative Commons.

Cylindrotoma

The terrestrial members of this genus (Figure 10) likewise spend their larval stage among terrestrial mosses or on marsh plants (Brinkmann 1997).

Figure 10. ***Cylindrotoma*** sp. larva, often a terrestrial moss inhabitant. Photo by Walter Pfliegler, with permission.

Phalacrocera

This genus is fairly restricted in its range with the exception of ***Phalacrocera replicata*** (Figure 11). This moss dweller is a cosmopolitan species, occurring in North America, northern Europe, and northern Asia (Wikipedia 2014). ***Phalacrocera replicata*** larvae (Figure 15) feed on ***Sphagnum*** (Figure 12) (Clymo & Hayward 1982) and also live on ***Warnstorfia exannulata*** (Figure 13-Figure 14).

Figure 11. ***Phalacrocera replicata*** adult, a moss dweller. Photo by CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 12. ***Sphagnum capillifolium***, food for larvae of ***Phalacrocera replicata***. Photo by Bernd Haynold, through Creative Commons.

Figure 13. ***Warnstorfia exannulata*** habitat and home for ***Phalacrocera replicata***. Photo by J. C. Schou, with permission.

Figure 14. ***Warnstorfia exannulata***, home for ***Phalacrocera replicata***. Photo by J. C. Schou, with permission.

The young larvae of the genus ***Phalacrocera*** (Figure 15) are transparent, permitting the green coloration of the moss to show through (Alexander 1920). Older larvae are

a brownish green with a striping that somewhat resembles the light and dark shades of moss branches. Long filamentous processes on the larvae help provide disruptive coloration that makes them more difficult to see. The larvae can survive for a long time under water, but also can survive a long time out of water. They can even survive frozen in ice for the duration of winter. They are sluggish and hang onto the mosses with their anal hooks, swaying back and forth. When they do move through the mosses, they alternately grab the moss with their mandibles and anal hooks. When they are disturbed, they roll into a ball like roly-polies. The female deposits her eggs in the leaf axils of the mosses.

Figure 15. ***Phalacrocera replicata*** larva, a moss dweller and moss consumer. Note the green color of the digestive tract and the transparency of the larva. Photo by Paul T, through Creative Commons.

Not surprisingly, these larvae remain in the mosses to pupate (Figure 16). When they emerge, they climb out the pupal encasement in its upright position (Figure 17), emerging from the top.

Figure 16. ***Phalacrocera replicata*** pupa on moss in Michigan, USA. Photo by Janice Glime.

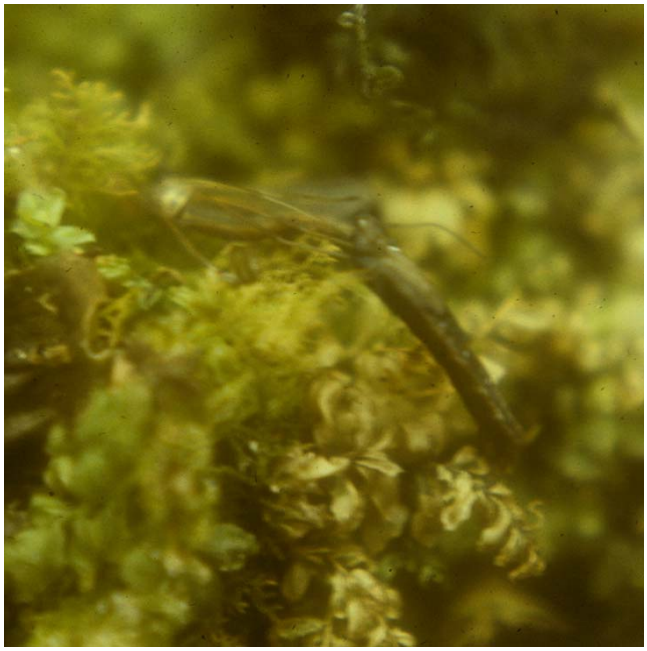

Figure 17. ***Phalacrocera replicata*** adult emerging from its pupa on moss in Michigan, USA. Photo by Janice Glime.

Phalacrocera tipulina (Figure 18) is another bog dweller in this family. It lives in or near the mountain peat bogs and as a larva eats mosses and other plants (Alexander 1942; Fetzner 2007).

Figure 18. ***Phalacrocera tipulina*** adult, a bog dweller. Photo by Chen Young, through Creative Commons.

Liogma

Liogma is one of the genera that exhibits cryptic coloration. The larvae live among mosses and feed on them (Alexander 1920; Byers 1961; Fetzner 2007). And they look like mosses in coloration and markings (Alexander 1920). One of these is ***Liogma nodicornis*** (Figure 19-Figure 21), a species that lives in ***Hypnum cupressiforme*** (Figure 22-Figure 23) as larvae and pupae.

Figure 19. ***Liogma*** sp. larva, a moss dweller with disruptive filaments. Photo by Bob Barber, through Creative Commons.

Figure 20. ***Liogma nodicornis***, a species that spends its larval and pupal life in mosses such as ***Drepanocladus***. Photo by Stephen Cresswell, with permission.

Figure 21. ***Liogma nodicornis*** mating, a species that spends its larval and pupal life in mosses such as ***Drepanocladus***. Photo by Stephen Cresswell, with permission.

Figure 22. Typical habitat of ***Hypnum cupressiforme*** and home for ***Liogma nodicornis***. Photo by Michael Lüth, with permission.

Figure 23. ***Hypnum cupressiforme***, home for ***Liogma nodicornis***. Photo by Michael Lüth, with permission.

Limoniidae

This family is often included as a subfamily in the **Tipulidae**. The species ***Limnophila alleni*** (Figure 24-Figure 25) was among early reports of members of this family that made use of mosses. Alexander (1919) reported that the females laid their eggs in mosses, flying low over the substrate until they find a suitable place.

Figure 24. ***Limnophila*** larva; some species hatch among mosses. Photo by Tom Murray, through Creative Commons.

Figure 25. ***Limnophila alleni*** adult, a species that oviposits among mosses. Photo by Chen Young, through Creative Commons.

The **Limoniidae** species tend to be in moist habitats. ***Paradelphomyia fuscula*** (Figure 26) was among the four most common species along springs in southern Finland (Salmela 2001).

Figure 26. ***Paradelphomyia fuscula*** adult, a common species along springs in Finland. Photo by Marko Mutanen, through Creative Commons.

Geranomyia vitiella has an unusual habit worth noting. Its larvae live on leaves of *Pandanus* in moist habitats of Fijian rainforest (Beaver & Ryan 1988). The larva makes a tube of jelly on the upper surface of the leaf, living and moving in it and emerging to feed on dead **epiphylls** (mosses, liverworts, fungi, algae, and lichens that live on the leaves) and the associated decaying matter and microbes (Beaver & Ryan 1988). When it is mature, it changes its position to the lower surface, producing an even larger mass of jelly. It pupates in the jelly. These jelly masses protect both larvae and pupae against both desiccation and natural enemies. Beaver and Ryan assumed that the eggs are laid among the epiphylls.

Hancock (2008) reports that Falk (1991) reared ***Gnophomyia viridipennis*** from moss collected from a fallen tree trunk of beech in Great Britain. Previous records indicate the species may prefer *Populus* species.

Arroyo-Rodríguez *et al.* (2007) experimented with ***Geranomyia recondita*** feeding in the lab. They offered three species of **Lejeuneaceae** – small leafy liverworts that are common among epiphylls. Only 30% of the larvae consumed the offered liverworts, but this demonstrates that they can eat live liverworts. They fed mostly on ***Lejeunea*** (Figure 27) and never ate ***Leptolejeunea*** (Figure 28). Arroyo-Rodríguez and coworkers suggested that this avoidance indicates they avoid liverworts with aromatic compounds. The larvae also consumed other epiphylls on the leaves. The jelly mass area had a negative correlation with the temperature, a relationship the authors interpreted as an indication the larvae are more active at night since the masses were larger at that time. The larger jelly mass would give them a larger foraging area.

Figure 27. ***Lejeunea*** *cf* ***epiphylla*** on ***Blechnum wattsii*** leaf; this liverwort is food for ***Geranomyia recondita.*** Photo by Tom Thekathyil, with permission.

Figure 28. ***Leptolejeunea elliptica***, member of a genus rejected as food by ***Geranomyia recondita***. Photo by Yan Jia-dang, through Creative Commons.

Geranomyia sexocellata near Cape Town, South Africa, uses a similar gelatinous tube, but it adds minute sand grains and attaches the tube to mosses in small trickles of water (Harrison & Barnard 1972). ***Limonia capicola*** larvae live among mosses at the edge of rapidly flowing small streams. Similarly, larvae of ***L. rostrata*** (=***Geronomyia rostrata***; Figure 29) live among mosses, liverworts, and filamentous algae on wet rocks (Rogers 1927). The larvae occur between the layers of liverwort thalli or in contact with stems of the mosses where they feed on the leaves. They seem to prefer the terminal leaves on the smaller stems in the lab, but in the field they are mostly found deep within the mat. Their translucent greenish color and slow movement make them hard to see. The larvae construct a tube and feed from its safety. Pupation occurs at the distal ends of the larval tubes. ***Limonia annulata*** (Figure 30-Figure 31) adults tend to occur on the moss-covered tree bases in forests (Fetzner 2008).

Figure 29. ***Limonia rostrata*** adult, a species whose larvae live between layers of liverworts or along stems of mosses that they feed on. Photo by Stephen Luk, with permission.

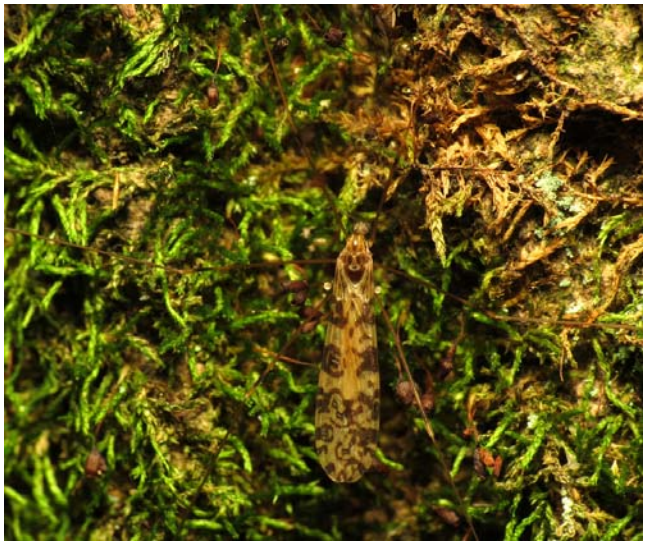

Figure 30. If you are having trouble finding the ***Limonia annulata*** adult on this moss, you can understand the value of its coloration. This species spends much of its adult time on moss-covered tree bases. Photo by Katja Schulz, through Creative Commons.

Figure 31. ***Limonia annulata*** adult, a species that hangs out on mosses at tree bases in its adult stage. Photo by Tom Murray, through Creative Commons.

The genus "***Gonomyia***" has been split into a number of genera, several of which include bryophyte dwellers. Byers (1961) reported use of bryophytes as habitat by at least some ***Erioptera*** larvae. Salmela (2001) found ***Erioptera pederi*** (Figure 32) among the **Nematocera** along springs and springbrooks in southern Finland.

Figure 32. ***Erioptera pederi*** adult, a species that lives along springs and springbrooks and larvae can occur among the bryophytes. Photo by Marko Mutanen, through Creative Commons.

Falk (1991) found that ***Ellipteroides alboscutellatus*** (previously in ***Gonomyia***; Figure 33) seemed to be associated with wooded mossy calcareous seepages. Several of the **Limoniidae** were published just as ***Gonomyia***, so other bryophyte dwellers may be lurking in

that former genus. In their search for indicator species, Salmela and Ilmonen (2005) recorded 29 species of craneflies (**Tipuloidea**) from Malaise traps in the Kauhaneva mire system in Finland. They found the highest diversity in mesotrophic sites, with the oligotrophic and ombrotrophic sites having equally low diversity. ***Erioptera flavata*** (Figure 34) and ***Phylidorea squalens*** (Figure 35) were indicators of mesotrophic sites (Figure 36), but they found no indicators for the low-nutrient sites.

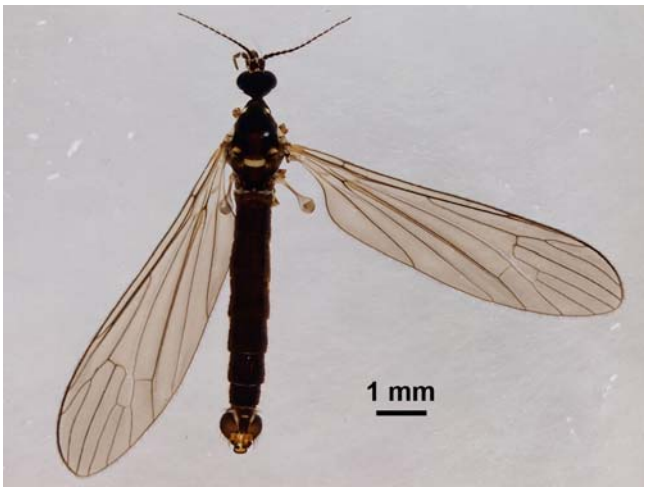

Figure 33. ***Ellipteroides alboscutellatus*** adult, a species associated with wooded mossy calcareous seepages. This museum specimen is unfortunately missing its long legs. Photo by Jukka Salmela, with permission.

Figure 34. ***Erioptera flavata*** adult, an indicator of mesotrophic sites. Photo by James K. Lindsey, with permission.

Figure 35. ***Phylidorea squalens*** adult male, an indicator of mesotrophic sites. Photo by James K. Lindsey, with permission.

Figure 36. ***Phylidorea squalens*** habitat in wet forest with mosses. Photo by James K. Lindsey, with permission

Elephantomyia aurantiaca (see Figure 37) is a limoniid that lives among damp mosses and liverworts near streams (Harrison & Barnard 1972).

Figure 37. ***Elephantomyia westwoodi*** male adult. ***Elephantomyia aurantiaca*** lives among damp mosses and liverworts near streams. Photo by Tom Murray, through Creative Commons.

Pediciidae

The **Pediciidae** (Figure 38) is another family that is often included as a subfamily in the **Tipulidae**. In addition to the two members of **Limoniidae**, Salmela and Ilmonen (2005) found that ***Pedicia rivosa*** (Figure 39-Figure 40) and ***Tricyphona immaculata*** (Figure 41) indicated mesotrophic sites in the Kauhaneva mire system, but there were no indicators for the low-nutrient sites. These two species and ***Pedicia straminea*** (Figure 42) were among the four most common species and often the most abundant species of the **Diptera** collected around southern Finnish springs (Salmela 2001).

Figure 38. ***Pedicia albivitta***, member of a genus that often occurs among mosses. Photo by Jason Neuswanger, with permission.

Figure 39. ***Pedicia rivosa*** adult, an indicator of mesotrophic sites, camouflaged here against the vegetation. James K. Lindsey, with permission.

Figure 40. ***Pedicia rivosa*** adult, an indicator of mesotrophic systems. Photo by Roger S. Key, with permission.

Figure 41. ***Tricyphona immaculata*** adult, indicator of mesotrophic sites. Photo by Malcolm Storey at <www.discoverlife.org>, through Creative Commons.

Figure 42. ***Pedicia straminea*** adult, an indicator of mesotrophic sites. Photo by Marko Mutonen, through Creative Commons.

Stephen Cresswell observed ***Pedicia auripennis*** (Figure 43) resting on a mossy rock overhang in the bed of a ravine in West Virginia, USA (Fetzner 2008). Flies can use such resting places to rehydrate and to maintain lower temperatures.

Figure 43. ***Pedicia auripennis*** adult resting. Mosses make good resting sites, especially cool, damp ones. Photo by Stephen Cresswell, with permission.

Figure 44. ***Tipula oleracea*** larval respiratory organ showing small papillae, but this species does not seem to be a moss dweller. Photo by Malcolm Storey, through Creative Commons.

Tipulidae – Craneflies

Most of the craneflies associated with bryophytes are aquatic, but a few terrestrial taxa give the bryophytes special importance. Alexander (1919) considered the **Tipulidae** family to serve as a major food group for the vertebrates. ***Tipula*** species on the Pribilof group in the Bering Sea are abundant in the summer. Larvae are especially common under mosses where they feed on the rhizoids. As many as 20 larvae can occur in a 30-cm square; considerable areas of mosses are killed by their activity (Figure 3). To add to destruction by the larvae, foxes dig up large areas of mosses to find the juicy larvae for food. Hofsvang (1997) noted the wide range of larval habitats, from water to mosses to dry logs. As adults, the **Tipulidae** typically live only a few days and some don't eat as adults.

In West Germany, changes in some of the fly populations are directly linked to changes in bryophyte cover (Wagner 1980). Morris (1986) reports on "an unusual habitat" for the overwintering of European cranefly larvae, but it appears that craneflies are the most important group utilizing the terrestrial bryological habitat. Craneflies are those insects that tend to cling around the ceiling and look like giant mosquitoes.

Figure 45. ***Tipula abdominalis*** larval respiratory disk with large grey papillae. This species likewise is not a moss dweller. Photo by Thomas Palmer (Ophis), with permission.

Adaptations

Some craneflies (**Tipulidae**) are highly adapted to their mossy habitat, with some taxa colored in such a way as to resemble a moss branch, as discussed under the various genera. Brindle (1957) observed that the **Tipulidae** that live among bryophytes have special anal papillae (Figure 44-Figure 45) to help them gain oxygen. I have been unable to verify that with the more recent data available.

Among the bryophytes they select, growth form is important (Gerson 1982). The compact species like ***Bryum argenteum*** (Figure 46) and ***Ceratodon purpureus*** (Figure 47-Figure 48) hinder tunnelling by the larvae, whereas loose growth forms like those of ***Climacium*** (Figure 49), ***Polytrichum*** (Figure 50), and ***Plagiomnium cuspidatum*** (Figure 51) are too diffuse for making tunnels (Byers 1961). Byers also concluded that ***Polytrichum*** and thallose liverworts were not soft enough. I have to wonder if secondary (antiherbivory) compounds might be important for protecting the thallose liverworts.

Figure 46. ***Bryum argenteum***, a compact species that hinders tunnelling by **Tipulidae** larvae. Photo by Michael Becker, through Creative Commons.

Figure 47. ***Ceratodon purpureus*** cushions, a compact species that hinders tunnelling by **Tipulidae** larvae. Photo by Michael Lüth, with permission.

Figure 48. ***Ceratodon purpureus*** cushion, a compact species that hinders tunnelling by **Tipulidae** larvae. Photo by Janice Glime.

Figure 49. ***Climacium dendroides*** showing openness of the clump, spaces unsuitable for tunnelling by **Tipulidae**. Photo by Janice Glime.

Figure 50. ***Polytrichum juniperinum*** showing open leaf overlap and open spaces in clump, unsuitable for tunnelling by **Tipulidae**. Photo by Janice Glime.

Figure 51. ***Plagiomnium cuspidatum*** showing the openness of the branches, unsuitable for tunnelling by **Tipulidae**. Photo by Michael Lüth, with permission.

Mosses can be a major portion of the diet of **Tipulidae** larvae (Richardson 1981; Pritchard 1983). However, the feces of some species have undigested vegetable particles in the feces, including mosses, suggesting that the food value may be from periphyton on the mosses and that the

mosses are not digested (Pritchard 1983). At least ***Tipula abdominalis*** (Figure 52-Figure 53) larvae have a high *p*H in the gut that permits them to digest leaf litter (Martin *et al*. 1980; Sharma *et al*. 1984). But leaf litter typically has fungi that begin the process to prepare them for digestion (Barlocher 1985). The mosses are living cells and thus gaining access to the contents inside the cell walls is more difficult.

Figure 52. ***Tipula abdominalis*** adult, a cranefly whose larvae have a high gut *p*H to digest detritus. Photo by Stephen Cresswell, with permission.

Figure 53. ***Tipula abdominalis*** larva, a species with a high gut *p*H to digest detritus. Photo by Tom Murray, through Creative Commons.

Tipula

Tipula (Figure 55-Figure 60) is a worldwide genus with 59 species in Britain alone (Freeman 1967). It is a typical wet habitat fly, especially in its larval stage. Using sweep nets (catching adults), Freeman (1968) found more species in wet or woodland habitats than in dry or non-woodland habitats. Not surprisingly, it feeds on the mosses in these habitats. And it is also not surprising that in the open and drier habitats the peak in number of species present occurs in spring and late summer, whereas in the more moist and shaded habitats the diversity remains relatively constant during the entire period of spring to late summer. And of course Freeman found more species in the more shaded or moist habitats.

Sevchenko (1966) found that larvae of ***Tipula stigmatella*** (Figure 55) / ***T. submaculata*** (Figure 56) live among dry mosses, especially ***Brachythecium velutinum*** (Figure 54) on tree roots, and feed on the moss. Savchenko (1964) likewise found that ***Tipula benesignata*** (Figure 57) feeds on mosses living under the forest cover. In fact, the association of fly larvae, and especially the craneflies (**Tipulidae**), is so strong that Oldroyd (1964) suggested that flies arose from ancestors that had larvae that lived in wet moss.

Figure 54. ***Brachythecium velutinum*** with capsules, a common home for ***Tipula stigmatella*/*submaculata*** on tree roots. Photo by Dick Haaksma, with permission.

Figure 55. ***Tipula stigmatella*** adult, a species whose larvae live among dry mosses such as ***Brachythecium velutinum***. Photo by James K. Lindsey, with permission.

Figure 56. ***Tipula submaculata*** adult, a species whose larvae live among dry mosses. Photo by Tom Murray, through Creative Commons.

Figure 57. ***Tipula benesignata***, a species that feeds as larvae on mosses under forest cover. Photo by Marko Mutanen, through Creative Commons.

Brindle (1960) found a correlation that may be a moss adaptation for moss-dwelling ***Tipula*** (Figure 58-Figure 59). The moss feeders always have four pairs of short anal papillae at the posterior end. They never have long papillae like the ones on larvae from wetter environments. On the other hand, this may simply be an evolutionary correlation of two divergent groups. But spiracular disk size also differs (Todd 1993) and it would be interesting to compare the size of this respiratory organ with available airspace within the bryophyte mat inhabited.

Figure 58. **Tipulidae** – herbivore on the moss ***Cratoneuron filicinum***. Photo courtesy of Misha Ignatov.

Figure 59. ***Cratoneuron filicinum*** – food for a **Tipulidae** larva. Photo courtesy of Misha Ignatov.

Zasypkina and Ryabukhin (2001) described the insects that lived in intermediate habitats in northeast Asia. They reported that the larvae of ***Tipula glaucocinerea*** live in wet depressions with no open water, living in moss litter under snowfields as well as those on the banks of bog pools and small lakes. Larvae of ***T. melanoceros*** live in boggy forest clearings, in peat mosses, or in decaying ***Sphagnum*** where they occur in groups.

Tipula confusa (Figure 61-Figure 60) not only chose to live in clumps of ***Brachythecium rutabulum*** (Figure 62) on walls and buildings, but it also consumed its mossy housing (Todd 1993). ***Tipula confusa*** had a significant preference for ***Dicranella heteromalla*** (Figure 63-Figure 64) (70.0±1.4% S.E. of observations), with ***Brachythecium rutabulum***, a woodland species, preferred second (47.3±1.3% S.E.); both a woodland species, ***Mnium hornum*** (Figure 65) (41.7±1.5% S.E.), and a moorland species, ***Sphagnum recurvum*** (Figure 66) (40.0±1.4% S.E.) were third in preference. ***Tipula subnodicornis*** (Figure 67) spent significantly more time on ***Eurhynchium praelongum*** (Figure 68) than on ***Sphagnum recurvum***, and exhibited the greatest preference for ***Eurhynchium praelongum*** (42.8±1.7% S.E. of obs), but not significantly higher than for ***Dicranum scoparium*** (Figure 69-Figure 70) (40.6±1.5% S.E.), for which preference was not significantly higher than that for ***Sphagnum recurvum*** (38.0±1.4% S.E.). Both ***Tipula confusa*** and ***T. subnodicornis*** preferred ***Polytrichum commune*** (Figure 71) significantly less than any other moss studied. Brindle (1960) found that on moorlands ***T. subnodicornis*** is typically associated with semi-aquatic mosses such as ***Sphagnum*** and "***Hypnum***" (presumably ***Drepanocladus*** s.l.; Figure 72).

Figure 60. ***Tipula confusa*** adult, a species whose larvae live among and feed upon ***Brachythecium rutabulum*** on walls. Photo by Janet Graham, through Creative Commons.

Figure 61. ***Tipula confusa*** adult, a species whose larvae live among and feed upon ***Brachythecium rutabulum*** on walls. Photo by James K. Lindsey, with permission.

Figure 62. ***Brachythecium rutabulum*** with capsules, habitat and second choice of mosses as food for ***Tipula confusa***. Photo by J. C. Schou, with permission.

Figure 63. ***Dicranella heteromalla*** habitat where one might find ***Tipula confusa***. Photo by Michael Lüth, with permission.

Figure 64. ***Dicranella heteromalla***, a choice habitat and food for ***Tipula confusa***. Photo by Michael Lüth, with permission.

Figure 65. ***Mnium hornum***, a moss that is eaten by ***Tipula confusa***. Photo by Michael Lüth, with permission.

Figure 66. ***Sphagnum recurvum***, among the food sources for ***Tipula confusa***. Photo by Malcolm Storey <www.discoverlife.com>, through Creative Commons.

Figure 67. ***Tipula subnodicornis*** adult, a species whose larvae prefer the moss ***Eurhynchium praelongum*** as food. Photo by James K. Lindsey, with permission.

Figure 68. ***Eurhynchium praelongum***, home and food source for ***Tipula subnodicornis***. Photo by Blanka Shaw, with permission.

Figure 69. ***Dicranum scoparium*** habitat and home for ***Tipula subnodicornis***. Photo by Janice Glime.

Figure 70. ***Dicranum scoparium,*** home and food for ***Tipula subnodicornis***. Photo by Janice Glime.

Figure 71. ***Polytrichum commune***, one of the least preferred moss species for food by ***Tipula confusa*** and ***T. subnodicornis***. Photo by Malcolm Storey <www.discoverlife.com>, through Creative Commons.

Figure 72. ***Drepanocladus exnnulatus***, a typical emergent moss home for ***Tipula subnodicornis***. Photo by Michael Lüth, with permission.

In lab choice experiments, Todd (1993) showed that ***Tipula confusa*** (Figure 61-Figure 60) preferred mosses from woodland habitats, whereas ***Tipula subnodicornis*** (Figure 67) did not show any overall preference for either woodland or moorland mosses. Todd found that eight (of 11 studied) species of ***Tipula*** were moss feeders, seven of which were in the subgenus ***Savtshenkia*** [***Tipula rufina*** (Figure 73), ***T. confusa***, ***T. pagana*** (Figure 74), ***T. staegeri***, ***T. limbata*** (Figure 75), ***T. alpium*** (Figure 76), ***T. subnodicornis***). Only ***Tipula montana*** (Figure 90) was in the separate subgenus ***Vestiplex***. On recently burned *Calluna* heath larvae live among and feed on dead introduced mosses, ***Campylopus introflexus*** (Figure 77). Falk (1991) reported that ***Tipula limbata*** also occurs in boggy forests in Scotland.

Figure 73. ***Tipula rufina*** adult; larvae of this species have small mandibles and eat small particles of moss. Photo by Malcolm Storey, through Creative Commons.

Figure 74. ***Tipula pagana*** adult, a moss feeder in Europe. Photo by Malcolm Storey, through Creative Commons.

Figure 75. ***Tipula limbata*** adult, a species whose larvae are moss feeders. Photo by Derek Sikes, through Creative Commons.

Figure 76. ***Tipula alpium*** adult, a species whose larvae eat mosses. Photo by James K. Lindsey, with permission.

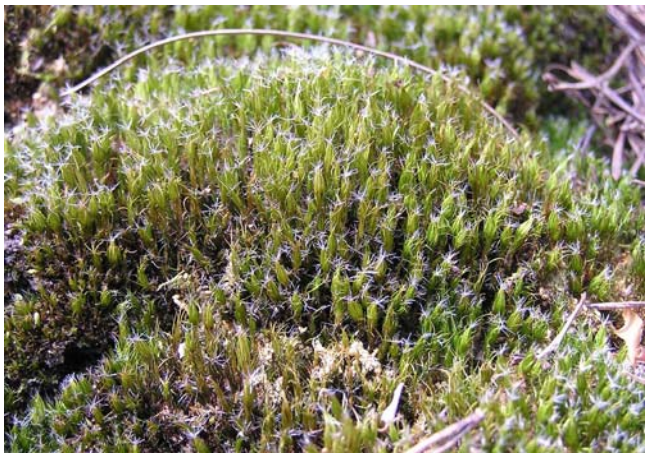

Figure 77. ***Campylopus introflexus***, an introduced moss in Europe that serves as home and food for some ***Tipula*** species. Photo by Michael Becker, through Creative Commons.

Approximately one fourth of the British species of ***Tipula*** feed on mosses, but in some species the ingested mosses depart in the feces with no evidence of breakdown (Todd 1993). That does not appear to be the case for ***Tipula montana*** (Figure 90) – it feeds exclusively on mosses. This species does not grow at temperatures below 7°C (Todd 1996). Perhaps the moss maintains a higher temperature where it can successfully complete its life cycle in a timely manner.

Mandible size seems to be an important character in bite size. **Grass feeders** typically have longer mandibles than moss feeders. ***Tipula paludosa*** (Figure 78-Figure 82) has significantly larger mandibles and ingests larger particles than the smallest mandibles of this group, exhibited by ***T. rufina*** (Figure 73), a species that ingests smaller particles. There was no evidence that the cell walls had been broken down, indicating that crushing of cells by the mandibles was the only means by which larvae could obtain the nutrients within the cells. Furthermore, biflavonoids in the cell walls of mosses apparently resist fungal invasion, thus making it difficult or impossible for the larvae to digest the cell walls. This explains the reason for the approach of taking the same size of particles throughout their growth because larger particles would not offer much more digestible food. Other kinds of insect larvae are known to increase particle size as they grow. The larvae apparently, as one might expect, eat from edge inward on the leaf, leaving less damage in the mid-cell region. Some ***Tipula*** species do switch moss species as they grow. Heavy metals accumulated by the bryophytes from pollution can also deter feeding.

Figure 78. ***Tipula paludosa*** larva, a species with large mandibles that feeds on mosses. Photo by Roger S. Key, with permission.

Figure 79. ***Tipula paludosa*** blending in with the surrounding twigs and needles. Photo by James K. Lindsey, with permission.

Figure 80. ***Tipula paludosa*** adult. Photo from <www.aphotofauna.com>, with permission.

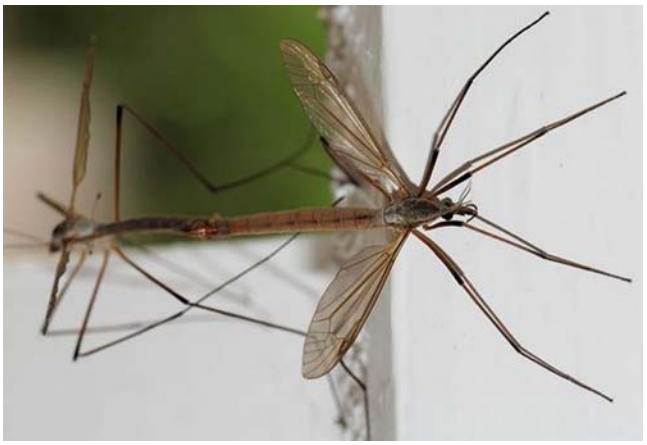

Figure 81. ***Tipula paludosa*** mating. Photo by Anki Engström <www.krypinaturen.se>, with permission.

Figure 82. Head, thorax, and halteres of ***Tipula paludosa***. Photo by Anki Engström at <www.krypinaturen.se>, with permission.

To these members of the subgenus ***Savtshenkia***, Savchenko (1964) adds ***Tipula benesignata*** (Figure 83). This species likewise feeds on mosses under forest cover.

Figure 83. ***Tipula benesignata***, a moss feeder under forest cover. Photo by Marko Mutanen, through Creative Commons.

It is of interest that the tipulid populations do not appear to support **Gause's law**. That is, in this group, closely related species tend to occur together. However, several factors may actually separate their niches. The adults in the same subgenus may be separated in time. Other factors such as mating behavior also help to keep the species from interbreeding.

Freeman (1967) explored **Gause's law** in the **Tipulinae**. Using a 350 x 350 m area, Freeman was able to demonstrate that each of the 23 species of ***Tipula*** was restricted to one or occasionally two of the five plant communities represented. Within each of those plant communities there was no evidence of competition for food in the soil-dwelling ***Tipula*** species, but some species, especially ***T. paludosa*** (Figure 78-Figure 81), became aggressive, directly attacking competitors. Ten species of ***Tipula*** were able to co-exist for nine years in one plant community, the **carr** (waterlogged wooded terrain). They seemed to accomplish this co-existence through use of microhabitats.

Coulson (1962) found that ***Tipula paludosa*** (Figure 78-Figure 81) was restricted to mineral soils in the Pennine, UK, moorland. Morris (1986) found a more unusual habitat for ***Tipula paludosa***. These cranefly larvae, known as leatherjackets in their larval stages and numbering in the hundreds, were living among mosses on the roof of a covered picnic table in Newfoundland, Canada. The roof shingles had accumulated sand and organic matter that sustained the mosses.

Tipula subnodicornis (Figure 67) has wide occurrence in the Pennine moorland of the UK, but it occurs only in areas with peat (Coulson 1962). It demonstrates niche separation from ***T. paludosa*** (Figure 78-Figure 81) in the moorland by emerging mostly within an 11-day period, whereas for ***T. paludosa*** emergence is spread mostly over 23 days in late July and early August. The time of day for emergence differed, with ***T. subnodicornis*** emerging around mid-day and ***T. paludosa*** emerging at 21:00 h, shortly after sunset. Mating of both species occurred shortly after emergence, thus separating the two species in time. Both species began laying eggs immediately after mating, with ***T. subnodicornis*** occurring deeper than those of ***T. paludosa***. Densities of final instar larvae of ***T. subnodicornis*** reached more than 100 per m^2 on *Juncus squarrosus* moorland (Figure 84) but was much lower on the ***Sphagnum*** (Figure 12; Figure 84) bog areas. In dry spells such at that of 1955, there was high mortality among eggs and first instars in ***T. subnodicornis***. Density similar to previous years was maintained only in areas such as ***Sphagnum*** flushes (Figure 84) where water was retained.

Figure 84. ***Sphagnum*** in flush with ***Juncus*** on Mt. Snowdon, Wales. Photo by Janice Glime.

With so many ***Tipula*** species occurring among mosses as larvae, we must assume that the mosses are suitable, perhaps preferred or exclusive egg-laying sites for many species (Figure 85. One such species that was identified early was ***Tipula nobilis*** (Figure 86) that laid eggs in mosses (Alexander 1919).

Figure 85. ***Tipula williamsiana*** female laying eggs on mosses. Photo by Chen Young, through Creative Commons.

Figure 86. ***Tipula nobilis*** adult, a species that uses mosses for oviposition. Photo by Chen Young, through Creative Commons.

Among this group are craneflies that eat mosses. Sevchenko (1966) found that craneflies live among and feed on dry ***Brachythecium velutinum*** (Figure 54) on tree roots. The larvae of ***Tipula oropezoides*** (Figure 87) are regular feeders on ***Rhizomnium punctatum*** subsp. ***chlorosum*** (see Figure 88) along streams in eastern deciduous forests of the United States (Wyatt & Stoneburner 1989). The larvae typically strip the leaves of their lamina, leaving the costa and border. Could it be that borders discourage feeding by some invertebrate herbivores?

Figure 87. ***Tipula oropezoides*** male, a species whose larvae feed on mosses such as ***Rhizomnium punctatum*** along streams. Photo by Tom Murray, through Creative Commons.

Figure 88. ***Rhizomnium punctatum***, home and food for ***Tipula oropezoides*** along streams in the eastern USA. Photo by J. C. Schou, with permission.

Some of the craneflies require 4 years to complete larval development, especially in Arctic ecosystems (MacLean 1980). The soil organisms there, and especially the **Diptera**, support the breeding populations of many breeding bird species, with craneflies being the most important prey. Hence, timing is important and the bird breeding is timed so that the young birds can feed on the emerging adult **Diptera** in early to mid July. In June and again in August, the **Diptera** larvae, especially craneflies, become the most important prey items. An overproduction of craneflies is necessary to compensate for the predation. These birds consume 35-70% of the annual production of ***Tipula carinifrons*** (Figure 89) and 50% of the peak emergence of all adult craneflies.

Figure 89. ***Tipula carinifrons*** male adult, a moss dweller in dry ***Sphagnum*** hummocks. Photo by Ashley Bradford, through Creative Commons.

In the blanket bogs of British moorland, larvae of ***Tipula subnodicornis*** (Figure 67) feed on liverworts (Coulson & Whittaker 1978; MacLean 1980). In a ***Sphagnum*** (Figure 12) bog, Smirnov (1958, 1961) found large quantities of ***Sphagnum*** leaves in gut analyses only in

Tipula larvae. In the coastal tundra of Barrow, Alaska, USA, ***Tipula carinifrons*** (Figure 89) is common in dry moss hummocks. Smirnov estimated that more than 25% of the energy consumed by cranefly larvae came from living plants.

Smith and coworkers (Smith 1997; Smith *et al*. 2001) examined the balance between the need for food and the need for shelter in the cranefly ***Tipula montana*** (Figure 90). Larvae were reared on single genera of mosses and the resulting growth in weight differed by a factor of two. When the larvae were given a choice between two genera, they chose the moss that had the most beneficial food quality. However, their response to ***Pleurozium schreberi*** (Figure 91-Figure 92) was a surprise. Although this food had the best food quality and resulted in the best growth, it was among the least eaten by the larvae. Fecal pellet analysis gave different results from those of observations, perhaps due to differences in digestibility. The sedge *Carex bigelowii* was eaten in preference to any of the mosses during the experiments, suggesting that the craneflies benefitted from using the bryophytes as a refuge, overriding the importance of dietary quality and making the trek to sedges less advantageous.

Figure 90. ***Tipula montana verberneae*** adult; larvae choose mosses as food based on quality. Photo by Pila Partanen, through Creative Commons.

Figure 91. ***Pleurozium schreberi*** habitat, displaying a habitat that appears suitable for ***Tipula*** larvae, but that is avoided by them as food. Photo by Michael Lüth, with permission.

Figure 92. ***Pleurozium schreberi***, a moss that is typically avoided as food for ***Tipula*** larvae. Photo by Bob Klips, with permission.

Tipulids are important contributors to the food web, and ***Tipula montana*** (Figure 90) is no exception. In Scotland the Dotterel (*Charadrius morinellus*; Figure 93) adults and chicks feed selectively, with adults eating mostly beetles, sawflies, and both adults and larvae of ***T. montana*** (Galbraith *et al*. 1993). The adult Dotterels contained a high proportion of beetles. The chicks, on the other hand, took more soft-bodied food. Every two years the adults of ***T. montana*** emerge *en masse*. At that time, both chicks and adults feast on tipulids. In one case, the larvae of ***T. montana*** formed much of the diet soon after the birds arrived at their breeding grounds and again just before they left in the autumn. The preferred feeding habitats were the moss ***Racomitrium lanuginosum*** (Figure 94) or the rush ***Juncus trifidus*** (Figure 95) heaths or the transition zone between the moss heath and montane bog. When the montane bogs were close to the ***R. lanuginosum*** heaths, they met the feeding needs of both the chicks and adults, respectively.

Figure 93. *Charadrius morinellus* (European Dotterel) male with chicks, consumers of moss inhabitants. Photo by Helwig Brunner, through Creative Commons.

Figure 94. ***Racomitrium lanuginosum*** hummocks in old drainage channels, home for ***Tipula montana***. Photo by Alan Silverside, with permission.

Figure 95. ***Juncus trifidus***, one of the preferred feeding habitats for ***Tipula montana***. Photo by Opioła Jerzy, through Creative Commons.

Tipula borealis (Figure 96) is a species of wet woodlands. The larvae occur in well-rotted logs, often occupying the interface space under the surface mosses (Gelhaus 1986).

Figure 96. ***Tipula borealis*** adult, a species whose larvae often live under mosses on rotten logs. Photo by Chen Young, through Creative Commons.

One of the more unusual relationships is the use of the hornworts ***Anthoceros agrestis*** (Figure 97) and ***Phaeoceros carolinianus*** (Figure 98) (Bisang 1996). ***Tipula*** sp. larvae consumed both the gametophytes and sporophytes of these hornwort species. ***Bryum*** sp. (see Figure 99) and several seedlings in the same pots were not eaten.

Figure 97. ***Anthoceros agrestis***, food for some ***Tipula*** larvae. Photo by Bernd Haynold, through Creative Commons.

Figure 98. ***Phaeoceros carolinianus*** with sporophytes, a hornwort that is food for some ***Tipula*** larvae. Photo by Hermann Schachner, through Creative Commons.

Figure 99. ***Bryum capillare***, a food source refused by hornwort-dwelling ***Tipula***. Photo by Michael Lüth, with permission.

Prionocera

In the coastal tundra at Barrow, Alaska, USA, ***Prionocera recta*** (Figure 100) is restricted to mossy depressions (MacLean 1980).

Figure 100. ***Prionocera recta*** adult, a species that in Alaska is restricted to mossy depressions. Photo by Jukka Salmela, with permission.

Dolichopeza

Alexander (1920 in Gerson 1982) and Byers (1961) reported that ***Dolichopeza*** lives in and eats the mosses. Like several other **Tipulidae** (*s.l.*), larvae of ***Dolichopeza americana*** (Figure 101) has cryptic coloration of green with irregular markings and dark lines, permitting it to blend with its mossy environment (Byers 1961).

Figure 101. ***Dolichopeza americana*** adult, a species whose larvae have cryptic coloration among bryophytes. Photo by Tony Gallucci, through Creative Commons.

Dolichopeza americana (Figure 101) and ***Oropeza*** larvae, also craneflies, have color patterns that make them inconspicuous among the mosses and permit them to browse without being easily detected by predators (Byers 1961). ***Dolichopeza barnardi, D. hirtipennis***, and ***D. peringueyi*** live in wet moss and liverwort cushions on the sides of waterfalls on Table Mountain, South Africa (Harrison & Barnard 1972). ***Dolichopeza*** females lay eggs in mosses (Gerson 1982). ***Dolichopeza*** larvae are bryophagous (Byers 1961).

Figure 102. This cranefly adult is emerging from its pupal case where it has spent the last few months in the moss mat. Photo by Janice Glime.

Lauren Russell (pers. comm.) found species of ***Dolichopeza*** in the Pacific Northwest, USA, to feed on living tissues of mosses and occasionally on liverworts. Roper (2001) reported ***Dolichopeza albipes*** (Figure 101) as a bryophage on mosses and liverworts in ghyll woodlands in Sussex, UK.

Figure 103. ***Dolichopeza albipes*** adult, a species whose larvae are bryophages on both mosses and liverworts. Photo by Janet Graham, through Creative Commons.

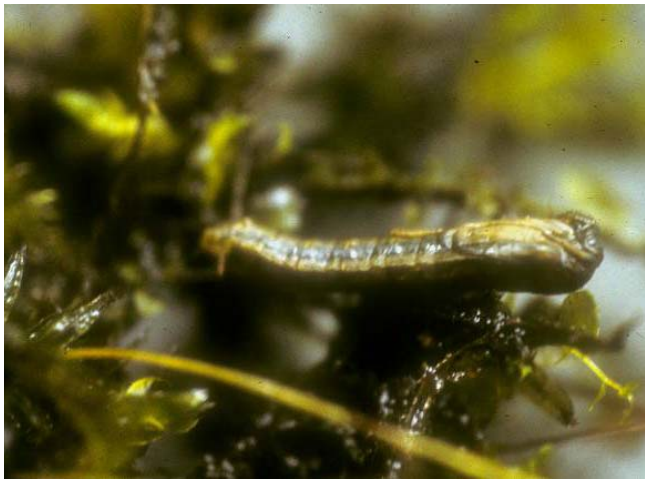

Figure 104. This pupa of a cranefly (**Tipulidae**) can be found among mosses. Photo by Janice Glime.

Dicranomyia

It is not unusual for bryophytes to house rare species. This habitat is time-consuming to sample, and sampling is destructive of the habitat, so the inhabitants are often overlooked. Most members of ***Dicranomyia*** (Figure 105) are aquatic, but ***D. lackschewitzi*** lives in seepages where there are sparse mosses in slumping coastal cliffs (Falk 1991). The species is considered extremely rare in Europe (Stubbs 1998).

Figure 105. ***Dicranomyia chorea*** adult; ***D. lackschewitzi*** lives in mosses in seepages on coastal cliffs. Photo by James K. Lindsey, with permission.

Dicranomyia goritiensis has a sporadic distribution (Kolcsár *et al*. 2015). It is associated with mosses and algae on rocks around waterfalls and rocky coastlines of Croatia and Greece.

Nephrotoma – Tiger Craneflies

Immature stages of ***Nephrotoma*** typically occur among mosses, in soil, and in decaying wood (Alexander & McAtee 1921). ***Nephrotoma virescens*** (Figure 106) larvae live among wet mosses (Johannsen 1969).

Figure 106. ***Nephrotoma virescens*** adult, a species whose larvae live among wet mosses. Photo by Odin Toness, through Creative Commons.

Summary

Many species of **Diptera** lay their eggs among bryophytes, develop as larvae there, and pupate there. Some eat the mosses. And some eat the associated algae, bacteria, fungi, and microorganisms. And they are often selective in their food choices. Others have looser associations, landing there for moisture regulation or hiding there to avoid predation or escape wind and cold. Bryophyte structure affects colonization, with very compact mosses making tunneling difficult, and very loose structure providing too little protection for some.

The several families that were once **Tipulidae** have numerous species that live among bryophytes both in the water and on land. Some of these (especially ***Triogma trisulcata***) are adapted to bryophyte living by being bryophyte mimics. Often members of ***Tipula*** seem to defy Gause's law, but on closer inspection we find they mate at different times of the day or in different time periods, live in different parts of the moss, or have other needs that separate their niches.

Acknowledgments

Thank you to all the wonderful photographers who have contributed images, given me permission, or put their images in Creative Commons.

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CHAPTER 12-19 TERRESTRIAL INSECTS: HOLOMETABOLA – DIPTERA NEMATOCERA 2

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CHAPTER 12-19
TERRESTRIAL INSECTS: HOLOMETABOLA – DIPTERA NEMATOCERA 2

Figure 1. Fungus gnat herbivory on ***Buxbaumia aphylla*** capsules. Note the topless setae. Photo by Jörg Müller, with permission.

Cecidomyiidae – Gall Midges

Some members of this family that are typical of trees can be found in moss tussocks or among the mosses on tree trunks. These include members of the genus ***Peromyia*** (Figure 2) (Perkovsky & Fedotova 2004). Mosses are so important to some species as to be the source of the name – including ***Bryocrypta dubia***, ***Cryptoneurus muscicola***, ***Bryomyia bergrothi***, and ***Peromyia muscorum***, as well as ***Peromyia palustris*** (Mamaev & Krivosheina 1993).

Stabaev (in Mamaev & Krivosheina 1993) found that larvae of gall midges comprised an important part of the fauna in primary soils under mosses. But Mamaev and Krivosheina comment that there has been little study of the moss-inhabiting gall midges, promising surprises for those who explore them.

Figure 2. ***Peromyia*** adult, a genus that sometimes lives among bryophytes on the ground and on tree trunks. Photo by Charley Eiseman, through Creative Commons.

Mycetophilidae – Fungus Gnats

This family primarily feeds on fungi, but a few species eat algae, mosses, and liverworts, while others are **saprophagous** (feeding on or obtaining nourishment from dead or decaying animal matter) in bird nests (Hackman *et al*. 1988; Økland 1994). ***Cordyla fusca*** (see Figure 3) is significantly correlated with mosses (Økland 1994). On the other hand, ***Boletina gripha*** (Figure 4) and ***Acnernia nitidicollis*** have high negative correlations with mosses. The correlation of some members of this family with mosses may relate to a concentration of host fungi in the soil that likewise correlates with the mosses or their habitat.

Figure 3. ***Cordyla fissa*** adult; the presence of ***C. fusca*** correlates with mosses in European forests. Photo by Hanna Koivula, through Creative Commons.

Pettet (1967) reported that larvae in the **Mycetophilidae** parasitize the thallose liverwort ***Riccia frostii*** (Figure 5). The infestation occurred when the Nile floodwaters receded in Sudan. The infestation spread and increased until virtually all thalli were infected and remained so until flooding returned. The infestation then completely disappeared and although Pettet watched for it closely for the next five years, it never returned. The larvae eat the internal tissues of the thalli, causing the thallus to become non-turgid and flabby. In the last stages of the infestation, the liverwort surface disintegrates. Each rosette revealed 5-25 small, yellow-orange larvae. Pupation likewise occurred inside the thallus. Such interactions can easily go unnoticed and close observation may reveal other interesting bryological habitats for insects.

Figure 4. ***Boletina gripha*** adult, a species that is negatively correlated with mosses. Photo by Hanna Koivula, through Creative Commons.

Figure 5. ***Riccia frostii***, a species that is parasitized by **Mycetophilidae**. Photo by Rosemary Taylor, with permission.

Müller (2012) found several adult fungus gnats (Figure 1, Figure 6) feeding on spores in capsules of ***Buxbaumia aphylla*** (Figure 7) in Germany. It is likely that at least some of the spores escape being eaten and are transported by the fungus gnats, later being deposited elsewhere.

Figure 6. Fungus gnat herbivory on capsules of ***Buxbaumia aphylla***. Photo courtesy of Jörg Müller.

Figure 7. ***Buxbaumia aphylla*** with fly. Photo courtesy of Sabovljevic.

Sciaridae – Dark-winged Fungus Gnats

Fungus gnats (**Sciaridae**) deposit eggs in organic matter, including mosses (Hurley 2006). When such habitats are present in greenhouses, the fungus gnats become pests. Shin *et al*. (2012) reported that these gnats inhabit peat bogs, thus making this a source of the gnats in nurseries and greenhouses. Peck and Moldenke (2010) are concerned with invertebrate invasions through commercial uses of mosses. Among those invertebrates, they found a few adult sciarid flies.

Ponge (1991) found that some of the **Sciaridae** larvae on the Scots pine (*Pinus sylvestris*) forest floor consumed mosses, but they also consumed fungi. But not all interactions of this family with bryophytes are so casual. Sawangproh (2014) notified me of finding the larvae of a black-winged fungus gnat, ***Scatopsciara cunicularius*** (Figure 8-Figure 14), feeding and tunnelling on a liverwort thallus, ***Marchantia polymorpha*** (Figure 8-Figure 10), in the greenhouse. The feeding causes serious damage to both growth and survival of the liverwort. The gnat population expands when the ambient temperature increases in early spring. When it is cool (12°C), the larvae take longer to develop and consequently do more damage to the thalli than when reared at 22°C (Sawangproh & Cronberg 2016; Sawangproh *et al*. 2016). Following the larval damage, the thalli are more susceptible to secondary attacks by other pests and fungal infections.

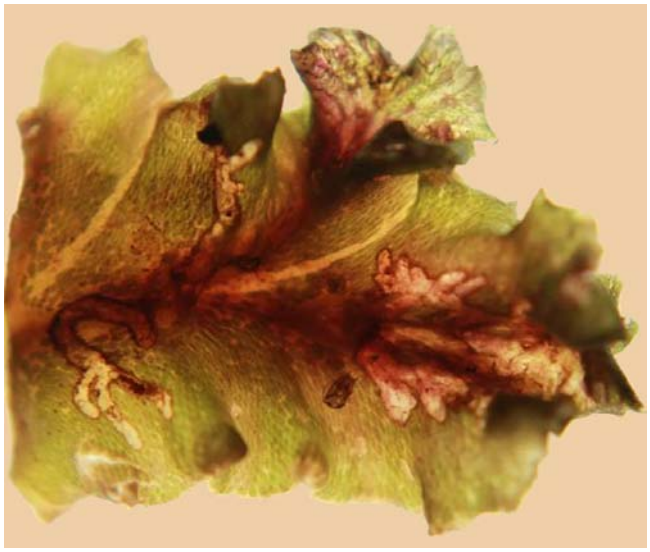

Figure 8. ***Scatopsciara cunicularius*** damage to ***Marchantia polymorpha*** by two third-instar larvae at 22°C in culture. Photo courtesy of Weerachon Sawangproh.

Figure 9. ***Scatopsciara cunicularius*** damage to ***Marchantia polymorpha*** by a group of larvae at day 2 after hatching. Photo courtesy of Weerachon Sawangproh.

Figure 10. ***Scatopsciara cunicularius*** larva on one of the wounded patches of ***Marchantia polymorpha***. Photo courtesy of Nils Cronberg.

Figure 11. ***Scatopsciara cunicularius*** larva from ***Marchantia polymorpha***. Photo courtesy of Weerachon Sawangproh.

Figure 12. ***Scatopsciara cunicularius*** mature pupal stage on a liverwort thallus. Photo by Weerachon Sawangproh.

Figure 13. ***Scatopsciara cunicularius*** pupa from ***Marchantia polymorpha***. Photo courtesy of Weerachon Sawangproh.

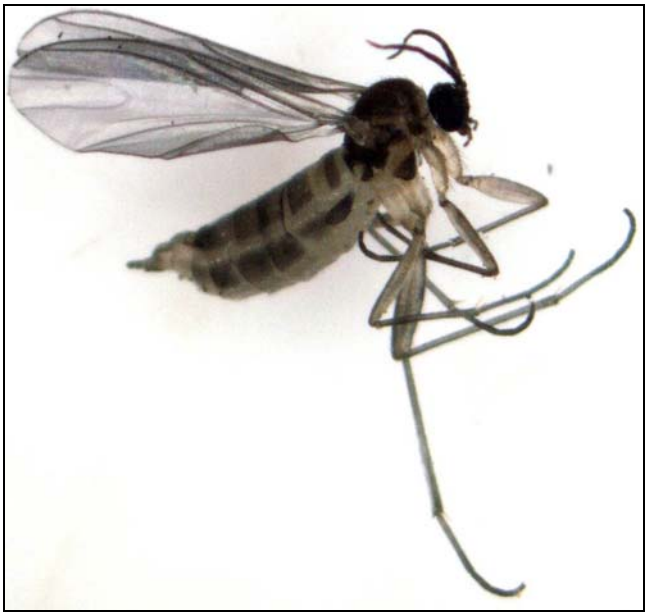

Figure 14. ***Scatopsciara cunicularius*** female adult. Photo courtesy of Weerachon Sawangproh.

It does not appear that these bryophagous fungus gnats need fungi. ***Scatopsciara cunicularius*** (Figure 8-Figure 14) can complete its entire life cycle with only liverworts as food (Sawangproh & Cronberg 2016; Sawangproh *et al*. 2016). This is an unusual relationship because few insects are known to eat liverworts. Sawangproh and coworkers (2016) suggested that the liverwort oil bodies with their essential oils may serve as a deterrent to herbivory. We still have little understanding of the mechanisms that permit some insects to eat the bryophytes, especially those with antiherbivore compounds, whereas most insects seem unable to. Just imagine what the world might be like with no insects. Bryophytes would most likely be far more speciose, whereas the insects may have eliminated those that did not develop antiherbivore compounds early in their evolution.

Bradysia sp. (Figure 15-Figure 16) larvae (Figure 15) can be found under several species of ***Bryum*** [***B. argenteum*** (Figure 17), ***B. dichotomum*** (Figure 18), and ***B. pachytheca*** (Figure 19)], at least in flower pots (Downing & Selkirk 1996). Downing and Selkirk observed that the mosses had a rough, patchy appearance, "like they had been ploughed." These larvae eat the moss rhizoids. My surprise was that after drenching the pots with a solution of 2 g Alsystrin in 10 L water the bryophytes grew back in two weeks!

Figure 15. ***Bradysia*** sp. larvae, ***Bryum*** inhabitants. Photo by David Cappaert, through Creative Commons.

Figure 16. ***Bradysia praecox***; some members of this genus live among the moss ***Bryum*** as larvae. Photo by James K. Lindsey, with permission.

Figure 17. ***Bryum argenteum***, a species where ***Bradysia*** sp. larvae hide under the clump. Photo by Janice Glime.

Figure 18. ***Bryum dichotomum*** with gemmae, home for some species of ***Bradysia***. Photo by David T. Holyoak, with permission.

Figure 19. ***Bryum pachytheca*** with capsules, cover for some ***Bradysia*** species. Photo by David Tng, with permission.

Ceratopogonidae – Biting Midges

One might not expect chocolate to be involved in this chapter, but certain members of the **Ceratopogonidae** (Figure 20) are associated with cacao (chocolate) flowers as important pollinators (Winder 1977). On the same trees, among the epiphytic mosses, one can find ***Atrichopogon*** (Figure 21-Figure 22), ***Stilobezzia*** (Figure 23), and ***Dasyhelea*** (Figure 24-Figure 26), all members of **Ceratopogonidae**.

Figure 20. ***Jungermannia exertifolia*** ssp ***cordifolia*** with **Diptera** larva (**Ceratopogonidae**?). Photo by Michael Lüth, with permission.

Figure 21. ***Atripogon*** larva, a dweller among epiphytic mosses. Photo from Waterbugkey, through EPA public domain.

Figure 22. ***Atripogon*** female adult, a species associated with epiphytic bryophytes. Photo by Tom Murray, through Creative Commons.

Figure 23. ***Stilobezzia*** female adult, a genus known from epiphytic mosses. Photo by Tom Murray, through Creative Commons.

Figure 24. ***Dasyhelea flavifrons*** larva weaving its way under the bark. Photo by Walter Pfliegler, with permission.

Figure 25. ***Dasyhelea flavifrons*** larvae; for some members of the genus this stage is spent in bryophytes on trees. Photo by Walter Pfliegler, with permission.

Figure 26. ***Dasyhelea*** male adult, a genus that can be found among bryophytes on trees. Photo by Christophe Quintin, through Creative Commons.

Many of the **Ceratopogonidae** have aquatic larvae, so it is natural that the adults hang out in moist conditions, near the water sources where they can lay eggs. Hence, some will naturally land on mosses to rest or obtain moisture (Figure 27).

Figure 27. **Ceratopogonidae** male on moss. Photo by Christophe Quintin, through Creative Commons.

Kolenohelea calcarata occurs among mosses in springs, and ***Serromyia femorata*** (Figure 28) occurs among damp mosses (Strenzke 1950). But ***Culicoides impunctatus*** (Figure 29) (biting midge) larvae at one site in western Scotland actually avoided most mosses (Blackwell *et al.* 1999). Their distribution and larval counts had a significantly negative correlation with all mosses other than species of ***Sphagnum***. This species increases its number of eggs when provided with ***Sphagnum*** egg-laying sites (Carpenter *et al.* 2001). Members of the genus ***Forcipomyia*** (Figure 30), another biting midge, also builds nests in ***Sphagnum*** (Oldroyd 1964).

Figure 28. ***Serromyia femorata*** female, a species associated with damp mosses. Photo by James K. Lindsey, with permission.

Figure 29. ***Culicoides impunctatus*** adult, a species that avoids mosses, except ***Sphagnum***. Photo by Orikrin, through Creative Commons.

Figure 30. ***Forcipomyia bipunctata*** adult, member of a genus that builds nests in ***Sphagnum***. Photo by James K. Lindsey, with permission.

Chironomidae – Midges

Bettis (2008) compared the abundance of invertebrate fauna in two different ***Grimmia*** (Figure 31) morphotypes, one on exposed granitic outcropping and one at a protected seasonal riparian habitat. In both cases, **Chironomidae** larvae were among the major invertebrates present. Some of the **Chironomidae** can emerge from mosses in large numbers (Figure 32), especially in polar regions, and adults cover mosses as they emerge (Figure 33) (pers. obs.).

Figure 31. ***Grimmia laevigata*** on boulder, potential home for **Chironomidae**. Photo by Alan Cressler, with permission.

Figure 32. **Chironomidae** swarming in moss garden, a typical scene in summer. Photo by J. Paul Moore, with permission.

Figure 33. **Chironomidae** adults on moss at Helfdi, Myvatn, Iceland. Photo by Janice Glime.

Although **Chironomidae** are abundant aquatic larvae, they also occur on land. The ***Cricotopus*** (Figure 34-Figure 35) larva occurs with **epilithic** (growing on rocks) and **epiphytic** (growing on plants, usually trees) liverworts in western Oregon and Washington, USA, and feeds on the leafy liverworts ***Calypogeia*** (Figure 36), ***Gyrothyra underwoodiana*** (Figure 37), ***Jungermannia rubra*** (Figure 38), ***Porella navicularis*** (Figure 39), and ***Scapania bolanderi*** (Figure 40) in the lab (Russell 1979). In the field they do considerable feeding damage to ***Calypogeia fissa*** (Figure 36) and ***Jungermannia rubra***.

Figure 34. ***Cricotopus annulator*** complex larva, member of a genus that occurs among liverworts on boulders and trees. Photo © Stroud Water Research Center, through Creative Commons.

Figure 35. ***Cricotopus*** adult, a genus whose larvae occur among liverworts on trees and boulders. Photo by G Drange, through Creative Commons.

Figure 36. ***Calypogeia fissa***, home and food for larvae of ***Cricotopus***. Photo by David T. Holyoak, with permission.

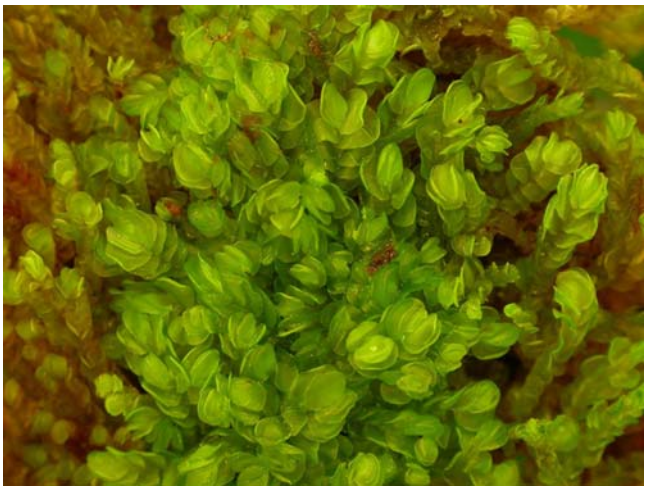

Figure 37. ***Gyrothyra underwoodiana***, home and food for ***Cricotopus*** larvae. Photo by Li Zhang, with permission.

Figure 38. ***Jungermannia rubra*** with perianth. This species provides home and food for ***Cricotopus*** larvae among epiphytes. Photo by Ken-ichi Ueda, through Creative Commons.

Figure 39. Branch with ***Porella navicularis***, home and food for larvae of ***Cricotopus***. Photo by Tanya Yoder, through Creative Commons.

Figure 40. ***Scapania bolanderi*** with capsules, a species that is home and food for ***Cricotopus*** larvae. Photo by Chris Wagner, with permission.

The **Chironomidae** may do an important service to some mosses. Harvey-Gibson and Miller-Brown (1927) reported that these midges, as adults, seem to be agents of fertilization for ***Polytrichum commune*** (Figure 41-Figure 42). In this species, the **paraphyses** (Figure 43) associated with both antheridia and archegonia exude mucilage (but no sugar). Small midges were among the continuous visitors to these gametangial areas. The insects lap the mucilage and get it on their body parts. If they visit at the right time, sperm may become attached as well and the midges that subsequently visit females may transfer live sperm to the appropriate location.

Figure 41. Field of ***Polytrichum commune*** with capsules, indicating successful fertilization. Photo by Michael Lüth, with permission.

Figure 42. ***Polytrichum commune*** with male splash cups that attract adult **Chironomidae** that carry sperm to the female plants that are mixed with them. Photo by Li Zhang, with permission.

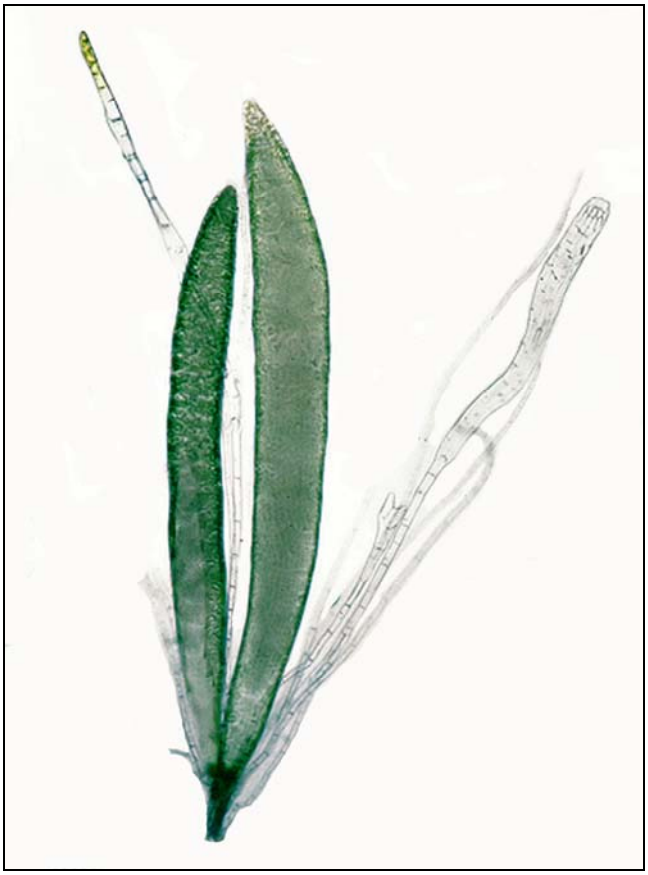

Figure 43. ***Polytrichum*** showing two antheridia with adjacent paraphyses. Photo by George J. Shepherd, through Creative Commons.

Moss-dwelling **Chironomidae** are abundant in and around springs. Lencioni *et al*. (2011) studied **Chironomidae** distribution in 81 springs in the Italian PreAlps and Alps. In 173 samples they found 26,871 **Chironomidae** representing all life stages except eggs. To illustrate the abundance of moss-dwelling **Chironomidae**, Nolte (1991) sampled and compared mosses that were intermittently out of the water on semi-submersed mosses near a spring with those in permanently submersed locations 700 m downstream. All of these larvae were small, and 98% were less than 5 mm in length. The total sampling revealed 65 species of chironomids in 26 genera, with greater species richness near the source in the semi-submersed mosses. But the mean abundance was 5X higher in the permanently submersed mosses compared to those that were semi-submersed at the spring. On the other hand, the maximum abundance anywhere was 830 larvae per 10 cm^2 in one semi-submersed sample. The dominance of the various chironomid taxa was dependent primarily on the location of the moss along the stream.

Ponge (1991) examined gut contents of forest floor animals in a 5x5 cm Scots pine litter. The subsequent feces were followed to determine the ultimate fate of the ingested material. Some of the fecal material included bryophytes and was the primary material in feces of both enchytraeid and lumbricid worms. In turn, the chironomid larvae consumed and digested the fecal material.

Chironomidae may play an important role in initial stages of both primary and secondary succession. These species specialize on open patches created by these

successional conditions and live in the early stage that is fallow, having mosses and lichens as pioneers (Frouz & Kindlmann 2001). The habitat generally has good quality food, but it is prone to severe desiccation in the summer that can decimate the larval population. In the Czech Republic and elsewhere, winter conditions permit the populations to replenish. The larvae are poor dispersers, but winged adults have the opportunity to move about. To explore the ability of these species to survive in this hostile environment, Frouz and Kindlmann studied ***Smittia aterrima*** (Figure 44), an abundant species in old fields. They found that eggs laid by the females from adjoining more developed vegetation were sufficient to replenish the lost populations.

Figure 44. ***Smittia aterrima*** adult, a species that includes mosses in its diet. Photo by James K. Lindsey, with permission.

Smittia aterrima (Figure 44) is common in disturbed areas, with up to 12,000 individuals per m^2 (Delettre & Lagerlöf 1992). These larvae live in the surface soil horizon and feed on plant litter, fungi, soil algae, and mosses (Frouz & Lukešová 1995). In České Budějovice, Frouz and Kindlmann (2001) tested the **source-sink hypothesis** [idea that organisms move from a favorable habitat (source), often as a result of overcrowding, to a sink that is less favorable, where they remain and accumulate] with this species and demonstrated that as their preferred open habitat became unsuitable, the larval population disappeared there. Ducrotoy (1980) and Delettre (1986) had observed the same phenomenon for terrestrial chironomids living among mosses on rocks, again as a result of drought. The larvae continue to exist in sub-optimal habitats during the drought and re-colonize the preferred habitats (including mosses) when favorable conditions return (Frouz & Kindlmann 2001). This migration maintains the source-sink survival strategy.

Other **Chironomidae** species have similar abundance patterns in these pioneer habitats. ***Bryophaenocladius*** cf. ***illimbatus*** (Figure 45) is a **parthenogenic** (having unfertilized eggs that develop into new individuals) moss dweller that lives in habitats with open and low vegetation (Frouz 1997). Both ***Bryophaenocladius cf. illimbatus*** and ***Smittia aterrima*** (Figure 44) decreased from the first to third year of the study as the field became less open and forbs taller than 20 cm became more prominent. Soil algae and mosses form an important component of food for both species (Frouz & Lukešová 1995).

Figure 45. ***Bryophaenocladius illimbatus*** adult, a species of mosses in sites with low, open vegetation. Photo by Marko Mutanen, through Creative Commons.

Sometimes one can find exciting new species by knowing the general habits of the genus. The snow-dwelling adults of ***Bryophaenocladius thaleri*** were discovered in barren areas of Dolomite Alps in Italy above 3100 m altitude. This species probably mates in **leks** (assembly areas where males gather during mating season to exhibit competing mating displays and attract females) on the ground because their males cannot fly (Willassen 1996). But the immature (larval) stages are so far unknown. Willassen suggests that we look for them among terrestrial mosses because that is a preferred habitat of other members of the genus. ***Bryophaenocladius virgo*** lives among mosses as larvae and adults and solves the flight problem by being **parthenogenetic** (giving birth without fertilization) (Cranston 1987). ***Bryophaenocladius vernalis*** (Figure 46) has been caught in the act of damaging rare mosses growing in chalk quarries in southern England.

Figure 46. ***Bryophaenocladius*** cf. ***vernalis*** adult male, a species that damages rare mosses in chalk quarries in England. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.

Limnophyes minimus (Figure 47-Figure 49) is likewise a pioneer that lives in the shallow soil that is formed by the mosses, lichens, and raw humus (Delettre 1986). On rocks, mosses trap dust and soon accumulate a thin soil on rock surfaces. This provides suitable habitat for ***Limnophyes minimus*** in Brittany, France. This species also occurs in the sub-Antarctic where the adult females are parthenogenic (Hänel & Chown 1998). And these females do not feed. As larvae, this species joins ***Pringleophaga marioni*** (**Lepidoptera**, **Tineidae**; Figure 50) in their contribution to nutrient recycling on sub-Antarctic Marion Island.

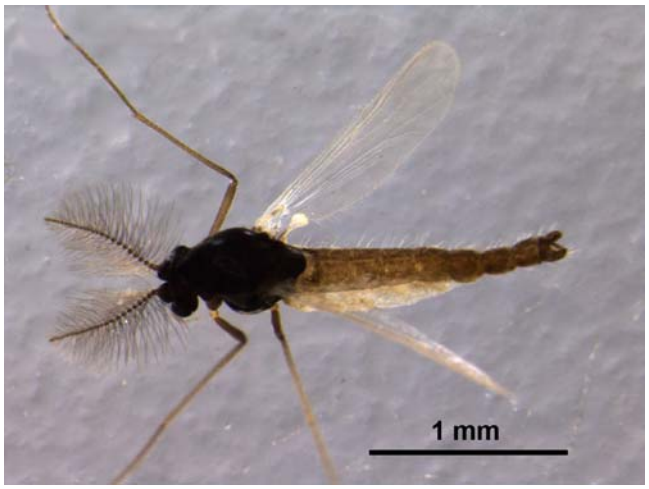

Figure 47. ***Limnophyes minimus***, a pioneer species in mosses on newly colonized areas. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.

Figure 48. ***Limnophyes minimus***, a pioneer among mosses. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.

Figure 49. ***Limnophyes minimus*** adult, a pioneer species among mosses in early succession stages. Photo by James K. Lindsey, with permission.

Figure 50. ***Pringleophaga marioni*** adult, a lepidopteran moss-dwelling contributor to nutrient cycling on Marion Island in the sub-Antarctic. Photo by Steven L. Chown, with permission.

The females of ***Eretmoptera murphyi*** (Figure 51) from the Antarctic and sub-Antarctic are **brachypterous** (short-winged), making dispersal difficult. Not only is the female apparently parthenogenic, but males are unknown (Cranston 1985). This species has terrestrial larvae that live among damp mosses and peat.

Figure 51. ***Eretmoptera murphyi*** on a leafy liverwort, Prince Olav Harbour, South Georgia. Photo courtesy of Roger S. Key.

As already seen in the aquatic midges, living among mosses could present a danger from parasitic mites (Stur *et al*. 2005). But when those mosses are semi-terrestrial, the **Chironomidae** become unavailable to those aquatic parasitic mites.

Belgica

One of the best known of the moss-dwelling **Chironomidae** is ***Belgica antarctica*** (Figure 52-Figure 54). These larvae are abundant in damp mosses, grass roots, detritus, and around penguin rookeries and seabird nests in the Antarctic (Wirth & Gressitt 1967; Cranston 1985). The species overwinters as larvae (Strong 1967); all four larval instars overwinter (Benoit *et al*. 2007). Some also occur in meltwater pools and small ponds with algae.

Belgica antarctica (Figure 52-Figure 54) is the largest arthropod in Antarctica and is wingless (Gressitt 1967). The females lay their eggs in a gelatinous mass in damp mosses and the larvae disperse among the mosses about 10 days later. The mosses most likely make survival of this larger animal possible by providing a warmer refuge than the ambient temperature. Gressitt showed that temperatures in ***Polytrichum*** (Figure 41-Figure 42) there exceed that of the air by as much as 13°C. The temperatures in ***Drepanocladus*** (probably ***Sanionia uncinata*** – Figure 55) were closer to those of the air.

Figure 52. ***Belgica antarctica*** eggs among mosses in Antarctica. Photo by Rick Lee, through Creative Commons.

Figure 53. ***Belgica antarctica*** larvae in Antarctica, a species that often lives among mosses. Photo by Rick Lee, through Creative Commons.

Figure 54. ***Belgica antarctica*** mating in Antarctica. Photo by Rick Lee, through Creative Commons.

Figure 55. ***Sanionia uncinata***, potential home for ***Belgica antarctica***, but temperatures in this moss differ little from that of the air. Photo by Franz Xaver, through Creative Commons.

Temperature is not the only factor limiting the distribution of ***Belgica antarctica*** (Figure 52-Figure 54). Hayward *et al*. (2007) considered moisture to be as important as cold resistance in these polar invertebrates. With temperatures most of the year below 0°C, water is hence inaccessible for a long period of time. Hayward and coworkers found that when the larvae were desiccated at a high relative humidity (98.2%) they were more tolerant of desiccation and also exhibited increased freezing tolerance to -10 and -15°C. Nevertheless, all larvae were frozen at -10°C. Slow drying was important for this acclimation. The researchers found that osmolality increased, reaching its highest levels after five days at 98.2% RH, but that these values returned to predesiccation values with just one hour of rehydration, well before water content returned to predesiccation levels. They found no evidence of heat-shock proteins contributing to desiccation tolerance. Membrane phospholipid adaptation and metabolite synthesis appeared to be the important physiological mechanisms that enhanced both cold tolerance and desiccation tolerance, a conclusion also supported by Lee *et al*. (2006). I would consider it likely that the mosses are important in ensuring a high initial humidity and a slow rate of desiccation, permitting the larvae to acclimate.

Teets *et al*. (2011) examined the effects of repeated cold exposure on survival, energy content, and stress protein expression of the larvae of ***Belgica antarctica*** (Figure 53). Most of the larvae (>95%) survived a single 12-hour stint of -5°C when frozen in both the presence of

water and in a dry environment. However, after five cycles of repeated cold exposure to -5°C, survival of frozen larvae dropped to below 70%. On the other hand, survival of controls and supercooled (dry) larvae remained unchanged. Freezing during these repeated cold exposures resulted in a drastic reduction in energy reserves. After five of these cold exposures, the larvae had 25% less lipid, 30% less glycogen, and nearly 40% less trehalose than supercooled larvae. There were further indications of protein damage in this frozen group. There seemed to be no difference in larvae frozen for 60 continuous hours and those that had a total of 60 hours accumulated from repeated cold exposure. Teets and coworkers concluded that both survival and energy conservation benefitted from a dry microhabitat that remained unfrozen during repeated cold exposures. Do bryophytes provide such an environment, or must the larvae migrate into the soil to survive?

The larvae of ***Belgica antarctica*** (Figure 53) spend most of the year (7-8 months) encased in ice with soil (Elnitsky *et al.* 2008; Lopez *et al*. 2009), creating desiccating conditions. Elnitsky *et al*. (2008) explored the possibility that they use cryoprotection to survive. They found that after 14 days of subzero exposure in the lab the larval survival remained above 95%. They interpreted this as an indication that the larvae underwent cryoprotective dehydration. But they also considered that in their natural environment **cryoprotection** (low-temperature protection) may be constrained by **inoculative freezing** (process in which organisms actually freeze) because of the close contact of the larvae with environmental ice. Their ability to undergo cryoprotective dehydration during slow cooling within frozen soil is dependent on the soil moisture. The percentage of larvae that were able to resist inoculative freezing increased as the soil moisture decreased. The researchers suggest that the larvae are likely to undergo cryoprotection under the right conditions.

Lee and coworkers (2006) demonstrated that rapid **cold-hardening** (physiological or anatomical preparation for cold) increases freezing tolerance in ***Belgica antarctica*** (Figure 53). Larvae that were summer acclimated had less cold tolerance at -10°C for 24 hours than those that were cold-acclimated. Cold-acclimated larvae had higher supercooling points than summer larvae. But when summer-acclimated larvae were maintained at 4°C, then transferred to -5°C for 1 hour prior to exposures to -10, -15 or -20°C, rapid cold hardening occurred; rapid cold hardening significantly increased larval freeze tolerance to both -15 and -20°C. Adults, which typically live for only a week, did not respond to rapid cold hardening. Living among mosses can protect the larvae from sudden changes in temperature, permitting them to acclimate.

But even during the summer the larvae are subject to summer storms, osmotic stress from salt spray, and desiccation due to wind and sunlight (Lopez-Martinez *et al*. 2009). In contrast to Hayward *et al*. (2007), Lopez-Martinez and coworkers found that the genes that were the most responsive to hydration changes were the ones encoding heat-shock proteins, as well as those for antioxidants, detoxiWcations, and those involved in altering cell membranes. Fast dehydration elicited both the highest expression and the greater number of genes expressed. As the larvae were rehydrated, most of the same genes were once again expressed. Fatty acid desaturase was the only gene upregulated during rehydration.

Strong (1967) considers the living mosses to serve only as shelter for ***Belgica antarctica*** (Figure 52-Figure 54), providing little nourishment. Instead, detritus, algae, lichens, and fungal hyphae are the primary food sources. Other researchers include mosses as part of the diet during the two-year life cycle (Sugg *et al*. 1983; Convey & Block 1996). But there is no comprehensive food study to indicate the diet throughout the life cycle and seasonal changes. The larvae demonstrate cryoprotectants, including erythritol, glucose, sucrose, and trehalose, but adults are freezing-susceptible and lack adequate quantities of these cryoprotectants (Baust & Edwards 1979). Maintenance on artificial diets indicate that cryoprotectant complexes are dependent on food source and temperature. We have seen how gene expression changes as freezing occurs. Could it be that these new compounds are supported by a change in diet to one that includes more bryophytes?

Leaf Miners

Most of us have seen the evidence of leafmining activity on deciduous leaves or herbaceous plants. But have you ever seen it on liverwort thalli? It is a world needing exploration.

Eisman *et al*. (2023) have just described the behavior of ***Paraphaenocladius exagitans*** in the thalli of ***Marchantia polymorpha*** (Figure 56). They discovered that unlike the miner *Metriocnemus*, which scatters its frass throughout its mines, the mines of ***P. exagitans*** are clean; the frass instead accumulates around the rim of the entry hole. These larvae were first noticed in Iowa in mid-October. On 23 November, the first adult emerged from an oblong, dark brown cocoon made of frass and located on the thallus of the liverwort. The larva had apparently fed on the surface of the thallus. However, two larvae were seen mining the fresh thallus in late December.

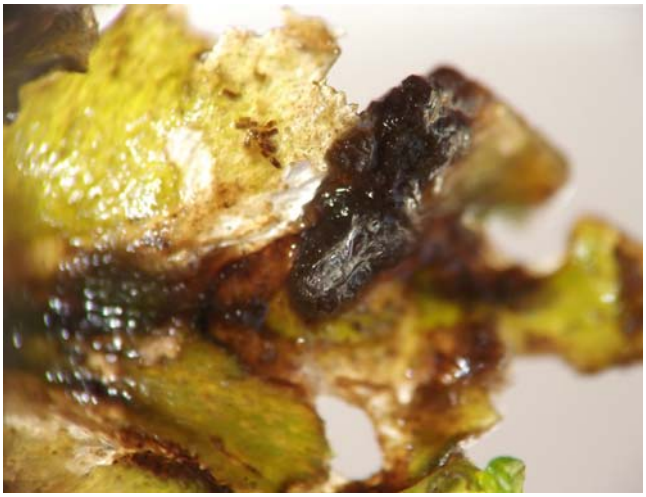

Figure 56. ***Paraphaenocladius exagitans*** pupa on a ***Marchantia polymorpha*** thallus. Photo courtesy of John van der Linden.

In a different collection, Eisman *et al*. (2023) found larvae of ***Paraphaenocladius exagitans exagitans*** and adults of ***Boreochlus persimilis*** in association with ***Marchantia polymorpha*** in Oregon, this time in late April. However, the authors were unable to determine what the midges were feeding on.

Culicidae – Mosquitoes

Gert Mogensen told an interesting mosquito story on Bryonet (13 March 2011). Arctic mosquitoes (Figure 57) struggle with low moisture on sunny days. They compensate for this dry atmosphere by spending much time on mosses, keeping in the shadows when possible. They are able to shelter on the undersides of leaves of shrubs (Figure 57), but there they are subject to spider predation. These spiders, in turn, are food for the group of birds called waders (Figure 58). The chicks of these waders benefit from the dwarfed nature of the shrubs. The females migrate south again once the eggs are laid and the males remain behind to care for the young!

Figure 57. Mosquito adult, member of a family (**Culicidae**) that struggles with low moisture in the Arctic. Photo by Brad Smith, through Creative Commons.

Figure 58. The Common Gallinule (***Gallinula galeata***), a wading bird that is part of the food chain of moss inhabitants (Culicidae→spiders→wading birds). Photo by Jim Rathert, USFWS, through public domain.

Simuliidae – Blackflies

I have discussed this family in the chapter on aquatic insects. But when I began researching the terrestrial **Diptera**, I was quite surprised to find that not all **Simuliidae** begin life in the water. ***Prosimulium hirtipes*** (see Figure 59-Figure 61), ***P. tomosvaryi***, and ***P. subrufipes*** all oviposit on moist terrestrial mosses, usually about 20 cm above streams (Zwick & Zwick 1990). This is no small contribution as they lay up to 20,000 eggs per cm^2. The eggs form a dense crust on mosses with small leaves, especially ***Brachythecium rivulare*** (Figure 62). These eggs are dependent on moisture and cannot survive complete desiccation.

Figure 59. ***Prosimulium hirtipes*** larva, a species that begins life on land among mosses at streamside. Photo by Janice Glime.

Figure 60. ***Prosimulium arvum*** adult, member of a genus in which some members lay their eggs among streamside mosses. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 61. ***Prosimulium*** female adult, member of a genus in which some members lay their eggs among streamside mosses. Photo by Tom Murray, through Creative Commons.

Figure 62. ***Brachythecium rivulare***, a site for egg-laying by ***Prosimulium hirtipes***, ***P. tomosvaryi***, and ***P. subrufipes***. Photo by Norbert Stapper, with permission.

Two Japanese blackfly species, ***Simulium japonicum*** and ***S. rufibasis*** (see Figure 63-Figure 66), lay their eggs in bryophytes (Baba & Takaoka 1989). These do not make large masses and lay their eggs singly on bryophytes on water-splashed rocks. Later, Baba and Takaoka (1991) discovered that ***Prosimulium kiotoense*** likewise oviposited on land, using mosses on riverbank rocks as their oviposition sites. They likewise laid eggs singly, but the females deposited many eggs in small areas, often forming large, irregular egg masses. These wet oviposition sites had dense bryophyte cover and were 0-15 cm above water level. If you want to watch, the event occurs mostly between 12:00 and 14:00 hours in the latter part of April on Kyushu Island, Japan.

Figure 63. **Simuliidae** larvae, a stage that is spent in fast water. Photo by Sarah Gregg, through Creative Commons.

Figure 64. ***Simulium heiroglyphicum*** pupa, an aquatic stage that is often on mosses. Photo by Luis Hernandez Triana, through Creative Commons.

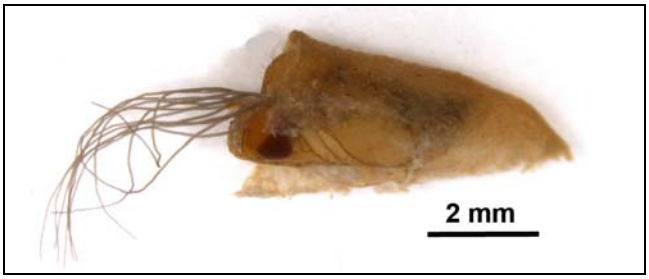

Figure 65. ***Simulium*** nr. ***metallicum*** pupa, a stage that is spent in fast water, often on bryophytes. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 66. ***Simulium equinum*** adult, member of a genus in which some species oviposit on land among mosses. Photo by Ladislav Tábi, with permission.

Psychodidae – Drain Flies, Sink Flies, Moth Flies, or Sewer Gnats

This family includes species with aquatic larvae, so it is not surprising that terrestrial species are often associated with bryophytes in locations where they can maintain high moisture. Roper (2001) reports several of these species in the ghyll woodlands (linear valley features cut into the sandy beds of the Weald of south-eastern England where temperatures are buffered and moisture levels are high; they have a rich flora of bryophytes). In Sussex, England, the very ornate ***Sycorax*** species occur among mosses near springs and "trickles" (Roper 2001).

Sycorax silacea larvae are wormlike and live on wet stones or mosses near cascades, springs, trickles (Andersen 1992), on mosses in the neighborhood of streams (Omelkova & Ježek 2012), and on mosses on half-submerged tree branches (Kroča & Ježek 2015), making them semiaquatic. Their decorations are quite ornate, permitting them to blend well among the mosses (Roper 2001).

Like ***Sycorax silacea***, many of the **Psychodidae** are semi-aquatic. ***Peripsychoda fusca*** lives in wet mosses and leaf litter piles in Europe (Kroča & Ježek 2015). Another European psychodid, ***Feuerborniella obscura***, lives among wet moss cushions, springs, and small streams. ***Parabazarella subneglecta*** (Figure 67) similarly prefers wet moss cushions, springs, and streams. ***Pneumia stammeri*** (Figure 68) lives among mosses in wetlands. Larvae of ***Bazarella neglecta*** occur among mosses around mill races and waterfalls (Roper 2001). This species has been reared successfully on the moss ***Platyhypnidium riparioides*** (Figure 69-Figure 70), a moss that typically occurs around the water-air interface where it is almost constantly wet or submerged. ***Parajungiella longicornis*** is a widespread and common species in Europe and western Siberia (Omelkova & Jezek 2012; Kroča & Ježek 2015). This species lives in both shaded and unshaded habitats in moss cushions on banks of streams, as well as ponds and forest seepages.

Figure 67. ***Parabazarella subneglecta*** adult, a species whose larvae prefer wet moss cushions and mosses of springs and streams. Photo from Bergen Museum, through Creative Commons.

Figure 68. ***Pneumia stammeri*** adult, a species that lives among mosses in wetlands. Photo by Aina Maerk Aspaas, NTNU University Museum, through Creative Commons.

Figure 69. ***Platyhypnidium riparioides***, showing its partly submersed and partly emergent location. Photo by Hermann Schachner, through Creative Commons.

Figure 70. ***Platyhypnidium riparioides***, home and food for ***Bazarella neglecta***. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Pericoma larvae (Figure 71-Figure 72) and pupae both live in damp locations along streams in the UK, frequently

among mosses (Satchell 1949). Suitable habitats can often support several species within a few meters. ***Pericoma*** species, including ***P. nubila*** (Figure 73-Figure 74), ***P. fuliginosa*** (Figure 75), and ***Tonnoiriella pulchra*** (syn.=*P. pulchra*) emerge in ghyll woodlands from rotting vegetation and mosses along streambanks (Roper 2001). ***Pericoma blandula*** (Figure 76) and ***P. fallax*** are both widespread species in Europe and parts of Asia, living among mosses in both shaded and unshaded locations (Omelkova & Jezek 2012; Kroča & Ježek 2015). The latter species is mostly aquatic, but also occurs in swampy meadows and bottomlands. ***Pericoma blandula*** is more common among mosses on riverbanks and the banks of springs (Duckhouse 1962).

Figure 71. ***Pericoma*** larva, a stage that often lives among bryophytes in damp places and along stream margins. Photo from <www.shl.uiowa.edu>, through public domain.

Figure 72. ***Pericoma*** larva, a stage that often lives among bryophytes in damp places and along stream margins. Photo from <www.dfg.ca.gov>, through public domain.

Figure 73. ***Pericoma nubila*** adult, a terrestrial stage often closely associated with aquatic habitats and mosses. Photo by Malcolm Storey, through Creative Commons.

Figure 74. ***Pericoma nubila*** adult, a stage often closely associated with aquatic habitats and mosses. Photo by Malcolm Storey, through Creative Commons.

Figure 75. ***Pericoma fuliginosa*** adult, a species that pupates in rotting vegetation and mosses on streambanks. Photo by James K. Lindsey, with permission.

Figure 76. ***Pericoma blandula*** adult, a species whose larvae live among mosses in both shaded and unshaded situations. Photo ©Nick Upton <www.diptera.info>, with permission.

For ***Psychoda cinerea*** (Figure 77) larvae, moisture is important, accounting for their habitat in mud and among mosses (Ježek 1990). ***Paramormia ustulata*** is more ubiquitous, living in a variety of habitats in both fresh and salt water, but it also includes mosses and moist soil (Vaillant 1971).

Figure 77. ***Psychoda cinerea*** adult. Larvae of this species live in mud and among mosses. Photo by Luis Miguel Bugallo Sanchez, through Creative Commons.

In some cases we don't know why the flies visit the mosses. Martin Cooper found a species of ***Philosepedon*** (Figure 78) resting on the capsules of a moss, but perhaps it was just a convenient resting place, serving no other purpose. Its larvae are known from dead snails (Corbet 2006)! It is clear that we need more behavioral studies on these flies and their interactions with bryophytes.

Figure 78. ***Philosepedon***, probably ***P. humeralis*** adult, on moss capsule. Photo by Martin Cooper, through Creative Commons.

Anisopodidae (=Rhyphidae) – Wood Gnats

I was introduced to the larvae (Figure 79) of this family when I found a larva feeding on mosses on a wet ledge. The larva was green and blended well with the bright green mosses. I watched for a time and found that mosses went in the mouth covered with detritus and came out the other end clean. It appeared the the larva was unable to digest the moss leaves it consumed.

Figure 79. **Anisopodidae** larva; some larvae in this family eat wet mosses, apparently to obtain the detritus and associated organisms on the moss surface. Photo by Walter Pfliegler, with permission.

Summary

Some adult members of fungus gnats (**Mycetophilidae**) feed on spores in the capsules of ***Buxbaumia aphylla***. Others, as larvae, develop within the thalli of liverworts, also completing pupation there. The dark-winged fungus gnats (**Sciaridae**) tunnel in liverwort thalli.

The midge (**Chironomidae**) adults include some members that are attracted to exudates from antheridia and archegonia of mosses, accomplishing the transfer of sperm to the eggs. And even the blackflies (**Simuliidae**) have some members that begin their lives among mosses on land. The moth flies (**Psychodidae**) live among bryophytes as larvae in both aquatic and terrestrial habitats. The biting midges (**Ceratopogonidae**) live in moist places and are common on mosses. Few mosquitoes (**Culicidae**) or gall midges (**Cecidomyiidae**) are known to use mosses.

Acknowledgments

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CHAPTER 12-20
TERRESTRIAL INSECTS: HOLOMETABOLA – DIPTERA BRACHYCERA

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CHAPTER 12-20
TERRESTRIAL INSECTS: HOLOMETABOLA – DIPTERA BRACHYCERA

Figure 1. Beefly (**Syrphidae**) on ***Cratoneuron filicinum***. Many flies use bryophytes for resting sites where the bryophytes reduce the danger of dehydration or the flies take a drink of water. Photo by Serhat Ursavas, with permission.

BRACHYCERA

Rhagionidae *sensu stricto* – Snipe Flies

The **Rhagionidae** is a worldwide family that has some members among the most primitive of the **Brachycera**. One of its diagnostic characters is that its head points downward when at rest (Figure 2), earning it the name of "downlooker flies."

In the Czech Republic, ***Rhagio latipennis*** (Figure 2) is a predaceous fly that prefers moist soil rich in organic matter (Farkač *et al*. 2005). Some prefer decaying wood, mosses, or liverworts along the sides of water courses.

Figure 2. ***Rhagio latipennis*** adult, a species that sometimes is associated with streamside mosses or liverworts. Note the downward-pointing head. Photo by João Coelho, through Creative Commons.

Spaniidae

Members of the **Spaniidae** family are often included in the **Rhagionidae**. The **Spaniidae** feeding habits may be assumed to be similar, in most cases, to those of the **Rhagionidae**.

Both adults and larvae typically eat small insects. The adults live in forests, especially near moist places. Larvae occur in moist meadow soil, among mosses, in decaying wood, under bark, and a few in water.

Imada and Kato (2016a) investigated **Diptera** in the **Rhagionidae/Spaniidae** to determine apparent adaptations to bryophyte consumption. The **Spaniidae** has larval members with multiple bryophyte-feeding habits. ***Spania*** (Figure 30-Figure 34) and ***Litoleptis*** (thallus-miners of thallose liverworts; Figure 3, Figure 17) both have a toothed form of apical mandibular sclerite with an orifice on its dorsal surface, contrasting with those of the members of **Rhagionidae** that possess a blade-like mandibular hook with an adoral groove. On the other hand, the moss stem borer ***Ptiolina*** (Figure 25) has a weak groove on the adoral surface of the mandible and has a highly sclerotized maxilla with toothed projections. Imada and Kato hypothesized that the toothed mandibles with the dorsal orifice would facilitate the leaf miners in scraping plant tissue and imbibing it along with a large quantity of cell sap. Their phylogenetic analysis indicated that the loss or reduction of the adoral mandibular groove and mandibular brush coincides with the evolution of bryophyte feeding.

Litoleptis (Figure 3)

Imada and Kato (2016b) reported the feeding strategy for ***Litoleptis*** (Figure 3, Figure 17) in Japan. The larvae of this genus mine the thalli of thallose liverworts in the families **Aytoniaceae** and **Conocephalaceae**. These include species of ***Conocephalum*** (Figure 4), ***Reboulia*** (Figure 5), and ***Asterella*** (Figure 6). It is clear that bryophyte miners are an overlooked group of species. While I was working on ththe original preparation of this chapter, Imada and Kato (2016b) provided me with six new species they described in the genus ***Litoleptis***, all from thallose liverworts, in Japan.

Figure 3. ***Litoleptis japonica*** adult on ***Conocephalum*** sp. Photo courtesy of Yume Imada.

Figure 4. ***Conocephalum conicum*** on wet rock; the dipteran ***Litoleptis japonica*** deposits eggs on its thallus and the larvae mine the interior. Photo by Fotis Samaritakis, through Creative Commons.

Figure 5. ***Reboulia hemisphaerica*** with archegoniophores, a potential host plant for species of ***Litoleptis***. Photo by Michael Lüth, with permission.

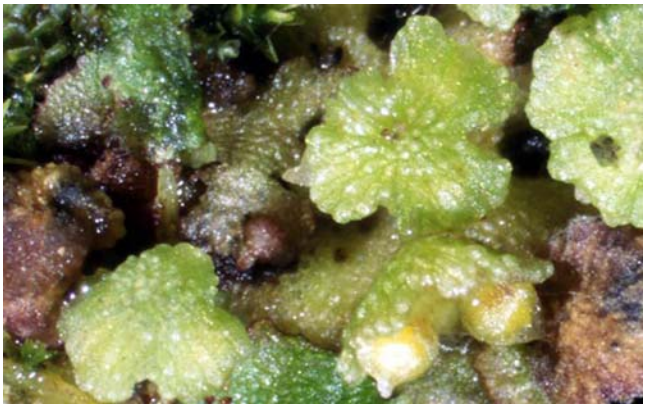

Figure 6. ***Asterella cruciata***, an endangered species in Japan and home of ***Litoleptis asterellaphile***. Photo by Misao Ito, with permission from Digital Museum of Hiroshima.

Litoleptis japonica (Figure 3) larvae occur in thalli of ***Conocephalum conicum*** (Figure 4) in shaded habitats in Japan (Figure 7-Figure 8). The adult female deposits eggs on the thallus of ***Conocephalum conicum*** (Figure 9-Figure 11), and its larvae (Figure 12-Figure 14) subsequently mine the thallus of this liverwort.

Figure 7. ***Litoleptis japonica*** habitat at Kibune, Kyoto Pref., Japan. Photo by Yume Imada, with permission.

Figure 8. ***Litoleptis japonica*** habitat in Nanataki in Wakayama Pref., Japan. Photo by Yume Imada, with permission.

Figure 9. ***Litoleptis japonica*** adult on ***Conocephalum conicum***. Photo by Yume Imada, with permission.

Figure 10. ***Litoleptis japonica*** ovipositing on ***Conocephalum conicum*** at Kibune, Kyoto Pref., Japan. Photo by Yume Imada, with permission.

Figure 11. ***Litoleptis japonica*** eggs (**arrows**), deposited on liverwort thallus. Photo by Yume Imada, with permission.

Figure 12. ***Litoleptis japonica*** first instar larva (**arrow**) mining in a thallus of ***Conocephalum conicum***. Photo by Yume Imada, with permission.

Figure 13. ***Litoleptis japonica*** larva. Photo by Yume Imada, with permission.

Figure 14. ***Litoleptis japonica*** larva mining ***Conocephalum conicum***. Photo by Yume Imada, with permission.

Figure 15. ***Litoleptis japonica*** pupa (**arrow**) on ***Conocephalum conicum***. Photo by Yume Imada, with permission.

Litoleptis kiiensis (Figure 16-Figure 17) occurs in ***Reboulia hemispherica*** (Figure 5) on rocky or clayey slopes in both evergreen and deciduous forests (Imada & Kato 2016b). ***Litoleptis kiiensis*** is a thallus miner on ***Reboulia hemisphaerica*** (Figure 5). The larvae mine the middle layer of the thalli, making mines nearly invisible from outside the thallus. The final instar of the larvae individually mine along the mid-vein and pupate near the adaxial layer of thalli in that mine in early spring. In their observations, this pupa was visible from the outside of the thallus. Adults emerge from the thallus later in the spring.

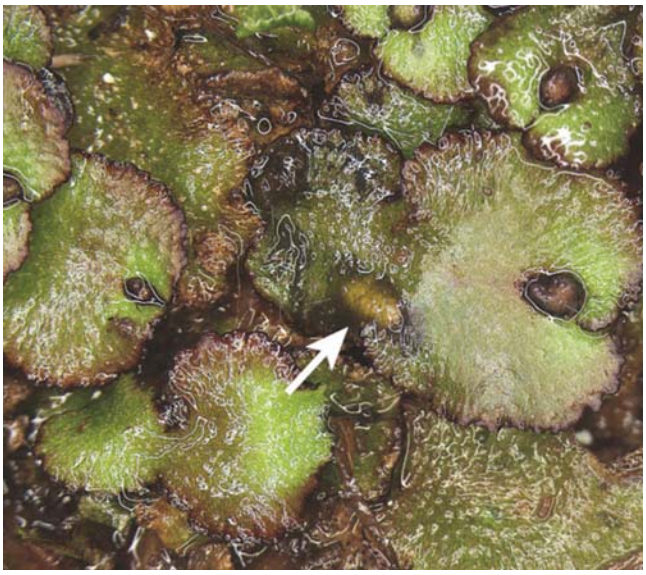

Figure 16. ***Litoleptis kiiensis*** larva (**arrow**) on thallose liverwort. Photo by Yume Imada, with permission.

Figure 17. ***Litoleptis kiiensis*** larva, a bryophyte inhabitant. Photo courtesy of Yume Imada.

Litoleptis niyodoensis occurs in ***Reboulia hemisphaerica*** (Figure 5) (Imada & Kato 2016b). ***Litoleptis himukaensis*** occurs along streams in ***Reboulia hemisphaerica***. ***Litoleptis izuensis*** occurs in ***Reboulia hemisphaerica*** on shaded clayey slopes along streams and roads in evergreen ***Castanopsis*** forests. ***Litoleptis asterellaphile*** (Figure 18) occurs in ***Asterella cruciata*** (an endangered species in Japan; Figure 6) on rocky cliffs along streams and roads in deciduous forests.

Figure 18. ***Litoleptis asterellaphile*** pupa (**arrow**) among liverworts. Photo by Yume Imada, with permission.

Ptiolina (Figure 19)

Lane and Anderson (1982) found immature adults of ***Ptiolina*** *cf.* ***zonata*** (Figure 19) by hand sorting moss-covered soil samples (Figure 20). Apparently mosses also provide oviposition sites for the genus (Figure 21-Figure 23), hence also providing homes for the larvae (Figure 24-Figure 26).

Figure 19. ***Ptiolina*** sp. on moss. Photo by Pristurus, through Creative Commons.

Figure 20. ***Ptiolina*** habitat at Kibune, Kyoto Pref., Japan. Photo by Yume Imada, with permission.

Figure 21. ***Ptiolina*** sp. ovipositing on ***Brachythecium buchananii*** at Kibune, Kyoto Pref., Japan. Photo by Yume Imada, with permission.

Figure 22. ***Ptiolina*** sp. ovipositing on moss; the two yellow areas at the tip of the abdomen are egg masses. Photo by Pristurus, through Creative Commons.

Figure 23. ***Ptiolina*** sp. eggs (**arrow**), deposited on ***Brachythecium buchananii***. Photo by Yume Imada, with permission.

Figure 24. ***Ptiolina*** sp. larva. Photo by Yume Imada, with permission.

Figure 25. ***Ptiolina*** sp. larva, a bryophyte inhabitant. Photo courtesy of Yume Imada.

Figure 26. ***Ptiolina*** sp. second-instar larva (**arrow**), boring a shoot of the moss ***Plagiomnium vesicatum***. Photo by Yume Imada, with permission.

Since that publication, we have learned that a number of species in this family are adapted to mining bryophytes, and they seem to be very specific about their choice of bryophyte. Furthermore, they deposit their eggs on the same bryophyte that the larvae will later eat. ***Ptiolina*** sp. (Figure 19-Figure 22) deposits eggs (Figure 21, Figure 23) on the moss ***Brachythecium buchananii*** (Figure 27), and the larvae (Figure 25) are stem borers on this same species (Imada & Kato 2016a).

Figure 27. ***Brachythecium buchananii***; ***Ptiolina*** deposits eggs on this species and larvae are stem borers in it. Photo by Michael Lüth, with permission.

Spania

The original record I found of a member of **Spaniidae** among bryophytes is that of ***Spania nigra*** (Figure 29-Figure 34). Larvae of this species live on mosses and liverworts in damp shade such as the ghyll woodlands of Sussex (Roper 2001). Boyce (2002) reported it from the

thallose liverwort ***Pellia*** (Figure 35) in England. Yume Imada (pers. comm.) has also found ***Spania*** sp. tunnelling in ***Conocephalum*** (Figure 34).

Figure 28. ***Spania*** sp. habitat. Photo by Yume Imada, with permission.

Figure 29. ***Spania nigra*** adult, a species whose larvae live among forest mosses and liverworts in the UK. Photo by Marko Mutanen, through Creative Commons.

Imada and Kato (2016a) observed that ***Spania*** sp. (Figure 29) deposited eggs exclusively on the thallus of the liverwort ***Pellia endiviifolia*** (Figure 35), a species it also mines.

Figure 30. ***Spania*** sp. adult on ***Brachythecium buchananii***, Japan. Photo courtesy of Yume Imada.

Figure 31. ***Spania*** sp. ovipositing on ***Pellia endiviifolia***, at Higashiyoshinomura, Nara Pref., Japan. Photo by Yume Imada, with permission.

Figure 32. ***Spania*** sp. eggs (**arrows**) on ***Pellia endiviifolia***. Photo by Yume Imada, with permission.

Figure 33. ***Spania*** sp. larva. Photo by Yume Imada, with permission.

Figure 34. ***Spania*** sp. larva tunnelling in ***Conocephalum***. Photo courtesy of Yume Imada.

Figure 35. ***Pellia endiviifolia*** males and females; thalli are home for some ***Spania*** larvae that mine the interior. Photo by David T. Holyoak, with permission.

Dolichopodidae – Long-legged Flies

The **Dolichopodidae** is likewise a family of water-loving species. I mention here a few that are somewhat amphibious. ***Dolichopus maculipennis*** (Figure 36) lives in calcareous wet habitats near small permanent pools, in bryophyte flushes (Figure 37), flushed grasslands, and wet mires (Horsfield & MacGowan 1997), but it also occurs in bogs (Ringdahl 1928). ***Hydrophorus rufibarbis*** (see Figure 39-Figure 38) seems to prefer small, peaty pools, but it also lives in grassy flushes and bryophyte springs (Horsfield & MacGowan 1997).

Figure 36. ***Dolichopus maculipennis*** adult, a species whose larvae live in bryophyte flushes. Photo by I. Grichanov, with online permission.

Figure 37. Bryophyte flush in Wales, potential home for some **Dolichopodidae**. Photo by Janice Glime.

Empididae – Dance Flies

The **Empididae** are somewhat common on aquatic bryophytes (Gootaert 2004), so it is no surprise that some terrestrial species likewise find bryophytes to be suitable homes. Plant (1993) found adult females of ***Monodromia fragilis*** (Figure 40) by sweeping the damp mosses on a cloud forest floor at 550 m asl in New Zealand. In Malaysia the adults are only 3-5 mm long and are mostly yellow or black Gootaert 2004). These seem to prefer boulders covered with mosses or a splash zone where there is constant high humidity.

Figure 38. ***Hydrophorus litoreus*** adult; ***H. rufibarbis*** lives in bryophyte springs and peaty pools. Photo by James K. Lindsey, with permission.

Figure 39. ***Hydrophorus oceanus*** larvae; ***H. rufibarbis*** lives in bryophyte springs and peaty pools. Photo by Hans Hillewaert, through Creative Commons.

The larvae of ***Hemerodromia*** (Figure 41) occur in fast-flowing streams and are predaceous. The adults are yellow or black and occur on moss-covered boulders or in the splash zone, both habitats that ensure moisture.

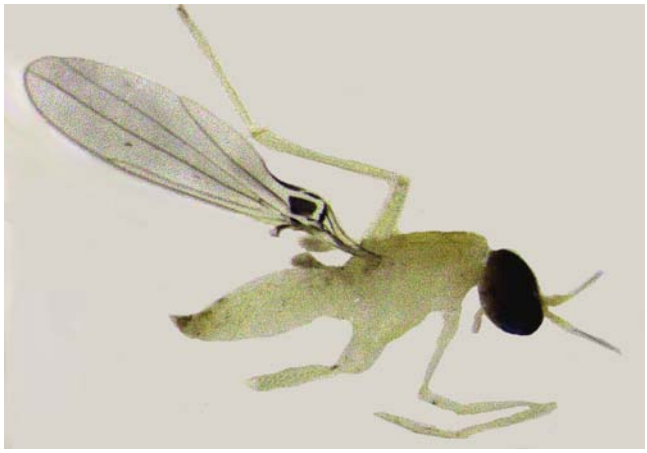

Figure 40. ***Monodromia fragilis*** adult, a species whose adults are associated with damp mosses on the floor of a New Zealand cloud forest. Photo modified from one by Stephen Thorpe, through Creative Commons.

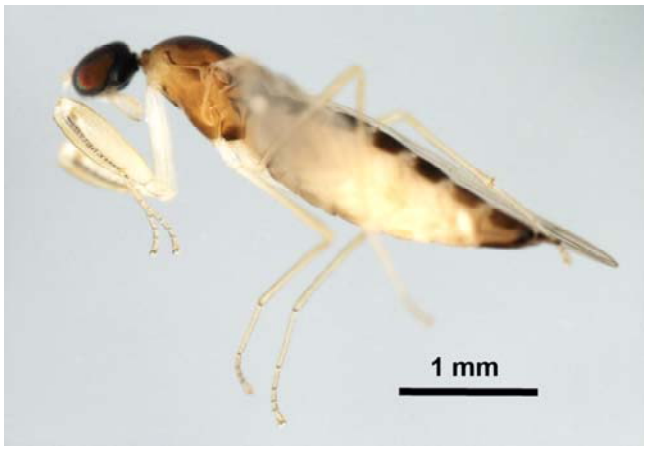

Figure 41. ***Hemerodromia*** adult, a genus whose adults are associated with moss-covered boulders or in the splash zone. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Some insects only use bryophytes as landing and resting places. That appears to be the case with the empidid fly in Sarah Lloyd's pictures below (Figure 42-Figure 44). This family is mostly predaceous on other small invertebrates (Tony Daley, pers. comm. 19 November 2011).

Figure 42. Empidoid fly, possibly **Hybotidae**, on a leafy liverwort. Note the greatly arched thorax and long legs. Photo courtesy of Sarah Lloyd.

Clinocera nivalis (*nivalis* refers to snow; Figure 44) in Scotland is primarily on wet stony and mossy slopes, especially below melting snow, and always above 850 m asl (Edwards 1933a, b; Horsfield & MacGowan 1997). It also is abundant on bryophyte springs and occurs in ***Racomitrium*** moss heaths (Figure 45) and moss-dominated snowbed communities. Horsfield and MacGowan consider that it might be restricted to areas with bryophyte springs and flushes, common in the highlands. J. M. Nelson found it in an ***Anthelia julacea*** (leafy liverwort; Figure 46-Figure 47) spring in Coire Raibert at around 1000 m.

Figure 43. Adult member of **Empididae** resting on a moss capsule. Photo courtesy of Sarah Lloyd.

Figure 44. ***Clinocera nivalis*** adult, a species of wet, stony, and mossy slopes and bryophyte springs. Photo by CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 45. ***Racomitrium lanuginosum*** heath, home for ***Clinocera nivalis***. Photo by Mike Pennington, through Creative Commons.

Figure 46. ***Anthelia julacea***, home for ***Clinocera nivalis***. 1 Photo by Jean Faubert., with permission.

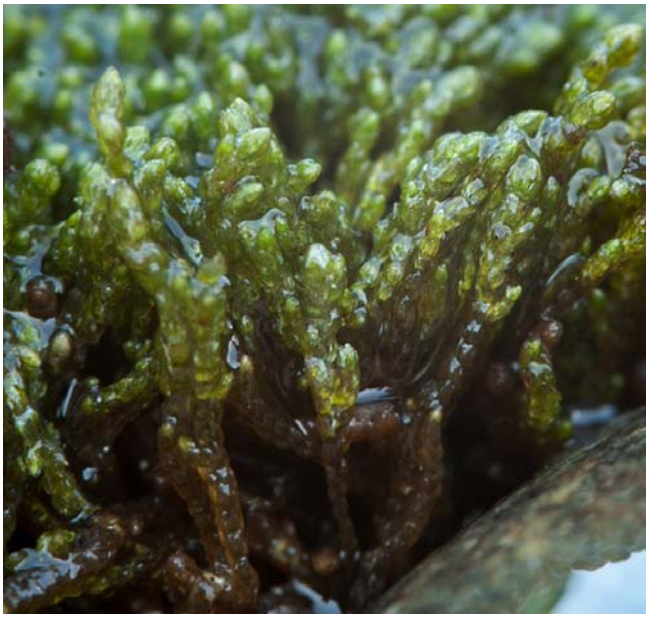

Figure 47. ***Anthelia julacea***, home for ***Clinocera nivalis***. Photo by Štěpán Koval, with permission.

Larvae of ***Wiedemannia impudica*** (see Figure 48) probably live in mosses on emergent boulders (Horsfield & MacGowan 1997), again where they will be constantly moist.

Figure 48. ***Wiedemannia*** *bistigma* adult; ***W. impudica*** is a likely moss inhabitant on emergent boulders. Photo by Marko Mutanen, through Creative Commons.

Hybotidae – Hybotid Dance Flies

Smith (1965) described a new species of ***Stilpon*** (Figure 49-Figure 50) from Portugal. The immature stages of this genus were still unknown, but the adults occur in grass tufts, heaps of cut sedge, and ***Sphagnum*** (Figure 51). The new species was similar to ***Stilpon nubilus***.

Figure 49. ***Stilpon*** sp. adult, a genus in which some adults occur in ***Sphagnum***. Photo by Tom Murray, through Creative Commons.

Figure 50. ***Stilpon curvipes*** adult, member of a genus in which some adults occur in ***Sphagnum***. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 51. ***Sphagnum warnstorfii***; ***Sphagnum*** is a genus that is home to adult ***Stilpon*** (and possibly the unknown larvae). Photo by Michael Lüth, with permission

Syrphidae – Syrphid Flies

This is a family of flies that often resemble bees. If you find a "bee" with only two wings and a pair of halteres, you have found a beefly. ***Platycheirus melanopsis*** (Figure 52) is known from moss-dominated summit heaths (Figure 45) and grasslands in Scotland (Horsfield & MacGowan 1997). ***Cheilosia sahlbergi*** (Figure 53) occurs in habitats where bryophytes are abundant, including ericaceous dwarf shrub heaths, flushes, and bryophyte springs.

Figure 52. ***Platycheirus melanopsis*** adult, a species from moss-dominated summit heaths. Photo from America Pink, with online permission.

Figure 53. ***Cheilosia sahlbergi*** adult, a species that occurs in habitats with abundant bryophytes. Photo by Ladislav Tabi, with permission.

Phoridae – Scuttle Flies

Mosses often provide a safe overwintering shelter. Herbert and Braun (1958) reported moss polsters as the overwintering quarters for adult dipterans in the family **Phoridae** (Figure 54).

Figure 54. **Phoridae** mating in Rock Creek Park, MD. Photo by Katja Schulz, through Creative Commons.

Agromyzidae – Mine Flies

This family has bryophyte specialists, but not on mosses. Rather, these bryobionts are known only from hornworts and liverworts (Spencer 1990). D'Aguilar (1945) described a new species of ***Liriomyza*** (Figure 55) from the thallose liverwort ***Ricciocarpos natans*** (Figure 56). ***Phytoliriomyza mesnili*** (formerly ***Liriomyza***; see Figure 57-Figure 58) is known from ***Ricciocarpos natans*** in France as well as being present on the thallose liverwort ***Riccia beyrichiana*** (Figure 59). It feeds in the thallus and pupates there and also pupates in the thallus of ***Nothoceros vincentianus*** (Figure 60-Figure 62) in Peru. In Mexico, it is known on ***Dumortiera*** (Figure 63) and ***Monoclea*** (Figure 64).

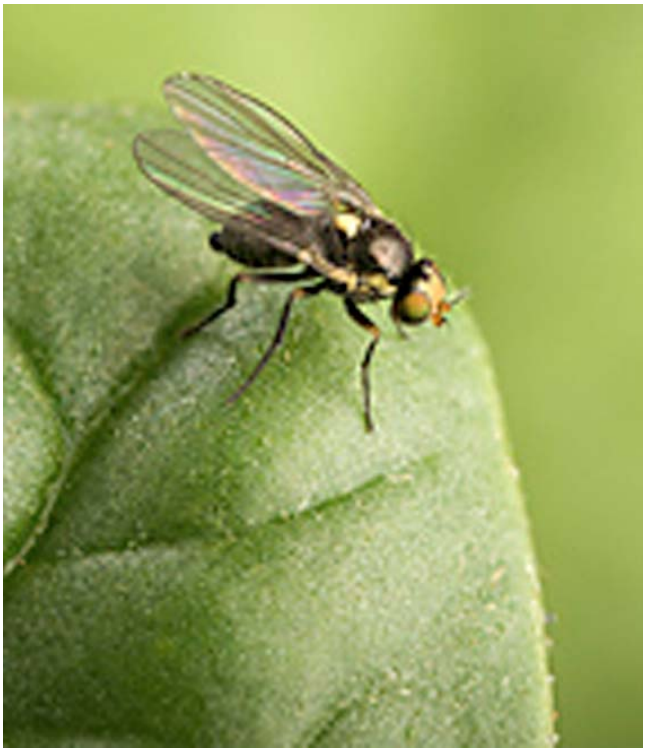

Figure 55. ***Liriomyza taraxaci*** adult, member of a genus known from the liverwort ***Ricciocarpos natans***. Photo by Peggy Greb, USDA, through public domain.

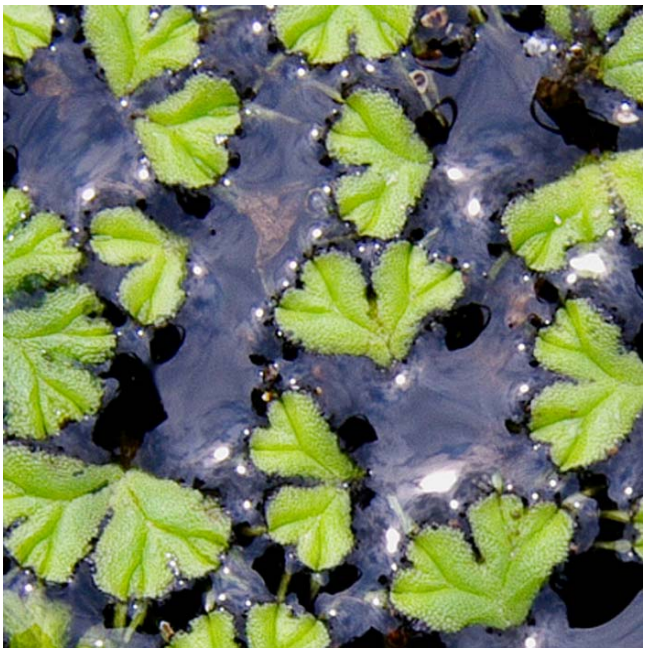

Figure 56. ***Ricciocarpos natans***, home for some species of ***Liriomyza***/***Phytoliriomyza***. Photo by Christian Fischer, through Creative Commons.

Figure 57. ***Phytoliriomyza arctica*** adult. Some members of this genus live in liverwort thalli. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 58. ***Phytoliriomyza melampyga*** larval tunnels in a leaf. Photo from Biodiversity Centre, through Creative Commons.

Figure 59. ***Riccia beyrichiana***, home and food for ***Phytoliriomyza mesnili***. Photo by Jan-Peter Frahm, with permission.

Figure 60. ***Nothoceros***, a genus where ***Phytoliriomyza mesnili*** is known to live in Peru. Photo by Juan Larrain, with permission.

Figure 61. ***Nothoceros*** with **Agromyzidae** leaf miners. Photo courtesy of Juan Carlos Villarreal.

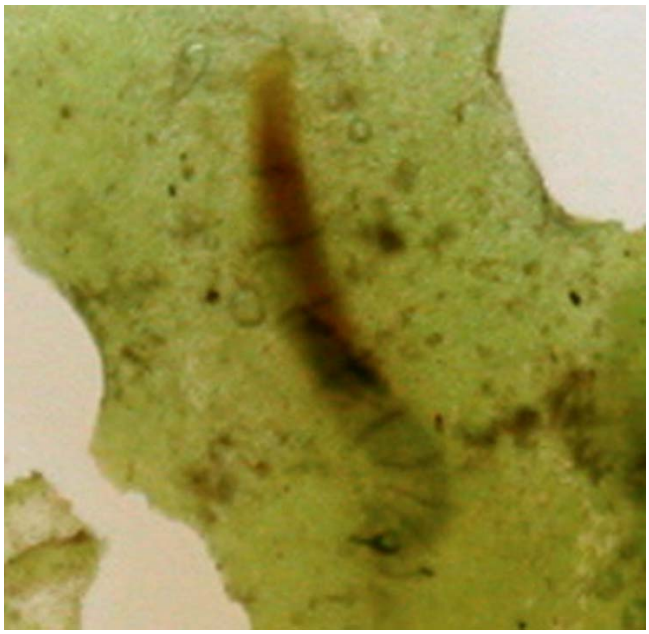

Figure 62. ***Nothoceros*** leaf miner seen through the thallus. Photo courtesy of Juan Carlos Villarreal.

Figure 63. ***Dumortiera hirsuta***, home to ***Phytoliriomyza mesnili*** in Mexico. Photo by Li Zhang, with permission.

Figure 64. ***Monoclea forsteri***, home to ***Phytoliriomyza mesnili*** in Mexico. Photo by Jan-Peter Frahm, with permission.

Reporting from Spain, Marta Infante and Patxi Heras (Bryonet 2 May 2019) described a larva living in ***Riccia cavernosa*** (Figure 65). They noted that it tried to defend itself from the dissecting needle. Later, they observed many pupae and larvae inside the thallus. The species proved to be ***Phytoliriomyza mesnili*** (Figure 66).

Ron Porley (Bryonet 3 May 2019) relayed a similar experience with ***Riccia cavernosa*** (Figure 65). Although he did not identify the insect, it was present as black pupae in the thalli of this species on the muddy margin of a reservoir in Algarve, Portugal, in November. Pettet (1967) reported a similar parasitism on ***Riccia frostii*** (Figure 67) by flies. Porley suggested that such habitation may only occur in section ***Ricciella*** because of its spongy thalli with large air chambers.

Figure 65. ***Riccia cavernosa***, home for pupae of ***Phytoliriomyza mesnili***. Photo from <www.aphotofauna.com>, with permission.

Figure 66. ***Phytoliriomyza melampyga*** adult; ***P. mesnili*** pupates within the thalli of ***Riccia cavernosa***. Photo through Wikimedia Commons.

Figure 67. ***Riccia frostii***, home for pupae of some **Agromyzidae**. Photo from Earth.com, with permission.

Manju Nair provided me with images of the pupae (Figure 68) of an **Agromyzidae** that appears to be

Phytoliriomyza (Figure 68). This pupa inhabits the thalli of ***Riccia beyrichiana*** (Figure 69) and ***Riccia hasskarliana*** (Figure 70).

Figure 68. ***Phytoliriomyza*** pupa from thallus of ***Riccia beyrichiana***. Photo by Manju Nair, with permission.

Figure 69. ***Phytoliriomyza*** pupa in thallus of ***Riccia beyrichiana***. Photo by Manju Nair, with permission.

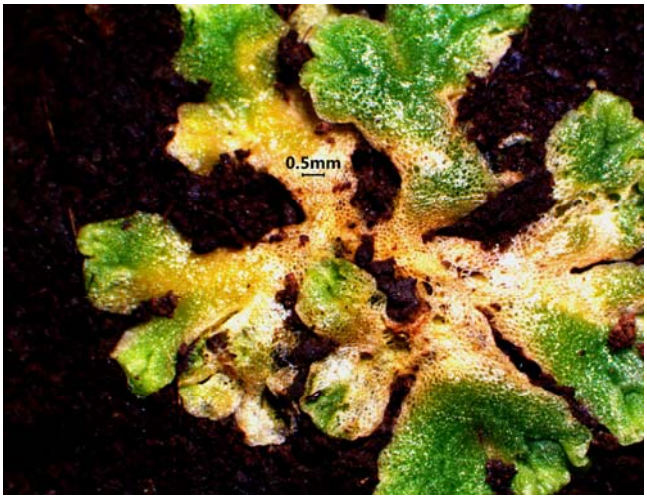

Figure 70. ***Riccia hasskarliana*** mined by ***Phytoliriomyza***. Photo by Manju Nair, with permission.

Some relationships of flies with their bryophyte hosts are obligatory. In Mexico, Juan Carlos Villarreal (pers. comm. 9 September 2014) found the larvae (Figure 71) of leaf-mining flies crawling within the hornwort ***Nothoceros aenigmaticus***, making traces. While in his custody, it became a pupa (Figure 72). Then one day a hatchling appeared. But it was not a young leaf miner. It was a parasitoid wasp that lived on the pupa! So far, no one has successfully reared the larvae or pupae of the agromyzid to adults, but using genetic bar-coding he determined it to be close to ***Phytomyza*** (Figure 73-Figure 78). He found similar **Diptera** from Panamanian ***Nothoceros vincentianus*** (Figure 75) and sequenced them. They most closely matched ***Phytomyza***. But with only an 87% match, perhaps this is a new species or even a new genus.

Figure 71. **Agromyzidae** larva from ***Nothoceros*** thallus. Photo courtesy of Juan Carlos Villarreal.

Figure 72. **Agromyzidae** pupa grown from larva that was living in ***Nothoceros***. Photo courtesy of Juan Carlos Villarreal.

Figure 73. ***Phytomyza*** egg from ***Nothoceros aenigmaticus*** Montage Mexico. Photo courtesy of Juan Carlos Villarreal.

Figure 74. ***Phytomyza ranunculi*** larval tunnels in a leaf, similar to those made by species in liverworts. Photo by James K. Lindsey, with permission.

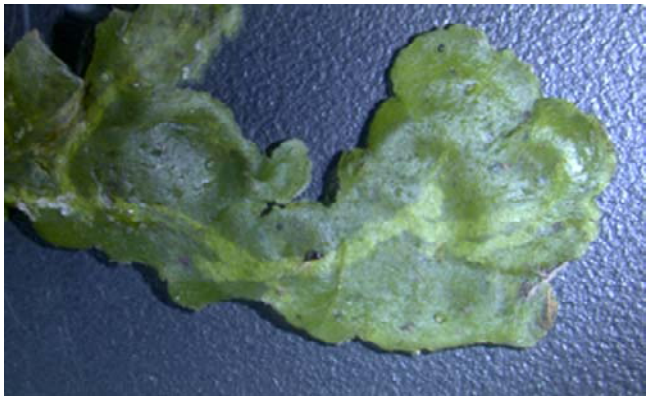

Figure 75. ***Nothoceros vincentianus*** with leaf miner, possibly ***Phytomyza*** sp., in Panama. Note the leaf miner trails on the thallus surface. Those are not midribs! Photo courtesy of Juan Carlos Villarreal.

Figure 76. ***Phytomyza vitalbae*** pupa, member of a genus with some members that live in liverwort thalli. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

Figure 77. ***Phytomyza ranunculi*** adult, member of a genus that sometimes lays eggs in liverwort thalli. Photo by Dick Belgers, through Creative Commons.

Figure 78. ***Phytomyza ranunculi*** adult, member of a genus in which some species live in liverwort thalli. Photo by James K. Lindsey, with permission.

Villarreal was able to determine (via a letter belonging to John Engel) that Proskauer had seen leaf miners in ***Megaceros*** (Figure 79) and ***Nothoceros*** (Figure 75). Hering (1957) described ***Phytoliriomyza*** sp. (see Figure 57-Figure 58) larvae and pupae from ***Megaceros***.

Figure 79. ***Megaceros*** sp. with capsules, home for some of the leaf-mining flies. Photo by David Tng <www.davidtng.com>, with permission.

In the larvae of ***Phytoliriomyza mesnili*** (see Figure 57-Figure 58), living in the hornwort ***Nothoceros vincentianus*** (Figure 75), the anterior spiracles of the larva penetrate the epidermis of the thallus to permit breathing (Herring 1966; Spencer 1990). Members of this family also mine ***Dumortiera hirsuta*** (Figure 63) and ***Monoclea*** (Figure 64) in Mexico (Spencer 1990). Although their substrate is generally thallose liverworts and hornworts (never mosses), some feed on ferns, but none is known to feed on flowering plants.

Mining flies seem to have a widespread distribution, albeit scattered. Herring (1957) found leaf-mining flies in ***Megaceros*** spp. (Figure 79) in the West Indies, Juan Fernandez Islands, and New Zealand. Several reports have revealed them in Europe. And Villarreal has found them in Mexico and Panama.

The combination of thallose liverworts or hornworts, mining fly, and parasitic wasp apparently also has far-reaching geographic presence, although the species involved may differ. Sara Altenfelder (pers. comm.) found ***Riccia glauca*** (Figure 80) and ***R. warnstorfii*** (Figure 81) with leaf-mining flies in arable fields in Germany, and these, like the ones found by Villarreal, were parasitized by wasps. She determined that the fly is ***Phytoliriomyza mesnili*** (see Figure 57-Figure 58), first described by Aguilar (1945) feeding on ***Ricciocarpos natans*** (Figure 56) and later reported by Sellier (1947) from ***Riccia beyrichiana*** (Figure 59). The larva eats the thallus, then pupates there (Spencer 1990). Fulnek (1962) mentioned a parasitic wasp – ***Dacnusa taras*** – that lives on some members of ***Phytoliriomyza***.

Figure 80. ***Riccia glauca***, home for ***Phytoliriomyza mesnili***. Photo by Bernd Haynold, through Creative Commons.

Figure 81. ***Riccia warnstorfii***, a species that is home to larvae of ***Phytoliriomyza mesnili***. Photo by Bernd Haynold, through Creative Commons.

In 2018, Ohgue *et al*. reported the first bryophyte galls (Figure 82) induced by insects. These were created by a species of **Agromyzidae**, probably related to ***Phytoliriomyza*** (Figure 57-Figure 58, Figure 66, Figure 68). These occur on the thallose liverwort ***Monoclea gottschei*** **subsp.** ***elongata*** (Figure 82) in a tropical mountain forest. The galls form swellings on the thallus surface, but they resemble the thallus, having no ornamentation or sclerotization. The larvae become pupae (Figure 83) within the gall and adult flies (Figure 84) emerge from the gall by making an exit hole in the upper epidermis of the galled thallus. The galls appear in the apical part of the thallus where archegonia or antheridia would normally occur. Although archegonia and antheridia were plentiful in the population, thalli with galls produced no sporophytes. The need to raise larvae to adults for identification has caused many of these thallus-inhabiting larvae to remain unnamed.

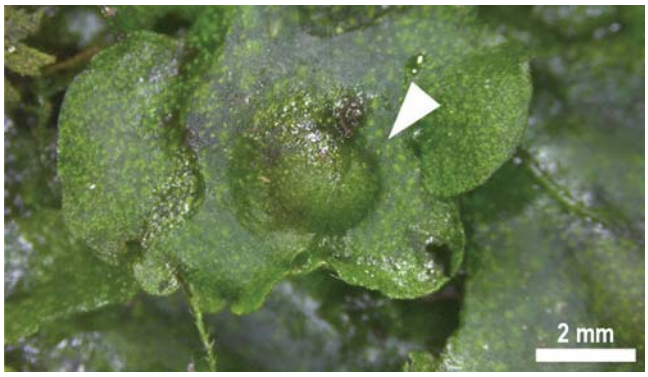

Figure 82. ***Monoclea gottschei*** thallus with a gall of **Agromyzidae**; triangle indicates gall. Photo by Takayuki Ohgue 2018, with permission from Yume Imada.

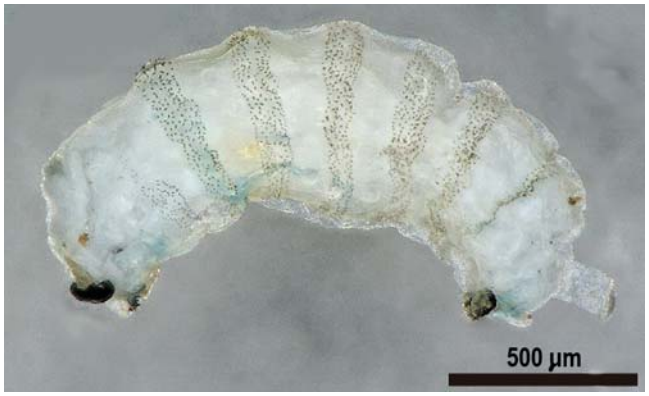

Figure 83. **Agromyzidae** thallus gall larva from ***Monoclea gottschei***. Photo by Takayuki Ohgue, with permission from Yume Imada.

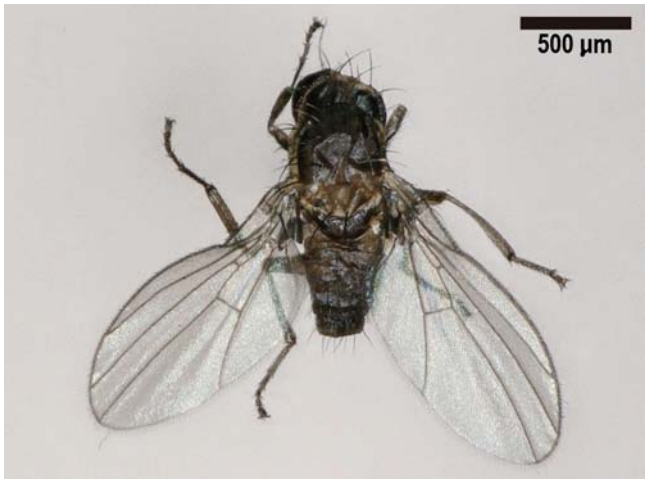

Figure 84. **Agromyzidae** thallus gall larva from ***Monoclea gottschei***. Photo by Takayuki Ohgue, with permission from Yume Imada.

Kato *et al*. (2022) found that liverwort-mining **Agromyzidae** were "overwhelmingly widespread and diverse" in the Japanese Archipelago. They found 39 species, 37 of which were new species! All of these were placed in ***Phytoliriomyza*** (*e.g.* Figure 57-Figure 58, Figure 66, Figure 68). Five of these were associated with ***Marchantia*** (Figure 85), two on ***Dumortiera*** (**Dumortieraceae**; Figure 63), three on ***Plagiochasma*** (Figure 86), one on ***Asterella*** (Figure 6), six on ***Reboulia*** (**Aytoniaceae**; Figure 5), one on ***Wiesnerella*** (**Wiesnerellaceae**; Figure 87), fifteen on ***Conocephalum*** (**Conocephalaceae**; Figure 4), and three on ***Riccia*** (**Ricciaceae**; Figure 59, Figure 65, Figure 67, Figure 70, Figure 80, Figure 81). Another 3 species were associated with hornworts: 1 on ***Folioceros*** (**Anthocerotaceae**; Figure 88), 1 on ***Megaceros*** (**Dendrocerotaceae**; Figure 79), and 1 on ***Notothylas*** (Figure 89), ***Phaeoceros*** (**Notothyladaceae**; Figure 90), and ***Anthoceros*** (**Anthocerotaceae**; Figure 91).

Figure 85. ***Marchantia polymorpha***; the genus ***Marchantia*** serves as home for species of ***Phytoliriomyza***. Photo by Denis Barthel, through Creative Commons.

Figure 86. ***Plagiochasma*** sp., home for species of ***Phytoliriomyza***. Photo by Zhang Li, with permission.

Figure 87. ***Wiesnerella denudata***, home for species of ***Phytoliriomyza***. Photo by Masaki Shimamura, with permission.

Figure 88. ***Folioceros cf glandulosus***, a hornwort in a genus that can serve as home for ***Phytoliriomyza***. Photo by Li Zhang, with permission.

Figure 89. ***Notothylas orbicularis***, a hornwort in a genus that can serve as home for ***Phytoliriomyza***. Photo by Blair Young, through Creative Commons.

Figure 90. ***Phaeoceros laevis***, a hornwort in a genus that can serve as home for ***Phytoliriomyza***. Photo by Oliver S. Beneutzer, through Creative Commons.

Figure 91. ***Anthoceros neesii*** with sporophytes dehiscing, a hornwort in a genus that can serve as home for ***Phytoliriomyza***. Photo from Earth.com, with permission.

Lauxaniidae

Sarah Lloyd described her experiences with some of the mine flies – ***Ceratolauxania atrimana*** (Figure 92-Figure 94). They like wet places (she never saw them in open, drier areas) and they tend to land on high points, but they sometimes also land on the mosses. That might be a location to rehydrate. They also oviposit on bryophytes, as shown on the ***Bazzania adnexa*** below (Figure 93).

Figure 92. ***Ceratolauxania atrimana*** laying eggs on ***Bazzania adnexa*** in Eucalypt forest in Tasmania. Photo courtesy of Sarah Lloyd.

Figure 93. ***Ceratolauxania atrimana*** laying eggs on ***Bazzania adnexa*** in Eucalypt forest in Tasmania. Photo courtesy of Sarah Lloyd.

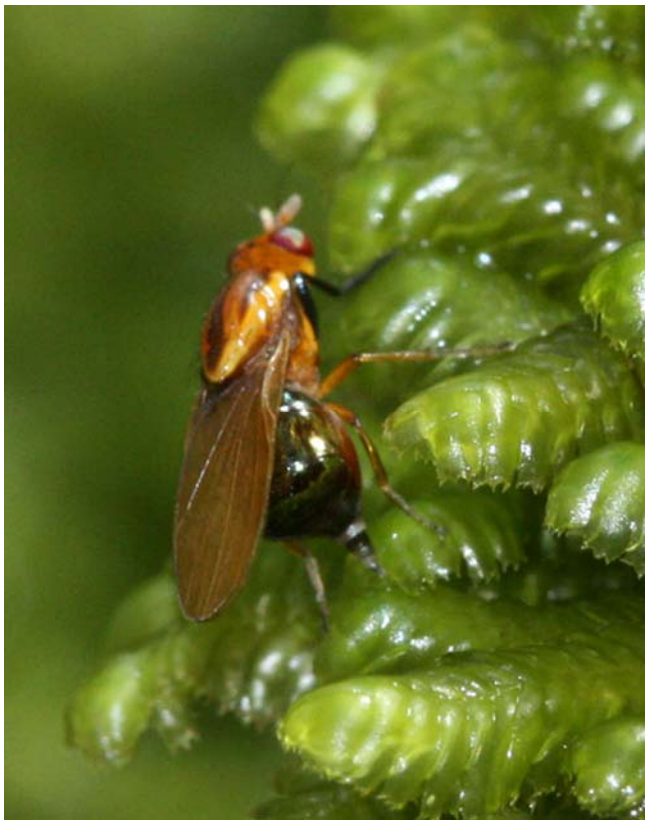

Figure 94. ***Ceratolauxania atrimana*** adult on ***Bazzania adnexa*** in a Tasmanian ***Eucalyptus*** forest. Photo courtesy of Sarah Lloyd.

Anthomyiidae – Root-maggot Flies

Thus far I can find only one paper that discusses the **Anthomyiidae** from bryophytes (Horsfield & MacGowan 1997). From very high altitudes in Britain, ***Alliopsis albipennis*** (see Figure 95) includes moss-dominated late snow-bed vegetation among its habitats, as well as flushes which are likely to be moss-dominated, but it is not restricted to these mossy habitats. ***Alliopsis atronitens*** (see Figure 95) exhibits one of its most frequent occurrences in ***Racomitrium lanuginosum*** moss heaths (Figure 45) on summit plateaus in Scotland.

Figure 95. ***Alliopsis billbergi*** adult; ***Alliopsis albipennis*** lives in moss-dominated late snowbeds. Photo by James K. Lindsey, with permission.

Delia caledonica (see Figure 96) occurs in blanket bogs and ***Racomitrium lanuginosum*** heath (Figure 45), among other montane habitats (Horsfield & MacGowan 1997). ***Delia piliventris*** (see Figure 96) occurs mostly in the ***Racomitrium lanuginosum***, grasslands, and tall herb communities in the montane area of Scotland.

Figure 96. ***Delia radicum*** adult. ***Delia caledonica*** is a species living in blanket bogs and ***Racomitrium lanuginosum*** heaths; ***D. piliventris*** lives mostly in ***Racomitrium lanuginosum*** heaths. Photo by Ladislav Tábi, with permission.

Botanophila moriens (see Figure 97-Figure 98) occurs in bryophyte springs and in ***Racomitrium lanuginosum*** (Figure 45) heaths at high elevations (760-1310 m alt) (Horsfield & MacGowan 1997). ***Zaphne spiniclunis*** (Figure 99) includes moss heaths (Figure 45) and bryophyte springs among its many habitats, mostly above 800 m near melting snow.

Figure 97. ***Botanophila*** larva, a species of bryophyte springs and ***Racomitrium lanuginosum*** heaths. Photo by Malcolm Storey, through Creative Commons.

Figure 98. ***Botanophila*** cf. ***fugax*** adult, a species of bryophyte springs and ***Racomitrium lanuginosum*** heaths. Photo by Martin Cooper, through Creative Commons.

Figure 99. ***Zaphne ambigua*** adult; ***Zaphne spiniculunis*** lives in moss heaths and bryophyte springs near melting snow. Photo by James K. Lindsey, with permission.

Heleomyzidae

Only ***Scoliocentra scutellaris*** (Figure 100) seems to utilize mosses for its habitat. This species in Scotland lives in moss heaths (Figure 45), as well as other montane habitats.

Figure 100. ***Scoliocentra scutellaris*** adult, a species of moss heaths. Photo by Gunnar M. Kvifte, through Creative Commons.

Muscidae – House Flies

This is one of the families you are undoubtedly familiar with because it includes the common housefly. The **Muscidae** have been discussed in part in the first of the **Diptera** subchapters because of their role in dispersing spores of the **Splachnaceae**. Hence we have already seen a relationship with ***Myospila meditabunda*** (Figure 101), ***Eudasyphora cyanicolor*** (Figure 102), ***Palpibracus chilensis***, and ***Palpibracus*** spp.

Figure 101. ***Myospila meditabunda*** female, one of the flies that facilitates transfer of spores in the **Splachnaceae**. Photo by James. K. Lindsey, with permission.

Figure 102. ***Eudasyphora cyanicolor*** adult male, one of the flies that facilitates transfer of spores in the **Splachnaceae**. Photo by Tristram Brelstaff, through Creative Commons.

In montane areas of Scotland, Horsfield and MacGowan (1997) both ***Phaonia subfuscinervis*** (Figure 103) and ***Spilogona triangulifera*** (see Figure 104) from ***Racomitrium lanuginosum*** heath (Figure 45), as well as other non-mossy habitats. These two flies have a habit of sunning themselves on rocks and typically associate with snowbeds. In Lithuania, the predaceous larvae of ***Phaonia fuscata*** (Figure 105-Figure 107) live in soil and mosses of broad-leaved forests (Gregor *et al*. 2002; Lutovinovas & Rozkošný 2009).

Figure 103. ***Phaonia subfuscinervis*** adult, a species of ***Racomitrium lanuginosum*** heaths. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 104. ***Spilogona*** *falleni* adult; ***Spilogona triangulifera*** lives in ***Racomitrium lanuginosum*** heaths. Photo by James K. Lindsey, through Creative Commons.

Figure 105. ***Phaonia subventa*** larva, pupa, adult male. Photo by Martin Cooper, through Creative Commons.

Figure 106. ***Phaonia fuscata*** adult female, a species whose larvae live among and under mosses in broad-leaved forests in Lithuania. Photo by James K. Lindsey, with permission.

Figure 107. ***Phaonia fuscata*** adult male, a species whose larvae live among and under mosses in broad-leaved forests in Lithuania. Photo by James K. Lindsey, with permission.

Limnophora is mostly aquatic in the larval stage (Roper 2001), but some are more limnoterrestrial. The carnivorous ***Limnophora exurda*** (current name not found) larvae and pupae live in tufts of wet mosses and liverworts that receive direct water or spray from waterfalls (Tate 1939). ***Limnophora riparia*** (Figure 108-Figure 109) adults occur singly on stones or mosses or algae in Armenia, but occasionally they may occur as small groups (Pont *et al*. 2011). Roberts (1971) suggested that the mouth parts and musculature of the carnivorous ***Limnophora riparia*** larvae (Figure 108) were adapted to the type of food they consumed. Larvae of this species are aquatic and prefer mosses as a substrate. They attach to their substrate to anchor themselves as they attack their prey, which includes other invertebrates, especially **Chironomidae** and **Simuliidae** larvae. ***Limnophora petallifera*** (Figure 110) females and others in the genus use mosses for oviposition, as well as algae (Werner & Pont 2006; Pont *et al*. 2011). They arrived for this purpose at about midday when the rock substrate was in direct sunlight with a temperature of 42°C (Werner & Pont 2006). The female was "running around the rock close to the water and stopped when she found a small indentation, then injected her eggs many times in the mosses and algae. Her forelegs were pointed upward and her abdomen pushed into the wet mosses. She laid the eggs singly, but each egg was placed next to the first one so that ultimately the eggs were in clusters.

Figure 108. ***Limnophora riparia*** larva, a species whose larval mouthparts are adapted for eating vegetable matter. Photo by Niels Sloth, with permission.

Figure 109. ***Limnophora riparia*** adult, a species whose adults often hang out on mosses. Photo by Marko Mutanen, through Creative Commons.

Figure 110. ***Limnophora petallifera*** adults eating larva of *Obuchovia popowae* (Simuliidae). ***Limnophora petallifera*** oviposits among mosses. Photo by Doreen Werner, permission pending.

Scathophagidae – Dung Flies

This is another poorly represented family in bryophytic habitats. ***Gonatherus planiceps*** (Figure 111) is a montane species in Scotland, and like many others there, one of its habitats is in ***Racomitrium lanuginosum*** heaths (Figure 45) (Horsfield & MacGowan 1997).

Figure 111. ***Gonatherus planiceps*** adult, a species of ***Racomitrium*** heaths. Photo by Marko Mutanen, through Creative Commons.

Bratton (2012) swept two females of ***Gimnomera tarsea*** (Figure 112) from mosses beside Loch a' Roe in the Outer Hebrides.

Figure 112. ***Gimnomera tarsea*** adult, a species whose adults hang out near mosses beside lakes. Photo by Marko Mutanen, through Creative Commons.

Calliphoridae – Blow Flies

And another! For the **Calliphoridae** I found only ***Calliphora stelviana*** (Figure 113) (Horsfield & MacGowan 1997). Like many other flies in the montane Scotland, these included ***Racomitrium lanuginosum*** among their habitats.

Figure 113. ***Calliphora stelviana*** adult, a species that lives in ***Racomitrium lanuginosum*** heaths. Photo by Marko Mutanen, through Creative Commons.

Summary

The **Rhagionidae** may live among bryophytes and lay their eggs there. The **Spaniidae** are leaf miners and ***Litoleptis*** species and some ***Spania*** species mine the thalli of thick thallose liverworts. The **Dolichopodidae** tend to be amphibious, living in wet bryophytes. The **Empididae** may be found on damp mosses as well as aquatic ones. Some **Hybotidae** live among ***Sphagnum*** as adults. The **Syrphidae** are likewise often aquatic, but some live among terrestrial mosses as larvae. The **Phoridae** are not normal bryophyte inhabitants, but they do overwinter in moss polsters. Several members of **Agromyzidae** are leaf miners in large thallose liverworts and hornworts. The **Lauxaniidae** like wet places and often land on protruding mosses; others oviposit on species of the leafy liverwort ***Bazzania***. **Anthomyiidae** live among mosses in late snow-bed vegetation; others live in ***Racomitrium*** heaths. One **Heleomyzidae** lives in moss heaths. The **Muscidae** are among the important spore dispersers for the moss family **Splachnaceae**. Others occur in ***Racomitrium*** heaths. The **Scathophagidae** and **Calliphoridae** also sometimes live in ***Racomitrium*** heaths.

Hence, ***Racomitrium***, with its often large hummocks, serves as a home for some members in many of the **Nematocera** families. This habitat is well insulated and capable of maintaining moisture for a longer time than most other terrestrial habitats.

Acknowledgments

Thank you to Yume Imada for sharing his research and images of the **Spaniidae**. Thank you to for alerting me to the mine flies (***Ceratolauxania atrimana***) that live on liverworts and sharing her research and images with me. Likewise, I appreciate Juan Carlos Villarreal for sharing his research on **Anthocerotophyta** and the flies that live in them, providing me with images for this chapter.

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CHAPTER 13
FISH

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CHAPTER 13
FISH

Figure 1. Rainbow trout (***Oncorhynchus mykiss***), a fish that spits out mosses. Photo by Eric Engbretson, through Creative Commons.

Fish Uses of Bryophytes

At the onset, I wasn't sure I could make a chapter on the relationship between bryophytes and fish. I was sure I had read a long time ago that the aquatic moss ***Fontinalis*** (Figure 3) was found in the gut of a fish, but I couldn't locate the information again. So we tried our own experiments. We placed ***Fontinalis*** in a tank with rainbow trout (***Oncorhynchus mykiss***; Figure 1, Figure 2). The moss was colonized by aquatic insects, so we considered it a suitable source of food. But these starved rainbow trout ignored it. Finally, in desperation, the grad student doing this experiment tried to force feed the fish. Most of the time, even these "strike-at-anything" fish spit the moss back out. Finally the student managed to get the moss into the mouth and swallowed by force feeding. But the moss passed through the digestive tract undigested (Figure 47). It didn't look good for my hypothesis that fish might serve as upstream dispersal agents for stream bryophytes.

The rainbow trout is native to tributaries of the Pacific Ocean in North America and Asia. The juveniles hang out near the bottom whereas the adults occur more in open water. Although the fish may behave as an **anadromous** fish (living in the ocean and migrating up freshwater streams to spawn), this seems to be mostly an opportunistic behavior, with many populations never venturing to the ocean. They are known to seek areas of streams that have overhanging vegetation and to subsist on a diverse diet that includes aquatic insects (NRCS 2000). Given these criteria, it would seem that they could take advantage of the bryophytes, especially dangling ones such as ***Fontinalis*** species, for cover, especially for young fish. And aquatic mosses provide a rich habitat of aquatic insects and other invertebrates that could serve as food. So we must ask ourselves if there really is little connection between fish and bryophytes, or is it simply a neglected area of study. In this chapter we will examine the relationships that have been reported in the hope that they will stimulate further research into natural habitats and the role of the bryophytes in the lives of fish.

As you will soon read, my original contention that at least some fish, in some circumstances, eat bryophytes, is true. But bryophytes provide other roles, probably more important to the fish than their role as a food source. Based

on the meager evidence I could locate, some fish use bryophytes for cover (especially small fish), spawning, and sources of invertebrates. Some even eat bryophytes.

Figure 2. Rainbow trout (***Oncorhynchus mykiss***), a commonly cultivated fish used for release to stock streams and lakes. These cultivated fish refused ***Fontinalis***, even when it had insects living on it. Photo by Janice Glime.

Habitat

One might expect that small fish like **minnows** would seek refuge or cover among large mosses like ***Fontinalis*** spp. But finding documentation about it is a challenge. Jones (1951) listed three small fish that used ***Fontinalis antipyretica*** (Figure 3) on bedrock as their habitat in a Welsh river: ***Phoxinus phoxinus*** (minnow; Figure 4), ***Gasterosteus aculeatus*** (three-spined stickleback, Figure 5), ***Barbatula barbatula*** (=***Nemacheilus barbatula***) (loach; Figure 6). He determined that fish mostly under 20 mm length preferred beds of moss and waterweed. Nevertheless, there was no evidence they ever ate the moss. Since fish like ***Phoxinus phoxinus*** may grow to 8-10 cm (Wikipedia 2012), it means that the mosses serve as a nursery – a place for the young fingerlings to hide from hungry predators.

Figure 3. ***Fontinalis antipyretica*** at the edge of a stream where it can provide cover for small fish. Photo by Andrew Spink at <http://www.andrewspink.nl/mosses/>, with permission.

Figure 4. ***Phoxinus phoxinus*** (minnows), fish small enough to hide among large mosses. Photo by Carlo Morelli, through Wikimedia Commons.

Figure 5. ***Gasterosteus aculeatus*** (three-spined stickleback). Photo by D. Ross Robinson, through EOL.com.

Figure 6. ***Barbatula barbatula***. Photo by Michal Maňas, through Wikimedia Commons.

In his study of mayfly life histories, Macan (1978) noted that ***Cottus gobio*** (bullhead) and ***Barbatula barbatula*** (stone loach) were taken in the moss samples. These mosses were colonies of ***Cinclidotus fontinaloides*** on permanently submerged rocks.

Spawning

Mills (1981) found that the roach (***Rutilus rutilus***; Figure 7) spawned in thick beds of ***Fontinalis antipyretica*** (Figure 3), placing their eggs throughout the fronds, but concentrating them away from the base of the moss and near the water surface, especially on those parts of the site that had relatively fast currents adjacent to the moss. This positioning afforded the eggs greater security against desiccation because the ends of the moss fronds could move up and down as the water level rose and fell.

Figure 7. **Roach** (***Rutilus rutilus***), a fish that is known to use the brook moss (***Fontinalis***) for spawning. Photo by T. Voekler, through Wikimedia Commons.

The roach spends larval steps 3-5 in water with macrophytes or woody debris, then moves out of the plant areas when it becomes older and larger (Copp 1990). Copp suggested that the young fish could perceive environmental change, as evidenced by their shift in habitat.

The pike-perch, ***Sander lucioperca*** (=*Stizostedion lucioperca*; Figure 8), so-named for its pointed nose, also will select mosses for nesting and spawning, in one case selecting the green parts of moss overgrown by bilberry, or moss and roots (Bastl 1969). Bastl recommended that such substrata can be used to improve spawning possibilities for this fish. These fish did not use the plastic strips provided as a substitute, so the moss must embody some beneficial property.

Figure 8. Pike-perch (***Sander lucioperca***). Photo by Piet Spaans, through Wikimedia Commons.

The spawning behavior of the pike-perch in natural habitats is poorly known (Lappalainen *et al*. 2003). One reason for this is the selection by the fish of murky habitats with 1-3 m depth, making them difficult to observe (Lappalainen *et al*. 2003; Zander 2010). Pike-perch typically inhabit deep, calm water of canals, lakes, reservoirs, and rivers (Luna & Bailly 2010). Their habit of feeding on other fish makes them a predator to hide from. The temperature of their habitat changes seasonally, forcing them to move to a different habitat. In autumn they prefer large pebbles in 1.2-1.8 m water, but as the temperature drops to 5ºC, they move to pits and trenches to spend the winter. In spring, a temperature of 2.8ºC signals the time to move upstream, where they spawn over large pebbles at 11ºC. Their pale yellow eggs attach to emergent vegetation or stones or gravel. The parents then drift downstream to pools, with many of the females dying after spawning.

The pike-perch can be a competitor of the roach, at least in lake habitats (Brabrand & Gaafeng 1993). Its presence can cause the roach to move from the open water to the littoral zone where vegetation is present. In this case, mosses such as ***Fontinalis*** could provide cover to protect the juveniles from predation by larger fish. But the littoral zone is not without its dangers. Perch (***Perca fluviatilis***; Figure 9) can eat the young fish and compete with them. However, in some situations there are sufficient Chironomidae (midge; Figure 10) larvae to feed the perch, and the perch don't bother the roaches (Persson 1987). One could suppose that if mosses are present, then Chironomidae are present (Glime 1994), and the mosses would provide a food source as well as protection. In this case, providing food for the predator of the roach is a bonus.

Figure 9. ***Perca fluviatilis***, a predator that drives fish to hide among dangling vegetation. Photo from Wikimedia Commons.

Figure 10. **Chironomidae**, illustrating their potential abundance. Photo by Simon Carmichael, through Creative Commons.

The things that show up when one does a Google search can be rather amusing, but sometimes one gets some real gems. More often, one must make some educated guesses and dig deeper. Such was the case in trying to find fish that use bryophytes for spawning. It seems logical that fish that use "vegetation" for spawning in mountain or rapid streams are likely to use mosses like ***Fontinalis*** species as an egg repository. But rarely is the "vegetation" identified further.

Wright, as early as 1901, recognized at least minimal vegetation differences when describing the spawning behavior of the "**stickleback**" (**Gasterosteidae**) in some detail. He noted that not all sticklebacks were the same and that their nest construction behavior differed. One variety (species?) makes a nest "like a muff among waterweeds." Another little fish collects straw, bits of grass, and moss with his mouth. He tucks these into the gravel and sand and presses them into place with his body. He then glues these with glue exuded from his own skin. This forms a floor, and he builds a small hut of woven fibers and moss. There is a small door at the top of the hut. The fish ultimately tests the strength of this hut by stirring up the nearby water with its tail.

The only other information I have found on nests of sticklebacks is 110 years later on a website (Coarse Fish 2011). In this case, the **nine-spined stickleback** (***Pungitius pungitius***; Figure 11), a circum-Arctic and widespread northern hemisphere fish of quiet water in streams, ponds, and lakes, uses "**willow moss**," a common name sometimes used for ***Fontinalis antipyretica***. The male ***P. pungitius*** builds the nest and cares for the young. The nest is near the bottom, typically built into the "vegetation." This is a tubular nest about 4 cm long and is made from threadlike algae and **willow moss**.

Figure 11. **Nine-spined stickleback** (***Pungitius pungitius***), a fish that occasionally builds its nest among ***Fontinalis antipyretica***. Photo through Creative Commons.

Nancy Auer (pers. comm. 20 Nov 2011), a larval fish expert, explains the scarcity of fish eggs among mosses. "Most moss is not that 'open' so adult fish may not use it and even larvae since most are in the water column."

Aquarium Fish

Aquarium fish keepers have discovered the advantages of adding aquatic mosses such as Java moss (which includes a variety of species, but is mostly ***Taxiphyllum barbieri***; Figure 12) for both decoration and spawning media (Benl 1958; Takaki *et al*. 1982). Axelrod and Vorderwinkler (1983) found that ***Fontinalis antipyretica*** var. ***gracilis*** (Figure 13) provided the best spawning grounds for certain tropical fish. The mosses also serve to provide hiding places for smaller fish being chased by larger ones or those fish that just prefer to hide during daylight hours.

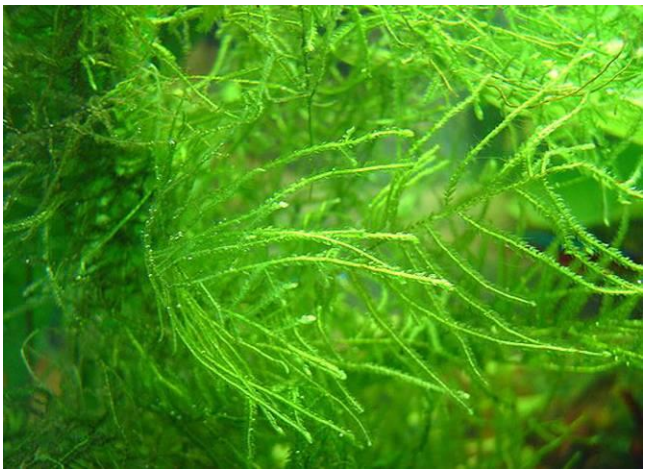

Figure 12. Java moss (***Taxiphyllum barbieri***). Photo by Buchling, through Creative Commons.

Figure 13. ***Fontinalis antipyretica*** var. ***gracilis***. Photo by Des Callaghan, with permission.

Bohlen (1999) used mosses in 40-liter aquaria to rear the spined loach (***Cobitis taenia***; Figure 14), a common freshwater fish of oxygen-rich water from Europe and Asia (Robotmam 1977). The fish laid their eggs in the most dense moss vegetation available (Bohlen 1999). The eggs lacked adhesion and easily fell through the gauze beneath the moss. Eggs numbering 2905-4282 were laid over a period of 101-120 days and were successfully reared using this method.

One website [Breeding my pencil fish (***Nannostomus beckfordi***; see Figure 15) 2007] provides a video of the golden pencil fish (***Nannostomus beckfordi***) breeding among the Java moss fronds in an aquarium. The pencil fish, widespread in its native South America (Wikipedia: Pencil fish), with a wide distribution in the lower Rio Negro and middle Amazonas river (AquaWorld: *Nannostomus beckfordi* 2011). It prefers slightly acidic water (pH 6.0-7.5), which is likewise suitable for many aquatic bryophytes. Java moss is especially good for scatter

breeders, serving like a safety net to catch the eggs. The moss needs to be kept clean to remain healthy, but this cleaning may be detrimental to the eggs that are housed there, as they, too, may be removed.

Figure 14. Spined loach (***Cobitis taenia***). Photo by J. C. Harf, through Wikimedia Commons.

Figure 15. ***Nannostomus beckfordi***, a genus in which some members deposit eggs among mosses. Photo by Jan Ševčík, through EOL Commons.

The website Aquamoss extols the benefits of **Java moss** for rearing **killifish** (Figure 16-Figure 17), **barbs** (Figure 18), and **characins** (Figure 19). Not only does the moss provide cover, but it helps to keep the aquarium clean by absorbing the nitrogen waste. Eggs among the mosses are protected from predation, and the moss provides a substrate for bacteria, detritus, and other food sources. The author of the site also claims that the young fry grow better when Java moss is in the tank.

Figure 16. One of many kinds of killifish, ***Nothobranchius rachovii*** (**bluefin notho**). Photo by Andreas Wretström, through Wikimedia Commons.

Figure 17. ***Heterandria formosa***, the **least killifish**. Photo by Brian Gratwicke, through Creative Commons.

Figure 18. Tinfoil barbs (**Cyprinidae**). Photo from Wikimedia Commons.

Figure 19. Red phantom tetra, ***Megalamphodus sweglesi*** (Characidae). Photo from Wikimedia Commons.

A native southeastern USA fish, ***Elassoma evergladei*** (Figure 20), the **pygmy sunfish**, is a very skittish fish when it has no cover. In an aquarium, **Java moss** serves well to provide cover for this small fish. In the wild, it seeks shelter among the vegetation and prefers to lay its eggs on *Ceratophyllum demersum*. The cover helps to protect the males against the aggressive behavior of othe territorial (especially larger) males.

Java moss (***Taxiphyllum barbieri***; Figure 12) may be the best of the mosses for removing nitrogen in multiple forms (Alghamdi 2003), withstanding the wide chemical range of aquarium water, and doing well at warm temperatures, but other mosses have also been used successfully. Takaki *et al*. (1982) report the use of the mosses ***Amblystegium*** (***Leptodictyum riparium***; Figure 21), ***Fontinalis*** spp. (Figure 13), ***Platyhypnidium riparioides*** (Figure 22), ***Rhacopilum***, ***Taxiphyllum*** spp.

(Figure 12), ***Vesicularia*** (Figure 23), and the liverworts ***Riccia fluitans*** (Figure 24), ***Ricciocarpos natans*** (Figure 25), and ***Chiloscyphus*** (Figure 26). I have been successful in using ***Bryum pseudotriquetrum*** (Figure 27) in an aquarium with alkaline water. Beware of dealers selling a club moss as an aquarium plant. It is neither a moss nor an aquatic species. It is a tracheophyte (*Lycopodium obscurum*) that will retain its green color for several months under water. For more information on use of mosses for aquaria, see Chapter 4 (Aquaria) of Volume 5, Uses.

Figure 20. ***Elassoma evergladei*** (**pygmy sunfish**) with a species of "**Java**" **moss**. Photo by Brian Gratwicke, through Creative Commons.

Figure 21. ***Leptodictyum riparium***, a suitable aquarium moss. Photo by Tan Sze Wei, Aquamoss website <www.aquamoss.net>, with permission.

Figure 22. ***Platyhypnidium riparioides***, a suitable moss for an aquarium. Photo by Des Callaghan, with permission.

Figure 23. ***Vesicularia montagnei***, Christmas Moss, in an aquarium. Photo by Tan Sze Wei, Aquamoss website <www.aquamoss.net>, with permission.

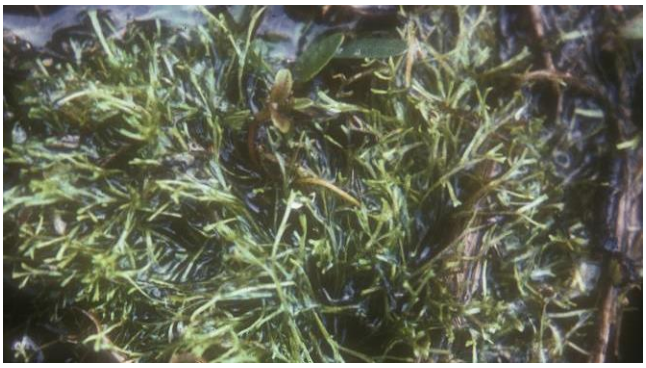

Figure 24. ***Riccia fluitans*** can be grown floating or in balls at the bottom of the aquarium in medium soft to hard water, *p*H 6-8, 15-30ºC (Aquatic Community). Photo by Janice Glime.

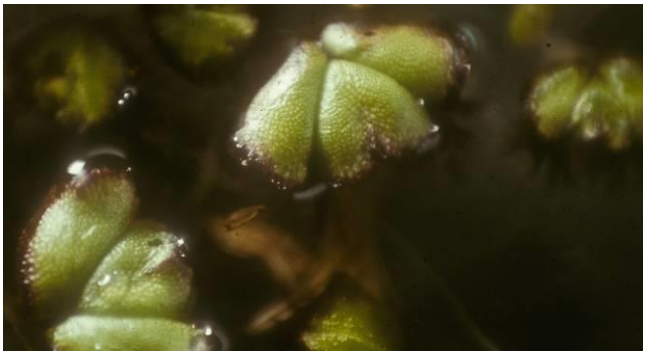

Figure 25. ***Ricciocarpos natans***, a floating thallose liverwort sometimes used in aquaria. Photo by Janice Glime.

Figure 26. ***Chiloscyphus polyanthos***, a leafy liverwort suitable for an aquarium. Photo by Jan-Peter Frahm, with permission.

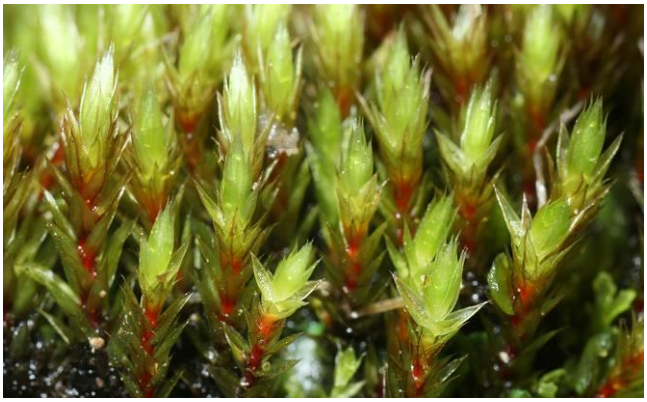

Figure 27. ***Bryum pseudotriquetrum*** (Marsh Bryum) grows in marshes and in shallow water at lake and stream edges. It can make an interesting small forest on the bottom of an aquarium. Photo by Barry Stewart, with permission.

Food

Bowden *et al*. (1999) pointed out that the roles of bryophytes in streams remain largely unexplored. Their role as a food source is one of these relatively unexplored areas. Specifically, they stated that it is "not clear whether fish benefit from an increase in abundance of insects often observed when bryophytes are present in a stream."

Cheney mentioned in 1895 that bryophytes serve as a food source for fish. Richards (1946) reported on the introduction of ***Fontinalis antipyretica*** into streams in South Africa in an effort to increase invertebrate populations that serve as fish food. Unfortunately, the insects in those streams were adapted to smooth rocks and bottom sediments and did not fare well on the rough structure of the mosses. Hence, their substrate was diminished and their numbers decreased. I know of no follow-up studies to see if this changed, with better adapted species arriving to fill the void.

Bryophytes can serve as a food source in two ways. The most obvious, but rarely used, is as a direct food source – eating the bryophyte. The other is that the bryophytes house numerous insects and other arthropods that serve as food. ***Fontinalis*** serves as a source of abundant food organisms, particularly chironomid larvae (Figure 10), for fish in the same stream (Mills 1981). Macan and Worthington (1974), in their book "Life in Lakes and Rivers," consider the mosses and liverworts that occur in thick mats to "profoundly influence fauna by providing a foothold for animals which otherwise could be swept away by curent."

Brusven *et al*. (1990) examined the importance of stream bryophytes as providers of drifting stream invertebrates that serve as potential fish food. They compared the density, biomass, and drift in various areas of the South Fork Salmon River, Idaho, USA, including areas with and without moss cover of ***Fontinalis neomexicana***. Insect densities were 4-18 times as great in moss clumps compared to moss-free areas. Simply being near the moss in mossy areas did not significantly increase invertebrate density compared to areas with no moss. And Brusven *et al*. were unable to determine any advantage to fish feeding in the daytime. It seems that despite the greater number of invertebrates living among the mosses, the daytime drift in that area was no greater than in the moss-free areas. That does not mean that there would be no differences at night when the greatest drifting occurs. If one assumes that daytime feeders only strike at drifting invertebrates, the mosses may not provide them with a feeding advantage until these invertebrates emerge as adults that fly above the stream within striking distance.

Muotka and Laasonen (2002) made it clear that retention of mosses was an important part of stream restoration in the channellized streams used for hauling out forest harvest, citing that when the mosses were dislodged they were replaced by periphytic algae and that only periphyton feeders increased when streams were restored by the addition of leaf litter that caused further loss of bryophytes.

Nurminen *et al*. (2003) explored the relationships of the rudd (***Scardinius erythrophthalmus***; Figure 28-Figure 29) and found that bryophytes were included among other aquatic macrophytes in their diet. In the period of 15 May to 15 June, bryophytes were more than half the diet by weight (26.2 g per g ww fish) for 6-year-old fish, but less for other ages and time periods. The **omnivorous** (eats plants and animals) common rudd is widely distributed in South America, Europe, and middle Asia (Common Rudd 2010). It prefers clean water of lakes, ponds, large rivers, small streams, and even thermal springs, with lots of plant cover, where they can feed on the plants at warmer temperatures (above 18ºC). Early stage larvae start their diet on small algae, then shift to cladocerans and copepods, before including the broad range of immature insects and vegetation that characterize the adult diet.

Figure 28. The rudd (***Scardinius erythrophthalmus***), a fish that actually eats bryophytes. Photo from Wikimedia Commons.

Figure 29. Juveniles of the rudd (***Scardinius erythrophthalmus***). Photo by Piet Spaans, through Wikimedia Commons.

Hypostomus margaritifer (Loricariidae), a relative of the common aquarium plecostomus (Figure 30), in the Upper Paraná River, Brazil, uses bryophytes and red algae as its primary food (Delariva & Agostinho 2001).

Figure 30. ***Hypostomus plecostomus***, a common aquarium fish that feeds on attached algae. Photo from Wikimedia Commons.

At least one observation provides definite proof that some fish eat bryophytes. On the Aquamoss website, we are warned not to put the Siamese algae eater, ***Crossocheilus siamensis*** (Figure 31), in a tank with Taiwan moss (***Taxiphyllum alternans***; Figure 32) because the fish will devour it – quickly! (Figure 32) .

Figure 31. Siamese algae eaters (***Crossocheilus siamensis***) nibbling on Taiwan moss (***Taxiphyllum alternans***). Photo from Tan Sze Wei, Aquamoss website <http://www.aquamoss.net/Articles/Siamese-Algae-Eater-And-Aquatic-Moss.htm>, with permission.

Jones (1951) discovered that plant material (including algae) was only discernible in the first part of the gut, being digested and amorphous by the more distal portions. In that portion, only impervious parts like chitinous arthropod exoskeletons could be identified. He expressed concern that studies that did not recognize this would give misleading proportions of the food choices.

Frost (1942) recognized the importance of bryophytes in providing a habitat for food organisms of fish. She had already demonstrated that these organisms were important in the diet of **brown trout** (***Salmo trutta***; Figure 33) at both Ballysmuttan and Straffan in Ireland (Frost 1939). Young salmon have feeding habits similar to those of trout and similarly consumed a large portion of their food from moss dwellers (Frost & Went 1940). And many of the smaller minnows "cropped" the moss fauna (Frost 1942). Not only do the mosses provide shelter for the immature stages of these food organisms, thus providing food at that stage, but it is likely that some of the consumed aerial adult forms spent their younger aquatic days among the mosses.

Figure 32. Taiwan moss (***Taxiphyllum alternans***). **Upper:** Before the introduction of the Siamese algae eater (***Crossocheilus siamensis***) into the tank. **Lower:** One day after the introduction of the Siamese algae eater. Photos from Tan Sze Wei, Aquamoss website <http://www.aquamoss.net/Articles/Siamese-Algae-Eater-And-Aquatic-Moss.htm>, with permission.

Figure 33. **Brown trout** (***Salmo trutta***) on a stream bed. Photo through Wikimedia Commons.

We know that the roach (***Rutilus rutilus***; Figure 34), a common fish in lakes and lowland rivers, spawns in mosses (Mills 1981). From that we can easily deduce that at least some individuals live in places where mosses occur. Roaches consume aquatic insect larvae and molluscs as they grow (Mann 1973), but switch to mostly plant material and algae as they get larger (Hellawell 1972; Mann 1973). It is a natural extension in logic then, to infer that organisms that live among the mosses are potential food organisms, whether it is while they are in the mosses, or only when they venture forth into the open water. So far there seems to be no documentation that the plant material includes mosses, but certainly some of the moss inhabitants must be eaten.

Figure 34. Roach, ***Rutilus rutilus***. Photo by Andreas Hartl, through Creative Commons.

Sayre (1936) reports a case in which rainbow trout (***Onchorhynchos mykiss***, formerly *Salmo gairdneri*; Figure 1) actually eats mosses (not ***Fontinalis***, apparently). When insects become scarce in streams in autumn, mosses can become part of the diet. A few strands of ***Scleropodium obtusifolium*** were found in the gut of one of these normally carnivorous individuals in a stream on the western slope of Colorado, USA. Sayre considered that they switched to algae and mosses because other food sources were scarce. It is possible, however, that such invertebrates as Chironomidae were still abundant among the moss leaves. She reported that the moss had lost some color but had not been digested, adding further support to the suggestion that it was only housing the real food.

As one might expect, mosses provide camouflage and cover for potential fish-food organisms. A particularly interesting case is that of the dragonfly ***Leucorrhinia dubia*** (Odonata) (Henrikson 1993). The naiads of this insect are able to change color to match the brown and green of local ***Sphagnum*** (Figure 35). They are significantly more abundant among ***Sphagnum*** and show a preference for this substrate in lab tests. Where lakes have large ***Sphagnum*** mats, this dragonfly is able to co-exist with fish.

Fish serve as human food, and in Alaska the mosses played an important but misunderstood role in their preservation. The Alaskan natives stored their fish and whale blubber in holes and packed them into holes lined with wood, skins, or leaves and covered them with mosses or leaves (Segal 1992). These were left to ferment for 1-2 months. With the introduction of modern technology, many switched to using plastic bags instead of the natural products. The result was that often the anaerobic conditions of the bags fostered the growth of ***Clostridium botulinum***, resulting in an increase of botulism from 1.2 cases per 100,000 population before 1966 to 15.2 cases per 100,000 by 1992.

Figure 35. ***Sphagnum cuspidatum***, showing brown and green colors that are matched by the naiad of the dragonfly ***Leucorrhinia dubia***. Photo by Michael Lüth, with permission.

Piscicidal Properties

One reason for the refusal of fish to eat bryophytes may be the chemical properties of the mosses. Asakawa *et al.* (1985) found a diterpenedial in the liverwort ***Lobatoriccardia yakishimensis*** that is potent in killing fish! We know that many bryophytes have secondary compounds that discourage herbivory and it is likely that there are many more than this one that discourage fish from eating the bryophytes. The strongest of these **piscicides** seem to be the (-)-polygodial from the ***Porella vernicosa*** complex (Figure 36) and sacculatal from ***Trichocoleopsis sacculata*** (Figure 37) and ***Pellia endiviifolia*** (Figure 38), ***Pallavicinia levieri*** (Figure 39), and ***Lobatoriccardia yakushimensis***, all liverworts (Asakawa 2007). These two compounds have a hot taste and can kill **killifish** (***Oryzia latipes***; Figure 40) within 2 hours at a concentration of only 0.4 ppm. Sacculatal and 1β-hydroxysacculatal are lethal to the **killifish** within only 20 minutes at 1 ppm. On the other hand, isopolygodial and isosacculatal from the same liverworts seem to be harmless at concentrations of 10,000 ppm.

Figure 36. ***Porella vernicosa***, member of a liverwort complex that produces the piscicide polygodial. Photo by Masanobu Higuchi, with permission.

Figure 37. ***Trichocoleopsis sacculata***, a leafy liverwort that produces the piscicide sacculatal. Photo by Rui-Liang Zhu, with permission.

Figure 38. ***Pellia endiviifolia*** with young capsules. Photo by Michael Lüth, with permission.

Figure 39. ***Pallavicinia levieri***, a thallose liverwort that produces sacculatal, a piscicide. Photo by Rui-Liang Zhu, with permission.

Figure 40. ***Oryzia latipes***. Photo through Wikimedia Commons.

Among the bryophytes, liverworts have received the most attention regarding piscicidal and other antibiotic activities. This is because liverwort cells have oil bodies that store lipophilic terpenoids and aromatic compounds that serve these purposes (Asakawa 2001).

Cover

The most important role of bryophytes, from a fish perspective, may be that of cover. ***Fontinalis*** (Figure 41) species, with their long, dangling branches, is especially good at providing cover and rarely is out of water during breeding season.

Figure 41. ***Fontinalis antipyretica*** forming a dense mat of streamers that can provide cover for eggs and young fish. Photo by Michael Lüth, with permission.

But not all bryophytes are advantageous as cover. In Norway, Heggenes and Salteit (2002) found that juveniles and adults of Atlantic salmon (***Salmo salar***; Figure 42) were less dense in areas where liverworts grew than where that bryophyte had been removed. They suggested that increases in liverwort density actually had a negative effect on the Atlantic salmon. Removal of the brook moss ***Fontinalis*** (Figure 41) had no significant effect on density of salmon. Brown trout (***Salmo trutta***; Figure 43-Figure 44), on the other hand, had higher densities in association with the ***Fontinalis***.

Figure 42. Atlantic salmon (***Salmo salar***). Photo by William Hartley, USFWS, through public domain.

The Atlantic salmon (***Salmo salar***) is one of those anadromous fish that migrate upstream to spawn, then the young fish return to salt water until breeding time (Atlantic Salmon 2010). Once independent of the yolk sack, the

juveniles begin eating tiny invertebrates, but as they become larger they eat small fish. Aquatic insects are a common food, and bryophytes can serve as either direct sources of the insects, or cover for these insects when they are not in open water. In any case, bryophytes generally increase numbers of insects in streams (see later chapter on aquatic insects).

The brown trout (***Salmo trutta***; Figure 43-Figure 44) likewise migrate upstream to spawn, but in this case they are migrating from lakes (Brown trout 2010). While in the streams or rivers, they are major predators on macroinvertebrates – shrimp, corixids, caddisflies, stoneflies, and mayflies. Cover is important protection from predators for them and they seek out submerged rocks, undercut banks, and overhanging vegetation, which could include mosses.

Figure 43. Brown trout (***Salmo trutta***), a fish that benefits in density from the presence of ***Fontinalis***. Photo by Jason Neuswanger at Troutnut.com, with permission.

Figure 44. Brown trout (***Salmo trutta***) jumping. Photos by Jason Neuswanger at Troutnut.com, with permission.

Douglas Burns (2008) tells about his friend who finds successful fishing for bass at strip mine ponds covered with moss. The only problem seems to be finding open water in which to work the lure. The advantage to those fishing is that these ponds are very productive and rarely have other persons fishing.

In Volume 5 on Uses, Chapter 4 (Aquaria), I have discussed the use of bryophytes in aquaria. For example, Tan (2003) reported that the Java moss (mostly ***Taxiphyllum barbieri***; Figure 12, Figure 31, Figure 32) is used by fish hobbyists around the world to decorate aquaria and provide cover.

Diversity

With the cover provided by bryophytes, one would assume there would be some correlation between fish communities and bryophyte cover. However, when Paavola (2003) tested this in an Arctic stream, there seemed to be little protective relationship. Rather, fish communities seemed to relate to oxygen levels, depth, and stream size, whereas bryophytes were more related to nutrient levels and in-stream complexity. Species richness did seem to correlate somewhat.

It appears that mosses might be able to help some fish survive drought conditions. McPhail (1999) experimented with the black mudfish (***Neochanna diversus***; Figure 45 - Figure 46) from New Zealand to determine how it might survive both hypoxia and drought. This fish is able to breathe air by rising to the surface and gulping an air bubble that it holds in the buccal cavity while still using its gills to get oxygen to its blood. In McPhail's study, when the water around it dropped to less than 2.5 mg L^{-1}, the fish all gulped air from the surface. At temperatures around 20-22ºC, the animals stayed alive on damp mosses for 10 weeks. They lost weight steadily, but all adults recovered upon re-immersion. Two young-of-the-year fish died. The black mudfish is on the IUCN Red List of Threatened Species and was thought to be extinct, but in a 2004 survey in New Zealand, a healthy population was found (World Conservation Monitoring Centre 1996). McPhail (1999) suggested that as a management strategy, mosses could be provided in restoration to help fish survive periods of drought.

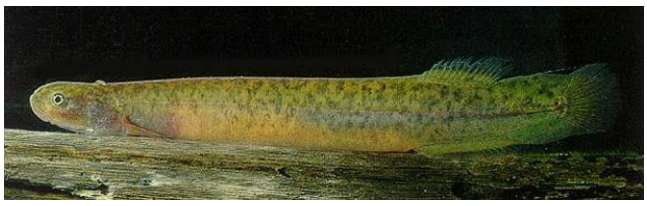

Figure 45. Brown mudfish, ***Neochanna diversus***. Photo by R. M. McDowell (NIWA), with permission.

Figure 46. Brown mudfish, ***Neochanna diversus***, showing its small size. Photo by Vince Kerr, permission pending.

Heino *et al*. (2005) and Paavola *et al*. (2003) found that bryophytes were not a good surrogate for fish diversity. Rather, species richness of this group seems to more related to geographic location, stream size, water color, and acidity. Hence, bryophytes are apparently not useful in predicting fish diversity. Paavola *et al*. (2006) further clarified this poor relationship by examining 101 boreal streams for concordance among fish, macroinvertebrates, and bryophytes. They found that spatial extent of the study was a critical factor in predictability (*i.e.* concordance) and that single river systems provided poor concordance.

Biodiversity of bryophytes can be threatened by fish-harvesting activities (Russell 2006). In the southernmost province of Chile, bryophytes are threatened by fish farming, among other things human activities.

Nutrient Relations

But are the bryophytes really a source of nutrition for the fish?

Sayre (1936) and Bland (1971) state that in Colorado streams rainbow trout will eat mosses when insects become scarce, but when we tried to feed ***Fontinalis*** to starved laboratory-reared rainbow trout (***Onchorhynchos mykiss***, formerly *Salmo gairdneri*), we were successful only occasionally when our graduate student forced the moss into their mouths (Paulson 1980). In the few cases where he was successful in force-feeding them, they later passed a small, cylindrical package of ***Fontinalis*** (Figure 47), essentially in tact, at the other end of the digestive tract! If they eat it in nature, it may be to get the insects that invariably live among the leaves.

Figure 47. Package of feces from rainbow trout (***Oncorhynchus mykiss***) containing undigested ***Fontinalis*** that had been force-fed. Photo by Janice Glime.

There does not seem to be any evidence that fish get nutrients from the bryophytes themselves. On the other hand, bryophytes may get nutrients from the fish! Peterson and Matthews (2009) found that the annual migration of salmon back to their streams can carry nutrients from the ocean to the streams. Using changes in ^{15}N, they measured C:N and C:P ratios in the bryophytes, among other things. When they compared channels with and without decomposing salmon, the bryophytes had lower C:N and C:P ratios in channels with salmon decomposing than in those without. This ratio is the result of higher N and P content, *i.e.*, more nutrients were stored in bryophytes of streams where the salmon returned during migration. Thus, bryophytes contribute to the capture of salmon-derived nutrients in the streams.

Movement of nutrients upstream in fish and ultimate arrival in bryophytes might be predictable, but finding ocean nutrients in **riparian** (banks of a natural water course) bryophytes is a bit of a surprise. Ben-David *et al*. (1998) found salmon-derived nutrients along forest trails near streams. Wilkinson *et al*. (2005) suggested that these nutrients are important contributions to the nutrient input of non-vascular plants. Bryophytes such as ***Hylocomium splendens*** absorb up to 90% of the dissolved nutrients. Through this pathway, the bryophytes retain nutrients that may later be released to the tracheophytes.

*p*H and *Sphagnum*

All is not well in ***Sphagnum*** land as far as fish are concerned. Dunson and Martin (1973) looked at the effects of this moss on downstream communities of fish. They examined the effects of *p*H on the fish through transplant experiments and distribution data. Brook trout (***Salvelinus fontinalis***; Figure 48 - Figure 49) of various ages were transplanted upstream, near the bog, where the *p*H was lower. The two adult trout both died within seven days in the zone closest to the bog (*p*H down to 3.7). For smaller fish (5 cm), half were dead in 4.5 days and all of them after 10 days, while the *p*H generally remained above 4.4. In a second experiment, the *p*H generally remained below 4.4 and all 50 fish (5 cm) died within 6.3 days. Although other factors could account for the deaths (differences in flow rate, stress from transplantation, confinement), these data suggest that low *p*H resulting from ***Sphagnum*** could be detrimental to some fish populations.

Figure 48. Brook trout, ***Salvelinus fontinalis***, a fish sensitive to low *p*H. Photo by Derek Ramsey, through Wikimedia Commons.

Figure 49. Brook trout (***Salvelinus fontinalis***). Photo through public domain at EPA website.

Hinder *et al.* (1996) found that liming improved the quality of water downstream from peatlands by raising the *p*H. Brown trout (***Salmo trutta***; Figure 43-Figure 44) survived even after the *p*H dropped back down to 5.2-5.3.

Table 1. Presence (+) of four fish species at increasing distances and *p*H downstream from Bear Meadows Bog in Pennsylvania, USA. Data from Dunson & Martin 1973.

	1	2	3	4	5	6	7	tributary
Brook trout (*Salvelinus fontinalis*)				+	+	+	+	+
White sucker (*Catostomus commersoni*)					+	+	+	+
Creek chub (*Semotilus atromaculatus*)						+	+	+
Blacknose dace (*Rhinichthys atratulus*)						+	+	+
Lowest *p*H	3.7	3.7	-	4.0	4.2	4.2	5.1	5.3

Pollution

Mosses are known for their ability to absorb and concentrate heavy metals. Huckabee and Blaylock (1972) demnstrated this mercury. Caines *et al*. (1985) demonstrated that both mosses and liverworts could decrease the metal concentrations in associated water, but that as the H^+ ion concentration increased in the water, the ability of mosses to bind the metal ions decreased. This is consistent with experiments done with ***Sphagnum***; flooding that moss with H^+ ions is one way to remove its attached cations. In the Scottish streams, Caines *et al*. found that the metal ions in the mosses remained there as long as the *p*H remained above 5.5. But if the stream *p*H drops below that level due to acid rain or drainage from peatlands, it can cause sufficient release of heavy metals to be lethal to fish.

Concentration of the heavy metals by macro-invertebrates can be even higher than that in bryophytes, depending on their position in the food web (Culioli *et al*. 2009). But fish, despite depending on smaller organisms for food, retained the smallest concentrations of arsenic, even lower than that in water. Mersch *et al*. (1993) likewise found that the aquatic moss ***Fontinalis antipyretica*** had much higher concentrations of heavy metals than did fish. In fact, for fish the concentration depended on the tissue, with copper accumulating in the liver and lead in the kidney. Mouvet *et al*. (1993) reported four different instances in which fish were killed but mosses survived, supporting the notion of using mosses as biomonitors of stream health.

If mosses live and fish die, the mosses need to give some sort of early warning. One such warning is loss of green color. Other symptoms include the discoloration of the terminal bud. And for those willing to do the testing, measuring accumulation of suspected toxins in the moss can indicate the degree of accumulated pollution.

Lithner *et al*. (1995) compared the ability of invertebrates, fish (***Perca fluviatilis***, ***Esox lucius***), and ***Fontinalis antipyretica*** at a location in Sweden to sequester and concentrate heavy metals as a function of *p*H. The found that when the *p*H decreased, so did the bioconcentration factor for Zn, Cd, Ni, Co in bryophytes, but the concentrations of Pb and Cu increased in fish with decreasing *p*H. This emphasizes the fact that bryophytes and other organisms may not be surrogate indicators for the suitability of heavy metal conditions for at least some fish.

A new twist on the use of **mosses** associated with **fish** is related to the administration of antibiotics to cattle and **fish** (Pouliquen *et al*. 2009). Oxolinic acid, florfenicol, flumequine, and oxytetracycline are all used in farming both fish and cattle. These ultimately end up in "freshwater." A study in France reveals the ensuing scenario. In this case, four fish farms and a sewage plant were located on the main course of the river. The famous mossbags were used, this time in the water. All four of these antibiotics could be measured in the bryophytes and sediments, but not in the water. Both Flumequine and oxytetracycline entered the water from fish farms, animal farms, and possibly human pharmaceutical sources. Accumulations of antibiotics could, through the course of time, alter the flora and fauna of the river. If carried into drinking water, antibiotics could affect the digestive bacteria needed by humans and other animals. And the impact on native mammals that drink from the river could be a concern. Therefore, bryophytes could serve as suitable organisms for testing to determine the levels of antibiotics in the water, particularly when the events of these entering the river are intermittent. The bryophytes, as accumulators, can permit assessment over a lengthy period of time.

Global Warming

The controversial global warming may have an indirect effect on fish that is mediated by changes from planktonic algae to deep-water bryophytes (Felley 2003). Loss of organic carbon in lakes of the southern boreal foerst of Ontario, Canada, previously depleted by acid rain damage, results in clearer water. Lake levels are falling due to declines in rainfall and increased evaporation due to increased temperatures. These factors, and the greater penetration of light, have depressed the planktonic algae in favor of the deep-water (down to 50 m) **bryophytes**. The lakes are now too warm for the cold-loving **trout** that previously lived there. This signals danger for the Arctic lakes that typically remain cold far into the summer. Warming there could seriously affect the fish populations adapted for cold water.

Surrogate Species

Surrogate species are those that can be used to assess the conditions of a habitat in lieu of another species or group. Virtanen *et al*. (2009) attempted to determine the usefulness of **bryophytes** in this role, compared to two groups of insects, the **Chironomidae** (midges) and four orders of insects, **Ephemeroptera**, **Plecoptera**, **Trichoptera** and **Coleoptera**. They found that the bryophytes were not good surrogates for spring insects. On the other hand, there seemed to be relatively good agreement among bryophytes, benthic insects, and fish in boreal headwater streams across a broad scale of water drainage systems, but not at the fine scale of streams in a single drainage system. Such research suggests that bryophytes could be used to assess the likely success rate of introducing fish into streams that have lost portions of their native fauna.

Summary

Bryophytes can provide cover, food, and spawning ground for fish. Although it seems that few fish eat bryophytes, many fish food organisms live there. In those cases where the fish eat the bryophytes, it is not clear whether they gain any nutrition from them. Little fish can take cover in bryophytes. And at least some fish use bryophytes for spawning sites. One variety of stickleback builds a hut in which mosses can be a major constituent. Others simply uses the mosses as they are growing. Some liverworts, including streambank species, are known to have **piscicidal** properties, but their ability to use these in habitats where the fish occur is not known.

A number of mosses, especially Java moss (***Taxiphyllum barbieri***), are used in aquaria for cover and spawning beds. Furthermore, Java moss is able to remove the fish nitrogen waste from the water.

Some insects can only survive fish predation when they have cover among mosses, and the naiads of ***Leucorrhinia dubia*** are able to change color to blend in with the ***Sphagnum***.

Sphagnum can acidify lakes and streams, making them uninhabitable for at least some kinds of fish.

Bryophytes can benefit fish as biomonitors, providing early warning signs that the water is contaminated, including more recent contamination with antibiotics. But sometimes the ability of bryophytes to accumulate substances differs from that of the fish.

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CHAPTER 14-1
AMPHIBIANS: ANURAN ADAPTATIONS

Janice M. Glime and William J. Boelema

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CHAPTER 14-1
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Figure 1. ***Dendrobates tinctorius*** (Dyeing Poison Frog), perched on a bed of mosses. Many species in the tropics use bryophytes to maintain hydration. This species is named for the use of the poisons in its skin. Its specific name, *tinctorius*, refers to the way indigenous tribes of Amerindians of the Amazon drainage and the Guianas rub the frogs' skin or blood onto the skin of plucked parrots, toxifying the skin and causing the new feathers to develop with a variety of different colors (Métraux 1944). Photo © Henk Wallays, through Creative Commons.

Bryophytes and Amphibians Share Commonalities

In searching for information on bryophytes and their amphibian inhabitants (frogs, toads, salamanders; Figure 1), I ran into Wachman's (2010) interesting question: "In what way are the bryophyte plants and the amphibian animals alike?" Wachman points out that bryophytes have shared the planet with amphibians since the Carboniferous era. Both are transitional organisms from living entirely in water to living at least part of their life cycle on land, a shift that occurred around 360–290 mya. Wachman claims both need a moist environment (I think most bryologists would take exception to that claim, and many treefrogs likewise have found ways around that requirement, although they do use mosses and other moist places to keep their skin moist). While it is true that most amphibians must find water to reproduce, this can be the basin of a bromeliad or tree hole, and a number of them lay their eggs on mosses or other vegetation in trees or on the ground.

Bryophytes need water to maintain the viability of their male gametes (sperm) while they travel to female reproductive organs, taking advantage of rainwater or dew in most cases. Both bryophytes and most amphibians have two distinctive phases of development – bryophytes have haploid leafy gametophytes and diploid sporophytes with a capsule; amphibians have larvae (not always free-living; usually known as tadpoles in frogs and toads) and adults. (But certain salamanders are neotenic in that they stay aquatic and have gills all their lives. Newts have three life phases: larva, then eft, then aquatic adult. They are somewhat able to go back to the eft stage if the standing water disappears – their skin becomes less permeable to water.) And both bryophytes and amphibians thrive best when far from populated areas. But bryophytes seem to be well armed against disease by their secondary compounds, whereas amphibians seem very susceptible to diseases. Since bryophytes are able to grow well in some areas, becoming a major part of the flora, it is to their credit that they provide cover and moisture for the amphibians there.

But in one way, bryophytes differ greatly from amphibians. Bryophytes have tolerance to extreme cold, occupying the northernmost and southernmost locations on the planet, sometimes even surviving on glaciers, whereas amphibians have very poor cold tolerance and most cannot occupy areas with permafrost. In central Alaska, only the Wood Frog (***Lithobates sylvaticus***) and Boreal Toad (***Anaxyrus boreas boreas***) occur, surviving the winter buried in frozen mud (National Park Service 2013).

Anura – Frogs and Toads

The tailless amphibians (Figure 1) are in the order **Anura**, a word that literally means without a tail. These include the frogs and toads. Most of the more familiar temperate frogs were included in the family **Ranidae** in the genus ***Rana***. The family occurs on all continents except Antarctica. However, only the Australian Wood Frog (***Hylarana daemeli***) represents this family in Australia, where it is restricted to the far north. The family has been revised and many of the familiar species are no longer in the genus ***Rana***.

Standard English names used here are according to Crother (2008) for North American species. **Common names** are local and not at all standardized, whereas the **Standard English names** have legal standing through an official published list (Crother 2007, 2008). Scientific (Latin) names are based on Frost (2011), using classification concepts based largely on recent molecular studies. Where possible, I have tried also to provide the older, more familiar names.

Ranid frogs range in size from the Wood Frog (***Lithobates sylvaticus***, previously *Rana sylvatica*; 2.5-7 cm long; Figure 2) to the Goliath Frog (***Conraua goliath***; up to 45 cm long).

Figure 2. ***Lithobates sylvaticus*** on a bed of mosses, the smallest of the "true" frogs (Ranidae). Photo © John White, with permission.

Role of Bryophytes for Anurans

Amphibians utilize bryophytes in a variety of ways, from nesting sites to substrata for maintaining or replenishing moisture to perches for calling to winter hibernacula. One of the more amazing discoveries I have made is to pick up a moss clump in late fall and discover a torpid toad beneath it. Indeed, many herpetologists seek out mossy sites when they are on amphibian hunts, as I well remember from my undergraduate days when I had the privilege to go in the field with a well-known **herpetologist** (one who studies amphibians and reptiles). But often the use of the bryophytes is passive or difficult to perceive. The bryophytes grow in the same sorts of habitats where these amphibians can survive, but does the bryophyte really contribute?

The evidence of bryophyte-amphibian interaction is modest and experiments to demonstrate the importance of the bryophytes are all but non-existent. Most of the reports on anurans only mention bryophytes casually. For example, Bosch and Martínez-Solano (2003) describe the factors that influence the presence of montane frogs in ponds and describe their study area as having moss with underwater caves. In many of the contacts I have made with herpetologists they have commented that the area (especially in the tropics) was covered with bryophytes and that surely the frogs make use of that habitat, but often published documentation is lacking. Nevertheless, it appears that loss of bryophytes could seriously impair many species in this highly vulnerable group of vertebrates that already are disappearing from the planet at an extraordinary rate.

Bryophytes provide a number of possible advantages to the anurans. For the tiny species, the bryophytes may be a full-time or part-time home where they can move about unseen by large predators like birds. As we wend our way through the many species that have been collected among the bryophytes, we will find that they provide mating and nesting sites, cover, calling sites, oxygen under water, and even food sources – both as food themselves and as sites for more traditional food items.

Bryophytes harbor many endangered species whose disappearance will increase with the loss of the bryophyte habitat. Some of these are tiny tropical anuran species that have not even been identified or named. Those that stay within the bryophyte mat are the least likely to have been collected (except perhaps by bryologists☺). Many occur on the IUCN (2011) list of endangered species.

Safe Sites

Safe sites, sometimes also known as predator-free sites, are important for amphibians, especially when they are calling or hibernating or nesting. Anurans are vulnerable to all sorts of predators, depending on their size. Large ones can suffer a brutal death by ducks that beat them to death on the water surface. Small ones can even become prey to insects, including those that can inhabit bryophytes, both on land (Figure 3) and in the water (Figure 4), or spiders (Figure 5) that lurk on ground and in the trees. Snakes lurk among the branches and leaf litter (Figure 6-Figure 7). For the amphibians, having colors of green, brown, and black can protect them when living among bryophytes, serving as camouflage. Furthermore, a large number of would-be predators are unable to maneuver among the small spaces provided among the bryophyte branches and leaves. Hence, for small frogs and salamanders the bryophytes provide safe sites. And for winter even larger amphibians can hide under them.

Figure 3. ***Pristimantis ridens*** that has fallen prey to an ant. This tiny frog most likely would have been just as vulnerable to ants within a mat of bryophytes, but would perhaps have been less obvious during its movements. Photo by Tobias Eisenberg, through Creative Commons.

Figure 4. ***Dytiscus*** (diving beetle) larva attacking the frog ***Xenopus***. This freshwater larva can be a threat to small frogs and tadpoles in pools and lakes. Photo by Brian Gratwicke, through Creative Commons.

Figure 5. Toad being eaten by spider in Costa Rica. Photo by Brian Gratwicke, through Creative Commons.

Figure 6. The Lora or Parrot Snake (***Leptophis ahaetulla***) eating the Evergreen Robber Frog (***Craugastor gollmeri***) with a much greater diameter than the snake. Photo by Brian Gratwicke, through Creative Commons.

Figure 7. ***Craugastor gollmeri***, a species adapted primarily for leaf litter, and resembling leaves. Photo by Brian Gratwicke, through Creative Commons.

Moisture and Temperature Conservation

Frogs and toads must maintain **moisture** without drowning, and mosses can provide that balance. As lung and skin breathers, it is more difficult for most anurans to obtain oxygen in water than in air, but the skin must remain moist to keep the cells functional and pliable. The moisture and temperature of the frogs are also important in attaining maximum jumping distance to avoid predators (Walvoord 2003).

Mosses can provide a moist environment at times when other habitats might be dry, playing a major role in the moisture conservation of many amphibians. Mazerolle (2001) demonstrated that the Wood Frog (***Lithobates sylvaticus***; Figure 2) had more predictable activity, based on weather, near the fragmented edges than in pristine bogs. This greater activity seemed to be more related to the amount of precipitation in the fragments than it was in the bogs, suggesting that the bogs are able to buffer the moisture changes for the frogs living there.

Walvoord (2003) demonstrated that for Cricket Frogs (***Acris crepitans*, Hylidae**) maximum jumping distance requires maintenance of appropriate interplay between

temperature and hydration. In lab experiments at 30°C, jumping distances of frogs at hydration levels of 85-95% significantly exceeded those at 75%. Furthermore, when the temperature was lowered to 15°C, the frogs had significantly poorer performance. However, at 15°C and 85% hydration, the frogs jumped as well as those at 95% hydration at 30°C. Air temperature was the best predictor of frog body temperature, and sky condition (sunny, cloudy) was the best predictor of hydration. The frogs are able to behaviorally modify their body temperature and their hydration to near optimum by choosing their location, thus permitting them maximal jumping distance and increasing their chances to avoid predators. In the field, the mean body temperature of 55 Cricket Frogs was 28.0°C and hydration was 97.4%. As we shall see, some frogs burrow into mosses during the day or go underground or under mosses, presumably optimizing their temperature and state of hydration.

Calling Sites

In anurans, calling by males is used as a means to attract females. But it also calls attention them by would-be predators (not to mention humans). In the cypress swamps of Georgia, USA, frogs often perch on mounds of moss in summer, using these as locations for breeding calls (Wright 2002), and possibly increasing the distance the call will travel by using an elevated location. But in the tropics, calling sites are often elevated on tree branches and leaves (Figure 8), or even located **within** bryophyte clumps. Presumably, this affords a place to hide while the frog is otherwise making itself more noticeable by calling.

Figure 8. ***Eleutherodactylus eileenae*** (Eileen's Robber Frog) perched on a tree leaf in Cuba to call during breeding season. Photo by Ariel Rodríguez, with permission.

One of the common genera calling from within mosses is ***Bryophryne*** (Figure 9). In southern Peru, at elevations of 3800-3850 m asl, Lehr and Catenazzi (2010) found ***Bryophryne abramalagae*** **(Strabomantidae)** calling from inside Peruvian feather grass clumps and in mosses at 11:00-13:00 hours. Likewise in Peru, ***Bryophryne cophites*** (Figure 9) calls from within moss clumps, despite its absence of a **tympanum** (exposed outer surface of ear drum).

Figure 9. ***Bryophryne cophites*** on a bed of mosses. Note the absence of a tympanum, the external evidence of an ear. Photo by Alessandro Catenazzi, with permission.

In the same location as ***Bryophryne abramalagae***, ***B. flammiventris*** called at 10:00-16:00 hours, again from within large moss mats (Lehr & Catenazzi 2010). Another species of ***Bryophryne*** (***B. gymnotis*;** Figure 10) and a different genus of strabomantid (***Psychrophrynella*** sp.; Figure 11) also call from moss hideouts. These calls were often heard from the opposite side of the valley, suggesting that the moss cover was likely to be an important safe site during calling, protecting them against detection and possible predation when they were making such loud sounds.

Figure 10. ***Bryophryne gymnotis***, a Peruvian frog that calls from within moss mats. Photo by Alessandro Catenazzi, with permission.

In Bolivia, as in Peru, the genus ***Psychrophrynella*** (syn. = *Phrynopus*) (**Strabomantidae**, formerly in Leptodactylidae) has a number of species that call from mosses (De la Riva 2007). At Cotapata, ***P. guillei*** begins as the mist rolls over the vegetation, calling from 5-10 cm deep within the mosses. ***Psychrophrynella iani*** calls from under stones and among the mosses. ***Psychrophrynella iatamasi*** (Figure 11) seems to stay in the forest floor mosses for its daytime calling (Aguayo & Harvey 2001). All of the Bolivian **páramo** ***Psychrophrynella*** species seem to call from secluded places such as mosses, with time of day or night depending on the species. The

páramo (Figure 12) is a misty alpine plateau with stunted trees and wide daily temperature fluctuations, creating a severe habitat. Luteyn (2011) describes the páramo as high, cold, inhospitable, wind and rain swept. I think I would seek shelter too.

Figure 11. ***Psychrophrynella*** (=*Phrynopus*) ***iatamasi*** on a bed of mosses. Photo by Ignacio de la Riva, with permission.

Figure 12. Chingaza páramo in the Eastern Cordillera of the Andes, Colombia. Photo by Andres Baron Lopez, with permission.

Peru seems to be one of the best-studied tropical countries for calling sites. ***Gastrotheca pacchamama*** (Ayacucho Marsupial Frog, **Hemiphractidae**; see Figure 13) males were found during the day, calling from moss-covered talus (Duellman 1987).

Figure 13. ***Gastrotheca testudinea***. Photo by Tiffany Kosch, with permission.

In east of Tanzania, from the moss forests at the summit of Morne Seychellois (1000 m), ***Sooglossus*** (=***Nesomantis*****) *thomasseti*** (**Sooglossidae**; Figure 16) calls from under objects, on cliff faces and boulders. Naomi Doak (pers. comm. 24 February 2011) reports that the three species of sooglossids that she studied [***Sooglossus sechellensis*** (Figure 14), ***S. gardineri*** (Figure 15), ***S. thomasseti*** (Figure 16)] call from mosses, and despite sooglossids being ground-dwelling frogs, they sometimes call from mosses on tree trunks.

Figure 14. ***Sooglossus sechellensis***, a species that sometimes calls from epiphytic mosses. Photo by Naomi Doak, with pernission.

Figure 15. Perhaps the world's tiniest frog, ***Sooglossus gardineri*** sits on a bed of moss in the Seychelles. Photo by Naomi Doak, with permission.

Figure 16. ***Sooglossus thomasseti*** sometimes calls from mosses on tree trunks. Photo by Naomi Doak, with permission.

In New Guinea, ***Choerophryne*** species (**Microhylidae**) call from steep, mossy-covered rocky cliff faces, as well as the forest floor and leaves of shrubs (Kraus & Allison 2001).

In a temperate forest in southern Chile, ***Eupsophus emiliopugini*** (Figure 17) (**Cycloramphidae,** formerly in Leptodactylidae**)** and its close relatives excavate burrows in mosses in bogs, from which they make their calls (Penna *et*

al. 2005). This species also calls from burrows hidden in the moss ***Racomitrium*** (Figure 18-Figure 19) and grasses or ferns on the margins of small streams. Stimuli from calls of nearest neighbors increase the calling intensity, creating a chorus, hence making a larger concentration of frogs that is advantageous for mating.

Figure 17. ***Eupsophus emiliopugini*** on a bed of mosses, probably ***Racomitrium*** sp. Photo by Rafael I. Marquez, with permission.

Figure 18. ***Racomitrium lanuginosum*** in Europe. Photo by Michael Lüth, with permission.

Figure 19. ***Racomitrium lanuginosum*** showing spaces where tiny frogs can hide while they call. Photo by Michael Lüth, with permission.

Males of ***Eupsophus calcaratus*** (Figure 20) use cavities within mosses to alter the resonance of their calls (Márquez *et al*. 2005). Hence, the females learn to recognize the resonance characteristics of the mossy burrow-like cavities where the males call. This moss cavity resonance contributes to the recognition by females of the males of their own species in an environment where several species may be calling at the same time.

Figure 20. ***Eupsophus calcaratus***, a frog that uses cavities among mosses to modulate its call resonance. Photo © Danté B. Fenolio <www.anotheca.com>, with permission.

It is somewhat of a surprise to find that a Macaya Burrowing Frog (***Eleutherodactylus parapelates***, **Eleutherodactylidae**, formerly in Leptodactylidae) was calling from within a large moss clump at 3 m high in a tree at the Massif de la Hotte of the Haitian Tiburon Peninsula, southwestern Haiti (Hedges & Thomas 1987). Many members of this genus call from mosses on the ground or on trees (*e.g.* ***E. richmondi***, Figure 21). One must interpret general references to the genus ***Eleutherodactylus*** with caution. This genus has recently been divided based on molecular evidence and some members now reside in different families and genera.

Even the larger frogs, in Ranidae, may call from within moss mats. In southwestern Sulawesi, Indonesia, ***Limnonectes*** (=***Rana***) ***arathooni*** calls from 4-10 cm depths within mosses, as well as from leaf litter and rotting roots (Brown & Iskandar 2000).

Figure 21. ***Eleutherodactylus richmondi*** calling from a bed of mosses. Note the really narrow toes that would be of little help in swimming. Photo by Luis J. Villanueva-Rivera, with permission.

Nesting and Reproduction

Some frogs and toads make use of bryophytes as **nesting sites**. Many more species for which the nesting sites are unknown, especially in the tropics, are likely to make use of bryophytes. Altig and McDiarmid (2007) described the arrangement of deposited eggs in amphibians, stating that semiterrestrial eggs need a source of free water without being submerged. Mosses at the edge of a bog or seepy talus often fulfill this need, where some frogs deposit their eggs in wet moss (McDiarmid & Heyer 1994). When the larvae of these species hatch, they do not feed, and they undergo their development right there in the moss bed.

For example, in the Philippines ***Limnonectes* (=*Rana*) *magnus* (Dicroglossidae)**, which is threatened by habitat loss, lays her eggs on rocks and moss (Wells 2007). ***Limnonectes*** (=***Rana***) ***leytensis*** (Swamp Frog, **Dicroglossidae;** Figure 22) also occurs in the Philippines, where it is endemic. The female most frequently deposits her eggs on mosses attached to roots or rocks, although she may also use leaves (Alcala 1962). Males call from the nest and guard the nest until the tadpoles hatch. By placing the eggs near the water, the female provides for the tadpoles to be washed into the water by rain – or to scramble there when disturbed.

Figure 22. The Swamp Frog, ***Limnonectes leytensis***. Photo by Wouter Beukema, with permission.

Frogs that call from mosses often lay their eggs there as well. Figure 23 shows ***Bryophryne cophites*** (**Strabomantidae**) tending her eggs on a bed of moss, perhaps at the same place the male has called to her.

Figure 23. ***Bryophryne cophites*** tending a clutch of eggs laid among mosses. Photos by Alessandro Catenazzi, with permission.

Experimental observations on ***Sooglossus gardineri*** (**Sooglossidae**; Figure 15), an endemic species from the moss forests of Mahe, Seychelles, suggest that wet substrata may be preferred in that species (Nussbaum 1980). In terraria, all observed **amplexus** (mating stage in which a male amphibian grasps a female with his front legs prior to depositing sperm on her eggs; Figure 24) occurred on damp paper towels or mosses. This is one of the tiniest frogs in the world at 9-12 mm long. This small size suggests that it would easily be at home within the epiphytic and ground bryophytes in the mossy forests where it lives. Fortunately, it is relatively widespread in the Seychelles and is not endangered in the way many of these tiny frogs are.

Figure 24. ***Hylarana temporalis*** in amplexus. The smaller frog on top is the male. Photo by Sandilya Theuerkauf, through Wikimedia Commons.

Living in a tree has unique environmental problems for young tadpoles that can't escape or change environmental conditions by swimming. Some species, like tree-dwelling ***Sooglossus seychelles***, have solved the problem by carrying the tadpoles on their backs (Figure 25). Bryophytes in their habitat may help to maintain their moisture.

Figure 25. ***Sooglossus sechellensis*** carrying its tadpoles on its back. Photo by Naomi Doak, with pernission.

Limnonectes* (=*Rana*) *arathooni (Djikoro Wart Frog, **Dicroglossidae)** in Indonesia, where it is endemic (BioDiversity Hotspots), deposits eggs under 4-10 cm of mosses, leaf litter, and rotting roots (Brown & Iskandar 2000). The male guards the eggs until they hatch and calls from within the nest while sitting on top of the eggs. When disturbed, nearly mature larvae can rapidly emerge from

the eggs and bounce down rocks, banks, etc to reach the nearby stream water. A further advantage of these streamside nest sites is that the splash of water from the stream keeps them humid, a necessity for these eggs and hatchlings. The height above the water protects the eggs from being washed away during high water periods. ***Limnonectes poilani*** (Figure 26) lives in streams and along their borders in the highlands of central and southern Vietnam and eastern Cambodia. As shown in Figure 26, bryophytes are often common in these habitats.

Figure 26. ***Limnonectes poilani*** **(Dicroglossidae)** on bryophytes in a stream, where its coloration matches that of the rocks. This is a member of a genus that often lays eggs among streamside mosses. Photo by W. Djatmiko, through Wikimedia Commons.

A Cuban species of the widespread bryophyte inhabitant ***Eleutherodactylus*** **(*E. rivularis***; Figure 27), laid its eggs, a clutch of 42, 4 m from the edge of the Jibacoa River at Las Mercedes (Díaz *et al*. 2001). These eggs where in a hole that had been excavated, presumably by the frog, under a piece of cloth and "moss sheaths."

Figure 27. ***Eleutherodactylus rivularis*** calling to attract a female. Photo by Ariel Rodríguez, with permission.

Many tropical treefrogs deposit their eggs in mosses. The extent of these occurrences is not well documented, and almost no experimental evidence exists to demonstrate any preference. ***Dendropsophus sarayacuensis*** (formerly *Hyla sarayacuensis*; **Hylidae**) (Shreve's Sarayacu Treefrog; Figure 28) from Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela will lay its eggs on either leaves (Figure 29-Figure 30) or moss-covered trees (Henzi 1987).

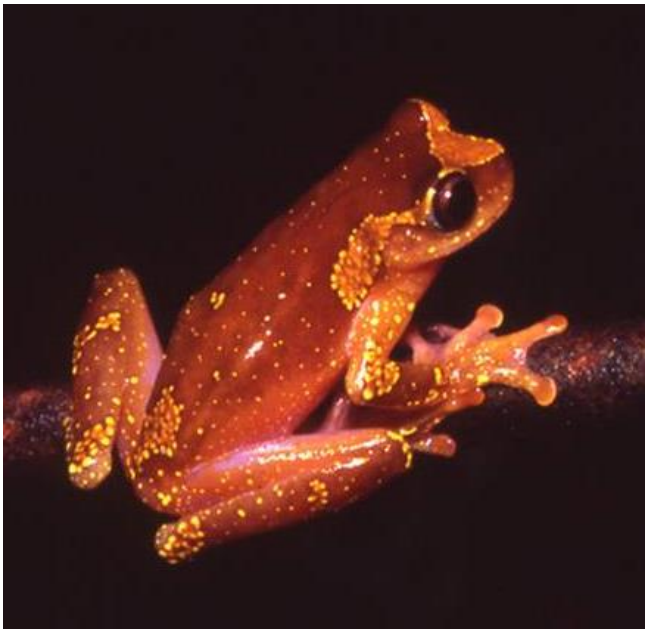

Figure 28. ***Dendropsophus sarayacuensis*** (Shreve's Sarayacu Treefrog) is adapted by its coloration to sitting on a tree branch and looking like lichens or dying leaves that have insect damage. Nevertheless, it also uses mosses as egg-laying substrate. Photo by Andreas Schlüter, through Wikimedia Commons.

Figure 29. Eggs of ***Dendropsophus sarayacuensis*** hanging from the underside of a leaf. Note how easily these masses can break and "drip" the froglets to the ground or water beneath. Photo by Andreas Schlüter, through Wikimedia Commons.

Figure 30. ***Teratohyla*** (formerly *Cochranella*) ***spinosa*** (**Glass Frog**) eggs dripping. Photo by Brian Gratwicke, through Creative Commons.

In North America, the east coast of the USA has several terrestrial species. Among these, we know that the Chorus Frog (***Pseudacris feriarum***; Figure 32) (central Pennsylvania inland south to southern Alabama and Georgia) deposits eggs in February to mid-May at the edge of wet patches (ponds and marshes), often on mosses (Livezey & Wright 1947).

Figure 31. ***Teratohyla*** (formerly *Cochranella*) ***spinosa*** (Glass Frog) on a leaf covered with lichen and liverwort epiphytes. Epiphytes hold moisture and help to keep the frogs moist. Photo by Brian Gratwicke, through Creative Commons.

Figure 32. ***Pseudacris feriarum***, a Chorus Frog that often deposits its eggs on mosses. Photo by John D. Willson, with permission.

The genus ***Mantella*** (Malagasy Poison Frog, Mantellidae) is endemic to Madagascar. It lays clutches of up to 130 eggs that are deposited under moss layers and other hidden places in their captive terrarium, but nesting behavior in the wild may differ (Glaw et al. 2000). ***Mantella laevigata*** (Figure 33) are **oophages** – they eat tadpole eggs, and these may be delivered to them by adult females, providing a type of parental care. Members of the genus ***Mantella*** frequently hybridize with each other, suggesting they aren't quite species yet (see Figure 34 for a member of this group).

Figure 33. ***Mantella aurantiaca*** (golden mantella) on a bed of bryophytes. Photo by Robert Lawton, through Wikimedia Commons.

Overwintering

Many frogs and toads use bryophytes for **cover** from cold and drought, especially in winter or dry weather. It is not uncommon to pick up a moss clump late in the fall and find a hibernating frog or toad under it (personal observation). For some frogs, the bryophytes are a hiding place, and an array of adaptive coloration patterns helps to disguise these amphibians, especially among the tree frogs, as discussed later.

Peatlands may be important temperature mediators for amphibians. Their openness permits warming in the sun, but their branches with air spaces provide a thick insulation from both heat and cold. Toads in north central Alberta, Canada, take advantage of this temperature buffering for hibernation locations (Browne & Paszkowski 2010). In the boreal forest there, 14 out of 21 hibernation sites were in cavities in peat hummocks (Table 1). Other locations were decayed root channels and red squirrel middens (refuse heaps).

Figure 34. ***Mantella expectata***, a species known to hybridize with ***Mantella laevigata***, on a bed of bryophytes. Photo by Paddy Ryan, with permission.

Peatlands in northern areas are known to freeze down to 80 cm. Toads are known to die at temperatures between

-1.5 and -5.2°C (Swanson *et al*. 1996). It is noteworthy that the hibernacula selected by toads in north central Alberta, Canada, rarely or never had temperatures below -5.2°C (Browne & Paszkowski 2010; Table 1). Furthermore, the toads hibernated in communal groups of up to 29 toads, most likely providing further insulation that was not detected by the temperature recorders, although groups of 2-5 were more common. By regularly exchanging positions, they could keep each other from freezing.

The importance of these sites is suggested by their use at distances ranging up to 1020 m from the breeding pond (Browne & Paszkowski 2010). It is likely that the insulation supplied by these peatland sites is crucial for overwintering in these northern sites that mark the limits of tolerance for temperature in ***Anaxyrus***. At the boreal forest site, the toads had a significantly higher selection for black spruce/tamarack stands than for other available habitats, with 79% of the toads hibernating there. Thus it appears that the peat/moss configuration of the forest floor provides the most important overwintering habitat in these northern locations.

Table 1. Site temperature characteristics of paired hibernation and reference sites for Western Toads (***Anaxyrus boreas***). Modified from Browne & Paszkowski 2010.

hibernation or reference	shelter type	depth (cm)	min (C)	consecutive days <0C	<-1.5C	<-5.2C
hibernation	red squirrel tunnel	45	-2.44	176	0.7	0
reference	organic soil under spruce	45	-1.06	154	0	0
hibernation	peat hummock cavities	53	-2.40	149	4.7	0
reference	peat hummock, no cavities	53	-3.37	176	22.2	0
hibernation	burned peat, cavities	47	-8.38	191	10.7	0.6
reference	burned peat, cavities	47	-1.40	163	0	0
hibernation	peat hummock, cavities	62	-9.46	175	41.9	3.2
reference	peat hummock, cavities	62	-6.31	150	21.7	0.7

Undulating Mosses and *Lithobates* (=*Rana*) *sylvaticus* (Wood Frog, Ranidae)

Imagine the mosses around you suddenly heaving and rising! The earliest known report of frogs freezing in winter is that of the Arctic explorer, Samuel Hearne (1769 in Hearne 1911). He reported that he frequently saw Wood Frogs, ***Lithobates sylvaticus*** (Ranidae; formerly placed in *Rana*; Figure 35) that were dug up with the moss when they pitched tents. These seemingly dead frogs could be "brought back to life" by wrapping them in skins and warming them slowly by the fire. For ***Lithobates sylvaticus***, the mosses not only ameliorate the temperature fluctuations, but also greatly reduce the water loss (Churchill & Storey 1993). And, these frogs may very well be frozen, only to start hopping around again in the spring! Despite being the smallest ranid, they are the only frog to be found north of the Arctic Circle (Conant & Collins 1998). Unprotected, the frozen frogs could die in 7-9 days from dehydration, so the moss is an important contributor to their survival.

Figure 35. Wood Frog, ***Lithobates*** (=*Rana*) ***sylvaticus***, among woodland **Polytrichaceae**. Photo by Michael Zahniser, through Wikimedia Commons.

It is not surprising that peatlands are one of the habitats providing a winter home for Wood Frogs. (Wikipedia 2008). Richard Andrus relays "a curious thing I've seen with Wood Frogs in our area (Adirondacks, New York, USA). These critters are explosive breeders in vernal pools for which the eggs and tadpoles are susceptible to predation. So they have a need to find pools that won't support larger frogs and fish. Several years ago I was at a floating mat bog in late April just as the ice was melting. There was ice and snow in the spruce forest around the pond but the mat itself had melted. When we reached the open mat we saw literally 1000's of Wood Frogs all over the mat, in the water, and pouring out of the forest. The reason for this huge number was apparently that the *p*H of the water (ca 4.0) was too low for fish and Green Frog tadpoles (***Lithobates clamitans***; Figure 36) but not too low for Wood Frogs (***Lithobates sylvaticus***; Figure 35). So this was a huge 'safety zone' for them to breed without these predators. They were coming from the north side as its southern exposure caused this to warm up first. On a hunch, the very next week I went out to another floating ***Sphagnum*** (Figure 37) mat I knew of and saw exactly the same thing repeated!! So apparently at least this species can escape egg and tadpole predation by using ***Sphagnum***-acidified ponds."

Figure 36. ***Lithobates clamitans*** (Green Frog) sitting on mosses. Photo by Matthew Niemiller, with permission.

Figure 37. ***Sphagnum lindbergii*** and ***S. balticum*** in Alaska. Photo by Matthew Johnson, for fair use.

Cold Water – *Rana temporaria* (Common Frog, Ranidae)

Despite their **ectothermic** (cold-blooded) nature, many frogs are able to survive winters that take them to below freezing (Koskela & Pasanen 1974). ***Rana temporaria*** (the European Common Frog; Ranidae; Figure 38-Figure 39) is not freeze-tolerant (Voituron *et al.* 2009a). Instead, as is common in northern Finland, ***Rana temporaria*** spends its winters under water to avoid freezing (Koskela & Pasanen 1974). From the time these frogs enter their winter habitat until they leave in April (mature individuals) or May (immature frogs), they disappear into the bottom muds or under bottom moss carpets, stones, or other hiding places. They are not in hibernation, and they can become active if disturbed, but they do not feed. When the air temperature exceeds 5ºC, the adult frogs emerge to land, with the juveniles emerging 1-3 weeks later. Following mating, a large mass of eggs with up to 2000 individuals is produced (Peatlands 2009). The eggs hatch into tadpoles within a week. In Northern Ireland the species is declining due to loss of peatlands and other wetlands. Hence, the species has been legally protected from capture for sale.

Figure 38. European Common Frog (grass frog, brown frog), ***Rana temporaria*** (Ranidae). Photo through Czech Wikipedia GNU Free Documentation License.

Figure 39. European Common Frogs, ***Rana temporaria***, amid their eggs at Cambourne, Cambridgeshire. Photo by Brian Eversham, with permission.

Freeze Tolerance – *Rana arvalis*

In contrast to ***Rana temporaria***, ***Rana arvalis*** (Moor Frog, **Ranidae**; Figure 40) is **freeze-tolerant** (Voituron *et al*. 2009a). It spends the winter not in the water, but in the soil under litter or mosses. The juveniles can survive freezing temperatures for about 72 hours at body temperatures of -3°C (Voituron *et al*. 2009b). In nature, they prepare for this when the temperature drops to the range of 4 to -1°C. In this temperature range, glucose increases 14-fold in the liver and 4-fold in the muscles. **Aerobic** metabolism (using oxygen) persists at a low level, decreasing with temperature, thus preventing the toxic conditions that would arise from **lactate** accumulation. Voituron *et al*. (2009b) suggest that their terrestrial habitat beneath mosses and litter layers provides a temperature regime that shortens the time they spend frozen. Allowance for temperatures to -3°C would permit them to live without freezing under the insulation of snow with the added insulation of the litter, including mosses.

Figure 40. ***Rana arvalis*** (Moor Frog) on a bed of mosses. Photo by Petr Balej, with permission.

Despite this cold tolerance, ***Rana arvalis*** (Figure 40) seems to be rare in the Czech Republic (Šandera *et al*.

2008). It requires nearby water with emergent vegetation where it can attach its eggs (Martin Šandera, pers. comm. 20 February 2011). Its breeding period is a short one week, and that is the time it is best to observe it. After that, even if found, it is difficult to identify.

Under Woodland Bryophytes - *Pelophylax* (Ranidae)

Other frogs **hibernate** in woodlands. ***Pelophylax lessonae*** (Pool Frog; Figure 41) and ***P. ridibundus*** (Edible Frog; Figure 42-Figure 43), both formerly placed in *Rana*, leave the ponds to prepare for winter (Holenweg & Reyer 2000). ***Pelophylax esculentus*** (Figure 44) is a hybrid of ***Pelophylax lessonae*** (Figure 41) and ***Pelophylax ridibundus*** (Marsh Frog, also formerly included in *Rana*), (Figure 42-Figure 43), but it is no longer recognized as a separate species by Frost (2011). In the woodlands, members of this frog group hibernate 3-7 cm below the surface, often under mosses, fallen leaves, or soil. Interestingly, they change hibernation sites during the winter, sometimes more than once. They seem able to find warmer spots – the hibernation sites had warmer temperatures than other spots that were sampled.

Figure 41. The Pool Frog (***Pelophylax lessonae***) from Europe. Photo by M. Betley, through Wikimedia Commons.

Figure 42. Marsh Frog, ***Pelophylax ridibundus***. Photo by Christian Fischer, through Creative Commons.

Figure 43. Marsh Frog, ***Pelophylax ridibundus***, with secreted white mucous that is most likely poisonous or distasteful to some of its would-be predators. Photo by Piet Spaans, through Creative Commons.

Figure 44. The Edible Frog, ***Pelophylax esculentus*** group. Photo by Leo Bogert, through Wikimedia Commons.

Bryophytes for Food and Food Locations

Strangely enough, Ting (1950) found that ***Sphagnum*** (Figure 37) mixed with egg yolk could serve as a food source when rearing various species of tadpoles. It has the added advantage of reducing the bacterial growth. Hartmann (1971) discovered that certain mosses produced **neurohormones** that stimulate frog hearts much like the action of **acetylcholine** (and have the same RF value). However, there is no conclusive evidence that mosses serve as an intended food source for adult frogs in nature.

Tadpoles may, however, consume at least some bryophytes in nature. We generally think of tadpoles as being algal and detrital feeders. However, at least in the terrestrial habitat, bryophytes may form part of the diet (Wickramasinghe *et al*. 2007). The semi-terrestrial tadpoles of ***Nannophrys ceylonensis*** (Ceylon Streamlined Frog, **Dicroglossidae**; Figure 45) in Sri Lanka, like most tadpoles, shift from a scraping food strategy as larvae to catching live prey as adults. During their larval stage, algae are an important part of their diet, with the majority of diatoms being ***Selenastrum*** (Figure 46). Surprisingly, in

the population studied by Wickramasinghe *et al*., ***Barbula*** sp. (*sensu lato*; Figure 47) accounted for most of the moss consumption. As the body size increases, the consumption of mosses decreases significantly, as does the consumption of diatoms. At the same time the mosses and diatoms diminish in the diet, so does the gut size. (Longer guts are needed to absorb nutrients from food organisms with cell walls, like algae and mosses.)

Figure 45. ***Nannophrys ceylonensis*** among the small plants of the moss ***Fissidens*** on the rock. Photo by Peter Janzen, with permission.

Figure 46. ***Selenastrum***, an alga that provides food for larval ***Nannophrys ceylonensis***. Photo by Yuuji Tsukii, with permission.

Figure 47. ***Barbula convoluta*** from Europe, member of a genus that can provide food for frogs. Photo by Michael Lüth, with permission.

Stebbins (1955) found the Tailed Frog ***Ascaphus truei*** (Figure 48) (Leiopelmatidae) in company of the Olympic Salamander ***Rhyacotriton olympicus*** under moss-covered rocks along the Pacific coast. Since the seepage where they were found was nearly completely hidden by the mosses, it is not clear that presence of the moss on the rocks was an important habitat consideration or simply that both frogs and mosses preferred the same conditions. But it seems that the two amphibians prefer the same food (Bury 1970). More specifically, young frogs eat a diet similar to that of the salamander. ***Ascaphus truei*** shifts from having mostly **Collembola** in the diet when young to eating more amphipods at older stages. But even when both are eating the same foods, the abundance of food items among the mosses prevents competition. ***Ascaphus truei*** climbs on rocks that are covered with mosses and algae, and Noble and Putnam (1931) suggested that these moss-covered rocks might provide a richer food source than locations within the rapid flow of the stream. Bury (1970) indicated that this habitat of ***Ascaphus truei*** was consistent throughout their range, where they lived in association with "small, water-washed or moss-covered rocks" in running water or along its borders.

Figure 48. Coastal Tailed Frog, ***Ascaphus truei***. Photo by James Bettaso, with permission.

Occasional Usage – A Place to Travel

In Panama, aerial frogs like the Banded Horned Treefrogs, ***Hemiphractus fasciatus*** (formerly ***Cerathyla panamensis*****; Hemiphractidae**) (Figure 49-Figure 53) may make indirect or intermittent use of bryophytes. This frog lives among **bromeliads** – those basket-shaped plants that capture water and live in trees (Stejneger 1917). The female ***Hemiphractus fasciatus*** carries her eggs and her young on her back (Myers 1966; Figure 49-Figure 50), suggesting that desiccation could become a problem. The bromeliads are abundant on both trees and the ground, and mosses are frequently present around them. It is difficult to imagine that these frogs do not take advantage of the cover, camouflage, and moisture of the mosses as they move from place to place. At the very least, one might expect to find these frogs when looking for bryophytic treasure on tropical tree branches. However, it appears that this species does not need to hide from many kinds of predators.

Instead, it rears up, arches its body, and throws up its head (Figure 51). The yellowish-orange tongue and large mouth present an imposing image (Figure 53). If a would-be predator makes contact, the frog has further defense by clamping two sharp tooth-like projections (Figure 53) into the attacker and hanging on with a strong grip (Figure 52), a painful experience that Myers knew all too well. The frog had to be pried loose!

Figure 49. ***Hemiphractus fasciatus*** female carrying eggs on her back. Photo by Edgardo J. Griffith, El Valle Amphibian Conservation Center (EVACC), Director, with permission.

Figure 50. ***Hemiphractus fasciatus*** female with juvenile frogs on its back. Eggs are retained in patches until the larvae develop into young adults, then remain for some time with the mother after hatching (Myers 1966). This behavior permits the adult to carry the young to locations with sufficient moisture. Photo by Brian Gratwicke, through Wikimedia Commons.

Figure 51. ***Hemiphractus fasciatus*** rearing up in a defensive position. Photo by Brian Gratwicke, through Creative Commons.

Figure 52. ***Hemiphractus fasciatus*** eating an earthworm. Note the two sharp teeth just to the right of the worm on the lower jaw. Photo by Edgardo J. Griffith, El Valle Amphibian Conservation Center (EVACC), Director, with permission.

Figure 53. ***Hemiphractus fasciatus*** with open mouth, showing yellow tongue and two sharp front teeth (in front lower jaw). Photo by Marcos Guerra, through fair use copyright.

Adaptations to Bryophyte Habitats

It is interesting that so many species of anurans exist sympatrically (same geographic area) in "mossy" habitats such as the mountain tops of tropical areas. Hofer *et al.* (2004) paraphrased Gause's Rule by stating that "If interspecific competition is a strong structuring force of

communities, ecologically similar species should tend to have spatial ranges at local scale that do not overlap." They used collected data to test the hypothesis and were surprised to find that whereas lizards and birds exhibited adjustments that reduced the potential for interspecific competition, the frogs did the opposite – there was a greater than chance co-occurrence of ecologically similar frog species. They suggested that resource requirements such as breeding sites may be more important for frogs than competition.

With this in mind, we can see that bryophytes can play a role in providing breeding sites that maintain moisture and provide cover that contributes to keeping the eggs safe. They furthermore provide moist respites for travelling anurans, and for many species can provide hiding places. Given this usage of bryophytes to define part of the anuran niche, we should expect adaptations to have evolved that make this bryological life somewhat easier.

An Altered Life Cycle

Alcala (1962) divided the tadpoles of anurans into three environmental categories. Stream dwellers have depressed bodies, strong tail muscles, and reduced body and tail fins (Figure 54); pond tadpoles have subspherical bodies, weak tail muscles, and high body and tail fins (Figure 55). Both of these aquatic larvae come from small eggs laid in large clutches. Larvae with direct development (out of water) have altered larval structures, including abdominal sacs instead of gills, and derive from large eggs in small clutches. A fourth category is those anurans that have no tadpoles at all, but that hatch directly into froglets.

Figure 54. ***Atelopus limosus***, showing the flattened body of a stream tadpole. Photo by Brian Gratwicke, through Creative Commons.

Figure 55. ***Paracrinia haswelli*** (**Haswell's Frog**) tadpole showing the high body and tail fins typical of pond tadpoles. Photo through Wikimedia Commons.

In the study area of Negros, Philippine Islands, more than 50% of the eggs are laid out of water (Alcala 1962). Among those in the study, some eggs were attached to mosses growing on rocks above a pool in a mountain stream, including ***Platymantis dorsalis*** (=*Cornufer meyeri*; **Ceratobatrachidae**; Figure 56) whose adults live on the montane forest floor, sometimes under moss mats.

Figure 56. ***Platymantis dorsalis***, a frog that seeks refuge under moss mats on the forest floor. Photo by Amir Hamidy, with permission.

Food Capture

Terrestrial adults require different adaptations to capture their food than do the aquatic larvae of their ancestors. One of these adaptations is an extremely fast tongue (O'Reilly & Nishikawa 1995). The anuran tongue is attached at the front, permitting a rapid and extended unfolding.

Escaping Predators and Flying Moss Frogs

When hiding among the mosses is not an option for avoiding predators, then a fast getaway might work. ***Ecnomiohyla rabborum*** (**Rabb's Fringe-limbed Treefrog**, **Hylidae**) is only known from the cloud forest in the mountains near El Valle de Anton, Panama, in the narrow elevational range of 900-1150 m asl (Mendelson *et al*. 2008; Mendelson 2009), where it lives in the canopy. Its large feet (Figure 57) permit it to glide downward from its arboreal habitat, effecting a rapid escape route. It lays its eggs in tree holes, just above the water line. Males remain near the eggs and defend them (Frost 2011). Although I could find no documentation that this species uses mosses, its habitat in the canopy of the cloud forest almost assures that it does.

Figure 57. ***Ecnomiohyla rabborum*** (**Rabb's Fringe-limbed Treefrog**, Hylidae), illustrating the large, very webbed feet used for gliding in the Costa Rican forest. Photo by Brian Gratwicke, through Creative Commons.

I thought I had finished adding new species to this chapter when I ran into "moss frogs." None of the names I had seen used this terminology except for the "mossy frogs" that mimicked mosses. But these were a whole new group of frogs, the genus ***Arthroleptella*** (**Moss Frogs, Pyxicephalidae**; southern Africa) and the family **Rhacophoridae** (Old World Tropics) (Wikipedia 2015a). Well – not quite all were new. ***Theloderma***, the genus of the Vietnamese Mossy Frog, is in the **Rhacophoridae** and will be discussed below.

Of interest is that some members of the genus ***Rhacophorus*** are known as **Flying Frogs** or **Parachuting Frogs**. ***Rhacophorus malabaricus*** (**Malabar Flying Frog**, **Rhacophoridae**; Figure 58-Figure 59) lives in the Western Ghats of India with an altitudinal range of 300-1200 m asl (Biju *et al*. 2004).

Rhacophorus malabaricus lives in tropical moist evergreen and deciduous forests as well as secondary forests and agricultural forests such as coffee plantations (Wikipedia 2011b). It spends its time in the lower canopy or understory and breeds in overhanging vegetation where tadpoles can drop from the foam nests into ponds and pools.

Rhacophorus malabaricus frogs are known as flying frogs because of their ability to glide from their arboreal habitat to the ground. Using their leg and toe spread (Figure 60) and unique morphology, they are able to minimize their descent (falling/gliding) speed and maximize their descent time (Emerson & Koehl 1990). Rather than relying on increasing horizontal travelling distance, their particular maneuverability permits them to actually decrease horizontal distance during descent. These gliding pathways can carry them 9-12 m, about 115 times their length (Wikipedia 2011b). Webbing between the toes further increases their gliding ability.

Figure 58. ***Rhacophorus malabaricus*** showing its narrow legs. Photo by L. Shyamal, through Wikimedia Commons.

Rhacophorus arboreus (**Japanese Green Treefrog**; **Kinugasa Flying Frog**; Figure 61-Figure 62) lives in Honshu, Japan, from sea level to 2000 m asl (Chantasirivisal 2011). It is a comparatively large treefrog; adult males are smaller (42-60 mm) than females (59-82 mm). During breeding season, they live in ponds and rice fields. Otherwise, they live in trees and leaf litter. They hibernate through the winter under moss or shallow soil. Unlike the moss frogs of ***Arthroleptella***, ***Rhacophorus arboreus*** females deposit eggs in a foam nest on vegetation near standing water where the larvae can easily enter the water. To protect the eggs, the female excretes an albumin-based fluid from her cloaca. She creates the foam by beating her hind legs, forming a nest to protect the 300-800 eggs. The male then fertilizes the eggs and the foam hardens, protecting the eggs from water loss and predators.

Figure 59. ***Rhacophorus malabaricus*** showing its ability to flatten against its substrate. Photo by L. Shyamal, through Wikimedia Commons.

Figure 60. ***Rhacophorus malabaricus*** in amplexus. Note the webbing between the toes that helps it to glide and maneuver to the ground. Photo by Sandilya Theuerkauf, through Wikipedia Commons

Figure 61. ***Rhacophorus arboreus*** (**Japanese Green Tree Frog; Kinugasa Flying Frog**). Photo by Peter Janzen, with permission.

Figure 62. ***Rhacophorus arboreus*** (**Japanese Green Tree Frog**) in its arboreal home. Photo © Danté B. Fenolio <www.anotheca.com>, with permission.

Arthroleptella bicolor (**Bainskloof Moss Frog**, **Pyxicephalidae**) lives in fynbos and heathland of Western Cape Province, South Africa at 300-2000 m asl (IUCN 2011). This species breeds in wet mossy areas usually near water, where it lays 8-10 eggs in terrestrial mosses or similar vegetation. Nevertheless, its eggs do not hatch into tadpoles, but develop directly into froglets.

Arthroleptella drewesii (**Drewe's Moss Frog, Pyxicephalidae**; Figure 63) is endemic to Table Mountain and other mountains, up to 1,000 m asl, in the Cape Peninsula of South Africa (IUCN 2011). It lives in fynbos and heathland, as well as forest. It lays its 5-12 unpigmented eggs in moss or similar vegetation in wet mossy areas similar to those of ***A. bicolor***. As in ***A. bicolor***, the eggs hatch directly into froglets.

Arthroleptella lightfooti (**Lightfoot's Moss Frog** or **Cape Chirping Frog**, **Pyxicephalidae**) is endemic to Table Mountain and to the other mountains of the Cape Peninsula, South Africa, where it occurs from sea level up to 1000 m asl (Frost 2011). Like the other ***Arthroleptella*** species thus far, it lives in fynbos, heathland, and forest (IUCN 2011). It lays its 5-12 eggs in mosses or similar vegetation in wet mossy areas, and likewise chooses locations near wet areas and streams (Rose 1929; Livezey & Wright 1947; Frost 2011). It, too, has direct development into froglets. Metamorphosis to adults occurs there on the mosses (Livezey & Wright 1947).

Figure 63. ***Arthroleptella drewesii*** on a bed of moss. Photo by Robert C. Drewes, with permission.

Arthroleptella villiersi (**De Villiers' Moss Frog, Pyxicephalidae**) is endemic to the western cape of South Africa, from sea level up to 1,000 m asl (IUCN 2011). It lives in lowland and montane fynbos and heathland, where it breeds in wet mossy areas similar to those of the other ***Arthroleptella*** species mentioned here. It lays its 10 eggs in moss and similar vegetation.

Anhydrophryne hewitti (**Hewitt's Moss Frog, Pyxicephalidae**; Figure 64) lives in forest and dense vegetation in the Drakensberg and midlands of Kwa-Zulu Natal, South Africa (IUCN 2011). Its breeding habitat is in wet mossy areas of riverine bush and forest near waterfalls and rapids. The 14-40 eggs are laid in moss and leaf-litter on edges of streams. Despite its preference for streamside habitats, the eggs develop directly without a larval stage.

Figure 64. ***Anhydrophryne rattrayi***, here blending with the leaf litter, shows the small size of these frogs. Another member of its genus, *A. hewitti*, lays its eggs in wet mossy areas along streams. Photo by Robert C. Drewes, with permission.

But most frogs don't glide. Some can hop quite high. I had a pet **Green Frog** (***Lithobates clamitans***) I soon named Mr. Wanderlust. He lived in my garden room on the main floor of the house, but he would often escape. I found him hopping across the TV room at the other end of the house several times, at the top of the stairs on the second story several times, and once I found him on top of the open door! I watched him jump one time as I saw him on the floor beside me at my desk. Then suddenly, he was on the desk beside me! But despite our usual vision of hopping frogs, many of them spend more time creeping and

climbing (Figure 65). That is how Mr. Wanderlust escaped under the hanging screen to get free from the garden room.

Figure 65. ***Lithobates clamitans*** attempting to climb a soil bank. Photo by Sheryl Pollock, with permission.

Camouflage and Mimicry

When you make a good dinner, it is helpful to be invisible. A number of species of frogs have disruptive coloration that would make them less conspicuous than a solid color. Greens and browns are common colors among frogs, again providing good camouflage for moss dwellers. But some have disruptive skin surfaces with warts and other extensions, making them blend with the mosses even more.

Importance of Being Still

One reason we know so little about the moss-dwelling frogs is that they do camouflage so well. Cooper *et al*. (2008) noted that camouflaged frogs should limit their movement to avoid detection by disrupting their crypsis. They experimented with ***Craugastor fitzingeri*** (formerly *Eleutherodactylus fitzingeri*; **Craugastoridae**; Figure 66-Figure 67) and demonstrated that when the frogs were motionless, four humans were able to detect only 60% of them in a 2 m diameter circle within 60 seconds. Over 90% of the individuals of five species of ***Craugastor*** remained motionless until the potential predator reached them.

Disruptive Coloration - *Boophis*

Vallan *et al*. (1998) reported on a new tree frog in the genus ***Boophis*** (**Bright-eyed Frogs**, **Mantellidae**; Figure 68) from Madagascar. This frog was especially adapted to blending with tree bark covered with lichens – it has tubercles and fringes and flattens against the branch when it is disturbed. It can change colors from whitish to brown, thus making it also camouflaged on some bryophytes. This mimicry makes it very different in appearance from other members of the genus, such as ***B. viridis*** (**Green Bright-eyed Frog**; Figure 69).

Figure 66. ***Craugastor fitzingeri*** on mosses. Photo by Brian P. Folt, with permission.

Figure 67. ***Craugastor fitzingeri***, with colors that blend with the soil. This one seems to be eyeing an ant, a potential food source. Sitting quietly not only protects it from being preyed upon, but also permits it to lie in wait for food organisms without being noticed. Photo by William Leonard, with permission.

Figure 68. ***Boophis lichenoides*** showing small tubercles, fringes and mottled (disruptive) coloration that help it to be inconspicuous among lichens on bark. Photo by Franco Andreone, through Creative Commons.

Figure 69. ***Boophis viridis*** (**Green Bright-eyed Frog**), a greenish member of the genus that looks very different from the lichen mimic, ***B. lichenoides***. Photo by Franco Andreone, through Creative Commons.

Ceratophrys ornata, A Bryophyte Mimic

Some frogs and toads really play it safe with both disruptive coloration and tubercles, making them look like the light and dark patches of a bryophyte clump. Such is the case for ***Ceratophrys ornata*** (up to 16.5 cm long), the Argentine Horned Frog, but it appears that this frog typically spends its time in grassland (except in captivity). In fact, moss in a terrarium can cause impaction if the frogs eat it. These frogs are unusual in having teeth and a strong jaw – strong enough to inflict pain on animals that attack them. The mouth is extremely large, and they feed on rodents, small reptiles, large spiders, and insects. Gut analysis of thirty-four specimens from Uruguay included 78.5% anurans, 11.7% passerine birds, 7.7% rodents, and 0.3% snakes, leaving only 1.8% as "other" (Basso 1990). They use a "lie-in-wait" strategy that is facilitated by their similarity to the bryophyte (or other) background. There are several color forms, ranging from mostly green to mostly brown. The larvae are also unusual – these are the only vertebrates to make calls in the larval state.

Figure 70. ***Ceratophrys ornata*** in a bed of moss. Photo through Flickr Creative Commons.

Figure 71. ***Ceratophrys ornata*** squatted among bryophytes. Photo by John White, from Wikimedia Commons.

Tubercles – *Theloderma corticale* (Vietnamese Mossy Frog, Rhacophoridae)

The **Vietnamese Mossy Frog, *Theloderma corticale*** (Figure 72-Figure 73), is one of many moss mimics among the amphibians, and perhaps the most famous. Literally translated from medical terminology, its generic name means nipple skin. Although it resembles a toad, it is not one. This strange animal can mimics both mosses and bird droppings, sometimes in the same animal! (Indraneil Das, pers. comm. 8 January 2012).

Figure 72. **Vietnamese Mossy Frogs**, ***Theloderma corticale***. Photo by Milan Kořínek, with permission.

It is an inhabitant of the karst zones of northern Vietnam, where it lives in flooded caves and other deep holes on the banks of mountain streams (Ryboltovsky 1999). Its skin is a mottled black and green that resembles a "bunch of moss." Numerous spines and tubercles add to the disruptive pattern that makes it quite invisible among the dense moss and lichen cover (Figure 73).

These frogs remain quiet in the daytime and hunt at night (Figure 73). When frightened, they will roll into a ball and play dead (Figure 74) (Wikipedia 2015b). They also avoid detection by being ventriloquists – throwing their voice to another location so they cannot be found while calling. This rare frog is now being bred as a terrarium pet. It appears that the starter pair has been

rescued from an area that is rapidly becoming unsuitable as a home. Despite its broad habitat range, it is threatened by habitat loss (Animal Photo Album 2007).

Figure 73. ***Theloderma corticale*** (**Vietnamese Mossy Frog**) camouflaged among bryophytes. Photo by Brian Gratwicke, through Creative Commons.

Figure 74. ***Theloderma corticale*** (**Vietnamese Mossy Frog**) on its back, feigning death. Photo © Chris Mattison <http://www.agefotostock.com/age/ingles/home01b.asp>, with permission.

Green and Wet – *Centrolene geckoideum* (Pacific Giant Glass Frog, Centrolenidae)

The Pacific Giant Glass Frog, ***Centrolene geckoideum*** (Figure 75), lives in tropical and South American cloud forests of Ecuador and Colombia (Glass Frogs: Centrolenidae), especially near waterfalls or rapids, where traversing mossy substrata must surely be a necessity in some locales. This is the largest of the glass frogs and its coloration of dark green to lime green, and skin covered with tubercles, most likely helps it to be inconspicuous among wet bryophytes and rocks. Clearing of forests for farming and chemical sprays from agriculture have reduced numbers so that this is listed as an IUCN vulnerable species (IUCN 2011).

Figure 75. ***Centrolene geckoideum***, the Pacific Giant Glass Frog, from near Tandayapa, Province of Pichincha, Ecuador. Note the tubercles and greenish color that helpsto camouflage this frog among bryophytes and lichens. Photo by William Duellman, courtesy of Biodiversity Institute, University of Kansas, with permission.

Changing Colors – *Platymantis* spp. (Ground Frogs, Ceratobatrachidae)

Platymantis macrosceles (Figure 76), endemic to Papua New Guinea, where it lives in montane forests, is not known for its arboreal behavior. However, when Foufopoulos and Brown (2004) found them in New Britain, two of them were perched on moss-covered branches of shrubs about 1 m above the ground and 2 m from a small stream. Their tubercles, combined with brown spots on green backs, made them all but invisible on their mossy perch. Interestingly, when removed from the mosses, they lost their patterned colors and became a yellowish green color (Figure 76; Johannes Foufopoulos pers. comm. 10 February 2009).

Figure 76. ***Platymantis macrosceles***, after losing its color when removed from its mossy perch. Photo by Johannes Foufopoulos, with permission.

Platymantis mamusiorum (**Ceratobatrachidae**; Figure 77), another little-known frog from the Nakanai Mountains of New Britain, Papua New Guinea, lives in montane rainforests where the ground and logs are thickly covered with moss (Foufopoulos & Brown 2004). It spends resting time on bushes and low branches up to about 1 m from the ground, but its cryptic coloration permits it to remain unseen against a mossy background. It is not as well camouflaged as the former species, lacking the brown spots and tubercles (Johannes Foufopoulos pers. comm. 10 February 2009).

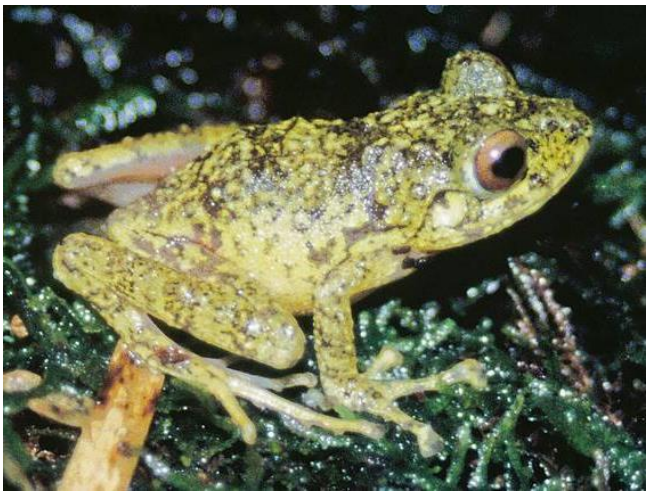

Figure 77. A ground frog, ***Platymantis mamusiorum*** showing cryptic coloration on a bryophyte-covered perch. Photo by Johannes Foufopoulos, with permission.

Colors Matter

As seen by the foregoing discussion, cryptic and disruptive coloration permit frogs to sit quietly without being seen. But it is not just blending with one particular substrate that provides an advantage. Having multiple color forms within a species increases chances for the species to survive. Forsman and Hagman (2009) demonstrated this in their studies of 194 species of Australian frogs. The polymorphic color patterns afforded larger ranges, more survival habitats, less negative population trends, and less vulnerability to extinction compared to species with non-variable color patterns. Among these, we can assume, is the ability for some color forms to utilize bryophyte habitats to their advantage where they are available. is a good example of multiple color morphs.

Oophaga pumilio has many color morphs (Pröhl & Ostrowski 2011; Figure 78-Figure 81) with estimates of 15-30 different forms (Summers *et al*. 2003). The green morphs typically remain within the moss mats and spend less time foraging compared to the brightly colored morphs that are more active (Pröhl & Ostrowski 2010). This dual strategy in a highly poisonous frog permits two different kinds of adaptations to operate in the same population. The brightly colored morphs advertise their poisonous nature through their warning coloration, whereas the green morphs are less conspicuous to us, to predators, and apparently also to potential mates.

Figure 78. Orange color morph of the Strawberry Poison Dart Frog, ***Oophaga pumilio***. Photo by Peter Janzen, with permission.

Figure 79. White color morph of the Strawberry Poison Dart Frog, ***Oophaga pumilio***. Photo by Peter Janzen, with permission.

Figure 80. Yellow color morph of the Strawberry Poison Dart Frog, ***Oophaga pumilio***. Photo by Peter Janzen, with permission.

Figure 81. Blue color morph of the Strawberry Poison Dart Frog, ***Oophaga pumilio***. Photo by Peter Janzen, with permission.

Does Size Matter?

Although some large frogs and toads make use of mosses for nesting and moisture retention, those that live within the mosses terrestrially are typically quite small. Bryophytes, particularly mosses, provide them with small spaces where they can navigate without being seen by hungry predators. But it appears that bryophytes might have had a role in their evolution and size characteristics.

The tiny ***Noblella pygmaea*** (**Noble's Pygmy Frog, Strabomantidae**; Figure 82) was found for the first time in southern Peru, where it occupied two habitat types, one along the montane ridge and the other in the elfin forest where moss cover was abundant (Lehr & Catenazzi 2009). This frog is the smallest in the Andes (females 12.5 mm, males 10 mm) and one of the smallest in the world. (Note that members of **Leptodactylidae** and related families have many small members and will be discussed later). Having a small size, while beneficial for hiding in mosses, is detrimental for venturing away from the moss during the drying heat of day. As size decreases, the surface area to volume ratio increases, providing relatively more surface area for losing water.

To understand the role of size and other parameters in the evolution of Neotropical amphibians, Gonzalez-Voyer *et al*. (2011) examined the correlates of species richness with habitat parameters and body morphology. They found that a greater age of the clade did not increase richness. Rather, ecological and morphological traits seemed most important. One of these traits that correlated well with greater terrestrialization and ability to live at high altitudes was the presence of greater vascularization in the ventral skin. This, presumably, may aid in moistening the body by ventral contact with moist substrates such as bryophytes.

Figure 82. Adult ***Noblella pygmaea*** on what appears to be a liverwort. Photo by Alessandro Catenazzi, with permission.

Since being small can also be a problem for eggs, having only two eggs permits ***Noblella pygmaea*** to make larger eggs with less relative surface area to suffer drying out (Figure 83) (Gonzalez-Voyer *et al*. 2011). The moss cover should help to protect both eggs and adults against water loss as well as provide camouflage, but the preferred egg-laying locations of many of these small species, including ***Noblella pygmaea***, are not known.

Figure 83. Adult ***Noblella pygmaea*** with its two eggs. Photo by Alessandro Catenazzi, with permission.

Although Gonzalez-Voyer *et al.* (2011) found no correlation between latitude and richness, Wiens (2007) and Moore and Donoghue (2007) found greater diversification rates in amphibians in lower latitudes. Amphibians seem to have evolved in contrast to **Bergmann's** (1847) **rule** (species of larger size are found in colder environments; usually applied to endotherms), having greater body size farther from the poles and small size at high elevations in the tropics (Feder *et al*. 1982; Adams & Church 2007; Lehr & Catenazzi 2009). Geist (1987) disagreed with Bergmann's rule and instead claimed that in mammals body size initially increases with latitude, but at latitudes of 53-65°N it reverses, with the result being small body sizes at the lowest and highest latitudes.

But does this relationship apply to ectotherms like anurans? Ashton (2002) found a distinct body size relationship with latitude and elevation in salamanders, with 13 of 18 species being larger in higher latitudes and elevations. But anurans seemed less likely to conform, with only 10 of 16 species showing these trends.

Part of the disagreement lies in what is being compared. The within species comparison of Ashton (2002) is not the same as comparing among species and genera. Blackburn and Hawkins (2004) quote Bergmann as saying that "on the whole. . . larger **species** live farther north and the smaller ones farther south."

For terrestrial frogs, Gonzalez-Voyer *et al*. (2011) found that larger body size correlated only marginally with latitude and elevation. In fact, they suggested that small-bodied species may diversify more than larger ones in the Neotropics, at least in the Andes, because they are able to partition the niches on a finer scale (see also Lomolino 1985; Purvis *et al*. 2003).

The first explanation that comes to mind regarding Bergmann's rule is that a larger body is less susceptible to losing heat due to a smaller surface area to volume ratio. While this is a reasonable explanation for endotherms, there does not seem to be any reason to assume this for ectotherms. In fact, Ashton (2002) found no clear relationship between body size of salamanders and environmental temperature.

One explanation for the ability of small frogs to survive at high altitudes is their ability to make a physiological activity shift in response to lower temperatures (Navas 1996, 2006; Lehr & Catenazzi 2009).

This ability permits them to occupy the "mosaic" of small patches where the habitat is suitable and a food source is available (Hutchinson & MacArthur 1959). These terrestrial frogs have the advantage that they do not need to migrate to water to lay their eggs, and generally their home range is small, sparing them of the dangers of moving among a patchwork of unfavorable habitats. Such small patches would be unsuitable for larger frogs with greater food demands and need for moisture.

Let us consider the genus ***Pristimantis***, a genus that includes arboreal bryophyte dwellers, in this discussion. ***Pristimantis*** (Figure 84) represents the clade with the greatest number of terrestrial species (Gonzalez-Voyer *et al*. 2011). Lynch and Duellman (1997) reported a correlation between small body size and arboreal species richness in this genus. Concomitantly, prey size correlates with body size, a phenomenon which Duellman (2005) suggested might indicate competitive release through resource partitioning, subsequently explaining high local diversity that can reach as high as 139 species in 6.5 km^2 in the Amazon (Bass *et al*. 2010).

One explanation for the successful niche partitioning is that large amphibians retain water more easily and maintain body heat at a more constant temperature (Shoemaker 1992). The presence of many body sizes permits greater niche partitioning, with each size group locating where moisture and temperature are optimal. In this regard, the variety of bryophyte growth forms available can provide a wide range of niches with different moisture and insulating abilities. Conversely, the divergent niches offered create divergent selection pressures that, coupled with the geographic isolation afforded by ridge and valley topography, provide suitable conditions for speciation (Lynch 1986; Lynch & Duellman 1997).

Figure 84. ***Pristimantis bacchus*** on a bed of mosses. Photo by Esteban Alzte, through Creative Commons.

One peculiar habit noted for small frogs in marshy areas of Suryamaninagar, Tripura, India, is that they form small groups as rain approaches, effectively becoming a large animal, but after it stops they separate from each other (Acharya 2011). One could hypothesize that this behavior may help to prevent overcooling during the rain, so it would be interesting to know if the same behavior would occur if they were able to sit within the cover of bryophytes.

The Frog or the Egg?

When frogs invaded bryophytes, whether on the ground or in the trees, did they invade because they were small, or did they become smaller as they adapted more and more to terrestrial living and bryophytic habitats? Did the tiny frogs invade first, or did they begin using bryophytes as egg-laying sites, taking advantage of UV protection, moisture, and protection from larger predators? If the latter, did birth among the mosses direct more and more of them to seek shelter there later in life, creating greater survival for those that did, and driving selection toward those with that behavior and miniature size? Did bryophytes drive anuran evolution in the tropics, or were they just convenient co-evolvers in time? In any event, being small permits a wider range of uses of bryophytes by anurans.

Enter the Bryophytes – and *Eleutherodactylus* (Eleutherodactylidae)

The genus ***Eleutherodactylus*** has many species of very small frogs associated with mosses. Their subtle coloring, often with disruptive patterns, makes them inconspicuous in a variety of habitats, including bryophytes. This is clearly demonstrated for ***E. cuneatus*** in Figure 85. So far, we do not know much about the moss interactions of this species. Is it pre-adaptive to becoming a moss-dweller when its environment becomes too dry for open exposure? Or is its coloration already an adaptation to the multiple habitats it must cross during its daily activities?

Figure 85. Some frogs, like this Cuban endemic ***Eleutherodactylus cuneatus***, blend in well with the mosses they cross by having a disruptive pattern of light and dark browns. This same coloration would serve it well as it crosses forest soil and patchy, decomposing leaf litter. Nevertheless, it is on the IUCN red list. Is it rare because it is disappearing, or only because we seldom see it due to its coloration? Photo by Ansel Fong, with permission.

Being tiny is one adaptation that permits some members of this genus to inhabit mosses. The smallest frogs known in the world are in this genus, measuring only 8.5 mm long (Wikipedia 2011a). The tiny ***Eleutherodactylus coqui*** (Figure 86) has invaded Hawaii, where it competes with native species (Kreaser *et al*. 2007). Frogs of this small size are likely invaders in the moss

trade, where they can travel unnoticed among the imported moss species. But of even greater concern is the trafficking of these tiny frogs in the plant trade.

Figure 86. ***Eleutherodactylus coqui*** on a tree bole, surrounded by bryophyte and algae growth. Photo by Alan Cressler, with permission.

One species of *Eleutherodactylus* appears in greenhouses so commonly through plant transport that it has been named the **Greenhouse Frog** (***Eleutherodactylus planirostris***; Figure 87) (Frost 2011). The natural distribution of this species is in Cuba, and the Isla de Juventud (0-720 m asl), Cayman Islands, and Caicos Islands. But they have been introduced into Florida, southern Louisiana, southern Georgia, Oahu, and the island of Hawaii, USA, and to Guam, Jamaica, Honduras, and Veracruz, Mexico. This terrestrial species lives in both mesic and xeric habitats, including forests, caves, beaches, nurseries, gardens, and urban areas (Hedges *et al*. 2004). In the Cayman Islands it has naturalized in bromeliads. No surprise, it is categorized as least concern by the IUCN.

Figure 87. ***Eleutherodactylus planirostris*** on moss. Photo by Brian Gratwicke, through Creative Commons.

When you are as small as these ***Eleutherodactylus*** species, even thin mats of bryophytes can help maintain moisture. Note in Figure 88 the wet leafy liverworts that are epiphyllous on the leaf, maintaining a moist location for this tiny ***Eleutherodactylus gryllus*** (**Cricket Robber Frog**; Figure 88-Figure 89). A native of interior uplands in Puerto Rico from 300-1182 m asl, it is known from only a few localities and is considered endangered (IUCN 2011). Mosses provide daytime retreats in its forest home. It calls from perches in trees and shrubs (Figure 88). Eggs still require water and are laid in basins of bromeliads, but Father Alejandro Sánchez found them under bryophytes (Figure 90). These develop young froglets, with no tadpole stage.

Figure 88. ***Eleutherodactylus gryllus*** (**Cricket Robber Frog**) calling from a leaf covered with epiphylls. Photo by Luis J. Villanueva-Rivera, USDA, with permission.

Figure 89. ***Eleutherodactylus*** sp. calling from a plant. Photo by Brian Gratwicke, through Creative Commons.

Figure 90. Eggs of ***Eleutherodactylus*** sp. under layer of moss on a tree trunk, El Yunque National Forest, Puerto Rico. Photo by Father Alejandro Sánchez, with permission.

Most of these species don't bear any coloration patterns that distinguish them as bryophyte dwellers. However, ***Pristimantis galdi*** (formerly *Eleutherodactylus galdi*) (Espada's Robber Frog; Figure 91) has both color patterns and tubercles to render it invisible in the right setting; *i.e*., it is a moss mimic. This species lives in both secondary and old-growth humid evergreen forests in Peru and the Cordillera of Ecuador from 1000 to 1740 m asl (Frost 2011; Rodríguez *et al*. 2004). It seems to prefer leaves at 1-2 m above the ground (Lynch & Duellman 1980). Its habitat is threatened by livestock farming, agriculture, and logging, classifying it at near threatened (Rodríguez *et al*. 2004).

Figure 91. ***Pristimantis galdi***, showing its tubercles from an arboreal branch. Photo © 2007 German Chavez, with permission for educational use.

Summary

Bryophytes and amphibians are both transitional organisms that have adapted to land. Their life cycles are characterized by two phases that have different requirements. Frogs need to maintain moist skin, so bryophytes can provide them with a suitable habitat. Mosses provide moist safe sites from the drying sun during the day and serve as mating and calling sites for many species. *Sphagnum* can offer a moisture refugium for migrating amphibians. The same moisture advantage is offered to eggs. The male Leyte Wart Frogs (***Limnonectes leytensis***) stay under the mosses with their eggs; tadpoles can later be washed into the nearby water by rain. In winter, the bryophytes can provide insulation for hibernating anurans that can become frozen up to 60%, as well as reducing the risk of desiccation. And some bryophytes can serve as food and even sources of oxygen. ***Sphagnum***, mixed with egg yolk, can even serve as food for rearing several species of tadpoles. At the very least, mosses provide refuge for a number of invertebrates that are suitable food for the anurans. For some species, using mosses as cover during overwintering may save their lives. In summer, some frogs may even return day after day to the same spot among the mosses.

Some Anura seem to be well adapted for the bryophyte habitat. Small size is an advantage for living among the stems or climbing across epiphytes on branches. Many have disruptive coloration of browns and greens. And some have protuberances that further disrupt the shiny surface, serving as additional camouflage. Some even change their color to blend with their substrate. Altered life cycles are adaptations to land in general, with such modifications as parental care of eggs, carrying eggs on their backs, having large but few eggs, and burying the eggs in mossy nests. Because of these anuran traits, bryophytes offer them **safe sites** against not only environmental conditions, but also against predation.

One means of escape for Moss Frogs and others is "flying." This is actually gliding, and some of these frogs have modified muscle placement that permits them to maneuver to a selected landing spot. Others simply hop or crawl.

Acknowledgments

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CHAPTER 14-2
ANURAN CONSERVATION ISSUES

Janice M. Glime and William J. Boelema

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CHAPTER 14-2
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Figure 1. ***Atelopus certus*** in its natural setting, streamside on a mossy rock. This species may soon only exist in captivity and is the object of a rescue operation. Photo by Brian Gratwicke, through Creative Commons.

Conservation Issues and Endangered Species

Many species of anurans, especially in the tropics, are disappearing because their ranges are small, restricted to mountain tops separated by uninhabitable valleys, preventing them from spreading to new locations (Figure 1). For some, extinction is imminent because their small range of habitat is being destroyed. Blaustein *et al*. (1994) suggest that amphibian species may not be able to recolonize areas where they have become extinct because of physiological constraints, low mobility, and site fidelity.

Knutson *et al*. (1999) examined landscape effects and wetland fragmentation on anuran abundance and species richness in Iowa and Wisconsin, USA. They found that there was a negative association with the presence of urban land, but a positive association with emergent wetlands and upland and wetland forests. For these larger species, a complex of habitats including wetlands is the best combination for success of the amphibian populations.

But amphibians are declining at an alarming rate worldwide. Factors of disease, parasites, deforestation, agriculture, heavy metals, herbicides, pesticides, increasing UV radiation, acid rain, fire, and other environmental changes all seem to have contributed to a rapid decline in anuran species.

Although the decline of amphibians is well known throughout the world, the causes are not so clear. It appears that the causes are multiple and that the tadpole stage, in particular, is very sensitive. This helps to explain why amphibians are endangered from pesticides, heavy metals, organic compounds, parasites (Figure 2), and bacteria. Tadpoles of many species are sensitive to low *p*H (Freda *et al*. 1991). Rising temperatures may play a role by increasing likelihood of bacterial, fungal (Halliday 1998), or parasitic infection (Blaustein & Dobson 2006). The rich diversity of arboreal amphibians in the tropics is particularly at risk, and we know almost nothing about where they place their eggs or how bryophytes may be essential in their life cycle survival. Meanwhile, their habitats are disappearing (Mazerolle 2003).

The anurans are negatively associated with urban development. This group of organisms often requires different habitats for breeding, hibernation, and summer feeding. When one of these habitats disappears or becomes inaccessible, the amphibians will disappear from the others as well. The genus ***Lithobates*** is a common peatland visitor that exemplifies common characteristics among disappearing anuran species: aquatic habit, montane distribution, and large body size (Lips *et al*. 2003).

Figure 2. ***Bufo bufo*** infected with parasitic fly larvae. Photo © Henk Wallays, with permission.

The amphibians are further limited by their latitudinal restrictions. While species richness decreases from low to high latitudes for all animal groups but birds and sawflies, the amphibians are nearly absent in the Arctic (Kouki 1999).

One contributing factor to the absence of amphibians at high latitudes, in addition to the short food season and cold temperatures, is the lack of canopy and higher levels of UV. As the ozone in the stratosphere diminishes, more UV-B radiation is able to penetrate the atmosphere and reach the Earth. Several researchers have hypothesized that it is increased levels of UV-B that have precipitated the massive losses of amphibians. This suggestion is in part due to the much greater decline in amphibians than that seen in birds or mammals (Bancroft *et al*. 2008). Bancroft *et al*. showed that UV-B radiation reduced amphibian survival by 1.9-fold compared to controls, with larvae (tadpoles) being more susceptible than embryos. Salamanders were even more susceptible than frogs. They concluded that the UV-B acted synergistically with other environmental stressors, such as those mentioned above. However, the results of multiple studies have been conflicting, with the same species acting differently at different life stages and even at the same life stage in the same population at the same time.

The complicating factor in explaining amphibian decline seems to be that there are multiple causes. For example, the Boreal Toad ***Anaxyrus boreas boreas*** (Figure 3) suffered total loss of 11 populations in the West Elk Mountains of Colorado between 1974 and 1982 (Carey 1993). In this case, it was the bacterium ***Aeromonas hydrophila*** that seemed to be the culprit. Carey concluded that stress caused a suppression of the immune system, increasing the sensitivity to infection. Such suppression would make the amphibians more susceptible to fungal, bacterial, viral, and parasite attacks.

Red leg: *Aeromonas hydrophila*

One of the most common infections of frogs in the lab, in my experience, is red leg, caused by a heterotrophic, Gram-negative, rod-shaped bacterium, ***Aeromonas hydrophila***. This bacterium travels through the bloodstream to the first available organ, where it produces an Aerolysin Cytotoxic Enterotoxin (ACT) (Wikipedia 2011a). Its very toxic infections are common in fish and amphibians, and can also affect humans. It is most likely to infect during times of environmental change, stress, temperature change, pollution, or in an otherwise unhealthy animal. One reason for the name of red leg is that the disease can cause internal hemorrhaging, a problem that can lead to death. For the disease to become manifest, both hemolysin and the endotoxin must be present (Rigney *et al*. 1978), resulting in bloating, lesions, hemorrhaging, and other serious problems in the frogs.

Figure 3. ***Anaxyrus boreas*** on a bed of mosses. Photo by William Flaxington, with permission.

Red leg may be a somewhat seasonal infection. Emerson and Norris (1905) observed more incidence of the disease in the warm weather of September and October, claiming that short periods in the cold chamber would delay death by the disease in infected frogs. But in 14 sites in Minnesota, USA, there were more infections in ***Lithobates pipiens*** (Leopard Frog; formerly ***Rana pipiens***) in March-June than in August-November (Hird *et al*. 1981), suggesting that either these frogs were more stressed early in the season after a winter of little food, or that the disease could grow better under spring conditions, possibly in lower temperatures. In that study, red-leg infections could not account for the declining populations of ***Lithobates pipiens*** (Hird *et al*. 1981).

Frogs are actually rather well protected from diseases such as those caused by ***Aeromonas*** species. Glands in their skin produce secretions containing a multitude of peptides with antimicrobial prosperities (Simmaco *et al* 1998). In ***Pelophylax lessonae*** (Edible Frog; formerly ***Rana esculenta***), 20-30 different peptides are secreted. Although these bacteria can grow freely in the blood of the frog, those in contact with the skin toxins are killed within 10 minutes.

Peatland Conservation

One might argue that the tropics and the peatlands are the two most vulnerable ecosystems under current circumstances. Peatlands are disappearing through mining and draining, and if they are replaced, it is frequently by a different vegetation type and hydrologic regime. But even when peatland pools are retained, lack of suitable habitat for summer retreats may cause amphibian losses (Marsh & Trenham 2001). Baldwin *et al*. (2006) and Bellis (1965) likewise concluded that summer refugia in peatlands were important for the Wood Frog (***Lithobates sylvaticus***; Figure 4), providing shade and moisture-laden ***Sphagnum*** (Figure 5).

Figure 4. ***Lithobates sylvaticus***, a frog with short lifespan and high fecundity. Photo by Bill Peterman, with permission.

Figure 5. Mer Bleue Bog with ***Sphagnum*** near Ottawa, Canada. Photo through Creative Commons.

Harper *et al*. (2008) concluded that current federal wetland law is inadequate to protect the amphibians, partly because it lacks protection for surrounding areas. They contend that state wetland regulations that protect no more than 30 m from the breeding pool cannot support the terrestrial habitat needs.

Life span can play a role in amphibian sensitivity, with a short life span and high fecundity, like that of the Wood Frog (***Lithobates sylvaticus***; Figure 4), being most sensitive to habitat loss and isolation. On the other hand, long life and low fecundity, like that of the Spotted Salamander (***Ambystoma maculata***), can lead to greater sensitivity to habitat degradation and lower adult survival. Furthermore, connections between wetlands are needed for recovery after population crashes (Baldwin *et al*. 2006; Harper *et al*. 2008).

Mining

Mining of peat changes the gross morphology of the peatland, removes the more open upper layers where it is easy for frogs and toads to nestle among the stems, and alters the hydrology. Such changes are likely to remove the aspects of peatlands that make these favorable habitats for amphibians.

Mazerolle (2003) demonstrated the negative impact of peat mining on amphibian abundance and diversity. Species richness and numbers of individuals both were lower in bog remnants (after mining) than in unmined bogs. The Wood Frog (***Lithobates sylvaticus***; Figure 4) was most abundant in areas far from the ponds when the area had not been mined. Only ***Anaxyrus americanus*** (formerly *Bufo americanus*; Figure 6) appeared to benefit from the increase in habitat complexity resulting from mined edges in fragmented peatlands. Knutson *et al.* (2000) suggest that more wetland patches are likely to increase the probability that at least one of those sites will be suitable for amphibian habitation. Mazerolle (2003) contended that amphibians would benefit from a management plan that maintained a complex mosaic of bog ponds, shrubs, and forest patches. Since peatlands are such important habitats for many amphibians, it is essential that we understand the role of their bryophytes in our attempts to restore their fauna along with wetland restoration (Mazerolle *et al*. 2006).

Figure 6. ***Anaxyrus americanus*** amid mosses and rocks. Photo by John D. Willson, with permission.

We can surmise from the foregoing information that some anurans would suffer from the loss of peatland habitat due to water loss during travels and daytime activity and to loss of egg-laying sites. Bellis (1962) stressed the importance of moisture provided by a spruce and tamarack bog in northern Minnesota, especially for smaller frogs.

But it appears there may be other consequences that result from mined peatlands. Mazerolle (2001) examined effects of fragmented bogs in southeastern New Brunswick, Canada. He found that the Wood Frogs **(*Lithobates sylvaticus***; Figure 4) that occurred in fragments were actually larger than those in pristine bogs. Leopard Frogs had a similar size relationship, but only in the 1998 year of study. Mazerolle attributed this relationship to be the result of larger frogs having a better chance of surviving than small frogs in the disturbed habitat of mined peatlands. Larger frogs would have a smaller surface area to volume ratio, thus decreasing their sensitivity to desiccation.

Old-growth Forests

Old-growth forests (Figure 7) with mature trees, continuous canopy, logs, snags, and often well-developed moss beds on the ground, logs, and branches, are likely to represent the third major habitat type where amphibians are rapidly disappearing. Logging and clearing for harvest or

agriculture greatly alters the old-growth habitat, eliminating vast acreage and replacing it with a drier cover with fewer niches.

Figure 7. Old-growth habitat of ***Ascaphus truei***. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Dupuis *et al*. (1995) demonstrated the importance of stand age in providing suitable habitat for amphibians. They found that logging could reduce terrestrial amphibian populations by up to 70% in old-growth forests in Canadian forests. Logging reduced the availability of moist habitats such as snags and logs, reduced shade, and often lost streamside buffer zones. As in peatland studies, they found that having connectivity between patches of suitable habitat was important. Bryophytes can play a role in these connections and in creating microhabitats that are moist and provide protection against UV-B radiation.

One of these disappearing species (the Coastal Tailed Frog, ***Ascaphus truei***; **Leiopelmatidae**; Figure 9) has been discussed earlier because it seems to find a rich food source among the streamside mosses. This is an unusual frog that can unlock keys to evolutionary processes. Although it is "tailed," it does not break the anuran rule of no tails because its "tail" lacks bone and is thus not a true tail. This is the only genus of frogs with internal fertilization (California Herps.com 2011).

Figure 8. ***Ascaphus truei*** tadpole in a stream with leafy liverworts. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Welsh (1990) found that the Coastal Tailed Frog occurred primarily in old-growth forests – those primeval coniferous forests that are disappearing rapidly from the Pacific Northwest in North America. Younger forests do not offer the needed microclimate required. It is only in the older forests that the preferred cover of the Coastal Tailed Frog (moss, rocks, and organic matter) exists. Their sucker-like mouths permit them to hang onto the rocks, where they presumably eat the attached algae. The importance of the bryophytes has not been studied experimentally, but Noble and Putnam (1931) suggested that these mossy habitats might provide an enriched food source for them. The tadpoles (Figure 8-Figure 10) occur in fast melt-water streams.

Figure 9. ***Ascaphus truei*** showing its fleshy tail. Stream edges such as this provide suitable feeding areas for the adults. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 10. ***Ascaphus truei*** tadpole showing its rasping suction cup mouth. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Tropics

There are possibly the greatest numbers of endangered amphibians in the tropics. That is where the smallest of vertebrate species live among bryophytes, lichens, and other epiphytes in the canopy, on tree trunks, and on the ground. Many of the anuran species remain to be described. But this habitat is in great danger of destruction to make way for farming and managed forestry, depleting the sites with bryophyte-covered habitats and replacing them with non-forest or with young trees that do not have established bryophyte cover.

A rapid decline in tropical anurans was first noticed in the 1980's (Bustamante *et al*. 2005; La Marca *et al*. 2005). Bustamonte *et al*. noted that 24 anuran species in the Ecuadorian Andes were in decline or had become extinct since the late 1980's. But the decline was not prevalent in

all species. Between 1988 and early 2000's, 56 of 73 species had declines, but 27 had increased in relative abundance. In six of seven localities, fewer species could be located, despite greater capture effort. It is noteworthy that they found greater differences for species with aquatic larvae (reduction from 34 to 17 species) than for those terrestrial species having direct development. For example, the genus ***Eleutherodactylus*** presented 28 species in both the earlier and recent surveys. Furthermore, six species had expanded their distributions to higher altitudes.

Fong and Hero (2006) explored eastern Cuba in an effort to document the extant anuran species so that losses with habitat destruction could be measured. They cited ***Eleutherodactylus cuneatus*** (Figure 11) as a species that is at high risk of disappearance if habitat loss were to occur in Cuba (Williams & Hero 1998; Lips *et al*. 2003; Hero *et al*. 2005; Fong & Hero 2006). In the tropics, at least in Latin America, species living close to streams seem to be the most vulnerable (Young *et al*. 2001).

Figure 11. ***Eleutherodactylus cuneatus***, a species that is at risk due to limited distribution. Photo by Ansel Fong, with permission.

Despite forest habitat destruction, Lips (1998) had also surmised that it was species with aquatic eggs and larvae that were most vulnerable to decline. Those with direct development such as ***Eleutherodactylus*** and some salamanders (***Bolitoglossa minutula***), both bryophyte inhabitants, typically arboreal, do not seem to be in decline. Lips further concluded that based on evidence in Australia, Brazil, and Costa Rica, it was an environmental contaminant such as chemicals or biotic pathogens, or a combination of factors that might include climate change. Laurance *et al*. (1996) concluded, based on worldwide spread patterns and presence of the disease in pristine environments that lacked environmental contamination, that the problem was caused by a disease.

Atelopus (Bufonidae)

The genus ***Atelopus*** (**Bufonidae**), the Neotropical Harlequin Frog – but actually a toad – seems to be particularly vulnerable. Of the known 113 species, 42 species have been reduced by at least 50% since earlier surveys, and only ten have stable populations (La Marca *et al*. 2005). Many of the species could not be relocated, and 30 have been missing from all previously known localities for at least 8 years. In this case, it seems to be those at higher elevations (above 1000 m) that are most vulnerable, with 75% disappearance, compared to 58% disappearance among lowland ***Atelopus*** species. Habitat loss did not seem to be the causal factor. Climate change may have played a role, but environmental contamination, pet trade, and introduction of competitor or predator species did not seem to have any role. Rather, 22 species had disappeared from protected areas! There is some good news, however. ***Atelopus varius*** (Figure 12) has recently been located in Costa Rica in a mossy stream (Solano Cascante *et al*. 2014).

Figure 12. ***Atelopus varius***, known from a mossy stream in Costa Rica. Photo by Brian Gratwicke, through Creative Commons.

Atelopus certus (Darien Stubfoot Toad; Toad Mountain Harlequin Frog; Figure 13-Figure 16) is an endemic to Panama, where it occurs at 500-1150 m asl. This golden-colored frog with spots like a giraffe is disappearing from Panama. It is one of the frogs targetted for a rescue operation to breed the frogs in captivity (Amphibian Rescue and Conservation Project 2011). On an expedition to capture these frogs for rescue, Mark Cheater (2011) reported finding the first few of these frogs on mosses, including a pair in amplexus. The frogs were placed in plastic cups lined with damp moss for transport.

Figure 13. ***Atelopus certus*** at edge of stream where wet mosses can keep it hydrated when it ventures landward. Photos by Brian Gratwicke, through Wikimedia Commons.

Figure 14. ***Atelopus certus*** male. These males climb shrubs and trees at night. Photo by Brian Gratwicke, through Creative Commons.

Figure 15. ***Atelopus certus*** (Darien Stubfoot Toad; Toad Mountain Harlequin Frog) male calling near stream. Photo by Brian Gratwicke, through Creative Commons.

Figure 16. ***Atelopus certus*** male calling. Its coloration serves it better as camouflage in its stream home than aloft on a mossy perch when calling. Photo by Brian Gratwicke, through Creative Commons.

An alarming factor was beginning to emerge. ***Batrachochytrium dendrobatidis***, a fungal disease organism that causes **chytridiomycosis** in amphibians and other animals, had arrived. And this fungus was present in populations of nine of the ***Atelopus*** species that have declined.

Chytridiomycosis

Although loss of cover and moisture will surely have a great impact on the anuran fauna, it appears that another serious threat is the rapid spread of the fungal disease **chytridiomycosis**. Anurans seem to be defenseless against fungi that are causing whole populations to disappear (Thompson 2010).

Catenazzi *et al*. (2011) found that the introduced fungal pathogen ***Batrachochytrium dendrobatidis*** caused the **chytridiomycosis** that accounted for a large portion of amphibian decline in the Andes of Peru. In its short known history, it has been responsible for both extinctions and **extirpations** (local extinctions) in Central America. In Peru, the overall number of species declined by 47%. The fungus seems to have a greater effect on aquatic and arboreal species (declined by 55% between 1999 and 2008) than on the terrestrial species. Abundance of frogs also declined during that period, following its discovery by Longcore *et al*. in 1999. The declines correspond with increases in the fungus (Catenazzi *et al*. 2011).

The fungus adheres to the skin of the amphibians, causing it to thicken, thus interfering with respiration (Denton 2008). That thickened skin inhibits the animal's ability to take in water and interferes with the salt-water balance in the body of the frog (Voyles *et al*. 2007). Furthermore, the fungus damages the nervous system (Denton 2008). This causes lethargy and ultimately death.

This fungal disease seems to be associated with a large number of amphibian declines worldwide (Berger *et al*. 1998; Piotrowski *et al*. 2004; Bovero *et al*. 2008; Brodman & Briggler 2008; Byrne *et al*. 2008; Reeves 2008; Gaertner *et al*. 2009), but the greater incidence of the disease could have multiple causes that weaken the amphibian resistance to the disease. Furthermore, it seems clear that chytridiomycosis is not the only cause of the decline (Daszak *et al*. 2003; Di Rosa *et al*. 2007).

In a summit-type meeting of herpetologists regarding the threat of amphibian extinctions in Latin America, 88 Latin American herpetologists and conservationists concluded that "at least 13 countries have experienced declines, and in 40 cases species are now thought to be extinct or extirpated in a country where they once occurred. Declines or extinctions have affected 30 genera and nine families of amphibians. Most declines have occurred in remote highlands, above 500 m in elevation in Central America and above 1000 m in the Andes. ...Climate Change appears to be important at one site and chytrid fungal disease has been identified at sites in three countries." (Young *et al*. 2001). Recognizing the importance of *in situ* studies, they concluded that it would be important to rear species in captivity to avoid imminent extinction.

One species targetted for *in situ* studies is ***Atelopus limosus*** (Limosa Harlequin Frog; Figure 17-Figure 22), an endemic to Panama, where it lives on stream banks in subtropical or tropical moist lowland forests and rivers (Wikipedia 2011b; Figure 13). Once a thriving species, it is now endangered by chytridiomycosis (Figure 21-Figure 22) as well as habitat destruction (IUCN 2011).

Figure 17. ***Atelopus limosus*** in its natural habitat. Photo by Brian Gratwicke, through Creative Commons.

Figure 18. A once healthy, reproductive species, ***Atelopus limosus*** is now endangered due to chytridiomycosis. Here it blends with mosses in its terrestrial habitat. Photo by Brian Gratwicke, through Creative Commons.

Figure 19. ***Atelopus limosus*** male and female in amplexus. Note the size differences between the male (smaller) and female in this lowland color form. Photo by Brian Gratwicke, through Creative Commons.

The Limosa Harlequin Frog has two color forms, a brown form with yellow nose and finger tips in the lowlands, and a green form with black patches on its back in the uplands (Wikipedia 2011b). The upland form is in the greatest danger, and the Amphibian Rescue and Conservation Project (2011) targeted this species and managed to maintain one upland female in captivity (Estrada 2011). They successfully bred the Limosa Harlequin Frog in captivity – no small feat.

This species, particularly the green and black upland variety, has been described several times as being camouflaged among the mosses and dark rocks (Amphibian Rescue and Conservation Project 2011; Price 2011). This ability to blend makes them difficult to locate, hence making the rescue operation difficult. Typical food for the genus includes beetles, ants, flies, and mites (Durant & Dole 1974), all of which can be found among and near bryophytes.

But they must leave these bryological hiding places during the dry season and return to fast-flowing rainforest streams (Amphibian Rescue and Conservation Project. 2011). It is here that the females lay their eggs. The rapidly moving water helps to protect the eggs from predation. Once the tadpoles emerge, they cling to the rocks with their suction cup mouths.

A more fundamental question is why this disease has suddenly become so widespread. One might look at acidification as a contributor, with frogs being more vulnerable and fungi typically being favored by a lower *p*H.

Figure 20. ***Atelopus limosus*** dead from chytridiomycosis caused by ***Batrachochytrium dendrobatidis*.** Photo by Brian Gratwicke, through Creative Commons.

Figure 21. ***Atelopus limosus*** dead from chytridiomycosis caused by ***Batrachochytrium dendrobatidis*.** Photo by Brian Gratwicke, through Creative Commons.

Figure 22. Dead ***Atelopus limosus***, a typical result of chytridiomycosis. Photo by Brian Gratwicke, through Creative Commons.

The danger from chytridiomycosis has gotten so severe that several scientists travelled to Panama to rescue as many frogs as they could (Goodman 2006; Figure 24-Figure 25). According to models of the spread of the fungus causing chytridiomycosis, attack on these

populations was imminent. So they packed hundreds of frogs into deli containers with wet mosses, placed them in carry-on suitcases, and began their adventure through airport customs back to Atlanta where they would attempt to breed them in captivity.

Figure 23. Swabbing a tropical frog for chytridiomycosis. Photo by Brian Gratwicke, through Creative Commons.

Figure 24. Swabbing a tropical frog for chytridiomycosis. Photo by Brian Gratwicke, through Creative Commons.

Figure 25. Testing a new and faster test for ***Batrachochytrium dendrobatidis***, the chytridiomycosis fungus. Photo by Brian Gratwicke, through Creative Commons.

Diagnosis

When organisms are under stress, whether it be temperature, pollution, or disease, one measure of the severity of that stress is an instability in development (St. Amour *et al*. 2010). The assumption is that it is costly to control symmetry (I am reminded of so many things that develop in a spiral, including at least some protonemata from spores imbedded in agar, and rhizoids before they touch a substrate). Therefore, the greater the evidence of asymmetry, the greater the indication of stress. In their study of asymmetry, St. Amour *et al*. found that ***Lithobates clamitans*** (Green Frog; Figure 4) had significantly higher levels of fluctuating asymmetry in individuals infected with chytridiomycosis.

A Cure?

One of the first steps in combating chytridiomycosis is to determine what conditions the fungus likes. Puschendorf *et al*. (2011) studied several species of the tree frog ***Litoria*** (Hylidae). They found that the fungus thrives where the environment is cool and moist, causing the highest outbreaks to occur in such areas. To support this conclusion, they demonstrated that in species with greater elevational ranges, populations disappeared at the higher elevations while surviving in the lowlands. To their surprise, they found a population of ***Litoria lorica*** and one of ***Litoria nannotis*** (Figure 26-Figure 27) in a stream at high elevation in a dry sclerophyll forest. In that and six additional surveys, 82.9% of the frogs had ***Batrachochytrium dendrobatidis*** (Figure 28). Among tadpoles of both species, 100% were infected. BUT none of the individuals had any signs of chytridiomycosis. This site had little canopy cover, low annual precipitation, and a more defined dry season than a nearby rainforest site. In that nearby site, ***L. nannotis*** was negatively affected by the disease chytridiomycosis. They hypothesized that the open habitat permitted the rocks where the frogs perched to warm up, having negative effects on growth and reproduction of the fungus.

Figure 26. ***Litoria nannotis***, an active frog that has frequent contact with habitats of other frogs. Note the color pattern that can easily blend with bryophytes during its travels. Photo through Wikimedia Commons.

Figure 27. ***Litoria nannotis*** tadpole. Photo by Jean-Marc Hero, through Wikimedia Commons.

Litoria nannotis (Figure 26-Figure 27) lives in fast streams, waterfalls, and cascades in the rainforest or wet sclerophyll forest of Australia (Liem 1974; McDonald 1992), where it is endemic (Williams & Hero 1998, 2001; Hodgkison & Hero 2001). The tadpoles are specially adapted to living in these torrents, including a streamlined body shape, large sucking mouthparts, and a muscular tail (Liem 1974; Richards 1992). At night, the frogs may venture up to 15 m from the stream in search of food, returning to the stream before dawn (Hodgkison & Hero 2001).

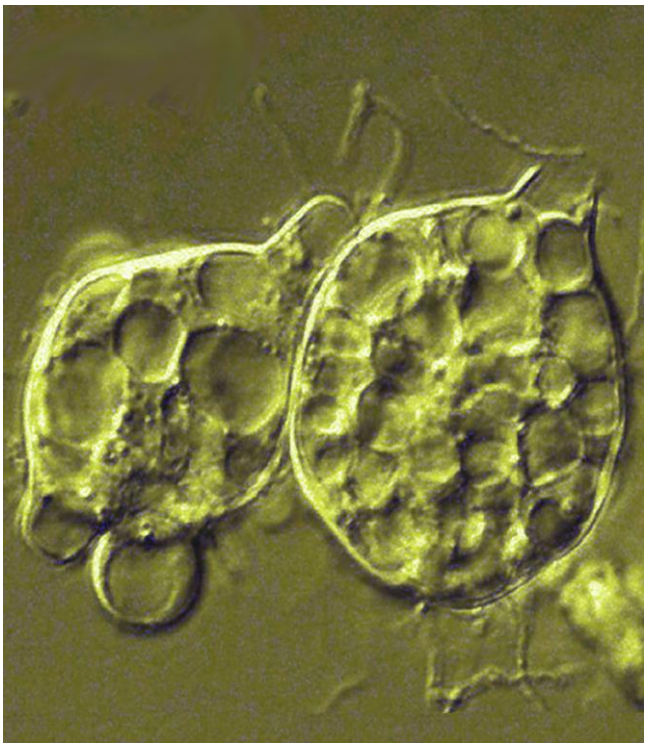

Figure 28. ***Batrachochytrium dendrobatidis***, a fungus causing chytridiomycosis. Photo by A. J. Cann, through Creative Commons.

Rowley (2006), and later Searle *et al*. (2011) found that some anuran species may be severely affected by chytridiomycosis while others in the same area are unaffected. Rowley suggested that behavior of the frogs played a role. Such factors as physical contact between frogs, contact with infected water, and contact with terrestrial substrates that serve as reservoirs all contribute to the likelihood of contracting an infection. In other words, the microenvironment plays a role. As in other studies, Rowley found that at elevations above 400 m asl the populations were more likely to decline due to chytridiomycosis, even while populations of the same species in the lowlands contracted no infection. Among three species of ***Litoria***, ***L. nannotis*** became locally extinct at all known high elevation sites. ***Litoria genimaculata*** (Figure 29) declined at the high elevation sites, then recovered. The third species, ***L. lesueurii*** (Stoney Creek Frog; Figure 30), had no known infection at any elevation. Ouellet *et al*. (2005) found similar confounding indications in Quebec, Canada. They examined specimens spanning the years 1895 to 2001 from 25 countries, totalling 3371 specimens. In recent studies, they found no evidence of mortality from chytridiomycosis in amphibians from Québec, despite the presence of the fungus in 17.8% of the amphibians from 1990-2001. Furthermore, epidermal infections were apparently absent in 440 amphibians from 23 other countries. It appears that despite the internal infection in seemingly healthy amphibians from eastern North America, the lethal expression of chytridiomycosis has complex causes that may require a predisposition to contract the disease.

Figure 29. ***Litoria genimaculata*** showing cryptic coloration and pronounced tubercles that permit it to blend with mosses and lichens. Photo by Jean-Marc Hero, with permission.

Figure 30. ***Litoria lesueurii*** in its stream home, exhibiting much smaller tubercles than its terrestrial congenerics. Photo through Wikimedia Commons.

Rowley (2006) demonstrated that the frequency of contact with other frogs and with water was greatest for ***L. nannotis*** (Figure 26), intermediate for ***L. genimaculata*** (Figure 29), and least for ***L. lesueurii*** (Figure 30), corresponding with the degree of infection mentioned above. Furthermore, ***L. lesueurii*** travelled farthest from the stream, whereas ***L. nannotis*** remained in the stream all day, moving only a short distance from the streams. These "travelling" patterns further separated the environment created for the fungus by creating temperature differences. For the most susceptible species, ***L. nannotis*** (Figure 26), the frogs rarely moved outside the temperature range that was optimum for the fungus. On the other hand, the uninfected species, ***L. lesueurii*** (Figure 30), were frequently at sites with temperatures above the temperature optimum and even the thermal tolerance for the fungus. ***Litoria nannotis*** even had the most suitable hydric conditions for development of the fungus. Hence, the "predisposition" seems to be the behavior of these three species. From our bryological perspective, the substrate used by the frogs can also play a role. Dewel *et al.* (1985) found that zoospores of chytrids are common on moss-covered rocks, and Letcher and Powell (2002) suggested that distance from moss could affect the safety of a given substrate where the frogs might sit.

Searle *et al*. (2011) looked at the differences between species somewhat differently, showing that even with the same degree of ***Batrachochytrium dendrobatidis***, the mortality rates differed among species. This would eliminate dispersal and contact as causal factors. Temperature seems to be emerging as an important distinction, but the work of Searle *et al*. seems to suggest that there is also a difference in immunity.

The spread of this disease around the world has been rapid. One contributing factor, perhaps the primary one, has been the human factor. Among these has been international trade in aquarium fish (Laurance *et al.* 1996). But even plant trade, with frogs as hitchhikers, contributes to the problem. And if the zoospores survive on mosses, then the moss trade can also spread the disease, either by spreading the zoospores, or by transport of infected frogs.

One interesting aspect of survival of the ***Batrachochytrium dendrobatidis*** is that rising temperatures, often viewed as a cause for disease increase, may actually improve the resistance of tadpoles to the disease. In experiments on tadpoles of ***Rana muscosa*** (Mountain Yellow-legged Frog; Figure 31-Figure 32), at 22°C, 50% died within 35 days, while 95% of those maintained at 17°C died (Andre *et al*. 2008). Nevertheless, Piotrowski *et al*. (2004) showed that growth of the chytrid fungus from the zoospores (Figure 33) was maximal in the range of 17-25°C.

There is perhaps some hope for at least some of the amphibians in this chytridiomycosis epidemic. There is strong evidence that some species of amphibians survive because of a co-habiting bacterium, dubbed the **anti-Bd skin bacterium** (Lam *et al*. 2009). The resistance seems to result from antimicrobial skin peptides and these anti-Bd skin bacteria. I have to wonder if any of the bryophyte antibiotic properties might help their inhabitants avoid fungal and other infectious invasions.

Figure 31. ***Rana muscosa*** (Mountain Yellow-legged Frog), a species whose tadpoles are susceptible to death from chytridiomycosis at temperatures of 17-25°C. Photo by USGS, through public domain.

Figure 32. ***Rana muscosa*** (Mountain Yellow-legged Frog) that has died from chytridiomycosis. Photo by Vance Vredenburg, NSF.gov website, through public domain.

Figure 33. Zoospores of the fungus ***Batrachochytrium dendrobatidis*** that causes **chytridiomycosis** in amphibians and other animals, in this case living on an arthropod. Photo by A. J. Cann, through public domain.

In summary, chytridiomycosis seems to be a major player in the decline of amphibians, but it is not the only cause. Amphibians are sensitive to stress, and stress can

exacerbate chytridiomycosis, but this same stress may be the primary cause. Furthermore, as will become obvious in the rest of this chapter, loss of habitat is a severe problem in parts of the world, particularly the Neotropics. In the Neotropics, it is likely that many species will disappear before they will even be described, and many of these are bryophyte inhabitants.

Moss Use in Captivity

Use of frogs in the pet industry is one of the causes for amphibian decline, but for most species this use may be minor compared to spread of disease and habitat loss. Nevertheless, it appears that the pet industry has helped in the spread of the disease.

Certain frogs have been targetted for rescue from tropical areas where their demise seems imminent (Amphibian Rescue and Conservation Project 2011). In the rescue efforts, bryophytes are often placed in plastic containers to provide a moist environment with cover that helps to keep the amphibians alive, especially during transport (Amphibian Rescue and Conservation Project 2011). In searching for various species and their relationships to mosses, I found many descriptions for preparing terraria for pets, including mosses as part of the habitat. Even biological supply companies often package frogs in mosses, especially ***Sphagnum*** (Figure 34), for shipping.

Figure 34. ***Sphagnum***, suitable packaging for amphibians. Photo by Hermann Schachner, through Wikimedia Commons.

Many species of anurans have suffered the fate of becoming pets. To this end, they are frequently sold along with a species of moss, often ***Sphagnum*** (Figure 34), to be placed with them in a terrarium or other container. The mosses can help to maintain moisture. ***Sphagnum***, in particular, can provide antibiotics that reduce chances of infections like red leg, a bacterial disease caused by any of several genera (***Aeromonas***, ***Citrobacter***, ***Escherichia coli***, ***Proteus***, ***Pseudomonas***, ***Salmonella***) (Hadfield & Whitaker 2005; PetEducation.com 2011). In the lab, we found presence of ***Sphagnum*** (Figure 34) in the aquarium/terrarium to prolong the life of the frogs and reduce incidence of red leg. It also reduced the effects of excreted ammonia and gave the frogs a place to get out of the water.

Making a Home – *Scaphiopus holbrookii* (Eastern Spadefoot, Scaphiopidae)

Like the fire-bellied toads, the Eastern Spadefoot (***Scaphiopus holbrookii***), often called the spadefoot toad, is not a member of the toad family Bufonidae. Its English name indicates its habit of using its hind feet to dig a hole in the sandy ground typical of its home, where it escapes the heat and drying atmosphere. My first experience with this unique animal was at a Girl Scout camp on the Eastern Shore of Maryland, USA, where we found it on the outdoor shower floor after dark. We put it in a jar for the night and released it the next day. To our amazement, it immediately dug a hole and disappeared! And its disappearance was rapid. Only a bit of disturbed soil indicated its former presence (Figure 35-Figure 37).

Figure 35. The Eastern Spadefoot Toad, ***Scaphiopus holbrookii***, begins to dig a hole in the ground in Maryland, USA. Photo by Janice Glime.

Figure 36. The Eastern Spadefoot Toad, ***Scaphiopus holbrookii***, digging a hole in the ground. Photo by Janice Glime.

Figure 37. The Eastern Spadefoot Toad, ***Scaphiopus holbrookii***, as it ultimately leaves only a bit of raised, disturbed soil. Photo by Janice Glime.

I don't know of any evidence that the Eastern Spadefoot uses bryophytes in its natural home, but it can make good use of them in captivity. Wright (2002) tells about a pet Eastern Spadefoot (***Scaphiopus holbrookii***; Figure 38) that made the most of the mosses provided for it as a winter home. The first batch of mosses seemed too wet, so Wright provided an additional set of dry ones. The spadefoot immediately began work and arranged the moss into an enclosure. At the rear was a thick pile of mosses, but the front had only a thin film through which the spadefoot could still see. Such instinctive behavior suggests that it may use mosses or similar vegetation structures in nature.

Figure 38. Eastern Spadefoot, ***Scaphiopus holbrookii***, on a bed of mosses. Photo © John White, with permission.

In the Aquarium - *Trachycephalus resinifictrix* (Amazon Milk Frog, Hylidae)

In aquaria, mosses such as Java moss serve as nesting substrata and hiding places for tadpoles. In Figure 39, the tadpoles of ***Trachycephalus resinifictrix*** (Amazon Milk Frog; **Hylidae**; Figure 40-Figure 42) are in the shelter of aquarium mosses. The milk frog derives its name from its habit of exuding a toxic, milky-white substance when threatened (Amphibian Rescue and Conservation Project 2010). Not only does this substance deter predators, but it helps to keep the frog hydrated, although it would seem to be stealing from itself to do so. This is one of the largest of the South American treefrogs, with males up to 10 cm and females 11.4 cm vent to snout. Their large size and concomitant large vocal sacs permit them to make very loud calls.

Figure 39. Tadpoles of the Amazonian Milk Frog ***Trachycephalus resinifictrix*** using mosses for cover in an aquarium. Photo by Milan Kořínek, with permission.

Figure 40. ***Trachycephalus resinifictrix*** adult. Photo by Milan Kořínek, with permission.

Figure 41. Adult ***Trachycephalus resinifictrix*** (Amazon Milk Frog) in amplexus. Photo by Milan Kořínek, with permission.

Figure 42. Adult ***Trachycephalus resinifictrix*** on a moss in nature at last! Note how different this morph is from the ones in the photo above. Photo by Philippe Kok, with permission.

Summary

Many of these anurans, especially in the tropics, are on the IUCN protected list, largely due to habitat loss and pollution. Stresses due to habitat changes most likely contribute to the increasing occurrences of the fungal disease **chytridiomycosis**. Most of the tropical anurans lack legal protection because they are so poorly

known, but they may be rapidly disappearing due to habitat loss and pollution. Peatland species may be especially vulnerable as the area of peatlands on the planet continues to diminish and become fragmented. Species in tropical forests may disappear due to habitat destruction before we even know they exist. Our lack of knowledge about the role of bryophytes in the various life stages of amphibians could hinder our ability to preserve these fascinating species.

Since most of these frogs have cryptic coloration that makes them almost invisible among lichens and bryophytes on trees, they are likely to be further endangered by air pollution that causes loss of this cryptogamic flora. Furthermore, in areas of deforestation, it will be many years before new forests develop the kind of epiphytic flora in which they are so well camouflaged. Under these circumstances they are likely to experience the same sorts of selection pressures for loss of some color variants as that seen in the classic example of the peppered moths (*Biston betularia*) due to loss of lichens.

Stresses make the amphibians more susceptible to disease. Among these is red leg, a common bacterial disease caused by ***Aeromonas hydrophila***. Its ability to cause hemorrhaging causes the legs to become red.

Chytridiomycosis, a fungal disease caused by ***Batrachochytrium dendrobatidis***, has been causing severe declines. In the tropics, it is the higher elevation populations that are most susceptible, offering the optimal temperature conditions. Hence, in these bryologically dense habitats, the anuran inhabitants may disappear. In some habitats, bryophytes may provide a safe resting place for chytrid zoospores that can eventually infect amphibians that journey across them. For frogs that are more mobile, there is more opportunity for contact with infected frogs or with deposits of zoospores on bryophytes and other substrates.

Mosses are used to provide suitable conditions for anurans in captivity. In experiments with spadefoot toads (***Scaphiopus holbrookii***), the toads rearranged the mosses to create their "comfortable" moisture level. Amphibian pet trade accounts for some of the losses of the colorful anurans. Mosses are often used in both transport containers and terraria for keeping these pets.

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CHAPTER 14-3
GROUND-DWELLING ANURANS

Janice M. Glime and William J. Boelema

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CHAPTER 14-3
GROUND-DWELLING ANURANS

Figure 1. ***Nannophryne variegata*** (previously *Bufo variegatus*) peering from a bed of the dung moss ***Tetraplodon mnioides*** in southern Chile. This toad is most likely only a casual visitor to the ***Tetraplodon***, although the attraction of these moss capsules for flies might make it an attractive feeding location for the toad. Photo by Filipe Osorio, with permission.

Peatland Habitats

Peatland habitats have been considered inhospitable for many species of frogs due to their acidity. Some frogs are tolerant enough to breed in the ***Sphagnum*** pools, but for others, mortality is too high. However, the ***Sphagnum*** mat and associated bryophyte serve other roles in the life cycles of these amphibians (Figure 1).

In Australia, the **Sphagnum Frog**, ***Philoria sphagnicolus*** (**Limnodynastidae**; Figure 2), has good reason for its name. This frog produces large eggs that are embedded in a foamy jelly (Debavay 1993). The male excavates a shallow burrow in clumps of ***Sphagnum*** or under stones on the forest floor. The females deposit the eggs in these burrows. The tadpoles complete development into adults within the nest. It is in small numbers worldwide and is on the IUCN red list of endangered species.

Figure 2. ***Philoria sphagnicolus***, the **Sphagnum Frog**. Photo by Evan, through Wikimedia Commons.

Mazerolle (2005) determined that male calling indicated that upland ponds were preferred by frogs over bog ponds, with calls emanating from 75% of the upland ponds, but only from 25% of the bog ponds, supporting the notion that the bog ponds may be too acid. None of the minnow traps in bog ponds caught tadpoles, whereas 58% of the upland ponds had at least one trapped tadpole. Several other studies likewise found few successful attempts of amphibians to breed in peatlands (Saber & Dunson 1978; Dale *et al*. 1985; Karns 1992b).

Furthermore, Mazerolle (2005) found no evidence that frogs moved from the forest to the bog in the summer, suggesting that the bog was not a significant refuge. However, there was back and forth movement between the bog and the upland, suggesting that the bog may provide a site for rehydration at times. Karns (1992a) and Mazerolle (2001), observing a number of amphibians, found that amphibians increased in bogs following the breeding season, so perhaps at least some frogs and other amphibians use them as summer sites.

But, it appears that **Green Frogs (*Lithobates clamitans*;** Figure 3**)** will use ***Sphagnum*** for rehydration (Mazerolle 2005). In an experiment where frogs were given the choice of ***Sphagnum***, upland sifted sandy loam, and well water with a *p*H of ~6.5 (upland pond water), the frogs showed no discrimination between the ***Sphagnum*** and the upland media as a source for rehydration.

Figure 3. ***Lithobates clamitans*** sitting among ***Sphagnum***. Photo by Alexander McKelvy, with permission.

Nevertheless, it appears that ***Sphagnum*** (Figure 4) peatlands are not as inhospitable to amphibians as formerly thought. In the boreal peatlands of North America, one might find the **Northern Leopard Frog** (***L. pipiens***; Figure 4), **Wood Frog** (***Lithobates sylvaticus***; Figure 5), **Green Frog** (***L. clamitans***; Figure 3), **Mink Frog** (***L. septentrionalis***; Figure 6), **Spring Peeper** (***Pseudacris crucifer***; Figure 7), **Western Chorus Frog** (***P. triseriata***; Figure 8), and **Gray Treefrog** (***Hyla versicolor***; Figure 9-Figure 10) (Desrochers & van Duinen 2006).

In Maine, the **American Bullfrog** (***Lithobates catesbeianus***; Figure 11) and **Pickerel Frog** (***Lithobates palustris***; Figure 12) are often found, as well as **Wood Frog** (***L. sylvaticus***; Figure 5), **Green Frog** (***L. clamitans***; Figure 3), **Northern Leopard Frog** (***L. pipiens***; Figure 4), **Spring Peeper** (***Pseudacris crucifer***; Figure 7), and **Gray Treefrog** (***Hyla versicolor***; Figure 9-Figure 10) (Desrochers & van Duinen 2006). Stockwell and Hunter (1989) also examined peatland amphibians in Maine, USA, and found twelve amphibian species. Of these, 94% of the captures were anurans. The most abundant of these was ***Lithobates sylvaticus*** (**Wood Frog**; Figure 5), comprising 59% of the captures. ***Lithobates clamitans*** (**Green Frog**; Figure 3) was the second most abundant, with 30% of the captures. Despite the presence of both sexes among adults in the Maine peatlands, Stockwell and Hunter concluded that none of the frogs except ***Lithobates sylvaticus*** (Figure 5) laid eggs in the peatlands. In Minnesota, the **American Toad** (***Anaxyrus americanus***; Figure 14) is added to the previous lists as one of the dominant species (Karns 1992a; Figure 13).

Figure 4. **Pickerel Frog**, ***Lithobates pipiens*** (Ranidae), among ***Sphagnum***. Photos by Janice Glime.

Figure 5. ***Lithobates sylvaticus*** on the moss ***Atrichum***. Photo by © John White, with permission.

Figure 6. **Mink Frog**, ***Lithobates septentrionalis*** (Ranidae). Photo by Twan Leenders, with permission.

Figure 7. **Spring Peeper**, ***Pseudacris crucifer*** (Hylidae). Photo by Matthew Niemiller, with permission.

Figure 8. **Mink Frog**, ***Pseudacris triseriata*** (Hylidae). Photo by Twan Leenders, with permission.

Figure 9. **Gray Treefrog**, ***Hyla versicolor*** (Hylidae). Photo by Janice Glime.

Figure 10. **Gray Treefrog**, ***Hyla versicolor*** (Hylidae), ventral view. Photo by Twan Leenders, with permission.

Figure 11. **American Bullfrog**, ***Lithobates catesbeianus*** (Ranidae). Photo by John D. Willson, with permission.

Figure 12. The **Pickerel Frog**, ***Lithobates palustris*** (Ranidae), on a bed of terrestrial mosses. Photo by Janice Glime.

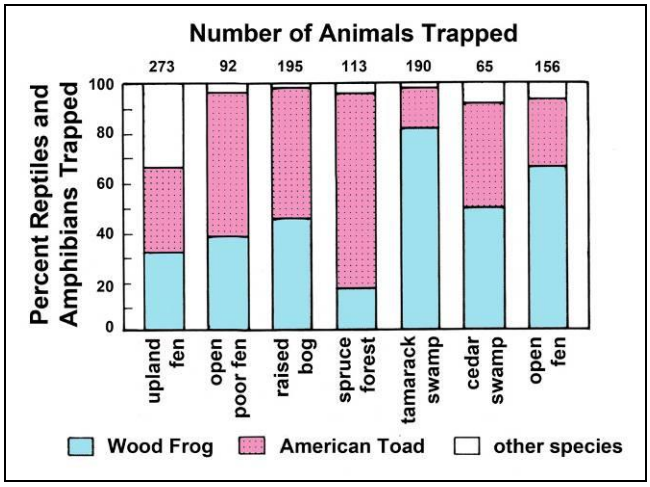

Figure 13. Comparison of percentage of **Wood Frogs** (***Lithobates sylvaticus***) with **American Toads** (***Anaxyrus americanus***) and other reptile and amphibian species trapped in various types of Minnesota peatlands. Redrawn from Karns 1992a.

The Tulula Wetlands, North Carolina, USA, have similar species to the boreal peatlands: **American Toad** (***Anaxyrus americanus***; **Bufonidae**; Figure 14), **Cope's Gray Treefrog** (***Hyla chrysoscelis***; Figure 15), **Green Frog** (***Lithobates clamitans***; Figure 3), **American Bullfrog** (***Lithobates catesbeianus***; Figure 11), **Wood Frog** (***Lithobates sylvaticus***; Figure 5), and **Spring Peeper** (***Pseudacris crucifer***; Figure 7) (Amphibians: Tulula Wetlands 2009). Knutson *et al*. (2000) suggest that the presence of **Pickerel Frog** (***Lithobates palustris***; Figure 12) is the best indicator of habitat quality in cold wetlands. Bog ponds can be especially enticing for amphibians because they harbor numerous insects and other invertebrates that serve as food (Desrochers & van Duinen 2006). Nevertheless, not all bogs seem to hold this attraction; in Estonia, frogs and toads are rare in bogs (H. Strijbosch in Desrochers & van Duinen 2006).

Figure 14. ***Anaxyrus americanus*** (**American Toad**) sitting on mosses. Photo by John D. Willson, with permission.

Figure 15. **Cope's Gray Treefrog**, ***Hyla chrysoscelis*** (Hylidae) with throat inflated while calling. Photo from US Geological Survey, through public domain.

Effects of *Sphagnum* Acidity

Because of its nearly continuous moisture, ***Sphagnum*** would seem to be an ideal habitat for frogs. But there is a caveat. ***Sphagnum*** acidifies its environment. And adult frogs typically avoid acidic conditions (Karns 1992a; Vatnick *et al*. 1999). Acidity can interfere with their development (Pough 1985; Leuven *et al*. 1986). Hence, it appears that low *p*H bog ponds might be of little or no importance in successful breeding and reproduction, but can be detrimental or lethal during tadpole development for most anurans (Gosner & Black 1957).

Rorabaugh (2008) found that the use of New Brunswick peatlands by the juvenile and adult **Northern Leopard Frogs** (***Lithobates pipiens***; Figure 4) peaked in August, a time when juveniles disperse from the breeding ponds (Mazerolle 2001). But *p*H is a problem for them. Tadpoles were unable to survive at *p*H less than 4, and even at less than *p*H 5.6 for more than 24 hours, mortality was high (Rorabaugh 2008).

As already suggested, ***Sphagnum*** can present problems for frogs because of the low *p*H conditions it creates. The **Wood Frog**, ***Lithobates sylvaticus*** (Figure 5), has tolerance to the lowest *p*H values measured in the New Jersey Pine Barrens, USA (Johnson 1985; Freda & Dunson 1986). In nine Maine bogs, Stockwell and Hunter (1985) found the **Wood Frog** to be the most common of the amphibians (59% of amphibians and reptiles). Karns (1979) never found tadpoles of this species at a *p*H lower than 5.0, although Johnson (1985) determined that eggs could develop normally at *p*H 4.0. Freda and Dunson (1985) showed that tadpoles of ***L. sylvaticus*** experienced lower sodium, chloride, and water concentrations in a low-*p*H pond (4.05-4.90) than did those from a nearby pond with a *p*H of 5.74-6.37. Higher sodium efflux occurred in both populations when placed in the lower *p*H pond, demonstrating the effect of low *p*H on ionic regulation in the tadpoles. This ability to exist in low *p*H water gives them an advantage – their predators are unable to survive the low *p*H, giving the tadpoles a huge advantage (See

discussion of overwintering and the anecdotal story by Dick Andrus).

Mazerolle and Cormier (2003) reported that they had captured **Green Frog** tadpoles in some of the bog ponds. However, they considered these ponds to be marginal, with an average *p*H of 3.67 (Mazerolle 2005), whereas the LC_{50} (*p*H at which 50% of frogs died) for **Green Frog** tadpoles in one study was 3.36 (Freda & Taylor 1992). Hence, the habitat was indeed marginal and indicated its importance despite its near-lethal *p*H. On the other hand, ***Lithobates clamitans*** (**Green Frog**; Figure 3) was among the most common (29%) of the amphibians and reptiles trapped in nine Maine, USA, bogs (Stockwell & Hunter 1985). In contrast, Brooks *et al*. (1987) found 13 amphibians and reptiles in peatlands of the Pocono Mountain region of Pennsylvania, USA, but none was common. The **Green frog** and ***Lithobates sylvaticus*** (**Wood Frog**; Figure 5) were not among the most common there. In Minnesota, the **Wood Frog** was the dominant amphibian (47% of all amphibian and reptile captures), but the **Green Frog** was conspicuously absent (Karns 1992a). Rather, in the Minnesota peatlands the **American Toad** (***Anaxyrus americanus***; Figure 14) was among the most common. Karns attributed this to more pools in the Maine peatlands, favoring the more aquatic **Green Frog**.

Not all amphibians are equally susceptible to the effects of low *p*H. Freda and Dunson (1986) found that in central Pennsylvania and the New Jersey Pine Barrens, USA, the **Jefferson Salamander** (***Ambystoma jeffersonianum*; Ambystomatidae**) and **Fowler's toad** (***Anaxyrus fowleri***, formerly *Bufo woodhousei*; Figure 16) were intolerant of water with a low *p*H. These two species had significantly higher mortality in ponds with low *p*H. In addition, ***Pseudacris triseriata***, ***P. crucifer***, ***Lithobates pipiens*** (Figure 4), ***Hyla versicolor*** (Figure 9-Figure 10), and ***Anaxyrus*** (=*Bufo*) ***americanus*** (Figure 14) were negatively affected by low *p*H water found in bog lakes. In laboratory experiments, ***Anaxyrus fowleri*** (Figure 16 and ***Hyla andersonii*** (**Pine Barren Treefrog**; Figure 17) exhibited significantly slower growth under acidic conditions, perhaps helping to explain the global decline in amphibians under the bombardment of acid rain. Freda and Dunson suggested that the small but erratic fluctuations of *p*H in the New Jersey ponds could contribute to their demise. They found that a *p*H change of only 0.2 units could alter hatching success. Contributions from acid rain could alter the *p*H sufficiently to kill sensitive eggs and larvae if the event were to occur at a critical time. In ponds where ***Sphagnum*** or other mosses are contributing H^+ ions, this additional input could to be lethal.

On the other hand, in these same locations the **Wood Frog** (***Lithobates sylvaticus***; Figure 5) and the **Pine Barrens Treefrog** (***Hyla andersonii***; Figure 17) tadpoles occurred in ponds with the lowest *p*H values, with the latter hatching at a *p*H as low as 3.70 (Freda & Dunson 1986). Ling *et al*. (1986) in Marquette County, Michigan, and Karns (1992b) in northern Minnesota, USA, found a similar tolerance for low *p*H in tadpoles of ***Lithobates sylvaticus*** (Figure 5). The larvae were seemingly unaffected when reared at *p*H as low as 3.0 (Ling *et al.* 1986). But further study is needed to explain the survival of ***Hyla andersonii*** at such low *p*H levels when the same authors (Freda & Dunson 1986) have demonstrated that low *p*H has a negative effect on its growth.

Figure 16. **Fowler's Toad** (***Anaxyrus fowleri***) sitting on ***Plagiomnium***. Photo by Twan Leenders, with permission.

Figure 17. ***Hyla andersonii*** (**Pine Barrens Treefrog**). Photo by Bruce Means, US Fish & Wildlife Service, with permission.

It is perhaps encouraging that proximal populations of ***L. sylvaticus*** (Figure 5) may differ. Karns (1992b) found that both embryos and larvae of ***L. sylvaticus*** from northern Minnesota peatlands had a greater tolerance for the low *p*H of bog water than did those that came from a circumneutral marsh in southern Minnesota. However, Karns concluded that the preference of this species for fen sites (higher *p*H) was due to being born there and not to avoidance of bog water.

Acid as a Refuge - *Rana arvalis* (Moor Frog, Ranidae)

The Moor Frog (***Rana arvalis***; Figure 18) occurs in many European countries. This frog can be the only frog species in some upland Lithuanian bogs (Đireika & Staðaitis 1999). As many as 20 individuals may be found in 0.1 hectare. However, throughout Europe it inhabits a wide range of habitats. In Siberia it occurs primarily in open swamps.

Figure 18. The **Moor Frog**, ***Rana arvalis*** on ***Sphagnum***. Photo by Piet Spaans, through Creative Commons.

This is one of the few species that is able to breed in acid peat bogs (Figure 19) because the acidic water is not suitable for frog egg development in most species (Klaus Weddeling, Bryonet 26 March 2011). Šandera (pers. comm. 20 February 2011) suggested that the frogs may hide in mosses in the summer to maintain moisture. Extensive fishery and agriculture threaten the future of ***Rana arvalis*** (Figure 18) (Šandera *et al*. 2008.

Figure 19. ***Rana arvalis*** in amplexus with the male on top. Notice the difference in coloration between the male and female. Photo by Martin Šandera, with permission.

Moisture Refuge

The **Wood Frog** (***Lithobates sylvaticus***; Figure 5) also may use ***Sphagnum*** as a "refugium" when it is migrating to its summer habitat and during the daytime in forested wetlands (Baldwin *et al*. 2006). The moisture and protection from the sun permit it to survive its trek to its new home. At least in Maine, USA, forested wetlands with *Sphagnum* are important in their migratory success. It is time to let the world know that to save the frogs we may need to save the mosses!

As already discussed, frogs need moisture. Hence, Mazerolle (2005) investigated the use of ***Sphagnum*** bogs (peatlands) by **Northern Green Frogs,** ***Lithobates*** (=*Rana*) ***clamitans melanota*** (Figure 20), in New Brunswick, Canada, to look for indications that the low *p*H would deter them from use of the moist habitat of the bog.

Figure 20. **Green Frog**, ***Lithobates clamitans***. Photo by Tony Swinehart, with permission.

Burrows in the Bog Moss

The **Common Frog** in Europe (***Rana temporaria***; Figure 21) inhabits raised bogs, blanket bogs, and fens (Peatlands 2009). Ida Bruggeman (pers. comm. 5 February 2009) observed them in her own Netherlands garden peatland, where they sometimes would burrow into holes dug by **Green Frogs** (***Pelophylax***). They never seemed to dig their own holes, however. She was able to observe ***P. rubicundus*** digging a burrow in which it would sit for hours (Figure 22-Figure 24). It would return to the same burrow for several consecutive days.

Figure 21. ***Rana temporaria*** (**Common Frog**) mating. Photo by Richard Bartz, through Wikimedia Commons.

Figure 22. A green frog, ***Pelophylax ridibundus***, in a ***Sphagnum*** bank in the garden of Ida Bruggeman in The Netherlands. This one is resting in the burrow it dug. Photo by Ida Bruggeman, with permission.

Figure 23. **Marsh Frog**, ***Pelophylax ridibundus*** peering out of resting burrow in ***Sphagnum***. Photo by Ida Bruggeman, with permission.

Figure 24. An empty burrow of the green frog, ***Pelophylax ridibundus***, in a ***Sphagnum*** bank in the garden of Ida Bruggeman in The Netherlands. Photo by Ida Bruggeman, with permission.

Figure 25. **European Common Spadefoot Toad** (***Pelobates fuscus***). Photo by Christian Fischer, through Wikimedia Commons.

Retreats – Mosses Instead of Sand

The **European Common Spadefoot** (***Pelobates fuscus***; Pelobatidae; Figure 25) can occur in ***Sphagnum*** peatlands, where its retreat-making behavior might be useful (Stachyra & Tchórzewski 2004). But its typical habitat is farmland, dunes, and pinewoods (Bosman & van den Munckhof 2006). This spadefoot is also known as the garlic toad because of the odor it emits as part of its noxious exudation defense mechanism. Like so many species of amphibians, this one is also disappearing. Its need for a suitable terrestrial habitat is emphasized by its predominantly beetle diet (Nicoară *et al*. 2005).

A Toxic Bog-dweller – *Bombina bombina* (European Fire-bellied Toad, Bombinatoridae)

Native to lowland swamps and wetlands (IUCN 2011), the **European Fire-bellied Toad** is named ***Bombina bombina*** (Figure 26). [**Tautonyms** (specific name repeats the generic name) are acceptable in zoological nomenclature, but are cause for rejection in botanical nomenclature and word processor grammar checkers!] ***Bombina bombina***, common in eastern and central Europe (IUCN 2011) and from the Balkans across central and eastern Asia (Staniszewski 1998), is one of the amphibians that inhabit the highland and transitional ***Sphagnum*** peatlands in Poland (Stachyra & Tchórzewski 2004), as well as bogs in other areas. It is not a true toad, but does have a warty skin. Its name derives from its bright red-orange belly that acts as warning coloration against predators, especially as it rears up to expose its bright underbelly. Despite its toxic skin, this and several other species of fire-bellied toads are kept as pets.

When it is time to shed its skin, this slightly toxic (to humans) toad first bloats itself, making a coughing sound, then tears off its skin with its mouth and eats it for added nutrition (Wikipedia 2008). When endangered, it rolls over, exposing its colorful belly, and covers its eyes with its feet (AmphibiaWeb: *Bombina bombina* 1999). In other cases, it may arch its back and expose its brightly colored underside (Wikipedia 2010). Despite its threatening color display and distasteful poison, it still is frequently eaten.

Figure 26. **European Fire-bellied Toad** (***Bombina bombina***). Photo by Mark Szczepanek, through Wikimedia Commons.

BSTI is a protease in the skin of these frogs that is a trypsin and thrombin inhibitor (Mignogna *et al*. 1996). Mignogna and coworkers suggest that the role of this protease in the skin is to prevent the premature release or breakdown of skin peptides. But it seems likely that the protease may also have toxic properties against predators. Certainly, inhibition of thrombin can cause excessive

bleeding, but the authors did not test this possibility in would-be predators. Despite its use of many kinds of habitats, the disappearance of wetlands is the greatest threat to this species (AmphibiaWeb: *Bombina bombina* 1999).

Ground-Dwellers: Bufonidae (Toads)

Although a number of amphibians have the common name of toad, only members of the Bufonidae are true toads. They differ from all other amphibian families by the presence of a pair of **parotoid** glands (Figure 27) at the back of the head, behind the eyes. Most of the Bufonidae have conspicuous warts, but so do members of many other Anuran species. Otherwise, they generally resemble frogs.

North American toads have recently been moved to a different genus, based on genetics and cladistics (Naish 2009), from the well known genus ***Bufo*** to ***Anaxyrus***, a genus restricted to the North American continent. However, this move is not acceptable to all herpetologists because it makes the remaining genus ***Bufo*** paraphyletic (Pauly *et al*. 2004, 2009). Furthermore, morphological characters that unite the genus ***Anaxyrus*** and separate it from ***Bufo*** have not yet been elaborated. Nevertheless, I shall use ***Anaxyrus*** for the North American members where it is appropriate, but be aware that other genera have also been split off from ***Bufo*** as well.

Most of us know the toads from childhood and may have been told that we would get warts from handling them. But toads don't cause warts. They do, however, emit secretions that can be irritants to some people. Toads have a pair of **parotoid glands** (Figure 27) on the backs of their heads. These excrete an alkaloid poison when the animals are stressed. There is a variety of compounds in these, differing among species. The term **bufotoxin** refers to any of these. The most toxic of these is from the Cane Toad, *Rhinella marina* (previously *Bufo marinus*).

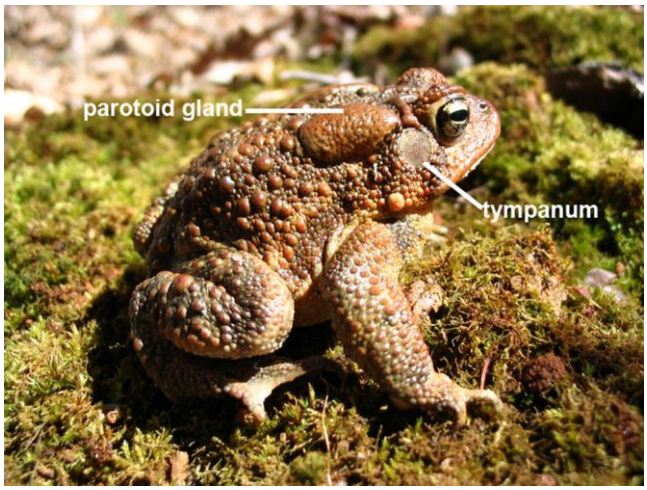

Figure 27. Head and thorax of the American Toad, ***Anaxyrus americanus***, illustrating the location of the parotoid gland and the tympanum, the external portion of the ear drum. Photo © Jason Gibson, with permission for academic use.

As already seen, toads certainly make use of bryophytes as hibernacula, where they spend the winter under the insulating blanket of clumps and thick mats. Toads spend less time in the water than do the true frogs. Hence, in addition to casual use, as is likely for ***Nannophryne variegata*** (previously *Bufo variegatus*) in Figure 1**,** we might expect somewhat different uses of the bryophytes than that seen for frogs.

Most toads lay their eggs in paired strings in open water (Figure 28) (Wikipedia 2015b). These eggs hatch into tadpoles except in ***Nectophrynoides***, whose eggs hatch directly into tiny toads.

Figure 28. ***Rhinella arunco*** (Bufonidae) strings of eggs. Photo © Danté B. Fenolio <www.anotheca.com>, with permission.

One of the strangest characteristics for toads is the ability of the male to change sex! These males have a **Bidder's organ** that can become an ovary under the right conditions (Wikipedia 2015b). But apparently this organ only becomes functional as an ovary when the testes are destroyed – an event most likely to occur in the lab (Wikipedia 2014). But it can also become functional when the testes are rendered non-functional by exposure to endocrine-disrupting chemicals. This may be somewhat adaptive in our polluted world.

Anaxyrus americanus (American Toad, Bufonidae)

Among the amphibians of the boreal peatlands in North America (Desrochers & van Duinen 2006) and the Tulula Wetlands in North Carolina, USA (Amphibians: Tulula Wetlands), one can find the widespread American Toad, ***Anaxyrus americanus*** (Figure 29-Figure 32). In Maine, USA, wetlands this species likewise occurred, but it was not abundant (Desrochers & van Duinen 2006).

It is likely that toads use bryophytes as part of a mosaic habitat. Their mottled browns and grays make them inconspicuous on the intermittent patches of soil. They can burrow under the bryophytes in winter to hibernate or burrow into them in summer to get cool or remain hydrated (Figure 30).

Terrestrial mosses may be more important than wetlands for toads. In the late autumn, I have more than once lifted a clump of moss for a collection, only to find a very quiet toad (**American Toad**, ***Anaxyrus americanus***; Figure 29) under the moss. I presumed that these animals were spending the winter there. It would seem likely that the moss would help to protect them from desiccation and cold during the winter months, and perhaps even lessen evaporative cooling. Kate Frego (personal communication 12 January 2008 and Bryonet 3 February 2009) relays this interesting story from Crepieul Township, northern Ontario (near town of Chapleau), Canada. She was working in an

upland white spruce post-fire forest, ~130 years old, with a thick carpet of ***Pleurozium schreberi*** (Figure 33). "It was quite startling! I arrived at my site before the snow melted (on purpose) and watched everything come to life. One day the ***Pleurozium*** carpet around some tree bases was literally pulsating. I was somewhat spooked, and watched for some time, from a distance!! Eventually there was a little break in the moss, and these toad feet 'swam' out, and a great fat **American Toad** pulled itself out of the opening it had made." The toad sat on the moss in the warm sun, then hopped off toward the pond. She estimates that the toad had been about 12 cm below the surface of the mosses. The pond nearby was full of **American Toad** tadpoles every year she was there, suggesting that this was an important breeding and overwintering habitat.

Figure 29. **American Toad**, ***Anaxyrus americanus***, peering through the sporophytes of ***Polytrichum***. Photo by Josh Vandermeulen, with permission.

Figure 30. Toad (***Anaxyrus***) burrowed into moss in July in the Adirondacks, eastern USA, perhaps to keep its skin moist. Photo by Sean Robinson, with permission.

To be of use to the toads, breeding habitats must be near water – ditches, pools, even vernal ponds. Eggs are laid in a long string or tube and young are hatched as tadpoles (Figure 34).

Figure 31. The common **American Toad**, ***Anaxyrus americanus***, on a bed of the moss ***Atrichum***. Photo by Twan Leenders, with permission.

Figure 32. **American Toad**, ***Anaxyrus americanus***, showing nostril, eye, tympanum, and warts. Photo by Janice Glime.

Figure 33. ***Pleurozium schreberi***, a moss where toads can emerge in the spring. Photo by Janice Glime.

Figure 34. Eggs and tadpoles of the common **American Toad *Anaxyrus americanus*** in a shallow pool. Photo by Janice Glime.

Anaxyrus boreas (Western Toad, Bufonidae)

Bartelt *et al.* (2004) used radio transmitters to demonstrate the movement patterns of 18 **Western Toads** (***Anaxyrus boreas***, previously *Bufo boreas*; Figure 35). The toads seemed to move at times and through habitats that maximized moisture conservation and selected moss cover for their movements 1.8% of the time, despite a frequency of this cover type that was near zero. Browne and Paszkowski (2010a) found that in north-central Alberta, Canada, this species used moss-covered peatland, among other habitats, during the foraging period, but they did not report use of mosses for hibernation (Browne 2010; Browne & Paszkowski 2010b).

Figure 35. ***Anaxyrus boreas*** on the forest floor where moss cover can help to maintain skin moisture. Photo by William Flaxington, with permission.

Bull (2009) found a similar preference by juveniles for mossy areas in Oregon. Young toads dispersed up to 2720 m from their site of birth within only 8 weeks after entering their adult stage. During their movement to their new summer home, they were subject to desiccation, predation (especially by birds), death by car, cattle trampling, and chytridiomycosis infection. Having mosses at 85% of the plots where juveniles occurred, compared to presence of mosses in only 3% of the area may only be a correlation with the need for the water. Mosses may have occurred in wetter areas. Nevertheless, Bull suggested that the mosses helped to provide protection from desiccation.

Bufo bufo (European Common Toad, Bufonidae)

The **European Common Toad** (***Bufo bufo***; Figure 36), which also extends into northern Africa, may be one of the few amphibians to eat bryophytes. Javier Martínez Abaigar (February 2009 pers. comm.) tells of finding bits of leaves of aquatic bryophytes, such as ***Fontinalis antipyretica*** (Figure 37), ***Chiloscyphus polyanthos*** (Figure 38), and other unidentified species, in the guts of tadpoles of this toad. Was this truly intended as food? Or did the rasping mouth tear these as it scraped algae from the leaves, or did they enter as detritus among the other edibles nestled among the bryophytes or on the bottom? In any event, I thought this would be worth exploring as a potential dispersal mechanism for the moss, but Javier says the tadpoles are confined to small, quiet pools and would provide no more dispersal than the fragment would have without the help of the tadpole, unless of course, the tadpole gets eaten.

Figure 36. Brown expression of the **European Common Toad**, ***Bufo bufo***, amid herbaceous plants and bryophytes. Photo by Milan Kořínek, with permission.

Figure 37. ***Fontinalis antipyretica***, shown here exposed out of water in early autumn, is an occasional food source for the **European Common Toad**, ***Bufo bufo***. Photo by Janice Glime.

Figure 38. ***Chiloscyphus polyanthos***, an occasional food source for the **European Common Toad**, ***Bufo bufo***. Photo by Des Callaghan, with permission.

This **European Common Toad** excretes a **bufagin** toxin that deters most predators. Unfortunately for the toad, grass snakes and hedgehogs, both predators on toads, are immune to it (Wikipedia 2015a). Females typically return to the pond where they were born to lay eggs in the spring. As adults, they are land-born, eating insects and other small invertebrates, but turnabout is fair play – larger toads may also eat grass snakes. These toads are on the IUCN (2010) red list of endangered species. They are often vulnerable when crossing roads to reach breeding grounds, causing some environmental groups to build tunnels under the road to permit safe crossing (Figure 39). Mazerolle (2005) indicates that drainage ditches may offer similar facilitation for frogs.

Figure 39. Tunnel under road to permit safe passage of the **European Common Toad *Bufo bufo*** to and from its breeding grounds. Photo by Christian Fischer, through Wikimedia Commons.

Incilius coniferus (formerly *Bufo coniferus*, Evergreen Toad, Bufonidae)

Incilius coniferus (formerly *Bufo coniferus*; **Evergreen Toad)** (Figure 40) is listed as a species of least concern (IUCN 2011), but it seems to be largely ignored. A Google search found nothing except its occurrence on several species lists. Its known distribution was on both Atlantic and Pacific slopes in east-central Nicaragua, Costa Rica, and Panama and into the Pacific lowlands of Colombia and northern Ecuador (Frost 2011).

Figure 40. ***Incilius coniferus*** (**Evergreen Toad**) blending with a bed of mosses and liverworts. Photo by Brian Gratwicke, through Creative Commons.

I could find nothing to indicate this species makes use of bryophytes for a habitat element, but the picture shown here (Figure 40) suggests that it might, and that it certainly would have good camouflage if it did. But this is not its only coloration. Most individuals are yellow-green to olive green, or even dull brown or gray, with little mottling, or sometimes with white or dark blotches (Savage 2002). The presence of warts helps to disrupt its coloration and facilitate blending with its environment. This individual seems to have combined these in just the right way to blend with the surrounding bryophytes. These color patterns help it to blend with its humid lowland forest and premontane habitat, where it is known up to 1550 m (Savage 2002). But it most likely also helps make it less conspicuous when it climbs, as much as several meters (Duellman & Schulte 1992; Savage 2002).

A further suggestion, besides its coloration, that bryophytes might be an important part of its habitat is that it eats ants and mites (Toft 1981), both of which can be abundant among bryophytes. Its oviposition doesn't offer any clues – it occurs at the beginning of the wet season, and the frogs place the eggs in temporary pools or depressions (Crump 1989). Tadpoles emerge from the eggs five days later, attesting to its aquatic, rather than terrestrial, affiliations. Is the coloration of ***Incilius coniferus*** (**Evergreen Toad;** Figure 40) just a co-incidence?

Pseudepidalea viridis (Green Toad, Bufonidae)

The green toad, ***Pseudepidalea viridis*** (previously *Bufo viridis*) (Figure 41) is a common inhabitant of peatlands in high elevation and transitional peat bogs in Poland (Stachyra & Tchórzewski 2004). This frog breeds over several months, presumably as a mechanism for greater survival in habitats that may dry up before tadpoles mature (Kovács & Sas 2009). When food gets scarce, the tadpoles may become cannibalistic, a phenomenon known in other tadpoles such as ***Anaxyrus boreas*** (Figure 35) (Jordan *et al*. 2004).

Figure 41. The **Green Toad**, ***Pseudepidalea viridis***, a peatland inhabitant. Its coloration suggests it might blend well with the mix of moss tops and dark spaces in the peatland. Photo by © John White, with permission.

Epidalea calamita (Natterjack Toad, Bufonidae)

Although this European frog, a close relative of ***Pseudepidalea viridis*** (Figure 41), inhabits sand dunes and gravel quarries (AmphibiaWeb: *Bufo calamita* 2006), the **Natterjack toad**, ***Epidalea calamita*** (previously *Bufo calamita*) (Figure 42-Figure 43), is likewise a common inhabitant of peatlands in high elevation and transitional peat bogs in Poland (Stachyra & Tchórzewski 2004). This is the only species of toad native to Ireland, where it lives near pools that stay warm (Wikipedia 2016). In The Netherlands, Strijbosch (1979) found this species selected the most eutrophic sites during its aquatic stage. Elsewhere in Europe it is common in heathlands.

Figure 42. Very young **Natterjack Toad**, ***Epidalea calamita*** climbing among the mosses. Photo by Piet Spaans, through Creative Commons.

In southern Britain, these toads avoid *Calluna* heaths, but they spend their entire lives in open areas where bare sand or short bryophyte turf dominates the landscape (Banks *et al*. 1993). It is interesting that introducing the cyprinid fish known as **ide** or **orfe** (***Leuciscus idus***; Figure 44) to the breeding pools reduced the predatory invertebrates, increasing survival of the tadpoles. Unfortunately, adults, especially males, fell prey to the grass snake (***Natrix natrix***; Figure 45).

Figure 43. Adult **Natterjack Toad**, ***Epidalea calamita***, at night. Photo by Christian Fischer, through GNU Free Documentation License.

Figure 44, ***Leuciscus idus*** (**ide** or **orfe**), a fish that reduces predators on the tadpoles of ***Epidalea calamita*** by eating the predators. Photo through Wikimedia Commons.

Figure 45. ***Natrix natrix*** (**Grass Snake**), a predator on adult **Natterjack Toads** (***Epidalea calamita***). Photo by Karl Larsaeus, through Wikimedia Commons.

Beebee (1977) attempted to determine the cause of 40 years of decline in this species. It is interesting that it was the inland heaths that had the greater decline, compared to the dunes. Climate change, human activity, and development did not seem to be a problem. Rather, large-scale changes in the heathland flora were responsible. Grazing stopped and forestry activity increased, permitting the invasion by taller vegetation and greater shade. These conditions were unsuitable for the **Natterjack Toad**, but a greater problem was the invasion of its competitor, ***Bufo bufo*** (Figure 36).

Leptophryne cruentata (Indonesia Tree Toad, Bleeding Toad, Bufonidae)

Leptophryne cruentata (Figure 46-Figure 47) is a true toad distributed in Southeast Asia, primarily Indonesia. Kusrini *et al*. (2007) found fifteen frogs hidden in a crevice covered by mosses in the wall of a waterfall. Its habit of hiding could explain its elusiveness. It is listed as critically endangered, at least partly because of the volcanic eruption of Mount Galunggung in 1982 (Wikipedia: Bleeding Toad 2008) that buried a large part of its range.

Figure 46. **Indonesian Tree Toad**, ***Leptophryne cruentata***, showing a pink-purple variety. Photo by Frank Yuwono, with permission.

Figure 47. ***Leptophryne cruentata***, the **Indonesian Tree Toad**, showing a red and yellow spotted variety. Photo by Georg Moser, with permission.

Atelopus zeteki (Panamanian Golden Frog, Bufonidae)

In tropical wet forest stream habitats, the critically endangered Panamanian Golden Frogs (***Atelopus zeteki***; Figure 48-Figure 49) can be found among mosses (Hong 2007; Lindquist *et al*. 2007). Technically a toad (Bufonidae), these amphibians look more like a tree frog. They may climb as much as 3 m near water falls, where they perch on large moss-covered boulders. But beware of these beautiful frogs. Their skin contains a highly toxic alkaloid that is an analog of **saxitoxin** (Fuhrman *et al*. 1969; Brown *et al*. 1977) and has the ability to block sodium channels in the nervous system (Yotsu-Yamashita *et al*. 2004).

Figure 48. **Panamanian Golden Frog** (***Atelopus zeteki***) sitting among bryophytes and ferns beside a stream. Photos by © John White, with permission.

Figure 49. ***Atelopus zeteki*** (**Panamanian Golden Frog**) with a conspicuous yellow dorsal view while sitting on a bed of moss. Photo by Dave Pape, through Wikimedia Commons.

Figure 50. Habitat of ***Atelopus zeteki*** (**Panamanian Golden Frog**). Photo by Brian Gratwicke, through Creative Commons.

Atelopus loettersi (Bufonidae)

This newly described species was located on the Amazonian slopes of southern Peru at 400-1000 m asl (De la Riva *et al*. 2011). Only tiny juveniles could be found, dwelling on mosses covering a large rock wall along a river bank. That appears to be all that is known about this species at this time.

Toads in the Trees: Bufonidae

Rhinella tacana (formerly *Chaunus tacana*, Bufonidae)

First named in 2006 (Padial *et al* 2006), ***Rhinella tacana*** (Figure 51) lives in the humid forest at only one known location in Bolivia at 1500 m asl (Frost 2011). It lives in Andean valleys and Amazonian slopes. Within its habitat, it climbs moss-covered tree trunks and rests on leaves or trunks at 1-4 m height (Padial *et al*. 2006). Its reproduction is unknown and too little is known about it for classification in the IUCN redlisting (IUCN 2011).

Figure 51. ***Rhinella tacana***, a toad that climbs mossy tree trunks in Bolivia. Photo by Sean Michael Rovito, with permission.

Ansonia latidisca (Borneo Rainbow Toad, Sambas Stream Toad, Bufonidae)

The **Sambas Stream Toad** (Figure 52) had not been seen since 1924 when Dr. Indraneil Das and his research team set out in 2011 to find it (Lin 2011). Just imagine the excitement of his graduate student, Pui Yong Min, who discovered it near the border of Indonesia and Malaysia, perched 2 m above ground on a moss-covered branch. But at this time, that is about all we know about it, except that it is a beautiful toad that would be a desirable pet for that reason. Therefore, to protect it, the location will not be published.

Figure 52. ***Ansonia latidisca***, **Borneo Rainbow Toad**, perched on mosses 2 m up in a tree. Photo by Indraneil Das, with permission.

Eastern Hemisphere Mossy Habitats

Arthroleptidae

Leptodactylodon albiventris (**Whitebelly Egg Frog;** see Figure 53) is endemic to Cameroon, Africa, in subtropical and tropical moist lowland forests, moist montane areas, rivers, and rocky areas (Amiet 2004). Living at 300-1000 m asl (Frost 2011), this species calls day and night from hidden locations; it finds a thin layer of water flowing under rocks or other cover and can only be located by removing the rocks, mosses, or looking among submerged roots (De la Riva *et al*. 2001).

Figure 53. ***Leptodactylodon*** sp. (**Whitebelly Egg Frog**) on leaf, member of a genus where some species hide under mosses in flowing water. Photo by Ignacio De la Riva, with permission.

Myobatrachidae

Pseudophryne (Myobatrachidae)

Several species in this genus, which is endemic to Australia, are known to be bryophyte inhabitants. Unique

to ***Pseudophryne*** species among the anurans, part of their defense is accomplished by a class of indolic alkaloids called **pseudophrynamines** (PS's). These compounds appear to be produced internally, either by the frog itself or by symbiotic organisms living within the frog (Smith et al 2002). In addition to these toxic alkaloids, they also possess **pumiliotoxins** (PTX's). The latter are found in all genera worldwide if those anurans (frogs & toads) contain lipophilic alkaloids. The PTX's appear to have a dietary source, with lab-reared animals lacking the compound. It is subsequently incorporated into the skin. An interesting consequence of high levels of this skin toxin is that it seems to inhibit the production of PS.

Pseudophryne corroboree & *P. pengilleyi* (Corroboree Frogs, Myobatrachidae)

The genus ***Pseudophryne*** is known only from Australia. The alpine species ***Pseudophryne corroboree*** (Figure 54) in New South Wales, Australia, has been split into two species with the northern one separated into ***P. pengilleyi*** (Osborne *et al.* 1996; Figure 55). Corroboree is the aboriginal name for a group meeting and the name of the frogs refers to the habit of gathering in large groups to form a chorus.

Figure 54. ***Pseudophryne corroboree***, an alpine corroboree frog from New South Wales, Australian, shown here in its peat moss (***Sphagnum***) habitat. Its bumblebee coloration is a better warning coloration than a camouflage. Photo by Scott Robinson <www.ifrog.us>, with permission.

Figure 55. The **Northern Corroboree Frog**, ***Pseudophryne pengilleyi***, in its native peatland habitat in northern New South Wales, Australia. Photo by Ken Thomas, with permission.

Both live in peatlands and often deposit their 10-38 eggs there (Pengilley 1973) in locations that become seasonally inundated. The male makes deep burrows in the ***Sphagnum*** or other substrate and proceeds to call from there to attract females. Males generally stay with the eggs for two-four weeks. Like several other moss-dwelling frogs, females may deposit several clutches of eggs, thus making smaller clutches and increasing the oxygen availability to all the eggs (Woodruff 1976). The southern species, ***P. corroboree*** (Figure 54), is in danger of extinction (Project Corroboree). Efforts to save the species include captive breeding.

Pseudophryne semimarmorata (formerly *Pseudophryne bibroni*) (Southern Toadlet, Myobatrachidae)

Pseudophryne semimarmorata (Figure 56) occurs in the extreme southeast of South Australia, southern Victoria, and eastern Tasmania, where it enjoys the status of least concern – an unusually safe designation for a small frog (IUCN 2010). It is called a toadlet due to its warty appearance, but it is not a true toad. Its typical habitats are dry forest, woodland, shrubland, grassland, and heath (Frogs of Australia 2011). The frogs hide under leaf litter or other debris (a designation that includes bryophytes) in depressions and other moist areas. They move about in their habitat by walking instead of the familiar hop we typically think of for frogs, but then many (most?) frogs walk or crawl when not trying to escape something.

Figure 56. ***Pseudophryne semimarmorata***, a species that hides under mosses in southern Australia. Note the absence of a tympanum behind the eye. Photo by John Wombey, through Creative Commons.

Males call, from burrows that the males construct, in late summer and autumn (FrogsAustralia 2005). But this species lacks any structural hearing organ (Figure 57) (Loftus-Hills 1973b; Parks & Wildlife Service, Tasmania 2010). One hypothesis is that they sense the sounds through the vibrations of the skull bones, a concept supported by the correlation between head width and auditory threshold (Loftus-Hills 1973a). They cease calling if ***Crinia victoriana*** begins calling nearby, and resume when this competing species stops (Littlejohn & Martin 1969). These two species use the same frequency band (~2500 Hz), so cessation of the call increases the efficiency of their communication.

Figure 57. ***Pseudophryne semimarmorata*** on a bed of mosses. Note the absence of a tympanum behind the eye. Photo by John Wombey, through Creative Commons.

It has an unusual reproductive behavior that befits its amphibious habitat. The nesting burrows, dug by the males, are located near water or boggy ground (FrogsAustralia 2005). The females lay their large eggs in loose clumps under litter in these shallow burrows (Frogs of Australia 2011). These must be located where they will later be flooded so that the aquatic tadpoles have a place to swim. The unusual aspect is that the eggs of one female may have up to eight different fathers and be placed in as many different nests (O'Brien 2011). These fathers stay with their fertilized eggs until they have developed into tadpoles (O'Brien 2011), a duty that lasts for at least 42 days (Parks & Wildlife Service Tasmania 2010). This promiscuous strategy by the females increases the chances that some of her eggs will be in nests that are suitably positioned for flooding at the right time (O'Brien 2011). If they are flooded too early, the eggs could be washed away, whereas if flooding is too late, the eggs can dry out. Since mosses often grow in such amphibious locations, they may play a role in the "debris" used for nesting and adult habitat.

Crinia nimbus & C. georgiana (Australian Moss Froglet, Myobatrachidae)

In Tasmania, you might hear what sounds like a ping-pong ball dropped on wood: took-tok-tok-tok-tok-tok, the call of the endemic **Australian Moss Froglet**, ***Crinia nimbus***, a cloud forest froglet (Wildlife Management 2014; Figure 58). The call of this common but narrowly distributed frog (southern mountains of Tasmania) is likely to come from its position under mosses or lichens in its nest, thus muffled by the overlying cover (Sopory & Hero 2008).

In ***Crinia nimbus***, the larval development time is greatly benefitted by temperatures as they increase from 5 to 15ºC (Mitchell & Seymour 2003). It would be interesting to learn whether the dark-colored mosses serve as black bodies to warm the habitat for these larvae in winter. If so, they could significantly increase survival because the larvae do not feed, and at 5ºC they can run out of yolk and die before reaching adulthood and food intake.

The **Australian Moss Froglet** requires mosses or lichens to maintain sufficient moisture for the development of its embryos (Mitchell 2002a). The female deposits 4-16 large eggs (Figure 59) in nests made from these in the subalpine regions of southern Tasmania (Mitchell & Seymour 2000). The frogs spend one year as larvae within any of about 10 species of mosses, lichens, and lycopods (Mitchell 2002b), and in southern Tasmania, this occurs under the snow (Mitchell & Seymour 2000). In laboratory experiments, embryos that experienced more drying than that experienced among the mosses had asymmetrical deformities and lower survivorship (Mitchell 2002a).

Figure 58. The **Australian Moss Froglet**, ***Crinia nimbus***, a small (up to 30 mm length) Tasmanian endemic that sounds like a ping-pong ball calling from its nest under mosses. Photo by Gerry Marantelli, compliments of the Amphibian Research Centre <http://www.frogs.org.au/>, with permission.

Figure 59. **Australian Moss Froglet**, ***Crinia nimbus***, eggs in their nest under mosses. Photo by Gerry Marantelli, compliments of the Amphibian Research Centre <http://www.frogs.org.au/>, with permission.

But moisture is not the only contribution of the moss. The thick gelatinous capsule around the eggs in this species affords further protection from desiccation, but it creates a formidable barrier to the entrance of oxygen (Mitchell & Seymour 2003). Models predict that the frogs should die at temperatures above 5ºC due to insufficient oxygen, but in reality, the frogs have an added advantage in the moss layers and rarely die at any of their natural temperatures (Mitchell 2002a). Not only does the moss permit aeration of both lower and upper surfaces, but the photosynthetic

oxygen production further supplements the oxygen available. At night it is safer for the frog to roam away from the protection of the moss. In the daytime, the nest of ***Crinia georgiana*** (Figure 60) in a moss bed had double the oxygen it had during pre-dawn hours (Seymour *et al*. 2000).

Figure 60. Two frogs of ***Crinia georgiana***, looking very much like two humans doing a dance! Photo by Jean-Marc Hero, with permission.

Byrne (2002) found ***Crinia georgiana*** (Figure 60) breeding in shallow temporary pools by a sloping, moss-covered granite outcrop where it "enjoys" the privilege of having a testes size at least four times that of any other species of ***Crinia***. This unusual size may be an adaptation to its habit of multiple matings (1-9) with a single female, creating sperm competition (Birkhead 1995; Byrne 2002).

Crinia tasmaniensis (Tasmanian Froglet, Myobatrachidae)

Crinia tasmaniensis, the **Tasmanian Froglet** (Figure 61), is endemic to Tasmania and must always be near water (ZipcodeZoo.com: ***Crinia tasmaniensis*** 2009). This requirement takes it to alpine areas, rainforests, bogs, swamps, fens, and peatlands, where mosses are part of its environment. Its call sounds like a bleating sheep.

Figure 61. The **Tasmanian Froglet**, ***Crinia tasmaniensis***, an inhabitant of bogs, swamps, and peatlands, among others. Photo through GNU Free Documentation License.

Geocrinia victoriana (Victoria Ground Froglet, Myobatrachidae)

Gollmann and Gollmann (1996) collected ***Geocrinia victoriana*** (Figure 62) in southwestern Victoria and from 180-1300 m in central Victoria from mosses in a roadside ditch and under grass tussocks. In laboratory experiments they demonstrated that populations from the mountains were larger when they hatched and grew faster than those from the lowland sites, but those from the southwest were similar to their counterparts at higher altitudes in central Victoria.

Figure 62. ***Geocrinia victoriana*** adult. Photo by Matt, through Creative Commons.

Summary

Although peatlands provide moist sites for adults to rest, bog ponds are often too acid. Acidification has resulted in extirpation of many species of frogs, interfering with development, but apparently the Wood Frog (***Lithobates sylvaticus***) is more tolerant and thus can inhabit low *p*H ponds without risk of predation by other amphibians. The tadpoles of the Green Frog (***Lithobates clamitans***) are apparently unsuccessful in surviving the low *p*H of bog ponds. ***Rana arvalis*** is one of the few species that is able to breed in acid peat bogs. Nevertheless, many frogs use peatlands in summer. Frogs such as ***Rana temporaria*** (European Common Frog) and ***Pelophylax*** spp. (green frogs) often make burrows in *Sphagnum* banks as a resting place in summer; other frogs may use those same burrows or tunnels and burrows made by small mammals. The ***Sphagnum*** Frog (***Philoria sphagnicolus***) male excavates a nest where the female deposits the eggs; the tadpoles remain in the nest. The destruction of peatlands can result in decreases in both numbers and diversity of anurans.

The **American Toad** (***Anaxyrus americanus***) is common in wetlands, including peatlands, as well as forests. Toads often spend the winter under bryophytes where both temperature and humidity are modulated. The bryophytes may be especially important during migrations. Some toads, such as tadpoles of the European common toad (***Bufo bufo***), may eat bryophytes, but it is possible these bryophyte fragments

come along with bacteria, algae, and other food items being scraped from their surfaces.

The Cloud Froglet Tadpoles (***Crinia*** spp.) require the moisture of mosses or lichens for the larvae to develop. The mosses also provide oxygen to the eggs and adults. Panamanian Golden Frogs (***Atelopus zeteki***) perch on mosses near waterfalls to maintain their moisture.

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CHAPTER 14-4
ANURANS: WATERFALLS, TREEFROGS, AND MOSSY HABITATS

Janice M. Glime and William J. Boelema

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CHAPTER 14-4
ANURANS: WATERFALLS, TREEFROGS, AND MOSSY HABITATS

Figure 1. Honduran cloud forest at Parque Nacional Montana de Santa Barbara at 2180 m asl that is habitat to many tropical anurans. Photo by Josiah Townsend, with permission.

Waterfalls

Sachatamia ilex (formerly *Centrolene ilex*) (Limon Giant Glass Frog, Centrolenidae)

A number of glass frogs are native to Central and South America where they live in streams and in subtropical or tropical moist lowland and moist montane forests. The Limon Giant Glass Frog, ***Sachatamia ilex*** (Figure 2), is also known as the Ghost Glass Frog and is nocturnal and **arboreal** (lives in trees) (Leenders 2001). It sleeps during the day on the upper surfaces of leaves where its green coloration makes it inconspicuous. Its habitat is in both primary and secondary wet forests where it often occurs in the spray zone of waterfalls and rapids of streams. Its color makes it inconspicuous when its perches are covered with mosses and it may be more common there than observations would indicate.

Figure 2. The **Limon Giant Glass Frog**, ***Sachatamia ilex*** (formerly *Centrolene ilex*). Its pose here makes one wonder if it is watching for dinner among the mosses, a place where insects often hide. Photo by Twan Leenders, with permission.

Frogs in the Trees

We know that mosses that live in trees must have xerophytic adaptations to survive the periods of no rain. The frogs that live there are most abundant and have the most species in the tropics (as will be seen below), where they share their habitat with epiphytes, including bryophytes (Figure 1). We can presume that bryophytes hold moisture and protect against UV light in these arboreal habitats, permitting at least some species to have a better survival chance than would be possible with no bryophytes.

Espadarana prosoblepon (formerly *Centrolenella prosoblepon*) (Emerald Glass Frog, Centrolenidae)

The Emerald Glass Frog, ***Espadarana prosoblepon*** (=*Centrolenella prosoblepon*) (Figure 3), is an arboreal frog (WWW.WildHerps.Com 2009). It has the coloration needed to blend with the many epiphytes, including bryophytes, on the mossy branches. These frogs take advantage of this coloration in their nest sites and calling locations among mosses and leaves. Jacobson (1985) studied this species at the Gaucimal River in Monteverde, Puntarenas Province, Costa Rica, at an elevation of 1360 m asl. She found that females deposit their eggs on leaf tops, moss-covered rocks, and moss-covered branches, where they attend the eggs immediately after depositing them (Jacobson 1985; Ryan & Lips 2004). Although in some species, attendance of eggs is important for removal of bacteria and fungi, it did not seem to improve larval survival for this species. Jacobson found 50 clutches of eggs, and these demonstrated a choice of moist micro-habitats. Five of the clutches were on constantly wet, mossy rocks on a river bank. Three were in water-laden mosses in forks of tree branches.

Figure 3. The Emerald Glass Frog, ***Espadarana prosoblepon*** (formerly *Centrolene prosoblepon*), blending in with the light green color of the mosses and liverworts. Photo by Twan Leenders, with permission.

Unlike many of the tropical arboreal frogs, ***Sachatamia ilex*** and ***Espadarana prosoblepon*** are not on the IUCN (2015) protected list and are not considered to be endangered (WWW.WildHerps.Com: *Centrolene prosoblepon*, Emerald Glass Frog).

Hylidae: North Temperate Treefrogs

The Britannica Online Encyclopedia defines the treefrogs as any frogs living in trees. Hence, they encompass several families. Among these, the **Hylidae** (Figure 4) are considered to be the "true" treefrogs, a taxonomic distinction rather than an ecological one. We prefer the definition from <dictionary.com> "any arboreal frog of the family Hylidae... They are strong jumpers and have long toes ending in adhesive discs, which assist in climbing," but common names ignore those requirements.

Figure 4. ***Hyla arborea*** (**Hylidae**) on moss. Photo by Milan Kořínek, with permission.

While some amphibians are most likely casual visitors, treefrogs in the tropics necessarily encounter bryophytes frequently. In tropical forests, biodiversity can be high, but many of these habitats remain unexplored (Tennesen 1998). Among these seemingly unknown habitats are the arboreal mosses – habitats where new species of frogs can be discovered on nearly every collecting trip to new areas. Each location may act like an island where contact with other such "islands" has been cut off by topography for a long enough period of time for genetic drift, differing selection pressures, and new mutations to create new species or variants. Such tiny frogs as are typical of these arboreal locations most likely don't travel far across open habitats without trees. Much like the human aborigines in some parts of the world, I doubt that they travel to a new mountain range very often.

The ground of many Peruvian forests is covered with wet ***Sphagnum***, and epiphytes abound on the trees. Although treefrogs need to maintain moist skin, there seems to be little direct evidence linking them to the use of these bryophytes to maintain moisture in their aerial habitat. Nevertheless, cryptic coloration that blends well with moss- and liverwort-covered branches suggests that such locations may be favorable resting places and may account for the limited observations that have been made of many species. Johannes Foufopoulos tells me he would never have discovered one of the new species in New Guinea (Foufopoulos & Brown 2004) if the frog hadn't called from its mossy perch. He had walked right by it without seeing it. It appears that some, perhaps many, can change colors to blend with their backgrounds or select backgrounds where their colors blend in. They become invisible to most searching eyes, especially those of the herpetologists.

Furthermore, nesting requirements and locations of eggs are virtually unknown in many of these species (*e.g.* Foufopoulos & Brown 2004). The same moisture advantage is offered to eggs and it is likely that eggs of

many species hide among the bryophytes and litter on the trees and forest floor.

We know that in the tropics, at least some treefrogs lay eggs among the mosses on the trees (Filipe Osorio pers. comm.). In Figure 5 the eggs resemble *Nostoc* balls and may thus be ignored by some carnivores because *Nostoc* has an unpleasant taste or just because they don't look like eggs. The terrestrial young of these species could remain protected from predators and desiccation within the mossy chambers until they develop to a sufficient size to move about easily.

Figure 5. Eggs of frogs on the tropical epiphytic liverwort ***Plagiochila* sp.** Can you find them in the upper picture? Photos by Filipe Osorio, with permission.

In these forests, animals have evolved reproductive specializations to the plants they live on, often being highly adapted to a single species or group of species. Frogs in particular have some special advantages that permit them to survive in an aerial habitat. Some sit on their eggs to incubate them. Others carry their tadpoles on their backs. And others lay eggs on leaves so that the young will fall into the river when they hatch. Most either have warning colors to threaten predators or have mottled colors that serve as camouflage (Figure 6).

Figure 6. This dart frog is not difficult to see when resting on epiphytic moss, but it is protected by its warning coloration of black and white and its poisonous skin. In some locations, its light and dark patches may hide it among sunflecks. Photo by Nate Warner, with permission.

At Monteverde, Costa Rica, temperatures in a sunlit moss mat or bromeliad basin may exceed the lethal temperature for the endangered tree-dwelling frogs that inhabit them (Pounds *et al*. 2006). Fortunately, these habitats are usually shaded, affording the frogs a safe place to live most of the time.

A variety of breeding niche diversifications, including mouth breeding, permit up to 80 different species of frogs and toads to co-occupy the same small forests in southern Chile, despite the absence of standing water in the treetops (Fogden & Fogden 1989). Their small size and susceptibility to dehydration causes the treefrogs to have narrow distributions, and many are **endemic** [exclusively occurring in just one locale (country, province, mountain, etc)] to a single or small group of mountains. Navas (2006) suggests the long history of amphibians at mid elevations in the Andes has permitted the many populations to adapt independently to the lower temperatures of the higher elevations. But high elevations require adaptations to other stressors as well, including UV radiation, especially for eggs. More recently, the more successful spread of chytridiomycosis in the lower temperatures at higher elevations has further reduced taxa there.

Hyla chrysoscelis (Cope's Gray Treefrog, Hylidae)

The Cope's Gray Treefrog (***Hyla chrysoscelis***; Figure 7-Figure 8) is a native American treefrog that lives on the bole and branches of trees. This species is listed as endangered in New Jersey, USA, but it is not federally listed (Southern Gray Treefrog, *Hyla chrysoscelis* 2011). It can change color from green to gray in only a few seconds to blend with its substrate (Reptiles and Amphibians of Minnesota 2009). It tends to occur in habitats with lots of mosses as ground cover, and moss is a recommended substrate for keeping the species in captivity [Costanzo *et al*. 1992; Girgenrath & Marsh 2003; Pollywog 2009]. Its coloration permits it to blend in with the lichens and mosses on tree bark. Despite its small size, ***Hyla chrysoscelis*** is able to withstand freezing, but where does it spend the winter? What use does it make of mosses and liverworts during its life cycle?

Figure 7. The Cope's Gray Treefrog, ***Hyla chrysoscelis*** in its grey coloration. When on a green substrate such as mosses, it can change rapidly to green. Photo by John D. Willson, with permission.

Figure 8. ***Hyla chrysoscelis*** (Cope's Gray Treefrog) in its greenish coloration, here blending with the bryophytes on the branch. This mossy branch seems to be a good night-calling position. Photo by Kerry Kriger, through SaveTheFrogs.com, for public use only.

Hyla versicolor (Gray Treefrog)

The specific name of ***Hyla versicolor*** means changing color, a capability of a number of treefrogs. ***Hyla versicolor*** is a similar species to ***H. chrysoscelis***, differing only in its call and its ploidy number, but lives farther north, overlapping with it at the southern end of its range. These species differ not only in range, but also in chromosome number, with ***H. chrysoscelis*** being diploid and ***H. versicolor*** being tetraploid (Ptacek *et al*. 1994). Like ***H. chrysoscelis***, it blends with the mosses of its tree bark environment (Rhode Island Vernal Ponds 2009; Figure 9). The AnimalsandEarth (2011) website describes ***Hyla versicolor*** as camouflaged on a moss-covered tree.

Figure 9. ***Hyla versicolor*** on a bed of moss. Photo by Brian Gratwicke, through Creative Commons.

Hyla arborea (Common Treefrog, Hylidae)

Hyla arborea, the Common Treefrog (Figure 10-Figure 11), typically occurs in open forests and open areas in Europe (Wikipedia: European Treefrog 2008). However, in Poland it is one of the species to be found in high elevational and transition bogs (Stachyra & Tchórzewski 2004). It is the only indigenous treefrog in mainland Europe and is endangered due to habitat loss and pollution (Wikipedia 2008).

Figure 10. Young ***Hyla arborea***, the Common Tree Frog, on a finger, demonstrating its tiny size. Photo by Christian Fischer, through Wikimedia Commons.

Figure 11. ***Hyla arborea*** on a bed of moss. Photo by Milan Kořínek, with permission.

Hyla gratiosa (Barking Treefrog, Hylidae)

Hyla gratiosa (Figure 12) is one of the larger hylids and is known from southeastern USA (Frost 2011). Wright (2002) reported it from a "moss-laden" black gum (*Nyssa sylvatica*) tree in Okefinokee Swamp, Georgia, USA.

Figure 12. ***Hyla gratiosa***, the **Barking Treefrog**, on a bed of bryophytes, where it sometimes calls to attract females. Photo by Brian Gratwicke, through Creative Commons.

Hylidae: Tropical Treefrogs

Ptychohyla dendrophasma (formerly *Hyla dendrophasma*) and *Ecnomiohyla minera* (formerly *Hyla minera*) (Fringe-Limbed Treefrogs, Hylidae)

The trunks of tropical cloud forest trees are typically covered with bryophytes. There hide numerous

inconspicuous frogs, still unknown to the world. Among these, ***Ptychohyla dendrophasma*** (formerly ***Hyla dendrophasma*** (a name meaning tree ghost) was discovered in 2000 from the Sierra Los Cuchumatanes in northwestern Guatemala (Campbell *et al*. 2000). This is a surprisingly large frog (84.1 mm) for bryophyte habitation, but it was hanging from a moss-covered tree branch about 1.2 m above a stream. At the same location, ***Ecnomiohyla minera*** spends its nights on the sides of moss-covered tree trunks and on branches. Duellman (1970) suggested that the resistance to desiccation and arboreal lifestyle of the Central American ***Ecnomiohyla miliaria*** (Figure 13) are evidence that its home is in the forest canopy. Its coloration would help to camouflage it among the canopy mosses. The large toe pads and scallops along the legs help it to maintain its hold in the canopy.

Figure 13. ***Ecnomiohyla miliaria*** blending with the multicolored bark of the branch. It occurs in humid rainforests and wet forested highlands of Colombia, Costa Rica, Nicaragua, and Panama. Note the fringes on the legs that may be helpful in holding onto branches, where it flattens itself against the substrate. Or perhaps they help it to glide. Photo by Joseph H. Townsend, through Wikimedia Commons.

Isthmohyla lancasteri (formerly *Hyla lancasteri*) (Lancaster's Treefrog, Hylidae) – Why Have Tubercles?

As noted earlier, the brown splotchy pattern on the green-colored ***Isthmohyla lancasteri*** (formerly *Hyla lancasteri*; Figure 14) should serve it well as camouflage among the mosses. But as elevation levels increase (to 1920 m asl in Panama), so do the elevations on the frog. That is, instead of the smooth skin seen at elevations between 650 and 910 m in Panama and Costa Rica (Figure 14), this higher elevation frog gets dorsal warts that are increasingly greater in size as elevation rises (Figure 15; Trueb 1968). It looks a bit like a miniature field of volcanoes.

One can only speculate on the selection pressure behind retention of such an innovation. Why should higher elevations favor conservation of larger tubercles? One might consider camouflage amid the moss or perhaps added protection against UV radiation. Or might it be a deterrent to would-be predators? Trueb (1968) seems to think that the protuberances provide cryptic coloration: "At 1920 m on Cerro Pando, the frogs were perched on branches covered with deep moss. The frogs were difficult to see because of their **tuberculate** skin and cryptic coloration – green, white, and brown mottling. At 1450 m, less moss is present and the frogs are correspondingly less tuberculate. Moss is less common at lower elevations, and frogs have fewer and less prominent protuberances and more subtle dorsal mottling. At elevations less than 910 m, the frogs are smooth, and the dorsal mottling is replaced by blotches on a unicolor background; these frogs are typically found on or near the ground, perched on leaves, branches, and stones." But Trueb also suggests that the protuberances on the legs and feet may help the frogs to hold onto the slippery branches. One might also speculate that they would help to keep a slippery, sleeping frog from falling through the mosses to the ground.

Figure 14. ***Isthmohyla lancasteri*** showing the low elevation (550 m asl) morph at Guayacan, Limon Province, Costa Rica. Note the color splotches and almost no tubercles. Photo by Brian Kubicki, with permission.

Figure 15. This is a higher elevation form of ***Isthmohyla lancasteri*** showing prominent tubercles. The photo was taken in Panama at Bocas del Toro Province, Parque Internacional La Amistad Caribbean side, Cerro Frío, at 1000 m asl. Photo by Angel Solís, with permission.

Agalychnis (Hylidae)

Agalychnis saltator (Misfit Leaf Frog; Figure 16-Figure 17) is one of those adorable green frogs with red eyes and large suction pads on its toes. It can be found in the Caribbean lowlands of northeastern Honduras, Nicaragua, and east-central Costa Rica at 15-1300 m asl. Pictures of frogs like this one frequently adorn ads, calendars, and other decorative positions. Bryophytes can provide a suitable substrate for laying its eggs, spread in a layer over the bryophyte mat (Figure 18). This species adds to its charm by **parachuting** (a free-fall descent that is less than 45° from the vertical) (Roberts 1994)!

Parachuting frogs display a tropical novelty that is part of the breeding activity. Males and females of ***Agalychnis saltator*** (Figure 16) gather in breeding aggregations on **lianas** (vines) above temporary swamps (Roberts 1994). From there, both genders parachute to the ground to join breeding aggregations there. They return to the canopy rapidly by a hand-over-hand movement up the **lianas** (vines). They lay grey eggs during the daylight hours, packed into the mosses that surround the lianas. They eggs are vulnerable to mortality caused by desiccation, submergence in water, and predation by ants, snakes, and birds. Roberts suggests that the parachuting behavior, followed by walking, may permit these frogs to live in the canopy where they are widely dispersed, then to gather in a short burst to breed in large numbers in isolated ponds.

Figure 16. ***Agalychnis saltator*** (Misfit Leaf Frog), a parachuting frog on a mossy branch. Photo by Twan Leenders, with permission.

Figure 17. ***Agalychnis saltator*** showing its greenish coloration patterning that blends with its aerial or ground mossy habitat. Photo by Jason Folt, through Creative Commons.

Figure 18. Eggs of ***Agalychnis saltator*** on leaf. Photo by Peter Janzen, with permission.

The related species ***Agalychnis spurrelli*** only occasionally lays eggs among the mosses (Gomez-Mestre & Warkentin 2007). These are laid in an irregular X shape only one layer deep (rarely in 2 layers). The tadpoles (Figure 19) drop into the water when they hatch. The eggs are subject to predation by egg-eating snakes. Tadpoles may be eaten by fish.

Figure 19. ***Agalychnis callidryas*** eggs – a treefrog that does not use mosses for oviposition. Photo by Geoff Gallice, through Creative Commons.

Charadrahyla nephila (Oaxacan Cloud-forest Treefrog, Hylidae)

Charadrahyla nephila (Figure 20) is endemic to Mexico, where it lives in subtropical or tropical moist lowland forests and moist montanes (cloud forests), and rivers at 680-2256 m asl, habitats that are all being destroyed, thus threatening its existence (Santos-Barrera & Canseco-Márquez 2004). It seems further to be suffering from **chytridiomycosis**, a fungal disease caused by ***Batrachochytrium dendrobatidis***, as suggested by the loss of keratinized mouthparts in tadpoles of southern Mexico. (See subchapter 14-2 for a discussion of this fungus disease.)

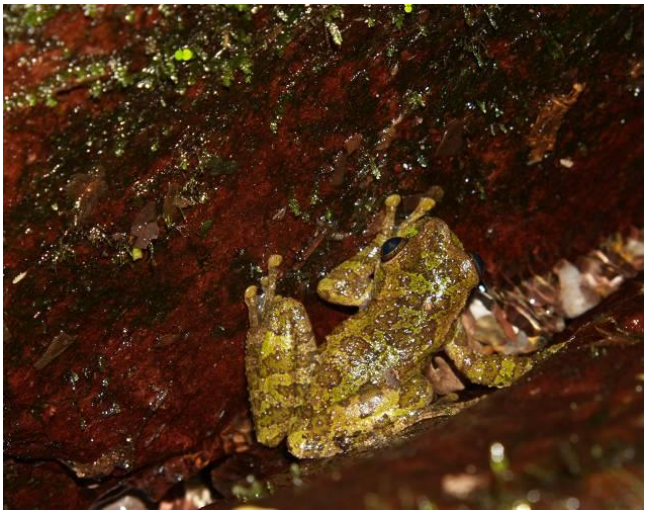

Figure 20. ***Charadrahyla nephila*** (Oaxacan Cloud-forest Treefrog) clinging to a tree and surrounded by bryophytes at La Chinantla, Oaxaca, Mexico. Photo by Omar Hernandez-Ordoñez, with permission.

Anotheca spinosa (Spine-headed Tree Frog, Hylidae)

Anotheca is a **monotypic** hylid genus. That is, there is only one species in the genus, ***Anotheca spinosa*** (Spine-headed Tree Frog, Figure 21). It is distributed in Costa Rica, Honduras, Mexico, and Panama in subtropical or tropical moist lowland forest and montane regions (Santos-Barrera *et al*. 2004) where it lives in cloud forests (Duellman 1970). It is active year-round, requiring it to choose habitats where it can maintain moisture through dry seasons. Unlike the tiny ***Eleutherodactylus***, this relatively large 80 mm species lays an average of 158 eggs per clutch (Jungfer 1996), keeping them wet in the basin of a bromeliad or a tree hole. The female stays with her eggs, and when she feels the tadpoles swimming against her, she releases a second set of eggs that serve as nutrient sources for the tadpoles.

The branches that hold these bromeliads in a cloud forest are typically covered with bryophytes, so being adapted to sit among them is beneficial. The bryophytes are most likely important in providing both camouflage and in maintaining moisture. For some they might provide sites for eggs that are adapted to the terrestrial environment. And the bryophytes hold numerous arthropods that serve as potential food items.

Figure 21. ***Anotheca spinosa*** (Spine-headed Tree Frog), shown here amid bryophytes on a tree at La Chinantla, Oaxaca, Mexico. It appears that looking like a leaf or bark is useful when bryophytes are sparse. Photo by Omar Hernandez-Ordoñez, with permission.

Litoria serrata (Green-eyed Treefrog, Hylidae)

Litoria serrata (Figure 22-Figure 23) lives in northeastern Queensland, Australia. Ross Alford (pers. comm. 28 March 2011) states that this species looks quite inconspicuous when it rests on mosses, which it often does in its natural habitat. This is facilitated by its tubercles and its brown-grey-green coloring.

Figure 22. ***Litoria serrata*** in its brown and green camouflage form. Photo by Jean-Marc Hero, with permission.

Figure 23. ***Litoria serrata*** in its lichen/moss camouflage form. Note the fringe projections on the legs that help hold it in place on tree branches and trunks. Photo by Jean-Marc Hero, with permission.

Ecnomiohyla miliaria (Cope's Brown Treefrog, Hylidae)

Ecnomiohyla miliaria (Figure 24) lives in rainforests in humid lowlands and premontane slopes from eastern Honduras and southeastern Nicaragua and central Colombia (Duellman 1970) to southeastern Costa Rica on the Atlantic slope (20-900 m) and on the Pacific slope in humid premontane areas of southwestern Costa Rica and western Panama at 600-1300 m asl (Frost 2011).

Figure 24. ***Ecnomiohyla miliaria***, demonstrating the flattened position that helps to make it inconspicuous. Its coloration helps to hide it among the lichens and mosses. Its large toes and fringes on the legs help it to clasp its arboreal substrate. Photo by Josiah H. Townsend, through Creative Commons.

Its actual habitat is unknown, although its thick, roughened skin, large toe suction pads, and fringes on the legs, as well as its ability to flatten its body, suggest that it is an arboreal species (Schoville 2000). Its coloration and tubercles suggest that it would blend well among bryophytes. It is listed as vulnerable because it is distributed over less than 20,000 km^2, its distribution is severely fragmented, and the extent and quality of its forest habitat in Nicaragua, Costa Rica, and Panama are in continued decline (IUCN 2010).

Smilisca sila (Panama Cross-banded Treefrog, Hylidae)

This Panama Cross-banded Treefrog lives in Colombia, Costa Rica, and Panama in subtropical or tropical moist lowland forests, rivers, and freshwater marshes (Frost 2011). These include mossy habitats, where it often traverses the bryophytes on the soil and trees (Figure 27). But its actual use of these substrata and their importance to its habitat have not been investigated. Habitat loss threatens its existence, so it is important to understand if this if bryophytes are a vital part of its niche.

Mantellidae

Spinomantis aglavei (Anamalozoatra Madagascar Frog, Mantellidae)

Spinomantis aglavei (Figure 25-Figure 26) is known from the Andringitra Mountains and eastern forests of Madagascar (Frost 2011). It occurs from sea level to 1500 m asl in slow-flowing streams, swamps, and fast-flowing streams of the rainforest, but does not tolerate secondary forests (Nussbaum & Vallan 2008). It is medium-sized (40-50 mm), greenish brown, and resembles tree bark with epiphytes (Glaw & Vences 2007). Its calls are emitted from the canopy, 1.5-3 m above ground, necessitating its travel up the tree where its coloration serves as camouflage. It deposits 30-38 eggs on leaves above streams and the hatching tadpoles drop into the streams to complete their development. Adults rest on the tree trunks during the day, relying on their cryptic coloration and skin fringes to hide them from harm. It is listed as a species of least concern because it is widely distributed and presumed to have a large population (IUCN 2010). It is likely that other species in this genus also use mosses (Figure 27).

Figure 25. ***Spinomantis aglavei***, showing the large toe suction pads and leg fringes typical or frogs living high in trees. Photo by Jörn Köhler, with permission.

Figure 26. ***Spinomantis aglavei*** at night on a tree trunk. Note how the large feet and fringe can help to hold this frog to this smooth bark while the colors serve as camouflage. Photo by Franco Andreaone, through Wikimedia Commons.

Figure 27. ***Smilisca sila*** (Panama Cross-banded Treefrog, **Hylidae**) climbing on roots and moss in Costa Rica. Photo by Brian Gratwicke, through Creative Commons.

Cloud Forests and Other Mossy Habitats

As I worked on this chapter, I discovered an interesting co-incidence that may actually reveal evolutionary adaptations. Based on concerns by an anuran systematist who was not accustomed to seeing my included taxa arranged in non-phylogenetic order, I rearranged

everything to a semblance of their current phylogenetic positions. I later decided this did not accomplish the ecological purpose of the book and began grouping the stories by habitat. By the time I finished the frogs and toads and was wrapping up the **Hylidae**, I realized that this chapter was mostly in habitat order already. Hence, as we end the discussion of the **Hylidae** and their close relatives, which are mostly tree-dwellers, (arboreal) we begin a group of families associated with bryophytes on the ground, rocks, or low branches (<2 m), but in "mossy" habitats they occur on trees as well. Note that I refer to bryophytes here and not just mosses because I believe that liverworts are often the substrate as well. However, most folks studying anurans are not bryophyte taxonomists and do not take note of the distinction, hence, I suspect, grouping the leafy liverworts into the broad category of mosses. Thus, as you read "mosses" below, keep in mind that they may include liverworts.

In tropical cloud forests, biodiversity can be high, but many of these habitats remain unexplored (Tennesen 1998). Many of the species are known from only one or two collections, and information on their biology and ecological preferences is extremely limited.

Cape Horn, South America

In her visit to the Cape Horn area, Blanka Shaw observed frogs among the very mossy habitats there (Figure 28-Figure 30). It's too bad we don't have joint herpetological and bryological field trips so that we can describe the habitats of these frogs more completely and so bryologists can be more familiar with the roles that bryophytes play in many mossy ecosystems.

Figure 28. Habitat for small frogs among liverworts in ***Nothofagus betuloides*** forest at Fjord Agostini, Provincia Magallanes, Chile. Photo by Blanka Shaw, with permission.

Microhylidae

The Microhylidae is a large family in the tropics and spans both eastern and western hemispheres. The species frequent mossy forests, among other habitats.

Albericus valkuriarum (Microhylidae)

Albericus valkuriarum inhabits the mid-montane rainforest and forest edge (Richards & Allison 2004) above 2000 m asl in Papua New Guinea (Frost 2011). Habitat degradation usually results in its disappearance (Richards & Allison 2004). Its breeding is unknown, but Richards and Allison suggest that it probably lays its eggs on the ground or in mosses on tree trunks. Richards and Zweifel (2004) make a similar statement about ***Albericus fafniri***.

Cophixalus *(Rainforest Frog, Microhylidae)*

With a name like **Microhylidae**, one would expect the tiny members of this family to be among the bryophyte fauna, taking advantage of the bryophyte moisture buffering to conserve moisture in the tiny animals with their large surface area to volume ratio.

Cophixalus sphagnicola lives in moss and leaf litter (Zweifel & Allison 1982; Kraus & Allison 2000) in very mossy rainforests near Wau, Morobe Province, Papua New Guinea. In Australia, ***Cophixalus ornatus*** (Figure 29) is an **arboreal** (tree-dwelling) frog that lives under logs and leaf litter in its New Guinea rainforest home. However, it often lays its eggs in moss (Figure 30) (Online Field Guide: Ornate Nursery Frog; Hoskin 2004). In one observation in Australia, the male attending the eggs began moving them when disturbed (Hoskin 2004). However, before moving them, he consumed some of them, then moved about half of those remaining to a more moist location. Those left behind failed to hatch. The male attendants apparently feed on ants that threaten survival of the eggs. The clutch size of this species is the largest of any known for Australian microhylids, with up to 22 eggs recorded.

Figure 29. ***Cophixalus ornatus***, a species wherein some females lay their eggs among mosses. The male is shown here in calling mode with an inflated vocal sac. Its relative, ***Cophixalus sphagnicola***, lives among the mosses. Photo by Jean-Marc Hero, with permission.

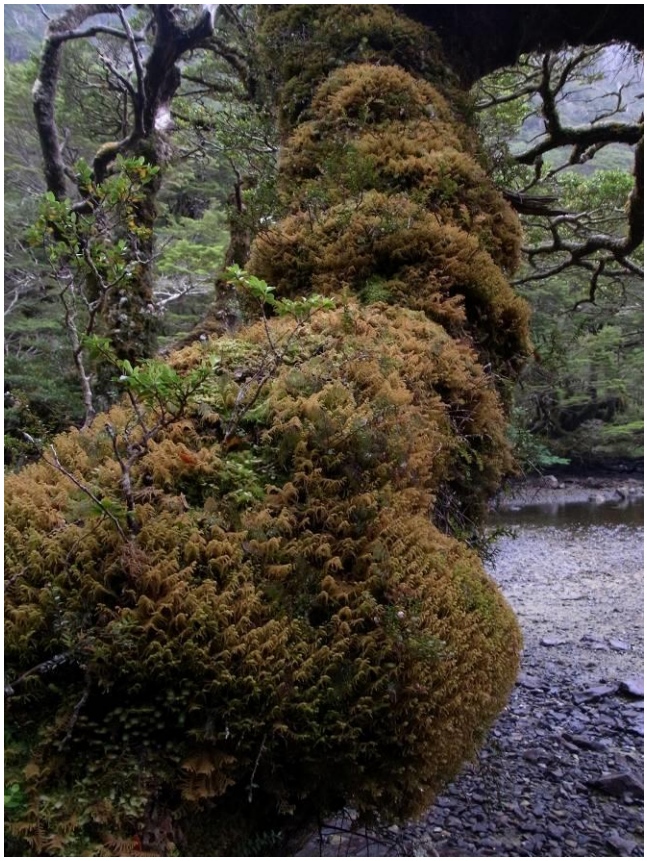

Figure 30. Leafy liverwort ***Lepicolea*** on bole at Tierra del Fuego, Peninsula Edwards, Cape Horn, Chile. This dense cover of epiphytic bryophytes provides ideal habitat where small frogs can hide. Photo by Blanka Shaw, with permission.

Choerophryne (Microhylidae)

Species of ***Choerophryne*** (Torricelli Mountain Frogs), a genus endemic to New Guinea, live on the forest floor and on leaves of shrubs, but also among mosses on steep rocky cliff faces, where they can be heard calling (Kraus & Allison 2001).

Dyscophus guineti (Sambava Tomato Frog, Microhylidae)

Dyscophus guineti (Figure 31-Figure 32) is broadly distributed beside slow-moving streams in the eastern rainforest belt of Madagascar from 150 to 900 m asl (Nussbaum *et al*. 2008). This is a very secretive species, making it difficult to locate. These are somewhat easier to find at night when they travel about on the forest floor. They lay hundreds of sticky eggs that are deposited in ponds (Glaw & Vences 2007), rendering sharp contrast to the single-digit egg clutches of terrestrial egg-layers.

Evans and Brodie (1994) used this frog (and others) in experiments to determine the ability of the surface secretions to slow down predators by creating a glue. But for our purposes, this is more interesting because these secretions make the frog sticky, permitting it to be a dispersal agent of bryophytes. In their discussion of the adhesive strength of these secretions, Evans and Brodie (1994) stated that they first washed the amphibians in their study to remove soil, debris, mosses, and other adhering substances. In this experiment, ***Dyscophus antongilii*** and ***D. guineti*** had the strongest glue among the eleven amphibians tested. The Common Garter Snake, ***Thamnophis sirtalis***, was able to free itself from secretions by ***Dyscophus*** in 7-39 seconds, a sufficient time for the frog to achieve some distance from its predator.

In an email discussion with Butch Brodie, he stated that he had not paid attention to bryophyte adherence in the field; the experiments were in the lab. But this sticky surface can indeed glue substances to the frogs, permitting such things as bryophytes to travel with the frog and potentially get dropped off elsewhere (see image of ***Ceuthomantis smaragdinus***, Figure 37). In my garden room, my Green Frog (***Lithobates clamitans***) was usually covered with bird seed shells because it spent much time under the bird feeder where fermenting seed shells nourished fruit flies.

Figure 31. ***Dyscophus guineti*** (**Sambava Tomato Frog**) male showing its duller coloration compared to the female. Photo by Franco Andreone, through Wikimedia Commons.

Figure 32. ***Dyscophus guineti*** female peering out from a seclusive spot among bryophytes. Photo by Tim Vickers, through Public Domain.

While getting these secretions on the belly of a snake in a place where it might be glued down seems a bit of a stretch, these secretions can be useful tactics against some animals. When encountering these frogs, the Lesser Hedgehog Tenrec, a mammal (***Echinops telfairi***) got its lips glued together and one eye and its toes were stuck together for the full thirty minutes of the trial (Evans & Brodie 1994). Furthermore, contact with the secretion caused the tenrec to turn in circles, snuffling and salivating profusely and rubbing the substrate with its head.

It appears that part of the strange behavior that permits ***Dyscophus guineti*** to escape predators could be the result of a trypsin inhibitor in the skin secretions (Conlon & Kim 2002). This differs from the α-helical antimicrobial peptides used by many frogs as a defense strategy, so Conlon and Kim speculated that it may be part of an alternative strategy of defense against microorganisms. But could it be part of a strategy against predators?

Platypelis grandis (Boulenger's Giant Treefrog, Microhylidae)

Platypelis grandis (Figure 33) lives in eastern and northwestern Madagascar (Frost 2011). Its habitat is subtropical or tropical moist lowland forests and moist montanes where it is threatened by habitat loss. It is usually arboreal, although it is occasionally found on the ground (IUCN 2010). It needs mature forest and breeds in tree holes. Its coloration and tubercles provide camouflage that help to protect it as it climbs on tree trunks and branches.

Figure 33. ***Platypelis grandis*** on tree bark with bryophytes and lichens. Photo by Jörn Köhler, with permission.

Hypopachus barberi (Barber's Sheep Frog, Microhylidae)

Hypopachus barberi (Figure 35) lives at 1470-2070 asl in the tropical countries of El Salvador, Guatemala, Honduras, and Mexico (Frost 2011). Its limited distribution is threatened by habitat loss in its native habitats of subtropical and tropical moist montane areas and freshwater marshes, although it is also able to live in plantations and rural gardens (Wikipedia 2011b).

Figure 34. ***Hypopachus barberi*** on a bed of moss where it is able to maintain hydration. Photos by Josiah Townsend, through Wikimedia Commons.

Figure 35. ***Hypopachus barberi*** from Guisayote Honduras on a bed of moss where it is able to maintain hydration. Photos by Josiah Townsend, through Wikimedia Commons.

Xenorhina (Snouted Frog, Microhylidae)

From the North Coast Ranges of Papua New Guinea, ***Xenorhina arboricola*** (Figure 36) is unique among members of ***Xenorhina*** there in being **arboreal** (tree-dwelling) (Allison & Kraus 2000). It lives among leaf litter collected in *Asplenium* (bird's nest fern) and in the mosses that surround the trees and epiphytes. Allison and Kraus found one frog guarding a clutch of 11 eggs that were "connected together by a single filament into a pearl-like string." ***Xenorhina zweifeli*** (formerly *Xenobatrachus zweifeli*) lives in the same North Coast range, where trees are covered with mosses (Kraus & Allison 2002). Like many of the frogs in that area, the extent of its use of mosses is unknown.

Ceuthomantidae

Ceuthomantis duellmani

New records of tiny, moss-dwelling frogs are common in the less-explored portions of the world. In 2010, Barrio-Amorós described a new species of ***Ceuthomantis*** from Sarisariñama Tepui, southern Venezuela. This species occurred in a dwarf forest that was completely covered by mosses and other epiphytes. ***Ceuthomantis duellmani*** called from within holes and hiding places in tree buttresses, undoubtedly taking advantage of the mosses as cover. It would be interesting to determine the density of these frogs within the moss mats during the daytime when moisture may be a problem elsewhere.

Figure 36. ***Xenorhina arboricola*** from New Guinea, a species that often lives among epiphytic mosses. Photo from Bishop Museum, with permission from Barbara Kennedy.

Ceuthomantis smaragdinus

Ceuthomantis smaragdinus (Figure 37) occurs at 1490-1540 m asl in Guyana (Heinicke *et al*. 2009). Its cloud forest habitat has broad-leafed trees up to 12 m tall, shrubs, and small tree ferns. These are covered with epiphytic bryophytes and bromeliads. Little is known about this frog, but it lives in a mossy habitat where it is likely to encounter bryophytes during its daily activities.

Figure 37. ***Ceuthomantis smaragdinus*** transporting what appear to be pieces of mosses. See discussion above on ***Dyscophus guineti*****.** Photo by D. Bruce Means, through Public Domain.

Hemiphractidae

Gastrotheca pacchamama (Ayacucho Marsupial Frog, Hemiphractidae)

Gastrotheca pacchamama (*cf*. Figure 38) is an endemic found along the Amazonian slopes of the Andes, known from three different areas: Machu Picchu, San Luis, and San Pedro in southern Peru (Frost 2011). It is known from 2000-3000 m asl. It is one of the **marsupial** frogs (direct-developing frogs that carry their developing eggs on their backs in a pouch until the eggs hatch) (Wikipedia 2015). The marsupial method in frogs is an adaptation to living in a terrestrial habitat. This species was found under rocks in wet grassland at Abra Tapuna in Peru (Duellman 1987). During the day, some of the males were calling from moss-covered talus. Presumably, the moss reduced the moisture loss and possibly provided camouflage.

Figure 38. Female ***Gastrotheca cornuta***, showing eggs in pouches on her back. Photo © Danté Fenolio <www.anotheca.com>, with permission.

Gastrotheca excubitor (Abra Acanacu Marsupial Frog, Hemiphractidae)

Gastrotheca excubitor (Figure 39) lives on the Amazonian slopes of the Andes in southern Peru at 2000-3000 m asl. It exhibits a green and brown pattern that would help make it less conspicuous among mosses, but there seems to be no verification that it lives among the mosses, where it may only be a casual visitor.

Figure 39. ***Gastrotheca excubitor*** on a bed of moss. The coloration would make this frog less conspicuous to its flying predators. Photo by Alessandro Catenazzi, with permission.

Stefania (Stefania Treefrogs, Hemiphractidae)

There are a number of records of collections of ***Stefania*** from mossy habitats in the tropics and subtropics. ***Stefania evansi*** (Figure 40) occurs in Guyana in tropical and subtropical moist lowland forests or moist montane forests up to 1400 m asl and in rivers (Wikipedia 2010). It carries its eggs on its back, and likewise carries the tadpoles, hence providing parental care. In Guyana, MacCulloch and Lathrop (2002) found several species of ***Stefania*** at night, sitting on moss-covered branches 1-4 m above the ground. Others were found in bromeliads, and one was collected from a mossy tree trunk. At the summit of Cerro Autana, Estado Amazonas, Venezuela, Barrio-Amorós and Fuentes (2003) found ***Stefania ginesi***, ***S. satelles***, and ***S. schuberti***, mossy inhabitants of the high summits of Tepui from 1750-2600 m. In addition to mossy habitats, these species occur along creeks, under rocks, and in bromeliads (*Brocchinia*) (Duellman & Hoogmoed 1984; Gorzula & Señaris 1998; Señaris *et al*. 1996).

Figure 40. ***Stefania evansi*** from Guyana carrying its eggs on its back. This is a strategy practiced by a number of arboreal frogs and permits them to move to places with sufficient moisture for the eggs. Photo by Philippe Kok, with permission.

Dendrobatidae

Oophaga pumilio (formerly *Dendrobates pumilio*) (Strawberry Poison-dart Frog, Dendrobatidae)

The Strawberry Poison Dart Frog is a small frog (17.5-22 mm) from Central America, where it lives in humid lowlands and premontane forest (Savage 2002; Wikipedia 2011c).

Frogs can be territorial over their personal patch of ***Sphagnum*** (or other substrate). The Strawberry Poison-dart Frog ***Oophaga pumilio*** (Figure 41-Figure 43) even exhibited dominance over intruders when it was placed into a new aquarium with the ***Sphagnum*** it had inhabited in its previous captive home (Figure 42; Baugh & Forester 1994), suggesting chemical markers were left in the moss. An earlier experiment (Forester & Wisnieski 1991) had demonstrated that, given a choice, these frogs exhibited a preference for their home aquarium, which had been lined with ***Sphagnum*** and contained a bromeliad. On Isla Colón, Bocas del Toro archipelago, Panama, this brightly colored frog can hide inconspicuously within the moss mat covering the trees (Sirota 2011). The males often use tree bases as calling places, likewise often being inconspicuous among the mosses (Pröhl & Ostrowski 2010).

Figure 41. The Strawberry Poison-dart Frog, ***Oophaga pumilio*** on a bed of *Selaginella*. Photo by Jason Folt, through Creative Commons.

Figure 42. Strawberry Poison-dart Frog, ***Oophaga pumilio***, in a chamber with ***Sphagnum*** where it had been previously, showing aggression toward the newcomer frog. Photo by Don Forester, with permission.

Figure 43. Strawberry Poison-dart Frog, ***Oophaga pumilio***, sitting on a tree trunk with bryophytes. Photo by John D. Willson, with permission.

The female Strawberry Poison-dart Frog deposits her tadpoles singly at each location and expends a great deal of energy to care for them (Savage, 2002; Wikipedia 2011c). She visits each tadpole every few days and deposits several of her unfertilized eggs to serve as food. This seems to be an essential food, as no other food form seems to work. The male contributes by transporting water in his **cloaca** (combined cavity used to release both excretory and genital products in amphibians, reptiles, fish, birds, and a few other groups) and watering the eggs to keep them hydrated (Wikipedia 2011c). Even so, success of the tadpoles is only 5-12%. The tadpoles take about one month to develop into young adults, but remain near their water sources a few more days while they absorb what remains of their tails.

These day-active Strawberry Poison-dart Frogs derive their poison from their diet of beetles and ants, primarily formicine ants (Daly & Myers 1967). Thus, the frog is harmless if its diet is confined to other foods, such as that of the ones kept for pets (Wikipedia 2010c).

This species has 15-30 color morphs, as discussed in Chapter 14-1 on adaptations. Among these, the green morphs typically remain within the moss mats and spend less time foraging compared to the more active, brightly colored morphs that advertise their poisons with their warning coloration (Pröhl & Ostrowski 2010).

Phyllobates (Poison-arrow Frog, Dendrobatidae)

Other wet forest frogs that may spend some of their time on or in mosses are even more poisonous [***Phyllobates terribilis*** (Golden Poison Frog; Figure 44-Figure 45), ***P. bicolor, P. aurotaenia***] (Dumbacher *et al*. 2000). Among these, ***P. terribilis*** (Figure 44) is the most poisonous; natives that use poison darts need only touch a dart to this frog to make it poisonous for a year! (Wikipedia: Golden Poison Frog 2011). Even touching the frog can be lethal for humans (Daly & Witkop 1971; Wikipedia: Golden Poison Frog 2011).

Figure 44. ***Phyllobates terribilus***, a very poisonous tree frog that has been used to make poison darts. Photo by Milan Kořínek, with permission.

Phyllobates terribilis lives in rainforests with 5 m or more rainfall! (Wikimedia 2011a). They occur at 100-200 m asl where the temperature is at least 26°C and relative humidity 80-90%. A large portion of the diet consists of ground-dwelling ants in the genera ***Brachymyrmex*** and ***Paratrechina***, contributing to their poisons. These frogs live in social groups of up to six individuals, perhaps protecting each other through their severe poisons. Surely only one would be eaten.

Figure 45. ***Phyllobates terribilus*** from the Pacific Coast of Colombia showing a color morph that serves as a warning color. Photo by Wilfried Berns, through Wikimedia Commons.

Silverstoneia flotator (Rainforest Rocket Frog, Dendrobatidae)

The tiny Rainforest Rocket Frog (Figure 46-Figure 48) lives in lowland rainforests and semideciduous forests in Panama and Costa Rica at elevations of 10-865 m asl. It is diurnal and hides among the leaf litter, but must often traverse bryophyte-covered areas to move around. The adults tend to hang out on the rocky sections of forest streams, but they deposit their eggs in leaf litter (Solís *et al*. 2004). The males transport the hatchling tadpoles to the streams where these young develop into adults (Figure 48).

Figure 46. ***Silverstoneia flotator*** on a bryophyte substrate. Photo by Brian Gratwicke, through Creative Commons.

Figure 47. ***Silverstoneia flotator*** (Rainforest Rocket Frog) jumping from a bryophyte substrate. Photo by Brian Gratwicke, through Creative Commons.

Figure 48. ***Silverstoneia flotator*** (Rainforest Rocket Frog) male with tadpoles on its back. Photo by Brian Gratwicke, through Creative Commons.

Leptodactylidae

This was once a much larger family that included the huge genus ***Eleutherodactylus*** (now in Eleutherodactylidae). Current thinking has divided the family and its largest genus.

Within the Leptodactylidae, some members make foam nests for their eggs, an adaptation to terrestrial life. Tadpoles remain in this frothy mass without eating, not exiting until they have completed metamorphosis. Their **development** is **direct** and they hatch into miniature frogs. That is, they have no tadpole stage.

In Brazil, the Marbled Tropical Bullfrog, ***Leptodactylus marmoratus*** (**Leptodactylidae**; Figure 49),

used mosses as cover for a foam nest on a road cut (Wassersug & Heyer 1988). However, nothing else is known that relates this frog to mosses (Mauro Teixeira pers. comm. 8 February 2009).

Figure 49. The Marbled Tropical Bullfrog, ***Leptodactylus marmoratus***, a frog known to nest under mosses. Photo © Mauro Teixeira Jr, with permission.

Eleutherodactylidae

This family lives in the tropics and subtropics of the western hemisphere. The genus ***Eleutherodactylus*** (Robber Frogs, Figure 50; **Eleutherodactylidae**) was the largest genus of frogs. However, many of the species have been placed in other genera and some in other families. It is interesting to see how many of these have gone back to the generic distinctions recognized in the 1800's. Our genetic information seems to have taken us full circle in many cases. What wonderful powers of observation those early herpetologists must have had!

Figure 50. ***Eleutherodactylus limbatus*** amid lichens and mosses on a tree branch at Gran Piedra, Cuba. Photo by Ariel Rodriguez, for educational use.

This family abounds from the ground to the treetops. The tiny size of the members of Eleutherodactylidae permits these species to live among mosses, especially in the canopy and on tree trunks. Some call from a perch on mosses (Figure 51). Many more may exist there unknown because many surveys don't seem to include searching among the bryophytes. Others seem only to lump the bryophytes into vegetation. When the habitat is a cloud forest, it is usually safe to assume that bryophytes are abundant.

Figure 51. ***Eleutherodactylus richmondi*** calling from a perch on mosses. Photo by Luis J. Villanueva-Rivera, with permission.

The Burrowing Frog **(*Eleutherodactylus parapelates*, Eleutherodactylidae**, formerly in Leptodactylidae), despite being a ground frog, was calling from within a large moss clump at 3 m high in a tree at the Massif de la Hotte of the Haitian Tiburon Peninsula, southwestern Haiti (Hedges & Thomas 1987).

Eleutherodactylus dolomedes (Figure 52) (Hedge's Robber Frog, Hispaniolan Ventriloquial Frog), likewise from Haiti, is difficult to locate, even when it is calling. It is a ventriloquist! Its 7-note call sounds a bit like a chirping bird and the ability of this frog to make it sound like the call is coming from somewhere else makes it difficult to locate the frog; its original finders spent an hour locating one calling specimen (Hedges & Thomas 1992).

Figure 52. ***Eleutherodactylus dolomedes***, the Hispaniolan Ventriloquial Frog, sitting on a fern frond in the mountains of Haiti. Photo from mongabay.com © Robin MooreiLCP, for educational use.

It is endemic to the high-elevation (1120 m asl) cloud forest of Massif de la Hotte, Haiti (Frost 2011) and had not been seen since 1991. But it was discovered again in 2010 in the mountains of southern Haiti (Burton 2011). Nevertheless, it is critically endangered. The IUCN report projects a population decline of greater than 80% over the next ten years because of the severe degradation of habitat in Haiti (IUCN 2010). Only 2% of the rainforest there remains.

While it has been recorded from forest edge, this is probably not suitable habitat (IUCN 2010). Eggs are laid on the ground, and it breeds by direct development.

The arguably smallest frog in the world (males 9.6-9.8 mm long, females 10.5 mm long) (Endangered Species

International: The World's Smallest Frog 2011), ***Eleutherodactylus iberia*** (Figure 53), was first discovered in 1996 in Monte Iberia, Cuba (Wikipedia 2010a). It seems to be the smallest known frog in the Northern Hemisphere, whereas the smallest in the Southern Hemisphere is the Gold Frog [***Brachycephalus didactylus*** (formerly *Psyllophryne didactyla*)] from Brazil (Allaboutfrogs.org 2011). Together they are tied for smallest frog and smallest tetrapod in the world. ***Brachycephalus didactylus*** may actually be smaller, with known males averaging 8-9 mm (Estrada & Hedges 1996).

Figure 53. ***Eleutherodactylus iberia***, the smallest known frog in the northern hemisphere, on a leaf. Photograph by Thomas Brown, through Wikimedia Commons.

Eleutherodactylus iberia (Figure 53) lives on the forest floor and requires a high humidity, so it stands to reason that habitats (rainforests) suitable for bryophytes in Cuba are also suitable for this frog (Allaboutfrogs.org). Only two populations are known, both in Holguín Province of eastern Cuba at elevations less than 600 m (Wikipedia 2010), making it critically endangered (Endangered Species International: The World's Smallest Frog 2011). One female has been found guarding a single egg. A small clutch size is common in the tiny frogs (Estrada & Hedges 1996), permitting more energy to be stored in each. It appears that the female of ***Eleutherodactylus iberia*** guards the eggs and may care for the young. Although the young are unknown, Estrada and Hedges (1996) suggest that the young may be as small as those in ***Stumpffia*** (**Microhylidae**), *i.e.* only 3 mm long!

The saga of this frog and its adaptations don't end with being small and inconspicuous. Did you wonder why it has the coloration of a bee or wasp (and a number of other poisonous beings)? This condition, known as **aposemitism**, is the familiar warning coloration that a number of poisonous, often unrelated, organisms share. Once a predator learns to recognize the color mix through a bad experience, it will avoid other potential prey items with that same color mix, just as we avoid several kinds of bees by recognizing the array of black mixed with yellow, orange, or red. It is noteworthy that this color combination prevails from tiny mites to large snakes. But some animals are **mimics**, displaying the colors without the poison or bad taste, thus taking advantage of the bad experiences with the truly nasty ones. These mimics must be in smaller numbers than their **models** (the ones with the real poison/bad taste) so that the predator is more likely to encounter the **model** first. Thus, the black, yellow, and white ***Eleutherodactylus iberia*** (Figure 53) could be a nasty model or an edible mimic.

A slight alkaloid odor among the collected ***E. iberia*** (Figure 53) frogs led Rodriguez *et al*. (2010) to test them and their close relatives in the area for poisonous alkaloids. They discovered that the skin of these frogs is endowed with a variety of poisonous alkaloids. They hypothesized that the poisons might originate from their diet, a convenient way to save your own energy and let someone else make your poisons. Indeed, they found that the diet consisted primarily of mites, ants, and springtails (Collembola). Among the 62 prey items in the gut, 71% were mites. Mites are known to contribute toxins used by other amphibians as skin toxins.

It appears that miniaturization in many of these frogs has been accompanied by a diet where mites play a major role (Caldwell 1996; Vences *et al*. 1998; Saporito *et al*. 2004; Rodriguez *et al*. 2010). Becoming smaller means the food items must also be smaller, and a smaller tongue can't reach as far to catch things. This switch to mites has resulted in the source of the sequestered alkaloids. Given the primary sources of food for ***E. iberia*** (Figure 53) – mites, ants, Collembola – one would expect these frogs to find bryophytes a particularly suitable foraging location because bryophytes often serve as a habitat for large numbers of these food items. Hence, tiny frogs most likely eat tiny mites that live among the tiniest of plants, the bryophytes.

This still very large genus of very tiny frogs in the **Eleutherodactylidae** extends from the ground to the treetops. The morphological variations also change through this vertical range, as shown by the ground to treetop array of ***Eleutherodactylus unicolor unicolor***, ***Eleutherodactylus wightmanae***, ***E. brittoni***, ***E. richmondi***, ***E. locustus***, ***E. antillensis***, ***E. portoricensis***, ***E. coqui***, ***E. cochranae***, ***E. gryllus***, and ***E. hedricki*** (Figure 54), with toe pads becoming larger as the height in the tree increases (pers. comm. Father Alejandro Sanchez, 24 February 2011). Although the moss often becomes dry and brittle, it serves as a suitably moist site for eggs in their season in the cloud forest.

In the Luquillo Experimental Forest of Puerto Rico, the well-known Coqui (***Eleutherodactylus coqui***; Figure 55-Figure 59) does a daily migration that must itself be a significant feat as they attempt to avoid predation by the whip scorpion ***Phrynus gervaisii*** (=*Phrynus palmatus*) (Formanowicz *et al*. 1981), tarantulas, snakes, screech owls, and other birds (Stewart 1985). At dusk the Coqui climb the tree trunks to search for food in the canopy. Often within minutes of peak climbing, the arachnid predators make their appearance. During this time, most adult male **Coqui** remain on understory call sites, but the others typically engage in this migration. At daybreak, the frogs return to the ground quickly by parachuting downward. A dry atmosphere reduces the number of frogs making this nightly migration. It appears that mosses contribute to the choice of climbing trees: those with more than 10 climbing frogs had either rough bark or the bark was covered with mosses. Could this correlation be due to hiding advantages, greater moisture, or both?

The Coqui, in turn, contribute to the nutrient dynamics of the forest. Beard *et al*. (2002) experimented with these frogs by using cubic meter enclosures and exclosures of the frogs. When Coqui were excluded, leaf washes had 83% less dissolved organic C, 71% less NH_4^+, 33% less NO_3^-, 60% less dissolved organic N, and 60-100% less Ca, Fe, Mg, Mn, P, K, and Zn. Exclusion of the Coqui had no effect on the foliar chemistry of plants transplanted into the exclosures. However, it did decrease nutrients available from decomposing leaf litter by 12% for K and 14% for P. C:N ratios increased by 13% in the litter. These changes appear to result from Coqui waste products, resulting from the conversion of their insect diet into nutrient forms that are more accessible for microbes and plants.

Figure 54. Toe pad sizes as they increase from ground level (**top left**) to treetop (**bottom right**) in the ***Eleutherodactylus***, a genus whose members commonly lay their eggs among the bryophytes.
Top from left to right: ***Eleutherodactylus unicolor***, ***Eleutherodactylus wightmanae***, ***Eleutherodactylus brittoni***,
Second row from left to right: ***Eleutherodactylus richmondi***, ***Eleutherodactylus locustus***, ***Eleutherodactylus antillensis***,
Third row from left to right: ***Eleutherodactylus portoricensis***, ***Eleutherodactylus coqui***, ***Eleutherodactylus cochranae***,
Fourth row from left to right: ***Eleutherodactylus gryllus***, ***Eleutherodactylus hedricki***.
Photos by Father Alejandro J. Sánchez Muñoz, with permission.

Figure 55. **Coqui**, ***Eleutherodactylus coqui***. Photo by Father Alejandro J. Sánchez Muñoz, with permission.

Figure 56. Coqui (***Eleutherodactylus coqui***) with eggs in a bromeliad basin. Photo by Rafael I. Marquez, with permission.

Figure 57. ***Eleutherodactylus coqui*** in its nest under mosses as it was uncovered on a tree in El Yunque, Puerto Rico. Photo by Father Alejandro Sanchez, with permission.

Figure 58. ***Eleutherodactylus*** with a set of eggs from an unknown species in the genus. Photos by Father Alejandro Sanchez, with permission.

Figure 59. ***Eleutherodactylus coqui*** eggs with a fully formed frog emerging from an egg. Photo by Father Alejandro Sanchez, with permission.

In a different Puerto Rican study, Drewry and Rand (1953) reported members of ***Eleutherodactylus*** (*sensu lato*; Figure 60-Figure 61) in high elevation mossy forests and the upper montane forest just below it. In Haiti, ***Eleutherodactylus limbensis*** spent the night on the wall of a ravine where there was a lush growth of moss (Lynn 1958).

Eleutherodactylus longipes (Figure 60) is endemic to Mexico. Its natural habitats are temperate, subtropical, or tropical dry pine-oak forests, subtropical or tropical moist montanes, and caves from 650-2000 m asl (Santos-Barrera & Canseco-Márquez 2010). It is threatened by habitat loss.

Eleutherodactylus gryllus (Cricket Coqui) is endemic to Puerto Rico. It lives in forest edge habitats or openings of subtropical or tropical moist lowland forests and subtropical or tropical moist montanes at 300-1182 m asl (Hedges & Rios-López 2008). During the day it hides in bromeliads or under mosses or rocks. Males call from bromeliads, most intensely at dawn (Villanueva-Rivera 2005), and eggs are laid in bromeliad basins, but development is direct into hatching froglets (Hedges & Rios-López 2008).

Figure 60. ***Eleutherodactylus longipes*** from ca. 2590 m on the N side of Cerro Pena Nevada near the community of Dulces Nombres in SE Nuevo Leon, Mexico (pers. comm. from Timothy Burkhardt, 17 February 2011). This frog may be taking advantage of the damp moss while blending in with the white lichens. Photo by Timothy Burkhardt <www.mexico-herps.com>, with permission.

Figure 61. ***Eleutherodactylus gryllus*** (Cricket Coqui) from El Yunque National Forest, Puerto Rico, sitting on a leaf covered with epiphyllous bryophytes. Such leaves are likely to maintain higher moisture levels than leaves without epiphyllous bryophytes. And these epiphylls are almost certainly liverworts. Photo by Luis J. Villanueva-Rivera, with permission.

To many people, ***Eleutherodactylus planirostris*** (Greenhouse Frog; Figure 62) is best known as an alien in greenhouses, where it was introduced in potted plants. ***Eleutherodactylus planirostris*** occurs in Cuba, the Bahamas, Grand Cayman, and Cayman Brac (AmphibiaWeb 2011). It has been introduced to Jamaica, and to Florida, Alabama, Georgia (Winn *et al.* 1999), Louisiana (Platt & Fontenot 1993), and Hawaii (Kraus *et al.* 1999), USA, and to Guam (Christy *et al.* 2007). Its altitudinal range is from sea level up to 727 m asl (AmphibiaWeb: *Eleutherodactylus planirostris* 2011).

Figure 62. ***Eleutherodactylus planirostris*** (Greenhouse Frog) on moss. Photo by Brian Gratwicke, through Creative Commons.

In Gainesville, Florida, USA, males of ***E. planirostris*** (Figure 62) call from April–September; breeding occurs under moist cover from late May to late September, peaking in July (Carr 1940; Goin 1947). Its 3-16 eggs are laid in moist depressions in the earth or in moist debris (Goin 1947; Lazell 1989; Bartlett & Bartlett 1999). These experience direct development and hatch as miniature froglets (Lazell 1989; Bartlett & Bartlett 1999) in June in Gainesville (Goin 1947) and from late May to early June in Key West, Florida (Lazell 1989). The adults are secretive and nocturnal except on warm, overcast, or rainy days (Carr 1940; Bartlett & Bartlett 1999). Their food depends on availability. In Florida they eat ants, beetles, and roaches, as well as other types of small invertebrates (Goin 1947; Duellman & Schwartz 1958; Lazell 1989). In Jamaica, they did not eat roaches, but instead ate numerous ants, mites, spiders, and harvestmen (Stewart 1979). In Hawaii, with densities in places of 12,500 frogs ha^{-1}, they have been known to consume up 129,000 invertebrates ha^{-1} $night^{-1}$ (Olson *et al*. 2011).

Diasporus hylaeformis (Pico Blanco Robber Frog; Figure 63), previously known as *Eleutherodactylus hylaeformis*, is a nocturnal species that lives at 1,500-2,500 m, where it can be found among the mosses and low vegetation in its native Costa Rica and Panama (Savage 2002). It includes mosses as egg-laying sites. Unlike most of the small bryophyte-dwelling frogs in the tropics, this one is relatively abundant and not endangered.

Figure 63. ***Diasporus hylaeformis*** among vegetation. Photo by Angel Solis, with permission.

Summary

Little seems to be known about treefrogs and their use of bryophytes, but it seems likely that bryophytes provide moisture and safe sites in an otherwise dry arboreal habitat. Life cycles are modified to accommodate the terrestrial habitat, including caring for eggs, carrying the eggs, supplying new eggs to tadpoles for food, and emergence of fully formed frogs from the eggs. Many of the tree frogs are tiny (including the smallest tetrapods) and produce only one to a few large eggs. Most have cryptic coloration that makes them nearly invisible among the bryophytes. Tubercles seem to aid some in camouflage. Some, however, have bright colors that advertise that they are poisonous (**aposemitism**), a result of their diet of ants, beetles, and/or mites that live on the ground or among the bryophytes.

Arboreal frogs have special behavioral and morphological adaptations to their lofty habitat. Females may sit on their eggs or carry them on their backs. Some lay eggs on low leaves where the young can fall into the river. Toe pads in ***Eleutherodactylus***, and probably other genera, increase in size as the habitat becomes more arboreal.

Cloud forests and other mossy habitats, especially in the tropics, house a large number of species of small to medium frogs. Some frogs hide deep within mosses to make their mating calls. Many lay their eggs on mosses. Like the treefrogs, these are poorly known and their relationships to mosses are often just speculation. They, like the treefrogs, have adaptations in their life cycles that conserve moisture for the eggs and tadpoles, including live birth of froglets or carrying tadpoles on their backs.

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CHAPTER 14-5
ANURANS: CENTRAL AND SOUTH AMERICAN MOSSY HABITATS

Janice M. Glime and William J. Boelema

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CHAPTER 14-5
ANURANS: CENTRAL AND SOUTH AMERICAN MOSSY HABITATS

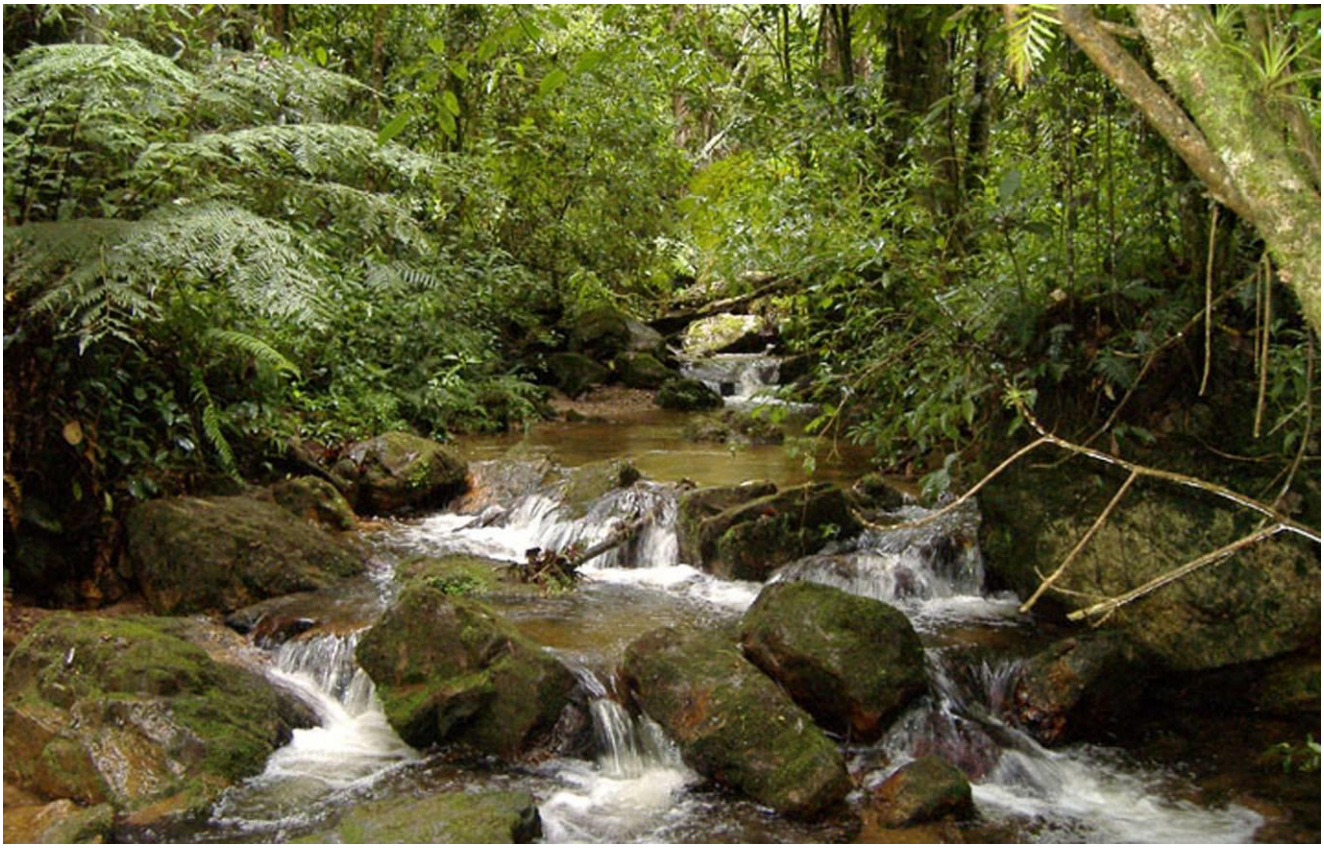

Figure 1. Waterfalls at Quebrada Cataguana Honduras, home to many disappearing anurans. Photo by Josiah Townsend, with permission.

Central and South American mossy habitats provide good places for tiny frogs. Some of these frogs are primarily stream dwellers that go ashore to feed as adults (Figure 1). Others live on the forest floor of mossy forests, or in the Páramo. But the most elusive are the ones that live in trees where mosses provide cover and moisture, as well as protection from UV light.

Strabomantidae

The giant genus ***Eleutherodactylus*** has been divided not only into a number of smaller genera, but also into several families. One of these is the **Strabomantidae**.

Bryophryne abramalagae (Strabomantidae)

Bryophyrne species inhabit the cloud forests in Peru, on the eastern slopes of the Andes (Leandro 2011). ***Bryophryne abramalagae*** is primarily known from its type locality of Abra Málaga at 4000 m asl, in the puna, Provincia de La Convención, Región Cusco, Peru (Lehr & Catenazzi 2010). The males call from inside moss, maintaining their cover during this vulnerable time. The mosses also provide a reproductive site for members of the genus.

Bryophryne flammiventris (Strabomantidae)

This species occurs along the road between Vilcabamba and Pampaconas, Provincia de La Convención, Región Cusco, Peru, at 3800-3850 m asl (Lehr & Catenazzi 2010). There is some suggestion that ***B. flammiventris*** was adapted to the habitat by having coloration on the ventral side similar to that of the tree roots where the mosses were providing habitats. The male calls, made at 10:00-16:00 hours, were made from within the moss clumps and could be heard on the other side of the valley.

Bryophryne bustamantei (Strabomantidae)

Bryophryne bustamantei (Figure 2) inhabits the transitional zone from the cloud forest to the humid grassy puna in the Umasbamba Valley, Provincia de La Convención, Peru, at 3555-3950 m asl (Lehr & Catenazzi 2008; Frost 2011). The frogs are active in both the rainy and dry seasons, living under stones, in bushes and grass, and under mosses (Chaparro *et al.* 2007; Lehr & Catenazzi 2008). They lack a tympanum, separating them from several members of the genus (Lehr & Catenazzi 2008). Despite the lack of this special hearing organ, the males

call from bushes (Chaparro 2008), suggesting they are still able to hear. Like many other terrestrial anurans, their development is presumed to be direct, lacking a tadpole stage. The species is endangered due to encroachment of human activities in its narrow habitat range.

Figure 2. ***Bryophryne bustamantei*** on a leaf. Note the absence of a tympanum. Photo by Alessandro Catenazzi, with permission.

Bryophryne zonalis (Strabomantidae)

Bryophryne zonalis (Figure 3) lives in the upper Marcapata valley, at elevations of 3129-3285 m asl along the road from Huallahualla to Quincemil, Quispicanchis, Peru (Frost 2011). This frog lays her eggs in moist habitats such as under mosses (Leandro 2011). The embryos do not become tadpoles, but rather become minute terrestrial froglets. The female remains nearby the eggs to tend them, protecting them from predation and desiccation. The 18-25 eggs are only 4-5 mm in diameter, with the hatchlings measuring about 5 mm snout to vent.

Figure 3. ***Bryophryne zonalis*** on a leaf. Photo by Alessandro Catenazzi, with permission.

Bryophryne gymnotis (Strabomantidae)

Bryophryne gymnotis (Figure 4) is known only from the montane cloud forest in its type locality, San Luis, at 3272-3354 m asl, Provincia de La Convención, Región Cusco, Peru (IUCN 2013). Its habitat is mossy and it calls from mosses, like other members of its genus (Lehr & Catenazzi 2010). Leandro (2011) reported that it is the only member of the genus with a tympanum. And like ***B. zonalis***, the female tends the eggs, which hatch into froglets, often among mosses (Leandro 2011).

Figure 4. ***Bryophryne gymnotis***. Photo by Alessandro Catenazzi, with permission.

Bryophryne cophites (formerly *Phrynopus cophites)* (Cuzco Andes Frog, Strabomantidae)

In the species ***Bryophryne cophites***, the name *cophites* means "deaf" and refers to the absence of the middle and external ear (tympanum) in this species (Figure 5), separating it from several other members of the genus.

Figure 5. ***Bryophryne cophites*** on bark, showing the absence of a tympanum. Photo by Tiffany Kosch, with permission.

The species is endemic to its type locality in the Páramo and elfin forest habitats on both north and south slopes of the Abra Acanacu on the northwestern end of the Cordillera Carabaya, Peru, at 3400-3450 m asl (Frost 2011). Mosses serve as a substrate for the eggs. Its narrow distribution and continuing decline of its Peruvian Andes habitat cause it to be classified as endangered (IUCN 2010).

Catenazzi *et al*. (2011) found that the introduced fungal pathogen ***Batrachochytrium dendrobatidis*** (see Chapter 14-1) caused **chytridiomycosis**, which accounted for a large portion of amphibian decline in the Andes of Peru, further endangering this species.

Bryophryne hanssaueri (Strabomantidae)

The endemic species ***Bryophryne hanssaueri*** (Figure 6) is known only from the immediate vicinity of the type

locality (Acjanaco, Manu National Park, Paucartambo, Peru) at 3266-3430 m asl (Frost 2011). The female tends her eggs (Figure 7), which develop directly into froglets (Figure 8). It lives in mossy habitats but, like many of these tropical species, its use of the moss remains a matter of speculation.

Figure 6. ***Bryophryne hanssaueri***, an endemic species from cloud forests in southeastern Peru. Photo by Alessandro Catenazzi, with permission.

Figure 7. ***Bryophryne hanssaueri*** female tending her eggs. Photo by Alessandro Catenazzi, with permission.

Figure 8. ***Bryophryne hanssaueri*** hatching froglet. Photo by Alessandro Catenazzi, with permission.

Bryophryne nubilosus (Strabomantidae)

Bryophryne nubilosus (Figure 9) lives in the mossy montane cloud forest and montane scrub at 2350-3215 m asl in the vicinity of Esperanza, in the Cosñipata Valley, Provincia de Paucartambo, Región Cusco, Peru (Frost 2011). Its relationship to mosses needs to be verified, but it seems to be sitting on a liverwort in the picture by Alessandro Catenazzi (Figure 9).

Figure 9. ***Bryophryne nubilosus***. Photo by Alessandro Catenazzi, with permission.

Noblella pygmaea (Noble's Pygmy Frog, Strabomantidae)

Noble's Pygmy Frog (Figure 10) has already been discussed in Chapter 14-1. This tiny frog is known only from its type locality in the Cusco Region, Peru, 3100 m asl (Frost 2011). It has not yet been rated by the IUCN (2012), but it is certainly endangered with such a small distribution. However, its tiny size and presence among mosses (Lehr & Catenazzi 2009) suggest it might be more widespread but not yet detected.

Figure 10. ***Noblella pygmaea*** (**Noble's Pygmy Frog**), a tiny moss-dweller. Photo by Alessandro Catenazzin, with permission.

Psychrophrynella (formerly *Phrynopus)* (Andes Frogs, Strabomantidae)

This genus has already been discussed because many of its species call from bryophytes, often from within the moss mat. The eggs are laid under mosses and stones, where they are seldom found. They presumably undergo direct development.

The **páramo** occurs at high elevations from about 2000 m asl (the upper forest line) to 5000 m (the permanent snow line), creating a uniquely harsh environment. In the páramo at Cotapata, Bolivia, members of ***Psychrophrynella*** (**Strabomantidae**, formerly members of *Phrynopus*) live under stones or among the grasses and mosses (De la Riva 2007). For example, ***P. condoriri*** spends the day under stones in a humid area of the páramo that has abundant mosses; ***P. illimani*** lives at the border of the elfin forest and wet páramo where both the ground and rocks are covered with mosses; ***P. katantika*** was even found among mosses and ferns on old walls and ruins. Likewise at Cotapata, ***P. guillei*** calls from deep within moss clumps and ***P. iani*** calls from under stones and among mosses. But ***P. iatamasi*** stays in the forest floor mosses, calling from there during the day (Aguayo & Harvey 2001). This genus deposits its eggs under mosses and stones, but these are rarely found (De la Riva 2007). As noted earlier, the mosses provide cover for calling males, who call day or night or both.

Psychrophrynella kempffi (Figure 11) usually occurs among the mosses or under stones and logs of the cloud forest. The latter species calls with a short whistle and is difficult to locate (De la Riva 1992), perhaps because it is hidden by the mosses.

Figure 11. ***Psychrophrynella kempffi***. Photo by Ignacio De la Riva, with permission.

Psychrophrynella usurpator (Strabomantidae)

Psychrophrynella usurpator (Figure 12) is another tropical frog, known only from the vicinity of Abra Acjanacu Peru at 3270-3539 m asl, a high pass in the Cordillera de Paucartambo, which is the easternmost Andean range facing the Amazonian lowlands in Departamento Cusco, Peru (Frost 2011).

Figure 12. ***Psychrophrynella usurpator*** on a bed of mosses. Photo by Alessandro Catenazzi, with permission.

Pristimantis (South American Rain Frogs; Strabomantidae)

If you do your searching in the daytime, you might miss some of the moss dwellers. At elevations of 2500-3275 m in the Cordillera Oriental of the central Peruvian Departamentos Huainuco, Junin and Pasco, Lehr *et al.* (2006) found ***Pristimantis platydactylus*** (formerly *Eleutherodactylus platydactylus*) **(Strabomantidae)** on low vegetation and moist moss at night. However, during the day they were under dry leaves on the ground or in terrestrial bromeliads. In western Ecuador, ***Pristimantis quinquagesimus*** (previously *Eleutherodactylus quinquagesimus*) has been seen at night on leaves and mossy branches less than 2 m above the ground in cloud forests between 2000 and 2700 m asl in Provincias Imbabura and Pichincha (Lynch & Trueb 1980). Many of these frogs are nocturnal, as witnessed by their night-time calling.

One adult female of ***Pristimantis vanadise*** (formerly *Eleutherodactylus vanadise*) (**Strabomantidae)** was captured on mosses on the walls of a creek canyon in the cloud forest of the mountains of Merida, western Venezuela (La Marca 1984). All the males and some juvenile females, on the other hand, were found among the litter on the forest floor, possibly including mosses, but not near the stream.

In Ecuador, ***Pristimantis simonbolivari*** (formerly *Eleutherodactylus simonbolivari*) spends the daytime under mosses on logs as well as in leaf litter and under rotten logs (Wiens & Coloma 1992). Near a small creek, ***Pristimantis appendiculatus*** (formerly *Eleutherodactylus appendiculatus*) (Figure 13) sits on moss-covered stems or exposed fern fronds at the edge of the road at night (Miyata 1980).

Figure 13. ***Pristimantis appendiculatus*** (**Pacific Robber Frog**) on a moss-covered tree trunk. Photo by William Duellman, courtesy of Biodiversity Institute, University of Kansas.

Some species rest on leaves that have **epiphylls** (plants living on leaves), including bryophytes, especially leafy liverworts in the **Lejeuneaceae**. The ability of epiphylls to hold moisture may provide a moist niche for some frogs. ***Pristimantis ridens*** (Figure 14) is a tiny frog that spends time on epiphyll-covered leaves in Costa Rica, Honduras, and Colombia from sea level to 1600 m asl (Solís *et al.* 2010a).

Figure 14. ***Pristimantis ridens*** with epiphylls on a palm leaf. Photo by Jason Folt, through Creative Commons.

Duellman and Hedges (2005) found ***Pristimantis stictogaster*** (formerly *Eleutherodactylus stictogaster*) on the western slopes of the Cordillera Yanachago in central Peru nestled under a moss on the ground. ***Pristimantis aniptopalmatus*** (formerly *Eleutherodactylus aniptopalmatus*) occurred at 2300-2600 m, also on the western slopes, where it is known only from under moss on tree trunks and under moss on the ground in the cloud forest.

The **Santa Cecilia Robber Frog** (***Pristimantis croceoinguinis***; Figure 15) is a nocturnal frog that lives in the eastern Amazonian lowland rainforest of Ecuador and central Peru (Panguana, 200 m asl, Huanuco, southern Peru; Pakitza, 350 m asl (Madre de Dios); and Tavara (Puno) (Castro *et al*. 2004b). In Colombia it occurs mostly in the Departamento de Putumayo at 400 m asl, but also is able to survive in the low cloud forest at the base of the Pastaza trench. Although its primary habitat is the lowland primary rainforest, it is able to invade low cloud forests as well. Typically, it occurs on low vegetation 0.5-1.5 m from the ground. Its development is unknown, but it is most likely directly into tiny frogs with no free-living tadpole stage.

Figure 15. ***Pristimantis croceoinguinis*** (**Santa Cecilia Robber Frog**) in a bed of mosses. Photo by Andreas Nöllert, with permission.

In Panama, ***Pristimantis museosus*** (**Robber Frog**; Figure 16-Figure 18) is a moss-dweller whose name (*museosus*) means mossy. Also named the Vanishing Frog, it is a moss mimic, with disruptive warts, green body, and disruptive patches of darker green and brown (Figure 16-Figure 17). I suspect it can vanish in plain view among the bryophytes. It lives among low vegetation, including the mossy forest floor of humid montane forests (IUCN 2010) of the Cordillera Central of Panama at 700-1000 m asl (Frost 2011). Its egg deposition niche is unknown. This unique frog is on the IUCN endangered list due to a fragmented habitat and narrow distribution (IUCN 2010).

Figure 16. ***Pristimantis museosus***, a Panamanian moss mimic. Photo by Justin Touchon, Smithsonian Tropical Research Institute, through Public Domain.

Figure 17. ***Pristimantis museosus*** on a twig, exposing the white ventral side. If this works as it is supposed to in birds, it would make the frog less conspicuous when viewed from below against a light-colored sky, while maintaining camouflage above against moss-covered bark. Photo by Marcos Guerra, Smithsonian Tropical Research Institute, through public domain.

Figure 18. ***Pristimantis museosus*** head, showing the tubercles and color patterning that provide it with good camouflage among the bryophytes. Photo by Justin Touchon, Smithsonian Tropical Research Institute, through public domain.

Pristimantis nervicus (Figure 19) lives in extreme southeastern Costa Rica to eastern Panama, and central Colombia from 20 to 200 m asl (Savage 2002). It maintains its moisture by being night-active and living in primary humid lowland and secondary forest. Adults live under surface debris (presumably including bryophytes) and in leaf litter, often near or in caves and rocky streambanks. Its development is directly from egg to froglet.

Figure 19. ***Pristimantis nervicus*** among mosses (***Thuidium*** sp.). Photo by Rafael Marquez, with permission.

Pristimantis gaigei (**Fort Randolph Robber Frog**; Figure 20) lives in drainage lowlands in extreme southeastern Costa Rica to Panama and central Colombia (Frost 2011) from 20-200 m asl (Savage 2002). This nocturnal species occupies humid lowland and secondary forests under surface debris and leaf litter near rocky stream banks where it is likely to encounter bryophytes.

Figure 20. ***Pristimantis gaigei*** (**Fort Randolph Robber Frog**). Photo by Esteban Alzate, through Creative Commons.

Pristimantis cerasinus (**Limon Robber Frog**; Figure 21-Figure 22) lives in Atlantic lowlands and premontane slopes of Nicaragua, Costa Rica, and Panama, western and central Panama, and northeastern Honduras at 19-1500 m asl (Savage 2002; Frost 2011). The adults live among the leaf litter in the daytime, but at night they roam among the vegetation, most likely including bryophytes (Pounds *et al*. 2004). They deposit their eggs on this low vegetation.

Figure 21. ***Pristimantis cerasinus*** (**Limon Robber Frog**). Is that a bryophyte or a fern under it? Photo by Jason Folt, through Creative Commons.

Figure 22. ***Pristimantis cerasinus*** (**Limon Robber Frog**). Photo by Brian Gratwicke, through Creative Commons.

Pristimantis bacchus (**Wine Robber Frog**; Figure 23) lives in Colombia at 1740-2300 m asl. This rare species was last seen in 2002 (Castro *et al*. 2004a). Its home among ground vegetation of cloud forests makes it difficult to locate. It is unlikely that it can avoid travelling among bryophytes in this habitat, but its further use is not known.

Figure 23. ***Pristimantis bacchus*** (**Wine Robber Frog**) on a thick moss bed. Photo by Esteban Alzate, through Creative Commons.

Pristimantis mutabilis (Strabomantidae) – A new kind of camouflage

This unusual frog stumped its collectors. They found it among mosses in the Ecuadorian Andes and brought it back to the house in a cup (Quenqua 2015). It was unusual in having tubercles that helped it blend in with its mossy habitat (Figure 24). But when they next looked in the cup, the tubercles were gone (Figure 25) and they at first thought they had collected the wrong frog. But when they added some mosses to the cup, the tubercles returned.

Figure 24. ***Pristimantis mutabilis*** on mosses, showing the protruding tubercles. Photo by Tim Krynak, with permission.

Figure 25. ***Pristimantis mutabilis*** on a leaf, showing the disappearance of tubercles. Photo by Tim Krynak, with permission.

Ranging 17-23 mm, this frog was a new species and an interesting anomaly (Guayasamin 2015). But the researchers wondered if this anomaly occurred elsewhere. Hence, they re-examined ***Pristimantis sobetes***, a member of a different species group. And there were the tubercles when the frog sat among mosses, but gone they were on other types of substrata. Might there be other moss mimics with this peculiar behavior?

Both species live in montane cloud forests that have abundant epiphytes and bryophytes.

Yunganastes ashkapara (Strabomantidae)

In Peru and Bolivia, ***Yunganastes ashkapara*** (formerly *Eleutherodactylus ashkapara*; **Strabomantidae**; Figure 26) in the ***Yunganastes fraudator*** group is a **nocturnal arboreal** species that apparently finds some advantage other than moisture among the mosses. This species calls from 2.5-10 m height during the rainy season, sitting inside mosses of the cloud forest canopy (Köhler 2000; Padial *et al*. 2007). Little information seems to be available on ***Y. pluvicanorus*** (Figure 27), but it appears to occupy similar mossy habitats.

Figure 26. ***Yunganastes ashkapara*** on a bed of mosses. This species calls from within thick moss mats. Photo by Jörn Köhler, with permission.

Craugastoridae

Other members of the former *Eleutherodactylus* genus, such as ***Craugastor catalinae*** (formerly *Eleutherodactylus catalinae*) (**Craugastoridae**) in Middle America (Panama to Mexico), may conserve their moisture when they sit at night on moss-covered boulders midstream where a rapid retreat into the water is possible (Campbell & Savage 2000).

Figure 27. ***Yunganastes pluvicanorus*** on a bed of mosses. This species calls from within thick moss mats. Photo by Jörn Köhler, with permission.

Craugastor lineatus (**Montane Robber Frog**; Figure 28) has been recorded from elevations of 300-2000 m asl on the Atlantic side from Guerrero, Oaxaca, and Chiapas, Mexico, southeast to Guatemala. On the Pacific side it occurs from eastern Oaxaca through Chiapas to the southwestern highlands of Guatemala, at elevations of 300-2000 m asl (Santos-Barrera *et al.* 2004). It occupies lower montane evergreen forests and requires nearby streams for development. Unfortunately, it is rapidly declining in

Mexico, probably due to the fungal infection **chytridiomycosis.** Habitat loss through agriculture, logging, and urbanization also threaten its survival.

Figure 28. ***Craugastor lineatus*** sitting on a bed of ***Sphagnum*** at La Chinantla, Oaxaca, Mexico. Photo by Omar Hernandez-Ordoñez, with permission.

Craugastor noblei (**Noble's Robber Frog**; Figure 29) lives in lowland and premontane evergreen forests of extreme eastern Honduras, through Nicaragua and Costa Rica, both slopes in central Panama, and in the lower portion of the premontane zone of southwestern Costa Rica, at 4-1200 m asl (Frost 2011). With its diurnal habit (Solís *et al*. 2010b) and brown color, it is dangerously visible on bryophytes, although its shape makes it look like a leaf.

Figure 29. ***Craugastor noblei*** (**Noble's Robber Frog**) on a mat of mosses in Costa Rica. Photo by Andrew J. Crawford, through Creative Commons.

Craugastor bransfordii (**Bransford's Robber Frog**; Figure 30-Figure 31) lives in humid lowlands and adjacent premontane slopes on the Atlantic mountainside from eastern Honduras and Nicaragua to central Costa Rica, 60-880 m asl (Frost 2011). It is a forest floor species, where it typically lives among leaf litter. However, as seen in Figure 30-Figure 31, it can traverse bryophytes and most likely finds a moist resting spot there.

Figure 30. ***Craugastor bransfordii*** (**Bransford's Robber Frog**) on a bed of mosses. Photo by Jason Folt, through Creative Commons.

Figure 31. ***Craugastor bransfordii*** (**Bransford's Robber Frog**) on a bed of mosses. Photo by Brian Gratwicke, through Creative Commons.

Craugastor crassidigitus (**Isla Bonita Robber Frog**; Figure 32) lives in northern Costa Rica, through Panama to the extreme northwestern border of Colombia, at 10-2000 m asl (Frost 2011). Its habitat is the humid lowland and premontane forests (Solís *et al*. 2004a).

Figure 32. ***Craugastor crassidigitus*** (**Isla Bonita Robber Frog**) on a bed of mosses. Photo by Sean Michael Rovito, through Creative Commons.

Craugastor gollmeri (**Evergreen Robber Frog**; Figure 33-Figure 35) lives in the lowland and premontane humid forests of Panama at 10-850 m asl and in eastern Costa Rica at 10-1520 m asl (Savage 2002). It lives among the leaf litter (Solís *et al*. 2004b), but where bryophytes are present they too can serve as cover or substrate during travels. Females attend the nest in this genus, but nesting sites of this species are not known.

Figure 33. ***Craugastor gollmeri*** (**Evergreen Robber Frog**) showing its leaf-like appearance. Photo by Brian Gratwicke, through Creative Commons.

Figure 34. ***Craugastor gollmeri*** (**Evergreen Robber Frog**) sitting on bryophytes. Photo by Brian Gratwicke, through Creative Commons.

Figure 35. ***Craugastor gollmeri*** (**Evergreen Robber Frog**) showing its underbelly coloration. Photo by Brian Gratwicke, through Creative Commons.

Cycloramphidae

Alsodes vittatus (Cycloramphidae)

It appears that some genera of **Cycloramphidae** in La Picada, Chile, may be dependent on mosses. ***Alsodes vittatus*** (formerly *Eupsophus vittatus*) (**Malleco Spiny-chest Frog**; see Figure 36) and ***Eupsophus roseus*** (**Cycloramphidae**; Figure 37) can be found under mosses, predominantly ***Hygroamblystegium*** (Figure 38; Formas & Vera 1980). The males of ***Alsodes vittatus*** (**Cycloramphidae**) occur under ***Sphagnum*** in water-filled cavities. Tadpoles were collected in water-filled cavities (*p*H 5.0) under ***Hygroamblystegium*** at the edge of a stream, with fifty tadpoles in one and sixteen in another cavity (Formas & Pugin 1978). Two clutches of eggs were found in similar ***Sphagnum***-covered water-filled cavities. Formas and Vera (1980) considered these two species to be derived from pond breeders, with the deposition of eggs and development of tadpoles in water-filled cavities under mosses as a derived character.

Figure 36. ***Alsodes igneus*** on a bed of bryophytes. Photo © Danté B. Fenolio <www.anotheca.com>, with permission.

Figure 37. ***Eupsophus roseus*** on a bed of bryophytes. Photo © Danté B. Fenolio <www.anotheca.com>, with permission.

Figure 38. ***Hygroamblystegium tenax*** from a dry streambed in a north-temperate stream. Photo by Janice Glime.

Eupsophus (Cycloramphidae)

In a temperate forest in southern Chile, ***Eupsophus emiliopugini*** calls from within clumps of the moss ***Racomitrium*** (Figure 39), and in bogs they excavate burrows where they can make their calls without being seen (Penna *et al.* 2005).

Figure 39. ***Racomitrium canescens*** in Iceland, demonstrating the types of mounds it can make – suitable for frogs to hide and call. Photo by Janice Glime.

Rhinoderma darwinii (Darwin's Frog, Cycloramphidae)

Protection of eggs from desiccation seems to have been one of the primary drivers in the evolution of terrestrial frogs. One of the strangest egg incubation techniques is that of the Darwin's Frog (***Rhinoderma darwinii***; Figure 40-Figure 46), a vulnerable species from Argentina and Chile. In southern Chile, these frogs live in the beech forests (Fogden & Fogden 1989). The female lays her eggs where it is somewhat damp, under litter or mosses. She abandons the eggs and several males take over the care for about 20 days (Vocal Sac-Brooding Frogs: Rhinodermatidae 2011), an unusual trait in itself. The males then each put a few eggs into their vocal sacs. Since calling season is over, the vocal sac is no longer needed for calling, so it makes a moist incubation pouch. The larvae feed on their own yolk (Jorquera 1982), but Goicoechea *et al*. (1986) used tracers to demonstrate that there is also a transfer of substances from the male to the developing larvae. In the sac for the next 50-70 days, these eggs hatch and the tadpoles complete their juvenile development (talk about a tickle in your throat!), leaving the males' mouths as froglets! (Vocal Sac-Brooding Frogs: Rhinodermatidae 2011). The males may gather a few eggs from several different clutches and not all the young will be at the same developmental stage. Meanwhile, the presence of the developing frogs makes the male look as if he is pregnant! (Figure 40).

The **Darwin's Frog** is a prey organism to birds, rodents, and snakes (Wikipedia 2011). It is protected from such attacks by camouflage. It comes in many combinations of greens and browns, typically looking like a leaf fallen on a moss, or just a leaf (Figure 46). Crump (2002) demonstrated that it selected substrate color based on its own color. Brown frogs selected brown substrata significantly more often than they selected green, and bicolored frogs likewise selected substrata that matched their color patterns. Green **Darwin's Frogs** (Figure 41), however, actually occurred less often on a green substrate, perhaps gaining an advantage by looking like a fallen green leaf or a plant on soil or other brown surface. Brooding males appeared on warmer surfaces than did non-brooding males or females.

Figure 40. Male **Darwin's Frog** (***Rhinoderma darwinii***) carrying developing tadpoles in its vocal sac, hence appearing to be pregnant. Photo by Claudio Soto-Azat, with permission.

Figure 41. Green variant of ***Rhinoderma darwinii***, blending in with the mosses and liverworts. Photo © Danté B. Fenolio <www.anotheca.com>, with permission.

This camouflage serves a second purpose. These frogs are ambush hunters, so they are able to sit undetected among the bryophytes to watch and wait for their own dinner (Figure 42).

One might ask why so many different patterns are necessary, but perhaps the predator would be able to learn a pattern if only one existed. If the frog is detected, it rolls over on its back and plays dead (Figure 43). The underside is black with white spots, a pattern recognized as warning coloration. If water is nearby, the frog jumps into the water, then floats downstream – on its back!

Figure 42. Darwin's frog (***Rhinoderma darwinii***) sitting on damp mosses in Chile. While this animal "leaf" sits still, an insect may land, unaware of the danger. At the same time, its predators often pass it by without noticing that it is a frog. Photo by Filipe Osorio, with permission.

Ceratophryidae

In Peru and Bolivia, ***Telmatobius timens*** (**Ceratophryidae**; similar species in Figure 44-Figure 45) lives in the páramo, where it spends the night sitting on rocks, on the ground, or in crevices and under mats of mosses along streams (Riva *et al*. 2005).

The specific name *timens* means frightened, scared, or alarmed (timid) and refers to the possible arrival of the infectious fungal disease **chytridiomycosis** to Bolivia (Riva *et al*. 2005). This disease has already devastated many amphibian species, including ***Telmatobius*** in Ecuador and Peru.

Figure 43. Darwin's Frog (***Rhinoderma darwinii***) playing dead by rolling on its back and exposing its black and white warning coloration. Photo by Claudio Soto-Azat, with permission.

Figure 44. ***Telmatobius culeus*** (Titicaca water frog) juvenile. Photo by Joshua Stone, through Wikimedia Commons.

Figure 45. ***Telmatobius*** sp. from northern Chile. Some members of this genus spend the night under mats of mosses near streams. Photo by José Grau de Puerto Montt, through Wikimedia Commons.

Figure 46. Color and pattern variants of Darwin's Frog, ***Rhinoderma darwinii***. Some color forms blend well with bryophytes while others are more suitable for leaf litter or other substrata. Photos by Claudio Soto-Azat, with permission.

Summary

Bryophytes offer opportunities for anurans to live in places where they might not otherwise survive. Among these are waterfalls where bryophytes provide a foothold and place to deposit eggs.

Pristimantis mutabilis is especially adapted to living among mosses by projecting tubercles that help it blend in with mosses, but withdrawing then when it is on a smooth substrate. In the cloud forests, genera such as ***Bryophryne***, ***Noblella***, ***Psychrophrynella***, ***Pristimantis***, ***Yunganastes*** use bryophytes for egg-laying, calling sites, and cover. ***Craugastor*** is more common in lowland and premontane forests where bryophytes can be common ground cover, providing moisture during travels. ***Alsodes vittatus*** lives under ***Sphagnum*** in water-filled cavities. ***Eusophus*** species call from within clumps of mosses in temperate forests in Chile. **Darwin's Frog** (***Rhinoderma darwinii***) has multiple color phases that permit the species to blend with a wide range of habitats, including bryophytes. In the páramo, ***Telmatobius timens*** finds refuge under moss mats.

In Australia, the Darwin's Frog (***Rhinoderma darwinii***) lays eggs in the mosses, then leaves them for the male to incubate, which they do in their vocal sacs after about a week of maternal care.

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CHAPTER 14-6
SALAMANDERS AND ADAPTATIONS

Janice M. Glime and William J. Boelema

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CHAPTER 14-6
SALAMANDERS AND ADAPTATIONS

Figure 1. **Four-toed Salamander** (***Hemidactylium scutatum***), predominantly a moss dweller, in a bed of mosses. Photo by John D. Willson, with permission.

Caudata (Urodela) – Salamanders

The term Caudata refers to having a tail (Figure 1), so the Caudata are the amphibians with tails. Caudata have four legs positioned at right angles to the body, and moist, smooth skin (except in newts). Some live entirely in the water, some live part of their life cycle in water and part on land, and others are entirely terrestrial or **arboreal** (in trees). Newts are salamanders that spend part of their adult life on land and part in the water.

Many salamanders live among bryophytes, and many live in areas where bryophytes form a dominant feature of the landscape. Others live in places where bryophytes are present, but scattered. Casual observations include finding salamanders in bryophyte collections, but we seldom know if this is a casual/accidental association, or if salamanders actually prefer the bryophyte habitat. Does the bryophyte offer any advantage to the salamander? There is no collection of data on the broad role of bryophytes, and most information is observational, thus not providing preferences or causality. The salamander sub-chapters represent an attempt to challenge researchers to make detailed studies on the relationships between bryophytes and salamanders.

In an attempt to be consistent with a worldwide fauna, Latin nomenclature in this chapter follows Frost (2011). English names are mostly based on the SSAR names list (Crother 2008) for North America north of Mexico, and AmphibiaWeb (Sandmeier 2010) or Frost (2011) for species that do not occur in North America north of Mexico. The order of families follows proposed phylogeny presented by Pearson and Pearson (2010), but the species presented do not, but rather one of related habitats and of convenience.

Distribution

The majority of species of salamanders occur in North America, with the largest family, Plethodontidae, being almost restricted to the western hemisphere. Of the ten families, only the Plethodontidae have a significant number of species that live in areas outside the temperate regions, *i.e.*, in the Neotropics.

If you live in the North Temperate Zone of North America, it is difficult to imagine that large parts of the world do not have salamanders. As somewhat late arrivals on the tree of life, salamanders are absent in Australia (Marc P. Hayes, pers. comm. 26 March 2011; Stan A. Orchard, pers. comm. 27 March 2011; Frost 2011) and in most of India, South America, Africa (Marc P. Hayes, pers. comm. 26 March 2011), and parts of Southeast Asia [Edmund (Butch) Brodie, Jr., pers. comm. 7 June 2011] and of course Antarctica (Frost 2011). The most species-rich areas are the Appalachian and Ozark Mountains, USA,

the Pacific coast of North America, western Europe, Japan, and China (Wake 2011). Only the Salamandridae extend into Northern Africa, southern foothills of the Himalayas, northern Vietnam, and southern islands of Japan.

The largest concentration of salamander species is in the Appalachian Mountains in eastern North America. Perhaps more striking is the distribution of the Plethodontidae, containing 70% of all salamander species. This large family is restricted to the USA, southern Canada, Mediterranean Europe, and the Korean Peninsula (1 species!). In Europe and Asia, the only plethodontids present are the limestone cave dwellers in the genus ***Speleomantes***, and only one of these (***S. supramontis***) is known to be associated with a mossy habitat. So, salamanders do not have worldwide distribution, and my North American bias in this presentation is justified.

Descriptions of salamander habitats often seem to lack detail. This is partly justifiable in that often a single individual represents the species when it is described for the first time. Even in surveys, it is typical to describe the general habitat and mention logs and rocks, but omit any mention of bryophytes. Salamanders that hide under bryophytes in the soil are treated as soil organisms and the bryophytes may or may not be mentioned. Epiphytic bryophytes that must be crossed to traverse the arboreal habitat are likewise often not mentioned. In some cases, these omissions are probably true representations of absence, but often they are in old-growth forests, cloud forests, and rainforests where this is unlikely to be the case.

I found it encouraging that Bryce A. Maxell (2005) of the Wildlife Biology Program, University of Montana, Missoula, MT, USA, not only recommended looking on and under bryophyte mats for amphibians, but the sample data sheet for ***Plethodon idahoensis*** specifically listed it among the habitats to record:

> under wood/vegetation
> under 4-20cm rock fragments
> under >20cm rock fragments
> under bryophyte mat
> on bryophyte mat
> in rock fracture
> other_____

This list would insure that habitat information on the bryophytes would be included in any survey using the form. On the other hand, encouraging searching of bryophytes could be seriously destructive to the bryophyte habitat. This seems to be a tricky problem.

Adaptations to Bryophytes

If you have to move through moss mats, it doesn't hurt to be shaped like a worm (Figure 2). For a salamander, that includes having short legs on an elongate body (Figure 2). Your diet necessarily changes to the mites, ants, beetles, and other small invertebrates (mostly arthropods) available. And if you wiggle and move, you attract attention, so your color should either blend in with the bryophytes or you should warn predators to beware by having bright colors that suggest you are poisonous. And if you fail to blend and someone grabs your tail, disengaging your tail while you run off can confuse your predator (Figure 3-Figure 5) (Wikipedia 2011a), especially if the detached tail continues to wiggle.

Figure 2. ***Oedipina pacificensis*** showing its small size, reduced appendages, and wormlike body that adapt it to maneuvering among mosses. Photo by Vide Ohlin, with permission for education.

Of these adaptations, most are adaptations to terrestrial living in general. Small size, short limbs, and cryptic (camouflage) coloration are the most bryological. Need for moisture is not an adaptation, but it increases the utility of the bryophytes in some habitats.

Tail Autotomy

Tail autotomy is the ability to drop the tail. Often if the salamander tail is simply dropped, it can continue to move and wiggle (Figure 3), providing a distraction that might permit the rest of the body to escape (Jim McCormac, pers. comm. April 2011). Not only that, but apparently some predators prefer the tail; consumption of the disengaged tail permits the remainder of the body more time for escape (Beneski 1989).

Figure 3. The Greenmountain Slender Salamander, ***Batrachoseps altasierrae***, with a waving disarticulated tail on the left and the escaping body in the upper left of the photo. Photo by Gary Nafis, © Gary Nafis at CaliforniaHerps.com, with permission.

And it doesn't hurt to be able to regenerate lost parts. But regeneration requires energy, and this apparently results in loss of reproductive capacity, at least in the salamander ***Batrachoseps attenuatus*** (California Slender Salamander; Maiorana 1977). On the other hand, Smits and Brodie (1995) demonstrated that in the moss-dwelling ***Oedipina uniformis*** (**Cienega Colorado Worm Salamander**) it does not appear to cause any increase in

respiratory cost. They measured respiration before and after activity of this salamander with and without an autotomized tail. Results suggest that the tail accomplishes the oxygen exchange/respiration the tail needs, but the tail is not needed to supply the rest of the salamander.

Figure 4. ***Bolitoglossa lincolni***, **Lincoln's Mushroomtongue Salamander**, with a complete tail. Note the constriction at the base of the tail that permits it to release. Photo by Sean Michael Rovito, with permission.

Salamanders have remarkable abilities to regenerate lost tissues (Figure 5), including other limbs as well as the tail (Endo *et al*. 2007; Keim 2009; Garza-García 2010). The exposed tissue after losing a tail is undoubtedly subject to bacterial infection, but following this self-amputation (**autotomy**), epidermal tissue migrates within 12 hours to cover the remaining stump (Mullen *et al*. 1996; Bryant, *et al*. 2002). In as little as twelve weeks after tail loss, some salamanders are able to achieve coordinated swimming behavior with their newly developing tails (Davis *et al*. 1990). It appears that the only serious price is loss of reproduction.

Figure 5. ***Bolitoglossa lincolni*** with short tail, suggesting it has been attacked by a predator and lost its tail, which is now regenerating. Photo by Sean Michael Rovito, with permission.

Toxicity

Living on land can often make salamanders more vulnerable to predation. They are more easily seen and more easily caught by small mammals, birds, and snakes than those in water where glares, shadows, and silt can make visibility poor. The salamanders have varying degrees of being poisonous through glands in their skin, and many either have no poison or it is too weak to be effective [Edmund (Butch) Brodie, Jr., pers. comm. 22 April 2011]. Fortunately for herpetologists, the poison is not a contact poison, but must be eaten to become noxious or dangerous. But when a snake flicks its tongue against this would-be dinner, it feels the effects of the poison from the more toxic ones.

Unfortunately for the salamander, it appears that not every snake is affected by the poison. In some cases, one or more species occurring in the same range, and with historically overlapping habitats to the salamander, have evolved immunity to the poison (Brodie *et al*. 2002; Williams *et al*. 2003; Ridenhour *et al*. 2004). For example, the garter snake (***Thamnophis*** spp.) has developed resistance to the neurotoxin **tetrodotoxin** (**TTX**). This resistance seems to have evolved independently in both related and unrelated snakes. The Sierra Gartersnake, ***Thamnophis couchii***, has elevated resistance to TTX, a toxin present in the **sympatric** (having overlapping distribution) newt ***Taricha torosa*** (**California Newt**, Salamandridae; Brodie *et al.* 2005). But the distantly related ***Thamnophis sirtalis*** (**Common Gartersnake**) also coevolved with its very poisonous sympatric newt prey, ***Taricha granulosa***, **Rough-skinned Newt**. These multiple predator-prey co-evolutions in ***Thamnophis*** seem to result from the simplicity of the genetic structure of TTX resistance in that genus, permitting the evolution of "extreme phenotypes" (Feldman *et al*. 2010), in this case, TTX resistance.

Not only does the ***Thamnophis*** snake with immunity have a broadened diet that includes newts, it becomes endowed with a bit of protection of its own! Some of these highly resistant snakes are able to ingest multiple newts safely in one meal (Williams *et al*. 2004). Williams *et al*. (2010) found that after consuming only one newt of ***Taricha granulosa***, the **Common Gartersnake** ***Thamnophis sirtalis*** retained significant amounts of active TTX in its liver for one month or more. The 42 μg in the liver that remained after three weeks is sufficient to incapacitate or even kill avian predators, and possibly also mammalian predators (Williams *et al.* 2010). Hence, the bryophytes in the ecosystem, through their housing of newts, could increase the number of snakes in the area through these interactions. ***Taricha torosa***, and all ***Taricha*** species, can dwell in bryophytes [Edmund (Butch) Brodie, pers. comm. 7 June 2011]. It is likely that other bryophyte-dwelling salamanders could be victims or promulgators of similar, as yet unexplored, relationships.

Several authors have attempted to determine the origin of the poison TTX. Possible sources include diet of poisonous arthropods, bacteria that manufacture the poison within the salamander, and manufacture by the salamander itself.

Some arthropods living among mosses are poisonous when eaten, especially mites and ants, and we know these can impart their poisons to some of the poisonous frogs that consume them (Daly & Myers 1967). Although Cardiff (2011) states that the same is true for salamanders, few salamanders eat the beetles, mites, or ants that are poisonous (David Wake, pers. comm. 21 April 2011), and no peer-reviewed study seems to be published to support this poison transfer claim.

Lehman *et al*. (2004) examined the possibility of bacterial origin of the poison TTX. Using PCR primers that amplify 16S rRNA genes, they were unable to detect any bacterial DNA in skin samples from the toxic ***Taricha***

granulosa. This provides a strong suggestion that bacteria are not involved.

Hanifin *et al*. (2002) examined the ability of ***Taricha granulosa*** to manufacture its own TTX by maintaining the newts in captivity. These newts were fed non-toxic earthworms, ***Tubifex*** worms, and crickets weekly. The levels of TTX actually increased by 20.7% after one year. Since none of these food items is poisonous, these results suggest that the newts manufacture their own poisons. Cardall *et al*. (2004) supported this view by stimulating the release of TTX in ***Taricha granulosa*** with a mild electric stimulation. Following reductions of 21-90% in TTX levels, these newts regenerated their original TTX levels in the skin during the next nine months in captivity.

It appears that toxins may be rare among the members of the largest family of salamanders, the Plethodontidae. Brandon and Huheey (1981) were the first to identify the composition of a skin toxin in the family Plethodontidae, a family with many bryophyte-dwelling species. This toxin, identified by them in ***Pseudotriton ruber*** (Figure 13) and ***P. montanus***, occurs in the skin and some organs but is most concentrated on the **dorsal** (back) surface. They determined this to be a **pseudotritontoxin**, a proteinaceous **neurotoxin**. When they experimented with its effects on mice, the mice responded by exhibiting hyperextension of their hind legs and lower back, having severe **hypothermia** (body temperature below normal), prolonged debility, coma, and death usually in 12 to 48 hours. Larger doses caused convulsions and death within as little as one hour. Young chickens, perhaps a closer model for their natural predators of reptiles and birds, had convulsions and death within minutes.

But reports of toxins in other plethodontid salamanders are rare. These salamanders are not as easy to experiment with as newts because of their small size, and for many tropical species, rarity. Brodie *et al*. (1991) have found toxicity in ***Bolitoglossa huehuetenanguensis*** (formerly *B. rostrata*), and ***B. subpalmata*** (Figure 6-Figure 7), so poisons may exist elsewhere.

Bolitoglossa subpalmata not only produces toxins, but also has behavioral responses to predators (snakes) that deter the predator (Brodie 1977; Ducey & Brodie 1991). In this case, the salamander rolls onto its back. Those salamanders from alpine areas where there were no snakes were less likely to respond with this behavior when making contact with a snake tongue.

Figure 6. ***Bolitoglossa subpalmata*** on its back in a defensive posture. Photo by Edmund (Butch) Brodie, with permission.

Figure 7. ***Bolitoglossa subpalmata*** adult with eggs. Photo by Edmund (Butch) Brodie, with permission.

Predator Avoidance

There is some suggestion that some sort of chemical cues may exist that warn other salamanders because at least some members of the family Plethodontidae are sensitive to skin chemicals from other salamanders, both their own species and others in their genus, that have been attacked. These are not documented as being poisonous, but rather elicit avoidance behavior in those salamanders sensing this danger signal (Lutterschmidt *et al*. 1994). Lutterschmidt *et al*. (1994) demonstrated this response for ***Desmognathus ochrophaeus*** (sometimes a moss-dweller) toward other ***D. ochrophaeus*** and also to others in its genus, but not to ***Plethodon richmondi*** skin extracts. This chemical does not seem to be present in the viscera of the salamanders or in damaged mealworms. Recognition of the released chemical from attacked individuals signals the nearby salamanders to flee or take cover.

Warning Coloration and Mimicry

A type of mimicry known as **disruptive coloration** helps to hide organisms in plain view and involves having a color pattern that resembles their surroundings. This is well known in the clothing worn by soldiers who need to blend with their surroundings. You probably noticed that the colors changed when the soldiers started fighting in desert habitats with little vegetation. Greens were replaced by grays.

For bryophyte-dwelling salamanders mimicry can involve resembling the bryophytes that surround them. Disruptive patterns of green, brown, and black give them the appearance of the bryophytes (Figure 8), at least from a distance. Nevertheless, most bryophyte-dwelling salamanders do not seem to mimic bryophytes. Instead, the non-colorful ones are typically shades of brown, instead mimicking the soil, bark, or a stick. This is perhaps reasonable since they could move within moss mats with little visibility, but would be conspicuous on the soil or bark where catching dinner may dictate surface movement. And brown salamanders on green moss do resemble a stick from a distance. I have not located any information to indicate that any salamanders have outgrowths that resemble moss or lichen growths, such as those seen on some frogs.

Figure 8. ***Aneides aeneus*** (**Green Salamander**) juvenile somewhat resembling its mossy habitat. However, one could argue that the blackish and yellow colors are also warning colors. Photo by Bill Peterman, with permission.

Some salamanders take advantage of camouflage on top so they are not noticed from a distance, but if a predator draws near, they can rear up and show a bright warning color on the ventral (lower) side, such as that seen for ***Taricha granulosa*** in Figure 9, or roll over onto their backs (Figure 10-Figure 11). If the predator has had a bad experience with that color combination, it is likely to retreat.

Figure 9. **Adult Rough-skinned Newt** (***Taricha granulosa***) demonstrating a defensive posture that is practiced by a number of the larger salamander species. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 10. The **Cascade Torrent Salamander**, ***Rhyacotriton cascadae***, demonstrating the brown dorsal surface that blends with the twigs among the mosses. Photo © Henk Wallays, through Creative Commons.

Figure 11. The **Cascade Torrent Salamander**, ***Rhyacotriton cascadae***. Behavior of rolling onto its back and revealing the warning color of yellow. Photo by Henk Wallays, through Creative Commons for educational use.

Müllerian mimicry is common among salamanders. **Müllerian mimicry** permits species that look like each other to protect each other through similar warning coloration. Less or non-poisonous species enjoy less predation because they look like a species that is highly poisonous. Thus a predator has a higher probability of encountering the highly poisonous common species first and learns to avoid things that look like it, including the less common weakly poisonous or non-poisonous species. Both relatively common, highly poisonous species and slightly poisonous species with small numbers can have varying degrees of red, yellow, and black warning color combinations. Interestingly, the same color combinations are prevalent among hurtful and toxic species elsewhere in the animal kingdom, including snakes, bees, and frogs.

Howard and Brodie (1971) first demonstrated the **Batesian mimetic** relationships of two toxic salamander species in the area at Highlands, North Carolina, USA. **Batesian mimicry** is the case where there is a toxic model and a non-toxic mimic that gains benefit by looking like a toxic species. It works best when the model is abundant and the mimic at least less abundant so that the predator is more likely to experience the model first. In the experiments by Howard and Brodie (1971), the highly toxic red **eft** (immature) stage of the **Eastern Newt**, ***Notophthalmus viridescens viridescens*** (Figure 12), a common moss visitor and a species that is both noxious and toxic, served as a model for the **Red Salamander**, ***Pseudotriton ruber schencki*** (Figure 13-Figure 15), a moss hibernator. After experiencing a noxious red eft, previously inexperienced chickens avoided the **Red Salamander** as well as the red eft. They still readily ate non-toxic species of ***Desmognathus***. Brandon and Huheey (1981) suggested that a **Müllerian mimicry** complex exists that has a variety of palatability levels. In **Müllerian mimicry**, a number of species, often unrelated, resemble each other and thus gain predation protection when a predator experiences another member of the group. This enhances the effectiveness of **Batesian mimics** as well because it increases the size of the pool of models. In the study by Brandon and Huheey, the poisonous (Müllerian) group includes the red eft of the **Eastern Newt** and at least some members of the **Red Salamander**; the non-poisonous Batesian species include such moss dwellers as the **Spring Salamander**, ***Gyrinophilus porphyriticus*** (Figure 16).

Figure 12. Red eft stage, ***Notophthalmus viridescens***, example of **Müllerian mimicry**. Photo by Alan Cressler, with permission.

Figure 13. ***Pseudotriton ruber***, a salamander with a strong neurotoxin, a Muellerian mimic of the red eft. This species is known to hibernate under mosses in ***Sphagnum*** peatlands. Photo by Mike Graziano, with permission.

Figure 14. ***Pseudotriton ruber***, where it is conspicuous on mosses. Photo by John White, through Creative Commons.

Figure 15. ***Pseudotriton ruber*** on mushrooms, where it is somewhat less conspicuous. Photo by John White, through Creative Commons.

Figure 16. ***Gyrinophilus porphyriticus***, a non-toxic Müllerian mimic of ***Pseudotriton ruber*** (Figure 13-Figure 15), giving it the advantage of looking like a poisonous species. Photo by Todd Pierson, with permission.

If you have no warning coloration and you are edible, it is not a good idea to advertise your presence. Instead, being still works well. And if the predator gets too close, try to look bigger or more dangerous – or drop your tail and run!

Locomotion

Locomotion provides an interesting story for bryophyte-dwelling salamanders. Limbs provide means of climbing trees and running across rocks, with arboreal species at times having large footpads that help them to cling to slippery surfaces (Wake 2011). But they also use sinuous body movements for rapid locomotion. For example, the genera ***Batrachoseps***, ***Oedipina***, ***Pseudoeurycea*** (formerly in ***Lineatriton***), and ***Phaeognathus*** have bryophyte-dwelling members with reduced limbs, and they use body movements for rapid locomotion. Some members of the often bryophyte-dwelling genus ***Bolitoglossa*** have highly webbed feet with nearly fused toes (Figure 17) that permit them to move across wet leaves and other smooth surfaces like bark. ***Aneides***, ***Chiropterotriton*** (Figure 18), ***Dendrotriton***, ***Nyctanolis*** (Figure 19), and ***Pseudoeurycea*** have bryophyte-dwelling species that are arboreal and use their long legs and toes with expanded tips to climb, but they are also aided by **prehensile tails** (tails that can be used to grasp, like that of a monkey) (Figure 18).

Figure 17. ***Bolitoglossa*** sp., illustrating the webbing on the foot that permits moving about on smooth surfaces. Photo by Ira Richling, <www.helicina.de >, with permission.

Figure 18. ***Chiropterotriton*** sp., demonstrating the long legs and prehensile tail that permit them to maneuver arboreal habitats. Photo by Timothy Burkhardt, with permission.

Figure 19. ***Nyctanolis pernix***. Photo by Todd Pierson, with permission.

Life Cycle

Having a life cycle with no aquatic stage is critical for tree dwellers, but many other species are restricted to living near water where they can lay their eggs (Figure 20-Figure 21). This is particularly true for the larger salamanders (newts) in the Salamandridae. For completely terrestrial species, having eggs that hatch into young salamanders (**direct development**) instead of tadpoles (Figure 22) facilitates this terrestrial transition. Others lay eggs near water where the larvae can easily drop or slither in.

Figure 20. Breeding adult **California Newts** (***Taricha torosa***). Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Role of Bryophytes

"One does not know whether a man killing an elephant or setting fire to the grassland is harming others until one knows the total system in which his act appears." Whereas this quote from Hardin (1968) was intended to illustrate the folly of our exploitations against whole ecosystems, it also characterizes our knowledge about the interaction of bryophytes with other members of the ecosystem. The salamanders are a group of organisms that is rapidly disappearing from the planet. As I researched this chapter, it became clear to me that for salamanders in particular, there is a huge gap in our knowledge. Many species live in "mossy" habitats, but little seems to be known about their use of the bryophytes.

Figure 21. Eggs of the **California Newt** (***Taricha torosa***). Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 22. Tadpole (aquatic) of **California Newt** (***Taricha torosa***). Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Pictures of salamanders on bryophytes abound on the web. But beware! Bryophytes are a favorite substrate for the photographers who often take these animals to the lab to be photographed. The bryophyte in the picture does not necessarily indicate that it is a preference for the salamander.

It is difficult to find documentation that salamanders actually depend on bryophytes, even when they are often found on or among mosses and liverworts (Figure 1). Others hide there in trees or peatlands. For example, Wilson (1992) reported finding one immature salamander

under a bryophyte mat at the base of a rock face in Idaho, USA. What does that really mean? Nevertheless, there is evidence that mosses can be beneficial to salamanders for maintaining moisture, camouflage, cover during hibernation and aestivation, nests, and in a few cases foraging sites.

Moisture

Salamanders have mucous-secreting glands that help to moisten and lubricate the skin. But these are insufficient to keep the skin moist in drier habitats, and not all salamanders are equally endowed with these glands.

The need of salamanders for moisture suggests that the bryophytes might play a vital role, albeit in a spurious way. When the soil is moist and the air is cool, bryophytes may simply be there, occasionally stepped on, and probably more often avoided because the soil and litter are easier to traverse. But when conditions begin to dry, the bryophyte offers a place to replenish moisture or a wetter place to take cover. Even for those species living in the soil, a bryophyte reduces water loss, making the soil more hospitable.

Almost no experiments exist to support the role of bryophytes in the habitat of salamanders. Using the **California Newt *Taricha torosa*** (Figure 23-Figure 25), Brown and Brown (1980) demonstrated the usefulness of mosses in hydrating salamanders. This animal can be up to 20 cm long (Wikipedia 2011b), and water maintenance is important, as it is to all salamanders. In their experiments, Brown and Brown (1980) found that water uptake from wet moss equalled 66% of that in fully submersed members of the species. Furthermore, external movement of water occurred along skin channels from the ventral (lower) to the dorsal (upper) surface, suggesting that a damp substrate such as moss could hydrate an animal resting on it or walking across it (Figure 23-Figure 25).

Figure 23. Adult **California Newt** (***Taricha torosa***) posed on a bed of mosses. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 24. Front view of adult **California Newt** (***Taricha torosa***) posed on a bed of mosses. Note its low profile, permitting the abdomen to contact the moss as it moves. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Despite the wonderful pictures above by Gary Nafis, it appears that ***Taricha torosa*** often lives in habitats lacking bryophytes. David Wake (pers. comm. 31 March 2011) concurs. Nevertheless, some ***T. torosa*** and ***T. granulosa*** do indeed live where the forest is humid and epiphytic mosses are common. In these locations, this newt lives among the mosses (Gary Nafis, pers. comm. 27 April 2011; Edmund (Butch) Brodie, pers. comm. 7 June 2011). In general, however, it appears that ***Taricha torosa*** prefers less humid climates than many of the other newt species (Wikipedia 2011b). Too bad – there has been a lot of research on this species. ***Taricha torosa*** further conserves water by storing it in the bladder (Brown & Brown 1980).

Figure 25. Adult **California Newt** (***Taricha torosa***) posed on a bed of mosses where it is able to replenish its water supply. Note the rough skin. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

This research on an animal of relatively dry habitats suggests that mosses could be critically important rehydration sources for other salamander taxa with higher moisture requirements. It is interesting that for their experiments Brown and Brown (1980) chose this species, which rarely encounters bryophytes in its California coastline and in the Sierra Nevada, USA, habitats. One must wonder if the species living in habitats with bryophytes have even better ability to make use of damp bryophytes for moisture regulation. Hopefully someone will investigate this role for salamanders in the "mossy" habitats occupied by amphibians, especially in the Neotropics.

Nesting Sites

Salamander nests are common among mosses, as well as grasses, sedges, and rotting logs (Wood 1955; Salthe 1967; Harris & Gill 1980). Studlar (Bryonet 8 September 2004) shared her observations that lungless salamanders (**Plethodontidae**) may lay their eggs in moss mats in the Appalachian Mountains, USA. Bryophytes help to maintain moisture as well as to provide cover that decreases visibility of the eggs. I wonder if they provide any antibiotic service? This could be especially helpful in preventing molds from developing on the eggs since many, perhaps most, bryophytes produce secondary compounds that have antibiotic properties. On the other hand, large areas of the eggs would not be in direct contact with the bryophytes and may, therefore, derive no antibiotic benefit from their bryological neighbors.

Food Source

As you will see later in this chapter, mosses are at least occasionally consumed by a few salamanders. But are they consumed as food, or merely ingested along with invertebrates or other food matter associated with them? No experimental work seems to be available to address this question.

On the other hand, bryophytes can be home to a number of food organisms, both in the water and on land. In peatlands, one attraction for salamanders in that mossy habitat is the presence of pools that harbor numerous insects, hence providing food (Desrochers & van Duinen 2006). Searching for the food available in the terrestrial bryophytes may impart cover as protection for them during foraging. Their predators may include reptiles, fish, birds, small mammals, and even spiders, with all but the latter being prevented from entering the small spaces within moss clumps.

Hibernation and Aestivation

When one considers **hibernation** (animal state of inactivity and metabolic depression, characterized by lower body temperature and slower breathing; used for passing winter) and **aestivation** (cessation or slowing of activity during summer, especially slowing of metabolism during a hot or dry period) sites, it appears that even less is known. Some salamanders in cooler climates hibernate in the winter and may seek the shelter of bryophytes for that purpose. However, as will be seen in the table at the end of this chapter, there seems to be documentation of this use for only a few species of salamanders. In many cases, the hibernation site is simply unknown.

Most salamander species are night-active. Some may spend the day among bryophytes, where they are less likely to be detected and where moisture is greater than on rocks or even in soil. In habitats where the summer is hot and dry most of the time, aestivation can occur. This likewise is not well documented, but at least a few species are known to use mosses as a summer refuge.

Bryophytes can help to buffer the temperature, maintaining a safer range for the salamanders. Vial (1968) found that ***Sphagnum*** in the mountains of Costa Rica maintained a relatively low range of stable temperatures (9.8-16°C). Peatland mosses, in particular, may help to cool the habitat through evaporative cooling. Gnaedinger and Reed (1948) found a temperature of 1.2°C under mosses while the air temperature was -3.3°C. The mosses apparently kept the soil from freezing, although the mosses themselves were frozen to a depth of 1 cm, as was the soil where mosses were absent.

This subchapter and the next will necessarily include a lot of anecdotal information and speculation in the hope that the information will stimulate further study. I hope in the following pages to suggest species that are worthy of further investigation to determine the role that bryophytes play in their life cycle – as hibernation sites, aestivation sites, remoistening sites, cover, and nesting sites.

Summary

Newts and salamanders are known as Caudata, a term referring to their tails. The majority are distributed in the Western Hemisphere. Lungless species (**Plethodontidae**) are almost completely restricted to North America and the Neotropics.

Salamander Adaptations: Arboreal bryophyte-dwelling salamanders tend to be small, shaped like a worm, with an elongate body and short legs. Their movements are often sinuous – they slither through a moss like a snake. And some have **prehensile tails** like a monkey, adding a fifth appendage for climbing, hanging, or clinging. Their colors are typically brown with various patterns of other colors (including **disruptive coloration**), and the ventral surface may be endowed with warning coloration. Hence, their defensive behavior may be to rear up or roll on their backs, exposing the **warning colors**. Some species are poisonous and colorful, and other species living in the same area may mimic their warning coloration (**Müllerian mimicry**). When attacked on the tail, salamanders can disarticulate the tail, which may continue wiggling, distracting the predator. They typically feed on ants, beetles, mites, and other small invertebrates. Their life cycle is either fully terrestrial, often with eggs hatching into young salamanders instead of tadpoles (**direct development**), or females locate their eggs near water where the larvae can easily drop or slither into the water when they hatch. Females often defend and tend the eggs, rotating them or cleaning them to reduce bacterial and fungal infection.

Role of Bryophytes: Bryophytes are important moisture reservoirs for salamanders, and at least some have channels in the skin that direct water, gained from bryophytes, upward to their backs. The plethodontid salamanders often lay eggs in mosses, thus satisfying their need for a wet or at least moist incubation environment. Some species use bryophytes exclusively for egg laying and are true **bryobionts**. Some use mosses for winter **hibernacula**, whereas others use them as summer retreats for aestivation. Thick bryophyte mats can buffer the temperature, providing soil that is frost-free longer, or cooled by evaporative cooling and shading. At least a few use the bryophytes as foraging sites.

Specific uses are often unknown, but the co-occurrence of certain salamanders with bryophytes in most of their known habitats suggests that the bryophytes may play an important role in their lives. At the very least, they can serve as indicators of the likely presence of salamanders.

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CHAPTER 14-7
HYNOBIIDAE, AMBYSTOMATIDAE, AND PLETHODONTIDAE

Janice M. Glime and William J. Boelema

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CHAPTER 14-7
HYNOBIIDAE, AMBYSTOMATIDAE, AND PLETHODONTIDAE

Figure 1. ***Desmognathus wrighti*** on a bed of moss, probably ***Hypnum* sp.** Photo by Bill Peterman, with permission.

Hynobiidae

This is a family of ca 36 species of medium-sized (to ~250 mm) terrestrial and semi-aquatic salamanders (Wake 2011). They occur in parts of Asia, south to Japan, and European Russia (Wikipedia 2011a). I could, however, find little information on their associations with bryophytes.

Hynobius tokyoensis (Tokyo Salamander)

Google made a link between ***Hynobius tokyoensis*** (**Tokyo Salamander**; Figure 2-Figure 3) and mosses, stating that when this species occurs on the forest floor, it can be found at the entrance of burrows, and under decayed logs, rocks, leaf litter, and moss mats (Kusano & Miyashita 1984). The eggs are deposited in water and the larvae are aquatic. The adults disperse up to 100 m from their breeding site by the time they are 4 years old, suggesting the importance of a suitable forest floor within that proximity.

This species has two completely disjunct distributions in Japan: Fukushima Prefecture southwestward to Kanagawa Prefecture and Aichi Prefecture of the Chubu District of Honshu (Matsui & Nishikawa 2001). It may be, however, that the Aichi population is actually ***Hynobius nebulosus*** (Matsui *et al*. 2001). This discontinuous distribution pattern is related to their need for areas kept moist by underground water oozing to the surface, a habitat found only in hills or small mountains (Ihara 2002). Its limited distribution makes it vulnerable to extinction (IUCN 2010).

Figure 2. ***Hynobius tokyoensis*** on a bed of moss. Photo by Henk Wallays, through Creative Commons.

Figure 3. ***Hynobius tokyoensis*** on a bed of moss. Photos © Henk Wallays, through Creative Commons.

Salamandrella keyserlingii (Siberian Salamander, Hynobiidae)

The **Siberian Salamander** seems to be the one Asian representative that has a notable association with bryophytes. It is distributed in northern Asia from Northern Hokkaido, Japan, and Sakhalin and Kurile Islands, Russia, from Kamchatka to eastern European Russia (to 45° E), south to northern Mongolia, northeastern China, and northern and northwestern Korea (Frost 2011).

It is an inhabitant of wet coniferous forests and mixed deciduous forests of the taiga, as well as riparian groves of the tundra and forest steppe (Kuzmin 1999).

This is one of the few amphibians to survive the cold of northernmost habitats. However, some salamanders do take advantage of mosses to provide their winter **hibernacula**. The **Siberian Salamanders** (***Salamandrella keyserlingii***; Figure 4), also known as Dybowski's Salamander, Manchurian Salamander, and Siberian Newt, are among the most cold-tolerant species (Potapov 1993). They can freeze for many years in the permafrost, then thaw out and go merrily on their way. Some may have been frozen for 10,000 years (Meat on the Web 2008)! This unusual animal can survive temperatures down to -50ºC, and they have been found preserved in ice with the wooly mammoth. However, there is no scientific evidence to support that ancient age for the salamanders. Rather, they probably fell into a crevasse.

Figure 4. ***Salamandrella keyserlingii***, the **Siberian Salamander**. Photo by Milõs Anděra, with permission.

The young **Siberian Salamanders** seek out vegetation where the temperature remains above -15ºC, but adults spend the winter in moss cushions near ponds and seldom experience temperatures below -3ºC (Potapov 1993). Nonetheless, adults can actually survive several weeks of temperatures below -50ºC. Amphibians use such cryoprotectants as glucose and glycerol, but the mechanism in this salamander is unknown. The nearness to ponds is critical when they do thaw because a moist salamander, caught in the freezing temperatures, is likely to die as ice crystals draw water out of the body. Nearness to the pond permits it to seek the safety of the water.

In summer, refugia under cover are important to modulate the temperature and maintain humidity (Hasumi *et al*. 2009). For example, at Shaamar, Mongolia, humidity under logs was 85.5% while the ambient air temperature was 48.3%. Light intensity in burrows and under logs was 27 lux compared to 17,000 lux at the surface. Some of these salamanders take cover in moss mats where they are seldom found by collectors. When captured and kept in the lab, ***Sphagnum*** will help to prevent desiccation.

Ambystomatidae (Mole Salamanders)

Ambystoma laterale (Blue-spotted Salamander)

This species is distributed from southern Canada and Alaska, USA, south to the southern edge of the Mexican Plateau. It lives under logs, mosses, and damp leaves or in burrows (LeClere 2011; NatureWorks 2011). The species migrates from wetlands to the forest floor where it spends the winter in underground retreats (Douglas & Monroe 1981). The migrants typically must travel 250 m or more to these sites.

The **Blue-spotted Salamander**, ***Ambystoma laterale***, also known as Lateral Salamander, Slender Salamander, Silvery Salamander, and Tremblay's Salamander (Figure 5), occurs in central and eastern North America, but it has become endangered in the lower part of its range (Ohio, Iowa) and is listed as a species of special concern in Indiana (Center for Reptile and Amphibian Conservation and Management). However, the IUCN (2010) lists it as a species of least concern. Clearcutting has been a major contributor to its increasing rarity, but acid precipitation also contributes to embryo mortality (Pough 1976). In northeastern North America it is threatened by acid rain (DeGraaf & Rudis 1983; Knox 1999). Not only is the *p*H detrimental to its development, but larval activity is lowered at *p*H levels less than 4.5-5.0, causing larvae to be preyed upon more easily (Brodman 1993; Kutka 1994).

Figure 5. The **Blue-spotted Salamander**, ***Ambystoma laterale***. Photo by Tony Swinehart, with permission.

Ambystoma maculatum (Spotted Salamander)

The **Spotted Salamander** occurs from Nova Scotia and Gaspe Peninsula west to central Ontario, Canada, and south through the eastern USA from Wisconsin to eastern Texas and east to southern Georgia, excluding the peninsula of Florida (Frost 2011).

The **Spotted Salamander, *Ambystoma maculatum*** (Figure 6-Figure 7), also known as Brown-spotted Salamander, Violet-colored Salamander, Yellow-spotted Salamander, Spotted Eft, Large Spotted Salamander is common in peatlands (Amphibians). Their typical home is in the deciduous forest, but they need vernal pools or ponds with no fish so that their eggs can avoid predation (Wikipedia: Spotted Salamander 2008; Figure 7). Oxygen is often a problem for salamander eggs, but ***A. maculatum*** has solved this problem by having a partner (Orr 1888; Gilbert 1944; Anderson 1971).

Figure 6. ***Ambystoma maculatum*** on mosses. Photo by John D. Willson, with permission.

Figure 7. Eggs of the Spotted Salamander, ***Ambystoma maculatum***. Photo by John D. Willson, with permission.

The salamander's eggs have a jelly coat that protects the eggs from drying out. However, this coating interferes with oxygen diffusion to the developing embryo. The salamander can solve the problem by partnering with the green alga ***Oophila amblystomatis*** (Figure 8-Figure 9) (name meaning "loves salamander eggs") (Hammen 1962; Bachmann *et al.* 1986). Through photosynthesis of the alga, the eggs obtain oxygen. The salamander returns the favor by providing the alga with much-needed CO_2 for photosynthesis (Figure 10). Ryan Kerney of Dalhousie University in Halifax, Nova Scotia, Canada, carried this story further, demonstrating that the algae were actually within the cells of the embryos, closely associated with the mitochondria, and that they benefitted from the nitrogen-rich waste produced by the embryos (Petherick 2010; Thoughtnomics 2011).

Researchers have questioned how these algae become associated and enter the cells, particularly in view of the typical immune response known for vertebrates. Kerney found that the algae could be present in the oviducts of adult females, the place where the jelly sacs that surround the embryos form. This suggests the possibility that the algae are passed to the embryos by the mother, but it does not explain how they enter the cells or what prevents the immune system from attacking them. Perhaps they, like the salamanders' own cells, are recognized as part of self at the time the embryo begins to form – an hypothesis that if true could be of tremendous benefit in our understanding of immunity.

Figure 8. Embryos of ***Ambystoma maculatum*** that have symbiotic algae, ***Oophila amblystomatis***, living with them. Photo by Renn Tumlison, with permission.

Figure 9. Embryo of ***Ambystoma maculatum*** showing the symbiotic algae, ***Oophila amblystomatis***, living within its egg. Photo by Renn Tumlison, with permission.

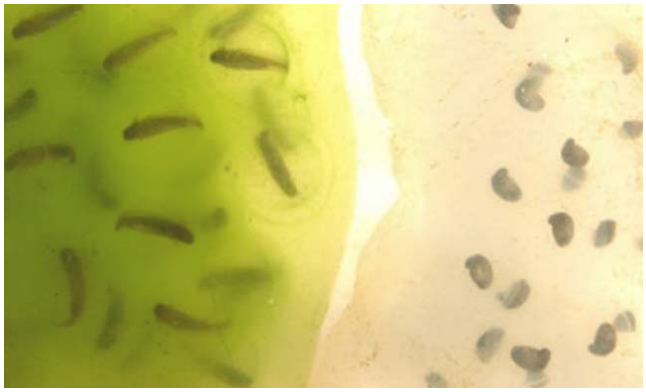

Figure 10. Comparison of embryos of ***Ambystoma maculatum*** that have symbiotic algae, ***Oophila amblystomatis***, on the **left** and no symbionts on the **right**. Photo by Renn Tumlison, with permission.

Embryos that were raised in continuous light hatched synchronously and at somewhat earlier developmental stages than those in either 12- or 24-hour darkness per day (Tattersall & Spiegelaar 2008). Those embryos without algae or in the dark moved more frequently than those with symbionts in the light. However, in later developmental stages, those in the light had more movements, suggesting that perhaps those without supplemental oxygen were conserving energy by not moving as much.

Like the frogs, larvae of salamanders are sensitive to low *p*H water. ***Ambystoma maculatum*** from three ponds in Marquette County, Michigan, USA, were raised at *p*H 3, 4, and 5 and in pond water *p*H (Ling *et al*. 1986). It took only 12 hours for the larvae to die at *p*H 3. At 4 and 5 the rates of development were significantly slower than those raised at *p*H above 5. Ling *et al*. (1986) found that 42% of the ponds in their study had *p*H levels below 5.5. Some of these were surrounded by a mat of ***Sphagnum***. In the pond with a central ***Sphagnum*** mat, and the lowest mean *p*H at 4.6, the researchers observed a slower rate of development. It is possible that under the stresses of laboratory conditions they were less tolerant of the lower *p*H than in their native ponds.

Ambystoma jeffersonianum (Jefferson Salamander)

The **Jefferson Salamander** (Figure 11) extends from central New Hampshire, USA, and southern Quebec, Canada, southwest to southern Indiana, and east to central Kentucky, western Virginia and West Virginia, USA (Frost 2011). Through a large part of this range it is able to hybridize with ***A. laterale***, complicating identification.

The Jefferson Salamander (***Ambystoma jeffersonianum***; Figure 11), also known as Granulated Salamander, Jefferson's Salamander, Plumbeous Salamander, and Brown Salamander, is among the many amphibians sensitive to conditions of low *p*H. In a study in central Pennsylvania and New Jersey Pine Barrens, USA, eggs could not hatch at *p*H below 4.5 (Freda & Dunson 1986). Those ponds with the lowest *p*H levels typically had abundant ***Sphagnum***. ***Sphagnum*** lowers the *p*H of the environment around it through cation exchange, releasing H^+ ions in exchange for cations such as Ca^{++} and Mg^{++} (Clymo 1963). In transplant experiments with embryos, mortality of ***A. jeffersonianum*** increased significantly as pond *p*H declined (Freda & Dunson 1986). The sensitivity helps to explain amphibian decline in the many sensitive species living with acid rain. A change of only 0.2 *p*H units can determine whether hatching occurs, making timing of the life cycle crucial for survival of the species.

Figure 11. ***Ambystoma jeffersonianum***. Photo by Todd Pierson, with permission.

Plethodontidae (Lungless Salamanders)

This large family is distributed on both sides of the Atlantic, from southern Alaska, USA, and Nova Scotia, Canada, south to eastern Brazil and central Bolivia, and in southern Europe and Korea (Frost 2011). But North America has most of the species. The family comprises 70% of the world's salamanders. These are known as **lungless salamanders** because they lack lungs and breathe through their skin. Most members of the large genus ***Plethodon*** prefer moist substrates (Taub 1961; Sugalski & Claussen 1997; Moore *et al*. 2001), hence making mosses near streams an ideal location for them. Nevertheless, in the tropics many species are land breeders, including many arboreal species. Bryophytes often play a role in keeping them moist as well as providing cover that hides them from predators. Their need for moisture is likely to be one reason for the preponderance of **nocturnal** (nighttime) activity among the plethodontid species.

Plethodon teyahalee, formerly *Plethodon oconaluftee* (Southern Appalachian Salamander)

Both ***Plethodon teyahalee*** (**Southern Appalachian Salamander**; also known as Teyahalee Salamander, Southern Appalachian Slimy Salamander, Balsam Mountains Salamander; Figure 12) and ***P. serratus*** (**Southern Red-backed Salamander**; Figure 13) may occur in peatlands (Amphibians: Tulula Wetlands 2009). ***Plethodon teyahalee*** is endemic to the United States, where it occurs at high elevations in the southern Appalachians, eastern USA, in other habitats as well as peatlands. Ash (1997) suggests that adults of the species may move into dry, clearcut areas to avoid competition with the smaller, immature salamanders of the same and other species in the more moist forest sites.

Figure 12. **Southern Appalachian Salamander** (***Plethodon teyahalee***). Photo by U. S. Geological Survey, through public domain.

Plethodon serratus (Southern Red-backed Salamander)

This species is also known as Ouachita Red-backed Salamander, Southern Redback Salamander, and Georgia Red-backed Salamander. The **Southern Red-backed Salamander** (Figure 13) is scattered into **disjunct** (disconnected) populations throughout southeastern USA (Frost 2011) where it hides under moss, as well as rocks and rotten logs, and migrates to seeps and springs during dry periods (Aardema 1999).

Figure 13. **Southern Red-backed Salamander** (***Plethodon serratus***). Photo by Henk Wallays, through Creative Commons.

Plethodon nettingi (Cheat Mountain Salamander)

The endangered relict **Cheat Mountain Salamander** (***Plethodon nettingi,*** **Plethodontidae**; Figure 14), an **endemic** in the Appalachian Mountains, West Virginia, USA, depends on bryophytes, especially the leafy liverwort ***Bazzania trilobata*** (Figure 15) (NationMaster 2008; Pauley 1985). While in the bryophyte mats, these amphibians feed on small invertebrates. Their territories are small and they seldom move more than a few meters in their lifetimes. Brooks (1945, 1948) reported finding 33 individuals on Cheat Mountain, crawling on moss-covered logs in dense stands of sapling and pole red spruce, sometimes with birch mixed in. On Bickle's Knob, West Virginia, these salamanders began appearing from mosses and under logs just after twilight (Brooks 1945).

Figure 14. **Cheat Mountain Salamander** (***Plethodon nettingi***) on bed of ***Bazzania trilobata***. Photo by Michael Graziano, with permission.

Figure 15. Branches of ***Bazzania trilobata***, home to the **Cheat Mountain Salamander**. Photo by Michael Lüth, with permission.

Plethodon cinereus (Eastern Red-backed Salamander, Plethodontidae)

The **Eastern Red-backed Salamander** (Figure 16) occurs in the northeastern USA and southeastern Canada, south through northeastern Wisconsin to southern Indiana, southern Ohio, and east of the Appalachian Divide south to northern North Carolina.

Plethodon cinereus poses a danger to the **Cheat Mountain Salamander** through competition with this much more widespread **Eastern Red-backed Salamander** (NationMaster 2008). The widespread distribution of ***Plethodon cinereus*** is reflected in having 18 English names listed by Frost (2011). This common salamander includes bogs among its habitats, where it can sometimes be found attempting to rob the pitcher plant leaves of their inhabitants (Hughes *et al*. unpubl.). Analysis of gut contents indicate a diet of midge larvae, ants, mites, and other small invertebrates that live in the bogs. I wonder if this diet makes it poisonous? The red-backed salamander can often be found under a clump of moss such as ***Leucobryum glaucum*** (Figure 17). At Cap des Rosiers, eastern Quebec, Canada, this salamander was mostly under stones and logs, but one specimen was under moss on a vertical limestone cliff face (Trapido & Clausen 1938).

Figure 16. ***Plethodon cinereus***, the **Eastern Red-backed Salamander**. Photo by Tony Swinehart, with permission.

Figure 17. ***Leucobryum glaucum*** cushions that provide suitable shelters for the **Eastern Red-backed Salamander**. Photo by Michael Lüth, with permission.

In this species, adults typically defend the territories surrounding their offspring. However, it appears that mothers cannot recognize their own offspring, nor could the offspring recognize their mothers (Gibbons *et al*. 2003). The young salamander offspring did not distinguish between mosses scented by their mothers and those with no scent or with scents of unfamiliar females. On the other hand, females chose unrelated offspring significantly more often over their own for acts of cannibalism.

Plethodon dorsalis (Northern Zigzag Salamander)

This salamander (Figure 18) often poses in a Z formation, hence its name. Other English names include Ashy Lizard, Zigzag Salamander, and Eastern Zigzag Salamander. It occurs in lower Midwestern USA from southern Indiana and southern and eastern Illinois to western Kentucky, central Tennessee, northern and western Alabama, and northeastern Mississippi (Frost 2011). Although Brode (1957) found it under sandstone slabs, Ferguson (1961) reported it from the bases of cliffs in Tishomingo County, Mississippi, USA, where it was under moist mosses, or from leaf litter.

Figure 18. ***Plethodon dorsalis***. Photo by Todd Pierson, with permission.

Plethodon welleri (Weller's Salamander)

Other English names for ***Plethodon welleri*** (Figure 19) include Spot-bellied Salamander and Spotbelly Salamander. **Weller's Salamander** occurs at higher elevations in Tennessee, north to mountains in Virginia (Frost 2011). Organ (1960) reported eight nests of this salamander, located from mid-August to early September between the upper rotting surfaces of conifer logs and the mat of 5-10 cm of mosses.

Figure 19. ***Plethodon welleri*** on a bed of mosses. Photo by Todd Pierson, with permission.

Plethodon elongatus (Del Norte Salamander)

In southwestern Oregon and northwestern California, USA, the **Del Norte Salamander** (***Plethodon elongatus***; Figure 20) is restricted to old-growth forests (Welsh 1990) and may require the moss cover that develops there. These forests range up to 560 years old and have more favorable microclimates than do the young forests. The **Del Norte Salamander** (***Plethodon elongatus***) rarely occurs in open water and seems to require the moisture of mosses, rocks, and organic matter. In northwestern California, Welsh and Lind (1995) sampled 57 sites and found a mean of 20 individuals at sites with moss as ground cover, but only 6.9 individuals at sites with none. The need for mosses meant that these salamanders also needed late successional stage forests where mosses had had time to develop significant cover. These habitats tended to be cooler with more moist microclimates among the mosses.

Figure 20. The **Del Norte Salamander**, ***Plethodon elongatus***. Photo by Henk Wallays, through Creative Commons.

Plethodon idahoensis (Coeur d'Alene Salamander)

Plethodon idahoensis (formerly *Plethodon vandykei idahoensis*), the **Coeur d'Alene Salamander** (Figure 21), lives further east in the drainage areas of the Selway River

of northern Idaho and the Bitterroot River of extreme western Montana, USA, as well as in the Duncan and Columbia River drainages of southeastern British Columbia, Canada (Frost 2011). The **Coeur d'Alene Salamander**, ***Plethodon idahoensis***, is the only plethodontid in the northern Rocky Mountains (AmphibiaWeb 2004).

This salamander can be found in springs, seepages, streamside, or spray zones of waterfalls (Discover Life 2012; Figure 21-Figure 22). These habitats often have bryophytes and the **Coeur d'Alene Salamander** can most likely be found on and under these bryophytes. Wilson (1990) reports one such case under bryophyte mats on cobbles along a stream at ~540 m in the Nez Perce National Forest, Idaho, USA.

The eggs of the **Coeur d'Alene Salamander** are produced in grapelike clusters, and larvae of this species develop within the eggs; thus, no tadpoles exist (Wikipedia 2011b).

Figure 21. The **Coeur d'Alene Salamander**, ***Plethodon idahoensis***. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

At Beauty Bay on Coeur d'Alene Lake, Idaho, USA, Dumas (1957) found two females and two immatures under moist moss on a stable talus slope. In the following year he found another immature under wet moss in a small seepage area on the south shore of the Chatcolet Lake.

Figure 22. Color variant of **Coeur d'Alene Salamander**, ***Plethodon idahoensis***. Photo by William Leonard, with permission.

Plethodon vandykei complex (Van Dyke's Salamander)

The **Van Dyke's Salamander** (Figure 23), also known as Van Dyke Salamander and Washington Salamander, occurs on the Olympic Peninsula and in the southern Cascade Range of western Washington, USA, at 0-1550 m asl (Frost 2011). This species, along with other members of its species complex, is frequent under moss mats (Slater 1933). ***Plethodon vandykei***, *sensu stricto*, is most common near streams, where it uses the mosses and moist slabs of bark at tree bases for cover.

During the day these salamanders are typically found under stones and mosses within streams, but when they search for food after dark they wander out of the water and hunt streamside. McIntyre *et al*. (2006) suggested that ***P. vandykei*** (Figure 23) is most common in habitats that are able to maintain both cool and hydric conditions; this species is sensitive to both heat and desiccation. Mosses provide such habitats, particularly in seeps. McIntyre and coworkers hypothesized that this would result in a positive association of this species with early successional stages that were dominated by bryophytes and graminoids, while having a negative association with leaf litter. Typically, in the Cascade Range of Washington State, USA, the mosses were associated with bedrock and small cobble, not soil. Surroundings of moist bryophytes would permit this and other members of the genus to absorb water directly through their skin (Spotila 1972). Seeps typically provide these ideal habitats by providing stability of both temperature and moisture (Hynes 1970; Huheey & Brandon 1973).

Figure 23. **Van Dyke's Salamander**, ***Plethodon vandykei*** on a log covered with mosses. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Plethodon larselli (Larch Mountain Salamander)

The **Larch Mountain Salamander**, ***Plethodon larselli*** (formerly *Plethodon vandykei larselli;* Figure 24), occurs in the Lower Columbia River Gorge of Oregon and Washington, USA (Frost 2011). It inhabits the lava talus slopes, and Burns (1962) found it among mosses on the side of a steep **andesite** (dark grey fine-grained volcanic rock) cliff.

Figure 24. ***Plethodon larselli***, the **Larch Mountain Salamander**. Photo © Henk Wallays, through Creative Commons.

Plethodon glutinosus (Northern Slimy Salamander)

The **Northern Slimy Salamander** (Figure 25) is a large (11.5-20.5 cm total length) terrestrial salamander (Virginia Department of Game and Inland Fisheries 2011a) that lives mostly in bottomland and wet hardwood forests of eastern USA (Beamer & Lannoo 2011a). This species lives under logs, rocks, and in tunnels in the soil; there seems to be no documentation that it lives among bryophytes. At night it traverses the forest floor, hunting for food. At that time, mosses may aid in rehydration, but this theory has not been tested. However, it does at times deposit eggs under mosses (Virginia Department of Game and Inland Fisheries 2011a). The eggs are a creamy white with an average of 5.5 mm diameter.

When handled, the **Northern Slimy Salamander** secretes a noxious sticky substance from its tail, a protection against predators (Virginia Department of Game and Inland Fisheries 2011a). Brodie *et al*. (1979) found that this secretion deterred shrews, causing them to avoid the salamander or to spend more time to kill it, resulting in less predation than that on the non-noxious ***Desmognathus ochrophaeus***. As an added deterrent it lashes its tail, further exposing the secreting glands.

Figure 25. ***Plethodon glutinosus*** on mosses. Photo by Henk Wallays, through Creative Commons.

Plethodon richmondi (Southern Ravine Salamander)

This salamander can be found in parts of Pennsylvania, Ohio, Kentucky, Indiana, and West Virginia (Pauley & Watson 2011). It is restricted to woodlands (Duellman 1954). Sexual maturity requires three years in males and four years in females (Nagel 1979). The Virginia Department of Game and Inland Fisheries (2011b) reports that this species has a spring courtship, followed by laying its eggs in damp logs and mosses in the early summer. On the other hand, Nagel (1979) found that in northeastern Tennessee, mating occurred from November to March, with a mean of 8.3 eggs deposited in May.

Plethodon metcalfi, formerly *Plethodon jordani metcalfi* (Southern Gray-cheeked Salamander)

The **Southern Gray-cheeked Salamander**, ***Plethodon metcalfi*** (Figure 26), is also known as Unspotted Salamander, Metcalf's Salamander, Clemson's Salamander, Clemson Salamander, Highland's Salamander, Highlands Salamander, Rabun Bald Salamander, Rabun Salamander, Frosted Salamander, and Southern Graycheek Salamander. It is surprising to have so many English names for a salamander that ranges only from the southwestern corner of North Carolina and extreme northwestern South Carolina into extreme northeastern Georgia, USA (Frost 2011). Organ (1958) found a courting pair on moss of the forest floor in mid August, but little else seems to be known of its relationship with bryophytes. The food of this species (snails, mites, spiders, insect larvae, springtails, millipedes, and centipedes) suggest that it could subsist on organisms found among bryophytes, making them potential hunting grounds (Whitaker & Rubin 1971).

Figure 26. ***Plethodon metcalfi***, the **Southern Gray-cheeked Salamander**, on a bed of mosses. Photo by Bill Peterman, with permission.

Plethodon jordani (Red-cheeked Salamander; Jordan's Salamander)

In the higher elevations of the Great Smoky Mountains, this species (Figure 27-Figure 28) is most abundant in the red spruce-Fraser's fir forest where the forest floor is covered with a heavy layer of mosses and little soil (King 1939). Its greater abundance in forests with a predominant bryophyte cover suggests that bryophytes may be important in maintaining the moisture required in its niche.

Although its range is somewhat small, it is widespread within that range and does not appear to be endangered (Beamer & Lannoo 2011b). Nevertheless, despite its protection within the Great Smoky Mountain National Forest, it could be endangered by the infestation of the balsam woolly adelgid beetle (***Adelges piceae***, Adelgidae, Hemiptera) that has caused considerable canopy changes. As new openings impact the bryophytes (Stehn *et al*. 2010a, b) by creating more light, potentially reducing their cover, this species could lose considerable habitat.

Figure 27. **Red-cheeked Salamander**, ***Plethodon jordani***, on a bed of ***Thuidium***. Photo by Matthew Niemiller, with permission.

Figure 28. ***Plethodon jordani*** on a bed of bryophytes. Photo by Bill Peterman, with permission.

Plethodon shermani (Red-legged Salamander)

Richard Bruce is an avid salamander hunter and has become interested in their mossy habitats. He has just sent me another picture, this time of ***Plethodon shermani***, adding another species to the list of bryophyte dwellers. The salamander was living in a species of ***Hypnum*** on a slope above the Nantahala River, North Carolina, USA. The species is mainly found under logs in daytime, and emerges on humid and rainy nights to forage on the forest floor (Richard Bruce, pers. comm. 4 November 2020). They are only occasionally found under moss cushions (unlike ***Desmognathus aeneus*** which is a moss specialist, and which co-occurs in forests with ***P. shermani***).

Figure 29. ***Plethodon shermani*** crawling on the moss ***Hypnum*** sp. where it lives. Photo courtesy of Richard Bruce.

Plethodon stormi (Siskiyou Mountains Salamander)

The **Siskiyou Mountains Salamander** (Figure 30) has a narrow distribution in southwestern Jackson County, Oregon, and northern Siskiyou County, California, USA (Frost 2011). Its narrow distribution and loss of habitat cause it to be listed as endangered (IUCN 2010). It is associated with moss-covered rocks (Gary Nafis, pers. comm. 28 April 2011). It appears that nothing is known about nests, eggs, or young (see Bury & Welsh 2011). Adults sit quietly and wait for their prey of collembolans, termites, beetles, moths, spiders, and mites (Nussbaum *et al*. 1983). They dart out from whatever cover they are using, so it is likely that some take advantages of the humidity and cooling ability of the mosses that abound in some of their talus habitats, using them as cover and re-moistening sites.

Figure 30. ***Plethodon stormi***. on a rock with mossy patches. Spotted coloration blends somewhat with the rock, but not with the moss. Photo © Gary Nafis through CaliforniaHerps.com, with permission.

Plethodon asupak (Scott Bar Salamander)

Like the previous species, the **Scott Bar Salamander** (Figure 31-Figure 32) is associated with moss-covered talus rocks (Figure 33; Gary Nafis, pers. comm. 28 April 2011), and it likewise has a restricted distribution, occurring in the Siskiyou Mountains (700-1300 m asl) at Muck-a-Muck Creek above Scott Bar, Siskiyou County, California, USA. ***Plethodon asupak*** is listed only as vulnerable (IUCN 2010),

being threatened by habitat loss (Lu 2009). It prefers north-facing slopes with closed canopy and talus rock (Lu 2009).

Figure 31. ***Plethodon asupak*** on a bed of mosses. Photo © Gary Nafis through CaliforniaHerps.com, with permission.

Figure 32. ***Plethodon asupak*** adult and juvenile. Photo by Timothy Burkhardt, with permission.

Figure 33. Rocky forest floor where mosses contribute to the habitat of ***Plethodon asupak***. Photo © Gary Nafis through CaliforniaHerps.com, with permission.

Gyrinophilus porphyriticus, formerly *Pseudotriton porphyriticus* (Spring Salamander)

This common species (Figure 34) has 25 English names in the 2011 list of Frost, even though its range is in just one area of North America: eastern USA from Canada to Georgia-Mississippi (Frost 2011). The most common alternative name among these is Blue Ridge Spring Salamander. The number may not be so surprising when one recognizes that there have been 34 Latin synonyms – it seems to be rather misunderstood. In Tishomingo County, Mississippi, Ferguson (1961) found a single salamander "resting" on a mat of mosses by a spring at the base of an over-hanging cliff. Scott LaGrecca (pers. comm. 11 August 2014) found "a couple" of them among ***Fontinalis*** in a stream in the Berkshires, Massachusetts, USA.

Figure 34. ***Gyrinophilus porphyriticus***, the **Blue Ridge Spring Salamander**, on a bed of mixed mosses. Photo by Bill Peterman, with permission.

Pseudotriton ruber (Red Salamander)

The **Red Salamander** (Figure 35) occurs from southern New York to northwestern Florida and west to eastern Ohio, central Kentucky and southeastern Louisiana, USA. Burger (1933) found a single adult in torpor under mosses of a drying bog in Pennsylvania in mid-summer. Bishop (1941) also observed adults under mats of ***Sphagnum***. As discussed earlier, this salamander has a complex of mimics that take advantage of its poisonous skin secretions.

Figure 35. The **Red Salamander**, ***Pseudotriton ruber***, on a bed of terrestrial mosses. Photo by John White, with permission.

Hemidactylium scutatum (Four-toed Salamander)

This seems to be the most famous of salamanders for dependence on mosses. Whenever I ask a North American herpetologist about salamanders associated with mosses, this species is mentioned, usually first. The **Four-toed Salamander** (Figure 36) is also known as Scaly Salamander, Scaly Lizard, and Eastern Four-toed Salamander. Its distribution is fairly continuous from

extreme southern Maine, USA, and extreme southern Quebec and Ontario, Canada, west to northern Wisconsin, USA, south to the **fall line** [area where an upland region (continental bedrock) and a coastal plain (coastal alluvia) meet; an unconformity] in North Carolina, South Carolina, Georgia, Alabama, and Tennessee, USA (Frost 2011). There may be additional disjunct populations in nearby areas.

Figure 36. ***Hemidactylium scutatum*** (**Four-toed Salamander**) on a bed of mosses. Photo by John D. Willson, with permission.

The **Four-toed Salamander** (***Hemidactylium scutatum***, Plethodontidae; Figure 37) is one of the best known of the amphibian moss inhabitants. Blanchard (1923) reported that all of his finds near Ann Arbor, Michigan, USA, were among ***Sphagnum*** clumps of woody bog shrubs within 15 cm above the water surface. the need for deep moss may be explained by the critical temperature maximum (CTM) for this species. In experiments, Hutchinson (1961) found the CTM to be 36.74°C, a temperature easily exceeded at the moss surface on a sunny day, but not likely to be achieved 15 cm below. The **Four-toed Salamander**, ***Hemidactylium scutatum*** (Figure 36), had a CTM of 36.7 + 0.11 C.

But, as early as 1918, Wright reported that this species was disappearing from New York due to draining of wetlands. Today the species is listed as endangered or rare in a number of states (Harris 2011), but is listed as a species of least concern on the 2010 IUCN Red List.

Fowler (1942) found a single adult under a ***Sphagnum*** mat in a shoreline bog of a lake in a Maine coniferous forest. King (1944) found it on fallen tree trunks and logs in a gum swamp in the Great Smoky Mountains National Park. Burger (1933) found two inactive individuals during the last week of March in Pennsylvania, again in swampy conditions. But apparently it has a broader habitat than just boggy or swampy land. Blanchard (1928) reported one adult male in ***Sphagnum*** in Reese's Bog, northern Michigan, USA, and argued that the apparent scarcity of the species may be due to its secretive habit of hiding among the ***Sphagnum***.

Habitat Characteristics

Bleakney (1953) revealed the role that mosses could play in the distribution of this species: "The first record for the province dates back to 1934 when the Arthur Dean's Nursery in Halifax sent a specimen to the Nova Scotia Museum of Science in Halifax. The salamander was correctly identified, but, because the northern limit of its range was believed to be southern Maine, the occurrence of this specimen was credited to introduction via ship's cargo. However, when in 1951 the nursery records were consulted, it was revealed that this **Four-toed Salamander** (Figure 36) had actually come from a load of moss gathered for the nursery from just outside the city."

Because so little was known of the habitat use of this species, Chalmers and Loftin (2006) investigated these relationships in order to build a predictive model of habitat. Among the predictors, a shoreline of ***Sphagnum*** species was important, along with wood substrate, water flow, and several plants. Interestingly, the shrub sheep laurel (*Kalmia angustifolia*) was a negative predictor, as was deciduous forest canopy. In Canaan Valley, West Virginia, USA, this species is likewise common in pond habitats with mosses, typically ***Sphagnum***, or loose bark on logs that can provide nest cover (Pauley 2007). After breeding season, the **Four-toed Salamanders** (Figure 36) leave the aquatic habitat to forage among the forest litter.

Mating

The species mates in late summer and into fall or even early winter. Courtship is an entertaining set of activities and responses, often occurring on peat mosses. The story reminds me of what we as children called Eskimo kisses. The male rubs his nose on the female's nose (Harding 1997; Petranka 1998). Then he circles her with his tail bent at a sharp right angle. If he is lucky, the female straddles his tail and presses her snout on the base of his tail. After a time, the male begins to move forward, tail undulating, and starts to deposit spermatophores. The female follows close behind, picking up the sticky spermatophores. With her snout still against the male's tail, she deposits the spermatophores in her **cloaca** (posterior opening for the intestinal, reproductive, and urinary tracts) while doing a straddle walk. After about 20 minutes the mating and fertilization are completed. It is not until spring that the female searches for a suitable nesting site to lay her eggs.

Figure 37. ***Hemidactylium scutatum*** (**Four-toed Salamander**) on mosses, ventral view. Flipping onto its back is one mechanism of responding to potential predators. Photo by John D. Willson, with permission.

Nest Sites

Numerous studies indicate that mosses are preferred nest sites for laying eggs. Wahl *et al*. (2008) found that when choices of moss, grasses, and sedges were available 89% of the nests at three montane pond sites in Virginia, USA, were in clumps of ***Sphagnum***. These sites had steeper banks, lower *p*H, and faced north more often than expected by chance. These three factors were correlated with embryonic survival. North-facing nests were cooler than those facing south.

The female typically lays her eggs among mosses at the edge of forest ponds and water holes (David Taylor, Bryonet 3 February 2009) where spaces will allow the larvae to wiggle down to the water (Linton & Gascho Landis 2005). Headstrom (1970) tells us that this salamander makes a simple cavity in ***Sphagnum*** (Figure 38-Figure 39), sometimes making use of a natural opening. Each cavity takes several minutes to construct, and it may take hours to provide for the entire clutch (Gates 2002). It is usually not far from open water and may be along the sides of a moss-covered rock that projects into the water. The eggs are sticky and adhere to the mosses. They have an added advantage – the eggs are unpalatable to insects, giving them protection in the mossy habitat that often houses insects (Hess & Harris 2000).

As already suggested, this species is best known for its occurrence among mosses in bogs and poor fens. Bleakney and Cook (1957) reported two females in Nova Scotia with eggs under ***Sphagnum*** mosses on logs. The logs hung over a stream and the two egg clutches had 36 eggs. It appears that the number of eggs in the clutch may be diminishing. Bishop (in Gilbert 1941) considered clutch sizes to range 40-60, with an average of 50 per female. But Cornell researchers found that after 1920 the averages were less than 50.

Figure 38. Female **Four-toed Salamander** (***Hemidactylium scutatum***) guarding her eggs in her nest of ***Sphagnum***. The ***Sphagnum*** has been parted so that the picture could be taken. Photo from Minnesota DNR, through public domain.

The females typically lay their eggs in such mosses as ***Sphagnum*** and ***Thuidium*** spp. (Wood 1955; Harris 2005). Chalmers (2004) found 238 nests in 36 wetlands in Maine, a state where the species is listed as one of Special Concern, along with eleven other states. Furthermore, it is listed as Threatened in Illinois and as Endangered in Indiana. Chalmers was able to locate these 36 new sites by using the predictive ability of shorelines with ***Sphagnum***. The nests were more common on shorelines with steeper slopes and deeper nesting vegetation, especially with moss and *Ilex verticillata* (winterberry), but were negatively associated with *Spiraea alba*, *Chamaedaphne calyculata*, and *Kalmia angustifolia* when they were within 1 m of the shoreline.

Figure 39. Eggs of ***Hemidactylium scutatum*** among non-***Sphagnum*** mosses. Photo by Jim McCormac <http://jimmccormac.blogspot.com>, with permission.

Wood (1955) reported that the **Four-toed Salamander** surrounds its nest with liverworts, as well as many species of ***Sphagnum***. ***Sphagnum*** is an important nest material (Wallace 1984), where the female deposits its eggs in mossy hummocks above the waterline where the eggs remain moist but don't drown (NJ Division of Fish & Wildlife 2009; Richard Andrus, pers. comm.; David Taylor, Bryonet 3 February 2009). Although many herpetologists assume that ***Sphagnum*** is preferred for nesting (Figure 38), females also deposit eggs under other species such as those of ***Atrichum*** (Figure 40) (David Taylor, Bryonet 3 February 2009), ***Sphagnum palustre*** (David Taylor, pers. comm. 25 October 2011), ***Thuidium*** (Figure 41), ***Mnium*** (probably now ***Plagiomnium*** or ***Rhizomnium***), ***Climacium*** (Gilbert 1941; Wood 1955; Easterla 1971; Petranka 1998; Harris 2009), ***Thamnobryum alleghaniense***, ***Hypnum*** sp., and in, as well as under, ***Aulacomnium palustre*** (Figure 42) (David Taylor, Bryonet 3 February 2009). In fact, in Kentucky, USA, John MacGregor (pers. comm. 4 February 2009) finds that most of the nests are under ***Thuidium*** (Figure 41). Many taxa of both mosses and liverworts surround the nests, contributing to the content of the nests (Harris 2009). The female often remains with the eggs until they hatch (Figure 40).

Figure 40. Female **Four-toed Salamander** (***Hemidactylium scutatum***) guarding her eggs in her nest amid the moss ***Atrichum* sp**. Photo by John D. Willson, with permission.

Figure 41. ***Thuidium delicatulum***, a common nest moss for the **Four-toed Salamander** (***Hemidactylium scutatum***). Photo by Michael Lüth, with permission.

Figure 42. ***Aulacomnium palustre***, a suitable moss for egg deposition by the **Four-toed Salamander**. Photo by Janice Glime.

Despite the numerous reports on eggs of this species in ***Sphagnum***, Wood (1953) found greater mortality for eggs in ***Sphagnum*** than for those laid on other genera. Overcrowding in large nests resulted in more dead eggs than for loosely placed eggs of small nests. Breitenbach (1982) found that solitary brooding was more likely to occur when there were abundant suitable nesting sites. In a Michigan study, only 12% of 109 nests were communal, with 13 of 14 nests in ***Sphagnum*** (Breitenbach 1982). Hence, greater reproductive success is likely to occur when there is more moss habitat available for cover. Nest disturbance can cause desertion of the nest, so nests hidden among mosses are less likely to be abandoned.

Wood (1955) found that the salamanders preferred thick mosses that contained many natural crevices where eggs could be placed, compared to shallow, thin mosses lacking such depressions. Gilbert (1941) similarly found that dense mosses such as those at tree bases and stumps or around hummocks did not seem to be desirable, whereas 27 out of 32 nests were in loose mosses along logs.

Hmmm...It appears that the habitat may alter the preferences for growth form and species. Gilbert (1941) found only five of these nests in ***Sphagnum***. He described the mosses being used as "loose and fluffy." But another factor could be temperature. Wood (1955) found that nest temperatures were warmer in the two ***Sphagnum*** habitats than in the seven ***Thuidium*** hummocks.

Gilbert (1941) found that the logs were located where water was within 7-10 cm. No nests were found where the water had completely dried up. Boyle (1914) found this species in Long Island, New York, by tearing mosses apart at the bases of dead trees at the edge of a pool. Green (1941) found a nest of 12 eggs in Kentucky, covered by a moss mat where a constant drip from a cliff face kept it continuously wet. These collections indicate that bogs are not essential for this species, but mosses apparently are.

Humphrey (1928) actually observed the female laying eggs in captivity. She had available to her ***Sphagnum*** in a dish. She actually turned upside down to lay the eggs on the overlying ***Sphagnum***. On a North Carolina, USA, coastal plain, three out of twenty **Four-toed Salamanders** laid their eggs on the underside of "sheet" moss (Schwartz & Etheridge 1954). Typically, the female repeatedly turns onto her back before laying eggs, perhaps to ensure the eggs are attached to the mosses instead of the underlying substrate (Noble & Richards 1932; Bishop 1941).

One problem that could further endanger such diminishing species as ***Hemidactylium scutatum*** is predation by inhabitants of the moss. Hess and Harris (2000) experimented with palatability of eggs and found that carabid beetles from the pond did not eat the eggs, but beetles from a stream punctured the eggs. However, they ate few of them. As noted earlier, Hess and Harris suggested that the eggs might contain a toxic or noxious chemical in their gelatinous layer. This avoidance of egg predation helps to explain the lack of nest defense and desertion of nests by this species. However, we have seen that the females seem to stay with the eggs at least some of the time.

Stereochilus marginatus (Many-lined Salamander, Plethodontidae)

The **Many-lined Salamander** (Figure 43), also known as Margined Triton and Margined Salamander, occurs on the Atlantic coastal plain from southeastern Virginia to northeastern Florida, USA (Frost 2011). Gerhardt (1967) found this species in a cypress swamp in Georgia, USA, among the ***Sphagnum*** in pine flatwoods, where it cohabited in the mosses with the **Broad-striped Dwarf Siren** (***Pseudobranchus striatus***), **Carpenter Frog** (***Lithobates virgatipes***) larvae, **Easter Lesser Siren** (***Siren intermedia***), and the **Mud Snake** (***Farancia abacura***).

Hatching can be fun to watch for both the **Four-toed Salamander** ***Hemidactylium scutatum*** and **Many-lined Salamander** ***Stereochilus marginatus*** (Figure 43) (both **Plethodontidae**) when they make their nests in ***Sphagnum*** or rotting wood (Blanchard 1934; Duellman & Trueb 1986). When the larvae hatch, they wriggle down the moss to the water. These larvae need to beware of cohabiting newts that like to have them for dinner (Wells & Harris 2001).

Adults of ***Stereochilus marginatus*** are somewhat safer than the larvae due to several anti-predator mechanisms. They secrete a glandular substance from the dorsal part of the tail, "threaten" by raising and undulating the tail, flip

over to expose the yellow venter with black spots (warning colors), secrete noxious substances from the skin, and lose their tails. The tail is lost when the salamander is attacked, even if the salamander has not been captured (Brodie 1977). The tail continues to wiggle after it has been detached (Gates 2002), possibly attracting the attention of the would-be predator.

Figure 43. The **Many-lined Salamander**, ***Stereochilus marginatus***. Photo by Michael Graziano, with permission.

In the Dismal Swamp, Virginia, where ***Sphagnum*** spp. are common, females seem to prefer laying their eggs on the brook moss ***Fontinalis*** sp. (Figure 44) (Wood & Rageot 1963; Rabb 1966). Bruce (1971) reported that females of ***Stereochilus marginatus*** in the Croatan National Forest in eastern North Carolina, USA, laid eggs underwater or just above the surface, with those underwater being laid singly or in small groups attached to stems of mosses.

Figure 44. ***Fontinalis antipyretica*** in a dry stream bed. During seasons of good flow, this is a suitable site for eggs of the **Many-lined Salamander**. Photo by Janice Glime.

Desmognathus fuscus (Northern Dusky Salamander)

The well-known salamander ***Desmognathus fuscus*** (Figure 45-Figure 47) occurs in Southern New Brunswick and southern Quebec, Canada, south of the Great Lakes to southeastern Indiana, western Kentucky, eastern Tennessee, and northeastern Georgia (excluding the coastal plain of North Carolina and South Carolina), USA.

Figure 45. The **Northern Dusky Salamander**, ***Desmognathus fuscus***. Photo by John D. Willson, with permission.

Figure 46. ***Desmognathus fuscus***. Photo by Todd Pierson, with permission.

The genus ***Desmognathus*** seems to be a common one under bryophytes. Adults may be located under mats of moss and other cover (Hom 1987). Their typical strategy when disturbed is to disappear into the mud (Tilley 1981). In New York, the Northern Dusky Salamander was the most common salamander species when Bishop compiled his list in 1922 (Bishop 1923). But lack of suitable sites may limit breeding and population growth throughout much of its range.

Figure 47. ***Desmognathus fuscus***. Photo by Bill Peterman, with permission.

In Tennessee, USA, Hom (1987) found nests mostly on the banks of streams (Figure 48) in moist soil under mosses [***Atrichum undulatum*** (Figure 51), ***Mnium affine***, ***Thuidium delicatulum*** (Figure 41)] and the leafy liverwort ***Trichocolea tomentella***, accounting for 85-95% of the observations over a three-year period.

Unlike many amphibians, most ***Desmognathus*** species do not have a larval stage, but instead begin life as miniature adults (Chippindale & Wiens 2005); *i.e.*, they have **direct development**. It appears that the most advanced forms have a larval stage that may have secondarily returned to the water, as in the Northern Dusky Salamander. The **Northern Dusky Salamander**, ***Desmognathus fuscus*** (Figure 47), selects sites in advance for laying eggs (Hom 1988). Burger (1933) found a cluster of eleven eggs under moss on a mountain slope in Lebanon County, Pennsylvania, USA, during the first week of September. These larvae were just ready to emerge, and when disturbed several did break through the egg membrane.

Females can occur in clusters, such as the three females hiding with their egg clusters under a 20-cm square of moss covering mucky soil of a springy swamp (Bishop 1923). Females of the species tended to brood their egg clutches under mosses (Hom 1987). Montague (1977) showed experimentally that ***Sphagnum*** served as a sufficiently moist site for a clutch of eggs in an environmental chamber at 14°C. Eggs are deposited in moist soil under mosses (Figure 49), rotting logs, rocks, and leaf litter (Dennis 1962; Snodgrass *et al*. 2007). Clutch size typically ranges 5-34 with a mean in the mid 20's (Means 2011). Hatching requires 45-60 days, and the female remains with the eggs during this time (Snodgrass *et al*. 2007). Females seem to recognize tradeoffs in parental care (Forester *et al*. 2005). In an experiment where eggs of several clutches were divided and placed at 13 and 21°C, those at the higher temperature developed faster. When the female was introduced to her two sets of eggs, she spent most of her time caring for those that were further developed. But when the young hatch, she leaves them to fend for themselves.

Figure 48. Habitat of ***Desmognathus fuscus***, Lumpkin County, Georgia, USA. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 49. ***Desmognathus fuscus*** that has been uncovered with its eggs. Photo by Todd Pierson, with permission.

Desmognathus ochrophaeus (Allegheny Mountain Dusky Salamander, Plethodontidae)

The **Allegheny Mountain Dusky Salamander** (Figure 50) occurs from the mountains of southeastern Kentucky, through the Adirondack Mountains, USA, to southern Quebec, Canada.

As for many salamanders, seeps provide this species with both moisture and temperature stability (Huheey & Brandon 1973). This is true even on rock faces, where they are able to maintain moisture among mosses. But this highly variable species also inhabits forest streambanks where it lives among mosses, under rocks, leaves, bark, and logs, and in rock crevices (Tilley 1972; Mushinsky 1976). Experiments indicate that the adults will select some habitats based on the one in which they experienced early development.

Figure 50. ***Desmognathus ochrophaeus*** (**Allegheny Mountain Dusky Salamander**) on a bed of ***Atrichum* sp**. Photo by John White, with permission.

Bruce (1990) tried to explain the selection pressures accounting for size differences between ***D. ochrophaeus*** and ***D. monticola*** (**Seal Salamander**). The more aquatic ***D. monticola*** is larger than ***D. ochrophaeus***. Bruce located most of the egg clutches under mosses at Wolf Creek in the Appalachian Mountains. Eggs of ***D. ochrophaeus*** were significantly smaller than those of ***D. monticola*** and also experienced earlier maturation, making them smaller as adults. Bruce suggested that the decrease in age at maturation in ***D. ochrophaeus*** accompanied the shift to a terrestrial habitat. The selection pressure could be competition or predation – or both.

Whereas Bruce suggests that the smaller size leads to greater predation, Forester (1979a) suggests that the predation is reduced by greater parental care of egg clutches in this species. Furthermore, those clutches unprotected by females were more susceptible to phycomycete fungi, in as little as 12 days after they were deposited. It appears that the female uses her head and mouth to remove infected eggs and to gently oscillate them through movements of the throat (**gular**) region; mechanically vibrated clutches likewise had a higher percentage of survival than non-vibrated controls. Females were able to defend their eggs against other members of their own species and against ground beetles, but were not so successful against larger salamanders or **Ringneck Snakes** (***Diadophis punctatus***). Nests often occurred under mats of the mosses ***Thuidium delicatulum*** (Figure 41), ***Atrichum undulatum*** (Figure 51), and ***Plagiomnium ciliare*** (Figure 52).

Figure 51. ***Atrichum undulatum***, a moss that provides a nesting site for several species of salamanders, including ***Desmognathus ochrophaeus***. Photo by Michael Lüth, with permission.

Figure 52. ***Plagiomnium ciliare***, a moss that is often home to eggs of ***Desmognathus ochrophaeus***. Photo by Annie Martin, Mountain Moss Enterprises, with permission.

Females in this species have a homing instinct for their own nests, at least over short distances (Forester 1974, 1979b). When 117 females were moved 2 m from their nests, 78% returned to their nests within 24 hours. They were attracted to unattended eggs, but were able to distinguish their own nests from others with unattended eggs, only occasionally selecting the eggs of another female in preference to their own. For example, seven females were nesting on a single moss-covered rock. When they were marked and moved, five of the seven returned to their own eggs. Females typically remain with their eggs and do not forage while attending them.

In an experiment, females were offered sites with depressions in soil, but only half of them were covered with moss (Forester 1979b). Females preferred holes with moss cover in all arrangements tested. That is some of the best evidence I have found indicating preference for bryophytes.

This species is known to avoid predation by early detection of a nearby predator. Chemicals released by wounded members of its own species and others in the genus serve as a warning to take cover (Lutterschmidt *et al.* 1994).

Desmognathus monticola (Seal Salamander)

This species (Figure 53) ranges from the central and southern Appalachians of western Pennsylvania to central Alabama (Camp & Tilley 2011) and is more aquatic than is ***Desmognathus ochrophaeus*** (Bruce 1990). It is typically found among mosses on rocks in streams (LeGrand *et al.* 2001). It lays its eggs in rapid streams where they are sometimes placed under mosses (Camp & Tilley 2011).

Figure 53. ***Desmognathus monticola*** on a bed of streamside mosses. Photo by Bill Peterman, with permission.

Desmognathus santeetlah (Santeetlah Dusky Salamander, Plethodontidae)

The **Santeetlah Dusky Salamander** (Figure 54) is restricted to the Great Smoky, Great Balsam, and Unicoi Mountains of the southwestern Blue Ridge Mountains in Tennessee and North Carolina, USA. ***Desmognathus santeetlah*** (Figure 54) is a higher elevation segregate of the **Northern Dusky Salamander** (***Desmognathus fuscus***) in the southern Appalachians, USA. One of the factors that maintains it as a separate species is that it has a different larval environment (Beachy 1993). This species broods its ca 20 eggs under mosses on logs and rocks at the edges of headwater streams (Jones 1986; Tilley 1988; Beachy 1993), compared to the soil depository under mosses, logs, and rocks for eggs of ***Desmognathus fuscus*** (Tilley 1973).

Instead of scurrying into the mud to hide, like ***D. ochrophaeus*** (**Allegheny Mountain Dusky Salamander**; Figure 50), this one remains motionless (Tilley 1981). Both ***D. santeetlah*** and ***D. ochrophaeus*** occur in the Southern Appalachians (Tilley 1973) and both seem to prefer brooding sites under mosses on logs or rocks. In some locations, only ***D. santeetlah*** nesting sites can be found (Tilley *et al.* 1978), but in others both species occur, suggesting that under some conditions there may be competition for suitable nesting sites. However, ***D.***

santeetlah oviposits mostly under mosses on rocks or logs in seepage areas.

Figure 54. ***Desmognathus santeetlah*** (**Santeetlah Dusky Salamander**), a high elevation salamander from the southern Appalachians. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Desmognathus aeneus (Seepage Salamander)

Also known as the Cherokee Salamander and Alabama Salamander, the **Seepage Salamander** (Figure 55) occurs from extreme southwestern North Carolina, adjacent Tennessee, and southwestward through northern Georgia (Figure 56) to north central Alabama, USA. In Georgia, Martof and Humphries (1955) found it under leaves, mosses, and stones, especially near seepages and other places of high humidity (Figure 56).

The 11-14 eggs of ***D. aeneus*** are deposited under mosses, as well as under logs, leaf litter, and mats of roots in seepage or wet areas near streams (Figure 56) (Bishop & Valentine 1950; Valentine 1963; Harrison 1967; Jones 1981; Collazo & Marks 1994). Females remain with the eggs during incubation (Brown & Bishop 1948; Bishop & Valentine 1950). Although this species is not considered a climber, Wilson (1984) observed them jumping from branch to branch in bushes and climbing up grasses. They feed mostly on insects, but their diet also includes nematodes, earthworms, land snails, isopods, amphipods, centipedes, arachnids, and millipedes, all items that can be found among mosses as well as leaf litter (Folkerts 1968; Donovan & Folkerts 1972; Jones 1981).

Figure 55. **Seepage Salamander**, ***Desmognathus aeneus*** on ***Atrichum***. Photo by Todd Pierson, with permission.

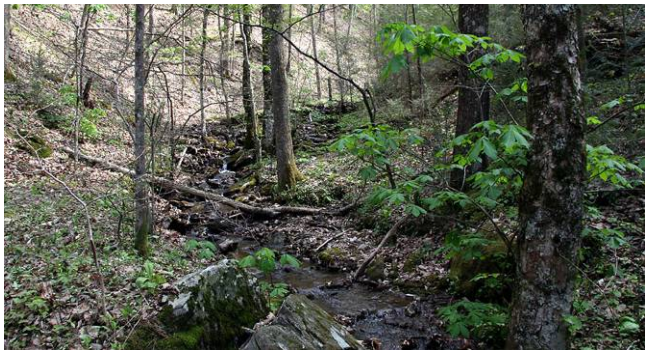

Figure 56. Habitat of the **Seepage Salamander** ***Desmognathus aeneus*** in Georgia, USA. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Desmognathus wrighti (Pygmy Salamander)

Known as the **Pigmy Salamander** (Figure 57), this small species occurs in woodland areas, especially above 1400 m asl within the southern Appalachians, including the Great Smoky Mountains of North Carolina and Tennessee, the Plott Balsam Mountains and Great Balsam Mountains of North Carolina, USA; it is also common between 950 m and 1400 m asl within the Cowee Mountains, Nantahala Mountains, and Unicoi Mountains of North Carolina, USA.

In the southern Nantahala Mountains, North Carolina, USA, ***Desmognathus aeneus*** (**Seepage Salamander**; Figure 55) and ***D. wrighti*** (**Pygmy Salamander**; Figure 57-Figure 58) are **sympatric** (ranges overlap) in high elevations (Hining & Bruce 2005). Both occupy clumps of moss, damp leaf litter, or shelter under stones or logs near streams and seepages in the deciduous forest during the spring (Figure 56). ***Desmognathus wrighti*** not only occupies wet areas, but can also be found up to two meters high in a tree on its leaves (Hairston, 1949; Organ, 1961). The two species manage to remain distinct by having different oviposition times, early May for ***D. aeneus*** and early August for ***D. wrighti*** (Harrison 2009).

Figure 57. **Pygmy Salamander**, ***Desmognathus wrighti***. Photo by Michael Graziano, with permission.

Richard Bruce (pers. comm. 10 August 2019; Bruce 2019) describes his experience with the Pygmy Salamanders: "I find the salamanders under moss cushions (especially ***Thuidium delicatulum***; Figure 58) on the soil but also in the mosses among the rhizoids, stems, and leaves. I find them in loosely organized mosses with a lot

of internal space, as opposed to more compact mosses. But the salamanders also occur in leaf litter and under logs. Of the 3 miniaturized species of ***Desmognathus***, ***D. aeneus*** seems to have the greatest affinity for moss, but the other two also occur frequently in mosses. Mosses provide shelter and moisture, but also an abundance of food, especially oribatid mites, as well as other mites, springtails, and other tiny arthropods. A recent paper by Bruckner *et al*. (1918), based on research in a German forest, reported that oribatids were more abundant in moss than in either leaf litter or dead wood. Pore size (spaces within the moss clump) can be an important factor in mobility as well as moisture retention.

Figure 58. ***Desmognathus wrighti*** that lives within the mats of ***Thuidium delicatulum*** and ***Atrichum*** sp. seen here. Photo courtesy of Richard Bruce.

Desmognathus quadramaculatus (Black-bellied Salamander)

From Monroe County, West Virginia eastward to Henry County, Virginia, and southward through eastern Tennessee, western North and South Carolina to northeastern Georgia, in the Appalachian Mountains, USA. Peatlands are good habitats for salamanders, and ***Desmognathus*** is certainly represented there. In the ***Sphagnum*** habitat of the Tulula Wetland, North Carolina, USA, one can find ***Desmognathus quadramaculatus*** (**Black-bellied Salamander**; Figure 59), typically in streams (Amphibians: Tulula Wetlands 2009). In North Carolina, it is known from among mosses in streams (LeGrand *et al*. 2001).

This species has a somewhat longer development time than some of the other ***Desmognathus*** species, requiring six years in males and seven in females to reach first reproduction in the southern Blue Ridge Mountains (Bruce 1988).

Beachy (1997) reported that ***D. quadramaculatus*** co-occurred with the salamander ***Eurycea wilderae***, another bryophyte dweller. Unfortunately for ***E. wilderae***, it provides dinner for ***D. quadramaculatus***. Larval growth rates of ***E. wilderae*** differed with different predator densities, but survivorship did not differ, suggesting that provided no advantage in the low productivity of Appalachian streams.

Figure 59. ***Desmognathus quadramaculatus*** (**Black-bellied Salamander**). Photo by Bill Peterman.

Desmognathus ocoee (Ocoee Salamander)

The **Ocoee Salamander** (Figure 60) occurs in two **allopatric** (non-overlapping) units, one in the Appalachian Plateau of northeastern Alabama and adjacent Tennessee, and the other in the southwestern Blue Ridge Physiographic Province of western North Carolina, eastern Tennessee, extreme western South Carolina, and northern Georgia, south of the Pigeon River (Balsam, Blue Ridge, Cowee, Great Smoky, Nantahala, Snowbird, Tusquitee, and Unicoi Mountains), USA (Frost 2011).

Along with ***D. quadramaculatus***, one can find ***D. ocoee*** in the ***Sphagnum*** habitat of the Tulula Wetland, North Carolina, USA (Amphibians: Tulula Wetlands 2009), where their typical habitat is streams. Petranka *et al*. (1993) estimated that timber-harvesting rates of the 1980's and early 1990's caused an annual loss of at least 14 million salamanders of all species in western North Carolina, increasing the importance of peatland refugia.

Typical predators on ***D. ocoee*** include beetles, but Hess and Harris (2000) showed that pond beetles did not eat their eggs. However, beetles from a stream punctured and consumed a large number of ***D. ocoee*** eggs.

Figure 60. ***Desmognathus ocoee*** (**Ocoee Salamander**). Photo by John D. Willson, with permission.

In Macon County, North Carolina, eggs were mostly in nests embedded in mosses growing on rocks on the stream

bank or in the stream (Hess & Harris 2000). Bruce (1996) likewise found that most of the eggs of this species were located under moss on logs, soil, or rocks at the edges of streams, where females care for the eggs.

Phaeognathus hubrichti (Red Hills Salamander)

The **Red Hills Salamanders** (Figure 61) occur in the wooded Alabama Coastal Plain, southern edge of the Red Hills region, USA (Frost 2011). They generally stay in burrows where the humidity is high (Dodd 2011), but when they leave the burrows to forage they can encounter mosses in their habitat and may use them as foraging sites. Their diet of mostly land snails, ants, beetles, and spiders are all likely moss dwellers and perhaps account for the mosses found in some fecal pellets (Gunzburger 1999).

Figure 61. ***Phaeognathus hubrichti***. Photo by John P. Clare, through Creative Commons.

Ensatina eschscholtzii (Monterey Ensatina)

When I was teaching species concepts, this was always one of my favorite examples. Armed with a film loop that showed the morphs and their habitats, I could introduce the difficulty in defining species in any practical way. At that time, several species were recognized, as suggested by breeding incompatibility between some populations, but now they are listed by Frost (2011) as a single species, ***Ensatina eschscholtzii*** (Figure 62), and, like Christopher (2005), Frost treats them as seven distinct subspecies.

The distribution of this superspecies is in Southwestern British Columbia and Vancouver Island, Canada, south through mesic Washington, Oregon, and California, USA, to northern Baja California, Mexico, in the Sierra San Pedro Martír and Sierra Juárez. Its distribution around the mountain range in western USA led to its designation as a **Rassenkreis**, a circle of races (Figure 70).

Hence, current thinking is that there is only one species within the genus. The subspecies are distributed up the Pacific coast of the USA, across the northern Central Valley, and south through the Sierras. The coastal and Sierran subspecies meet in the mountains of southern California and they behave as separate species. Nevertheless, although some of these subspecies look quite different in the pictures that follow, adjacent salamanders recognize each other and can hybridize. For example, ***Ensatina eschscholtzii eschscholtzii*** hybridizes with ***E. e. xanthoptica*** and ***E. e. klauberi***.

Figure 71 demonstrates the habitat of ***Ensatina eschscholtzii oregonensis***. The recognized variants of ***Ensatina eschscholtzii***, not including hybrids, are:

Ensatina eschscholtzii eschscholtzii (Figure 62)
Ensatina eschscholtzii klauberi (Figure 64)
Ensatina eschscholtzii xanthoptica (Figure 63)
Ensatina eschscholtzii picta (Figure 65)
Ensatina eschscholtzii oregonensis (Figure 66-Figure 67)
Ensatina eschscholtzii platensis (Figure 68)
Ensatina eschscholtzii croceater (Figure 69)

Figure 62. ***Ensatina eschscholtzii eschscholtzii***. Photo by William Flaxington, with permission.

Figure 63. ***Ensatina eschscholtzii xanthoptica*** on moss. Photo by William Leonard, with permission.

Figure 64. ***Ensatina eschscholtzii klauberi***. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 65. ***Ensatina eschscholtzii picta***. Photo by William Flaxington, with permission.

Figure 66. ***Ensatina eschscholtzii oregonensis***. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 67. ***Ensatina eschscholtzii oregonensis*** amid mosses. Photo by Henk Wallays, through Creative Commons.

Figure 68. ***Ensatina eschscholtzii platensis***. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 69. ***Ensatina eschscholtzii croceator***. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

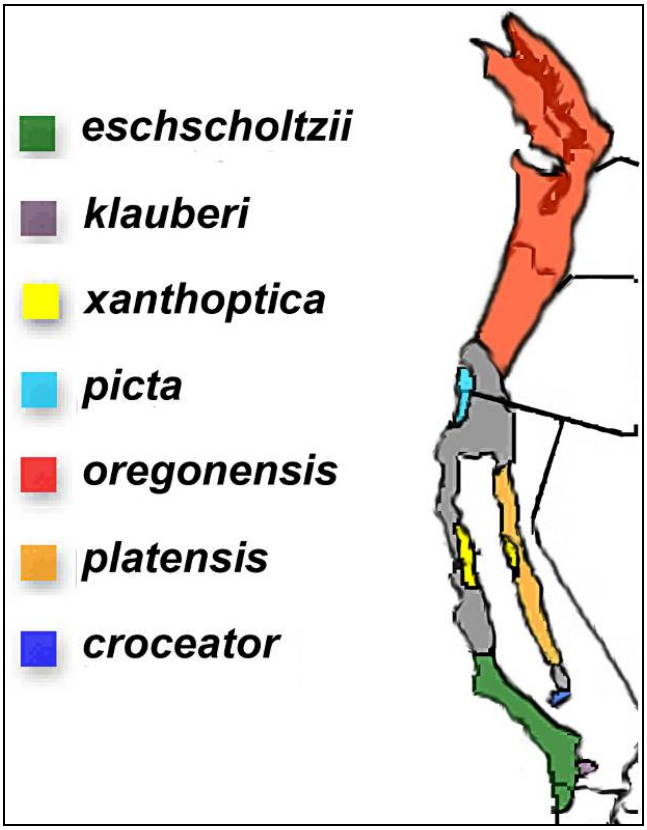

Figure 70. *Rassenkreis* of subspecies of ***Ensatina eschscholtzii***. Redrawn from Gary Nafis, © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 71. ***Ensatina eschscholtzii oregonensis*** habitat. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Gnaedinger and Reed (1948) pointed out that the importance of the moss habitat for ***Ensatina eschscholtzii*** had apparently been overlooked. At that time, several species were recognized, and when we combine them we need to recognize that the former species did not all have the same habitat, hence requiring caution in applying species habitat descriptions. Gnaedinger and Reed reported the salamander to occur between the moss and the ground, easily visible when the moss was removed. Such moss cover was found in 31.5% of their observations, exceeded only by the grouping of leaves, grass, and twigs. Relative numbers of those individuals found under mosses were 52.4% young, 16.7% juvenile, and 13.6% adults. This suggests that eggs may be laid on or in moss patches. The mosses may have been important in temperature regulation. The young were active under mosses at 1.2°C when the air temperature was -3.3°C, suggesting an insulating effect. The ground where salamanders were located was not frozen, apparently due to the protective cover of mosses. Unprotected soil, leaf litter, and surface of the mosses were frozen to a depth of about 1 cm and almost to the depth where the salamanders were active.

Hydromantes brunus (Limestone Salamander)

This species is known only from the area along the Merced River and North Fork Merced River, Mariposa County, California, USA, at 300-760 m asl (Frost 2011). The type was found under a moss-covered rock in Mariposa County, California, USA (Gorman 1954).

Hydromantes shastae (Shasta Salamander)

This species (Figure 72) is an endemic to the limestone substrates south of Mount Shasta near the Shasta Reservoir, Shasta County, California, USA at 300-910 m asl (Frost 2011). The type specimen was found under a small mossy log at a cave entrance (Gorman & Camp 1953). Eggs are terrestrial and have only been found in caves.

Road construction, quarrying, and changes in water levels cause this species to be vulnerable (IUCN 2010).

Figure 72. ***Hydromantes shastae*** on mosses. Photo by Henk Wallays, through Creative Commons.

Hydromantes ambrosii

Andreas Nöllert kindly sent me images of two subspecies of this salamander from mossy habitats. He found both in northwestern Italy. ***Hydromantes ambrosii ambrosii*** was living on a mossy cliff and ***H. a. blanchii*** was living in a mossy forest.

Figure 73. ***Hydromantes ambrosii ambrosii***, a cliff dweller. Photo by Andreas Nöllert, with permission.

Figure 74. ***Hydromantes ambrosii ambrosii*** habitat in NW Italy. Photo by Andreas Nöllert, with permission.

Figure 75. ***Hydromantes ambrosii blanchii***. Photo by Andreas Nöllert, with permission.

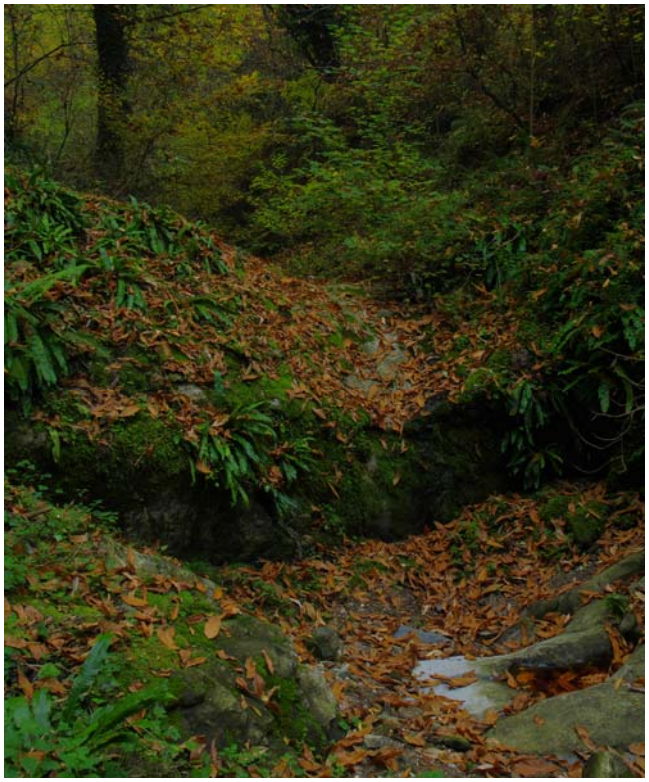

Figure 76. ***Hydromantes ambrosii bianchii*** habitat in Italy. Photo by Andreas Nöllert, with permission.

Summary

The Hynobiidae is a small family in Asia and Europe, with ***Hynobius tokyoensis*** migrating to the forest floor where mosses are among its hiding places. ***Salamandrella keyserlingii*** is also Asian and European and is one of the most cold-tolerant species of salamanders, spending winter in moss **hibernacula** and even surviving freezing in the permafrost for many years.

The Ambystomatidae extend from southern Canada to Mexico, living under mosses, among other forest floor habitats. Some species (*e.g.* ***Ambystoma maculatum***) are common in peatlands. This species provides oxygen to its jelly-coated eggs by partnering them with the green alga ***Oophila amblystomatis***.

In the Western Hemisphere, the Plethodontidae, including the large genus ***Plethodon***, is a large family of temperate zone salamanders. Many of these are bryophyte dwellers. The **Cheat Mountain Salamander** (***Plethodon nettingi***) is usually associated with the leafy liverwort ***Bazzania trilobata***, a rare example of a salamander associated with a specific bryophyte other than the genus ***Sphagnum***. ***Plethodon cinereus*** often lives in ***Sphagnum*** peat, where it attempts to rob the pitcher plant leaves of the invertebrates living there. But it can also live under forest floor mosses such as ***Leucobryum glaucum***. ***Desmognathus*** is found with mosses both in peatlands and in old-growth forests.

Peatlands are especially important for some species, such as members of ***Plethodon*** and ***Ambystoma***. Nevertheless, ***Sphagnum*** and associated ponds are typically too acid for most salamanders. ***Hemidactylium scutatum*** (**Four-toed Salamander**) apparently uses ***Sphagnum***. The **Four-toed Salamander** is the best known of the bryophyte dwellers, depositing its eggs under a variety of bryophytes, especially ***Thuidium*** and ***Sphagnum***. Mosses appear to be critical in its habitat, and loss of wetlands is a threat to its existence.

Stereochilus marginatus lays its eggs underwater on the moss ***Fontinalis***. ***Desmognathus fuscus*** lays eggs in the moist soil of stream banks, under mosses; a number of ***Desmognathus*** species use mosses for egg-laying sites.

Ensatina eschscholtzii subspecies form a **Rassenkreis** in California, USA, and mosses are often an important niche, where they can be found on the soil surface just under the moss.

Unknown species like ***Hydromantes brunus*** are likely to be living among mosses, invisible to the collector.

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CHAPTER 14-8
SALAMANDER MOSSY HABITATS

Janice M. Glime and William J. Boelema

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CHAPTER 14-8
SALAMANDER MOSSY HABITATS

Figure 1. ***Bolitoglossa rostrata*** on the moss ***Thuidium*** sp. Photo by Sean Michael Rovito, with permission.

There are a number of habitats where bryophytes dominate either the ground cover (Figure 1) or the arboreal portion. In these, traversing bryophytes by salamanders is unavoidable. Since the Plethodontidae bryophyte inhabitants are too numerous for one subchapter of downloadable size, I have chosen to subdivide them into the mosses present vs mosses dominant and discuss them in these habitats. Please keep in mind that reference to "mosses" might actually include liverworts as well because the collectors were not trained to recognize the difference.

Tropical Mossy Habitats - Plethodontidae

The Neotropics provide a wide array of niches for bryophytes in trees, and elfin cloud forests literally look as if they have been draped by a bryophytic mat. The epiphytic bryophytes provide moisture-holding capacity that enables bromeliads and other epiphytes to be successful there. This arboreal system is home to a myriad of salamander species that use bryophytes for homes, cover, nests, moisture, and foraging sites. Small size and limited mobility have contributed to the evolution of many related species on mountains separated by valleys that prohibit their interbreeding, resulting in numerous microspecies and more conspicuous species.

Rich salamander fauna is associated with bryophyte mats in cloud forests of Talamancan central America, where they can sometimes be very abundant in the cloud forests. In Costa Rica salamanders use moss mats more commonly than do salamanders farther north and west. This is especially true for ***Nototriton*** and ***Oedipina***. Fossorial ***Lineatriton*** (now ***Pseudoeurycea***) and ***Oedipina*** occur only below the lower elevational limit of cloud forests in Veracruz, Mexico, and in Nuclear Central America. On the other hand, in cloud forests of Costa Rica and Panama, elongate members of ***Oedipina*** are common in moss mats covering soil banks, downed logs, and stumps at elevations up to at least 2000 m. Likewise, in Costa Rica ***Nototriton*** species, as well as at least two species of ***Bolitoglossa*** (Figure 1), occur among cloud forest mosses. The mid-elevational cloud forest locations tend to have the most salamanders, and at that elevation, mosses are the more commonly used habitat.

Terrestrial and Arboreal Adaptations

Wake (1987) considers mid-elevation cloud forests to have been critical in the evolution of Neotropical salamanders. Salamanders in the arboreal habitat of the Neotropics represent the epitome of adaptations for salamanders living on land. Wake (1987) considers the epiphytic habitat for tropical salamanders to have diverged into two habitat groups: mosses and bromeliads (Figure 3). The epiphytic bryophyte habitat is actually a composite including roots, club mosses, stems, ferns, and small flowering plants. Altig and McDiarmid (2007) summarized the terrestrial adaptations, which are largely coincidental to adaptations for living among terrestrial bryophytes, especially in the arboreal habitat. Epiphytic bryophyte-dwelling salamanders are not as easy to characterize as the bromeliad dwellers (Wake 1987). They are typically slender with short legs, presumably making movement within the moss mat easier. But living on land, especially in trees, made life cycle adaptations essential.

Nests need to be placed where they have both cover/camouflage and moisture maintenance. Bryophytes can provide both, so their use in arboreal habitats, especially for live-bearers, is a viable option for those not using bromeliad basins.

Eggs (Figure 2) cannot move about to adjust to the changes in their environment, hence they exhibit some of the most important of the terrestrial adaptations. They require tradeoffs among need for gas exchange, need for mechanical support, same-species sperm attraction, other species sperm avoidance, heat conservation or cooling, predator defense, moisture retention, UV light protection, prevention of polyspermy (multiple fertilizations by sperm), and protection from bacteria and the water molds ***Saprolegnia*** and ***Achlys*** (Altig & McDiarmid 2007). Together, these needs influence the number of layers, thickness, and physical characteristics of the layers of the eggs. Salthe (1963) suggests that having 8 jelly layers is the primitive condition and that changes in number of layers can occur through the loss of the most external layers (*e.g.* **Ambystomatidae**), loss of more internal layers (especially **Plethodontidae**), or having eggs with three layers for which we do not understand the homologies. Salthe further suggested that loss of layers of terrestrial eggs in **Plethodontidae** results from changes of internal layers whereas the tough outer layer remains for protection.

Figure 2. ***Bolitoglossa hartwegi***, a moss dweller, tending its eggs. Photo by Bill Peterman, with permission.

Figure 3. Bromeliads and mosses on the floor of the cloud forest in Puerto Rico, illustrating the types of habitats available to small salamanders such as ***Nototriton*** species. Photo by Janice Glime.

Important adaptive features of the jelly layer include elasticity, stickiness, toughness, turgidity, and wateriness. Those eggs laid in the water are typically spherical in the water but sag on surfaces in the air. Terrestrial eggs typically have jelly that is turgid and retains its spherical shape in air. Terrestrial salamanders and frogs that experience direct development to adults lay eggs that have a tough outer jelly that permits proper development, oxygenation, and protection from trampling by the parents. Pigmentation has received insufficient study. However, there is evidence that those eggs laid in the open have melanic pigments at the animal pole (Altig & McDiarmid 2007). Buried eggs usually are pale or lack pigmentation. Pigments can absorb heat and increase rate of development, protect against heat, and protect against specific wavelengths (Barrio 1965; Jones 1967; Hassinger 1970).

Egg placement (Figure 2) necessarily must protect eggs from desiccation. The semiterrestrial eggs have not yet abandoned their aquatic history. These are usually deposited adjacent to a water source, not submerged, where hatchlings can easily move or drop into the water (Altig & McDiarmid 2007). They frequently are laid among mosses in seeps or beside bog ponds.

Development and hatching of eggs is often modified from that of aquatic species. Females of many terrestrial species care for the eggs, cleaning and turning them – an activity that seems to reduce the bacterial and fungal colonization. Some species are **viviparous** (have live birth). Some have embryos that develop directly into young salamanders with no larval stage. But some still require water for development of their larvae and therefore lay their eggs near water where larvae have easy access.

Hatching is similar among most salamanders, using an enzyme to break through the jelly, but in some terrestrial salamanders there is an egg tooth similar to that in birds.

Bolitoglossa (Tropical Climbing Salamanders, Plethodontidae)

Sean Rovito has told me about finding several species of tropical climbing salamanders (***Bolitoglossa***; Figure 4) in the páramo in the Cordillera de Talamanca, Costa Rica, under thick mats of moss. Wake (1987) reported that members of this genus use mats of vegetation, including mosses and liverworts surrounding tree branches and twigs.

Species in this genus are able to propel themselves forward by an "explosive tail flip" that carries them off the vegetation – a protective device when in danger during its daylight resting hours (Leenders & Watkins-Colwell 2003). Another protective behavior is to raise its tail as an offering to a predator. If the tail is grabbed, the salamander can **disarticulate** and run off, leaving the predator with only the tail (Lee 2000).

Figure 4. **La Loma Salamander**, also known as the Ridge-headed Salamander, ***Bolitoglossa colonnea*** occurs in Costa Rica and Panama. Photo by Twan Leenders, with permission.

Arboreal adaptations include elongated fingers, contrasting with webbing used by aquatic species to move through water, and increased efficiency of the suction cups (Wikipedia 2011a). The arboreal body size is smaller, making it easier to cling (and easier to move through moss mats).

Bolitoglossa diaphora (Plethodontidae)

Although ***Bolitoglossa diaphora*** (Figure 5) was described by McCranie and Wilson in 1995, it still has no English name (Frost 2011). It is known from 1470-2200 m asl in cloud forests of the Sierra de Omoa on the Atlantic side of the mountains of northwestern Honduras. It was described as a species based on a specimen at Cerro Jilinco at 2200 m asl from under a moss mat in a small hole. Its decreasing population is listed as critically endangered (IUCN 2010b).

Figure 5. ***Bolitoglossa diaphora*** on a fern. Photo by Josiah Townsend, with permission.

Bolitoglossa diminuta (Quebrada Valverde Salamander, Plethodontidae)

This is a tiny (35 mm) bryophyte-mat-inhabiting Costa Rican salamander, known only from the type locality of lower montane rain forest, near Quebrada Valverde, Cartago Province, on the Atlantic slope of Costa Rica at 1300-1650 m asl. For a long time the only known adult was collected with its egg mass in a mat of liverworts (Robinson 1976; Wake 1987). Wake (pers. comm. 31 March 2011) says that this species specializes in living in balls of mosses attached to vines suspended far from the ground or the trees to which the vines are attached. Eggs are typically laid in these moss balls. This salamander is considered vulnerable because it is known from only one location (IUCN 2010b).

Bolitoglossa hartwegi (Hartweg's Mushroomtongue Salamander, Plethodontidae)

Bolitoglossa hartwegi (Figure 2, Figure 6-Figure 7) lives in Guatemala and Mexico in subtropical and tropical moist montane forests (IUCN 2010b; Frost 2011), 1200-2800 m asl (Encyclopedia of Life 2011). It is also able to live in heavily degraded forests, but loss of habitat still renders it threatened. Its presence in moist montane forests suggests that it might be an occasional moss dweller, or use them at moist sites.

Figure 6. ***Bolitoglossa*** *cf.* ***hartwegi*** on a bed of ***Thuidium***. Photos by Sean Michael Rovito, with permission.

Figure 7. ***Bolitoglossa*** *cf.* ***hartwegi*** blending with mosses and lichens on a rock. Photos by Sean Michael Rovito, with permission.

Bolitoglossa helmrichi (Plethodontidae)

The tiny ***Bolitoglossa helmrichi*** (Figure 8-Figure 9) is near threatened in its arboreal home in the cloud forests of Guatemala (IUCN 2010b). Its scarcity accounts for the little information we have on it, but its small size and habitat suggest it spends at least part of its time among mosses.

Figure 8. ***Bolitoglossa helmrichi*** resting on a leaf. Photo by Todd Pierson, with permission.

Figure 9. ***Bolitoglossa helmrichi***. The lower photo shows how small these salamanders are. Photo by Todd Pierson, with permission.

Bolitoglossa jugivagans (Plethodontidae)

The species ***Bolitoglossa jugivagans*** (Figure 10-Figure 11) causes one to ask about potential adaptations among these mossy habitat salamanders. This is a newly described species from Panama, where it lives in a mossy habitat (Hertz *et al*. 2013). Its life habits are poorly known, but it has one habit that offers possibilities as an adaptation to its mossy neighborhood – it changes from a highly patterned coloration during the day (Figure 10) to a more uniform coloration at night (Figure 11). Andreas Hertz (pers. comm. 14 January 2016) tells me that the trigger(s) for its change in coloration are currently unknown, but other salamanders are known to respond to changes in light, background coloration, temperature, and stress. Such ability could provide adaptations for salamanders living within bryophyte mats or running about and resting on top of them. He pointed out that while we know about mechanisms for these changes in only a few species, we know that these mechanisms do differ among species.

Figure 10. ***Bolitoglossa jugivagans*** exhibiting its daytime coloration while sitting on a moss. Photo by Andreas Hertz, with permission.

Figure 11. ***Bolitoglossa jugivagans*** exhibiting its nighttime coloration while sitting on a solid-colored leaf. Photo by Andreas Hertz, with permission.

Bolitoglossa lincolni (Lincoln's Mushroomtongue Salamander, Plethodontidae)

Bolitoglossa lincolni (Figure 12) is known from the central plateau of the Chiapas, Mexico, and mountainous areas of western Guatemala at 1200-3000 m asl (IUCN 2010b). It lives in low vegetation (probably including mosses), under bark, and in bromeliads, with a broad enough habitat that its populations are not declining. However, due to destruction of habitat, it is listed as a species near threatened on the IUCN list.

Figure 12. ***Bolitoglossa lincolni*** (**Lincoln's Mushroomtongue Salamander**). Photo by Bill Peterman, with permission.

Bolitoglossa longissima (Plethodontidae)

Bolitoglossa longissima is restricted to intermediate elevations (1840-2240 m asl) on the Atlantic side of Pico La Picucha in the Sierra de Agalta, Honduras (Frost 2011) where it is critically endangered (IUCN 2010b). This species is known from under leaves and moss on the ground and from moss-covered tree trunks at ~2.0-3.5 m above the ground (McCranie & Cruz 1996).

Bolitoglossa marmorea (Crater Salamander, Plethodontidae)

This species (Figure 13) is distributed in Costa Rica and Panama, where it lives in subtropical or tropical moist

montane regions and areas where the forest has been highly degraded (Wikipedia 2011b) at 1,920-3,444 m asl (IUCN 2010b). It hides under rocks in the daytime, but climbs over moss mats on tree trunks and branches at night (Wake *et al.* 1973). It is moderately sized – large for a moss dweller (adults range 128-134 mm in total length), and has long limbs (AmphibiaWeb 2009c). Habitat loss and degradation due to agricultural expansion threaten its existence, causing it to be listed as endangered (IUCN 2010b).

Figure 13. ***Bolitoglossa marmorea***, a species that traverses mosses on tree trunks at night in the Neotropics. Photo from Division of Herpetology, University of Kansas, permission through Rafe Brown.

Bolitoglossa mexicana (Mexican Mushroomtongue Salamander, Plethodontidae)

Bolitoglossa mexicana (Figure 14) occurs from the Chiapas, Mexico, to the Honduras (IUCN 2010b). It primarily lives in trees where it hangs out in bromeliads and other epiphytes, presumably including bryophytes. Their broad distribution and abundance cause them to be classified as a species of least concern.

Figure 14. ***Bolitolgossa mexicana*** on mossy bark at Selva Lacandona, Chiapas, Mexico. Photo by Omar Hernandez-Ordoñez, with permission.

Bolitoglossa obscura (Tapantí Giant Salamander, Plethodontidae)

Hanken *et al.* (2005) examined the members of ***Bolitoglossa*** in Costa Rica and Panama in an effort to understand the taxonomy there. They found that ***Bolitoglossa obscura***, known only from the type locality in the Parque Nacional Tapanti, Provincia Cartago, Costa Rica., is **sympatric** (having overlapped distributions) with two other tiny (35 mm) moss-mat-inhabiting plethodontid species, ***B. diminuta*** **(Quebrada Valverde Salamander)** and ***Nototriton picadoi*** (discussed below). The existence of ***Bolitoglossa obscura*** is vulnerable, but its population trend is unknown (IUCN 2010b).

Bolitoglossa robusta (Robust Mushroomtongue Salamander, Plethodontidae)

The **Robust Mushroomtongue Salamander** (Figure 15), also known as the Ringtail Salamander, occupies humid premontane and lower montane areas in the mountains of north-central and eastern Costa Rica at 500-2048 m asl and in Bocas del Toro Province, Panama at 50-2100 m asl (Frost 2011). It is often found under fallen logs, in thick leaf litter, or under mosses (Hanken *et al.* 2005). Although its populations are decreasing, it is still listed as a species of least concern (IUCN 2010b).

Figure 15. ***Bolitoglossa robusta***. Photos by Eduardo Bozo, with permission.

Bolitoglossa rostrata (Longnose Mushroomtongue Salamander, Plethodontidae)

The species ***Bolitoglossa rostrata*** (Figure 16) of Guatemala and Mexico occurs in high elevation forests and is often arboreal (Raffaëlli 2011a). One could expect to find it among epiphytic bryophytes since the genus is well adapted to the small spaces provided by them. The species is vulnerable and decreasing in population size (IUCN 2010b).

Figure 16. ***Bolitoglossa rostrata*** on ***Thuidium***. Photo by Sean Michael Rovito, with permission.

Bolitoglossa rufescens (Northern Banana Salamander, Plethodontidae)

Bolitoglossa rufescens (Figure 17) is distributed from Mexico to Honduras (Frost 2011) where it occupies rainforests in lowlands (sea level to 1500 m asl) (McCoy 1990). It is arboreal and night active (McCoy 1990), living mostly in bromeliads (Frost 2011). The bryophytes in its habitat most likely contribute to keeping it hydrated when it moves about in search of food. Ants are the most important food source (Anderson & Mathis 1999), thus we should expect it to venture away from the bromeliads to find them. It is listed as a species of least concern (IUCN 2010b). It defends itself by flicking its tail, a behavior that distracts the predator, usually a snake, from the more vulnerable parts of the body (Brodie *et al*. 1991). If deemed necessary, it will **disarticulate** its tail (Lee 2000). Unlike ***B. palmata*** and ***B. rostrata***, this species is not noxious to snakes. In one case, Buttenhoff (1995) observed an attack by the mantid ***Choeradodis strumaria*** (see Figure 18) on an adult ***B. rufescens***. Although mantids would not seem to have much connection to bryophytes, some are excellent bryophyte mimics and hang out among the arboreal bryophytes.

Figure 17. ***Bolitoglossa rufescens*** on a bed of mosses. Photo by Sean Michael Rovito, with permission.

Figure 18. ***Choeradodis strumaria***, a mantid predator on ***Bolitoglossa rufescens***. Photo by C. Horwitz through Creative Commons.

Bolitoglossa sombra (Shadowy Web-footed Salamander, Plethodontidae)

Bolitoglossa sombra (Figure 19) occurs on Pacific slopes of the Cordillera de Talamanca of Costa Rica and extreme western Panama at 1500-2300 m asl (Frost 2011) and is found on moss-covered tree trunks, under mosses on tree trunks, and on stumps at 0.6-2.0 m above the ground, but was also found on a concrete structure providing access to an underground aqueduct and between mossy buttresses of a tree on top of leaf litter (Hanken *et al*. 2005). Like most of the tropical amphibians, it is red-listed, but is listed only as vulnerable (IUCN 2010b).

Figure 19. ***Bolitoglossa sombra***, a bryophyte dweller in the tropics. Photo © 2013 Don Filipiak, through online permission.

Bolitoglossa subpalmato (La Palma Salamander, Plethodontidae)

The **La Palma Salamander** (Figure 20) occurs in humid lower montane and montane zones, marginally into the premontane belt on both slopes of the Cordillera de Guanacaste, Cordillera de Tilarán, Cordillera Central to central and northern Costa Rica at 1245-2900 m asl (Frost 2011). Its habitat is subtropical or tropical moist montane regions, pastureland, plantations, rural gardens, and heavily degraded former forests (Wikipedia 2011c), where its habitat is threatened by habitat loss and fragmentation due to the encroachment of agriculture, causing it to be listed as endangered by the IUCN (IUCN 2010b).

Figure 20. ***Bolitoglossa subpalmata*** on a leaf. Photo by Ira Richling, <www.helicina.de>, with permission.

This species enjoys one of the most extensive studies done on tropical salamanders. Vial (1968) found that its niche changes with elevation in Costa Rica. In the middle portion of its elevational range (2400-2700 m asl), its most frequent microhabitat is in the dense carpet of ***Sphagnum*** (Figure 21) and club mosses, where it is able to maintain its hydration. These salamanders are not active when the humidity is less than 51%. The mossy habitats also afford a relatively low, stable temperature (9.8-16°C).

Figure 21. ***Sphagnum balticum*** from Costa Rica, home for a variety of salamanders. Photo from Biopix, through Creative Commons.

The species is nocturnal, spending the day under rocks, mosses, and plant debris where these are either deeply imbedded in the soil or have well-developed borders of lichens and mosses (Vial 1968). At night they may climb branches of moss-covered trees to 2 m above ground. They nest under well-imbedded rocks or in decaying logs. Adults attend the eggs (Houck 1977). When the nest is disturbed, the adults abandon the eggs and development ceases. They require a site that has been undisturbed for several years, permitting it to develop a good cover of lichens and mosses. Mosses clearly play a role in maintaining the species in at least the middle elevations of its range.

This species seems to be ideal prey for small snakes, but it has an effective defense mechanism (Wikipedia: *Bolitoglossa* 2011). It, and ***B. subpalmata***, are poisonous. The skin secretes a toxin that is effective on particular snake species. The initial contact causes the snake to become immobile and unable to respond to its prey. The salamander remains still, taking advantage of the behavior of the snake to contact the salamander when the snake flicks its tongue. This contact paralyzes the snake and permits the salamander to run.

Bolitoglossa suchitanensis (Plethodontidae)

The type specimen of ***Bolitoglossa suchitanensis*** (Figure 22), buried in moss on a log, was collected in Guatemala in 1999 (Campbell *et al*. 2010). However, it was not named and described until 2010. Subsequent collections came from tree trunks and under logs, but not in mosses. Its known habitat is a humid deciduous forest with abundant mosses and epiphytes. It lacks an IUCN status evaluation (IUCN 2010b).

Figure 22. ***Bolitoglossa suchitanensis***, an inhabitant of mossy logs and forests. Photo by Sean Michael Rovito, through Creative Commons.

Bolitoglossa xibalba (Plethodontidae)

Campbell *et al*. (2010) reported that most of the individuals of ***Bolitoglossa xibalba*** (Figure 23) were taken from under loose bark or mosses at bases of rotting tree trunks. These were found at 1980-2760 m asl in wet montane forests of Guatemala. Little seems to be known about the species, and it lacks an IUCN status evaluation (IUCN 2010b).

Figure 23. ***Bolitoglossa xibalba***. Note the webbing of the feet. Photo © Jonathan Campbell, with permission.

Chiropterotriton (Splayfoot Salamanders, Plethodontidae)

This genus of twelve species is known from West-central Tamaulipas in the north to the mountains of northern Oaxaca in the south, Mexico (Frost 2011). Tim Burkhardt (pers. comm. 17 February 2011) found an unidentified member of ***Chiropterotriton*** (Figure 24) at 2440 m asl on the NW slope of Cerro Cofre de Perote, Veracruz, Mexico. It was beneath a mat of mosses on the rocky wall of a ravine.

Figure 24. ***Chiropterotriton*** sp. from the wall of a ravine where it was beneath sheets of moss on Cerro Cofre de Perote, Veracruz, Mexico. Photo by Timothy Burkhardt <www.mexico-herps.com>, with permission.

Chiropterotriton chiropterus (Common Splayfoot Salamander, Plethodontidae)

Chiropterotriton chiropterus (Figure 25) is known only from central Veracruz, near Huatusco, Mexico, at 1000-1200 m asl (IUCN 2010b). Its niche includes mosses and bromeliads and it has direct development. IUCN lists it as critically endangered and possibly extinct, although it was once abundant. It seems unable to live in degraded habitats.

Figure 25. ***Chiropterotriton chiropterus***, a moss dweller in Mexico. Photo by César L. Barrio Amorós, with online permission for educational use.

Cryptotriton alvarezdeltoroi (Alvarez del Toro's Salamander, Plethodontidae)

Timothy Burkhardt (pers. comm. 17 February 2011) suggested to me that the salamanders in ***Nototriton*** and ***Cryptotriton*** are the ones most closely associated with mosses. ***Cryptotriton*** is a recent segregate of the genus ***Nototriton***.

In Mexico, ***Cryptotriton*** (formerly *Nototriton*) ***alvarezdeltoroi*** (**Alvarez del Toro's Salamander**; Figure 26), a salamander of ~2.6 cm length (Raffaëlli 2011b), was found at 1200-1550 m asl in the cloud forest of the Chiapas, climbing up a moss bank at night (Papenfuss & Wake 1987). It is known only from this type locality. The IUCN Red List of this species has been changed from endangered (2004) to vulnerable (2008) (IUCN 2010b). This change is because it is now known in less than 20,000 km^2, all individuals are known in fewer than five locations, and there is continuing decline in the extent and quality of its habitat in Chiapas, Mexico. Its known habitat is restricted to the cloud forest, where it seems to require microhabitats with very high humidity. Like many terrestrial salamanders, it has direct development into froglets that hatch from the eggs.

Figure 26. ***Cryptotriton alvarezdeltoroi***, a species that occurs among mosses in the cloud forest of Mexico. Photo by Sean Michael Rovito, through Creative Commons.

Cryptotriton monzoni (Monzon's Hidden Salamander, Plethodontidae)

This little fellow, ***Cryptotriton monzoni*** (Figure 27), measures only 2.2 cm (Whittaker 2010) and is listed as critically endangered by the IUCN Red List (IUCN 2010b). It is known only from its type locality at 1570 m asl in Zacapa, Guatemala, thus occurring in less than 100 km^2 and fewer than five localities, while suffering from a continuing decline in its habitat, especially due to deforestation. Its known habitat is in the cloud forest, and it may occur in additional, unexplored sites of cloud forest. The type specimen was found in a bromeliad and its use of mosses is unknown. Most likely they contribute to keeping it moist while it is foraging.

Figure 27. ***Cryptotriton monzoni***, known only from lower montane wet forest at its type locality in lower montane wet forest, near La Unión, Zacapa, Guatemala, at 1570 m asl. Photo by Sean Michael Rovito, with permission.

Dendrotriton cuchumatanus (Forest Bromeliad Salamander, Plethodontidae)

In Guatemala, ***Dendrotriton cuchumatanus*** (also known as Cuchumatanas Bromeliad Salamander; Figure 28-Figure 29) lives under moss mats on oak trees (Sean Michael Rovito pers. comm. 7 February 2009). It is endemic to its type locality in Guatemala (Acevedo & Wake 2004) at Sierra de los Cuchumatanes southwest of San Juan Ixcoy (Frost 2011). Despite its common name, it is not known to inhabit bromeliads, but does live both in moss banks and under mosses on fallen trees (ZipcodeZoo.Com 2008a).

Figure 28. Cuchumatanas Bromeliad Salamander, ***Dendrotriton cuchumatanus*** on a leaf covered with epiphyllous algae and bryophytes. Photo © Jonathan Campbell, with permission.

Figure 29. ***Dendrotriton cuchumatanus*** on a mossy log. Photo by Sean Michael Rovito, with permission.

Nototriton (Moss Salamanders)

In Costa Rica, and other neotropical countries, a genus of tiny **Moss Salamanders** (***Nototriton***; Figure 30) lives among mosses on trees as well as among leaf litter on the ground (Good & Wake 1993; García-París *et al.* 2000a). Seven species of **Moss Salamanders** have been discovered among the mossy habitats in diversity hotspots in Costa Rica (ZipcodeZoo.Com 2008d). In the cloud forest they can be abundant in moss clumps (Taylor 1954), where they are difficult to find (Good & Wake). In other Neotropical countries, most of the species live in bromeliads (Good & Wake 1993). Some species of ***Nototriton*** are so small that young ones can fit completely on a man's thumbnail (National Geographic News 2009)! The long, thin bodies maximize surface area for oxygen exchange in this lungless salamander (Edge 2009).

Figure 30. **Santa Barbara Moss Salamander**, ***Nototriton limnospectator***, a moss salamander of lower montane wet forests of the Parque Nacional Santa Barbara. It occurs at intermediate elevations (1640-1980 m asl) of the Montaña de Santa Bárbara on the Atlantic side of western Honduras where it is threatened by habitat loss. That, plus its limited distribution, cause it to be listed as endangered (IUCN 2010b). Its use of mosses is unknown. Photo by Sean Michael Rovito, with permission.

This genus, as currently configured, is the result of an evolutionary radiation of bolitoglossine salamanders (**Plethodontidae**) that has tremendous diversification of both form and ecology (García-París & Wake 2000). They range from the large, robust terrestrial taxa such as ***Pseudoeurycea bellii*** to the much smaller moss dwellers of ***Nototriton*** such as ***N. abscondens*** (Figure 31).

The genus ***Nototriton*** is small and slender, with a long tail and moderately long to short legs, with moss dwellers having short legs (García-París & Wake 2000). The feet are small, especially in the arboreal moss dwellers. This is an interesting contrast to the tree-dwelling frogs, where the foot pads are larger with increasing elevation above the ground, providing better suction for holding on. One can assume that such suction ability is not needed for wormlike salamanders that live within the moss mat.

This genus differs from many of the terrestrial plethodontid salamanders in its care of the eggs. Instead of guarding them, the females deposit the eggs in clumps of bryophytes in trees and abandon them (McCranie & Wilson 1992; Good & Wake 1993). This suggests that the bryophytes provide sufficient moisture. But does this suggest that the bryophytes afford such good protection that parental care is unnecessary? Might the bryophytes provide antibiotics that keep the eggs safe from disease?

The larvae of ***Nototriton*** develop completely within the eggs, and the eggs hatch into small salamanders, not tadpoles. Papenfuss and Wake (1987) describe members of this diverse genus as "rare, secretive, and poorly known." ***Nototriton*** is characterized by a delicate pattern of colors that are quite beautiful under the dissecting microscope, but to the unaided eye, these colors usually blend to create a dull brown (Figure 37). Wake suggests that miniaturization in this genus permits its members to occupy habitats not available to other species. For some, the habitat appears to be the spaces among bryophytes (see Figure 3).

Nototriton abscondens (Plethodontidae)

Like many of the moss-dwelling salamanders that have been seen only a few times, ***Nototriton abscondens*** (Figure 31) has no English name. It is known from sub-humid and humid premontane and humid montane forests of the Cordillera de Tilarán and Cordillera Central of Costa Rica, 960-2050 m asl (Good & Wake 1993). This one has been known longer than most, with Taylor (1954) reporting them from moss mats hanging from trees and bushes, occasionally horizontal limbs, and mosses that cover dirt banks, large boulders, or stumps. They also seem to be common in lightly disturbed areas along trails and roads, again in clumps of moss. Good and Wake (1993) found them again in these habitats, but also in mosses on tree trunks and branches in the cloud forest and on mosses on logs. They consider this to be a species that specializes on mosses (**bryobiont**).

Figure 31. ***Nototriton abscondens***. Photo by Eduardo Boza Oviedo, with permission.

Nototriton barbouri (Yoro Salamander, Plethodontidae)

Nototriton barbouri (Figure 32) is an endemic living at moderate and intermediate elevations (860-1990 m asl) on the Atlantic mountainside from northwestern to north-central Honduras (Frost 2011). This species occurs in an area of less than 5000 km^2, has fewer than ten known locations, and suffers from continuous decline of its habitat, making it an endangered species on the IUCN Red List (IUCN 2010b). In this lower montane forest, it lives among moss, low vegetation, on the forest floor, and on tree trunks (ZipcodeZoo.Com 2008b). Its clutch size of 5-19 eggs is a bit larger than that of ***Nototriton picadoi*** (McCranie & Wilson 2002).

Figure 32. ***Nototriton barbouri*** on mosses covering decaying wood. Photo by Josiah Townsend, with permission.

Nototriton gamezi (Monteverde Moss Salamander, Plethodontidae)

This species (Figure 33) lives in the premontane and lower montane rainforests of the Reserva Biologica Monteverde, Cordillera de Tilarán, Costa Rica, at 1550-1650 m asl. The species is listed as vulnerable, but stable (IUCN 2010b).

Figure 33. ***Nototriton gamezi***. Photo by Sean Michael Rovito, with permission.

Two specimens of ***Nototriton gamezi*** (Monteverde Moss Salamander**,** Figure 33-Figure 36) were collected in thick mats of moss in Monteverde Cloud Forest Reserve, Costa Rica, in August, 1987, in forest openings near the divide (García-París & Wake 2000). The type specimen and one other were collected nearby from mosses growing on a tree. García-París and Wake (2000) found specimens by searching through heavy moss mats in openings in the forest. The temperatures within the mats ranged 20.0-21.5°C.

Figure 34. ***Nototriton gamezi*** on a bed of mosses. Photo by Sean Michael Rovito, with permission.

Figure 35. ***Nototriton gamezi***. Photo by Sean Michael Rovito, with permission.

Figure 36. ***Nototriton gamezi***. Photo by Eduardo Boza Oviedo, with permission.

Nototriton guanacaste (Guanacaste Moss Salamander, Plethodontidae)

Nototriton guanacaste (also known as Volcan Cacao moss salamander) is known primarily from collections of moss from tree trunks and branches, up to 4 m from the ground, in the cloud forests and premontane rainforests of Costa Rica (Tosi 1969; Good & Wake 1993). It is known only from humid, lower montane moss-laden, low-stature forests near the summits of Volcán Orosí and Cerro Cacao, in the Cordillera de Guanacaste, Province of Guanacaste, northwestern Costa Rica, at 1420 and 1580 m asl (Frost 2011). It has a narrow temperature activity range of 17.1-18.1°C (Good & Wake 1993), suggesting that the bryophytes may serve to buffer its temperature climate, or at least provide a safe haven during inactivity.

Figure 37. ***Nototriton guanacaste***. Photo by Javier Sunyer, with permission.

Nototriton picadoi (Picado's Moss Salamander, Plethodontidae)

Nototriton picadoi (Picado's Moss Salamander) is restricted to premontane and lower montane wet forest (in the northern end of the Cordillera de Talamanca in cloud forest, Costa Rica, at 1200-2200 m asl (Frost 2011). Although a few individuals have been found in moss balls up to 8 m high, associated with vines (Wake 1987; David Wake, pers. comm. 31 March 2011), most ***Nototriton picadoi*** seem to be almost restricted to hanging mosses on tree limbs and tree trunks, but they have also been collected in bromeliads (Good & Wake 1993; Savage 2002). Bruce (1999) considers the species to be a "specialist on moss." In a collecting trip to Tapanti, Bruce was able to locate only 38 individuals in 270 person hours. Of these, three were in moss mats on the ground and 35 were above ground to about 8 cm, all but one being in mosses.

Eggs of ***Nototriton picadoi*** have been found only in and under mosses in the same habitats where adults are known (Good & Wake 1993; Savage 2002). Nevertheless, it appears that the adults do not attend their eggs (Bruce 1998), an unusual behavioral omission for terrestrial salamanders (Duellman & Trueb 1994). Bruce (1998) suggests that this lack of care may represent a tradeoff with other adaptations that minimize desiccation, predation, and fungal infections in the eggs. Like the tiny frogs, this species has few eggs (1-8), permitting eggs to be larger and more protected. The eggs are laid over an extended period of several months that begins with the wet season in May. All hatching is completed before the dry season, ending in December. Development of the embryos requires 2.5-3 months.

Nototriton richardi (Richard's Salamander, Plethodontidae)

Nototriton richardi (Figure 38-Figure 39) lives in moss banks (Wake 1987) and leaf litter of the humid lower montane rainforest and to a lesser degree in upper premontane rainforest of higher altitudes (1370-1800 m asl) on the Atlantic slopes of the Cordillera Central of Costa Rica (Good & Wake 1993; ZipcodeZoo.Com 2008c; Frost 2011). Good and Wake (1993) also found it among mosses covering tree trunks and stumps in Costa Rica. It is listed as near threatened on the IUCN red list (IUCN 2010b).

Figure 38. ***Nototriton richardi***. Photo by Eduardo Boza Oviedo, with permission.

Figure 39. ***Nototriton richardi***. Photo by Eduardo Boza Oviedo, with permission.

Nototriton saslaya (Plethodontidae)

Nototriton saslaya (Figure 40) is an endemic known only from the cloud forest near its type locality on the south slope of Cerro Saslaya, Atlántico, Nicaragua, at 1280-1370 m asl (Köhler 2002; IUCN 2010a; Frost 2011). The cloud forest is characterized by an abundant bryophyte cover, so it is almost inevitable that the salamanders will traverse them. They would make ideal safe spots for eggs, but the location of eggs has not been documented. The species is listed as vulnerable (IUCN 2010b).

The species ***Nototriton saslaya*** not only lives in moss, but the eggs hatch there and juveniles develop there; *i.e.*, they are not dependent upon submersion as are eggs of many salamanders (ZipcodeZoo.Com 2008d).

Figure 40. ***Nototriton saslaya*** on leaf. Photo by Gunther Koehler, with permission.

Nototriton tapanti (Tapanti Moss Salamander, Plethodontidae)

This species is known only from its type locality, the humid premontane Atlantic slope forest near Tapanti, Costa Rica, where it lives in the humid premontane Atlantic slope at the north end of the Cordillera de Talamanca (Frost 2011). It lives among mosses that cover tree trunks and stumps, on road banks, and probably in leaf litter in the Orosi River Valley (Savage 2002). This and other recent species in Costa Rica suggest that a number of species have evolved there through miniaturization, a good adaptation to living among mosses (Good & Wake 1993). In other locations, the species of ***Nototriton*** are primarily bromeliad dwellers. This species is currently listed as endangered on the IUCN Red List due to its very restricted distribution and may possibly be critically endangered due to continued habitat loss (Bolaños *et al*. 2004, 2008). However, lack of data makes it hard to assess its status.

Nyctanolis pernix (Nimble Long-limbed Salamander, Plethodontidae)

Nyctanolis pernix (Figure 41) occurs in Guatemala and Mexico in subtropical or tropical moist montanes (IUCN 2010b) at 1200-1610 m asl (Frost 2011). It is listed as endangered due to its small distribution and threatened habitat (IUCN 2010b). It is not found in disturbed habitats. Its habitat is humid pine-oak forests and cloud forests, where it lives under moss and bark and is most active on rainy evenings (Elias & Wake 1983; Stuart *et al*. 2008), suggesting it has high sensitivity to moisture loss. Breeding is direct with no tadpole stage.

Figure 41. ***Nyctanolis pernix*** on a leaf. Photo by Sean Michael Rovito, with permission.

Oedipina (Plethodontidae)

The genus ***Oedipina*** has also been segregated from the genus ***Nototriton***, based on both molecular and morphological characteristics (García-París *et al*. 2000b).

This genus has fifteen recognized species and is the most specialized genus in the Plethodontidae (Brame 1968). It seems to have evolved around Costa Rica and western Panama, then extended southward from Estado de Chiapas, Mexico, southward through western Colombia to extreme northwestern Ecuador. It occurs primarily in lowlands or low montane areas up to 2286 m asl. The genus is primarily **fossorial** (adapted to digging and living underground) and is often found under very wet mosses along road cuts or in and under rotting logs in pastures of forested areas.

Species of ***Oedipina*** at intermediate altitudes occur in cloud forests, typically in moss mats covering downed vegetation and soil banks (Wake 1987).

Oedipina carablanca (Los Diamantes Worm Salamander, Plethodontidae)

In Guayacan, Limon Province, Costa Rica, this species occurs in humid Atlantic lowlands (Frost 2011) in places like rotting logs and under moss mats (Kubiki 2011). It is barely known and its population status is known. IUCN (2010b) lists it as endangered.

Oedipina elongata (Central American Worm Salamander, Plethodontidae)

Oedipina elongata (Figure 42-Figure 43), also known as Galliwasp and White-crowned Worm Salamander, occurs at low and moderate elevations from north-central Chiapas, Mexico, and near the Caribbean coast of eastern Belize, across the Guatemalan Atlantic foothills to the Montañas del Mico and into adjacent northwestern Honduras (Townsend *et al*. 2006; Frost 2011). It is known from elevations up to 1035 m asl in Honduras, where it occupies channels within logs, termite nests, leaf litter, and tree stumps (IUCN 2010b). Its preference for moist microhabitats suggests that one should also seek it in mosses. Its development is direct. This lucky salamander is listed by IUCN as one of "least concern" (IUCN 2010b). Nevertheless, like its sister species, it is threatened by deforestation. Fortunately, it does tolerate modest disturbance.

Figure 42. ***Oedipina elongata*** (**Central American Worm Salamander**), shown here on a log at Selva Lacandona, Chis, Mexico. Photo by Omar Hernandez-Ordoñez, with permission.

Figure 43. ***Oedipina elongata*** (**Central American Worm Salamander**). Photo by Edmund (Butch) Brodie, with permission.

Oedipina gracilis (Long-tailed Worm Salamander, Plethodontidae)

Oedipina gracilis (Figure 44) lives in low to moderately high elevation (3-710 m asl) in Costa Rica along the Caribbean coast and into Panama (Savage 2002; Guyer & Donnelly 2005). Habitat destruction is causing populations to decrease and it is listed as endangered (IUCN 2010b).

Figure 44. ***Oedipina gracilis*** (Long-tailed Worm Salamander) on ***Monoclea***, probably ***M. gottschei***. Photo by William Leonard, with permission.

Oedipina gracilis (Figure 44) is nocturnal (Bruce 2003) and inhabits predominantly moist, hidden environments, such as leaf litter, burrows made by insects, and underneath or near rotting logs (Leenders 2001). It finds these habitats in humid Atlantic lowlands of Costa Rica and extreme northwestern Panama (Frost 2011). The eggs occur in the same places as adults, but degree of parental care is unknown (Bruce 2003). Its use of bryophytes is unknown, but likely.

Oedipina pacificensis (Plethodontidae)

Oedipina pacificensis (Figure 45-Figure 46) is known from the humid lowlands and premontane slopes of southwestern Costa Rica and adjacent southwestern Panama at 5-730 m asl (Frost 2011). The pictures below demonstrate its tiny diameter (Figure 45-Figure 46). Its wormlike morphology is suitable for its habit of burrowing underground, sometimes going under mats of wet moss or rotten logs (Höbel 2008).

Figure 45. ***Oedipina pacificensis*** showing its small size. Photo by Angel Solis, with permission.

Figure 46. Close view of ***Oedipina pacificensis***. Photo by Angel Solis, with permission.

Oedipina poelzi (Quarry Worm Salamander, Plethodontidae)

Oedipina poelzi (Quarry Worm Salamander; Figure 47) occurs in the Cordillera de Tilarán, Cordillera Central, and Cordillera de Talamanca of Costa Rica at 775-2050 m asl (Frost 2011). Individuals were taken from moss and lichen mats covering the road cuts near the falls where water seepage was constant (Wake 1987). This species occurs in subtropical or tropical moist montanes, rivers, and previously forested land (Frost 2011). It is threatened by habitat loss.

Figure 47. ***Oedipina poelzi***, a moss dweller in Costa Rica. Photo from Division of Herpetology at University of Kansas Biodiversity Institute, with permission through Rafe Brown.

Oedipina pseudouniformis (Plethodontidae)

Oedipina pseudouniformis lives in humid lowland and premontane areas of the Atlantic slope of central Costa Rica and on both slopes in northern Costa Rica at 19-1213 m asl, and in Nicaragua at 730-945 m asl (Frost 2011). It was described from a salamander taken from moss growing beneath bushes on a steep, sloping hill about 0. 25 km north of a swamp (Brame 1968). Wake (1987) lists it as an arboreal moss dweller. Additional specimens of ***O. pseudouniformis***, in large numbers, were in or under moss covering the east facing slopes, north of the swamp, or under logs in the deep woods to the northwest of the swamp. Its small population size and human activity have caused its populations to grow even smaller, causing it to be listed as endangered (IUCN 2010b).

Oedipina uniformis (Cienega Colorado Worm Salamander, Plethodontidae)

This worm salamander lives in the mountains and lowlands of central Costa Rica (Volcan Tenorio, Meseta Central) to the Panama border at 750-2150 m asl. It is an arboreal moss dweller (Wake 1987) that is decreasing in population size and is near threatened (IUCN 2010b).

Pseudoeurycea juarezi (Juarez Salamander, Plethodontidae)

The **Juarez Salamander** (Figure 48) occurs in the cloud forests of the Sierra Juárez and Sierra Mixe, Oaxaca, Mexico at 2400-3000 m asl (IUCN 2010b). It inhabits pristine moist forests under loose bark, under fallen trees, and under mosses on rocks and logs. Its development is direct, with no tadpoles. Logging, agricultural expansion, and human settlement threaten it with habitat loss. Parra-Olea *et al*. (2008) suggest that it has declined by 80% in the last ten years, and the IUCN has listed it as critically endangered (IUCN 2010b).

Figure 48. This ***Pseudoeurycea juarezi*** was located by lifting the moss at Sierra de Juarez Oaxaca, Mexico. Photo by Omar Hernandez-Ordoñez, with permission.

Pseudoeurycea rex (Royal False Brook Salamander, Plethodontidae)

Pseudoeurycea rex (Figure 49) lives in the high elevations (2450-4000 m asl) of western Guatemala (Frost 2011) and Mexico (although that may prove to be a different species) and is known to live predominantly in arboreal mosses (Wake 1987). This species has direct development and therefore does not depend upon open water for larval development.

Although it was formerly listed as a species of least concern by IUCN (Wikipedia 2011f), it is threatened by habitat loss. But the whole cause of its decline is unknown; it is declining or disappearing even in areas that still maintain the habitat of former populations. It was once considered to be the most abundant species in Guatemala, but now it is extremely rare, with its population size dropping by 80% in ten years, and its status has been changed to that of critically endangered (IUCN 2010b).

Figure 49. ***Pseudoeurycea rex*** on bark. Photo © 2003 Jonathan Campbell, with permission.

Pseudoeurycea scandens (Tamaulipan False Brook Salamander, Plethodontidae)

The Tamaulipan False Brook Salamander (Figure 50-Figure 51) lives in Southwestern Tamaulipas in the caves of the Biósfera El Cielo, Mexico, at 1050-1800 m asl, and from the type locality at ~28 km northeast of Ciudad del Maiz in San Luis Potosí, Mexico (Frost 2011). This

species can also live among arboreal mosses (Wake 1987), presumably benefitting from the moisture and cover they provide. Its direct development precludes the need for open water.

This species has fared better than most and is listed only as vulnerable by IUCN (2010b). Nevertheless, it has not been seen since the mid 1980's, but this may be due to limited searching. Its mossy habitat can easily hide it from an undiscerning eye.

Figure 50. ***Pseudoeurycea scandens*** on moss-covered log where it blends well with the bark and the patchy environment. Photo by Sean Michael Rovito, with permission.

Figure 51. More muted color patterns on another ***Pseudoeurycea scandens*** (**Tamaulipan False Brook Salamander**) on bark where it blends well with the bark and lichens, permitting it to be inconspicuous among the patches of mosses as well. With no mating call and small size, these salamanders are difficult to locate and may be lurking nearby undetected. Photo by Timothy Burkhardt, with permission.

Pseudoeurycea werleri (False Brook Salamander, Plethodontidae)

Pseudoeurycea werleri (Figure 52), a lower elevation salamander, lives in the rainforest and cloud forest from 900-1500 m asl on Sierra de los Tuxtlas, Veracruz, Mexico, where it is endangered due to its small distribution and declining habitat (Flores-Villela & Martínez-Salazar 2009; IUCN 2010b). Its home is in the arboreal mosses, where its direct development permits it to survive without pools of water.

Wake (1987) stated that bromeliads and moss mats in mid-elevational wet and rain forests provide "ideal" microhabitats for insectivorous, direct developing amphibians. This suggests that we may be overlooking such secretive species as this one.

Figure 52. This ***Pseudoeurycea werleri*** came very close to being dinner, with its entire tail being disarticulated in an attack. Photo by Sean Michael Rovito, with permission.

Lineatriton (placed in ***Pseudoeurycea*** by Frost 2011) (Plethodontidae)

This genus is combined into ***Pseudoeurycea*** by Frost (2011). In its narrow ***Lineatriton*** sense, it is a relatively rare Mexican genus with three described species. The systematics of these species is uncertain and they may actually represent more or fewer species. It uses moss mats to some degree (Wake 1987) and is secretive, nearly always under cover in the rainforest floor (Brodie *et al*. 2002 for ***L. orchimelas***). When predators approach, it propels itself by coiling and uncoiling its body rapidly.

Pseudoeurycea lineola (Veracruz Worm Salamander; Figure 53) lives only at 800-1250 m asl in a small area of oak-pine forest in the Sierra Madre Oriental of Veracruz, Mexico (Frost 2011). It lives under stones, logs, and debris, possibly including mosses, and in subterranean hideouts. Its need for moisture suggests that mosses might be a suitable habitat. This species is endangered due to its small, fragmented distribution and continuing loss of habitat (IUCN 2010b). None of its known locations is protected by law.

Figure 53. ***Pseudoeurycea lineola***. Photo by Sean Michael Rovito, with permission.

Pseudoeurycea orchileucos (Sierra de Juárez Worm Salamander) lives around Yetla and Vista Hermosaat 800-1390 m asl on the humid northern slope of the Sierra de Juárez, Oaxaca, Mexico (Frost 2011). In these cloud forests it can live below ground (**fossorial**), making it difficult to locate. It does not survive in disturbed habitats, probably due to its need for moisture (IUCN 2010b). Its development is direct, so pools of water are not needed. Hence, mosses might be used to keep its body moist. The species is endangered due to its small population size and limited distribution; logging contributes to its loss of habitat (IUCN 2010b). None of its habitats is on protected land.

Pseudoeurycea orchimelas (San Martin Worm Salamander) lives at 100-1300 m asl in the Sierra de Los Tuxtlas and adjacent Sierra de Santa Marta, Veracruz, Mexico (IUCN 2010b). It is fossorial (lives below ground) in leaf litter. Its direct development does not necessitate open water. Its relationship to bryophytic habitats is unclear. Wake (1987) considered the genus to make some use of bryophytes, but there is no specific mention for this species. This species likewise is endangered because of its small population, limited distribution, and habitat destruction, despite being abundant within its distribution (IUCN 2010b). Unlike the other two species of the former ***Lineatriton***, it is protected where it occurs in the Reserva de la Biósfera Los Tuxtlas.

Thorius (Mexican Pigmy Salamanders, Plethodontidae)

Thorius dubitus (Acultzingo Pigmy Salamander, Plethodontidae)

Thorius (Figure 54) represents the smallest of the tailed amphibians (Hanken 1983), with some members less than 2 cm, including the tail (Wikipedia 2010). The genus occurs in the pine-oak cloud forest on high mountain crests of west-central Veracruz and adjacent Puebla, Mexico at 2475-2800 m asl (Frost 2011). ***Thorius dubitus*** occurred under mosses (Wake 1987) and other plants and occurred at slightly higher elevations than the other salamander species of the area (Hanken 1983).

Figure 54. ***Thorius arboreus***, a relative of ***T. dubitus***, and possible a moss dweller. Photo by Sean Michael Rovito, with permission.

Old-growth Temperate Habitats

Old growth forests offer a variety of microhabitats not available in younger secondary forests. Dense growths of bryophytes there ameliorate the temperature, providing safe sites that help to cool by evaporation as well as provide dense shade from the dangers of the sun. These same bryophytes likewise provide a haven of moisture when bare soil and branches become dry (Figure 28). Hence, they are able to harbor an array of interesting miniature communities about which we really know very little.

Aneides aeneus (Green Salamander, Plethodontidae)

Aneides aeneus (Figure 55-Figure 57), also known as Web-footed Salamander, Bronzy Salamander, or Bronzed Salamander, lives in the Appalachian region from southern Ohio, southern Indiana, and southwestern Pennsylvania to western South Carolina, Tennessee, northern Georgia, northern Alabama, and northeastern Mississippi, USA (Frost 2011). It eats a diet that can easily be found among, under, or on top of mosses. In Bat Cave, North Carolina, USA, Rubin (1969) found that one individual had eaten 53% ants, 32% spiders, 13% shed salamander skin, and 2% unidentified insect larvae. But when Lee and Norden (1973) examined gut contents of 25 individuals from Coopers Rock, West Virginia, USA (at the northern limit of their range), they found some interesting organic matter – leaf fragments, humus, mosses, and hemlock needles, as well as sand grains.

Figure 55. ***Aneides aeneus*** adult in crevice in its mossy habitat. Photo by Bill Peterman, with permission.

Canterbury (1991) found that juveniles remained with their mother for about a month. They climbed up the rock faces from their birth crevices toward moss-covered ledges. Cryptic coloration of mottled green and dark colors would render these youngsters almost invisible (Figure 56). Adults live in crevices in boulders and retreat deep into the crevice to hibernate for the winter (Figure 57) (Gordon 1952).

Figure 56. ***Aneides aeneus*** juvenile in its mossy habitat. Photo by Bill Peterman, with permission.

Figure 57. ***Aneides aeneus*** adults with eggs in crevice in its mossy habitat, North Carolina, USA. Photo by Bill Peterman, with permission.

Aneides vagrans (Wandering Salamander, Plethodontidae)

Aneides vagrans (Figure 58) lives in coastal northern California, USA, from northwestern Sonoma County to Smith River near Crescent City, and has been introduced and is widespread on Vancouver Island, British Columbia, Canada (Frost 2011). Nevertheless, its populations are decreasing and its IUCN status is near threatened (IUCN 2010b).

Although the ground-dwelling **Wandering Salamander**, ***Aneides vagrans*** (Plethodontidae) (Figure 58) lives under bark of fallen trees, arboreal members living on large coast redwoods (*Sequoia sempervirens*; Figure 67) may inhabit mosses as well (Spickler *et al*. 2006). Like most of the arboreal salamanders, the species is lungless and the young are hatched fully formed, *i.e.*, they do not form larvae first. Hence, they require high moisture and high oxygen levels. Sillett (1995) found this species among the branches of the moss ***Antitrichia curtipendula*** (Figure 59-Figure 61) at 30 m above ground. However, the moss study was not designed to be quantitative, and the more quantitative study on mats of the epiphytic fern *Polypodium scouleri* suggests that ***A. vagrans*** spends much time among the fern mats, occupying tunnels and cavities left by dead roots and rhizomes (Spickler *et al*. 2006). (I have to guess that these tunnels may actually be in mosses.) Nevertheless, the moist habitat and production of photosynthetic oxygen provided by mosses suggest that mosses should be suitable habitats for these salamanders as well. In any event, the salamanders are at least indirectly dependent on the bryophytes. *Polypodium scouleri* requires either bryophytes or litter to provide the moist substrate needed for their gametophytes to establish (Lovelace 2003).

Figure 58. The **Wandering Salamander**, ***Aneides vagrans***. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 59. ***Antitrichia curtipendula***, a good candidate for protection of small organisms in mature forests of the Pacific Northwest, USA. Photo by Michael Lüth, with permission.

Figure 60. ***Antitrichia curtipendula***, moist and expanded. Photo by Michael Lüth, with permission.

Figure 61. ***Antitrichia curtipendula***, dry, with capsules. Photo by Michael Lüth, with permission.

Batrachoseps wrighti, formerly *B. wrightorum* (Oregon Slender Salamander, Plethodontidae)

Batrachoseps wrighti (**Plethodontidae**; Figure 62-Figure 63) [85-120 mm total length (Bury 2011)] is also known as the Western Four-toed Salamander. It is endemic to the northwestern USA, where it occurs from the Columbia River Gorge of northwestern Oregon, USA, southward along the slopes of the Cascade Mountains in Oregon, from sea level to about 1430 m asl (Kirk 1991; Kirk & Forbes 1991; Frost 2011). It lives in temperate zone forests of moist Douglas fir (*Pseudotsuga menziesii*), maple (*Acer*), and red cedar (*Juniperus*) (Bury 2011) and is considered vulnerable on the IUCN Red List due to continuing habitat loss (IUCN 2010b).

Figure 62. ***Batrachoseps wrighti*** on a bed of mosses. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

The specific habitats of these salamanders include decayed logs and stumps, especially in older decay classes (Bury 2011). However, they have also been found under moss-covered bark in termite channels in decaying logs (Storm 1953) and under large rocks that are moss covered (Bury 2011). It is possible that they require the mosses when they venture out for food, using the mosses to maintain their moisture. On the other hand, as far as we know, they seem to spend their time in burrows underground or deep within large logs except in early spring just after snowmelt.

They develop without a larval stage, emerging from eggs as froglets (Lannoo 2005), an adaptation to terrestrial living.

Figure 63. ***Batrachoseps attenuatus*** on moss. Photo by Brian Gratwicke, through Creative Commons.

Rhyacotriton cascadae (Cascade Torrent Salamander, Rhyacotritonidae)

The Cascade Torrent Salamander (***Rhyacotriton cascadae***; Figure 64-Figure 65), also known as Cascade Salamander and Cascades Torrent Salamander, lives in torrents (AmphibiaWeb 2009a) on the western slope of the Cascade Mountains from just north of Mount St. Helens, Washington, south to northeastern Lane County, Oregon, USA (Frost 2011). Although it seems to occur where there are lots of mosses, documentation of its actual use of the moss as a place of shelter or laying eggs is lacking. There is only one published record of its nest, which was under cobble in a quiet area of a small stream (MacCracken 2004). Since this genus is apparently the least desiccation-tolerant genus of salamanders (Ray 1958), it is likely that the salamanders migrate to mosses during times of diminished flow.

Figure 64. Cascade Torrent Salamander, ***Rhyacotriton cascadae***. Photo by John Clare, through Creative Commons.

Figure 65. Ventral side of the Cascade Torrent Salamander, ***Rhyacotriton cascadae***. Photo by Henk Wallays, through Creative Commons.

Rhyacotriton olympicus (Olympic Torrent Salamander, Rhyacotritonidae)

The Olympic Torrent Salamander (***Rhyacotriton olympicus***; Figure 66), also known as Mountain Salamander, Olympic Salamander, Olympic Mountain Salamander, and Northern Olympic Salamander, is another inhabitant restricted to old-growth forests of northern California and southwestern Oregon (Anderson 1968; Welsh 1990). The Olympic Torrent Salamander (***Rhyacotriton olympicus***), like ***Plethodon elongatus***, rarely occurs in open water and likewise seems to require the moisture of mosses, rocks, and organic matter (Welsh 1990) (Figure 67-Figure 68).

Figure 66. ***Rhyacotriton olympicus***, the Olympic Torrent Salamander. Photo by Michael Graziano, with permission.

As we have seen in other taxa, ***R. olympicus*** (Figure 66) often occurs under moss-covered stones in both larval and adult stages, particularly in seepage areas (Stebbins 1955). Stebbins found that the stream was mostly hidden by the moss-covered rocks. Slater (1933) noted that collectors generally hunt for them only during the day. On his night trips he noted that they were on stones and moss a meter or so away from the water (Figure 68). He suggested that they made these excursions onto the mosses in search of food. The mossy habitat would help to conserve their moisture during these wanderings.

Figure 67. Coast redwood forest (*Sequoia sempervirens*), home of ***Rhyacotriton*** and ***Dendrotriton*** salamanders. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 68. Rainforest in the Olympic National Park, Washington, USA, home of ***Rhyacotriton olympicus***. Photo by Andreas Nöllert and published in a calendar by Druckhaus Gera GmbH, Jacob-A.-Morand-Strasse 16, D-07552 Gera, Thuringia, Germany, with permission.

Rhyacotriton variegatus (Southern Torrent Salamander, Rhyacotritonidae)

The Southern Torrent Salamander (Figure 69-Figure 70) is also known as the Southern Olympic Salamander and the California Mountain Salamander. As its name implies, it has a more southerly distribution in the coast ranges from southern Mendocino County, California, north to the Little

Nestucca River and the Grande Ronde Valley in Polk, Tillamook, and Yamhill counties, Oregon and the western slope of the Cascade Mountains near Steamboat, Oregon, USA (Frost 2011).

Figure 69. ***Rhyacotriton variegatus*** on a bed of mixed mosses. Photo by Henk Wallays, through Creative Commons.

Figure 70. ***Rhyacotriton variegatus*** creeping across a moss. Photo by William Flaxington, with permission.

Welsh and Lind (1996) conducted an extensive survey of ***Rhyacotriton variegatus*** (Figure 69-Figure 70) in northwestern California to identify those attributes most important to its location. They determined that it has a rather narrowly defined niche that is encompassed by cold, clear headwaters to low-order streams that have loose, coarse substrata (little sedimentation), in humid forests with large conifers affording more than 80% canopy closure and abundant ground-layer moss. That defines old-growth, undisturbed forest. Their preference for shallow, cold, percolating water with cover of moss and rocks is supported by observations of Anderson (1968), Nussbaum & Tait (1977), Nussbaum *et al*. 1983, Stebbins (1985), Bury (1988), Bury & Corn (1988), Corn & Bury (1989), Welsh (1990), Bury *et al*. (1991), Good & Wake (1992), and Leonard *et al*. (1993). Large conifers, moss, and high canopy closure indicated sites with this species, whereas those with grass and stumps lacked the species (Welsh & Lind 1996). As reported by Bingham and Sawyer (1991), significantly greater moss abundance occurs in old-growth compared with young forests in northwestern California. The moss appears to be important in maintaining moisture in this salamander, but so far there seems to be no direct evidence they live there.

Asia – One Plethodontid!

I was nearly finished with this chapter when I suddenly realized that the salamander chapter had a strong western hemisphere bias. A little checking revealed that the eastern hemisphere does not have many species of these little 4-footed creatures, but I was certain at least some might make use of mosses. Google didn't get me very far, so I appealed to bryonetters for help.

Karsenia koreana (Korean Crevice Salamander, Plethodontidae)

Known in Korea as the Moss Salamander (Figure 71) (Hiromi Matsui, pers. comm. 25 March 2011), or Ikkee dorongyong (Wake 2005), ***Karsenia koreana*** is a disjunct curiosity. But what is so special about this salamander? It is the first and only plethodontid salamander found in Asia (Min *et al*. 2005)! The world plethodontid specialist David Wake is quoted as saying, "I've discovered and named nearly 50 species of salamanders – more than 10 percent of the total in the world. I've discovered new genera in Guatemala and Costa Rica. But this tops everything I've ever found by a long ways. For me, this is the most stunning discovery in the field of herpetology during my lifetime. It's so utterly unexpected, so completely unexpected." (Sanders 2005).

Figure 71. ***Karsenia koreana***, the only known plethodontid in Asia. Photo by Todd Pierson, with permission.

Figure 72. ***Karsenia koreana*** in a mossy habitat in Asia. Photo by Todd Pierson, with permission.

But that is not the only remarkable circumstance. It was not described until 2005 (Min *et al.* 2005) when a high school teacher from Illinois, Stephen J. Karsen, was on a field trip with his Korean students looking for salamanders in the same sorts of places (Figure 72) he might find them in Illinois (Wake 2005). But in South Korea, this was not considered as a likely habitat because the terrestrial plethodontid species so common in North America were totally unknown and thought to be absent here. Discovered at 210 m asl (Min *et al*. 2005) and endemic to the middle portion of the Korean Peninsula, South Korea, the species is now known from 16 locations in three provinces of South Korea (Wake 2005). With this many locations, it is listed as a species of least concern on IUCN Red List (IUCN 2010b).

This was not, however, the first find of the species. It had been collected 34 years earlier by a Japanese-Korean collecting team but never described as a species (Nishikawa 2009).

Karsenia koreana (Figure 71) was both a new species and a new genus in the family Plethodontidae, representing a considerable disjunction from this predominantly western hemisphere family, and raising questions about its venture to Asia 100 million years ago (Sanders 2005). It averages 42 mm snout to vent length and only superficially resembles the North American ***Plethodon*** (Wake 2005). It occurs in rock slides and on damp, mossy slopes, causing the Koreans to call it the moss salamander. Its habitat is young forests of hardwoods and pines, 15-50 years old, in limestone areas. Its resting habitat seems to be under small rocks and slices of limestone in areas with fine-grained soil. Since it requires moisture, bryophytes are likely to play a role in maintaining its hydration.

Europe – One Plethodontid Genus

Speleomantes supramontis (Supramonte Cave Salamander, Plethodontidae)

The Plethodontidae in Eurasia are limited to ***Karsenia koreana*** in Korea and ***Speleomantes***, a genus of six limestone cave dwellers (Marc P. Hayes, pers. comm. 26 March 2011). Of these six, it appears that ***S. supramontis*** (Figure 73) from east Sardinia (around the Gulf of Orosei, Italy, from 100-1360 m asl) is the only one frequently associated with bryophytes. In the Mediterranean oak forests it occurs under mosses on rocks near streams (Nöllert & Nöllert 1992). Not surprisingly, a species such as this with a limited habitat and distribution is endangered (IUCN 2010b).

Figure 73. ***Speleomantes supramontis*** (**Supramonte Cave Salamander**) on a rock ledge. Photo by Franco Andreone, through Wikimedia Commons.

Peatlands and Wetlands

Peatlands would seem to provide an ideal habitat for many kinds of amphibians. They have open areas where the amphibians can bask, they have open water for tadpoles and larvae, and they provide moist mosses that keep the amphibians hydrated (Figure 74). This combination also makes them ideal sites for nesting for some species. But there is a caveat – acidity!

Stan A. Orchard of BulfrogControl.com Inc. (pers. comm. 27 March 2011) gave me this summation of his observations: "I have routinely found amphibians (toads, frogs, semi-aquatic salamanders, newts) in and around ***Sphagnum*** bogs, but they tend to be found in and around open water pools (Figure 74) that are used for spawning, larval stage development, and over-wintering. Amphibian associations with ***Sphagnum*** (Figure 21) bogs seem to me to be co-incidental and the result of a need by both for damp conditions. However, Plethodontid salamanders, for example, that require damp, shady conditions but reproduce on land are not so likely to be found in a peat bog as on a damp shaded forest floor. Conversely, amphibian species that are found in bogs tend to have migrated in specifically to escape summer dehydration, to forage, and to utilize permanent or seasonal pools for reproduction. ***Sphagnum*** patches do not seem to be attractive sites for over-wintering for semi-terrestrial species because they are too water soaked in the winter and subject to water table fluctuations, as opposed to damp but drained upland habitats. It is also possible that peat bogs may be uncomfortably acidic for some species."

Figure 74. Developing peatland, seen from upland at Lawrence Lake, Michigan, USA. Photo by Janice Glime.

Despite the acidity, some salamanders are able to tolerate ***Sphagnum*** habitats. Most of these have been discussed in the subchapter on Ground-dwelling Anurans, including results of various experiments on acidity. In peatlands of Maine, USA, twelve species of amphibians appeared in traps (Stockwell & Hunter 1989). Of the 2179 amphibians captured, only 4.5% were salamanders. Nevertheless, four species were present: ***Ambystoma laterale*** (Blue-spotted Salamander; Figure 75), ***Desmognathus fuscus*** (Northern Dusky Salamander; Figure 76), ***Eurycea bislineata*** (Northern Two-lined Salamander; Figure 77), and ***Notophthalmus viridescens*** (Eastern Newt - **Salamandridae**; Figure 106).

Figure 75. ***Ambystoma laterale*** (**Blue-spotted Salamander**), a peatland salamander that occurs in eastern USA and Canada (Frost 2011). Photo by Henk Wallays, through Creative Commons.

In addition to the salamanders just mentioned, at least occasional ***Sphagnum*** (Figure 21) dwellers include some members of the genera ***Bolitoglossa***, ***Eurycea***, ***Hemidactylium***, ***Lissotriton***, ***Pseudotriton***, ***Stereochilus***, and ***Triturus***. Some ***Ambystoma*** species in ***Sphagnum*** waters seem to suffer lower developmental rates and reduced activity, but survive; some, however, suffer death in the acid water (see chapter on Ground-dwelling Anurans). The relationship of some ***Eurycea*** species to wetlands with ***Sphagnum*** are discussed here, and later those of the Salamandridae.

Figure 76. Northern Dusky Salamander, ***Desmognathus fuscus***. Photo by Janice Glime.

Figure 77. The Northern Two-lined Salamander, ***Eurycea bislineata***. Photo by Henk Wallays, through Creative Commons.

Eurycea wilderae (Blue Ridge Two-lined Salamander, Plethodontidae)

The Blue Ridge Two-lined Salamander lives in the Southern Appalachian Mountains, USA. In the Tulula Wetlands, North Carolina, USA, one can find ***Eurycea wilderae*** (Blue Ridge Two-lined Salamander, Figure 78-Figure 81) and ***E. guttolineata*** (Three-lined Salamander; Figure 82-Figure 83) among the ***Sphagnum*** (Amphibians: Tulula Wetlands 2009). Although it would seem that ***Sphagnum*** would provide a safe site for eggs, both lay their eggs in the water, presumably because they have aquatic larvae. Instead, their preferred habitat for egg laying appears to be streams and stream banks (AmphibiaWeb 2010).

Figure 78. ***Eurycea wilderae*** on a moss mat. Photo by Todd Pierson, with permission.

Figure 79. ***Eurycea wilderae*** on a mat of mosses. Photo by Michael Graziano, with permission.

Figure 80. ***Eurycea wilderae***, showing its small size compared to a US quarter. Photo by Todd Pierson, with permission.

Figure 81. ***Eurycea wilderae***. Photo by John D. Willson, with permission.

Eurycea guttolineata (Three-lined Salamander, Plethodontidae)

Eurycea guttolineata (Figure 82-Figure 83) is also known as Holbrook's Triton and Southern Long-tailed Salamander. It lives in the southeastern USA where it is found in the Mississippi Embayment from eastern Louisiana to extreme western Kentucky and western Tennessee, throughout most of Mississippi and Alabama, the panhandle of Florida and northward through Georgia, South Carolina, North Carolina, to the eastern half of Virginia (Frost 2011).

In the Tulula Wetlands, North Carolina, USA, it lives among the ***Sphagnum*** (Figure 74) (Amphibians: Tulula Wetlands). Nevertheless, it lays its eggs in the water, presumably because the larvae are aquatic, preferring streams and stream banks (AmphibiaWeb 2010). This very long-tailed ***Eurycea guttolineata*** is common in swampy areas and along the margins of sluggish streams in Georgia, USA (Salamanders of Georgia and South Carolina 2010).

Figure 82. ***Eurycea guttolineata*** at the edge of a stream. Photo by Michael Graziano, with permission.

Figure 83. ***Eurycea guttolineata*** on a bed of mosses. Photo by Matthew Niemiller, with permission.

Streams and Springs

Eurycea bislineata (Northern Two-lined Salamander, Plethodontidae)

Eurycea bislineata (Figure 84-Figure 85) lives in eastern North America from the St. Lawrence River in Canada and northeastern Ohio, USA, to northern Virginia, USA. It is widespread and known enough to have ten additional English names (Frost 2011). This species frequently uses mosses for nests and shelter. Eggs may be laid on rocks and logs, but Bahret (1996) found clutches of eggs, fully exposed, on the uppermost leaves of an aquatic moss, ***Sphagnum trinitense*** (Figure 86-Figure 88). Jobson (1940) found larvae and adults in patches of moss in a swift stream. Richmond (1945) found a nest with 42 eggs among underwater roots under a clump of mosses and other plants. When he turned the mosses back and left them undisturbed for an hour, he returned to find that the salamander had returned to its nest.

Figure 84. ***Eurycea bislineata***. Photo by Twan Leenders, with permission.

Figure 85. Aquatic larva of ***Eurycea bislineata***. Photo by John White, with permission.

Figure 86. Habitat of ***Sphagnum trinitense*** in South Carolina, USA. Photo by Blanka Shaw, with permission.

Figure 87. Emergent ***Sphagnum trinitense***. Photo by Jan Janssens, with permission.

Figure 88. Close view of submerged ***Sphagnum trinitense*** in South Carolina, USA. Photo by Blanka Shaw, with permission.

Eurycea lucifuga (Cave Salamander, Plethodontidae)

The Cave Salamander (Figure 89) is also known as the Spotted Tailed Triton, Hoosier Salamander, and Spotted-tail Salamander. It appears to be limited to limestone areas near and in limestone caves at higher elevations of the Appalachian Mountains from eastern Tennessee northward almost to Maryland, USA, and in the Ozark uplift of northeastern Oklahoma, southeastern Kansas, northern Arkansas and central and southern Missouri, southern Illinois, southern Indiana and southwestern Ohio through Kentucky and Tennessee to northeastern Mississippi, northern Alabama, and northwestern Georgia (Frost 2011). This species is common in large springs in Oklahoma, hiding in wet mosses and other vegetation (Bragg 1955).

Figure 89. ***Eurycea lucifuga***. Photo by Danté Fenolio, with permission.

Eurycea multiplicata (Many-ribbed Salamander, Plethodontidae)

Also known as the **Many-ribbed Triton**, the species ***Eurycea multiplicata*** (Figure 90) occurs in the Ouachita Mountains of west-central Arkansas and southeastern Oklahoma, USA (Frost 2011). Its apparent avoidance of acidic conditions was exemplified by Bragg (1955) when he placed them in an aquarium with peat moss (***Sphagnum***) at one end. The entire aquarium, including the sand, was moistened, but after two days of drying, the salamanders had not collected in the peat moss as expected, but rather were curled up on the dry limestone from their native habitat. After several more days they died from desiccation. A limestone rock-dwelling moss may have been a more appropriate choice, but the ***Sphagnum*** avoidance suggests that it has properties that keep these salamanders away from it, possibly its acidity due to its cation exchange ability.

Figure 90. ***Eurycea multiplicata***, a ***Sphagnum*** avoider. Photo by Michael Graziano, with permission.

The natural habitat of this species is cave springs, cave runs, and cold streams (IUCN 2010b). Despite its apparent aversion to peat mosses in the experiments of Bragg (1955), some mosses do seem to play a role in its life. Dundee (1947) reported that during winter these salamanders remain active, taking cover under rocks, logs, and mosses near streams. It is only during extreme cold that they actually go into **torpor** (state of inactivity), and this may occur under mosses.

Eurycea tynerensis, formerly *Eurycea griseogaster* (Oklahoma Salamander, Plethodontidae)

Eurycea tynerensis (Figure 91) (formerly *Eurycea griseogaster*), was once considered part of ***E. multiplicata***. This species likewise occurs on the Ozark Plateau of southwestern Missouri, extreme southeastern Kansas, northern Arkansas, and northeastern Oklahoma, USA, where it lives in streams, springs, and seeps. Dundee (1947) found the species under rocks, logs, and clumps of moss at the edges of streams.

Figure 91. ***Eurycea tynerensis*** (**Oklahoma Salamander**) on a liverwort, ***Conocephalum* sp**. Photo by Michael Graziano, with permission.

Proteidae

This is a small family of salamanders with only one known representative that makes use of bryophytes.

Necturus punctatus (Dwarf Waterdog, Proteidae)

Necturus punctatus (Figure 92) ranges along the coastal plain from southeastern Virginia to central Georgia, USA. This species is unusual in retaining its gills as an adult. Its typical habitats are slow-moving muddy or sandy streams, deep irrigation ditches, cypress swamps, stream-fed rice fields, and mill ponds (IUCN 2010b).

Neill (1948) found as many as twelve individuals of this species hibernating in decaying hardwood logs, under bark, or in beetle tunnels, but also in insect burrows under thick moss on sunny slopes in Richmond County, Georgia, USA.

Figure 92. ***Necturus punctatus*** among mosses in water. Photo by Todd Pierson, with permission.

Salamandridae

The **Salamandridae** are the newts, a naming choice that will always be a mystery, or at least a point of consternation, for me. But a newt is really just a salamander that differs enough from members of the large **Plethodontidae** family to be distinguished by its own family. One major difference is the life cycle of newts. They have three stages rather than two. Their **larval** stage is aquatic. They then metamorphose into juveniles that are terrestrial, known as the **eft** stage. Finally, as **adults**, they return to the water, but can at times venture onto land, often including peatlands. In their adult stage, a number of them are sold as aquarium pets, but they need a way to get above water occasionally.

Newts are more common than other salamanders in Eurasia, and they often live in mossy habitats or make use of them at times during their wanderings (Marc P. Hayes, pers. comm. 26 March 2011). The newt family **Salamandridae** occurs in Africa in the Mediterranean fringe (Stan A. Orchard, pers. comm. 27 March 2011). Asia has an endemic newt family, the Hynobiidae, mostly known from Japan.

Klaus Weddeling (Bryonet 26 March 2011) informed me that all the European species of salamanders use mosses for shelter during hibernation and during dry periods. Young adults use the wet mosses and soil as shelter for 2-3 years while they mature. But that doesn't mean you are likely to find one. Des Callaghan (Bryonet 26 March 2011) reported that there are only three species of salamanders in Britain, all of them newts in the **Salamandridae**. Although these might traverse bryophytes, they are not particularly associated with them.

Calotriton asper, formerly *Euproctus asper* (Pyrenean Brook Salamander, Salamandridae)

In the French Pyrenees, Michael Lüth and fellow bryologists found the endemic ***Calotriton asper*** (Figure 93-Figure 94) among mosses close to a waterfall (Figure 94; Bryonet 26 March 2011). Its distribution is the Pyrenees Mountains of France, Spain, and Andorra at 175-3000 m asl. This species is also known as Pyrenean Mountain Newt, Pyrenean Mountain Salamander, Pyrenees Mountain Newt, Pyrenees Mountain Salamander, Pyrenean Salamander, and Pyrenean Newt.

Figure 93. ***Calotriton asper*** that has been living among mosses in the Pyrenees. Photo by Michael Lüth, with permission.

Figure 94. Habitats of ***Calotriton asper*** in the French Pyrenees. Photos by Michael Lüth, with permission.

As a cave dweller, this species faces food deprivation for extended periods up to a year. Issartel *et al*. (2010) attempted to follow the physiological responses to 42 days of fasting, followed by 10 days of refeeding in a subterranean and an epigean population of ***Calotriton asper***. The control subterranean population exhibited hypometabolism together with higher glycogen (+ 25% in liver and muscles) and triglyceride stores (+ 50% in muscles), suggesting it was ready to fast. While fasting, the subterranean cave individuals had a 20% decrease in $\dot{V}O_2$ (liters of oxygen used per minute) while epigean individuals showed little change. Furthermore, the underground population maintained a higher energetic reserve. It appears that the cave population is genetically better adapted to fasting, inducing a decrease in metabolism and greater capacity to accumulate energy reserves. But one must ask if this is, rather than a genetic change, one that has been induced by the prior experiences in the cave. In either case, those organisms with this ability to retain reserves are the ones who will be more likely to survive to breed.

This advantage is almost ensured by the limited dispersion of individuals. Montori *et al*. (2008) demonstrated that the mean distance this species migrated in a year was less than 50 m. There did not seem to be any seasonal migration. Suitable habitats that favored abundance relate to the number of refugia: woody debris, stones, and fissures, places where the salamander can hide and remain hydrated. Larval abundance is correlated with streambed structure. With the limited movement in this species, suitable adult and larval habitats must be in close proximity.

Chioglossa lusitanica (Golden-striped Salamander, Salamandridae)

Chioglossa lusitanica (

Figure 95-Figure 96) is known from northwestern Spain (Iberian Peninsula) and the northern-central part of Portugal (Frost 2011) where it occurs in forested streams (IUCN 2010b) and uses mosses as a refuge (Goux 1957; Marc P. Hayes, pers. comm. 26 March 2011; Iñigo Martínez-Solano, pers. comm. 30 March 2011).

Its limited distribution, pollution, and loss of habitat contribute to its listing as vulnerable (IUCN 2010b).

Figure 95. The **Golden-striped Salamander**, ***Chioglossa lusitanica***. Photo by Andreas and Christel Nöllert, with permission.

Figure 96. Close view of the **Golden-striped Salamander**, ***Chioglossa lusitanica***. Photo by Andreas and Christel Nöllert, with permission.

Euproctus platycephalus (Sardinian Mountain Newt, Salamandridae)

In Sardinia, Italy, there seems to be a salamander species that makes use of mosses. Michael Lüth (Bryonet 26 March 2011) informed me of ***Euproctus platycephalus*** (Figure 97); a group of bryologists disturbed one in wet mosses, ***Thamnobryum alopecurum*** (Figure 98). In the hot, dry summer of the Mediterranean (Figure 99), mosses provide a place to aestivate.

Figure 97. ***Euproctus platycephalus*** photographed on the leafy liverwort ***Porella platyphylla***, but it was under a moss when it was disturbed. Photo by Michael Lüth, with permission.

Figure 98. ***Thamnobryum alopecurum***, home to a population of ***Euproctus platycephalus***. Photo by Michael Lüth, with permission.

The **Sardinian Mountain Salamander** is also known as Sardinian Newt, Pyrenean Brook Salamander, Sardinia Mountain Salamander, Sardinian Brook Salamander, and Flat-headed Salamander. It is endemic to the mountains of Sardinia, Italy, at 50-1800 m asl (Frost 2011). This rare species is red-listed as endangered (IUCN 2010b). It is threatened by treatment of water bodies with DDT in the 1950's in the battle against malaria, introduction of trout that may eat the larval and possibly adult salamanders or compete with them for food, and reduction of water levels due to increasing pressures from human activities including tourism and agriculture (Boehme *et al.* 1999).

Figure 99. Habitat of ***Euproctus platycephalus*** in Sardinia, Italy. Photo by Michael Lüth, with permission.

This salamander spends its larval stage in primarily calm, but also running water (Meijden 1999). The terrestrial phase is always near water, under stones, but also in root zones of bushes and trees and under mosses. The size is 120-140 mm for males and 100-130 for females, total length. This is the opposite of many species of salamanders where the female is the larger gender.

Eggs are only 3 mm in diameter, achieving 4-5 mm with the gelatinous envelope (Meijden 1999). The female lays them over a 3-5.6 month period and development averages 37.6 days at 15°C, or 12.7 days at 14.5°C. Larval development can take 376-453 days at 15°C, exposing the small larvae to predation for a dangerously long time. Even at 20.5°C, development takes 184-260 days.

Lissotriton boscai (Bosca's Newt)

This species (Figure 100) is endemic in the western Iberian Peninsula, excluding southwestern Portugal, and southernmost Spain from sea level to 1800 m asl (Frost 2011). Its habitats include peat moss, running water, and deep, still waters, but it prefers small, shallow ponds with aquatic plants (AmphibiaWeb 2000). In its terrestrial phase, it lives near ponds and hides in humid, shady places under roots, stones, mosses, and trees.

Figure 100. ***Lissotriton boscai***, a peatmoss dweller in the Iberian Peninsula. Image through public domain.

Lissotriton helveticus, formerly *Triturus helveticus* (Palmate Newt, Salamandridae)

This species (Figure 101) occurs in western Europe, including Great Britain (Wikipedia 2011e). Smaller than most newts, males reach only 8.5 cm and females 9.5 cm. It has a wide range of habitats, including terrestrial forests, pastures, and agricultural land, as well as aquatic ponds, lakes, canals, and marshes. It is more tolerant of lower *p*H levels than most amphibians, permitting it to range into more habitats. In the moorlands it can occupy acid pools, and it occurs in peatlands, so Marc P. Hayes (pers. comm. 26 March 2011) suggested that it might make some use of mosses. It is likely that this mostly aquatic species uses the mosses to maintain hydration when it ventures onto land.

Figure 101. Water form of a male **Palmate Newt**, ***Lissotriton helveticus***. Photo by H. Krisp, through Creative Commons.

Lissotriton montandoni, formerly *Triturus montandoni* (Carpathian Newt, Salamandridae)

This newt, also known as Montadon's Newt (Figure 102), lives in the Carpathian and Tatra Mountains of Europe, where it makes use of streams (Frost 2011), but also forest habitats rich in mosses (Marc P. Hayes, pers. comm. 26 March 2011). Like ***L. helveticus***, it tolerates acid more than most other amphibians, permitting it to occupy a wider range of habitats.

Figure 102. ***Lissotriton montandoni***, a moss dweller in European forests. Photo by Maciej Pabijan, through Creative Commons.

Lissotriton vulgaris, formerly *Triturus vulgaris* (Smooth Newt, Salamandridae)

The **Smooth Newt** (Figure 103) has pages of Latin synonyms and a good share of English names. It occurs in Europe in the British Isles and western France west through southern Norway and southern Finland to the Urals and south to the northern Balkans, northwestern Turkey, and Kazakhstan (Frost 2011). Forests are critical to its existence, but it can occur in meadows and shrub land where forests existed previously, and even occurs in gardens, parks, and fields (AmphibiaWeb 2009d). In the steppe zone it is present in wooded river valleys. In Northern Ireland, this species is legally protected, but it is listed as a species of least concern worldwide (IUCN 2010b).

Figure 103. ***Lissotriton vulgaris***, the **Smooth Newt**. Photo by Andreas & Christel Nöllert, with permission.

Newts are not common among mosses, with adults needing a place to swim, but peatlands with open water seem suitable for some. In Ireland, the Smooth Newt (***Lissotriton vulgaris***; Figure 103) prefers the moist habitat of peatlands (Peatlands 2009). After courtship and mating, the female gathers the sperm packets and lays her eggs on aquatic plant leaves that she rolls around the sticky eggs, thus necessitating peatlands that have open water.

This species is rapidly disappearing. Kinne (2006) attempted to determine factors that would improve its habitat and foster greater survival. He determined that the terrestrial phase would hide, especially in the daytime, under mosses, as well as rotting wood, roots of trees and bushes, log piles, and earth holes. When this species was maintained in a terrarium, it chose mosses for its overwintering habitat. There seems to be no documentation of its overwintering activities among mosses in nature.

Notophthalmus viridescens (Eastern Newt, Salamandridae)

This species of newt (Figure 104-Figure 106) is widespread in the eastern USA and into the Midwest (Hunsinger & Lannoo 2011). Its life cycle is unusual, taking it to a variety of habitats. The eggs (Figure 104) are laid in streams, where the larvae develop. Juveniles migrate to land where they may spend 2-7 years in the red eft stage (Figure 105. As mature adults (Figure 106), they are amphibious, spending most of their time in water, but also traversing the land.

Figure 104. Eggs of ***Notophthalmus viridescens***. Photo by Tom Murray, with permission.

Figure 105. Terrestrial red eft stage of the **Eastern Newt**, ***Notophthalmus viridescens***, displaying warning coloration and Muellerian mimicry that announce its toxic skin. Photo by Janice Glime.

Figure 106. Aquatic adult stage of **Eastern Newt**, ***Notophthalmus viridescens***. Photo by Janice Glime.

The eft and adults both make use of mosses for cover, as well as a variety of other cover types (leaves, branches, logs, rocks, grass) (Roe & Grayson 2008). The bright orange coloration of the red eft contrasts sharply against the green bryophytes, but acts as a warning coloration to ward off predators who could have a bad experience with the toxins in the skin (Brodie 1968). The brightly colored efts are more than 10X as toxic as the adults. Only 0.005 cc of eft back skin killed white mice in 10 minutes.

Salamandra salamandra (European Fire Salamander, Salamandridae)

European Fire Salamanders occur in central and southern Europe, from the Iberian Peninsula to Iran and North Germany to North Africa (Kuzmin 1999), mostly at altitudes of 400-1000 m asl (Wikipedia: Fire Salamander 2011). In the Balkans and Spain, they can be at even higher altitudes. Of these, ***Salamandra salamandra*** (Figure 107-Figure 109) is the best known species, living in deciduous forests in hilly areas. Its abundance classifies it as a species of least concern (IUCN 2010b). Although its primary habitat is among fallen leaves, it also lives on mossy tree trunks (Wikipedia 2011d).

Figure 107. ***Salamandra salamandra*** on a mossy rock. Photo by Marek Szczepanek, through Wikimedia Commons.

Figure 108. ***Salamandra salamandra*** on a wet day in the Harz National Park in central Germany. This colorful salamander is hiding in a minicave made by tree roots. The mosses are ***Schistostega pennata*** and ***Atrichum undulatum***. Photo by Katja Reichel, with permission.

This species gets its English name of fire not from its yellow spots, but from its behavior (Wikimedia: Fire Salamander 2011). Adults often hide in crevices in logs. When the logs are used as fire wood, the heat drives them from their hiding places and a number of them may appear "from the flames." Hence, they have earned the name of Fire Salamander.

As Klaus Weddeling pointed out on Bryonet (26 March 2011), the adults of ***Salamandra*** species are completely terrestrial, using terrestrial habitats even for spawning, having no need for spawning waters any more. Eggs are developed internally and larvae are deposited into the water as they "hatch" (Manenti *et al*. 2009; Wikipedia: Fire Salamander 2011). Adult life spans are known up to 50 years.

You might ask why this salamander has such a bright black and yellow coloration, thus advertising its presence (Figure 109). This is one of the **warning color** combinations, also seen in a number of species of bees, butterflies, and snakes. And yes, this is a poisonous species. But many salamanders are poisonous when consumed. This one is, however, one of the most, perhaps the most, poisonous (Mebs & Pogoda 2005). Its poison glands are concentrated around its head and are usually associated with the colored spots. When disturbed, it assumes a defensive posture and actually sprays, at high velocity (>3 m s^{-1}), defensive alkaloid poisons and **salamandrin** (Brodie & Smatresk 1990; Oracle Thinkquest 2000). **Salamandrin** is a strong alkaloid neurotoxin that usually causes convulsions (Oracle Thinkquest 2000; Wikipedia: Fire Salamander 2011), hypertension, and hyperventilation in all vertebrates (Wikipedia: Fire Salamander 2011). However, it is only dangerous if swallowed, thus not dangerous to humans, but washing one's hands after handling it is highly advisable (Oracle Thinkquest 2000). The secretions probably do double duty in protecting against bacteria and fungi (Wikipedia: Fire Salamander 2011).

Figure 109. ***Salamandra salamandra*** on a bed of mosses, in plain view, advertising its warning coloration of black and yellow. Photo by Iocopo Buttini, through Creative Commons.

Triturus cristatus (Great Crested Newt, Salamandridae)

This species (Figure 110), with at least ten English names, occurs in northern and middle Europe to the Alps, westward to middle and eastern France, and eastward to central Russia (Frost 2011). This species is diminishing, despite considerable protection of its habitats in many countries in Europe.

Figure 110. The **Great Crested Newt**, ***Triturus cristatus***. Photo by Milan Kořínek, with permission.

Müllner (2001) found a distinct preference for forested sites over grassland, attributing this to increased structural diversity that offered better shelter and higher humidity. In the highland and transitional peatlands of Poland, ***Triturus cristatus*** (Figure 111) inhabits the peatlands. In their land phase, the newts hide in the daytime, using stones, mosses, dead or rotting wood, tree roots, shrubs, log piles, and holes to hide in or under (Kinne 2006). In Europe this **Great Crested Newt** (***Triturus cristatus***; Figure 110-Figure 111) uses mossy habitats from June until March (Klaus Weddeling, Bryonet 26 March 2011). In winter, the adult newts move to land where they hide in mosses and moist grasses (Kinne 2006).

During breeding season, peat mosses may again become important, but in the water. Dag Dolmen (pers. comm. through Karen Thingsgaard 4 April 2011) of NTNU The Museum, Trondheim, Norway, advised me that both ***Triturus cristatus*** (Figure 110-Figure 111) and ***Lissotriton vulgaris*** (Figure 103) often attach eggs to ***Sphagnum*** (Figure 21) in the ponds where they breed.

This species seems to be rapidly disappearing, largely due to disappearance of its habitat (UK Biodiversity Action Plan 1995). This newt was fairly common in Europe and has been protected by law in England and elsewhere in Europe (HCT 2009), including prohibition of habitat destruction. Nevertheless, both its terrestrial habitat and ponds needed for its young are disappearing rapidly (AmphibiaWeb 2009b). Protected peatlands may be its last holdout.

Global warming is also likely to impact this species by changing the sex ratio (Wallace & Wallace 2000). At temperatures of 18-24°C the sex ratio is generally 1:1. At higher temperatures, the population develops more males than females, whereas at lower temperatures than 18°C, the number of females increases significantly. Thus, at higher temperatures one might expect a lower reproductive rate due to the smaller number of females.

Figure 111. The **Great Crested Newt**, ***Triturus cristatus***. Photo from Wikimedia Commons.

This newt seems to be one of the species that utilizes the moist mosses during migrations. Stein (1938) observed "great numbers" near Sunderland, Massachusetts, USA, during their migration toward a pond. Many were on the moist mossy bank. As they climbed out of the stream, they travelled along the projecting mosses toward the top of a waterfall. Stein was able to collect over 1000 individuals without exhausting the population. At the very end of their journey the newts had to ascend a dam with a perpendicular wall. It seems that the mosses permitted them to maintain a foothold against the force of the water.

Importance of the Bryophyte Amphibian Community

The bryophytes not only support large amphibians and reptiles like green frogs and rattlesnakes, but more importantly, they provide critical habitat for a number of smaller amphibians and reptiles. Araujo (1999), working in Portugal, concluded that these small amphibians and reptiles may be better indicators of biodiversity than the larger, more conspicuous species. That suggestion is even more applicable in the tropics among the arboreal bryophyte fauna.

Salamanders may play a much greater role in the ecosystem than most of us realize (Conniff 2014). Conniff considers them to be at least one of the top predators in North American forests. In many locations, they have a high abundance and eat a lot. He reports that an average salamander eats 20 ants, 2 flies or beetle larvae, 1 adult beetle, and half a springtail in a single day. But this is an ecosystem, and nothing acts alone. Their food consists almost entirely of shredding invertebrates – those organisms that shred and eat the leaf litter. And when these shredders eat, they release carbon from the leaves, carbon that comprises 47.5% of the litter. When the shredders are eaten by the salamanders, less carbon is released to the atmosphere.

To assess the importance of salamanders in the carbon cycle, Dr. Hartwell H. Welsh Jr., a herpetologist at the United States Forest Service research station in Arcata, California, and Dr. Michael L. Best, currently at the College of the Redwoods in Eureka, California, built exclosures that permitted free access to invertebrates but kept salamanders out of half of them (Conniff 2014). The results – fly and beetle larvae and adult beetles and springtails declined significantly when in enclosures with salamanders. Welsh and Best calculated that the density of salamanders in their study would account for 179 pounds (81.2 kg) of carbon per forest acre being stored in the soil instead of contributing to atmospheric gases that affect global climate.

The small size and lack of lungs in most salamanders translates to a small caloric need. This permits them to eat really small invertebrates that provide insufficient calories for birds and mammals. Bryophytes contribute part of the habitat where many of these salamanders reside.

Summary

Bryophyte-dwelling terrestrial salamanders, particularly arboreal ones, are typically slender with short legs, presumably making movement within the moss mat easier. Terrestrial life cycle adaptations are essential. Egg construction requires tradeoffs among need for gas exchange, need for mechanical support, same-species sperm attraction, other species sperm avoidance, heat conservation or cooling, predator defense, moisture retention, UV light protection, prevention of polyspermy, and protection from bacteria and fungi. Terrestrial eggs are turgid compared to aquatic eggs, usually have a tough outer layer, and may have pigments. Parental care of eggs helps to minimize bacteria and fungi. Eggs may hatch into tadpoles, but many hatch directly into young salamanders, skipping the larval stage.

Many undescribed species of tiny salamanders most likely lurk among the mosses in the tropical forests. Those that are known are limited in distribution and are threatened by habitat loss. In Costa Rica, the moss salamander ***Nototriton*** and the climbing salamander ***Bolitoglossa*** can be found in such habitats, and in Mexico ***Cryptotriton*** occupies bryophytes in the cloud forest. These three genera are tiny and seem to be moss specialists, with large eggs, long development times, and no larval stages. In Guatemala, the similarly adapted ***Dendrotriton cuchumatanus*** may occupy moss mats. ***Oedipina*** species, a Central American group, may live on the ground or be arboreal, using bryophytes for moisture and cover.

In the temperate zones, old growth forests are likely to have more developed bryophyte communities than younger forests. Bryophyte growths are often well developed in old growth, and small amphibians can find refuge from desiccation and predation and in some cases use them as an oxygen source. In old-growth forests of northern California and southwestern Oregon, moss dwellers include species of ***Batrachoseps***, ***Rhyacotriton***, and ***Plethodon***. The wandering salamander ***Aneides vagrans*** seems to be dependent on mosses among the coast redwoods. ***Aneides vagrans*** salamanders benefit from the photosynthetic oxygen produced by the bryophytes, while remaining moist among their masses. They also use tunnels made by rhizomes and roots of the fern *Polypodium scouleri*, which seems to depend on the bryophytes to develop its gametophytes successfully.

Asia has only one Plethodontid species; Europe has one genus, of which only ***Speleomantes supramontis*** has known bryophyte associations.

North American streams and springs can have species of ***Eurycea*** among the bryophytes, especially on streambanks.

Peatlands support salamanders and newts, including ***Eurycea*** species (lined salamanders), ***Necturus punctatus*** (Dwarf Waterdog), ***Lissotriton vulgaris*** (Smooth Newts), ***Triturus cristatus*** (Great Crested Newt), ***Notophthalmus viridescens*** (Eastern Newt), ***Ambystoma laterale*** (Blue-spotted Salamander), and ***Desmognathus fuscus*** (Northern Dusky Salamander).

The bryophyte amphibian fauna, especially the small species, are good indicators of biodiversity.

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Bryophyte-dwelling Salamander Checklist

species	distribution	habitat	bryophyte use: mossy habitats	under or in mosses	nests	aestivation	hibernation	foraging	source
Hynobiidae									
Hynobius tokyoensis Tokyo Salamander	Japan	forest floor		x					Kusano & Miyashita 1984
Salamandrella keyserlingii Siberian Salamander	northern Asia	wet forest of taiga		x		x	x		Potapov 1993; Hasumi *et al*. 2009
Ambystomatidae									
Ambystoma laterale Blue-spotted Salamander	western N. Amer.	deciduous & mixed forest		x					LeClere 2011
Ambystoma maculatum Spotted Salamander	eastern N. Amer.	peatlands	x						Amphibians: Tulula Wetlands
Ambystoma jeffersonianum Jefferson Salamander	central E. N. Amer.	forest floor & wetlands	x						Freda & Dunson 1986
Plethodontidae									
Plethodon teyahalee Southern Appalachian Salamander	high elev S. Appalachians	decid. forest & peatlands	x						Amphibians: Tulula Wetlands
Plethodon serratus S. Red-backed Salamander	SE USA	forest floor			x				Aaradema 1999
Plethodon nettingi Cheat Mountain Salamander	Cheat Mtn, WVa, USA	red spruce forest floor		x	x		?		Pauley 1985
Plethodon cinereus E. Red-backed Salamander	NE USA, SE Canada	peatlands, forest floor	x	x					Hughes *et al*. unpubl.
Plethodon dorsalis Northern Zigzag Salamander	lower midwest USA	rocky slopes		x					Ferguson 1961
Plethodon welleri Weller's Salamander	mtns of TN to VA, USA	conifer logs		x					Organ 1960
Plethodon elongatus Del Norte Salamander	SW OR to NW CA	old growth forest	x						Welsh & Lind 1995
Plethodon idahoensis Coeur d'Alene Salamander	northern Rocky Mtns	seeps, springs, waterfalls		x					Wilson 1990; Dumas 1957
Plethodon vandykei Van Dyke's Salamander	Washington, USA	coniferous forest floor		x					Slater 1933
Plethodon larselli Larch Mountain Salamander	Columbia R Gorge USA	talus slopes		x					Burns 1962
Plethodon glutinosus Northern Slimy Salamander	eastern USA	bottomland			x				VA Dept Game Inland Fish 2011
Plethodon richmondi Southern Ravine Salamander	eastern USA	ravines, hillsides, mesic forest			x				VA Dept Game Inland Fish 2011
Plethodon metcalfi Southern Gray-cheeked Salamander	S Blue Ridge Mtns USA	forest floor	x						Organ 1958
Plethodon jordani Red-cheeked Salamander	Great Smoky Mtns	spruce-fir forest	x	x					King 1939
Plethodon stormi Siskiyou Mountains Salamander	S Oregon, N California	talus		x					Gary Nafis 28 April 2011
Plethodon asupak Scott Bar Salamander	S Oregon, N California	talus		x					Gary Nafis 28 April 2011
Gyrinophilus porphyriticus Spring Salamander	eastern N Amer	mature hdwd forest	x						Ferguson 1961
Pseudotriton ruber Red Salamander	eastern USA	tamarack wetlands	x	x			x		Burger 1933
Hemidactylium scutatum Four-toed Salamander	eastern N Amer	mature forest, peatlands	x	x	x				Gilbert 1941; Wood 1955; Petranka 1998; Harris 2009
Stereochilus marginatus Many-lined Salamander	Atlantic coastal plain, USA	wetlands	x	x	x				Blanchard 1934; Duellman & Trueb 1986

Desmognathus fuscus Northern Dusky Salamander	eastern N Amer	forest streams			x				Burger 1933; Hom 1987
Desmognathus ochrophaeus Alleghany Mountain Dusky	Appalachian Mtns, USA	seeps	x	x	x				Tilley 1972; Mushinsky 1976
Desmognathus monticola Seal Salamander	central & S Appalachians	streams			x				Camp & Tilley 2011
Desmognathus santeetlah Santeetlah Dusky Salamander	SW Blueridge Mtns	headwater streams			x				Beachy 1993
Desmognathus aeneus Seepage Salamander	SE USA	seepage in deciduous forest			x				Martof & Humphries 1955; Jones 1981
Desmognathus wrighti Pygmy Salamander	S Nantahala Mtns, NC, USA	deciduous & spruce-fir forest		x					Hining & Bruce 2005
Desmognathus quadramaculatus Black-bellied Salamander	Appalachian Mtns, USA	cool steep streams, peatlands	x						Amphibians: Tulula Wetlands
Desmognathus ocoee Ocoee Salamander	SW Blue Ridge; Piedmont Physiogr	peatlands; streams	x		x				Amphibians: Tulula Wetlands
Phaeognathus hubrichti Red Hills Salamander	Alabama coastal plain USA	forest						x	Gunzberger 1999
Ensatina eschscholtzii Monterey Ensatina	W N Amer	mossy ground		x					Gnaedinger & Reed 1948
Hydromantes brunus Limestone Salamander	Mariposa Co, CA, USA	limestone rock		x					Gorman 1954
Hydromantes shastae Shasta Salamander	Shasta Co, CA, USA	limestone rock		x					Gorman & Camp 1953
Hydromantes ambrosii	Italy	forest, cliffs	x						Andreas Nöllert, pers. comm. 22 January 2016
Nototriton abscondens	Costa Rica	premontane & humid montane	x	x	?				Taylor 1954
Nototriton guanacaste Guanacaste Moss Salamander	Costa Rica	cloud forest	x	x	?				Tosi 1969; Good & Wake 1993
Nototriton picadoi Picado's Moss Salamander	Costa Rica	cloud forest	x	x	x			?	Good & Wake 1993; Savage 2002
Nototriton saslaya	Nicaragua	cloud forest	x	x	x				ZipcodeZoo.Com 2008c
Nototriton gamezi Monteverde Moss Salamander	Costa Rica	rainforest	x	x	?				García-Paris & Wake 2000
Nototriton ricardi Richard's Salamander	Costa Rica	rainforest	x	x	?				Good & Wake 1993
Nototriton tapanti Tapanti Moss Salamander	Costa Rica	humid premontane	x	x	?				Savage 2002
Nototriton barbouri Yoro Salamander	Honduras	lower montane forest floor	x	x	?				ZipcodeZoo.Com 2008b
Chiropterotriton chiropterus Common Splayfoot Salamander	Veracruz, Mexico	arboreal	x						IUCN 2010
Cryptotriton alvarezdeltoroi Alvarez del Toro's Salamander	Chiapas, Mexico	cloud forest		x					Papenfuss & Wake 1987
Cryptotriton monzoni Monzon's Hidden Salamander	Zacapa, Guatemala	cloud forest	x						IUCN 2010
Oedipina poelzi Quarry Worm Salamander	Costa Rica	moist montanes	x	x	?				Wake 1987
Oedipina uniformis Cienega Colorado Worm Salamander	Costa Rica; Nicaragua	arboreal	x	x					Wake 1987
Oedipina pseudouniformis Cienega Colorado Worm Salamander	Costa Rica & Nicaragua	arboreal		x					Brame 1968
Oedipina elongata Central American Worm Salamander	Mexico to Honduras	soil & wood channels	x						IUCN 2010
Oedipina gracilis Long-tailed Worm Salamander	Costa Rica; Panama	moist litter & burrows	x						Leenders 2001
Oedipina pacificensis	SW Costa Rica & Panama	lowlands	?	?					Frost 2011
Oedipina carablanca Los Diamantes Worm Salamander	Costa Rica	lowlands		x					Kubiki 2011
Bolitoglossa obscura Tapanti Giant Salamander	Costa Rica & Panama	arboreal		x					Wake 1987
Bolitoglossa diminuta Quebrada Valverde Salamander	Costa Rica	arboreal		x					Wake 1987

Bolitoglossa sombra Shadowy Web-footed Salamander	Costa Rica; Panama	arboreal		x					Hanken *et al*. 2005
Bolitoglossa robusta Robust Mushroom-tongue Salamander	Costa Rica; Panama	ground in lower montane		x					Hanken et al. 2005
Bolitoglossa diaphora	Honduras	cloud forest	?						McCranie & Wilson 2009
Bolitoglossa rostrata Longnose Mushroomtongue Salamander	Guatemala; Mexico	arboreal high mountain	x						Raffaëlli 2011
Bolitoglossa longissima	Honduras	ground & arboreal		x					McCranie & Cruz 1996
Bolitoglossa mexicana Mexican Mushroomtongue Salamander	Veracruz, Mexico to Honduras	arboreal in rainforest	x						IUCN 2010
Bolitoglossa subpalmato La Palma Salamander	Costa Rica	moist montane		x	x				Robinson 1976; Wake 1987
Bolitoglossa marmorea Crater Salamander	Costa Rica; Panama	moist montane	x						Wake *et al.* 1973
Bolitoglossa hartwegi Hartweg's Mushroomtongue Salamander	Guatemala; Mexico	moist montane forest	?						IUCN 2010
Bolitoglossa helmrichi	Guatemala	arboreal in cloud forest	?						IUCN 2010
Bolitoglossa lincolni Lincoln's Mushroomtongue Salamander	Guatemala; Mexico	forest, somewhat arboreal	?						IUCN 2010
Bolitoglossa rufescens Northern Banana Salamander	Mexico to Honduras	bromeliads in wet forest	?						McCoy 1990
Bolitoglossa suchitanensis	Guatemala	humid deciduous forest	x	x					Campbell *et al*. 2010
Bolitoglossa xibalba	Guatemala	wet montane forest	x	x					Campbell *et al*. 2010
Thorius dubitus Acultzingo Pigmy Salamander	Veracruz & Puebla Mexico	pine-oak cloud forest		x					Hanken 1983; Wake 1987
Pseudoeurycea juarezi Juarez Salamander	Oaxaca, Mexico	cloud forest	x	x					IUCN 2010
Pseudoeurycea rex Royal False Brook Salamander	western Guatemala	arboreal		x					Wake 1987
Pseudoeurycea scandens Tamaulipan False Brook Salamander	Mexico	arboreal		x					Wake 1987
Pseudoeurycea werleri Werler's False Brook Salamander	Veracruz Mexico	arboreal; rainforest & cloud forest		x					IUCN 2010
Pseudoeurycea lineola Veracruz Worm Salamander	Veracruz Mexico	oak-pine forest	x	?					Frost 2011
Pseudoeurycea orchileucos Sierra de Juárez Worm Salamander	Oaxaca Mexico	cloud forest	x						IUCN 2010
Pseudoeurycea orchimelas San Martin Worm Salamander	Veracruz Mexico	litter	?						IUCN 2010
Nyctanolis pernix Nimble Long-limbed Salamanders	Mexico; Guatemala	humid pine-oak & cloud forest		x					Elias & Wake 1983; Stuart *et al.* 2008
Dendrotriton cuchumatanus Forest Bromeliad Salamander	Guatemala	oak forest		x					ZipcodeZoo.Com 2008a
Batrachoceps wrighti Oregon Slender Salamander	NW USA	temperate forest	x						Storm 1953; Bury 2011
Aneides vagrans Wandering Salamander	N coastal CA, USA; BC, Canada	redwood forest		x					Sillett 1995; Spickler *et al*. 2006
Aneides aeneus Green Salamander	mid - E USA	boulders & rock cliffs		x				x	Gordon 1952; Lee & Norden 1973; Canterbury 1991
Rhyacotriton olympicus Olympic Torrent Salamander	N CA, SW OR, USA	old growth forest	x	x					Slater 1933; Welsh 1990
Rhyacotriton cascadae Cascade Torrent Salamander	Cascade Mtns, USA	riffles; underground streams	x	?					Frost 2011
Rhyacotriton variegatus Southern Torrent Salamander	Cascade Mtns CA; OR USA	humid forest headwaters	x	?					Welsh & Lind 1996
Karsenia koreana Korean Crevice Salamander	Korea	rock slides in young forest	x						Wake 2005
Speleomontes supramontis Supramonte Cave Salamander	east Sardinia, Italy	caves; oak forest		x					Nöllert & Nöllert 1992
Eurycea wilderae Blue Ridge Two-lined Salamander	S Appalachian Mtns	peatlands	x	x					Amphibians: Tulula Wetlands

Eurycea guttolineata Three-lined Salamander	SE USA	swampy areas	x	x					Amphibians: Tulula Wetlands
Eurycea multiplicata Many-ribbed Salamander	Ouichita Mtns, USA	limestone streams						x	Dundee 1947
Eurycea tynerensis Oklahoma Salamander	Ozark Plateau, USA	streams, springs, seeps		x					Dundee 1947
Eurycea bislineata Northern Two-lined Salamander	E USA	peatlands, small streams	x	x	x				Jobson 1940; Richmond 1945; Bahret 1996
Eurycea lucifuga Cave Salamander	mid-S Appalachian Mtns, USA	limestone caves, springs		x					Bragg 1955
Proteidae									
Necturus punctatus Dwarf Waterdog	SE coastal plain, USA	hardwoods		x					Neill 1948
Salamandridae									
Notophthalmus viridescens Eastern Newt	Eastern USA	streams; forest floor		x					Roe & Grayson 2008
Salamandra salamandra European Fire Salamander	Central & S Europe	deciduous forest		x					Wikipedia: Fire Salamander 2011
Euproctus platycephalus Sardinian Mountain Newt	Sardinia, Italy	rivers		x		x	?		Michael Lüth (Bryonet 26 March 2011)
Calotriton asper Pyrenean Brook Salamander	Pyrenees	streams & lakes		x					Michael Lüth (Bryonet 26 March 2011)
Triturus cristatus Great Crested Newt	Europe	forest & peatlands	x	x	x	?	x		Kinne 2006
Taricha torosa California Newt	Coastal California, USA	epiphytic mosses; dry forest	x	x					Gary Nafis, 27 Apr 2011; Edmund Brodie, 7 Jun 2011
Lissotriton helveticus Palmate Newt	W Europe	peatlands	x						Wikipedia: Palmate Newt 2011
Lissotriton montandoni Carpathian Newt	Carpathian & Tatra Mtns	forest; rivers	x						Marc Hayes pers. comm. 26 March 2011
Lissotriton vulgaris Smooth Newt	Europe	forest	x						Peatlands 2009
Lissotriton boscai Bosca's Newt	W Iberian Peninsula	shallow ponds; peatlands	x	x					AmphibiaWeb: *Lissotriton boscai* 2000

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CHAPTER 15
REPTILES

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CHAPTER 15
REPTILES

Figure 1. A hatchling Spotted Turtle, ***Clemmys guttata***, traversing mosses near its wetland home. Photo courtesy of Steve Soldan, Woodlot Alternatives.

Vertebrates

A chipmunk scampers across a log. A bird builds a nest in the tree above. A toad awakens from its winter nap. A bear gathers grubs to fill its empty gut. These and many more animals have interacted in secret ways with the bryophytes of the forest, dispersing them, using them for nesting and bedding, escaping the cruel crystals of ice by hiding beneath them, eating the tiny invertebrates among them. Reptiles are no exception, using them for nesting sites and hibernacula. So many animals use the mosses in so many untold ways. And surely many more secrets remain to be discovered.

With reptiles I must face a capitalization dilemma. Whereas only proper nouns in plant names are generally capitalized, reptiles, like birds, have official English names that are capitalized. Hence, I shall be inconsistent and capitalize these names, although it bothers me, and I will not capitalize those of plants.

Order Testudines – Turtles

The moist environs of the ***Sphagnum*** peatlands (Figure 2) make ideal habitats for aquatic turtles like the Spotted Turtle ***Clemmys guttata*** (Figure 1; Wright 1919; Folkerts & Skorepa 1967) and the Painted Turtle ***Chrysemys picta*** (Krawchuk & Brooks 1998; Rydin & Jeglum 2006) and their eggs (Figure 3).

Figure 2. Viru raised bogs, Estonia. Photo by Lysy, through Creative Commons.

Clemmys guttata (Spotted Turtle, Emydidae)

Clemmys guttata (Figure 1) is globally endangered (IUCN 2011). In New York, USA, ***Clemmys guttata*** is rare in ***Sphagnum*** peatlands (Figure 2), particularly those suitable for cranberries. But in Pennsylvania, USA, it has been known to congregate on the peatlands in May and June (Netting 1936). In the Georgian Bay, Ontario, Canada these animals hibernate in the ***Sphagnum*** swamps from September until April (Litzgus & Brooks 2000). Litzgus *et al*. (1999) found that the turtles actually have two types of hibernation niches in Georgian Bay: ***Sphagnum*** hummocks with cave-like spaces created by tree roots (Figure 4) and rock caverns at the shores of the swamps (Figure 5), both requiring ***Sphagnum*** peatlands. The stable temperature of the hummocks protects the turtles from freezing, permitting them to maintain a body temperature of 0.3-3.9ºC at the northern limits of their range, despite air temperatures that reach -35ºC.

Figure 3. Eggs of the Painted Turtle, ***Chrysemys picta***, exposed from their underground home. Photo by John White, with permission.

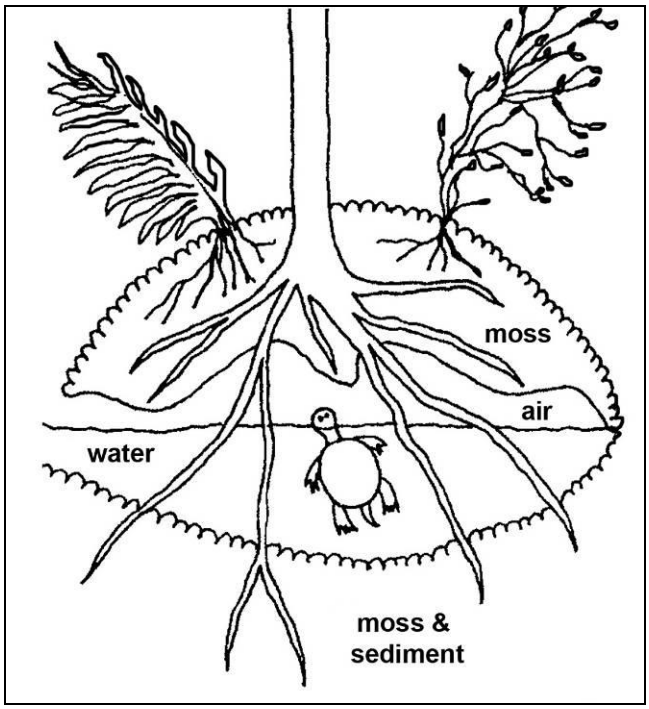

Figure 4. Spotted Turtle, ***Clemmys guttata*** in air pocket beneath moss hummock, with body submersed and head above water. Redrawn from Litzgus *et al*. 1999.

Clemmys guttata (Figure 1, Figure 6-Figure 7), a shallow-water turtle, prefers a soft bottom substrate with both submerged and emergent vegetation. Therefore, boggy ponds, fens, and ***Sphagnum*** (Figure 2) seepages provide suitable habitats. In the spring the turtles travel to seasonal pools, then search for suitable nesting sites (Milam & Melvin 2001). Babcock (1938) reported finding nests among damp logs and moss. Nesting sites include ***Sphagnum***, among others (Hunter *et al*. 1992; Ernst *et al*. 1994). Dick Andrus (pers. comm.) found "a bunch of little ones buried in a ***Sphagnum*** hummock (Figure 13) once on Long Island." In summer, the turtles frequently wander onto land between their wetlands, where they may aestivate for weeks at a time (Figure 6) (Ernst *et al*. 1994; Harding 1997, 2002). They seldom wander very far; turtles in a Massachusetts, USA, study travelled an average maximum distance of 265 m from their winter hibernacula, although some travelled as far as 1025 m (Milam & Melvin 2001).

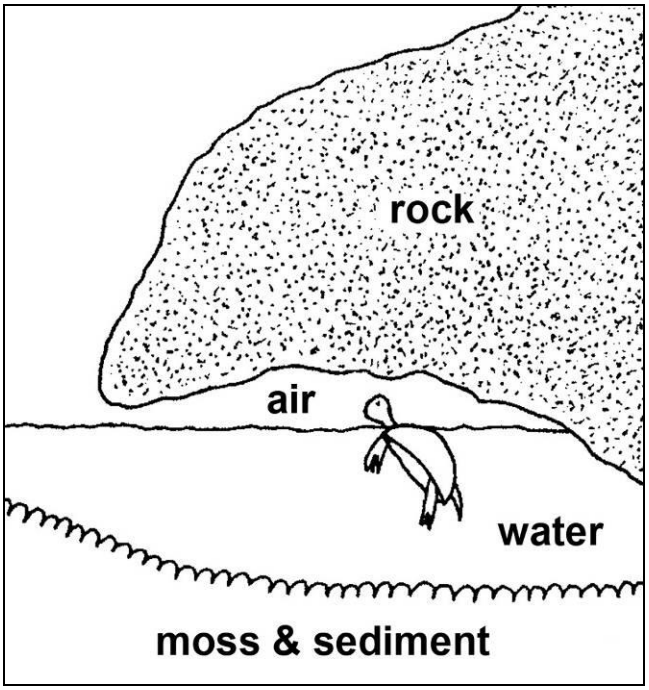

Figure 5. Relationship of hibernating Spotted Turtle, ***Clemmys guttata***, in an air pocket under the safety of a rock. Redrawn from Litzgus *et al*. 1999.

Milam and Melvin (2001) demonstrated that even though these turtles do not wander far from their winter hibernacula in the peatlands, they wander farther than the buffer protected by the Massachusetts' Wetlands Protection Act. The act provides buffers of 30 and 60 m in uplands around the wetlands, but in this study, females nested 75 – 312 m from the wetlands and aestivated at distances up to 412 m. To maintain turtle populations, larger surrounding areas will need to be preserved along with the wetlands.

But not all Spotted Turtles spend their lives in association with peatlands. In Georgian Bay, Ontario, Canada, one island population of Spotted Turtles placed their nests in shallow soil of exposed Precambrian Shield rock outcrops (Litzgus & Brooks 1998). Although there were patches of lichens and mosses among the rocks, it is doubtful that these were large enough to provide habitat for the turtle. On the other hand, the low-lying ***Sphagnum*** interspersed among the rocks may have been essential for

maintaining hydration and could provide a suitable nesting site. The authors speculated that the rocks provided the warmth needed for incubation. Milam and Melvin (2001) found that the dominant ground cover in the habitat of spotted turtles in their Massachusetts, USA, study was ***Sphagnum*** spp, although they only mentioned three (out of 19) hibernacula in abundant ***Sphagnum***, in an area of shrub wetlands where there was a slow current of shallow water.

Figure 6. This sleepy-looking fellow is a hatchling Spotted Turtle, ***Clemmys guttata***, and he is wearing a radio transmitter. Photo courtesy of Steve Soldan, Woodlot Alternatives.

Figure 7. ***Clemmys guttata*** sunning on a rock. Photo by S. Duranceau, through Wikimedia Commons.

Chrysemys picta (Painted Turtle, Emydidae)

Although the Painted Turtle (***Chrysemys picta***; Figure 8-Figure 10) is common in ponds, lakes, marshes, and other forms of slow-moving water with a muddy bottom, it can also be found in fens and bogs (Rydin & Jeglum 2006) – habitats where bryophytes predominate. It has in interesting courtship in which the male uses his long claws, palms facing outward, to stroke the female on the cheeks and neck (Wikipedia 2011b). Females lay the eggs in several events in sandy soil exposed to the sun, preferably with open water within 200 m. The nest is shallow (5-11 cm deep), but doesn't need to protect the next generation over the winter. Instead, the eggs hatch in 72-80 days and the independent young dig their way out.

Figure 8. ***Chrysemys picta*** on moss-covered roots. Photo by John White, with permission.

Figure 9. ***Chrysemys picta*** sunning on a log. Photo © Gary Nafis, with permission.

Figure 10. ***Chrysemys picta*** on its back, revealing the decorated plastron. Photo © Gary Nafis, with permission.

Winter is a dangerous season for the young turtles. Although they tolerate freezing down to -6ºC (Churchill & Storey 1992), contact with soil causes ice crystals to penetrate their integument when the soil is just below freezing (Packard *et al*. 2000). At temperatures below -2.5ºC, apparently these hatchlings increase their ability to tolerate cold as the winter continues, extending an initial survival of 3 days at -2.5ºC to survival for 11 days at that temperature (Churchill & Storey 1992). It appears that ingestion of nesting soil raises their temperature of crystallization by increasing their ice-nucleating activity and hence decreases their survival at winter temperatures in the field (Costanzo *et al*. 2003). This effect can last for a month and can account for greater survival of laboratory-

reared turtles that are deprived of these soil-derived ice-nucleating proteins.

The muddy pond or lake bottom provides a place for the adult turtles to hibernate during the winter, using the calcium and magnesium in their bones and shell to buffer the lactic acid produced by their anaerobic respiration (Storey & Storey 1990; Storey 1996; Jackson 2002). At the same time 40-45% of the lactic acid is stored into the bone and shell and remains there until the turtle ceases hibernation and once again obtains fresh oxygen. Along with a severe depression in metabolism, this mechanism, known only from turtles, permits the turtle to remain in anoxic hibernation for months at a time.

Like snakes, the turtles must bask in the sun to gain enough heat to digest their food (Wikipedia 2009). On the other hand, too much heat will kill them within minutes.

Glyptemys (formerly *Clemmys*) *muhlenbergii* (Bog Turtle, Emydidae)

The Bog Turtle, ***Glyptemys*** (= *Clemmys*) ***muhlenbergii*** (Figure 11), inhabits many of the same locations as the spotted turtle, so it is not surprising that hybrids exist (Ernst 1983). As the name implies, the Bog Turtle, also known as the cranberry turtle, lives largely in ***Sphagnum*** peatlands (Ashley 1948; Barton & Price 1955). (The term bog must be interpreted liberally because it is relatively recently that North Americans began using the narrower European definition of bog; previously, almost anything with ***Sphagnum*** was considered a bog.) The moist peat is most likely important in keeping the turtles hydrated. ***Clemmys*** (= *Glyptemys*) ***muhlenbergii*** (Figure 11) is the smallest of the turtles in North America (NRCS 2006). It has been diminishing in numbers due to over-collection and destruction of habitat. As early as 1918 Wright considered it to be disappearing due to destruction of peatlands. The northern population lives in the eastern United States from Massachusetts to Maryland; the southern population lives in southwestern Virginia, south to northern Georgia.

Their small size permits them to traverse peatlands through tunnels that at times afford them protection from predators – and human collectors. This secretive behavior makes them to be more rare than they really are. In a study of several ***Sphagnum*** peatlands in Pennsylvania and New Jersey, USA, Ernst *et al*. (1989) found that some Bog Turtle tunnels appeared to have been made by meadow voles (***Microtus pennsylvanicus***; Figure 12) and widened for use by the turtle. In fact, few of the tunnels appeared to be strictly the results of the labor of the turtles.

All things considered, one might think of these turtles as lazy inhabitants of peatlands. Carter *et al*. (2000) used threadspooling to determine their movements and found that 75% of their movements remained within 20 m. Only 2% of the movements took them more than 100 m. Hence, they seldom moved between wetlands, underscoring the importance of individual wetlands and the unlikelihood that restored wetlands will be easily recolonized by these turtles.

It appears that despite its common name of Bog Turtle, ***Glyptemys muhlenbergii*** (Figure 11) does not require peatlands. In Maryland, USA, turtles from two locations lived in wetlands dominated by low grasses and sedges in one area and by cattle and sheep pasture in the other (Morrow *et al*. 2001). Almost no ***Sphagnum*** (Figure 13) peat was present.

Figure 11. ***Glyptemys*** (=*Clemmys*) ***muhlenbergii***, the Bog Turtle. Photo by US Army Corps of Engineers, licensed under Wikimedia Commons.

Figure 12. The vole ***Microtus pennsylvanicus*** at entrance a tunnel. Photo by Daderot, through Creative Commons.

Figure 13. ***Sphagnum magellanicum*** hummock, a moist location for bog herps. Photo by James K. Lindsey, with permission.

Nevertheless, Bog Turtles do use ***Sphagnum*** (Figure 13) for basking and as a nesting site where eggs incubate for 42-56 days (NRCS 2006). Mating occurs in spring and nesting occurs from May to July (Smith 2006). These nests

generally are close to the hibernacula. Barton and Price (1955) describe a nest among ***Sphagnum*** (Figure 13) extending about 12 cm above the water surface with hatchlings emerging. Apparently the female had buried herself in the moss, deposited the eggs, and crawled out, allowing the mosses to close over behind her, camouflaging the eggs.

Although the turtles prefer to feed on slugs, worms, spiders, and insects, they will also eat mosses (NRCS 2006; Smith 2006). However, one must ask if this is an accidental consumption in an attempt to eat invertebrates.

Glyptemys (formerly *Clemmys*) *insculpta* (Wood Turtle, Emydidae)

The Wood Turtle, ***Glyptemys*** (=*Clemmys*) ***insculpta*** (Figure 14-Figure 15) seems to prefer open areas and cornfields to hemlock swamp with mosses (Kaufmann 1992). In a study in central Pennsylvania, only one turtle chose the hemlock forest that had a thick carpet of ***Sphagnum***. Was she the outcast, or did she have the sole privilege of staying in this damper habitat?

Figure 14. Wood Turtle, ***Glyptemys*** (=*Clemmys*) ***insculpta***. Photo by USGS, licensed as public domain.

Figure 15. ***Glyptemys insculpta*** among vegetation. Photo by Steve Silluzio, with permission.

Emydoidea blandingii (Blanding's Turtle, Emydidae)

In Nova Scotia, juveniles of Blanding's Turtle (***Emydoidea blandingii***; Figure 16) selected habitats with ***Sphagnum*** (Figure 13), sweet gale (*Myrica gale*), and leatherleaf (*Chamaedaphne calyculata*) (McMaster & Herman 2000). Butler and Graham (1995) found that hatchlings often sought refuge under ***Sphagnum*** in dry vernal pools. After a literature and field study, the U. S. Fish and Wildlife Service (2007) concluded that the best place to release hatchlings might be in beds of ***Sphagnum***.

Figure 16. Blanding's Turtle, ***Emydoidea blandingii***. Photo by Phil Myers, through Creative Commons.

Power *et al.* (1994) provided a plausible explanation for the choice of sphagnous habitats, among others. In their study of the Kejimkujik National Park in Nova Scotia, Canada, they found that they could predict the occurrences of this turtle by the color of the water. Within the park, the turtles would seek out highly colored bodies of water, typically small streams and lakes draining peatlands. In addition to data from 1572 captures (60 turtles), three turtles that left one body of water migrated through more lightly colored waters to settle in another location that was highly colored. Graham (1992) made similar observations on the preference for highly colored water in Maine, USA. These highly colored waters typically drain peatlands that provided the source of the coloration. Kerekes and Freedman (1989) indicated that these colored areas were high in secondary productivity, especially aquatic invertebrates, that would serve as a food source for the turtles. It is the same colored organic material coming from the peatlands that provides the food for this greater invertebrate productivity.

I have to wonder if the colored water of vernal pools in peatlands might offer another advantage. Packard *et al.* (2000) found that these turtles do not overwinter in the nests where they were born. They can survive to -6ºC, but that when they are in contact with frozen soil their integument is penetrated by ice crystals at temperatures barely below 0ºC. The freezing is fatal at temperatures below -2.5ºC. Since dark-colored water should absorb more heat than clear water, perhaps these colored ponds are a mechanism to keep them warm.

Chelydra serpentina (Snapping Turtle, Chelydridae)

A snapping turtle is not one that would come to mind as a moss eater. Those powerful jaws that one must avoid when trying to capture this large freshwater turtle don't suggest a diet of bryophytes. But Ralph Pope provided me with a picture that may represent snpping turtle feeding on ***Sphagnum capillifolium*** (Figure 17) – or was it those beetles we can see? The wide swath suggests to me it was eaten by something larger than a beetle.

Figure 17. ***Sphagnum capillifolium*** with middle portion eaten, lacking its capitula. This may have been done by the snapping turtle that was found nearby (dead!), or was it the two beetles on the right side of the picture? Photo by Ralph Pope, with permission.

Marine Turtles

At the risk of perpetuating a myth, I found an interesting reference to marine turtles that fed on mosses! Fritts (1981) reported that Dampier (1906) had found that the marine turtles on the Galapagos Islands and adjacent areas were "rank, fat, and fed on moss." Fritts considered it likely that these were Olive Ridley Turtles, based on their size and habits, but he also stated that Dampier had mentioned loggerhead turtles (***Caretta caretta***?, Cheloniidae; Figure 18) fed on moss and were rank. I doubt that the moss made them rank, and I have to wonder if it was true moss or another mosslike plant, like Spanish moss (a bromeliad) that also grows there.

Figure 18. ***Caretta caretta*** (Loggerhead Sea Turtle) swimming in a marine habitat. Photo by Ukanda, through Wikimedia Commons.

Testudo (Spur-thighed Tortoise, Testudinidae)

Serhat Ursavaş wrote to me that he saw a turtle [***Testudo*** (*graeca*) ***ibera***, Spur-thighed Tortoise or Greek tortoise; Figure 19] in the Kirzil Mountain National Park near Beysehir Lake, Turkey (1234 m asl). The overstory vegetation was *Pinus nigra* subsp. *pallasiana*, *Salix alba*, and *Populus tremula*. The turtle was eating a mixture of moss (***Calliergonella cuspidata***; Figure 20) and grass on very wet, muddy soil. When approached, it stopped eating.

This species is widespread in the Mediterranean, where it survives relatively dry conditions (Highfield 1992). It is a relatively large tortoise, with females reaching up to 30 cm. Typical food plants include vetches (*Vicia*), dandelions (*Taraxacum*), mallows (*Malva*), and numerous species of the legume family (Fabaceae).

Figure 19. ***Testudo*** (*graeca*) ***ibera*** eating the moss ***Calliergonella cuspidata*** and grass in a muddy field in Turkey. Photo by Serhat Ursavaş, with permission.

Figure 20. ***Calliergonella cuspidata*** in a wetland where the Spur-thighed Tortoise can eat it. Photo by Michael Lüth, with permission.

Dispersers

The Snapping Turtle (***Chelydra serpentina***, Chelydridae; Figure 21-Figure 23) is not thought of as a moss dweller and spends much of its time in the water. But it has a different relationship with bryophytes. It contributes to dispersal, at least for ***Riccia rhenana*** (Figure 22), dragging fragments from one place to another (McGregor 1961). Apical segments of these liverworts can survive two months of desiccation and five weeks embedded in ice, despite the death of older parts. My own experience with dispersal involved a Box Turtle (***Terrapene carolina***, Emydidae). My ***Conocephalum conicum*** (Figure 24) spread in my garden room when I had a Box Turtle, but not at any other time.

Figure 21. ***Chelydra serpentina*** (Snapping Turtle) on land, showing the algae growing on its back. Photo by Todd Pierson, with permission.

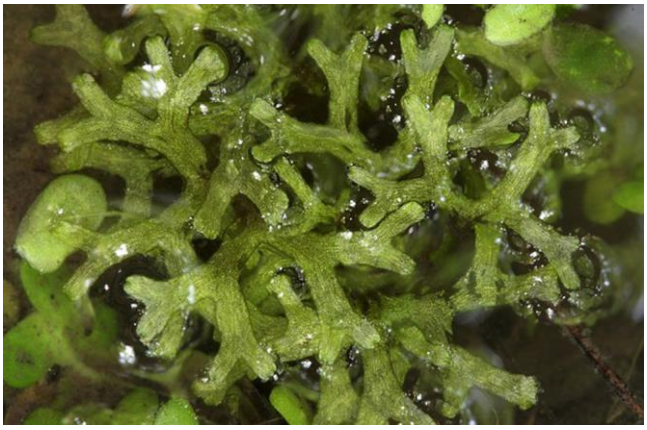

Figure 22. ***Riccia rhenana***, a species that is dispersed by the Snapping Turtle (***Chelydra serpentina***). Photo by Štěpán Koval, with permission.

Winter

Winter presents particular challenges for reptiles. Species in higher altitudes generally have better freezing survival than those of lower elevations (Storey 2006). Adults also are more freeze tolerant than juveniles. Live bearers have better long-term freezing survival than do egg bearers. And juveniles that hibernate in bogs go to greater depths than do adults. Thus, mosses help in the survival of at least some reptiles by providing insulation that keeps temperatures warmer than air temperatures in winter.

Figure 23. ***Chelydra serpentina*** (**Snapping Turtle**) on land, showing its huge feet and strong jaws. Photo by Todd Pierson, with permission.

Figure 24. ***Conocephalum conicum***, a liverwort that may be eaten by the Box Turtle (***Terrapene carolina***). Note the circular cut from the thallus. Photo by Janice Glime.

Order Squamata – Lizards

Lizards bring images of rocks, fence posts, and other dry habitats. But some include mosses as important habitat characteristics. Block and Morrison (1998) reported that ***Sceloporus*** (Figure 25) lizards in dry California oak woodlands were positively associated with mosses. Other lizards make rather unique uses of mosses.

Figure 25. ***Sceloporus magister*** in its typical rocky habitat where its disruptive coloration resembles rocks and lichens. Photo by Kalderi, through Wikimedia Commons.

Adaptations

Lizards are predominately terrestrial. There is one marine species and a few aquatic ones, including the Jesus Lizard (*Basiliscus plumifrons*), a basilisk lizard. Hence, adaptations to the bryophyte habitat do not necessarily differ from those of lizards in general – they are terrestrial adaptations.

Among the more common bryophyte-associated lizards are some members of the genus ***Anolis***. Whenever considering terrestrial adaptations, the life cycle is often a major factor, and ***Anolis*** seems to exemplify an extreme adaptation to its somewhat hazardous terrestrial life. Instead of the multiple-egg clutch size typical of other lizards, it has a clutch size of one! (Andrews & Rand 1974). This small number is, however, compensated by laying an egg at intervals of 1-2 weeks. This staggered and frequent production of eggs has several advantages: the female is able to produce larger eggs without a great increase in weight (light weight is important for escaping); the eggs each experience different weather conditions so that it is more likely that at least some will survive. With a generation time of only 4 months, this is a high reproductive potential.

The protection of the eggs is of paramount importance to reproductive success. Andrews and Sexton (1981) examined the water relations of eggs for *Anolis auratus* and ***Anolis limifrons*** (a bryophyte dweller; Figure 26). They found that rate of water loss from the egg surface had a linear relationship with egg mass in both species. *Anolis auratus* lost water more slowly, a factor related to its thicker calcium carbonate eggshell. These differences permitted *A. auratus* to live in the drier grasslands, whereas ***A. limifrons*** was confined to wetter habitats, *i.e.* the rainforest.

Figure 26. ***Anolis limifrons*** on a bed of mosses and liverworts. Photo by Peter Janzen, with permission.

The arboreal habitat poses its own hazards, *i.e.*, climbing and potentially falling. Adhesive toe pads facilitate climbing (Andrews & Rand 1974), but come at a price. Toe pad size increases by the square of the length. Body weight, on the other hand, increases by the cube of length. Hence, larger animals put more burden on the toe pads, causing a selection for smaller animals in arboreal habitats. Since many bryophytic habitats are arboreal, these adaptations can coincide with bryophyte dwellers.

Andrews and Rand (1974) suggest that this relationship of toe pad size to body weight and a foraging habit likewise put a limit on the egg weight at a given time. But another selection pressure on clutch size is the climate itself. In temperate and seasonal habitats of the tropics, clutch size is larger than in more moderated tropical climates. Hence, in those habitats with short-term fluctuations in rainfall, opportunistic reproducers are more likely to be successful. This strategy is likewise a safer approach in this habitat that likewise typically has high predation.

Predation can be an important factor in the strategy of a forager. The movement that permits these animals to chase or look for prey also makes them more conspicuous to their own predators. Anoles not only provide food for adult birds, but in Costa Rica birds such as the Bare-necked Umbrella Birds are known to capture the anole ***Anolis capito*** (syn.=***Norops capito***; Figure 27) from moss-covered tree trunks and feed them to their young (Losos 2011). These birds can detect the lizard from 10 m. Losos reports seeing a bird swipe a lizard from 2-3 m in front of him when the lizard had been invisible to him until the catch.

Figure 27. ***Anolis capito*** (=***Norops capito***), a cloud forest anole from Nicaragua. Photo by Josiah Townsend, with permission.

Both unpredictable weather conditions and opportunistic reproduction favor **r-selected life strategies** (high growth rate and many offspring with low probability of survival to adulthood, beneficial in less crowded niches and unpredictable habitats). Anoles exhibit the small body size, early maturity, short generation time, and high fecundity of an **r-strategist**. Arboreal anoles, in particular, are **iteroparous** (having multiple reproductive events), another r strategy.

Vitt and Congdon (1978) expanded on these ideas. They suggested that the "sit and wait" **ambush predators** were able to sustain a high clutch mass, whereas predator escape and foraging selected for small clutch size/mass. The anoles are foragers. They escape the problems of high egg mass by having only one egg at a time.

Even the **dewlap** (Figure 28, Figure 29), that often brightly colored flap of skin under the head that anoles (and others) flash to announce their aggressive defense of territory and attract females (Williams & Rand 1977), can relate to habitat/climate. Seasonally dry climates force reproduction into a short window of time annually. In these conditions, rapid choice of a mate is important, and males are selected for brightly colored, relatively large dewlaps (Fitch & Hillis 1984). In such seasonal environments, the males are typically larger than the females. In tropical rainforests and cloud forests, on the other hand, the breeding season is prolonged or even year-round, and dewlaps tend to be relatively small. In this case, some are brightly colored and others dull brown, tan, or white. Williams and Rand (1977) found that where populations of numerous species contact or overlap, the dewlap colors and patterns are sufficiently different to aid recognition. But Nicholson *et al*. (2007), in studying species of ***Anolis***, failed to demonstrate any link between dewlap color and size with similar habitat specialization. They furthermore were unable to show that greater variation in dewlap morphology exists among sympatric (overlapping distribution) species, and suggested that the role of the dewlap in sexual selection still needs to be tested.

Figure 28. Brown Anole (***Anolis sagrei***) displaying its dewlap. Photo through Wikimedia Commons.

Anolis (Anole, Polychrotidae)

The tropical cloud forests hide numerous species of lizards (Wilson & McCranie 1982, 2004; McCranie *et al*. 1993b), but finding specific relationships with bryophytes is a story of a needle in a haystack. Among these genera is the well-known genus ***Anolis*** (Figure 31).

This genus is best known for its use as a pet and laboratory organism, especially the Green Anole, also known as the American Chameleon, ***Anolis carolinensis*** (Figure 29), that is able to change color in response to temperature. This arboreal lizard parachutes to the ground when disturbed (Oliver 1951). ***Anolis carolinensis*** sometimes lays its eggs (Figure 30) among mosses (Greenberg & Noble (1944). In this case, the female uses her forelegs to part the branches, but the snout does most of the digging. Some individuals deposit their eggs deep in ***Sphagnum*** (Figure 13).

Figure 29. ***Anolis carolinensis***, a species that sometimes uses mosses for nesting sites and oviposition. Note the red dewlap. Photo by Jeff Heard, through Creative Commons.

Figure 30. ***Anolis carolinensis*** and egg. Note the soil on the snout that was used to dig the hole for the egg. Photo by J. Cody Parmer, from <www.discoverlife.org>.

The adult ***Anolis limifrons*** (Figure 26) seems to prefer grass for its habitat, whereas the related ***A. humilis*** (syn.=***Norops humilis***; Figure 31) prefers leaf litter (Talbot 1977). But for laying eggs, ***Anolis limifrons*** (Figure 26) may use mats of moss at the base of bromeliads, as well as leaf litter or clumps of decaying vegetation in tree crotches 1-2 m above ground.

The cloud forest is home to a number of anole species (*e.g.* Wilson & McCranie 1982; McCranie *et al*. 1993a; Townsend & Wilson 2009). In the cloud forests of Honduras, there are 27 known species of lizards (Wilson & McCranie 2004). Since the cloud forest is also home to many bryophytes, the anoles must necessarily interact with the bryophytes daily in many of the niches. For example, the anole ***Anolis morazani*** in Figure 32 is running across bryophytes on a branch. It is likely that bryophytes provide a means of moistening the ventral surface, as shown for salamanders, and can provide a collection substrate for drops of moisture collected from clouds, providing a suitable drinking location for the anoles and other arboreal lizards.

Figure 31. ***Anolis humilis*** (=***Norops humilis***). Photo by John D. Willson, with permission.

Figure 32. ***Anolis morazani***, a cloud forest anole from Honduras. Photo by Josiah Townsend, with permission.

The montane ecotype of the Dominican Anole (***Anolis oculatus montanus***; Figure 33) lives in high elevation rainforests of central Dominica (Wikipedia 2012). This ecotype form lives on moss-covered tree trunks and has a deep green color to match. Occasional splotches and spots form a disruptive pattern, more closely resembling the non-uniform pattern of these bryophytes.

Figure 33. ***Anolis oculatus montanus***, showing the green coloration with disruptive spots for this bryophyte-dwelling anole. Photo by Hans Hillewaert, through Creative Commons.

Brookesia vadoni (Mossy Pygmy Leaf Chameleon, Chamaeleonidae)

This lizard doesn't cultivate bryophytes. It resembles them! A native of Madagascar, the rare Mossy Pygmy Leaf Chameleon looks like it has mosses and lichens growing on its back, enabling it to blend in with similar surroundings (Brygoo & Domergue (1968). Most members of this plant-mimic genus are slow-moving and hide under litter. ***Brookesia vadoni*** (Figure 34-Figure 35) lives in the northeastern part of Madagascar where more than 330 days have rain, and mosses and lichens abound.

Figure 34. The Mossy Pygmy Leaf Chameleon (***Brookesia vadoni***) exhibiting green patches that blend with these mosses and lichens. Photos from Flickr, through Creative Commons license.

Figure 35. The Mossy Pygmy Leaf Chameleon (***Brookesia vadoni***) exhibiting tubercles that give it the disruptive look that blends with mosses. Photos from Flickr, through Creative Commons license.

Rhampholeon spectrum (Spectral Pygmy Chameleon, Chamaeleonidae)

Rhampholeon spectrum (Figure 36) develops growths of liverworts on its body (Böhme & Fischer 2000). But this lizard does not restrict this to a head dress (Figure 36-Figure 37). Rather, it can have its entire body covered in liverworts! It is interesting that the only cryptogams inhabiting it are liverworts, and not mosses or lichens, but these liverworts are all in the family **Lejeuneaceae**, the family that is so common among the epiphyllous bryophytes.

These dwarf chameleons were collected in the montane cloud forest of Mt. Nlonako, Cameroon, at approximately 1200 m asl (Figure 38). Böhme and Fischer write that the "strikingly greenish coloration is not caused by a pigment, but by the overgrowth of otherwise epiphyllous liverworts." In all, they could identify four different species of liverworts, and claimed the first reported case of more than one species on the same individual.

Figure 36. This ***Rhampholeon spectrum*** appears to have liverworts on the eye socket, and there are enough to color the head green. Photo by Wolfgang Böhme, with permission.

Figure 37. These liverworts appear dangerously close to the eye of this ***Rhampholeon spectrum***. Photo by Wolfgang Böhme, with permission.

Figure 38. Cloud forest in Cameroon where ***Rhampholeon spectrum*** was collected, adorned with leafy liverworts. Photo by Wolfgang Böhme, with permission.

Figure 39. Green, liverwort-covered male and interested "naked" female Spectral Pygmy Lizard (***Rhampholeon spectrum***) in Cameroon. Photo by Wolfgang Böhme, with permission.

Cololejeunea jovetastiana (formerly ***Aphanolejeunea jovetastiana***; see Figure 41) and ***Colura digitalis*** (see Figure 42) had the greatest abundance on the lizards, whereas Böhme and Fischer found only a few plants of ***Cololejeunea*** sp. and only two samples of ***Lejeunea*** (Figure 45-Figure 46). In addition to liverwort camouflage (Figure 40), this lizard is able to change color in the range of dull shades of tan to gray (Wikipedia 2011c). The rough surface created by the scales gives sufficient topography for lodging of the spores and establishment of the liverworts (Figure 43).

Figure 40. This Spectral Pygmy Chameleon (***Rhampholeon spectrum***) seems to be in early stages of liverwort colonization, but it appears that soon they may impair its vision. Photo by Wolfgang Böhme, with permission.

Figure 41. ***Cololejeunea minutissima***. ***Cololejeunea jovetastiana*** is a common member of the liverwort flora on the lizard ***Rhampholeon spectrum***. Photo by David T. Holyoak, with permission.

Figure 42. ***Colura calyptrifolia***. ***Colura digitalis*** is one of the two most abundant species of liverworts on ***Rhampholeon spectrum***. Photo by David T. Holyoak, with permission.

Not only does the green covering of liverworts help to camouflage the lizard, but the researchers observed that one male so-adorned aroused the sexual interest of a nearby female! (Figure 39; translated from Böhme & Fischer by Rob Gradstein, pers. comm. 14 November 2011). Such a benefit must surely be considered a symbiosis.

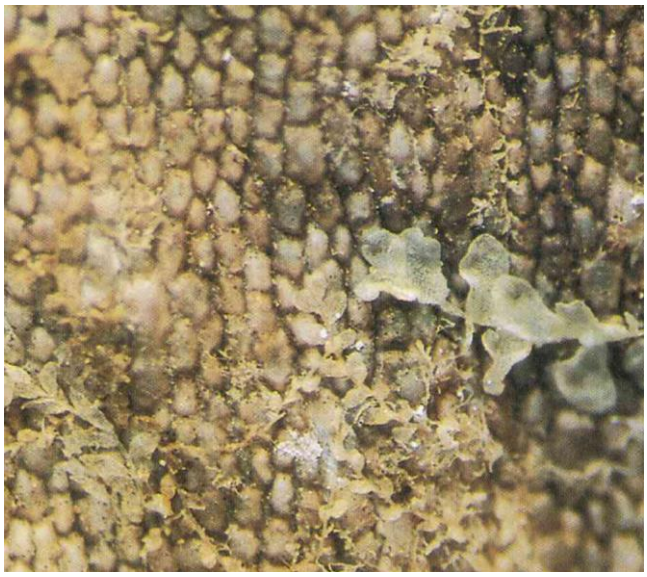

Figure 43. Close view of scales of ***Rhampholeon spectrum*** with several species of leafy liverworts attached. Photo by Wolfgang Böhme, with permission.

Corytophanes cristatus (Helmeted Iguana, Chorytophanidae)

There is another lizard that reverses the relationship of habitat and inhabitant. It's hard to imagine walking around with a garden growing on your head. But for the Helmeted Iguana ***Corytophanes cristatus*** (Figure 44) in the lowland rainforest of the Chiapas, southern Mexico, not only algae, but also the leafy liverwort ***Lejeunea obtusangula*** (Figure 45-Figure 46), grow from their heads (Figure 47) (Gradstein & Equihua 1995).

Figure 44. The Helmeted Iguana/Basilisk, ***Corytophanes cristatus***. Note the scoop-shaped head where bryophytes are able to grow. Photo © John Sullivan, Ribbit Photography, with permission.

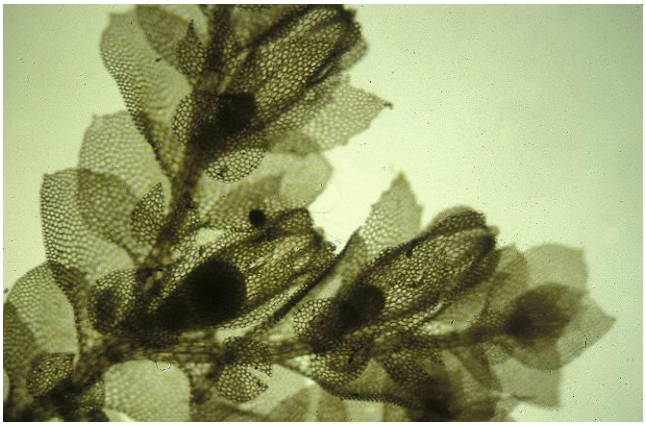

Figure 45. The leafy liverwort ***Lejeunea obtusangula***. This liverwort has been identified from the head of the Helmeted Iguana, ***Corytophanes cristatus***. Photo by Elena Reiner-Drehwald, with permission.

The liverwort in this story grew among a mat of algae comprised of four species in the Chlorophyta and Cyanobacteria. These included the common genera *Cladophora*, *Rhizoclonium*, and *Trentepohlia*. Together they resulted in a tear-drop shape of green on the head of the lizard. A picture by Twan Leenders from Costa Rica indicates that more than one species of liverwort can grow there as well (Figure 48).

Figure 46. Ventral view of ***Lejeunea*** such as that cultured on the head of the Helmeted Iguana. Members of this family are common as epiphyllous liverworts in the tropics. Photo by Michael Lüth, with permission.

The head seems to be especially adapted for green colonizers. The algae and liverworts reside in a depression in the head (the crest) that creates a catchment area where it could remain moist enough to support the growth of these photosynthetic organisms (Gradstein & Equihua 1995). The liverwort, ***Lejeunea*** (Figure 46), is a common epiphyte in the Neotropical rainforest, including living epiphyllous on tracheophyte leaves. Sporophytes of the liverwort were common in the forest and most likely represented its means of colonizing the lizard.

But what is the real function of this depression on the head? Although no one seems to have witnessed the act directly, it is likely that the head serves as a shovel to excavate a nest (Leenders 2002). Many lizards are known

to use their heads to excavate nests; their legs are weak and of little use for heavy digging (Twan Leenders, pers. comm. 20 February 2009). And, the one observation indicating nesting behavior was of a female with mud on her head standing over a hole in the ground that held two eggs. Since spores and fragments collect in the soil sporebank as they rain from the tree branches, the digging may also be at least one means of accomplishing the head gardening.

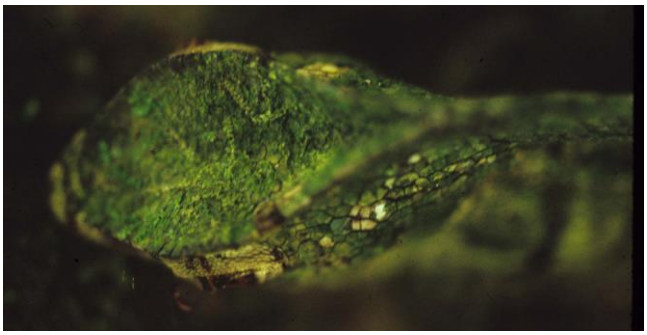

Figure 47. Head of the Helmeted Iguana ***Corytophanes cristatus*** showing the leafy liverwort ***Lejeunea obtusangula*** growing in the crest. Photo by Clementina Equihua, with permission.

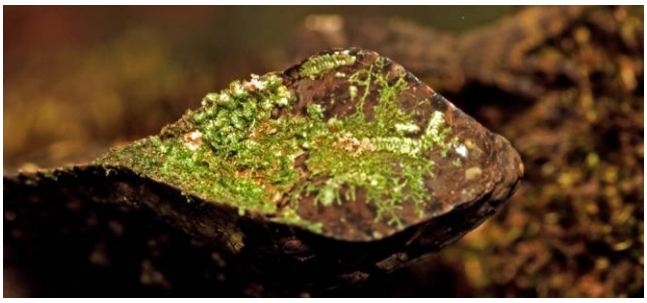

Figure 48. Head of Crested Basilisk/Helmeted Iguana, ***Corytophanes cristatus***, or possibly a different species, in the Rara Avis Rainforest Preserve, Costa Rica, showing at least two different leafy liverworts. Rob Gradstein (pers. comm. 14 November 2011) has suggested these liverworts may be ***Symbiezium transversale*** and ***Lejeunea flava*** (Figure 49), two species that are locally common, but not typically as epiphylls. Photo by Twan Leenders, with permission.

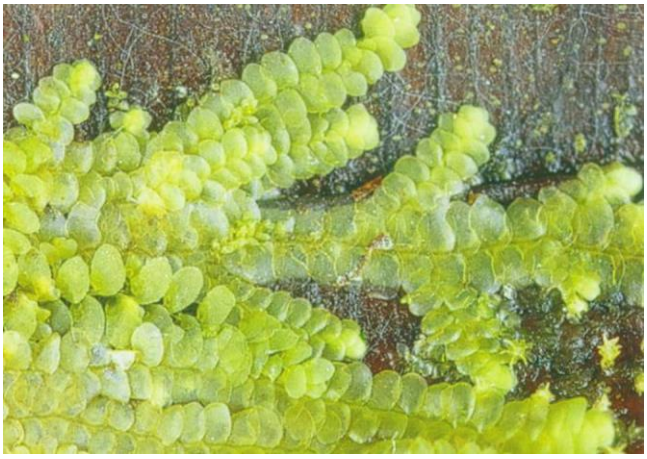

Figure 49. ***Lejeunea flava***, a tiny liverwort that might colonize the head of ***Corytophanes cristatus***. Photo by Jia-dong Yang, through Creative Commons.

One would assume that colonization of liverworts on the lizard's head would be challenging because the lizard most likely sheds its skin several times annually. Thus it's not surprising that the bryophytes are epiphyllous species of ***Lejeunea*** (Figure 45-Figure 46) that are already adapted to a transient habitat. The rainforest is moist and the lizard is able to move quickly if needed, but it spends many hours without moving (Figure 50) (Twan Leenders pers. comm. 31 January 2009), earning it the nickname of Old Man Lizard. Further supporting its name, its long life provides a combination that makes such colonization possible. It would be interesting to see what happens to the crown garden when the skin is shed. Perhaps fragments from the disposable garden are able to colonize the new crest immediately. The lizard may gain a camouflage advantage as it hangs out on trees with patches of epiphytes on the bark (Figure 51).

Figure 50. ***Corytophanes cristatus***, looking a bit like its bryophyte habitat. Photo © 2007 Petrovan Silviu, with online permission for academic use.

Figure 51. Helmeted Iguana, ***Corytophanes cristatus***, on a trunk covered with leafy liverworts. A crown of liverworts would have made it less conspicuous. Photo by John D. Willson, with permission.

Sasa and Monrós (2000) reported that both ***Corytophanes cristatus*** (Figure 47-Figure 51) and ***C. hernandezii*** (Figure 52) had remains of bryophytes in the guts of several individuals. It is possible these were consumed while targetting invertebrate food.

Figure 52. ***Corytophanes hernandezii***, a species that occasionally eats mosses. Photo through Creative Commons.

Ceratophora karu (Agamidae)

The name ***Ceratophora*** literally means horn-bearer, referring to the horn at the tip of the snout on the males. This genus is endemic to Sri Lanka (Bahir & Surasinghe 2005). ***Ceratophora karu*** (Figure 53) is rare and critically endangered, living in a 10 km^2 area at 900-1070 m asl in tropical moist montane forest. All the endangered agamid species in Sri Lanka are forest-dwellers. The genus ***Ceratophora*** is considered a geographical relict (de Silva 2006). In 2011, researchers Janzen & Bopage were unable to locate ***Ceratophora karu*** near its known Morningside Estate location. The lack of protection for this species forebodes its likely extinction.

Figure 53. ***Ceratophora karu***, an endemic of Sri Lanka with mosses growing on its back and head. Photo by Friedrich Wilhelm Henkel, with permission.

Thanks to Wolfgang Böhme and Friedrich Wilhelm Henkel, we are able to document here the occurrence of mosses growing on the back of at least one of these rare ***Ceratophora karu*** (Figure 53).

Zootoca (formerly *Lacerta*) *vivipara* (Viviparous Lizard, Lacertidae)

Lizards are generally found in dry habitats where their scales help them to avoid desiccation. The common ***Zootoca*** (=*Lacerta*) ***vivipara*** (Viviparous Lizard; Figure 54-Figure 55) may be the only lizard to frequent peatlands in northern Europe, where it reproduces (H. Strijbosch in Desrochers & van Duinen 2006). It is one of a number of reptiles that have live birth instead of depositing eggs. In highland areas, this lizard is able to increase its ability to resist ice formation during its hibernation, which it spends under 2-4 cm of peatmoss or grass litter (Grenot *et al*. 2007). A contributing factor is that it can increase its blood glucose levels about 4-fold from September to March, followed by a rapid decline when it exits hibernation. The mosses act as insulation that reduces daytime temperatures and keeps nighttime temperatures warmer.

Zootoca vivipara (Figure 54-Figure 55) is most typical in raised bogs that transition into pine or pine-birch forests (Èeirâns 2004). These areas are characterized by wet ***Sphagnum*** (Figure 2).

Figure 54. The Viviparous Lizard, ***Zootoca*** (formerly *Lacerta*) ***vivipara***. Photo by Marek Szczpanek, from Wikipedia Commons.

The Viviparous Lizard, as its name implies, gives birth to live young. The courtship is a rather strange one in which the male grabs the female's head in his mouth (Peatlands 2009). Following copulation, the female must stay warm for the next three months, basking in the sun, so that the eggs can develop properly. In Northern Ireland they are legally protected not only from direct harm or capture, but also from disturbance.

Figure 55. The Viviparous Lizard, ***Zootoca*** (=*Lacerta*) ***vivipara***. Photo by Marek Szczpanek, from Wikipedia Commons.

Plestiodon (formerly *Eumeces*) *anthracinus* (Coal Skink, Scincidae)

The Coal Skink, ***Plestiodon*** (formerly *Eumeces*) ***anthracinus*** (Figure 56), can be found on the edge of swamps (Wright 1919), but it is more common among boulders on limestone cliffs, under ledges, sandstones slabs, and under rocks (Virginia Department of Game and Inland Fisheries 2009). It is rarely seen and has an interesting habit when pursued – it jumps into a shallow stream and hides under rocks or debris (ZipCode Zoo 2008). Females defend their eggs, which are usually placed under rocks or logs on land. The young can be recognized by their blue tails (Virginia Department of Game and Inland Fisheries 2009). In Tennessee it is considered very rare or imperiled (Atlas of Reptiles in Tennessee 2008). But information on its dependence on or use of bryophytes is lacking, aside from its occurrence on the edge of a swamp. The ability of bryophytes to ameliorate temperature and maintain moisture suggests that there are most likely many more reptiles that make use of bryophytes, but we have very little information on their use of this habitat.

Figure 56. Coal Skink, ***Plestiodon*** (formerly *Eumeces*) ***anthracinus***. Photo through Creative Commons.

Lobulia (Scincidae)

The genus ***Lobulia*** in the family Scincidae has several species that utilize mosses in the high altitude areas of New Guinea (Greer *et al*. 2005), where it is endemic. ***Lobulia subalpina*** is common in shrubby-grassy clearings of forests with dense moss cover, but may not actually use the mosses. ***Lobulia alpina***, on the other hand, is common on fallen, decaying logs of tree ferns (*Cyathea* spp.) that are covered with mosses, their primary habitat. ***Lobulia stellaris*** sometimes occurs in mossy clumps. Greer *et al*. found one active at around 0900 hrs at the base of a moss mound. ***Lobulia*** species use mossy-grassy clumps in the alpine grassland for sunning themselves. The landscape is dotted with large mounds about 1 m high and 1-2 m in diameter, providing ideal sunning locations. They not only give good sun exposure, but serve as shelter sites. Nevertheless, none of the ***Lobulia*** were found in the dense moss forest.

Cnemaspis spinicollis (Geckonidae)

Cnemaspis spinicollis (Figure 57) from Cameroon is poorly known, recorded only from the Takamanda Forest Reserve in the southwest province of Cameroon (LeBreton 2003). Its home is larg rainforest trees that are covered with layers of mosses, stems of vines, and exfoliating bark.

Figure 57. ***Cnemaspis*** sp. ***Cnemaspis spinicollis*** lives among mosses on the rainforest trees of Cameroon. Photo by L. Shyamal through Creative Commons.

Uroplatus sikorae – Mossy Leaf-tailed Gecko

Ourá means tail and *platys* means flat, referring to the flattened tail of the genus ***Uroplatus*** (Wikipedia 2015). It ranges 15-20 cm from its nose to the base of its tail as an adult. The Mossy Leaf-tailed Gecko is an endemic lizard in Madagascar, occurring in both primary and secondary forests.

Uroplatus sikorae (Figure 58) can change its skin color to match its surroundings and even has dermal flaps to break up its smooth appearance when at rest (Wikipedia 2015). But more to our interests, it looks like it has bryophytes growing on its scales, enough so that I thought from the picture that they were real bryophytes. It rests head down on tree trunks during the day, blending well with its surroundings. ***Uroplatus sikorae*** is a nocturnal tree dweller where it feeds on insects. These geckos die very quickly if the humidity is too low, requiring a range of 60-100% (Dunlop 2016).

Figure 58. ***Uroplatus sikorae*** (leaf-tailed gecko) in Madagascar, with bryophytes on scales. Photo by Paul Bertner, with permission.

Order Squamata – Snakes

Like the lizards, the mention of snakes does not bring bryophytes to mind, but of course some make use of mosses in their habitat. The mosses can help provide moisture and may be suitable hiding places for smaller species.

Diadophis punctatus punctatus (Ringneck Snake, Colubridae)

If one imagines snakes among mosses, it is small ones like ***Diadophis punctatus*** (Figure 59-Figure 60) that come to mind. This primarily nocturnal species is known from insect burrows under thick mosses of sunny slopes, although it might be more common in the soft tissues of decaying logs, under bark, or in beetle (*Passalus cornutus*) tunnels (Neill 1948).

Figure 59. ***Diadophis punctatus*** on a bed of the moss ***Plagiomnium* sp.** Photo by John White, with permission.

This nocturnal species is a native North American, occurring from southeastern Canada to Mexico. Although they are slightly venomous, they are no danger to humans. Their greater resource against predation seems to be their ability to roll up and expose the underside of the tail, displaying a bright red warning coloration (Figure 60).

Figure 60. ***Diadophis punctatus*** showing the warning coloration of the underbelly. Photo by William Flaxington.

In northern and western areas these snakes are typically located in open woodlands near rocky hillsides or in wetter environments that have good cover, including coarse woody debris (Stebbins 2003). But southern populations live primarily in arid habitats within riparian and wet environments (Dundee & Miller 1968).

Pseustes poecilonotus (Dos Cocorite, Colubridae)

Pseustes poecilonotus (Figure 61) lives in Amazonian South America (Boos 2001) where it is a species of IUCN least concern (Lee *et al.* 2007). It is known from sea level to 1200 m asl. This diurnal snake lives in humid lowland forest and savannas. It feeds on frogs, lizards, birds, and small mammals. These are all available in its arboreal habitat where it also encounters bryophytes. It is too large to live under bryophytes or hide in them, but they could provide moisture or egg-laying sites.

Figure 61. ***Pseustes poecilonotus*** on tree trunk in Tortuguero, Costa Rica. Photo by John D Willson.

Sibon longifrenis (Stejneger's Snail Sucker, Colubridae)

Sibon longifrenis (Figure 62) is an egg-layer that lives in Costa Rica, Honduras, Nicaragua, and Panama (McCranie 2007; Lewis 2009; Hosek 2011). Kofron (1990) considered this and several other ***Sibon*** species to be synonyms of *S. dimidiata*, but later Savage and McDiarmid (1992) provided convincing argument that this species is distinct. ***Sibon longifrenis*** is a nocturnal moss mimic, with patches of white, green, and brown in a disruptive pattern that makes it blend well in its arboreal tropical habitat. Its diet consists of snails, slugs, and amphibian eggs, all of which can be found among the epiphytic bryophytes. Other members of the genus in Costa Rica have similar green coloration (Solórzano 2001).

Figure 62. ***Sibon longifrenis*** in a tropical tree among mosses and liverworts where it is almost invisible. Photo by Josiah Townsend.

Ryan and Lips (2004) found that the most common food for the related species ***Sibon argus*** (Figure 63) is slugs, but some eat eggs of anurans, gaining the species the common name of goo-eater. The researchers found a snake of this species in Panama with its head hidden in a moss clump. When the snake was pulled out, it was swallowing eggs of ***Espadarana prosoblepon***. At night this species moves along branches, flicking its tongue at moss clumps and undersides of leaves, apparently searching for eggs.

Figure 63. ***Sibon argus***, a species that eats amphibian eggs in moss clumps. Photo by Twan Leenders, with permission.

Virginia valeriae (Smooth Earth Snake, Colubridae)

Virginia valeriae (Figure 64) is not a snake one would probably associate with bryophytes, but Tobias Landberg found an unlikely connection. This is a snake that lives in the soil and leaf litter where it eats earthworms and soft-bodied arthropods. But just by chance, Landberg found this species dispersing moss spores!

Figure 64. Smooth Earth Snake, ***Virginia valeriae***, sunning itself on a moss. Photo by Tony Gerard through Creative Commons.

Figure 65. Smooth Earth Snake, ***Virginia valeriae***, wending its way among moss capsules. Photo by Tobias Landberg.

Figure 66. Smooth Earth Snake, ***Virginia valeriae***, showing moss spores that have collected on its head. Photo by Tobias Landberg.

Natrix Natrix (Grass Snake, Colubridae)

Natrix natrix (Figure 67) in Eastern Europe is frequent on poor ***Sphagnum*** and *Carex* peat in drained pine forests (Èeirâns 2004). They also occur around flooded peat mines in raised bogs, but they avoid pre-drained forest types and active raised bogs.

Figure 67. ***Natrix natrix***, a ***Sphagnum*** inhabitant. Photo by Fafner, through Creative Commons.

Sistrurus catenatus catenatus (Eastern Massasauga Rattlesnake, Viperidae)

Some moss inhabitants you would rather not meet. Such is most likely the case for the Eastern Massasauga Rattlesnake, ***Sistrurus catenatus catenatus*** (Figure 68). It inhabits low-lying areas including peatlands, where it uses temperature sense organs on its head to locate small prey such as mice, voles, and shrews (Johnson 1992, 1995). When winter approaches, these snakes seek places where the temperature does not drop below freezing, and at least in New York, USA, the raised hummocks of ***Sphagnum*** often provide a suitable place (Johnson & Breisch 1993, 2000; Johnson *et al*. 2000; Department of Environmental Conservation 2010). These hummocks typically overlie branching roots that provide spaces for the snakes.

Figure 68. The poisonous Eastern Massasauga Rattlesnake, ***Sistrurus catenatus catenatus***. Photo by John White.

Vipera berus (European Viper, Viperidae)

The common European Viper (***Vipera berus***; Figure 69-Figure 70) may easily be encountered in peatlands, where the presence of juveniles indicates that reproduction in the peatland is successful (H. Strijbosch in Desrochers & van Duinen 2006). Its bite can be dangerous or fatal to the very young and very old, but generally it is not fatal, the poison being mild.

Figure 69. The common European Viper (***Vipera berus***) amid the ***Sphagnum*** and cranberries. Photo by Twan Leenders, with permission.

Figure 70. The European Viper (***Vipera berus***) in a bed of ***Sphagnum***. Photo from Wikipedia Commons.

North of the Arctic Circle in Sweden, ***Vipera berus*** (Figure 69-Figure 70) lives between 300 and 450 m asl (Andersson 2003). Its chosen hibernation sites are always within 1 km of peat bogs and marshlands where they fed on voles during their active season of mid-June to mid-August.

Bothriechis schlegelii (Eyelash Viper, Viperidae)

The Eyelash Viper (Figure 71) derives its name from the superciliary scales above the eyes, believed to disrupt the contrast between the smooth body and its surroundings, making it less conspicuous to would-be predators and to its own prey (Wikipedia 2011a). This somewhat small (75 cm) species is characterized by a rainbow of color variants, some of which mimic the lichen and bryophyte encrusted bark of its arboreal habitat.

Figure 71. ***Bothriechis schlegelii*** (Eyelash Viper), demonstrating its color pattern that blends with bark, lichens, and bryophytes, where it waits quietly for its food. Note the upturned scales above the eyes. Photo by Josiah Townsend, through Creative Commons.

The Eyelash Viper is a pit viper, and thus is poisonous, sensing its prey through heat-sensitive glands between the eyes and nostrils. It lives in dense foliage of the mesic forests of Southern Mexico, south to Colombia and Venezuela at elevations from sea level to 2640 m asl (Wikipedia 2011a). The bryophyte collector must beware –

this venomous snake lies quietly in wait, an **ambush predator.** It is inconspicuous on branches, sometimes among mosses or tangled among vines, until it detects its prey. It is nocturnal and preys on other arboreal animals such as lizards, frogs, small rodents, and birds. As a likely adaptation to their arboreal habit, they are **ovoviviparous**, giving annual birth to 10-12 live young.

Visitors

The common Eastern Garter Snake (***Thamnophis sirtalis***; Figure 72-Figure 73) (Stockwell & Hunter 1989) and Green Snake (***Opheodrys vernalis***; Figure 74-Figure 75) also appear in peatlands (Rochefort in Desrochers & van Duinen 2006), but they are widespread elsewhere.

Figure 72. Eastern Garter Snake, ***Thamnophis sirtalis***. Photo by Janice Glime.

Figure 73. ***Thamnophis sirtalis tetrataenia*** flicking its tongue. Photo by Brian Gratwicke, through Creative Commons.

Figure 74. Green Snake, ***Opheodrys vernalis***, sunning on a rock near a patch of mosses. Photo © Gary Nafis, with permission.

Figure 75. Green Snakes, ***Opheodrys vernalis***, hatching from eggs. Photo by John White, with permission.

The rough green snake (***Opheodrys aestivus***) lives in dense brush of lakeshores, streambanks, upland ravines, and forest edges, where they obtain their water by sucking droplets of dew from leaves (Goldsmith 1984). Bryophytes can provide droplets as well, especially early in the morning. Goldsmith observed this species two different times sucking water from piles of damp ***Sphagnum*** in its terrarium. Clark (1949) observed 5 eggs of the species in mosses beside a decaying log in Louisiana, USA. Nevertheless, it may be more of a visitor to bryophytes.

Figure 76. ***Opheodrys aestivus***, a species that obtains water from mosses. Photo by James Harding, through Creative Commons.

Order Crocodilia – Crocodiles (Family Crocodylidae)

In the Philippines, ***Sphagnum*** is used for nesting material in crocodile farms for incubating eggs (Tan 2003). At crocodile breeding stations, wild-collected eggs are cushioned or layered in ***Sphagnum*** for incubation. But information on natural uses of mosses by crocodilians is lacking.

Reptiles in Captivity

Bryophytes are popular in terraria, albeit difficult to keep healthy. Even reptiles seem to benefit from bryophytes in their captive homes (Brough & Rearick 2011; Foster & Smith Inc 2012), and use of bryophytes in live sample containers is a common practice for collectors (LeBreton *et al*. 2011).

At Reptile and Supply Co Inc (2010), New Zealand *Sphagnum* is recommended as the best *Sphagnum* for reptiles due to its water-holding capacity. They also sell sheet moss (US$13.99 per 6.75" circle) and cushion moss (US$9.99 per sq ft) for lizard terrariums.

Kaplan (1997) recommends ***Sphagnum*** as a suitable substrate for reptiles, but admonishes that it can cause fungal infections to those who handle it. She recommends that it be dried thoroughly periodically and baked at 121°C for one hour to kill and fungal growth that may be occurring. The moss provides moisture and maintains air humidity.

One possible caution is that the lizard might eat the moss. One pet owner wrote to Just Answer.Reptile (2012) with concern that her Leopard Gecko had passed bits of "Fluker's" moss in her feces and had stopped eating. [It appears that Fluker's is a trade name and includes true moss and Spanish moss (a bromeliad)]. It is not clear that the moss played any role in the loss of appetite because the lizard had just shed and was also provided night temperatures that were too cool. The advice from Just Answer.Reptile was to provide moist towels instead of moss for the "moist pot." I would think a fine mesh or cloth over the moss might be a good alternative. On the other hand, the primary concern was that the moss might cause an obstruction, but X-ray indicated that did not seem to be the case.

Summary

Peatlands are especially important for some of the reptiles, particularly turtles. ***Chrysemys guttata*** (Spotted Turtle) uses ***Sphagnum*** swamps for hibernation, being protected from freezing by the insulation. Later it uses ***Sphagnum*** and other mosses for nesting. ***Glyptemys muhlenbergii*** (Bog Turtle) lives primarily in peatlands, apparently using the mosses to maintain their hydration. They travel within the peatlands in small rodent tunnels. The *Sphagnum* is used for nesting. Turtles such as the Snapping Turtle may help in dispersal of bryophytes.

Sistrurus catenatus (Massasauga Rattlesnake) and ***Vipera berus*** (European Common Viper) live in low-lying areas such as peatlands and often hibernate in raised hummocks where the temperature is buffered. ***Thamnophis sirtalis*** (Eastern Garter Snake) and ***Opheodrys vernalis*** (Green Snake) also can live in peatlands.

In Europe, the Viviparous Lizard (***Zootoca vivipara***) frequents peatlands, hibernating under the moss. Coal Skinks (***Plestiodon anthracinus***) can occur on the edge of swamps.

The Helmeted Iguana (***Corytophanes cristatus***) can have leafy liverworts growing on the crest of its head, possibly providing camouflage, whereas species of ***Brookesia*** have color patterns that resemble bryophytes. Species of the arboreal snake genus ***Sibon*** also blend with the bryophytic epiphytes in their habitat.

Many reptilian caretakers use ***Sphagnum*** in the cages, and even crocodile eggs can be reared in ***Sphagnum***.

Several snakes use bryophytes, some for sites of finding food, others to rehydrate, and some to modulate their temperature.

The only connection between bryophytes and crocodiles seems to be for breeders who use mosses for rearing the eggs.

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CHAPTER 16-1
BIRDS AND BRYOPHYTES INTERSECT

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CHAPTER 16-1
BIRDS AND BRYOPHYTES INTERSECT

Figure 1. ***Lepidocolaptes affinis***, Spot-crowned Woodcreeper, a bird that specializes on foraging among bryophytes and lichens, especially epiphytes such as these. Photo by Larry Thompson, through DiscoverLife <www.discoverlife.org>.

Where Birds and Bryophytes Intersect

Bryophytes, including epiphytes (Figure 1), form an important source of food and habitat for many birds in the tropical rainforests (Gradstein *et al*. 1996). Nadkarni (1994) considered that the epiphytes contributed to the diversity of birds by adding to the resources available, providing more opportunities for resource specialization, and spread the available resources in the canopy throughout the year. These included retention of nutrients in the canopy, providing habitat for invertebrates, and providing a foraging substrate in the canopy (Nadkarni *et al*. 2004).

There is a positive relationship between bryophytes, vascular plants, and breeding birds in marginal habitats bordering agricultural areas (Wuczyński *et al*. 2014). A study in Lower Silesia, Poland, revealed 47 species of birds and 90 of bryophytes in 70 of these marginal habitats. These numbers were topped by 414 species of tracheophytes. The number of species of bryophytes was positively correlated with the number of species of breeding pairs of birds. These relationships suggest that bryophytes are good biodiversity indicators and can be used as a surrogate taxon for overall species richness. But do the birds use the bryophytes in some way, or do both simply like the same habitats? Bryophyte species richness was significantly correlated with the number of trees and shrubs, explaining 49% of the variability.

Birds have the potential to play a major role in bryophyte use and dispersal (Takaki 1957). It only took me a short time to realize how destructive my finches were to the mosses in my garden room due to their continuous nest-building activities.

Some interactions with mosses may not even involve use of the mosses. Davis (1981) reports that Skuas on Signy Island in the maritime Antarctic were disruptive to the moss community because of their activities there. Once the Skuas have pulled up the mosses, the wind will transport them elsewhere.

Bryophytes also provide microclimate buffers, offering thermal protection (Wolf 2009). This not only provides an ameliorated "climate" for birds' feet, but also affects their food organisms living under and in the bryophyte mat.

Unfortunately, observer location introduces bias into the sampling (Wolf 2009). Ground-level birds were more difficult to observe. The presence of bryophytes, lichens, and **Cyanobacteria** increases the roughness of the canopy. This microtopography provides important ecological functions that include nesting and foraging. In the Pacific Northwest states of Oregon and Washington, 100 bird species breed in the coniferous forests, using bryophytes, lichens, or mistletoe among construction materials in their nests. In North America, nearly 40% of the 262 bird species use either lichens or bryophytes in their nests. In the coniferous forests of Oregon and Washington, 65% use lichens or bryophytes, and 45 species use both. Wolf argues for the maintenance of old-growth forests to support these relationships.

Even the Northern Spotted Owl (***Strix occidentalis caurina***; Figure 2) depends on bryophyte and lichen epiphytes because this owl eats the northern flying squirrel (***Glaucomys sabrinus***; Figure 3), a species that depends on lichens and mosses extensively for both food and nesting materials (FEMAT 1993).

Figure 2. ***Strix occidentalis caurina***, Northern Spotted Owl , a species that benefits from mosses because they eat northern flying squirrels that feed on and make nests with mosses. Photo from Bureau of Land Management, through Creative Commons.

Figure 3. ***Glaucomys sabrinus***, the northern flying squirrel that uses mosses for food and nesting, but then itself becomes food for the Northern Spotted Owl. Photo by Bob Cherry, through public domain.

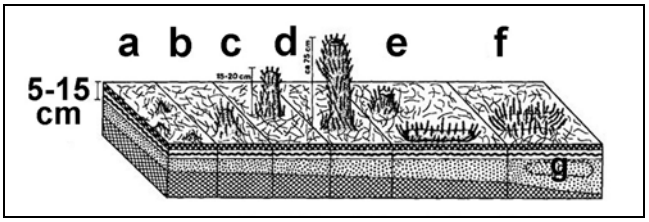

Figure 4. Developmental stages of bird watchtowers made of bryophytes. **a**. moss hummocks among morasses; **b.** early developmental stage of tower; **c.** immature tower; **d.** tower at optimum development stage; **e.** tower after collapse; **f.** collapsed tower overgrown by ***Polytrichum*** shoots; **g.** tower fragment remaining in peat. Modified from Kuc 1996.

Watch Towers and Sentinels

If you search for information on birds and watch towers, you are likely to find many articles on dangers of tall buildings, towers, and windmills to birds in flight. But in the tundra, where topography can be somewhat monotonous due to lack of trees and vertical structure, some birds use watch towers that they construct or that occur naturally in the landscape (Figure 4; Kuc 1996). And some of these birds use mosses as watch towers (Figure 5-Figure 6). This is known on Insla Grande de Tierra del Fuego, but mounds of mosses are likely used elsewhere as well.

Spending time on these towers detracts from the time spent foraging and thus is a tradeoff (Metcalfe & Furness 1984; Wickler 1985). The importance depends in part on how conspicuous the bird is and on the hunting tactics of the predators (Lendrem 1983a, b). The cost of this vigilance is reduced when it is shared with other birds, including those of other species (Metcalfe 1984; Sullivan 1984).

Hollén *et al*. (2008) demonstrated that in the Pied Babblers (***Turdoides bicolor***; Figure 7) the foragers gain more weight when these sentinels are in cooperative calling groups.

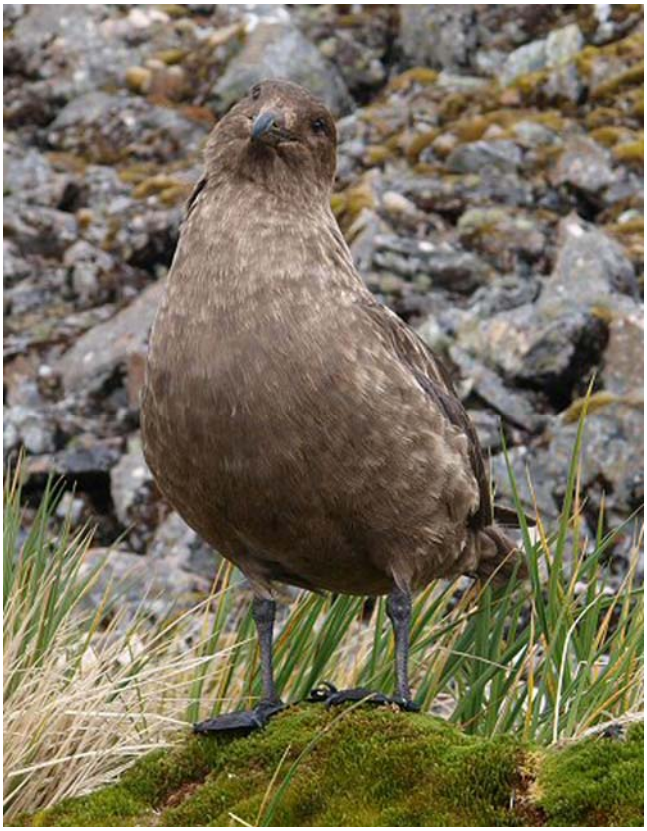

Figure 5. ***Stercorarius antarcticus***, Antarctic Skua sentinel on moss mound on South Georgia. Photo by Roger S. Key, with permission.

Figure 6. ***Anas georgica georgica*** (Yellow-billed Pintail), foraging while another is on a moss mound as a sentinel on South Georgia in the Antarctic. Photo by Roger S. Key, with permission.

Bathing

But bath mats? Appressed bryophytes on branches and limbs of trees provide bathing opportunities in the canopy, escaping the predators on the forest floor. One adult male Pacific Wren (***Troglodytes pacificus***; Figure 8) was using the mat of ***Dicranum*** spp. (Figure 9) 1.5 m above ground for his private bath, dipping into the creek beneath repeatedly, then rubbing his head and plumage into the moss to preen his feathers. But the moss was also wet, saturated by heavy fog in the morning. Winter Wrens (***Troglodytes troglodytes***; Figure 10) in Europe (now considered a separate species from those in North America) also bathe in dew-covered vegetation (Armstrong 1955). In Amazonia, the Conures (Figure 11), a kind of parrot in the subfamily **Arinae**, bathe communally in wet moss mats 23 m above the forest floor (Brightsmith 1999). Even the pelican may use mosses as a bathmat (Figure 12).

Figure 7. ***Turdoides bicolor***, Southern Pied Babbler. Photo by Derek Keats, through Creative Commons.

Figure 8. ***Troglodytes pacificus***, Pacific Wren, a bird that uses mosses as a bath mat. Photo by Upupa4me, through Creative Commons.

Figure 9. ***Dicranum scoparium***, a potential "bath mat" for the Pacific Wren. Photo by Misha Ignatov, with permission.

Figure 10. ***Troglodytes troglodytes***, European Winter Wren. Photo from Oskare Photography, through Creative Commons.

Figure 11. ***Aratinga solstitialis***, Sun Conure (**Arinae**), a Conure that might bathe in wet moss mats. Photo by Anshu, through Creative Commons.

Figure 12. Pelican drying on moss. Photo by Kapa, through public domain.

Thirsty Birds

Sometimes the mosses are the best source of a drink of water. In the Sandwich Isles of Hawaii, the Hawaii Mamo (***Drepanis pacifica***; Figure 13) obtains water from the epiphytic mosses, using rapid darts of the tongue on the wet mosses (Perkins 1903). The stomach contained no insects, so that could not explain the behavior.

Figure 13. ***Drepanis pacifica***, Hawaii Mamo, a bird that obtains water from epiphytic mosses. Photo by Hiart, through Creative Commons.

Fertilizer Effects of Birds on Bryophytes

Owls have yet another effect on bryophytes. Owl perches in Alaska provide a unique habitat for a few not-so-unique mosses: ***Bryum argenteum*** (Figure 14), ***Dicranum elongatum*** (Figure 15), ***Orthotrichum speciosum*** (Figure 16), and ***Syntrichia ruralis*** (Figure 17) (Steere 1976).

Figure 14. ***Bryum argenteum*** with capsules, a moss that can live on owl perches in Alaska. Photo by Ivanov, with permission.

Figure 15. ***Dicranum elongatum***, a moss that can grow on owl perches in Alaska. Photo by Michael Lüth, with permission.

Figure 16. ***Orthotrichum speciosum***, an epiphytic moss that can grow on owl perches in Alaska. Photo by Michael Lüth, with permission.

Figure 17. ***Syntrichia ruralis***, a species that can grow on owl perches in Alaska. Photo by David Holyoak, with permission.

Similarly, in Svalbard the "manuring" causes production of moss carpets that have a thin active layer (Vanderpuye *et al*. 2002). Beneath that is an accumulation of thick peat with no standing water. These manure deposits from the seabirds provides needed nutrients in this low-nutrient habitat.

Aplodon wormskioldii (**Splachnaceae**; Figure 18), includes owl pellets (Figure 19) among its substrates (Koponen 1990). Owl pellets are not guano, but rather are the regurgitated mass of indigestible materials.

Figure 18. ***Aplodon wormskioldii*** in Spitzbergen, a species that includes owl pellets among its substrates. Photo by Michael Lüth, with permission.

Figure 19. Owl pellet, substrate for ***Aplodon wormskioldii*** in Alaska. Photo by Gail Hampshire, through Creative Commons.

In the more temperate UK, Ken Adams (20 February 2014) reports on a ***Metzgeria violacea*** (Figure 20) on the side of a *Crataegus* bough. This location was so dense in a blackthorn bower that he supposed it could only have been introduced on a bird's foot. Air movement in the valley was too restricted to imagine that it had arrived that way. Recalling that ***Ulota phyllantha*** (Figure 21) supposedly prefers the nitrogen-rich bird droppings, he mused that this could be a similar situation. Or are these bryophytes simply tolerant of the droppings. It could also be that gemmae are simply deposited on branches where the birds perch. We know little of these relationships in the temperate zone.

Figure 20. ***Metzgeria violacea***, a species that might be dispersed by birds and may benefit from the guano. Photo by David Holyoak, with permission.

Figure 21. ***Ulota phyllantha***, a species that might be dispersed by birds and possibly benefit from the guano. Photo by Janice Glime.

Guano

Some birds favor certain mosses by large quantities of **guano** (accumulation of feces). Some seabirds tend to choose certain cliffs for roosting and defecating. The resulting **guano** (Figure 23) is high in some nutrients and provides the ideal substrate for its own unique flora. Among these plants are a number of **ornithocoprophilous** bryophytes – those that grow on bird dung. The most common of these include ***Ceratodon purpureus*** (Figure 22), ***Eurhynchium praelongum*** (Figure 24), and ***Mnium hornum*** (Figure 25), all species with a wide ecological amplitude (Watson 1964).

Figure 22. ***Ceratodon purpureus*** with capsules, a species that is able to grow on and may benefit from bird dung. Photo by Michael Lüth, with permission.

Figure 23. Guano of gulls and puffins on Farne Islands. Photo by Matthew Wills, through Creative Commons.

Figure 24. ***Eurhynchium praelongum***, a species that is able to grow on and may benefit from bird dung. Photo by Blanka Shaw, with permission.

Figure 25. ***Mnium hornum***, a species that is able to grow on and may benefit from bird dung. Photo by Des Callahan, with permission.

On Svalbard, near the Arctic Circle, Kuc (1996) reported an interesting relationship between the bryophytes and the Parasitic Jaeger (***Stercorarius parasiticus***; Figure 26). In the Nornsund Area, the moss ***Syntrichia ruralis*** (Figure 17) forms dense, high tufts in rings immediately

adjacent to the nests. Likewise, the moss ***Drepanocladus exannulatus*** (Figure 27), another dominant species, surrounded the nests, but in some areas this species was significantly degraded by the activities of the Parasitic Jaeger. In the dry tundra, the terrain was dominated by the moss ***Racomitrium lanuginosum*** (Figure 28-Figure 29), a moss that was heavily fertilized by guano from the Parasitic Jaeger.

Figure 26. ***Stercorarius parasiticus***, Arctic Jaeger, a species that seems to encourage the growth of ***Syntrichia ruralis*** near its nest. Photo by Donald Macauley, through Creative Commons.

Figure 27. ***Drepanocladus exannulatus***, a species common near the nests of the Arctic Jaeger (***Stercorarius parasiticus***), but that suffers from their activity. Photo by Michael Lüth, with permission.

Figure 28. ***Racomitrium*** in Iceland, a moss that is often fertilized by the Arctic Jaeger. Photo by Janice Glime.

Figure 29. ***Racomitrium lanuginosum***, a common species that lives in the tundra where the Arctic Jaeger provides it with a heavy fertilization by guano. Photo by Juan Larrain, with permission.

Megaphorura arctica (Figure 30), an Arctic springtail, feeds on a variety of bryophyte species (Hodkinson *et al*. 1994). These springtails form dense aggregates under bird cliffs, presumably benefitting from the guano, perhaps indirectly through the bryophytes. The bryophytes include ***Sanionia uncinata*** (Figure 31), ***Polytrichastrum alpinum*** (Figure 32), and ***Racomitrium lanuginosum*** (Figure 29).

The most fascinating association of bryophytes with bird droppings is that of some members of **Splachnaceae**. The moss ***Tayloria dubyi*** (Figure 33) seems to live exclusively on bird dung in the subAntarctic Magallanes ecoregion (Jofre *et al*. 2011). In fact, it may be restricted to the dung of the Upland Goose, ***Chloephaga picta*** (Figure 34).

Figure 30. ***Megaphorura arctica***, a springtail that lives among mosses under cliffs where guano drips. Photo by Arne Fjellberg, through Creative Commons.

Figure 31. ***Sanionia uncinata***, a moss that seems to benefit from bird drippings on cliffs. Photo by Michael Lüth, with permission.

Figure 32. ***Polytrichastrum alpinum***, a moss that lives under bird drippings on cliffs. Photo by Michael Lüth, with permission.

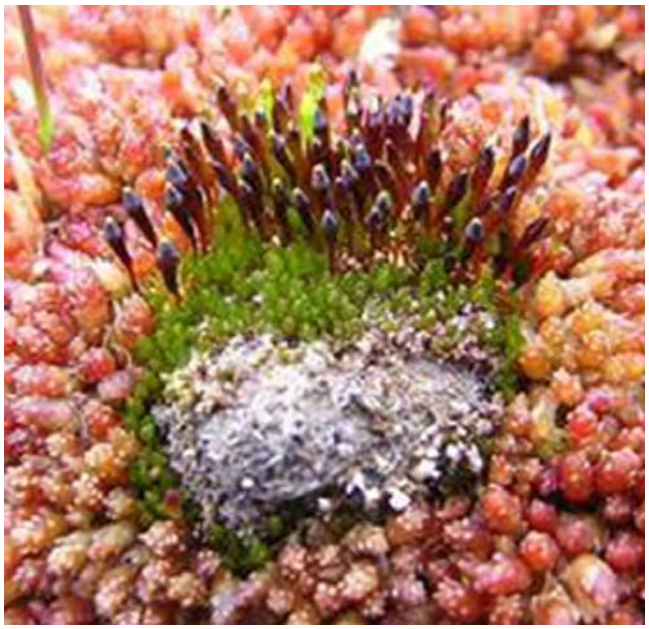

Figure 33. ***Tayloria dubyi*** with capsules, a species that lives on bird dung, especially of the Upland Goose, in the subAntarctic Magallanes ecoregion. Photo by Jocelyn Jofré, through Creative Commons.

Figure 34. ***Chloephaga picta***, Upland Goose, the bird whose dung provides the substrate for ***Tayloria dubyi*** in the subAntarctic. Photo by Fabien Dany <www.fabiendany.com>, with online permission.

But not all guano benefits are restricted to polar regions. In western North Carolina, USA, it is not the seabirds bringing oceanic nutrients to the cliffs, but rather nitrogen sources originate in the highly productive forests and are transferred to nutrient-poor terrestrial cliffs by birds (Langevin 2015). Among these, in particular, are common Ravens (***Corvus corax***; Figure 35) and Peregrine Falcons (***Falco peregrinus***; Figure 36). These birds frequently nest on cliffs in the southern Appalachian Mountains, excreting N-rich guano that increases the nitrogen below the nesting sites. Langevin showed that the ammonia levels were significantly higher below the nest sites. Likewise, there was a significant difference in vegetation, with particular lichens known to prefer high N being more common there. Beneficial effects of these forest N sources on bryophytes remain to be documented.

Figure 35. ***Corvus corax***, Raven, a species that brings nutrients from rich forests to cliffs where the nutrients are deposited as guano. Photo by Ingrid Taylar, through Creative Commons.

Figure 36. ***Falco peregrinus***, Peregrine Falcon and guano on cliff edge where it perches. Photo by Mike Baird through Creative Commons.

But guano does not always favor the mosses. In the polar Mac. Robertson Land, guano has reached toxic levels, making the coastal slopes barren of mosses and lichens (Bergstrom & Seppelt 1990). This is largely due to Antarctic Petrels (***Thalassoica antarctica***; Figure 37) that breed along these slopes, with a mean nest density of 0.82 m^{-1} (Alonso *et al.* 1987)! But the area also serves as breeding grounds for Southern Fulmars (***Fulmarus glacialoides***; Figure 38) and Adélie Penguins (***Pygoscelis adeliae***; Figure 39).

Figure 37. ***Thalassoica antarctica***, Antarctic Petrel flying. Photo by François Guerraz, through Creative Commons.

Figure 38. ***Fulmarus glacialoides***, Antarctic Fulmar roosting; their guano prevents establishment of bryophytes. Photo by Samuel Blanc, through Creative Commons.

Penguins

Penguins deserve special note because of their extensive role in N transfer from rich oceanic sources to land in the Antarctic. Cocks *et al*. (1998) reported a range of 13.1-25.9% of the Antarctic N to be from seabird guano, with similar results in other studies (Erskine *et al*. 1998; Bokhorst *et al*. 2007a, b; Lee *et al*. 2009). Wasley *et al*. (2012) interpreted this input to be from ancient penguin rookeries (Figure 39) that have been abandoned for thousands of years (Emslie & Woehler 2005). Bryophytes have elevated δ15N signatures (>15%), indicating their use of animal-derived N through repeated trophic transfer by microbial activity since the original deposition.

Figure 39. ***Pygoscelis adeliae***, Adelie Penguin on Antarctica, illustrating the large number of birds that can create guano. Photo by Murray Foubister, with permission

In the case of the Adelie Penguin (***Pygoscelis adeliae***; Figure 39), dung left 3000-8000 years ago remains, at least partly frozen in ice (Gill 2012). Mosses are able to derive nutrients from these deposits, giving them much needed resources that are so scarce in the sand and gravel substrate of Antarctica.

Penguin rookeries on King George Island in the maritime Antarctic are an important source of nutrients and have a strong influence on the vegetation patterns and diversity (Smykla *et al*. 2007). The nutrient input, as guano, creates a zonation pattern. The first zone includes those areas under the immediate influence of fresh guano and trampling, supporting little or no vegetation. The second zone is adjacent to the first and is covered with nitrogen-loving green algae and sometimes Cyanobacteria. The third zone is dominated by Antarctic hair-grass. The fourth zone is dominated by mosses. The fifth and last zone under the rookery influence is dominated by lichens.

Peatland Habitats

Brewer (1967) pointed out that studies on bog vegetation were much more numerous than those on the animal populations. To help remedy this situation, he studied the breeding bird populations on two peatlands in lower Michigan. In the years 1961-1966 he noted 24 species of breeding birds in Portage Bog. These included the Song Sparrow (***Melospiza melodia***; Figure 40), Field Sparrow (***Spizella pusilla***; Figure 41), Yellowthroat (***Geothlypis trichas***; Figure 42), Yellow Warbler (***Setophaga petechia***; Figure 43), Nashville Warbler (***Leiothlypis ruficapilla***; Figure 44), Eastern Towhee

(***Pipilo erythrophthalmus***; Figure 45), Brown-headed Cowbird (***Molothrus ater***; Figure 46), Catbird (***Dumetella carolinensis***; Figure 47), American Goldfinch (***Carduelis tristis***; Figure 48), Traill's Flycatcher (***Empidonax traillii***; Figure 49), Black-capped Chickadee (***Poecile atricapillus***; Figure 50), Mourning Dove (***Zenaida macroura***; Figure 51), Cedar Waxwing (***Bombycilla cedrorum***; Figure 52), Yellow-shafted Flicker (***Colaptes auratus***; Figure 53), Cardinal (***Cardinalis cardinalis***; Figure 54), Brown Thrasher (***Toxostoma rufum***; Figure 55), Ruby-throated Hummingbird (***Archilochus colubris***; Figure 56), Mallard (***Anas platyrhynchos***; Figure 57), Marsh Hawk (***Circus cyaneus***), Eastern Bluebird (***Sialia sialis***; Figure 58), Tree Swallow (***Tachycineta bicolor***; Figure 59), Robin (***Turdus migratorius***; Figure 60), Whip-poor-will (***Caprimulgus vociferus***; Figure 61), and Veery (***Catharus fuscescens***; Figure 62). Among these, the Mallards were the only species for which the researchers located a nest, and the nest occurred in three of the six years. About 425 pairs were located there per hectare. Brown-headed Cowbirds were the most dense and Song Sparrows were the most abundant, the latter having an average of 138 territorial males per hectare. Others with a density of more than 24 per hectare were Yellowthroats, Field Sparrows, Eastern Towhees, and, perhaps, Brown-headed Cowbirds.

Figure 40. ***Melospiza melodia***, Song Sparrow, a species that commonly occurs in bogs during breeding season. Photo by Len Blumin, through Creative Commons.

Figure 41. ***Spizella pusilla***, Field Sparrow, a species that commonly occurs in bogs during breeding season. Photo by Jeff Whitlock, through Creative Commons.

Figure 42. ***Geothlypis trichas***, Yellowthroat, a species that commonly occurs in bogs during breeding season. Photo by Dan Pancamo, through Creative Commons.

Figure 43. ***Setophaga petechia***, Yellow Warbler, a species that commonly occurs in bogs during breeding season. Photo by Dick Daniels, through Creative Commons.

Figure 44. ***Leiothlypis ruficapilla***, Nashville Warbler, a species that commonly occurs in bogs during breeding season. Photo by Jerry Oldeneffel, through Creative Commons.

Figure 45. ***Pipilo erythrophthalmus***, Eastern Towhee, a species that commonly occurs in bogs during breeding season. Photo by Ken Thomas, through Creative Commons.

Figure 48. ***Carduelis tristis***, American Goldfinch, a species that commonly occurs in bogs during breeding season. Photo by MDF, through Creative Commons.

Figure 46. ***Molothrus ater***, Brown-headed Cowbird, a species that commonly occurs in bogs during breeding season. Photo through Creative Commons.

Figure 49. ***Empidonax traillii***, Willow Flycatcher, a species that commonly occurs in bogs during breeding season. Photo by Dominic Sherony, through Creative Commons.

Figure 47. ***Dumetella carolinensis***, Grey Catbird, a species that commonly occurs in bogs during breeding season. Photo by Steve, through Creative Commons.

Figure 50. ***Poecile atricapillus***, Black-capped Chickadee, a species that commonly occurs in bogs during breeding season. Photo by Zac Cota, through Creative Commons.

Figure 51. ***Zenaida macroura***, Mourning Dove, a species that commonly occurs in bogs during breeding season. Photo by R. L. Sivaprasad, through Creative Commons.

Figure 52. ***Bombycilla cedrorum***, Cedar Waxwing, a species that commonly occurs in bogs during breeding season. Photo by Cephas, through Creative Commons.

Figure 53. ***Colaptes auratus***, Yellow-shafted Flicker, a species that commonly occurs in bogs during breeding season. Photo by Minette Layne through Creative Commons.

Figure 54. ***Cardinalis cardinalis***, Cardinal in snow in Pickerington, OH, USA, a species that commonly occurs in bogs during breeding season. Photo courtesy of Eileen Dumire.

Figure 55. ***Toxostoma rufum***, Brown Thrasher, a species that commonly occurs in bogs during breeding season. Photo by E. Monk, through Creative Commons.

Figure 56. ***Archilochus colubris***, Ruby-throated Hummingbird, a species that commonly occurs in bogs during breeding season. Photo by Dan Pancamo, through Creative Commons.

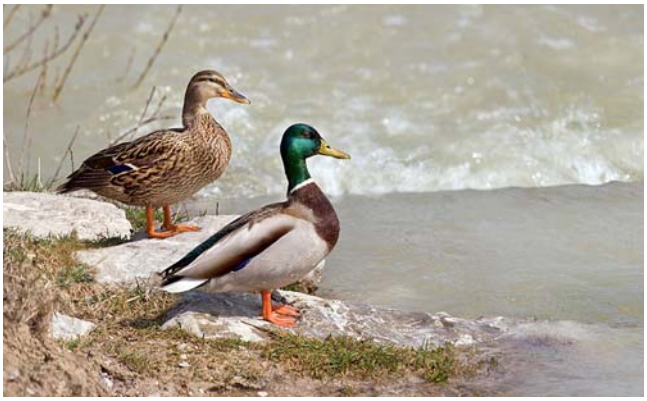

Figure 57. ***Anas platyrhynchos*** female (left) and male (right), a species that commonly breeds and nests in bogs. Photo by Richard Bartz through Wikimedia Commons.

Figure 58. ***Sialia sialis***, Bluebird male, a species that commonly breeds in bogs. Photo from Sandy's Photos 2009, through Creative Commons.

Figure 59. ***Tachycineta bicolor***, Tree Swallow, a species that commonly occurs in bogs during breeding season. Photo by John Benson, through Creative Commons.

Figure 60. ***Turdus migratorius***, Robin, a species that commonly occurs in bogs during breeding season. Photo by Dakota Lynch, through Creative Commons.

Figure 61. ***Caprimulgus vociferus***, Whip-poor-will, a species that commonly occurs in bogs during breeding season. Photo by Jerry Oldeneffel, through Creative Commons.

Figure 62. ***Catharus fuscescens***, Veery, a species that commonly occurs in bogs during breeding season. Photo by Dominic Sherony, through Creative Commons.

In bogs studied by Brewer (1967), as the high thicket gave way to low thicket, some of the bird species changed, including the arrival of the Nashville Warbler (***Leiothlypis ruficapilla***; Figure 44) in 1965. The trees in the bog were not suitable for cavity-nesting birds during the study. Among these birds, Field Sparrows (***Spizella pusilla***; Figure 41) preferred open bog and Song Sparrows

(***Melospiza melodia***; Figure 40) preferred thickets, as did the Towhee (***Pipilo erythrophthalmus***; Figure 45), Yellowthroat (***Geothlypis trichas***; Figure 42), and Catbird (***Dumetella carolinensis***; Figure 47). The number of species in the open bog was about 13, whereas in the thicket it was about 21. When examining peatlands on a larger scale, Niemi and Hanowski (1992) found 110 species of birds that frequented Minnesota peatlands.

Brewer (1967) concluded that most of the birds came to the bog only for feeding. For example, Robins (***Turdus migratorius***; Figure 60) nested in the deciduous areas but came to the bog for feeding. This was especially true when berries were ripe, with both juveniles and adults coming to feed. Based on these habitat relationships, it is not surprising that most of the species in this bog were forest edge species. Brewer also considered it likely that some of the visitors, like the Meadowlark (***Sturnella magna***; Figure 63), mistook the open bog for an open field.

Figure 63. ***Sturnella magna***, Eastern Meadowlark, a bird that may occasionally mistake an open bog or fen for an open field. Photo by Jim F. Bleak, through Creative Commons.

Brewer (1967) only observed birds in the Sugarloaf Bog for two years. This site had 26 breeding bird species during that time, with the average per year of about 20 species. The density was high, with about 675 males per hectare. The **Black-capped Chickadee** (***Poecile atricapillus***; Figure 50) was the most abundant, with about 100 males per hectare (compared to 10 at Portage Bog).

Only nine species were common to both locations (Brewer 1967). In a larger study based on literature, Brewer found that there is little commonality among species of the open bog. Birds of the spruce forest, on the other hand, are similar to those of a cedar forest or a spruce thicket. It became clear that species of the bogs depended on the vegetation of that stand and on the vegetation of adjacent areas, as well as the geographic distribution of the species. Few birds were present in the winter, reflecting the poor winter food supply and insufficient cover.

Calmé and Desrochers (1999, 2000) and Calmé *et al*. (2002) investigated the birds in 67 southern Quebec, Canada, peatlands. They expressed concern over the loss of peatlands to urban sprawl, agriculture, forestry, and peat mining, particularly in eastern Canada (Calmé & Desrochers 2000). This loss further fragments the peatlands, making natural re-introductions more difficult. This isolation causes the peatlands and their bird populations to behave with island dynamics. Among ten species of birds studied in detail, two rely primarily on peatlands for nesting sites. Bird species richness was primarily related to microhabitat richness and heterogeneity. The Palm Warbler (***Dendroica palmarum***; Figure 64) and Upland Sandpipers (***Bartramia longicauda***; Figure 65) depended on having larger, non-isolated peatlands.

Figure 64. ***Dendroica palmarum***, Palm Warbler, a species that depends on large, non-isolated peatlands. Photo by Wolfgang Wander, through Creative Commons.

Figure 65. ***Bartramia longicauda***, Upland Sandpiper, a species that depends on large, non-isolated peatlands. Photo by Johnath, through Creative Commons.

Calmé *et al*. (2002) found 17 species of birds that were significantly more frequent in peatlands than in the surrounding habitats. For some, the peatland was one of several habitats, but some were significantly more frequent in peatlands.

In studying 28 southeastern Quebec, Canada, peatlands, Desrochers *et al*. (1998) found that harvesting

effects on birds depended on the type of harvesting. Block harvesting had the least effect, presumably because it retained most of the topography and microhabitats. Vacuum harvesting, on the other hand, did alter the bird communities. Ten of the 28 species responded negatively to peatland perturbation. The Palm Warbler (***Dendroica palmarum***; Figure 64), in particular, was closely associated with the unperturbed sites.

The Palm Warbler (***Dendroica palmarum***; Figure 64) is an area-sensitive bird and in southern Québec it is restricted to peatlands (Poulin 2002). The within-site habitat configuration strongly affects the physical efficiency of this species but not necessarily functional effectiveness. While it is clear that having a number of peatlands available is important to the Palm Warbler, the biological factors they provide remain elusive.

When Lachance *et al.* (2005) investigated 16 peatlands in southern Quebec, Canada, they found 36 bird species and 154 plant species. They found that afforestation altered the vegetation structure in ways that changed the bird species composition. In particular, there were fewer mosses and shrubs, but more trees.

One reason for the diminished number of birds in disturbed peatlands is the loss of eggs and nestlings to predation. Haddad *et al*. (2000) assessed the effects of harvesting peat mosses on the survival of bog-dwelling songbirds [Palm Warbler (***Dendroica palmarum***; Figure 64), Common Yellowthroat (***Geothlypis trichas***; Figure 42), Hermit Thrush (***Catharus guttatus***; Figure 66), and several species of sparrows (**Passeridae**; Figure 40-Figure 41)]. They found greater risk of nest predation in harvested bogs.

Figure 66. ***Catharus guttatus***, Hermit Thrush, a species that loses more eggs to predation in harvested bogs than in undisturbed bogs. Photo by Cephas, through Creative Commons.

Another possibility to explain loss of birds on harvested peatlands is disruption of the habitat of food organisms. **Diptera** larvae, especially the cranefly ***Tipula*** (Figure 67), live and pupate among the mosses in the peatland (MacLean 1980). The birds consume 35-70% of annual production of ***Tipula carinifrons*** and consume 50% of adults at peak emergence. The cranefly larvae feed on liverworts in these bogs (Coulson & Whittaker 1978). Paasivirta *et al*. (1988) likewise noted the importance of emerging insects for feeding birds in peatlands.

Figure 67. ***Tipula***, leatherjacket larva, a genus that is eaten in great numbers by birds in bogs. Photo by Rasbak, through Creative Commons.

Effects on Bryophyte Community Structure

Birds can have considerable influence on bryophyte communities, especially in Arctic wetlands. We have already seen that guano from seabirds can provide nutrients that are otherwise limiting. And Pheasants (Figure 68) can disrupt the community while searching for food (Erkamo 1976).

Figure 68. ***Phasianus colchicus***, Pheasant, a forager that can disturb bryophytes while foraging. Photo by Hugh J. Griffiths, through Creative Commons.

In the Arctic, **geese** (Figure 69) can play a role in community structure (Jasmin *et al*. 2008). Although one might expect such feeding disruption to reduce the number of species, Jasmin and coworkers found greater bryophyte species richness following 11 years of goose presence, compared to that in goose exclosures. The non-protected areas exhibited more variation in time and space than within the exclosures, promoting greater coexistence of bryophyte species at the microscale of 1 cm.

Figure 69. ***Chen caerulescens***, migratory Snow Geese, foraging. Photo by Bradley Davis, through Creative Commons.

Conservation Issues

Agricultural areas might actually help bird species diversity in tropical forests (Hughes *et al.* 2002; Sekercioglu *et al*. 2007). Although we typically think of deforestation for agriculture as being detrimental to bird diversity, researchers found that most of the 144 bird species used the agricultural areas for foraging, often travelling several kilometers from their forest home (Hughes *et al.* 2002). They estimated that 46% of the native birds were using the agricultural countryside in southern Costa Rica. The authors suggest that diversity will suffer less if tall trees and edge habitats are maintained.

In an effort to understand how to protect birds with minimal effort, we have often chosen indictor species (Simberloff 1998). Unfortunately, these are not as indicative as we might hope. It is difficult to know what species should be the indicator and on just what it should indicate. Simberloff suggested instead that the species should be an "umbrella species,... one that needs such large tracts of habitat that saving it will automatically save many other species."

A flagship species is typically a charismatic large vertebrate, such as the panda or a snowy owl (Anonymous, USDA; Simberloff 1998). It is useful because it causes both public interest and sympathy (Simberloff 1998). It suffers some of the same problems – it may not be in an area that protects many other species, and it might be expensive to protect. And management of one flagship species may conflict with that of managing another. "The recognition that some ecosystems have keystone species whose activities govern the well-being of many other species suggests an approach that may unite the best features of single-species and ecosystem management. If we can identify keystone species and the mechanisms that cause them to have such wide-ranging impacts, we would almost certainly derive information on the functioning of the entire ecosystem that would be useful in its management."

Even keystone species can get complicated. As seen in a Colorado subalpine ecosystem, there may be subtle interdependencies (Daily *et al*. 1993). The Red-naped Sapsuckers (***Sphyrapicus nuchalis***; Figure 70) actually have two keystone roles. Their excavation activities to make nests in fungus-infected aspens are essential to two species of swallows, and when they drill sap wells into willows they nourish not only themselves, but also make this rich food source available to Hummingbirds (Figure 56), Orange-crowned Warblers (***Vermivora celata***; Figure 71), chipmunks (***Tamias striatus***), and other sap robbers. Thus for this community to persist, it requires the complex interactions of sapsuckers, willows, aspens, and a heartwood fungus.

As an example, the penguin (Figure 39) can be a keystone species in the maritime Antarctic (Barcikowski *et al*. 2005). We have seen above that the guano produced by the penguins can form the base for an entire community by providing an important supplement to the rare nutrients. In areas where the guano enriches the substrate with nutrients originating in the ocean, the grasses *Colobanthus quitensis* (Figure 72) and *Deschampsia antarctica* (Figure 73) predominate. Where the guano is absent, mosses such as ***Polytrichum piliferum*** (Figure 74) predominate.

Figure 70. ***Sphyrapicus nuchalis***, Red-naped Sapsucker, a keystone bird species. Photo by Dominic Sherony, through Creative Commons.

Figure 71. ***Vermivora celata***, Orange-crowned Warbler, a species that depends on the Red-naped Sapsucker as a keystone species. Photo by Linda Tanner, through Creative Commons.

Figure 72. ***Colobanthus quitensis***, a dominant Antarctic species in areas enriched by guano. Photo by John Clark, through Creative Commons.

Figure 73. ***Deschampsia antarctica***, a dominant Antarctic species in areas enriched by guano. Photo by John Clark, through Creative Commons.

Figure 74. ***Polytrichum piliferum***, a moss that avoids areas with guano in the maritime Antarctic. Photo by Bob Klips, with permission.

To put this in a bryological perspective, we may find that a species is dependent on mosses in spring before herbaceous plants are available or in winter when tracheophytes cease growing. The bryophytes might depend on one or more species of birds for the bulk of their dispersal. Or the bryophytes might serve as emergency foods during years when the weather is not suitable for good productivity of other, more preferred foods. With so many possibilities, we have just begun to understand the interrelationships.

Dispersal Agents

If you have ever reared Zebra Finches (***Taeniopygia guttata***; Figure 75), you know that they are incessant nest-builders. It was impossible to keep mosses in my garden room when I had finches because these mosses were prime nest-building material. But as you would also observe, not all selected mosses made it to the nest. Pieces would fall as the birds flew, and even the nest itself would occasionally lose pieces, but fragments would especially get dropped beneath the nest as the building progressed, in some cases deliberately as the birds determined that piece to be too recalcitrant to become part of the architecture.

In addition to fragments and propagules travelling among feathers, it is also possible for bryophyte parts to travel in the digestive system of birds (Behling *et al*. 2016). On Navarino Island, at the Cape Horn Biosphere Reserve, these researchers recovered bryophyte diaspores from fecal samples from the Upland Goose (***Chloephaga picata***; Figure 34) and the White-bellied Seedsnipe (***Attagis malouinus***). Viability remains to be established.

Figure 75. ***Taeniopygia guttata***, Zebra Finch, a pet that is an incessant nest builder and uses mosses, among other things. Photo from Sky High Butterfly, through Creative Commons.

Davison (1976) describes the role of birds in the dispersal of mosses. Indeed, it was not the nest-building activities, but feeding activities that caught his attention. Where leaf litter is somewhat scarce, such as older beech woods, and mosses are abundant, foraging requires that the birds poke around among the mosses. **Blackbirds** (***Turdus merula***, Figure 76) in particular foraged among ***Mnium hornum*** (Figure 25) and ***Polytrichastrum formosum*** (Figure 77), breaking the plants and scattering them much like the Japanese do when planting a moss garden. Davison reports that within a two-month period these birds moved 34 clumps of moss from one place to another within an area of about 5 m^2, but also brought to the area an additional 18 pieces.

Figure 76. ***Turdus merula*** (Blackbird), a species that forages among ***Mnium hornum*** and ***Polytrichastrum formosum***. Photo by Mario Modesto Mata through GNU Free Documentation.

Figure 77. ***Polytrichastrum formosum***, a moss where Blackbirds forage, disturbing the moss. Photo by David T. Holyoak, with permission.

But it appears that might not be the only reason to cause **Blackbirds** (***Turdus merula***; Figure 76) to scatter bryophytes. Robin Stevenson reports (Bryonet 25 April 2010) observing a male of this same species of bird throwing clumps of mosses off a roof, alternately with mid air attacks by another Blackbird – a classic example of displacement! There was too much activity to discern if both birds were moss throwers. Apparently the two were fighting over territory or some other disagreement and the mosses were handy objects to throw from their rooftop habitat. In this case, the lucky roof mosses were ***Grimmia pulvinata*** (Figure 78), ***Hypnum cupressiforme*** (Figure 79), and ***Syntrichia montana*** (Figure 80). When on the ground they threw cockle shells and other things.

Figure 78. ***Grimmia pulvinata***, a moss thrown about by a Blackbird during a territorial competition. Photo by Michael Lüth, with permission.

In another instance, Davison (1976) found spores of a moss on the feet of a dead Song Thrush (***Turdus philomelos***; Figure 81). Although most of the scavenging activity probably only transports moss fragments and spores for short distances, spores might occasionally be transported by feet, feathers, and beaks to considerable distances following such activity.

Figure 79. ***Hypnum cupressiforme***, a species thrown about by Blackbirds in displacement activity. Photo by Jan-Peter Frahm, with permission.

Figure 80. ***Syntrichia montana*** (Intermediate Screw-moss), a species thrown about by Blackbirds in displacement activity. Photo by Barry Stewart, with permission.

Figure 81. ***Turdus philomelos***, Song Thrush, a bird known to carry mosses on its feet. Photo by Brian Eversham, with permission

But birds are imperfect in their industrious movement of moss from natural substrate to nest. Bits fall, and hence alight in a new location. This facilitated dispersal, while

somewhat random, can be quite helpful in moving rarely fruiting mosses about. Chmielewski and Eppley (2019) found that when birds use bryophyte-covered areas for foraging and gathering nesting material, they can acquire propagules on their legs, feet, and tails. The researchers successfully germinated propagules from among the 242 propagules and 1512 spores they collected from 224 birds, comprised of bird 34 species. They found the tail feathers to be the greatest dispersal agents among bark and foliage species. Hence, birds are potential dispersal agents.

The Pintail Duck (***Anas acuta***; Figure 82) is a likely agent of dispersal of ***Riccia rhenana*** (Figure 83) (McGregor 1961). In this liverwort, the older parts die, but the apices survive two months of drought and five weeks submersion in ice, making it likely that they would survive transport among the feathers of the Pintail Duck.

Figure 82. ***Anas acuta***, Northern Pintail male and female, agents of aquatic bryophyte dispersal, especially ***Riccia rhenana***. Photo by J. M. Garg, through Creative Commons.

Figure 83. ***Riccia rhenana***, a species dispersed by pintail ducks. Photo by Štěpán Koval, with permission.

Lewis *et al*. (2014b) suggested that ***Tetraplodon*** (Figure 84) species were distributed long-distances by birds. They reasoned that the absence of wind patterns to account for their distribution in the New World and the sensitivity of the spores to extreme environmental conditions, bird dispersal, probably on feathers, was the most reasonable explanation. In support of this possibility, Lewis *et al*. (2014a) demonstrated bryophyte diaspores among the feathers of transequatorial migrant birds.

Figure 84. ***Tetraplodon mnioides*** with mature capsules; this species may be distributed by birds. Photo by Richard Caners, with permission.

Des Callaghan filmed a site where the White Wagtail (***Motacilla alba***; Figure 85) frequently perches on a particular branch. That branch is covered by ***Splachnum vasculosum*** (Figure 86-Figure 87). Does the bird simply like the soft moss and its location? Is the moss dispersed by the feathers and feet of the birds? Or might it be deposited in feces, indicating the birds ate the capsules?

Figure 85. ***Motacilla alba alba***, White Wagtail, a species that spends much time on a branch with ***Splachnum vasculosum*** in Wales. Photo by Luis Garcia, through Creative Commons.

Figure 86. ***Splachnum vasculosum*** growing on a branch next to a stream and the site where the White Wagtail, ***Motacilla alba***, prefers to perch. Photo courtesy of Des Callaghan.

Figure 87. ***Splachnum vasculosum*** capsules. Photo by Dick Haaksma, with permission.

In some way the petrels and other sea birds seem to be responsible for the locations of members of **Calymperaceae** in the Chathams and other areas around New Zealand. Fife and Lange (2009) suggest dispersal by birds. They consider it likely that the sea birds may have contributed to dispersal of the moss ***Calymperes tenerum*** (Figure 88) on the Chatham Islands and the Kermadecs to the north and east of New Zealand, respectively. Peter de Lange (pers. comm. 12 June 2017) reported that until 80-100 years ago, Tube Nose Petrels, especially ***Pterodroma*** spp. (Figure 92-Figure 93), were influential, but Broad-billed Prions (***Pachyptila vittata***) and shearwaters (***Puffinus griseus***; Figure 89) also were common in the areas where ***Calymperes*** grows now, but that these birds disappeared 80-100 years ago.

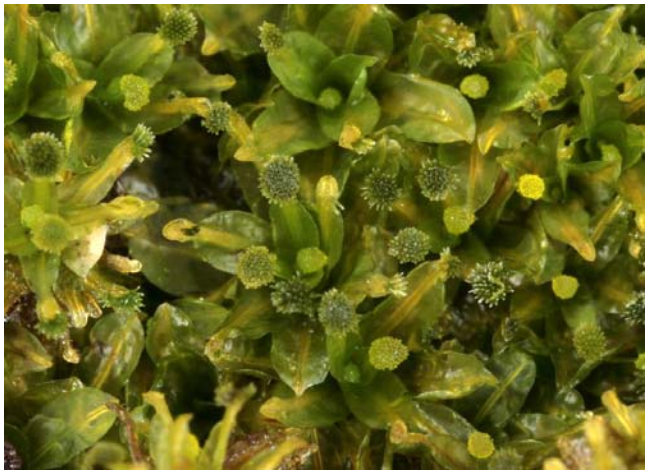

Figure 88. ***Calymperes tenerum***, a species that may have been dispersed long distance by the Shearwater. Photo by Jan-Peter Frahm, with permission.

Later, de Lange (Peter de Lange, pers. comm. 12 June 2017) found ***Syrrhopodon armatus*** (Figure 90-Figure 91) on the smallest of the main Chatham Island, Rangatira. This island is free of predators and supports a million plus seabirds. The ***S. armatus*** grows on tree trunks that are used by the petrels and Broad-billed Prions (***Pachyptila vittata***) as runways. They also grow around the burrows of these birds, especially those of the Chatham Petrel (***Pterodroma axillaris***). On Rabbit Island, ***Syrrhopodon*** grows around the active burrows of shearwaters (***Puffinus griseus***; Figure 89) and diving petrels.

Figure 89. ***Puffinus griseus***, Sooty Shearwater, a possible dispersal agent for ***Calymperes tenerum*** (Figure 88). Photo from USGS photograph by Jonathan Felis, through public domain.

Figure 90. ***Syrrhopodon***, a genus that might be dispersed by sea birds in islands around New Zealand. Photo by Jan-Peter Frahm, with permission.

Figure 91. ***Syrrhopodon armatus*** leaf, a possible propagule carried by sea birds to islands around New Zealand. Photo from Natural History Museum, London, through Creative Commons.

In addition to these islands, on the Chatham island of Rekohu and the Pitt island of Rangiuria, ***Calymperes*** (Figure 88) is found only in locations there the

pterodromids once had dense nesting locations, as indicated by remains of their burrows (Peter de Lange, pers. comm. 12 June 2017). At the location where de Lange first found ***C. tenerum*** (Figure 88) there are still seabirds, including Taiko (***Pterodroma magentae***), a critically endangered species (Fife 2009).

In New Zealand at Te Paki, ***Calymperes*** (Figure 88) again is associated with ***Pterodroma nigripennis*** (Figure 92) and ***P. gouldi*** (Peter de Lange, pers. comm. 12 June 2017). And on Raoul Island, all the locations found by de Lange were also in areas frequented by the Kermadec Petrel (***Pterodroma neglecta neglecta***; Figure 93) until the rats wiped them out early in the 20th Century. As on the Chatham Islands, the birds used the trees with ***Calymperes*** (Figure 88) as runways.

Figure 92. ***Pterodroma nigripennis***, a species that seems to be associated with ***Calymperes*** (Figure 88) and may disperse it. Photo by Christopher Watson, through Creative Commons.

Figure 93. ***Pterodroma neglecta***, Kermadec Petrel, a species always found with ***Calymperes*** on Raoul Island. Photo by Lance Andrewes, through Creative Commons.

On the Poor Knights Islands, Jessica Beever has similarly collected ***Syrrhopodon armatus*** (Figure 90-Figure 91) associated with a heavily burrowed petrel area (Allan Fife, pers. comm. 12 June 2017).

Based on what we know about these seabird-**Calymperaceae** relationships there are three plausible explanations for the relationships. The birds may fertilize the bark with guano, thus providing nitrogen for the mosses. The birds may serve as dispersal agents. The mosses may provide foraging substrate for the birds. Felicisimo *et al*. (2008) provided evidence that the Cory's Shearwater (***Calonectris diomedea***; Figure 94) follows wind patterns that could explain dispersal patterns. Cameron *et al*. (2006) have suggested that Buller's Shearwater (***Puffinus bulleri***; Figure 95) best explains the presence of the fern *Asplenium pauperequitum* on the Chatham Islands group, a distance of 1245 km from its nearest neighbor. This bird is a New Zealand endemic species and has large breeding populations on the Poor Knights Islands where *Asplenium pauperequitum* was originally described (Allan Fife, pers comm. 12 June 2017). In the Chathams it does not breed, but it is a regular visitor. Any and all of these explanations for the **Calymperaceae**-seabird associations may be true.

Figure 94. ***Calonectris diomedea***, Cory's Shearwater flying, permitting it to disperse bryophytes over long distances. Photo by A. H. Kopelman, through Creative Commons.

Figure 95. ***Puffinus bulleri***, Buller's Shearwater, a species that might disperse mosses to islands near New Zealand. Photo by Tom Tarrant, through Creative Commons.

Chmielewski (2015) sought to support these suggestions by culturing propagules found on birds caught with mist nets. Using cotton swabs, he sampled feet, legs, and flight feathers. The spores obtained were cultured on nutrient agar. The resulting bryophyte plants were identified by PCR amplification and Sanger sequencing of the trnL region of the chloroplast genome. We shall have

to look forward to the revelation of these species when this work is published.

Dispersal of bryophytes by birds is discussed in more detail in subchapters 4-9 and 4-11 of Volume 1.

Soft Landings

Pole jumpers have sand pits or mats to protect them when they land. To me it seems reasonable that birds might choose soft landing sites as well. Birds in captivity often get a condition known as **bumblefoot** (Figure 96) (Halliwell 1975; Hawkey *et al*. 1985), but the condition can occur in wild populations, albeit much less commonly (Gentz 1996). Bumblefoot can be caused by rough perches, sandpaper on the perch, sharp corners, dirty perches, or all perches of the same size. In the wild these problems are largely absent, explaining the scarcity of bumblefoot in nature. Do wild birds select landing spots on the basis of the presence of the spongy bryophytes and lichens (Figure 97)?

Figure 96. Eagle bumblefoot, a common condition for birds of prey in captivity. Photo by Richard Jakowski, through Creative Commons.

Figure 97. Bird on moss perch – Is it a sentinel, or just cooling its feet on the moss? Photo by Ervin Gjata, through public domain.

Summary

Birds interact with bryophytes by foraging among them, eating them, eating capsules, getting a drink, building nests or parts of nests with them, using them as breeding grounds, using moss hummocks as **watch towers**, throwing them in displacement behavior, bathing among them, and getting dry on them. On the other hand, the birds may help the bryophytes as dispersal agents and by providing fertilizer as guano. Or they may seriously disturb them during their foraging. Others provide so much guano that the bryophytes are intolerant of it. Soft bryophytes might also help to prevent bumblefoot in wild birds.

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CHAPTER 16-2
BIRDS AND BRYOPHYTIC FOOD SOURCES

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CHAPTER 16-2
BIRDS AND BRYOPHYTIC FOOD SOURCES

Figure 1. ***Branta bernicla hrota***, Brant, juvenile foraging; foods include bryophytes. Photo by MPF, through Creative Commons.

Many birds do depend on bryophytes for food. Some eat the leafy gametophytes, especially in the Arctic. Others use the more nutrient-rich capsules. And others, probably many more than we know, forage for macroinvertebrates among the bryophytes, especially epiphytes.

Capsules

A. J. Grout, one of the earliest of North American bryologists, observed birds pecking the capsules of ***Polytrichum commune*** (Figure 2), a story retold by Lewis Anderson (Bryonet 10 April 2003). To this story, Frank Cook (Bryonet 15 May 2001) contributed his own observations of White-throated Sparrows (***Zonotrichia albicollis***; Figure 3) "vigorously nipping the capsules from ***Polytrichum*** in a white pine (***Pinus strobus***; Figure 4) stand in Algonquin Park, Ontario.

Figure 2. ***Polytrichum commune*** capsules, food for White-throated Sparrows (***Zonotrichia albicollis***) and Norwegian Grouse (***Tetrao urogallus***?) chicks. Photo by Bob Klips, with permission.

Figure 3. ***Zonotrichia albicollis***, White-throated Sparrow, a consumer of ***Polytrichum*** capsules. Photo by Dorothy Pugh, with permission.

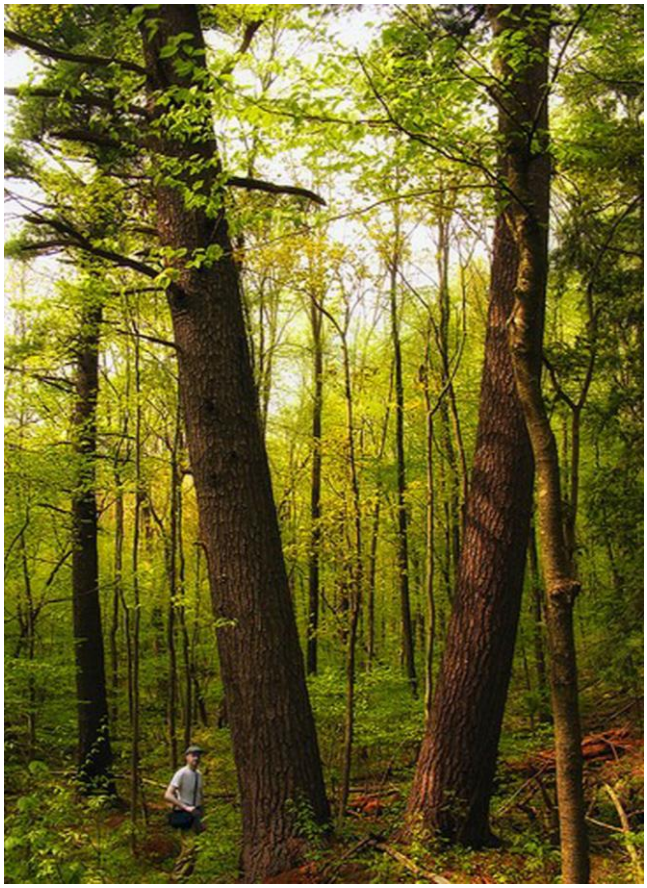

Figure 4. ***Pinus strobus*** (white pine) forest, Pennsylvania. Photo by Nicholas T., through Creative Commons.

Richardson (1981) reported moss-feeding by mammals and birds in northern areas. Capsules of ***Bryum*** (Figure 5) and ***Polytrichum*** (Figure 2) are eaten by the Norwegian Grouse chicks (***Tetrao urogallus***?; Figure 6), apparently as the main food, whereas other kinds of capsules are eaten by Scottish Red Grouse (***Lagopus lagopus scotica***; Figure 7) (Lid & Meidell 1933). The Wyoming Sage Grouse (***Centrocercus urophasianus***; Figure 8) eats small amounts of moss, Snow Buntings (***Plectrophenax nivalis***; Figure 9) eat ***Bryum algovicum*** capsules (Figure 10), and the Moorhen (***Gallinula chloropus***; Figure 11), Blackbird (***Turdus merula***; Figure 12), Song Thrush (***Turdus philomelos***; Figure 13), and Fieldfare (***Turdus pilaris***; Figure 14) all eat mosses. In Britain, the Blue Tits (***Cyanistes caeruleus***; Figure 15) and Marsh Tits (***Poecile palustris***; Figure 16) feed on capsules of ***Dicranoweisia cirrata*** (Figure 17) (Betts 1955). Catherine La Farge reported on Bryonet (15 January 2008) that high Arctic moss capsules are consumed by lemmings and Arctic hares. Thus it would not be surprising if birds also consume them when the capsules are still green.

Figure 5. ***Bryum arcticum*** with capsules that serve as food for Norwegian Grouse (***Tetrao urogallus***?) chicks in Norway. Photo by Michael Lüth, with permission.

Figure 6. ***Tetrao urogallus***, Norwegian Grouse female, on moss. Chicks of this species eat capsules of ***Bryum*** and ***Polytrichum***. Photo by Honza Sterba, through Creative Commons.

Figure 7. ***Lagopus lagopus scotica***, Red Grouse, a species that eats moss capsules. Photo by MPF, through Creative Commons.

Figure 8. ***Centrocercus urophasianus***, Greater Sage Grouse, a consumer of small amounts of mosses. Photo by Gordon Sherman, with online permission.

Figure 9. ***Plectrophenax nivalis***, Snow Bunting, a herbivore on the capsules of ***Bryum pendulum***. Photo by Cephas, through Creative Commons.

Figure 10. ***Bryum algovicum*** with capsules that are eaten by the Snow Bunting. Photo by Barry Stewart, with permission.

Figure 11. ***Gallinula chloropus***, Moorhen, a moss consumer. Photo from Anemone Projectors, through Creative Commons.

Figure 12. ***Turdus merula***, a Blackbird that eats mosses. Photo by Mario Modesto Mata through GNU Free Documentation.

Figure 13. ***Turdus philomelos***, Song Thrush, in Cambridgeshire, a bird that eats mosses. Photo by Brian Eversham, with permission.

Figure 14. ***Turdus pilaris***, Fieldfare, a bird that eats mosses. Photo by Frankie Fouganthin, through Creative Commons.

Figure 15. ***Cyanistes caeruleus***, Blue Tit, in winter, a bird that eats capsules of ***Dicranoweisia cirrata***. Photo through public domain.

Figure 16. ***Poecile palustris***, Marsh Tit, a species that eats capsules of ***Dicranoweisia cirrata***. Photo by Luc Viatour, through Creative Commons.

Figure 17. ***Dicranoweisia cirrata*** with capsules that are eaten by Blue Tits and Marsh Tits. Photo from BioPix, through Creative Commons.

Dan Norris (Bryonet, 22 November 1995 & 19 November 2006) reported that the Green Eastern Rosella Parrot (***Platycercus eximius***; Figure 18) in Tasmania selects the green, but mature, capsules of ***Polytrichum juniperinum*** (Figure 19) on clay soil banks as a primary food source. He watched the parrots for over an hour, then examined the area to find that they clipped the setae at 45º angles and left a miniature forest of setae with a litter of calyptrae that were split off, falling 5-10 mm to the right of the sporophyte. The number of barren setae suggested that harvest in this manner was widespread. Further examination on other clay banks of the island revealed that similar patterns were common in the forested mid-elevation habitats throughout the island.

Ptarmigans

In northern Europe and Alaska, the Willow Ptarmigan (***Lagopus lagopus***; Figure 20-Figure 21, Figure 23) chicks consume moss capsules of ***Polytrichum*** *s.l.* (Figure 19) and ***Pohlia*** (Figure 22) (Weeden 1969; Gardarsson & Moss

1970; Spidsø 1980; Martin & Hik 1992). Pullianen and Eskonen (1982) considered that moss capsules could be a source of high quality food in this Arctic environmental at a time when they were too small to handle large food items.

Figure 18, ***Platycercus eximius diemenensis***, Green Eastern Rosella Parrot male, a species that selects green capsules of ***Polytrichum juniperum*** as food. Photo by J. J. Harrison, through Creative Commons.

Figure 19. ***Polytrichum juniperinum*** mature capsules that are still green under the calyptra, providing food for the Green Eastern Rosella Parrot (***Platycercus eximius***). Photo by Ian Sutton, through Creative Commons.

Figure 20. ***Lagopus lagopus lagopus***, Willow Ptarmigan in summer plumage. Chicks of this species consume mosses. Photo by George Lesard, through Creative Commons.

The consumption of these moss capsules by Willow Ptarmigan chicks appears to be a regular event every spring as the capsules appeared in the diet in three consecutive years (Martin & Hik 1992). It is likely that they supply needed lipids; they contain about 20% lipids, a level higher than that in the other available vegetation (Pakarinen & Vitt 1974). In two cases the large numbers of capsules consumed suggest food selection rather than accidental ingestion (Martin & Hik 1992).

Figure 21. ***Lagopus lagopus lagopus***, Willow Ptarmigan in winter plumage. Chicks of this species eat capsules of ***Polytrichum*** and ***Pohlia***. Photo through Creative Commons.

Figure 22. ***Pohlia nutans*** with capsules. Capsules from this genus are eaten by the Willow Ptarmigan in the North. Photo by Michael Lüth, with permission.

Martin and Hik (1992) found the crops of Willow Ptarmigan chicks (***Lagopus lagopus***; Figure 23) stuffed with capsules of the moss ***Distichium inclinatum*** (Figure 24). The researchers suggested that the sporophytes might be easily accessible forage for these chicks. Could the capsules possibly act as grinding agents for other foods?

Figure 23. ***Lagopus lagopus lagopus*** *cf* ***pullus***, Willow Ptarmigan juvenile, a consumer of moss capsules of ***Polytrichum*** and ***Pohlia***. Photo by Walter Pfliegler, with permission.

Figure 24. ***Distichium inclinatum*** with capsules. Willow Ptarmigan chicks eat the capsules and they can be found in the crops of the birds. Photo by Michael Lüth, with permission.

Grouse

Grouse (**Tetraoninae**) chicks (Figure 7) are known to eat moss capsules (Richardson 1981). In fact, the clutch size and mean egg weight are dependent on the food of the mother (Naylor & Bendell (1989). The two most preferred foods were the trailing arbutus (*Epigaea repens*; Figure 25) and capsules of ***Polytrichum*** (Figure 19), and their availability was important, but not the size of the hen or her scaled body weight. Egg size, on the other hand, was not related to spring diet, but was instead related to the size of the hen. Therefore, the spring diet was important in providing the nutrients required for clutch formation.

Figure 25. ***Epigaea repens***, one of the two most preferred foods of grouse chicks. Photo by Fritz Flohr Reynolds, through Creative Commons.

Titmice

Titmice eat moss capsules in the temperate zone (Richardson 1981). Haftorn (1954) on five occasions observed the Crested Titmouse (***Baeolophus*** sp.; Figure 26) on snow-free rocks with mosses. The birds were pulling at the tips of the moss and Haftorn surmised that they were probably eating the capsules.

Figure 26. ***Baeolophus***, Crested Titmouse, a genus that grazes on the tips of mosses, perhaps to eat capsules. Photo by Dick Daniels, through Creative Commons.

Betts (1955) considered that in oak woodlands the Great Tit (***Parus major***; Figure 27) and the Blue Bit (***Cyanistes caeruleus***; Figure 15) can compete for food with the Coal Tit (***Periparus ater***; Figure 28) and the Marsh Tit (***Poecile palustris***; Figure 29). Using gizzard analyses, she determined that the Great Tit and Blue Tit had different diets, with the former feeding mostly on adult insects, especially weevils, and the Blue Tit on scale insects, small larvae, and pupae. The Coal Tit fed mostly on small, free-living insects and scales. The Marsh Tit ate mostly adult insects, scales, and a few larval forms. But in winter the diet changed. The Blue Tit consumed large numbers of capsules from the moss ***Dicranoweisia cirrata*** (Figure 30), ignoring the capsules of all other species. It had so many capsules in its gizzard that the gizzard was a vivid green (300-450 capsules per gizzard). One Coal Tit had consumed a few capsules and one Marsh Tit had 233 capsules in the gizzard.

Figure 27. ***Parus major***, Great Tit, a consumer of adult insects. Photo by Francis Franklin, through Creative Commons.

Figure 28. ***Periparus ater***, Coal Tit, a species that feeds on small, free-living insects and scales, but consumes large numbers of moss capsules in winter. Photo by David Kesl, through Creative Commons.

Figure 29. ***Poecile palustris***, Marsh Tit, a species that switches to eating moss capsules in the winter. Photo by Luc Viatour, through Creative Commons.

Figure 30. ***Dicranoweisia cirrata*** with capsules that provide winter food for the Blue Tit (***Cyanistes caeruleus***; Figure 15). Photo from BioPix, through Creative Commons.

In Norway, one might see the Crested Tit (***Parus cristatus***; Figure 31) pulling on moss tips that are free from snow on rocks in December (Haftorn 1954).

Figure 31. ***Parus cristatus***, Crested Titmouse, a species that harvests mosses in early winter. Photo by Jiří Duchoň, through Creative Commons.

Kōkako

The Kōkako/Blue-wattled Crow (***Callaeas wilsoni***; Figure 32) in New Zealand feeds on moss capsules (Jessica Beever, Bryonet 2 May 2003, based on observations by personnel from the Department of Conservation). Of 912 observations, 26 were feeding on moss capsules. When it was a good year for tracheophytes, only 3 out of 217 observations were of capsule feeding, but in a poor-fruit year, this increased to 6 out of 178 on mosses. These are probably within normal variation, but it suggests that the moss capsules may serve as an emergency food. The Kōkako forage along the branches, snipping off the capsules with the edge of the beak. Although they also feed on invertebrates from the bark and mosses, their action in obtaining the mosses by deliberate cutting is different from the pecking used to obtain insects. Eating the capsules is no accident.

The Kōkako (***Callaeas wilsoni***) make their greatest use of mosses in spring and summer (3%) when the capsules are most abundant, but they also may consume some in winter (0.75%) (Jessica Beever, Bryonet 2 May 2003, based on observations by personnel from the Department of Conservation). The actual consumption may be larger as it is more difficult to observe moss feeding than that on bright-colored fruits.

Figure 32. ***Callaeas wilsoni***, Kōkako, a bird that feeds on moss capsules. Photo by Duncan, through Creative Commons.

Fruit Mimicry by Capsules?

Michael Lüth (Bryonet 16 January 2008) has observed that some members of the **Splachnaceae** change their odor as they mature. ***Tetraplodon mnioides*** (Figure 33) has violet-colored capsules that smell like blueberries when the capsules are still closed. Once the capsules open, the odor changes to the smell of dung. A similar change occurs in ***Splachnum ampullaceum*** (Figure 34). When this species has immature capsules, the capsules have a strong, sweet odor like berries. But once the capsule opens it smells like dung. Could it be that in these early fruity stages the capsules are eaten by the local fauna, including birds? Patricia Geissler once expressed the idea that birds eat the capsules of ***Voitia nivalis*** (Figure 35) that occur among the buds of *Salix herbacea* (Figure 36), an early season food for some of the Arctic birds. If so, this is another potential dispersal mechanism. One might be able to make some interesting observations from within a duck blind, or using time-lapse photography.

Figure 33. ***Tetraplodon mnioides*** with mature capsules that might be eaten by the local fauna. Photo by Richard Caners, with permission.

Figure 34. ***Splachnum ampullaceum***, showing capsules that resemble some of the nearby fruits. Photo by Michael Lüth, with permission.

Figure 35. ***Voitia nivalis*** with capsules on Svalbard. These capsules resemble fruits of *Salix herbacea* (Figure 36) and may be eaten along with them. Photo by Michael Lüth, with permission.

Figure 36. *Salix herbacea* fruits in Austria, resembling capsules of ***Voitia nivalis***. Photo by El Grafo, through Creative Commons.

While in Tasmania in December for the Australasian Bryological Workshop, Paddy Dalton and Rod Seppelt showed their fellow bryologists ***Pleurophascum grandiglobum*** (Figure 37), a moss of the button grass plains in SW Tasmania. Allison Downing (Bryonet 18 January 2008) was "intrigued by the capsules (Figure 37), which are extremely large, globular, cleistocarpous, and on quite long setae, and was curious about dispersal, particularly the possibility that this species might be dispersed by birds. The capsules are light green, fading to pale yellow, and to me, had much in common with the fruits of many Epacridaceae (Ericaceae) and also of *Persoonia* (Proteaceae; Figure 38) that grow in this area." Emma Pharo stated that there are a number of birds that do feed on the ground in the button grass plains (Allison Downing, Bryonet 18 January 2008). The birds might not gain any nutrition from the capsules and their contents, but mimicry is used by many plants for pollination so why not for dispersal? The New Zealand species of ***Pleurophascum***, similarly, has globular fruits that become orange/red with maturity, and the color (red, orange) would make them even more attractive to birds.

Figure 37. ***Pleurophascum grandiglobum*** with capsules that are large and may be eaten by birds and dispersed by them. Photo by Christopher Taylor, Australian National Botanic Gardens, with online permission.

Figure 38. *Persoonia levis* fruit; ***Pleurophascum grandiglobum*** capsules (Figure 37) mimic these and may be eaten by some of the same bird species. Photo by John Tann, through Creative Commons.

Michael Lüth's comment about ***Tayloria*** (Figure 39-Figure 41) reminded Downing that three species of ***Tayloria***, ***T. octoblepharum*** (Figure 39), ***T. gunnii*** (Figure 40), and ***Tayloria tasmanica*** (Figure 41), all with abundant and conspicuous capsules, grow in the same habitat as ***Pleurophascum*** (Figure 37). Perhaps they, too, are fragrant (like the fruits of some Ericaceae) in their early stages of development and dispersed by birds before they reach the 'dung'-smelling stage of their life cycle.

Figure 39. ***Tayloria octoblepharum*** with capsules, possible mimics of some of the fruits in the Ericaceae. Photo by Janice Glime.

Figure 40. ***Tayloria gunnii*** with capsules, possible mimics of some of the fruits in the Ericaceae. Photo by Christopher Taylor, Australian National Botanic Gardens, with online permission.

Figure 41. ***Tayloria tasmanica*** with capsules, possible mimics of some of the fruits in the Ericaceae. Photo by Paddy Dalton, with permission.

Bird Color Vision

To understand bird choice based on color, it is necessary to understand how birds see color. Most studies on bird responses to color have assumed that they see colors the same way as humans do (Bennett *et al*. 1994). However, this is not true. The human eye design is different from that of birds and has different spectral abilities. Birds have four types of cones in the retina, compared to our three (Finger & Burkhardt 1994). Among their differences, at least some birds are able to see UV light, and feathers of some birds reflect UV light (Bennett & Cuthill 1994).

Using gene coding for UV- or violet-absorbing opsin in the retina, Ödeen & Håstad (2003) were able to assess color sensitivities on living birds. Their color vision can be put into two classes: short-wavelength sensitivity biased toward violet and another biased toward UV. The violet sensitivity is ancient among birds, and sensitivity to UV has evolved independently in four evolutionary lines. Many members of the orders **Psittaciformes** (parrots) and **Passeriformes** (perching birds) present UV-sensitive type color vision, but within the **Passeriformes**, the **Corvidae** (Jays, Magpies, & Crows) and **Tyrannidae** (Tyrant Flycatchers) do not. At least some members of **Laridae** (Skuas, Gulls, Terns, & Skimmers – **Charadriiformes**) and **Struthionidae** (flightless birds – **Struthioniformes**) likewise have UV-sensitive vision. Birds of prey (**Accipitridae** & **Falconidae** – **Falconiformes**), on the other hand, have the violet type.

The colorations of songbirds are significantly more conspicuous to other songbirds than they are to raptors and covids in the coniferous and deciduous forests (Finger & Burkhardt 1994; Håstad *et al*. 2005). This difference permits the **Passeriformes** to advertise their colors for mating purposes while not advertising to the raptors (birds of prey) that are their predators.

In addition to their cones birds have a complex of oil droplets in their retinas that may alter the color hues they perceive and that may also alter brightness and saturation (Bennett *et al*. 1994). Bennett and coworkers caution us that color is a product of the perception of the observer.

This brings us to the question of bird choice of bryophyte capsules and leafy stalks based on color. We know that bryophytes often serve as emergency food. Consider the observation of Bennett and Théry (2007) that plants are most likely to produce conspicuous fruit colors at times when frugivorous bird abundance is low. By contrast, if seeds, or bryophyte spores, are dispersed by birds, then I would think it would be beneficial for the fruits and capsules if they were bright-colored when it is appropriate for dispersal.

But capsules are not the only parts of bryophytes that are eaten. As you will soon see, leafy parts are as well. And we know that at least some bryophytes have fluorescent cell walls. For example, the bulbils of ***Pohlia*** are fluorescent under UV light (Nordhorn-Richter 1984). The value of this fluorescence for dispersal by birds remains unexplored.

Leafy Plants

It is uncommon for birds to use leafy bryophytes for food, but they may do so when food is scarce (Sillett 1994; Rhoades 1995; Wolf 2009). Among the few birds that actually eat the leafy bryophytes, we know that the Red-throated Loon (***Gavia stellata***; Figure 42), Brant (***Branta bernicla***; Figure 1), White-tailed Ptarmigan (***Lagopus leucura***; Figure 43), Willow Ptarmigan (***Lagopus lagopus lagopus***; Figure 44**),** and Rock Ptarmigans (***Lagopus muta***; Figure 45) all eat bryophytes in the Pacific Northwest, USA (Palmer 1962; Martin & Hik 1992; Braun *et al*. 1993; Hannon *et al*. 1998).

Figure 42. The Red-throated Loon, ***Gavia stellata***, and young. This species actually eats the leafy bryophytes in the Pacific Northwest, USA. Photo by David Karnå, through Creative Commons.

Figure 43. ***Lagopus leucura***, White-tailed Ptarmigan, Rocky Mountains, Alberta, a species that eats leafy bryophytes in the Arctic. Photo by John Hill, through Creative Commons.

Figure 44. ***Lagopus lagopus lagopus***, Willow Ptarmigan, with summer plumage, sitting on its dinner plate of leafy bryophytes. Photo by George Lesard, through Creative Commons.

Figure 45. ***Lagopus muta***, Rock Ptarmigan in summer plumage, a species that eats leafy bryophytes. Photo by Böhringer Friedrich, through Creative Commons.

Ducks and Food Availability

For ducks, bryophytes are not a preferred food. Ring-necked Ducks (***Aythya collaris***; Figure 46) in temporary wetlands use mostly plants, but those in more permanent wetlands choose animal foods for half their diet. The period during pre-laying and laying is an important time for females to obtain protein, and in the northern long days of Minnesota, USA, the females may feed up to 19 hours a day to obtain needed protein. However, when their usual food sources are unavailable, Ring-necked Ducks (***Aythya collaris***) may eat bryophytes (Hohman 1985). In 1980, reduced protein content in Class II juveniles seemed to be the result of a large percentage of aquatic mosses and caddisflies in cases. In that year, aquatic mosses comprised 18% of the diet, whereas in other years there were only trace amounts.

Figure 46. ***Aythya collaris***, Ring-necked Duck male, a species that obtains protein from mosses. Photo by Alan Vernon, through Creative Commons.

Geese

Geese seem to have a love-hate relationship with mosses as a food source. Sometimes they are essential to the diet, but in other times and places, they are deliberately avoided. The Canada Goose (***Branta canadensis***; Figure 47) selectively consumes the riverweed *Podostemum ceratophyllum* (Figure 48) over the moss ***Fontinalis novae-angliae*** (Figure 49) in a riverine system, despite the dominance (89% of biomass) of moss in that system. This preference may have been due to the presence of C18 acetylenic acid, octadeca-9,12-dien-6-ynoic acid in the mosses, a compound that deters crayfish feeding.

Figure 47. ***Branta canadensis***, Canada Geese and goslings. This species avoids eating the moss ***Fontinalis***. Photo by Janice Glime.

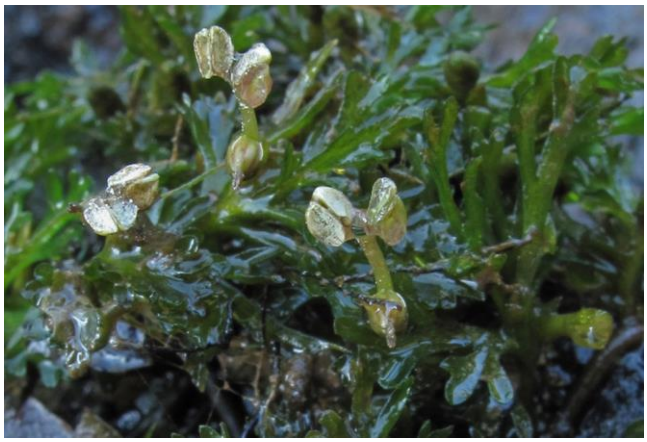

Figure 48. *Podostemum ceratophyllum*, a flowering plant species that is preferred over mosses as food by Canada Geese. Photo by Alan Cressler, with permission.

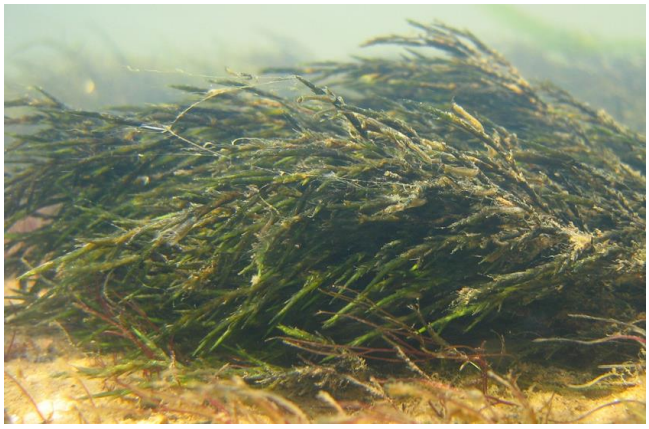

Figure 49. ***Fontinalis novae-angliae*** protecting invertebrates from Canada Goose grazing because the geese won't eat it. Photo by John Parker, with permission.

By contrast, polar and alpine habitats seem to encourage the consumption of bryophytes, including by geese (Longton 1992). Gloutney *et al*. (2001) report that at Karrak Lake, NT, Canada Geese (***Branta canadensis***; (Figure 47), Lesser Snow Geese (***Chen caerulescens caerulescens***; Figure 50) and Ross's Geese (***Chen rossii***; Figure 51) eat primarily mosses, chickweed (*Stellaria* spp.; Figure 52), and sedges (*Carex* spp.; Figure 53). In the Svalbard breeding season, mosses form a considerable part of the diet of Barnacle Geese (***Branta leucopsis***; Figure 54) (Prop *et al*. 1980).

Figure 50. ***Chen caerulescens***, Lesser Snow Geese, grazing on sedges. Photo by Walter Siegmund, through Creative Commons.

Figure 51. ***Chen rossii***, Ross's Goose, grazing on sedges. Photo by Andrew C., through Creative Commons.

Figure 52. ***Stellaria humifusa***; members of this genus are eaten by several species of geese. Photo by Lynn J. Gillespie, through Creative Commons.

Figure 53. ***Carex aquatilis*** var. ***minor*** in water; members of this genus are eaten by several species of geese. Photo by Jeffery M. Saarela, through Creative Commons.

Figure 54. ***Branta leucopsis***, Barnacle Goose, grazing. This species grazes largely on mosses in the Arctic. Photo by Arthur Chapman, through Creative Commons.

Barnacle Geese (***Branta leucopsis***; Figure 54) arrive in Spitzbergen, Scandinavia, after a long migration, but before flowering plants are available (Prop & Vulink 1992). Thus mosses are eaten heavily during pre-laying and laying periods (62% in feces) (Fox & Bergersen 2005). The young goslings also consume the mosses, and sampling revealed that 27 out of 28 samples of adult and gosling droppings contained mosses (Prop & Vulink 1992). Snow Geese (***Chen caerulescens caerulescens***; Figure 50) and Pink-footed Geese (***Anser brachyrhynchus***; Figure 55) consume mosses to a lesser extent than the Barnacle Geese. It is interesting that moss in the diet increased as the temperature increased (Fox *et al*. 2006).

Figure 55. ***Anser brachyrhynchus***, Pink-footed Geese, foraging among grasses. Photo by Brian Eversham, with permission.

The Barnacle Goose (***Branta leucopsis***; Figure 54) grazes the top layer of mosses when the ***Calliergon*** (Figure 56) is still frozen (Prop & de Vries 1993). Along the water's edge, the geese dug for large lumps of mosses, consuming them as soon as they appeared. Fortunately, the mosses were a nearly inexhaustible food supply, but the geese seemed to prefer them when they were still anchored in ice. That made it possible for them to scrape the upper, most nutritious part with their bills without having to attempt separating them from their lower parts that were sealed in ice. Grasses began to grow when the moss beds began to thaw and within one week the young leaves appeared and were immediately consumed by the geese. During the earliest stages of this thaw, the geese fed on **forbs** (herbaceous flowering plant other than grass) and xerophytic mosses on the few snow-free patches. Then the forbs became the dominant food for about ten days. Then the moss meadows became available and the females switched to feeding on mosses, with their forbs proportion dropping to only 50%. As they became more available, graminoids gradually took on more importance in the diet of both males and females. However, at that time the proportion of mosses in the male diet was greater than that of females, both making great use of mosses in the moss meadows for food.

Figure 56. ***Calliergon cordifolium***, a genus that is grazed by Barnacle Geese (***Branta leucopsis***; Figure 54) when the moss is still encased in ice. Photo by Janice Glime.

One factor in determining suitable food is retention time (Prop & Vulink 1992). Since plant cell walls are difficult to digest, and bryophytes have a higher cell wall to cell content ratio, the bryophytes are more difficult to digest than herbaceous foods. The Barnacle Goose (***Branta leucopsis***; Figure 54) increased its retention time 2-4-fold as the short days of winter increased to the continuous light of summer in their Arctic breeding area. This permitted greater digestion of their food from 37% in winter to 56% in summer and allowed them to expand their food choices to include bryophytes – often the only food available in their summer range.

Competition may force some geese to eat mosses. When Barnacle Geese (***Branta leucopsis***; Figure 54) and Pink-footed Geese (***Anser brachyrhynchus***; Figure 55) coexist during molting time, their diet of sedges and grasses shifts to include more mosses, especially in the Barnacle Goose, reaching 33% of the diet, whereas mosses only reached 17% of the Pink-footed Goose diet (Madsen & Mortensen 1987). The Pink-footed Goose seems to be able to keep the Barnacle Goose from feeding in the preferred sedge and grass food patches. Mosses are suboptimal for both nutrients and fiber content compared to sedges and grasses.

Ardea and Sage (1982; Sage & Ardea 1982) note that the Barnacle Geese (***Branta leucopsis***; Figure 54) begin eating mosses as soon at they arrive in their Arctic breeding grounds. The authors suggest that this is necessary for them to build up **arachidonic acid**, a fatty acid in cell membranes. This notion is supported by Prins (1982). Several species of geese are known to eat mosses in their Arctic breeding grounds, including the Snow Goose (***Chen caerulescens***; Figure 50), Pink-footed Goose (***Anser brachyrhynchus***; Figure 55), Barnacle Goose, and Brant Goose (***Branta bernicla***; Figure 1). Prins suggested that the arachidonic acid helped to keep the membranes pliable as they move about on the frozen Arctic ground. The Canada Goose (***Branta canadensis***; Figure 47) instead eats horsetails (*Equisetum*; Figure 57), which are likewise rich in arachidonic acid, but mosses have the highest contents known.

Figure 57. *Equisetum arvense*, a source of arachidonic acid for Canada Goose (***Branta canadensis***). Photo by MPF, through Creative Commons.

When snow melt is delayed, as it has been recently along Hudson Bay shores, a predicted outcome of global warming, as many as 100,000 Snow Geese (***Chen caerulescens caerulescens***; Figure 50) stay for weeks instead of 1-2 days as in the past. The result is devastation of salt marsh and wetland plants, and only the moss carpet seems able to grow.

In the high Andes of sub-Antarctic South America, ***Attagis malouinus*** (White-bellied Seedsnipe; Figure 58), ***Chloephaga picta*** (Upland Goose; Figure 59), and ***C. poliocephala*** (Ashy-headed Geese; Figure 60) frequently consume bryophytes (Russo *et al* 2020). The fragments, including both leafy stems and capsules, occurred in 84.6% of the seedsnipe (26 samples) and 90.9% of the Chloephaga goose fecal samples (22 samples; Figure 61). At least one of the ***Chloephaga*** species consumes the mosses ***Polytrichum strictum*** (Figure 62) and ***Notoligotrichum trichodon*** (Figure 63). Of 11 collected goose droppings, more than 50% contained fragments of the **Polytrichaceae**. Such consumption suggests the possibility of dispersal of this moss family in bird feces.

Figure 58. ***Attagis malouinus*** in mountain area of Patagonia, a sub-Antarctic bird that eats mosses. Photo courtesy of Sebastian Saiter.

Figure 59. ***Chloephaga picta***, a sub-Antarctic bird that eats mosses. Photo by Peter Prokosch, through Creative Commons.

Figure 60. ***Chloephaga poliocephala***, sub-Antarctic bird that eats mosses on Ushuaia, Tierra del Fuego, Argentina. Photo through Creative Commons.

Figure 61. ***Chloephaga feces*** with mosses in it. Photo courtesy of Nick Russo, modified by Janice Glime.

Figure 62. Male plants of ***Polytrichum strictum***, a common food of ***Attagis malouinus***, ***Chloephaga picta***, and ***Chloephaga poliocephala***. Photo by Kristian Peters, through Creative Commons.

Figure 63. ***Notoligotrichum trichodon*** with capsules; both leafy stems and capsules are common foods of ***Attagis malouinus***, ***Chloephaga picta***, and ***Chloephaga poliocephala***. Photo by Bernard Goffinet, with permission.

Blood Pheasant

The Blood Pheasant (***Ithaginis cruentus***; **Phasianidae**; Figure 64) is protected in China, where it lives in shrublands on high, cold plateaus. Mosses are an important part of its diet (Shi & Li 1985; Nan *et al*. 2011). Yao (1992) dissected 46 gizzards to analyze for food preferences. This revealed 32 species of mosses, comprising 22 genera and 14 families. The preferred mosses comprised 24-54% of the content, second preference comprised 11-17%, third preference 4-9%, and those occasionally eaten comprised less than 2.1%.

Figure 64. ***Ithaginis cruentus***, Blood Pheasant, a species for which mosses are an important diet component. Photo from EOL China Regional Center, through Creative Commons.

Other foods of the Blood Pheasant include grasses, and both mosses and grasses are taken during prolonged feeding expeditions in which the birds bob up and down like a slow sewing machine needle at the rate of 50 pecks per minute (Nan *et al*. 2011). In 528 observations, all individuals consumed mosses. Although it was difficult to distinguish which bryophytes were being consumed, the researchers were able to identify ***Actinothuidium hookeri*** (Figure 65), ***Funaria hygrometrica*** (Figure 66), ***Hedwigia ciliata*** (Figure 67), ***Homomallium connexum*** (see Figure 68), ***Pogonatum perichaetiale*** (Figure 69), and ***Rhytidium rugosum*** (Figure 70). It appeared that the birds preferred mosses that were soft and easily fragmented for ease of swallowing. On the other hand, some of these mosses may help to grind food in the gizzard. Grasses were also eaten in large supply, but since they were abundant, it did not appear that the mosses served as emergency food or a source of fiber. Furthermore, it did not appear that the mosses were eaten as a source of insects because the insects were in low supply. Hence, it appears that the mosses were a preferred food.

Figure 65. ***Actinothuidium hookeri***, food of the Blood Pheasant (***Ithaaginis cruentus***). Photo by Li Zhang, with permission.

Figure 66. ***Funaria hygrometrica*** capsules, food for the Blood Pheasant. Photo by Frank Vincentz, through Creative Commons.

Figure 67. ***Hedwigia ciliata*** drying, a species eaten by the Blood Pheasant. Photo by Janice Glime.

Figure 68. ***Homomallium incurvatum***; ***H. connexum*** is among the mosses consumed by the Blood Pheasant. Photo by Hermann Schachner, through Wikiwand.

Figure 69. ***Pogonatum perichaetiale*** with capsules. This species is eaten by the Blood Pheasant. Photo by Li Zhang, with permission.

Figure 70. ***Rhytidium rugosum***, food for the Blood Pheasant. Photo by Michael Lüth, with permission.

Kakapo

On Stewart Island, the third largest island of New Zealand, the Kakapo (***Strigops habroptilus***; Figure 71) "plucks" the mast of the moss ***Dicranoloma*** (Figure 72), the sedge *Oreobolus*, the grass *Centrolepis*, the flowering plant *Astelia*, and the Asteraceae member *Celmesia* (Best 1984). Signs on ***Dicranoloma*** were rare, typically represented as foliage that had been pulled from the ground.

Figure 71. ***Strigops habroptilus***, Kakapo, camouflaged among leaves in NZ. The coloration camouflages it among the vegetation, including while it feeds among bryophytes. Photo by Mnolf, through Creative Commons.

Figure 72. ***Dicranoloma billardieri*** in NZ, a species often pulled up by the Kakapo. Photo by Jan-Peter Frahm.

Turkeys?

Glover and Bailey (1949) reported that turkey droppings indicated that bryophytes formed a common food source from January to April in the beech-birch-maple-hemlock forest. However, it appears that the "mosses" in this case were instead actually *Lycopodium*, referred to elsewhere in the paper as a bryophyte.

Dispersal

The birds in some cases return the "favor." The Mallard, ***Anas platyrhynchos*** (Figure 73) and Lapwing ***Vanellus vanellus*** (Figure 74) both eat bryophytes. Wilkinson *et al*. (2017) found a large fragment of the moss ***Didymodon insulanus*** (Figure 75) in the feces of the Mallard in Cumbria, England, and similarly in the Lapwing feces. These fragments were cultured and proved to be viable. This suggests that consumption of bryophytes by birds can in some cases be a means of dispersal. Could this be more true for species that benefit from guano deposits?

Figure 73. ***Anas platyrhynchos***, Mallards, birds that eat bryophytes. The mosses can remain live in the feces. Photo courtesy of Eileen Dumire.

Figure 74. ***Vanellus vanellus***, Northern Lapwing, a bird that consumes bryophytes. The bryophytes can remain viable in the feces. Photo by Andreas Trepte, through Creative Commons.

Figure 75. ***Didymodon insulanus***, a moss that can survive the digestive tract of Mallards and Lapwings Photo by David T. Holyoak, with permission.

Nutritional Value of Bryophytes

These records raise the question of nutritional value of bryophytes. Why do birds eat bryophytes? Sugawa (1960) found that puppies and chickens will eat the pendent moss ***Neodicladiella pendula*** that is pulverized and used as a food additive. These animals seemed to suffer no ill effects. In fact, they gained more weight than the controls. Sugawa found that these mosses contained considerable Vitamin B_2. Mosses can have high contents of vitamins, especially B_2 (Sugawa 1960; Margaris & Kalaitzakis 1974).

The greatest known use of bryophytes as food for birds occurs in the Arctic tundra. In these mosses, the caloric content is ~4.5-5.0 kcal g^{-1} (Pakarinen & Vitt 1974). The flowering plants consist of about 15% protein and 5% fats, whereas mosses have about 4% protein and 2% fats. Much of the moss biomass is bound in lignin-like compounds. Sugars in these mosses comprise ~1.5%. These sugars include mannose, melibiose, maltose, and deoxyribose in the mosses ***Syntrichia princeps*** (Figure 76), ***Rhynchostegium*** sp. (Figure 77), ***Platyhypnidium riparioides*** (Figure 78), and ***Homalothecium*** spp. (Figure 79) (Margaris & Kalaitzakis 1974).

Figure 76. ***Syntrichia princeps*** with capsules. Photo by Michael Lüth, with permission.

Figure 77. ***Rhynchostegium alopecuroides***. Photo by Michael Lüth, with permission.

Figure 78. ***Platyhypnidium riparioides*** with capsules, an emergent aquatic moss. Photo by Michael Lüth, with permission.

Figure 79. ***Homalothecium lutescens*** Europe 2 Michael Lüth, with permission.

Forman (1968) examined caloric values of thirteen bryophyte species from Mt. Washington, NH, USA. Values for fresh bryophytes varied from 3747 cal g^{-1} dry weight for ***Dicranella heteromalla*** (Figure 80) to 4305 cal g^{-1} in ***Thuidium delicatulum*** (Figure 81). But then, spinach has only 0.23 cal g^{-1} of fresh spinach (1 cup) (Wikipedia 2017). When species were transplanted to a high-temperature and high-humidity environment, the caloric content decreased. On the other hand, bryophyte species that originated from the coniferous and northern hardwoods forests all had higher caloric values than those from the higher alpine area or the lowland oak forest. On Mt. Washington, the bryophytes are among those plants with the lowest caloric values.

Mosses can affect the nutritional value of forbs and grasses in Arctic wetlands (Kotanen 2002). Moss presence did not prevent the rapid uptake of nitrogen by other forage species. However, most of added N nevertheless ended up in the moss layer. Hence, the mosses are able to divert N away from the tracheophyte forage plants and into long-lasting peat. This sequestering can make it more difficult for freshwater tracheophyte forage plants to recover from excessive foraging by Snow Geese (***Chen caerulescens atlantica***; see Figure 50). On the other side of the coin, the Snow Geese fertilize the moss layer in the polygon fens (Pouliot 2006).

Figure 80. ***Dicranella heteromalla***, a moss with ~3700 cal g^{-1} dry weight. Photo by Michael Lüth, with permission.

Figure 81. ***Thuidium delicatulum***, a moss with ~4300 cal g^{-1} dry weight. Photo by Michael Lüth, with permission.

Solheim *et al*. (1996) showed that grazing geese had a significant impact on nitrogen fixation in the Arctic Svalbard. In areas with grazing there was 10X as much N fixation as in areas with no grazing. Bird droppings under cliffs likewise increased N fixation.

Atmospheric pollutants are having a large impact on the N content of bryophytes. Pitcairn *et al*. (1995) found that atmospheric N deposition caused a significant rise in tissue N of 38% in central Scotland to 63% in Cumbria during just two decades.

Crafford and Chown (1991) suggested that herbivory by curculionid beetles on bryophytes originated in response to an absence of flowering plants during glacial periods. For birds, it appears that Arctic birds that eat bryophytes likewise have occupied a feeding niche that at least during part of the year is devoid of flowering plants.

Palatability

Bryologists for a long time assumed that bryophytes were inedible. This could result from bad taste, low nutrient value, or toxic effects. But, in fact, bryophytes are eaten. To humans they may taste terrible, with Crum (1973) describing ***Dicranum*** (Figure 82) as having a strong, somewhat peppery taste, ***Rhodobryum giganteum*** (Figure 83) as having a sickening sweet taste, and most tasting like raw green beans. But are these the tastes registered by the birds? Feeding preference tests of birds with choices of leafy bryophytes and capsules seem to be lacking. Are there species preferences? Does color matter? Do they provide some essential nutrient that is more abundant in bryophytes than in other foods?

Foraging

As already discussed in earlier chapters, many invertebrates reside among the bryophytes. These include grubs, beetles, bugs, worms, mites, spiders, and other macroinvertebrates. Many of these organisms are desirable food for birds. Hence, many birds forage among bryophytes, and some are specially adapted for this bryophyte foraging behavior.

Figure 82. ***Dicranum scoparium*** with capsules, a moss in a genus Crum described as tasting peppery. Photo by Janice Glime.

Figure 83. ***Rhodobryum giganteum***, a moss with a sickening sweet taste. Photo by David Long, with permission.

Ground Foragers

The Common Blackbird (***Turdus merula***; Figure 12) forages among mosses when snow still covers part of the ground (see film by Shutterstock 2017). It is likely that other early arrivals take advantage of the moss fauna when most insects are in the egg or pupal stage, often hidden under bark or in the soil and immobile.

Arctic Foraging Effects

In the Arctic breeding grounds, mosses are typically the dominant vegetation. The thickness of the moss mats influence the temperature of the underlying soil (van der Wal *et al*. 2001). Herbivores, including birds, can reduce that mat thickness by trampling, consumption, or foraging. When Barnacle Geese (***Branta leucopsis***; Figure 54) and reindeer were excluded from areas with moss cover at Spitsbergen, the moss mat increased in thickness and the soil temperature was reduced by 0.9°C. In all sites, the soil temperature was negatively correlated with the thickness of the moss mat. This temperature change had no effect on the moss growth rate, but the Arctic meadow-grass (***Poa arctica***; Figure 84) and polar cress [***Cardamine pratensis*** (= ***C. nymanii***); Figure 85] experienced a 50% reduction in biomass on the chilled soils.

Figure 84. ***Poa arctica***, an Arctic grass that diminishes in cover at lower temperatures. Photo by R. J. Soreng, through Creative Commons.

Figure 85. ***Cardamine pratensis***, a species that has less growth at lower soil temperatures. Photo by Aiwok through Creative Commons.

Arctic foraging can have detrimental effects on the plants in this fragile ecosystem, but at times they benefit the bryophytes. The Lesser Snow Goose (***Chen caerulescens caerulescens***; Figure 50) in the Arctic coastal region can be very destructive while foraging among roots and rhizomes for grubs and other food (Jefferies 1988). At the rate of foraging exhibited, Jeffries estimated that the sedge meadow would convert to a moss carpet in about five years.

Foraging on Epiphytes

Bryophytes are often torn up by foraging birds, presumably in search of insects and other invertebrates. In the Pacific Northwest, USA, 44% of the foraging among epiphytes was on bryophytes. These were mostly pendant bryophytes (Figure 86), followed by foliose lichens (Figure 87), then appressed bryophytes (Figure 88). In these forests, 20% of the bryophyte foraging was on the abundant moss ***Isothecium myosuroides*** (Figure 86). The bark insectivorous birds were the most frequent foraging guild on the bryophyte and lichen substrates.

Figure 86. ***Isothecium myosuroides***, most common epiphytic moss foraged by birds in the Pacific Northwest. Photo by Dale Vitt, with permission.

Figure 87. ***Flavoparmelia caperata***, a foliose lichen like those foraged by birds in the Pacific Northwest. Photo by Robert Klips, with permission.

Figure 88. ***Hypnum imponens*** on log, an appressed bryophyte like those that are less preferred for foraging by birds in the Pacific Northwest. Photo by Janice Glime.

As an example, we know that the Blue Tit (***Cyanistes caeruleus***; Figure 15) eats larvae of ***Erannis*** (Lepidoptera) in winter (Betts 1955) – a moth associated with forests with lots of bryophyte cover (Kiadaliri *et al*. 2005). Females of at least some species of ***Erannis*** lay eggs under mosses as well as in crevices, making this a good foraging site for birds hunting larvae.

Wolf (2009) questioned the value of epiphyte foraging to birds in coniferous forests of the Pacific Northwest. Of the 735 foraging records, ~30% occurred on epiphytic substrates. The data indicated selectivity by the Chestnut-backed Chickadee (***Poecile rufescens***; Figure 89), Red-breasted Nuthatch (***Sitta canadensis***; Figure 90), Brown Creeper (***Certhia americana***; Figure 91), Hairy Woodpecker (***Picoides villosus***; Figure 92), and Gray Jay (***Perisoreus canadensis***; Figure 93). Furthermore, the position in the canopy influenced their choices. In the mid and upper crown, lichens were preferred, whereas in the lower crown the bryophytes were preferred. Weikel and Hayes (1999) suggested that the bryophyte cover may house more arthropods that serve as food, but at the same time they hide the arthropods, making them less available to these birds.

Figure 89. ***Poecile rufescens***, Chestnut-backed Chickadee, a species that typically forages among epiphytic bryophytes in the Pacific Northwest, USA. Photo by Walter Siegmund, through Creative Commons.

Figure 90. ***Sitta canadensis***, Red-breasted Nuthatch, a species that forages among epiphytic bryophytes in the Pacific Northwest. Photo by Matt MacGillivray, through Creative Commons.

Figure 91. ***Certhia americana***, Brown Creeper, on a tree where it often forages among mosses and lichens. Photo by Walter Siegmund, through Creative Commons.

In the Pacific Northwest coniferous forests of Washington and Oregon, USA, eleven species of birds use the bryophytes for foraging (Wolf 2009). However only four bird species comprised 79% of the foraging records. These were the Pacific Winter Wren (now named ***Troglodytes pacificus***; Figure 94; 33 records), Brown Creeper (***Certhia americana***; Figure 91; 13 records), Gray

Jay (***Perisoreus canadensis***; Figure 93; 14 records), and Chestnut-backed Chickadee (***Poecile rufescens***; Figure 89; 13 records). Among these, the Brown Creeper (***Certhia americana***), Hermit Thrush (***Catharus guttatus***; Figure 95), and Winter Wren used the bryophytes in more than 20% of their foraging excursions.

Figure 92. ***Picoides villosus***, Hairy Woodpecker, a species that forages among epiphytic mosses. Photo by Will Pollard, through Creative Commons.

Figure 93. ***Perisoreus canadensis***, Gray Jay, a species that forages among epiphytic bryophytes. Photo by Franco Folini, through Creative Commons.

Figure 94. ***Troglodytes pacificus***, Pacific Wren, a forager among bryophytes. Photo by Carly Lesser & Art Drauglis, through Creative Commons.

Figure 95. ***Catharus guttatus***, Hermit Thrush, a species that frequently forages among bryophytes. Photo by Cephas, through Creative Commons.

The behavior differed among these birds (Wolf 2009). The Brown Creeper (***Certhia americana***; Figure 91) and Hairy Woodpecker (***Picoides villosus***; Figure 92) hung vertically or upside-down on the epiphytes as they probed, hammered, pecked, or otherwise inspected the epiphytic bryophytes, using mostly prostrate mosses (esp. ***Hypnum***; Figure 96) on the bole. The arthropods that are the victims of their searches use the epiphytes for refuge, forage, rest, aestivation, and thermoregulation (Richardson & Young 1977; Rhoades 1995; Shaw 2004). The dense mats accumulate soil, providing further habitat for invertebrates (Winchester & Ring 1996). The birds contribute a selection pressure that selects for cryptic coloration and other forms of camouflage in the arthropods (Richardson & Young 1977).

Figure 96. ***Hypnum cupressiforme***, a common epiphytic genus for foraging by Brown Creepers and Hairy Woodpeckers. Photo by Jan-Peter Frahm, with permission.

With the wide range of bryophytes in the Neotropics, certainly some are better sources of food items than others. The Ochraceous Wren and Common Bush-Tanager forage among the dead organic matter and bryophytes more frequently than they do among other (tracheophyte) epiphytes (Nadkarni & Matelson 1989).

In Costa Rica, The Ruddy Treerunner (***Margarornis rubiginosus***; Figure 97) is an epiphyte specialist, foraging on bryophytes (Sillett 1994). The Spot-crowned Woodcreeper (***Lepidocolaptes affinis***; Figure 98) is a Central American foraging specialist on bryophytes and

foliose lichens, but the bryophytes were used less proportionately than lichens.

Figure 97. ***Margarornis rubiginosus***, Ruddy Treerunner, a species that specializes on foraging among bryophytes. Photo by Dominic Sherony, through Creative Commons.

Figure 98. ***Lepidocolaptes affinis***, Spot-crowned Woodcreeper, foraging among mosses. Photo by Carmelo López Abad, through Creative Commons.

The Blue-capped Ifrita (***Ifrita kowaldi***; Figure 99), a poisonous bird, is restricted to the highlands of New Guinea (Figure 100), mostly above 2000 m asl (Dumbacher *et al*. 2000). They live in mossy, moist montane forests, where they behave much like the nuthatches, foraging for insects and worms among mosses, on tree trunks, and on major branches in the midstory of the forest. They are rarely seen alone, typically travelling in groups of up to six individuals.

Figure 99. Blue-capped Ifrita, ***Ifrita kowaldi***, a poisonous bird that lives in mossy forests where it forages among midstory mosses. Photo by Jerry Oldenettel, through Creative Commons.

Figure 100. New Guinea Highlands, Papua New Guinea. Photo from eGuide Travel, through Creative Commons.

Pendant bryophytes (Figure 101) can protect some arthropods from foragers. These arthropods are able to dwell at some distance from the branch, away from the perches of the birds (Wolf 2009). These mosses are too unstable for many kinds of birds to perch. Among the birds that were not deterred by the pendant branches, the Pacific-slope Flycatcher (***Empidonax difficilis***; Figure 102) used a sally, hover, and glean foraging behavior to capture insects on the dangling bryophytes. The Chestnut-backed Chickadee (***Poecile rufescens***; Figure 89) used short flights and hops to forage, but occasionally hovered or hung from the bryophytes to snatch an insect from the pendant portion. Furthermore, 70% of the nests of this species contained bryophytes (Dahlsten *et al*. 2002).

Peterson *et al*. (1989) sampled trunk-surface arthropods from American beech (*Fagus grandifolia*; Figure 103) and sugar maple (*Acer saccharum*; Figure 104). The arthropod resources did not differ significantly between trees. Furthermore, they were not correlated with bark texture or bryophyte cover.

Figure 101. ***Pseudobarbella mollisima***, a pendant moss in Japan. Photo by Janice Glime.

Figure 102. ***Empidonax difficilis***, Pacific-slope Flycatcher, a species that is able to forage among dangling mosses. Photo by Ron Knight, through Creative Commons.

Figure 103. *Fagus grandifolia* forest in winter. Photo by Dcrjsr, through Creative Commons.

Pheasants (***Phasianus colchicus***; Figure 105) do not seem to have any particular use for the mosses themselves, but the mosses seem to be in their way on the forest floor of a wetland forest (Wiegers 1983). When they are foraging, they turn the bryophyte cover upside down in search of food. Following these events, some mosses, including ***Dicranum scoparium*** (Figure 106) and ***Mnium hornum*** (Figure 107), that were turned upside down develop into moss balls.

Figure 104. *Acer saccharum* autumn leaves and trunk. Photo by Janice Glime.

Figure 105. ***Phasianus colchicus***, Pheasant, a species that often disturbs bryophytes while foraging. Photo by Gary Noon, through Creative Commons.

Figure 106. ***Dicranum scoparium***, a moss that gets turned upside down by foraging pheasants. Photo by J. C. Schou, through Creative Commons.

Rod Seppelt (Bryonet 26 February 2013) has observed Skuas (***Catharacta lonnbergi***; Figure 108) upturning upland moss polsters of ***Ditrichum strictum*** (see Figure 109) on subAntarctic islands, searching for earthworms. It is puzzling because there are easier food items available than these relatively small worms.

Figure 107. ***Mnium hornum***, a moss that gets turned upside down by foraging pheasants. Photo by Kristian Peters, through Creative Commons.

Figure 108. ***Catharacta lonnbergi***, Skua, on nest on South Georgia, a species that upturns mosses to forage. Photo by Christo Barrs, through Creative Commons.

Figure 109. ***Ditrichum gracile***; ***D. strictum*** is commonly upturned by foraging Skuas on sub-Antarctic islands. Photo by Hermann Schachner, through Creative Commons.

In Eugene, Oregon, USA, the Steller's Jay (***Cyanocitta stelleri***; Figure 110) tears up mosses from the oaks as it forages for arthropods that hide there (Wagner 2013). In other locations it is Crows (Figure 112) and Scrub Jays (***Aphelocoma californica***; Figure 111).

Figure 110. ***Cyanocitta stelleri***, Steller's Jay, a species that forages on mosses on oaks in the Pacific Northwest, USA. Photo by Alan D. Wilson, through Creative Commons.

Figure 111. ***Aphelocoma californica***, Scrub Jay, a species that tears up mosses on oak trees. Photo by Minette Layne, through Creative Commons.

Crows (***Corvus***; Figure 112) are among those birds that can be quite destructive to bryophytes. Erkamo (1976) reported that some animal had upturned mosses on flat, open rocks in Finland. These mosses were typically only a few cm across, but some were up to 10-15 cm. Since the observations are indirect, based only on the upturned mosses, it is possible that voles, pheasants, seagulls, or crows were responsible, but crows seemed most likely. Erkamo has, at other times, seen crows engaging in such activity, presumably searching for insects or worms.

Birds keep bryophytes from growing well on red wood ant (***Formica rufa*** group; Figure 113) mounds due to the bird foraging activity on the ants (Heinken *et al*. 2007).

Motley and Bosanquet (2004) reported a neglected flower pot that contained ***Petalophyllum ralfsii*** (Figure 114). Meanwhile, the surface had been colonized by various species of moss and the thallose liverwort ***Aneura***

(Figure 115). The surprise came when birds attacked the bryophytes, pulling them out and most likely taking them for nesting material. But they were selective. They avoided taking the ***P. ralfsii***.

Figure 112. ***Corvus corax***, Crow, a species that is destructive of bryophytes while foraging. Photo by Ingrid Taylar, through Creative Commons.

Figure 113. ***Formica rufa*** sideview, an ant that builds mounds and birds keep bryophytes from growing on them. Photo by Richard Bartz, through Creative Commons.

Figure 114. ***Petalophyllum ralphsii***, a species that is avoided when birds collect bryophytes for nests. Photo by Michael Lüth, with permission.

Figure 115. ***Aneura pinguis***, a bryophyte among those collected by birds, presumably for nesting material. Photo by Michael Lüth, with permission.

Juncos

The Dark-eyed Junco (***Junco hyemalis***; Figure 116) in the Pacific Northwest, USA, is most active in the low understory, but it may go to the upper canopy to search for prey items among the lichens (Wolf 2009). But they may also forage on ***Dicranum*** sp. (Figure 82, Figure 106) and ***Isothecium*** (Figure 86), where Wolf observed them on a horizontal tree bole and branch of *Tsuga heterophylla* (Figure 117) at 0.7 m and 3 m respectively.

Figure 116. ***Junco hyemalis***, Dark-eyed Junco, a species that forages on ***Dicranum*** sp. and ***Isothecium***. Photo by Factumquintus, through Creative Commons.

Figure 117. ***Tsuga heterophylla*** (hemlock) forest, home of the Dark-eyed Junco. Photo by Willow & Monk, through Creative Commons.

Weaver Birds

In the Udzungwa Mountains of Tanzania, the disturbed humid forest serves as home for at least 70 species of birds (Fjeldså 1999). Many of the birds search for their food among the epiphytic lichens, mosses, and ferns in the mature forests. The Tasmanian Mountain Weaver, ***Ploceus nicolli*** (Figure 118), is a vulnerable species that occurs in the tall forest of the Eastern Arc Mountains. It is associated with locations having large cover of epiphytic mosses and lichens.

Figure 118. ***Ploceus velatus***, Southern Masked Weaver and nest; ***P. nicolli*** lives in areas with a large cover of epiphytic mosses. Photo by Chris Eason, through Creative Commons.

Tropical Birds

In the tropics, some birds use epiphytes as their feeding substrates. These include at one end of the spectrum those birds that choose the substrate where they prefer to feed, and at the other end the birds choose the prey item, going to the substrate if it potentially has that prey organism. In Costa Rica, Sillett (1994) studied eight species that use epiphytes among their feeding substrates. Four species were epiphyte specialists. These included two that chose bryophytes: Ruddy Treerunner (***Margarornis rubiginosus***; **Furnariidae**; Figure 97) on just bryophytes and Spot-crowned Woodcreeper (***Lepidocolaptes affinis***; **Dendrocolaptidae**; Figure 98) on bryophytes and lichens.

Orians (1969) and Remsen (1985) have provided evidence of bryophyte utilization by tropical birds, but otherwise, little documentation of this tropical resource exists. In Neotropical Costa Rica, Nadkarni and Matelson (1989) report three birds that feed upon bryophyte inhabitants (Table 1). The Emerald-chinned Hummingbird (***Abeillia abeillei***; Figure 119) and Amethyst-throated Hummingbird (***Lampornis amethystinus***; Figure 120) feed upon insects associated with the mosses and other bryophytes. The Rufous-tailed Hummingbird (***Amazilia tzacatl***; Figure 121) utilizes the flowers that are anchored in the bryophytic substrate. In fact, the Ochraceous Wren (***Troglodytes ochraceus***; Figure 122) and Common Bush-Tanager (***Chlorospingus ophthalmicus***; Figure 123) foraged in mosses more frequently than expected. Avian resources nestled among the bryophyte mats include fruits, flowers, seeds, water, and invertebrates.

Table 1. Percentage (and total number) of foraging visits to epiphytes by birds that probed moss mats and dead organic matter in the Monteverde field study, 1 July to 28 August 1985. Frequent foragers had 10 or more foraging visits recorded during the study period. Infrequent foragers had less than 10 foraging visits recorded. From Nadkarni and Matelson (1989).

Frequent foraging visits (> 10 foraging visits)	
White-throated Mountain-gem, *Lampornis castaneoventris*	95 (150)
Ochraceous Wren, *Troglodytes ochraceus*	89 (19)
Common Bush anager, *Chlorospingur ophthalmicus*	57 (511)
Olive-striped Flycatcher, *Mionectes olivaceus*	46 (37)
Slate-throated Redstart, *Myioborus miniatus*	45 (47)
Prong-billed Barbet, *Semnornis fiantzii*	30 (23)
Golden-browed Chlorophonia, *Chlorophonia callophrys*	33 (187)
House Wren, *Troglodytes aedon*	26 (57)
Three-striped Warbler, *Basileuterus tristriatus*	20 (10)
Mountain Robin, *Turdus plebejus*	< 10 (146)
Infrequent foragers (< 10 total foraging visits)	
Spotted Barbtail, *Premnoplex brunnescens*	

Figure 119. ***Abeillia abeillei***, Emerald-chinned Hummingbird, a tropical bird that feeds on insects associated with bryophytes. Photo by Scott Bowers, through Creative Commons.

Figure 120. ***Lampornis amethystinus***, Amethyst-throated Hummingbird, a tropical bird that feeds on insects associated with bryophytes. Photo by Juan Carlos Pérez M., through Creative Commons.

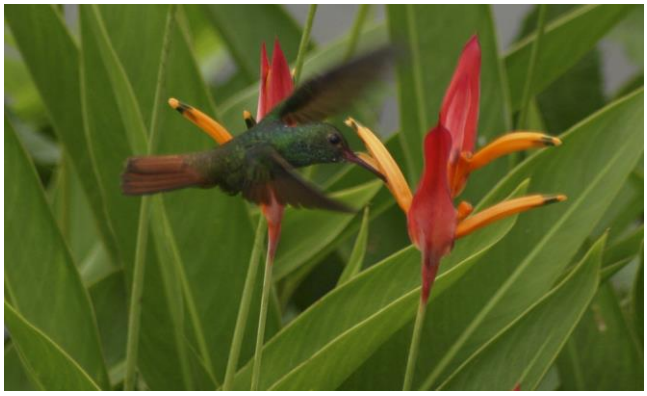

Figure 121. ***Amazilia tzacatl***, Rufous-tailed Hummingbird, a bird that feeds on flowers that are anchored in bryophytes. Photo by Brian Gratwicke Creative Commons.

Figure 122. ***Troglodytes ochraceus***, Ochraceous Wren, on mosses, a location where it forages. Photo by Annika Lindqvist, through Creative Commons.

Figure 123. ***Chlorospingus ophthalmicus***, Common Bush Tanager, on bryophytes where it forages. Photo by Cephas, through Creative Commons.

In subtropical evergreen forests, Dinesen (1995, 1997) reported on Shelley's Greenbul (***Arizelocichla masukuensis***; Figure 124). These birds found most of their food among the epiphytic mosses.

Figure 124. Shelley´s Greenbul, ***Arizelocichla masukuensis***, a species that forages among epiphytic mosses. Photo by Per Holmen, with permission.

Jamaican Blackbird

Another tropical bird, the Jamaican Blackbird, ***Nesopsar nigerrimus*** (Figure 125), lives in the moist montane of Jamaica above 515 m (Cruz 1978). Its food includes insects, and its foraging behavior among the epiphytes, dead leaves, and moss-covered tree trunks and branches seems to be part of its adaptive evolution on the island. Its shorter legs, more curved claws, and longer, narrower bill adapt it for arboreal rummaging in crevices and among bryophytes.

Figure 125. ***Nesopsar nigerrimus***, Jamaican Blackbird, foraging amid lichens. Photo by Dominic Sherony, through Creative Commons.

Summary

Both capsules and leafy portions of bryophytes are eaten by some birds. This is particularly true in polar climates where tracheophytes are scarce or absent. These birds include grouse and pheasants, as well as

song birds. Even some parrots feed on capsules of ***Polytrichum***. In tundra regions, the ptarmigan and grouse chicks often depend on bryophytes, especially the high quality food of capsules. Some birds use bryophyte capsules as emergency food, and one might describe all use of bryophytes as emergency food, although in some habitats, the emergency is long-lived. This capsule feeding can be seasonal, can depend on a bad year for tracheophytes, or can be used in a habitat with low productivity.

Use of color by birds to locate food is a topic wide open for research. Several hypotheses have suggested that members of the **Splachnaceae** with their brightly colored capsules and fruity odors may get dispersed as a result of attracting birds. This may also occur for the moss ***Pleurophascum***. The ability of most songbirds and some others may enable the birds to see UV reflections that we have not discovered for capsules, or to locate bulbils and other bryophyte structures.

Leafy plants may be eaten as well, including by some diving birds and ptarmigans. Blood Pheasants, in particular, seem to consume large quantities of leafy bryophytes. In other cases, antiherbivory compounds keep the birds away, protecting the invertebrates living among the bryophyte branches. On the other hand, bryophytes may provide high concentrations of some vitamins, and one study on caloric content indicates that levels in leafy bryophytes may be high. Bryophytes can compete for nutrients, especially nitrogen, making the forbs less nutritious. Some birds may use the bryophytes to obtain arachidonic acid in preparation for winter.

The high ratio of cell wall to cell contents requires a long retention time of consumed bryophytes. This can reduce the feeding rate, causing the birds to remain quiet and less conspicuous. On the other hand, it might provide the bryophytes with a means of long-distance dispersal; some bryophytes survive passage through the digestive tract.

Perhaps the greatest food contribution of the bryophytes is through foraging. Many invertebrates reside there. This can be good or bad for the birds, with some specializing on bryophyte foraging and others unable to locate the invertebrates hidden by the bryophytes. Among these, the hanging bryophytes require the greatest specialization by the bird foragers, thus providing a safe haven for many invertebrates. On the other hand, the birds disturb the bryophytes on the ground and elsewhere, providing possible dispersal.

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CHAPTER 16-3
BIRD NESTS

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CHAPTER 16-3
BIRD NESTS

Figure 1. Nest with mosses, lichens, and baby birds. Photo by Kytka through public domain.

Nests

Within a thick and spreading hawthorn bush
That overhung a molehill large and round,
I heard from morn to morn a merr thrush
Sing hymns of rapture, while I drank the
Sound with joy – and oft an unintruding guest,
I watched her secret toils from day to day;
How true she warped the moss to form her nest,
and modell'd it within with wood and clay.

The Thrush's Nest, by Claire
(in Marshall 1908)

Nests are complex structures that often consist of structural differences within a single nest. Most bird nests occur in unique habitats and are constructed of specific materials (Heinrich 2000). The nests themselves are typically so unique that the owner/builder can be identified by the nest. In some cases, false nests are built by the male to discourage would-be suitors from enticing the female away.

The greatest vulnerability in the life cycle is typically during the time the young birds are in the nest (Heinrich 2000). Thus the construction and location of the nest are important survival factors (Heinrich 2000; Mainwaring *et al*. 2012). Most nests are built by the females, but in some cases it is the male who builds the nest(s), using them as sex attractants (Heinrich 2000). But the female typically chooses the site.

Although many nests are built for one-time use by the builder, some nests are reused by the same bird or by other animals for other purposes (Heinrich 2000). For example, the deermouse climbs the tree to find a bird nest, then relocates it near the ground and fills it with seeds to store for the winter.

The importance of bryophytes in the Antarctic is illustrated at Vestfold Hills, East Antarctica. There was greater species diversity of mosses and lichens in sites

adjacent to nests than away from them. Is this a **guano** (bird droppings) benefit to the bryophytes, a moisture or insulation benefit to the birds, or a combination of both? Or do the bryophytes simply like the same locations as the birds? Soil nutrients were not significantly associated with moss diversity or abundance. Rather, both species and abundance of mosses have a positive association with soil water content. So it may be that the birds prefer nesting sites that are also preferred by the mosses.

Types of Nests

Wikipedia (2017) defines nine types of nests. The most common and familiar of these is the **cup** nest that is the product of many of the passerine birds.

The **scrape** nest (Figure 2) is the simplest. It is merely a depression in the soil or vegetation, but it may benefit from the addition of materials, such as bits of vegetation, small stones, shell fragments, or feathers. Mosses may form the base of such a nest. It usually has a rim to prevent eggs from rolling away. This type of nest is the most exposed, thus offering the least protection. This nest style is used by ostriches, many kinds of ducks, most shorebirds, most terns, some falcons, pheasants, quail, partridges, bustards, and sand grouse.

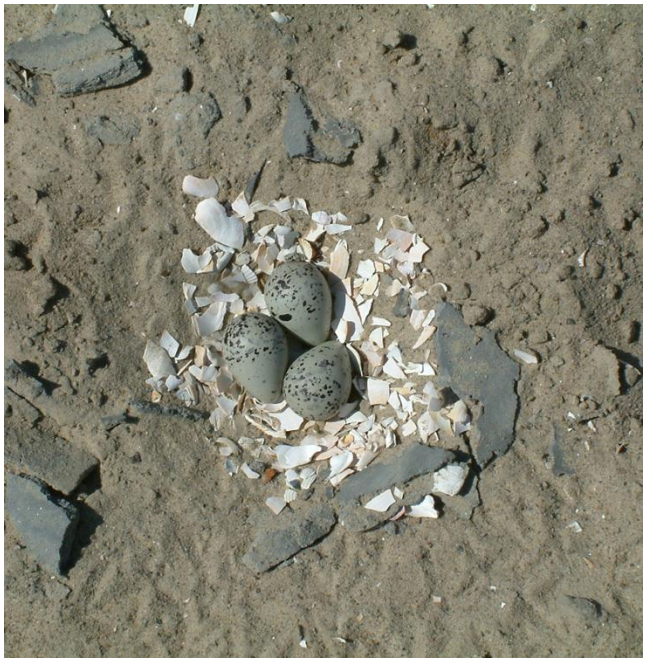

Figure 2. The **scrape** nest of ***Charadrius*** sp., a plover. This nest is lined with shells to support the eggs when the soil or sand become muddy. Photo by Gniazdo Sieweczki RB, through Creative Commons.

The **mound** nest (Figure 3) is typically made of soil, branches, sticks, twigs, and/or leaves (Wikipedia 2017). The females lay their eggs within the mounds, and the rotting vegetable matter generates heat that helps to warm and incubate the eggs. The largest of these nests is that of the Australasian megapodes. In some cases, as in the Australian Brush Turkey (*Alectura lathami*), the gender of the hatched eggs is affected by the temperature, with more females at higher temperatures (Göth 2007). Others building mound nests include the horned coot and the flamingo (Wikipedia 2017).

Figure 3. Malleefowl **mound** nest. Photo by Glen Fergus, through Creative Commons.

The **burrow** is an underground excavation that may be created by the bird or repurposed from a previous mammalian or tortoise owner (Wikipedia 2017). These are sometimes lined with mosses and usually have a tunnel entrance to an egg chamber. The bird occupants include white-browed tits, puffins, shearwaters, some megapodes, motmots, todies, most kingfishers, the crab plover, miners, and leaftossers.

Figure 4. The Sand Martin, *Riparia riparia*, in **burrow** nest. Photo by Bruce, through Creative Commons.

The **cavity** nest (Figure 5) is built in living or dead wood, tree ferns, or some cacti (Wikipedia 2017). The **cavity** nester is more likely to use bryophytes than the above-named nest builders. These are used to line the cavity and to elevate the base to a suitable height for entering and feeding the young birds. Some of the birds excavate their own cavities (woodpeckers, trogons, some nuthatches, many barbets). But far more species (parrots, tits, bluebirds, most hornbills, some kingfishers, some owls, some ducks, some flycatchers) must find holes already large enough.

Figure 5. *Dryocopus martius* (Black Woodpecker) with its **cavity nest**. Photo by Alastair Rae, through Creative Commons.

When most people think of a bird nest, it is the **cup** nest (Figure 6) that they visualize. These nests are open from the top and smoothly hemispherical inside, with a deep depression to house the eggs (Wikipedia 2017). The materials used are mostly pliable and some species specifically use bryophytes, either in the construction, the lining, or the outermost layer – perhaps as camouflage. The nest mass often correlates with the weight/size of the adult bird it must support. The insulation quality of the nest relates to nest mass, nest wall thickness, nest depth, nest weave density and porosity, surface area, height above ground, and elevation above sea level. Among the many cup builders are the robin and the tiny hummingbird. Some are attached to the branch with saliva, and some hummingbirds use spider webs to affix the nest.

Figure 6. ***Passerculus sandwichensis***, Savannah Sparrow **cup** nest. Photo by Kati Fleming, through Creative Commons.

The **saucer** or **plate** nest is somewhat similar to the cup nest, but has very little, if any, depression (Wikipedia 2017). This nest may be within the range of nest variation for a cup builder.

The **platform** nest (Figure 7) is large and flat. It is occasionally lined with mosses (Wikipedia 2017). This nest type is common among some ducks and birds of prey. This more permanent structure can be used y the same pair of birds for many years.

Figure 7. Osprey (*Pandion haliaetus*) and **platform** nest. Photo by Tibor Duliskovich, through Creative Commons.

The **pendant** nest (Figure 8) is an elongated sac that hangs from a branch (Wikipedia 2017). Pendant nest builders include Oropendolas, caciques, orioles, weavers, and sunbirds. Some of these birds construct their nests from bryophytes.

Figure 8. ***Ploceus castaneiceps*** (Taveta Golden-weaver) **pendant** nest. Photo by Robert Lawton, through Creative Commons.

The **sphere** nest (Figure 9) is a globe-shaped nest that is completely enclosed except for a small opening which may be near the bottom (Wikipedia 2017).

Figure 9. Weaver (**Ploceidae**) on **sphere** nest. Photo by Bernard Dupont, through Creative Commons.

Bryophyte Advantages in Bird Nests

Use of mosses for bird nests is not uncommon. Annie Martin (Bryonet 1 June 2010) reports that as many as forty different types of birds use mosses in constructing their nests. While that may be a local number, many more examples are known worldwide. Birds have long been recognized as consumers of mosses and liverworts for nesting materials (Figure 10) (Takaki 1957, Breil & Moyle 1976 – SE USA; Takeshita 1978, Furuki & Onuma 1996 – Japan; Hribek 1985 – Europe; Abolina 1991 – Lithuania; Cao & Caihua 1991, Cao *et al*. 2010 – China), to name a few. Richardson (1981) listed 53 British birds that use mosses to some degree in their nests; Campbell and Ferguson-Lees (1972) reported 52 from that region. Jadin and Billiet (1979) described the activities of birds building nests with mosses and liverworts on Reunion Island in the Indian Ocean.

Figure 10. Cup nest made of leafy liverworts in Costa Rica. Photo courtesy of Dave Fenlon.

Birds and bryophytes can have close relationships that permit both of them to reproduce. Some birds have an incessant need to make nests, and mosses can be a favorite building material. I found it impossible to develop any kind of moss garden in my garden room when it housed 10 Zebra Finches (***Taeniopygia guttata***; Figure 11) because within days or even hours every scrap of the moss had been moved from my chosen location to the midst of the bamboo clump, where it aided in forming massive 3-story apartment nests. I ultimately had to get rid of the finches and traded them for Society Finches, birds that have a little more reverence for mosses and don't find nest building to be an essential daily activity!

Figure 11. ***Taeniopygia guttata***, Zebra Finch, a bird that often uses mosses in its nests, at least when choices are limited. Photo by Peripitus, through Creative Commons.

The families of birds using mosses to some degree in their nests ranges widely. We need consider only a few examples to illustrate this. In the **Passeriformes**, Hribek (1985) found that among others in the **Paridae**, the Great Tit (***Parus major***; Figure 18-Figure 19) and the Blue Tit (***Cyanistes caeruleus***; Figure 22) use mosses in their nests, as does the Pallas Dipper (***Cinclus pallasii***; Figure 12) in the **Cinclidae** (Nishimura *et al.* 1980). In the **Apodiformes: Apodidae**, the Philippine Swiftlet (***Aerodramus mearnsi***; Figure 13) uses bryophytes (Tan *et al*. 1982). In the **Podicipediformes: Podicipedidae**, breeding populations of the Red-necked Grebe (***Podiceps grisegena***; Figure 14-Figure 15) in the Northwest Territories use ***Sphagnum*** (Figure 16) in addition to cattails and other emergent vegetation in nest construction (Fournier & Hines 1998). Even the huge American Bald Eagle (***Haliaeetus leucocephalus*** in the **Falconiformes: Accipitridae**; Figure 17) in Alaska uses mosses in old-growth forests in their nests atop tall spruce trees (Holleman 1997).

Figure 12. ***Cinclus pallasii***, Brown dipper, Pallas Dipper, in stream. This species collects aquatic mosses to make its nest. Photo by Alpsdake, through Creative Commons.

Figure 13. ***Aerodramus mearnsi***, Philippine Swiftlet, with its challenging moss nest. Photo by Angie Cederlund, with permission.

Figure 14. ***Podiceps grisegena***, Red-necked Grebe with ducklings, a species that uses mosses in its nest. Photo through public domain.

Figure 15. ***Podiceps grisegena***, Red-necked Grebe, on its nest with nestlings on its back. Photo by Lukasz Lukasik, through Creative Commons.

Figure 16. ***Sphagnum fimbriatum***; ***Sphagnum*** is used as a nest material for the Red-necked Grebe. Photo by James K. Lindsey, with permission.

Figure 17. ***Haliaeetus leucocephalus***, American Bald Eagle landing on nest. This species uses mosses in building its nest in Alaska. Photo by Murray Foubister, through Creative Commons.

With such a large number of birds using bryophytes in their nests, we must ask why? Do they provide some special attributes that make them desirable? Or are they simply easy to collect and available?

Alabrudzińska *et al*. (2003) found that the quantity and proportion of mosses in nests and the nest size can influence the success of eggs as well as of the nestlings, as seen in the Great Tits (***Parus major***; Figure 18-Figure 19). They considered that nest size and composition must satisfy contradictory pressures needed for survival. The nest must be kept moist with a relatively constant temperature. It must also protect the eggs and young from predation and limit disease and parasites.

Figure 18. ***Parus major***, Great Tit male, a bird that includes mosses in its nest. Photo by Charles J. Sharp, through Creative Commons.

Figure 19. ***Parus major*** nest with moss, down, and nestlings. Photo by Notts Ex Miner, through Creative Commons.

Insulation

Bryophytes can have beneficial effects that are not provided by other nesting materials. Providing insulation may be the first use that comes to mind. Birds often use grasses, feathers, and fur to regulate the nest temperature (Bartholomew *et al.* 1976; Winkler 1993; Blem & Blem 1994; Lombardo *et al.* 1995), much as we put on a winter coat or sleep under a quilt. But bryophytes can provide insulation as well.

Several studies have indicated the importance of nest temperature. Olson *et al*. (2006) used Zebra Finches (***Taeniopygia guttata***; Figure 11) to evaluate the importance of temperature on embryo development. They found that after 12 days of incubation, periodic cooling resulted in lower embryo mass and yolk reserves compared to controls incubated at 37.5ºC. When the eggs were cooled to 20ºC regularly, the embryos had higher mass-specific metabolic rates and delayed development.

Peréz *et al*. (2008) experimentally heated the nests of the Tree Swallow (***Tachycineta bicolor***; Figure 20) during incubation. They found that incubating females maintained better body condition and fed nestlings at a greater rate. Their nestlings similarly had higher body mass and better body condition. In contrast, Ardia *et al*. (2008) examined the effects of cooling on the same species. They found that cooled eggs required longer incubation periods and the nestlings had a lower immunity to bacteria. Embryos that were exposed to experimental cooling resulted in nestlings that had lower residual and absolute body mass. The cooled females made fewer feeding trips, but this seemed to have no effect on nestling immunity to bacteria.

Figure 20. ***Tachycineta bicolor***, Tree Swallow, a species in which nest temperature affects health of the nestlings. Photo by John Benson, through Creative Commons.

One means by which birds can alter the temperature of a nest is by increasing its size or thickness. This mechanism is used by the Great Tit, ***Parus major*** (Figure 18-Figure 19) (Alabrudzińska *et al*. 2003). Clutch size (Figure 21) correlates negatively with total nest mass, but is positively correlated with the proportion of nest mass in the lining. Successful performances of eggs and nestlings are attributable to the quantity and proportion of moss in the nest structure as well as the nest size. Alabrudzińska and coworkers suggest that nest size and composition may affect moisture, temperature, protection, and/or sanitary conditions of the nest, thus supporting the hypothesis that mosses serve as more than structural materials.

Figure 21. ***Parus major***, Great Tit, nest with moss and eggs in nest box. Photo by Notts Ex Miner, through Creative Commons.

Deeming *et al*. (2012) extended this study to determine what triggers affect usage of more mosses in the nests of the Blue Tits (***Cyanistes caeruleus***; Figure 22) and Great Tits (***Parus major***; Figure 18-Figure 19, Figure 21). They found that nest mass is inversely related to temperatures experienced by the female during nest construction. Nest cup mass in particular is related to the temperatures experienced by the females during the seven days prior to the beginning of egg laying. This behavior is independent of latitude (Deeming *et al*. 2012), but nests are heavier at higher latitudes (Mainwaring *et al*. 2012).

Figure 22. ***Cyanistes caeruleus***, Blue Tit adult, feeding. Photo by Dave Howes, through Creative Commons.

The Sociable Weaver (***Philetairus socius***; Figure 36-Figure 37) can serve to illustrate the role nesting materials might play and give us some insight into the role mosses could play. The nest of the Sociable Weaver consists of multiple chambers, and in summer each chamber is occupied by 1-2 birds, whereas in winter there may be up to 5 birds in a chamber, with some chambers remaining empty (Bartholomew *et al.* 1976). Bartholomew and coworkers found that for the Sociable Weaver in the Kalahari Gemsbok National Park, South Africa, the nest temperatures varied only 7-8ºC when the outside temperatures ranged from 16-33.5ºC. This temperature is controlled largely by the number of birds in a chamber. Van Dijk *et al.* (2013) further found that nest volume had no effect on its thermoregulatory benefits. Nevertheless, the central part of the nest had the most stable conditions.

Blem and Blem (1994) suggested that the moist bryophytes could alter the nest temperature, presumably cooling it through evaporative cooling, and certainly maintaining a cool temperature longer against the hot (~43ºC) body temperature of the birds, much like a runner putting a wet band around his or her head. On the other hand, I suggest that the dark-colored mosses can also absorb sunshine like a dark body and warm the nest on cool days before leaves appear on the trees.

The nest of the **Prothonotary Warbler** (***Protonotaria citrea***; Figure 23), a cavity nester, consists of a cup made of grasses, leaves, and rootlets placed on a thick mat of moist, green bryophytes – both mosses and liverworts (Bent 1953; Petit 1989; Blem & Blem 1992). These bryophytes remain moist during the incubation and nestling stages (Blem & Blem 1994). It is likely that this nest composition affects the nest living conditions (Mertens 1977 a, b). The bryophyte composition of these nests ranges 74.7-80.2% of the dry mass of the nest. ***Anomodon attenuatus*** (Figure 24) is the most used of the five moss and two liverwort species. The other bryophytes found in nests were the mosses ***Haplocladium microphyllum*** (Figure 25), ***Amblystegium varium*** (Figure 26), ***Plagiomnium cuspidatum*** (Figure 27), and ***Thuidium delicatulum*** (Figure 28), and the liverworts ***Porella platyphylla*** (Figure 29) and ***Frullania eboracensis*** (Figure 30). The woven bryophyte nest is also able to expand as the baby birds grow, maintaining a tight fit to the tiny eggs, but expanding as the young birds grow.

Figure 23. ***Protonotaria citrea***, Prothonotary Warbler, a species that builds its nest on a mat of moist, green mosses. Photo by William H. Majoros, through Creative Commons.

Figure 24. ***Anomodon attenuatus***, a pleurocarpous moss used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Michael Lüth, with permission.

Figure 25. ***Haplocladium microphyllum***, a pleurocarpous moss used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Robin Bovey, with permission through Dale Vitt.

Figure 26. ***Amblystegium varium***, a pleurocarpous moss used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Michael Lüth, with permission.

Figure 27. ***Plagiomnium cuspidatum***, a plagiotropic moss used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Michael Lüth, with permission.

Figure 28. ***Thuidium delicatulum***, a pleurocarpous moss used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Janice Glime.

Figure 29. ***Porella platyphylla***, a leafy liverwort that grows on rocks and trees and is used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Tim Waters through Creative Commons.

Figure 30. ***Frullania eboracensis***, a leafy liverwort that grows on bark and is used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Robert Klips, with permission.

Most of the evidence of the importance of bryophytes as insulators is inconclusive. Mainwaring *et al*. (2012) found that insulative properties of nest linings decreased as

the season progressed. The Blue Tit (***Cyanistes caeruleus***; Figure 22) exhibited seasonal changes in the nest composition, but the mass of mosses in the base of the nest showed no seasonal variation (Mainwaring *et al*. 2014). On the other hand, there was a seasonal decline in the mass of materials used to line the cup (Mainwaring & Hartley 2008).

Deeming and Mainwaring (2015) found that the Blue Tits (***Cyanistes caeruleus***; Figure 22), European Pied Flycatchers (***Ficedula hypoleuca***; Figure 31), and Common Redstart (***Phoenicurus phoenicurus***; Figure 32) used different nesting materials in the same types of nest boxes. Blue Tits used mostly mosses with hair, fur, and feathers (Figure 33); Flycatchers used leaves and grass (Figure 34); Redstarts used leaves, grass, moss, and lots of feathers. (Figure 35). Nevertheless, all three nest types have similar insulating properties.

Figure 31. ***Ficedula hypoleuca***, European Pied Flycatcher, a non-moss user. Photo by Ron Knight, through Creative Commons.

Figure 32. ***Phoenicurus phoenicurus***, Common Redstart, with earwig; this species uses mosses and other materials. Photo by Yerpo, through Creative Commons.

Figure 33. ***Cyanistes caeruleus***, Blue Tit, nest with mosses, feathers, and hair. Photo by Arnstein Ronning, through Creative Commons.

Figure 34. ***Ficedula hypoleuca***, European Pied Flycatcher, eggs with leaves and grass in the nest; mosses are not used. Photo by Arnstei Rønning, through Creative Commons.

Figure 35. ***Phoenicurus phoenicurus***, Common Redstart nest with moss, grasses, feathers, and eggs. Photo by Roberto Zanon, through Creative Common.

Humidity Control

Humidity control can be important for young birds, and nest materials can be used to buffer changes in humidity. We can use the Sociable Weaver (***Philetairus socius***; Figure 36) once more to illustrate this role, perhaps in the extreme.

Figure 36. ***Philetairus socius***, Sociable Weaver, a bird that builds a huge apartment nest that regulates humidity. Photo by Charles J. Sharp, through Creative Commons.

The Sociable Weaver (***Philetairus socius***; Figure 36) builds the largest bird nest (Figure 37) on the planet (van Dijk *et al*. 2013), housing at times over 100 pairs of birds (White *et al*. 1975). The nest is usually constructed in trees, using large twigs to construct the roof (Sociable Weaver 2017). Dry grasses separate the chambers and sharp spikes of straw deter predators from traversing the entrance tunnels. Inside, soft plant material, fur, cotton, and fluff line the nesting chambers. I can't help but wonder if bryophytes would be included if they were available in its habitat.

For the Sociable Weaver, the nest materials absorb the humidity, maintaining a lower humidity than that in the outside air (Bartholomew *et al.* 1976). The Sociable Weaver (***Philetairus socius***; Figure 36) does not use bryophytes, probably due to scarcity in its dry habitat, but where the bryophytes grow and are used by birds, I would expect them to have a significant role in absorbing and retaining humidity. I have taken bryophytes from a desiccator and watched their weight rise as I tried to weigh them. Bryophytes are able to take moisture out of the atmosphere, and thus they could also absorb moisture created by the birds' bodies. On the other hand, when the atmosphere is dry, the bryophytes could absorb moisture at night and help to keep baby birds, with scant covering of feathers, from drying out during the day.

Wimberger (1984) noted that the use of fresh bryophytes raised the humidity in nest cavities. This could prevent egg desiccation and increase hatching success (see also Clark & Mason 1985). On the other hand, the Fieldfare (***Turdus pilaris***; Figure 38-Figure 40) has an open nest, using grass and mud with very little moss or lichen. Compared to other species, the Fieldfare lost water rapidly. Within 10 minutes of removal of a water source, only 54% humidity remained in the nest, whereas the Redwing (***Turdus iliacus***; Figure 41) nest had 66%, the Eurasian Blackcap (***Sylvia atricapilla***; Figure 42-Figure 44) 71%, the Pied Flycatcher (***Ficedula hypoleuca***; Figure 31, Figure 34) 73%, the Chaffinch (***Fringilla coelebs***) 80%, and the Brambling (***Fringilla montifringilla***) 81%. Thrushes (**Turdidae**) made dense nests that still contained considerable water several days later. When the water content of the mosses and lichens was increased from 30% to 60%, the water content of the nest 24 hours later rose from 27% to 41%.

Figure 37. The very large nest of ***Philetairus socius***, Sociable Weaver. Photo by Harald Süpfle, through Creative Commons.

Figure 38. ***Turdus pilaris***, Fieldfare, with worm. This species uses little or no moss in its nest and the nest loses water rapidly. Photo by Grzegorz Golebiowski, through Creative Commons.

Figure 39. ***Turdus pilaris***, Fieldfare fledgling. Photo by Ernst Vikne, through Creative Commons.

Figure 40. ***Turdus pilaris***, Fieldfare, babies in nest – a species that uses few or no mosses in its nest. Photo by Arnstein Rønning, through Creative Commons.

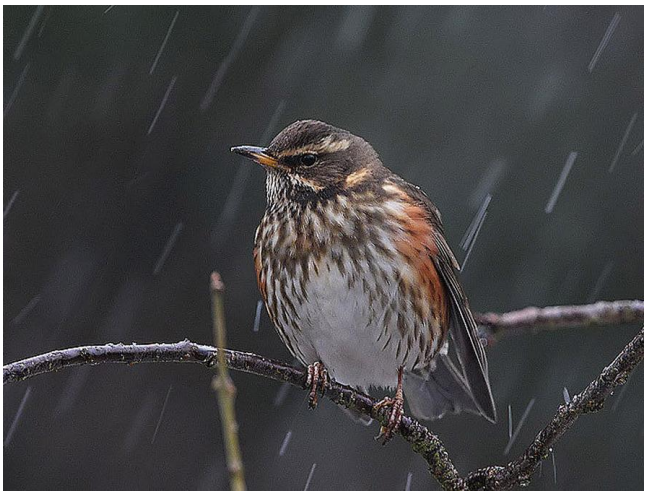

Figure 41. ***Turdus iliacus***, Redwing, a bird that builds a nest that maintains moisture. Photo by Steve Garvie, through Creative Commons.

Figure 42. ***Sylvia atricapilla***, European Blackcap. Photo by S. Drozd Lund, through Creative Commons.

Figure 43. ***Sylvia atricapilla***, European Blackcap, a nest that is able to hold moisture. Photo by James K. Lindsey, with permission.

Figure 44. ***Sylvia atricapilla***, Eurasian Blackcap, nest with nestlings. Photo through Creative Commons.

Fontúrbel *et al*. (2020) noted that hummingbirds benefit from moisture retention by mosses, preventing eggs from drying out (see also Breil & Moyle 1976; Blem & Blem 1994).

In a study on passerine birds, Slagsvold (1989b) found that the width of the interior of the nest cup correlated negatively with the amount of mosses and lichens used in construction. It would seem, then, that using more mosses and narrowing the interior of the nest would provide a more insulated, more moist environment, and that bryophytes can be major contributors to those effects.

Elasticity

Elasticity can be important for both insulation and humidity. Slagsvold (1989a) noticed that the Chaffinch (***Fringilla coelebs***; Figure 45-Figure 46) and Brambling (***Fringilla montifringilla***; Figure 47) construct nest cups that expand in proportion to the number of young. This would also permit the nest to expand as the nestlings grow, continuing to maintain a warm blanket effect around them.

Slagsvold (1989a) considered selection for elastic nesting materials such as mosses and lichens as important criteria. But it appears that it is the ability to absorb rainwater rapidly, then to dry slowly, that is important.

Among the passerine birds, Slagsvold surmised that narrow nest cups were especially common with small-sized birds that nest above ground. These nests are typically open and include large quantities of mosses and lichens.

Figure 45. ***Fringilla coelebs***, Chaffinch, a bird that selects nesting materials, such as bryophytes, that expand as nestlings grow. Photo by Andreas Trepte, through Creative Commons.

Figure 46. ***Fringilla coelebs***, Chaffinch, expandable nest with mosses. Photo by Trachemys, through Creative Commons.

Figure 47. ***Fringilla montifringilla***, Brambling male, a species for which mosses keep the nest moist. Photo by M. M. Lolek, through Creative Commons.

Antibacterial, Antiparasitic?

There are lots of hungry predators, albeit tiny, that enjoy living on birds. These can take a toll on survival. Adults and juveniles of the Cliff Swallow (***Petrochelidon pyrrhonota***; Figure 48) occupying parasite-free (fumigated) colonies had an average of 4.4% (adults) and 62.2% (juveniles) greater daily survival than their counterparts in naturally infested colonies (Brown & Brown 2004). Several researchers (Wimberger 1984; Clark & Mason 1985) suggest that the bryophytes may serve as insecticidal and anti-pathogenic agents in the nest. Clark and Mason examined the European Starling (***Sturnus vulgaris***; Figure 49) as a likely recipient of such help because it uses the same nest for multiple years, thus increasing the chances for parasite and pathogen encounter. This species chooses fresh green material in its nest, restricting its selection to a small number of species and choosing plants with volatile compounds that are likely to inhibit arthropod hatching or bacterial growth. These plants typically possess greater concentrations of mono- and sesquiterpenes than the local flora in general.

Figure 48. ***Petrochelidon pyrrhonota***, Cliff Swallow, a bird that has lots of parasites. Photo by Ingrid Taylar, through Creative Commons.

Figure 49. ***Sturnus vulgaris***, European Starling, a species that re-uses its nest and incorporates plants that contain greater concentrations of mono- and sesquiterpenes than the local flora in general. Photo by Luzmaria, through Creative Commons.

Igic *et al*. (2009) found that the Song Thrush (***Turdus philomelos***; Figure 50) used cigarette butts in its nest (Figure 51). This raised the question of anti-predatory nesting materials, as shown by Strecker (1926) and Schuetz (2005) for shed snake skins and carnivore scat. But mosses and odiferous leaves may serve this function as well, protecting birds against ectoparasites (Clark & Mason 1988; Banbura *et al*. 1995; Lambrechts & Santos 2000).

Figure 50. ***Turdus philomelos***, Song Thrush, a bird that may use anti-predatory nesting material. Photo by Yvan, through Creative Commons.

Figure 51. ***Turdus philomelos***, Song Thrush, feeding babies in New Zealand nest. Photo from ZipCodeZoo, through Creative Commons.

Blue Tits (***Cyanistes caeruleus***; Figure 22) use odor cues to determine when to replace green plant materials (Mennerat 2008). The female Blue Tits bring fresh plants to their nests (Banbura *et al*. 1995), so there is reason to believe that these plants may be chemically endowed in a way that helps to protect the nest. Both parents hesitated longer before entering the nest box when the experimenter added green tracheophyte material compared to addition of mosses. Banbura concluded that we cannot rule out antiparasite functions of green plant material in the Blue Tit nests, but neither can we say conclusively that they serve this purpose.

On Corsica, Mennerat *et al*. (2009a, b) found that despite adding aromatic plants to their nests, the Blue Tit (***Cyanistes caeruleus***; Figure 22) experiences just as many parasites as without them. However, their growth is improved. The researchers found that the bacterial community in the nest was significantly affected by these plants, being reduced on nestlings. This offered the further advantage that the bacteria reduced most on the chicks with the worst infestations of the blood-sucking blowfly larvae (*Protocalliphora*). On the other hand, birds in nests where aromatic plants were replaced by mosses did not experience the benefits experienced in accompaniment of the aromatic plants: chick mass gain, higher haematocrit levels, faster feather development (Mennerat *et al*. 2009b).

Shutler and Campbell (2007) added greenery to nests of the non-greenery-using Tree Swallows (***Tachycineta bicolor***; Figure 20). They found no evidence that feathers had reduced parasites, but the added green plant material did result in lower numbers of ectoparasites in the nests. Nevertheless, there was no increase in breeding success.

Dawson *et al*. (2011) investigated the use of feathers to line nests in the Tree Swallow (***Tachycineta bicolor***; Figure 20). They found that adding feathers to nests actually increased the abundance of ectoparasites in those nests, a conclusion previously noted by Lombardo *et al*. (1995). Dawson and coworkers interpreted this to mean that the feathers separated the nestlings from the parasites. This conclusion supported that of Winkler (1993) in a study that showed that removal of feathers from Tree Swallow nests caused higher mite and lice infestation on nestlings, coinciding with lower growth rates of the nestlings, compared to controls. But there is also a cost to males that spend more time to gather more feathers – they are more likely to lose their mate to another male!

Wimberger (1984) further showed that birds in **Falconiformes** that used their nests in successive years were more likely to include green foliage, including bryophytes, than those species that did not reuse their nests. This suggests that the bryophytes may have some sort of protective function.

If birds choose nesting materials based on their antibiotic properties, it would seem that they would need to detect the odors caused by the compounds that facilitate this antibiotic use. But the **Passeriformes** (the birds that more often use bryophytes in their nests) are known to have a very small relative **olfactory** (odor-sensing) bulb size (Mennerat *et al*. 2005). Thus we have assumed that these birds have poor olfactory senses.

It appears that this wisdom is misleading, at least for some passerine birds (Mennerat *et al*. 2005; Strandh *et al*. 2012). The Blue Tit (***Cyanistes caeruleus***; Figure 22) uses mosses in her nest and this species is one of the birds that is sensitive to the odor of lavender (Mennerat *et al*. 2005). If birds choose vegetation based on the odor of volatile compounds, then I am surprised that the aromatic thallose liverworts do not seem to be used in nests.

Brian Dykstra (pers. comm. 10 December 2011) asked an interesting question. Liverworts such as species of ***Frullania*** (Figure 30) often house rotifers in their lobules (Figure 52). Could it be that these bacteria consumers actually help the birds by reducing the abundance of pathogens?

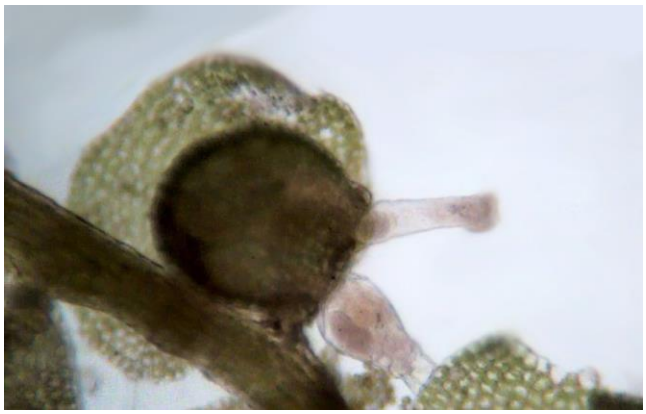

Figure 52. ***Frullania eboracensis*** lobule with rotifer. Photo courtesy of Lisa Pokorski.

We know that bryophytes themselves often have antibacterial properties (*e.g.* Basile *et al.* 1999; Alabrundzinska *et al.* 2003; Ariyo *et al.* 2011; Bukvicki *et al.* 2012; Asakawa *et al.* 2013; Yu *et al.* 2014), but until now, no study has demonstrated conclusively that they serve this purpose in the nests of birds.

At last, Fontúrbel *et al.* (2020) have shown that "Mamma knows best." They found that the hummingbird Picaflor Rubi (***Sephanoides sephaniodes***; Figure 53-Figure 54) selects the mosses ***Ancistrodes genuflexa*** (in 100% of the nests; Figure 55), ***Weymouthia mollis*** (27%; Figure 56), and ***Weymouthia cochlearifolia*** (17%; Figure 57) based on samples in austral South America, but ***A. genuflexa*** is particularly scarce in the forest while comprising up to 97% of the moss nesting material. They identified five compounds with antibacterial properties (Figure 58) in ***A. genuflexa***.

Figure 53. ***Sephanoides sephaniodes***, a hummingbird that uses ***Ancistrodes genuflexa*** selectively in its nests, giving the nests antibiotic properties. Photo by Felipe Bernala, through Creative Commons.

Figure 54. ***Sephanoides sephaniodes*** nest made with mosses. Photo by Diucón, through Creative Commons.

Figure 55. ***Ancistrodes genuflexa***, the most common moss in nests of Picaflor Rubi (***Sephanoides sephaniodes***). Photo by Felipe Osorio Zúñiga, with permission.

Figure 56. ***Weymouthia mollis***, a moss used in nests of Picaflor Rubi (***Sephanoides sephaniodes***). Photo by Juan Larrain, with permission

Figure 57. ***Weymouthia cochlearifolia***, a moss used in nests of Picaflor Rubi (***Sephanoides sephaniodes***). Photo by Juan Larrain, with permission.

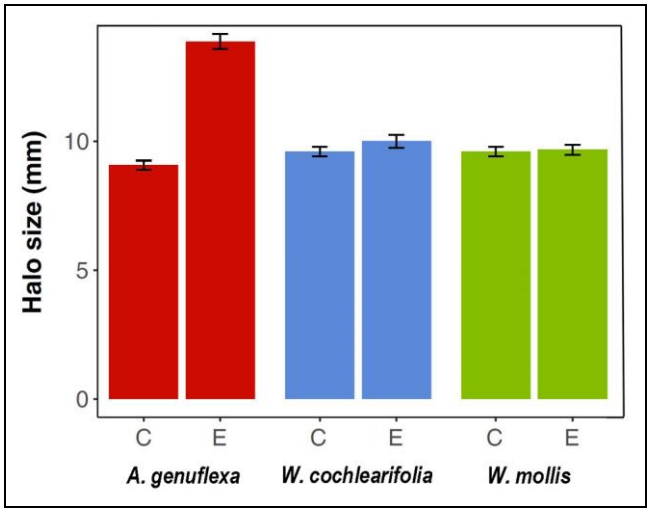

Figure 58. Antimicrobial activity of control (**C**) and moss extracts (**E**) from ***Ancistrodes genuflexa***, ***Weymouthia mollis***, and ***Weymouthia cochlearifolia***) against five common bacteria strands. Error bars represent standard error. Modified from Fontúrbel *et al*. 2020.

We know from other studies that birds may prefer materials that have antibiotic properties. Doctoral student Sarah Knutie became curious when one of Darwin's finches (Figure 59) pulled at cotton threads on the clothes line rope to use as nesting material (Pety 2020). She followed up with an experiment using cotton balls. Half of them had antibiotic solution (1% permethrin) and half had just water. These were available in wire-mesh dispensers. Of the 26 active nests examined, 85% contained cotton. Of these, 13 nests had permethrin-treated cotton and 9 had untreated cotton. Only 4 had no cotton. Of the 8 nests with at least 1 g of treated cotton, 7 had no parasites and the eighth had only 4. Hence, it appears that the birds may select materials with antibiotic properties. That could explain at least some of the selection of bryophytes for nesting material.

Figure 59. Darwin's finch with bryophytes in its beak, a bird that sometimes collects cotton balls with antibiotics for nesting. Photo by Rudy R., through Creative Commons.

There is a wide array of research projects needed to understand the role of bryophytes in nests. What is their elasticity compared to other nesting materials? Do they provide antibiotic properties that reduce parasites, fungi, or bacteria? Do they serve as better insulators than other materials? Do they keep the nest at a more constant humidity than other materials? Are they easier to work with or to carry than other materials?

Cavity Nest Elevation

Bryophytes have an additional function for cavity-nesting birds. They are often used to raise the nest cup so that the baby birds can be reached easily by the parents when feeding the birds and the birds can get in and out easily (Hamao *et al*. 2016). The bryophytes can also serve to separate the nest cups from cavity walls that may remain too moist, at the same time absorbing the excess moisture (Hamao *et al*. 2016).

Selection of Nest Materials

Just how choosy are the birds about the mosses they use? Breil and Moyle (1976) found that 11 birds had used 60 different species of mosses, including aquatic species, in their nests, suggesting that preference may simply depend on availability. Pant (1989) investigated the nests of five bird species in the Kumaon Himalaya and found that the primary mosses used were pleurocarpous. He supposed that these were preferred because they were easier to shape to suit the shape of the nest. This might also account for the use of larger leafy liverworts, in addition to pleurocarpous mosses, in the nest of the Streaked Laughing Thrush (***Trochalopteron lineatum***; Figure 60) (Pant & Tewari 1984). Furthermore, Abolina (1991) found that the large leafy liverworts ***Radula complanata*** (Figure 61) and ***Lophocolea heterophylla*** (Figure 62) were used for nesting material in Lithuania.

In their study of nests of twelve bird species, Breil and Moyle (1976) found that most birds chose the bryophytes that were most abundant locally. These included the aquatic mosses ***Fontinalis*** (Figure 63) and ***Hygrohypnum*** (Figure 64), and ***Sphagnum*** (Figure 16). Terrestrial mosses were mostly the pleurocarpous ***Brachythecium***

(Figure 65), ***Hedwigia*** (Figure 66), and ***Thuidium*** (Figure 67), plus the epiphytic bryophytes ***Frullania*** (Figure 30) and ***Platygyrium repens*** (Figure 68).

Figure 60. ***Trochalopteron lineatum***, Streaked Laughing Thrush, one of the few birds known to use leafy liverworts in its nest. Photo by P. Jeganathan, through Creative Common.

Figure 61. ***Radula complanata***, a nesting material for birds in Lithuania. Photo by Hermann Schachner, through Creative Commons.

Figure 62. ***Lophocolea heterophylla***, a nesting material for birds in Lithuania. Photo by Bob Klips, with permission.

Figure 63. ***Fontinalis antipyretica***; some members of this genus are used in bird nests. Photo by Andrew Spink, with permission.

Figure 64. ***Hygrohypnum ochraceum***, ; some members of this genus are used in bird nests. Photo by Michael Lüth, with permission.

Figure 65. ***Brachythecium rutabulum***, representing a genus commonly used in bird nests. Photo by Kristian Peters, through Creative Commons.

Figure 66. Dry ***Hedwigia ciliata*** with capsules, a pleurocarpous species commonly used in bird nests. Photo by Hugues Tinguy, through Creative Commons.

Figure 67. ***Thuidium delicatulum***, representing a genus commonly used in bird nests. Photo by Janice Glime.

Figure 68. ***Platygyrium repens***, an epiphytic moss commonly used in bird nests in the Appalachians, USA. Photo by Hermann Schachner, through Creative Commons.

Other birds appear to be especially choosy. In Hawaii, one bird nest (most likely of a non-native species) made its nest almost entirely from the setae and capsules of ***Pyrrhobryum*** (***Rhizogonium***) ***spiniforme*** (Figure 69-Figure 70) (Brandon Stone, Bryonet 9 April 2003).

Figure 69. ***Pyrrhobryum spiniforme***, a moss used exclusively in some bird nests in Hawaii. Photo by Alan Cressler, with permission.

Figure 70. ***Pyrrhobryum spiniforme*** with capsule and seta that are used for nests by some birds in Hawaii. Photo by Janice Glime.

In the Uluguru Mountains of Tanzania, Tamás Pócs (Bryonet 2 June 2010) observed a nest of a small bird made purely of ***Orthostichella rigida*** (Figure 71), a common hanging epiphyte.

Figure 71. ***Orthostichella rigida*** from Tasmania, a pendent moss used in bird nests there. Photo courtesy of Tamás Pócs.

In Kenya, Min Chuah Petiot (Bryonet 2 June 2010) has collected an abandoned and fallen nest made with the hanging moss ***Papillaria africana*** (Figure 72). This moss was still green and alive.

Figure 72. ***Papillaria africana***, nesting material in Kenya. Photo by Bruno Senterre, with permission.

Gustavo Tomás and Andrew Spink (Andrew Spink, Bryonet 2 June 2010) collected moss samples from a large number of Blue Tit (***Cyanistes caeruleus***; Figure 22) and Coal Tit (***Periparus ater***; Figure 73) nests from a woodland in the eastern Netherlands. The most common species in nests was ***Hypnum cupressiforme*** (Figure 74-Figure 75), which is common in the area. However, other locally common mosses were less common in the nests, indicating that the birds clearly selected certain species. It is interesting that different species were used in different parts (top/bottom) of the nest.

Figure 73. ***Periparus ater***, Coal Tit, a species that commonly uses ***Hypnum cupressiforme*** (Figure 74) in its nests in The Netherlands. Photo from Biopix, through Creative Commons.

Figure 74. ***Hypnum cupressiforme***, a moss commonly used in nests of Blue Tits and Coal Tits, covering the log. Photo by Michael Lüth, with permission.

Figure 75. ***Hypnum cupressiforme*** var ***cupressiforme***, a preferred moss in nests of Blue Tits and Coal Tits. Photo by David Holyoak, with permission.

In the Pacific Northwest of Oregon and Washington, all seven thrush species (**Turdidae**) and six hummingbird species (**Trocholidae**) use either bryophytes or lichens in their nests (Wolf 2009). All nine crows and jays (**Corvidae**) except the Black-billed Magpie (***Pica hudsonia***; Figure 76-Figure 77) use bryophytes for nesting material. These Pacific Northwest bryophytes include ***Alsia*** (Figure 78), ***Brachythecium*** (Figure 65), ***Calliergon*** (Figure 79), ***Dendroalsia*** (Figure 80), ***Dicranum*** (Figure 81), ***Eurhynchium*** (Figure 82), ***Homalothecium*** (Figure 83), ***Hypnum*** (Figure 74), ***Isothecium*** (Figure 84), ***Pogonatum*** (Figure 85), ***Pohlia*** (Figure 91), ***Polytrichum*** (Figure 86), ***Porella*** (Figure 88), and ***Sphagnum*** (Figure 87).

Figure 76. ***Pica hudsonia***, Black-billed Magpie, a bird that does not use bryophytes in its nest. Photo by Carplips, through Creative Commons.

Figure 77. ***Pica hudsonia***, Black-billed Magpie, nest showing mud and vegetable matter, but no bryophytes. Photo by Rich Mooney, through Creative Commons.

Figure 78. ***Alsia californica*** with capsules, a moss used in nests in the Pacific Northwest, USA. Photo by Paul Wilson, with permission.

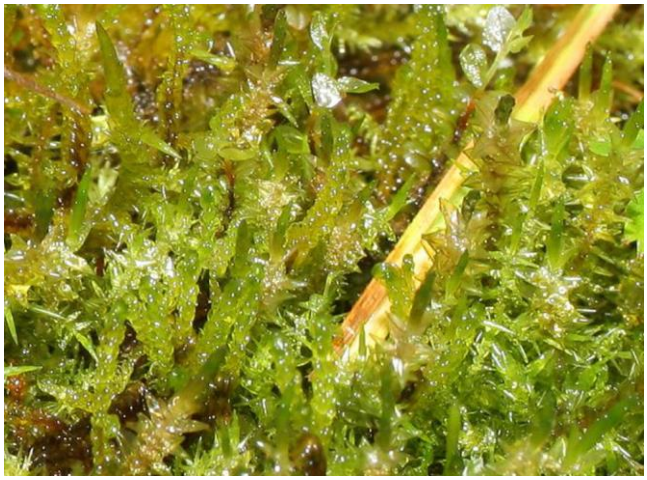

Figure 79. ***Calliergon giganteum*** with ice, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Kristian Peters, through Creative Commons.

Figure 80. ***Dendroalsia abietina***, a species used commonly in bird nests in the Pacific Northwest, USA. Photo by Michael Lüth, with permission.

Figure 81. ***Dicranum scoparium***, one of the mosses available for use in bird nests in the Pacific Northwest, USA. Photo by J. C. Schou, through Creative Commons.

Figure 82. ***Eurhynchium praelongum***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Janice Glime.

Figure 83. ***Homalothecium sericeum***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Michael Lüth, with permission.

Figure 84. ***Isothecium myosuroides***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Dale Vitt, with permission.

Figure 85. ***Pogonatum urnigerum***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Janice Glime.

One commonality to surmise from these studies is that short, acrocarpous mosses are rarely used. In the first report of bryophytes in bird nests in Chin, Cao and Gao (1991) found only pleurocarps among the 18 species used. These were mostly hanging mosses in **Meteoriaceae** (Figure 71), **Pterobryaceae** (Figure 89), and **Trachypodaceae** (Figure 90). Mosses that are long, mostly pleurocarpous species or those with a **plagiotropic** (growing inclined or nearly horizontally) habit, and larger

leafy liverworts comprise almost all of the bryophytes in bird nests. (Most leafy liverworts grow horizontally.)

Figure 86. ***Polytrichum juniperinum***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Vincent de Boer, through Creative Commons.

Figure 87. ***Sphagnum fimbriatum***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by David T. Holyoak, with permission.

Figure 88. ***Porella navicularis***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Rosemary Taylor, with permission.

Figure 89. ***Pterobryon densum*** (**Pterobryaceae**), in one of the three most common bryophyte families in Chinese bird nests. Photo by Michael Lüth, with permission.

Figure 90. ***Bryowijkia ambigua*** (**Trachypodaceae**), in one of the three most common bryophyte families in Chinese bird nests. Photo by Li Zhang, with permission.

Even in the case of the acrocarpous moss ***Pohlia nutans*** (Figure 91) in a nest, it was only the sporophytes that were used (Crum 1973). Mrs. Cuthbert, of Mount Pleasant, Michigan, USA, reported that she found a bird nest lined with moss sporophytes (a hundred or so, as in Figure 92), giving a gold-colored look to the interior on a wet day (Crum 1973). Crum identified the moss as ***Pohlia nutans*** (Figure 91).

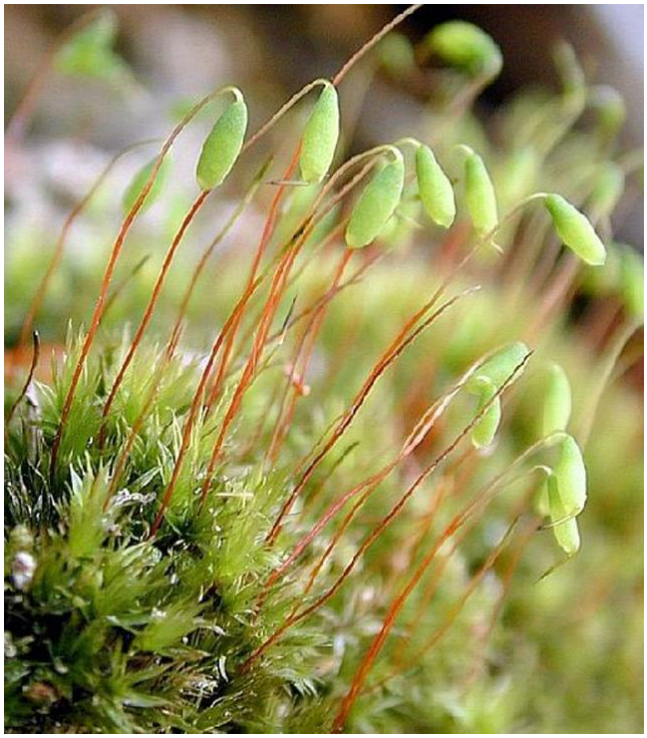

Figure 91. ***Pohlia nutans*** with capsules; setae of this moss are used in some bird nests. Photo by Michael Lüth, with permission.

Figure 92. Nest with sporophyte setae and capsules, possibly from ***Pohlia nutans*** (Figure 91). Photo courtesy of Lovatt.

Who Uses Mosses in Nests?

Breil and Moyle (1976) examined a number of nests of 12 eastern USA birds, identifying 65 species of mosses used in construction. They reported that all North American passerine birds use bryophytes in their nests, emphasizing the importance of bryophytes as an ecosystem component. These 65 species of bryophytes included 5 species of leafy liverworts. Of the nests examined, only the Indigo Bunting (***Passerina cyanea***; Figure 93) nest (Figure 94) lacked bryophytes.

Wolf (2009) conducted an extensive survey of bryophyte usage by birds in the Pacific Northwest (Oregon and Washington), USA. These are listed by orders, along with other records, in the following nest subchapters.

Figure 93. ***Passerina cyanea***, Indigo Bunting, on moss, although it did not include these in its nest in the eastern USA study. Photo by Steve Trynoski, with permission.

Figure 94. ***Passerina cyanea***, Indigo Bunting, nest with eggs, showing total lack of bryophytes. Photo by Richard Bonnett, through Creative Commons.

Summary

Birds often use bryophytes in their nests. This inclusion may help to maintain a safe temperature, to maintain suitable moisture, to prevent disease and parasitism, to provide a soft lining, to camouflage the nest, to permit the nest to expand as nestlings grow, and to help hold the nest together.

The use of bryophytes in nests is much more common among the **Passeriformes** (perching birds) than among the other orders of birds. Some birds are very specific in their choices, using only one or a few species when many are in the area. Most birds choose bryophytes with a plagiotropic growth habit and avoid acrocarpous mosses. Some select sporophytes, especially setae, to serve as nest linings.

What is clear is that we know little about the advantages that bryophytes may give birds when the bryophytes are included in the nests.

Acknowledgments

Thank you to Brian Dykstra for sending me the wonderful thesis on birds and epiphytes by Adrian Wolf, as well as other references and personal observations. David Dumond shared the references he got from Bryonetters. Tamás Pócs took a number of pictures of ***Orthostichella rigida*** just for this project. Thank you to Janet Marr for a critical reading of the manuscript.

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CHAPTER 16-4
BIRD NESTS – NON-PASSERIFORMES, PART 1

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CHAPTER 16-4
BIRD NESTS – NON-PASSERIFORMES, PART 1

Figure 1. Bird nest among ferns, with mosses surrounding nest cup. Photo courtesy of JeriLynn Peck.

Anseriformes Screamers, Ducks, *etc*

Anatidae – Swans, Geese, & Ducks

Wolf (2009) found eleven species of **Anatidae** that use bryophytes in their nests in North America:

Anser brachyrhynchus (Pink-footed Goose; Figure 2-Figure 3)
Anser albifrons (Greater White-fronted Goose; Figure 4-Figure 5)
Branta bernicla (Brant; Figure 6-Figure 7)
Branta canadensis (Canada Goose; Figure 8-Figure 10)
Cygnus columbianus (Tundra Swan; Figure 11-Figure 12)
Cygnus cygnus (Whooper Swan; Figure 13)
Aythya collaris (Ring-necked Duck; Figure 14)
Clangula hyemalis (Long-tailed Duck; Figure 15-Figure 20)
Mergus merganser (Common Merganser; Figure 23)
Somateria fischeri (Spectacled Eider; Figure 24-Figure 26)
Somateria mollissima (Common Eider; Figure 27)

Pink-footed Goose (*Anser brachyrhynchus*)

The Pink-footed Goose (***Anser brachyrhynchus***) may use bryophytes in the nest in parts of North America. But in the Arctic they choose dry vegetation patches for their nests. Having moist bryophytes nearby is important in nest selection sites, however. These bryophyte areas are used for foraging (Jensen *et al*. 2008; Wisz *et al*. 2008).

Figure 2. ***Anser brachyrhynchus***, Pink-footed Goose, a bird that uses bryophytes in its nests in North America. Photo by Hilary Chambers, through Creative Commons.

Figure 3. ***Anser brachyrhynchus***, Pink-footed Goose, on mossy nest. Photo by Otto Plantema, with permission.

Figure 4. ***Anser albifrons***, Greater White-fronted Goose, a species that uses mosses in their nests in North America. Photo by John B., through Creative Commons.

Figure 5. ***Anser albifrons albifrons***, White-fronted Goose, on nest. Photo by Tim Bowman, USFWS, through public domain.

Figure 6. ***Branta bernicla***, Brant, a species that uses mosses in their nests in parts of North America Photo by Jeroen Reneerkens, through Creative Commons.

Figure 7. ***Branta bernicla***, Brant, nest with eggs. Photo by Bob Gill, USFWS, through public domain.

Figure 8. ***Branta canadensis***, Canada Goose, a species that uses mosses in their nests in North America. Photo courtesy of Eileen Dumire.

Figure 9. ***Branta canadensis***, Canada Goose, nest with eggs and down lining. Photo by James K. Lindsey, with permission.

Figure 10. ***Branta canadensis***, Canada Goose, nest with no special lining, demonstrating differences one can find among nests (compare to Figure 9). Photo by Notts Ex Miner, through Creative Commons.

Figure 11. ***Cygnus columbianus***, Tundra Swan, a species that uses bryophytes in their nests in North America and elsewhere. Photo by Tim Bowman, through public domain.

Figure 12. ***Cygnus columbianus***, Tundra Swan, on nest. Photo from USFWS, through public domain.

Figure 13. ***Cygnus cygnus***, Whooper Swans, a species that uses bryophytes in their nests in North America. Photo by Sciadopitys, through Creative Commons.

Figure 14. ***Aythya collaris***, Ring-necked Duck, on water, a species that uses bryophytes in their nests in North America. Photo by MDF, through Creative Commons.

Long-tailed Duck (*Clangula hyemalis*)

I suspect that bryophytes are not the normal nesting material for the Long-tailed Duck (***Clangula hyemalis***; Figure 15-Figure 16). Its nest is typically built on the ground near water, using vegetation and lined with down (Wikipedia 2016). But Susan Studlar (pers. comm. 12 July 2017) reported to me that they built large nests (Figure 17-Figure 20) of ***Rhytidiadelphus*** cf. ***loreus*** (Figure 21) when that was the only material provided to them at the Sealife Center in Seward, Alaska. I suspect most birds are adaptable, using the materials that are most available to them at the time of nest building. The Horned Puffin (***Fratercula corniculata***; Figure 22), on the other hand, ignores all those mosses in the landscape and lays its eggs in a crevice among the rocks (Wikipedia 2017).

Figure 15. ***Clangula hyemalis***, Long-tailed Duck, a species that uses bryophytes in their nests in North America. Photo by Wolfgang Wander, through Creative Commons.

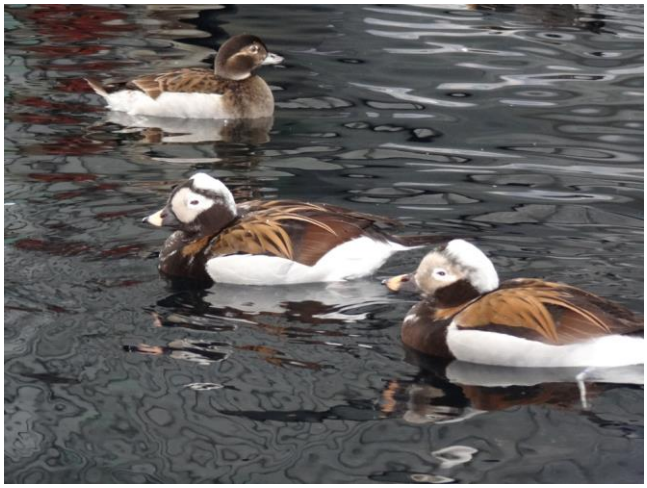

Figure 16. ***Clangula hyemalis***, Long-tailed Duck, a species that will use mosses to build a nest when other materials are not available. Photo courtesy of Sue Studlar.

Figure 17. ***Clangula hyemalis***, Long-tailed Duck, female on nest. Photo by Tim Bowman, USFWS, through public domain.

Figure 18. ***Clangula hyemalis***, Long-tailed Duck, on nest on a bed of mosses. Photo through public domain.

Figure 19. ***Clangula hyemalis***, Long-tailed Duck, nest made of ***Rhytidiadelphus*** cf. ***loreus*** – the only material available to it. Photo courtesy of Sue Studlar.

Figure 20. ***Clangula hyemalis***, Long-tailed Duck, ***Rhytidiadelphus*** cf. ***loreus*** nest lined with down. The moss was the only material provided to it. Photo courtesy of Sue Studlar.

Figure 21. ***Rhytidiadelphus*** cf. ***loreus*** in nest of ***Clangula hyemalis*** (Long-tailed Duck). Photo courtesy of Sue Studlar.

Figure 22. ***Rhytidiadelphus*** cf. ***loreus*** and Horned Puffin (***Fratercula corniculata***) in Seward, Alaska. The moss looks inviting, but the Puffin usually lays its one egg in a crevice or cavity among the rocks without a nest. Photo courtesy of Sue Studlar.

Figure 23. ***Mergus merganser***, Common Merganser, a species that uses bryophytes in their nests in North America. Photo by John Bennett, through Creative Commons.

Figure 24. ***Somateria fischeri***, Spectacled Eider female, a species that uses bryophytes in their nests in North America. Photo by Dick Daniels, through Creative Commons.

Figure 25. ***Somateria fischeri***, Spectacled Eider pair, a species that uses bryophytes in their nests in North America. Photo by Laura Whitehouse, USFWS, through public domain.

Figure 26. ***Somateria fischeri***, Spectacled Eider, nest. Photo by USFWS, through public domain.

Figure 27. ***Somateria mollissima***, Common Eider, colonial nesting with Canada geese. Photo by Caroline Bond, USGS, through public domain.

Snow Goose (*Chen caerulescens*)

It is not surprising to find that in the far north, where mosses are a prominent feature of the landscape, birds like the Snow Goose (***Chen caerulescens***; Figure 28) use mosses as a major component of their nests (Figure 29) (Gianetta 2000). The Greater Snow Goose (***Chen caerulescens atlanticus***; Figure 30) in Jungersen Bay, northern Baffin Island, uses three habitat types for nesting (Giroux *et al*. 1984). One of these is wet moss-covered meadows with up to 5 cm of standing water, dominated by *Carex aquatilis* var. *minor* (Figure 31), *Dupontia fisheri* (Figure 32), *Calamagrostis stricta* (Figure 33), and *Arctagrostis latifolia* (Figure 34).

Figure 28. ***Chen caerulescens*** (Snow Goose) grazing; this species uses mosses as a major component of their nests. Photo by Walter Siegmund, through Creative Commons.

Figure 29. ***Chen caerulescens***, Snow Goose, nest with nestlings and often containing bryophytes. Photo by James K. Lindsey, with permission.

Figure 30. ***Chen caerulescens atlanticus***, Greater Snow Geese foraging. Photo by D. Gordon and E. Robertson, through Creative Commons.

Figure 31. ***Carex aquatilis*** var ***minor*** in the Northwest Territories, common in the home of the Greater Snow Goose. Photo by Jeffery M. Saarela, through Creative Commons.

Figure 32. ***Dupontia fisheri***, common in the habitat of the Greater Snow Goose. Photo from Smithsonian Institution, National Museum of Natural History, through Creative Commons.

Figure 33. ***Calamagrostis stricta*** in the Northwest Territories, common in the habitat of the Greater Snow Goose. Photo by Matt Lavin, through Creative Commons.

Figure 34. ***Arctagrostis latifolia*** subsp. ***latifolia*** in the Northwest Territories, common in the habitat of the Greater Snow Goose. Photo by Jeffery M. Saarela, through Creative Commons.

McCracken *et al*. (1997) found that among the Ross' Geese (***Chen rossii***; Figure 35) and Lesser Snow Geese (***Chen caerulescens caerulescens***; Figure 37), the nest size (Figure 36) differed with habitat. The smallest were among heath, then rock, then mixed, with the largest nests among mosses. Temperature was an important factor for these Arctic breeders. Could it be that mosses tended to insulate the eggs, but at the same time prevented the warmer temperatures that could speed up development? Were the mosses too compact and tight to be good insulators? Or did the mosses indicate a cooler ground temperature?

Figure 35. ***Chen rossii***, Ross's Snow Goose, a species whose nest size is largest when among mosses. Photo by Dominic Sherony, through Creative Commons.

Figure 36. ***Chen rossii***, Ross' Goose, nest with mosses and eggs. Photo by James K. Lindsey, with permission.

Figure 37. ***Chen caerulescens caerulescens***, Lesser Snow Goose, a species that makes larger nests among mosses than among heath vegetation. Photo by Walter Siegmund, through Creative Commons.

Phasianidae – Quail, Pheasants, *etc*

Wolf (2009) found five species of **Phasianidae** that use bryophytes in their nests in parts of North America:

Falcipennis canadensis (Spruce Grouse; Figure 38-Figure 39)
Lagopus lagopus (Willow Ptarmigan; Figure 40-Figure 42)
Lagopus muta (Rock Ptarmigan; Figure 43-Figure 44)
Dendragapus obscurus (Blue Grouse; Figure 45-Figure 46)
Tympanuchus phasianellus (Sharp-tailed Grouse; Figure 47-Figure 48)

Figure 38. ***Falcipennis canadensis***, Spruce Grouse, on mossy log. Photo by MDF, through GNU Free Documentation.

Figure 39. ***Falcipennis canadensis***, Spruce Grouse, nest with eggs. Photo by Mark Yezbick and Willi Shrinx, through Creative Commons.

Figure 40. ***Lagopus lagopus***, Willow Ptarmigan female, among mosses in Alaska, a species that uses bryophytes for nesting. Photo by David Menke, USFWS, through Creative Commons.

Figure 41. ***Lagopus lagopus***, Willow Ptarmigan nest with eggs. Photo by James K. Lindsey, with permission.

Figure 42. ***Lagopus lagopus***, Willow Ptarmigan, nest among mosses. Photo by Mlkniemi, through Creative Commons.

Figure 43. ***Lagopus muta***, Rock Ptarmigan, a species that uses bryophytes for nesting. Photo by Friedrich Böhringer, through Creative Commons.

Figure 44. ***Lagopus muta***, Rock Ptarmigan, nest. Photo by Valugi, through Creative Commons.

Figure 45. ***Dendragapus obscurus***, Blue Grouse, a species that uses bryophytes in their nests in North America. Photo by S. King, NPS, through public domain.

Figure 46. ***Dendragapus obscurus***, Blue Grouse, male. Photo from USNPS, through public domain.

Figure 47. ***Tympanuchus phasianellus***, Sharp-tailed Grouse, a species that uses bryophytes in their nests in parts of North America. Photo by Barbara Muenchau, through Creative Commons.

Figure 48. ***Tympanuchus phasianellus***, Sharp-tailed Grouse, nest with eggs. Photo from USFWS, through public domain.

Gaviiformes: Loons

Gaviidae – Loons

Wolf (2009) found three species of **Gaviidae** that use bryophytes in their nests in parts of North America:

Gavia stellata (Red-throated Loon; Figure 49)
Gavia pacifica (Pacific Loon; Figure 50)
Gavia immer (Common Loon; Figure 51-Figure 52)

Figure 49. ***Gavia stellata***, Red-throated Loon on nest. Photo by Dave Menke, through public domain.

Figure 50. ***Gavia pacifica***, Pacific Loon, on nest. Mosses may be included in these nests. Photo from USFWS, through public domain.

Figure 51. ***Gavia immer***, Common Loon, with chick. Photo from NPS, through public domain.

Figure 52. ***Gavia immer***, Common Loon, on nest. Photo by Dana Moos, through Creative Commons.

Podicepidiformes: Grebes

Podicepididae – Grebes

Red-Necked Grebe (*Podiceps grisegena*)

Breeding populations of the **Red-necked Grebe**, ***Podiceps grisegena*** (Figure 53), in the Northwest Territories use ***Sphagnum*** (Figure 107) in addition to cattails and other emergent vegetation in nest construction (Figure 54) (Fournier & Hines 1998).

Figure 53. ***Podiceps grisegena***, Red-necked Grebe, with ducklings. Photo by Donna Dewhurst, through public domain.

Figure 54. ***Podiceps grisegena***, Red-necked Grebe, a species that includes ***Sphagnum*** in their nests. Photo by Lukasz Lukasik, through Creative Commons.

Pelecaniformes: Tropicbirds, Pelicans, *etc*

Phalacrocoracidae – cormorants

Wolf (2009) found two species of **Phalacrocoracidae** that use bryophytes in their nests in North America:

Phalacrocorax penicillatus (Brandt's Cormorant; Figure 55)
Phalacrocorax pelagicus (Pelagic Cormorant; Figure 56-Figure 57)

Figure 55. ***Phalacrocorax penicillatus***, Brandt's Cormorants, on nests. Photo by Franco Folini, through Creative Commons.

Figure 56. ***Phalacrocorax pelagicus***, Pelagic Cormorant, female and chicks on nest. This species uses bryophytes in their nests in parts of North America. Photo by Alan Vernon, through Creative Commons.

Figure 57. ***Phalacrocorax pelagicus***, Pelagic Cormorant, on nest. Photo by Alan Vernon, through Creative Commons.

Falconiformes: Vultures, Hawks, & Falcons

Accipitridae – Hawks, Old World Vultures & Harriers

Despite their large size and predatory habits, Wolf (2009) found seven species of **Accipitridae** that use bryophytes in their nests in the Pacific Northwest of the USA.:

Aquila chrysaetos (Golden Eagle; Figure 58-Figure 60)
Buteo brachyurus (Short-tailed Hawk; Figure 61)
Buteo lagopus (Rough-legged Hawk; Figure 62-Figure 63)
Buteo lineatus (Red-shouldered Hawk; Figure 64-Figure 65)
Elanoides forficatus (Swallow-tailed Kite; Figure 66)
Elanus leucurus (White-tailed Kite; Figure 67-Figure 68)
Haliaeetus leucocephalus (Bald Eagle; Figure 69)

Figure 58. ***Aquila chrysaetos***, Golden Eagle, a species that uses bryophytes in their nests in parts of North America. Photo by Richard Bartz, through Creative Commons.

Figure 59. ***Aquila chrysaetos***, Golden Eagle, nest. Photo by Wildxplorer, through Creative Commons.

Figure 60. ***Aquila chrysaetos***, Golden Eagle, egg and baby on nest. Photo by Johann Jaritz, through Creative Commons.

Figure 61. ***Buteo brachyurus***, Short-tailed Hawk, in flight, a species that uses bryophytes in their nests in parts of North America. Photo by Dario Sanches, through Creative Commons.

Rough-legged Buzzard/Hawk (*Buteo lagopus*)

The Rough-legged Buzzards (***Buteo lagopus***; Figure 62) use mosses to line their nests (Figure 63) (The Hawk Conservancy 1996-2001).

Figure 62. ***Buteo lagopus***, Rough-legged Hawk, a species that lines their nests with mosses. Photo by Walter Siegmund, through Creative Commons.

Figure 63. ***Buteo lagopus***, Rough-legged Buzzard, nest with lining of moss and hatching nestlings. Photo from USFWS, through public domain.

Figure 64. ***Buteo lineatus***, Red-shouldered Hawk, a species that uses bryophytes in their nests in parts of North America. Photo by Mike Baird, through Creative Commons.

Figure 65. ***Buteo lineatus***, Red-tailed Hawk, nest. Photo by Bill Majoros, through Creative Commons.

Figure 66. ***Elanoides forficatus***, Swallow-tailed Kite, in flight. This species uses bryophytes in their nests in parts of North America. Photo by Andrea Westmoreland, through Creative Commons.

Figure 67. ***Elanus leucurus***, White-tailed Kite, carrying nesting material. In parts of North America it includes bryophytes in the nest. Photo by Ken Penicle Jr., through Creative Commons.

Figure 68. ***Elanus leucurus***, White-tailed Kite, on nest. Photo by Maria Teresa Jaramillo, through Creative Commons.

American Bald Eagle (*Haliaeetus leucocephalus*)

It is of some consolation to those who fear extensive loss of mosses that protected birds use mosses for their nests. Even the huge **American Bald Eagle** (***Haliaeetus leucocephalus***; Figure 69) in Alaska uses mosses in old-growth forests to form nests (Figure 69) atop tall spruce trees (Holleman 1997). One can hope that in our efforts to protect our national symbol we will learn to protect those aspects of its habitat that are important to its success. This, hopefully, will protect the mosses.

Figure 69. ***Haliaeetus leucocephalus***, American Bald Eagle, landing on nest. Photo by Murray Foubister, through Creative Commons.

Gruiformes: Cranes, Rails, *etc*

Gruidae – Cranes

Wolf (2009) found one species of **Gruidae** whose members use bryophytes in their nests (Figure 70) in parts of North America of the USA: ***Grus canadensis*** (Sandhill Crane; Figure 71).

Figure 70. ***Grus canadensis***, Sandhill Crane, tending eggs in nest. Photo by Andrea Westmoreland through, Creative Commons.

Figure 71. ***Grus canadensis pratensis***, Sandhill Crane, a species that uses bryophytes in their nests. Photo by Albert Herring, USFWS, through Creative Commons.

Rallidae

Chestnut Forest-Rail (*Rallina rubra*)

The Chestnut Forest-Rail (***Rallina rubra***; see Figure 72) from the Tari Gap, Southern Highlands Province, Papua New Guinea, builds a large, globular nest (Frith & Frith 1990). This domed structure is made of mosses, leaves, and ferns. Its entrance is on the side and the nest sits ~2m above the ground in the crown of the pandanus

palm. Despite the large size of the nest, this rail places only one very large egg in the nest. Although both birds incubate the eggs for their 34-37 days of incubation, the eggs are often left alone long enough that they become cold.

Figure 72. *Rallina fasciata*, Red-legged Crake; the species ***Rallina rubra*** uses mosses in their nests in Papua New Guinea. Photo by J. Wee, through Creative Commons.

Figure 73. ***Charadrius morinellus***, Dotterel male, a species that uses bryophytes in their nests. Photo by Helwig Brunner, through Creative Commons.

Charadriiformes

Charadriidae – Plovers, *etc*

Wolf (2009) found four species of **Charadriidae** that use bryophytes in their nests in parts of North America:

Charadrius semipalmatus (Semipalmated Plover; Figure 76)
Pluvialis apricaria (European Golden-Plover; Figure 77-Figure 78)
Pluvialis dominica (American Golden-Plover; Figure 79-Figure 80)
Pluvialis squatarola (Black-bellied Plover; Figure 81)

Dotterel (*Charadrius morinellus*)

In Scotland, the rare Dotterel (***Charadrius morinellus***; Figure 73) prefers the *Carex bigelowii*-***Racomitrium lanuginosum*** (Figure 74) moss heath (Welch *et al*. 2005). It feeds largely on beetles, sawflies, and both larvae and adults of ***Tipula montana*** (a common moss inhabitant in its larval stage; see Figure 75) (Galbraith *et al*. 1993). The preferred feeding habitats for these birds are flat or gently sloping ***Racomitrium lanuginosum*** or *Juncus trifidus* heaths or the transition zone between moss heath and montane bog. The most frequently used habitats are those where the montane bogs with best food for juveniles were adjacent to the ***R. lanuginosum*** heaths with the best food for adults.

Figure 74. ***Racomitrium lanuginosum***, a moss commonly used in nests of the Dotterel. Photo by Niels Klazenga, with permission.

Figure 75. ***Tipula abdominalis*** larva, a moss dweller in a genus that provides food for the Dotterel. Photo through Creative Commons.

Figure 76. ***Charadrius semipalmatus***, Semi-palmated Plover, a species that uses bryophytes in their nests in parts of North America. Photo by Donna Dewhurst, through public domain.

Figure 77. ***Pluvialis apricaria***, European Golden-Plover. Members of this species use bryophytes in their nests in parts of North America. Photo by Bjørn Christian Tørrissen, through Creative Commons.

Figure 78. ***Pluvialis apricaria***, European Golden-Plover, nest with eggs amid lichens and bryophytes. Photo by Mike Pennington, through Creative Commons.

Figure 79. ***Pluvialis dominica***, American Golden Plover, a species that uses bryophytes in their nests in parts of North America. Photo by O. W. Johnson, USFWS, through public domain.

Figure 80. ***Pluvialis dominica***, American Golden Plover, eggs and nest. Photo by Meegs C, through Creative Commons.

Figure 81. ***Pluvialis squatarola***, Black-bellied Plover, a species that uses bryophytes in their nests in parts of North America. Photo by Peter Wallack, through Creative Commons.

Scolopacidae – Sandpipers, *etc*

Wolf (2009) found eighteen species of **Scolopacidae** that use bryophytes in their nests in parts of North America:

Tringa melanoleuca (Greater Yellowlegs; Figure 82)
Tringa flavipes (Lesser Yellowlegs; Figure 83)
Actitis macularius (Spotted Sandpiper; Figure 84-Figure 85)
Numenius phaeopus (Whimbrel; Figure 86)
Numenius tahitiensis (Bristle-thighed Curlew; Figure 87)
Limosa lapponica (Bar-tailed Godwit; Figure 88)
Arenaria interpres (Ruddy Turnstone; Figure 89-Figure 90)
Aphriza virgata (Surfbird; Figure 91-Figure 92)
Calidris mauri (Western Sandpiper; Figure 93)
Calidris minutilla (Least Sandpiper; Figure 94)
Calidris fuscicollis (White-rumped Sandpiper; Figure 95)
Calidris ptilocnemis (Rock Sandpiper; Figure 96)
Tryngites subruficollis (Buff-breasted Sandpiper; Figure 97)
Limnodromus scolopaceus (Long-billed Dowitcher; Figure 98)
Gallinago gallinago (Common Snipe; Figure 99)
Phalaropus tricolor (Wilson's Phalarope; Figure 100-Figure 101)
Phalaropus lobatus (Red-necked Phalarope; Figure 102-Figure 103)
Phalaropus fulicarius (Red Phalarope; Figure 104)

Figure 82. ***Tringa melanoleuca***, Greater Yellowlegs, a species that uses bryophytes in their nests in parts of North America. Photo by Dick Daniels, through Creative Commons.

Figure 83. ***Tringa flavipes***, Lesser Yellowlegs chicks. Members of this species use bryophytes in their nests in parts of North America. Photo by S. Kropidlowski, USFWS, through public domain.

Figure 84. ***Actitis macularia***, Spotted Sandpiper, a species that uses bryophytes in their nests in parts of North America. Photo by Mike Baird, through Creative Commons.

Figure 85. ***Actitis macularius***, Spotted Sandpiper, nest with eggs. Photo by Robert A. Hamilton, through Creative Commons.

Figure 86. ***Numenius phaeopus***, Whimbrel, a species that uses bryophytes in their nests in parts of North America. Photo by Valter Jacinto, through Creative Commons.

Figure 87. ***Numenius tahitiensis***, Bristle-thighed Curlew, a species that uses bryophytes in their nests in parts of North America. Photo by Gregory Smith, through Creative Commons.

Figure 88. ***Limosa lapponica***, Bar-tailed Godwit, a species that uses bryophytes in their nests in parts of North America. Photo by Steve Maslowski, USFWS, through public domain.

Figure 89. ***Arenaria interpres***, Ruddy Turnstone, a species that uses bryophytes in their nests in parts of North America. Photo by Dick Daniels, through Creative Commons.

Figure 90. ***Arenaria interpres***, Ruddy Turnstone, on nest. Photo by Tim Bowman, USFWS, through Creative Commons.

Figure 91. ***Aphriza virgata***, Surfbird, a species that uses bryophytes in their nests in parts of North America. Photo by Marlin Harms, through Creative Commons.

Figure 92. ***Aphriza virgata***, Surfbird, nest with young birds. Photo by Terry Hall, through public domain.

Figure 93. ***Calidris mauri***, Western Sandpiper, a species that uses bryophytes in their nests in parts of North America. Photo by Caleb Slemmons, through Creative Commons.

Figure 96. ***Calidris ptilocnemis***, Rock Sandpiper, a species that uses bryophytes in their nests in parts of North America. Photo by Alan D. Wilson, through Creative Commons.

Figure 94. ***Calidris minutilla***, Least Sandpiper, on shore rock, a species that uses bryophytes in their nests in parts of North America. Photo by Britta, through Creative Commons.

Figure 97. ***Tryngites subruficollis***, Buff-breasted Sandpiper, a species that uses bryophytes in their nests in parts of North America. Photo by Cláudio Dias Timm, through Creative Commons.

Figure 95. ***Calidris fuscicollis***, White-Rumped Sandpiper, a species that uses bryophytes in their nests in parts of North America. Photo by Cláudio Dias Timm, through Creative Commons.

Figure 98. ***Limnodromus scolopaceus***, Long-billed Dowitcher, a species that uses bryophytes in their nests in parts of North America. Photo by Tim Bowman, through Creative Commons.

Figure 99. ***Gallinago gallinago***, Common Snipe, a species that uses bryophytes in their nests in parts of North America. Photo by Alpsdake, through Creative Commons.

Figure 100. ***Phalaropus tricolor***, Wilson's Phalarope, in pond, a species that uses bryophytes in their nests in parts of North America. Photo by Blake Mathson, through Creative Commons.

Figure 101. ***Phalaropus tricolor***, Wilson's Phalarope, male on nest. Photo from NPS, through public domain.

Figure 102. ***Phalaropus lobatus***, Red-necked Phalarope, a species that uses bryophytes in their nests in parts of North America. Photo by Andreas Trepte, through Creative Commons.

Figure 103. ***Phalaropus lobatus***, Red-necked Phalarope on water. Photo by Blake Matheson, through Creative Commons.

Figure 104. ***Phalaropus fulicarius***, Red Phalarope, in shore vegetation, a species that uses bryophytes in their nests in parts of North America. Photo from USFWS, through public domain.

Broad-billed Sandpiper (*Limicola falcinellus*)

The Broad-billed Sandpiper (***Limicola falcinellus***; Figure 105) builds nests in fens dominated by mosses and wet sedges. The nests are built on shallow hummocks, typically in transition zones between vegetation types. Once the baby birds hatch, they are moved from the nest to wetter fen areas nearby. Rae *et al*. (1998) found one nest concealed between two small bryophyte hummocks – one of ***Sphagnum*** *cf.* ***capillifolium*** (Figure 107) and the other possibly ***Aulacomnium*** sp (Figure 108). One was in a *Carex* tussock in a wet fen with 30% ***Hamatocaulis*** *cf* ***vernicosus*** (Figure 109). The nests were often surrounded by a high cover of dark brown bryophytes. The eggs (Figure 106) and chicks were both colored dark chocolate brown, a coloration that Rae and coworkers suggested was an adaptation of **crypsis** (ability to avoid detection) to protect them against predation. Importance of matching color patterns is known in other birds, such as the Stone Curfew (***Burhinus oedicnemus***; Figure 110-Figure 111) (Solis & Lope 1995). These researchers demonstrated that mismatches in coloration between eggs (Figure 112) and the ground in the Stone Curfew increase the predation rate; these birds benefitted by choosing both nest building materials and nest substrate that increased camouflage.

Figure 105. ***Limicola falcinellus***, Broad-billed Sandpiper, a species that nests in mossy wetlands. Photo by Sreedev Puthur, through Creative Commons.

Figure 106. ***Limicola falcinellus***, Broad-billed Sandpiper, eggs that blend with the background of brown mosses. Photo by Klaus Rassinger and Gerhard Cammerer, through Creative Commons.

Figure 107. ***Sphagnum capillifolium***, a species often found in the nesting sites of the Broad-billed Sandpiper (***Limicola falcinellus***). Photo by Juan Larrain, with permission.

Figure 108. ***Aulacomnium palustre***, a species found in nesting sites of the Broad-billed Sandpiper (***Limicola falcinellus***). Photo by Kristian Peters through Creative Commons.

Figure 109. ***Hamatocaulis vernicosus***, one of the brown mosses common in the nesting habitat of the Broad-billed Sandpiper (***Limicola falcinellus***). Photo by Michael Lüth, with permission.

Figure 110. ***Burhinus oedicnemus***, Stone Curfew, a species that relies on matching the background colors to the coloration of its eggs. Photo by Artemy Voikhansky, through Creative Commons.

Figure 111. ***Burhinus oedicnemus***, Stone Curlew nesting, a species that relies on matching the background colors to the coloration of its eggs. Photo by Max Pixel, through Creative Commons.

Figure 112. ***Burhinus oedicnemus*** eggs matching their environment. Photo from <www.aerien.ch> through Creative Commons.

Laridae – Skuas, Gulls, Terns, & Skimmers

Wolf (2009) found seventeen species of **Laridae** that use bryophytes in their nests in parts of North America:

Stercorarius parasiticus (Parasitic Jaeger; Figure 114-Figure 115)
Stercorarius pomarinus (Pomarine Jaeger; Figure 116)
Stercorarius longicaudus (Long-tailed Jaeger; Figure 117-Figure 118)
Chroicocephalus philadelphia (Bonaparte's Gull; Figure 119-Figure 120)
Larus canus (Mew Gull; Figure 121-Figure 122)
Larus argentatus (Herring Gull; Figure 123-Figure 124)
Larus thayeri (Thayer's Gull; Figure 125)
Larus glaucoides (Iceland Gull; Figure 126-Figure 127)
Larus hyperboreus (Glaucous Gull; Figure 128-Figure 129)
Larus marinus (Great Black-backed Gull; Figure 130-Figure 131)
Rissa tridactyla (Black-legged Kittiwake; Figure 138)
Rissa brevirostris (Red-legged Kittiwake; Figure 139)
Rhodostethia rosea (Ross's Gull; Figure 140)
Pagophila eburnea (Ivory Gull; Figure 141)
Hydroprogne caspia (Caspian Tern; Figure 142)
Sterna paradisaea (Arctic Tern; Figure 143-Figure 144)
Onychoprion aleuticus (Aleutian Tern; Figure 145)

Stercorarius spp. (Figure 114-Figure 118) prefer mosses, especially ***Polytrichum juniperinum*** (syn. = ***P. alpestre***; Figure 113) (Deeming & Reynolds 2015). Over 60% of their nest material (Figure 115) is mosses.

Figure 113. ***Polytrichum juniperinum,*** a species common in nests of ***Stercorarius*** species. Photo by Vincent de Boer, through Creative Commons.

Figure 114. ***Stercorarius parasiticus***, Arctic Skua/Pomarine Jaeger, a species that uses bryophytes in their nests. Photo by Billy Lindblom, through Creative Commons.

Figure 115. ***Stercorarius parasiticus***, Parasitic Jaeger, nest with eggs and lot of moss. Photo by James K. Lindsey, with permission.

Figure 116. ***Stercorarius pomarinus***, Pomarine Jaeger, a species that uses bryophytes in their nests. Photo by Patrick Coin, through Creative Commons.

Figure 117. ***Stercorarius longicaudus***, Long-tailed Jaeger, nesting. This is a species that uses bryophytes in their nests in parts of North America. Photo by Don Henise, through Creative Commons.

Figure 118. ***Stercorarius longicaudus***, Long-tailed Jaeger, possibly nesting here. Photo through public domain.

Figure 119. ***Chroicocephalus philadelphia***, Bonaparte's Gull, on shore, a species that uses bryophytes in their nests in parts of North America. Photo by Dick Daniels, through Creative Commons.

Figure 120. ***Chroicocephalus philadelphia***, Bonaparte's Gull, nesting in Alaska. Photo by David Menke, USFWS, through public domain.

Figure 121. ***Larus canus***, Mew Gull, a species that uses bryophytes in their nests in parts of North America. Photo by Kari Pihlaviita, through Creative Commons.

Figure 122. ***Larus canus***, Mew Gull, on nest amid mosses and stones. Photo by John Haslam, through Creative Commons.

Herring/Glaucous Gull Hybrid (*Larus argentatus*/*hyperboreus*)

Ólafsson (1982) found a pair of gulls, one a Herring Gull (***Larus argentatus***; Figure 123-Figure 124) and the other a Glaucous Gull (***Larus hyperboreus***; Figure 128-Figure 129). Their nest was in a small, collapsed cave. It was constructed almost exclusively of the common moss ***Racomitrium*** (Figure 74). Only one arthropod, a mite, was found among these nest materials.

Figure 123. ***Larus argentatus***, Herring Gull, a species that uses mosses in their nests. Photo by Tony Brierton, through Creative Commons.

Figure 124. ***Larus argentatus***, Herring Gull, nest with mosses under the grass, and eggs. Photo by Finn Rindahl, through Creative Commons.

Figure 125. ***Larus thayeri***, Thayer's Gull, a species that uses mosses in their nests. Photo by Liam O'Brien, through Creative Commons.

Figure 126. ***Larus glaucoides***, Iceland Gull, a species that uses bryophytes in their nests in parts of North America. Photo by Seabamirum, through Creative Commons.

Figure 127. ***Larus glaucoides***, Iceland Gulls, in nesting area. Photo by Seabamirum, through Creative Commons.

Figure 128. ***Larus hyperboreus***, Glaucous Gull, with fledgling. Photo by A. Wieth, through Creative Commons.

Figure 129. ***Larus hyperboreus***, Glaucous Gull, nest with eggs. Photo by Peter Davis, USFWS, through public domain.

Figure 130. ***Larus marinus***, Great Black-backed Gull, a species that uses bryophytes in their nests in parts of North America. Photo by Andreas Trepte, through Creative Commons.

Figure 131. ***Larus marinus***, Great Black-backed Gull, nest and eggs. Photo by Banangraut, through Creative Commons.

Kelp Gull (*Larus dominicus*)

In the Argentine Islands the primary constituent of the Kelp Gull (***Larus dominicus***; Figure 132) nest (Figure 133) is the grass *Deschampsia antarctica* (Figure 134) (Parnikoza *et al*. 2012). The researchers postulated that in making the nests the gulls were responsible for the spread of this grass species on the islands. But the Kelp Gull also uses mosses extensively in its nests. In the Argentine Islands, ***Sanionia uncinata*** (Figure 135) was common and likewise was common in nests. It is particularly suitable because of its pleurocarpous growth form and lack of attachment to its substratum. I would expect that these gulls are similarly able to disperse the mosses.

Figure 132. ***Larus dominicus***, Herring Gull; in the Argentine Islands, this species uses ***Sanionia uncinata*** in their nests. Photo by Cláudio Dias Timm, through Creative Commons.

Figure 133. ***Larus domesticus***, Kelp Gull, nest in Patagonia in a habitat where grasses are readily available, but mosses are not. Photo by Erik Thuesen, through Creative Commons.

Figure 134. *Deschampsia antarctica* (large patch), the grass used for Herring Gull nests in the Argentine Islands. Photo by Sharon Chester, through Creative Commons.

Figure 135. ***Sanionia uncinata***, a moss commonly used in nests of the Kelp Gull. Photo by Hermann Schachner, through Creative Commons.

Lesser Black-Backed Gull (*Larus fuscus*)

When Surtsey arose from the ocean near Iceland in a volcanic explosion, no life existed (Magnússon *et al*. 2008). Slowly plants and flying animals arrived. Among the early bryophytes was the moss ***Racomitrium*** (Figure 74), and this serves as the main nesting (Figure 136) material for the Lesser Black-Backed Gull (***Larus fuscus***; Figure 137) during this austere period.

Figure 136. ***Larus fuscus***, Lesser Black-Backed Gull nest, eggs, & chicks. Photo by Sam Sam, through Creative Commons.

Figure 137. ***Larus fuscus***, Lesser Black-backed Gull, an early Surtsey colonist that uses the moss ***Racomitrium*** for nesting. Photo by Peter Ertl, through Creative Commons.

Figure 138. ***Rissa tridactyla***, Black-legged Kittiwake, on nest. Photo by Sciadopitys, through Creative Commons.

Figure 139. ***Rissa brevirostris***, Red-legged Kittiwakes, at nest. Photo by Art Sowls, through public domain.

Figure 140. ***Rhodostethia rosea***, Ross's Gull, a species that uses bryophytes in their nests in parts of North America. Photo by J. P. Siblet, through Creative Commons.

Figure 141. ***Pagophila eburnea***, Ivory Gull adult, feeding. This species uses bryophytes in their nests in parts of North America. Photo by Alan Vernon, through Creative Commons.

Figure 142. ***Hydroprogne caspia***, Caspian Tern, a species that uses bryophytes in their nests in parts of North America. Photo by B. J. Stacey, through Creative Commons.

Figure 143. ***Sterna paradisaea***, Arctic Tern, a species that uses bryophytes in their nests in parts of North America. Photo by Blake Matheson, through Creative Commons.

Figure 144. ***Sterna paradisaea***, Arctic Tern nest with eggs. Photo by James K. Lindsey, with permission.

Figure 145. ***Onychoprion aleuticus***, Aleutian Tern, a species that uses bryophytes in their nests in parts of North America. Photo by F. Deines, through Creative Commons.

Alcidae – Auks, Murres, & Puffins

Wolf (2009) found four species of **Alcidae** that use bryophytes in their nests in parts of North America:

Brachyramphus marmoratus (Marbled Murrelet; Figure 146-Figure 149)
Brachyramphus brevirostris (Kittlitz's Murrelet; Figure 154-Figure 155)
Ptychoramphus aleuticus (Cassin's Auklet; Figure 156-Figure 157)
Cerorhinca monocerata (Rhinoceros Auklet; Figure 158-Figure 160)

Marbled Murrelet (*Brachyramphus marmoratus*)

When mosses are endangered, few people care, but when a bird shows evidence of disappearance, environmentalists and nature-lovers join forces to protect them. Protecting these birds in pristine habitats can, however, protect mosses as well. The Marbled Murrelet (***Brachyramphus marmoratus***; Figure 146) provides one such story.

Figure 146. ***Brachyramphus marmoratus***, Marbled Murrelet. Photo by Kiliii Yu, through Creative Commons.

Figure 147. ***Brachyramphus marmoratus***, Marbled Murrelet, on mossy nest high in a tree. Photo by Sierra Club, permission pending, site not found.

Figure 148. ***Brachyramphus marmoratus***, Marbled Murrelet chick. Photo by Peter Halasz, through Creative Commons.

Some of our big trees have moss mats that are 30 cm deep on the old firs and Sitka spruce (Krajick 1995a). These mats take centuries to develop and supply

nourishment for canopy-specific birds such as the Marbled Murrelet (***Brachyramphus marmoratus***; Figure 147).

Tompkins (2004) reported that 17 million pounds of mosses had been harvested in 2003 in parts of North America, including Appalachia, with an estimated recovery rate of only 1% per year. The endangered and elusive seabird, the federally threatened Marbled Murrelet (***Brachyramphus marmoratus***; Figure 146), nests (Figure 149) on these moss mats (Figure 147) along the Pacific Coast of the USA (Donahue 1999; Tompkins 2004).

Figure 149. Nest of the Marbled Murrelet (***Brachyramphus marmoratus***) with common moss in the Willamette Valley of the Pacific Northwest, USA. Photo by JeriLynn Peck.

Neville Winchester (in Tompkins 2004) found more than 300 species of mosses in the canopy mats where the Murrelets live. They are so important to the Marbled Murrelet that these birds fly miles inland to build their nests on the mats (Skow 1998; Tompkins 2004). The nest is the size of a baseball and is fashioned into a cup nestled in mosses on a wide tree branch where overhanging branches hide it from its Raven (***Corvus corax***; Figure 150) and Steller's Jay (***Cyanocitta stelleri***; Figure 151) predators (Donahue 1999). The Murrelets prefer trees with high limbs that support wide moss beds. These must be camouflaged by branches to protect the chicks (Figure 148) from predators like jays (Krajick 1995b). Saving the current nesting sites of the birds is essential because these birds return to the same nesting site year after year and rarely change locations (Donahue 1999).

Figure 150. ***Corvus corax***, Raven, a predator of the Marbled Murrelet. Photo by Frank Vassen, through Creative Commons.

Figure 151. ***Cyanocitta stelleri***, Steller's Jay, eating; this is a predator on the Marbled Murrelet. Photo by Rick Leche, through Creative Commons.

The Marbled Murrelet (***Brachyramphus marmoratus***; Figure 146-Figure 148) is distributed from central California to Alaska, living in mature forests of large coastal conifers (Singer *et al*. 1991). Although most of the nests are simple depressions in the moss or lichen mats, others are more constructed. The Marbled Murrelet uses epiphytic mosses (especially ***Isothecium*** spp.; Figure 152) extensively as nesting material (Hamer & Nelson 1995). In California the Marbled Murrelet prefers the moss ***Brachythecium*** (Figure 153) instead (Brian Dykstra, pers. comm. 10 December 2011). Where it is protected, lots of bryophytes are also protected.

Figure 152. ***Isothecium myosuroides***, a species available for nests of the marbled Murrelet. Photo by Adolf Ceska, with permission.

Figure 153. ***Brachythecium rutabulum***, a species available for nests of the marbled Murrelet. Photo by Michael Lüth, with permission.

Figure 154. ***Brachyramphus brevirostris***, Kittlitz's Murrelet, a species that uses bryophytes in their nests in parts of North America. Photo by Ron Niebrugge, through Creative Commons.

Figure 155. ***Brachyramphus brevirostris***, Kittlitz's Murrelet, nest. Photo by USFWS, through public domain.

Figure 156. ***Ptychoramphus aleuticus***, Cassin's Auklet, a species that uses bryophytes in their nests in parts of North America. Photo by Blake Matheson, through Creative Commons.

Figure 157. ***Ptychoramphus aleuticus***, Cassin's Auklet, on nest. Photo by L. Lauber, USFWS, public domain.

Figure 158. ***Cerorhinca monocerata***, Rhinoceros Auklet, a species that uses bryophytes in their nests in parts of North America. Photo by Dick Daniels, through Creative Commons.

Figure 159. ***Cerorhinca monocerata***, Rhinoceros Auklet, nest burrows. Photo by through Creative Commons.

Figure 160. ***Cerorhinca monocerata***, Rhinoceros Auklet, nest burrow and female. Photo by NOAA, through public domain.

Summary

The use of bryophytes in nests is much more common among the **Passeriformes** than among the non-**Passeriformes**. The latter are mostly ground-nesting birds. Some build their nests on the mosses and others gather bryophytes to include in their nests. In the Arctic and Antarctic, use of bryophytes in nest construction is common due to the limited vegetation available. There, even water birds commonly use bryophytes.

Burrowing birds may use bryophytes as liners in the burrows, sometimes providing a nest for rodents that move in later. Hummingbirds often use mosses and lichens on the outsides of nests, presumably as camouflage. The Picaflor Rubi is one of the birds that can make its entire nest with bryophytes.

Some birds require mossy wetlands nearby their nesting sites because those wetland sites provide food needed for the young.

Protection of birds such as the Marbled Murrelet, a species that flies inland to mossy habitats to nest, may effectively protect the bryophytes as well.

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CHAPTER 16-5
BIRD NESTS – NON-PASSERIFORMES, PART 2

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CHAPTER 16-5
BIRD NESTS – NON-PASSERIFORMES, PART 2

Figure 1. Bird's nest with living moss in Malaysia rain forest at 110 m alt. Photo courtesy of Tamas Pocs.

Columbiformes: Pigeons & Doves

Columbidae – Pigeons & Doves

Wolf (2009) found only one species of **Columbidae** that uses bryophytes in their nests in parts of North America: ***Patagioenas fasciata*** (Band-Tailed Pigeon; Figure 2-Figure 3).

Figure 2. ***Patagioenas fasciata***, Band-Tailed Pigeon, the only member of **Columbidae** that uses mosses in their nests in parts of North America. Photo by Gary Kramer, through public domain.

Figure 3. ***Patagioenas fasciata***, Band-tailed Pigeon, on nest. Photo by Cgates326, through Creative Commons.

Cuculiformes: Cuckoos & Relatives

Cuculidae – Typical Cuckoos

Wolf (2009) found one species of **Cuculidae** that uses bryophytes in their nests in parts of North America: ***Coccyzus americanus*** (Yellow-billed Cuckoo; Figure 4). Unlike the European Cuckoo, the Yellow-billed Cuckoo usually builds its own nest, only occasionally laying eggs in the nest of another species (Wikipedia 2017).

Figure 4. ***Coccyzus americanus***, Yellow-billed Cuckoo, a bird that uses mosses in nests. Photo by Factumquintus, through Creative Commons.

Strigiformes: Owls

Strigidae – Typical Owls

Wolf (2009) found five species of **Strigidae** that use bryophytes in their nests in parts of North America:

Bubo virginianus (Great Horned Owl; Figure 5-Figure 6)
Bubo scandiacus (Snowy Owl; Figure 7)
Glaucidium gnoma (Northern Pygmy Owl; Figure 8)
Strix nebulosa (Great Gray Owl; Figure 9-Figure 10)
Aegolius acadicus (Northern Saw-whet Owl; Figure 11-Figure 12)

Figure 5. ***Bubo virginianus***, Great Horned Owls, in nest where mosses are often used. Photo by John Kees, through Creative Commons.

Figure 6. ***Bubo virginianus***, Great Horned Owl chicks. Photo by G. M. Stolz, through Creative Commons.

Snowy Owl (*Bubo scandiacus*)

Snowy Owls (***Bubo scandiacus***; Figure 7) use mosses as nest liners (Giannetta 2000).

Figure 7. ***Bubo scandiacus***, Snowy Owl. Members of this species use mosses to line their nests. Photo by David Syzdek, through Creative Commons.

Figure 8. ***Glaucidium gnoma***, Northern Pygmy Owl, a species that uses bryophytes in their nests in parts of North America. Photo by Ken-ichi Ueda, through Creative Commons.

Figure 9. ***Strix nebulosa***, Northern Pygmy Owl. Members of this species use bryophytes in their nests in parts of North America. Photo by jok2000, through Creative Commons.

Figure 10. ***Strix nebulosa***, Northern Pygmy Owl, on nest. Photo by Kuva, through Creative Commons.

Figure 11. ***Aegolius acadicus***, Northern Saw-whet Owl. Members of this species use bryophytes in their nests in parts of North America. Photo by Robert L. Curtis, through Creative Commons.

Figure 12. ***Aegolius acadicus***, Northern Saw-whet Owl, young. Photo by Kathy and Sam, through Creative Commons.

Burrowing Owls (*Athene cunicularia*)

Thomsen (1971) reminds us that Burrowing Owls (***Athene cunicularia***; Figure 13-Figure 14) decorate their burrows (Figure 15) with mosses, among other things. The burrowing owl often does not make its own burrow, but rather uses the underground village of a marmot or prairie dog (Rennie 1857). At St. Domingo the owl digs a burrow 70 cm deep and deposits its eggs on a bed of moss.

Figure 13. ***Athene cunicularia***, Burrowing Owls, ground-nesting birds that use burrows. Photo by Travelwayoflife, through Creative Commons.

Figure 14. ***Athene cunicularia hypugaea***, Burrowing Owl. Members of this species decorate their burrows with mosses. Photo by Teddy Llovet, through Creative Commons.

Figure 15. ***Athene cunicularia***, Burrowing Owl, nest hole. Photo by USFWS, through Creative Commons.

Caprimulgiformes: Goatsuckers & Relatives

Caprimulgidae – Goatsuckers

Wolf (2009) found one species (***Chordeiles minor*** – Common Nighthawk; Figure 16) of **Caprimulgidae** that uses bryophytes in their nests (Figure 17-Figure 18) in parts of North America.

Figure 16. ***Chordeiles minor***, Common Nighthawk, on a bed of mosses. Photo by Gavin Keefe Schaefer, through Creative Commons.

Figure 17. ***Chordeiles minor***, Common Nighthawk, eggs in nest of mosses. Photo by Mike Allen, through Creative Commons.

Figure 18. ***Chordeiles minor***, Common Nighthawk, hatchlings in nest. Photo by Mike Allen, through Creative Commons.

Apodiformes: Swifts & Hummingbirds

Apodidae – Swifts

Wolf (2009) found only two members of the **Apodidae** that use bryophytes in their nests in parts of North America:

Cypseloides niger (Black Swift; Figure 19-Figure 20)
Aeronautes saxatalis (White-throated Swift; Figure 21-Figure 22)

Figure 19. ***Cypseloides niger***, Black Swift, adult on mossy nest. Photo by Terry Gray, through Creative Commons.

Figure 20. ***Cypseloides niger***, Black Swift, nest. Photo through Creative Commons.

Figure 21. ***Aeronautes saxatalis***, White-throated Swift, at cliff. Members of this species use bryophytes in their nests in parts of North America. Photo by Richard Crossley, through Creative Commons.

Figure 22. ***Aeronautes saxatalis***, White-throated Swift, in flight. Photo by Michael Woodruff, through Creative Commons.

Glossy Swiftlets (*Collocalia*)

Medway (1966) found that at least some of the European swiftlets (***Collocalia*** and ***Aerodramus***) build bracket-shaped nests of mosses and other bryophytes that are bound together. The Glossy Swiftlets (***Collocalia esculenta***; Figure 23) include bryophytes in their nests, along with horse-hair fungi and palm fibers (Sick 1957; Medway 1962).

Figure 23. ***Collocalia esculenta***, Glossy Swiftlet, a species whose members build nests made entirely of bryophytes in the Philippines. Photo through Creative Commons.

In the Philippines, Tan *et al*. (1982) discovered three nests of ***Collocalia esculenta*** (Glossy Swiftlet; Figure 23) that contained only bryophytes. One was a nest of a single species of the leafy liverwort ***Frullania*** (Figure 24). One nest was constructed of stems of the tiny leafy liverwort ***Mastigolejeunea*** sp. (85%) with scattered mosses [***Papillaria fuscescens*** (see Figure 25), ***Meteorium*** (Figure 26), ***Acroporium*** (Figure 27)]. The third nest had a large compartment of only the leafy liverwort ***Frullania*** and a small one of the mosses ***Papillaria fuscescens*** and ***Aerobryidium*** *cf.* ***filamentosum*** (Figure 28). In all three nests the bryophytes were neatly glued together with saliva from the birds. Some of the bryophytes continued to grow

in the nests, but the shoots were attenuated and the leaf shapes abnormal. Of the mosses, only pleurocarpous species were used, and all the bryophytes were epiphytic high in the canopy of a dipterocarp forest. Furthermore, the bryophytes used were only common close to the summit of the mossy forest. Abundant ground species were completely ignored.

Figure 24. ***Frullania*** sp., a leafy liverwort used to make nests of ***Collocalia esculenta*** in the Philippines. Photo by Li Zhang, with permission.

Figure 25. ***Papillaria***, a genus used in nests of ***Collocalia esculenta*** in the Philippines. Photo by Michael Lüth, with permission.

Figure 26. ***Meteorium***, a genus used in nests of ***Collocalia esculenta*** in the Philippines. Photo by Janice Glime.

Figure 27. ***Acroporium pungens***, member of a genus used in nests by ***Collocalia esculenta*** in the Philippines. Photo by Michael Lüth, with permission.

Figure 28. ***Aerobryidium filamentosum***, a moss species used in nests of ***Collocalia esculenta*** in the Philippines. Photo by Taiwan Liverworts Color Illustrations, through Creative Commons.

Unlike most birds I have seen, ***Collocalia esculenta*** carry their nesting materials with their feet, flying at the tufts of epiphytes, grabbing with their feet and leaning back (Medway 1962). They beat their wings and tug at the bryophyte fronds. Carrying the mosses in their feet makes

the birds tail-heavy and flying is laborious. Fragments are often dropped, and long strands may hang from the nest until the birds are able to weave them into the nest. The mosses are held in place by gumming them to the underlying debris or cave wall. Nests are often deep in caves. This species is able to echo-navigate, so total darkness in the cave is no hindrance.

Mossy-nest Swiftlet (*Aerodramus salangana*)

The moss use by the Mossy-nest Swiftlet (***Aerodramus salangana***; Figure 29) is obvious by its name. The Mossy-nest Swiftlet in Malaysia builds a rounded nest made of plant material (Figure 30) (Medway 1962). Among three nests examined by Medway, the components were *Selaginella* sp. (a lycophyte; Figure 31) 75%, ***Piloecium pseudorufescens 5%***, ***Piloecium pseudorufescens*** 90%, ***Octoblepharum albidum*** (Figure 32) a little; ***Neckeropsis lepineana*** (Figure 33) 80%, ***Pinnatella kuehliana*** 10%, These are all epiphytic mosses except *Selaginella*, a genus that often resembles a moss. ***Octoblepharum*** is the only acrocarpous genus.

Figure 29. ***Aerodramus salangana***, Mossy-nest Swiftlet, showing its cave habitat. Photo by Bernard Dupont, through Creative Commons.

Figure 30. ***Aerodramus salangana natunae***, Mossy-nest Swiftlet nest and nestlings, showing mosses in nest. Photo by Bernard Dupont, through Creative Commons.

Figure 31. ***Selaginella willdenowii***, a moss-like lycophyte in a genus used in nests of the Mossy-nest Swiftlet in Malaysia. Photo copyright Patrick Blanc, permission implied.

Figure 32. ***Octoblepharum albidum***, a moss included in the nests of the Mossy-nest Swiftlet (***Aerodramus salangana***). Photo by Bramadi Arya, through Creative Commons.

Figure 33. ***Neckeropsis lepineana***, a moss included in the nests of the Mossy-nest Swiftlet (***Aerodramus salangana***). Photo by Colin Meurk, through Creative Commons.

Mascarene Swiftlet (*Aerodramus francicus*)

Billiet and Jadin (1979, Jadin & Billiet 1979) reported that the **Mascarene Swiftlet** (***Aerodramus francicus***; Figure 34) uses mosses, liverworts, and lichens glued together with saliva.

Figure 34. ***Aerodramus francicus***, Mascarene Swiftlet, a bird that uses bryophytes in its nests. Photo by Eliane Küpfer, through Creative Commons.

Philippine Swiftlet (*Aerodramus vanikorensis amelis*)

The Philippine Swiftlets (***Aerodramus vanikorensis amelis***; Figure 35) use both lichens and mosses in their nests (Tan *et al*. 1982).

Figure 35. ***Aerodramus vanikorensis amelis***, Philippine Swiftlet, sitting on its mossy nest. Photo by Guy Poisson, with permission.

Trochilidae – Hummingbirds

Wolf (2009) found eight members of the **Trochilidae** that use bryophytes in their nests in parts of North America:

Hylocharis leucotis (White-eared Hummingbird; Figure 36)
Eugenes fulgens (Magnificent Hummingbird; Figure 37)
Archilochus alexandri (Black-chinned Hummingbird; Figure 38-Figure 40)
Calypte anna (Anna's Hummingbird; Figure 43-Figure 46)
Stellula calliope (Calliope Hummingbird; Figure 47-Figure 48)
Selasphorus platycercus (Broad-tailed Hummingbird; Figure 49-Figure 51)
Selasphorus rufus (Rufous Hummingbird; Figure 52-Figure 53)
Selasphorus sasin (Allen's Hummingbird; Figure 54-Figure 55)

Figure 36. ***Hylocharis leucotis***, White-eared Hummingbird, a bird that uses bryophytes in its nests in parts of North America. Photo by Amado Demesa, through Creative Commons.

Figure 37. ***Eugenes fulgens***, Magnificent Hummingbird, a bird that uses bryophytes in its nests in parts of North America. Photo by Dmitry Mozzherin, through Creative Commons.

Figure 38. ***Archilochus alexandri***, Black-chinned Hummingbird, a bird that uses bryophytes in its nests. Photo by Greg Lasley, through Creative Commons.

Figure 39. ***Archilochus alexandri***, Black-chinned Hummingbird. Members of this species use bryophytes in their nests. Photo by Jerry Oldenettel, through Creative Commons.

Figure 40. ***Archilochus alexandri***, Black-chinned Hummingbird, nest. Photo by Benedict Gagliardi, through Creative Commons.

Ruby-throated Hummingbird (*Archilochus colubris*)

The Ruby-throated Hummingbird (***Archilochus colubris***; Figure 41) builds a tiny nest (Figure 42) to house two pea-sized eggs (Bell 2001). These nests are located on thin branches of understory trees. They consist of an inner cup lined with fine plant down and camouflaged on the outside with small pieces of mosses and lichens. These are held together with spider webs, which are also used to affix the nest to the branch.

Figure 41. ***Archilochus colubris***, Ruby-throated Hummingbird. Members of this species use mosses and lichens on the outsides of their nests, creating camouflage. Photo by Matt Tillett, through Creative Commons.

Figure 42. ***Archilochus colubris***, Ruby-throated Hummingbird, on nest. Photo by Choess, through Creative Commons.

Figure 43. ***Calypte anna***, Anna's Hummingbird. Members of this species use bryophytes in their nests. Photo by Don Loarie, through Creative Commons.

Figure 44. ***Calypte anna***, Anna's Hummingbird, head. Photo by James Maughn, through Creative Commons.

Figure 45. ***Calypte anna***, Anna's Hummingbird, nest with mosses. Photo by Steve Berardi, through Creative Commons.

Figure 46. ***Calypte anna***, Anna's Hummingbird, nest with mostly lichens on the outside, but with a few bryophytes mixed in. Photo by Emily Hoyer, through Creative Commons.

Figure 47. ***Stellula calliope***, Calliope Hummingbird. Members of this species use bryophytes in their nests. Photo by Jerry Oldenettel, through Creative Commons.

Figure 48. ***Stellula calliope***, Calliope Hummingbird, feeding young in nest. Photo by Katia Schulz, through Creative Commons.

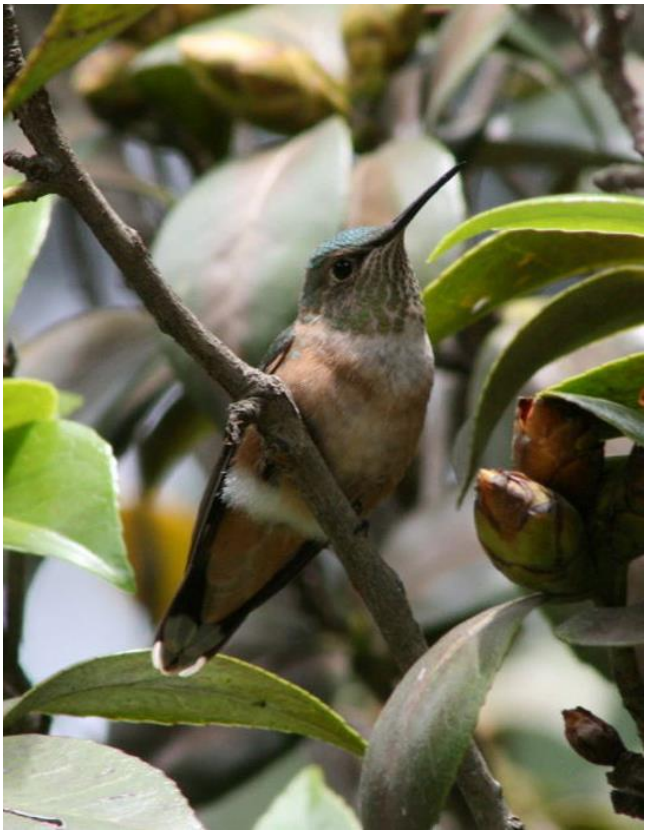

Figure 49. ***Selasphorus platycercus***, Broad-tailed Hummingbird. Members of this species use bryophytes in their nests. Photo by Alfonso Gutiérrez Aldana, through Creative Commons.

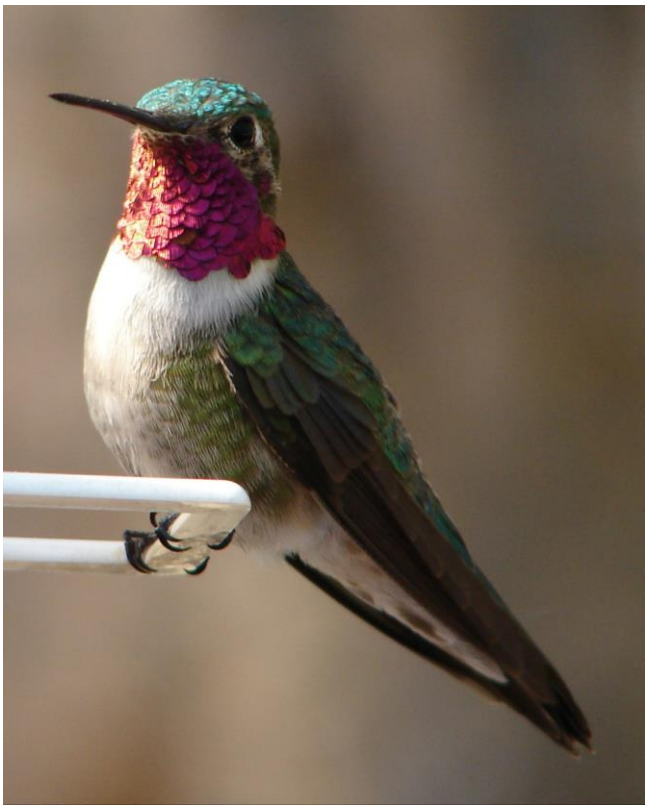

Figure 50. ***Selasphorus platycercus***, Broad-tailed Hummingbird. Photo by Michele Lynn Reynolds, through Creative Commons.

Figure 51. ***Selasphorus platycercus***, Broad-tailed Hummingbird, feeding young in nest. Photo by Bill Ratcliff, NPS, through public domain.

Rufous Hummingbird (*Selasphorus rufus*)

The Rufous Hummingbird (***Selasphorus rufus***; Figure 52) breeds in open areas and forest edges of western North America (Wikipedia 2011). It nests the farthest north of any hummingbird and the female builds its nest (Figure 53) in a shrub or conifer where it is protected. The male aggressively defends this tiny nest. The nests are built in lower branches in spring, benefitting from the temperature amelioration by the canopy. In summer the nests are built higher in the tree (Horvath 1964).

Figure 52. ***Selasphorus rufus***, Rufous Hummingbird male. Photo by Rick Leche, through Creative Commons.

Figure 53. ***Selasphorus rufus***, Rufous Hummingbird, female on nest with mosses and lichens on the exterior of the nest. Photo by Rick Leche, through Creative Commons.

Figure 54. ***Selasphorus sasin***, Allen's Hummingbird. Members of this species use bryophytes in their nests. Photo by Jesse Rorabaugh, through Creative Commons.

Figure 55. ***Selasphorus sasin***, Allen's Hummingbird, on nest that has a few bryophytes. Photo by Asicnewbie, through Creative Commons.

Picaflor Rubí (*Sephanoides sephaniodes*)

The Picaflor Rubí, also known as the Green-backed Firecrown or Picaflor Chico, is a South American hummingbird named ***Sephanoides sephaniodes*** (Figure 57). This tiny bird uses mosses and lichens for its nest (Figure 56), including the moss ***Ancistrodes genuflexa*** (Figure 56-Figure 58) (Torres-Dowdall *et al*. 2007). It seems it prefers this to other pendent mosses in the same family, such as ***Weymouthia cochlearifolia*** (Figure 59) and ***W. mollis*** (Figure 60). On the other hand, in Chile, the Picaflor Rubi uses the tree fern ***Lophosoria quadripinnata*** (Figure 61) in all of the "garments" (materials located inside nest), providing a soft texture and a brown color to the nests (Osorio Zúñiga 2012). The pendent mosses ***Weymouthia cochlearifolia***, ***W. mollis***, and ***Ancistrodes genuflexa*** occur on the outside as 16.6, 26.6, and 100% of the nests, respectively. Among these latter species 20, 37.5 and 40% produced reproductive structures in the nests (Figure 62). In older nests, reproductive structures still occurred on ***Eriodon conostomus*** (Figure 63), ***Ptychomnion ptychocarpon***, and ***Dicranoloma robustum*** (Figure 64). Most of these mosses were taken at heights of 10-18 m from the ground and were not the most abundant species found there. Thus, there is selectivity of the bryophytes used for nesting material.

Figure 56. A nest of the Picaflor Chico (***Sephanoides sephaniodes***), with the bird's tail barely visible, for which the nesting material is primarily ***Ancistrodes genuflexa***. Photo courtesy of Felipe Osorio Zúñiga.

Figure 57. ***Sephanoides sephaniodes***. Members of this species often build their nests almost entirely of mosses. Photo by Greg Lasley, through Creative Commons.

Figure 58. The pendent moss ***Ancistrodes genuflexa*** in Chile, a moss used in the nests of ***Sephanoides sephaniodes***, known there as the Picaflor Chico. Photo courtesy of Felipe Osorio Zúñiga.

Figure 59. ***Weymouthia cochlearifolia***, a pendent moss used in the nests of ***Sephanoides sephaniodes***. Photo by Juan Larrain, through Creative Commons.

Figure 60. ***Weymouthia mollis***, a pendent moss used in the nests of ***Sephanoides sephaniodes***. Photo by Juan Larrain, through Creative Commons.

Figure 61. ***Lophosoria quadripinnata***, a fern used in the nests of ***Sephanoides sephaniodes***. Photo by Franz Xaver, through Creative Commons.

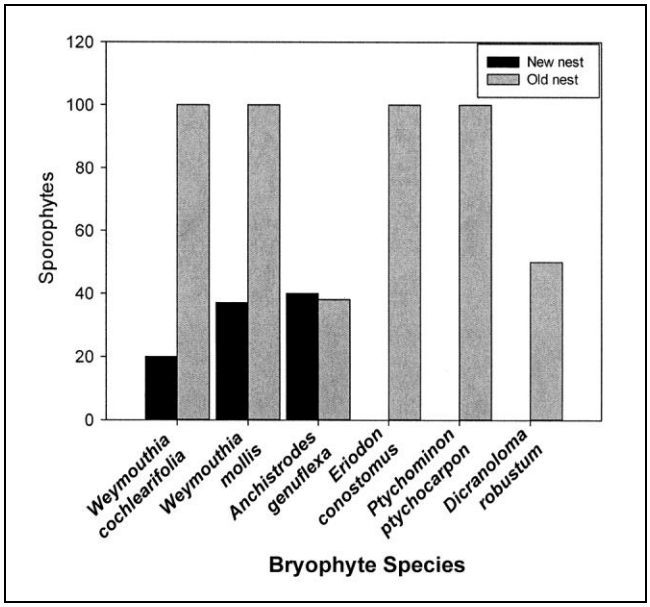

Figure 62. Number of sporophytes vs bryophyte species and nest age of the Picaflor Chico (***Sephanoides sephaniodes***) in Chile. Redrawn from Osorio Zúñiga 2012.

Figure 63. ***Eriodon conostomus*** with capsules, a moss that produces capsules in older nests of Picaflor Rubi. Photo by Juan Larrain, through Creative Commons.

Figure 64. ***Dicranoloma robustum*** with capsules, a moss that produces capsules in older nests of Picaflor Rubi. Photo by Juan Larrain, with permission.

In Patagonia, Argentina, ***Sephanoides sephaniodes*** (Figure 57) is known as the Green-backed Firecrown (Calvelo *et al*. 2014). This species, and the White-sided Hillstar, ***Oreotrochilus leucopleurus*** (Figure 65), likewise used primarily mosses in their nests, but they both interestingly selected mosses with **falcate** (sickle-shaped – see leaves of ***Dicranoloma***; Figure 64) leaves. These were entangled with spider webs and concealed on the outside with spider cocoons, leprose lichens, feathers, and hairs.

Figure 65. ***Oreotrochilus leucopleurus***, White-sided Hillstar. Members of this species like falcate mosses for their nests. Photo by Pablo Caceres Contreras, through Creative Commons.

Osorio-Zuñiga *et al*. (2014) determined that ***Sephanoides sephaniodes*** (Figure 57) was selective in its nesting materials. The bulk of the nest was made from the fern ***Lophosoria quadripinnata*** (Figure 61) (and the moss ***Ancistrodes genuflexa*** – Figure 58). Six other mosses were included in lesser quantities, although 19 species were

available in the area. The birds were further selective in collecting higher densities of reproductive mosses than that represented in the environment. These reproductive structures remained for more than a year, suggesting that this nest-building behavior could be an effective dispersal mechanism. By placing the sporophytes at a greater height, the birds enable dispersal to a greater distance.

More recently, Fontúrbel *et al*. (2020) reported that ***Ancistrodes genuflexa*** occurs in 100% of the nests, makes up 97% of the moss biomass in the nests, but is only 0.1% of the total moss biomass in the forest. The other two mosses that are present in any regularity are ***Weymouthia mollis*** (in 27% of nests) and ***W. cochlearifolia*** (in 17% of nests). These two species provide only 3% of the moss biomass in the nests, but comprise 94% of the moss biomass in the forest. Knowing that mosses often have antibiotic properties, reasoned that this attribute might account for the selection. Hence, the researchers tested the three primary nest components for their antibacterial agents. In ***A. genuflexa***, they found 14 compounds. Of these, five are known to have antibacterial properties, one has antifungal properties, and one repels insects (Asakawa *et al*. 2013)! Although the two ***Weymouthia*** species are known to have antimicrobial properties, neither species was effective against the five common bacteria tested. Furthermore, when the mosses were kept in the lab at 4ºC, both ***Weymouthia*** species were attacked by fungi and rotted after six months, whereas the ***A. genuflexa*** samples were unharmed for a year. Since ***Sephanoides sephaniodes*** may reuse its nest for several years, it is likely that it experiences greater survival when it uses ***A. genuflexa*** at its primary nesting material. As Fontúrbel and coworkers titled their article, "Mamma knows best."

The hummingbirds commonly use mosses and lichens in their nests, so it is not surprising that the endemic Juan Fernandez Firecrown (***Sephanoides fernandensis***; Figure 66-Figure 67) makes its nest almost entirely of mosses (Figure 68) (Jaime Jiminez, pers. comm. 19 May 2020).

Figure 66. ***Sephanoides fernandensis*** (Juan Fernandez Firecrown) female in Juan Fernandez area. Photo courtesy of Jaime Jiminez.

Figure 67. ***Sephanoides fernandensis*** (Juan Fernandez Firecrown) female in Juan Fernandez area. Photo courtesy of Jaime Jiminez.

Figure 68. ***Sephanoides fernandensis*** (Juan Fernandez Firecrown) female on nest in Juan Fernandez area. Photo courtesy of Jaime Jiminez.

Trogoniformes

Trogonidae – Trogons

Wolf (2009) found only one species of **Tyrannidae** whose members use bryophytes in nests in parts of North America: ***Trogon elegans*** (Elegant Trogon; Figure 69).

Figure 69. ***Trogon elegans***, Elegant Trogon, a species that uses bryophytes in nests in parts of North America. Photo by Dominic Sherony, through Creative Commons.

Summary

Burrowing Owls may use bryophytes as liners in the burrows, sometimes providing a nest for rodents that move in later. Some swiftlets make extensive use of mosses in their nests. Hummingbirds often use mosses and lichens on the outsides of nests, presumably as camouflage. The Picaflor Rubi is one of the hummingbirds that can make its entire nest with bryophytes, selecting ***Ancistrodes genuflexa*** in much greater proportion than its presence in the forest, apparently for its antibiotic properties.

Pleurocarpous bryophytes are the most common in nests, and tree-nesting tropical birds typically use epiphytic bryophytes, including pendent species.

Acknowledgments

Thank you to Brian Dykstra for sending me the wonderful thesis on birds and epiphytes by Adrian Wolf, as well as other references and personal observations. David Dumond shared the references he got from Bryonetters. Filipe Osorio Zúñiga provided me with information and images for the Picaflor Chico. Jaime Jiminez provided me with images and natural history information on ***Sephanoides fernandensis***. Thank you to these and all the photographers who made their images available to me online or gave me permission.

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CHAPTER 16-6
BIRD NESTS – PASSERIFORMES, PART 1

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BIRD NESTS – PASSERIFORMES, PART 1

Figure 1. Moss nest from the Pacific Northwest, USA. The bryophytes include ***Isothecium*** and ***Neckera***. Photo courtesy of Jerilyn Peck.

Passeriformes: Perching Birds

This is a large order (>5000 species) and comprises most of the birds that use bryophytes in their nests. But then, it also includes more than half the bird species in the world (Wikipedia 2017). The order is distinguished by having three toes pointing forward and one pointing back, permitting these to be perching birds. Passerines also are **altricial** (hatched or born in undeveloped state and requiring care and feeding by parents).

Richardson (1981) reports that a quarter of the bird species breeding in Great Britain use bryophytes in the construction of their nests. Hansell (2000) likewise reports that numerous small to medium-sized bird species use bryophytes.

Large passerine birds tend to build larger nests relative to their body size when compared to small birds (Slagsvold 1989). The depth of the inner nest cup size of these birds does not relate to the size of the bird. Birds that nest off the ground in open nests have a narrow nest cup, but those with a domed nest or which build in a cavity have a broad nest cup. Birds in exposed nests are less likely to survive than those reared in nest cavities (Nice 1937, 1957). There seem to be no data on the success of birds reared in nests made totally of mosses. Mosses and lichens alter the nest cup size, with the inner nest cup being narrower when more are used (Slagsvold 1989). Use of mosses and lichens also depends on season, with those birds nesting early in the breeding season using significantly more mosses and lichens than are used in later nests.

In coniferous forests, bryophytes are often abundant. Several species of birds that breed there build nests exclusively of bryophytes. These include the Winter Wren (see below; Hejl *et al*. 2002), Marbled Murrelet (see Chapter 16-7; Nelson 1997), and Golden-crowned Kinglet (see Chapter 16-7; Ingold & Galati 1997). In addition, Sakai (1988) described a Hammond Flycatcher nest (see below) made with two epiphytic lichens and five bryophytes, including the epiphytic moss ***Isothecium*** sp. (Figure 11) and liverwort, ***Porella navicularis*** (Figure 17).

Tyrannidae – Tyrant Flycatchers

Wolf (2009) found fifteen species of **Tyrannidae** that use bryophytes in their nests in North America:

Contopus sordidulus (Western Wood-Pewee; Figure 2)
Empidonax flaviventris (Yellow-bellied Flycatcher; Figure 4)
Empidonax alnorum (Alder Flycatcher; Figure 5)
Empidonax minimus (Least Flycatcher; Figure 6)
Empidonax difficilis (Pacific-slope Flycatcher; Figure 7-Figure 8)
Empidonax hammondii (Hammond's Flycatcher; Figure 13)
Empidonax occidentalis (Cordilleran Flycatcher; Figure 18)
Sayornis nigricans (Black Phoebe; Figure 19)
Sayornis phoebe (Eastern Phoebe; Figure 20-Figure 21)
Sayornis saya (Say's Phoebe; Figure 26-Figure 27)
Pitangus sulphuratus (Great Kiskadee; Figure 28)
Tyrannus melancholicus (Tropical Kingbird; Figure 31)
Tyrannus couchii (Couch's Kingbird; Figure 32)
Tyrannus forficatus (Scissor-tailed Flycatcher; Figure 33)
Pachyramphus aglaiae (Rose-throated Becard; Figure 37)

Figure 2. ***Contopus sordidulus***, Western Wood Pewee. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Olive-sided Flycatcher (*Contopus cooperi*)

The Olive-sided Flycatchers (***Contopus cooperi***; Figure 3) typically hide their nests in a cluster of needles and twigs at distal ends of horizontal conifer branches (Johnsgard 2009). These may occur anywhere from 5-13 m above the ground. They use twigs, lichens, mosses, and needles to construct a cup ~12-15 cm in diameter.

Figure 3. ***Contopus cooperi***, Olive-sided Flycatcher. Members of this species often include mosses in their nests. Photo by Jerry Oldenettel, through Creative Commons.

Yellow-bellied Flycatcher (*Empidonax flaviventris*)

In the eastern United States, Yellow-bellied Flycatcher (***Empidonax flaviventris***; Figure 4) nests close to mature stands of lowland coniferous forest (Harrison 1975; Hawrot & Niemi 1996). These forests often have a well-developed layer of mosses and these mosses appear to be necessary for the bird's nesting. The Yellow-bellied Flycatcher nests on the ground in a layer of mosses.

Figure 4. ***Empidonax flaviventris***, Yellow-bellied Flycatcher. This species builds nests on a bed of mosses on the ground. Photo by Cephas, through Creative Commons.

Figure 5. ***Empidonax alnorum***, Alder Flycatcher. Members of this species often include mosses in their nests. Photo by Cephas, through Creative Common.

Figure 6. ***Empidonax minimus***, Least Flycatcher. Members of this species often include mosses in their nests. Photo by MDF, through Creative Commons.

Pacific-slope Flycatcher (*Empidonax difficilis*)

The Pacific-slope Flycatcher (***Empidonax difficilis***; Figure 7-Figure 8) typically builds nests on ledges or crevices of canyon walls (Johnsgard 2009). These are often concealed by mosses or ferns. When the nest is built on trees, they are supported from below and from the rear, occurring in a crotch or on a limb that projects far from the main trunk. They contain a variety of materials, frequently including mosses (Figure 8-Figure 9).

Figure 7. ***Empidonax difficilis***, Pacific-slope Flycatcher, a species that uses ***Isothecium*** in their nests in Douglas fir forests of the Pacific Northwest, USA. Photo by Ron Knight, through Creative Commons.

Figure 8. ***Empidonax difficilis***, Pacific-slope Flycatcher mossy nest with eggs. Photo from USFWS, through Creative Commons.

Figure 9. ***Empidonax difficilis***, Pacific-slope Flycatcher, nest with mosses and young bird. Photo by Don Loarie, through Creative Commons.

In the Pacific Northwest, USA, Wolf (2009) found a nest of the Pacific-slope Flycatcher (Figure 8) on a fractured piece of bark on the tree bole of ***Pseudotsuga menziesii*** (Figure 10) at ~4 m above the ground. The bird had woven strands of the moss ***Isothecium*** (Figure 11) into the rim of the nest and decorated the exterior with fragments of the lichen ***Sphaerophorus globosus*** (Figure 12). The ***Isothecium*** had been relocated from elsewhere in the forest understory.

Figure 10. ***Pseudotsuga menziesii*** bark where Pacific-slope Flycatchers (***Empidonax difficilis***) build their nests in crevices. Photo by Walter Siegmund, through Creative Commons

Figure 11. ***Isothecium myosuroides***, representing a genus among those used in nests of the Pacific-slope Flycatcher (***Empidonax difficilis***). Photo by Hermann Schachner, through Creative Commons.

Figure 12. ***Sphaerophorus globosus***, one of the lichen materials used in nests of the Pacific-slope Flycatcher (***Empidonax difficilis***). Photo by Einar Timdal, through Creative Commons.

Hammond's Flycatcher (*Empidonax hammondii*)

The Hammond's Flycatcher (***Empidonax hammondii***; Figure 13) has a nest that is distinctly different from that of the Pacific Slope Flycatcher (***Empidonax difficilis***; Figure 7-Figure 9) (Sakai 1988). The Hammond's Flycatcher nest is taller, more tightly woven, and mimics the surrounding substrate. The outer bowl of the only retrieved nest was made with mostly white scale lichens, mosses ***Dendroalsia abietina*** (Figure 14), ***Homalothecium nuttallii*** (Figure 15), ***Isothecium*** sp. (Figure 11), ***Alsia*** sp. (Figure 16), and the leafy liverwort ***Porella navicularis*** (Figure 17). By comparison, in the 22 Pacific-slope Flycatcher nests, the material was mostly mosses. They often lacked the camouflage effect because they used the same materials on all substrates. The nests were held together with spider webs that were also used to secure the nests to the substrate.

Figure 13. ***Empidonax hammondii***, Hammond's Flycatcher. Members of this species often include mosses in their nests. Photo by Pablo Leautaud, through Creative Commons.

Figure 14. ***Dendroalsia abietina***, a nest component of the Hammond's Flycatcher in the Pacific Northwest. Photo by James Maughn, through Creative Commons.

Figure 15. ***Homalothecium nuttallii***, a species used in nests of the Hammond's Flycatcher in the Pacific Northwest. Photo by Doug Murphy, through Creative Commons.

Figure 16. ***Alsia californica***, member of a genus used in nests of the Hammond's Flycatcher in parts of North America. Photo by John Game, through Creative Commons.

Figure 17. ***Porella navicularis***, a leafy liverwort used in nests of the Hammond's Flycatcher in the Pacific Northwest. Photo by Matt Goff <www.sitkanature.org>, with permission.

Figure 18. ***Empidonax occidentalis***, Cordilleran Flycatcher. Members of this species often include mosses in their nests. Photo from Amado Demesa, through Creative Commons.

Figure 19. ***Sayornis nigricans***, Black Phoebe. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Eastern Phoebe (*Sayornis phoebe*)

I picked up my copy of "A Complete Field Guide to Nests in the United States" with eager anticipation. I quickly scanned the keys that depended on nesting location and materials and found several that mentioned mosses or peatlands. As I looked up each appropriate item in the key, I soon discovered only one bird was cited as a bryophyte user, the Eastern Phoebe – ***Sayornis phoebe*** (Figure 20) (Headstromn 1970). The Eastern Phoebe builds a cup-shaped nest (Figure 21) lined with mud and fibrous plant material. It uses mosses as a binding material with mud in the inner cup (Breil & Moyle 1976). It also uses mosses to line the cup. The outermost layer is also covered with moss (Headstromn 1970). Bent (1963) provided interesting bryological information. In a single nest, ***Mnium stellare*** (Figure 22), ***Funaria*** sp. (Figure 23), ***Polytrichum*** sp. (Figure 24), ***Hypnum*** "***cristatum***," and ***Climacium dendroides*** (Figure 25) were used as construction materials.

Figure 20. ***Sayornis phoebe***, Eastern Phoebe, a bird that can be identified by the mosses in its nest. Photo by John Benson, through Creative Commons.

Figure 21. ***Sayornis phoebe***, Eastern Phoebe, nest. Photo by Bernard Goffinet, through Creative Commons.

Figure 22. ***Mnium stellare***, a moss used in the Eastern Phoebe (***Sayornis phoebe***) nests. Photo by Hermann Schachner, through Creative Commons.

Figure 23. ***Funaria hygrometrica*** with immature capsules, a species used in nests of the Eastern Phoebe. Photo by Hermann Schachner, through Creative Commons.

Figure 24. ***Polytrichum commune***, member of a genus used in construction of nests of the Eastern Phoebe. Photo by Hermann Schachner, through Creative Commons.

Figure 25. ***Climacium dendroides***, a moss used in nests of the Eastern Phoebe. Photo by Stan Phillips, through public domain.

Figure 26. ***Sayornis saya***, Say's Phoebe. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 27. ***Sayornis saya***, Say's Phoebe, nest with young. Photo by Tom Grey, with permission.

Figure 28. ***Pitangus sulphuratus***, Great Kiskadee. Members of this species often include mosses in their nests.. Photo by Tom Grey, with permission.

Eastern Kingbird (*Tyrannus tyrannus*)

The Eastern Kingbird (***Tyrannus tyrannus***; Figure 29) of the Great Plains typically lives in forests where the canopy level is uneven, providing high points for observation and foraging (Johnsgard 2009). The female picks the nest site and builds the nest (Figure 30). She places it on outer branches of shrubs or small trees and often incorporates mosses in the construction.

Figure 29. ***Tyrannus tyrannus***, Eastern Kingbird. Members of this species often include mosses in their nests. Photo by MDF, through Creative Commons.

Figure 30. ***Tyrannus tyrannus***, Eastern Kingbird, nest with eggs. Photo by Anc516, through Creative Commons.

Figure 31. ***Tyrannus melancholicus***, Tropical Kingbird. Members of this species often include mosses in their nests.. Photo by Tom Grey, with permission.

Figure 32. ***Tyrannus couchii***, Couch's Kingbird. Members of this species often include mosses in their nests. Photo by Ruben, through Creative Commons.

Figure 33. ***Tyrannus forficatus***, Scissor-tailed Flycatcher. Members of this species often include mosses in their nests.. Photo by Tom Grey, with permission.

Yellow-bellied Chat-tyrant (*Ochthoeca diadema*)

Miller and Greeney (2008) described the nest of the Yellow-bellied Chat-tyrant (***Ochthoeca diadema***; Figure 34). They found a partially domed cup built into a vertical mat of mosses that hung from a horizontal vine. The cup was thick and composed of bryophytes with a sparse lining of feathers. The dome covered only about one-third of the cup. Closer examination revealed that the nest was actually build into the vertical sheet of mosses.

Figure 34. ***Ochthoeca diadema***, Yellow-bellied Chat Tyrant. Members of this species sometimes build their nests into vertical hanging mats of mosses. Photo by Andres Cuervo, through Creative Commons.

Crowned Chat-tyrant (*Ochthoeca frontalis*)

Miller and Greeney (2008) found the Crowned Chat-tyrant (***Ochthoeca frontalis***) where it built its nest into a clump of mosses that was hanging 50 cm below a horizontal tree trunk (Miller & Greeney 2008). This provided good concealment by vegetation on the upper side. The nest was a partial dome made of mosses built into growing mosses and ferns.

Other species, such as Rufous-breasted Chat (***Ochthoeca rufipectoralis***; Figure 35) and Slaty-backed Chat-tyrant (***O. cinnamomeiventris***; Figure 36) also place their mossy cups on ledges (Hilty & Brown 1986; Greeney 2007).

Figure 35. ***Ochthoeca rufipectoralis***, Rufous-breasted Chat Tyrant. Members of this species often include mosses in their nests. Photo by Dick Cook, through Creative Commons.

Figure 36. ***Ochthoeca cinnamomeiventris***. Members of this species place mossy cups on ledges. Photo by Ken-ichi Ueda, through Creative Commons.

Figure 37. ***Pachyramphus aglaiae***, Rose-throated Becard. Members of this species often include mosses in their nests. Photo by Dominic Sherony, through Creative Commons.

Laniidae – Shrikes

Wolf (2009) found two species of **Laniidae** that use bryophytes in their nests in North America:

Lanius ludovicianus (Loggerhead Shrike; Figure 38)
Lanius excubitor (Northern Shrike; Figure 39)

Figure 38. ***Lanius ludovicianus***, Loggerhead Shrike. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 39. ***Lanius excubitor***, Northern Shrike. Members of this species often include mosses in their nests. Photo by Smudge 9000, with permission.

Vireonidae – Typical Vireos

Wolf (2009) found three species of **Corvidae** that use bryophytes in their nests in North America:

Vireo griseus (White-eyed Vireo; Figure 40)
Vireo cassinii (Cassin's Vireo; Figure 41-Figure 42)
Vireo huttoni (Hutton's Vireo; Figure 43)

Figure 40. ***Vireo griseus***, White-eyed Vireo. Members of this species often include bryophytes in their nests. Photo by Andy Reago and Chrissy McClarren, through Creative Commons.

Figure 41. ***Vireo cassinii***, Cassin's Vireo. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 42. ***Vireo cassinii***, Cassin's Vireo, nest with female. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 43. ***Vireo huttoni***, Hutton's Vireo. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Rhipiduridae – Fantails

The Grey Fantail (***Rhipidura albiscapa***) in Tasmania builds a tidy nest of grass, moss sporophytes, bark, other plant fibers, ad spider webs (Lloyd 2013). The webs are used to attach the nest to a branch. The moss sporophytes are used to line the cup of the nest. These nests are built by the males and females in the understorey shrubs and small trees and both birds contribute to feeding.

Figure 44. ***Rhipidura albiscapa*** (Grey Fantail), a species that lines its nest with moss sporophytes. Photo by Patrick Kavanagh, through Creative Commons.

Figure 45. ***Rhipidura albiscapa*** (Grey Fantail) nest and nestlings. Photo by Benjamint444, through Creative Commons.

Monarchidae – Monarch Flycatchers

The Rarotonga Flycatcher (***Pomarea dimidiata***; Figure 46), an endangered species in the Cook Islands of Polynesia, makes a nest entirely from mosses (Figure 46-Figure 47), mostly **Meteoriaceae** (Figure 48) (John Game, Bryonet 22 June 2016).

Figure 46. ***Pomarea dimidiata***, Rarotonga Flycatcher, at mossy nest. Photo by G. McCormack © CINHP <www.cookislands.bishopmuseum.org>, with online permission.

Figure 47. ***Pomarea dimidiata***, Rarotonga Flycatcher, on nest of mosses. Photo by G. McCormack © CINHP <www.cookislands.bishopmuseum.org>, with online permission.

Figure 48. ***Weymouthia mollis***, member of **Meteoraceae** that is common in bird nests. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Myiagra cyanoleuca (Migratory Satin Flycatcher; Figure 49) builds a nest on a dead horizontal branch 5-25 m

above ground (Lloyd 2013). It uses bark strips and moss tightly bound with spider webs, making it neat and well disguised.

Figure 49. ***Myiagra cyanoleuca*** (Satin Flycatcher) male, a species that includes mosses in its nests. Aviceda at English Wikipedia, though Creative Commons.

Corvidae – Jays, Magpies, & Crows

Wolf (2009) found nine species of **Corvidae** that use bryophytes in their nests in North America:

Perisoreus canadensis (Gray Jay; Figure 50)
Cyanocitta stelleri (Steller's Jay; Figure 51)
Cyanocitta cristata (Blue Jay; Figure 52)
Cyanocorax yncas (Green Jay; Figure 53)
Aphelocoma californica (California Scrub-jay; Figure 54)
Gymnorhinus cyanocephalus (Pinyon Jay; Figure 55)
Nucifraga columbiana (Clark's Nutcracker; Figure 56)
Corvus brachyrhynchos (American Crow; Figure 57)
Corvus caurinus (Northwestern Crow; Figure 58)
Corvus corax (Common Raven; Figure 59)

Figure 50. ***Perisoreus canadensis***, Gray Jay. Members of this species often include mosses in their nests. Photo by Walter Siegmund, through Creative Commons.

Figure 51. ***Cyanocitta stelleri***, Steller's Jay. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 52. ***Cyanocitta cristata***, Blue Jay. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 53. ***Cyanocorax yncas***, Green Jay. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 54. ***Aphelocoma californica***, California Scrub-jay. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 55. ***Gymnorhinus cyanocephalus***, Pinyon Jay. Members of this species often include mosses in their nests. Photo by James St. John, through Creative Commons.

Figure 56. ***Nucifraga columbiana***, Clark's Nutcracker. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 57. ***Corvus brachyrhynchos***, American Crow. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 58. ***Corvus caurinus***, Northwestern Crow. Members of this species often include mosses in their nests. Photo by T Greyfox, through Creative Commons.

Common Raven (*Corvus corax*)

The Raven (***Corvus corax***; Figure 59) uses mosses to line its nest (Giannetta 2000).

Figure 59. ***Corvus corax***, Raven. Members of this species often include mosses in their nests. Photo by Dick Daniels, through Creative Commons.

Hirundinidae – Swallows

Wolf (2009) found only two species of **Hirundinidae** that use bryophytes in their nests in North America:

Tachycineta bicolor (Tree Swallow; Figure 60-Figure 61)
Stelgidopteryx serripennis (Northern Rough-winged Swallow; Figure 62)

Tree Swallow (*Tachycineta bicolor*)

Tree Swallows (***Tachycineta bicolor***; Figure 60) are known to construct a basket nest (Figure 61) of sticks with an "upholstery" of moss, grass, and animal fur (Heinrich 2000). Heinrich assumed these to provide insulation and to cushion the eggs.

Figure 60. ***Tachycineta bicolor***, Tree Swallow, male. Members of this species use bryophytes in their treehole nests. Photo by Tom Grey, with permission.

Figure 61. ***Tachycineta bicolor***, tree swallow, in a nest where bryophytes were used. Photo through public domain.

Figure 62. ***Stelgidopteryx serripennis***, Northern Rough-winged Swallow. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Paridae – True Tits

Wesołowski (unpublished data) found that the tits typically gathered moss for their nests in the immediate vicinity of the nest cavity, but they also would travel up to 80 m to gather nesting materials. Wolf (2009) found eight species of **Paridae** that use bryophytes in their nests in North America:

Poecile atricapillus (Black-capped Chickadee; Figure 74)
Poecile gambeli (Mountain Chickadee; Figure 89)
Poecile rufescens (Chestnut-backed Chickadee; Figure 90)
Poecile hudsonicus (Boreal Chickadee; Figure 91)
Poecile cinctus (Gray-headed Chickadee; Figure 92)
Baeolophus inornatus (Oak Titmouse; Figure 93)
Baeolophus ridgwayi (Juniper Titmouse; Figure 94)
Baeolophus bicolor (Tufted Titmouse; Figure 95)

Wesołowski and Wierzcholska (2018) compared the nesting materials used by three species of tit (Figure 63) and demonstrated that they were selective. Furthermore, the selections differed among the species. They avoided the abundant ***Brachythecium rutabulum*** (Figure 64), and ***Plagiothecium nemorale*** (Figure 65) and almost never used ***Anomodon longifolius*** (Figure 66) or ***Brachythecium oedipodium*** (Figure 67). Of the 54 available species, 21 were never used. Most plots associated with the nests had an average of 10.2-11.6 moss species/plot. The liverwort ***Metzgeria furcata*** (Figure 68) was used exclusively by Marsh Tits, and in greater proportion than in the environment. ***Brachythecium salebrosum*** was used only by Blue Tits, who also used large quantities of two forms of ***Hypnum cupressiforme*** (Figure 103). Great Tits under-used ***Hypnum cupressiforme*** forms but used ***Anomodon viticulosus*** (Figure 69), and possibly also ***Pleurozium schreberi*** (Figure 70) in greater proportion than their

availability. Wesołowski and Wierzcholska found no difference in water uptake between used and unused mosses. The Great Tits used mosses (***Anomodon viticulosus***, ***Isothecium alopecuroides*** (Figure 71), ***Pleurozium schreberi***) with stems twice as thick as those used by the Marsh Tits [***Hypnum cupressiforme*** mod. ***filiforme*** (Figure 72), ***Neckera complanata*** (Figure 73)].

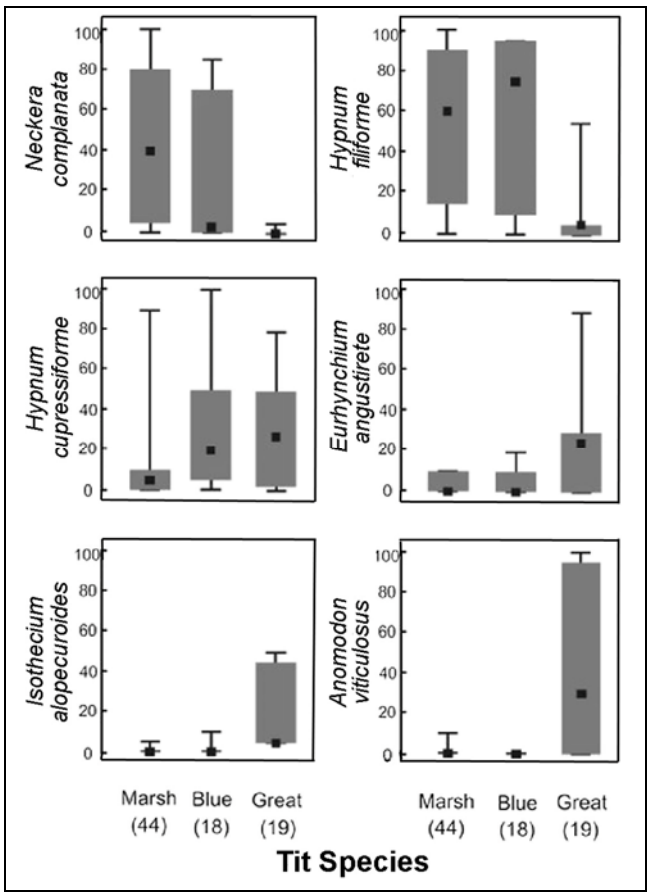

Figure 63. Moss choice in nests of three species of tits in Poland. The percent represents to the percent of volume of mosses in the moss layer of nests that had mosses. Small squares represent the medians, boxes indicate 25-75% quartiles, and whiskers show the ranges. Numbers in parentheses are sample sizes. Modified from Wesołowski & Wierzcholska 2018.

Figure 64. ***Brachythecium rutabulum***, an abundant moss avoided by tits. Photo by Janice Glime.

Figure 65. ***Plagiothecium nemorale***, an abundant moss that is avoided by tits as a nesting material. Photo by Michael Luth, with permission.

Figure 66. ***Anomodon longifolius***, an abundant moss that is rarely used by tits for their nests. Photo by Hermann Schachner, through Creative Commons.

Figure 67. ***Brachythecium oedipodium***, an abundant moss that is rarely used by tits for their nests. Photo by Michael Luth, with permission.

Figure 68. ***Metzgeria furcata***, a liverwort that often occurs in tit nests, but in small quantity. Photo by Michael Luth, with permission.

Figure 69. ***Anomodon viticulosus***, a preferred moss for nests by Great Tits. Photo by Janice Glime.

Figure 70. ***Pleurozium schreberi***, a preferred moss for nests of Great Tits. Photo by Janice Glime.

Figure 71. ***Isothecium alopecuroides*** with capsules, mosses with thick stems that preferred by Great Tits for nest materials. Photo by David T. Holyoak, with permission.

Figure 72. ***Hypnum cupressiforme*** mod. ***filiforme***, a moss with thin stems and that is used for nest materials by Marsh Tits. Photo by Jan-Peter Frahm, with permission.

Figure 73. ***Neckera complanata***, a moss with thin stems and that is used for nest materials by Marsh Tits. Photo by Michael Lüth, with permission.

But why did these birds travel as much as 80 m to gather some species when unused ones were much closer? When Wesołowski and Wierzcholska (2018) used human

plucking of the mosses used in nests and compared them to plucking of the unused species, they found that the used species yielded larger (heavier) bundles of moss and contained longer shoots than of those mosses that were ignored by the birds. This suggests that there is an energy benefit when using the selected species.

Black-capped Chickadee (*Poecile atricapillus*)

Allen (2017) observed a Black-capped Chickadee (***Poecile atricapillus***; Figure 74) busily gathering dry moss for its nest, then flying to the nestbox. The stream had lots of moss, but the bird ignored these, preferring the dry patch next to the stream. The Robin, on the other hand, preferred the wet moss for its open, mud-lined nest.

Figure 74. ***Poecile atricapillus***, Black-capped Chickadee. Members of this species gather dry mosses near a stream for their nests. Photo by Tattooed Dreamer, through Creative Commons.

Carolina Chickadee (*Poecile carolinensis*)

Erichsen (1919) describes the appearance of "down" on the cinnamon and royal ferns as a signal that the Carolina Chickadee (***Poecile carolinensis***; Figure 75) will begin its nest building (Figure 76). The Carolina Chickadee often begins this nest (Figure 77) by placing a thick mat of green moss (often ***Hypnum***; Figure 78) from the tree trunks into the nesting cavity (Figure 77). This always occurs first, followed by the soft down of the ferns.

Figure 75. ***Poecile carolinensis***, Carolina Chickadee. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 76. ***Poecile carolinensis***, Carolina Chickadee, with nesting materials. Photo by Tom Grey, with permission.

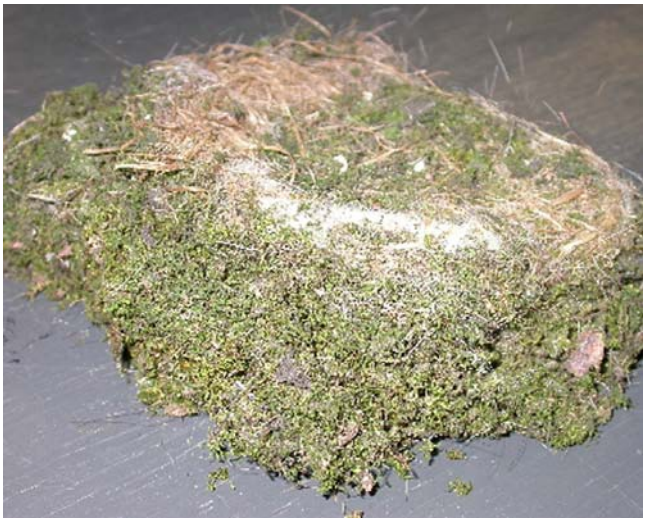

Figure 77. ***Poecile carolinensis***, Carolina Chickadee, nest. Photo courtesy of Diane Lucas.

Figure 78. ***Hypnum imponens***, a common species in a genus used for nests of the Carolina Chickadee. Photo by Janice Glime.

Andreas (2010) observed nests of two Carolina Chickadees (***Poecile carolinensis***; Figure 75). These included ten mosses and two liverworts. The dominant species were the pleurocarpous moss ***Platygyrium repens*** (Figure 79) and the leafy liverwort ***Frullania eboracensis*** (Figure 80) plus a few others, which comprised 55% of the nesting material by volume. In another year, the bryophytes comprised 70.4% of the nest material. The selection of bryophytes was not in proportion to their abundance and all species used were epiphytic on bark. Andreas suggested that they may select ***Frullania eboracensis*** for its chemical properties, possibly protecting them from mites (Figure 113). Only **corticolous** (growing on tree bark) bryophytes were used, with the exception of a single piece of ***Bryoandersonia illecebra*** (Figure 81) in one nest. But even clumps of **acrocarpous** (mostly upright with archegonia and capsules forming at tip of stem) mosses were removed from the tree trunks as tiny tufts for nest usage, including ***Orthotrichum ohioense*** and ***Dicranum montanum*** (Figure 82). Other corticolous bryophytes, including ***Anomodon attenuatus*** (Figure 83), ***Brachythecium laetum*** (Figure 84), ***Clasmatodon parvulus*** (Figure 85), ***Hypnum pallescens*** (Figure 86), and ***Ulota crispa*** (Figure 87), were ignored.

Figure 79. ***Platygyrium repens*** with bulbils, a moss used in nests of Carolina Chickadees. Photo by Hermann Schachner, through Creative Commons.

Figure 80. ***Frullania eboracensis***, a leafy liverwort used in nests of Carolina Chickadees. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 81. ***Bryoandersonia illecebra***, the only non-epiphytic moss used in a Carolina Chickadee nest. Photo by Bob Klips, with permission.

Figure 82. ***Dicranum montanum***, an acrocarpous moss used in the nest of a Carolina Chickadee. Photo by Hermann Schachner, through Creative Commons.

Figure 83. ***Anomodon attenuatus*** with capsules, an epiphytic moss that was ignored when the Carolina Chickadee built its nest. Photo by Bob Klips, with permission.

Figure 84. ***Brachythecium laetum***, an epiphytic moss that was ignored when the Carolina Chickadee built its nest. Photo by Bob Klips, with permission.

Figure 85. ***Clasmatodon parvulus***, an epiphytic moss that was ignored when a Carolina Chickadee built its nest. Photo by A. Newman, through Creative Commons.

Figure 86. ***Hypnum pallescens***, an epiphytic moss that was ignored when a Carolina Chickadee built its nest. Photo by Michael Lüth, with permission.

Figure 87. ***Ulota crispa***, an epiphytic moss that was ignored when a Carolina Chickadee built its nest. Photo by Michael Lüth, with permission.

In Cashiers, NC, a Carolina Chickadee (***Poecile carolinensis***; Figure 75) used ***Thuidium delicatulum*** (Figure 88) in its nest in an English Boxwood shrub (Annie Martin, Bryonet 1 June 2010).

Figure 88. ***Thuidium delicatulum***, a ground moss used in the nest of a Carolina Chickadee. Photo by Janice Glime.

Figure 89. ***Poecile gambeli***, Mountain Chickadee. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 90. ***Poecile rufescens***, Chestnut-backed Chickadee. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 91. ***Poecile hudsonicus***, Boreal Chickadee. Members of this species often include mosses in their nests. Photo by David Mitchell, through Creative Commons.

Figure 92. ***Poecile cinctus***, Grey-headed Chickadee. Members of this species often include mosses in their nests. Photo by Jargal Lamjav, through Creative Commons.

Figure 93. ***Baeolophus inornatus***, Oak Titmouse, with its nest in the large hole at the bottom left. Members of this species include bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 94. ***Baeolophus ridgwayi***, Juniper Titmouse. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 95. ***Baeolophus bicolor***, Tufted Titmouse. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Varied Tit (*Sittiparus varius*)

The Varied Tit (***Sittiparus varius***; Figure 96) lives in coniferous forests, mixed forests, and bamboo in eastern Japan, Korea, and some parts of northeastern China and extreme southeastern Russia (southern Kurile Islands). It is one of the birds that uses bryophytes for nesting material (Sakai 2007).

Figure 96. ***Sittiparus varius***, Varied Tit. Members of this species often include mosses in their nests. Photo by Alpsdake, through Creative Commons.

Figure 97. ***Parus major***, Great Tit,. Members of this species often include bryophytes in their nests. Photo by Paul Gulliver, through Creative Commons.

Figure 98. ***Parus major***, Great Tit, nest with bryophytes and eggs. Photo by Oh Wei, through Creative Commons.

Blue Tit (*Cyanistes caeruleus*), Great Tit (*Parus major*), and Japanese Tit (*Parus minor*)

The Great Tit (***Parus major***; Figure 97-Figure 98) and the Blue Tit (***Cyanistes caeruleus***; Figure 99-Figure 101) both use mosses to build their nests (Figure 98) (Hribek 1985). Likewise, Gustavo Tomás and Andrew Spink (pers. comm. 2010) have collected mosses from a large number of Blue Tit (***Cyanistes caeruleus***) and Coal Tit (***Periparus ater***; Figure 102) nests in the Netherlands. The most common species in the nest is the locally common ***Hypnum cupressiforme*** (Figure 103). But other locally common species are not common in the nests, suggesting a preference. It appears that different species may be used in different parts of the nest, but so far there is no quantitative analysis available to support this. Figure 108 demonstrates the use of a ***Hypnum*** species (with ***Thuidium***) in the nest of an unknown bird in Pennsylvania, USA.

Figure 99. ***Cyanistes caeruleus***, Eurasian Blue Tit,. Members of this species build their nests with mosses. Photo by Francis C. Franklin, through Creative Commons.

Figure 100. ***Cyanistes caeruleus***, Blue Tit, mossy nest and eggs. Photo by Notts Ex Miner, through Creative Commons.

Figure 101. ***Cyanistes caeruleus***, Blue Tit, nest with moss and nestlings. Photo by Notts Ex Miner, through Creative Commons.

Figure 102. ***Periparus ater***, Coal Tit. Members of this species often include mosses in their nests, preferring ***Hypnum cupressiforme***. Photo by Aviceda, through Creative Commons.

Figure 103. ***Hypnum cupressiforme***, a preferred moss in the nests of Blue Tits and Coal Tits. Photo by Michael Lüth, with permission.

Although the population may use a wide variety of mosses, a few species of bryophytes typically comprise the nest. For example, the Japanese Tit, ***Parus minor***, used 21 species of bryophytes in the nests, but among 91% of the 47 nests, more than 50% of the volume was comprised of only three bryophyte species (Hamao *et al.* 2016). In this case, the preference seems to relate to a potential food source. The Japanese Tits preferred pleurocarpous mosses. In thse nests, seven species of moths emerged from the nesting material and were more frequent in nests with successful fledgine than in failed nests.

Figure 104. ***Parus minor***, Japanese Tit, a species that seems to be selctive in choice of mosses for its nests. Photo by Hyun-tae Kim, through Creative Commons.

In the Czech Republic, Hříbek (1985) found that Blue Tits (Figure 99-Figure 101) used mostly softer species (***Hypnum cupressiforme*** (Figure 103), ***Leptodictyum riparium*** (Figure 105), whereas the Great Tits used mostly the large-stemmed mosses such as ***Calliergonella cuspidata*** (Figure 106) and ***Rhytidiadelphus squarrosus*** (Figure 107).

Figure 105. ***Leptodictyum riparium***, a favorite nesting material of Blue Tits in the Czech Republic, with capsule. Photo by Michael Lüth, with permission.

Figure 106. ***Calliergonella cuspidata***, one of the nesting materials of Great Tits in the Czech Republic. Photo by David T. Holyoak, with permission.

Figure 107. ***Rhytidiadelphus squarrosus***, one of the nesting materials of Great Tits in the Czech Republic. Photo by Michael Lüth, with permission.

Álvarez *et al*. (2013) asserted that the properties and structure of a nest affect breeding performance. This drives the selection of behavior that produces nests characteristic of the species, including the appropriate nesting materials. Where preferred materials are low, birds select alternative materials, often at the cost of reduced breeding success. The researchers set out to support this hypothesis with the Great Tit, a species that has a wide range of habitats, using populations in four different Mediterranean habitats. Interestingly, the clutch size decreased as moss mass increased in the four sites. However, hatching success increased as the moss mass increased in one site. And in all the habitats, the nestling condition was poorer in nests with a greater proportion of sticks and feathers.

Mainwaring *et al*. (2012) reported that the nests of Blue Tits (***Cyanistes caeruleus***) and Great Tits (***Parus major***; Figure 97-Figure 98) in Great Britain consist of a "pad of moss mixed with dry grass and other plant material placed at the base of the nest box" (Figure 109) (Cramp & Perrins 1993; Mainwaring *et al*. 2008; Mainwaring & Hartley 2008, 2009; Britt & Deeming 2011). The nest cup is lined with fine dry grass, hair, wool and feathers. In this case, it appears that the mosses may be used to regulate the temperature and insulate the eggs and young birds. When temperatures increase, the female reduces the amount of lining material.

Figure 108. ***Hypnum*** and ***Thuidium*** in unidentified nest. Photo courtesy of Jeri Peck.

Figure 109. ***Parus major***, Great Tit, with eggs in nest on mosses. Photo by Notts Ex Miner, through Creative Commons.

When Great Tits (***Parus major***; Figure 97) built a second nest in nest boxes after rearing their first brood, they still used mosses in the nest, but there was no lining or inner layer – or any eggs (Slagsvold 1984).

Rydgren *et al*. (2023) compared the mosses used in nests of ***Parus major*** to those available nearby. There was a clear preference for highly branched pleurocarpous species, especially ***Pleurozium schreberi*** (Figure 70), ***Rhytidiadelphus squarrosus*** (Figure 107), and ***Sanionia uncinata*** (Figure 110). They avoid common species that are only sparsely branched. They also used the same species in the same nest boxes in subsequent years. The nesting materials were collected close to the nest, predominantly within 5 m, supporting the hypothesis that collecting nest materials is costly (Figure 111). The researchers suggested that studies are needed to reveal cost of gathering nest materials, to determine the suitability (advantages?) of the materials chosen, and to see if the choices are inherited. It would be interesting to run choice experiments with materials having a variety of properties and to compare nesting materials of the same species in different locations.

Figure 110. ***Sanionia uncinata***, a preferred species for nests of the Great Tit (***Parus major***). Photo by Claire Halpin, with permission.

Figure 111. ***Parus minor*** making nest with branched moss. Photo by Alpsdake, through Creative Commons.

The Corsican Blue Tit (***Cyanistes caeruleus ogliastrae***; Figure 112) includes 1-5 aromatic herbs in its nest (Lambrechts & Dos Santos 2000). Herbs are included in a number of kinds of bird nests, and researchers have suggested that they may serve an anti-parasite function (Figure 113) (Wimberger 1984; Bucher 1988; Cowie & Hinsley 1988; Clark 1991; Banbura *et al.* 1995). Using an herb removal experiment when the young hatched, these researchers found that the parents brought fresh aromatic greens to the nest. They proposed the Potpourri hypothesis that included at least seven functional causes for materials used in the nests. When the Blue Tits breed in cavities, they use predominately mosses, but also include other materials, including fresh herbaceous leaves. They suggested that mosses may optimize the microclimate in the nest cavity. The aromatic herbs are likely to serve an anti-parasitic function.

Figure 112. ***Cyanistes caeruleus ogliastrae***, Corsican Blue Tit. Members of this species often include mosses in their nests. Photo by Valter Jacinto, through Creative Commons.

Figure 113. ***Cyanistes caeruleus***, Eurasian Blue Tit, with mite infestation causing balding. Photo by Michael Palmer, through Creative Commons.

Ground Tit (*Pseudopodoces humilis*)

Ground Tit, also known as Hume's Jay, (***Pseudopodoces humilis***; Figure 114) has been considered the smallest member of the Jay and Crow family (Lipske 2004). But more recently it appears that it should be classified in the **Paridae** with the Chickadees. These birds are common in forests and woody suburbs of Europe and North America, but it appears that their ancestors lived on the dry, treeless Tibetan plateau. They nest in cavities where they build nests of grasses and mosses. Like Jays, they rarely fly, but they do not run like the Jays; rather, they hop.

Figure 114. ***Pseudopodoces humilis***, Ground Tit. Members of this species build nests of grasses and mosses. Photo by David Blank, through Creative Commons.

Pipridae – Manakins, Piprites

Black-capped Piprites (*Piprites pileata*)

Only one example in this family has emerged. The Black-capped Piprites (***Piprites pileata***; Figure 115) builds a spherical nest made of mosses (Cocckle *et al*. 2008).

Figure 115. ***Piprites pileata***, Black-capped Piprites. Members of this species often build their nests of mosses. Photo by Bruno Lima, through Creative Commons.

Aegithalidae – Long-tailed Tits

Wolf (2009) found one species of **Aegithalidae** whose members use bryophytes in their nests (Figure 116) in North America: ***Psaltriparus minimus*** (Bushtit; Figure 117).

Figure 116. ***Psaltriparus minimus***, Bushtit, at mossy nest. Photo by Walter Siegmund, through Creative Commons.

Figure 117. ***Psaltriparus minimus***, Bushtit, pulling on nest materials. Photo by Mikul, through Creative Commons.

Long-Tailed Tit (*Aegithalos caudatus*)

The Long-tailed Tit (***Aegithalos caudatus***; Figure 118-Figure 119) has been separated from other tits and has different feeding and nesting (Figure 120) habits from them. These are not seed-eaters, eating mostly insects from bark crevices and buds. The families stay together, so that a flock will contain only related birds. Relatives that have lost their family members will join the flock. Nests may be tended by 1-8 adults. The female sits on the eggs and the male brings the food. Once the dozen or more babies hatch, helper adults gather food to feed them.

Figure 118. ***Aegithalos caudatus***, Long-tailed Tit, a species whose members build nests with mosses. Photo by drplokta, through Creative Commons.

Figure 119. ***Aegithalos caudatus***, Long-tailed Tit juvenile. Photo by Charles J. Sharp, through Creative Commons.

Figure 120. ***Aegithalos caudatus***, Long-tailed Tit, building her nest in a hedgerow. Photo by Gail Hampshire, through Creative Commons.

The nests are bag-shaped and woven from mosses, bound with spider webs (Burton 1996). The birds cover the outside of the nest with lichens, sometimes substituting plastic and newspaper in areas of human habitation. This nest is insulated on the inside with feathers. The tits may accumulate ~1130 km of travel to gather nest materials. Hansell (2002) reported a nest with 5000-6000 pieces of material, including short-leaved mosses and cocoons intertangled, creating a Velcro effect with a few hundred sprigs of mosses.

Sittidae – Nuthatches

Wolf (2009) found two species of **Sittidae** that use bryophytes in their nests in North America:

Sitta carolinensis (White-Breasted Nuthatch; Figure 121)
Sitta pygmaea (Pygmy Nuthatch; Figure 123)

Figure 121. ***Sitta carolinensis***, White-breasted Nuthatch. Members of this species often include bryophytes in their nests. Photo by Tom Grey, with permission.

Red-Breasted Nuthatch (*Sitta canadensis*)

The Red-breasted Nuthatch (***Sitta canadensis***; Figure 122) builds its nest in tree holes, generally about 2.5 cm in diameter (Heinrich 2009; Moss Musings 2017). Inside the hole it lines the nest with mosses, down, and fibers. In fact, its nest can be recognized from those of woodpeckers because they never line their nests.

Figure 122. ***Sitta canadensis***, Red-breasted Nuthatch, outside the mossy nest in the treehole. Photo by Cephas, through Creative Commons.

Figure 123. ***Sitta pygmaea***, Pygmy Nuthatch, at tree hole. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission

Certhiidae – Holarctic Treecreepers

Wolf (2009) found one species of **Certhidae** whose members use bryophytes in their nests in North America: ***Certhia americana*** (Brown Creeper; Figure 124-Figure 125).

Figure 124. ***Certhia americana***, Brown Creeper, with a beak full of dinner. Photo by Alan and Elaine Wilson, through Creative Commons.

Figure 125. ***Certhia americana***, Brown Creeper, a bird that uses mosses to construct its nests. Photo by Badjoby, through Creative Commons.

Troglodytidae – Wrens

Wolf (2009) found five species of **Troglodytidae** that use bryophytes in their nests in North America:

Salpinctes obsoletus (Rock Wren; Figure 126)
Catherpes mexicanus (Canyon Wren; Figure 127)
Thryothorus ludovicianus (Carolina Wren; Figure 128-Figure 129)
Thryomanes bewickii (Bewick's Wren; Figure 130)
Troglodytes pacificus (Pacific Winter Wren; Figure 133-Figure 135)

Figure 126. ***Salpinctes obsoletus***, Rock Wren. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 127. ***Catherpes mexicanus***, Canyon Wren. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Carolina Wren (*Thryothorus ludovicianus*)

The tiny Carolina Wren (***Thryothorus ludovicianus***; Figure 128) is revered in places like Virginia because of its penchant for eating lots of insects (Harrison 2003). They nest mostly in nooks and crannies, so nest boxes are especially suitable for them. Their nests (Figure 129) often contain mosses, along with leaves, twigs, rootlets, weed stalks, and even cast-off snake skins. Both males and females are the nest builders, but it is she who lines the nest with feathers, hair, fine grass, and moss. These prolific breeders will typically lay a second set of eggs as soon as the young birds leave the nest and may even have a third set.

Figure 128. ***Thryothorus ludovicianus***, Carolina Wren. Members of this species often include mosses in their nests and nest linings. Photo by Ken Thomas, through public domain.

Figure 129. ***Thryothorus ludovicianus***, Carolina Wren, nest with a considerable proportion of mosses, and nestlings. Photo by Marvin, through Creative Commons.

Figure 130. ***Thryomanes bewickii***, Bewick's Wren. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Pacific Wren (*Troglodytes pacificus*) and Winter Wren (*T. hiemalis*)

The Winter Wren has been divided into two species, the Pacific Wren (***Troglodytes pacificus***; Figure 131) and the Winter Wren (***Troglodytes hiemalis***; Figure 132), the eastern species (Toews & Irwin 2008). Where their breeding ranges overlapped, the two species were distinguishable by their songs and lack of cross mating. This evidence was supported by DNA analysis.

Figure 131. ***Troglodytes pacificus***, Pacific Wren. Members of this species often include mosses in their nests. Photo by Tom Talbott, through Creative Commons.

The Pacific Wren (***Troglodytes pacificus***; Figure 131) breeds in the coiferous forests of the Pacific Northwest and constructs a nest almost entirely of mosses (Hejl *et al*. 2002). These wrens protect their nests with a dome and small side entrance (Heinrich 2009). The winter wren places green mosses and small evergreen twigs on the outside. Some birds place their nests in hanging mosses near the ground, but more commonly they place them on tip-up mounds formed by roots of fallen trees.

The Pacific Wren builds a round nest of grass, moss, lichens, or leaves that it stuffs into a hole in a wall, crack in a rock, corner of a building, or tree trunk, but can also put it in bushes or overhanging boughs (Wikipedia 2010).

Eastern Winter Wren (*Troglodytes hiemalis*)

Piers (1897) reported two Winter Wren (***Troglodytes hiemalis***; Figure 132) nests in Nova Scotia, Canada, built in moss that was constantly saturated by water trickling from the bank above. Piers suspected that the second nest was a later one built by the same pair as the first.

Figure 132. ***Troglodytes hiemalis***, Winter Wren. Members of this species often include mosses in their nests. Photo by Paul Stein, through Creative Commons.

Figure 134. ***Troglodytes troglodytes***, Eurasian Wren, feeding young in nest of mosses and other materials. Photo by Sonja Kübelbeck, through Creative Commons.

Eurasian Wren (*Troglodytes troglodytes*)

Nests of the Eurasian Wren (***Troglodytes troglodytes***; Figure 133) can make its nest almost entirely of bryophytes (Figure 134). The Japanese variety (***Troglodytes troglodytes fumigatus***) likewise uses mosses (Figure 135).

Figure 133. ***Troglodytes troglodytes***, Eurasian Wren, a bryophyte nest builder. Photo by Dibyendu Ash, through Creative Commons.

Figure 135. ***Troglodytes troglodytes fumigatus***, Japanese Winter Wren, shown here gathering mosses for its nest. Photo by Alpsdake, through Creative Commons.

Cinclidae – Dippers

Wolf (2009) found one species of **Cinclidae** whose members use bryophytes in their nests in North America: ***Cinclus mexicanus*** (American Dipper; Figure 136-Figure 137), also known as the Water Ouzel.

Figure 136. ***Cinclus mexicanus***, American Dipper, on mosses on the streambank. Photo by Stephen Shunk, through Creative Commons.

Figure 137. ***Cinclus mexicanus***, American Dipper, gathering moss for its nest. Photo by Frank D. Lospalluto, through Creative Commons.

The American Dipper (Figure 136-Figure 137) is the only aquatic songbird in North America (Rosentreter 2014). It is a year-round resident, maintaining its streamside territorial defense year-round. It is known for its diving ability, down to nearly 7 m below the surface, and lives along unpolluted streams with riffles, cascades, and waterfalls. It makes a ball-shaped nest with a side entrance, placed on a cliff face, in a crevice, or under a bridge abutment, positions that help it to avoid predators. The outer shell of this nest is moss with its inner chamber made of pine needles. It uses stream mosses that it dives to obtain, hence they are dripping wet. These are woven into the nest, still wet, and as they dry they tighten the weave and help to affix the nest to its vertical substrate.

I have seen the nest of an American Dipper (Figure 136-Figure 137) in Colorado with the busy expectant mother diving into the water to collect ***Platyhypnidium riparioides*** (Figure 138) for the construction. The nest (Figure 139), wedged under the cliff behind a waterfall, appeared to be made entirely of mosses. Dan Norris (Bryonet 22 November 1995) reports that this bird is indeed selective, using mosses with a different frequency from that found in their habitat.

Figure 138. ***Platyhypnidium riparioides***, a common moss used in nests of the American Dipper (***Cinclus mexicanus***). Photo by Stan Phillips, through public domain.

Figure 139. ***Cinclus mexicanus***, American Dipper, nest of ***Hygrohypnum*** and ***Hygroamblystegium***. Photo by Janice Glime.

Terry McIntosh (Bryonet 2 June 2010) identified mosses in Dipper (***Cinclus mexicanus***; Figure 136-Figure 137) nests from northern Idaho. To his surprise, he found only one species, ***Scouleria marginata*** (Figure 140), a somewhat rare moss, despite the much greater abundance of ***S. aquatica*** (Figure 141). He attributed this selection to the stronger plants of ***S. marginata***. By contrast, Ellen Anderson (Bryonet 2 June 1010) found 30 moss species and 5 liverwort species (plus a few unknowns) in 7 dipper nests in the area around Juneau, Alaska, USA. Most of the nests had only traces of mosses, but nevertheless had quite a few species, numbering 1, 7, 10, 11, 13, 14, and 16 (plus 5 unknowns).

Figure 140. ***Scouleria marginata***, a common component of the American Dipper nests. Photo by Martin Hutten, with permission.

Figure 141. ***Scouleria aquatica***, a common moss that is ignored as nesting material for the American Dipper when ***S. marginata*** is present. Photo by Matt Goff, with permission.

Roger Rosentreter (pers. comm. 20 January 2014) observed numerous American Dipper (***Cinclus mexicanus***; Figure 136-Figure 137) nests on the Payette River, Idaho, USA, reaching up to 2 nests per kilometer. In this case, the nests were composed primarily of the aquatic moss ***Scouleria aquatica*** (Figure 141), an abundant moss in the river.

Brown Dipper (*Cinclus pallasii*)

The Brown Dipper, also known as the Pallas Dipper, (***Cinclus pallasii***; Figure 142), is an Asian dipper that uses mosses in its nests (Nishimura *et al*. 1980).

Figure 142. ***Cinclus pallasii pallasii***, Brown Dipper, a bird that uses aquatic bryophytes in its nests Photo by Alpsdake, through Creative Commons.

Summary

The Passeriformes is the largest order of birds and contains the majority of birds that use bryophytes in their nests. Nevertheless, they seem to be a small proportion of the total species in the order.

In this first part, the members using bryophytes include Tyrant Flycatchers, shrikes, Vireos, Jays and Crows, Swallows, Tits, Piprites, Nuthatches, and Wrens. Among these, the American Dipper is an aquatic bird that often dives for mosses to build its nest. Their selective choices may be energy savings by being able to gather larger bryophyte materials, providing nest-inhabiting food organisms, and in some cases possibly providing more constant moisture.

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BIRD NESTS – PASSERIFORMES, PART 2

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CHAPTER 16-7
BIRD NESTS – PASSERIFORMES, PART 2

Figure 1. ***Grallaricula peruviana*** is a rare bird, shown here with bryophytes in its nest. Photo by Harold Greeney, through Creative Commons

Grallariidae

The Peruvian Antpitta (***Grallaricula peruviana***) is a rare species that uses bryophytes in its nest, as seen in Figure 1.

Regulidae – Kinglets

Wolf (2009) found two species of **Regulidae** that use bryophytes in their nests in North America:

Regulus satrapa (Golden-Crowned Kinglet; Figure 2)
Regulus calendula (Ruby-Crowned Kinglet; Figure 4)

The Golden-crowned Kinglet (***Regulus satrapa***; Figure 2) breeds in the coniferous forests (Figure 3) of the Pacific Northwest and constructs a nest almost entirely of mosses (Ingold & Galati 1997).

Figure 2. ***Regulus satrapa***, Golden-crowned Kinglet. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

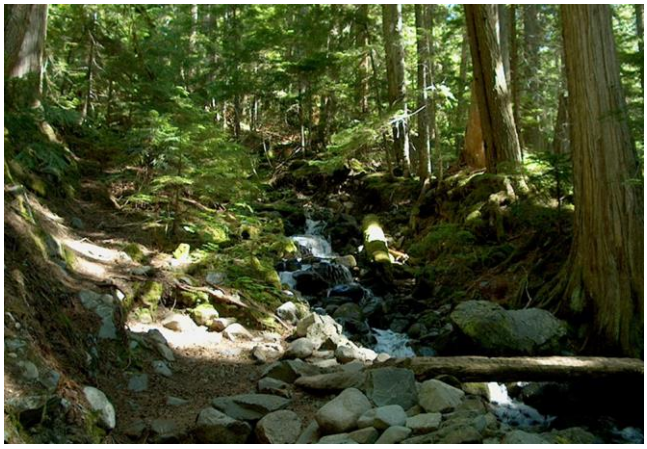

Figure 3. Conifer forest, Garibaldi National Park, BC, home to the Golden-crowned Kinglet, ***Regulus satrapa***. Photo by The Simkin, through public domain.

Figure 4. ***Regulus calendula***, Ruby-crowned Kinglet. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Sylviidae – Old-World Warblers & Gnatcatchers

Wolf (2009) found one species of **Sylviidae** that use bryophytes in their nests in North America: ***Phylloscopus borealis*** (Arctic Warbler; Figure 5).

Figure 5. ***Phylloscopus borealis***, Arctic Warbler. Members of this species use bryophytes in their nests. Photo by Osado, through Creative Commons.

Turdidae – Thrushes

Wolf (2009) found thirteen species of **Turdidae** that use bryophytes in their nests in North America:

Luscinia svecica (Bluethroat; Figure 6)
Oenanthe oenanthe (Northern Wheatear; Figure 7)
Sialia mexicana (Western Bluebird; Figure 8)
Myadestes townsendi (Townsend's Solitaire; Figure 9)
Catharus fuscescens (Veery; Figure 11)
Catharus minimus (Gray-Cheeked Thrush; Figure 12)
Catharus bicknelli (Bicknell's Thrush; Figure 13)
Catharus ustulatus (Swainson's Thrush; Figure 14)
Catharus guttatus (Hermit Thrush; Figure 15-Figure 16)
Turdus pilaris (Fieldfare; Figure 18-Figure 19)
Turdus iliacus (Redwing; Figure 20)
Turdus migratorius (American Robin; Figure 21-Figure 22)
Ixoreus naevius (Varied Thrush; Figure 38)

Figure 6. ***Luscinia svecica***, Bluethroat. Members of this species use bryophytes in their nests. Photo by Andreas Trepte, through Creative Commons.

Figure 7. ***Oenanthe oenanthe***, Northern Wheatear. Members of this species use bryophytes in their nests. Photo by Craig Nash, through Creative Commons.

Figure 8. ***Sialia mexicana***, Western Bluebirds. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 9. ***Myadestes townsendi***, Townsend's Solitaire. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 10. ***Myadestes palmeri***, Puaiohi, nest in a mossy cavity. Photo by Lucas Behnke, with permission.

Figure 11. ***Catharus fuscescens***, Veery. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 12. ***Catharus minimus***, Gray-cheeked Thrush. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 13. ***Catharus bicknelli***, Bicknell's Thrush, on mossy nest. Photo by Kent McFarland, through Creative Commons.

Figure 14. ***Catharus ustulatus***, Swainson's Thrush. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 15. ***Catharus guttatus***, Hermit Thrush. Members of this species use bryophytes in their nests. Photo by Cephas, through Creative Commons.

Figure 16. ***Catharus guttatus***, Hermit Thrush nest and hatchlings. Photo by Per ver Donk, with permission.

Hermit Thrush (*Catharus guttatus*)

Once again, the female is the sole nest-builder in the Hermit Thrush (***Catharus guttatus***; Figure 15-Figure 16) (Cornell Lab of Ornithology). Her bulky handiwork includes mosses in addition to twigs, bark strips, ferns, and grasses. It is not lined with mosses, but rather with conifer needles, rootlets, and plant fibers.

Figure 17. Bird nest in Coast Range of the Pacific Northwest, USA, with mosses still growing. Photo by JeriLynn Peck.

Figure 18. ***Turdus pilaris***, Fieldfare. Members of this species use bryophytes in their nests. Photo by Allan Drewitt, through Creative Commons.

Figure 19. ***Turdus pilaris***, Fieldfare, nest, showing occasional mosses mixed with grasses in the nest. Photo by Andreas Trepte, through Creative Commons.

Figure 20. ***Turdus iliacus***, Redwing. Members of this species use bryophytes in their nests. Photo by Ómar Runólfsson, through Creative Commons.

American Robin (*Turdus migratorius*)

The American Robin (***Turdus migratorius***; Figure 21) uses mosses as a binding material with mud in the inner cup of the nest (Figure 22-Figure 23) (Breil & Moyle 1976). It also uses mosses to line the cup. It seems to have a preference for ***Thuidium delicatulum*** (Figure 24), ***Plagiomnium cuspidatum*** (Figure 25), ***Brachythecium acuminatum*** (Figure 26), ***B. salebrosum*** (Figure 27), and ***Amblystegium varium*** (Figure 28).

Figure 21. ***Turdus migratorius***, American Robin. Members of this species sometimes use mosses as a binder for the mud linings of their nests. Photo by Tom Grey, with permission.

Figure 22. ***Turdus migratorius***, American Robin, on nest. Photo by Jane and Phil, through Creative Commons.

Figure 23. ***Turdus migratorius***, American Robin, nest and young. Photo by Tom Grey, with permission.

Figure 24. ***Thuidium delicatulum***, a moss used as a mud binder to line the Robin's nest. Photo by Janice Glime.

Figure 25. ***Plagiomnium cuspidatum***, a moss used as a mud binder to line the Robin's nest. Photo by Hermann Schachner, through Creative Commons.

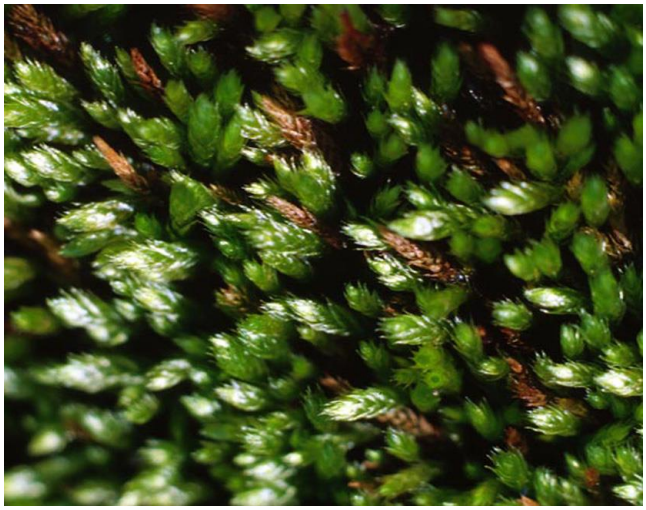

Figure 26. ***Brachythecium acuminatum***, a moss used as a mud binder to line the Robin's nest. Photo by Charles T. Bryson, through Creative Commons.

Figure 27. ***Brachythecium salebrosum*** with capsules, a moss used as a mud binder to line the Robin's nest. Photo by Michael Lüth, with permission.

Figure 28. ***Amblystegium varium***, a moss used as a mud binder to line the Robin's nest. Photo by J. C. Schou, through Creative Commons.

Other members of the genus, such as the Yellow-legged Thrush (***Turdus flavipes***; Figure 29-Figure 30), place bryophytes on the outside of the nest.

Figure 29. ***Turdus flavipes***, Yellow-legged Thrush. Members of this species use mosses on the outsides of their nests. Photo by David R. Santiago, through Creative Commons.

Figure 30. ***Turdus flavipes***, Yellow-legged Thrush, nest with eggs and bryophytes. Photo by David R. Santiago, through Creative Commons.

Chinese Thrush (*Turdus mupinensis*)

In a Chinese study (Zhao *et al*. 2005), nests of the Chinese Thrush (***Turdus mupinensis***; Figure 31) were collected from Xiaolongmen Nature Reserve of Beijing. Nests exhibited seven bryophyte species: ***Anomodon*** sp., ***A. minor*** (Figure 32), ***Entodon*** sp. (Figure 33), ***Lindbergia sinensis*** (see Figure 34), ***Brachythecium*** sp. (see Figure 27), ***Herpetineuron*** sp. (Figure 35), ***Plagiomnium*** sp. (see Figure 25), and ***Myuroclada maximowiczii*** (Figure 36). ***Anomodon minor*** was one of the major nest components.

Figure 31. ***Turdus mupinensis***, Chinese Thrush. Members of this species use mosses in their nests in China. Photo by Charles Lam, through Creative Commons.

Figure 32. ***Anomodon minor***, a species that is used in nests of the Chinese Thrush. Photo by Michael Lüth, with permission.

Figure 33. ***Entodon concinnus***, in a genus that is used in nests of the Chinese Thrush. Photo by Hermann Schachner, through Creative Commons.

Figure 34. ***Lindbergia koelzii*** with capsules, member of a genus used in nests of the Chinese Thrush, ***Turdus mupinensis***. Photo by Michael Lüth, with permission.

Figure 35. ***Herpetineuron toccoae***, member of a genus used in nests of the Chinese Thrush, ***Turdus mupinensis***. Photo by Li Zhang, with permission.

Figure 36. ***Myuroclada maximoviczii***, a species that is used in nests of the Chinese Thrush. Photo by Janice Glime

Blackbird (*Turdus merula*)

The Common Blackbird (***Turdus merula***; Figure 37) makes a bulky cup in its nest, using dry grasses, twigs, stalks, and yes, mosses (Snow 1958). These are plastered with mud or muddy leaves and lined with fine grass, thin dead stems, or rootlets. Mainwaring *et al.* (2014) found that as spring temperatures increased in the lower latitudes, the quantity of mosses used in the nests decreased, suggesting that mosses may be needed for insulation at cooler temperatures (Mainwaring *et al*. 2012).

Figure 37. ***Turdus merula***, Common Blackbird, nesting. Members of this species use bryophytes in their nests. Photo by J. J. Harrison, through Creative Commons.

Nest size of birds is limited on the upper end by becoming more conspicuous and requiring more energy to prepare (Møller 1990). On the small end, it loses insulating ability, stability, and protection to prevent nestlings from falling out of the nest. Møller manipulated nest size of the Blackbird (***Turdus merula***; Figure 37), a species that makes an open-cup woodland nest. When nests were exchanged for smaller or larger nests, there was no effect on nest egg predation by the exchange itself, but larger nests experienced more predation. But real nests that experienced predation were not significantly larger than successful nests. Møller suggested that nest size in nature is dependent on nest site.

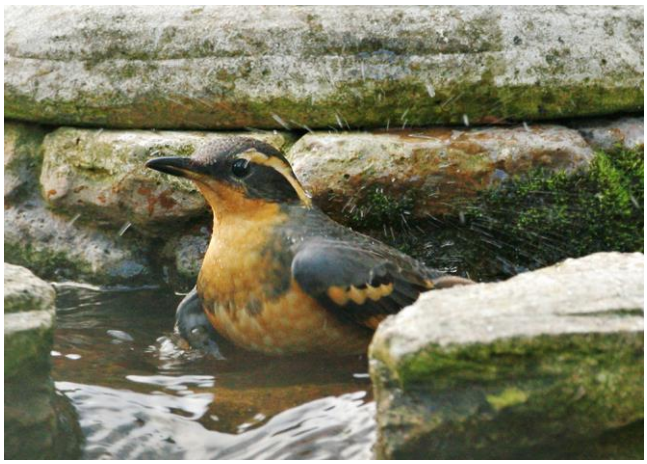

Figure 38. ***Ixoreus naevius***, Varied Thrush. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Muscicapidae – Old World Flycatchers

In the same Chinese study (Zhao *et al*. 2005), nests of three members of this family [Narcissus Flycatcher (***Ficedula narcissina***; Figure 39), Blue-and-white Flycatcher (***Cyanoptila cyanomelana***; Figure 40-Figure 41), Daurian Redstart (***Phoenicurus auroreus***; Figure 42)] were collected from Xiaolongmen Nature Reserve of Beijing. These nests, like those of the Chinese Thrush, exhibited the same seven bryophyte species, with the moss ***Anomodon minor*** (Figure 32) as the main component of nests of all three bird species.

Figure 39. ***Ficedula narcissina***, a Chinese species. Members of this species use bryophytes in their nests. Photo by Alpsdake, through Creative Commons.

Figure 40. ***Cyanoptila cyanomelana***, Blue-and-white Flycatcher male, a species that uses bryophytes to make nests. Photo by Alpsdake, through Creative Commons.

Figure 41. ***Cyanoptila cyanomelana***, Blue-and-white Flycatcher male. Members of this species make their nests with bryophytes. Photo by Alpsdake, through Creative Commons.

Figure 42. ***Phoenicurus auroreus***, Daurian Redstart male. Members of this species use bryophytes in their nests. Photo by Alpsdake, through Creative Commons.

Petroicidae – Australian Robins

Australian Pink Robin (*Petroica rodinogaster*)

The **Australian Pink Robin** (***Petroica rodinogaster***; Figure 43) includes both lichens and mosses in its nest (Figure 44) (Newman & Bratt 1976).

Figure 43. ***Petroica rodinogaster***, Australian Pink Robin. Members of this species build their nests of mosses, especially ***Thuidiopsis sparsa***. Photo by J. J. Harrison, through Creative Commons.

Pharo and Meagher (2011) reported finding a Pink Robin's nest that was made almost entirely from mosses. It was located in a mountain ash forest in Victoria, Australia, in an area that had been lightly burned two years earlier. The nest was "extraordinarily tiny on a branch of *Olearia agrophylla*." The nest was woven exclusively from ***Thuidiopsis sparsa*** (Figure 45) except for a few strands of grass. It is interesting that the moss was not even growing at the site. Therefore, the birds deliberately hunted that moss. The nest has a loose weave, but was strong, with intertwined moss branches. The nest was attached to a branch by numerous strands that were wrapped around the main branch and a smaller branch.

Figure 44. The tiny Australian Pink Robin's nest woven from ***Thuidiopsis sparsa*** (Figure 45), with Emma´s index finger for 'scale.' Photo courtesy of Emma Pharo and David Meagher.

Figure 45. ***Thuidiopsis sparsa***, a moss used to make the nest of the Australian Pink Robin (***Petroica rodinogaster***). Photo through Creative Commons.

Sturnidae – Starlings, *etc.*

Wolf (2009) found one species of **Sturnidae** whose members use bryophytes in their nests in North America: European Starling (***Sturnus vulgaris***; Figure 46-Figure 47).

Figure 46. ***Sturnus vulgaris***, European Starling, the only member of this family that uses mosses in its nest in North America. Photo by Ingrid Taylar, through Creative Commons.

Figure 47. ***Sturnus vulgaris***, European Starling, at nest. Photo by Gynti 46, through Creative Commons.

The European Starling "prefers" to use the wild carrot *Daucus carota* (Figure 48) or the fleabane *Erigeron philadelphicus* (Figure 49) in its nest, both of which have known abilities to suppress parasitic mites in nests (Clark & Mason 1985). We can only wonder if the bryophytes might serve a protective role against mites and other parasites in forested sites.

Figure 48. *Daucus carota* leaves, a species included in nests of the European Starling, presumably to reduce parasite infections. Photo by BioImages, through Creative Commons.

Figure 49. *Erigeron philadelphicus*, a species included in nests of the European Starling, presumably to reduce parasite infections. Photo by Fritzflohr Reynolds, through Creative Commons.

Motacillidae – Wagtails & Pipits

Wolf (2009) found one species of **Motacillidae** whose members use bryophytes in their nests in North America:

Motacilla alba (White Wagtail; Figure 50-Figure 51)
Anthus cervinus (Red-throated Pipit; Figure 54)
Anthus rubescens (American Pipit; Figure 55)

White Wagtail (*Motacilla alba*)

Des Callaghan (Bryonet 23 June 2016) reported that while in the wonderful north of Finland one summer, a fine place for **Splachnaceae**, he noticed an intriguing association between ***Splachnum vasculosum*** (Figure 52-Figure 53) and the insectivorous passerine bird ***Motacilla alba*** (Figure 50). Could the Wagtails be attracted by the odor? Are the mosses a food source? Or do the ***S. vasculosum*** and ***Motacilla alba*** simply like the same habitat? Callaghan recorded this interesting habitat <https://youtu.be/DdlJ7njn3Vg>. Mosses are included in nests (Figure 51) of this wagtail species (Bouglouan 2016).

Figure 50. ***Motacilla alba alba***, White Wagtail. Members of this species use bryophytes in their nests. Photo by Luis Garcia, through Creative Commons.

Figure 51. ***Motacilla alba***, White Wagtail, nest with eggs, a nest that often includes bryophytes. Photo by Walcoford, through Creative Commons.

Figure 52. ***Splachnum vasculosum*** colony, a preferred perch for White Wagtail (***Motacilla alba***). Photo by Des Callaghan, with permission.

Figure 53. ***Splachnum vasculosum*** with capsules and males. Photo by Dick Haaksma, with permission.

Figure 54. ***Anthus cervinus***, Red-throated Pipit. Members of this species use bryophytes in their nests. Photo by Tom Grey with permission.

Figure 55. ***Anthus rubescens***, American Pipit, with insect. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Small Kauai Thrush (*Myadestes palmeri*)

The Small Kauai Thrush or Puaiohi (***Myadestes palmeri***; Figure 56), a small Hawaiian endemic, builds a cavity nest (Figure 57) along a stream bank comprised mostly of bryophytes and tiny ferns, with a weave of fine grass (Kepler & Kepler 1983). The bryophytes trail out of the cavity mouth from the base of the nest, providing an opportunity for these bryophytes to attach and grow on the stream bank. Included bryophytes were the mosses ***Dicranum speirophyllum*** (Figure 58) and ***Campylopus*** sp. (Figure 59) and the liverworts ***Bazzania*** sp. (Figure 60) and ***Lepidozia*** sp. (Figure 61).

Figure 56. ***Myadestes palmeri***, Small Kauai Thrush. Members of this species use bryophytes in their nests. Photo by Eike Wulfmeyer, through Creative Commons.

Figure 57. ***Myadestes palmeri***, Puaiohi, nest with mosses in a cavity. Photo by Lucas Behnke, with permission.

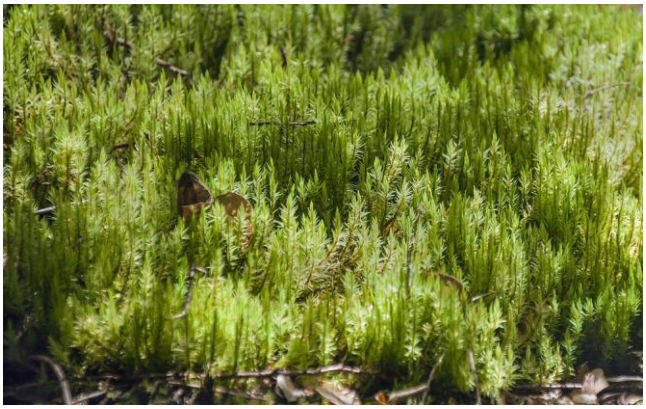

Figure 58. ***Dicranum speirophyllum***, a moss used in the Puaiohi (***Myadestes palmeri***) nest. Photo by John Game, through Creative Commons.

Figure 59. ***Campylopus umbellatus***, a moss representing a genus used in the Puaiohi (***Myadestes palmeri***) nest. Photo by Michael Lüth, with permission.

Figure 60. ***Bazzania*** sp., a leafy liverwort representing a genus used in the Puaiohi (***Myadestes palmeri***) nest. Photo by Ondřej Zicha, through Creative Commons.

Figure 61. ***Lepidozia*** sp., a leafy liverwort representing a genus used in the Puaiohi (***Myadestes palmeri***) nest. Photo by Ken-ichi Uedo, through Creative Commons.

Bombycillidae – Waxwings

Wolf (2009) found two species of **Bombycillidae** that use bryophytes in their nests in North America:

Bombycilla garrulus (Bohemian Waxwing; Figure 62)
Bombycilla cedrorum (Cedar Waxwing; Figure 63-Figure 64)

Figure 62. ***Bombycilla garrulus***, Bohemian Wax Wing. Members of this species use bryophytes in their nests. Photo by Randen Pederson, through Creative Commons.

Cedar Waxwing (*Bombycilla cedrorum*)

The Cedar Waxwing (***Bombycilla cedrorum***; Figure 63) nests in edge habitat, using small evergreens and deciduous trees to hold its nests (Figure 64) (Heinrich 2009). The nest is somewhat similar to that of a Robin in size and rough appearance, but it has no mud lining. The outside typically is decorated with lichens and mosses, probably providing camouflage.

Figure 63. ***Bombycilla cedrorum***, Cedar Waxwing. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 64. ***Bombycilla cedrorum***, Cedar Waxwing, nest with moss & eggs. Photo by Rich Mooney, through Creative Commons.

Peucedramidae – Olive Warbler

Wolf (2009) found one species of **Peucedramidae** that uses bryophytes in their nests in North America: ***Peucedramus taeniatus*** (Olive Warbler; Figure 65).

Figure 65. ***Peucedramus taeniatus***, Olive Warbler. Members of this species use bryophytes in their nests. Photo by Ron Knight, through Creative Commons.

Parulidae – Wood Warblers, *etc.*

Wolf (2009) found 27 species of **Parulidae** that use bryophytes in their nests in North America:

Oreothlypis ruficapilla (Nashville Warbler; Figure 67)
Oreothlypis celata (Orange-crowned Warbler; Figure 66, Figure 68)
Oreothlypis virginiae (Virginia's Warbler; Figure 69)
Dendroica coronata (Yellow-rumped Warbler; Figure 70)
Setophaga pitiayumi (Tropical Parula; Figure 71)
Setophaga magnolia (Magnolia Warbler; Figure 72)
Setophaga tigrina (Cape May Warbler; Figure 73)
Setophaga caerulescens (Black-throated Blue Warbler; Figure 74-Figure 75)
Setophaga nigrescens (Black-throated Gray Warbler; Figure 76)
Setophaga virens (Black-throated Green Warbler; Figure 77)
Setophaga townsendi (Townsend's Warbler; Figure 78)
Setophaga occidentalis (Hermit Warbler; Figure 79)
Setophaga kirtlandii (Kirtland's Warbler; Figure 80)
Setophaga striata (Blackpoll Warbler; Figure 81)
Setophaga cerulea (Cerulean Warbler; Figure 82)
Setophaga ruticilla (American Redstart; Figure 83)
Setophaga citrina (Hooded Warbler; Figure 84-Figure 85)
Protonotaria citrea (Prothonotary Warbler; Figure 86)
Helmitheros vermivorum (Worm-eating Warbler; Figure 88)
Limnothlypis swainsonii (Swainson's Warbler; Figure 90)
Seiurus aurocapilla (Ovenbird; Figure 91-Figure 92)
Parkesia noveboracensis (Northern Waterthrush; Figure 97)
Parkesia motacilla (Louisiana Waterthrush; Figure 98)
Oporornis agilis (Connecticut Warbler; Figure 99)
Geothlypis trichas (Common Yellowthroat; Figure 100)
Cardellina pusilla (Wilson's Warbler; Figure 101)
Cardellina canadensis (Canada Warbler; Figure 102)

Figure 66. ***Oreothlypis celata***, Orange-crowned Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 67. ***Oreothlypis ruficapilla***, Nashville Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 68. ***Oreothlypis celata***, Orange-crowned Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 69. ***Oreothlypis virginiae***, Virginia's Warbler. Members of this species use bryophytes in their nests. Photo by Jerry Oldenettel, through Creative Commons.

Figure 70. ***Dendroica coronata***, Yellow-rumped Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 71. ***Setophaga pitiayumi***, Tropical Parula. Members of this species use bryophytes in their nests. Photo by Dario Sanchez, through Creative Commons.

Figure 72. ***Setophaga magnolia***, Magnolia Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 73. ***Setophaga tigrina***, Cape May Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 74. ***Setophaga caerulescens***, Black-throated Blue Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 75. ***Setophaga caerulescens***, Black-Throated Blue Warbler, feeding young in nest. Members of this species use bryophytes in their nests. Photo by USFWS, through public domain.

Figure 76. ***Setophaga nigrescens***, Black-throated Gray Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 77. ***Setophaga virens***, Black-throated Green Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Townsend's Warbler (*Setophaga townsendi*)

Some birds have very specific uses for the bryophytes. The Townsend's Warbler (***Setophaga townsendi***; Figure 78) lines its nest with the **setae** (stalks of moss capsules) of mosses (and hair) (Baicich & Harrison 2005).

Figure 78. ***Setophaga townsendi***, Townsend's Warbler. Members of this species use bryophytes in their nests. Photo by Jerry Oldenettel, through Creative Commons.

Figure 79. ***Setophaga occidentalis***, Hermit Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Kirtland's Warbler (*Setophaga kirtlandii*)

In Michigan the Kirtland's Warbler (***Setophaga kirtlandii***; Figure 80) harvests moss sporophytes (Brian Dykstra, pers. comm. 10 December 2011).

Figure 80. ***Setophaga kirtlandii***, Kirtland's Warbler, in Jack pine. Members of this species harvest moss sporophytes, presumably for their nests. Photo by Ron Austing, through Creative Commons.

Figure 81. ***Setophaga striata***, Blackpoll Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 82. ***Setophaga cerulea***, Cerulean Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 83. ***Setophaga ruticilla***, American Redstart. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 84. ***Setophaga citrina***, Hooded Warbler. Members of this species use bryophytes in their nests. Photo by Mary Elliott, through Creative Commons.

Figure 85. ***Setophaga citrina***, Hooded Warbler. Members of this species use bryophytes in their nests. Photo by USFSW, through public domain.

Prothonotary Warbler (*Protonotaria citrea*)

The Prothonotary Warbler (***Protonotaria citrea***; Figure 86) nests in abandoned holes made by woodpeckers. Although it sometimes uses few mosses in the actual nest, it does build it on a bed of bryophytes, both mosses and liverworts (Bent 1953; Petit 1989; Blem & Blem 1992, 1994). When building in a nest box, the mosses go in first to form the bed. Then the nest is built on top of them. The bryophytes remain moist, but the cup is not. Blem and Blem found that 75-80% of the dry mass of the nests they studied is composed of mosses and liverworts. They identified five species of mosses and two liverworts (Table 1), with the moss ***Anomodon attenuatus*** (Figure 87) predominating. They suggested that the bryophytes maintain the needed environment within the nest cavity (*e.g.* Mertens 1977a, b). In addition to ameliorating the moisture, bryophytes may serve to reduce pathogens and parasites (Clark & Mason 1985). I have seen several pictures of these nests, but unfortunately I could not find the name of the photographer on those sites.

Figure 86. ***Protonotaria citrea***, Prothonotary Warbler, a species that uses a bed of bryophytes under its nest. Photo by David Inman, through Creative Commons.

Table 1. Occurrence of bryophytes in Prothonotary Warbler (***Protonotaria citrea***) nests in nest boxes along the James River, Virginia, USA. From Blem & Blem 1994.

	Percent occurrence			
Species	**Top**	**Mid-dle**	**Bot-tom**	**Total**
Mosses				
Anomodon attenuatus	97.3	96.4	91.4	95.0
Haplocladium microphyllum	20.6	13.4	21.0	18.3
Amblystegium varium	6.7	7.6	1.3	5.2
Plagiomnium cuspidatum	2.7	1.3	3.1	2.4
Thuidium delicatulum	0.4	1.3	0.0	0.6
Liverworts				
Porella platyphylla	21.9	27.3	32.1	27.1
Frullania eboracensis	0.4	0.8	0.8	0.7

Figure 87. ***Anomodon attenuatus*** with capsules, the primary bryophyte used in the nest of the Prothonotary Warbler. Photo by Bob Klips, with permission.

Worm-eating Warbler (*Helmitheros vermivorum*)

The Worm-eating Warbler (***Helmitheros vermivorum***; Figure 88) uses stems of ***Polytrichum*** in its nest (Figure 89) (Baicich & Harrison 2005).

Figure 88. ***Helmitheros vermivorum***, Worm-eating Warbler. Members of this species use bryophytes in their nests. Photo by Jerry Oldenettel, through Creative Commons.

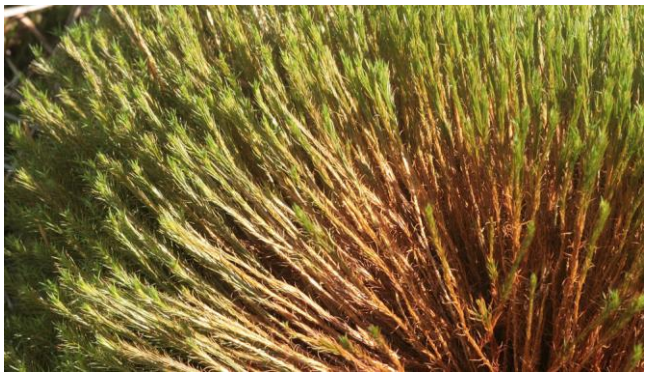

Figure 89. ***Polytrichum commune***, a moss in a genus used in nests of ***Helmitheros vermivorum***, Worm-eating Warblers. Photo by Hermann Schachner, through Creative Commons.

Figure 90. ***Limnothlypis swainsonii***, Swainson's Warbler. Members of this species use bryophytes in their nests. Photo by Carol Foil, through Creative Commons.

Ovenbird (*Seiurus aurocapilla*)

The seclusive Ovenbird (***Seiurus aurocapilla***; Figure 91-Figure 92) may be dependent on mosses in its environment. Apfelbaum and Haney (1981) reported the disappearance of the Ovenbird from a severely burned Jack pine (***Pinus banksiana***; Figure 93-Figure 95) forest in the Great Lakes area. In that fire, ~80% of the feather moss (Figure 96) communities suffered severe loss due to the fire. But other factors related to the fire may have caused them to disappear.

Figure 91. ***Seiurus aurocapilla***, Ovenbird, a ground nester that may be dependent on mosses in its habitat. Photo by Tom Grey, with permission.

Figure 92. ***Seiurus aurocapilla***, Ovenbird, nest and nestlings. Photo by Fredlyfish4, through Creative Commons.

Figure 93. Jack pine (***Pinus banksiana***) healthy forest. Photo by M. Ricon, through Creative Commons.

Figure 94. ***Pinus banksiana*** after fire in Baraga, Michigan, USA. Photo by Janice Glime.

Figure 95. Burned moss in Jack pine forest, Baraga, MI. Photo by Janice Glime.

Figure 96. ***Pleurozium schreberi***, a feather moss that covers vast areas of ground in conifer forests. Photo by Sture Hermansson, with online permission.

Figure 97. ***Parkesia noveboracensis***, Northern Waterthrush. Some members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 98. ***Parkesia motacilla***, Louisiana Waterthrush. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 99. ***Oporornis agilis***, Connecticut Warbler. Members of this species use bryophytes in their nests. Photo from connecticut-warbler-audubon-field-guide, free stock photos.

Figure 100. ***Geothlypis trichas***, Common Yellowthroat. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 101. ***Cardellina pusilla***, Wilson's Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 102. ***Cardellina canadensis***, Canada Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Furnariidae – Neotropical Ovenbirds

In the Neotropical ovenbirds (**Furnariidae**) moss use in nesting materials seems to have at least somewhat followed evolutionary lines (Zyskowski & Prum 1999). ***Premnoplex brunnescens*** (Figure 103) builds a domed nest of mosses (Figure 104-Figure 106). This nest may be suspended from structures such as logs.

Figure 103. ***Premnoplex brunnescens***, Spotted Barbtail. Members of this species build domed nests of bryophytes. Photo by Murray Cooper, through Creative Commons.

Figure 104. ***Premnoplex brunnescens***, Spotted Barbtail, nest of bryophytes. Photo by Juan Ignacio Areta, through Creative Commons.

Figure 105. ***Premnoplex brunnescens***, Spotted Barbtail, nest of bryophytes. Photo by Harold Greeney, through Creative Commons.

Figure 106. ***Premnoplex brunnescens***, Spotted Barbtail, nest of bryophytes. Photo by Gustavo Londoño, through Creative Commons.

In the Neotropical ***Cranioleuca albiceps*** group (see Figure 107), ***Margarornis*** (Figure 108-Figure 109), ***Premnoplex brunnescens*** (Figure 103-Figure 106), ***Siptornis*** (Figure 110), and Plain Softtail, (***Phacellodomus fusciceps***; see Figure 111), a "pensile" nest (Figure 109) is constructed (Zyskowski & Prum 1999). This is a large nest with a small brood chamber that is entered from below. It is constructed from top down by draping long strands of green mosses or strips of other plant material. The nest hangs down from a log or rocky overhang and in ***Premnoplex brunnescens*** it may also hang from vines. ***Asthenes*** (Figure 112) species construct an ovoid nest (Figure 113) using fresh ***Sphagnum*** (Figure 114). An outer shell of herbaceous stems loosely surrounds it.

Figure 107. *Cranioleuca pallida*, Pallid Spinetail, in Brazil. Members of the ***Cranioleuca albipes*** group build pensile nests that incorporate bryophytes. Photo by Ciro Albano, through Creative Commons.

Figure 108. ***Margarornis rubiginosus***, Ruddy Treerunner. Members of this species make nests among bryophytes. Photo by Carmelo López Abad, through Creative Commons.

Figure 109. ***Margarornis squamiger***, Pearled Treerunner, pensile nest imbedded in bryophytes and rootlets with an entrance at the bottom. Photo by Harold Greeney, through Creative Commons.

Figure 110. ***Siptornis striaticollis***, Spectacled Prickletail, nest. Photo by Harold Greeney, through Creative Commons.

Figure 111. ***Phacellodomus ruber***, Greater Thornbird. Members of this species construct their nests using mosses and other plant material. Photo by Cláudio Dias Timm, through Creative Commons.

Figure 112. ***Asthenes anthoides***, Austral Canastero, Members of ***Asthenes*** incorporate bryophytes in their nests. Photo by Collaerts brothers, through Creative Commons.

Figure 113. ***Asthenes flammulata,*** Many-striped Canastero nest in Ecuador. Photo by Harold Greeney, through Creative Commons.

Figure 114. ***Sphagnum austinii***, member of a genus used in nests of ***Asthenes***. Stan Phillips, through public domain

White-browed Spinetail (*Hellmayrea gularis*)

In the Andean cloud forests, the White-browed Spinetail (***Hellmayrea gularis***; Figure 115) nests (Figure 116) were embedded in hanging masses of epiphytic mosses, but rather than being pendulous, the nests were supported from below or from the sides by stems (Greeney & Zyskowski 2008). These nests were ball-shaped with a side entrance. The exterior consisted of green moss, whereas the internal side consisted of dry bamboo leaves. The nest was lined with soft materials, either *Tillandsia* seed down (Figure 117) or tree-fern scales (Figure 118).

Figure 115. ***Hellmayrea gularis***, White-browed Spinetail, bringing grub to nest. Photo by Murray Cooper, through Creative Commons.

Figure 116. ***Hellmayrea gularis***, White-browed Spinetail, nest embedded in mosses. Photo by Harry Greeney, through Creative Commons.

Figure 117. *Tillandsia schiedeana*; the down (coma) of seeds in this genus are used in the nests of the White-browed Spinetail (***Hellmayrea gularis***). Photo by Roger Culos, through Creative Commons.

Figure 118. Hairy tree fern frond showing scales and hairs used in nests of the White-browed Spinetail, ***Hellmayrea gularis***. Photo by Janna Schreier <janna@jannaschreier.com>, with permission.

Thraupidae – Tanagers & Honeycreepers

Wolf (2009) found one species of **Thraupidae** that use bryophytes in their nests in North America: ***Piranga ludoviciana*** (Western Tanager; Figure 119).

Figure 119. ***Piranga ludoviciana***, Western Tanager. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Yellow-bellied Dacnis (*Dacnis flaviventer*)

The Yellow-bellied Dacnis (***Dacnis flaviventer***; Figure 120) is a bird of the high canopy and nests in this genus are largely unknown. Sheldon and Greeney (2008) were fortunate enough to find one nest and describe it. Although most of the nest is made of ferns, mosses comprise the sparse lining of the cup, woven with rootlets and dried grasses in a circular fashion.

Figure 120. ***Dacnis flaviventer***, Yellow-bellied Dacnis male. Members of this species line their nests with mosses. Photo by Patty McGann, through Creative Commons.

Emberizidae – Emberizines

Wolf (2009) found thirteen species of **Emberizidae** that use bryophytes in their nests in North America:

Spizella arborea (American Tree Sparrow; Figure 121-Figure 122)
Pooecetes gramineus (Vesper Sparrow; Figure 123-Figure 124)
Ammodramus savannarum (Grasshopper Sparrow; Figure 125-Figure 126)
Passerella iliaca (Fox Sparrow; Figure 127)
Melospiza lincolnii (Lincoln's Sparrow; Figure 128)
Zonotrichia albicollis (White-Throated Sparrow; Figure 129)

Zonotrichia querula (Harris's Sparrow; Figure 130)
Zonotrichia leucophrys (White-Crowned Sparrow; Figure 131-Figure 132)
Zonotrichia atricapilla (Golden-Crowned Sparrow; Figure 133)
Junco hyemalis (Dark-Eyed Junco; Figure 134-Figure 137)
Junco phaeonotus (Yellow-Eyed Junco; Figure 138)
Calcarius lapponicus (Lapland Longspur; Figure 139-Figure 140)
Plectrophenax nivalis (Snow Bunting; Figure 141)

Figure 121. ***Spizella arborea***, American Tree Sparrow. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 122. ***Spizella arborea***, American Tree Sparrow, nest and nestlings. Photo from USFWS, through public domain.

Figure 123. ***Pooecetes gramineus***, Vesper Sparrow. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 124. ***Pooecetes gramineus***, Vesper Sparrow, nestlings in nest, begging. Photo by Kati Fleming, through Creative Commons.

Figure 125. ***Ammodramus savannarum***, Grasshopper Sparrow. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 126. ***Ammodramus savannarum***, female Grasshopper Sparrows in nest. Photo by Janet Ruth, USGS, through public domain.

Figure 127. ***Passerella iliaca***, Fox Sparrow. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 128. ***Melospiza lincolnii***, Lincoln's Sparrow. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 129. ***Zonotrichia albicollis***, White-throated Sparrow. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 130. ***Zonotrichia querula***, Harris's Sparrow. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 131. ***Zonotrichia leucophrys***, White-crowned Sparrow. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 132. ***Zonotrichia leucophrys***, White-Crowned Sparrow, nest with eggs. Photo by Jacob W. Franks, NPS, through public domain.

Figure 133. ***Zonotrichia atricapilla***, Golden-crowned Sparrow. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Junco (*Junco hyemalis*)

The common Junco (***Junco hyemalis***; Figure 134) spends its winter in snowy places in the northern USA, then returns to even more northern locations in late April to build its nest of grasses, moss, and rootlets nestled in a mossy bank (Figure 135) or along a woodland trail (Figure 136) (Harrison 2000). Ken-ichi Ueda found a similar construction in a stream bank (Figure 137).

Figure 134. ***Junco hyemalis***, Dark-eyed Junco. Members of this species use bryophytes in their nests. Photo by USFWS, through public domain.

Figure 135. ***Junco hyemalis***, Dark-eyed Junco, nest with eggs in mossy cavity. Photo from USFWS, through public domain.

Figure 136. ***Junco hiemalis***, Dark-eyed Junco, nest with ***Hedwigia ciliata***. Photo courtesy of Susan Studlar.

Figure 137. Junco nest in mossy stream embankment. Photo by Ken-ichi Ueda, through Creative Commons.

Figure 138. ***Junco phaeonotus***, Yellow-eyed Junco. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 139. ***Calcarius lapponicus***, Lapland Longspur. Members of this species use bryophytes in their nests. Photo by Ómar Runólfsson, through Creative Commons.

Figure 140. ***Calcarius lapponicus***, Lapland Longspur, nest. Photo by James K. Lindsey, with permission.

Figure 141. ***Plectrophenax nivalis***, Snow Bunting,. Members of this species use bryophytes in their nests. Photo by Cephas, through Creative Commons.

Eastern Towhee (*Pipilo erythrophthalmus*)

The Eastern Towhee (***Pipilo erythrophthalmus***; Figure 142), formerly the Rufous-sided Towhee, nest (Figure 143) is somewhat unusual in its moss component. The lining can consist of a single material – 70-80 strands of ***Polytrichum ohioense*** setae (Figure 144) interwoven to form the lining (Breil & Moyle 1976). A few had **gametophyte** (leafy plants) fragments or capsules attached.

Figure 142. ***Pipilo erythrophthalmus***, Eastern Towhee male. Members of this species that use setae of ***Polytrichum ohioense*** (Figure 144) to line their nests in the southeastern USA. Photo by Bill Thompson, through Creative Commons.

Figure 143. ***Pipilo erythrophthalmus***, Eastern Towhee, nest. Photo by Bill Thompson, through Creative Commons.

Figure 144. ***Polytrichum ohioense*** showing setae that can be used to line the nests of the Eastern Towhee (***Pipilo erythrophthalmus***). Photo by Bob Klips, with permission.

Savannah Sparrow (*Passerculus sandwichensis*)

Mosses comprised more than 30% of the mass of nesting materials in the southeastern Ontario, Canada, populations of the ground-nesting Savannah Sparrow (***Passerculus sandwichensis***; Figure 145-Figure 146) compared to less than 20% in the northern Manitoba populations (Crossman *et al*. 2011). Although these differences were not statistically significant (p >0.05), they may reflect the somewhat smaller, more compact nests in the northern Manitoba population. But does it vary with climate as an adaptive means to maintain more favorable temperatures? Indeed Crossman and coworkers found that whereas the external dimensions of the nest did not differ, the inner nest cup was significantly shallower in northern Manitoba, indicating a thicker bottom that could provide greater insulation in the northern Manitoba population. But alas, we do not know if the mosses contributed to any insulating properties.

Figure 145. ***Passerculus sandwichensis***, Savannah Sparrow, a species for which moss usage and nest size vary with latitude. Photo by Tom Grey, with permission.

Figure 146. ***Passerculus sandwichensis***, Savannah Sparrow, nest with eggs. Photo by James K. Lindsey, with permission.

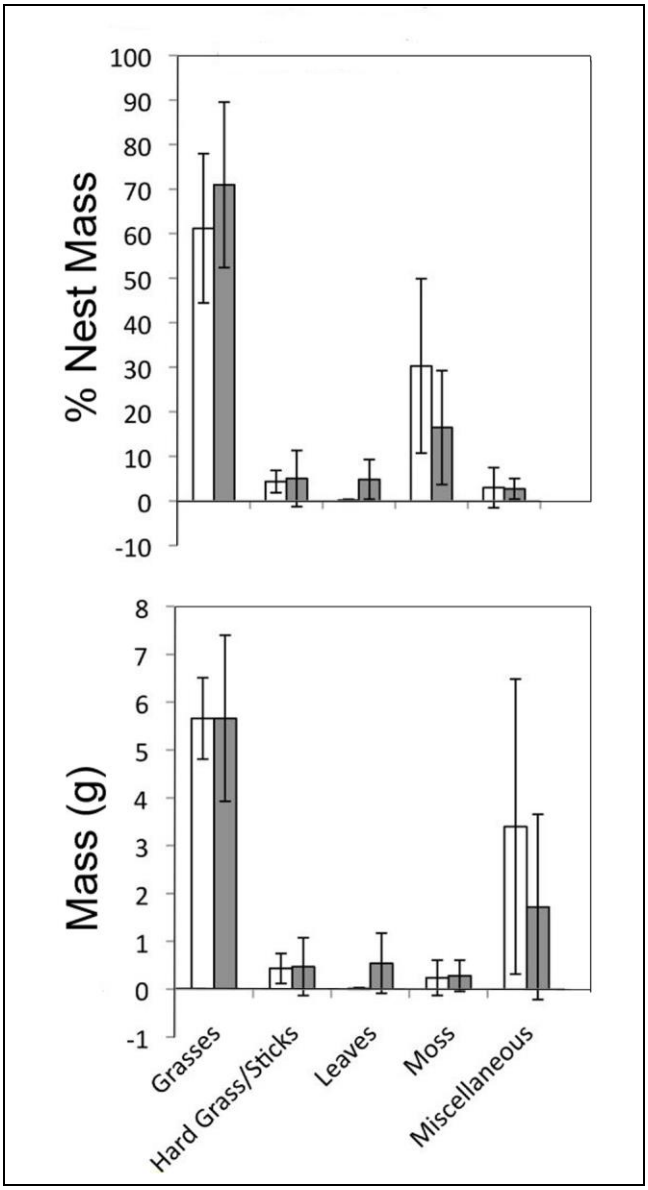

Figure 147. Nest composition for materials comprising ≥1% of nest mass of the Savannah Sparrows (***Passerculus sandwichensis***; Figure 145-Figure 146) that bred in southeastern Ontario (white bars) and northern Manitoba (grey bars). Bars represent dominant nesting materials ≥1% of nest dry mass. Those materials comprising <1% of nest mass are combined into miscellaneous. Plots show means (± SD). Modified from Crossman *et al*. 2011.

Ipswitch Sparrow (*Passerculus sandwichensis princeps*)

The Ipswich Sparrow (***Passerculus sandwichensis princeps***; Figure 148) is endemic on Sable Island, Nova Scotia, Canada. Dwight (1895; Mills & Lucas 2016) notes that mosses are included in their nests. As is typical in many kinds of nests, these are composed of two distinct parts. The outer shell is made of coarse materials including dead weed stalks, grasses, and "little bits" of mosses. The inner cup has finer materials, including hair of ponies and cattle, grasses, and sedges. These nests differ from those of the Savannah Sparrow on the mainland, where the nest is scraped out to form hollows and contain no mosses or lining materials.

Figure 148. ***Passerculus sandwichensis princeps***, Ipswich Sparrow. Members of this subspecies are endemic to Nova Scotia and often include mosses in the linings of their nests. Photo through Creative Commons.

Icteridae – Blackbirds, Orioles, *etc.*

Wolf (2009) found three species of **Icteridae** that use bryophytes in their nests in North America:

Euphagus carolinus (Rusty Blackbird; Figure 149-Figure 150)
Euphagus cyanocephalus (Brewer's Blackbird; Figure 151)
Icterus bullockii (Bullock's Oriole; Figure 152-Figure 154)

Figure 149. ***Euphagus carolinus***, Rusty Blackbird. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 150. ***Euphagus carolinus***, Rusty Blackbird, female on nest. Photo by USFWS, through public domain.

Figure 151. ***Euphagus cyanocephalus***, male Brewer's Blackbird. Members of this species use bryophytes in their nests. Photo by Alan D. Wilson, through Creative Commons.

Figure 152. ***Icterus bullockii***, Bullock's Oriole. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 153. ***Icterus bullockii***, Bullocks Orioles. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 154. Hanging nest of ***Icterus bullockii***, Bullock's Oriole. Members of this species use bryophytes in their nests. Photo by Eugene Zelenko through Creative Commons.

Fringillidae – Fringilline Finches

Wolf (2009) found eleven species of **Fringillidae** that use bryophytes in their nests in North America:

Leucosticte tephrocotis (Gray-crowned Rosy Finch; Figure 155)
Leucosticte atrata (Black Rosy Finch; Figure 156)
Leucosticte australis (Brown-capped Rosy Finch; Figure 157)
Pinicola enucleator (Pine Grosbeak; Figure 158)
Carpodacus purpureus (Purple Finch; Figure 159-Figure 160)
Loxia curvirostra (Red Crossbill; Figure 161)
Loxia leucoptera (White-winged Crossbill; Figure 162)
Carduelis flammea (Common Redpoll; Figure 163-Figure 164)
Carduelis pinus (Pine Siskin; Figure 165)
Carduelis psaltria (Lesser Goldfinch; Figure 166-Figure 167)
Coccothraustes vespertinus (Evening Grosbeak; Figure 168)

Figure 155. ***Leucosticte tephrocotis***, Gray-crowned Rosy Finch, in British Columbia. Members of this species use bryophytes in their nests. Photo by Nigel, through Creative Commons.

Figure 156. ***Leucosticte atrata***, Black Rosy Finch, in British Columbia. Members of this species use bryophytes in their nests. Photo by Peter Wallack, through Creative Commons.

Figure 157. ***Leucosticte australis***, Brown-capped Rosy Finch. Members of this species use bryophytes in their nests. Photo by Dominic Sherony, through Creative Commons.

Figure 158. ***Pinicola enucleator***, Pine Grosbeak. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 159. ***Carpodacus purpureus***, Purple Finch. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 160. ***Carpodacus purpureus***, Purple Finch, feeding young in nest. Photo by Robert Kuhn <www.theonlinezoo>, through Creative Commons.

Figure 161. ***Loxia curvirostra***, Red Crossbill. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 162. ***Loxia leucoptera***, White-winged Crossbill male. Members of this species use bryophytes in their nests. Photo by John Harrison, through Creative Commons.

Figure 163. ***Carduelis flammea***, Cock Redpoll. Members of this species use bryophytes in their nests. Photo by Gail Hampshire, through Creative Commons.

Figure 164. ***Carduelis flammea***, Common Redpoll, feeding young in nest. Note mosses woven into the exterior. Photo by Peter Reese, through nzbirdsonline.org.nz, online permission.

Pine Siskin (*Carduelis pinus*)

The Pine Siskin (***Carduelis pinus***; Figure 165) breeds from SE Alaska to Newfoundland (Van Woerkom 1999). They remain year-round along the Pacific Coast where they prefer coniferous forests and mixed woodlands. Their nests are saucer-shaped, constructed with twigs, grasses, strips of bark, and lichens. These are lined with hair, moss, thistledown, or feathers. The young leave the nest in two weeks. The female remains in the nest with the young and the male brings food for her and she regurgitates food for the nestlings.

Figure 165. ***Carduelis pinus***, Pine Siskin. Members of this species use bryophytes in their nests. Photo by Cephas, through Creative Commons.

Figure 166. ***Carduelis psaltria***, Lesser Goldfinch male. Members of this species use bryophytes in their nests. Photo by Gail Hampshire, through Creative Commons.

Figure 167. ***Carduelis psaltria***, Lesser Goldfinch female. Members of this species use bryophytes in their nests. Photo by Alan D. Wilson, through Creative Commons.

Figure 168. ***Coccothraustes vespertinus***, Evening Grosbeaks, getting drink. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Brambling (*Fringilla montifringilla*)

The Brambling (***Fringilla montifringilla***; Figure 169) has a name that literally means "mountain fringilla" (Wikipedia 2016a) It lives in birchwoods and coniferous forests of northern Europe and Asia. It is migratory, overwintering in southern Europe, north Africa, north India, northern Pakistan, China, and Japan. This small passerine bird uses mosses, hair, and wool to line its nest (Stevenson 1987).

Figure 169. ***Fringilla montifringilla***, Brambling. Members of this species use bryophytes in their nests. Photo by M. Nishimura, through Creative Commons.

Chaffinch (*Fringilla coelebs*)

Based on the pictures I have seen, the Chaffinch (***Fringilla coelebs***; Figure 170) commonly uses bryophytes extensively in its nests (Figure 171-Figure 173).

Figure 170. ***Fringilla coelebs***, Chaffinch female. Members of this species use bryophytes in their nests. Photo by James K. Lindsey, with permission.

Figure 171. ***Fringilla coelebs***, Chaffinch, nest made largely of bryophytes. Photo by James K. Lindsey, with permission.

Figure 172. ***Fringilla coelebs***, Chaffinch, nest with extensive use of bryophytes. Photo by Trachemys, through Creative Commons.

Figure 173. ***Fringilla coelebs***, Chaffinch, nest of bryophytes. Photo by Nottsexminer, through Creative Commons.

Poo-uli (*Melamprosops phaesoma*)

The Poo-uli (***Melamprosops phaeosoma***; Figure 174) is a Hawaiian honeycreeper, a rare species nearing extinction (Engilis *et al*. 1996;). Its nest is an open cup which it constructs from twigs and bryophytes. Coarse mosses are used to fill the spaces between the twigs, reminiscent of human uses of mosses for chinking. Both nests examined contained ***Homaliodendron flabellatum*** (Figure 175), ***Thuidium plicatum***, ***Trachypodopsis auriculata*** (Figure 176). One nest also contained ***Aerobryopsis wallichi***; the other contained ***Floribundaria floribunda*** (Figure 177). The lining is made from fern rootlets. Leaves and stems of graminoids and dicots constituted less than 5% of the material in the nest.

Figure 174. ***Melamprosops phaeosoma***, Poo-uli, a rare species. Members of this species use bryophytes in their nests. Photo by Paul E. Baker, through public domain.

Figure 175. ***Homaliodendron flabellatum***, a species used in the nest of the Poo-uli, ***Melamprosops phaeosoma***. Photo by Yao, through Creative Commons.

Figure 176. ***Trachypodopsis auriculata***, a species used in the nest of the Poo-uli, ***Melamprosops phaeosoma***. Photo through Creative Commons.

Figure 177. ***Floribundaria floribunda***, a species used in the nest of the Poo-uli, ***Melamprosops phaeosoma***. Photo through Creative Commons.

Kākāwahie or Moloka'i Creeper (*Paroreomyza flammea*)

Kākāwahie or Moloka'i Creeper (***Paroreomyza flammea***; Figure 178) is an extinct member of this family, originally native to Hawaii (Wikipedia 2016b). It fed primarily on larvae of beetles and Lepidoptera. The birds constructed a nest with an exterior of moss.

Figure 178. ***Paroreomyza flammea***, Moloka'i Creeper (bottom 2 birds), an extinct bird that placed mosses on the exterior of the nest. Photo by Frederick William Frohawk, through Creative Commons.

Leiothrichidae – Laughing Thrushes

Nilgiri Laughing Thrush (*Trochalopteron cachinnans*)

The Nilgiri Laughing Thrush (***Trochalopteron cachinnans***; Figure 179) gathers bryophytes and uses them to build nests. These typically include several species.

Figure 179. ***Trochalopteron cachinnans***, Nilgiri Laughing Thrush. Members of this species use bryophytes in their nests. Photo by Antony Grossy, through Creative Commons.

Ptilonorhynchidae – Bower Birds

Bower Birds have some of the most interesting mating behavior in the bird world. The male bower bird builds a mating tunnel or similar structure to attract his mate (Hansell 2000). This tunnel typically involves a column of sticks around a stem of a sapling or small fern that serves

as a central feature of the bower. Depending on the species, this bower is often decorated with blue objects.

Vogelkop Bowerbird (*Amblyornis inornata*)

The Vogelkop Bowerbird (***Amblyornis inornata***; Figure 180) of New Guinea and Australia builds a conical hut (Figure 181) up to 2 m wide by 3.3 m high (Uy 2002). The pathway to this doorway of this hut is paved with a carpet of moss. This mossy path is decorated with rhododendron flowers, red ginger berries, iridescent blue beetle carapaces, and feathers from other birds. One isolated population in the Kumawa Mountains builds a spire around saplings, forming an umbrella-like structure over a circular mossy foundation.

Figure 180. ***Amblyornis inornata***, Vogelkop Bowerbird. Members of this species pave the pathways to their huts with mosses. Photo by Carmelo López Abad, through Creative Commons.

Figure 181. ***Amblyornis inornata***, Vogelkop Bowerbird, bower with hut. Photo by Carmelo López Abad, through Creative Commons.

The females of the Vogelkop Bowerbird (***Amblyornis inornata***; Figure 180) are slightly smaller than the males (Lananhbirds 2010). The dull coloration is offset by one of the largest and most colorful bowers. The bower is a 100-cm-high cone with a 160-cm diameter. Like many human homes, the birds have a front lawn that is cleared and carpeted with mosses. The lawn is the site of flowers, fruit, beetle wings, dead leaves, and other objects in an "artistic" arrangement. Males maintain these objects, replacing ones that are no longer suitable or replacing ones stolen by neighbors.

Because of the dull plumage, this species is of less interest than other Bowerbird species and therefore is of Least Concern on the IUCN Red List (BirdLife International 2004). That is, if humans don't like it, they don't hunt it for its plumage.

Macgregor's Bowerbird (*Amblyornis macgregoriae*)

The Macgregor's Bowerbird (***Amblyornis macgregoriae***; Figure 182) contrasts with the Vogelkop Bowerbird by having the "simplest" bower (Hansell 2000). It builds a maypole tower that is 2-3X the height of the male. This is made of a few hundred fine, interlocked sticks in the center of a moss platform. The platform lacks other adornment.

Figure 182. ***Amblyornis macgregoriae***, Macgregor's Bowerbird. Members of this species use bryophytes in their nests. Photo by Katerina Tvardikova, through Creative Commons.

Golden-fronted Bowerbird (*Amblyornis flavifrons*)

The Golden-fronted Bowerbird (***Amblyornis flavifrons***) builds a bower similar to that of Macgregor's Bowerbird, but the lawn is decorated by little piles of yellow, green, and fruit (Hansell 2000).

Acanthizidae – Scrubwrens, Thornbills, and Gerygones

The Brown Thornbills (***Acanthiza pusilla***; Figure 183) are very active birds, searching for tiny invertebrates (Lloyd 2013). They make an untidy nest (Figure 184)of bark shreds, grass, spider webs, spider egg sacs, amd moss. This nest is hidden close to the ground in tussock grass, saggs or bracken.

Figure 183. ***Acanthiza pusilla*** (Brown Thornbill), a bird that includes mosses in its nest. Photo by Patrick Kavanagh, through Creative Commons.

Figure 184. ***Acanthiza pusilla*** (Brown Thornbill) nest that often includes mosses. Photo by J. J. Harrison, through Creative Commons.

Rhinocryptidae – Tapaculos

Silvery-fronted Tapaculo (*Scytalopus argentifrons*)

In a Costa Rican cloud forest, the nest of the Silvery-fronted Tapaculo (***Scytalopus argentifrons***; Figure 185) was a "substantial" globular structure (Young & Zuchowski 2003). It was made mostly of mosses placed into a subterranean cavity at the end of a short, narrow tunnel.

Figure 185. ***Scytalopus argentifrons***, Silvery-fronted Tapaculo, Members of this species put mosses in their underground nests. Photo by Francesco Veronesi, through Creative Commons.

Callaeatidae – New Zealand Wattlebirds

The Kōkako (***Callaeas wilsoni;*** Figure 186), endemic to the North Island of New Zealand, sometimes includes moss capsules to line its nest (Figure 187). They use lichens, mosses, and liverworts, together with rotten wood and some mud in a central layer of the nest (Jessica Beever, Bryonet 2 May 2003).

Figure 186. ***Callaeas wilsoni***, Kōkako, a New Zealand endemic species. Members of this species use moss capsules to line their nests. Photo through Creative Commons.

Figure 187. ***Callaeas wilsoni***, Kōkako, in a nest with lots of mosses. Photo by Dick Veitch, © Department of Conservation, NZ, with limited online permission.

Zosteropidae – White-eyes

The White-eye (***Zosterops lateralis***; Figure 188-Figure 189) builds a nest (Figure 190) with mosses on the outside (Wikipedia 2017). This tiny nest is suspended from a fork in the branches.

Figure 188. ***Zosterops lateralis***, Wax-eye, a bird that cloaks the outside of its nest in mosses. Photo by Phil Bendle, with permission.

Figure 189. ***Zosterops lateralis***, White-eye. Photo by fir002, through Creative Commons.

Figure 190. ***Zosterops lateralis***, White-eye nest with mosses. Photo by Phil Bendle, with permission.

Effect of Cavity-nesting Birds on Bryophyte Communities

We have already discussed dispersal of bryophytes by birds, but nesting birds can have other effects on bryophyte communities as well. Tatsumi *et al*. (2017) investigated the effects of birds on the tree bole surrounding cavities where birds have nested (Figure 191-Figure 194). They suggested that tree holes (Figure 195-Figure 198) that are inhabited can be enriched with nutrients from those organisms, and those nutrients can escape down the tree trunk. Using the trees *Aria japonica* and *Cercidiphyllum japonicum* in a Japanese temperate forest, they investigated the bryophyte and lichen communities above and below tree holes.

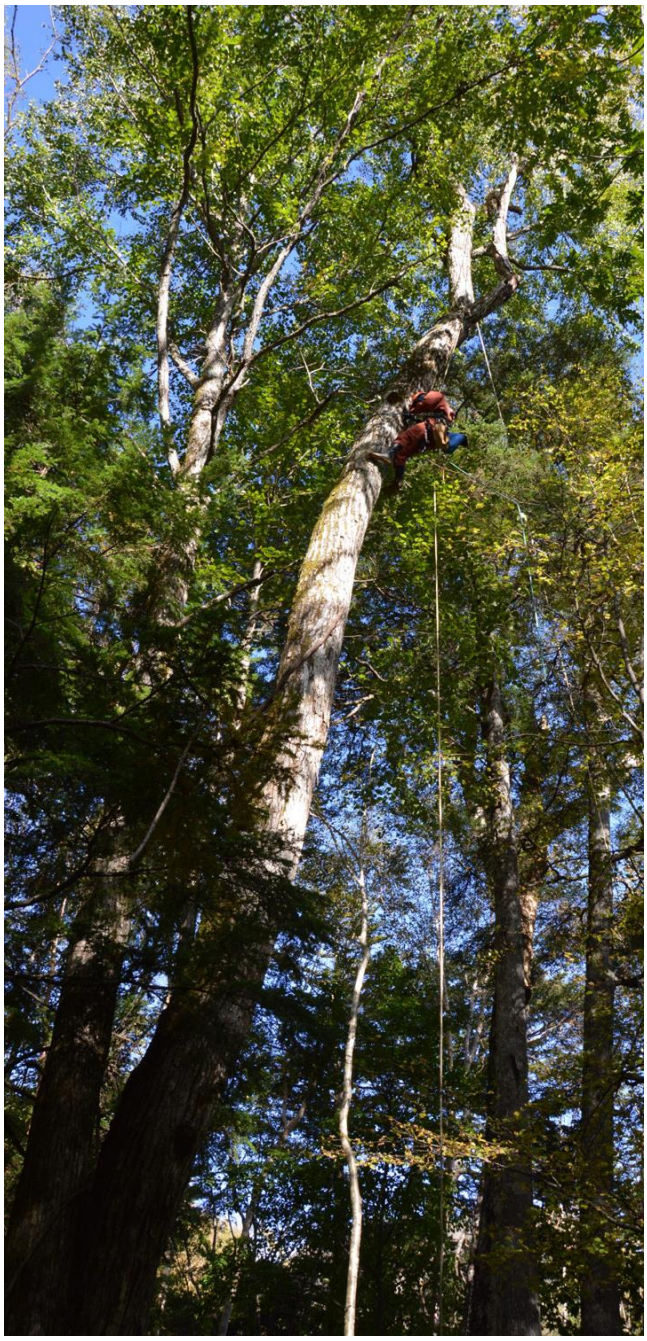

Figure 191. Scaling large trees to investigate the tree hole nesters. Photo courtesy of Shinichi Tatsumi.

Figure 192. Tree hole methods – one of the researchers prepares to place a quadrat frame. Photo courtesy of Shinichi Tatsumi.

Figure 193. Tree hole methods, with a quadrat positioned above the tree hole. Photo courtesy of Åsa Ranlund.

Figure 194. Tree hole methods showing quadrat below the tree hole. Photo of courtesy of Yume Imada.

Figure 195. Tree hole showing diversity above and below the hole. Photo courtesy of Wakana Azuma.

Figure 196. Elongate tree hole and climbing equipment. Photo courtesy of Wakana Azuma.

Figure 197. View of inside of tree hole. Photo courtesy of Wakana Azuma.

Figure 198. Close view of tree hole vegetation. Photo courtesy of Shinichi Tatsumi.

The richness of bryophyte and lichen species did not differ above and below the tree holes (Tatsumi *et al*. 2017). But the species composition of bryophytes differed significantly. The moss ***Anomodon tristis*** (Figure 199) and liverwort ***Porella vernicosa*** (Figure 200) were significantly more common below than above tree holes. On the other hand, the liverwort ***Radula japonica*** (Figure 201) and four lichen species were more frequent above than below the holes. Tatsumi and coworkers suggested nutrient and moisture differences as possible reasons for the species differences. I have to wonder how much the activity of the parents going in and out of the cavity could affect the bryophytes surviving there. These could have two impacts, dispersal and damage. More fragile species might not be able to survive the activity. Others might be transported there on feathers and feet.

Figure 199. ***Anomodon tristis***, a moss that is more common below tree holes than above. Photo by Bob Klips, with permission.

Figure 200. ***Porella vernicosa***, a liverwort that is more common below tree holes than above. Photo by Masanobu Higuchi, with permission.

Figure 201. ***Radula japonica***, a liverwort that is more common above tree holes than below. Photo by Taiwan Mosses, through Creative Commons.

Edible Nests

An interesting twist to the food concept is the use of bird nests as food for humans. I have not documented that any of those used contain mosses, but Salgado *et al*. (1998) found mosses in neotropical bird nests that they examined for **zoopharmacognosy** (behavior in which non-human animals apparently self-medicate by selecting and ingesting or topically using plants, soils, insects, or psychoactive drugs to prevent or reduce harmful effects of pathogens and toxins).

Summary

These passerine birds use mosses for a variety of purposes in their nests. Some put them inside as liners, some make the bottom of the nest thicker, and some weave them on the outside as camouflage. But in most cases we don't know what the function of the mosses really is – insulation, moisture, camouflage, or parasite protection. Or could it be all of these, or simply the mosses are the most available building materials?

The choice of bryophytes usually seems to depend on availability. But in other cases, the species chooses particular bryophytes, even if they are less abundant. Some bowerbirds use mosses to decorate their bowers – making a green path to the nest.

Birds can have an impact on the bryophytes themselves. Aside from being destructive by removing the bryophytes, and dispersing them to new locations, they have an impact on the species found above and below the tree holes where they nest.

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CHAPTER 17-1
RODENTS – MUROIDEA: MURIDAE

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CHAPTER 17-1
RODENTS – MUROIDEA: MURIDAE

Figure 1. Rodent among mosses and lichens, Auckland Island. Photo by James Russell, with permission.

Mammals

Scattered references to mammals using bryophytes for nests or habitat appeared early in the literature. However, until search engines were able to do the massive reading required to find these, bryologists were able to find little documentation of these uses.

Mammals are warm-blooded animals, so it is logical that in northern climates some of them would use bryophytes as nesting materials, taking advantage of their insulating properties. But as this chapter will reveal, they have found a variety of uses for bryophytes, especially in northern habitats.

Rodentia – Rodents

The term "rodent" is derived from the Latin word *rodere*, meaning to gnaw (Wikipedia 2017a). They comprise the order **Rodentia**, distinct in having a single pair of incisors (cutting teeth) that grow continuously. They comprise 40% of the mammal species and are common and abundant on all continents except Antarctica.

Even larger animals are known to use bryophytes for nesting purposes. But rodents seem to have the most uses. Le Blanc *et al*. (2010) determined that in eastern Canada, moss cover and vertical cover were the predominant influences on community structure of small mammals, whereas for forest birds it was conifer basal area, vertical cover, and snag availability. Kaminski *et al*. (2007), in the Allegheny Mountains of West Virginia, USA, demonstrated through principal component analysis that moss cover and abundant seedlings were important for specialist rodents in habitats with coarse woody debris.

One can find numerous studies in which mosses were made available as nesting materials in the lab (*e.g.* McGuire & Sullivan 2001; Pulfer 2007). In trapping studies, mosses have been used for insulation and food in the trap (Lentfer 1975; Peterson & Batzli 1975). Those studies that describe actual wild nests are much fewer than might be expected from the lab. Nevertheless, mosses are not uncommon in nests, but they are usually only minor components.

Bryophytes as Food

Until somewhat recently, we assumed that mammals did not eat bryophytes. Batzli and Cole (1979) reported that mosses produced low metabolizable energy for **microtine** rodents (members of the subfamily **Microtinae**, with teeth adapted for herbivory).

Nevertheless, both bovines and rodents use mosses as part of their diets. Prins (1982) observed that in cold environments mosses are eaten by a variety of herbivores, suggesting that the mosses might provide the secondary compound arachidonic acid that would help to keep the membranes of the footpads pliable on the cold ground and snow.

Microtine rodents in northern climates select mosses as part of their diet (Batzli & Jung 1980). Batzli (1983) likewise suggests that it may be secondary compounds that drive these rodents to consume bryophytes – such compounds as arachidonic acid? Or might it be a sort of winter tonic that helps to prevent bacterial infections? The well-known cycling of these northern rodents does not seem to correlate with nutrient fluctuations, and mosses are more difficult for rodents to digest than flowering plants (Tahvanainen *et al.* 1991), but Batzli contends that we cannot rule out secondary compounds for the changes in diet. In addition to making use of arachidonic acid, a fatty acid not found in flowering plants, Prins (1982) reminded us that mosses are high in fiber, low in nitrogen, and low in digestible energy, seemingly giving the rodents little reason to eat them unless the mosses provided something special and important – like arachidonic acid.

This seemingly non-nutritional status of bryophytes is supported by the study of 35 bryophyte species from the high Arctic tundra (Figure 2) of Devon Island, Canada (Pakarinen & Vitt 1974). They demonstrated that the highest nitrogen content is in the green portion, and that the fraction is higher in hydric species than in mesic or xeric species. Mean contents (%) for the green portion of these species are total nitrogen, 1.00 (1.08 ash-free) and total carbon, 45.9 (48.7 ash-free). By contrast, the percent N content of *Nephrophyllidium crista-galli* (a dicot; Figure 3) in Alaska ranged ~3-3.8% in areas where Sitka deer gathered and 2-3% in areas where they were absent (Klein 1965). In the five Arctic tracheophyte species measured for carbon percentage by Tolvanen and Henry (2001), all were inferior to that in the Pakarinen and Vitt (1974) moss study except that of the shrub *Cassiope tetragona* (Figure 4), which was only slightly higher. Barkley *et al.* (1980) and Batzli and Pitelka (1983) consider mosses to have a nutrient content that does not differ from that of other plants in the same region.

Figure 2. Nunavut tundra, Canada. Photo by A. Dialla, through Creative Commons.

Turchin and Hanski (2001) suggested that interaction with the food supply was one possible explanation for rodent cycling in far northern habitats. Nevertheless, based on their models they concluded that predation was the best explanation for population cycling, but they allowed for the possibility of food to play a role in cycles of lemmings, rodents that rely on mosses for food.

Figure 3. *Nephrophyllidium crista-galli*, an Arctic plant with 3-3.8% nitrogen content in Alaska. Photo by Alpsdake, through Creative Commons.

Figure 4. *Cassiope tetragona*, an Arctic plant with nitrogen content only slightly higher than that of mosses. Photo by Bjoertvedt, through Creative Commons.

One example of the role of secondary compounds is the hormonal precursors found in graminoids (Hansson & Henttonen 1988). But that would fail to explain the cycles in shrub and moss eaters. Are we missing something? Both the arctic rodents and the bryophytes reproduce in early spring. Is there a time in winter, or late fall, when bryophytes produce a hormone precursor, if not the hormone itself? Or is it the shift to a greater percentage of bryophytes in the diet that triggers hormone production? Hansson and Henttonen concluded that the cycles are complex, that they are regular in only a minority of the rodents, and that extrinsic factors are important in regulating these cycles.

One of the mechanisms used by the woodrat genus *Neotoma* is that of caching to reduce toxin intake (Torregrossa & Dearing 2009). Although this study did not include bryophytes, it is a topic that should be considered in understanding bryophyte relationships. Among the three non-bryophyte feeders in the study, the white-throated woodrat (*N. albigula*; Figure 5) made a terpene-free cache. In nature, dismantled middens of this species revealed no alpha-pinene, despite its occurrence in the surrounding trees. The desert woodrat (*Neotoma lepida*; Figure 6) instead decreased total food intake, but did not decrease the terpene-containing food. The third species, Bryant's woodrat (*N. bryanti*; Figure 7), did nothing to regulate

terpene intake. Nevertheless, in the food cage all three species abandoned a greater amount of food when it contained terpene.

Figure 5. The white-throated woodrat, *Neotoma albigula*, a species that makes a terpene-free cache. Photo by J. N. Stuart, through Creative Commons.

Figure 6. *Neotoma lepida*, a species that does not decrease terpene-containing foods. Photo by Lloyd Glenn Ingles, through Creative Commons.

Figure 7. Bryant's woodrat, *Neotoma bryanti*, a species that does nothing to regulate terpene intake. Photo by Alan Harper, through Creative Commons.

This raises the question of phenolic compounds in bryophyte food organisms. Some of these are aromatic, suggesting that they will evaporate from the bryophytes with time, or at least decrease in concentration. Do these phenolic compounds also decrease in winter when the bryophytes are mostly inactive? Do stored bryophytes in nests lose their phenolic compounds?

Little is known about seasonal variation in phenolic concentrations of bryophytes. Hribljan (2009; in prep) found no significant change in phenolic concentrations from September to November in the moss ***Pleurozium schreberi*** (Figure 8) in the Keweenaw Peninsula of Michigan, USA (Figure 9). But do concentrations decrease as the mosses rest under the snow of winter? Do they decrease during hot, dry periods of summer? And if so, do rodents change their feeding habits in response?

Figure 8. ***Pleurozium schreberi***, a boreal forest moss that showed no change in phenolic content from September to November. Photo by Sture Hermansson, with online permission.

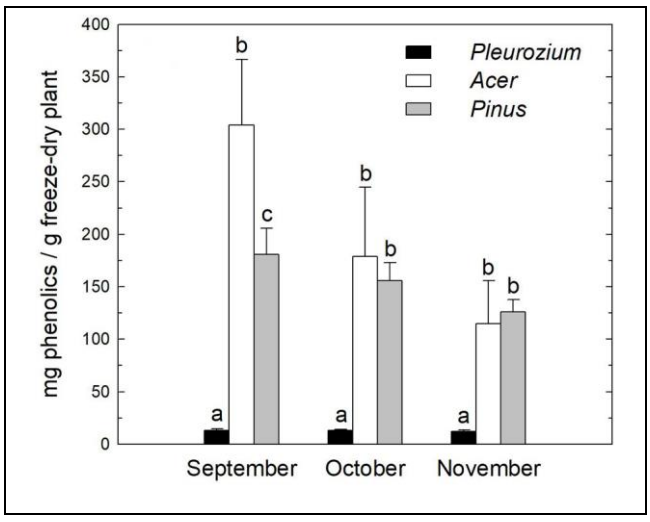

Figure 9. Seasonal phenolics in ***Pleurozium schreberi***, leaves of a deciduous maple tree (*Acer*), and needles of the conifer *Pinus*. Drawn by John Hribljan, with permission.

Several studies have indicated that rodents eat moss capsules (see study by Matt Dami below under Dispersal). One reason for this food choice may be the high concentration of lipids (Gellerman *et al*. 1972; Pakarinen & Vitt 1974). It can be as high as 30% in the capsules, compared to 5% in the leafy gametophyte.

Impacts on Bryophytes

Rodents are common in mires (Bostrom & Hansson 1981) and can be a major influence on bryophyte dynamics there, particularly in boreal and northern climates. Their use of bryophytes as food, the trimming of runways, and uses for nesting materials all remove bryophytes, sometimes faster than the bryophytes can regrow.

Grazing

Ericson (1977) found that not only the dwarf shrubs and grasses, but also the mosses in northern Sweden were impacted by grazing by small rodents (moles and lemmings). Mean moss cover declined in 1974 and 1975, but experienced a strong increase in 1976. Ericson attributed these changes entirely to grazing and other activities of the microtine rodents. The rodents typically bite off tips of mosses in the snow-free season, but in the snow-covered season they bite the shoots close to the bases.

In 1974, the decrease in mosses was primarily the result of summer grazing and runways (Figure 10), whereas in 1975 it was a further response to these activities during the winter period until the rodent population crash (Ericson 1977). These rodents included primarily the wood lemming ***Myopus schisticolor*** (Figure 10), a species that prefers mosses (Kalela *et al*. 1963a). The strongest bryophyte declines included the mosses ***Ptilium crista-castrensis*** (Figure 11) (73%), ***Dicranum scoparium*** (Figure 12) (57%), ***D. polysetum*** (Figure 13) (53%), ***D. majus*** (Figure 14) (37%), ***Hylocomium splendens*** (Figure 15) (30%), and ***Pleurozium schreberi*** (Figure 8) (12 %). On the other hand, species on windthrows and tree stumps [***Dicranum montanum*** (Figure 16), ***Sanionia uncinata*** (Figure 17)] were largely spared.

Figure 10. Wood lemming, ***Myopus schisticolor***, by its path through ***Hylocomium splendens***. Photo by Risto S. Pynnönen through Wikimedia Commons.

Although Kalela *et al*. (1963a) considered ***Plagiothecium denticulatum*** (Figure 18) to be a rejected species by ***Myopus schisticolor*** (Figure 10), this species was eaten at least sometimes in the Ericson (1977) study. Ericson also noted that ***Pleurozium schreberi*** (Figure 8) was not eaten as frequently as its abundance would suggest (see also Kalela *et al*. 1963a, b; Helminen & Valanne 1963). In 1975, the picture was reversed, with ***Pleurozium schreberi*** decreasing by 19% while ***Ptilium crista-castrensis*** (Figure 11) increased by 43% and ***Dicranum scoparium*** (Figure 12) increased by 70%! This decrease-increase trend is a common phenomenon by forest floor mosses, demonstrating a one-year time lag relative to the microtine rodent peak years.

Figure 11. ***Ptilium crista-castrensis***, the bryophyte that experiences the strongest decline when in the presence of the wood lemming ***Myopus schisticolor***. Photo by Michael Lüth, with permission.

Figure 12. ***Dicranum scoparium***, a species that declines in the presence of the wood lemming ***Myopus schisticolor***. Photo by Janice Glime.

Figure 13. ***Dicranum polysetum***, a species that declines in the presence of the wood lemming ***Myopus schisticolor***. Photo by Janice Glime.

Figure 14. ***Dicranum majus***, a species that is damaged and declines when wood lemmings are present. Photo by Michael Lüth, with permission.

Figure 15. ***Hylocomium splendens***, a species for which cover diminishes in the presence of the wood lemming. Photo through Wikimedia Commons.

Figure 16. ***Dicranum montanum***, a species that lives on stumps and tree bases and is spared from damage by wood lemmings. Photo by Michael Lüth, with permission.

Figure 17. ***Sanionia uncinata***, a species of stumps and windthrows and that is not harmed by wood lemmings. Photo by Michael Lüth, with permission.

Figure 18. ***Plagiothecium denticulatum***, a species that is rejected by the wood lemming ***Myopus schisticolor***. Photo by Michael Lüth, with permission.

Weft and other dominant species growth forms benefit from the rodents through regeneration from rhizomes in ***Polytrichum commune*** (Figure 19) and ***P. juniperinum*** (Figure 20) (Meusel 1935; Wigglesworth 1947) and ***Dicranum*** spp. (Figure 12-Figure 14, Figure 16) (Meusel 1935), from broken or bitten tips of ***Hylocomium splendens*** (Figure 21) (Correns 1899), and from isolated leaves and leaf fragments of ***Dicranum*** spp. and ***Polytrichum commune*** (Correns 1899).

Figure 19. ***Polytrichum commune***, a species that regenerates from rhizomes. Photo by A. J. Silverside, with permission.

Figure 20. ***Polytrichum juniperinum***, a species that regenerates from rhizomes. Photo by Janice Glime.

Figure 21. ***Hylocomium splendens***, a species that exhibits broken and bitten tips when rodents feed on it. Photo by Amadej Trnkoczy through Creative Commons.

Hansson (1969) reports frequencies of 86, 90, and 50% mosses in the diet of the bank vole ***Myodes glareolus*** (Figure 22) in Sweden in three successive years, and mosses form a regular part of the diet in all seasons (Hansson 1971). Contrarily, Holisová (1966) found only traces of mosses in their diet in lowland oak forests. Kalela (1957) found that ***Pleurozium schreberi*** (Figure 8) is especially eaten by the grey red-backed vole ***Myodes rufocanus*** (Figure 23), although mosses form only a minor part of the diet.

Figure 22. ***Myodes glareolus***, bank vole, eating mosses in the Netherlands. Photo by Andrew Spink, with permission.

Figure 23. ***Myodes rufocanus*** (grey red-backed vole), a vole that eats the moss ***Pleurozium schreberi***. Photo by Zbyszek Boratynski, through Creative Commons.

Hansson (1969) likewise reported a high frequency of mosses in the diet of the field vole ***Microtus agrestis*** (Figure 24) at Ammarnäs in Scandinavia, although he found that they usually contribute only a minor part of the diet elsewhere. Grazing by rodents during their peak years was so great in Scandinavia that moss cover declined significantly, many plots by more than 50%, for two consecutive years (Ericson 1977).

Figure 24. ***Microtus agrestis*** (field vole) among mosses. Photo from Wikimedia Commons.

Experimental evidence in England supports the role that small rodents can have in altering the vegetation. Summerhayes (1941) used areas that were fenced with fine mesh wire to keep the field vole ***Microtus agrestis*** (Figure 24) out. Control plots were similar but lacked the fencing. The original plots had mostly the grass *Melica caerulea* (Figure 25), but also the grasses *Holcus mollis* (Figure 26) and *Deschampsia caespitosa* (Figure 27). The exclosures resulted in almost total disappearance of mosses within them during the sampling period of 1932 to 1939. Summerhayes attributed this to the increased competition by the dominant plants when the vole attack was prevented.

Figure 25. *Melica* sp., the primary ground cover when vole exclosures were erected. Photo from iNaturalist, through Creative Commons.

Figure 26. *Holcus mollis*, one of the plants in the habitat of ***Microtus agrestis***. Photo by James K. Lindsey, through Creative Commons.

Figure 27. *Deschampsia caespitosa* in winter, one of the plants in the habitat of ***Microtus agrestis***. Photo by Sten Porse, through Creative Commons.

Virtanen *et al*. (1997) similarly established exclosures against the Norwegian lemming (***Lemmus lemmus***; Figure 28) in the late snowbeds of Finnish Lapland. Eight years later they found considerable changes in the vegetation. Mosses had expanded their coverage. ***Polytrichum*** (Figure 19-Figure 20) species had reached a carpet that was three times as thick as that in the open areas. The mosses experienced vertical growth in undisturbed conditions. Inside the exclosures the liverworts and some prostrate **tracheophytes** (lignified vascular plants) were absent. The open (disturbed) plots were the only place where the bryophytes with good colonizing ability occurred.

Figure 28. ***Lemmus lemmus*** on ***Sphagnum***. Photo by Andreaze, through Creative Commons.

Lemmings in North America can consume up to 90% of the primary production during a peak population year (Schultz 1968; Moen *et al*. 1993). In Scandinavia, they consumed 66% of the mosses and only 33% of the graminoids during these peaks (Moen *et al.* 1993) Bryophytes are a winter staple for the Norwegian lemming (***Lemmus lemmus***; Figure 28) (Virtanen 2000). After 5 years in an exclosure (Figure 29) experiment in a mountain snowbed of northwestern Finland, absence of grazing by lemmings and reindeer (***Rangifer tarandus***; Figure 30) caused an increase in moss biomass (Figure 31). After 15 years, the moss family **Polytrichaceae** (Figure 19-Figure 20) still dominated, but some of the graminoids had also increased (Figure 31). On the other hand, the moss ***Kiaeria*** (Figure 32) decreased or became completely absent in the exclosures, apparently due to competition from

tracheophytes. Virtanen concluded that the assumption that herbivore grazing in low productivity environments was of little consequence was an incorrect assumption. Grazers can have a significant impact on both bryophytes and tracheophytes in these environments.

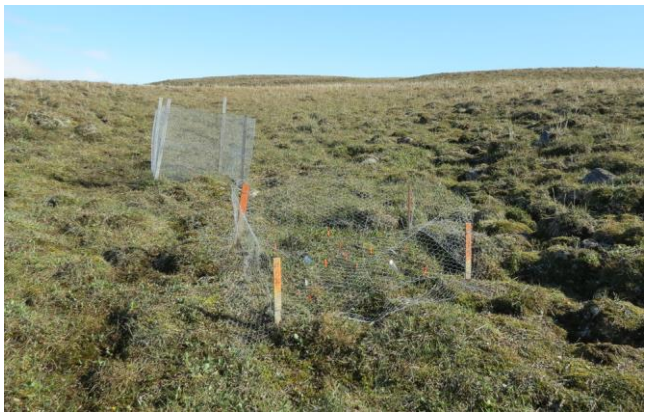

Figure 29. Lemming exclosure 1x1 m on Bylot Island. Photo courtesy of Dominique Fauteux.

Figure 30. ***Rangifer tarandus*** (reindeer), a species that often co-exists with lemmings and negatively impacts moss biomass. Photo by Dean Biggins, USFWS, through public domain.

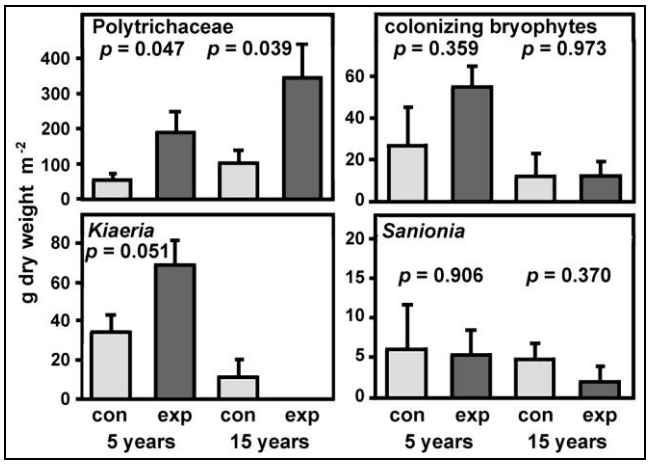

Figure 31. Dry weight of bryophytes after 5 and 15 years in controls (**con**) and exclosures (**exp**). Modified from Virtanen 2000.

Figure 32. ***Kiaeria starkei***, a moss that benefits from grazing by mammals. Photo by Michael Lüth, with permission.

Andersson and Jonasson (1986) conducted a similar study on rodent exclosures in the alpine heath of Lapland in northern Sweden. Several plants were greatly reduced by the rodents and flowering frequency of food plants decreased. The lemmings (***Lemmus lemmus***; Figure 28) and voles (***Myodes***; Figure 22-Figure 23) both eat the mosses ***Polytrichum commune*** (Figure 19) and ***P. juniperinum*** (Figure 20) (Kalela 1957, 1962; Koshkina 1962; Kalela & Koponen 1971; Kalela *et al.* 1971). Andersson and Jonasson (1986) found that ***Polytrichum*** declined, but they attributed the decline to depression by luxurious growth of tracheophyte species. The ***Polytrichum*** species have a slower growth rate than that of tracheophytes.

It is the lemmings that make mosses a large part of their diet, differing considerably from the vole diet (Kalela 1957, 1962; Koshkina 1962; Stoddart 1967; Kalela *et al.* 1971, Kalela & Koponen 1971, Baltruschat & Uberbach 1976). Hence, Andersson and Jonasson (1986) concluded that the voles and lemmings may not experience severe competition for food.

The grazing causes good and bad years for bryophytes, sometimes permitting tracheophytes to get established. These tracheophytes can sometimes out-compete the bryophytes. Thus, the rodents can have a major impact on the construct of the vegetation.

Runways, Burrows, and Nests

But consumption is not the only influence on the changing bryophyte communities. The runways and exposed tunnels (Figure 33) are colonized by mosses (Figure 34), especially ***Ceratodon purpureus*** (Figure 35), ***Plagiothecium curvifolium*** (Figure 36), ***P. denticulatum*** (Figure 18), ***Pohlia nutans*** (Figure 37), and ***Brachythecium starkei*** (Figure 38) (Ericson 1977). These small turf or mat species are unable to colonize the weft-moss-covered areas and benefit from the disturbance of the runways. The runway species also differ from those of windthrows that are colonized by ***Amblystegium serpens*** (Figure 39), ***Sanionia uncinata*** (Figure 17), and ***Dicranum montanum*** (Figure 16).

Figure 33. ***Microtus*** and ***Apodemus*** tunnels, illustrating destruction of the vegetation. Photo by Marijke Verhagen, Saxifraga, with online permission.

Figure 34. ***Microtus*** and ***Apodemus*** tunnels, showing colonization by mosses. Photo by Marijke Verhagen, Saxifraga, with online permission.

Figure 35. ***Ceratodon purpureus*** with immature capsules, a colonizer on rodent runways. Photo courtesy of Dale Sievert.

Figure 36. ***Plagiothecium curvifolium***, a colonizer on rodent runways. Photo by Michael Lüth, with permission.

Figure 37. ***Pohlia nutans***, a colonizer on rodent runways. Photo by Michael Lüth, with permission.

Figure 38. ***Brachythecium starkei***, a colonizer on rodent runways. Photo by Michael Lüth, with permission.

Figure 39. ***Amblystegium serpens***, a colonizer of windthrows. Photo by Michael Lüth, with permission.

The role of these rodents in leafy liverwort population dynamics is less clear. Kalela *et al*. (1963a) reported that ***Myopus schisticolor*** (Figure 10) rejected ***Ptilidium ciliare*** (Figure 40), but it appears that ***Barbilophozia lycopodioides*** (Figure 41) experiences at least some foraging. Both species are poor competitors that are able to colonize the exposed substrate of the runways.

Figure 40. ***Ptilidium ciliare***, a species rejected by ***Myopus schisticolor***. Photo by Li Zhang, with permission.

Figure 41. ***Barbilophozia lycopodioides***, a leafy liverwort that is sometimes eaten by rodents. Photo by Michael Lüth, with permission.

Duncan (1954) found that rodents compress the ***Sphagnum*** (Figure 42) and reduce its growth rate. Duncan found more seedlings (11% germination) of black spruce (***Picea mariana***; Figure 43) on the "fine" mosses [***Mnium*** (Figure 44), ***Drepanocladus*** *s.l.* (Figure 45), ***Helodium*** (Figure 46)] compared to non-compressed ***Sphagnum*** (4.5%). However, compressed ***Sphagnum*** mats appear to be the best of these substrata for black spruce seedlings.

Figure 42. ***Sphagnum magellanicum***, in a genus that gets compressed by rodent "traffic." Photo by Michael Lüth, with permission.

Figure 43. ***Picea mariana*** sapling in a bed of ***Sphagnum***. Photo by Joseph OBrien, USDA Forest Service, through Creative Commons.

Figure 44. ***Mnium hornum***, in a moss genus that can provide microhabitat for black spruce germination. Photo by Michael Lüth, with permission.

Figure 45. ***Drepanocladus exannulatus***; black spruce seeds can germinate among some members of this genus. Photo by Michael Lüth, with permission.

Figure 46. ***Helodium blandowii***; black spruce seeds can germinate among branches of this species. Photo by J. C. Schou, through Creative Commons.

Tabata and Iwasa (2013) found that Smith's red-backed vole, ***Phaulomys smithii***, occurred in rocky terrains at the base of Mt. Fuji, Japan, where bryophytes were common. But the role of these rodents in promoting the growth of the bryophytes or in distributing them remains unknown.

Otomys sloggetti (**Muridae**; Figure 88) typically occupies rocky habitats, living in crevices in nests of weeds and grass (Lynch 1989). However, in boggy and spongy habitats of South Africa, they occupy extensive burrow systems similar to those of *Parotomys brantsii* (Figure 47). The area is characterized by numerous hummocks that are ~200 mm high and ~300 mm in diameter. Lynch (1992) suggested that the moles (***Cryptomys hottentotus***; Figure 48) were the engineers of the hummocks. But it appeared that ***O. sloggetti*** further enlarged and cleaned them, creating greater habitat variety and colonization by a greater variety of plants, including mosses. The mosses become repeatedly "top-dressed" with soil, creating the hummocky landscape. However, not all agree with this interpretation of the hummock origin, suggesting instead that such non-animal agents as freeze-thaw cycles could account for the hummocks (van Zindern Bakker & Werger 1974).

Figure 47. ***Parotomys brantsii***, Brant's whistling rat, South Africa, nibbling on grass. Photo by Derek Keats, through Creative Commons.

Figure 48. ***Cryptomys hottentotus***, a hummock-building vole that prepares the way for Photo by Daderot, through Creative Commons.

The tiny moss ***Acaulon triquetrum*** (Figure 49) grows in calcareous grasslands in Southwest Germany (Ahrens 2003). The upper layer of the substrate is colonized by rhizomes that branch and from which young shoots develop. This species is able to colonize the bare surfaces of the loess soil that is created by burrowing small mammals (and these rodents could contribute to dispersal by carrying rhizoids, rhizomes, propagules, and leaf fragments on their footpads and fur.

Figure 49. ***Acaulon triquetrum***, a moss species that occupies bare soil created by burrowing rodents. Photo by Michael Lüth, with permission.

Another possibility is that plant fragments are carried in the gut and deposited at a different location. The first question to arise here is whether they are viable after their adventure in the gut. John Hribljan (unpublished) cultured microtine rodent scat from Isle Royale, Michigan, and

several fragments germinated (Figure 50) to produce new plants.

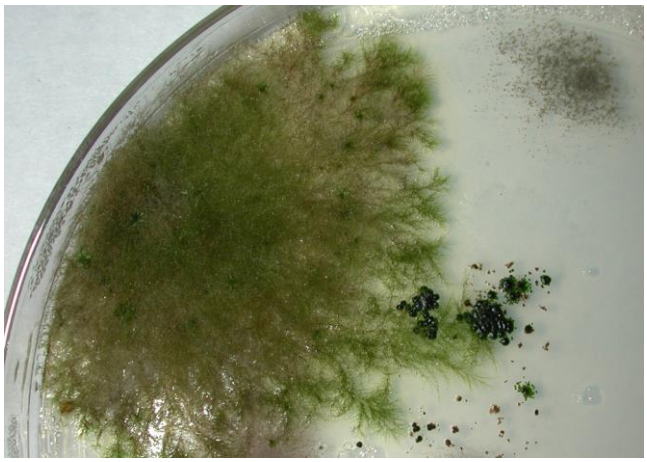

Figure 50. Culture of ***Funaria hygrometrica*** derived from feces collected from moss from Alaska. The size of the feces suggests these were microtine rodents. Photo by John Hribljan, with permission.

Beavers (***Castor canadensis***; Figure 51) are not known to use mosses, but they are ecological engineers that can change whole habitats. Their disturbance is often instrumental in the creation of wetlands (Adams 1993; Ponomarenko & Ponomarenko 2003). Such disturbances often result in the invasion of bryophytes and graminoids from wetlands into upland habitats (Ponomarenko & Ponomarenko 2003).

Figure 51. ***Castor canadensis*** – beaver – an engineer that creates wetlands. Photo by MSR, through Creative Commons.

Rodent Cycles

Rodent cycles have puzzled biologists for many decades (Turchin *et al*. 2000). The cycles were once understood to be 3-4 years, but now we understand that they are not so simple (Hansson 2002). They are characterized by lag phases and may be resource-driven. But lag phases can also be caused by predator effects. These drivers can force the population to spread to suboptimal patches. Hansson reports that some rodents appear to be limited by food, especially mosses. The mosses recover slowly from overgrazing and are further limited by temperature.

Rodents can be responsible for considerable changes in the abundance of bryophytes (Rydgren *et al*. 2007). Early reports on increases in the bryophyte annual production and abundance suggest that climate change provides more favorable conditions (Økland 1997; Økland *et al*. 2004; Knorre *et al*. 2006). But more recently data suggest that in the boreal forests, rodent cycles impact the feather moss ***Hylocomium splendens*** (Figure 15). When rodents have long cycles, their peak years have the greatest impact, causing the greatest reduction in growth of the moss. The role of bryophytes in these ecosystems is typically as a food source (Hansson 1969; Tast 1991; Bondrup-Nielsen 1993), although bryophytes can also provide cover and nesting material. Further impact on moss persistence results from trampling (Rydgren *et al*. 2007). Runways open the carpet due to removal of tissue (Kalela & Koponen 1971; Ericson 1977). Furthermore, species such as ***Brachythecium starkei*** (Figure 38) and ***Ceratodon purpureus*** (Figure 35) rapidly colonize runways in the first year. Summer foraging on the shoot apex does not have a severe effect on the mosses, but winter grazing can exterminate a species clone, as seen in species of ***Dicranum*** (Figure 12-Figure 14, Figure 16) (Ericson 1977).

In Norway, fluctuations in rodent populations have profound impact on the success of the moss ***Hylocomium splendens*** (Figure 15) (Rydgren *et al*. 2007). The moss has its highest growth rate when the rodents are acyclic and becomes reduced when the periodicity and severity of the peak disturbance by rodents increases. Even its means of reproduction changes, with mature segments surviving in less variable environments, and regeneration from older branches responding to more variable environments. Rodent herbivory and trampling contribute to fragmentation from the mosses.

Such regeneration from older parts makes the population less fit than survival of mature stems (Rydgren *et al*. 2007). This is because large segments will survive for decades, but fragmentation results in small segments. These, in turn, have lower branching frequencies and lower probability of survival. Because of their small size, bryophytes such as ***Hylocomium splendens*** (Figure 15) may be able to use only two of the three resistance mechanisms known to tracheophytes (defense, escape, tolerance), lacking the size and lignin needed for physical defense against trampling and fragmentation. Rather, they seem to rely on tolerance through compensatory growth, greater photosynthesis, reallocation of resources, and activation of the meristem (Boege & Marquis 2005). The latter is triggered by damage to the apex that removes apical dominance, a phenomenon well known among many dicots.

For ***Hylocomium splendens*** (Figure 21), and many other large boreal mosses, reproduction by spores is rare, and growing tips provide the major form of reproduction (Økland 1995; Rydgren & Økland 2002; Cronberg *et al*. 2006). Fragmentation contributes to the diaspore bank, but there is a delay in growth, if it is successful at all (Rydgren *et al*. 2007). Nevertheless, it requires a severe impact of

30% loss of growing points and 15% loss of segments to reduce the population to a no-gain state under favorable growing conditions. Thus, with rodent cycles of 3-5 years and disturbance severities of only 15-30%, ***Hylocomium splendens*** (Figure 15) will survive.

Scenarios of climate effects on the microtine rodent cycles suggest that those cycles may change to become more irregular (Rydgren *et al*. 2007). Specifically studying the responses of the boreal moss ***Hylocomium splendens*** (Figure 15), Rydgren and coworkers found that the growth rates are higher in the acyclic scenarios, but that the population growth rates are progressively reduced when peak disturbance severities increase. When the environment is less variable, the mature segment of ***H. splendens*** (Figure 21) is the primary contributor to population growth rate. In a more variable environment, regeneration from branches of older parts becomes more important, a process that leads to reduced population fitness. Hence, if the cycles break down, abundance of ***H. splendens*** and other large bryophytes in boreal forests such as those of Norway will increase.

Snowbed bryophytes seem to be particularly vulnerable to rodents, perhaps because these sites are covered predominately by bryophytes. Moen *et al*. (1993) found that lemmings in northern Norway reduced the cover of graminoids by 33% and of mosses by 66% during the winter population peak. They considered this to be an important impact that helped to explain the snowbed vegetation dynamics.

As is usual in ecology, nothing operates alone. And the effects of large herbivores such as sheep can affect the impact of rodents on bryophytes, particularly in alpine ecosystems (Austrheim *et al*. 2007). Using exclosures, Austrheim and coworkers kept sheep out, but permitted access to rodents. This resulted in a significant increase in the grass *Deschampsia flexuosa* (Figure 52) within the exclosures. Frequencies of graminoids, herbs, and dwarf shrubs did not change in response to grazing, but of the 15 bryophyte species, cover of six bryophyte species groups changed, with three increasing and three decreasing significantly.

In their exclosure experiments, Austrheim *et al*. (2007) lumped bryophytes that were difficult to distinguish in the field to avoid taxonomic errors. Those that decreased in the exclosures were the ***Plagiothecium*** group [***P. nemorale*** (Figure 53), ***P. denticulatum*** (Figure 18), ***P. laetum*** (Figure 54)] and the ***Brachythecium*** group [***B. reflexum*** (Figure 55), ***B. salebrosum*** (Figure 56), ***B. starkei*** (Figure 38)], whereas ***Straminergon stramineum*** (Figure 57), ***Pohlia nutans*** (Figure 37), and ***Cephalozia bicuspidata*** (Figure 58) increased in the exclosures. At the same time, ***Polytrichum*** [***P. commune*** (Figure 19), ***Polytrichastrum formosum*** (Figure 59), ***P. longisetum*** (Figure 60), ***P. alpinum*** (Figure 61)] increased in the grazed plots, whereas the leafy liverwort ***Neoorthocaulis floerkei*** (Figure 62) decreased in these grazed plots. The moss ***Pleurozium schreberi*** (Figure 8) and leafy liverwort ***Ptilidium ciliare*** (Figure 40) tended to increase in exclosures.

Figure 52. ***Deschampsia flexuosa***, a grass that increased in exclosures that keep out sheep but permit an increase in rodent numbers. Photo by Miguel Porto, through Creative Commons.

Figure 53. ***Plagiothecium nemorale***, a species that decreases in exclosures in alpine regions. Photo by Michael Lüth, with permission.

Figure 54. ***Plagiothecium laetum***, a species that decreases in exclosures in alpine regions. Photo by Christian Peters, with permission.

Figure 55. ***Brachythecium reflexum***, a species that decreases in exclosures in alpine regions. Photo by Michael Lüth, with permission.

Figure 56. ***Brachythecium salebrosum***, a species that decreases in exclosures in alpine regions. Photo by Michael Lüth, with permission.

Figure 57. ***Straminergon stramineum***, a species that increases in exclosures in alpine regions. Photo by David Holyoak, with permission.

Figure 58. ***Cephalozia bicuspidata***, a short-lived colonizer, with perianths. Photo by Hermann Schachner Wikimedia Commons.

Figure 59. ***Polytrichastrum formosum***, a species that increases in exclosures in alpine regions. Photo by David T. Holyoak, with permission.

Figure 60. ***Polytrichastrum longisetum***, a species that increases in exclosures in alpine regions. Photo by Michael Lüth, with permission.

Figure 61. ***Polytrichastrum alpinum***, a species that increases in exclosures in alpine regions. Photo by David Holyoak, with permission.

Figure 62. ***Neoorthocaulis*** (=*Barbilophozia*) ***floerkei***, a species that is reduced in frequency by sheep. Photo by Janice Glime.

It was successional bryophytes that increased, along with the preferred fodder grass *Deschampsia flexuosa* (Figure 52) (Austrheim *et al*. 2007). The net result, however, was that neither tracheophyte nor bryophyte species richness was affected, nor was the total cover of either. It is interesting that when the sheep were excluded from grazing, the level of rodent grazing also diminished.

Austrheim and coworkers (2007) suggested four potential contributing factors for the changes in the bryophyte communities:

1. Exclusion of sheep reduces typical disturbance-favored pleurocarpous species such as the ***Brachythecium*** (Figure 38) and ***Plagiothecium*** (Figure 18, Figure 53-Figure 54) species groups.
2. Frequency of short-lived colonizers such as ***Pohlia nutans*** (Figure 37) and ***Cephalozia bicuspidata*** (Figure 58) increases.
3. Grazing favors grazing-resistant ***Polytrichum*** group species (Figure 19-Figure 20) (Helle & Aspi 1983; Väre *et al.* 1996; Virtanen 2000; Olofsson *et al.* 2004).
4. Herbivores cause a decrease in frequency of the leafy liverworts ***Barbilophozia lycopodioides*** (Figure 41) (sheep & rodents) and ***Neoorthocaulis*** (syn. = ***Barbilophozia***) ***floerkei*** (Figure 62) (sheep).

Bryophyte recovery can influence the structure of the rodent cycle. In their comparison of rodent cycling at Barrow, Alaska, USA, with that of North Fennoscandian lemmings, Oksanen *et al*. (2008) considered that the contrasting population fluctuations between these two areas probably depended on the different growth rates of the mosses. Based on data from Barrow, Turchin and Batzli (2001) assumed that it would take only two years for a complete recovery of mosses, based on the data from the wet tundra there (Tieszen *et al*. 1980). However, in North Fennoscandian habitats where lemmings over-winter, recovery from grazing requires at least ten years (Oksanen 1983).

Dispersal

Feces created by the rodents have the potential to provide a means of dispersal. Vole digestion time varies considerably, depending on the diet (Lee & Houston 1993). Nevertheless, voles have a very efficient digestion for plants. This high efficiency in the digestion of vegetal matter may lie in their habit of **coprophagy**. That is, they consume their own feces and cycle their food through their digestive system a second time. Seed diets can take considerably longer than leaf diets. But how long does it take for a moss diet to traverse the gut?

Whatever the residence time, feces of rodents may be deposited in their habitat, including among the local bryophytes, but also along runways or on other soil. If the rodent fails to re-ingest these feces, the moss provides a suitable habitat for germination, and the rodent may carry it some distance to a new location. Hribljan (unpublished data) provides support for this possibility; mosses germinated from feces collected from among mosses in Alaska (Figure 63).

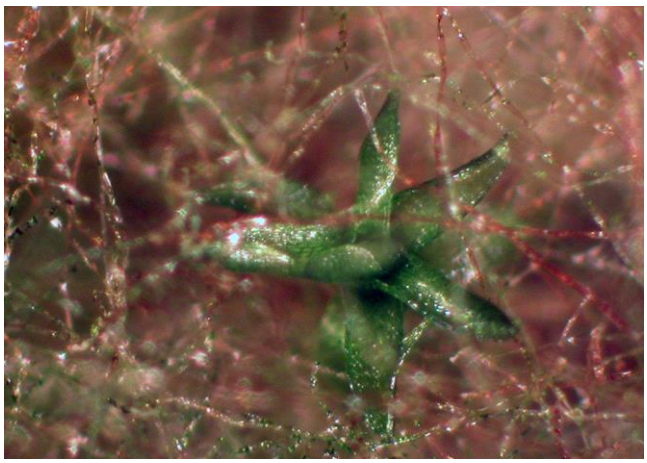

Figure 63. Developing ***Funaria hygrometrica*** from a culture of rodent feces collected from moss in Alaska. Photo by John Hribljan, with permission.

The experimental evidence of bryophyte dispersal by rodents is limited. Kimmerer and Young (1996) examined the effect of gap size and regeneration niche on the

coexistence of bryophyte species. Based on their study on two epixylic mosses, ***Tetraphis pellucida*** (Figure 64-Figure 65) and ***Dicranum flagellare*** (Figure 66), rodents appear to play a major role in both dispersal and distribution. Their activity creates gaps that ***Dicranum flagellare*** can colonize on the tops of logs. ***Tetraphis pellucida*** occurs primarily on the vertical surfaces at the sides of the logs. Both species produce propagules that can adhere to the rodents.

Figure 64. ***Tetraphis pellucida***. a species that lives on vertical surfaces of logs and is dispersed by rodents. Photo by Jan-Peter Frahm, with permission.

Figure 65. ***Tetraphis pellucida*** gemma, the dispersal unit carried by rodents. Photo by UBC Botany Website, with permission.

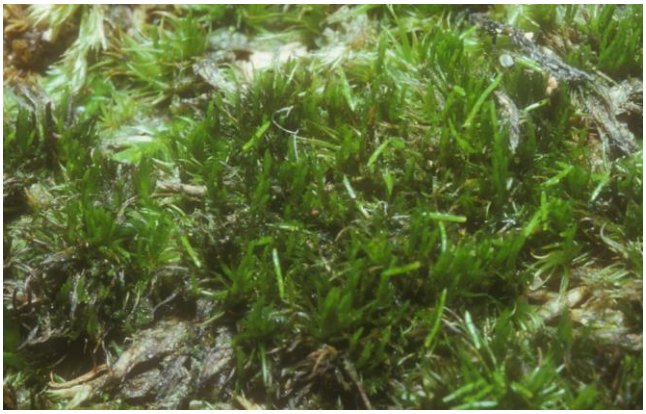

Figure 66. ***Dicranum flagellare*** with brood branches, many of which are broken off and lying on the moss in this image. Photo by Janice Glime.

Determining the ability of rodents to disperse bryophyte propagules is a multistep process that often exceeds the time limits and expertise of graduate students. However, Matt Dami (2014) has succeeded in this multistep process to demonstrate that rodents (mice) eat moss capsules (Figure 67), pass them in feces, and that the spores in the feces germinate (Figure 68). For ***Polytrichum commune*** (Figure 19, Figure 68), most are able to develop to full plants, whereas for ***Dicranum flagellare*** (Figure 66), few are successful (Figure 69).

Figure 67. Laboratory mouse consuming ***Dicranum scoparium*** sporophytes. Photo courtesy of Matt Dami.

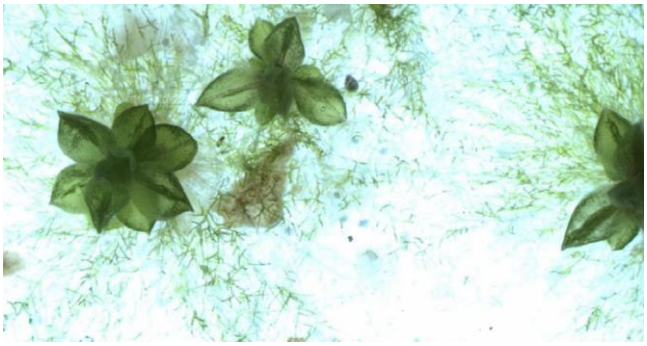

Figure 68. ***Polytrichum commune*** young plants cultured from spores in mouse feces in laboratory. Photo courtesy of Matt Dami.

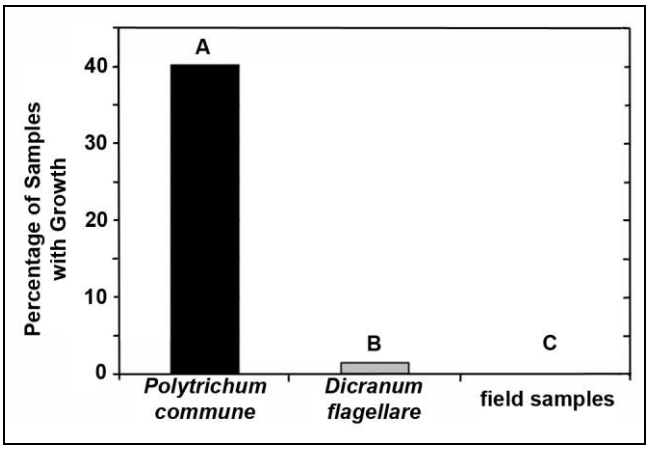

Figure 69. Percentage of cultured ***Polytrichum commune***, ***Dicranum flagellare***, and unidentified field samples that formed gametophores. Modified from Matt Dami 2014.

Dami (2014) conducted the study in central New York, USA, where he trapped 77 rodents in three forested sites. He collected 6 fecal pellets in each site, then used centrifugation to separate the spores (Figure 70) to demonstrate natural feeding concentrations in the feces and to assess viability. They found an average of 1,626 unidentified bryophyte spores per 3-pellet sample in the field collections (Figure 71). In the lab they provided 20 sporophytes with associated gametophytes of the two mosses ***Dicranum flagellare*** (Figure 72) and ***Polytrichum commune*** (Figure 73) to each of 18 laboratory mice. They collected three pellets from each mouse every 24 hours for four days. In this case, they found an average of only 28 ***D. flagellare*** spores but 4,333 of ***Polytrichum commune*** (Figure 74). The two species likewise differed in number of samples exhibiting germination and growth, with only 1.4% of ***D. flagellare*** and 40.3% of ***P. commune*** samples reaching gametophore stage. On the other hand, none of the spores from the field samples produced gametophores. On the other hand, ***D. flagellare*** samples contained many more vegetative fragments (Figure 66) than did ***P. commune*** (Figure 19).

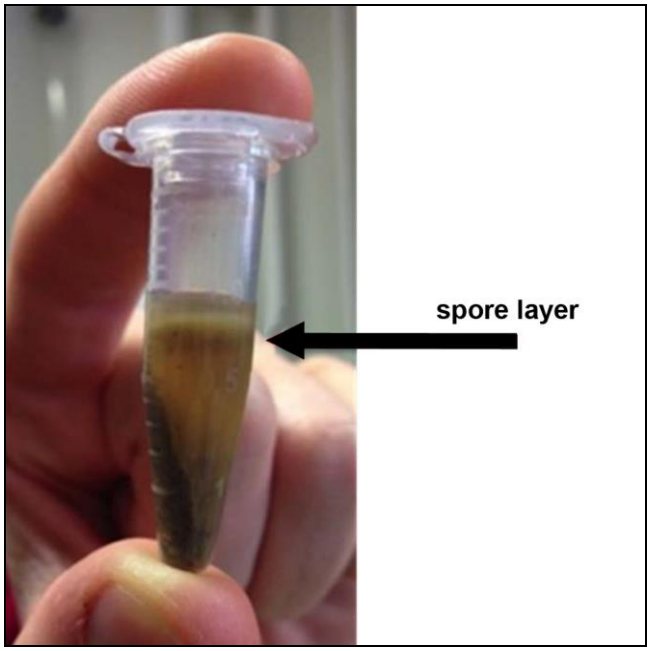

Figure 70. 1.5 µL microcentrifuge tube containing fecal sample in 25% Ludox solution after density centrifugation. Photocourtesy of Matt Dami.

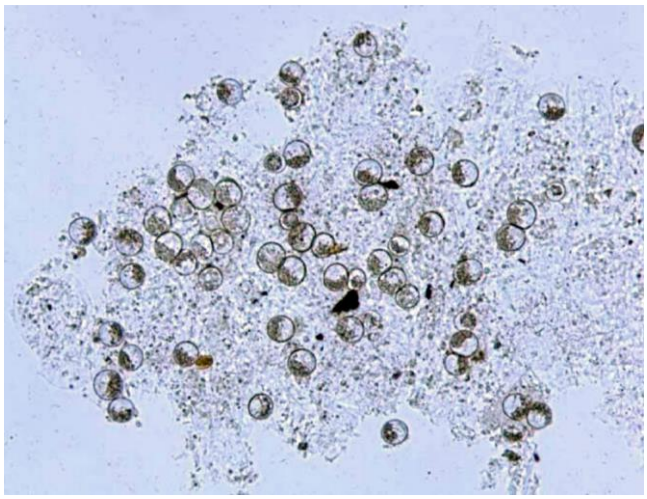

Figure 71. Light microscope image of spores from field sample. Photo courtesy of Matt Dami.

Figure 72. ***Dicranum flagellare*** with capsules. Photo by Rob Routledge, through Creative Commons.

Figure 73. ***Polytrichum commune*** capsules, food for rodents. Photo by Michael Lüth, with permission.

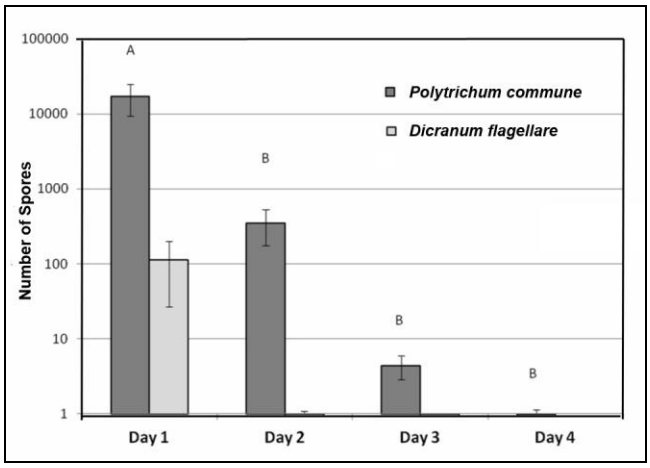

Figure 74. Number of spores detected in laboratory feces samples over the four collection days. Modified from Matt Dami 2014.

Field collections revealed additional insight into the role rodents could play in bryophyte dispersal. After capturing 77 rodents in one summer, Dami (2014) found that 37.66% carried spores and 12 individuals also carried gametophyte fragments. Two were identifiable as ***Platygyrium*** sp. (Figure 75) and ***Sphagnum*** sp. (Figure 43). Attempts to sterilize the fragments made them inviable.

Figure 75. ***Platygyrium repens*** showing masses of bulbils at the tips, structures that easily dislodge and adhere to fur and hair. Photo by Jan-Peter Frahm, with permission.

This still calls into question the viability of these spores in feces in the field where they must endure the feces conditions until decay permits them to reach a suitable substrate. My own experience with fish feces suggests that what might be viable at the time of expulsion may not retain viability with continued exposure to the conditions of the feces.

Muroidea – Hamsters, Voles, Lemmings, and New World Rats and Mice

Muridae – Mice, *etc.*

This is the largest family of rodents and the largest of mammals (Wikipedia 2016). Although the family name is derived from the Latin *mus*, meaning mouse, it also includes some kinds of voles, rats, and others. None is native to North America, but a number of species have arrived here, presumably with humans.

Micromys minutus – Eurasian Harvest Mouse

The Eurasian Harvest Mouse (***Micromys minutus***; Figure 76-Figure 78) has a wide distribution in the temperate and humid climate zone of East Asia and western Europe (Harris & Trout 1991). In urban environments, the habitat may differ, but Dickman (1986) found that even in such a setting fecal pellets can contain small amounts of moss.

Figure 76. ***Micromys minutus***, Eurasian harvest mouse, a mouse that consumes mosses. Photo by Bj. Schoenmakers, through Creative Commons.

Figure 77. ***Micromys minutus*** constructing a nest. Photo by Hajotthu, through Creative Commons.

Figure 78. Completed summer nest of ***Micromys minutus***. Photo by Alexis Martin, through Creative Commons.

Myodes = *Clethrionomys* – Red-backed Voles

It seems that there is no agreement among systematists as to the preferred generic group name for these voles. I have chosen to use ***Myodes***, but with nothing more than convenience to back up my choice. Furthermore, rodents with the common name of vole are in both the **Muridae** and the **Cricetidae** (covered in the next subchapter).

Longton (1992) states that mosses are "freely consumed" by Arctic and alpine voles. Voles seem to at times make important uses of mosses. In her messages to Bryonet on 3 December 2004 and 12 January 2008, Kate Frego described some of the relationships of the voles to bryophytes. She reported that they clipped the ***Dicranum polysetum*** (Figure 13) they had earlier avoided as food. Frego states that this is only anecdotal data, but she observed quite extensive "clipped" pathways of ***Dicranum polysetum*** as the snow melted, with some areas resembling "rooms" with nests, others with copious mouse droppings. In the sub-nivean tunnels that they made, they had trimmed off all the moss tips into neat, compact carpets!

Mosses are able to offer other advantages to both the rodents and their food plants. The moss layer provides a temperature stabilizing factor (Fuller *et al*. 1969). The temperature lag is greater in the moss than in the layer under the snow. Furthermore, when snow melts and refreezes, the structure of the snow changes, causing a sharp increase in its thermal conductivity. Hence, the snow layer experiences wide temperature fluctuations, whereas these are considerably damped in the moss layer (Figure 79).

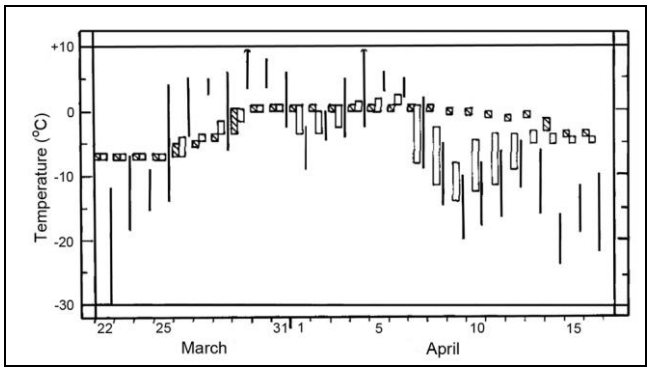

Figure 79. Daily moss (**cross-hatched box**), snow 5 cm above moss (**open box**), and air temperatures (**vertical line**). Beginning 1 April, physical structure of the snow was changing. Redrawn from Fuller *et al*. 1969.

In the Alaskan Arctic tundra, experiments in which mosses were removed demonstrated that ***Sphagnum*** (Figure 42) removal permitted an increase in the shrub *Betula nana* (Figure 80) (Gough *et al*. 2007). Hence, vole activity could change the vegetation patterns in these Arctic systems. Unfortunately, Gough *et al*. (2007) did not have any data on the relationship of ***Sphagnum*** to vole activity.

Figure 80. ***Betula nana***, a shrub that benefits when a rodent damages the ***Sphagnum***. Photo by Foledman, through Creative Commons.

The diet of ***Myodes*** differs among species, but also differs within species among habitats (Hansson 1985). For example, ***Myodes glareolus*** (Figure 24) feeds mostly on seeds in the deciduous forest and on fungal tissues in coniferous forests.

Myodes rufocanus – Grey Red-backed Vole

The grey red-backed vole (***Myodes rufocanus***; Figure 23) extends through a large range in the northern Palaearctic from northern Fennoscandia through northern Russia, and northeastern and northern Korea and the islands of Sakhalin (Russia), and Japan (Abe *et al.* 2005), then far south to northern parts of Mongolia and China (Wilson & Reeder 2005).

Myodes rufocanus (Figure 23) is often common in areas where Norwegian lemmings (***Lemmus lemmus***; Figure 28) reside, but unlike the lemmings, the voles do not usually eat the mosses, preferring blueberry plants (*Vaccinium myrtillus*; Figure 81) and other dicots instead (Kalela 1957; Virtanen *et al*. 1997). This separation of diets keeps them from competing for food in this food-limited environment.

Figure 81. ***Vaccinium myrtillus***, common food of ***Myodes rufocanus***, the grey red-backed vole. Photo by Anneli Salo, through Creative Commons.

The summer nest of ***Myodes rufocanus*** is constructed of grass, leaves, lichens, and moss (Chester 2016).

Myodes rutilus – Northern Red-backed Vole

The northern red-backed vole (***Myodes rutilus***; Figure 82) is distributed in the northern Holarctic, including northern Fennoscandia, European Russia, Siberia, north Xinjiang Province in China, through Mongolia, to northeast China and northern parts of the Korean peninsula, the islands of Sakhalin (Russia), Hokkaido (Japan), Alaska (USA), and Canada (Linzey *et al*. 2016). It lives in the subarctic birch forest zone and in northern parts of the boreal forest zone. Its greatest abundance is in productive (**eutrophic** or **mesotrophic**) forests, with a dense understory of grasses, herbs, or moss. It prefers mature old-growth forests, but, unlike other ***Myodes*** species, it is absent from clear-felled areas. It is herbivorous, eating green parts of grasses and herbaceous plants, nuts, seeds, bark, lichen, fungus, and insects, storing food for winter. In the autumn it stores seeds.

Figure 82. ***Myodes rutilus***, a species that lives in mossy spruce forests. Photo by Zbyszek Boratynski, through Creative Commons.

The habitat of the northern red-backed vole (***Myodes rutilus***; Figure 82) can change with seasons. In the Daisetsu Mountains of Japan, the vole was captured in areas with dense cover of the bamboo *Sasa* and a thin cover of mosses in July (Onoyama 1989). However, in September it showed a preference for dense tree cover.

In Alaska, West (1977) found a seasonal difference in the dispersion pattern of the northern red-backed vole. In summer, they lacked any pattern of aggregation. During midwinter they had moved to just one section of the trapping grid. In early spring, they once more dispersed with no pattern of aggregation. When West analyzed the vegetation structure, he found that the area of winter aggregation had a significantly thicker moss layer than the areas used in the summer. West considered this to indicate that the aggregation was the result of a limited area of suitable moss cover for overwintering.

The food of ***Myodes rutilus*** (Figure 82) is primarily seeds from dwarf shrubs and forbs, lichens, and above and belowground fungi (West 1982). I found no evidence that the voles eat bryophytes, so it is likely that the mosses serve to provide space for moving around between the snow and the frozen ground.

Myodes gapperi – Southern Red-backed Vole

The southern red-backed vole (***Myodes gapperi***; Figure 83) is also known as ***Clethrionomys gapperi***, living in Canada and the northern United States (Wikipedia 2017b). Pivorum and Bunch (2005) stated that its ideal habitat would be mesic with an abundance of litter, rotting logs, moss-covered rocks, exposed roots, and rock crevices. It often is restricted to mossy habitats (Headstrom 1970). It may burrow beneath ***Sphagnum*** (Figure 42) to make its nest, concealing it from view (Headstrom 1970). In peatlands it uses moss, among other bits of vegetation, to line the nest (Linzey & Brecht 2002).

In these peatlands and elsewhere it uses natural runways among the mosses, roots, and rocks (Linzey & Brecht 2002). ***Myodes gapperi*** (Figure 83) uses runways in warm weather, but tunnels through the snow in winter (Wikipedia 2017b). In New Jersey, USA, the red-backed vole lives only in ***Sphagnum*** peatlands of the pine barrens, where during winter, the moss is often frozen, necessitating using food gathered earlier for its winter supply (Stone & Cram 1902).

Figure 83. ***Myodes gapperi***, southern red-backed vole, with ***Sphagnum***. Photo by Phil Myers, through Creative Commons.

In humid forests it often occurs among mossy rocks (Komarek & Komarek 1938). Craig *et al*. (2014) hinted at the possibility that mosses may contribute to needed cover in areas with limited or no downed wood. It is the most abundant mammal among the tundra vegetation on Mt. Washington, New Hampshire, USA, where it lives among mosses, rocks, and dwarf willows. In a study comparing this species with ***Peromyscus keeni*** (mice) in Alaska, the southern red-backed vole preferred habitats with more moss cover than that of ***P. keeni*** (Smith *et al*. 2005). In fact, the growth of the young mice is inversely correlated to the percent cover of mosses on the forest floor. But in spring, even the voles have a negative correlation with moss, perhaps due to those sites being wetter.

Hodson *et al*. (2010) found that the southern red-backed voles responded to moisture availability. When moss cover was low, the voles had either reduced maximum potential fitness or an increased relative rate of decline of fitness with density. This species has high water requirements (Getz 1968) and generally occurs in mesic forests with moist microclimates and moss cover (Morris 1996; Orrock *et al*. 2000). The most abundant mosses in their habitats were ***Pleurozium schreberi*** (Figure 8), ***Ptilium crista-castrensis*** (Figure 11), and ***Sphagnum*** spp. (Figure 42). Hodson and coworkers (2010) found that in cut vs uncut forest stands, moss cover was the most important parameter in determining success of ***Myodes gapperi*** (Figure 83). They did not determine if the moss was essential, but rather it could be that the moss also occurred in the most moist habitats.

The red-backed voles (***Myodes*** spp.) are both omnivorous and opportunistic, with a diet that changes with the seasons and availability (Boonstra & Krebs 2012). In North America in spring and late fall, they mainly feed on dicot leaves. In summer and fall they eat seeds, berries, fruits, and insects. Throughout the year they also include monocots, mosses, and lichens (Perrin 1979; Vickery 1979; Merritt & Merritt 1978; Merritt 1981; Martell 1981).

Côté *et al*. (2003) reported 3% or more bryophytes in the gut of ***Myodes gapperi*** (Figure 83) in a black spruce (*Picea mariana*; Figure 84) forest. In a study in West Virginia, USA, small amounts of moss were retrieved from a few red-backed vole stomachs, but these never formed a major food source (Schloyer 1977). Maser and Maser (1988) emphasized that lichens were particularly important in winter in the Cascade Mountains of North America. However, these become depleted under the snow, forcing the voles to eat vascular plants and mosses. This is especially important because these voles do not hibernate, but are active year-round.

Figure 84. ***Picea mariana*** forest and bog, Lake County, Minnesota, USA. Photo by Jason J. Husveth, with online permission.

Myodes glareolus – Bank Vole

The bank vole, known by ***Myodes glareolus*** (Figure 85) and ***Clethrionomys glareolus*** (depending on your perspective), occurs from Europe through Central Asia (Jonsson *et al*. 2000; Macdonald 2001). This species builds its nest in a hole under the ground, but spends much of the day active above ground (EOL 2017a).

Figure 85. ***Myodes glareolus*** peering out of a tree hole. Photo by Johan Dierckx, Nature Diary.

In Poland, ***Myodes glareolus*** (Figure 85) was present in live and snap traps in ***Sphagnum*** (Figure 42) peat bogs and were predominant in that type of trapping (Cienchanowski *et al.* 2012). Torre and Arrizabalaga (2008) determined the habitat preferences of ***Myodes glareolus*** in a Mediterranean mountain range. They found that mosses accounted for far more (90%) of the variance than other measured environmental parameters. The bank voles preferred moist habitats where mosses were more abundant. But were the mosses important to them, or was it that the same habitat suited both the mosses and the bank voles? This is a recurring question with the voles and needs to be experimentally tested.

Myodes glareolus (Figure 85) does not appear to eat mosses as a regular diet component, but it is a herbivore, eating leaves of woody plants, soft fruits and seeds, and leaf litter (in winter) (Watts 1968). The mosses do occasionally enter consumption Figure 86), perhaps because it is an easier means to get the seeds or the springtime arthropods when they are present among the mosses. Bank voles in northern Sweden consumed mosses at a frequency of about 20% of their diet (Hansson 1979), suggesting that habitat, and perhaps latitude, may influence diet choices.

Figure 86. ***Myodes glareolus***, bank vole eating mosses in the Netherlands. Photo by Andrew Spink, with permission.

In European forests, the bank vole is the dominant small rodent species (Hansson 1983). It uses the moss ***Mnium hornum*** (Figure 44) for winter cover, as well as odd decaying logs (Kikkawa 1964). In these habitats, it consumes small amounts of moss, but bark is its primary food, especially in some winters (Hansson 1983). Gębczyńska (1976) likewise found mosses in gut analyses, being present in 30% of the vole stomachs in spring in an oak hornbeam forest. Nevertheless, vegetative parts of plants and insects comprised the major portion of the diet.

Apodemus sylvaticus – Wood Mouse

The ubiquitous wood mouse, ***Apodemus sylvaticus*** (Figure 87), is distributed throughout Europe (with the exception of Finland and northern parts of Scandinavia, the Baltic, and Russia) and parts of North Africa (Schlitter 2016). It uses mosses, leaves, and grass to construct its nest (Duke 2011). In Berkshire, UK, winter cover is provided by the moss ***Mnium hornum*** (Figure 44) (Kikkawa 1964). The wood mouse does not appear to eat mosses as a regular diet component, but rather is a seed eater (Watts 1968). The mosses do occasionally enter consumption, perhaps because it is an easier means to get the seeds and the springtime arthropods when they are present among the mosses.

Figure 87. ***Apodemus sylvaticus***, wood mouse, a species that uses mosses in its nest. Photo by Mick E. Talbot, through Creative Commons.

Pseudohydromys and *Mirzamys* – Moss Mice

These little-known genera have several species in the mossy forests of New Guinea (Helgen & Helgen 2009). I have been unable to find out why these are called moss mice. Perhaps it is because many of the species live in mossy forests. Likewise, little is known of their biology. We can only infer that mosses have some importance in the choice of habitat by some species. These moss-dwelling Papua New Guinea species include ***Pseudohydromys eleanorae***, ***P. murinus***, and ***P. ellermani*** in mossy montane forest; ***P. occidentalis*** (Indonesia and Papua New Guinea) and ***P. fuscus*** in mossy mid and upper montane forest; ***P. musseri*** in mossy upper montane forest (Helgen & Helgen 2009; Helgen & Wright 2017).

The related genus ***Mirzamys*** likewise is known from mossy upper montane forests in New Guinea (Helgen & Helgen 2009). ***Mirzamys louiseae*** occurs here and ***M. norahae*** lives in mossy rainforest habitats that can be characterized as elfin or upper montane forest.

Otomys sloggetti – Sloggett's Vlei Rat

The Sloggett's Vlei Rat (***Otomys sloggetti***; Figure 88) occurs typically in habitats with xeric soils and rocky outcrops of South Africa, but Lynch (1992) found it to be in large numbers in a mesic bog with no rocky outcrops. In the bog habitat, it was a burrower, occupying an extensive burrow system. The young are born during the warm wet months of October to March.

Figure 88. ***Otomys sloggetti***, a species that lives in boggy habitats. Photo by Terry Rosenmeier, through Creative Commons.

The boggy habitats are characterized by numerous hummocks about 20 cm high and 30 cm in diameter. Lynch (1992) suggested that these were originally formed by burrowing by ***Cryptomys hottentotus*** (Figure 48). Then the ***O. sloggetti*** (Figure 88) enlarged and cleaned the tunnels. These excavated areas are colonized by various tracheophytes, especially dwarf sedges, and mosses. The activity of the voles adds soil to the top, creating the hummock landscape. Others consider the hummocks to originate from freeze-thaw activity and not by the rodent activity.

Rattus rattus – Black Rat

The black rat (***Rattus rattus***; Figure 89) has travelled with humans, earning it the alternative name of ship rat. As a result of this human association, it is known from all continents (EOL 2017b).

Figure 89. ***Rattus rattus***, black rat, in tree in New Zealand, a species that includes mosses in its varied diet. Photo by James Russell, with permission.

The diet of the black rat is almost as varied as its distribution. Clout (1980) found that in a *Pinus radiata* plantation it consumed invertebrates, fungi, and plant material, including mosses and pine needle fragments. Unlike many of the voles, no seeds or fruits were eaten. Tobin *et al*. (1994 found seasonal changes in the diet of rats in a Hawaiian macadamia orchard. Mosses occurred in 48% of the rat stomachs, with a mean of 4% of the diet. The moss ***Sematophyllum caespitosum*** was a ubiquitous moss there on branches and tree trunks.

Leptomys – Water Rats

The genus ***Leptomys*** (Figure 90) generally occurs in mossy locations where it is endemic in New Guinea (Musser *et al.* 2008). Their habitats are often in the montane forests where they tend to be terrestrial but amphibious and are often similar to small-bodied mice or shrews that specialize on foraging among dense mosses and litter. Both ***Microhydromys*** (Figure 91) and ***Pseudohydromys*** (Figure 92) in New Guinea seem to be similarly adapted for foraging in dense moss and leaf litter. ***Paraleptomys*** likewise has a body form similar to that of ***Leptomys***. Musser and coworkers suggested that their small size and movements adapt ***Leptomys*** species to moving over the forest floor by hopping, and they have the ability to escape predators by "leaping in unexpected directions." The genus is nocturnal and carnivorous. Members live underground in nests they dig in the forest floor of tropical lowland evergreen and tropical montane evergreen rainforests.

Figure 90. ***Leptomys signatus***, in a genus that is endemic in mossy forests in New Guinea. Photo by Michael Pennay, through Creative Commons.

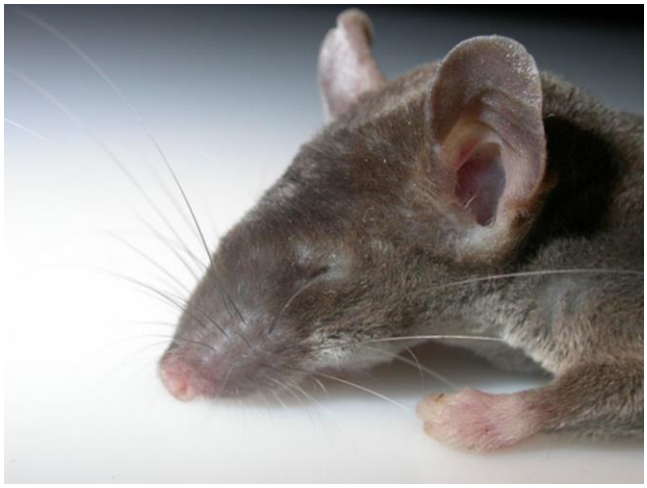

Figure 91. ***Microhydromys argenteus***, southern groove-toothed moss-mouse. Photo by Michael Pennay, through Creative Commons.

Figure 92. ***Pseudohydromys*** sp., in a New Guinea genus that is adapted for foraging in dense mosses and leaf litter. Photo from Alchetron, through Creative Commons.

Shrew Rats

Tucked away in the mossy forest of Sulawesi (Figure 93) in Indonesia is a group of Muridae known as shrew rats (Esselstyn *et al.* 2012). These are unique in lacking cheek teeth. They furthermore lack gnawing incisors, but instead have bicuspid upper incisors.

Figure 93. Sulawesi Moss Forest Gandangdewata. Photo courtesy of Kevin C. Rowe, Museums Victoria

Sulawesi is an island of Indonesia, formerly known as the Celebes. Approximately 62% of the mammalian species are endemic (Wikipedia 2018). The shrew rats are among these endemic species (Esselstyn *et al*. 2012). They run about among the mossy forest, and one must wonder if their peculiarities have been selected for the structure of their habitat.

Paucidentomys vermidax

The generic name ***Paucidentomys*** of this unusual mouse translates into few-toothed mouse, while ***vermidax*** refers to it as a worm devourer (Pappas 2012). These shrew rats were trapped in pitfalls in wet mossy forests at high elevations on Sulawesi Island in Indonesia.

Figure 94. ***Paucidentomys vermidax*** in Sulawesi. Photo courtesy of Kevin C. Rowe, Museums Victoria.

The newly described ***Paucidentomys vermidax*** (Figure 94) was collected in two pitfall traps in the mature forest. The diet of soft-bodied earthworms is consistent with the lack of grinding teeth. Esselstyn *et al*. 2015) suggested that ***P. vermidax*** was a specialist on earthworms of the moist forests above ca 1500 m. The researchers conjecture that the mouth was used only for food capture, not for processing it.

Hyorhinomys stuempkei

Paucidentomys (Figure 94) was not the only shrew rat to be running around among the mosses in Sulawesi forests. In 2015, Esselstyn *et al*. named ***Hyorhinomys stuempkei*** (Figure 95-Figure 96) as another shrew rat there. It has a distinctive large, flat, pink nose in which the nares face forward like a pig's (Figure 94). It is further distinctive in having especially large ears. But alas, so far only five of these are known, so habitat needs are speculative.

Figure 95. New genus and species (***Hyorhinomys stuempkei***) of hognose rat in Sulawesi. Photo by Kevin C. Rowe, Museums Australia, with permission.

Figure 96. ***Hyorhinomys stuempkei*** in Sulawesi. Photo courtesy of Kevin C. Rowe, Museums Victoria.

In addition to ***Paucidentomys*** (Figure 94) and ***Hyorhinomys*** (Figure 95-Figure 96), shrew rats on Sulawesi include ***Echiothrix*** (Figure 97), ***Melasmothrix*** (Figure 98), ***Sommeromys*** (Figure 99), and ***Tateomys*** (Figure 100-Figure 101) (Esselstyn *et al.* 2015). The addition of ***Paucidentomys*** brings the number of shrew rats on Sulawesi to six genera and eight species. The habitat for this latest species is undisturbed lower montane forest where mosses are abundant and cover much of the surfaces, including canopy epiphytes.

Figure 97. ***Echiothrix centrosa*** from lowland forest of Sulawesi; some members of this genus occur in the mossy forest, but not this one. Photo courtesy of Kevin C. Rowe, Museums Victoria.

Figure 98. ***Melasmothrix naso*** in Sulawesi. Photo courtesy of Kevin C. Rowe, Museums Victoria.

Figure 99. ***Sommeromys macrorhinus*** in a mossy Sulawesi forest. Photo courtesy of Kevin C. Rowe, Museums Victoria.

Figure 100. ***Tateomys macrocercus*** in a Sulawesi mossy forest. Photo courtesy of Kevin C. Rowe, Museums Victoria.

Figure 101. ***Tateomys rhinogradoides*** in a Sulawesi mossy forest. Photo courtesy of Kevin C. Rowe, Museums Victoria.

Gracillimus radix

The slender root rat, ***Gracillimus radix*** (Figure 102-Figure 103), was discovered in 2016 in the Indonesian island of Sulawesi (Rowe *et al*. 2016). This species forages among the roots (Phillips 2016), where it eats both plants and animals (Rowe *et al*. 2016). Phillips suggested that its excessive whiskers (Figure 104-Figure 105) may help it find food (presumably roots and insects) among the mosses and roots of its native forest.

Figure 102. ***Gracillimus radix*** in Sulawesi mossy forest. Photo by Kevin C. Rowe, Museums Victoria, with permission.

Figure 103. ***Gracillimus radix*** in Sulawesi, showing the small digits on the paw. Photo by Kevin C. Rowe, Museums Victoria, with permission.

Bunomys

Eight species of ***Bunomys*** are present on Sulawesi (Musser 2014). All are nocturnal, terrestrial, and endemic to the island. Not enough is known about the physiology or behavior of the genus to generalize on the importance of the mosses to its habitat. They could maintain the moisture needed for the ***Bunomys***, or for its food organisms. They could be important cover against predators. They might provide nesting materials – mosses were used in nests made in cages in the lab. But the ***Bunomys*** species may simply prefer the same habitats where these mosses thrive.

Figure 104. ***Gracillimus radix*** in Sulawesi mossy forest,, showing the long whiskers. Photo by Kevin C. Rowe, Museums Victoria, with permission.

Figure 105. ***Gracillimus radix*** in Sulawesi, showing the unusual nose. Photo by Kevin C. Rowe, Museums Victoria, with permission.

Bunomys chrysocomus is relatively widespread on the island, occurring in both lowland tropical evergreen and montane rainforests, occupying an elevational range of 250-2200 m) (Musser 2014). It was found one night in a runway beneath a rotting, moss-covered tree trunk of the forest floor. On another occasion it was 1.5 m above a stream in a damp, moss-covered rock cliff face. Others were in dense undergrowth with no mosses. The ***B. chrysocomus*** seem to have a broad diet of invertebrates, small vertebrates, and fruit, with earthworms appearing to be one of the preferred foods. The latter are broken into pieces in the mouth.

Figure 106. ***Bunomys chrysocomus*** in mossy forest of Sulawesi. Photo courtesy of Kevin C. Rowe, Museums Victoria.

Bunomys coelestis is endemic to montane forests on Gunung Lompobatang, the high volcano at the southern end of the southwestern peninsula of Sulawesi (1829-2500 m) (Musser 2014).

Bunomys prolatus is only known from the mountain forest on Gunumg Tambusisi (1982 m), where it has been captured among mosses (Musser 2014). The habitat is one of short trees (4 m) with a heathlike vegetation and deep moss cover. All but one individual was trapped at night. That one was in deep moss during the day, suggesting the mosses may serve as daytime cover.

Bunomys torajae is from montane forest on Gunung Gandangdewata (2500-2600 m) (Musser 2014).

Bunomys fratrorum (Figure 107) seems to be restricted to the northeastern end of the northern peninsula, occupying lowland tropical evergreen and montane rainforests (coastal plain to 1982 m) (Musser 2014).

Bunomys andrewsi occurs mainly in lowland tropical evergreen rainforests in the core of Sulawesi and the coastal plain to 1600 m (Musser 2014). It is not restricted to primary forest, occurring also in secondary growth and even village gardens. Some of its habitats are very mossy. Stomach contents included figs, seeds, termites, and insects, especially larvae. In one case fragments of moss were found in the stomach, possibly being consumed along with insects.

Bunomys penitus (Figure 108) seems to be restricted to montane regions of the west-central mountain block and Pegununan Mekongga (1285-2287 m) (Musser 2014). It was collected in a runway beneath a moss-covered tree trunk on the forest floor. Among the collections, many were caught in traps placed in runways in the spaces beneath the moss-covered tree roots or associated with decaying moss-covered trunks. However, in an area with thick mosses (2.5 cm), there was no path worn in the moss. Nevertheless, in the primary tropical lower and upper montane rain forest (1740-2287 m) this species frequently was trapped beneath old treefalls that had become covered with dense moss, decaying into the wet forest floor or in other association with mosses. The mosses may actually have been an impediment to food capture. Earthworms and other invertebrates would require excavation from beneath the thick moss mat. ***Bunomys penitus*** has short front claws compared to those of ***B. chrysocomus***, ***Melasmothrix***, and ***Tateomys***, making it difficult for ***B. penitus*** to extract the food items. Snails were eaten by biting away edges of the shell to get at the soft body. Bits of moss were sometimes consumed when they adhered to consumed fungi.

Figure 107. ***Bunomys fratrorum*** in mossy forest of Sulawesi. Photo courtesy of Kevin C. Rowe, Museums Victoria.

Figure 108. ***Bunomys penitus*** in mossy forest of Sulawesi. Photo courtesy of Kevin C. Rowe, Museums Victoria.

Bunomys karokophilus is currently known only from lowland tropical evergreen rainforest in the northern portion of the west-central mountain block (823-1150 m)

(Musser 2014). It is often associated with mossy habitats. It gets its name because it seems to feed almost exclusively on karoko, an ear fungus, *Auricularia delicata* (Figure 109). The karoko grows only on wet, decaying tree trunks and limbs on the ground. These are usually free of other kinds of fungi and lack extensive moss cover.

Figure 109. ***Auricularia delicata*** group, primary food for ***Bunomys karokophilus***. Photo by Josef Papi, through Creative Commons.

Summary

Rodents can have major impacts on the bryophyte communities, especially in the Arctic. Many rodents have mosses in the gut and feces, but these often seem to be the result of accidental intake. Nevertheless, some rodents seem to include bryophytes as an important part of the diet, often increasing the percentage of intake in winter. Researchers have suggested that this switch may be a need for nitrogen, arachidonic acid, or fiber. In other cases, it may be a simple matter of availability. A number of **Microtine** rodents consume mosses in the winter, even though the mosses are poorly digested, being high in fiber, and providing little nitrogen or digestible energy, but often the nutrient content in the Arctic is superior or differs little from that of tracheophytes in the region.

The shoot tips seem most desirable for food, but in winter the moss may be clipped at the bottom. Some records indicate that moss capsules are also eaten. Such grazing in northern habitats can have severe impacts on the moss communities, as indicated by exclosures. A 1-year time lag between feeding and the evidence of bryophyte species changes is common. Weft and other large species can benefit from regeneration from rhizomes and dispersal of fragments or propagules.

Many rodents use mosses in the construction of nests, particularly as part of the lining. In bogs, several species may coexist in a single bog, some using them for food or to make nests, tunnels, or runways.

Bryophytes are impacted by the rodents in multiple ways. Negative impacts include diminished cover and competition from flowering plants. But at other times they may benefit through exposed soil and removal of taller grasses. The rodents can also serve as dispersal agents, and runways open new habitats where colonizers can grow, increasing diversity.

Moss users in the **Muridae** include ***Micromys minutus*** (minor food), ***Myodes rufocanus*** (among nest materials), ***M. rutilus*** (aggregate in mosses in winter), ***M. gapperi*** (mossy habitats, minor food), ***M. glareolus*** (mossy habitats, winter cover, minor food), ***Apodemus sylvaticus*** (minor food, winter cover), ***Pseudohydromys*** (mossy rainforest), ***Mirzamys*** (mossy rainforest), ***Otomys sloggetti*** (makes hummocks in bogs), and ***Rattus rattus*** (minor food).

Shrew rats seem to be primarily associated with mossy areas and some seem to be physically adapted to foraging among the bryophytes. There is no evidence thus far that they choose bryophytes as food.

Acknowledgments

This chapter has benefitted greatly from anecdotal records sent to me by bryologists and friends who observed these small rodents interacting with mosses in the field. Kate Frego has provided invaluable anecdotal experience to me. Kevin Rowe was particularly helpful in sharing papers, photographs, and personal observations.

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Figure 1. This exposed runway of the heather vole (***Phenacomys intermedius*/*ungava***) shows the clippings of mosses and barren nature of their path. According to Kate Frego, this appearance is common when the snow melts in the spring. Photo courtesy of Kate Frego.

Cricetidae – Hamsters, Voles, Lemmings, and New World Rats and Mice

The voles, lemmings, and muskrats are known as the microtine rodents, the **Microtinae**. This subfamily comprises the largest numbers among the **Rodentia** in the Northern Hemisphere. They are distinguished by their molar teeth, which have prismatic cusps in the shape of alternating triangles. These sharp teeth are suitable for grinding and are an adaptation to the herbivorous diet. Batzli and Jung (1980) demonstrated that microtine rodents near Atkasook, Alaska, eat mosses.

Chionomys nivalis – Snow Vole

The snow vole (***Chionomys nivalis***; Figure 2) is distributed from southern Europe to the Near and Middle East (Castiglia *et al*. 2009), extending to the Caucasus, Turkey, Israel, Lebanon, Syria, and Iran (Shenbrot & Krasnov 2005). The European populations are restricted to rocky and mountainous areas at mostly higher elevations (Castiglia *et al*. 2009).

Figure 2. ***Chionomys nivalis***, a species that may suffer from heavy metal toxicity by eating bryophytes and lichens. Photo by Svíčková, through Creative Commons.

Janiga *et al*. (2016) reminded us of the role mosses could play in consumption of lead and other pollutants by this and other microtine species. The concentrations of Pb, Cd, Zn, and S in mosses from the Alps revealed rising levels with altitude, despite the scarcity of polluters at higher elevations (Zechmeister 1995; Šoltés 1998). These pollutants seem to have arrived with the precipitation through long-distance transport. Several researchers have suggested that mosses (and lichens) may have a significant influence on the lead concentrations in ***Chionomys nivalis*** (Figure 2) (Sivertsen *et al*. 1995; Belcheva *et al.* 1998; Metcheva *et al*. 2008; Janiga *et al*. 2012). Janiga and coworkers considered this to be a special problem due to winter consumption of mosses.

Microtus agrestis – Field Vole

The field vole (***Microtus agrestis***; Figure 3) is a widespread European Palaearctic species, ranging from western Europe eastwards through Russia to Lake Baikal in south-east Siberia.

Figure 3. ***Microtus agrestris*** among mosses. Photo from Wikimedia Commons.

It is not just in the Arctic that rodents eat mosses. Ferns (1976) found that ***Microtus agrestis*** (Figure 3) eats both mosses and liverworts in a larch plantation in Great Britain. The mosses comprised 20% of the area of materials in the **feces** (scat) under the microscope. ***Microtus agrestis*** exhibits seasonal differences in diet. Grasses are the primary food, with the greatest consumption rate in winter (Faber & Ma 1986). Herbs and mosses are also important, especially in spring and summer. Considerable variability occurs in the diet, depending on the kind of habitat and time of year. The moss ***Hypnum cupressiforme*** (Figure 4) forms an important part of the diet, but it is interesting that it seems not to be consumed in winter.

In a study of small rodents in Scandinavia, Hansson (1971) demonstrated the need of more water by herbivores than that needed by granivores. This can explain their choice of mossy habitats and may even explain their consumption of the mosses.

Microtus agrestis (Figure 3) in Fennoscandia exhibits population cycles (Turchin & Hanski 2001). Many researchers have attempted to model these cycles, but causes are still controversial. Turchin and Hanski concluded that their evidence supports the predation hypothesis. Many models have considered food to be the driving factor, but Turchin and Hanski considered this to hold only in systems like the moss-eating lemmings. Nevertheless, a disappearance of mosses due to consumption, runways under snow, or fires could make the habitat unsuitable for these small, moisture-dependent rodents.

Figure 4. ***Hypnum cupressiforme*** var ***cupressiforme***, an important food for ***Microtus agrestis***. Photo by David Holyoak, with permission.

Like ***Chionomys nivalis*** (Figure 2), ***Microtus agrestis*** (Figure 3) are subject to consumption of heavy metals that have become incorporated into their food items (Ma *et al*. 1991). And these can enter their bodies with mosses as the carrier. Fortunately, ***Microtus agrestis*** consumes only small amounts of ***Hypnum cupressiforme*** (Figure 4) in these areas, a moss known to contain considerably more lead and cadmium than the flowering plants in the diet.

Microtus pennsylvanicus – Meadow Vole

The meadow vole (***Microtus pennsylvanicus***; Figure 5) is the North American counterpart of ***M. agrestis*** (Figure 3). It occurs throughout most of Canada and Alaska, USA, south through the northern half of the United States, to Oregon, northern Utah, central New Mexico, Kansas, northern Missouri, Georgia, and South Carolina; it is disjunct (by 500 km) in Florida, USA, and Chihuahua, Mexico (Hall 1981; Cassola 2016a).

Figure 5. ***Microtus pennsylvanicus***, a species that makes paths among mosses. Photo by John White, with permission.

These voles occupy a wide variety of habitats, ranging from dry pastures and wooded swamps to marshes and orchards (Cassola 2016a). The soil needs to be loose and organic to permit tunneling. Their underground tunnels are extensive. In Wisconsin, Getz (1970) found that the meadow vole inhabits areas that have a dense, spongy mat comprised of several moss species. The voles make paths among these mosses, but the paths do not have the character of distinct runways.

The meadow vole seems to prefer introduced species over native ones for its food (Thompson 1965), perhaps indicative of its European ancestors. When given 30 plant species choices from a variety of habitats, eight of the top ten chosen foods were introduced species. By contrast, the native boreal plants and bog plants occupied the last eight positions of preference. Peat moss (***Sphagnum***; Figure 6) was scarcely touched.

Figure 7. ***Ptilium crista-castrensis***, a moss eaten by ***Phenacomys intermedius***. Photo by Janice Glime.

Figure 6. ***Sphagnum capillifolium***, in a genus among the least preferred among the 30 plants provided to ***Microtus pennsylvanicus*** as food choices. Photo by David Holyoak, with permission.

Figure 8. ***Pleurozium schreberi***, a moss eaten by ***Phenacomys intermedius***. Photo by Janice Glime.

Kate Frego relates that during her summer PhD research in the boreal forest of northern Ontario, Canada, she observed both red-backed voles (***Myodes***) and meadow voles (***Microtus pennsylvanicus***; Figure 5) eating moss shoots, tips first. "I did a little test with the meadow voles (which are placid enough to sit on my hand and eat!), and offered them choices which I ranked. I have to say it was a small sample size, 4 voles as I recall, but they were very consistent! They seemed to 'prefer' ***Ptilium crista-castrensis*** (Figure 7), and ***Pleurozium schreberi*** (Figure 8), would occasionally take ***Ptilidium ciliare*** (Figure 9), and politely declined all the ***Dicranum*** spp. I had at hand [***D. polysetum*** (Figure 10) and ***D. scoparium*** (Figure 11)]. Unfortunately, I have no info on whether the munched vegetative bits survived passage through their guts. (I actually have photos of one meadow vole scoffing down a ***Ptilium*** shoot)."

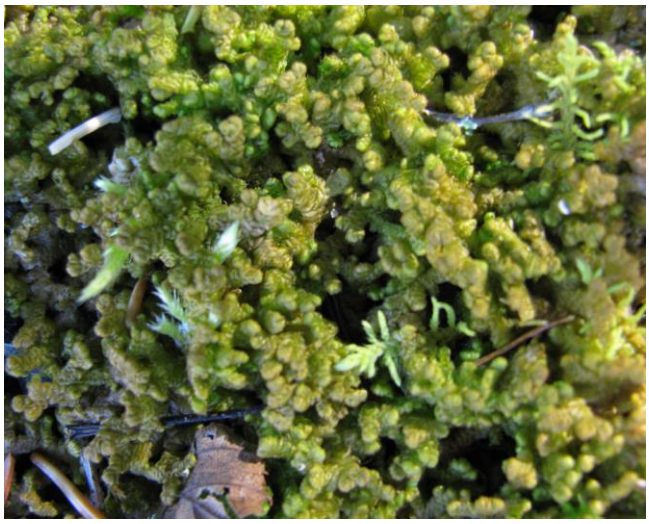

Figure 9. ***Ptilidium ciliare***, a leafy liverwort eaten by ***Phenacomys intermedius***. Photo by Janice Glime.

Figure 10. ***Dicranum polysetum***, a moss eaten by ***Phenacomys intermedius***. Photo by Janice Glime.

Figure 11. ***Dicranum scoparium***, one of the preferred forest mosses for the wood lemming. Photo by Janice Glime.

Linzey (1984) cautioned that estimates of mosses in fecal samples of this and other rodents may be overestimates of the diet percentage because they, along with monocots, have poor digestibility (Batzli & Pitelka 1971), giving them over-representation. Linzey found that mosses were only eaten by ***Microtus pennsylvanicus*** in winter, whereas Frego observed them eating mosses in summer.

Microtus oeconomus – Tundra Vole

The tundra vole, ***Microtus oeconomus*** (Figure 12), has the northernmost distribution of any of the North American species of ***Microtus***, and is common also in the northern parts of Eurasia (known there as root voles) (EOL 2017a). Although the habitat preference is moist meadows near water, the tundra vole can also inhabit ***Sphagnum*** bogs (Figure 13) (Ciechanowski *et al*. 2012).

Alaskan populations of the tundra vole consume mosses, but these comprise less than 10% of the diet (Batzli & Jung 1980). Batzli and Jung (1980) suggested that grazing pressure by the tundra voles may be competitive with both the brown lemmings (***Lemmus sibiricus***; Figure 14) and collared lemmings (***Dicrostonyx torquatus***) because of overlapping food niches, thus restricting the distribution of the voles through competition with lemmings.

Figure 12. ***Microtus oeconomus***, a species that can be found in ***Sphagnum*** bogs. Photo by аимаина хикари, through Creative Commons.

Figure 13. ***Picea mariana*** forest with ***Sphagnum***, Lake County, MN. Photo by Jason J. Husveth, with online permission.

Figure 14. ***Lemmus sibiricus***, a potential competitor for food with ***Dicrostonyx torquatus***. Photo by Ansgar Walk, through Creative Commons.

Microtus pinetorum – Pine Vole, Woodland Vole

The woodland vole (***Microtus pinetorum***; Figure 15) is distributed from extreme southern Ontario, Canada, and throughout the eastern United States with the exception of peninsular Florida and the coastal plains of the southeastern

states; there is a disjunct population in Texas (Cassola 2016b). The rock vole (***Microtus chrotorrhinus***; Figure 16) and the woodland vole (***Microtus pinetorum***) both live where there are rocks, mosses, ferns, and forbs in North America (Kirkland & Knipe 1979; Christian & Daniels 1985; Merritt 1987). This relationship suggests that these voles may depend on the bryophytes, but detailed studies seem still to be needed.

Figure 15. ***Microtus pinetorum***, a woodland vole that lives in habitats with bryophytes and uses them in nesting and runways. Photo by Phil Myers, through Creative Commons.

Pine voles (***Microtus pinetorum***; Figure 15) use bryophytes for nest sites and runways (Rhodes & Richmond 1985). Given the choice of mixed loam with peat moss (3:1 vol/vol), base mixture with added gravel (3:2 v/v), or (1:1 v/v), the moles chose the loam/peat moss mixture for subsurface tunnels and nests over the other choices. In fact, they always avoided the soil/stone mix. One reason for their choice of mossy habitats may be their need for temperatures below 30ºC (Rhodes & Richmond 1985). I would expect dark soil to heat more readily than moist, aerated mosses. We need data to support this, however, because we also know that mosses easily reach temperatures higher than that of air, especially at the surface (Nørgaard 1951; Hribljan & Glime, unpublished data). On the other hand, the sub-surface temperature can experience a much smaller diurnal temperature range (Nørgaard 1951).

Microtus xanthognathus – Taiga Vole

The taiga vole (***Microtus xanthognathus***) inhabits northwestern Canada to Alaska (Wikipedia 2017). It lives in forested habitats near streams, lakes, or bogs. Its runways are a combination of underground and surface runways (EOL 2017c). These voles construct communal nests and food caches in August and September. The nests are made of dry grasses and are located ~15-20 cm underground. The food supply must be reached through the nest. The taiga voles huddle together in groups of 5-10 individuals, keeping each other warm and sharing the food during winter. The life span is short, as in most other voles. The young voles are born in the summer and breed the next summer. They do not survive the following winter.

The taiga vole (***Microtus xanthognathus***) requires an abundant supply of rhizomes for winter food (Wolff & Lidicker 1980; Conroy & Cook 1999). In summer it feeds on horsetails, grasses, and berries. But mosses provide it with ground cover and are a necessary part of its habitat.

Microtus chrotorrhinus – Rock Vole

The rock vole (***Microtus chrotorrhinus***; Figure 16) is distributed in Canada from Labrador through the Gaspé Peninsula, New Brunswick, west to Ontario, and in the USA from northeastern Minnesota southward at higher elevations to New England, New York, and northeastern Pennsylvania, and disjunctly in the southern Appalachians to Virginia, western North Carolina, and eastern Tennessee (Kirkland & Jannett 1982; Handley & Pagels 1991).

Figure 16. ***Microtus chrotorrhinus***, a species that is most abundant in moist mossy areas. Photo by Roger W. Barbour, Smithsonian Institutes, with online permission.

The rock vole in Virginia, USA, lives in sites with abundant vegetation, mosses, talus- and rock-laden slopes, typical of the habitats for this species (Orrock *et al*. 1999). In contrast to these rocky sites, in Labrador and other areas they are most common in moist mossy areas near streams and ponds, thick brush, and open-canopy forests (Buech *et al*. 1977; Kirkland & Knipe 1979; Kirkland & Jannett 1982; Lansing 2005).

Orrock and Pagels (2003) found that more mosses were present in yellow birch and other forests with rock voles than those without these rodents. The ability of mosses to ameliorate the effects of air temperature may contribute to their preference for mossy habitats (Fuller *et al*. 1969). Kirkland and Jannett (1982) considered the moss cover of yellow birch and rock vole sites to be indicative of the cool, moist microclimate there, but suggested that the mosses also may serve as a reserve food source.

One rock vole (***Microtus chrotorrhinus***; Figure 16) in New York, USA, was actually snap-trapped with the moss ***Atrichum undulatum*** (Figure 17) in its mouth! (Whitaker & Martin 1977). The stomach also contained the same moss in a relatively unchewed state. Among those voles examined, leafy portions of ***A. undulatum*** comprised 5.2% of the stomach contents.

Figure 17. ***Atrichum undulatum***, a moss that forms part of the diet of ***Microtus chrotorrhinus***. Photo by Brian Eversham, with permission.

These voles also pull clumps of ***Sphagnum*** (Figure 6) for building their nests (Martin 1971), which are lined with grass and have multiple entrance tunnels (North Carolina GAP Analysis Project 2005). In the Appalachian and Adirondack Mountains of eastern North America, this species occurs in small populations that live among large, moss-covered rock fragments (Kilpatrick & Crowell 1985).

Phenacomys intermedius – Western Heather Vole

Phenacomys intermedius was once considered to include the eastern North America populations, but some authors have separated the eastern populations into ***Phenacomys ungava*** (Cassola 2016c). Nevertheless, some consider ***P. ungava*** to be only a subspecies. Since it is not always clear which species is included in the study, I will use ***Phenacomys intermedius*/*ungava*** to designate my uncertainty.

The distribution of the western heather vole (***Phenacomys intermedius***; Figure 18) extends across northern Canada from Labrador to the Yukon Territory and in the USA from the western mainland south to New Mexico (Banfield 1974; Fitzgerald *et al*. 1994). It is active both night and day.

Kate Frego (Bryonet) relays her experience with heather voles in northern Ontario, Canada: "In the summer, while trying to photograph a Heather Vole (in my hand; Figure 18), I tickled its nose with a sprig of moss, and was stunned when it grabbed the moss and ate the whole sprig."

Figure 18. ***Phenacomys intermedius*/*ungava***, eastern heather vole. Photo courtesy of Kate Frego.

The western heather vole (***Phenacomys intermedius***; Figure 18) lives in mountains in the areas near or above **timberline** (altitude at which trees cease to grow into actual trees; treeline; Figure 19) (EOL 2017d). Their food is typically leaves, seeds, berries, and bark of willow and other shrubs. Their summer nests are underground, but winter nests occur at ground level next to a bush, rock, or stump. Their nests are comprised of twigs, leaves, and grass. Males are territorially aggressive during mating season, but in winter they may nest together to maintain warmth.

Figure 19. Treeline on mountain over Firth River in Ivvavik National Park, YT. Photo by Daniel Case, through Creative Commons.

In Minnesota, USA, the heather vole (***Phenacomys intermedius*/*ungava***; Figure 18) occurs in a wide range of habitats. These include open pine and spruce forests with an understory of heath, shrubby vegetation, and moist, mossy meadows (Banfield 1974; Christian 1999). These locations are not above timberline, but winters are long, cold, and snowy.

It appears that the connection of heather voles with mosses may be accidental in some cases, at least in some cases. Côté *et al*. (2003) reported that ***Phenacomys intermedius*/*ungava*** in a black spruce forest in eastern Canada had 3% or more bryophytes among the material retrieved from the gut. Other observations demonstrate that this species does indeed eat mosses (Glime 1996). It was caught in the act grabbing and nibbling the moss ***Ptilium crista-castrensis*** (Figure 7), from tip down to base. This vole also ate ***Pleurozium schreberi*** (Figure 8) and ***Ptilidium ciliare*** (Figure 9). On the other hand, it rejected ***Dicranum polysetum*** (Figure 10). The winter runways, constructed at the ground surface under the snow, were conspicuous after snowmelt by the closely clipped ***Dicranum*** with its clippings lying nearby (Figure 1).

Phenacomys ungava – Eastern Heather Vole

The eastern heather vole (***Phenacomys ungava***; Figure 20-Figure 21) is widely distributed across Canada, but its populations seem to be sparse (EOL 2017e), partly due to its avoidance of traps. Recently most authors consider it to be part of the species ***P. intermedius*** (Figure 18) (Cassola 2016c). It seems to avoid traps, making it hard to estimate the population sizes (EOL 2017e). These voles often pile their food near their burrows at night,

making it accessible for daytime food. They don't hibernate, and their winter food source is unknown. Nevertheless, they clip mosses in their runways (Figure 22), potentially dispersing them to other locations.

Figure 20. ***Phenacomys ungava***, a species that uses mosses in its nests. Photo by Gerda Nordquist, MN DNR.

Figure 21. ***Phenacomys intermedius*/*ungava***, heather vole, a species that clips ***Dicranum*** (Figure 10) species in winter and is known to eat other boreal bryophytes. Photo courtesy of Kate Frego.

Figure 22. Close view of heather vole runway in May, showing moss clippings. Photo courtesy of Kate Frego.

Phenacomys ungava (Figure 20-Figure 21) constructs its nests just below the ground surface, using grass, moss, and other materials (Foster 1961). Braun *et al*. (2013) described the summer nests similarly as constructed of soft materials, including grass, moss, leaves, and plant down. Its habits are poorly known because of the difficulty of trapping it and of keeping it alive.

Arborimus albipes – White-footed Vole

The white-footed vole (***Arborimus albipes***; Figure 23) lives in trees in dense forests of the Pacific Northwest of North America, seldom seeing direct sunshine through the canopy (Jewett 1920). They commonly live near rivers or streams (EOL 2017f). Their home is on the moss-covered forest floor (Jewett 1920). Their burrows have never been observed, but their claws suggest that they are adapted for burrowing (EOL 2017f). They are active year-round.

Figure 23. ***Arborimus albipes***, white-footed vole, an inhabitant of moss-covered forests. Photo by Michael Durham, through Creative Commons.

The abundant mosses in their native forests provide them with some of their food; seeds, fruits, fungi, and animals were absent among their ingested material (Verts & Carraway 1995).

Arborimus longicaudus – Red Tree Vole

The red tree vole (***Arborimus longicaudus***; Figure 24) is another native of the Pacific Northwest (Manning & Maguire 1999). It is likely that ***Arborimus longicaudus*** is not a committed moss user. It eats conifer needles. Nevertheless, the nests (see discarded resin ducts in Figure 25) can contain mosses (Biswell *et al*. 2017). "From the ground, red tree vole nests generally appear as dark haphazard accumulations of twigs, needles, moss, and/or lichens on the topside of a large branch or whorl of branches against the bole of a tree." Some are known to nest under the mosses that cover large branches of old trees (Carey, in Wilson & Ruff 1999).

Figure 24. ***Arborimus longicaudus***, red tree vole, in a spruce tree. This species includes mosses among its nesting materials. Photo by Stephen DeStefano, through public domain.

Figure 25. Discarded resin ducts from Douglas fir, discards from nest-making activity of ***Arborimus longicaudus*** (tree vole). Photo by Petrelharp, through Creative Commons.

Peromyscus maniculatus – Deer Mouse

Deer mice (***Peromyscus maniculatus***; Figure 26) are the most widespread of the North American rodents (EOL 2017g), extending from the northern treeline in Alaska and Canada southward to central Mexico, but absent in the eastern United States (Baker *et al*. 1983). They likewise have a wide range of habitats, occupying almost every kind of habitat available (EOL 2017g). They can easily climb, tunnel through snow, or run about on the surface. Nests in this species are typically located in dead trees, under logs and stumps, or among mosses (Sharpe & Millar 1991). Their association with humans includes nesting in such human creations as mattresses (EOL 2017g).

Figure 26. ***Peromyscus maniculatus*** in a spruce tree. Photo by Phil Myers, through Creative Commons.

I opened my email one day to find a delightful story unfolding from a former undergraduate student of mine, Steve Juntikka. A fat little mouse, which was later identified as ***Peromyscus maniculatus*** (Figure 27), on Isle Royale was busily consuming capsules from the moss ***Funaria hygrometrica*** (Figure 28). Isle Royale National Park is the largest island in Lake Superior on the border of USA and Canada. The mice most likely arrived as stowaways.

Figure 27. Juvenile ***Peromyscus maniculatus*** on Isle Royale, Michigan, devouring capsules of ***Funaria hygrometrica***. Photo courtesy of Steve Juntikka.

Figure 28. ***Funaria hygrometrica*** one day after the mouse dined on it, showing the orange tips of setae where capsules have been removed. Photo courtesy of Steve Juntikka.

Juntikka described the lunching behavior of the mouse (Figure 27), "Looks like the capsules were the best tasting and you have never seen those little whiskers move so fast. I could not believe the front feet moving with a doggy paddle motion to rake in the capsules. The hind legs were spread apart to balance the weight while each capsule disappeared with delight." The next day there weren't many capsules left (Figure 28).

Like most of the rodents, deer mouse populations fluctuate, typically 3-5 years, and this seems at times to be correlated with food availability (EOL 2017g). Deer mice are night active, feeding opportunistically on seeds, nuts, fruits, berries, insects, and other animal matter, as well as any human food scraps they find.

Bryophytes are not a major part of the diet, but Côté *et al*. (2003) found that the gut contained 3% or more mosses

in their black spruce habitat. The diet changes between juveniles and adults (Van Horne 1982). In a coniferous forest, the adults consumed more hard-bodied insects than did juveniles. They ate few monocots, including grasses, concentrating on dicots and ferns, but a few mosses were eaten.

Neotoma cinerea – Bushy-tailed Woodrat

The bushy-tailed woodrats (***Neotoma cinerea***; Figure 29) extend from the Yukon Territory and Northwest Territories of Canada south to Arizona and New Mexico, USA, and from California east to the Badlands in South Dakota (EOL 2017h). They are very territorial, with both males and females marking their territories with a musky scent and white color on rock ridges. They pile vegetation and other collected items, making middens of a conspicuous size. These are not mere temporary constructions, but edifices on which the animals may defecate or urinate. When the middens bake in the sun, they become as hard as rocks and can last for tens of thousands of years!

Figure 29. ***Neotoma cinerea***, a species that uses dry mosses and grasses in its nests. Photo by Ken Cole, USGS, through public domain.

Based on observations in five localities, Brown (1968) found that the nests themselves must be dry, relatively dark, and create inaccessibility to would-be predators (Figure 30). The portion constructed by the woodrat is often an open, cup-shaped nest composed of dry mosses and grass.

Figure 30. ***Neotoma*** sp., Packrat, midden in Nevada, USA. Photo by Toiyabe, through Creative Commons.

Foraging occurs at long distances from the nest, up to 470 m for females (Topping & Millar 1996). Topping and Millar suggested that this long distance may be related to availability of appropriate food. This nighttime activity is affected by the brightness of moonlight, most likely avoiding the increased predation in bright moonlight as they cross open areas to reach foraging areas with greater cover (Topping *et al*. 1999). Morton and Pereyra (2008) verified nighttime haying behavior of these rodents in Wisconsin, USA, where they gathered mostly poisonous flowering plants. They found that the food plants were cut and stacked to dry before they were placed within the dens, possibly decreasing the toxicity.

Neotoma fuscipes – Dusky-footed Woodrat

The dusky-footed wood rat (***Neotoma fuscipes***; Figure 31) lives in the extreme western United States, from the Columbia River in western Oregon south to the inner Coastal Range of west-central California, and the north Sierra Nevadas, east-central California (EOL 2017k). It typically lives in woods that have a dense understory. Even though they are very small, they build large (up to 1 m in diameter and height), elaborate houses made of sticks (Figure 32). These may be located on the ground, in the tree canopy, on rocky slopes, or even in abandoned buildings. These "houses" typically include several nesting and resting chambers as well as several used for storing food and "treasures" collected from among human creations. English (1923) reported that this species uses mosses to line compartments of its nests, keeping them clean and well kept. The toilet may be within the house or outside it (EOL 2017k). Although the woodrats are solitary, these houses may be used successively by a number of woodrats. Mosses do not seem to be part of the diet.

Figure 31. ***Neotoma fuscipes***, a species that uses mosses to line its nests. Picture by Mbmceach, through Creative Commons.

Figure 32. ***Neotoma fuscipes*** nest. Photo by Donna Pomeroy, through Creative Commons.

Neotoma magister – Allegheny Woodrat

The Allegheny woodrat (***Neotoma magister***; Figure 33), an endangered species (Mengak 2002), is the only woodrat in the Appalachian Mountain range in eastern USA (EOL 2017j). The species is able to occupy a wide range of macrohabitat conditions (Castleberry *et al*. 2002). On the other hand, it chooses its habitat based on conditions of the microhabitat. Castleberry and coworkers suggested that this selection may relate to the high mobility of the species and its herbivore diet.

Figure 33. ***Neotoma magister***, a species that ingests a small amount of moss. Photo by Alan Cressler, through Creative Commons.

The Allegheny woodrat forages only at night, consuming primarily fruits, nuts, seeds, leaves, and fungi (EOL 2017j). Castleberry *et al*. (2002) found that the diet typically had more than 2% moss in the Allegheny Plateau of West Virginia and Virginia, USA. There are no studies to indicate if this is digested, or if it simply comes along with seeds and fungi found among the moss stems.

Lemmus – Lemmings

Lemmings (***Lemmus***) are well known moss consumers, in addition to sedges and grasses (Batzli 1993). The story of the importance of mosses to their survival has been evolving over the many years of my career.

Ever since Walt Disney filmed lemmings plunging over cliffs into the ocean during mass migrations, lemmings have gotten the reputation of being suicidal. But rumors claim that the suicidal tendency is mere fiction and that the Disney crew drove the lemmings off with helicopters.

Mosses may actually help to explain the Disney film that shows lemmings committing suicide (Ekerholm *et al*. 2001). It is doubtful that they really have any intention of committing suicide, but lemmings do tend to eat themselves literally out of house and home during the winter, then become fully exposed when the snow melts. That means they must scurry to a new location for both food and shelter. And sometimes they **might** scurry too far and reach the fiords where they **could** plummet to the ocean and be unable to climb the steep cliffs to safety. But there seems to be no scientific documentation that they actually do plummet to their deaths (Turchin *et al*. 2000). In fact, Ekerholm *et al*. (2001) contend that those lemmings that do not "jump the cliff" are actually the ones that commit suicide.

It was 1924 when Charles Elton reported that lemming populations reach the maximum density their environment permits, remain there until their predators catch up, then crash because the predator overeats. But Turchin *et al*. (2000) claim this is not true for lemmings, although it is true for voles. We do know, however, that lemmings cycle through mass migrations as a result of overpopulation that depletes their habitat. And Turchin and coworkers (2000) claim that it is the absence of mosses that triggers this moving carpet of furry bodies. Foraging on mosses on the rocky tundra, lemmings soon remove these slow-growing plants faster than the mosses can re-grow, say Turchin and coworkers. Hence, they are forced to move elsewhere or starve. Unfortunately, many fail to negotiate the dangers and energy required to cross rivers and lakes, ultimately drowning and adding credence to the Disney story.

In a 20-year study in northern Norway, Ekerholm and colleagues (2001) found a "vague" 10-year cycle for the highland lemmings. This cycle corresponds with the time required for snowbed mosses to recover from their grazing and reach a 100 g m^{-2} biomass (Kyllönen & Laine 1980; Oksanen 1983). Furthermore, the crashes in lemming populations correspond to times of massive destruction of the highland mosses (Oksanen & Oksanen 1981; Moen *et al*. 1993; Ekerholm *et al*. 2001). In some areas, the lemming population can recover using grassy habitats, but in the more northern areas, recovery of mosses is necessary before a real "outbreak" of lemmings can occur (Ekerholm *et al*. 2001).

Batzli (1983), in reviewing the responses of Arctic lemmings to nutritional factors, concluded that the availability of high quality forage drives the differences in densities of the Arctic rodents between habitats and in different seasons. But in addition to nutritional quality, fluctuations in plant secondary compounds may also play a major role. The Norwegian lemming (***Lemmus lemmus***; Figure 34) continues to eat monocots in winter, but it increases its intake of mosses (Koshkina 1962; Batzli & Pitelka 1983), even though the monocots are more digestible than the mosses (Batzli & Cole 1979). As Prins (1982a) suggested, perhaps it was the secondary compound arachidonic acid that made mosses desirable, especially in preparation and duration of winter, by providing better protection against the cold.

Figure 34. ***Lemmus lemmus***, the Norwegian lemming, a species that supplements its winter diet by increasing moss consumption. Photo by Argus Fin, through Creative Commons.

Turchin *et al*. (2000) questioned whether it was prey or predation that controlled lemming numbers. As predators, these rodents eat mosses, especially in winter. The lemmings (***Lemmus***; Figure 34, Figure 43) can destroy ~90% of the moss cover and cut off all the monocot shoots in their habitats (Batzli 1981), creating an open field where they must run to find food. The mosses regrow slowly, leaving the lemmings exposed when the snow melts, particularly in large populations (Turchin *et al*. 2000). This causes the predators to have a particularly easy time finding and catching the lemmings as prey. The extra food results in an increase in the predator population (Snowy Owl and others) resulting from highly successful reproduction. The Snowy Owls are strong fliers. When the lemming population subsequently crashes from the owl predation, the owls are able to migrate to other areas where prey is sufficiently abundant (Line 1997). Using graphic models of the population dynamics, Turchin and coworkers (2000) concluded that the various rodent cycles are not due to a single mechanism, making a universal explanation unlikely.

Based on the low amounts of digestible energy that lemmings appear to derive from mosses, Prins (1982a) suggested that lemmings and other vertebrates of cold climates eat mosses for reasons other than nutrition. He hypothesized that ingestion of a highly unsaturated fatty acid, arachidonic acid, may be an adaptive mechanism that helps protect against low temperatures, making the footpads more pliable. Animals do not synthesize arachidonic acid and its concentration in mosses (up to 35 % of fatty acids) is the highest reported in plants.

In addition to the leaves and stems of mosses, high Arctic lemmings also consume the capsules of mosses (Catherine La Farge, Bryonet 15 January 2008); the mosses have often been decapitated (Catherine La Farge, Bryonet 30 March 2016). Little is known about the secondary compounds of capsules, particularly with regard to seasonal changes in them.

In addition to gut analyses, flattened moss beds, and observations of lemmings eating mosses, habitat choice supports the importance of mosses in the life of a lemming (Oksanen 1983). The sites where lemmings (***Lemmus*** sp.; Figure 34) were observed have five times as much moss meadow as sites where lemmings did not visit. Following the population crash of the lemmings, there was an 8.4-fold increase in the moss biomass.

Lemmings have the disadvantage of being attacked from above. They are the main food of the Snowy Owl (*Bubo scandiacus*; Figure 35), a powerful bird with a 1.5 m wingspan (Line 1997). The lemmings protect themselves in summer by living in shallow burrows or under lichen-covered rocks. However, in winter these same lemmings curl up in balls of grasses and mosses under the snow and ice. They create a maze of tunnels and emerge only to feed on buds, twigs, and bark of the dwarf tundra shrubs. It is on these feeding forays that the Snowy Owl is able to catch them for food. An adult Snowy owl will eat 3-5 lemmings per day; a pair of owls with its brood will consume 1900 to 2,600 lemmings in the period of May to September. Their breeding success is tied to years when the lemmings are numerous.

Figure 35. The Snowy Owl, ***Bubo scandiacus***, male, a major lemming predator. Photo by Michael Gäbler, through Creative Commons.

In addition to the effects of harvesting mosses for food, lemmings affect the bryophyte diversity of their Arctic habitats through the construction of runways and burrows. Lemming runways and burrows provide openings in the tundra that provide some bryophyte species with the reduced competition they need. Among these are ***Bryum wrightii*** (Figure 36), ***Desmatodon leucostoma*** (Figure 37), and ***Funaria polaris*** (Steere 1976).

Figure 36. ***Bryum wrightii***, a species that colonizes lemming runways and burrow openings. Photo by Jean Faubert, with permission.

Figure 37. ***Desmatodon leucostoma***, a species that colonizes lemming runways and burrow openings. Photo by Jonathon Sleath, BBS website, with permission.

Dale Vitt (pers. comm. January 2018) has shared his lemming experiences with me. On the Canadian Arctic Devon Island (Figure 38-Figure 39), he found that both ***Funaria polaris*** and ***F. microstoma*** (Figure 40) grew on the openings to lemming burrows (Figure 41).

Figure 38. Truelove Lowlands, Devon Island. Photo by Martin Brummell, through Creative Commons.

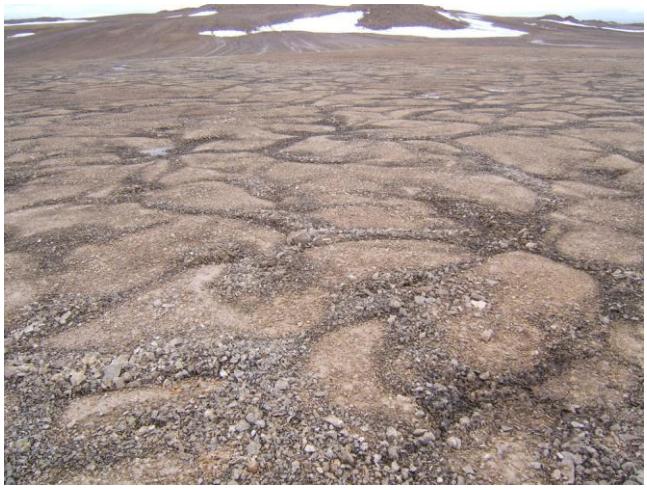

Figure 39. Devon Island showing permafrost. Photo Anthonares, through Creative Commons.

Figure 40. ***Funaria microstoma***, a moss found at the openings of lemming burrows in the Arctic. Photo courtesy of Dale Vitt.

Figure 41. Lemming burrow on Devon Island showing bryophytes at entrance of the burrow. Photo courtesy of Dale Vitt.

Although some lemmings partition their niches by having different diets, there can be considerable overlap. Soininen *et al*. (2015) used DNA metabarcoding of feces to demonstrate diet overlap among high Arctic lemmings in the winter. Contrasting to previous analyses, they found that *Salix* dominated the diets of both collared lemmings (***Dicrostonyx groenlandicus***) and brown lemmings (***Lemmus trimucronatus***) on Bylot Island, whereas mosses were a relatively minor contribution. *Salix* is abundant on the island, and feeding by the two lemming species has little impact on its cover. Despite the paucity of bryophytes in the winter diet, Dominique Fauteux (pers. comm. January 2018) has observed the lemmings on Bylot Island eating ***Polytrichum*** and ***Aulacomnium*** heads "many, many times."

Gruyer *et al*. (2008) found, using exclosures (Figure 42)), that on Bylot Island the lemmings have little impact on plant biomass, even in peak years. This contrasts with the effects of other herbivores on the island.

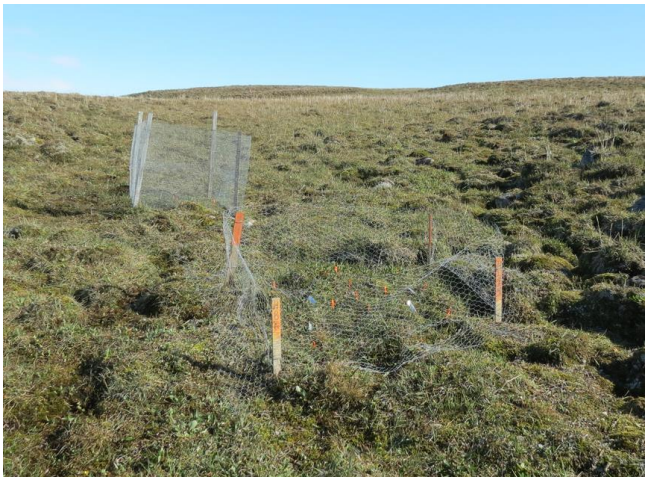

Figure 42. Lemming exclosure 1x1 m on Bylot Island in 2014. Photo courtesy of Dominique Fauteux.

Lemmus lemmus – Norwegian Lemming)

The Norwegian lemming (***Lemmus lemmus***; Figure 43) is the only **endemic** (not occurring outside a restricted area) vertebrate species in Fennoscandia (Tast 1991). It typically lives in the alpine tundra (Eurola *et al*. 1984), but may expand to forests during peak population years (Tast 1991). The species faces potential extinction as a result of climate warming. It is adapted for cold weather, and geography prevents it from moving to colder regions.

Figure 43. ***Lemmus lemmus***, the Norwegian lemming, a moss eater. Photo through Creative Commons.

Norwegian lemmings reproduce year-round and often reproduce under snow (Tast 1991). They can have up to 100 offspring per pair in one year (EOL 2017k). The Norwegian lemmings consume mosses year round as their primary food item, including all habitats (Tast 1991; Turchin & Batzli 2001). Nevertheless, the proportion in the diet decreases toward the end of the main breeding season. When moss consumption again rises, breeding resumes. These mosses grow even in winter in the Arctic, providing fresh food all year.

At the highest population peaks, winter consumption by various lemming species can remove the growing portions of 90-100% of both mosses and graminoids (Thompson 1955; Pitelka 1957; Koshkina 1961; Schultz 1968; Kalela & Koponen 1971; Kiryuschenko 1979; Henttonen & Jävinen 1981; Chernyavsky *et al.* 1981; Moen *et al.* 1993). In the Kilpisjaervi region, Finnish Lapland, no large invasion of ***Lemmus lemmus*** (Figure 43) occurred between 1971 and 1984, resulting in continuous increase in the bryophyte biomass (Eurola *et al*. 1984). Timo Koponen (Bryonet 13 January 2008) considered ***Dicranum*** (Figure 10) species essential for these lemmings to survive.

Further evidence of lemming-moss relationships comes from exclosure experiments in snowbeds at Kilpisjärvi in Finnish Lapland. Despite low lemming densities during the study period, Virtanen (2000) and coworkers (1997) found "profound" changes in an 8-year exclosure, with a three-times thicker cover of haircap mosses [**Polytrichaceae**: ***Polytrichastrum alpinum*** (Figure 44), ***P. sexangulare*** (Figure 45), ***Polytrichum commune*** (Figure 46), ***P. hyperboreum*** (Figure 47), ***P. juniperinum*** (Figure 48), ***P. piliferum*** (Figure 49)] and a few graminoids (Figure 50). After 15 years, polytrichaceous mosses in the exclosures had a large number of dead shoots and Virtanen (2000) suggested that they may actually depend on grazing for maintenance (Figure 50). Virtanen *et al*. (1997) suggested that polytrichaceous mosses had the advantage of a significant subterranean rhizome that permitted their survival during periods of heavy grazing. Outside the plots, one could find plants of low stature (Figure 50), including liverworts [***Cephalozia*** spp. (Figure 51), ***Gymnomitrion*** spp. (Figure 52), ***Moerckia blyttii*** (Figure 53)] and the low moss ***Kiaeria starkei*** (Figure 54). ***Kiaeria*** was absent in the exclosures after 15 years (Virtanen 2000). It was only in the open that colonizing species such as ***Pohlia nutans*** (Figure 55) and ***P. drummondii*** (Figure 56) were present (Figure 50). Hence, the lemmings had a strong influence on the species composition of the moss communities. Thus, in this exclosure experiment in a mountain snowbed, the biomass of mosses increased within the exclosures during 5 years of experiments (Virtanen 2000).

Figure 44. ***Polytrichastrum alpinum***, a species that can increase 3-fold when lemming herbivory is prevented. Photo by David Holyoak, with permission.

Figure 45. ***Polytrichastrum sexangulare***, a species that can have 3X thicker cover in lemming exclosures. Photo by Hermann Schachner, through Creative Commons.

Figure 46. ***Polytrichum commune***, a species that can have 3X thicker cover in lemming exclosures. Photo by A. J. Silverside, with permission.

Figure 47. ***Polytrichum hyperboreum*** with capsules, a species that can reach 3X thicker cover in lemming exclosures. Photo by Michael Lüth, with permission.

Figure 48. ***Polytrichum juniperinum***, a species that can reach 3X thicker cover in lemming exclosures. Photo by Janice Glime.

Figure 49. ***Polytrichum piliferum***, a species that can reach 3X thicker cover in lemming exclosures. Photo by Li Zhang, with permission.

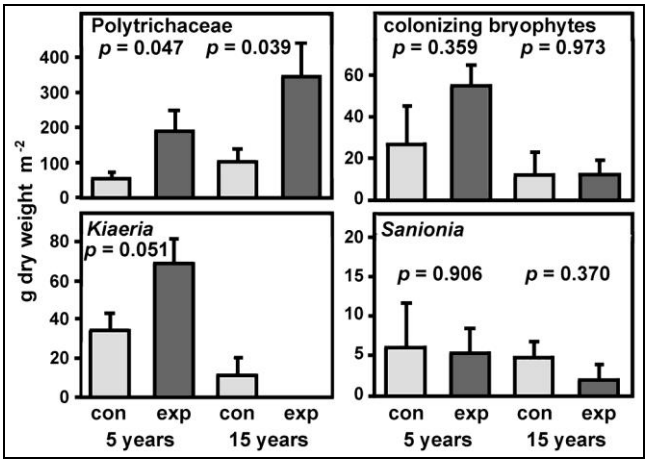

Figure 50. Effect of grazing exclosures (**exp**) compared to controls (**con**) on bryophytes in a lemming habitat at Kilpisjärvi in Finnish Lapland after five and fifteen years of exclosure from herbivory. Redrawn from Virtanen 2000.

Figure 51. The leafy liverwort, ***Cephalozia bicuspidata***, with perianths, member of a genus that is able to grow outside the lemming exclosures. Photo by Hermann Schachner, through Wikimedia Commons.

Figure 52. ***Gymnomitrion concinnatum***, member of a genus that is able to grow outside the lemming exclosures. Photo by Hermann Schachner, through Creative Commons.

Figure 53. ***Moerckia blyttii***, a species that is able to grow outside the lemming exclosures. Photo by Michael Lüth, with permission.

Figure 54. ***Kiaeria starkei***, a moss that completely disappears in lemming exclosures after 15 years. Photo by Michael Lüth, with permission.

Figure 55. ***Pohlia nutans***, a colonizing species, in the Khibiny Mountains, Apatity, Murmansk. Photo by Michael Lüth, with permission.

Figure 56. ***Pohlia drummondii*** with bulbils, a colonizing species, that occupies open areas. Photo by David T. Holyoak, with permission.

Do lemmings control the mosses, or do mosses control the lemmings? Oksanen (1983) found five times as much moss on a site visited by lemmings (***Lemmus*** sp.; Figure 57) as found at a site they did not visit. But it appears that it was in fact a two-way control; after a population crash at Kilpisjarvi, Finland, there was an 8.4-fold increase in moss biomass on the site the lemmings had grazed. When the

moss "dies," lemmings leave or die. When lemmings leave, mosses rebound.

Ims *et al*. (2008) considered the suggestion that Norwegian lemmings (***Lemmus lemmus***; Figure 57) are especially sensitive to winter climatic conditions. They reasoned that this may be due to their reliance on mosses. These low plants exist at the base of the snow collection and are probably locked in ice when adhering water refreezes after a melt, making periods of time when even this food is unavailable. Hence, warmer climates where freezing and thawing are common throughout the winter may be unfavorable because of food unavailability.

The Norwegian lemming (***Lemmus lemmus***; Figure 57) in forest tundra eats more mosses than the less available grasses and sedges (Koshkina 1961), and the Nearctic brown lemming (***Lemmus trimucronatus***; Figure 58), a species of circumpolar tundra, eats more mosses in winter when monocots are least available (Batzli 1975).

Figure 57. ***Lemmus lemmus***, the Norwegian lemming, a species that devours mosses in the tundra. Photo by Andreaze, through Creative Commons.

Figure 58. ***Lemmus trimucronatus***, the Nearctic brown lemming, a species that increases its moss consumption in winter. Image from EOL, through Creative Commons.

One should expect that grazing would change the structure of the bryophyte community, but in fact, the predicted changes did not occur on the Arctic islands studied (Virtanen 2000). ***Sanionia uncinata*** (Figure 59) is common on Arctic islands lacking grazers, but in the 15 years of exclosure experiments it remained a subordinate species in both exclosures and non-exclosures. Furthermore, the expected change in colonizing species – small liverworts and ***Pohlia*** spp. (Figure 55-Figure 56) (Oksanen & Ranta 1992) did not occur in either treatment (Virtanen 2000).

Figure 59. ***Sanionia uncinata***, a species that is common when grazers are absent, but that was only a subordinate species after 15 years in exclosures. Photo by Michael Lüth, with permission.

In some locations, the Norwegian lemming (***Lemmus lemmus***; Figure 34, Figure 43, Figure 57), along with reindeer, can have a profound effect on bryophyte vegetation. They eat the competing graminoids, resulting in more space for bryophytes to obtain sufficient sunlight. In exclosure experiments, Virtanen (2000) showed that mosses such as ***Kiaeria*** (Figure 54) were reduced to low biomass or total absence after 15 years of exclusion of these herbivores. The **Polytrichaceae** (Figure 44-Figure 49) still dominated the habitat, but its litter had increased. But in the shorter experiment of only five years, mosses increased, no doubt due to the absence of winter feeding by lemmings. This suggests that the 4-5-year cycles of lemmings in many areas may be in tune with the growth rate of the bryophytes, affording them sufficient recovery time. Virtanen concluded that even in such a low productivity environment as the Norwegian Arctic, herbivory has a major impact in controlling the ecosystem, a system where mosses and lichens are typically the dominant vegetation.

Another study in the Fennoscandian mountain range of northernmost Sweden and Norway likewise demonstrated that Norwegian lemmings (***Lemmus lemmus***; Figure 57) can have a significant impact on the vegetation (Olofsson *et al.* 2004). Both ***Dicranum*** (Figure 10) and ***Polytrichum*** (Figure 46-Figure 49) species increased significantly in the exclosures. These are preferred winter forage for lemmings (Kalela 1961). The liverwort ***Ptilidium ciliare*** (Figure 9), on the other hand, became greatly reduced when herbivory disappeared in the exclosures. Liverworts are known to be weak competitors that benefit from grazing (on competing plants) and disturbance (Gjaerevoll 1956; Moen *et al*. 1993; Virtanen *et al.* 1997); presumably, grazing on the surrounding plants provided the ***P. ciliare*** with the exposure it needed.

Not only do the lemmings reduce the mosses by foraging, but they also use them in nests. The Norwegian lemming builds a dry nest lined with mosses and lichens, then includes mosses as the bulk of its diet (Anonymous 2005). A moss population crash occurs when the lemmings exhaust the moss flora, which regrows slowly, leaving the

lemmings to seek new locations to forage (Turchin *et al*. 2000). Thus, lemmings can be seen running in large numbers in search of food and shelter.

We have seen that metal pollutants accumulated by mosses have been detrimental to populations of other small rodents. Kataev *et al*. (1994) further reported that the decline in ***Lemmus lemmus*** (Figure 43, Figure 57) in regions with high SO_2 and heavy metal emissions may be due to the decrease in abundance of mosses due to the pollution.

Apparently capsules also form part of the diet. Olga Belkina (pers. comm. 13 November 2012) observed ***Oligotrichum hercynicum*** (Figure 60) with setae but no capsules (Figure 61) in a Lapland State Nature Biosphere Reserve. Feces of ***Lemmus lemmus*** were nearby (Figure 62). On another occasion, her research team identified fragments of ***Hylocomium splendens*** (Figure 63) and ***Sanionia uncinata*** (Figure 59) in the gut. Kalela *et al*. (1961) found that the forest populations of the Norwegian lemming typically survives winter by eating ***Pleurozium schreberi*** (Figure 64) and ***Hylocomium splendens***.

Figure 60. ***Oligotrichum hercynicum*** with capsules bitten by lemmings. Photo courtesy of Olga Belkina.

Figure 61. ***Oligotrichum hercynicum*** with capsules bitten by lemmings. Photo courtesy of Olga Belkina.

Figure 62. ***Oligotrichum hercynicum*** with capsules bitten by lemmings and scat that reminds us of their former presence. Photo courtesy of Olga Belkina.

Figure 63. ***Hylocomium splendens***, winter staple food for the Norwegian lemming. Photo by Daniel Mosquin, Botany Website, UBC, with permission.

Figure 64. ***Pleurozium schreberi***, winter staple food for the Norwegian lemming. Photo by Janice Glime.

Lemmus sibiricus/*trimucronatus* – Brown Lemmings

The brown lemming (***Lemmus sibiricus***; Figure 14) has been divided into subspecies, and the North American (Nearctic) portion of the species has been named as a separate species, ***Lemmus trimucronatus*** (Figure 58)

(Wilson & Reeder 2005); the Nearctic brown lemming. ***Lemmus sibiricus*** *s.s.* (black-footed lemming) is distributed in the Palaearctic tundra zone from the White Sea to Kolyma (Russian Federation). Unfortunately, I have found no lemming studies mentioning mosses for the eastern Palaearctic.

Brown lemmings near Barrow, Alaska, (presumably ***Lemmus trimucronatus***; Figure 58) eat mosses, as well as grasses and sedges, in winter, and in drier habitats the mosses form up to 40% of the diet (Batzli & Pitelka 1983). When lemming numbers peak in their 4-6 year cycle, such mosses as ***Calliergon*** (Figure 65), ***Dicranum*** (Figure 10), and ***Polytrichum*** (Figure 46-Figure 49) species can form 5-20% of the diet in summer and 30-40% in winter (Bunnell *et al*. 1975). Lemmings actually prefer mosses (Chapin *et al*. 1986). Mosses show seasonal carbohydrate fluctuations, with a decline in brown tissues in summer and an increase in autumn. ***Aulacomnium*** (Figure 66) species show greater seasonal fluctuation of carbohydrate concentration in brown material than do ***Polytrichum***/***Pogonatum***/***Polytrichastrum***? (Figure 44-Figure 49) species. Mosses have the highest concentrations of lignin-like materials, whereas *Eriophorum* (cottongrass; Figure 67) and lichens have the lowest. The preference ranking of the lemmings, who specialized on mosses and graminoids, correlate positively with fiber and negatively with mineral nutrient contents, suggesting that fiber may be important in the diet.

Figure 65. ***Calliergon giganteum***, in a genus that forms up to 40% of the diet of the brown lemming in Alaska. Photo by A. Neumann, Biopix, through Creative Commons.

Figure 66. ***Aulacomnium turgidum***, in a genus that shows large seasonal fluctuation of carbohydrates in brown material. Photo by Michael Lüth, with permission.

Figure 67. ***Eriophorum vaginatum***, a genus with low concentrations of lignin-like materials. Photo by Roger D. Bull, through Creative Commons.

Schultz (1968) estimated that in their peak years, brown lemmings (***Lemmus sibiricus***; Figure 68) consume up to 90% of the primary production in their North American habitats; Batzli (1975) found the same 90% consumption in the low Arctic, where mosses and monocots were the primary winter food. In Scandinavia, Norwegian lemmings consume 66% of the mosses (Moen *et al*. 1993).

Figure 68. ***Lemmus sibiricus***, a species that eats mostly mosses and grasses in winter. Photo by Ansgar Walk, through Creative Commons.

In northern Alaska, ***Lemmus trimucronatus*** (Figure 58) specializes on monocots and mosses, whereas the other small rodents eat primarily flowering plants (Batzli & Jung 1980; Batzli 1983). ***Lemmus trimucronatus*** continues consuming monocots in the winter, leaving behind the basal 1 cm and permitting regrowth. However, their moss consumption increases (Koshkina 1962; Batzli & Pitelka 1983; Batzli 1983; Rodgers 1990; Turchin & Batzli 2001), reaching up to 40% of the diet (Batzli & Pitelka 1983). Batzli (1983) determined that mosses are the least digestible group for the rodents (Batzli & Cole 1979), providing much less energy. Nevertheless, they can be up to 40% of the diet in drier habitats, where they are more important than in moist habitats (Batzli & Pitelka 1983). Batzli (1983) reasoned that instead they must provide a nutrient supplement. On the other hand, Rodgers (1990) suggests that when graminoids become senescent at the end

of summer, the lemmings are forced to eat a greater proportion of mosses. In cafeteria-style experiments, lemmings that had been fed artificial diets chose mosses in the same proportion as those individuals that had been raised on a natural diet, indicating the choice of mosses was genetically based (Rodgers & Lewis 1985). Food choice indicated that preference was based primarily on macronutrients and caloric content. Habitat made no difference in diet choices (Rodgers & Lewis 1986).

Nevertheless, the Alaskan brown lemmings (***Lemmus trimucronatus***; Figure 58) cannot survive and reproduce on a diet exclusively of mosses. It appears that in Barrow, Alaska, USA, the summer digestibility is poor and the consumption by these lemmings is low (Batzli & Cole 1979). But in winter, if densities are medium to high (~>30 lemmings per hectare), they rapidly exhaust the graminoids and must live on a diet of 100% mosses (Turchin & Batzli 2001).

With the low digestibility of mosses (Batzli & Cole 1979), it is not surprising that captive Nearctic brown lemmings (***Lemmus trimucronatus***; Figure 58) lost weight on a moss-only diet, supporting the suggestion that mosses must serve some function other than as a source of energy. Batzli and Cole (1979) suggest that the high concentrations of calcium, magnesium, and iron may be beneficial.

In a feeding experiment using ***Funaria hygrometrica*** (Figure 28), the lemmings of Devon Island ate only the capsules (Pakarinen & Vitt 1974). Pakarinen and Vitt suggested that the choice of capsules may have been related to the high lipid content of the spores. The availability of the highly polyunsaturated fatty acid arachidonic acid (Gellerman *et al*. 1972) almost exclusively in mosses (and also *Equisetum*) may be especially important to these small mammals that must run about on and under the snow (Prins 1982b). Northern climates seem to increase the predation on mosses, perhaps because the arachidonic acids might help to keep the fats in the foot pads from changing from a liquid to a solid phase on the cold ground in winter (Prins 1982a), or perhaps because there are fewer choices for food. Arachidonic acid has a low melting point of -49.5^{o}C, supporting the foot pad theory. Few other plants have arachidonic acid, yet it is present in high concentrations in the blood of Arctic animals, perhaps contributing to increased limb mobility and protecting cell membranes at low temperatures. Interestingly, Hansen and Rossi (1991) found that arachidonic acid comprised 30% of the fatty acids in ***Rhytidiadelphus squarrosus*** (Figure 69) and ***Eurhynchium striatum*** (Figure 70) at 20ºC, but concentrations shifted toward more eicosapentaenoic acid at lower temperatures, with a slight decrease in arachidonic acid.

Synaptomys borealis – Northern Bog Lemmings

The range of the northern bog lemming (***Synaptomys borealis***; Figure 71) extends from Alaska, USA, eastward to Labrador, Canada, and southward to southeastern Manitoba, then southward in the USA to Washington, Montana, and northern New England (Clough & Albright 1987; Cassola 2017).

Figure 69. ***Rhytidiadelphus squarrosus***, a species in which dominance of arachidonic acid is shifted to dominance of eicosapentaenoic acid at low temperatures. Photo by Johan N., through Creative Commons.

Figure 70. ***Eurhynchium striatum*** with capsules, a species in which dominance of arachidonic acid is shifted to dominance of eicosapentaenoic acid at low temperatures. Photo by J. C. Schou, with permission.

Figure 71. ***Synaptomys borealis***, a species that prefers mossy habitats. Painting by Todd Zalewski, Smithsonian Institutes, through public domain.

Mosses seem to play a prominent role in habitat preference. In the Athabaska-Mackenzie Region of Canada, Preble (1908) reported habitats for the northern bog lemming (***Synaptomys borealis***; Figure 71). These

included the border of a small meadow, a wet, swampy area, proximity of small muskeg ponds, and a marsh. To these, Banfield (1974) reported Canada black spruce bogs as the primary habitat, but also wet subalpine meadows, alpine, and sagebrush. In Churchill, Manitoba, Scott and Hansell (1989) found them in the *Carex*-moss-*Salix* community and the *Salix* community; Wrigley (1974) similarly found them in a sedge-moss tundra (Figure 72). Cowan (1939) found them in muskegs in British Columbia, Canada. Booth (1947) also considered them to be inhabitants of wet, boggy places in the North Cascades, Canada, as did Manville and Young (1965) and Osgood (1904) for Alaska, USA. Groves and Yensen (1989) (also Bursik 1993) reported them from ***Sphagnum*** bogs (Figure 73) in Idaho, USA, as did Johnson and Cheney (1953) for Idaho and Washington and Layser and Burke (1973) for Washington. In Montana, Reichel and Beckstrom (1993, 1994) found them in thick mats of ***Sphagnum*** (Figure 74), and found this habitat to be the best predictor for finding them. For Minnesota, USA, Coffin and Pfannmuller (1988) listed the habitat as dominated by ***Sphagnum*** and graminoids, including forested bogs and open ericaceous shrublands.

Christian *et al*. (1999) concurred, but expanded the Minnesota habitats to include spruce forest (Figure 73) with moss on the forest floor, wet alpine meadows, and alpine tundra. Clough and Albright (1987) reported them from wet sedge meadows in the northeastern USA. Near the base of Mount Washington, New Hampshire, USA, Preble (1899) found them in swampy habitats densely carpeted with moss. On the other hand, in Montana, USA, Pearson (1991) found them in an old-growth hemlock *Tsuga heterophylla* forest (Figure 75) that lacked the typical bog/fen habitat, although most of the sites were more typical.

Figure 72. Sedge-moss tundra, Nunavut, northern Canada. Photo by A. Dialla, through Creative Commons.

In British Columbia, Canada, Cowan (1939) found that ***Synaptomys borealis*** (Figure 71) creates a honeycomb of tunnels in the mossy carpets of the muskegs. These tunnels are strewn with fecal pellets, indicating where feeding occurred. The nests are above ground in winter and below ground in summer (Banfield 1974).

Figure 73. Mountain bog/fen in Idaho, USA, with spruce forest in the background. Photo by Robert Marshall, through Creative Commons.

Figure 74. ***Sphagnum capillifolium***, a common bog/fen species. Photo by David Holyoak, with permission.

Figure 75. ***Tsuga heterophylla*** forest. Photo by pxhere, through Creative Commons.

The "house" that is less likely to disappear is a house of ***Sphagnum*** (Figure 74) (Cowan 1939). The bog lemmings ***Synaptomys borealis*** (Figure 71) usually live in small colonies among the wet mosses (Osgood 1904). Their runways are among the mosses rather than among the

grasses and other weeds. Although rare even in Alaska, they tend to be more common in peatlands (Preble 1908; Osgood 1909), where they make nests beneath the moss (Headstrom 1970). For these lemmings in their more southern extensions of their range, where they are also rare, it is in the peatlands that they survive (Coffin & Pfannmuller 1988).

Runways not only carry clippings of new bryophyte species, but open habitat to mosses that otherwise could not occur there. Among these in Arctic Alaska is the colonizing species, ***Funaria polaris*** (Batzli *et al*. 1980).

While it is clear that mosses, especially ***Sphagnum*** (Figure 74), are important in defining the habitat of the northern bog lemming, it is less clear why. Perhaps a small indication is the presence of ***Hylocomiastrum pyrenaicum*** (Figure 76) in the mouth of one individual (Harper 1961), but this may just be a gathering to line the nest. Moisture could be an important factor, but there seem to be no physiological studies to test this idea.

Figure 76. ***Hylocomiastrum pyrenaicum***, a species that has been seen in the mouth of a northern bog lemming (***Synaptomys borealis***). Photo by Michael Lüth, with permission.

Rand (1945) provides examples that support this suggestion of the importance of moisture. In this study, seven individuals were captured in wet grassy glades and twelve in marshy sedges of dwarf birch flats (Yukon and Northwest Territories, Canada), although another seven trapped by Rand were in typical spruce swamps with mosses. The common factor is moisture.

Synaptomys cooperi – Southern Bog Lemming

The bog lemming (***Synaptomys cooperi***; Figure 77), as its name implies, is a bog species (Connor 1959; Banfield 1974), ranging from southern Manitoba, Canada, south to Arkansas and Tennessee, USA (EOL 2017m). Nevertheless, it can occupy a wide range of habitats, including grasslands, mixed deciduous and coniferous woodlands, spruce-fir forests, and freshwater wetlands (EOL 2017m). In Minnesota, USA, Christian *et al*. (1999) found that it was significantly more abundant in bogs than in sedge meadows or lowland conifer habitats. Connor (1959) reported it from New Jersey. Goodwin (1932) found this species in Connecticut, USA, on a dark forest floor that was overgrown with ferns, ***Sphagnum*** (Figure 74), and other mosses. No surface runways were visible, but there were definite tunnels beneath the surface.

Figure 77. ***Synaptomys cooperi***, bog lemming, makes tunnels under ***Sphagnum***. Photo by Phil Myers, through Creative Commons.

Despite its typical bog habitat, Hamilton (1941) found this species in quite different circumstances in Albany County, New York, USA. These "bog" lemmings were in a beech-hemlock forest with a forest floor of spring perennials and lots of black leaf litter. Mosses were apparently not an important component.

The bog lemming eats grasses, sedges, mosses, fungi, fruit, bark, and roots (EOL 2017m). Using fecal analysis, Linzey (1984) found that even in southwestern Virginia, USA, the bog lemming subsisted on the broom grass *Andropogon* (Figure 78) in the summer but on mosses in winter. Both of these foods are low in digestible nutrients.

Figure 78. *Andropogon virginicus*, summer food for the bog lemming (***Synaptomys cooperi***) in Virginia, USA. Photo by P. B. Pelser, through online permission.

Dicrostonyx – Collared Lemming

Once again, we encounter recent changes in our understanding of the species. ***Dicrostonyx torquatus*** *sensu stricto* (Figure 79) is now considered to be distributed only in the Arctic and sub-Arctic tundra and forest-tundra in the Palaearctic region – *i.e*., in Northern Europe and Asia (Wilson & Reeder 2005). ***Dicrostonyx*** is the only rodent (order **Rodentia**) that changes to white for the winter.

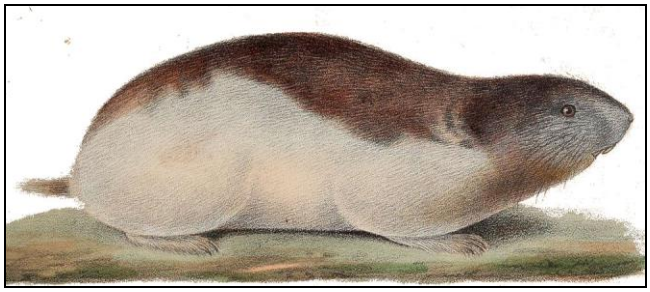

Figure 79. ***Dicrostonyx torquatus***, the collared lemming in the Palaearctic region. Photo by Ellicrum, through Creative Commons.

Dicrostonyx groenlandicus – Northern Collared Lemming

The northern collared lemming (***Dicrostonyx groenlandicus***; see related species in Figure 80) is distributed in northern Greenland and Queen Elizabeth Islands to northern North America above the tree line, including northern Alaska, USA (Musser & Carleton, in Wilson & Reeder 2005).

Like other genera of lemmings, mosses form part of the diet of ***Dicrostonyx***. Not just any moss will do either. It is perhaps not surprising to learn that northern collared lemmings (***Dicrostonyx groenlandicus***) graze on ***Polytrichum*** (Figure 46-Figure 49) gametophytes during summer on both Devon Island and Ellesmere Island (Pakarinen & Vitt 1974; Longton 1980). But when they were offered fruiting material of ***Funaria arctica***, only capsules were eaten (Pakarinen & Vitt 1974). Pakarinen and Vitt suggested that this preference may be related to the high lipid content of some moss spores.

Mosses generally provide less than 10% of the diet of the collared lemming (*cf.* Figure 79) in Alaska (Batzli & Jung 1980). It appears that this Alaskan lemming must now be ***Dicrostonyx groenlandicus***, although it was reported as ***D. torquatus***. The common sedge *Carex aquatilis* (Figure 81) contains one or more compounds that are deleterious to collared lemmings (Batzli & Jung 1980). The common evergreen shrub (***Ledum palustre***; Figure 82) is likewise deleterious to the collared lemming, but also to the tundra vole (***Microtus oeconomus***; Figure 83) and brown lemmings (***Lemmus sibiricus***; Figure 68). Differing secondary compounds separate the diets of the two lemmings, but the tundra vole is more of a generalist, overlapping the diets of both lemmings.

Figure 80. ***Dicrostonyx nelsonii*** (=*D. exsol*), one of three North American species, and a bryophyte consumer. Photo courtesy of Tim Menard.

Figure 81. *Carex aquatilis*, a species that is deleterious if eaten by the collared lemming (***Dicrostonyx***). Photo by Matt Lavin, through Creative Commons.

Figure 82. ***Ledum palustre*** with flowers, a species that is deleterious if eaten by the collared lemming (***Dicrostonyx***). Photo by Kristian Peters, through Creative Commons.

Figure 83. ***Microtus oeconomus***, a species that suffers deleterious effects from eating ***Ledum palustre***. Photo by аимаина хикари, through Creative Commons.

Gut content analysis indicates that moss capsules form a substantial part of the diet of several North American and Eurasian Arctic lemming species (Batzli & Jung 1980).

And Ron Lewis Smith (Bryonet, 21 November 2006) reports large-scale grazing by lemmings on the capsules of ***Polytrichum*** (Figure 46-Figure 49) and ***Polytrichastrum*** (Figure 44-Figure 45) in northern Sweden. When grazing on capsules, lemmings prefer mature capsules in which the spores have a high lipid content (Pakarinen & Vitt 1974).

Wooding (1982) reported the diet of Canadian brown lemmings (***Lemmus trimucronatus***?; Figure 58) was comprised of willow buds, fruits, flowers, grasses, and twigs. However, in captivity they will eat mushrooms and mosses. This supports the concept that availability is an important determinant of the diet. Rodgers and Lewis (1985) came to an interesting conclusion regarding diet differences between the brown lemming (***Lemmus trimucronatus***; Figure 58) and the northern collared lemming (***Dicrostonyx groenlandicus***). The brown lemming preferred graminoids and moss, whereas the northern collared lemming preferred shrubs and herbs. They demonstrated that diet preferences were heritable. The diet preferences for both species were based on macronutrients and caloric content, but the differences between the species depended on secondary compounds and physical characteristics of the plants. They concluded that the northern collared lemming has a greater capacity to deal with secondary compounds or the presence of plant hairs than does the brown lemming.

Myopus schisticolor – Wood Lemming

Wood lemmings, ***Myopus schisticolor*** (Figure 84), are distributed in the northern Palaearctic, ranging from western Norway, through Sweden and Finland through northern and central Russia to the Pacific coast and Sakhalin Island (Russia) (Shenbrot & Krasnov 2005). They live in mossy bogs and coniferous forests in cool climates. In the Ural Mountains, they are rare and are restricted to swampy moss habitats (Bolshakov & Berdjugin 1990). Their runways often traverse moss beds as well as under fallen trees and roots.

Figure 84. ***Myopus schisticolor*** by its path through the moss ***Hylocomium splendens***. Photo by Risto S. Pynnönen, through Wikimedia Commons.

Using food preference experiments, Kalela *et al*. (1963a, b) showed that in northern Sweden, the wood lemmings highly preferred a large number of the most abundant forest mosses, including ***Brachythecium reflexum*** (Figure 85), ***Dicranum fuscescens*** (Figure 86), ***D. polysetum*** (Figure 10), ***D. scoparium*** (Figure 11), ***Hylocomium splendens*** (Figure 63), ***Pleurozium schreberi*** (Figure 8), ***Ptilium crista-castrensis*** (Figure 7), ***Pohlia nutans*** (Figure 55), ***Polytrichum commune*** (Figure 46), ***P. juniperinum*** (Figure 48), and ***Rhodobryum roseum*** (Figure 87). In eastern Finland, ***Dicranum*** and ***Polytrichum*** seem to be their favorites, which happen also to have the highest nitrogen content, even though ***Pleurozium schreberi*** and ***Hylocomium splendens*** are more abundant (Eskelinen 2002). They rejected most herbaceous species, but only rejected a few bryophytes such as ***Ptilidium ciliare*** (Figure 9) and ***Plagiothecium denticulatum*** (Figure 88) (Kalela *et al*. 1963a, b). In one area this species used ***Aulacomnium palustre*** (Figure 89) extensively, but this seems to be a rare occurrence (Lepp 2008).

Figure 85. ***Brachythecium reflexum***, one of the preferred forest mosses of the wood lemming. Photo by Michael Lüth, with permission.

Figure 86. ***Dicranum fuscescens***, one of the preferred forest mosses of the wood lemming. Photo by Hermann Schachner, through Creative Commons.

Figure 87. ***Rhodobryum roseum***, one of the preferred forest mosses of the wood lemming. Photo by Hermann Schachner, through Creative Commons.

Figure 88. ***Plagiothecium denticulatum***, one of the rejected forest mosses of the wood lemming. Photo by Christian Peters, with permission.

Figure 89. ***Aulacomnium palustre***, a species that is sometimes eaten as a major food source by the wood lemming. Photo by Kristian Peters, through Creative Commons.

During the snow-free season ***Myopus schisticolor*** (Figure 84) feeds on only the green topshoots of the mosses, whereas during the snow-covered season, these lemmings bite off the shoots at the base (Kalela *et al.* 1963a, b). Their order of preference in Sweden seems to be ***Dicranum scoparium*** (Figure 11) > ***Hylocomium splendens*** (Figure 63) > ***Pleurozium schreberi*** (Figure 64) > ***Sphagnum girgensohnii*** (Figure 90). This order provides an interesting contrast to the choices of the heather vole (***Phenacomys intermedius***; Figure 18, Figure 21-Figure 22) that Kate Frego described. That vole seemed uninterested in ***Dicranum scoparium***. The wood lemming in Finland had some similar preferences to those in Sweden, with ***Dicranum*** and ***Polytrichum*** (Figure 46-Figure 49) as top choices, despite a greater availability of ***Pleurozium*** and ***Hylocomium*** (Lepp 2008; Figure 91).

Figure 90. ***Sphagnum girgensohnii***, a preferred moss for food by ***Myopus schisticolor***. Photo by Hermann Schachner, through Creative Commons.

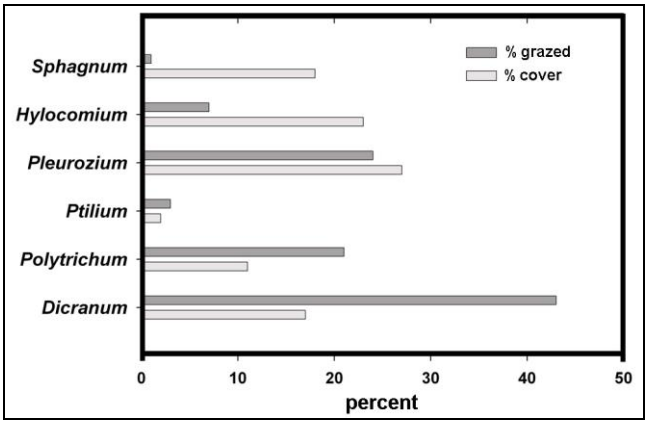

Figure 91. Percent grazing vs cover represented in a lemming habitat in Sweden. Based on data from Lepp 2008.

The species choices changed somewhat in the winter storage holes, which were located in drier sites (Lepp 2008). About 85% of their stored mosses were ***Dicranum*** (Figure 10), 11% ***Pleurozium schreberi*** (Figure 64), and only 3% ***Hylocomium splendens*** (Figure 63). They did still forage in winter, still preferring ***Dicranum***, but their second highest nibblings were on ***Ptilium*** (Figure 7), which occurred in only 30% of the study plots. In fact, for whatever reason, they did not forage on ***Polytrichum*** (Figure 46-Figure 49) in winter, despite its greater abundance than that of ***Ptilium***.

The wood lemming will graze for a long time on the same moss species, hence making it possible to identify its recent food by the color of the feces (Lepp 2008). Those with ***Pleurozium schreberi*** (Figure 64) and ***Hylocomium splendens*** (Figure 63) are light brown, ***Polytrichum***

(Figure 46-Figure 49) dark brown, ***Dicranum*** (Figure 10) dark green, and ***Ptilium crista-castrensis*** (Figure 7) light green.

One explanation for the choice of mosses for the wood lemming may be the nitrogen content (Lepp 2008). ***Dicranum*** (Figure 10) and ***Polytrichum*** (Figure 46-Figure 49) have the highest nitrogen content among the mosses in the study area. Secondary compounds such as phenols may discourage consumption of some species that are abundant, but no data are available for the study site. Since such content could differ based on environmental conditions, we can only speculate. On the other hand, Eskelinen (2002) suggested that the high carbon:nitrogen content of ***Dicranum*** (Caut *et al*. 2009; Codron *et al*. 2011) might account for ***Dicranum*** as the preferred food, and sometimes only food, for this species in Finland.

Ericson (1977) found that ***Myopus schisticolor*** (Figure 84) had a high preference for many forest moss species in preference experiments. Their preferred mosses were ***Dicranum scoparium*** (Figure 11), ***Hylocomium splendens*** (Figure 63), ***Pleurozium schreberi*** (Figure 64), and ***Sphagnum girgensohnii*** (Figure 90). In fact, they rejected most of the herb species. Some bryophytes were also rejected, including the leafy liverwort ***Ptilidium ciliare*** (Figure 9) and the moss ***Plagiothecium denticulatum*** (Figure 88). In summer the wood lemming eats only the green tops of shoots, but in winter when the bryophytes are snow covered, they eat them down to the base.

Young wood lemmings cannot survive on mosses alone; to grow faster, they need to eat other plants as well (Andreassen & Bondrup-Nielsen 1991; Lepp 2008). Adults, however, can subsist on mosses alone. Nevertheless, both growth and reproduction are negatively affected when the diet is 100% moss, compared with a diet that also includes grasses and shrubs.

Bathyergidae – Blesmoles and Mole Rats

Cryptomys hottentotus – Hottentot Mole-rat

The Hottentot mole-rat (***Cryptomys hottentotus***; Figure 92Figure 93) is widely distributed in South Africa (Bishop *et al*. 2004). Colonies have 2-14 individuals that permanently live in a network of burrows, locating their food as they burrow (Spinks 1998) The Hottentot mole-rat builds hummocks through its burrowing activity (Lynch 1992) in mesic bog soils (Bishop *et al*. 2004). It may not need a mossy habitat, but some mosses seem to benefit from its presence. The excavated soil is colonized by a lawn-like cover that includes mosses (Lynch 1992).

Figure 92. ***Cryptomys hottentotus*** (Hottentot mole-rat), a species that creates habitat for some mosses. Photo by Lloyd Glenn Ingles, through Creative Commons.

Figure 93. ***Cryptomys hottentotus*** adult showing dense fur. Photo by Daderot, through Creative Commons.

Myoxidae – Dormice and Hazel Mice

Muscardinus avellanarius – Hazel Dormouse

In England, the hazel dormouse (***Muscardinus avellanarius***; Figure 94), a somewhat rare nocturnal rodent, gets its name from the Anglo-Norman term *dormeus*, which means "sleepy" (Wikipedia 2008). This refers to its habit of becoming torpid and cold in the winter, waking only occasionally to eat food stored nearby. Hibernation is triggered by temperatures below 16ºC (Habril & Passig 2008).

Figure 94. ***Muscardinus avellanarius*** – hazel dormouse, a species that uses mosses in its winter hibernacula. Photo by Danielle Schwarz, through Creative Commons.

Its habitat is typically an unshaded understory where there is high species diversity (Bright & Morris 1990). Bright and Morris (1991) contend that this species is entirely arboreal, detouring considerable distances to avoid crossing open ground. They seldom venture more than 100 m from the nest. They seem to prefer nesting in tree hollows, but when these are scarce they select a location with shrub cover and proximity to the forest edge (Berg & Berg 1998). Despite living in trees, they do not seem to include mosses in the diet (Bright & Morris 1993).

Mosses may be more important for a **hibernaculum** (shelter occupied during the winter by a dormant animal). The hazel dormice hibernate in winter, 6-7 months in Lithuania (Juškaitis 1999). Bright and Morris (1996) reported that the dormice covered their surface hibernaculum with a thin layer of mosses or leaves. Such shallow surface hibernacula make the hibernating animals vulnerable to floods, trampling, and predation (Juškaitis 1999).

In a Ukraine study, Zaytseva (2006) found that mosses comprise about 5% of the nesting material in nest boxes used by the hazel dormouse, which sleeps there throughout the day. The globose summer nest is shaped much like a wren's nest with a door (Habril & Passig 2008). Both summer and winter nests often have mosses in them, but the winter nest is more likely to be in a tree hollow or stump. Some dormice may spend their winter on the ground under moss and litter.

Van Laar and Dirkse (2010) examined the nesting materials and found that this species used the epiphytic mosses ***Brachythecium rutabulum*** (Figure 95) and ***Orthotrichum lyellii*** (Figure 96). But they also used the primarily ground-dwelling species ***Cirriphyllum piliferum*** (Figure 97), ***Hypnum cupressiforme*** (Figure 4), ***Calliergonella cuspidata*** (Figure 98), ***Eurhynchium hians*** (Figure 99), and ***Thuidium assimile*** (Figure 100). All nest materials were pleurocarpous mosses. Van Laar and Dirkse considered the moss choice to be due to the physical properties of the moss that helped the hazel dormouse to maintain a certain degree of humidity in the nests.

Figure 95. ***Brachythecium rutabulum***, an epiphyte used for nesting material by the hazel dormouse, ***Muscardinus avellanarius***. Photo by Michael Lüth, with permission.

Figure 96. ***Orthotrichum lyellii***, an epiphyte used for nesting material by the hazel dormouse, ***Muscardinus avellanarius***. Photo by Michael Lüth, with permission.

Figure 97. ***Cirriphyllum piliferum***, a ground species used as nesting material for the hazel dormouse, ***Muscardinus avellanarius***. Photo by Michael Lüth, with permission.

Figure 98. ***Calliergonella cuspidata***, a ground species used as nesting material for the hazel dormouse, ***Muscardinus avellanarius***. Photo by Tim Waters, through Creative Commons.

Figure 99. ***Eurhynchium hians***, a ground species used as nesting material for the hazel dormouse, ***Muscardinus avellanarius***. Photo by Michael Lüth, with permission.

Figure 100. ***Thuidium assimile***, a ground species used as nesting material for the hazel dormouse, ***Muscardinus avellanarius***. Photo by Hermann Schachner, through Creative Commons.

Gliridae – Dormouse

Glirulus japonicus – Japanese Dormouse

The Japanese dormouse (***Glirulus japonicus***; Figure 101)), an endemic to Japan, is nocturnal, searching a relatively large area to find food at night (EOL 2017b). Its name derives from the Anglo-Norman word *dormeus*, which means sleepy one. However, it is not its daytime sleeping that gives it this name, but rather its long hibernation period. The males awaken in May to find a mate.

Figure 101. ***Glirulus japonicus***, a species that uses bryophytes in its lair. Photo by Katuuya, through Creative Commons.

It easily climbs trees, where it feeds on seeds, fruits, insects, and bird eggs (EOL 2017b). It can run as easily on the lower side of a branch as on the upper side. This species lacks a caecum, and thus should not be expected to digest cellulose, making mosses an inefficient food and explaining their absence in the dormouse diet.

The Japanese dormouse (***Glirulus japonicus***; Figure 101) uses bryophytes in its lair (Figure 102) (Watanabe 1978), a fact noted much earlier in Britain by Tripp (1888). These bryophytes are useful in building suitable nests. Even in arboreal habitats at warmer latitudes, the Japanese dormouse uses bryophytes for its lair (Watanabe 1978; Minato & Doei 1995; Doei & Minato 1998). After examining 21 nests, Minato and Doei (1995) reported 42 species of mosses and 15 species of liverworts as constituting the majority (53.1% by weight) of the nest materials. Like most of the bird nest bryophytes, the majority of those used by the Japanese dormouse were pleurocarpous, and consistent with the dormouse habitat, they were mostly epiphytic. The six most commonly used species were the leafy liverwort ***Frullania tamarisci*** subsp. ***obscura*** (Figure 103), and the mosses ***Hypnum tristo-viride*** (Figure 104), ***Isothecium subdiversiforme*** (Figure 105), ***Anomodon rugelii*** (Figure 106), ***Entodon scabridens***, ***Anomodon longinervis***. The leafy liverwort ***Frullania tamarisci*** subsp. ***obscura*** was often the most abundant bryophyte in the nest. This species is typically abundant nearby, spreading over the surface of tree trunks in large mats, often making it easier for the dormouse to harvest.

Figure 102. ***Glirulus japonicus*** sleeping in nest. Photo by Yamaneseisokubunpuik, through Creative Commons.

Figure 103. ***Frullania tamarasci*** subsp ***obscura***, a mat-forming pleurocarpous moss used for nesting material by the Japanese dormouse (***Glirulus japonicus***). Photo from <www.naver.com>, through Creative Commons.

Figure 104. ***Hypnum tristo-viride***, a pleurocarpous moss used for nesting material by the Japanese dormouse (***Glirulus japonicus***). Photo by Jiang Zhenyu, Mou Shanjie, Xu Zaiwen, and Chen Jianzhi, through Creative Commons.

Figure 105. ***Isothecium subdiversiforme***, a pleurocarpous moss used for nesting material by the Japanese dormouse (***Glirulus japonicus***). Photo from Digital Museum, Hiroshima University, with permission.

Figure 106. ***Anomodon rugelii***, a pleurocarpous moss used for nesting material by the Japanese dormouse (***Glirulus japonicus***). Photo by Janice Glime.

Watanabe (1978) found 25 bryophyte species in 8 nests. He found an average of 4 bryophyte species per nest, whereas Minato and Doei (1995) found an average of 6.8 species.

Myoxus glis – Fat Dormouse; Edible Dormouse

The fat dormouse (***Myoxus glis***; Figure 107) occurs throughout much of mainland western Europe and on a number of Mediterranean islands (Milazzo *et al*. 2003).

Figure 107. ***Myoxus glis***, a species that eats mosses, but most likely accidentally. Photo by Marcus Ostermann through Creative Commons.

Gigirey and Rey (1998) reported that 12 of 32 stomachs of the fat dormouse, ***Myoxus glis*** (Figure 107), had moss remains. Gigirey and Rey (1999) subsequently found mosses of this species in the feces. However, in both cases they considered these mosses to be ingested accidentally.

Whereas mosses may not be a desirable diet item, they do provide nesting materials (Drăgoi & Faur 2013). They typically construct these nests using leaves and mosses (Grzimek 2003). The mosses are typically pleurocarpous mosses, including the epiphytes ***Brachythecium rutabulum*** (Figure 95), ***Isothecium myosuroides*** (Figure 108), and ***Eurhynchium praelongum*** (Figure 109), but also nearby forest floor species including ***Brachythecium glareosum*** (Figure 110), ***Ctenidium molluscum*** (Figure 111), ***Eurhynchium striatum*** (Figure 70), and ***Eurhynchium hians*** (Figure 99) (van Laar & Dirkse 2010).

Figure 108. ***Isothecium myosuroides***, a pleurocarpous epiphyte used for nesting by the edible dormouse (***Myoxus glis***). Photo by Malcolm Storey, DiscoverLife, with online permission.

Figure 109. ***Eurhynchium praelongum***, a pleurocarpous epiphyte used for nesting by the edible dormouse (***Myoxus glis***). Photo by Janice Glime.

Figure 110. ***Brachythecium glareosum***, a pleurocarpous ground species used for nesting by the edible dormouse (***Myoxus glis***). Photo by Michael Lüth, with permission.

Figure 111. ***Ctenidium molluscum***, a pleurocarpous ground species used for nesting by the edible dormouse (***Myoxus glis***). Photo by Michael Lüth, with permission.

They locate their nests high in trees, using the cup formed by branching, although some may use abandoned bird nests (Juškaitis 2006).

Dryomys nitedula – Forest Dormouse

The forest dormouse (***Dryomys nitedula***; Figure 112) lives in Switzerland through eastern and southern Europe, Asia Minor and the Caucasus to central Russia and central Asia. It is a tree dweller, living in forests (EOL 2017n).

Figure 112. ***Dryomys nitedula***, the forest dormouse. Photo by Domodi, through Creative Commons.

Like ***Myoxus glis*** (Figure 107), ***Dryomys nitedula*** (Figure 112) uses mosses in its nests (Drăgoi & Faur 2013). The nests are round with either a side or top entry. The exterior is rough, constructed of branches, but the interior is padded, using grasses, feathers, hair, or mosses. And like the fat dormouse, ***Dryomys nitedula*** sometimes uses empty bird nests (Adamik & Kral 2008).

Summary

Many rodents have mosses in the gut and feces, but these seem to be the result of accidental intake. But some seem to include them as an important part of the diet, often increasing the percentage in winter. Researchers have suggested that this switch may be a need for nitrogen, arachidonic acid, or fiber. In other cases, it may be a simple matter of availability. The shoot tips seem most desirable for food, but in winter the moss may be clipped at the bottom. Some records indicate that moss capsules are eaten.

Known consumers of mosses include ***Chionomys nivalis***, and several members of ***Microtus***, ***Phenacomys***, ***Peromyscus maniculatus*** (capsules). Lemmings, in particular, are dependent on mosses in the diet. These may provide arachidonic acid, a more pliable fatty acid at cold temperatures. When their population peaks, they may destroy their moss cover under the snow, making them dangerously visible to predators when the snow melts.

Many rodents use mosses in the construction of nests, particularly as part of the lining. In bogs, several species may coexist in a single bog, some using them for food or to make nests, tunnels, or runways. Pleurocarpous mosses are preferred by most of the rodents that use mosses as nesting materials.

Bryophytes are impacted by the rodents in multiple ways: diminished cover, competition from flowering

plants. But at other times they may benefit. The rodents can serve as dispersal agents, and runways and burrow openings open new habitats where colonizers like ***Funaria*** can grow, increasing diversity.

Acknowledgments

This chapter has benefitted greatly from anecdotal records sent to me by bryologists and friends who observed these small rodents interacting with mosses in the field. Steve Juntikka, a former plant taxonomy student of mine, sent me an excited email from Isle Royale after observing the young mouse devouring capsules of ***Funaria hygrometrica***. Leah Vucetich and Rolf Peterson, Isle Royale researchers, provided me with the identification of the juvenile ***Peromyscus maniculatus*** based on the picture alone.

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CHAPTER 17-3
RODENTS AND BATS – NON-MUROIDEA

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CHAPTER 17-3
RODENTS AND BATS – NON-MUROIDEA

Figure 1. ***Lepus arcticus*** in its summer coloring. Photo from Gilad.rom, through Creative Commons.

Soricomorpha

Soricidae – Shrews

In 25 bogs and ombrotrophic mires of Poland, Ciechanowski *et al*. (2012) found that shrews dominated among the mammals captured in pitfall traps. The traps produced 598 individuals distributed among 12 mammal species. Typical wetland species included ***Neomys fodiens*** (Eurasian water shrew; Figure 2), ***Neomys anomalus*** (Mediterranean water shrew; Figure 3), and ***Microtus oeconomus*** (tundra vole; Figure 4). The most numerous species was the Eurasian pigmy shrew (***Sorex minutus***; Figure 5), and it was sometimes the only rodent present in the habitat. It was most common in undisturbed, treeless parts of bogs where ***Sphagnum*** (Figure 6) dominated.

Figure 2. ***Neomys fodiens***, The Eurasian water shrew, a typical wetland species that is found in bogs and mires. Photo from Saxifraga – Rudmer Zwerver, with online permission.

Figure 3. ***Neomys anomalus*** (Eurasian water shrew), a typical wetland species that is found in bogs and mires. Photo by Mnolf, through Creative Commons.

Figure 4. ***Microtus oeconomus*** (tundra vole), a typical wetland species. Photo from Saxifraga, Janus Verkerk, with online permission.

Figure 5. ***Sorex minutus*** (Eurasian pigmy shrew), the most common rodent species in Polish bogs. Photo from Saxifraga – Rudmer Zwerver, with online permission.

Figure 6. ***Sphagnum rubellum***, in a genus that dominates bogs. Photo by Michael Lüth, with permission.

Sorex cinereus – Long-tailed Shrew

The long-tailed shrew (***Sorex cinereus***; Figure 7) occurs from Alaska, USA, east to Labrador/Newfoundland, Canada, south in the USA to Washington, Utah, New Mexico, Northern Great Plains, southern Indiana and Ohio, through the Appalachian Mountains to northern Georgia and western South Carolina, and on the east coast to New Jersey and northern Maryland, where it commonly occurs with mosses (Youngman 1975; Whitaker 2004). It seems often to be present in traps set for lemmings. Hamilton (1941) found ***Sorex cinereus*** near the summit of Big Black Mountain in Harlan County, Kentucky, USA, at ~1220 m. Of these, six of the seven specimens were taken from runways at the sides of moss-covered logs in damp, deciduous thickets. In the thickets of Maine and New Hampshire, USA, traps set for lemmings also captured shrews (Clough & Albright 1987). These included ***Blarina brevicauda*** (northern short-tailed shrew; Figure 8) and ***Sorex cinereus***. Groves and Yesen (1989) likewise found species of ***Sorex*** in lemming traps in a ***Sphagnum*** "bog" in Idaho, USA (Figure 9), as did Pearson (1991) in Glacier National Park and Reichel and Beckstrom (1993) in western Montana.

Figure 7. ***Sorex cinereus*** (long-tailed shrew), a species that seems to have an affinity for moss-covered logs in its runways. Photo by Phil Myers, through Creative Commons.

Figure 8. ***Blarina brevicauda*** (northern short-tailed shrew), a species caught in lemming traps in thickets of Maine and New Hampshire, USA. Photo by Gilles Gonthier, through Creative Commons.

Figure 9. Mountain bog (poor fen?) in Idaho, USA. Photo by Robert Marshall, through Creative Commons.

Sciuromorpha

Sciuridae

Records indicating that squirrels use mosses to line their nests are old (Tripp 1888). But sometimes, the mosses use squirrel activity to their advantage (Ken Adams, Bryonet 30 April 2020). In the Epping Forest, UK, ***Zygodon viridissimus*** competes with ***Z. forsteri*** for space on the grooves created by squirrel gnawing. The former often out-competes the latter.

Tamias merriami – Merriam Chipmunk

The Merriam chipmunk (***Tamias merriami***) has a small distribution in central and southern California, USA (Harvey & Polite 1999). There seems to be little documentation of chipmunks eating or using mosses. Imagine the surprise when Brent Mishler and his team (Mishler & Hamilton 2002) caught a chipmunk (Figure 10-Figure 11) grabbing a chunk of the moss ***Syntrichia princeps*** (Figure 12-Figure 13) from the very middle of their field of view (Figure 12) through a CAMcorder (see Grant *et al*. 2006 for setup). Mishler (pers. comm. 12 January 2008) suggests that the Merriam chipmunk (***Tamias merriami***; Figure 10-Figure 11) may have been after the water adhering to the moss (***Syntrichia princeps***), as it had just been moistened earlier in the day for an experiment; the surroundings were dry.

Figure 10. ***Tamias merriami***, a chipmunk that harvests mosses. Photo by James Maughn, through Creative Commons.

Figure 11. Chipmunk (***Tamias merriami***), caught in the act by a camcorder as it eats mosses, ***Syntrichia princeps***). Photo courtesy of Brent Mishler.

Figure 12. ***Syntrichia princeps*** with red ellipse indicating where moss was removed by ***Tamias merriami***. Photo courtesy of Brent Mishler.

Figure 13. ***Syntrichia princeps*** with capsules. Photo by F. Guana, Modoc National Forest.

Tamiasciurus hudsonicus – American Red Squirrel

The American red squirrel (***Tamiasciurus hudsonicus***; Figure 14) seems to eat just about anything. It is more tame than most squirrels, and I have even had a confused squirrel climb my leg! It also seems to like decorating its

abode, using paper, moss, and other local objects it can find (Hanrahan 2012).

Figure 14. ***Tamiasciurus hudsonicus*** (American red squirrel) uses mosses to decorate its home. Photo by Cephas, through Creative Commons b

Sciurus vulgaris – Eurasian Red Squirrel

The Eurasian red squirrel (***Sciurus vulgaris***; Figure 15-Figure 16) is distributed across the northern parts of Europe (Greene 1887). It makes a nest in the fork of a tree. This nest is an interwoven structure of twigs, leaves, and mosses.

Figure 15. ***Sciurus vulgaris***, a species that uses pleurocarpous mosses in its nest boxes. Photo from Saxifraga – Mark Zekhuis, with online permission.

Nest boxes used by the Eurasian red squirrel (***Sciurus vulgaris***; Figure 15-Figure 16) displayed pleurocarpous mosses (van Laar & Dirkse 2010). Two of these were ground species [***Hypnum cupressiforme*** (Figure 17), ***Homalothecium sericeum*** (Figure 18)]. The Eurasian red squirrel used only one epiphytic species (***Orthotrichum*** sp.; Figure 19), but van Laar and Dirkse suggested that all of the mosses may have been collected from a nearby tree. The nest included ~470 g spruce twigs and ~180 g of these mosses. In addition, the squirrel had included insulation material from the roof of a nearby house. Quinton (1997) reported finding a nest under ***Sphagnum*** (Figure 6) in the boreal forest of North America.

Figure 16. ***Sciurus vulgaris***, a species that uses pleurocarpous mosses as nesting materials. Photo from Saxifraga – Mark Zekhuis, with online permission.

Figure 17. ***Hypnum cupressiforme***, a moss used in nests of ***Sciurus vulgaris***. Photo by Michael Lüth, with permission.

Figure 18. ***Homalothecium sericeum***, a moss used in nests of ***Sciurus vulgaris***. Photo by Michael Lüth, with permission.

Figure 19. ***Orthotrichum cupulatum*** with capsules, a moss used in nests of ***Sciurus vulgaris***. Photo by Jutta Kapfer, with permission.

Pulliainen and Raatikainen (1996) studied the effect of various nesting materials on nest temperature of the red squirrel in Finland. The wind speed had a large effect on differences between inside and outside the nest. During windless times, the temperature difference could be as much as 30ºC in nests made of mosses, proving mosses to be superior insulators to the beard lichen (*Usnea*; Figure 20). Juniper bark provided the poorest insulation among the materials tested. A plastic plate under grass greatly increased the inside temperature by restricting the air current throughout the nest.

Figure 20. ***Usnea filipendula***, a nest material that has less insulating ability than the tested mosses. Photo by Jerzy Opioła, through Creative Commons.

TalkTalk (2011) describes the nest of the red squirrel as having a layer of twigs with a layer of moss or bark fragments. It is likely that availability is a major influence on the nest materials used.

Sciurus carolinensis – Grey Squirrel

The grey squirrel (***Sciurus carolinensis***; Figure 21-Figure 22) lives in the eastern USA, but is an invasive in Europe (Steele *et al*. 1996; Goheen & Swihart 2003). It builds a nest the size of a football (YPTE 2011). It is comprised of twigs, often with their leaves remaining attached, and is perched high in a tree. The squirrels line the nest with dry grass, shredded bark, moss, and feathers. The summer nest is typically flimsy and located among small branches.

Figure 21. ***Sciurus carolinensis***, grey squirrel, a species that uses mosses as one of its nest lining materials. Photo by Janice Glime.

Figure 22. ***Sciurus carolinensis***, a species that uses mosses as one of its nest lining materials. Photo by John White, with permission.

Spermophilus parryii – Arctic Ground Squirrels

Like the pikas, it appears that Arctic ground squirrels (***Spermophilus parryii***; Figure 23-Figure 24) survive winter in the "warmth" of hibernacula (Barnes 1989). These rodents can wake up and run around when their core temperature is as low as -2.9°C. Temperatures much lower than that can be lethal for such small homeotherms. Maintenance of a temperature as low as -3°C could save up to ten times as much energy as maintenance of a body temperature above 0°C. It is quite possible that for the pikas, the mosses permit the maintenance of sufficiently "warm" temperatures to survive.

Figure 23. ***Spermophilus parryii*** and tunnel entrances. Photo from National Park Service, through public domain.

Figure 24. ***Spermophilus parryii***, Arctic ground squirrel, a species that seems to benefit from the insulating ability of mosses in the nest. Photo Jim McCarthy, through public domain.

Arctic ground squirrels actually cache bryophytes. They preferentially decapsulate bryaceous mosses and store the capsules in their nests for winter food reserves (Zazula *et al*. 2006).

Nest materials for these Arctic ground squirrels in the Yukon include mosses and lichens and these are the most common materials found in the pouches of females (Gillis *et al*. 2005). Carrying these materials was most common prior to and during lactation. These mosses and lichens are absent in male pouches.

Glaucomys – Flying Squirrels

Glaucomys are active all year, but have little resistance to cold (Marchand 2001). Instead, they keep warm by huddling together in tree cavities lined with grass, moss, or bark. The nests can be as much as 30º warmer than the surrounding air outside the nest. These huddles typically have about 10 squirrels, but there may be as may as 50.

Glaucomys sabrinus – Northern Flying Squirrel

The northern flying squirrels (***Glaucomys sabrinus***; Figure 25) has a wide distribution throughout northern North America from Alaska, across Canada to the eastern provinces, with several extensions into northern USA. Like the southern flying squirrel, this squirrel is nocturnal (IUCN 2017).

Figure 25. Northern flying squirrel, ***Glaucomys sabrinus***, a species that uses mosses in its nests. Photo by Phil Myers, through Creative Commons.

The northern flying squirrel (***Glaucomys sabrinus***; Figure 25) builds a cavity nest, using various mosses (Patterson *et al*. 2007). Patterson and coworkers found trace amounts of peat moss (***Sphagnum***; Figure 6), dried grasses, cedar leaves, and twigs in the nests in southern Ontario.

Glaucomys volans – Southern Flying Squirrel

The smaller southern flying squirrels (***Glaucomys volans***; Figure 26) occur along the southern USA north to New England (Marchand 2001). They have tiny bodies, weighing only 57-113 g. They are nocturnal, thus most people have never seen them. Nevertheless, they are the most abundant squirrel in the eastern US.

Figure 26. Southern flying squirrel, ***Glaucomys volans***, a species that uses mosses in its nests. Photo by Ken Thomas, through Creative Commons.

Lagomorpha – Hares, Rabbits, and Pikas

Leporidae – Rabbits and Hares

Lepus arcticus – Arctic Hare

In the high Arctic, the Arctic hare (***Lepus arcticus***; Figure 1, Figure 27) seems to prefer eating developing bryophyte capsules (Catherine LaFarge, Bryonet 30 March 2016). LaFarge often found decapitated sporophytes, although the lemmings helped in the consumption.

Figure 27. ***Lepus arcticus*** in white phase. Photo by Chmee2, through Creative Commons.

Oryctolagus cuniculus – European Rabbit

The European rabbit (***Oryctolagus cuniculus***) is present in all Western European countries, Ireland and UK, Austria, Sweden, Poland, Czech Republic, Hungary, Romania, Ukraine, and Mediterranean, Croatia, and Slovakia (Smith & Boyer 2008).

Rabbits, with their noses to the ground, would seem ideally suited for nibbling on bryophytes. However, it seems they may not find them to their liking. Bhadresa (1977) reported that in a food preference test, the rabbit ***Oryctolagus cuniculus*** (European rabbit – the only domesticated rabbit; Figure 28) in Norfolk – actually disliked ***Dicranum scoparium*** (Figure 29). But then, that is only one moss. Davidson *et al*. (1990) found leaf fragments of ***Mnium*** (Figure 30-Figure 31), ***Brachythecium*** (Figure 32), ***Hypnum*** (Figure 17), and ***Polytrichum*** (Figure 36) species in feces of rabbits in southeast England, but never forming more than 5% of the plant material in a fecal pellet. Rabbits eat a mixed diet (European Rabbit 2009), and it appears that mosses may be part of it – or they are ingested accidentally.

Figure 28. European rabbit, ***Oryctolagus cuniculus***, a species that consumes at least some mosses. Photo by Aiwok, through Creative Commons.

Figure 29. ***Dicranum scoparium*** with capsules, a species that the European rabbit dislikes. Photo by Janice Glime.

Figure 30. ***Mnium spinosum*** cushions, in a genus found in the feces of the European rabbit. Photo by George Shepherd, through Creative Commons.

Figure 31. ***Mnium spinosum***, in a genus found in the feces of the European rabbit. Photo by Michael Lüth, with permission.

Figure 32. ***Brachythecium rutabulum***, in a genus found in the feces of the European rabbit. Photo by J. C. Schou, with permission.

Rabbits can have a negative impact on bryophytes. After a fire in the heathlands of Brittany, rabbits, along with roe-deer, damaged the bryophytes by scraping (Clément & Touffet 1981). The bryophytes were important as initial colonizers after the fire, so the scraped areas suffered from their loss in succeeding plant and animal colonization. The mosses ***Funaria hygrometrica*** (Figure 33) and ***Ceratodon purpureus*** (Figure 34) are important in rebuilding the organic matter following fires and their loss is unfavorable to invertebrate development. ***Polytrichum s.l.*** species have a strong competitive ability compared to tracheophytes in colonizing these nutrient-poor sites. In particular, ***Polytrichastrum formosum*** (Figure 35) and ***Polytrichum commune*** (Figure 36) have a higher density and growth rate and can produce 7-8 tons ha^{-1} yr^{-1}, preventing new species from becoming established and retarding the growth of those already present. As in cases with other rodents, the rabbits may facilitate the development of these **Polytrichaceae** colonies.

Figure 33. ***Funaria hygrometrica***, a species that rebuilds organic matter after a fire. Photo by Michael Lüth, with permission.

Figure 34. ***Ceratodon purpureus***, a species that rebuilds organic matter after a fire. Photo by Janice Glime.

Figure 35. ***Polytrichastrum formosum*** with capsules, a species that is highly competitive on nutrient-poor sites opened up by browsing. Photo from UBC Botany website, with permission.

Figure 36. ***Polytrichum commune***, a species that is highly competitive on nutrient-poor sites opened up by browsing. Photo by Michael Lüth, with permission.

But rabbits (***Oryctolagus cuniculus***; Figure 28) can also create habitat for bryophytes. Callaghan (2015) reports that some mosses thrive due to grazing activities by rabbits in the UK. A more spectacular find occurred at an old tin works in Cornwall, where the rare copper moss ***Scopelophila cataractae*** (Figure 37) benefits by the creation of habitats by rabbits. As succession proceeds on the exposed mineral soil, the tracheophytes replace the bryophytes. However, when the rabbits arrive, the rabbits

create a network of runways and tunnels, exposing the metal-rich soil where the copper moss thrives. These serve as refugia for this moss species that is disappearing as the more coarse vegetation develops. The entrances to burrows are clothed in a mat of protonemata (Figure 38) that have abundant gemmae (Figure 39). Callaghan speculates that the rabbits must disperse thousands of these gemmae on their fur, and the entrance to the tunnel is often the benefactor substrate.

Figure 37. Mature plants of ***Scopelophila cataractae***, a species that benefits from rabbits making tunnels. Photo by Blanka Shaw, with permission.

Figure 38. ***Scopelophila cataractae*** protonemata in a rabbit hole. Photo courtesy of Des Callaghan.

Figure 39. ***Scopelophila cataractae*** protonema and gemma. Photo by Des Callaghan, with permission.

The European rabbit has multiplied from the 24 introduced to Australia in 1859 to over 600 million in less than a century (European Rabbit 2009), suggesting that this rapid multiplier could present considerable destruction to mosses, or could favor their increase by destroying lichens. In areas where rabbits have been introduced, they often have no natural enemies. Australia is a case in point. In such cases, the virus causing **myxomatosis** may be their only enemy. While this has been used successfully to help control the rabbits, the ones currently remaining in Australia are now immune to it.

In a dune system in Wales, the advent of myxomatosis caused changes in the vegetation. This area had been the site of severe rabbit grazing. In 1954, myxomatosis began to spread to the area and Ranwell (1960) anticipated the loss to the rabbit population. In May of 1955 rabbit pellets were common and thick on the transects across turf areas. Mosses were very evident among the 1-2 cm high turf, but were much less evident in the deep turf. During the succeeding years of rabbit decline, grasses, sedges, and pleurocarpous mosses [***Ditrichum flexicaule*** (Figure 40), ***Pseudoscleropodium purum*** (Figure 41), ***Rhytidiadelphus squarrosus*** (Figure 42), ***R. triquetrus*** (Figure 43)] increased, surviving in the ungrazed turf. ***Eurhynchium praelongum*** (Figure 44) and ***Plagiomnium undulatum*** (Figure 45) also increased during the study period. At the same time, decreases were evident in the acrocarpous mosses ***Bryum*** sp. (Figure 46), ***Climacium dendroides*** (Figure 47), ***Dicranum scoparium*** (Figure 29), ***Syntrichia ruralis*** (Figure 48). ***Rhodobryum roseum*** (Figure 49) disappeared from 1955 to 1958. Overall, the bryophyte richness remained unchanged. The greatest losses of mosses occurred only after 3-4 years of recovery from grazing.

Figure 40. ***Ditrichum flexicaule*** in Norway, a species that increased when rabbits declined. Photo by Michael Lüth, with permission.

Figure 41. ***Pseudoscleropodium purum***, a species that increased when rabbits declined. Photo by Janice Glime.

Figure 42. ***Rhytidiadelphus squarrosus***, a species that increased when rabbits declined. Photo by Jan-Peter Frahm, with permission.

Figure 43. ***Rhytidiadelphus triquetrus***, a species that increased when the rabbit population declined. Photo courtesy of Eric Schneider.

Figure 44. ***Eurhynchium praelongum***, a moss that increased in response to rabbit population decline. Photo by Michael Lüth, with permission.

Figure 45. ***Plagiomnium undulatum***, a moss that increased in response to rabbit population decline. Photo by Michael Lüth, with permission.

Figure 46. ***Bryum caespiticium***, in a moss genus that declined when rabbit population declined. Photo by Bob Klips, with permission.

Figure 47. ***Climacium dendroides***, a moss that declined when rabbit populations declined. Photo by Janice Glime.

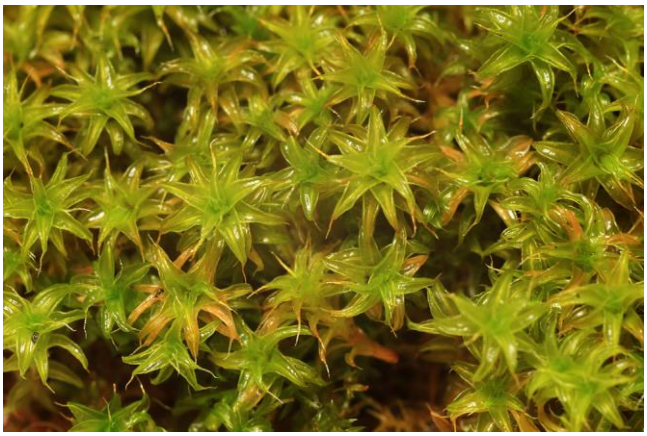

Figure 48. ***Syntrichia ruralis*** ssp ***ruralis***, a moss that declined when rabbit populations declined. Photo by Barry Stewart, with permission.

Figure 49. ***Rhodobryum roseum***, a species that disappears when rabbit herbivory declines. Photo by Hermann Schachner, through Creative Commons.

The results of Ranwell (1960) differ somewhat from those of Watt (1957), who showed that disappearance of rabbits resulted in the decrease of mosses in ungrazed pasture over long periods of time. Watt found 29 bryophyte species, but ***Rhytidiadelphus squarrosus*** (Figure 42) is found only in the ungrazed community. This is in contrast to its common presence in grazed pasture on the South Downs and other locations in Breckland, England. On the other hand, 11 species occur exclusively in the grazed area. These are all small and 10 of the 11 are acrocarpous. As in the Ranwell (1960) study, Watt found that mosses in the ungrazed turf are tall and mostly pleurocarpous. The small mosses seem to be unable to survive competition with taller vegetation, including competition for light. The larger mosses, on the other hand, seem to thrive in the ungrazed conditions. Watt considered these results to support the hypothesis that "in the grazed community the competitive power of the potentially taller growing plants is reduced by grazing sufficiently to allow the smaller species to survive and that in the ungrazed the unchecked growth of taller growing species eliminates or tends to eliminate the smaller, whether they are annual or perennial of varied life-forms."

Gillham (1955) also stressed the importance of rabbit grazing, considering it to be less important than exposure. This contention was supported by the abundance of mosses that are intolerant of extreme exposure, but that are able to reach their maximum in the "closely nibbled swards." Heavy grazing caused moss cover to reach 25%, mostly of the moss ***Ceratodon purpureus*** (Figure 34) – a moss that is not shy of sunlight. In early spring, when the rabbits were most hungry, the lanes between the grazed heather bushes were dominated by the mosses ***Rhytidiadelphus squarrosus*** (Figure 42) and ***Hypnum cupressiforme*** (Figure 17). Gillham (1954) found that bryophyte fragments were only occasionally present in the rabbit dung and concluded that they were probably only eaten when mixed with other plant material. Although the bryophytes are important components of the turf in heavily grazed inland areas, they have little importance on sea cliffs due to their exposure to wind and salt there (Gillham 1955).

Ochotonidae – Pikas

Ochotona princeps – American Pika

The American pika (***Ochotona princeps***; Figure 50) is distributed widely in British Columbia and the western USA (Defenders of Wildlife 2017). Mosses are often a dominant feature of their landscape.

Figure 50. ***Ochotona princeps*** among mosses. Photo courtesy of Mallory Lambert, through Johanna Varner.

The presence of pikas is usually a good indicator of regions with rocky, mesic, cool habitat (Figure 51) with long winters and short summers (Simpson 2009). Although

the American pikas (***Ochotona princeps***; Figure 51) are a high elevation species in western North America, in the Columbia River Gorge they live near sea level (Horsfall 1925; Varner & Dearing 2014a, b). But at low elevations in the southern part of the Columbia River Gorge, Oregon, USA, the known temperature range was extended and the long winters and typical snow accumulation were not present.

Figure 51. ***Ochotona princeps*** among the rocks and mosses of a talus slope. Photo courtesy of Johanna Varner.

Dr. Erik Beever (pers. comm.), research ecologist for the National Park Service Inventory & Monitoring program, reported to me that pikas occur at low elevations (less than 150 m) in a valley fed by a snowmelt river in the Cascade Range of western USA. The valley is cold, and he theorizes that their ability to survive the winter without their usual snow cover is due to the thick (>20 cm) moss mats that provide cover and insulation for them (Figure 52).

Figure 52. ***Ochotona princeps*** emerging from tunnel covered with ***Hylocomium splendens*** and ***Selaginella*** sp. Photo courtesy of Johanna Varner.

Varner and Dearing (2014b) supported this assessment, finding that the moss cover insulates the interstices of the talus slopes from temperature fluctuations. Varner and Dearing (2014a) speculated that the mosses could cool the microclimates of the talus in the valley (Figure 51), making the climate suitable for the pikas. The pikas are able to travel long distances beneath the thick moss cover. Even their extensive moss consumption only removes about 0.002% of the moss in their home ranges in one year. Hence, unlike the lemmings, the pikas can enjoy the cover of the mosses without the danger of eliminating it.

In this unusual habitat they subsist on what is for most rodents an unusual food – mosses (Varner & Dearing 2014a, b). These mosses comprise more than 60% of the diet at the two sites studied. At this rate, the pikas consume ~7.31 g/day and 2.67 kg/year of mosses. The mosses are available all year, thus making food caches unnecessary.

Richardson (1981) considered mosses to be a difficult food for mammalian herbivores, having a high fiber content, low nitrogen, and low digestible energy compared to other food choices. Varner and Dearing (2014a) reported the same high fiber and low nitrogen (<1%) in the mosses of the Columbia River Valley. But the pikas re-ingest their fecal pellets. As a result, the **caecal pellets** (partially digested foods passed as fecal pellets, then re-ingested) of these pikas were far more nutritious, having low fiber content and high nitrogen content, thus allowing the pikas to gain greater nutritional value than that available to other herbivores that do not re-ingest their fecal material.

At high elevations, these talus dwellers forage on the surrounding vegetation (Figure 53) (Huntly *et al*. 1986). Their foraging intensity decreases with distance from the **talus** (rock fragments accumulated at base of cliff or slope), but their selectivity increases with distance, consistent with the "central place foraging theory." In this case, plant abundance increased with distance from the talus. The pikas would travel greater distances to harvest plants for caching (Figure 54) rather than for immediate consumption. For these haying forays, higher proportions of forbs and tall grasses were selected. The haypiles serve to sustain the pikas during winter (Dearing 1997a).

Figure 53. ***Ochotona princeps*** eating a sedge in the Rockies, a rodent that runs around under the moss layer. Photo by Sevenstar, through public domain.

Figure 54. ***Ochotona princeps*** (pika) hay pile. Photo courtesy of Bob Krear.

Dearing (1996) tested the hypothesis that plant secondary compounds may be higher in the winter diet either because they function as preservatives or because pikas delay consumption of these species until the toxins degrade. Dearing found little evidence suggesting that morphology excluded any plants from the winter diet, nor was plant size of importance. Even nutrient content showed only a weak relationship. On the other hand, the winter diet was significantly lower in water content and higher in total energy content, but no other nutrients had any consistent pattern. The manipulation of secondary compounds was, however, important. The winter diet contained more total phenolics and had greater astringency.

Dearing (1996) suggested that these secondary compounds helped to preserve the cache, but it also made an additional (initially toxic) food source available. In a follow-up study, Dearing (1997b) found that following 10 months of storage, the winter diet retained 20.5% more biomass with a higher level of energy while being lower in fiber and equal in nitrogen when compared to the summer diet of these pikas. Experiments demonstrated that the pikas preferred foods with a lower phenolic content compared to species with a high content, and they delayed eating those high phenolic species in the haypile until the phenolic content had decreased (due to microbial activity). This need to store a winter cache occupied almost 55% of the surface activity and the evolution of territoriality most likely relates to the need for sufficient vegetation for the winter food cache (Conner 1983).

Behavioral differences between high elevation and low elevation populations of pikas also contributed to their survival at the lower elevations (Smith 1974). At high elevations (3,400 m) the pikas were active throughout the day. At a lower altitude site (2,550 m) they were mostly active in the morning and late afternoon. During their inactive times at high temperatures, survival made it necessary for them to retreat to favorable microclimates among the rockslides. While onset of vocalization and parturition occurred about six weeks earlier at the low altitude site, as one might expect, it seems strange that the onset of hay storage likewise occurred six weeks earlier. But the timing of vocalization and haying were actually correlated with the amount of precipitation during the previous winter. When the winter was dry with little snow and spring was early, the pikas responded by earlier vocalization and haying. [Perhaps the earlier haying was to ensure more moisture or higher nutrient content of the food items?]

In warm weather, the American pikas have only short bursts of surface activity, typically less than 2.5 minutes at a time (MacArthur & Wang 1974). Instead, they remain in the cooler microclimate beneath the rocks and regulate their body temperature to only 2-3ºC below their upper lethal temperature.

The mean body temperature of a pika ranges 37.9-42.7 in an ambient temperature range of -9.3 to 24ºC (MacArthur & Wang 1973). Hyperthermia causes death after only two hours of exposure to ambient temperatures higher than 28ºC. Its ability to maintain a high body temperature through high metabolism and thick insulation permits it to survive in its high elevation habitat where food storage is limited. Climatic shifts that cause warmer temperatures put the pikas in peril of at least local extinctions (Beever *et al*. 2010). Such local extinctions have already occurred for the American pika living in the Great Basin (Beever *et al*. 2010, 2011). The survival of mosses that ameliorate the high temperatures will be critical to the survival of pikas in these habitats.

Ochotona collaris – Collared Pika

The collared pika (***Ochotona collaris***; Figure 55) is distributed in Alaska and the Yukon (Defenders of Wildlife 2017). They live on a diet of grasses and grass-like plants called sedges, but will include flowering plants, twigs, moss, and lichens among food items. Koju and Chalise (2014) assumed that the poor quality of food in winter caches for this species were due to predation pressure that limited their foraging radius to 10 m.

Figure 55. ***Ochotona collaris***, a species that will include some mosses among its food items. Photo by Jacob W. Frank, through public domain.

An interesting mechanism by at least some collared pikas is the selection of food that has previously experienced herbivory by caterpillars (Barrio *et al*. 2013). Could they be seeking food that had higher levels of secondary compounds, stimulated by the herbivore attacks? Or were these herbivore activities signals of suitable food of high quality?

Like ***Ochotona principes*** (Figure 50-Figure 54), ***O. collaris*** (Figure 55) can run across the talus slope under the moss cover (Morrison *et al*. 2004) in its Yukon, Canada, home (Morrison *et al*. 2009). This most likely reduces predation risk as well as modulating the temperatures they

experience (Morrison *et al*. 2004). Nevertheless, choice of food nutrition level does not seem to be dictated by predation risk. On the other hand, in experiments total amount of forage removed by the pikas was inversely related to predation risk.

Erinaceidae – Hedgehogs

The European hedgehog (***Erinaceus europaeus***) is a nocturnal species of Europe and Central Asia. As its name inplies, it is common in hedgerows. The hedgehog (***Erinaceus europaeus***; Figure 56) is the only British mammal to have spines (Wildscreen 2010). They have fairly short tails, long legs, and small ears. They eat mostly insects, but may include other small animals, like frogs and rodents.

Figure 56. The hedgehog, ***Erinaceus eupopaeus***, a species that uses pleurocarpous mosses for nesting materials. Photo by Jörg Hempel, through Creative Commons.

When young hedgehogs are born, they have a coat with soft, white spines under the skin to protect the mother during birth. After a few hours these emerge. After about 36 hours, a second coat of dark-colored spines emerges, then later a third set emerges. By day eleven, the hedgehogs are able to curl into a ball, and finally after 14 days their eyes open. They are nocturnal, having large eyes, but they may also be active in the daytime (Wikipedia 2017a). They are solitary animals, and only the female takes care of the young.

They rest in the daytime in nests made of twigs, leaves, grass, pine needles, and other foliage. The "other foliage" includes mosses (Figure 57), sometimes in large quantities! Fortunately, the nest is re-used by another individual. The hedgehog selects pleurocarpous mosses that are available near the nest among its nesting materials (van Laar & Dirkse 2010). The authors suggest that the mosses may be selected to maintain a suitable humidity in the nest.

Figure 57. ***Erinaceus eupopaeus***, hedgehog, carrying moss, presumably for a nest. Photo through Creative Commons.

CHIROPTERA – Bats

Pteropidae – Flying Foxes

Pteropus conspicillatus – Spectacled Flying Fox

The flying fox of Australia is really a kind of bat associated with the rainforest habitats of the Wet Tropics bioregion of northeastern Queensland, Australia (Parsons *et al*. 2007). The spectacled flying fox (***Pteropus conspicillatus***; Figure 58-Figure 59) seems like an unlikely candidate for eating mosses, but... this bat ingests mosses, as evidenced by feces (**splat**) comprised of 14% moss (Andi Cairns, pers. comm. 4 December 2004). Samples from the wet complex notophyll vine forest had the greatest occurrence of bryophytes in fecal samples (22.8% of 685 samples) (Parsons *et al*. 2007). The fragments represented a diversity of bryophytes (15 families of mosses, thallose and leafy liverworts) and ranged from whole plants to detached leaves. The bryophytes evidenced effects of being eaten: highly fragmented, abraded, tightly interwoven with hair and fiber content. The bryophytes mixed with hair suggested that they may have been ingested during grooming.

Figure 58. ***Pteropus conspicillatus***, the spectacled flying fox, with folded wings. This bat is a moss disperser. Photo by Shek Graham, through Wikimedia Commons.

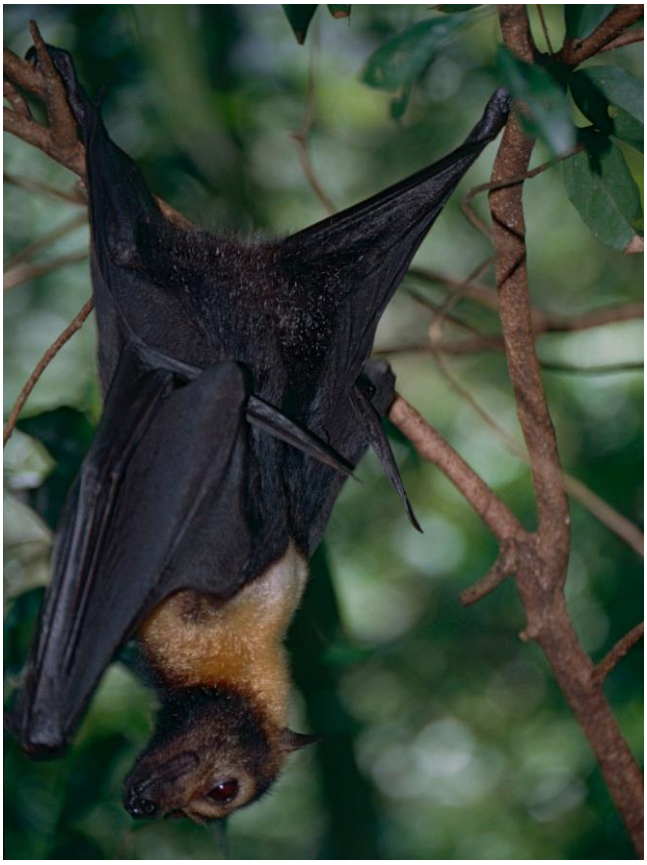

Figure 59. ***Pteropus conspicillatus*** showing the bat wings. Photo by Bernard Dupont, through Creative Commons.

The use of bryophytes as food may be accidental or at least of only minor significance. On the other hand, the flying fox appears to be an effective dispersal vector. Using material from the interior of the feces (Figure 60-Figure 61), Parsons (Figure 60) and coworkers (2007) demonstrated that 52% of 48 fragments developed rhizoids and/or shoots in culture. Seasonal effects were evident, with those collected early in the season having greater germination success (17 of 28 fragments) than those collected later in the growing season (7 of 20).

Figure 60. ***Jennifer Parsons*** and splat trap for ***Pteropus conspicillatus***. Photo courtesy of Andi Cairns.

Figure 61. ***Pteropus conspicillatus*** splat on a leaf. Photo courtesy of Andi Cairns.

Summary

Larger rodents make use of bryophytes, particularly for nesting materials, but a few eat them. Bryophytes make habitats for some of these, especially in bogs, fens, and other wetlands, and in Arctic regions. Such common bog dwellers include shrews,

The Merriam chipmunk gathers mosses, presumably for nesting material, but it could possibly be for food. The Eurasian red squirrel uses mosses in its nest, possibly to buffer the temperature, and possibly also explaining use by the Arctic ground squirrels in their hibernacula. Flying squirrels include mosses in the nest, presumably for the same purpose. The grey squirrel includes mosses to line the nest. The red squirrel uses mosses to decorate its home. Pikas use the mosses as a cool cover during hot days. Pleurocarpous mosses are often preferred for nesting.

Uses for food are less common among these larger rodents, but the Arctic ground squirrels cache moss capsules for winter food. The Arctic hare likewise consumes moss capsules. The European rabbit eats the leafy portions, but it is choosey about which species it eats. Pikas eat mosses when they are abundant. They re-ingest their feces, permitting them to obtain more

nutrients from ingested mosses. Even the flying fox (actually a bat) ingests mosses, and in the process it serves as a dispersal agent.

Scraping activity by rabbits can destroy bryophytes, but this favors the growth of ***Polytrichum*** species and creates disturbed habitats suitable for ***Funaria*** and ***Ceratodon***. And a rabbit burrow provided a suitable habitat (and probably dispersal) for the rare ***Scopelophila cataractae***. In Australia, rabbits caused the disappearance of some species and appearance of others, maintaining similar bryophyte species richness. ***Rhytidiadelphus squarrosus*** benefits from grazing in England, but disappears with rabbit grazing in Australia.

Acknowledgments

This chapter has benefitted greatly from anecdotal records sent to me by bryologists and friends who observed these small rodents interacting with mosses in the field. Steve Juntikka, a former plant taxonomy student of mine, sent me an excited email from Isle Royale after observing the young mouse devouring capsules of ***Funaria hygrometrica***. Leah Vucetich, an Isle Royale researcher, provided me with the tentative identification of a juvenile ***Peromyscus*** based on the picture alone. Andi Cairns alerted me to the study on the spectacled flying fox. Johanna Varner helped me get images of pikas. Thank you to Brent Mishler for helping me to get all the information I needed regarding the CAMcorder observations of the Merriam chipmunk and to Des Callaghan for helping me retell the story of the role of rabbits in making a habitat for ***Scopelophila cateractae***.

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CHAPTER 18-1
LARGE MAMMALS: RUMINANTS - CERVIDAE

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CHAPTER 18-1
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Figure 1. ***Rangifer tarandus groenlandicus*** scraping and browsing in the Arctic. Photo by Erwin and Peggy Bauer, U.S. Fish and Wildlife, through public domain.

Ruminantia - Ruminants

Tiny bryophytes seem unlikely foodstuffs for large ruminants, but there are in fact records of their consumption by a variety of these cud-chewing beasts (Figure 2). What seems unlikely is that bryophytes ever provide a major portion of the diet of these animals, and their consumption may often be accidental.

If you have read about "reindeer moss," notably eaten by reindeer and caribou, you have been fooled by an inappropriate common name. The moss in this case is not a moss at all, but a lichen. And a lichen is not even a plant. Rather, it is a fungus with a partner. That partner can be one of the algae (usually Chlorophyta) or one of the Cyanobacteria. Together, they make a whole new type of organism that often can live in places where neither partner can live alone. The fungi provide protection from UV light and from desiccation. The photosynthetic algae or Cyanobacteria provide the carbohydrate energy source through photosynthesis.

Figure 2. Domestic cow (***Bos taurus***) chewing cud. Photo by foxypar4, through Creative Commons.

Wild ungulates may deliberately eat mosses or ingest them accidentally along with a preferred browse. Even large animals such as the Mylakhchinsk bison (Figure 3) have been found with mosses in the alimentary tract (Ukraintseva *et al*. 1978). Peary caribou (***Rangifer tarandus pearyi***; Figure 6) in the Canadian Arctic archipelago can have up to 58% mosses in their rumen (Thomas & Edmonds 1983), hardly indicative of accidental ingestion. Nevertheless, the nutritive value of bryophytes for warm-blooded animals has been questioned (Sugawa 1960).

Figure 3. European bison (***Bison bonasus***); mosses have been found in the alimentary tract of Mylakhchinsk bison. Photo by Michael Gäbler, through Creative Commons.

Figure 4. ***Hypnum cupressiforme***; ***Hypnum*** was found in the alimentary tract of a Mylakhchinsk bison. Photo by Michael Lüth, with permission.

Figure 5. ***Polytrichum commune***; ***Polytrichum*** sp. was found in the alimentary tract of Mylakhchinsk bison. Photo by Rob Routledge, through Creative Commons.

Figure 6. Peary caribou (***Rangifer tarandus pearyi***) in winter. Photo by L. David Mech, through Creative Commons.

High concentrations of polyphenolic lignin-like compounds in cell walls of bryophytes make the cellular contents less accessible to digestive enzymes (Prins 1982). They furthermore often have polyphenols that have antibiotic properties, thus inhibiting the ability of digestive bacteria in ruminants to break down the bryophytes.

Prins (1982) observed that in cold environments mosses are eaten by a variety of herbivores, both mammals and birds, including the ruminants Peary caribou (***Rangifer tarandus pearyi***; Figure 6), Spitsbergen reindeer (***Rangifer tarandus platyrhynchus***; Figure 7), Soay sheep (***Ovis orientalis***; Figure 8-Figure 9), and musk-oxen (***Ovibos moschatus***; Figure 10). Although mosses have similar caloric values to those of tracheophytes, they are difficult for these ruminants to digest (Hegnauer 1962).

Figure 7. ***Rangifer tarandus platyrhynchus*** grazing among grasses and mosses. Photo by Billy Lindblom, through Creative Commons.

Figure 8. Herd of European mouflon Sheep (***Ovis orientalis musimon***) feeding and lying down, both of which can have an effect on the vegetation. Photo by Frank Vincentz, through Creative Commons.

Figure 9. European mouflon sheep (***Ovis orientalis musimon***), a moss eater. Photo by Frank Vincentz, through Creative Commons.

Figure 10. Musk-ox (***Ovibos moschatus***), a herbivore that eats mosses. Photo through Creative Commons.

One explanation that has been suggested for ruminant herbivory on mosses is that mosses contain high concentrations of highly polyunsaturated fatty acids such as arachidonic acid (Gellerman *et al*. 1972). This fatty acid is also a component of animal cell membranes and other multi-unsaturated C-20 and C-22 fatty acids (Gurr & James 1971; Huneck 1983; Hegnauer 1986). Arachidonic acids have 4 double bonds, whereas the others have 5 double bonds. These are unique in mosses, being absent in seed plants where the highest level of unsaturation is usually two or three double bonds (Swanson *et al*. 1976). Mosses, on the other hand, may have up to 35% of their fatty acids as arachidonic acid, the highest known in any plants (Gellerman *et al*. 1972; Suire & Asakawa 1979). Gellerman *et al*. (1972) and Swanson *et al*. (1976) suggest that in mosses this acid contributes to the special properties of the chloroplast and other tissues that enable them to survive extreme environmental conditions.

Prins (1982) suggested that consumption of mosses with their arachidonic acids permits Arctic animals to have a higher activity level at low temperatures by making their cell membranes, especially in foot pads, more fluid at low temperatures. These fatty acids decrease the temperature at which the membrane undergoes a phase change from a liquid crystalline state to a solid or gel-like state. This behavior of membranes has been demonstrated for cold-acclimated fish; these fish show a higher degree of unsaturation in the lipids of the cell membrane than do warm-acclimated fish (Caldwell & Vernberg 1970; Cossins *et al*. 1977; Smit 1980). Nevertheless, no direct evidence is available to demonstrate the real fate of arachidonic acid derived from a diet including mosses (Prins 1982). If the Arctic animals do eat mosses to gain arachidonic acid, they may have to eat large quantities because of the limited digestibility of the moss.

Some seeds have been protected from mammal predation by neighboring bryophytes (Ukraintseva 1979). In the late Pleistocene, bryophytes reduced post-dispersal predation, whereas ^{14}C dating indicated that some animals had consumed bryophytes.

Van der Wal and Brooker (2004) found that few studies on the impacts of herbivores on the vegetation addressed impacts in the Arctic. They specifically sought understanding of the impact of the moss layer. This layer maintains warmer soils that potentially benefit the tracheophytes. Their results suggest that grazers impact the moss depth, subsequently altering soil temperature, and that this temperature change may impact some tracheophyte abundance. These impacts vary with growth form of the tracheophytes. The moss layer is altered by both grazing and trampling. Furthermore, the feces and urine benefit the tracheophytes, encouraging their expansion.

Impact of Ruminants on Bryophytes

Grazing

A number of studies have indicated that heavy grazing reduces bryophyte and lichen dominance in both oceanic and continental areas (Austrheim *et al*. 2007). Such reductions favor the establishment or increase of more resistant bryophytes such as ***Dicranum*** (Figure 11) species and members of the large mosses in the **Polytrichaceae** (Figure 5) (Helle & Aspi 1983; Väre *et al*. 1996; Virtanen 2000; Olofsson *et al*. 2004).

Hanley (1982) considered food selection by ungulates to involve four morphological parameters:

1. body size
2. type of digestive system (caecal or ruminant)
3. rumino-reticular volume to body weight
4. mouth size.

They considered large ungulates and caecal digesters to be limited by time compared to small ungulates and ruminant digesters. The high **rumino-reticular** (part of a cow's four stomachs) volume to body weight ratio adapts them to gaining nourishment from plants such as graminoids with thick cell walls and high cellulose content. Conversely, a low rumino-reticular volume to body weight ratio adapts those animals to thriving on browse plants (leaves, twigs, or other high-growing vegetation) with thin, lignified cell walls.

Figure 11. ***Dicranum scoparium***, in a genus favored by heavy grazing. Photo by Michael Becker, through Creative Commons.

Milchunas and Noy-Meir (2002) suggest that such environments as cliffs and other small geological formations that prevent herbivory are likely to have greater diversity. They found that 86% of studies in small refuges indicated positive effects of these refuges on plant diversity, whereas only 50% of large refuges had such an impact.

Takala and coworkers (2012) demonstrated the importance of reestablishing herbivory to restore bryophyte communities that were familiar from the days of pasturing large herbivores in the area. They identified three of these restored bryophyte species as suitable indicators of "valuable" grassland habitats: ***Abietinella abietina*** (Figure 12), ***Climacium dendroides*** (Figure 13), ***Syntrichia ruralis*** (Figure 14). In addition, ***Rhytidiadelphus squarrosus*** (Figure 15) is indicative of rich soil and survives at least moderate grazing (Ingerpuu *et al*. 1998).

Figure 12. ***Abietinella abietina***, a moss indicator of valuable grassland habitat. Photo by Hermann Schachner, through Creative Commons.

Figure 13. ***Climacium dendroides***, an indicator of valuable grassland habitat. Photo by Krzysztof Ziarnek, through Creative Commons.

Figure 14. ***Syntrichia ruralis***, an indicator of valuable grassland. Photo by David T. Holyoak, with permission.

Figure 15. ***Rhytidiadelphus squarrosus*** growing among grasses where it seems to benefit from grazing. Photo by Johan N., through Creative Commons.

On the other hand, van der Wal and Brooker (2004) demonstrated that in the High Arctic, mosses can mediate the impact of grazers on the abundance of grasses through their effects on soil temperature.

White-tailed deer (***Odocoileus virginianus***; Figure 16-Figure 17) is among a number of ungulates that have a strong impact on the vegetation in its habitat (Rooney & Waller 2003). Herbivory can cause trophic cascades and even modify the physical structure of the habitat. In the Great Lakes region of North America and elsewhere, the white-tailed deer has experienced population surges due to the annihilation of its natural predators. In response, herb diversity is declining while grasses, sedges, and some ferns are increasing. We can expect that these changes will eventually impact the bryophyte communities (Rooney 2009).

Figure 16. White-tailed deer (***Odocoileus virginianus***) lying down. Photo through Creative Commons.

Figure 17. White-tailed deer (***Odocoileus virginianus goudotii***), a rapidly multiplying species with no natural enemies. Photo by Petruss, through Creative Commons.

Peatlands (Figure 18) seem to be especially susceptible to damage from large herbivores (Bleasdale 1998). The white-tailed deer (***Odocoileus virginianus***; Figure 16-Figure 17), in particular, often enters ombrotrophic bogs and minerotrophic fens in search of food or cover (Pellerin *et al*. 2006). These researchers compared five peatlands (Figure 18) that had been subjected to heavy deer browsing for 75 or more years with five peatlands on deer-free islands. They found that the deer had little impact on cover and species composition in the bogs, but cover of lichens was reduced and that of grasses and sedges increased. But the surface area of bare peat also increased. By contrast, the grazed fens differed significantly from the ungrazed fens. The floristic composition differed, with plant diversity being greater in undisturbed fens, especially for shrubs, sedges, and liverworts (Figure 29-Figure 31). Dunne and Doyle (1998) documented changes in *Molinia*-dominated (Figure 19) blanket bogs in Ireland, where the impact was caused by Kerry cattle, likewise citing impacts on liverworts.

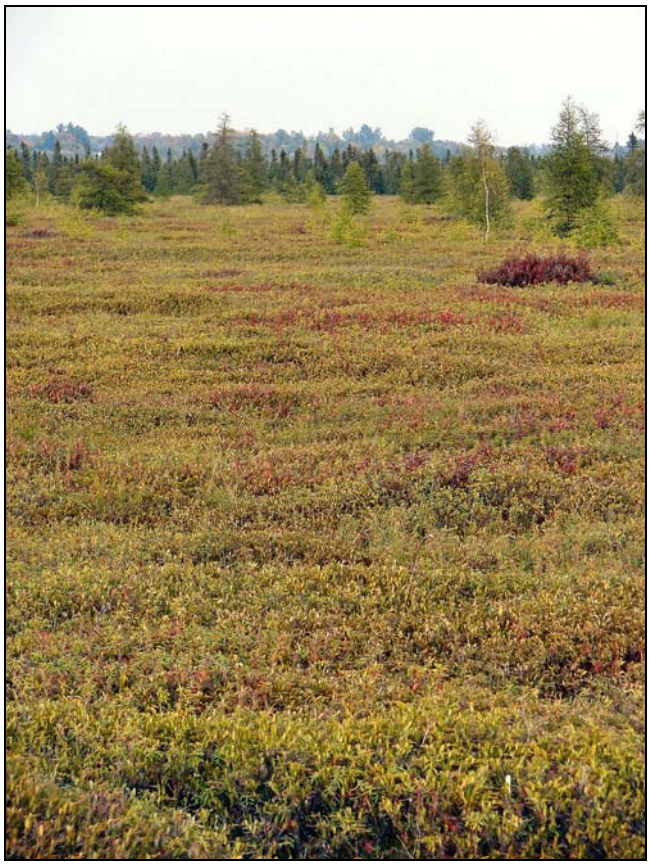

Figure 18. Peatland in Ontario, Canada, a habitat especially vulnerable to browsing and trampling. Photo through Creative Commons.

Figure 19. ***Molinia*** (=***Melica***) ***caerulea*** in wetland, a blanket bog species where cattle can change the bryophyte vegetation. Photo by Lamiot, through Creative Commons.

The effects are not the same in all ecosystems. Olofsson *et al.* (2002) used exclosures against herbivores in two Arctic-alpine (Figure 20) plant communities. Exclosures in the snowbed (Figure 21-Figure 22) resulted

in significant biomass increases of both tracheophytes and cryptogams (including bryophytes), but no corresponding changes occurred in the tall herb meadow. The least competition occurred in the open snowbed plots, a condition the researchers attributed to the mammalian herbivores. Excluding the herbivores permits the plant biomass to build up and eliminate the competitive differences.

Figure 20. Arctic landscape. Photo from USFWS, through Creative Commons.

In northwestern Finnish Lapland, Pajunen *et al*. (2008) used exclosures from 1999-2006 to compare the effects of reindeer grazing in a forest-tundra ecotonal area (Figure 21). The area included tundra heath, frost heath, and riparian habitats. They found a general increase in total cover in all exclosures. However, while the dominant tracheophyte groups increased, the bryophytes diminished in both cover and species richness within the exclosures. Like the cattle, it appears that the reindeer maintain a habitat suitable for bryophytes by reducing tracheophyte competition for light.

Figure 21. Forest-tundra ecotones in Rocky Mountain National Park, USA. Photo by Michael Kirsh, through Creative Commons.

Van der Wal and Brooker (2004) investigated the impact of large herbivores on Arctic plant communities (Figure 22-Figure 23), particularly with attention to the impact on the depth of the moss layer. They found that grazing had a domino effect by impacting the depth of the moss layer (Figure 22-Figure 23), subsequently causing a rise in the soil temperature (see Figure 25 for moss effect on soil temperature). That, in turn affected the seed plant abundance and community structure, especially promoting growth of grasses. The grazing and trampling are both effective in reducing the depth of the moss layer. The grasses benefit not only from the warmer temperatures, but also from the added nutrients from grazer **feces** (poop) and urine.

Figure 22. Moss layer at Nunavut tundra, Northern Canada, showing late snowbed. Photo by A. Dialla, through Creative Commons.

Figure 23. Vegetation in the tundra at Nunavut in the Canadian Arctic Archipelago. Photo by A. Dialla, through Creative Commons.

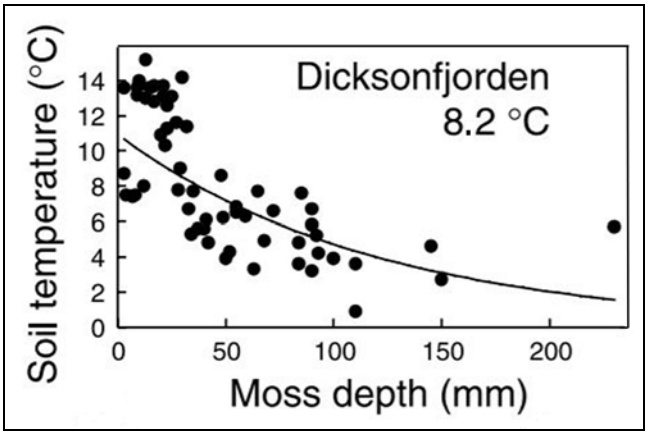

Figure 24. Typical example of moss depth effects on soil temperature in Spitzsbergen. Temperature given is ambient temperature at Dicksonfjorden. Modified from van der Wal and Brooker 2004.

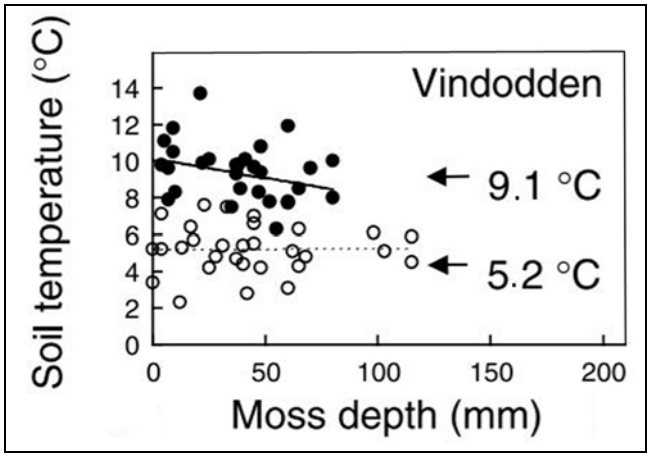

Figure 25. Typical example of moss depth effects on soil temperature at Vindodden in Spitzsbergen. Dark and open circles represent two different days with different ambient air temperatures, as indicated. Modified from van der Wal and Brooker 2004.

Similarly, Elkington (1981) found that sheep and rabbit exclosures on limestone grasslands (Figure 26) in Teesdale, England, caused the grassland structure to become more open, largely through the loss of the grass ***Festuca ovina*** (Figure 27) and reduction of bryophyte and lichen cover. In Utah, USA, the cryptogamic crust (Figure 28) suffered "considerably" from domestic grazing (Anderson *et al*. 1982a, b). In this sensitive ecosystem, the cryptogamic cover was able to recover in 14-18 years.

Figure 26. Limestone grassland in Swindale Wood, England. Photo by Andrew Curtis, through Creative commons.

Porley and Rose (2001), being bryologists, expressed regret that the liverwort mat (*Scapanietum asperae*; Figure 29-Figure 39) was disappearing in English chalklands, dropping from 30 known localities 50 years earlier to 8 or fewer. These communities consisted of the bryophytes ***Scapania aspera*** (Figure 29), ***Frullania tamarisci*** (Figure 30), ***Porella arboris-vitae*** (Figure 31), ***Hypnum lacunosum*** (Figure 32), ***Ctenidium molluscum*** (Figure 33), ***Dicranum scoparium*** (Figure 11), ***Pseudoscleropodium purum*** (Figure 34), ***Calliergonella cuspidata*** (Figure 35), ***Neckera crispa*** (Figure 36), ***Homalothecium lutescens*** (Figure 37), and occasionally ***Ditrichum gracile*** (Figure 38) and ***Tortella tortuosa*** (Figure 39). These communities have suffered from release from grazing, being replaced by other species. The loss for bryologists is supported by the absence of these communities on the continental chalklands and the conservation importance of the community.

Figure 27. ***Festuca ovina*** var. ***glauca***, a grass lost to grazing in limestone grasslands. Photo by David J. Stang, through Creative Commons.

Figure 28. Cryptogamic crust in Hovenweep National Monument (in Colorado and Utah). Photo from NOS, through Creative Commons.

Figure 29. Leafy liverwort, ***Scapania aspera***, dominant species in the liverwort mat (*Scapanietum asperae*). Photo by Hermann Schachner, through Creative Commons.

Figure 30. ***Frullania tamarisci***, a leafy liverwort member of the liverwort mat in English chalk grasslands. Photo from Proyecto Musgo, through Creative Commons.

Figure 31. ***Porella arboris-vitae***, a leafy liverwort member of the liverwort mat in English chalk grasslands. Photo by J. C. Schou, with permission.

Figure 32. ***Hypnum lacunosum***, a moss member of the liverwort mat in English chalk grasslands. Photo by Hermann Schachner, through Creative Commons.

Figure 33. ***Ctenidium molluscum***, a moss member of the liverwort mat in English chalk grasslands. Photo by Hermann Schachner, through Creative Commons.

Figure 34. ***Pseudoscleropodium purum***, a moss member of the liverwort mat in English chalk grasslands. Photo by Hermann Schachner, through Creative Commons.

Figure 35. ***Calliergonella cuspidata***, a moss member of the liverwort mat in English chalk grasslands. Photo by David T. Holyoak, with permission.

Figure 36. ***Neckera crispa***, a moss member of the liverwort mat in English chalk grasslands. Photo by Uniprot, through Creative Commons.

Figure 37. ***Homalothecium lutescens***, a moss member of the liverwort mat in English chalk grasslands. Photo by David T. Holyoak, with permission.

Figure 38. ***Ditrichum gracile***, a moss that sometimes occurs in the liverwort mat in English chalk grasslands. Photo by Hermann Schachner, through Creative Commons.

Figure 39. ***Tortella tortuosa***, a moss that sometimes occurs in the liverwort mat in English chalk grasslands. Photo by David T. Holyoak, with permission.

As late as 1997, Bullock and Pakeman voiced concerns over the effects of reintroducing grazing to lowland heath (Figure 40) in England, citing the lack of information to guide management in these ecosystems. They found that introducing grazing or increasing stocking rates caused a general increase in plant species richness, grass, forb, bryophyte, and lichen cover, and area of bare ground. At the same time, litter depth and cover of dwarf shrubs and scrubs.

Figure 40. Lowland heath in England, a habitat that suffers from the effects of over-grazing. Photo by Roger Key, with permission.

One source of understanding the impact of browsers is through introductions. The Sitka black-tailed deer (***Odocoileus hemionus sitkensis***; Figure 41-Figure 42) to Haida Gwaii in the Queen Charlotte Islands, BC, Canada, in the late 19th Century provided such an opportunity (Stockton *et al*. 2005). The temperate rainforest is a habitat where little information exists on the impact of herbivory by large mammals. This system fortunately gave us a time table because among the 7 islands, there was representation of no deer, deer for less than 20 years, and deer for more than 50 years. When the deer were introduced, their natural predators (wolves and cougars) were absent. Where deer were never present, lower vegetation cover exceeded 80%, whereas it was less than 10% on islands that had

experienced deer browsing for more than 50 years. Interestingly, species richness was similar on all 7 islands, whereas diversity at the plot scale (314 m^2) was 20-50% lower on islands with more than 50 years of deer browsing. Hence, the deer have simplified the ecosystem. This raises the question of the effects on bryophytes in this temperate rain forest. Typically, bryophyte cover is high, and the forests on Queen Charlotte Island are draped in bryophytes (Figure 43) (*e.g.* Hong & Glime 1997).

Figure 41. Sitka black-tailed deer (***Odocoileus hemionus sitkensis***), a species that has devastating effects on vegetation on some islands among the Queen Charlotte Islands, British Columbia, Canada. Photo by D. Gordon E. Robertson, through Creative Commons.

Figure 42. Sitka black-tailed deer (***Odocoileus hemionus sitkensis***). Photo by Wanetta Ayers, through public domain.

Figure 43. Hoh rainforest, with epiphytes on maples, a scene similar to that on the nearby Queen Charlotte Islands. Photo by Kevin Muckenthaler, through Creative Commons.

Contrary to many of these studies, Suominen *et al*. (1999) demonstrated in two Swedish pine forests (Figure 44) that moss cover was higher in unbrowsed plots (by moose, ***Alces alces***; Figure 45), and lichen cover was higher in browsed plots. They considered this difference to be a response to the differences in the amount of light reaching the forest floor. In the greater light, the drought-resistant lichens could outcompete the shade-tolerant mosses, reaffirming the differences in response between habitats. Invertebrates differed as well, with higher numbers in unbrowsed plots, but diversity was higher in the browsed plots. This is an aspect that has not been examined relative to bryophyte communities of invertebrates. It also raises the question of the impact of moose browsing on the epiphytic bryophyte flora. Even if the mosses are not eaten, the higher light and lower moisture levels caused by browsing on trees could have an impact.

Figure 44. Pine forest in Sweden. Photo from Pixabay, through Creative Commons.

Figure 45. ***Alces alces*** bull moose grazing among shrubs. Photo from Denali National Park, Alaska, USA, through Creative Commons.

Brotherson *et al*. (1983) examined the long-term effects of grazing on **cryptogamic crusts** (bryophytes, lichens, algae, and bacteria; Figure 28) in the Navajo National Monument, Arizona, USA. They found that grazing over 40 years had greatly impacted both the

tracheophyte (plants with lignified vascular tissue) and cryptogamic communities. The cryptogamic community suffered the most, exhibiting the greatest reduction in cover. Algae were much more tolerant than the lichens and bryophytes. In Idaho, Hilty *et al*. (2004) suggested that following fire in these rangelands, a resting period from livestock grazing would reduce invasive grasses and benefit the native mosses.

Not surprisingly, air pollution, in particular nitrogen pollution, plays a role in the relationship of grazing and bryophytes. Van der Wal *et al*. (2003) found that as livestock grazing increased concurrently with increased N deposition, large-scale degradation of both natural and seminatural ecosystems occurred. Using an experimental approach, these researchers demonstrated that the interplay between grazing and N deposition has led to the replacement of moss-dominated habitats by those dominated by grasses and sedges.

Trampling

Even when large mammals don't eat bryophytes, they can impose serious damage through trampling (Figure 46). Liddle (1997) considered mosses to be particularly sensitive to disturbances such as trampling. Thus, when trampling is reduced, we should expect bryophyte abundance to increase (Jónsdóttir 1991; Økland 1997; van der Wal *et al*. 2003). But the response is not quite so simple, because it also depends on the response of the rodent community (Austrheim *et al*. 2007). This trampling effect becomes most important in sensitive, slow-growth ecosystems such as those in the Arctic (Callaghan *et al*. 2001).

Figure 46. Introduced reindeer on South Georgia, Ocean Harbour, showing how hoofs could kick up and trample the vegetation. Photo by Roger S. Key, with permission.

In addition to trampling, some hoofed mammals such as roe deer (***Capreolus capreolus***; Figure 47) scrape the ground (Figure 48), dislodging the bryophytes and often exposing bare ground (Clément & Touffet 1981).

Although the role in destruction creates a major impact, trampling and scraping (Figure 1) can at times facilitate dispersal of bryophytes. Pénzes-Kónya (2003) documented the role of disturbance in dispersal of the cushion moss, ***Leucobryum juniperoideum*** (Figure 49), in the Bukk Mountains of northern Hungary where it is the dominant bryophyte on the ground. Both deer (**Cervidae**) and mouflons (***Ovis orientalis orientalis***, a subspecies of wild sheep) are instrumental in turning over whole cushions during the extremely dry spring. But ***L. juniperoideum*** actually benefits somewhat from this behavior. It responds to the change in light direction and gravitational pull by growing in a ball (Figure 50). And it has **caducous** (able to break off) leaves that behave like gemmae for reproduction (Figure 51).

Figure 47. Roe deer (***Capreolus capreolus***) male and female. Photo by Juan Lacruz, through Creative Commons.

Figure 48. Roe deer (***Capreolus capreolus***) tracks, indicating the depth of penetration of hoofs. These same hoofs can carry bryophyte fragments and "plant" them elsewhere. Photo by James K. Lindsey, with permission.

Figure 49. ***Leucobryum juniperoideum***, a species that forms a ball and grows on the new upper side when turned over by disturbance. Photo by David T. Holyoak, with permission.

Figure 50. ***Leucobryum juniperoideum*** cushion that has been turned upside down and experienced new growth on its new top side. This ball-shaped form is typical after such disturbance. Photo courtesy of Erika Pénzes-Kónya.

Figure 51. Leaf of ***Leucobryum juniperoideum*** that was turned to under side of clump, showing the development of rhizoids. Photo courtesy of Erika Pénzes-Kónya.

While the stems of ***L. juniperoideum*** are upside down, rhizoids form on the leaf tips (Figure 51). These plants, and their detached tips, form new plants and can be dispersed by the hooves. Even the leaf lamina cells can produce filaments when the plants are turned over (Figure 52). Nevertheless, during the dry season the disturbance is greater than the regeneration. The new growth occurs faster in the rainy periods. ***Leucobryum glaucum*** (Figure 53-Figure 54) has similar behavior when turned upside-down (Erika Pénzes-Kónya, Bryonet 13 June 2011).

But cryptogamic crusts (Figure 28) are not so fortunate (Anderson *et al*. 1982b). Domestic grazing greatly reduces the lichens, mosses, and algae forming the crusts. This destruction coincides with soils with heavier texture and greater salinity. Recovery seems to be moderately fast, with crusts usually becoming re-established within 14-18 years.

In three sagebrush communities (Figure 55) in east-central Idaho, USA, cryptogamic crusts (Figure 28; Figure 55) are important in maintaining the ecosystem (Kaltenecker *et al*. 1999). These biological crusts typically have bryophytes that help to retain water and collect it from dew. Following ~10 years of exclosure to browsing, the crust doubled compared to areas where browsing continued. However, in the area of low sagebrush (*Artemisia arbuscula*; Figure 56), there was the least crust cover and this cover did not differ in exclusion areas there, apparently limited by the gravelly soil surface and dominance of rhizomatous grasses.

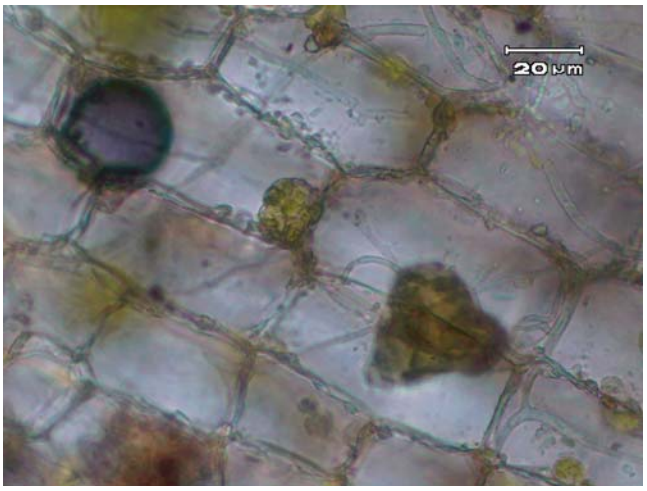

Figure 52. Green cells of ***Leucobryum juniperoideum*** that developed filaments when moved to the top of the clump. Photo courtesy of Erika Pénzes-Kónya.

Figure 53. ***Leucobryum glaucum*** in Epping Forest. Photo by Barry Samuels, with permission.

Figure 54. Cushion moss (***Leucobryum glaucum***), a species that forms a ball and grows on the new upper side when turned over by disturbance. Photo by Rob Routledge, through Creative Commons.

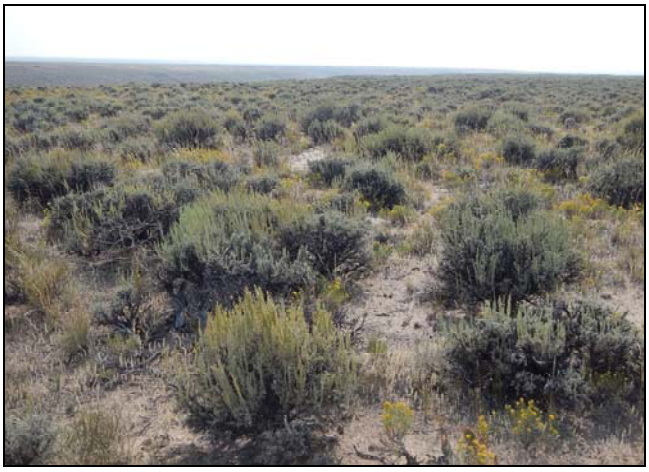

Figure 55. Sagebrush steppe in Grand Teton National Park, USA. Photo by Matt Lavin, through Creative Commons.

Figure 56. ***Artemisia arbuscula***, a sagebrush in areas where cryptogamic crusts are limited. Photo by Matt Lavin, through Creative Commons.

Yet another response to trampling can be found in fens (Figure 57) (Stammel & Kiehl 2004). Low light availability limits seed germination, accompanied by litter accumulation and competition by mosses.

Figure 57. Fen, sometimes referred to as a flow-through bog. Photo through Creative Commons.

Manuring

We use manure (Figure 58) to fertilize crops, so it is reasonable to ask what effect ruminant manure has on the one-cell-thick moss leaves. Vanderpuye *et al*. (2002) examined the effects in the ***Luzulion nivalis*** (Figure 59) snowbeds (Figure 60 at Sassendalen, Svalbard. This location has a low water table, whereas moss tundras usually have no standing water. In these cold environments, manure seems to explain the moss tundra vegetation. The mammals contributing this manure are non-migratory Svalbard reindeer (***Rangifer tarandus platyrhynchus***; Figure 7).

Figure 58. Manure-straw mix to be used in agriculture. Photo by Malene Thyssen, through Creative Commons.

Figure 59. ***Luzula nivalis***, the species for which the *Luzulion nivalis* is named. Photo by Jeffery M. Saarela, through Creative Commons.

Figure 60. Late snowbeds, Great Britain. Photo by Nigel Brown, through Creative Commons.

Several authors have demonstrated that manure from mammalian grazers and enhanced nutrient cycling resulting from grazing can cause an increase in the graminoids and a concurrent decrease in bryophyte abundance in Arctic-alpine tundra (Olofsson *et al*. 2001; Stark *et al*. 2002).

Van der Wal *et al*. (2004) tested the hypothesis that large herbivores manipulate their own food supply by modifying soil nutrient availability. To do this in a Spitzbergen tundra, they added feces of the reindeer ***Rangifer tarandus platyrhynchus*** (Figure 7) for four years, thus simulating the effect of feces impact by a larger herd. After the third year, the standing crop of grasses had clearly increased in both shoot density and biomass per shoot. At the same time, the increase in feces and grass productivity did not result in increased grazing pressure. The added feces caused an increase in soil microbial biomass carbon and nitrogen, especially under wet conditions that promoted decay rates. Under dry conditions, the grasses benefitted from the fecal additions. On the other hand, the moss layer depth was significantly impacted by the fecal addition. Areas with the greatest soil microbial biomass likewise had the greatest reduction in moss depth. Van der Wal and coworkers suggested that the moss reduction was due to greater decomposition of the mosses by the enhanced microbes. It is common for Arctic seabirds to affect the tundra vegetation, but here the non-migratory Svalbard reindeer have replaced the seabirds and created an intense manuring effect (Vanderpuye *et al*. 2002). This illustrates yet another mechanism by which grazers impact the bryophyte community, especially in the tundra (van der Wal *et al*. 2004). But Vanderpuye and coworkers consider the reindeer manuring to explain the presence of moss tundras in this Spitzbergen landscape where seabird colonies are absent. Perhaps it is all about the size of the herd.

Life on Manure – Splachnaceae

A discussion of manuring and bryophytes would not be complete without describing the fascinating relationships of the moss family **Splachnaceae** with manure.

While some bryophytes suffer from the manure of reindeer and caribou, others find these to be their most suitable habitat. These dung mosses include, in particular, many members of the **Splachnaceae**. Included are ***Aplodon wormskjoldii*** (Figure 61), ***Splachnum luteum*** (Figure 62), ***S. sphaericum*** (Figure 63), ***Tayloria*** spp. (Figure 64), ***Tetraplodon mnioides*** (Figure 65), ***T. paradoxus*** (Figure 66), and ***Voitia hyperborea*** (Figure 67) (Steere 1976). See also Volume 1, Chapter 4-9, Adaptive Strategies: Spore Dispersal Vectors.

Figure 61. ***Aplodon wormskjoldii*** with capsules, an Arctic dung moss. Photo by Taimyr Anabar Fedosov, with online permission.

Figure 62. ***Splachnum luteum*** in Alaska, a dung moss with its capsules. Photo courtesy of Andres Felipe Baron Lopez.

Figure 63. ***Splachnum sphaericum*** with capsules, an Arctic dung moss. Photo by Madcowcult, through Creative Commons.

Figure 64. ***Tayloria serrata*** with capsules, an Arctic dung moss. Photo by Hermann Schachner, through Creative Commons.

Figure 65. ***Tetraplodon mnioides*** with capsules, a dung moss in the Arctic. Photo by Hermann Schachner, through Creative Commons.

Figure 66. ***Tetraplodon paradoxus*** with capsules, a dung moss in the Arctic. Photo by Michael Lüth, with permission.

Figure 67. ***Voitia hyperborea*** with capsules, a dung moss in the Arctic. Photo by Michael Lüth, with permission.

I am most familiar with these mosses on moose droppings. My first experience was spectacular. I was walking along a path on Isle Royale (Figure 68-Figure 69), Michigan, USA. This is the largest island in Lake Superior (Figure 68) and has a large moose (***Alces alces***) population. My student was ahead of me, searching for the ***Splachnum rubrum*** (Figure 70-Figure 71) he had seen before I arrived. Suddenly an iridescent purplish red caught my eye! My immediate response was "What in the world?…**IT'S SPLACHNUM!**"

Figure 68. Lake Superior, with Isle Royale indicated by the arrow. Photo from NASA, through public domain.

Figure 69. Isle Royale and its associated smaller islands. Photo by Todd VerBeek, through Creative Commons.

Figure 70. Winter moose dung with ***Splachnum rubrum*** on Isle Royale. Photo by Janice Glime.

Figure 71. ***Splachnum rubrum*** capsules on Isle Royale, Michigan. Photo by Janice Glime.

Splachnum rubrum (Figure 70-Figure 71) is picky, occupying only the winter dung (Figure 72), the dung that drops as small cylinders. It differs from the large, moist "cow pies" of summer because the winter food consists of twigs and branches and other foods low in nutrients and moisture content.

Figure 72. Moose (***Alces alces***) winter scat. Photo by Cephas, through Creative Commons.

In spring, the capsule odor attracts flies. With luck, the flies have visited another patch of these dung cylinders where ***Splachnum rubrum*** (Figure 70-Figure 71) has grown and produced capsules. In their mature stage, these capsules smell like dung and attract the flies that subsequently get spores on them. These are transferred to the next patch of dung they encounter. Details of this wonderful family will be provided later in the Habitats volume.

Cervidae – Deer, Elk, Moose, and Caribou

In the Arctic, members of this family are often dependent on mosses for food, but some members of the family may also impact bryophytes in lower latitudes. Chollet *et al*. (2013) reported that the deer family **Cervidae** has increased in abundance in temperate and boreal forests. The impact of these over-abundant deer is well documented (Kirby 2001), but little is known about the impact on bryophytes (Chollet *et al*. 2013).

White-tailed Deer – *Odocoileus virginianus*

The white-tailed deer (***Odocoileus virginianus***; Figure 73) has a significant impact on the tracheophyte vegetation, damaging forest vegetation and crops (Horsley *et al*. 2003). Using exclosures (Figure 74), Stewart and Burrows (1989) found that the lichen-moss cover changed little between exclosures and non-exclosures from 1979 to 1985.

Figure 73. ***Odocoileus virginianus***, white-tailed deer, seems to have little effect on the bryophyte vegetation. Photo by Scott Bauer, USDA, through public domain.

Figure 74. Exclosures, **near** for reindeer, **far** (with young trees) for both rodents and reindeer, at Abisko in sub-Arctic Sweden. Photo by Monteuxs, through Creative Commons.

In many parts of the eastern USA the increases in deer populations indicate that effects on plant communities may increase in the future (Stromayer & Warren 1997). The impact of heavy deer browsing seems to be particularly exacerbated in swamps by the mossy and soupy peat. Quantitative studies are needed to assess the impact of the white-tailed deer on bryophyte communities.

Black-tailed Deer – *Odocoileus hemionus*

Chollet *et al*. (2013) compared the impact of browsing by the black-tailed deer (***Odocoileus hemionus***; Figure 75-Figure 76) in two island groups, one with the deer and one without, in the Haida Gwaii archipelago of British Columbia, Canada. In this case, the deer totally avoided browsing, as determined by observations on their feeding. The islands with the black-tailed deer had greater density, cover, and diversity of bryophytes than the islands with no deer. This presumably is due to reduced competition with tracheophytes for light and the total avoidance of foraging on bryophytes by the black-tailed deer.

Figure 75. ***Odocoileus hemionus sitkensis***, Sitka Deer, at Haida Gwaii, Vancouver Island, Canada. Photo by D. Gordon E. Robertson, through Creative Commons.

Figure 76. ***Odocoileus hemionus sitkensis***, a subspecies found on Vancouver Island, Canada. Photo by Wanetta Ayers, through public domain.

Reindeer/Caribou – *Rangifer tarandus*

Reindeer and caribou (***Rangifer tarandus***; Figure 77) are different names for the same ungulate in different parts of the world. Their browsing on lichens, especially those known as reindeer "mosses" (*Cladina* spp.; Figure 78), is well known (Väre *et al*. 1995; Olofsson *et al*. 2004), but their consumption of bryophytes is less well understood.

Figure 77. ***Rangifer tarandus*** (caribou) grazing. Photo by Peter Nijenhuis, through Creative Commons.

Figure 78. ***Cladina*** spp. in Tyresta National Park, Sweden – preferred food of reindeer. Photo by Peder Curman, through Creative Commons.

Importance of Mosses in Diet

Several authors claim that reindeer/caribou seldom eat mosses, despite the limited availability of other foods (Person *et al*. 1980; White & Trudell 1980; Olofsson *et al*. 2004). In a study of food preferences in northern Sweden, Danell *et al*. (1994) found that these animals had a high preference for lichens in winter, but a low one for the common moss ***Pleurozium schreberi*** (Figure 79). The researchers were unable to explain this difference by nitrogen content, organic matter digestibility, or fiber.

Figure 79. ***Pleurozium schreberi***, a common moss often avoided by reindeer and caribou. Photo by J. C. Schou, with permission.

Crête *et al*. (1990) compared lactating caribou in two tundra habitats (Figure 80), one where lichens occupied more than 50% of the ground cover and one where mosses, bare soil, and graminoids dominated the vegetation. The rumen contents reflected the differences in the two habitats. Fewer lichens were eaten in the habitat dominated by mosses and graminoids. Nevertheless, selection for lichens was intense, with lichen cover 25X less but only 1.5-2X less abundant in the rumina.

Figure 80. Barren-ground caribou (***Rangifer tarandus groenlandicus***) grazing in the tundra. Photo from USFWS, through public domain.

Klein (1979) found that the Peary caribou (***Rangifer tarandus pearyi***; Figure 6, Figure 82) – a subspecies in the high Arctic islands of Canada's Nunavut and Northwest territories – eat a smaller percentage of lichen than do caribou on the mainland. Rather, they rely on vascular plants and a greater quantity of mosses. Rumen contents contained an average of 58% mosses in Peary caribou of five regions of the Canadian Arctic archipelago during winter, representing five regions (Thomas & Edmonds 1983). Nevertheless, they still prefer the rather scarce foliose lichens in winter (Klein 1979).

In Arctic ecosystems (Figure 81), tracheophyte food can be scarce and mosses subsequently form a major component of the diet of many vertebrate herbivores. In addition to the rodents and birds already discussed in earlier chapters as bryophyte herbivores, ruminants in the Arctic also depend on mosses as a component of their diet. These include reindeer and caribou (***Rangifer tarandus***; Figure 80-Figure 82) and muskox (***Ovibos moschatus***; Figure 83) (Prins 1982; Prop & Vulink 1992; Longton 1997; van der Wal *et al*. 2000; Joly *et al*. 2007).

Figure 81. Arctic tundra from air. Photo by Robert Berdan, with permission.

Figure 82. ***Rangifer tarandus pearyi***, a moss eater. Photo by Morgan Anderson, Environment, with online permission.

Figure 83. Muskox (***Ovibos moschatus***), a tundra moss eater. Photo through Creative Commons.

Manseau *et al*. (1996) considered the habitat of caribou (***Rangifer tarandus***; Figure 80) to be very susceptible to both grazing and trampling by the caribou. In fact, it appears that the herd size is regulated by the amount of available forage in its summer range. They found that the lichen mat was absent in grazed areas of the shrub tundra and that those areas were either bare or occupied by fragments of dead lichens and mosses.

On the other hand, lichens are very important to the caribou diet. Pharo and Vitt (2000) reported that in the montane forests of western Canada, the lichens preferred by the endangered woodland caribou (***Rangifer tarandus caribou***; Figure 84) were abundant, but the ground cover was dominated by feather mosses, especially ***Pleurozium schreberi*** (Figure 79).

Figure 84. Caribou (***Rangifer tarandus caribou***) feeding in tundra, Northwest Territories, Canada. Photo by Robert Berdan, with permission.

The Svalbard reindeer (***Rangifer tarandus platyrhynchus***; Figure 7) includes coprophagy among its feeding strategies (van der Wal & Loonen 1998). That is, they feed on the feces of barnacle goose (***Branta leucopsis***; Figure 85). In fact, the majority of the reindeer in the research area were seen feeding on these droppings instead of vegetation. The number of goose droppings eaten were enough to supply the daily energy requirements for 68 reindeer. But they were very selective in their choice of droppings, choosing those containing grass and avoiding those with moss fragments. There did not appear to be important differences in nitrogen, phosphorus, magnesium, calcium, sodium, potassium, or energy content between the two types of feces. Fiber, on the other hand, differed between grass- and moss-dominated droppings, with less fiber associated with the mosses. Thus, the grass-dominated droppings were more digestible.

Nevertheless, Arctic herbivores, including ***Rangifer tarandus***; Figure 80, Figure 84), do consume substantial quantities of bryophyte biomass (van der Wal & Brooker 2004) and further damage them through trampling. Liddle (1997) has shown that trampling can be particularly destructive to mosses in Arctic ecosystems because of their slow growth rate and recovery (Callaghan *et al*. 2001).

Figure 85. Barnacle Geese (***Branta leucopsis***); Svalbard reindeer eat the feces of this goose, but avoid feces with mosses. Photo by Allan Hopkins, through Creative Commons.

Digestibility

Several authors have attributed the usual lack of consumption to the low digestibility of mosses (Person *et al*. 1980; White & Trudell 1980; Thomas & Kroeger 1981). Nevertheless, on Arctic islands with little lichen availability, the caribou herds eat mosses (Staaland *et al*. 1979).

Robert Pegau, in correspondence with Howard Crum, reported that reindeer in Alaska scarcely digest mosses (Crum 1973), although they do graze on ***Polytrichum*** (Figure 5), ***Aulacomnium turgidum*** (Figure 86), and ***Hylocomium splendens*** (Figure 87) (Bland 1971). A high content of moss (up to 12%) in winter in the rumen of reindeer at Hardangervidda, Norway, may be ingested unavoidably while grazing on lichens (Gaare & Skogland 1975). Lichens, on the other hand, are readily digested (Crum 1973).

Figure 86. ***Aulacomnium turgidum*** in Norway, a moss species eaten by Alaskan reindeer. Photo by Jutta Kapfer, with permission.

Figure 87. ***Hylocomium splendens***, a moss species eaten by Alaskan reindeer. Photo by Rob Routledge, through Creative Commons.

Nevertheless, when lichens are overgrazed, reindeer may turn to mosses. On Svalbard, where desirable lichens are scarce, Svalbard reindeer (***Rangifer tarandus platyrhynchus***; Figure 7) had a rumen content of 32-39% mosses, hardly an accidental accompaniment to lichens (Reimers 1977). In fact, van der Wal (2006) considers Svalbard reindeer to be moss specialists, consuming up to 54% of their winter diet as mosses, a figure similar to that of Peary caribou (***Rangifer tarandus pearyi***; Figure 6, Figure 82) in northern Canada (Klein 1979). Rather than eating lichens, reindeer in the High Arctic seem to have replaced lichens as winter forage with bryophytes (Staaland *et al*. 1983; Staaland 1986; Longton 1997). Staaland *et al*. (1983) found that the mosses on Svalbard provided a higher mineral content than the food available in Norway, but at the same time, the mosses had lower digestibility than the lichens and browse in Norway.

In a different study, Bjorkvoll *et al*. (2009) found that the winter diet of Svalbard reindeer (***Rangifer tarandus platyrhynchus***; Figure 7) was only 22-30% mosses during the three-year period of the study. Effects of snow cover in late winter affected the dietary composition. ***Polytrichum*** (Figure 5) was the most common bryophyte and comprised a relatively high proportion in the early winter diet.

In the southern Northwest Territories, Canada, the barren-ground caribou (***Rangifer tarandus groenlandicus***; Figure 1, Figure 88) included mosses, lichens, and shrubs in its diet (Thomas *et al*. 1984). Using fermentation in ruminal fluids in test tubes, Thomas and coworkers found that the dry matter biomass of shrubs was reduced by 37-51%, whereas the bryophytes were reduced only 7-28%. The lichens averaged 49% reduction in 180 hours. In a different case, Thomas and Kroeger (1981) examined *in vitro* digestion in ruminal fluids from ***Rangifer tarandus groenlandicus*** that had been shot in its winter range in southern Northwest Territories, Canada. This animal had poor digestion (15-27%) of two species of mosses and a liverwort.

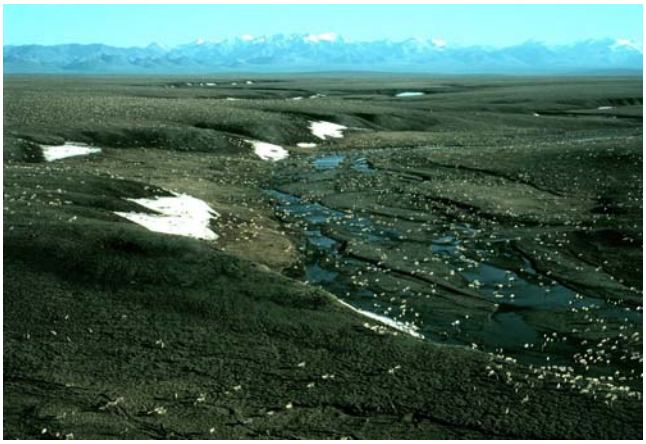

Figure 88. Barren-ground caribou (***Rangifer tarandus groenlandicus***) herds. Such numbers cause considerable damage to the vegetation, including bryophytes. Photo from U.S. Fish and Wildlife, through public domain.

In Aoluguya, Great Khingan Mountain Range of Inner Mongolia, Feng and Bai (2011) examined factors related to bryophyte consumption and digestion. The bryophytes have high concentrations of acid-detergent fiber, making them indigestible. This raises the question, what permits some reindeer to subsist largely on bryophytes, especially in winter?

Staaland and coworkers (1979) suggest that the reindeer (***Rangifer tarandus platyrhynchus***; Figure 7) on Svalbard may be adapted to eating mosses. These reindeer have an enlarged caecum-colon complex that appears to be an adaptation to a bryophytic diet by using the assistance of bacteria. These reindeer also have a high number of fiber-digesting rumen bacteria (Orpin *et al*. 1985), facilitating digestion. The rumen bacteria of the Svalbard reindeer are very effective in facilitating fiber digestion and nitrogen metabolism, providing an important adaptation for living in high Arctic habitats with poor nutritional conditions.

The Svalbard reindeer (***Rangifer tarandus platyrhynchus***; Figure 7) eat mosses in the winter because they are unable to migrate to forested lichen habitat (Longton 1992). Nevertheless, digestibility of mosses by these caribou is typically low, only 11-35% in summer and 3-11% in winter (Thomas & Kroeger 1980). Thus, one must ask just what the mosses provided for the animals. If ruminants, with their massive digestive bacteria flora, are unable to digest the mosses, one would assume they would be even less digestible for most other large mammals. There are likely to be other populations with similar winter grazing problems. Callaghan *et al*. (2004) considered deep snow to be a deterrent from winter grazing in some Arctic areas in some years. Areas of deep snow could force these ruminants into lower elevations or lower latitudes and prevent them from finding enough of the desired winter food source of lichens.

If mosses are difficult to digest and provide limited nutritional value, why are they heavily consumed in the Arctic? Ardea and Sage (1982) claim that the reindeer must consume 7 kg of mosses to extract the same energy they would get from just 0.5 kg of tundra grass.

We have seen that Prins (1982) suggested that they eat mosses for their arachidonic acid because of its ability to remain flexible in winter. These acids are major constituents of animal fats, especially in phospholipids of

cell membranes (Ardea & Sage 1982). These make the membranes more fluid, especially at the low temperatures of winter.

Feng and Bai (2011) added to the arachidonic acid possibilities. Reindeer are not able to synthesize arachidonic acid, but that which is ingested can provide several benefits to them. This acid is a precursor for some prostaglandin hormones, it has a low melting point that could lower the freezing point of the reindeer extremities, and it provides protection to cell membranes in the cold.

Effects on Soil Temperature

In the wet meadow vegetation of Barrow, Alaska, USA, Miller *et al.* (1980) found that in exclosures (Figure 74) the moss increased and the thaw depth decreased, suggesting that the mosses insulated the permafrost (Figure 89) against warming, and thus against thawing. Van der Wal and Brooker (2004) examined effects of reindeer herbivory on a moss layer of ***Sanionia uncinata*** (Figure 90), ***Tomentypnum nitens*** (Figure 91), and ***Aulacomnium*** spp. (Figure 92). Moss depth in the grazed controls was 38±6 mm compared to 57±10 mm in the ungrazed exclosures. Furthermore, NH_4-N was considerably lower inside the exclosures, but nitrogen mineralization potential was reduced by greater moss depth. A 10-cm-thick mat of mosses causes ~4.4ºC drop in soil temperature, with the temperature decreasing with moss depth (Figure 93). Manipulating the soil temperature had no effect on moss growth, but the grass *Poa arctica* and flowering plant *Cardamine nymanii* (Figure 94) both were reduced by 50% biomass in the chilled soils (van der Wal *et al*. 2001). These temperature decreases not only affect roots and rhizomes of tracheophytes, but they also affect decomposer communities by affecting the soil microbes and consequently affecting nutrient cycling (Harrison & Bardgett 2008).

Figure 89. Digging in permafrost in the tundra, using a jackhammer. Photo by Nick Bonzey, through Creative Commons.

Figure 90. ***Sanionia uncinata***, a moss species affected by reindeer grazing. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 91. ***Tomentypnum nitens***, a moss species affected by reindeer grazing. Photo by Scot Loring, through Creative Commons.

Figure 92. ***Aulacomnium palustre***, a moss species affected by reindeer grazing. Photo by Kristian Peters, through Creative Commons.

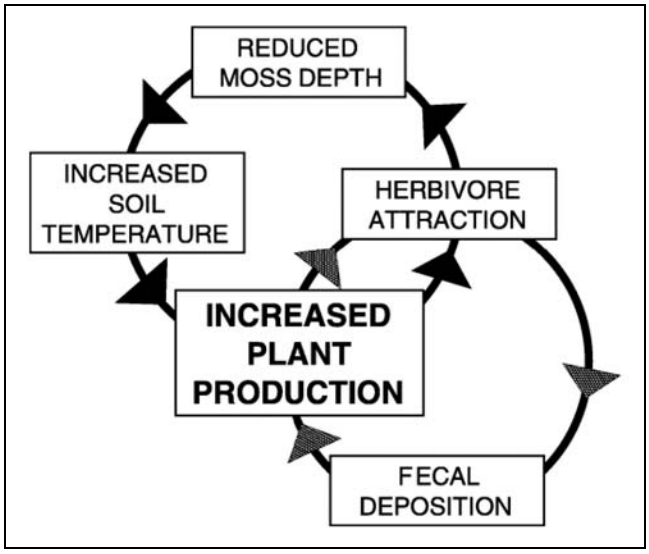

Figure 93. Relationship of mosses, herbivores, and soil temperature as conceptualized by van der Wal and Brooker 2004.

Figure 94. ***Cardamine nymanii*** in flower in Spitzbergen, a food much eaten by ruminants in Alaska. Photo by Bjoertvedt, through Creative Commons.

Microbial Responses to Grazing

Väre *et al*. (1996) found that microbial activity was significantly depressed at sites grazed by reindeer. This seems to be the result of reduced soil moisture at the grazed sites, especially during dry periods. Furthermore, grazing reduced the levels of all exchangeable nutrients by 30-60% in the organic layer of the soil. These factors contributed to the reduction of fine roots.

Temporal Differences

Both food choice and digestibility vary by season. Thomas and Kroeger (1980) found summer digestibility of mosses to range 11-35%, whereas winter digestibility ranged only 3-11%.

Thompson and McCourt (1981) studied the phenology of diet in the porcupine caribou herd (***Rangifer tarandus granti***; Figure 95) in the northern Yukon. The winter diet was dominated by lichens (66.7%) with most of the remainder being mosses (28.8%). In summer they shifted to primarily tracheophytes, especially sedges in spring, but shrubs dominated (>98%) after calves were born. The diet of shrubs declined and lichens again became prominent beginning in August.

Figure 95. Porcupine caribou (***Rangifer tarandus granti***) grazing. Photo by Dean Biggins, through public domain.

In the Great Khingan Mountain Range of Inner Mongolia, bryophyte consumption by reindeer also varied by season (Feng & Bai 2011). In April bryophytes comprised 5.63% of the feces, dropping to 2.2% in June, and rising to 12.9% in September. The four most common genera of bryophytes were ***Pleurozium*** (Figure 79), ***Dicranum*** (Figure 11), ***Aulacomnium*** (Figure 86, Figure 92), and the leafy liverwort ***Ptilidium*** (Figure 96). ***Pleurozium schreberi*** (Figure 79) comprised over 70% of the bryophyte total. But some seasonal differences are present. ***Polytrichum juniperinum*** (Figure 97) only occurred in large amounts in September. Despite the seasonal changes in amount of bryophytes eaten, the relative proportions among the other bryophyte species did not change appreciably between seasons. Nevertheless, sampling of the dominant forest floor bryophytes revealed that the reindeer are selective. ***Hylocomium splendens*** (Figure 87), ***Sphagnum*** spp. (Figure 98), and ***Pleurozium schreberi*** (Figure 79) are dominant bryophytes in the four types of forests investigated, but of these only ***Pleurozium schreberi*** was eaten. Additionally, ***Didymodon*** (Figure 99) and ***Racomitrium*** (Figure 100) occurred only occasionally in the feces.

Figure 96. ***Ptilidium ciliare***, leafy liverwort in a genus that is one of the four most common bryophytes in the reindeer grazing grounds of the Great Khingan Mountain Range of Inner Mongolia. Photo by Hermann Schachner, through Creative Commons.

Figure 97. ***Polytrichum juniperinum***, a moss species that occurred in its greatest amounts in reindeer feces in September in the Great Khingan Mountain Range of Inner Mongolia. Photo by Janice Glime.

Figure 98. ***Sphagnum austinii***, a dominant moss in Mongolian reindeer habitats, but was not eaten by them. Photo by Michael Lüth, with permission.

Figure 99. ***Didymodon rigidulus*** var ***icmadophilus***, member of a genus that is occasionally consumed by reindeer in the Great Khingan Mountain Range of Inner Mongolia. Photo by Michael Lüth, with permission.

Figure 100. ***Racomitrium*** in grey-green mounds, a genus that occasionally is consumed by Mongolian reindeer. Photo by Manfred Morgner, through Creative Commons.

In the five regions studied, Thomas and Edmonds (1983) found that monocots and mosses comprised 13% and 58%, respectively, of the rumen content of Peary caribou (***Rangifer tarandus pearyi***; Figure 6) in the Canadian Arctic archipelago. However, the digestibility of mosses for caribou is low, with the summer digestibilities of mosses ranging 11-35%, whereas lichens range 18-86% (Thomas & Kroeger 1980, 1981). In winter the mosses drop to 3-11% digestibility, suggesting they are not being consumed primarily for their nourishment. Perhaps it fools the caribou into "thinking" that they are full.

Thomas *et al*. (1984) also found that the dry matter disappearance of 22 plant species was significantly higher in March of 1981 than in tests performed one year earlier. The variation in the ruminal fluids coincided with differences in the physical condition of the caribou, which may have resulted from their nutritional history.

Site Differences

Based on these observations, we can expect the diet to differ by location. Pearce (1997) found that in the Kara area of Russia, 14% of the moss sites and 10% of the lichen sites experienced severe damage from reindeer activity. On

the other hand, in Norway,73% of the moss sites and 85% of the lichen sites suffered from grazing and trampling. The reindeer populations of Norway had doubled in the previous years, resulting in soil erosion in 75% of the sites. Only 8% of the Russian sites suffered from erosion.

Sørmo *et al*. (1999) examined fragments in the rumen of Svalbard reindeer (***Rangifer tarandus platyrhynchus***; Figure 7) in the western parts of Spitsbergen at Nordenskiöld where tundra vegetation is somewhat abundant and on the island of Nordaustlandet where they live in a polar desert with scarce vegetation. On Nordenskiöld the rumen contents were primarily mosses and grasses, whereas on Nordaustlandet they were primarily the flowering plants *Saxifraga* spp. (Figure 101).

Figure 101. ***Saxifraga cespitosa*** on Svalbard. This genus is the primary food of the Svalbard reindeer on Nordaustlandet. Photo by Victor M. Vicente Selvas, through Creative Commons.

Grazing Effects on Bryophytes and Vegetation

Van der Wal (2006) considered the ruminant herbivores to cause predictable changes in the ecosystem vegetation. Van der Wal points out that reindeer can deplete the lichens and switch to mosses (Staaland *et al*. 1993) with no detrimental effects to the reindeer population (Cooper & Wookey 2001). In fact, the carrying capacity for large ungulates increases when the vegetation switches to mosses, and increases again when it converts to grasses after extensive herbivory on mosses. A similar succession from lichens to mosses to graminoids is known where caribou (reindeer) range in Greenland (Thing 1984), Russia (Vilchek 1997), North America (Palmer & Rouse 1945; Klein & White 1987; Manseau *et al*. 1996), Fenno-Scandia (Helle & Aspi 1983, Gaare 1997), and the high arctic islands (Van der Wal *et al.* 2001). Even domesticated reindeer in boreal forest ecosystems cause the conversion of lichen vegetation to mosses (Väre *et al* 1996; Mäkipää 1998). And in Norway the moss-dwarf shrub heath gives way to grass domination under the pressure of reindeer grazing (Olofsson *et al*. 2001, 2004). Thing (1984) interpreted this progression of species as ecosystem damage.

Sarvas (1937) found that mosses like ***Polytrichum juniperinum*** (Figure 97) can survive feeding and trampling because they have rhizomes and rhizoids that can survive the above-ground feeding. These underground parts are able to germinate and form new plants. Oksanen (1978) found that ***Polytrichum hyperboreum*** (Figure 102) in northern Norway is very resistant to trampling by reindeer. It is likely that ***Polytrichum*** species are also dispersed by the reindeer, and some of these are delivered to areas where competition with species of ***Cladonia*** (Figure 103) is avoided (Helle & Aspi 1983).

Figure 102. ***Polytrichum hyperboreum*** with capsules, a moss species that is very resistant to trampling. Photo by Kristian Hassel, through Creative Commons.

Figure 103. ***Cladonia cornuta***, a member of the lichen genus that competes with the moss ***Polytrichum***. Photo through Creative Commons.

Van der Wal (2006) suggests the change in species begins with selection of lichens over mosses, causing greater lichen losses. This change is further promulgated by trampling, which is more damaging to lichens than to mosses, especially when they are dry (Cooper *et al*. 2001). If grazing is suppressed, the system may change back to lichen domination, but the change is slow (Crettenden 2000; Cooper & Wookey 2001; Den Herder *et al*. 2003). In fact, as lichens recover, they may "smother" the mosses (Gaare 1997; Van der Wal *et al.* 2001). A more likely explanation is the allelopathic effect of the many lichen secondary compounds (Lawrey 1995).

In *Pinus sylvestris* forests (Figure 104) of Fennoscandia, in 50-year-old exclosures indicate that

certain bryophytes benefit from reindeer grazing (Väre *et al*. 1995). This was particularly true for ***Dicranum*** spp. (Figure 11) and ***Pleurozium schreberi*** (Figure 79). In heavily grazed sites, the food lichen species ***Cladina*** spp. (reindeer "moss"; Figure 78) disappears. However, in ungrazed sites, ***Cladina*** species replace the ***Cladonia*** (Figure 103) lichen species and small bryophytes like ***Barbilophozia*** spp. (Figure 105), ***Pohlia nutans*** (Figure 106), and even ***Polytrichum*** spp. (Figure 102).

Figure 104. ***Pinus sylvestris*** (Scots pine) forest with mosses. Photo by Hermann Falkner, through Creative Commons.

Figure 105. ***Barbilophozia floerkei***, a leafy liverwort among the species replaced by ***Cladina*** in ungrazed sites. Photo by Hermann Schachner, through Creative Commons.

Figure 106. ***Pohlia nutans*** in Svalbard, among the moss species replaced by the lichen ***Cladina*** in ungrazed sites. Photo by Michael Lüth, with permission.

Virtanen (2000) used exclosures to determine the effects of herbivory on vegetation of a mountain snowbed in northwestern Finland. Unlike Sarvas (1937) and Oksanen (1978), Virtanen found that the dead plant material of **Polytrichaceae** (Figure 97, Figure 102) in the 15-year exclosures had increased; the moss ***Kiaeria*** (Figure 107) had disappeared. His results contradicted the assumption of other researchers that herbivory was unimportant in areas of low productivity. In these snowbeds, it clearly had an impact.

Figure 107. ***Kiaeria starkei***, a moss species that disappears in exclosures. Photo by Hermann Schachner, through Creative Commons.

Olofsson *et al*. (2001) examined the effects of summer grazing on the tundra heath vegetation in northern Norway. Comparing winter grazed, lightly summer grazed and heavily summer grazed vegetation at four different sites. They concluded that the highest productivity occurs at intermediate grazing pressure. They found that intensive grazing may be responsible for the transition from a moss-rich heath tundra to a productive grass-sedge-dominated steppe-like tundra vegetation. Intermittent grazing can actually enhance summer productivity.

In the sub-Antarctic on South Georgia, experimental reindeer exclosures demonstrated the changes to the vegetation after 1 year (Leader-Williams *et al*. 1987). Native grasses (*Poa flabellata*; Figure 108) and dwarf shrubs (*Acaena magellanica*; Figure 109) increased in response to the absence of grazing. The moss ***Polytrichum*** (Figure 97, Figure 102) likewise increased, but to a lesser extent. This is reminiscent of the responses in rodent exclosures (see Chapter 17). Macrolichens showed little change, as did moss-bank communities. The lichen cover is likely to require decades to recover.

Using approximately 3000 permanent plots in Finland and more than 10,000 plots in all in three different surveys, Mäkipää and Heikkinen (2003) measured changes in the vegetation. During this time, the forest floor moss ***Hylocomium splendens*** (Figure 87) decreased in abundance while ***Dicranum polysetum*** (Figure 110) increased. In the northern part of Finland, grazing by semi-domestic reindeer coincided with a decline of ***Cladina*** (Figure 78) lichens, a favorite food, while the mosses ***Dicranum*** spp. increased. ***Polytrichum juniperinum*** (Figure 97), ***Pohlia nutans*** (Figure 106), and ***Brachythecium*** sp. (Figure 113), moss species typical of disturbed sites, increased. ***Sphagnum*** (Figure 98)

abundance decreased, especially in western Finland where the moss ***Pleurozium schreberi*** (Figure 79) also was favored.

Figure 108. ***Poa flabellata*** on South Georgia, a species that increases when grazing stops. Photo by Roger Key, with permission.

Figure 109. ***Acaena magellanica***, a shrub that increases when grazing is stopped. Photo by El Grafo, through Creative Commons.

Figure 110. ***Dicranum polysetum***, a moss species that increased in permanent plots. Photo by Hermann Schachner, through Creative Commons.

Hansen *et al*. (2007) followed vegetation changes for 26 years following the reintroduction on the northwest coast of Spitsbergen, Svalbard, of the Svalbard reindeer (***Rangifer tarandus platyrhynchus***; Figure 7). The population size fluctuated, and when it reached high numbers, it caused a top-down effect on the vegetation that included a decrease in the cover of mosses. The preferred winter forage, fruticose lichens, almost disappeared. When the grazing pressure was relieved, the mosses not only recovered completely, but within six years they exceeded the pre-reindeer levels.

In the Arctic and alpine tundra, reindeer (***Rangifer tarandus***; Figure 77) consume 22-30% of their winter diet as moss (Heggberget *et al*. 2010). These researchers expressed concern that climate change, predictably greater in these northern areas, could compromise the available winter forage. Lichens are likely to be impacted, forcing the reindeer to seek other forage. In some populations, a larger alimentary tract has adapted to the reindeer diet.

Roe Deer – *Capreolus capreolus*

Several studies have revealed the ability of hoofed mammals to transport bryophyte propagules. One such study demonstrated the **epizoochorous** dispersal of bryophyte fragments by roe deer (***Capreolus capreolus***; Figure 111) (Heinken *et al*. 2001). They found 106 bryophyte fragments, almost all stem fragments, lodged in the coats and hooves of 15 roe deer and 9 wild boar (***Sus scrofa***; Figure 112). These represented 12 bryophyte species, with the most abundant being ***Brachythecium velutinum*** (Figure 113), ***Hypnum cupressiforme*** (Figure 4), and ***Eurhynchium hians*** (Figure 114). These were typically about 3.6 mm long, but ranged 0.5-35 mm. The species that were most common were slender pleurocarpous mosses (growing horizontally) with erect, acute leaves. Robust acrocarpous mosses (growing upright) that formed tall turfs were generally absent.

Figure 111. Roe deer (***Capreolus capreolus***) male and female, showing the hooves that can transport bryophyte fragments. Photo by Jojo through Wikimedia Commons.

Roe deer can do considerable damage to bryophyte vegetation (Clément & Touffet 1981). Following fire in the Brittany heathlands, roe deer were responsible for bryophyte disappearance due to scraping by roe deer.

Figure 112. Wild boar (***Sus scrofa***), a species that can transport bryophytes in its long hair and on its hooves. Photo by Jerzy Strzelecki, through Creative Commons.

Figure 113. ***Brachythecium velutinum***, a moss that is one of the most abundant bryophytes transported by sheep. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 114. ***Eurhynchium hians***, one of the most abundant moss species carried by roe deer (***Capreolus capreolus***). Photo by Michael Lüth, with permission.

Bryophytes do not appear to serve as food for this species (Tixier *et al*. 1997). Although they are generalist feeders by using a variety of types of food, they are selective within the food types. Their use of food species correlates negatively with fiber content. Bryophytes were specifically avoided in all seasons. Even so, they preferred plants that had high concentrations of protein-binding phenolic compounds, leading Tixier and coworkers to suggest that they might have specific mechanisms for deactivating these compounds. For many animals, protein-binding compounds prevent the animals from obtaining nutrition from the proteins they eat, even from accompanying foods that don't have the binding compounds.

Hog Deer – *Axis porcinus*

In southeastern Australia, both introduced mammals and native species consume plants (Davis *et al*. 2008). Whereas the swamp wallabies (***Wallabia bicolor***; Figure 115) consume the largest proportion of tree browse, the hog deer (***Axis porcinus***; Figure 116) consume the largest proportion of mosses, however only removing less than 0.01%.

Figure 115. ***Wallabia bicolor*** and large joey. Photo by Peripatus, through Creative Commons.

Figure 116. ***Axis porcinus***, a moss consumer. Photo by Brent Huffman, through Creative Commons.

Summary

Bryophytes and ruminants interact in various ways. Some of these animals eat the bryophytes, particularly reindeer in Arctic regions, and most are capable of creating disturbance that can damage the bryophytes. Trampling and scraping break and dislodge the

bryophytes, but at the same time these activities can contribute to dispersal as the fragments adhere to hooves and fur/hair/wool.

Reindeer/caribou (***Rangifer tarandus***) typically cannot digest bryophytes well, but on Svalbard, where they have no place to go for winter, mosses are a staple in the diet. They seem to have adapted by being able to absorb more of the nutrients from the mosses through an enlarged caecum-colon complex.

Both black-tail (***Odocoileus hemionus***) and white-tail (***Odocoileus virginianus***) deer and roe deer (***Capreolus capreolus***) apparently avoid eating bryophytes.

When grazing is light, it can favor such mosses as ***Rhytidiadelphus squarrosus***, **Polytrichaceae**, and ***Brachythecium***. Colonizers like ***Pohlia nutans*** can benefit from disturbance and increased light. Leafy liverworts like ***Barbilophozia floerkei*** decrease with grazing. But the bryophyte communities depend on the site, with Arctic and alpine communities responding differently from more temperate ones. Rodents likewise can have a profound effect on the bryophytes, with communities responding differently depending on the foraging ruminants present.

Bryophytes suffer from manuring and urine, perhaps due to increased microbial decomposition, or to greater competition from the enriched tracheophytes.

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CHAPTER 18-2
LARGE MAMMALS: RUMINANTS – NON-CERVIDAE

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CHAPTER 18-2
LARGE MAMMALS – RUMINANTS

Figure 1. ***Ovis aries*** (Soay sheep) resting on mat of mosses and grasses. Their herbivory on grasses can benefit the mosses. Photo from Biopix, through Creative Commons.

Moschidae – Musk Deer – *Moschus*

Green (1987) found that for Himalayan musk deer (***Moschus chrysogaster***; Figure 5), the choice of mosses as food was highly seasonal and usually avoided. They preferred forbs and woody plants in autumn and winter, positively avoiding bamboo leaves and mosses.

Ihl and Barboza (2007) compared the digestible value of a typical ruminant food for Arctic muskoxen (***Ovibos moschatus***; Figure 2) with that of the mosses ***Hylocomium splendens*** (Figure 3) and ***Tomentypnum nitens*** (Figure 4) from two locations in Alaska, USA. First they acclimated the muskoxen to mosses for 15 consecutive days. Using forages from ruminally **fistulated** muskoxen (having passageway cut from rumen to outside) they determined that ruminal degradation was not affected by previous acclimation to mosses.

Ruminal digestion caused a loss of dry matter during 48 hours of ruminal incubation of grasses (-49%), but mosses actually gained dry matter (44-57%) (Ihl & Barboza 2007). These changes were unaffected by suspending the forages in the rumen for 15 consecutive days, a procedure that could induce digestive enzymes in response to previously uneaten food sources. The incubated mosses gained 435-680% N and 18% fiber!

Figure 2. ***Ovibos moschatus***, a species that does not acclimate to digestion of mosses. Photo by Laurent Bélanger, through Creative Commons.

Figure 3. ***Hylocomium splendens***, a species common in the habitat of Arctic musk oxen. Photo from Botany Website, UBC, with permission.

Figure 4. ***Tomentypnum nitens***, a species common in the habitat of Arctic musk oxen. Photo by Jutta Kapfer, with permission.

Ihl and Barboza (2007) suggested that the gain in mass by the mosses was due to microbial colonization and adsorption of fibrous particles onto the absorbent mosses. When digested with acid-pepsin, the ruminally incubated mosses lost little nitrogen, whereas the hay lost 23% nitrogen. Ihl and Barboza suspected that winter consumption of mosses may be the result of selecting other plants that grow mixed within the moss community, thus explaining the presence of mosses in feces. The times when mosses occurred in the feces of these animals indicated low availability of preferred foods. As noted in an earlier chapter, Arctic birds likewise experience periods of low availability of desired foods, but their digestive processes differ, so studies on ruminants may not be indicative of digestibility for birds, or *vice versa*.

Figure 5. Himalayan musk deer (***Moschus moschiferus***), a species that eats mosses seasonally. Photo by Николай Усик, through Creative Commons.

Bovidae – Antelopes, Cattle, Gazelles, Goats, Sheep, and Relatives

Sheep – *Ovis*

Sheep can have a serious impact on the bryophyte communities. Downing (1992) suggested their impact on limestone bryophyte vegetation at Attunga, Australia. Rieley *et al.* (1979) reported that sheep graze in Welsh oakwoods on grasses until ultimately the bryophytes increase in abundance. Austrheim *et al*. (2007) found a similar increase in bryophytes, particularly ***Plagiothecium*** (Figure 6) and ***Rhodobryum roseum*** (Figure 7), under heavy grazing pressure of sheep in an alpine habitat in southern Norway.

Figure 6. ***Plagiothecium succulentum***, member of a moss genus that increases under heavy grazing of sheep in alpine areas of southern Norway. Photo by Hermann Schachner, through Creative Commons.

Figure 7. ***Rhodobryum roseum***, a moss species that increases under heavy grazing of sheep in alpine areas of southern Norway. Photo by Hermann Schachner, through Creative Commons.

In a study of ruminants from the Canary Islands, Rodríguez Suárez *et al*. (1990) found that mouflons [wild sheep; ***Ovis aries musimon*** (Figure 8) – an endangered species that has been successfully cloned (Loi *et al*. 2001; Trivedi 2001)] and Barbary sheep (***Ammotragus lervia***; Figure 9), native of northern Africa and introduced to Europe in the late 1800's) consumed bryophytes. Rodríguez Suárez and coworkers examined the stomach contents of 46 Corsica mouflons and 19 Barbary sheep from the highest area of La Palma and Tenerife islands. They found that 11 stomachs contained ***Grimmia laevigata*** (Figure 10), ***Grimmia*** sp., ***Racomitrium heterostichum*** (Figure 11), and 2 ***Didymodon*** sp. (Figure 12). These species grow on rocks in very dry habitats where other plants usually considered more suitable for consumption are generally absent. This suggests that the consumption of mosses is deliberate.

Figure 8. Mouflon (***Ovis aries musimon***), a moss consumer. Photo through Creative Commons.

Figure 9. Barbary sheep (***Ammotragus lervia***), a moss consumer, eating. Photo by Peripitus, through Creative Commons.

Figure 10. ***Grimmia laevigata***, a moss species consumed by mouflons and Barbary sheep in the Canary Islands. Photo by Hermann Schachner, through Creative Commons.

Figure 11. ***Racomitrium heterostichum***, a moss species consumed by mouflons and Barbary sheep in the Canary Islands. Photo by J. C. Schou, with permission.

Figure 12. ***Didymodon rigidulus*** var ***icmadophilus***, in a moss genus sometimes consumed by mouflons and Barbary sheep in the Canary Islands. Photo by Michael Lüth, with permission.

Like the roe deer (***Capreolus capreolus***; Figure 13), grazing sheep are often transporters of bryophyte fragments and other propagules (Müller & Heinken 2011). Pauliuk *et al*. (2011) compared transport by two breeds of sheep. The twelve sheep in the study carried 16 species of mosses, but these represented only 40% of the moss species in the pasture (Figure 14). The belly and tail (Figure 13) were especially good at transport. The two breeds favored different species and frequencies. Those sheep that had a dense, curly fleece were able to carry larger species and more fragments than the breed with a fine, smooth fleece. The horizontally growing pleurocarpous mosses, as with roe deer, were more common than upright acrocarpous species; small species and mats were likewise more common than other forms. Large species, acrocarpous species, wefts, and turfs were underrepresented. Hooves, on the other hand, carried primarily acrocarpous colonist species.

Figure 13. Roe deer (***Capreolus capreolus***) lying down, a position that can put bryophyte fragments on the underbody and tail. Photo through Creative Commons.

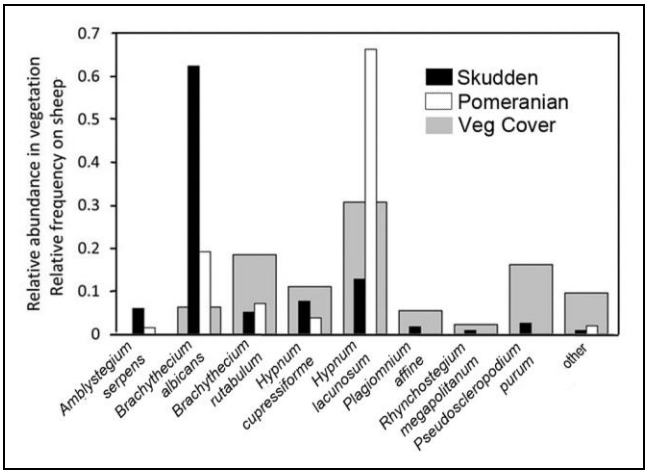

Figure 14. Comparison of bryophyte transport by two breeds of sheep: Skudden (n = 5, 117 fragments) and Pomeranians (n = 7, 2096 fragments). Grey bars indicate relative cover in the vegetation of the study site. Modified from Pauliuk *et al*. 2011.

It appears that at least some bryophytes receive other benefits from the sheep. They appear to maintain a habitat where these bryophytes can thrive. When the pasture is abandoned, bryophytes disappear due to their limited ability to compete with the invading tracheophytes (Takala *et al*. 2012). In southwestern Finland, cover, species richness, species density, and species diversity of bryophytes were all significantly higher in pastures that had been continuously grazed than those in abandoned grasslands. Takala defined three grassland habitats: (1) continuously grazed pastures, (2) previously abandoned pastures where grazing was re-established during 1990s, and (3) abandoned pastures. Among these, 17 species of bryophytes were suitable indicators of the three grassland types. Four of these indicated valuable grassland habitat.

In some areas, sheep graze in bogs (Rawes 1983). In two high altitude blanket bogs in the North Pennine uplands of England, cessation of sheep grazing led to major changes in the species composition, vegetation pattern, and structure of the bogs. Colonization of bare peat was slow in the exclosures. In particular, the leafy liverwort ***Diplophyllum albicans*** (Figure 15) declined, whereas it had previously been a constant companion for the cottongrass *Eriophorum* (Figure 16).

Figure 15. ***Diplophyllum albicans***, a leafy liverwort species that declines in the absence of sheep. Photo by Hermann Schachner, through Creative Commons.

Figure 16. Cottongrass (*Eriophorum vaginatum*), member of a common genus in peatlands of English uplands. Photo through Creative Commons.

Lee *et al*. (2013) examined blanket bog plant communities following various types of disturbance, including low-intensity sheep grazing. In the low-intensity grazing areas, ***Hypnum jutlandicum*** (Figure 17) cover and bryophyte species richness both increased in the least-disturbed plots. Overall bryophyte cover, however, did not. In fact, low-level grazing had little impact on the bryophyte communities. The most-disturbed plots, with a 10-year burn cycle, had an increase in ***Sphagnum*** spp. (Figure 18) over a 10-year period. I have to wonder if drafts created by the burning contributed to dispersal from neighboring communities.

Figure 17. The moss ***Hypnum jutlandicum*** with capsules. Photo by J. C. Schou, through Creative Commons.

Figure 18. ***Sphagnum girgensohnii***, representing a genus that increases in number of represented species following fire disturbance. Photo by Jutta Kapfer, with permission.

A common bryophyte in northern open areas is the moss ***Racomitrium lanuginosum*** (Figure 19). On a Scottish montane plateau, an area was fenced to provide a ski corridor (Scott *et al*. 2007). This area was used to establish permanent quadrats for a 12-year study. The fencing created a gradient in snow-lie and sheep use. ***Racomitrium lanuginosum*** cover was initially lower immediately adjacent to the fence. After 12 years, cover was reduced significantly in the 10 m adjoining the fence, whereas it was relatively stable further away. Scott and coworkers attributed the decline near the fence to greater snow-lie and heavier sheep usage. Grass cover near the fence increased. At the same time, ***Dicranum fuscescens*** (Figure 20) increased significantly near the fence. At more interior locations, there was a significant increase in ***Polytrichastrum alpinum*** (Figure 21) (Welch *et al*. 2005).

Figure 19. ***Racomitrium lanuginosum*** (white), a common moss species in Arctic and alpine areas, in Iceland. Photo by Manfred Morgner, through Creative Commons.

Figure 20. ***Dicranum fuscescens***, a moss species that increased near the exclosure fence. Photo by Michael Lüth, with permission.

During and Willems (2003) reported that many species of mosses have disappeared "almost completely" from the Dutch chalk grasslands (see Figure 22) after grazing ceased. These included characteristic acrocarpous mosses such as ***Tortella*** spp. (Figure 23), ***Trichostomum*** spp. (Figure 24), ***Aloina*** spp. (Figure 25), and ***Pleurochaete squarrosa*** (Figure 26), but also the pleurocarpous species ***Abietinella abietina*** (Figure 27) and ***Homalothecium lutescens*** (Figure 28) have experienced drastic reductions. Litter indicator species such as ***Brachythecium rutabulum***

(Figure 29) are concurrently increasing. As in other studies, these changes seem to be the result of cessation of grazing.

Figure 21. Alpine hairy cap moss, ***Polytrichastrum alpinum***, with capsules, a species that increased in interior regions of exclosure fence. Photo by David T. Holyoak, with permission.

Figure 22. Chalk grassland similar to those in the Netherlands. Photo by Rose and Trev Clough, through Creative Commons.

Figure 23. ***Tortella tortuosa***, a species that has disappeared from pastureland after grazing ceased. Photo by Hermann Schachner, through Creative Commons.

Figure 24. ***Trichostomum crispulum***, in a moss genus that lived in Dutch chalk grasslands but has disappeared where grazing is no longer present. Photo by David T. Holyoak, with permission.

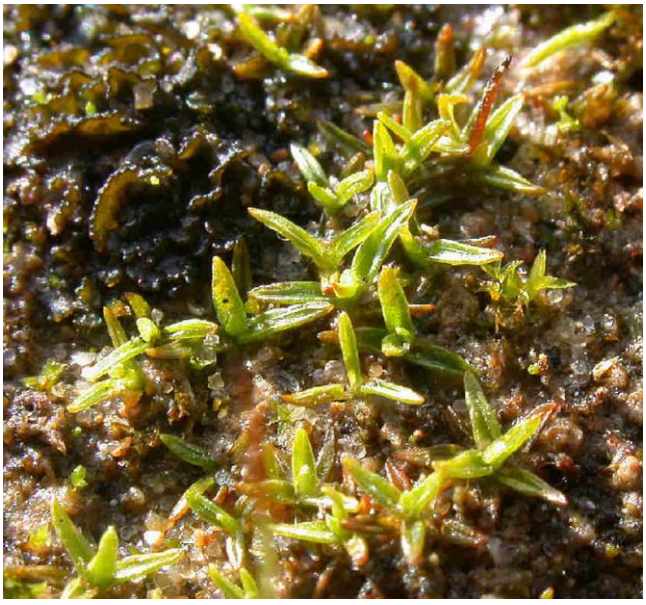

Figure 25. ***Aloina aloides***, in a moss genus that lived in Dutch chalk grasslands but has disappeared where grazing is no longer present. Photo by David T. Holyoak, with permission.

Figure 26. ***Pleurochaete squarrosa***, a moss species that lived in Dutch chalk grasslands but has disappeared where grazing is no longer present. Photo by David T. Holyoak, with permission.

Figure 27. ***Abietinella abietina***, a species that has experienced severe decreases from pastureland after grazing ceased. Photo by Hermann Schachner, through Creative Commons.

Figure 28. ***Homalothecium lutescens***, a species that has experienced severe decreases from pastureland after grazing ceased. Photo by J. C. Schou, Biopix, with permission.

Figure 29. ***Brachythecium rutabulum*** with capsules, a species that has increased in Dutch chalk grasslands after grazing was withdrawn. Photo by J. C. Schou, with permission.

Maelfait *et al*. (2007) similarly found that when dune vegetation was short-grazed by sheep (***Ovis aries***; Figure 30), the previously lichen-moss domination decreased. But one site changed during the same time to a cover of ~95% clipped grasses, mosses, and herbs, a physiognomy created by the grazing of sheep.

Figure 30. ***Ovis aries***, domestic sheep that causes lichen-moss domination to decrease. Photo through Creative Commons.

One of the operators in the moss vs tracheophyte story in pastureland is nitrogen (van der Wal *et al*. 2003). Air pollution has increased nitrogen deposition, causing massive invasion of grasses, sedges, and rushes in habitats ranging from forests to upland heaths. At the same time, grazing by livestock has increased in many locations, further degrading natural ecosystems. In the Scottish montane ecosystem, grazing and nitrogen deposition interact, causing a loss of the moss-dominated habitat and takeover by grasses and sedges.

One of our techniques to maintain diversity is to create green spaces where normal (non-pasture) vegetation is allowed to grow. However, even in these situations adjacent land use can significantly alter the bryophyte (and tracheophyte) communities of the natural vegetation (Piessens *et al*. 2008). Fortunately, these effects occur only within 5 m or less of the borders into heathland patches. In these transition zones adjacent to the borders, the invasive moss ***Campylopus introflexus*** (Figure 31) is common at grazed sites.

Figure 31. ***Campylopus introflexus***, an invasive moss species common in transition zones of grazed areas. Photo by Fitis-Sytske Dijksen, with online permission through <freenatureimages.com>.

Hill *et al*. (1992) found that ***Polytrichum commune*** (Figure 32) declined steadily in sheep exclosures (Figure 34) in Snowdonia, Wales. When sheep were fenced out of some areas, ***Polytrichum commune*** declined consistently,

presumably due to competition for light by larger tracheophytes. Subsequent to sheep exclosure (Figure 33-Figure 35), voles became dominant among the herbivores and considerable growths of pleurocarpous mosses like ***Hylocomium splendens*** (Figure 3) and ***Pleurozium schreberi*** (Figure 36) invaded the mats of dead grass.

Figure 32. ***Polytrichum commune*** with capsules, a species that declines when sheep are removed. Photo by Bas Kers, through Creative Commons.

Figure 33. Nature Reserve, Helfdi, Iceland, in area where sheep are allowed to browse. Photo by Janice Glime.

Figure 34. Nature Reserve, Helfdi, Iceland, in exclosure where sheep are unable to browse. Photo by Janice Glime.

Figure 35. Wool on fence and plants on near side of fence in Iceland where grasses have been eaten by sheep. The exclosure prevents browsing on the opposite side where the grass is abundant. Photo by Janice Glime.

Figure 36. ***Pleurozium schreberi***, a species that becomes dominant among dead grass in sheep exclosures when voles invade. Photo by Rob Routledge, through Creative Commons.

But do sheep eat bryophytes? Rodriguez Suárez *et al*. (1990) reported 15 cryptogams in the stomachs of goats and sheep. The winter diet of feral Soay sheep (***Ovis aries***; Figure 30) at St. Kilda, Scotland, is comprised of 20-30% mosses (Milner & Gwynne 1974). When Virtanen and Crawley (2010) assessed the relationships of bryophytes with these St. Kilda sheep, they found that bryophytes and tracheophytes had opposite trends relative to elevation and sheep preference. The bryophytes reached their highest species richness at mid to high elevations and were negatively correlated with levels of sheep preference.

In a 1500 m^2 plot in a sheep pasture of the Netherlands, the moss layer disappeared almost totally, concomitant with the introduction of artificial fertilizer application and liquid manure (Arnolds 1989). This coincided with changes in the fungal populations, and those fungi associated with litter or bryophytes decreased in numbers.

In the alpine communities of the Scottish Highlands (Figure 37), one can find rare species (Miller *et al*. 2010). Nevertheless, this community is often heavily grazed by sheep. Many have suggested that the sheep hold the community in a **plagioclimax** (habitat or area in which influences of humans have prevented further ecosystem development). By excluding sheep from spring until fall for 10 years, Miller and coworkers found that graminoids initially increased in cover and the vegetation became taller. However, this stage did not last, and a decline in

graminoid cover followed, with bryophytes becoming much more abundant. Permanent removal of sheep could cause a shift to a bryophyte-rich habitat tall-herb or scrub vegetation.

Figure 37. Alpine area in Scotland, where sheep often graze. Photo through Flickr Creative Commons.

Large herbivores can have an especially severe effect on bryophytes and other plants in Arctic and alpine regions (Austrheim *et al*. 2007). Using exclosures in an oceanic alpine ecosystem to stop sheep grazing, Austrheim and coworkers found that tracheophyte height increased, but the grass ***Deschampsia flexuosa*** (Figure 38) was the only tracheophyte that increased in cover in these exclosures. At the same time, six bryophyte species changed in abundance, favoring successional bryophytes. The mosses ***Straminergon stramineum*** (Figure 39) and ***Pohlia nutans*** (Figure 40) and the leafy liverwort ***Cephalozia bicuspidata*** (Figure 41) increased when sheep grazing ceased.

Figure 38. *Deschampsia flexuosa*, the only seed plant in an oceanic alpine ecosystem that increased in cover inside sheep exclosures. Photo by M. Porto, through Creative Commons.

Figure 39. ***Straminergon stramineum***, a species in an oceanic alpine ecosystem that increases when sheep grazing stops. Photo by Jutta Kapfer, with permission.

Figure 40. ***Pohlia nutans*** in Svalbard, a moss that benefits when sheep grazing stops. Photo by Michael Lüth, with permission.

Figure 41. ***Cephalozia bicuspidata***, a leafy liverwort species that increases when sheep grazing stops. Photo by Botany Website, UBC, with permission.

For ***Pohlia nutans*** (Figure 40), this is a surprise as it tends to occur in open, disturbed sites, and it also typically disappears when reindeer are fenced out (see above). Species of the mosses ***Brachythecium*** (Figure 29) and ***Plagiothecium*** (Figure 6) likewise decreased in the exclosures, while ***Polytrichum*** (Figure 32) species actually

increased with grazing, as already noted in Wales by Hill *et al*. (1992) and elsewhere (Helle & Aspi 1983; Väre *et al*. 1996; Virtanen 2000; Olofsson *et al*. 2004), causing Austrheim *et al*. (2007) to consider the genus to be grazing resistant. The leafy liverworts ***Barbilophozia lycopodioides*** (Figure 42) and ***B. floerkei*** (Figure 43) decreased with grazing, whereas the latter disappeared in the exclosures in the Arctic reindeer study by Väre *et al.* (1995), where it was replaced by the lichen ***Cladina*** (Figure 44), a preferred food of reindeer. Nevertheless, exclosures did not result in changes in tracheophyte or bryophyte species richness or total cover of bryophytes and lichens in the Austrheim *et al*. study. A side effect of the exclosures and cessation of sheep grazing was that rodent grazing was also reduced.

Figure 42. ***Barbilophozia lycopodioides***, a leafy liverwort species that diminishes with sheep grazing. Photo by Hermann Schachner, through Creative Commons.

Figure 43. ***Barbilophozia floerkei***, a species that decreases with grazing but can disappear in exclosures. Photo by Hermann Schachner, through Creative Commons.

Figure 44. ***Cladina*** spp., a genus that replaces ***Barbilophozia floerkei*** in reindeer exclosures in the Arctic. Photo by Peder Curman, through Creative Commons.

Goats – *Capra*

Goats are known to eat everything, right? So we shouldn't be surprised that in Washington State's Olympia National Park (Figure 45), invasive goats, introduced from Canada and Alaska for hunting, were destroying the sensitive ecosystem (Wright 1996). In particular, the very rare Olympic Mountain milk vetch (*Astragalus cottonii*; Figure 46) was a favorite food. But like we might expect of goats, these goats ate everything, including mosses. They further affected the habitat by trampling and wallowing. Rodriguez Suárez *et al*. (1990) also found that goats on the Canary Islands consumed mosses.

Figure 45. Olympic rainforest, Washington, USA, with bigleaf maples and epiphytic mosses. Photo from NPS, through public domain.

Figure 46. *Astragalus cottonii*, a rare but favorite food of goats in the Olympic Mountains, USA. Photo by Paul Slichter, with permission.

Nevertheless, feral goats (*Capra hircus*; Figure 47-Figure 48) in New Zealand avoided mosses, even though mosses were very abundant compared to preferred foods like *Schefflera digitata* (Figure 49) and ferns (Mitchell *et al*. 1987).

Figure 47. *Capra hircus aegagrus*, a feral goat and moss avoider in New Zealand. Photo by Murat Göktas through Creative Commons.

Figure 48. Wild goat, *Capra hircus aegagrus*, a goat that avoids eating mosses. Photo by Quartl, through Creative Commons.

Figure 49. *Schefflera digitata* in New Zealand, a preferred food of feral goats. Photo by Kahuroa, through Creative Commons.

Cattle – *Bos*

It is hard to imagine a big cow choosing to eat mosses, but Esteban *et al*. (2012) reported that in the Southern Patagonian *Nothofagus* forests (Figure 50), mosses, along with grasses, were the most grazed vegetation by cattle (***Bos taurus***; Figure 51). But contrasting with many rodent herbivores, the cattle consumed erect herbs and mosses in the summer, switching to shrubs in spring and winter. In fact, while sheep primarily grazed prostrate herbs, cattle grazed mosses, except in autumn.

With this kind of preference for mosses, it might be surprising that removing cattle herbivory can cause a decline in bryophytes. But further examination in southwestern Finland reveals that these weak moss competitors are actually disappearing as tracheophyte biomass increases (Takala *et al*. 2012). By contrast, in continuously grazed grasslands, bryophyte cover, species richness, species density, and species diversity were significantly higher than in abandoned grasslands. The importance of cattle grazing for maintaining the bryophyte species richness is further supported by Humphrey and Patterson (2000) in a riparian pasture and an upland conifer forest of the UK. Furthermore, they found almost no evidence that trampling had any effect on the bryophytes.

Figure 50. ***Nothofagus pumilio*** forest in Patagonia, a forest type where mosses are grazed by cattle (***Bos taurus***). Photo by through public domain.

Figure 51. ***Bos taurus***, Italian cattle, a species that consumes mosses and herbs in summer, but shrubs in spring and winter. Photo by Justine Peacock, through Creative Commons

Yet Ludvíková *et al*. (2014a, b) found that in their experimental comparisons in temperate *Agrostis capillaris* (Figure 52) grassland, it was the non-trampled plots that had the highest composition of bryophytes, with ***Rhytidiadelphus squarrosus*** (Figure 53) being the dominant species (95%). However, the non-trampled plots also had the lowest evenness index, indicating few dominant species and lots of uncommon species. Soil compaction played an important role in determining species composition (Ludvíková *et al*. 2014b).

Figure 52. *Agrostis capillaris*, a dominant grass where the moss ***Rhytidiadelphus squarrosus*** co-exists where trampling is limited. Photo by Kristian Peters, through Creative Commons.

Figure 53. ***Rhytidiadelphus squarrosus***, the dominant bryophyte in non-trampled plots in temperate grassland. Photo by Michael Lüth, with permission.

Ingerpuu and Sarv (2015) studied 15 Estonian coastal meadows (Figure 54) to compare effects of two different grazing pressures. During a 10-year period, the intensive grazing area experienced an increase in bryophyte diversity, but tracheophyte diversity did not increase, nor did that of the diaspore bank. Litter cover suppressed tracheophyte diversity. Nevertheless, tracheophyte and bryophyte diversity were positively correlated. And species composition remained unaffected by grazing intensity.

Figure 54. Estonian coastal meadow. Photo by KalervoK, through Creative Commons.

The Austrian agricultural landscapes (Figure 55) are rich in bryophytes, with a total of 506 species, 135 of which are considered to be endangered (Zechmeister *et al*. 2002). The upland landscapes dominated by moderately intensive cattle farming have significantly more endangered species than do the lowland landscapes with primarily intensive farming styles. Similarly, in comparing 24 grazed and 24 abandoned sites, Oldén *et al*. (2016) demonstrated that grazing had more impact on tracheophytes than on bryophytes in boreal wooded pastures. These are low-intensity livestock grazing areas in forested sites.

Figure 55. Austrian agricultural landscape. Photo through Creative Commons.

In Finnish seminatural grasslands, Takala *et al*. (2014) used 420 plots in 21 grasslands to examine species richness and cover of bryophytes. They found that grazing promotes bryophyte species richness, with colonists and perennial bryophytes in particular increasing. As expected, colonists were strongly associated with sites having a high proportion of bare ground.

Among the most sensitive ecosystems that must endure grazing are the cryptogamic crusts (Figure 56) in prairie areas. In a study in southeastern British Columbia, Rosentreter (2006) found that rock cover decreased significantly(?), $p>0.10$, in the Cattle Only Area from 1994 to 2004, whereas in the Wildlife Only Area there were no significant changes in litter, soil, bryophyte, or rock cover. Bryophytes and litter provided the predominant soil cover. But bryophyte cover overall increased nearly 70% from

1991 to 2003 ($p<0.10$), somewhat complicating the comparisons. Decreases in bryophyte cover in the exclosure area was driven by the increases in vascular plants and litter cover. Hence, bryophyte cover decreased with time in the exclosure, only the bryophytes increased in the wildlife and cattle area, and bryophytes did not change in the cattle only or wildlife only areas. Bryophytes are important contributors to these ecosystems by providing soil stability, nitrogen fixation, maintaining greater soil moisture, preventing runoff, facilitating infiltration, and enhancing seed germination and subsequent plant growth (Anderson *et al*. 1982a, b; Johnston 1997; McCune 2000).

Figure 56. Cryptogamic crust in Natural Bridges National Monument, Utah. Photo by Hihonjoe, through Creative Commons.

Some endangered species are benefitted by cattle and pony grazing. The disturbance by the cattle and wheel ruts in salt marshes (Figure 57) where they graze creates open soil patches that can be colonized by ***Bryum marratii*** (Figure 58) (Holyoak 2015). But the occurrence of the species in wheel tracks was short-lived because grazing was light and competitive grasses (*Agrostis stolonifera*; Figure 59) excluded it within two years (Callaghan 2017). In Ireland, when salt marsh grazing stopped, a dense saltmarsh grass cover developed, leading to extinction of the moss in Northern Ireland and threatening the species in other Irish locations (Lockhart *et al*. 2012).

Figure 57. ***Bryum marratii*** habitat at bay of Meallabhan, Scotland, a salt marsh. Photo by Michael Lüth, with permission.

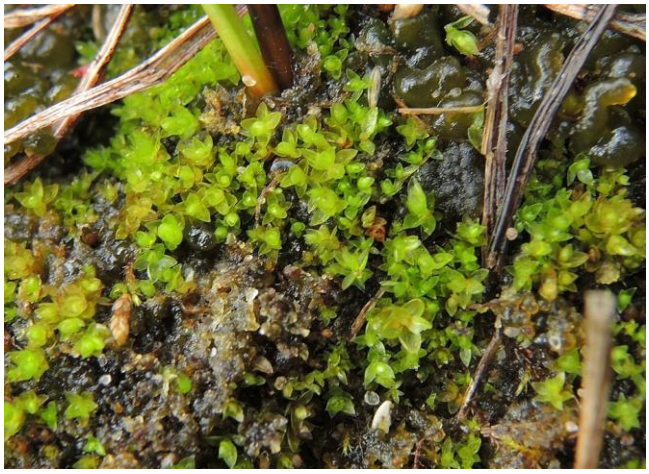

Figure 58. ***Bryum marratii***, in a salt marsh in Scotland. Photo by Michael Lüth, with permission.

Figure 59. *Agrostis stolonifera*, a salt marsh species that crowds out ***Bryum marratii***. Photo by Matt Lavin, through Creative Commons.

Bison – *Bison*

Even large, herbivorous, late Pleistocene mammals such as the Mylakhchinsk bison (see Figure 60-Figure 61) have died with bryophytes in their alimentary tract (Ukraintseva *et al*. 1978; Ukraintseva 1979).

Ukraintseva (1981) examined the gastrointestinal tracts of a variety of herbivorous mammals, including ***Bison*** (Figure 60-Figure 61), preserved from various periods during the Kargin interglacial period in the Indigirka River basin (Wisconsin period, 45,000-30,000 BP). During that time bogs spread, concurrent with the reduction of herbaceous communities suitable for pasturing. At the same time, rumen analysis indicated that the food composition changed for these large mammals, shifting to plants (Ukraintseva *et al*. 1978), including ***Sphagnum*** (Figure 62), from moist and water-logged communities (Ukraintseva 1981). These plants had considerably different nutrient quality, and the diet change led to the extinction of some of the herbivores.

Figure 60. American buffalo, ***Bison bison***, grazing. The Mylakhchinsk bison died with mosses in its gut. Photo through Creative Commons.

Figure 61. The European bison, ***Bison bonasus***, grazing amid grasses and mosses. Photo by Michael Gäbler, through Creative Commons.

Figure 62. ***Sphagnum austinii***; species of ***Sphagnum*** entered the food chain when climate change caused more bogs to develop. Photo by Michael Lüth, with permission.

Summary

Activities of sheep and other ruminants can contribute to dispersal of bryophytes as the fragments adhere to hooves and fur/hair/wool.

Many goats eat mosses, but feral goats in New Zealand seem to avoid them. Musk oxen may actually lose nutrients due to adsorption onto mosses they accidentally ingest. On the other hand, some sheep (***Ovis***) will eat bryophytes as a significant portion of their diet. Some goats (***Capra***) will eat them and others avoid them. In southern Patagonia, cattle (***Bos taurus***) will eat mosses in summer, but not in winter.

When grazing is light, it can favor such mosses as ***Rhytidiadelphus squarrosus***, **Polytrichaceae**, ***Brachythecium***, and ***Plagiothecium***. Colonizers like ***Pohlia nutans*** can benefit from disturbance and increased light. Leafy liverworts like ***Barbilophozia lycopodioides*** and ***B. floerkei*** decrease with grazing. Similarly, the moss ***Straminergon stramineum*** and the leafy liverwort ***Cephalozia bicuspidata*** benefit from exclosures. But the bryophyte communities depend on the site, with Arctic and alpine communities responding differently from more temperate ones. Rodents likewise can have a profound effect on the bryophytes, with communities responding differently depending on the foraging ruminants present.

Bryophytes suffer from manuring and urine, perhaps due to increased microbial decomposition, or to greater competition from the enriched tracheophytes.

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CHAPTER 18-3
LARGE MAMMALS – NON-RUMINANTS

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CHAPTER 18-3
LARGE MAMMALS – NON-RUMINANTS

Figure 1. ***Ursus americanus***, black bear cubs playing in mosses. Photo through public domain.

Canidae – Dogs

When we think of the impacts of dogs (***Canis lupus familiaris***) on bryophytes, we tend to think of their habit of urinating (Figure 2) to mark their territory and record their presence. This raises concerns about permitting dogs on nature trails.

I was surprised to find a statement in 2012 that "very little is known about the nutrient composition of dog urine and its impacts on habitats" (White *et al*. 2012). Instead, these researchers refer to the ability of urine to "scald" vegetation, while acknowledging that it provides some enrichment of soil nitrogen (Taylor *et al*. 2005). White and coworkers also stated that dog urine does more damage on dry soils because the salts are unable to disperse quickly. Gilbert (1989) reported that dog urine has significant effects on algal crusts and lichen communities at tree bases. Unfortunately, bryophytes were not mentioned.

Webb (2002) studied the effects of human traffic, including dog walkers, in Lye Valley, Oxford, England. She found that the effect of dog urine was especially damaging to plants in very low nutrient ecosystems, like the calcareous fen areas and the dry calcareous grasslands. The implication is that these negative effects included damage to fen mosses. Some fast-growing grasses benefit.

Figure 2. ***Canis lupus familiaris*** marking territory. Photo by Daniel Mott, through Creative Commons.

In urban areas, it is mostly ***Bryum argenteum*** (Figure 3) that finds its way into the cracks in the sidewalks and along their borders (Sam Bosanquet, Bryonet 8 June 2011). But in natural areas, rarer species may be affected. Bosanquet asked if anyone knew of the impacts of dog urine and feces on bryophytes, citing the known negative impacts of human urine on the leafy liverwort ***Lepidozia cupressina*** (Figure 4) and the filmy fern ***Hymenophyllum tunbrigense*** (Figure 5), often killing both.

Figure 3. ***Bryum argenteum*** in crack in parking lot. Photo by Paul Davison.

Figure 4. ***Lepidozia cupressina***, a species that is negatively impacted by dog urine. Photo by Michael Lüth, with permission.

Figure 5. ***Hymenophyllum tunbrigense***, a fern that is negatively impacted by urine. Photo through Creative Commons.

In her moss gardens, Annie Martin (Bryonet 9 June 2011) has observed frequent visits from a St. Bernard who left sizeable deposits of feces. Fortunately, this does not seem to have caused any harm to the garden, even if left there for several days.

Rod Seppelt (Bryonet 8 June 2011) relays his own experience. Mosses such as ***Eurhynchium*** (***Kindbergia***; Figure 6) and ***Brachythecium albicans*** (Figure 7) are able to regrow rapidly after urine damage, probably initially through lack of competition from the grasses that die off, but later come back. But dog urine is concentrated, so some bryophytes are likely to experience toxic effects. What seems to be the worst component for plants is ammonia, particularly the high concentration of nitrogen <www.dogster.com>. In the Arctic (Figure 8), urine enriches the nutrients, and if these nutrients are too high, seed plant vegetation benefits, to the detriment of the poorly competing bryophytes (see Chapter 18-1).

Figure 6. ***Eurhynchium praelongum***, a species that regrows quickly after being sprayed with urine. Photo by Juan Larrain, with permission.

Figure 7. ***Brachythecium albicans***, a species that regrows quickly after being sprayed with urine. Photo by Michael Lüth, with permission.

Figure 8. Tundra with dwarf willow, blueberry, and bearberry in Alaska, a habitat enriched by nutrients in urine of large mammals. Photo by Nathanael Coyne, through Creative Commons.

Bryophytes are known to require lower nutrient concentrations than that of tracheophytes. Cape and coworkers (2009) presented evidence that we should re-evaluate our perspective on the critical ammonia levels for plants. They suggested 1 µg NH_3 m^{-3} for bryophytes, whereas they suggested 3 ± 1 µg NH_3 m^{-3} was appropriate for herbaceous tracheophytes.

As I read these comments about the lack of response of bryophytes to dog urine, I must wonder about the impact of climate on this seeming lack of response. In a humid climate where bryophytes remain hydrated and rain is frequent, might the urine be washed away before enough of it enters the moss to harm it? On the other hand, might a dry climate result in concentration and dose the moss with lots of it at once when rehydration occurs, especially with fog or night-time dew? Would the urine convert to uric acid and hence be more harmful in that state?

Macropodidae – Wallabies and Kangaroos

Most wallabies don't seem to have a direct interaction with bryophytes, but they can have a major impact on them by damaging and browsing or grazing on competing vegetation. Unlike the damage done by deer and goats in other areas of New Zealand, the damage to vegetation on Kawau Island, New Zealand, is the result of four species of introduced Australian wallabies [***Macropus eugenii*** – Dama wallaby (Figure 9), ***Macropus parma*** – parma wallaby (Figure 10), ***Petrogale penicillata penicillata*** – brush-tailed rock wallaby (Figure 11), and ***Wallabia bicolor*** – swamp wallaby (Figure 12)] (Wilcox *et al*. 2004). The activities of these wallabies in the forest damage the tracheophyte vegetation and create a lawn of bryophytes (Figure 13). This appears to be the result of greater tolerance on the part of bryophytes, rather than superior competition. The most common species are the mosses ***Campylopus clavatus*** (Figure 14), ***Dicranoloma billardierei*** (Figure 15), ***Leucobryum candidum*** (Figure 16), and ***Ptychomnion aciculare*** (Figure 17), especially ***Dicranoloma billardierei***. A few patches of the large liverwort ***Chandonanthus squarrosus*** (Figure 18) are also present, with large areas of ***Cladina*** (Figure 19) and ***Cladia*** (Figure 20-Figure 21) lichens. The researchers consider this lawn to be the result of superior tolerance of stress by the bryophytes and lichens.

Figure 9. ***Macropus eugenii***, the Dama wallaby, with Joey. This species, introduced to New Zealand, destroys the ground vegetation, and it becomes replaced by bryophytes. Photo by Mathae, through Creative Commons.

Figure 10. ***Macropus parma*** (parma wallaby) with joey. This species, introduced to New Zealand, destroys the ground vegetation, and the vegetation is replaced by bryophytes. Photo by Matthias Kabel, through Creative Commons.

Figure 11. ***Petrogale penicillata penicillata*** (brush-tailed rock wallaby). This species, introduced to New Zealand, destroys the ground vegetation, and it becomes replaced by bryophytes. Photo by Roy at NatureMap, through Creative Commons.

Figure 12. ***Wallabia bicolor*** (swamp wallaby). This species, introduced to New Zealand, destroys the ground vegetation, which is replaced by bryophytes. Photo by Patrick K59, through Creative Commons.

Figure 13. Bryophyte lawn created by wallabies on Kawau Island, New Zealand. Photo courtesy of Mike Wilcox.

Figure 14. ***Campylopus clavatus***, a common species of moss in forest bryophyte lawns of Kawau Island following invasion of Australian wallabies. Photo from Canberra Nature, through Creative Commons.

Figure 15. ***Dicranoloma billardierei***, a common species of moss in forest bryophyte lawns of Kawau Island following invasion of Australian wallabies. Photo by Michael Lüth, with permission.

Figure 16. ***Leucobryum candidum***, a common species of moss in forest bryophyte lawns of Kawau Island following invasion of Australian wallabies. Photo by Phil Bendle, through Creative Commons.

Figure 17. ***Ptychomnion aciculare***, a common species of moss in forest bryophyte lawns of Kawau Island following invasion of Australian wallabies. Photo by Nathan Fell, through Creative Commons.

Figure 18. ***Chandonanthus squarrosus***, a less common liverwort in forest bryophyte lawns of Kawau Island following invasion of Australian wallabies. Photo by David Tng, with permission.

Figure 19. ***Cladina mitis***; the genus ***Cladina*** is common in forest lawns of Kawau Island following invasion of Australian wallabies. Photo by Triin Lillemets, through Creative Commons.

Figure 20. ***Cladia retipora*** lawn, in a common genus of lichen in forest lawns of Kawau Island following invasion of Australian wallabies. Photo by Chris Lindorff, through Creative Commons.

Figure 21. Close view of ***Cladia retipora***, in a common genus of lichen in forest lawns of Kawau Island following invasion of Australian wallabies. Photo by Vanessa Ryan, through Creative Commons.

Sankaran *et al*. (2008) found that the eastern grey kangaroo (***Macropus giganteus***; Figure 22) and the common wombat (***Vombatus ursinus***; Figure 23), on the other hand, are more effective at increasing woody plant abundance than the introduced hog deer (***Axis porcinus***; Figure 24) or native swamp wallabies (***Wallabia bicolor***; Figure 12), both of which are browsers. The hog deer is the largest consumer of mosses (less than 0.01%) in southeastern Australia (Davis *et al.* 2008).

Hobbs (1996) likewise considered that browsing by herbivorous ungulates on grasses, forbs, and shrubs could give competitive advantage to trees, ferns, and mosses. This assumption is partly supported on Yanakie Isthmus (connecting Wilsons Promontory to mainland Victoria, Australia) by the observed increase in moss cover in their presence, while grass cover decreased (University of Ballarat 1999).

Figure 22. ***Macropus giganteus***, eastern grey kangaroo, a species in New Zealand that is responsible for increasing woody plant abundance. Photo by Danielle Langlois, through Creative Commons.

Figure 23. ***Vombatus ursinus***, common wombat, a species in New Zealand that is responsible for increasing woody plant abundance. Photo by P. Baum, through Creative Commons.

Figure 24. ***Axis porcinus***, a browser that also eats mosses. Photo by Simon J. Tonge, through Creative Commons.

Dendrolagus – Tree-kangaroo

The Lumholtz tree-kangaroo (***Dendrolagus lumholtzi***; Figure 25) is known from the rainforests of Northeast Queensland, Australia. It is the smallest (~0.5m body length) of the tree-kangaroos and is somewhat territorial. It consumes mosses, as well as lichens, ferns, and flowers (Heise-Pavlov 2017).

Figure 25. ***Dendrolagus lumholtzi***, a moss consumer. Photo by Kenneth Bader, through Creative Commons.

Mosses seem to be more commonly consumed among the tree-kangaroos than among other wallabies. The Huon tree-kangaroo (***Dendrolagus matschiei***; Figure 26) is a generalist leaf eater, including leaves, fruits, and mosses in its diet (Betz 2001). In the rainforests of their native Papua New Guinea, they live where the forest floors are covered by a variety of moss species (Porolak 2008). Lichens and **lianas** (vines) are uncommon at the altitudinal range (1,000-3,000 m) where they live.

Figure 26. ***Dendrolagus matschiei***, a generalist plant eater, including mosses. Photo by Cyndy Sims Parr, through Creative Commons.

Macropus – Australian Wallabies (and others)

Species of ***Macropus*** (Figure 27) make **hip holes** to use as resting sites, especially in hot weather (Eldridge & Rath 2002). **Hip holes** are shallow, kidney-shaped depressions these kangaroos construct next to trunks of many trees and shrubs in arid and semi-arid Australia. Although these hip holes average less than 10 cm deep (Eldridge & Rath 2002), that is enough digging to cause considerable destruction to the thin cryptogamic crust of lichens, bryophytes, and bacteria (Eldridge & Greene 1994).

Figure 27. ***Macropus parma***, a species introduced to New Zealand, that destroys the ground vegetation, which is replaced by bryophytes. Members of this genus destroy bryophyte vegetation by digging hip holes. Photo by Mistvan, through Creative Commons.

Vombatidae – Wombats

Jones and Pharo (2009) questioned the importance of bryophytes in the buttongrass moorland in Australia following fire. Moss patches there become visible between the charred tussocks of grass. These researchers established twenty wire cages (30 cm x 30 cm x 20 cm) as exclosures that permitted insect access but not vertebrates. In addition, 20 patches with a minimum diameter of 10 cm of either of the mosses ***Campylopus*** spp. (Figure 14) or ***Dicranoloma*** spp. (Figure 15) were divided by a cage to test whether these mosses would become food to large herbivores after the fire. However, using stem length measurements, they were unable to find any differences in mosses inside and outside exclosures.

One possible reason for the absence of evidence is that suitable feeding grounds were close enough to the burned area that wombats did not need to rely on poor quality food sources such as mosses (Jones & Pharo 2009). For wombats, the mosses are hard to digest. They are hindgut fermenters (Hume 1999). Polyphenolic compounds in mosses can have antibiotic properties that inhibit the digestion of hindgut fermenters (Prins 1982). Interestingly, the Parks & Wildlife Service (2008) considered mosses to be a "particular delicacy" for the wombats, with native grasses being their primary food, as well as shrubs, roots, sedges, bark, and herbs.. Triggs (1996) considered that some mosses provide the wombats with water when they are moist and green; they are ignored when they are dry.

Jones and Pharo (2009) also considered the possibility that the wombats might only consume the capsules, but no capsules were observed at the study site. However, in a different buttongrass moorland they had observed evidence of grazing on capsules of the moss ***Tayloria tasmanica*** (Figure 28). In another report, Lyn Cave (in Fife 2015) concluded that the primary habitat of ***Tayloria tasmanica*** is wombat dung. For some reason, little attention has been given to the potential of moss capsules as food.

Figure 28. ***Tayloria tasmanica***, a dung moss species possibly grazed on by wombats. Photo by Niels Klazenga, with permission.

When large herbivores live at high elevations with deep snow cover, they face a challenge getting enough of the right foods to balance their needs. This is further complicated by the slow regrowth of alpine plant species following disturbance. Thus, Green *et al*. (2015) hypothesized that responses of wombats (***Vombatus ursinus***; Figure 23) to disturbance by fire at high elevations would differ from those at low elevations. To test their hypothesis, they examined the winter diet of common wombats in the Snowy Mountains of Australia in the ten years following a fire. Optimal foraging theory predicts that these herbivores should respond to scarce food resources by widening their food choices. However, these wombats expanded their diet choices only slightly at the higher elevations compared to those at the lower elevations, with no expansion in number of food species. Rather, they are able to exploit the improved food quality resulting from nutrients released by fire.

Wombats may actually contribute to bryophyte diversity. I have observed ***Mittenia plumula*** (Figure 29) growing at the entrance (Figure 30-Figure 31) of a wombat burrow. The opening provided the disturbed soil and cave environment needed by this species.

Figure 29. Close view of ***Mittenia plumula***. Photo by David Tng, with permission.

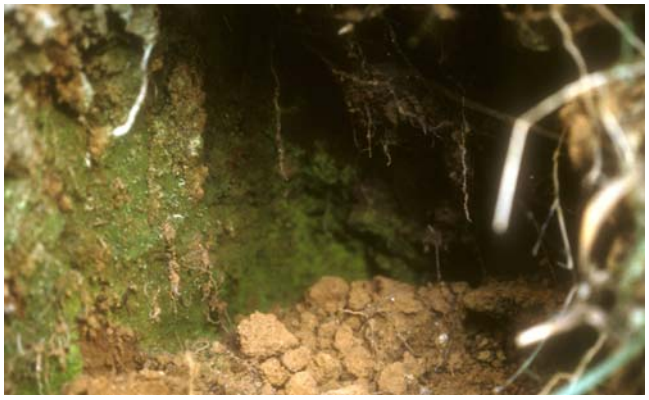

Figure 30. ***Mittenia plumula*** in wombat burrow opening in Australia. Photo by Janice Glime.

Figure 31. ***Mittenia plumula*** in wombat burrow opening in Australia. Photo by Janice Glime.

Phalangeridae

Common Brushtail Possum – *Trichosurus vulpecula*

I doubt that the Australian possum uses bryophytes, but the moss uses it. I have seen the moss ***Tayloria octoblepharum*** (Figure 32) growing on the dung of the common brushtail possum (***Trichosurus vulpecula***; Figure 33) in Australia. Like other members of the **Splachnaceae**, this species uses dung as its substrate and the capsules smell like dung at maturity, attracting flies that disperse the spores.

Figure 32. ***Tayloria octoblepharum*** on possum dung at Rainbow Mountain, NZ. Photo by Janice Glime.

Figure 33. ***Trichosurus vulpecula***; dung of this species is a substrate for the moss ***Tayloria octoblepharum***. Photo by J. J. Harrison, through Creative Commons.

Elephantidae – Elephants, Mammoths

Elephants – *Elaphus*

One might expect elephants, the giants of the four-legged creatures, to be destructive of bryophytes, but in a ***Sphagnum*** (Figure 34) bog of Peninsula Malaysia, elephants (***Elephas maximus***; Figure 35) maintain the plant communities with their trampling (Yao *et al*. 2009).

Figure 34. ***Sphagnum orientale***, a moss that can be found in bogs of the Malaysian Peninsula. Photo by Blanka Shaw, with permission.

Figure 35. ***Elephas maximus*** (Asian elephant). Ancestors of this genus perished in the Wisconsonin era, perhaps due to the conversion of suitable pasture into bog habitat. Photo by Bernard Dupont, through Creative Commons.

Mammoths – *Mammuthus*

The prehistoric woolly mammoth (***Mammuthus primigenius***; Figure 36) ate mosses – and became entombed in the ice with a meal of ***Polytrichum*** (Figure 37) and ***Hypnum*** (Figure 38) in its stomach (Bland 1971).

Figure 36. Woolly mammoth (***Mammuthus primigenius***), a prehistoric moss consumer. Image from Flying Puffin, through Creative Commons.

Figure 37. ***Polytrichum commune***, possibly food of the woolly mammoth. Photo by J. R. Crellin, through Creative Commons.

On the other hand, van Geel *et al*. (2011) considered the mosses in the Palaeo gut sample from a mammoth calf from Yamal Peninsula, northwest Siberia, to be accidental. They considered that a one-month-old calf most likely ate fecal material that had been deposited on mosses and that associated mosses were consumed at the same time.

Figure 38. ***Hypnum lindbergii***, possibly food of the woolly mammoth. Photo by Michael Lüth, with permission.

Ukraintseva (1981) similarly examined the gastrointestinal tract of large mammals from the Pleistocene, looking for possible causes of extinction. He found, using C^{14} analysis from the horse (***Equus***; Figure 39), mammoth (***Elaphas***; Figure 35), and bison (***Bison***; Figure 40), that these animals perished during the Wisconsin period, 45,000-30,000 BP. During that time period, bogs and forests spread while herbaceous communities (pastures) diminished, changing the quality of the food they consumed. Instead of their usual pasture food, they had to feed in water-logged sedge, cottongrass, grass, moss, and ***Sphagnum*** (Figure 34) communities. Hence their nutrient consumption changed, a change that Ukraintseva considered to be the cause of their extinction.

Figure 39. ***Equus caballus*** (Dartmoor pony). Ancestors of this genus perished in the Wisconsonin period, perhaps due to the conversion of suitable pasture into bog habitat. Photo by Simon J. Tonge, through Creative Commons.

Figure 40. ***Bison bison*** (buffalo). Ancestors of this genus perished in the Wisconsonin period, perhaps due to the conversion of suitable pasture into bog habitat. Photo through Creative Commons.

Ursidae – Bears

Researchers have questioned whether bears consume bryophytes by choice. Elgmork and Kaasa (1992) contended that they are consumed only accidentally. But Dalen *et al*. (1996) reported that brown bear (***Ursus arctos***; Figure 41) feces contained 50-90% bryophytes, hardly an accidental percentage. Nevertheless, Dalen and coworkers found this only in May for a bear and her two cubs, again suggesting that bryophyte consumption was not a normal occurrence. At other times, some feces contained 15% ***Brachythecium reflexum*** (Figure 42), but it appeared that these mosses were consumed when the bears ate ants. Nevertheless, Wilson and Ruff (1999) noted that bears are omnivores, thus eating a variety of plant foods, including mosses.

Figure 41. ***Ursus arctos arctos*** (brown bear), a subspecies that eats lots of bryophytes. Photo by Jiří Bukovský, through Creative Commons.

Figure 42. ***Brachythecium reflexum***, a species reaching as much as 15% of content in feces of the brown bear (***Ursus arctos arctos***). Photo by Michael Lüth, with permission.

Iversen (2011; Iversen *et al*. 2013) studied the diet of polar bears (***Ursus maritimus***; Figure 43) from Svalbard. She reported 13 species of mosses in the feces, with ***Polytrichastrum alpinum*** (Figure 44) being the most frequent. Only 32.8% of the feces contained terrestrial vegetation. Of these, 27% contained mosses. Not only

were mosses relatively frequent, they also made up a significant portion of the biomass. Only two scats could be attributed to juveniles, but both contained mosses. On the other hand, Lønø (1970) found moss in only 2 of the 172 stomachs examined from Svalbard polar bears.

Figure 43. ***Ursus maritimus*** (polar bear), a moss consumer. Photo courtesy of Bob Krear.

Figure 44. ***Polytrichastrum alpinum***, food of the polar bear on Svalbard. Photo by David Holyoak, with permission.

It appears that brown bears (***Ursus arctos***; Figure 41) have found another use for ***Sphagnum*** (Figure 48). The bears sometimes put peat mosses with carcasses that they cache, a behavior suggesting that the moss may be used to reduce bacterial and fungal attack on their food (Elgmork 1982). Hyvönen (1990) reported that bears often bury their prey in forests with mats of ***Polytrichum*** (Figure 37). Hyvönen reported on the Finnish coin that has a bear on one side and ***Polytrichum*** on the other side, suggesting that the association of these two organisms on the same coin related to the habit of the bears to bury their food in forests with ***Polytrichum*** ground cover.

Hyvönen (1990) reminds us that Linnaeus reported that bears (***Ursus arctos arctos***; Figure 41) gather ***Polytrichum*** (Figure 37) tufts to cushion their winter holes, whereas Dr. Erik Nyholm contends that bears are indiscriminate in choosing padding, using the more abundant species of ***Pleurozium schreberi*** (Figure 45) and ***Hylocomium splendens*** (Figure 46). They also seem to use bryophytes for napping, as I have seen in several photographs posted on the internet.

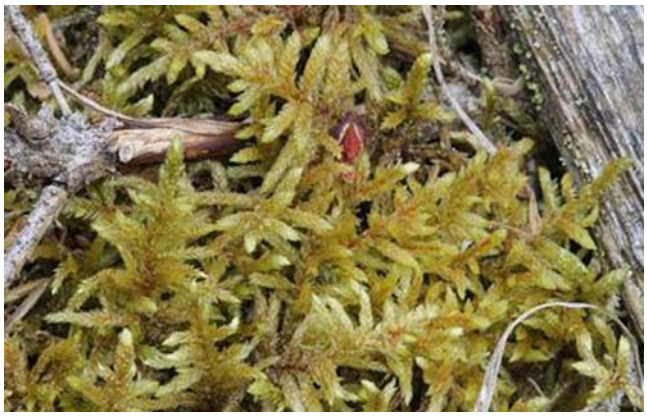

Figure 45. ***Pleurozium schreberi***, a species used by brown bears (***Ursus arctos arctos***) to pad their winter holes. Photo by Rob Routledge, through Creative Commons.

Figure 46. ***Hylocomium splendens*** on spruce forest floor, a species used by brown bears (***Ursus arctos arctos***) to pad their winter holes. Photo by Janice Glime.

Grizzly bears (***Ursus arctos*** ssp; Figure 47) are a subspecies of brown bears, but are carnivorous (Wilson & Ruff 1999). Nevertheless, they reputedly eat moss, especially when they come out of hibernation, a report I have been unable to verify. Storie (1973) and Compton (1993) reported that grizzly bears eat unidentified mosses (Figure 48). It seems these bears eat mosses along with ants and soil when they are desperate, which doesn't say much for a discriminating appetite at that time!

Bears could damage some of the epiphytic bryophytes. They at times rip bark off trees to find insects for food (Zyśk-Gorczyńska *et al*. 2015). If bryophytes are growing there, they will come off with the bark. This leads me to wonder if the bears ever attempt to get insects from the mats of bryophytes on trees, another potential source of bryophyte destruction.

Bears are also known to contribute to the nutrient regime of bryophytes, but not as you might expect. They catch fish, then transport them to land (Figure 49) before consuming them. The remainder of the carcass provides a nitrogen source (Wilkinson *et al*. 2005).

Figure 47. ***Ursus arctos*** ssp. (grizzly bear), a species that consumes mosses in an effort to get the ants. Photo by Gregory Smith, through Creative Commons.

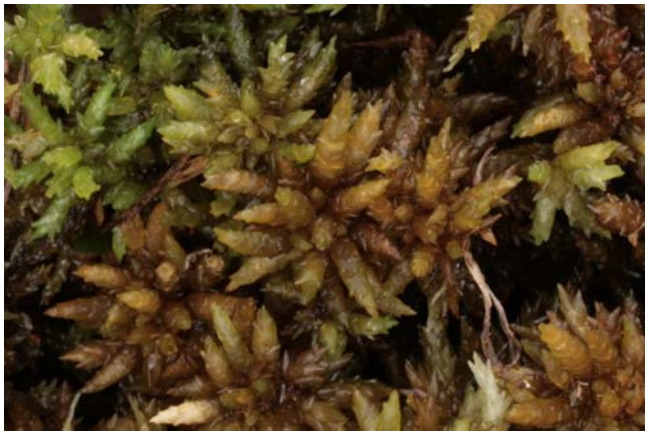

Figure 48. ***Sphagnum perichaetiale***, a potential food source for grizzly bears in the Arctic. Photo by Jan-Peter Frahm, with permission.

Figure 49. ***Ursus americanus*** (black bear) carrying fish to land. Photo by Aaron Huelsman, through Creative Commons.

Hominidae – Primates

Chimpanzees

Egdar (1997) examined the habitats of China's monkeys, past and present. The environmental changes in the last 50 million years forced the animals to adapt to changing food availability. Some remained in the "diminishing rainforests" where they could find enough fruits and protein to survive. But others adapted to new habitats. Among these adapters was the Yunnan snub-nosed monkey (***Rhinopithecus bieti***; Figure 50-Figure 51) that moved to the high-altitude pine forests (Figure 50). Here the most consistent food sources were hanging mosses and lichens on rocks.

Figure 50. Yunnan snub-nosed monkey (***Rhinopithecus bieti***), a species that eats hanging mosses and lichens when it is forced to move to the mountains. Photo from EOL China Regional Center, through Creative Commons.

Figure 51. Close view of the Yunnan snub-nosed monkey (***Rhinopithecus bieti***). Photo from EOL China Regional Center, through Creative Commons.

But monkeys are smarter than most other animals. Lamon *et al*. (2017) were studying the behavior of wild chimpanzees (***Pan troglodytes***; Figure 52) in Budongo Forest Reserve in Western Uganda and discovered an unusual tool use. They were using mosses as sponges! This was a new behavior that first appeared in the population in 2011. Three years later, they found that the sponging behavior was still present and had spread to some of the other members of the community. Hanging mosses are common in areas inhabited by chimpanzees (Figure 53-Figure 56). The moss species used were ***Pilotrichella cuspidata*** (Figure 54), ***Racopilum africanum***, and ***Pinnatella minuta***, as well as two leafy liverworts – ***Plagiochila strictifolia*** and ***Plagiochila pinniflora*** (Hobaiter 2014).

Figure 52. ***Pan troglodytes schweinfurthii*** in its natural habitat. Photo by Bernard Dupont, through Creative Commons.

Figure 53. Hanging moss from Riparian forest, home of chimpanzees, Chappal Hendu, border of Cameroon, Taraba State Nigeria at 2000 m asl. Photo courtesy of Bup-Olu Oyesiku.

Three years after the initial 2011 moss sponging behavior, Lamon and coworkers (2017) decided to experiment to see if the mosses were a preferred method to obtain water. Using the same population that had learned the behavior, they selected a site where a clay pit had two ground water holes at the bottom of two trees. These cavities contained rainwater enriched with minerals. The experimenters hung the moss ***Pilotrichella welwitschii*** (see Figure 54), collected in swamp areas within the natural range of the chimpanzees, in trees around the clay pit. A wide choice of leaves was available naturally. Of 40 chimpanzees included in the study, 33 used moss sponges during at least one of the experimental trials. Five of these were among the original 8 sponge users and 17 were new at this behavior. Those who had tried the mosses seemed to prefer that method, as 18 of those 22 used only moss sponges to obtain water. Furthermore, Hobaiter *et al*. (2014) had noted only 8 of 32 individuals using moss sponges; leaf sponging was the predominant technique, with 83% of the individuals using it at least once and 18 were exclusive leaf spongers, although 22 chimpanzees used the mosses at least once. Three years later, mosses seemed to be the preferred tool among those that had learned the behavior.

Figure 54. ***Pilotrichella*** sp., one of the mosses available to chimpanzees for moss sponges. Photo by Lena Struwe, through Creative Commons.

A similar sponging behavior occurred in chimpanzees (***Pan troglodytes***; Figure 55) in the Virunga National Park in the Democratic Republic of the Congo (Lanjouw 2002). When water was scarce, the chimpanzees gathered water from that collected in tree branches. When they could not access it directly, they prepared tools, including the use of sponges developed from mosses. The chimps collected mosses from trees. They then rolled them into a bundle about the size of a golf ball. These balls were inserted into the hollow of the branches. When the chimpanzees extracted the moss sponge, it had absorbed water. The chimpanzees sucked the water from the moss sponge, repeating this procedure to get additional drinks.

The chimpanzees are known for getting water from the many hanging mosses in the rainforests (Min Chuah-Petiot, pers. comm. 1 March 2018). Among these hanging water sources (Figure 56) are ***Pilotrichella cuspidata*** (Figure 54), ***Squamidium brasiliense*** (Figure 57-Figure 58), and ***Papillaria africana*** (Figure 59-Figure 60).

Figure 55. ***Pan troglodytes*** (chimpanzee) with moss sponge. Photo courtesy of Catherine Hobaiter.

Figure 56. ***Pilotrichella cuspidata***, ***Papillaria africana***, and ***Squamidium brasiliense*** in Grande Comore, Africa, showing the hanging mosses that are typical of chimpanzee habitats where they are used as sponges. Photo courtesy of Min Chuah-Petiot.

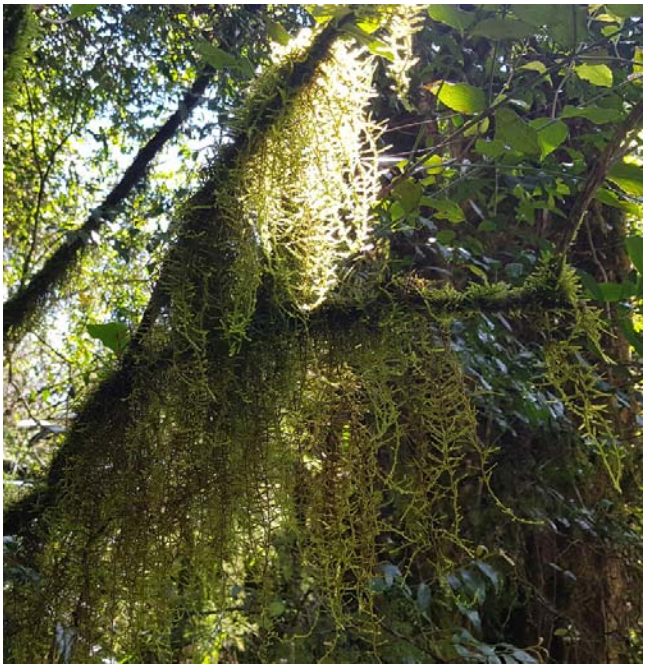

Figure 57. ***Squamidium brasiliense***, one of the mosses available to chimpanzees for moss sponges. Photo by Richard Gill, through Creative Commons.

Figure 58. ***Squamidium brasiliense***, one of the mosses available to chimpanzees for moss sponges. Photo by Nick Helme, through Creative Commons.

Figure 59. ***Papillaria africana***, a leafy liverwort that grows on trees and causes allergic contact dermatitis. Photo by Craig Peter, through Creative Commons.

Figure 60. ***Papillaria africana***, a leafy liverwort that grows on trees and causes allergic contact dermatitis. Photo by Nick Helme, through Creative Commons.

Humans

Humans can suffer from contact with some bryophytes (Schmidt (2000). In addition to fungal diseases from contact with ***Sphagnum*** (Figure 34, Figure 48) inhabitants, members of ***Frullania*** can cause wood cutter's disease. Contact with this leafy liverwort can cause dermatitis even for others who handle the clothing. Bancons and Maleville (1967) found that ***Frullania*** is a powerful allergen that can cause asthmatic attacks as well as skin reactions. The allergen is very volatile, permitting it to cause infections at a distance with no contact. In young trees, the fraction that diffuses through the bark is sucked into the sapwood.

Mitchell (1981) reported 112 cases of allergic contact dermatitis caused by ***Frullania*** in British Columbia during a 10-year period. Mitchell *et al*. (1970) found that sesquiterpene lactones with alantolactone as the most active compound. Quirce *et al*. (1994) found similar results among 7 infected persons who apparently contracted the condition during a stroll in the park. All tested positive to ***Frullania dilatata*** (Figure 61-Figure 62) and three also tested positive to ***F. tamarisci*** (Figure 63-Figure 64).

Figure 61. ***Frullania dilatata***, a leafy liverwort that grows on trees and causes allergic contact dermatitis. Photo by Sture Hermansson, with online permission.

Figure 62. ***Frullania dilatata***, a leafy liverwort that grows on trees and causes allergic contact dermatitis. Photo by Sture Hermansson, with online permission.

Figure 63. ***Frullania tamarsici***, a leafy liverwort that grows on trees and causes allergic contact dermatitis. Photo by Claire Halpin, with permission.

Figure 64. ***Frullania tamarsici***, a leafy liverwort that grows on trees and causes allergic contact dermatitis. Photo by Claire Halpin, with permission.

The genus also causes allergy skin problems in places like France where charcoal is burned (Jeff Duckett, pers. comm. 21 December 2017). See also Bonhôte *et al*. 2000.

Whales

Whales seem like an unlikely animal to interact with bryophytes. However, whale bones can serve as a substrate for at least some species (Figure 65-Figure 66). Jeff Duckett (2017) reported ***Bryum argenteum*** (Figure 67), ***Ceratodon purpureus*** (Figure 68), ***Rhytidiadelphus squarrosus*** (Figure 68), ***Tetraplodon mnioides*** (Figure 69), and ***Ulota phyllantha*** (Figure 67) among a number of others. His publication summarizes reports of bryophytes on whale bones around the world.

Figure 65. Humpback whale bones with mosses. Photo by Jeff Duckett, with permission.

Figure 66. Humpback whale bones with mosses. Photo by Jeff Duckett, with permission.

Figure 67. ***Bryum argenteum*** and ***Ulota phyllatha*** on whale vertebra. Photo by Jeff Duckett, with permission.

Figure 68. ***Ceratodon purpureus*** with ***Rhytidiadelphus squarrosus*** growing over it on humpback whale skeleton. Photo by Jeff Duckett, with permission.

Figure 69. ***Tetraplodon mnioides*** on blue whale skull. Photo by Jeff Duckett, with permission.

Summary

Large vertebrates may use bryophytes or harm them – or both. Dogs can damage them with urine and feces, but we have little scientific knowledge of these effects. Wallabies and kangaroos can damage the leafy vegetation, making the habitat suitable for bryophytes. ***Dendrolagus*** species, the tree-kangaroos, eat mosses. On the other hand, ***Macropus*** species, Australian wallabies, make hip holes, damaging the bryophytes as they dig.

Wombats make burrows, and mosses like ***Mittenia*** are able to establish on the recently disturbed soil at the opening. Some researchers suggest that wombats might consume mosses for their adhering water. They also consume capsules of the dung moss ***Tayloria tasmanica***.

The dung moss ***Tayloria octoblepharum*** grows on the dung of the common brushtail possum (***Trichosurus vulpecula***).

Elephants can actually maintain some bryophyte communities through their trampling. And Pleistocene mammoths were preserved in ice with bryophytes in their gut. But a change from pasture habitats to boggy and mossy habitats may have led to their extinction.

Bears use the bryophytes to line the winter "nest." Others use growing bryophytes for napping. Bryophytes also occur in feces, but may be there through consumption of inhabiting ants. However, polar bears can eat large quantities of bryophytes. Brown bears also bury mosses with their food, presumably to help preserve the food. Bears can also drag fish into the forest to eat them, with the remains providing nutrients that benefit bryophytes.

The Yunnan snub-nosed monkey (***Rhinopithecus bieti***) subsists in a habitat where hanging mosses and rock lichens are the primary food source. Some chimpanzees (***Pan troglodytes)*** in African rainforests have learned to use the pendent mosses as sponges to gather water from tree holes and other difficult to reach places.

Acknowledgments

Ron Porley kindly notified me of the publication on chimpanzees using mosses as sponges to drink. Jessica Beever provided me with the paper and helped me obtain the image of the moss lawn on Kawau Island, kindly provided by Mike Wilcox. Eileen Dumire critically reviewed the chapter. Thank you to David Taylor for notifying me of an error in the text.

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CHAPTER 19-1
BACTERIAL EFFECTS ON BRYOPHYTES

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CHAPTER 19-1
BACTERIAL EFFECTS ON BRYOPHYTES

Figure 1. Nodules of the nitrogen-fixing bacterium ***Bradyrhizobium*** with mosses on ***Acacia koa***. Photo courtesy of James Leary.

This is the most exciting chapter I have written thus far! The study of bacterial interactions between bryophytes and bacteria is quite new, and fascinating relationships are unfolding.

Nomenclature for phyla in this are from Oren and Garrity (2021) (see Euzéby 1997)

There have been few explorations of the bacteria that are naturally associated with bryophytes (Koua *et al*. 2015). Koua and coworkers explored the bacteria on eight bryophyte species. They identified 42 bacterial species in 90 DGGE gel bands. The bacterial genus ***Clostridium*** (Figure 2) predominated, comprising 21.4% of the total bacterial community.

Bacteria could influence their bryophyte substrates in a number of ways. For dead and dying bryophytes, they could contribute to decomposition. For living bryophytes, they could block light needed for photosynthesis. But at the same time they could produce CO_2 through respiration, contributing to higher photosynthetic rates. But beyond these more easily conceived roles, they can contribute hormones and other substances that might influence the development of the bryophytes or the community where they both live. And even more interesting relationships are unfolding.

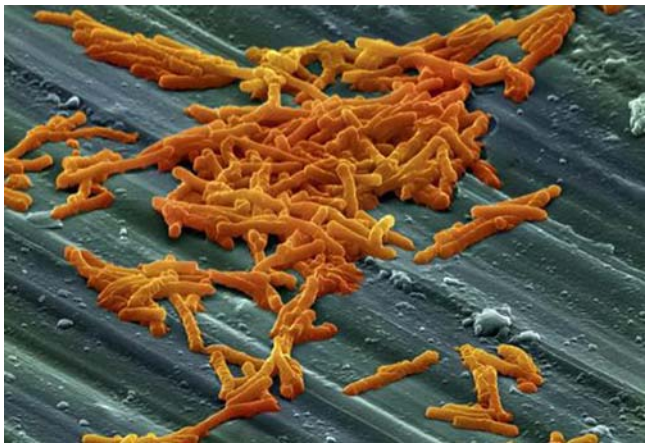

Figure 2. ***Clostridium difficile***, a predominant bacterial genus on some bryophytes. Photo through Creative Commons.

Bacteria Communities on Bryophytes

During and van Tooren (1990, 2008) reminded the ecologists that bryophytes in the ecosystem may be influenced by their interactions with other organisms, including bacteria. Such interactions might involve mineral nutrition, carbon economy, herbivory, and growth and development of gametophytes.

Among the abundant bacteria associated with bryophytes in Japan are strains of ***Burkholderia*** (ubiquitous obligately aerobic, rod-shaped, Gram-negative, genus of **Pseudomonadota** (previously Proteobacteria); Figure 3), ***Hafnia*** (facultatively anaerobic, rod-shaped, Gram-negative genus of **Pseudomonadota**; Figure 4), ***Methanobacterium*** (nonmotile, anaerobic genus of **Archaea**; Figure 5), ***Methylobacterium*** (pink-pigmented, facultatively anaerobic, straight rod-shaped, Gram-negative genus of **Pseudomonadota**; Figure 6), ***Pantoea*** (yellow-pigmented, Gram-negative genus of **Pseudomonadota**; Figure 7), and ***Serratia*** (facultatively anaerobic, rod-shaped, Gram-negative genus of **Pseudomonadota**; Figure 8), occurring as endophytes, epiphytes, or both (Opelt & Berg 2004; Bragina *et al*. 2013; Koua *et al*. 2015).

Figure 3. ***Burkholderia pseudomallei***; ***Burkholderia*** is one of the abundant bryophyte-dwelling bacterial genera in Japan. Photo by Gavin Koh, through Creative Commons.

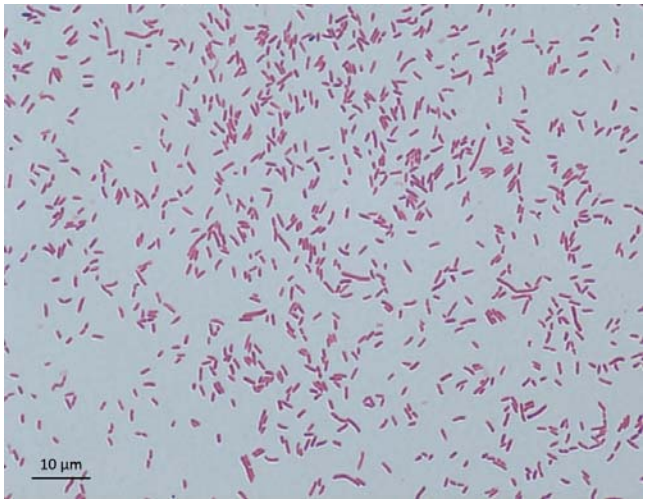

Figure 4. ***Hafnia alvei***, in one of the abundant bryophyte-dwelling bacterial genera in Japan. Photo by Antoine2003, through Creative Commons.

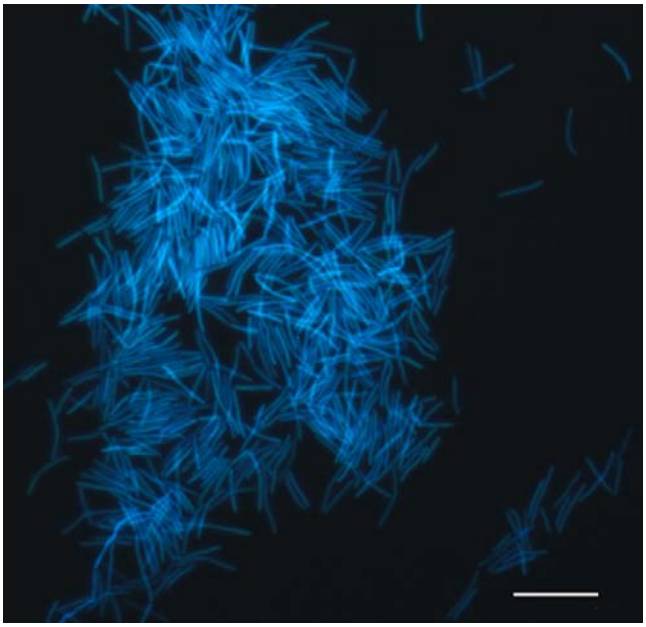

Figure 5. ***Methanobacterium*** sp., one of the abundant bryophyte-dwelling bacteria genera in Japan. Photo from JAMSTEC, through Creative Commons.

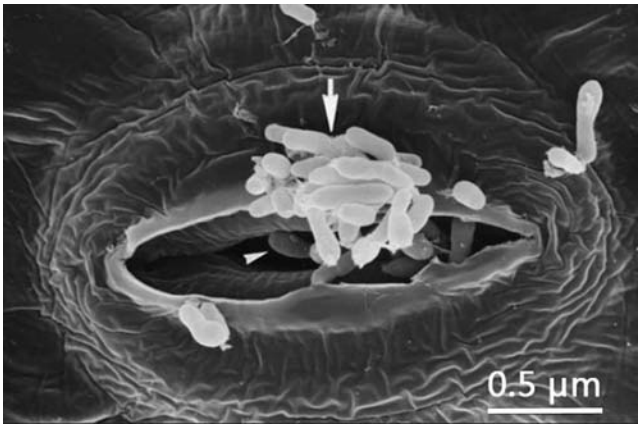

Figure 6. ***Methylobacterium*** sp. in sunflower stoma, one of the abundant bryophyte-dwelling bacterial genera in Japan. Photo by U. Kutschera, through Wikimedia Commons.

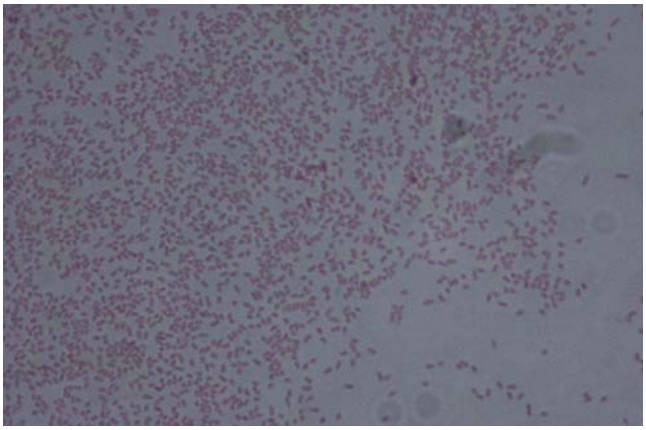

Figure 7, ***Pantoea agglomerans*** Gram stain, a species that occurs on bryophytes and is antagonistic toward some pathogenic bacteria and fungi. Photo by Dr. Sahay, through Creative Commons.

Figure 8. ***Serratia marcescens*** bacteria on bread slice; ***Serratia*** is an abundant genus on bryophytes in Japan and is antagonistic toward them. Photo by DBN, through Creative Commons.

On the other hand, some bacteria are antagonistic toward the bryophytes, including species such as ***Bacillus*** sp. (**Bacillota** – syn. = **Firmicutes**; Figure 9), ***Pseudomonas putida*** (**Pseudomonadota**; see Figure 10), ***Serratia*** sp. (Figure 8), and ***Xanthomonas*** sp. (**Pseudomonadota**; Figure 11) (Opelt *et al.* 2007). ***Serratia liquefaciens*** (see Figure 8), predominant in the mosses ***Sphagnum*** (Figure 12) and ***Aulacomnium*** (Figure 13), and ***Serratia proteamaculans*** (see Figure 8) are the most effective antagonists among the bacterial isolates from these same mosses (Opelt & Berg 2004).

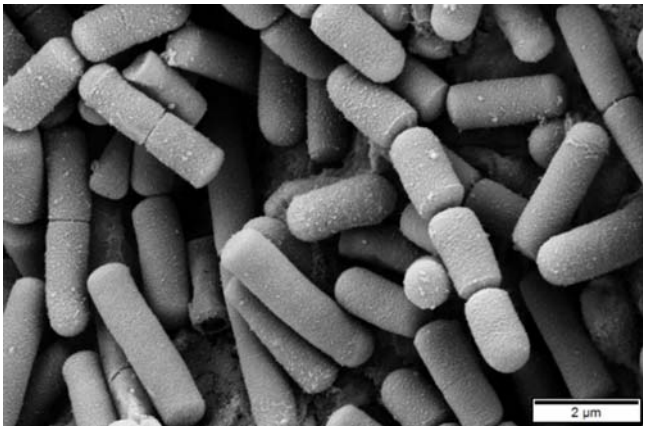

Figure 9. ***Bacillus cereus*** SEM, in an abundant genus on bryophytes in Japan and antagonistic toward them. Photo by Mogana Das Murtey and Patchamuthu Ramasamy, through Creative Commons.

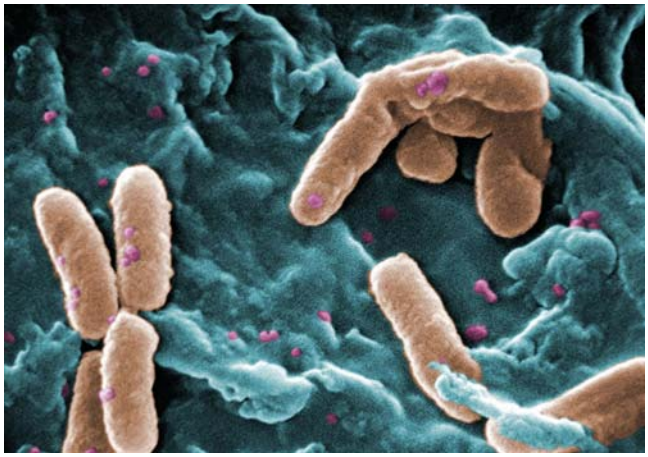

Figure 10. ***Pseudomonas aeruginosa***; ***Pseudomonas putida*** is antagonistic toward bryophytes. Photo by Janice Haney Carr, CDC, through Public domain.

Figure 11. ***Xanthomonas oryzae*** pv. **oryzicola** infecting a leaf; some members of this bacterial genus are antagonistic toward bryophytes.. Photo by S. Q. An *et al*., through Creative Commons.

Figure 12. ***Sphagnum*** blanket bog, habitat for ***Serratia liquefaciens***, one of the strongest antagonists against bryophytes. Photo through Creative Commons.

Figure 13. ***Aulacomnium palustre***, habitat for ***Serratia liquefaciens***, one of the strongest antagonists against bryophytes. Photo by Hermann Schachner, through Creative Commons.

Koua and coworkers (2015) found bacterial colonizers of bare-rock bryophytes in their Japanese collections to be γ-**Proteobacteria** (**Pseudomonadota**) [***Buttiauxella***, ***Enterobacter*** (Figure 14), ***Erwinia*** (Figure 15), ***Pantoea*** (Figure 7), ***Pseudomonas*** (Figure 10), and ***Salmonella*** (Figure 16)] and **Bacillota** [***Anaerobacter*** (Figure 17), ***Clostridium*** (Figure 2)] – a group that can survive extreme conditions, especially desiccation, through production of endospores. ***Citrobacter*** (**Pseudomonadota**; Figure 18), ***Clostridium*** (**Bacillota**), ***Pseudomonas*** (**Pseudomonadota**), and ***Serratia*** (Figure 8) were common among highly populated soil and bare-rock-associated bryophytes. ***Anaerobacter*** (**Bacillota**), ***Buttiauxella*** (**Pseudomonadota**), ***Erwinia***, and ***Pantoea*** were limited to the bryophytes associated with bare rocks.

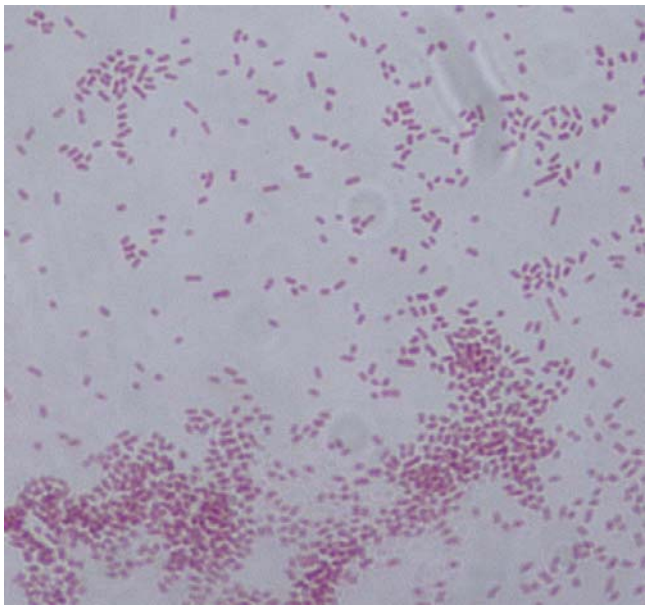

Figure 14. ***Enterobacter aerogenes***; the genus ***Enterobacter*** is a bacterial colonizer of bare-rock bryophytes in Japan. Photo by Riraq25, through Creative Commons.

Figure 15. ***Erwinia tracheiphila*** causing flower wilt; the genus ***Erwinia*** is a bacterial colonizer of bare-rock bryophytes in Japan. Photo by Howard F. Schwartz, through Creative Commons.

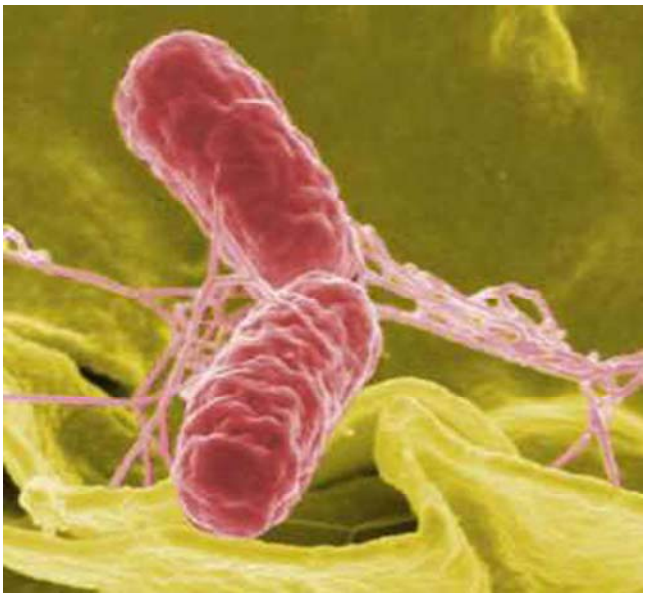

Figure 16. ***Salmonella***, bacterial colonizer of bare-rock bryophytes in Japan. Photo by JohnnyMrNinja, through Creative Commons.

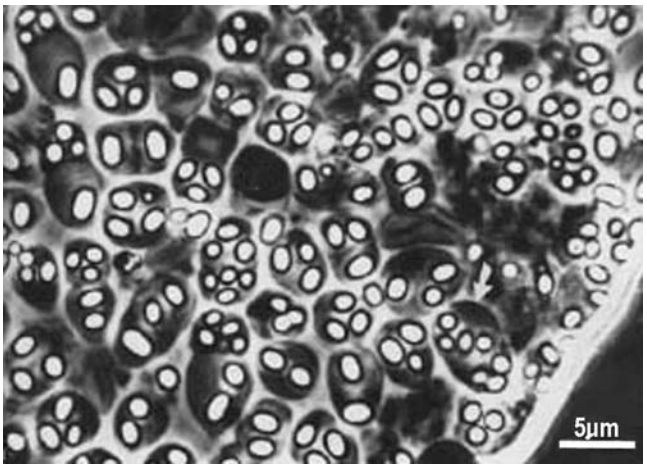

Figure 17. ***Anaerobacter polyendosporus***; members of this genus can survive extreme conditions, especially desiccation, through production of endospores. Photo by Abtop, through Creative Commons.

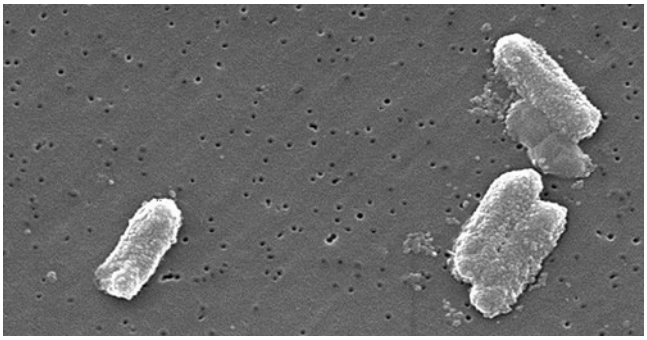

Figure 18. ***Citrobacter freundii*** SEM; some members of ***Citrobacter*** are common bacteria among highly populated soil and bare-rock-associated bryophytes. Photo through public domain.

Some bryophyte-dwelling bacteria, especially **Proteobacteriaceae**, are fussy, selecting only bryophytes of highly populated soil habitats: ***Dickeya*** (Figure 19)**,** ***Klebsiella*** (Figure 20), ***Obesumbacterium***, and ***Pectobacterium*** (Figure 21) (Koua *et al*. 2015). ***Serratia proteamaculans*** (see Figure 8) occurred exclusively in the moss ***Trachycystis microphylla*** (Figure 22) of both bare rocks and highly populated soils. These contrast with ***Clostridium*** (**Bacillota**; Figure 2), which was present on all species of bryophytes in all habitats in the Japanese study.

Figure 19. ***Dickeya*** *cf.* ***dadantii*** or ***Pectobacterium carotovorum*** on onion; some species of ***Dickeya*** are selective for bryophytes of highly populated soil plots. Photo through Creative Commons.

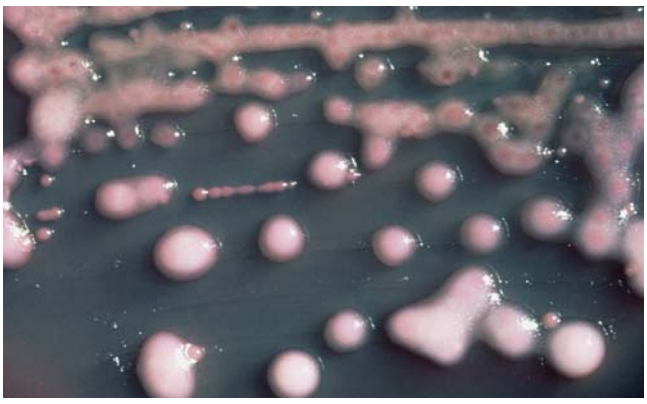

Figure 20. ***Klebsiella pneumoniae*** pink colonies; some species of ***Klebsiella*** are selective for bryophytes of highly populated soil plots. Photo from CDC, through public domain.

Figure 21. ***Pectobacterium carotovorum*** on lettuce; some species of ***Pectobacterium*** are selective for bryophytes of highly populated soil plots. Photo Gerald Holmes, Strawberry Center, Cal Poly San Luis Obispo, through Creative Commons.

Figure 22. ***Trachycystis microphylla***; ***Serratia proteamaculans*** occurred exclusively on this moss species in a Japanese study. Photo by Harum Koh, through Creative Commons.

Scheirer and Dolan (1983) found an unidentified bacterium, similar to ***Agrobacterium*** (**Pseudomonadota**; Figure 23), on both surfaces of ***Polytrichum commune*** (Figure 24) leaves. The terminal cells of the moss lamellae act like a pseudoepidermis (Figure 25), providing a microhabitat suitable for the bacteria and other microorganisms. The bacteria did not occur in the cell interiors.

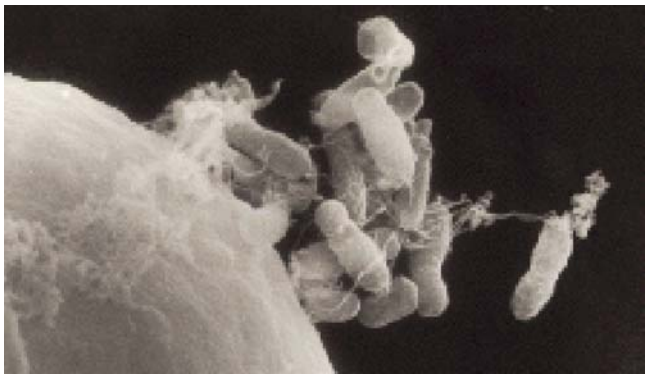

Figure 23. ***Agrobacterium tumefaciens***; an unidentified bacterium similar to ***Agrobacterium***, occurs on both surfaces of ***Polytrichum commune*** leaves. Photo through Creative Commons.

Figure 24. ***Polytrichum commune***; an unidentified bacterium similar to ***Agrobacterium*** occurs on both surfaces of leaves of this moss. Photo by Bob Klips, with permission.

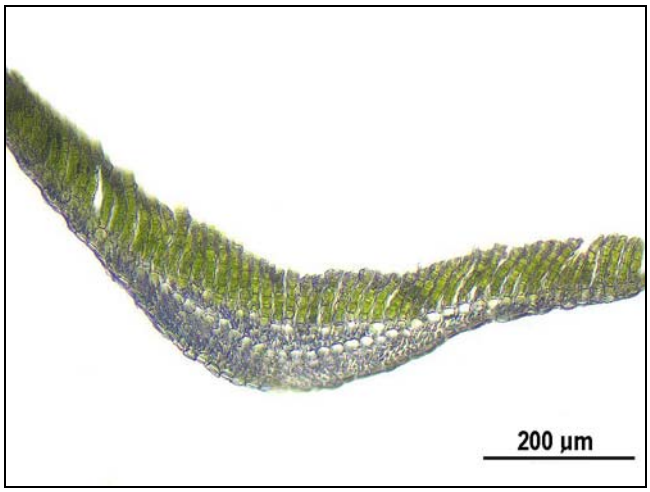

Figure 25. ***Polytrichum commune*** leaf section showing lamellae that act like an epidermis. Photo by Kristian Peters, through Creative Commons.

Tang *et al*. (2016) again noted that our understanding of the relationships of the abundant bacteria on bryophyte hosts is largely lacking. They analyzed the bacterial community associated with ten liverwort and ten moss host species in Tibet, China. They found no obvious differences in bacterial richness between mosses and liverworts. Nevertheless, the diversity was significantly higher with liverworts than with mosses. The bacteria that were most constantly present were members of the phyla **Acidobacteriota**, **Actinomycetota**, **Armatimonadota**, **Bacteroidota**, **Planctomycetota**, and **Pseudomonadota**. Those in the phyla **Chloroflexota**, **Fibrobacterota**, **Gemmatimonadota**, and **Chlamydiota** appeared among only some of the bryophytes. The most constant genera among the bryophytes were ***Burkholderia*** (**Pseudomonadota**; Figure 3), ***Frankia*** (**Actinomycetota**; Figure 26), ***Frondihatitans***, ***Granulicella*** (**Acidobacteriota**), ***Hafnia*** (Figure 4), ***Haliangium*** (**Pseudomonadota**; Figure 27), ***Mucilaginibacter*** (**Bacteroidota**), ***Novosphingobium*** (**Pseudomonadota**; Figure 28), ***Rhizobacter*** (**Pseudomonadota**), and ***Sorangium*** (**Pseudomonadota**). Eleven of the bacteria couldn't be classified, suggesting that there may be many new bacteria to be identified among the bryophytes. Tang and coworkers concluded that the phylogeny of hosts has a strong influence on the associated bacterial community and that niche also plays an important role when the hosts are phylogenetically more similar.

Figure 26. ***Frankia alni*** nodules on ***Alnus glutinosa*** roots; members of ***Frankia*** are among the most common genera on bryophytes in Tibet. Photo by Cwmhiraeth, through Creative Commons.

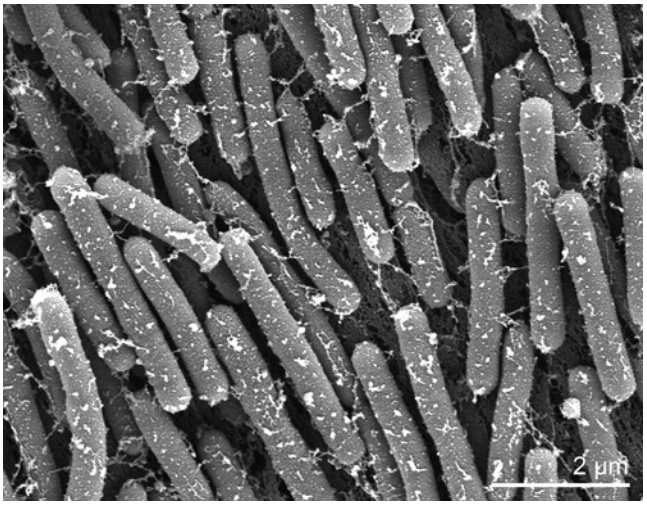

Figure 27. ***Haliangium ochraceum***, in one of the most common genera of bacteria among bryophytes in Tibet. Photo by Manfred Rohde, through Creative Commons.

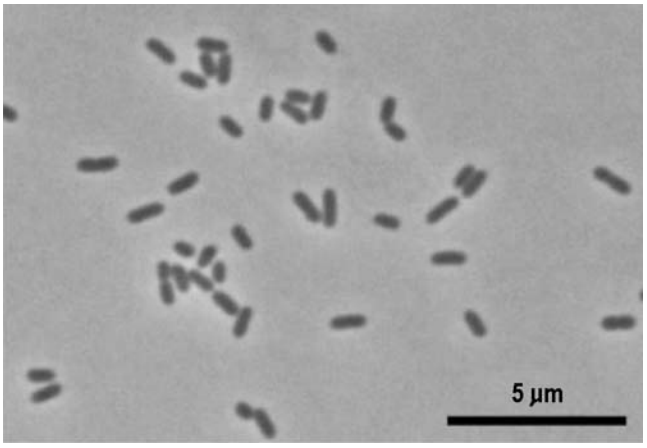

Figure 28. ***Novosphingobium***, one of the most constant genera among bryophytes in Tibet. Photo by Nierychlo *et al.*, through Creative Commons.

Schauer and Kutschera (2013) concluded that some methylobacteria (Figure 6) prefer to colonize bryophytes. ***Methylobacterium funariae*** (see Figure 6) was described as a new species from ***Funaria hygrometrica*** (Figure 29). Further evidence suggests that ***Methylobacterium*** species (Figure 6) prefer gametophytes (1*n* tissues), including liverwort and moss protonemata and fern prothalli. They appear to be symbionts, a relationship already known for some species of the genus living on tracheophyte leaves, where they consume the methanol emitted from stomatal pores and supply growth-promoting phytohormones.

Figure 29. ***Funaria hygrometrica***, substrate from which ***Methylobacterium funariae*** was described as a new species. Photo by James K. Lindsey, through Creative Commons.

Tani and Sahin (2013) named two new species ***Methylobacterium haplocladii*** (see Figure 6) and ***Methylobacterium brachythecii*** (see Figure 6) from bryophytes. These pink bacteria were isolated from ***Haplocladium microphyllum*** (Figure 30) and ***Brachythecium plumosum*** (Figure 31), respectively.

Figure 30. ***Haplocladium microphyllum***, a species where a new species of ***Methylobacterium*** (***M. haplocladii***) was discovered. Photo by Bob Klips, with permission.

Figure 31. ***Brachythecium plumosum*** with capsules, a species where a new species of ***Methylobacterium*** (***M. brachythecii***) were discovered. Photo by Hermann Schachner, through Creative Commons.

Saumya *et al*. (2019) added to our knowledge by examining the bacterial flora of the mosses ***Anoectangium clarum*** (see Figure 32), ***Atrichum undulatum*** (Figure 33), and ***Hyophila involuta*** (Figure 34) on Mount Abu in India. Like the study by Koua *et al*. (2015) in Japan, they found the bacteria to belong mostly to the family **Methylobacteriaceae** and phylum **Bacillota**, with **γ-Proteobacteria** predominating. Genera that are most common in the various habitats of soil, near water, and on rocks are ***Aeromonas*** (**Pseudomonadota**; Figure 35), ***Halobacillus*** (**Bacillota**), ***Pseudomonas*** (**Pseudomonadota**; Figure 10), and ***Raoultella*** (Figure 36).

Figure 32. ***Anoectangium compactum***; ***Anoectangium clarum*** in India supports mostly **Pseudomonadota** and **Bacillota**. Photo by Jan-Peter Frahm, with permission.

Figure 33. ***Atrichum undulatum*** in India supports mostly **Pseudomonadota** and **Bacillota**. Photo by Hermann Schachner, through Creative Commons.

Figure 34. ***Hyophila involuta*** in India supports mostly **Pseudomonadota** and **Bacillota**. Photo by Bob Klips, with permission.

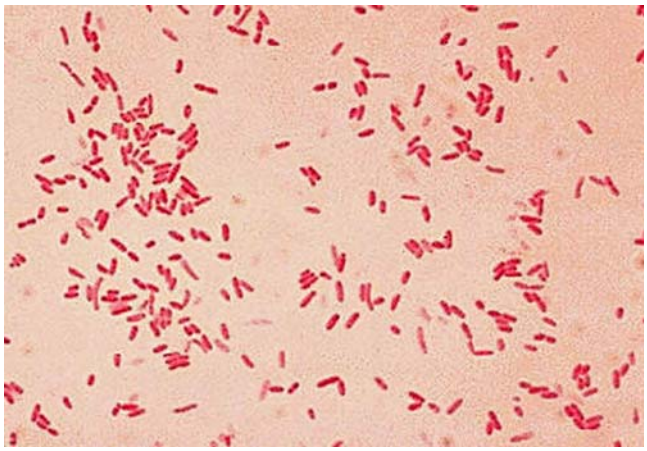

Figure 35. ***Aeromonas hydrophila***, in one of most common bacterial genera on bryophytes in the various habitats of soil, near water, and on rocks in Japan. Photo by W. A. Clark, CDC, through public domain.

Alcaraz *et al*. (2018) noted that microbiomes influence plant establishment, development, nutrient acquisition, pathogen defense, and health. They compared the microbiomes of ***Marchantia polymorpha*** (Figure 37) and ***Marchantia paleacea*** (Figure 38) to the microbiomes on their soil substrates and to plants grown from gemmae collected in the same populations of ***Marchantia***. They identified ***Bryobacter*** (**Acidobacteriota**; Figure 39), ***Lysobacter*** (**Pseudomonadota**; Figure 40), ***Methylobacterium*** (Figure 6), ***Paenibacillus*** (**Bacillota**; Figure 41), ***Pirellula*** (**Planctomycetes**), ***Rhizobium*** (**Pseudomonadota**; Figure 42), and ***Steroidobacter*** (**Pseudomonadota**; Figure 43) associated with the ***Marchantia***, genera that contribute to plant-growth promotion, complex exudate degradation, nitrogen fixation, methanol conversion, and disease suppression. They suggested that these ***Marchantia*** species could be used as surrogates for testing the roles of bacteria in plants.

Figure 36. ***Raoultella planticola*** culture, in one of most common bacterial genera on bryophytes in the various habitats of soil, near water, and on rocks in Japan. Photo by A. Doubt, through Creative Commons.

Figure 37. ***Marchantia polymorpha*** with gemmae, a species that is host to bacteria that contribute to plant growth promotion, complex exudate degradation, nitrogen fixation, methanol conversion, and disease suppression. Photo by Holger Casselmann, through Creative Commons.

Figure 38. ***Marchantia paleacea***, a species that is host to bacteria that contribute to plant growth promotion, complex exudate degradation, nitrogen fixation, methanol conversion, and disease suppression. Photo by Naufal Urfi Dhiyaulhaq, through Creative Commons.

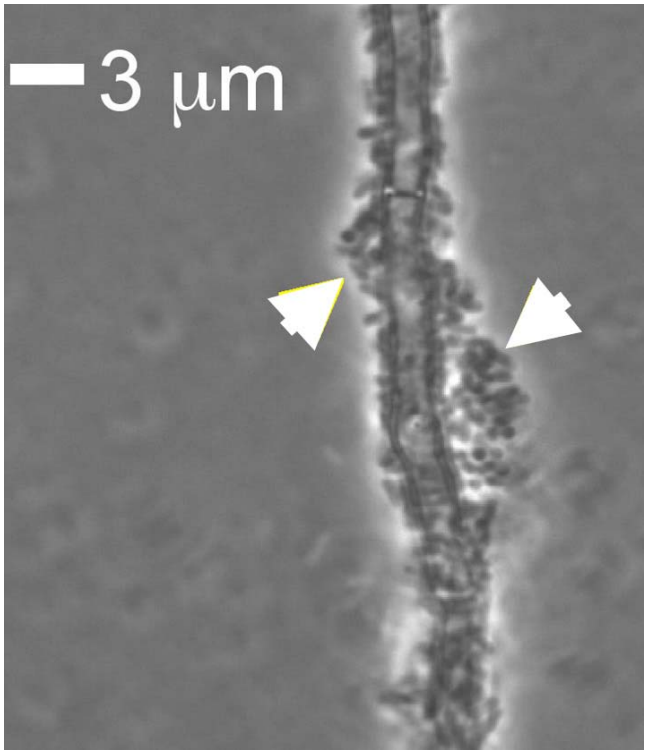

Figure 40. ***Lysobacter***, a genus that contributes to plant-growth promotion, complex exudate degradation, nitrogen fixation, methanol conversion, and disease suppression in species of ***Marchantia***. Photo through Creative Commons.

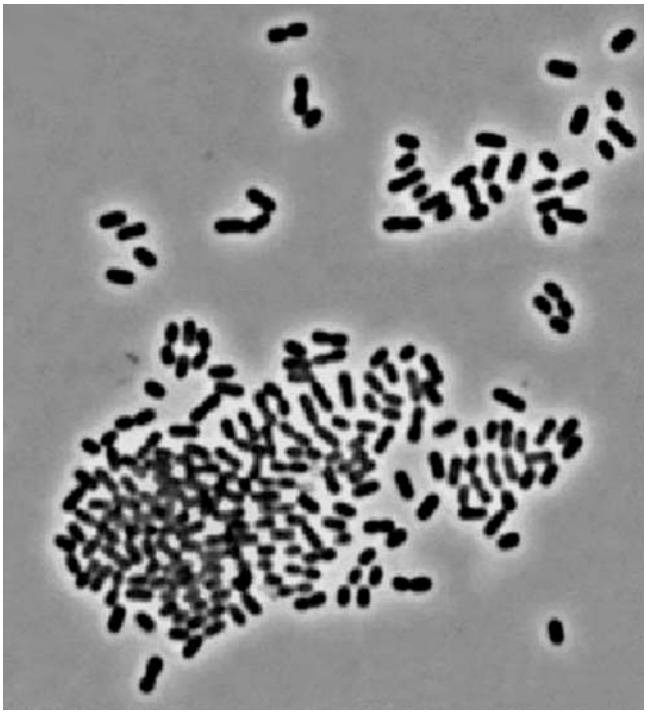

Figure 39. ***Bryobacter aggregatus***, in a genus that contributes to plant growth promotion, complex exudate degradation, nitrogen fixation, methanol conversion, and disease suppression in species of ***Marchantia***. Photo courtesy of the U.S. National Library of Medicine.

Figure 41. ***Paenibacillus dendritiformis***, in a genus that contributes to plant growth promotion, complex exudate degradation, nitrogen fixation, methanol conversion, and disease suppression in species of ***Marchantia***. Photo by Eshel Ben-Jacob, through Creative Commons.

Figure 42. ***Rhizobium*** nodules attached to roots of ***Vigna unguiculata*** (cowpea). ***Rhizobium*** species contribute to plant growth promotion, complex exudate degradation, nitrogen fixation, methanol conversion, and disease suppression in species of ***Marchantia***. Photo by stdout, through Creative Commons.

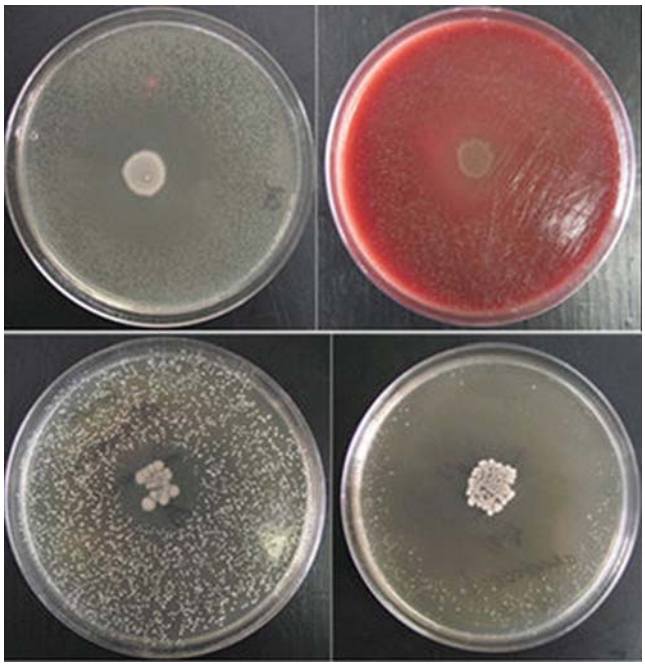

Figure 43. ***Steroidobacter denitrificans*** growth inhibition zones on various media; members of this genus contribute to plant growth promotion, complex exudate degradation, nitrogen fixation, methanol conversion, and disease suppression in species of ***Marchantia***. Photo through Creative Commons.

Marks *et al*. (2018) compared the bacterial community of ***Marchantia inflexa*** (Figure 44-Figure 45) between sexes and among habitats. Using common garden conditions, they found that the bacterial community associated with the liverwort is abundant and diverse. The particular taxonomic assemblages of bacteria may serve functional roles that allow the liverworts to better acclimate to their local environment. Furthermore, the differences in communities on the two sexes of the plants may contribute to subtle differences in their physiology and form.

Figure 44. ***Marchantia inflexa***, a species that benefits from bacteria to improve acclimation to the local environment and may depend on them to create subtle differences in physiology and form between the sexes. Photo by Scott Zona, through Creative Commons.

Figure 45. ***Marchantia inflexa*** plants expressing female characters. Photo by Alan R. Franck, through Creative Commons.

Aschenbrenner *et al*. (2017) compared communities associated with different substrata of bark, mosses, and lichens in Austria and revealed significant differences in community structures. The lichen microbial communities are less complex and less densely interconnected than the moss- and bark-associated communities. Generalists were mostly **Pseudomonadota**, with ***Sphingomonas*** (Figure 46) being the most abundant genus. The researchers suggested that the generalists benefitted each other and the community by maintaining a pool of species that were available to colonize new plants where they provided nitrogen fixation and other supporting functions. This sharing of hosts lends stability to the microbial community.

Figure 46. ***Sphingomonas phyllosphaerae***, member of a generalist bacterial genus that can occur on bryophytes. Photo by Alan Rockefeller, through Creative Commons.

Tian and Li (2017) similarly found **Pseudomonadota** and **Bacteroidota** to be the most dominant phyla in their study of the mosses ***Entodon compressus*** (matrix under tree; Figure 47), ***Grimmia montana*** (exposed rock surface; Figure 48), and ***Hygroamblystegium noterophilum*** (stream bank; Figure 49) at the Beijing Songshan National Nature Reserve, China. The greatest species richness occurred on ***Entodon compressus***, followed by ***Grimmia montana*** and ***Hygroamblystegium noterophilum***, based on 16s rDNA libraries. On the other hand, the 16s rRNA libraries indicated that richness was of the order 73, 18, and 45, respectively. The **Pseudomonadota** comprised 33.7-86.1% of the communities and **Bacteroidota** 8.4-54.9% as the dominant phyla regardless of moss species. Nevertheless, the ratio and composition of the groups varied widely.

Figure 47. ***Entodon compressus***, a species with the greatest bacterial richness in a Chinese study, with **Pseudomonadota** and **Bacteroidota** being the most dominant phyla. Photo by Martin Hutten, with permission.

Figure 48. ***Grimmia montana***, a species with high bacterial richness in a Chinese study, with **Pseudomonadota** and **Bacteroidota** being the most dominant phyla. Photo by Des Callaghan, through Creative Commons.

Figure 49. ***Hygroamblystegium noterophilum***, a species with less bacterial richness than ***Entodon compressus*** or ***Grimmia montana*** in a Chinese study, with **Pseudomonadota** and **Bacteroidota** being the most dominant phyla. Photo by Jean Faubert, with permission.

Actinomycetota and **Acidobacteriota** were abundant on ***Entodon compressus*** (Figure 47) (Tian & Li 2017). This moss supported a community of ***Sphingomonas*** (Figure 46), ***Pseudonocardia*** (**Actinomycetota**; Figure 50), ***Bryobacter*** (**Acidobacteriota**; Figure 39), ***Flavisolibacter*** (**Bacteroidota**), ***Acidiphilium*** (**Pseudomonadota**), and ***Roseateles*** (**Pseudomonadota**). ***Sphingomonas*** is tolerant of low temperatures and produces growth-promoting substances. ***Pseudonocardia*** has antibacterial activity. ***Acidiphilium*** is able to solubilize rock phosphates. ***Roseateles*** can degrade aliphatic and aliphatic-aromatic co-polyesters. The researchers speculated that this bacterial community might be important in community dynamics in the organic matter associated with the ***Entodon compressus***. Associated with ***Grimmia montana*** (Figure 48) they found ***Rheinheimera*** (**Pseudomonadota**; Figure 51), a genus that might be useful for the growth of this species on exposed rock with very little matrix by inhibiting the production of other microbes. This genus occurred in multiple locations and has antibiotic properties that might inhibit other bacteria.

Figure 50. ***Pseudonocardia*** on ***Acromyrmex*** worker, a bacterium cultured by the ant to protect fungus farms. This bacterium occurs on the moss ***Entodon compressus***. Photo by João Pedro Sá Medeiros, through Creative Commons.

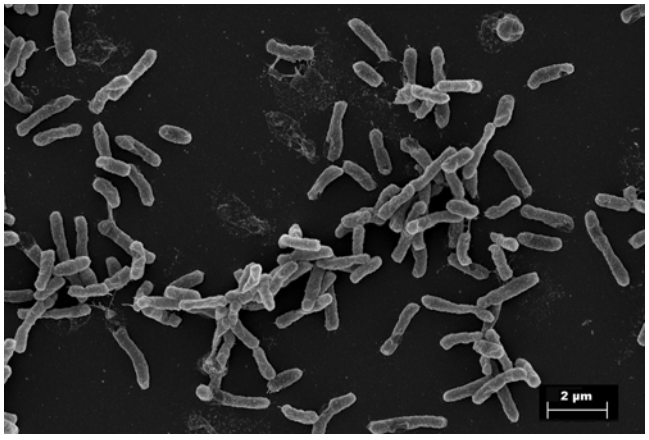

Figure 51. ***Rheinheimera baltica*** SEM; some members of this genus grow in association with ***Grimmia montana*** on bare rocks, where they are suspected of enhancing the moss growth by inhibiting other microbes. Photo by Manfred Rohde, through Creative Commons.

Saha *et al*. (2021) investigated the bacteria associated with the moss ***Plagiomnium rostratum*** (Figure 52). They found that the predominant bacterial species were members of the families **Bacillaceae (Bacillota**), **Enterobacteriaceae** (**Pseudomonadota**; Figure 14), **Lactobacillaceae** (**Bacillota**), **Moraxellaceae** (**Pseudomonadota**), and **Pseudomonadaceae** (**Pseudomonadota**). Many of the bacteria isolated were able to solubilize phosphates and scavenge nitrogen efficiently, as well as degrade starch, cellulose, and casein. They found that variation in the bacterial association was significantly correlated with total carbohydrate and phosphorus contents of the moss gametophytes.

Figure 52. ***Plagiomnium rostratum***, a moss colonized mostly by members of the **Bacillota** and **Pseudomonadota**. Photo by Hermann Schachner, through Creative Commons.

Effects on Bryophytes

The relationships between bacteria and bryophytes has been almost totally neglected (Jessica M. Nelson, Bryonet 22 April 2021). Recently a few researchers have begun to uncover exciting roles that these might play in the physiology of bryophytes. In sharp contrast, we are now learning about exciting interactions between these two groups of organisms.

Carella and Schornack (2018) described the relationship between bacteria and bryophytes as an association "with a strong and directed effort [by bacteria] to reprogram host cells [of bryophytes] in order to permit, promote and sustain microbial growth. In response to colonization, hosts accommodate or sequester invading microbes by activating a set of complex regulatory programs that initiate symbioses or bolster defenses."

Alvarez *et al.* (2016) found that the level of expression of antibacterial genes by the mosses were dependent on the developmental stage of the mosses. There was greater expression by the gametophore tissue than by the protonema tissue. Could these relate to habitat conditions at the time of development? Or is there an energy limitation on the protonema? Production of secondary compounds used for defense requires resources that compete with resources needed for growth and reproduction. Therefore, there is most likely a tradeoff, with the bryophyte optimizing its production of secondary compounds by producing them when they are needed most for the continuation of the species. On the other hand, having bacteria that produce defenses against the pathogenic bacteria in the association would be an important savings of resources.

Symbiosis

There is limited direct evidence of symbiotic relationships between bryophytes and bacteria. The evidence that exists suggests that this is an area that warrants our attention. At the very least, the relationship does not seem to be neutral, with cases of protocooperation, commensalism, and antagonism, as well as symbiosis.

Nitrogen Fixation

The nitrogen-fixing bacterial genus ***Bradyrhizobium*** (**Pseudomonadota**; Figure 1, Figure 53) forms a symbiotic connection with the adventitious roots of its host, ***Acacia koa*** (Figure 54) in Hawai'ian mesic forests. Leary *et al.* (2004) discovered that when these symbioses occur in mosses growing in the canopy, they form more and larger nodules than when associated with roots in soil.

Figure 53. ***Bradyrhizobium*** nodules with moss on ***Acacia koa***. Photo courtesy of James Leary.

Figure 54. ***Acacia koa***, a tree that benefits from mosses associated with its nitrogen-fixing ***Bradyrhizobium*** nodules. Photo by Forest and Kim Starr, through Creative Commons.

Methylobacteria

The **methylobacteria** are a group of bacteria that are able to use methanol as their sole source of carbon and energy (Corpe & Basile 1982). They have been isolated from the surfaces of bryophytes. There is evidence that these pink, facultative methylotrophs are beneficial to the plants on which they grow. Evidence suggests this includes bryophytes.

Alcalde *et al.* (1996) demonstrated a little-known interaction between the moss ***Bartramia*** (Figure 55) and the genus ***Methylobacterium*** (Figure 6) in Spain, a relationship discussed elsewhere in this chapter for peatland habitats. Bryophytes and tracheophytes have pectin in their cells walls, causing them to emit methanol. The pink-pigmented ***Methylobacterium*** (Figure 6) species are able to colonize leaf surfaces and use the methanol as their only source of carbon and energy (see also Raghoebarsing *et al.* 2005; Liu *et al.* 2014).

Kutschera (2007) found that the tracheophytes failed to respond to the relationship. However, development of both the mosses and liverworts in the study was affected. Organ development in moss protonemata and in liverwort thalli was "considerably" enhanced. ***Methylobacterium*** secretes both cytokinins and auxins that can initiate or control developmental stages. This seems only to affect haploid stages (gametophytes) and the interaction has been lost in tracheophytes that are apparently able to sufficiently produce and control their own growth hormones.

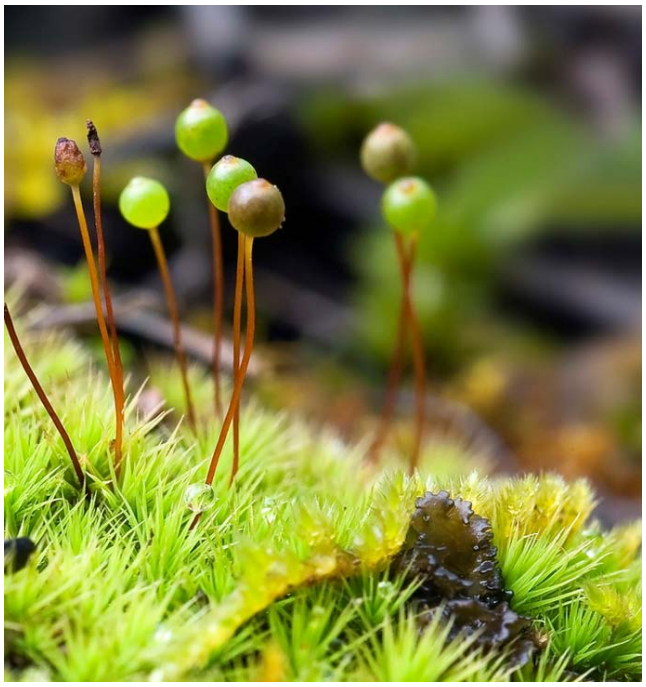

Figure 55. ***Bartramia stricta*** with capsules; a species of ***Methylobacterium*** in Spain uses methanol as its only source of carbon and energy. This is emitted by the moss and provides needed carbon for the ***Methylobacterium***, which in turn releases CO_2 used by the moss. Photo by John Game, through Creative Commons.

In bryophytes, ***Methylobacterium*** (Figure 6) enhances cell growth (Kutschera *et al.* 2007). Bacteria isolated from the upper surface of the thalli of ***Marchantia polymorpha*** (Figure 37) proved to be an undescribed species of ***Methylobacterium***, now known as ***Methylobacterium marchantiae*** (Schauer *et al.* 2011; see Figure 6). This bacterium stimulates the surface expansion of isolated gemmae (Figure 37, Figure 56) from ***M. polymorpha*** by about 350% (Kutschera *et al.* 2007)! In water suspension, the ***Methylobacterium marchantiae*** from the liverwort forms dense clusters of up to 600 cells. But when ***Methylobacterium mesophilicum***, a tracheophyte associate, is cultured in water, only single cells are formed. Kutschera and coworkers suggested that the clusters on the liverwort inhabitant were an adaptation to surviving on the liverwort when it underwent desiccation in its natural habitat.

Figure 56. ***Marchantia polymorpha*** gemma. The bacterium ***Methylobacterium marchantiae*** stimulates the surface expansion of such isolated gemmae. Photo by Des Callaghan, through Creative Commons.

Kutschera and Koopmann (2005) discovered that the thallose liverworts ***Marchantia polymorpha*** (Figure 37) and ***Lunularia cruciata*** (Figure 57) serve as host plants for the genus ***Methylobacterium*** (Figure 6) that secretes phytohormones on the surfaces of the thalli. These hormones promote the growth of isolated gemmae (Figure 56) on agar and appear to be a necessary component for the completion of the life cycle. When bryophytes first evolved, it appears that they depended on external sources such as bacteria for critical factors in their life cycles. They spent their evolutionary capital developing numerous secondary compounds so that they could survive the bacteria fungi, protozoa, and herbivores that threatened their existence.

Figure 57. ***Lunularia cruciata*** showing gemmae that respond to hormones secreted by ***Methylobacterium***. Photo by Hermann Schachner, through Creative Commons.

Tian and Li (2017) identified the dominant methylamine-utilizing bacteria from ***Hygroamblystegium noterophilum*** (Figure 49) as ***Methylotenera***, ***Methyloversatilis***, and ***Tepidimonas***. These genera contribute primarily to denitrification and methanol metabolism.

Hornschuh *et al*. (2002) found that bacteria were numerous on the leaf surfaces of moss ***Funaria hygrometrica*** (Figure 29). In particular, they occurred in the grooves between adjacent lamina cells (Figure 58). Isolated strains of ***Methylobacterium mesophilicum*** (see Figure 6) and ***Methylobacterium*** sp. elicited the same response as cytokinin application on protonemal bud formation (Figure 59) and promoted growth of the protonemal filaments. This suggests that these bacteria have an important role in the development of ***Funaria hygrometrica***.

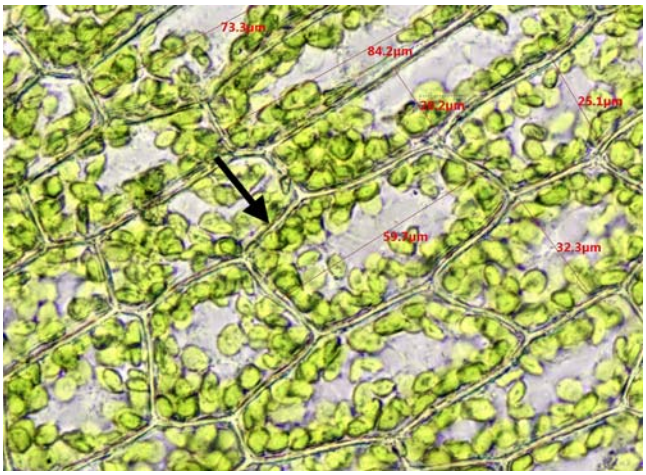

Figure 58. ***Funaria hygrometrica*** leaf cells; **arrow** indicates groove between two adjacent lamina cells where bacteria often grow. Photo by Claire Halpin, with permission.

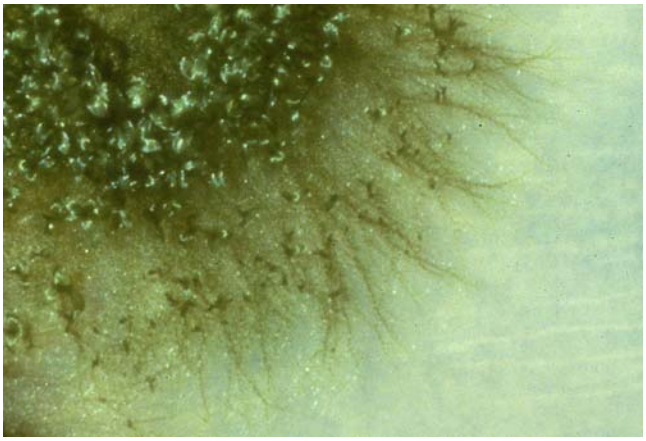

Figure 59. ***Funaria hygrometrica*** cultures with young gametophores and gametophore buds near the ends of the protonemata. ***Methylobacterium*** elicits a cytokinin type of response in the growth and bud formation of the protonema. Photo by Janice Glime.

Schauer and Kutschera (2011) further investigated the bacterium now known as ***Methylobacterium funariae*** (see Figure 6) isolated from ***Funaria hygrometrica*** (Figure 29). These bacteria provide cytokinins and auxins to the moss associates. In the association, methanol is emitted by the mosses and used by the bacteria as their carbon source. Schauer and Kutschera suggested that amino acids leached from the bryophytes might be important as sources of carbon and nitrogen for the bacteria.

CO_2 Source

One of the first considerations regarding bryophyte interactions with bacteria was that bacteria provide a source

of CO_2 for the bryophytes, particularly in aquatic habitats. Wetzel *et al*. (1985) noted that algae and aquatic plants are rapidly limited by low availability of CO_2 even at low *p*H in the range of 4-6. They found that 25-40% of the carbon fixed by leaves can originate from the sediments. When more CO_2 becomes available in the rhizosphere sediments, the reliance on CO_2 diminishes.

In the remote location of Antarctica, Tarnawski *et al*. (1992) noticed differences in growth of the moss ***Schistidium chrysoneurum*** (Figure 60). This moss grows as turf in wet locations and as cushions at relatively dry sites. Tarnawski and coworkers discovered that the CO_2 concentrations within these two communities differed "substantially." At the beginning of the growing season, both communities had the same CO_2 concentrations of about 350 ppm. But in the turf, the CO_2 levels rose tenfold during the growing season while those in the cushions changed little. This provided ideal growing conditions in the turf. The researchers attributed the higher CO_2 levels to respiration of rhizoids and heterotrophic communities, including the bacterial component.

Figure 60. ***Schistidium chrysoneurum*** in Antarctica, a species that benefits from the CO_2 produced by bacteria. Photo by Sharon Robinson, with permission.

In another example a surprisingly large colony of ***Fontinalis*** *cf*. ***novae-angliae*** (Figure 61-Figure 62) was discovered on the floor of Yellowstone Lake, a 119-m-deep lake in Yellowstone National Park, USA, at 2,357 m asl (Lovalvo *et al*. 2010). Due to its elevation and location, the lake averages a temperature of 5ºC. We would expect that the attenuation of light and the cold temperatures at that depth would discourage the growth of any photosynthetic organism other than some highly adapted algae. In the lake, the mosses were associated with geothermal vents where the water was supersaturated with CO_2. This situation illustrates the ability of high CO_2 levels to enhance photosynthesis in otherwise limiting conditions. Thus, we should look for aquatic mosses at depths where heterotrophic bacteria benefit from organic sediments and release respiratory CO_2 that is available to the aquatic bryophytes.

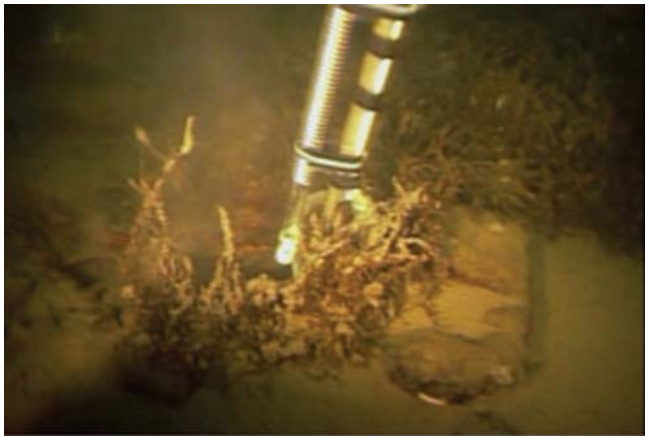

Figure 61. ***Fontinalis*** *cf*. ***novae-angliae*** from Yellowstone Lake geothermal vent, where bacterial respiration most likely contributes to its needed CO_2. Photo from Lovalvo *et al*. 2010.

Figure 62. ***Fontinalis novae-angliae*** habitat in a stream; bacteria associated with the moss most likely contribute CO_2 for photosynthesis by the moss. Photo by Janice Glime.

Gimeno *et al*. (2017) suggested that bacterial partners could contribute to carbonyl sulphide production (COS) in bryophytes. Uptake of COS, a surrogate for measuring photosynthesis, could be significant in bryophyte cells at night, as suggested by their experiments, because bryophytes are able to take in COS in the dark, using the light-independent carbonic anhydrase, not relying on light to open stomata as is the case for tracheophytes. Carbonyl sulfide is an intermediate between carbon dioxide and carbon disulfide (Wikipedia 2022). With sufficient humidity or water in association with bases, carbonyl sulfide decomposes to carbon dioxide and hydrogen sulfide. Could this help to account for the bryophytes that occur in highly alkaline waters? It is unclear if the bryophytes can benefit the bacteria at night, but in the daytime they could provide O_2.

Growth Hormones

One of the important discoveries in the bryophyte-bacteria relationship is that bacteria can provide hormones that are necessary for the development of bryophytes through the life cycle. Researchers have discovered that optimal growth conditions, including development and reproduction, often require interactions with

microorganisms in a parasitic, mutualistic, or protocooperative relationship (Spiess *et al*. 1984a, 2019).

Bud Induction

I suspected such a relationship between bacteria and protonemal development in the 1980's when I cultured ***Fontinalis squamosa*** (Figure 63-Figure 64) from spores (Glime & Knoop 1986). I cultured these in the lab of Martin Bopp in Germany and had to abandon them to return to my responsibilities in the USA. My colleague, Bernd Knoop, continued to watch the cultures until they became contaminated, at which time they were discarded. But he reported to me that the only buds (see Figure 65) on my cultures were on the contaminated cultures. That suggested to me that my sterile cultures needed something that was produced by partner organisms in nature. Ares *et al*. likewise concluded that the developmental differences between the axenic cultures of ***Fontinalis antipyretica*** (Figure 66) and those contaminated with bacteria (or fungi) were likely to be due to interaction with the contaminants.

Figure 63. ***Fontinalis squamosa*** in stream at Cwm Idwal National Nature Reserve, Wales. This species seems to require bacterial hormones to complete its development. Photo by Janice Glime.

Figure 64. ***Fontinalis squamosa*** protonema; this species seems to need hormones from bacteria to advance to the bud stage. Photo by Janice Glime.

Figure 65. Moss protonema with young bud. Development of this stage often seems to require hormones from bacteria. Photo by Chris Lobban, with permission.

Figure 66. ***Fontinalis antipyretica***, a species that seems to gain developmental benefits from microbes. Photo by Misha Ignatov, with permission.

As we now have observed in many other axenic cultures of bryophytes, the protonemata of ***Hyophila involuta*** (Figure 34) failed to produce buds on basal Knop's + Nitsch's minor salts (Rahbar & Chopra 1982). Furthermore, addition of auxins, gibberellic acid, abscisic acid, chelates, vitamin B_{12}, activated charcoal, coconut milk, and altered hydration, *p*H, temperature, light intensity and duration all failed to stimulate bud formation. Cytokinins could initiate multicellular gemmae on the protonemata, but failed to initiate buds. Only the interaction of IAA with either kinetin or DMAAP stimulated formation of buds and normal gametophore development. Such observations suggest that in nature some exogenous source, perhaps from bacteria or fungi, contributes the hormones necessary to initiate the next developmental stage.

Reutter *et al.* (1998) found that application of cytokinins to ***Physcomitrium patens*** (syn. = ***Physcomitrella patens***; Figure 67) cultures enhances bud formation but fails to stimulate the subsequent gametophore development. Most of the cytokinin and auxin occur in extracellular pools and appear to be involved in hormone transport in mosses. Gonneau *et al*. (2001)

further demonstrated that development in ***Physcomitrium patens*** is regulated by environmental signals and hormones. Cytokinins are required to give rise to the leafy gametophore, but it appears to be regulated to different concentrations in the bud stage compared to elongation of the gametophore.

Figure 67. ***Physcomitrium patens***; AHLs from bacteria promote spore germination in this moss. Photo by Hugues Tinguy, with permission.

My suspicion of bacterial hormone contributions was influenced by the early research of Luretta Spiess and her coworkers. They were able to demonstrate that the bacterium ***Agrobacterium tumefaciens*** (Figure 68) influenced the development of the epiphytic moss ***Pylaisiella selwynii*** (Figure 69), including initiation of gametophore buds more quickly (Spiess *et al*. 1971). After 35 days, mosses cultured axenically exhibited only 0-24% gametophore formation, whereas those inoculated with ***A. tumefaciens*** had at least 96% gametophore formation. Bacterial-assisted cultures also produced 4-6 gametophores per culture, compared to 1 in the absence of the bacteria. The supernatant from the cultures did not cause any changes in bud production.

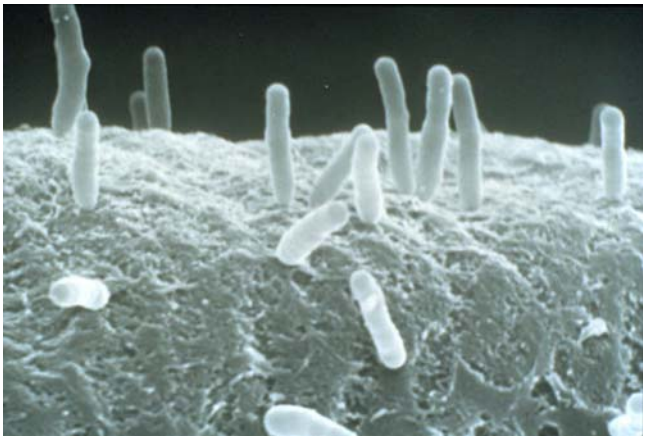

Figure 68. ***Agrobacterium tumefaciens***, a species that provides hormones needed for the development of ***Pylaisiella selwynii***. Photo by Martha Hawes, University of Arizona through NSF public domain.

Figure 69. ***Pylaisiella selwynii***, a moss that has a hormonal benefit from the bacterium ***Agrobacterium tumefaciens***. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Spiess *et al*. (1972) explored the possible influence of bacteria by testing the effects of various hormones on ***Pylaisiella selwynii*** (Figure 69). They found that indoleacetic acid (IAA) and ethrel increased bud formation at a narrow concentration range. But bud formation responded well at various concentrations of cytokinins. Nevertheless, the cytokinin-induced buds failed to develop into normal gametophores. This is not surprising because Bopp and Jacob (1986) later found that in the moss ***Funaria hygrometrica*** (Figure 29) the concentration of cytokinin that effects branching of caulonemata requires pico-molar concentrations, whereas bud formation requires micro-molar concentrations.

More encouraging for Spiess *et al*. (1972) was the fact that octopine, lysopine, and octopinic acid from crown-gall tumors increased ***Pylaisiella selwynii*** (Figure 69) bud formation at 10^{-3} M. In particular, lysopine stimulated the formation of buds that developed into typical gametophores. However, octopine initiated the formation of gemma-like structures, but no gametophores. Culturing with l-arginine from octopine and l-lysine from lysopine failed to induce gametophore formation. γ-guanidinobutyric acid induced bud formation at 10^{-3} M concentrations; the buds produced highly abnormal gametophores. Reminiscent of the ineffectual influence of the supernatant, Spiess *et al*. (1976) found that physical contact was necessary for the bacteria to be effective in production of gametophores.

Whatley and Spiess (1977) demonstrated that LPS (lipopolysaccharide) from ***Agrobacterium tumefaciens*** (**Pseudomonadota**; Figure 68) inhibited gametophore development by preventing the bacterium from binding, providing further evidence that direct contact was needed between the moss and the bacterium. This effect is apparently only effective for a short time; if the LPS was added 24 hours after the addition of the bacterial cells, it had no effect in reducing the development of the gametophore.

Protonemal growth of ***Pylaisiella selwynii*** (Figure 69) was slightly accelerated by cAMP (Spiess 1979). IAA (10^{-6} M) alone, or with cAMP, inhibited protonemal elongation but when added at 10^{-12} M it increased filament growth, demonstrating the importance of the concentration. When adenosine and guanosine were added together (depending on the ratio), they caused a marked increase in rapidly elongating normal gametophores.

After ten years of study with ***Agrobacterium*** (Figure 68), Spiess *et al*. (1981a) still could not assign the bacterial isolates from three other species of mosses and ***Pylaisiella selwynii*** (Figure 69) from another location to the genus ***Agrobacterium***. Many of these isolates elicited developmental changes in the protonemata of ***Pylaisiella selwynii*** (Figure 69) that were similar to those of the ***Agrobacterium***. In any case, it was becoming clear that in nature bacteria can influence the developmental stages of mosses.

Spiess *et al*. (1981b) again pursued the effects of octopine and cytokinin on the growth and gametophore formation of ***Pylaisiella selwynii*** (Figure 69). Octopine is an unusual amino acid, but it occurs in crown gall tumors. In combination with cytokinin it increased the number of gametophores and decreased the time required for them to develop. This effect was similar to that seen with ***Agrobacterium*** (Figure 68) in ***Pylaisiella selwynii*** cultures. But concentration was important. More common amino acids alone or in combination with auxins or cytokinins generally had a neutral effect on the moss development.

There is an interesting inhibitory action by the cell walls of ***Pylaisiella selwynii*** (Figure 69). Cell walls of several dicots, but not of tested monocots, inhibited the induction of buds and gametophore development by ***Agrobacterium tumefaciens*** (Figure 68) (Spiess *et al*. 1984b). Both pectin and polygalacturonate were inhibitory. Protonemal cell walls inhibited gametophore induction; gametophores were less inhibitory. But cell walls from the moss ***Polytrichum commune*** (Figure 24) protonema and gametophores caused little inhibition. On the other hand, ***Agrobacterium*** is ineffective in increasing bud formation in ***Polytrichum commune***. If the ***Polytrichum*** protonemata or gametophore cell walls are treated with pectinesterase, they do inhibit the developmental stimulation of ***Agrobacterium*** on ***Pylaisiella selwynii*** and pectinesterase increases the inhibitory effect by ***Pylaisiella*** gametophore cell walls. Conversely, pectinesterase treatment of the ***Polytrichum*** protonema makes it more sensitive to the ***Agrobacterium***, causing increased bud and gametophore formation. Spiess and coworkers reasoned that the bacteria require suitable adherence sites and that the addition of the pectinesterase made these sites available in ***Polytrichum***.

One effect of at least some bryophytes on ***Agrobacterium tumefaciens*** (Figure 68) is the ability to induce the expression of its virulence gene (Primich-Zachwieja & Minocha 1991). This was evident by the β-galactosidase activity in the bacteria.

While Spiess and coworkers were attempting to understand the relationships of bacteria with ***Pylaisiella selwynii*** (Figure 69), Chopra and Vashistha (1990) explored the effect of auxins and antiauxins on the shoot bud induction and growth form of the moss ***Bryum atrovirens*** (Figure 70). In culture, various auxins induced buds on the protonemata, whereas without these added hormones the sterile culture conditions were not conducive to bud formation. Again, concentration was important, with higher levels causing adverse effects on the morphology.

Figure 70. ***Bryum atrovirens***; various auxins induced buds on the protonemata, whereas without these added hormones buds were absent; bacteria most likely supply these auxins in nature. Photo by Jan-Peter Frahm, with permission.

The study of hormones and their effects on bryophytes has been largely confined to auxins and cytokinins (Sabovljević *et al*. 2014). Gibberellic acid (GA) has been mostly ignored, with investigations suggesting that it did not evolve its interaction with GID1-DELLA until after bryophytes diverged from other land plants (Yasumura *et al*. 2007). ABA and its sister compound lunularic acid have been studied somewhat extensively (Decker *et al*. 2006).

Chopra and Dhingra-Babbar (1984) also found that indoleacetic acid (IAA), gibberellic acid, abscisic acid, chelates, salicylic acid, and altered temperature, *p*H, agar, sucrose levels, light levels, and photoperiod do not induce buds in the moss ***Trematodon brevicalyx*** (see Figure 71). Only cytokinins elicited a bud response in sterile cultures. In fact, even at concentrations of cytokinins that induced buds, varying concentrations of IAA reduced the number of buds considerably.

Figure 71. ***Trematodon longicollis*** on a wet roadside bank; ***Trematodon brevicalyx*** requires cytokinins to induce bud formation in culture, hormones most likely supplied by bacteria in nature. Photo by Michael Lüth, with permission.

Yasumura *et al*. (2007) demonstrated a lack of GA production in ***Physcomitrium patens*** and suggested the pathway to it production arose after the bryophyte lineage. Nevertheless, gibberellic acid, a known product of bacteria (MacMillan 2002; Yamaguchi 2008) has a positive effect on morphogenesis in ***Bryum argenteum*** (Figure 72) (Sabovljević *et al.* 2010) and interferes with gravitropism in ***Ceratodon purpureus*** (Figure 73) (Chaban *et al*. 1999). Since bacteria that inhabit plants are able to produce gibberellic acid (Katznelson & Cole 1965; MacMillan 2002; Karakoç & Aksöz 2006; Zhang *et al*. 2012; Ambawade & Pathade 2015; Desai 2017), this interaction should be explored with bryophytes *in situ* and in the lab.

Figure 72. ***Bryum argenteum***, a moss species that is positively affected by gibberellic acid. In nature this is probably supplied by bacteria and other microorganisms. Photo by Tushar Wankhede, with permission.

Figure 73. ***Ceratodon purpureus***, a species in which gibberellic acid interferes with gravitropism. Photo by Janice Glime.

If mosses respond to different concentrations in different ways, how do bacterial levels coordinate the developmental stages? Do the bacteria respond to environmental signals so that protonemata branch while the bacteria are at low numbers (that would give bacteria more cover and hold moisture better), then the bryophytes develop gametophores when the bacterial numbers increase (that would ensure a large colony of mosses that can help to conserve moisture within the colony)? Do differences in developmental responses occur among bryophyte species? If so, how important are the bacteria species in determining the success of specific bryophyte species in particular habitats?

Growth

The moisture-loving leafy liverwort ***Scapania nemorea*** (Figure 74) has a regular association with the bacterium ***Pseudomonas extorquens*** (see Figure 10) (Basile *et al*. 1969). When ***S. nemorea*** gametophytes were inoculated with this bacterium in culture, they grew larger and reached reproductive maturity more quickly than those cultures without the bacteria. It is likely that this stimulus occurs in nature as well.

Figure 74. ***Scapania nemorea*** with gemmae, a species with a regular positive association with the bacterium ***Pseudomonas extorquens***. Photo by Blanka Aguero, through Creative Commons.

Tani *et al*. (2011) explored ***Racomitrium japonicum*** (Figure 75) with the intent of increasing its growth rate for culture as a green-roof plant. They isolated ***Pseudomonas*** (Figure 10), ***Rhodococcus*** (**Actinomycetota**; Figure 76), and ***Duganella*** (**Pseudomonadota**) species from hydroponic culture of the moss. The researchers characterized these bacteria by their plant interactions such as auxin production, **siderophores** (molecules that bind and transport iron in microorganisms), or hydrogen cyanate, growth in absence of added nitrogen source, calcium phosphate solubilization, utilization of sugars, polymers, or aliphatic compounds, and antifungal activity. Such activities cause the bacteria to stabilize production and enhance the growth of ***Racomitrium japonicum***.

Figure 75. ***Racomitrium japonicum***; environmental bacteria (especially ***Duganella***, ***Pseudomonas***, and ***Rhodococcus***) stabilize production and enhance the growth of ***Racomitrium japonicum***. Photo from Digital Museum, Hiroshima University, with permission.

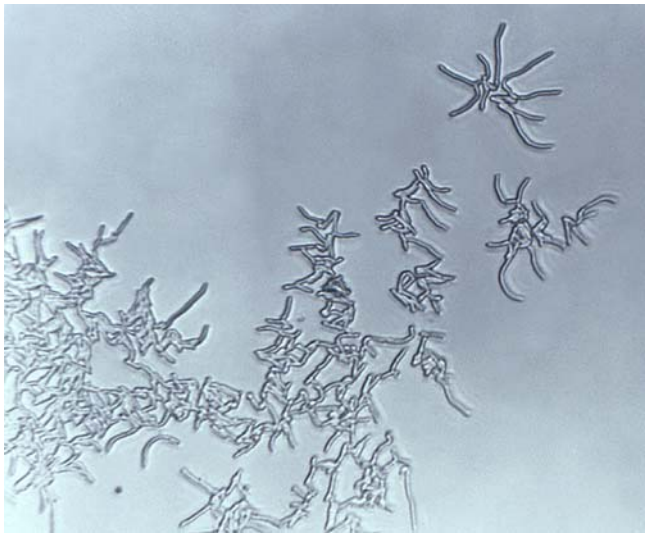

Figure 76. ***Rhodococcus***, a bacterium that enhances growth and production of ***Racomitrium japonicum***. Photo by David Berd, CDC, through public domain.

Rhizoids

Sheldrake (1971) determined that the concentrations of auxins in the soil were in the same range as those known to stimulate the formation of rhizoids in liverworts. Sheldrake further considered that the greatest concentration of auxins would occur in areas with the highest nutrient levels. This mechanism would cause the bryophytes to produce the most rhizoids in microhabitats with the highest concentrations of nutrients. Sheldrake concluded that the bryophytes did not produce auxins and that they depended on the environment to supply them. Hence, the bacteria could provide an important role in signalling environmental conditions to the bryophytes. This increased production of bryophyte rhizoids could be beneficial in high-nutrient environments that would also increase competition from other plant species.

Khan *et al*. (1997) found that rhizoids of mosses could also stimulate the growth of bacteria. This was particularly true for the bacterium ***Bacillus*** (Figure 9). Where do these mutual stimulation partnerships end?

Quorum Sensing

It is important to realize that bacteria do not live as solitary cells, but that they require the coordination of a colony with intercellular communication that permits them to adjust to changing environmental conditions (Whitehead *et al*. 2001). This communication, as we might expect, is through chemical signals. These signals are dependent on cell density and growth phase.

Bacteria use **quorum sensing** as a way of monitoring their population density and interacting with their environment (Vesty *et al*. 2020). Quorum sensing requires intercellular signalling mechanisms (ISMs) that serve as a means of recognizing cell density (Whitehead *et al*. 2001). In the environment, the expression of virulence depends on the synthesis of and response to diffusible signalling metabolites (Manefield & Turner 2002). Thus far, only the **Pseudomonadota** are known to produce the necessary AHL (N-acyl-L-homoserine lactone) compounds used for signalling, thus limiting the availability of such signalling. This may account for the preponderance of the **Pseudomonadota** in association with bryophytes. However, widespread testing of signalling among bacteria and to bryophytes is lacking. For example, <1% of all bacteria that are present in any environment can be cultured in the lab using standard media, so many more AHL-producing bacteria are possible (Vesty *et al*. 2020). Recent DNA techniques may help us to elucidate these bacteria.

As Whitehead *et al*. 2001 suggested, Williams *et al*. (2007) found that bacteria associated with bryophytes, instead of being the passive autonomous organisms we thought, are highly communicative. As the population density increases, the production of quorum sensing molecules also increases, increasing their presence in the external environment. Quorum sensing enables a bacterial population to achieve a co-operative response that improves access to nutrients or specific environmental niches, promotes collective defense against other competitor prokaryotic or eukaryotic defense mechanisms, and facilitates differentiation into forms that promote survival by making the cells better able to combat environmental threats. Quorum sensing can be exploited or inactivated by both plants and mammals, and it appears that bryophytes are among the users of this phenomenon.

Spore Germination

Among the Gram-negative bacteria, the quorum sensing molecules are N-acylhomoserine lactones (**AHL**s) (Vesty *et al*. 2020). These AHLs can affect the spore germination of the moss ***Physcomitrium patens*** (Figure 67). AHLs promote this spore germination at sub-micromolar concentrations but inhibit spore germination at concentrations above 1 µM. Even the sporophytes of some wild isolates of ***Physcomitrium patens*** are associated with AHL-producing bacteria. Many of the ***Pseudomonas*** (Figure 10) isolates, most of the ***Serratia*** (Figure 8) isolates, and one of the ***Aeromonas*** (Figure 77) isolates, all known from bryophytes, produced AHLs in their study. Furthermore, there are many bacteria that thus far have not been cultured, so there could be many additional sources of AHL's in the bryophyte habitats.

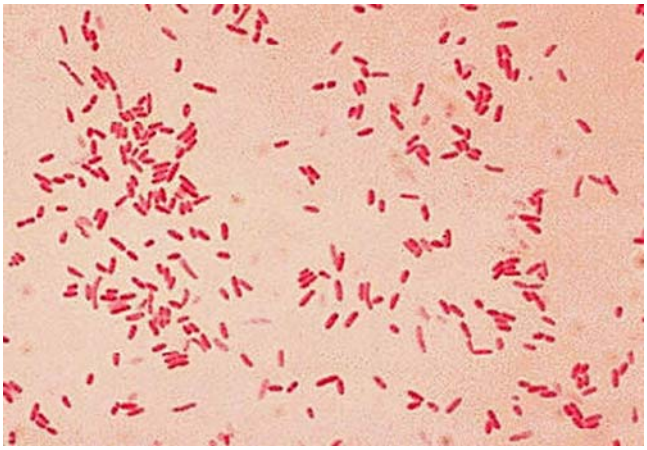

Figure 77. ***Aeromonas hydrophila***, a bacterium that produces AHLs as signalling compounds. Photo by W. A. Clark, CDC, through public domain.

Vesty *et al*. (2016) concluded that endogenous hormone signalling networks that control germination of spores and seeds as environmental responses may have evolved independently in spores and seeds. Such parallel evolution is a testimony to the importance of the relationship.

Vitamins

Algae use **vitamin B_{12}** that is manufactured by bacteria, a symbiotic need generated by the lack of B_{12}-dependent enzymes in algae (Croft *et al*. 2005). Bryophytes likewise obtain vitamin B_{12} from bacteria (Basile *et al*. 1985), although it does not seem to have a direct role. Its presence in bryophyte-associated bacteria, however, could be important for animals feeding there, particularly large herbivores that use bryophytes as emergency food. Growth of ***Liochlaena lanceolata*** (Figure 78) and ***Gymnocolea inflata*** (Figure 79) was significantly stimulated by the pink facultative methylotrophic bacteria that both synthesize and accumulate vitamin B_{12}. These bacteria commonly associate with bryophytes, but the physiological role of vitamin B_{12} is elusive (Marsten 1952).

Figure 78. ***Liochlaena lanceolata***, a species that is stimulated by the pink facultative methylotrophic bacteria that both synthesize and accumulate Vitamin B_{12}. Photo by Bob Klips, with permission.

Figure 79. ***Gymnocolea inflata***, a liverwort species that is stimulated by the pink facultative methylotrophic bacteria that both synthesize and accumulate Vitamin B_{12}. Photo by Michael Lüth, with permission.

Water Relations

Could bacteria help bryophytes in their recovery from desiccation? Or are they a threat to be reckoned with?

Minibayeva and Beckett (2001) suggested that the oxidative burst seen upon rehydration in a hornwort (***Anthoceros natalensis*** – Figure 80) and two thalloid liverworts [***Dumortiera hirsuta*** (Figure 81), ***Pellia epiphylla*** (Figure 82)] is actually a defense mechanism against pathogenic fungi and bacteria. Li *et al*. (2010) found a similar response to both biotic and abiotic stresses in ***Dumortiera hirsuta***. When bryophytes desiccate, their membranes become leaky. When they rehydrate, bacteria and fungi can enter the leaky cells as the water rehydrates them (Minibayeva & Beckett 2001). Hence the oxidative burst can help to prevent those pathogens from damaging the cells of the bryophyte. It is interesting that mosses and at least some leafy liverworts tested lacked the oxidative burst and its absence may be related to their desiccation tolerance. We need experiments and observations to determine how well the oxidative burst correlates with desiccation tolerance, and is it needed more in those with higher moisture requirements?

Figure 80. ***Anthoceros*** sp. with capsules; ***Anthoceros natalensis*** seems to use oxidative burst seen upon rehydration as a defense against bacteria. Photo from USFWS, through public domain.

Figure 81. ***Dumortiera hirsuta***; a liverwort that seems to use the oxidative burst seen upon rehydration as defense against bacteria. Photo by Shyamal L., through Creative Commons.

Figure 82. ***Pellia epiphylla***; this liverwort seems to use the oxidative burst seen upon rehydration as defense against bacteria. Photo by Valentin Hamon, through Creative Commons.

Bacteria can confound measurements of productivity in bryophytes. From an ecosystem point of view, it may be legitimate to express the productivity of the bryophyte-periphyton association, but from a physiological perspective of the bryophyte alone, this is not acceptable. Gupta (1977) noted that following desiccation in the mosses ***Dicranella palustris*** (Figure 83), ***Mnium hornum*** (Figure 84), and ***Syntrichia ruralis*** (Figure 85), and the liverworts ***Porella platyphylla*** (Figure 82) and ***Scapania undulata*** (Figure 86) the external water collected from them after 22 hours had large numbers of microorganisms. The burst of respiration following rehydration was due to these microorganisms. But does this respiratory activity indicate damage to the bryophytes, providing leaked carbohydrates to the bacteria, or could it be a benefit by providing additional CO_2 for photosynthesis?

Do bacteria help in the uptake of nutrients in bryophytes? For the bean, *Phaseolus vulgaris*, 42 hours after 10 nM homoserine lactone (HL) was supplied to roots the transpiration and stomatal conductance increased significantly. Although the experiments were done with tracheophytes, the same effect could occur with bryophytes, especially those that form cushions. They lack stomata, but transpiration still occurs from the cushion. Joseph and Phillips (2003) considered the bacteria in the soil to have a role in plant water and nutrient relations. As water diffuses from the plant to the atmosphere, the action helps to move diffusion-limited nutrients such as phosphorus from the soil to the plant and also to the microbes.

Figure 83. ***Dicranella palustris***, a species that has large numbers of microorganisms in its external water, causing a burst of respiration upon rehydration of the moss. Photo by Andrew Hodgson, with permission.

Figure 84. ***Mnium hornum***, a species that has large numbers of microorganisms in its external water, causing a burst of respiration upon rehydration of the moss. Photo by Bob Klips, with permission.

Figure 85. ***Syntrichia ruralis***, a species that has large numbers of microorganisms in its external water, causing a burst of respiration upon rehydration of the moss. Photo by Bob Klips, with permission.

Figure 86. ***Scapania undulata***, a liverwort species that has large numbers of microorganisms in its external water, causing a burst of respiration upon rehydration. Photo by Hermann Schachner, through Creative Commons.

By contrast, Krochko *et al*. (1978) found that respiration in the semiaquatic moss ***Cratoneuron filicinum*** (Figure 87) does not occur upon rehydration following rapid drying. They, too, cautioned that contamination by bacteria could cause false readings of the respiration by the moss.

Figure 87. ***Cratoneuron filicinum***, a moss that does not exhibit a rapid respiration following rehydration. Photo by Claire Halpin, with permission.

Freezing Protection

Liquid pure water does not freeze at 0ºC, but requires the temperature to drop to -38ºC before it freezes, and even lower in very small samples (Moffett 2015). But water does not occur in the ecosystem in its pure state. Instead it has many nucleating materials, including bacteria, that permit it to crystallize at a temperature near 0ºC. In fact, it is the bacteria that permit it to freeze at the highest temperatures. The **ice nucleation** bacteria seem to be limited to a small number of plant pathogens that use specific proteins to cause freezing. The resulting damage permits them to gain nutrients from the plants. Moffett showed that ice nucleation is likewise an active process in both mosses and liverworts. In fact, those tested harbor 106-107 g L^{-1}, an order of magnitude greater than that known for lichens. But Moffett failed to find more than a few bacteria on the surfaces of mosses cultured on selective media, thus concluding that ice nucleation activity is unlikely to be caused by surface bacteria. But there seem to be many bacteria that have never been cultured because we don't know their requirements (Vesty *et al*. 2020). Could it be that tiny nucleating bacteria are present, but not yet detected by traditional methodology?

When ice forms on bryophytes, it grows at the expense of the bryophyte by pulling water from the cells or scavenging it from the surface. This is a particular problem for those species that are dependent on fog, dew, and cloudwater. Moffett *et al*. (2009a, b) suggested that mosses produce ice nuclei that are very different from those produced by bacteria. Instead, they are proteins that show only distant relationship to the classical bacterial ice nuclei. Moffett *et al*. suggest that these ice nuclei are used as a water harvesting mechanism by the bryophytes, removing it from atmospheric moisture rather than from the bryophyte cells.

On the other hand, some bacteria do have a sneaky trick to gain entry into plant cells. These are a small number of ice-nucleating bacteria (Moffett 2015). The bacteria use certain proteins to induce freezing that damages the plants, permitting the bacteria to gain nutrients (Lindow 1983). But for bryophytes, it is possible that they help the plants gain water (Moffett 2015). Ice crystals are hygroscopic, gathering water from the atmosphere. This could be an advantage following the desiccating effects of freezing. Size matters, and smaller ice nucleating bacteria could prevent large crystal formation by out-competing the larger bacteria, a phenomenon used by Florida orange growers to prevent ice damage to the oranges on cold nights. Moffett found that all mosses and liverworts tested have active ice nucleation. This benefit for bryophytes survived as a water-gathering mechanism. Moffett suggested a number of hypotheses:

1. Ice nucleation is a ubiquitous feature of bryophytes.
2. Ice nucleation is used as a water-gathering mechanism.
3. Ice nucleation is of greater selective advantages to bryophytes growing in habitats such as rock and tree surfaces.
4. Ice nucleation in bryophytes is due to a surface expressed protein.
5. Ice nuclei from bryophytes become airborne and influence atmospheric processes.

All of these hypotheses need to be tested. Could the finding of a protein on the surface of the liverwort be a product of some unknown bacterium that didn't have the right conditions to appear in culture, rather than of the liverwort (see Kazda *et al*. 1980; Vesty *et al*. 2020)?

Weber (2016) provided evidence that spores (Figure 88) of ***Polytrichum commune*** (Figure 24) in the atmosphere are ice nucleators. This nucleation ability was active at -7ºC when the spores were contaminated with bacteria, compared to -12ºC for spores contaminated with microorganisms. Hence, moss spores can affect precipitation patterns, with the more common contaminated spores having the greater effect by causing freezing at a higher temperature.

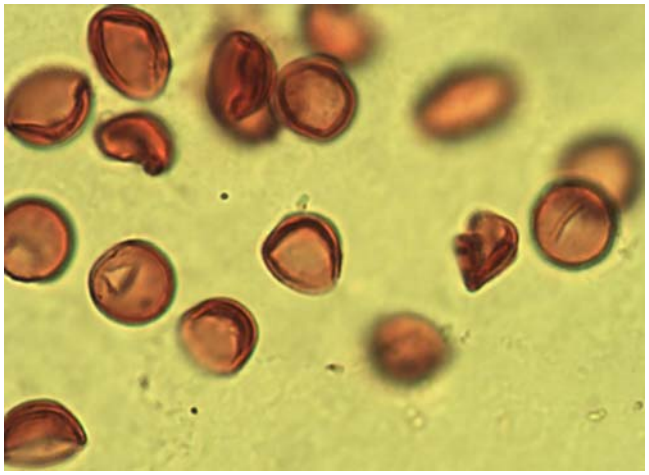

Figure 88. ***Polytrichum commune*** spores; these serve as ice nucleators in the atmosphere and are active at even higher temperatures when they have bacteria. Photo by Global Pollen Project, through Creative Commons.

Nutrients

Šoltés *et al*. (2015) attempted to understand the seasonal variation of bryophytes in a calcareous mire in Slovakia. In a detailed examination of ***Campylium stellatum*** (Figure 89) and ***Drepanocladus cossonii*** (Figure 90), they found that distribution of these two mosses was limited primarily by decreasing concentrations of NH_4^+ and increasing concentrations of NO_3^+. They determined that this seasonal variation in bryophyte cover was the result of the synergistic relationship with the nitrifying bacteria and by the unstable water table. The bacteria were instrumental in the decomposition of the organic substances in the soils, thus returning nutrients that benefitted the bryophytes.

Figure 89. ***Campylium stellatum***, a species limited primarily by decreasing concentrations of NH_4^+ and increasing concentrations of NO_3^+. Seasonal variation in this bryophyte cover resulted from a synergism with nitrifying bacteria and by an unstable water table. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 90. ***Drepanocladus cossonii***, a species limited primarily by decreasing concentrations of NH_4^+ and increasing concentrations of NO_3^+. Seasonal variation in this bryophyte cover resulted from synergism with nitrifying bacteria and by unstable water table. Photo by Hermann Schachner, through Creative Commons.

Some plants, especially graminoids, require silica (Si). It increases resistance to various forms of stress. But Si has limited availability to plants because of its insolubility. Bryophytes grow in locations where high levels of silica are present in rocks, so Hu *et al*. (2019) investigated the associated bacteria in the widespread moss ***Hypnum plumaeforme*** (Figure 91). They did indeed find that a strain in the bacterial genus ***Kosakonia*** was able to release Si from feldspar and quartz. These bacteria significantly increased the water-extractable Si in the soil, improved Si uptake by *Zea mays*, and promoted seedling growth. Hence the bryophyte rhizoids can provide the environment needed for the bacteria that release needed Si. We need research on this partnership role in habitats where both grasses and bryophytes grow. And do any of the bryophytes use silica?

Figure 91. ***Hypnum plumaeforme***; the bacterium ***Kosakonia*** lives in the moisture provided by rhizoids of this moss and is able to release Si from feldspar and quartz. Photo by Janice Glime.

Epiphyllous liverworts can benefit nitrogen-fixing bacteria and **Cyanobacteria** by maintaining leaf moisture for a longer period of time, thus improving the usable N content in the canopy (Bentley & Carpenter 1980).

Decomposition

When one thinks of bacteria in natural habitats, decomposition usually comes to mind. Nevertheless, we know that decomposition of bryophytes is notoriously slow (Fenton *et al*. 2010). Instead, the bryophytes retain high levels of soil carbon, retain excessively high soil water content, cool the soil, and slow nutrient cycles.

Sphagnum (Figure 12) decomposition can require specialized bacteria, with the abiotic environmental conditions having more importance than in other systems because of this bacterial specialization (Kulichevskaya *et al*. 2007). These bacteria are primarily members of the phyla **Actinomycetota**, **Planctomycetota**, and **Pseudomonadota** (**Alphaproteobacteria**). Kulichevskaya *et al*. found that the numbers of **Bacillota** and **Bacteroidota**, which are believed to be the primary decomposers in eutrophic wetlands, are low. As the decomposition reached its final stage, the numbers of **Planctomycetota** increased. Representatives of the **Pseudomonadota** were able to utilize galacturonic acid, the only low-molecular-weight organic compound detected in the water samples of the decomposing peat. The bacterial community involved in ***Sphagnum*** decomposition appears to be fundamentally different from that which decomposes the dead plant parts in eutrophic ecosystems at neutral *p*H. Even where ***Sphagnum*** is present, decomposition of the other bryophytes is significantly higher than that of the ***Sphagnum*** (Lang *et al*. (2009). The loss of mass in these other species correlates with the initial nitrogen, without influence of incubation conditions.

Kulichevskaya *et al*. (2010) named a new genus and species [***Bryobacter aggregatus*** (Figure 39) in **Acidobacteriota**] for three strains of chemo-organotrophic bacteria isolated from acidic ***Sphagnum*** bogs (Figure 12). These bacteria preferred substrates of sugars (heteropolysaccharides, galacturonic acid, and glucuronic acids) – substances released during ***Sphagnum*** decomposition. These grew at *p*H 4.5-7.2 and 4-33ºC.

Again in 2014 Kulichevskaya *et al*. described a new species, genus, and family of bacteria from ***Sphagnum***. The species, ***Roseiarcus fermentans***, is a microaerophilic fermentive bacterium in the **Pseudomonadota**.

Bamforth (2007) noted that protozoa are important in stimulating bacterial activity for decomposition. In a tropical forest in Puerto Rico, he found that the high moisture content of the tropical rainforest litter (including bryophytes) and soils provided the connected soil water needed for protozoan transport. Often there needs to be consideration of protozoan potential because of their dormancy status. Nevertheless, the large numbers of protozoa suggest that a major proportion of these contribute to stimulation of the bacterial decomposition for this organic matter.

Mikola and Hintikka (1956) experimented with decomposition of five forest litter types. One of these was the moss ***Pleurozium schreberi*** (Figure 92). Others were the grass *Deschampsia flexuosum* (Figure 93), shrub *Alnus incana* (Figure 94), deciduous tree *Populus tremula* (Figure 95), and conifer tree *Pinus sylvestris* (Figure 96). Of these, the ***Pleurozium schreberi*** litter had the lowest bacterial number and highest fungal count. The researchers noted that the related moss ***Hylocomium splendens*** (Figure 97) is very acid and decomposes differently from tracheophyte leaves (Mikola 1954). Since these mosses are closely related species and occur in overlapping acidic habitats, it is possible that the acid conditions are unfavorable to bacteria while being favorable to the fungi.

Relative to lichen-dominated sites, bryophytes are associated with higher soil nutrient concentrations and a greater production of easily decomposable substrates that provide better maintenance of microbial activities (Ohtonen & Vare 1998). Do the bryophytes contribute to these better conditions, or are they simply indicators of the better conditions?

Figure 92. ***Pleurozium schreberi***, a species, when compared with litter from four tracheophytes, had the lowest bacterial number and highest fungal count. Photo by Bob Klips, with permission.

Figure 93. ***Deschampsia flexuosa***, a grass used by Mikola and Hintikka for comparison of bacterial activity in decomposition. Photo by James K. Lindsey, through Creative Commons.

Figure 94. ***Alnus incana*** leaf, a shrub used by Mikola and Hintikka for comparison of bacterial activity in decomposition. Photo by Vassil, through public domain.

Figure 95. ***Populus tremula*** leaf, a tree used by Mikola and Hintikka for comparison of bacterial activity in decomposition. Photo by Willow, through Creative Commons.

Figure 96. ***Pinus sylvestris*** litter, a conifer used by Mikola and Hintikka for comparison of bacterial activity in decomposition. Photo by Beentree, through Creative Commons.

Figure 97. ***Hylocomium splendens***, a species that decomposes differently from tracheophyte litter, possibly due to its acidity. Photo by Claire Halpin, with permission.

Bastardo (1979) experimented with decomposition in ***Fontinalis antipyretica*** (Figure 98). Satake and Miyasaka (1984) found, by using TEM, that the leaves of the aquatic liverwort ***Solenostoma vulcanicola*** (Figure 99) exhibit rod-shaped bacteria and numerous holes in the liverwort cell walls. They suggested that these bacteria contribute to the decomposition of this liverwort.

Figure 98. ***Fontinalis antipyretica*** with silt and microorganisms. Photo copyright Malcolm Storey, with online permission.

Figure 99. ***Solenostoma vulcanicola***, a leafy liverwort species that gets numerous holes in its cell walls due to rod-shaped bacteria. Photo courtesy of Angela Ares.

Van Tooren *et al*. (1988) found that nutrients released by decomposing bryophytes in spring and summer are incorporated by the tracheophytes, thus ensuring their retention in the system. In ecosystems where they are associated with nitrogen-fixing bacteria, such as mires and grasslands, they enhance the N in the ecosystem (Oechel & van Cleve 1986). Hence the nutrient content of the bryophytes affects the nutrient cycle of the whole ecosystem.

Fauna and Bryophagy

Bacteria often play a role in feeding the animals that live among the bryophytes. In peatlands, ***Sphagnum*** is often a suitable substrate for a number of Protozoa (Mieczan 2006). The bactivorous Protozoa were in the highest numbers in all the moss samples, whereas the algivorous ones were the lowest.

Nematodes are common among bryophytes in some habitats. Among these, members of the genus ***Panagrolaimus*** (Figure 100) are bacterial feeders that are known from terrestrial mosses in both the Antarctic and temperate ecosystems (Shannon *et al*. 2005). In a Balkan oak forest, Lazarova *et al*. (2000) found a similar relationship, with bacterial feeders being the most abundant group of nematodes on the moss ***Hypnum cupressiforme*** (Figure 101). Merrifield (1992) likewise found that the moss-dwelling nematode ***Plectus*** sp. (Figure 102) is a bacteria feeder.

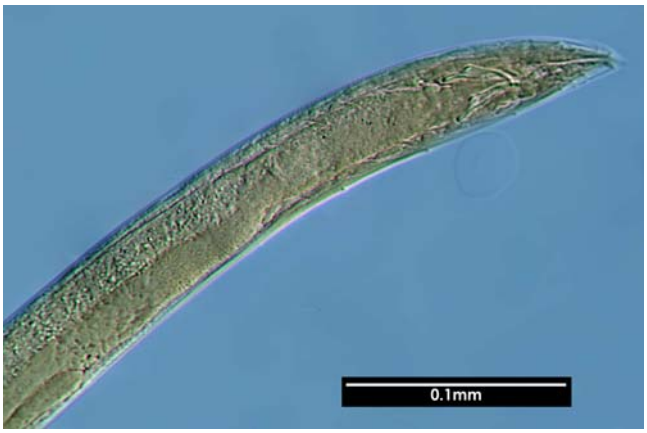

Figure 100. ***Panagrolaimus davidi***, in a nematode genus that has bacterial feeders that live among bryophytes. Photo from Smithsonian, through Creative Commons.

Many tardigrades are well adapted to living among mosses. They have the ability to dry out and rehydrate under the same water regimes as their moss hosts. Although one group of tardigrades has a stylet that permits them to feed on mosses, some of the tardigrades, particularly smaller ones, feed on bacteria that they find among the mosses (Tardigrada 2005; Schill *et al*. 2011).

Bryophyte communities often have associated arthropods. There is a body of evidence that many of these arthropods feed on the associated bacteria (Varga 1992).

Figure 101. ***Hypnum cupressiforme***, where nematode residents are predominantly bacteria feeders. Photo by Kurt Stüber, through Creative Commons.

Figure 102. ***Plectus murrayi***; a moss dweller in this genus is a bacteriovore. Photo from Bold Systems, by A. Velasco, through Creative Commons.

Although we often think of isopods as scavengers, they can be quite common among and under bryophytes. ***Porcellio scaber*** can come to the surface to feed on the softer apical tissues at night (Hribljan & Glime, in prep.). Because bryophytes have many substances that are difficult to digest, it is likely that they need some help. Zimmer (1999) found that oxidation of phenolics, common in many bryophytes, is primarily due to endosymbiotic bacteria. Furthermore, the gut has oxygen zones such that the outer, peripheral portion is anaerobic while the inner portion is aerobic. This range of conditions permits both aerobic and anaerobic bacteria to survive in the gut. Furthermore, the beginning of the gut is acidic, whereas the hindgut is neutral. It is not clear if these bacteria are gained from the bryophytes, but their presence could make bryophytes a good source of food.

Isopods also have bacteria in the gut that help them break down complex carbohydrates (Zimmer & Brune

2005). On the other hand, phenolics such as those present in mosses can reduce the gut flora needed for breaking down lignocelluloses (Zimmer 1999; Zimmer & Brune 2005). When the gut flora was reduced they were unable to hydrolyze gallotannins. When they ingested gallic acid, it reduced both the palatable fungi and the bacteria, but at the same time it increased the gut microflora. Thus, it would appear they cannot benefit from eating tracheophyte litter and bryophytes at the same time. This suggests that eating foods with hydrolyzable tannins, as found in some mosses, can inhibit the digestion of other foods in the diet of this species.

Pyszko *et al*. (2019) pointed out that we still lack an understanding of the gut bacterial flora of the moss-eating insects. Among the true bugs, the moss bugs (**Peloridiidae**; Figure 103) are obligately associated with endosymbiotic bacteria (Kuechler *et al*. 2013). The Malpighian tubules (part of the excretory system) have most of their nuclei infected by **Pseudomonadota** in the genus ***Rickettsia*** (Figure 104). The connection to bryophytes as food is not clear. Could the bugs subsequently eat the excreted uric acid complex? Or might the feces benefit from these bacteria, permitting the bugs to reingest them and benefit from them?

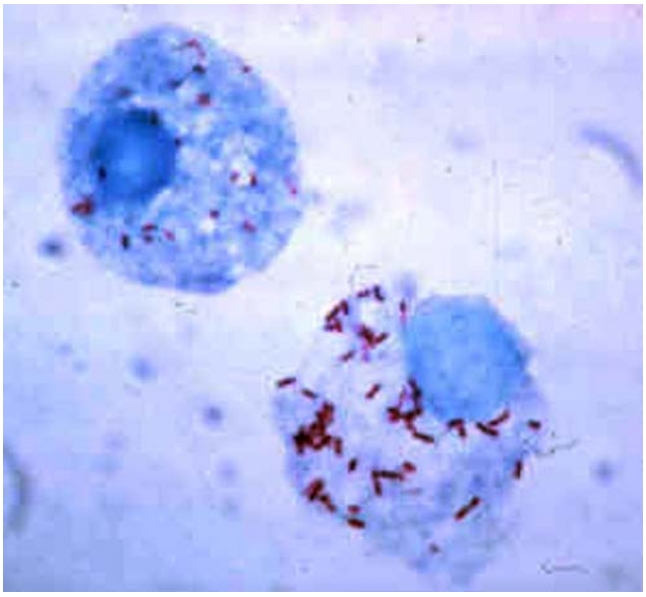

Figure 104. ***Rickettsia rickettsii***, a bacterium found in the Malpighian tubules of the moss bugs (**Peloridiidae**). Photo from CDC, through Creative Commons.

Figure 103. ***Hemiodoecellus fidelis*** (**Peloridiidae**) on ***Sphagnum***, a moss bug that cultures ***Rickettsia*** bacteria in its Malpighian tubules. Photo by Simon Grove, through Creative Commons.

Figure 105. ***Simplocaria semistriata***, a bryophyte-eating beetle that seems to have a gut flora that helps it digest bryophytes. Photo by Boris Loboda, through Creative Commons.

Using two bryophagous species of beetles in the **Byrrhidae** [***Simplocaria semistriata*** (Figure 105) and ***Curimopsis paleata*** (Figure 106)], Pyszko *et al*. (2019) found that the gut flora differed considerably from the abdominal flora in the same individual beetle (Figure 107). Furthermore, both differed substantially from the substrate surface bacterial flora. The dominant bacteria in the guts and abdomens were all **Pseudomonadota**: ***Novosphingobium*** (Figure 28), ***Bradyrhizobium*** (Figure 1, Figure 53), ***Ralstonia*** (Figure 108), and ***Caulobacter*** (Figure 109). These bacteria are involved in detoxification of secondary metabolites or in nitrogen fixation. Since these genera are less common in the substrate surface samples, it is likely that they are associated with the specific ability of bryophages to feed on mosses.

Figure 106. ***Curimopsis paleata***, a bryophyte-eating beetle that seems to have a gut flora that helps it digest bryophytes. Photo by M. Virtala, through Creative Commons.

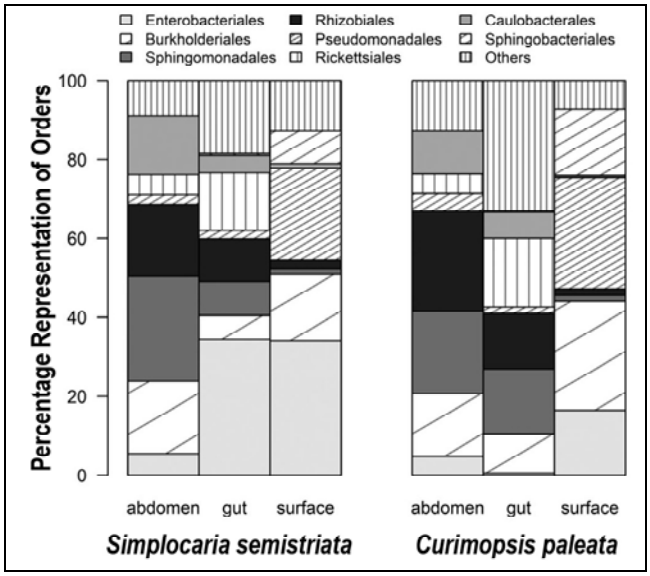

Figure 107. Composition of orders of bacteria in communities associated with abdomens, guts, and surfaces of the bryophyte-eating beetles ***Simplocaria semistriata*** and ***Curimopsis paleata***. Modified from Pyszko *et al*. 2019.

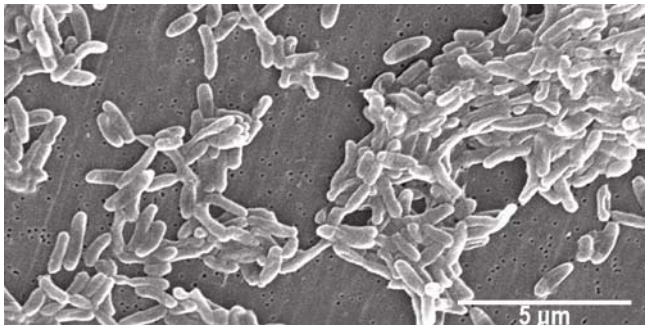

Figure 108. ***Ralstonia mannitolilytica***, a bacterium involved in nitrogen fixation or detoxification of secondary metabolites and that occurs in the guts of the bryophage beetles ***Curimopsis paleata*** and ***Simplocaria semistriata***. Photo by Judith Noble-Wang, CDC, through public domain.

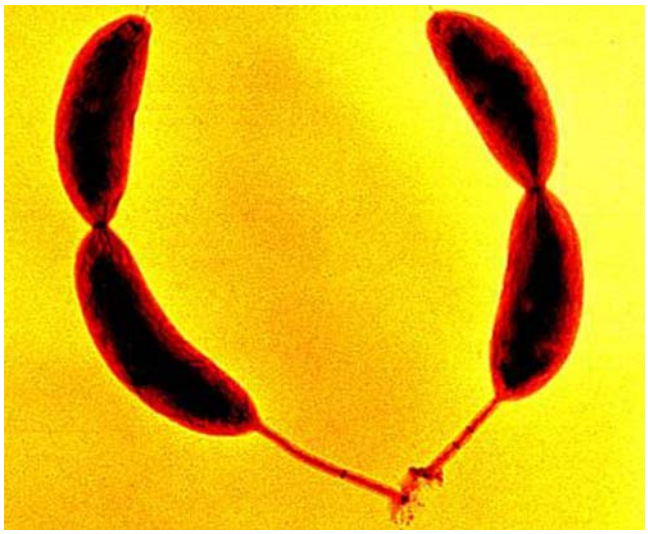

Figure 109. ***Caulobacter crescentus***, a bacterium involved in detoxification of secondary metabolites or nitrogen fixation and that occurs in the guts of the bryophage beetles ***Curimopsis paleata*** and ***Simplocaria semistriata***. Photo from USDA, through public domain.

Some of the bacteria found in the **Byrrhidae** (pill beetles) guts are nitrogen fixers, *e.g.* ***Bradyrhizobium*** (Figure 1, Figure 53) (Pyszko *et al*. 2020). Since nitrogen is typically deficient in plants (Benemann 1973), the ability to extract more of it from food items may be especially beneficial. Rapid travel through the gut reduces this ability (Pyszko *et al*. 2020). Therefore, having nitrogen fixers in the guts of bryophyte eaters may be useful. Other benefits may include detoxification, such as the ability of the bacteria ***Novosphingobium*** (Figure 28) and ***Ralstonia*** (Figure 108) to degrade phenols and aromatics.

In bryophyte-dwelling ***Cytilus sericeus*** (**Byrrhidae**; Figure 110) treated with bactericides and fungicides, the bactericides actually had a positive effect on egg hatching and larval development, whereas the fungicides were detrimental to their fitness, particularly during hatching (Pyszko *et al*. 2020). When the larvae were supplied with adult feces, the feces did not improve fitness. Hence, the beneficial fungi are associated with the eggs, but are not transmitted in the feces. Could the bryophytes be providing bactericides that make the environment favorable to the developing eggs and larvae?

Figure 110. ***Cytilus sericeus*** on moss; bactericides actually had a positive effect on egg hatching and larval development. Bryophytes are likely to provide these bactericides in nature. Photo by James K. Lindsey, with permission.

Wolf and Rockett (1984) assessed the bacteria in the alimentary canals of two oribatid mites (***Rhysotritia*** sp. (Figure 111) and ***Pergalumna*** sp.). These included ***Acinetobacter*** (Figure 112), **Actinomycetota**, ***Alcaligenes*** (Figure 113), ***Bacillus*** (Figure 9), ***Citrobacter*** (Figure 18), ***Corynebacterium*** (Figure 114), ***Flavobacterium*** (Figure 115), ***Mycobacterium*** (Figure 116), and ***Pseudomonas*** (Figure 10). The frequency of ***Bacillus*** and ***Pseudomonas*** was considerably lower in mites taken directly from natural habitats than from those found in moss-soil habitats. Both of these bacterial genera are common on mosses, so it is possible that the moss was the source of the bacteria. After being cultured in the lab (with no moss), both mite species showed dramatic shifts in their gut flora.

Figure 111. ***Rhysotritia*** sp., a mite that occurs on mosses and has a variety of bacterial genera in its gut. Photo by Scott Justis, with permission.

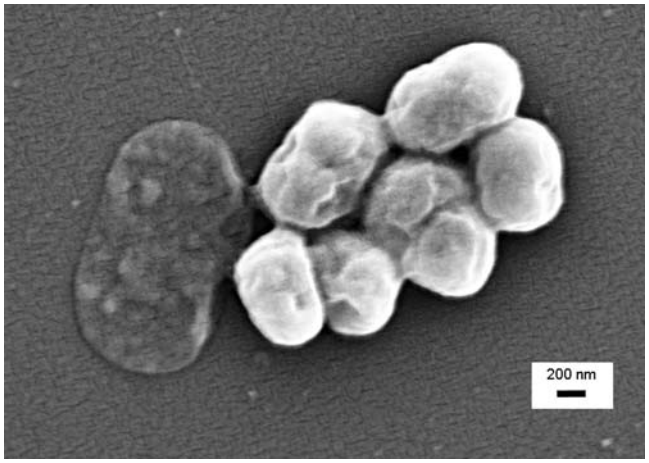

Figure 112. ***Acinetobacter baumannii*** SEM, in a genus that occurs in the alimentary canals of two oribatid mite genera. Photo by Vader1941, through Creative Commons.

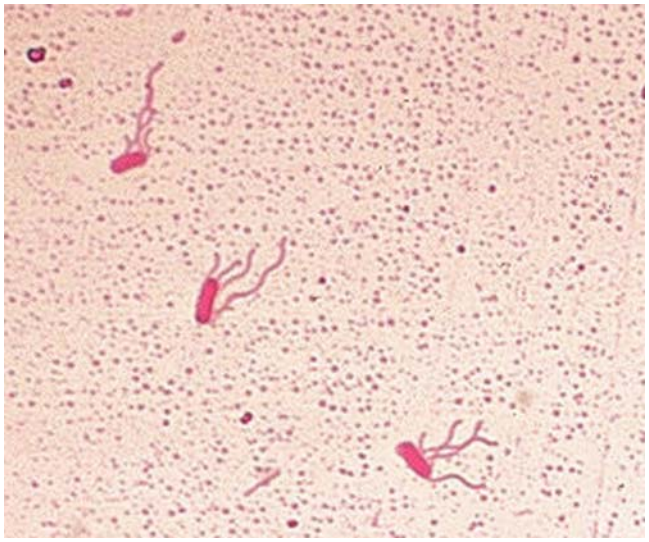

Figure 113. ***Alcaligenes faecalis***, in a genus that occurs in the alimentary canals of two oribatid mite genera. Photo by W.A. Clark, CDC, through public domain.

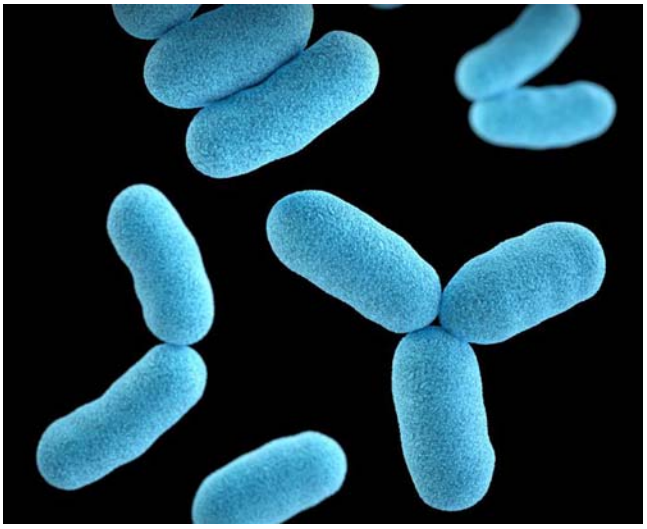

Figure 114. ***Corynebacterium diphtheriae*** SEM, in a genus that occurs in the alimentary canals of two oribatid mite genera. Photo by Jennifer Oosthuizen, CDC, through public domain.

Figure 115. ***Flavobacterium columnaris***, in a genus that occurs in the alimentary canals of two oribatid mite genera, shown here in the gill of a chinook salmon. Photo from USFWS, through public domain.

Figure 116. ***Mycobacterium tuberculosis*** SEM, in a genus that occurs in the alimentary canals of two oribatid mite genera. Photo by NAIAD, through Creative Commons.

Moquin *et al.* (2012) found that for both **soil crusts** and mites the dominant phyla of bacteria were **Bacteroidota**, **Acidobacteriota**, and **Pseudomonadota**. The bacterial community and prevalence of **Bacteroidota** in the bryophytic crusts appear to be affected by high carbon availability. The bacterial communities associated with the bryophytic crusts are distinctly different from those of the cyanobacterial crusts and soils. **Acidobacteriota** prevailed in the mites, and the bacteria present in the gut are the same as those known as symbionts in ***Tetraponera*** (Figure 117) ants.

Figure 117. ***Tetraponera punctulata***, an ant that has **Acidobacteria** as gut bacteria symbionts. Photo by Farhan Bokhari, through Creative Commons.

Mammals also may benefit from bacteria by getting more energy from bryophytes than would be possible otherwise. Pikas (***Ochotona princeps***, Figure 118) store plant foods for winter. They manipulate the decomposition of their food by storing with them plants with a high content of secondary compounds, including bryophytes (Dearing 1997). This permits them to store the plants for longer periods and to maintain higher levels of biomass and nutrients until they are eaten. Eating plants with high phenolic compounds is delayed until the phenolic content has decreased due to the microbial activity.

Figure 118. ***Ochotona princeps***, an alpine rodent (pika) that stores plants with secondary compounds among its stored foods to preserve them longer. Photo by Linette Elliott, through Creative Commons.

Bjorkvoll *et al.* (2009) suggested that the Svalbard reindeer (***Rangifer tarandus platyrhynchus***, Figure 119) may be a specialist in consuming mosses. The fermentation chambers of the rumen are increased in size and have a very high number of fiber-digesting rumen bacteria. ***Polytrichum*** (Figure 24) was the most frequent moss consumed.

Figure 119. ***Rangifer tarandus platyrhynchus*** (Svalbard reindeer), apparently a specialist in moss consumption, probably due to the large number of bacteria in the rumen. Photo by Buiobuione, through Creative Commons.

Pathogens

Not all bacteria are friendly symbionts among their bryophyte neighbors. Lawton and Saidasan (2009) showed that ***Physcomitrium patens*** (Figure 67) is susceptible to a range of bacterial pathogens that can infect and multiply on the moss. In defense against these pathogens, it uses a variety of mechanisms: production of reactive oxygen species, synthesis of secondary metabolites, changes in gene expression, and activation of the programmed cell death pathway. These responses can be elicited by toxins as well as directly by the bacteria and are under genetic control.

The lab rat of mosses, ***Physcomitrium patens*** (Figure 67), is susceptible to a range of bacterial pathogens that can infect and multiply on the moss plants (Lawton & Saidasan 2009). One of the responses of the moss is to produce **reactive oxygen species**, as well as synthesis of secondary metabolites, changes in gene expression, and activation of the programmed cell death pathway.

One of the common bacteria on bryophytes is ***Bacillus cereus*** (Figure 9) (Sabovljević *et al*. 2010). On the other hand, the leafy liverwort ***Lophocolea heterophylla*** (Figure 120) and moss ***Polytrichum commune*** (Figure 24) produce antibiotics that are effective against this bacterium species (Nikolajeva *et al*. 2012) and in another study extracts of ***Atrichum undulatum*** were the most effective against ***B. cereus*** (Sabovljević *et al*. 2010).

Figure 120. ***Lophocolea heterophylla***, a species that produces antibiotics against ***Bacillus cereus***, a bacterial species that is antagonistic toward bryophytes. Photo by Kristian Peters, with permission.

In many of these studies, it is likely that more bacteria exist that are not stimulated to grow on the media being used. Kazda *et al*. (1980) cultured bacteria from 122 samples of ***Sphagnum*** (Figure 12) and other moss vegetation using foot pad inoculation. They found that of the 759 foot pads examined 20% had noncultivable acid-fast ***Bacillus*** (Figure 9). The frequency was significantly higher in the ***Sphagnum cuspidatum*** habitat (Figure 121).

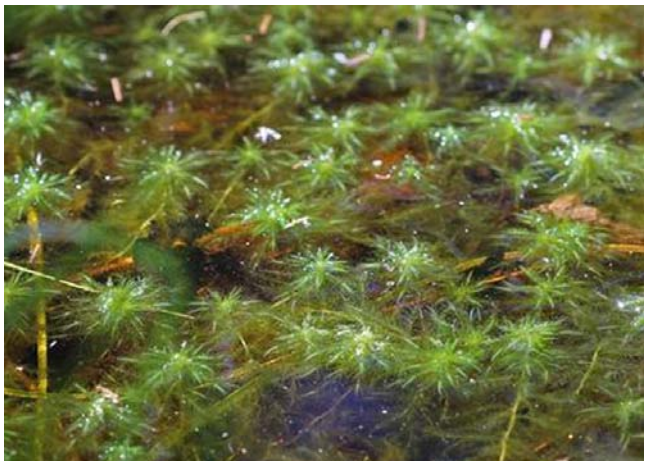

Figure 121. ***Sphagnum cuspidatum***, a habitat where ***Bacillus*** has a high frequency. Photo by Rob Routledge, through Creative Commons.

This suggests that bryophytes could be reservoirs of bacteria that are pathogenic to other organisms. D'aoust *et al*. (1990) found that ***Salmonella poona*** (see Figure 16) and ***S. arizonae*** (see Figure 16) are frequently encountered in fertile eggs of pet turtles (***Trachemys scripta elegans***, Figure 122) and in the mosses used for packing the turtles. Since these species of bacteria became resistant to the antibiotics, the turtles were taken off the market to protect the children who would otherwise choose them as pets and possibly get infected by the bacteria.

Figure 122. ***Trachemys scripta elegans***, a species of turtle that carries ***Salmonella poona*** and ***S. arizonae*** from the mosses used for packing material. Photo by Jf268, through Creative Commons.

Bacterial Source of Antibiotics Useful to Bryophytes

Pantoea agglomerans (Figure 7) is known from bryophytes, in particular ***Sphagnum fallax*** (Figure 123-Figure 124) (Opelt *et al*. 2007). This bacterial species is an active producer of antibiotics that are effective against many plant pathogens among the bacteria and fungi (Dutkiewicz *et al*. 2016). This species of ***Pantoea*** does this by competition, releasing antibiotics, and induction of plant resistance. Bryophytes such as ***Sphagnum fallax*** can serve as a reservoir for the bacteria so that they become available to animals and annual plants and plant parts (Opelt *et al*. 2007). It is further useful, especially to rooted plants, by preventing the penetration of harmful industrial contaminants. But how does this latter feature affect bryophytes? Could it hold high concentrations near the soil surface where they may be harmful to bryophytes?

Figure 123. ***Sphagnum fallax***, a species that can serve as a reservoir of bacteria needed by other plants and animals. Photo by Hugues Tinguy, with permission.

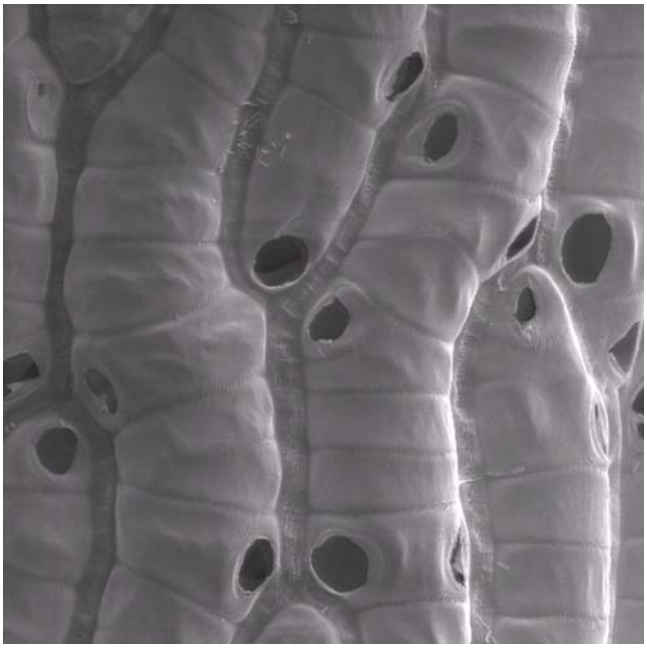

Figure 124. ***Sphagnum fallax*** hyaline cells with bacteria. Photo by Gabi Berg, with permission.

Opelt and Berg (2004) used ***Syntrichia ruralis*** (patches on sand dunes; Figure 85), ***Aulacomnium palustre*** (edge of non-calcareous mire; Figure 13), and ***Sphagnum rubellum*** (open part of mire; Figure 125) to represent typical moss species of nutrient-poor communities on the Baltic Sea coast of Germany and examine the antagonistic potential of bacteria associated with them. They found a high degree of specificity of the bacteria for the particular moss. This specificity was also manifest in the bacterial antagonistic behavior. For example, the antagonistic activity against the fungus ***Verticillium dahliae*** (Figure 126) ranged from 31% for ***Sphagnum rubellum***, to 17% for ***Aulacomnium palustre***, to 5% for ***Syntrichia ruralis***. The antifungal role of the antagonistic bacteria is remarkable – 99% of those associated with mosses produced antifungal compounds.

Figure 125. ***Sphagnum rubellum***, a strong antagonist against ***Verticillium dahliae***. Photo by J. C. Schou, through Creative Commons.

Figure 126. ***Verticillium dahliae*** showing wilt disease. Photo by Howard F. Schwartz, through Creative Commons.

Out of the 52 species of bryophytes tested with 12 species of microorganisms, 29 (56%) were active against at least one of the test bacteria, but none exhibited any antifungal property (Banerjee & Sen 1979). Anyone who has tried to grow mosses in a closed space with a high humidity recognizes that fungi can be a threat to the moss health, so these antifungal roles of bacteria could be exceedingly important.

After searching through many papers on bacteria and bryophytes, it is unclear to me in many cases which bacteria can serve as pathogens to the bryophytes and which are either neutral or offer some antagonistic advantage to the bryophytes by inhibiting other bacteria or fungi. And some bryophytes produce antibiotics against specific antagonistic bacteria whereas others do not. This is a huge field of bryological interaction where we have just begun to scratch the surface in our understanding.

Speculation

What a fantastic world of interaction! The bacteria got here first and developed all sorts of signals. Bryophytes took advantage of all those signals and developed quorum sensing. This made a close dependence possible and beneficial. So what might remain that we haven't even considered?

Could it be that the inhibition of gemmae germination on the thallus of ***Marchantia*** species (Figure 37, Figure 38) is due to a lack of germination signals from bacteria? The ***Marchantia*** produces secondary compounds that inhibit bacteria. Thus, germination might be prevented because the gemmae need hormones from the bacteria. On the other hand, ***Methylobacterium marchantiae*** (see Figure 6) isolated from ***Marchantia polymorpha*** (Figure 37) stimulates the surface expansion of isolated gemmae. But what is the timing? Under what environmental conditions? Does this only work if the thallus is dying? Do the numbers of bacteria signal the right season to germinate?

Spore germination signals are another potential role for bacteria. Some desert seeds have chemical inhibitors that prevent their germination. When there is a heavy rain, the inhibitors are washed away and the seeds germinate. This prevents them from germinating in a light shower or dew that provides insufficient water for continued survival of the germinated seedling. Do spores use bacteria as a similar signal? AHLs inhibit spore germination at high concentrations, but stimulate it at low concentrations.

Could the rain wash away the AHLs and permit the spores to germinate only when there is enough water for successful protonemal survival?

Summary

The predominant members of the bryophyte bacterial communities belong to the **Pseudomonadota**. The **Bacillota** are common in some habitats, and a number of other bacterial phyla are less common.

I found it fascinating that the bryophytes have in many cases relied on bacteria to provide them with needed hormones for their growth and development. In such small plants, economy of resources is an important survival mechanism, so using products of reliably associated organisms is an adaptive advantage. These hormones were most likely available before the bryophytes originated, making the production of these substances by the bryophytes unnecessary.

A number of unrelated bryophytes require bacterially produced hormones to change stages in their life cycle. This is best known in producing buds on the protonema and in development of the buds into gametophores, explaining why some mosses won't develop in sterile culture with no added hormones.

The **Methanobacteria** typically are able both to break down methane to form CO_2 (then available to bryophytes for photosynthesis) and to fix atmospheric nitrogen (also used by bryophytes). This implies that theses bacteria somehow provide anaerobic conditions within the cells to permit nitrogen fixation to occur.

At least some, perhaps all, bryophytes obtain vitamin B_{12} from bacteria, but the physiological roll seems to be unknown – it does enhance growth and development in culture. The oxidative burst seen on rehydration of bryophytes can be a defense against pathogenic fungi and bacteria. Bacteria interfere with measurements of primary productivity of bryophytes, especially aquatic ones. They may help in the movement of water and nutrients up the bryophyte stems as water evaporates from the tips. Some bacteria provide freezing protection through ice nucleation. Others gain entry by causing freezing damage to bryophyte cell membranes. They can contribute to release of elements from rock, making them available to the community of plants. Bryophytes benefit bacteria by maintaining moisture for a longer period of time.

Some bacteria are pathogens to bryophytes, whereas others produce antibiotic compounds that protect the bryophytes from these pathogens. Bacteria are particularly important in producing antifungal compounds used by bryophytes, particularly liverworts. Bryophytes themselves produce many antibiotic compounds against bacteria. When the bacteria multiply, the bryophytes can respond to increased numbers (**quorum sensing**) to produce antibiotics needed for protection.

Many of the invertebrates that live among the bryophytes consume the bacteria or depend on them in other ways. Some bryophagous insects incorporate nitrogen-fixing bacteria in their gut to permit them to gain usable nitrogen from consumed bryophytes. Bacteria associated with some bryophytes might prepare them for consumption by giving access to nutrients that were bound in recalcitrant tissues.

As a newly explored habitat, bryophytes have revealed new species and even new families of bacteria. Furthermore, many bacteria remain as unculturable, likely comprising a large number of new species. Their roles could be important to both the bryophytes and the larger plant community.

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CHAPTER 19-2
BRYOPHYTE BACTERIA EFFECTS ON COMMUNITIES

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CHAPTER 19-2
BRYOPHYTE BACTERIA EFFECTS ON COMMUNITIES

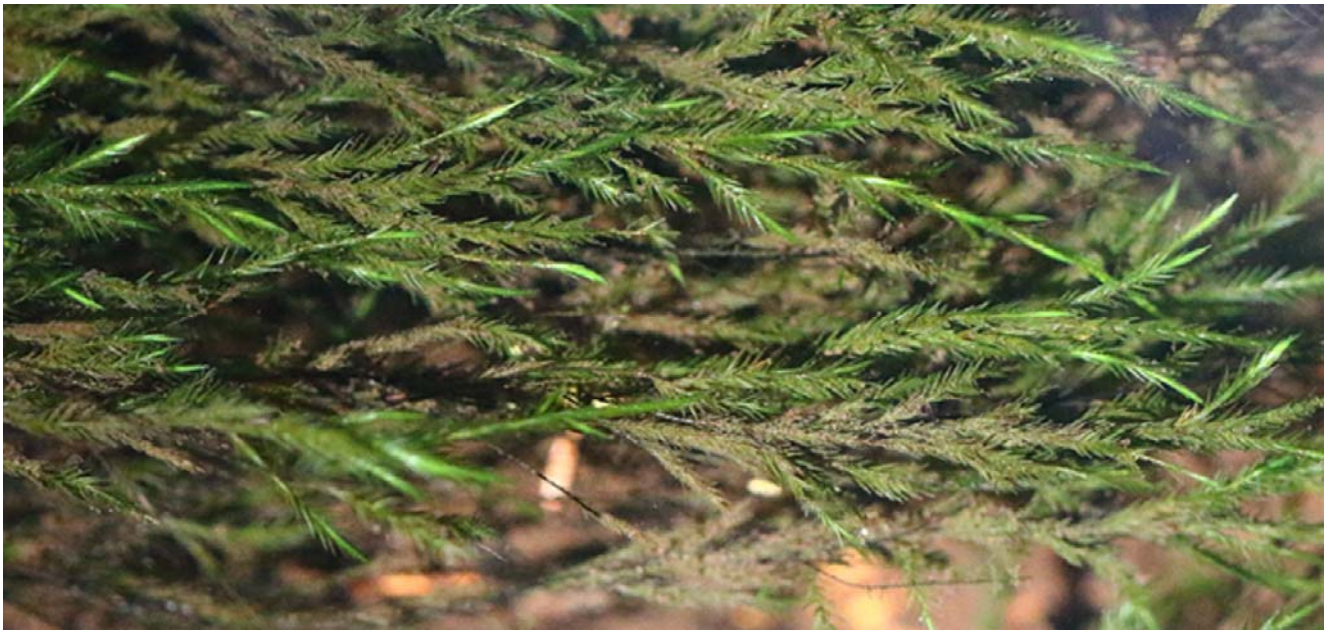

Figure 1. ***Fontinalis dalecarlica*** showing collection of sediments that harbor many bacteria, including ***Methylocystis*** that oxidizes CH_4, releasing CO_2. Photo by Jean Faubert, with permission.

Community Effects

During and van Tooren (1990) noted that bryophytes occur in microhabitats that are formed by the physical environment and typically modified by the tracheophyte vegetation occurring with them, but the bryophytes are typically treated as if they are isolated from other plants and other organisms in the environment. More realistically, we are now beginning to realize the importance of the interactions between bryophytes and other organisms. These interactions are involved in competitive, parasitic, symbiotic, and mutualistic relationships. During and van Tooren pointed out that information regarding the relationships of bryophytes with other organisms, including bacteria, is essential for understanding mineral nutrition, carbon economy, herbivory, growth, development, and the overall ecological role of the bryophytes.

Reboledo and León (2021) again pointed out the importance of bryophyte-microorganism interactions. They pointed out that these interactions had developed during coevolution of the bryophytes with microorganisms. Some of the interactions took the place of substances the bryophytes would otherwise have needed to produce themselves, thus saving them energy. They also avoided complex pathways that responded to environmental differences and changes such as seasons.

Sun *et al*. (2017) used bryophyte removal experiments to learn that absence of bryophytes caused a change in the soil microbial community in the conifer-dominated forest and an ericaceous shrubland of the alpine Tibetan Plateau. Frahm *et al* (2012) suggested that bacterial contamination may affect the antibiotic effect of bryophytes on seed germination.

Ma *et al*. (2017a) examined the bacterial communities on four moss species [***Campyliadelphus polygamus*** (Figure 2), ***Cratoneuron filicinum*** (Figure 3)***, Grimmia pilifera*** (Figure 4), ***Pylaisia polyantha*** (Figure 5)]. They found a total of 279 genera comprised of 558 **OTU's** (operational taxonomic units). Of the 16 bacterial phyla found, the **Pseudomonadota** and **Actinomycetota** were the two most abundant phyla. The most common bacterial genera were ***Bosea, Cellvibrio***, ***Friedmanniella***, ***Jatrophihabitans***, ***Lapillicoccus***, and ***Oligoflexus***. The two wet-habitat mosses (***Campyliadelphus polygamus, Cratoneuron filicinum***) had similar bacterial communities, differing from those of the two relatively dry habitat species (***Grimmia pilifera***, ***Pylaisia polyantha***) that also had similar bacterial communities. The bacterial communities in the summer and autumn were most similar on each moss species. However the season was not the most important factor in causing community differences.

Figure 2. ***Campyliadelphus polygamus***, a moss species that hosts mostly **Pseudomonadota** and **Actinomycetota**. Photo by Jean Faubert, with permission.

Figure 3. ***Cratoneuron filicinum***, a moss species that hosts mostly **Pseudomonadota** and **Actinomycetota**. Photo by David T. Holyoak, with permission.

Figure 4. ***Grimmia pilifera***, a moss species that hosts mostly **Pseudomonadota** and **Actinomycetota**. Photo by Wayne Lampa, through Creative Commons.

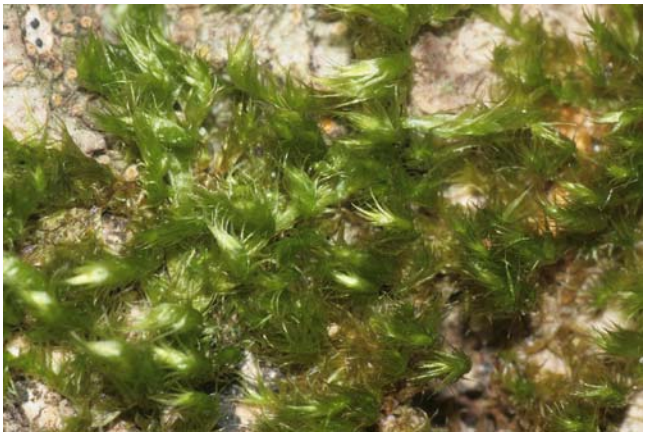

Figure 5. ***Pylaisia polyantha***, a moss species that hosts mostly **Pseudomonadota** and **Actinomycetota**. Photo by Hermann Schachner, through Creative Commons.

Tang *et al*. (2016) were curious about the specificity of the bacteria on the bryophytes. They investigated ten liverworts and ten mosses from Tibet, China, using sequencing techniques. Six of the mosses had bacterial communities with a higher community similarity, but the remaining four mosses had communities that were more similar to those of the ten liverworts. Tang and coworkers concluded that the phylogeny of hosts has a strong influence on the associated bacterial community and that niche also plays important roles when the hosts are phylogenetically more similar.

Harris and Tibbles (1997) compared bacterial productivity in four Antarctic habitats. These included soils from four different habitats: beneath moss beds, from nests of snow petrel (*Pagodroma nivea*), exposed unvegetated soil (polygon soil) 5 m away from nests, and exposed polygon soil on nunataks without nests of breeding birds. The moisture levels from nest entrances and beneath mosses were much higher than in those from unvegetated exposed polygons. Mosses also modify temperatures, providing much cooler summer temperatures than exposed polygons on continental Antarctica, which are greater than 20°C at midday, and exhibited less temperature fluctuation. Harris and Tibbles considered these moss beds to be bacterial "hotspots," although based on temperature "coolspots" might be more appropriate. They considered that bacterial productivity in moss soils was typically nutrient limited, whereas in the polygons moisture was a more important factor.

Opelt and Berg (2004) considered the bryophytes to serve as a diverse community reservoir of bacteria that provided antibiotics against plant pathogens. Koua *et al*. (2015), in Japan, found that many of the bacteria associated with bryophytes played critical roles in soil nutrient enrichment, especially in nitrogen fixation. They seem to be especially important as hosts of nitrogen-fixing bacteria, contributing to biogeochemical cycling (Cornelissen *et al*. 2007).

Vollár *et al*. (2018) found that among the 42 bryophyte species in their study, the families **Brachytheciaceae** and **Amblystegiaceae** produced the greatest numbers of antiproliferative extracts – extracts that worked against the proliferation of cancer cells. ***Plagiomnium cuspidatum*** (Figure 6) seemed to be the most active, affecting 8 bacterial strains. As in several other bryophyte studies (*e.g.*

Bodade *et al*. 2008; Liu & Wang 2010; Liyanage *et al*. 2015; Sabovljević *et al*. 2010), ***Staphylococcus aureus*** (Figure 7) was the most susceptible to the antiproliferation activity. ***Paraleucobryum longifolium*** (Figure 8) exhibited the highest activity.

Figure 6. ***Plagiomnium cuspidatum***, most active among 42 species of bryophytes, affecting 8 bacterial strains. Photo by Hermann Schachner, through Creative Commons.

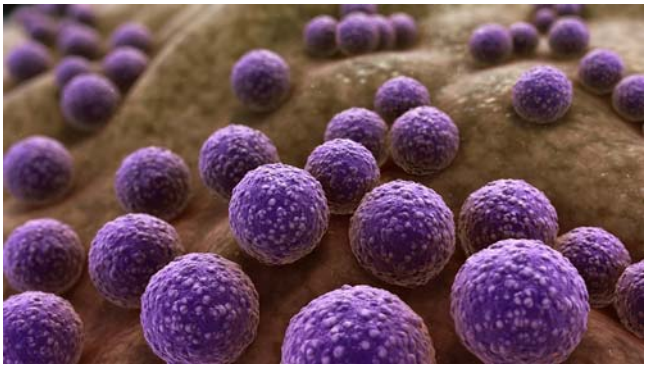

Figure 7. ***Staphylococcus aureus***, a species that among the most susceptible to inhibition by bryophyte extracts. Photo from <www.scientificanimations.com>, through Creative Commons.

Figure 8. ***Paraleucobryum longifolium***, the species with the greatest antibacterial activity among 42 species of bryophytes tested. Photo by Hermann Schachner, through Creative Commons.

Koua *et al*. (2015) reiterated that little is known about the bryophyte-associated microbial diversity or their role in soil enrichment and nitrogen fixation. As community members, the bacteria associated with bryophytes have the potential to infect other members of the community. This is especially true for plant pathogens, but the bryophytes can also serve as a refuge for bacteria that affect animals and fungi.

Zhu *et al*. (2006) assayed 60 bryophyte species for their antibacterial activity and found that 93.3% of the species demonstrated antibacterial activity against at least two of the seven tested bacterial species [***Priestia megaterium*** (Figure 9) – syn. = *Bacillus megaterium*, ***Bacillus subtilis*** (Figure 10), ***Bacillus thuringiensis*** (Figure 11), ***Escherichia coli*** (Figure 12), ***Pseudomonas aeruginosa*** (Figure 13), ***Pseudomonas putida*** (see Figure 13), and ***Staphylococcus aureus*** (Figure 7)]. This activity was particularly strong in the liverwort genera ***Conocephalum*** (Figure 14), ***Frullania*** (Figure 15), ***Herbertus*** (Figure 16), ***Marchantia*** (Figure 17), ***Mastigophora*** (Figure 18), and ***Porella*** (Figure 19. But what does this activity against human tracheophyte pathogens mean for the communities where these bryophytes live?

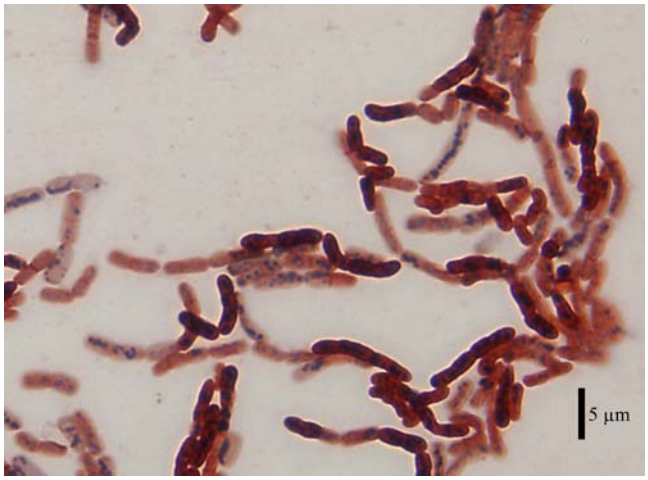

Figure 9. ***Priestia megaterium*** DSM-90 cells colored with Sudan black and safranin, a species that is affected by antibacterial compounds from bryophytes in China. Photo by Osmoregulator at English Wikipedia, through Creative Commons.

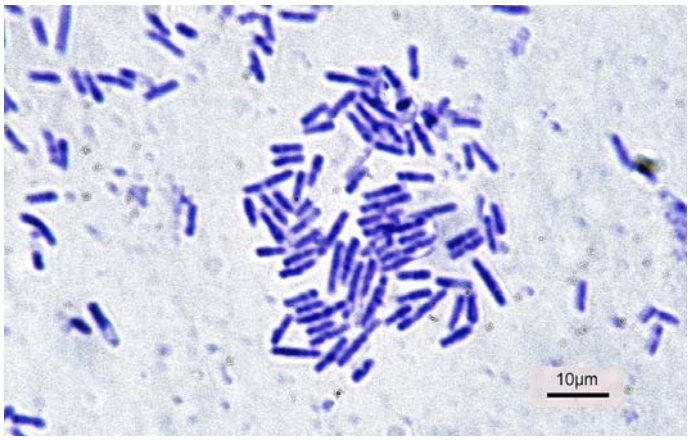

Figure 10. ***Bacillus subtilis***, a species that is affected by antibacterial compounds from bryophytes in China. Photo by Graham Beards, through Creative Commons.

Figure 11. ***Bacillus thuringiensis***, a species that is affected by antibacterial compounds from bryophytes in China. Photo by Dr. Sahay, through Creative Commons.

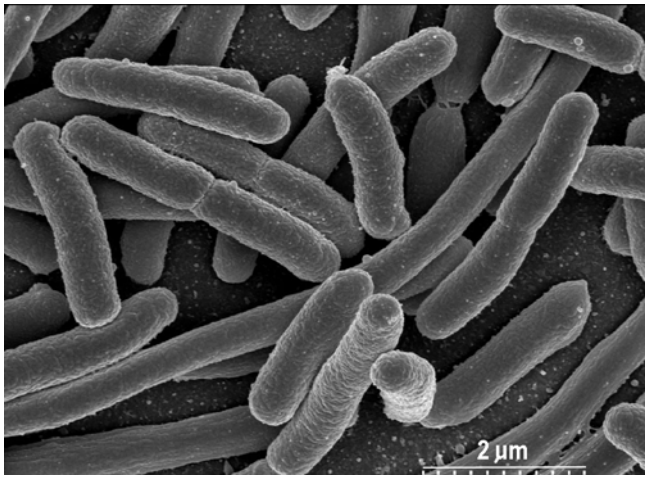

Figure 12. ***Escherichia coli***, a species that is affected by antibacterial compounds from bryophytes in China. Photo by Rocky Mountain Laboratories, NIAID, NIH - NIAID, through public domain.

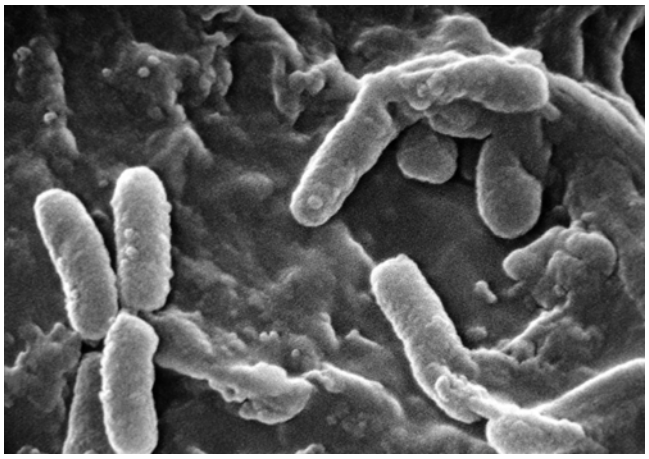

Figure 13. ***Pseudomonas aeruginosa*** SEM, a species that is affected by antibacterial compounds from bryophytes in China. Photo by Janice Haney Carr, CDC, through public domain.

Figure 14. ***Conocephalum***, a genus in China with particularly strong antibacterial activity. Photo by Don Loarie, through Creative Commons.

Figure 15. ***Frullania dilatata***, in a genus in China with particularly strong antibacterial activity. Photo by Bernd Haynold, through Creative Commons.

Figure 16. ***Herbertus aduncus***, in a genus in China with particularly strong antibacterial activity. Photo from Botany Website, UBC, with permission.

Figure 17. ***Marchantia polymorpha***, in a genus in China with particularly strong antibacterial activity. Photo by Denis Barthel, through Creative Commons.

Figure 18. ***Mastigophora woodsii***, in a genus in China with particularly strong antibacterial activity. Photo by Jo Denyer, with permission.

Figure 19. ***Porella platyphylla***, in a genus in China with particularly strong antibacterial activity. Photo by Hermann Schachner, through Creative Commons.

In one study ***Pseudomonas putida*** (see Figure 13) is most sensitive to the extracts of mosses, and ***Bacillus subtilis*** (Figure 10) is most sensitive to the extracts of liverworts (Zhu *et al*. 2006). ***Staphylococcus aureus*** (Figure 7) is the most resistant of the seven tested bacteria to the extracts of both liverworts and mosses, contrasting with its widespread susceptibility to bryophyte extracts in a number of other studies (*e.g.* Bodade *et al*. 2008; Liu & Wang 2010; Liyanage *et al*. 2015; Sabovljević *et al*. 2010). This suggests that some bryophytes could serve as a refuge for the ***Staphylococcus aureus***, but there is evidence that suggests that the antibiotics against ***S. aureus*** from some of the bryophytes are only produced when the bacteria are present (Sabovljević *et al*. 2010).

The importance of this inducible response to the community has not been investigated. If the antibiotics manufactured by bryophytes are effective against these bacteria that are not known to be pathogenic to bryophytes, how might these antibiotics affect other bacteria in the ecosystem? What selection pressures kept these antibiotic properties in the library of secondary compounds produced by bryophytes that weren't harmed by them? How can we explain that ***Bacillus subtilus*** is the most sensitive of the seven tested bacteria to liverwort extracts and that ***Pseudomonas putida*** is the most sensitive to moss extracts (Zhu *et al*. 2006)? And why do 99% of the bacteria found with mosses produce antifungal compounds (Opelt and Berg 2004)? Why are there no compounds produced by any liverwort as protection against fungi (Banerjee & Sen 1979)? Why should bryophytes produce so many compounds that protect other organisms, but at the same time depend on bacteria to produce some compounds that protect the bryophytes?

Many of the bacteria associated with bryophytes appear to be unknown because they do not grow on standard media (see Vesty *et al*. 2020).

Are some of these undetected bacteria the sources of any of the antibiotic compounds that we attribute to the bryophytes? Are we missing some antibiotic compounds when we culture the bryophytes axenically before testing them, thus failing to elicit any inducible responses (see Sabovljević *et al*. 2010)? Among these bacteria, how important are they to soil nutrient cycling? Are they nucleators that affect our weather? Are the bryophytes a reservoir for ice-nucleators that may be beneficial or detrimental to other kinds of plants? What sorts of selection pressures exist for these less known or unknown bacteria?

Using DNA and RNA techniques we are able to assess such differences without the need to name the bacteria involved. In China, Wang *et al*. (2018) found abundant bacteria associated with all the mosses they sampled and identified in this manner. These were mostly in the phyla **Pseudomonadota** and **Actinomycetota**. Their OTU level hierarchy separated the bacteria into two main branches of aquatic vs terrestrial. The aquatic habitat showed larger differences in the bacterial community composition than did the terrestrial habitat. Thus, the habitat of the host bryophyte is an important factor in determining the community.

Streams and Rivers

Bryophytes in streams typically are covered with bacteria, making it difficult to assess productivity of the bryophytes alone (Arscott *et al*. 1998). These are difficult to remove, and the role of the bacteria in producing CO_2 that bryophytes can use in photosynthesis needs to be assessed. Furthermore, the bryophytes trap silt and organic

matter (Figure 20) that flows in the stream or river, making them an important habitat for some kinds of bacteria.

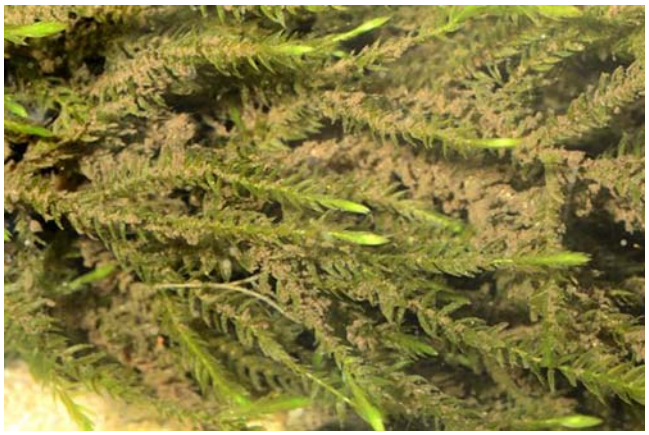

Figure 20. ***Fontinalis antipyretica*** with detritus that can serve as food for bacteria and macroinvertebrate scrapers. Photo by J. C. Schou, with permission.

In their study of carbon sources used by primary consumers in two oligotrophic rivers, McWilliams-Hughes *et al*. (2009) found that tracheophyte macrophytes and **Cyanobacteria** were unimportant as food sources for insect scrapers. Rather, 98% of the scrapers exhibited δ13C values that were enriched with bryophyte δ13C values, especially when slow-flowing habitats were excluded from the analysis. ***Fontinalis*** sp. (Figure 21) was abundant in headwater (low order) streams, where it exhibited more dependence by scrapers than the dependence by scrapers associated with the ***Drepanocladus*** (Figure 22) sp. of the high-order streams (with higher order streams having more combining tributaries). This is consistent with the greater cover by bryophytes in the headwater streams. They suggested that scrapers might switch to marginal food sources such as bryophytes in the headwaters where productivity and nutrients are low. But what is really providing their food? Might it be the bacteria and other periphyton that are always associated with the mosses? I have seen a Dipteran larva eat "dirty" mosses (Figure 20) and watched the feces come out as clean moss fragments.

Figure 21. ***Fontinalis antipyretica***, home for macroinvertebrate scrapers in streams. Photo by Claire Halpin, with permission.

Figure 22. ***Drepanocladus aduncus***, in a genus in slower water in streams than that of ***Fontinalis*** and where scrapers are less dependent on it for food. Photo by Hermann Schachner, through Creative Commons.

Špoljar *et al*. (2012) found that when the bryophyte coverage was scattered the diversity of algae, protozoa, and meiofauna was governed by the amount of suspended organic matter and epiphytes. They concluded that this was the result of enrichment by seston travelling downstream. One can assume that bacteria are associated with this seston (Bowden *et al*. 2017), but what is their role? Are the bacteria food themselves, or are they only important in releasing nutrients from the seston?

Heino *et al*. (2015) examined the metacommunity structure by surveying the diatoms, bacteria, bryophytes, and invertebrates in three drainage basins in Finland. The species were mostly distributed independently of one another in the southernmost drainage basin, but in the northernmost drainage basin there were discrete community types. These relationships seem only to be related to geography and not to environmental heterogeneity. They suggested that environmental variables may vary between organismal groups.

Stream conditions would seem to be ideal for many kinds of bacteria. The constant supply of sediments that get carried during times of rapid flow are trapped by the bryophytes, where these sediments can accumulate. But what protections do the stream bryophytes have against this potential associated bacterial onslaught? Basile *et al*. (1998) used an acetone extract to assess the bacterial activity of the stream moss ***Platyhypnidium riparioides*** (Figure 23) against 11 strains of bacteria. They found that this extract was active against some Gram-negative strains. Are these antibacterial properties effective against the bacteria that normally inhabit this moss? Most of the testing has been with human pathogens, but early assessments did not determine the natural bacterial flora of the mosses.

What quickly becomes evident by these studies is that we know little about the bryophyte bacteria and their role in the stream ecosystems. Meyer *et al*. (2007) commented that whereas we have an understanding of stream fungal diversity and know that fungi are critical to the organic matter dynamics and food webs in headwater streams, we know little about bacterial diversity.

Figure 23. ***Platyhypnidium riparioides***, a stream moss with antibacterial activity against 11 strains. Photo by J. C. Schou, with permission.

Demars *et al*. (2020) showed that addition of carbon caused a rapid increase in both photosynthesis and heterotrophic respiration in a stream. In the control stream, with no added carbon, the carbon exchange between the autotrophs and bacteria accounted for ~49% of the bacterial production and 37% of the net primary production during periods of stable flow. The researchers considered the bryophyte contribution to primary productivity to be negligible, so they did not include them in their food flow calculations. Furthermore, the added sucrose (carbon) in the experiment did not end up in the bryophytes. It is likely that such carbon exchange between the bacteria and bryophytes in an important occurrence when the predominant autotrophs are bryophytes.

Yakubik *et al*. (2000) noted that some bacteria in bryophyte mats contribute to denitrification. This can be accentuated in lower reaches of a stream where the water is slower. This lower flow rate results in less mixing and permits the bacteria to colonize the mosses more easily, and provides a longer residence time for the denitrification to occur.

On the other hand, Leppänen (2013) demonstrated that N_2 fixation can occur in association with ***Fontinalis dalecarlica*** (Figure 1), although the rates are low. The highest activity was in the upper, green portion, compared to the lower, brown portion of the plants. In boreal forest streams in Finland, it oxidized CH_4 at the highest rate among the boreal mosses investigated, which included peatland and feather mosses. It seems certain that the N_2 fixation is dependent on an external energy source and is closely connected with the oxidation of CH_4. But N fixation must take place in an oxygen-free environment. As much as 74% of this fixation is tied to the nifH sequences best identified as the bacterium ***Methylocystis*** (Figure 24). This evidence, coupled with the high CH_4 rates, suggests that ***Fontinalis dalecarlica*** is important in the CH_4 of boreal rivers. The bacteria are located on the leaf, in the cavity between the leaf and stem, but can also occur inside the outer stem cells. There is a mucous-like substance in the cells of the moss that may be important in the relationship. Solheim *et al*. (2004) suggested that the mucous might result from or contribute to a symbiotic relationship between the bacteria and moss. On the other hand, Postgate (1998) suggested that it could be a protective strategy to create an anaerobic environment for the nitrogenase to work.

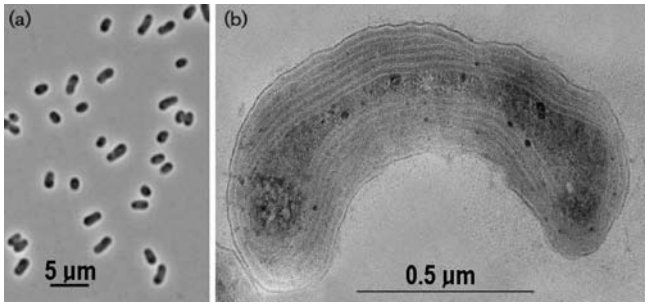

Figure 24. ***Methylocystis bryophila*** extracted from peat. **a.** Phase-contrast micrograph of cells. **b.** Electron micrograph of an ultrathin section of a cell. From Belova *et al*. 2013, with permission from Svetlana Dedysh.

Martinez-Abaigar *et al*. (1993) evaluated the effects of organic pollution on the mosses ***Fontinalis antipyretica*** (Figure 20, Figure 21) and ***Brachythecium rivulare*** (Figure 25) and the leafy liverwort ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 26) in rivers in Spain. They suggested that the morphology of the bryophytes influenced the sensitivity to the pollution, resulting from differences in their ability to capture suspended organic materials (Figure 20). This organic matter promotes the growth of bacteria and their ability to degrade and cause senescence in the bryophytes.

Figure 25. ***Brachythecium rivulare***, a species that captures organic materials that promote the growth of bacteria. Photo by Hugues Tinguy, with permission.

Figure 26. ***Jungermannia exsertifolia*** subsp. ***cordifolia***, a species that captures organic materials that promote the growth of bacteria. Photo by Claire Halpin, with permission.

The leafy liverwort ***Solenostoma vulcanicola*** (Figure 27) exhibits rod-shaped bacteria associated with numerous holes in its cell walls, suggesting that bacteria play a role in its decomposition (Satake & Miyasaka 1984).

Figure 27. ***Solenostoma vulcanicola*** in Japan, a species with colonies of rod-shaped bacteria that create numerous holes in its cell walls. Photo by Masaki Shimamura, with permission.

Faunal Connections

Bryophytes can play a key role in food for stream nematodes (Dražina *et al*. 2014). Dražina *et al*. (2013) found that it is the suction-feeding nematodes that dominate among the stream bryophytes, the same group that is common among terrestrial mosses in Europe (Barbuto & Zullini 2006). The nematodes use their stylets to pierce the bryophyte cells and suck out the contents (Traunspurger 2002; Dražina *et al*. 2013). Other nematodes feed on the epiphyton and deposits associated with the bryophytes (Suren 1992; Majdi *et al*. 2011). Thus, not only do some stylet-feeding nematodes eat bryophytes, but bryophytes provide the substrate for detrital pathways for nematode food. Furthermore, uptake of bacterial-respired CO_2 by the bryophytes (and algae) finds its way into these photosynthetic bryophytes, thus increasing the food available to both stylet bryophyte-feeding nematodes and other invertebrates (Demars *et al*. 2021).

In contrast to many earlier studies, Demars *et al*. (2021) suggested that the aquatic bryophytes covered by periphyton might contribute to the macroinvertebrate diet, a suggestion already supported by some earlier researchers (Jones 1949; Dangles 2002; Parker & Huryn 2006; Carroll *et al*. 2016). This also contrasts with their earlier conclusion (Demars *et al*. 2020) that this bryophyte-periphyton association does not contribute much to primary productivity. Stream ecologists are beginning to rethink the role of bryophytes in streams.

Antarctic

Christie (1987) contrasted the nitrogen in a wet carpet and dry peat in the Antarctic. The numbers of sulphate-reducing bacteria [***Desulfovibrio*** (Figure 28) and ***Desulfotomaculum*** (Figure 29) and of ***Clostridium*** (Figure 30) were very low, even in the wet carpet. The low acetylene reduction activity of these bacteria and absence of ***Azotobacter*** (Figure 31) suggest that nitrogen fixation was not an important contributor to nitrogen present. There furthermore were no nitrifying bacteria. However, there were substantial numbers of proteolytic and nitrate-respiring bacteria as well as a small number of denitrifying bacteria. The heterotrophic groups were more abundant in the wet carpet than in the dry turf.

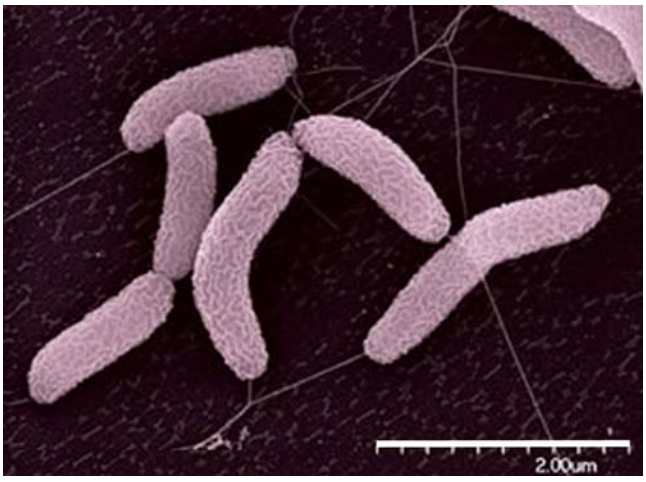

Figure 28. ***Desulfovibrio desulfuricans***, a sulfate-reducing bacterium in a genus with low numbers in the Antarctic peat. Photo through public domain.

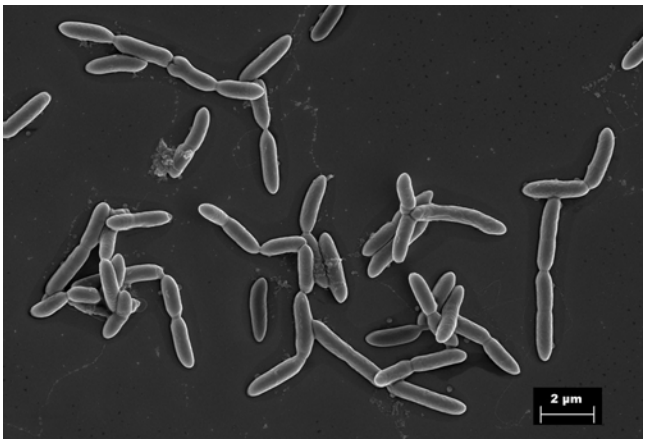

Figure 29. ***Desulfotomaculum***, a sulfate-reducing bacterium with low numbers in the Antarctic peat. Photo by Manfred Rohde, through Creative Commons.

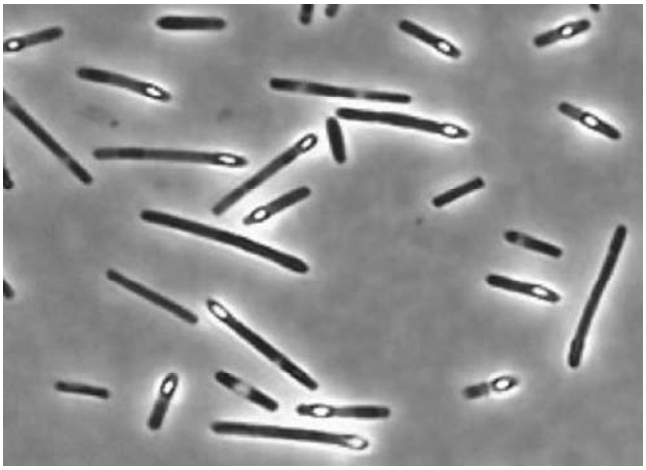

Figure 30. ***Clostridium perfringens*** sporulating, in a bacterial genus with low numbers in the Antarctic peat. Photo by Oregon State University, through Creative Commons.

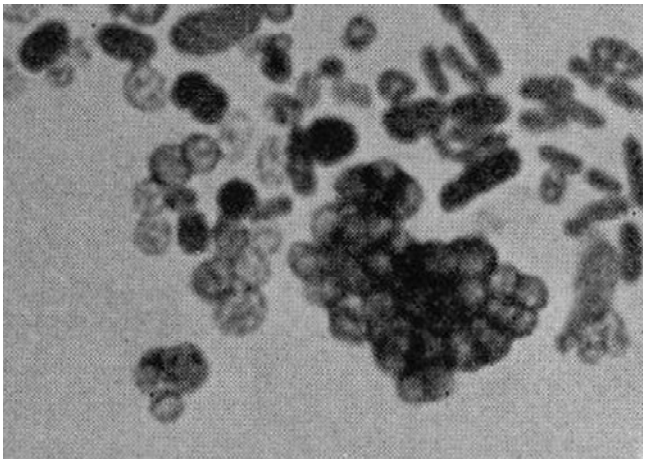

Figure 31. ***Azotobacter***, a nitrogen-fixing bacterium that is absent in the Antarctic peat. Photo by Dan H. Jones, through public domain.

Park *et al*. (2013) investigated the neglected bacterial relationships among Antarctic bryophytes, using the moss ***Sanionia uncinata*** (Figure 32). They found that the **Pseudomonadota** was the dominant phylum, comprising 65.5% of the associated bacteria. The **Bacteroidota** (29.1%) and **Actinomycetota** (11.7%) were also important. The bacteria on the mosses exhibited zonation, with the **Alphaproteobacteria** comprising only 2% of the bacterial flora in the upper green parts, but were in significantly greater proportion at 22.2% in the lower brown portions. Park and coworkers considered it likely that there were specific relationships between these endophytes and the host moss.

Figure 32. ***Sanionia uncinata***, a species with **Proteobacteria** comprising 65.5% of the associated bacteria in an Antarctic study. Photo by Hermann Schachner, through Creative Commons.

Raymond (2016) answered a question I raised earlier, before reading this – Is it the bryophyte or the bacterium that produces the external ice-binding proteins? A strong ice-pitting activity was known in the Antarctic moss ***Bryum argenteum*** (Figure 33). Raymond realized that this was a sign of ice-binding proteins that protect against freezing damage. He found that this ice-binding activity is the result of ice-binding proteins produced by bacteria living on the moss leaves. These were mostly **Actinomycetota** and **Bacteroidota**. He found 42 bacterial ice-binding proteins. These operate in a symbiotic relationship with the moss, with the latter providing the sustaining energy source and the bacteria protecting the moss from freezing damage.

Figure 33. ***Bryum argenteum***, an Antarctic moss with a strong ice-pitting activity. Photo by Claire Halpin, with permission.

Arctic Alpine

Löffler *et al*. (2008) found that an increase in the occurrence of bryophytes and shrubs along an arctic-alpine gradient in Scandinavia would also increase the microbial activity. They also found that higher temperatures promoted greater soil microbial activity in the summer. Whereas these temperatures are expected to promote shrub growth as the climate warms, the higher moisture expected with climate change is expected to promote bryophyte growth. Both temperature and moisture increases should increase the microbial activity in the soil in heathlands in Scandinavia. Spruce forests (Figure 34) had the highest bacterial α-diversity, whereas the aspen forests (Figure 35) exhibited greater turnover (β-diversity) and higher γ-diversity.

Figure 34. ***Picea mariana*** in Alaskan taiga, a forest type that had the highest bacterial α-diversity in Scandinavia. Photo from NOAA, through public domain.

Figure 35. ***Populus tremuloides*** (aspen), a forest type that had the highest turnover (β-diversity) and higher γ-diversity of microbes in Scandinavia. Photo by Famartin, through Creative Commons.

Boreal Forest

The boreal forest bryophyte bacterial communities have thus far been widely neglected. Only the **Cyanobacteria** (Figure 36) have attracted the attention of researchers. They will be covered in a separate chapter, but their relative role needs to be clarified here.

Figure 36. ***Chroococcus***, one of the common **Cyanobacteria** associated with ***Sphagnum***. Photo by M. Lorenz, through Creative Commons.

In boreal forests in Finland and elsewhere, the feather mosses ***Hylocomium splendens*** (Figure 37) and ***Pleurozium schreberi*** (Figure 38) predominate (Leppänen 2013). The N fixation activity associated with these mosses is well known (Meeks 1998; DeLuca *et al*. 2002; Gundale *et al*. 2012). As in ***Fontinalis dalecarlica*** (Figure 1), Gavazov *et al*. (2010) found higher nitrogen fixation in the upper portions of ***Hylocomium splendens***. This suggests that light has an important role in the fixation (Meeks 1998; Gundale *et al*. 2012), implicating **Cyanobacteria**. But in the boreal forests of Finland, there was no significant amount of methane (CH_4) oxidation activity, a phenomenon that Leppänen (2013) attributed to the low concentrations of CH_4 in the forest habitats and moisture conditions that are unsuitable for methanotrophs (Larmola *et al*. 2010). Since methane oxidation is often accompanied by nitrogen fixation, this leaves us wondering which organisms are contributing to these higher levels of nitrogen fixation in younger portions of the mosses.

Figure 37. ***Hylocomium splendens***, a boreal forest feather moss that is important in hosting bacteria that fix nitrogen. Photo by Clare Halpin, with permission.

Figure 38. ***Pleurozium schreberi***, a moss shown to be less important in driving bacterial communities in the boreal forest than the forest type. Photo by Hugues Tinguy, with permission.

DeLuca *et al*. (2002) reported that the **Cyanobacteria** (Figure 36) association with ***Pleurozium schreberi*** (Figure 38) alone fixes 1.5-2.0 kg N ha^{-1} yr^{-1} in the mid to late successional forests of northern Scandinavia and Finland. Gavazov *et al*. (2010) found that liverworts did not fix detectable amounts of N_2 in the boreal/sub-Arctic forests. Lichens had the highest rates of fixation, but because of their greater biomass, the mosses served as the nitrogen sink through their nitrogen fixation associations.

Rodríguez-Rodríguez *et al*. (2022) hypothesized that moss species would be the driver in the composition of the ecologically important bacterial communities associated with them. They quantified changes in bacterial communities as a function of host species [mosses ***Pleurozium schreberi*** (Figure 38) and ***Ptilium crista-castrensis*** (Figure 39)] and forest type [coniferous black spruce (Figure 34) versus deciduous broadleaf trembling

aspen (Figure 35)] in eastern Canada. But in fact, it was forest type, not moss host species, that was the main factor affecting bacterial community composition on the mosses.

Figure 39. ***Ptilium crista-castrensis***, a moss shown to be less important in driving bacterial communities in the boreal forest that the forest type. Photo by M. Porcius Cato, through Creative Commons.

Among these boreal bryophytes, at least some of the nitrogen fixation seems to occur without the activity of **Cyanobacteria** (Figure 36), as for example associations with members of ***Dicranum*** (Gundale *et al*. 2011). ***Pleurozium schreberi*** (Figure 38) and ***Sanionia uncinata*** (Figure 32) exhibited relatively similar mean rates of N_2-fixation (46.1 µg N g^{-1} day^{-1} and 52.4 µg N g^{-1} day^{-1} respectively), despite a dominance of **Alphaproteobacteria** N_2-fixers 21.4% vs 6..8% **Cyanobacteria**) on ***Pleurozium schreberi*** and a dominance of **Cyanobacteria** (79%) on ***Sanionia uncinata***, with only 7.2% **Alphaproteobacteria** as N_2-fixers (Holland-Moritz *et al.* 2018).

Holland-Moritz *et al*. (2018) indicated that the moss microbiome in the boreal forest is highly diverse, includes many undescribed taxa (including an undescribed phylum), and is a major contributor to nitrogen fixation beyond that from the **Cyanobacteria**. The average richness is 924 phylotypes per sample, dominated by 8 bacterial phyla: **Pseudomonadota** (44.8% of reads across all samples), **Acidomycetota** (10.8%), **Verrucomicrobiota** (9.8%), **Bacteroidota** (9.3%), **Cyanobacteria** (6.5%), **Candidate phyla WPS-2** (5.7%), **Planctomycetota** (5.2%), and **Actinomycetota** (4.2%). Cutler *et al*. (2017) found similar relative abundances on ***Pleurozium schreberi*** (Figure 38). Many of these bacteria are novel and undescribed lineages within the **Alphaproteobacteria** sub-phylum and the **Verrucomicrobiota** phylum (Bragina *et al.* 2015).

But many of the boreal forest phylotypes could not be classified beyond phylum or class (Holland-Moritz *et al*. 2018), emphasizing how little we know about these communities. Contrasting with the study of Rodríguez-Rodríguez *et al*. (2022) in eastern Canada, the identity of the moss species was more important than the site in determining the composition of the bacterial communities associated with the mosses near Fairbanks, Alaska, USA, with moss species accounting for 63% of the variation in bacterial community composition. The pleurocarpous moss ***Sanionia uncinata*** (Figure 32) had communities quite distinct from those of the other 6 moss species [***Pleurozium schreberi*** (Figure 38), ***Tomentypnum nitens*** (Figure 40), ***Aulacomnium palustre*** (Figure 41), ***A. turgidum*** (Figure 42), ***Dicranum elongatum*** (Figure 43), and ***Sphagnum capillifolium*** (Figure 44)]. Of the bacteria on ***Sanionia uncinata***, 59% were unique to that moss species. Only 77% of the 30 most abundant phylotypes present on the other mosses were present on ***S. uncinata***, whereas 90% of the 30 most abundant phylotypes were found on all the other moss species.

Figure 40. ***Tomentypnum nitens***, a species of fen mosses with bacteria that are similar to most of the other dominant fen mosses near Fairbanks, Alaska, USA. Photo by Hermann Schachner, through Creative Commons.

Figure 41. ***Aulacomnium palustre***, a species of fen mosses with bacteria associates that are similar to those of most of the other dominant fen mosses near Fairbanks, Alaska, USA. Photo by Kristian Peters, through Creative Commons.

Figure 42. ***Aulacomnium turgidum***, a species of fen mosses with bacteria that are similar to those of most of the other dominant fen mosses near Fairbanks, Alaska, USA. Photo by Mark Hill, with permission.

Figure 43. ***Dicranum elongatum***, a species of fen mosses with bacteria that are similar to those of most of the other dominant fen mosses near Fairbanks, Alaska, USA. Photo by Hermann Schachner, through Creative Commons.

Figure 44. ***Sphagnum capillifolium***, a species of fen mosses with bacteria that are similar to those of most of the other dominant fen mosses near Fairbanks, Alaska, USA. Photo by Blanka Aguero, with permission.

The moss-associated bacteria are likely to be anoxygenic phototrophs capable of carbon fixation via Rubisco, with an ability to utilize by-products of photorespiration from hosts via a glyoxylate shunt (Holland-Moritz *et al*. 2018). Furthermore, whereas most of the mosses were dominated by **Acetobacteraceae** (**Alphaproteobacteria**), **Acidobacteriaceae** (**Acidobacteriota**), and **Methylacidiphilales** (**Verrucomicrobiota**), ***Sanionia uncinata*** (Figure 32) had either a low abundance or total absence of these bacterial taxa. It was dominated instead by **Comamonadaceae**. (**Betaproteobacteria**), **Nostocacaceae** (**Cyanobacteria**), and **Chitinophagageae** (**Bacteroidota**). But why are these communities on ***Sanionia uncinata*** so different? Is it differences in microhabitat, or are the chemical defenders of these mosses different?

In an attempt to predict the effect of climate change on nitrogen fixation in the boreal forest, Gundale *et al*. (2012) assessed the effects of elevated temperatures on the relationship between bacteria and the feather moss substrate. They surmised that ***Pleurozium schreberi*** (Figure 38) may become a larger source of N in boreal forests relative to ***Hylocomium splendens*** (Figure 37) as climate warming progresses. Although the feather mosses have been considered to be cyanobacterial hosts, it is quite possible that these are also accompanied by Methanobacteria or other forms of non-cyanobacterial bacteria that are able to fix atmospheric nitrogen.

De Long *et al*. (2016) found that global warming altered the microbial communities in the soil, favoring communities based on bacteria. These, however, were mediated by mosses and shrubs, varying with successional stage. Mosses can serve as a buffer, like a heavy quilt, in modifying the soil temperature, as well as slowing the loss of moisture from the soil.

Peatland Bacterial Flora

Peatlands (Figure 45), often dominated by ***Sphagnum*** (Figure 46) as the keystone species, contain dead plant material accumulated over thousands of years (Kamal & Varma 2008). This habitat covers ~5-8% of the world's surface and contains ~3-3.5 times the amount of carbon stored by tropical rainforests. Weston *et al.* (2015) noted the importance of ***Sphagnum*** as a keystone species in a habitat that holds more than one-third of the terrestrial carbon on the planet Earth.

Figure 45. Peatland in Estonia. Photo by Martin Küttim, through Creative Commons.

Figure 46. ***Sphagnum*** spp. in Estonia. Photo by Martin Küttim, through Creative Commons.

In this role, ***Sphagnum*** (Figure 46) plays an important role, along with its associated microbiome, in carbon and nitrogen cycling (Kamal & Varma 2008). The combination of high acidity, low temperatures, and extremely low concentrations of nutrients in many ***Sphagnum*** habitats suggests that we should find unique communities of bacteria associated with these bryophytes.

Kostka *et al*. (2016) noted that ***Sphagnum*** (Figure 46) displays a diverse community of microorganisms on its surface and within the tissues. The prokaryotes and fungi can act as mutualists, symbionts, or antagonists. In these roles, methanotrophic and nitrogen-fixing bacteria may provide up to 20-30% of ***Sphagnum*** carbon and nitrogen.

Methane Oxidation

The production of methane (CH_4) in peatlands has become a hot topic recently because of its potential role in global warming. Wetlands, including peatlands, are the largest natural sources of atmospheric methane (Raghoebarsing *et al*. 2005). Nevertheless, most of the methane formed in wetlands stays in wetlands, where it is recycled. ***Sphagnum*** (Figure 46) species in peatlands use this methane through symbiosis with partly endophytic methanotrophic bacteria. These bacteria occur both on the stem leaves and in the hyaline cells of the ***Sphagnum***. The methane is rapidly oxidized by the bacteria to form CO_2 that is then fixed by the ***Sphagnum*** in photosynthesis and ultimately into plant sterols. The methane, through this pathway, provides 10-15% of the carbon source for ***Sphagnum***.

Nevertheless, peatlands are a major source of methane (Larmola *et al*. 2010). But ***Sphagnum***-dominated peatlands (Figure 45) have lower methane emissions than those known for other mire types. These researchers found that all 23 species of ***Sphagnum*** (*e*.g. Figure 46) in a boreal mire supported methanotrophic bacteria. Furthermore, transplanted ***Sphagnum*** with no indication of these methanotrophic bacteria exhibited the bacteria in their new location, showing rapid movement and/or activation of the bacteria among the ***Sphagnum***, and the importance of habitat. Water level is important in regulating the methane oxidation. The methanotroph ***Methylocystis*** (Figure 24) was present with ***Sphagnum*** plants that exhibited both active and inactive in methane oxidation, suggesting that its activity depended on water availability. Larmola and coworkers concluded that there is a loose symbiosis between the ***Sphagnum*** species and methanotrophic bacteria that contributes to 10-30% of the ***Sphagnum*** carbon.

In 2013, Belova *et al*. discovered a new species of ***Methylocystis***, ***M. bryophila*** (Figure 24), that could convert methane to CO_2 and could also fix nitrogen. This species was isolated from an acidic ***Sphagnum*** (Figure 46) peat-bog lake in Germany and from a peat bog in northern Russia. They attributed the nitrogen-fixing capability to an aerotolerant nitrogenase.

The most abundant methanotrophs in peatlands typically are **Alphaproteobacteria** and **Gammaproteobacteria** (Kip *et al*. 2010). Within the hyaline cells, ***Sphagnum*** hosts other bacteria that decrease the O_2 concentration and increase the CO_2 concentration in these cells (Granhall & Hofsten 1976), thus favoring photosynthesis in the nearby photosynthetic cells and benefitting the **Cyanobacteria** living in the hyaline cells. These **Cyanobacteria** fix N_2 that could be used by both the moss and the other bacteria (Leppänen 2013). But ***Sphagnum*** (Figure 46) can also house methanotrophic bacteria in these same cells, and these bacteria are capable of N_2 fixation as well. These methanotrophic bacteria can provide up to 30% of the carbon in the moss (Raghoebarsing *et al*. 2005) because they can fix nitrogen and oxidize CH_4 at the same time (Leppänen 2013). Most of the N_2 is fixed in the dark in aerobic conditions in the peat, indicating activity of heterotrophic bacteria (Kravchenko & Doroshenko 2003).

Nitrogen Sources

Aldous (2002) demonstrated that atmospheric nitrogen deposited among ***Sphagnum*** (Figure 46) plants was translocated to the capitula, with 11% to >80% in the lower and higher influx sites, respectively. Gerdol *et al*. (2006) noted that ***Sphagnum papillosum*** (Figure 47-Figure 48) was able to grow more when it had higher capitulum N concentrations. Both research groups noted that high water level favored the movement. Gerdol *et al*. (2006) found that the microbial nitrogen fixers were able to increase the nitrogen in the ***Sphagnum*** peatland. As with atmospheric nitrogen sources, these bacteria (no **Cyanobacteria** found) that occurred in senescing plant tissues, followed by upward transport of the fixed nitrogen, positively affected the growth of ***Sphagnum papillosum***. In dry growing seasons, enhancement of fixed nitrogen in the rhizosphere promoted growth of tracheophytes that subsequently increased their competition against the ***Sphagnum***. Experimental additions of nitrogen benefitted the ***Sphagnum*** only when the growing conditions inhibited the bacterial colonies.

Figure 47. ***Sphagnum papillosum*** in a peatland; microbial nitrogen fixers in senescing cells of this species are able to increase the nitrogen and benefit growth. Photo from Botany Website, UBC, with permission.

Figure 48. ***Sphagnum papillosum***, a species positively affected by increased nitrogen that is often contributed by bacteria. Photo by David T. Holyoak, with permission.

Bragina *et al*. (2013) found that genes for nitrogenase were both high in abundance and diverse among the ***Sphagnum*** (Figure 46). These were usually specific for each ***Sphagnum***. The methanotrophs, on the other hand, exhibited highly similar patterns among species. The sporophyte of the ***Sphagnum*** had a high proportion of specific **diazotrophs** (organisms able to grow without external sources of fixed nitrogen) (4%) but lacked methanotrophs. The nitrogen-fixing bacteria were highly specific and were transferred with the sporophyte.

Waughman and Bellamy (1980) found that nitrogen fixation rates were lower at the nutrient extremes, with that in bogs being especially low. The highest activity measured was >100 nmol C_2H_4 mL peat^{-1} d^{-1}. Nitrogenase activity had a positive correlation with *p*H and K and a negative correlation with Ca. Lower latitudes have a greater nitrogenase activity in peat than do higher latitudes, even when temperatures are factored in. In the south German mires the nitrogen fixed annually by the heterotrophic bacteria were 2100 mg N m^{-2} in fens, 530 in poor fens, and 70 in bogs.

Comparisons of *Sphagnum* Species

Bragina *et al*. (2012) compared the communities of bacteria on ***Sphagnum fallax*** (Figure 49) and ***S. angustifolium*** (Figure 50), two closely related species with distinct habitat nutrient preferences in weakly acid, mesotrophic situations influenced by minerotrophic groundwater. The two species also produce similar secondary metabolites. The two species exhibited high similarity (minimum of 95.5%) of bacterial colonization patterns. The interior of hyaline cells of the leaves were colonized primarily by **Alphaproteobacteria** (in **Pseudomonadota**). This group of bacteria was represented by a high degree of diversity, including ***Acidocella***, ***Acidisphaera***, ***Phenylobacterium***, and ***Rhodopila*** as the major bacterial taxa on both species of ***Sphagnum***, with no statistically significant differences between the microbial communities of the two ***Sphagnum*** species. The composition of the subdominant **Caulobacteraceae** did, however, vary between mosses, being more abundant with ***S. fallax***. In this group ***Phenylobacterium*** was detected all over, whereas ***Caulobacter*** (Figure 51), ***Gluconacetobacter*** (Figure 52), ***Methylocystis*** (Figure 24), ***Methylosinus***, and ***Rhizobium*** (Figure 53) occurred only with ***S. fallax***. The associated microbial community fulfills functions that can only be accomplished by the cooperation with the ***Sphagnum*** community. These include nitrogen fixation, solubilizing phosphorus, and providing carbon from peat-derived methane (Raghoebarsing *et al.* 2005; Opelt *et al.* 2007c). Bragina and coworkers considered the moss-bacterial communities to have the same close relationships that are present between ***Sphagnum*** and the ecology and function of the bog ecosystem.

Figure 49. ***Sphagnum fallax***, a species of weakly acid mesotrophic habitats with mostly **Verrucomicrobiota** and **Planctomycetota** as bacterial associates. Photo by Hugues Tinguy, with permission.

Figure 50. ***Sphagnum angustifolium***, a species that grows in weakly acid, mesotrophic situations influenced by minerotrophic groundwater. This species is colonized by a highly diverse group of **Alphaproteobacteria** in the hyaline cells of the leaves. Photo by Hermann Schachner, through Creative Commons.

Figure 51. ***Caulobacter crescentus***, in a genus that occurs with ***Sphagnum fallax***, but not with ***S. angustifolium***. Photo by USDA, through public domain.

Figure 52. ***Gluconacetobacter*** cellulose biofilm, a genus that occurs with ***Sphagnum fallax***, but not with ***S. angustifolium***. Photo through Creative Commons.

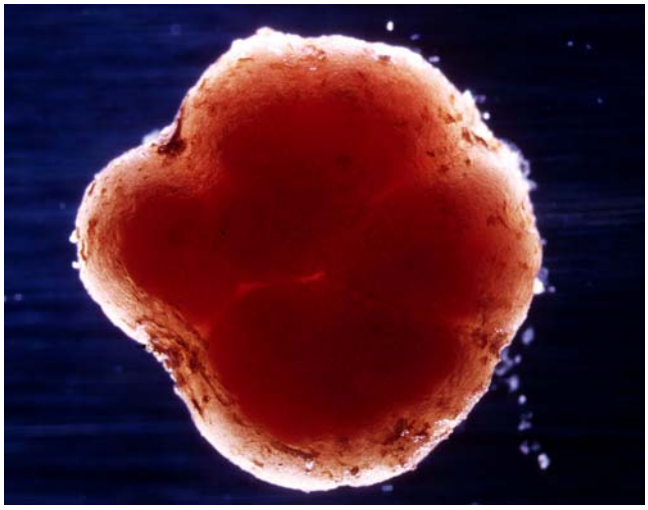

Figure 53. ***Rhizobium*** bacteria nodule, a genus that occurs with ***Sphagnum fallax***, but not with ***S. angustifolium***. Photo from CSIRO, through Creative Commons.

Bragina *et al*. (2012) also compared the bacterial diversity on ***Sphagnum divinum*** or ***S. medium*** (previously considered part of ***S. magellanicum***) (Figure 54) and ***S. fallax*** (Figure 49) in three alpine bogs in Austria. ***Sphagnum divinum*/*medium*** characterizes strongly acid habitats with poor nutrients, whereas ***S. fallax*** inhabits weakly acid mesotrophic habitats. ***Sphagnum divinum*/*medium*** was inhabited mainly by **Gammaproteobacteria** (in Phylum **Pseudomonadota**), whereas associates of ***S. fallax*** (Figure 55) were mainly in the phyla **Verrucomicrobiota** and **Planctomycetota**. Although the bacterial colonies occurred in high abundance in the dead hyaline cells, they were always connected with living photosynthetic cells (Figure 55). Bragina and coworkers found that nutrient richness and *p*H were the most important determining factors for bacterial communities. They found it interesting that the bacterial diversity was transferred from the sporophyte to the gametophyte, contrasting with the transfer from the soil in tracheophyte communities. Microbial fingerprints showed that bacterial species from different bogs had a high similarity within the same bryophyte species. They considered the plant to plant transfer of bacteria, rather than through a soil intermediary, to be a possible explanation of the high specificity of ***Sphagnum***-associated bacteria over long distances.

Figure 54. ***Sphagnum cf. divinum***, a species of strongly acid habitats with poor nutrients, and mostly with **Gammaproteobacteria**. Photo by Michael Lüth, with permission.

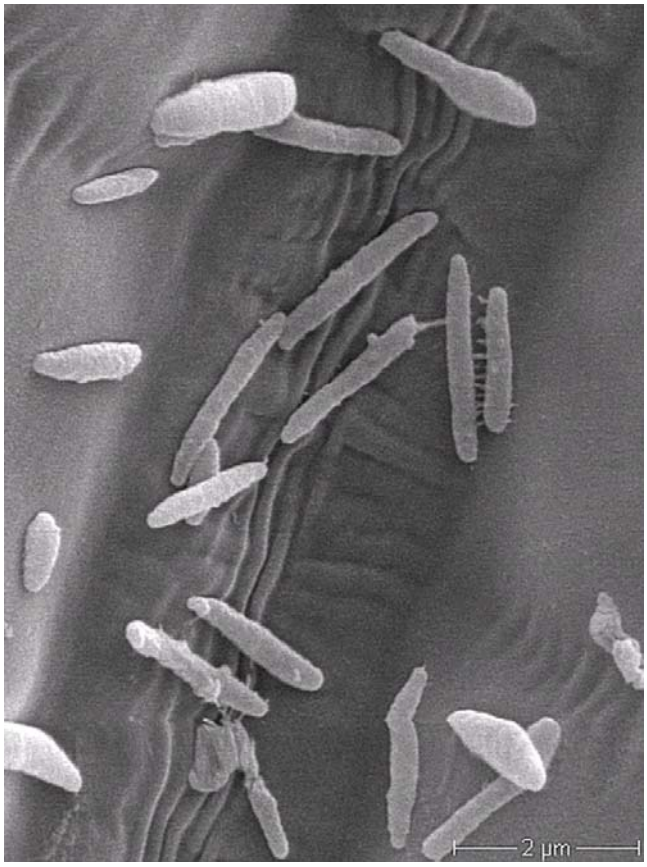

Figure 55. ***Sphagnum fallax*** bacteria SEM. Photo courtesy of Gabi Berg.

Shcherbakov *et al*. (2015) isolated bacterial populations from gametophytes of ***Sphagnum*** (Figure 54) from various geographic regions of Russia. Among the more than 400 strains isolated, ribosomal data indicated that the isolates were in the genera ***Pseudomonas*** (Figure 13) (20-57%), ***Collimonas*** (7-10%), ***Flavobacterium*** (Figure 56) (6-8%), ***Burkholderia*** (Figure 57) (5-6%), and ***Serratia*** (Figure 58) (3%). These are similar to the bacteria taxa reported for ***Sphagnum*** from the Austrian Alps (Bragina *et al*. 2015).

Figure 56. ***Flavobacterium columnare*** on gills of ***Delistes luxatus***; this bacterial genus is common on Russian ***Sphagnum***. Photo by S. Vanderkoo, through Creative Commons.

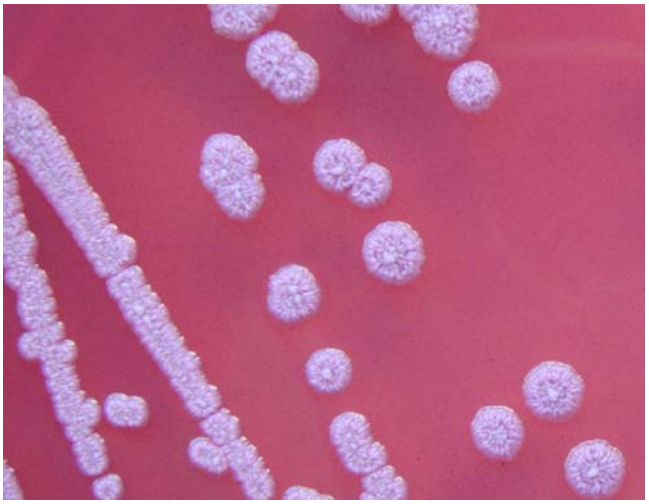

Figure 57. ***Burkholderia pseudomallei***, in a genus of bacteria that are antagonistic toward bryophytes in Germany. Photo by Gavin Koh, through Creative Commons.

Figure 58. ***Serratia marcescens*** antibiogram, in a genus among the most common antagonists toward bryophytes in Germany. Photo by Stefan Walkowski, through Creative Commons.

Tian *et al*. (2019) compared the microbial community associated with the brown (lower) and green portions of ***Sphagnum palustre*** (Figure 59) peat. **Alphaproteobacteria** (in phylum **Pseudomonadota**) were dominant in all samples. Members of the phylum **Acidobacteriota** were abundant in the ***S. palustre*** peat, whereas **Gammaproteobacteria** (in phylum **Pseudomonadota**) dominated the brown layer. **Cyanobacteria** dominated the green portion. They considered the structural differences in the microbiome to be mainly due to microhabitat differences. The microbial communities of the ***Sphagnum palustre*** peat was significantly influenced by the water table and the total nitrogen content.

Figure 59. ***Sphagnum palustre***, a species where **Alphaproteobacteria** is very frequent; **Gammaproteobacteria** dominates in the lower brown layer. Photo by Hugues Tinguy, with permission.

Opelt *et al*. (2007a, b) explored the bacterial relationships with ***Sphagnum divinum*/*medium*** (Figure 54) and ***S. fallax*** (Figure 49) from three locations in Germany and three in Norway. They particularly looked for bacteria that exhibited antagonistic activity against fungal pathogens; these comprised 48% of the isolates. ***Sphagnum divinum*/*medium*** housed 24% of the antagonists compared to only 19% for ***S. fallax***. Nevertheless, ***S. fallax*** bacterial communities exhibited a significantly higher diversity $\{H' = -\Sigma^{s}_{i=1} [(ni/N)\ln(ni/N)]\}$ than did the ***S. divinum*/*medium*** associates. More of the inhabitants of ***S. divinum*/*medium*** were specific to that species. The researchers suggested that the higher nutrient levels in the ***S. fallax*** habitat could explain the higher bacterial diversity.

Most of the antagonists in the Germany/Norway study were in the genera ***Serratia*** (Figure 58) (15%), ***Burkholderia*** (Figure 57) (13.5%), ***Staphylococcus*** (Figure 7) (13.5%), and ***Pseudomonas*** (Figure 13) (10%) (Opelt *et al*. 2007a). Whereas most of the antagonist strains had a high moss specificity, ***Burkholderia*** and ***Serratia*** had similar molecular fingerprints on both ***Sphagnum*** (Figure 49, Figure 54) species. A high proportion of the antagonist strains [***Hafnia*** (Figure 60), ***Pantoea*** (Figure 61)**,** ***Staphylococcus***, and ***Yersinia*** (Figure 62)] are known as facultative pathogens of humans.

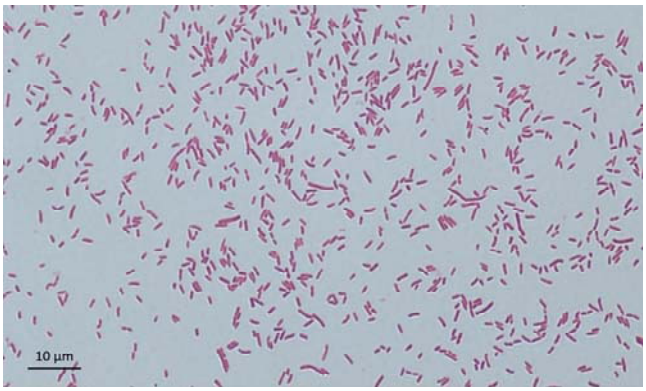

Figure 60. ***Hafnia alvei***, in a genus of bacteria that is antagonistic toward bryophytes in Germany and also a facultative pathogen of humans. Photo by Antoine2003, through Creative Commons.

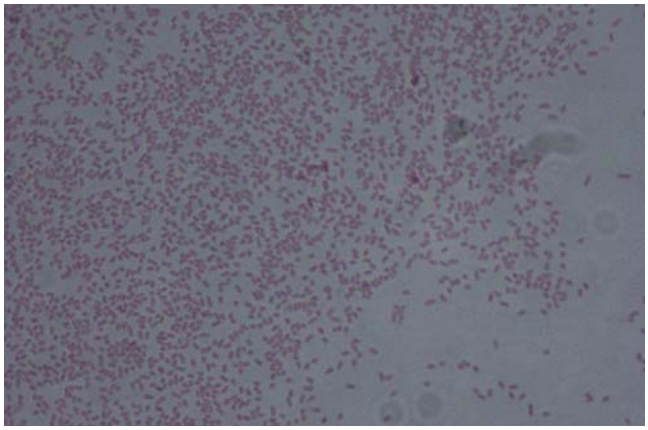

Figure 61. ***Pantoea agglomerans*** Gram stain, in a genus of bacteria that is antagonistic toward bryophytes in Germany and also a facultative pathogen of humans. Photo by Dr. Sahay, through Creative Commons.

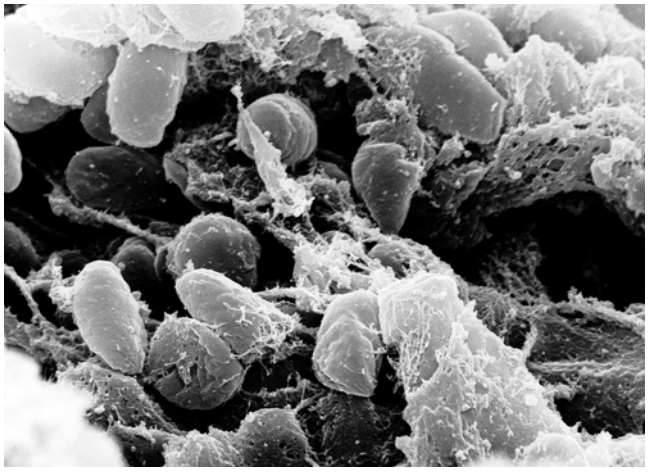

Figure 62. ***Yersinia pestis*** in gut of flea, in a genus among the most common antagonists toward bryophytes in Germany. Photo from CDC, through Creative Commons.

Antibiotic Role

Bacteria associated with bryophytes often serve as protectors, providing the antibacterial or antifungal compounds needed to protect the bryophytes. Whereas Opelt *et al.* (2007c) found a high proportion (26%) of antifungal bacteria, they found only 0.4% antibacterial strains. Among these antagonists, there was a high diversity of ***Burkholderia*** (Figure 57) isolates in the **endophytic** (living within cell) and **ectophytic** (living on plant surface) habitats of ***Sphagnum*** (Figure 49, Figure 54). The researchers suggested that these antagonistic bacteria could account for the high level of antimicrobial activity of ***Sphagnum***. It seems likely that the high level of antimicrobial compounds in at least some ***Sphagnum*** species could account for the specificity of the bacteria that grow there. The researchers also found a high diversity of nitrogen-fixing bacteria, especially inside ***Sphagnum***.

Because of these antagonistic properties, Sarolta *et al.* (2010) sought new types of medically useful antagonists in the Borsáros Raised Bog in Romania. They explored the communication forms that make the bacterial antagonism successful, analyzing the biofilm formation of single strains and co-cultures.

Szentes *et al*. (2011) found that rhizobacteria produced plant-growth-promoting substances that interacted in various ways, including competing with pathogens for nutrients. This research team found ***Bacillus*** (Figure 10-Figure 11), ***Cedecea***, ***Delftia*** (Figure 63), ***Lysinibacillus*** (Figure 64), ***Pseudomonas*** (Figure 13), ***Serratia*** (Figure 58), ***Stenotrophomonas*** (Figure 65), and ***Viridibacillus***. ***Bacillus***, ***Pseudomonas***, and ***Serratia*** were the dominant bacterial genera associated with bryophytes. *In vitro* cultures showed that a high number of the isolates inhibited the growth of fungal and bacterial plant pathogens such as ***Pectobacterium carotovorum*** (Figure 66) or produced secondary metabolic substances with biocontrol properties. ***Serratia fonticola*** BB17 (see Figure 58) and ***Pseudomonas fluorescens*** (Figure 67) BE8 were the most efficient against plant pathogens, with effectiveness up to 48.28% and 55.17% respectively.

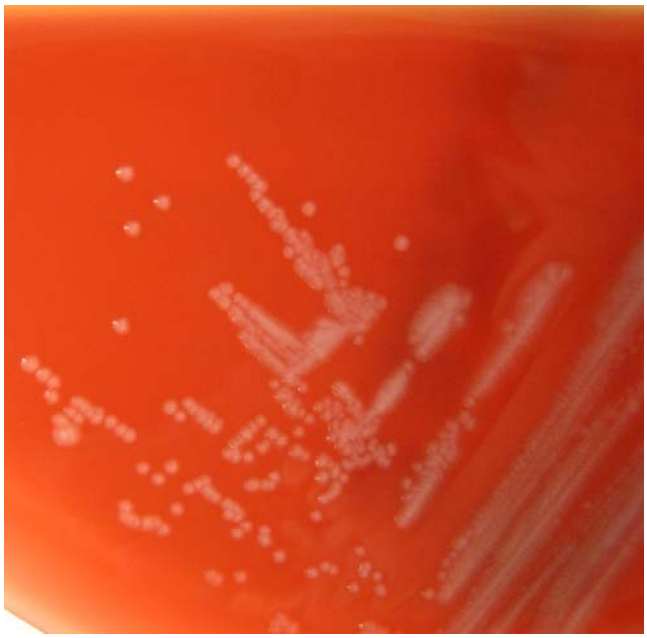

Figure 63. ***Delftia***, a genus that can be among the dominant bacteria associated with bacteria. Photo by mostly harmless, through Creative Commons.

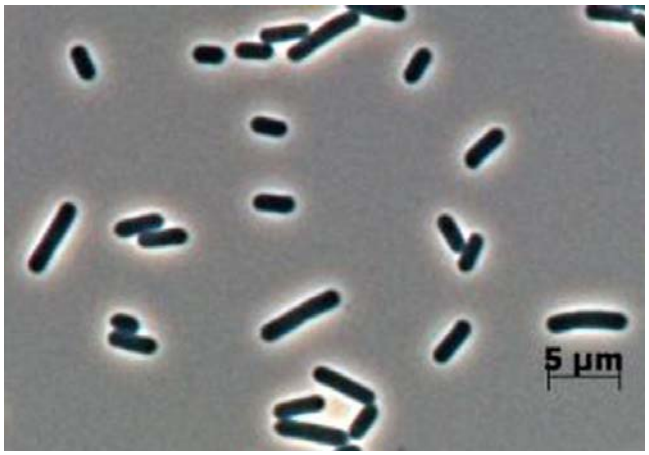

Figure 64. ***Lysinibacillus***, a genus that can be among the dominant bacteria associated with bacteria. Photo from Leibniz-Institut DSMZ, through Creative Commons.

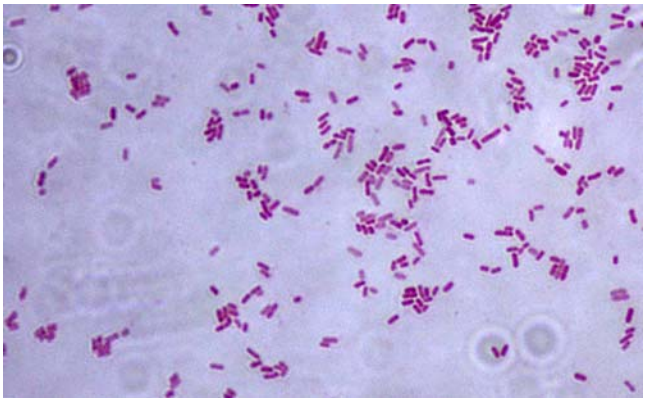

Figure 65. ***Stenotrophomonas maltophilia***, in a genus that can be among the dominant bacteria associated with bryophytes in peatlands. Photo by Riraq25, through Creative Commons.

Figure 66. ***Pectobacterium carotovorum***, a species that is inhibited by many bacterial isolates from bryophytes. Photo by Paul Bachi, through Creative Commons.

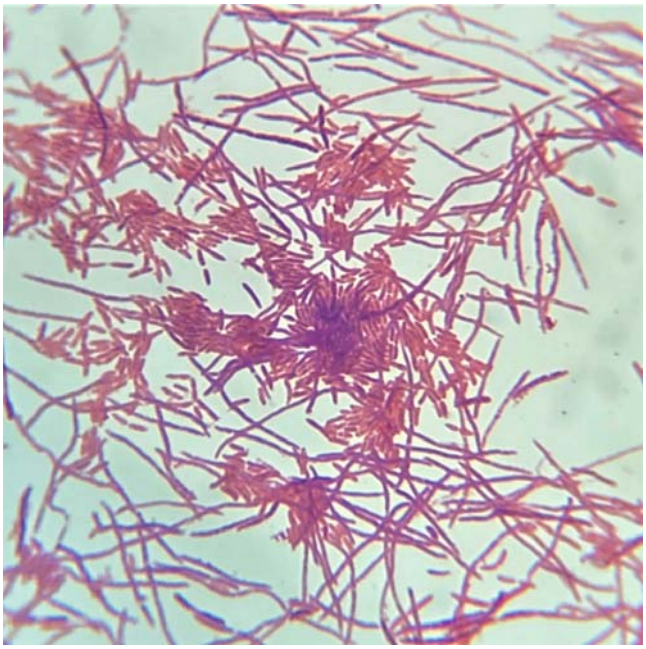

Figure 67. ***Pseudomonas fluorescens*** Gram stain, one of the most efficient bryophyte bacteria against plant pathogens. Photo by B. Domangue, through Creative Commons.

Ecosystem Roles

Robroek *et al*. (2021) approached the "rewiring" of peatland plant-microbe interactions and communities using a network approach. They found that the prokaryotic communities differed between sites. This was manifest in a more rapid turnover in the plant-microbial interactions than in the communities they inhabited. They found that the turnover in the bacterial network composition was driven mostly by the establishment of new interactions between the plant community and that of the microorganisms, a phenomenon that was shared among all the sites.

Wicaksono *et al*. (2021a, b) produced evidence that the tracheophytes tended to have specific bacteria, whereas the bryophytes presented greater bacterial species richness and diversity. Nevertheless, Bragina *et al*. (2015) was able to demonstrate that the plants and lichens of bogs shared a core microbiome over the entire ecosystem, forming a transkingdom metacommunity. All of these bog organisms are connected to the keystone ***Sphagnum*** (Figure 49, Figure 54) species through the microbial species such as ***Burkholderia bryophila*** (see Figure 57) This bacterial species was associated with a wide array of host plants and provides a beneficial plant-microbe interaction.

Bragina *et al*. (2014) were among the early researchers attempting to unravel the roles of the symbiotic and protocooperation effects of the ***Sphagnum*** (Figure 49, Figure 54) microbiome. It appears that the microbiome is important in facilitating survival in the extreme conditions found in the ***Sphagnum*** habitats. The microbiome provides abundant subsystems that facilitate coping with oxidative and drought stresses, resistance to detrimental environmental factors, repair, and self-controlling mechanisms. Microbe-microbe and plant-microbe interactions are important in biofilm formation, interaction via quorum sensing (see Chapter 19-1 of this volume), and nutrient exchange. Their involvement in the nitrogen cycle and recycling of organic material are important contributions to the nutrient supply.

In addition to the products produced by the bacteria that are associated with ***Sphagnum*** (Figure 49, Figure 54), the bacteria can alter the response to a change in physical growth conditions as well. With the threat of global warming looming over the cold-climate peatlands, the ability of bacteria to rapidly acclimatize may promote the survival of ***Sphagnum*** through host-microbiome acquired thermotolerance (Carrell *et al*. 2021). First the researchers showed that elevated temperatures decreased the growth of sterile ***Sphagnum*** without addition of microbes. The addition of a microbiome from a thermal habitat matching the experimental temperatures returned the ***Sphagnum*** to its pre-warming growth rates. Warming changed the structure of the microbiome and induced a plant heat shock response. They suggested that the thermally conditioned microbiomes provided thermal conditioning to the ***Sphagnum*** host. The same results occurred when the microbiomes were isolated from ***Sphagnum*** warming experiments in Iceland, Sweden, and France.

But we may have barely scratched the surface of the interactions in the peatland community. As reported by Dedysh (2011) in her review, these uncultivated and unidentified bacteria form a large proportion of the microbial communities in acidic, cold, nutrient-poor, and water-saturated peatlands, hiding from us unknown physiologies and roles in the peatland ecology. New genetic techniques are permitting us to enumerate the number of strains present, and our culturing techniques are improving for these more elusive organisms.

Decomposition

Sphagnum litter has a very slow decomposition, with first year loss of mass ranging 0.1-25% (Clymo 1965; Aerts *et al*. 2001; Scheffer *et al*. 2001; Dedysh 2011). This has been attributed to acidity (that favors fungi more than bacteria), phenolic compounds and waxes (mostly from shrubs) that are highly resistant to decay (Verhoeven & Liefveld 1997; Dedysh 2011), low nutrient content, especially N and P in ***Sphagnum***, low temperatures, and anoxic conditions (Dedysh 2011). When decay occurs, the end-products are transferred into methane. This methane diffuses into the living, aerobic parts of the peat where Methanobacteria oxidize it and release CO_2.

Bacteria affect the decay of ***Sphagnum*** (Figure 49, Figure 54), or more accurately, its near absence. Using ***Sphagnum fallax*** (Figure 49) from a fen woodland, Brock and Bregman (1989) found that after 12 months, the original N and P content associated with the moss had diminished little. Furthermore, the cells lacked much damage and had poor colonization by bacteria.

Patra (2020) reminded us of the role of ***Sphagnum*** (Figure 49, Figure 54) in secreting acids, making acid conditions that are unfavorable for the growth of most decomposing bacteria. The decomposition is further slowed by the absence of oxygen in the lower peat layers, causing an accumulation of dead material we know as peat.

Xeric

Liu *et al*. (2014) investigated the endophytic bacterial community in the xerophytic moss ***Grimmia montana*** (Figure 68). Using a 212 sequence library, they identified 54 genera of bacteria in 4 phyla (**Pseudomonadota**, **Bacillota**, **Actinomycetota**, and ***Cytophaga*** /***Flexibacter***/**Bacteroids**). As in many other bryophyte bacterial communities, the **Pseudomonadota** were dominant (45.9%), with **Bacillota** being second (27.6%). The most abundant genera included ***Acinetobacter*** (Figure 69), ***Aeromonas*** (Figure 70), ***Enterobacter*** (Figure 71), ***Leclercia***, ***Microvirga***, ***Paenisporosarcina***, ***Planococcus***, ***Planomicrobium***, ***Pseudomonas*** (Figure 13), and ***Rhizobium*** (Figure 53). They did not determine the role of the bacteria in the association, but some were known to have beneficial effects on their hosts. Some of the genera isolated differed from those detected by the molecular method, thus emphasizing that our methods may often miss important genera and species due to inappropriate culture conditions. At the same time, some taxa may not be in the molecular library.

Figure 68. ***Grimmia montana*** with capsules, a rock-dwelling species with 54 known genera of bacteria in its cells, spanning 4 phyla, with **Pseudomonadota** being dominant. Photo from Earth.com, with permission.

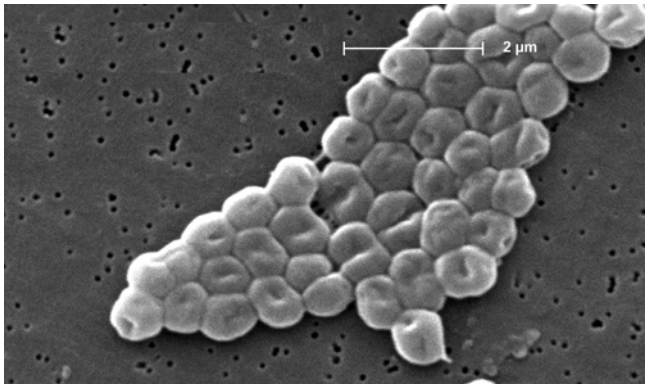

Figure 69. ***Acinetobacter baumannii***, in one of the more abundant genera on ***Grimmia montana***. Photo by Janice Carr, through Creative Commons.

Figure 70. ***Aeromonas hydrophila***, in one of the more abundant genera on ***Grimmia montana***. Photo by Nathan Reading, through Creative Commons.

Figure 71. ***Enterobacter cloacae***, in one of the more abundant genera on ***Grimmia montana***. Photo from CDC, through public domain.

Soil Crusts

Soil crusts are a community of organisms that together colonize and stabilize soil surfaces. These are most common in dry areas where their ability to survive long periods of drought permit them to survive with little competition (Weber *et al*. 2019). These crusts occupy approximately ~12% of the terrestrial surface of the planet Earth (Weber *et al*. 2019). It is important that we understand these processes as they relate to ecosystem processes, especially in cryptogamic soil crusts (Deane-Coe & Stanton 2017), as our Earth remains in a state of continuous change.

The biocrusts may be dominated by **Cyanobacteria**, lichens, or bryophytes (Warren *et al*. 2019; Weber *et al*. 2019). The communities differ significantly from each other (Maier *et al*. 2018). Their organisms include free living, lichenized, and mycorrhizal fungi, **Cyanobacteria**, chemoheterotrophic bacteria, diazotrophic bacteria and archaea, eukaryotic algae, and bryophytes (Warren *et al*. 2019; Weber *et al*. 2019). The organisms are characterized by desiccation and extreme temperature tolerance, production of various soil-binding chemistries, almost exclusive dependency on asexual reproduction, pattern of aerial dispersal over impressive distances, and universal vulnerability to a wide range of human-related perturbations (Warren *et al*. 2019).

The role of bacteria in the bryophyte-lichen matrix of soil crusts remains poorly known. Weber *et al*. (2019) found that bacterial community composition changed in a stepwise manner along with biocrust succession, while bare soil communities were completely different. As the climate changes and land use destroys these communities, it is important that we understand the role of interactions, including those between the bacteria and bryophytes.

Weber *et al*. (2012) explored the soil crusts in the succulent Karoo of South Africa. They found that leaching from mosses may cause the high rates of soil respiration. The leaching creates microsites with high nutrient levels, favoring the growth of the microorganisms.

Moquin *et al*. (2012) examined the bacterial diversity in bryophyte-dominated soil crusts. They found the dominant phyla to be **Acidobacteriota**, **Bacteroidota**, and **Pseudomonadota**. Although tracheophytes are not a common member of the crusts, they found bacterial root associates, especially in the family **Oxalobacteraceae**. The presence of **Bacteroidota** suggests that the bacterial community in these crusts is affected by high carbon availability. The bacterial communities of soils and the **Cyanobacteria**-dominant crusts differed from those of the bryophyte-dominated ones. Bamforth (2008) noted that the microorganisms are important in the nutrient cycling of the crust community and subsequently contribute nutrients to the underlying soils.

In southwestern China, Cao *et al*. (2020) found that not only moss species, but also the types of karst rocky desertification, affect the microbial communities. Mosses were by far the more impacting factor, with changes in moss species bringing drought-resistant factors that affected the bacterial community, or *vice-versa*. The bacteria were able to provide proline content, superoxide dismutase activity, and peroxidase activity. These compounds are closely related to the drought adaptability of mosses.

Maier *et al*. (2018) found that alpha diversity of the crust community increases as succession progresses, with a concomitant shift from more generalized to more specialized organisms. At the same time, the CO_2 gas exchange exhibits significantly larger respiration rates in later successional stages. The NO and HONO emission patterns also change during succession. Thus, as the photosynthetic organisms change, they facilitate specific microbial communities, and these microbial changes in turn influence the physiological properties of the biocrusts and their contributions to both local and global nutrient cycles. The three dominance types of biocrusts have significantly different communities.

In the ***Didymodon rigidulus*** (Figure 72) community, there are endophytic bacteria, including ***Bacillus cereus*** (Figure 73), ***Bacillus pumilus***, ***B. subtilis*** (Figure 10), ***Bacillus*** sp, ***Neobacillus niacini***, ***Peribacillus simplex*** (see Figure 74), and ***Priestia aryabhattai*** (all previously in *Bacillus*; see Figure 9) (Ma *et al*. 2017b). The dominant species was ***B. subtilis***. They found that at the test concentrations of petroleum ether, ethyl acetate, and n-butyl alcohol extracts, ***B. cereus*** and ***B. subtilis*** did not significantly alter the bryophyte spore germination. On the other hand, the protonema growth was inhibited to varying degrees by the same extracts. Hence, we know that bacteria can use their secondary metabolites to affect the development of bryophytes and alter the community composition.

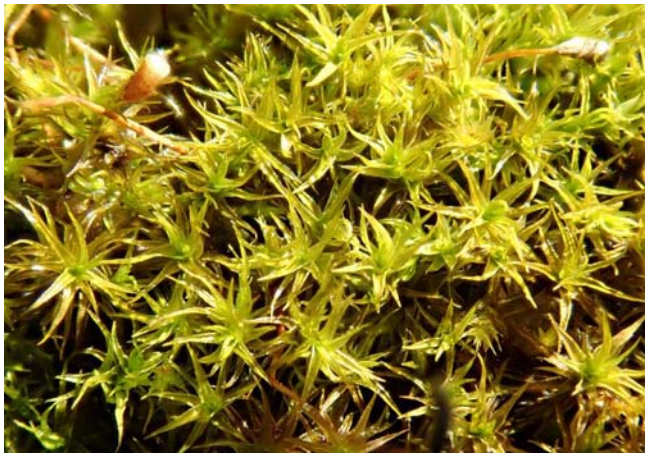

Figure 72. ***Didymodon rigidulus***, a species with a number of endophytic bacteria; ***Bacillus subtilis*** is dominant. Hugues Tinguy, with permission.

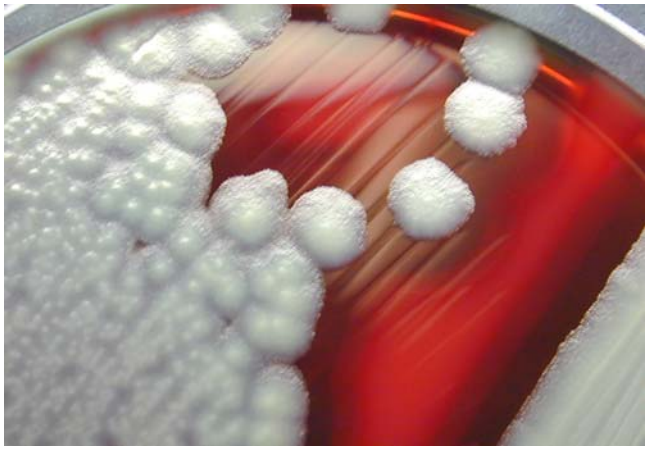

Figure 73. ***Bacillus cereus*** showing hemolysis on sheep blood; this is one of the endophytic bacteria found in ***Didymodon rigidulus***. Photo by Larry Stauffer, through public domain.

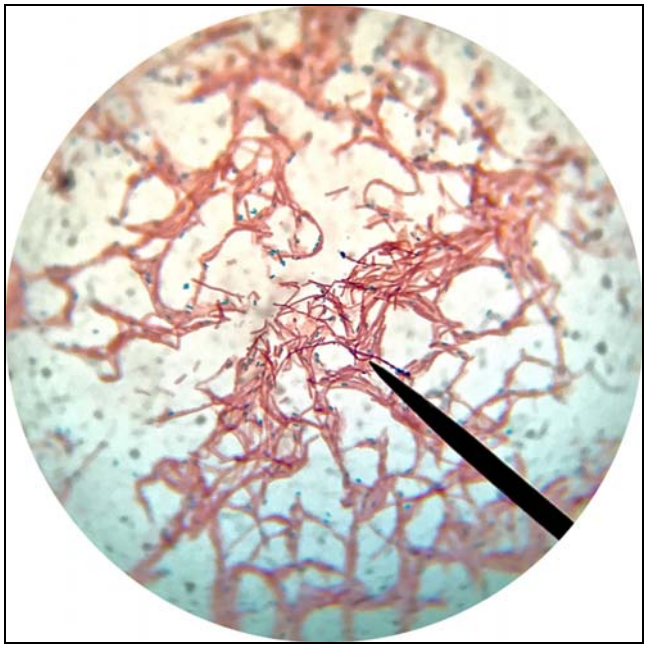

Figure 74. ***Peribacillus subtilis*** with endospores; ***P. simplex*** is one of the endophytic bacteria found in ***Didymodon rigidulus***. Photo by W M Rapids, through Creative Commons.

Honeybees

Honeybees can benefit from the antibacterial activity of bryophytes against bacteria. And without honeybees, the plant community can suffer due to absence of pollination. Gahtori *et al*. (2011) identified the bacterium ***Medisscoccus plutonius*** as the cause of the European foulbrood disease in honeybees (Figure 75). They extracted antibacterial compounds from three different bryophytes and tested them against this bacterium. All of the tested extracts exhibited good antibacterial activity against the foulbrood bacteria. The maximum activity derived from ***Dicranum undulatum*** (Figure 76) and ***Marchantia polymorpha*** (Figure 17) and was comparable to that of the standard drug in use against these bacteria.

Figure 75. ***Apis mellifera*** (honeybee) on comb. Photo by A. Szalansk, through Creative Commons.

Figure 76. ***Dicranum undulatum***, a species that has compounds that are antibacterial against the foulbrood bacteria in honeybees. Photo by Robin Bovey, with permission through Dale Vitt.

Sevim *et al*. (2017) tested the antibacterial activity of 23 bryophyte species in Turkey against ***Paenibacillus larvae*** (Figure 77) isolates from honeybee larvae; these bacteria are responsible for the American foulbrood diseases in the honeybee larvae. Of the 23 bryophytes sampled, they found 10 [liverwort ***Metzgeria conjugata*** (Figure 78); mosses ***Calliergonella cuspidata*** (Figure 79), ***Calliergonella lindbergii*** (Figure 80), ***Grimmia alpestris*** (Figure 81), ***Isothecium alopecuroides*** (Figure 82), ***Polytrichastrum formosum*** (Figure 83), ***Polytrichum commune*** (Figure 84), ***Syntrichia calcicola*** (Figure 85), ***Syntrichia intermedia*** (Figure 86), ***Tortella densa*** (Figure 87)] that exhibited good antimicrobial activity against ***P. larvae*** isolates.

Figure 77. ***Paenibacillus larvae***, a bacterium in honeycombs that affects the larvae of the honeybee. Photo from Georgia Department of Agriculture, through Creative Commons.

Figure 78. ***Metzgeria conjugata***, a liverwort that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Hermann Schachner, through Creative Commons.

Figure 79. ***Calliergonella cuspidata***, a wetland moss that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Hugues Tinguy, with permission.

Figure 80. ***Calliergonella lindbergii***, a wetland moss that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Hermann Schachner, through Creative Commons.

Figure 81. ***Grimmia alpestris***, a rock-dwelling moss that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Hermann Schachner, through Creative Commons.

Figure 82. ***Isothecium alopecuroides***, a rock-dwelling moss that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Hermann Schachner, through Creative Commons.

Figure 83. ***Polytrichastrum formosum***, a soil-dwelling moss that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Kent Brothers, Botany Website, UBC, with permission.

Figure 84. ***Polytrichum commune***, a wetland moss that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Riken Mon, through Creative Commons.

Figure 85. ***Syntrichia calcicola***, a xerophytic moss that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Hermann Schachner, through Creative Commons.

Figure 86. ***Syntrichia intermedia***, a xerophytic moss that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Acta Plantarum, through Creative Commons.

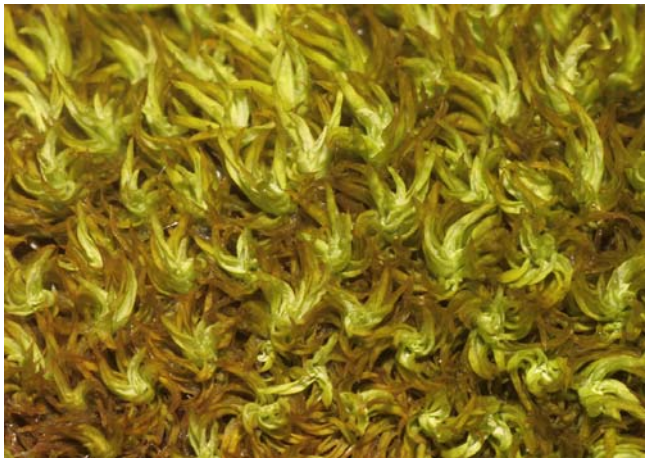

Figure 87. ***Tortella densa***, a moss of mostly rather dry habitats that makes compounds that are effective against the bacterial American foulbrood disease in honeybee larvae. Photo by Hermann Schachner, through Creative Commons.

But does this protection work in nature? Are honeybees able to bring mosses to the hive to prevent the growth of the bacteria? Do they have behavioral adaptations that cause them to move about among the mosses to sanitize themselves? What an interesting relationship it would be if such activities were true. But we don't know; perhaps nature was simply waiting for humans to do the sanitizing job.

Pollution Relationships

Meyer *et al*. (2010a) compared bryophyte microbial communities in rural, urban, and industrialized communities. The particulate atmospheric pollution affects the bryophyte-microorganism complexes. They found that microalgae, bacteria, rotifers, and testate amoebae biomasses were significantly higher in the rural site. The physico-chemical variables (NO_2, relative humidity, temperature, site) and the trace elements accumulated in bryophytes (copper, strontium, lead) explained 69.3% of the variance in the microbial community. These numbers suggest that bacteria in a community are potential biomonitors of atmospheric pollution.

Rojas *et al*. (2016) reported that bryophytes dominated control precipitates, whereas the **Basidiomycota** fungi were most abundant under reclaimed precipitates at an acid mine drainage reclamation site in central Pennsylvania, USA. Furthermore the reclaimed precipitates had more bacterial diversity than did the controls. Bacteria under bryophytes were more common under unreclaimed (control) soils.

Meyer *et al*. (2010b) found that the bryophytes did not accumulate the low concentrations of metallic trace elements. However, the **Cyanobacteria**, testate amoebae, and fungi all decreased in the microbial community in response to the particle deposition. Thus, the composition of the microbe community could serve as a useful indicator of pollution effects.

Reclamation Communities

Bryophytes can help to reclaim despoiled areas in a number of ways. Kyyak *et al*. (2020) found that they could colonize saline substrates of tailings storage, where they provide extended surface area for the accumulation of organic matter. The organic carbon under moss turfs increased 2.2-5.0 times compared to areas with no bryophytes. The dense-turf mosses ***Didymodon rigidulus*** (Figure 72) and ***Ptychostomum pseudotriquetrum*** var. ***bimum*** (Figure 88) accumulated the most organic matter, compared with loose turf formed by ***Barbula unguiculata*** (Figure 89) and ***Funaria hygrometrica*** (Figure 90). The moss turfs facilitate a 0.2-0.5 unit increase in acidity of the aqueous solutions of the tailings. Bacterial quantity increased significantly under mosses in reclaimed mine tailings, achieving a biomass under the moss turfs of ***Didymodon rigidulus*** and ***Funaria hygrometrica*** of 5.09-6.10 µg C g^{-1} dry weight soil. Without mosses, bacteria reached only 3.19-11.27 µg C g^{-1} dry weight soil.

Figure 88. ***Ptychostomum pseudotriquetrum*** var. ***bimum*** where organic matter accumulates in greater amounts than in the tailings beneath the loose moss turfs. Photo by Hugues Tinguy, with permission.

Figure 89. ***Barbula unguiculata*** dry, where less organic matter accumulates in the tailings beneath the moss loose turfs than in dense turf areas. Photo by Bob Klips, with permission.

Figure 90. ***Funaria hygrometrica*** where less organic matter accumulates in the tailings beneath the moss loose turfs than in the dense turf areas. Photo by Kurt Stueber, through Creative Commons.

The microbial biomass in the tailings beneath the moss turfs depended on the species characteristics of the mosses (Kyyak *et al*. 2020). The microbial biomass index almost doubled with the high level of salinization under turfs of ***Didymodon rigidulus*** (Figure 72) and ***Funaria hygrometrica*** (Figure 90). The moss cover also promoted a significant increase in the primary ecological and trophic groups of microorganisms (saprophytes, cellulose-destroying bacteria, oligonitrophils, and nitrogen fixers). Thus the pioneer bryophytes are important in the accumulation of organic matter, increase in acidity, improvement of the redox regime of the substrate, and promotion of development of the important soil microbiota (DeLuca *et al*. 2002; Gavazov *et al*. 2010; Stewart *et al*. 2011; Kyyak *et al*. 2020). In particular, they increased the productivity of cellulose-degrading bacteria.

Summary

It is only in the 21st century that much research has addressed the bacterial communities associated with bryophytes. It appears that these communities have important roles in the ecosystems they inhabit.

Bryophytes in rivers and streams trap organic sediments. These provide rich habitats for bacteria, which in turn provide food for invertebrates both large and small. We now know that they can cause denitrification, whereas others are important in nitrogen fixation, while at the same time converting methane to free CO_2 that is used by the bryophytes. Their role in nitrogen fixation in peatlands, the boreal forest, cryptogamic crusts, and other low-nutrient habitats is significant. They are also, at least in part, responsible for degradation, senescence, and decomposition of the bryophytes, thus contributing to nutrient cycling. However, in acidic peatlands, the decomposition is slow.

Some bacteria produce ice-binding proteins that help bryophytes, especially in the polar and alpine regions, to survive freezing by preventing large crystals from forming in the bryophyte cells.

Some communities are very similar on a number of bryophyte species in an area, while at the same time some bryophytes can have unique communities. But we do not understand what causes the bacterial community differences with bryophyte species – microhabitat needs, bryophyte secondary compounds, bryophyte structure, bacteria-bacteria interactions?

There are many habitats where the bacterial associates of bryophytes have not been assessed. Their roles in these communities could be critical for some of the vital ecosystem functions. It is likely that there are multiple connections for some of these roles and that the community composition will change with climate change, probably before we begin to understand these connections.

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CHAPTER 19-3
BRYOPHYTE DEFENSES AGAINST BACTERIA

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CHAPTER 19-3
BRYOPHYTE DEFENSES AGAINST BACTERIA

Figure 1. ***Salmonella typhi***, a human pathogen that is very sensitive to bryophyte extracts. Photo from CDC, through public domain.

Defenses Against Bacteria

Bryophytes generally seem to lack damage by bacteria and other pathogens. Although some bacteria can be pathogens on bryophytes, others actually help to protect the bryophytes.

Martínez-Abaigar and Núñez-Olivera (2021) referred to bryophyte defenses as "the outstanding capacity of bryophytes to produce bioactive compounds with diverse biological functions." In addition to the great variety of terpenoids produced by liverworts, all three bryophyte lineages can produce phenolic derivatives (from simple cinnamic acids to complex flavonoids), alkaloids, and lipids. Among these defenses, the liverwort bisbibenzyls and sesquiterpenoid derivatives and the moss diterpenoid derivatives momilactones are the most important compounds.

We now know that bryophyte defenses include phenylquinone, aromatic and phenolic substances, oligosaccharides, polysaccharides, sugar alcohols, amino acids, fatty acids, and aliphatic compounds (Alam *et al*. 2012). Bryophytes also produce polyunsaturated C_{20} fatty acids. These include arachidonic acid and eicosapentaenoic acid (Ponce de León *et al*. 2015). These can be oxidized and transformed into bioactive compounds.

More than 1600 terpenoids have been identified from bryophytes (Chen *et al*. 2018). Some of these are unique to bryophytes. These terpenoids have a variety of functions, but they are particularly useful as defenses against both biotic and abiotic stresses.

Until 2016 momilactones were known only from rice and the moss ***Hypnum plumaeforme*** (Figure 2) (Okada *et al*. 2016). These compounds are diterpenoid phytoalexins with antimicrobial and allelopathic functions. A similar transcription response to stresses was identified in ***Physcomitrium patens*** (Figure 3), suggesting a similarity between mosses and tracheophytes in response to stresses, including pathogens. On the other hand, jasmonic acid seems to be absent in bryophytes, whereas it is a signalling mechanism in tracheophytes, initiating plant defenses (Ponce de León *et al*. 2015; Okada *et al*. 2016).

Figure 2. ***Hypnum plumaeforme*** moist, source of momilactones that are antibiotic and allelopathic. Photo by Janice Glime.

Figure 3. ***Physcomitrium patens***, a new source of momilactones. Photo by Michael Lüth, with permission.

Liverworts seem to have the most diverse array of secondary compounds with antibiotic properties (Russell 2010). Among the 14 species tested, 88% had antibiotic activity, whereas only 33% of the moss species exhibited any activity against the three bacterial strains tested. The liverwort ***Lunularia cruciata*** (Figure 4) presented the greatest activity against the three bacteria tested. But this is only a small sampling of bacteria and bryophytes. A wider array of bacterial species would most likely reveal even more kinds of activity.

The liverworts are known for their often distinctive odors. They also have distinctive **oil bodies** in the cells, and these are unique enough that they are often of taxonomic value. We now know that these oil bodies are the sites of many defense compounds – secondary compounds that seem to have no other metabolic functions (Asakawa 2011). The oil bodies are known only from the liverworts and are the site for storing terpenoids (He *et al*. 2013). These include the mono-, sesqui- and di-terpenoids, aromatic compounds like bibenzyl, bis-bibenzyls, and acetogenins (Asakawa *et al*. 2013) – compounds that serve to protect the liverworts against both herbivory and pathogens (antimicrobial, antifungal, and antiviral). On the other hand, mosses and hornworts produce primarily di- and triterpenes (Zhan *et al*. 2015). Among the liverworts, more than 40 new carbon skeletons of terpenoids and aromatic compounds have been found (Asakawa & Ludwiczuk 2017).

Figure 4. ***Lunularia cruciata***, a species with the greatest antibacterial activity among species in one test. Photo from Botany Website, UBC, with permission.

Wang *et al*. (2006) suggested that the lower inhibitory activity of ***Cylindrocolea recurvifolia*** (Figure 5) compared to that of ***Pleurozia subinflata*** (Figure 6), both leafy liverworts, could be due to the lower contents of oil bodies in the former, where they are both smaller and fewer. On the other hand, Zhu *et al*. (2006) found that there was no correlation between antibacterial activity and size or number of oil bodies in 38 liverwort species.

Figure 5. ***Cylindrocolea recurvifolia***, a leafy liverwort with small and few oil bodies and less antibiotic activity than that of ***Pleurozia subinflata***. Photo from Museum of Hiroshima University, with permission.

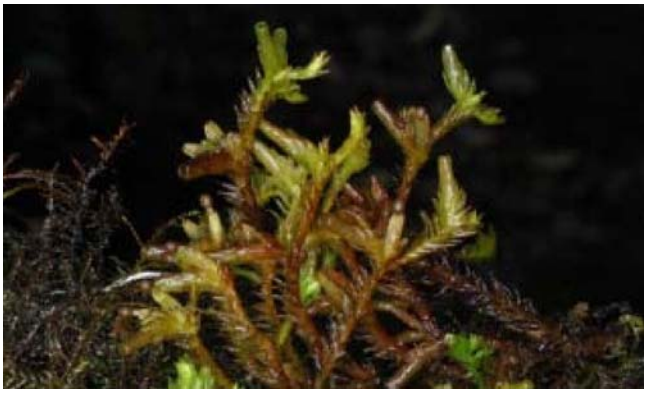

Figure 6. ***Pleurozia subinflata***, a leafy liverwort with larger and more numerous oil bodies than those of ***Cylindrocolea recurvifolia*** and with greater antibiotic activity. Photo by Jan-Peter Frahm, with permission.

Mosses and liverworts seem to lack tissue-specific antibody binding against the lignin-like polymers homoguaiacyl (G) and guaiacyl/syringyl (GS) (Ligrone *et al*. 2008). On the other hand, the hornworts ***Megaceros pellucidus*** (Figure 7) and ***Nothoceros fuegiensis*** (see Figure 8) exhibited more intense labelling with the GS antibody of the pseudoelaters and spores than in the other cell types.

Figure 7. ***Megaceros pellucidus***, a species in which GS antibody labelling of the pseudoelaters and spores was greater than for other cell types. Photo by Ashley Bradford, through Creative Commons.

Figure 8. ***Nothoceros aenigmaticus***, a species in which GS antibody labelling of the pseudoelaters and spores was greater than for other cell types. Photo by Juan Carlos Villareal, with permission.

Antibiotic Response by Bryophytes

Banerjee and Sen (1979) reported that 56% of the bryophytes they tested were active against at least one bacterial species. Our knowledge of moss antibiotic properties is much less than that of liverworts (Provenzano *et al*. 2019). Only 3.2% of the mosses and 8.8 of the hornworts have been characterized. This is probably because the liverworts seem to a more promising variety of interesting secondary compounds that could be useful to humans.

Van Hoof *et al*. (2013) found that the moss ***Hypnum cupressiforme*** (Figure 9) had strong antimicrobial effects. In this case, at least, the activity was greater against plant bacteria than it was against human bacteria.

Figure 9. ***Hypnum cupressiforme***, a species with strong antibacterial effects against plant bacteria. Photo by J. C. Schou, with permission.

Sawant and Karadge (2010) found that extracts of the cave liverwort ***Cyathodium cavernarum*** (Figure 10) were mostly inactive against the bacteria tested, whereas other liverworts [***Plagiochasma intermedium*** (Figure 11), ***Asterella wallichiana*** (Figure 12), ***Targionia hypophylla*** (Figure 13)] in these tests exhibited good antimicrobial activity. Chavhan (2017) likewise found that ***Targionia hypophylla*** exhibited a high level of antibiotic activity against two bacterial strains. And ***Cyathodium tuberosum*** (Figure 14) exhibited the least. Is there a pattern to the absence of antimicrobial properties in cave mosses? This would seemingly save energy in these low-energy systems.

Figure 10. ***Cyathodium cavernarum***, a thallose cave liverwort that doesn't seem to possess antibodies. Photo by Cédric de Foucault, through Creative Commons.

Figure 11. ***Plagiochasma intermedium***, a liverwort species with good antibiotic activity. Photo from Earth.com, with permission.

Figure 12. ***Asterella wallichiana*** with young archegonial heads, a liverwort species with good antibiotic activity. Photo by Shyamal L., through Creative Commons.

Figure 13. ***Targionia hypophylla***, a liverwort species with good antibiotic activity. Photo by Hugues Tinguy, with permission.

Figure 14. ***Cyathodium tuberosum*** a liverwort with the weakest antibiotic activity among those tested. Photo by Silvia Pressel and Jeff Duckett, with permission.

Zhu *et al*. (2006) found that 93% of the 60 tested bryophytes exhibited antibacterial activity. All liverworts tested (38) had activity against at least two bacterial species tested. Of the 60 bryophyte species, 17 were active against all seven of the tested bacterial species (Gram positive: ***Bacillus megaterium*** (Figure 15), ***Bacillus subtilis*** (Figure 16), ***Bacillus thuringiensis*** (Figure 17), ***Staphylococcus aureus*** (Figure 18); Gram negative: ***Escherichia coli*** (Figure 19), ***Pseudomonas aeruginosa*** (Figure 20), ***Pseudomonas putida***). The activity was especially high in the liverwort genera ***Conocephalum*** (Figure 21), ***Frullania*** (Figure 22), ***Herbertus*** (Figure 23), ***Marchantia*** (Figure 24), ***Mastigophora*** (Figure 25), and ***Porella*** (Figure 26). Among these, ***Staphylococcus aureus*** was the most resistant to bryophyte extracts from both mosses and liverworts, in sharp contrast to a number of other studies in which it was the most susceptible to bryophyte extracts (*e.g.* Bodade *et al*. 2008; Liu & Wang 2010; Liyanage *et al*. 2015; Sabovljević *et al*. 2010). The most sensitive bacterial species to moss extracts was ***Pseudomonas putida***; sensitivity to liverwort extracts was greatest in ***Bacillus subtilis***. When negative results are found, it is possible that the bryophyte had not received the proper signals to make the antibiotic compounds. This would be particularly true in sterile cultures.

Figure 15. ***Bacillus megaterium***, one of seven bacterial species inhibited by 17 of 60 bryophyte species tested. Photo by Alexastely, through Creative Commons.

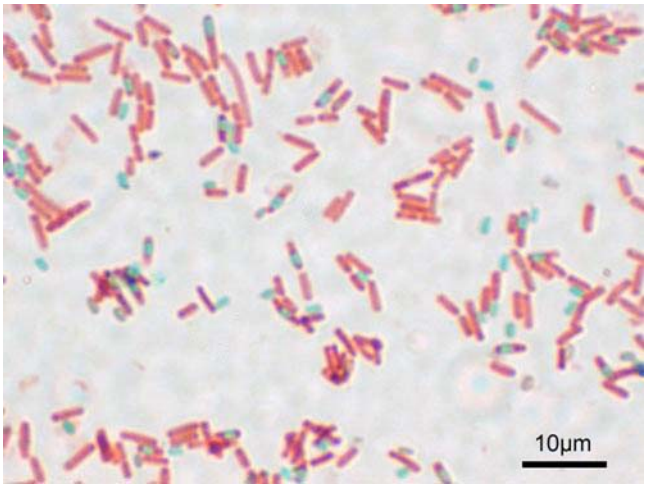

Figure 16. ***Bacillus subtilis*** forming spores, one of seven bacterial species inhibited by 17 of 60 bryophyte species tested. Photo by Y. Tambe, through Creative Commons.

Figure 17. ***Bacillus thuringiensis***, one of seven bacterial species inhibited by 17 of 60 bryophyte species tested. Photo by Todd Parker, CDC, through public domain.

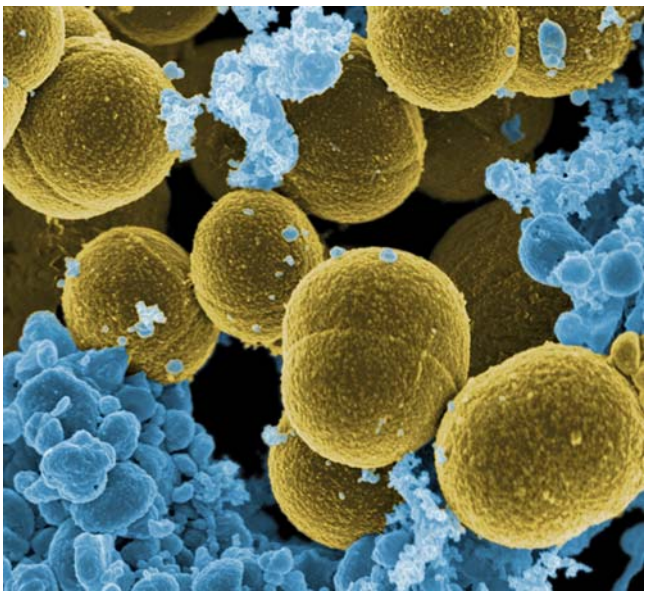

Figure 18. ***Staphylococcus aureus***, one of seven bacterial species inhibited by 17 of 60 bryophyte species tested. Photo from NIAID-RML, through public domain.

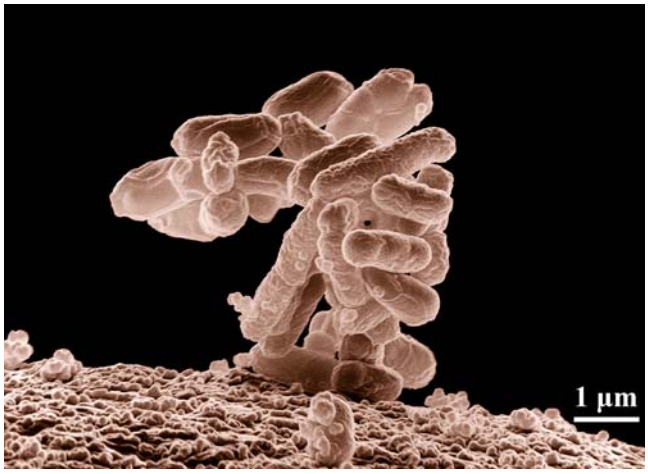

Figure 19. ***Escherichia coli***, one of seven bacterial species inhibited by 17 of 60 bryophyte species tested. Photo by Erbe, digital colorization by Christopher Pooley, both of USDA, ARS, EMU, through public domain.

Figure 20. ***Pseudomonas aeruginosa***, a bacterial species resistant to multiple drugs and one of seven bacterial species inhibited by 17 of 60 bryophyte species tested. Photo by Jennifer Oosthuizen, CDC, through public domain.

Figure 21. ***Conocephalum conicum*** from the UK, in a genus with especially high antibacterial activity. Photo by Lairich Rig, through Creative Commons.

Figure 22. ***Frullania dilatata***, in a genus with especially high antibacterial activity. Photo by Paul Bowyer, through Creative Commons.

Figure 23. ***Herbertus aduncus***, in a genus with especially high antibacterial activity. Photo from Earth.com, with permission.

Figure 24. ***Marchantia polymorpha***, a species that responds to the bacterium ***Pseudomonas syringae*** by producing antibacterial compounds. Image copyright Stuart Dunlop <www.donegal-wildlife.blogspot.com>, with permission.

Figure 25. ***Mastigophora woodsii***, in a genus with especially high antibacterial activity. Photo by Claire Halpin, with permission.

Figure 26. ***Porella platyphylla***, in a genus with especially high antibacterial activity. Photo by Hermann Schachner, through Creative Commons.

When Shirzadian and Afshari Azad (2010) tested the activity of 11 Iranian bryophytes, they found that only ***Xanthomonas citri*** pv. ***malvacearum*** (pv. = pathovar; Figure 27) failed to show any response to extracts from the bryophytes. The other bacteria [***Erwinia amylovora*** (Figure 28), ***Pectobacterium carotovora*** (Figure 29), ***Ralstonia solanacearum*** (Figure 30), ***Agrobacterium tumefaciens*** (Figure 31)] responded to the extracts.

It is interesting that the **α-DOX** (α-dioxygenase) in the moss ***Physcomitrium patens*** (Figure 3) is both part of the defense system and a controlling agent in development (Machado *et al.* 2015). α-DOX contributes to the synthesis of **oxylipins**, permitting plant signaling against both biotic and abiotic stresses. On the other hand, Bressendorff *et al*. (2016) found that the moss ***Physcomitrium patens***, unlike tracheophytes, uses a different signalling pathway for immunity than the one used to respond to osmotic stress.

The evolution in bacteria only got part way to having a successful jasmonic acid defense (Monte *et al*. 2018). They have the genes for the JA-Ile (jasmonoyl-isoleucine) signalling pathway, but they do not produce JA-Ile.

Figure 27. ***Xanthomonas citri*** pv ***malvacearum*** on cotton leaf, a bacterium that failed to respond to bryophyte extracts from Iran. Photo from Clemson University - USDA Cooperative Extension Slide Series, through Creative Commons.

Figure 28. ***Erwinia amylovora*** on apples, a bacterium that was inhibited by extracts from Iranian bryophytes. Photo from University of Georgia Plant Pathology, University of Georgia, <Bugwood.org>, through Creative Commons.

Figure 29. ***Pectobacterium carotovora*** on elm, a bacterium that was inhibited by extracts from Iranian bryophytes. Photo by Ninjatacoshell, through Creative Commons.

Figure 30. ***Ralstonia solanacearum*** wilt symptoms; this bacterium was inhibited by extracts from Iranian bryophytes. Photo from Clemson University - USDA Cooperative Extension Slide Series - USDA Forest Service, through Creative Commons.

Figure 31. ***Agrobacterium tumefaciens***, a bacterium that was inhibited by extracts from Iranian bryophytes. Photo by William Jacobi, Colorado State University, <Bugwood.org>, through Creative Commons.

Habitat Differences?

It seems reasonable to hypothesize that bryophytes from damp habitats are more likely to provide a suitable habitat for bacteria and fungi. Therefore, we can also hypothesize that bryophytes of moist habitats should have more defense compounds than those from dry habitats. Or could these be obtained through partnerships?

Liu and Wang (2010) noted that the moss ***Ditrichum pallidum*** (Figure 32) was able to defend against the bacteria ***Staphylococcus aureus*** (Figure 18), ***Escherichia coli*** (Figure 19), and ***Proteus vulgaris*** (Figure 33) to different degrees. Could this indicate differences in abundance of these three bacteria in the habitat of the

Ditrichum pallidum used in the tests? Or is it just specificity to the individual species and their relative abundance in bryophyte habitats?

Figure 32. ***Ditrichum pallidum***, a moss that has different degrees of response to bacteria, depending on the bacterial species. Photo by Hugues Tinguy, with permission.

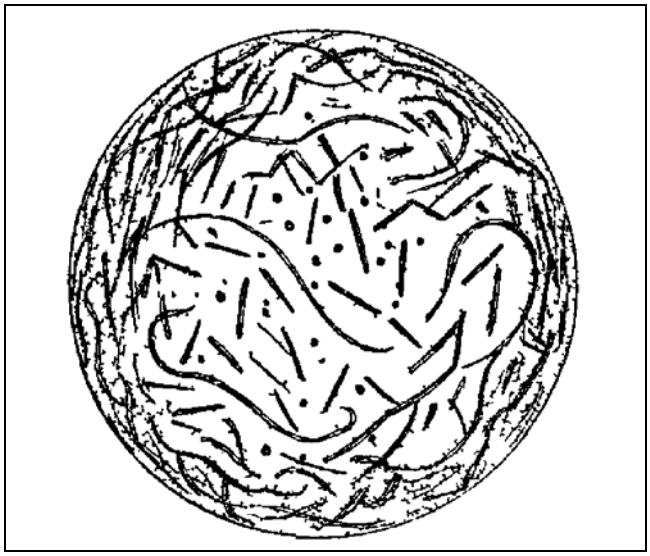

Figure 33. ***Proteus vulgaris*** drawing, the species that suffered the least effect by ***Ditrichum pallidum*** extracts in bests by Liu and Wang (2010). Image from Project Gutenberg Distributed Proofreaders, Encyclopædia Britannica, 1911, through public domain.

Bodade *et al*. (2008) similarly found that the dry habitat moss ***Racomitrium crispulum*** (Figure 34) did not provide any effective antibacterial compounds against the bacteria tested [including ***Escherichia coli*** (Figure 19) and ***Staphylococcus aureus*** (Figure 18)], whereas other bryophyte species in the test were all effective at least some of the time.

Dulger *et al*. (2005) tested 8 mosses from relatively dry habitats of rocks, soil, and tree trunks in Turkey and found that they inhibited 11 species of bacteria. The most susceptible bacteria among these were ***Bacillus subtilus*** (Figure 16) and ***Pseudomonas aeruginosa*** (Figure 20). The antiyeast activity was weak.

Figure 34. ***Racomitrium crispulum*** with capsules, an exposed-rock moss that was ineffective against the tested bacteria. Photo by Larry Jensen, with permission.

Leptodictyum riparium (Figure 35), a moss of wet habitats, had the best inhibitory power against all eight bacteria tested when compared to that of the thallose liverwort ***Conocephalum conicum*** (Figure 21) and the moss ***Plagiomnium undulatum*** (Figure 36) (Castaldo-Cobianchi *et al*. 1988). They commented there is competition between species growing in the water where one might find ***L. riparium***.

Figure 35. ***Leptodictyum riparium***, a moss that is even more inhibitory toward eight bacteria than the strongly inhibitory ***Conocephalum conicum***. Photo by Hermann Schachner, through Creative Commons.

Figure 36. ***Plagiomnium undulatum***, a moss that is less inhibitory toward eight bacteria than the strongly inhibitory ***Leptodictyum riparium***. Photo by Hermann Schachner, through Creative Commons.

Altuner *et al*. (2014) found that the antibacterial activity of the forest floor species ***Dicranum polysetum*** (Figure 37) was especially strong against ***Staphylococcus carnosus*** (see Figure 18). It is interesting that such a strong activity against ***Staphylococcus carnosus*** exists when this bacterial species in not known from any natural habitat **and** it has no known pathogenicity (Löfblom *et al*. 2017)! Furthermore, it lacks any pathogenicity genes. Altuner *et al*. (2014) found that all three mosses in their study [***Calliergonella cuspidata*** (Figure 38), ***Dicranum polysetum***, and ***Hypnum cupressiforme*** (Figure 9)] were active against several species of Gram positive and Gram negative pathogenic bacteria.

Figure 37. ***Dicranum polysetum***, a species with especially strong antibacterial activity against the non-pathogenic ***Staphylococcus carnosus***. Photo by Kristian Peters, through Creative Commons.

Figure 38. ***Calliergonella cuspidata***, a species active against several Gram positive and Gram negative pathogenic bacteria. Photo by Claire Halpin, with permission.

Dey *et al*. (2015) found that elevation made a difference in antibacterial activity of ***Pellia endiviifolia*** (Figure 39) from the eastern Himalayas. Those collected at higher elevations had significantly higher antimicrobial activity. They suggested this might be due to differences in UV light levels, with the intensity increasing at higher elevations.

Figure 39. ***Pellia endiviifolia***, a species with significantly higher antibacterial activity at higher altitudes. Photo by David T. Holyoak, with permission.

By contrast, Mukherjee *et al*. (2012) found that in the thallose liverwort ***Dumortiera hirsuta*** (Figure 40) those specimens from a higher elevation had slightly lower antibacterial activity than those from lower elevations. Clearly more detailed information is needed about the habitats to determine the differences in antibacterial activity.

Figure 40. ***Dumortiera hirsuta***, a species with slightly lower antibacterial properties at higher elevations. Photo by Mutolisp, through Creative Commons.

Out of 29 species of bryophytes from Sri Lanka, only ***Pogonatum marginatum*** (a species of wet soil and shady banks; Figure 41) failed to respond with antibiotics against any of the test bacteria [***Lysinibacillus sphaericus*** (MTCC511), ***Staphylococcus aureus*** (Figure 18) (ATCC25923), ***Klebsiella pneumoniae*** (Figure 42) (ATCC700603), ***Pseudomonas aeroginosa*** (Figure 20) (ATCC27853)] (Liyanage *et al*. 2015).

Figure 41. ***Pogonatum urnigerum***; ***Pogonatum marginatum*** from Sri Lanka failed to produce any antibiotic in response to test bacteria. Photo by Hermann Schachner, through Creative Commons.

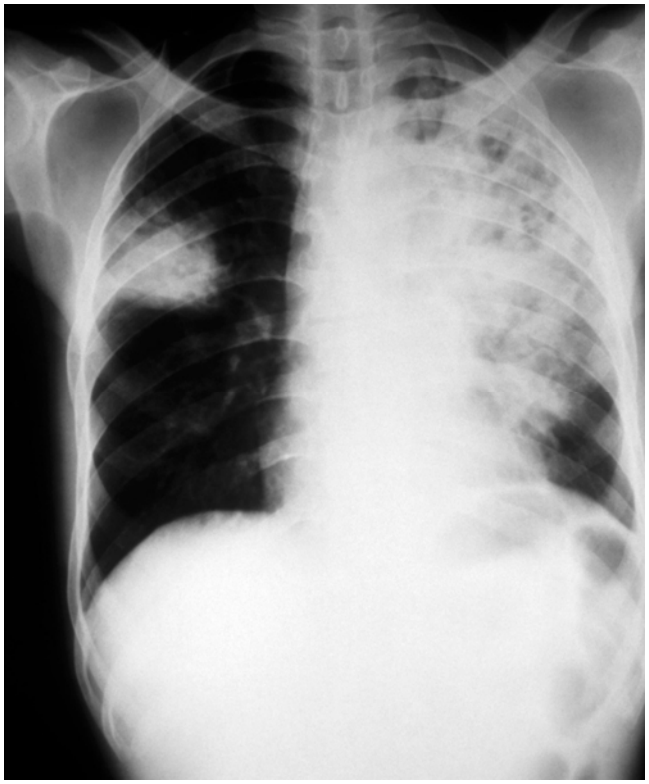

Figure 42. Human lung X-ray showing damage by ***Klebsiella pneumoniae***, especially in left lung; ***Pogonatum marginatum*** fails to respond to this bacterium. Photo through Creative Commons.

Bacterial Defense Partners

Bacteria themselves can often be of antibiotic benefit to the bryophytes. They can provide antagonistic compounds that serve as defense compounds against other bacteria and fungi. I wonder if the bacteria ever serve as deterrents to larger herbivores such as insects, birds, and rodents. One would expect the insects to avoid some of the bryophytes because they produce insect repellant (Ludwiczuk & Asakawa 2019), but it seems that the bacteria could also serve this role.

Mechanisms of control of microorganisms by bryophyte-associated bacteria include secretion of metabolic substances (*e.g.* antibiotics, **siderophores** - small, high-affinity iron-chelating compounds secreted by microorganism), controlling proliferation, and competitive exclusion of plant pathogens (Glick & Bashan 1997; Muleta *et al*. 2007; Svzntes *et al*. 2010). Among these antagonistic bacteria Szentes *et al*. (2010) found the genera ***Azospirillum*** (Figure 43), ***Bacillus*** (Figure 15, Figure 16, Figure 17, Figure 74), ***Burkholderia*** (Figure 44), ***Enterobacter*** (Figure 45), ***Pseudomonas*** (Figure 20), and ***Rhodococcus*** (Figure 46).

Figure 43. ***Azospirillum*** promoting root hair growth (**upper**) compared to roots with no ***Azospirillum*** (**lower**). Members of this genus control proliferation and facilitate competitive exclusion of plant pathogens that occur on bryophytes. Photo by T. A. Toennisson, through Creative Commons.

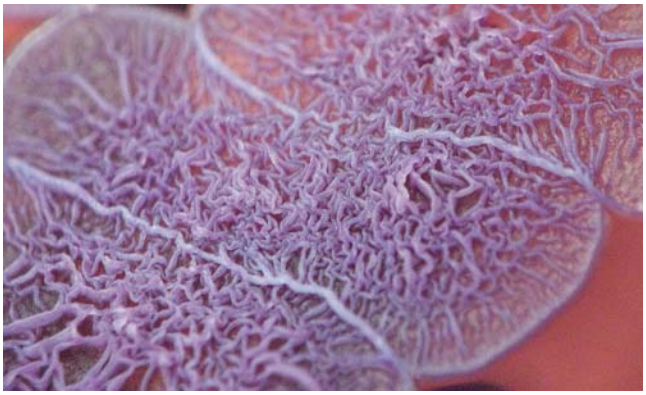

Figure 44. ***Burkholderia thailandensis***; members of this genus control proliferation and facilitate competitive exclusion of plant pathogens that occur on bryophytes. Photo through Creative Commons.

Figure 45. ***Enterobacter cloacae***; members of this genus control proliferation and facilitate competitive exclusion of plant pathogens that occur on bryophytes. Photo from CDC, through public domain.

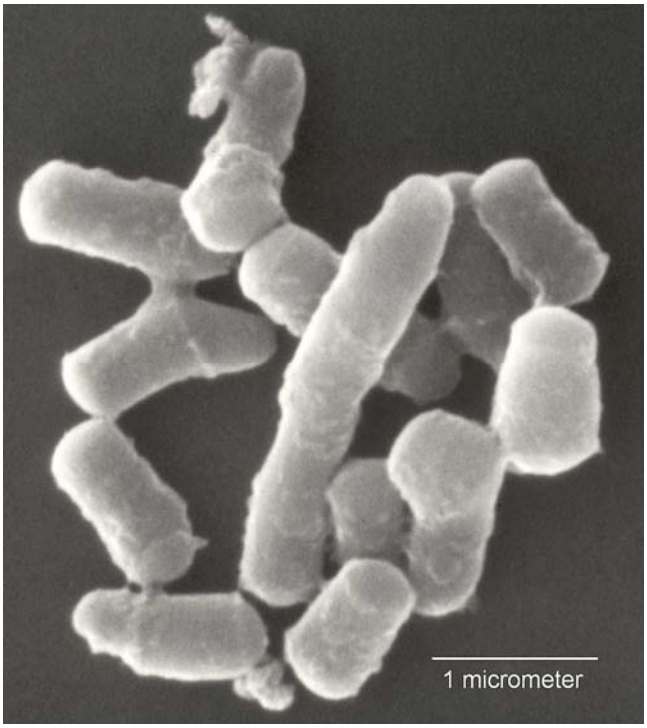

Figure 46. ***Rhodococcus***; members of this genus control proliferation and facilitate competitive exclusion of plant pathogens that occur on bryophytes. Photo by Jerry Sims, through public domain.

Banerjee and Sen (1979) found that the liverwort family **Rebouliaceae** (Figure 47) had especially good antibiotic activity in all 5 tested species. The moss ***Brachythecium procumbens*** and the liverworts ***Asterella wallichiana*** (Figure 48) and ***Marchantia paleacea*** (Figure 49) showed the widest range of antibiotic activity. ***Salmonella typhi*** (Figure 1) was the most sensitive of the microorganisms used in the tests.

Figure 47. ***Reboulia hemisphaerica***, in a family (**Rebouliaceae**) with especially good antibiotic activity. Photo by Hermann Schachner, through Creative Commons.

Figure 48. ***Asterella wallichiana*** with young archegonial heads, among the species with the widest range of antibiotic activity. Photo by Shyamal L., through Creative Commons.

Figure 49. ***Marchantia paleacea***, among the bryophyte species with the widest range of antibiotic activity. Photo by Des Callaghan, with permission.

It is interesting that some newly recognized strains of bacteria present among the bryophytes have toxicity to things that presumably never affect the bryophytes. For

example, 12 new strains of ***Bacillus thuringiensis*** (Figure 17) were isolated from among 76 bryophyte species (Zhang *et al*. 2007). A strain of this bacterium harbored a new gene that exhibited activity against the Asian tiger mosquito ***Aedes albopictus*** (Figure 50). This mosquito species is a vector of chikungunya virus, dengue virus, and dirofilariasis, and is rapidly expanding its range due to human activity. But perhaps it is more likely that this strain and others of the species ***Bacillus thuringiensis*** are active against multiple pathogens, some of which do affect bryophytes. The bryophytes may also provide a service to the community by maintaining a reservoir of these bacteria that are available to the other plant species and able to render their antagonistic effects there.

Figure 50. ***Aedes albopictus***, a species of mosquito that is sensitive to a bryophyte-inhabiting strain of the bacterium ***Bacillus thuringiensis***. Photo by James Gathany, CDC, through public domain.

Inducible Defenses

Bodade *et al*. (2008) provided indirect evidence that an inducible reservoir of defense compounds might be the case in the bryophytes they tested. They found that the antibacterial extracts were not always effective against the same bacterium, nor was the magnitude of inhibition consistent. This suggests the possibility of environmental stimulation by the bacteria themselves or by the environmental conditions with the possibility of seasonal changes. The interactions of bacteria with their bryophyte substrates are a new field of study with many questions needing answers.

Gimenez-Ibanez *et al*. (2019) noted that to that date no bacterial pathogens had been discovered in association with the widespread liverwort ***Marchantia polymorpha*** (Figure 24). In addition to this lack of evidence of bacterial pathogens, the researchers discovered an ancient immune system that governs plant-microbe interactions between ***M. polymorpha*** and the plant pathogenic bacterium ***Pseudomonas syringae*** (Figure 51). The presence of this bacterium on the liverwort activates the immune response, including effector activities inside the liverwort cells. This response also appears to be very specific and differs among the strains of ***Pseudomonas syringae***.

Figure 51. ***Pseudomonas syringae*** on lilac leaf. This bacterium also induces ***Marchantia polymorpha*** to produce antibiotics. Photo by Jerzy Opioła, through Creative Commons.

Thus, it appears that at least some of the defenses are inducible. This saves energy and permits the bryophyte to maintain a larger library of defenses. Sabovljević *et al*. (2010) found that all extracts (in DMSO) from their investigated bryophytes [***Atrichum undulatum*** (Figure 52), ***Marchantia polymorpha*** ssp. ***ruderalis*** (Figure 53), ***Physcomitrium patens*** (Figure 3)] produced antibacterial compounds against the bacteria ***Escherichia coli*** (Figure 19) ATCC 35210, ***Pseudomonas aeruginosa*** (Figure 20) ATCC 27853, ***Salmonella typhimurium*** (Figure 54) ATCC 13311, ***Enterobacter cloacae*** (human isolate; Figure 45), ***Listeria monocytogenes*** (Figure 55) NCTC 7973, ***Bacillus cereus*** (human isolate; Figure 56), ***Micrococcus flavus*** (Figure 57) ATCC 10240 and ***Staphylococcus aureus*** (Figure 18) ATCC 6538). Extracts from naturally grown bryophytes demonstrated better antibacterial activity than did those from laboratory-grown bacteria, suggesting that the presence of bacteria in the environment could stimulate production of defense compounds.

Figure 52. ***Atrichum undulatum***, a moss species that produced antibacterial compounds against a number of tested bacteria. Photo by Michel Langeveld, through Creative Commons.

Figure 53. ***Marchantia polymorpha*** ssp. ***ruderalis***, a species that produced antibacterial compounds against a number of tested bacteria. Photo by David T. Holyoak, with permission.

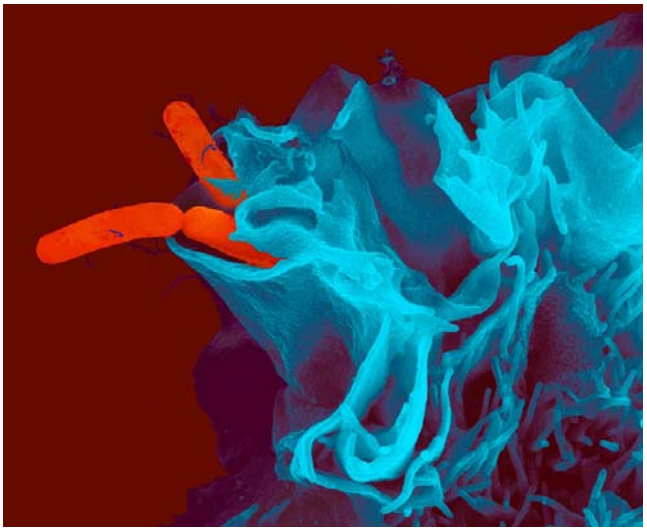

Figure 54. ***Salmonella typhimurium*** in human epithelial cell, a bacterial species affected by antibacterial compounds from several bryophytes. Photo by David Goulding, Wellcome Trust Sanger Institute, through Creative Commons.

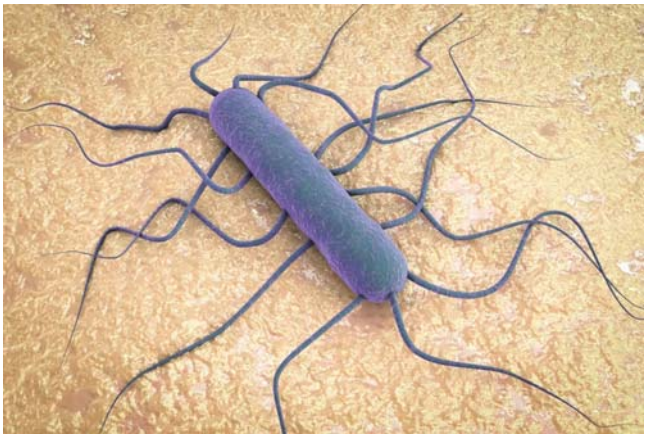

Figure 55. ***Listeria monocytogenes***, a bacterium inhibited by ***Atrichum undulatum***, ***Marchantia polymorpha*** ssp. ***ruderalis***, and ***Physcomitrium patens***. Photo by Kateryna Kon, TheConversation.com, through Creative Commons.

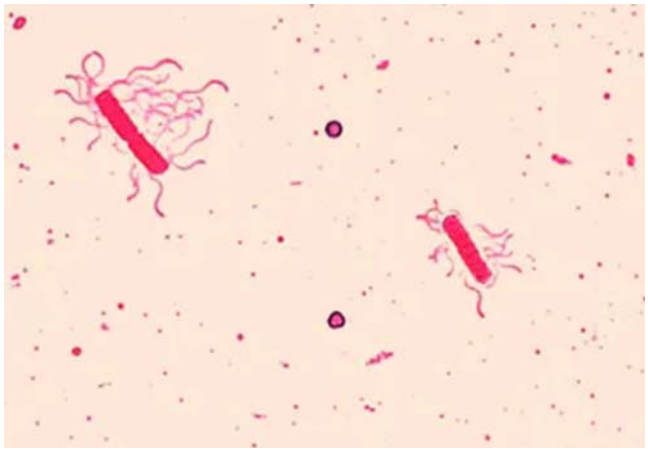

Figure 56. ***Bacillus cereus***, a bacterium inhibited by ***Atrichum undulatum***, ***Marchantia polymorpha*** ssp. ***ruderalis***, and ***Physcomitrium patens***. Photo by William A. Clark, CDC, through public domain

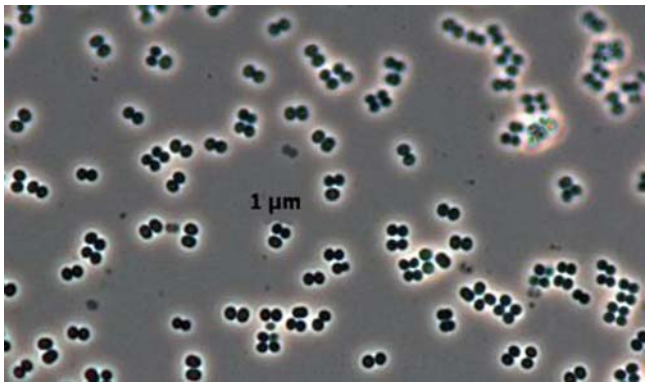

Figure 57. ***Micrococcus flavus***, a bacterium inhibited by ***Atrichum undulatum***, ***Marchantia polymorpha*** ssp. ***ruderalis***, and ***Physcomitrium patens***. Photo Leibniz-Institut DSMZ, through Creative Commons.

Ponce de León and Montesano (2017) noted that early bryophytes needed adaptations to combat both abiotic stresses and pathogenic microorganisms. They reported that several of the defense mechanisms against microbial pathogens were retained in the evolution of flowering plants and they provided evidence that defense compounds can, in fact, be induced. The moss ***Physcomitrium patens*** (Figure 3) uses plasma membrane receptor(s) to sense the pathogen. It then transduces the signal through a MAP kinase cascade that leads to activation of defenses associated with the cell wall and expression of genes encoding for proteins with various roles in plant resistance. Other responses include activation of the production of reactive oxygen species (ROS), induction of an HR-like reaction, and an increase in some hormone levels.

Alvarez *et al*. (2016) noted that the shikimate, phenylpropanoid, oxylipins, and auxin pathways were all activated by introducing the bacterium ***Pectobacterium carotovorum*** (Figure 29) to the moss ***Physcomitrium patens*** (Figure 3). The **shikimate pathway** leads to the production of phenolic compounds, which are known inhibitors of bacteria (Santos-Sánchez *et al*. 2019). **Phenylpropanoids** can work synergistically with most antibiotics and provide enhanced antibacterial activity (Hemaiswarya & Doble 2010). **Oxylipins** signal the regulation of plant growth and development, senescence,

sex determination of reproductive organs, and of importance here, the defense against biotic and abiotic stress and programmed cell death (Christensen & Kolomiets 2011). **Auxin** is a growth hormone for which concentrations, and relative concentrations, matter (Leyser 2017).

In experiments with ***Physcomitrium patens*** (Figure 3), Ponce de León *et al*. (2007) clearly demonstrated induction. This was achieved with the pathogenic bacterium ***Pectobacterium carotovorum*** ssp. ***carotovorum*** (Figure 29). Infection with this bacterium caused severe maceration, whereas ***carotovorum*** caused only mild symptoms. Both the species and subspecies induce a defense response in the moss, as evidenced by enhanced expression of conserved plant defense-related genes.

Inducible defense mechanisms in ***Physcomitrium patens*** (Figure 3) include reinforcement of the cell wall, production of reactive oxygen species, programmed cell death, activation of defense genes, and synthesis of secondary metabolites and defense hormones (Ponce de León & Montesano 2013). These responses are induced by the exposure to the pathogens.

All of this evidence indicates that the defense responses by the bryophytes are inductive, but it is unlikely that they are entirely inductive.

Antioxidants and ROS

The oxidative burst is "a rapid, transient production of huge amounts of reactive oxygen species (ROS)" (Wojtaszek 1997). Changes in cell wall *p*H are important in controlling this production. H_2O_2 (hydrogen peroxide) is produced and is directly toxic to micro-organisms (Samoĭlenko *et al*. 1983). The peroxide can disturb the structure and permeability of the bacterial cell wall and the cytoplasmic membrane, as well as inducing ribosomal lesions and rupturing the DNA.

In addition to being an antibacterial phenomenon, the oxidative burst is important in other plant defenses, including oxygen consumption, production of phytoalexins, systemic acquired resistance, immobilization of plant cell wall proteins, changes in membrane permeability and ion fluxes, and an apparent role in hypersensitive cell death (Wojtaszek 1997).

Unlike animal systems, plant cells are able to produce ROS, primarily as H_2O_2, in significant amounts (Wojtaszek 1997). This production is mostly exocellular and is regulated by such factors as hormones, light, and wounding. Whereas it is generally absent in elongating cells of tracheophytes, it can exhibit significant production in wounded cells or those undergoing mechanical stress. Its half-life of 10^{-9} s makes it difficult to follow the sequence of reactions. In suspension cultures, pathogens such as fungi and bacteria (**elicitors**) usually elicit a response in 1-2 minutes, reaching a maximum response in several minutes (Figure 58). The reaction is completed within 30-60 minutes after initiation. Time intervals for intact plants seem to be much longer. And response time varies with the elicitor and plant species. Furthermore, the specific compound responsible for the elicitation varies among species of elicitor, as does the degree of response. But is all this true in bryophytes?

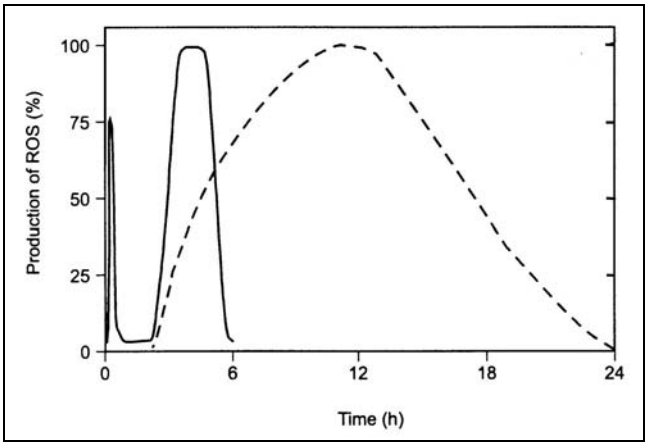

Figure 58. Oxidative burst of plant cells in response to bacterial elicitation (—) and ROS generation by plants in response to treatment with OGA (oligo-1,4-α-D-galacturonide) (– –), a known elicitor of an oxidative burst in many plants. Modified from Wojtaszek 1997.

Minibayeva and Beckett (2001) were among the first to report details on the oxidative burst in bryophytes. They found that among the plants they tested, it was best developed in the cyanobacterial lichens, the hornwort ***Anthoceros natalensis***, and two thalloid liverworts [***Dumortiera hirsuta*** (Figure 40; Figure 59), ***Pellia epipylla*** (Figure 60)]. The four mosses (Figure 59) and leafy liverwort in the test were almost completely unresponsive. Among the responsive species, production of O_2 was generally higher in species from moist habitats and correlated well with plant water content at full turgor. Unfortunately, at the time of these experiments we were unaware of the importance of rate of drying on the survival success of bryophytes to dehydration. Their drying regime was extended from full hydration to an **RWC** (relative water content) of 0.05-0.10 in only 2.5 hours (Minibayeva & Beckett 2001), a time which usually prevents bryophytes from preparing for desiccation (Stark *et al*. 2013; Greenwood & Stark 2014). Nevertheless, in ***Anthoceros natalensis*** the rate of oxygen production was more than 1000 μmol g^{-1} dry mass h^{-1}, a rate 100 times that recorded for the roots of wheat (Minibayeva *et al*. 1998)!

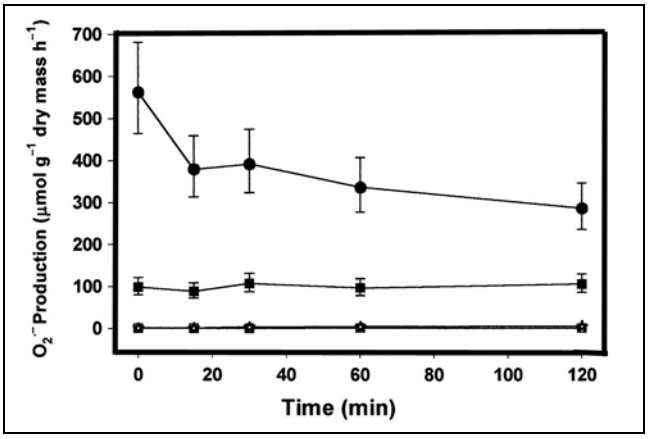

Figure 59. Superoxide production (oxidative burst) upon hydration in hydrated (**solid squares**) and desiccated (**solid circles**) ***Dumortiera hirsuta*** (Figure 40), and hydrated (**open squares**) and desiccated (**star**) moss ***Atrichum androgynum*** (Figure 61). Modified from Minibayeva & Beckett 2001.

Figure 60. ***Pellia epiphylla***, a thallose liverwort that experiences a high level of oxidative burst when it is rehydrated. Photo by Bernd Haynold, through Creative Commons.

Mayaba *et al*. (2002) found that the moss ***Atrichum androgynum*** (Figure 61) produced an oxidative burst of hydrogen peroxide during rehydration, an **ROS** response. They suggested that this oxidative burst might provide protection against bacterial and fungal attempts to invade the cells. As additional support for this hypothesis, Lawton and Saidasan (2009) found that the moss ***Physcomitrium patens*** (Figure 3) produces reactive oxygen species (ROS) in response to pathogenic bacteria. Mayaba *et al*. found a burst of H_2O_2 (oxidative burst) during rehydration during the first 15 minutes in ***Atrichum androgynum***. They found that the production increased as the desiccation time of the moss increased. Light and the hormone ABA (abscisic acid) influenced the rate.

Figure 61. ***Atrichum androgynum***, a species that produces an oxidative burst of hydrogen peroxide during rehydration. Photo by Nick Helme, through Creative Commons.

Lyapina *et al*. (2021) found that mosses had a higher number of small secreted peptides (SSPs) in their genomes than did either the liverwort ***Marchantia polymorpha*** (Figure 24) or the hornwort ***Anthoceros*** sp. (Figure 62). Synthetic peptide elicitors like those of tracheophytes triggered reactive oxygen species production in the protonema of the moss ***Physcomitrium patens*** (Figure 3), suggesting that even tracheophytes could elicit the ROS response in the bryophytes, thus perhaps aiding in their ability to defend against invading bacteria in the protonema stage. This moss also secretes peptides that respond specifically to a chitosan treatment, indicating a possible role in immune signalling. Could these elicitors from tracheophytes be a signal to help the bryophytes determine a suitable place to become established?

Figure 62. ***Anthoceros punctatus***; a tested species in this genus has fewer small secreted peptides (SSPs) in its genome than do tested mosses. Photo by Malcolm Storey, <DiscoverLife.org>, with online permission.

But reactive oxygen can be dangerous for cells because it can react in so many ways. Antioxidants can be of valuable protection to bryophytes, particularly during rehydration, scavenging the oxygen quickly before it can do too much damage (Mayaba *et al*. 2002). Seel *et al*. 1992) suggested that the antioxidants may be more important than the levels of H_2O_2 in desiccation survival of bryophytes.

Vats and Alam (2013) evaluated this ROS potential in the moss ***Barbula javanica***. The moss had a total phenolic content of 30 ± 0.96 mg GAE/gdw. It exhibited substantial antioxidant behavior against several oxidation agents, with a reducing activity at 1259±1.56 μM L^{-1}. Vats and Alam suggested that the high phenolic content might account for this activity. The moss ***Cryphaea heteromalla*** (Figure 63) similarly has a high level of protection against reactive oxygen species (ROS), which can be induced by tert-butyl hydroperoxide (Provenzano *et al*. 2019).

Figure 63. ***Cryphaea heteromalla***, a moss with a high level of protection against reactive oxygen species (ROS). Photo by Hermann Schachner, through Creative Commons.

Differences in Plant Parts

One might expect that bryophytes would protect the parts that need protection the most, thus saving energy by not producing secondary compounds where they are not needed. But which tissues are the most vulnerable for the species? Mukherjee *et al*. (2012) compared antibacterial activity in the reproductive thallus to that of the vegetative thallus of ***Dumortiera hirsuta*** (Figure 40). They found that the reproductive thallus showed the least antibacterial activity of the two. This appears to be an interesting aspect that needs lots more study.

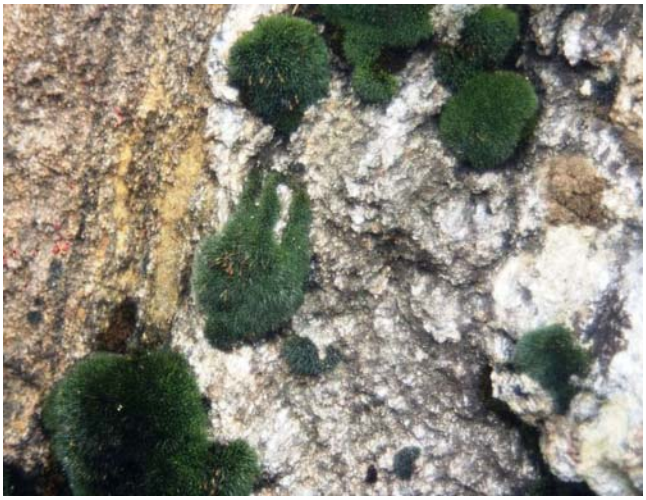

Figure 65. ***Grimmia alpestris***, on rock, with capsules, a species that is active against ***Paenibacillus*** obtained from larvae of the honeybee. Photo by Henk Greven, with permission.

Defending Others?

Bryophytes could accomplish community service by providing antibacterial activity against pathogens that affect roots and seeds. But do they?

We do know that some bryophytes produce antibacterial substances that could protect larvae. Sevim *et al*. (2017) found that 10 [***Calliergonella cuspidata*** (Figure 38), ***Calliergonella lindbergii*** (Figure 64), ***Grimmia alpestris*** (Figure 65)***, Isothecium alopecuroides*** (Figure 66), ***Metzgeria conjugata*** (Figure 67), ***Polytrichastrum formosum*** (Figure 68), ***Polytrichum commune*** (Figure 69), ***Syntrichia calcicola*** (Figure 70), ***Syntrichia montana*** (Figure 71), ***Tortella inclinata*** var. ***densa*** (Figure 72)] out of 23 tested species of bryophytes were active against ***Paenibacillus*** (Figure 73) obtained from larvae of the honeybee (***Apis mellifera***). Although it is unlikely that any honeybee larvae will be living among bryophytes, other kinds of larvae do occur there and these antibiotics might protect them against bacteria as well.

Figure 66. ***Isothecium alopecuroides***, a species that is active against ***Paenibacillus*** obtained from larvae of the honeybee. Photo by Herman Schachner, through Creative Commons.

Figure 64. ***Calliergonella lindbergii***, a species that is active against ***Paenibacillus*** obtained from larvae of the honeybee. Photo by Bob Klips, with permission.

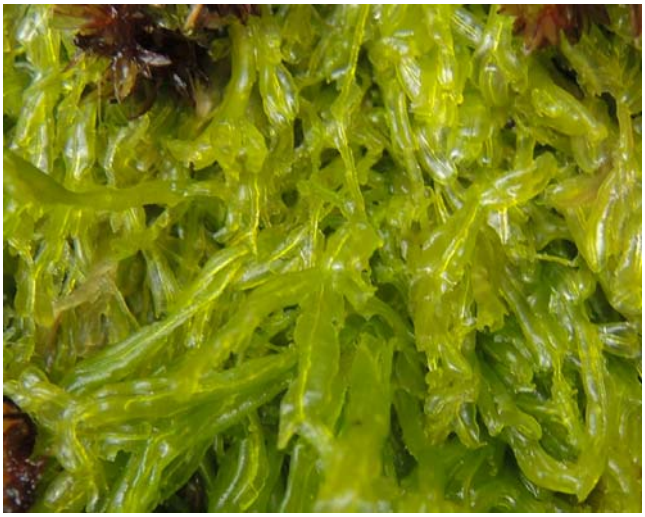

Figure 67. ***Metzgeria conjugata***, a species that is active against ***Paenibacillus*** obtained from larvae of the honeybee. Photo by Jo Denyer, with permission.

Figure 68. ***Polytrichastrum formosum***, a species that is active against ***Paenibacillus*** obtained from larvae of the honeybee. Photo by David T. Holyoak, with permission.

Figure 69. ***Polytrichum commune***, a species that is active against ***Paenibacillus*** obtained from larvae of the honeybee. Photo by Kristian Peters, through Creative Commons.

Figure 70. ***Syntrichia calcicola***, a species that is active against ***Paenibacillus*** obtained from larvae of the honeybee. Photo by Hermann Schachner, through Creative Commons.

Figure 71. ***Syntrichia montana***, a species that is active against ***Paenibacillus*** obtained from larvae of the honeybee. Photo by Claire Halpin, with permission.

Figure 72. ***Tortella inclinata*** var. ***densa***, a species that is active against ***Paenibacillus*** obtained from larvae of the honeybee. Photo by Hermann Schachner, through Creative Commons.

Figure 73. ***Paenibacillus larvae*** infecting a hive. Photo by Tanarus, through Creative Commons.

Potential Uses

Bryophytes can have a number of functions in the ecosystem resulting from their providing a welcoming habitat for bacteria. For example, ***Bacillus thuringiensis*** (Figure 17) (*Bt*) is the source of the antibiotics in some

kinds of pesticides (Figure 74), especially against beetles, mosquitoes, black flies, caterpillars, and moths (Perez *et al*. 2015). Zhang *et al*. (2007) found that ***Bacillus thuringiensis*** occurs naturally on bryophytes. *Bt* is non-toxic to most animals and non-pathogenic to birds, fish, and shrimp (Perez *et al*. 2015). Some of pesticides using *Bt* are even approved for use in organic gardens. Lin *et al*. (2017) found that the bacterium ***Bacillus thuringiensis*** strains could be isolated from bryophyte populations in Turkey, suggesting that the bryophytes could serve as a reservoir for this important bacterium. These bacteria became established as long-term inhabitants of leaves and stems within 26 days of inoculation.

Figure 74. ***Bacillus thuringiensis*** damage by larvae (**left**) and protected by Bt genes (**right**). Photo from Agricultural Research Service, USDA, through public domain.

Tani *et al*. (2011) cultured bacteria in hydroponic cultures of the moss ***Racomitrium japonicum*** (a roof-greening moss; Figure 75) and reported that these bacteria had the potential to serve as biofertilizers for production growth of this moss species. They further found that ***Methylobacterium*** (Figure 76) species formed a mutualistic relationship with the moss (Tani *et al*. 2012). The moss has natural populations of methylotrophic bacteria. And the moss produces methanol. The bacteria use the methanol as a carbon source, converting methanol to CO_2. When these bacteria are present in cultures of ***Racomitrium japonicum***, they increase the growth of the moss – a desirable phenomenon for mosses grown in production quantities.

Figure 75. ***Racomitrium japonicum***, a species that benefits from the oxidation of methanol by ***Methylobacterium*** and for which other associated bacteria serve as a "fertilizer" by enhancing growth. Photo by Masaki Shimamura, with permission.

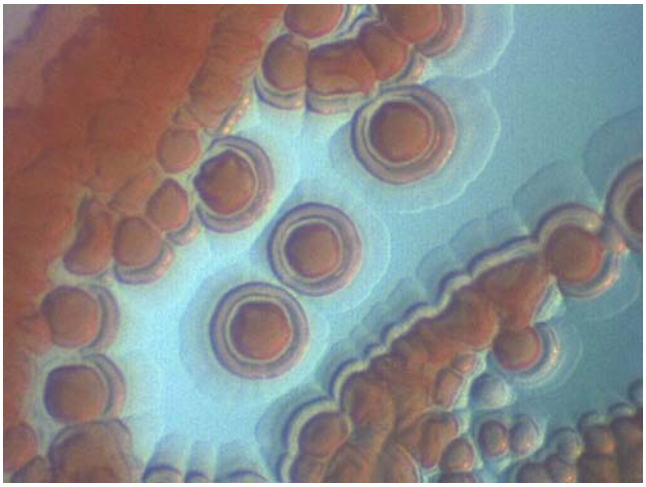

Figure 76. ***Methylobacterium symbioticum***, in a bacterium genus that benefits ***Racomitrium japonicum*** through the oxidation of methanol. Photo by Symborg, through Creative Commons.

Mishra *et al*. (2014) remind us that many bacteria have developed resistance to most of our traditional antibiotics. They suggest the use of bryophyte antibiotic substances as potential replacements (see also Pant 1998). These bryophytes and bacteria have been living together for millions of years, perhaps longer, and the bryophyte antibiotics are still effective.

We have already seen the potential use of bryophyte compounds to inhibit multiplication of ***Melissococcus plutonius*** (Figure 77), one of the causal bacteria for European foulbrood disease in honeybees. Research in developing culture techniques and enhancing growth are proceeding on ***Physcomitrium patens*** (Figure 3) and ***Marchantia polymorpha*** (Figure 24) (Schwartzenberg *et al*. 2004; Horn *et al*. 2021).

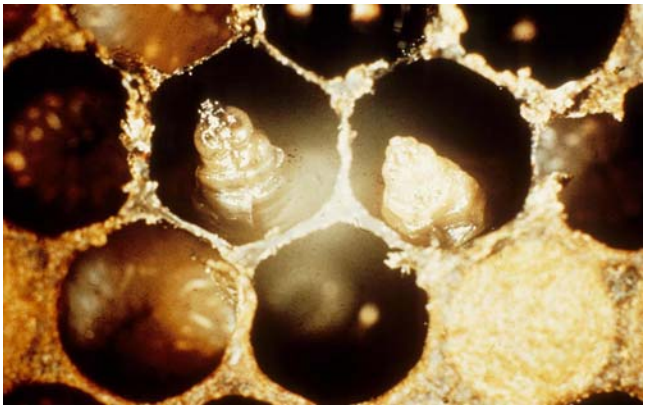

Figure 77. ***Melissococcus plutonius*** causing European foulbrood disease. Photo from Georgia Department of Agriculture, <Bugwood.org>, through Creative Commons.

Frahm (2004) reported that experiments at Bonn University in Germany were able to culture the first *in vivo* bryophytes for extraction of biomedical compounds. The products of all 20 tested bryophytes had effects on a variety of crop infections with various fungi. Products from bryophytes are now available commercially in Germany. In addition, successful field experiments have been completed in Peru and Bolivia. These products are

antifungal on human pathogenic fungi. But are these *in vivo* products produced by the bryophytes or by their fungal associates?

Singh *et al*. (2011) found that several bryophytes used by traditional healers were effective in the treatment of burns. The bryophyte extracts are especially effective against ***Staphylococcus aureus*** (Figure 18).

Mosses harbor **Actinomycetota** that include ***Micromonospora chalcea*** (Figure 78), a bacterium with growth promoting potential (Insuk *et al*. 2020). This species also codes for genes for phosphate solubilization, permitting the bacteria to survive in the nutrient-limited environment so common where bryophytes thrive. Their production of glycine-betaine and trehalose contribute to tolerance of drought. They have genes for heat shock proteins, cold shock proteins, and oxidative stress.

Figure 79. ***Archidium ohioense***, a moss that produces substances that could provide a safer replacement for NSAIDs. Photo by Li Zhang, with permission.

Figure 78. ***Micromonospora chalcea***, a bacterium that can promote plant growth and enhance drought tolerance. Photo from Leibniz-Institut DSMZ, through Creative Commons.

Figure 80. ***Bryum coronatum*** with capsules, a moss that produces substances that could provide a safer replacement for NSAIDs. Photo by Geoffrey Cox, through Creative Commons.

For arthritis sufferers, bryophytes have the potential to support anti-inflammatory functions. ***Archidium ohioense*** (Figure 79), ***Bryum coronatum*** (Figure 80), and ***Racopilum africanum*** (Figure 81) all produced substances that acted against inflammatory agents, but Ayinke *et al*. (2015) found that concentration was important. This includes protection of red blood cells effectively against heat and hypotonic induced lyses. The effects were comparable to those of expensive and somewhat dangerous non-steroidal anti-inflammatory drugs. Should we be looking for use by wild mammals for anti-inflammatory purposes, especially in the Arctic?

Figure 81. ***Racopilum africanum***, a moss that produces substances that could provide a safer replacement for NSAIDs. Photo by Jan-Peter Frahm, with permission.

The potential uses of bryophytes and their associated bacteria in the pharmaceutical industry have been reviewed many times by various authors and will not be discussed further in this chapter. But it could be worthwhile to review these for their potential as a pharmaceutical chest for other animals in the wild.

Sterilizing Bryophytes

Sterilizing bryophytes has been a challenge for bryologists. Many of the standard cleaning agents are as dangerous to the bryophytes as they are to the bacteria. Some detergents can even encourage bacterial growth (pers. obs.).

Yet it is often desirable to isolate bryophyte processes from those closely allied bacterial contributions. Hence, the decision to use sterile culture must depend on the purpose of the culture. Is it needed to understand biochemical and physiological pathways of the bryophyte, or is it needed to ascertain potential roles in the ecosystem?

This chapter has revealed that bryophytes often depend on bacteria to carry out normal life functions. On the other hand, Gupta (1977) demonstrated that the large number of bacteria associated with several bryophytes accounted for the respiratory activity measured upon rehydration of the bryophytes. They suggested that this respiration could provide an indication of survival or injury of some bryophytes, but that it presented serious limitations as indication of the cell viability of the bryophytes.

For those conditions where sterile bryophytes are needed, one must establish the conditions for growth and propagation. Schelpe (1953) tried the method of using abscised apical parts of elongated stems of mosses that have been kept in a moist atmosphere and low light intensity. Unfortunately, he had little success in obtaining bacteria-free cuttings. Lack of success in culturing bryophytes is all too common and methods differ among species.

Rowntree (2006) reported on their most successful method to date in preparing bryophytes for the Millennium Seed Bank of threatened UK bryophytes. These are held in sucrose-free ¼ or ½ Murashige & Skoog or Knops minimal medium. These were successfully sterilized first (pre-cultured) with 1% (w/v) for 3 min and 0.5% (w/v) for 2 min. Sporophyte cultures were more successful than those of gametophytes due to less contamination (see also Vujičić *et al*. 2011). They found that some sterilizing treatments could cause the bryophytes to develop resistance to the toxic effects of the biocide. Vujičić *et al*. (2011) also suggested the use of sugar-free medium for ***Hypnum cupressiforme*** (Figure 9). They found that lower temperatures (18-20°C) also helped.

Perhaps Shaw (1986) has a better solution to culturing bryophytes while retaining the necessary interactions with bacteria, as needed for ecological studies. He has successfully cultured them by drying the bryophyte gametophytes, grinding them to a fine powder, and sowing this powder on native soil or other desired substrate. This method has the advantage of producing bryophytes with normal morphology – something that is often missing in sterile culture.

Summary

For whatever reason, bryophytes have many secondary compounds that are antibiotic to many types of human and plant pathogens. In some cases, these are effective against bacteria that could affect the bryophytes. For both types, they are often produced only in response to the presence of certain bacteria or other microorganism. Of greater interest here are the bacteria that protect the bryophytes.

There are some implications that there are differences in quantity of antibacterial substances that depend on habitat. These differences are unclear, with some aquatic species having many such compounds and some cave thallose liverworts, a bryophyte type that usually produces high concentrations of antibacterial compounds, can have none! Part of the problem might relate to sterile culturing, or the bacteria might be unculturable species. In any case, much more must be learned before any generalizations can be made.

Among the protections exhibited by some bryophytes are oxidative bursts upon rehydration. It is suggested that this serves to protect the bryophytes at a time when their membranes are damaged and could provide easy access for the bacteria. To accompany this burst, the bryophytes can accelerate the production of antioxidants, a necessity for the bryophyte to avoid damage by free radicals of oxygen.

Little is known about differences in defense or bacterial numbers among plant parts. In some cases, reproductive parts are less protected.

Some of the bacteria produce compounds such as *Bt* that can protect honeybee larvae from disease. Our knowledge of this is very limited, but the ability of these compounds to serve as antibiotics against multiple organisms suggests that this could be a fertile area for research. The bacteria that live among bryophytes suggest that the bryophytes could serve as a reservoir of these bacteria, and that in turn the bacteria could provide antibiotics for other organisms in the ecosystem, including humans.

Bacteria can present a problem in studying the physiology of bryophytes because they contribute to the measured photosynthesis and respiration. But sterilizing the bryophyte can keep the bryophyte from developing normally or from producing substances that you are trying to measure.

It has become clear that the bacteria associated with a bryophyte can have profound effects on its success, including successful establishment, development, and growth. This is an important consideration for those attempting production levels of moss culturing.

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CHAPTER 1-1
FIELD TAXONOMY AND COLLECTION METHODS

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CHAPTER 1-1
FIELD TAXONOMY
AND COLLECTION METHODS

Figure 1. Zen Iwatsuki on a collecting trip in Iceland. Photo by Janice Glime.

Collection

Vanderpoorten *et al*. (2010) suggest that to find a high species richness, look for a habitat with lots of bryophyte cover (Figure 1). Species diversity has a high positive correlation with the carpet density. Such a habitat suggests an appropriate moisture level, and the large clumps of bryophytes can create microhabitats where moisture is lost more slowly, permitting smaller species to develop among them.

Stevenson (2005) reminds us that when you focus on one habitat, you begin to ask questions about how and why plants are growing there. These questions form the bases of hypotheses. And when you accept the rigors of recording your habitat observations, these hypotheses are more likely to take form. They are also much more reliable for later descriptions than your memory will be. These notes will help you to formulate better data collection sheets, and you should spend time field-testing these sheets before you begin an actual comprehensive study.

For ecological studies, there are at least two reasons to collect specimens (Vanderpoorten *et al*. 2010). First, you need to collect to verify your field identification and to look for minute species hiding among the more obvious ones. Second, you need to collect **voucher specimens** for your collections. Collections for quantitative or systematic sampling will be discussed later in a chapter on Sampling. For vouchers, you will probably want some for your own herbarium, but you also need one for your institution or other permanent herbarium that is available to other researchers and one for the person who verifies the species for you. **If you are collecting in another country,** especially a country where the bryophyte flora is poorly known, you should also prepare an identified specimen to give to a national or other public herbarium in that country. By doing this, you help to pay back your debt of collecting there and help the field of bryology progress in that country.

Collection methods have been described many times and in multiple languages (*e.g.* Loeske 1925; Iwatsuki 1970; Kildyushevsky 1973; O'Shea 1989; Buck & Thiers 1996; Gradstein *et al*. 2003). Loeske (1925), interpreted in English by Raup (1926), stressed the importance of a systematic study, rather than a random one. Even at that early date, he opined that a region seldom offers many new or rare mosses. Instead, he espoused the value of studying a bryophyte in relation to its habitat, way of living, and relationship to the rest of the flora.

Bryophytes are the easiest of all plants to collect (Buck & Thiers 1996). They rarely need to be pressed, but rather can be placed in a **paper bag** (Buck & Thiers 1996) or **packet** and permitted to air dry (Smith Merrill 1990). Some bryologists (*e.g.* Ireland 1982) prefer packets made of newspaper because it allows more rapid water loss than brown paper bags. And very wet specimens may cause the bags to come unglued.

The collection depends somewhat on the substrate of the bryophyte. Buck and Thiers (1996) point out that if plants grow in loose tufts or mats or are pendent, they can be easily picked up by hand. Extra adhering soil can, and should, be removed, provided that does not cause the colony to fall apart. Small plants or those tightly adhering to their substrate will be best served if they are collected with a small portion of their substrate to keep them together and to retain the growth habit. Likewise, epiphytic species should be collected with a shallow strip of the bark. Epiphylls should be collected with their underlying leaf. Those on branches can be collected with clippers.

Some collection methods are unique, permitting collection of difficult specimens. Snider and He (1991) suggest using a **flashlight** to peer into crevices and under cliff overhangs. It should be one that can be locked into the on position rather than requiring continuous pushing of a button switch.

Obtaining the Sample

In most cases, the bryophytes can be sampled by a hand grab. However, bryophytes on bark or those that have grown for decades may require extraction with the help of a knife. As Patricia Eckel put it in Evansia (1996), using a knife can have its hazards: having plants blow away from the blade, getting cut, getting poked by the knife in the pocket, losing one's balance while balancing on a talus slope, and shutting sand in with the blade, making opening and closing more difficult.

The Sposs

After losing all her knives and seemingly suitable tools, Eckel (1996) discovered the "**sposs**" (Figure 2). This is a hybrid form of spoon boss, a tool that doesn't hurt and that catches the loosened bryophyte before the wind can carry it away. Her husband, Richard Zander, invented and named the sposs. The official sposs has its handle bent back so it can be hung over the belt and one can have a firmer grip. Eckel recommends a 30 cm cooking spoon with a 15 cm boss (bowl part) for gathering bryophytes from under cacti and avoiding snakes and other animals enjoying the cool of the same tracheophyte as the bryophyte. This tool works equally well for the bryophytes in a crevice, on a rock ledge, or in the fragile arrangement of sand in the desert. And it is not confiscated from your pack at the airport!

Figure 2. Spoon bent to make a **sposs** for collecting soil bryophytes. Image by Patricia Eckel.

Chisel

If you typically collect bryophytes on rock or bark, especially tiny ones that require bringing the substrate with them, you might want to invest in a good chisel (Schofield 1985). McCune (1994) recommends one available from Miners Inc. (catalog # AO 601). This is currently available for US $50.80. It has a tungsten carbide cutting edge that makes it strong and durable, and it is lighter in weight than most chisels (Figure 3). On the other hand, a much cheaper putty knife will work well for soil samples and even some bark samples.

Figure 3. Carbide-tipped hand chisel for removing bits of wood or rock. Photo by Miners Inc.

Masking Tape Sampler

Some species are so tiny that the eye cannot discern them even in good light, or they may be within reach but out of view. Once a possible site for tiny bryophytes is located, extraction of the bryophyte can be accomplished with the aid of masking tape (Snider & He 1991). The tape should be at least 5 cm wide (Figure 4). The tapes differ in their ability to adhere, but none adhered well to very wet or dripping rocks. The vinyl packaging tape was least useful because it easily wrinkled, stuck to itself easily, and was unmanageable in the field. Duck tapes, bandaging tapes, and thicker vinyl repair tapes worked well in the field, but weighed more and were difficult to cut or tear; they were also difficult to work with after samples were acquired. Only painter's tape (masking tape) seemed to be adequate for the job. Even if the tape did not adhere well to moist surfaces, it did a good job of removing and holding the bryophytes.

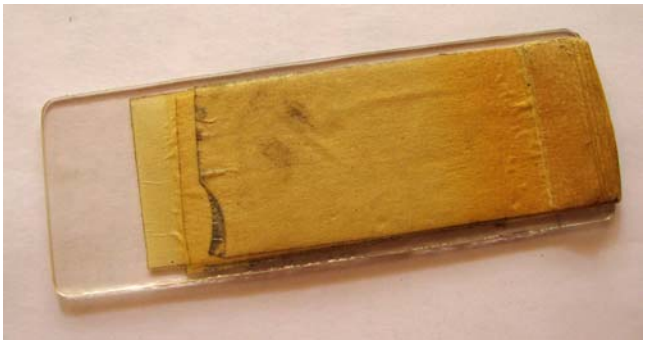

Figure 4. Masking tape bryophyte sampler with masking tape on a strip of plexiglass. Edges of the plexiglass have been sanded to make them smooth. Photo by Janice Glime.

Snider and He (1991) prepared the tapes by cutting them in 5x17 cm strips, then folding over 2 cm at one end (Figure 5). These were attached at one end to a piece of 6 cm x 17 cm x 5 mm plexiglass. The folded end was used to

pull the tape off the plexiglass to take a sample. Once the sample was in place (Figure 6-Figure 7), they attached the sticky side to the other side of the plexiglass and wrote collection data on the non-sticky side of the tape. When the specimen is returned to the lab, it can be removed by moistening the specimen with water or a wetting agent like Pohlstoffe (See Chapter 2-2 in this volume). They used the method to discover such findings as protonemal trumpets of ***Diphyscium foliosum***, protonemal flaps of ***Tetraphis pellucida*** (Figure 8-Figure 9), asexual propagules of various bryophytes, and several minute leafy liverworts such as ***Cephaloziella*** (Figure 10). These flat samples can even be photographed by a scanner without glares or need for a tripod (Figure 11-Figure 12). They can be enlarged as scanned or later in Photoshop.

Figure 5. Masking tape sampler, showing folded over ends. Photo by Janice Glime.

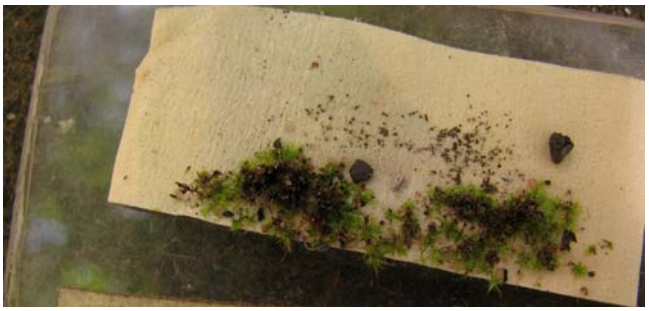

Figure 6. Masking tape sampler with sample of ***Bryum*** from crack in stone. Photo by Janice Glime.

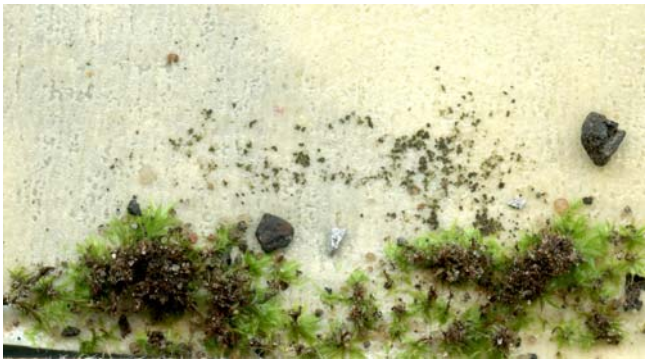

Figure 7. Masking tape sampler with sample of ***Bryum*** sp. from crack in stone. Photo by Janice Glime using Epson V500 scanner.

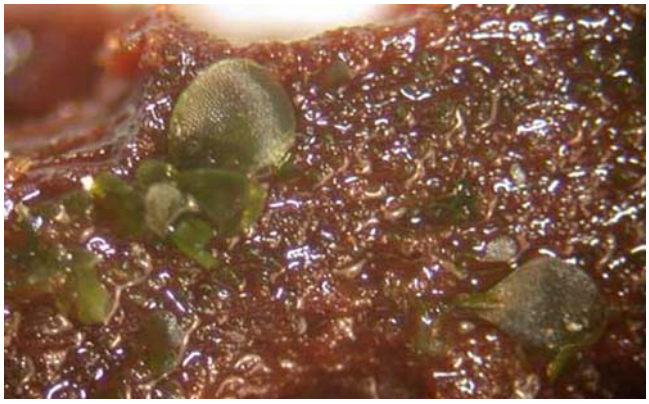

Figure 8. Protonemal flaps of ***Tetraphis pellucida***. Photo from University of British Columbia website.

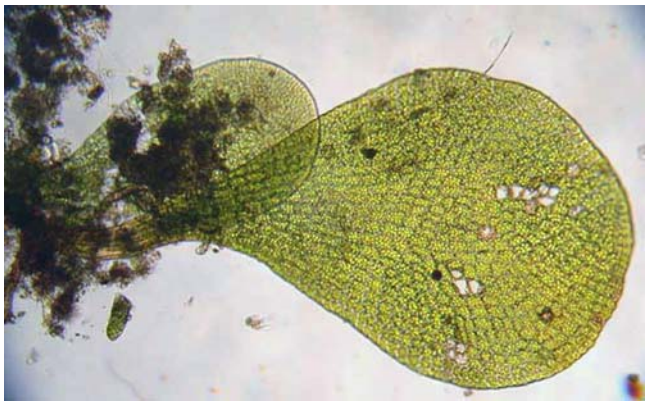

Figure 9. Microscope view of protonemal flaps of ***Tetraphis pellucida***. Photo from University of British Columbia website.

Figure 10. ***Cephaloziella massalongi***, a very tiny liverwort. Photo by Des Callaghan.

Figure 11. Masking tape sampler with sample of ***Bryum*** sp. from crack in stone. Photo by Janice Glime using Epson V500 scanner to make image.

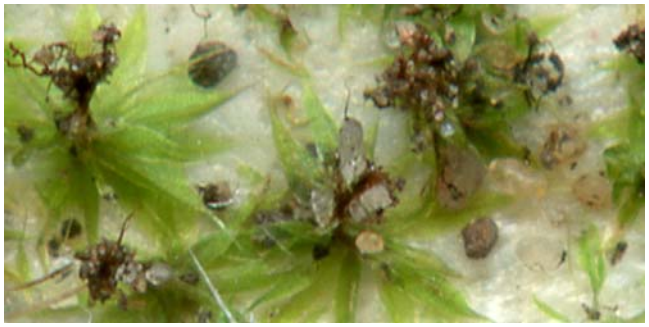

Figure 12. Enlarged view of masking tape sample of ***Bryum*** sp. from crack in stone. Photo by Janice Glime using Epson V500 scanner.

Seasons

Some bryophytes are seasonal or annual. Although winter is a good season for epiphytes that don't require capsules for identification, it is often not a good collecting season for other bryophytes that may be buried under snow. Flood plain species are only discernible for a period of time after the water recedes following flooding. Species of arable fields are mostly ephemerals that disappear in a relatively short period and often are present in only either spring or fall. Preston *et al*. (2010) found that autumn, winter, and early spring were suitable times to inventory fields in Great Britain. And capsules are only in a mature state with spores intact for a short time. Most of the sexual structures mature in spring or fall, or when the rainy season occurs. Nevertheless, some mature in winter. Hence, the season most suitable for collection depends on the purpose of the collection, the species, and the location.

What to Sample – the Miniscule

Many different kinds of characters are used to identify bryophytes, and reproductive structures also provide ecological life cycle strategy information. Sporophytes on bryophytes like ***Orthotrichum*** provide important, and sometimes essential, characters needed for identification. Additional searching can sometimes reveal local hidden capsules from a previous year or young, developing capsules from the current year. Tubers and bulbils are also important for both taxonomic and ecological purposes (Vanderpoorten *et al*. 2010). Unstable habitats such as riverbanks, arable fields, and flood plains are likely to have rhizoidal tubers buried in the soil beneath the bryophytes, so 1-3 cm of soil should be collected with the bryophytes (Whitehouse 1966; Porley 2008). Unfortunately, most countries won't permit soil to come into the country, so these must be cleaned and at least some propagules carefully preserved in a **minipacket** along with the specimen.

Minipackets are useful for a number of rare structures and species (Vanderpoorten *et al*. 2010). These can be made in advance, or as needed, so be sure you have some light-weight paper to use. If small species occur among a clump of larger species, place at least a sample of each of the smaller species in a **minipacket**. These packets can be made like the large packets (see Chapter 3 on Herbarium Methods and Exchanges in this volume). If a small species is left to dry with the larger clump, it can become glued to the larger bryophyte when it dries. It will also be brittle when dry and easily broken if you try to remove it then. Rewetting to remove it can reduce the ability to extract DNA from the bryophyte. At least some plants of an especially small specimen like ***Ephemerum*** spp. should also be placed in a minipacket, and if only a few plants have reproductive structures, these, too, should be placed in a minipacket (Rothero & Blackstock 2005). Small species on soil are likely to become invisible if the soil dries and loses its cohesiveness, so extracting a few individuals into a minipacket is again useful.

Sample Size

The amount to collect is an important consideration. An ideal sample is about the size of the palm of your hand (Miller 1988; Smith Merrill 1990; Buck & Thiers 1996; Vanderpoorten *et al*. 2010), but that is not always feasible or wise. Conservation should be a foremost consideration. If you must deposit a sample in an institutional herbarium, send to someone to verify identification, and keep some for yourself, be sure to take enough for all those purposes (Buck & Thiers 1996). Only small samples of suspected rare species should be collected, and then only if absolutely necessary and more than that amount is left intact where you found it. **DO NOT collect rare species** just to add to your personal or institutional herbarium or to use for exchange. Be sure to protect the edges if you take part of a clump, at least for species that seem rare in that location or overall. You can do this by placing a rock against the exposed edge or by packing soil against it to protect against desiccation inside the clump. Even another species of bryophyte might help, but try to avoid ones that might overtake a rare species.

When I joined a field trip with the British Bryological Society (BBS), I was warned not to collect more than a thumbnail (or about a 1.5 cm diameter). On the other hand, if you are collecting for exchange or gifts to herbaria, you usually need at least half a palm size for the herbarium to accept the material. Of course if it is a small species with only small clumps, such size will not be possible, or will require several clumps. The danger of several clumps is that they could turn out to be different species or microspecies, and they should certainly all come from the same small area within a location where it is most likely that they have originated from spores or fragments of the same population.

Mixed Collections

The usefulness of mixed collections depends largely on the use of the collection. These provide us with information and should be treated somewhat differently. If the sample collection contains mixed species (Figure 13), they can be separated partially into minipackets in the field, or separation can occur later in the lab. Each packet can be given a different letter while retaining the original collection number; the species occurring together should be noted on the packets. If these are just small bits among a larger collection, they can be placed in minipackets that are kept with the original collection. It is important that packet labelling makes clear which specimen belongs with which name. This can be clarified with minipackets (David Wagner, Bryonet 20 January 2023).

Figure 13. ***Hypnum jutlandicum*** (pinnate) + ***Hypnum lacunosum*** (thick branches) + ***Dicranum scoparium*** (acrocarpous, bright green) in Denmark, illustrating typical species mixes one might encounter. Photo by Lars Hedenäs.

Mixed populations of closely related species can reveal both genetic differences and ecological information. Both species presumably are exposed to the same conditions, so one might assume that differences in morphology (or physiology) are the result of genetic differences. But Wyatt *et al*. (1985) remind us that the microclimate within a bryophyte clump is not uniform. Young individuals resulting from spores that germinate within the clump will experience different growing conditions than did the spores that germinated to form the original colony.

Thus the question arises as to the usefulness of mixed collections (Wyatt *et al*. 1982, 1985). Consider that whether they are all one species or distinguishable as different species, the multiple morphologies contribute important ecological information about the past history of the clump and its microhabitat conditions.

On the other hand, as common garden information, the mixed collection usually falls short. These will be discussed in more detail in the chapter on bryophyte – bryophyte interactions in the Bryophyte Interactions volume. Isoviita (1985), however, argues that in some cases they can be useful to represent common garden conditions. First of all, bryophytes can be difficult to cultivate, and morphologies of cultured bryophytes are likely to change, being unrepresentative. Secondly, the equipment to conduct common garden experiments is not always available.

To understand when mixed collections might be useful, we can consider the arguments of Wagner and Wagner (1983). "Cohabitation of two or more species without successful interbreeding demonstrates biological discreteness and confirms that the character differences are most likely genetically fixed." They used the technique in their study of the fern genus *Botrychium*. This is a fascinating genus with underground prothalli that depend on mycorrhizal fungi. The sporophyte of some species spends little time above ground. This genus can occur intermixed in ways that have little effect on the environment of each other, thus possibly providing information on niche separation. But their most convincing argument is that most of the species in the genus are endangered, so that this is a means of gaining ecological information with minimal disturbance that could create further endangerment in a species that is difficult to culture.

In Papua, New Guinea, handfuls of ***Frullania*** often produced two or more species of ***Frullania*** (Glime *et al*. 1990). Multiple collections of these indicated associations that were rather frequent. Other mixed pairs of species in the same genus (**congeneric**) include ***Syntrichia laevigata*** and ***S. papillosa*** (Figure 14) (Robert Klips, pers. comm. 10 August 2012) and ***Grimmia anodon*** and ***G. plagiopodia*** growing intermixed on sandstone outcrops in western Montana (Roxanne Hastings, pers. comm. 10 August 2012). Intermixed species will be discussed in detail in the Bryophyte Interactions volume in the chapter on bryophyte – bryophyte interactions.

Figure 14. ***Syntrichia laevigata*** and ***S. papillosa*** growing intermixed in Columbus, Ohio, USA. Photo by Robert Klips.

In short, for ecological work intermixed collections can be useful and should not be totally avoided. Rather, for verification purposes, use minipackets to store a small sample of each species, but leave most of the mix intact for whatever use might later be needed, including DNA analysis. All identified species should be listed on the packet.

Epiphytes and Epiphylls

In some habitats, especially the tropics, the greatest diversity and abundance occur in the canopy. These require special collecting (Perry 1978) and preservation techniques. Furthermore, only outer bark should be collected with the bryophyte, keeping enough of the bark on the tree to protect the wood against disease. Nevertheless, at least the outer layer of bark should be collected to maintain the slender species that would otherwise be lost (Buck & Thiers 1996).

Epiphytic bryophytes often have directional, vertical, and bark type preferences, and these need to be noted on the herbarium label. Hence, when collecting these, note the host species, the type of bark (rough, smooth, flaking, fissured), height on the tree, and side/aspect of the tree (N-S-E-W). It is also important to note if the substrate was vertical, on a branch or lean, and whether it was on the top, side or bottom of leaning or horizontal structures.

Some bark bryophytes will come off easily, but for some you will need to make a slice of the underlying bark with a sharp knife or chisel in order to keep the growth form of the bryophyte intact.

Canopy

Bryophytes in the canopy present the greatest challenges. These are typically out of reach, so short of bringing a trained monkey, one needs to develop special

techniques. Several researchers have been successful using a single rope to aid tree climbing (Perry 1978; Ter Steege & Cornelissen 1988; Gradstein *et al*. 1996, 2003) (to be covered in chapter on Sampling in this volume). Smaller branches can be sawed off and lowered by ropes.

But not all of us are so agile. Developing archery skills can help, allowing you to shoot epiphytes from the tree, but not all bryophytes will cooperate, and your arrow may lodge in the canopy without returning the prize. Ropes with a weight or hook on one end can sometimes help; with a little skill you might be able to toss it over a branch to pull the branch down. But this method is limited to lower branches because there is too much congestion to be successful in reaching an adequate number of epiphytes in upper branches. Some studies (for insects and other animals) have used a helium-filled dirigible (Hallé 1990) to reach the canopy, but that has another set of dangers.

You (but not the forest) may get lucky and have the advantage of a hurricane or other wind storm to bring branches down from the canopy, but Gradstein *et al*. (2003) point out that fallen branches are inadequate to sample the canopy diversity. One needs to be careful that these are recent falls and represent canopy colonizations rather than post-fall additions. This should be recognizable by the newness of the break on the branch. This method of collecting has the disadvantage that you don't know the height from which the branch has fallen, and sampling is likely to be biased by size class, position in the canopy, and species of tree. Even the age of the tree can be a factor, especially in heavy wind storms.

Epiphytes with their bark substrate may be subject to squashing, especially if you collect in packets, so you might want to pack paper wads around them to protect against such flattening.

Epiphylls should be collected on their substrate leaves to keep the colonies intact, to help in identification of the substrate leaf, and to recognize patterns of colonization. If the leaf is too large, it can be cut so that your collection includes the base, the middle, and the tip (tip morphology is often important in determining the species that collect there). These should be kept in a plant press or other means of keeping the leaf flat for later examination. These are sites for tiny liverworts, especially those in the **Lejeuneaceae**, and should be explored in the lab with the dissecting microscope. Since there are likely to be fungi and Cyanobacteria as cohabitants, the collected leaves need to be dried quickly. Newspapers are useful absorbent materials, but they or other absorbents must be changed daily, especially in humid climates, to discourage overgrowth by the Cyanobacteria and fungi. Especially wet leaves should be blotted dry before the leaf is put in the plant press.

Aquatic Samples

Aquatic bryophytes tend to be quite "dirty." When the bryophytes dry, this mix of silt, bacteria, fungi, and algae becomes glued to the plants, making it difficult to see cells. Hence, aquatic bryophytes need to be washed in the water of their habitat to remove as much of the adhering material as possible. Once the adhering material is removed as best as practical, the bryophyte should be squeezed or pressed, but not wrung, to remove excess water. Then it should be shaken lightly to loosen up the branches and leaves so they don't all stick together. It may be helpful to remove a few branches and dry them in a minipacket where they can be spread out singly. Otherwise, you may find leaves hopelessly glued together by the adhering algae and bacteria.

For some of the more delicate species, like ***Fontinalis flaccida***, the plants can be floated on a 3"x5" (~7x13 cm) card and branches arranged so that some are clear. This may be especially useful for herbaria that glue specimens to sheets, but the cards can also be put in packets and the specimens are easily removed from the cards.

Conservation Issues

Collecting anywhere that is not slated for another destruction is always a conservation issue. Not only is sampling a potential means of destroying the entire colony by disturbing rhizoids and increasing moisture loss, the trampling involved can also be destructive. Wagner () follows the 1-in-20 rule. That is, don't remove more than 1 plant in 20 or more than 5% of a plant to conserve its life. This same rule has been adopted independently in Australia and at the New York Botanical Garden, suggesting that 1-in-20 is a good rule.

Removal depends partly on the moss species and its growth habit. There are a few "rules" you can follow:

1. If you have permanent plots, sample pieces outside, but adjacent, to the plot when sampling is essential, such as reproductive phenology studies.
2. Don't disturb the cushions and other growth forms that are needed to maintain water relations of the bryophyte.
3. Collect pleurocarpous branches from the edge of the colony.
4. Generally don't remove specimens from the center of a colony, especially of acrocarpous species, because it changes moisture-holding ability.
5. If there is only a small population, avoid removing any, except perhaps a small branch if it is absolutely essential, placing it in a mini packet so it doesn't get lost.
6. Be aware of potentially rare species and take only pictures.
7. Be careful what you tread on and how often. Sometimes a plastic sled can be used for standing or squatting to minimize damage.
8. The objective is to collect in a way that the bryophytes can fill in the vacated space before other species invade.
9. For teaching, I kept a teaching collection (plus photography) that students could use for study without having to collect their own.
10. Some herbaria won't accept specimens smaller than the palm of your hand, but I found that the British get upset if you collect a sample larger than your thumbnail on their forays.
11. Always have permission before collecting.

Collecting Permits

The temptation to pick up a bit of moss anywhere you find it is compelling, especially if it looks new and interesting. And, unfortunately, most land owners don't care about the bryophytes. But in many places, especially parks at any level, a collecting permit is required. At the very least, you need permission of the land-owner. It would be futile to try to list places where one might obtain such a permit, but it is very important. Not only is it embarrassing to be caught "stealing" a specimen, but there may be fines and even sanctions. As a representative of your institution, you can bring bad publicity to that institution and even to your country if you are in another country from your own.

A search of Google for **collecting permit** will get you lots of addresses and websites, but a narrower search for the country, state, or municipality may get just what you need. If you are unable to find anything for that country or state, you can usually get pointed to the right place by contacting a local bryologist. If there is no bryologist, try the Department of Agriculture website to see if it provides any leads – or contact them directly with an explanation of what you want to collect, how much, the purpose of the collection, and a query about who to contact for permission to collect and export. A useful website telling you contact information for various countries and various agencies in the USA is called The Skeptical Moth <http://skepticalmoth.southernfriedscience.com/techniques/collecting-permits/>.

One of the most embarrassing things you could do is to take a class collecting somewhere when you don't have permission. And even if you have standing permission, it is often a good idea to notify the owner you are coming so you don't inadvertently enter upon an event where it would be dangerous or awkward.

Don't be surprised if there is a fee for a collecting permit. And that may differ, depending on who you are and where you are from! For example, West Virginia, USA, provides the permits free of charge to academics, students, and researchers from West Virginia, USA, but charges $25 for the same group out of state. Permits for commercial use are much higher and apply to everyone.

Keep your permit with you in the field. You might want to keep it in a Ziploc bag so it remains legible. When we were in Yellowstone, off trail and out of sight, a ranger approached us and we had to show our permit. Our parked car had attracted his attention.

Bryological Collector Arrested

Collecting without permission is taken seriously, at least in New Zealand. One eager collector in New Zealand was arrested for collecting without a permit. The arrested collector became temporarily famous through journals such as Commercial Horticulture (January 1993), with the article titled "US botanist fined for taking native mosses" (Alan Whittemore, Bryonet 29 September 1999). The botanist was collecting material to screen it for natural products, not for herbarium records. In addition to his infamy, he was fined. The mosses had been collected in national parks in quantities for which personnel would not have issued a permit.

In some countries you will be asked to leave your collections behind with a local herbarium or museum and may never see them again (Willem Meijer, Bryonet 28 September 1999). Meijer suggests working with young students from that country who are eager to learn. They may be more willing to send a portion of your specimens from a herbarium just to get them identified.

Record-keeping

When in the field, do fieldwork. Minimal time should be spent doing other record-keeping chores. BUT, do keep complete records. A common way for bryologists to do this is to prepare packets or small paper candy bags in advance (Figure 15). This is done by numbering them consecutively and keeping a small record book (Figure 16). If you keep a life list of numbers, you also have a record of how much collecting you have done. There are numbering machines that use stamp pad ink. These allow you to set the starting number and each time you press it onto a bag or packet, the number advances.

Figure 15. Candy bag collection bags, pre-numbered. Photo by Janice Glime.

When you arrive at a collecting site, record in the notebook the **starting collection number**, **date**, **location**, general features of the **habitat**, **altitude**, and **GPS coordinates** (Figure 17). It is also important to record characters that might change as the specimen dries, including **color**, **growth form**, and **fertility** (Rob Gradstein, pers. comm. 28 July 2012). Be aware that different nationalities abbreviate dates differently, so 3/5/12 means 5 March 2012 in the USA, but means 3 May 2012 in Germany. It is safest to **write out the month**. A good way to be sure your information is not lost due to rain or other mishap is to photograph the beginning page if you have a camera. This also serves to mark the beginning of pictures taken at the site.

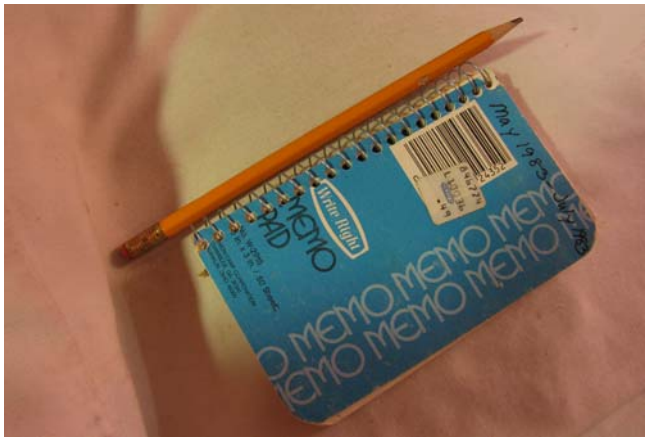

Figure 16. Record book showing dates of collection included. Photo by Janice Glime.

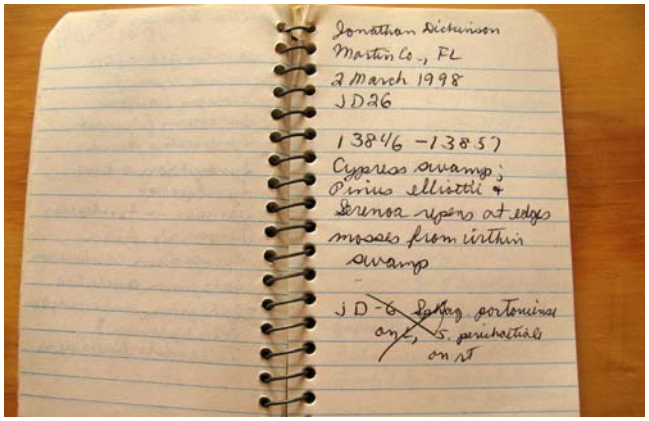

Figure 17. Field notebook record of a collection site, including general habitat description and record of collection numbers. GPS was not available. Photo by Janice Glime.

A partial alternative to notebooks or writing on bags is a field packet labelled with habitat characteristics to circle (Figure 18-Figure 19). I was introduced to this in Japan by Zen Iwatsuki. I found I could write just about as fast as I could locate the right word to circle, but I suspect that after one uses the method for awhile it would be faster. It does provide the advantage that the collector is more likely to include more detail about habitat information.

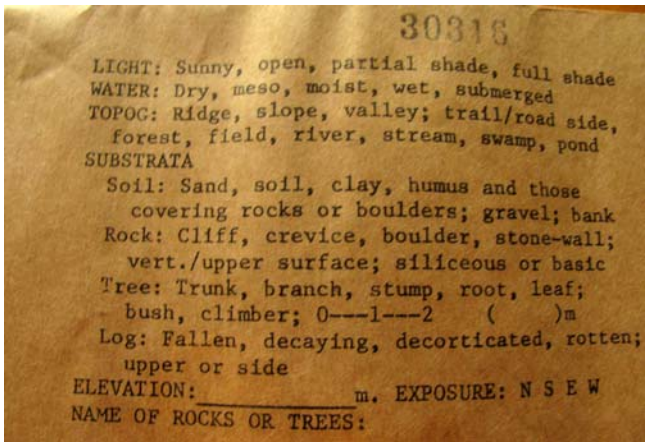

Figure 18. Collecting packet from Zen Iwatsuki, demonstrating a habitat circling system used by some bryologists. Photo by Janice Glime.

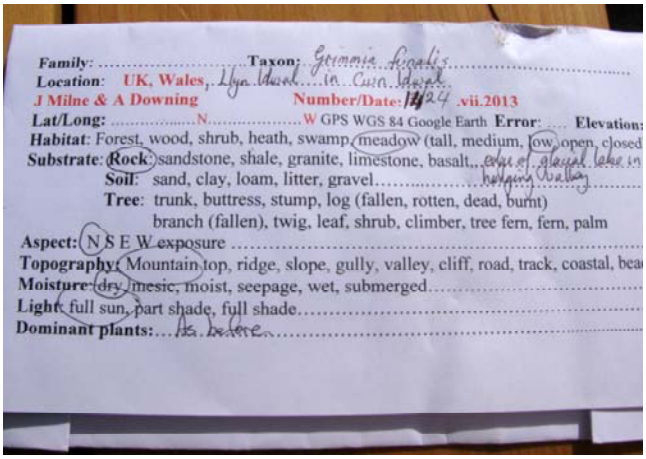

Figure 19. Field packet used by Allison Downing and Pina Milne. Photo by Janice Glime.

When collecting the bryophyte, squeeze out excess water and put the bryophyte in the bag or packet. (See chapter on Herbarium Methods and Exchanges to learn one way of folding a packet.) Be sure the numbered packets or bags are kept in order before use. I do this by having an apron with pockets (see Figure 32-Figure 36 below). The pocket is long enough and wide enough for the bags I use to fit easily with an end sticking out for easy grabbing. Always remove the bag or packet from the top of the pile, then record the **elevation**, **substrate**, **exposure**, **indication of moisture**, and **specific habitat** and **microhabitat** information that is not included with your general habitat information (Buck & Thiers 1996; Figure 20). It is helpful to put your **best guess name** on the packet, with a question mark if there is any doubt. That can make it easier to find the specimen later when you want a specific one, and it also makes identification easier because you have used the clues provided by growth habit and microhabitat. Try to avoid putting more than one collection or species in the same bag or packet unless they are tightly intermixed or the mix is needed for ecological study.

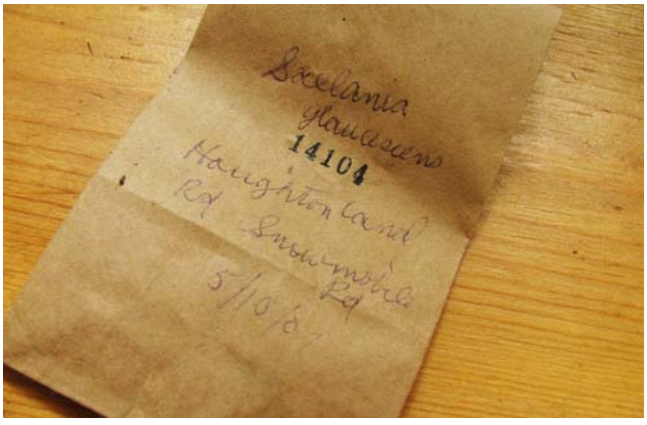

Figure 20. Bag with sample and tentative name. It is missing substrate information; hopefully that is in the field notebook. Photo by Janice Glime.

When you are ready to leave the site, finish your notebook page by recording the last collection number. Add any further observations that might help. It is also helpful to take another picture of the page to mark the end of that collection site among your pictures. If you take

bryophyte pictures along the way, you might want to photograph the packet or bag with your identification guess to help you recognize your pictures. If you are on an extended collecting trip, it might be awhile before you are able to process them, and bryophytes in pictures are not easy to recognize. And don't forget to include some pictures of the habitat for your collections.

An alternative option for the age of technology is to use a mobile phone app such as EpiCollect (Franks 2013). This app was originally designed for recording epidemiological data, but can be used conveniently for plant field records (Aanensen *et al*. 2009). You can design your own database for a specific project, as Franks has done. Data recorded on your phone can be synched into a Google Cloud that is available through the internet anywhere. The phone GPS system can assign the coordinates, date, and elevation, and you can even link a picture, taken by the same phone, to the data entry. For closer images, a hand lens over the phone's lens can magnify your image considerably. The only drawbacks are carrying extra batteries, risk of getting the phone wet, and having to spend a bit more time entering data while in the field. Thus far, the app cannot duplicate location and habitat from one record to the next, but it is only a matter of time before someone designs a repeat button for that purpose. Franks has created a bryological app that permits you to click on a specific point on Google Maps or Google Earth to see all the data fields for that point and any linked photographs. This application is part of the QBry project at <http://epicollectserver.appspot.com/project.html?name=QBry>.

Data Sheets

If consistent habitat information is needed, especially if more than one person is collecting the information, field data sheets can be useful (Shevock 2021; , . For ecological studies, it is best to create a preliminary list of species, allowing plenty of space to add to it as needed. This can be done by a reconnaissance trip and lab identifications prior to a more detailed study, or by a quick reconnaissance on the day of the data collection. In the latter case, the team should combine their lists and discuss possible identification conflicts and annotations for unknown species. At the end of the day, the added species should be coordinated and their temporary names unified to avoid confusion later. Data sheets will be discussed in more detail in the chapter on Sampling in this volume.

Coll. No. _____ Taxon _____

LIGHT: sunny, open, filtered, partial shade, full shade
WATER: dry, mesic, moist, seep, wet, saturated, submerged to __ m
TOPOG: ridge, slope, swale, valley, trail, roadside
HABITAT: dense/open/cut forest, woodland, savannah, grassland, heath, chaparral, tropical, sub-tropical, temperate, subalpine, alpine, desert, riparian, spring/seep, meadow, bog/fen, swamp, pond, lake, vernal pool, river/stream/creek bank, intermittent streamlet, rivulet, rheophytic
SUBSTRATE: igneous (granite, volcanic), metamorphic (slate, shale, marble, limestone), sedimentary (sandstone), other _____
Soil: sand, loam, gravel, clay, rocky, litter, humus, peat
Rock: outcrop, cliff, crevice, top/wall of boulder, rock-slab, underhang
Tree: base, buttress, trunk, stump, snag, log, fallen/dead/rotten trunk, branch, exposed roots, bark, leaf, shrub, climber, liana, __ m above ground
Type: conifer, podocarp, hardwood, tree fern, palm, bamboo, _____
Dominant plants: _____

Figure 21. Field data sheet from Shevock 2021; circle descriptors that fit.

Permanent Ink

I (Glime) learned as a graduate student to use a Rapidograph pen with India ink to write labels. This permanence was especially important because I was placing labels into 1 dram vials that housed preserved insects I had removed from stream bryophytes. Since ball point pen ink was readily soluble in the alcohol preservative, and external labels frequently came off the vials, the Rapidograph solved both the permanence problem and the need to write very small on a label small enough to fit in the vial and still be legible.

Zander (2004) pointed out the problems in using Rapidograph pens. The ink easily clogs in the small diameter point, filling them is not easy, and they are expensive. He suggests using a modified ball point pen. In particular, the Beifa "Tank" pen is available in dollar stores and is cheap (Figure 22).

Figure 22. Permanent ink Beifa ball point pen. Photo by Richard Zander.

Although the ink is supposed to be "permanent," Zander replaces it with India ink (Figure 23). To do this, he removes the point stem with its disks using a pair of pliers, then replaces the ink with India ink such as the Rapidograph ink (it comes in a handy squeeze bottle). The stem is then replaced in the pen. Zander has used this modification for a long time without experiencing a point jam.

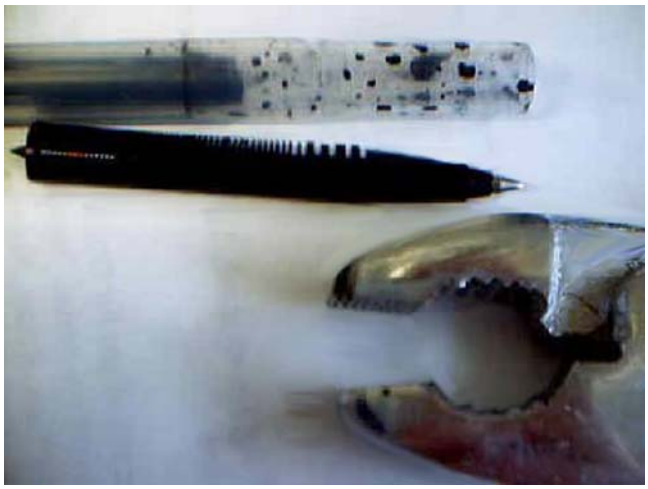

Figure 23. Permanent ink ball point pen, with original ink replaced with permanent India ink. Photo by Richard Zander.

If your bags and notebooks get wet, not much will work for record-keeping. I keep a felt pen (Sharpie) with me because it has a little more success on wet paper. Pencils just dig up the paper, although they are somewhat more successful on damp paper than most pens. I haven't tried India ink on wet surfaces. Richard Zander (pers. comm. 12 August 2012) recommends a crayon or wax pencil as backup. Zander also suggested waterproof paper such as that from Forestry Suppliers (Rite in the Rain® Field-Flex Notebooks). If you can keep a notebook in a dry place and be able to write in it without getting wet, you can put your notes on a sheet of paper there and put that page into the packet or bag. For this purpose, it helps to have a plastic bag that is large enough for you to write within it. The notebook can be wrapped inside it.

GPS Coordinates

Technology has even improved fieldwork in bryology. A simple hand-held GPS unit permits one to record exact locations, with degree of accuracy depending on the quality of the meter, and of course, its price. And many of the new digital cameras will automatically record GPS coordinates with you pictures. Now even cell phones come with GPA software. Once this information is recorded with the specimen, it is possible to relocate the population much more easily than was possible in most cases before this technology. Furthermore, Jan-Peter Frahm (Bryonet 31 May 2012) reports that he has had a program created that permits him to record a list of species in *.txt format. By clicking on the name, one can record the name with its coordinates, date and hour of collection, and altitude. The records can be transferred to a PC in Excel or a Google file, then imported to the database FLORKART (in German meaning plant map) to produce a map output or to display on Google Earth. This can be used with Android smart phones or with Windows Mobile Smart phones that have a built-in GPS. Unfortunately its website is no longer available.

Voucher Specimens

As noted by Shevock *et al*. (2014), understanding of biodiversity is critical to determining distribution, abundance, rarity, and conservation priorities. To document these, one must place voucher specimens in stable herbaria for later verification and new species concepts. As already mentioned, **every** study, whether it is taxonomic, ecological, physiological, or biochemical, should provide voucher specimens so that later researchers can verify or compare the identifications. This does not imply that you have misidentified the species. Rather, it adds to our comparisons by providing material for species to be checked for possibility of a segregate when they are later split. This will undoubtedly become more common as we increase our DNA knowledge base. And of course if someone studies the same location later, but finds species differences, the voucher specimens will permit checking to be sure the two studies haven't determined different names for the same species. This collection can also be studied by the next researcher before embarking on the field study to learn to recognize the species and prepare the mind for spotting them. Storage of these specimens should take into account that they might be later used for DNA testing, baseline records of pollutants, or other purposes that require careful treatment.

For voucher specimens to be useful, any publication on the study should clearly state where the specimens are located and how they can be identified as belonging to that study. This is typically done by specifying the **collection numbers** (your field numbers) or **accession numbers** (numbers assigned by the herbarium) in the publication. It also helps to label them as voucher specimens and identification of the study name. This can help to protect them from being discarded or moved without notifying the bryological community. With the digitizing of herbarium records, it should eventually be easier to track such collections.

Field Preservation

Most specimens are easily kept in paper packets or in paper bags until such time as herbarium packets are made, but some require special attention. It is important that the specimens are dried relatively quickly. Schuster (1966) warns that keeping them moist, especially in a confined, warm place, will encourage growth of fungi, and the bryophytes may continue to grow, becoming **etiolated**. **Never** store them in plastic bags as that encourages mold.

It is useful to maintain the growth form, but this will be disturbed when leaves are removed. To facilitate examination, it is helpful to separate a few specimens from the edge of the clump or from a neighboring clump so that these can be used for close observation and leaf removal.

Vanderpoorten *et al*. (2010) advise that material collected for DNA extraction should be cleaned and immediately air-dried, then kept dry. Subsequent moistening can lead to degradation of the DNA so that it cannot be used for molecular analysis.

Liverworts will lose their oil bodies upon drying, so if at all possible they should be kept hydrated until they have been examined. Make drawings or take pictures of the oil bodies, or at least make a detailed description, because these cannot be preserved. In some cases, they will become reestablished after a number of hours of rehydration.

Chris Cargill (Bryonet 12 August 2021) reports using A4 sheets of used photocopy paper to enclose the bryophytes while they dry. This prevents curling in soil specimens as they dry and also reduces or eliminates the effects of light during drying, making the specimens more useful for later study. Wire baskets can be used for faster drying. She further recommends keeping loose soil from the specimens in small Ziploc bags, stored with the specimen. The separate packaging prevents abrasions. Specimens with soil can be wrapped in tissue paper inside the packet to prevent further loss of soil.

Liverworts and other Flat Plants

Although some liverworts, especially ***Riccia*** species of flood plains, can revive after long periods of desiccation, many thallose liverworts can dry out, break, or become irrevocably distorted when they dry. These are best identified while still fresh and moist, but if this is impossible, add water to rehydrate them. Herbarium specimens should not be preserved in any preservative

because it makes them unusable for DNA or other molecular analysis. If one is concerned about maintaining the natural habit, a small portion of the sample could be preserved (Ohta 1991) or stored in the preservative phenyl-acetic acid-alcohol (Rob Gradstein, pers. comm. 26 July 2012), with the bulk of the specimen being kept dry and having a cross reference to indicate where the preserved specimen is located.

Liverworts typically need light pressing. This can be done between sheets of a newspaper, or in a phone book, but do not apply pressure, *i.e.*, do not put them in a tight plant press. Buck and Thiers (1996) suggest removing excess soil and debris and placing them between papers or in a folded packet, then placing them in a plant press with light pressure and no heat for 24 hours.

Oil bodies typically disappear upon drying. Flash freezing and other methods that work in the lab might not be available for prolonged fieldwork. Jeff Duckett (Bryonet 5 October 2021) recommends keeping a bottle of 25% glutaraldehyde or formaldehyde on hand and diluting to 1% for use. ETOH should not be used if preservation of oil bodies is desirable.

Tiny Bryophytes

Tiny bryophytes can also be a problem. Richard Zander (pers. comm. 27 July 2012) was kind enough to contribute to dealing with this problem. He suggests that one can use a squirt bottle of water to wash away powdery soil from small plants. In some cases, especially on wet clay, one might be able to put these on a card (3x5" is a good size) and have the clay substrate glue itself to the card. This won't work with dry sand. Using an empty squirt bottle or other type of hand air pump to blow away powdery soil might expose enough of the plant clump that it can be separated from the soil and placed in a minipacket or small envelope so it doesn't get lost. In fact, Zander (pers. comm. 29 July 2012) triple-packets them. He puts the sample (dust and bryophytes) into a large inner packet, then puts each bryophyte species into a small packet inside that.

Keeping a sand-dwelling or clay-dwelling colony intact is a special challenge. Zander (pers. comm. 29 July 2012) tells me he used Elmer's glue once. He says the polyvinyl alcohol available now is soluble in water, so bryophytes can be glued to paper, then removed with water for examination later. I haven't tried it.

Aquatic Species

If wet aquatic species are stored with other bryophytes, they will keep the others from drying. For species like ***Sphagnum*** and other wet bryophytes, remove as much water as possible by squeezing them (Vanderpoorten *et al.* 2010). If possible, fluff them out again before putting them in their packets or bags. Make their containers triple thick so the water is less likely to cause the container to tear or come apart. If the bryophyte is really wet, put it in a plastic bag, but be sure to take it out as soon as you reach a place where you can dry your collections.

Fornwall (1977) compared three storage methods for the aquatic moss ***Fontinalis duriaei***. He found that storage dry at room temperature, and dry packed in coolers with cold packs both caused the mosses to lose color and appear to be quite unhealthy after being rehydrated and cultured in fresh stream water at 10°C for seven days. However, those mosses that were stored in bags of stream water with cool packs for three weeks (and opened every night to allow gas exchange) exhibited levels of photosynthesis and respiration after storage that did not differ from the measurements prior to storage.

Drying Specimens

Getting specimens dried before they have an opportunity to mold or curl can be a challenge on extended field trips in faraway places. Generally, they can be dried by opening the bags and spreading them around your room or laboratory (Figure 24-Figure 25). If you are travelling by car, bryophytes in their collection bags or packets can be placed in a net or burlap bag and affixed to the top of the car to air dry. It is best not to leave them there when you are not in attendance because it could rain. They also should not be baked in the hot sun.

Figure 24. Jim Shevock in "drying room" with packets on left and specimen bags opened for drying on right. Photo by Blanka Aguero.

Figure 25. Drying bryophytes during Nordic Bryological Society foray. Photo by Michael Lüth.

Croat (1979) addressed this problem in a big way by modifying a truck into a processing lab and modifying a refrigerator by adding a portable propane gas oven to use for field drying. Fortunately, such elaborate equipment is usually not necessary for bryophytes, but in humid warm climates of the tropics, drying can still at times be a challenge.

Frahm and Gradstein (1986) constructed a dryer that is light weight and inexpensive for use in such humid climates (Figure 26). The drying source is a pair of kerosene stoves. The legs of the dryer are made of aluminum, making them light weight. They are about 1 m high and extend above the platform where they support a cotton curtain to hold in the dry heat. The shelf is made of wire screening and packets or open bags can be distributed across it. Of course, these must be protected against wind or your prized collection will escape to freedom! Frahm and Gradstein warn against use of polyester or nylon for the curtains or screen because they are more flammable. Be sure to do a little experimenting so you know just how high to place your shelf and how often the apparatus should be checked or your specimens could turn to charcoal – or worse.

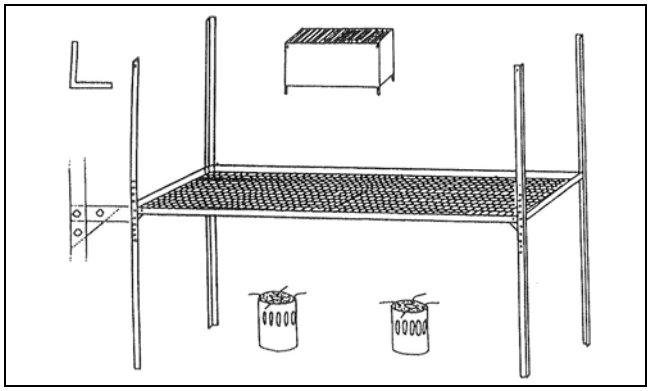

Figure 26. Field drying rack for bryophytes. Note the two kerosene stoves beneath and the inset of the curtained part of the platform above. Image from Frahm & Gradstein 1986, Bryological Times 38: 5.

David Wagner (2014), a constant innovator of bryological methods, has devised a simple, rapid, and inexpensive method for drying bryophyte specimens. He uses the spring type of clothespins to attach specimens first to a rod or rope, than to attach additional ones to the specimen above (Figure 27). This method has the advantage of permitting air to reach both sides of the specimens. He devised this method for field packets, but it should work as well for paper bags, provided they are not so wet that they tear under the added weight and pressure of the clothes pins. Bulldog clips (Figure 28) are more compact for travelling and may even be easier to find for purchase. A fan can be used to speed up drying even more. The paper in the packets is kraft paper.

Once the specimens are **thoroughly** dry, they should be packed in sealed plastic bags (unless the air is dry) to avoid having these hygroscopic plants once again take up water. Please note that if they are not completely dry, they are likely to mold inside the plastic bags.

Figure 27. Drying packets clipped together with wooden clothes pins. Photo by David Wagner.

Figure 28. Drying packets clamped together with bulldog clips. Photo by David Wagner.

Once dry, specimens can be kept dry by sealing them in bags containing silica gel ($SiO_2 \cdot nH_2O$) (Greene 1986). Greene reports that the method worked excellently in the southern Chilean rainforest. If the silica gel has absorbed moisture prior to use, it can be dried along with the bryophytes on the drying rack.

If floating species like ***Riccia fluitans*** (Figure 29) are to be kept, a good way to collect them is to float them on an index card that will fit inside a packet. The algae and other detritus will glue them to the card. Once dry, they can be put in a packet like other bryophytes.

Field Stains

Occasionally you may want to see something more clearly in the field. For ecological studies, being able to identify every individual can sometimes be tedious but necessary. In some cases, field stains can help in this endeavor, such as seeing fimbriate stem leaves on ***Sphagnum***. Jan Janssens (Bryonet 4 October 2012) suggested using crystal violet or gentian violet solution. It works well when filled into a rinsed and dried felt-tip pen. He suggests pulling off the ***Sphagnum*** capitulum and squeezing the ***Sphagnum*** somewhat dry before applying

stain at the top of the broken stem. This technique also works well in the lab. If no stain is available, you can hold plants up to diffuse skylight to get a somewhat better view.

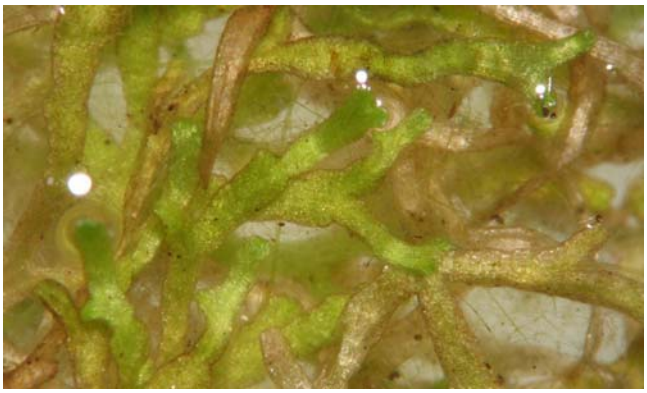

Figure 29. ***Riccia fluitans*** that is "floating" on paper. Photo by Kristian Peters, with permission.

Adam Hölzer (Bryonet 4 October 2012) likewise uses **crystal violet** (Merck Art. 1408), enabling him to see pores under the microscope. Dissolve some powder in 50 ml distilled water and add alcohol to preserve. Add new alcohol from time to time as the alcohol evaporates. Use alcohol for cleanup.

Field Gear – Collecting Equipment

If you have the motto "Be prepared" you might want to keep your collecting pack ready to go, or at least keep a checklist. Loeske (1925), interpreted by Raup (1926), suggested that essential equipment consisted of a good lens, paper envelopes, and notebook. I would suggest a bit more to increase efficiency. Here is what I would recommend.

Field Gear Checklist
(essentials are in bold)

hand lens on lanyard or string (Figure 40-Figure 43)
indelible pen
pencil
knife with protected point (Figure 36)
prenumbered packets or bags (Figure 15)
bag for collections
Ziploc plastic baggies (Figure 34)
field notebook (Figure 16)
masking tape sampler (Figure 4-Figure 7)
back pack
collecting pockets (Figure 31-Figure 36)
squirt bottle for moistening specimens
cloth measuring tape (Figure 30)
GPS
altimeter
metric ruler
water
sun glasses
hat
pocket raincoat
bug repellant
food (added the day of the trip)
field guide

Figure 30. Cloth measuring tape with metric units on one side and English units on the other. This can be helpful for measuring height on tree, diameter of tree, size of population, and various other distances. Photo by Janice Glime.

Attire

Although attire is mostly dictated by preference and the climate of the collecting location, one might consider a few accessories. Sun protection is important for those working in the open sun, and Eckel (1996) suggests carrying a small, collapsible umbrella to gain some relief from an intense sun. I prefer a wide-brimmed cloth hat that I can fold into a pocket or pack when it isn't needed. Sun glasses that flip up during hand lens use are important for protecting one's eyes.

Collecting Apron

Keeping bags, pens, hand lenses, camera, knife, record book, and other items close at hand but out of the way during a field trip can be a challenge. Back packs can hold a lot, but they are not handy, and sometimes there is no place to set one down. In others, they may throw you off balance, causing a fall and even endangering your life. To solve the problem, I created a set of pockets that I tie around my waist (Figure 31-Figure 34). These can be designed to meet your own needs with pockets to hold your equipment while holding it secure against loss. I recommend a heavy cloth like denim, or even double cloth. Stitching should be in double lines, and ends and corners should be reinforced with criss-cross stitches or other means of reinforcement. Mine are designed to tie, and my last set has the pockets sewn onto the ties. I like my former design better, where the pockets, or at least the front ones, are threaded onto the ties like curtains on a rod. When this is done, don't use loops, as they are easily torn if the pocket gets caught when you are hiking through brush. You could also use a belt, but with some clothing it can be uncomfortable. In either case, try the pockets on before stitching them down to be sure the pockets locate themselves where you want them. The two flank pocket panels provide easiest access when they meet near the middle of the front.

I carry 3x5" cards with me for a variety of uses (Figure 33). They can be helpful for scooping floating bryophytes from the water. They can be used to mount these wet specimens by floating them on the card and letting them

dry there. This permits the specimen to spread out and glue itself to the card instead of the plants gluing themselves together. This may also be useful for some small liverworts that may otherwise get lost in the bag, although minipackets are usually a better way to handle these. Cards can also provide a smooth surface for epiphylls and thallose liverworts and they help create rigidity for packets with thin soil layers.

Figure 31. Janice Glime wearing collecting pockets in geothermal field, Karapiti, NZ. Photo by Zen Iwatsuki.

Figure 32. Set of three pocket panels. Note the bulky middle pocket that hangs over one's rump to hold collected specimens and field guides. The whistle on the tie is for calling missing students or calling for help when you are lost from your companion. Photo by Janice Glime.

Figure 33. Pockets for numbered bags, cards, field notebook. Note the small pockets above the bag pockets. These are suitable for batteries, hand lenses, and other small items. See detailed image of these in Figure 35. Photo by Janice Glime.

Figure 34. Pockets for pens, knives, flash, phone, or camera, or, in this case, plastic bags in case very wet species are collected. Note that the back pocket on the left is gathered at the top to make the inside larger to keep the contents from falling out. Photo by Janice Glime.

It is useful to have small sheets of paper to make mini-packets for small species or small objects such as capsules that might get lost in the collecting bag or among other bryophytes. Pages from the field notebook can serve this purpose, provided that their removal does not cause the remaining pages to come apart.

Small pockets help to keep tools in easy reach and avoid tangling (Figure 35). Long, narrow pockets can hold knives, pens, or pencils (Figure 36).

Figure 35. Small pockets with potential uses shown by the lenses sitting on them. Note the double stitching at the bottom of the pocket. Photo by Janice Glime.

My back pocket is large and is not flat, being larger across the bottom edge (Figure 34). It can hold packets with mosses in them and a field guide. It's a good idea to keep the field guide in a Ziploc bag to protect it from dirt and water.

Some carpenters' aprons may serve your purposes and are made to carry heavy tools, so they are durable. You may have to add your own back pocket and some small pockets if you need them. It depends on your needs – and how ambitious you are.

Figure 36. Long, narrow pockets house pens and knives. Photo by Janice Glime.

Collection Bags

Bryophyte collections can be damp or even soggy. If you are staying in a hotel or have much travelling to do, these must be placed where they won't mold and can begin to dry. In Japan, I was introduced to hand-made collecting bags for holding the paper bags (Figure 37). If you don't go too may places, you can use a separate bag for each collection site. It is usually possible to tie these to your belt or to the collection apron (Figure 38). Bright colors help you to locate a bag you have left on the ground.

Figure 37. Bryophyte collection bag. Photo by Janice Glime.

Figure 38. Zen Iwatsuki warming his hands over a geothermal vent in Iceland. Note the collecting bag hanging from his belt. Photo by Janice Glime.

Eckel (1996) extols the benefits of a Naugahyde (vinyl-coated fabric) flat bag. In the morning it is filled with empty packets that are replaced during the day with filled packets. It can double as a pillow for sitting, a cushion for sliding down a slope, a shield against cacti, and protection for crossing a barbed wire fence.

Hand Lenses (Loupes)

Hand lenses are essential for seeing the details needed for identifying bryophytes. And they also reveal the beauty of the bryophyte world. Lenses come in a variety of magnifications and sizes (Figure 39). The most commonly used is a 10X loupe, but you might even be able to use one up to 30X. The small ones are the most convenient because they weigh less and are often easier to focus, especially if you wear glasses. A reading magnifying glass offers some help but is not nearly as helpful as a 10X hand lens, and it is heavy and bulky.

When using a hand lens, hold it close to your eye and bring the bryophyte toward you until it is in focus (Figure 40). One advantage of the lens is that it permits you to focus on something close to your eye. The exact positioning will depend on the correction in your glasses.

Figure 39. Small 20X and larger 10X hand lens with nylon string. Photo by Janice Glime.

Figure 40. Janice Glime demonstrating the use of a hand lens while wearing eye glasses. Photo by Jill Nissila.

It is a good idea to carry several hand lenses with you. In damp, cold, or rainy weather, the lens can fog up and it may take an hour before it is usable again. And there is always the chance you will lose one. By all means attach your hand lens to something. A lanyard is good, but a heavy string will work well and is flexible and light weight. If your lens is hanging around your neck, you can tuck it inside your coat when it is raining or cold, and it will always be handy without being lost easily.

A few bryophytes have been shown to have fluorescent propagula, and such propagula are often difficult to see in the field. For the taxonomist, the solution is to collect and identify later, but for the ecologist, field identification is important. More importantly, the same species needs to be distinguished from similar species during field studies, even if verification must come later. Zimmermann (2011) introduced us to a 10X hand lens that provides the UV light needed to see this fluorescence in the field Figure 41-Figure 42) (Zimmermann 2012). The lens now is available at 10X, 15X, and 20X with color temperatures of 4500, 600 (neutral), and 8000 K. Norbert Stapper (Bryonet 16 July 2013) recommends the neutral, with cool white not showing the typical yellow color of a the lichen *Flavoparmelia*. Nick Hodgetts (Bryonet 1 December 2011) adds his endorsement to this lens. The lens is a bit costly at 195 Euros plus postage.

Figure 41. Lichen candelaris UV hand lens. Photo by Erich Zimmermann.

Figure 42. Lichen candelaris UV hand lens showing inside. Photo by Erich Zimmermann.

Technical details:

- Cold white light through two laterally shifted LEDs (prevents shadows). LED with low power consumption and high lifespan
- Operation time: 8,000 x 5 sec flashes until low battery indicator lights up, additional 300 flashes to battery empty
- 3V Lithium-batteries (3 pcs. CR 2023 Renata): High energy density and extended shelf life
- Active power source results in constant luminous intensity over the whole battery life cycle and extended temperature range
- Lens system x10, Æ20mm, (triplet, aplanate, achromate, closely glued)
- Submerged key, anodized Alloy-box, water spray proof IP67, your name is laser labelled on special order.
- Weight 76 g
- Swiss made, 1 year warranty
- Included in delivery: 10X magnifying glass, 2 pcs Lanyard, 3 replacement batteries, instruction manual with technical details

Hand lenses have been a popular topic on Bryonet, and members have their own preferences that may help you in your consideration. Werner Pflaum (Bryonet 30 November 2011) recommends the Lichen candelaris despite its high price. He considers the light source to be excellent. Norbert Stapper (Bryonet 30 November 2011) warns that the lens is not waterproof because it lacks an O-ring to seal the electronics and battery compartment. The lens system is a sealed triplet, which eliminates fogging, an important consideration for rainy days or cold weather.

David Wagner (Bryonet 16 July 2013) recommends the 20X hand lens by Iwamoto, claiming it is worth the $100 or so it costs because of exceptional clarity and wide field of the lens. In USA it can be ordered from Minerox <http://www.minerox.com>.

Less expensive lenses lack the light source and generally have only two lenses, not three. David DuMond (Bryonet 28 November 2011) recommends a hand lens with LED source from Miners <https://minerox.com/index.cfm?fuseaction=category.display&category_ID=2>. This 20X lens has a 21 mm diameter and triplet glass (Figure 43). It is only US $24.95, complete with leather carrying case.

Figure 43. Handlens with LED. Photo by Miners.

The Weinschenk hand lens has excellent optics with sealed triplet lenses, available in 10X and 20X, but no light source. Norbert Stapper (Bryonet 15 July 2013) combines

the 20X Weinschenk hand lens with the Lichen candelaris 10X to obtain 28X magnification. The Weinschenk lens is available through Industrieoptik Fischer, Wetzlar, Germany <http://www.iof-wetzlar.de> or from <http://www.kruess.de/shop/Lupen/Weinschenk-Lupe:::21_44.html>. Rune Halvorsen (Bryonet 15 July 2013) considers it "an absolute must for bryologists!" Martin Godfrey (Bryonet 29 November 2011) recommends hand lenses from Quicktest <www.quicktest.co.uk>. This company supplies lenses for the jewelry trade and carries hand lenses that range in cost from £1.50 to £95.00 for a 10X lens. Marshall Crosby (Bryonet 2 February 2012) recommends BioQuip for hand lenses at a range of prices <http://www.bioquip.com/specials/product_special.asp>.

McCune (1994) recommended an illuminated lens by Bausch and Lomb, available through Forestry Suppliers for US $43.75, but it no longer seems to be available from them. However, they now have one that is 10X instead of the original 7X lens, also by Bausch and Lomb, but for only US $28.25. It requires two AA batteries and is the size of a fountain pen (if you remember what that is!). McCune found it very useful in the field for examining bryophytes and lichens in a permanent plot when you must get so close you block the daylight.

Jesús Muñoz (Bryonet 15 July 2013) uses both the 14X and 20X Bausch & Lomb Hastings Triplet hand lenses, available from Forestry Suppliers <http://www.forestry-suppliers.com/product_pages/View_Catalog_Page.asp?mi=52491&title=Bausch+%26+Lomb%AE+Hastings+Triplet+Pocket+Magnifiers>.

Sean Edwards (Bryonet 1 August 2013) has found the 10X Ruper triplet lenses from Summerfield Books <www.summerfieldbooks.com> to be excellent for all his uses. These are aplanatic Japanese lenses at a reasonable cost. This company also stocks lanyards. They are also stocking an ultraviolet LED triplet hand lens. Although this is designed for detection of mineral fluorescence, they may be helpful for detecting fluorescent structures such as ***Pohlia*** bulbils on bryophytes. This is also a triplet lens that corrects for both aplanatic aberrations to improve the field of view (21 mm) and achromatic distortion for true color viewing at the reasonable price of only £21.

Des Callaghan (Bryonet 1 August 2013) advises that one should be sure the lenses are cemented together (usually sold as cemented doublet or cemented triplet). Otherwise, one must seed assurance that the housing is waterproof. And some of the cheaper models have lenses held by a threaded ring that can easily unscrew, causing you to lose the lenses. When lenses are not sealed, they easily steam up inside, especially in cold or wet weather.

Field Microscopes

When you are examining small plots for total bryophyte cover, and you must name every species and determine how much cover it provides, a field microscope can be useful. But when looking with such closeness, it becomes more difficult to avoid missing some parts and overlapping others.

Rod Seppelt (Bryonet 9 February 2012) reports on a field microscope that Gert Steen Mogensen introduced to him many years ago. This microscope was mounted on a miniature train track, maintaining a consistent distance of the lens from the ground and facilitating a consistent movement. When the train track is on the ground, one can move the microscope along the track. A camera could even be attached to an eyepiece, especially if a trinocular microscope is used. This system provides stability and helps to solve the problem of vibration. It should be adaptable for stacking. I haven't tried it, but the ability to photograph and enlarge the picture later might even permit one to do the cover estimates accurately later in the lab.

You are less likely to need a compound microscope for the field, but you might want to check some things for verification in the evening after a day in the field. Tamás Pócs (Bryonet 10 February 2012) reports great satisfaction with the BioLux NV (Figure 44), made by BRESSER, Meade Instruments Europe Bmbh & Co. KG, Gutenbergstrasse 2, DE-456414 Rhede/Westf. Germany at a price of about 100 Euro. Its magnification ranges 20-128 X. It is lit by LEDs (with transmission and overhead light) and also has a digital camera ocular. It has a movable stage and several built in filters. More information is available at <http://www.astroshop.eu/monocular-microscopes/bresser-microscope-biolux-nv/p,14667>.

Figure 44. BioLux NV field microscope, made by BRESSER. Photo modified from Bresser website.

Norbert Stapper (Bryonet 11 February 2012) suggests two good sites for light-weight field microscopes: <http://www.blam-hp.eu/swift_br.pdf> and <http://dominique.voisin.pagesperso-orange.fr/technique/pyrennee/index.htm>.

Return at the End of the Day

Rob Gradstein (pers. comm. 28 July 2012) recommends that all information gathered on the specimens should be written in the field notebook. This depends in part on whether legible information with indelible ink is on the collecting packet or bag. Certainly general habitat notes should be in the notebook since that was most likely not repeated on each collection bag. Each specimen should receive a unique collection number, preferably already done in advance. (If the collection contains mixed species

and is separated later, each packet can be given a different letter while retaining the original collection number.) If there wasn't time to clean the specimens in the field, they **should be cleaned as well as possible and excessive substrate removed.** The specimens need to be spread to dry. I have many memories of collecting bags spread around hotel rooms at bryological meetings. It might be a good idea to alert the hotel staff so your specimens don't get tossed or mixed up. Be sure these collections remain in a paper container that won't permit them to escape if someone opens a window or door. If there is such a danger, place the collection packets/bags in a broad weave bag(s) and hang these where they get good air circulation. I still recall bags of mosses blowing around when we opened our hotel room balcony doors to cool the room (no air conditioner) and a storm came up. First the packets were blown around and some where dumped. Then some got soaked when the rain came in. We were scrambling in the middle of the night to move and protect the collections.

Thallose liverworts and epiphylls should be pressed lightly between sheets of absorbent paper (newspaper works well) and the paper changed daily. Place a sample of any liverwort capsules in a small envelope or minipacket with the rest of the sample to help keep some of the capsules unopened (but keep some intact as well). These capsules tend to release when they dry. It is also important to keep part of the liverwort sample alive/moist for later study of **oil bodies** (Rob Gradstein, pers. comm. 28 July 2012). You can accomplish this by keeping them in plastic at a cool (but not freezing) temperature. Examine them as soon as possible with a microscope and carefully describe the oil bodies. If possible, photograph them through a microscope; if not, draw them. Oil bodies will begin to disintegrate within a few days, or hours in a dry climate, and their morphology can change, even if they don't disappear.

Getting your Specimens Home – Customs and Inspection

Transporting your specimens requires a little attention. Some become brittle when they dry, so they should be packed to protect them. The bags or packets help to protect them. They should be tight enough that they will not move around in their shipping or transporting box, but loose enough that they don't crush each other (Buck & Thiers 1996).

Getting your specimens back into your own country can sometimes be problematic. Be sure you know both the import and export requirements for your home country and the country you are sending specimens from. As a courtesy, you should always provide a set of specimens, preferably identified, to the country where you collected them. Ask permission from a national herbarium or other prominent herbarium to give them the specimens. If you are sending them later, follow the protocol for "Sending Specimens for Identification" in Chapter 3 of this volume.

Hedenäs (1993) raised questions about various requirements of some countries. It is important that you understand these. Some countries require deposit of a duplicate set of specimens before you leave the country. This is impractical in most cases, as it is unlikely that you will be able to identify positively all of the specimens in a country where the flora is poorly known. Nevertheless, if that is the law, it is important that you comply. You can send a list of species and collection numbers later. Instead, if leaving a set is not required, it might be better to send a duplicate set after they have been examined in the lab and identifications verified.

One aspect that can cause import/export problems is rare or protected species (Willem Meijer, Bryonet 28 September 1999). You might need proof that each specimen is not an endangered species. Customs agents are not familiar with mosses and may not even recognize that it is a moss, much less a liverwort.

Frahm (2000) reports on difficulties with specimens mailed to him from other herbaria, requiring him to go to the customs office at the German port of entry. It was no longer sufficient to label the package as "dried specimens" or "dried plants for scientific study." Rather, it is necessary to include a CITES certificate. This requires a declaration of the species enclosed. But bryophytes are not yet on the CITES list. Frahm suggests that the bryophytes be assigned a monetary value below the customs limit. He further suggests that it might help to make the statement that the enclosed bryophytes are not on the CITES list. Therefore Frahm concluded that a customs declaration indicating “Dried herbarium specimens – bryophytes: no CITES required, value $10” could solve most problems.

When sending collections, divide them into small sets. Large sets (many specimens) may discourage inspectors, causing delays in getting the specimens to you.

Bill Buck (Bryonet 19 July 2012) assures us that there are no restrictions about bringing bryophytes into the United States, nor are any permits required. But importation of soil is problematic. Even a small amount attached to your specimens can result in having your specimens confiscated and destroyed. The process for bringing soil is complex and may include an onsite inspection. Buck showed the customs agents the freezers where new material is placed, and then the herbarium, with its multiple levels of security, where the material will ultimately be stored. But, as Wim Meijer warned, any bryophytes that get on the CITES list will most likely change the whole process. Jim Shevock (Bryonet 19 July 2012) fully agrees that it is best to mail the specimens back, at least to the USA. If you bring specimens into the USA and do not have the needed paperwork, you risk having the entire collection destroyed. In any case, specimens are likely to cause delays at customs at the port of entry and could cause you to miss a connecting flight. It is best if you mail them to yourself in care of the herbarium.

Summary

Collect in individual paper bags or envelopes. Ecological collections should include voucher specimens. Recorded data should include location, date with month written out, GPS coordinates or latitude and longitude, elevation, habitat, substrate, and collection number. Sample size depends on abundance and expected use, with palm-size collections being best for common species. Permission of the owner or a collection permit is important.

A collecting apron can make field equipment orderly and handy without being in your way. Cloth bags for collection bags facilitate drying.

A hand lens is usually essential in the field to permit tentative identification. Care should be taken to obtain one with sealed lenses. A light source (LED or UV) may be useful, depending on expected use. Field dissecting microscopes on a track can also be useful for finding small species and to facilitate consistent and thorough sampling.

If specimens must pass through customs, it is best to mail them to your herbarium. Be aware of customs guidelines for all countries in your travels before collecting.

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CHAPTER 2-1
LABORATORY TECHNIQUES: EQUIPMENT

Janice M. Glime and David H. Wagner

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CHAPTER 2-1
LABORATORY TECHNIQUES: EQUIPMENT

Figure 1. Dries Touw at a microscope in the Hattori Botanical Laboratory, Nichinan, Japan, 1983. Photo by Janice Glime.

Lower Plants

Moss and lichen – lower plants,
the higher plant people say;
But if you give them half a chance,
they'll really make your day.
Miniature beauty – ecology too,
enough for your interest forever;
You'll need a scope and some chemicals few,
to unlock their secrets most clever.
So get out there – look around,
learn from the lichen and moss;
Treasure the mysteries of lower plants found,
and you'll never be at a loss.

- Ray Showman

Lab bench Setup

A well stocked lab bench (Figure 1) will save you time and make your work more efficient. Usually this bench will be located near the herbarium specimens for easy checking of your identification and for processing and accessioning specimens (Figure 2).

Figure 2. Working area in the herbarium at the Missouri Botanical Garden. Specimen compactors are on the left and benches with microscopes and other equipment are on the right. Photo by Paul J. Morris through Flickr Creative Commons.

Although making slides seems relatively routine for anyone who has done this often, there are lots of tricks to make it fully effective. Having a set of tools that are in one place is a tremendous time-saver, and it encourages one to

identify that specimen picked up on the way to work rather than tuck it away for later. This can be accomplished easily if you have a workbench reserved for that purpose, but if not, create a sturdy box that holds your needed tools.

This is a **list of supplies** you will probably want to have handy so that you can proceed efficiently:

Desirable Lab Bench Supplies

compound microscope with its own base light source (Figure 5)
dissecting microscope with top mounted light or lights on each side (Figure 8-Figure 9)
blue filters for microscope lights
microscope slides (Figure 33)
coverslips (Figure 31)
single-edged razor blades
microforceps or watchmaker forceps
a curved one and a straight one are helpful (Figure 25)
whetstone
emory board
dropper bottle with narrow tip and water (Figure 29)
ocular micrometer
stage micrometer
lens paper
paper towels
Petri plate(s)
Syracuse watch glass (Figure 3)
hot plate for warming water to soften tissues
jar or beaker of water
slide labels
permanent mounting medium
methylene blue or similar stain

Figure 3. Syracuse watch glass.

Microscopes

As Rockcastle and Barr (1968) pointed out, observing bryophytes requires a "bits made big" technique. Identification of bryophytes usually requires two microscopes, a dissecting/stereo microscope with a zoom (preferred) viewing range of ~3X to 40X and a compound microscope with a viewing range of 40X (or less) to 400X total magnification. Magnification is determined by multiplying the ocular (eyepiece) magnification by that of the objective lens. Higher magnification may be required, depending on your needs.

The dissecting microscope is needed for several purposes. It is usually the first microscope you will want to use to get a clearer view of leaf insertion, paraphyllia, decurrencies, general habit, and other surface features. It is also needed for locating small bryophytes, especially tiny leafy liverworts, from among the dominant bryophytes. It is also needed for locating the fauna. The other important use of this microscope is to guide your hands when you make sections or remove leaves.

The compound microscope is used with microscope slides. It permits you to see cell shape, number of cells wide, borders, costae, and teeth on the leaves. On the sporophyte you can see such details as peristome decorations and imbedded stomata. The compound microscope is also needed for a clear view of your sections of leaves and stems. It will also help you see special structures like gemmae, bulbils, paraphyllia, and reproductive organs.

There is a wide range in quality of microscopes. It is very useful to have trinocular microscopes that can hold a camera (see the two microscopes in Figure 1) or to have a USB connection, or that have a direct image transfer to your computer. Once you have a little experience, you can take pictures that are adequate for identification. This can avoid the need, in some cases, for sending specimens to experts, and it will save them lots of time because you have already made sections and spent the time to get good views of the leaves, insertions, and stem sections. You can also introduce these images on Bryonet <Bryonet-L@mtu.edu> or a web site where you can request help for troublesome species. (Caution: try to keep the total of all image sizes under 2 MB when sending them to an email list such as Bryonet.)

One can usually count on Olympus and Nikon microscopes to be of good quality, but these tend to be rather expensive for a beginner. Tamás Pócs (Bryonet 10 February 2012) reports great satisfaction with the BioLux NV (Figure 5), a compound microscope made by Bresser, Meade Instruments Europe Bmbh & Co. KG, Gutenbergstrasse 2, DE-456414 Rhede/Westf. Germany at a price of about 100 Euro <http://www.astroshop.eu/monocular-microscopes/bresser-microscope-biolux-nv/p,14667>. Its magnification ranges 20-128 X. It is lit by LEDs (with transmission and overhead light) and also has a digital camera ocular. It also has a movable stage and several built in filters, as well as a carrying case for field work. An added advantage is that it has a carrying case, making it more convenient for field work.

Figure 4 outlines the principal parts of a **compound** microscope. Since manufacturers vary, the microscope

available to you may differ somewhat. You will note that some microscopes have one eyepiece (**monocular**; Figure 5), whereas others have two (**binocular**; Figure 9). **Ocular** refers to the eyepiece.

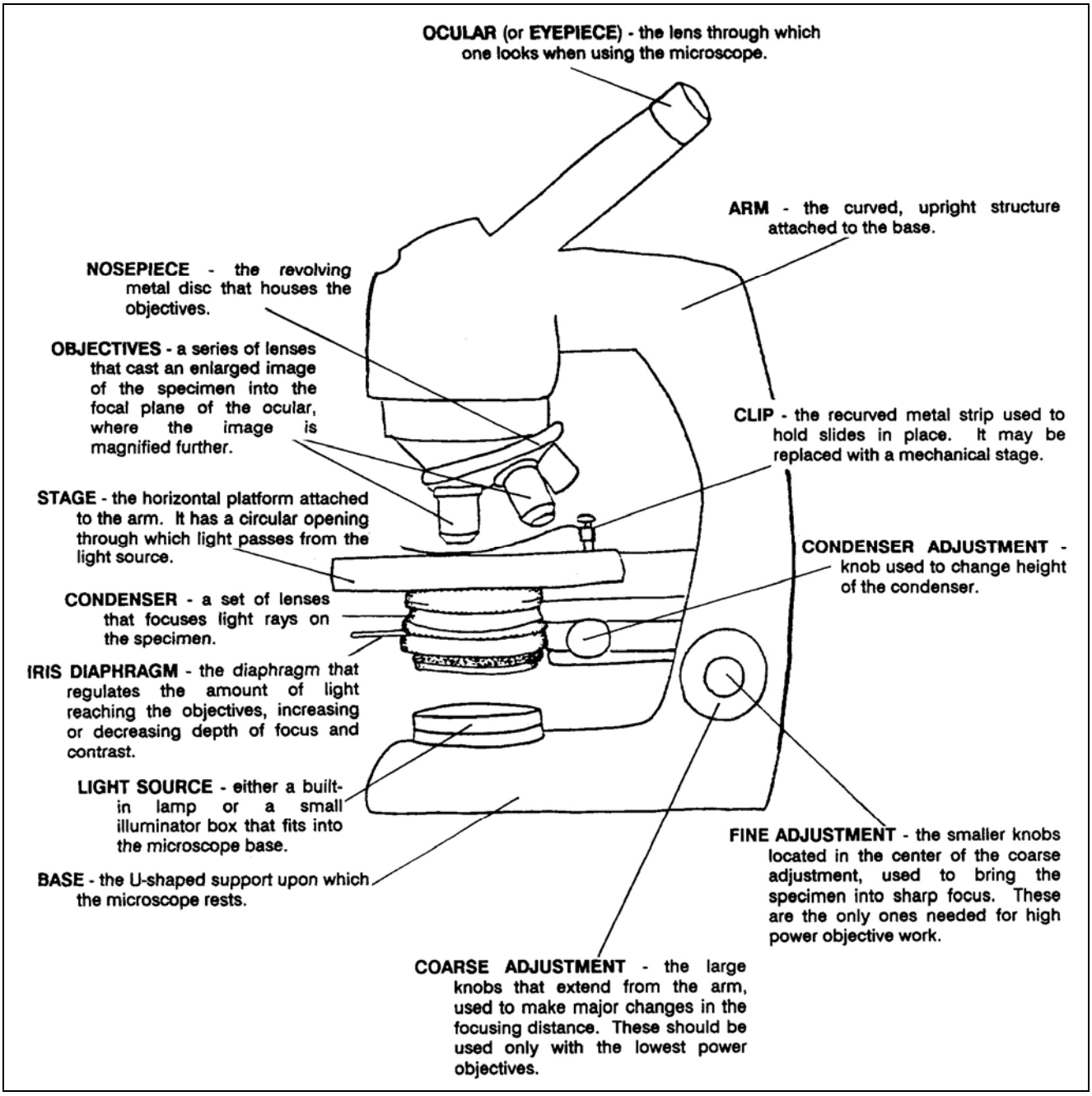

Figure 4. Compound microscope showing parts. Drawing by Janice Glime.

Figure 5. BioLux NV compound microscope, made by Bresser. Photo modified from Bresser website.

The **mechanical stage** (not shown) has numbers in both directions that you can move the slides, so that you can note the coordinates on the numerical scales, then remove the slide. When you replace it you can go easily to the same location.

Your microscope should be **parfocal** (having all lenses adjusted to the same focal distance, making it possible to switch objective lenses with minimal refocusing). That means that when you change from one objective to another, the ocular distance is still correct and the object should still be close to being in focus. When you start using a different microscope, it will most likely be somewhat fuzzy for several reasons. You have increased the magnification and it is easier to see that it is not in perfect focus. The oculars may not all be screwed in completely, changing the focal distances. However, in most cases you can adjust this by using the fine adjustment. Different people have different focal distances, and these change with time. Hence, some initial adjustment is needed, with fine-tuning occasionally.

Parfocal Adjustment

Binocular microscopes may require adjustment so that both oculars focus at the same distance. If there is also a camera tube, this also needs to be adjusted.

Procedure

1. Position the objective turret above the subject.
2. Set both eyepiece diopters to "0."
3. Set the microscope near the middle of its focus range.
4. Focus with the microscope on the lowest magnification setting, using first just one ocular (eyepiece). Use the fine adjustment until the image is clear.
5. Focus with the other ocular by turning the diopter ring on the ocular until the image is clear and sharp. Do not move the fine adjustment. If you can't get the focus clear, put it in the best position, use the fine adjustment, and readjust the other ocular. Repeat until both oculars provide clear focus.
6. Move to the next highest setting and repeat the process.
7. Finally, move to the highest setting and repeat the process. If you will not be using the oil immersion lens, then use the highest magnification below that.
8. Tighten the diopter lock button if there is one and record the setting.
9. Repeat the procedure with the microscope tube.
10. Do this whenever using a microscope that is new to you. As your eyes change, the settings may need adjustment.

Microscope Use

First, it is important that you learn to use the microscope correctly, or you will not be able to see all the things that you should. After you understand how to set up your microscope, make a slide of one of your samples and determine the best way to adjust your microscope.

Adjusting Light and Learning to Focus

1. Start with a **prepared slide**; diatoms are a good choice because of the fine detail of the pores and striations. The diatom *Amphipleura pellucida* is often used. Its striae (lines of pores) have a mean of 0.25 µm distance apart, the theoretical limit of resolution of light optics. If you can see them clearly, it is an indication of a good quality of microscope. If you don't have access to a diatom slide, you can use an onion skin (the thin layer) or other thin, nearly transparent subject in a drop of water with a coverslip.
2. On the slide you can often **locate the organism** by a change in color as you scan, but a more reliable way is to begin by focusing on the edge of the coverslip. This will put your view in the right plane so you can scan the slide.
3. Once you locate the specimen, **focus first with the coarse adjustment**, always starting by focusing upward so you don't run the objective into the slide.
4. Once you have gotten the clearest image possible with coarse adjustment, use the fine adjustment to get and even more distinct image.
5. Using a nearly transparent slide, you can learn to **adjust lighting**. This should be done by adjusting the diaphragm under the condenser. It should **not** be adjusted with the light intensity of the light source because with most microscope lighting systems, lowering the light intensity changes the light quality to the red end. Changing the light intensity by using the rheostat to change the intensity of the light source should only be used to adjust the light for your eye comfort.
6. If the light has a red cast, it can be balanced with a **blue filter** (see Figure 6-Figure 7). This can be especially important for photography. Usually it just requires a blue glass filter over the light or in the condenser housing under the diaphragm, and often one is supplied with the microscope.

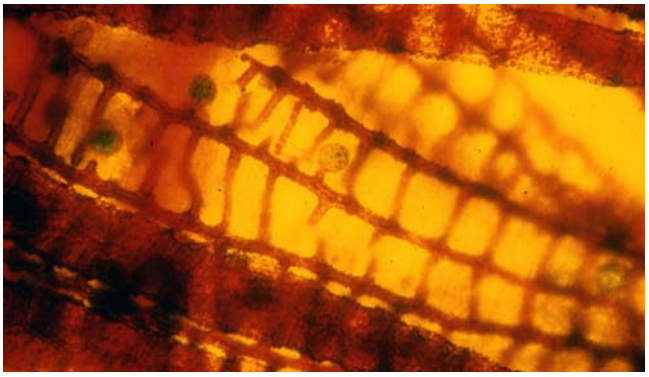

Figure 6. Peristome of ***Fontinalis squamosa*** with tungsten light of microscope and no blue filter. Photo by Janice Glime.

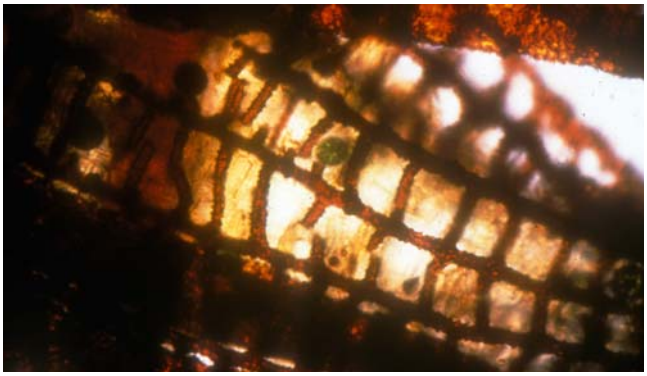

Figure 7. Peristome of ***Fontinalis squamosa*** with blue filter covering tungsten light of microscope. Photo by Janice Glime.

Adjusting the Focus and Ocular Distance

1. If you are using a binocular microscope, you need to adjust the oculars. If you are right-handed, look through the right ocular with your right eye and get the object into clear focus. Even if you are left-eyed, start with the right ocular, but use your left eye. (If you are right-handed, you are likely to be right-eyed.) You might have to shut the other eye to do this.
2. **Always start with the coarse adjustment and focus upward.** It is safest to adjust the objective downward with the coarse adjustment while watching the slide from the side without using the ocular, bringing the objective as close as possible to the slide without touching it. Then be sure you focus in the opposite direction (upward) **slowly** with the coarse adjustment while watching through the microscope. If you are inexperienced, focus on the edge of the coverslip to get into the right plane.
3. Adjust to the best focus using the **fine adjustment**.
4. Then use your left ocular, still using your right eye, and get it into focus, but this time **turn the left ocular** to adjust the focus. This is usually done by turning a ring at the base of the ocular housing, not the ocular itself.
5. If it is impossible to get a clear image this way, you may have to move the right ocular so it is closer to the middle of its range, then refocus with the fine adjustment before focusing the left ocular. Repeat this until you are able to see clearly with both oculars.
6. Use both eyes, and **move the oculars together** and **apart slowly** until you can see through both of them. At first, you might see two images; adjust the distance between the oculars carefully until you can see only one image in 3-D.
7. When the images are clear, observe the dial or **vernier scale** between the oculars to see what number is indicated. (Some microscopes, especially dissecting microscopes, might not have this scale.) Then set each of the two oculars at that number. This adjusts the focal distance because you have changed it when you changed the distance between the oculars.
8. **Write that number** on your lab notebook, or on a piece of tape on the microscope if you are the only user. You can always set any microscope at this number and save much time in trying to adjust the ocular distance. You will probably have to set the number on the vernier scale every time you come to lab if different people use the microscope because they will have different distances between their eyes.
9. **Re-focus** with the coarse and fine adjustment until you have the best single clear image.
10. After you are more comfortable using your binocular microscope, try adjusting the ocular distance again and record the new number if you find a better position.

Adjustments for Glasses

1. When you adjust the microscope to see the image clearly, you are also adjusting the focal distance to work best with your eyes. This will compensate for near-sightedness or far-sightedness. However, it will not adjust for astigmatism. Examine the object on the microscope slide to see if it is clearer with or without your glasses. This will require a new adjustment.
2. If you prefer to wear your glasses, then you need to take precautions to prevent scratching them. You can use a bit of masking tape on two sides of the ocular to provide a soft cushion for your glasses. Some microscopes will be equipped with rubber caps that protect glasses. The rubber or plastic extensions that fit around your eyes generally get in the way when you wear glasses.

Dissecting Microscope

In addition to the compound microscope (the one you will use with slides), you will also be using a **dissecting** microscope (microscope with low stage and long focal distance that permits you to dissect an object while viewing). That gives you a large viewing and working space that permits you to work with larger objects that you can dissect while viewing them.

The principles of the dissecting microscope are the same as those for the compound microscope, but this microscope will always have two oculars, and lighting will usually be from above, giving you reflected light. Some microscopes have a light in the base, but I (Glime) find these uncomfortable to work with because they make the stage high (Figure 8) and I cannot rest my hands on the lab bench.

Figure 8. Dissecting microscope with two foam pads and a cork board to permit moving the stage up and down while still working. Photo by David H. Wagner.

Self-focusing Foam Stage for a Dissecting Microscope

David Wagner offers suggestions for working with a dissecting microscope when your plane of focus keeps changing. This can be a problem when searching for propagules or reproductive structures and when sorting for the interesting invertebrate fauna. When you move one hand to the focusing knob, it is easy to lose track of the object of interest. He has created his own vertically movable stage. A foam pad can help (

There are foot-controlled, electric focusing stages, but these are very expensive. Wagner's solution is to place a stack of foam pads such as artificial sponges (must be soft when dry) on the stage of the dissecting microscope and placing a cork board on top to provide a solid surface (Figure 8). Set the focus of the microscope to the surface of the cork board. The specimen will be above this, so you can focus on any part of a specimen by pressing down on the board with the heels of your hand without setting down your tools. It is also easy to tip a specimen from side to side while keeping a particular point of interest in view and in focus (Figure 9), even with magnification set at the highest level. With this system, one seldom needs to touch the focusing knob after the initial focus. Glime thinks you might want to add sponges, pillows, or a box on each side of the stage so that you have something on which to rest your hands and forearms. They would be steadier that way, and it would be less tiring. Hence, for that reason Glime prefers a microscope that has a low stage. A lower bench or higher seat might help make you more comfortable.

Figure 9. Dissecting microscope showing the ability to tilt a stage with two foam pads and a cork board. Photo by David H. Wagner.

Summary of Microscope Care

1. Always carry the microscope with **two hands**. Do not attempt to carry anything else at the same time.
2. Avoid touching the lenses with your fingers.
3. Always start your examination of a specimen with the **low power objective**. Rotate the nosepiece to a higher objective if greater magnification is desired.
4. **Focus away** from the specimen. Lower the objective only when you are watching from the side.
5. Keep **both eyes open** during microscope use.
6. Remember to keep the **condenser slightly below its highest position** and to adjust the **iris diaphragm** to achieve the best possible image.
7. **Never focus down** with the coarse adjustment when the high power or oil immersion objectives are in place.
8. Use **oil immersion** whenever the numerical aperture marked on an objective is greater than 1.00.
9. Clean the lenses with **lens tissue** and **water** or **saliva** only. Avoid cleaning with powerful solvents like acetone or xylene.
10. When you are done, **rotate the low power objective** into position and **remove the slide**. Turn off the light source and cover the microscope.

Microscope Light Sources

A compound microscope typically has a tungsten light source in its base. This usually causes the image to have a reddish cast, so it is desirable to place a **blue filter** under the condenser or over the light to balance the light. For the dissecting microscope, an even white light makes the best viewing. There are a number of choices for these lights.

For reflected light, I (Glime) have used a dual gooseneck fiber optic light (Figure 10). This provides bright, good quality light and avoids heat of tungsten bulbs, although some of the new LED lights are probably better. Most of them can be focused and the size of the light circle can be adjusted by changing the distance and focus.

Figure 10. Dual gooseneck fiber optic lights. Photo from online advertising.

Regular tungsten microscope lights are hot and are a nuisance to replace when they burn out. **LED lights** last much longer and are cooler. Wagner has marvelled over the amazing products appearing on the market. He has been especially impressed with the intensity of lights now marketed as headlamps for bicyclists. These are intended to be mounted on handlebars or the top of helmets. They are bright enough to serve as truly effective headlights, almost as bright as those for automobiles.

These lights are somewhat expensive, but cost less than a ringlight flash. The 250 lumen Cygolite (Figure 11) is US $130. Some models in cycling stores have up to a 400 lumen rating, costing about a dollar per lumen. Eventually, as production volume increases, costs should come down.

Figure 11. LED light source for lab or field. Photo by David H. Wagner.

These headlamps are compact (10 cm long, 4 cm diameter) with a rechargeable battery that plugs into either a wall receptacle or a computer's USB port. The latter is very useful because it means you can recharge it on a bench without looking for the wall outlet. Once charged, you can move it from dissecting scope to compound scope easily because no wires tether it (Figure 12). The batteries are rated to have a five-hour working time per charge, making the light useful for extended field work. The light can be directed on a colony of bryophytes in a dark forest. Having a steady light source, an image can be composed in a way not possible with a flash.

Figure 12. LED light source mounted for use with a microscope. Photo by David H. Wagner.

Zander (2006) suggests using a unit with three 1-watt Luxeonwarm-white LED's, which he has attached to his dissecting microscope with duck tape (Figure 13-Figure 16).

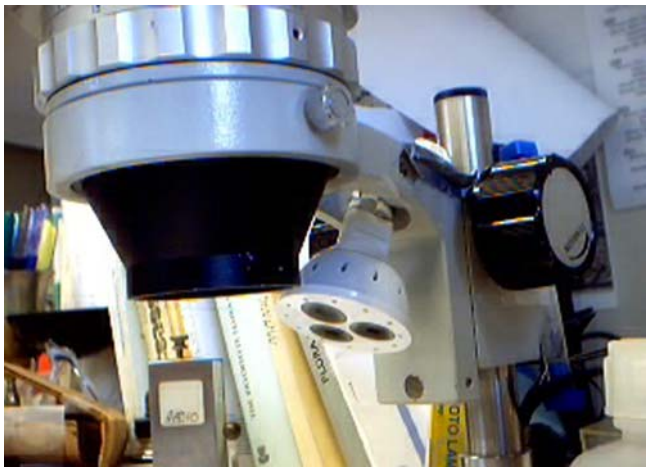

Figure 13. Triple 1-watt Luxeonwarm-white LED unit mounted on dissecting microscope with duck tape. Photo by Richard Zander.

When the LED light is bright enough to be mounted some distance from an object, the light doesn't cause the glare of fiber optic sources, yet is as cool as fiber optic

sources. It is useful in adding **reflected light** to images made with a compound microscope, thanks to stacking software. Compare the two images of ***Jungermannia atrovirens*** androecia (Figure 14), one with transmitted light and the second supplemented by reflected light from an LED headlamp.

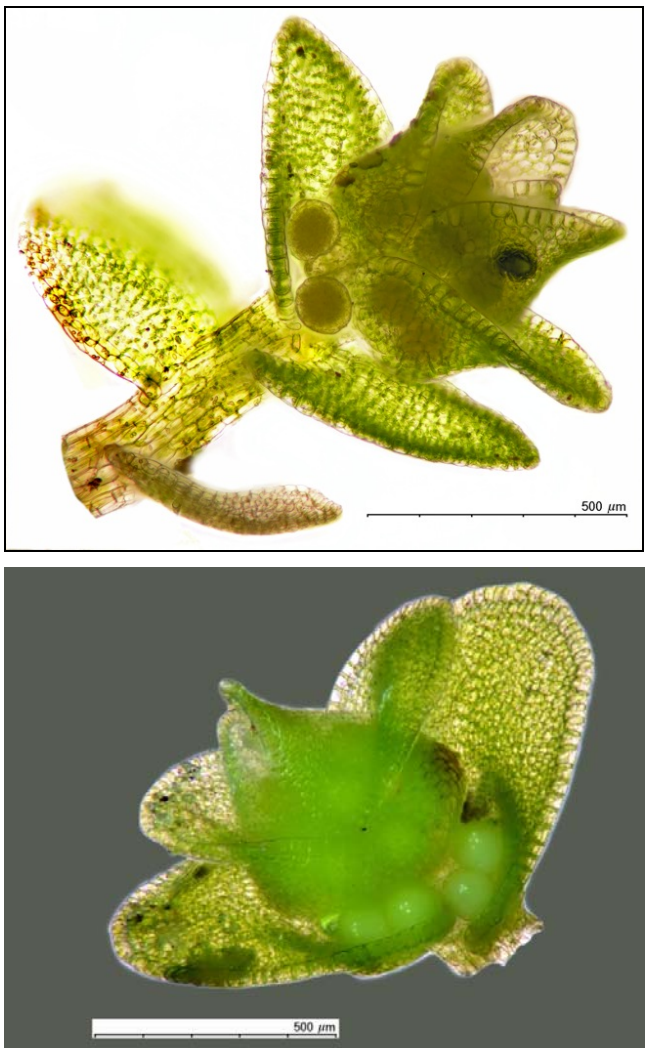

Figure 14. Comparison of light sources for microscopy. Note pasted-in scalebars. **Upper:** transmitted light. **Lower:** transmitted + reflected light. Photos by David H. Wagner.

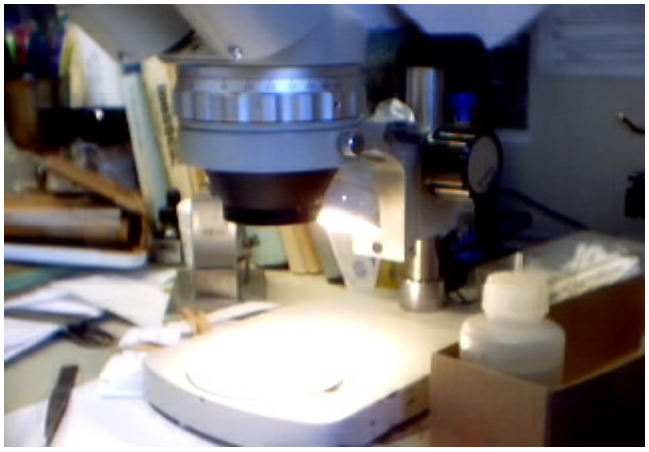

Figure 15. This unit provides an even, warm white light spread over the base of the microscope. Photo by Richard Zander.

Figure 16. The three items needed to provide this LED light system. Photo by Richard Zander.

Three items are needed (Figure 16):

W-15-12 UpLight Power Supply
MR16/MR11 Socket - GX5.3/G40
MR16-WLX3 Warm White LED bulb - Medium 30°

These are available for about US $51 from:

Super Bright LEDs, Inc.
100 Washington St.
Florissant, MO 63031
314-972-6200
<http://www.superbrightleds.com/cgi-bin/store/commerce.cgi?product=MR16>

To set up your light, cut the connector off the end of the line that comes from the transformer. Stuff the copper wires into the holes in the base of the socket, and affix them there with a little duck tape. Plug the transformer into a multi-plug extension cord and use the on-off switch of the extension cord to turn the lamp on and off. For more concentrated light, a narrow-beam 10° bulb is also available.

Differential Interference

Interference microscopy was somewhat popular in the decades from 1940 to 1970. But its complicated design and use caused it to fall into disuse as better microscopes were developed. Its basic principle was to shine two separate beams of light, providing much greater lateral separation than that used in phase contrast microscopy. Gabrys (1978) used it to determine the refractive index of the cell wall of the moss ***Funaria hygrometrica***, demonstrating that for both ***F. hygrometrica*** and the tracheophyte *Lemna trisulca*, the mean refractive index was in the range of 1.41-1.42.

DIC microscopy is one possible way to improve the images. DIC stands for differential interference contrast microscopy and is also known as **Nomarski interference contrast** (NIC) or Nomarski microscopy. This technique enhances contrast in unstained, transparent biological materials. It is the lighting scheme that produces the image, similar to that of phase contrast microscopy, but without producing the diffraction halo that detracts from the latter. This technique has been used for many of the images in the illustrated dictionary produced by Bill and Nancy Malcolm (2006) and in the book *California Mosses* by Malcolm *et al.* (2009).

Ha'penny Optics

Bill and Nancy Malcolm (Bryonet 18 August 2012) have created beautiful images in their well-known *Mosses and Other Bryophytes, an Illustrated Glossary* (second edition). They suggest that to be able to see the delicate details of bryophytes you need differential interference optics. This permits even a transparent specimen to cast a shadow, making it visible (Figure 17). Cheaper microscopes do not have this system, and microscopes from North America and Europe are much more expensive. To solve this cost problem, the Malcolm's recommend a technique called **ha'penny optics**.

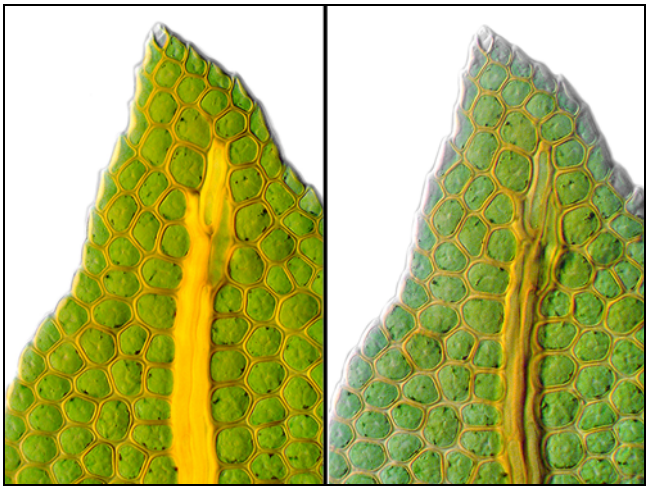

Figure 17. ***Fissidens pusillus*** showing differences in detail in light microscopy (**left**) and **ha'penny microscopy** (**right**). Photos by Bill and Nancy Malcolm.

Ha'penny optics cost only about half a cent, hence the name. The Malcolm's suggest placing a whole mount of a moss or liverwort leaf on your microscope and focusing it under the 40X objective. They slide a memo-sized piece of opaque paper across the underside of the condenser lens. When the edge of he paper reaches the midpoint of the condenser lens, the specimen will appear to be lighted from only one side, with the other side appearing to be in a strong shadow. This creates a 3-d look, revealing the structure of the leaf in excellent detail. This technique, if effective on your microscope, is especially useful for leaf margins, cell walls, papillae, and other textural surfaces. Although this technique works better on some microscopes, it will at least improve the effects on most microscopes. If sliding the paper across the condenser doesn't work, then try sliding it across the light source in the base. The effect is usually best with the diaphragm wide open, but experiment with closing it down slightly. Note that some microscopes have a diaphragm on the condenser and another on the light source.

If this technique works for you, you can make a more permanent **ha'penny** shadow source that is easier to use:

1. **Measure** the diameter of the condenser lens of the microscope (or light source if it works better).
2. Draw a **circle** of the same diameter onto a piece of stiff black paper or stiff plastic (Figure 18).
3. Inside that circle, draw a **second circle** that has a diameter 20 mm less, *i.e.*, making a doughnut 10 mm thick.
4. If the underside of the condenser is curved where it attaches to its mount, a circular doughnut won't lie flat. That can sometimes be solved by making the shape be **D** instead of **O** (Figure 18).

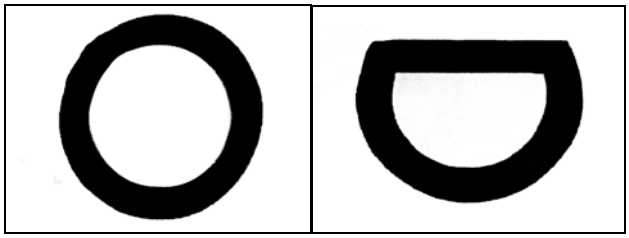

Figure 18. Ha'penny differential interference paper of Malcolm and Malcolm. **Left:** O-shaped interference for flat lenses. **Right:** D-shaped interference that may work better on curved lenses. Drawing by Janice Glime.

5. Cut the **O** or **D** using a sharp utility knife or single-edged razor blade.
6. Make a movable **lever** (Figure 19), using the same plastic or black paper, roughly 160 x 20 mm that will partially block the light reaching your specimen.

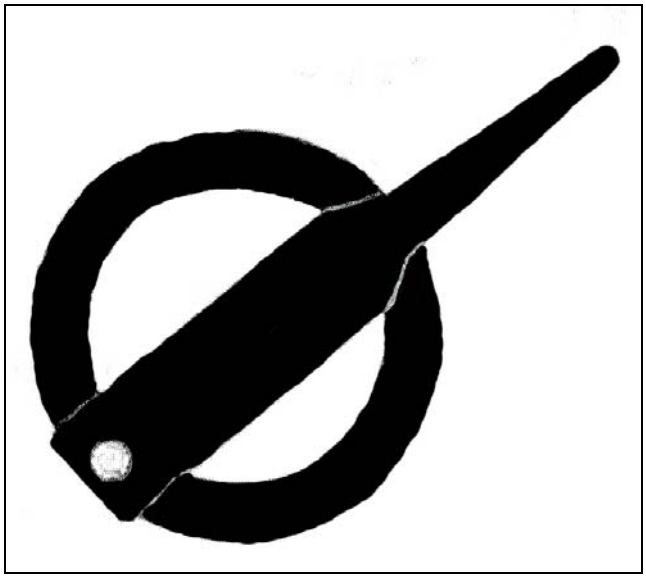

Figure 19. Ha'penny differential interference paper of Malcolm and Malcolm with lever attached. Drawing by Janice Glime.

7. Use a small **eyelet** to hinge the wide end of the lever to the rim of the doughnut (**O** or **D**).
8. Place the apparatus on the light or condenser with the lever on the upper side of the doughnut so that the edge of the lever is approximately at the center of the doughnut when in use, but it must be possible to pull the **lever** completely out of the light path when you don't need its interference. If you are right-handed, you will probably want the lever to be pointing toward the right.
9. **Tape** the doughnut firmly to the condenser or light with the lever on the upper side of the doughnut. Tape the doughnut in three places, making sure the tape does not interfere with the movement of the lever.

Polarized Light

Polarized light can sometimes make certain structures more visible (Amann 1923, 1931; Kolvoort 1966; Nordhorn-Richter 1988). It requires a special microscope with the right optical system and filters.

Plane polarized light can be used to see lignin and lignin-like compounds in vascular tissue and various other tissues where crystalline structure is suitable. Brilliant colors result from the lignin crystals in the cell walls, where the crystals bend the light rays to give the effect you see.

In bryophytes, this might be a tool to find lignin-like compounds in cell walls. The effect is much like a psychedelic panorama. In tracheophytes the lignin occurs between cells such as parenchyma cells and in the secondary walls of sclerenchyma cells. You can see these bright colors in the xylem, but the phloem and cortex cells will be pale or even disappear under plane polarized light. These bright colors are only seen easily in the cross sections of the stem (Figure 20). Certain dyes might also make tissues become visible in plant polarized light.

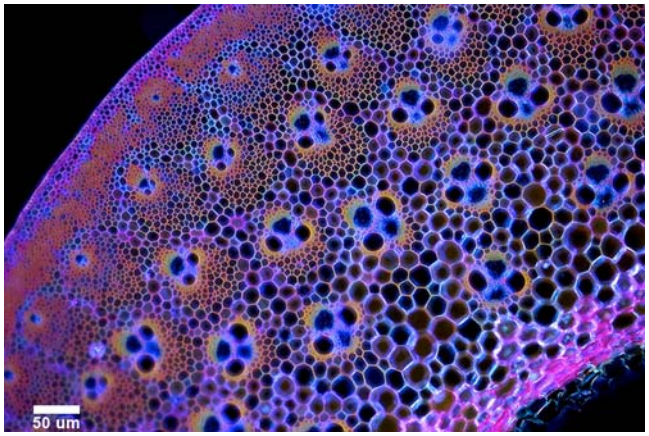

Figure 20. *Fargesia* sp. (bamboo) stem cross section in polarized light. Photo by Eckhard Völcker through Flickr.

Polarized light can tell us about the structure of bryophyte cells. That structure cannot be seen directly, but the presence and direction of crystalline structures can be determined by their response to polarized light (Taylor 1959). They can be seen only when examined in a direction perpendicular to their length, becoming dark (invisible) when viewed in the same direction as their length. For example, the crystals can be seen as brilliant colors in xylem when the stem is viewed in cross section, but not when viewed in longitudinal section.

Leaf Borders and Costae

Adams (2009) has devised a cheap Polaroid system for observing the border and costa of moss leaves. For example, in ***Fissidens***, it makes it easier to see if the costa joins the border at the tip of the leaf. In this case, and others, the moss cell walls have a regular crystalline nature with the cellulose fibers stacked so tightly and in precisely oriented parallel arrays that they rotate plane polarized light. But when the fibers are dispersed in an amorphous hemicellulose matrix, this effect is minimized.

Adams (2009) recommends making **two Polaroid lenses** from a pair of cheap Polaroid sunglasses. These can be cut to fit the filter holder just beneath the substage condenser and to fit the eyepiece lens. If the eyepiece lens is cut larger than the lens, it can be taped on its edges to the ocular. The ocular can then be rotated to block the light (when the gel alignment of the two lenses is perpendicular) and only the properly aligned cell walls will be visible, *i.e.* the border and costa.

Fluorescence

Fluorescence is most widely understood in mosses in chlorophyll fluorescence (Figure 21-Figure 22) (*e.g.* Shi *et al*. 1992; Deltoro *et al*. 1998; Proctor & Smirnoff 2000; Smith 2002; Heber *et al*. 2006; de Carvalho *et al*. 2011). **Fluorescence** is the emission of light from a substance while it is irradiated by light energy (Nordhorn-Richter 1988). Such cell parts as carotenoids, chlorophyll, and phenolic compounds have the necessary conjugated double bonds to cause fluorescence. In addition to these familiar sources of fluorescence, other fluorescing substances include proteins, flavonoids, oils, and waxes. Fluorochromes can combine with specific cell compounds, making it possible to see very small structures with a microscope because these combinations produce secondary fluorescence.

Figure 21. ***Fontinalis squamosa*** protonema using tungsten microscope light with blue filter. Photo by Janice Glime.

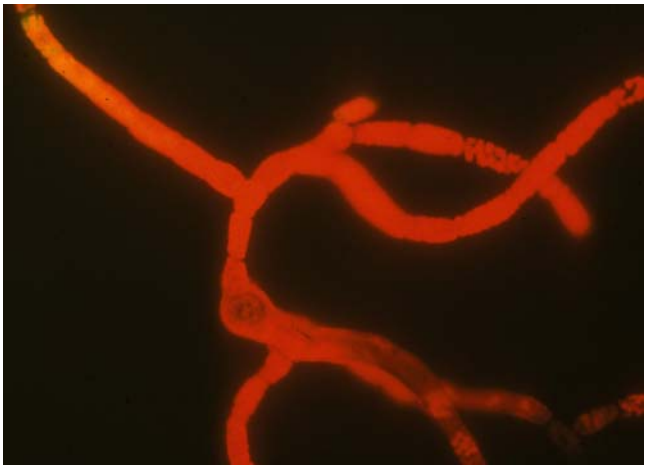

Figure 22. ***Fontinalis squamosa*** protonema using fluorescence microscopy and UV light source. Note that the chlorophyll fluoresces red. Photo by Janice Glime.

To view fluorescence, a fluorescence microscope is needed, equipped with a UV light source. An excitation filter (BP 350-410 or BP 450-490) is needed to absorb all wavelengths except the violet light at 350-410 nm or blue

light at 450-490 nm wavelengths (Nordhorn-Richter 1988). The microscope has a light-splitting mirror, which combined with the filtering system provides a light that permits observation and photography of structures that meet the chemical requirements.

When electrons absorb energy, they are elevated to a higher energy level. This is an unstable state that lasts for only about 10^{-15} seconds, during which they emit light as fluorescence (Nordhorn-Richter 1988). For fluorescence to be visible, the substance must be illuminated with UV light or blue light and the fluorescence is seen as yellow, orange, or red. The reaction requires that the energy content of the radiation source corresponds with the energy conditions of the electrons of the excited substance, requiring a broad spectrum of light energy so that the needed wavelength is present.

Details on applications of fluorescence microscopy are in Chapter 2-2 of this volume.

Dark Field Microscopy

Dark field microscopy takes advantage of the differences in light patterns between the specimen and the blank portion of the slide (Figure 23). The specimen will scatter light, whereas the area with no specimen will transmit the light with no scatter. Dark field microscopy uses ? to exclude the part of the image that does not scatter light. That is, it blocks light from anywhere but the specimen. The result is a greater contrast for the specimen.

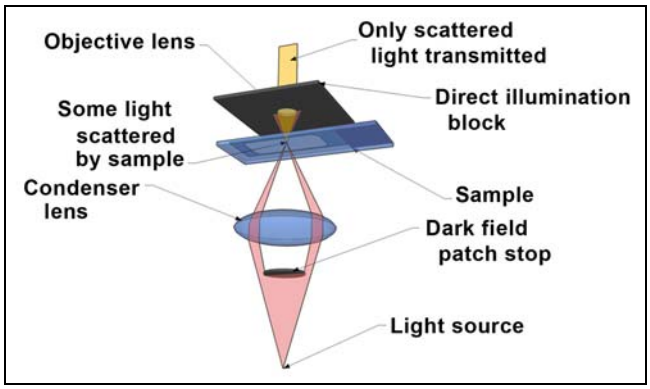

Figure 23. Dark field microscopy setup. Illumination modified from Wikimedia Creative Commons.

Phase Contrast Microscopy

The technique of phase contrast microscopy converts phase shifts by the light passing through a somewhat transparent specimen to make changes in the brightness of the image reaching the eye (or camera) (Figure 24).

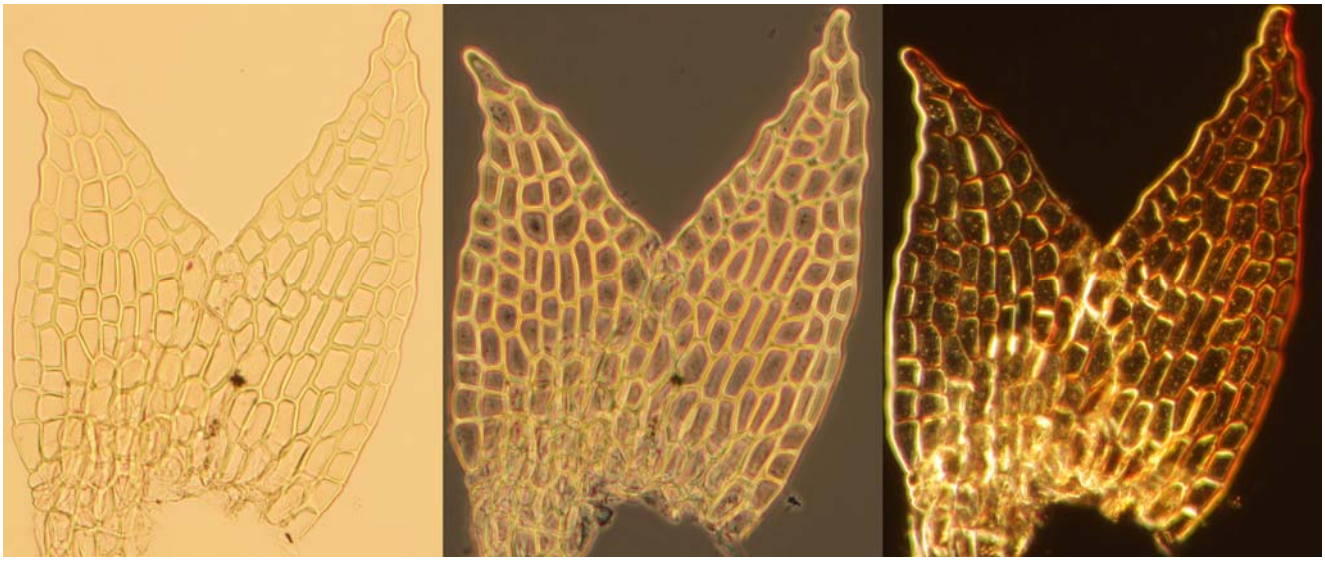

Figure 24. Comparison of microscopical techniques of ***Anthelia juratzkana***. **Left:** light microscopy. **Middle:** phase contrast microscopy. **Right:** dark field microscopy.

Small Equipment

Microforceps

Examining a bryophyte in the lab usually begins with a dissecting microscope and a pair of forceps. And that begins an adventure!

Forceps permit one to widen the spaces between the plants, sometimes revealing an interesting arthropod or gastropod fauna. Rhizoids, gemmae, and other propagules become visible. And it is possible to grasp a single leaf and remove it. **Microforceps** are essential for removing leaves or teasing out tiny liverworts. Standard lab forceps simply are too big.

Do you have leg scars because your forceps fell from you hands and landed point down (Bill Buck, David H. Wagner, Bryonet 5 January 2012)? Some are so expensive that the risk of scars is preferable to buying a new pair. The microforceps, also known as watchmaker forceps, seem to range in price from US $14.95 for a set of 5 on Amazon to US $295.00 from an electron microscopy supply company. But why so costly? Bryophyte parts are tiny. Ordinary lab forceps are much too broad to clasp a single leaf. Hence, one needs those fine-pointed forceps used by jewelers and watchmakers (Figure 25). And those hurt both your vulnerable legs and your pocketbook.

Figure 25. Typical steel microforceps used for work with bryophytes. Photo by Janice Glime.

Prices of US $20-40 are more common for microforceps like the ones in Figure 25. Carolina Biological Supply has extra fine microforceps for US $10.05 (like those in Figure 26-Figure 27). Terry McIntosh (Bryonet 13 May 2010) has found durable steel needle-nose forceps at Canadian $1.00 each that work just as well as the expensive ones. These are available at a liquidator place (Midland Liquidators) in Vancouver, Canada. I (Glime) also have found that the cheap ones work as well as the expensive ones, and last as long. The only problem with some forceps, especially for larger male hands, is that these tend to be a bit shorter, giving large hands less control. I (Glime) have used these in botany and bryology labs – they withstood student use.

Figure 26. These forceps are inexpensive but work well. Photo by Janice Glime.

Figure 27. Forceps with points (and people) protected by a short piece of tubing. Photo by Janice Glime.

Bryonetters (January 2012) discussed the pros and cons of a variety of forceps. Wagner recommends BioQuip #4524 for around $20. Charles Epsey (Bryonet 3 January 2012) and Guy Brassard (Bryonet 3 January 2012) recommend **Dumont** (style 3) in Switzerland for superfine, precisely aligned tips at a reasonable price. I have to agree with the assessment of affordable good quality of the Dumont forceps. They are available at <http://www.finescience.com/Special-Pages/Products.aspx?ProductId=306&CategoryId=29> or <http://www.dumonttweezers.com/>. Richard Zander (Bryonet 3 January 2012) recommends forceps from Micro-Mark. Carl Wishner (Bryonet 3 January 2012) finds ultra-fine and microfine forceps at Fry's Electronics (ER0P5SA stainless, anti magnetic, anti-acid).

Some forceps are "stiff." There is little that can be done, and don't spread your good forceps because they too will become stiff. Once you find a brand you like, stick with it.

For students, cheaper versions of microforceps are sufficient for short-term use, especially if you are supplying them for their use. I recommend keeping one pair of curved microforceps (Figure 25). There are some leaves that are easier to grab with these, and they are good for holding a stem firm with one hand while the other does the pulling. They are also good for removing debris or small arthropods from among the bryophyte stems.

René Schumacker (Bryonet 9 July 2008) suggests also searching for watchmaker tweezers (numbers 4 or 5). Richard Zander and others (Bryonet 8 July 2008) suggest Micromark <http://www.micromark.com/> as a source for inexpensive fine-tipped forceps.

Forceps will last longer if they are kept in a case. Some come in a clear plastic case with a foam sponge to hold them in place so the points don't get knocked around and damaged, but the hinges break easily and you may want a more permanent solution. Cairns (2013) suggests using a pocket reading glasses case for storage (Figure 28). The case should be cushioned at the end where the points go to avoid damaging them. You can cut the tip from a plastic pipette to protect the tips.

Figure 28. Forceps case using a pocket reading glasses case. Note that the upper pair is protected by the tip cut from a pipette. Photo by David Meagher.

Forceps Repair

The inevitable microforceps dropping is likely to require some repair work. They seem to land naturally on their points, blunting and bending them. I have been able to do reasonable straightening on a pair of those cheap student forceps used for ordinary animal dissection. I find that using a curved pair works best – you can stroke the ends of your microforceps like you are milking a cow.

Keep a fine-grain whetstone for needed sharpening or shortening of one side when they are unequal. One approach for restoring the fineness of the tips is to use a

dissecting microscope and whetstone to file the points down to a finer tip (Brian Heitz, Bryonet 3 January 2012). Carl Wishner (Bryonet 3 January 2012) recommends use of a dissecting scope and microfine or fine file "Washita stone." Wagner claims he can upgrade many poorer quality forceps by working with a fine (or extra fine) diamond jeweler's file under a dissecting microscope, but they do not reach the quality of a good pair of Swiss jeweler forceps. Claudio Delgadillo Moya (Bryonet 5 January 2012) suggests putting a final touch on the forceps with fine-grained sandpaper, working under the dissecting microscope. You can also use fine-grained sandpaper to file them, but a whetstone, albeit a more expensive initial investment, is ultimately cheaper because it is usable for a long time.

Ken Kellman (Bryonet 3 January 2012)#has some success in bending forceps back into shape by grabbing both arms of the forceps in fine needle-nose pliers. He then uses a diamond double-sided nail file (emery boards are usually too coarse, but better than nothing), and lightly pinches the forceps around the file and files the inside edges of the forceps (Bryonet 20 March 2023). This tends to get rid of the uneven grip of bent forceps. This even filing of both points simultaneously eliminates the little gaps that prevent you from gripping moss leaves and can even improve cheaper new forceps. File until you can no longer see any gaps under the dissecting microscope.

If your forceps have become bowed, you might want to wrap them in a soft cloth or paper towel to prevent scratches and force them together with pliers. For those broken tips, if possible, file down the longer tip to match the shorter length and file the sides to make the narrow width you need. A whetstone might be needed if the break is very far from the end. Ordinary emery boards will work also, but need to be replaced often.

Although dropped forceps with damaged points can be filed to make them sharp again, if you need to do this often, you soon get to wider and thicker portions that cannot be sharpened adequately. To reduce breakage and bending, store them with a tip protector such as seen in Figure 7.

Microdissecting Needles

Microdissecting tools are often needed with tiny leaves (Deguchi & Matsui 1987), such as those of ***Cephaloziella*** or ***Ephemerum***. I (Glime) learned to make a fine tool from entomologist friends. Such a needle can be made by cutting off the head end of an insect pin, leaving about 2-3 cm at the point end, and embedding the dull end into the end of a wooden matchstick. Cut off the flame end of the matchstick with a pair of pliers and you have a microdissecting needle. A slightly larger point can be made with a sewing needle embedded into the handle in place of the needle part of a cheap lab dissecting needle.

Dropper Bottles

Dropper bottles are used to make slides, but can also be used to moisten a portion of the bryophyte sample without making the entire sample wet or removing a portion of the clump for soaking. This also removes the need to dry the sample again if the moisture is confined to a small portion.

Needle Dropper Bottle

A small, ordinary dropper bottle, even one from the pharmacy, will work for most purposes, but sometimes a smaller drop is desirable, especially if you need to add only a tiny bit of water to the edge of a slide. Wagner (Bryonet 11 May 2010) shared a contribution from one of his students who brought a needle dropper bottle to class (Figure 29). These cost US $3-4 and are made by Gaunt Industries. They are available directly from that company <http://www.gauntindustries.com/2_Ounce_Products-HYPO_25.html> or from plastics fabrication stores such as Tap Plastics <http://www.tapplastics.com/shop/product.php?pid=409&> or art supply stores. Those with 23 gauge needles are best. An added advantage is that they don't spill if knocked over.

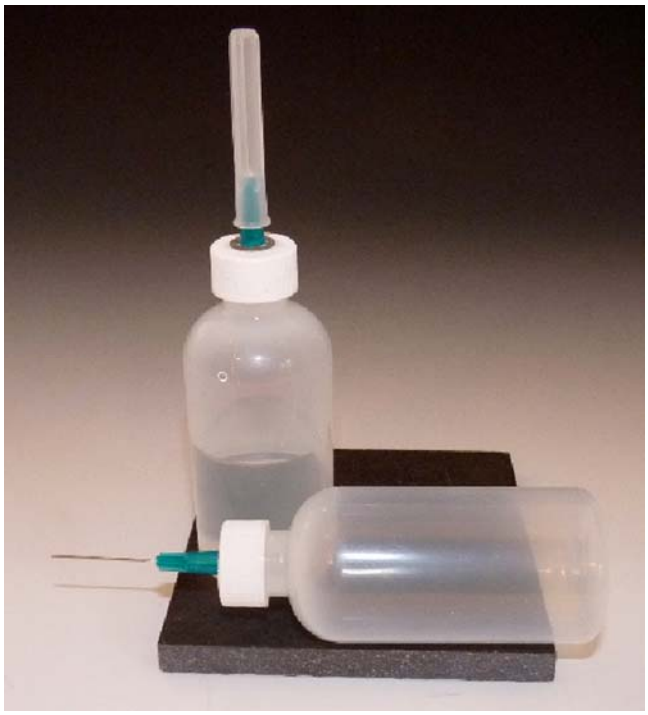

Figure 29. Needle dropper bottle for wetting mosses or adding water to a slide. Photo by David H. Wagner.

Slides

Slides are pretty standard, so little need be said. Occasionally a **depression slide** may be useful so that the bryopFigure 27hyte can maintain its 3-d relationships. Depression slides may be especially useful for observing the fauna in association with the bryophyte.

Coverslips

Plastic or glass? Plastic is cheap and throw away. But plastic is an oil product, so you are using a non-renewable energy resource. That said, there are other issues that are more important for your viewing pleasure. Glass is less likely to get scratched and has different adhesion properties with water. But thin glass coverslips get dirty and break easily. To clean them, get them wet and lay them on a paper towel. Then rub another part or different paper towel over them while they lie flat on a table. Do not try to wipe them between your fingers. They will break most of the time.

Housing for Coverslips

If you have lots of things on your lab bench, It is easy to overturn the coverslips. Zander (1993) suggests gluing the coverslip box to the base of the microscope or to a tray that holds your tools.

Wagner (Bryonet 2011) prefers to keep his coverslips ready for use on a small **polyurethane foam pad** (Figure 30). A small piece, 5 X 10 cm and .5 to 1 cm thick is all that is needed for two or three coverslips. This arrangement makes them easy to pick up by pressing thumb and finger into the foam on either side of the coverslip (Figure 31). The coverslip is then transferred to forceps for careful placement on the slide. But coverslips can be hard to control with forceps because the glass coverslip is slippery. I prefer to hold the coverslip gently by the edges, then with one edge touching the slide, I lower the opposite edge onto the slide with a dissecting needle (See Chapter 2-2 for diagram).

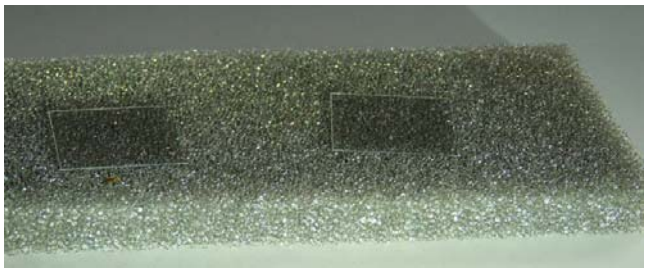

Figure 30. Polyurethane foam for holding microscope slides. Photo by David H. Wagner.

Figure 31. Demonstration of picking up a coverslip from a foam pad. Photo by David H. Wagner.

Standard microscope slides can be placed on a foam pad the same way as coverslips but Wagner prefers to keep them flat on the lab bench. This prevents the drop of water for mounting leaves from getting tipped off. After placing the coverslip on the mount, slip the slide to the edge of the bench to put it on the compound microscope stage. Otherwise, as often as not, the water drop is not added to the slide until it is on the stage of the dissecting microscope and dissections are complete.

Coverslips and Slides in Box

Wagner (Bryonet 2011) keeps his foam pad with coverslips in a wooden box (Figure 32), so that when he's away from the bench for a period of time he can close the lid to keep dust off the coverslips. Cut out a place at one end to store a small stock of coverslips and stack a similar stock of slides at the other end of the box (Figure 33). A reticule for measuring or counting is tucked into a slot in the foam. A fresh razor blade can be stored along the top edge. Wagner's box is not just any old cigar box, it is a box made by a craftsman. It is a way to have an article of beauty on the lab bench, something that can be important to a scientist with an active aesthetic sense.

Figure 32. Storage box used by David H. Wagner for storing slides and coverslips. Photo by David H. Wagner.

Figure 33. Open storage box used by David H. Wagner for storing slides and coverslips. Photo by David H. Wagner.

Other Useful Tools

Annie Martin (Bryonet 13 May 2010) gives us the perspective of an amateur beginner. She tells us that as she entered the world of bryology and started her own closer inspection of mosses, she discovered a couple of "creative"

tools of benefit. First, Paul Davison suggested a **syringe** as a sharp tool for cutting small fragments. She found a package for about $5 available at a local drug store (but she had to ask the pharmacist to retrieve them from behind the counter).

An idea she claims as her own hillbilly thinking – use a **camping headlight** (cut off the head strap) for a portable light source for microscopes. These head lamps are super bright with several settings, including a spot light. They have a foam backing that keeps them from sliding around on the surface. They actually provide better light than the battery lamps with goosenecks and range in price from US $5-$25. The lamps are available in outdoor stores or camping sections of superstores.

Being the daughter of a dentist, Martin found several dental tools with sharp points that work. When you are not affiliated with a university or have access to a research lab, it becomes necessary to find all kinds of creative, cheap solutions.

Photomicrography

Photography has been improving rapidly with the onset of digital cameras (Frahm 2000a, b, 2002) and stacking. But taking pictures through the microscope is still somewhat challenging – and can be expensive to set up. Some suggestions will be discussed here, but more detail will follow later in a chapter on photography in this volume.

There are several ways to get images of microscopic structures: cameras, digital connections to a computer, and scanners.

Scanners

Scanners can sometimes make relatively good images of flat objects and can therefore be used to show larger leaves or whole plants (Figure 34-Figure 35). The only magnification you can get is digital, but it is sometimes adequate when you want to get a quick image at home.

Figure 34. ***Plagiomnium*** sp. image (drying) from an Epson V500 scanner. Photo by Janice Glime.

Figure 35. ***Fissidens*** sp. image from an Epson V500 scanner. Photo by Janice Glime.

Experimentation with a scanner demonstrated that one can get reflected images that way, and in the absence of a camera that is able to get close to the subject, it can at least provide a habit image of some bryophytes. But the Epson V500, which is a good flatbed scanner that does an excellent job of transforming 35 mm slides into digital images, is unable to recognize the mosses as an image when using the transmitted light as one would for an image of a 35 mm slide (positive film). I (Glime) was unable to cajole the scanner into making a transmitted light scan of ***Fissidens*** or ***Plagiomnium***. It might be useful for making images of microscope slides of a sufficiently large specimen, or even of larger samples of bryophytes directly on the glass, but that remains to be demonstrated.

Malcolm and Malcolm (2006) describe using a scanner for photographing bryophytes. They recommend using at least **2400 dpi** resolution and then enhancing the image in Photoshop. The white inner lid of the scanner can be replaced with an upside-down tray at least 5 cm deep and spray painted flat black (or some other desirable color), with the spray painting avoiding the brush strokes. Avoid a white background because it can present uneven glares. For light-colored capsules and some bryophytes, use a grey background instead of black to avoid too great a contrast.

The specimen should be well **hydrated**, but not dripping. If condensation occurs, you can warm the platen (glass) of the scanner with a hair dryer. Clean the platen with a cotton cloth between scans to remove dirt, being careful not to scratch it with adhering sand.

Place the specimen upside down on the platen, using one of the upper corners. This will give the appearance of light coming from one side as it would in nature. You might want to test the scanner with a uniform, highly detailed color pattern that covers the platen. That will tell you if the scanner has "sour" areas that do not focus well or render colors well.

Choose **reflective** mode on the scanner and select an area slightly larger than the specimen. Use 100% scale (**original**). **Turn off** sharpening and compression and do all manipulating in Photoshop. The gamma should be set at 1.8.

To improve the image clarity and contrast in Photoshop, experiment using LEVELS (and select PREVIEW). Adjust colors as needed and sharpen last. Keep your original completed image as a TIFF or PICT file and make a copy before changing to jpg or other lower resolution format. The 2400 dpi resolution will permit you to crop your image while retaining sufficient detail.

Cameras

Michael Lüth (pers. comm.) recommended a Nikon Coolpix 990. This camera can be placed directly onto the ocular of the microscope. A wide field ocular is best to avoid having a circular image. This camera lens is the right size to fit well and exclude stray light. You can look directly at the camera screen to see the microscope image. The camera can be used on both compound and dissecting microscopes, as well as being a general-use camera for close-ups or scenery shots. For both types of microscopes, a third lens dedicated to the camera works best because it is level. It is often necessary to do some adjusting to make its focal plane match that of the other two oculars. But since it

is relatively easy to see the image with the camera, focusing can be done using the camera view.

Many microscopes now are being sold with a digital ocular that connects directly with the computer. Usually you can view the image on the computer screen, making focusing easy. Some of these have excellent quality, but some have very poor quality, being very pixilated due to low resolution. Don't order one unless you can see what it is capable of doing.

If you already have a camera tube on your microscope, or even the right diameter normal ocular, you can make the connection to your computer with an inexpensive attachment such as the one by GeckOOptics (Figure 36-Figure 37) for Australian $125. The included software package allows you to view, save, and edit images.

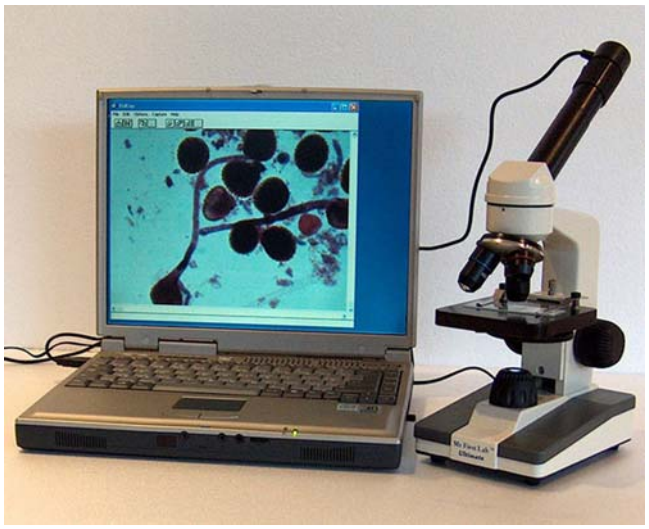

Figure 36. Computer screen with USB hookup to microscope. Photo by GeckOOptical. PERMISSION PENDING

Figure 37. USB attachment for microscope from GeckOOptical. Photo by GeckOOptical. PERMISSION PENDING.

Scalebar

For demonstrations of cellular structures or spores, size is important. Hence, providing a scale with the image is important. Rod Seppelt (Bryonet 14 April 2010) suggested taking a picture of a stage micrometer (special microscope slide with a microscopic scale). This should be done for all magnifications that you are likely to use. The image could then be included beside or within all pictures you take at each magnification to provide a reliable scale or even super-imposed on the picture as a scale bar. This can be accomplished with Photoshop or similar program. Once the scale is attached to the original image, the image size can be changed and the scale will change with it. Be sure to label the length of the scale bar on the picture.

An alternative to the Photoshop cut-and-paste approach, suggested by Andrew Spink (Bryonet 16 April 2010) is to use the free software **Combine ZP** <http://www.hadleyweb.pwp.blueyonder.co.uk/CZP/Installation.htm>. If you know the actual distance between two points on the photo, this program can add a scale bar (Figure 38). This same program is designed to stack several photos taken at slightly different focus, but it also permits this ability to stack a scale bar.

Figure 38. ***Lophocolea heterophylla*** with scale bar added using Combine ZP. Photo by Andrew Spink.

Inserting Scales into Images Using Photoshop

David Wagner provides us with a means of making a set of scales to use for various magnifications.

In Photoshop, open three files:

1. page with scales (Figure 39)
2. subject
3. image of stage micrometer at same magnification as subject. (Wagner photographs a stage micrometer at every photo session, at all the magnifications used in that session.)

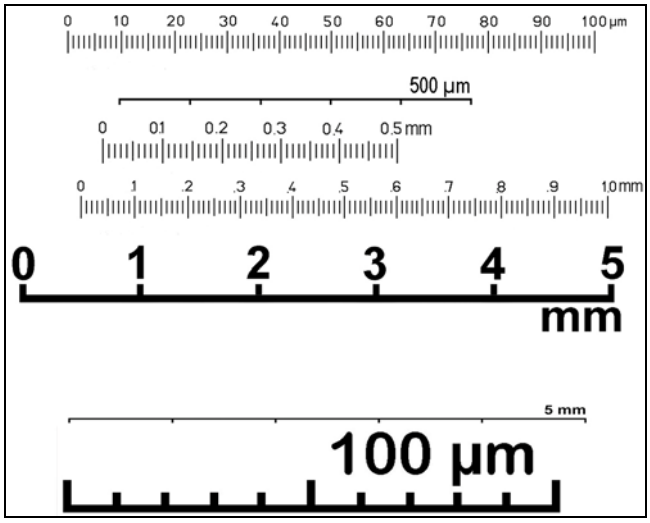

Figure 39. Scalebars that can used to label microscope images. Provided by David H. Wagner.

4. Bring file #1 (Figure 39) to the top and select the appropriate scale. (The top one, 100 µm, Wagner uses only with the highest magnification (40X objective), middle ones for 10X objective, and bottom ones for 4X and multi-image mosaics.)
5. Copy the selected scale to the clipboard.
6. Bring file #3 to the top and paste the copied scale onto the micrometer image. (see Picture 1, attached).
7. Use the move tool (in Photoshop CS3 you need also to set the move tool with Edit/Transform/Scale) to adjust the scale to the micrometer.
8. Flatten layers (Layer menu).
9. Select the calibrated scale and paste it onto the subject image (Figure 40). NEVER resize images before the calibrated scale is pasted in!

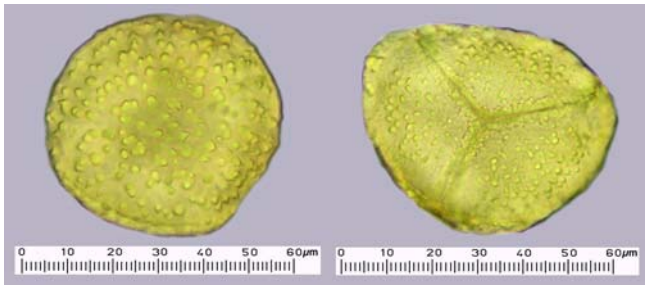

Figure 40. ***Phaeoceros oreganus*** spores with image stacking and added scalebar (from Photoshop) using both transmitted and reflected light. Photo by David H. Wagner.

Stacking

Manual stacking, using Photoshop, is also possible, albeit more time-consuming. Stacking in photography is the process of taking multiple images of the same subject, each at a slightly different focus. Software such as Combine ZP is used to put the images together, using the best focus portions of each to make a combined image with outstanding depth of field (Figure 41-Figure 42). This approach is also known as **deep focus** (David H. Wagner, Bryonet 19 April 2010).

Figure 41. Gemma cup of ***Marchantia polymorpha*** showing all gemmae in focus, a result of stacking 8 images in Photoshop. Note that the 1 mm text is hidden by the dark background. Text on a dark background should be in white or black framed in a white box. Photo by David H. Wagner.

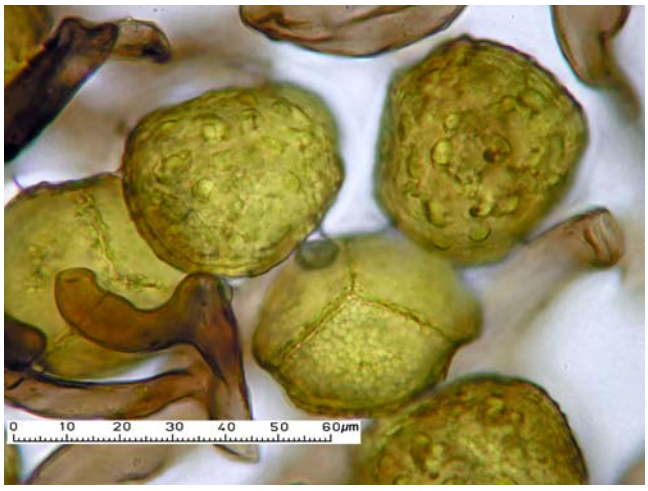

Figure 42. ***Phaeoceros pearsonii*** spores with image stacking and scalebar, using both transmitted and reflected light. Photo by David H. Wagner.

In creating the images in Figure 41-Figure 42, David H. Wagner (Bryonet 16 April 2010) used this stacking technique to create greater focus for the image of ***Marchantia polymorpha*** gemmae (Figure 41). This image was created from a stack of eight images, adding one image at a time. The spore image in Figure 42 used stacking with both transmitted and reflected light to make the details clearer.

Norbert Stapper demonstrates the use of stacking to photograph leaves and other parts of a moss under the microscope (Figure 43-Figure 44). He likewise used Combine Z.

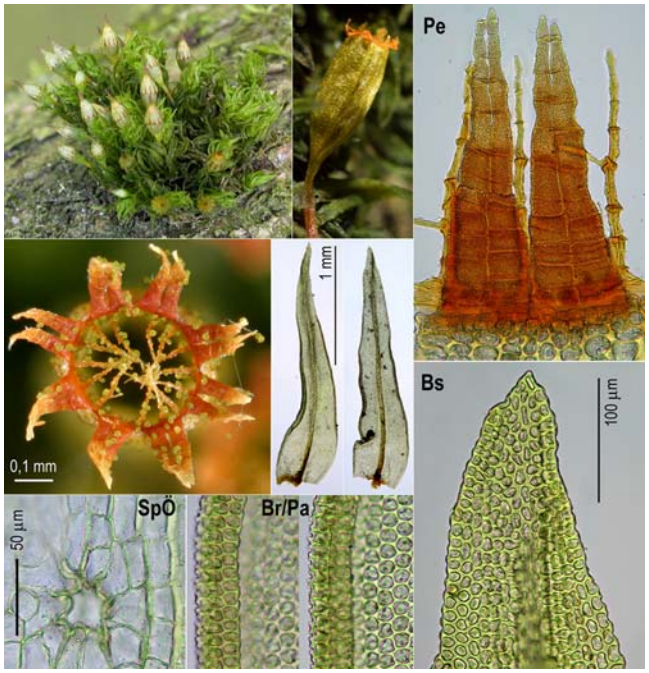

Figure 43. Stacked images, using Combine Z, of ***Orthotrichum patens***. Photos by Norbert Stapper, with permission.

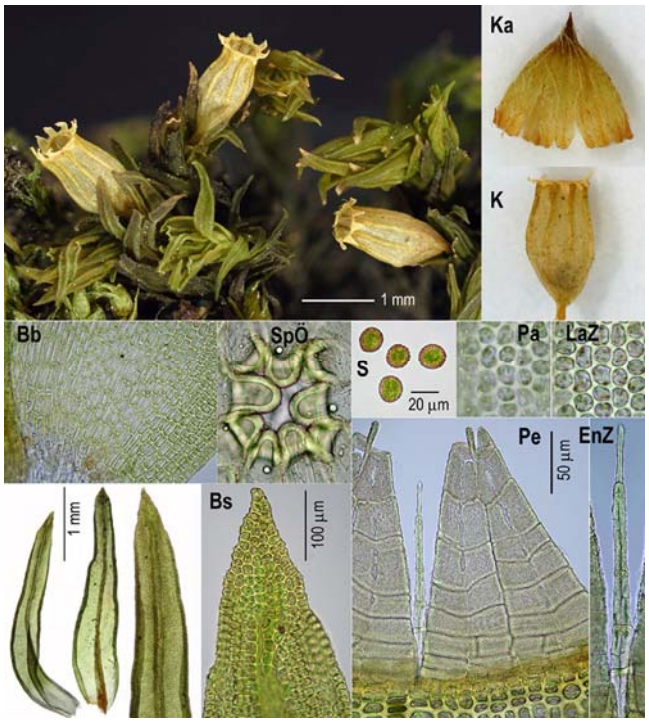

Figure 44. Stacked images, using Combine Z, of ***Orthotrichum pulchellum***. Photos by Norbert Stapper.

Standardizing Focus Increments For Image Stacking Photomicrography

Stacking software has reached widespread use in bryology because it makes it possible to greatly increase the depth of field for these small objects. Its principle is to take a series of images, each at a slightly greater focal distance. These are combined using the best focus areas of each with software such as Z or built-in software in the Olympus Tough camera. Objects such as bryophyte shoots photographed in reflected light with the clear focus of stacking have a three-dimensional appearance that can be very beautiful. This set of instructions is only slightly modified from those of Wagner on Bryonet (19 April 2010).

The stacking software works best if photos are taken in evenly graduated, overlapping focal planes. When the overlap is optimal, usually about 25%, neither too many nor too few pictures need be taken. Precise, expensive equipment is available that performs this process automatically. But obtaining excellent results by careful manual focusing is easily managed. Wagner has installed a handmade metering dial on his microscope that has served well in this regard.

Draw a **circle** on a card and divide it into **10°** segments using a protractor (Figure 45). Draw in the **radii** for each segment (Figure 46). There is nothing special about 10°; it is simply convenient and easy to see for this process.

Cut out the center of this dial, using a hole diameter that will fit around the fine focus knob on one side of the microscope (Figure 46).

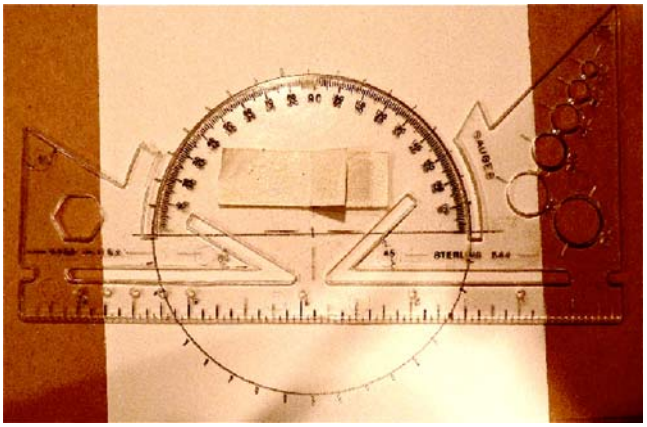

Figure 45. Protractor Photo by David H. Wagner.

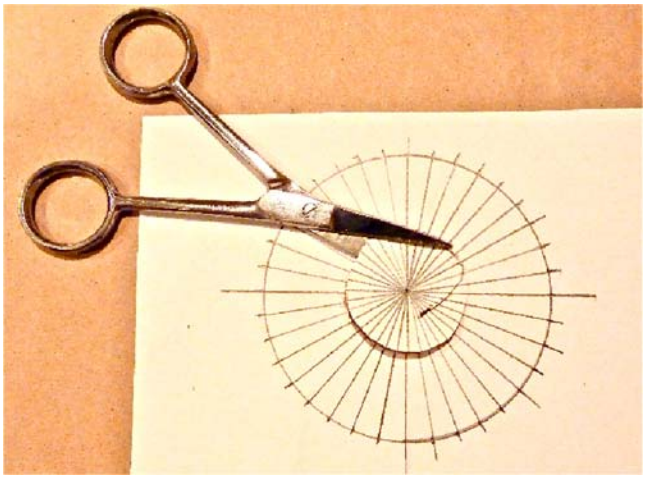

Figure 46. Card with 10° increments of radii. Photo by David H. Wagner.

Trim the card to fit and tape it to the microscope so that the fine focus knob is centered in the middle of the card's dial (Figure 47). Attach a "needle" firmly to the center of the focusing knob, so that the needle reaches to the edge of the dial. Wagner has used artist's putty to

attach it and for a needle has used a piece of black binding tie that comes with power cords. Plastiline modeling clay and a toothpick or bobby pin would work about as well.

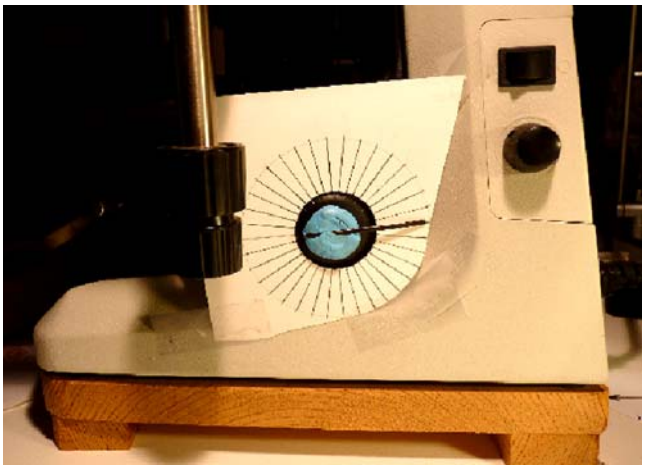

Figure 47. Stacking radii taped to microscope. Photo by David H. Wagner.

Mount a mirror in such a way that the needle and dial are visible as you use the microscope (Figure 48). Although this is not essential, it helps to be able to monitor the view through the microscope, adjusting focus with one hand while taking photographs with the camera's remote shutter release in the other hand.

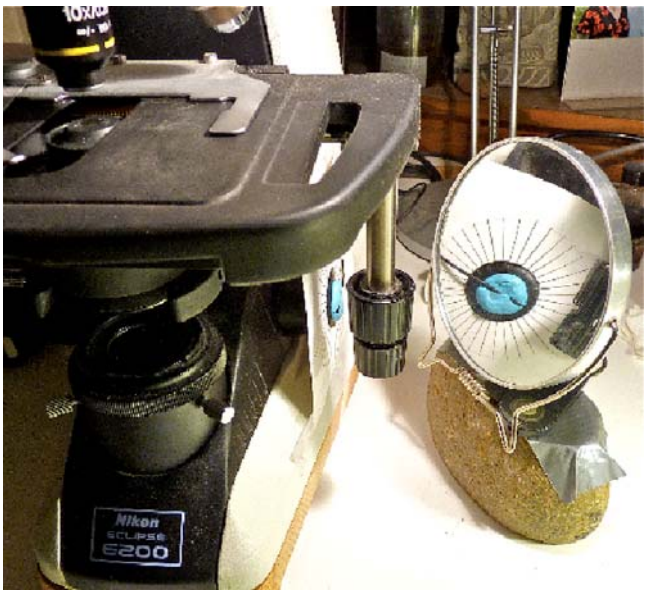

Figure 48. Mirror mounted so that needle and dial are visible while using the microscope. Photo by David H. Wagner.

For any particular object, first determine how many turns around the dial are necessary for a complete series of images. Focus on the top of the object and note where the needle is on the dial. Then focus down to the lowest focal plane you want to capture to determine the number of revolutions needed. For most slide-mounted objects it usually requires 1-3 complete revolutions around the dial to focus from top to bottom (near to far) focal planes.

Experimentation is necessary to use this system effectively. Wagner has found that with a Nikon Eclipse E200 microscope and a Nikon Coolpix camera, focus levels that work well are:

4X objective: 6 increments of the dial per image
10X objective: 2 increments of the dial per image
40X objective: 0.5 increments, or even better is to take three images per increment. (Oil-bodies in liverwort cells come into and out of focus with very slight touches of the fine focus knob.)

Practice is needed for consistent results. These guidelines provide about 25% image overlap, which works well with Helicon Focus. Maximum resolution settings on the camera help the stacking program to work optimally.

Once the object is properly staged, keep an eye on the dial and an ear on the shutter sounds. Turn the knob for the pre-determined number of increments with one hand on the fine focus knob, then activate the shutter release with other hand, turn the focus to the next stop, push the shutter release, *etc.*, until you have completed the number of revolutions of the needle on the dial to make a complete set of images from top focus to bottom focus.

For most bryophyte images, 10-30 images are likely to be adequate. Nothing is lost by taking extra images, and some are likely to be discarded. The useful ones are exported to a stacking program such as Combine Z. Once the stacking is completed, you can use Photoshop or other image management software to clean up debris, resize, sharpen, or whatever is needed.

Culture and Viewing Chamber

Paul Davison (2006; pers. comm. 22 February 2012; Davison & Kittle 2004) has made a viewing/photography cell that is useful for viewing aquatic bryophytes and bryophyte inhabitants (Figure 49-Figure 51). This uses two microscope slides with a spacer (foam) between them, temporarily bound together by vice or binder clips. The spacer must leave enough marginal space to squirt silicone between the panes as a sealant. Once the silicone sets, remove the spacer.

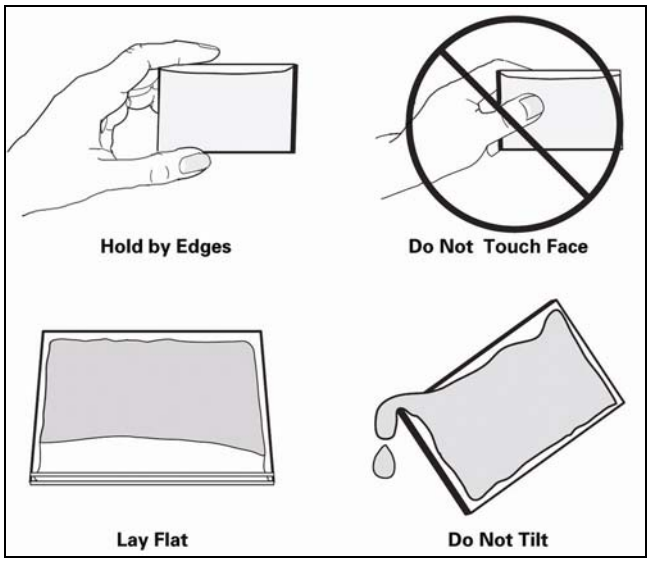

Figure 49. Method for constructing a microchamber for observing bryophytes and small invertebrates. This chamber can be used for projecting the images on a screen for teaching purposes. Modified from Davison 2006.

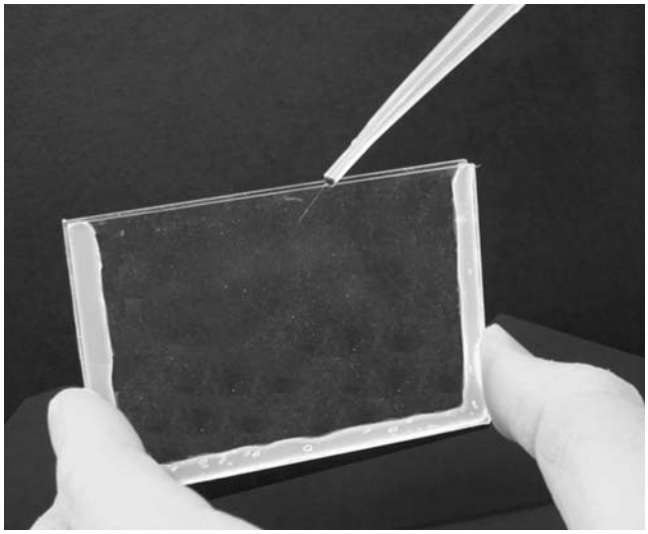

Figure 50. Filling completed microchamber built by above construction. Photo by Paul G. Davison from Davison 2006.

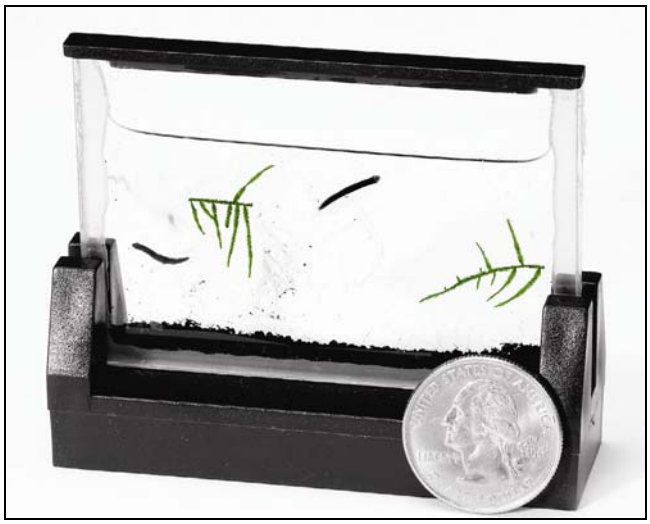

Figure 51. Occupied microchamber (with invertebrates and moss). Image modified from Davison 2006.

Summary

Adjust your microscope for the best possible viewing by adjusting the ocular distance and parfocus. Keep frequently used equipment at the microscope desk in a place that is easy to reach. Protect equipment such as microforceps against damage and sharpen tools as needed. Use a scalebar with the microscope and be sure that images have a scale reference.

Put small inhabitants into small chambers to minimize movement for photography. Use stacking equipment and software for the best images.

Acknowledgments

Bryonetters have been invaluable in providing the information used in this chapter.

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CHAPTER 2-2a
LABORATORY TECHNIQUES: SLIDE PREPARATION AND STAINS

Janice M. Glime and David H. Wagner

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CHAPTER 2-2a
LAB TECHNIQUES:
SLIDE PREPARATION AND STAINS

Figure 1. ***Polytrichum juniperinum*** leaf cross section using a cryostat and displaying natural colors. Photo courtesy of John Hribljan.

Preparing the Specimen

Fresh specimens are the most fun to work with. They are bright green and require little or no hydration before placing them in a drop of water on a slide. Chloroplasts migrate in cyclosis. And tiny invertebrates crawl about to entertain and distract you. But most often we don't have the pleasure to observe fresh material under the microscope. Instead, we have dry, often brittle, specimens collected in great numbers in a day-long or even months-long collecting trip. But don't dismay – the bryophytes will still freshen up to make good slides.

Cleaning Bryophytes

Washing Machine (Jewett 1913)

Jewett (1913) suggests a small "**washing machine.**" The bryophytes are placed on a fine screen – we assume that cloth window screening would work – and sprayed with a nozzle to clean them.

Embroidery Hoop (Mayfield *et al*. 1983)

Mayfield *et al*. (1983) suggested a similar cleaning procedure using a net, but they suggested placing the netting (mosquito or bridal veil netting) tightly in an **embroidery hoop**. This is particularly useful for thallose liverworts. They should be collected with ~3 mm substrate to protect rhizoids and scales. The liverworts are placed on the hoop netting with a second net placed over them. They are then washed with a stream of water. This may take some practice because too much water will damage the plants whereas a weak stream will not succeed in removing the soil and debris. Mayfield and coworkers suggest that a suitable stream of water can be achieved by attaching an eyedropper to pliable tubing. If the tubing is connected to a tapered laboratory water faucet, water flow can be adequately controlled. Specimens can then be pressed suitably in a telephone book, using folded waxed paper to hold the specimens between the pages of the book. Dried specimens are affixed to a 2x5" (5x12.5 cm) card with water-soluble glue. Specimens can be rehydrated when needed with boiling water. Contemporary workers discourage pressing or gluing specimens.

Wash Bottle (Wagner 2011)

Wagner (2011) suggests having a small **wash bottle** (125 ml) for rinsing the bryophytes and cleaning slides and coverslips for reuse (Figure 2). The water can also be used to wash away the wetting agent. The same ability of a wetting agent (see below) to reduce trapped bubbles also causes the water drop on your slide to lose its cohesion and adhesion, causing the water drop to run all over the place, so start with a small drop.

Figure 2. Water bottle and ceramic washing cup. David Wagner says he likes "to use a pretty, wood-fired stoneware cup, much more pleasing to the eye than the usual beaker." Photo by David Wagner.

HCl (Zander 1993)

Zander (1993) suggests using dilute HCl to clean away limy incrustations. It can also indicate whether the collection was made from a calcareous habitat because, if it is calcareous and bits are present with the sample, it will produce bubbles.

Ultrasound

Jan-Peter Frahm (Bryonet 11 December 2013) suggested using a sonicator to clean bryophytes before making slides, especially when they are used for photography. The bryophyte can be suspended by forceps into the vibrating bath. These are available for cleaning jewelry and watches in small sizes at relatively inexpensive prices. I tried this for cleaning ***Fontinalis***, but it disrupted the cell contents without dislodging adhering diatoms like ***Cocconeis*** (Figure 3-Figure 4). On the other hand, Randal Mindell (pers. comm. 2 January 2022) successfully cleaned ~24,000-year-old bryophyte subfossils.

It might be helpful to add a cleaning agent to the water to facilitate removal. Rod Seppelt (Bryonet 11 December 2013) suggests Tween 80 as a detergent. He dilutes it (lots) with water to clean capillary ink pens.

Aquatic Bryophytes (Landry 1973)

Aquatic bryophytes can be particularly challenging. They typically are covered with epiphytes, some of which (*e.g.*, the diatom ***Cocconeis***; Figure 3-Figure 4) embed themselves into the surfaces of the leaves. Landry (1973) experimented with various cleaning techniques on ***Fontinalis*** (Figure 5). He found that household bleach, diluted to 0.5%, causes no chlorophyll bleaching, but at 0.10% bleaching appeared in 15 seconds. Solutions diluted to 0.25% caused bleaching in 5 seconds. Bleaching in these cases occurred in the lower (older) leaves and may have been tied to senescence. Unfortunately, these methods did not appear to remove the epiphytes. Ultimately, 5 minutes cleaning with 3% peroxide (H_2O_2) and agitation seemed to remove approximately 85-90% of the epiphytes (Figure 5). Tumbling the moss at 30 revolutions per minute still only removed only about 85% of the epiphytes. Swirling improved the removal. Higher concentrations of peroxide and/or longer time periods caused bleaching of the chlorophyll.

Figure 3. ***Cocconeis placentula*** cemented to an algal strand. Photo by Bernd Kaufmann, through Creative Commons.

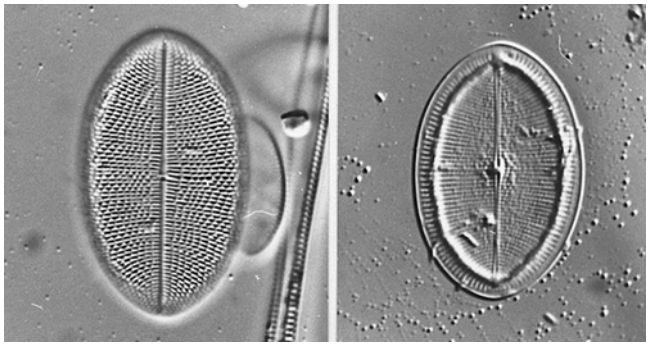


Figure 4. Both valves of ***Cocconeis placentula***, a common diatom that imbeds itself into the cell wall of aquatic bryophytes. Photo by Pauli Snoeijs, Nordic Microalgae <www.nordicmicroalgae.org>, through Creative Commons.

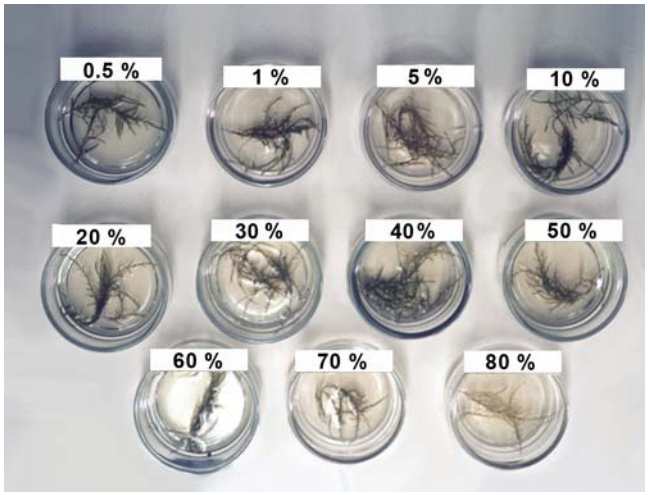


Figure 5. Experiment on cleaning ***Fontinalis*** sp. with household hydrogen peroxide at various concentrations. Note the bleaching at 70 and 80%. Photo by Janice Glime.

Dealing with Old Specimens

Old samples can be brittle and fragile. Placing them in water to soak can further degrade them so that they fall apart when cut. Adam Hoelzer (Bryonet 11 January 2016) takes from an old sample a single branch and puts it on a slide in a drop of water without soaking. Even if the branch is flattened from storage in a packet, that is helpful. Under a stereo microscope, Hoelzer keeps the branch affixed with his left index finger in position in the drop of water and cuts thin slices of the branch with a single-edged razor blade. You need some experience but that is the quickest and easiest way. Do not soak the parts as they get very soft. There is no need of using *Sambucus* or anything else to hold the moss. After cutting you can heat the sections carefully for swelling for a very short time with the help of a very small amount of KOH under the cover slip.

Sorting the Plants

A classic mistake in identifying bryophytes is looking at the sporophyte of one species and the leaves of another. Sporophytes often originate deep in the clump and may actually belong to a species that achieved sufficient dominance in a previous year to produce a capsule. But another species can easily encroach or simply intermix enough to confuse the unwary. Be sure to track the sporophyte down and locate its attached gametophyte. You might find it belongs to a small pleurocarpous moss that is weaving in and out among your acrocarpous cushion. This sorting should be done with bryophytes that are moist enough to be soft, but not soaked. Dry mosses are likely to break before you can pull the gametophyte out from among its trappings.

Wetting Agents

Assuming your specimens have not been collected in the same day and have gotten dry and brittle, the first step is to re-wet them before attempting to make a slide or even examine them with the dissecting microscope. Dry bryophytes are often brittle and will break easily if you begin manipulating them without wetting them first. However you wet them, we recommend watching them with a dissecting microscope as the water moves through the capillary spaces among the stems. It is a fascinating display and is sure to grab the attention of first-time viewers such as students.

Most bryophytes will wet up adequately by dipping them in water or dropping water or misting on the desired portion of the sample. Once the specimen has regained its wet shape and is pliable, leaves can be removed by holding the tips of the stems with a pair of forceps (can be ordinary lab forceps if the specimen is not tiny) or a dissecting needle (probe) and a second pair of microforceps should be used to pull down on the desired leaf, being careful to hold the leaf in a position close to the stem to get as much of its base as possible. For smaller species, curved microforceps often work best for holding the stems.

But some mosses simply don't wet well. In fact, some bryophytes repel water and may even trap large air bubbles that further keep them from getting wet. Members of the **Mniaceae** (Figure 6) are notorious for this, and **Polytrichaceae** (Figure 7) can be contrary as well if water cannot reach the leaf bases easily. In particular, wetting agents help to avoid the air bubbles trapped in leaf folds by reducing or eliminating the surface tension of the water. Warm water can sometimes actually increase the bubbles. Soap is a wetting agent, and it doesn't take much. One drop in your dropper bottle is likely to be more than needed. But beware, soap and the other wetting agents, as well as heating, will usually kill the bryophytes and destroy the cell contents.

Figure 6. ***Plagiomnium*** sp. branch resisting wetting. Photo possibly courtesy of Derek Bewley.

Figure 7. ***Pogonatum urnigerum*** (**Polytrichaceae**), a genus where water must enter the leaf bases where there is less wax. Photo by David Holyoak, with permission.

One solution to getting some of these to get wet is to drop them in **hot (not boiling) water** (Jewett 1913; Lucas 2009). I have to wonder if this distorts anything, and it most likely melts waxes such as one might find on the Polytrichaceae. But it does make most of them flexible rather quickly, and lost wax is usually not a problem. Some bryologists actually keep a hot plate nearby with hot water while they work.

Koponen (1974) dips members of **Mniaceae** (Figure 6) into 70-90% ethanol, then into 2% KOH, ultimately washing away the KOH with water. The specimens are ready for examination in one minute and the chloroplasts are destroyed, making other cell contents visible and the cell walls a yellowish to brownish color. This is especially helpful when the corners of the cells must be seen clearly.

A traditional wetting agent is one known by the German word **Pohlstoffe**. This is a non-technical name for a wetting agent (di-octyl sodium sulfosuccinate) available from Fisher Scientific, known as **Aerosol OT** (Wagner 1981; Bryonet 23 July 2008); it is mixed in a 1:24:75 ratio with methanol and water. Wagner suggested omitting the methanol, finding that this modified mix brings leafy bryophytes, dry capsules, and peristomes to turgidity rapidly, virtually everything except thallose liverworts. Schofield (1985) likewise suggested using only Aerosol OT and water with a dilution of 1:100. It is named for Richard Pohl (Diana Horton, Bryonet 19 September 1999) who presented the formula as a softening agent for dried plant parts (Pohl 1954).

Wagner recommends a half dropper of the 10% solution in 50 ml of water in a dropping bottle. The Aerosol OT can be difficult to obtain, especially if you are not affiliated with an institution. A Google search only located sites that sold it in huge quantities at costs of $500 or more. Wagner (Bryonet 11 May 2010) learned from his students that the critical substance is also known as **docusate sodium**, the active ingredient of stool softener! Hence, it is available at the drugstore for about US $5.00 for 60 caplets (Figure 8). Wagner determined that one caplet with a liquid center (100 mg docusate sodium), not solid pills, in 25 ml of water works well as Pohlstoffe. The carriers (glycerine, gelatin, propylene glycol, polyethylene glycol) do not appear to leave any noticeable residue.

Figure 8. Examples of stool softeners with docusate sodium. Photos modified by Janice Glime.

Soap (Tom Thekathyil, Bryonet 12 May 2010)

Another solution to wetting bryophytes is to use **soap** or detergent as a wetting agent. Tom Thekathyil (Bryonet 12 May 2010) suggests diluted kitchen detergent. It doesn't take much. One drop in your dropper bottle is likely to be more than needed. **A word of caution**: Soap can destroy the oil bodies of leafy liverworts! Warm water with patience is a better approach, but hot water can destroy the oil bodies.

Agral 600 (Tom Thekathyil, Bryonet 12 May 1210)

Tom Thekathyil also uses **Agral 600** (horticultural wetting agent). The latter kills the animal life that often accompanies the bryophytes but does not seem to affect the plants. This is useful to avoid introducing dermestids and other hungry creatures into the herbarium.

Rehydrating Capsules

DulcoEase

Des Callaghan (Bryonet 28 January 2016) raised the question of rehydrating ***Weissia*** capsules (Figure 9) that are full of spores. He needed them to regain normal size so he could obtain measurements. He tried the laxative DulcoEase (containing docusate sodium) for rehydrating capsules, but in this case, the interior spores remained dry, presumably insulated from the water by the outer spores. This kept the capsule partially dehydrated and did not permit it to obtain its fresh size as needed for measurements.

Figure 9. ***Weissia controversa*** capsules. Photo by Michael Lüth, with permission.

Catherine La Farge and Stephen Rae (Bryonet January 2016) both suggested using hot water to rehydrate. David Wagner (Bryonet January 2016) suggested adding docusate to a 50% solution of ethyl alcohol. It can speed the rehydration. A closed capsule can be rehydrated more quickly by putting tiny pricks through the wall using an insect pin.

Terry McIntosh (Bryonet January 2016) suggested a variation on this technique. He puts a complete stem into a shallow glass or plastic dish and sprays them with a fine mist until the leaves open. Then he covers the dish with a tall, clear plastic or glass container and places it outside in a protected area. The next morning the plant appears field-fresh, including capsules.

A mild solution (5-10%) of dish soap (Dawn) in tap water, heated to ~90°C is good for hydrating liverwort capsules (and probably also works on moss capsules). The soap breaks up the surface tension (Scott Schuette, Bryonet January 2016).

Jessica Budke (Bryonet January 2016) had a more sophisticated suggestion. She puts capsules in a low-level vacuum while they are in solution. That is helpful in preparation for TEM. It also helps to cut the capsule lengthwise to excise more tissue. Arno van der Pluijm (Bryonet January 2016), when working with ***Orthotrichum***, first punctures the capsule with a minute insect needle into the spore sac. After adding water it then quickly rehydrates and nothing is damaged.

Howard Matcham and Jan Janssens (Bryonet January 2016) both use 2% KOH or stronger to soak capsules. This technique causes the lids to pop, but it is useful for viewing stomata. Matcham suggests a single drop onto a slide, then a 5 minute soak before viewing. Janssens suggests soaking in nearly boiling water before adding KOH.

Rather than KOH, Jurgen Nieuwkoop (Bryonet January 2016) uses a drop of alcohol in water to wet difficult tissues. Norbert Stapper (Bryonet January 2016) suggests using a humidifying air chamber at close to 100% relative humidity. He advises to increase the humidity very slowly to avoid forming condensate on the capsules. This avoids the bubble formation from air expelled from the capsule.

After evaluating the suggestions made by Bryonetters, Des Callaghan (Bryonet 3 February 2016) found that to rehydrate the ***Weissia*** capsules (Figure 9), this was the method that worked the best:

1. Put the capsules in a drop of 2% KOH on a glass slide
2. Puncture one side of each capsule (I do this with the tip of very fine forceps)
3. Gently heat the KOH solution with a naked flame beneath the slide

This appears to rehydrate most capsules to their original dimensions, though some can be very stubborn.

Clearing Leaves

I (Glime) have never tried clearing leaves – I wish I had known about this for some of those dirty aquatic species! Des Callaghan (Bryonet 30 August 2012) has demonstrated cleared specimens of ***Anthelia juratzkana*** (Figure 5) in brightfield, phase contrast, and darkfield.

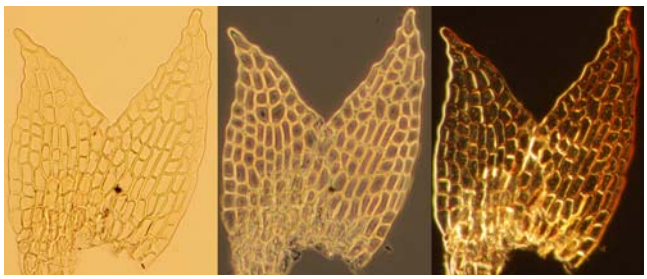


Figure 10. Cleared leaves of ***Anthelia juratzkana***. **left:** brightfield, **mid:** phase contrast, **right:** dark field. Photos by Des Callaghan, with permission.

Lactic Acid

The lactic acid clears all the gunk from the cells, making the walls much easier to see (Rod Seppelt, Bryonet 13 May 2010). Rod Seppelt (Bryonet 13 May 2010) uses lactic acid to clear leaves. One drop on a whole mount is sufficient (particularly if small), or with leaves and sections. The lactic acid may also be added under the cover glass of stems and leaves that have been mounted moist, but not flooded. Gently warm the slide using heat from an incandescent desk lamp. In the lab, if you don't have an incandescent lamp, you can use a hot plate, an alcohol burner, or even a candle, but you will need to clean the carbon off the slide if you wave the slide through the flame or place the slide above the flame. A Bunsen burner is too hot and could result in boiling the solution, a mishap to be avoided!

Unfortunately, lactic acid has its problems. It is somewhat a health hazard if you make contact with it, but less so than phenol, and it is not permanent on the slide. Specimens need to be examined (and drawn if desired) within a few days to weeks.

Water boils more quickly and suddenly than lactic acid, so less water is better. One Bryonetter suggested that a few air bubbles under the cover glass can be a useful **indicator** of imminent danger. When the bubbles begin to expand rapidly, it is time to remove the slide and let it cool so it doesn't boil. If the solution reaches boiling, you will most likely lose most of your dissected leaves and stems as bubbles escape.

KOH or NaOH

Usually these methods will only require a few minutes to clear the specimens. However, for especially dirty ones, you may need to leave the specimen overnight to clear. Potassium hydroxide (KOH) or sodium hydroxide (NaOH) will also clear tissues – particularly if the material is in contact with the air.

Chloral Hydrate

Chloral hydrate works well as a clearing agent, but please read the discussion of its use in Chapter 2-4 of this volume. It is a controlled substance and is dangerous to your health.

If you should choose to use it, the following protocol, developed for clearing parts of the flowering experimental plant *Arabidopsis thaliana*, may be a useful start (Berleth & Jurgens 1993). Substitute solutions for clearing can be tried in place of the chloral hydrate – experiment:

1. Fix plant tissue in 9:1 parts ethanol:acetic acid. Use vacuum infiltration to facilitate penetration of the fix – approximately 2 hours at ambient temperature.
2. Wash tissue twice with 90% ETOH for 30 minutes each wash.
3. Make solution of chloral hydrate or substitute in 30% glycerol. (Note that another substitute might already contain some glycerol.)
4. Add enough clearing agent (chloral hydrate or substitute) to cover the tissue in an Eppendorf tube (ca. 500 mL). Allow tissue to clear several hours.
5. Dissect tissue further if needed, using dissecting microscope. Mount dissected, cleared plant parts in chloral hydrate/glycerol or substitute under coverslip. Seal slide with clear fingernail polish if desired.

Richard Zander (Bryonet 5 March 2017) recommended the use of polyvinyl alcohol-glycerol glue. He originally used a 50:50 mixture, but found it to be too syrupy. He now recommends 70% polyvinyl alcohol glue:30%glycerol. This mix dries to a thick gum. Be generous with this mountant because it is about half water and that will evaporate. Polyvinyl alcohol glue is sold as Elmer's Clear School Glue or Colorations Clear School Glue. The glue also is good for sticking labels to microscope slides. Ready stick on labels dry and fall off in 5-10 years, whereas this glue lasts longer.

Dehydration

Usually specimens are air dried and this is adequate for most species. Some thallose liverworts require preservation, but mosses rarely do. For higher quality specimens, cleaned specimens can be dehydrated with a series of ETOH (70, 90, 100%) (Mayfield *et al*. 1983). Following the dehydration series, specimens are placed in a 1:1 ethyl alcohol:xylene solution, then transferred to 100% xylene. Remove any remaining dislodged soil particles with fine needles. The thalli can then be placed on glass slides in a xylene-soluble mounting medium such as Permount with coverslips that are weighted down with small weights like nuts (of nuts and bolts) or metal washers.

Stains

For most observations, stains are not necessary. But some things are simply too transparent or lack contrast. The series of images of ***Moerckia blyttii*** (Figure 11-Figure 14) by David Wagner illustrate what stains can do to aid visibility of the thallus structure.

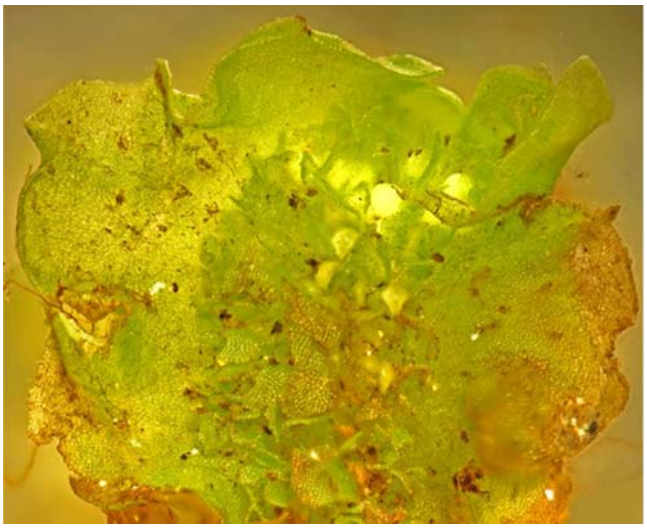


Figure 11. ***Moerckia blyttii*** fresh plant. Photo by David Wagner.

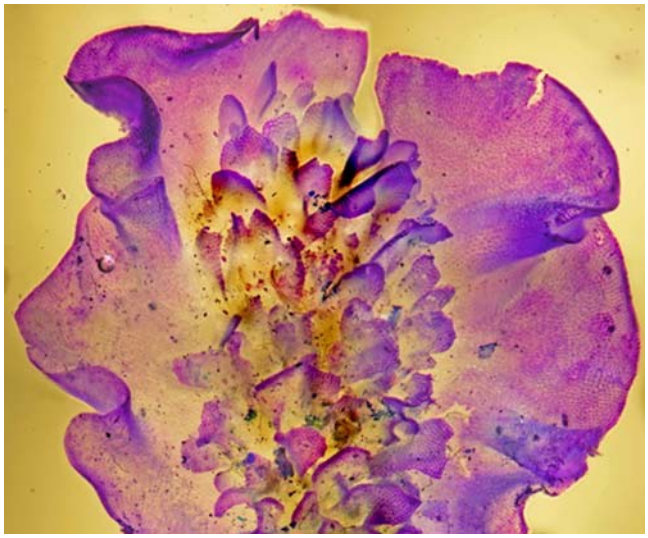


Figure 12. ***Moerckia blyttii*** cleared and stained with methylene blue. Photo by David Wagner.

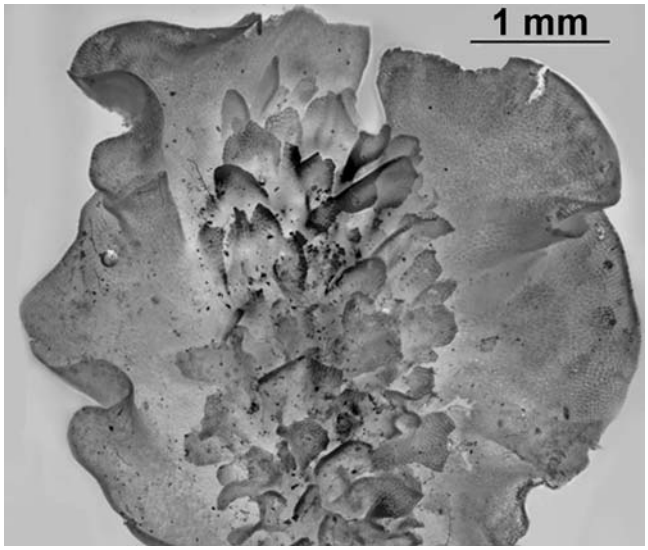


Figure 13. ***Moerckia blyttii*** cleared and stained, grey scale. Photo by David Wagner.

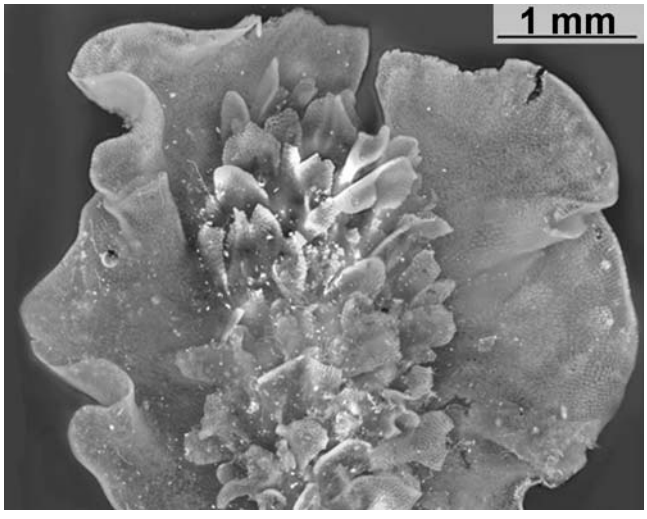


Figure 14. ***Moerckia blyttii*** cleared and stained; gray scale positive image converted to negative. Photo by David Wagner.

Stains can be used for a variety of purposes. They can distinguish cell types, make pores visible, clarify cell walls, make starch visible, and solve other problems in distinguishing special structures. Most stains are readily available, some are toxic, and others are household items.

Tom Thekathyil (Bryonet 13 May 2010) suggests using household chemicals such as those provided by Maier (2012). These include one drop of red or blue **food coloring** in 30 mL of water, or for greater detail and contrast, a mix of one or two drops each of red and blue **food coloring**, five drops water, two to three drops **white vinegar**, and three to five drops **rubbing alcohol**.

Staining Stems

Stems usually have specialized cells, including the epidermis, the cortex, and often a central strand. Others may have hydroids and leptoids and a second distinguishable layer inside the epidermis. In some species, natural colors distinguish the layers, but other specializations may not be easily recognizable.

Triple Stains

Ralf Wagner (pers. comm. 2012) suggests two triple stains that can be used to distinguish cell differences, the Etzold Stain (credited to Dr. Etzold) and W3A. The latter is described (in German) at <http://www.mikroskopie-bonn.de/_downloads/Arbeitsplan_W3Asim.pdf>.

Etzold Stain

Dissolve in 1L water:

Acetic acid (100 %):	20 ml
Fuchsin (bas.)	0.1 g
Chrysoidin	0.143 g
Astralblue	1.25 g

Color Results

non-ligneous cell walls: blue
ligneous cell walls, sclerenchym and xylem: red
Phloem: blue

Kawai Stem Staining Techniques

Kawai did extensive studies on stem sections using a variety of dyes (Kawai 1971a, b, c, 1974, 1975, 1976, 1977a, b, 1978, 1979, 1980a, b, 1981, 1982, 1989, 1991a, b; Kawai & Ochi 1987; Kawai *et al*. 1985, 1986) (Figure 27-Figure 63). He cut stems in 5 or 10 µm, even 15 µm sections (Isawo Kawai, pers. comm. 5 October 1989). Most of the information we have is the result of personal communication and a set of images he sent to me (Glime) many years ago. The effectiveness and time required varied among species and even within a species, perhaps indicating differences in age of the tissue or habitat where it grew.

For his early studies on mosses [**Hypnaceae**, **Thuidiaceae** (Figure 15)], Kawai (1971c, 1975, 1976) rehydrated the mosses by boiling them for half an hour to an hour in water. He then used a standard technique of ethylalcohol-butylalcohol-parafin for fixation. Sections were usually 5 µm thick.

Figure 15. ***Thuidium*** stem with leaves and paraphyllia. Photo by Paul Davison, with permission.

As his work progressed, he experimented with various methods of staining. In early studies, he used **acid fuchsin**, **fuchsin**, **fast green**, and **methyl green** (Figure 25-Figure 27) to stain members of **Bartramiaceae**, **Dicranaceae**, **Entodontaceae**, and **Fissidentaceae** (Kawai 1971). In some cases (**Amblystegiaceae** *sensu lato*, **Dicranaceae**, **Fontinalaceae**, **Hedwigiaceae**, **Lembophyllaceae**, **Leucodontaceae**, **Meteoriaceae**, **Neckeraceae**, **Pterobryaceae**, **Trachypodiaceae**), he used just **gentian violet** and **acid fuchsin** (Kawai 1977b, 1978, 1979). In others (**Amblystegiaceae**, **Bartramiaceae**, **Dicranaceae**, **Hypnaceae**, **Leucobryaceae**) he stained with **gentian violet**, **acid fuchsin**, and **potassium iodide**, using 5 µm sections (Kawai 1980a, b, 1981, 1982). As part of his experimentation with methods, he used 15 µm sections with the **Bryaceae** (Figure 16) (Kawai & Ochi 1987).

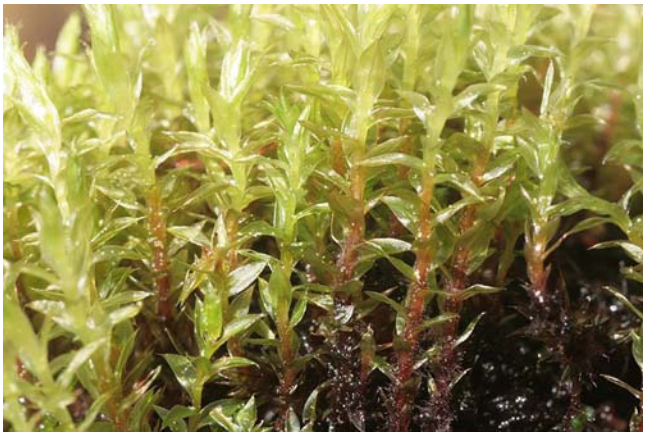


Figure 16. ***Bryum pseudotriquetrum***, a species Kawai cut in 15 µm sections. Photo by Hermann Schachner, through Creative Commons.

Some mosses were much more resistant to the stains. In particular, members of the **Polytrichaceae** (Figure 7) and **Fontinalaceae** (Figure 17) were difficult to stain so that cell types could be seen clearly (Kawai, pers. comm. 5 October 1989). Kawai *et al*. (1985, 1986) ultimately developed a lengthy and more complex protocol that gave satisfactory results. Even this differed between species within the family.

Figure 17. ***Fontinalis antipyretica*** shoot, a family in which Kawai found stems difficult to stain. Photo by Kristian Peters, with permission.

For ***Polytrichum commune*** (Figure 18), Kawai *et al*. (1985) tried three methods. **1) Aniline Blue-Eosin-Methyl Green Method:** They placed the moss in a solution of **aniline blue** and **eosin** for **48 hours**, followed by **washing** and a second solution of just **eosin** for another **48 hours**. Finally, the preparation was **washed** again and placed in a solution of **methyl green** for another **48 hours**. After **washing** the stems were cut in **15 µm** sections with a cryo-microtome and mounted in **gum arabic**. **2) Janus Green-Eosin-Methyl Green Method:** The specimen was soaked in a solution of **Janus green** and **eosin** for **48 hours**, **washed**, and soaked another **48 hours** in just **eosin**. The specimen was **washed** again and soaked in **methyl green** for **48 hours** before the final **washing**, **sectioning**, and **mounting**. **3) Gentian Violet+Congo Red-Eosin-Methyl Green Method:** The specimen started in a solution of **gentian violet** and **Congo red** for **32 hours**. As in the other procedures, it was **washed** and soaked in **eosin**, this time for **40 hours**. Finally it was **washed** and placed in a solution of **methyl green** for **32 hours**, **washed**, **sectioned**, and **mounted**.

Figure 18. ***Polytrichum commune***, a species Kawai used to experiment with stem staining techniques. Photo by Des Callaghan, with permission.

For ***Pogonatum contortum*** (Figure 19), Method 1 was successful, but specimens were soaked in each solution for **32 hours**, except for **40 hours** for just **eosin** (Kawai *et al*. 1985). For ***Rhizogonium*** (Figure 20) and ***Mnium*** (Figure 21), Method 1 was successful, but specimens were soaked in each solution for **72 hours**. For ***Fissidens*** (Figure 22-Figure 23), Method 2 was successful, but specimens were soaked in each solution for **36 hours**. In general, Kawai used the following concentrations:

eosin 0.2 g per 100 cc
methyl green 0.005 g per 100 cc

Figure 19. ***Pogonatum contortum*** with fly taking a drink. Photo from Botany Website, UBC, with permission.

Figure 27-Figure 63 illustrate the responses of a variety of species in various soaking times.

Figure 20. ***Rhizogonium spiniforme*** with capsule, a genus that required soaking in the staining solution for 72 hours. Photo by Janice Glime.

Figure 21. ***Mnium stellare***, a genus that required soaking in the staining solutions for 72 hours. Photo by Des Callaghan, with permission.

Figure 22. ***Fissidens crispus*** shoot, a genus that must be soaked in each staining solution for 36 hours. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

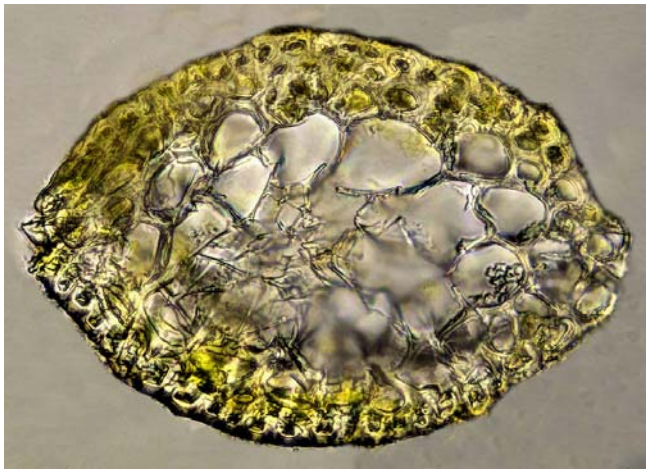


Figure 23. ***Fissidens bryoides*** stem cs, unstained. Photo by Dick Haaksma, with permission.

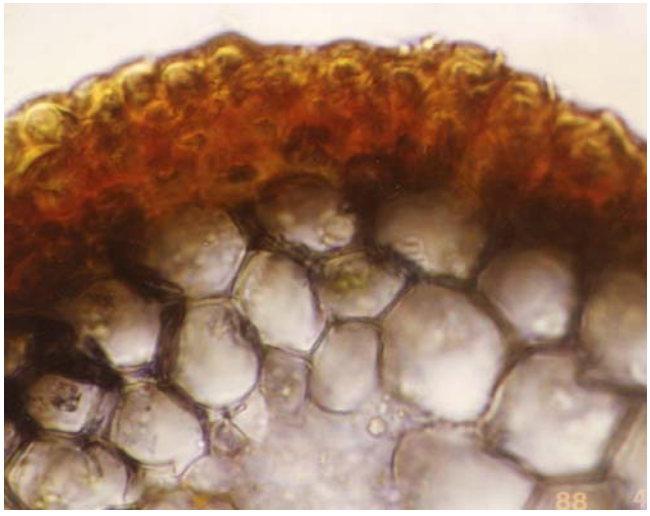


Figure 24. ***Bryoxiphium*** sp. stem cross section stained with **aniline blue** for 1 hour. Photo courtesy of Isawo Kawai.

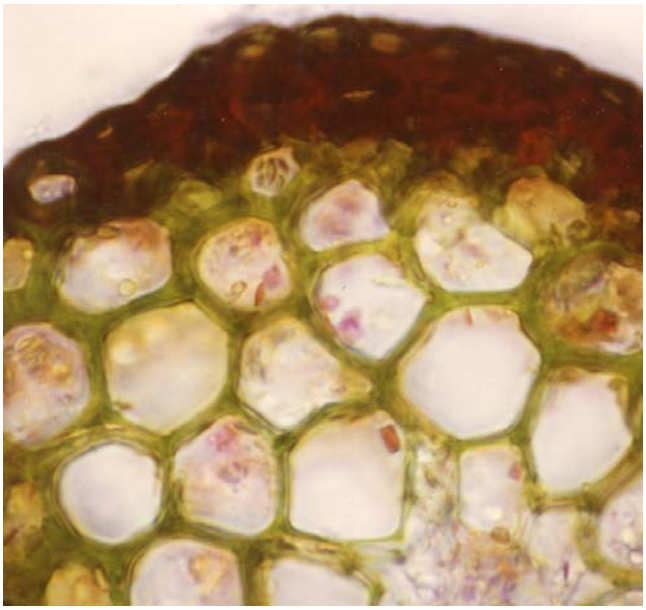


Figure 25. ***Bryoxiphium*** sp. stem cross section stained with **eosin** for 2 hours and **methyl green** for 30 seconds. Photo courtesy of Isawo Kawai.

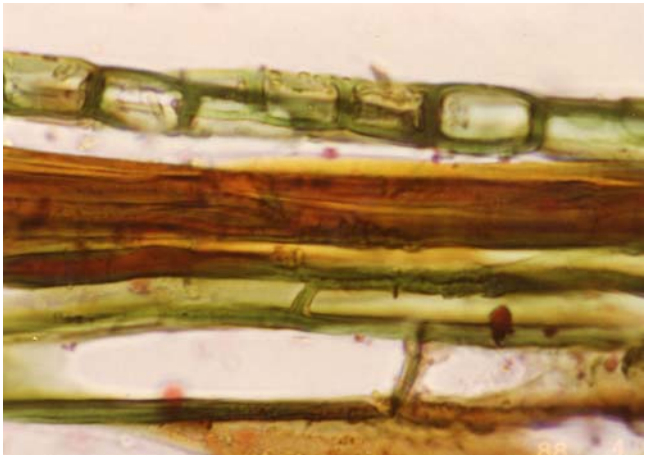


Figure 26. ***Bryoxiphium*** sp. stem longitudinal section stained with **eosin** for 2 hours and **methyl green** for 30 seconds. Photo courtesy of Isawo Kawai.

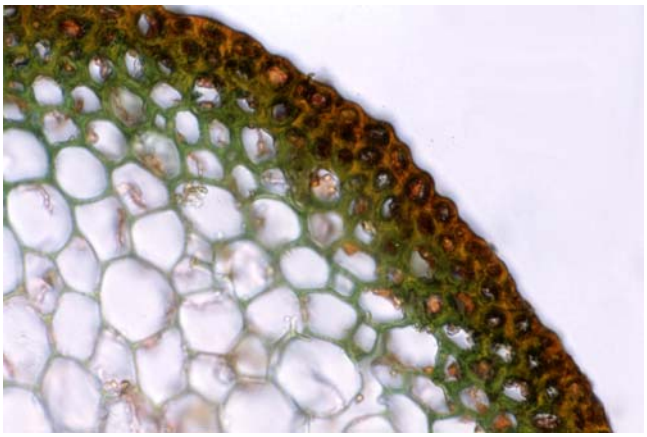


Figure 27. ***Fontinalis antipyretica*** stem cross section stained with 0.005 g per 100 cc **methyl green** for 10 seconds, then stained with 0.2 g per 100 cc **eosin** for 50 minutes. The blue-green/green color clearly shows the inner layer of "epidermal" portion of the stem. Photo courtesy of Isawo Kawai.

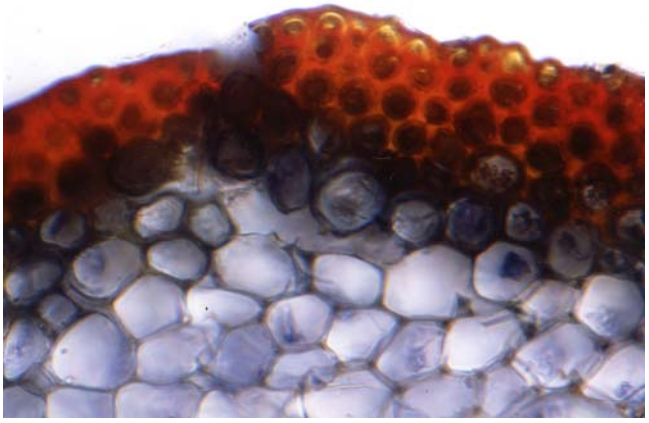


Figure 28. ***Fontinalis antipyretica*** stem cross section stained in **aniline blue** for 20 minutes. Photo courtesy of Isawo Kawai.

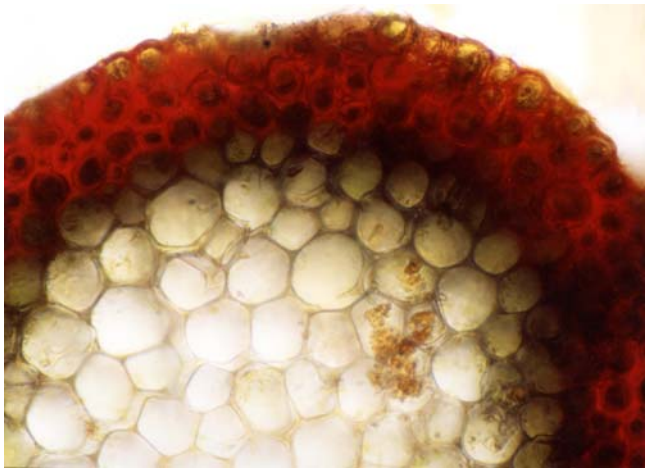


Figure 31. ***Fontinalis antipyretica*** stem cross section stained in **aniline blue** + **eosin** for 1 hour. Compare this to the previous picture (Figure 32) to see differences that can occur under the same staining protocol. These differences may relate to age of the tissues or possibly the habitat. Photo courtesy of Isawo Kawai.

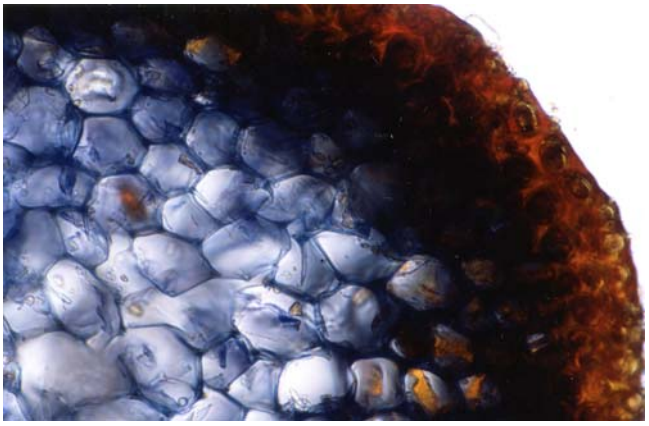


Figure 29. ***Fontinalis antipyretica*** stem cross section stained with **aniline blue** for 30 minutes. Photo courtesy of Isawo Kawai.

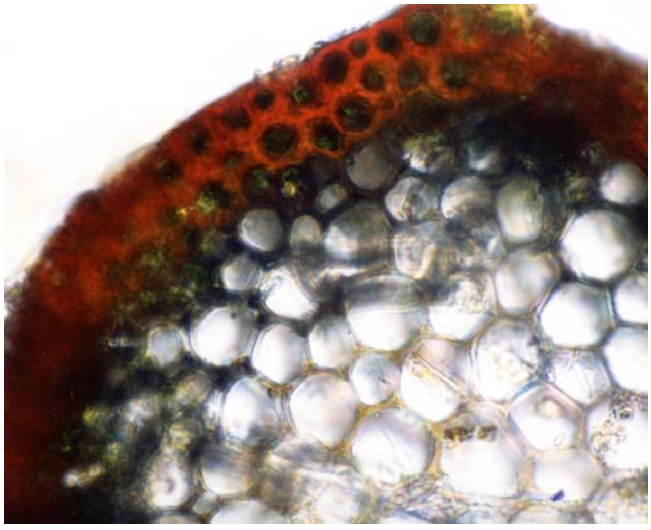


Figure 32. ***Fontinalis antipyretica*** stem cross section stained in **aniline blue** + **eosin** for 1 hour. Photo courtesy of Isawo Kawai.

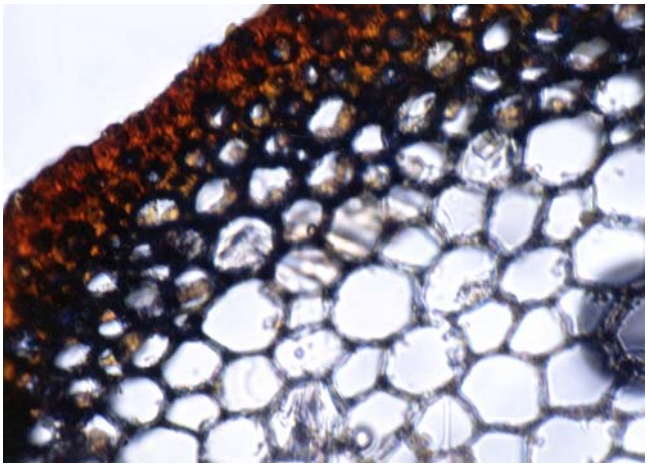


Figure 30. ***Fontinalis antipyretica*** stem cross section stained with **aniline blue** for 1 hour. Photo courtesy of Isawo Kawai.

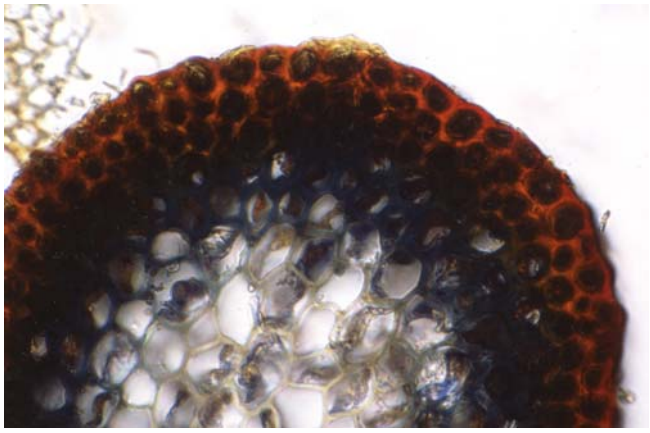


Figure 33. ***Fontinalis gracilis*** stem cross section stained with **aniline blue** for 5 minutes. Photo courtesy of Isawo Kawai.

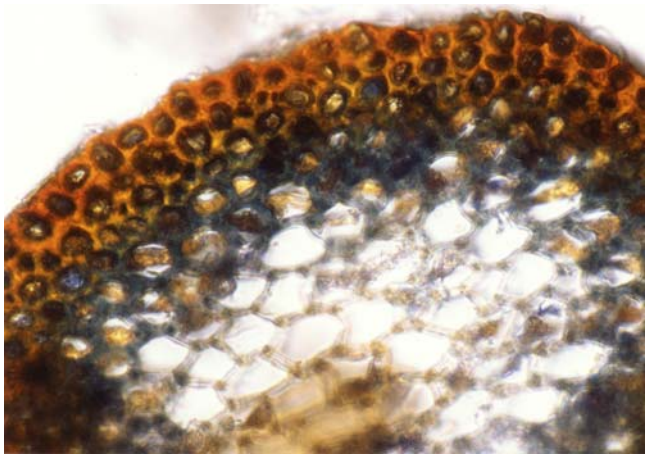


Figure 34. ***Fontinalis gracilis*** stem cross section stained with **aniline blue** for 5 minutes. Photo courtesy of Isawo Kawai.

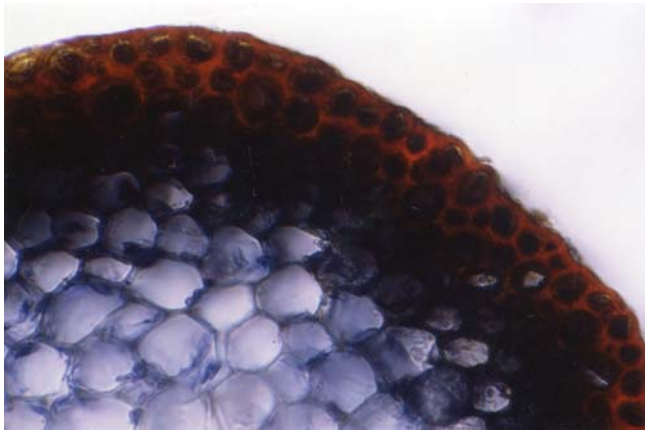


Figure 35. ***Fontinalis gracilis*** stem cross section stained with **aniline blue** for 1 hour. Photo courtesy of Isawo Kawai.

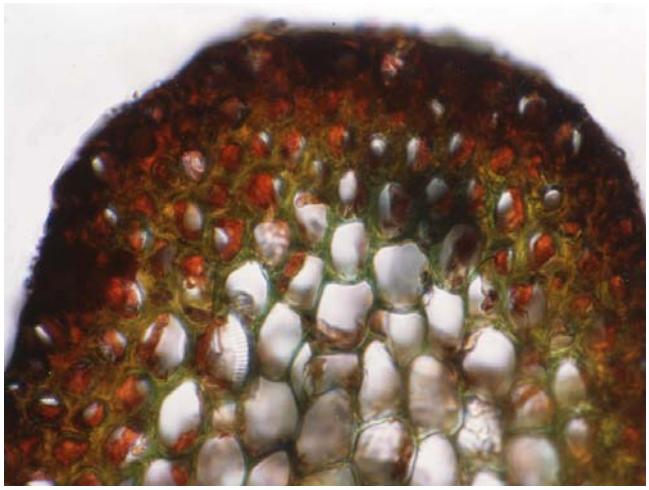


Figure 36. ***Fontinalis gracilis*** stem cross section stained with 0.005 g per 100 cc **methyl green** for 10 seconds, then stained with **methyl green** + 0.2 g per 100 cc **eosin** for 15 minutes. Photo courtesy of Isawo Kawai.

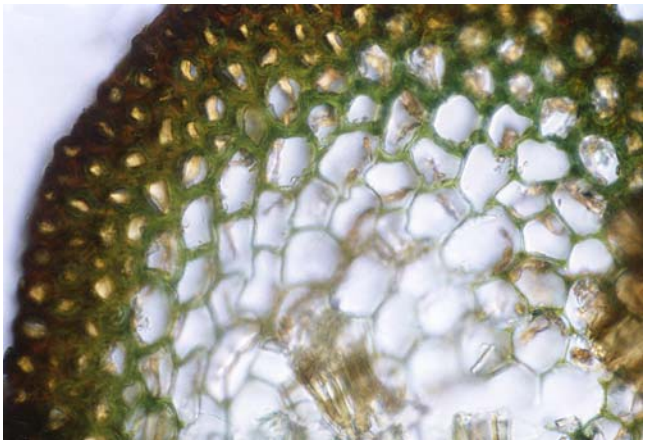


Figure 37. ***Fontinalis gracilis*** stem cross section stained with 0.005 g per 100 cc **methyl green** for 10 seconds, then stained with **methyl green** + 0.2 g per 100 cc **eosin** for 1 hour. Photo courtesy of Isawo Kawai.

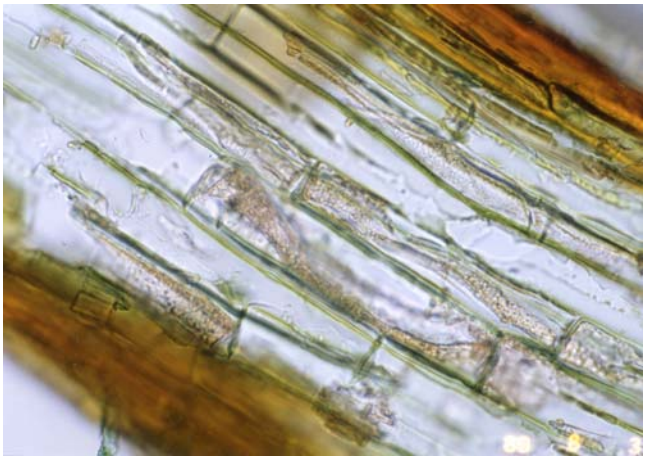


Figure 38. ***Fontinalis gracilis*** stem longitudinal section stained with 0.005 g per 100 cc **methyl green** for 10 seconds, then stained with **methyl green** + 0.2 g per 100 cc **eosin** for 15 minutes. Photo courtesy of Isawo Kawai.

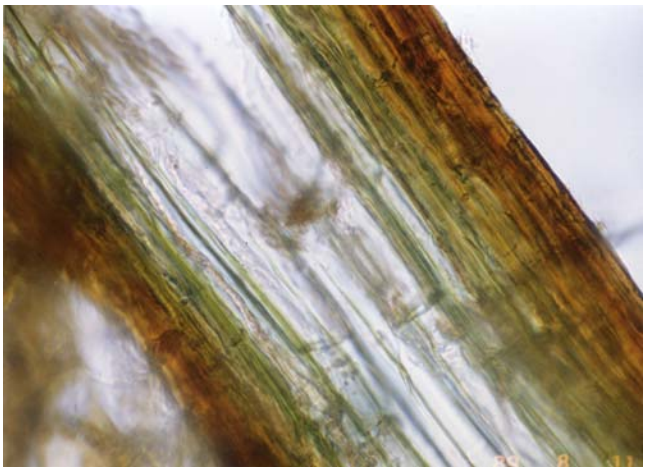


Figure 39. ***Fontinalis gracilis*** stem longitudinal section stained with 0.005 g per 100 cc **methyl green** for 10 seconds, then stained with **methyl green** + 0.2 g per 100 cc **eosin** for 1 hour. Photo courtesy of Isawo Kawai.

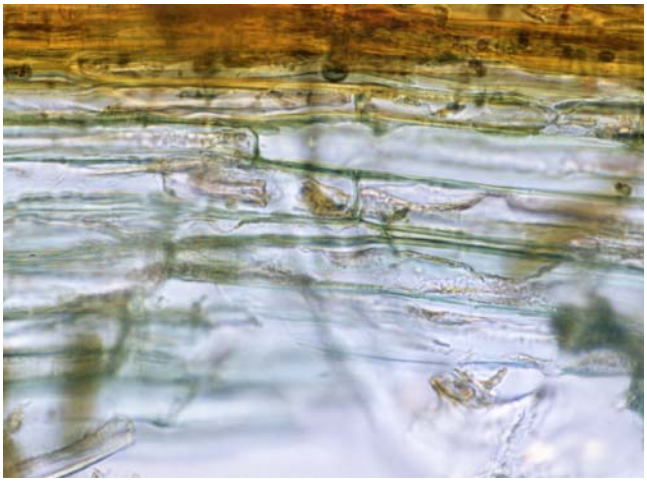


Figure 40. ***Fontinalis gracilis*** stem longitudinal section stained with **eosin** for 1 hour, **washed**, then stained with **methyl green** for 30 seconds. Photo courtesy of Isawo Kawai.

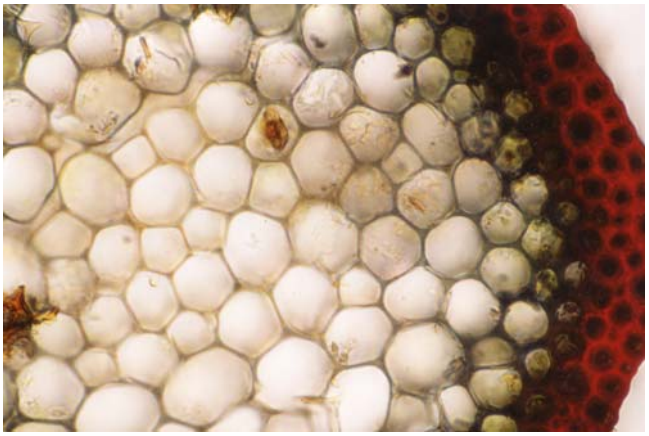


Figure 41. ***Fontinalis hypnoides*** stem cross section stained with **aniline blue** for 30 minutes. Photo courtesy of Isawo Kawai.

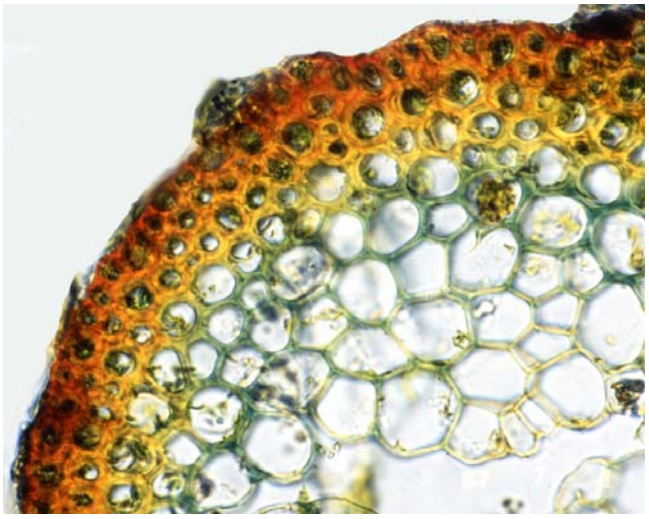


Figure 42. ***Fontinalis hypnoides*** stem cross section stained with **aniline blue** + **eosin** for 3 hours. Photo courtesy of Isawo Kawai.

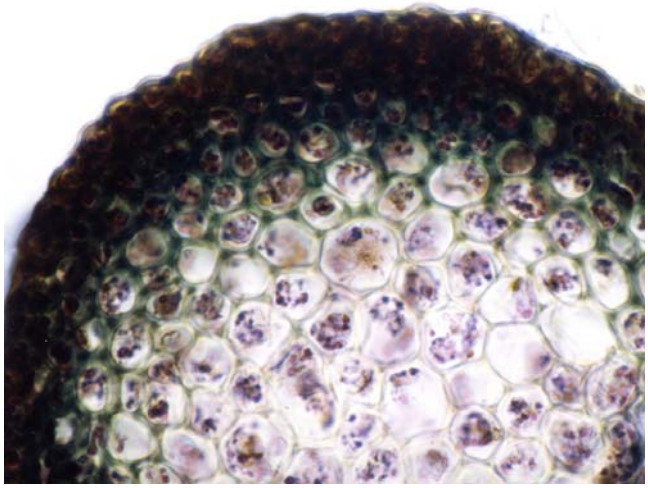


Figure 43. ***Fontinalis hypnoides*** stem cross section stained with **aniline blue** + **eosin** for 7 hours. Photo courtesy of Isawo Kawai.

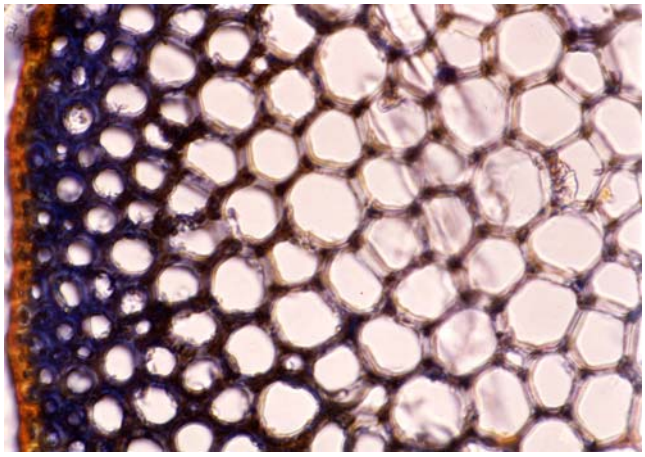


Figure 44. ***Hylocomium*** sp. stem cross section stained with **aniline blue** for 3 hours. Photo courtesy of Isawo Kawai.

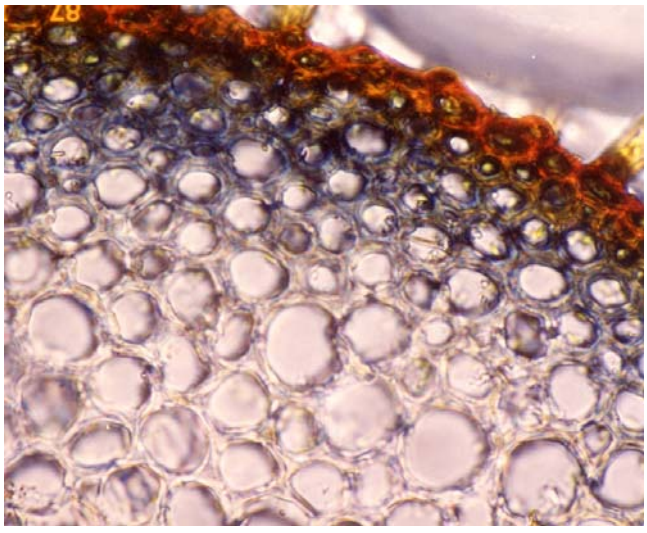


Figure 45. ***Hylocomium*** sp. stem cross section (5 µm thick) stained with **aniline blue** + **eosin** for 2 hours. Photo courtesy of Isawo Kawai.

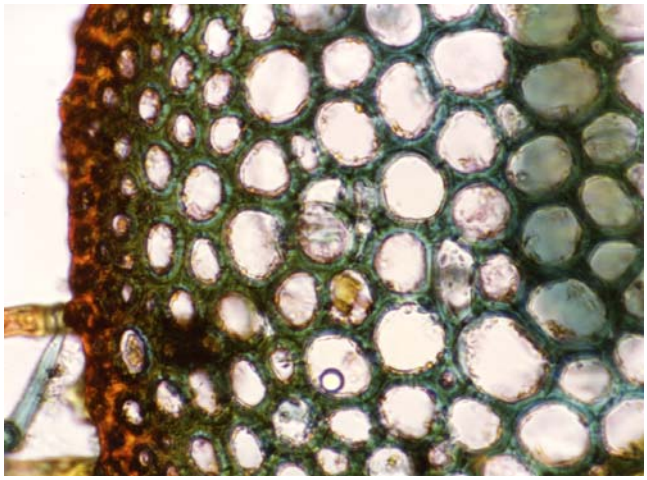


Figure 46. ***Hylocomium*** sp. stem cross section stained with **eosin** for 1 hour, then with **methyl green** 1 minute. Photo courtesy of Isawo Kawai.

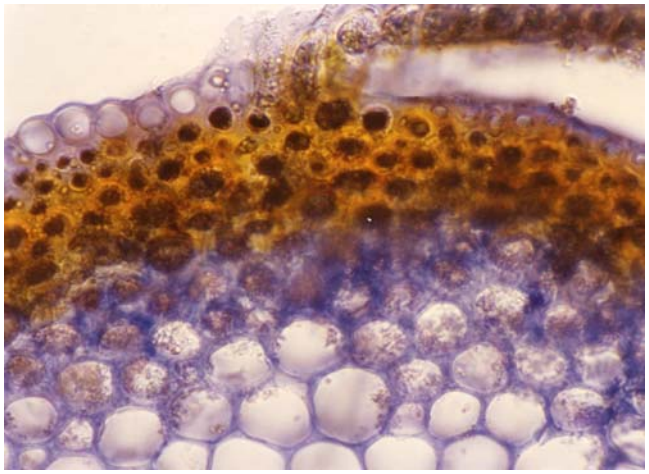


Figure 47. ***Hypnum*** sp. stem cross section stained with **aniline blue** for 1 hour. Photo courtesy of Isawo Kawai.

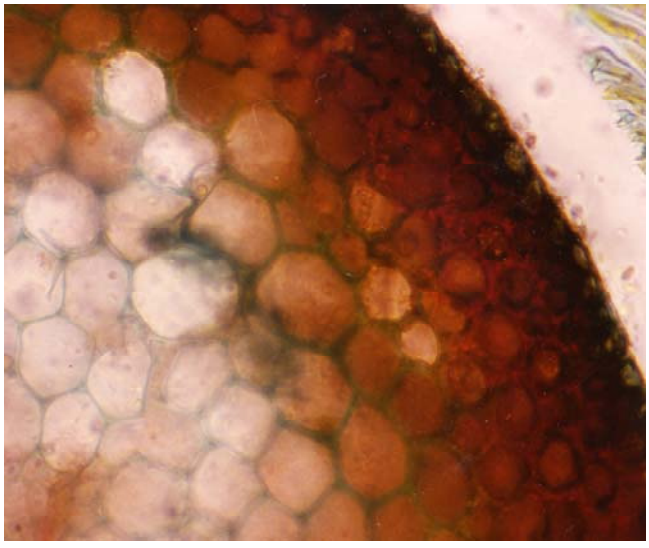


Figure 48. ***Hypnum*** sp. stem cross section stained with **eosin** for 1 hour, **washed**, then stained with **methyl green** for 0.5-1 minutes. Photo courtesy of Isawo Kawai.

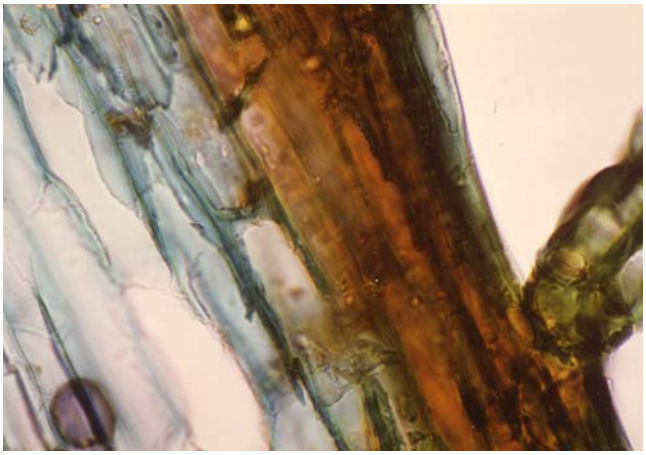


Figure 49. ***Hypnum*** sp. stem longitudinal section stained with **eosin** for 1 hour, then stained with **methyl green** for 30 seconds. Photo courtesy of Isawo Kawai.

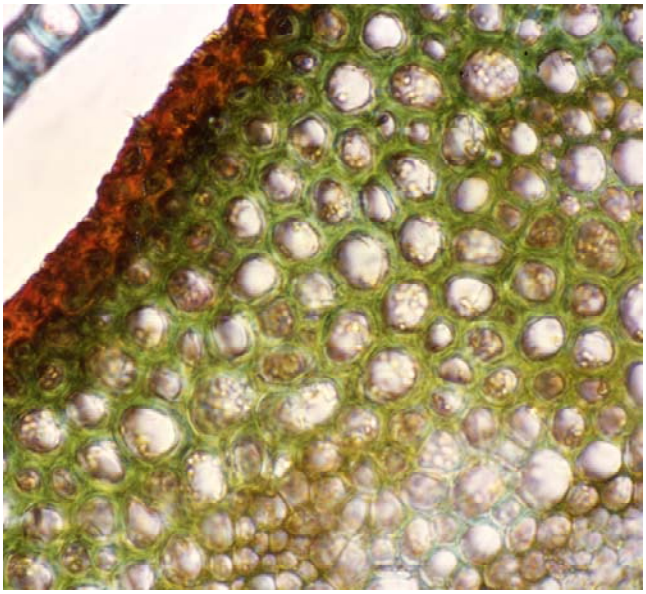


Figure 50. ***Polytrichum*** sp. stem cross section stained with **eosin** for 1 hour, then stained with **methyl green** for 2 minutes. Photo courtesy of Isawo Kawai.

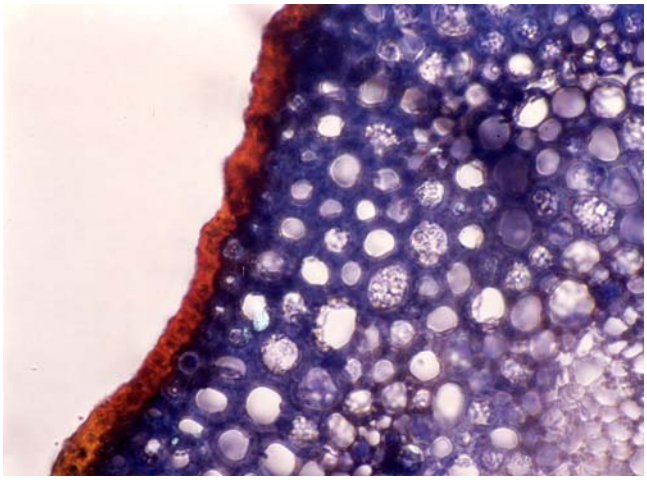


Figure 51. ***Polytrichum*** sp. stem cross section stained with **aniline blue** for 2 hours. Note the cell inclusions in these cortex cells. Photo courtesy of Isawo Kawai.

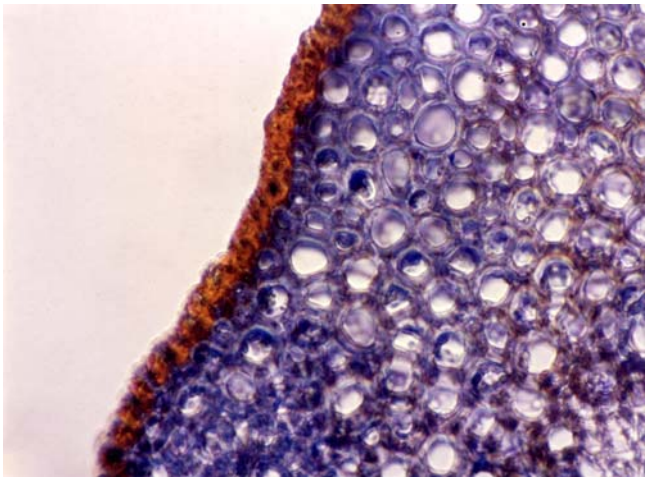


Figure 52. ***Polytrichum*** sp. stem cross section stained with **aniline blue** for 2 hours. Photo courtesy of Isawo Kawai.

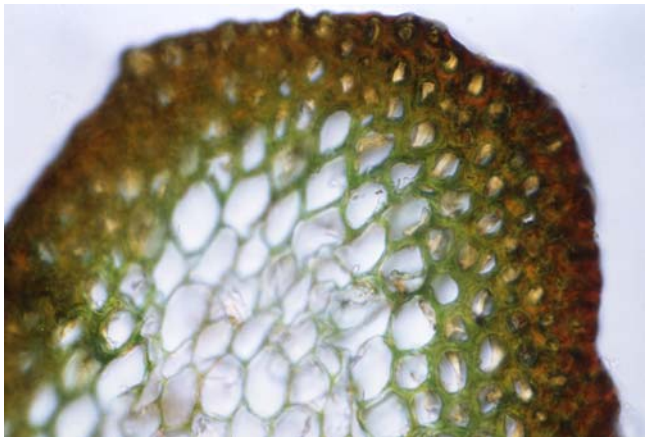


Figure 55. ***Polytrichum*** sp. stem cross section stained with 0.01g per 100 cc **methyl green** for 50 seconds, then stained with 0.3 g per 100 cc **eosin** for 2 hours. Photo courtesy of Isawo Kawai.

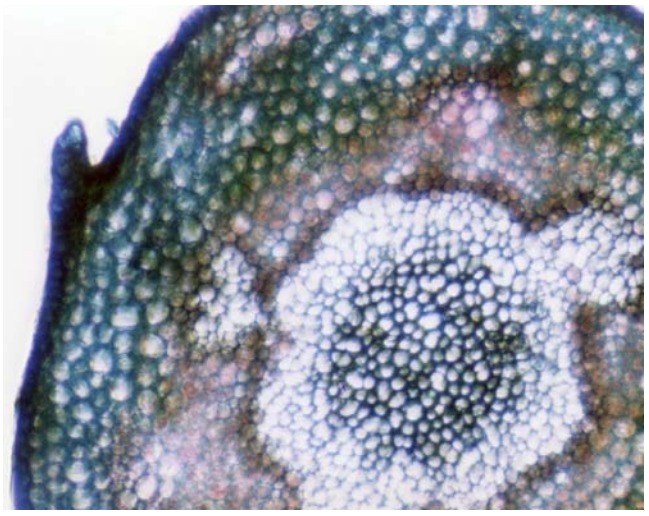


Figure 53. ***Polytrichum*** sp. 10 µm stem cross section stained with 0.01g per 100 cc **methyl green** for 50 seconds, then 0.3 g per 100 cc **eosin** was added for 2 hours, then **washed** with water. Photo courtesy of Isawo Kawai.

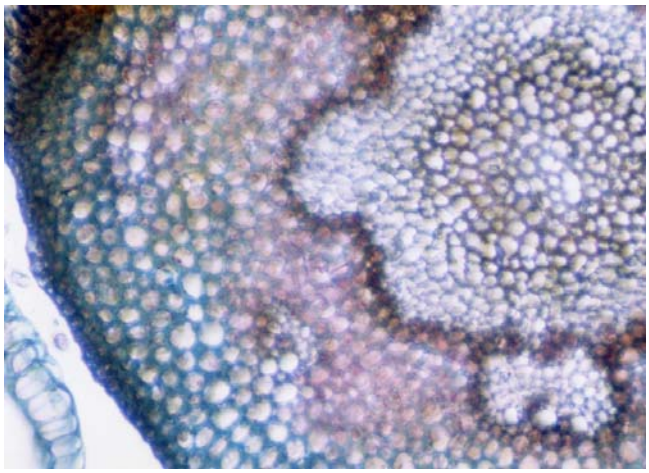


Figure 56. ***Polytrichum*** sp. stem cross section stained with 0.01g per 100 cc **methyl green** for 3 minutes, then stained with **eosin** for 2 hours. Photo courtesy of Isawo Kawai.

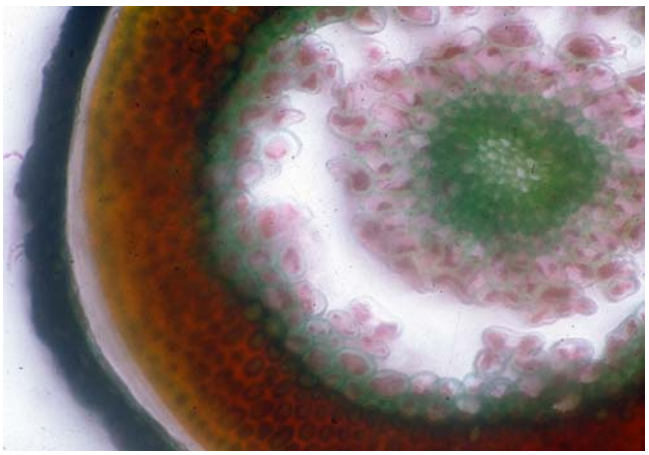


Figure 54. ***Polytrichum*** sp. stem cross section. The cortex cell walls are blue-green from **methyl green**. The hydrome cells are violet-brown. Photo courtesy of Isawo Kawai.

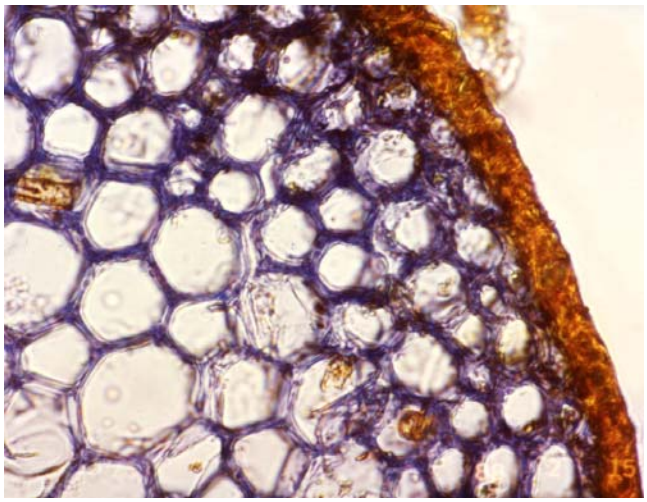


Figure 57. ***Rhizogonium*** sp. stem cross section stained with **aniline blue** for 1 hour. Photo courtesy of Isawo Kawai.

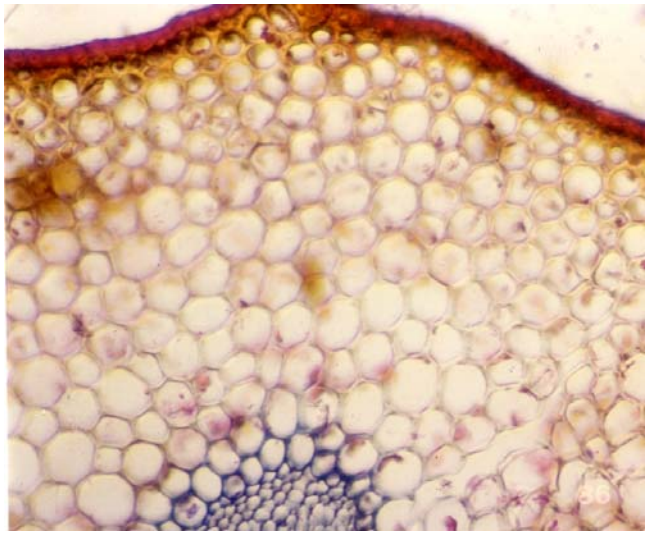


Figure 58. ***Rhizogonium*** sp. stem cross section stained with **aniline blue** + **eosin** for 3 days. Photo courtesy of Isawo Kawai.

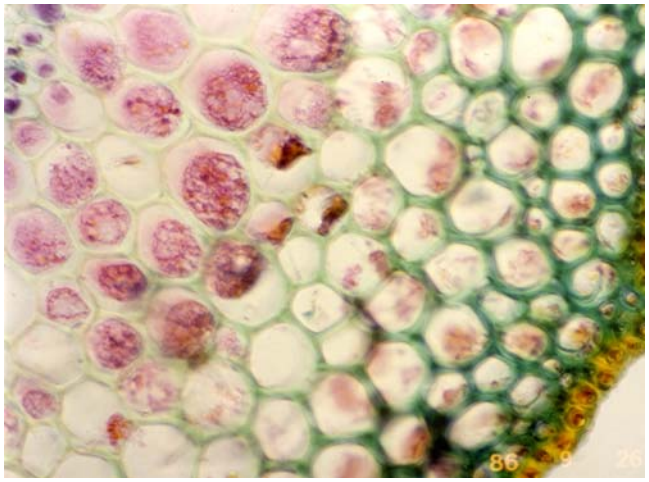


Figure 59. ***Rhizogonium*** sp. stem cross section stained with **aniline blue** + **eosin** for 3 days, washed, stained with **eosin** 3 more days, then stained with **methyl green**. Photo courtesy of Isawo Kawai.

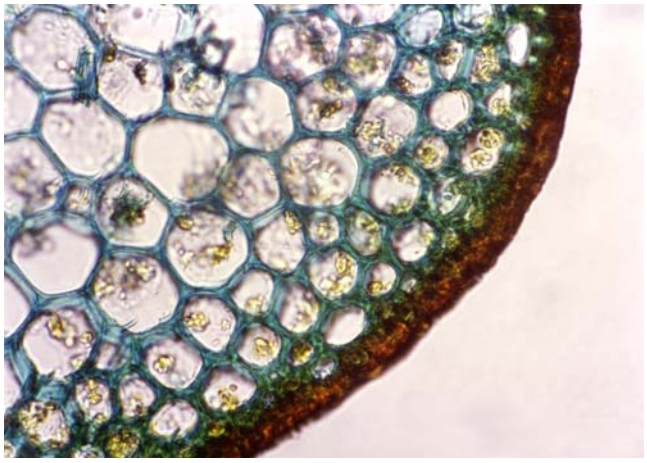


Figure 60. ***Rhizogonium*** sp. stem cross section stained with **eosin** for 2 hours, **washed**, then stained with **methyl green** for 1 minute. Photo courtesy of Isawo Kawai.

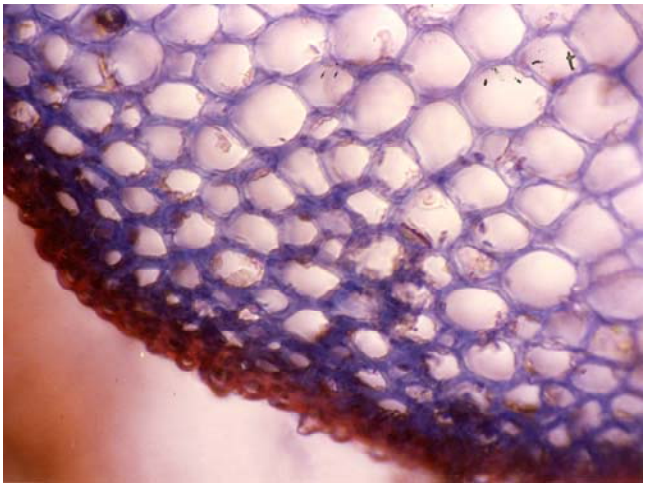


Figure 61. ***Thuidium*** sp. stem cross section stained with **aniline blue** + **eosin** for 2 hours. Photo courtesy of Isawo Kawai.

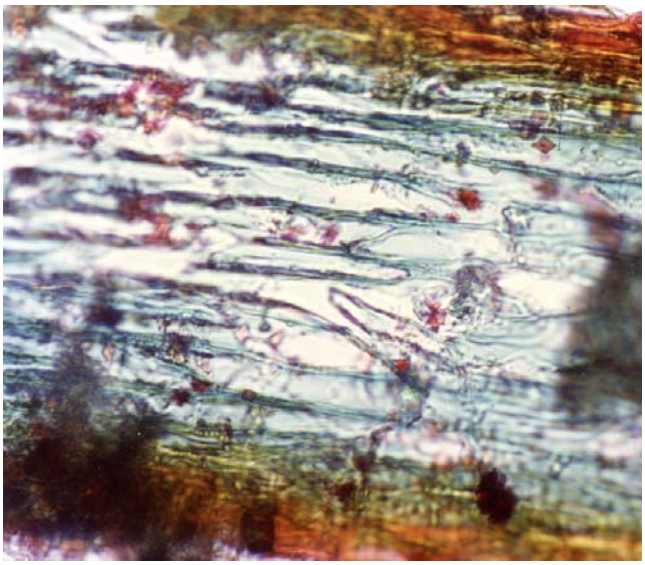


Figure 62. ***Thuidium*** sp. stem longitudinal section stained with **aniline blue** + **eosin** for 2 hours. Photo courtesy of Isawo Kawai.

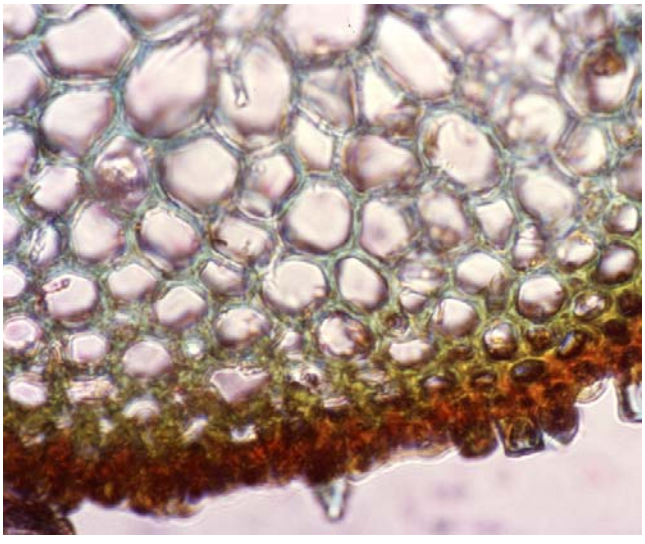


Figure 63. ***Thuidium*** sp. stem cross section stained with **eosin** for 2 hours, washed, then stained with **methyl green** for 1 minute. Photo courtesy of Isawo Kawai.

Acid Fuchsin

Acid fuchsin has been used to stain a variety of plant, animal, and fungal tissues. Kawai (1980b) used **acid fuchsin**, along with **I_2KI** and **gentian violet** to distinguish the internal anatomy of stems in the **Leucobryaceae** (Figure 64). Using 5 µm sections, he was also able to examine the structure in ***Atrichum undulatum*** (Figure 65), ***Bartramia pomiformis*** (Figure 66), ***Dicranum nipponense*** (Figure 67), ***Leucobryum neilgherrense***, and ***Hypnum plumaeforme*** (Figure 68) (Kawai 1981).

Figure 64. ***Leucobryum glaucum***, a genus in which Kawai used acid fuchsin, along with I_2KI and gentian violet to distinguish the internal anatomy of stems. Photo by Janice Glime.

Figure 65. ***Atrichum undulatum*** with capsules, a species in which 5 µm stem sections work well. Photo by Martin Hutten, with permission.

Figure 66. ***Bartramia pomiformis***, a species in which 5 µm stem sections work well. Photo by Ivanov, with permission.

Figure 67. ***Dicranum nipponense*** with capsules, a species in which 5 µm stem sections work well. Photo by Misha Ignatov, with permission.

Figure 68. ***Hypnum plumaeforme***, a species in which 5 µm stem sections work well. Photo by Jan-Peter Frahm, with permission.

Aniline Blue (Kawai & Glime 1988)

Kawai used **aniline blue** to stain several species, including ***Fontinalis*** spp. (Figure 28-Figure 35; pers. comm. 5 July 1988), ***Polytrichum commune*** (Figure 18), and ***Pogonatum contortum*** (Figure 19) (Kawai *et al*. 1985). It stained the epidermal (outermost layers of stem) red and those just inside the red ones were stained blue.

1. Place moss in solution of **aniline blue** and **eosin** for 48 hours. The hydrome cell walls stain violet-brown.
2. After **washing**, place the moss in **eosin** for absorption for 48 hours to stain epidermal cell walls and leptome red.
3. **Wash** again and place moss in solution of **methyl green** for another 48 hours to stain cell walls of cortex blue-green.

Congo Red (Kawai & Glime 1988)

1. Place leafy gametophyte into solution of **gentian violet** and **Congo red** for 48 hours to stain hydrome cell walls violet-brown.
2. **Wash** moss and place in solution of **eosin** for another 48 hours to stain cell walls of epidermis, cytoplasm of leptome, and chloroplasts red.
3. **Wash** again and place moss in solution of **methyl green** for another 48 hours to stain cortex cell walls blue-green.

Eosin

Eosin is a red dye that stains cytoplasm. It is water-soluble and thus can be used to follow water movement through plants. It has been used in the tracheophyte *Arabidopsis* sp. to indicate photodamage to the photosynthetic apparatus (Havaux *et al*. 2000).

Kawai (pers. comm. 8 July 1989) used **eosin** as one of the stains to distinguish cells in ***Fontinalis antipyretica***. This stains the outer cells of the stem ("epidermis") (Figure 27) and the cell walls of the cortex red. **Eosin** likewise stained the cytoplasm of the **leptom** and the chloroplasts red. As noted earlier, this stain works well in most bryophytes to stain cell walls and cytoplasm red.

Fast Green

Fast green is the green dye used in food coloring, but it is known to have tumorogenic effects. It is a protein stain and is one of the stains used by Kawai (1971).

Fuchsin

The dye **fuchsin** is a biological stain that is produced by oxidation of a mixture of **aniline** and **toluidine**, producing a brilliant bluish red. Kawai (1971) used it to stain bryophyte stems.

Gentian Violet (=Crystal Violet)

The color of stain by **gentian violet** depends on the acidity. At *p*H 1.0, the dye is green, but in an alkaline solution it is colorless.

Kawai (1980b) used **gentian violet**, along with **acid fuchsin** and **I_2KI** to distinguish structures within the stems in members of the **Leucobryaceae**.

Janus Green

Janus green is a vital stain that changes color based on the level of oxygen in a cell (Wikipedia 2012). Kawai (pers. comm.) has used it in combination with other stains to stain the **hydrom** of moss stems.

Methyl Green

Isawo Kawai (pers comm. 8 July 1989) used 0.005 g per 100 cc of **methyl green** for 10 seconds to stain cells in 10 µm sections of the stem of ***Fontinalis antipyretica*** (Figure 27). This was followed by **eosin** (0.2 g per 100 cc) added to it. This mix was allowed to stand for 50-60 minutes, then **washed** for observation. **Eosin** stained the outer cells of the stem red and **methyl green** stained those just inside the outermost layers a blue-green color (Figure 27). The central tissue did not stain with this combination.

1. Place leafy moss in solution of **Janus green** and **eosin** for 48 hours to stain hydrome cell walls violet-brown.
2. After **washing**, place moss in solution of **eosin** for further 48 hours to stain cell walls of epidermis, cytoplasm of leptome, and chloroplast red.
3. **Wash** again and place moss in solution of **methyl green** for another 48 hours to stain the cortex cell walls blue-green.

Kawai and coworkers (Kawai *et al*. 1985; Kawai, pers. comm. 5 October 1989) found that the leaf cell walls of ***Polytrichum*** sp. (Figure 54), ***Fissidens*** sp. (Figure 22), and ***Bartramia*** sp. (Figure 66; stained blue-green with **methyl green**, but the cell walls of several species of ***Fontinalis*** (Figure 17) leaves (Kawai, pers. comm. 5 October 1989) would not stain with methyl green.

Leaves

I_2KI – Lugol's Solution (Kruijer & Klazenga 1994)

Kruijer and Klazenga (1994) consider **methylene blue,** a common ***Sphagnum*** (Figure 69) stain (see chapter on *Sphagnum* Staining in this volume), to be somewhat problematic for other leaves, sometimes staining too darkly. Instead, they recommend staining with a diluted solution of **iodine-potassium iodide** (I_2KI), or Lugol's solution (Johansen 1940). This is the well known stain for starch, causing it to turn blue to purple to nearly black. But it can also stain **cellulose** if tissues are first hydrolyzed with sulfuric acid and **hemicellulose** if hydrolyzed with hydrochloric acid. Kruijer and Klazenga used **I_2KI** successfully on leaves and cross sections of members of the **Hypopterygiaceae** (Figure 70) and the genus ***Dicranoloma*** (Figure 71). Cell walls became brighter, but remained nearly colorless except for the middle lamella, which sometimes became bright yellow.

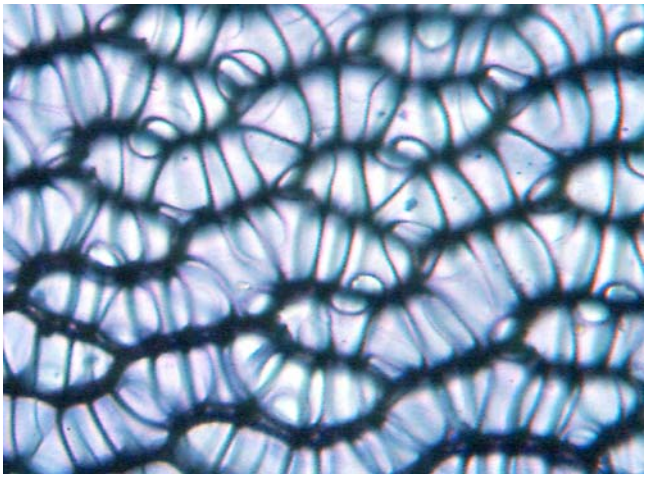


Figure 69. ***Sphagnum*** leaf cells stained with methylene blue to make pores visible. Photo by Janice Glime.

Figure 70. ***Canalohypopterygium filiculaeforme***. Some members of its family (**Hypopterygiaceae**) can be stained with I_2KI. Photo by Jan-Peter Frahm, with permission.

KOH (Zander 1989, 1993)

KOH in concentrations from 2% to saturated will stain cell walls of many mosses. It can be used on whole leaf mounts and on sections. In the **Pottiaceae** the resulting colors can be used as diagnostic characters. Zander (1993) uses it to rehydrate mosses as well. The **KOH** should not be kept in glass dropper bottles because it reacts with the glass to form a precipitate. If the specimen will later be mounted with an acidic mountant, add a drop or two of dilute **HCl** to the specimen.

Figure 71. ***Dicranoloma billardieri***. Some members of its genus can be stained with I_2KI. Photo by Michael Lüth, with permission.

KOH is useful in distinguishing between genera in the **Pottiaceae** (Zander 1993). For example, the lamina color reaction in ***Tortula*** (Figure 72) and ***Ganguleea*** is yellow, whereas in ***Syntrichia*** (Figure 73), ***Dolotortula***, ***Chenia*** (Figure 74), ***Hilpertia*** (Figure 75), ***Sagenotortula*** (Figure 76), ***Stonea***, and ***Hennediella*** (Figure 77) it is red, and in ***Saitobryum*** (Figure 78), deep red (Zander 1989).

Figure 72. ***Tortula intermedia***, in a genus that stains yellow in KOH. Photo by Michael Lüth, with permission.

Figure 73. ***Syntrichia ruralis***, in a genus that stains red in KOH. Photo by Michael Lüth, with permission.

Figure 74. ***Chenia leptophylla*** in arable field, in a genus that stains red in KOH. Photo by Jonathan Sleath, with permission.

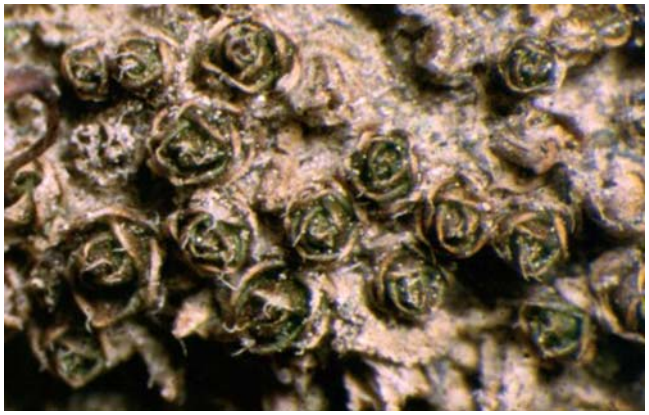


Figure 75. ***Hilpertia velenovskyi***, in a genus that stains red in KOH. Photo by Jan-Peter Frahm, with permission.

Figure 76. ***Sagenotortula quitoensis***, in a genus that stains red in KOH. Photo by Claudio Delgadillo Moya, with permission.

Figure 77. ***Hennediella stanfordensis***, in a genus that stains red in KOH. Photo by Paul Wilson, with permission.

Figure 78. ***Saitobryum peruvianum***, in a genus that stains deep red in KOH. Photo by Claudio Delgadillo Moya, with permission.

Safranin O / Fast Green (Rod Seppelt, Bryonet 15 August 2012)

Rod Seppelt (Bryonet 15 August 2012) considers this a good general stain for plant sections. It works well for bryophytes on specimens that have been fixed and embedded and on sectioned material. Bill and Nancy Malcolm (2006) have used this combination to obtain high-contrast color effects. The technique is somewhat time-consuming, requiring a schedule of dehydration and rehydration. They suggest a quicker option using **toluidine blue**. If it is used simply to clear the cells, then the hydrolyzation step is unnecessary.

Lisa Op den Kamp (Bryonet 4 October 2012) also uses **safranin**. She applies this directly to the leaves or capitula of ***Sphagnum*** (Figure 79), then washes them in water, all before cutting the ***Sphagnum*** to make the desired sections. Safranin normally dyes lignin red; although ***Sphagnum*** doesn't have typical lignin, safranin stains the lignin-like compounds in the tissues. She has kept the solution for 12 years and it still works well.

Figure 79. ***Sphagnum auriculatum*** capitula, not stained. Photo by Jan-Peter Frahm, with permission.

Sphagnum Stains

In particular, ***Sphagnum*** (Figure 69) leaves typically need to be stained for the pores to be visible. Rudi Zielman (Bryonet 4 October 2012) considers there to be four ***Sphagnum*** stains (see Chapter 2b for details):

aniline blue
methylene blue
gentian violet (=crystal violet)
toluidine blue O

These can be applied in two ways: supply a bit of it directly in a few drops of alcohol or water or make a stock solution based on alcohol or water.

To enhance the pores on ***Sphagnum*** (Figure 80) leaves, Rod Seppelt (Bryonet 13 May 2010) suggests **toluidine blue**, **aniline blue**, or **methylene blue**. A drop or two in 100 ml of water should be sufficient. Schofield (1985) recommends **methylene blue**, **gentian violet**, or **crystal violet** in a 1-2% aqueous solution. If the stain is very dark, simply dip the moss in quickly and then rinse it in clear water. If it gets too much stain, you will see even less than with no stain. Be careful – these stains also stain fingers and clothing! If you don't have the standard stains, try experimenting. We wonder if beet juice would work. It might need a bit of vinegar to make it colorfast for permanent mounts.

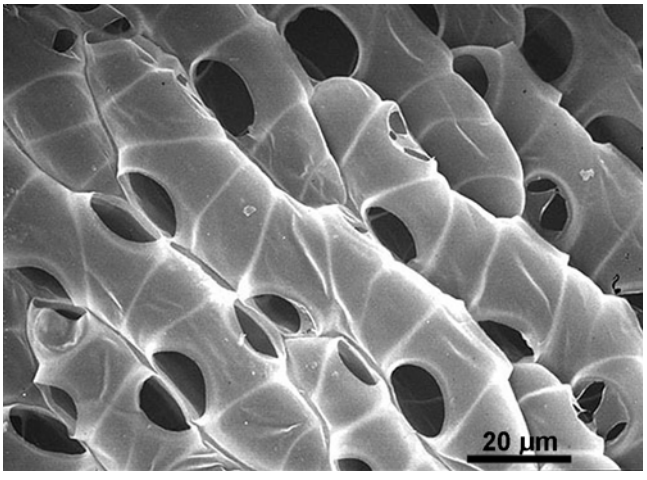


Figure 80. SEM of ***Sphagnum*** hyaline cells and pores. Photo from Botany Website, UBC, with permission.

Methylene Blue (Kruijer & Klazenga 1994; Wagner, Bryonet 11 May 2010)

When staining ***Sphagnum*** (Figure 69) pores, it is important not to stain too heavily. Kruijer and Klazenga (1994) use a 1-2% aqueous solution of **methylene blue**. Or, place a drop of full strength dye on a slide or in a Syracuse watch glass. Dip the ***Sphagnum*** branch quickly into the dye to cover the branch, then dip the branch into clean water to wash the dye off. Don't allow the branch to remain in the dye. After washing, the moss should be ready for viewing.

David Wagner (Bryonet 11 May 2010) brings us a simple solution for staining ***Sphagnum*** (Figure 69), a contribution from one of his students. Since **methylene blue** is used as an antibiotic for aquarium fish for hatching eggs or getting rid of fungal infections, it is readily available at tropical fish stores. A half ounce bottle (ca 12 ml) of VERY concentrated **methylene blue** is only about US $4.25 and will be a lifetime supply.

Crystal Violet/Gentian Violet

Crystal violet, also known as gentian violet or methyl violet 10B, is the compound hexamethyl pararosaniline chloride, or pyoctanin(e), and is a triarylmethane dye.

Adam Hölzer (Bryonet 4 October 2012) reports that he can see even the pores of ***Sphagnum obtusum*** (Figure 81) very well with **crystal violet**. He dissolves some powder in about 50 ml of distilled water with the addition of some alcohol to preserve it. He adds new alcohol occasionally to compensate for evaporation. He puts the moss leaves in a drop of water. Then uses his forceps to dip into the solution and transfer only a small drop into the drop of water. He covers the drop with a cover glass. The color stains the cellulose of the leaves Excess stain can be removed by adding water to one side and drawing off the solution on the other with tissue paper. The 50 ml of solution will last for several years even if you use it every day. Stains on the desk can be cleaned with alcohol.

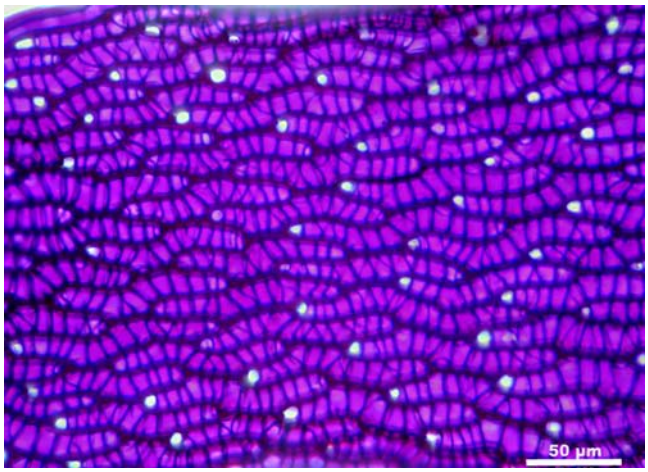


Figure 81. ***Sphagnum obtusum*** stained for pores. Photo by Ralf Wagner.

Crystal violet and gentian violet solutions can be used to fill well-rinsed and dried felt-tip pens (Joannes (Jan) A. Janssens, Bryonet 4 October 2012). These pens can be used in the field to stain ***Sphagnum*** (Figure 81) that has been squeezed somewhat dry.

Toluidine Blue O (Rod Seppelt, Bryonet 15 August 2012)

Rod Seppelt (Bryonet 15 August 2012) considers this to be the most useful stain for general tissue differentiation in fresh material, but it is not useful for permanent mounts. It can help to distinguish the ventral row of leaves in **liverworts**. It also will reveal the pores and stem leaves in ***Sphagnum*** (Figure 81).

Simple method:

0.2%-0.25% toluidine blue O in water (be sure it is O), or 1 drop in 10 drops of water

Stain moss in solution for 10-30 seconds, place on slide, apply cover glass, and examine (without washing excess stain away). If too dark, dilute the stain further before use, or wash the moss quickly to remove some of the excess.

In vascular plants, its multiple color responses can indicate tissue type: phloem green, xylem blue, parenchyma purple, lignified tissue of bundle caps pale whitish-green. Similar color distinctions may occur in bryophytes. Unfortunately, the color is not permanent.

More complex recipe:

0.610 g KH_2PO_4
0.970 g K_2HPO_4
0.050 g Toluidine Blue O
In 100 ml distilled water

Des Callaghan (Bryonet 4 October 2012) likewise recommends Toluidine Blue O and Safranin O for ***Sphagnum*** (Figure 81). Simply dip the branch in the stain and it works almost immediately. You can find the stains on eBay cheaply (*e.g.* items 261098492176 and 261107216623). But he cautions that for non-aqueous permanent mounts, these stains are not suitable. Instead, Bismark Brown provides a nice stain.

Reproductive Structures

Iron Haematoxylon / Fast Green (Rod Seppelt, Bryonet 15 August 2012)

This stain works very well to show archegonia and spermatogenous cells in antheridia (Rod Seppelt, Bryonet 15 August 2012).

Bulbils and Spores

Fluorescence and Fluorescent Dyes (Nordhorn-Richter 1988)

Gisela Nordhorn-Richter (pers. comm.) discovered the fluorescence of bulbils in ***Pohlia*** (Figure 82-Figure 83) when a microscope salesman visited her institution. No one was visiting the display and she felt sorry for the salesman, so she took some of her specimens to look at them. She was amazed at the ease of finding bulbils with the fluorescence technique.

Figure 82. ***Pohlia bulbifera*** with bulbils that can be located by their fluorescence. Photo by Misha Ignatov.

Figure 83. ***Pohlia bulbifera*** bulbils that can be located by their fluorescence. Photo by Des Callaghan, with permission.

Preparation of bryophytes for fluorescence microscopy is mostly what not to do. They can be prepared on a slide with water or as permanent slides (Nordhorn-Richter 1988). However, some of the embedding materials have phenolic compounds as preservatives or may have a synthetic resin. These produce fluorescence that interferes with seeing the bryophyte structures. Air bubbles are another potential problem because they can scatter the light. Dry plants can only be rewet once because the membranes typically are destroyed by drying. When the plants are rewet, water soluble substances leak from the cell. When they dry once again, the water-soluble fluorescing substances disappear, ending fluorescence.

In the dried condition, fluorescing substances of bryophytes are very stable, with rhizoid bulbils (Figure 84) of ***Pohlia*** that are more than 100 years old still exhibiting brilliant fluorescence. Chlorophyll, on the other hand, loses its fluorescent ability upon drying.

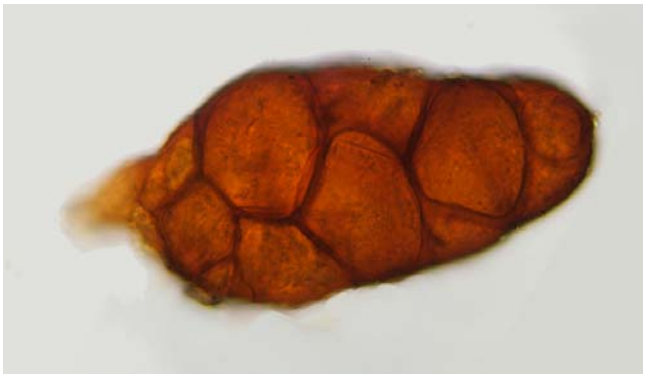


Figure 84. ***Pohlia wilsonii*** rhizoidal tubers. Photo by Guillermo M. Suárez, with permission.

To hide the fluorescence of chlorophyll, which can interfere with fluorescence of other substances, a suppression filter of 650 nm can absorb its red fluorescence (Nordhorn-Richter 1984a, b, 1985a, b, 1988). Alternatively, the chlorophyll can be extracted by 80% acetone or DMSO without interfering with other fluorescent substances.

The fluorescence technique for bryophytes permits one to find rhizoid gemmae hiding in a sandy substrate (Nordhorn-Richter 1988). Live spores exhibit red fluorescence, permitting estimation of vitality that can be quantified with a fluorescence spectrophotometer (Figure 85; Ridgway & Larson 1966; Paolillo & Kass 1973; Genkel & Shelamova 1981). Phenolic acids, including ***Sphagnum*** acid (Tutschek 1975), lignin-like compounds in cell walls (Lal & Chauhan 1982; Nordhorn-Richter 1984a, 1985), peristome structure (Nordhorn-Richter 1985b), and papillae (Nordhorn-Richter 1984b) become visible. Even small bryophytes can be found by using a UV light (366 nm) at night! (Nordhorn-Richter 1983). Gambardella *et al*. (1993) used fluorescence microscopy to examine the cytoskeleton of the columella in ***Timmiella barbuloides*** (Figure 86). Animal tissues exhibit only secondary fluorescence, making it possible to distinguish between animal galls and bryophyte propagules (Nordhorn-Richter 1988).

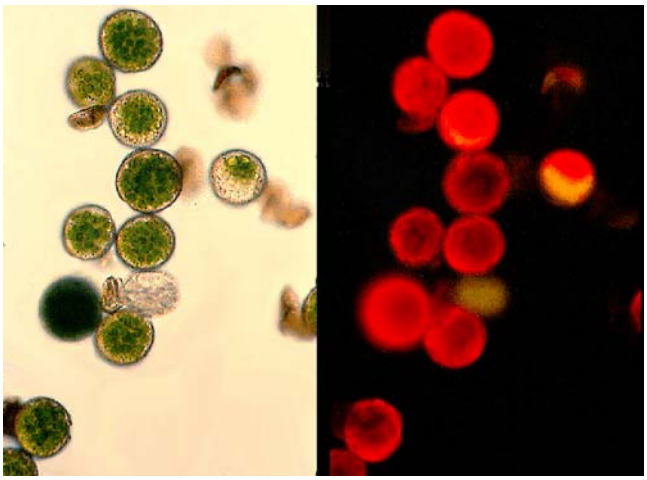


Figure 85. Spores of ***Fontinalis squamosa*** showing spores in white light on left and fluorescing under UV light on right. Note that the living spores show up as red under fluorescence, whereas dying and dead spores are yellow or invisible. Photos by Janice Glime.

Figure 86. ***Timmiella barbuloides***, the species used by Gambardella and coworkers to examine the cytoskeleton with fluorescence. Photo by Jonathan Sleath, with permission.

Shellhorn *et al*. (1964) demonstrated that both fresh and fossil pollen could be detected with **fluorochromes**, with better results if **acridine orange** was added to enhance detail. Ridgway and Larson (1966) extended the fluorescence technique to provide better viewing of the features of the hornwort ***Anthoceros*** (Figure 87). The images of spores of ***Fontinalis squamosa*** demonstrate that the use of fluorescence microscopy can help to distinguish living from dead spores in mosses (Figure 85). The yellow fluorescence in the image suggests that the exine is fluorescing, as it does in pollen (Ridgway & Larson 1966).

Figure 87. ***Anthoceros agrestis***, a hornwort in which fluorescence microscopy helps to reveal its structures. Photo by Bernd H through Creative Commons.

Stains can provide one with the ability to see structures using fluorescence microscopy. Brandes (1967) explained the use of **acridine orange** as a vital stain for use with fluorescence microscopy of protonemal pro-buds and buds. The stain moves to the cytoplasm, combining with the RNA. This technique shows the increase of cytoplasmic RNA immediately after the induction of the pro-buds. Hence, kinetin-induced buds, as well as non-induced branches, can be detected ten hours after the beginning of a kinetin treatment.

Fluorescent dyes can have various purposes, including using them as growth markers in the field (Russell 1988). **Fluorochrome** 3,3'Dihexyloxacarbocyanine iodine [$DiOC_6(3)$] can be used to locate selectively the fungal hyphae among the rhizoids of bryophytes (Duckett & Read 1991). Ascomycetous hyphae are visible when concentrations of 0.01-5 µg ml^{-1} are used, whereas to see Basidiomycetes that form endophytic associations, the concentration needs to be at least 50 µg ml^{-1}. Some fungi, such as VA fungi in liverworts, do not stain with **fluorochrome** at any concentration. Others require a much lower concentration than these. One advantage to this method is to recognize the extent of the fungal hyphae in the association.

Staining Liverwort Capsules (Von Konrat *et al*. 1999)

Von Konrat *et al*. (1999) devised a technique to examine the multiple layers of the capsule wall of liverworts. First the layers need to be separated using a **pectinase** preparation. Then the layers need to be cleared and stained to make the details easier to see.

They recommended doing all the treatments on the same slide – results were less satisfactory when the specimen was moved from one reagent to another. Solutions can be removed between treatments by using filter paper cut into strips. The capsule was mounted on a coverslip and the fully stained capsule was mounted between two coverslips so that both surfaces could be examined.

1. Treat with FAA for 24 hours or until decolored

FAA (Formalin-Acetic-Alcohol)	**(100 ml)**
Ethyl alcohol	50 ml
Glacial acetic acid	5 ml
Formaldehyde (37-40%)	10 ml
Distilled H_2O	35 ml

2. **Rinse** in water three times.
3. Clear partially with 80% **lactic acid** at 60°C for 30-60 minutes in container saturated with water vapor.
4. **Wash** again at least three times in water.
5. Add enough 1% (v/v) **pectinase** preparation of *Aspergillus niger* in water to cover specimen. Let stand for a maximum of 1 hour at 37°C with slide in container saturated with water vapor.

   Catalog # P-9179
   Sigma Chemical Co.
   St. Louis, MO, USA

6. At this stage, you should be able to find the cell layers separated or at least tissue fragments from internal layer separated from the epidermal layer, permitting adequate comparisons. Longer digestion causes digestion of the tissue and thus digestion should stop after 1 hour even if tissues are not separated.
7. **Rinse** with water three times.
8. Add 1 drop of water and 3.5% **sodium hypochlorite** (household bleach) for 30-120 sec or until capsule becomes nearly transparent. (Monitor under dissecting microscope.)
9. **Rinse** with water three times for 30-60 sec each time.
10. Add **dye** for 60-120 seconds, depending on dye (see Table 1 below).
11. **Rinse** again for 60 sec in water.
12. Examine capsules in water or **glycerol**. Water can cause surface tension problems and material may scatter, making glycerol preferable (Zander 1997).
13. If necessary, gentle tapping or squashing with a pair of fine forceps may help to separate the internal layer.
14. Mountants may include **Aqueous Mountant** or **glycerol** in **glycerin jelly** (Zander 1997). Hoyer's solution is not suitable because the dye will fade.

Table 1. Von Konrat *et al*. (1999) tested coloration methods on the cell walls of the leafy liverwort ***Frullania***.

	Internal Layer		Epidermal Layer	
Stain	Cell walls	Thickening	Cell walls	Thickening
Alcian blue (0.02% w/v in water)	blue +	blue ++	blue +	blue ++
Autofluorescence	blue +	 –	blue +	 –
Bismark brown Y (1.0% w/v in 5% w/v aqueous phenol soln)	orange/brown +	orange/brown +	orange/brown +	orange/brown +
Calcofluor white (0.01% w/v in water)	blue +	 –	blue +	 –
Methylene blue (0.05% w/v in water)	blue +	blue +	blue +	blue +
p–Nitrobenzenediazonium tetrafluoroborate (0.5% w/v in 0.1 M sodium phosphate buffer pH 7.0 for 10 min at 4°C)	 –	orange +	 –	orange +
Ruthenium red (0.02% w/v in 1% w/v aqueous soln ammonium acetate)	 –	red ++	 –	red ++
Toluidine blue O (0.05% w/v on sodium benzoate buffer pH 4.4)	 –	pink–purple +	 –	pink–purple +
Nile blue A (0.01% in water)	–	–	–	–
Phloroglucinol-HCl (1 ml 2% w/v in 95% v/v aqueous ethanol + 2 ml 10M HCl	–	–	–	–
Sudan red 7B (0.1% w/v in 50% v/v polyethylene glycol + 45% v/v glycerol + 5% v/v water)	–	–	–	–

Figure 88. ***Frullania tamarisci***, in a genus that exhibits a variety of cell wall colors in various solutions (Table 1). Photo by Tim Waters, through Creative Commons.

*p*H Testing (Zander 1980; Long 1982)

Lichenologists are quite familiar with testing *p*H reactions, but this technique has not been widely used on bryophytes. Zander (1980) used *p*H responses (acid-base color reactions) to separate ***Triquetrella californica*** (Figure 89) from ***Barbula fallax* var. *reflexa*** (Figure 90) and to remove ***Bryoerythrophyllum calcareum*** and ***B. inaequalifolium*** (Figure 91) from the genus ***Barbula***. Long (1982) similarly tested four species of **Pottiaceae** and was able to distinguish them on the basis of color change. He used concentrated **HCl**, 10% **KOH**, **concentrated nitric acid**, and 2:1 concentrated $\mathbf{H_2SO_4}$, obtaining, respectively, the following results:

Bryoerythrophyllum wallichii (Figure 92) – pale brown, red-brown, red-brown, dark red-brown
Bryoerythrophyllum caledonicum (Figure 93) – pale greenish-brown, red-brown, red-brown, dark red-brown

Leptodontium flexifolium (Figure 94) – green, orange, red, brown & green
Chionoloma recurvifolium (syn. = ***Bryoerythrophyllum recurvifolium***; Figure 95) – green, orange, red, dark brownish-green

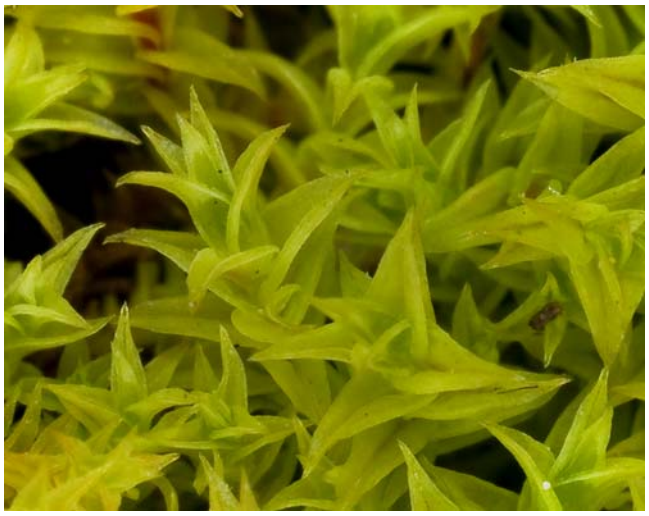


Figure 89. ***Triquetrella californica***, a species for which *p*H reactions help in identification. Photo by John Game, with permission.

Figure 90. ***Barbula fallax*** var. ***reflexa***, a species that can be separated from ***Triquetrella californica*** based on its reaction to *p*H changes. Photo by David T. Holyoak, with permission.

Figure 91. ***Bryoerythrophyllum inaequalifolium***, a species separated from ***Barbula*** by its *p*H reaction. Photo by Jonathan Sleath, with permission.

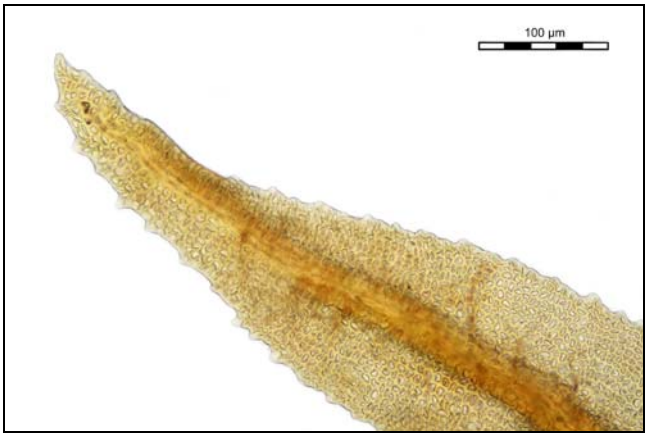


Figure 92. ***Bryoerythrophyllum wallichii*** leaf cells, a species that changes color ranging from pale brown to dark red-brown in response to decreasing *p*H. Photo from Trustees of the Natural history Museum, London, through Creative Commons.

Figure 93. ***Bryoerythrophyllum caledonicum***, a species that ranges from pale greenish brown to dark red-brown in response to changes in *p*H. Photo by Rory Hodd, with permission.

Figure 94. ***Leptodontium flexifolium***, a species that may be green, orange, red, or brown, depending on the *p*H. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 95. ***Chionoloma recurvirostrum***, a species that exhibits colors of green, orange, red, dark brownish-green, depending on the *p*H. Photo by Michael Lüth, with permission.

Weak Alkali (Lane 1978)

Lane (1978) used a saturated solution of sodium bicarbonate (Hill 1976) in distilled water (weak alkali, final *p*H ~10) to effect color change in red-pigmented ***Sphagnum***. The branches or capitula were flooded by pipette, then permitted to stand for 1-2 minutes (Lane 1978). He then permitted the flooded branches to dry overnight, compared them to known specimens again, and flooded them with a weak acid (*e.g.* vinegar) of *p*H ~3 to check for color change reversibility. Of the 17 species tested, Lane found that there was no color change in subgenera ***Rigida***, ***Subsecunda***, or ***Cuspidata***, although ***Subsecunda*** became redder. ***Sphagnum magellanicum*** (subgenus ***Sphagnum***; Figure 96-Figure 97) became dark brown-black. ***Sphagnum wulfianum*** (subgenus ***Polyclada***; Figure 98) became chocolate brown. The nine species in subgenus ***Acutifolia*** all turned blue or dark blue. The test works equally well on fresh, freshly dried, and herbarium material.

Figure 96. ***Sphagnum magellanicum*** showing normal color variant. Photo by Michael Lüth, with permission.

Figure 97. ***Sphagnum magellanicum***, showing normal color variation compared to that in Figure 96. Photo by Jan-Peter Frahm, with permission.

Figure 98. ***Sphagnum wulfianum***, a species that turns chocolate brown at *p*H 10. Photo by Rob Routledge, through Creative Commons.

Cleaning Up Stains

Spilled stains are hard to remove. David Wagner's experience testing kitchen cleaning agents for removing stains from floors or bench tops has found "Bar Keepers Friend"™ with oxalic acid is better than most.

Leaf Removal and Making Slides

For identification, cells, margins, costa, and insertion of leaves must be seen clearly. In some cases, especially leafy liverworts, these can be seen by making a slide of the branch or stem intact. But for most mosses, it is too difficult to see everything that is needed. Removing a leaf from a moss is usually a necessity to attain this clarity. It is advisable to mount a number of leaves when leaf and cell characters need to be examined. These will represent various surfaces and positions, and greater numbers of leaves will usually provide more specimens with no interfering air bubbles.

There are a number of publications on preparing slides for viewing bryophytes (Murray 1926). I have extracted from these what works for me:

1. First **moisten the moss** by placing it in a beaker of water.
2. Place a stem on a glass slide and **strip the leaves** by pulling them downward from the tip with a pair of

microforceps while holding the tip of the branch or stem with another pair of forceps. Alternatively, you can run the convex side of a pair of curved microforceps down the stem to break off leaves. Some bryologists remove leaves by running a dissecting needle down the stem while holding the tip with forceps on a glass slide. Still others (Lucas 2009) use a spear point to run down the stem to remove leaves. Lucas points out that the spear tip tends to leave other structures such as paraphyllia on the stem where they are more easily observed.

3. **Remove most of the branches** from the portion of the stem you will observe on the slide (Lucas 2009) so that the coverslip can flatten the stem better for easier viewing. But you will also need to compare branch and stem leaves, which differ in some species.
4. Put a **drop** of water on the leaves and/or stems and spread them out so some are dorsal and others ventral in position.
5. Hold the **coverslip** by its edges and lower one side of the coverslip gently with a needle or forceps to avoid trapping air bubbles (Figure 99). If you drop the coverslip straight down, there will be no chance for bubbles to escape. If the stem is bulky and the leaves small, you might want to put them on separate slides.

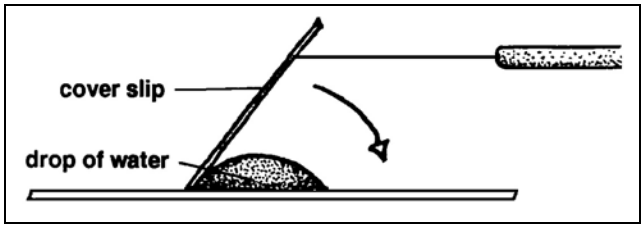


Figure 99. Technique for making a slide with minimal air bubbles. Drawing by Janice Glime.

6. If the coverslip is **floating**, remove some of the water by touching a paper towel edge to one coverslip edge. If there is **not enough water**, add water to the edge of the coverslip with a dropper. This should be added where there is adequate water at the edge to avoid trapping air as the water enters. Too much water will allow your images to move about and wiggle, making examination difficult. Too little will cause the water to draw around the specimen and cause distortions of the light.
7. Examine with the **compound microscope**. The magnification depends on the size of the specimen and what you are trying to see. It is usually best to locate the specimen and focus on 40X or 100X, then move to 400X when more detail is needed.
8. To see papillae, decurrencies, projecting costa tips, and perhaps other surface features, you need to see the leaf in side view, so it is best to observe the leaves that remain on the stem for these features. Most other features are best seen on detached leaves that are more or less flattened by the coverslip. Look around and observe several of the leaves.

Ken Kellman (pers. comm. 5 June 2015) provided me with an alternative method:

1. Etch the collection number onto a clean glass slide. I use a carbide scribe for this. I can't tell you how many times I have gotten confused about what specimen I am looking at before I started doing this.
2. First soak and dissect in a drop of water, then drop 10% glycerol onto the water drop.
3. Set that overnight to evaporate. This leaves the plants moist with most of the water gone.
4. Arrange the specimen and add a small amount of the glycerine jelly. Estimating the amount is very difficult, but you want the jelly to migrate at least to all corners of the cover slip. Too much just makes a mess. Ideally, end up with a small 5mm x 5mm x 1mm thick square.
5. Heat on a hot plate and take it off as soon as the jelly has melted.
6. Put the coverslip on and press it down to make sure the jelly goes out to the perimeter of the slip.
7. Let it cool with a weight on it. (Nuts from nuts and bolts work well).
8. After cooling, scrape the exuded jelly around the edge of the coverslip and use q-tips (cotton swabs) to wipe the perimeter of the coverslip. This has to be clean for the nail polish **lutant** (sealer) to stick. It often takes several wipes. You have to be a little careful as you don't want to keep smearing the jelly that is under the coverslip onto your slide. Keeping the q-tip wrung out helps, also continually changing the q-tip prevents smearing what is on the q-tip from previous wipes.
9. When finally clean, let the slide dry and put a coat of clear nail polish on.
10. Let that dry and put a second coat on so that the nail polish gets just over the top of the coverslip. Note that it is impossible to make this "pretty and neat." The seal is very important since it prevents (or at least drastically slows) the jelly from drying up.
11. Write a stick-on label and store it horizontally in a slide box. The etched number also helps if the label dries up and falls off, you always know what specimen the slide came from.

Avoiding Air Bubbles

Because of the small spaces among the leaves, bryophyte shoots often trap air bubbles that distort the image and make photographs less pleasing. These are hard to coax out. Sometimes it is effective to bounce the coverslip up and down with a dissecting needle or forceps.

Rod Seppelt (Bryonet September 2017) uses a mild vacuum pump attached to a water faucet to extract the air from the tissues. This is made with a Büchner funnel with a rubber bung in the top and. A Tyson of thick rubber tube is attached to the side vent of the funnel on one end and to the side vent of the faucet on the other. When the faucet is turned on, it creates a weak vacuum as it passes the side vent. The plants are put in water in the flask for this weak vacuum to remove the air. A piece of glass tubing is passed through the bung. The vacuum is controlled by the water speed through the faucet and by applying pressure with your fingers on the tube.

Anne Mills (Bryonet September 2017) reports that Bill Buck keeps a beaker full of hot water for dipping moss shoots. The added heat causes the bubbles to dissipate. The same can be accomplished by flaming a prepared slide quickly. Flaming is faster with the coverslip on, but it will sometimes break the coverslip (Dave Kofranek, Bryonet 12 April 2021).

Bubbles often get trapped in the medium when the coverslip is applied. This is especially a problem when the coverslip is dropped straight down. Most of the bubbles can be avoided by using a dissecting needle or fine forceps. With one edge of the coverslip in contact with the slide, use the needle or forceps to slowly lower one edge of the coverslip until it is entirely in contact with the water.

We need to consider a special problem with liverworts. Oil bodies in their cells are especially important in recognizing species of liverworts (David Wagner, Marc Favreau, Bryonet 12 April 2021). However, they are typically absent in dried material in the herbarium. In cases of herbarium material, wetting with hot water or using a wetting agent like Pohlstoffe or detergent that reduces surface tension is useful for combating the bubbles. The advantage of hot water is that it not only has a reduced surface tension, the heating has driven off dissolved gasses so bubbles in the mount will be dissolved. **But** all methods that use reduced surface tension for wetting are hard on liverworts. Fresh, living specimens are necessary for good photographic documentation of oil body character. These should be mounted directly in water. Stacking photography helps to visualize the oil bodies. (See Liverworts and Oil Bodies below.)

Chris Cargill (Bryonet 14 April 2021) found that heating a slide and specimen in water by using a match beneath the slide worked "perfectly" to remove air bubbles in air cavities in fresh sections of ***Ricciella***-type ***Riccia*** plants.

David Wagner (Bryonet 12 April 2021) found that best practice is to submerge the specimen in water, cover, and set aside in a small Petri dish overnight. Squirt each shoot vigorously before the plunge. The swishing helps but he thinks the overnight submersion results in the gas bubbles dissolving in the water. It is not always perfect but usually helps a lot.

Sectioning

Sectioning bryophytes is typically a hit or miss endeavor. For this reason, it is prudent to make a lot of sections (at least 10) so that at least some are likely to show what you need. If you need to see a cross section, the sections need to be thin enough for them to rest on their sides.

It seems that bryologists have developed a number of methods for sectioning bryophytes (*e.g.* Singh 1942; Foster 1977; Nishimura 1997). Nevertheless, Sean Edwards (Bryonet 30 July 2002) points out that bryologists have tended to avoid cutting sections of moss leaves for several reasons:

1. Microtome sectioning involves some considerable delay owing to the various preparations required (moreover, microtomes are often not available, especially to amateurs, when needed).
2. Pith sectioning is unsatisfactory because of the difficulty in controlling section thickness, and in separating the pith debris without damaging the sections.
3. In both microtome and pith sectioning it is almost impossible to be certain of the exact part of the leaf from which the sections were taken.
4. In both methods of sectioning, considerable care and time are needed to maintain a suitable cutting edge.

Nevertheless, there are several methods used by bryologists for making sections of stems and leaves (*e.g.* Singh 1942; Frolich 1984; Nishimura 1997). One is to place the stem with leaves on a dry glass slide and chop, like cutting parsley! The idea is that with lots of cuts, some of them will yield a usable section.

Razor Blades

Razor blades are the standard tool for cutting sections. Hutchinson (1954) recommends use of a normal (double-edged) razor blade that is divided into four sections. The blade should be placed between pieces of blotting paper and broken down the center the long way. Each of these pieces is broken again perpendicular to the previous break. She found she could use used blades because only the sharp points are needed. The blades can even be broken again when the points become dull.

Zander (2022) recommends using sharper razor blades – thin blades cut from very hard steel with a narrow bevel on each side. Triple cut bevels are more like a rounded edge and do not cut as well. Comparisons are available on the Refined Shave website <https://www.refinedshave.com/razor-blade-sharpness-summary/>. Smith (1980) claims that double-edge blades give better results than single-edge blades for free-hand sectioning, recommending those of the Feather brand.

Cutting Techniques

In the many techniques that create sections, placement of the sections is important. Once the specimen sections are in a drop of water on the slide, Hutchinson (1954) recommends stirring the water to distribute the specimens, while looking through the eyepiece of a dissecting microscope. Be sure the water is not sufficient to exceed the area of the coverslip when it is applied or you will use the smallest, hence the best, specimens. As the slide begins to dry, add 5% glycerine at the edge of the coverslip. If the best specimens need to be moved to another slide, you can use a dental applicator (Figure 100) dipped in a 5% solution of glycerine. When placed over the desired section, this combination will lift it up. The applicator can be dipped into a drop of the same solution on the new slide and the section shaken off.

Figure 100. Dental Disposable Micro-Applicators. White is superfine, yellow is fine. Photo modified from AliExpress.

Hepenstrick (2018) describes a method using a magnet to secure the slide (Figure 101). A second slide is placed across it to provide a guide for cutting (Figure 102). An instructional video is available at < https://doi.org/10.6084/m9.figshare.4781254.v1>. Beginning students who tried the magnet method agreed that it was better than the dissecting microscope with a razor blade, as seen in Figure 103.

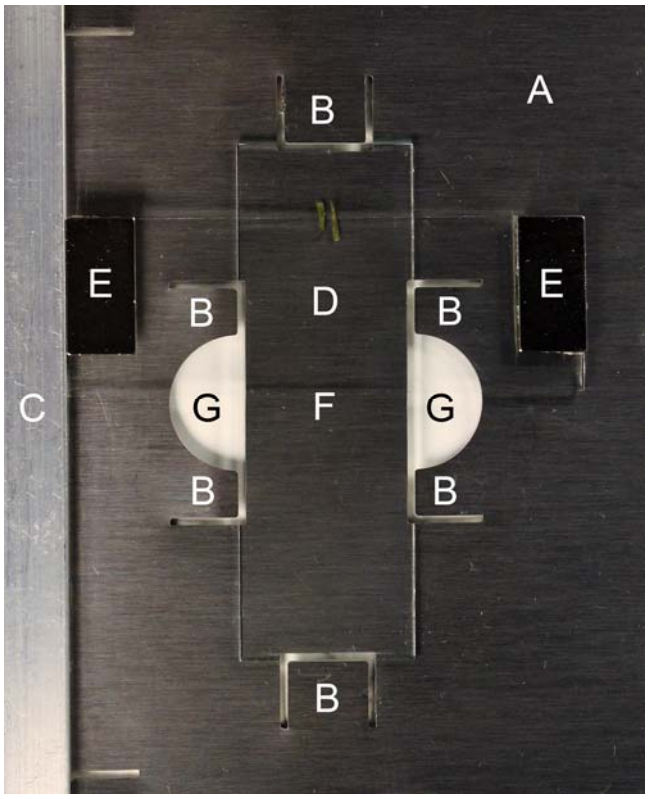


Figure 101. A magnetic sectioning aid with fixed ***Polytrichum*** leaves ready for sectioning. The support plate (**A**) is a magnetic, rust-free steel sheet with laser cut tongues (**B**) which are slightly bent upwards, and a non-magnetic strip (**C**) which helps to align the magnetic slide (**D**) with its attached neodymium magnets (**E**) centrally on the lower slide (**F**) in order to fix the specimen for sectioning. Sections can be cut under a dissecting microscope with a razor blade that is guided with both hands. The semicircle slots (**G**) help to place and grasp the lower slide. Photo courtesy of Daniel Hepenstrick.

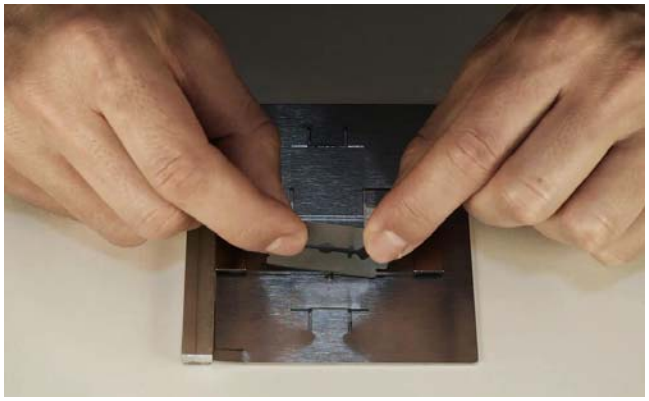


Figure 102. Sectioning with razor blade and magnetic slide holder. Photo courtesy of Daniel Hepenstrick.

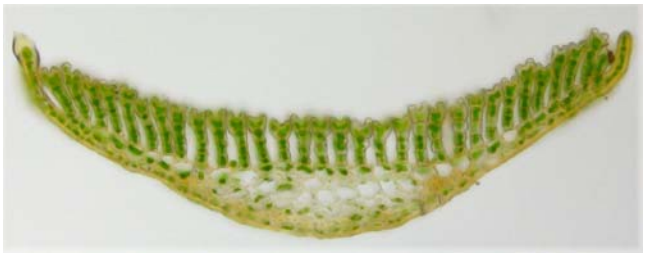


Figure 103. ***Polytrichum commune*** section cut with magnetic holder. Photo courtesy of Daniel Hepenstrick.

Wax Mounts (Taylor 1957)

Taylor (1957) found a different solution to positioning leaves and stems for cutting. He first coats them with water-soluble wax. These include Carbowax and some kinds of crayons.

Taylor makes two solutions: **Solution A** is 20% aqueous polyethylene glycol 600 with a small quantity of Quaternary amine disinfectant to prevent development of fungi in permanent mounts. **Solution B** consists of polyethylene glycols 1540 and 4000, which can be used alone or in combination. However, 1540 alone may be too soft, and 4000 too crumbly.

1. Place solution B on a slide and melt.
2. Place a piece of stem in molten drop to cover stem. The drop needs to be thick enough to support the blade during cutting.
3. Cool wax for ~1 minute with slide on cool metal surface.
4. Use quarter of razor blade to trim drop at one end to point where sectioning is to start, keeping blade vertical and at right angle to stem.
5. Keep sharp corner of cutting edge on slide with cutting edge slanting upward toward you. This keeps cutting edge sharp.
6. Move blade sideways against squared end of drop, making thinnest section possible while watching through dissecting microscope.
7. If leaves curl, soak in solution A at room temperature until solution reaches consistency of glycerin.
8. Remove leaves and touch to filter paper to remove excess liquid.
9. Transfer blotted moss to molten B and proceed from #1.
10. Transfer cut sections with adhering wax to water with small amount of wetting agent if need to keep from floating. Taylor prefers enough water to cover bottom of Syracuse watch glass.
11. Sections can be transferred by tapping slide on rim of watch glass.
12. Polyethylene glycol is not compatible with gelatin, so sections should stay in water until wax completely dissolves – a few minutes in warm water.
13. Remove sections and put in dilute glycerin onto slide.

Cutting Block (Flowers 1956)

Flowers (1956) used a 2x2x15 cm cutting block made of soft wood. She then made a jellyroll arrangement of the bryophyte in tracing paper (a thin paper):

1. Put bryophyte in boiling water to relax it and select several good, clean shoots.
2. Remove excess water by pressing the bryophyte gently between absorbent paper towels or blotters.
3. Roll a 5-10 x 30-40 mm strips of hard-surfaced, thin transparent tracing paper (such as that used by architects) lengthwise into a tight scroll. The size depends on the size of the strips. Open the roll and place the bryophyte shoots longitudinally into the first coil of the roll, using fine curved forceps.
4. Carefully roll the shoots up in the strip, using thumbs and index fingers of both hands.
5. Hold this roll up to the light to locate the upper ends of the shoots and grasp the roll just above the shoot tip with a pair of forceps.
6. Lay a strip of good quality, smooth, white cardboard (10x40 mm) parallel with the proximal edge of the cutting block.
7. Place the bryophyte roll longitudinally upon the white paper near the proximal edge, holding it down with the left index fingernail at the shoot apex.
8. Using a sharp safety razor blade, cut off the anterior portion of the paper roll and discard.
9. Begin cutting sections of stems and leaves through the tracing paper, using your fingernail as a guide. After each cut, move the blade back slightly before making the next cut.
10. As sections are cut, dip the razor blade in a drop of water on a glass slide to remove the sections.
11. Remove the sections of tracing paper from among the leaves, adding a few drops of water to facilitate the removal.
12. Excess water can be removed by holding the slide over an alcohol lamp, leaving only a thin layer.
13. Large leaves like those of ***Polytrichum*** (Figure 18) can be treated in the same way as the stems.

Pith Sandwich Cutting Tool (Trotter 1955)

1. Cut a piece of pith from common elder (*Sambucus niger*) 3-4 cm long x 1 cm wide. Make sure ends are cut clean to make a cylinder.
2. Cut cleanly as possible with sharp safety razor blade down the middle to avoid fraying.
3. Put drop of water on clean slide.
4. Lay half of pith on convex side.
5. Place **dry** specimen at end on flat side, slightly extended beyond pith.
6. Make a sandwich by placing other half of pith flat side onto the first flat side of pith, being careful to align edges.
7. Hold sandwich firmly and dip end with moss into water.
8. Place sandwich onto a glass slide without losing grip and make a first cut close to end that holds moss, using sharp, clean safety razor blade, and discard that cut.
9. Dip to wet end of sandwich again.
10. Press firmly down on the pith above the specimen and cut first section as thinly as possible **next to** the end of the pith, taking care not to cut the pith. You may want to do this while watching through a dissecting microscope.
11. After making several cuts, use razor blade or dissecting needle to move cut sections to opposite end of slide and into drop of water or wetting agent.
12. Repeat until you have enough sections.
13. Place coverslip onto cut sections and water.
14. Add extra water at edge of coverslip if needed.
15. To examine, close down the diaphragm that controls the light and examine on low power (40X total).

A modification of this method uses a razorblade instead of a slide on top (Figure 104). This is thinner and makes it easier to work with the bryophyte specimen.

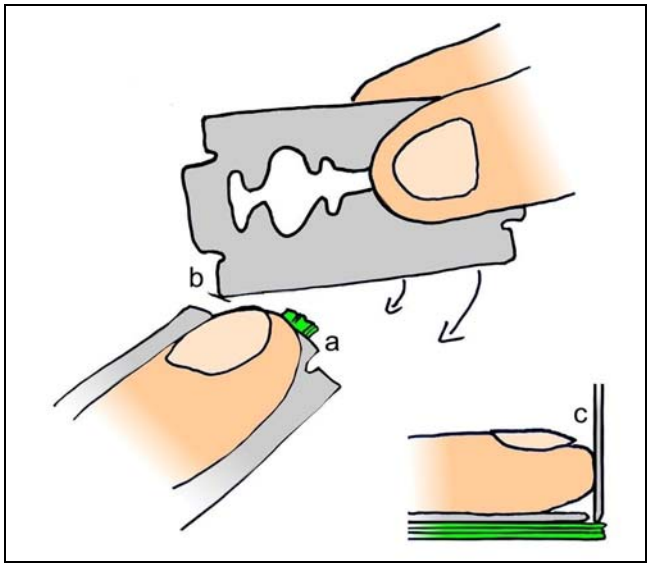


Figure 104. Lüth leaf sectioning. The bryophyte is green, shown at **a** and in the side view at **c**. The cutting position of the double-edge razor blade is at **b**. Photo courtesy of Steve Rae.

Note that sections that are visible to the naked eye are probably too thick to be useful. Note also that stems with oblique leaves, like those of ***Fissidens*** (Figure 22), may have to be placed with stems in an oblique position so that leaves are perpendicular to the cutting edge. Furthermore, plants with very brittle cells, like ***Rhabdoweisia*** (Figure 105), may make it difficult to get good sections.

Figure 105. ***Rhabdoweisia crispata***, a short species with brittle cell walls. Photo by Amelia Merced, with permission.

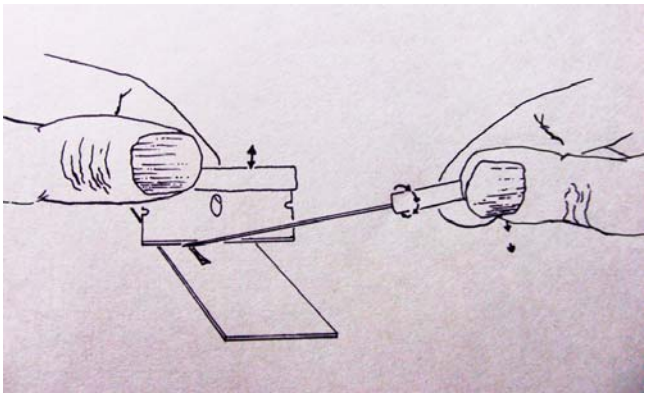


Figure 106. The roll-and-chop method of sectioning bryophytes. This would usually be done while looking through a dissecting microscope. Modified from Wilson (1990).

Chopping Method

Some bryologists subscribe to a chopping technique. They use a moist, but not flooded, stem with leaves, placed on a glass slide. These are chopped with a razor blade from the apex towards the base. Using some very fine forceps, usually adding a very small amount of water (in addition to that held between the tips by capillary action), they are spread about the water drop where the coverslip will go. After the coverslip is added, this preparation can be cleared, if necessary, by infiltrating it with a drop or two of lactic acid, and warming as discussed under Clearing Spores above. I (Glime) have always felt this chopping method was a waste of time since any chopped bits must be examined afterwards, and often none of them is useful. Most, if not all, of the sections will be wedge-shaped and won't lie on their sides. Perhaps I just gave up too soon before I perfected my skill.

Roll and Chop (Wilson 1990; Zander, Bryonet 8 July 2008)

Wilson (1990) presented a method he calls the "roll and chop" method (Figure 106). He uses a dissecting needle to hold the leaf or stem on a glass slide. After each cut, the needle is rolled back a tiny bit and cut again with the razor blade against the needle. I haven't tried this method, but I do have a concern. If one starts cutting from the bottom of the stem, the leaves become detached after the first cut, reducing the chances they will subsequently be cut in thin sections. If one starts at the tip, rolling the needle will butt into leaf tips and roll under them instead of on top of them. I asked Richard Zander for his advice on this, and he agreed that if you start at the bottom of the plant the leaves fall off. Rather, he always does "one leaf at a time if possible, since results are better. Hold the leaf down, apex away, then chop across the middle of the leaf while rolling. A substitute for rolling the needle (probe) is to hold the leaf down at an angle and slowly chop while dragging the blade down the needle; results are the same. Sometimes one can hold the whole plant down with a needle across the plant apex at an angle perpendicular to the leaves and chop across many leaves. This results in a mess but sometimes cross sections result. Less tedious than doing one leaf at a time, though."

Richard Zander (Bryonet 8 July 2008) recommends that single-edge razor blades (Figure 107) for sectioning should be discarded after five to ten uses because they become dull. He described his technique, essentially that of Wilson, on Bryonet: "One holds a leaf or stem crosswise with a stiff dissecting needle, then slices the material with a razor blade held longitudinally against the far side of the needle, meanwhile rolling the needle slowly towards oneself to gradually expose uncut portions of the material.

Figure 107. Box of single-edge razor blades. Photo by Micromark.

Practice (and a relatively fresh blade) makes this technique quite effective, even for very small leaves. Remember to scrape off sections (especially stem sections) adhering to the razor blade with a dissecting needle after cutting. The usual pair of compound and dissecting microscopes are needed, but using an additional illuminator with the dissecting microscope for fine dissections rather than just a single lamp will prove surprisingly advantageous for observation of fine features." Zander and others (Bryonet 8 July 2008) suggest Micromark <http://www.micromark.com/> as a source for razor blades.

Modified Roll and Chop (Kellman 2005)

Kellman (2005) criticized this roll and chop method because it is difficult and often produces sections that are too thick. The pressure needs to be even and sufficient to prevent the leaf from tearing. He recommended solving the first problem of thick sections by making a special needle using a sewing needle. The needle is cut to the desired length (about 7.5 cm) and inserted into a 4 cm piece of a 1 cm wooden dowel by drilling a 1.6 mm hole into the end to a depth of about 1.2 cm. The large diameter of the dowel provides one with a better grip and makes it easier to roll the needle a shorter distance. Kellman finds that the best needle is a 7.5 cm (3") soft sculpture doll needle 1 mm in diameter (Dritz product #56D). The cut end of the needle should be dipped into a drop of glue and put into the hole in the dowel. The short end of the needle can then be wedged into the hole beside the needle to position it firmly. Kellman warns that cutting the needle often results in having the cut off end flying across the room, so he recommends that it be cut inside a cloth or plastic bag so that it can be retrieved easily. The next step creates the tread that helps the needle grip the leaf. Run an emery board or sandpaper along the length of the needle, rotate the needle and repeat until the entire needle has a tread. Do not run the emery board or paper around the needle because that will not create the lengthwise treads needed.

Kellman solves the tearing and uneven pressure problem by stacking several leaves on top of each other to cut them. This also provides more sections, saving time.

1. To prepare the sections, place the stem on right-hand side of a clean slide and remove leaves under a dissecting microscope.
2. Select the leaves you want to section and move them to the left side of the slide without adding more water.
3. Once you have moved the chosen leaves, stack them together like spoons, stacking at least 3 leaves.
4. When the stack is ready, place the needle over the stack, pressing down lightly.
5. Use a sharp blade to cut along the away side of the needle. Use a chopping type of cut instead of a slice, a method not feasible with a single leaf. The full edge of the blade should reach the slide at one time.
6. Move the cut piece away and roll the needle as little as possible back toward you.
7. Make another cut, making the first section.
8. If sections get stuck to the blade, place a drop of water in the middle and dip the blade in it to remove the sections.
9. Continue this procedure until you have enough sections. Then make a slide as usual. You can place a coverslip on the stem and remaining leaves on the right to view whole leaves and another on the sections, all on one slide.

Dissecting Microscope Hand Sections (Welch 1957; Schofield 1985)

This method works well for leafy stems, branches, and large leaves. Some bryophytes, like ***Polytrichum*** (Figure 18), require leaf sectioning to view special structures like the lamellae (Figure 1). Because this is a large leaf, it is a good representative for a beginner to use for practice. Welch (1957; Schofield (1985) published the technique that works best for me (Glime):

1. Place a wet ***Polytrichum*** (Figure 18) leaf or leafy branch/stem on a dry slide.
2. Put a drop of water on one side of the slide, away from the leaf.
3. Cut away the tip with a sharp razor blade about 1/3 from the tip end of the leaf.
4. Discard your first cut.
5. While viewing through a dissecting microscope, cut as close to the previous cut as possible. Use one hand to cut and the other to guide and steady the cutting hand while holding the specimen with a fingernail or a pair of curved microforceps.
6. Cut 8-10 very thin sections and dip your razor blade in the drop of water to free them.
7. Examine the sections with the dissecting microscope to see if any of them are lying in cross section.
8. Continue cutting until you have about 30-40 sections.
9. If there are satisfactory sections, put a coverslip on the slide and examine the leaves under low and high power on the compound microscope.

With this technique I can usually get 5-8 sections (Figure 108) that will lie on their sides as they should.

Figure 108. ***Polytrichum juniperinum*** leaf cs showing several sections on a slide. Photo courtesy of John Hribljan.

Double Slide Sectioning Technique

Sean Edwards (pers. comm. 20 July 2012) has provided us with his double slide sectioning technique, based on his thesis (Edwards 1976 – see Adams 1981; Edwards 2012). The following description is only slightly modified from his description.

This method allows, with very little practice, good clean sections of about 10 µm thickness to be taken from any required part of the moss leaf, with no preparation or specialized equipment, and within a matter of seconds. The equipment required is the normal laboratory dissecting microscope (or good close eyesight), two 7.5 × 2.5 cm standard glass slides, and a supply of double-edged or single-edged razor blades. As noted by Adams in the Floating Slide Miniblade Technique, throw-away twin-bladed razors are currently in plentiful supply. By carefully prising apart the plastic mounts, two very thin, but easily hand-held ultra-sharp blades can be recovered that are ideal for section cutting (Adams 1981).

Selected moist leaves are arranged parallel with each other on a glass slide, with the parts to be sectioned aligned as shown by the arrows in Figure 109. The second slide is laid (with care) over the leaves, so that its long edge is also aligned with the parts to be sectioned (Figure 110-Figure 111). This may be checked with a dissecting microscope if necessary, and individual leaves adjusted. Firm pressure is applied to the upper slide by the finger of one hand, and half a double-edged razor blade is drawn with the other hand across the leaves, using the upper slide as a guide (Figure 110, Figure 111). Only a corner of the blade is used, but if the 'angle of elevation' of the blade is sufficiently small (about 15°-20°, perhaps less than that indicated in Figure 110), the cut is perfectly clean.

Sections are made by adjusting the tilt of the razor blade for each successive cut; the first cut is made with the blade leaning somewhat (about 15°) towards the upper slide, and this angle is progressively lessened. The situation is shown diagrammatically in Figure 112, where θ is the angle of tilt and P_1 is the fulcrum. The angle of tilt is surprisingly easy to control, and even a relatively coarse adjustment will give a fine control over the section thickness. After the tilt of the blade has passed 0° (vertical), the fulcrum moves down to P_2, resulting in an even finer control over the thickness of the last few sections. Although the sections must in theory be slightly wedge-shaped because of 15° angle, this is not noticeable in practice.

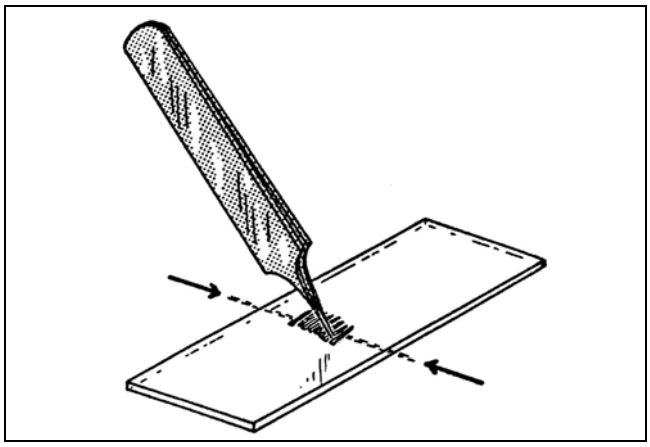


Figure 109. Placing specimen on slide in first step of the double slide sectioning technique of Sean Edwards. Drawing by Sean Edwards.

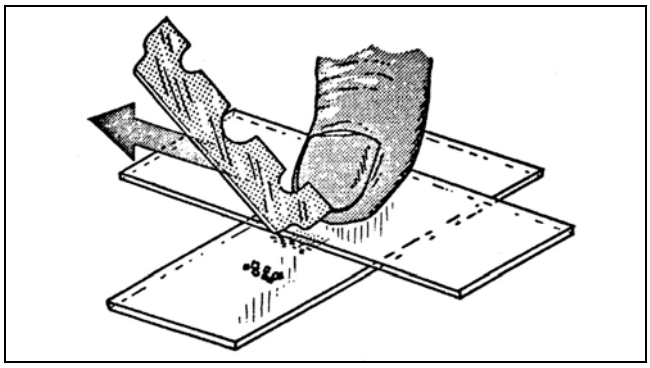


Figure 110. Alignment of slide and specimens in double slide sectioning technique of Sean Edwards. Drawing by Sean Edwards.

Figure 111. Sectioning setup of double slide sectioning technique of Sean Edwards. Photo by Sean Edwards.

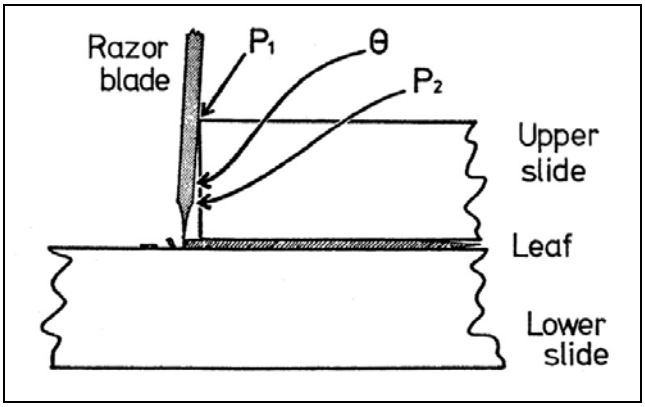


Figure 112. Cutting position of the razor blade in the double slide sectioning technique of Sean Edwards. θ is the angle of tilt and P_1 is the fulcrum. P_2 is the position of the fulcrum after the tilt of the blade has passed 0° (vertical). Drawing by Sean Edwards.

Pressure on the blade has to be judged by experience, but it should be no more than is necessary to cut the leaves. One blade corner may provide many series of sections, but such economy is usually not necessary; only with very old and fragile material should a fresh corner be used for each operation. It seems that an 'angle of elevation' of about 15°-20° enables the pressure to be taken by the less vulnerable curved corner of the blade, while allowing the razor edge unimpeded access to the leaves. It is clearly advantageous to keep this angle constant. If the broken corner of a half-blade immediately above the cutting corner is bent somewhat, just before it is first used, then the unused cutting corners can be recognized without confusion, and a packet of ten blades can be used to section at least forty plants. Particular advantages of this method lie in the degree of control and inspection allowed before and during cutting, by the transparency of the glass cutting-guide, and also in the world-wide availability and cheapness of double-edged razor blades.

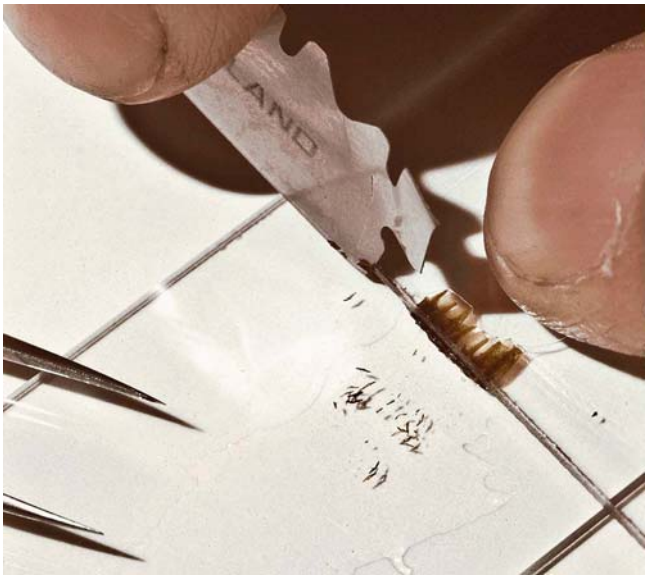


Figure 113. Cutting sections along edge of top slide in double slide sectioning technique of Sean Edwards. Note cut sections in water on the lower slide. Photo by Sean Edwards.

Figure 114. Cut sections along edge of top slide in double slide sectioning technique of Sean Edwards. Note the alignment of multiple stem pieces under top slide. Photo by Sean Edwards.

Floating Slide Miniblade Technique (Adams 1981)

This technique is nearly the same as the Double Slide Sectioning Technique of Sean Edwards, but a few modifications may be helpful to some people. The Floating Slide Miniblade Technique likewise involves two microscope slides. However, double-edged razor blades are hard to find and are really too thick to control the sectioning adequately. The second problem with the Edwards Double Slide Sectioning Technique is that the angle of tilt ensures that none of the sections are truly vertical slices with parallel slides.

Use the more readily available twin-bladed razors and pry the plastic mounts apart to obtain two very thin ultra-sharp blades. The second refinement requires the obligate use of a dissecting microscope (as also recommended by Tony Smith).

1. Mount a clean slide under the center of the low power field at ~45º to the left-right plane (near left to away right).
2. Place a large drop of water on the slide, and then mount your selection of leaves etc., in a line across the middle of the slide for sectioning.
3. Finally, add the second slide at right angles as per Edwards' technique, carefully trapping the leaves at the level you need the sections, and most importantly, a film of water between the slides.
4. Then, if you are right-handed use the second (longest) finger of your left hand (N.B. not your thumb as in Edwards' technique) to hold the upper slide down tightly onto the leaves, and using a blade in the right hand, slice away the unwanted projecting leaf segments with a gentle (so as not to blunt the blade) horizontal slice. Hold the blade vertically, but with the cutting edge tilted at ~30º towards your right hand, and slide it along the edge of the top slide, gripping the blade between the thumb and second finger, and – doing something you can't do easily with half a double-edged blade – resting your index finger along the top edge to provide that extra control.
5. Now comes the innovative bit. Because you have a film of water trapped between the slides, if you flex your left second finger slightly, you can retract the upper slide (observing all the time under the microscope) and expose new tiny projecting segments of the leaves you wish to slice.
6. Keeping your blade in the vertical plane, but with the sharp edge inclined towards your right hand at ~30º as before, you can now slice a beautifully thin section with vertical, parallel sides. With a bit of practice, it is fairly easy to retract the upper slide on its film of water, a potential slice at a time, and go on cutting ultra-thin vertical slices.

You can modify this technique by using a coverslip instead of the top slide:

1. Hold the coverglass in place with your left forefinger, with your left thumb held sideways (nail facing right), pressing down on the slide underneath. The thinness of the glass has the advantage of making it easier to see the projecting leaf segments that you are about to cut, since in the case of a slide, the edge of the glass gives you a double image. It is also easier to trap a film of water under it.
2. If you clean away unwanted bits of leaf you can lift the forward edge of the coverglass slightly with your blade, and pull it forward over the sections all in one operation, the water under it being dragged along with it and serving to suspend the sections.
3. Gripping a bunch of leaves or a shoot between thumb and forefinger, with the soft side of the thumb slightly higher, place a drop of water on the leaves and slice away against your thumb. If you are careful, you can cut a collection of slices, which stick in a film of water at the bottom of the blade, without too much damage to your thumb!
4. On dispersing the sections in a drop of water on a slide, you may find however, that they are not quite

thin enough and insist on lying flat instead of edge on. Don't despair! Pick up the best section with a pair of forceps, and mount it on the edge of a microscope slide in a film of water, as close as possible to the upper face.

5. Now despite the fact that it is lying flat on the edge of the slide, if you look at it under the microscope you will see it edge on. This is usually sufficient to enable you to observe the cell structure of a costa, and whether a margin is bistratose.

Figure 115. ***Polytrichum juniperinum* leaf section** using a cryostat. Photo by John Hribljan.

Cryostat Sections

If you are fortunate enough to have a cryostat, you can get excellent, consistent sections. I inherited a freezing cryostat that had been obtained as government surplus. The principle is that it freezes your specimen in ice. The specimen is prepared by turning the cold stage to a very cool temperature and building up an ice base with a few drops of water, waiting for each drop to freeze before adding the next. Then the specimen is placed there vertically. If you are cutting small leaves, you may want to position several of them on the ice. Once the specimen is positioned, continue to add drops of water, letting each freeze before adding the next. Once you have covered the portion of the specimen you need, you can cut off any excess with a sharp razor blade. The disk is then clamped into a holder in front of a blade. This blade (or perhaps the holder) can be moved by "winding" much like an old Victrola. Each time the blade comes down, it cuts a narrow slice from the ice and bryophyte. These must be collected on a cold, dry slide placed under the ice ribbon created – something that must be done quickly. A pair of microforceps can help to remove all the ribbon from the blade. To make the slide cold, keep it inside the cryostat while you are building the ice mound and doing the sectioning. A warm slide will melt the ribbon immediately and you can lose your slices.

The icy ribbon can be moved to the center of the slide if done quickly before it melts. Then you can add a drop of water and coverslip as you would for any slide.

The cryostat can be adjusted for the thickness of the sections. The necessary thickness depends on the thickness of the specimen (leaf, stem; see Figure 115). Capsules are a bit more difficult once they form an internal air chamber because the air will be trapped inside. If this becomes a problem, you might try adding a bit of wetting solution inside the capsule before sectioning. Be careful that the wetting agent does not get on the ice mount because the water drops will run off before they can freeze. (We haven't really tried this, so we don't know if it will work.)

Adam Hoelzer (Bryonet 5 December 2013) likewise uses a cryostat. He reports that the slices are not as thin as one can achieve with paraffin, but they are definitely adequate. Rather than using pure water, he uses the mounting medium provided by the manufacturer of the cryostat – a medium that consists mostly of polyvinyl alcohol. This is the typical medium used by hospitals that use cryostats for histology.

Stems and Small Leaves

Mosses lack lignified vascular tissue in their stems, but they may have vascular elements called **hydroids** (water-conducting elements) and **leptoids** (photosynthate-conducting elements). Additionally, the center of the stem may contain small, thick-walled cells that serve as strengthening tissue (Figure 116), but that does not seem to have any conduction function. None of these structures can be seen without sectioning the stem. Furthermore, it is difficult to section small leaves by themselves, so they are best sectioned on an intact stem or branch. This is the method that works for me (Glime):

1. Place a wet moss stem on a **dry slide**.
2. Put a **drop of water** on one side of the slide, away from the stem.
3. While viewing through a dissecting microscope, use a **sharp razor blade** to cut as close to the end of the stem as possible. Use a fingernail or finger of one hand to guide (the one holding the stem) and steady the hand holding the blade. Alternatively, you might find it easier to press down on the stem with a pair of curved forceps instead of holding it with your finger.
4. **Discard** your first cut.
5. **Cut 8-10 very thin sections** and dip your razor blade in the drop of water to free them.
6. Examine the sections with the dissecting microscope to see if any of them are **lying in cross section**, indicating they are thin enough.
7. If there are satisfactory sections, put a **coverslip** on the slide and examine the stems under low and high power on the **compound microscope**.
8. Use a microscope with **plane polarized light** to see cells with phenolic compounds in the stem.

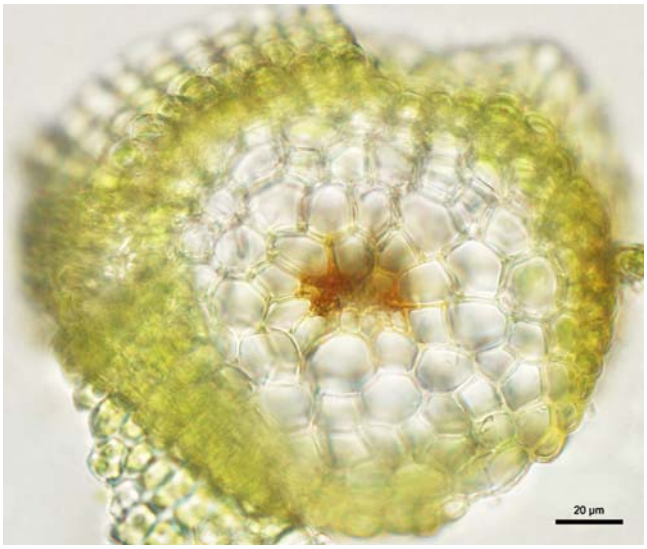


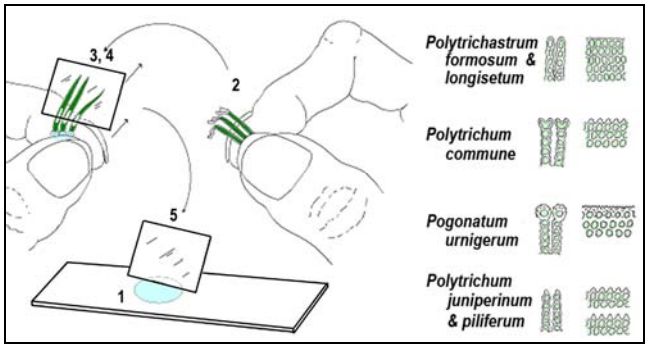
Figure 116. Stem cross section of the moss ***Molendoa sendtneriana*** showing central strand. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Lamellae

This sectioning technique, including the figure, is modified from the protocol by Ken Adams (2018).

When examining ***Polytrichum*** / ***Polytrichastrum*** / ***Pogonatum*** that do not have leaf margins folded over the lamellae, to determine the species, it is difficult for many people to cut very thin transverse sections. The late Peter Wanstall provided a simple solution to the problem, but beginners nevertheless seem to have difficulty with it. Hence this short procedural account:

1. Put a drop of water on a clean slide, and have some water in a dish plus a coverglass close at hand.
2. Assuming most of you are right handed, pull off a bunch of freshly wetted expanded leaves by their laminas with your right thumb and forefinger, then carefully grip the transparent sheathing leaf bases with your left thumb and forefinger so that the laminas lay across the flesh of your forefinger, before you let go with the right hand, as being springy and being bent at right angles they will otherwise fly out of line.
3. Then dip your second right finger in the water and transfer a good sized drop into the groove between your thumb and forefinger.
4. Take the coverglass in your right hand, dip the edge in this droplet, and move it away from you, gently scraping it against several laminas at once, several times, until you can see that patches of the green of the lamellae have given way to the clear tissue of the leaf lamina.
5. Dozens of lamella fragments will now be collected in a film of water along the bottom edge of your coverglass – but you are unlikely to be able to see anything – just be reassured that they are there, and dip the edge in the droplet of water you have prepared on the slide.



6. Add a cover glass and examine with the 10x objective and you should see plenty of torn-off lamellae looking like bits of green brick wall lying on their sides.

Beginners are often bewildered by these and fail to see what has happened. Imagine they really are bits of brick wall on their side. Along what was the top of the wall will be an edge with a constant repeating pattern, while along the other long edge the tissue will be torn and ragged from where it was ripped off the lamina. Students with no prior experience of microscopy may not even realize that the walls may be upside down! The top row of cells are heavily cutinized to prevent water loss, and slightly larger than the rest of the lamella cells, so that when the leaf loses turgor in dry conditions and the lamina curves slightly upwards at the edges, the top row of cells of one lamella come in contact with the top rows of lamellae on either side, thus closing off the moisture saturated air cavities in between, effectively minimising drying out of the lamellae. Using this technique the morphology of the top row cells is observed from the side, as opposed to end on as would be seen in a transverse section of the leaf. Nevertheless, because ***Polytrichum commune*** has top row cells with four large rounded bosses at their corners, in both TS and from the side two rounded bosses will be seen topping each cell, whereas in ***Polytrichastrum formosum*** and ***Polytrichastrum longisetum*** the top surface will be gently undulating in side view.

Techniques for Special Structures

Clearing Spores

Tom Blockeel (Bryonet 24 January 2012) sought a method to make it easier to see the very dark or blackish spores of species like those of ***Riccia*** (Figure 117). The ornamentation of the spores can help in identification, but it is not possible to observe it clearly with transmitted light.

Wagner (Bryonet 24 January 2012) suggested using a combination of transmitted and reflected light. The reflected light can be a strong LED light from a bicycle headlamp. This, combined with stacked images, can provide excellent quality (Figure 118).

Figure 117. Spore of ***Riccia sorocarpa*** showing its dark color and density, preventing one from seeing spore wall details without special techniques. Photo from EOL through Creative Commons.

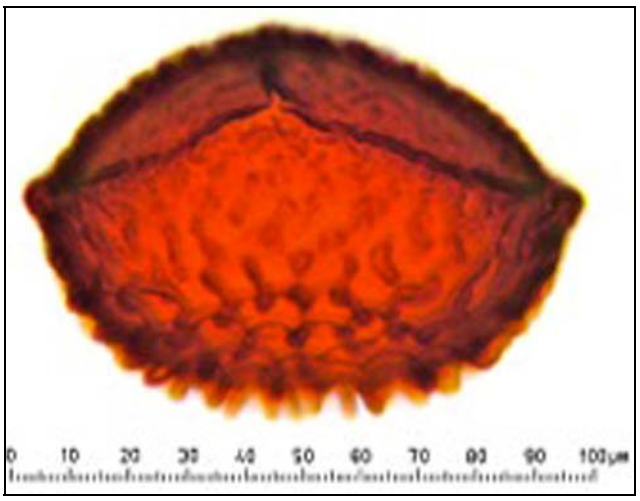


Figure 118. Spore of ***Riccia sorocarpa*** using both transmitted and reflected light plus stacking. Compare the clarity to that of the same species in Figure 117. Photo by David Wagner, with permission.

Marko Sabovljevic (Bryonet 24 January 2012) suggested using 5-10% **Clorox bleach** (NaOCl – 8% of active chlorine) for 1-3 minutes to clear the spores, a method also suggested by Richard Zander and Jörn Hentschel in the same Bryonet thread. Hentschel also suggested **calcium hypochlorite** ($Ca(ClO)_2$), the C-Solution used by lichenologists for their spot test. Martin Godfrey (Bryonet 25 January 2012) uses **gum chloral** to clear dark, dense specimens and also make a permanent preparation. But Upton (1993) reports that gum-chloral slides deteriorate steadily with time and specimens become irretrievably lost. Several bryologists (Richard Zander, Rod Seppelt, Bryonet 24 January 2012) also suggested **lactic acid**, but it wasn't clear that they had actually tried it for black spores. Seppelt also suggested a strong detergent like **Tween 80** because it reduces the black pigment in some lichens. Tom Blockeel reported that the bleach "does the trick perfectly well!" (Bryonet 6 February 2012).

An excited Richard Zander sent me an email on 15 November 2020 to share a discovery! He had been trying to clear the spores of thalloid liverworts using either 100% Clorox or lactic acid with little success. Then, he mixed the two and tried the mix on the spores of ***Ricciocarpos natans*** (Figure 119). A few bubbles arose, and "the spores decolorized and turned a very light, translucent brown, with morphologic details perfectly visible." He also used 5% Clorox and lactic acid on spores of **Targionia** (first one, then the other), and the spores again retained a brownish color. But, sadly, David Wagner tried the mix of Clorox 1:5 dilution with a drop of vinegar on spores of ***Riccia nigrella***; before he could wash them, the spores turned to mush!

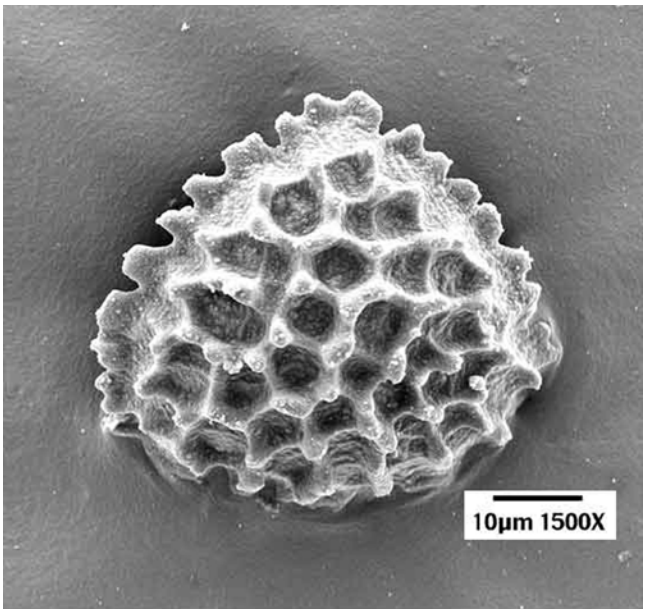


Figure 119. Distal SEM view of ***Ricciocarpos natans*** spore. Photo by William T. Doyle, with permission.

Spore Clumping and Cohesion Problems

Spores in a drop of water will tend to clump, making observations difficult. A drop of Extran® in 5 ml of water will break these apart. It might be useful to keep a bottle of water with detergent for making slides where surface tension or cohesion among leaves create problems. A little experimentation will determine appropriate amounts of detergent for various brands.

Gum Chloral Recipe for Mounting

Martin Hausler (pers. comm. 18 July 2012) provided me with this method for chloral hydrate, with the recipe originally from Watson's British Mosses and Liverworts:

Distilled water 100 ml
Gum arabic 40 g
Glycerine 20 ml
Chloral hydrate 50 g

1. Dissolve the gum arabic first in cold water, which can take a day or so as it is best not to stir to avoid getting masses of air bubbles which take an age to come out.
2. When dissolved add the glycerine and chloral hydrate and heat until dissolved; filter hot if necessary.

3. Put a drop on a slide, then add your wet specimen to it.
4. Leave the slide horizontal for a few days for the gum to set - in this time any clearing will take place. It is great for things like ***Fossombronia*** spores (Figure 120). For whole mounts of perianths or similar structures, the clearing properties will show up lots of structure without the need to dissect.

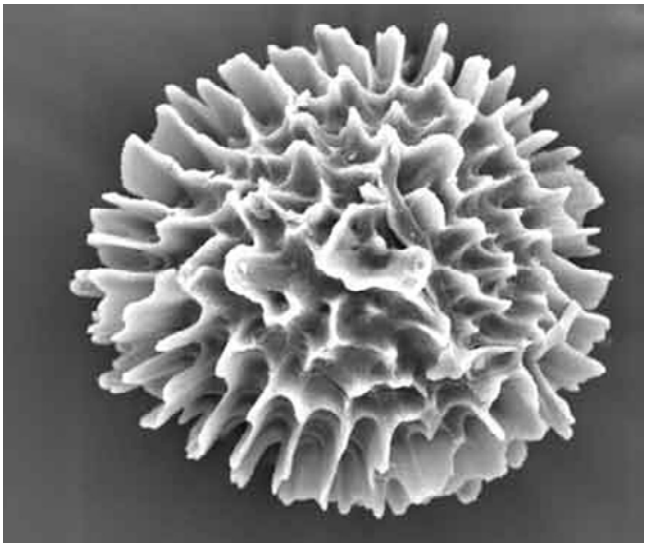


Figure 120. ***Fossombronia longiseta*** spore proximal SEM. Photo courtesy of William T. Doyle.

5. Although not strictly necessary, you may want to seal your coverslips with a couple of coats of nail varnish as it stops the gum from drying out. Technically this is a temporary mount but some slides last over 30 years old and are fine. It does tend to shrink delicate specimens so when if you don't need its clearing properties, use glycerine jelly as per Richard Zander in "Genera of the Pottiaceae."

Rod Seppelt (Bryonet 14 November 1997) suggested staining spores with **malachite green**, **acid fuchsin**, and **orange G**, a method used for testing pollen (Alexander 1969). The viable pollen stains deep red-purple, whereas the aborted pollen stains green. This recipe uses **chloral hydrate**, a controlled substance in the US. The solution uses 10 ml ethanol; 1 ml 1% malachite green in 95% ethanol; 50 ml distilled water; 25 ml glycerol; 5 gm phenol; 5 gm chloral hydrate; 5 ml 1% acid fuchsin in water; 0.5 ml 1% orange G in water; and 1-4 ml glacial acetic acid (for very thin to very thick walls). This should work as well for bryophyte spores.

SEM

Scanning Electron Microscopy (SEM) can reveal details not visible with an ordinary light microscope. Miyoshi (1969) demonstrated the intricate detail of ***Schistostega pennata*** and ***Hedwigia ciliata*** by using the Scanning Electron Microscope (SEM), compared to images using the light microscope. The image in Figure 121 was taken using SEM photography and can be compared to that of the same species using ordinary light (Figure 117) or both transmitted and reflected light (Figure 118). The SEM technique is somewhat complex and time-consuming and will not be covered at this time. Methods can be found in Hofmann *et al*. 1996, Zhang *et al*. 2007, and Srivastava *et al*. 2011, and many others.

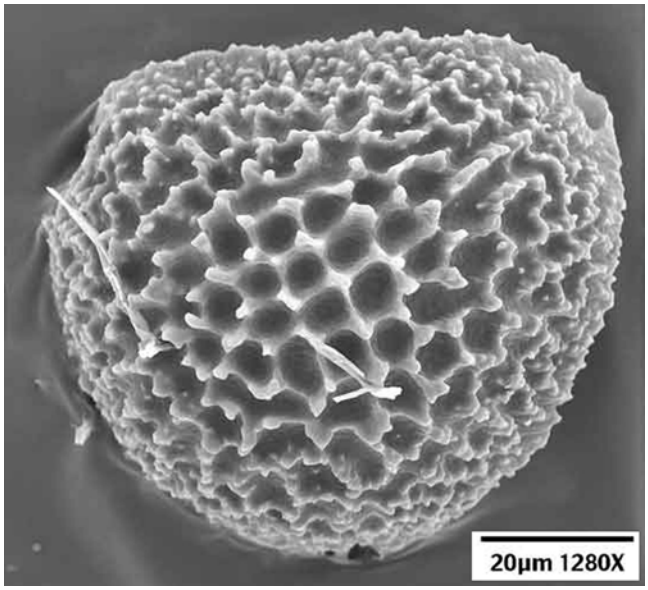


Figure 121. ***Riccia sorocarpa*** distal spore wall SEM. Photo courtesy of William T. Doyle.

Vacuoles

Many bryologists seemed to consider that bryophytes did not have vacuoles, but it appears this is only true for some taxa (Rod Seppelt, Bryonet 14 November 1997; Jeff Bates, Bryonet 14 November 1997). It is interesting that Seppelt reports that vacuoles seem to be absent in most Antarctic mosses. This suggests that absence of vacuoles may be an adaptation to cold temperatures – an interesting correlation to examine.

One indicator that a cell has a vacuole is the position of the chloroplasts (Michael Christianson, Bryonet 14 November 1997). If they are crowded around the periphery of the cell, it is likely that a vacuole is occupying the center of the cell. In Figure 122, fluorescent microscopy demonstrates the position of the chloroplasts at the periphery of the leaf cells of ***Funaria hygrometrica***, whereas in Figure 123 that is more difficult to see.

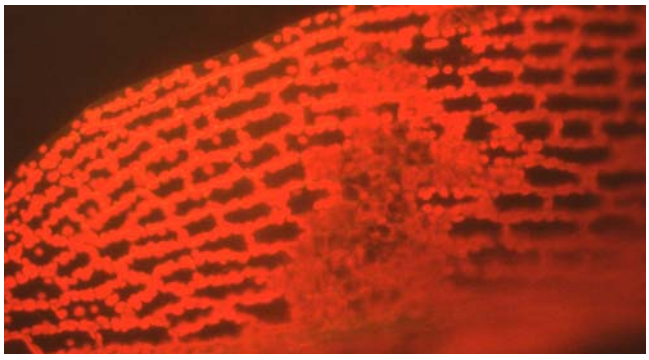


Figure 122. Leaf of ***Funaria hygrometrica*** showing chlorophyll fluorescence and demonstrating the clustering of chloroplasts at the cell margins. Such positioning indicates the presence of a vacuole. Photo by Janice Glime.

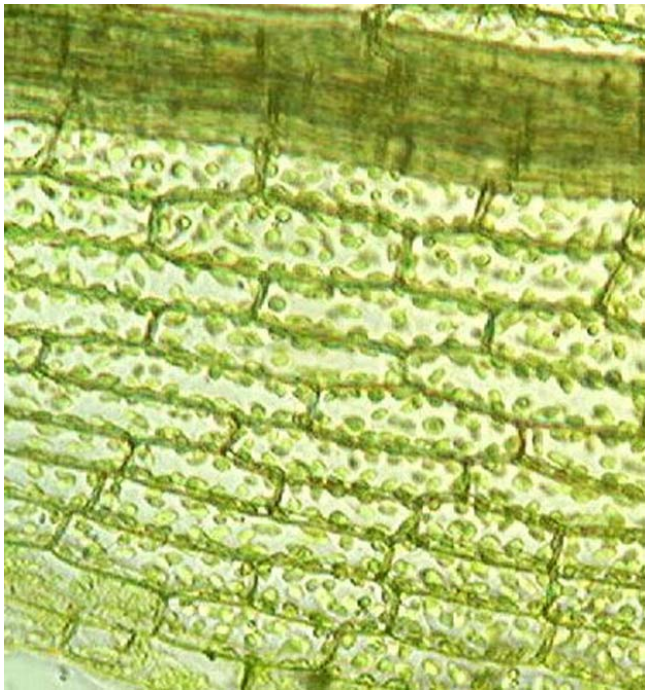


Figure 123. ***Funaria flavicans*** leaf cells showing chloroplasts on cell margins, indicating presence of a cell vacuole. Photo by Frederick B. Essig, with permission.

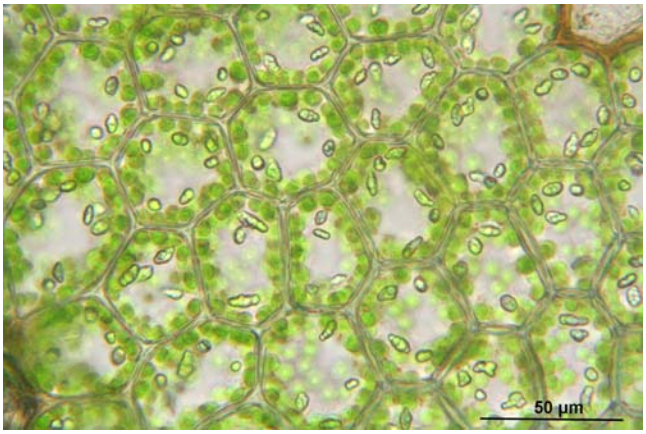


Figure 124. ***Calypogeia muelleriana*** leaf cells showing oil bodies. Photo by Hermann Schachner, through Creative Commons.

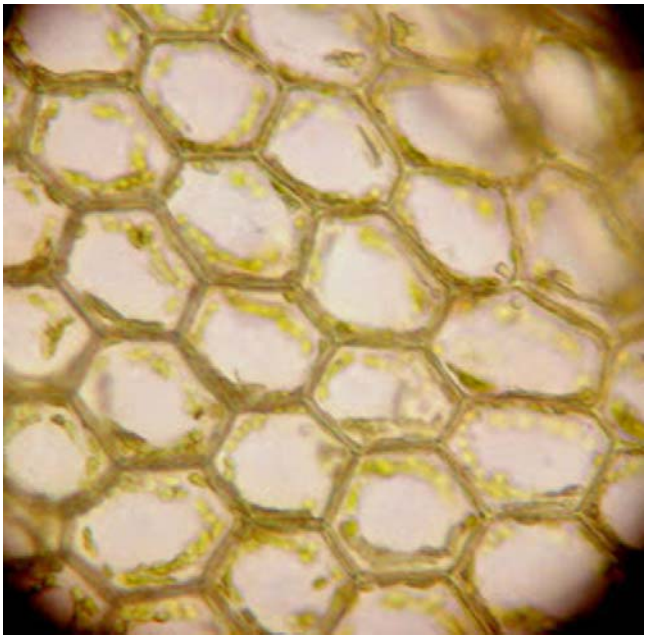


Figure 125. ***Calypogeia muelleriana*** dried leaf cells where oil bodies have disintegrated. Photo by Jutta Kapfer, with permission.

Liverworts and Oil Bodies

Oil bodies can be a problem because they disappear as the liverwort dries (Tom Thekathyil, pers comm. 27 August 2012; Wagner 2013), in some species disappearing within hours despite a moist state of hydration. David Wagner (Bryonet 5 September 2012) considers it a general rule that when cells with oil bodies die, the oil bodies dissipate. Liverworts on rotting logs (which are moisture sinks) never dry out in nature, but when they dry, they die. Unlike other bryophytes, they are not desiccation tolerant. ***Calypogeia*** (Figure 124-Figure 125) species must be examined for oil-body characters before they dry. Once dry, the oil bodies are gone forever and slow drying doesn't help. On the other hand, liverworts that grow in extreme environments, like ***Marsupella*** spp. (Figure 126) on rocks in alpine situations, are as desiccation tolerant as any bryophyte. If air dried, herbarium specimens will retain oil bodies for years because the cells are NOT dead. They live for years in a desiccated condition. To have any chance of seeing oil-bodies in dried specimens, they must be rehydrated slowly with plain water.

Sometimes Wagner has been surprised at getting good results. Also be aware that oil bodies can change character as they age after collecting. There's no substitute for immediate observation upon collections, although this period can be prolonged if they are stored in a refrigerator or cooler (Wagner 2013). On the other hand, extended periods in the dark will alter their appearance or cause them to disappear. There are some mysterious anomalies. ***Scapania gymnostomophila*** (Figure 127-Figure 128) has oil bodies that persist for decades, itself a distinctive taxonomic character.

Figure 126. ***Marsupella emarginata*** var ***pearsonii***. Alpine rock-dwelling members of this genus retain their oil bodies when they are dried. Photo by Michael Lüth, with permission.

Figure 127. ***Scapania gymnostomophila*** with gemmae. Photo by Štěpán Koval, with permission.

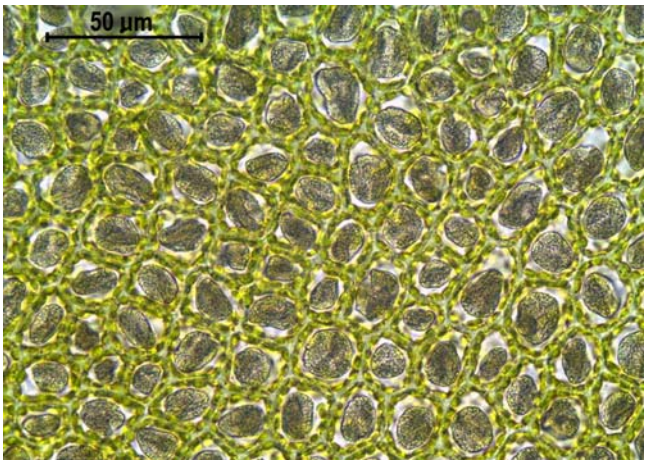


Figure 128. ***Scapania gymnostomophila*** leaf cells showing oil bodies. Photo by Hugues Tinguy, with permission.

Nevertheless, liverworts survive wetting and drying in nature. Rod Seppelt (Bryonet 27 August 2012) reported that Jeff Duckett told him that the liverworts must dry SLOWLY for the oil bodies to survive, but does this always work, or does the death of oil bodies explain why so many liverworts seem to require a moist environment?

Oil bodies are often essential for identification. Several methods of liverwort preservation have been suggested (Lehman & Schulz 1982; Ohta 1991). Lehmann and Schulz suggest a method of fixation that preserves the oil bodies, as do Müller-Stoll and Ahrens (1990). The latter researchers provide a method of staining oil bodies in live cells with diachromes and fluorochromes. If you can read the language, these may be helpful.

Peristome Teeth

Niels Klazenga (Bryonet 9 April 2014) reports the method he uses, taught to him by Dries Touw. He uses it to see teeth without having too many spores to interfere with the view. He cuts the capsule in half transversely so that you have a top half and a bottom half. Then cut the top half in four parts longitudinally. Transfer the four parts to a different slide after removing the columella and washing off excess spores. On the new, clean slide put two parts with the inside up and two parts with the outside up, so that you can see both the inside and outside of the peristome. You can do the same thing for the bottom half to see stomata, but it is rare that you need to see the inside of the bottom. These parts tend to be a bit temperamental, so they don't always end up the way you want them. Rod Seppelt added that the peristomes of some mosses assume a very different shape when wet. Instead of being straight, they bend from near the base, so that the upper parts of the teeth become strongly reflexed, completely reversing their direction. "Trying to wedge the peristome under a coverglass before wetting is tricky and does test the patience."

Brent Mishler (Bryonet 9 April 2014) suggested that one should select a recently dehisced capsule and make a longitudinal cut through the peristome (Figure 129-1&2), followed by a transverse cut slightly below the peristome insertion (Figure 129-3, 4, & 5). The endostome (attached to the spore sac) will then usually separate from the exostome with fine forceps (Figure 129-6, Figure 130-Figure 133). If a large number of spores obscure the peristomial structures, a drop of 95% ethanol added before adding water will usually disperse the spores; then excess spores can be scraped or wiped off before adding water. "Treatment with ethanol also causes the separation of the exostome and endostome, facilitating their dissection and observation. If no dehiscent capsules are available, peristome details often can be observed adequately (*i.e.* adequately for identification purposes) by removing the operculum from a nearly mature capsule by immersing the capsule in water, adding a cover slip, and boiling the slide gently over a heat source. This is usually sufficient to cause the operculum to dehisce."

To study peristomes in plane polarized light, the ventral and dorsal laminae of the teeth (not outer and inner peristomes) must be separated (Taylor 1959). Examination may even require viewing a cross section of a tooth.

1. Split capsule vertically with a razor blade.
2. Soak teeth in groups of 3-4 in 5% solution of pectinase for 24 hours.
3. Wash in 3 or more baths of distilled water.
4. Make gum syrup mountant
   A: 40 g gum arabic
      0.5 g phenol crystals
      60 cc water
   B: 52 parts cane sugar
      30 parts water (by volume)
   Combine 25 cc A, 15 cc B, and 2 g glycerin.
5. Cover a small area of a slide with a thin coating of the gum syrup mountant.
6. For peristomes, permit gum arabic to become almost dry.
7. Transfer teeth in groups of 3-4 to mountant, making sure some groups show the ventral and others dorsal surface.
8. If peristome teeth curl, they can be moistened slightly with a damp (not wet) fine water color brush (# 00000).

9. The gum arabic can be remoistened if needed, especially if used for leaves and other structures.
10. The teeth can be flattened on the slide with a needle or the damp brush.
11. Make sure the gum syrup is nearly hard, but soft enough to flow under pressure. This will take practice to prevent ripples from too much liquid, but must permit the teeth to pull apart.
12. To make teeth very flat (desirable), cover part of slide lightly with light coating of paraffin wax or other substance to prevent the adhesive from sticking to it.
13. Press the coated slide against the teeth until they are tightly pressed against the mountant.
14. Permit the gum arabic mountant to harden.
15. Remove uppermost surface of lamina on each set of teeth by gentle scraping, using a dull tool such as a discarded side-cutting dental tool.
16. Remove the loosened particles with a dry brush.
17. Lightly moisten the gum syrup to get a smooth surface and allow to dry.
18. To make the slide permanent, add the desired finisher, such as gum-chloral.

To View Teeth:

19. Place the finished slide on the rotating stage of a polarizing microscope and turn stage to a position where light is extinguished when viewing slide.
20. Insert gypsum tube into microscope tube and rotate stage clockwise.
21. If tooth lamina becomes blue or green, chains run N-S when tooth is returned to this extinction position.
22. If tooth lamina becomes yellow after rotation, search for a position at right angles and repeat the test.
23. Be careful not to rotate counter-clockwise.
24. If all chains are parallel, you will not find the bright color change, but usually at least some will show an acute angle between two sets of chains.

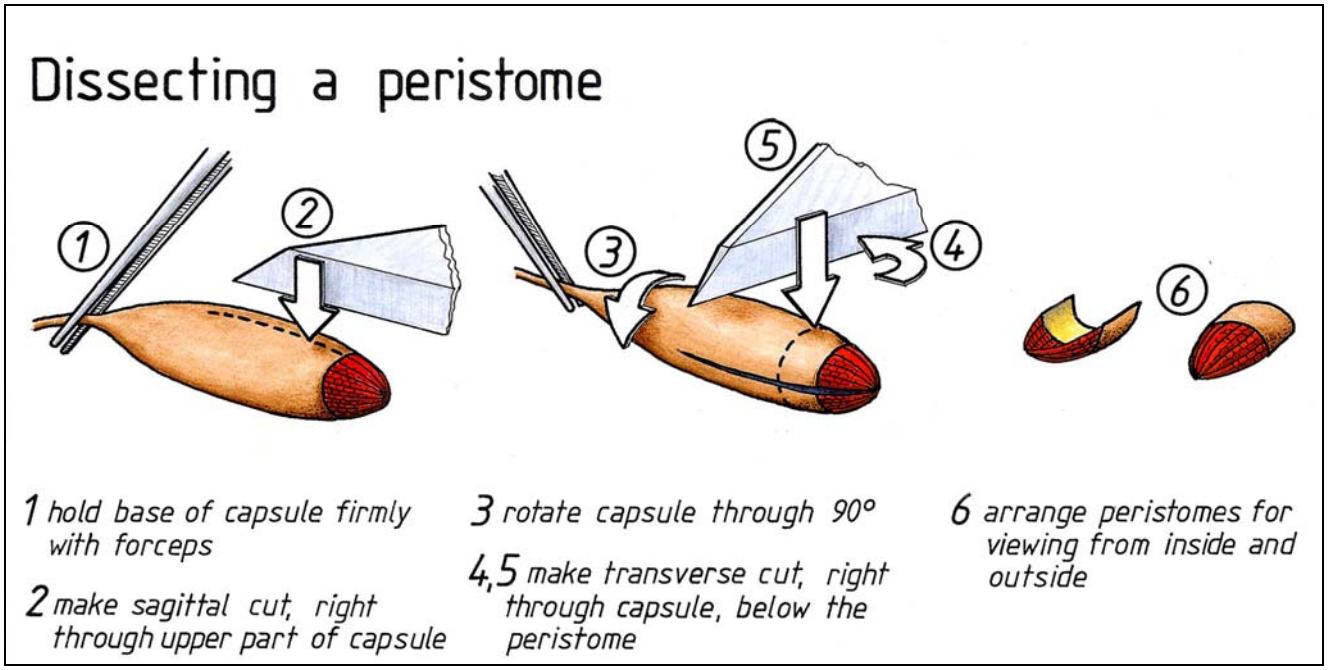


Figure 129. Cutting method for capsule to display peristome teeth on a slide. Drawings by Sean Edwards.

Javier Penalosa (Bryonet 12 April 2014) found that slightly boiling the slide makes the operculum pop off the capsule (see Figure 130, Figure 132). He was successful in using this technique to see peristomes of ***Bryum*** (Figure 130, Figure 132) and ***Brachythecium*** (Figure 133). Once the operculum is off, a drop of alcohol will disperse spores on the slide. This exposes the **nodose cilia** in ***Brachythecium rutabulum*** (Figure 133) and appendiculate cilia in ***Brachythecium oedipodium***.

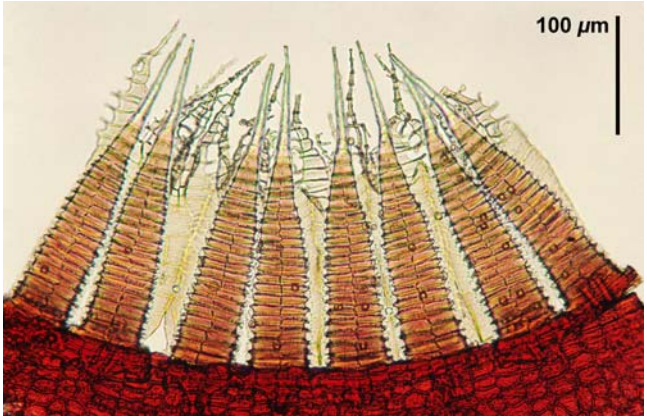


Figure 130. Peristome teeth of ***Bryum dichotomum***. Photo by Sean Edwards.

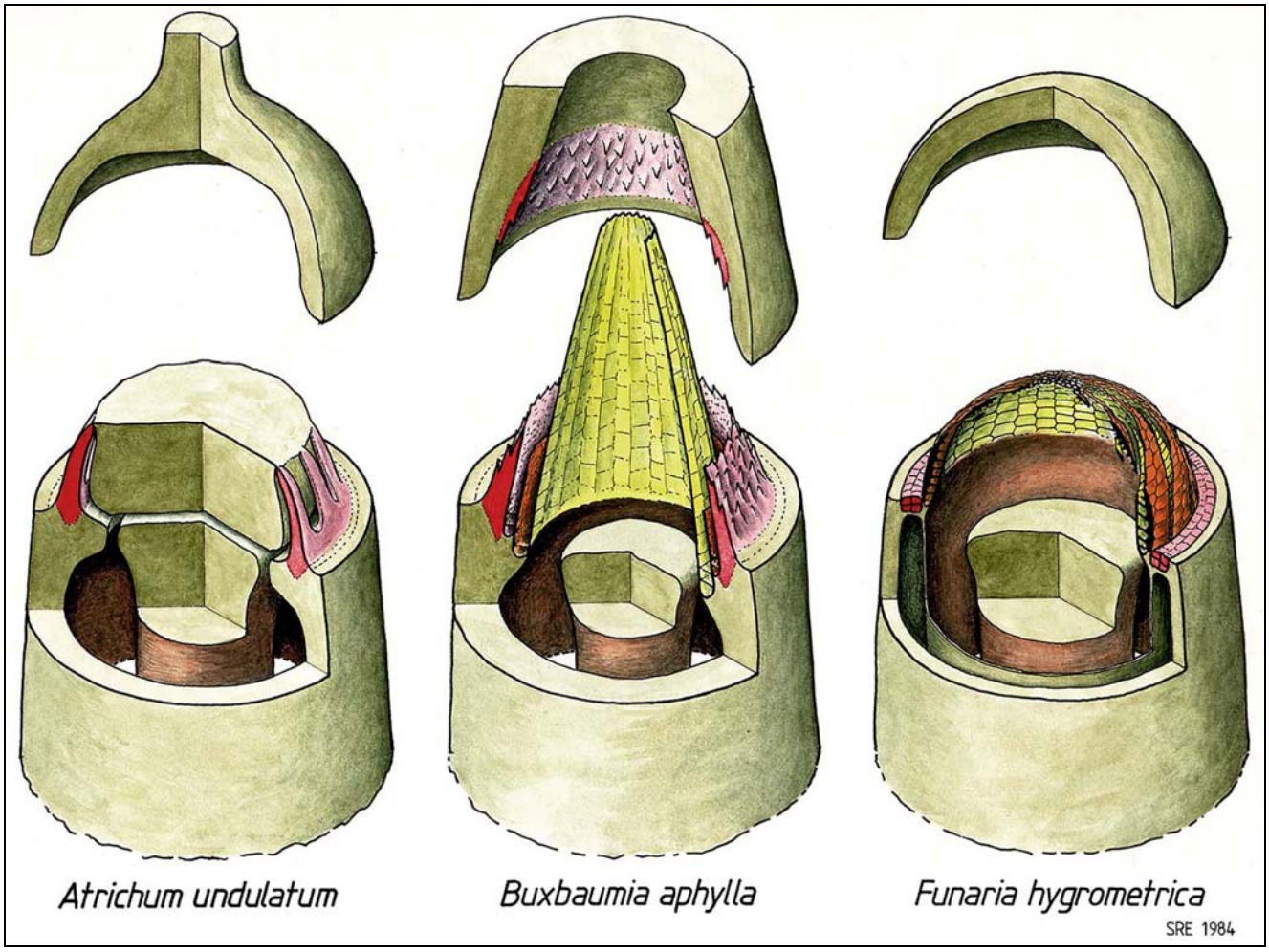


Figure 131. Three species with the operculum removed to reveal differences in peristome types. Drawings by Sean Edwards.

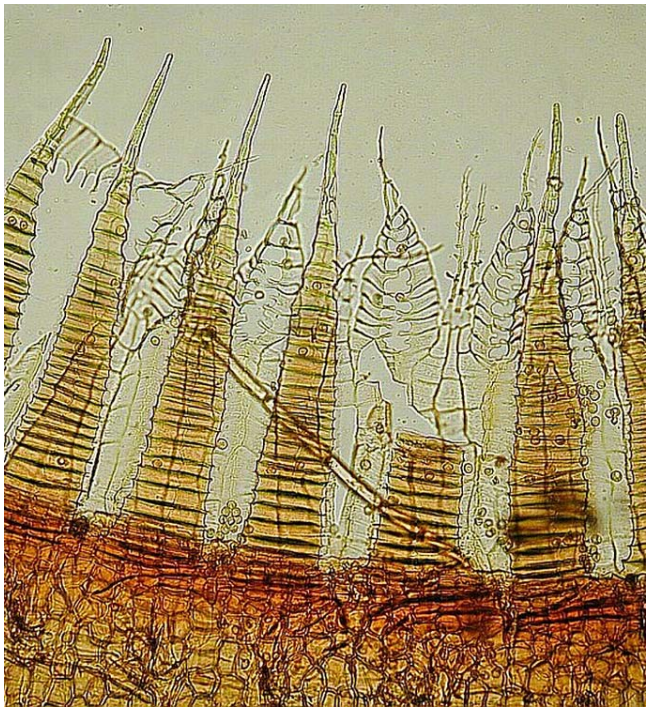


Figure 132. ***Bryum caespiticium*** peristome showing peristome teeth and cilia. Photo by Michael Lüth, with permission.

Figure 133. ***Brachythecium rutabulum*** peristome showing nodose cilia (see sever in upper part of image between inner and outer peristome). Photo by Laurie Knight <www.laurieknight.net>, with permission.

Summary

Bryophytes often need to be cleaned before they are mounted for observation. Methods for doing this include a special bryophyte washing machine, netting on an embroidery hoop, wash bottle, HCl, H_2O_2, and agitation. Dried bryophytes need to be rehydrated using a wetting agent such as water, soap, detergent, heated water, 2% KOH, Pohlstoffe (docusate sodium), or Agral 600. Some leaves need to be cleared before cell wall papillae and wall structure can be seen clearly, using reagents such as lactic acid, KOH, NaOH, or chloral hydrate. Some species require air drying or dehydration in ETOH to prepare them for making a slide.

Stains permit further clarification of structures such as pores and wall markings and permit determination of cell types. They can be as simple as food coloring or an array of chemical stains used singly or in combination. Identification of ***Sphagnum*** usually requires a stain to discern the leaf cell pores. Archegonia and spermatogenous cells can be stained with fast green. Fluorescent dyes coupled with a fluorescence microscope can reveal bulbils and determine if spores are viable. A pectinase preparation can be used to stain liverwort capsules.

Some bryophytes (esp. Pottiaceae) produce different colors in reaction to a mix of HCl, KOH, concentrated H_2NO_3, and H_2SO_4. Some ***Sphagnum*** subgenera respond to *p*H and have distinctive colors in $NaHCO_3$.

Removing leaves from stems is aided by a dissecting microscope and microforceps. Sharp razor blades can be used to make sections of leaves and stems. Cutting is best done under a dissecting microscope, with the method being largely a matter of preference, including chopping, wax mounts, pith sandwich, cutting block, and double slide sectioning. If you are lucky enough to have a cryostat, you can use it to make sections.

Some structures require special treatment, such as clearing spores, using SEM, seeing vacuoles, preserving and seeing oil bodies, and seeing details of peristome teeth.

Acknowledgments

Numerous discussions by Bryonetters have contributed heavily to this chapter. I appreciate the additional help from Richard Zander who answered my many questions quickly and thoroughly and alerted me to his websites. He also did further testing of the clearing technique. Isawo Kawai kindly sent me numerous pictures and information on his staining procedure. Ralf Wagner provided me with the instructions for the Etzold staining and W3A staining.

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CHAPTER 2-2b
SPHAGNUM STAINING

H. Rudi Zielman and Janice M. Glime

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CHAPTER 2-2b
SPHAGNUM STAINING

Figure 1. ***Sphagnum russowii***, a species for which pores are seen more easily when stained. Photo by Des Callaghan, with permission.

Following a discussion on Bryonet and the diminishing size of his trusty aniline pencil (Figure 2), Rudi Zielman set out to compare various stains used to make the pores of ***Sphagnum*** leaves and stems more visible. This subchapter is the result of that investigation. Another driver for this investigation is the toxicity of aniline. Furthermore, newer versions of this pencil simply didn't work – they didn't color wet leaves (Figure 3-Figure 4). And an aniline solution did not color the leaves easily. Then the leaves lost their color when they were placed in water.

Figure 2. Aniline blue pencil used to stain ***Sphagnum***. Photo by Rudi Zielman.

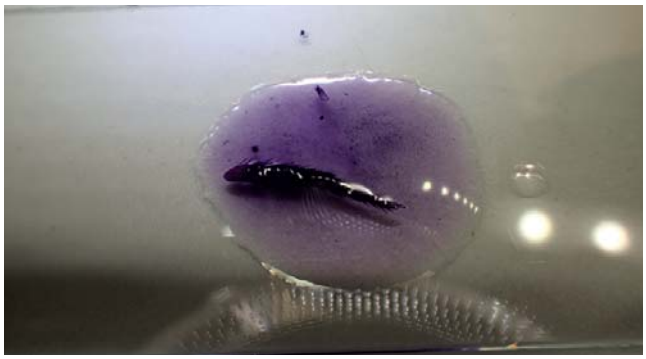

Figure 3. ***Sphagnum obtusum*** branch in water with aniline blue pencil scrapings. Photo by Rudi Zielman.

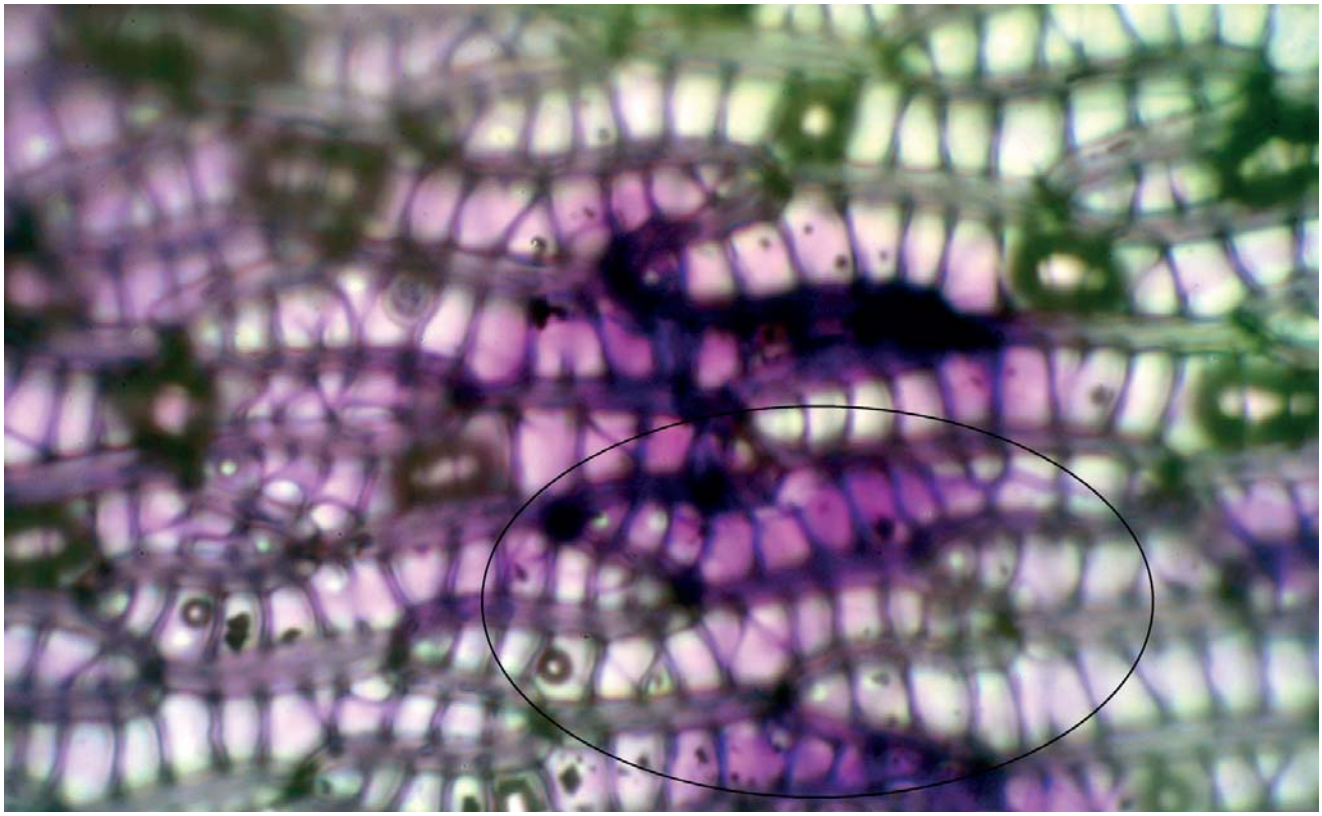

Figure 4. ***Sphagnum obtusum*** stained with an old aniline pencil. The branch was stained, leaves carefully removed, and placed on a slide in water. The pores became more visible, as seen in the area inside the ellipse. Photo by Rudi Zielman.

The dyes used are all dyes with a ring structure; especially with toluidine blue it is emphasized that it should be the toluidine blue-O, *i.e*. the methyl and amine groups in the ortho position. This is also true with safranin, and apparently is the case in all the stains described here and currently available for staining the moss. Methylene blue and safranin are sold at (web) stores that also sell microscopy equipment.

Toluidine blue is currently the most difficult to obtain; when Zielman collected all the materials about 8 years ago he was able to collect the needed materials from a web shop and a university lab; gentian violet was also a problem at that time, now to a lesser extent; one needs a doctor's prescription to get it from a pharmacist. It is used in the treatment of **thrush** (a fungal infection) in infants, and can apparently also be found at shops that focus on supplies for breastfeeding. An advantage is that all these dyes are, in contrast to aniline, non-toxic. A 10 ml ready-to-use solution costs approximately 15-20 euros. Methylene blue, toluidine blue-O, and gentian violet are also available as a powder (quite difficult); to use them one places a few grains (forceps tip) on a slide and dissolves this in water or ethanol. You can also use the powder to prepare a "stock solution" (additional recipes on the internet; several are listed here, but unfortunately no URL's or author names were available), but then some stirring and filtering facilities are required. For the staining effects it does not matter whether you use the solution or the powder, but the solution works more easily.

A word about safety: methylene blue is the most annoying of these four dyes tested here. It is non-toxic, but it can cause eye and skin irritations. All solutions contain alcohol and are therefore slightly irritating. Spilled dyes can be easily removed with a tissue and some methylated alcohol.

Methods

The stains used are:

No colorant (stain) applied
Methylene Blue
Toluidine Blue (actually tolonium chloride)
Gentian Violet (also called crystal violet or methylrosanaline)
Safranin

Methylene Blue from Powder

Prepare a saturated solution of methylene blue by adding 1.5 g powdered methylene blue to 100 mL 95% ethyl alcohol. Slowly add the alcohol to dissolve the powder. Add 30 mL saturated alcoholic solution of methylene blue to 100 mL distilled water and 0.1 mL 10% potassium hydroxide. Always make these in a 1% ETOH solution, a saturated solution in water.

Toluidine Blue-O from Powder

Dissolve the toluidine blue powder in distilled water (0.1 g of toluidine blue in 100 ml of distilled water). Check the *p*H of the solution, it is very important. The stock solution should be *p*H 2.3 (and less than 2.5), achieved with 5 ml 1% sodium chloride in 45 ml; mix well. The working solution should be *p*H 2.0-2.5. Make this solution fresh and discard after use.

Alternatively, mix powder to dissolve and adjust *p*H to 2.0~2.5 using glacial acetic acid or HCl.

Gentian Violet Powder

Dissolve 2 g of gentian violet powder dye in 20 ml of 95% ethanol (Histanol 95) and mix with 80 ml of 1% aqueous solution of ammonium oxalate. Dip the moss quickly and rinse in water (Figure 5).

Figure 5. ***Sphagnum*** stained with gentian violet. Photo by Don Avery, with permission.

Safranin-O

Mix 10 ml of basic solution with 90 ml of distilled/demineralized water.

Applying Stain

For each stain, a dry branch or stem piece is quickly dipped in a few drops of the stain, stirred and slightly pressed to make sure the stain is distributed everywhere. If you dip too briefly, the leaf parts (often the proximal half) may not be properly stained because the stain solution could not reach them. After dipping, the branches or stem pieces are rinsed in demineralized water. Do this carefully; ***Sphagnum*** mosses very easily lose leaves or become damaged. Just dip in water, replace drops, re-dip, until the water no longer colors. After that, the material is mounted on the slide.

Microscopic images in this subchapter were taken with a Leica DM E microscope with 40 X achromatic objective and trinocular head with a Leica 1 X photo lens on which a Nikon D5300 camera body was attached. The diaphragm opening of the microscope is equal for all photos; the exposure intensity is not. Because a microscopic image has no depth of field, stacking is needed. First focusing is done slightly above the leaf blade or section and then the fine adjustment knob is used manually through small steps to change the focal plane through the cell wall, going deeper and deeper. The recordings are then stacked with CombineZM and reworked (color levels automatically balanced, stack edges clipped) with GIMP 2.10. (It is also possible to have a camera that does automatic stacking and combining the images.) The resulting photos are composed of a variable number of individual photos, depending on visual evaluation (or the number provided by an automatic camera).

Results

In the overviews below we show a few species in which pores are important to observe. For each species in the images shown, the different stains were applied to adjacent branches of the same stem just below the capitulum. The order is always no coloring, methylene blue, toluidine blue-O, gentian violet, safranin. This sequence shows a fairly even gradient in the colors seen, from blue through purples to orange-red.

Sphagnum divinum (Figure 6-Figure 16)

First of all, ***Sphagnum divinum***, where the width of pores in the proximal part of branch leaves and the thickness of the wall between **chlorocytes** (cells with chloroplasts) and **hyalocytes** (colorless cells) are important to observe. What you see in these images of ***Sphagnum divinum*** is that the pores in the hyalocytes are clearly visible and are less than half the width of the cell. The leaf cross section is less clear. This is caused by the sigmoid cell pattern; the wall between hyalocytes and chlorocytes is visible through many sections behind one another, and thus is often blurred in stained leaf transections, so it is recommended to inspect these in unstained condition.

Figure 6. ***Sphagnum divinum***, Ireland, a segregant from ***Sphagnum magellanicum*** that can be identified more easily when stained. Photo by David Long, with permission.

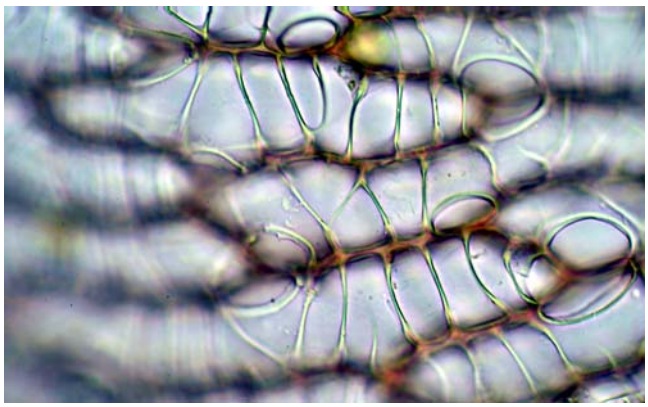

Figure 7. ***Sphagnum divinum*** leaf cells with no staining. Photo by Rudi Zielman.

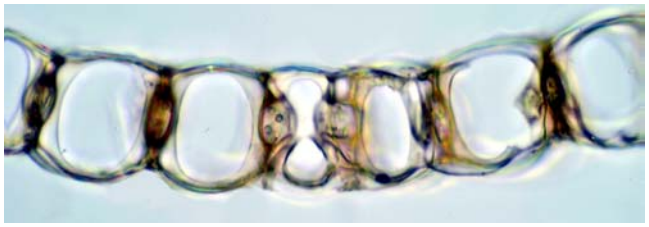

Figure 8. ***Sphagnum divinum*** leaf cross section with no staining. Photo by Rudi Zielman.

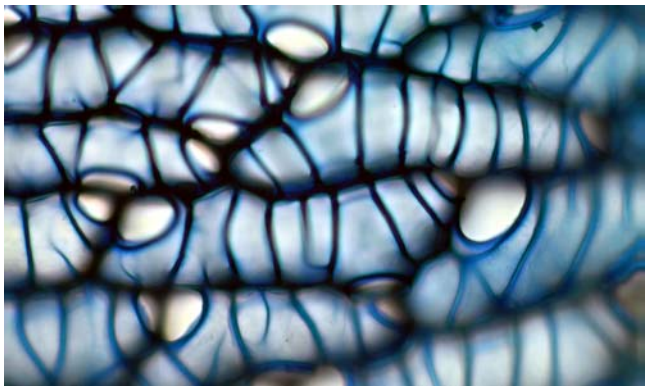

Figure 9. ***Sphagnum divinum*** leaf cells stained with methylene blue. Photo by Rudi Zielman.

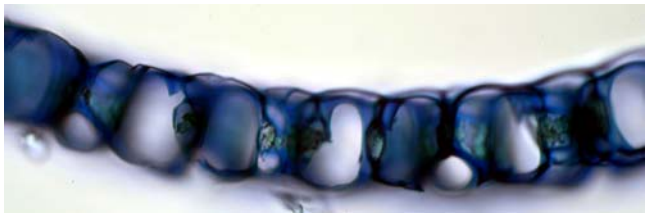

Figure 10. ***Sphagnum divinum*** leaf cross section, stained with methylene blue. Photo by Rudi Zielman.

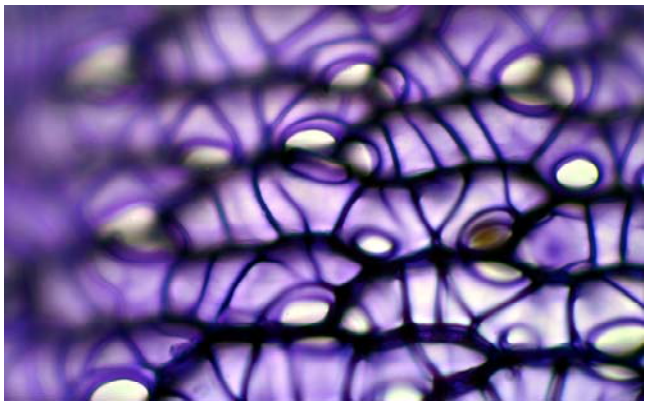

Figure 11. ***Sphagnum divinum*** leaf cells stained with toluidine blue-O. Photo by Rudi Zielman.

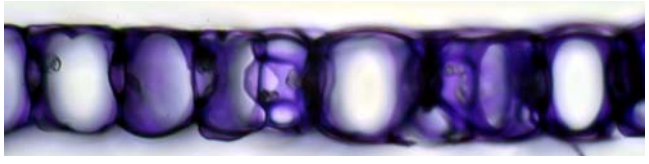

Figure 12. ***Sphagnum divinum*** leaf cross section, stained with toluidine blue-O. Photo by Rudi Zielman.

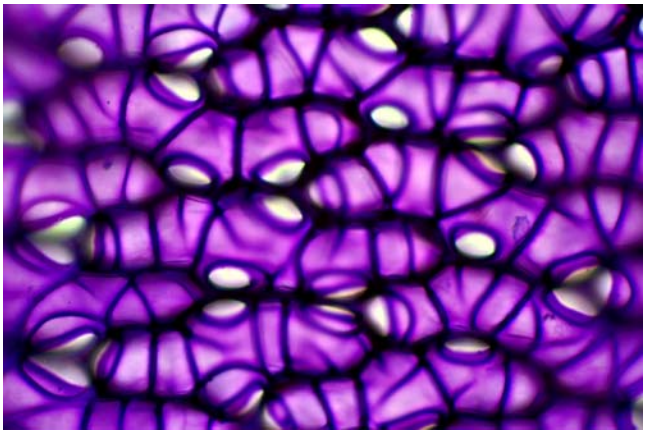

Figure 13. ***Sphagnum divinum*** leaf cells stained with gentian violet. Photo by Rudi Zielman.

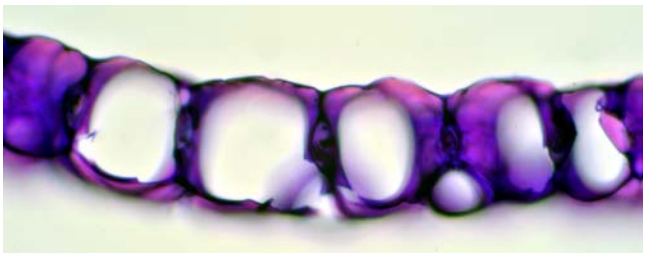

Figure 14. ***Sphagnum divinum*** leaf cross section, stained with gentian violet. Photo by Rudi Zielman.

Figure 15. ***Sphagnum divinum*** leaf stained with safranin. Photo by Rudi Zielman.

Figure 16. ***Sphagnum divinum*** leaf cross section, stained with safranin. Photo by Rudi Zielman.

Sphagnum obtusum (Figure 4, Figure 17-Figure 27)

A true challenge with staining lies in making visible the very small and very unclear pores of ***Sphagnum***

obtusum. The cell wall thinnings that matter most are primarily located proximally in the leaf at the lateral sides; this zone is therefore always pictured.

Figure 17. ***Sphagnum obtusum***, a species with faint pores that require staining for observation. Photo by Michael Lüth, with permission.

It should be clear that all stains enhance the visibility of the structures in the branch leaf cells of ***Sphagnum obtusum***, while without such staining the faint pores remain invisible. But again, the stained cross-sections of the branch leaves are more difficult to interpret than the unstained ones.

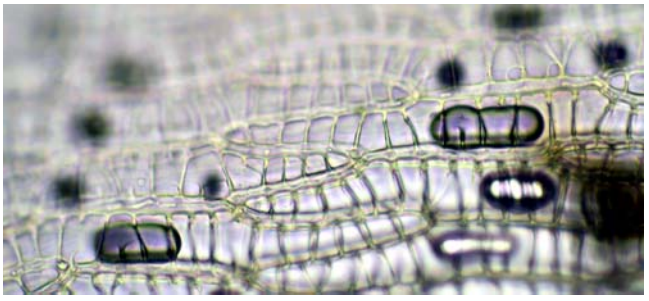

Figure 18. ***Sphagnum obtusum*** leaf cells, with no staining. Photo by Rudi Zielman.

Figure 19. ***Sphagnum obtusum*** leaf cross section, with no staining. Photo by Rudi Zielman.

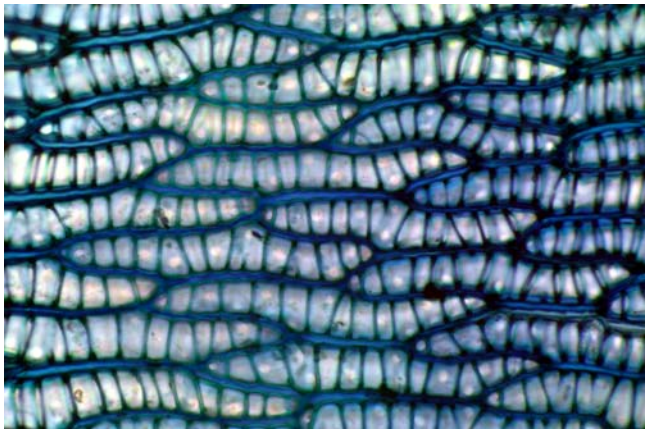

Figure 20. ***Sphagnum obtusum*** leaf cells, stained with methylene blue. Photo by Rudi Zielman.

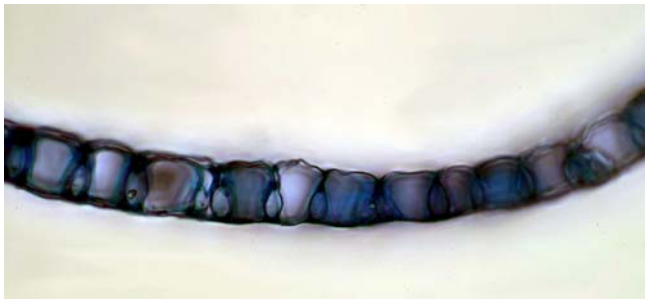

Figure 21. ***Sphagnum obtusum*** leaf cross section, stained with methylene blue. Photo by Rudi Zielman.

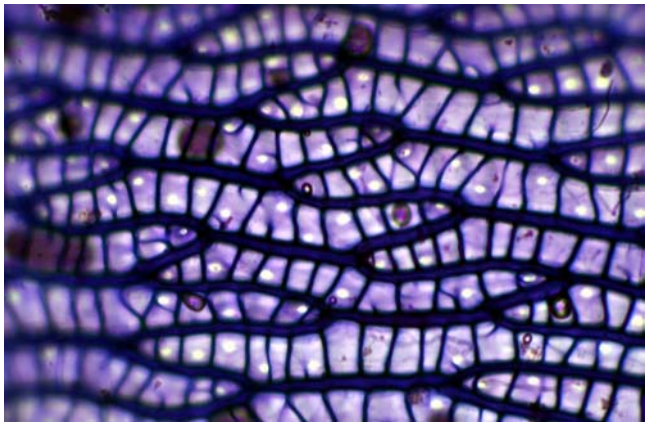

Figure 22. ***Sphagnum obtusum*** leaf ells, stained with toluidine blue-O. Photo by Rudi Zielman.

Figure 23. ***Sphagnum obtusum*** leaf cross section, stained with toluidine blue-O. Photo by Rudi Zielman.

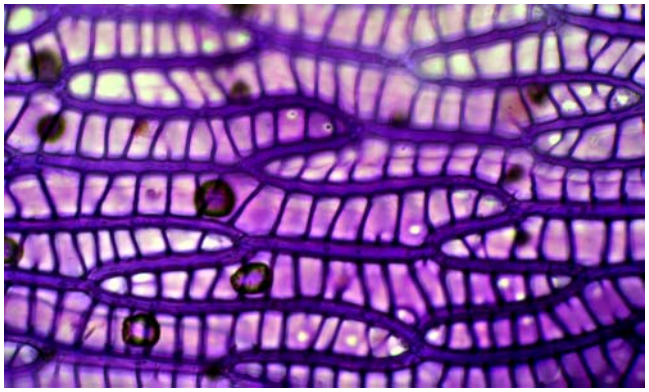

Figure 24. ***Sphagnum obtusum*** leaf cells, stained with gentian violet. Photo by Rudi Zielman.

Figure 25. ***Sphagnum obtusum*** leaf cross section, stained with gentian violet. Photo by Rudi Zielman.

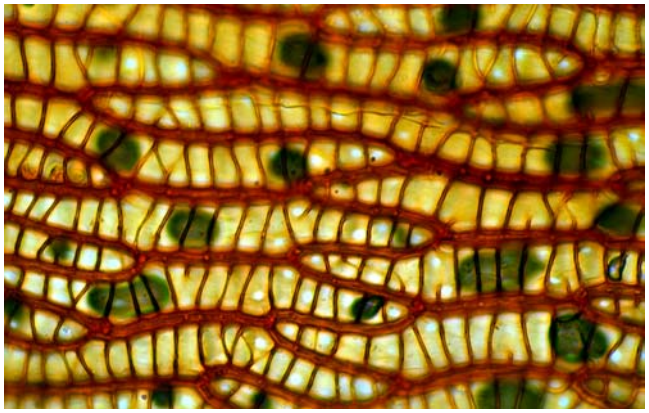

Figure 26. ***Sphagnum obtusum*** leaf cells, stained with safranin. Photo by Rudi Zielman.

Figure 27. ***Sphagnum obtusum*** leaf cross section, stained with safranin. Photo by Rudi Zielman.

Sphagnum russowii (Figure 28-Figure 38)

In ***Sphagnum russowii***, the **pseudopores** (thin spots in the cell wall) of the stem epidermis are of importance. The easiest way to prepare them is by holding a piece of stem with forceps and then cut the whole stem diagonally with a razor blade; sometimes it even works to get rid of the tissue below that epidermis completely (*e.g.* in the gentian violet preparation in Figure 36). Hölzer (2010) also mentions the large pores on the ventral side of branch leaves as characteristic (Figure 29); figs 30, 32, 34, 36 show the same pore structure.

Figure 28. ***Sphagnum russowii***, a species with pores that are more easily seen with staining. Photo by Hermann Schachner, through Creative Commons.

Figure 29 is the non-stained version of ***Sphagnum russowii*** leaf pores; this image comes close to what we see through the microscope. In all pictures of the stem epidermis (Figure 32, Figure 34, Figure 36, Figure 38), except the unstained (Figure 30), the faint pores are clearly visible. Also the large pores on the ventral side in the branch leaves are easily recognizable. Please realize that the white holes are a view where a pore on the ventral and dorsal side are aligned with each other!

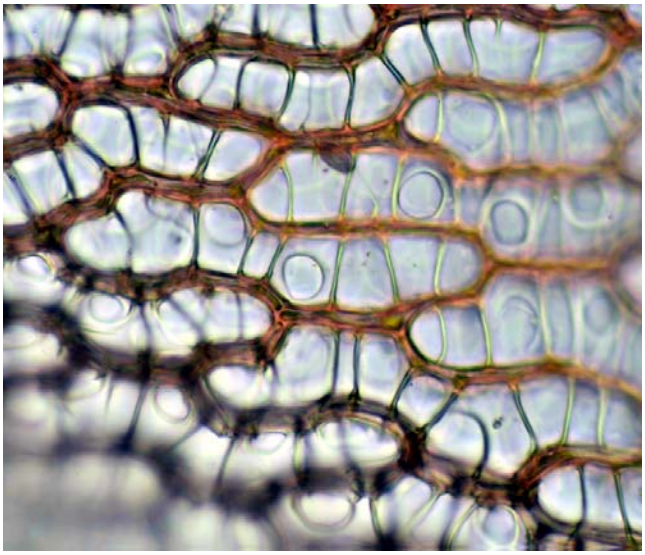

Figure 29. ***Sphagnum russowii*** leaf cells showing pores with no stain. Photo by Rudi Zielman.

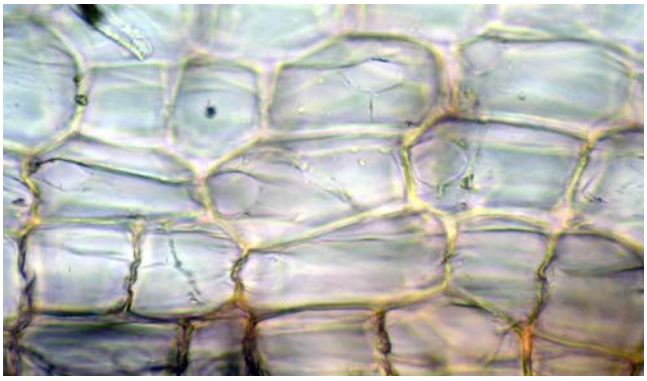

Figure 30. ***Sphagnum russowii*** stem epidermis, with no stain. Photo by Rudi Zielman.

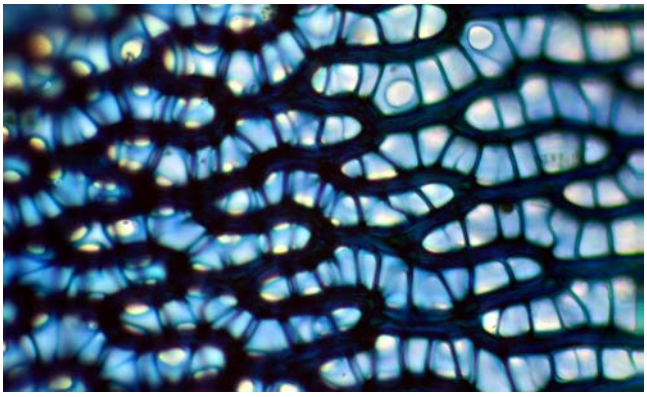

Figure 31. ***Sphagnum russowii*** leaf cells, stained with methylene blue. Photo by Rudi Zielman.

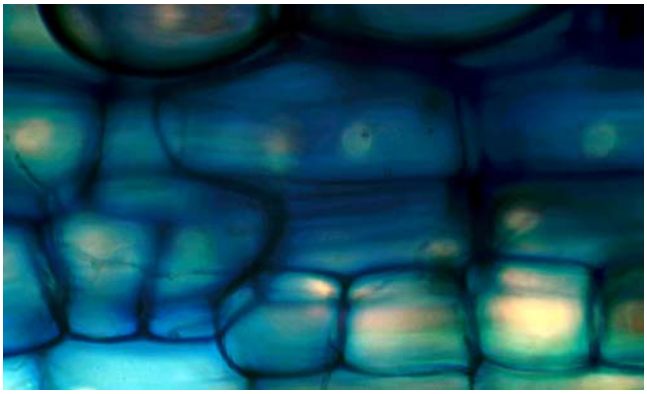

Figure 32. ***Sphagnum russowii*** stem epidermis, stained with methylene blue. Photo by Rudi Zielman.

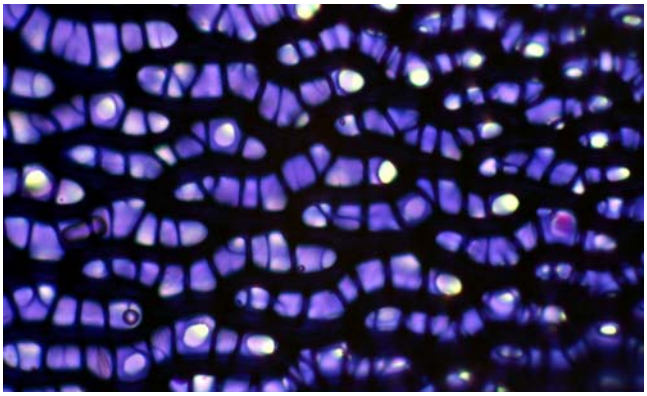

Figure 33. ***Sphagnum russowii*** leaf cells, stained with toluidine blue-O. Photo by Rudi Zielman.

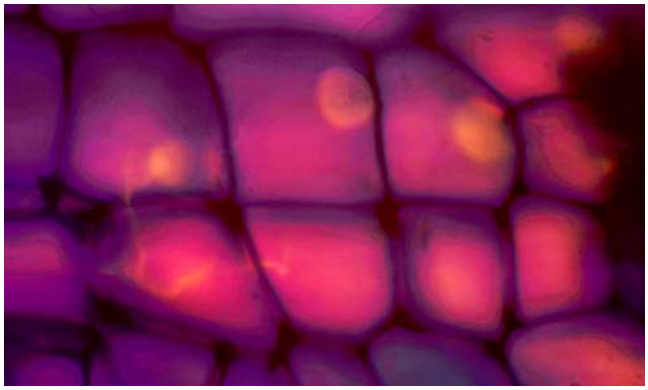

Figure 34. ***Sphagnum russowii*** stem epidermis, stained with toluidine blue-O. Photo by Rudi Zielman.

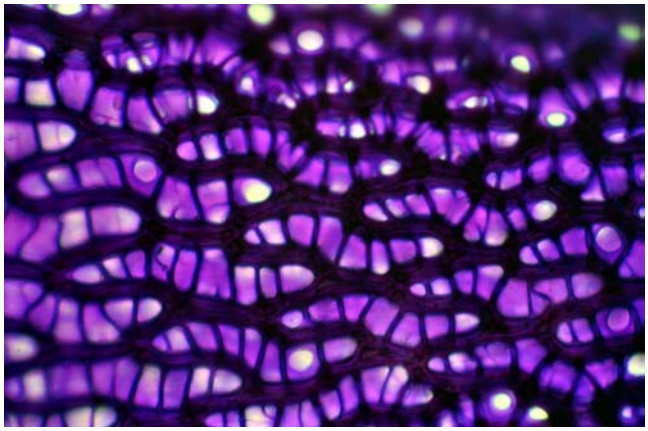

Figure 35. ***Sphagnum russowii*** leaf cells, stained with gentian violet. Photo by Rudi Zielman.

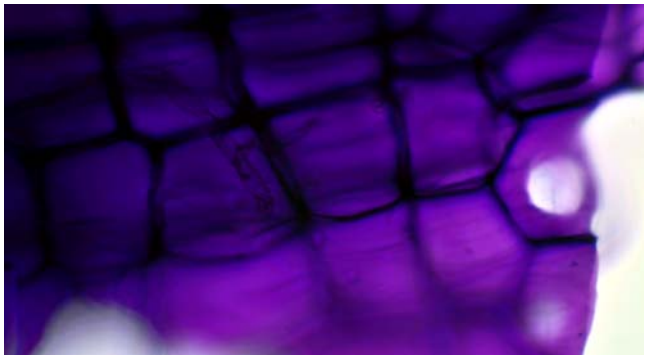

Figure 36. ***Sphagnum russowii*** stem epidermis, stained with gentian violet. Photo by Rudi Zielman.

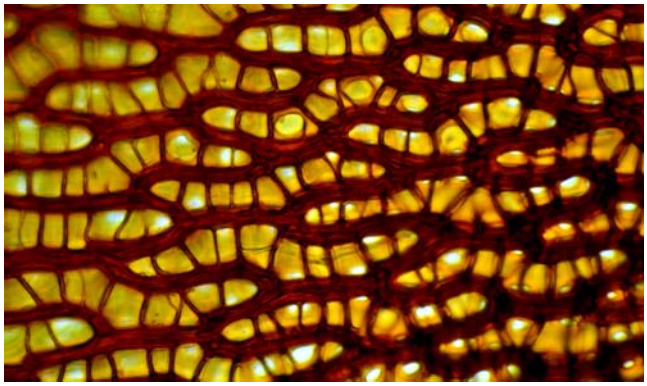

Figure 37. ***Sphagnum russowii*** leaf cells, stained with safranin. Photo by Rudi Zielman.

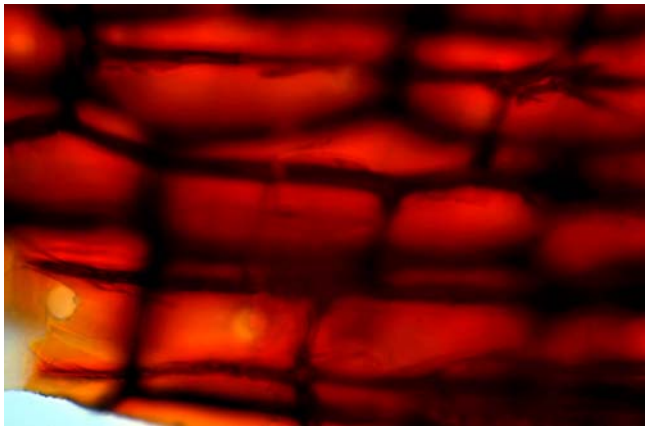

Figure 38. ***Sphagnum russowii*** stem epidermis, stained with safranin. Photo by Rudi Zielman.

Judgment Call

The staining of ***Sphagnum*** helps in making pores visible, as unstained gaps in stained walls, but is not always necessary. As an example, one can make a good judgment on ***Sphagnum divinum*** (Figure 6-Figure 16) and ***Sphagnum centrale*** (Figure 39-Figure 42) without staining. Differentiating these species depends on the thickening of the cell walls of chlorocysts as seen in section, most obvious on the adaxial (= ventral) leaf side. Staining can help in assessing this wall. In general, however, we recommend the location of chlorocytes to be assessed by unstained cross-sections.

Figure 39. ***Sphagnum centrale***. Photo by Hermann Schachner, through Creative Commons.

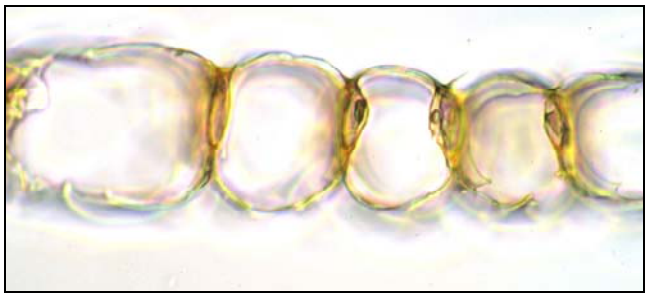

Figure 40. ***Sphagnum centrale*** unstained leaf cross section showing the almost hidden chlorocytes and thicker walls on the adaxial side of the hyalocytes. Photo by Rudi Zielman.

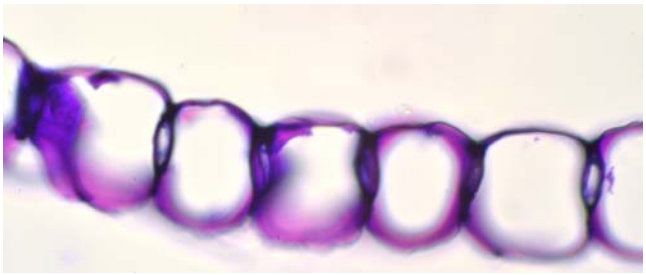

Figure 41. ***Sphagnum centrale*** leaf cross section with gentian violet stain. Photo by Rudi Zielman.

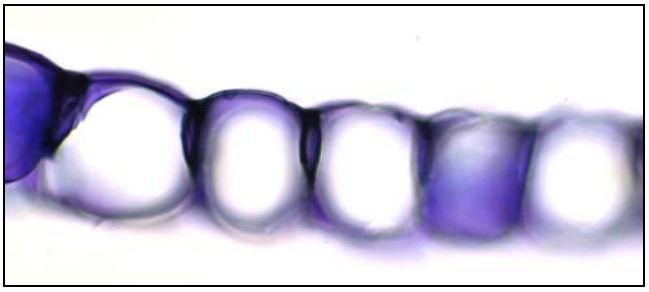

Figure 42. ***Sphagnum centrale*** leaf cross section with toluidine stain, giving a slightly better view of the thicker adaxial walls of the hyaline cells than in the gentian violet stain. Photo by Rudi Zielman.

If a decision has to be made as to whether faint pores or pseudopores are at hand, staining must be used. The dye which is used is less important as long as it is a cationic dye as already noted by Daniels and Eddy (1990). If I (Zielman) had read this in 2012 more carefully… For the rest it is merely a matter of taste; Adam Hölzer (2010) only wants to use gentian violet; Lisa op den Kamp (Bryonet, October 2012) has a strong preference for safranin; this is also the stain that was used by Laine *et al*. (2009), whereas in Australia all staining of botanical tissue is standardly done with toluidine blue (Rod Seppelt, pers. comm.). In general methylene blue, that used to be widely used, is considered a staining which is uncomfortably harsh and dark. Because of this I am, for the ease of use and availability, using more and more safranin, after my first bottle of gentian violet was empty. But after completing the work for this article, I tend to use toluidine blue, although it is tricky to obtain, or gentian violet. All in all it remains a tad a matter of personal taste, so not a firm conclusion. But I am going to use stains more often again, for an easier assessment.

Summary

Sphagnum pores are usually difficult or impossible to distinguish in unstained material. Some stains in use in the last century are toxic. And some current ones are difficult to obtain. Among the ones tested here, safranin and methylene blue are both safe and available from internet sources, gentian violet or toluidine blue might be preferred if obtainable. Some of the staining solutions can be made from powders, but it is easier to just buy the solutions ready-made.

Acknowledgments

This chapter is based mostly on a publication in Dutch (Zielman 2020). We all owe Rudi Zielman a vote of thanks for documenting the differences among the available stains.

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CHAPTER 2-3
LABORATORY TECHNIQUES: MAKING OBSERVATIONS

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CHAPTER 2-3
LABORATORY TECHNIQUES: MAKING OBSERVATIONS

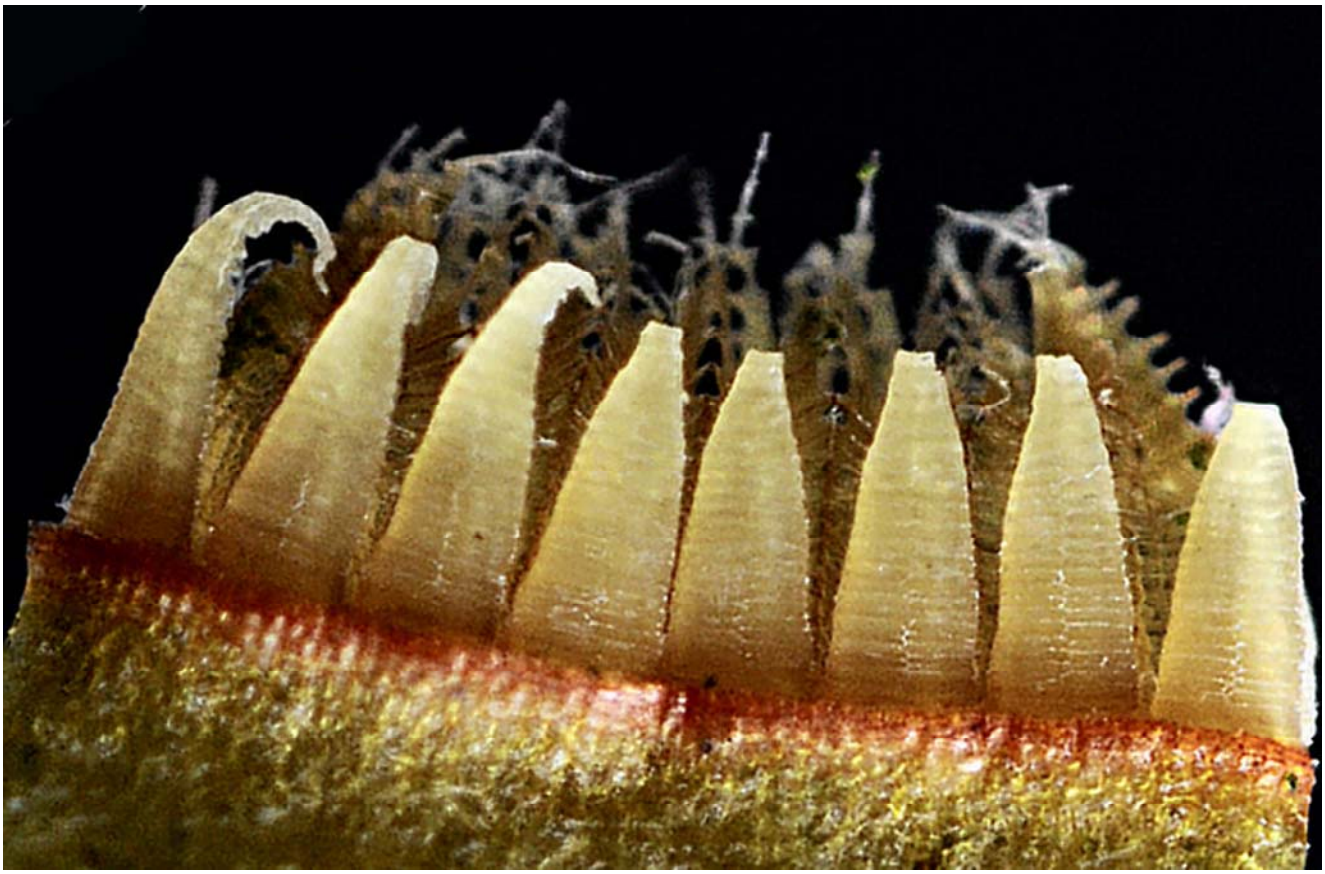

Figure 1. ***Plagiomnium rhynchophorum*** peristome ready to perform its dispersal of spores. Photo by George Shepherd through Flickr.

Sporophytes

Stomata

One of the most difficult things to see on a moss is the stomata at the base of the capsule. Rod Seppelt (Bryonet 27 August 2012) suggests clearing the capsules with lactic acid to make them easier to see. This method works well also to make it easier to see cell walls, cell content, papillae, and exothecial cells, including those on liverworts as well as mosses. The material should first be wet on a microscope slide and covered with a coverslip. Then place a drop or two of lactic acid on the edge of the coverslip and allow it to diffuse into the mount. **Gently warm the slide over a spirit flame** (a gas flame is too hot); this mix boils very quickly. The lactic acid gets rid of most of the cytoplasmic contents, thus clearing the tissues. If you want to make the mount permanent, then you must be sure all the lactic acid has been removed by heating, then add a permanent mounting medium at the edge of the coverslip.

Opening Immature Capsules (Lauridsen 1972)

Removing an operculum while keeping the peristome intact is difficult to impossible. Lauridsen (1972) tested a method that "fools" the capsule into behaving as if it is ripe, releasing the operculum. This is done with alternate immersion in **KOH** and **NaOCl**. The amount of KOH and NaOCl varies with species and ripeness and needs to be tested each time. This is best accomplished by dousing the capsule first with a drop of NaOCl for a few seconds, then in a solution of KOH until the mouth of the capsule becomes reddish. This may take 10 sec – 3 minutes. Zander (1993) recommends 2% KOH for Pottiaceae.

Although the method did not work well with ***Funaria hygrometrica*** (Figure 2) (14% opened), it was more than 90% successful in ***Bryum argenteum*** (Figure 3), ***B. intermedium*** (Figure 4), ***Distichium inclinatum*** (Figure 5), ***Mnium hornum*** (Figure 6), and ***Polytrichum commune*** (Figure 7) (Lauridsen 1972). The biggest disadvantage of the method is that the peristome teeth and exothecial cells

both become reddish in KOH, and the coloration remains. If possible, some capsules should be kept intact with no chemicals to retain natural colors. The treatment and color changes should be noted on the packet so as not to confuse further researchers with the altered colors. These chemicals should be washed away before mounting the specimen in Hoyer's or returning them to the packet. KOH plus Hoyer's will present a white precipitate, and excess NaOCl will eventually discolor the capsules.

Figure 2. ***Funaria hygrometrica*** capsule, with a lid (operculum) that is hard to remove. Photo by George Shepherd, through Creative Commons.

Figure 3. ***Bryum argenteum*** capsules, with opercula easily removed with KOH. Photo by Dick Haaksma, with permission.

Figure 4. ***Bryum intermedium*** with capsules; the operculum in this species is easily removed with KOH. Photo by David T. Holyoak, with permission.

Figure 5. ***Distichium inclinatum*** with capsules; the operculum in this species is easily removed with KOH. Photo by Michael Lüth, with permission.

Figure 6. ***Mnium hornum*** with capsules; the operculum in this species is easily removed with KOH. Photo by J. C. Schou, with permission.

Figure 7. ***Polytrichum commune*** capsules; the operculum in this species is easily removed with KOH. Photo by David T. Holyoak, with permission.

Zander (1993), working with **Pottiaceae**, suggests that if the operculum does not come off, the slide can be heated with a butane cigarette lighter, taking care not to let the flame touch the glass. A coverslip will reduce evaporation. If the peristome has a habit of breaking at the base, soak the intact capsule in a mix of **KOH** and **Pohlstoffe** for 15-20 minutes, or longer. To avoid precipitation that occurs with Pohlstoffe in KOH, one alternative is to add 1-2 drops of concentrated (4 g in 20 cc water) stock solution of **sodium N-lauroylsarcosine** (Gardol) to the bottle of KOH instead.

Britton (1890) found that capsules did not retain their ability to expand when rewet after drying, so she suggested that they should be kept in a moist dish under cover until needed for observation.

Peristomes

Miller (1988) reminded us of both the beauty and interesting behavior of peristome teeth (Figure 1). He advised that to see the details of the peristome, split the newly opened capsule lengthwise. Mount half in water with the outside surface upward and the other half with the inside surface upward. Adjust the light on the microscope, using the **diaphragm**, to get the best view of the details.

Sean Edwards (pers. comm. 22 April 2014) excites his students by demonstrating what he calls the karate-chop method, using a ***Polytrichum*** peristome (Figure 8). Using this method, he distinguishes peristomes in three species of the **Polytrichaceae**.

Figure 8. ***Polytrichum*** epiphragm showing peristome teeth. Photo by George Shepherd Creative Commons.

To observe the hygroscopic movement of the teeth, Miller (1988) suggested removing the sporophyte with its seta intact. Thread the seta through a pinhole in a stiff piece of paper to position the capsule firmly in a vertical position. In some mosses, like **Mniaceae**, you can see movement of an exposed peristome (Figure 9) and spore dispersal by breathing on the dry peristome, providing a change in moisture. Observe the teeth at 40X and 100X while blowing moist breath across the teeth. This works best when a second person supplies the breath so that you can observe it with the microscope at the same time. This will only work well if the capsule is mature and the spores are still inside, but the peristome can still respond even if the spores are gone.

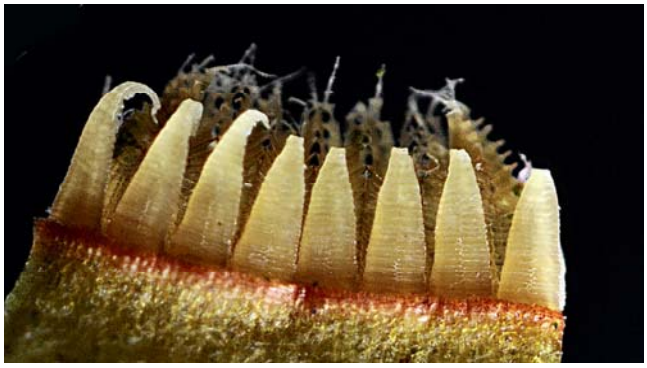

Figure 9. ***Plagiomnium rhynchophorum*** (**Mniaceae**) peristome – one that flexes in response to humidity in one's breath. Photo by George Shepherd, with permission.

I have had success in observing peristome movement with ***Dicranella heteromalla*** (Figure 10-Figure 11) by keeping the capsule and seta attached to the moss. The moss needs to be rehydrated by placing one or more drops of water on the leaves near the seta insertion. Exercise caution to avoid getting water on the seta or capsule. The nearby moisture first causes the seta (Figure 10) to gyrate, delighting the students; then the peristome teeth (Figure 11) begin to flex. Breathing on it might give the same result.

Figure 10. ***Dicranella heteromalla*** with capsules; setae in this species will gyrate in response to moisture changes. Photo by Bob Klips, with permission.

Figure 11. ***Dicranella heteromalla*** capsule showing peristome teeth that will respond to moisture changes. Photo from Botany 321 Website, UBC, with permission.

Anchoring Specimens in Clay

Conard developed a unique idea for examining peristomes and their activities. He suggested placing a bit of clay (any color) 5-8 mm across and 1-2 mm thick on a slide. A capsule, with its seta removed, can be placed in any desired position for observation with high power on a compound microscope. The right clay will remain soft, so the slide can be kept for several years and the capsule can still be repositioned. This can also be useful for demonstrating peristome movement to students and for other uses where positioning is important.

Counting Spores

Britton (1890) detailed a way to examine the capsule and its contents. She suggested that observing a dry capsule on a microscope slide under low power on a compound microscope (4x or 10x objective) could lead to the breaking of the annulus that holds the lid (operculum) to the capsule. If the annulus releases the lid, the dryness will cause capsule compression and spores will be pushed out. If there are still too many spores in the capsule, put a drop of water on one edge of the coverslip and draw it through with a piece of paper towel or blotter on the opposite edge. The spores will be drawn out as the water moves.

If this procedure is unsuccessful, you can encourage the spores to come out by holding the slide over the flame of an alcohol lamp until the water boils (Britton 1890). This drives the air out of the capsule and the spores with it. BE CAREFUL with this technique because if the slide gets too hot it can break, sometimes explosively. Withdraw the slide before the water dries up completely.

Most of the recent spore counting techniques have been copied from pollen counts. To obtain a sense of variability, one capsule is not enough, despite the large number of spores in most species. Fifteen is a reasonable number, but they should, if possible, be distributed among 15 clumps to minimize the bias of a single genotype. One drop of Extran® in 5 ml distilled water can prevent clumping. These can be spread in 5 ml water in a **Newbauer chamber** (used for counting platelets and red cells in blood). This chamber is designed for a thick crystal slide with the size of a glass slide (30 x 70 mm, but 4 mm thickness). The counting area is located in the center of the slide. Counting can be done at 100x, with further replication achieved by four counts per sample. The mean number of spores per sporangium is used. Size uses the greatest diameter and can be based on photomicrographs analyzed with ImageJ software (Rasband 1997-2002).

Spores can be difficult to observe because of their density. Miyoshi (1969) compared the visibility of the special surface ornamentation under light and SEM microscopy, demonstrating the superiority of SEM for this purpose. Other methods are covered in Chapter 2-2 of this volume.

David Wagner (Bryonet 22 January 2020) suggested a method that is used for pollen grains in anthers. The anther or capsule is wetted with a small amount of wetting agent. This keeps the spores in a clump instead of floating to the edges of the drop. Smash the capsule in a small drop of glycerine that will fit under the coverslip. Instead of a normal coverslip, use a **reticle** (series of fine lines or fibers in eyepiece of optical device such as microscope, used as measuring scale or aid in describing location of objects) with a 1 cm grid marked in millimeters. A grid of this size will have one square visible under the 10X objective of a compound microscope. This magnification is high enough to count the spores one square at a time, from top right to lower left, 100 squares. It is tedious but gives a very accurate result with a single mount.

Efrain De Luna (Bryonet 22 January 2020) suggested that to avoid the tedious stem, you can use the NIH Image (ImageJ, free software) or purchase ImagePro (Media Cybernetics) to recognize such discrete objects as cells, spores, *etc*. and determine their size and counts with the software.

Tom Ottley (Bryonet 22 January 2020) suggested a more mathematical approach.

Wagner assumes that evolutionary selection would result in the maximum number of spores being packed into a capsule. Then one can measure the internal diameter of the capsule and the diameter of a spore. Capsule diameter, divided by spore diameter, cubed x 0.6 would give the number of spores. He then multiplies by 0.5 to compensate for other structures (such as the columella) taking up space. This should actually be calibrated for each species by comparing to actual counts, and spores would probably need to be at the same stage of development. Ottley also suggesting that weighing a few (~10) ripe capsules, then emptying the spores and reweighing the capsule could give you an estimate of the spore weight. You could calculate the weight from a measured diameter by assuming a density of 1. This requires a sensitive balance.

Nicholas McLetchie (Bryonet January 2020) suggests the alternative method of using a hemocytometer, following methods for counting blood cells.

One method for calibrating counts, used by palynologists, is to purchase a tablet with a known number of *Lycopodium* spores – usually with ~10,000 each (Bent Vad Odgaard, Bryonet 22 January 2020). One tablet is added to the solution containing the liverwort spores and a few drops of HCl are added to dissolve the calcium carbonate that that holds the tablet together. Since you know the number of *Lycopodium* spores, and if you assume an equal and even dispersion of both kinds of spores, you can compare the counts of the two kinds of spores under the field of view and use the ratio to calculate the total number on the slide.

Adam Hölzer (Bryonet 22 January 2020) suggests putting spores of several capsules in a measured amount of water (50 or 100 ml) with some glycerin. You will need to test several amounts of glycerin to find the appropriate amount. Then shake the mix very well and quickly remove 1 or 0.5 ml to a slide before the spores can settle. These can then be counted by one of the above methods.

Surface ornamentation and shape are likewise important in examining spores (Kristian Peters, Bryonet 13 November 2019). Some of these ornamentations are important in dispersal and may differ between aquatic and terrestrial species.

Flotability can also be an indication of density. Misha Ignatov (Bryonet, 12 November 2019) reported that he had heard about one experiment where **Polytrichaceae** spores remain floating on the water surface despite various

attempts to sink them, but after adding TRIS (reducing surface tension) they all sank immediately. Thus, their density is slightly greater than 1. Using solutions of various density one might like find out spore density quite precisely, if necessary.

Spore diameter is provided in most descriptive bryophyte floras for each species (Misha Ignatov, Bryonet 12 November 2019). For a description of shape, size, and ornamentation of moss spores in Europe, see Boros and Járai-Komlódi (1975).

Spore Dispersal

Place mosses or liverworts with mature capsules where the heat of a lamp is focused on them. Allow the bryophytes and their capsules to dry with the heat until the operculum comes off (mosses) or the capsule splits (liverworts). If it is a moss, the peristome teeth will begin to move as the capsule dries further and the seta may begin to gyrate. If it is a liverwort, the elaters will begin to twist, aiding in the dispersal of the spores.

This demonstration could be even more interesting by placing the capsule on an agar plate (see chapter on culturing) for the above procedure (we haven't tried this, so it might not work). Set the capsule into the agar so that it is upright. It might be necessary to put a narrow cellophane collar around it to keep the capsule from absorbing moisture from the agar. When spores disperse, they will land on the agar. The plate can then be covered to allow the spores to germinate.

Another method for determining dispersal distance is to place a capsule upright by one of the methods described earlier and place microscope slides coated in glycerine at designated distances from the capsule. The spores that are dispersed will be trapped by the glycerine and can be observed under the microscope. This could likewise be done with plates of agar. I would suggest the small Petri plates (35 or 50 mm) to save agar and space. This same technique will work in the field as well as in the lab. There will undoubtedly be contamination, but since the goal is only to locate spores and the distance travelled, contamination need not be a concern.

Living spores in the capsule or elsewhere can be distinguished from dead ones by several techniques. Fluorescence (see Chapt. 2-2 in this volume) will make living spores and living parts of spores visible when viewed using a UV light source. When using an ordinary light microscope, living spores can be distinguished using acetocarmine stain (Mogensen 1978). Living spores stain deep red, whereas dead spores do not stain at all.

Sperm

The first problem for observing sperm (Figure 12) is finding the antheridia at the right stage. By the time the male inflorescence is distinguishable, the sperm are likely to be dispersed (Jeff Duckett, Bryonet 11 January 2012). While many bryophytes are adapted to take advantage of spring rains for dispersal of sperm, we are learning that mites and springtails can disperse them, and some bryophytes take advantage of autumn water. ***Polytrichum*** (Figure 13-Figure 14) typically disperses sperm in early spring, ***Sphagnum*** (Figure 15) in autumn (Jeff Duckett, Bryonet 11 January 2012). ***Pellia*** (Figure 16), which has the largest sperm, disperses in early summer. Reese (1955) suggests that sperm are best collected during a dry period because rain will cause them to disperse and you will miss them. Of course if you see new growth arising from the antheridial head, you have missed the dispersal event (Figure 13).

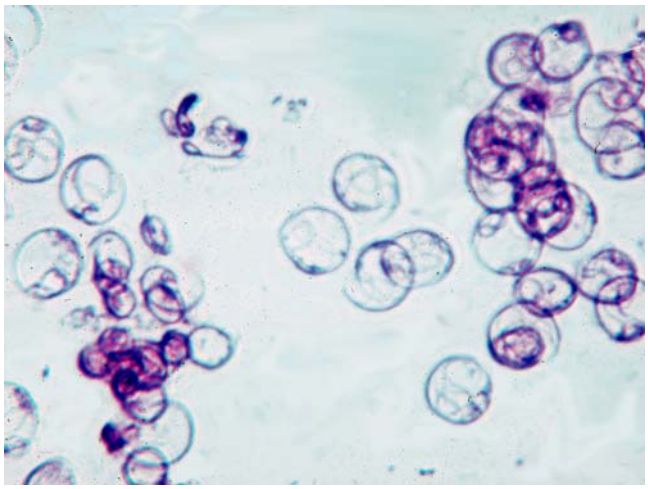

Figure 12. Stained bryophyte sperm. Image modified by Janice Glime.

Figure 13. ***Polytrichum juniperinum*** with splash cups that display new growth and hence have no viable antheridia in them. Photo by Janice Glime.

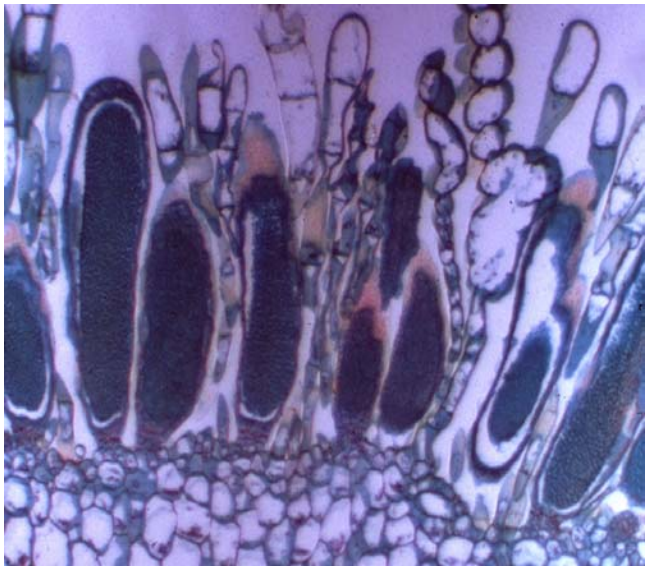

Figure 14. ***Polytrichum*** antheridia, where sperm are produced. Photo by Janice Glime.

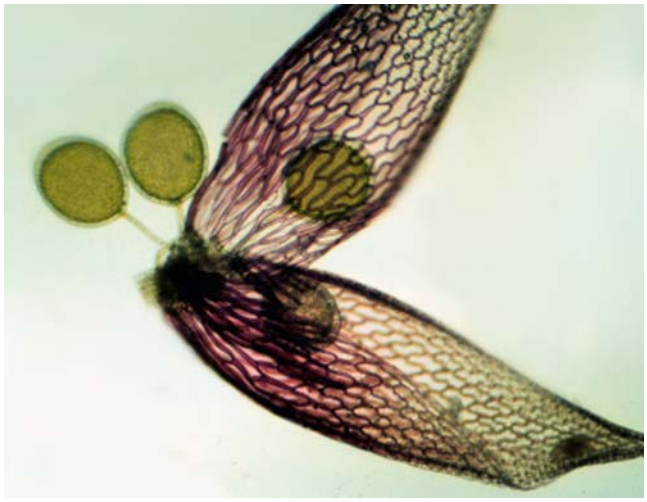

Figure 15. ***Sphagnum*** antheridia; these release sperm in autumn. Photo courtesy of Yenhung Li.

Figure 16. ***Pellia neesiana*** antheridia; these release large sperm in early summer. Photo by Michael Lüth, with permission.

If you are lucky enough to find ripe antheridia, you may need special techniques to actually see the sperm. First, you will probably need to squash the antheridia to release the sperm, a feat you can accomplish by pressing lightly on the coverslip, preferably while observing the antheridia through the microscope so you don't overdo it.

Once you have freed the sperm, they may not be as easy to observe as you might expect. They are in constant motion, so it might help to add a bit of **methyl cellulose** to the medium to slow them down (Rod Seppelt, Bryonet 11 January 2012). Even so, they are transparent, eluding detailed observation. Use the diaphragm of your microscope (NOT the rheostat) to decrease the light and increase contrast.

Reese (1955) presented a method for observing sperm. He suggested clipping off the antheridial heads or branches with perigonia and inverting several in a drop of water on a slide. The source of water is important, with chlorine in tap water killing the sperm, and distilled water likewise having deleterious effects, perhaps causing the cells to take in water and explode. Reese suggests letting tap water sit overnight. The slides can be put aside in Petri dishes with damp filter paper until the water on the slide becomes milky, indicating that spermatozoids have been released. At this point, the antheridial parts should be removed, leaving only water and sperm on the slide. Set the slide somewhere to dry in preparation for staining. The dry sperm can be stained with a 1% aqueous solution of gentian violet. You can immerse the slides in the gentian violet or place a few drops of the stain on the slide. All that is needed is 30-60 seconds to stain the material. Then wash the slide with distilled water and de-stain it in 50% ethanol for 10-20 seconds. Wash it again in distilled water, allow it to dry, and mount it in your choice of mounting media.

To observe live antherozoids, Reese (1955) recommends smearing a small amount of fresh egg albumen on a slide and adding a drop of water with freshly discharged antherozoids. You can add a cover slip if you wish to observe. The albumin helps to slow down the movements of the antherozoids. Using darkfield illumination helps in observing these, or close the diaphragm down as far as it will go.

Des Callaghan has created a film that shows sperm in motion <http://youtu.be/Jdh8flxvZgk>. These were not stained, but instead used differential interference microscopy (DIC) to create the contrast needed for the sperm to be visible.

If you just want to find sperm, and possibly count them, you can probably succeed with Sperm VitalStain™. We have not tried this – it is designed for human sperm and it can distinguish between living and dead sperm. The stain contains both eosin and nigrosine. The eosin will be absorbed by the dead cells – those with a damaged plasma membrane – and will stain these cells red. Nigrosine is a counterstain that facilitates the visualization of the living (unstained) cells. Instructions are available on their web page.

Nelly Horst (pers. comm. 3 February 2013) reports that DAPI staining (available from chemical suppliers) works nicely as a stain (Figure 17).

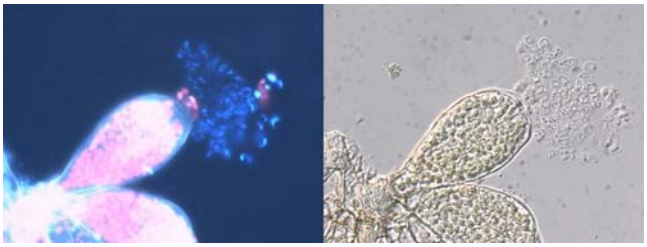

Figure 17. Sperm with DAPI stain (**left**) compared to fresh material (**right**). Photos courtesy of Nelly Horst.

Paraphyllia

Seeing these small structures can be challenging, even in large species. Rod Seppelt (Bryonet 26 October 2022) offers suggestions to make it somewhat easier: For **pseudoparaphyllia**, he finds that by using a pair of very fine forceps (*e.g.* Watchmakers No. 5, but they are about AU$50 in Australia) it is possible to press slightly on the stem and at the same time clasp the base of a branch and tear/slice away the branch base. This will have a bit of the stem and, with any luck, the pseudoparaphyllia if they are present. It is a bit frustrating, however.

Axillary Hairs

Seppelt (Bryonet 26 October 2022) relates that early on he asked Bill Buck where to look for axillary hairs. The reply was to look at the very apex of the shoots. He may have been primarily referring to pleurocarps. But, in general terms, carefully remove a number of leaves, clear the leaves in lactic acid (gets rid of the cellular contents making cell details more easily visible), and then go hunting, examining the basal attachment part of the leaves. They are often very small, sometimes with 1-2 tinted (yellowish or brownish) basal shorter cells. Length varies and it is a moot point as to what constitutes a "mature" axillary hair. Seppelt has also found that axillary hairs are not always to be found in the shoot apices. In some ***Fissidens*** (Figure 18) species, for example, they can still be found in the axils of leaves several pairs of leaves below the shoot apex.

Figure 18. ***Fissidens adianthoides***; in some species of ***Fissidens*** one can find axillary hairs at some distance below the apex. Photo by Hermann Schachner, through Creative Commons.

Jeff Duckett (Bryonet 27 October 2022) has found that the best way to see axillary hairs is to cut the stem apex longitudinally and squash it with the cut surfaces uppermost. This will make the hairs readily visible in the axils of the young leaves. These hairs are short-lived and thus one is unlikely to find them among older leaves.

Hedenäs (1989) examined the axillary hairs of 200 pleurocarpous moss species. He pulled the leaves off the terminal ~5 mm of the stems. He found that the branches usually have fewer and weaker axillary hairs. Hairs could often be found attached to the bases of detached leaves where stem portions remained, but in other cases it was necessary to squash the tips.

Leaf Movement

Beginning students are often in awe when they drop water onto a moss like ***Hedwigia ciliata*** (Figure 19-Figure 20). The leaves spread before their eyes like a well-orchestrated ballet. Place a moss branch on a glass slide or in a Syracuse watch glass and add water to one end. As students watch the leaves spread, this permits a good discussion on why. They can compare species and further investigate to try to determine why some spread more easily than others.

Hedwigia (Figure 19-Figure 20) is great for a spreader (Figure 20), **Mniaceae** for non-spreaders (Figure 21) (without special coaxing). They can compare this behavior to that of dry tracheophyte leaves. It is an interesting exercise to try to determine what mechanism causes the leaf spread. For example, in ***Polytrichum*** species (Figure 13), the large, non-chlorophyllous area at the base of the leaf (Figure 22-Figure 23) fills with water and forces the leaf out. One can compare a variety of species and examine the leaf structure to see what facilitates the movement. This simple exercise can lead to lots of questions and simple observations and experiments – role of temperature of the water, other liquids, leaf structure (alar cells, borders, costa), staining to track where the water goes, etc.

Figure 19. Dry ***Hedwigia ciliata***. Photo by Des Callaghan, with permission.

Figure 20. Wet ***Hedwigia ciliata***, showing spreading of the leaves. Photo by Li Zhang.

Figure 23. ***Polytrichastrum alpinum*** (**Polytrichaceae**) leaf base showing hyaline cells and absence of lamellae. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 21. ***Plagiomnium*** branch resisting rewetting. Photo courtesy of J. Derek Bewley.

Figure 22. ***Polytrichum juniperinum*** showing leaf base that lacks lamellae (arrow) and illustrating the spreading of hydrated leaves. Photo by Janice Glime.

Water Movement

Water enters bryophytes in various ways. For the majority of bryophytes, entry is through the leaves and in at least some it occurs most easily at the tips of the stems. But for some it is able to enter through rhizoids, and others absorb water throughout the plant. Once water gains access, various structures can help to move the water more quickly. Hydroids in stems seem to function like tracheids and vessels, moving the water upward in the plant through elongate capillary spaces of the hydroid cells. Alar cells can facilitate entry of water at leaf bases and from there it might enter the costa, travelling more quickly through the elongate cells of the costa because it has fewer cell walls to cross. But water will also move across the leaf lamina from cell to cell. And in mosses like ***Polytrichum*** spp., there are leaf traces (Figure 24) that can facilitate movement of water from the stem into the leaf. There is little published data to demonstrate how each of these structures affects the speed of movement and how that differs among taxa. Of even greater interest is a comparison of these structures and their effects on water movement as it relates to habitat.

Water movement can be demonstrated with dyes placed at various positions on the moss (Figure 25). Dyes at the tip can demonstrate how far downward the stain is able to go in a period of time and how it gets there – central strand? stem cortex? leaves? external capillary spaces? Plants positioned with their rhizoids in a dye can demonstrate the ability of rhizoids to take up water and the ability of the plant to move it upward.

After the dye has been placed on the portion of the plant of interest, one can cut sections at intervals to look for the presence of the dye in various parts of the plant. Care must be taken to prevent external dye from reaching other tissues when the specimen is mounted on the slide, so it is best to apply the dye, permit it to enter the plant for the time desired, then thoroughly wash the outside of the plant until it no longer discolors the wash water.

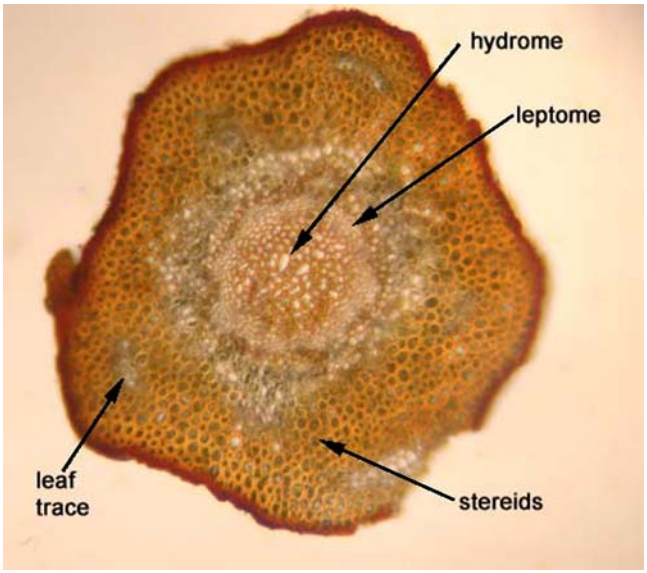

Figure 24. ***Polytrichum commune*** stem cross section showing leaf traces. Photo from UBC botany website, with permission.

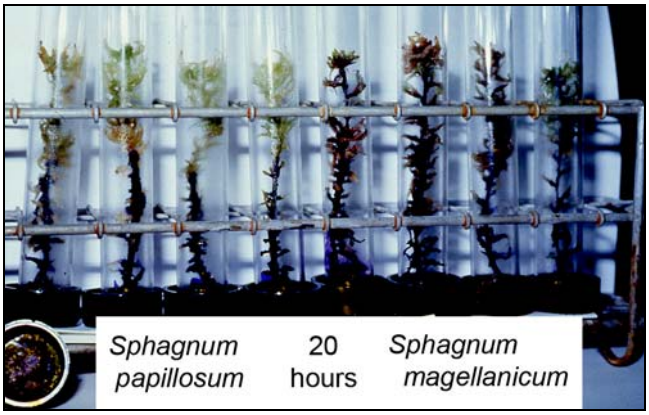

Figure 25. Demonstration of external water conduction in two species of ***Sphagnum***. Note that it has travelled much farther in ***Sphagnum magellanicum*** than in ***S. papillosum***. Photo by Yenhung Li.

intensities to see what that particular bryophyte responds to. Studies on bryophyte tropisms are limited (See Volume 1, Chapter 5-5), so new discoveries are almost certain.

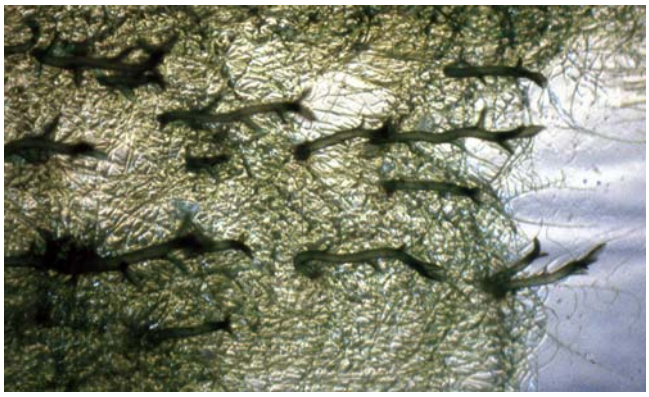

Figure 26. Phototropism of ***Funaria hygrometrica*** with light coming from right side of Petri plate. Photo by Janice Glime.

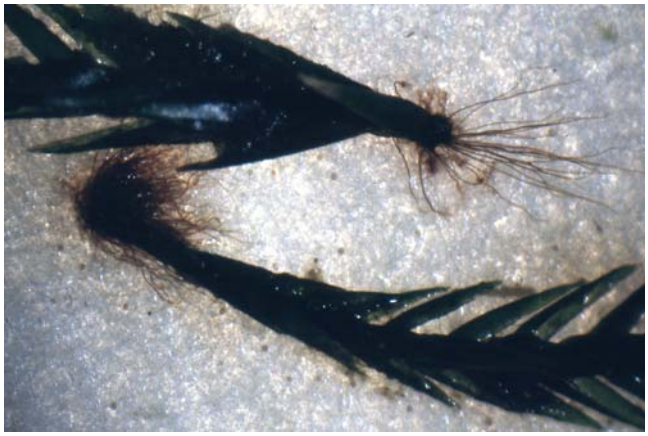

Figure 27. ***Fontinalis squamosa*** rhizoids exhibiting negative phototropisms to light coming from the left. Photo by Janice Glime.

Tropisms

Most, perhaps all, mosses exhibit tropisms. But do any, or all, liverworts do the same? Tropisms can be exhibited by culturing spores and using gravity (in darkness) or light from one side to test for these two tropisms (Figure 26-Figure 27). But a simpler method is to use a plastic bag and arrange the bryophytes to change direction of gravity or light. If testing for effects of one of these, be sure that the other cannot have any effect. For gravitropism, the clump can be placed on its side and light excluded. For phototropism, the clump should remain in its normal upright position and light should come from one side (Figure 26). Figure 28 demonstrates a combination of light and gravity on mosses on agar plates to test which has the stronger effect. Once a phototropism has been observed, one can experiment with various colors of light and

Figure 28. Paper rolls used to test the combined effects of light and gravity on tropisms. Photo by Janice Glime.

Etiolation

Etiolation can be demonstrated by placing bryophytes in a sealed plastic bag and giving them almost no light, such as that in a desk drawer or cabinet with the door closed. Within a few days or a week your bryophyte is likely to become elongated and spindly. I (Glime) sometimes see this in my terrarium where mosses grow from spores and have less light intensity than outdoor light.

Splash Cup Dispersal

The distribution of gemmae from the gemma cup of ***Marchantia*** (Figure 29-Figure 30) can be shown, and this might be applied to other splash dispersal structures in bryophytes. The splashing is effected by dropping colored ink or food coloring from a titration column onto the splash cup. The liverwort should be surrounded by white paper. As the dye hits the splash cup from the titration column, it splatters around the splash cup and makes blue spots on the white paper. This is a minimal approximation of the ability of raindrops to splash the gemmae. The distance of the water dropping is much less than that of a real raindrop, hence not having the same impact and resulting in shorter splash distances. The person doing the "splashing" should wear an apron or other protection during this demonstration.

Figure 29. ***Marchantia polymorpha*** gemmae cups. Photo by Michael Lüth, with permission.

Figure 30. ***Marchantia polymorpha*** gemmae cups with a few gemmae escaping in the upper chamber. Photo by Walter Obermayer, with permission.

Determining Oicy

Determining whether sexual organs occur on one plant or on separate plants is not an easy task. As Roxanne Hastings (Bryonet 14 April 2014) asserts "In order to be certain one must tackle the problem with systematic thoroughness." Using more traditional methodology, Hastings states that you must ensure that your clump of mosses is complete, including all the basal attachments, in order to determine **cladautoicous** (with antheridia on separate branch of same plant) mosses. She recommends taking a large clump, soaking it, and spreading it out on a slide or Petri dish. Then carefully tweeze the stems apart and remove any stems that are not basally attached. (You can't tell if they are part of the same or different plant.) Such fragments are only useful if the plant is **gonioautoicous** (having male and female reproductive parts on the same branch).

Then the tedium begins. Take a single stem and use needle-nose forceps, starting at the base, to carefully pull back each and every leaf to examine carefully for reproductive structures. When you reach the stem tip, remove that stem from the clump and set it aside. Then repeat the process on the next stem and every stem/branch of the clump until both sexes are located or you are certain only one is present. Yes, it can take several hours to peruse only one clump! Unfortunately, finding only one sex by this method is not definitive. Male organs typically develop before female organs do, or you might just be unlucky in finding only one of the sexes on your branches. And beware of the dwarf males (see Chapter 3).

But there is another way. And it even works for plants that are not producing sexual material at the time. Using the rarely reproducing dioicous moss ***Drepanocladus turgescens*** (Figure 31), Hedenäs *et al*. (2016) developed a method using a female-targetting marker that was previously developed for ***Pseudocalliergon trifarium*** (syn. ***D. trifarius***; Figure 32) and ***D. lycopodioides*** (Figure 33). When male and female portions of ***D. turgescens*** were sequenced and amplified, this method was successful in consistently revealing differences between males and females at five sequence positions. Alas, this method is likewise time-consuming and complicated, but it is reliable.

Figure 31. ***Drepanocladus turgescens***, a dioicous species for which a female-targetting marker can identify the gender. Photo by Michael Lüth, with permission.

Figure 32. ***Pseudocalliergon trifarium***, a species for which a female-targetting marker can be used to determine sex. Photo by Michael Lüth, with permission.

Figure 33. ***Drepanocladus lycopodioides***, a species for which a female-targetting marker can be used to determine sex. Photo by Michael Lüth, with permission.

Brownian Movement

Motion within a cell can often surprise the observer, especially a beginner. If you see chloroplasts moving as a group in something approaching a circle, it is most likely **cytoplasmic streaming**. However, if the movement is more like a vibration, it is most likely Brownian movement. Molecules are in constant motion, and these bump structures like oil bodies, causing them to move. Smaller particles within the cell will most likely also be in motion, but are less obvious. Ken Adams (Bryonet 2 February 2012) explains that at the small dimensions of cells, the thermal collisions of molecules against oil bodies is unbalanced. Thus, in any instant the number of collisions on one side of the oil body exceeds that on the other side.

Jeff Duckett (Bryonet 2 February 2012) reminds us that cytoplasmic streaming is unlikely to cause motion of liverwort oil bodies because there is almost no cytoplasm surrounding them.

Plasmolysis

Cyndy Galloway (Bryonet) uses the moss ***Physcomitrium*** (Figure 34) to demonstrate plasmolysis to students. A fairly strong salt solution causes the protoplasts to look like little basketballs. However, she said that adding water for deplasmolysis caused the cells to take in water too rapidly, causing them to burst. Perhaps that could be solved with some tinkering – a lower salt concentration, and replacement by water with some amount of salt that would be close to isotonic. ***Fontinalis duriaei*** (Figure 35) demonstrates plasmolysis caused by a copper solution (Figure 36). Observations on plasmolysis can be an assessment tool for contamination by heavy metals and will most likely be useful for other types of pollution as well.

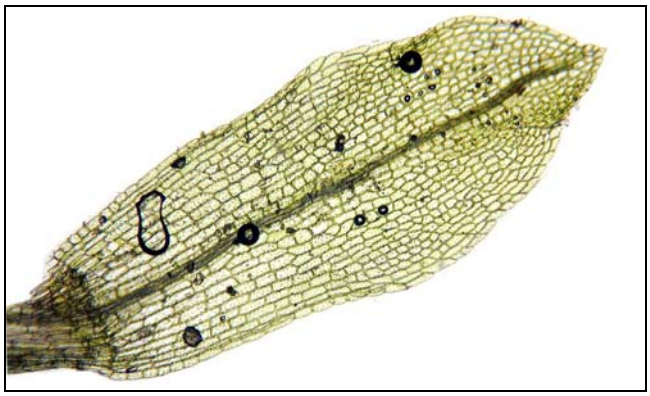

Figure 34. ***Physcomitrium sphaericum*** leaf cells, a good species for demonstrating plasmolysis. Photo by Michael Lüth, with permission.

Figure 35. ***Fontinalis duriaei***, a species that plasmolyzes in copper solutions. Photo by Michael Lüth, with permission.

Nutrient Cycling

There is a very easy, inexpensive exercise that can be done to demonstrate the role of bryophytes in nutrient cycles. Unfortunately, I don't know who contributed this, so if it is yours, please let me know!

Half fill a series of clear plastic (polycarbonate) cups with water – rainwater or distilled water is best. Add **methylene blue** dropwise to sets of three cups, one drop, two drops, and three drops for each cup in the set. (A small bottle of a concentrated solution of methylene blue can be obtained at a tropical fish store. It is a cationic stain that every bryologist should have on the lab bench.) The number of sets is determined by the number of samples.

Into each set place a moss or liverwort sample. Divide each sample into three parts. Add nearly equal amounts to each of the three cups in the set. A set = 3 cups, one with 1 drop, one with 2 drops, and one with 3 drops of stain. Volume by sight will work, but weighing is better. The sample should be small enough to be completely immersed in the methylene blue solution; bring the level up to about three quarters. It is interesting to compare nutrient sequestering abilities of ***Sphagnum*** (Figure 37), ***Eurhynchium*** (Figure 38), and forest floor leaf litter, for example.

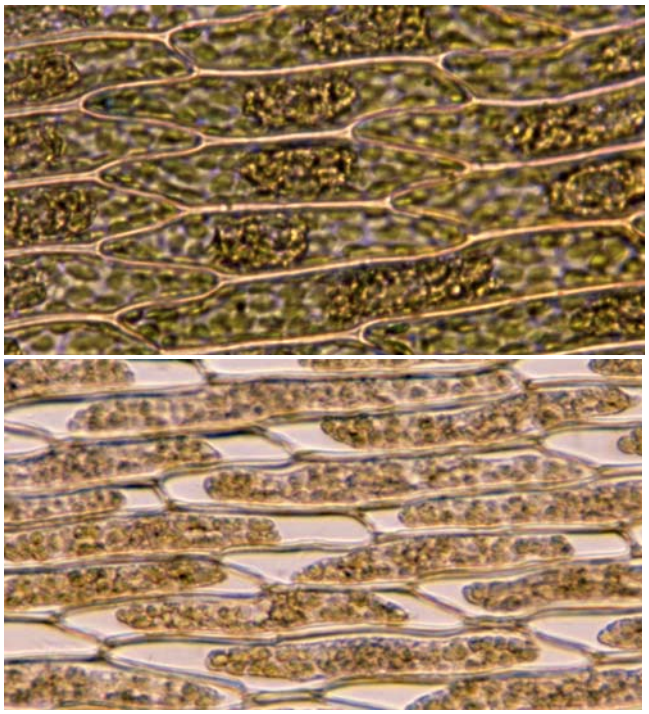

Figure 36. ***Fontinalis duriaei*** leaf. **Upper:** healthy leaf cells in water, demonstrating normal cell protoplasm arrangement. **Lower:** ***Fontinalis duriaei*** leaf cells in 100 µg L^{-1} copper, showing plasmolysis of cell contents.

Leave the sets overnight. The solution with moss will be clear in all of the cups (usually) while the dicot leaves and leaf litter water will still be blue. The graduated series of stain concentration helps visualize the effectiveness of the various samples. If you add an aquatic plant, you might get different results, so habitat comparisons could be quite interesting.

This demonstration shows how cations are scavenged by the cryptogams. In nature they pick out the micronutrients from rainfall that provide nutrition for the ecosystem or move them in solutions from the soil, using capillary spaces. Others remove them from water in streams and lakes. In industrial applications bryophytes clean water by picking out toxic metal ions and other cationic pollutants. This simple experiment can demonstrate rate differences among mosses and give an indication of their ability to extract nutrients from their ecosystems.

Figure 37. ***Sphagnum centrale*** with leaf litter. Photo by Janice Glime.

Figure 38. ***Eurhynchium oreganum***. Photo by Matt Goff, with permission.

Depending on the size of the cups, it may be necessary to start with a more dilute solution of stain than comes out of the bottle. Try adding lichens to the experiment for another comparison.

Measuring

Most of the material viewed using the microscope is too small to be measured with an ordinary ruler. Instead, we use a device called the **ocular** (eye) **micrometer** (reticule; Figure 39), which is a small disk that fits inside the eyepiece of the microscope. The disk has a tiny scale etched on it, and when we view a specimen, the image of the scale is superimposed on the object image.

The ocular micrometer scale is usually divided into units of 10 (Figure 39). To measure an object, simply count the number of units superimposed on the object. Thus the object shown in the margin is 10 **units** long.

Note that the measurement is reported in units, not microns or millimeters. We cannot assign a label to the units until the ocular micrometer has been **calibrated** (Figure 40-Figure 42). The scale needs to be calibrated with each objective on the microscope because the magnification of the scale never changes, whereas the magnification of the object does. An ocular micrometer placed in a 10X eyepiece is always magnified 10 times,

whereas an object under the objective is magnified by the power of the objective **and** the ocular.

To calibrate the ocular micrometer, you need to compare the scale with a scale of known dimensions that fits on the stage of the microscope (Figure 40-Figure 42). Remember that the stage is where all your organisms will sit on slides and perform for you (Figure 42). This special slide is known as a **stage micrometer**. It is a microscope slide with a tiny ruler etched on it. The marks on the ruler are exactly 0.01 mm apart (0.01 mm = 10 microns, µm).

Figure 39. Microscope ocular, showing where the ocular micrometer is inserted. Photo from Wikimedia Creative Commons.

Calibrate

1. Begin to calibrate the ocular micrometer by placing the stage micrometer on the stage and focusing on it with low power.
2. Move either the ocular or the stage micrometer until the two scales are superimposed.
3. Now move the stage micrometer laterally until the lines at one end coincide with each other. Call this point A.
4. Look for another line on the ocular micrometer that coincides with one on the stage micrometer. Call this point B.
5. Count the number of divisions on the ocular micrometer between points A and B.
6. Count the number of divisions on the stage micrometer between points A and B. Multiply this number by 0.01 mm to find the actual length of these divisions.
7. To find out how many mm equals 1 unit on the ocular micrometer, divide the answer to line 6 by the number of ocular micrometer units (line 5). (stage number of divisions/ocular number of divisions):

$$\frac{\text{mm}}{\text{ocular unit}} = \frac{0.01(\text{\# stage divisions})}{\text{\# ocular divisions}}$$

For example, in Figure 40 below, the number of stage micrometer divisions between points A and B is 6. The number of ocular micrometer divisions in this distance is 3. Therefore, the mm/unit on the ocular micrometer is:
(6 x 0.01 mm)/3 = 0.02 mm/unit or 20 µm.

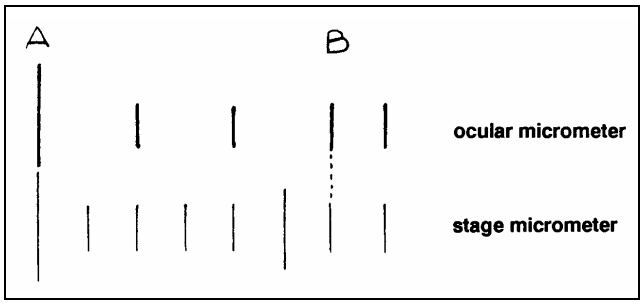

Figure 40. Alignment of scale of ocular micrometer (reticule) with that of the stage micrometer as seen in the eyepiece of the microscope. Drawn by Shelly Meston.

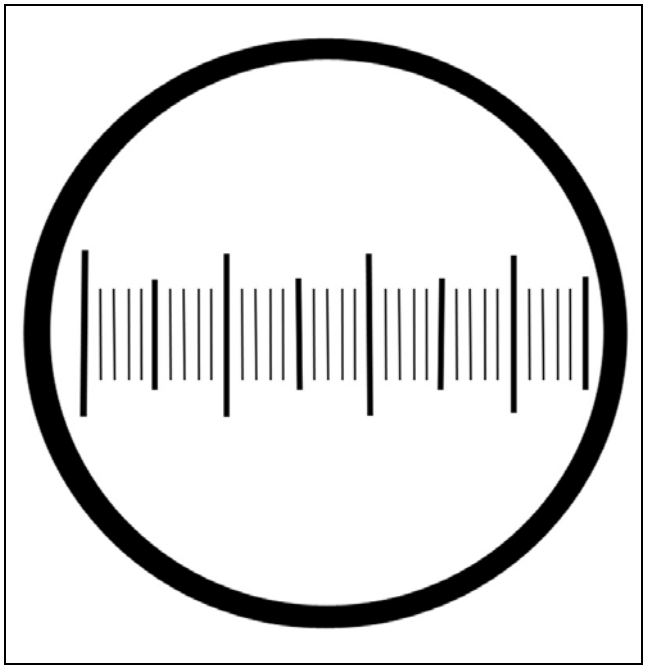

Figure 41. View of an ocular micrometer (reticule) in the eyepiece of the microscope. Drawn by Janice Glime.

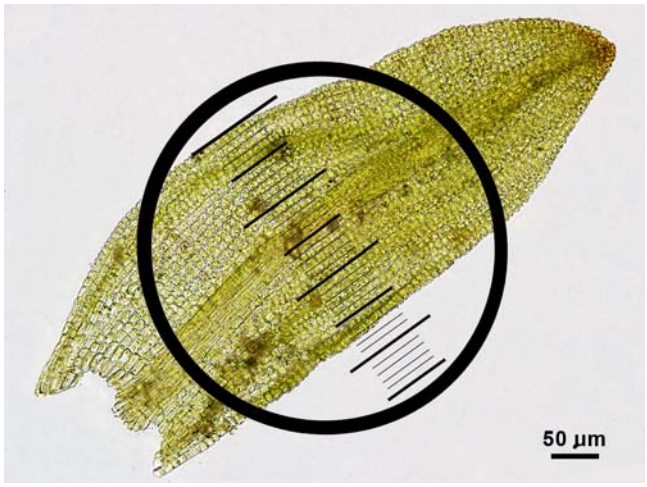

Figure 42. Reticule in position to measure width of midleaf of ***Barbula convoluta***. Measured width is 28 units and must be calibrated against stage micrometer. Leaf image by Dale A. Zimmerman; reticule by Janice Glime.

An object under this ocular and this objective measuring 8 units would be 0.16 mm long. Calibrate your ocular micrometer for each objective on your microscope and record the conversions below to keep as a reference.

low power:
stage micrometer units ____
ocular micrometer units ____
mm/unit ____

medium power:
stage micrometer units ____
ocular micrometer units ____
mm/unit ____

high power:
stage micrometer units ____
ocular micrometer units ____
mm/unit ____

oil immersion:
stage micrometer units ____
ocular micrometer units ____
mm/unit ____

You should also include the scale when you make drawings. Follow the instructions above for calibrating an **ocular micrometer**, which is a small ruler that fits in the eyepiece of your microscope. Using this ruler, you can measure things you see under the microscope. If you do not have an ocular micrometer available, you can estimate the size of objects using only a **stage micrometer**. The stage micrometer is a special slide that has a tiny ruler etched on it. Place the stage micrometer on the stage of your microscope and focus on the ruler with low power. Each mark on the micrometer is 0.01 mm apart. Use the ruler to measure the diameter of your field of view. Do this for each power on your microscope and record the diameters in the blanks below. Be very careful when focusing under the higher power objectives because the stage micrometer is very expensive. Then, use this information to estimate the size of objects seen under each power and to include a scale with each drawing you make.

field of view diameters:
low power ____
medium power ____
high power ____

Leaf Measurements

It is challenging to measure leaf cells because, unlike bricks, they are not rectangular. Rather, their sides are not parallel and their width and length change along the cell. In an attempt to solve this measurement problem, Ivanov and Ignatov (2011) developed a method to digitize the "cell net." Using this software, one can measure cell length, width, and area. They compared the published cell width for five moss species in five different publications (Table 1).

Table 1. Comparison of published cell width data for five pleurocarpous moss species in µm (from Ivanov & Ignatov 2011).

	Noguchi		Lawton		Ignatov & Ignatova
		Smith	Limpricht		
	1992	2004	1971	1885-1904	2004
Ptilium crista-castrensis	2	4-5	3-5	5	4-6
Callicladium haldanianum	4-4.5	-	5-7	6	5-8
Calliergonella lindbergii	3-4	5.0-6.5	4-7	6-7	5-7
Isopterygiopsis muelleriana	4-4.5	4-6	-	5-6	-
Hylocomium splendens	3-4	5-7	4-6	5	5-6

Later, Ivanov and Ignatov (2013) developed a 2-d digitization of plant cell aerolation using polarized light microscopy. This microscopic image is photographed into a digital photo. Using ***Plagiomnium elatum*** **(**Figure 43-Figure 44**)** and ***P. medium*** (Figure 45-Figure 46), they digitized the cell arrangement of the oblique rows (Figure 44) on these unistratose leaf lamina. They proposed a "computer analytic method that allows transferring visible images into coordinates of intracell boundaries and their **vertices** (points where three or more cells contact), *i.e.*, into a digital cell net. After such a digitizing it is possible to estimate many geometrical parameters of cells and their complexes under relatively simple mathematic treatment." Chemical or physical coloring methods should be used to permit distinction between cell boundaries and intracellular space. In some cases, this might be done by fluorescence microscopy. The method is somewhat complex, so I refer the reader to the original paper as I have not tried it myself.

Figure 43. ***Plagiomnium elatum***. Photo by Michael Lüth, with permission.

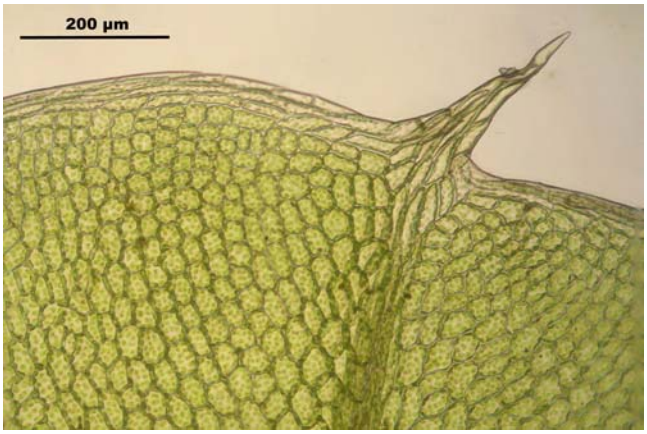

Figure 44. ***Plagiomnium elatum*** showing oblique rows of leaf cells. Photo by Hermann Schachner, through Creative Commons.

Figure 45. ***Plagiomnium medium***. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University.

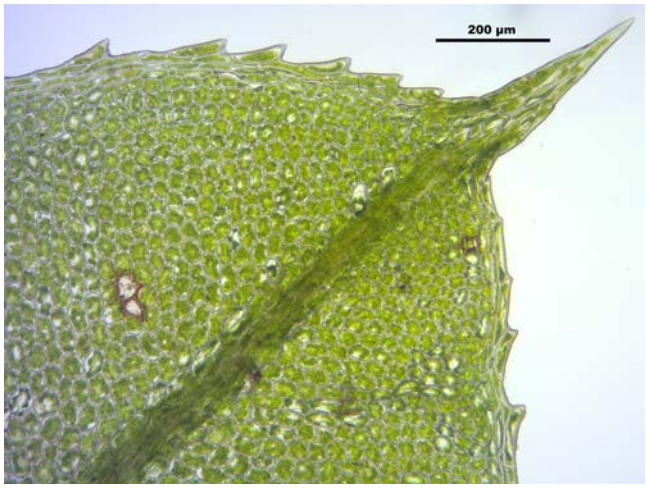

Figure 46. ***Plagiomnium medium*** demonstrating the difficulty in measuring cells in such irregular arrangements. Photo by Hermann Schachner, through Creative Commons.

Leaf Angles

A simple ocular protractor can be constructed using an ocular micrometer (Christy 1987). These instructions are modified only slightly from their publication in The Bryological Times.

1. Using an index card or heavy paper, draw a circle with a diameter equal to that at the top of your microscope eyepiece.
2. Use a protractor and ruler to draw 10 radii in 20° increments in a 90° segment of the circle (Figure 47, **a**).
3. Cut out the circle from (1) and cut a rectangle ~3 x 10 cm from the same card or paper.
4. At the points where the 10° radii meet the edge of the circle, draw corresponding marks along one of the long edges of the rectangle (Figure 47, **b**). Do this along the entire edge of the rectangle to form a scale calibrated in 10° intervals. Discard the circle (or save it for making replacement **collars**).
5. On the rectangle, draw a smaller mark midway between each 10° mark. Midway in the scale, label one of the 10° marks "0," then count in each direction from 0 and mark off 45, 90, 135, and 180°. This makes a scale calibrated in 5° intervals (Figure 47, **c**).
6. Wrap the scale, calibrations on upper edge, around the side of the eyepiece tube, and using adhesive tape, secure the overlapping end to the other end to form a ring of paper around the eyepiece tube (Figure 47, **d**). This is the **collar**, for which the fit should be loose enough that it can be rotated on the tube, but tight enough for friction to hold it at any setting.
7. Put a V-shaped scratch or pencil mark, on the rim of the eyepiece, on a radius parallel to the scale line of the ocular micrometer to serve as an index mark (Figure 47, **e**).

Use of the Ocular Protractor

1. Rotate the eyepiece or move the microscope slide until one of the scale increment lines on the ocular

micrometer is parallel with one side of the angle to be measured. While holding the eyepiece stationary with one hand, rotate the collar with the other hand and set the zero point of the collar at the index mark on the rim of the eyepiece (Figure 47, **f**).

2. While holding the collar stationary with one hand, rotate the rim of the eyepiece with the other hand until the other side of the angle is parallel to one of the scale increment lines on the ocular micrometer (Figure 47, **g**). The degrees of the angle can then be read on the collar at the point directly below the index mark on the rim of the eyepiece.

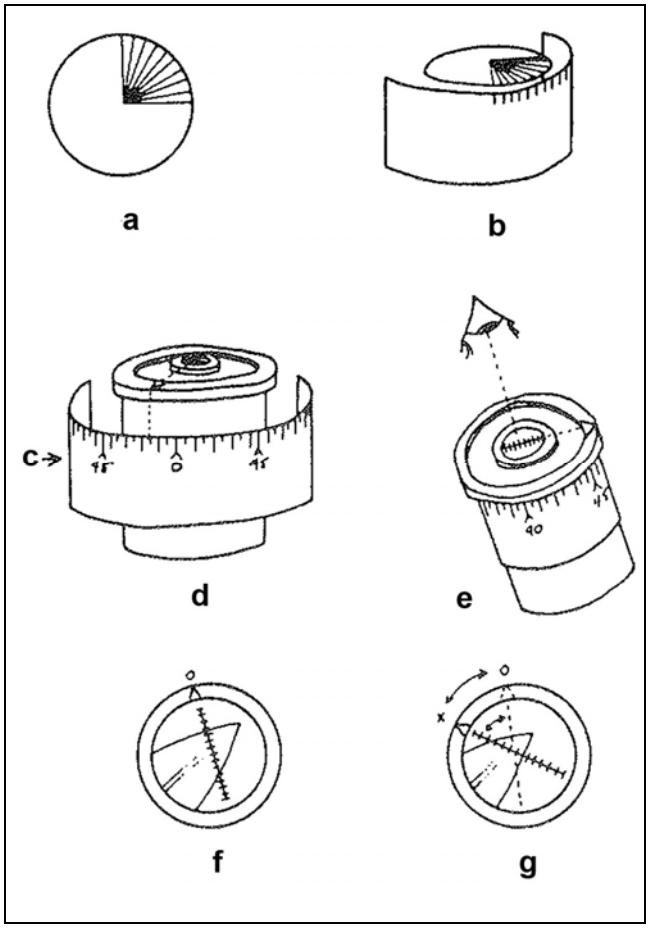

Figure 47. Ocular protractor for measuring angles. Modified from Christy 1987.

Rigidity Index

To calculate the **rigidity index** of **Polytrichaceae** leaves, Sean Edwards (pers. comm. 22 April 2014) multiplies the mean height of leaf **lamellae** (thin sheet of cells standing up along costa of leaf; Figure 48) and divides by the mean width of the **lamina** (expanded portion or blade of leaf; Figure 48), both as mid-leaf number of cells. This permits you to quantify the rigidity of the leaves as a rigidity index. This can be used to characterize different species, even within environmental variation.

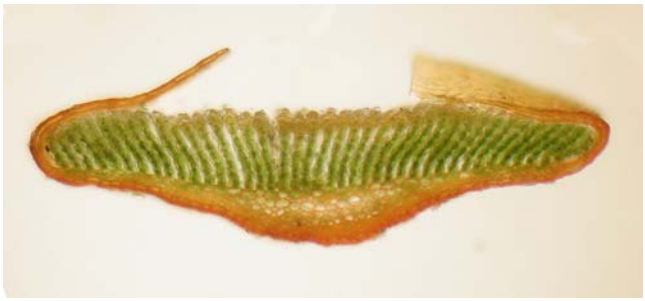

Figure 48. ***Polytrichum juniperinum*** leaf cross section showing vertical lamellae and width of leaf lamina. Photo courtesy of John Hribljan.

Making Drawings

Rod Seppelt (Bryonet 30 December 2022) reports that he was shown a way to use black and white prints to make line drawing images. First, go over the outlines with India ink. Then clear the print in potassium permanganate. This leaves you with the outlines on a white background. But Rod doesn't use this technique because he is able to make excellent drawings by hand.

Older bryologists will remember the camera lucida. This method uses a mirror attached to the ocular of the microscope. Hence, while looking through the microscope you can see the sheet of white paper at the same time and trace around what you see.

David H. Wagner (Bryonet 30 December 2022) has posted a youtube video <https://www.youtube.com/watch?v=pXbVEVnSX4c&t=28s> to demonstrate using photographs to make pen and ind drawings. The method is useful for both macro- and microphotographs.

Summary

Bryophytes have a number of interesting performances, and these can be enhanced by clearing tissues with lactic acid. Capsules can be opened with KOH and NaOCl or heating the slide, depending on the species. To see peristomes under the compound microscope, the capsule should be split. Teeth on whole capsules are best viewed if positioned carefully so they are vertical. Clay can serve as an anchor. Moisture modification can cause the teeth to flex. Spore dispersal can be demonstrated on an agar plate.

Observation of sperm requires a knowledge of the delicate timing. Sperm can be slowed in methyl cellulose and the diaphragm should be adjusted to increase contrast. Other options are DIC microscopy or use of a vital stain such as Sperm VitalStain™.

Adding water to dry leaves can cause leaf movements. placing the base of a plant in dye can demonstrate the movement of solutions in the capillary spaces. Tropisms can be demonstrated on agar plates or other positioning. Etiolation is easily demonstrated in low light.

Dispersal can be demonstrated in splash cups using food coloring. Brownian movement in cells is easily

observed in live leaves. Adding a salt solution to the edge of the coverslip can demonstrate plasmolysis.

Nutrient cycling can be demonstrated by the ability of bryophytes to clear a dye solution in a small cup.

Measurements are important for identification and making descriptions. These will require an ocular micrometer and stage micrometer. These must be calibrated for each microscope and user. Measuring leaf angles may require making your own simple equipment.

Acknowledgments

I thank all the Bryonetters who have shared their excitement and discovery with the rest of us. Please continue to contribute your wonderful stories and demonstrations that excite your students.

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CHAPTER 2-4
LABORATORY TECHNIQUES: PRESERVATION AND PERMANENT MOUNTS

Janice M. Glime and David M. Wagner

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CHAPTER 2-4
LABORATORY TECHNIQUES: PRESERVATION AND PERMANENT MOUNTS

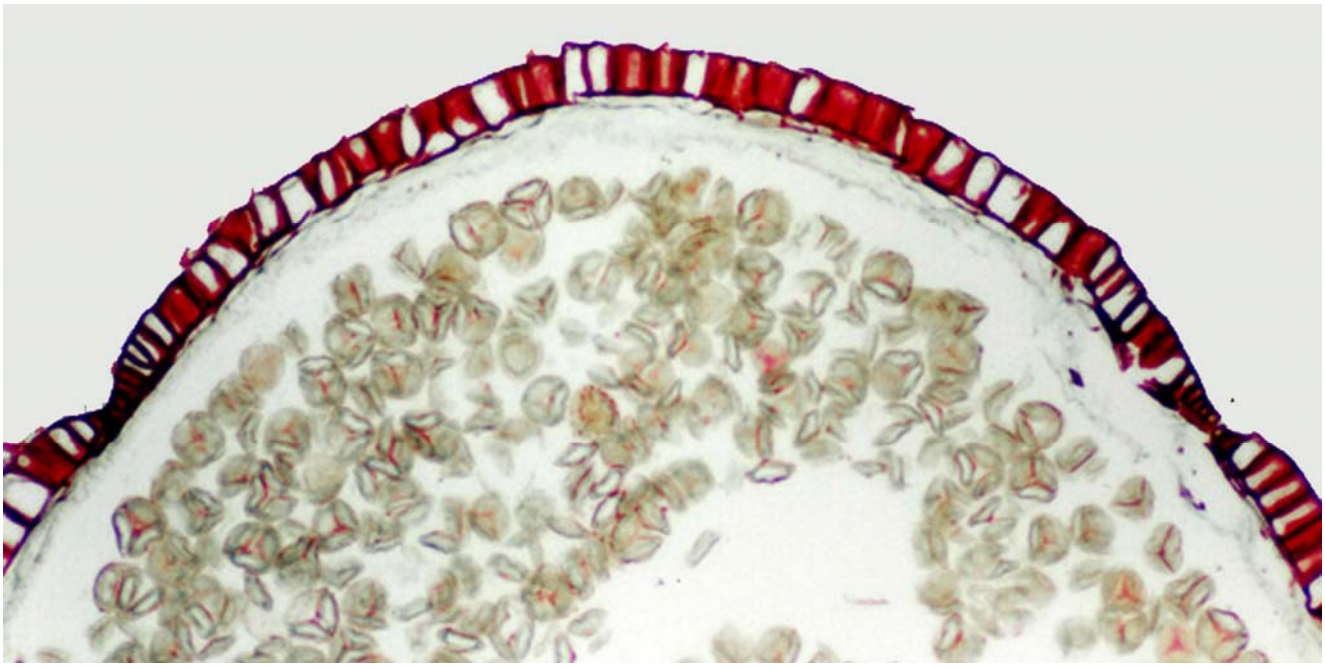


Figure 1. Stained permanent mount of ***Sphagnum*** capsule from Triarch. Photo by Janice Glime.

Permanent and Semi-Permanent Slides: Mounting Media – Mountants

There are lots of considerations in making permanent mounts – ease of use, availability of ingredients, drying time, clearing effect (Angela Newton, Bryonet 16 February 2011). Most people would like their permanent mounts to be durable, surviving being "tossed around." Each mounting medium seems to have its problems, satisfying some, but not all the criteria (Holzinger 1900; Yuncker 1921; Jennings 1935; Iwatsuki 1955; Bowers 1964; Wilberforce 1970; Zander 1983, 1993; Frahm 1990). Nevertheless, as seen in the professionally prepared slide in and available at <http://digitalcommons.mtu.edu/bryophyte-ecology/>., details can become more visible with staining and made to last.

Traditionally, mounting was accomplished with balsam mounts (Jennings 1935) or a synthetic resin like Permount, but slides made with these had to be stored horizontally or the mountant would drift to one slide, carrying the specimen(s) with it. The balsam procedure is time-consuming, requiring dehydration of the specimen in an alcohol series until it is ready to accept an organic solvent such as **xylene** that will mix with the resin. This means that the **mountant** cannot simply be added to a slide once one determines that the mount is suitable for preservation. Furthermore, xylene is highly toxic. MSDS guidelines recommend protection with goggles, respirator, lab coat, and gloves to avoid potential toxicity to "blood, kidneys, liver, mucous membranes, bone marrow, or central nervous system (CNS). Repeated or prolonged exposure to the substance can produce target organs damage."

Des Callaghan (Bryonet 14 December 2018) notes that delicate species with thin cell walls do not preserve well in most mountants. The cell walls collapse in glycerine jelly. A detailed but time-consuming method for mounting delicate liverworts is provided by David Copestake (2015).

Rod Seppelt (Bryonet September 2017) advises making the mountant more viscous by varying the percentages of the glycerol-water mix or the Karo syrup-water mix.

Glycerine to Gum Arabic

Sayre (1941) suggested a gum arabic **mountant** (mounting medium) for bryophytes. At the time, this was a new approach that was superior to glycerine, although Wagner finds that the glycerine mounts of thin sections can

be made overnight and will last for decades if handled carefully. Sayre reports that a combination of glycerine and gum arabic can last for more than a year:

1. Mix 20 g gum arabic in 60 cc distilled water.
2. Let stand covered several hours.
3. Filter through coarse paper.
4. Add 10 cc glycerine and 4 cc formalin (more glycerine may be needed in a dry climate).
5. Place specimen in drop of mix (mountant).
6. Allow to dry for 24 hours in flat position at room temperature.
7. Store flat.
8. Store the mountant in bottle with pipette stopper.

Hoyer's Solution

Hoyer's Solution, also known as gum chloral, was one of the earliest mountants in widespread use for bryophytes (Anderson 1954; Conard & Redfearn 1979; Schofield 1985):

distilled water	50 cc
gum arabic (USP flake)	30 g
chloral hydrate	200 g
glycerine	20 cc

Schofield (1985) recommended allowing the solution to stand for several hours to reduce the number of bubbles; a magnetic mixer can help in this regard as well. Store in air-tight bottles.

Anderson (1954) reported that it was suitable for all mosses he tried (he did not study liverworts) except **Mniaceae** (Figure 3) and ***Tortella*** (Figure 2). In the latter mosses, **Hoyer's solution** caused cell shrinkage and distortion in some species. Lightowlers (1980) expressed frustration at the cell distortion. Anderson did report that both H. L. Blomquist and R. M. Schuster used Hoyer's solution for **liverworts** and that these had held up well, as did ***Sphagnum*** (Figure 4). Schofield (1985) likewise recommended Hoyer's, stating that it results in distortion in leaves of some bryophytes, but it is suitable for most. Hoyer's solution has the added advantage of being an effective clearing agent, so it is helpful for such structures as peristome teeth, capsule exothecial cells, and dense papillae (Anderson 1954). It has the added advantage of not needing **luting** (sealing edges with something like nail polish) (Zander 1993) although unsealed slides will dry out or crystallize much faster than sealed slides.

Figure 2. ***Tortella tortuosa***, a genus in which cell shrinkage occurs in some species when placed in Hoyer's solution. Photo by Des Callaghan.

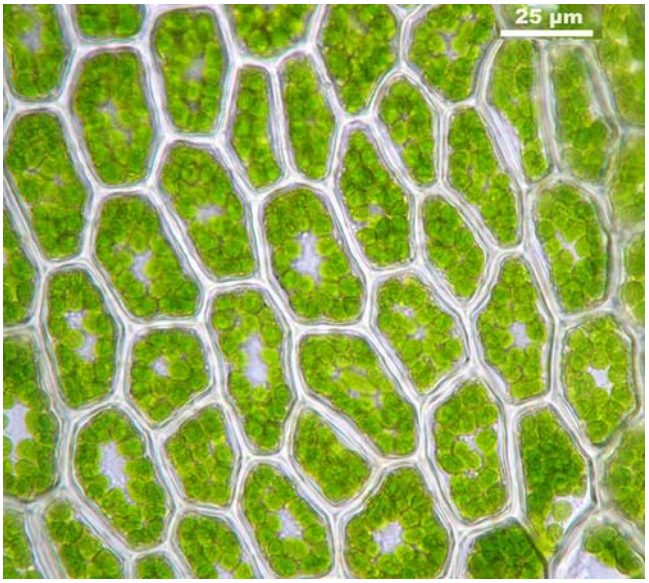


Figure 3. ***Mnium spinosum*** leaf cells. Cells of members if this family (Mniaceae) exhibit cell shrinkage and distortion in Hoyer's solution. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.

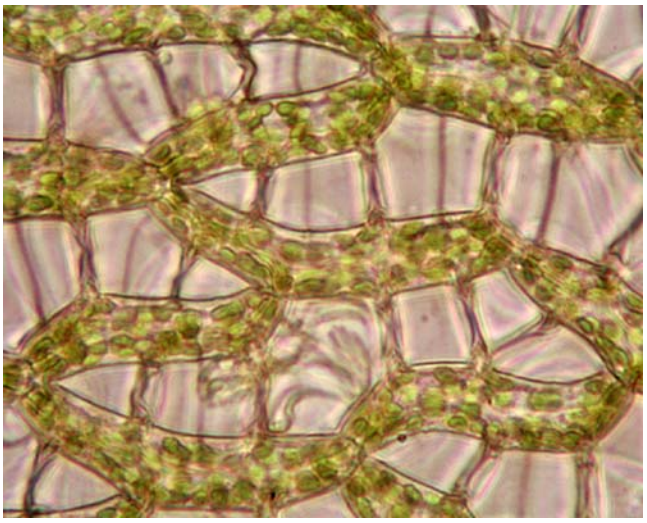


Figure 4. ***Sphagnum palustre*** cells. Cells in **Sphagnaceae** are able to retain their shape in Hoyer's solution. Photo by Malcolm Storey through Creative Commons.

Water Glass Alternative (WGG) for Hoyer's Solution plus Glycerin

This chapter was posted for less than a week when Richard Zander posted this alternative Zander 2013). He touts it as a way to avoid the "tedium of heating slides to melt glycerin jelly." It does not solidify as quickly as glycerin jelly, and its longevity is not known but may be at least as long as a glycerin mount. Even if it crystallizes around the edges, it will still render the bryophyte acceptable.

2 parts water glass solution (sodium silicate solution 40-42 Be)
1 part glycerin (glycerol) mixed with a little water to help it dissolve in the water glass

1. Mix and stir well.

2. Put in capped squeeze bottle or dropper bottle (not a glass-stoppered bottle).
3. Soak specimen in water or 2% KOH solution or water or aerosol solution.
4. If cells are large and thin-walled and apt to collapse, add a drop of pure glycerin and heat to force glycerin into the cells, but this is usually unnecessary even for species with moderately large laminal cells.
5. Add a few drops of WGG over the moist specimen and add cover glass.

In addition to the slow drying time, the basic *p*H may cause some interesting color reactions similar to those when using KOH. On the other hand, its high index of refraction and tinting of leaf cells may make stains unnecessary for ***Sphagnum*** leaves. If stains are needed, they must be basic with this mountant.

Modified Hoyer's for Chromosomes

Concerned about the distortion effects on ***Mnium*** (Figure 3) and ***Tortella*** (Figure 2, Figure 5), Bowers (1964) developed a technique to give better results for making chromosome preparations.

1. First place the material in concentrated HCl, water, and stain (1:3:3).
2. Mix the modified Hoyer's medium:

gum arabic (U.S.P. flake)	20	g
distilled water	60	cc
chloral hydrate	5	g
glycerine	10	cc

3. Mix in above order at room temperature. The solution may need to stand for several hours for bubbles to dissipate. It should be clear and with no precipitate. Store in glass, air-tight bottle.
4. Add stain to Hoyer's medium (1:1) and place drop on slide.
5. Transfer plant material to the medium-stain mixture.
6. Macerate by tapping.
7. Add coverslip.
8. Smear with pressure from a finger.
9. For recently fixed (aceto-alcohol 30:70) or fresh material, use one part aceto-orcein to one part medium. For material stored for a long time, aceto-carmine gives better results.

Figure 5. ***Tortella rigens*** leaf cells, member of a genus in which cells of some species collapse in Hoyer's solution. Photo by Kristian Peters.

Gum Chloral Solution

This solution can serve both as a clearing agent and for making permanent mounts. This recipe has the same ingredients as Hoyer's solution, but in different proportions. The following recipe is from Watson, courtesy of Martin Godfrey:

distilled water	100	ml
gum arabic	40	gm
glycerine	20	ml
chloral hydrate	50	g

1. Dissolve gum arabic first in cold water for 1-2 days.
2. Do not to stir – you will get masses of air bubbles.
3. When dissolved, add glycerine and chloral hydrate and heat until dissolved.
4. Filter hot if necessary.
5. Put drop on a slide and add wet specimen to it.
6. Leave slide horizontal for 2-3 days for gum to set and clear.

Godfrey (Bryonet) reports that gum chloral is great for things like ***Fossombronia*** spores (Figure 6). For structures like perianths, the clearing properties will make the interior structures visible without the need to dissect. The slide can be sealed with a few coats of nail polish to stop the gum from drying out, permitting it to last more than 30 years. Beware, however, that delicate specimens may shrink. If these don't need to be cleared, you can use glycerine jelly, as suggested by Richard Zander. And this actually causes little distortion (Zander 1997).

Figure 6. ***Fossombronia*** spores and elaters. Gum chloral works well as a mountant for these spores. Photo by Tom Thekathyil.

David Long (Bryonet 11 October 2009) reminds us that Hoyer's solution is especially good for liverworts because it can both clear the tissue and preserve it. However, it can cause health issues. Long-term use of **chloral hydrate**, a constituent of Hoyer's solution, can cause addiction, rashes, gastric discomfort, and severe renal, heart, and liver failure (Gelder *et al*. 2005). It should not be used for classroom studies.

Its reputation as a health hazard has made Hoyer's solution difficult to obtain. David Wagner (Bryonet 31 May 2010) tells us that "the primary deterrent to availability of Hoyer's Solution for use as a clearing agent is that it is a controlled substance. In the USA it is a

Schedule IV drug, classed with barbiturates, tranquilizers and sedatives. A prescription is necessary to obtain it. It is/was known by the street name 'Mickey Finn,' a knockout or date rape drug. It has been used (and misused) as a sedative and sleep-inducing agent for over a century and a half; its hypnotic effects seem to be a reason for its abuse as a recreational drug."

A recent product might have some value as a substitute, but its track record is unknown (Villani *et al.* 2013). This product, Visikol™, is made with polychlorinated alcohol and is considered a replacement for chloral hydrate as a clearing agent. It already contains glycerol and works successfully for flowering plant tissues, clearing them in 20-30 minutes, although the authors warn that larger samples may require up to three days. It also works for insects, fungi, and protists, but its usefulness for bryophytes and its effect on bryophyte tissue shrinkage and effectiveness over time remain to be tested.

But it has problems as a mountant as well. It can badly distort specimens by drying them, clear them so much they are nearly invisible, or suffer crystallization (Wagner, Bryonet 31 May 2010). Considering the relative safety issues and undesirable traits of Hoyer's solution, glycerine jelly is a much wiser choice for a mountant.

The distortion problem can be mostly eliminated by soaking the plants thoroughly and adding a little heat to eliminate trapped air (Angela Newton, Bryonet 25 June 1999). Flowers (1973) suggests using a warm coverslip to reduce the bubbles. Then, once the specimen is in the glycerine, it is necessary to wait until the tissues relax before putting on a coverslip (Angela Newton, Bryonet 25 June 1999). An additional problem is the invasion of bubbles from the edges of the coverslip. Interestingly, round coverslips seem to reduce this invasion, but sealing the edges may be a better plan. One can also refill the coverslip during the first few weeks to reduce this problem.

Jonathan Sleath (Bryonet 24 June 1999) agrees with Newton. He has used Hoyer's solution (or gum chloral) successfully for a number of years, following the recipe given in Smith (1978). "The slides have kept well, and could probably be made permanent by sealing the edges of the coverslip with clear nail polish. The material does distort a little at first as water is drawn out by osmosis, but once equilibrium is reached the cell walls seem to regain their normal shape. Of course the cell contents are lost, but the clearing properties of the solution can be quite useful." Despite all the concern over health issues, Sleath reports that chloral hydrate, the major constituent of Hoyer's solution, is still occasionally used in pediatric practice in the United Kingdom because it is so safe. Chloral hydrate is not a controlled substance in the United Kingdom at this time (Wikipedia, 2013). When he makes a permanent mount, he seals the coverslip on all four sides, unlike the corner technique of Wagner.

Allan Fife (Bryonet 24 June 1999) suggested that soaking dissected bryophyte tissue overnight in **90% lactic acid** will largely prevent the cell wall collapse that is a common feature of Hoyer's mounts, particularly of thinner-walled cells. But, that does not remove its dangers from its chloral hydrate. The Oxford MSDS gives the ORL-RAT LD50 480 mg kg^{-1}. (ORL=Oral, RAT=rat, LD50=the dosage that killed 50% of the rats). So, if you weigh 70 kg, you would need to ingest 33.6 grams of choral hydrate to have a 50% probability of death (assuming you were a rat). According to Anderson's recipe there are 0.2 grams of chloral hydrate per ml of Hoyer's Solution. Therefore if you imbibed ca. 160 ml of Hoyer's Solution you would have a high likelihood of not seeing the next sunrise. The Oxford MSDS recommends safety glasses and ventilation when handling chloral hydrate. It is listed as a skin, eye, and respiratory irritant. You should also wear gloves and take care when using Hoyer's, and make a point of rinsing your hands after using it.

Belen Albertos (Bryonet 25 June 1999) reported that his lab uses **Kaiser's glycerol gelatin** to make permanent slides for microscopy. This is available in Europe, Asia, South America, and Australia from Merck, ready to use. Interestingly, it is not available through this supplier in Canada or the United States, although it is available in Mexico. To use it, you need to warm a portion of the solution to about 40°C. Once your slide is prepared as a water mount, place a drop of the warm solution on the edge of the coverslip. If there is excess liquid, pull the glycerol under the coverslip by placing the edge of a paper towel on the opposite edge of the coverslip. Albertos suggests placing the slide on a slope to let the glycerine run down and displace the water, but the paper towel method is probably the most effective. When solution completely covers the material, place the slide on a level surface to cool. The coverslip will keep the specimen in position during storage, but there might be a slight loss of color. Albertos reports that slides made in this way are still in good condition after five years. However, he warned that a colleague found that liverworts get altered quickly.

Lightowlers (1981) suggested a modification of gum chloral to preserve the shape of cells:

1. Presoak the specimen in an aqueous solution of 50% polyethylene glycol (PEG) 400 grade for about 12 hours (until thoroughly penetrated). 50-100% glycerol or 100% lactic acid are somewhat less effective.
2. Remove from solution after soaking and blot thoroughly with tissue paper. Too much PEG reacts with gum arabic to make an opaque precipitate. Too much glycerol slows the setting time. Excess lactic acid crystallizes upon drying.
3. Place specimen in drop of mountant on slide & dissect as needed.
4. Tease out bubbles and cover with coverslip.

Glycerine, Glycerol, and Glycerine Jelly

Hoyer's solution has been used for many decades as a mountant, but its toxicity (chloral hydrate) has decreased its availability and popularity. Furthermore, with Hoyer's solution, slides remain sticky and are easily smeared. Glycerine seems to be a viable alternative.

Glycerol is made from glycerine (=glycerin). Glycerine is the solid state, whereas glycerol is the liquid state. The formula is the same. Several Bryonetters have recommended this alternative (Ida Bruggeman, Cyndy Galloway, Martin Godfrey, Paul Davison, David Wagner, Richard Zander).

In 1900(!), Holzinger suggested mounting bryophytes in **glycerine jelly**. He improved upon the method of using mounts in jelly between mica sheets (replaced now by

coverslips) by using two thicknesses of paper – one ordinary writing paper, one cardboard that is slightly heavier than postal card paper (poster paper?).

1. Cut these into strips the length of a microscope slide and slightly wider.
2. Fasten at one end with paste to keep them from slipping.
3. Lay glycerine jelly mount in center of paper slide.
4. Cut through both thicknesses with sharp pointed pen-knife.
5. Cover inside of cardboard with paste.
6. Lay jelly mountant down over it.
7. Press down the thin paper, being careful not to misplace anything.
8. The two thicknesses of paper form a frame for the mount with margin of white paper to put data about the specimen.

Ida Bruggeman, Bryonet, reports that specimens in Hoyer's mounting medium will dry out after a while, losing contrast and making many details invisible. In comparison, many of her glycerine gelatin slides, sealed with nail polish, have lasted more than ten years, but they, too, dry out or get fungal infections after 15-30 years.

Glycerine appears to be the simplest and safest method of making permanent slides. Once you are through observing anything that might move and are ready to make it permanent, you can simply add a drop of glycerine at the edge of the coverslip (David Wagner, Bryonet 12 February 2001). It can be drawn under the coverslip by placing a bit of paper towel on the opposite edge of the coverslip and letting capillary action pull the excess water away. If the slide is left in the open for several days, water will evaporate and the glycerine will penetrate the specimen. Once the specimen is impregnated with glycerine, affix the coverslip by placing a drop of clear nail polish at the corners of the coverslip. Wagner recommends NOT trying to seal all the sides with nail polish because they seem to leak, but the ones affixed at the corners can last 20 years or more. Centering the coverslip will minimize the leakage of glycerine from the slide. You can clean the coverslip when needed on this more-or-less permanent mount by using alcohol on a cotton swab. Unfortunately, the oil bodies will not preserve.

It takes practice to determine how much glycerine to use. The needed amount varies with the thickness of the specimen, with a thin mount of leaf sections typically requiring only a single drop. More glycerine can be added, but as the slide dries, air may be drawn under the coverslip, trapping bubbles when more is added. If you add too much, you can blot it with thin strips (5 x 20 mm) of tissue paper, toilet paper, or paper towel. This process should be repeated until the glycerine barely starts to draw back from the edge of the coverslip.

Some bryophytes will shrink and curl when the glycerine is added. This is an indication that the change has been too quick. Dilute the glycerine and add it more slowly, allowing some of the liquid to evaporate, then adding more.

Glycerine quickly follows capillary spaces. While this is an advantage for drawing it under the coverslip, it is likewise a danger for drawing it out. If the slide contacts another slide next to the coverslip, the glycerine will creep to the edge of the slide, then follow the capillary spaces between the slides, ultimately travelling in the capillary spaces under the slides. Within a few days to weeks, all the glycerine will have followed this capillary route and will vacate the coverslip space. To help prevent this, be sure the coverslip is perfectly centered on the slide before you add nail polish. Wagner finds that it is best to add the nail polish right after the glycerine has been applied and before it is set aside for drying.

In 1997, Zander retracted his earlier advice (Zander 1983) on the use of lactophenol gel made with methyl cellulose. While this seemed to be a good alternative for clearing without collapsing the cell wall structure, making nice mounts, it dried out within six months, making the mounts unusable (Zander, pers. comm. 19 July 2012). Zander (2007) contends that the perfect mounting medium still does not exist, despite the many presented by past bryologists (Davis 1909; Sayre 1941; Anderson 1954; Bowers 1964; Wilberforce 1970; Lightowlers 1981; Zander 1983; Frahm 1990). He (Zander 1997, 2007) recommends mounting in **glycerine jelly** (= a mixture of glycerine and gelatin that is used in histology for mounting specimens). This glycerine jelly medium sets fast, is safe for delicate tissues, preserves the color responses of cell walls to potassium hydroxide, has a high index of refraction, has a long life, and the ingredients are safe and inexpensive. Its slow evaporation rate makes it virtually permanent with **luting** (sealing with a paste, nail polish, or other sealant around the coverslip).

Glycerine jelly requires a longer procedure because it must be melted before it can be used. But melting degrades the gelatin so it does not set, so it must be melted just before it is used. If the slide gets too hot, it will destroy delicate organs such as axillary hairs. Coloration from KOH tests will disappear in a few days. And, the glycerine will evaporate over a period of years. Evaporation can be retarded by storing the slides in a closed container, but that presents an additional nuisance.

Glycerine Jelly Preparation (Zander 2003)

Richard Zander (2003) has suggested using glycerine jelly instead.

1. Take 2 packets (7 g each) of gelatin (Knox brand works fine).
2. Mix in 50 ml cold water to hydrate.
3. Heat but don't boil, while still stirring, until the liquid is clear or at least there is no undissolved gelatin.
4. Swirl it to dissolve all gelatin.
5. Add glycerine to make 200 ml.
6. [Optional: Add a crystal of thymol to keep down bacteria and fungi.]
7. Heat for about an hour until everything dissolves and the liquid is clear.
8. Pour on a clean PVC (polyvinyl chloride) pan with a flat bottom to make a thin layer.
9. Leave uncovered or cover with cloth to prevent dust overnight to several days to allow most of the water to evaporate.
10. Peel off the thin, flat sheet of glycerine jelly.
11. Roll into a kind of jelly roll.
12. Slice the roll crosswise into neat, tight curlicues or helices about 0.5 cm wide.

13. Store in a plastic box.
14. Pinch off a small piece when wanted.
15. If there are bubbles, reheat in a beaker (water bath is helpful) and let stand as liquid. Do not keep hot for a very long time, as heat denatures the gelatin.
16. The glycerine jelly will be hard to remove from the plate unless the water portion has evaporated. It is best to evaporate the water portion with heat since glycerine absorbs water, to some extent, from the air.

Using Glycerine Jelly

1. Place bryophyte material in a drop of water on a slide and soak it.
2. If the water is not absorbed readily, heat the slide slightly with a butane cigarette lighter, or start with warmed (not boiling) water.
3. Make desired sections and arrange the material on the slide.
4. Pinch off a bit of the glycerine jelly and place on slide and heat the slide evenly. (Heating one spot can break the slide.)
5. Arrange the material and add a coverslip.
6. The jelly hardens in a minute and may be mailed after cooling.
7. If clearing is needed, first dip the moist plant in lactic acid for a minute or so, or heat in pure lactic acid before preparing the glycerine jelly mount.
8. The jelly can be kept liquid for a short time on a hot plate, but prolonged heat turns the jelly brown and the gelatin breaks down so that it won't harden.
9. NOTE: Glycerine will eventually dissolve calcium carbonate.

Making Semi-permanent Mount

1. From wet mount, blot specimen to remove excess water.
2. Add small drop or drops of glycerol to slide with specimen.
3. Heat with lighter under slide till boiling (this pumps up the tissues after an initial collapse).
4. Do dissections if needed.
5. Add piece of glycerine jelly and heat until melted (try to avoid boiling a second time).
6. [Try transferring boiled specimen atop solid piece of glycerine jelly on clean slide, then heat just to melting; this helps minimize bubbles and helps minimize mess.]
7. Arrange specimen quickly and if needed cover with a coverslip.
8. Add label on left side and store slide flat in air-tight box.

Dave Wagner has been mounting liverworts on his slides in just glycerin for years, and seems to have much success. However, Des Callaghan (Bryonet 25 November 2013) found that some bryophyte species, such as ***Thuidium*** (Figure 7), do not reach "full turgor" and remain somewhat dehydrated in glycerol plus alcohol (the alcohol evaporates, leaving the glycerol).

Richard Zander (Bryonet 6 December 2013) suggests heating the slide of water-mount cells in added glycerol on a hot plate or coffee cup warmer. Cells of such sensitive species as ***Tortula hoppeana*** (Figure 8) expand to full turgor and stay that way. He also recommends using a 1 to 1 mixture of glycerol and Elmer's Clear School Glue (apparently a thick polyvinyl alcohol solution). The index of refraction remains high. When the water in the glue is evaporated it makes a semi-solid mount. If the cells collapse, heat on a hot plate or cup warmer as with pure glycerol. Make sure the glue and glycerol are well mixed or the slide will seem to "weep" glycerol.

Figure 7. ***Thuidium delicatulum***, a species that does not rehydrate well in glycerol plus alcohol. Photo by Michael Lüth, with permission.

Figure 8. ***Tortula hoppeana***, a sensitive species that expands well in water plus glycerol with heat. Photo by Paul Wilson, with permission.

Clearing

If you need a more transparent specimen, you can clear it first by using a mixture (1:1) of glycerol and lactic acid [see step 7 in "Using Glycerine Jelly" above (Zander 1997)]. You can make mounts more quickly by adding glycerine jelly directly to a blotted wet mount and heating to boiling (bubbles may be troublesome). Dip the moist plant in lactic acid for a minute or so (or heat in the pure acid) before preparing the glycerine jelly mount.

Alternatively, you can keep a small hot plate near your microscope. Set a microscope slide with the wetted plant (or sectioned material) in a little water (or a mixture of water and a little glycerine) and a cube of glycerine jelly on the hot plate. After a moment or two, the glycerine jelly melts and some of the extra water evaporates. Remove the slide, arrange the material, and put a coverslip on it. The hot plate can be one of those coffee warmers you can pick up in a flea market cheaply. This eliminates heating a cube of glycerine jelly on a slide, which can break the slide if it is not heated evenly with the cigarette lighter or other point-source heat source. You can rig it so that the hot plate warms up whenever the microscope light is on.

Zander (1997) adds that glycerine will eventually dissolve calcium carbonate. Also, if you make the glycerine jelly with a high concentration of gelatin, then if you work on your specimen in a water/glycerine mixture (which slows sections from flying around when you make them), any added glycerine jelly will not be too dilute (when mixed with the pure glycerine on the slide) to harden.

For **Mniaceae** (Figure 9) and other large-celled bryophytes, you may need modifications. Richard Zander (Bryonet 9 November 2009) suggests that you strip leaves in water or Pohlstoffe solution or 2% KOH, then add 2 tiny drops of pure glycerine to the water or solution mount. Make cross sections and arrange leaves nicely in the unmixed water/glycerine mount, add a fingernail-sized clod of glycerine jelly, heat with one of those butane lighters with the nice torch flame, taking care to heat the slide fairly evenly so it does not break. Heat until the glycerine jelly just melts, or before it is completely melted, rearrange the leaves and whatever else is on the slide before placing a coverslip on it. After it cools it should be solid and ready to mail or bang around the lab without drying. Don't use 2% KOH with liverworts as the leaf cell walls are attacked.

Figure 9. ***Plagiomnium cuspidatum*** dry, a moss that repels water instead of absorbing it. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University.

Dan Marsh (Bryonet) similarly suggests Frahm's (1990) Solution, 1:1:1 glycerine, water, mucilage (the brown glue-type from school supply sections of stores). For study of variation in ***Sphaerocarpos*** spores (Figure 10), this solution served not only as a satisfactory mounting medium but also cleared the spores quite nicely.

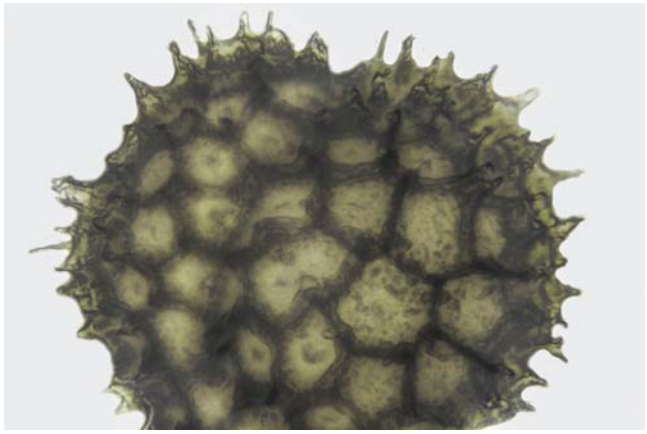


Figure 10. ***Sphaerocarpos michelii*** spore, a structure that clears well in Frahm's solution of glycerine, water, and mucilage in equal parts. Photo by Dick Haaksma, with permission.

DMHF (5,5-dimethyl Hydantoin Formaldehyde)

In his search for a better mountant, Zander (2007) uncovered 5,5-dimethyl hydantoin formaldehyde (DMHF), discussed by Steedman (1958). It is a water-soluble resin generally used in such products as cosmetics, adhesives, coatings, inks, and textiles. Although a similar chemical is used to gradually release the carcinogenic formaldehyde, DMHF releases little or none. Zander found the solution easy to use with tested species of ***Tortula*** (Figure 11) and ***Mnium*** (Figure 3) but, when hardened, the mountant resulted in somewhat collapsed laminal cells and a low index of refraction. Although DMHF would indeed make permanent mounts of bryophytes that are less collapsed than, *e.g.*, acrylic solutions, the low index of refraction makes it difficult to examine anatomical details such as laminal papillae. When mixed with glycerine, visibility improves but the material will not set well.

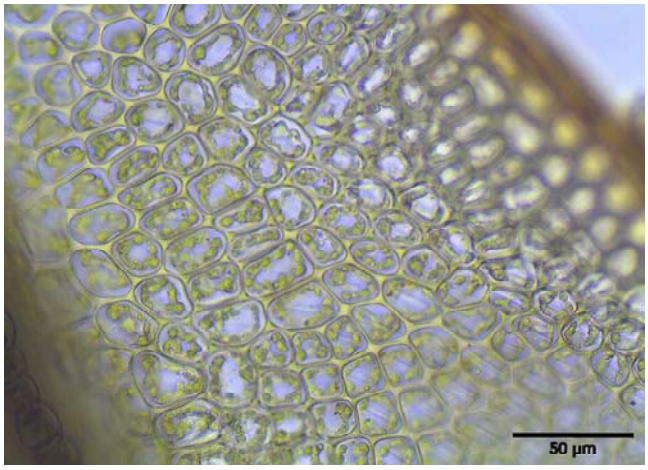


Figure 11. ***Tortula subulata*** leaf lamina cells, member of a genus wherein mountants may collapse the laminal cells. Photo by Kristian Peters.

PVA

Zander (2007) credits Howard Webb with alerting him to polyvinyl alcohol with glycerol (PVAG) and polyvinyl alcohol with glycerol and borax (PVAGB) media (Salmon 1954; Dioni 2007; Webb 2007). However, Anderson (1954) cautions against use of PVA (polyvinyl alcohol) as a mountant because after a few months the plants begin to shrink and distort, ultimately becoming unrecognizable. The addition of glycerol and borax had the potential to prevent those problems.

If in fact PVA is an acceptable medium, it is easy to obtain. It is the primary ingredient of transparent glues and glue gels, and one could experiment with these as well. Carolina Biological Supply has a powdered form that can be made into a thick syrup by heating it for a long time in water. Zander points out that when used alone the PVA causes the same problems as in Anderson's warning, those also known for acrylic resins and DMHF, where cell walls collapse and the index of refraction is low. Zander reports that the addition of glycerine gives the mountant a high index of refraction, but the resulting hardened medium is cloudy. The addition of borax does not help, nor does decreasing the water. He couldn't recommend it.

Elmer's glue consists of PVA, water, ethanol, and acetate. It can serve as a mounting medium, as shown by David Meagher (Figure 12).

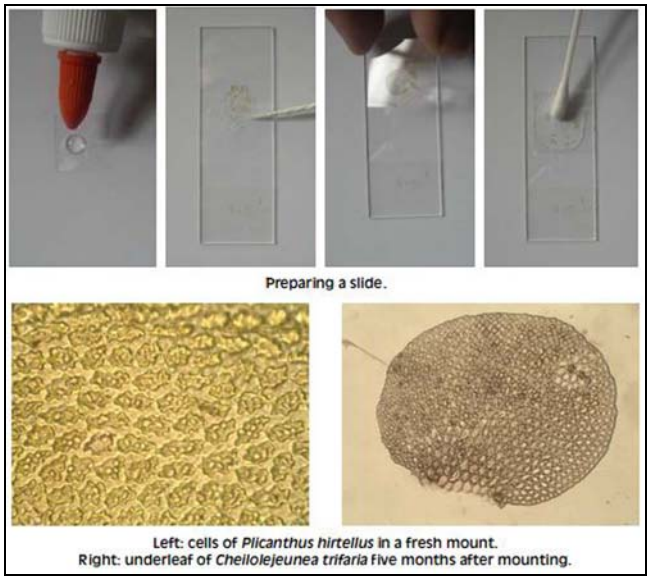


Figure 12. Meagher permanent mounting methods using glue. Photos by David Meagher, with permission.

Karo Syrup

A cheap and readily available mountant is Karo Syrup. This is the mountant of choice at the State Herbarium of South Australia. Graham Bell (pers. comm.) reports that it works better than other media in that dry climate. He adds phenol (2-3 %) to the dilute Karo mix to prevent fungal and bacterial contaminants. Standard dilutions of the Karo syrup are 20, 50, and 80%. It is often necessary to start with a lower concentration, let the slide dry for a day or two, then backfill it with more Karo solution at a higher concentration. Some of the slides made in this manner are more than 70 years old and still useable. Some stains seem to present problems, but once the slides stabilize they remain in good condition.

Polyvinyl Lactophenol

This mountant has the advantage that it need not be luted (Zander 1993) because it actually sets, which Hoyer's does not (Fisk 1991). However, cells collapse in it. Zander (1983b) suggests instead a lactophenol gel because it usually does not collapse the cells. It also has a high index of refraction. However, Rod Seppelt (Bryonet 12 February 2001) warns that heating solutions with **phenol** needs to be done with care. The MSDS data sheet considers it to be very hazardous when in contact with skin or eyes and dangerous if ingested or inhaled. It can cause corneal damage or blindness if it contacts the eye and can cause blistering of the skin. Severe over-exposure can cause lung damage, choking, unconsciousness, or even death. Use a hood if available and avoid breathing the fumes:

lactic acid (=2-hydroxypropanoic acid)	20 cc
phenol, crystal (=carbolic acid)	15 g
distilled water	15 cc
methyl cellulose powder (=cellulose methyl ether, of viscosity 25 cP in 2% solution of lowest viscosity available)	6 g
ethylene glycol (=1,2-ethanediol)	35 cc

Procedure:

1. Mix phenol with lactic acid, dissolving with gentle heat.
2. Add water and stir.
3. Heat to just boiling (**use fume hood**).
4. Add methyl cellulose powder and stir vigorously into hot solution to dissolve (reheat if necessary).
5. Add ethylene glycol last.
6. Pour into glass cylinder and let stand to allow bubbles and undissolved material to rise.
7. Allow to settle for a day or two, then remove any floating particles.
8. Pour clear liquid into storage bottle.
9. Use small bottle with applicator wand in lid or plastic squeeze bottle with fairly wide opening (4 mm) to place drop or two on slide.
10. If specimen is incrusted with carbonates, first soak them in drop or two of dilute HCl to prevent bubble formation in lactophenol gel.
11. Specimens previously soaked in KOH should be neutralized with drop or two of dilute HCl before mounting in lactophenol gel.
12. Moist plants may form a precipitate in the lactophenol gel, but it will dissolve with stirring.
13. Arrange the plants and leaves on a **clean** slide while the gel is still liquid.
14. Add coverslip to preserve for 1-2 months.
15. For semi-permanent slides, it is best to seal the mount with a **lutant** like clear fingernail polish. Nail polish does not adhere well to glass, so varnish might be substituted. Some bryologists (*e.g.* Watson 1963) prefer **circular coverslips** because their lack of corners makes them adhere better.

16. For a more permanent lutant you can use one of the following:
    poly (ethyl methacrylate) with butyl benzyl phthalate as plasticizer (Krystalon®Harleco, Gibbstown, NY 08027 USA) (an artificial balsam)
    polyurethane gloss finish (used for wood floors) – keep slide out of light
17. Apply lutants liberally to make a good seal, but avoid having a ridge that might interfere with changing objectives on the microscope.
18. Keep lutants in a balsam bottle or small disposable applicator bottle; keep more than half full to help exclude air.
19. Keep disposable wipers on hand to keep tools and hands clean from the reagents.
20. A fan may be needed to carry away vapors.

Aquamount Improved

Matt von Konrat (Bryonet 25 June 1999) suggests Aquamount Improved, from BDH Laboratory, an improvement over Aquamount that contained phenol. This solution comes ready to use and is relatively cheap. It avoids the problems of tissue shrinkage.

Figure 13. Kleermount, sold in 100 ml bottles from Carolina Biological Supply Co. Photo by Carolina Biological Supply Co.

Kleermount, Xylene solution #2

Kleermount (Figure 13), suggested by Volkmann-Kohlmeyer and Kohlmeyer (Kohlmeyer & Kohlmeyer 1972; Volkmann-Kohlmeyer 1996) for fungi, works well for bryophytes as well (Martin Wigginton, Bryonet). Kleermount is available from Carolina Biological Supply Company, 2700 York Road, Burlington, NC 27215-3398. International orders: (+1) 910-584-0381; FAX (+1) 910-584-3399). They provide a Material Safety Data Sheet (MSDS) for the solution, which warns that it is harmful by inhalation, possibly causing irritation to the respiratory tract. Prolonged exposure may result in an allergic reaction; it can cause eye and skin irritation. If ingested it may cause gastrointestinal discomfort. It is also a fire hazard: closed containers of Kleermount Xylene solution exposed to heat may explode. In short, its use requires caution and common sense.

Serge Hoste (Bryonet 24 June 1999) adds that Kleermount causes serious plasmolysis in ***Plagiomnium*** (Figure 14), ***Funaria*** (Figure 15), ***Amblystegium*** (Figure 16), and others. He advocates "using a medium with the highest water content possible. A gelatine-glycerol-water and PVA-glycerol-water, with a few drops of thymol added as fungicide, is claimed to keep for more than 20 years and conserve color to a much larger extent than with the use of chloral hydrate. Good sealing around the edges of the cover slide is paramount but can easily be obtained by applying two (or more) generous coatings of clear nail varnish around the edges of the cover glass."

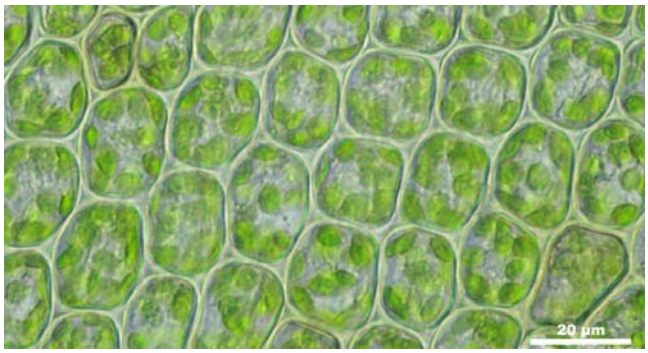


Figure 14. ***Plagiomnium undulatum*** leaf cells. This is a member of a genus in which leaf cells plasmolyze in Kleermount. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.

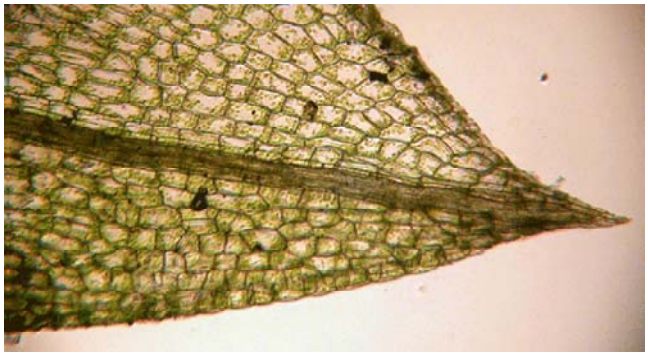


Figure 15. ***Funaria hygrometrica*** leaf cells. This is a member of a genus in which leaf cells plasmolyze in Kleermount. Photo by Bob Klips.

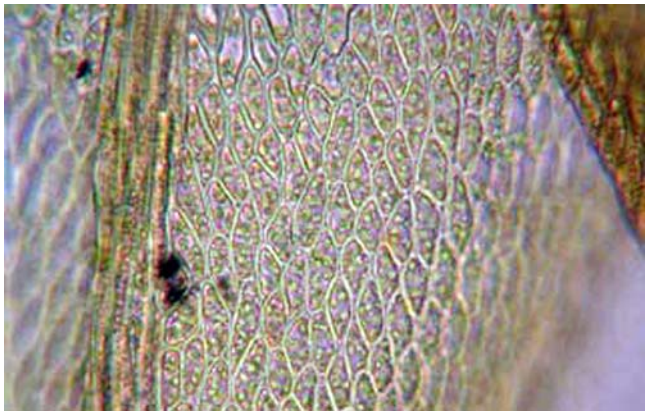


Figure 16. ***Amblystegium varium*** leaf cells. This is a member of a genus in which leaf cells plasmolyze in Kleermount. Photo by Bob Klips.

Fluoromount-G

Bernard Goffinet (Bryonet 12 February 2012) recommends Fluoromount-G. This mountant is available from Fisher (OB100-01, 25 ml for 25$ before discount, good for "500 slides"). It is toxic and should be handled with care. The MSDS data sheet states that it is potentially harmful if ingested and warns "Do not get on skin, in eyes, or on clothing. Potential skin and eye irritant." It has the advantage that it does not bleach the leaves, nor alter them in any way (at least within the two weeks following its use). It is water soluble, so it can be used for mounting wet specimens.

Gray-Wess Mountant

Uwe Schwarz (Bryonet 12 February 2012) suggests Gray-Wess as an alternative mountant:

polyvinylalcohol	2 g
glycerine	5 ml
lactic acid	5 ml
water	10 ml

Mix everything together and heat it in a test tube in hot water until the liquid becomes clear. If the specimen has calcareous incrustations, you should skip the lactic acid because it will cause a lot of bubbles.

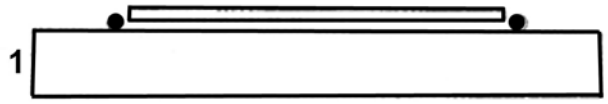
Double-Coverslip Method

Martin Wigginton (Bryonet) suggested the double-coverslip method (Figure 18), published for fungi (Figure 17) by Volkmann-Kohlmeyer and Kohlmeyer (1972; 1996), but originally introduced by Diehl in 1929. Although this method was developed for preserving fungal spores, it works well for bryophytes. The method is more time-consuming than just using fingernail polish, but the results are much more permanent. This method should be used by anybody who needs to prepare voucher specimens, and it should always be used for preserving type material where slides are needed.

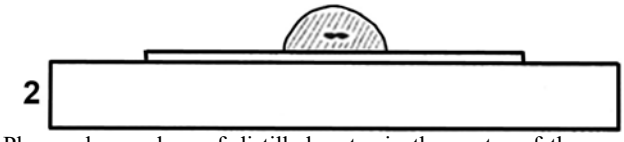
Figure 17. Ascospores of a fungus, using a double coverslip, with appendages perfectly preserved after 29 years. Photographed using Nomarski interference contrast and quartz filter. Photo from-Kohlmeyer & Kohlmeyer 1996.

Tocci noted that shellac was used in the 1800's and lasts about 100 years. One can also use Paraloid B-72 in acetone. But she also recommends the double cover slip method that is popular for mounting fungi (Kohlmeyer & Kohlmeyer 1972), and that can be used with glycerine. It permits observation of living material that can subsequently be made into a permanent mount.

Double Coverslip Method of Kohlmeyer and Kohlmeyer:



Place a 25 x 25 mm coverslip on a clean 76 x 26 mm glass slide, sealed to it with two drops of distilled water.

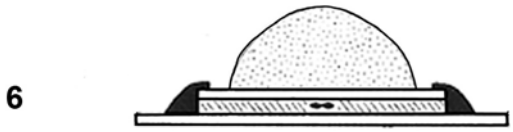


Place a larger drop of distilled water in the center of the cover glass. Add the specimen to the drop.

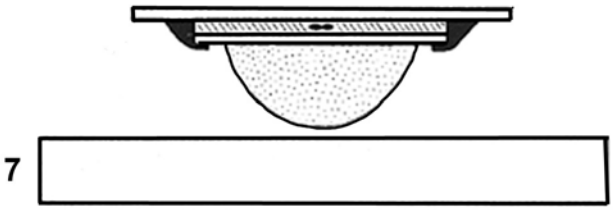
Use the smaller coverslip (18 x 18 mm) to cover the drop with the specimen, permitting immediate viewing of the living material with a compound microscope. Immersion oil can be used if necessary, but it is messy and must be cleaned off, endangering what has been accomplished. It is better to save it until the slide has been sealed and dried.

After making all the observations, measurements, and photographs you need for now, add a droplet of concentrated glycerine to the water at one or two sides of the small coverslip to prevent drying out. The slide must be stored horizontally in a dustproof container for a few days to allow the water to evaporate. Excessive water plus glycerine can be removed from the edges of the larger coverslip easily with filter paper – or if needed, add more glycerine.

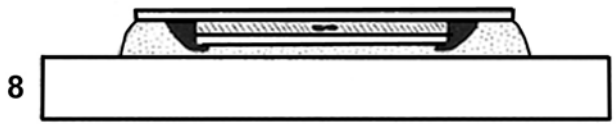
Seal the mount with a thin ring of clear fingernail polish. It is best to repeat this step after an hour to be sure the glycerine is perfectly sealed.



When the nail polish is fully dried, remove the large cover glass from the slide using a needle. Place a drop of mounting medium on the small cover glass. It will take some experimentation to get the right amount.



Turn over the preparation and place it on the slide, gluing it to the slide.



The drop of mounting medium flattens out, but this will happen more readily if a small weight is put on top, *e.g.* some of the larger nuts from a nut and bolt set. These are small, so a supply can easily be kept in the lab. The medium will ooze out and surround the edges of the small cover glass, permanently sealing in the small cover glass and nail polish. Any excess medium squeezed out at the sides can be taken off with a needle syringe. The preparation must be stored horizontally until the medium is hardened, but it can be used after a day, should further microscopy be necessary. The sealing procedures are best done under a hood to avoid breathing the toxic fumes of the medium.

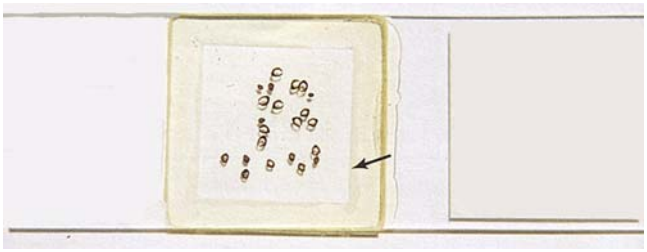


Figure 18. Double-coverslip slide showing smaller top coverslip (arrow) and nail polish seal. Note the blank label on the right. Paper labels can easily come off, so using a slide with frosted glass on one end may be a preferred solution. Labelling should be done with waterproof ink and a Rapidograph pen. Photo modified from Volkmann-Kohlmeyer and Kohlmeyer 1996.

Since this slide and specimen can be used again and again, it is wise to check it for visual clarity of important structures before beginning the sealing process. Be sure that both sides of the leaf can be seen, that at least one leaf base can be seen clearly, and that papillae, if present, can be seen. The latter often requires showing a bent surface of a leaf. Once the process is complete and thoroughly dry, the slide can be placed in a minipacket for protection and stored in the packet with the specimen. This will serve the added advantage of preserving more of the specimen because it won't be necessary to use more material to make more slides.

The method requires two coverslips of different sizes, a large one (25 x 25 mm) and a smaller one (18 x 18 mm). The large coverslip is attached to a clean slide (76 x 26 mm) by using two droplets of distilled water (to avoid mineral deposits). A somewhat larger drop of water is placed on the coverslip and the specimen added. The smaller coverslip is then used to cover the specimen and water.

This method seems to lack a preservative, so one might want to follow the advice of Norbert Stapper (Bryonet 13 February 2001) and add camphor or phenol. We don't know their long-term effects on the slides, but see the warnings of health risks of phenol discussed above.

Lutants – Sealing Slides

Once the mounting medium is reasonably dry, it is usually necessary to seal the coverslip (Diehl 1929). The medium remains somewhat fluid, so the coverslip is essentially floating. David Wagner (Bryonet 31 May 2010) recommends painting with a **lutant** of clear fingernail polish on the two sides of the coverslip parallel with the length of the slides. He cautions against enclosing the coverslip completely because it may become necessary to add more glycerine later. Glycerine at the edges may prevent the nail polish from sticking, in which case the slide may need to be cleaned. Excess liquid should be drawn off first with a paper towel at the edge of the coverslip. You should finish the cleaning of the remaining residue with alcohol or a wetting agent on a cotton swab. It is a good idea to check to be sure that the specimen(s) remains in a suitable position before affixing it permanently. The polish should be spread well away from the edge of the coverslip to give the polish more adherence outside the influence of the glycerine.

In addition to keeping the specimen moist, a coverslip that is tacked down is much easier to clean. Dust will easily accumulate over time and glycerine may invade the surface from a neighboring slide. Wagner advises cleaning lengthwise with a cotton swab moistened with alcohol, being careful to avoid the open edges of the mount so the alcohol is not drawn under the coverslip.

Nail polish has been criticized as not being permanent, but permanent slides need to be sealed with a **lutant** (sealer). Richard Zander (Bryonet 12 December 2018) recommends a 70:30 mixture of clear glue (*e.g.* Elmer's) and glycerin. The glue is a polyvinyl alcohol and lasts a long time. Since lutants usually don't last more than a decade, it is necessary to make sure you can easily soak the slide and remount the specimen. The polyvinyl alcohol is suitable for this purpose because it is soluble in water.

But David Wagner argues that Sally Hansen's "Hard as Nails" clear fingernail polish will last more than 40 years as a lutant, with pure glycerine as a **mountant**

(mounting medium). Instead of ringing the cover glass, he uses it to tack the cover slip in place. This permits the cover slips to be cleared of dust in later years without disturbing the mount. The mountant of glycerine is placed at the edge of the water mount over night so that the glycerine can slowly replace the water. Once the mountant has permeated the mount, the cover glass can be tacked in place with the nail polish.

Reviving Dried Slides

All is not lost if your slides dry out. Glycerine mounts can be revitalized by adding water with a good wetting agent around the open edges of the coverslip (David Wagner, Bryonet 31 May 2010). This will gradually loosen the coverslip so it can be removed carefully with your needle-point forceps. Nail polish usually comes off with the coverslip and can easily be broken off. Polish left on the slide can be scraped away. Make sure the material you need is still on the slide before placing a new coverslip. Otherwise, if important specimens are stuck to the removed coverslip, it is best to re-use that coverslip. Flood the surface of the mount area with your wetting agent mix and gently lower the coverslip as you would with a fresh mount. Add glycerine to the edge of the coverslip and let it sit to dry and infiltrate the specimen. Continue processing it as you would a new mount.

Cleaning Slides

Des Callaghan (Bryonet 11 December 2013) has a great way to clean your dirty slides, whether for re-use or permanent slides that have become smeared. Rub them with a paste-type cleaner between your fingertips. Callaghan uses the UK brand Astonish; a tub will last a lifetime. The paste washes off easily and leaves the glass surface spotless.

Labels

Stick-on labels are available, but these eventually come off. A more permanent solution is to use a slide with an etched area for writing (Chris Cargill, Bryonet 11 December 2013). There is nothing to come off, and Cargill says that permanent markers do not wash off with water and if stored in the dark do not fade appreciably. Non-permanent ink does come off. One can also use a diamond-tipped pen to inscribe the slide permanently. This can be done with an accession number, but the accession list could get misplaced, so it is better to put all information on the slide.

David Wagner (Bryonet 10 December 2013) has used Scotch brand Magic Mending Tape for years, long enough to consider it of archival quality (good for at least a couple of decades). It is quick, easy, and reversible (Figure 19):

1. Strip off a 2 inch (5 cm) length of 3/4 inch (~2 cm) wide tape and tape the slide to the work bench. This holds the slide tightly in place so that writing very small is possible.
2. Write specimen information on the tape. I always use a pencil because there's no wait for ink to dry. Erasable, too. This is the stage to add glycerine to the edges of the coverslip for a semipermanent mount.
3. Cut the edge cleanly with a razor blade.

Figure 19. Application of Scotch Magic Tape labels. Photo by David Wagner.

Jan-Peter Frahm (Bryonet 11 December 2013) suggests another alternative for quick, long lasting labels using a computer and Brother P-Touch labelling machine connected through a USB port (Figure 20). This printer also works as a printer for MS Word so that one can make a template in Word. The labels are superior because they are plastified and do not flake off as is often the case with other labels. The print is superior to handwriting for legibility.

Figure 20. Slide label made using Brother P-Touch labelling machine. Photo by Jan-Peter Frahm.

Des Callaghan (Bryonet 11 December 2013) suggests using a laser printer, then cutting labels to size and attach them with PVA glue or double-sided sticky tape (Figure 21). The labels can be sprayed with hair lacquer **before** sticking them to the slide to protect them from abrasion.

Figure 21. Slide labels using a laser printer, PVA glue, and hair lacquer. Photo by Des Callaghan.

Richard Zander (Bryonet 11 December 2013) considers all commercial slide labels to be inadequate, coming off the slide within a few decades. He feels all slides should be kept for students to use in the future. This is especially important for rare collections with little material. Zander cuts rectangular labels from buffered paper and stores a supply in a box. When needed, they are glued on a slide with Elmer's white glue (polyvinyl acetate – "a superb glass adhesive"). This can also be used to re-attach labels that fall off. The glue is kept half cm deep in a balsam applicator bottle so that no glue collects around the edges of the top and is has a glass applicator rod in it. The glue should be slightly diluted with water and the lid of the balsam bottle should be coated with mineral oil on the ground glass to make a better seal. Only a tiny drop of glue should be rubbed on the back of label and label pressed on the slide. Information is added to the label with permanent, non-fading ink, but print carefully so it can be read by people whose first language uses a different alphabet.

Slide Storage

Mounting media of "permanent slides" tend to settle if the slide is placed on its side. Hence, horizontal storage is usually essential. Richard Zander (11 September 1998) makes "trays" using corrugated cardboard. Strips of cardboard are glued across the tops and sides, and one down the middle. This provides the right space to keep slides lined up and the height keeps the next "tray" from making contact with the slide. He recommends gluing a small tag on the bottom edge of the "tray" that tells the contents of that group of slides.

Wagner stores his slides on trays the size of plant press boards or herbarium sheets so they fit on shelves of a standard herbarium cabinet. Three rows can be placed from end to end. Its durability was tested when he dropped a tray of slides in a parking lot. The tray was sandwiched between cardboard press boards so when the bundle hit the pavement upside down, only one slide was thrown out and broken. The rest survived unscathed even though tumbled.

Storage trays need not be made of expensive material. Some bryologists use cardboard trays, although they may suffer loss of rigidity if they get wet. Wagner is currently using foam core board. It helps to line the bottom with blotting paper or similar absorbent material to help absorb any glycerine that travels there by capillarity. It also helps to super glue borders and dividers that are 1.8 cm wide by .4-.5 cm thick as a means of keeping the slides in place.

Preserving Bryophyte Plants for Dioramas

The following advice for preparing dioramas is from Roxanne Hastings and Donna Cherniawsky, Curators of Botany, Royal Alberta Museum, Canada. The recipe came from a display tech, Ludo Bogart, long since retired and where he got it from nobody knows, including him.

Field Collections

1. It is critical that you get the plants into the tank as fresh as possible… especially with vascular plants, less important for bryophytes and lichens but absolutely critical for gymnosperms. Large plastic bags work well (museum specimen bags of heavy poly count – not Safeway Ziploc) or sheets; wrap the plants into them in the field and put them into the largest thermos tubs available, with ice packs. For conifer shrubs and long branches, you can wrap them in plastic and put them on top of blocks of dry ice to get them back home from the field. You have maybe two days at most to get the plants from field and into the vat. Having walk-in refrigeration at both a field station and at the museum will go an awful long way to the success of preservation. Putting the plants into Tupperware-like containers and storing them in refrigeration will buy you several days time. Getting conifers in the tank the same day you get back from the field, no matter how late, is important. The other material, if stored in refrigeration, can wait a day or two.
2. Hastings and Donna Cherniawsky would go into an area and spend the first few days just scouting the sites and tagging all the spots where they wanted to collect. And then in the last 2-3 days they went back to all the sites and collected the stuff in a mad rush.
3. What works superbly for collecting sheets of mosses is large plastic under-the-bed storage trays with snap-on lids. The depth is about perfect for the height of mosses and the trays can be easily stacked on top of one another, which makes transport in the back of a van or minibus that much easier. Also get a number of smaller plastic containers to pick up smaller samples of evergreen shrubs and specific mosses that you can weave into your display when you build your diorama. These will make for a more realistic forest floor, and having the specimens in separate tubs

makes it easier to find them when you are building your display. Tupperware will become your friend for this project.

4. Collect at least twice as much as you think you are going to need for the display. Some specimens will just fall apart in the processing or will just not look as good as you thought they would when you saw them in the field. Having more diversity available will help you create better displays. Any extra material will find a happy home in a teaching collection. People absolutely love handling specimens that they can see on display in your gallery and they make for gorgeous open house/public appreciation days material.

Preservation Protocol (From Roxanne Hastings, pers. comm. 11 October 2012)

1. Assemble the equipment:
   stainless steel tank with a lid
   perforated stainless steel paddle or spoon
   stainless steel wire mesh
   roll of stainless steel wire
   fume hood
   source of hot tap water
   sink hose
   big funnel
2. Assemble personal safety equipment:
   Wrap around eye goggles
   Nose and mouth mask – medical or industrial
   Long rubber gloves
   Rubber boots – safety toes if working with barrels of liquids
   Knee length lab coats
   Breathing mask is good idea if working with industrial volumes

   NB you must wear proper safety equipment. Acetone and alcohol are dangerous. At the minimum you need safety goggles for your eyes and you should have an eye rinse station in the area and wear elbow length rubber gloves. With big tanks you need rubber boots, maybe even safety toes depending if you have to roll drums yourself. Breathing masks are advised for big jobs. You must work in a ventilated room and the tank must be used under a fume hood. The process sounds a lot worse than what it is. It becomes routine. But you must pay attention to safety. Cover your eyes and cover your mouth and nose. There will be splashing and it will hit you in the face. A trip to an industrial safety supply shop will easily resolve your concerns.

3. Prepare the preservative:
   1 part Acetone
   1 part Isopropyl Alcohol at 70%
   2 part Glycerine

   The acetone evaporates the water in the plants, whereas the alcohol and glycerine enter. The alcohol preserves the plants and the glycerine gives them their lifelike feel and luster. Acetone can remove chlorophyll color and cause some species to become black or grey. Fortunately, mosses and lichens usually came out unscathed and required no touch up. To ensure accurate color rendition, take photographs in the field with color charts and also write down the color numbers so you can match the colors later. You can use standard paint chips available free at paint shops to match colors.

4. These fluids are all **thoroughly** mixed together at once. This takes some effort because they have significant density differences. For large batches, you can use perforated steel shelves built so that they can be put into a large tank on a ledge built all around the inside face of the tank at half height. This allows two layers of specimens without them all piling up in the bottom of the tank.
5. Moss specimens will easily fall apart in a big tank so it helps to wrap the sheets of mosses in stainless steel mesh - what concrete people use to provide structure for a sidewalk when they pour concrete into it. You will need a strong set of metal clippers to cut the mesh and a long roll of wire to stitch the mesh together once you have wrapped your specimens. The mesh is reusable. Wear leather work gloves because the wire mesh is really sharp once it is cut.
6. If you are doing a big job and need to order your chemicals by the drum, then you will need a stainless steel hand pump to get the fluid from the barrel into the tank. You must ground the pump with a wire to prevent friction sparking when you pump. Plastic pumps won't spark but they are useless for pumping viscous liquids like glycerine and will melt in Acetone. And obviously you cannot use electric pumps. If you are doing a smaller job you can buy the supplies by the liter and just dump it into the tank. Then you won't have sparking issues.
7. It takes a lot of stirring; a perforated stainless steel spoon or paddle works best. Plastic will eventually melt in the acetone and is not strong enough to stir glycerine. The perforations provide better mixing and glides more easily through the glycerine.
8. Put your specimens into the tank and keep pushing them down. They will float for a few hours to a few days while they absorb the fluid and the air gets beat out of them. Gently stir them until they settle. In a big tank you may have to come back the next day and gently stir them again. Let them sit for a few weeks. Mosses go through the process in a matter of weeks. Small trees or branches in the order of a meter or so long will take a few months.
9. Put a lid on the tank; it should also be stainless steel. You MUST do this in a fume hood. Smaller tanks can be put in a lab fume hood.
10. Then you have to fish them out. A 3 m long stainless steel rod with a hook on it to grab the mesh works well. Large plants will be really, really heavy! Lift them out and let them drain into the tank. Then you have to rinse them, still in the screens, with very hot tap water. Rinse them until the water runs clear and not brown. Don't let this water go down a drain! Rinse them back into your now empty chemical drums. You can use a big plastic funnel with screens in it; put the funnel over the drums and rinse into that.
11. Once the plants are drained, open up the screens and lay out the specimens **in the fume hood** to dry. This will take at least a week. Keep checking.

12. Now your plants are ready to process. They will be lustrous and flexible with various amounts of fading that may require some airbrushing – or not. Some specimens still look very good after 40 years. Specimens that were processed in 2008 were still in perfect condition in 2012 and you could still smell the aroma of the sap of the pine trees. All the pines still have their needles and are flexible (2012). You can use leftovers for hands-on teaching with school kids and the public; they are still perfectly life like, in fact they are tougher because they are a tiny bit like rubber cement.

Preserving Liverworts

Despite Rob Gradstein's claim that thallose liverworts can be dried like mosses (see chapter on Field Taxonomy and Collecting Methods in this volume), Wagner considers preservation in liquid a necessity for examination of morphological characters. He recommends using rubber-topped vials used for drawing blood and reports that some are 20 years old, but have not lost any appreciable amount of liquid.

Susan Moyle Studlar (Bryonet 20 September 1999) has observed that some of the thallose liverworts retain their green color and are easy to work with after air drying in a plant press. She has had success with this treatment of species of ***Conocephalum*** (Figure 24), ***Pellia*** (Figure 23), and ***Pallavicinia*** (Figure 22).

Figure 22. ***Pallavicinia lyellii***, a liverwort that can be preserved by drying. Photo by Jan-Peter Frahm.

Jesús Muñoz (Bryonet 19 February 1999) suggests two formulas for preserving liverworts:

10:1:1:8 96% ethanol : glutaraldehyde : glycerol : water

or

1:1:18 glutaraldehyde : glacial propionic acid : 70% ethanol

Muñoz reports that you can use formaldehyde instead of glutaraldehyde, but that glutaraldehyde gives better results. The bottles must close tightly or the ethanol evaporates. Unfortunately, the mixtures degrade chlorophyll and lipids, so although morphology and anatomy remain as in live plants, oil-bodies and natural color disappear. As suggested in the chapter on Field Taxonomy and Collecting Methods in this volume, it is a good idea also to keep a herbarium sample cross-referenced to the liquid sample so that there is still material for DNA or chemical analysis.

Figure 23. ***Pellia endiviviifolia*** near Swallow Falls, Wales. This liverwort can be preserved by drying. Photo by Janice Glime.

Figure 24. ***Conocephalum conicum***, a liverwort that can be preserved by drying. Photo by Dick Haaksma.

David Wagner (Bryonet 19 September 1999) agrees that these two formulas work well. He advises against Pohlstoffe for thallose liverworts and compares working with the revived specimens to working with boiled lettuce. Even leafy liverworts do not fare well in Pohlstoffe because the oil bodies disintegrate in that and other wetting agents. The oil bodies sometimes survive drying if water, but no wetting agent, is added to rehydrate them. Wagner uses FAA (formalin-acetic acid-alcohol), which is similar to the suggestions of Muñoz except for the presence of 5% acetic acid and lack of glycerine. But Wagner points out that the

glycerine is important to keep the tissues soft if they accidentally dry out. The downside of glycerine is that it can interfere with the embedding process if one wants to prepare the specimen for microtome sectioning.

David Wagner (Bryonet 5 November 2022) uses a 50:50 mix of denatured alcohol and distilled white vinegar as a liquid preservative. The denatured alcohol is available at hardware stores in the paint section where paint thinners, paint strippers, solvents, *etc*. are found. A common one has the brand name Klean Strip and actually has a high percentage of methanol, which is why it is a good glass cleaner and marine stove fuel. Of course, it is really poisonous if consumed. The vinegar is 5% acetic acid, from a grocery store; it helps preserve proteinaceous cell structure. The advantage of this method is that it is cheap and readily available to most people. Wagner used this method to preserve ***Riella americana*** with sporophytes (Figure 25).

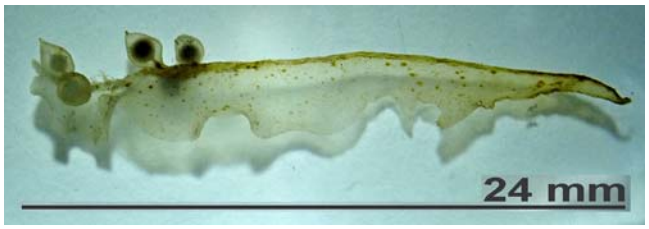


Figure 25. ***Riella americana*** with sporophytes, preserved with methanol and vinegar. Photo by David Wagner, with permission.

Michael Christianson (Bryonet 19 September 1999) raised the possibility of using **lyophilization** (freeze-drying), suggesting it should keep such important organelles as chlorophyll and oil bodies intact. If the material is put into ampoules after lyophilization, these could be sealed. If the ampoule is further treated by replacing the air with nitrogen, Christianson predicts that DNA would be preserved for decades.

One of the problems in preservation is that such specimens require maintenance about once a year to replace the liquid that has evaporated from them. Angela Newton (Bryonet 20 September 1999) suggested that this labor can be greatly reduced by placing a group of vials in a larger jar that can easily be topped off. Furthermore, it will provide a head of liquid that will last much longer than that of a small vial. This also helps to reduce swirling motion that can damage small specimens during the refill process.

Kronestedt and Echlin (1982) suggested freeze-drying the thallose liverwort ***Ricciocarpos natans*** (Figure 26) instead of acetone or ethanol dehydration in preparation for critical point drying for scanning electron microscopy because freeze-drying causes less cell collapse.

Figure 26. ***Ricciocarpos natans*** thallus, one whose cells collapse in acetone or ethanol. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.

Summary

Permanent slides usually require use of a mounting medium. Ideally, these must dry quickly, be effective in clearing, be durable, and be easily available. Older mounts used glycerine, other mountants include gum arabic, Hoyer's solution, gum chloral, DMHF (5,5-dimethyl Hydantoin Formaldehyde), PVA, Polyvinyl Lactophenol, Aquamount, Kleermount, Fluoromount-G, Gray-Wess Mountant. Slides can also be sealed with a lutant like fingernail polish, including those using the double-coverslip method. Most of these methods permit repair when the slide dries out too much. Storage usually must be flat to prevent movement of the mountant and specimen.

Caution is needed in selecting a mountant. Chloral hydrate (in Hoyer's solution) is toxic, and some mountants distort the cells or cause plasmolysis.

A mix of glycerol and lactic acid can be used to clear specimens. Liverworts may require special preservation, but some thallose specimen can simply be dried.

Acknowledgments

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CHAPTER 3-1
HERBARIUM METHODS AND EXCHANGES

Janice M. Glime and David H. Wagner

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CHAPTER 3-1
HERBARIUM METHODS AND EXCHANGES

Figure 1. Benito Tan and herbarium cabinets for bryophytes at the Hattori Botanical Laboratory in Nichinan, Japan. Photo by Janice Glime.

Folding Packets

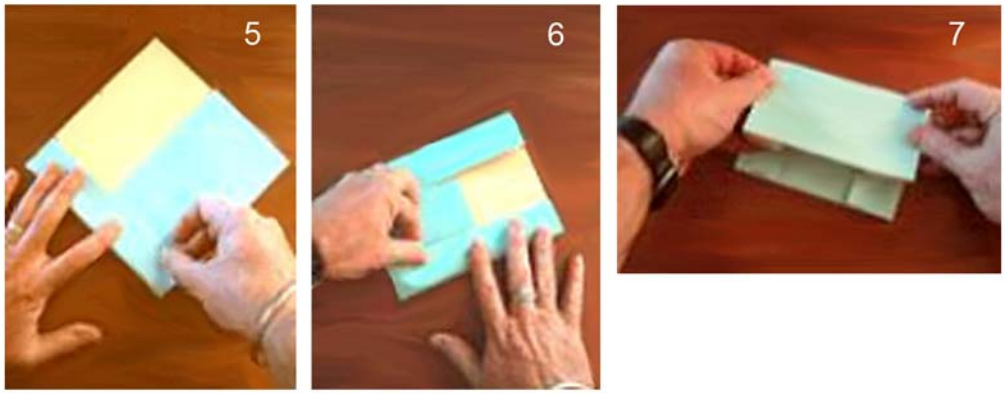
The standard for bryophyte storage is to put them in packets. These are made from a sheet of white paper, preferably acid-free, 100% cotton to reduce decomposition of brittle paper. Some herbaria use brown packets made from shelf liners or grocery bags (*e.g.* Kraft paper), and use of these is somewhat common in the field. Those are not quite as easy to read, but they do last well. Wagner uses 3" margins for the packets, but Glime finds that 1-1.5" margins work well. The size depends in part on the size of the herbarium box or drawer used to hold the packets. Having an exact size isn't critical, so after a little practice it probably won't be necessary to measure. If the housing for the packets permits larger sizes, larger packets may be desirable for some large taxa. Note that the outside (last) fold should be a little shorter than the others (Schofield 1985). This permits more space for the bryophyte and makes it clear which side is to be opened.

At CAS, curators use Strathmore ultimate white 100% pure cotton 24 lb watermarked paper, available in reams of 500 sheets, CODE 318003 (US standard size 8.5 x 11 in) (Jim Shevock, Bryonet 8 April 2015). CAS also uses Strathmore 25 percent cotton fiber paper for printing of herbarium labels and to process additional labels for specimen exchange. Both are acid free and of archival quality and print well on photocopiers. Karen Golinski (Bryonet 8 April 2015) similarly uses 100% cotton, acid free, Avon Brilliant White, wove finish, 24 basis <http://www.neenahpaper.com/finepaper/morebrands/cottonpapers/classiccottonpapers/productdetail?color=Avon+Brilliant+White&finish=Wove>. Mary Zimmerman (Bryonet 8 April 2015) uses Byron Weston Linen Record Ledger Paper from Talas: 100% cotton ('linen' is just the slight texture on the paper) and it has the year of manufacture watermarked into the sheets

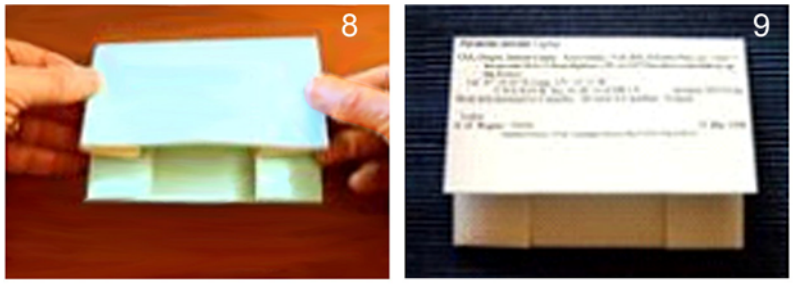
<http://apps.bnt.com/ecom/catalog/product_specific.cfm?ClientID=15&ProductID=24235>

Bryophyte specimens should be placed into the packets. An 8 1/2 x 11" (21.6 x 28 cm) sheet of paper, or size close to that such as the standard European size, should be folded in thirds like a business letter (Figure 2). After the first fold, the two open ends are folded inward. It is an important consideration that the first fold is up, then the sides are folded in before the top is folded down. This folding is less likely to lose specimens and fits more neatly into the box or drawer than those where sides are folded last. And it is the only folding system that works well when the packet is glued to a herbarium sheet. The typical resulting packet is 4x6" (10x15 cm), a convenient size for storage in shoe boxes. These packets may be stored in boxes as packets or glued to a herbarium sheet, with the packet glued across the middle section of the back so the opening flap faces you like the flap of a pocket. See storage below.

Left to right: 1. Mark 3" (7.6 cm) in from top of 8.5x11" (21.6x25.4 cm) sheet. **2.** Mark 3" in from other side at top. **3.** Mark 3" from top using 3" card template. **4.** Fold bottom up to mark 3" down side. [Change 3" on sides to 1.5" 3.8 cm) if you desire.]



Left to right: 5. Fold left edge to mark 3" (7.6 cm) from left. **6.** Fold right edge to mark on right. **7.** Fold top flap down.



Left to right: 8. Crease well. Packet is complete. **9.** Packet with preprinted label data.

Figure 2. Steps for folding herbarium packets. Colors were used to make it easier to see the folds in these images. Photos by David Wagner.

Packet Machine

Miller (1988) offers an alternative way to expedite making packets. He uses a file folder to make a **packet machine**. We have modified it here to make the same type of packet as the one shown in Figure 2 and to maintain packet size close to 4x6" (10x15 cm) with maximum space on the flap for the label [3.5" (8.9 cm)] (Figure 3-Figure 13) (Schofield 1985).

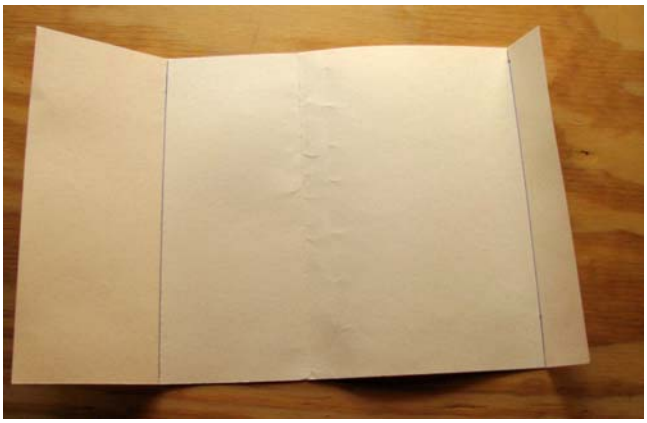


Figure 3. Cut the tabs from the folder to leave all edges straight and square. Then carefully measure 3.75" (9.5 cm) wide on one end of the opened folder, parallel to the folder fold. Score this line with a ball point pen and ruler to make it easy to fold. Photo by Janice Glime.

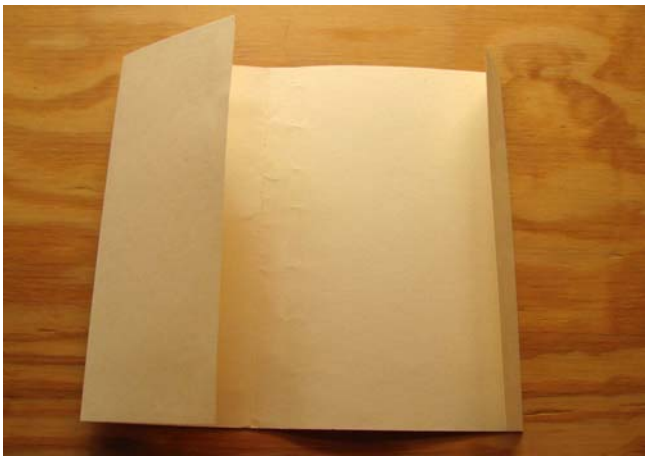


Figure 4. On the opposite end prepare a similar pocket; measure 1.25" (3.2 cm) from that end, score, and fold both ends to make pockets. Photo by Janice Glime.

Figure 5. Line up the pocket creases carefully and press them with a spoon or your fingernail. Photo by Janice Glime.

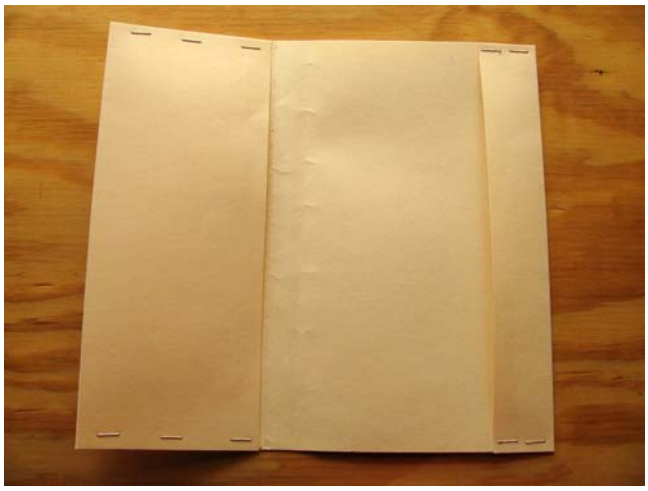


Figure 6. Staple or tape the ends so that it forms a pocket. Once stapled, this packet machine is ready to prepare packets. Photo by Janice Glime.

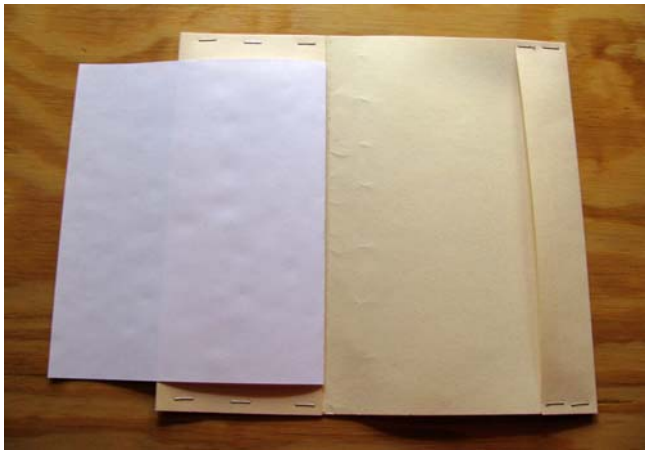


Figure 7. The machine is now complete with staples. For the first fold, 2-3 sheets can be folded together. Place one end of the 8.5" (21.6 cm) wide paper in the 3.75" (8.9 cm) pocket and fold it over the pocket. An old stainless steel spoon under the thumb or just the thumbnail helps to get a good crease on the packet. Photo by Janice Glime.

Figure 8. Separate the sheets and place one side that is perpendicular to the fold into the 1.25" (3.2 cm) pocket. Photo by Janice Glime.

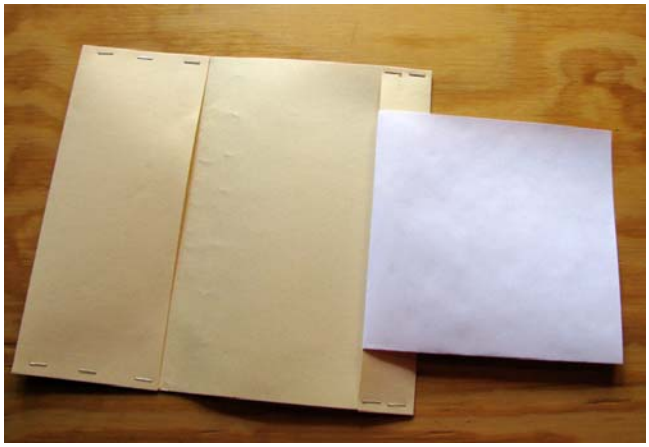


Figure 9. Fold the packet over the pocket and crease. Photo by Janice Glime.

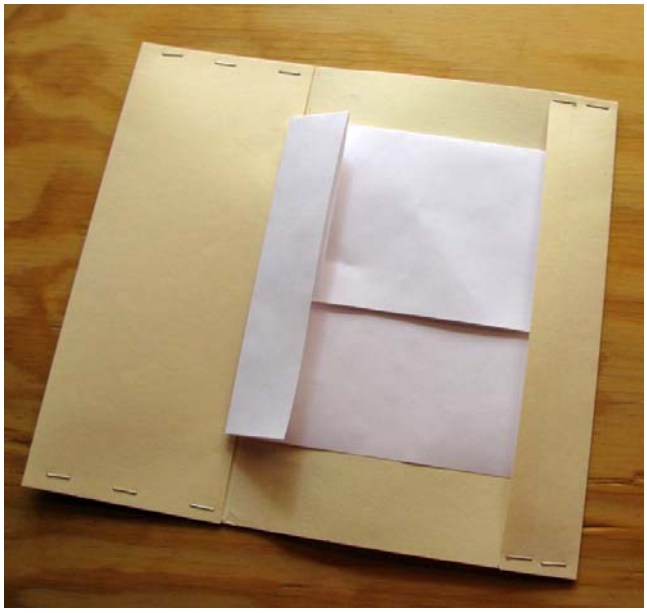


Figure 10. Repeat the operation on the other side of the packet. Photo by Janice Glime.

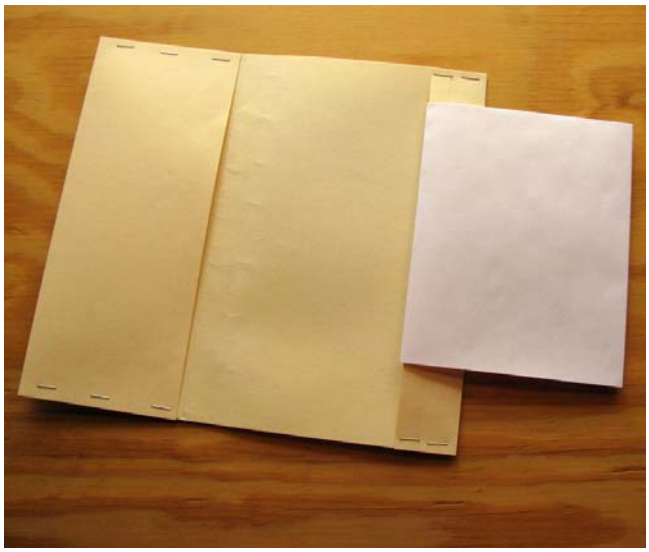


Figure 11. After you fold this side of the packet, you have an envelope and only the top flap needs to be folded down. Photo by Janice Glime.

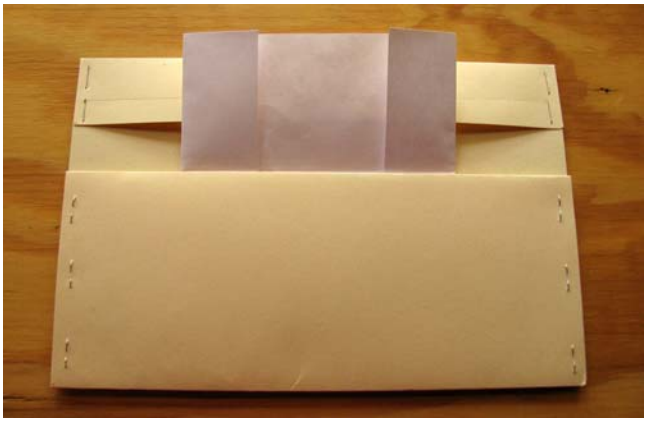


Figure 12. Place the bottom folded edge of the packet into the 3.75" (9.5 cm) pocket of the folder and fold the exposed part of the sheet over the pocket just above the pocket top edge so that when folded the dimensions are 3.75x6" (9.5x15 cm) with the last flap being 3.5" (8.9 cm). You won't be able to fold along the edge of the folder pocket this time, but must fold just above it. Photo by Janice Glime.

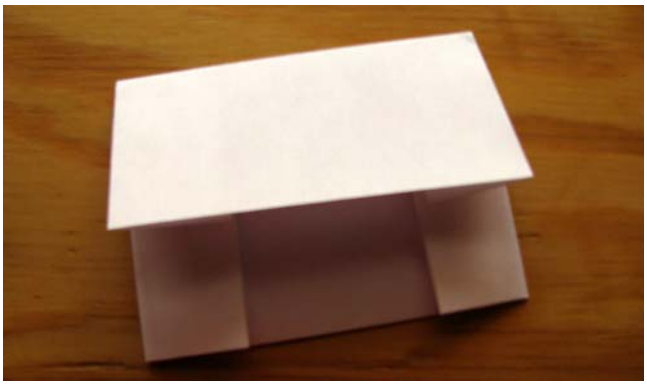


Figure 13. Now it is ready to use. The label should be placed on the top flap. Photo by Janice Glime.

Followers

David Wagner (pers. comm. 2009) has found a way to keep folded packets neatly stacked, in order, under constant but light pressure. This also works for sorting, since specimens can be added anywhere in the row with ease and it will expand readily to fit. The trick is to use a cylinder (can of beans in this case) in a tray that is propped up to provide an incline for the can to roll against the packets (Figure 14).

Figure 14. Packets held in place with food can in inclined box. Photo by David Wagner.

Card files (4x6" card size ≈ 10x15 cm) have a movable back on the drawers that can be adjusted to hold the packets upright. Shoe boxes can be packed with wadded paper in back to keep packets upright.

Herbarium Sheets

Jerry Jenkins (Bryonet 31 January 3013) reports getting good herbarium paper from Herbarium Supply <http://www.herbariumsupply.com/nu_listCategoriesAndProducts.asp?idCategory=31> in Bozeman, Montana.

Herbarium Labels

Rob Gradstein (pers. comm. 26 July 2012) states that "labels should be a little smaller than herbarium packets and glued on the outer surface (top, not bottom!) of the packet." But we agree with Schuster (1966) that the label should be printed directly on the front flap of the packet. This saves time, and glued-on labels have a tendency to come loose from packets after time in storage. This can result in loss of data, or worse, incorrect information when the label is matched to the wrong specimen. (Glime inherited a herbarium where loose and lost labels were a serious problem.) If the specimen needs to be put in a new packet, the label can always be cut from the original packet and glued to it or stored inside if a new label is printed on the packet. In either case, the label should be on the opening face of the packet.

Label data should include **name of the species** (if known), the **author** of the scientific name, **altitude**, **habitat**, **substrate**, **date** of collection (with month written out), and **location** (country, state, county, distance to nearest town), **GPS** coordinates, name of **collector**, **collection number**, **determiner** (name of person identifying or verifying identification). Persons adding identifications or verifications to specimens often precede their names with an **exclamation mark (!)** to indicate determined by. Additional information may include name of associated species, color, height of plant, abundance or other information not evident from the pressed specimen. For liverworts, it should include descriptions of the oil bodies because these will disappear upon drying.

The family name is less commonly used for bryophyte labels because the family concept is less stable than in flowering plants and there are fewer families and genera. Specimens are usually stored alphabetically by genus (see Herbarium Arrangement below).

The label will usually also include the name of the **herbarium** and the **accession number** for that herbarium. The herbarium name aids in getting loans back to the rightful owner.

A sample herbarium label is shown in Figure 15. Note that the **date is written out in full** to avoid confusion among different country annotations, and a detailed collection location is included.

CRYPTOGAMIC HERBARIUM OF
MICHIGAN TECHNOLOGICAL UNIVERSITY

FAMILY: Fontinalaceae
SPECIES: *Fontinalis duriaei* Schimp.
DATE: 1 May 1969
LOCATION: USA, New Hampshire, Grafton Co., 1 km. north of Plymouth in woods on left of Texas Hill Rd.
45°8'N, 71°40'W, R21, T15, sec 6 ELEV. 300 m
HABITAT: on granite rock in mountain stream in *Tsuga canadensis* woods
NOTES: few dark capsules with ends abraded away; plants dark green with little algal growth
COLLECTED BY: Janice Glime COLLECTION NUMBER: 281
DETERMINED BY: Janice Glime ! Winona Welch
ACCESSION NUMBER: 12896

Figure 15. Sample herbarium label from Michigan Technological University. Designed by Janice Glime.

Multiple Species

Bryophytes often grow intermixed (Figure 16). Here need of ecologists and taxonomists/systematists differ. For ecological studies, the associations contribute important information. I (Glime) am reminded of a letter I received from Sin Hattori, along with his careful notes on the species in a set of collections of ***Frullania***. Most of the collections contained multiple species. He encouraged me to "do something" with the information of the mixes – so I did (Li *et al.* 1989; Glime *et al.* 1990).

On the other hand, when Niels Klazenga (Bryonet 15 July 2013) collected bryophytes in Borneo in 1997, he grabbed what he could – as told to by his PhD supervisor, hence including many mixed collections. Curation officers at the museum spent ten years cleaning up the mess.

Figure 16. At least 3 species are tucked in between lobes of ***Conocephalum conicum***. When mixes like these are in collections it is best to make a minipacket if the mixed-in species are important. In any case, they should be noted on the label. Photo by Janice Glime.

Jean Faubert (Bryonet 15 July 2013) disagrees. Rather, he admonishes not to try to make single species collections. Grab the lot, put it in the bag and DO identify everything you see in it when back in the lab. Sure enough, that is when the goodies show up. He declares that most of his lifetime big finds were made that way. Philip E. Hyatt (Bryonet 15 July 2013) agrees and adds that since most info is slowly going on line, someone who is desperate to find a specimen won't have too much problem running it down in the future like we might have had to do with mixed collections in the past. In 1990, if you were not in a herbarium you probably didn't know the specimen existed. Life changes.

In habitats like the Sahara Desert or epiphylls, species are often not separable. Tamás Pócs (Bryonet 14 December 2015) makes a packet with one good specimen of the mix, then makes as many copies of the label as the number of species present. Packets with just labels (no specimens) or just labels are filed by each species, with the appropriate species for that location underlined.

As Philip Hyatt suggested, the herbarium in Trondheim is databasing every species (present in the same packet) as a separate record. They have a way to track which of the species is the 'main' species in the packet, *i.e.* in what cabinet the specimen is stored. This is more practical for the data users (and less practical for the herbarium curators), and curation of synonyms is easier this way, too.

The practices and reasons are varied, as demonstrated by a Bryonet discussion in mid July 2013. There are certainly pros and cons for both approaches. Separating the species is likely to lose the growth habit. Parts may be broken and underground structures lost. One loses the information gained by determining which species form associations and how reliable those associations are. Baranabas Malombe (Bryonet 15 July 2013) also considers it important to collect and retain all the species in the collections to demonstrate the diversity of the site.

If it is desirable to have archival specimens of more than one species, then removal to a separate packet is necessary. If only one species is of interest, it is safest to make minipackets to represent the accompanying species and to include their names in the notes on the packet label, or at least indicate that it is mixed with other species. Keep in mind that beginners may use this collection to learn species. Rod Seppelt (Bryonet 16 July 2013) agrees. "While it may be desirable to have monospecific collections, in practice it is rarely possible." For example, Seppelt states "I have been looking at ***Fissidens*** (collected by the late Ilma Stone); the label clearly indicates that the packet also contains fruiting material of two, sometimes three, additional ***Fissidens***. It would be impossible to separate these into separate collections and still have a meaningful herbarium voucher." As Seppelt points out, "if all threads/plants of a particularly species are removed from a mixed collection, what can be important information about associated taxa is lost."

While it is desirable to separate species into separate packets, exemplars of intermixed species can be housed in minipackets within the herbarium packet. When accompanying species are removed to separate packets, the collection numbers should be retained, but individualized by adding a letter at the end of the collection number. The parent packet should retain the letter **a**, alerting the researcher that there are other packets. If the other taxa have been identified, they should be listed in the notes along with their collection number and letters.

David Wagner suggests a way to have all the specimens catalogued in the herbarium: Make duplicate labels and file the duplicates for the subordinate species in their appropriate places, but indicate the specimen label where the actual specimens are located. This does cause problems when the systematics are updated, but can be helpful in locating the smaller associates.

Alas, in large herbaria, as noted by Ambroise Baker (Bryonet 16 July 2013), 1 specimen =1 species at 1 location at 1 collection date. This is also true for higher plants, but it is easier to do for them. As stated by Niels Klazenga (Bryonet 15 July 2013), "mixed collections are not okay." But Jon Shaw (Bryonet 15 July 2013) disagrees.

My (Glime) own solution to the mixed collection is to make minipackets in which a bit of each minor species is placed. A sample of the dominant species can also be placed in a minipacket to assure the right specimen/species is examined. If the community is important, only samples of each species are removed, but if the specimen is important for taxonomic purposes, I might attempt to remove all the minor associates. Blanka Shaw, herbarium curator at Duke, likewise treats the plants that are mixed together and a separation is not an option by making small fragment packets with a few plants of each named species separated from the rest. "If you spend the extra time to name more than one taxon in the packet, definitely do make a fragment packet. There is nothing more frustrating than having a specimen with a rare liverwort in it, that is present in few stems only, and there's no way to find it out among all the other dried species that look identical in the dissecting scope." Blanka Shaw further distinguishes between plants associated in the same microhabitat in the field and those associated in the collection/packer.

Blanka Shaw (Bryonet 15 July 2013) does issue a warning about only listing the species on the same packet as associated species. These species might not be searchable in some databases. The bryophyte portal <http://bryophyteportal.org/portal/index.php> currently doesn't enable one to search the associatedTaxa field. However, the field is available there for this purpose, and you can get at the data by downloading the result of your search. In the Duke database, there are about 5,000 specimens with the associatedTaxa field filled in (out of ca. 160,000 records). But this information is rarely used – she has never considered it when preparing species lists. When a species name is updated, the name(s) in the associatedTaxa field does not get updated automatically (=you have to search for every synonym). So, it is not very practical for the data users. Hence, David Wagner's method of making a separate label to be filed as if it were a herbarium packet would put it into the database and enter it in both the search and nomenclatural updates.

Dorothy J. Allard (Bryonet 15 July 2013) suggests the following from the perspective of a bryophyte collector and curator:

- If you have enough material, split all of it into separate packets and establish one collection for each species. Then in an "associated taxa" field, indicate which other

species are present. Separating material can sometimes be difficult and destructive.

- If it is easy and non-destructive you can separate the material into individual packets. Information on the associated taxa is still useful to express on the label.
- If you don't have enough material, label the specimen with a single species and include information about the other species in the packet in an associated species field. If possible include one smaller packet inside for each of the associated species with its own label.

It is not unusual for one of the minor species to be the one of interest. Dorothy J. Allard (Bryonet 15 July 2013) reports that sometimes she collects a specimen because of a small and interesting liverwort, for example, embedded within a clump of ***Brachythecium***. In this case she labels the specimen with the name of the liverwort and indicates that it is within a matrix of the ***Brachythecium*** in a habitat field, but she also lists the ***Brachythecium*** in an associated taxa field. In essence she treats the ***Brachythecium*** as the liverwort's substrate.

Ken Kellman (Bryonet 15 December 2015) separates a collection out when the identification is made. Each will become a separate collection with a suffix like a,b,c etc. On the front of the label, you can then put "growing with *Tortula muralis*, *Didymodon fallax*...) and this information is included on all the separated packets. But he only does this if there is some special reason to separate the collection: 1) the separated plant needs to be documented for a study; 2) the separated plant is rare or disjunctive etc. It would take so much time to separate out all collections that you have to prioritize. In any event, he tries to put all species found in a collection on the label so future workers can read what he was seeing.

Genevieve Lewis-Gentry (Bryonet 14 December 2015) and coworkers use three different options for a mixed collection:

1. Put a separate barcode for each different biological organism on the single packet. Use this to track name changes/annotations for each.
2. Use a single barcode that corresponds to the packet. Add many biological organisms to this one identifier.
3. Only use a single barcode, pretend it is a simple specimen, and note all the other species in a remarks field. (This is exclusively what was done with older systems, but this is never done now.)

Their database and workflow centers around barcodes. Everything has to have at least 1 to go into their computer. Their system is flexible so that depending on the situation they can choose to either put many barcodes on a single packet/sheet/slide/etc. or to put a single barcode with the packet etc. and tell the computer that this preparation has multiple organisms they would like to track separately.

As Claudio Delgadillo-Moya (Bryonet 15 July 2013) summed it up, "What and how you collect mosses and other small plants depends on where you live, the purpose of your research, or what you want the herbarium for."

Annotations

Sometimes labels are filled with information and little room remains for further annotation. A common practice is to glue one end of a slip of paper to the edge of the packet label for name changes, verifications, or other notes. However, this slip of paper can easily come loose, so several options are used. One is to glue the packet to a larger card and attaching the paper, fully glued, to that. This seems to defeat some of the advantages of the packets and can create storage problems, unless the packets are in palm folders, but packets could get tangled with each other, causing glue to come loose. Another alternative is to place the annotations in a waxed envelope and to place that inside the packet. (Putting it in without protection could result in smudging or mold.) The disadvantage is that one must open the packet to know that something has been added. If the addition is extensive, one could place a note on the outside label instructing one to see inside.

At the University of Colorado Museum, William Weber reports that annotations are placed on the back of the packet (with packets stored in boxes or palm packets, not on herbarium sheets).

NEVER DISCARD THE ORIGINAL LABEL. Handwritten and even typed labels must be interpreted, and sometimes that interpretation is in error. Keeping the original label permits researchers to check for possible alternative interpretations. And there is always the possibility of transcription error.

Multiple Access

Guido van Reenen (Bryonet 15 December 2015) has refined his relational database to overcome the problems mentioned above. In his database structure the specimen information is basically stored in two tables, an 'Observation' table and a 'Collection' table. In the 'Observation' table the information of the specimen is stored (taxon name, determiner, date, substrate, phenology, if there is a microscope slide and/or a photo, etc.). If the specimen is also collected (that is not necessarily the case) a link is established to the 'Collection' table. In database jargon: the 'Observation' table has a many-to-one relation to the 'Collection' table. In other words a collection can contain one or more specimen.

In the case of multiple specimen in a collection, van Reenen defines one specimen as the 'main' specimen. Mostly this is the most abundant specimen in the collection. Under this specimen the collection is stored in the herbarium. The herbarium label also lists the names of the other specimens in the collection. He also uses the method of placing cards in the herbarium to reference to the physical collection, but that takes too much time and requires a lot of discipline, especially after a name change. And it is not necessary anymore because all the information is now in the database. He does most of the queries in the 'Observations' table, because all other tables in the database are linked to this table and it gives him all the information I need, including herbarium information.

Van Reenen also maintains a 'Taxa' table with information on the name, if it is a synonym, if it contains synonyms, place in the taxonomic hierarchy, etc., a 'Location' table, a 'Persons' table and a 'Relevé' table, to name the most important. The last one gives some headaches as well, because when collecting in a 400 m^2 relevé, often one species was collected more than once. And a percentage cover should only be attached to every unique species in the relevé.

The printing of the herbarium labels is done from the 'Collections' table (Figure 17). The collection is stored in the herbarium under ***Fissidens ornatus***.

BRYOPHYTES OF COLOMBIA

Collected by G.B.A. van Reenen & C. Schulte Fischedick

No. 04366 15 August 1981

Fissidens ornatus Herzog

\+ *Fissidens flexinervis* Mitt.

\+ *Fissidens intermedius* Müll. Hal.

Identified by R.A. Pursell, 1988.

Figure 17. Sample herbarium label for a mixed collection from Colombia. Courtesy of Guido van Reenen.

Storage

Cabinets

Herbarium cabinets are the standard method for storage of preserved plant material. For most tracheophyte specimens, pest control is essential and it is important that the cabinets be sealed or nearly so to keep specimens dry and to discourage pests. Bryophytes, on the other hand, are usually not bothered by pests, so in less humid climates, less expensive storage cabinets are acceptable.

But cabinets require lots of space, so many larger herbaria with larger budgets have converted to compactors (Figure 18) that are used for both bryophytes and other plants. Although these can be a nuisance at times, they are great space savers and also make it somewhat easier to control humidity and pests because access is reduced.

Packet Storage

Nearly everyone stores bryophytes in packets, but some herbaria glue the packet to a standard size herbarium sheet. This has the advantage that the herbarium can use the same storage method for the bryophytes as they use for tracheophytes. But the packets take much more room this way, and a herbarium sheet is difficult or impossible to put under the microscope for closer inspection. It also makes your working space more crowded. My biggest concern is that the large format forces me to remove the specimen to observe it under the microscope, and when comparing several specimens, it is easy to mix them up, returning specimens to the wrong packet. Single packets can be placed under the microscope without removing the bryophyte from the packet.

Dale Kruse conducted a survey of bryonet members in 2008 and got a mixed response. Susana Rams Sánchez has worked with specimens at MA, MUB, BM, E, S, MO and others. She finds the method at MO (Missouri Botanical Garden) to work the best, *i.e.*, packets. Others using packets included Noris Salazar Allen (Herbarium, University of Panama), Chris Cargill (Canberra), Stephen Rae (MUSCI Natural Resource Assessment). Rudolf Schuster (1966) considered packets in shoe boxes, trays, or drawers to be "much better" than pasting the packets to herbarium sheets. He also recommended that if the packet must be affixed to a herbarium sheet, it should be stapled rather than glued so that it can be removed without destroying the packet.

Figure 18. Herbarium compactor at Missouri Botanical Garden showing cabinet with open door. Labels on the ends denote the contents of that section. Photo by Paul J. Morris through Flickr Creative Commons.

Cargill (Canberra) reports that one can prevent specimens from falling to the bottom of the packets by storing the specimens in polypropylene archival bags. In some cases they are also wrapped in Kimwipes® before placing them in the bag.

Kerry Barringer (Brooklyn Botanic Garden) reported that they were changing their method from packets on sheets to packets in cardboard boxes (51 x 16.5 x 6.3 cm). The boxes are open and two will fit lengthwise on a standard herbarium cabinet shelf. They made new packets and photocopied disintegrating old ones to store inside the packet.

Those who disliked the placement of packets onto herbarium sheets cited concerns such as glue yellowing the packet, glue coming lose, packets getting caught and being torn off, glue catching dirt, difficulty in removing packets from the sheet (resulting in loss of specimens), greater cost for sending loans, more storage space required. To this list, one must consider where the packet is to be placed on the sheet. If it is placed in the lower right corner, where a label would normally go, then the stack becomes very lopsided. If packets are arranged at random on different sheets, then it makes sorting through the sheets to find a particular specimen a more difficult job. Placement of more than one packet on a sheet brings its own problems – renaming some, but not all, specimens; shipping for loans or

verification of identification, and still has the problem of locating the labels when sorting through to find something.

David Long (Royal Botanic Garden, Edinburgh), a proponent of herbarium sheets, cited advantages of gluing packets to herbarium sheets: being able to use standard herbarium cabinets, species covers, and genus covers; specimens do not get lost as easily as those in loose packets; it is easier to flick through sheets to find individual specimens (if packets are in a standard position and only one per sheet); hunting for specimens requires less handling and thus less chance for damage; specimens are kept horizontal so that soil does not collect at the bottom of the packet and damage specimens; specimens are better protected when sent on loan; there is greater ease to arrange packets geographically by sheets (this could also be accomplished in a palm folder); types can have the traditional red folder and be easier to spot; useful literature can be placed in the folder with them (Bryonet July 2008).

Bill Buck (New York Botanical Garden) further supports the use of packets glued onto herbarium sheets. The greater protection of the specimen seems to be a primary concern for supporters of this method, including problems with settling in vertical packets and provision for extra padding without tight packing. The herbarium sheet also will accommodate large packets for such taxa as ***Spiridens*** (Figure 19) and ***Polytrichum***; when just packets are used, large specimens must either be cut into sections or stored elsewhere. And packets, due to their small size, are more easily lost, especially when sent out on loan. Catherine La Farge England (Bryonet 18 July 2008) reports the same reasoning for the University of Alberta Herbarium, an approach established by Dale Vitt.

Type Specimens

Colored folders are traditionally used for tracheophytes to indicate special collections. Red is standard for type specimens, whereas blue or other color may be used to indicate a particular geographic area. The same system can be used if bryophytes are stored on herbarium sheets and provides one of the arguments in favor of this method. A red felt pen run across the top of a packet will serve the same purpose (Figure 20-Figure 21), or a red herbarium folder can be cut to fit around the packet (Figure 22).

Figure 19. ***Spiridens flagellosus***, a large epiphytic moss. Photo by John Game through Flickr Creative Commons.

Figure 20. Type specimen packet (red top) among other packets. The red top is made by a red felt pen. Photo by Janice Glime.

Figure 21. Close view of type specimen packet among other packets. The red top is made by a red felt pen. Photo by Janice Glime.

When a palm folder is used, a felt pen can be used to make a colored dot on the folder to indicate the presence of a type specimen (Figure 25).

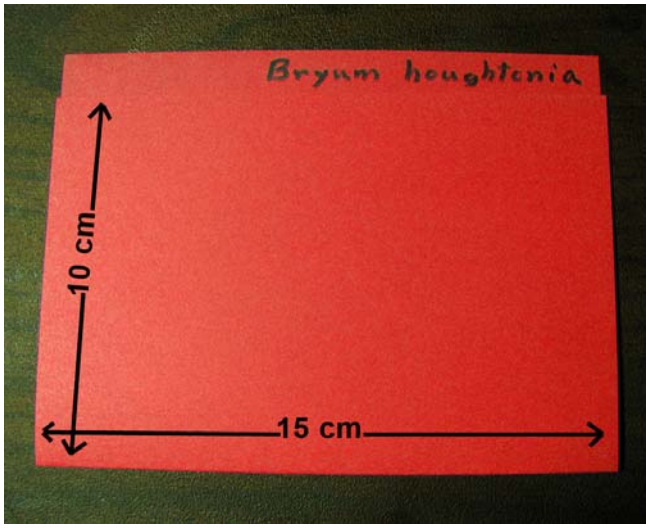


Figure 22. Sample type specimen folder for bryophyte packet. Photo by Janice Glime.

When slides are made of the type specimen, it is important to retain the slide with its specimen (Singh Deo & Majumdar 2020). These can be mounted in a permanent medium, or allowed to dry on the slide. For the latter, in particular, the slide should be placed in a small packet to prevent loss of the specimen. These latter ones can be rewet to position the specimen as needed.

It might be tempting to keep a "**kleptotype**" (stolen specimen or part of specimen of type) when working with type specimens, but this should never be done. With other herbarium specimens, it should be done only with permission of the owner/curator (Katagiri & Majumdar (2020). In the International Code of Nomenclature for Algae, Fungi and Plants, Rec. 7A.1 (Turland *et al.* 2018), it is strongly recommended that the material on which the name of a taxon is based, especially the holotype, be scrupulously conserved. Nevertheless, the Code does not explicitly prohibit the taking of fragments of a type specimen. Katagiri and Majumdar have proposed the following language be added to the Code:

> "8A.n. The unauthorized division of a type specimen should be prevented to avoid a loss of the type specimen. Such action most likely complicates the work of future generations and the resulting reduced collections may give a misleading concept of the species. When found, such "kleptotype" specimens should not be destroyed but preserved as duplicates. Formal notification of the existence and location of these specimens should also be published."

Storage Containers

For those using 4x6 (10x15 cm) packets, a 4x6 card file cabinet can be used to hold the packets. It has a pull-out drawer that can be removed and a movable back that can hold the packets up even when the drawer is not full.

Brian Eversham uses plastic boxes that can hold a double row if the packets are folded small enough (Figure 23). I use shoe boxes because they are free at the local shoe stores and keep the packets covered, avoiding excess dust. It is easy to attach a label to the end of the box to indicate the part of the alphabet contained therein. I try to leave enough room for half as many more packets to be added, *i.e.*, 2/3 full.

Figure 23. Herbarium drawer with packets. Photo by Brian Eversham.

Packets on herbarium sheets can be stored in a standard herbarium cabinet, and that seems to be the main asset for those who prefer them. The boxes or drawers, however, can also be stored in a herbarium cabinet and require much less space than a packet plus herbarium sheet.

Bryophytes are seldom eaten by pests in a herbarium, unlike tracheophytes, so most bryologists store them without mothballs or other deterrents.

Palm Folders

Palm folders were originally constructed to handle large or thick tracheophyte specimens like palms, hence the name. Palm folders can hold 10-20 packets, or even more, depending on the size and thickness of the packets. Those using packets placed in palm folders (Bryonet July 2012) included Jaakko Hyvönen (Plant Biology, Helsinki), Dan Norris (Berkeley University Herbarium), Xiaolan He-Nygren (Helsinki), and Jim Shevock (California Academy of Sciences). This method permits the packets to lie flat, overcoming the crushing problem and the problem of having specimens collect at the bottom of the packet in a pile of soil.

Dan Norris (Bryonet July 2012) cites the flexibility offered by palm folders for having different sizes of packets to accommodate large specimens. The folders are 30.5 mm x 56 mm and have additional flaps on each side, top, and bottom (Figure 24). The large size of the folder, like the large herbarium sheet, can accommodate large specimens like ***Spiridens*** (Figure 19) or ***Dawsonia***.

Palm folders can be stacked so that 6-7 will fit on one standard herbarium shelf (Figure 25). The folders will allow specimens up to 27 mm thick. This permits a collection of various sizes to remain together. Jim Shevock points out that a further advantage is that the 27 mm thickness permits labelling the end of the folder (Figure 25), making it easier to find the right folder.

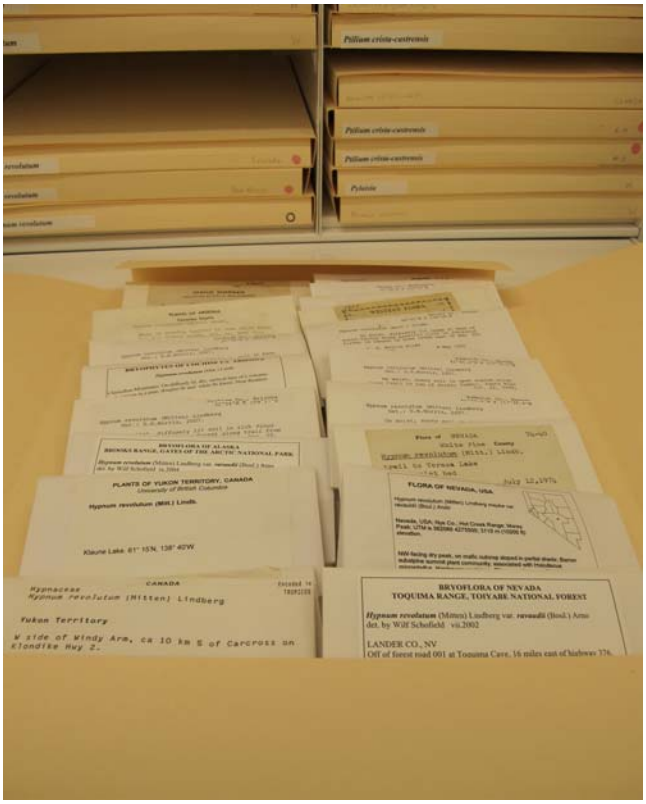


Figure 24. Herbarium palm folders showing arrangement of packets with a variety of labels, some as part of the packet, others glued on. Note the map on one of the labels indicating its location in the state of Nevada. Photo by Jim Shevock.

Susana Rams Sánchez warns against making species sheets with more than one packet glued to them. These will soon be a problem as identifications change with revisions. And when specimens are sent for loan, all the packets must be shipped, making them unavailable at the home herbarium and increasing shipping costs.

Figure 25. Herbarium cabinet with palm folders. Photo by Jim Shevock.

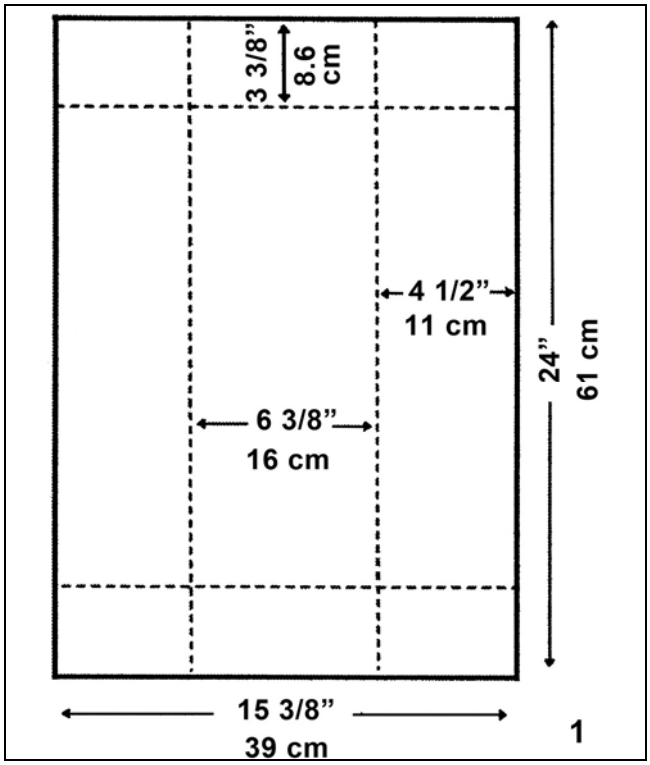


Figure 26. To make boxes, use scissors, razor knife, or paper cutter to remove 4.2 cm from long side of a 43x61 cm genus cover. Save trim as template for trimming additional genus covers. Score with hard metal edge such as door key and fold/unfold along indicated lines. Scoring controls exact line of fold. Rub smooth, hard object down folded edge to make creases sharp. To save measuring scoring lines, create template strips from cardboard or genus covers to guide scoring tool.

Storage Boxes from Genus Covers

If you are familiar with large herbaria, you are familiar with the heavy poster board or Manila folder quality of genus covers used for storing tracheophytes. Davison (2002) suggests using these for making storage boxes for bryophyte packets. These are similar to the palm folders, but the ones Davison has designed are the width of a "standard" packet and are not covered. The following instructions (Figure 26-Figure 28) are only slightly modified from his:

The finished box occupies the full length of a standard herbarium cabinet. Two boxes fit side by side on the shelf. The boxes can hold 40-130 upright specimens, depending on the size of the specimens. Be sure to measure the shelf size of your cabinet before making the boxes because the cabinet sizes can vary somewhat.

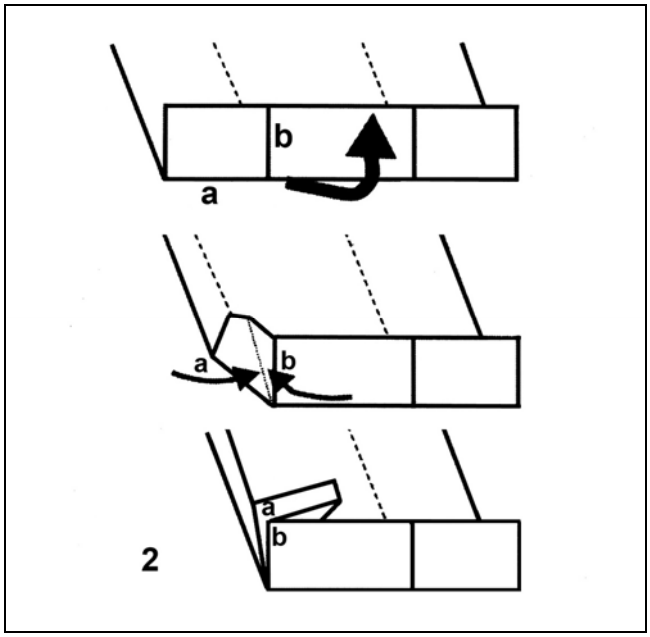


Figure 27. To form corners of box, push slightly inward at arrows and align edge **a** with edge **b**. Hold edges **a** and **b** firmly together and crease from inside. The corner crease will find itself as you align, meet, and hold edge **a** to **b.** Press firmly while creasing. Fold/unfold all four corners.

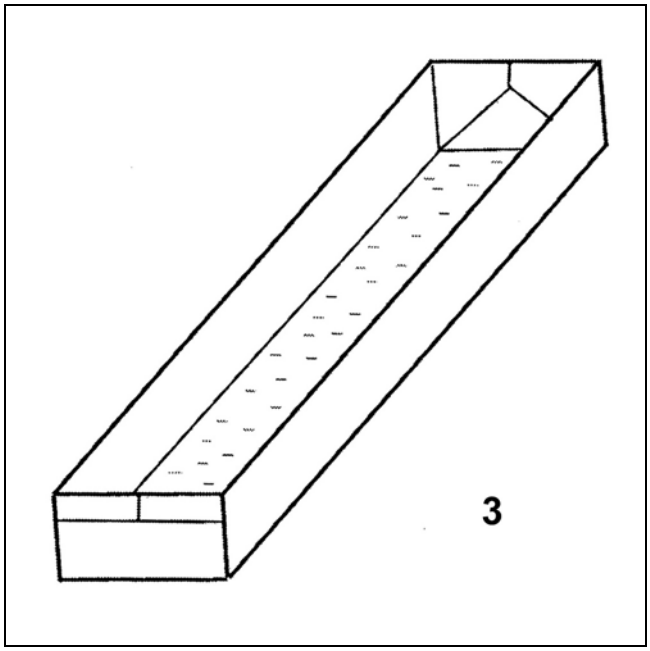


Figure 28. Once all folds have been made, shape the box and adhere each end with tape, glue, or staples. Davison uses clear 2" (5 cm) wide commercial-grade box packing tape and cover the entire outer face of each end. The tape provides a tear-resistant surface for taping and removing labels that identify the box contents. If handled carefully, as specimens should be, the boxes are adequately sturdy. Placing cardboard inside the upright ends strengthens the boxes but is not required.

Specially Made Storage Boxes

Jay Cordeiro of the Northeast Natural History & Supply Co. supplies herbarium drawers and trays to your specifications (Figure 29-Figure 34). Specimen drawers and unit trays are designed for curation, storage, rehousing, and display. They can be used for shells, minerals, skeletal material, feathers, eggs, skins, anthropological objects, fossils, glass vials, and memorabilia, as well as bryophytes. Archival trays are custom manufactured to any dimension; they are rigid, unbuffered, and acid-free with neutral pH. Trays are constructed of white corrugated cardboard, come free-assembled (not flat and self-folding), are overwrapped, and nested for maximum storage efficiency. Archival drawers are available in standard sizes to fit typical Cornell, California Academy, and National Museum of Natural History style storage cabinets. Trays can be lined with plastazote or ethafoam, unbleached cotton, or polyester batting for use with delicate specimens. Lids are optionally available for better protection from ambient environmental damage and for use in layered storage. The trays are sturdy and affordable.

The company does not have an online catalog because their product is custom designed. The trays and drawers can be purchased in sets of 100 or more. Sample sizes and prices include:

Size 1 (2 3/8 x 1 5/8 x 7/8): ~pricing range $0.50 to $0.63

Size 2 (2 3/8 x 3 5/16 x 7/8): ~pricing range $0.62 to $0.76

Size 3 (4 3/4 x 3 3/8 x 7/8): ~pricing range $0.72 to $0.88

Size 4 (7 5/16 x 4 15/16 x 7/8): ~pricing range $0.93 to $1.19

Size 5 (9 5/8 x 6 7/8 x 7/8): ~pricing range $1.59 to $1.91

Purchase is direct from:
Jay Cordeiro
Northeast Natural History & Supply Co.
Distributor: HH Elements, Inc.
24 North Grove Street
Middleboro, MA 02346 USA
<unionid@comcast.net>

Figure 29. Wooden tray. Photo by Jay Cordeiro, Northeast Natural History Supply Co.

Figure 30. Wooden tray. Photo by Jay Cordeiro, Northeast Natural History Supply Co.

Figure 31. Wood pull of wooden tray. Photo by Jay Cordeiro, Northeast Natural History Supply Co.

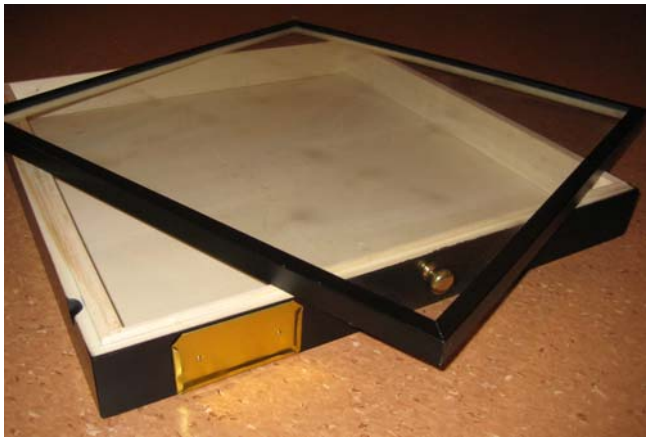


Figure 32. Box opener of wooden tray. Photo by Jay Cordeiro, Northeast Natural History Supply Co.

Figure 33. Herbarium drawer with boxes. Photo by Jay Cordeiro, Northeast Natural History Supply Co.

Figure 34. Trays. Photo by Jay Cordeiro, Northeast Natural History Supply Co.

Preservation

Most specimens will keep well in packets if they are not packed together too tightly. If a specimen has fragile parts sticking out, it helps to pack crumpled tissue paper around the specimen. An alternative is to cut out space for the specimen in a piece of styrofoam or corrugated cardboard of appropriate thickness and dimensions. However, if the specimen falls out of the styrofoam, it may suffer even greater damage than with no packing, so it might be necessary to staple or tape a minipacket in the cut out space. Small jewelry boxes can sometimes be useful. Glime once stored ***Splachnum ampullaceum*** in a plastic film can.

Preservatives should be avoided so the material can be used later for DNA or chemical analysis. If preservation is necessary for maintaining the morphology of a liverwort, maintain some of the specimens in preservative and others dried, and in some cases (flat thallose species), like ***Conocephalum*** (Figure 35), pressed. Rob Gradstein (pers. comm. 26 July 2012) suggests using FAA (fenyl-acetic-alcohol). This preservative served Barbara Crandall-Stotler for her morphological work and Rudy Schuster for making the drawings used in his liverwort volumes.

Figure 35. ***Conocephalum conicum***, a mostly flat thallose liverwort that preserves better if it is pressed. Photo by Robert Klips.

Gradstein (pers. comm. 26 July 2012) also suggests that dry, shrunken herbarium material of thallose liverworts can be rehydrated and stained with methylene blue (see Rico 2011), a method that works well for him in studying ***Riccardia*** (Figure 42). Rico developed this method of rehydrating the moss in a solution of sodium hypochlorite (commercial bleach) diluted to 20% in distilled water. This restores the form of the liverwort and the structure of the cells. The cells are cleared, making observation easier.

Species like ***Riccia fluitans*** (Figure 36) can be teased apart and floated onto a 3x5 (7.6x12.7 cm) card. The algae on these aquatic plants will serve as a glue to make them adhere to the card. Once affixed, they will retain their shape and remain flat.

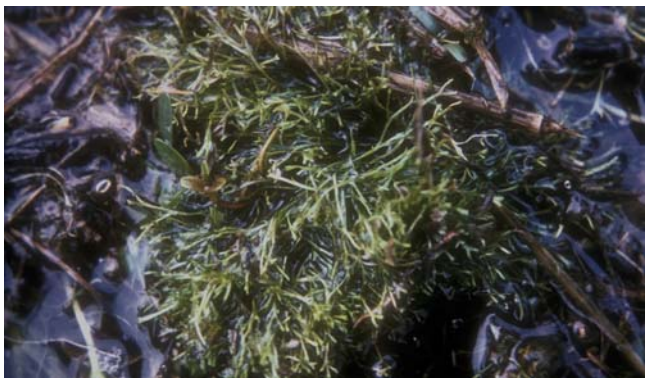


Figure 36. Floating form of ***Riccia fluitans***, a species that can be floated on a card before putting it in a packet. Algae help to glue it to the card. Photo by Janice Glime.

Since leafy liverworts will lose their oil bodies upon drying, one should preserve them by a photograph that shows details of the oil bodies. In addition, describe the oil bodies in detail.

Cool Preservation

Bryophytes prosper in cool temperatures, so it is not surprising that cooling them during drying can improve the quality of the specimen over air-drying. Victor Ardiles H. (Bryonet 25 September 2013) reports that both gametophytes and sporophytes look better when fresh samples, still in their paper bags, are placed in a freezer for 15 days at 7°C, 37% Relative humidity. The method discourages fungal growth and retains colors, leaf details, structure of thallose and leafy liverworts, bottle liverworts, and hornworts. The low temperature slows the dehydration of the tissues, a more natural approach.

Minute Species and Special Structures

The really tiny species can present special problems because they are easily lost among the soil in the packet. Several methods can help to make these locatable in the future. One popular method is to remove some of the specimens from the soil and place them in a minipacket (Rothero & Blackstock 2005) or small envelope without the soil. Another possibility, suggested by Richard Zander (pers. comm. 1 August 2012) is to glue the plants (without soil) to a white card with a polyvinyl-alcohol-based glue. That glue is water soluble, so the specimens can be soaked loose.

In some cases, only a few plants may have capsules, antheridia, archegonia, or propagules. To help avoid loss of these important structures, make a small packet or use a small envelope to store these within the species packet (Rothero & Blackstock 2005). Microscope slides can also be put in a small packet and stored within the species packet. They may survive better in a waxed paper envelope because the slide can be sticky and the paper may stick to the slide. The waxy surface can reduce this but won't necessarily eliminate it.

Herbarium Arrangement

There are two choices in widespread use in the arrangement of bryophyte herbaria – systematically or alphabetically. They each have their advantages and disadvantages, so one needs to choose based on resources and needs. The majority of those who commented on this to Dale Kruse in his survey preferred a strictly alphabetical system.

The systematic arrangement provides groupings that make it easier for someone making a systematic study. All members of a family would be grouped together. This method is further divided into choices – systematic or alphabetical arrangement of genera. Richard Zander (Bryonet 13 November 2008) considers this family grouping with alphabetical arrangement of genera to be "a nice compromise." Rod Seppelt (Australian Antarctic Division) practices a further compromise to group genera into the family, but to arrange the families alphabetically. This solves the problem of trying to linearize the non-linear systematics of families. One could also arrange the species systematically, but that does not seem to be a common practice.

The disadvantage of systematic arrangements is that our knowledge of bryophyte systematics is constantly changing. The publication of Shaw and Goffinet (2000) moved a lot of genera to other families and split some families. Because of the instability of our understanding of the systematics, the cabinets would require an updated list of the locations of each genus and family. Flora North America is making further changes. As we gather more molecular information we keep moving things. Hence, this arrangement can be expensive because it would require constant monitoring and rearrangement whenever a taxon has been moved or redefined.

The alphabetical arrangement is more practical. In some cases, the packets are arranged in families with an alphabetical arrangement of families. In other herbaria, the genera are arranged alphabetically with no family groupings. The latter arrangement is the most stable arrangement.

Jim Shevock reports that the University of California herbarium files their bryophytes alphabetically by genus (Figure 25). My own experience is that most bryological herbaria use that method because it is easier and less expensive to maintain. Missouri Botanical Garden uses family groupings. At the California Academy of Sciences the genera are filed by family, but the genera and species are filed alphabetically within the family, and the families are arranged alphabetically.

I like the advice of Jaakko Hyvönen (Bryonet July 2008) regarding phylogenetic vs alphabetical: we are...still too far away from the classification that would enable arrangement accordingly. Alphabets have been pretty stable for quite some time and this makes it easy for ALL people (most of whom are NOT bryologists) to locate specimens in collections. On the long run one would be able to save a LOT of precious volunteer, student *etc*. herbarium time by adopting this simple system. At the same time, need for rearrangement is minimized.

Guide Cards

A practical way to help the user is to provide guide cards. William Weber (University of Colorado Museum) uses blue cards for Colorado material and yellow for other areas. A salmon guide card indicates the genus, yellow the species. Alternatively, one could color code the top of the packets with a felt pen. Note that red is reserved for type specimens.

When a herbarium is rearranged or names change, guide cards can be placed where the alternative name would occur, directing the user to the location of that group. This can be useful if staff lack the time to rearrange the collection. A guide card can be placed where the new name should be, directing users to the name on the packets.

Herbarium Care

Soil

More information is retained if the substrate is collected with the specimen. However, this brings its own problems. It can be bulky, bring plant pests, and prevent you from taking or sending specimens across borders. But Brent Mishler (Bryonet 2 March 2021) warns us that if it is removed, rhizoids, tubers, and other underground structures can be damaged or removed. Furthermore, the soil helps to keep the clump intact. Hence, for taxonomic and

ecological purposes, it is best not to remove soil in contact with rhizoids or stems. Mishler recommends using window screening to gently rub away excess soil.

Wet soil is likely to cling to the clump, but dry soil may have dried to fine parts like glue. Sometimes a gentle washing by dipping the bases of the clumps in water can help to remove water with minimal damage to the underground parts, but caution is needed. Heavy soil clumps can pull on the rhizoids and break them loose.

Chris Cargill (Bryonet, 2 March 2021) faces similar problems at the Australian National Herbarium (CANB), especially with specimens like ***Riccia*** (Figure 37) and hornworts that typically have soil attached. The soil detaches over time as researchers access the collections, often just by disturbing the packet without removing anything. To improve maintenance of the collection integrity, they wrap terricolous collections carefully in archival tissue paper, sometimes on a piece of card for rigidity, and then place the whole wrapped specimen into an archival quality polypropylene bag. This reduces the movement of the specimens and inside the packet and therefore any rubbing from loose soil or small pebbles. They place any loose soil in a separate small archival plastic ziplock bag and place it with the specimen.

Figure 37. ***Riccia*** showing rhizoids clinging to soil. Photo by Bernd Haynold, through Creative Commons.

Ken Kellman (Bryonet, 2 March 2021) agrees with the importance of keeping soil. If there is a lot of powdery soil, wrap the sample in a smaller packet inside your herbarium packet. Fragment packets work well. That tends to minimize the inevitable settling of the soil.

Richard Zander (Bryonet, 2 March 2021) finds that, within limits, the more soil the better:

1. Rhizoidal gemmae, fallen calyptrae, and other plant parts may be found in the debris
2. Other organisms are present in the packet, and I think maybe in the future the best place to search for new taxa or significant species will be among soil in packets already in the herbaria.

Brent Mishler (Bryonet, 2 March 2021) raised an additional concern. The specimens may be used later for extracting DNA [or heavy metals in soil vs bryophytes], so washing can give false results. Initial wetting can cause a lot of damage and loss of cellular contents. This is particularly true if they dry out again before being able to repair the damage. Hence, if specimens must be cleaned, Mishler recommends doing it dry.

Brent Mishler, Bryonet 2 March 2021

Pest Control

Pests can be a problem in a herbarium, and methods to eliminate or minimize them can be detrimental to future studies that rely on untreated material for historical pollution studies or DNA testing. In November of 2010 there was a discussion on bryonet-L regarding means of eliminating pests without compromising future studies.

Historically, most bryophyte herbaria have not treated for pests with the same care as that used for vascular plants. For example, beetles can be real pests among tracheophytes and some algae, but are usually not rampant among bryophytes. The popular belief that nothing eats them let of a somewhat false confidence in storing the with no pesticide treatments. However, if you have ever tried to import them into a country, you know that the border quarantine agents are concerned about pests in the soil, and this alone should suggest that the bryophytes may introduce pests into the herbarium. Scattered publications, and especially more recent ones, as cited in the interactions volume on this website, demonstrate that our assumption that nothing eats bryophytes was incorrect.

Agral 600

As mentioned in the Laboratory Techniques subchapter on Slide Preparation and Stains, Tom Thekathyil (Bryonet 12 May 1210) submerses the bryophytes in **Agral 600** (horticultural wetting agent). It kills the animal life that often accompanies the bryophytes but does not seem to affect the plants.

Moth Balls (Naphthalene)

For tracheophytes, the standard treatment has been to put **moth balls** in the cabinets. These have contained such compounds as **naphthalene** (highly flammable and carcinogenic), **1,4-dichlorobenzene**, or **camphor**. These all have strong odors that are very offensive to some people, especially when they work for many hours in that environment.

Rod Seppelt (Bryonet 26 November 2010) reports using fumigation with *Pyrethrum* in a spray. The plant that produces the Pyrethrin[tm], however, is known to cause human health problems among long-term growers of the plant.

Microwave Oven

A more recent method for killing bryophyte inhabitants has been to put them in the microwave oven, but such treatment renders the bryophytes unusable for future DNA studies due to the ability of the gamma rays to alter the DNA. Lars Hedenäs (Bryonet 30 November 2010) reports that the Swedish Museum of Natural History would never send material to another herbarium if there is the danger that the material on loan would be subjected to microwaves. The risk of destroying DNA would "seriously reduce its value for future research."

Wagner finds that the microwave is not effective, largely because of the uneven distribution of microwaves inside the oven. The oven has the further problem of being

too small unless you purchase a commercial grade oven. Wagner had a friend who trapped a fly inside his otherwise empty microwave, turned it on for 60 seconds, and when he opened it the fly flew out. It had survived by cowering in a safe corner. Some herbarium material absorbed microwaves and overheated. Wagner has even had charred herbarium specimens, and blackened paper under them, that resulted from too long a treatment.

Bromomethane (Methyl Bromide)

Juan Larraín (Bryonet 13 April 2016) raised concerns that Chile requires that all specimens with soil, including bryophytes, must be treated with bromomethane before entering the country. While this may be a good means to prevent the introduction of agricultural pests, Rod Seppelt (Bryonet 13 April 2016) warns that it should not be used on specimens to be used for molecular work. Rather, he recommends freezing.

Freezing

It appears that the safest and most common method in current use is freezing. And this is standard practice in many herbaria (Figure 38). In this method, one recommendation is to freeze the packets for 24-48 hours; the process should be repeated annually to maintain the pest-free environment (Denis Oliver, Bryonet 26 November 2010). Rod Seppelt (Bryonet 26 November 2010) recommended three days at -18ºC for material collected in the region or -18ºC for seven days if it has come from a different biogeographic region or outside the country. He later modified this (Bryonet 6 February 2012), based on a response from the herbarium in Auckland, New Zealand. They found that a more effective treatment was to use cycles of room temperature to -15ºC over a few days. It is kinder to the bryophytes and more effective against insects. At Christchurch (CHR), freezing is for 7 days at -20°C (Allan Fife, Bryonet 15 August 2002).

At the University of Alberta Herbarium (ALTA) specimens are frozen at -20°C (Catherine La Farge England, Bryonet 15 August 2002). The specimens are stacked as single sheets or only a few sheets overnight; larger stacks are stored at that temperature for four days to be sure the center gets cold enough. The specimens are sealed in poly freezer bags in the freezer and kept in them until they reach room temperature afterwards, for up to a day for larger stacks. A similar procedure is followed at the New York Botanical Garden (NYBG) and Missouri Botanical Garden (Marshall Crosby, Bryonet 15 August 2002), where freezing is for 3-4 days (Barbara Thiers, Bryonet 15 August 2002).

At the Helsinki Herbarium (H), all loans are frozen for at least a week before putting them in herbarium cabinets (Johannes Enroth, Bryonet 15 August 2002). The same procedure is followed at the British Museum (Brian O'Shea, Bryonet 15 August 2002). At the Chicago Field Museum (Matt von Konrat, Bryonet 15 August 2002), new specimens and loans are frozen unless they are to be used for DNA analysis or study of oil bodies in liverworts. The concern is more for the protection of other plants and fungi in the herbarium since bryophytes are seldom eaten by herbarium pests. Fungi are particularly vulnerable.

Figure 38. New specimens are being placed into the freezer at Beaty Biodiversity Museum in Vancouver, BC, Canada. Photo by Derek Tan, copyright Beaty Biodiversity Museum

Lloyd Stark (Bryonet 15 August 2002) warns that freezing as described above may be too effective, killing the bryophytes as well as the pests. In regeneration tests on specimens from UC, MO, and Cal Acad, mosses were not able to regenerate, but members of Pottiaceae that had not been frozen were able to regenerate several years later. At the University of Nevada Herbarium (UNLV), the dry climate makes freezing unnecessary. David Wagner agrees that low humidity is almost as effective as low temperature for controlling typical herbarium pests.

Rod Seppelt (Bryonet 16 August 2002) reports the additional precaution of freezing specimens that have been taken out of the herbarium cabinets for more than a few hours. If the specimens are kept in the herbarium facility, overnight freezing is usually adequate. If they reside anywhere else while outside the cabinets, they are frozen for several days.

At the Provincial Museum of Alberta (PMAE), the procedure is even more extreme. They do a quick freeze to -70°C for small accessions (fewer than 50 specimens). For larger collections they fumigate. Roxanne Hastings (Bryonet 16 August 2002) reports that creatures are killed within 24 hours at the very low temperature and have no chance to acclimate to it.

Herbarium personnel have done some experimenting, although it may not appear in the literature. John Braggins reported to Rod Seppelt (Bryonet 26 November 2010) that **multiple freezing events** were more effective than a single event. He found at AK that silverfish could be killed with a number of cycles, from room temperature down to -6ºC or -10ºC and back to room temperature. That procedure was more effective than just one cycle to -10ºC. Freezing overnight is most likely useless. After all, these organisms survive such cycles in nature in many parts of the world. Rod Seppelt (Bryonet 6 February 2012) also reported that he had greater success with several low temperature (-1°C)/warm temperature cycles for several days. The multiple freezing event treatment seems to be gaining popularity, and many of the herbaria cited above may already be using it.

Domestic freezers vary in their temperatures, but generally only go down to about -15ºC, and depending on their arrangement may have zones that are warmer or slightly colder.

Jeff Duckett (Bryonet 26 November 2010) points out that one advantage to freezing the bryophytes is that it does not **always** kill the bryophytes, despite killing their inhabitants. These are plants that can spend the winter, often for three months, under snow, or in many cases exposed with no snow ab below freezing temperatures. In the polar regions they survive in areas that may be snow-free for some time at very low temperatures. Yet these species survive. Such is probably not the case for tropical bryophytes.

Adequate freezing facilities are not available in many herbarium locations. David Wagner (Bryonet 16 August 2002) suggests that baking or poisoning, coupled with closely contained quarantining may be necessary instead, particularly in the tropics. An alternative in temperate climates is an air-conditioning system that chills the air before heating it, thus dehumidifying it. Keeping vulnerable specimens, especially fungi, away from the bryophytes solves a lot of the problems, especially if low humidity can be maintained.

The downside to all this pest control is that the specimens are no longer suitable for longevity tests on spores or plant tissues and might not be usable for DNA testing. The **specimen label should indicate treatments** such as these to protect against faulty conclusions by people using the specimens for physiological purposes or DNA analysis.

Eva Krab (Bryonet 3 February 2012) found that a number of approaches did not work. After a number of failed attempts, she took the approach of flushing the moss cores [***Sphagnum fuscum*** (Figure 39) and ***Hylocomium splendens*** (Figure 40)] in a gas-closed chamber with 100% CO_2 for 12 hours, then leaving the cores at room temperature for 24 hrs (so that eggs would hatch) before freezing them at -20°C. But even after 3 rounds of all those treatments – and still no success – the springtails were still active! (It worked a lot better in the ***Hylocomium*** cores than in the ***Sphagnum*** cores.) The mosses actually survived these treatments surprisingly well. These were subarctic springtails, so maybe temperate springtails might be more sensitive to the freezing part of the cycle.

Figure 39. ***Sphagnum fuscum***, a hummock moss that survives cryopreservation with a pretreatment in 100% CO_2 to eliminate pests. Photo by Michael Lüth.

I like the suggestion from Javier Martínez-Abaigar (Bryonet 3 February 2012). He suggested using a Berlese funnel (Figure 41) to chase the springtails out of the moss, then returning them to their natural habitat.

Figure 40. ***Hylocomium splendens***, a moss that survives cryopreservation with a pretreatment in 100% CO_2 to eliminate pests, but invertebrates do not survive as well as those on ***Sphagnum***. Photo by Janice Glime.

Insect Traps

Some passive means include insect traps, apparently somewhat standard procedure in large herbaria, but these are ineffective against eggs that may be dormant for long periods, causing new outbreaks when new material is introduced. What traps adults may not work for larvae that sit and chew on bryophytes and packets for weeks or months.

Drowning

Eleanor Edye (Bryonet 2 February 2012) found that washing the collections with a surfactant before drying them increases the effectiveness in killing them. She reports that springtails usually have a very hydrophobic cuticle and thus tend to float. Forced immersion in water will reduce their populations. If bryophytes are the only concern, some of the predatory mites will eat the springtails but not the bryophytes.

Steam Sterilization

Soil can be sterilized with steam. While this will most likely kill the pests, it will likewise kill the bryophytes. Rod Seppelt (Bryonet 16 December 2009) reported that Alison Downing found that some bryophyte spores, such as the thick-walled spores of ***Riccia*** species, survive standard autoclaving of soil.

UV radiation can be used to sterilize the air and even for a short distance (a few cm) into water (Javier Martinez-Abaigar, Bryonet 16 December 2009). However, soil shields it, so it is not an effective tool for sterilizing soil adhering to bryophytes, and most likely will not kill invertebrates hiding among the bryophytes.

Moisture Control

Moisture is another challenge in some herbaria, especially in the tropics. Fungi may appear as tiny hairs projecting upward or as a mass of hairs forming a mat. In worse cases they may form spores that spread easily to

other specimens and that are not healthy to breathe. Roxy Hastings (Bryonet 26 November 2010) found that fungi could be a problem at relative humidities above 40%.

Dehumidifier

Use of a dehumidifier may be sufficient in some cases to prevent the growth of fungi and bacteria, but it adds to the operating expenses and may be insufficient in large herbaria in very humid climates.

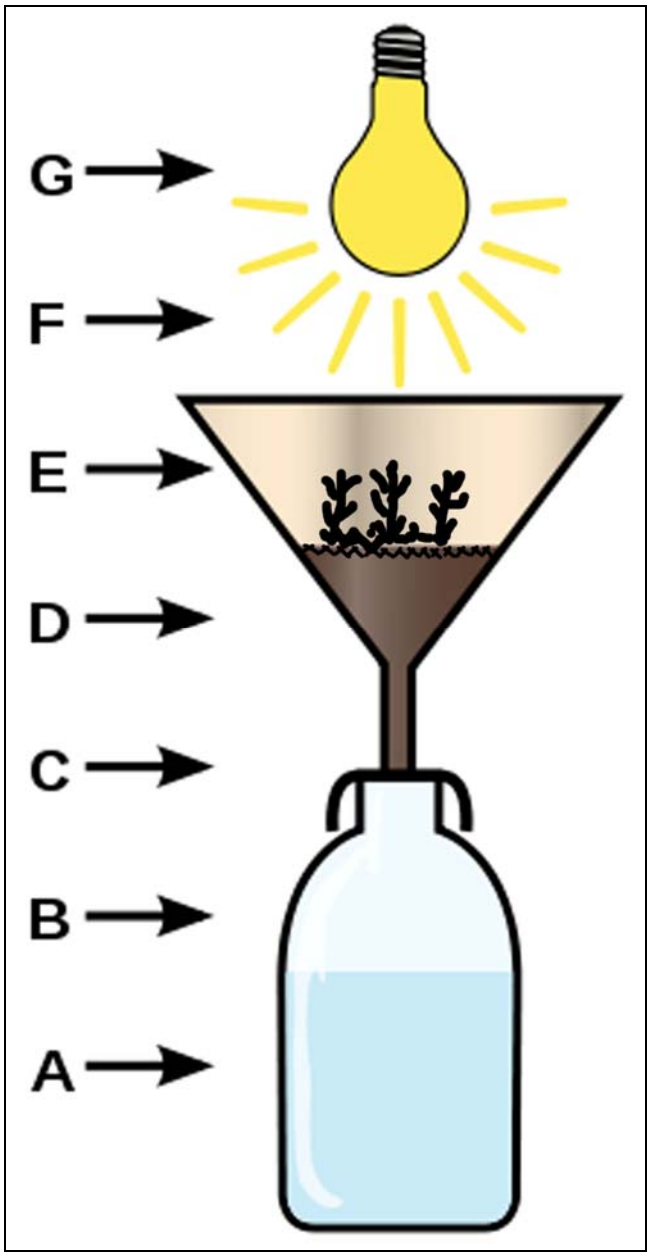


Figure 41. Berlese funnel showing its parts. **A** = liquid for trapping insects (not needed if you want to keep them alive). **B** = air space above liquid in jar or bottle. **C** = lid with hole for funnel end. **D** = open funnel area with screen or wider mesh on top. **E** = area of funnel where sample is placed. **F** = space above funnel to avoid scorching bryophyte sample. **G** = light/heat source that causes invertebrate inhabitants to go downward to escape. Drawing from Creative Commons.

Silica Gel

Modest problems can be controlled with silica gel packs, available from herbarium suppliers (Roxy Hastings, Bryonet 26 November 2010). They are available from "Herbarium Supplies" to maintain various humidity levels in the range of 25-40%. These packs can be "recharged" by putting them in an oven to dry and usually provide a color indicator of their state of moisture.

Herbarium Cabinet Materials

If you choose to make your own cabinet for herbarium specimens, be aware that particle board can contain formaldehyde in the glue, presenting a long-term health risk (Rod Seppelt, Bryonet 26 November 2010). Herbarium cabinets are usually made of metal with a somewhat spongy material around the door to seal it. A good cabinet will not allow pests to gain entry unless they travel with the herbarium specimen.

Sending Specimens for Identification

Understanding accepted courtesy and rules for sending bryophyte specimens can make it easier for one to get much needed help. These guidelines should keep you out of trouble and avoid misunderstandings:

1. Assign each of your collections a unique collection number. Many bryologists pre-number collection bags and keep a life list of numbers to avoid ambiguity.
2. When mailing a specimen for identification, keep part of the sample yourself and be sure it has the same collection number on both yours and the identifier's packets. This will permit correspondence with the least ambiguity.
3. Be prepared to donate the collection to the person doing the identification (Loeske 1925; Raup 1926; Zander 1993). This is a courtesy for the time that person spends helping you. Be aware that some recipients will assume that the specimen is now theirs.
4. Make it clear who will be considered author(s) of any scientific publications resulting from the identification. If possible, offer to make the determiner a co-author. If there is a reason you can't do this, explain why you must be the only author. Establishing this at the onset can avoid awkward misunderstandings.
5. Include details of name of collector, collection number, date, substrate, habitat, and location on the packets, including latitude, longitude, and more precise coordinates, including GPS if possible.
6. Include on the packet label any notes that might be important. Information included in an accompanying letter will usually not be added to the label by others.
7. Check and follow the import/export laws regarding herbarium specimens in both yours and the receiving

countries. Usually it is sufficient to label a package as "herbarium specimens, no commercial value," but some countries have very rigorous import standards to protect against introducing soil organisms and disease, and more recently, against collections of rare or endangered species. For example, specimens entering Australia and New Zealand require paperwork in advance and treatment protocols (Rod Seppelt, Bryonet 12 July 2012). The sender or recipient may have to pay inspection and/or fumigation costs, the alternative being destruction of the specimens. And in some countries you could get the recipient in trouble because the necessary paperwork is lacking. A Google search for **plant import regulations** and the name of the country can be a good start.

8. Remove as much soil as possible.
9. Be sure the specimen is dry and in paper, not plastic, to avoid mold.
10. Get permission from the recipient before sending the specimen. Otherwise, you might never see your specimen or any identification again.
11. Provide a clear address and email address for providing you with the names of bryophytes identified.
12. If you have a target deadline, be sure you discuss that with the person identifying before you send the specimens.
13. Try not to send more than three specimens at a time so the task will not seem so daunting to the recipient (Zander 1993).
14. Don't include more than one species in a packet if you can avoid it. If not, tease out the individual species and put some branches of them in small packets within the larger one, giving each the same collection number but a unique letter to distinguish it (and keep duplicates of the individuals). It is important to maintain the growth form to help in identification.
15. If you are borrowing samples for DNA analysis or other destructive purpose, be sure the person/institution loaning them understands that, and be sure that at least some material is left for verification by anyone later. Actual plants from which DNA analysis is made should be maintained in minipackets (triangular packets) and kept both in the original voucher specimen packet, entered in the herbarium database, and linked to the voucher specimen in Genbank (Brent Mishler, Bryonet 20 January 2023).
16. Include in your packet a carefully prepared slide with a semi-permanent or permanent mount of the specimen of interest, including stem leaves, branch leaves from the middle of the branch, a short branch from which the middle leaves have been removed, and if available, a peristome (Holzinger 1900). It is also very helpful to provide a permanent mount slide of leaf cross sections. These inclusions will save considerable time for the identifier and make it more likely that you will get your identifications in a timely manner. These should be protected in a small envelope within the packet.
17. Karen Golinski (Bryonet 12 July 2012) suggests providing a spreadsheet with the collection numbers and collection information with space for adding the name. This makes it easy for the identifier to provide you the names and makes it easier for that person (or you) to add the information to a herbarium database.
18. Make an attempt to identify your specimens before you send them to experts. Not only will you learn more this way, but it makes the task less daunting for those helping you. And some bryologists will take the time to tell you where you went wrong in those that are identified incorrectly. David Wagner (Bryonet 12 July 2012) states "First, for anybody sending specimens to an expert you have not had communication with before, send only one or two specimens with your best guess as to identification. This is far more likely to get a prompt response. As soon as somebody sends me a box with a dozen or more specimens, it gets put on a shelf as a 'when I get time to do it' task. This shelf has accumulated specimens for many years with most boxes advancing only very slowly to the top of priority tasks. Send me one specimen and I'll look at it and respond within 24 hours. Offering to pay helps to advance priority ranking, of course." Wagner also points out that your identifications will give the expert some idea of your level of expertise.
19. Make use of the internet to see if your identification matches the images there. But of course be aware that some ID's shown there may be wrong.
20. If you took pictures of the bryophytes and their habitats, send the best of these to the person doing identification (Figure 42-Figure 44). Field growth habit can help in the identification, and if the pictures are good, they are an additional way of saying thank you to the one helping you. Photographs of microscopic characters are even better.

Figure 42. ***Riccardia cf. elata***, posted to Bryonet by Zhang Li for help in identification. With only this view, Bryonetters suggested the fern *Hymenophyllum*. A view showing its habitat and growth habit might have helped. Cellular structure and other microscopic views are needed. Photo by Zhang Li.

Figure 43. ***Riccardia cf. elata***, posted later to Bryonet by Zhang Li for help in identification. With the addition of this view, Bryonetters could be more certain the species was one of ***Riccardia***. Photo by Zhang Li.

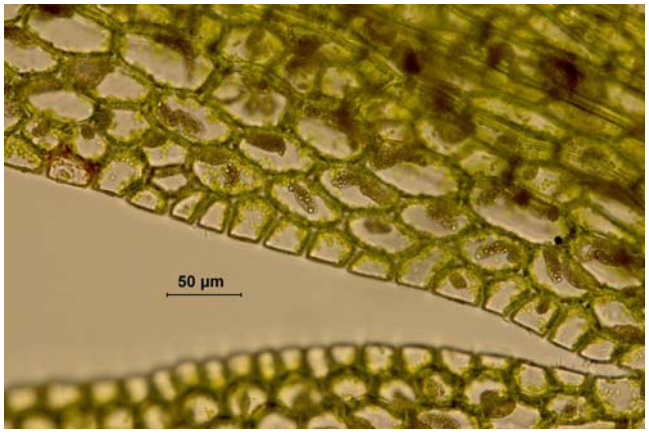


Figure 44. ***Riccardia cf. elata*** microscopic view posted to Bryonet by Zhang Li for further help in identification. This view enabled Bryonetters to be certain the species was not a fern, but rather one of the liverwort ***Riccardia***. Note the oil bodies. The suggestions were narrowed to ***Riccardia elata*** or ***R. prehensilis***. Photo by Zhang Li.

References

Current Names

The choice of references depends on your geographic location, so it would most likely be of little help for us to make suggestions. Old references can be useful if you check the names in TROPICOS <http://www.tropicos.org/> for nomenclatural changes. If you can't locate them there, Google might help, or The Plant List <http://www.theplantlist.org/tpl/record/tro-35156923>. Be careful of your spelling – these lists don't find similar spellings. They don't care about capitalization. For liverworts and hornworts, the best source currently is Söderström *et al*. (2016).

Bryologists will always disagree among themselves about generic placement using the Linnean naming system. This generates healthy discussion about relationships, but creates problems for a herbarium and the ability to relocate a specimen. It is best for a herbarium to choose a published classification system and be consistent in its use. If a different system is chosen, then the entire collection should be updated. This might be at the generic or family level, not necessarily at the level of the entire herbarium. But it should not be store partly by phylogeny and partly by alphabet at the same hierarchical level.

Easy sources for names, authors, synonyms, and currently accepted legitimate names are Söderström *et al*. (2016), **TROPICOS** <http://www.tropicos.org/>, a service of the Missouri Botanical Garden, and **The Plant List** <http://www.theplantlist.org/>, a collaboration between the Royal Botanic Gardens, Kew, and the Missouri Botanical Garden. I (Glime) don't like the higher level classification used by the Missouri Botanical Garden (it puts the bryophytes in the class Equisetopsida to use classification levels considered commensurate with those of animals). At least I don't have to look at them in the Kew list!

Indexing

Wagner recommends indexing your taxonomic reference books. He found the books more inviting when they were easier to use, and found that the accuracy of his work definitely increased as a result. With bryophytes he indexes the major genera. Figure 45 shows an indexed copy of Paton's "The Liverwort Flora of the British Isles." Figure 46 shows the thumb tabs in greater detail and Figure 47 shows the method for cutting them. An index card serves as template for the area to be cut out. A cutting mat is placed ON TOP of the page to be indexed. Wagner uses a #11 scalpel blade to cut through forty pages (twenty sheets of paper). The important part is to plan which pages will be indexed. It is easy to want to do too many and run out of space on the outer margin of the book.

Figure 45. Index tab indentations in The Liverwort Flora of the British Isles. Photo by David Wagner from Bryological Times #136 (2012).

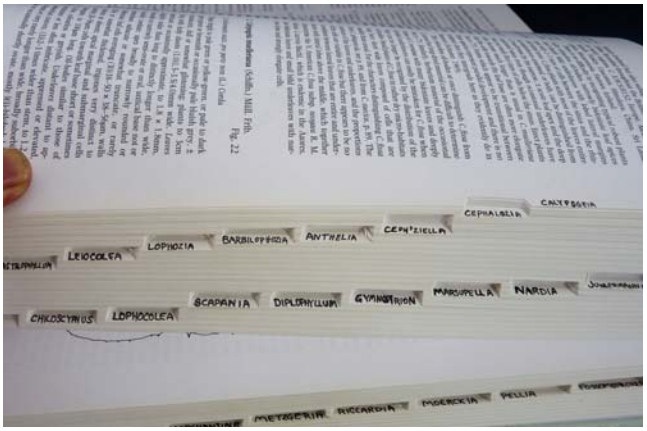


Figure 46. Close view of index tab indentations in The Liverwort Flora of the British Isles. Photo by David Wagner from Bryological Times #136 (2012).

Figure 47. Tools for cutting indentations in page edges. Photo by David Wagner from Bryological Times #136 (2012).

The second type of index Wagner uses is an invention that began with an address book. The index is printed on only one side of the paper and stapled on the right side. This might seem counterintuitive because most booklets have the binding on the left side when it is face up. However, because our writing is from left to right, it means the words to be indexed will appear lined up on the left side of a sheet. (This might need to be reversed for some Asian countries.) By staggering the sheets and trimming on the left, any item is quickly found. There are two examples here. The first (Figure 48) shows an index to the five most common references Wagner uses for liverworts, directing one to the pages for species of liverworts found in Oregon. The species are designated by six letter codes. This index is kept with the appropriate books on the workbench or book shelf.

Figure 48. Excel file printout of six-letter liverwort codes, showing reference where it can be found and page. Photo by David Wagner from Bryological Times #136 (2012).

The second example of this kind of index is an older one, made in 1998 when Wagner was doing extensive cryptogam inventories in southwestern Oregon. It has all the mosses and liverworts known from the entire state, almost 700 names (Figure 49). It is useful to check spelling or authority of a name when typing memos, labels, or annotating. Again, the names are designated by six letter codes manufactured for rapid data entry both in the field and when databasing. By using small type all 678 names fit onto 14 pages.

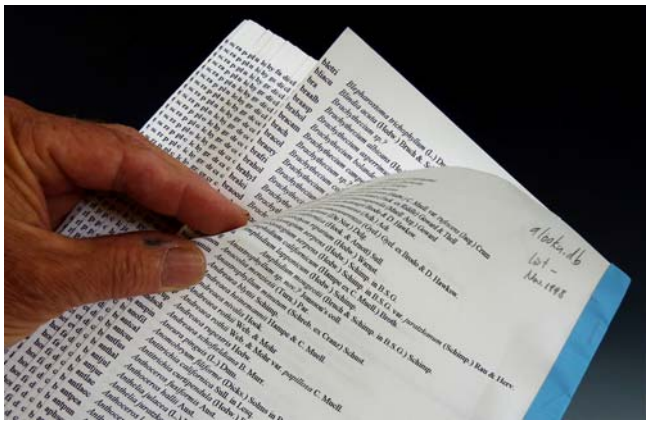


Figure 49. List of all bryophytes found by David Wagner in Oregon, used to check spelling and supply authors. Photo by David Wagner from Bryological Times #136 (2012).

Herbarium Label Programs

There are several programs on the internet, *e.g.* <http://www.flmnh.ufl.edu/herbarium/pl/>, to help make it easier for you to produce labels and make a herbarium database. If you can use Access, UC Davis has a free Herbarium Management System to download <http://herbarium.ucdavis.edu/database.html> that allows you to print up labels from Access data (Stephen Lodder, Bryonet 12 July 2012).

Specify 6 is another free herbarium program <http://specifysoftware.org/>, funded by the U.S. National Science Foundation. This program can handle specimen data for computerizing collections, tracking specimen and tissue management transactions, and moving species data to the internet. It runs on Windows, Mac OS X, and Linux operating systems.

One consideration for computer programs is that their database is compatible with other programs in widespread use. Current efforts to create a national database of US holdings are underway, supported by government funding. Part of this effort includes converting the many individual databases into a single one that is accessible online. This will permit researchers to find the location of needed specimens and to determine the contact person(s) for loans.

Shipping Live Bryophytes

Bryophytes don't like to be wet and hot at the same time, and this can be exacerbated by also being dark. Such conditions are ideal for fungi to grow, and once a fungus attacks the bryophytes, they most likely won't recover. Hence, shipping live bryophytes can be a major challenge. To reduce these ideal fungal conditions, whenever possible pack some of those frozen picnic cooler gels with your bryophytes to keep them cool and use an insulated container, or insulate one with something like crumpled paper or styrofoam peanuts. If the bryophyte is drought tolerant, send it dry. If you are shipping aquatic

bryophytes, seal them with clean water in plastic bags and keep them cool. Use a rapid shipping method to ensure the best results. Don't provide nutrients as they will encourage growth of algae, fungi, and bacteria on the surface. I have had some success packing aquatic mosses with wet paper towels or newspaper, but heat will quickly spoil all your efforts.

Your first concern may be to keep the bryophytes alive, but getting them across the border might be even more challenging. Even within the same country, it might be necessary to have a **nursery license** to ship plants across state borders. For example, in North Carolina, the Department of Agriculture and Consumer Services requires a nursery license for shipping within the US (Annie Martin, Bryonet 8 December 2010). All live plants and bryophytes need to be inspected for nematodes, insects, or diseases in advance. A certificate documenting certification must be included in any shipment of live plants (bryophytes). For international shipments, at least from the USA, a local inspector must examine each and every shipment that leaves the country. Shipping overseas is a laborious process and shipping is costly.

Sharing Images

Many herbaria have web pages where they provide images of bryophytes. If you choose to set up your own web page, a few guidelines will make it more useful.

Make it clear what you consider fair use. If you prefer restricted use or permission, provide contact information for those seeking permission and make clear what information you will need to give that permission (*e.g.*, intended use, size and resolution, whether it will be modified, attribution, web address). When I (Glime) request images for this book, I state that the image is for an online book on Bryophyte Ecology <www.bryoecol.mtu.edu>, sponsored with no financial support by the International Association of Bryologists and the Department of Biological Sciences of Michigan Technological University. I clearly state that I will give credit for the image and ask if there is additional attribution they would like included besides the name of the photographer.

Sending large images by email can really slow down the system at both ends, so you might want to share images with specific individuals through a free downloadable program called DropBox <www.dropbox.com>. There are also a number of websites where you can post images that are available to everyone, or by becoming a "friend" for that group, much like FaceBook. If you give full permission for use, provide the attribution information you would like the user to include.

BE SURE OF IDENTIFICATION! It is okay to post species where your identification is doubtful, but be clear that it is doubtful, or ask for help when you post the picture.

Don't post pictures taken by anyone else without getting their permission and all the information discussed above.

Some posters restrict the resolution and size of the images they post to avoid having them used commercially for profit as posters, calendars, or advertisements. Many posters give permission for educational use, but not for other purposes. If you have no plans of publishing your pictures, or using them for profit, why not give permission for all but commercial use? This book is built on the willingness of people to share. And the less time one must spend hunting for a contact person to gain permission, the more time can be spent on creating and sharing the final product.

Herbaria

There are numerous herbaria around the world, and many of them are able to loan specimens to other herbaria. When requesting specimens, it is important to state the use you will make of them and anticipated return date. If you need them for DNA or chemical analysis, or any other destructive sampling, be sure the loaning herbarium understands that. NEVER use type specimens for destructive sampling. And likewise, avoid using voucher specimens unless the destruction is necessary to verify identification or compare then and now. Try not to use the entire specimen.

Index Herbariorum <http://www.nybg.org/bsci/ih/ih.html> provides a list of the registered herbaria of the world. The index lists 1610 herbaria in 117 countries. The site permits searching by institution, city, state, acronym, staff member, correspondent, and research specialty.

Herbarium Specimen Mapping

Some herbaria include a dot map on the herbarium label (Figure 50). Phytogeographers need to understand plant distributions, and floras typically include the distributions of the species. The size of the map depends on the level of detail needed for that herbarium or project. For instance, specimens collected for the BBS vice county records will have a dot in the county of collection.

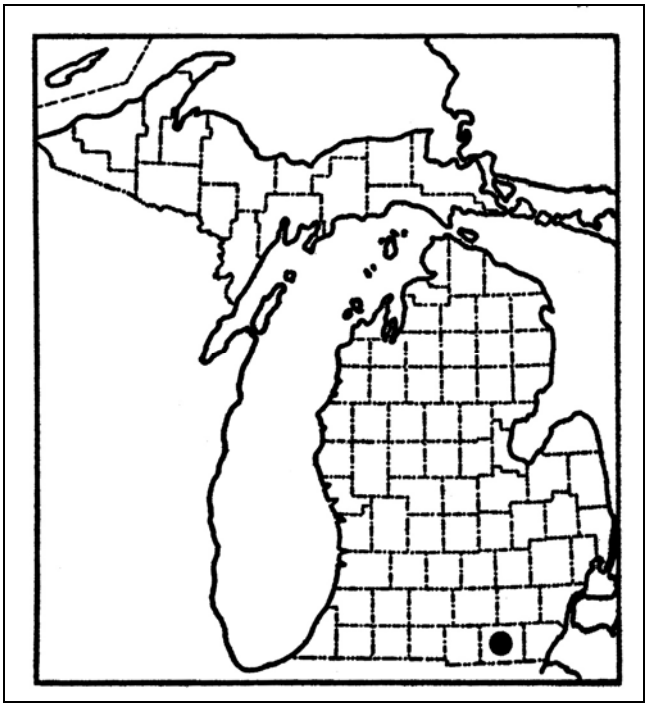


Figure 50. Dot map for Michigan, USA, indicating location of a specimen in one county. From Voss 1996.

Computers have brought us mapping programs that greatly facilitate these tasks. Brent D. Mishler (Bryonet 13 July 2008) has alerted us about the free program BerkeleyMapper <http://berkeleymapper.berkeley.edu/>. This program uses Google maps and places GIS-based points on the maps.

The best way to look at a map is to run the query first at <http://ucjeps.berkeley.edu/bryolab/UC_bryophytes.html>. For example:

1. Search for Scientific name ***Mnium*** (or any other)
2. Submit query
3. Select on the return page the link: "Map the results using BerkeleyMapper (192 records with coordinates [those with a light green checkbox])"

Live Collections

Maintenance of live collections requires a solid background in the ecological and physiological needs of the species to be cultured. These details will be covered elsewhere in this volume. In the present chapter, we wish to caution you that cultured species may not look like the same species in the field. For genes to be expressed, the right nutrients must be present for development. Hence, caution should be used in using cultured bryophytes for taxonomic identifications. Nevertheless, live cultures are one way to maintain rare species on the verge of extinction.

An alternative to living, growing cultures, is cryopreservation. Michael Christianson (Bryonet 10 June 1999) reported that he had taken over the culture collection established by Malcolm Sargent and that he had begun using cryopreservation of the species, including successful cryopreservation of liverworts.

Cryopreservation

Before we have scratched the surface of the complexity of evolution and biogeographic pathways, many plants and animals are disappearing from the planet forever. We have struggled with our fossil record to make sense of the small samplings we have through time and we do not want to compound our struggle for understanding by losing the species we have today. Nature does not preserve species as fossils on a regular basis, so to ensure these disappearing taxa remain available for study, we as scientists must help out.

We knave known for a very long time that most bryophytes have the ability to survive being frozen (Gubin *et al*. 2003), so our knowledge about cryopreservation for this group of animals already has a sound scientific basis. Some of the early studies on cryopreservation for scientific purposes have included bryophytes (Sugawara *et al*. 1980). But several bryologists led the way toward building a collection of cryopreserved endangered and rare bryophyte species (Burch & Wilkinson 2002; Burch 2003; Burch & Ramsay 2003).

Developing such a collection requires considerable testing to be assured that most of the cultures will survive and begin growth again. However, this method for conservation has advantages over the traditional live culture methods. It requires much less maintenance time once the species has been cryopreserved, and it is less likely to get contaminated while frozen. Furthermore, cultured bryophytes tend to lose vigor over time and both their physical and physiological characters may change in the unnatural conditions of culture, making them look like a different species (Christianson 1998).

As in standard culture, it is desirable to obtain a pure culture free of algal and fungal contaminants. Burch and Ramsay (2003) and Christianson (1998) suggest eliminating algae by growing protonemata **in** (not on) a medium where they will grow toward the light. The photosynthetic ends of these protonemata will emerge from the medium free of algae.

Dehydration prior to freezing will minimize the formation of ice crystals that damage cells. Desiccation-tolerant species are able to survive the prolonged dehydration that makes this successful, but desiccation-intolerant species may not (Burch 2003). Survival of these intolerant species is more likely to be successful if the growth medium is supplemented with abscisic acid (ABA) and sucrose (see volume 1 for a discussion of desiccation tolerance in bryophytes) (Christianson 1998; Burch 2003; Burch & Ramsay 2003). Exact levels needed will require experimentation, with needs differing by species.

Preparation of the bryophytes can be important to their survival, and as you might expect, the ones from wet habitats lack desiccation tolerance, making them more difficult to preserve through cryopreservation (Burch 2003). Christianson (1998) found that only 3-4 days in a medium supplemented with 10^{-5} M ABA and 100 mM proline prepared the mosses ***Ceratodon purpureus*** (Figure 51), ***Funaria hygrometrica*** (Figure 52), ***Physcomitrella patens*** (Figure 53), and two species of ***Sphagnum*** (Figure 39) to survive at least one year in cryopreservation at -80°C.

Figure 51. ***Ceratodon purpureus***, a widespread moss that survives when treated with ABA and proline prior to cryopreservation. Photo by Michael Lüth.

Figure 52. ***Funaria hygrometrica***, a disturbed habitat soil moss that survives when treated with ABA and proline prior to cryopreservation. Photo by Janice Glime.

Figure 53. ***Physcomitrella patens***, a disturbed habitat soil moss that survives when treated with ABA and proline prior to cryopreservation. Photo by Janice Glime.

In a study of a desiccation-tolerant, a non-desiccation tolerant, and an intermediate-tolerant bryophyte, Burch verified this expectation (Figure 54Figure 57). Burch tested a protocol in which the moss protonemata were cultured on sucrose-free 1/2 strength MS medium (Murashige & Skoog 1962), *p*H 5.8, solidified with 3.5 g L^{-1} Gelrite®. These were cultured in 5 cm Petri plates sealed with Micropore® tape and maintained at 20±2°C with 16:8 hour light:dark cycle. Light was provided by Growlux® and cool white fluorescent tubes (22-29 µmol m^{-2} s^{-1}). After sufficient cultured material developed, the protonemata were air dried for 18 days with half the cultures encapsulated and half not. The **encapsulation** process started with a double thickness sterile filter paper cut into 0.5x1.5 cm strips placed into sucrose-free 1/2 MS, 3% sodium alginate (from Sigma) encapsulation medium. This medium was solidified using 100 mM calcium chloride solution. The two pieces of filter paper were separated so that one side was coated in alginate. 2-4 mm diameter circles of protonemata were embedded in the alginate, re-immersed in 3% sodium alginate, and set again using 100 mM calcium chloride solution (Wilkinson *et al*. 1998). Each strip of filter paper had only one sample protonemata, and each strip was placed separately in a 5 cm Petri plate. An equal number of samples was cultured the same way, but without the encapsulation procedure. When these were transferred onto fresh control media, and little difference was visible between the cultures. After 18 days of dehydration in empty Petri plates sealed with Micropore® tape, they were again tested for viability. The three species exhibited 100% survival of the desiccation-tolerant species, 40% for the intermediate species, and 0% survival for the desiccation-intolerant species. After 18 days, one strip was placed in each cryovial and immersed directly into liquid nitrogen, cooling rapidly to -196°C. After 20 hours of cryopreservation, the protonemata were warmed rapidly by immersing the vials in a 40°C water bath for two minutes. The thawed samples were transferred once again to 12 MS medium and returned to the original cultural conditions. This procedure indicated that encapsulation did little to affect the survival of cryopreservation in these species. Hence, Burch concluded that for desiccation-tolerant species, pretreatment may be unnecessary.

Figure 54. ***Bryum rubens***, a desiccation-tolerant bryophyte that survives dehydration and cryopreservation. Photo by Michael Lüth, with permission.

Figure 55. ***Ditrichum cornubicum***, a bryophyte with intermediate desiccation tolerance that has partial survival following dehydration and freezing. Photo by Des Callaghan, with permission.

Figure 56. ***Cyclodictyon laetevirens***, a bryophyte that lacks desiccation tolerance and that has no survival following dehydration and freezing. Photo by Sean Edwards.

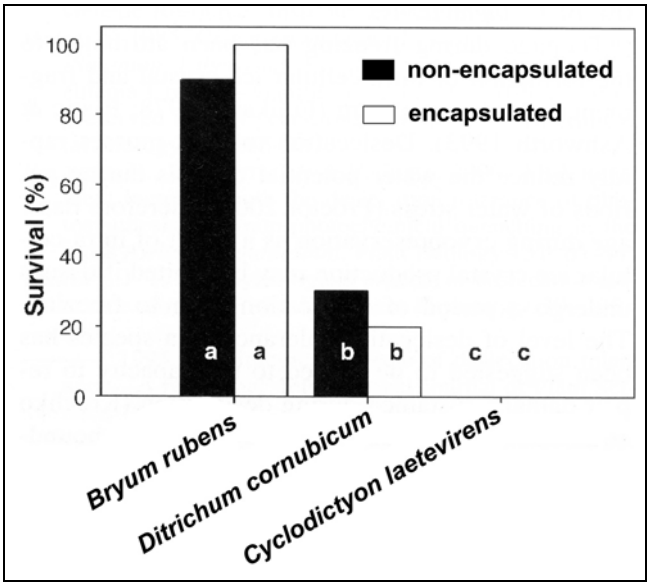


Figure 57. Comparison the effects of encapsulation in alginate on survival in a desiccation-tolerant (***Bryum rubens***), an intermediate-tolerant (***Ditrichum cornubicum***), and an intolerant (***Cyclodictyon laetevirens***) bryophyte species. Bars with the same letter are not significantly different from each other ($\alpha = 0.05$). Redrawn from Burch 2003.

Pence (1998) developed a protocol similar to that of Burch (2003), testing three liverworts and one moss. The thallose aquatic ***Riccia fluitans*** (Figure 36) was sensitive to desiccation and required either abscisic acid (ABA) pretreatment or encapsulation in alginate beads with 0.75 M sucrose to achieve 100% survival of drying. ABA had little effect on the leafy liverwort ***Plagiochila*** sp. (Figure 58); it survived with simply drying, encapsulation, and liquid N exposure. The thallose liverwort ***Marchantia polymorpha*** (Figure 59) required both ABA and encapsulation. Hence, ABA was needed as pretreatment for both thallose species to avoid total mortality upon drying. Rowntree and Ramsay (2009) reported that pretreatment methods, including ABA and encapsulation, were successful for 22 species of bryophytes having a broad range of moisture and other ecological requirements. Some species had 100% survival, and overall regeneration rates were more than 68% for all species tested.

Figure 58. ***Plagiochila asplenioides***, member of a genus for which ABA had little effect on survival of cryopreservation. Photo by Dick Haaksma.

Duckett *et al*. (2004) suggest ways of streamlining the cryogenic process. Spores, gemmae, and vegetative fragments can be surface sterilized and grown in Petri plates on media with inorganic salts. Phytogel or Gelrite are preferable to most traditional agars because these are often toxic due to impurities. And some bryophytes benefit from dilution of nutrients. Spore availability can be extended by storing ripe capsules at 4°C. Temperatures >25°C can cause excess respiration and reduce the health of the propagule/culture; light intensity should be much lower than that in nature to prolong the culture viability.

Figure 59. ***Marchantia polymorpha***, a thallose liverwort species that requires both ABA and encapsulation before cryopreservation. Photo by Jan-Peter Frahm.

Bryophytes such as ***Ditrichum plumbicola*** that produce specialized propagules may be easier to preserve through desiccation and cryopreservation (Rowntree *et al*. 2007). Some species cultured in preparation for cryopreservation will produce protonemal gemmae hitherto unknown in nature (***Ditrichum cornubicum***, ***Saelania glaucescens***, ***Seligeria camiolica***, and ***Zygodon gracilis***) (Duckett *et al*. 2004). Protonemal gemmae suspensions are an ideal way to re-introduce these species to the natural environment.

Ditrichum plumbicola protonemata exhibited unexpectedly low survival of cryopreservation (Rowntree *et al*. 2007). Rowntree *et al*. (2007) found that pretreatment of ***Ditrichum plumbicola*** protonemata with ABA and sucrose caused protonemal growth to be arrested and propagules induced. Most protonemal cells died, but those that survived were char by thick, deeply pigmented walls, numerous small vacuoles, and lipid droplets in their cytoplasm. The protonemal propagules were highly

desiccation- and cryopreservation-tolerant, behaving like the desiccation tolerant rhizoids in the natural environment where they are induced by extreme conditions.

Not all mosses need to be cultured as protonemata to preserve well. Schulte and Reski (2004) used fresh plants to preserve 140,000 mutants by cryopreservation (Figure 60-Figure 61). They used a combination of several of the pre-treatment techniques described above, but with some additions. They used a complete Knop medium (Egener *et al*. 2002), amended with 920 mg L^{-1} ammonium tartrate, 87 g L^{-1} mannitol (Grimsley & Withers 1983), 10 µM ABA dissolved in DMSO (dimethyl sulfoxide), and 100 mM proline (Christianson 1998). The liquid medium was filter sterilized; the solid medium was supplemented with 1.2$ (w/v) agar. Macro- and microelements, $FeSO_4$ x $7H_2O$, glucose, and mannitol were autoclaved. The other supplements were filter-sterilized with a 0.22 µm millipore filter and added to the medium after it was autoclaved. The medium *p*H was adjusted to 5.8 before autoclaving and before filter sterilizing.

Figure 60. Cryopreservation equipment in Ralf Reski's IMSC lab <http://www.moss-stock-center.org/>. Photo by Ralf Reski.

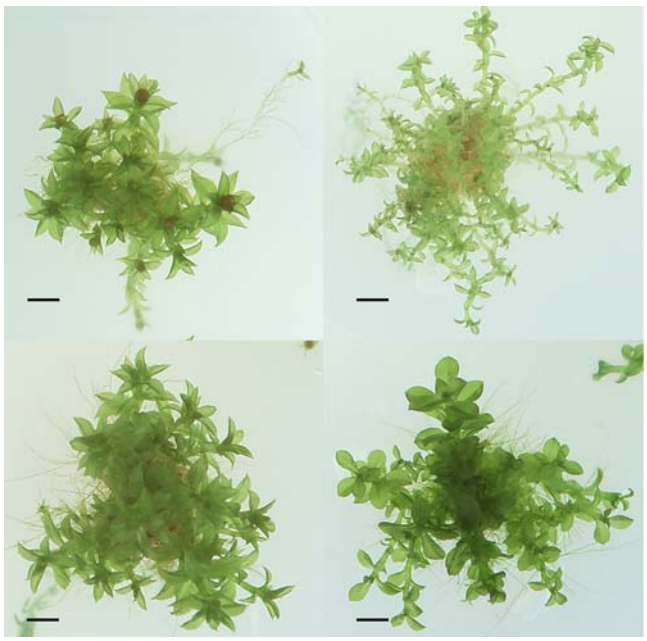


Figure 61. Four ecotypes of ***Physcomitrella patens*** in culture in Ralf Reski's IMSC lab <http://www.moss-stock-center.org/>. Photo by Ralf Reski.

When You Depart – Willing Your Herbarium

Your personal herbarium is valuable, but non-botanists might not recognize its value (Miller 1988). Therefore, it is wise to be sure you have either included it in your will or your heirs understand its value and where it should go. Since herbaria will not always be willing to accept collections, it is wise to make arrangements with the receiving herbarium so you know they will accept your specimens. It is the responsibility of the receiving herbarium to let the bryological community know that they have received your herbarium. If your herbarium is a personal herbarium and is duplicated elsewhere, consider giving it to an exchange program or to a struggling bryologist where the herbarium is inadequate. And be sure provisions are made for return of any specimens you might have on loan.

Exchange Programs

Several of the bryological societies sponsor bryophyte exchange programs. For example, the ABLS (American Bryological and Lichenological Society) program has separate liverwort and moss exchanges. To join the program, one needs to send several species with five duplicates to the current appropriate director of exchange. For each specimen you send, you can select a species from the next exchange list. Hence, if you send six species with five specimens of each, you are eligible to receive 30 specimens from among the forthcoming lists. Specimens contributed must be of adequate size, typically palm size, but this depends on the abundance and size of the species. Sending rare species for exchange should be avoided. The packets must have complete label information, as discussed earlier in this chapter.

Borrowing Specimens

Funk (2007), US National Herbarium, has provided a good introduction into the many uses of a herbarium <http://www.virtualherbarium.org/vh/100UsesASPT.html> . Top among these uses for ecologists is to compare your specimens with those of others to verify your identification.

If you are not near with a large herbarium, it may be necessary to borrow specimens to verify your identifications. There is an etiquette for borrowing and asking in the right way is more likely to get you the specimens you need. Visit the New York Botanical Garden website for instructions on how to borrow specimens <http://sciweb.nybg.org/science2/herb/tips.asp.html>.

Type Specimens

You should only borrow type specimens when non-types will not do. This would include revisions of a genus or species when you must verify the original description. Type specimens must be handled with utmost care and returned to the loaning herbarium quickly. This method of verification may change somewhat as our use of molecular identification becomes more common and a larger database is available.

The first problem in borrowing a type specimen is to locate it. Generally there are multiple paratypes placed in multiple herbaria, but there is only one holotype. The location of the holotype can be determined by checking the Index Herbariorum <http://sciweb.nybg.org/science2/hcol/bryotypes/index.asp.html>. Index Herbariorum provides the physical location of a herbarium, its web address, holdings (number and type of specimens), history, staff, areas of expertise of associated staff, and contact information. Only permanent collections with active management and accessibility to scientists are included.

When using Index Herbariorum, you can locate herbarium personnel by entering the person's name on the Text Search page. For example, when I entered "Deguchi," it provided me Person: Hironori Deguchi; Herbarium Acronym: HIRO; Institution: Hiroshima University; Location: Japan, Hiroshima; Research Pursuits: Taxonomy; morphology; and ecology of bryophytes.

To locate a herbarium where a type specimen is housed, one can use the Virtual Herbarium for Bryophytes and visit the Type Specimen Catalog.

Always return type specimens as quickly as possible by a method that insures they won't get lost.

Summary

Most bryophytes are stored in packets folded in thirds of a standard sheet of 100% rag paper. It is easy to make your own packet folding machine. Labels can be designed on a word processor or produced by a herbarium label program. Labels need to include **name of species**, **author** of the scientific name, **altitude**, **habitat**, **substrate**, **date** of collection, **location** (country, state, county, distance to nearest town), **GPS** coordinates, name of **collector**, **collection number**, and **determiner** (name of person identifying or verifying identification). Once they are placed into the herbarium collection, an accession number should be added. Packets with multiple species should indicate so; methods of storing and labelling depend on the purpose of the collection. Storage cabinets need to protect from pests but usually do not require moth balls. Keeping specimens dry is most important.

Herbaria have preferences for specimen storage, including boxes, drawers, folders, and herbarium sheets. Cool preservation works best, but is expensive. Minute species and special structures may require liquid preservation or minipackets. Arrangement in the herbarium may be alphabetical (for ease of filing) or phylogenetic (useful for systematic studies). Type specimens are usually indicated by red folders, but other marks of red can be used.

Killing inhabitants and soil pathogens is necessary for new collections, whether fresh from the field or obtained from another herbarium. This can be accomplished by Agral 600, moth balls, microwave, freezing, steam, insect traps, moisture control, or drowning.

A herbarium should be equipped with both dissecting and compound microscopes and equipment named in Chapter 2-1. Its workspace should include good taxonomic references, and it helps to add indexing tabs. A computer station is useful for entering data, using online keys, updating nomenclature, making dot maps, and finding images, as well as making herbarium labels.

When shipping specimens to other countries, be sure you know and comply with pertaining laws. Most prohibit soil. Be sure the recipient knows they are coming, and whenever possible, ship to a herbarium where the recipient can receive them. There are many acts of courtesy that can help when you ask others to identify your specimens. Posting pictures online to ask for identification help should include as much information as possible, show habit, plant, leaf, and cross sections, and be kept small so as not to clog inboxes or be slow in loading. Be sure you have permission to post pictures that are not yours.

Living culture can maintain rare species and permit testing without decimating the extant populations. Cryopreservation can also maintain the genome for later study and cultivation.

Exchange programs are available through some of the societies, *e.g.* the American Bryological Society, where members of the program can exchange specimens with others in the group to build the diversity in a herbarium.

Herbaria can borrow specimens from each other, but loans to individuals might be refused. Type specimens are more likely to be carefully protected, so you might have to travel to the host herbarium.

Acknowledgments

Dale Kruse kindly sent me a printout of all the emails he received on Bryonet and offline regarding herbarium practices.

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CHAPTER 1-1
AQUATIC AND WET ANTHOCEROTOPHYTA

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CHAPTER 1-1
AQUATIC AND WET ANTHOCEROTOPHYTA

Figure 1. ***Phymatoceros bulbiculosus*** with capsules, a species that can occur in European streams and rivers. Photo by Ken Kellman, through Creative Commons.

Nomenclature for this chapter is based primarily on Söderström *et al*. (2016). In addition, Lars Söderström provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. These unverifiable taxa have been included in the species. Listed synonyms are those I encountered in the aquatic literature and are not complete with all possible synonyms.

To develop this list, I used my own bibliography, collected over the past 56 years, and Google Scholar. These papers soon led me to others. I do not pretend that this is complete. It concentrates on streams, but includes lakes and other wetlands. It deliberately ignores bogs and mostly ignores fens, but nevertheless includes a few of these species because they were found in a wetland study. Bogs and poor fens have been treated in whole books and provide an extensive literature; fens seem somewhat less studied. They would require considerably more review and time. Thus I felt that less-reviewed topics, particularly the aquatic habitats with which I am most familiar, should be given priority. Nevertheless, some of the citations took me into that literature.

Many of the species on this list are not typical wetland or aquatic species. They were, however, found in a wetland or aquatic study. Their relative frequency can be suggested based on the number of references cited.

The **Anthocerotophyta** (hornworts) is a small group when compared to the other two bryophyte phyla. Few of these occur in wet habitats, although some have been reported from mountain streams. Four of the five families have appeared among the studies cited herein.

Anthocerotaceae

Most systematic treatments include only ***Anthoceros*** and ***Folioceros*** in this family, but a number of studies use the name ***Aspiromitus***, a genus that is considered a synonym of ***Anthoceros*** by Söderström *et al*. (2016), but some species have not been studied sufficiently to determine their affinities. These are listed here in ***Aspiromitus*** until their affinities are better understood.

Anthoceros (Figure 2, Figure 5, Figure 6, Figure 7)

The genus ***Anthoceros*** (Figure 2, Figure 5, Figure 6, Figure 7) occurs mostly on **arable** (suitable or used for growing crops) fields (Porley 2020). My own limited experience suggests that it is a non-competitor that benefits from the disturbance and reduction of "weeds" as competitors in such situations. It is perhaps these same factors that permit it to occasionally live in wet habitats.

Anthoceros agrestis (Figure 2)

(syn. = *Anthoceros punctatus* var. *cavernosus*)

Distribution

Anthoceros agrestis (Figure 2) occurs primarily in the temperate zone in central Europe, ranging in northern and eastern Europe as well (Paton 1979), but is rather rare in the Mediterranean-Atlantic parts (www.iucnredlist.org). It grows in arable fields and gardens, or in ditches in open habitats or woodlands (www.iucnredlist.org).

Figure 2. ***Anthoceros agrestis*** with capsules in an area that becomes muddy. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

The only wetland/aquatic study that I found including this species reported it in mountainous streams on Madeira Island, Portugal (Luis *et al*. 2015). ***Anthoceros agrestis*** (Figure 2) is not uncommon, but difficult to find, because both the thallus and sporophytes are short-lived, and tend to occupy ephemeral habitats, such as the still-wet soils of receding rivers and lakes in the spring. In New Brunswick, Canada, it is found on wet soil and humus in boggy habitats (Haughian 2019). Kresáňová (2002) reported it from Slovakia, where it has been under-recorded. Paton (1979) considered it to have a more restricted distribution and ecology than that of ***Anthoceros punctatus*** (Figure 6-Figure 7).

Reproduction

Anthoceros agrestis (Figure 2) is **monoicous** (having male and female reproductive organs on same plant) (Paton (1979). The antheridia may number up to 45 in a chamber. Archegonia are embedded in the thallus and the egg is enclosed within that thallus. Szövényi *et al*. (2015) demonstrated its advantages as a model organism, demonstrating that the plants grew faster when provided with continuous light than when given long-day photoperiods when the light was at or below 300 µE m^2 s^{-1}. In the British Isles, it is a summer annual. Sporophytes (Figure 2) mature July to December. Colonies of ***Nostoc*** sp. (Figure 4) occur in mucilage cavities scattered in the ventral tissue.

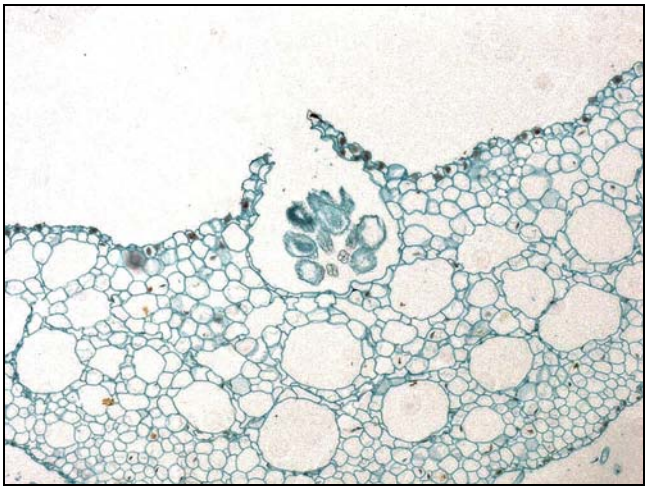

Figure 3. ***Anthoceros*** thallus cs showing large parenchyma cells and pore with ***Nostoc***. Photo from Botany Website, UBC, with permission.

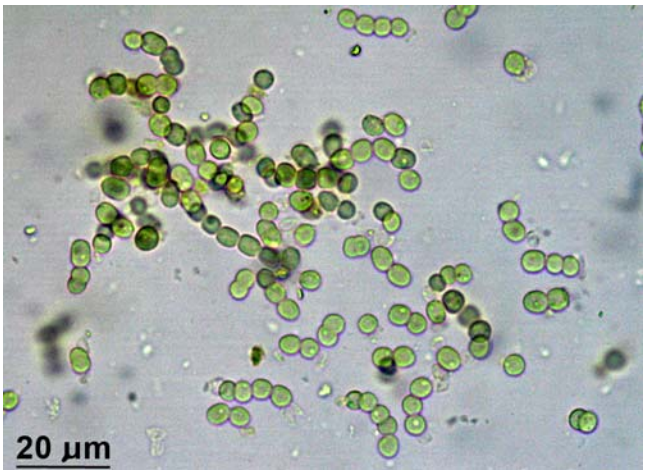

Figure 4. ***Nostoc*** from ***Anthoceros agrestis***. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Biochemistry

Several biochemical studies have used this hornwort as a model organism. These have revealed alkaloids, a number of glutamic acids (Trennheuser *et al*. 1994), and cinnamic acid (accumulated as rosmarinic acid) (Peterson 2003). Soriano *et al*. (2018) considered that rosmarinic acid might aid in UV filtering, but none of the variables they measured seemed to respond significantly to the UV exposures used in the experiments. However, all of them had an increasing trend under the combination of PAR UV-A UV-B radiation.

Anthoceros caucasicus (Figure 5)

Distribution

Anthoceros caucasicus (Figure 5) is European (GBIF 2019), occurring mostly in Macaronesia, with a few localities in the Azores, Portugal, Italy, southern Spain, and the Caucasus (During *et al*. 1996). The only wetland study in which I found this species is that of Luis *et al*. (2015) in mountainous streams on Madeira Island, Portugal. In a broader search on the species, I found that in 1994, it was discovered along a rivulet in The Netherlands (During *et al*. 1996).

Reproduction

It is **dioicous** (having separate male and female plants) in The Netherlands, but **monoicous** elsewhere (During *et al*. 1996). These plants in The Netherlands apparently originated from the large spores that were buried when the site was covered by sand 35 years earlier. The land was unfertilized at the time of discovery. Its general habitat includes rural mosaics with forest, hedges, pastures, and crops, as well as sublittoral sediment (GBIF (2019). In addition, GBIF (2019) reports it from sublittoral sediment, in addition to its presence in rural mosaic habits of woods, hedges, pastures, and cropland.

Figure 5. ***Anthoceros caucasicus***, a stream that sometimes includes streams and rivulets among its habitats. Photo by Rosalina Gabriel, with permission.

Anthoceros punctatus (Figure 6-Figure 7)

Distribution

Anthoceros punctatus (Figure 6-Figure 7) occurs in Europe, Asia, and North and South America (MBG 2020).

Aquatic and Wet Habitats

Anthoceros punctatus (Figure 6-Figure 7) presents near absence in wetland studies; like the previous species, only one of the wetland studies I have reviewed reports this species, likewise from mountainous streams on Madeira Island, Portugal (Luis *et al*. 2015). By contrast, Wagner (2011) reports that in Oregon, USA, it occurs mostly on recently disturbed soil in urban areas and is not common away from towns.

Figure 6. ***Anthoceros punctatus*** with sporophytes, in Madeira, Portugal. Photo by Michael Lüth, with permission.

Figure 7. ***Anthoceros punctatus*** with maturing sporophytes beginning to dehisce. Photo by Malcolm Storey, with online permission.

Role

A well-known symbiosis occurs between members of the **Anthocerotophyta** and **Cyanobacteria**. Campbell and Meeks (1989) found that all ***Nostoc*** (Figure 4) species that

were able to become symbionts in association with ***Anthoceros punctatus*** (Figure 6) formed **hormogonial filaments** (gliding filaments; Figure 8) in great frequency in its presence. The production of hormogonia was induced when ***A. punctatus*** grew in nitrogen-limited culture conditions. These symbiotic filaments lacked **heterocysts** (Figure 6), were mobile, and were comprised of "distinctly" smaller cells than those of "vegetative" filaments. These small cells were the result of continued cell division without biomass increase. During this time of rapid division, nitrogen fixation disappeared and CO_2 fixation decreased by 30%, accompanied by a 40% reduction in NH_4^+ assimilation. These, however, returned to normal rates within 72 to 96 hours after hormogonia induction. Likewise, the hormogonia reverted to their vegetative growth state and differentiated heterocysts. One mutant was able to form chill-resistant akinetes.

Figure 8. ***Nostoc punctiforme***, a **Cyanobacterium** that can be a symbiont in cells of ***Anthoceros punctatus***. The colorless round cell at the lower left is a **heterocyst**. Photo from UTEX, through Creative Commons.

Wong and Meeks (2002) examined the ability of non-heterocystic strains of the **Cyanobacterium** ***Nostoc punctiforme*** (Figure 8) to form a symbiotic relationship with ***Anthoceros punctatus***. With ammonium deprivation, vegetative cells of another ***N. punctiforme*** mutant randomly lysed, thus forming short filaments (**hormogonia**). These mutants were equally able to infect the hornwort compared to the wild type, but the association did not support the growth of the hornwort.

Fungal Interactions

The symbioses of this species are of interest regarding both its ecology and its evolution. When spores of the **Glomales** fungus ***Claroideoglomus claroideum*** (syn. = *Glomus claroideum*) (**Basidiomycota**; Figure 9) contact the thalli of ***Anthoceros punctatus*** (Figure 6-Figure 7), they develop hyphae that appear within the thallus as branched hyphae (Schüßler 2000). By 45 days in culture, these have formed arbuscules and vesicles. This is the first record of an identified Glomalean arbuscular mycorrhiza-like symbiosis with a bryophyte.

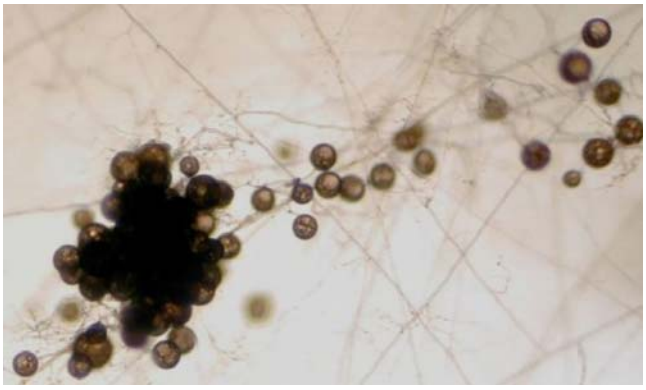

Figure 9. ***Claroideoglomus claroideum***, an endophytic fungus that can occur within cells of ***Anthoceros punctatus***. Photo by V. A. Silvani, M. Pérgola, and S. Fracchia, through Creative Commons.

Aspiromitus (Figure 10)

Most of the members of the genus ***Aspiromitus*** (Figure 10) have been included in the genus ***Anthoceros*** (Figure 2, Figure 5, Figure 6, Figure 7) (Söderström *et al*. 2016). The four listed here have not yet been transferred or synonymized and must therefore still be treated in the genus ***Aspiromitus***. Their apparent limited distribution has left them as neglected taxa. All of them are reported in only one paper on wetlands, that by Ruttner (1955).

Aspiromitus asper

Aspiromitus asper can occur in wetland areas in the tropics (Ruttner 1955). It is reported from Java (Söderström *et al*. 2010). I have been unable to find additional information on its distribution or ecology.

Aspiromitus bullosus

Aspiromitus bullosus can occur in wetlands in the tropics (Ruttner 1955). It likewise has been reported from Java (Söderström *et al*. 2010)

Aspiromitus lobatus (Figure 10)

For ***Aspiromitus lobatus*** (Figure 10) Ruttner (1955) gave the most information, indicating that it occurs above water level, in water spray in the tropics. Söderström *et al*. (2010) reported the species from Java.

Figure 10. ***Aspiromitus lobatus***, a species that can grow in waterfall spray in the tropics. Photo through Creative Commons.

Aspiromitus squamulosus

Ruttner (1955) indicated that ***Aspiromitus squamulosus*** occurs over water in the tropics. Information on this species is so scarce that I am unable to determine where it is known to occur.

Folioceros (Figure 11, Figure 12)

Folioceros (Figure 11, Figure 12) is a tropical and subtropical genus in and near Asia, where it grows on moist rocks, in fallow fields, and near waterfalls (Wikipedia 2019).

Folioceros fuciformis (Figure 11)

(syn. = *Aspiromitus falsinervius*)

Folioceros fuciformis (Figure 11) is often reported in checklists from various tropical locations and countries in Asia (TROPICOS 2020a), but its habitat is not included.

Figure 11. Wet ***Folioceros fuciformis*** with capsules, a species that lives in the zone above the water level in the tropics. Photo by Li Zhang, with permission.

Aquatic and Wet Habitats

The only wetland record I could find was that of Ruttner (1955), indicating that it occurs up to about 30 cm above water level in the tropics. The only labels in the online Consortium of North American Bryophyte Herbaria are from Hawaii, Micronesia (on steep clay and sand bank, associated with *Philonotis revoluta* and *Selaginella* sp.), Guam (abundant on moist clay bank), and India (in dense jungle beside a stream on a moist cliff and in wet soil of marshy area in jungle).

Folioceros glandulosus (Figure 12)

(syn. = *Aspiromitus glandulosus*)

Folioceros glandulosus (Figure 12) is known from waterfalls in the Asian tropics (Ruttner 1955; TROPICOS 2020b). Like ***Folioceros fuciformis*** (Figure 11), little information seems to be published about it.

Figure 12. ***Folioceros cf. glandulosus***, a species that occurs in waterfalls of the Asian tropics. Photo by Li Zhang, with permission.

Dendrocerotaceae

Megaceros (Figure 13)

Of the nine species of ***Megaceros*** (Figure 13) listed by Söderström *et al*. (2016), only two occurred in the wetland studies I reviewed. Both are primarily tropical.

Megaceros flagellaris (Figure 13)

(syn. = *Megaceros salakensis*)

Distribution

Megaceros flagellaris (Figure 13) is widely distributed in the Eastern Hemisphere, especially the tropics, including Angola, China, Japan, India, Sri Lanka, Thailand, Philippines, Borneo, Indonesia, Papua New Guinea, New Caledonia, Samoa, Society Islands, Tahiti, Hawaii, Vanuatu, Australia, New Zealand, and Tanzania (Chantanaorrapint 2014; Ruklani *et al*. 2016).

Figure 13. ***Megaceros flagellaris*** with sporophytes, a species of waterfalls and permanently wet habitats, among others. Photo by Scott Zona, through Creative Commons.

Aquatic and Wet Habitats

Ruttner (1955) reported ***Megaceros flagellaris*** (Figure 13) from waterfalls in the tropics. Cargill *et al*. (2013) considered its typical habitat to be shaded soil, over pebbles, rocks, and boulders, on fallen logs, and at the bases of tree ferns. It is usually in permanently wet habitats such as streambanks or in creeks and streams. In Thailand, Chantanaorrapint (2014) found it on wet rocks and tree logs in shady areas inside the forest. Ruklani *et al*. (2016) found this species on wet rocks and tree logs, in shady areas inside the forest of Sri Lanka.

Reproduction

The species is **monoicous** (Chantanaorrapint 2014). Desirò *et al*. (2013) did not find any colonization of this species by fungi, although some other **Anthocerotophyta** are known to serve as suitable substrates.

Megaceros tjibodensis

The only wetland or aquatic report for ***Megaceros tjibodensis*** is in the listing of Ruttner (1955) for the tropics. None of the online label publications by the Consortium of North American Bryophyte Herbaria includes habitat information except an occasional mention of forest. From these labels, we learn that the species occurs in montane forest in Micronesia and *Myristica* forest of the Caroline Islands. Other locations include Indonesia and Java.

Phymatocerotaceae

Phymatoceros (Figure 1, Figure 14-Figure 16)

Phymatoceros (Figure 1, Figure 14-Figure 16) is the only genus in this family (Söderström *et al*. 2016) and only one of its two species occurred in the aquatic/wetland studies reviewed here.

Phymatoceros bulbiculosus (Figure 1, Figure 14)

(syn. = *Phaeoceros bulbiculosus*)

Distribution

Proskauer (1957) reports ***Phymatoceros bulbiculosus*** (Figure 1, Figure 14) as widespread in the Mediterranean region of Europe and Africa, and it is also present in North and South America.

Aquatic and Wetland Habitats

Phymatoceros bulbiculosus (Figure 1, Figure 14) is the only member of this small family of two species (Söderström 2016) that seems to be reported from any wetland or aquatic habitat. Ferreira *et al*. (2008) reported it from rivers. Luis *et al*. (2015) found it in mountain streams on Madeira Island, Portugal.

Distribution and Wet Habitats

It occurs on shaded soils in slow-to-dry or summer-dry habitats (Doyle & Stotler 2006). These include hillsides, creek banks, road and trail banks, and margins of sloping meadows. Kresáňová (2002) reported the species as agricolous in Slovakia, but protected (red-listed), suggesting that it might be under-recorded.

Figure 14. ***Phymatoceros bulbiculosus***, a species that can occur in rivers and mountain streams. Photo by David Wagner, with permission.

Reproduction

The species is **ephemeral** (short-lived), appearing in open sites during the rainy season and producing abundant tubers (Figure 15-Figure 16) (Stotler *et al*. 2005) that presumably permit its survival when in a dormant state resulting from insufficient water.

This perennial species is distinguished from the other species of ***Phymatoceros*** by the presence of stalked tubers on the ventral thallus surface (Figure 15-Figure 16) (Doyle & Stotler 2006). In some cases, the population consists entirely of only males or only females, persisting through these tubers.

Figure 15. ***Phymatoceros bulbiculosus*** showing numerous ventral tubers. Photo by Donna Pomeroy, through Creative Commons.

Figure 16. ***Phymatoceros bulbiculosus*** with young tubers. Photo by David Wagner, with permission.

Notothyladaceae

Phaeoceros (Figure 18-Figure 21)

This genus has 34 species recognized by Söderström *et al*. (2016). Of these, only two have been reported among the aquatic/wetland species reported here.

Ridgeway (1967a) described the ***Nostoc*** (Figure 17) relationship in the genus ***Phaeoceros***. The ***Nostoc*** enters the thalloid cavities and produces typical globose **endophytic** (occurring within plant tissues) colonies. In this event, or when the ***Nostoc*** is cultured on a nitrogen-free substrate, but in intimate contact with the ***Phaeoceros*** thalli, **chlorosis** (abnormal reduction of green color in plant tissues) did not occur to the degree that it occurred in control cultures. Ridgeway considered this evidence that the ***Nostoc*** fixed nitrogen that was available to the hornworts. He also suggested that ***Nostoc*** might benefit if it could catabolize the carbohydrate components of the mucilaginous thalloid cavity.

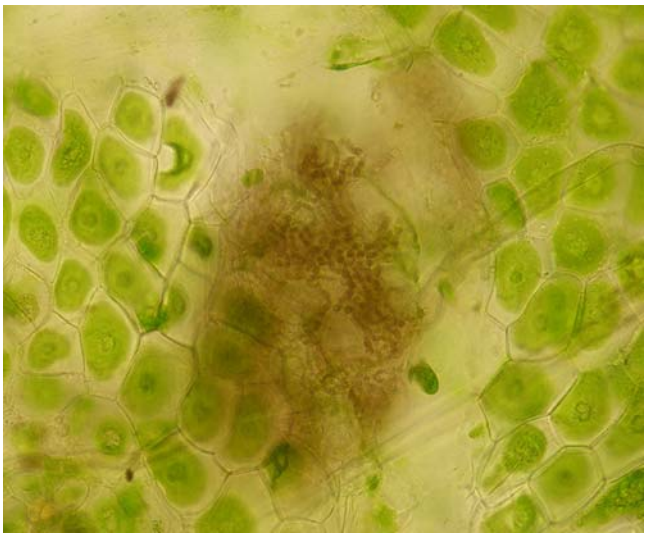

Figure 17. ***Nostoc*** (brown) in hornwort. Note the strings of round cells that form the hormogonia. Photo by Chris Lobban, with permission.

Phaeoceros carolinianus (Figure 18)

(syn. = *Anthoceros carolinianus*, *Anthoceros laevis* var. *carolinianus*, *Phaeoceros laevis* var. *carolinianus*)

Phaeoceros carolinianus (Figure 18) is a worldwide, ubiquitous species (Campbell & Outred 1995; Cargill & Fuhrer 2008). It was reported in only one wetland aquatic study included here; Ferreira *et al*. (2008) reported it from rivers. It is known in Australia from banks of waterways, as well as more terrestrial locations. This is the most common of the ***Phaeoceros*** species in New Zealand (Campbell & Outred 1995).

Figure 18. ***Phaeoceros carolinianus*** with capsules, a species for which wet habitats include rivers and stream banks. Photo by Hermann Schachner, through Creative Commons.

Reproduction

This is a **monoicous** species (Cargill & Fuhrer 2008). Penjor *et al*. (2016) reported that no tubers were present on this species at Coi Suthep, Chiang Mai, Thailand, despite their widespread occurrence among hornworts as a means of surviving unfavorable conditions. They suggested that the habitat might not be suitable for their formation. The **antheridia** (Figure 19) follow the typical pattern of green when young, turning yellow-orange at maturity. This color change results from the loss of green chlorophyll due to conversion of chloroplasts to chromoplasts in the antheridial cells. The genus is characterized by yellow spores with spines (Figure 20). In their study in Thailand, Penjor *et al*. (2016) found that the sporophyte tissue can continue spore production throughout the growing season.

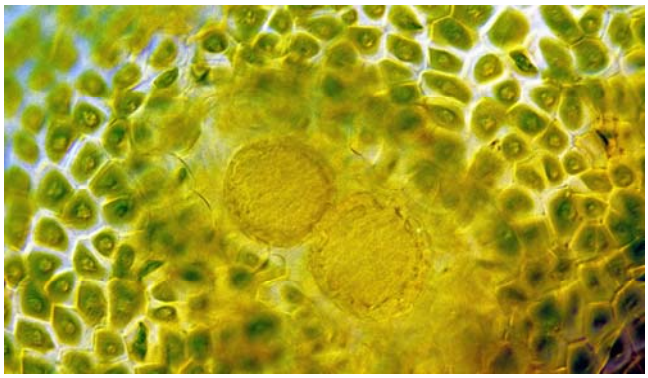

Figure 19. ***Phaeoceros*** antheridia in their yellow-orange mature stage. Photo by George Shepherd, through Creative Commons.

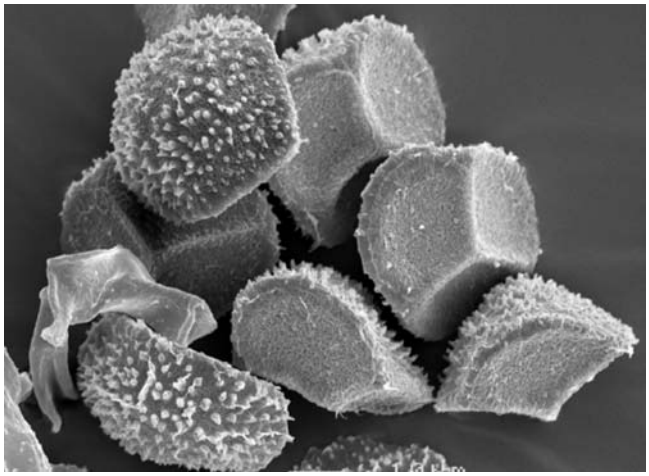

Figure 20. ***Phaeoceros carolinianus*** spores SEM. Photo by Christine Cargill, through Creative Commons.

Phaeoceros laevis (Figure 21)

Distribution

(syn. = *Anthoceros laevis*)

Phaeoceros laevis (Figure 21) is cosmopolitan, occurring in North America, South America, Europe, and Asia, but avoiding more northern locations above 60º N latitude (Schuster 1992). It has been reported from South Island, New Zealand, but the Southern Hemisphere records should be viewed with caution, as they are probably all misidentified ***Phaeoceros carolinianus*** (Figure 18) (Cargill & Fuhrer 2008).

Aquatic and Wet Habitats

Phaeoceros laevis (Figure 21) occurs on moist rock surfaces or springy banks of ravines in Connecticut, USA (Nichols 1916). Watson (1919) reported that it occurs on ground associated with fast water. In South Island, New Zealand, plants so-named are positively correlated with bankfull discharge in 48 streams (Suran & Duncan 1999). It survives in steep streams in the high rainfall area of South Island, New Zealand (Lepp 2012). For ***Phaeoceros laevis*** there was little or no difference in drag forces between bare rocks and hornwort-bearing rocks (Lepp 2012). ***Phaeoceros laevis*** can be found in rivers (Ferreira *et al*. 2008); and occurs in mountainous streams in Madeira Island, Portugal (Luis *et al.* 2015).

Figure 21. ***Phaeoceros laevis*** with sporophytes, a Northern Hemisphere hornwort that occurs in rivers, streams, and on wet soil. Photo by David Holyoak, with permission.

This species is common in areas that have abundant moisture, including moist soil in fields, sides of ditches and streams, and is sometimes even submerged (Isaac 1941).

Reproduction

One of the earliest reports of ***Phaeoceros laevis*** (Figure 21) is that it can be **aposporous** (producing 2*n* gametophytes from sporophyte tissue with no meiosis) (Lang 1901). It is dioicous (Cargill & Fuhrer 2008) and behaves as a short-day plant for antheridial initiation, but requires no critical temperature for initiation (Ridgeway 1967b). It grows well and forms gametangia at both 10ºC and 21ºC under **short-day** (occurring only after being exposed to light periods shorter than a critical length, as in early spring or fall) conditions, whereas liverworts and mosses in the same experiment were more specific in their requirements (Benson-Evans 1964).

Fungal Interactions

In addition to ***Nostoc*** (Figure 17) symbionts, Ligrone (1988) identified an aseptate fungus living as an endophyte in ***Phaeoceros laevis*** (Figure 21). This fungus forms **extracellular** (on outside of cell) thick-walled hyphae, **intercellular** (between cells) thin-walled hyphae, and **intracellular** (within cells) **arbuscules** (treelike growth of filaments in certain mycorrhizal fungi). **Vesicles** (swollen end cells, thought to be storage organs for food reserves in fungi) can be formed by either inter or intracellular hyphae that swell. These are common in summer. The fungus colonizes the host parenchyma, but is absent at the growing apices and epidermal cells. The infected cells of the hornwort increase their cytoplasmic contents while the chloroplast loses starch and its **pyrenoid** (protein body in chloroplasts of algae and hornworts, involved in carbon fixation and starch formation and storage). The arbuscule forms numerous convoluted branches intermingled with the **arbuscular hyphae** (Figure 22-Figure 23). Eventually the arbuscule degenerates, leaving intracellular clumps of collapsed hyphae. These hornwort cells can become re-infected. Ligrone and Lopes (1989) reported that in some strains of this hornwort **sessile** (unstalked) or shortly stalked tubers can form near the growing points or on the ventral surface.

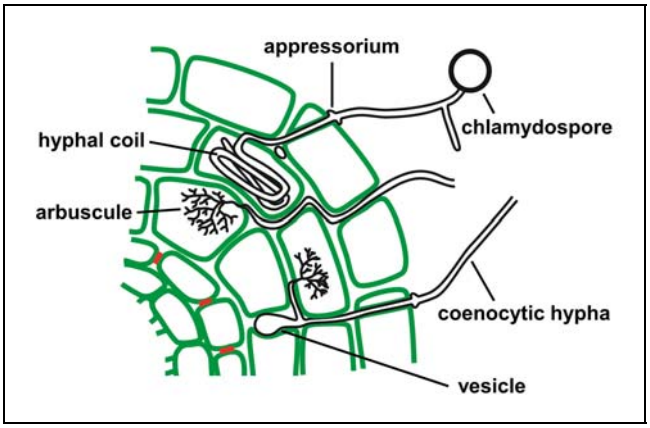

Figure 22. Diagram of arbuscular mycorrhiza, **Glomeromycota**, in a root. Diagram by M. Piepenbring, through Creative Commons.

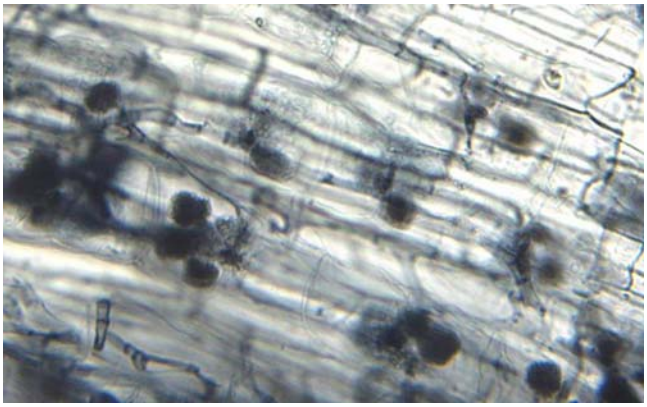

Figure 23. Arbuscular mycorrhizae in root cells. Photo by M. S. Turmel, through public domain.

Summary

Four families of hornworts have members that are associated with aquatic or wetland habitats. These representatives are rarely submersed. Some have Cyanobacteria partners that aid by producing usable nitrogen through nitrogen fixation. Others have associated fungi, but their role requires further investigation.

Anthoceros agrestis, ***Anthoceros caucasicus***, ***Anthoceros punctatus***, ***Megaceros flagellaris***, ***Phymatoceros bulbiculosus***, and ***Phaeoceros laevis*** occur in streams, especially mountain streams.

Acknowledgments

I appreciate Lars Söderström, who helped me find the current acceptable names for a number of older taxa. Thank you to all those who have put their images in Creative Commons or given me permission to use them. Llo Stark has contributed by noting minor errors in the chapter.

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CHAPTER 1-2
AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES: CEPHALOZIINEAE 1

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CHAPTER 1-2
AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA, ORDER JUNGERMANNIALES: CEPHALOZIINEAE 1

Figure 1. Alpine tundra lake, late snowbeds, and small streams where some members of the **Cephaloziineae** may take advantage of the longer availability of moisture. Photo courtesy of Bob Janke.

Nomenclature for the liverwort subchapters is based on Söderström *et al*. (2016). In addition, Lars Söderström provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. These unverifiable taxa have been included in the species.

As in the subchapter on **Anthocerotophyta**, I used my own bibliography, collected over the past 56 years, and Google Scholar. These papers soon led me to others. I searched in Google Scholar for additional information on the species in that constructed list. I do not pretend that this is complete. It concentrates on streams, but includes lakes and other wetlands. It deliberately ignores bogs and mostly ignores fens, but nevertheless includes a few of these species because they were found in one or more other wetland studies. Bogs and poor fens have been treated in whole books and provide an extensive literature; fens seem somewhat less studied. They would require considerably more review and time. Thus I felt that less-reviewed topics, particularly the stream habitats with which I am most familiar, should be given priority.

I have thus far found no records of **Haplomitriopsida** in these studies. Hence I have not included that class in this chapter. Söderström *et al*. (2016) list 5 suborders in the order **Jungermanniales** of the **Jungermanniopsida**. This subchapter includes the suborder **Cephaloziineae**. In that suborder, most of the species outside the **Scapaniaceae** are only marginally associated with water. Although many of the species in the **Cephaloziineae** are not typical wetland or aquatic species, those included here were, nevertheless, found in a wetland or aquatic study. Their relative frequency can be noted based on the number of references cited.

The human propensity for trying to pigeon-hole members of a continuum is no more obvious anywhere than it is among "aquatic" bryophytes. Not only do they not pigeon-hole into neat habitat categories, the species tend to have wide physiological and at least some morphological variance, causing them to be named as multiple species when they are in fact environmental variations of one species. I have included the synonyms that I found in the aquatic literature, but many additional ones often exist.

Adelanthaceae

Only two members of this family appeared in my search for wetland and aquatic studies. These both occur in tropical regions where few studies are available regarding their ecology.

Cuspidatula flexicaulis (see Figure 3)

(syn. = *Jamesoniella balansae*, *Jamesoniella flexicaulis*, *Jamesoniella affinis* fo. *minor*)

Distribution and Wet Habitats

Cuspidatula flexicaulis (see Figure 2-Figure 3) is distributed in Malaysia, Indonesia, Papua New Guinea, and New Caledonia (GBIF 2020a). Ruttner (1955) listed it among the wetland and aquatic species in the tropics. In New Zealand it is an abundant species in subalpine forests (Scott 1970).

Figure 2. ***Cuspidatula monodon***; ***Cuspidatula flexicaulis*** is a species that sometimes occurs in wetlands. Photo by David Tng, with permission

Figure 3. ***Cuspidatula monodon***; ***Cuspidatula flexicaulis*** is a species that sometimes occurs in wetlands. Photo by David Tng, with permission.

Syzygiella sonderi (Figure 4)

(syn. = *Cryptochila grandiflora*)

Distribution

Syzygiella sonderi (Figure 4) is a widespread species, occurring in the Southern Hemisphere, including high elevations in the Neotropics (southeastern Brazil, tropical Andes, and Central America) (Gradstein & da Costa 2016). In the Eastern hemisphere it occurs on Réunion Island in the Mascarenes and in New Guinea and Borneo (Váňa *et al*. 2014).

Figure 4. ***Syzygiella sonderi***, a Southern Hemisphere species that benefits from high water levels of mountain streams. Photo by Juan Larrain, through Creative Commons.

Aquatic and Wet Habitats

In the Andes, Gradstein *et al*. (2018) listed ***Syzygiella sonderi*** (Figure 4) as a submerged liverwort from higher elevation lakes. In the northern maritime Antarctic it occurs on heated ground on volcanic islands. It is positively correlated with bankfull discharge in 48 streams on South Island, New Zealand (Suren & Duncan 1999); Lepp (2012) found it associated with steep streams in high rainfall areas on South Island. Nevertheless, on sub-Antarctic Marion Island this species occurs in **feldmark** (plant community characteristic of sites where plant growth is severely restricted by extremes of cold and exposure to wind, typical of alpine tundra and sub-Antarctic environments) in dry situations, typically associated with other bryophytes. In the Antarctic region, ***Syzygiella sonderi*** occurs on volcanic ash and debris, on rock ledges, and on gravel in protected moist areas (Bednarek-Ochyra *et al*. 2000).

On Marion and Prince Edward Islands, the mire drainage line peats are less acidic, and with higher Ca and Mg concentrations than peats of other mire habitats (Chown & Froneman 2008). On the more mineral soils, ***Syzygiella sonderi*** (Figure 4) is restricted to mire drainage lines, where it is one of the dominant species.

Adaptations

Syzygiella sonderi (Figure 4) has a moderate or low optimum for photosynthetically active radiation (PAR) and low photoinhibition, while also having high photoprotective capability when desiccated, characteristics that are beneficial at high elevations (Tonkie 2016). Nevertheless, it has only moderate photosynthetic capacity with low effective quantum yield and relatively low photoprotective capability. This species achieves its moderate photosynthetic rate at a moderate optimal PAR and has low to moderate response to light at low levels. Photochemistry ceases at moderate to very high **relative water content** [RWC; RWC = ((fresh mass-dry mass)/(saturated mass-dry mass)) × 100]. Nevertheless, it has high ability to recover its photochemistry upon rehydration.

Anastrophyllaceae

Anastrophyllum assimile (Figure 5)

Distribution

Anastrophyllum assimile (Figure 5) is widespread in Asia, Europe, and North America, and extends to Malesia. Known locations include Austria, Switzerland, Italy, Norway, Alaska, Yukon, British Columbia, Labrador, Greenland, Japan, Korea, Borneo, and Papua New Guinea (Schill & Long 2003). It is an alpine species, extending down into the montane *Abies-Rhododendron* forests. In the Upper Bureya River (Russian Far East), where it is rare, it occurs on wet cliffs (Konstantinova *et al*. 2002). In Arctic and alpine areas of North America, this species is associated with **siliceous** (containing or consisting of silica) substrates (Horton 1977).

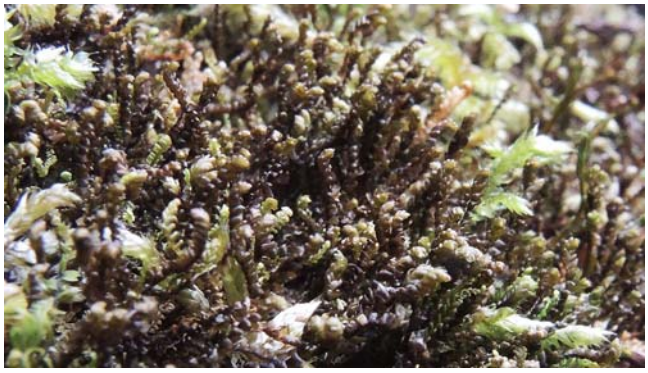

Figure 5. ***Anastrophyllum assimile***, a Northern Hemisphere species that can occur on wet cliffs and submergence areas around lakes and other wet areas. Photo by Kristian Hassel, through Creative Commons.

Aquatic and Wet Habitats

Anastrophyllum assimile (Figure 5) occurs in wet cliff crevices along the shoreline of Takakia Lake, Queen Charlotte Islands, British Columbia, Canada (Hong 2007). It is among the numerous rare species that are vulnerable to changes in lake water level, including also the rare and unusual ***Takakia lepidozioides*** (Figure 6).

In higher altitudes in China and the Himalayas In higher altitudes in China and the Himalayas ***Anastrophyllum assimile*** (Figure 5) occurs on both soil and rocks, including both acidic and calcareous rocks, on open rocky slopes below cliffs, in block screes and boulder fields, on cliffs, on mossy banks, and in wetter habitats including boulders by streams and wet rocks by waterfalls (Schill & Long 2003). In the forest it is usually mixed with other bryophytes and does not grow as an epiphyte. Schill and Long considered it to be tolerant of wetter substrates at high altitudes.

Adaptations

Schofield (1985) describes this species as one that can be quite large, growing in **tall turfs** of more or less erect shoots. These occur predominantly in open sites, forming **mats** of creeping shoots and firmly attached by rhizoids. Mägdefrau (1982) notes that these life forms have good capillary action that permits them to hold "considerable" amounts of water.

Figure 6. ***Takakia lepidozioides*** in wet habitat, a species that occurs in habitats similar to those of ***Anastrophyllum assimile*** along the shoreline of Takakia Lake on the Queen Charlotte Islands. Photo from Botany Website, UBC, with permission.

The leaf color is variable when the liverwort is moist, but when it is dry it is very dark brown, purplish brown, or blackish (Figure 5) (Schill & Long 2003). Herzog (1926) observed that liverworts with dark coloration usually occur in open habitats at higher altitudes where the light is very intense. The dark color is able to protect against these high light levels. In colder seasons, the dark pigments absorb more heat, maintaining a higher temperature in the mat. Capsules are unknown.

Anastrophyllum michauxii (Figure 7)

(syn. = *Sphenolobus michauxii*)

Distribution

Anastrophyllum michauxii (Figure 7) is widely distributed in the Holarctic region (Váňa 1996). It is a montane species that occurs in Europe (Austria, Bulgaria, France, the Czech Republic and Slovakia, Germany, Hungary, the former Yugoslavia, Italy, Romania, Poland, Finland, Sweden, Norway), in Asia (China, Japan), and in a few sites in North America (Dulin & Philippov 2012).

Figure 7. ***Anastrophyllum michauxii***, a Holarctic species that prefers rotten logs, especially near streams and other wet areas. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

On the Soyda River bank in the Russian Federation, Dulin and Philippov (2012) found ***Anastrophyllum michauxii*** (Figure 7) in the fern and herb spruce forest on a rotten spruce log. Choi *et al*. (2012) reported it as occurring near streams on Mt. Jiri-san in Korea. Nichols (1918) found it on wet rock cliffs on Cape Breton Island, Canada. Despite its occasional associations with water, the species seems most commonly to appear on rotten wood (Schuster & Patterson 1957; Dulin & Philippov 2012; Sofronova 2014).

Barbilophozia barbata (Figure 8)

Distribution

Barbilophozia barbata (Figure 8) is widespread in the Northern Hemisphere, especially in the boreal and mountain regions (Düll 2004; Wagner 2009).

Aquatic and Wet Habitats

Wagner described it as a species of terrestrial peaty substrates over rock where it usually occurs with other mosses and liverworts. In the West Carpathians, Mamczarz (1970) found it in rock communities associated with streams near Lacko. Papp *et al*. (2006) reported it from the Iskur River, Bulgaria, and its main tributaries. Düll (2004) reported it from siliceous rocks in Sicily and Erzberger (2002) from Hungary. Cain and Fulford (1948) found it to be common on moist igneous rock cliffs and boulders in Ontario, Canada, where it was often associated with other species of moist habitats, including ***Scapania nemorea*** (Figure 9), ***Lepidozia reptans*** (Figure 9), and ***Ptilidium ciliare*** (Figure 10).

Figure 8. ***Barbilophozia barbata***, a widespread Northern Hemisphere leafy liverwort from boreal and mountain regions, mostly in terrestrial habitats, but sometimes associated with streams. Photo by Hermann Schachner, through Creative Commons.

But it can also be found in wetter habitats. Lee (1944) reported it from a collection near a "little pool" in the low, partially grass-covered, tundra-like valleys of Greenland. Yamada and Iwatsuki (2006) reported it from fine-grained soil along a stream on the western slope of Chamga Mt. in Sakhalin Province, Japan, at 1406 m asl. In mountainous regions and the tundra, ***Barbilophozia barbata*** (Figure 8, Figure 11-Figure 12) can have an important role in ground cover **coenosis** (community of living beings belonging to different species and associated by way of inter-species interdependence or mutualism such as a food chain) (Troeva *et al*. 2010).

Figure 9. ***Lepidozia reptans*** (**small, pinnate liverwort**) and ***Scapania nemorea*** (**several larger leafy branches in lower left quadrant**), species that may accompany ***Barbilophozia barbata***. Photo by Bernd Haynold, through Creative Commons.

Figure 10. ***Ptilidium ciliare***, a species that may accompany ***Barbilophozia barbata*** on moist igneous cliffs. Photo by Hermann Schachner, through Creative Commons.

Figure 11. ***Barbilophozia barbata*** in a patch on a boulder (see arrow). Photo by Sture Hermansson, with online permission.

Reproduction

In their study of propagule banks in boreal old-growth spruce forest in SE Norway, Rydgren and Hestmark (1997) found it among the living vegetation and as propagules in the soil. However, they only achieved ~5% germination from the soil bank propagules. On the other hand, Ross-Davis and Frego (2004) found that the similarity between aerial propagules and the extant flora of bryophytes in New Brunswick, Canada, was greater than the similarity of the buried propagules with the extant flora.

Figure 12. ***Barbilophozia barbata*** ventral side showing rhizoids that help it adhere to rocks. Photo by Hermann Schachner, through Creative Commons.

Biochemistry

There have been a number of biochemical studies on this genus, particularly indicating sesquiterpenes (Anderson *et al*. 1973; König *et al*. 1994; Nagashima *et al*. 1996, 1999; Asakawa 2001). Despite these sesquiterpenes and other substances that can serve as antibiotics, Bidartondo and Duckett (2010) reported the presence of the **Basidiomycota** fungus ***Sebacina*** (Figure 13) in association with ***Barbilophozia barbata*** (Figure 8, Figure 11-Figure 12) collected from Switzerland and the UK.

Figure 13. ***Sebacina incrustans*** on moss, a genus known to occur in association with ***Barbilophozia barbata***. Photo through Creative Commons.

Barbilophozia sudetica (Figure 14-Figure 15)

(syn. = *Lophozia sudetica*)

Figure 14. ***Barbilophozia sudetica***, an arctomontane species sometimes found on wet cliffs and stream banks. Photo by Hugues Tinguy, with permission.

Distribution

Barbilophozia sudetica (Figure 14-Figure 15). ***Barbilophozia sudetica*** is an **arctomontane** (occurring in Arctic habitats and mountain habitats farther south) species that is common in the northern Holarctic, but distribution extends to mountain ranges in East Asia, Spain, and Portugal and even to subtropical islands in Madeira at 32ºN (Bakalin 2004). In North America, Rahill (2018) found it among the tundra vegetation on Mount Washington, NH, USA.

Figure 15. ***Barbilophozia sudetica*** showing a color variant. Photo by Štěpán Koval, with permission.

Aquatic and Wet Habitats

Konstantinova *et al*. (2002) found this species on a wet cliff and soil banks of a small creek of the Upper Bureya River in the Russian Far East. In Iceland, this species occurs on lava fields where the temperature does not exceed 39ºC (Buda *et al*. 2018). In the Aleutian Islands, Alaska, USA, the species is common, forming dark strands overgrowing the tundra ***Sphagnum*** (like Figure 78) and ***Sphagnum*** at the edge of a pond (Talbot *et al*. 2018). It also occurs on the bank of a streamlet, on the slope of a late snow area, on an outcrop face with ***Pohlia*** (Figure 16), in an alpine fellfield, on a old pier, and on damp humus on a cliff shelf.

Figure 16. ***Pohlia wahlenbergii*** with water beads, in a habitat suitable for ***Barbilophozia sudetica***. Photo by Michael Lüth, with permission.

Fungal Interactions

Like ***Barbilophozia barbata*** (Figure 8, Figure 11-Figure 12), ***B. sudetica*** (Figure 14-Figure 15) is known to form symbiotic mycorrhizal fungal associations (Wang & Qiu 2006) with the **Sebacinaceae** (Figure 13) (Kottke *et al*. 2003).

Gymnocolea inflata (Figure 17-Figure 18, Figure 20, Figure 22)

Distribution

Gymnocolea inflata (Figure 17-Figure 18, Figure 20, Figure 22) is distributed in Africa, Europe, northern and southern Asia, and North America (Alaska, Canada, USA) (ITIS 2020a).

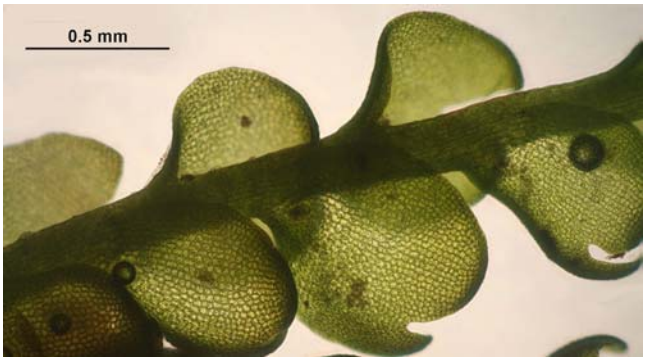

Figure 17. ***Gymnocolea inflata***, a species with widespread distribution that can occur in or out of water. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Gymnocolea inflata (Figure 17-Figure 18, Figure 20, Figure 22) is a **hydroamphibiont** (living in transition zone between water and land, depending on water level; compare to euhydrobiont and geoamphibiont) (Figure 18), occurring in acid water (*p*H 3.5-4.2) in streams of Gory Stolowe Mountains, Poland (Szweykowski 1951). In Europe it often occurs with *Carex goodenoughii*, but is uncommon with ***Eleocharis quinqueflora*** (Figure 76) and ***Paludella squarrosa*** (Figure 19) (Geissler & Selldorf 1986). In streams of the Harz Mountains of Germany it occurs in the upstream reaches (Bley 1987). It also occurs in small lakes in southern Finland (Toivonen & Huttunen 1995).

Figure 18. ***Gymnocolea inflata*** growing in a wet habitat. Photo by Michael Lüth, with permission.

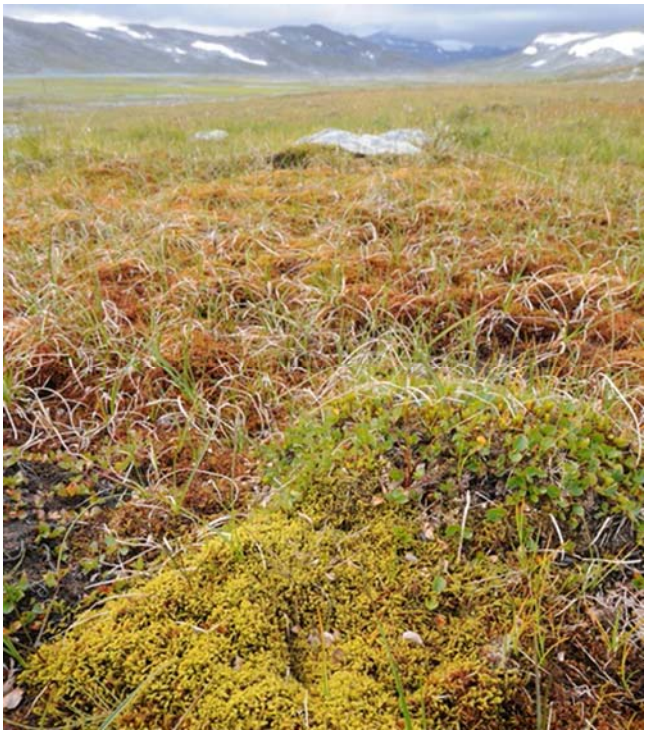

Figure 19. ***Paludella squarrosa*** habitat where ***Gymnocolea inflata*** avoids cohabiting with ***Paludella squarrosa*** and ***Eleocharis quinqueflora***. Photo by J. C. Schou, through Creative Commons.

In the Azores of Portugal, ***Gymnocolea inflata*** (Figure 20) occurs at 860-990 m asl (Schumacker & Gabriel 2002). Its habitat is permanently wet **pseudogley** (gley resulting from temporary or seasonal waterlogging due to poor drainage, rather than from permanent existence of high water table) soil overlain by a thin layer of **moor** (poor soil covered mainly with grass and heather; common in high latitudes and altitudes). The species is relatively common in wet heaths and bogs in Europe. Tyler *et al*. (1973) reported it from the ***Rhynchospora fusca*** (Figure 21) community where it covered the bottom of shallow depressions in heathland between bars.

Figure 20. ***Gymnocolea inflata*** showing one of its dark color forms. Photo by Michael Lüth, with permission.

Watson (1919) reported ***Gymnocolea inflata*** (Figure 17-Figure 18, Figure 20, Figure 22) as form ***laxa*** on peaty sides of fast water streams, on banks with frequent submergence, and submerged in slow water with poor mineral salts.

Figure 21. ***Rhynchospora fusca***, a community that often has ***Gymnocolea inflata*** in heathland low areas. Photo by Peter M. Dziuk, with online permission for educational use.

In Westfalens, northwestern Germany, ***Gymnocolea inflata*** (Figure 17-Figure 18, Figure 20, Figure 22) occurs between ***Sphagnum*** (Figure 22) (Koppe 1945). Tori *et al*. (1993) sampled peat profiles and found ***Gymnocolea inflata*** as part of the liverwort dominance with sparse ***Sphagnum*** cover. In the bare peat layer, only a few sedges occurred – no notable bryophytes. In Cataracts Provincial Park, Newfoundland, Canada, Weber (1976) found ***Gymnocolea inflata*** as a typical bog bryophyte, occupying open areas with a *p*H 3-4. Albinsson (1997) found that ***Gymnocolea inflata*** is among the liverworts that have narrow ecological amplitudes in mire habitats. Other smaller species tend to have wider amplitudes. Albinsson referred to those liverworts that required a habitat formed by other living bryophytes as using a **compromise strategy**. Those liverworts that prefer peat or litter as their substrate are included in the **avoidance strategy**. Albinsson found that those species that occur predominantly with ***Sphagnum*** (Figure 22) include those that are typically sterile, *i.e.*, not forming sexual reproductive structures. Frequently fertile species (*e.g.*, ***Cephalozia*** spp.; Figure 45-Figure 60) tend to occur on peat or litter, rather than on living ***Sphagnum***.

Figure 22. ***Gymnocolea inflata*** in Perrault Fen, Houghton Co., MI, USA, with ***Sphagnum***. Photo by Janice Glime.

Gough *et al*. (2006) found that ***Gymnocolea inflata*** (Figure 17-Figure 18, Figure 20, Figure 22) colonized and covered **ferricrete**-cemented (hard, erosion-resistant layer of sedimentary rock, usually conglomerate or breccia, cemented together by iron oxides) silty alluvial sediments within seeps and streams in undisturbed, highly acidic, metal-rich habitats in east-central Alaska. These liverwort-covered sediments have high concentrations of metals, including Al, As, Cu, Fe, Hg, La, Mn, Pb, and Zn. The ***G. inflata*** thalli here are very small and compact, forming intimate associations with the iron-rich sediments of the seeps and streams. When the liverworts become covered by silt, the thalli grow upward, creating a dense fibrous ferricrete sediment below them. The dominance of ***G. inflata*** causes these areas to appear black. This species dominates both in very damp sites and in areas with flowing water.

Basile and Basile (1980) examined the effects of ammonium ions on form and hydroxyproline content of cell wall proteins in ***Gymnocolea inflata*** (Figure 17-Figure 18, Figure 20, Figure 22). The presence of ammonium ions causes ventral leaves to develop, and the form of lateral leaves and branching pattern change due to a morphoregulatory role. This type of reaction might alter the appearance of this and other liverworts in the field as a result of the available nutrients.

Isopaches bicrenatus (Figure 23-Figure 24)

(syn. = *Lophozia bicrenata*)

Distribution

Isopaches bicrenatus ; Figure 23-Figure 24) is a widespread species in the temperate regions of the Northern Hemisphere (Gradstein *et al*. 2018). But it has appeared in a few widely separated areas, including southeastern Brazil, New Zealand, high elevations (>4000 m asl) in the Andes, Colombia (Gradstein *et al*. 2018), and the Dominican Republic in Central America (Bakalin 2008).

Figure 23. ***Isopaches bicrenatus***, a widespread species in temperate regions where it can occur on river banks, but is often on wood or in wet depressions. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

The habitat of this species includes earthy and gravelly substrates on river banks in the Haute Ardenne rivers of Belgium (Leclercq 1977). It is predominantly a terrestrial liverwort, often in association with other leafy liverworts, often on wood, but can also occur on wet soil in hollows or inundated shrublet-moss spruce forest, making pure patches or occurring with other liverworts (Dulin 2014).

Reproduction

Fulford (1955) described development of ***Isopaches bicrenatus*** (Figure 23-Figure 24). Like the typical liverworts, the spore germinates to produce a thalloid protonema. But under adverse conditions, it can produce a filamentous protonema instead, a phenomenon that has been observed in a number of liverworts. The mature plants produce a number of reddish gemmae (Figure 24) in clusters. These, and leaf fragments that regenerate easily, make reproduction and spread easy for this species.

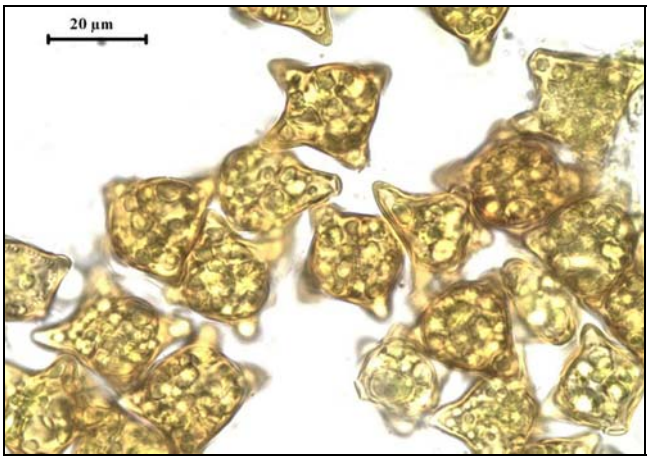

Figure 24. ***Isopaches bicrenatus*** gemmae; these become reddish at maturity. Photo by Hugues Tinguy, with permission.

Rivulariella gemmipara (Figure 25)

(syn. = *Chiloscyphus gemmiparus*)

Rivulariella gemmipara (Figure 25) seems to be a liverwort without a home – or with many homes. Whereas Wagner (2013) moved it from ***Chiloscyphus*** in the **Lophocoleaceae** to ***Rivulariella*** in the **Jungermanniaceae**, Patzak *et al*. (2016) consider its alignment to be with the **Scapaniaceae** *s.l.* Stotler and Crandall-Stotler (2017) argue for its placement in the **Anastrophyllaceae**, a family formerly included within the **Scapaniaceae**.

Distribution

Rivulariella gemmipara (Figure 25) is a subalpine or alpine species that is endemic to western North America (Wagner 2013). It is a species of concern, with only six known locations, those in Alaska, Oregon, California, and Utah, all in the USA.

Figure 25. ***Rivulariella gemmipara*** leaves from upward-growing stem. Photo courtesy of David Wagner.

Aquatic and Wet Habitats

Rivulariella gemmipara (Figure 25) grows in moderately fast water where there are small rocks (small pebbles to fist-sized cobbles) and gravel (Figure 26-Figure 31), avoiding areas with organic debris or muck over the substrate (Wagner 2013). It also avoids areas where the water surface is smooth or where the flow is very rapid. The suitable areas are typically permanent springs that keep the streambed submerged at all times, and that are exposed to sun most of the day, but that seldom have rapid flow due to any runoff. Rocks are its only known substrate. It is often associated with ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 27), ***Chiloscyphus polyanthos*** (Figure 28), and ***Scapania undulata*** (Figure 29).

Figure 26. ***Rivulariella gemmipara*** habitat in springfed stream. Photo courtesy of David Wagner.

Adaptations

Rivulariella gemmipara (Figure 25) lacks rhizoids in adults, but these are produced in germinating gemmae (Evans 1928). Perhaps this is enough to enable attachment, but it is an unusual characteristic for a bryophyte that grows on rocks in flowing water. Its slightly flattened stems are more in line with its habitat.

The species has horizontal, flattened stems (Figure 30) and upright, leafy stems (Wagner 2013). These flattened stems adhere closely to the substrate and lack rhizoids (David Wagner, pers. comm. 3 June 2020). The erect shoots differ distinctly from these pioneering horizontal stems. The latter lack underleaves, but the upright stems produce them, these eventually being as large as the lateral shoot leaves and transversely inserted. When the stone gets overturned, as it does sporadically, the upright leafy stems die and disappear, probably due to abrasion or decomposition, but the flat stems remain tightly adhered to the rocks, leaving blackish tracks (Figure 30, Figure 32). This method of gluing to the substrate seems to be a unique adaptation of this species.

Figure 27. ***Jungermannia exsertifolia*** subsp. ***cordifolia*** from a wet habitat. Photo by Des Callaghan, with permission.

Figure 28. ***Chiloscyphus polyanthos***, a frequent species in siliceous mountain brooks where ***Jungermannia atrovirens*** is able to grow. Photo by Hermann Schachner, through Creative Commons.

Figure 29. ***Scapania undulata***, a species that associates with ***Marsupella aquatica*** on rocks in Maine, USA. Photo by Jan-Peter Frahm, with permission.

Figure 30. ***Rivulariella gemmipara*** flat horizontal stems on rock that was overturned. Photo courtesy of David Wagner.

Figure 31. ***Rivulariella gemmipara*** on pebbles in springfed stream. Photo courtesy of David Wagner.

Reproduction

Rivulariella gemmipara (Figure 25) is **monoicous**, thus facilitating sexual reproduction (Wagner 2013). It has marginal gemmae (Figure 33) on its leaves and these develop rhizoids as they germinate.

Figure 32. ***Rivulariella gemmipara*** on rock showing the upright plants on one side and the tracks of stems on a side that has been buried. Photo courtesy of David Wagner.

Figure 33. ***Rivulariella gemmipara*** leaf with gemmae. Photo courtesy of David Wagner.

Schljakovia kunzeana (Figure 34)

(syn. = *Lophozia kunzeana*, *Orthocaulis kunzeanus*)

Distribution

Schljakovia kunzeana (Figure 34) is widespread as an Arctic-alpine, circumboreal tundra species. It extends southward into the coniferous forest of the Great Lakes and alpine areas of Europe (Schuster 1969).

Figure 34. ***Schljakovia kunzeana*** is a widespread circumboreal species that can be found on some river banks and other wet habitats. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Watson (1919) described ***Schljakovia kunzeana*** (Figure 34) as a liverwort of alpine wet ground associated with fast water. Konstantinova *et al*. (2002) reported it from a boggy valley of a small creek of Upper Bureya River in the Russian Far East. In the Komi Republic of northwestern Russia, it occurs with other leafy liverworts on soil among sedges along the bank of the Ugum River (Dulin 2014). In the Russian Arctic National Park, Fedosov *et al*. (2018) reported that it occurs in willow and moss-dominated communities on smooth terraces, typically accompanied by other leafy liverworts.

Sphenolobus minutus (Figure 35, Figure 38-Figure 41)

(syn. = *Anastrophyllum minutum*)

Distribution

Sphenolobus minutus (Figure 35, Figure 38-Figure 41) is widely distributed in the Holarctic region (Schuster 1969), as well as Madagascar, Mexico, and the Russian Federation (TROPICOS 2020). Other reported locations include Norway, Czech Republic, Nova Scotia, Gaspé Peninsula, and Yukon in Canada, and Japan (Consortium of North American Bryophyte Herbarium 2020).

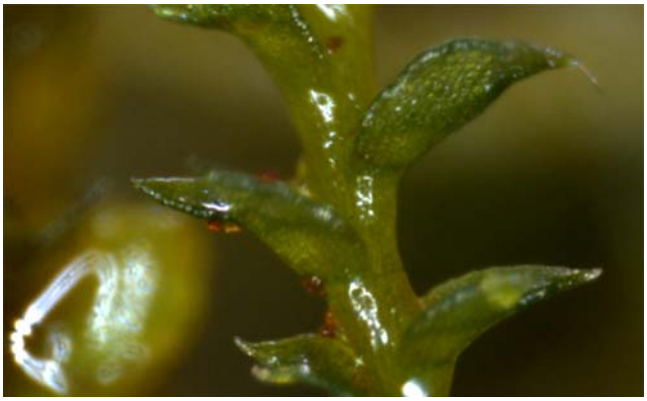

Figure 35. ***Sphenolobus minutus***, a widely distributed Holarctic liverwort that is less common further south except on the mountains; it lives on peaty soil and areas of high moisture, but can become submerged in montane streams. Photo by Jouko Rikkinen, through Creative Commons.

Aquatic and Wet Habitats

In western Canada ***Sphenolobus minutus*** (Figure 35, Figure 38-Figure 41) occurs submerged as a hemicalciphilous species in montane streams and on stream banks (Figure 36) (Vitt *et al*. 1986; Glime & Vitt 1987). In these habitats, it forms mats (Figure 38). It is especially common on peaty soil, but it can also occur on north-facing cliffs where there is little or no seepage but high atmospheric moisture (Schuster 1969). In the flume (Figure 37) at Franconia Notch, New Hampshire, USA it occurred on the flume wall (Glime 1982).

Figure 36. Calcareous stream in BC, Canada, where one might find ***Sphenolobus minutus***. Photo by Janice Glime.

Figure 37. Flume, Franconia Notch, NH, site where one can find ***Sphenolobus minutus*** on the walls. Photo by Janice Glime.

Figure 38. ***Sphenolobus minutus*** forming a mat. Photo by Jouko Rikkinen, through Creative Commons.

Reproduction

Like most of the leafy liverworts, ***Sphenolobus minutus*** (Figure 38) produces gemmae (Figure 39-Figure 41). These provide a means of surviving unfavorable conditions as well as dispersal.

Figure 39. ***Sphenolobus minutus*** with gemmae. Photo by Jouko Rikkinen, through Creative Commons.

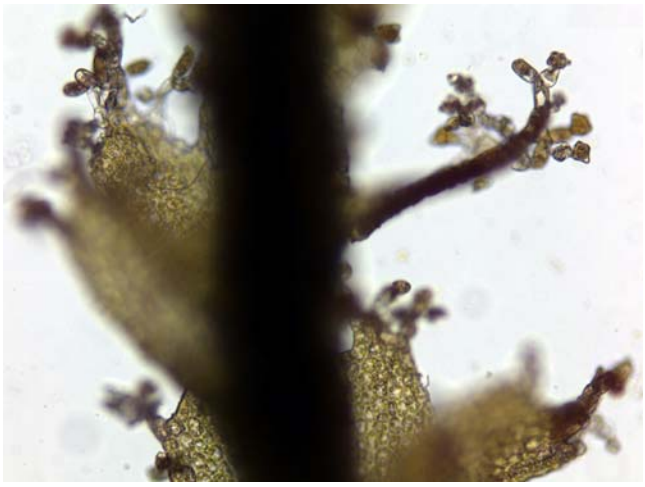

Figure 40. ***Sphenolobus minutus*** with gemmae on leaf tips. Photo by Jouko Rikkinen, through Creative Commons.

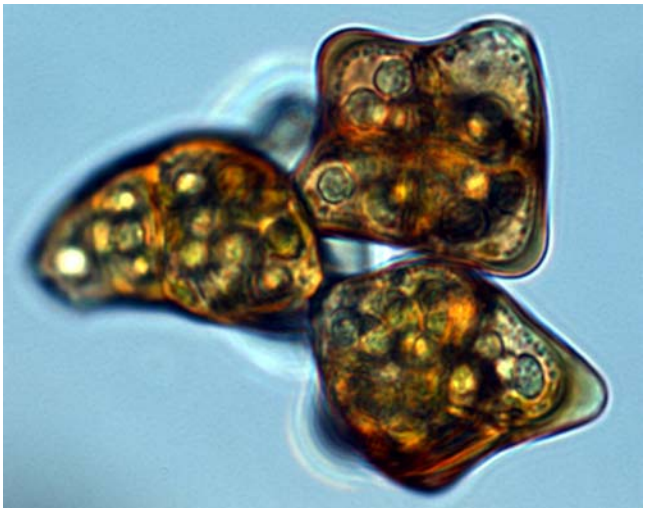

Figure 41. ***Sphenolobus minutus*** gemmae, showing their angular construction. Photo by Jouko Rikkinen, through Creative Commons.

Role

Kitagawa (1974) reported nematode galls (Figure 43-Figure 42) on ***Sphenolobus minutus*** (Figure 35, Figure 38-Figure 41) from Nepal. But other more common interactions seem to be lacking. For example, in their study on mycorrhizae in liverworts, Wang and Qiu (2006) could find no records of mycorrhizae for this species.

Figure 42. Nematode similar to the ones that can form galls on ***Sphenolobus minutus***. Photo by courtesy of Andi Cairns.

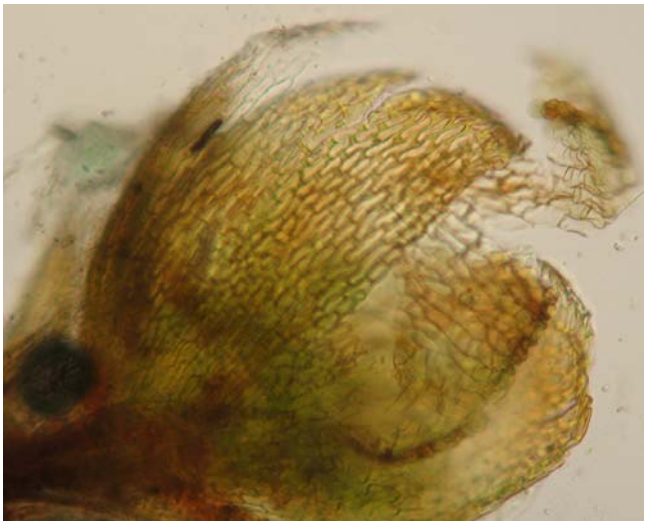

Figure 43. ***Bryum argenteum*** nematode galls, a parasitic attack that also occurs in ***Sphenolobus minutus***. Photo courtesy of Claudio Delgadillo Moya.

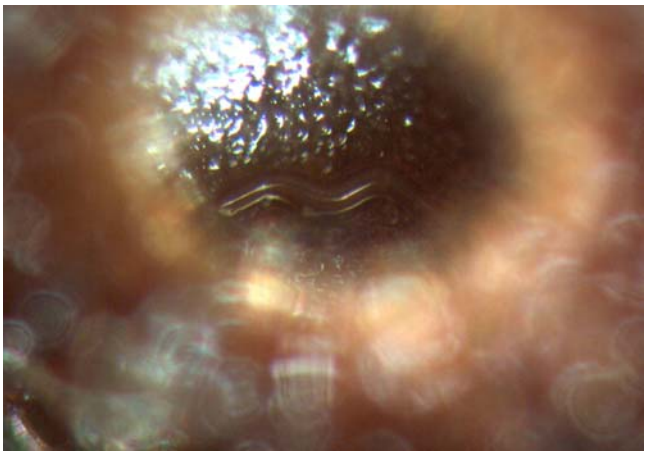

Figure 44. ***Buxbaumia aphylla*** nematode in gall showing nematode. Photo by Misha Ignatov, with permission.

Tetralophozia filiformis

(syn. = *Chandonanthus filiformis*, *Chandonanthus pusillus*)

Distribution

Tetralophozia filiformis has a very disjunctive distribution in Asia, Europe, and North America (Urmi 1983, 2015). Because its collections are widely separated (Japan, Himalayas, and Canada) and more recently in Russia (Konstantinova 2002b), it was originally treated as several species that have since been combined (Laine 1970).

Aquatic and Wet Habitats

In the Cantabrian Mountains of Spain it occurs on sheltered siliceous rocks with oceanic conditions (Urmi 1983). The records seem to be rather limited, but at least one record indicates that it occupies a dripping cliff near a waterfall of the Upper Bureya River in the Russian Far East (Konstantinova *et al*. 2002).

Cephaloziaceae

Cephalozia (Figure 45-Figure 59)

Cephalozia (Figure 45-Figure 59) occurs in small ponds of coastal barrens, Cape Breton Island, Canada (Nichols 1918). Albinsson (1997) found that ***Cephalozia*** species tended to have wider ecological amplitudes in Swedish mires than did the larger liverworts. The ***Cephalozia*** species are frequently fertile and seem to prefer peat and litter rather than living ***Sphagnum*** (like Figure 78) as a substrate, using an **avoidance strategy**.

Cephalozia ambigua (Figure 45-Figure 46)

Distribution

Cephalozia ambigua (Figure 45-Figure 46) is listed for China and Russia in TROPICOS (TROPICOS 2020). Geissler (1976) reported it from the Swiss Alps. Lorenz (1915) listed it for Scandinavia and Ellesmere Island in the Arctic Archipelago. Potemkin and Sofronova (2013) considered ***Cephalozia ambigua*** to be circumpolar, occurring in Arctic, alpine, and subalpine areas. In Europe it extends southward to the French Pyrenees, Spain, and Bulgaria. It extends from southern Polar Deserts to northern Taiga, mountain tundras, and elfin wood areas in the Far East.

Figure 45. ***Cephalozia bicuspidata*** complex; ***C. ambigua*** is a species from China and Russia and high elevations elsewhere in the Northern Hemisphere where it can occur on wet cliffs and lakeshore rocks or peaty soil. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

In the Swiss Alps, ***Cephalozia ambigua*** (Figure 45-Figure 46) occurs in alpine streams (Geissler 1976). In the Upper Bureya River of the Russian Far East, the species occurs on wet cliffs and rocks at the lake shore, often accompanied by other leafy liverworts (Konstantinova *et al*. 2002). It occurs on acid to neutral soil (incl. peaty soil and soil over the rocks) (Potemkin & Sofronova 2013).

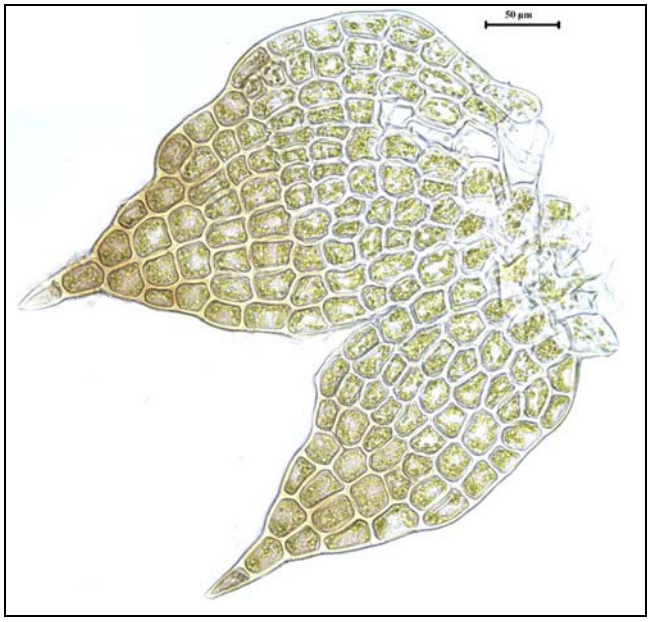

Figure 46. Leaf from ***Cephalozia bicuspidata*** complex. Note the thickened walls of the terminal cells compared to those at the base. Photo by Hugues Tinguy, with permission.

Adaptations

Potemkin and Sofronova (2013) noted that most species of ***Cephalozia*** never develop any secondary pigmentation, thus always occurring as green or whitish green (Figure 45). However, members of the ***Cephalozia bicuspidata*** complex [***C. ambigua*** (Figure 45-Figure 46), ***C. bicuspidata*** (Figure 47, Figure 53-Figure 56, Figure 59, Figure 60), ***C. hamatiloba*** (Figure 48)] from sunlit habitats are typically brown and/or purple. Furthermore, ***C. catenulata*** (Figure 49), ***C. macrostachya*** (Figure 50), ***C. loitlesbergeri*** (Figure 51) and ***Nowellia curvifolia*** (syn. = *Cephalozia curvifolia*; Figure 52) often develop brown pigmentation.

Figure 47. ***Cephalozia bicuspidata*** exhibiting reddish-brown color from exposure to direct sunlight. Photo by Hermann Schachner, through Creative Commons.

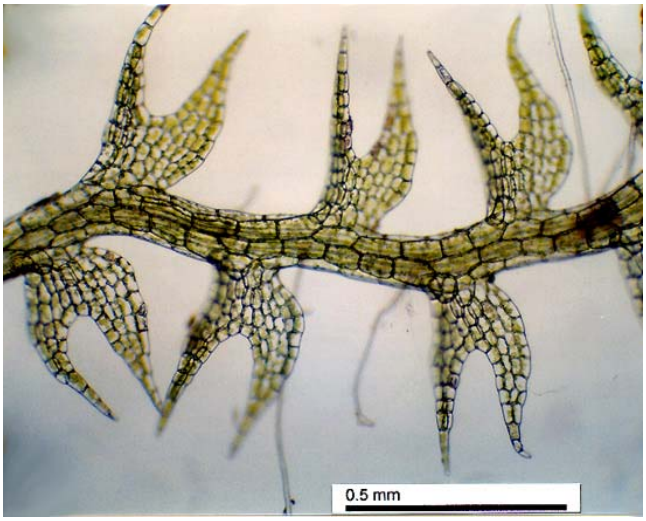

Figure 48. ***Cephalozia hamatiloba***, from the ***C. bicuspidata*** complex, is usually brown or purple in sunlit habitats. Photo by David H. Wagner, with permission.

Figure 49. ***Cephalozia catenulata***, a species that can develop brown pigmentation in direct sunlight. Photo by Michael Lüth, with permission.

Figure 50. ***Cephalozia macrostachya***, a species that can develop brown pigmentation in direct sunlight. Photo by Michael Lüth, with permission.

Figure 51. ***Cephalozia loitlesbergeri***, a species that can develop brown pigmentation in direct sunlight. Photo by Des Callaghan, with permission.

Figure 52. ***Nowellia curvifolia***, formerly in the genus ***Cephalozia***, red form from sunlit area. Photo by Hugues Tinguy, with permission.

Potemkin and Sofronova (2013) found that in ***Cephalozia ambigua*** (Figure 45-Figure 46) the extra thickenings of the apical wall of the terminal cells (Figure 46) is flexible, with the thickenings usually absent on soil, but present in populations growing on logs where humidity conditions are intermittent.

Cephalozia bicuspidata (Figure 47, Figure 53-Figure 56, Figure 59, Figure 60)

Distribution

Cephalozia bicuspidata (Figure 47, Figure 53-Figure 56, Figure 59, Figure 60) has a widespread distribution in the Northern Hemisphere, with scattered reports from South America and Africa (DiscoverLife 2020a). ***Cephalozia bicuspidata*** occurs mostly in northern and temperate Eurasia (not known in Asia south of Taiwan), Azores, North America, northern South America, Macaronesia, Africa (central African mountains, South Africa), and from remote islands of southern Indian (Reunion, Marion I., Crozet Is.) and Atlantic (Tristan da Cunha group) oceans, Chili, South Georgia, and Tasmania (Schuster 1974; Piippo 1990; Váňa 1993; Damsholt 2002).

Figure 53. ***Cephalozia bicuspidata***. Photo by Jay Avery, through Creative Commons.

Figure 54. ***Cephalozia bicuspidata*** on a wet log. Photo by Rambryo, through Creative Commons.

Aquatic and Wet Habitats

In his early summary of aquatic bryophytes, Watson (1919) described ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60) as a species to be found on stream banks of streams with slow water and that provided frequent submergence. Light (1975) reported it from small lakes with low ion concentrations in Scottish mountains where ice cover lasted 4-7 months. Geissler (1976) found the species in alpine streams of the Swiss Alps. Similar habitats around Europe and North America support the species – earthy and gravelly substrates of river banks in Haute Ardenne rivers, Belgium (Leclercq 1977); as calciphilous emergents of montane streams and streambanks in western Canada (Vitt *et al.* 1986; Glime & Vitt 1987), contrasting with Schuster's (1953) statement of

intolerance of lime; upper and middle stream reaches in the Harz Mountains of Germany (Bley 1987); irrigation ditches (Beaucourt *et al*. 1987); in the ***Platyhypnidium-Fontinalis antipyretica*** association (Figure 55) of Thuringia, Germany (Marstaller 1987); in small lakes in southern Finland (Toivonen & Huttunen 1995); soil bank of a small creek of Upper Bureya River in the Russian Far East (Konstantinova *et al*. 2002); on the Southern Kuril Islands in the Goryachyee Lake area on fine-grained ground in crevices of a tufa cliff where they were splashed by water from the lake Bakalin 2007); in and along rivers (Ferreira *et al*. 2008). The most common sites for this species are sunny sites where the species uses decorticated rotting wood, rock, or bare mineral soil as substrate (Botany Website 2020).

Figure 55. ***Fontinalis antipyretica***, a species that, along with ***Platyhypnidium***, can be found in association with ***Cephalozia bicuspidata***. Photo by Michael Lüth, with permission.

Potemkin and Sofronova (2013) reported ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60) on acid and occasionally more or less neutral substrata – bare soil, rocks, rotten wood (Figure 54), among mosses and among ***Sphagnum*** (like Figure 78), particularly, at bases of trees. Schuster (1953, p. 507) considered the ***C. bicuspidata*** complex to have no tolerance for even tiny amounts of lime.

One of the more unusual occurrences of ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60) is in the Kootenay Paint Pots (Figure 57), British Columbia, Canada (Wehr & Whitton 1983). These are natural springs enriched with heavy metals and a *p*H range of 3.2-4.0. The springs have high levels of iron and zinc. These springs are home to 14 species of algae, but only one liverwort (***Cephalozia bicuspidata***) and one moss (***Dicranella heteromalla***; Figure 58). The latter occurred only as protonemata.

Figure 56. ***Cephalozia bicuspidata***, showing its mat growth form and a perianth in the upper right. Photo by Malcolm Storey, DiscoverLife.com, with online permission.

Figure 57. Kootenay National Park Paint Pots, where ***Cephalozia bicuspidata*** and ***Dicranella heteromalla*** are the only bryophytes able to grow in the iron-laden springs. Photo by Marek Ślusarczyk, through Creative Commons.

Figure 58. ***Dicranella heteromalla*** with young capsules, one of two bryophyte species able to grow at the Kootenay Paint Pots on the iron-rich mud. Photo by Janice Glime.

Adaptations

Potemkin and Sofronova (2013) observed that ***C. bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60), like ***C. ambigua*** (Figure 45-Figure 46), has flexible cell

wall thickenings (Figure 59) that seem to respond to intermittent humidity by developing stronger thickenings.

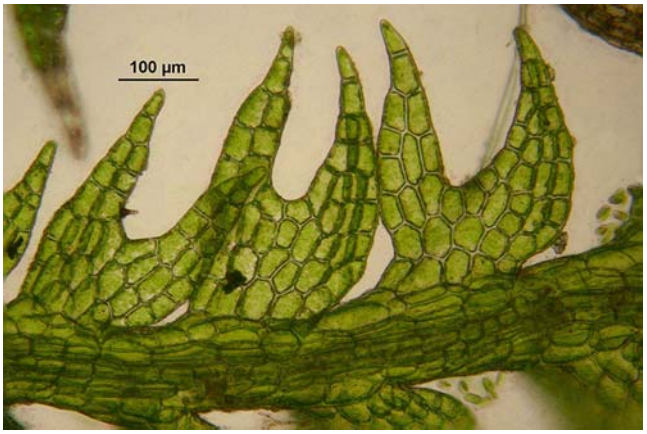

Figure 59. ***Cephalozia bicuspidata*** showing cell walls, in this case with no obvious thickening. Photo by Hermann Schachner through Creative Commons.

Proctor (1982) determined that the photosynthetic activity of the sporophytes of ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60) is very low when compared with that of the gametophyte structures [perianth (Figure 60), bracts and uppermost leaves] associated with the sporophyte. In fact, the CO_2 uptake by the sporophyte is only a small percent of that translocated to it from the gametophyte. The greatest transport to the sporophyte seems to occur when the sporophyte has reached full size but is still green.

Figure 60. ***Cephalozia bicuspidata*** with numerous gametophyte perianths that dominate what you see. Photo by Michael Lüth, with permission.

The subspecies ***Cephalozia bicuspidata*** subsp. ***lammersiana*** (syn. = *Cephalozia lammersiana*, *Jungermannia lammerisiana*) occurs submerged in slow water with poor mineral salts (Watson 1919).

Role

At Tuckerman Ravine on Mt. Washington, New Hampshire, USA (1300 m asl), Duckett and Slack (2013) found ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59 on wet vertical rocks where it was associated with ***Scapania undulata*** (Figure 61), ***Solenostoma hyalinum*** (Figure 62), ***Blindia acuta*** (Figure 63), ***Philonotis fontana*** (Figure 64), ***Pohlia nutans*** (Figure 65), ***Racomitrium fasciculare*** (Figure 66), and ***R. heterosticum*** (Figure 67). ***Cephalozia bicuspidata*** on the mountain had no sexual reproductive structures, but they displayed extensive subterranean shoots that were leafless and contained fungi, most likely **Mucoromycotina**.

Figure 61. ***Scapania undulata*** (red with green edges) with the moss ***Philonotis fontana***, two species often associated with ***Cephalozia bicuspidata*** on wet vertical rocks. Photo by David T. Holyoak, with permission.

Figure 62. ***Solenostoma hyalinum*** with capsule, a species often associated with ***Cephalozia bicuspidata*** on wet vertical rocks. Photo by Michael Lüth, with permission.

Figure 63. ***Blindia acuta***, a species often associated with ***Cephalozia bicuspidata*** on wet vertical rocks. Photo by David Holyoak, with permission.

Figure 64. ***Philonotis fontana***, a species often associated with ***Cephalozia bicuspidata*** on wet vertical rocks. Photo by Janice Glime.

Figure 65. ***Pohlia nutans*** a species often associated with ***Cephalozia bicuspidata*** on wet vertical rocks. Photo by Michael Lüth, with permission.

Figure 66. ***Racomitrium fasciculare***, a species often associated with ***Cephalozia bicuspidata*** on wet vertical rocks. Photo by Janice Glime.

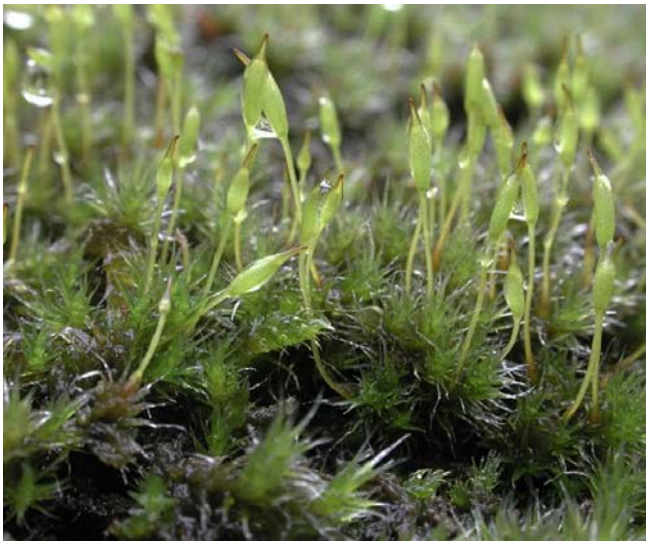

Figure 67. ***Racomitrium heterostichum***, a species often associated with ***Cephalozia bicuspidata*** on wet vertical rocks. Photo by Jan-Peter Frahm, with permission.

Reproduction

Duckett and Clymo (1988) found that many leafy liverworts regenerate from slabs cut from various depths of peat cores. They found that species that lack underground axes regenerate most abundantly at the surface, but not below 9 cm depth. Species like ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60) that have such underground structures often have poor regeneration from the surface, but have much more regeneration down to 12 cm and even grow from samples down to 24-30 cm. This relationship proved to be true for both the cores from live ***Sphagnum***-covered surface (like Figure 78) and from the much older cut peat surface that had been recently colonized by liverworts. The researchers interpreted this to mean that most of the regeneration of ***C. bicuspidata*** is from underground axes rather than from spores or gemmae. The underground axes typically have a large biomass. All the axes had fungal associates that could be partially saprophytic or parasitic.

Fungal Interactions

Pressel and Duckett (2006) found that ***Mniaecia jungermanniae*** (Figure 68), a parasitic **Ascomycota**, associated with ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60). They hypothesized that the fungus could form a symbiotic relationship, producing swollen rhizoids on the liverwort. However, when cultured with ***Cephalozia bicuspidata***, the ***Mniaecia*** remained extracellular. Rather, it induced the formation of giant perichaetia that contained supernumerary archegonia followed by **parthenogenetic** (reproduction from egg without fertilization) and **apogamous** (reproduction in which sporophyte develops from gametophyte without fusion of gametes). They also observed similar giant perichaetia and abnormal perianths in the field.

Mniaecia jungermanniae (Figure 68) is known from 17 species of liverworts, including ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60) as one of the most frequently inhabited liverwort species (Egertová *et al*. 2016). In the Czech Republic all the substrata of this liverwort were acidic and included soil, rocks, and boulders. The liverworts and their symbionts were typically located in the shade of both coniferous and broad-leafed forests. The fungus produces turquoise apothecia (Figure 68) on the liverworts (Duckett *et al*. 2004). In ***Cephalozia bicuspidata***, these occur on the shoots from January to March. This fungus does not colonize the rhizoids of ***C. bicuspidata***.

Figure 68. ***Mniaecia jungermanniae***, an **Ascomycota** fungus growing on ***Cephalozia bicuspidata***. Photo courtesy of Jan Gaisler.

Liepina (2012) reported the occurrence of fungal structures in the cell walls of ***Cephalozia bicuspidata*** (Figure 59) from a swamp. Kowal *et al*. (2018) noted that the rhizoids of leafy liverworts are often colonized by the **Ascomycota** fungus ***Pezoloma ericae*** (see Figure 69), forming associations that might carry out the same functions as mycorrhizae from members of the heath family **Ericaceae** in which there is bi-directional phosphorus for carbon exchange. These researchers measured exchanges of P and CO_2 in the liverwort-fungal association using tracers. They demonstrated the transfer of P from the fungus to the liverwort and transfer of carbon fixed by the liverwort to the fungus. The mycorrhizal liverworts also exhibited increased growth compared to those with no fungal partner.

Figure 69. ***Pezoloma ciliifera***; ***Pezoloma ericae*** occurs on ***Cephalozia bicuspidata***. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Hasselbring (1911) provided an early report of fungi in the rhizoids of liverworts. When the fungal hypha makes contact with the rhizoid, a thickening appears on the inside of the opposite wall. As the hypha grows into the cell, cellulose is deposited ahead of the growing point, surrounding the hypha with a sheath of cellulose. Hasselbring isolated ***Mucor rhizophilus*** (Figure 70) in the **Zygomycota** from nine liverwort species and successfully cultured it with ***Gymnocolea inflata*** (Figure 17-Figure 18, Figure 20, Figure 22), ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60), ***Cephaloziella*** sp. (Figure 100-Figure 105), and ***Lophozia ventricosa*** (Figure 112-Figure 116). This association appears to be neither mycorrhizal nor parasitic, although when the liverworts become strongly infected the plants experience an unfavorable reaction.

Figure 70. ***Mucor mucedo***; ***Mucor rhizophilus*** is known from nine liverwort species, including ***Gymnocolea inflata***. Photo by Lena Wild, through Creative Commons.

Fuscocephaloziopsis albescens (Figure 71-Figure 72)

(syn. = *Pleurocladula albescens*)

Distribution

Fuscocephaloziopsis albescens (Figure 71-Figure 72) is reported by GBIF (2020b) from Canada, USA, Iceland, Greenland, Russian Federation, Norway, Sweden, Switzerland, UK, and Japan. The species is also known from the Tatra Mountains of Poland and Slovakia (Górski 2015, 2016).

Figure 71. ***Fuscocephaloziopsis albescens***, a mostly Arctic and alpine species from Europe and North America, plus Japan, a species occasionally found in mires, seepage streamlets, and snowbeds. Photo by Des Callaghan, through Creative Commons.

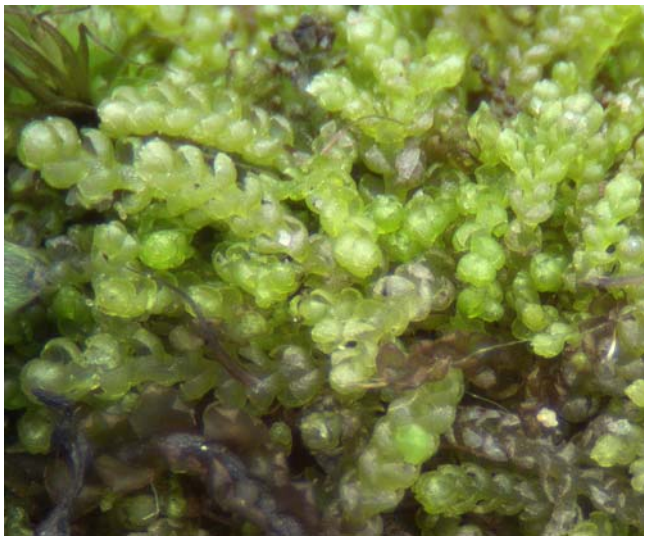

Figure 72. ***Fuscocephaloziopsis albescens*** forming a mat. Photo by Tomas Hallingbäck, with permission.

Aquatic and Wet Habitats

This is not a frequent wetland species. Konstantinova *et al*. (2002) reported it from wet rocks of the Upper Bureya River in the Russian Far East. Górski (2015) reports it from snowbeds in the Tatra Mountains of Poland and Slovakia. There it occurred in an association with ***Pohlia nutans*** (Figure 65) (Górski 2016). Talbot *et al*. (2018) found it on Attu Island of the Aleutian Islands, again rare, on rock cliff outcrops, late snowbeds, cliff crevices, mesic mires, and seepage streamlets. It was sometimes mixed with other leafy liverworts.

Fuscocephaloziopsis connivens (Figure 73-Figure 78)

(syn. = *Cephalozia connivens*)

Distribution

Fuscocephaloziopsis connivens (Figure 73-Figure 78) is a Holarctic species, mostly occurring in boreal and temperate areas with a more or less humid microclimate (Potemkin & Sofronova 2013). This distribution includes records from Africa, the Caribbean, Europe, northern Asia, Middle America, Alaska, Canada, continental USA, Mexico, Oceania, and South America, even occurring on the Hawaiian Islands (ITISb).

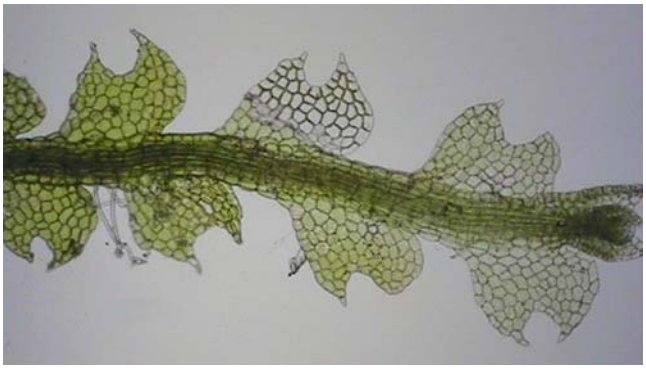

Figure 73. ***Fuscocephaloziopsis connivens***, a holarctic species on streambanks and in wetlands. Photo by Paul Davison, with permission

Figure 74. ***Fuscocephaloziopsis connivens***, the smaller liverwort mixed here with a larger liverwort. Photo by Jan-Peter Frahm, with permission.

Aquatic and Wet Habitats

Watson (1919) included this species in his list of aquatic and wetland species. It occurs on banks with frequent submergence and slow water (Figure 75). Geissler and Selldorf (1986) considered it to be uncommon in association with ***Eleocharis quinqueflora*** (Figure 76)**.** Henriques *et al*. (2017) considered ***Fuscocephaloziopsis connivens*** (Figure 73-Figure 78) to be a **humicolous** (thriving on humus) specialist.

Reproduction

Cores in peatlands demonstrate the regeneration capacity of ***Fuscocephaloziopsis connivens*** (Figure 77-Figure 78). Duckett and Clymo (1988) found it remarkable that this species was nearly absent at the surface where there were actively growing ***Sphagnum*** capitula (like Figure 78), but that it was able to regenerate from lower layers in the cores (3-12 cm depth). Nevertheless, Michael Lüth has photographed it growing well with ***Sphagnum*** (Figure 78).

Figure 75. ***Fuscocephaloziopsis connivens*** growing in a wetland habitat near water. Photo by Michael Lüth, with permission.

Figure 76. ***Eleocharis quinqueflora***, sometimes an associate of ***Fuscocephaloziopsis*** in alpine regions. Photo by Max Licher, through Creative Commons.

Figure 77. ***Fuscocephaloziopsis connivens*** with young capsule and perianth and demonstrating the light green leaf color. The spores have the potential to join the upper layers of peat in the spore bank. Photo by Des Callaghan, with permission.

Figure 78. ***Fuscocephaloziopsis connivens*** growing with ***Sphagnum*** and other bog/poor fen vegetation. Photo by Michael Lüth, with permission.

Fuscocephaloziopsis lunulifolia (Figure 79, Figure 81-Figure 82)

(syn. = *Cephalozia lunulifolia*, *Cephalozia media*)

Distribution

Fuscocephaloziopsis lunulifolia (Figure 79, Figure 81-Figure 82) is widespread in the Northern Hemisphere (Hong 2007). TROPICOS specifically lists it for China, Japan, the Russian Federation, and the USA. Potemkin and Sofronova (2013) list it as a Holarctic boreal species, extending in the Eastern Hemisphere to Japan and SW China (Yunnan) but having a disjunct location in Cuba, as well as Guatemala (Gradstein & Váňa 1994).

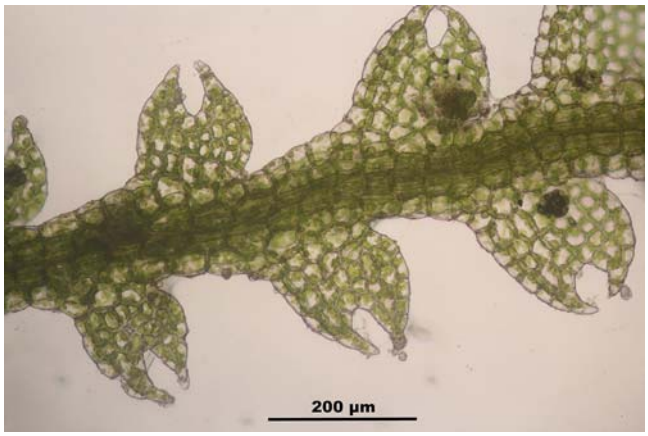

Figure 79. ***Fuscocephaloziopsis lunulifolia***, a widespread species in the Northern Hemisphere, occurring on rotten wood, soil, rocks, or among other mosses. It is associated with lakes, stream banks, and bare peat in subalpine zones and the taiga. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Potemkin and Sofronova (2013), from their experience in Russia, describe this species as one found among ***Sphagnum*** (like Figure 78), on rotten wood, more rare among other mosses, on humus soil, rocks, or fine sandy soil. The ***Fuscocephaloziopsis lunulifolia*** plants are medium-sized, whitish green, and lack secondary pigmentation (Figure 79, Figure 81).

Nichols (1918) reported this species from moist hollows between ***Sphagnum*** hummocks (Figure 80) on

Cape Breton Island, Canada. In the Altai Mountains of Russia, Váňa and Ignatov (1995) considered it rare in the upper taiga and subalpine zones, where it occurred on sides of hummocks, lake shores just above the water level, and on bare peat of bogs. In the Takakia Lake area of the Queen Charlotte Islands, western Canada, Hong (2007) found it on shaded decayed wood, wet rocks, and stream banks. Jonsson (1996) reported ***Fuscocephaloziopsis lunulifolia*** (Figure 79, Figure 81-Figure 82) from the riparian zone of the H. J. Andrews Experimental Forest in the western Cascades, Oregon, USA.

Figure 80. ***Sphagnum*** hummocks and hollows, similar to the ones where ***Fuscocephaloziopsis lunulifolia*** can occur. Photo by Nicholas A. Tonelli, through Creative Commons.

Figure 81. ***Fuscocephaloziopsis lunulifolia*** forming a mat on its substrate. Photo by Michael Lüth, with permission.

Adaptations

Fuscocephaloziopsis lunulifolia (Figure 79, Figure 81-Figure 82) presents evenly thickened leaf cell walls (Figure 82) that are unable to develop extra thickenings in the apical wall of the terminal cells in **xylicolous** (living on wood that has lost its bark) habitats, making it less flexible in these adaptations compared to ***Cephalozia bicuspidata*** (Figure 53-Figure 56, Figure 59, Figure 60) (Potemkin & Sofronova 2013).

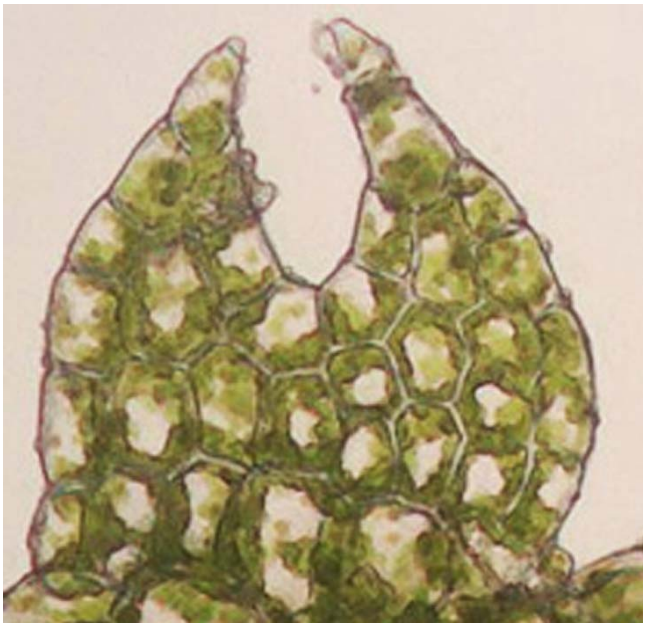

Figure 82. ***Fuscocephaloziopsis lunulifolia*** cells showing walls that are evenly thickened. Photo by Hermann Schachner, through Creative Commons.

Reproduction

Fuscocephaloziopsis lunulifolia (Figure 79, Figure 81-Figure 82) can be dioicous or autoicous. The propagule bank seems to be rather inconsequential for this species. In their study in a boreal old-growth spruce forest in SE Norway, Rydgren and Hestmark (1997) observed germination in fewer than 5% of the samples. However, it likewise was poorly represented in the extant flora sampled, occurring in only 1 of 50 samples.

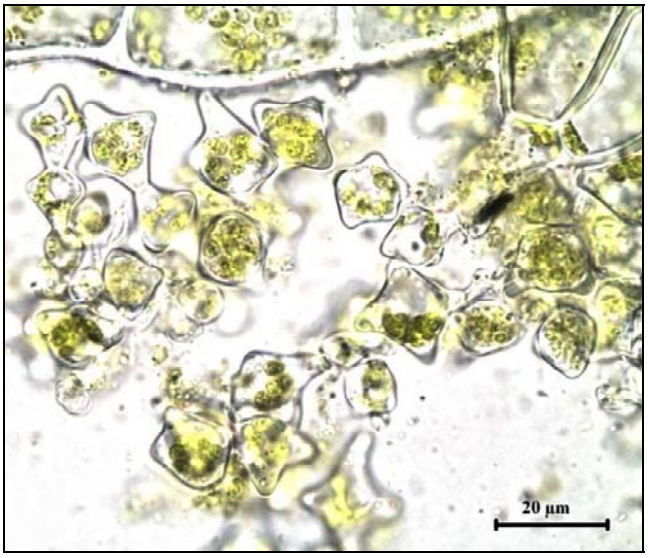

Figure 83. ***Fuscocephaloziopsis lunulifolia*** gemmae, potential members of the sporebank in upper layers of peat. Photo by Hugues Tinguy, with permission.

Fungal Interactions

Wang and Qiu (2006) reported mycorrhizal relationships with ***Fuscocephaloziopsis lunulifolia*** (Figure 79, Figure 81-Figure 82).

Odontoschisma elongatum (Figure 84, Figure 89-Figure 90)

(syn. = *Odontoschisma denudatum* subsp. *elongatum*)

Distribution

Odontoschisma elongatum (Figure 84, Figure 89-Figure 90) presents a distribution in the Caribbean, Europe, Northern Asia, Alaska, Canada, and the continental USA (ITIS 2020c).

Figure 84. ***Odontoschisma elongatum***, a Northern Hemisphere species that can occur in mires. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

This species likewise is not a common member of wetland communities. Geissler and Selldorf (1986) found it with *Trichophorum cespitosum* (Figure 85) and *Carex chillanensis*, and uncommonly with *Eleocharis quinqueflora* (Figure 76) and ***Paludella squarrosa*** (Figure 19). Albinsson (1997) reported this species from ***Sphagnum*** associations (like Figure 78) in mires, noting that liverworts were encountered more often among species of ***Sphagnum*** in the subgenera ***Sphagnum*** (Figure 86) and ***Acutifolia*** (Figure 87) than in subgenus ***Cuspidata*** (Figure 88).

Figure 85. ***Trichophorum cespitosum***, a sedge species that sometimes contributes to making a suitable habitat for ***Odontoschisma elongatum***. Photo by Peter M. Dziuk, with online permission for educational use.

Figure 86. ***Sphagnum magellanicum***, a member of the subgenus ***Sphagnum***. Photo by Michael Lüth, with permission.

Figure 87. ***Sphagnum capillifolium***, a member of the subgenus ***Acutifolia***. Photo by Blanka Shaw, with permission.

Figure 88. ***Sphagnum tenellum***, a member of the subgenus ***Cuspidata***. Photo by David Holyoak, with permission.

Adaptations

Odontoschisma elongatum (Figure 84, Figure 89-Figure 90) can be a bright green (Figure 89), but more commonly has a yellowish or brownish pigment (Figure

90) (Evans 1912). Even a deep blackish purple color is relatively common. Shoots initially produce branches very sparingly, producing unbranched ascending axes. As the stems become longer, they become prostrate and produce the typical intercalary branches, some lateral and some ventral. A few of these are flagelliform (Figure 89) and grow downward, holding the plant in place, especially in its ***Sphagnum*** habitat, and rhizoids are scarce.

Figure 89. ***Odontoschisma elongatum*** with flagelliform stolon (**arrow**) and green color. Photo by Norbert Schnyder, with permission.

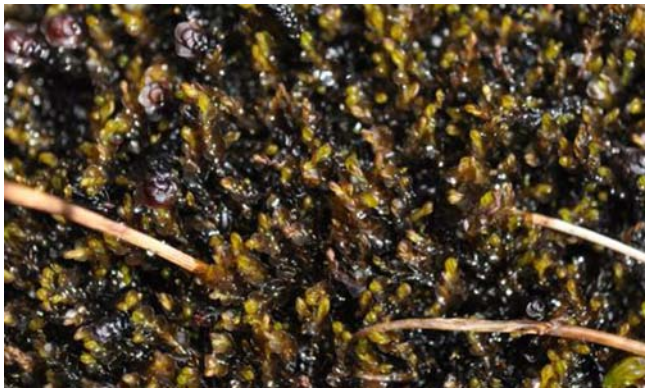

Figure 90. ***Odontoschisma elongatum*** from a wetland community, exhibiting brownish and golden coloration. Photo by Andrew Hodgson, with permission.

Role

Cyanobacteria (Figure 91) can be involved in symbiotic relationships with leafy liverworts (Rikkinen 2017). These can be important sources of fixed nitrogen that is available to the liverworts. Although Rikkinen investigated terrestrial populations, this relationship might as well occur in wetland species. In ***Odontoschisma elongatum*** (Figure 84, Figure 89-Figure 90) the slime papillae at the margins and surface of reduced underleaves near the growing tip were uninfected with any symbiont. But contrary to earlier observations, Rikkinen found that both bacteria and fungal hyphae could attach to the surface of the young slime papillae. The fungus would eventually infect the papilla with its haustoria. In later stages one can observe heavy fungal infections of the slime papillae, and these papillae are eventually shed from the plant.

Figure 91. ***Nostoc linckia***, a **Cyanobacterium**; some species of ***Nostoc*** are common on leafy liverworts as symbionts. Photo from Proyecto Agua, through Creative Commons.

Reproduction

The species is dioicous and male plants are apparently rare (Evans 1912). Despite the difficulty of sexual reproduction, gemmae are also rather rare. This suggests that fragments may be an important means of reproduction and spreading.

Fungal Interactions

Pocock and Duckett (1985) found no mycorrhizal fungi in ***Odontoschisma elongatum*** (Figure 84, Figure 89-Figure 90) among British liverworts. Likewise, Wang and Qiu (2006) found no records of mycorrhizae in ***Odontoschisma elongatum***. Nevertheless, Duckett *et al.* (1991) reported not only flagelliform branches, but also rhizoidal fungi from British ***O. elongatum***.

Odontoschisma fluitans (Figure 92-Figure 93)

(syn. = *Cephalozia fluitans*, *Cladopodiella fluitans*)

Distribution

Odontoschisma fluitans (Figure 92-Figure 93) is distributed in temperate regions of the northern hemisphere and occurs in Europe and eastern North America (Gradstein & Ilkiu-Borges 2015).

Figure 92. ***Odontoschisma fluitans***, a species of Northern Hemisphere temperate regions, known from stream banks, heathlands, peat bogs, and small lakes. Photo by Jean Faubert, with permission.

Aquatic and Wet Habitats

Few records seem to exist for this species in wetlands. Nevertheless, Watson (1919) included it in his treatment of aquatic and wetland species, attributing it to banks with frequent submergence and slow water (Figure 93). Koppe (1945) reported it from ***Sphagnum*** moors in Westfalens, northwestern Germany. It is typically associated with ***Sphagnum*** in heathlands and peat bogs (Gradstein & Ilkiu-Borges 2015). But Toivonen and Huttunen (1995) reported it from small lakes in southern Finland.

Figure 93. ***Odontoschisma fluitans*** forming mats. Photo by David T. Holyoak, with permission.

Reproduction

Unlike some members of the genus, ***Odontoschisma fluitans*** lacks gemmae (Figure 92-Figure 93) (Gradstein & Ilkiu-Borges 2015).

Odontoschisma sphagni (Figure 94-Figure 97, Figure 99)

(syn. = *Jungermannia sphagni*, *Odontoschisma prostratum*)

In North America, this species has been widely known as *Odontoschisma prostratum*, but based on molecular data, Gradstein and Ilkiu-Borges (2015) considered it to belong to the same species as the European ***O. sphagni*** (Figure 94-Figure 95). ***Odontoschisma sphagni*** is exceptional in the genus in being autoicous; other members are dioicous (Gradstein & Ilkiu-Borges 2015).

Figure 94. ***Odontoschisma sphagni***, a species that is both Holarctic and tropical, especially occurring in bogs and other peatlands. Note the whitish underground shoots. Photo by Des Callahan, with permission.

Figure 95. ***Odontoschisma sphagni.*** Photo by Michael Lüth, with permission.

Distribution

Odontoschisma sphagni (Figure 94-Figure 97, Figure 99) occurs in tropical America as well as the Holarctic region, including records from Europe, North America, Mexico, and the Greater Antilles (Gradstein & Ilkiu-Borges 2015).

Aquatic and Wet Habitats

Bley (1987) legitimizes ***Odontoschisma sphagni*** (Figure 94-Figure 97, Figure 99) as an aquatic species (Figure 96-Figure 97), reporting it from the upper reaches of streams in the Harz Mountains of Germany. Gradstein and Ilkiu-Borges (2015) summarize its habitats to include "raised bogs between ***Sphagnum***, on moist, often somewhat peaty soil, on rotten or dead wood, or on thin soil over moist sandstone rock in evergreen or deciduous forests. Sometimes the species grows over ***Leucobryum*** (Figure 98) or among other mosses" (Figure 99).

Figure 96. ***Odontoschisma sphagni*** well hydrated, showing its (mostly) green form. Photo by Michael Lüth, with permission.

Figure 97. ***Odontoschisma sphagni*** in a dry state, showing its reddish color form. Photo by Michael Lüth, with permission.

Figure 98. ***Leucobryum glaucum***; ***Odontoschisma sphagni*** will sometimes grow over members of this moss genus. Photo by Amadej Trnkoczy, through Creative Commons.

Figure 99. ***Odontoschisma sphagni***, growing here with the moss ***Polytrichum***. Photo by Michael Lüth, with permission.

Reproduction

Duckett and Clymo (1988) found that ***Odontoschisma sphagni*** (Figure 94-Figure 97, Figure 99) occurred in core samples from 12-23 cm depth, but was absent from the surface. Because this species does not produce gemmae, but exhibits the same regeneration patterns as species that do, Duckett and Clymo considered the regeneration of liverworts in these habitats not to be the result of gemmae. It is more likely that they are underground shoots (Figure 94). It is also possible that in ***Odontoschisma sphagni*** they result from spores because this species is **autoicous** (having male and female organs on same plant but on separate branches) (Gradstein & Ilkiu-Borges 2015).

Cephaloziellaceae

Cephaloziella (Figure 100-Figure 105)

Cephaloziella (Figure 100-Figure 105) is a widespread genus in a variety of habitats. In the maritime Antarctic, it forms bryophyte carpets in wet areas and depressions around melt pools and streams (Gimingham & Birse 1957). In southern Finland, it occurs in small lakes (Toivonen & Huttunen 1995).

Cephaloziella hampeana (Figure 100-Figure 101)

Distribution

Cephaloziella hampeana (Figure 100-Figure 101) has a scattered distribution that may include disjunct locations or just missing collection areas. When Flores *et al*. (2017) discovered it in Argentina, they raised the question of its disjunct distribution, noting the importance of high elevation locations for species like this. It is widely distributed in the Northern Hemisphere, with its most southern localities previously known from Vera Cruz in Mexico and El Quiche in Guatemala.

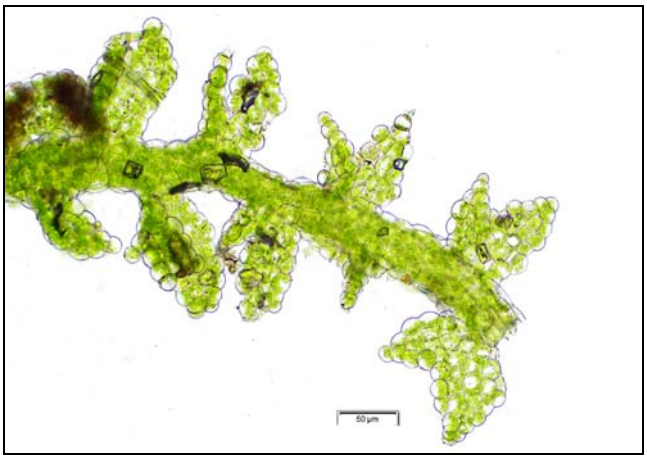

Figure 100. ***Cephaloziella hampeana***, a species widely distributed in the Northern Hemisphere, but also at high elevations in the Southern Hemisphere, where it can be found in fens and mires and similar wetlands. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman and Karen Blisard.

Aquatic and Wet Habitats

Cephaloziella hampeana (Figure 100-Figure 101) appears to be mostly terrestrial, but its tolerance of moisture permits it to live in wetland habitats. Ingerpuu *et al*. (2014) report it from fens and mires in Estonia. In Argentina, as with a number of other Neotropical liverworts, ***C. hampeana*** occurs on soil, associated with

wetlands (Flores *et al*. 2017). In Tennessee, USA, at Abrams Falls Trails, it occurs on moist soil. In Connecticut, USA, the liverwort occupies crevices or the surface of drier cliffs in a ravine (Nichols 1916). In Turkey Run State Park, Indiana, USA, Ellis (1973) found ***Cephaloziella hampeana*** on moist ground on peat mosses, on the sides of ditches, and on sandy and turfy ground. Sass-Gyarmati *et al*. (2015) found ***Cephaloziella hampeana*** on one of the control plots in their experiments on temperature increase and drought. In that heathland vegetation, the species typically grows on acidic or neutral substrates, requiring a somewhat colder temperature range that might not be available as the climate warms, but it has a wide tolerance for moisture levels.

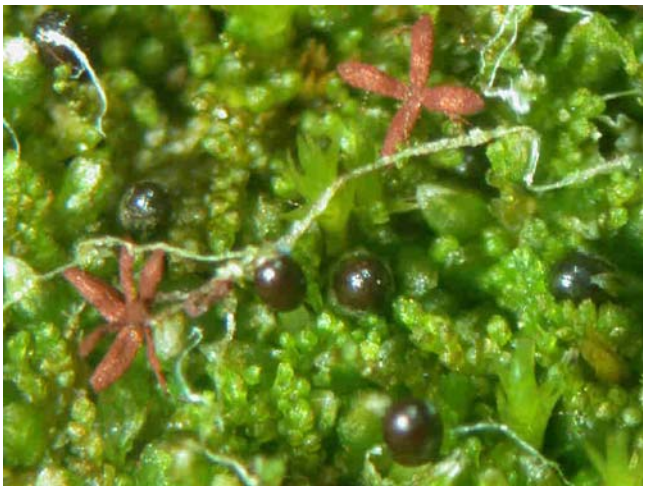

Figure 101. ***Cephaloziella hampeana*** with both gemmae and sporophytes. Photo by David T. Holyoak, with permission.

Fungal Interactions

As for many liverwort species, Wang and Qiu (2006) list it among the species that have fungal associations. The nature of this association needs to be explored.

Cephaloziella rubella (Figure 102-Figure 105)

Distribution

Cephaloziella rubella (Figure 102-Figure 105) occurs in the Northern Hemisphere, mostly in the Temperate Zone: Europe, Asia, North America (ITIS 2020d)

Figure 102. ***Cephaloziella rubella***, a species of the temperate Northern Hemisphere that occurs occasionally on montane stream banks. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

This species occurs as a submerged hemicalciphilous species in montane streams and on stream banks in western Canada (Figure 103) (Vitt *et al.* 1986; Glime & Vitt 1987). But elsewhere, reports of its wetland presence are rare. Strout (1976) found it in Larks Lake, Michigan, USA, where it hosted an apparent symbiont in the **Cyanobacteria** (see Figure 91). In addition to its cyanobacterial symbiont, ***Cephaloziella rubella*** (Figure 102-Figure 105) has fungal associations (Wang & Qiu 2006).

Figure 103. Glacial melt stream where ***Cephaloziella rubella*** grows in BC, Canada. Photo by Janice Glime.

Figure 104. ***Cephaloziella rubella*** showing its growth pattern in mats. Photo by Michael Lüth, with permission.

Figure 105. ***Cephaloziella rubella*** showing the large, dense mats it can form. Photo by Michael Lüth, with permission.

Kymatocalyx (Figure 106-Figure 111)

(syn. = *Ruttnerella*, *Stenorrhipis*)

Kymatocalyx (Figure 106-Figure 111) is a leafy liverwort known from Andean streambeds (S. Robbert Gradstein pers. comm. 3 November 2011). This is a pantropical rheophytic genus that grows in or near running water, on periodically submersed rocks, in waterfalls, on wet cliffs, and similarly wet habitats. Members of this genus produce very small erect leafy shoots from creeping, stoloniform axes.

Kymatocalyx africanus (Figure 106)

Distribution

Kymatocalyx africanus (Figure 106) occurs in the Uluguru Mts. (1600-2350 m asl) of Tanzania, and Mt. Mulanje (1200-2220 m asl), Malawi.

Figure 106. ***Kymatocalyx africanus***, a species of limited known distribution in eastern Africa where it can grow partially submerged in streams and wet places. Photo courtesy of Tamás Pócs.

Aquatic and Wet Habitats

The species occurs in montane forest areas on shady granitic rocks and boulders, on soil banks or on thin peat over rocks in streams or wet places, partially submerged in water (Gradstein & Váňa 1999). The type was found on Mt. Mulanje in the bed of a seasonal stream on thin gritty soil over a granite boulder at 1740 m asl.

Reproduction

Kymatocalyx africanus (Figure 106) is **cladautoicous** (having male sexual organs on special branch separate from female organs) (Gradstein & Váňa 1999).

Kymatocalyx cubensis (Figure 107)

In Madagascar, ***Kymatocalyx cubensis*** (Figure 107) can occur 0.3-1 m above the tidal surface, suggesting that it is salt-tolerant (Pócs 1998). Its only claim to being hydrophilic is its nearness to the ocean water.

Figure 107. ***Kymatocalyx cubensis***, a species that occurs within a meter of the tidal surface in Madagascar. Photo courtesy of Tamás Pócs.

Kymatocalyx dominicensis (Figure 108)

Distribution

Kymatocalyx dominicensis (Figure 108) is known from Cuba (1210 m asl), Puerto Rico (900 m asl), Dominica (800 m asl), St. Vincent Is., Guyana (150-1200 m asl), Venezuela (500 m asl), Colombia (1800 m asl), Bolivia (850 m asl), and Brazil (10-1850 m asl) in the Western Hemisphere and in Madagascar (1 m asl) in the Eastern Hemisphere (Gradstein & Váňa 1999).

Figure 108. ***Kymatocalyx dominicensis***, a species known from the Neotropics and Madagascar where it can occur on shaded rocks along rivers, in waterfalls, and at times be partly submerged. Photo courtesy of Tamás Pócs.

Aquatic and Wet Habitats

Like other taxa of the genus, ***Kymatocalyx dominicensis*** (Figure 108) grows on shaded rocks along rivers, in waterfalls, etc., often partly submerged, in moist tropical lowland and lower montane areas (Gradstein & Váňa 1999). It was very common as dark green mats on volcanic stones along the trail in Dominica (Gradstein 1989).

Kymatocalyx madagascariensis (Figure 109-Figure 110)

Distribution

Kymatocalyx madagascariensis (Figure 109-Figure 110) seems to be restricted to the East African islands: Madagascar (0.3-1380 m asl), Mauritius (700 m asl), Reunion (200-1800 m asl), and Comoro Archipelago (500-1580 m asl). Material from mainland Africa belongs to ***K. africanus*** (Figure 106) (Gradstein & Váňa 1999).

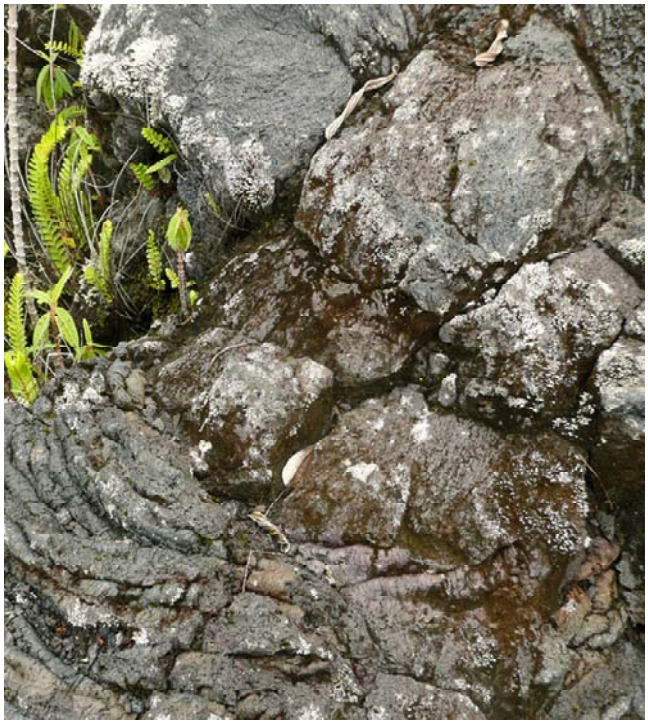

Figure 110. ***Kymatocalyx madagascariensis*** in crevices on old lava flow, Reunion Island. Photo courtesy of Tamás Pócs.

Figure 109. ***Kymatocalyx madagascariensis***, a species endemic to east African islands, occupying lava rocks where they may be submerged at times of high rainfall. Photo courtesy of Tamás Pócs.

Aquatic and Wet Habitats

Kymatocalyx madagascariensis (Figure 109-Figure 110) grows on shaded granite and basaltic lava rocks, on cliffs and boulders near waterfalls, partly submerged or irrigated, in moist tropical lowland and montane rainforest areas (Gradstein & Váňa 1999). In Madagascar, Comores, and the Mascarenes it occurs mostly on volcanic rocks of temporary water flows (see Figure 111), but also occurs on wet soil on roadsides. On Réunion Island it occurs in shady cracks in 5-20-year-old lava flows (Figure 110) (Tamás Pócs, pers. comm. 3 March 2020).

Figure 111. ***Kymatocalyx madagascariensis*** temporary water flow habitat on old lava flow, Reunion Island. Photo courtesy of Tamás Pócs.

Kymatocalyx rhizomatica

(syn. = *Ruttnerella rhizocaula*)

Distribution

Kymatocalyx rhizomatica was reported from tropical wet areas by Ruttner (1955). It is a pantropical species from Malaysia, Sarawak (300 m asl), Sumatra, Costa Rica (150-600 m asl), Panama (150-300 m asl), and Colombia (700 m asl) (Gradstein & Váňa 1999).

Aquatic and Wet Habitats

Kymatocalyx rhizomatica grows on volcanic rock, stones, or moist earth in and along rivulets, in waterfalls and on trails in lowland and submontane rainforest areas (Gradstein & Váňa 1999).

Reproduction

Kymatocalyx rhizomatica is cladautoicous and gemmae observations are rare (Gradstein & Váňa 1999).

Lophoziaceae

Lophozia (Figure 112-Figure 121)

In western Canada, Glime and Vitt (1987) considered members of ***Lophozia*** in their stream study to be a restricted terrestrial of montane streams and streambanks. These are not submersed species.

Lophozia ventricosa (Figure 112-Figure 116)

Distribution

Records of ***Lophozia ventricosa*** (Figure 112-Figure 116) are almost entirely restricted to the Northern Hemisphere, from the Arctic to the subtropics (DiscoverLife 2020b). It occurs in the Antarctic/Southern Ocean region on an island off the southern coast of Australia, Europe, Asia, and North America (Alaska, Canada, Continental USA) (ITIS 2020e).

Figure 112. ***Lophozia ventricosa*** occurs from the Arctic to the subtropics in the Northern Hemisphere. Its wet habitats include being submerged in small lakes, on river banks, and in fens. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Lophozia ventricosa (Figure 112-Figure 116) can be truly aquatic in small lakes in the Scottish mountains where the ice cover lasts 4-7 months and the water is low in ions (Light 1975). In Belgium, Leclercq (1977) reported it on earthy and gravelly substrates of river banks (Figure 113) in the Haute Ardenne rivers. Lenz (2011) reported this species from fens in the Bighorn National Forest, Wyoming, USA.

Figure 113. ***Lophozia ventricosa***, appearing here with other bryophytes on a gravelly substrate. Photo by Hermann Schachner, through Creative Commons.

Reproduction

Lophozia ventricosa (Figure 112-Figure 116) produces gemmiferous shoots (Figure 114-Figure 116). Algar-Hedderson *et al*. (2013) found little difference in the gemma production between a boreal population in central Norway and one in the Arctic tundra on Svalbard. There was a significant difference in that shoots in the boreal site tended to produce somewhat more gemmae and form larger, denser colonies. This combination results in a somewhat higher colony level output in the boreal site.

Figure 114. ***Lophozia ventricosa*** with gemmiferous branches. Photo by Jan-Peter Frahm, with permission.

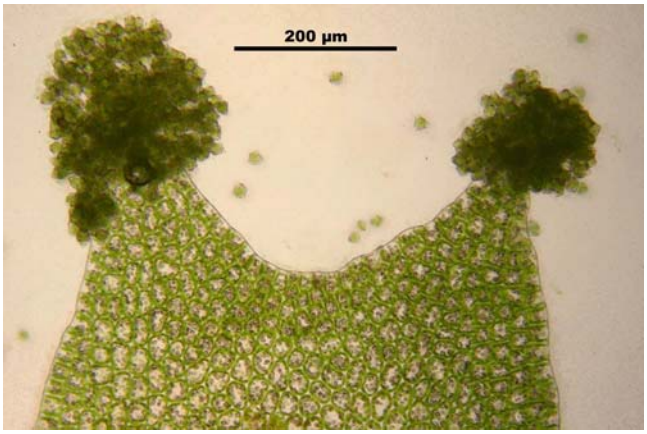

Figure 115. ***Lophozia ventricosa*** leaf showing gemmae at the tips of the leaf lobes. Photo by Hermann Schachner, through Creative Commons.

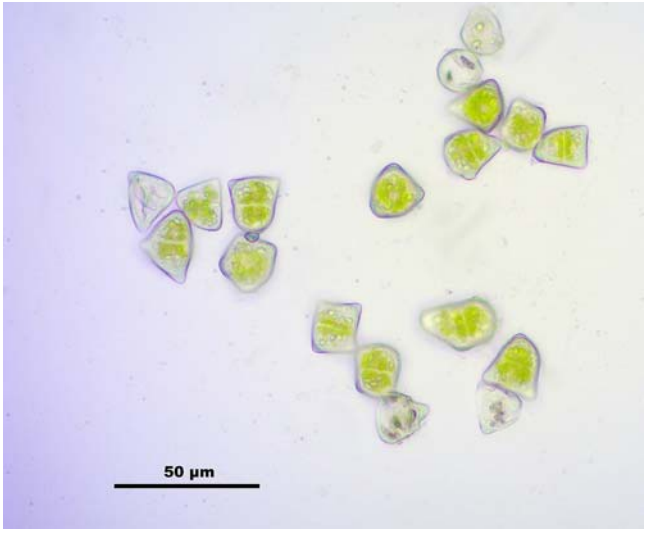

Figure 116. ***Lophozia ventricosa*** gemmae. Photo by Hermann Schachner, through Creative Commons.

Figure 117. ***Lophozia ascendens*** with gemmae, a species that produces gemmae later than do ***L. ventricosa*** and ***L. longifolia***. Photo by Michael Lüth, with permission.

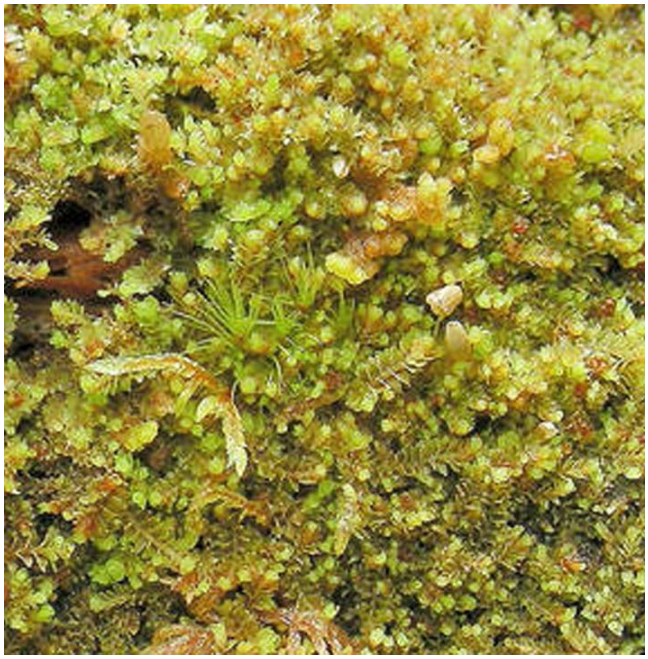

Figure 118. ***Lophozia longiflora***, a species that has earlier gemma production compared to ***L. ventricosa***. Photo by Earth.com, with permission.

Lophozia ventricosa (Figure 112-Figure 116) is a common liverwort in the National Nature Reserve in the Sumava Mountains, Bohemian Forest, Czech Republic. Holá *et al*. (2011) found that gemma production of the rare ***L. ascendens*** (Figure 117) was delayed in the growing season when compared to the more common ***Lophozia ventricosa*** and ***L. longiflora*** (Figure 118). The researchers concluded that air humidity was an important factor in the germinability of these gemmae. Gemma germination was low in early spring, reaching its highest level in August and September, and decreasing slightly in October. The researchers suggested that the rather mild winters of the Czech Republic assure a lower mortality of shoots in winter, thus decreasing selection pressure toward production of dormant gemmae of these species.

Fungal Interactions

Like many liverworts, ***Lophozia ventricosa*** (Figure 112-Figure 116) associates with members of the **Ascomycota** fungus ***Sebacina vermifera*** (see Figure 13) species complex (Bidartondo & Duckett 2010). It is known to share identical ***Sebacina vermifera*** DNA with the fungus on the leafy liverwort ***Nardia scalaris*** (Figure 119).

Biochemistry

Lophozia ventricosa (Figure 112-Figure 116) most likely benefits from its antimicrobial activity (Bukvicki *et al*. 2015). This species proved to have a number of compounds that are active against a variety of bacteria and fungi.

Figure 119. ***Nardia scalaris***, a leafy liverwort species that shares the fungus ***Sebacina vermifera*** having the same DNA as that fungus occurring on ***Lophozia ventricosa***. Photo by Hermann Schachner, through Creative Commons.

Lophozia ventricosa (Figure 112-Figure 116) possesses a variety of secondary compounds (Lu *et al*. 2005). The essential oils include sesquiterpenoids (Lu *et al*. 2005; Song *et al*. 2007) and terpenoids (Tori *et al*. 1993). Thus far, we have little information on the advantage these compounds give to specific liverworts, but it is likely that at least some of them serve as antiherbivore compounds. This is beneficial for organisms with slow growth rates, where the rate of herbivory could be greater than the growth rate. These antifeedant compounds could help the liverwort win the race.

Lophozia wenzelii (Figure 120-Figure 121)

Distribution

Lophozia wenzelii (Figure 120-Figure 121) is an arctomontane species (Bakalin 2004) distributed in Europe, Asia, and North America from Alaska, through the continental USA (ITIS 2020f). It extends from Greenland to India, China, and Japan in the Eastern Hemisphere, and to New Mexico, USA, in the Western Hemisphere (GBIF 2020c). It is unknown in the high Arctic except for Greenland (Bakalin 2004).

Figure 120. ***Lophozia wenzelii***, an arctomontane species that can occur in alpine streams, mountain bogs, and marshy areas. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

Váňa (2005) considers that this species occurs mostly in mountain bogs and marshy areas. It occurs more rarely on wet rocks or rock debris. But in the Swiss Alps, Geissler (1976) found it in alpine streams, occurring uncommonly with ***Carex goodenoughii*** and ***Eleocharis quinqueflora*** (Figure 76) (Geissler & Selldorf 1986). In Russia at the Ushkovskii Volcano, Bakalin (2005) ***Lophozia wenzelii*** (Figure 120-Figure 121) occurs in glacial areas on stones of stream banks as well as on light soil between hummocks. This hummock soil is mixed yearly by freezing and thawing dynamics.

Figure 121. ***Lophozia wenzelii*** showing its growth habit. Photo by Štěpán Koval, with permission.

Bakalin (2005) reports that ***Lophozia wenzelii*** (Figure 120-Figure 121) grows among mosses and liverworts, but rarely forms pure **mats**. In moss tundra and oligotrophic bogs it is interspread within the boreal forest zone. In rare circumstances it grows along the peaty banks of streams on fine-granulated soil or on somewhat dry rocks. In the tundra it is able to grow in microdepressions between heath-lichen or moss patches. Frequently it occurs in wet (var. ***wenzelii***) or dry (var. ***groenlandica***) crevices of gravelly barrens and rocks (including seacoast cliffs). The main habitats, however, are oligotrophic bogs, where ***L. wenzelii*** sometimes grows in pure mats or mixed with ***Gymnocolea inflata*** (Figure 17-Figure 22), ***Scapania*** spp. (most frequently with ***S. paludicola*** – Figure 122), ***Cephalozia*** spp. (Figure 45-Figure 60), and ***Odontoschisma fluitans*** (Figure 92-Figure 93) (Bakalin 2004).

Figure 122. ***Scapania paludicola***, a species that often accompanies ***Lophozia wenzelii***. Photo by Michael Lüth, with permission.

In the Upper Puiva River in the Urals of Russia, Konstantinova and Lapshina (2017) found ***Lophozia wenzelii*** (Figure 120-Figure 121) on soil and bare loamy soil of the tundra, in snowbed communities, between boulders in rock fields, in dwarf shrub-sedge-***Sphagnum*** bogs, in seepages, on banks of brooks, and on road sides. Here they occur in pure mats or mixed with a variety of other leafy liverworts and mosses.

Adaptations

In Europe and northern Asia, var. ***litoralis*** exhibits rusty brown to red-brown plants. These live in places with disturbed vegetation cover, on soil near brook banks, or in the subalpine belt on mountains. Where vegetation is disturbed they occur on finely granulated soil or among mosses in lax **mats**. The occurrence on wet cliffs is rare.

Lophozia wenzelii (Figure 120-Figure 121) is a critically endangered species in the Czech Republic (Čihal & Kaláb 2017). In a model to determine the most important habitat characters for their presence, several factors emerged. The probability of presence is lower when the temperatures are higher in the warmest month. Higher precipitation values in the driest month also favor habitation. Since the least precipitation in the Czech Republic occurs in winter (January or February), the winter precipitation is important.

Lophoziopsis excisa (Figure 123-Figure 124)

(syn. = *Lophozia excisa*)

Distribution

Lophoziopsis excisa (Figure 123-Figure 124) is a highly variable and wide-ranging species (Schuster 1969). Its distribution is bipolar, ranging from Greenland southward to Italy and Spain in the Eastern Hemisphere and to some of the mountain forests in the southern Appalachian Mountains in eastern USA and to California in western USA. It has been found on Antarctica, in New Zealand, southern Chile, and southern Argentina. GBIF (2020d) includes it in Northern Asia as well, probably in alpine regions of Japan (Kitagawa 1965).

Figure 123. ***Lophoziopsis excisa*** with gemmae, a bipolar species extending south into mountains of the temperate zone. It most commonly occurs with other bryophytes on cliffs along streams and in bogs. Photo by Štěpán Koval, with permission.

Figure 124. ***Lophoziopsis excisa*** with gemmae. Photo by Jan-Peter Frahm, with permission.

Aquatic and Wet Habitats

The habitats of this species suggest that it is indifferent to *p*H within most of the normal range (Schuster 1969). It occurs primarily on mineral substrata, but is also able to live on exposed loamy, acid soil. It is always mixed with other bryophytes, especially other leafy liverworts, in the Upper Puiva River basin of the Ural Mountains in Russia (Konstantinova & Lapshina 2017). Geissler and Selldorf (1986) found it was uncommon with *Carex goodenoughii* in bogs in Ticino, Switzerland. In ***Rhododendron lapponicum*** (syn. = *Ledum groenlandicum*; Figure 125) bogs of the glacial relict lake areas of the Komi Republic of northwestern Russia, it occurs on decaying wood and slightly matted soil, and on soil in a ***Menyanthes-Comarum Sphagnum*** mixed forest (Dulin 2015). In the

Timpton River Basin, South Yakutia, Russia, Sofronova (2017) found ***Lophoziopsis excisa*** (Figure 123-Figure 124) mixed with other liverworts on soil of moist south-facing cliffs along the river bank as well as on fine soil in cliff cracks. But it is also found on soil in between stones of the stone field on south-facing slopes, where it can occur in pure mats or mixed with other liverworts.

Figure 125. ***Rhododendron groenlandicum*** bog, a habitat where it occurs on decaying wood and slightly matted soil in northwestern Russia. Photo by Wynn Anderson, through Creative Commons.

Reproduction

Lophoziopsis excisa (Figure 123-Figure 124) is **paroicous** with red gemmae (Konstantinova & Savchenko 2018).

Fungal Interactions

Newsham and Bridge (2010) noted the presence of fungi belonging to **Sebacinales** (Figure 13) in ***Lophoziopsis excisa*** (Figure 123-Figure 124) at Léonie Island in the southern maritime Antarctic. Newsham *et al*. (2014) reported the occurrence of ***Cladophialophora*** (Figure 126) and related fungi in the tissues of ***Lophoziopsis excisa*** from Léonie Island. Fungal partners are fairly well known among bog plants (Thormann 2006), including liverworts (Duckett & Clymo 1988) so the presence of fungi with this liverwort species on peaty soils is not surprising.

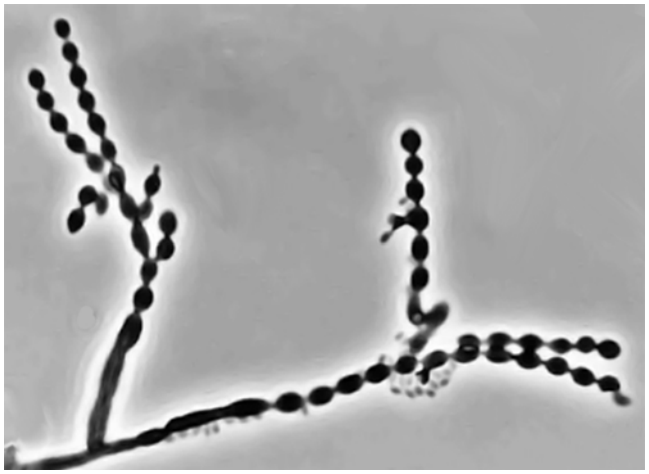

Figure 126. ***Cladophialophora*** sp.; some species of this fungal genus are found in tissues of ***Lophoziopsis exicisa***. Photo by Medmyco, through Creative Commons.

Trilophozia quinquedentata (Figure 127-Figure 128)

(syn. = *Tritomaria quinquedentata*)

Distribution

Trilophozia quinquedentata (Figure 127-Figure 128) is widely distributed in the Northern Hemisphere from the Arctic to northern USA and to at least one location each in China and Japan (TROPICOS 2020).

Figure 127. ***Trilophozia quinquedentata***, a Northern Hemisphere mostly terrestrial species that can occur on wet cliffs, dripping rock surfaces, and associated with waterfalls. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

This mostly terrestrial species is at least tolerant of water, occurring on wet cliffs of the Upper Bureya River in the Russian Far East (Konstantinova *et al*. 2002). It also occurs on dripping steep rock surfaces of granite at the margins of shaded permanent waterfalls, where it is only loosely attached (Figure 128) (Vieira *et al*. 2005). It is also typically associated with ***Chiloscyphus polyanthos*** (Figure 129) and ***Aneura pinguis*** (Figure 130) in mountain streams of northwest Portugal.

Figure 128. ***Trilophozia quinquedentata*** loosely attached to its substrate. Photo by Hugues Tinguy, with permission.

Figure 129. ***Chiloscyphus polyanthos***, a common associate of ***Trilophozia quinquedentata***. Photo by Štěpán Koval, with permission.

Figure 130. ***Aneura pinguis***, a common associate of ***Trilophozia quinquedentata***. Photo by Hermann Schachner, through Creative Commons.

Tritomaria exsecta (Figure 131-Figure 136)

(syn. = *Sphenolobus exsectus*)

Distribution

Tritomaria exsecta (Figure 131-Figure 136) extends in a wide range including Australiia, Asia, Europe, and North America from Mexico to Alaska (ITIS 2020g). It has also been reported from eastern Africa (BFNA 2020) and New Zealand (Engel 2006).

Aquatic and Wet Habitats

Its inclusion in aquatic and wetland studies seems to be rare. Nichols (1916) reported it as a **calciphobic** (avoiding calcium) species along rivers in Connecticut, USA. Glime (1982) reported it from the wall of the humid flume (Figure 37) at Franconia Notch, New Hampshire, USA.

Figure 131. ***Tritomaria exsecta***, a wide-ranging mostly terrestrial species, occurring as a calciphobe along rivers and on humid canyon walls. Photo by Hermann Schachner, through Creative Commons.

Figure 132. ***Tritomaria exsecta***. Photo by Michael Lüth, with permission.

Reprodution

It forms mats and can produce apical gemmae (Figure 133-Figure 136).

Figure 133. ***Tritomaria exsecta*** in a mat with gemmae at the apex of shoots. Photo by Hermann Schachner, through Creative Commons.

Figure 134. ***Tritomaria exsecta*** with apical gemmae. Photo by Michael Lüth, with permission.

Figure 135. ***Tritomaria exsecta*** with gemmae. Photo by Michael Lüth, with permission.

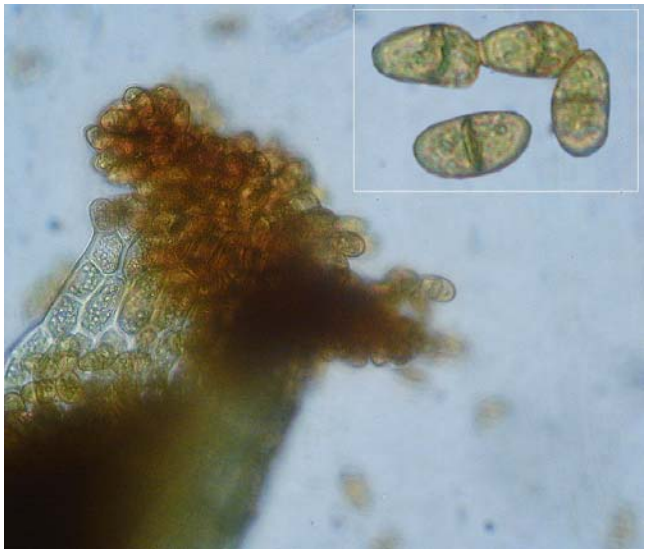

Figure 136. ***Tritomaria exsecta*** gemmae. Photo by Michael Lüth, with permission.

Tritomaria exsectiformis (Figure 137, Figure 141-Figure 143)

Distribution

Tritomaria exsectiformis (Figure 137, Figure 141-Figure 143) is an Arctic-alpine, circumboreal species (Harpel & Dewey 2005). It is distributed in North America from Greenland and Alaska southward to Colorado, Iowa, Michigan, and Pennsylvania in the USA, It is also present in Europe, Asia, and Africa (Hong 2002).

Figure 137. ***Tritomaria exsectiformis***, a species distributed from the Arctic to the temperate region in the Northern Hemisphere, occurring mostly at high elevations where it often occurs in areas of perennial flow at or near springs and seeps. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

In Greenland, Hassel *et al.* (2014) found ***Tritomaria exsectiformis*** (Figure 137, Figure 141-Figure 143) growing on rocks in a heathland of ***Vaccinium uliginosum*** (Figure 138) with the mosses ***Saelania glaucescens*** (Figure 139), ***Bartramia ithyphylla*** (Figure 140), and liverwort ***Scapania*** sp. (*e.g.* Figure 122).

Figure 138. ***Vaccinium uliginosum*** with fruit, the dominant species in heathland where one can find ***Tritomaria exsectiformis***. Photo by David Gaya, through Creative Commons.

Figure 139. ***Saelania glaucescens***, a species growing with ***Tritomaria exsectiformis*** on rocks in blueberry heathlands. Photo by Michael Lüth, with permission.

Figure 140. ***Bartramia ithyphylla***, a species growing with ***Tritomaria exsectiformis*** on rocks in blueberry heathlands. Photo by J. C. Schou, with permission.

In western USA, Harpel and Dewey (2005) found ***Tritomaria exsectiformis*** (Figure 137, Figure 141-Figure 143) to be typical of open to shaded coniferous forest where it is associated with low volume, perennial water flow at or near springs and seeps. These typically occur on very gentle topographic gradients. Its substrate is usually decaying wood (Figure 141) in stage four decay and having direct contact with water. It is never present where there is high volume flow.

Figure 141. ***Tritomaria exsectiformis*** on wet, decaying wood. Photo by Stan Phillips, through public domain.

Reproduction

This perennial species occurs mostly at high elevations where snow remains a long time into spring and summer, usually at elevations above 1500 m (Harpel & Dewey 2005). This gives it a short growing season with a late summer and fall. Reproduction occurs only by gemmae (Figure 142-Figure 143) and other vegetative means. The species is a restricted terrestrial associated with the montane streams and streambanks of western Canada (Figure 103) (Vitt *et al.* 1986; Glime & Vitt 1987). Hong (1994) reported it from creek banks, decayed wood, and humus over decayed wood in forests ranging from 0 to 2300 m asl.

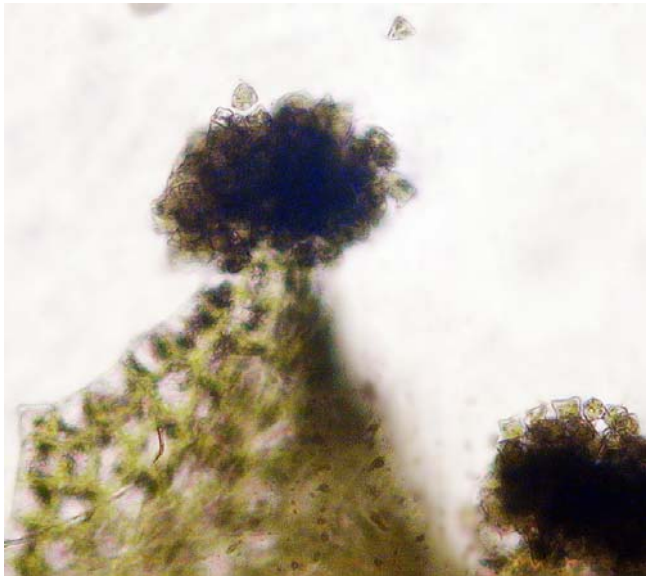

Figure 142. ***Tritomaria exsectiformis*** with clusters of gemmae on leaf tips. Photo by Michael Lüth, with permission.

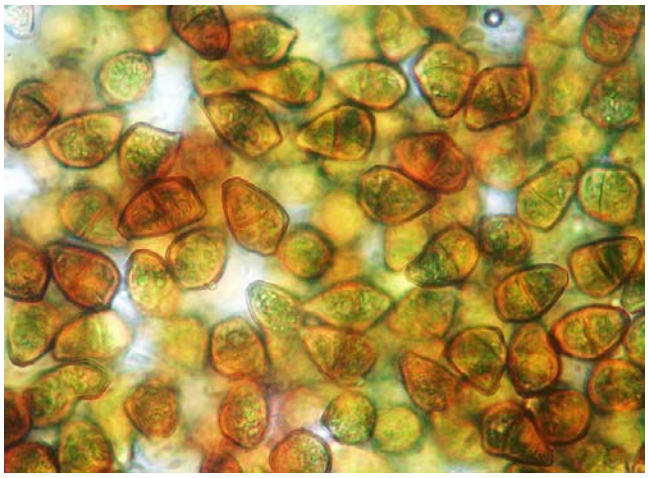

Figure 143. ***Tritomaria exsectiformis*** gemmae. Photo by Michael Lüth, with permission.

Tritomaria exsectiformis (Figure 137, Figure 141-Figure 143) is dioicous, thus rarely producing sporophytes. Harpel and Dewey (2005) suggested that dispersal is most likely accomplished by moving water and possibly invertebrates. It requires a substrate that provides a constant water supply without the dangers of scouring.

Summary

The **Cephaloziineae**, except for **Scapaniaceae**, are not common in wet habitats, and especially rare in the water. The **Adelanthaceae** has only 2 species in 2 genera that have appeared in wetland habitats, with ***Syzygiella sonderi*** being submerged in high elevation lakes in the Andes. The **Anastrophyllaceae** is predominantly terrestrial, but may appear on wet cliffs and wet rocks of stream banks and waterfalls. I have identified only 9 species (7 genera) in such wet habitats. The mostly tiny **Cephaloziaceae** seem somewhat more aquatic, occurring in small ponds and mires as well as wet cliffs and rocks of lake shores and stream banks, but with only 9 species (3 genera) included in the literature surveyed. They often occur among other bryophytes, thus protecting the from frequent desiccation. Some become submerged. Some species regenerate from buried stolons. The **Ascomycota** ***Mniaecia jungermanniae*** can inhabit members of ***Cephalozia***, and ***Pezoloma ericae*** can occur on the rhizoids. The **Zygomycota** species ***Mucor rhizophilus*** occurs on rhizoids in several genera of **Cephaloziaceae**. The **Cephaloziellaceae** is represented by 8 species (2 genera) in carpets of wet areas in the Antarctic and lakes of Finland, but it is mostly terrestrial. The **Lophoziaceae** is represented by 6 species (2 genera) here, again by species that grow mostly terrestrially. Nevertheless, some occur in mountain lakes and others in bogs and marshy areas. Seeps and dripping rock surfaces are suitable for some. Some take advantage of the water from late snow melt.

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CHAPTER 1-3
AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES: CEPHALOZIINEAE 2

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CHAPTER 1-3
AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA, ORDER JUNGERMANNIALES: CEPHALOZIINEAE 2

Figure 1. ***Scapania undulata*** and habitat, showing its close adherence to water without necessarily being submerged. Many of the leafy liverworts treated in this chapter occupy niches that maintain moisture without submergence. Photo by Jean Faubert, with permission.

Scapaniaceae

It is interesting that very similar mosaic infection patterns in **Lophoziaceae** and **Scapaniaceae** add strength to the molecular link between the two families (Duckett *et al*. 2006). Both are in Cephaloziineae.

Diplophyllum albicans (Figure 2, Figure 12, Figure 14-Figure 15)

Distribution

Diplophyllum albicans (Figure 2, Figure 12, Figure 14-Figure 15) is an amphi-oceanic species, but rarely penetrates away from the oceanic climate (Bakalin & Vilnet 2018).

Figure 2. ***Diplophyllum albicans***, an amphi-oceanic species of wet cliffs and lake shores as well as fast streams. Photo by Štěpán Koval, with permission.

Aquatic and Wet Habitats

In Scotland, this species sometimes covers the hill lake shore rocks (West 1910). Nichols (1918) reported ***Diplophyllum albicans*** (Figure 2, Figure 12, Figure 14-Figure 15) from wet rock cliffs on Cape Breton Island, Canada. But by contrast, Watson (1919) considered the species to be associated with fast water. This is more consistent with their habitat on moist stones and rocks in the stream beds of the Gory Stolowe Mountains in Poland (Szweykowski 1951), on rocks in streams near Lacko in the Western Carpathians (Mamczarz 1970), upper and middle stream reaches in Harz Mountains of Germany (Bley 1987), in aquatic habitats of eastern Odenwald and southern Spessart with ***Heterocladium heteropterum*** (Figure 3) (Philippi 1987), and in rivers (Ferreira *et al*. 2008).

Figure 3. ***Heterocladium heteropterum***, a species that may accompany ***Diplophyllum albicans*** on gravelly river banks. Photo by Štěpán Koval, with permission.

Other habitats are wet, but not submersed. In the Haute Ardenne rivers in Belgium, Leclercq (1977) found ***Diplophyllum albicans*** (Figure 2, Figure 12, Figure 14-Figure 15) on earthy and gravelly substrates of river banks. In the British Isles, Orange (2001) found the species on a shaded damp rock face by a wooded stream. In the Upper Bureya River of the Russian Far East, Konstantinova *et al.* (2002) reported it from a wet cliff and rocks at the lake shore, occurring with ***Blepharostoma trichophyllum*** (Figure 4), ***Cephalozia ambigua*** (Figure 5), ***Gymnomitrion concinnatum*** (Figure 6), ***Barbilophozia sudetica*** (Figure 7), ***Marsupella boeckii*** (Figure 8), ***M. emarginata*** **subsp.** ***tubulosa*** (Figure 9), and ***Fuscocephaloziopsis albescens*** (Figure 10).

Figure 4. ***Blepharostoma trichophyllum***, a species that may accompany ***Diplophyllum albicans*** on wet cliffs and lake shore rocks. Photo by Hermann Schachner, through Creative Commons.

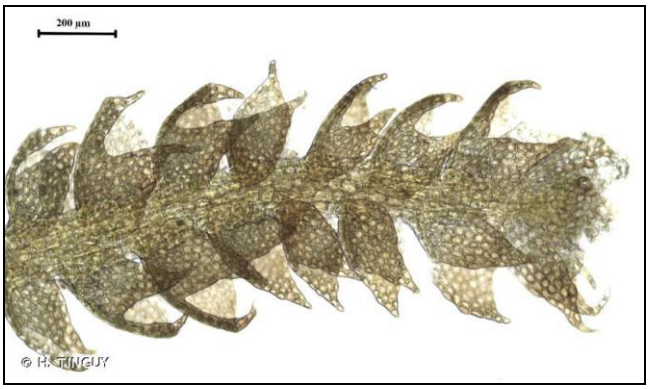

Figure 5. ***Cephalozia ambigua***, a species that may accompany ***Diplophyllum albicans*** on wet cliffs and lake shore rocks. Photo by Hugues Tinguy, with permission.

Figure 6. ***Gymnomitrion concinnatum***, a species that may accompany ***Diplophyllum albicans*** on wet cliffs and lake shore rocks. Photo by Michael Lüth, with permission.

Figure 7. ***Barbilophozia sudetica***, a species that may accompany ***Diplophyllum albicans*** on wet cliffs and lake shore rocks. Photo by Hugues Tinguy, with permission.

Figure 8. ***Marsupella boeckii***, a species that may accompany ***Diplophyllum albicans*** on wet cliffs and lake shore rocks. Photo by Earth.com, with permission.

Figure 9. ***Marsupella emarginata*** subsp. ***tubulosa***, a species that may accompany ***Diplophyllum albicans*** on wet cliffs and lake shore rocks. Photo from Taiwan Moss Color Book, through Creative Commons.

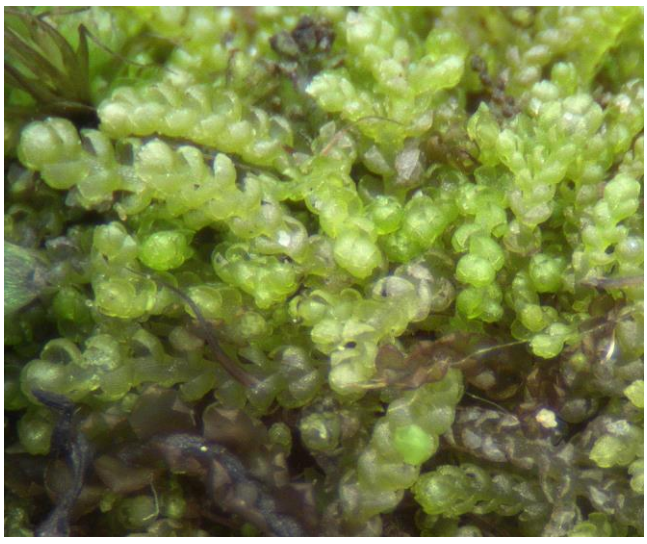

Figure 10. ***Fuscocephaloziopsis albescens***, a species that may accompany ***Diplophyllum albicans*** on wet cliffs and lake shore rocks. Photo by Tomas Hallingbäck, with permission.

Not all of the reported habitats are associated with water. Leach (1930) found them on non-calcareous British scree, associated with ***Racomitrium*** (Figure 11) species. In southern Chile, ***Diplophyllum albicans*** (Figure 2, Figure 12, Figure 14-Figure 15) occurs on sea cliffs where they are subject to seawater spray (Engel & Schuster 1973). The researchers suggest that bryophytes are able to survive the salt spray on these cliffs because of high rainfall and forest drainage that provide fresh water. In the humid Queen Charlotte Islands, Glime and Hong (2002) found ***Diplophyllum albicans*** as epiphytes.

Figure 11. ***Racomitrium heterostichum***; members of this genus accompany ***Diplophyllum albicans*** on non-calcareous British scree. Photo by Jan-Peter Frahm, with permission.

Physiology

Clausen (1964) demonstrated the need for water by ***Diplophyllum albicans*** (Figure 2, Figure 12, Figure 14-Figure 15). In experiments, most cells of this species died at humidities less than 63% at 20ºC. Most stream environments where this species occurs would rarely reach these conditions at this low humidity and this degree of heat. Nevertheless, its tolerance is greater than that of ***Calypogeia arguta*** (Figure 13).

Figure 12. ***Diplophyllum albicans*** in a hydrated state, showing the overlapping shoots. Photo by Hermann Schachner, through Creative Commons.

Figure 13. ***Calypogeia arguta***, a species with poor tolerance of low humidity. Photo by Des Callaghan, with permission.

Reproduction

This species is dioicous, limiting its ability to reproduce sexually (Schuster 1974). However, it can produce abundant gemmae (Figure 14-Figure 15).

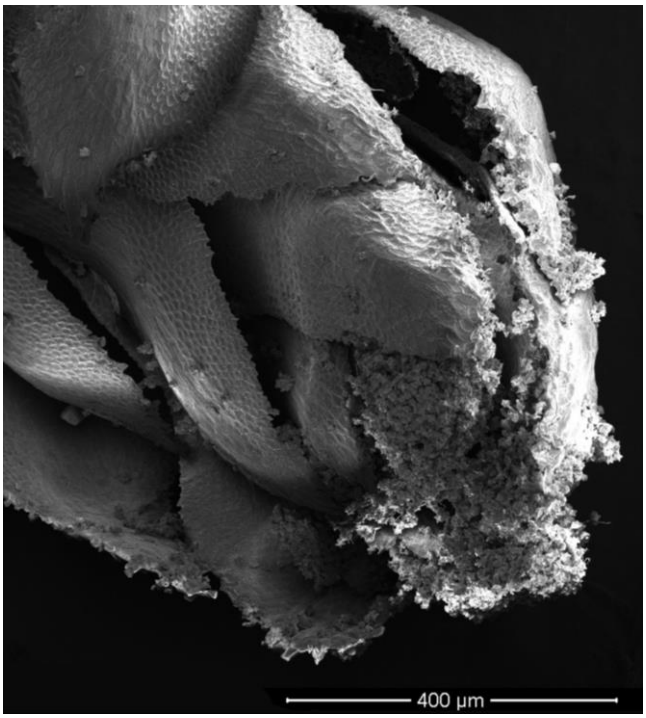

Figure 14. SEM of ***Diplophyllum albicans*** leaves with gemmae. Photo courtesy of Jeff Duckett and Silvia Pressel.

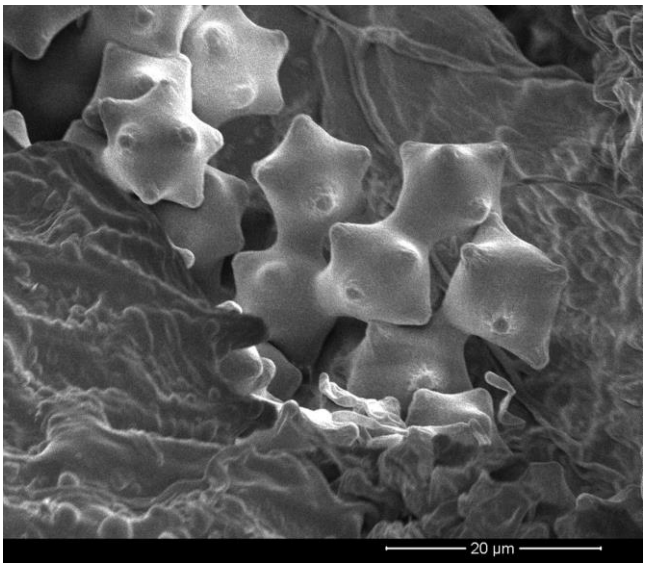

Figure 15. SEM of ***Diplophyllum albicans*** gemmae. Photo courtesy of Jeff Duckett and Silvia Pressel.

Interactions

That ***Diplophyllum albicans*** (Figure 2, Figure 12, Figure 14-Figure 15) is a poor competitor has been demonstrated in high altitude blanket bogs (Rawes 1983). When sheep grazing ceased, this species declined, suggesting that the ability of other plant species, especially ***Calluna vulgaris*** (Figure 16), to increase may have created competition against the ***D. albicans***.

Figure 16. ***Calluna vulgaris***, a species that increases when sheep grazing ceases. Photo by Willow, through Creative Commons.

Diplophyllum albicans (Figure 2, Figure 12, Figure 14-Figure 15) occurring in mossy ravines is frequently a substrate for **Myxomycetes** (slime molds) (Ing 1983). The nature of this relationship is not known.

Fungal Interactions

Like many of the leafy liverworts, ***Diplophyllum albicans*** (Figure 2, Figure 12, Figure 14-Figure 15) can serve as host for the parasitic **Ascomycota** fungus ***Mniaecia jungermanniae*** (Figure 17) (Pressel & Duckett 2006). Although the fungus does not seem to penetrate the cells, its colonization coincides with the formation of giant perichaetia and abnormal perianths, conditions that were also present in wild populations of ***Diplophyllum*** and other species. The association does not appear to cause long-term damage, although it can cause a local reduction of perianth development. Henderson (1972) concluded that this fungus favors **moribund** (at point of death) ***Diplophyllum albicans*** as its substrate.

Figure 17. ***Mniaecia jungermanniae*** on ***Cephalozia bicuspidata***; ***M. jungermanniae*** causes enlarged perianths on ***Diplophyllum albicans***. Photo courtesy of Jan Gaisler.

Biochemistry

This raises the question of its ability to survive and thrive within some plant communities, but not others. Like other liverworts, ***Diplophyllum albicans*** (Figure 2, Figure 12, Figure 14-Figure 15) produces sesquiterpenoids. Their abundance and diversity are evidenced by the discovery of six new sesquiterpenoids and two new norsesquiterpenoids from three liverworts (Adio & König 2007; see also Benešová *et al*. 1975), with one from ***Diplophyllum albicans***. Asakawa *et al*. (1979) had already named "pungent sesquiterpene lactones" from this species. All of these exhibited inhibitory activity toward germination and root elongation in rice husks, suggesting a competitive advantage for the slower-growing liverworts.

Tadesse (2002) found natural plant products in ***Diplophyllum albicans*** (Figure 2, Figure 12, Figure 14-Figure 15) that exhibited antifungal activity, but these were not tested on ***Mniaecia jungermanniae*** (Figure 17). They are known to act against the common fungi ***Botrytis cinerea*** (Figure 18-Figure 19) and ***Alternaria solani*** (Figure 20-Figure 21) (Mekuria *et al*. 1999; Tadesse 2002). Saxena and Harinder (2004; Olofin *et al*. 2013) noted the presence of diplophyllin from ***Diplophyllum albicans***. This compound is active against human epidermoid carcinoma (Ohta *et al*. 1977).

Figure 18. ***Botrytis cinerea*** on tomato; this is a fungus that is inhibited by extracts from ***Diplophyllum albicans***. Photo by Paul Bachi, USDA, through Creative Commons.

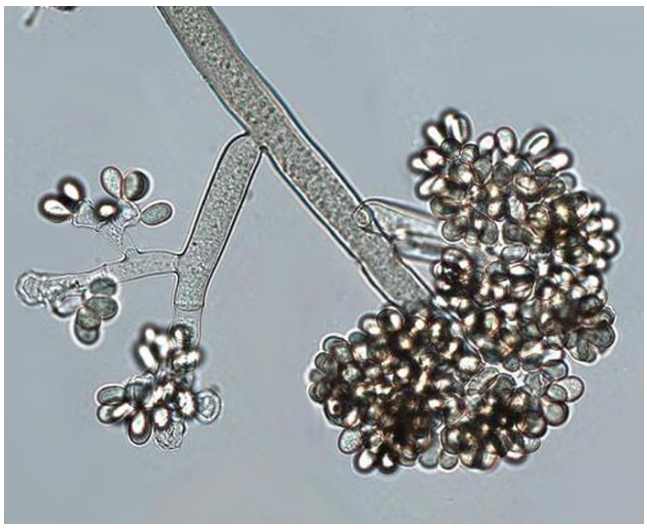

Figure 19. ***Botrytis cinerea*** a fungus that is inhibited by extracts of ***Diplophyllum albicans***. Photo by Paul Bachi, USDA, through Creative Commons.

Figure 20. ***Alternaria solani*** causing stem lesions; this fungus is inhibited by extracts from the liverwort ***Diplophyllum albicans***. Photo from Clemson University USDA, through Creative Commons.

Figure 21. ***Alternaria solani*** spore. Photo by Paul Bachi, through Creative Commons.

Diplophyllum taxifolium (Figure 22-Figure 23, Figure 29)

Distribution

Diplophyllum taxifolium (Figure 22-Figure 23, Figure 29) is a Northern Hemisphere taxon, mostly from temperate and boreal zones in Europe, Asia, Oceania, Alaska, Canada, USA (ITIS 2020a). It extends from Greenland in the East southward to Newfoundland, Labrador, Nova Scotia, Ontario, Maine, south as far as North Carolina and Tennessee and in the west from Alaska, USA, to British Columbia and New Brunswick in Canada, southward to Washington state in the USA (Redfearn 2008).

Figure 22. ***Diplophyllum taxifolium***, a Northern Hemisphere species that extends southward into the mountains. It occurs on humid and wet rock cliffs, rocky stream banks, and on alder hummocks. Photo by Michael Lüth, with permission.

Figure 23. ***Diplophyllum taxifolium*** showing its growth habit. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

On Cape Breton Island, Canada, Nichols (1918) reported ***Diplophyllum taxifolium*** (Figure 22-Figure 23, Figure 29) from rock cliffs associated with streams. Choi *et al*. (2013) found it on wet cliffs along a stream in a mixed conifer-broadleaf forest of Mt. Deogyu National Park at 680-1160 m asl in the Republic of Korea. Here it was often in association with ***Bazzania denudata*** (Figure 24) and ***Calypogeia tosana*** (Figure 25). In the Endybal River Basin, Yakutia, in Russia, ***Diplophyllum taxifolium*** occurs on soil of rocky outcrops along stream banks (Sofronova & Kopyrina 2016). It is typically mixed with ***Cephaloziella varians*** (Figure 26), ***Marsupella emarginata*** (Figure 27), ***Scapania crassiretis*** (Figure 36), and ***Sphenolobus minutus*** (Figure 28). In a different region of Yakutia (Indigirka River), ***Diplophyllum taxifolium*** likewise occurred on wet cliffs, but forming less cover than some of the other liverwort species (Sofronova 2018). At the Ushkovskii Volcano in Kamchatka, Russia, Bakalin (2006) found this species growing between the hummocks and on spots of light soil shaded by alder. In North America, Redfearn (2008) found that it occurs at 0-1950 m asl on shaded rocks, cliffs, soil banks, humus, and frequently along streams.

Figure 24. ***Bazzania denudata***, a species in association with ***Diplophyllum taxifolium*** on rock cliffs by streams. Photo by Kent Brothers, with permission through UBC Botany website.

Figure 25. ***Calypogeia tosana***, a species in association with ***Diplophyllum taxifolium*** on rock cliffs by streams. Photo from Digital Museum, Hiroshima University, with permission.

Figure 26. ***Cephaloziella varians***, a species in association with ***Diplophyllum taxifolium*** on rock cliffs by streams. Photo by Kristian Peters, with permission.

Figure 27. ***Marsupella emarginata***, a species in association with ***Diplophyllum taxifolium*** on rock cliffs by streams. Photo by Hermann Schachner, through Creative Commons.

Figure 28. ***Sphenolobus minutus***, a species in association with ***Diplophyllum taxifolium*** on rock cliffs by streams. Photo by Jan-Peter Frahm, with permission.

Terrestrial

Diplophyllum taxifolium (Figure 22-Figure 23, Figure 29) does occur in habitats that one would expect to get dry (Figure 29). Růžička *et al.* (2012) reported it from periglacial areas in low-altitude scree slopes. The air circulation through these talus slopes creates microclimates that have lower temperatures, often experiencing temperatures <0ºC during snow-free periods. These allow ice to accumulate year-round, as seen on Kamenec Hill in North Bohemia, Czech Republic at only 330 m asl. These habitats serve as refugia for boreal and Arctic bryophytes. The slow melt may keep the atmosphere near the ice sufficiently moist to provide for the needs of the liverworts.

Figure 29. ***Diplophyllum taxifolium*** in a terrestrial habitat. Photo by Michael Lüth, with permission.

Reproduction

Diplophyllum taxifolium (Figure 22-Figure 23, Figure 29) is dioicous (Redfearn 2008). The male and female plants typically are in separate patches, resulting in little fertilization. The male plants are smaller. Hong (1980) states that gemmae are abundant, but none of the pictures I found showed any.

Biochemistry

Diplophyllum taxifolium (Figure 22-Figure 23, Figure 29) exhibits ent-eudesmanolides and entprenylaromadendrones, compounds that provide biological activities that may increase its competitive ability (Wang *et al*. 2016). This species of ***Diplophyllum*** seems to avoid colonization by fungi (Bidartondo & Duckett 2010). We need to test the effectiveness of these secondary compounds in deterring the colonization of common liverwort-inhabiting fungi. These secondary compounds do not seem to prevent at least some fungi from colonizing this species

Douinia ovata (Figure 30)

(syn. = *Harpalejeunea ovata*)

Distribution

Douinia ovata (Figure 30) is a subarctic species, distributed on the Pacific coast of North America from Alaska, USA, to British Columbia, Canada (Váña 1996). It also is known from the Atlantic side of Europe and from Japan.

Figure 30. ***Douinia ovata***, a species distributed along the Pacific coast of North America, the Atlantic side of Europe, and Japan. It is only occasionally submerged. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

Douinia ovata (Figure 30) is not usually an aquatic species, but Watson (1919) reported it as being occasionally submerged. It is among the most common species of the **Lophoziaceae-Scapaniaceae** complex north of the tropics (Söderström *et al*. 2007). Its occurrence is oceanic, suggesting it may be intolerant of a climate with a wide variation.

Adaptations and Reproduction

Douinia ovata (Figure 30) has a **mat** life form and is a perennial stayer (Miyashita 2013). It lacks specialized asexual reproductive structures.

Fungal Interactions

Like ***Diplophyllum taxifolium*** (Figure 22-Figure 23, Figure 29), Wang and Qiu (2006) found no records of fungal associations for this species.

Saccobasis polita (Figure 31)

(syn. = *Sphenolobus politus*)

Distribution

Saccobasis polita (Figure 31) occurs in Austria, Russian Federation (TROPICOS 2020), North America from Alaska to Washington and Colorado, USA (Hong 1994), the Swiss Alps (Geissler 1976), and Norway (Zander 1983).

Figure 31. ***Saccobasis polita***, a species from North America and northern Europe where it occurs in alpine streams. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Watson (1919) reported ***Saccobasis polita*** (Figure 31) in alpine areas on wet ground associated with ***Harpanthus flotovianus*** (Figure 32) and ***Mesoptychia bantriensis*** (Figure 33). Geissler (1976) similarly reported it from alpine streams. Bakalin (2008) found this species in the Nabil'sky Range at 1406 m asl in Russia, where it occurred on fine-grained soil along a stream.

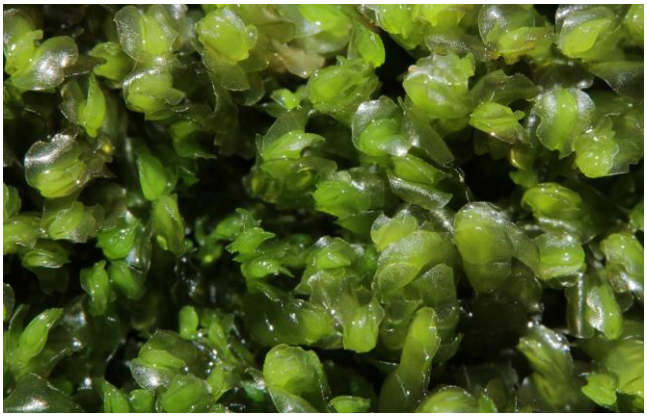

Figure 32. ***Harpanthus flotovianus***, a species associated with ***Saccobasis polita*** in alpine areas on wet ground. Photo by Hermann Schachner, through Creative Commons.

Figure 33. ***Mesoptychia badensis***, a species associated with ***Saccobasis polita*** in alpine areas on wet ground. Photo by Štěpán Koval, with permission.

Reproduction

In Norway, ***Saccobasis polita*** (Figure 31) plants produce gemmae, but these appear to be different from those reported elsewhere for the species and appear to represent at least a different variety (Damsholdt 1983). Jóhannsson (1984) found that ssp. ***polita*** is widely distributed, but that in Iceland one can find ssp. ***polymorpha*** as well. This latter purported subspecies produces prolific gemmae there on the sandy lava, differing from ssp. ***polita*** that prefers stream banks, bogs, and otherwise very wet habitats. But Jóhannsson argues that the taxonomic character of gemmae used to separate the subspecies does not separate them at all.

Scapania (Figure 34-Figure 158)

Scapania (Figure 34-Figure 158) presents a number of species that occur in or near water. Vuori *et al*. (1999) noted a number of these in small, pristine streams of the Tolvajärvi region in the Russian Karelia.

Scapania aspera (Figure 34-Figure 35)

Distribution

Scapania aspera (Figure 34-Figure 35) is distributed throughout Europe, but is also known from subarctic eastern Siberia (Borovichev *et al*. 2016).

Figure 34. ***Scapania aspera***, a European calcicole. Photo by Hermann Schachner, through Creative Commons.

Figure 35. ***Scapania aspera*** showing its mat habit. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Scapania aspera (Figure 34-Figure 35) occurred at a spring in Tara River canyon and Durmitor area, Montenegro (Papp & Erzberger 2011).

Reproduction

Harrington (1966a, b) experimented with ***Scapania aspera*** (Figure 34-Figure 35) and determined that neither spores nor gemmae would germinate in the absence of calcium. Spore germination was even reduced at 10 mg L^{-1} calcium. Borovichev *et al*. (2016) supported this preference for calcareous rock by their discovery of the species in Siberia at least 3000 km from the nearest known location of the species. The area is known for its calcareous rock outcrops. It is interesting that the molecular distances between these populations and the European populations are extremely low.

Biochemistry

When Bukvicki *et al*. (2013) extracted the chemical constituents from this species using solid phase micro extraction gas chromatography-mass spectrometry, they

were able to identify 96 compounds. These demonstrated inhibitory activity against yeast and bacterial strains, with a higher zone of inhibition for yeast than for bacteria. The activity against fungi needs ecological investigation. It is possible that these liverworts could interfere with mycorrhizal relationships needed by rooted plants near them.

Scapania crassiretis (Figure 36)

(syn. = *Scapania nemorea* subsp. *crassiretis*)

Distribution

Scapania crassiretis (Figure 36) is a Northern Hemisphere species known from Greenland to Colorado, USA (EOL 2020). It occurs in Europe and Asia as well (ITIS 2020b).

Figure 36. ***Scapania crassiretis***, a species in association with ***Diplophyllum taxifolium*** on rock cliffs by streams. Photo from Earth.com, with permission.

Aquatic and Wet Habitats

Vitt and Horton (1979) found ***Scapania crassiretis*** (Figure 36) on an east-facing shale cliff in the Olgivie Mountains in the Yukon, Canada. Konstantinova and Vasiljev (1994) found the species in the Malaya Golaya River mouth of southern Siberia, where it occurred on the river bank, or rocks at 1100 m asl and was associated with ***Scapania rufidula*** and ***Tritomaria exsecta*** (Figure 37). In the Lower Golaya River Konstantinova and Vasiljev found it on a cliff associated with ***Sphenolobus minutus*** (Figure 28) and ***Diplophyllum obtusifolium*** (Figure 38). Konstantinova *et al*. (2002) found the species on the soil bank of a small creek and on alpine wet cliffs of the Upper Bureya River in the Russian Far East.

Figure 37. ***Tritomaria exsecta***, a species associated with ***Scapania crassiretis*** on river banks in southern Siberia. Photo by Michael Lüth, with permission.

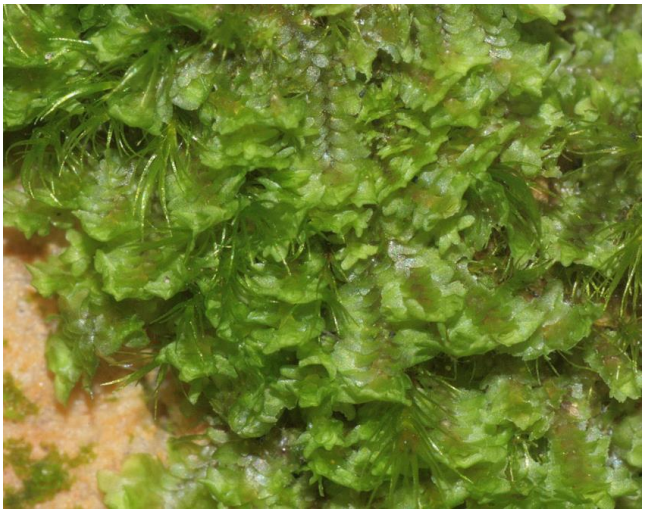

Figure 38. ***Diplophyllum obtusifolium***, a species associated with ***Scapania crassiretis*** on river banks in southern Siberia. Photo by Hermann Schachner, through Creative Commons.

Scapania cuspiduligera (Figure 39, Figure 43-Figure 44)

Distribution

Scapania cuspiduligera (Figure 39, Figure 43-Figure 44) occurs in the mountains of China (Cao *et al*. 2003) and the Chichibu Mountains of Japan (Inoue 1958). It is known from the Russian Federation (TROPICOS 2020), Europe, North America, and South America (ITIS 2020c), but it is absent in the tropics (DiscoverLife 2020). In western North America it is Arctic-alpine (Hong 1980). Puglisi *et al*. (2013) described the species as a circumpolar boreo-Arctic montane species, but it is very rare in the Mediterranean area where it only occurs in Spain, France, and Italy.

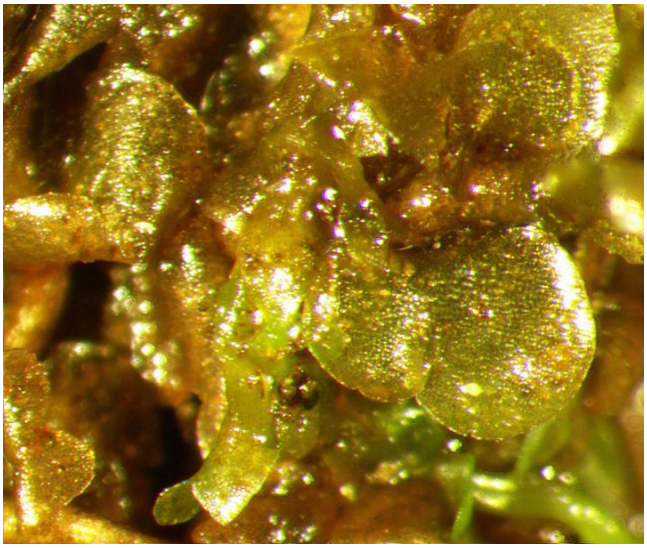

Figure 39. ***Scapania cuspiduligera***, a boreo-Arctic circumpolar montane species that extends to the Mediterranean area. It can be aquatic, but also prefers calcareous terrestrial habitats. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman and Karen Blisard.

Aquatic and Wet Habitats

In Finland, Koponen *et al*. (1995) considered this species to be aquatic. Bosanquet (2020), based on his experience in the British Isles, described this as a species mostly from upland habitats. It creeps over ***Gymnostomum aeruginosum*** (Figure 40) and other mosses that occur in crevices in damp, base-rich crags. Its habitats in Wales include drier habitats such as calcareous turf on spoil heaps of limestone quarries. In Scotland, it occurs at sea level on the damp ground found in calcareous dunes. In the Machtum-Kelsbaach of Luxembourg, ***Scapania cuspiduligera*** (Figure 39, Figure 43-Figure 44) occurs in a calcareous ravine (Werner & Caspari 2002). In the Sayan Mountains of southern Siberia it occurs in cliff crevices of the high mountains, often associated with ***Blepharostoma trichophyllum*** (Figure 4), but also with ***Mesoptychia gillmanii*** (Figure 41) and ***Preissia quadrata*** (Figure 42) at 1050 m asl on rocks at the river bank (Konstantinova & Vasiljev 1994).

Figure 40. ***Gymnostomum aeruginosum***; ***Scapania cuspiduligera*** creeps over this and other species in crevices in damp, base-rich crags. Photo by Bob Klips, with permission.

Figure 41. ***Mesoptychia cf. gillmanii***, a species that occurs with ***Scapania cuspiduligera*** in cliff crevices of the high mountains. Photo by Michael Lüth, with permission.

Figure 42. ***Preissia quadrata***, a species that occurs with ***Scapania cuspiduligera*** in cliff crevices of the high mountains. Photo by Andy Hodgson, with permission.

In western Canadian montane streams, this species can be classified as a restricted terrestrial species (Vitt *et al*. 1986), occurring in montane streams and on stream banks (Glime & Vitt 1987).

Reproduction

Gemmae are common in the genus ***Scapania***, including reddish to brownish gemmae in ***Scapania cuspiduligera*** (Figure 43-Figure 44).

Figure 43. ***Scapania cuspiduligera*** with patches of brown gemmae on leaves near the tips. Photo by Hugues Tinguy, with permission.

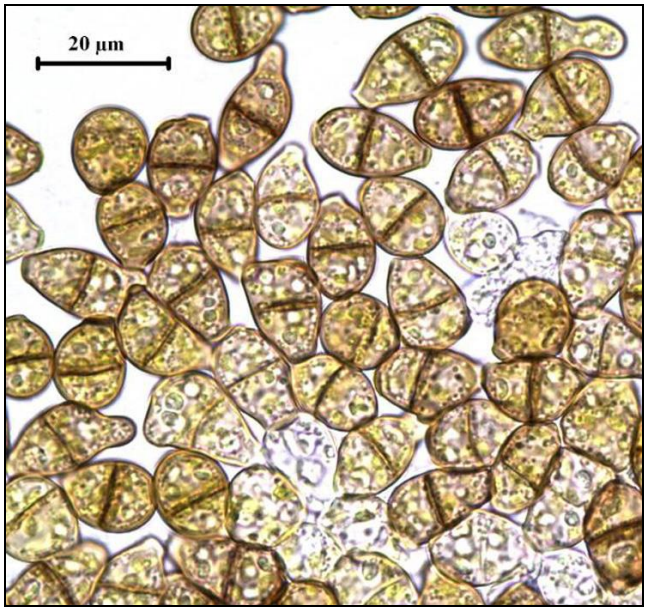

Figure 44. ***Scapania cuspiduligera*** gemmae showing their 2-celled structure. Photo by Hugues Tinguy, with permission.

Fungal Interactions

Wang and Qiu (2006) found no records of mycorrhizae on ***Scapania cuspiduligera*** (Figure 39, Figure 43-Figure 44). But in 2010, Bidartondo and Duckett found UK populations in association with ***Sebacina*** (Figure 45). It is of interest that they found identical fungal DNA from two locations; they suggested that this might result from long-distance dispersal of either the liverwort or the fungus, perhaps together.

Figure 45. ***Sebacina sparassoidea*** on moss, in a fungus genus that forms associations with ***Scapania cuspiduligera***. Photo by Dave W., through Creative Commons.

Scapania hyperborea (Figure 46, Figure 50)

Distribution

Scapania hyperborea (Figure 46, Figure 50) is almost exclusively Arctic, but it does extend into some alpine areas in North America (3900 m in Colorado, USA), but is not known from European alpine areas (Schuster 1974).

Figure 46. ***Scapania hyperborea***, an Arctic-alpine species that inhabits sunny areas of wetlands. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Scapania hyperborea (Figure 46, Figure 50) forms golden brown to reddish brown patches or dense mats (Figure 46) (Schuster 1974). In the Arctic it is often associated with other wetland bryophytes [***Paludella squarrosa*** (Figure 47), ***Drepanocladus*** *s.l.* (Figure 48), ***Gymnocolea inflata*** (Figure 49), ***Fuscocephaloziopsis albescens*** (Figure 10), and others] in sunny areas with seepage or around rock pools and tarns. In low-lying swales and marshy areas it exhibits vigorous growth, but when growing over dead peat the creeping growth can be very small, typically under 2 mm wide.

Figure 47. ***Paludella squarrosa***, an associate of ***Scapania hyperborea*** in wetlands. Photo by Hermann Schachner, through Creative Commons.

Figure 48. ***Drepanocladus aduncus***; some species of ***Drepanocladus*** are associates of ***Scapania hyperborea*** in wetlands. Photo by Hermann Schachner, through Creative Commons.

Figure 49. ***Gymnocolea inflata***, an associate of ***Scapania hyperborea*** in wetlands. Photo by Michael Lüth, with permission.

Koponen *et al*. (1995) reported ***Scapania hyperborea*** (Figure 46) as aquatic in Finland. Choi *et al*. (2012) report it from Russia in hummocky sedge-moss communities and wet, peaty roadsides in the tundra zone, ranging from 14 to 1300 m asl. Sofronova and Potemkin (2018) report it from 700-1859 m asl in Russia, growing typically on acid rocks in sheltered niches with other leafy liverworts. In the tundra belt it occurs on moist soil on rocky outcrops, also associated with other leafy liverworts. In Sweden, Ohlson *et al*. (1997) found it in old-growth swamp forests.

Terrestrial

In the forest and tundra belt of Yakutia, Russia, ***Scapania hyperborea*** (Figure 46, Figure 50) occurs at 700-1859 m asl, typically growing on acid rocks (Figure 50) and in sheltered niches (Sofronova & Potemkin 2018). It frequently associates with ***Lophoziopsis excisa*** (Figure 51), ***Scapania microdonta*** (Figure 70), ***Scapania sphaerifera***, ***Scapania spitsbergensis***, ***Sphenolobus saxicola*** (Figure 52), ***Sphenolobus minutus*** (Figure 28), ***Tetralophozia setiformis*** (Figure 53), and ***Trilophozia quinquedentata*** (Figure 54).

Figure 50. ***Scapania hyperborea***, growing here on a dry rock. Photo by Michael Lüth, with permission.

Figure 51. ***Lophoziopsis excisa***, a species that grows with ***Scapania hyperborea*** at high elevations and in boreal regions. Photo from Earth.com, with permission.

Figure 52. ***Sphenolobus saxicola***, a species that grows on acid rocks with ***Scapania hyperborea*** at high elevations and in boreal regions. Photo by Jean Faubert, with permission.

Figure 53. ***Tetralophozia setiformis***, a species that grows on acid rocks with ***Scapania hyperborea*** at high elevations and in boreal regions. Photo by Michael Lüth, with permission.

Figure 54. ***Trilophozia quinquedentata***, a species that grows on acid rocks with ***Scapania hyperborea*** at high elevations and in boreal regions. Photo by Hugues Tinguy, with permission.

Scapania irrigua (Figure 55-Figure 56)

Distribution

Scapania irrigua (Figure 55-Figure 56) is a widely distributed Holarctic species that extends southward to the Coniferous Forest Biome and the northernmost edge of the Deciduous Forest Biome (Schuster 1974). It occurs throughout Europe, south to England, and is recorded from Japan.

Figure 55. ***Scapania irrigua***, a widely distributed Holarctic species that occurs in standing and running water and in bogs and in other wet habitats. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman and Karen Blisard.

Figure 56. ***Scapania irrigua*** growing in a mat with mosses. Photo by David T. Holyoak, with permission.

Aquatic and Wet Habitats

Scapania irrigua (Figure 55-Figure 56) is considered by Watson (1919) as occasionally submerged (Watson 1919). Geissler (1976) reported it from alpine streams in the Swiss Alps; Geissler and Selldorf (1986) noted that it occurred with the sedge ***Baeothryon cespitosum*** (Figure 57), but was uncommon with ***Eleocharis quinqueflora*** (Figure 58) and the moss ***Paludella squarrosa*** (Figure 47). Koponen *et al*. (1995) considered it to be aquatic in Finland. Schuster (1974) stated that it is usually associated with standing water, although the later observations of Geissler would seem to broaden that habitat to running water. It is often in bogs with ***Sphagnum*** and ***Polytrichum*** (Figure 59), occurs on peat at lake margins (Figure 60), can withstand *p*H below 4, and seems to be most frequently associated with sunny rock pools (Schuster 1974). By contrast, it also occurs in wet, springy depressions of calcareous ***Thuja*** swamps (Figure 61) and on moist, loamy soil (Schuster 1974). On the Isle of Arran off the coast of

Scotland, Travis (1917) reported this species from wet soil on the shore.

Figure 57. ***Baeothryon cespitosum***, a species that accompanies ***Scapania irrigua*** in the Swiss Alps. Photo by Hermann Schachner, through Creative Commons.

Figure 58. *Eleocharis quinqueflora*, a species where ***Scapania irrigua*** is an uncommon companion in the Swiss Alps. Photo by Max Licher, through Creative Commons.

Figure 59. ***Polytrichum commune*** and ***Sphagnum*** habitat suitable for ***Scapania irrigua***. Photo with online permission.

Figure 60. Perrault Fen peat surrounding small lake in the Keweenaw Peninsula of Michigan, USA. Photo by Janice Glime.

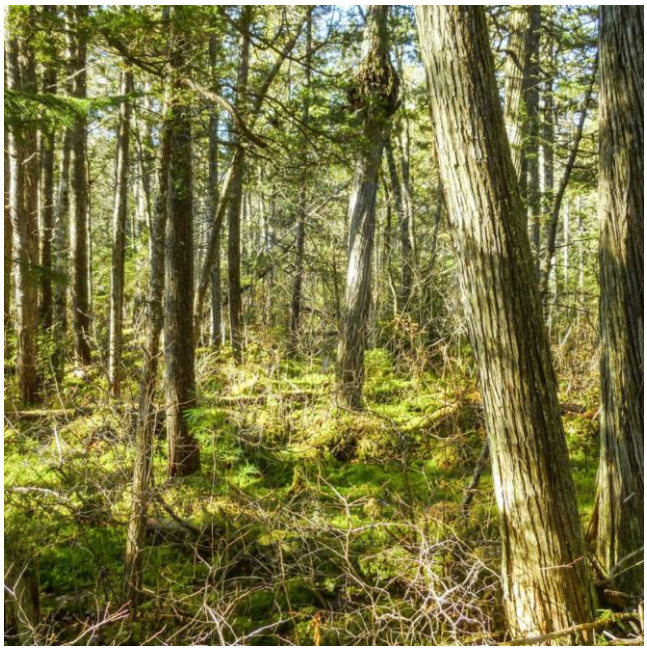

Figure 61. ***Thuja*** swamp habitat suitable for ***Scapania irrigua***. Photo by Allen Norcross, with permission.

In central Europe, ***Scapania irrigua*** (Figure 55-Figure 56) forms part of the *Cardamino-Montention* suballiance (Zechmeister & Mucina 1994). This alliance is comprised of ***Scapania irrigua***, *Carex frigida* (Figure 62), and *Luzula*

alpinopilosa (Figure 63). These species all have an alpine distribution in spring communities.

Figure 62. ***Carex frigida***, a member of the alliance with ***Scapania irrigua*** in central Europe. Photo by Michael Kesl, through Creative Commons.

Figure 63. ***Luzula alpinopilosa***, a member of the alliance with ***Scapania irrigua*** in central Europe. Photo by Hugues Tinguy, through Creative Commons.

In the Algama River Basin of southeastern Yakutia, Russia, ***Scapania irrigua*** (Figure 55-Figure 56), occurs on sand between rocks, where it often occurs with ***Blasia pusilla*** (Figure 64) and ***Solenostoma confertissimum*** (Figure 65) (Sofronova 2013). It also occurs on river banks, on rotting wood, and in habitats with ***Gymnocolea inflata*** (Figure 49) and ***Scapania paludicola*** (Figure 84-Figure 88). In the Franconia Mountains of New Hampshire, USA, ***S. irrigua*** occurs on the shores of Eagle Lake where it is associated with ***Mylia anomala*** (Figure 66), ***Gymnocolea inflata***, and ***Calypogeia sphagnifolia*** (Figure 67) on the ***Sphagnum*** (Figure 59) (Lorenz 1908).

Figure 64. ***Blasia pusilla***, a species that often occurs with ***Scapania irrigua*** on sand between rocks. Photo by Hermann Schachner, through Creative Commons.

Figure 65. ***Solenostoma confertissimum***, a species that often occurs with ***Scapania irrigua*** on sand between rocks. Photo by Hermann Schachner, through Creative Commons.

Figure 66. ***Mylia anomala*** with ***Sphagnum***, two taxa that often occur with ***Scapania irrigua***. Photo by Blanka Aguero, with permission.

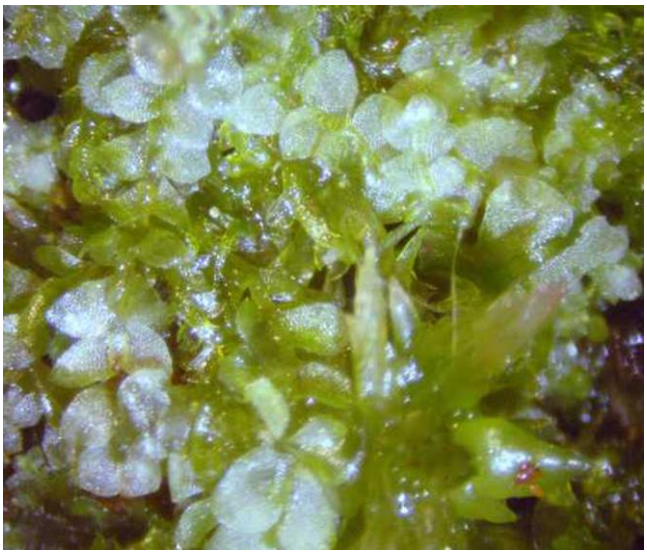

Figure 67. ***Calypogeia sphagnifolia***. Photo by Scot Loring, through Creative Commons.

Adaptations

In bright light, ***Scapania irrigua*** can develop brown protective pigments (Figure 68). The gemmae (Figure 69) in this species are not as protected as in some species.

Figure 68. ***Scapania irrigua*** showing a brown form. Photo by J. C. Schou, with permission.

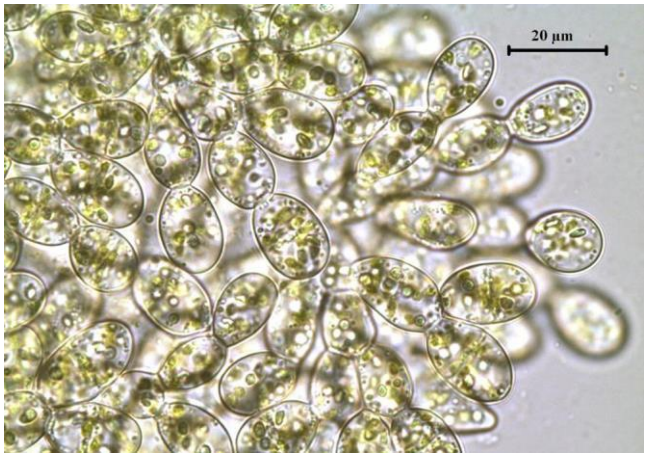

Figure 69. ***Scapania irrigua*** gemmae showing thin walls. Photo by Hugues Tinguy, with permission.

Biochemistry

Scapania irrigua (Figure 55-Figure 69) is among the many bryophytes that have been tested for secondary compounds. Zhang *et al*. (2015) have identified diterpenoids that are active against some human cancer cell lines. Although many liverworts have exhibited anti-cancer properties, the medical and pharmaceutical professions have done little to pursue this ability as an actual treatment.

Scapania microdonta (Figure 70)

Distribution

Scapania microdonta (Figure 70) has an amphi-Pacific distribution (Kuznetsova *et al*. 2010) in the Arctic and subarctic of North America and Asia (Wagner 2017).

Aquatic and Wet Habitats

Scapania microdonta (Figure 70) occurs on shaded rocks, cliffs, and crevices in gravelly barrens (Wagner 2017). Konstantinova *et al*. (2002) reported it from a wet cliff on the south-facing slopes and rocks on the lake shore of the Upper Bureya River in the Russian Far East.

Figure 70. ***Scapania microdonta*** (herbarium specimen), a species that can occur on wet cliffs and lake shores. Photo by CBG Photography Group, through Creative Commons.

In the forest and tundra belt of Yakutia, Russia, ***Scapania microdonta*** (Figure 70) occurs at 700-1859 m asl, typically growing on acid rocks and in sheltered niches (Sofronova & Potemkin 2018). It frequently associates with ***Lophoziopsis excisa*** (Figure 51), ***Scapania hyperborea*** (Figure 46-Figure 50), ***Scapania sphaerifera***, ***Scapania spitsbergensis***, ***Sphenolobus saxicola*** (Figure 52), ***Sphenolobus minutus*** (Figure 28), ***Tetralophozia setiformis*** (Figure 53), and ***Trilophozia quinquedentata*** (Figure 54). It seems to rarely be in wet habitats.

Scapania nemorea (Figure 71-Figure 79)

(syn. = *Scapania nemorosa*, *Scapania nemorosa* var. *uliginosa*)

Distribution

Scapania nemorea (Figure 71-Figure 79) occurs from Europe to Asia, south to Oceania, and in North America from Alaska to the continental USA to Hawaii (UNB 2020). This seems inconsistent with the amphi-Atlantic distribution given by Kuznetsova *et al*. (2010). In fact, Schuster (1974) puts it mostly in temperate regions, but extending northward in Europe to Sweden, Norway, and Finland and in North America as far south and inland as Louisiana. In much of its range it is the most ubiquitous species of ***Scapania*** (Schuster 1974).

Figure 71. ***Scapania nemorea***, a Northern Hemisphere species, south to Hawaii, but mostly temperate. It is typical in moist habitats in a zone above ***Scapania undulata*** (Figure 125-Figure 136). Photo by Hermann Schachner, through Creative Commons.

Figure 72. ***Scapania nemorea*** showing a lighter color form. Photo by Rick Ballard, through Creative Commons.

Figure 73. ***Scapania nemorea*** with apical gemmae. Photo by Blanka Aguero, with permission.

Aquatic and Wet Habitats

Koponen *et al*. (1995) found ***Scapania nemorea*** (Figure 71-Figure 79) to be aquatic in Finland. It occurs along rivers (Figure 74) and on wet or moist cliffs of ravines in Connecticut, USA. On Cape Breton Island, Canada (Nichols 1918) and in the Appalachian Mountains, USA (Glime 1968), it is likewise associated with streams. In New Hampshire, USA, it occurs on rocks that are normally above the water level in a headwater stream (Glime 1970). In the Haute Ardenne rivers of Belgium it occurs on earthy and gravelly substrates on river banks (Leclercq 1977). It is rare in upstream reaches in the Harz Mountains of Germany (Bley 11987). In marshes it is usually associated with fast water (Watson 1919). Coroi *et al*. (2004) considered to be a diagnostic streamside species in southern Ireland.

Figure 74. ***Scapania nemorea*** growing just above the water level. Photo by Bernd Haynold, through Creative Commons.

But it can also occur in less aquatic habitats. At the Flume of Franconia Notch, New Hampshire, USA, it occurs on bedrock near the stream edge, on the flume wall, and on ledges in the flume (Glime 1982). Cleavitt (1996) likewise found it to be common growing on moist rock ledges in the White Mountain National Forest, New Hampshire, as well as on rocks in streams.

In the northwestern European region of Russia, Potemkin (2018) found it with ***Calypogeia fissa*** (Figure 75) both in a rock crevice with seepage and on soil in a rock fissure with seepage. In the alder swamps of southern Sweden, Darell and Cronberg (2011) found it only close to the ground on "stools" and stones where it was both humid and shaded; they did not find it in streams, but only on their banks, as well in flooded black alder stools. Thus, it occurs not only on rocks in streams, but also in moist habitats such as on moist rocks, moist rotting logs, and loam or clay on stream banks (UNB 2020).

Figure 75. ***Calypogeia fissa***, a species that occurs with ***Scapania nemorea*** in a rock crevice with seepage and on soil in a rock fissure with seepage. Photo by Hermann Schachner, through Creative Commons.

In my own experience, this species occurred in association with Appalachian Mountain streams, but it was always in less wet locations than was ***Scapania undulata*** (Figure 125-Figure 136), especially when it was only centimeters away. Weber (1976) reported similar moisture relationships, with ***S. undulata*** in Cataracts Provincial Park, Newfoundland, Canada, being confined to submerged or emergent rocks and ***S. nemorea*** (Figure 71-Figure 79) growing optimally in the inundation zone – a narrow strip along the river that is submerged only periodically (Figure 76). There ***S. nemorea*** is also part of the rich bryophyte flora on dripping rock faces and other seepage areas.

Figure 76. ***Scapania nemorea*** on rock, near Swallow Falls Park, Maryland, growing just above water level. Photo by Janice Glime.

Scapania nemorea (Figure 71-Figure 79) is calciphobic (Nichols 1916). Dulin (2008) described it as a rare **nemoral** (inhabiting woods or groves) amphi-oceanic species that was confined to rare substrates on the bank of the Bolshaja Khozja River in the Komi Republic of Russia. Adlassnig *et al.* (2013) found that this species formed lush carpets in a metal-contaminated site in Salzburg, Austria, where the substrate was the acidic soil of a spoil heaps on both banks of Brown Creek.

Reproduction

Reproduction by gemmae (Figure 77) is likely to be important in this species. Laaka-Lindberg *et al*. (2003) considered size of propagules to be important in determining the number produced. ***Scapania nemorea*** (Figure 71-Figure 79) typically produces up to 500-700 one-celled gemmae per leaf (Figure 77-Figure 79), whereas ***Radula complanata*** (Figure 80) produces multicellular gemmae that number only 15-45 per leaf (Figure 80-Figure 81).

Figure 77. ***Scapania nemorea*** with gemmae at the shoot tips. Photo by William Schachner, through Creative Commons.

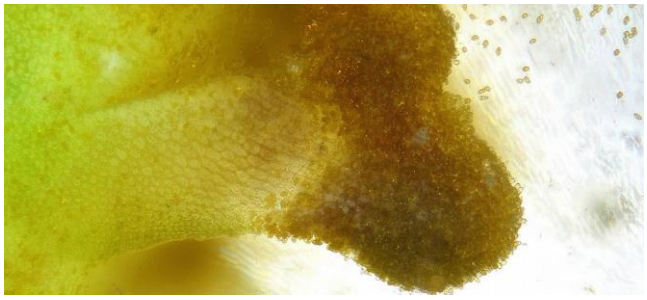

Figure 78. ***Scapania nemorea*** gemmae, showing how numerous they are. Photo by Dick Haaksma, with permission.

Figure 79. ***Scapania nemorea*** gemmae. Photo by Dick Haaksma, with permission.

Figure 80. ***Radula complanata*** with multicellular gemmae on leaf margin. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman and Karen Blisard.

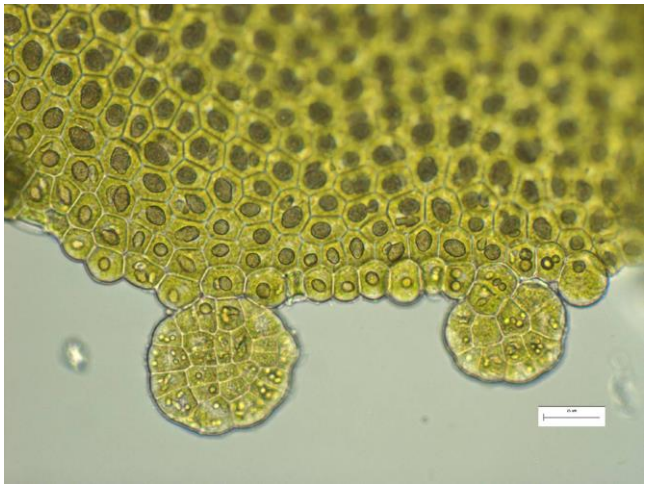

Figure 81. ***Radula complanata*** multicellular gemmae. Photo by Blanka Aguero, with permission.

Nevertheless, this species produces sporophytes (Figure 82), indicating successful sexual reproduction, as seen here from a population near Swallow Falls Park, Maryland, USA.

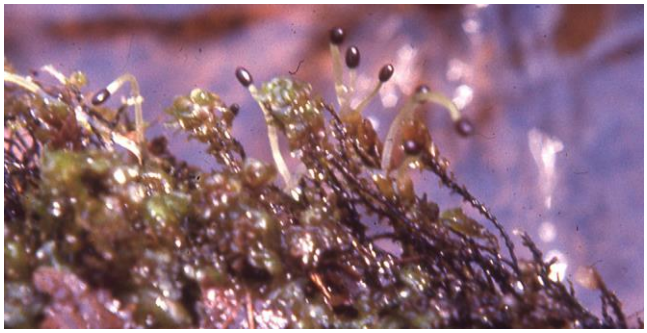

Figure 82. ***Scapania nemorea***, near Swallow Falls Park, Maryland, USA, showing capsules with water nearby.

Fungal Interactions

We know from the work of Egertová *et al*. (2016) that ***Mniaecia jungermanniae*** (Figure 17) is a bryophyte-loving ascomycetous fungus that occurs on ***Scapania nemorea*** (Figure 71-Figure 74, Figure 76), although this fungus is more common on another member of the **Scapaniaceae**, ***Diplophyllum albicans*** (Figure 2, Figure 12, Figure 14-Figure 15). All of the locations where the association occurred had acidic bedrock and included sandstone, granite, and phyllite. These were typically in the shade of coniferous or broad-leafed forests where there was a rich liverwort cover.

Biochemistry

Knowledge of biochemistry can help us to separate difficult taxa. In 1981, Zehr undertook the investigation of variation in ***Scapania nemorea*** (Figure 71-Figure 79). He found that variation of terpenes correlated with the substrate, suggesting a potential plastic adaptation to the habitat. These results also indicate that terpene constituents are not suitable for demarcating species or lower levels of classification in ***Scapania***.

Scapania nemorea (Figure 71-Figure 79) produces volatile compounds such as sesquiterpenes that exhibit antimicrobial activity against the common yeast, ***Saccharomyces cerevisiae*** (Figure 83) (Bukvicki *et al*. 2014). Whereas these studies were conducted to consider the potential for preservation of foods, we need to examine their importance in determining the ability of these liverworts to survive in wet habitats that could be otherwise suitable for fungi.

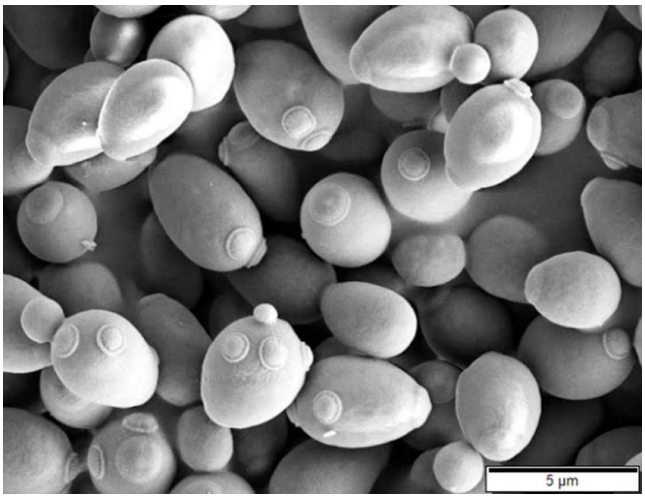

Figure 83. ***Saccharomyces cerevisiae*** (yeast) SEM. Photo by Mogana Das Murtey and Patchamuthu Ramasamy, through Creative Commons.

On the one hand, it is good news that bryophytes may help us to solve both cancer problems and food preservation, but this can be bad news for the bryophytes. Studlar and Peck (2007) considered not only the harvesting of the bryophytes for various uses, especially horticultural, but also the incidental species that often are harvested with them, to be detrimental to their success. They considered ***Scapania nemorea*** (Figure 71-Figure 74, Figure 76) to be only a facultative aquatic and expressed concern regarding its incidental harvesting in mesic habitats.

Scapania paludicola (Figure 84-Figure 88)

Distribution

Scapania paludicola (Figure 84-Figure 88) is circumboreal and circumpolar (Schuster 1974). In North America, it extends southward to New York and Michigan in the eastern USA and from Alaska, USA, through the Northwest Territories, Yukon, and Alberta in Canada, south to Montana, USA (Hong 1980). In Eurasia it extends from central Europe northward to Scandinavia and eastward to Russia and Siberia, reaching Japan in the south and Iceland in the north.

Figure 84. ***Scapania paludicola***, a species that is circumboreal and circumpolar, extending southward into the mountains. Photo by Jan-Peter Frahm, with permission.

Figure 85. ***Scapania paludicola*** in a common upright growing position. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Scapania paludicola (Figure 84-Figure 88) is almost completely restricted to bogs (or poor fens; Figure 88), but in the tundra it can occur on wet granite rocks, especially at the margins of pools and shallow lakes (Schuster 1974). In these habitats it typically occurs with other liverworts. In peat bogs it is sometimes submerged, but it also grows among ***Sphagnum*** (Figure 59) where it is barely above the water level. In shaded spots, it is green, but in sunny spots it is purplish black to copper red. It seems to prefer a *p*H of 5.5 or lower, occurring widely in granitic mountain areas. Geissler and Selldorf (1986) found it associated with *Carex goodenoughii* and uncommonly with ***Eleocharis quinqueflora*** (Figure 58) in moors of Switzerland. ***Scapania paludicola*** (Figure 84-Figure 88) occurs in the Upper Karasu River, Turkey, at 1850 m and in a swampy meadow near a pool (Konstantinova & Vasiljev 1994). Sofronova (2018) reported ***S. paludicola*** from 500 to 1200 m asl along the upper course of the Indigirka River, eastern Yakutia, Russia, where it was present on the soil of grass mires and on brook and river banks. Color forms vary (Figure 87-Figure 88).

Figure 86. ***Scapania paludicola***, Perrault Fen (poor fen), Michigan, USA. Photo by Janice Glime.

Figure 87. ***Scapania paludicola*** illustrating green color and growth habit. Photo by David T. Holyoak, with permission.

Figure 88. ***Scapania paludicola*** showing a dark brown form. Photo by Michael Lüth, with permission.

Scapania paludosa (Figure 89-Figure 92)

Based on his studies on the isozymes of a number of ***Scapania*** species, Zehr (1981) concluded that ***Scapania paludosa*** (Figure 89-Figure 92) should be combined with ***Scapania uliginosa*** (Figure 103-Figure 109). Söderström *et al*. (2016) have not recognized this combination, so I shall maintain separate discussions for these two species.

Distribution

Scapania paludosa (Figure 89-Figure 92) seems to be either rare or infrequent in alpine and subalpine areas and has a restricted distribution (Schuster 1974). It is Holarctic, mostly in the Spruce-Fir Biome and southern tundra. In Europe it occurs in the Alps, north to Scandinavia and east to Siberia; it also occurs in Iceland, Greenland, and Japan. In North America it extends from Alaska south to Oregon in the west and in the east on Isle Royale, Michigan, USA, reaching as far south as Massachusetts along the eastern coast.

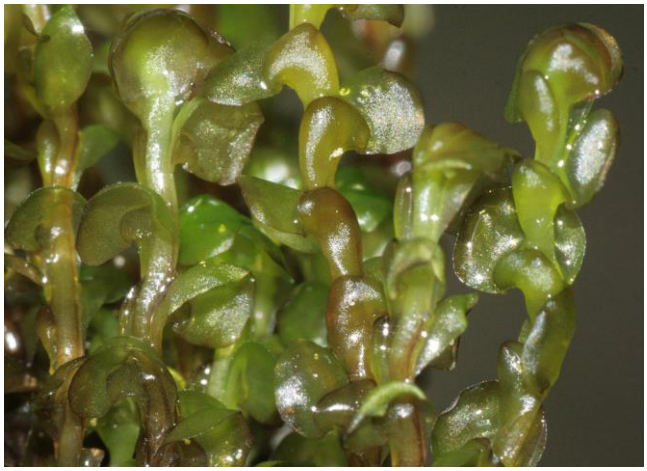

Figure 89. ***Scapania paludosa***, a Holarctic species that is mostly restricted to alpine rills and springs. Photo by Hermann Schachner, through Creative Commons.

Figure 90. ***Scapania paludosa*** in a wet habitat such as a spring. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Koponen *et al*. (1995) listed ***Scapania paludosa*** (Figure 89-Figure 92) as an aquatic species in Finland. The habitat differs from that of ***Scapania paludicola*** (Figure 84-Figure 88) by the occurrence of ***S. paludosa*** restricted to alpine rills and springs (Figure 91-Figure 92), but not swift streams (Schuster 1974). It attaches to rocks, sticks, or stones and may be submerged or submersed in the spring. But it can also occur in alpine bogs. It frequently associates with other members of the genus. It can also occupy stones in snow-water brooks.

Figure 91. ***Scapania paludosa*** growing at the side of a spring or rill with tracheophytes encroaching into the mounds of liverworts. Photo by Hermann Schachner, through Creative Commons.

Figure 92. ***Scapania paludosa*** showing the density its mats can form. Photo by Hermann Schachner, through Creative Commons.

Shacklette (1965) found that the stems of ***Scapania paludosa*** (Figure 89-Figure 92) on Yakobi Island, Alaska, USA, could become intertwined to a degree that could dam the swift mountain rivulet, causing a series of terraced pools. The liverworts are able to close the pool surface, permitting tracheophytes to invade the mat. Lepp (2012)

reported it from the edges of a small stream through a steep ravine in Alaska. Sjörs and Een (2000) found ***Scapania paludosa*** in numerous springs in Muddus National Park in northern Sweden. Likewise, Smieja (2014) reported 51 taxa of liverworts at springs in the Polish Tatra Mountains. Among these, ***Scapania paludosa*** finds its optimum ecology in the **crenic** (referring to a spring and brook water flowing immediately from it) habitats. Figure 95-Figure 96 show the preferred temperatures, altitude, and water *p*H that make these alpine habitats suitable for the species, where it is entirely restricted to bryophyte-dominated springs, forming extensive, swollen turfs.

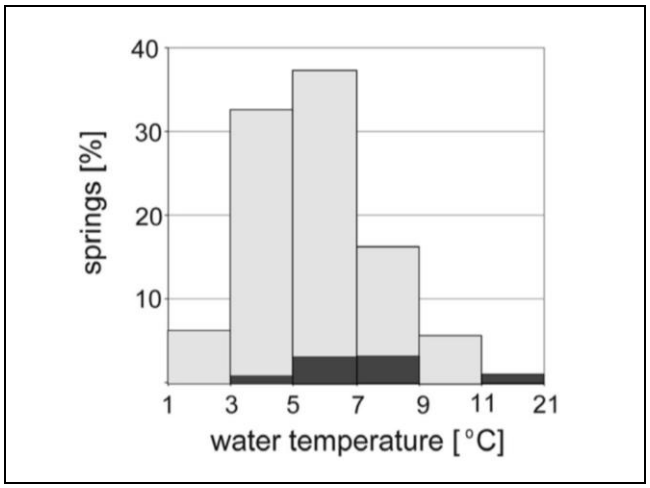

Figure 93. The temperature range of ***Scapania paludosa*** in the Tatra National Park springs, where it occurs in the upper montane zone. Black bars represent bryophytes; gray bars represent tracheophytes. Modified from Smieja 2014.

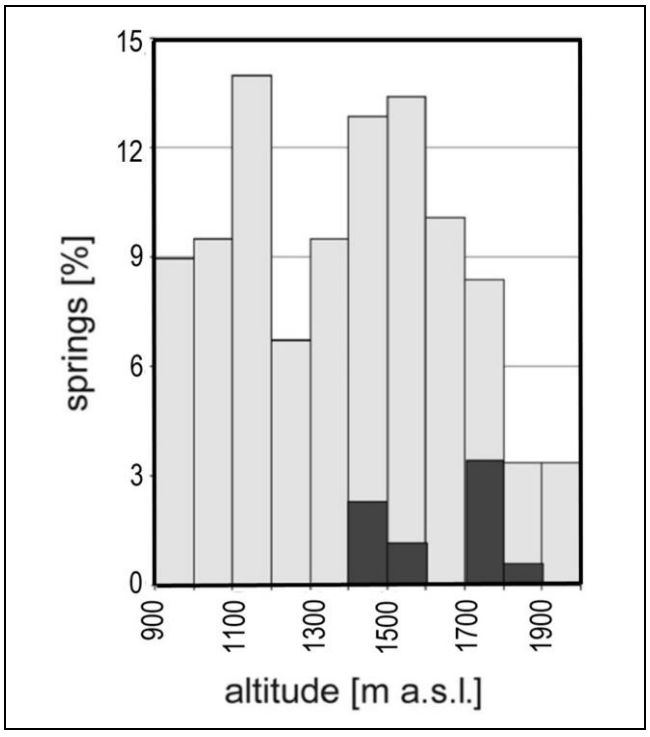

Figure 94. The distribution and temperature range of ***Scapania paludosa*** in the Tatra National Park springs. Black bars represent bryophytes; gray bars represent tracheophytes. Modified from Smieja 2014.

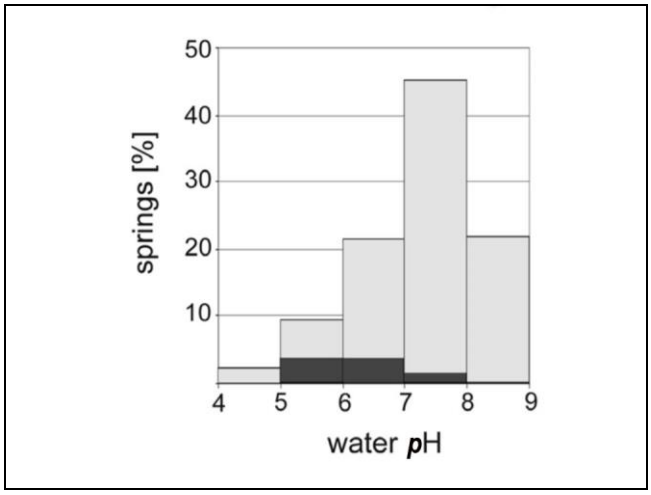

Figure 95. The distribution and habitat range of ***Scapania paludosa*** in the Tatra National Park springs, where it occurs in the upper montane zone. Black bars represent bryophytes; gray bars represent tracheophytes. Modified from Smieja 2014.

Scapania rigida (Figure 97-Figure 96)

(syn. = *Scapania rigida* fo. *minor*)

Scapania rigida (Figure 97-Figure 96) seems to be a little-known species with almost no published information. The only information I have found is that of Ruttner (1955), who considered it to be among aquatic liverworts and reported it from the wall of a bay in the tropics.

Figure 96. ***Scapania rigida*** growing on a branch. Photo by Naufalurfi, through Creative Commons.

Figure 97. ***Scapania rigida*** growing as an epiphyte. This is a little-known tropical species known from the wall of a bay. Photo by Naufalurfi, through Creative Commons.

Scapania rufidula

Distribution

Scapania rufidula is a species with the narrow distribution of Europe and northern Asia, *i.e.* in Siberia (Steere 1954; ITIS 2020d).

Aquatic and Wet Habitats

Scapania rufidula occurs on soil banks of small creeks and rivers of Upper Bureya River (Russian Far East) (Konstantinova *et al*. 2002). In the Indigirka River of eastern Yakutia, Russia, ***S. rufidula*** is the most frequently occurring liverwort and occurs on the banks of small brooks, on numerous rock outcrops, and in rock fields (Sofronova 2018). In southern Siberia in the Sayan Mountains, ***S. rufidula*** occurs at the Malaya Golaya River mouth at 1100 m asl on rocks of the stream bank (Konstantinova & Vasiljev 1994). Here it is associated with ***Scapania crassiretis*** (Figure 36). In the Lower Malaya Golaya River, it occupies soil deposits on river bank rocks, as well as occurring in rock fields and on rocks covered with humus. In the latter habitat it is often mixed with ***Trilophozia quinquedentata*** (Figure 54).

Scapania subalpina (Figure 98-Figure 102)

Distribution

Scapania subalpina (Figure 98-Figure 102) is a montane and alpine species with a circumboreal distribution (Gesierich & Rott 2004). It occurs from California and Colorado, USA, northward to Alaska (Schuster 1974). In Europe it occurs from the Alps and Pyrenees northward to Scandinavia, Siberia, and Iceland. It also occurs in alpine areas of Japan.

Figure 98. ***Scapania subalpina***, a circumboreal alpine and montane species that is facultatively aquatic in streams, springs, cascades, and other wet areas. Photo by Michael Lüth, with permission.

Figure 99. ***Scapania subalpina*** showing its growth habit. Photo by Andy Hodgson, with permission.

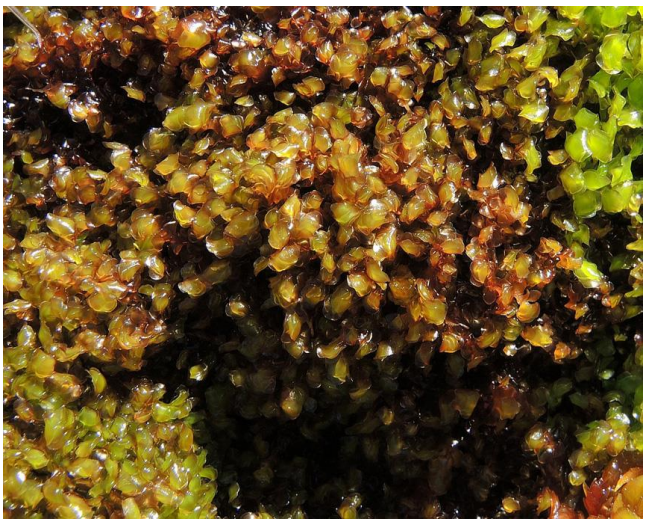

Figure 100. ***Scapania subalpina*** showing various color forms. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Koponen *et al*. (1995) reported ***Scapania subalpina*** (Figure 98-Figure 102) as aquatic in Finland, although

Virtanen (1995) considered it to be a facultative aquatic liverwort in Finland. Ferreira *et al*. (2008) reported it from rivers. Gesierich and Rott (2004) considered it to be a montane species on moist and wet earth (Figure 101) in the catchment of a glacial stream in Austria. There they considered it to be potentially endangered in the perialpine area where it is one of two dominating liverwort species in the fen.

Figure 101. ***Scapania subalpina*** growing with a variety of other species. Photo by Michael Lüth, with permission.

The ecology of ***Scapania subalpina*** (Figure 98-Figure 102) is similar to that of ***Scapania undulata*** (Figure 125-Figure 136) (Schuster 1974). This restricts it mostly to wet ledges, borders of rocky springs, cold streams, and cascades. It lives where it is kept wet at all times either by high humidity or by spray. However, it avoids locations where it is permanently submerged. It seems to prefer shaded, acid rocks (Figure 102), although it can occur on weakly basic rocks. Watson (1919) ascribed to it a habitat of gravelly detritus associated with fast water.

Figure 102. ***Scapania subalpina*** growing in a habitat that can dry out. Photo by Jean Faubert, with permission.

Physiology

In experiments, ***Scapania subalpina*** (Figure 98-Figure 102) from Greenland tolerated temperatures down to -10ºC in ice for 34 days (Clausen 1964). In the same set of experiments, it withstood 1 day in ice at -40ºC, likewise with no cellular damage. It was among the most cold-tolerant species in the experiments on the 32 liverwort species tested.

Reproduction

Schuster (1974) reports that ***Scapania subalpina*** (Figure 98-Figure 102) commonly produces gemmae but rarely produces capsules.

Scapania uliginosa (Figure 103-Figure 109)

(syn. = *Scapania obliqua*)

Distribution

Scapania uliginosa (Figure 103-Figure 109) has a restricted range in Arctic-alpine areas, extending from the European Alps to northern Scandinavia (Schuster 1974). Although it is frequent in Iceland and Greenland, it is not known from Spitzbergen. In North America it extends from Alaska southward to high mountains in Colorado, USA.

Figure 103. ***Scapania uliginosa*** is restricted to Arctic-alpine areas where it grows in streams and small lakes. Photo by Jan-Peter Frahm, with permission.

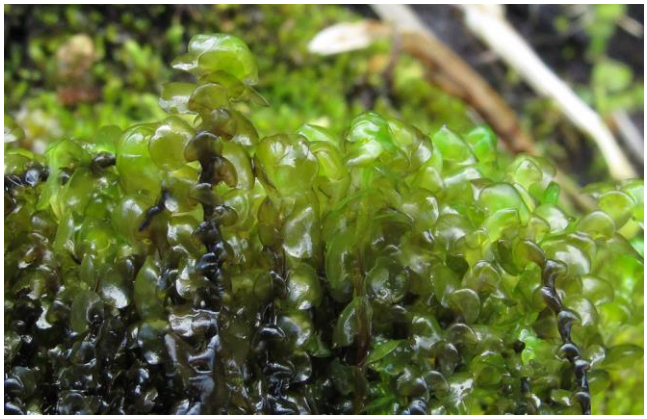

Figure 104. ***Scapania uliginosa*** showing its upright growth habit. Photo by Michael Lüth, with permission.

Figure 105. ***Scapania uliginosa*** showing a brown form with fist-like branch apices. Photo by Dick Haaksma, with permission.

Aquatic and Wet Habitats

Watson (1919) reported ***Scapania uliginosa*** (Figure 103-Figure 109) from alpine or subalpine areas where it grows submersed in fast water. Geissler (1975, 1976) supported this description by reporting it from European alpine streams. Kozlowski *et al*. (2017) reported that ***Scapania uliginosa*** was among the bryophytes covering stream bottoms in streams of Tatra National Park in Poland. Likewise, other researchers reported that ***Scapania uliginosa*** grows in streams (Dohnal 1950; Sykora & Hadac 1984).

But this species, while apparently needing a steady water supply [Koponen *et al*. (1995) considered it to be aquatic in Finland], does not always grow in streams. Light (1975) found it in small lakes in the Scottish mountains, where the lakes are covered with ice 4-7 months a year and the ion concentration is low.

In high mountains ***Scapania uliginosa*** (Figure 103-Figure 109) is restricted to seepage-moistened rocks or cold springs and streams (Figure 106-Figure 108) (Schuster 1974). It sometimes occurs on stony, marshy ground in cold regions of high altitude or latitude (Figure 109). Schuster describes the species as occurring in large, swelling tufts at the sides of alpine rills, the types of sites where one might find ***Scapania undulata*** (Figure 125-Figure 136), ***S. paludosa*** (Figure 89-Figure 92), ***Marsupella aquatica*** (Figure 110), and ***M. sphacelata*** (Figure 111). ***Scapania uliginosa*** (Figure 103-Figure 109) occurs in sites that remain submerged for at least part of the year and apparently avoids calcareous rocks. Cantonati and Lange-Bertalot (2011) reported that ***S. uliginosa*** was the dominant substrate for diatoms from springs in Nature Parks of the south-eastern Alps.

Figure 106. ***Scapania uliginosa*** in an alpine seepage. Photo by Michael Lüth, with permission.

Figure 107. ***Scapania uliginosa***, shown here in the middle, joins other bryophytes and a saxifrage in a seepage area. Photo by Michael Lüth, with permission.

Figure 108. ***Scapania uliginosa*** in a seepage area. Photo by Michael Lüth, with permission.

Figure 109. ***Scapania uliginosa*** in a marshy habitat. Photo by Michael Lüth, with permission.

Figure 110. ***Marsupella aquatica***, a species that occurs on the sides of alpine rills similar to the ones to occupied by ***Scapania uliginosa***. Photo by Barry Stewart, with permission.

Figure 111. ***Marsupella sphacelata***, a species that occurs on the sides of alpine rills similar to the ones to occupied by ***Scapania uliginosa***. Photo by Hermann Schachner, through Creative Commons.

In Sweden, Sjörs and Een (2000) found this species in springs. In the Upper Tissa River of southern Siberia, Konstantinova and Vasiljev (1994) found ***S. uliginosa*** (Figure 103-Figure 109) on the stream bank in a ***Larix*** forest (Figure 112). Here it occurred with the leafy liverworts ***Blepharostoma trichophyllum*** subsp. ***brevirete*** (Figure 113), ***Mesoptychia heterocolpos*** (Figure 114), ***Lophoziopsis excisa*** (Figure 51), ***Scapania subalpina*** (Figure 98-Figure 102), and ***Trilophozia quinquedentata*** (Figure 54). Geissler (1982) reported ***Scapania uliginosa*** growing in deep and sometimes overflowing spring fens. In an alpine catchment in Austria, Gesierich and Rott (2004) considered it to be potentially endangered, a case where extinction would greatly alter the fens where it is one of two dominant liverworts. They surmised that it avoids calcareous habitats.

Figure 112. ***Larix*** forest, a suitable habitat for ***Scapania uliginosa*** on a stream bank. Photo through public domain.

Reproduction

Although this plant apparently produces gemmae in Scotland, gemmae appear to be rare throughout the Arctic-alpine range (Aleffi 1992).

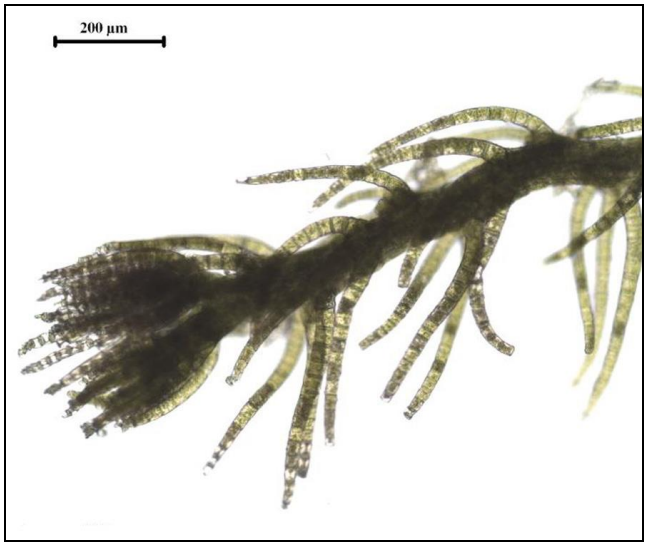

Figure 113. ***Blepharostoma trichophyllum*** subsp. ***brevirete***, a species that occurs with ***Scapania uliginosa*** on stream banks. Photo by Hugues Tinguy, with permission.

Figure 114. ***Mesoptychia heterocolpos***, a species that occurs with ***Scapania uliginosa*** on stream banks. Photo by Blanka Aguero, with permission.

Physiology

Scapania uliginosa (Figure 103-Figure 109) exhibits a degree of tolerance to a variety of heavy metals. Samecka-Cymerman *et al*. (1991) found this species to contain up to a maximum in mg kg^{-1} dry plant weight of 518 B, 418 Ba, 16 Cd, 180 Co, 119 Cr, 292 Cu, 11 Li, 10,700 Mn, 694 Mo, 243 Ni, 464 Pb, 955 Sr, 123 V, and 2067 Zn in Sudetan streams of Poland and Ardennes streams in Belgium and western Germany. Whitton (2003) likewise chose this liverwort for monitoring heavy metals in fresh water.

Role

Egorov (2007) examined the ability of associated **Cyanobacteria** (Figure 115) to fix nitrogen. The biological assimilation of atmospheric nitrogen by such microorganisms associated with ***Scapania uliginosa*** (Figure 103-Figure 109) during the growing period was 0, compared to 0.09 mg cm^{-2} on a species of the moss ***Bryum*** (Figure 116). This is somewhat surprising to me due to the wet habitats where this liverwort is found.

Figure 115. ***Nostoc***, one of the **Cyanobacteria** that occur on bryophytes and can fix nitrogen. Photo by Proyecto Agua, through Creative Commons.

Figure 116. ***Bryum capillare***; some members of the genus ***Bryum*** support nitrogen-fixing **Cyanobacteria**. Photo by Michael Becker, through Creative Commons.

Scapania umbrosa (Figure 117-Figure 124)

Distribution

Scapania umbrosa (Figure 117-Figure 124) ranges from Lapland southward to the Azores, Russia, and Scotland, but it is unknown in Asia (Schuster 1974). In North America it occurs on both coasts but is rare further inland. It extends from Alaska south to California and from Newfoundland and Labrador to New York.

Figure 117. ***Scapania umbrosa***, a species from coastal regions of the Northern Hemisphere where it occurs in moist habitats, but only occasionally submerged. Photo by Michael Lüth, with permission.

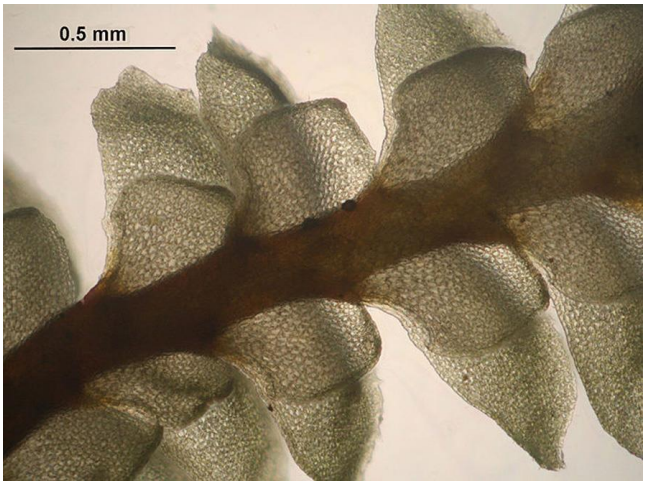

Figure 118. ***Scapania umbrosa*** showing leaf folds. Photo by Hermann Schachner through Creative Commons.

Figure 119. ***Scapania umbrosa*** showing a moist, pale color form. Photo by Hermann Schachner, through Creative Commons.

Figure 120. ***Scapania umbrosa*** showing the upright habit and claw-like tips. Photo by Hugues Tinguy, with permission.

Figure 121. ***Scapania umbrosa*** showing a drier and darker appearance. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Schuster (1974) considers ***Scapania umbrosa*** (Figure 117-Figure 124) to be restricted to locations where it is continually moist. These can include decaying, damp, shaded logs (Figure 122) or moist rocks. It is known from both igneous rock and calcareous or noncalcareous sandstone. Watson (1919) noted that it was occasionally submerged.

Figure 122. ***Scapania umbrosa*** on decaying wood. Photo by Hermann Schachner, through Creative Commons.

In Russia, Choi *et al*. (2012) reported ***Scapania umbrosa*** (Figure 117-Figure 122) from fine-grained soil on wet roadsides in the dark coniferous forest belt, ranging 60-1400 m alt. At Eagle Lake in the Franconia Mountains, New Hampshire, USA, ***Scapania umbrosa*** similarly occurred along the trail above 915 m, in this case on wet rocks (Lorenz 1908).

Reproduction

Gemmae in this species are apical and 2-celled (Figure 123-Figure 124).

Figure 123. ***Scapania umbrosa*** with apical gemmae. Photo by Hermann Schachner, through Creative Commons.

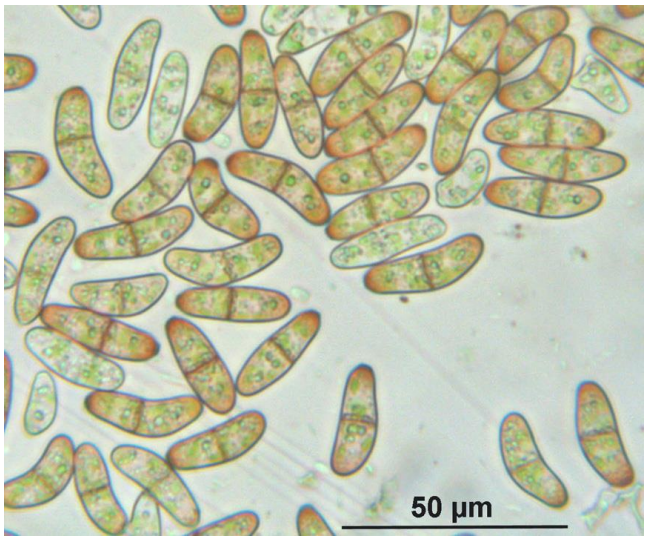

Figure 124. ***Scapania umbrosa*** gemmae. Photo by Hermann Schachner, through Creative Commons.

Fungal Interactions

Bidartondo and Duckett (2010) reported that the fungus ***Sebacina*** (Figure 45) associates with this species.

Scapania undulata (Figure 125-Figure 136)

(syn. = *Martinellius undulata*, *Plagiochila undulatum*, *Pleurozia cochleariformis*, *Scapania dentata*, *Scapania intermedia*)

Distribution

Scapania undulata (Figure 125-Figure 136) is distributed widely throughout the Arctic, southward on high mountains (Schuster 1974). In eastern North America it extends southward in the Appalachian Mountains into the Mixed Mesophytic Forest and the Hemlock-Hardwoods Forest. In western North America it extends from Alaska and the Yukon southward to California. In the Rocky Mountains it extends southward to New Mexico. In the Eastern Hemisphere it extends from Europe to North Africa, Korea, and Japan.

Figure 125. ***Scapania undulata***, a species widely distributed throughout the Arctic, southward on high mountains. This species is predominantly aquatic, occurring in both streams and lakes, but also on banks where it is usually wet. Photo by Florent Beck, through Creative Commons.

Figure 126. ***Scapania undulata*** showing its growth habit. Photo by Hermann Schachner, through Creative Commons.

Figure 127. ***Scapania undulata*** showing shoot apices. Photo by David T. Holyoak, with permission.

Figure 128. ***Scapania undulata*** with only the shoot apices emergent. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Of all the aquatic liverworts, ***Scapania undulata*** (Figure 125-Figure 136) seems to be the most widespread and abundant. Because of its widespread importance, I will provide more detail on its ecology. ***Scapania undulata*** ranges from hydric to almost xeric (Schuster 1974). In the Haute Ardenne rivers of Belgium, it is strictly aquatic (Leclercq 1977). Satake (1983) likewise reported it as aquatic from Kyushu, Japan. Koponen *et al*. (1995) considered it aquatic in Finland, whereas Virtanen (1995) reported it to be common in both Finnish streams and other wet habitats. Koppe (1945) reported it in water in Westfalens, northwestern Germany. Ferreira *et al*. (2008) simply reported it from rivers. Weber (1976) found ***S. undulata*** to be confined to submerged or emergent rocks (Figure 129-Figure 130) in the Cataracts Provincial Park, Newfoundland, Canada. Its wide-ranging moisture requirements permit it to also occupy the narrow riverbank strip that is periodically submerged and exposed as the stream level changes, a zone in which it achieves its optimum growth in these streams. It is even at least somewhat salt-tolerant, living where it becomes submersed in seawater at high tide, leading Shacklette (1961) to consider it to be a facultative halophyte.

Figure 129. ***Scapania undulata*** and habitat on rock just above the water. Photo by Jean Faubert, with permission.

Figure 130. ***Scapania undulata*** on rock in stream. Photo by Bernd Haynold, through Creative Commons.

Streams

This species typically prefers upstream habitats. It occurs in fast water of the River Rheidol, but it can't compete with flowering plants in slow water downstream (Jones 1955). Holmes and Whitton (1975) found it to be among the most common bryophytes in the extreme upper reaches and tributaries of the River Tweed in the UK. Holmes and Whitton (1977) found it in the upper upstream of the River Swale in Yorkshire, UK, but in the River Tyne, UK, it was more scattered (Holmes & Whitton 1981). In northern England, it occurs in streams and rivers (Wehr 1983). Weekes *et al*. (2014) reported ***Scapania undulata*** (Figure 125-Figure 136) to be the most common bryophyte in small streams in Ireland, where it forms turfs (Figure 131). It is among the commonest species in English and Welsh rivers (Scarlett & O'Hare 2006).

Figure 131. ***Scapania undulata*** in a dry montane stream bed, showing how abundant it can become. Photo by Michael Lüth, with permission.

Figure 132. ***Scapania undulata*** habitat on a dripping cliff. Photo by Dick Haaksma, with permission.

Scapania undulata (Figure 125-Figure 136) has been well-known from other parts of Europe as well. It occurs in European alpine streams (Figure 133), also generally being fast-flowing headwaters (Geissler 1975, 1976). It has been reported from streams in Polish and Czech Sudety Mountains (Samecka-Cymerman & Kempers 1998) and Szoszkiewicz *et al*. (2018) found that ***Scapania undulata*** was among the three most abundant leafy liverworts in Tatra and Sudeten streams, with bryophytes being especially important to macroinvertebrates in the siliceous rivers of Tatra. In the Maritsa River, Bulgaria, it is a hygrophyte in the upper course of the river where conductivity and sulfates had low values (Gecheva *et al*. 2011) and is likewise reported from other Bulgarian rivers (Gecheva *et al*. 2010, 2013). It occurs in streams in northeastern Finland (Heino & Virtanen 2006). Virtanen (1995) found ***S. undulata*** to be "rather common" in the 8 streams in his study in Lohja parish in southern Finland. Vieira *et al.* (2005) reported it from mountain streams of northwest Portugal, and it is common in mountain fluvial microhabitats of northwest and center-west Portugal (Vieira *et al*. 2012a), with ***Scapania undulata*** being among the most common species in 187 streams in Portugal (Vieira *et al*. 2012b). This species also occurs in upstream areas in mountainous streams in Madeira Island off the northwest coast of Africa (Luis *et al.* 2015).

Figure 133. Alpine stream, northwestern Georgia, southeastern Europe. Photo by Lodian, through Creative Commons.

In the streams I have studied in eastern North America, ***Scapania undulata*** (Figure 125-Figure 136) was certainly the most common of the submersed liverworts. In North

America, it occurs in fast-flowing streams in the Adirondack Mountains, USA, streams (Slack & Glime 1985; Glime *et al*. 1987). Glime (1970) likewise found it to be the dominant bryophyte at upstream locations with fast water and an absence of tracheophytic macrophytes in the headwaters of a New Hampshire, USA, stream. In Quaker Run, a stream originating at 700 m asl near the Pennsylvania-New York border, ***S. undulata*** covers many of the small rocks that are submerged in the stream, forming luxurious mats (Matthews 1932). Lanfear (1933) reported it as submerged in deep, swift, clear water in Pennsylvania, USA. Knapp and Lowe (2009) found it in streams in the Great Smoky Mountains National Park, Kentucky, USA. Porter (1933) reported it submerged in a small stream in Albany County, Wyoming, USA, attached to rocks.

On the other hand, it is dominant not only in middle and upstream reaches, but also in lower stream reaches in the Harz Mountains of Germany (Bley 1987) and midstream in the unpolluted upper and middle parts of streams of eastern Odenwald and southern Spessart (Philippi 1987).

It can survive permanent submergence (Schuster 1974). But it can also survive in the constant spray of water near a waterfall of Upper Bureya River in the Russian Far East (Konstantinova *et al*. 2002). Hence, one can frequently find it on emergent rocks where it remains wet even when above water (Figure 134-Figure 136).

Figure 134. ***Scapania undulata*** on rock in stream. Photo by Michael Kesl, through Creative Commons.

Figure 135. ***Scapania undulata*** on the sides of a rock, partly in and partly out of water, at Cranberry Lake, New York, USA. Photo by Janice Glime.

Figure 136. ***Scapania undulata*** partially submersed at Cranberry Lake, New York, USA. Photo by Janice Glime.

While ***Scapania undulata*** (Figure 125-Figure 136) is often the most common or abundant liverwort in streams, in upland Welsh streams it was surpassed by ***Nardia compressa*** (Figure 137) (71% cover) compared to its 23% cover (Wilkinson & Ormerod 1994). The researchers found that acidification and subsequent liming changed the bryophyte community composition, with ***N. compressa*** decreasing. However, in the five years following liming, no other species replaced the ***Nardia***.

Figure 137. ***Nardia compressa*** a species that can surpass ***Scapania undulata*** in upland Welsh streams. Photo by Barry Stewart, with permission.

Hall *et al*. (2001) used TWINSPAN to asses the important parameters determining the suitable streams for plants, including bryophytes. For ***Scapania undulata*** (Figure 125-Figure 136), these include an area of medium percent open water, lowest *p*H, and lowest mean height above water table. As noted earlier, ***S. undulata*** occupied a lower mean height above water table than did ***S. nemorea*** (Figure 71-Figure 79).

Lakes

Although it is almost always associated with running water, this species is not restricted to streams. It occurs to 5 m depth in a Yorkshire, UK, reservoir, and in small lakes with low ion concentration in Scottish mountains with ice cover 4-7 months of the year (Light 1975). At the margins of large lakes wave action seems to replace running water

(Schuster 1974). It is particularly common at the water's edge where spray from the water keeps it constantly wet.

Nygaard (1965) reported ***Scapania undulata*** var. ***purpurascens*** as rare in the deepwater of a lake at 11.5 m deep. This variety no longer has taxonomic status. Nygaard commented that the clear lake was disappointing for fishing, with perch being the only fish present.

Scapania undulata (Figure 125-Figure 136) is abundant in and out of water on rocks and stones at lake margins and on boggy shores (Figure 138) in Scotland (West 1910). Tremp (2003) reported it forming turfs in oligotrophic water.

Figure 138. ***Scapania undulata*** as it could appear on boggy shores or lake margins. Photo by Michael Lüth, with permission.

Associations

Marstaller (1987) found it as part of the ***Platyhypnidium*** (Figure 139)-***Fontinalis antipyretica*** (Figure 161) association in streams in Thuringia, Germany. Gregor and Wolf (2001) likewise found it in locations where these two species also occurred. I have frequently found it in Appalachian Mountain streams, USA, where ***Fontinalis dalecarlica*** (Figure 140) occurred.

Figure 139. ***Platyhypnidium riparioides***; ***Scapania undulata*** frequents streams with this species and ***Fontinalis antipyretica***. Photo by David T. Holyoak, with permission.

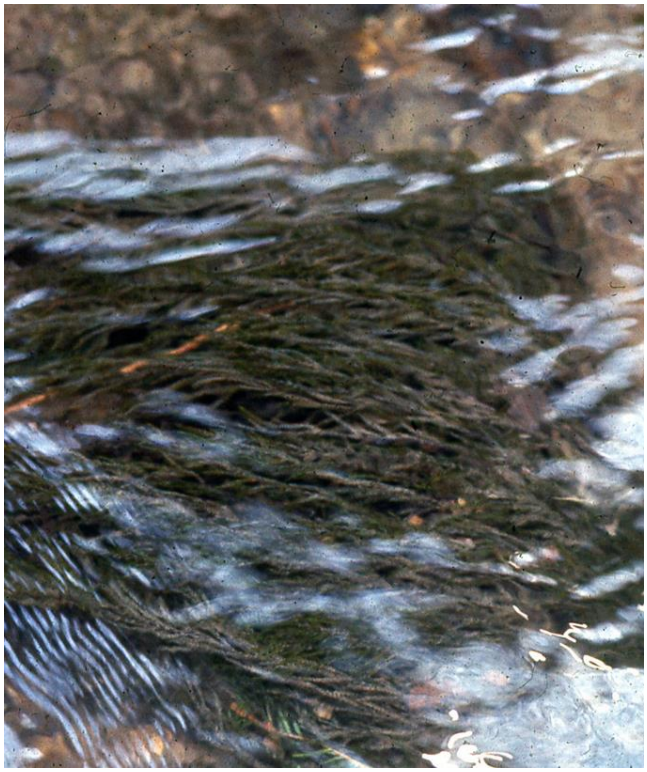

Figure 140. ***Fontinalis dalecarlica***, a species characteristic of streams that also have ***Scapania undulata***. Photo by Janice Glime.

Because of their ubiquity and ability to become relatively abundant, the plants of ***Scapania undulata*** (Figure 125-Figure 136) have been useful accumulator plants for inorganic **xenobiotics** (substances foreign to body or to ecological system) in the Tatra streams, Poland (Samecka-Cymerman *et al.* 2007). In Portugal, Vieira *et al*. (2012a) used it, along with ***Platyhypnidium lusitanicum*** (Figure 141), ***Fissidens polyphyllus*** (Figure 142), and ***Fontinalis*** (Figure 140), as characteristic bryophytes to assess the fluvial status of mountain streams. Lang and Murphy (2012) considered ***S. undulata*** to be an indicator of upland **oligotrophic** (relatively low in plant nutrients) acidic streams with base-poor waters.

Figure 141. ***Platyhypnidium lusitanicum***, one of the species used to assess fluvial status in Portuguese streams. Photo by Barry Stewart, with permission.

Figure 142. ***Fissidens polyphyllus***, one of the species used to assess fluvial status in Portuguese streams. Photo by David T. Holyoak, with permission.

Spitale (2009) found that seasons affect the competition vs facilitation of bryophyte community members. As seasons change, so does the water level. Spitale tested the effects of these changes on two species adjacent to the moss ***Warnstorfia exannulata*** (Figure 143): ***Sphagnum warnstorfii*** (Figure 144) and ***Scapania undulata*** (Figure 125-Figure 136). However, he was unable to show that the seasonal water gradient affected the competition vs facilitation relationships. Nevertheless, climatic fluctuations that affected the length of the water gradient also changed the competitive hierarchies of these species on a seasonal scale.

Figure 143. ***Warnstorfia exannulata***, a species subjected to water level fluctuations. Photo by Michael Lüth, with permission.

*p*H

Scapania undulata (Figure 125-Figure 136) is almost entirely restricted to acidic rocks, but in the Lake Superior region it may be closely adjacent to basaltic, neutral to basic rock outcrops. Tremp and Kohler (1991) found it submersed in low-buffered water of streams. It occurs in waters affected by mineralization zones in the Sudeten Mts, Poland (Samecka-Cymerman & Kempers 1993) and its preferred *p*H range is 3.89-6.6 in West Virginia, USA, mountain streams (Stephenson *et al.* 1995). It can also occur in acid waters in Japan (Satake *et al*. 1989a). Shilland and Monteith (2010) found that ***Scapania undulata*** increased in cover of the stream bed during their acid waters monitoring.

Figure 144. ***Sphagnum warnstorfii***, a species, along with ***Scapania undulata***, that occurs in locations with water level fluctuations. Photo by Michael Lüth, with permission.

In Denmark it occurs in streaming water at *p*H 7.2 (Sørensen 1948), whereas it is an acidophilic (*p*H 4.0-6.0) hydroamphibiont in streams of Gory Stolowe Mountains, Poland (Szweykowski 1951). Hübschmann (1957) reported it from acid water in the mountains, and Glime (1968) reported it from acid springs and brooks in the Appalachian Mountains, USA. Papp *et al*. (2006) likewise found that it prefers waters with low concentrations of dissolved minerals in the Iskur River, and its main tributaries, in Bulgaria. Weekes *et al*. (2014) found it to be a strong indicator species of non-calcareous conditions.

Scapania undulata (Figure 125-Figure 136) had the highest constancy value of the macrophytes identified to species in the study by Weekes *et al*. (2014). The species was typically associated with ***Racomitrium aciculare*** (Figure 145) and ***Hyocomium armoricum*** (Figure 146), all common in fast-flowing acidic streams.

Figure 145. ***Racomitrium aciculare***, a species often associated with ***Scapania undulata***. Photo by Michael Lüth, with permission.

Figure 146. ***Hyocomium armoricum***, a species often associated with ***Scapania undulata***. Photo by Dick Haaksma, with permission.

Scarlett and O'Hare (2006) found that ***Scapania undulata*** (Figure 125-Figure 136) distribution is correlated with low cation concentrations in the Bosge and Black Forest mountains. It is capable of regulating proton levels within the protoplasts and thus might serve as an indicator species for acidic geology.

The *p*H of the water affects the sensitivity of the bryophyte to heavy metals. Thiébaut *et al*. (2008) examined the cellular distribution of heavy metals in ***Scapania undulata*** (Figure 125-Figure 136) in two streams with different acidity (*p*H 5.20 & 6.57) in the Vosges Mountains in eastern France. Little difference was observed in the apparent health of the liverwort, and it remained green in both streams. However, in the most acidic stream lipid droplets accumulated in some of the leaf cells. This acid-tolerant species accumulated more Fe and less toxic Al when compared to the non-acid-tolerant ***Platyhypnidium riparioides*** (Figure 139), where the relationship was reversed. The researchers suggested that the ability to control metal uptake may help to explain the acid tolerance of some species of bryophytes.

Stephenson *et al*. (1995) found that when the streams in their West Virginia mountain stream study had sandstone beds, the species diversity declined as the *p*H declined. At *p*H 3.15, no bryophytes were present. In the highly acidic streams, ***Scapania undulata*** (Figure 125-Figure 136) predominated. When transplanted from a stream with *p*H 5.97 to one with *p*H 3.15, ultrastructural damage was present within three months. These streams also had a heavy load of SO_4 and Al that most likely contributed to the damage.

In upland Welsh streams, Ormerod *et al*. (1987) likewise found that the bryophyte community composition related most strongly to *p*H and aluminium concentration. ***Scapania undulata*** (Figure 125-Figure 136) was characteristic of streams with a mean *p*H of 5.2-5.8. Streams with ***S. undulata*** generally had impoverished macroinvertebrate populations. Since at least some of these invertebrates can feed successfully on the acid-tolerant plants such as ***S. undulata***, the researchers postulated that it was the *p*H, and not the liverworts, that kept the invertebrates out of these streams.

Water Relations

Gupta (1977a) suggested that in ***Scapania undulata*** (Figure 125-Figure 136), the ability of reabsorbing solutes from damaged cells upon rewetting may help in survival. Gupta (1977b) also found that ***S. undulata*** exhibited a peak in photosynthesis after 6 hours of desiccation at 96.5% RH, whereas the more drought-resistant xerophytic ***Porella platyphylla*** (Figure 147) reached its peak after 2 hours. Both species continued to lose water up to 50 hours at that humidity. Furthermore, at 84% relative humidity, ***S. undulata*** had few living cells remaining, but at 93% it had ~3/4 of the cells still living (Clausen 1964). Thus, it can be out of water, but only if the humidity is still high (Figure 148-Figure 149).

Figure 147. ***Porella platyphylla***, an epiphytic species that has good drought resistance. Photo by Hugues Tinguy, with permission.

Figure 148. ***Scapania undulata*** habitat, in this case, emergent but wet. Photo by Dick Haaksma, with permission.

Figure 149. ***Scapania undulata*** in Roaring Creek, West Virginia, USA, where it is only slightly above water and fully hydrated. Photo by Janice Glime.

Temperature

The streams where ***Scapania undulata*** (Figure 125-Figure 136) occurs demonstrate its ability to tolerate cold temperatures, at least down to 0ºC (Figure 150).

Figure 150. ***Scapania undulata*** in an Appalachian stream with snow, showing its ability to tolerate low temperatures. Photo by Janice Glime.

Temperature affects the kinetics of nutrients and heavy metals. Duncker (1976) found that the rate of uptake of zinc by dead ***Scapania undulata*** at 32ºC at zinc concentrations of 2 mg L^{-1} was greater than that of live material at 14ºC. There was some indication that uptake was also greater at 24ºC than at 14ºC in live material. Such temperature differences can affect the rate at which the liverwort obtains nutrients in different seasons, but this needs to be explored.

Photosynthetic Products

We have little understanding of the role played by the various photosynthetic products produced by leafy liverworts. Suleiman *et al*. (1980) noted the possibility that these products could be used taxonomically, identifying **mannitol** in ***Scapania undulata*** and **volemitol** and **sedoheptulose** in some other leafy liverworts. These products are formed in addition to sucrose and fructans. But how do they relate to habitat adaptations, or do they?

Reproduction

We know somewhat more about the role of reproduction in permitting a species to live and prosper where it does. Grainger (1947) discovered that ***Scapania undulata*** (Figure 125-Figure 136) produces its gametangia in the cold months of December to April in a stream near Huddersfield, England, with fertilization occurring near the air-water interface. Production of capsules follows (Figure 151).

Figure 151. ***Scapania undulata*** with capsules. Photo by Michael Lüth, with permission.

Scapania undulata (Figure 125-Figure 136) is a dioicous species (Holá *et al*. 2014), making its fertilization difficult in its flowing water habitats. Based on 100 plots in ten streams in southern Finland, the sex ratio was male biased, contrasting with the female-biased sex ratio of most dioicous bryophytes (Holá *et al*. 2014). It was not unusual for plots to have only one sex. Females produced only one sexual branch per shoot, and no sex-expressing branches also had gemmae. The researchers interpreted this to indicate presence of a trade-off between sexual and asexual reproductive structures. Nevertheless, sporophytes can be produced (Figure 152).

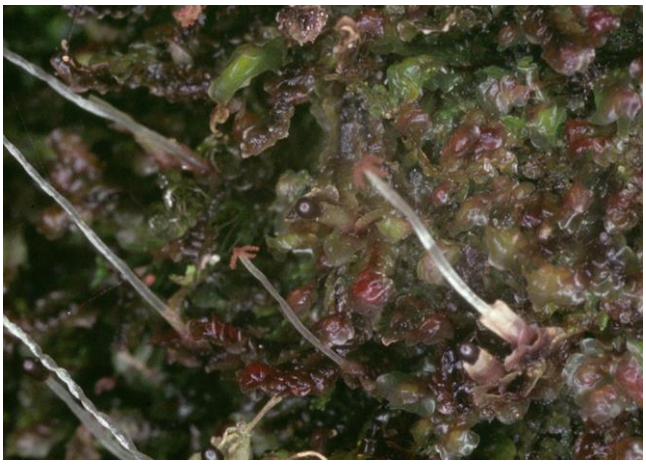

Figure 152. ***Scapania undulata*** with capsules. Photo by Malcolm Storey, with online permission through DiscoverLife.

The gemmae in this species are small, having only 1, or mostly 2, cells (Figure 153) (Potemkin 1998). Their walls are thin and they vary from green to red (Figure 154).

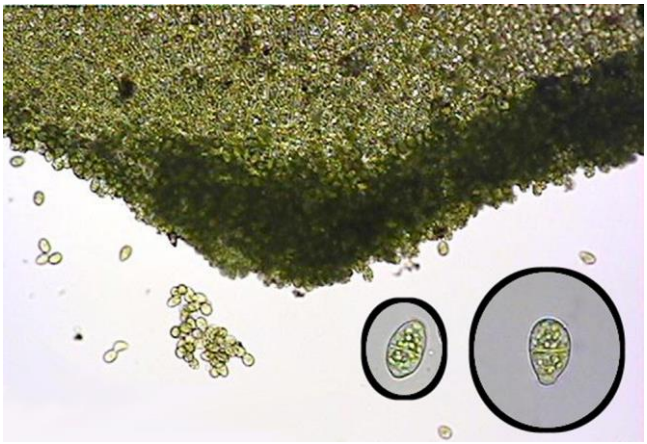

Figure 153. ***Scapania undulata*** gemmae on leaf. Photo by Paul Davison, with permission.

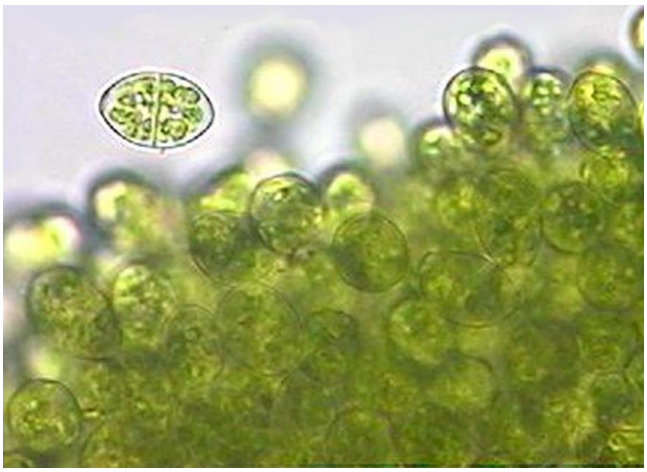

Figure 154. ***Scapania undulata*** gemmae. Photo by Paul Davison, with permission.

But this species may have another, possibly more successful, means of reproduction. Its detached leaves can germinate to produce new plants (Figure 155) (Glime 1970). This mechanism can permit wide dispersal in the stream and provide more surface area to help it attach in a new location. It is also possible, but not yet demonstrated, that it has access to the nutrients remaining in the leaf.

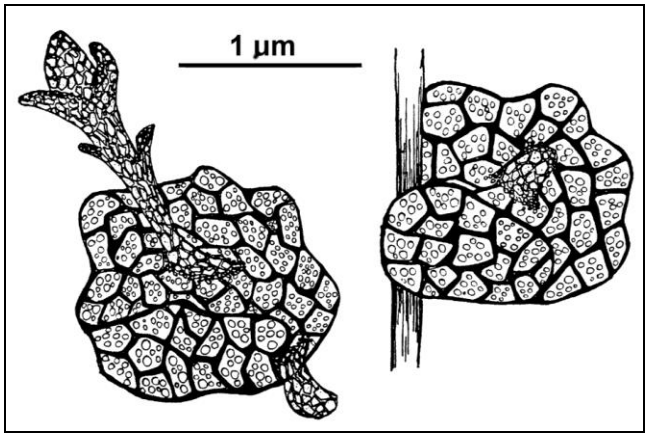

Figure 155. ***Scapania undulata*** plantlets on leaves from a stream in New Hampshire, USA. Drawings by Flora Mace.

Biochemistry

Like so many liverworts, ***Scapania undulata*** (Figure 125-Figure 136) has a variety of secondary compounds, including terpenoids (Huneck *et al*. 1986; Mues *et al*. 1988; Nagashima *et al*. 1993, 1994; Adio *et al*. 2004). What we lack is an understanding of the biological importance of these compounds to the liverwort. It is eaten by some caddisflies (Ito 1991), suggesting these compounds are at least not always effective as antiherbivore compounds.

Pigments

Pigments can be important to bryophytes to trap more light energy in low light and to protect the chlorophyll (Figure 156) and DNA in high light environments. In direct sunlight, there is a dentate, pigmented form of ***Scapania undulata*** (Figure 157-Figure 158), but this expression seems to occur only north of the Southern Appalachians, USA (Schuster 1974). This suggests that it is at least partly genetically controlled.

Figure 156. ***Scapania undulata*** showing non-red form. Photo by Michael Lüth, with permission.

Figure 157. ***Scapania undulata*** showing red pigments in a European population. Photo by Michael Lüth, with permission.

Figure 158. ***Scapania undulata***, a pigmented form from Europe. Photo by Michael Lüth, with permission.

López and Carballeira (1989; see also Martínez-Abaigar *et al*. 1994) found that the aquatic bryophytes they studied, including ***Scapania undulata*** (Figure 125-Figure 136), exhibited higher chlorophyll concentrations than did terrestrial bryophytes. Pigment ratios were indicators of stress from organic and metal pollution, with ***Scapania undulata*** being the most sensitive of the five bryophytes tested (although no other liverworts were included). On the other hand, its chlorophyll *a* and *b* as a percent of dry weight did not decrease as a result of increasingly poor water quality.

Martínez-Abaigar *et al*. (1994), in addition to supporting the higher concentration of chlorophyll in aquatic bryophytes compared to terrestrial ones, also demonstrated that concentrations in aquatic bryophytes, including ***Scapania undulata*** (Figure 125-Figure 136), were similar to those of epilithic river algae. Chlorophyll *a*:*b* ratios and the carotenoid index were lower than in terrestrial bryophytes. Of the 14 species of aquatic bryophytes tested, they found that ***S. undulata*** had a total chlorophyll content of 150±7 mg m² within a range of 97-351 mg m² per shoot area. In this species, the chlorophyll concentration increased in spring when shade developed and light decreased. At the same time, the *a*/*b* ratio decreased due to an increase in chlorophyll *b*. Chlorophyll *b* serves as an antenna pigment to capture more light energy.

Martínez-Abaigar *et al*. (2009) attempted to show the effects of UV-B on six aquatic bryophytes, including ***Scapania undulata*** (Figure 125-Figure 136). They found a greater response to the culture conditions than to the enhanced UV-B conditions. However, the culture conditions did not impede growth. UV-B affected some pigment variables, but did not affect photosynthetic performance or growth. They attributed the muted response to the fact that these bryophytes were collected from high elevations where they were already acclimated to high light intensities.

Kunz *et al*. (1993) reported the presence of riccionidin A in ***Scapania undulata*** (Figure 125-Figure 136), a pigment it shares with the floating liverwort ***Ricciocarpos natans*** (Figure 159) and the streambank liverwort ***Marchantia polymorpha*** (Figure 160).

Figure 159. ***Ricciocarpos natans***, a species with the pigment riccionidin A. Photo by Murray Fagg, Australian National Botanic Gardens, with online permission.

Figure 160. ***Marchantia polymorpha*** with gemmae, a species with the pigment riccionidin A. Photo by Hermann Schachner, through Creative Commons.

Nutrient Relations

Nitrogen is often a limiting nutrient in streams. In the Hubbard Brook Experimental Forest in New Hampshire, USA, Yakubik *et al*. (2000) tested the effect of nitrate releases on ***Scapania undulata*** (Figure 125-Figure 136) and its rate of nitrate uptake. In low discharge releases there is more contact between the liverwort and the nitrate than in high discharge releases, thus affecting the ability of the liverwort to absorb and store the nitrate. Thus, through removal the bryophytes had a greater effect on stream nitrate concentrations in low discharges.

In addition to nitrogen experiments at the Hubbard Brook Experimental Forest, Meyer and Likens (1979) conducted similar experiments within the forest in the stream system. They found that ***Scapania undulata*** (Figure 125-Figure 136) that occurred in first and second order streams readily absorbed P, another limiting nutrient in streams, from the water, even when it occurred in relatively low concentrations. Inputs to these ***S. undulata*** streams were essentially balanced with outputs, resulting in no annual net retention of P in the stream.

Vanderpoorten and Klein (1999) showed the importance of *p*H on the ability of bryophytes to tolerate minerals in the water. ***Scapania undulata*** (Figure 125-

Figure 136) can tolerate a neutral *p*H if the mineral concentration is low. Such waters have low buffering capacity, causing greater responses to slight changes in the chemical balance. This is consistent with its use as a bioindicator of oligotrophic, acidified to weakly acidified, and poorly buffered streams (Thiébaut & Muller 1999). Effluent from villages or trout hatcheries cause an increase of dissolved Mg^{++}, K^{+}, and NO_3^{+}, causing species like ***Scapania undulata*** to disappear (Vanderpoorten & Klein 1999). Hence, Grasmück *et al*. (1995) considered that ***S. undulata*** served as an indicator for weakly mineralized, oligotrophic water.

Samecka-Cymerman *et al*. (2007) compared the effects of various substrates (granites/gneisses, limestones/dolomites, and sandstones) on absorption levels of an array of elements, including both nutrients and heavy metals. The bryophytes from the Tatra mountains streams in Poland, including ***Scapania undulata*** (Figure 125-Figure 136), varied in their behavior depending on the substrate. Those from granites/gneisses had higher concentrations of Cd and Pb. Those from sandstones had higher concentrations of Cr. And those from limestones/dolomites had higher concentrations of Ca and Mg.

Heavy Metals

Nutrients become toxic at higher levels. Heavy metal pollutants typically exceed those levels. Bryophytes are great accumulators, and in some cases they are able to sequester the heavy metals and survive. In other cases, they die from the exposure. For this reason, they can be used as bioindicators of heavy metals, or of clean water, and ***Scapania undulata*** (Figure 125-Figure 136) is a species that has been used in a number of bioindicator studies (Samecka-Cymerman 1989).

When compared to ***Fissidens polyphyllus*** (Figure 142), ***Fontinalis antipyretica*** (Figure 161), ***Platyhypnidium riparioides*** (Figure 139), and ***Brachythecium rivulare*** (Figure 162), ***Scapania undulata*** (Figure 125-Figure 136) had the highest accumulation capacity for heavy metals (López & Carballeira 1993). Metal accumulation is affected by the concentration of the metal in the water, *p*H, sulfate concentration, nitrite and ammonia, and filtrable reactive phosphate. In their study, they found the relationship between concentration in the water and that in ***S. undulata*** to be statistically significant except for Cd, Pb, and Co.

Vázquez *et al*. (1999) examined the distribution of a variety of heavy metals in the plants of ***Scapania undulata*** (Figure 125-Figure 136). They found that for most metals, more was taken up by the extracellular compartment than the intracellular compartment; the particulate fraction was negligible. The relationship between the metal concentration of the water and that of the liverwort followed **Michaelis-Menten** kinetics for enzymes, an asymptotic curve that increases with the concentration gradient. They also found that heavy metal uptake caused considerable loss of intracellular K, probably due to membrane damage. It also caused loss of extracellular Mg, most likely due to displacement on cation binding sites. Of the species tested, loss of intracellular K was greatest in ***S. undulata***. By contrast, this species had the least loss of extracellular Mg.

Figure 161. ***Fontinalis antipyretica***, a species that has less capacity for heavy metal accumulation than ***Scapania undulata***. Photo by Dick Haaksma, with permission.

Figure 162. ***Brachythecium rivulare***, a species that has less capacity for heavy metal accumulation than does ***Scapania undulata***. Photo by Michael Lüth, with permission.

Satake *et al*. (1990) explored the effects of mercury sulfide crystals in ***Scapania undulata*** (Figure 125-Figure 136). In transplant studies, they found that mercury compounds accumulated in the cell walls. Likewise, this species accumulated Pb in the cell wall, but not in the nucleus or other cell components (Satake *et al*. 1989b). They found that PbS was undetectable in the liverwort, but the insoluble $PbSO_4$ accounted for ~3% of the total Pb in the shoots.

Vincent *et al*. (2001) examined the effects of *p*H on accumulation of Al, Mn, Fe, Cu, Zn, Cd, and Pb in ***Scapania undulata*** (Figure 125-Figure 136) in the English Lake District. They found that the metals had accumulated more in older parts of the plants, whereas the studies noted previously here used apical portions only. They found that there was greater aluminium accumulation in the two more acidic streams (*p*H 5.35 and 5.81). Fe showed no preference. Cu, Zn, and Cd accumulated mostly in the liverworts from the highest *p*H (7.26). Pb accumulated most at the middle and highest *p*H. The **accumulation enrichment factor** (amount of metal in plants divided by stream water concentration) followed the

sequence of Zn<Cd<Cu<Mn<Pb<Al<Fe, making Fe the most enriched.

As in other studies, Duncker (1976) found that zinc uptake was correlated with concentration, reaching a saturation at 60 mg L^{-1}. This was essentially constant after half an hour or two days. Light affected the uptake rate at low concentrations, with a 15% greater rate in the light with a 1 mg L^{-1} concentration. Temperature seemed to affect the rate, but it was not definitive. Duncker was unable to demonstrate any genetic differences in plants from high vs. low concentrations of zinc.

Other Pollutants

Scapania undulata (Figure 125-Figure 136) has also been used to assess fluoride in streams (Samecka-Cymerman & Kempers 1990). It has the ability to accumulate fluoride, dependent on the concentration in the water. In water with a concentration of 250 ppm, the concentration in the plants increased by 21-67%.

López and Carballeira (1989) found that, based on pigment contents among the five aquatic bryophytes they tested, ***Scapania undulata*** was the most sensitive to pollution. On the other hand, Stephenson *et al*. (1995) found this species to have an exceptionally high tolerance to both acidity and toxic metals in their North American sites. Could these be differences in physiological races?

Disturbance

Rudolf *et al*. (2012) noted that lower parts of streams in the Tatra Mountains of Slovakia are typically characterized by disturbance events, including road construction and use, clearings, buildings, avalanches, insect infestation (especially bark beetles), windthrows, and ski resorts. ***Scapania undulata*** (Figure 125-Figure 136) was among the bryophytes that was present more than three times in their survey of 78 sites spread across 28 streams, with altitudes ranging 639-2002 m asl. They also noted that nutrient relationships of stream bryophytes are poorly known, and that these disturbances often increase the nutrients in the streams.

Role

Scapania undulata (Figure 125-Figure 136) serves in a variety of roles in streams, lakes, and other wetlands. In streams, they are typically home to may insects and other aquatic invertebrates. In my own experience, if the stream was suitable for ***S. undulata***, the liverwort was suitable as a home for a variety of insects (Glime 1968, 1978).

Some studies have demonstrated the use of ***Scapania undulata*** (Figure 125-Figure 136) as food for caddisflies (Cairns & Wells 2008). A more interesting documentation is that several caddisflies use this species to make their cases (Glime 1968). The species of liverwort depends on availability, with cases of ***Paleagapetus celsus*** from the eastern USA known from ***Scapania nemorea*** (Figure 71-Figure 79) (Flint 1962; Glime 1978) and several other leafy liverworts, including ***S. undulata***. Ito (1998) found that all four species of ***Paleagapetus*** that he reviewed used ***Scapania undulata*** (and ***Chiloscyphus polyanthos*** – Figure 163) for their cases. Ito (1991) found that ***Paleagapetus rotundatus*** feeds on the leaves and lives among the plants, preferentially. It appears that all known members of the genus have this same strong dependence on leafy liverworts, including those in the eastern part of the former Soviet Union (Botosaneanu & Levanidova 1987), Japan (Ito & Hattori 1986; Ito 1988, 1991), and North America (Flint 1962; Glime 1978).

Figure 163. ***Chiloscyphus polyanthos***, a leafy liverwort found in the cases of the caddisfly ***Paleagapetus*** spp. Photo by Bernd Haynold, through Creative Commons.

In Japan, the caddisfly ***Ptilocolepus granulatus*** (Figure 164) uses ***Scapania undulata*** (Figure 125-Figure 136) (and ***Chiloscyphus polyanthos*** – Figure 163) to make its cases <https://www.youtube.com/watch?v=7uZBMz_Qyuk>, to serve as its substrate, and to become food (Ito 1998; Waringer & Graf 2002). Depisch (1999) and Ito and Higler (1993) also found that this caddisfly species commonly lives among and feeds on the liverwort ***Scapania undulata***.

Figure 164. Larva of the caddisfly ***Ptilocolepus granulatus*** carrying its case made with leafy liverworts. Photo by Michel-Marie Solito de Solis, YouTube - permission needed.

Habitat Summary

It is difficult to describe the habitat of this species because of its variability. In Connecticut, USA, it is hydrophytic in rock ravines and calciphobic along rivers (Nichols 1916). On Cape Breton Island, Canada, it occurs in ravines (Nichols 1918). Watson (1919) summarized the information known to him to describe the species as submerged in slow or fast water with poor mineral salts,

often in marshy places, on wet rocks or soil associated with fast water, occasionally submerged. To these habitats, Verdoorn (1932) added that it occurs in water on emergent basket-ball-sized rocks in shallow water, an observation supported by Glime (1970) for occurrences on rocks just above and below the water surface of a headwater steam in New Hampshire, USA.

Summary

The **Scapaniaceae** has four genera with members that occur in wet or aquatic habitats. Of these, ***Scapania*** has the most aquatic members. Among these, ***Scapania undulata*** is usually submersed and has been the subject of a variety of studies.

The wetland and aquatic species of the **Scapaniaceae** can be found from the tropics to the Arctic, but in the tropics they are mostly confined to the high altitudes in the mountains. They are relatively common at the interface of water and air, occurring on emergent rocks and stream banks. Some are common in bogs, where they grow over or among the ***Sphagnum***. They can often develop red and brown pigments in response to prolonged bright sunlight. They mostly occur in cool or cold water and some can withstand temperatures down to -10ºC in ice for at least 34 days. Many produce abundant gemmae. Some are associated with ***Mniaecia jungermanniae*** and other fungi.

Some caddisflies use leaves of several species of ***Scapania*** to make their cases. And some eat the leaves, despite the presence of antibiotics and potential antifeedants. The aquatic species are usually good accumulators, often with a high tolerance to both acidity and toxic metals. Their nutrient requirement is low.

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CHAPTER 1-4
AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES: JUNGERMANNIINEAE

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CHAPTER 1-4
AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES: JUNGERMANNIINEAE

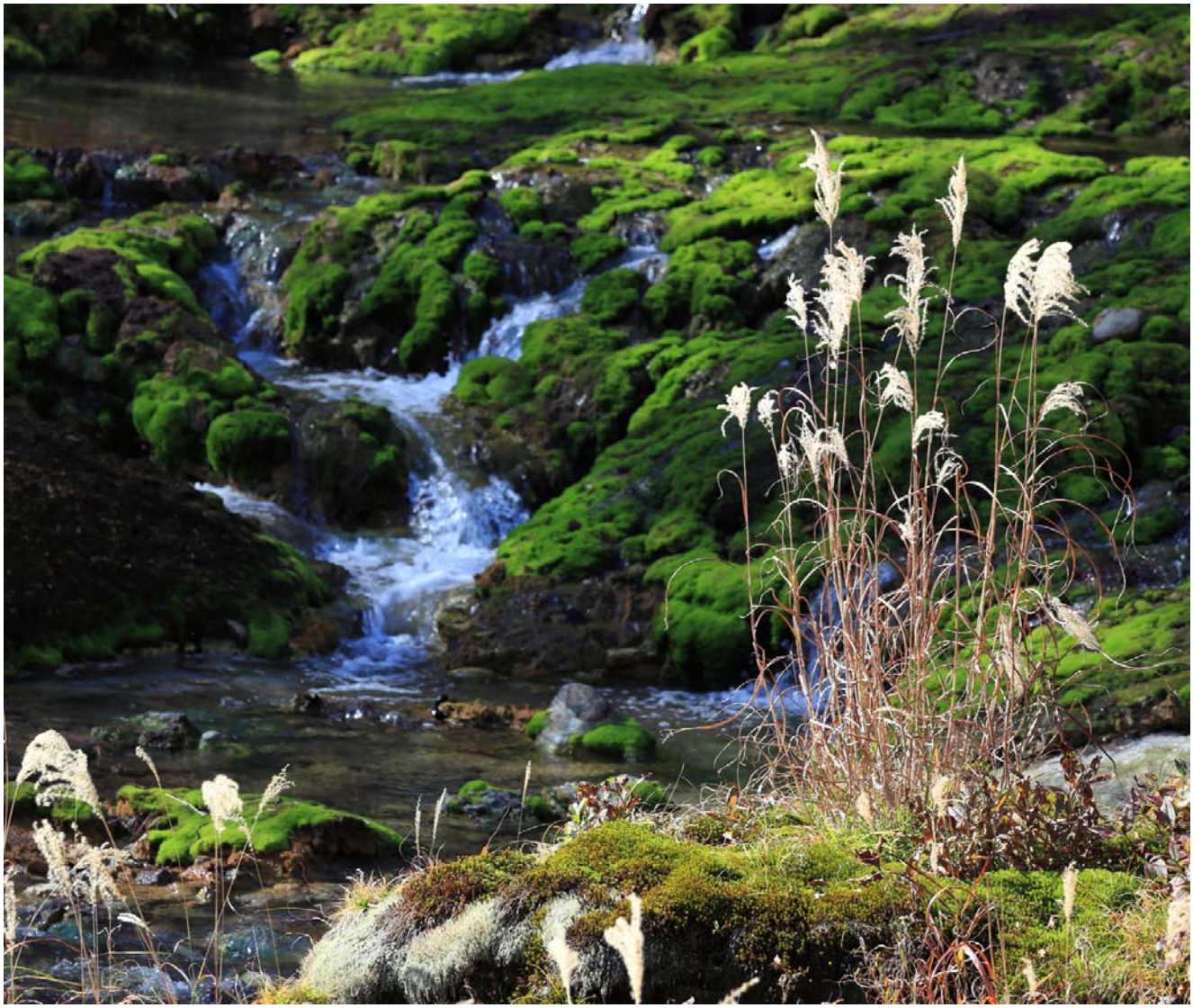

Figure 1. A sulfur stream in Japan where the dominant vegetation is ***Solenostoma vulcanicola***. Photo by Juuyoh Tanaka, through Creative Commons.

Antheliaceae

Anthelia julacea (Figure 2-Figure 3)

Distribution

Anthelia julacea (Figure 2-Figure 3) is somewhat Holarctic, being absent in the northernmost part of the tundra (Schuster 1974). In Europe it extends southward from Iceland to Austria and the Czech Republic in alpine regions. It is present in eastern Siberia, but not in European Russia. It also extends into China, India, and Japan. Its North American distribution is more scattered and rare, with records often proving to be ***Anthelia juratzkana*** (Figure 7-Figure 10). ***Anthelia julacea*** seems to be concentrated on the west coast, from the Aleutian Islands and Alaska southward to Oregon and possibly California. But it is also known from Quebec (Kucyniak 1949).

Figure 2. ***Anthelia julacea***, a holarctic and alpine species common in springs and ***Sphagnum*** hummocks, mixed here with other bryophytes. Photo by Michael Lüth, with permission.

Aquatic And Wet Habitats

West (1910) described this as a species of wet sandy or peaty shores of mountain lakes in Scotland. This liverwort seems to be rather consistently present in the damp tundra (Schuster 1974). In the damp tundra Shimwell (1972) named the ***Anthelion julaceae*** alliance for the sub-alpine spring vegetation dominated by this species. The masses of these liverworts resemble polsters of ***Sphagnum*** hummocks of **ombrogenous** (dependent on rain for its formation) bogs (Figure 3). Jerram (2003) found it in a spring **flush** (area where water from underground flows out onto surface to create area of saturated ground, rather than well-defined channel; piece of boggy ground, especially where water frequently lies on surface; swampy place; pool of water in field) in Cumbria, UK. ***Anthelia julacea*** (Figure 2) occurred with ***Sphagnum auriculatum*** (Figure 4) on flushed slabs of granite. Bajzak and Roberts (2011) found it in tundra-like meadows where ***Sphagnum lindbergii*** (Figure 5) and ***Paludella squarrosa*** (Figure 6) dominated. It covered the ground in some places that were open, forming a dense crust.

Figure 3. ***Anthelia julacea*** forming hummocky mats. Photo by Jean Faubert, with permission.

Figure 4. ***Sphagnum auriculatum***, a species that occurs with ***Anthelia julacea*** on flushed slabs of granite. Photo by Bernd Haynold, through Creative Commons.

Figure 5. ***Sphagnum lindbergii***, a species that occurs with ***Anthelia julacea*** in tundra-like meadows. Photo by J. C. Schou, with permission.

Figure 6. ***Paludella squarrosa***, a species that occurs with ***Anthelia julacea*** in tundra-like meadows. Photo by Hermann Schachner, through Creative Commons.

Adaptations

Anthelia julacea (Figure 2) is a relatively robust plant that occurs in patches or mats (Figure 3). It is typically dark green to deep yellowish green to brown, often is crowded, forming shrub-like mounds.

I have found little information on its photosynthesis and productivity. Dilks and Proctor (1975) found that the photosynthetic response to temperature in ***Anthelia julacea*** (Figure 2) did not differ significantly from that of most lowland species. The species seem to be protected from intracellular freezing to at least -5ºC.

Reproduction

The species is **dioicous** (Jessup 2019), accounting for the fact it is usually lacking sporophytes.

Anthelia juratzkana (Figure 7-Figure 10)

Distribution

Anthelia juratzkana (Figure 7-Figure 10) is mostly Arctic-alpine and bipolar (Schuster 1974). In the Southern Hemisphere it is present in New Zealand, Bolivia, at Tierra del Fuego, Argentina, South Georgia, and Livingston Island, Antarctica. In the Northern Hemisphere, it extends as far northward as the exposed land. It extends southward from there in high alpine summits, extending from Spitsbergen through Scandinavia to England and the central European Alps. In North America it extends southward to Quebec, Canada, and Maine, USA.

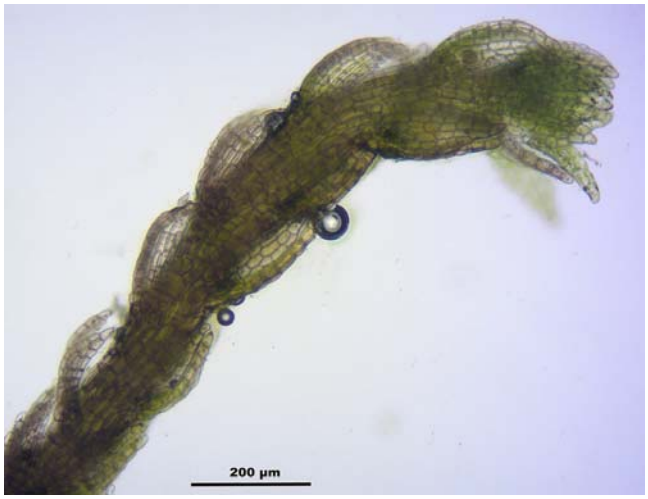

Figure 7. ***Anthelia juratzkana***, an Arctic-alpine and bipolar species that occurs in streams, on the banks of streams and lakes, and on wet cliffs. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Anthelia juratzkana (Figure 7-Figure 10) is typical of perennially wet microhabitats (Jessup 2019). Bakalin (2005) found ***Anthelia juratzkana*** (Figure 7-Figure 10) in a sedge-moss mire on Bering Island in northwestern Russia. It also occurred on peaty banks of small lakes with several other leafy liverworts, and on hummocks or hollows in moss-shrub or moss-sedge mires and is also relatively common on the island on peaty banks of lakes, on fine-grained soil in wet crevices, on rocks near small waterfalls, and along streams. It is not common elsewhere in northwestern Asia.

The species is typical of cold, damp sites exposed to full sun for at least part of the growing season (Schuster 1974). It frequently occupies moist, snow-fed slopes (Figure 10) in the Far North. It occurs in alpine streams in the Swiss Alps (Geissler 1976) and on wet cliff and rocks at the lake shore of the Upper Bureya River in the Russian Far East (Konstantinova *et al*. 2002).

Figure 8. ***Anthelia juratzkana*** habitat showing silvery mats. Photo by Michael Lüth, with permission.

Figure 9. ***Anthelia juratzkana*** mats showing closer view with hummocky appearance. Photo by Michael Lüth, with permission.

Figure 10. ***Anthelia juratzkana*** habitat at receding snow bank. Photo by Michael Lüth, with permission.

Role

Anthelia juratzkana (Figure 7) forms thin, silvery gray or decolorate patches on bare ground, sometimes forming dense mounds and appearing bluish gray to gray-green (Schuster 1974). The individual branches are minute.

The bluish coloring is often due to the presence of **Cyanobacteria**. ***Anthelia juratzkana*** (Figure 7-Figure 10) has the blue-green bacterium ***Gloeocapsa montana*** (see Figure 11) associated with it (Riedl 1977). These bacterial colonies give it a gelatinous sheath that causes a waxy, whitish appearance, with a fungus growing in the sheath and another forming a mycorrhiza-like symbiosis with the liverwort.

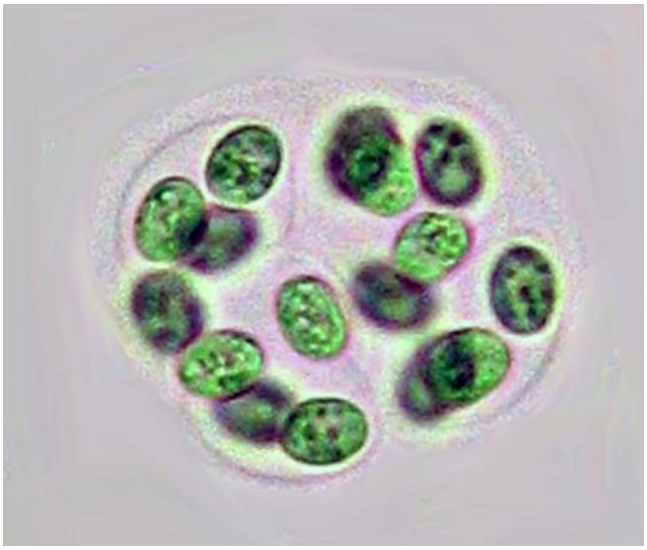

Figure 11. ***Gloeocapsa*** sp.; ***Gloeocapsa montana*** is a **Cyanobacterium** that associates with ***Anthelia juratzkana***. Photo by John, through Creative Commons.

Adaptations

Both species of ***Anthelia*** expresses a variety of phenotypes in response to light, moisture, temperature, and substrate. Both species form lax patches, sods, mounds and **turfs** of elongate stems (2–4 cm) in perennially wet microhabitats.

Lösch *et al*. (1983) found that only the uppermost 4 mm layer of ***Anthelia juratzkana*** (Figure 7-Figure 10) had enough pigment concentration to accomplish photosynthesis. At light saturation, its optimum temperatures were 6-11ºC. In those conditions, maximum CO_2 uptake was 0.7 mg CO_2 g^{-1} dw h^{-1}, compared to 1.5 mg for ***Polytrichastrum sexangulare*** (Figure 12). ***Anthelia juratzkana*** has its low temperature **compensation point** at -4ºC (compensation point is level at which photosynthesis gain is offset by respiration loss). On the other end of the scale, this species cannot sustain photosynthesis at 30ºC. The photosynthetic rate is not damaged by nine months of storage in dark, cold, wet conditions, securing its ability to survive in Arctic and alpine areas.

Reproduction

Anthelia juratzkana is **paroicous** and produces sporophytes frequently (Jessup 2019). It is abundant in the Arctic in midsummer; spore dispersal there occurs as bird migrations begin, increasing opportunities for spores and miniscule stem fragments to be dispersed in the dusted feathers of these birds.

Figure 12. ***Polytrichastrum sexangulare***, a species with a maximum CO_2 uptake of 1.5 mg compared to only 0.7 mg CO_2 g^{-1} dw h^{-1} for ***Anthelia juratzkana***. Photo by Štěpán Koval, with permission.

Balantiopsidaceae

Balantiopsis convexiuscula (Figure 13-Figure 14)

Distribution

Balantiopsis convexiuscula (Figure 13-Figure 14) seems to be restricted to New Zealand and Australia (Simpson 1977; GBIF 2020a).

Figure 13. ***Balantiopsis convexiuscula***, a species of New Zealand and Australia, where it occurs on stream banks, logs, and near waterfalls. Photo by Shirley Kerr, with permission.

Aquatic and Wet Habitats

Balantiopsis convexiuscula (Figure 13-Figure 14) occurs on streambanks in New Zealand (Fineran). Simpson (1971) found it on a bank near a waterfall in Nelson Lakes National Park, New Zealand. Referring to it as **hygrophilic**, Mark *et al*. (1989) noted that it was absent in stands of the Fiord Ecological Region of New Zealand that lacked flowing water. Instead, they are typical in watercourses.

Figure 14. ***Balantiopsis convexiuscula*** forming a vertical mat as one might find on a stream bank. Photo by Shirley Kerr, with permission.

Suren and Duncan (1999) found that ***Balantiopsis convexiuscula*** (Figure 13-Figure 14) is positively correlated with bankfull discharge in their study of 48 streams in South Island, New Zealand. Simpson (1977) found it on logs and on a bank near a waterfall of Coldwater Creek, New Zealand.

Reproduction

Female stems of ***Balantiopsis convexiuscula*** (Figure 13-Figure 14) form an archegonium (Allison & Child 1975). After fertilization, a marsupium forms around the archegonium, from which the capsule emerges. However, capsules are relatively rare. Spores are small.

Calypogeiaceae

Calypogeia (Figure 15-Figure 21, Figure 23-Figure 46)

Geissler (1976) reported ***Calypogeia*** (Figure 15-Figure 21, Figure 23-Figure 46) as ***C. trichomanis*** in alpine streams of the Swiss Alps. Unfortunately, this name has been used for a variety of species and I cannot be sure which one she found. The name is no longer in use.

Stephenson *et al*. (1995) reported ***Calypogeia*** (Figure 15-Figure 21, Figure 23-Figure 46) species from West Virginia, USA, mountain streams. The preferred *p*H was around 5.95.

Calypogeia arguta (Figure 15-Figure 16)

Distribution

Calypogeia arguta (Figure 15-Figure 16) is widely distributed, from the Faeroe Islands and Scandinavia through India, Korea, Japan, and many provinces of China, to South Africa, and New Caledonia (GBIF 2020b). In the Western Hemisphere, it seems to be unknown farther north than Nova Scotia or farther south than Cuba.

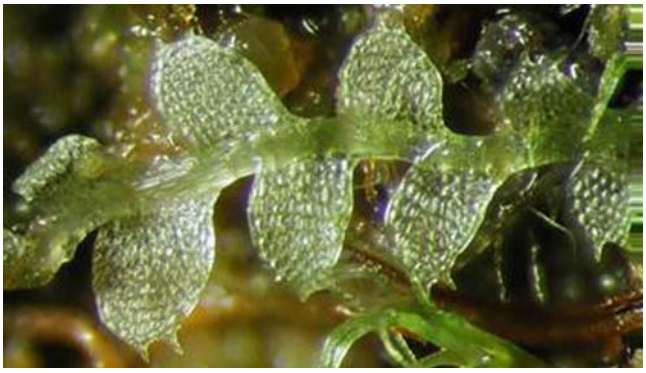

Figure 15. ***Calypogeia arguta***, a widely distributed species in the Northern Hemisphere, of moist soil and wet sites. Photo by Bat Whittler, through Creative Commons.

Aquatic and Wet Habitats

Ferreira *et al*. (2008) reported ***Calypogeia arguta*** (Figure 15) from rivers. ***Calypogeia arguta*** is relatively common on moist soil (Figure 16) in Hong Kong (So & Zhu 1996). It occurs there along with ***Kurzia gonyotricha***, ***Heteroscyphus argutus*** (Figure 17), ***Pallavicinia subciliata*** (Figure 18), and ***Notoscyphus lutescens*** (Figure 19). Those populations vary considerably in size and color. Alam (2011) reports that the species forms smooth mats in the Nilgiri Hills, Tamil Nadu, India. In the Azores, Gabriel and Bates (2005) reported this as a species characteristic of the wettest sites, although it also was most commonly found on rocks.

Figure 16. ***Calypogeia arguta*** habitat at a stream edge on moist soil. Photo by George G., through Creative Commons.

Figure 17. ***Heteroscyphus argutus***, an associate of ***Calypogeia arguta*** in some habitats. Photo by Lin Shanxiong, through Creative Commons.

Figure 18. ***Pallavicinia subciliata***, an associate of ***Calypogeia arguta*** in some habitats. Photo by Lin Shanxiong, through Creative Commons.

Figure 19. ***Notoscyphus lutescens***, an associate of ***Calypogeia arguta*** in some habitats. Photo by David Tng, with permission.

Kitagawa (1978a) considered ***Calypogeia arguta*** (Figure 15-Figure 16) to be a pioneer on the sterile soil of a roadside bank in Mts. Hokkôda, Japan, but also was abundant on soil along sulfur-rich streams.

Adaptations

Its need for water was demonstrated by Clausen (1964). She found that few cells were alive after 12 hours at 20ºC and 93% humidity. At 96% humidity, only about half the cells were alive. But low temperatures are also detrimental; few cells were alive from plants from the Faeroe Islands when subjected to two days on ice at -10ºC.

Reproduction

One possible explanation for the widespread distribution of this species is its ability to survive in diaspore banks. Bisang *et al*. (2003) found that this species germinated from a turf diaspore bank in the Malaysian rainforest.

Fungal Interactions

Calypogeia arguta (Figure 15-Figure 16) is among the liverwort species that apparently inhibit the parasitic ascomycete ***Mniaecia jungermanniae*** (Figure 24-Figure 26) (Pressel & Duckett 2006). Two other liverwort species in the bryophyte association were infected and produced apothecia. Benkert and Otte (2006), on the other hand, observed ***M. jungermanniae*** using ***Calypogeia arguta*** as host. The fungus is most common in the colder periods of the year (March to May) in the Liberec Region of the Czech Republic (Egertová *et al*. 2016).

Calypogeia azurea (Figure 20-Figure 21)

Distribution

Calypogeia azurea (Figure 20-Figure 21) is a widespread, subboreal-montane species (Buczkowska *et al*. 2016), being widely distributed through the northern hemisphere, including North America (rare; in Pacific Northwest), Europe, and eastern Asia (Buczkowska *et al*. 2018).

Figure 20. ***Calypogeia azurea***, a species widely distributed in the Northern Hemisphere. Photo by Hermann Schachner, through Creative Commons.

Figure 21. ***Calypogeia azurea*** showing gemmae. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

It occurs on loamy soil, humus, peat, wet stones and rocks, to rotten logs (Buczkowska *et al*. 2018). Watson (1919) considered it (as *Calypogeia trichomanis*) to be a

species of stream or river banks that experienced frequent submergence and slow water. Thus, the populations would occasionally become submerged. Geissler and Selldorf (1986) reported it occurring with *Carex goodenoughii* and uncommonly with ***Eleocharis quinqueflora*** (Figure 22) in European mountains.

Figure 22. ***Eleocharis quinqueflora***, a sedge species that sometimes has ***Calypogeia azurea*** at its base. Photo by Max Licher, through Creative Commons.

In the ***Calypogeia azurea*** complex, ***C. sinensis*** prefers wet open cliffs and partly shaded cliff caves in the waterfall spray zone, or mesic tree trunk bases and decaying wood in broad-leaved, evergreen, subtropical to southern subtropical montane forests (Buczkowska *et al*. 2018). It has only two known localities. The first is subtropical montane forest near Xiniu Waterfall in the Chinese province of Guizhou at about 1300 m asl. The second locality is a subtropical montane forest in southern North Vietnam, at about 2000 m asl.

Adaptations and Variations

Calypogeia azurea (Figure 20-Figure 21) is one of the few members of ***Calypogeia*** that has blue oil bodies (Figure 23) (Buczkowska *et al*. 2016), giving it a bluish color and accounting for the epithet *azurea*. The species presents a variety of environmentally induced morphological differences.

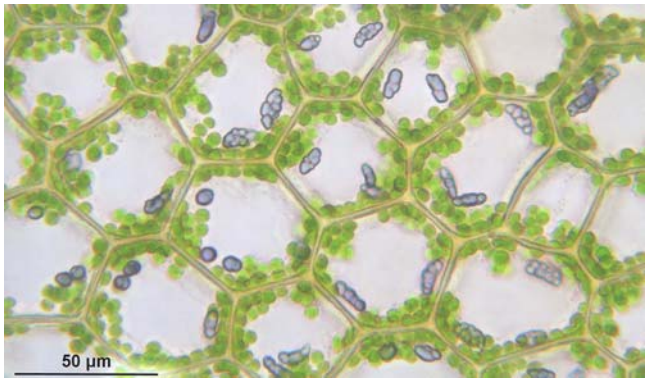

Figure 23. ***Calypogeia azurea*** leaf cells showing bluish oil bodies. Photo by Hermann Schachner, through Creative Commons.

Reproduction

Calypogeia azurea (Figure 20-Figure 21) is **autoicous** (Paton 1999; Damsholt 2002), although Damsholt also questions the possibility it is sometimes **paroicous**.

Fungal Interactions

Calypogeia azurea (Figure 20-Figure 21) is a species where the fungal parasite ***Mniaecia jungermanniae*** (Figure 24-Figure 26) finds suitable habitat and host (Egertová *et al*. 2016). These occurrences include liverworts growing on wet soil.

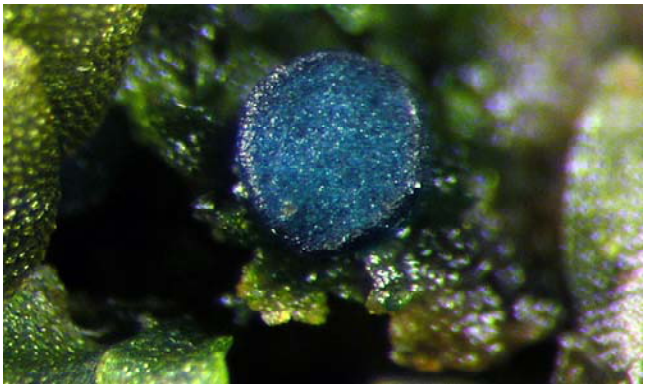

Figure 24. ***Calypogeia azurea*** with fungal parasite ***Mniaecia jungermanniae***. Photo by Walter Obermayer, with permission.

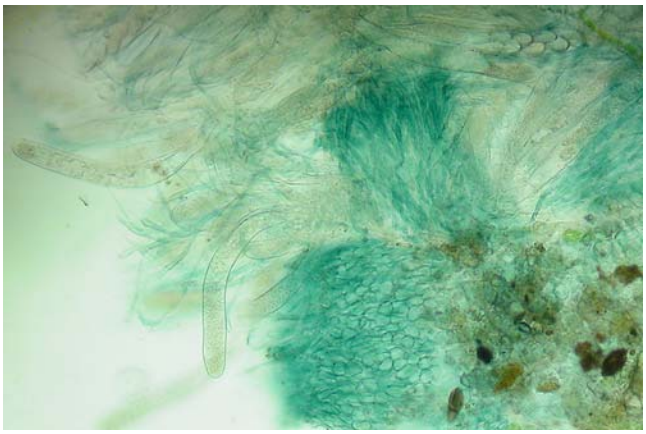

Figure 25. ***Calypogeia azurea*** with fungal parasite ***Mniaecia jungermanniae*** asci in the upper right corner of the image. Photo by Walter Obermayer, with permission.

Figure 26. ***Calypogeia azurea*** with asci of the fungal parasite ***Mniaecia jungermanniae***. Photo by Walter Obermayer, with permission.

Biochemistry

A number of studies have examined the secondary compounds in ***Calypogeia azurea*** (Figure 20-Figure 21). Among these, Nakagawara *et al*. (1992) looked at the azulenes in their study of sesquiterpenoids. One of these azulenes exhibits anti-inflammatory and anti-ulcer activity. Tazaki *et al*. (1998) likewise isolated a new sesquiterpenoid from the species.

Calypogeia fissa (Figure 27-Figure 29, Figure 33-Figure 34)

Distribution

Calypogeia fissa (Figure 27-Figure 29, Figure 33-Figure 34) has a suboceanic distribution pattern in North America, Europe, Asia, and North Africa (Potemkin 2018).

Figure 27. ***Calypogeia fissa***, a species with a suboceanic distribution in the Northern Hemisphere, occurring in a variety of wet habitats. Photo by Hermann Schachner, through Creative Commons.

Figure 28. ***Calypogeia fissa***. Photo by Štěpán Koval, with permission.

Figure 29. ***Calypogeia fissa*** ventral side showing under leaves. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Watson (1919) attributed this species to peaty ground, associated with fast water. Clapham (1940) reported it from the sides and tops of tussocks in calcareous fens in the Oxford District, UK. Its occurrence in the River Tweed, UK, was not common (Holmes & Whitton 1975a). It can occur in irrigation ditches (Beaucourt *et al*. 1987). In southern Finland it occurs in small lakes (Toivonen & Huttunen 1995). ***Calypogeia fissa*** (Figure 27-Figure 29, Figure 33-Figure 34) in the study area in northwestern European Russia grows on more or less wet humus as well as sandy soils and rotten wood near temporary water courses in coastal communities (Potemkin 2018). It also occurs in rock crevices with seepage where one might also find ***Scapania nemorea*** (Figure 30). ***Calypogeia fissa*** frequently forms rather extensive mats resulting from frequent production of gemmae (Figure 33) and probably regular spore production (Figure 34).

Figure 30. ***Scapania nemorea***, a species that can occur in rock crevices with ***Calypogeia fissa***. Photo by Michael Lüth, with permission.

Genetic and Physiological Differences

Buczkowska *et al.* (2011) identified two morphologically distinct groups of the ***Calypogeia fissa*** (Figure 27-Figure 29, Figure 33-Figure 34) complex in Europe. These were supported by statistical analysis of 34 morphological characters as well as by genetic distance. Furthermore, PCR indicates that the European and North American populations represent two subspecies of ***Calypogeia fissa*** (Buczkowska *et al*. 2012a): ***Calypogeia fissa*** subsp. ***fissa*** (Figure 31) in Europe and ***C. fissa*** subsp. ***neogaea*** (Figure 32) in North America (Buczkowska *et al*. 2015). These could be distinguished by both genetic and molecular markers. In Europe, there is a haploid group and a diploid group, with an isozyme pattern that suggests an **allopolyploid** (having two haploid sets of chromosomes that are dissimilar and derived from different species; *i.e.*, a hybrid which has a functional set of chromosomes from each parent of two species) origin of the diploid group. Such differences can express themselves in physiological differences without necessarily showing morphological differences. This can account for finding the species in different habitats on different continents.

Figure 31. ***Calypogeia fissa*** subsp. ***fissa***, the subspecies typical in Europe, showing underleaves. Photo by Hermann Schachner, through Creative Commons.

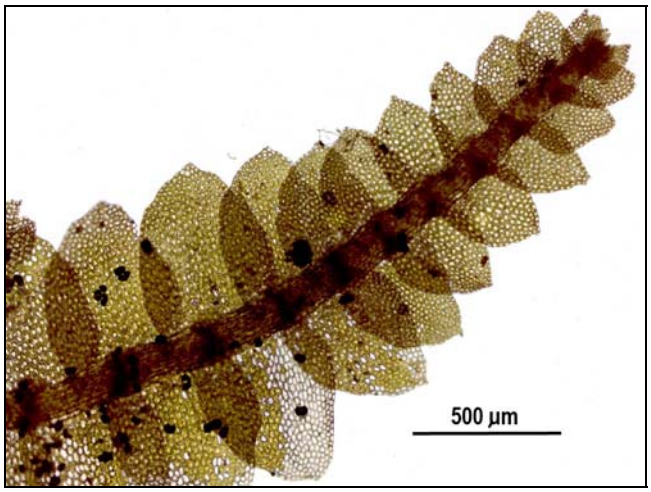

Figure 32. ***Calypogeia fissa*** subsp. ***neogaea***, the subspecies typical in North America; ventral leaves in the photo are the darkened areas across the stem.. Photo by Blanka Aguero, with permission.

Reproduction

Calypogeia fissa frequently forms rather extensive **mats** resulting from frequent production of gemmae (Figure 33) and probably regular spore production (Figure 34) (Schuster 1969; Potemkin 2018). ***Calypogeia fissa*** (Figure 27-Figure 29, Figure 33-Figure 34) is **autoicous** or **paroicous** (Schuster 1969).

Figure 33. ***Calypogeia fissa*** with gemmae. Photo by Štěpán Koval, with permission.

Figure 34. ***Calypogeia fissa*** with nearly mature capsule. Photo by Malcolm Storey, through Creative Commons.

It is able to regenerate from peat slabs (Duckett & Clymo 1988). Unlike some leafy liverworts, ***Calypogeia fissa*** lacks underground shoots (Figure 29). Therefore, it regenerates most abundantly at the surface, failing to have regenerative parts below 9 cm depth in the peat.

Fungal Interaction

Wang and Qiu (2006) found a report of fungal association with ***Calypogeia fissa*** (Figure 27-Figure 29, Figure 33-Figure 34), but I have not found details of this record.

Biochemistry

Warmers and König (1999) found four new sesquiterpenes in ***Calypogeia fissa*** (Figure 27-Figure 29, Figure 33-Figure 34). Their role remains unknown, but they are likely to play a role in antiherbivory. The oil bodies (Figure 35) typically house such secondary compounds.

Figure 35. ***Calypogeia fissa*** leaf cells showing colorless oil bodies. Photo by Hermann Schachner, through Creative Commons.

Calypogeia goebelii (Figure 36)

(syn. = *Kantia goebelii* fo. *thermarum*)

Distribution

Calypogeia goebelii (Figure 36) is distributed in Australia, Oceania, and southern Asia (Guala & Döring 2019).

Figure 36. ***Calypogeia goebelii***, a species that lives in thermal acidic sprays, from Australia, Oceania, and southern Asia. Photo through Creative Commons.

Aquatic and Wet Habitats

Ruttner (1955) reported this species from areas with thermal acidic spray in the tropics. Elsewhere, Kitagawa (1978b) reported ***Calypogeia goebelii*** (Figure 36) from 1550-1600 m asl in the evergreen forest of Thailand as terrestrial and listed its distribution as Java, Sumatra, New Guinea, and Micronesia.

Calypogeia muelleriana (Figure 37-Figure 40)

Like many of the liverworts, the taxonomy has been confusing for ***Calypogeia muelleriana*** (Figure 37-Figure 40). Buczkowska (2010) found that among 52 samples from Poland that resembled ***Calypogeia muelleriana***, 21 belonged to a new taxon, as identified with isozyme markers. Based on Chloroplast DNA sequences, this new taxon more closely resembles ***C. azurea*** (Figure 20-Figure 21) than it does ***C. muelleriana*** and this unnamed new species has also been identified in the USA (Buczkowska *et al*. 2013)

Distribution

Calypogeia muelleriana (Figure 37-Figure 40) is widespread in Europe, but was poorly known in North America (Stotler & Vitt 1972). It is circumpolar and bipolar (Emerson & Loring 2010). Hong (1990) added a number of locations in western USA and Canada, including shaded decaying logs, moist loam, and shaded damp stream banks. He described two new forms (fo. ***schofieldii*** and fo. ***shieldsii***) in this western North American region. It is also known in eastern North America from Manitoulin Island, Ontario, Canada (Williams & Cain 1959), in North and South Carolina, USA (Raczka 2014), and in Pickle Springs, Missouri, USA (Stotler & Vitt 1972).

Figure 37. ***Calypogeia muelleriana***, a species widespread in Europe on stream and river banks and in lakes. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

In the Pickle Springs, Missouri, USA, ***Calypogeia muelleriana*** (Figure 37-Figure 40) occurred on sandy soil of stream banks (Stotler & Vitt 1972) and in North and South Carolina, USA, along the Waccamaw River (Raczka 2014). Leclercq (1977) also reported it from earthy and gravelly substrates of river banks in Haute Ardenne rivers, Belgium. In Germany, it occurs in upper and middle

stream reaches in the Harz Mountains (Bley 1987). In southern Finland it occurs in small lakes (Toivonen & Huttunen 1995). These latter two suggest that it is facultatively aquatic.

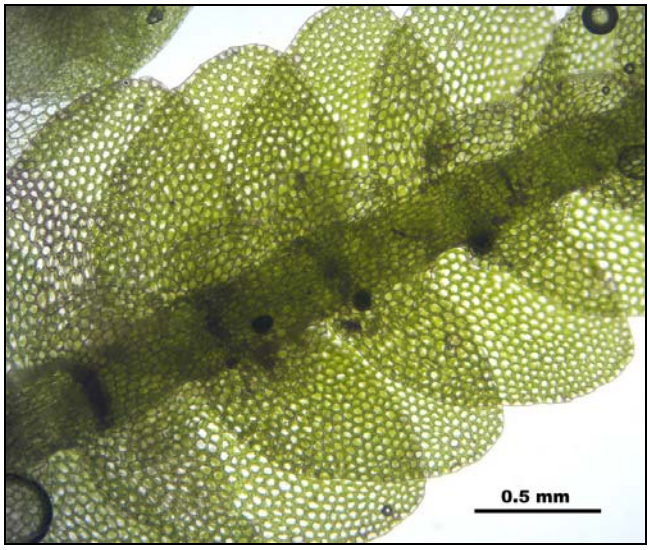

Figure 38. ***Calypogeia muelleriana*** ventral side with underleaves. Photo by Hermann Schachner, through Creative Commons.

Reproduction

Calypogeia muelleriana (Figure 37-Figure 40) is **monoicous**, with both male and female reproductive organs developing from short lateral branches (Schuster 1969). After fertilization, a spore-bearing capsule develops, splits, and releases spores to the wind. Sometimes gemmae develop near the tips of its leafy stems (Figure 39-Figure 42) or around the leaf margins. These gemmae eventually detach, after which they can form new clonal plants under favorable conditions.

Figure 39. ***Calypogeia muelleriana*** habitat showing plants with gemmae. Photo by Michael Lüth, with permission.

Figure 40. ***Calypogeia muelleriana*** with gemmae. Photo by David T. Holyoak, with permission.

Figure 41. ***Calypogeia muelleriana*** with terminal gemmae. Photo by Des Callaghan, with permission.

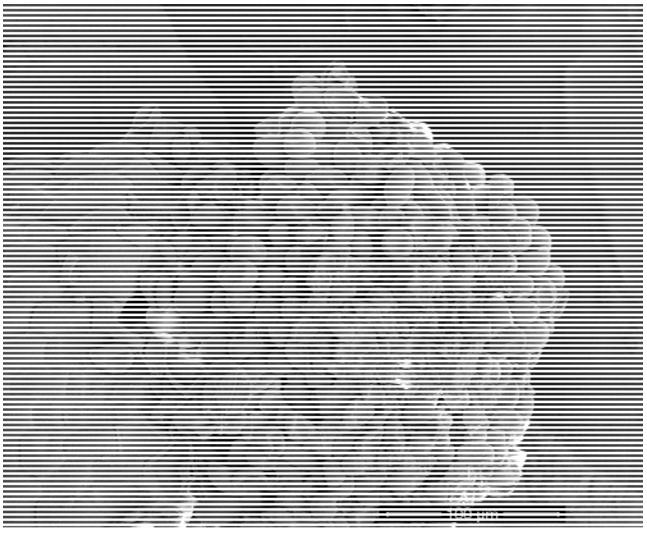

Figure 42. SEM of ***Calypogeia muelleriana*** leaf with gemmae. Photo by Jeff Duckett and Silvia Pressel. with permission.

Biochemistry

Some of its secondary compounds have been identified. Warmers *et al*. (1998) investigated the lipophilic constituents and reported three new sesquiterpene compounds. Such compounds often occur in the oil bodies (Figure 43).

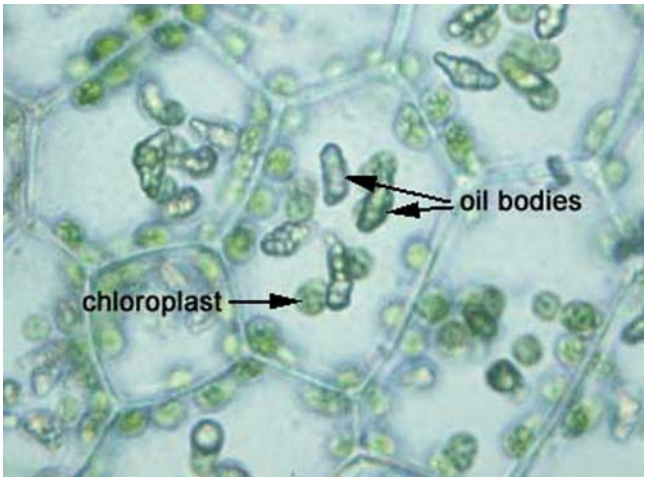

Figure 43. ***Calypogeia muelleriana*** showing oil bodies in leaf cells. Photo from Botany Website, UBC, with permission.

Calypogeia sphagnicola (Figure 44-Figure 46)

(syn. = *Calypogeia muelleriana* fo. *sphagnicola*)

Distribution

Calypogeia sphagnicola (Figure 44-Figure 46) is widely distributed, occurring in the subarctic and alpine areas in northern and central Europe, from Greenland southward, and North America, with a report from Japan (Schuster 1969). In North America it extends from Alaska southward to Alberta and British Columbia in the west and from Newfoundland (Weber 1976), Quebec, and Ontario to West Virginia in the east (Schuster 1969). In the southern extensions it is primarily in spruce and tamarack bogs – habitats that are often considered **refugia** (locations which support isolated or relict population of once more widespread species) and suggest it may have had a wider distribution at one time.

Aquatic and Wet Habitat

Of the many references I found documenting the presence of this species, all but one indicated it was associated with ***Sphagnum*** (Figure 46). Thus, I question the record from North Carolina, USA, indicating that it was found on moist soil (Blomquist 1936) and suggest it may have been a misidentification – or incomplete habitat information.

Figure 44. ***Calypogeia sphagnicola***, a species from sub-Arctic and alpine areas in the Northern Hemisphere. Photo by Erika Mitchell, through Creative Commons.

Figure 45. ***Calypogeia sphagnicola*** showing underleaf. Photo by Scot Loring, through Creative Commons.

Figure 46. ***Calypogeia sphagnicola*** with ***Sphagnum***. Photo by David T. Holyoak, with permission.

Calypogeia sphagnicola (Figure 44-Figure 46) has earned its name because it occurs almost exclusively in ***Sphagnum*** bogs, but also on ***Sphagnum***-capped crests of cliffs (Schuster 1969; Emerson & Loring 2010). ***Calypogeia sphagnicola*** occurs at the summits of ***Sphagnum*** hummocks in southern France (Hugonnot 2011). They are able to colonize degenerating mats in communities with other leafy liverworts. It is one of the species that has high conservation value because of its restriction to specific microhabitats, especially dying ***Sphagna***. Kitagawa (1978a) likewise reported this species from oligotrophic moors where it grows among ***Sphagna*** in the alpine zone of Ödake, Japan, but its primary distribution is in the Arctic, with only three locations in Japan in Japan's northern mountains. Near Gladkovskaya Bay in Russia, Bakalin (2005) found it to occur on the peaty banks of ponds in a peat moss-sedge mire, typically occurring with other liverworts. Bakalin *et al.* (2016) reported it from bare peat of peat moss tussocks in mires in the Putorana Plateau of eastern Siberia, where it grew with other liverworts.

Albisson (1997) considered ***Calypogeia sphagnicola*** (Figure 44-Figure 46) to have a somewhat wider ecological

amplitude than some of the mire specialists. They also found that these liverworts occur more frequently with ***Sphagnum*** species in subgenera ***Sphagnum*** (Figure 47) and ***Acutifolia*** Figure 48) than in subgenus ***Cuspidatum*** (Figure 49). This is consistent with the observations of Souto *et al*. (2015) who found that ***C. sphagnicola*** was associated with dense carpets of ***Sphagnum magellanicum*** (Figure 47), a moss in subgenus ***Sphagnum***.

Figure 47. ***Sphagnum magellanicum***, subgenus ***Sphagnum***, showing a dense carpet that can serve as substrate for ***Calypogeia sphagnicola***. Photo by Dale Vitt, with permission.

Despite its relative rarity, ***Calypogeia sphagnicola*** (Figure 44-Figure 46) is able to successfully compete with other liverworts by over-growing the ***Sphagnum*** capitula in the hummocks, but this is further supported by other liverworts that overgrow the ***Sphagnum*** and reduce its growth rate (Nordbakken 1996). Hugonnot *et al*. (2015) suggest that ***C. sphagnicola*** grows over actively growing ***Sphagnum*** capitula (Figure 46), whereas some leafy liverwort species avoid the ***Sphagnum*** competition by growing on bare peat as well as among ***Sphagnum***.

Figure 48. ***Sphagnum girgensohnii***, subgenus ***Acutifolia***, representing the more preferred substrate group for ***Calypogeia sphagnicola***. Photo by Kari Pihlaviita, through Creative Commons.

In the Alaskan black spruce forest, ***Calypogeia sphagnicola*** (Figure 44-Figure 46) forms small patches or even isolated shoots (Seppelt *et al*. 2008). These are green to pale green to yellowish-green, but older parts are frequently yellowish-brown.

Reproduction

Calypogeia sphagnicola (Figure 44-Figure 46) is **monoicous** (Schuster 1969). Gemmae are common (Bosanquet 2021).

Figure 49. ***Sphagnum cuspidatum*** (subgenus ***Cuspidatum***) submersed; this species prefers wetter habitats than most ***Sphagnum*** species and is not a preferred substrate for ***Calypogeia sphagnicola***. Photo by Bernd Haynold, through Creative Commons.

Biochemistry

Buczkowska *et al*. (2012b) used isozymes to determine that two forms of ***Calypogeia sphagnicola*** (fo. ***sphagnicola*** and fo. ***paludosa***) represent genetically distinct species. The former is haploid and the latter is diploid. They likewise differ distributionally in Poland. "***Calypogeia sphagnicola*** fo. ***sphagnicola*** occurs exclusively in the lowlands of the northern part of the country on raised peat bogs; ***C. sphagnicola*** fo. ***paludosa*** is found only in the mountains of southern Poland, mainly in the subalpine zone, where it grows on ***Sphagnum-Polytrichum*** hummocks (Figure 50) on the upper part of north-facing slopes."

Figure 50. ***Sphagnum capillifolium*** and ***Polytrichum commune*** forming a hummock where ***C. sphagnicola*** fo. ***paludosa*** is able to grow. Photo by Sheila, through Creative Commons.

Fungal Interactions

Wang and Qiu (2006) reported that ***Calypogeia sphagnicola*** (Figure 44-Figure 46) has fungi associated with it.

Calypogeia sullivantii (Figure 51)

Distribution

Calypogeia sullivantii (Figure 51) occurs from Maine to Florida and Puerto Rico and west to Ohio, Missouri, Mississippi, Kentucky, and Louisiana, all in the eastern half of the USA (Pagán 1939; Schuster 1969). In the eastern states, Schuster and Patterson (1957) considered it to be a mostly mountain species.

Figure 51. ***Calypogeia sullivantii***, a species previously considered a variety of ***C. arguta***, occurs around springs. Photo by Blanka Aguero, with permission.

Aquatic and Wet Habitats

Wittlake (1950) found that ***Calypogeia sullivantii*** (formerly placed in ***C. arguta*** as a variety; Figure 51) occurred around springs at Spy Rock Hollow, Arkansas, USA, in association with other mosses and liverworts. Guerke (1971) reported this species from moist ditch banks in Louisiana, USA. In West Virginia, it lives in a sandstone cave where there is a constant drip from the ceiling of the cave, along with seepage, that keeps the cave continuously wet (Ammons 1933). In southern Illinois, Skorepa (1968) found it on wet clay and rocks and under a sandstone ledge. Pagán (1939) found it on wet banks and on rocks in Puerto Rico.

But its habitat is not always wet. Vitt (1967) reported it from sandy soil in the forest above and below a cliff area at Pickle Springs, Missouri, USA. Fulford (1934) found it on moist, sandy soil in Kentucky, USA. Evans (1907) found that it usually grows scattered among other plants or in loose thin tufts. Schuster (1969) lists a variety of habitats, including stream banks, along cascading brooks, and on moist or damp soil in deep shade.

Reproduction

Calypogeia sullivantii (Figure 51) is **autoicous** (having separate male and female branches but on same plant) (Schuster 1969). They reproduce asexually by gemmae.

Geocalycaceae

Geocalyx graveolens (Figure 52-Figure 54)

Distribution

Geocalyx graveolens (Figure 52-Figure 54) is a widespread species in oceanic Holarctic regions (Szweykowski & Kozlicka 1974; Schäfer-Verwimp & Váňa 2011; Hugonnot 2014). In North America, it is abundant from Alaska to California and from Labrador to North Carolina and Tennessee (Hugonnot 2014). Nevertheless, it does not reach the tundra (Schuster 1980). It is much less common in Europe, and Asia exhibits only local occurrences.

Figure 52. ***Geocalyx graveolens***, a Holarctic species that extends southward into the mountains, occurring in such wet habitats as humus, peat, and mires. Photo by Hugues Tinguy, with permission.

Figure 53. ***Geocalyx graveolens*** ventral side showing underleaf at the red star. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Its most common habitats seem to be on humus, peaty soil, or decayed forest litter in mires, often on banks or sides of ledges (Simó *et al.* 1978; Schuster 1980; Damsholt 2002; Nebel & Philippi 2005). Gabriel and Bates (2005) considered it to be indicative of the wettest sites in the Azores.

In Germany ***Geocalyx graveolens*** (Figure 52-Figure 54) is very rare, occurring in calcareous alder breaks with "brisk" water (Rätzel *et al*. 2004). In western Canada, Vitt *et al*. (1986) found that it fell in the restricted terrestrial category when associated with montane streams. In eastern Canada, in Ontario, Cain and Fulford (1948) reported it from wet rotten logs, humus, and peat in deep shade, being very common throughout the province. Similarly, Evans and Nichols (1935) reported it on logs in swampy woods in the Upper Peninsula of Michigan, USA, and Steere (1934) likewise found it on rotten wood and humus in swamps and wet woods on Sugar Island, Michigan. Sharp (1944) made a similar habitat observation at Mountain Lake, Virginia, USA. Järvinen (1976) reported similar habitats in eastern Fennoscandia.

In the Himalayas, Long (2005) found it in mossy carpets under dripping cliffs. Several researchers have found it on the banks of brooks and rivers (*e.g.* Figure 54) (Plitt 1908 in Maryland, USA; Greenwood 1910 in Massachusetts, USA; Burnham 1919 in the Lake George area of New York, USA). In Massachusetts, these habitats also include damp soil on the edge of streams (Greenwood 1915). Darlington (1938) found it on moist ground near Glen Lake in Michigan, USA. Clee (1937) found it on shaded hedge banks that had an abundance of water. Mogensen and Damsholt (1981) found it in habitats with percolating water. Further attesting to its broad ecological amplitude, Váňa and Ignatov (1996) found it in the Altai Mountains in eastern Asia on a sand bar that was temporarily flooded in a stream running through a narrow canyon. Fulford (1934) found it growing over moist, shaded sandstone cliffs in Kentucky, USA. Ingerpuu *et al*. (2014) considered it to be a facultative fen species in Estonian mires.

Figure 54. ***Geocalyx graveolens*** on stream bank. Photo by Michael Lüth, with permission.

In contrast to these wet habitats, it occurs on sandstones in Baden Wurtemberg (Nebel & Philippi 2005) and Vosges (Frahm 2002) in the oriental Pyrenees (Hugonnot 2014). Furthermore, in North America (Schuster 1953) and Nordic countries (Damsholt 2002) ***Geocalyx graveolens*** (Figure 52-Figure 54) seems to tolerate subcalcareous situations, but this is not the case in the British Isles (Paton 1999). Zubel (2009) found that in southeastern Poland, it occurs on rock, sandstone, mineral soil, and humus in the mountains, but in the lowlands it occurs on rotting wood, humus, and tree bases in wet and very wet sites in alder forests and other wet forest types or boggy forests.

In North America, Schuster (1953) considered that the species showed a decided tolerance for subcalcareous conditions, and Damsholt (2002) for basic rocks in Nordic countries, which apparently is not the case in the British Isles (Paton, 1999).

Reproduction

Geocalyx graveolens (Figure 52-Figure 54) forms extensive creeping mats over ***Sphagnum*** species (Figure 47). Sharp (1944) described it as having a peculiar yellowish color (Figure 52). It typically produces numerous capsules. Ross-Davis and Frego (2004) found its diaspores in diaspore rain and buried propagule banks. Its rarity, particularly in Europe, would not seem to be caused by a limited number of suitable habitats or propagules.

Role

These mats can serve as home for the boreid beetle, ***Caurinus dectes*** (Figure 55), where the beetles feed on the liverwort on decaying logs (Russell 1979). Asakawa (1998) reported a turpentine-like odor in this liverwort species. It is possible that this odor discourages some of the potential insect herbivory, but it apparently has no negative effect on ***Caurinus dectes***.

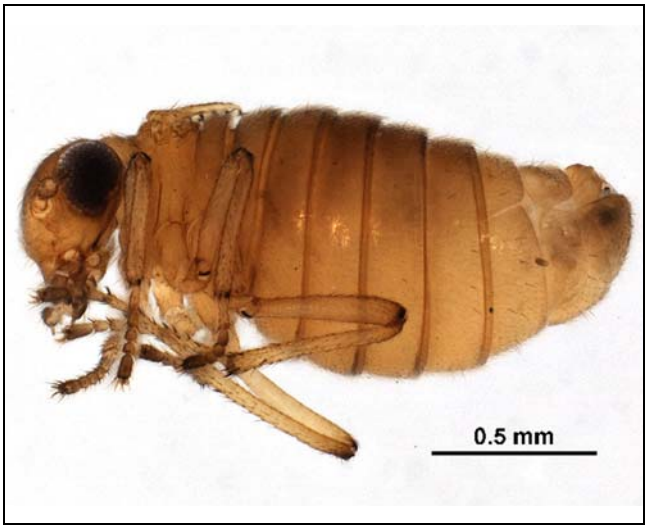

Figure 55. ***Caurinus dectes***, a boreid beetle that feeds on ***Geocalyx graveolens***. Photo by CBG Photography Group, through Creative Commons.

Fungal Interactions

In their study on liverwort-fungal symbioses, Bidartondo and Duckett (2010) were only able to find **Ascomycetes**. This was different from the previous reports of **Basidiomycetes** on this species.

Gymnomitriaceae

Gymnomitrion commutatum (Figure 56)

(syn. = *Marsupella commutata*)

Distribution

Gymnomitrion commutatum (Figure 56) occurs in Europe, Siberia, Russian Far East, China, eastern Asia, Indian Subcontinent, Malesia, subarctic America, western Canada, northwestern USA (Váňa *et al*. 2010), Iceland, and South Greenland (Konstantinova 2000).

Figure 56. ***Gymnomitrion commutatum***, a Northern Hemisphere wet habitat liverwort. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Konstantinova *et al*. (2002) found ***Gymnomitrion commutatum*** (Figure 56) on wet cliffs and cliff crevices associated with the Upper Bureya River in the Russian Far East. Bakalin (2008) found it on cliffs near streams in the tundra belt in several locations in the Sakhalin Province, Russia. Choi *et al*. (2013) found it at elevations of 1400-1614 m asl in Mt. Deogyu National Park in the Republic of Korea, where it occurred on shaded cliffs and rocks. Its records are few, and it is included in the Red Data Book for Russia (Sofronova *et al*. 2015). ***Marsupella commutata*** grows on crystalline substrates in streams on the Ushkovskii Volcano, Kamchatka (Bakalin 2006).

Adaptations

This high altitude species is blackish-brown (Mamontov *et al*. 2018), a characteristic that most likely protects it from the high levels of UV radiation at those altitudes.

Reproduction

Gymnomitrion commutatum is only occasionally fertile and capsules are rare in the UK (Smith 1990).

Gymnomitrion crenulatum (Figure 57-Figure 58)

Distribution

The distribution of ***Gymnomitrion crenulatum*** (Figure 57-Figure 58) is in question because of misidentifications. Váňa *et al*. (2010) consider it confined to northern and southwestern Europe, with other locations representing misidentifications. However, GBIF (2020c) still includes Norway, Finland, Britain, Ireland, France, Portugal, Spain, Yamal-Nenets, Tibet (Xizang), Sichuan, Yunnan, Japan, Alaska, Nunavut, British Columbia, Washington, and South Georgia.

Figure 57. ***Gymnomitrion crenulatum***, a Northern Hemisphere species with a poorly understood distribution; it seems to prefer emergent rocks of streams, but can get submersed. Photo by Andrew Hodgson, with permission.

Aquatic and Wet Habitats

This species seems to do best above the low flow water level in exposed streambed conditions, preferring moderately stable boulders (Figure 58) that are easily submerged (Vieira *et al*. 2005). It is tolerant of acid water, perhaps preferring it, especially in mountain streams of northwest Portugal. Casas *et al*. (1999) reported it on rocks by a stream in shrubby heathland in Spain.

Figure 58. ***Gymnomitrion crenulatum*** habitat in rock crevices. Photo by Andrew Hodgson, with permission.

One of the populations studied was reduced considerably by a strong fire, causing rock sediments to erode the bryophyte communities in the streambed (Vieira *et al*. 2004). In more protected locations it typically forms dense patches.

Reproduction

When Rawat *et al*. (2016) reported ***Gymnomitrion crenulatum*** (Figure 57-Figure 58) from India for the first time, they reported that they found no fertile plants. Its rarity most likely contributes to lack of observations on reproduction, but conversely, the rarity of reproduction probably contributes to the rarity of plants. In the UK, the plant is only occasionally fertile and capsules are very rare (Smith 1990).

Marsupella (Figure 59-Figure 62, Figure 63-Figure 67, Figure 70-Figure 87, Figure 89)

Marsupella (Figure 59-Figure 62, Figure 63-Figure 67, Figure 70-Figure 87, Figure 89) has more than one species in aquatic habitats, and these have at times been registered as the genus only. These include a dominance in the upper and middle reaches in the Harz Mountains of Germany (Bley 1987) and occurrence in small, pristine streams of the Tolvajärvi region, Russian Karelia (Vuori *et al*. 1999).

Marsupella aquatica (Figure 59-Figure 62)

(syn. = *Marsupella emarginata* var. *aquatica*)

Marsupella aquatica (Figure 59-Figure 62) seems to be confined to alpine or subalpine regions (Evans 1904). ***Marsupella emarginata***, on the other hand, extends downward into the plains, at least in eastern North America.

Distribution

Marsupella aquatica (Figure 59-Figure 62) has an **arctomontane** (in Arctic and in montane regions at lower latitudes) semi-circumpolar distribution with oceanic affinities (Konstantinova 2000). More specifically, Váňa *et al*. (2010) list it for northern and southwestern Europe, Asia, including Macaronesia, Siberia, Russian Far East, Caucasus, subarctic America, Canada, and northwestern and northeastern USA. They consider other records in North America to be misidentifications.

Figure 59. ***Marsupella aquatica***, an Arctic-montane semi-circumpolar species from wet and submerged rocks of streams and rivers. Photo by Štěpán Koval, with permission.

Aquatic and Wet Habitats

Nichols (1918) reported ***Marsupella aquatica*** (Figure 59-Figure 62) from ravines on Cape Breton Island, Canada. Lorenz (1924) reported it on rocks in Deer Brook on Mt. Desert, Maine, whereas the more western species ***M. emarginata*** (Figure 65-Figure 66) was frequent on wet rocks. Watson (1919) considered ***Marsupella aquatica*** to be a species that grows submerged in slow water with poor mineral salts and to occupy more aquatic rocks than ***Marsupella emarginata***. Dulin *et al*. (2009) likewise reported ***M. aquatica*** from streams with poor mineral salts in the Vologda Region of Russia, where it frequently occurred with ***Scapania undulata*** (Figure 60) and ***Fontinalis dalecarlica*** (Figure 61). Koppe (1945) reported it from stones in streams in the Westfalens of northwestern Germany. Koponen *et al*. (1995) merely listed it as aquatic in Finland. Vieira *et al.* (2005) reported it from mountain streams in northwest Portugal. By contrast, Lepp (2012) reported that it occurs to depths of 30 m in Australia, and Heggenes and Saltveit (2002) reported that it forms a carpet down to almost 40 m in the regulated River Suldalslågen in western Norway. This lake in the river is free of ice only from July to October.

Figure 60. ***Scapania undulata***, a species that associates with ***Marsupella aquatica*** on rocks in Maine, USA. Photo by Jan-Peter Frahm, with permission.

Figure 61. ***Fontinalis dalecarlica***, a species that associates with ***Marsupella aquatica*** on rocks in Maine, USA. Photo by J. C. Schou, with permission.

Bodin and Nauwerk (1968) studied the biology of the leafy liverwort ***Marsupella aquatica*** (Figure 59-Figure 62), the dominant member of the well-developed bryophyte vegetation of Latnajaure, a mountain lake (maximum depth 43.5 m) in the Abisko area of Sweden. ***Marsupella aquatica*** increases in size and robustness with depth in Latnjajaure in Swedish Lappland.

Monteith (1996) reported that ***Scapania undulata*** (Figure 60) may be replacing ***Marsupella aquatica*** (Figure 59-Figure 62), a common inhabitant in acid streams, following an experimental burn.

Adaptations

Marsupella aquatica can reach 10 cm long and is dark green to almost black, not red-brown (Smith 1990; Wagner 2008). In contrast to Wagner, Evans (1904) describes the color as bright green to reddish. The latter dark coloration can protect it from the high UV radiation in its alpine habitat. The stems branch little and are very firm (Evans 1904). A cross-sectional view reveals that stem cells are all about the same size. Those in the middle have thin walls, grading to thicker walls toward the outer cells. The outermost layer has shorter cells than the interior.

Figure 62. ***Marsupella aquatica***, exhibiting a red form. Photo by Barry Stewart, with permission.

Reproduction

Marsupella emarginata is **dioicous** (Smith 1990).

Biochemistry

Marsupella aquatica (Figure 59-Figure 62) has received less biochemical attention than some of the previously mentioned bryophytes. Huneck *et al*. (1982) identified an Ent-longipinane derivative from the species. Nagashima *et al*. (1994) identified a new gymnomitrane-type sesquiterpenoid from it, as well as others that were previously known. Adio *et al*. (2002) identified volatile compounds from ***Marsupella aquatica***. Leong *et al*. (2002) identified amorphane sesquiterpenoids from the species in Scotland. Later Adio *et al*. (2007) determined nine amorphane sesquiterpenoid constituents of the species from Austria.

Marsupella boeckii (Figure 63)

Distribution

Marsupella boeckii (Figure 63) occurs in the Antarctic-Southern Ocean area, Europe, including Svalbard (Konstantinova & Savchenko 2008), Asia, and North America from Alaska to continental USA (ITIS 2020a).

Figure 63. ***Marsupella boeckii***, a species of scattered locations worldwide, occurring in wet habitats such as the edges of springs and wet cliffs. Photo from Earth.com, with permission.

Aquatic and Wet Habitats

Koponen *et al*. (1995) reported it as aquatic in Finland. Konstantinova and Savchenko (2008) found it in Svalbard at the edge of a spring that was covered with mats of ***Marsupella arctica*** (Figure 64) where both occurred on shallow sandy soil (<1 cm) overlying rocks. Sofronova (2018) found that it created "minute" cover up to 1 cm square on wet cliffs, compared to carpets of more than 1 sq m of ***Marsupella emarginata*** (Figure 65-Figure 67) in the same habitat in eastern Yakutia, Russia.

Figure 64. ***Marsupella arctica*** herbarium specimen, a species that forms mats at the edges of springs. Photo by CBG Photography Group, through Creative Commons.

Reproduction

Marsupella boeckii is **dioicous** (Smith 1990; Konstantinova & Savchenko 2008).

Marsupella emarginata (Figure 65-Figure 67)

(syn. = *Nardia emarginata*)

Distribution

Marsupella emarginata (Figure 65-Figure 67) is a widespread Laurasian species that extends into the tropics in the high mountains (Váňa 1993). It occurs in Europe, Asia, North America from Alaska to Mexico, South America (ITIS 2020b), and Africa (Váňa 1993).

Figure 65. ***Marsupella emarginata***, a widespread Northern Hemisphere species that extends into the high mountains of the tropics where it is common in streams and rivers and banks. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Marsupella emarginata (Figure 65-Figure 67) is the most common species in the genus, as noted by Scarlett and O'Hare (2006), in English and Welsh rivers. It is common and abundant in wet or damp acidic places, especially on rocks or gravel both in and beside streams and rivers. Its less wet habitats include humid woodland rocks in woods, wet crags, lake margins, wet gravel tracks, and near snowbeds. Sofronova (2018) similarly found it in places of late snow melt in East Yakutia, Russia. It often occurs in mountain streams (Vieira *et al*. 2005 – northwest Portugal; Knapp & Lowe 2009 – Great Smoky Mountains National Park, Kentucky, USA; Luis *et al*. 2015 – Madeira Island).

Figure 66. ***Marsupella emarginata*** in its green form, showing mat growth. Photo by Barry Stewart, with permission.

West (1910) reported this species from wet rocks and shores, often submersed, in Scotland. In Connecticut, USA, it occurs on wet or moist cliffs of ravines, but it is calciphobic along rivers (Nichols 1916). On Cape Breton Island, Canada, Nichols (1918) found it again on rocks of a ravine stream bank and on wet rock cliffs associated with streams. Sofronova (2018) found it on wet cliff habitats in carpets of more than 1 sq. m. Watson (1919) attributed its most common occurrence to rocks in fast water, on banks with frequent submergence in slow water that is low in mineral salts, in waterfalls, and on mostly submerged rocks in fast streams. Weber (1976) likewise found it in Newfoundland, Canada, in the narrow zone that is periodically submerged along the river (Figure 67).

Figure 67. ***Marsupella emarginata*** in its habitat, forming mats on a bank where it can be periodically submerged. Photo by Chris Wagner, through Creative Commons.

It also occurs in European springs, particularly in the Central Alps (Zechmeister & Mucina 1994). In the Altai Mountains, Váňa and Ignatov (1996) found it on wet rocks of deep canyons and near a waterfall in the lower forest zone, but also in the alpine zone among rocks in rock fields, and in the subalpine covering wet cliffs with extensive pure mats.

Koponen *et al*. (1995) considered it to be an aquatic species in Finland. Ferreira *et al*. (2008) reported it as growing in rivers. Szweykowski (1951) considered it to be an acidophile (*p*H 4.0-6.0) in streams of Gory Stolowe Mountains, Poland, terming it a **hydroamphibiont** in streams. Thiébaut *et al*. (1998) considered it to be an acidophilous stream species in the Vosges Mountains of northeastern France, being sensitive to high ion concentrations. Geissler (1975, 1976) termed it a **helokrene** (living in marsh spring communities) in European alpine areas. Vanderpoorten and Klein (1999a) found that it could tolerate neutral *p*H if it is in **oligomineral** (having few dissolved minerals) waters; sewage effluent causes populations to decrease. Light (1975) reported it from small lakes in the Scottish mountains, where it experienced ice cover 4-7 months of the year; again, it preferred low ion concentrations. Satake *et al*. (1989) reported in from the acid river Akagawa, Japan. Tremp and Kohler (1991) likewise reported it as

submersed in low-buffered streams and Bahuguna *et al*. (2013) reported that it grows only in water low in solutes. Kohler and Tremp (1996) found ***Marsupella emarginata*** (Figure 65-Figure 67) to be an indicator of silicate rock areas with acidic water. Birk and Willby (2010) likewise found it to be somewhat common in siliceous mountain streams. In view of these low-ion occurrences, Tremp 2003) classified the species as **oligotrophic** (preferring low nutrients). Vanderpoorten (2012) considered it to be an indicator species for acidic waters with low buffering capacity.

In West Virginia, USA, ***Marsupella emarginata*** (Figure 65-Figure 67) preferred a *p*H of around 4.17 in mountain streams (Stephenson *et al*. 1995). In the Haute Ardenne rivers of Belgium, it is known from earthy and gravelly substrates of river banks (Leclercq 1977). But it also occurs near water on the wall of the Flume at Franconia Notch, New Hampshire, USA (Glime 1982). In the Canary Islands, it is never dominant and occurs on moist, shaded, soft volcanic rocks of the laurel forest (Dirkse 1985). Wagner *et al*. (2000) reported it from 40 and 70 m depth in Waldo Lake, Oregon, USA.

It occurs in association with ***Scapania undulata*** (Figure 60) in aquatic habitats of eastern Odenwald and southern Spessart (Philippi 1987) and in the ***Platyhypnidium*** (Figure 68)***-Fontinalis antipyretica*** (Figure 69) association in Thuringia, Germany (Marstaller 1987).

Figure 68. ***Platyhypnidium riparioides***, a species that can occur in association with ***Marsupella emarginata***. Photo by Hermann Schachner, through Creative Commons.

Figure 69. ***Fontinalis antipyretica*** in dried out small pool, a species that can occur in association with ***Marsupella emarginata***. Photo by Matt Goff, with permission.

Janauer and Dokulil (2006) report that when the water flow is too fast or runoff is too irregular, tracheophytic macrophytes are unable to become established, but bryophytes can become dominant. ***Marsupella emarginata*** (Figure 65-Figure 67) is one of those bryophytes to take advantage of these conditions (Lottausch *et al*. 1980).

In the River Dee, Maitland (1985) found dense liverwort growth, ***Marsupella emarginata*** (Figure 65-Figure 67) on most rock surfaces, reaching about 3 m diameter, but only 20 cm in depth (*e.g.* Figure 67).

Adaptations

Thiebaut *et al*. (1998) considered ***Marsupella emarginata*** (Figure 65-Figure 67) to be acidophilous and sensitive to high concentrations of cations. It disappears when Mg is too high and *p*H reaches 7.0. But they found that it was the cation concentration, not the *p*H that discouraged its presence. They concluded that it must have a physiological mechanism to regulate the difference in H^+ concentration between the cell and the surrounding water. They suggested that cations such as Mg and Ca limit the penetration of other elements needed by the plant cells.

Marsupella emarginata varies from bright green to reddish (Evans 1904). Reddish colors can help to protect the plants from damage by UV rays, particularly at high elevations, whereas green colors are more typical of bryophytes growing at lower light levels and lower elevations.

Reproduction

Marsupella emarginata (Figure 65-Figure 67) is **dioicous** with only occasional capsules that appear in late winter or spring in the UK (Smith 1990).

Fungal Interactions

Wang and Qiu (2006) report ***Marsupella emarginata*** (Figure 65-Figure 67) as having associations with fungi, but with no mycorrhizal relationships known. Egertová *et al*. (2016) found ***Mniaecia jungermanniae*** (Figure 24-Figure 26) in three samples of this species. Hopefully studies like that of Adio and König (2007) on sesquiterpenoids and other terpenes will help us to understand why some species have fungal partners or parasites and others do not.

***Marsupella emarginata* subsp. *tubulosa* (Figure 70)**

(syn. = *Marsupella tubulosa*)

Distribution

Marsupella emarginata* subsp. *tubulosa (Figure 70) has been identified in several studies. It is a subspecies of the Northern Hemisphere, primarily in eastern Asia and nearby islands, but also reported from fewer known locations in Europe and North America (GBIF 2020d). However, in their revision of the **Gymnomitriaceae**, Bakalin *et al*. (2021) exclude it from these latter areas and from the Russian far East continental mainland as incorrect identifications, based on the absence of the biconcentric character of the oil bodies there, confining it to the insular and peninsular areas in Amphi-Pacific Boreal and Temperate Eastern Asia

Aquatic and Wet Habitats

Bakalin *et al*. (2021) considered ***Marsupella emarginata*** subsp. ***tubulosa*** (Figure 70) to be acidophilic and meso- to hygrophytic. The species occupies sandy soils and mineral substrates, over wet to moist, and sometimes mesic cliffs, being most common along streams near running water in the Korean Peninsula. Song and Yamada (2006) reported it from wet rocks on Jeju (Cheju) Island, Korea. It occurs on a soil bank of a small creek of the Upper Bureya River in the Russian Far East (Konstantinova *et al*. 2002). On Mts. Hakkôda in northern Japan, it occurs on moist rocks (Kitagawa 1978a). Records of this subspecies with habitat data are harder to find despite its recorded number of locations.

Figure 70. ***Marsupella emarginata*** subsp. ***tubulosa*** forming mats in a small creek. Photo from Taiwan Mosses, through Creative Commons.

Biochemistry

Despite the paucity of readily available ecological information, Matsuo *et al*. (1979) isolated three new sesquiterpenoids from this species.

Marsupella koreana (Figure 71-Figure 73)

Distribution

Marsupella koreana (Figure 71-Figure 73) is probably an endemic species of the montane-temperate (Bakalin *et al*. 2021) Korean Peninsula, but is quite common there and has a highly variable morphology (Bakalin *et al*. 2019b). As a result, it may occur elsewhere, hiding under different names.

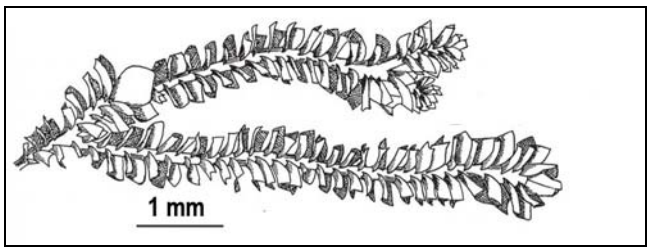

Figure 71. ***Marsupella koreana***. Drawing modified from Bakalin *et al*. 2021.

Figure 72. ***Marsupella koreana***, an apparent endemic of the Korean Peninsula. Photo modified from Bakalin *et al*. 2019; permission pending.

Figure 73. ***Marsupella koreana***. Photo modified from Bakalin *et al*. 2019;, permission pending.

Aquatic and Wet Habitats

Bakalin *et al*. (2019b) consider ***Marsupella koreana*** (Figure 71-Figure 73) to be acidophilic to neutro-tolerant and meso- to hygrophytic. It occupies mesic, rarer moist or dry substrata in open to partly shaded places.

Adaptations

The brownish green to deep green coloration of ***Marsupella koreana*** (Figure 71-Figure 73) (Bakalin *et al*. 2019b) suggest an adaptation to high light intensity. They form loose mats that are somewhat rigid (Bakalin *et al*. 2021). They have few or no rhizoids, but rhizoids are

common on geotropic stolons, a feature that should aid in their spread locally. Stems have hyaline epidermal cell with thick inner walls (Figure 74).

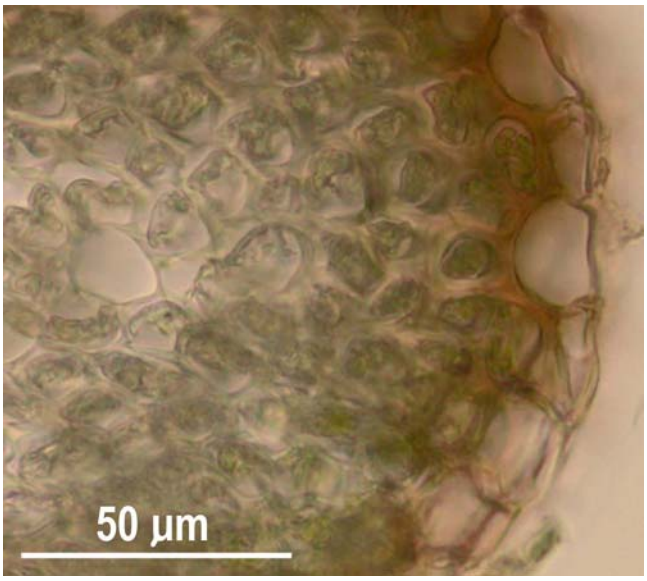

Figure 74. ***Marsupella koreana*** stem cross section showing thick inner walls of epidermal cells. Photo modified from Bakalin *et al.* 2019; permission pending.

Reproduction

Marsupella koreana (Figure 71-Figure 73) is **dioicous** (Bakalin *et al*. 2019b). Its spores are small (10-11 µm) and papillose.

Biochemistry

This rare endemic lacks biochemical studies, and it is not clear if it has oil bodies (Figure 75).

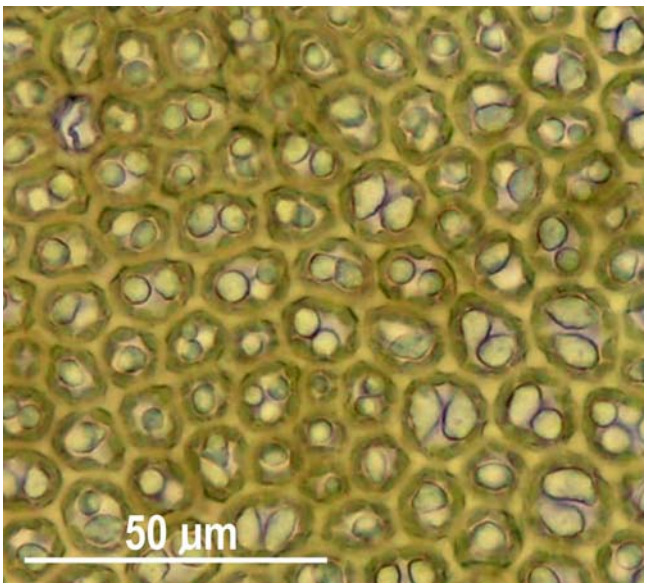

Figure 75. ***Marsupella koreana*** leaf cells with oil bodies? Photo modified from Bakalin *et al*. 2019; permission pending.

Marsupella pseudofunckii (Figure 76-Figure 77)

Distribution

Marsupella pseudofunckii (Figure 76-Figure 77) is a Temperate Montane East Asian species, known from Korea, China, Taiwan, the Russian Far East, and Japan (Bakalin *et al*. 2021).

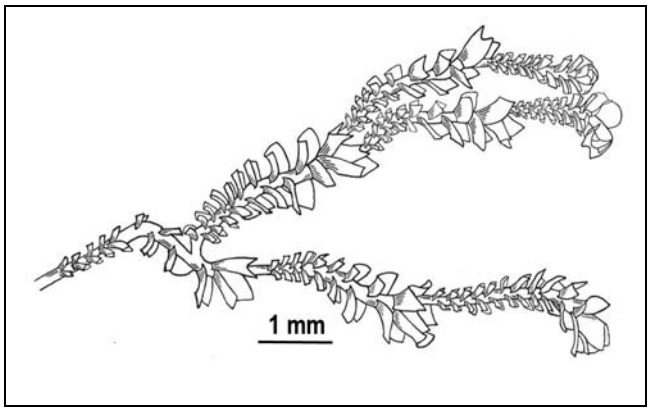

Figure 76. ***Marsupella pseudofunckii*** female plant. Drawing modified from Bakalin *et al.* 2021.

Figure 77. ***Marsupella pseudofunckii***. Photo from Bakalin *et al*. 2019; permission pending.

Aquatic and Wet Habitats

Marsupella pseudofunckii (Figure 76-Figure 77) is acidophilic and occurs as a mesophyte to hygrophyte (Bakalin *et al*. 2021). It occurs on dry to moist cliffs, rarely on wet rocks or stones near streams, in open or, more commonly, partly shaded places. Choi *et al*. (2013) list cliffs along streams, sometimes accompanied by ***Scapania undulata*** (Figure 60).

Adaptations

The species can at least sometimes form mats (Figure 78). These should help it to conserve water when it is not in a wet location. Its leaves also fold, further conserving water.

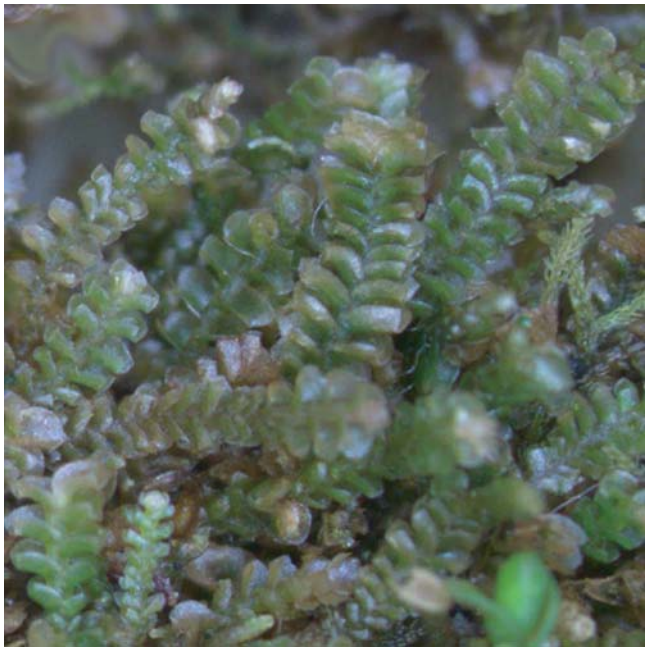

Figure 78. ***Marsupella pseudofunckii***, a montane east Asian species. Photo from Bakalin *et al*. 2019; permission pending.

Reproduction

Marsupella pseudofunckii (Figure 76-Figure 78) is **dioicous** (Bakalin *et al*. 2021).

Biochemistry

There seems to be nothing published on biochemistry of ***Marsupella pseudofunckii*** (Figure 76-Figure 78), and the oil bodies (Figure 79) are not described.

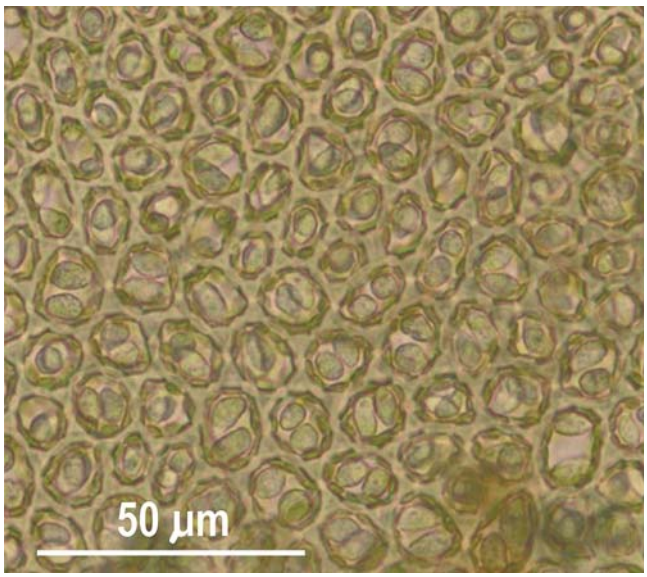

Figure 79. ***Marsupella pseudofunckii*** cells with oil bodies? Photo modified from Bakalin *et al*. 2019; permission pending.

Marsupella sparsifolia (Figure 80-Figure 81)

Distribution

Marsupella sparsifolia (Figure 80-Figure 81) is a bipolar species, mostly from Arctic-alpine and high subarctic areas (Schuster 1974). It occurs in Europe from Greenland and Scandinavia south to Great Britain and alpine central Europe. It also occurs in Uganda and the Cape of Good Hope, South Africa. In North America it occurs in the mountains of British Columbia and Alberta, Quebec, Canada, and in the USA on Mt. Washington, New Hampshire and in the Huron Mtns, Michigan. It also occurs in New Zealand.

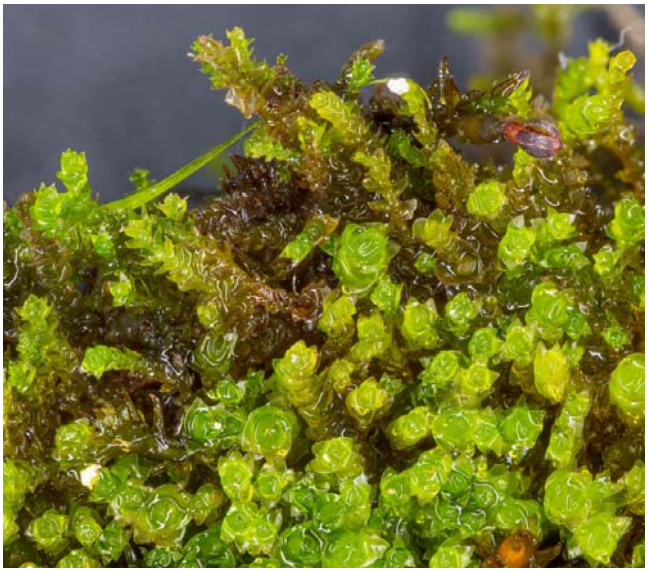

Figure 80. ***Marsupella sparsifolia*** in a wet habitat. Photo by Kristian Peters (Kersey Online; Sage bud), with permission.

Figure 81. ***Marsupella sparsifolia,*** is a bipolar Arctic-alpine species that occurs on stream banks and other wet habitats. Photo by Kristian Peters (Kersey Online; Sagebud), with permission.

Aquatic and Wet Habitats

Koponen *et al*. (1995) considered this species to be aquatic in Finland. Schuster (1974) attributes it to alluvial sand or sandy soil adjacent to streams, in acid late snow areas, on siliceous rock faces receiving water. Like ***Marsupella emarginata*** (Figure 65-Figure 67), it avoids calcareous sites but tolerates frequent inundation. Hong (1980) reported ***Marsupella sparsifolia*** (Figure 80-Figure 81) from soil in the North Cascades Range, Washington, USA. It also occurs on moist cliffs where it can form close mats, as seen along Cliff River in the Huron Mountains, Michigan, USA (Nichols 1935).

Figure 82. ***Marsupella sparsifolia*** habitat. Photo by Kristian Peters (Korseby Online; Sagebud), with permission.

Reproduction

Marsupella sparsifolia (Figure 80-Figure 81) is **paroicous** (Smith 1990). It is usually fertile and frequently produces capsules.

Marsupella sphacelata (Figure 83-Figure 86)

Distribution

Marsupella sphacelata (Figure 83-Figure 86) is Holarctic, occurring in boreal and low-Arctic regions (Schuster 1974). Its terrestrial form extends further south than does the aquatic form. This species is widespread in Europe, from Greenland southward to England, Spain, and the Azores. It is widespread in Japan, but is poorly known elsewhere in Asia. In North America it extends from Alaska south to California and in the east from Newfoundland to North Carolina.

Figure 83. ***Marsupella sphacelata*** clone. Photo by Hermann Schachner, through Creative Commons.

Figure 84. ***Marsupella sphacelata***, a boreal and low-Arctic species mostly of slow streams. Photo by Štěpán Koval, with permission.

Figure 85. ***Marsupella sphacelata***. Photo by Giovanni Bergamo Decarli, through Creative Commons.

Figure 86. ***Marsupella sphacelata*** showing its mat growth habit and dark pigments. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Watson (1919) considered ***Marsupella sphacelata*** (Figure 83-Figure 86) to be an alpine species submerged in fast water. Geissler (1975) likewise found it in European alpine streams. At 1400 m in the Sayan Mountains of southern Siberia, Konstantinova and Vasiljev (1994) reported it submerged on rocks in brooks, mixed with other liverworts. But in the eastern USA, it occurs in mountain streams that are not alpine (Glime 1968), and Vieira *et al*. (2005) found it in mountain streams of northwest Portugal. Sharp (1939) reported it from boulders in brooks in Tennessee, USA, where it was rare. It also occurs on a rock cliff associated with Katrine Lake in Sudbury, Ontario, Canada and on wet rock of a small stream at Pinetree Lake in Algonquin Park at 600 m or less, also in Ontario (Williams & Cain 1959). At Cumberland Falls State Park (327 m) in Kentucky, USA, it occurred on moist rocks (Norris 1967).

Koponen *et al*. (1995) considered this species to be aquatic in Finland. The typical aquatic form grows attached to rocks and rock walls of mountain streams, usually in small pools and in slow water (Figure 87) (Schuster 1974). It seems to be absent from calcareous rocks. It can form pure patches, but also grows with ***Marsupella emarginata*** (Figure 65-Figure 67), ***Scapania undulata*** (Figure 60), and ***S. subalpina*** (Figure 88). Its lax tufts are typically dull green and brownish-tinged above (Figure 83-Figure 86, Figure 89).

Figure 87. ***Marsupella sphacelata*** in submersed habitat. Photo by Hermann Schachner, through Creative Commons.

Figure 88. ***Scapania subalpina***, a species that often grows with ***Marsupella sphacelata*** in mountain streams. Photo by Andy Hodgson, with permission.

But ***Marsupella sphacelata*** (Figure 83-Figure 86) can also be found in wet areas not associated with streams. Kitagawa (1978a) found it to be locally abundant on damp soil at the edge of moors below the summit of Odake, Japan.

Adaptations

The terrestrial forms of ***Marsupella sphacelata*** (Figure 83-Figure 86) are able to grow in direct sun, often with intermittent seepage (Figure 89) (Schuster 1974). They are able to endure long dry periods. Their life form is small to large tufts (Smith 1990). These forms create blackish patches. This attests to a wide physiological range for the species (Schuster 1974).

Marsupella sphacelata (Figure 83-Figure 86, Figure 89) can produce UV-B-absorbing compounds (Figure 86, Figure 89) in mountain streams where this radiation is high. Arróniz-Crespo *et al*. (2004) verified that these differed among populations, but we need to verify whether these are environmentally induced or genetically different.

Reproduction

Marsupella sphacelata (Figure 84-Figure 87, Figure 89) is **dioicous** (Smith 1990). Fertile plants are rare and capsules very rare.

Figure 89. ***Marsupella sphacelata*** habitat on wet substrate, showing dark pigments that absorb UV radiation. Photo by Hermann Schachner, through Creative Commons.

Marsupella subemarginata (Figure 90)

Distribution

Collections of ***Marsupella subemarginata*** (Figure 90) thus far suggest that it is **oro-boreal** (boreal mountains and mountainous regions), with records from Switzerland, Russia, and Japan (Bakalin *et al.* 2019b).

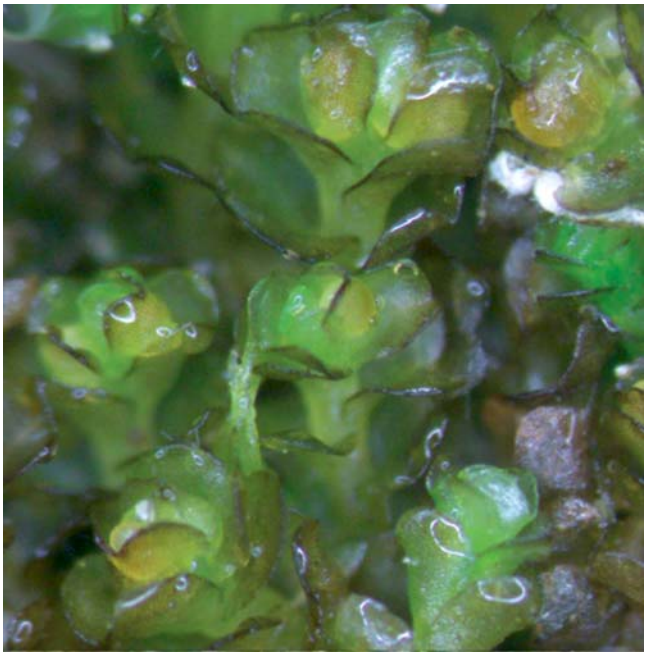

Figure 90. ***Marsupella subemarginata***, a species from an Eastern Hemisphere oro-boreal region. Photo modified from Bakalin *et al.* 2019; permission pending.

Aquatic and Wet Habitats

Marsupella subemarginata (Figure 90) occurs on temporarily wet cliffs and boulders in areas with a mild climate and even distribution of precipitation around the year (Bakalin *et al.* 2019). In Kamchatka it occur on moist boulders near temporary streams in mountain tundra.

Adaptations

Plants of ***Marsupella subemarginata*** (Figure 90) are greenish brownish to rusty (Bakalin *et al.* 2019); the darker colors can filter out the high UV light one would expect in its mountain environments. Its stem has marginal cells of the hyaloderm with thickened walls on all sides (Figure 91), possibly protecting them from gushes of water when it rains or preventing water loss when it does not. Nevertheless it has few rhizoids.

Reproduction

Although ***Marsupella subemarginata*** (Figure 90) is **dioicous**, Bakalin and coworkers (2019) reported it as freely producing spores that frequently germinate within the cushions.

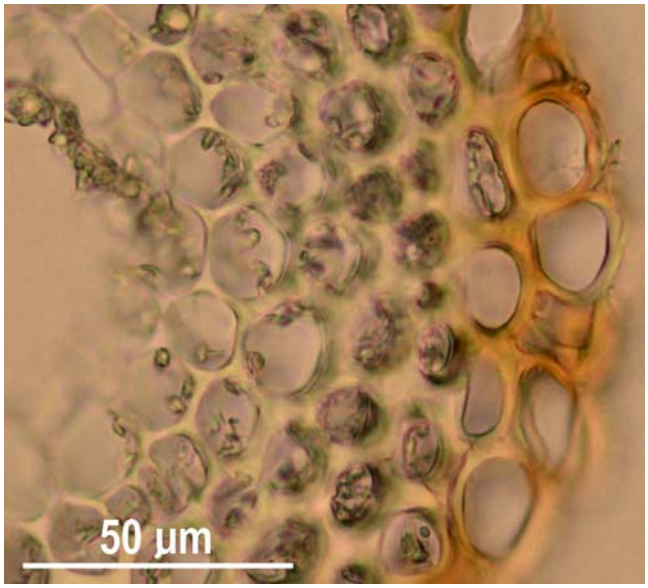

Figure 91. ***Marsupella subemarginata*** stem cross section showing thickened walls on the epidermal cells. Photo modified from Bakalin *et al*. 2019; permission pending.

Biochemistry

There seem to no studies on the biochemistry of ***Marsupella subemarginata*** (Figure 90) and oil bodies are not described (Figure 92).

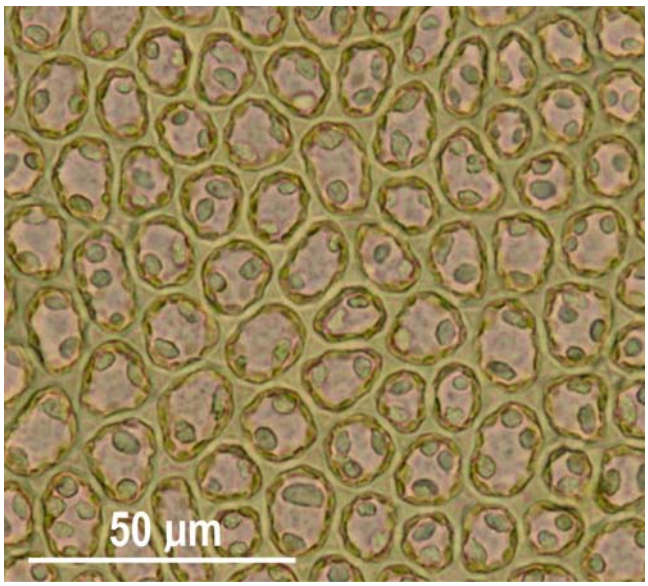

Figure 92. ***Marsupella subemarginata*** leaf cells with oil bodies? Photo modified from Bakalin *et al.* 2019; permission pending.

Marsupella vietnamica (Figure 93)

Distribution

So far, ***Marsupella vietnamica*** (Figure 93) is known only from North Vietnam, but Bakalin and coworkers suggest it should be found in Yunnan, China, as well (Bakalin *et al.* 2019b).

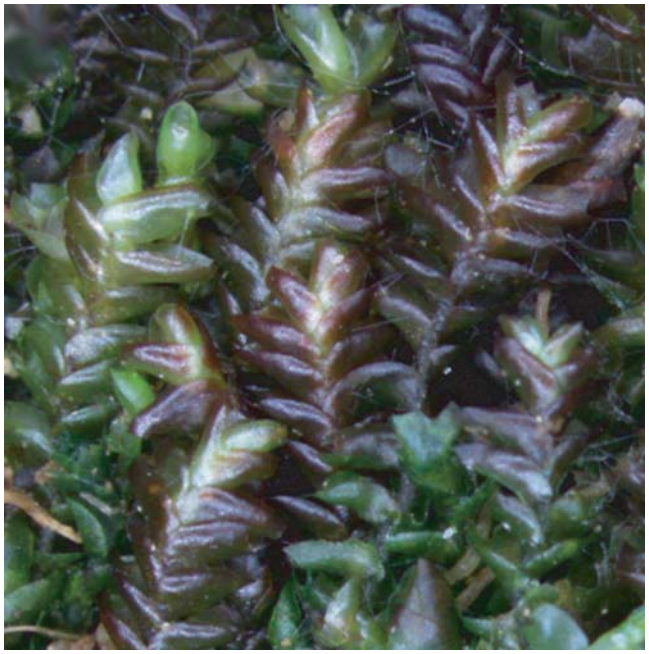

Figure 93. ***Marsupella vietnamica***, a species from North Vietnam. Photo modified from Bakalin *et al.* 2019; permission pending.

Aquatic and Wet Habitats

Marsupella vietnamica (Figure 93) is thus far a meso-hygrophytic species and an acidophile. It prefers shaded to semi-open moist to wet cliffs near streams where there is sufficient water even during the so-called "dry season" in the tropical zone. The species occurs in middle mountain elevations.

Adaptations

No special adaptations seem to be described for ***Marsupella vietnamica*** (Figure 93). The stem appears to have somewhat thickened walls in the outer layers (Figure 94). The leaf cells have huge trigones and in the photo they have brown cell walls (Figure 95).

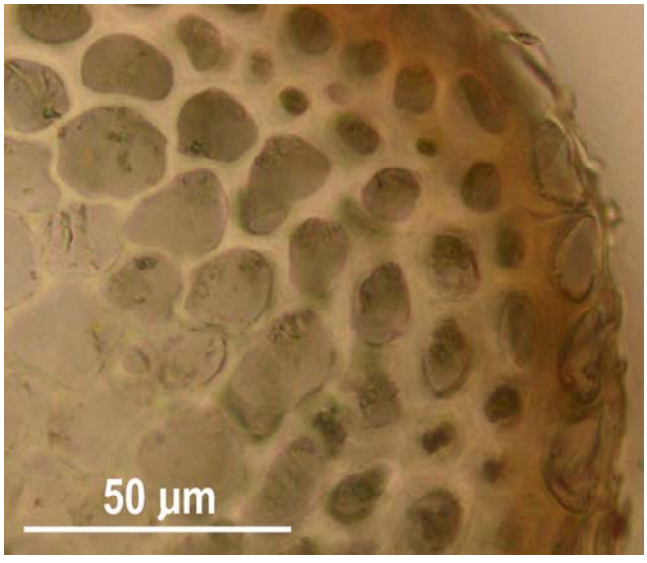

Figure 94. ***Marsupella vietnamica*** stem cross section. Photo modified from Bakalin *et al.* 2019; permission pending.

Reproduction

The sexual condition is unknown, but Bakalin *et al.* (2019b) indicated that ***Marsupella vietnamica*** (Figure 93) is **probably dioicous** because they found no antheridia or sporophytes.

Biochemistry

There seem to be no studies on the biochemistry of ***Marsupella vietnamica*** (Figure 93), but there appear to be distinct oil bodies in the leaf cells (Figure 95).

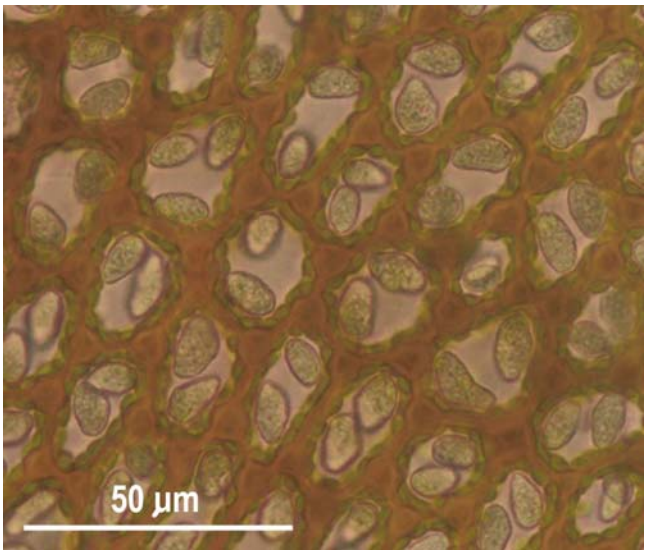

Figure 95. ***Marsupella vietnamica*** leaf cells and oil bodies? Photo modified from Bakalin *et al.* 2019; permission pending.

Marsupella yakushimensis

Distribution

Marsupella yakushimensis is a south temperate to subtropical Montane East Asian endemic species known in China, the southern part of the Korean peninsula, and the southern half of Japan (Bakalin *et al*. 2021).

Aquatic and Wet Habitats

Marsupella yakushimensis is an acidophilic hygro- to hydrophyte (Bakalin *et al*. 2021). It occurs on wet cliffs at some distance from water courses or on stones washed with sluggishly running water in partly shaded habitats in the middle elevations of mountains with evergreen to deciduous broadleaved forests. Choi *et al*. (2012, 2013) found it on humid soil of a steep mountain slope and on wet cliffs along a stream in Korea.

Adaptations

Commonly, ***Marsupella yakushimensis*** forms pure patches, but more rarely it is associated with ***Scapania undulata*** (Bakalin *et al*. 2021). It can have purple to red pigmentation, especially in Japanese populations, perhaps protecting it from UV light in the mountains.

Reproduction

Marsupella yakushimensis is **dioicous** and seems to produce antheridia regularly, but it rarely has archegonia (Bakalin *et al*. 2021). Even where Bakalin *et al*. found the two sexes intermixed there was no evidence of fertilization or a fully developed perianth.

Nardia assamica

Distribution

Nardia assamica is an east Asian species that extends into the Caucasus (Bakalin *et al*. 2009), but also extends into alpine areas in Europe (Geissler 1975) and Australia (ITIS 2020c). Hicks (2003) also includes Alaska.

Aquatic and Wet Habitats

Geissler (1975) reported ***Nardia assamica*** in European alpine streams. Hicks (2003) listed its habitats as wet exposed soil with water seepage. Bakalin *et al*. (2009) reported on its presence in the South Kuril Islands, East Asia. There, its less aquatic habitats, compared to those in the alpine streams, include oligotrophic peatlands, wet open places, fumaroles and hot sulfur springs at 50ºC, areas of bare clayish or sandy ground in places with destroyed vegetation cover (stream banks, travertine cones in hot stream areas), rocks along cool and hot sulfur springs in forested and forestless areas, cliff wall in *Salix-Duscheckia* wet community, among mosses in hummocks in sedge-moss mires, between patches of ***Eriophorum*** (Figure 96) and ***Eleocharis*** (Figure 22) in wet depression in wind-stressed community of ***Sasa*** (bamboo; Figure 97) and small herbs. It frequently occurs with other leafy liverworts.

Figure 96. ***Eriophorum scheuchzeri*** in the Swiss Alps. ***Nardia assamica*** lives among plants of this genus in the Alps. Photo by Simon A. Eugster, through Creative Commons.

Figure 97. ***Sasa*** ground cover in spruce forest at Bihora Pass Japan. ***Nardia assamica*** lives in association with ***Sasa*** in wet depressions. Photo by Janice Glime.

Biochemistry

The oil bodies are large (Figure 98). Although there seem to be no biochemical studies, one could conjecture that such large oil bodies might contain some interesting biochemicals.

Figure 98. ***Nardia assamica*** cells showing large oil bodies. Photo by Yang Jia-dong, Taiwan Encyclopedia of Life, through Creative Commons.

Nardia compressa (Figure 99-Figure 102)

(syn. = *Alicularia compressa*)

Distribution

Nardia compressa (Figure 99-Figure 102) has a worldwide distribution, but avoids the hot tropics, occurring there only at high elevations (DiscoverLife.org 2020).

Figure 99. ***Nardia compressa***, a species with worldwide distribution outside the tropics, occurring in lakes and streams. Photo by Hermann Schachner, through Creative Commons.

Figure 100. ***Nardia compressa*** showing stoloniferous shoots. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Based on early studies, West (1910) reported ***Nardia compressa*** (Figure 99-Figure 102) to be abundant on wet and submersed rocks (Figure 101) in Scotland, sometimes occurring down to 1 m depth in lakes. Light (1975) reported it from small lakes of the Scottish mountains where it experiences 4-7 months of ice cover and low ion concentrations.

Figure 101. ***Nardia compressa*** habitat by a stream. Photo by Hugues Tinguy, with permission.

Watson (1919), on the other hand, reported ***Nardia compressa*** (Figure 99-Figure 102) as a species submerged in slow water with poor mineral salts, as well as rocky and stony beds of fast streams. In the Haute Ardenne rivers of Belgium it seems to be strictly aquatic (Leclercq 1977). In Thuringia, Germany, Marstaller (1987) found it in association with ***Platyhypnidium*** (Figure 68) and ***Fontinalis antipyretica*** (Figure 69).

Lepp (2012) reported ***Nardia compressa*** (Figure 99-Figure 102) from the edges of a small stream running through a steep ravine in Alaska. In swift mountain streams of Yakobi Island, Alaska, USA, Shacklette (1965) found that the intertwined stems can dam the stream, creating a series of terraced pools. The growth of the liverwort closes the pool surface (*e.g.* Figure 102), permitting tracheophytes to invade the mat.

Vieira *et al*. (2004, 2005) described ***Nardia compressa*** (Figure 99-Figure 102) in Portugal as the dominant species from granite slabs of the streambed, where it is immersed, often in fast-flowing acidic water. It is most common in high mountain areas, but often in exposed peat bog areas at 700-1400 m asl. It seems to form extensive populations anywhere it can become established. This includes exposed peat bog areas associated with ***Fissidens polyphyllus*** (Figure 103), ***Marsupella aquatica*** (Figure 59-Figure 62), ***Marsupella sphacelata*** (Figure 83-Figure 87), ***Platyhypnidium lusitanicum*** (Figure 104), and ***Scapania undulata*** (Figure 60), in these mountain streams of northwest Portugal (Vieira *et al*. 2005).

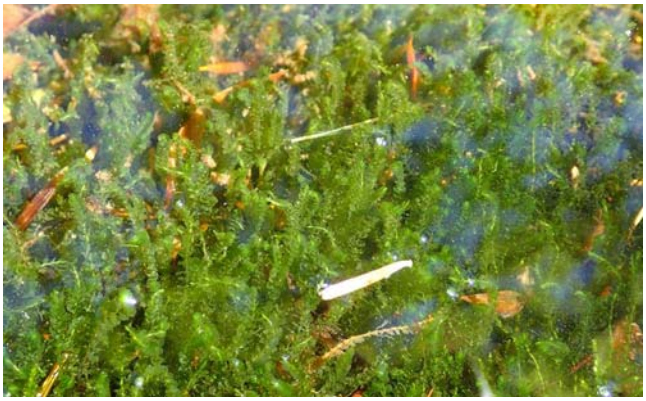

Figure 102. ***Nardia compressa*** submersed. Photo by Hugues Tinguy, with permission.

Figure 103. ***Fissidens polyphyllus***, a species that occurs with ***Nardia compressa*** in exposed peat bog areas. Photo by David T. Holyoak, with permission.

Figure 104. ***Platyhypnidium lusitanicum***, an associate with ***Nardia compressa***. Photo by Barry Stewart, with permission.

Geissler (1975) considered ***Nardia compressa*** (Figure 99-Figure 102) to be a helokrene species associated with alpine streams. Ferreira *et al*. 2008) considered it to be a species of rivers. Scarlett and O'Hare (2006) found it to be among the commonest species in English and Welsh rivers.

Nardia compressa (Figure 99-Figure 102) apparently is unable to tolerate alkaline water well. Wilkinson and Ormerod (1994) studied the effects of catchment liming on bryophytes in upland Welsh streams. ***Nardia compressa*** had the greatest cover exhibited in any one stream, reaching up to 71% cover. Liming was used to restore acidified streams. Under this treatment, the cover of ***N. compressa*** declined significantly from 39% to 5%.

Rothero (2020) found it on permanently wet or frequently inundated rocks and stones in acidic turbulent streams and rivers. It can occasionally be embedded in sand and gravel. It typically forms spongy masses, especially in cold, slow-flowing headwaters of upland streams, but it also occurs in **burns** (streams or small rivers) and flushes associated with late-lying snow fields, often forming pure patches of many square meters.

Adaptations

Nardia compressa (Figure 99-Figure 102) varies in color from deep green to reddish-brown or deep purple (Smith 1990). The plants are robust and form large tufts.

Reproduction

Nardia compressa (Figure 99-Figure 102) is **dioicous** and is rarely fertile in the UK (Smith 1990). Gemmae are unknown.

Nardia geoscyphus (Figure 105-Figure 106)

Distribution

Nardia geoscyphus (Figure 105-Figure 106) is a boreal species occurring in Europe, Asia, and North America (Natcheva 2020). Overall, it has a restricted distribution with low population density (Natcheva 2020).

Figure 105. ***Nardia geoscyphus***, a boreal Northern Hemisphere species from stream banks and constructed ditches. Photo by Štěpán Koval, with permission.

Figure 106. ***Nardia geoscyphus*** habitat on a stream bank. Photo by Martine Lapointe, with permission.

Beaucourt *et al*. (1987) reported ***Nardia geoscyphus*** (Figure 105) from irrigation ditches. It also grows on eroded soil beside roads and on stream banks (Figure 106) (Natcheva 2020).

Adaptations

Nardia geoscyphus (Figure 105-Figure 106) rarely occurs in dense **mats** and the shoots are usually prostrate and closely adhere to the soil (Evans 1912). Rhizoids are numerous (Smith 1990). Its coloration ranges from green to reddish brown or purplish . It often grows among other bryophytes, likely retaining more water due to their presence.

Reproduction

Nardia geoscyphus (Figure 105-Figure 106) is **paroicous** (having archegonia and antheridia on same branch), permitting it to frequently produce capsules (Smith 1990).

Nardia scalaris (Figure 107-Figure 108, Figure 111)

(syn. = *Alicularia scalaris*, *Alicularia scalaris* var. *distans*, *Alicularia scalaris* var. *procerior*, *Alicularia scalaris* var. *rivularis*)

Distribution

Nardia scalaris (Figure 107-Figure 108, Figure 111) is distributed in the North Pacific in Alaska, British Columbia, California, Oregon, Washington in North

America; Chukotka, Kamchatka, Magadan, and Sakhalin in Russia (Bakalin 2012). Elsewhere, it is reported from Tennessee, USA (Sharp 1939), Scotland (West 1910), Serbia (Pantović & Sabovljević 2013), and the Azores (Sjögren 1997). ITIS (2020d) also reports it from southern Asia and Africa.

Figure 107. ***Nardia scalaris***, a species from the Northern Hemisphere, southward into the mountains, growing on peaty soils and in springs. Photo by J. C. Schou, with permission.

Figure 108. ***Nardia scalaris*** forming continuous carpet. Photo by Hermann Schachner, through Creative Commons.

Figure 109. ***Saxifraga ferruginea***, a species that can grow on carpets of ***Nardia scalaris*** in Alaska. Photo by Paul Slichter, with permission.

Aquatic and Wet Habitats

West (1910) reported ***Nardia scalaris*** (Figure 107-Figure 108, Figure 111) from wet sandy-peaty shores in Scotland, where it is often abundant. Also in Scotland, Harriman and Morrison (1982) found ***Nardia scalaris*** [and several ***Scapania*** (*e.g.* Figure 60) species] to be the most abundant species of bryophytes in the streams. Watson (1919) described it as a species submerged in fast water, on ground or rocks, on banks with frequent submergence and slow water, and in usually drier sites with fast water.

Sharp (1939) reported it on moist, peaty soil in Tennessee, USA, but there it was rare, being more common farther north. Pantović and Sabovljević (2013) found ***Nardia scalaris*** (Figure 107-Figure 108, Figure 111) on rock by a stream and on soil on Mt. Boranja in western Serbia. Sjögren (1997) found it in a single collection as "accidentally" epiphyllous in the Azores Islands.

In Alaska ***Nardia scalaris*** (Figure 107-Figure 108) can form continuous carpets (Figure 108) that seem to support the growth of ***Saxifraga ferruginea*** (Figure 109) (Shacklette 1961). These areas typically are highly disturbed and contaminated with copper, for which these two species seem to have good tolerance. The liverwort provides an organic layer about 1 cm thick. It grows on a variety of substrates and is tolerant of the sulfide found in pyrite. It is often a snowbed species and has a strong requirement for abundant water and light with little or no competition.

The ***Scapania*** (Figure 60)-***Nardia*** (Figure 107-Figure 108, Figure 111) community on Yakobi Island colonizes mountain rivulets, forming carpets that permit ***Nephrophyllidium crista-galli*** (syn. = *Fauria crista-galli*; Figure 110) to colonize and eventually succeed to a copperbush community (Shacklette 1965).

It is likely that this species has some salt tolerance, as Evans (1912) reported it growing on cliffs at about 3 m above the high tide level in Nova Scotia and New Brunswick, Canada.

Reproduction

Nardia scalaris (Figure 107-Figure 108, Figure 111) is **dioicous** and rarely produces capsules (Figure 111), at least in North America (Evans 1912; Smith 1990). It typically produces prostrate shoots that become suberect when growing in compact mats.

Figure 110. ***Nephrophyllidium crista-galli***, a species that colonizes the ***Scapania-Nardia*** community on Yakobi Island. Photo by Andy Tasler, through public domain.

Figure 111. ***Nardia scalaris*** with capsules. Photo by J. C. Schou, with permission.

Fungal Interactions

Bidartondo and Duckett (2010) found that ***Nardia scalaris*** (Figure 107-Figure 108, Figure 111) predominantly and consistently associates with the ***Sebacina vermifer*** species complex (see Figure 169). An unusual find was that the DNA sequence of the fungus on this liverwort was identical to that on ***Lophozia ventricosa*** (Figure 112) at Ben Wyvis, Scotland. The only other shared DNA found in their study was for this fungus species on both ***Nardia scalaris*** and ***Schistochilopsis opacifolia*** at St. Gotthard, Switzerland. But what are the biological implications of this shared DNA, other than a local population that is able to inhabit more than one host? Does it mean it did so recently?

Biochemistry

This species has been the subject of a number of biochemical studies. Beneš *et al*. (1981) reported on a triterpenoid present in the species, one already known from other liverworts. Then they found a new diterpenoid, nardiin, from the species (Beneš *et al*. 1982). Langenbahn *et al*. (1993) further described terpenes from the species, revealing 12 diterpene malonates. The aromatic compounds give ***Nardia scalaris*** (Figure 107-Figure 108, Figure 111) its distinctive carrot-like odor (Beike *et al*. 2010).

Figure 112. ***Lophozia ventricosa***, a liverwort that shares the fungus ***Sebacina vermifer*** with the same DNA as that of the one on ***Nardia scalaris***. Photo by Hermann Schachner, through Creative Commons.

Harpanthaceae

Harpanthus flotovianus (Figure 113-Figure 116)

Distribution

Harpanthus flotovianus (Figure 113-Figure 116) occurs in Europe, Asia, and North America (ITIS 2020e), where it is widespread in boreal and montane regions.

Aquatic and Wet Habitats

In early records, ***Harpanthus flotovianus*** (Figure 113-Figure 116) was found on the sides of fast alpine streams (Watson 1919). Koponen *et al*. (1995) considered it to be aquatic in Finland. In eastern Fennoscandia it occurs in wet habitats – near springs and streams, and in fens and moist forests (Figure 117) (Järvinen 1976). Dulin (2015) reported it from the vicinities of glacial relict lakes, occurring on decaying wood in herbal-***Sphagnum*** mixed and birch forests. It occurred there in pure patches and with other liverworts.

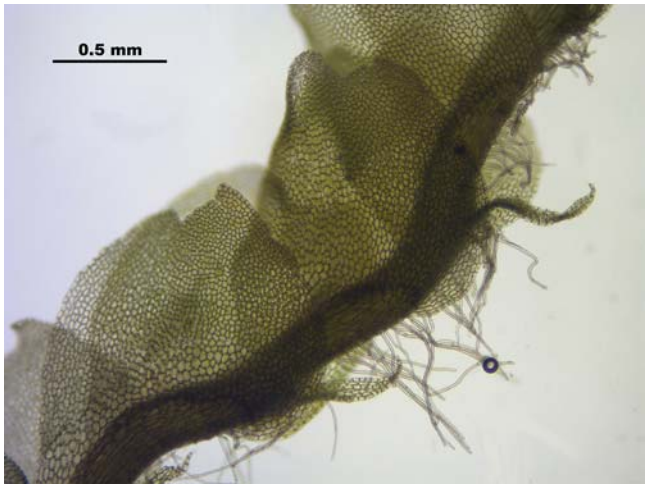

Figure 113. ***Harpanthus flotovianus***, a widespread boreal-montane species, occurring in streams, springs, lakes, their banks, and other wet habitats. Photo by Hermann Schachner, through Creative Commons.

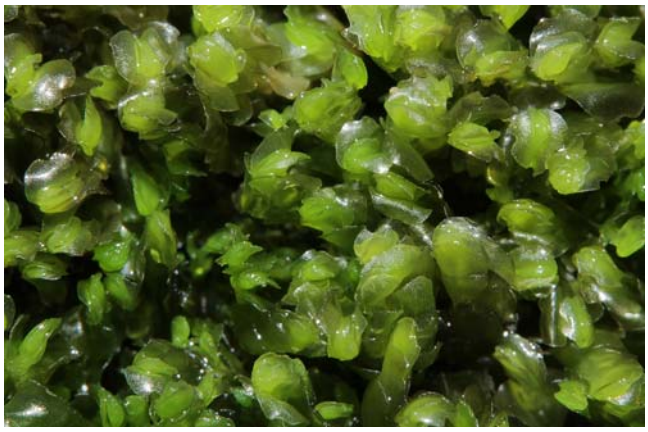

Figure 114. ***Harpanthus flotovianus***. Photo by Hermann Schachner, through Creative Commons.

Figure 115. ***Harpanthus flotovianus***. Photo by Štěpán Koval, with permission.

Figure 116. ***Harpanthus flotovianus*** showing its mat growth. Photo by Hermann Schachner, through Creative Commons.

Figure 117. ***Harpanthus flotovianus*** habitat in a wet spruce opening. Photo by Scot Loring, through Creative Commons.

In Estonia, ***Harpanthus flotovianus*** (Figure 113-Figure 116) occurs in fens, transitional mires, and bogs (Figure 118) (Ingerpuu *et al*. 2014). Emerson and Loring (2010) likewise found it associated with ***Sphagnum*** in the Rogue River-Siskiyou National Forest. In this forest it formed an association including ***Calypogeia sphagnicola*** (Figure 44-Figure 46), ***Pohlia sphagnicola*** (Figure 119), ***Cephaloziella spinigera*** (Figure 120), and ***Kurzia makinoana*** (Figure 121.

Figure 118. Peatland habitat suitable for ***Harpanthus flotovianus*** and associated ***Pohlia sphagnicola***. Photo by Michael Lüth, with permission.

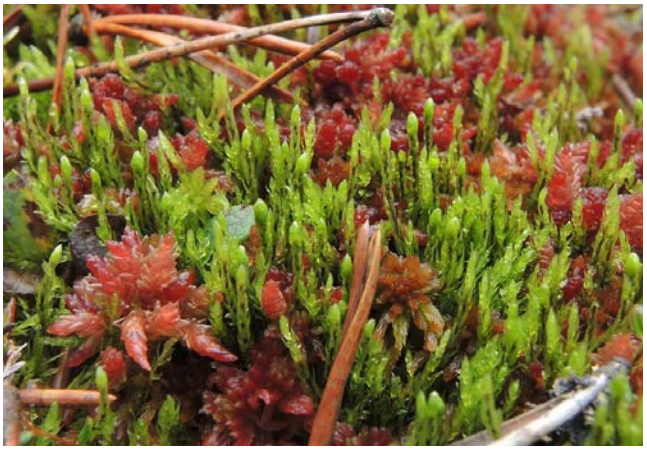

Figure 119. ***Pohlia sphagnicola***, often an associate of ***Harpanthus flotovianus*** in bogs and poor fens. Photo by Michael Lüth, with permission.

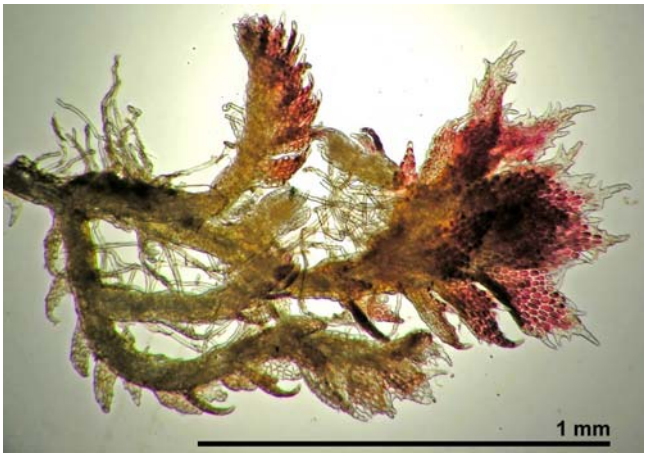

Figure 120. ***Cephaloziella spinigera*** autoicous shoot, an associate of ***Harpanthus flotovianus*** in bogs and poor fens. Photo by David Wagner, with permission.

Figure 121. ***Kurzia makinoana***, an associate of ***Harpanthus flotovianus*** in bogs and poor fens. Photo by Blanka Aguero, with permission.

Reproduction

Fertile plants of ***Harpanthus flotovianus*** (Figure 113-Figure 116) are unknown in the Pacific Northwest (Schofield 2002) and are rare in the British Isles (Paton 1999), where they are **dioicous** (Smith 1990). The paucity of sexual reproduction and lack of gemmae undoubtedly contributes to the rarity in this region. The species is perennial and should be identifiable throughout the year.

Fungal Interactions

Wang and Qiu (2006) found no records of any associated mycorrhizal fungus with this species.

Hygrobiellaceae

Hygrobiella laxifolia (Figure 122)

Distribution

Hygrobiella laxifolia (Figure 122) occurs in Europe, Asia, and North America. However, in 2014, Bakalin and Vilnet explored the genomic makeup of populations from northwestern Europe, Far Eastern Russia, and western USA. They found that the Far Eastern specimens separated from each other and from the North American population. They named the Far Eastern clades as ***Hygrobiella intermedia*** and ***Hygrobiella squamosa***. These two species and ***Hygrobiella laxifolia*** are **sympatric** (sharing part of their distributional area) in the northern Pacific region. Pigmentation, form of perianth and leaves, stem cross section anatomy, and length of underleaves can be used to separate the species morphologically.

Aquatic and Wet Habitats

Under the name of ***Hygrobiella laxifolia*** (Figure 122), Nichols (1918) reported the species from a rock ravine streambank on Cape Breton Island, Canada. Watson (1919) considered it to be subalpine, occasionally being submerged. Koponen *et al*. (1995) considered populations under this name to be aquatic in Finland.

Luis *et al*. (2007) reported populations from Madeira Island off the northwest coast of Africa as ***Hygrobiella laxifolia*** (Figure 122). It grew on rocks in the spray zone

of the stream margins where it was associated with other bryophytes.

Figure 122. ***Hygrobiella laxifolia***, a Northern Hemisphere species of stream banks. Photo by Martine Lapointe, with permission.

Adaptations

The plants of ***Hygrobiella laifolia*** range in color from green to greenish-brown or reddish-brown (Smith 1990). Its ability to grow mixed with other bryophytes can help it to maintain hydration.

Reproduction

Hygrobiella laxifolia is **dioicous** (Smith 1990).

Jungermanniaceae

Eremonotus myriocarpus (Figure 123-Figure 126)

Distribution

Eremonotus myriocarpus (Figure 123-Figure 126) is distributed in Europe, Asia, and North America (ITIS 2020f). The species is a rather rare Arctic-alpine species from north and central Europe, China, Japan, the Far East of Russia, and several localities in Greenland and North America (Konstantinova & Savchenko 2008). Although records are widespread, they are not frequent.

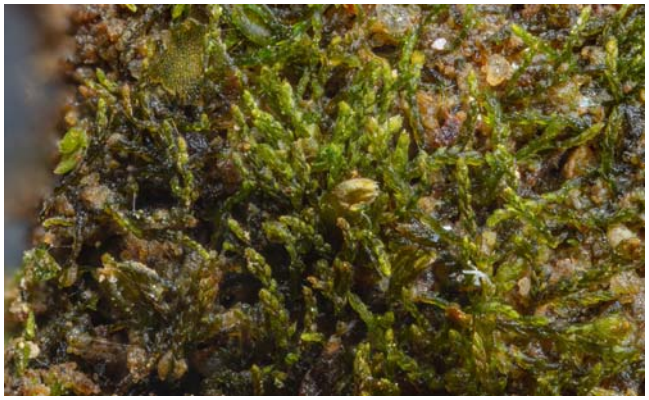

Figure 123. ***Eremonotus myriocarpus***, a rather rare Arctic-alpine species in the Northern Hemisphere, where it is occasionally submerged. Photo by Kristian Peters, with permission.

Figure 124. ***Eremonotus myriocarpus*** showing a green mat form. Photo by Kristian Peters, with permission.

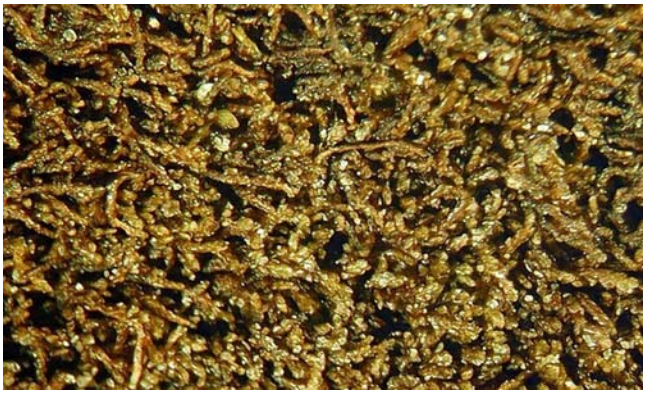

Figure 125. ***Eremonotus myriocarpus*** showing a color variant, perhaps in response to high light intensity. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Watson (1919) considered this to be a subalpine species that is occasionally submerged (Figure 126). Long (1982) reported it from a damp rock face.

Figure 126. ***Eremonotus myriocarpus*** habitat. Photo by Michael Lüth, with permission.

Adaptations

Eremonotus myriocarpus is minute (Smith 1990). It forms reddish-brown patches, a color uncommon in most submersed species, but beneficial for species in exposed sites. The coloration, however, is also advantageous in cold habitats, even when the plants are submersed.

Reproduction

Eremonotus myriocarpus is **dioicous** (Smith 1990). It lacks gemmae. In the United Kingdom, male plants are frequent while female plants are only occasional.

Fungal Interactions

Fungi seem to find this species to be a suitable habitat. However, Bidartondo and Duckett (2010) found only Ascomycetes in the usually basidiomycete-containing ***Eremonotus myriocarpus*** (Figure 123-Figure 126) from locations in Europe.

Jungermannia (Figure 127-Figure 128, Figure 130-Figure 133, Figure 135-Figure 137, Figure 140-Figure 143)

Jungermannia (Figure 127-Figure 128, Figure 130-Figure 133, Figure 135-Figure 137, Figure 140-Figure 143) ***vs. Solenostoma*** (Figure 170-Figure 176, Figure 177-Figure 189, Figure 193-Figure 196) – These two genera have been divided and many species have been moved to ***Solenostoma***. They occur in small lakes in southern Finland (Toivonen & Huttunen 1995), small, pristine streams of the Tolvajärvi region, Russian Karelia (Vuori *et al*. 1999), and occur as west African rheophytes (Shevock *et al*. 2017).

Jungermannia atrovirens (Figure 127-Figure 128, Figure 130)

(syn. = *Aplozia riparia*, *Aneura riparia* fo. *potamophila*, *Aneura riparia* var. *rivularis*, *Aplozia riparia* var. *rivularis*, *Haplozia riparia* var. *potamophila*, *Haplozia riparia* var. *rivularis*, *Jungermannia riparia*, *Plectocolea riparia*, *Solenostoma triste*)

Distribution

Jungermannia atrovirens (Figure 127-Figure 128, Figure 130) is listed by ITIS (2020g) for Europe, Asia, Africa, and North America.

Aquatic and Wet Habitats

Jungermannia atrovirens (Figure 127-Figure 128, Figure 130) is often completely submerged and truly aquatic in fast streams, on banks with frequent submergence and slow water, and wet, rocky places associated with fast water (Watson 1919). This description is supported by its occurrence in the Linth River, Switzerland (Koch 1936); in water in Westfalens, northwestern Germany (Koppe 1945); the only bryophyte in four streams of the Black Mountain District of South Wales (Jones 1948); hydrophytic or hydrophilic in the Rhine area, Germany (Philippi 1968); among the most common in upstream and extreme upper reaches and tributaries of the River Tweed, UK (Holmes & Whitton 1975b; Birch *et al*. 1988); above (Figure 128) and below water in the upper reaches of the River Wear, UK (Holmes & Whitton 1977a); in the river and on the river bank of the River Tees, UK (Holmes & Whitton 1977b); in upper to midstream of the River Swale, Yorkshire, UK (Holmes & Whitton 1977c); throughout the River Tyne, UK (Holmes & Whitton 1981); in the ***Platyhypnidium*** (Figure 68)-***Fontinalis antipyretica*** (Figure 69) association, Thuringia, Germany (Marstaller 1987); among the commonest species in English and Welsh rivers (Scarlett & O'Hare 2006); at spring and river in Tara River canyon and Durmitor area, Montenegro (Papp & Erzberger 2011); and on damp rock face in the Canary Islands (Crundwell *et al*. 1978).

Figure 127. ***Jungermannia atrovirens***, a relatively widespread, predominantly Northern Hemisphere species submerged in streams and lakes. Photo by Hermann Schachner, through Creative Commons.

Figure 128. ***Jungermannia atrovirens*** wet above the water level. Photo by Bernd Haynold, through Creative Commons.

In the UK this species grows in a variety of calcareous situations, including rock, tufa, or soil. On sandstone cliffs, as well as limestone cliffs, it is abundant. But it also occurs on less wet habitats, including forestry tracks with limestone or tufaceous rock. Konstantinova *et al*. (2009) reported it from moist cliffs and rocks on stream banks, primarily in calcium-rich sites. Birk and Willby (2010) considered it to be a species of siliceous mountain brooks, indicating a high quality site, but less frequently than ***Scapania undulata*** (Figure 60) or ***Chiloscyphus polyanthus*** (Figure 129).

Figure 129. ***Chiloscyphus polyanthos***, a frequent species in siliceous mountain brooks where ***Jungermannia atrovirens*** is able to grow. Photo by Hermann Schachner, through Creative Commons.

Adaptations

Jungermannia atrovirens is small, forming yellowish-green to dull green patches (Smith 1990). It often grows through patches of other bryophytes where they can help it to retain moisture.

Reproduction

Although the species is **dioicous**, males and females (Figure 130) are typically both abundant (BBS 2020), reducing the disadvantage of separate sexes. Although perianths are frequent, capsules are produced only occasionally in the UK, in spring and summer (Smith 1990).

Figure 130. ***Jungermannia atrovirens*** with abundant perigynia. Photo by Hugues Tinguy, with permission.

Jungermannia borealis (Figure 131)

Distribution

The distribution of ***Jungermannia borealis*** (Figure 131) must be viewed with caution because of a number of misidentifications. It seems to be in northern Europe, Asia, and North America, extending southward in the mountains.

Figure 131. ***Jungermannia borealis*** with perigynium, a species of the Northern Hemisphere, living on stream and river banks and near waterfalls. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

Jungermannia borealis (Figure 131) occurs in water near a waterfall of the Upper Bureya River (Russian Far East) (Konstantinova *et al*. 2002). In Yakutia, also in Asian Russia, this species occurs on stream and river banks in the upper course of the Indigirka River (Sofronova 2018). Damsholt and Váňa (1977) describe the habitat as typically in basic on shaded rocks and soil.

Reproduction

Like most leafy liverworts, this species is **dioicous** (Figure 131) (Damsholt & Váňa 1977).

Fungal Interactions

Wang and Qiu (2006) found no records of fungi associated with this species.

Jungermannia callithrix (Figure 132)

(syn. = *Solenostoma callithrix*)

Distribution

Jungermannia callithrix (Figure 132) is primarily Neotropical (Schumaker & Váňa 1999), but is known off the coast of Africa (Luis *et al*. 2015).

Figure 132. ***Jungermannia callithrix***, a mostly Neotropical species from narrow mountain streams. Photo by Tomas Hallingbäck, with permission.

Aquatic and Wet Habitats

Luis *et al*. (2015) reported it from a low altitude, narrow stream and low flow in mountain streams on Madeira Island off the northwest coast of Africa.

Jungermannia exsertifolia (Figure 133)

Distribution

Jungermannia exsertifolia (Figure 133) is another Northern Hemisphere species, known from Europe, Asia, and North America (ITIS 2020h). There are a few additional outlying locations on islands. It is a widely distributed Holarctic species with considerable morphological variation throughout its range (Zubel 2008). Váňa (1973) considered European populations of this species to differ somewhat from Asian plants and to represent a different subspecies, ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 140), discussed below. This subspecies occurs in the European sub-arctic-boreal-subalpine region. Records of this species should be viewed with caution because it has been confused with ***Jungermannia atrovirens*** (Figure 127-Figure 128, Figure 130) as well as failure to recognize it as a subspecies in some European records (Zubel 2008).

Figure 133. ***Jungermannia exsertifolia*** is a widely distributed Holarctic species, primarily in cold-water streams. Photo by Paul Bowyer, through Creative Commons.

Aquatic and Wet Habitats

Koponen *et al*. (1995) considered ***Jungermannia exsertifolia*** (Figure 133) to be aquatic in Finland. It occurs in regulated portions of the River Rhine (Vanderpoorten & Klein 1999b) and in the Alpine Rhine to the Middle Rhine (Vanderpoorten & Klein 1999c). Yet few aquatic studies seem to have recorded it.

This species seems to have an aversion to warm water. In sub-Arctic streams of Iceland ranging 7.1 to 21.6°C, it occurs in low densities in cold streams, but it is absent in the warmest streams (Gudmundsdottir *et al*. 2011a, b).

Adaptations

Like most of the species in this family, ***Jungermannia exsertifolia*** ranges in color from dull green to blackish-purple or even black. The dark coloration most likely protects it from photoinhibition in cold streams. It forms tufts or patches. It has few rhizoids, a character that would seem to be a disadvantage in moving water of streams.

Reproduction

Jungermannia exsertifolia is **dioicous** and lacks gemmae (Smith 1990), suggesting that fragmentation may be an important means of reproduction.

Interactions

Jensen *et al*. (2008) found that ***Jungermannia exsertifolia*** (Figure 133) was among the first liverworts that showed good dose-dependent activity against the malaria parasite ***Plasmodium falciparum*** (Figure 134). It is interesting that these liverworts were collected from Iceland where malaria is unknown.

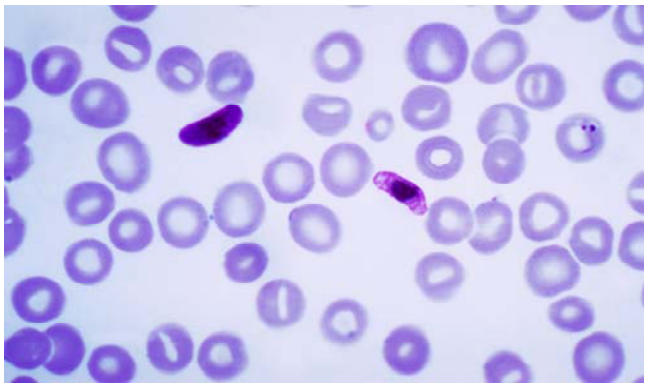

Figure 134. ***Plasmodium falciparum*** macro and microgametocyte. Photo from CDC - Dr. Mae Melvin Transwiki, through public domain.

Jungermannia exsertifolia subsp. *cordifolia* (Figure 135-Figure 137, Figure 140)

(syn. = *Aplozia cordifolia*; *Jungermannia cordifolia*; *Jungermannia eucordifolia*; *Solenostoma cordifolia*)

Distribution

Jungermannia exsertifolia* subsp. *cordifolia (Figure 135-Figure 137, Figure 140) occurs in Europe, Asia, and North America (ITIS 2020i) where it is sub-Arctic-boreal-subalpine in its distribution (Zubel 2008).

Figure 135. ***Jungermannia exsertifolia*** subsp. ***cordifolia***, a sub-Arctic-boreal-subalpine species of fast water. Photo by Des Callaghan, with permission.

Figure 136. ***Jungermannia exsertifolia*** subsp. ***cordifolia*** from a wet habitat. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

Nichols (1918) reported this subspecies from ravines on Cape Breton Island, Canada. Watson (1919) considered it to be alpine or subalpine, occurring on submerged rocks in fast water (Figure 137). Geissler (1976) found it in alpine streams in the Swiss Alps. Koponen *et al*. (1995) considered it to be aquatic in Finland; Heino and Virtanen (2006) reported it from streams in northeastern Finland. In Thuringia, Germany, Marstaller (1987) found it in the ***Platyhypnidium*** (Figure 68)-***Fontinalis antipyretica*** (Figure 69) association – a stream association.

Figure 137. ***Jungermannia exsertifolia*** subsp. ***cordifolia*** on a partly submerged rock in fast water. Photo by Dick Haaksma, with permission.

When Martinez-Abaigar *et al*. (1993) transplanted several species of bryophytes to polluted water in the River Iregua in northern Spain, ***Jungermannia exsertifolia*** **subsp.** ***cordifolia*** (Figure 135-Figure 137, Figure 140) proved to be very sensitive to pollution events; ***Fontinalis antipyretica*** (Figure 69) was more tolerant. This research team (Martínez-Abaigar *et al*. 2002) also found that this subspecies accumulated phosphorus (P) and potassium (K) dependent on the concentration of KH_2PO_4 in the water in 15 days of exposure. However, K accumulations fluctuated rather widely, presumably due to the ease with which it can be leaked from the cells. The accumulation of P in the liverwort seems to reach saturation at 20 mg L^{-1}. Increasing the P concentration in the water and tissues failed to increase net photosynthesis. The researchers suggested that the liverwort might be deficient in other mineral nutrients such as N, or that it had an intrinsic inability to use the excess nutrients. When P concentration in the tissues reached 0.45% of the dry mass, net photosynthesis declined with added P, suggesting that it had reached toxic concentrations. Furthermore, P enrichment did not affect chlorophyll concentration, but the *a*/*b* ratio declined, as did the proportions of chlorophylls to phaeopigments. At the same time, the proportions of carotenoids to chlorophylls increased. These responses likewise suggested P toxicity. In P-enriched aerated and nonaerated conditions, anoxia greatly reduced the P accumulation in just three days. This was likely due to blockage of mitochondrial respiration. This was followed by a distinct net loss of P, suggesting membrane damage. The photosynthetic response to K was lower than that to P.

Adaptations

Jungermannia exsertifolia subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140) has been the subject of many studies on the effects of enhanced UV. This interest has resulted in part from the loss of ozone in the stratosphere. Ozone serves as a filter against UV radiation. Hence, when fluorine in the atmosphere destroys ozone, the UV reaching the Earth increases.

One of the leading researchers on the effects of UV-B radiation on bryophytes is Martínez-Abaigar. He and his coworkers have laid the foundation for this research. In particular, they have concentrated on aquatic bryophytes. At higher elevations, the atmosphere is thinner, permitting more UV-B radiation to reach the surface of the Earth. Hence, mountain stream bryophytes are at particular risk because they lack a thick cuticle to help reduce the UV-B light. Martínez-Abaigar *et al*. (2006) specifically named ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140) as a good bio-indicator species for UV-B levels. Fv/Fm ratio, the concentration of UV-absorbing compounds (especially if they are analyzed individually), and DNA damage are good indicator variables for UV damage.

Fabón *et al*. (2011) pursued the effects of UV radiation on DNA in bryophytes, using ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140). DNA damage was significantly greater in PAB (PAR + UV-A + UV-B) treatments than in P (only photosynthetically active radiation, PAR) or PA (PAR + UV-A) treatments, making this species a good biomarker for UV-B damage. Under PAB treatment, DNA damage increased in thymine dimers following a period of high Par plus UV. But after UV cessation and return of PAR only, there was a rapid and complete repair. The net result showed little damage to this liverwort, indicating it is well adapted to the levels of UV in the lab experiment.

Temperature can make a difference in the amount of UV damage because of the reduced metabolism at low temperatures. Núñez-Olivera *et al*. (2005) cultured

Jungermannia exsertifolia subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140) and ***Fontinalis antipyretica*** (Figure 69) at 2ºC for 78 hours with continuous radiation to determine whether acclimation to sun or shade affected the UV-B response. The ***F. antipyretica*** was more sensitive to UV-B, showing significant decreases in several physiological variables. The sensitivity was present in both sun and shade plants, with shade plants being more sensitive. ***Jungermannia exsertifolia*** subsp. ***cordifolia***, on the other hand, had no difference in effect in shade- vs sun-acclimated plants.

Soriano *et al*. (2019) likewise found that ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140) acclimates to UV radiation intensity. Its response differences between sun and shade plants were moderate compared to those of ***Marchantia polymorpha*** (Figure 138-Figure 139), but greater than those of ***Fontinalis antipyretica*** (Figure 69).

Figure 138. ***Marchantia polymorpha*** gemmae cups on a wet population. Photo by Rudolf Macek, with permission.

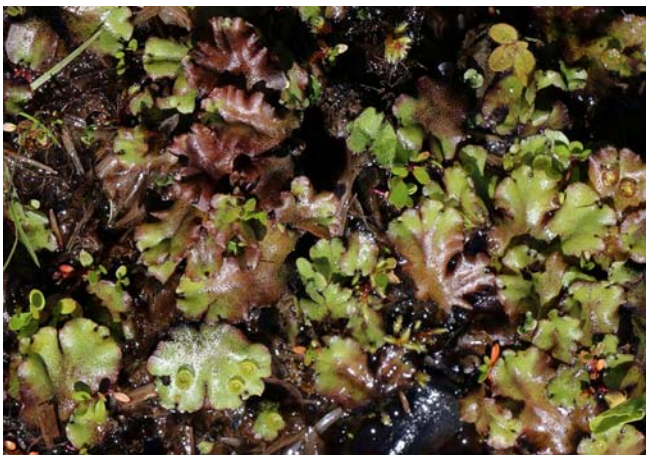

Figure 139. ***Marchantia polymorpha*** with red thallus, often a result of sun exposure. Photo by Paul Slichter, with permission.

Arróniz-Crespo *et al*. (2006) compared the responses of ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140) from mountain streams at a series of altitudes (1140-1816 m asl). They discovered two new caffeic acid derivatives, and the concentrations of these increased significantly with altitude. There was a significant linear relationship with altitude for additional measured parameters: MEUVAC (methanol-extractable UV-absorbing compounds), the maximal apparent electron transport rate through PSII (ETRmax), and the maximal non-photochemical quenching (NPQmax) all increased with altitude. Photoinhibition percentage decreased with altitude, suggesting that those populations from higher altitudes were exhibiting acclimation.

Martínez-Abaigar *et al.* (2009) likewise found evidence of acclimation to high UV radiation in populations of this species from high elevations. In their experiments, UV-B had little negative effect on photosynthetic performance or growth except in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140). However, some pigments were affected negatively. UV-B protective compounds rarely increased (Figure 140). They attributed these muted responses to acclimation at their field altitudes of 1850-2000 m asl.

Figure 140. ***Jungermannia exsertifolia*** subsp. ***cordifolia*** on rock at edge of stream, emergent and underwater. Photo by Dick Haaksma, with permission.

Monforte *et al*. (2015a) similarly found little effect on Fv/Fm or DNA damage levels, hence making them inadequate as UV damage indicators. They supported the hypothesis of a strong acclimation capacity in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140). On the other hand, coumarins were positively correlated with UV levels.

Martínez-Abaigar *et al*. (2003) found little response by ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140) to UV-A, but it did respond to UV-B. While the moss responded negatively in a number of measured parameters, the liverwort showed only a decreased Fv/Fm ratio, suggesting that this might be the most sensitive physiological variable. In addition, the concentration of UV-absorbing compounds increased with increased UV-B radiation.

Martínez-Abaigar *et al.* (2008) explored the effects of added phosphate on the UV-B response in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140). They measured photosynthetic pigment composition, chlorophyll fluorescence, photosynthesis and respiration rates, and the accumulation of protecting UV-absorbing compounds – both the commonly used bulk UV-

absorbance of methanol extracts and the concentrations of five hydroxycinnamic acid derivatives in this liverwort. Although most of these variables were affected by the level of UV-B radiation, added phosphate had no significant effect on them except the vitality index (OD430/OD410) in the liverwort. They suggested that the liverwort has low nutrient requirements and that the added phosphate was stored as a luxury nutrient.

Monforte *et al*. (2015b) used 90 herbarium samples from Spain to assess usefulness of ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140) for UV radiation biomonitoring. They assessed both soluble (mostly vacuolar) and insoluble (bound in cell wall) UV-absorbing compounds. These provide a post-event means of assessment. For example, the soluble compound p-coumaroylmalic acid exhibited significantly higher concentrations after ~1975 when stratospheric ozone degradation was initiated. The bulk level of insoluble ultraviolet-absorbing compounds had the best spatial correlation with UV levels based on altitude and latitude. Summer and autumn samples differed significantly in both soluble and insoluble UV-absorbing compounds, reflecting the reduction of UV light in autumn in Spain.

Using a longer period of 82 days, Arróniz-Crespo *et al*. (2008) considered the response of five hydroxycinnamic acid derivatives to UV levels in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140) from mountain streams. They found that the liverwort was tolerant to UV radiation, with the accumulation of three UV-absorbing hydroxycinnamic acid derivatives: p-coumaroylmalic acid, 5″-(7″,8″-dihydroxycoumaroyl)-2-caffeoylmalic acid, and 5″-(7″,8″-dihydroxy-7-O-β-glucosyl-coumaroyl)-2-caffeoylmalic acid being likely contributors to that tolerance. Thus, these three compounds are potential bioindicators of elevated UV levels.

Fabón *et al*. (2010) examined the effects of UV-B radiation on hydroxycinnamic acid derivatives from different cell compartments in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140). They found a higher UV absorbance by the soluble fraction when compared to that of the cell-wall-bound fraction. Absorbance for both fractions increased when UV-B radiation was enhanced. The researchers identified five hydroxycinnamic acid derivatives in the soluble fraction and two more in the cell-wall-bound fraction. Of these, only p-coumaroylmalic acid in the soluble fraction and p-coumaric acid in the cell-wall-bound fraction increased under enhanced UV-B. DNA damage exhibited a strong increase under the enhanced UV-B, while the maximum quantum yield of PSII decreased.

Otero *et al*. (2006) assessed the effects of cadmium and enhanced UV radiation on ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140). Both caused degradation of chlorophyll and a decrease in the maximum quantum yield of photosystem II. At the same time, the xanthophyll index increased, permitting an increase in non-photochemical dissipation of energy. Cadmium elicited more stress than did the UV radiation, causing a decrease in net photosynthesis. UV radiation caused the level of trans-p-coumaroylmalic acid to increase, and cadmium caused trans-phaselic and feruloylmalic acids to increase. Elevated UV radiation alone resulted in DNA damage, and that was exacerbated when cadmium was elevated. This combined effect is probably a function of the ability of cadmium to inhibit DNA repair.

Fabón *et al*. (2012) found that PAB (PAR + UV-A + UV-B) samples increased in the bulk UV absorbance of both soluble and insoluble fractions; this response was most likely due, at least in part, to increases in the concentrations of p-coumaroylmalic acid in the soluble fraction and p-coumaric acid in the cell wall. They found seven hydroxycinnamic acid derivatives in the soluble and insoluble fractions. Most of these showed diel changes, responding within a few hours to radiation changes, but more strongly to UV-B. Significant and rapid changes occurred for Fv/Fm, ΦPSII, NPQ, and the components of the xanthophyll cycle in response to high PAR, UV-A, and UV-B radiation.

Núñez-Olivera *et al*. (2009) considered the seasonal variations in the UV-absorbing compounds and physiological changes with seasons in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140). Using monthly collections for three years from a mountain stream, they found no DNA damage. The tender young shoots of summer-autumn with high Fv/Fm accumulated higher amounts of several hydroxycinnamic acid derivatives than did shoots collected in winter-spring. The p-coumaroylmalic acid proved to be the compound best associated with radiation changes.

Reproduction

Jungermannia exsertifolia subsp. ***cordifolia*** is **dioicous** and lacks gemmae (Smith 1990), suggesting that fragmentation may be an important means of reproduction.

Biochemistry

In addition to studies on compounds that protect against high light intensity and elevated UV radiation, there have been studies on other secondary compounds in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140). Cullmann *et al*. (1999) found the typical liverwort **lignans** (any of class of polyphenolic compounds and noted for having antioxidant and estrogenic activity) and added three new ones. Nagashima *et al*. (1996) found eight new diterpenoids, added to the seven previously known. These have known biological activity against various cancer cell lines, plant-growth regulating properties, phytotoxic activity on root growth, as well as antiplasmodial, hypoglycemic, hypolipidemic, antimicrobial, antiviral, antifouling, larvicidal, algicidal, and insect antifeedant activities (Banerjee *et al*. 2008; Li *et al*. 2016; Lin-Gen *et al*. 2016; Pal *et al*. 2016; Bao *et al*. 2017; Li *et al*. 2017). They help to explain how a slow-growing liverwort can compete with bigger plants and ward off hungry insects.

To these, Scher *et al*. (2010) added a new diterpene derivative from this liverwort and found three previously known compounds. All of these demonstrated noticeable activity against a virulent tuberculosis pathogen.

Jungermannia pumila (Figure 141-Figure 143)

(syn. = *Aplozia pumila*, *Jamesoniella ruttneri*, *Solenostoma pumila*)

Distribution

Jungermannia pumila (Figure 141-Figure 143) is distributed in Europe, Asia, and North America (ITIS 2020j).

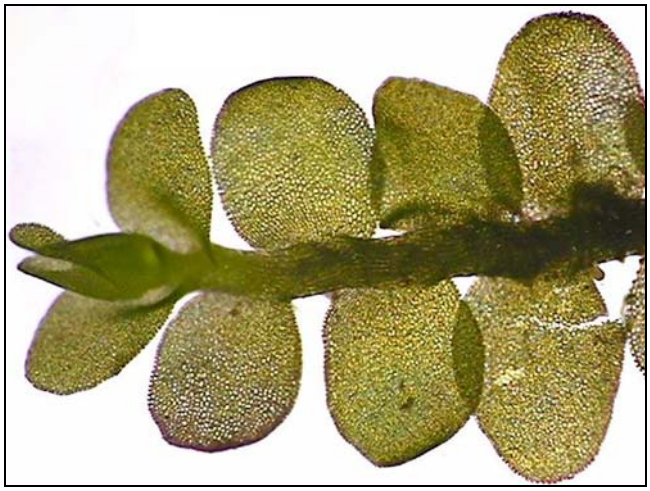

Figure 141. ***Jungermannia pumila***, a Northern Hemisphere species that can be found in some fast streams and deep in ponds. Photo by Paul Davison, with permission.

Figure 142. ***Jungermannia pumila***. Photo by Rambryo, through Creative Commons.

Figure 143. ***Jungermannia pumila*** forming a mat. Photo by Rambryo, through Creative Commons.

Aquatic Wet Habitats

Watson (1919) attributed ***Jungermannia pumila*** (Figure 141-Figure 143) to rocks or gravel associated with fast streams, waterfalls, more aquatic in fast streams. Ruttner (1955) reported it submersed in a pond and <40 cm above water level in the tropics. Philippi (1987) considered it rare in aquatic habitats of eastern Odenwald and southern Spessart, Germany. Marstaller (1987) noted its occurrence in the ***Platyhypnidium*** (Figure 68)-***Fontinalis antipyretica*** (Figure 69) association in Thuringia, Germany. Heino and Virtanen (2006) affirmed its occurrence in streams in northeastern Finland. And Luis *et al*. (2015) found it in mountainous streams on Madeira Island. In the UK, ***J. pumila*** (Figure 141-Figure 143) usually grows on damp rock on cliffs, low rock outcrops in woodlands, or low down on rock faces by rivers; sometimes it occurs on soil (BBS 2020).

Adaptations

Like many of the species in this genus, ***Jungermannia pumila*** (Figure 141-Figure 143), this species is small and exhibits a dull green to blackish coloration (Smith 1990). Unlike many of the wet-habitat species in this genus, it produces numerous rhizoids. It often grows with other bryophytes, a behavior that can help it to maintain moisture.

Reproduction

Jungermannia pumila (Figure 141-Figure 143) is **paroicous** and perianths (Figure 144) are common (Smith 1990; Hodgson 2021). Capsules are likewise common, produced in winter and spring. Gemmae are absent.

Figure 144. ***Jungermannia pumila*** fertile branches with females in center and male bracts below them. Photo by Andrew Hodgson, with permission.

Jungermannia quadridigitata

(syn. = *Lepidozia setacea*, *Microlepidozia setacea*)

Distribution

Jungermannia quadridigitata is listed by Söderström *et al*. (2016) as being of serious doubt. It is possible it is now included in one of the other taxa listed here. For this reason, I am unable to provide distribution information.

Aquatic and Wet Habitats

The species is not a true aquatic, but occurs in moist hollows between ***Sphagnum*** hummocks (Figure 145) on Cape Breton Island, Canada (Nichols 1918). Weber (1976) also included it among bog bryophytes in Cataracts Provincial Park, Newfoundland, Canada, considering it a typical bog bryophyte.

Figure 145. Raised bog with ***Sphagnum fimbriatum*** surrounded by ***Sphagnum magellanicum***, where ***Jungermannia quadridigitata*** can occur in the hollows between hummocks like these. Photo through Creative Commons.

Mesoptychia badensis (Figure 146-Figure 148, Figure 150)

(syn. = *Lophozia badensis*)

Distribution

Mesoptychia badensis (Figure 146-Figure 148, Figure 150) is listed by TROPICOS for China and Russia. Crandall-Stotler *et al*. (2013), however, considered it to be widely distributed in the northern hemisphere.

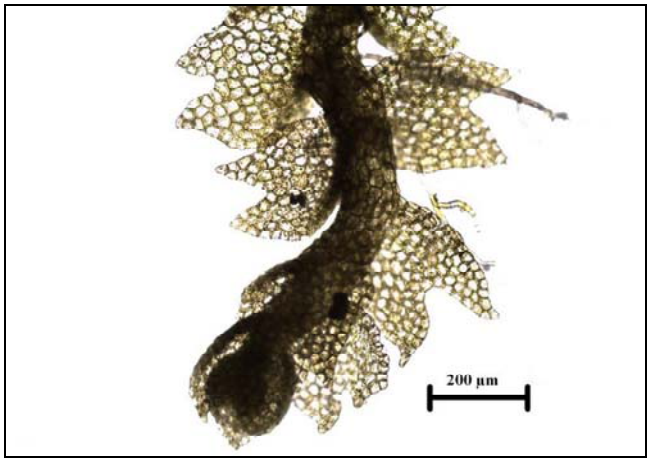

Figure 146. ***Mesoptychia badensis***, a species widely distributed in the Northern Hemisphere in calcareous habitats, including streams and rivers. Photo by Hugues Tinguy, with permission.

Figure 147. ***Mesoptychia badensis***. Photo by Štěpán Koval, with permission.

Aquatic and Wet Habitats

Nichols (1916) reported this species from calcareous rivers in Connecticut, USA. Watson (1919) treated it as occasionally submerged. In the Lorraine River, Belgium, it occurred in the travertine ***Cratoneuron*** (Figure 149) association (de Sloover & Goossens 1984). Bakalin *et al*. (2019a) found the species in the krummholz and tundra-like habitats where it grew in open wet to mesic limestone cliff crevices and on fine limestone deposits near small streams in the Balagan Mountain and Vengeri River Valley (Sakhalin Island, North-West Pacific).

Figure 148. ***Mesoptychia badensis***. Photo by Štěpán Koval, with permission.

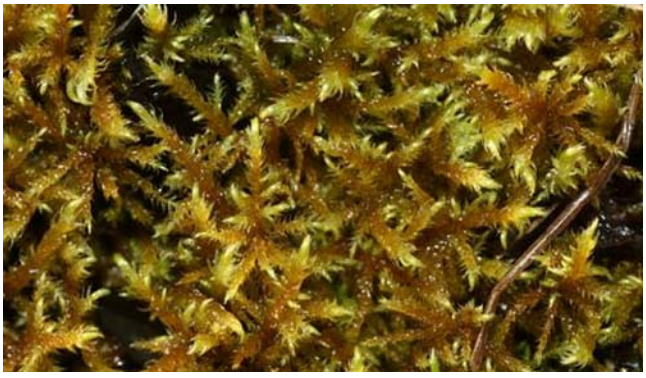

Figure 149. ***Cratoneuron filicinum***; ***Mesoptychia badensis*** occurs in association with ***Cratoneuron*** in the travertine. Photo by Barry Stewart, with permission.

Reproduction

The species is **dioicous**, but at least sometimes produces capsules (Figure 150). On the other hand, it does not produce gemmae (Potemkin *et al*. 2015). We should look for its ability to reproduce from fragments, especially in the field. This could be especially important in rivers, streams, and areas subject to flooding.

Figure 150. ***Mesoptychia badensis*** with capsules, despite being dioicous. Photo by Štěpán Koval, with permission.

Mesoptychia bantriensis (Figure 151-Figure 153)

(syn. = *Leiocolea bantriensis*)

Distribution

Mesoptychia bantriensis (Figure 151-Figure 153) occurs in Europe, Asia, and North America (Bakalin 2018). Hodgetts (2015) listed it specifically from Norway, Sweden, United Kingdom, and Italy in Europe.

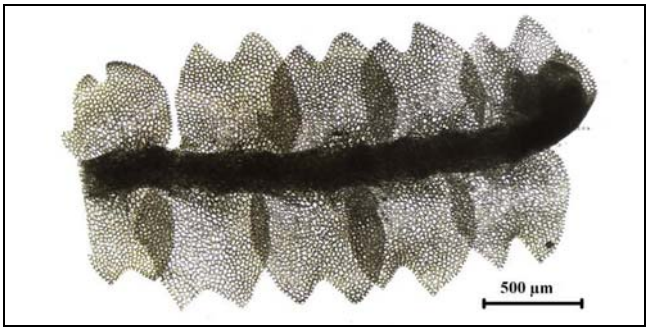

Figure 151. ***Mesoptychia bantriensis***, a Northern Hemisphere liverwort of streams, rivers, lakes, and their banks, as well as mires and moist tundra. Photo by Hugues Tinguy, with permission.

Figure 152. ***Mesoptychia bantriensis*** showing growth habit. Photo by Štěpán Koval, with permission.

Aquatic and Wet Habitats

Watson (1919) listed this species as one of alpine and subalpine rocks and on soil by fast water. Heino and Virtanen (2006) reported it from streams in northeastern Finland. Bakalin *et al*. (2016) reported it from moist soil or on mineral ground of mesic tundras, but also along streams and on lake shores, on cliffs near waterfalls, on peat in mires, on peat in minerotrophic bogs, on silty alluvium along lake shores, and on fine soil and humus along watercourses on the Putorana Plateau in East Siberia. It forms mats on its substrate (Figure 153).

Adaptations

Mesoptychia bantriensis (Figure 151-Figure 153) forms green to reddish-brown tufts and patches (Smith 1990). This coloration can be beneficial in locations where it is exposed to bright light and low temperatures at the same time by protecting it from photoinhibition.

Figure 153. ***Mesoptychia bantriensis*** showing mat formation. Photo by Barry Stewart, with permission.

Reproduction

Mesoptychia bantriensis is **dioicous** and lacks gemmae (Smith 1990). Perianths can be seen only occasionally and capsules are rare.

Mesoptychia collaris (Figure 154)

(syn. = *Leiocolea collaris*, *Lophozia muelleri*)

Distribution

Mesoptychia collaris (Figure 154) occurs in Europe, Asia, Africa, and North America (ITIS 2019).

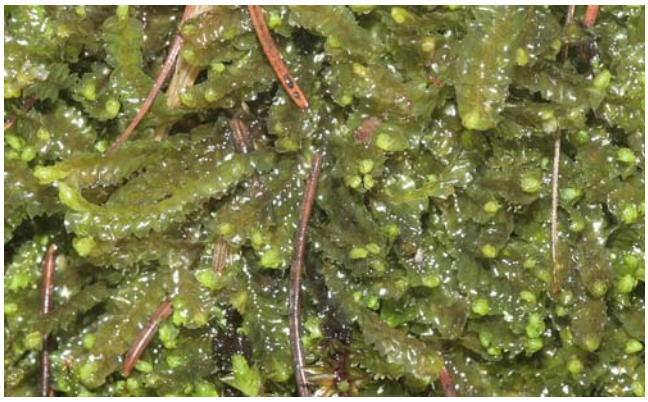

Figure 154. ***Mesoptychia collaris***, a Northern Hemisphere species that is hemicalciphilous in cold streams and seepage areas. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Mesoptychia collaris (Figure 154) was considered by Watson (1919) to occur on alpine and subalpine rocks by fast water. In western Canada it is submerged in montane streams where it is hemicalciphilous (Vitt *et al*. 1986; Glime & Vitt 1987). In Thuringia, Germany, it occurred in the ***Platyhypnidium*** (Figure 68)-***Fontinalis antipyretica*** (Figure 69) association (Marstaller 1987). In the Tara river canyon and Durmitor area of Montenegro it occurred at a spring and river (Papp & Erzberger 2011). Konstantinova and Lapshina (2014) considered it to be calciphilous in seepage areas on schists on a steep rocky slope to the valley of a rivulet in the eastern subpolar Urals in Russia.

Adaptations

Mesoptychia collaris (Figure 154) forms green to brown patches (Smith 1990), suggesting the possibility of protection from high light intensities. It often grows through patches of other bryophytes, providing a greater opportunity to maintain moisture.

Reproduction

Mesoptychia collaris (Figure 154) is **dioicous** (Smith 1990). Perianths occur only occasionally and capsules are rare. Gemmae are absent.

Mesoptychia gillmanii (Figure 155)

(syn. = *Leiocolea gillmanii*)

Distribution

Mesoptychia gillmanii (Figure 155) is widespread around the northern hemisphere in boreal and montane regions, although it is considered vulnerable in Europe (Hodgetts *et al*.).

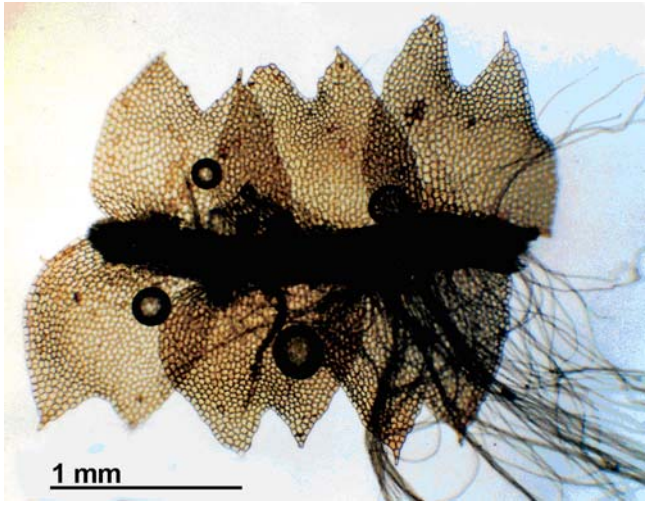

Figure 155. ***Mesoptychia gillmanii***, a species from boreal and montane regions of the northern hemisphere. It is a calciphile in streams, on peaty soil, and on cliffs and ledges. Photo by David Wagner, with permission.

Aquatic and Wet Habitats

In Finland, ***Mesoptychia gillmanii*** (Figure 155) occurs in streams (Heino & Virtanen 2006). In North America, this species is found on peaty soil, typically on cliffs or ledges. Nevertheless, it is an obligate calciphile (Schuster 1969). The species often occurs at elevations where the snow leaves late in the growing season, giving it a short growing season.

Adaptations

Mesoptychia gillmanii (Figure 155) lacks the coloration seen by many members of this family, instead displaying only green to yellowish-green coloration (Smith 1990). Like many members of the family, it grows among other bryophytes, a behavior that can help it to maintain moisture.

Reproduction

Mesoptychia gillmanii (Figure 155) is a perennial that, like most members of the genus, produces no gemmae. This means its dispersal must be primarily by spores or fragments (Wagner 2018). It is, however, **paroicous (Smith 1990)**, increasing the potential for fertilization and spore production.

Mesoptychia turbinata (Figure 156-Figure 157)

(syn. = *Lophozia turbinata*)

Distribution

Mesoptychia turbinata (Figure 156-Figure 157) is apparently restricted to the Mediterranean area of Europe and North Africa (Schuster 1969).

Aquatic and Wet Habitats

Watson (1919) considered ***Mesoptychia turbinata*** (Figure 156-Figure 157) to be a species on stream banks that experience frequent submergence and to occasionally be submerged. Papp *et al*. (2018) reported it from limestone rock at a rivulet in Albania. This species is a calcicole and does best in a *p*H range of 4-8 with 3.0 mM Ca^{++} (Jefferies 1969). The K^{+} efflux appears to be unaffected by the Ca^{++} concentration in this species.

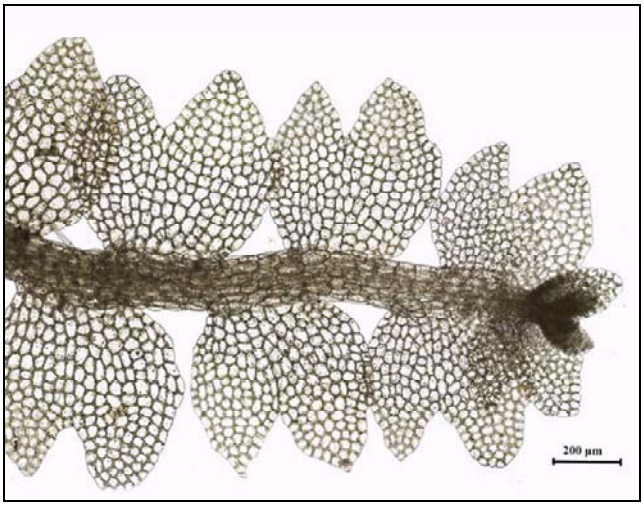

Figure 156. ***Mesoptychia turbinata***. Photo by Hugues Tinguy, with permission.

Adaptations

Like the previous species, ***Mesoptychia turbinata*** (Figure 156-Figure 157) lacks the protective reds and browns that might protect it from exposure to bright light. Instead, its coloration ranges from pale green to yellowish-green (Figure 157). It most likely gains moisture retention

where it grows among other bryophytes. or through its rather dense mats (Figure 157).

Figure 157. ***Mesoptychia turbinata*** showing the extensive mats that are possible. Photo by Hugues Tinguy, with permission.

Reproduction

Mesoptychia turbinata (Figure 156-Figure 157) is **dioicous**, but nevertheless produces frequent perianths in the UK (Smith 1990). Capsules, however, are only occasional, appearing in winter or spring in the UK.

Notoscyphaceae

Notoscyphus lutescens (Figure 158)

(syn. = *Notoscyphus paroicus*)

Distribution

Notoscyphus lutescens (Figure 158) occurs in the Western Ghats (Udar & Kumar 1981; Singh *et al*. 2016) and in Hong Kong and mainland China, sometimes on wet soil (So & Zhu 1996). It extends into the southern hemisphere to New Zealand (Braggins *et al*. 2014), and is known from South Africa, Madagascar, India, China, Japan, Philippines, Indonesia, Papua New Guinea, north-eastern Australia (Queensland), as well as New Caledonia, Hawaii, Fiji, and Samoa (Schuster 2002). Not surprisingly, it has more recently been found in Australia.

Figure 158. ***Notoscyphus lutescens***, an Eastern Hemisphere species, occurring where it is aquatic or wetland, including river banks and seeping cliffs. Photo by David Tng, with permission.

Aquatic and Wet Habitats

Ruttner (1955) reported ***Notoscyphus lutescens*** (Figure 158) as an aquatic or wetland species in the tropics. In Malawi, O'Shea *et al*. (2001) found it on river banks and on both dry and moist granitic and sandstone rocks, among other terrestrial habitats. Pócs and Streimann (2006) reported it from a riverside earth bank in Australia. Omar *et al*. (2016) documented it from a wetland in South Africa. It is also known from a seeping cliff at 900 m in the Nguru Mountains of Tanzania (Pócs & Váňa 2015).

Reference to aquatic habitats are rare or non-existent among the reports on its localities. Nevertheless, this species is sold in some areas as an aquarium plant <https://aquaticarts.com/, Brownsburg, IN, USA>.

Adaptations

Members of ***Notoscyphus*** are typically yellowish-green, but can become red with age (Winterton *et la*. 2018).

Reproduction

Notoscyphus lutescens (Figure 158) is dispersed by spores and stem fragments (Winterton *et al*. 2018).

Biochemistry

Wang *et al*. (2014) reported ten new diterpenoids from this species. One of the compounds exhibited activity against human prostate cancer cells. So and Chan (2001) found a new cyclic bis (bibenzyl) derivative with activity against bacteria *Bacillus subtilus* (Figure 159) and two strains of *Staphylococcus aureus* (Figure 160). Zhu *et al*. (2006) found antibacterial activity against all five bacteria they tested, but were unable to find any oil body characters that were linked statistically to antibiotic activity. It is likely that some of these compounds are also inhibitory to environmental pathogens.

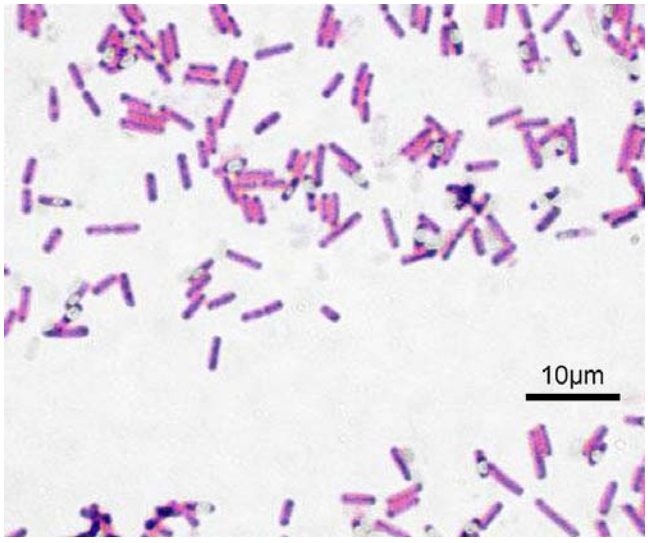

Figure 159. ***Bacillus subtilis*** with Gram stain, a species that is inhibited by extracts of ***Notoscyphus lutescens***. Photo by Y. Tambe, through Creative Commons.

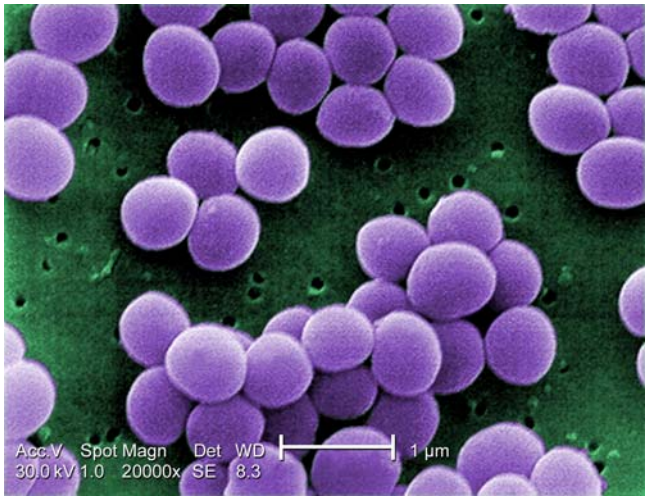

Figure 160. ***Staphylococcus aureus***, a species that is inhibited by extracts of ***Notoscyphus lutescens***. Photo by Janice Haney Carr, through public domain.

Figure 162. ***Saccogyna viticulosa*** with branches in a semi-upright position. Photo by Dick Haaksma, with permission.

Saccogynaceae

Saccogyna viticulosa (Figure 161-Figure 163)

Distribution

Saccogyna viticulosa (Figure 161-Figure 163) is listed for Europe, Africa, and Asia by ITIS (2020k). Mateo *et al*. (2013) treat it as a hyper-oceanic species along the Atlantic Ocean. Kürschner (2010) added it to southwest Asia, describing its previous known distribution as western Mediterranean and Atlantic region.

Figure 163. ***Saccogyna viticulosa*** forming a mat. Photo by Dick Haaksma, with permission.

Figure 161. ***Saccogyna viticulosa***, a species mostly along the eastern side of the Atlantic Ocean where it is wet for long periods or even submerged. Photo by Dick Haaksma, with permission.

Aquatic and Wet Habitats

This species is one occurring with high humidity, sometimes being wet for long periods of time or even submerged. In northwestern Portugal, ***Saccogyna viticulosa*** (Figure 161-Figure 163) occurs in small crevices with humus and high humidity in the stream or waterfall margins that may be subjected to inconstant splashes or inundation. It is never extensive, always mixed with other bryophytes, often associated with ***Pellia epiphylla*** (Figure 164), ***Fissidens polyphyllus*** (Figure 103), ***Hyocomium armoricum*** (Figure 165-Figure 166), ***Plagiothecium nemorale*** (Figure 167), and ***Riccardia multifida*** (Figure 168) in wetter situations, with ***Radula holtii*** in dripping conditions, and in mountain streams (Vieira *et al.* 2004, 2005). In the Laurel forest of the Canary Islands, it occurs on periodically moistened, rather exposed volcanic rocks (Dirkse 1985). On Madeira Island, it occurs in low altitude, narrow streams and low flow in mountainous

streams (Luis *et al.* 2015). In the British Isles, it occurs in many small, rocky streams (Averis & Hodgetts 2013).

Figure 164. ***Pellia epiphylla*** showing an associated leafy liverwort. Photo by Jan-Peter Frahm, with permission.

Figure 165. ***Hyocomium armoricum*** habitat such as those where we might find ***Saccogyna viticulosa*** in association. Photo by Dick Haaksma, with permission.

Figure 166. ***Hyocomium armoricum***, sometimes an associate of ***Saccogyna viticulosa***. Photo by Michael Lüth, with permission.

Figure 167. ***Plagiothecium nemorale***, sometimes an associate of ***Saccogyna viticulosa***. Photo by Hermann Schachner, through Creative Commons.

Figure 168. ***Riccardia multifida*** showing its habitat with a leafy liverwort on the right. Photo by Rick Ballard, through Creative Commons.

In northwestern Portugal, ***Saccogyna viticulosa*** (Figure 161-Figure 163) was never extensive and always occurred in mixtures with other bryophytes – a behavior suggesting its need for constant moisture (Vieira *et al.* 2004). However, in experiments, ***Saccogyna viticulosa*** had survival down to 51% relative humidity with only a few cells surviving down to 33% relative humidity (Clausen 1964). It is likely that it would have even greater survival in nature where the drying time would be more extended, permitting the cells to prepare (*e.g.* Stark *et al.* 2013). At -10ºC in ice, undeveloped apical cells died within 1-2 days. In other experiments, Proctor (2010) showed that ***Saccogyna viticulosa*** cells are easily damaged by bright light during initial rewetting. Dilks and Proctor (1974) found that despite the rapid damage and slow recovery of assimilation, this species has the capacity to survive long dry periods. At the beginning of rehydration, dark respiration typically shows a slight stimulation, followed by a longer-term buildup after a moderate or prolonged desiccation. Pressel *et al.* (2009) found that this species can withstand several weeks of natural drying. The estimated recovery time is 0.4 hours. The species typically occurs in shaded sites where they probably are never subject to intense desiccation. Of the species tested in this study, ***Saccogyna viticulosa*** (Figure 161-Figure 163) lives

in niches with the lowest irradiance and least severe desiccation, especially avoiding direct summer sun.

Reproduction

One reason for the scarcity of ***Saccogyna viticulosa*** (Figure 161-Figure 163) in some areas is its **dioicous** habit, limiting spore production (Watson & Dallwitz 2019). In northwestern Portugal, Vieira *et al*. (2004) never found the species fertile. This problem is compounded by the absence of gemmae, at least in the UK (Watson & Dallwitz 2019).

Fungal Interactions

Wang and Qiu (2006) reported fungal associations with this species. ***Saccogyna viticulosa*** (Figure 161-Figure 163) is known to host the fungus ***Sebacina*** (Figure 169) (Bidartondo & Duckett 2010). It produces numerous hyphae associated with the branched rhizoid apex. Döbbeler (2011) found that the **Ascomycete** fungus ***Octosporella fortunata*** occurs on terricolous populations of ***Saccogyna viticulosa*** on the Canary Islands. This fungus produces its spores in sacs that are hidden within the mats of liverworts. Ing (1983) found **Myxomycetes** to be frequently associated with ***Saccogyna viticulosa*** in wooded ravines in Highland Britain.

Figure 169. ***Sebacina incrustans***, in a genus that is known from ***Saccogyna viticulosa***, shown here on a moss. Photo through Creative Commons.

Biochemistry

Several biochemical studies have revealed the array of secondary compounds in ***Saccogyna viticulosa*** (Figure 161-Figure 163). Suleiman *et al*. (1980) demonstrated that even photosynthetic products in this species may differ from that in other families that have been considered closely related. Connolly *et al*. (1994) found two new sesquiterpenoids in ***Saccogyna viticulosa***. Hackl *et al*. (2004) identified several new sesquiterpenes from populations on Madeira and unravelled some of the pathways involved in making the volatile essential oils in this species.

Solenostomataceae

Solenostoma (Figure 170-Figure 176, Figure 177-Figure 189, Figure 193-Figure 196)

Solenostoma (Figure 170-Figure 176, Figure 177-Figure 189, Figure 193-Figure 196) has **psychrorithral** (cold upper stream reaches) species in European alpine streams (Geissler 1975).

Solenostoma ariadne

(syn. = *Nardia ariadne*)

Solenostoma ariadne is known from India and China. Ruttner (1955) reported it as a wetland/aquatic species from the tropics.

Solenostoma gracillimum (Figure 170-Figure 172)

(syn. = *Jungermannia gracillima* fo. *crenulata*, *Solenostoma crenulatum*)

Distribution

Solenostoma gracillimum (Figure 170-Figure 172) is known from Europe, Asia, Africa, North America, and South America (ITIS 2020l).

Figure 170. ***Solenostoma gracillimum***, a species known from both the Northern and Southern Hemispheres, living in streams, small lakes, and in other wet areas. Photo by Hugues Tinguy, with permission.

Figure 171. ***Solenostoma gracillimum*** showing its growth habit. Photo by David T. Holyoak, with permission.

Aquatic and Wet Habitats

Most of the wet habitat reports are relatively recent. Bley (1987) reported ***Solenostoma gracillimum*** (Figure 170-Figure 172) from upstream reaches in the Harz Mountains of Germany. Toivonen and Huttunen (1995) found it in small lakes in southern Finland. It occurs in mountain streams of northwest Portugal (Vieira *et al.* 2005) and in Madeira Island (Luis *et al.* 2015). Ferreira *et al.* (2008) listed it for European rivers. In North America its wet habitats include ditches and ravine walls (Breil 1970).

The plants become reddish (Figure 172) when exposed to the sun (Breil 1970).

Figure 172. ***Solenostoma gracillimum*** showing red coloration often seen with sun exposure. Photo by Barry Stewart, with permission.

Solenostoma gracillimum (Figure 170-Figure 172) is one of the species that can facultatively live in areas with metalliferous mine waste (Holyoak 2008). In Ireland, it was indicative of copper waste, but it does not require excess copper to colonize. This is a habitat where drying would appear to be frequent.

Solenostoma gracillimum (Figure 170-Figure 172) seems to have an unusual tolerance for zinc. In the Hautes-Pyrénées, this species was one of only three present where Zn had reached such high concentrations that it formed a white precipitate of **anglesite** (Figure 173), along with ***Pohlia cruda*** (Figure 174) and ***Schizothrix*** sp. (Figure 175) (Say & Whitton 1982). Similarly, Brown and House (1978) found it growing near a lead mine and on spoil from a copper mine in southwest England.

Figure 173. Anglesite, a rock type that can precipitate onto bryophytes. Photo by Parent Géry, through Creative Commons.

Figure 174. ***Pohlia cruda***, a species that occurs with ***Solenostoma gracillimum*** in areas with high levels of zinc. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman and Karen Blisard.

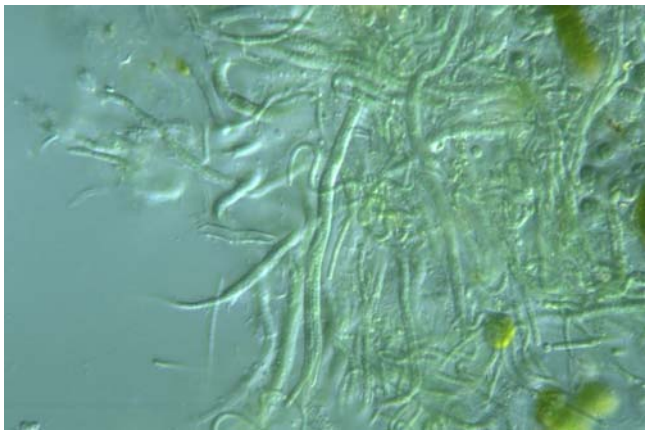

Figure 175. ***Schizothrix*** sp., member of a genus that occurs with ***Solenostoma gracillimum*** in areas with high levels of zinc. Photo by Yuuji Tsukii, with permission.

Reproduction

Solenostoma gracillimum (Figure 170-Figure 172) is **dioicous** (Figure 176) (Breil 1970), but has a widespread distribution that suggests that at least some spores have dispersed. It does not produce gemmae (Bakalin 2012).

Figure 176. ***Solenostoma gracillimum*** with numerous perianths. Photo by David T. Holyoak, with permission.

Fungal Interactions

Solenostoma gracillimum (Figure 170-Figure 172) is one of the hosts of the fungus ***Mniaecia jungermanniae*** (Figure 24-Figure 26) (Egertová *et al*. 2016). Pressel and Duckett (2006) found that it infected some liverwort species, but not others.

Solenostoma hyalinum (Figure 177-Figure 179)

(syn. = *Eucalyx hyalina*, *Jungermannia hyalina*)

Distributions

Solenostoma hyalinum (Figure 177-Figure 179) is widespread in Europe, south to northern Africa, but up to 1969 only one Asian country had a recorded species (Schuster 1969). It occurs in North America from Quebec, Canada, southward to North Carolina, USA, and westward through the Midwest to Mexico.

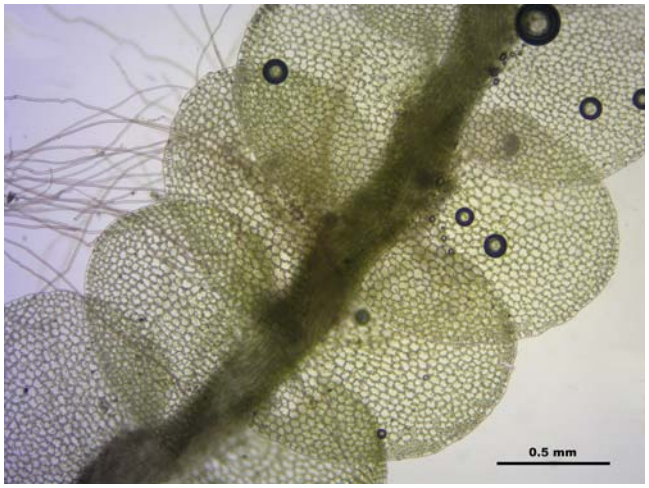

Figure 177. ***Solenostoma hyalinum***, a Northern Hemisphere species that lives where it is constantly wet or submerged. Photo by Hermann Schachner, through Creative Commons.

Figure 178. ***Solenostoma hyalinum***, a Northern Hemisphere species that lives where it is constantly wet or submerged. Photo by Hermann Schachner, through Creative Commons.

Solenostoma hyalinum (Figure 177-Figure 179) in North America occurs primarily at median and low elevations (Schuster 1969). Although it has rare occurrences in the taiga, it does not reach higher elevations in the southeastern states of the USA. It is able to form extensive mats on river banks. Schuster has never observed it any considerable distance from streams. It seems to require at least some soil, not occurring on bare rocks.

Early in aquatic studies, Watson (1919) reported ***Solenostoma hyalinum*** (Figure 177-Figure 179) as a species that is occasionally submerged. But others have documented a wider and wetter range of habitats. Vieira *et al*. (2004, 2005), based on their studies in northwest Portugal, reported it from vertical faces of boulders subjected to splashes or constant drippings and in the margins of waterfalls, associated with ***Scapania undulata*** (Figure 60), ***Hyocomium armoricum*** (Figure 165-Figure 166), ***Fissidens polyphyllus*** (Figure 103), and ***Platyhypnidium lusitanicum*** (Figure 104), as well as in mountain streams. Ferreira *et al*. (2008) reported it from rivers. It occurs in mountain streams on Madeira Island (Luis *et al.* 2015). Duckett and Slack (2013) found it on vertical wet rocks in Tuckerman Ravine on Mt. Washington, New Hampshire, USA. Hong (1972) reports the species from several streams in Montana, USA. Weber (1976) considered it to be a river bank species in the Cataracts Provincial Park, Newfoundland, Canada. Likewise, Kitagawa (1978a) found it on river banks where it can form large, compact mats on rocks.

Reproduction

In northwest Portugal, ***Solenostoma hyalinum*** (Figure 177-Figure 179) has only been found sterile in pure or mixed well-developed patches (Vieira *et al*. 2004). Nevertheless, it can produce capsules (Figure 179) when both genders are present.

Figure 179. ***Solenostoma hyalinum*** with a capsule, indicating that some populations can successfully reproduce sexually. Photo by Michael Lüth, with permission.

Fungal Interactions

Solenostoma hyalinum (Figure 177-Figure 179) is one of the known hosts for the Ascomycete fungus ***Mniaecia jungermanniae*** (Figure 24-Figure 26) (Egertová *et al*. 2016). The exact relationship needs to e explored.

Solenostoma inundatum (Figure 180-Figure 181)

(syn. = *Jungermannia inundata*)

Distribution

Solenostoma inundatum (Figure 180-Figure 181) occurs in Australia and New Zealand (Allison & Child 1975; ITIS 2121).

Figure 180. ***Solenostoma inundatum***, a species from Australia and New Zealand. Photo owned by the University of Auckland, with online permission for educational use.

Figure 181. ***Solenostoma inundatum***, a species that can be found in some mountain streams. Photo owned by the University of Auckland, with online permission for educational use.

Aquatic to Wet Habitats

Solenostoma inundatum (Figure 180-Figure 181) occurs on soil or rocks in wide-ranging habitats from mountain streams to dry pumice banks (Allison & Child 1975). Its name implies that it lives where it can at least some of the time become submersed. Scott (1985) described it as occurring on wet clay banks in wet sclerophyll forest where it is a common pioneer. It often occurs with other bryophytes, especially ***Jackiella*** and ***Isotachis.***

Figure 182. ***Jackiella javanica***, a liverwort that frequently serves as a substrate for ***Solenostoma inundatum***. Photo from Taiwan Mosses Color Illustrations, through Creative Commons.

Figure 183. ***Isotachis*** sp., a liverwort that frequently serves as a substrate for ***Solenostoma inundatum***. Photo by Phil Bendle, with permission through John Grehan.

Adaptations

When submersed, the plants of ***Solenostoma inundatum*** (Figure 180-Figure 181) are bright green, but when on exposed banks they are bright red (Allison & Child 1975). The red coloration is most likely induced by the bright light in exposed sites and can protect for UV damage, especially when dry.

Reproduction

The sexual status of ***Solenostoma inundatum*** (Figure 180-Figure 181) is unclear, with Scott (1985) listing it as

dioicous and Bakalin (2014) listing at as **dioicous** with a question mark. Smaller plants produce bright pink perianths (Figure 184) that can at times be quite numerous (Allison & Child 1975). The capsules mature (Figure 185) and dehisce with spiral cleavage (Figure 186).

Figure 184. ***Solenostoma inundatum*** with perianth. Photo owned by the University of Auckland, with online permission for educational use.

Figure 185. ***Solenostoma inundatum*** capsule. Photo owned by the University of Auckland, with online permission for educational use.

Figure 186. ***Solenostoma inundatum*** dehiscing capsule. Photo owned by the University of Auckland, with online permission for educational use.

Solenostoma javanicum

(syn. = *Aplozia javanica*)

Solenostoma javanicum occurs in Australia and southern Asia (ITIS 2020m). The only report of a wet habitat I could find was that of Ruttner (1955). He reported it from sulfur springs in the tropics.

Solenostoma obovatum (Figure 187)

(syn. = *Eucalyx obovata*, *Eucalyx obovata* fo. *elegatus*, *Eucalyx obovata* fo. *laxus*, *Eucalyx obovata* var. *rivularis*, *Jungermannia obovata*, *Nardia obovata*, *Plectocolea obovata*)

Distribution

Solenostoma obovatum (Figure 187) occurs sparingly in the Arctic, then southward in the mountains of Europe and North America (Schuster 1969).

Figure 187. ***Solenostoma obovatum***, a species from the Arctic southward to the mountains of Europe and North America, occurring in rivers and streams and on their banks. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

An early report by Nichols (1918) attributed ***Solenostoma obovatum*** (Figure 187) to a rock ravine streambank, Cape Breton Island, Canada (Nichols 1918). Watson (1919) reported it from rocks or soil of fast streams, usually on submerged rocks, and on banks with frequent submergence and slow water. In the mountains of Westfalens, northwestern Germany, it occurs in shallow water (Koppe 1945). But others attribute it to more aquatic habitats. It occurs in alpine streams in the Swiss Alps (Geissler 1976). In Thuringia, Germany, it occurs in the ***Platyhypnidium*** (Figure 68)***-Fontinalis antipyretica*** (Figure 69) association (Marstaller 1987). And it occurs in the Iskur River, Bulgaria, and its main tributaries (Papp *et al*. 2006). Light (1975) reported a species he questionably attributed to ***Solenostoma cf. obovatum*** from small lakes in Scottish mountains with ice cover 4-7 months per year and low ion concentrations.

Reproduction

Solenostoma obovatum (Figure 187) is **paroicous** (Schuster 1969). It apparently lacks gemmae, as is typical for this family.

Solenostoma sphaerocarpum (Figure 188-Figure 189, Figure 193)

(syn. = *Aplozia sphaerocarpa*, *Haplozia sphaerocarpa*, *Jungermannia sphaerocarpa*)

Distribution

Solenostoma sphaerocarpum (Figure 188-Figure 189, Figure 193) occurs across Siberia and is known from Japan (Váňa *et al*. 2013). ITIS (2020n) lists Europe, Asia, Africa, Oceania, Australia, North America from Alaska to Mexico, and South America.

Figure 188. ***Solenostoma sphaerocarpum***, a worldwide species from streams and rivers and their banks. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

Szweykowski (1951) reported ***Solenostoma sphaerocarpum*** (Figure 188-Figure 189, Figure 193) from moist stones and rocks in stream beds in the Gory Stolowe Mountains of Poland. Konstantinova and Vasiljev (1994) found it on rocks on a stream bank, mixed with ***Blepharostoma trichophyllum*** (Figure 190), ***Mesoptychia heterocolpos*** (Figure 191), ***Tritomaria scitula***, and ***Lophoziopsis excisa*** (Figure 192) in the Sayan Mountains of southern Siberia. Miller and Shushan (1964) reported it from stream banks in Oregon, USA. Geissler (1976) found it in alpine streams in the Swiss Alps. It occurs in the upper and middle reaches of streams in the Harz Mountains of Germany (Bley 1987), and in the ***Platyhypnidium*** (Figure 68)***-Fontinalis antipyretica*** (Figure 69) stream association in Thuringia, Germany (Marstaller 1987). Ferreira *et al*. (2008) considered it to be a species of rivers. Tremp and Kohler (1991) consider it to be a species of low-buffered water of streams.

Figure 189. ***Solenostoma sphaerocarpum*** showing its matted growth habit. Photo by Hugues Tinguy, with permission.

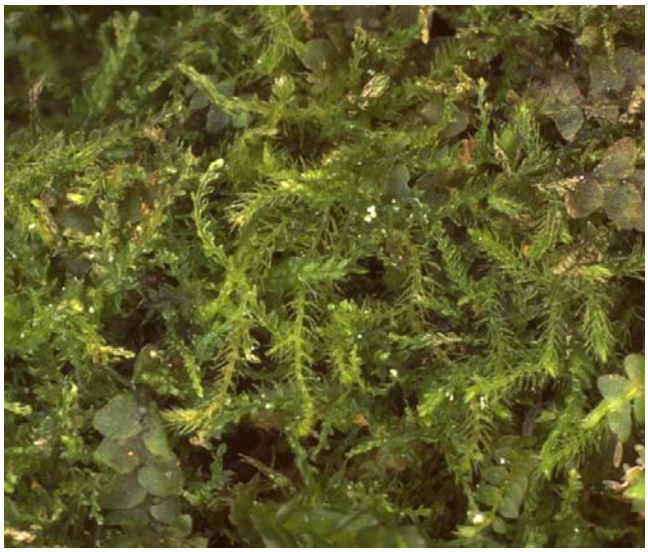

Figure 190. ***Blepharostoma trichophyllum***, an associate of ***Solenostoma sphaerocarpum*** on stream banks. Photo by Jan-Peter Frahm, with permission.

Figure 191. ***Mesoptychia heterocolpos***, an associate of ***Solenostoma sphaerocarpum*** on stream banks. Photo by Jan-Peter Frahm, with permission.

Figure 192. ***Lophoziopsis excisa***, an associate of ***Solenostoma sphaerocarpum*** on stream banks. Photo by Štěpán Koval, with permission.

Adaptations

Solenostoma sphaerocarpum (Figure 188-Figure 189, Figure 193) is very **polymorphous** (expressing multiple forms). It becomes red-colored in exposed situations (Váňa *et al*. 2013).

Reproduction

Solenostoma sphaerocarpum (Figure 188-Figure 189, Figure 193) is **heteroicous** (male & female organs on same plant; Figure 193), leading to its classification among several species, including ***S. rossicum*** in Russia and ***S. pyriflorum*** subsp. ***purpureum*** in west Greenland. Newton (1983) followed the spore germination and sporeling development. She found up to six gametophytes could be produced by one protonema. It is interesting that in mature leaves the oil bodies were fewer, but larger, when compared with immature leaves and protonemata. It is one of the few liverworts to possess purple rhizoids.

Figure 193. ***Solenostoma sphaerocarpum*** with perigynia visible. Photo by Hugues Tinguy, with permission.

Solenostoma stephanii

(syn. = *Aplozia stephanii*)

Distribution

Solenostoma stephanii occurs in Australia, Oceania, and southern Asia (ITIS 2020).

Aquatic and Wet Habitats

Ruttner (1955) reported ***Solenostoma stephanii*** as submersed in the **littoral** (relating to or situated on shore of sea or lake, usually shallow) zone in the tropics.

Solenostoma tetragonum

(syn. = *Nardia tetragona*)

Distribution

Solenostoma tetragonum is known from Australia, Oceania, and southern Asia (ITIS 2020p). This includes southeast Asia, from Himalayas, India, and Srí Lanka to China, Japan, Micronesia, Samoa, New Guinea, and northern Australia (Li & Váňa 2015).

Aquatic and Wet Habitats

The only wetland study that lists ***Solenostoma tetragonum*** is that of Ruttner (1955) for **tuff** (fine-grained volcanic rock) walls in the tropics. Gupta and Asthana (2016) list this species for soil and dry or wet racks at mid and upper altitudes.

Some people have found this liverwort to be desirable for aquaria (Elo500 2014), indicating its ability to be aquatic.

Solenostoma truncatum (Figure 194)

(syn. = *Nardia truncata*)

Distribution

Solenostoma truncatum (Figure 194) is widespread mostly in southeastern Asia and northern Australia (Li & Váňa 2015). It is very variable in leaf shape, cell texture, and perianth characters (Li & Váňa 2015), resulting in many synonyms (*e.g.* Váňa & Long 2009; Li *et al*. 2017).

Figure 194. ***Solenostoma truncatum***, a species mostly from southeastern Asia and northern Australia, occurring on wet rocks, moist soil, and sulfur springs, as well as some drier habitats. Photo from Hong Kong Flora, with permission.

Aquatic and Wet Habitats

Ruttner (1955) reported ***Solenostoma truncatum*** (Figure 194) as a species of sulfur springs in the tropics. Li and Váňa (2015) considered it to be the commonest species of ***Solenostoma*** in southeast Asia. In the Ghats of India it grows on moist soil in shady habitats, either in pure patches or with other bryophytes, expressing the variety ***kodaikanalensis*** (Alam *et al*. 2012).

The species occurs on soil, wet rocks, and soil-covered rocks at middle and upper altitudes in the Pachmarhi Biosphere Reserve, India (Gupta & Asthana 2016).

Solenostoma vulcanicola (Figure 195-Figure 196)

(syn. = *Jungermannia vulcanicola*, *Nardia vulcanica*)

Distribution

Solenostoma vulcanicola (Figure 195-Figure 196) has a relatively small distribution in Indonesia, Japan, and India (Singh & Singh 2015).

Figure 195. ***Solenostoma vulcanicola*** removed from clump to show individual plants. This species has a limited distribution in Asia and is restricted to sulfur springs. Photo courtesy of Angela Ares.

Figure 196. ***Solenostoma vulcanicola*** showing dense clumps from an acid spring in Japan. Photo by Juuyoh Tanaka, through Creative Commons.

Aquatic and Wet Habitats

In 1955, Ruttner listed ***Solenostoma vulcanicola*** (Figure 195-Figure 196) as one from sulfur springs in the tropics. Satake and coworkers have published multiple papers on its tolerance of the chemistry of Japanese springs and spring-fed streams (Satake 1983). It is able live and thrive in a *p*H range of 3.6 to 4.6, disappearing at 5.5 (Satake *et al*. 1989). In fact, it has not been recorded at a *p*H above 4.6, but it is known from Kusatsu hot spring (Japan) at *p*H 1.9! At such low *p*H levels, iron oxide accumulates on the shoots and is difficult to remove. Potassium in the shoots reached as much as 5%.

Bacteria can occur in the cell wall of ***Solenostoma vulcanicola*** (Figure 195) in acid (*p*H 4.2-4.6) stream water (Satake & Miyasaka 1984b), suggesting a possible role in decomposition.

Satake (1983) explored the accumulation of various elements in stream waters and in their bryophytes. Satake *et al*. (1989) demonstrated that few species were able to tolerate a variety of heavy metals in their water environment. ***Solenostoma vulcanicola*** (Figure 195-Figure 196), growing in a *p*H range of 4.0-4.6, were covered with a precipitate of $Fe(OH)_2$ that accounted for 5-13% of its dry weight. Its K accumulation was up to 5%.

Shiikawa (1956, 1959, 1960, 1962) found that the liverwort ***Solenostoma vulcanicola*** (Figure 195-Figure 196) plays an active role in deposition of iron ore. Since Japan has few native sources of usable iron, Ijiri and Minato (1965; Wickens 2001) suggested producing limonite ore artificially by cultivating this liverwort and other bryophytes in fields near iron-rich springs.

Satake and Miyasaka (Satake & Miyasaka 1984a; Satake *et al*. 1990) reported the accumulation of mercury in ***Solenostoma vulcanicola*** (Figure 195-Figure 196) from a stream (Figure 1) at *p*H 4.2-4.6. Satake *et al*. (1983; 1984) found the highest mercury content (12,100 Hg g^{-1}) in basal segments (1.3%, Satake 1985) of ***Solenostoma vulcanicola*** from an acidic stream in Japan (Figure 1). Satake and coworkers demonstrated that mercury is accumulated from stream water primarily in the cell walls of this species (Satake *et al*. 1983, 1988, 1990; Satake & Miyasaka 1984a; Satake 1985), and not in the **plasmalemma** (cell membrane) or chloroplasts (Satake & Miyasaka 1984a).

The mercury forms electron-dense particles as a mercury-sulfur compound, probably mercuric sulfide, which is not toxic to living organisms.

In addition to mercury, ***Solenostoma vulcanicola*** (Figure 195) from rivers, streams, lakes, and springs accumulates scandium (Satake & Nishikawa 1990). Among the 18 bryophytes analyzed, only this species and ***Scapania undulata*** showed a substantial accumulation.

Adaptations

Solenostoma vulcanicola (Figure 195) can become brownish black to black (Figure 197), but not red or purple (Bakalin 2014). Their stems are mostly erect, permitting them to form tight cushions (Figure 196-Figure 197). The rhizoids are sparse.

Reproduction

Solenostoma vulcanicola (Figure 195) is **dioicous** (Bakalin 2014). Despite the difficulty of its sexual reproduction, it can form huge cushiony mats in the right conditions (Figure 1, Figure 197).

Figure 197. ***Solenostoma vulcanicola*** habitat showing extensive cushions. Photo courtesy of Angela Ares.

Summary

The **Jungermanniineae** are represented by 11 families in wet and aquatic environments. Some of these, such as ***Jungermannia exsertifolia***, ***Marsupella aquatica***, ***M. sphacelata***, ***Nardia compressa***, and ***Solenostoma vulcanicola*** can be classified as truly aquatic, only occasionally being out of water, although they may occur on emergent rocks where they are constantly saturated. The others in this subchapter occur in wet habitats, but are not restricted to aquatic habitats.

The **Jungermanniineae** typically grow in mats, but several grow among or on ***Sphagnum***. Some are known to host fungi. They often have terpenoids that may serve as antibacterial and antiherbivore agents. Their protective coloration seems to go more to brown than red, but some species do form red pigments.

Acknowledgments

Lars Söderström helped me find the current acceptable names for a number of older taxa. Thank you to Ken Adams, Andi Cairns, David Long, Martha Nungesser, and Chris Preston for helping me to define burn.

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CHAPTER 1-5
AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES: LOPHOCOLEINEAE, PART 1

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Figure 1. ***Chiloscyphus polyanthos*** habitat. Photo by Michael Lüth, with permission.

Suborder Lophocoleineae

Blepharostomaceae

Blepharostoma trichophyllum (Figure 2-Figure 3)

Distribution

Blepharostoma trichophyllum (Figure 2-Figure 3) has a widespread Holarctic distribution, but has also been reported from high tropical mountains in both the Eastern and Western Hemispheres (Gradstein *et al*. 1977).

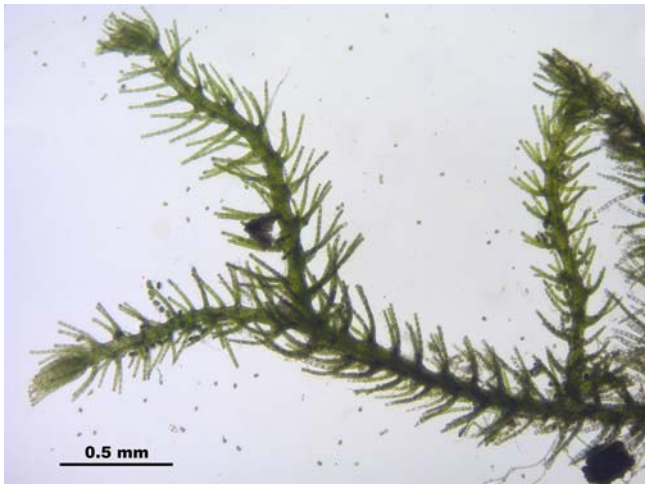

Figure 2. ***Blepharostoma trichophyllum*** individual plant showing finely divided leaves. Photo by Hermann Schachner, through Creative Commons.

Figure 3. ***Blepharostoma trichophyllum*** forming mats that are typical of its growth habit. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Blepharostoma trichophyllum (Figure 2-Figure 3) has a broad range of habitats. Watson (1919) reported it from ground, rocks, and stumps associated with fast water. Mamczarz (1970) found it in the ground community associated with streams near Lacko, Western Carpathians. Similarly, Rastorfer *et al*. (1973) found it to be hydro-mesic at Prudhoe Bay, Alaska.

Gradstein *et al.* (1977) reported ***Blepharostoma trichophyllum*** (Figure 3) from the boggy páramo (Figure 4), associated with species of ***Sphagnum*** (Figure 5). On Svalbard, it similarly occupied the moss-***Sphagnum*** tundra (Figure 5), where it was mixed with ***Schistochilopsis opacifolia***, ***Fuscocephaloziopsis pleniceps*** (Figure 6), ***Cephalozia bicuspidata*** (Figure 7), and ***Cephaloziella varians*** on the side of a hillock (Konstantinova & Savchenko 2008). In the Italian Alps, it occurs in peat bogs and on logs (Figure 8) (Privitera *et al*. (2010). In the Pyrenees, Hugonnot (2014) found it colonizing the compacted and decaying ***Sphagnum***, along with ***Liochlaena lanceolata*** (Figure 9)**.**

Figure 4. Marshes at Páramo de Ocetá, the type of site where one might find ***Blepharostoma trichophyllum***. Photo by Álvaro Siabatto and José Próspero Hurtado Caro, through Creative Commons.

Figure 5. ***Sphagnum*** in tundra, a habitat suitable for ***Blepharostoma trichophyllum***. Photo from NPS, through public domain.

Figure 6. ***Fuscocephaloziopsis pleniceps***, a species that often grows mixed with ***Blepharostoma trichophyllum*** in the tundra. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.

Figure 7. ***Cephalozia bicuspidata***, a species that often grows mixed with ***Blepharostoma trichophyllum*** in the tundra. Photo by Michael Lüth, with permission.

Figure 8. ***Blepharostoma trichophyllum*** in a typical habitat on a log. Photo by Hermann Schachner, through Creative Commons.

Figure 9. ***Liochlaena lanceolata***, a liverwort that associates with ***Blepharostoma trichophyllum*** in the Pyrenees. Photo by Hugues Tinguy with permission.

Hong (1977) found ***Blepharostoma trichophyllum*** (Figure 3) on wet soil, rocks, and decayed wood in Wyoming, USA, but Söderström (1989), working in Sweden, never found it in the earliest decay stages (stages 1-3), occurring in later stages with ***Calypogeia suecica*** (Figure 10), ***Fuscocephaloziopsis leucantha*** (Figure 11), and ***Neoorthocaulis attenuatus*** (Figure 12). Glime (1982) reported it from the humid wall of the Flume at Franconia Notch in New Hampshire, USA.

Figure 10. ***Calypogeia suecica***, a liverwort that occurs with ***Blepharostoma trichophyllum*** on late-decay-stage logs in Sweden. Photo by Michael Lüth, with permission.

Figure 11. ***Fuscocephaloziopsis leucantha***, a liverwort that occurs with ***Blepharostoma trichophyllum*** on late-decay-stage logs in Sweden. Photo by David T. Holyoak, with permission.

Figure 12. ***Neoorthocaulis attenuatus***, a liverwort that occurs with ***Blepharostoma trichophyllum*** on late-decay-stage logs in Sweden. Photo from Earth.com, with permission.

In the Republic of Buryatia, Russia, Konstantinova *et al*. (2018) found ***Blepharostoma trichophyllum*** (Figure 3) on soil-covered rocks, on soil between rocks, on banks of rivers, on trails under roots sticking out and on mossy logs (Figure 8) in mixed forests, in pure mats or mixed with other bryophytes. In the moist alpine tundra of the Canadian Yukon, Hong and Vitt (1977) found it was frequently associated with ***Mesoptychia heterocolpos*** (Figure 13), ***Schljakovia kunzeana*** (Figure 14), and ***Scapania irrigua*** (Figure 15). In the Sette-Daban Range of eastern Yakutia, Sofronova and Sofronov (2010) found it with mixed with ***Radula complanata*** (Figure 16) on stream banks. Dulin (2008) found it on stream and river banks, as well as on rotting logs, in the Komi Republic of Russia.

Figure 13. ***Mesoptychia heterocolpos***, a species that often accompanies ***Blepharostoma trichophyllum*** in the moist alpine tundra. Photo by Blanka Aguero, with permission.

Figure 14. ***Schljakovia kunzeana***, a species that often accompanies ***Blepharostoma trichophyllum*** in the moist alpine tundra. Photo by Michael Lüth, with permission.

Figure 15. ***Scapania irrigua***, a species that often accompanies ***Blepharostoma trichophyllum*** in the moist alpine tundra. Photo by David T. Holyoak, with permission.

But it was also a submerged hemicalciphilous liverwort in montane streams and on streambanks in western Canada (Vitt *et al.* 1986; Glime & Vitt 1987). In the wetter habitats, and when submersed, it often occurs with other leafy liverworts. Sofronova (2013) likewise found it in water, on the soil of a shallow, temporary brook in southeastern Yakutia, where it occurred with the leafy liverworts ***Scapania crassiretis*** (Figure 17) and ***Plagiochila porelloides*** (Figure 18). Lepage (1953) found it on a moist bank of the Roggan River in Québec, Canada, where it was accompanied by ***Fossombronia pusilla*** (Figure 19), ***Scapania mucronata*** (Figure 20), and ***Fuscocephaloziopsis pleniceps*** (Figure 6). In the Sayan Mountains of southern Siberia, Konstantinova and Vasiljev (1994) found it on rocks at the stream bank, typically associated with ***Mesoptychia heterocolpos*** (Figure 13), ***Lophoziopsis excisa*** (Figure 21), ***Schistochilopsis opacifolia***, ***Solenostoma confertissimum*** (Figure 22), ***Solenostoma sphaerocarpum*** (Figure 23), ***Tritomaria scitula*** (Figure 24), and ***Marchantia polymorpha*** subsp. ***montivagans*** (Figure 25); on a brook bank it was mixed with ***Fuscocephaloziopsis pleniceps***, ***Mesoptychia heterocolpos*** (Figure 13), ***Lophozia ventricosa*** (Figure 26), ***Schljakovianthus quadrilobus*** (Figure 27), ***Scapania*** *cf.* ***irrigua*** (Figure 15), and ***Solenostoma confertissimum*** (Figure 22).

Figure 16. ***Radula complanata*** with capsules, a species that occurs with ***Blepharostoma trichophyllum*** on stream banks in the Sette-Daban Range of eastern Yakutia. Photo by Hermann Schachner, through Creative Commons.

Figure 17. ***Scapania crassiretis***, a species that occurs with ***Blepharostoma trichophyllum*** in temporary brooks in southeastern Yakutia. Photo from Earth.com, with permission.

Figure 18. ***Plagiochila porelloides***, a species that occurs in temporary brooks in southeastern Yakutia with ***Blepharostoma trichophyllum***. Photo by Štěpán Koval, with permission.

Figure 19. ***Fossombronia pusilla***, a species that occurs with ***Blepharostoma trichophyllum*** on moist river banks. Photo by Clive Shirley, Hidden Forest <hiddenforest.co.nz>, with permission.

Figure 20. ***Scapania mucronata***, a species that occurs with ***Blepharostoma trichophyllum*** on moist river banks. Photo by Tomas Hallingbäck, with permission.

Figure 21. ***Lophoziopsis excisa***, a species that occurs with ***Blepharostoma trichophyllum*** on stream bank rocks in Siberia. Photo from Earth.com, with permission.

Figure 22. ***Solenostoma confertissima***, a species that occurs with ***Blepharostoma trichophyllum*** on stream bank rocks in Siberia. Photo by Michael Lüth, with permission.

Figure 23. ***Solenostoma sphaerocarpum***, a species that occurs with ***Blepharostoma trichophyllum*** on stream banks in Siberia. Photo by Hugues Tinguy, with permission.

Figure 24. ***Tritomaria scitula*** with gemmae, scattered in this mix with ***Blepharostoma trichophyllum*** and other bryophytes on stream bank rocks in Siberia. Photo from Earth.com, with permission.

Figure 25. ***Marchantia polymorpha*** subsp. ***montivagans***, a species that occurs with ***Blepharostoma trichophyllum*** and other bryophytes on stream bank rocks in Siberia. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 26. ***Lophozia ventricosa***, a species that occurs with ***Blepharostoma trichophyllum*** on a brook bank in Siberia. Photo by Hermann Schachner, through Creative Commons.

Figure 27. ***Schljakovianthus quadrilobus***, a species that occurs with ***Blepharostoma trichophyllum*** on a brook bank in Siberia. Photo by Štěpán Koval, with permission.

Reproduction

Unlike most aquatic species, where development of early stages is unknown, the sporelings, gemmalings, and regeneration of ***Blepharostoma trichophyllum*** (Figure 3) were described early by Fulford (1955). Arzeni (1948) described the perianth (Figure 28-Figure 29) and rare gemmae from populations in Reese's, Bog, Michigan, USA.

Biochemistry

Blepharostol, a sesquiterpenoid alcohol, as well as other terpenoids, has been described from this species (Feld *et al.* 2004).

Figure 28. ***Blepharostoma trichophyllum*** with perianths (brownish) and capsules (nearly black). Photo by Hermann Schachner, through Creative Commons.

Figure 29. ***Blepharostoma trichophyllum*** showing sporophytes. Photo by Michael Lüth, with permission.

Herbertaceae

Herbertus sendtneri (Figure 30)

(syn. = *Herbertus armitanus*, *Herbertus circinatus, Herbertus dicranus*)

Not surprisingly, Feldberg *et al*. (2004) found cryptic species among the ***Herbertus sendtneri*** (Figure 30) populations. Differences are described as morphological "tendencies," suggesting that the similarity in morphology has developed independently. Furthermore, the differences in leaf shapes between Austrian and Macaronesian populations or Neotropical populations may reflect differences in suboptimal climate in the Austrian Alps where ***H. sendtneri*** grows in shaded rock crevices of large boulder slopes, compared to other populations such as those in Macaronesia.

Distribution

Herbertus sendtneri (Figure 30) is widespread, especially in the Northern Hemisphere, where it is known from Arctic and alpine areas. ***Herbertus dicranus*** was originally considered to be unique to the tropics, but later Heinrichs *et al*. (2009) determined it to be conspecific with European and Asian populations of ***H. sendtneri***. Like many species, it exhibits **polyphyly** (derived from more than one common evolutionary ancestor or group), but molecular studies allied the tropical populations with the European and Asian populations (Heinrichs *et al*. 2009). Discovery of ***H. armitanus*** and ***H. circinatus*** as synonyms has extended the distribution to east Africa (Tanzania) and Malesia (Papua New Guinea and the Solomon Islands).

Aquatic and Wet Habitats

In Alaska on Attu Island, ***Herbertus sendtneri*** (Figure 30) is uncommon, occurring on damp banks of the tundra, on the wall of a humus hole of a periodic streamlet, on the bank of a gully in the subalpine, on a shaded wall of a gully, and associated with a snow bed (Talbot *et al*. 2018).

One surprising occurrence of ***Herbertus sendtneri*** (Figure 30) was in a glacial lake (4120 m) in the Andes of Colombia (Gradstein *et al*. 2018). These were previously identified as ***H. oblongifolius*** due to their dwarf stature and obtuse leaf tips, known as rare from Brazil. This rare taxon was subsequently placed in synonymy with ***H. sendtneri***, a widespread taxon. This lake population may have originated from a rock-inhabiting population that dispersed into the lake through caducous branches or other fragments that washed into the lake. Gradstein and coworkers estimated that such an event occurred in the last 12,000-21,000 years when the lake was ice-free. Such a submersed population is rare for liverworts in the tropics and is unlikely to occur at lower elevations because of the higher temperatures and paucity of dissolved CO_2.

Figure 30. ***Herbertus sendtneri***, a widespread Arctic-alpine species known mostly from the Northern Hemisphere. Photo from Earth.com, with permission.

Adaptations

Mägdefrau (1982) described ***Herbertus sendtneri*** as having a **tall turf** life form (Figure 31).

Reproduction

Herbertus sendtneri (Figure 30) is **dioicous**, and as of 2004, males were still unknown (Feldberg *et al*. 2004). Sporophytes are rare (He & Sun 2017), but He and Sun (2017) found them from a herbarium specimen collected in Austria. The spores are papillose, typical of the Northern Hemisphere, whereas those from the Southern Hemisphere are tuberculate or shortly spinose.

Fungal Interactions

It serves as host for the fungal endophyte ***Paenibacillus herberti***, a taxon from Ga Walloon Glacier (Bomi County, Tibet, China) that thus far appears to be unique to this ***Herbertus*** species (Guo *et al*. 2015). Subsequently, Guo *et al*. (2016) isolated another member of the genus, ***Paenibacillus marchantiophytorum***, from this same species of ***Herbertus*** at Gawalong glacier, Tibet.

Figure 31. ***Herbertus sendtneri*** showing its **tall turf** life form. Photo by Michael Lüth, with permission.

Biochemistry

Sun *et al*. (2010) used extracts from five bryophyte species, including ***Herbertus sendtneri*** (Figure 30-Figure 31), to determine effects on seed germination and seedling physiology of the cucumber. They found that all of these extracts promoted growth of the radicle at some concentrations and that ***Herbertus sendtneri*** extracts could enhance chlorophyll content. It could also enhance the content of soluble sugar.

Lepidoziaceae

Bazzania denudata (Figure 36-Figure 32)

Distribution

Bazzania denudata (Figure 36-Figure 32) is distributed in North America from Alaska, southward to Oregon, Montana, and Kentucky, USA (Clark & Frye 1942). It also occurs in Greenland and Central Europe (Schuster 1969).

Figure 32. ***Bazzania denudata***, an epiphyte, but also occurring on moist sandstone canyon walls. Photo from Botany Website, UBC, with permission.

Aquatic and Wet Habitats

Bazzania denudata (Figure 36-Figure 32) is predominantly an epiphyte (*e.g.* Cain 1935; Kitagawa 1978; Hong 1988; Peck *et al*. 1995), especially at tree bases (Schuster 1969). These tend to be in relatively moist forests, and Bakalan (2016) notes that it avoids dry substrata. But it can also occur in wet or very humid places. Fulford (1934) found this species on moist, shaded sandstone in Kentucky, USA. Schuster and Patterson (1957) reported it from a damp recess in a cliff in Virginia, USA, where it occurred with ***Metzgeria leptoneura*** var. ***breviseta*** (Figure 33) and ***Radula tenax*** (Figure 34). McKnight (1985) found it to be occasional on a moist, shaded sandstone wall in Indiana, USA (a westward extension) with ***Bryoxiphium norvegicum*** (Figure 35). Glime (1982) found it on the wall of the Flume at Franconia Notch, New Hampshire, USA. Bakalin (2016) considers it an acidophilic mesophyte.

Figure 33. ***Metzgeria leptoneura***, a species occurring with ***Bazzania denudata*** in damp recesses of a cliff. Photo by Blanka Aguero, with permission.

Figure 34. ***Radula tenax***, a species occurring with ***Bazzania denudata*** in damp recesses of a cliff. Photo from Earth.com, with permission.

Figure 35. ***Bryoxiphium norvegicum*** on a sandstone wall, a habitat where it can occur with ***Bazzania denudata***. Photo by Bob Klips, with permission.

Adaptations

The leaves of ***Bazzania denudata*** are deep green to brownish green or yellowish green (Bakalin 2016) – color variations that are most likely environmentally induced. It lacks rhizoids, forming loose patches. This means it would most likely be unable to establish under water, but it can live well in moist habitats.

Reproduction

Bazzania denudata is dioicous, limiting opportunities for sexual reproduction. The leaves in this species are easily deciduous (Figure 36) (Bakalan 2016), presumably serving as propagules, albeit with somewhat limited dispersal.

Figure 36. ***Bazzania denudata***, a species mostly distributed in northern parts of the Northern Hemisphere. Photo from Botany Website, UBC, with permission.

Biochemistry

Bazzania denudata has homogenous oil bodies (Bakalan 2016). The secondary compounds contained in these seem to have received little study.

oil bodies homogenous

Bazzania praerupta (Figure 37)

(syn. *Bazzania longa*, *Bazzania lehmanniana*)

Distribution

Bazzania praerupta (Figure 37) is a species of the Palaeotropics (Gradstein 2017). Aryanti and Gradstein (2007) considered its distribution to be Asiatic, but there are reports from some areas of Africa (*e.g.* Müller 1996). The known distribution has been complicated by the discovery of synonyms. Gradstein (2017) reduced ***Bazzania longa*** (from Australia only) and ***B. lehmanniana*** to synonymy with ***B. praerupta***, extending the known distribution of ***B. praerupta*** to Australia.

Aquatic and Wet Habitats

In the Ailao Mountains, SW China, it forms smooth mats on forest trees (Song *et al*. 2011). Like the previous species, this is primarily an epiphyte, as seen on tree branches in Java (Meijer 1960). It seems to prefer bamboo forests in Ethiopia, often occurring on the stems (Hylander 2014). Nevertheless, it can behave like a wet habitat species, as seen by growth in the thermal acidic spray in the tropics (Ruttner 1955).

Figure 37. ***Bazzania praerupta***, a Palaeotropical species that can live in acidic thermal spray zones. Photo through Creative Commons.

Reproduction

Bazzania praerupta is **dioicous**, a characteristic of the genus (Bakalan 2016). Little seems to have been published about its reproduction and dispersal.

Biochemistry

Because of its limited distribution, this species has received little biochemical attention. Kondo *et al*. (1990) confirmed the presence of three previously known sesquiterpenoids. Kudwiczuk and Asakawa (2010) noted that drimenol and albicanol help characterize the species. Drimanes are characteristic, but limonene, anastreptene, trinoranastreptene, ent-α-selinene, and spahulenol are also present.

Bazzania tricrenata (Figure 38)

Distribution

Bazzania tricrenata (Figure 38) is a circumboreal species, extending southward in the mountains (Schuster 1969) to Taiwan, Japan, and the Korean Peninsula (Bakalan 2016). In North America it extends from the Aleutians and Alaska south to California and east to Ellesmere, southward to Tennessee (Bakalan 2016).

Figure 38. ***Bazzania tricrenata***, an epiphytic and saxicolous species that can occur on wet cliffs in alpine areas. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

This is not an aquatic species, but it does seem to at least tolerate wet habitats. Nichols (1918) reported it from rock cliffs associated with streams on Cape Breton Island, Canada. Glime (1982) found it on the humid wall of the Flume at Franconia Notch, New Hampshire, USA. Konstantinova *et al*. (2002) found it on a wet cliff on a south-facing slope of the alpine zone of the Bureya River in the Russian Far East, where it was associated with ***Anastrophyllum assimile*** (Figure 39), ***Mylia taylorii*** (Figure 40), and ***Scapania microdonta*** (Figure 41). Bakalan (2016) considered it to be an acido- and basi-tolerant mesophyte, preferring mesic cliff crevices and open (but not full sun) rocks, rarely occurring in shady sites.

Figure 39. ***Anastrophyllum assimile***, a species associated with ***Bazzania tricrenata*** on a wet cliff in the Russian Far East. Photo by Norbert Schnyder, with permission.

Figure 40. ***Mylia taylorii***, a species associated with ***Bazzania tricrenata*** on a wet cliff in the Russian Far East. Photo by Hugues Tinguy, with permission.

Other habitats are not so moist. Ji *et al*. (2001) reported it as epiphyllous in the Matoushan Nature Reserve of Jiangxi Province, China. Schuster (1969) summarized its habitat as occurring almost uniformly on soil-covered damp to moist rock, especially on shaded, acidic ledges and usually avoiding calcareous areas.

Figure 41. ***Scapania microdonta***, a species associated with ***Bazzania tricrenata*** on a wet cliff in the Russian Far East. Photo from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

Knowing its typical habitats on rocks, desiccation tolerance of ***Bazzania tricrenata*** is not surprising. In samples from the Faroe Islands, about half the cells remained alive down to 33% relative humidity, but none at 15% (Clausen 1964).

Adaptations

Bazzania tricrenata is yellowish brownish to greenish brown, colors that would seem to enable it to occur in bright light (Bakalan 2016), a trait not consistent with its preference for shaded sites. It forms loose patches and typically lacks rhizoids.

Reproduction

Bazzania tricrenata does not have caducous leaves (Bakalan 2016). The species, like the rest of the genus, is **dioicous**. Its capsules are relative uncommon and are unknown in some regions. Spores are small. This raises the question of its ability to spread. The flagelliform branches that are produced ventrally can help it survive during unfavorable times through protection by the over-arching branches. These flagelliform branches can help it to enlarge its clone, but do they play a role in dispersal and colonization?

Fungal Interactions

Wang and Qiu (2006) found no reports of mycorrhizal fungi associated with this species.

Biochemistry

Bazzania tricrenata has smooth oil bodies (Bakalan 2016). Like other species of liverworts, this one has terpenoids, which could account for its lack of fungi – a relationship that needs to be explored. Sangaiah and Rao (1982) reported the synthesis of a phenolic sesquiterpene from this species. Suleiman *et al*. (1980) determined that the photosynthetic products in this species are volemitol and sedoheptulose in addition to sucrose and fructans.

Bazzania trilobata (Figure 42)

Distribution

Bazzania trilobata (Figure 42) is circumboreal, including Western Europe, eastern and western coastal North America, and Japan (Buckowska *et al*. 2010). In Poland, distribution coincides with two parts of the natural distribution range of Norway spruce.

Figure 42. ***Bazzania trilobata***, a species common in ***Thuja*** swamp and poor fen forests. Photo by Allen Norcross, with permission.

Aquatic an Wet Habitats

This is not an aquatic species, but it does like moist or humid places. I know it from ***Thuja*** swamps and a hemlock forest adjoining a poor fen. It occurs on ledges in the Flume at Franconia Notch, New Hampshire, USA (Glime 1982). In Germany it is reported from upstream reaches of the Harz Mountains (Bley 1987). And in the Great Smoky Mountains, USA, Cain (1935) found it on wet rocks; in Ohio, USA. Hall (1958) found it on moist sandstone and occasionally on adjacent mossy soil. In the Czech Republic it occurs in water-logged spruce stands where it dominates, often along with ***Sphagnum girgensohnii*** (Figure 43) (Neuhäuslová & Eltsova 2002).

Figure 43. ***Sphagnum girgensohnii***, a species occurs in water-logged spruce stands with ***Bazzania trilobata***. Photo by Hermann Schachner, through Creative Commons.

Figure 44. ***Bazzania trilobata*** showing a common growth form. Photo by Michael Lüth, with permission.

Figure 45. ***Bazzania trilobata*** at Hocking Hills, Ohio, USA, in a moist canyon. Photo by Janice Glime.

Jackson (2015) assessed the potential effects of the hemlock woolly adelgid on the hemlock forest and subsequent effects on ***Bazzania trilobata*** (Figure 44-Figure 47). She concluded that increases in light intensity and temperatures can cause damage to this species, causing its cover to diminish. On the other hand, we know that ***B. trilobata*** can survive freezing, perhaps benefitting from insulation by snow (Figure 46).

Figure 46. ***Bazzania trilobata*** in snow, demonstrating its ability to survive freezing temperatures. Photo by Allen Norcross, with permission.

Figure 47. ***Bazzania trilobata*** stolons. Photo by Janice Glime.

In the primarily red spruce, yellow birch, or spruce-dominated forests, this liverwort can serve as home for the endemic Cheat Mountain Salamander (***Plethodon nettingi***) (West Virginia, USA) (Figure 48) (Dillard *et al*. 2008; Pauley 2008). ***Bazzania trilobata*** forms **tall turfs** (Figure 44) or **wefts**, depending on the habitat characteristics (Uniyal *et al*. 2007), providing ample space for the salamanders to move about.

Figure 48. ***Bazzania trilobata*** with ***Plethodon nettingi***. Photo by Michael Graziano, with permission.

Paratley and Fahey (1986) found that one type of swamp in New York, USA, could be termed the ***Bazzania trilobata*** swamp. It is characterized by a low water table and "favorable" flow. In these swamps, bryophyte richness was high when there was a base-rich inflow and extensive microrelief. Bakalan (2016) considered the species to be an acidophilic to neutro-tolerant mesophyte. It rarely occurs in limestone areas, and when it does, it occurs on thick litter that provides an acidic substrate.

Cleavitt *et al*. (2007) examined the effect of water availability on the seasonal growth of ***Bazzania trilobata*** (Figure 44-Figure 47) on boulders of an eastern hemlock (*Tsuga canadensis*) stand at Hubbard Brook in New Hampshire, USA. There, it is able to form pure colonies on the boulders. They found that an increase in water availability did not cause a straightforward growth increase. Rather, it appeared to have a short-term initial effect, causing biomass gain with a moderating effect on elongation. Biomass gain of the stems appeared to be limited by the cost of respiration, but further research is needed to confirm this. Branching was stimulated over stem elongation in less dense stems where light intensity was greater.

Adaptations

Bazzania trilobata (Figure 44-Figure 47) is a large species that can grow prostrate to erect (Bakalan 2016). It forms somewhat loose patches or **tall turfs** (Figure 44) and **wefts** (Uniyal *et al*. 2007). Its color is typically deep green and shiny, but it can become yellowish green or brownish green. It lacks rhizoids.

Reproduction

Like other members of ***Bazzania***, ***B. trilobata*** (Figure 44-Figure 47) is **dioicous**.

Stolons (flagelliform branches) are a common form of asexual reproduction among liverworts in bogs and fens (Duckett *et al*. 1991). These are abundant in ***Bazzania trilobata*** (Figure 44-Figure 47) and may contribute to their success as a propagule below the surface where moisture remains much longer, and as a way of accomplishing rapid spread once they become established in a new location.

Figure 49. ***Bazzania trilobata*** stolons, a means of perenniation and asexual reproduction. Photo by Dick Haaksma, with permission.

Fungal Interactions

Fungi are often common on bryophytes, especially in humid habitats. Raudabaugh *et al*. (2011) assessed water stress factors for both the epiphytic and endophytic fungi, including those of ***Bazzania trilobata*** (Figure 44-Figure 47). Eleven of the twelve endophytic fungi had only limited biomass production at the weakest water matric potential (*ca*. 0 MPa).

Duckett *et al*. (1991) characterized ascomycetous fungi from a number of leafy liverworts. They found that most of the relationships were formed in the **Lepidoziineae** (including ***Bazzania trilobata***) and **Cephaloziineae**. Many members of these families have flagelliform axes (stolons) that extend deep into the peat. These frequently bear rhizoids that are infected with fungi. But if these are grown in sand or water, the fungal infection does not develop. Each rhizoid or cluster of rhizoids must be infected

independently – there is no internal connection between them.

Oil Bodies and Biochemistry

Oil bodies have been of taxonomic importance, but bryologists have wondered about their function for the liverworts. Pihakaski (1972) explored these structures in ***Bazzania trilobata*** (Figure 50). They found that whereas proteins are present in the chloroplast stroma, they are not present in the globules (oil bodies) embedded in the stroma. Instead, the globules are comprised of unsaturated neutral lipids. In ***B. trilobata*** it appears that the globules are surrounded by a single membrane, differing in that regard from the oil bodies of ***Pellia epiphylla*** (Figure 51). Huneck *et al*. (1984) examined seasonal dependence on essential oil in ***Bazzania trilobata*** and described the stereochemistry of (-)-5-hydroxycalamenene.

Figure 50. ***Bazzania trilobata*** leaf cells showing oil bodies. Photo by Walter Obermayer, with permission.

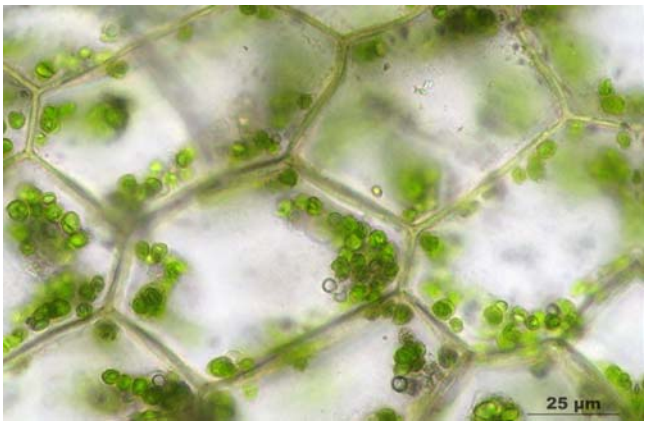

Figure 51. ***Pellia epiphylla*** thallus cells showing smaller oil bodies. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

There have been a number of biochemical studies on this species. Nagashima *et al*. (1996) identified a new myltaylane-type sesquiterpene alcohol and nine known sesquiterpenoids from ***Bazzania trilobata*** (Figure 44-Figure 47). Martini *et al*. (1998a) isolated 10 bisbibenzyl derivatives and two biphenyl linkages from ***Bazzania trilobata***. Warmers and König (1999) added two more sesquiterpenes. Scher *et al*. (2004a) isolated antifungal compounds from ***Bazzania trilobata*** and determined them to be effective against ***Botrytis cinerea*** (Figure 52), ***Cladosporium cucumerinum*** (Figure 53-Figure 54), ***Phytophthora infestans*** (Figure 55-Figure 56), ***Pyricularia oryzae*** (Figure 57-Figure 58), and ***Zymoseptoria tritici*** (Figure 59). They were able to isolate six antifungal sesquiterpenes and three bisbibenzyls. Scher *et al*. (2004b) isolated Bazzanin S as a new chlorinated bisbibenzyl from ***B. trilobata***. Konečný *et al*. (1985) obtained a series of sesquiterpenoids from Czech populations and determined a number of these were identical to those found in the same species from Japan. They added additional secondary compounds to the known list and presented the seasonal variation in essential oils. They also detailed the wax components in this liverwort.

Figure 52. ***Botrytis cinerea***, a fungus inhibited by sesquiterpenoids from ***Bazzania trilobata***, on strawberry. Photo by Rasbak, through Creative Commons.

Figure 53. ***Cladosporium cucumerinum*** on leaf, a fungus that is inhibited by antifungal compounds from ***Bazzania trilobata***. Photo by T. A. Zitter, with online permission from <DiscoverLife.org>.

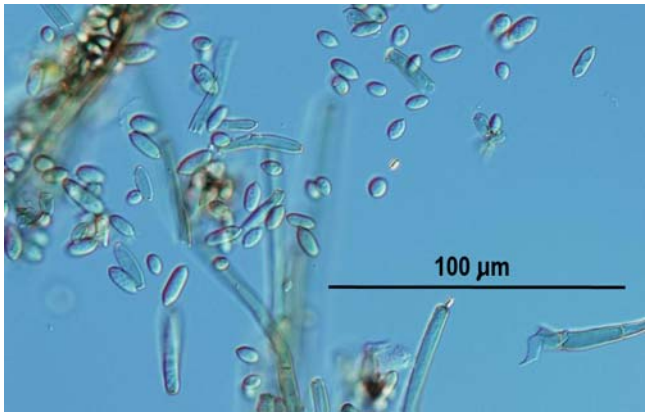

Figure 54. ***Cladosporium cucumerinum***, a fungus that is inhibited by extracts from ***Bazzania trilobata***. Photo by Bruce Watt, through Creative Commons.

Figure 55. ***Phytophthora infestans***, a species of fungus that is inhibited by secondary compounds from ***Bazzania trilobata***, on leaf. Photo by Howard F. Schwartz, through Creative Commons.

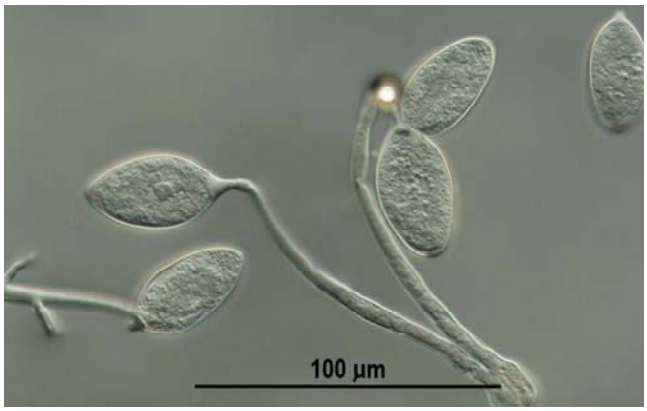

Figure 56. ***Phytophthora infestans***, a species of fungus that is inhibited by secondary compounds from ***Bazzania trilobata***. Photo by Bruce Watt, through Creative Commons.

Secondary compounds such as these often serve to protect the bryophytes from pathogens and herbivory. Tadesse *et al*. (2003) tested extracts from 17 different bryophyte species against mycelial growth of ***Botrytis cinerea*** (Figure 52) and ***Alternaria solani*** (Figure 60-Figure 61), including extracts from ***Bazzania trilobata*** (Figure 44-Figure 47). Extracts from this liverwort inhibited the mycelial growth of both fungi by more than 50%. Extracts from ***B. trilobata*** and ***Diplophyllum albicans*** (Figure 62) were more effective than those of the other bryophytes tested. Fungal disease control was ineffective after 4 hours, but showed some antifungal activity after 2 days. Nevertheless, the liverwort extracts were less effective than the fungicide dichlofluanide.

Figure 57. ***Pyricularia oryzae***, a species of fungus that is inhibited by secondary compounds from ***Bazzania trilobata***. Photo by Donald Groth, Louisiana State University AgCenter, Bugwood.org, through Creative Commons.

Figure 58. ***Pyricularia oryzae***, a species of fungus that is inhibited by secondary compounds from ***Bazzania trilobata***. Photo by Donald Groth, through public domain.

Figure 59. ***Zymoseptoria tritici***, a species of fungus that is inhibited by secondary compounds from ***Bazzania trilobata***. Photo by Mary Burrows, Montana State University, Bugwood.org, through Creative Commons.

Figure 60. ***Alternaria solani*** leaf lesions, a species of fungus that is inhibited up to 50% by secondary compounds from ***Bazzania trilobata***. Photo from Clemson University – USDA Cooperative Extension Slide Series, through Creative Commons.

Figure 61. ***Alternaria solani*** conidia; this species is inhibited up to 50% by extracts from ***Bazzania trilobata***. Photo by E. McKenzie, Landcare Research, Australia, through Creative Commons.

Figure 62. ***Diplophyllum albicans***, a species that is one of the best inhibitors of ***Alternaria solani*** and ***Botrytis cinerea*** among the bryophytes tested. Photo by David T. Holyoak, with permission.

Biochemistry

But in addition to the secondary compounds that seem to be useful in protecting the plants from pathogens and herbivory, the liverworts can also possess **lignan** (phytoestrogens; class of polyphenolic compounds including many found in plants and noted for having antioxidant and estrogenic activity) derivatives (Martini *et al*. 1998b; Scher *et al*. 2003).

Hygrolembidium boschianum

(syn. = *Lembidium boschianum*)

Distribution

Hygrolembidium boschianum occurs in the Southern Hemisphere, including southern South America, Australia, and nearby islands (EOL 2021).

Aquatic and Wet Habitats

Hygrolembidium boschianum occurs in sulfur springs in the tropics (Ruttner 1955). Gradstein (2011) verified this habitat with his report of the species submerged in sulfur springs in Indonesia. There seems to be little known about it ecologically.

Kurzia makinoana (Figure 63)

Distribution

Kurzia makinoana (Figure 63) is distributed in Europe, Asia, and western North America (ITIS 2020). Piippo (1990) considered it to be widely distributed in East Asia, with records from Guanxi and Zheijang in China and from Taiwan, and from Japan (BLM 1996). In North America, the species is widely distributed from Alaska to California (Bakalin 2018).

Figure 63. ***Kurzia makinoana***, a widely distributed Northern Hemisphere species, living in a wide range of wet and damp habitats. Photo by Blanka Aguero, with permission.

Aquatic and Wet Habitats

Kurzia makinoana (Figure 64) prefers the banks of streams and other watercourses (Bakalin 2018). In North America it occurs in acidic to moderately neutral mesophytic sites as a hygrophyte. It prefers partly to strongly shaded places and can be found on moderately moist peaty banks of streams in more northern sites and on

sandy-loamy banks of ditches in more southern sites and occasionally on acid rock. In its northern locales, it occurs in open swampy areas near the sea coast, whereas in the south it is more frequent in woody evergreen swamps. But it also grows over acidic rocks, ***Sphagnum*** (Figure 5), and other bryophytes at higher elevations in the Appalachian Mountains. At lower elevations it is confined to peaty and sandy banks of streams. In the Rogue River of the Siskiyou National Forest, Oregon and California, USA, it is associated with ***Sphagnum*** (Emerson & Loring 2010).

Figure 64. ***Kurzia makinoana*** forming a loose mat/turf. Photo from Earth.com, with permission.

In Korea, Choi *et al*. (2013) found ***Kurzia makinoana*** (Figure 63-Figure 64) on cliffs along streams in a broad-leaved forest in the range of 580-1446 m asl. On Bering Island, northwest Russia, it occurs on the peaty banks of ponds formed by freezing and thawing of ground material overlying permafrost (**cryogenic processes**), and in peat moss-shrub mires, occurring with ***Diplophyllum taxifolium*** (Figure 65), ***Fuscocephaloziopsis albescens*** (Figure 66), ***Gymnocolea inflata*** (Figure 67), and ***Odontoschisma elongatum*** (Figure 68) (Bakalin 2005). On Sakhalin Island in the West Pacific, ***Kurzia makinoana*** (Figure 63-Figure 64) occurs among mosses on raised oligotrophic dwarf shrub-peat moss mires (Bakalin *et al*. 2005). In Tottori Prefecture, Japan, Bakalin *et al*. (2013) found it on the wet clay of road crust and on tree trunks in the partial shade of broad-leaved or coniferous forests, often on rotten logs. It can be in pure mats or with ***Bazzania tridens*** (Figure 69), ***Blepharostoma minor***, and ***Plagiochila ovalifolia*** (Figure 70). In Mts. Hakkôda in northern Japan, Kitagawa (1978) found that it was rather common on soil from montane to alpine zones. It occurs in those regions on rotten logs, soil, and rocks, being abundant on the soil along sulfur-rich streams where it is associated with ***Diplophyllum albicans*** (Figure 62), ***Scapania parvitexta***, ***Calypogeia arguta*** (Figure 71), and ***C. fissa*** (Figure 72).

Figure 65. ***Diplophyllum taxifolium***, a species that occurs with ***Kurzia makinoana*** in peat moss-shrub mires of northwest Russia. Photo by Hermann Schachner, through Creative Commons.

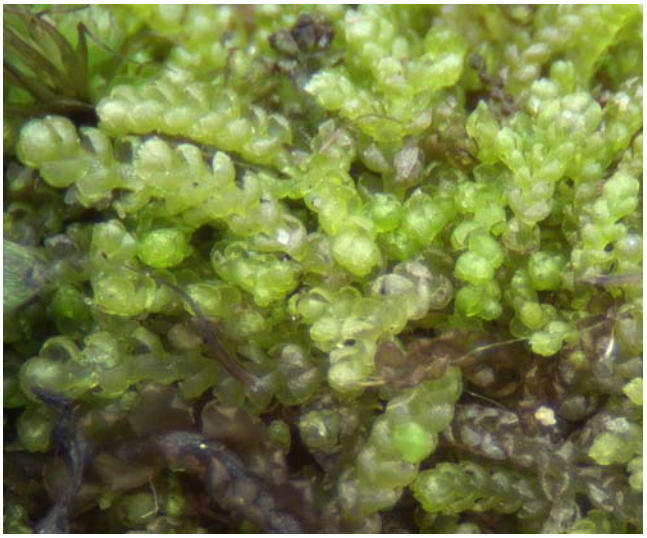

Figure 66. ***Fuscocephaloziopsis albescens***, a species that occurs with ***Kurzia makinoana*** in peat moss-shrub mires of northwest Russia. Photo by Tomas Hallingbäck, with permission.

Figure 67. ***Gymnocolea inflata***, a species that occurs with ***Kurzia makinoana*** in peat moss-shrub mires of northwest Russia. Photo by Michael Lüth, with permission.

Figure 68. ***Odontoschisma elongatum***, a species that occurs with ***Kurzia makinoana*** in peat moss-shrub mires of northwest Russia. Photo by Andrew Hodgson, with permission.

Figure 69. ***Bazzania tridens***, a species that occurs with ***Kurzia makinoana*** in Tottori Prefecture, Japan. Photo from Taiwan Color Illustrations, through Creative Commons.

Figure 70. ***Plagiochila ovalifolia***, a species that occurs with ***Kurzia makinoana*** in Tottori Prefecture, Japan. Photo from Earth.com, with permission.

Figure 71. ***Calypogeia arguta***, a species that occurs on the soil along sulfur-rich streams on Mts. Hakkôda, Japan. Photo by George G., through Creative Commons.

Figure 72. ***Calypogeia fissa***, a species that occurs on the soil along sulfur-rich streams on Mts. Hakkôda, Japan. Photo by Hermann Schachner, through Creative Commons.

At higher altitudes in Japan, the plants of ***Kurzia makinoana*** (Figure 63-Figure 64) become atypical, approaching the appearance of the European ***K. trichoclados*** (Figure 73).

Figure 73. ***Kurzia trichoclados***, a species similar to ***Kurzia makinoana***. Photo by David T. Holyoak, with permission.

Adaptations

Kurzia makinoana (Figure 63-Figure 64) is a tiny leafy liverwort, dull or deep green to brownish-green (BLM 1996). It occurs in dense tufts or patches with interwoven stems and occasionally creeps among the stems of other bryophytes. Such growth patterns can help it to maintain moisture.

Reproduction

Kurzia makinoana (Figure 63-Figure 64) is **dioicious** (BLM 1996).

Biochemistry

The tiny ***Kurzia makinoana*** (Figure 63-Figure 64) is aromatic (BLM 1996). It produces the monoterpene limonene as well as a number of sesquiterpenoids (Toyota *et al*. 1997). The chemical constituents differ from those of other **Lepidoziaceae** (Asakawa 1982). Among these compounds in ***Kurzia makinoana*** several (sesquiterpene lactones) (Asakawa *et al.* 2013) are known for their cytotoxic activity against P-388 lymphocytic leukemia cells (Asakawa 1995).

Kurzia pauciflora (Figure 74)

(syn. = *Jungermannia pauciflora*, *Jungermannia quadridigitata*, *Kurzia setacea*, *Lepidozia setacea*, *Microlepidozia setacea*)

Distribution

Schuster (1958) predicted that ***Kurzia pauciflora*** (Figure 74) would prove to be transcontinental. Based on a variety of studies, we now know that it occurs in North and South America, Europe, Asia, and Africa (ITIS 2020). It is circumboreal and extends throughout temperate Europe, being common in central Europe (Reinoso & Rodríguez-Oubiña 1988).

Figure 74. ***Kurzia pauciflora***, a circumboreal species in the Northern Hemisphere, extending into the European temperate zone. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Watson (1919) included ***Kurzia pauciflora*** (Figure 74) as an aquatic species that occurs on banks that are frequently submerged and in slow water with poor mineral salts. This latter habitat is consistent with the low-nutrient bog sites where it has been reported frequently.

Bakalin (2018) describes *Kurzia pauciflora* (Figure 74) as a species occurring as single shoots between ***Sphagnum*** (Figure 5) and ***Leucobryum*** (Figure 75) in mires. It is sometimes accompanied by ***Mylia anomala*** (Figure 76), ***Odontoschisma fluitans*** (Figure 77), ***Cephaloziella spinigera*** (Figure 78), and other liverworts. Hong (1988) contrasts this with his experience in western North America, where it usually grows in pure patches in peat bogs. Less commonly, it occurs on the bare peat of heaths, wetlands, and on wet cliffs and stones in association with ***Bazzania denudata*** (Figure 36-Figure 32) or ***Herbertus aduncus*** (Figure 79). Bakalin finds that it is confined to ***Sphagnum*** carpets in bogs (Figure 5) with *p*H below 3.8. Schuster (1958) noted its occurrence in a bog near Burt Lake in Michigan, USA. Karofeld and Toom (1999) found it on decaying ***Sphagnum*** in Mannikjarve bog in central Estonia. Ingerpuu *et al*. (2014) considered the species to be common in bogs in Estonia. Weber (1976) found it in the Cataracts Provincial Park, Newfoundland, Canada, where it occurred in open boggy areas (*p*H 3-4) in areas where ***Sphagnum*** spp. predominated. Miller (1960) likewise noted its intimate association with ***Sphagnum*** in the Laurentian Mountains of Canada. Weber and Brassard (1976) considered to be typical in ombrotrophic bogs in Newfoundland. Van Geel (1978) reported it from peat bog fossils in Germany and the Netherlands – the only liverwort representative that partially fossilized there.

Figure 75. ***Leucobryum glaucum***; ***Leucobryum*** is sometimes a habitat for ***Kurzia pauciflora*** in mires. Photo by Amadej Trnkoczy, through Creative Commons.

Figure 76. ***Mylia anomala***, a species that often grows with ***Kurzia pauciflora***. Photo by Blanka Aguero, with permission.

Figure 77. ***Odontoschisma fluitans***, a species that often grows with ***Kurzia pauciflora***. Photo by David T. Holyoak, with permission.

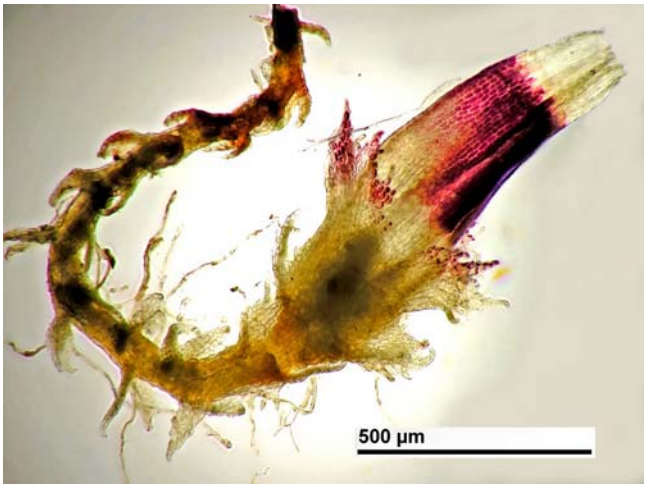

Figure 78. ***Cephaloziella spinigera*** female shoot, a species that often grows with ***Kurzia pauciflora***. Photo by David Wagner, with permission.

Figure 79. ***Herbertus aduncus***, a species that often grows with ***Kurzia pauciflora*** on bare peat of heaths, wetlands, and on wet cliffs and stones. Photo by Botany Website, UBC, with permission.

In the Atlantic blanket bogs in the maritime regions of North-western Europe, water table and *p*H were major determinants of the bryophyte flora, whereas ammonia was important in determining the tracheophyte flora (Sottocornola *et al*. 2009). ***Kurzia pauciflora*** (Figure 74), along with ***Mylia anomala*** (Figure 76) were the most common species in the sampling, with ***K. pauciflora*** along with species of ***Cephalozia*** (Figure 80) exhibiting optimal conditions at a lower *p*H than that of other bryophytes.

Figure 80. ***Cephalozia bicuspidata***; some species of ***Cephalozia*** share habitats at optimal conditions of low *p*H with ***Kurzia pauciflora***. Photo by Hugues Tinguy, with permission.

On the other hand, van Baaren *et al*. (1988) found it to be characteristic of mesotrophic fens in the Netherlands, typically as a dominant species.

But Redfearn (19622) also found it in association with the moss ***Tetraphis pellucida*** (Figure 81) on moist, shaded, vertical dolomite of east-facing bluffs in Douglas County, Missouri, USA.

Figure 81. ***Tetraphis pellucida***, a moss species associated with ***Kurzia pauciflora*** on moist, shaded, vertical dolomite bluffs. Photo by Hermann Schachner, through Creative Commons.

Albinsson (1997) determined that ***Kurzia pauciflora*** (Figure 74) belongs to a group of liverworts with a relatively wide ecological amplitude. One secret to its success in habitats with other bryophytes might be its extensive system of underground axes (Hugonnot *et al*. 2015). These exhibit profuse branching and can reach a maximum depth of 10 cm. They permit the colonization of successive layers of substrate, contributing to the success of the species. They do best on dead rather than live ***Sphagnum*** (Figure 5) and therefore benefit from disturbance.

Van Diggelen *et al*. (2015) report ***Kurzia pauciflora*** (Figure 74) as a red-listed species that often achieves as high a cover value as ***Sphagnum*** (Figure 5) species in restoration sites for acidified and eutrophied fens, most likely due to its regeneration from dead peat layers.

Reproduction

Kurzia pauciflora is **dioicous** (Earth.com 2021), but it seems to have other mechanisms for regeneration and asexual reproduction. Duckett and Clymo (1988) found that ***Kurzia pauciflora*** (Figure 74) and other species with well-developed underground axes regenerate poorly at the surface, but that their regeneration is much more successful down to 12 cm or so below the surface; they can still be found at 24-30 cm depth. Their presence in these lower layers occurs in both bogs with a live ***Sphagnum***-covered surface (Figure 5) and from a much older cut peat surface recently recolonized by liverworts. These results support the contention that regeneration is mainly from the underground axes rather than from spores or gemmae. The underground biomass of these species is typically large.

Interactions

All the axes of ***Kurzia pauciflora*** (Figure 74) have fungal associates, and it is possible that the fungi are partially saprophytic or parasitic (Duckett & Clymo 1988). Liepiņa (2012) reported that fungal infection causes swollen rhizoids in this species.

Wang and Qiu (2006) noted reports of mycorrhizal relationships with ***Kurzia pauciflora*** (Figure 74). But earlier, Duckett *et al*. (1991) considered that the rhizoid-Ascomycete associations and flagelliform branches seen in ***Kurzia pauciflora*** represent secondary parasitic infections rather than a mutualistic relationship. They further argued that the nitrogen fixation observed in these liverworts was due to **Cyanobacteria** (Figure 82) on the surface of the plants.

Figure 82. ***Microcoleus*** (**Cyanobacteria**), a nitrogen-fixing periphyton organism such as those you might find on ***Kurzia pauciflora***. Photo by Yuuji Tsukii, with permission.

Kowalczyk *et al*. (1997) used ***Kurzia pauciflora*** (Figure 74), among nine others, to demonstrate sterilization techniques. Using commercial bleach (Ace) diluted with distilled water at 1:1 and 1:3 ratios of bleach to water. The optimal sterilization time was 0.5-2.0 minutes. They determined that the fragments to be sterilized should not be larger than 3x3 mm, taken from the terminal portions of the thallus or leafless shoots of the leafy gametophytes. Greater success is achieved with healthy plants that are turgid.

Pressel *et al*. (2008) found that when ***Kurzia pauciflora*** (Figure 74) is infected with the Ascomycete fungus ***Rhizoscyphus ericae*** (Figure 83), the fungus forms a mutualistic association with the rhizoids. This fungus induces branching and septation in the rhizoids in this and a variety of liverworts. This fungus is also associated with members of the **Ericaceae** (heath family), permitting both host groups to provide inoculum for the other (Duckett & Read 1995).

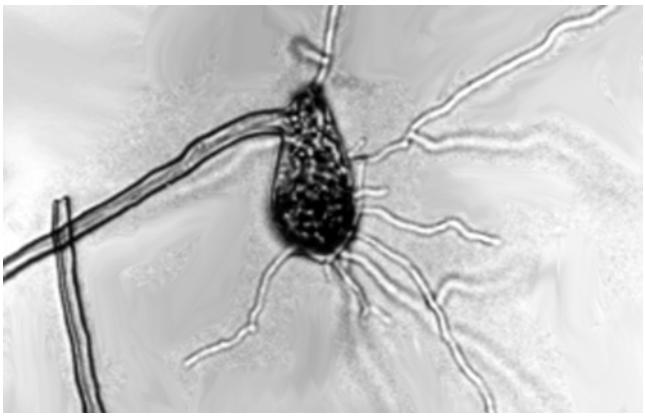

Figure 83. ***Kurzia pauciflora*** swollen rhizoid tips with fungal hyphae. Photo modified from Duckett & Read 1995.

In a study of 43 bryophyte species, 21 mosses lacked arbuscular mycorrhizal fungi and these were present in only 4 of 21 liverworts, all epigeous species (Liepiņa 2012). Liepiņa considered these fungi to be symbiotic.

Kurzia trichoclados (Figure 85)

(syn. = *Lepidozia trichoclados*)

Distribution

Kurzia trichoclados (Figure 85) is known from Europe, North America, and Southeast Asia, with a recent report from India (Rawat *et al*. 2016). Unfortunately, as is often the case, many collections have been misidentified as ***K. pauciflora*** (Figure 74) in Belgium (Stieperaere & Schumacker 1986). Despite this rather widespread distribution, the species is red-listed as vulnerable for the Iberian Peninsula (Sergio *et al*. 2007) and as endangered in Poland (Klama & Górski 2018). Nevertheless, Gradstein and Váňa (1987) remind us that this is a very small liverwort that is easily overlooked.

Figure 84. ***Kurzia trichoclados*** forming mats such as those one might find in heaths and bogs. Photo by David T. Holyoak, with permission.

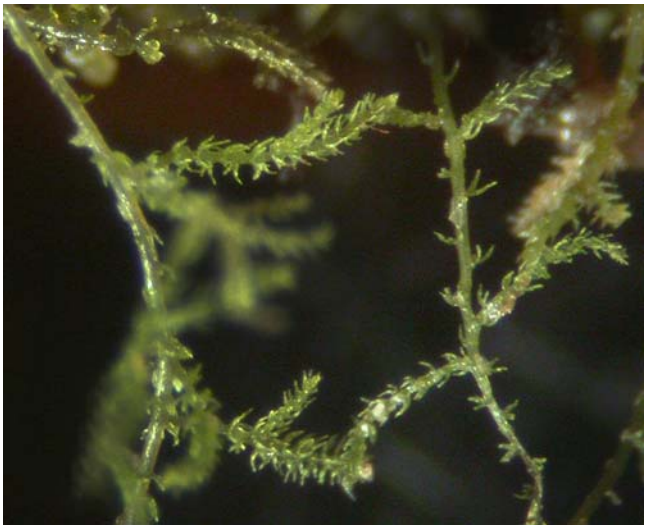

Figure 85. ***Kurzia trichoclados***, a tiny Northern Hemisphere liverwort. Photo by Tomas Hallingbäck, with permission.

Aquatic and Wet Habitats

There seems to be little information on this species, in part due to misidentifications. Watson (1919) reported it as occasionally submerged, but I found no more recent record of its aquatic affinities. On the other hand, it is common in peatlands. In the mid-west coast of Britain, within the Oceanic Temperate Region, ***Kurzia trichoclados*** (Figure 84) is exclusively found on upland heaths and bogs (Callaghan & Ashton 2008).

But it appears that habitats need not even be wet. Porley (2001) reported the species as frequent on the sandstone scarps of the Lough Navar Forest region, Co Fermanagh, in the UK.

Adaptations

Kurzia triclados varies in coloration from pale yellow and translucent to brown and slightly opaque (Paton 1986, 1993). These may be responses to differences in light intensity.

Reproduction

Paton (1986, 1993) reported that populations in Great Britain and Ireland are known to have bulbils. These appear on older stems. They are positioned by a short stalk in the axil of an underleaf on leafy stems or of rudimentary leaves on flagella or terminally on long, slender flagella. They readily break away from the stem. They are wider than long and possess three regular vertical rows of diminutive leaves with protuberant basal cells. Although their obvious function would seem to be as propagules, this function has not been observed. These bulbils occur more frequently in deep turfs than in shallow ones, suggesting that they might be developed in response to burial. Like ***Kurzia pauciflora*** (Figure 74), this species has subterranean axes and swollen rhizoids that most likely contribute to its success in peatlands, particularly since it rarely produces gemmae or capsules (Pocock & Duckett 1985).

Fungal Interactions

With so few studies, it is not surprising that Wang and Qiu (2006) found no records of mycorrhizae on this species. On the other hand, Duckett and Read (1995) considered it to typically contain rhizoidal Ascomycetes. Furthermore, Pocock and Duckett (1985) reported fungi in association with the subterranean axes. Von Reuß *et al*. (2004; Adio *et al*. 2007) identified a number of sesquiterpene constituents from ***Kurzia pauciflora*** (Figure 74), perhaps playing a role in limiting the number of fungi that can invade this liverwort.

Lepidozia reptans (Figure 86-Figure 88)

Distribution

Lepidozia reptans (Figure 86-Figure 88) is a relatively cosmopolitan species, occurring in Africa, the Caribbean, Europe, Northern and Southern Asia, North America, Central America, and South America (ITIS 2020).

Figure 86. ***Lepidozia reptans***, cosmopolitan species, often occupying river banks. Photo by Hermann Schachner, through Creative Commons.

Figure 87. ***Lepidozia reptans*** rhizoids showing branched tips. Photo from Botany website, UBC, with permission.

Aquatic and Wet Habitats

Lepidozia reptans (Figure 88) occurs on earthy and gravelly substrates of river banks in Haute Ardenne rivers, Belgium (Leclercq 1977); cracks in the flume at Franconia Notch, New Hampshire, USA (Glime 1982); and middle reaches in the Harz Mountains of Germany (Bley 1987), qualifying it as wetland or aquatic. Cain and Fulford (1948) found it was widely distributed and common on wet rocks, logs, and humus in Ontario, Canada. It was usually mixed with other bryophytes and was especially common in bogs and swamps. Arzeni (1948) found that ***Blepharostoma trichophyllum*** (Figure 2-Figure 3) was intertangled with ***Lepidozia reptans*** on rotten logs in Reese's Bog, Michigan, USA.

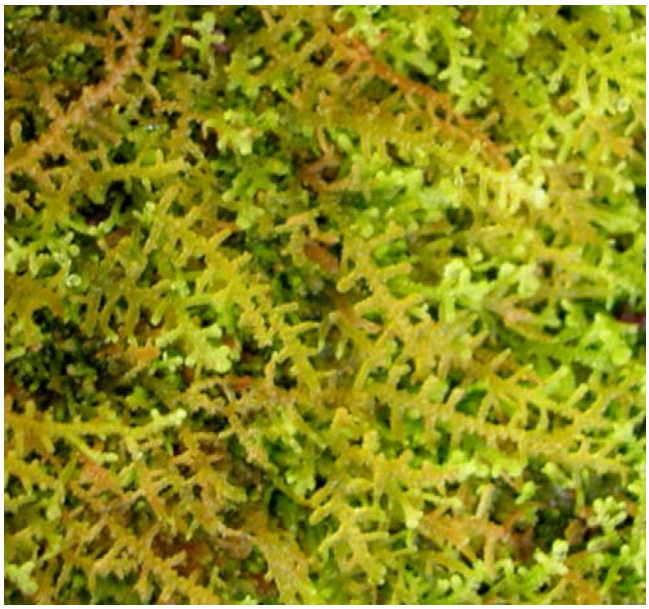

Figure 88. ***Lepidozia reptans*** forming mats as one might find on logs or stream banks. Photo from Botany Website, UBC, with permission.

Söderström (1989 noted that ***Lepidozia reptans*** (Figure 86-Figure 88) in Sweden is typically epixylic and does not occur on logs that have much remaining bark. Brūmelis *et al*. (2017) likewise emphasized the importance of **decortication** (loss of bark) for this species to occur on logs in ***Picea abies*** (Figure 89) forests in Latvia, attributing ***Lepidozia reptans*** (Figure 88) to mid stages in decay, after the bark was gone but before epigeous species became dominant. It occurs especially near water in shady sites on decaying wood and moist soil, often with ***Tetraphis pellucida*** (Figure 81) and species of ***Calypogeia*** (Figure 10, Figure 71, Figure 72) (Botany Website 2020).

Adaptations

Lepidozia reptans occurs in dull, gray-green **mats**, with its branches forming close to right angles (Crum 1991). It sometimes forms flagelliform tips on the branches, but lacks the ventral stolons seen in ***Bazzania***.

Bączkiewicz (2013) found a low genotypic diversity within populations of ***Lepidozia reptans*** (Figure 86-Figure 88, Figure 90) from three regions in Poland, whereas the number of rare alleles in any species in the study was among the greatest in this species.

Figure 89. ***Picea abies*** forest in Sweden, similar to the ones in Latvia where ***Lepidozia reptans*** occurs on mid-decay logs. Photo by Enfore, through Creative Commons.

Figure 90. ***Lepidozia reptans*** demonstrating color variation compared to that in Figure 88; this could be environmentally induced or genetic. Photo from Botany Website, UBC, with permission.

Russell (2010) found an inhibition zone of 1.0 mm from ethanolic extracts of ***Lepidozia reptans*** (Figure 86-Figure 88), but there was no antibiotic activity against Gram-negative ***Escherichia coli*** (Figure 91) or ***Klebsiella pneumoniae*** (Figure 92).

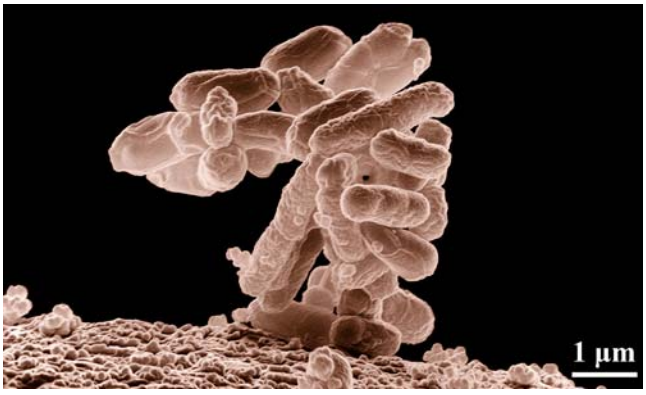

Figure 91. ***Escherichia coli***, a species that experiences no antibiotic activity by ***Lepidozia reptans***. Photo by Eric Eribe, through public domain.

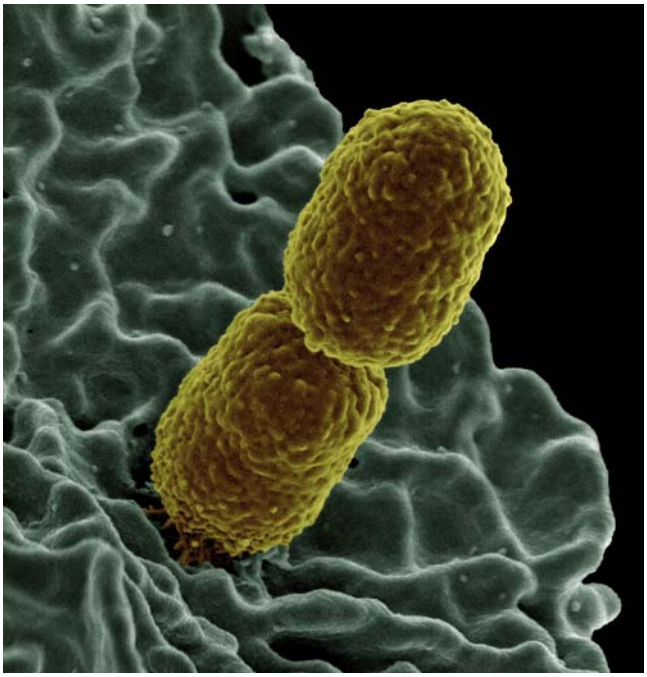

Figure 92. ***Klebsiella pneumoniae***, a species that experiences no antibiotic activity by ***Lepidozia reptans***. Photo by IAID, through Creative Commons.

In ravine habitats, it can provide substrate for slime molds (Ing 1983). The nature of this relationship needs to be explored – is it mutualism, competition, or just a preference for the same habitat?

Reproduction

Lepidozia reptans (Figure 86-Figure 88, Figure 90) is **autoicous**, making it easier to achieve sexual reproduction (Crum 1991). On the other hand, its lack of ventral stolons denies it of that reproductive advantage as seen in ***Bazzania***.

Biochemistry

Several biochemical studies have included this species. Connolly *et al*. (1986) described the structure of a sesquiterpene diol from ***Lepidozia reptans*** (Figure 86-Figure 88, Figure 90). Rieck *et al*. (1997) determined the structure of another new sesquiterpene alcohol. Zhang *et al*. (2010) identified lignans and described a new cadinane sesquiterpenoid lactone from this species. Li *et al*. (2018) identified five new terpenoids and nine known ones from Chinese populations of ***Lepidozia reptans***, screening them for anti-inflammatory compounds. Suleiman *et al*. (1980) identified volemitol and sedoheptulose as photosynthetic products.

Lepidozia trichodes

Distribution

Lepidozia trichodes has been known for a long time from Java and Bolivia (Stapf 1894-1896). Chuah-Petiot (2011) reported it from Malaysia. Gao and Bai (2002) considered it to be endemic to China and Taiwan, but in fact it is now known from a number of islands north of Australia (DiscoverLife (2020). Even before Gao and Bai considered it to be endemic, it was reported from the Philippines (del Rosario 1967). Pócs and Ninh (2005) subsequently reported it from Vietnam, Lai *et al*. (2008) from Thailand, and Aryanti and Gradstein (2007; Ariyanti *et al*. 2009) from Sulawesi, Indonesia. Siregar *et al*. (2018) added distributio in Papua New Guinea, Japan, and India.

Aquatic and Wet Habitats

Ruttner (1955) reported ***Lepidozia trichodes*** from acidic thermal spray in the tropics. Kitayama (1995) likewise reported it from the tropics, occurring in the cloud forest of Mount Kinabalu, Sabah, Malaysia, in dense "moss balls" with other leafy liverworts. Piippo (1984) found it in both the rainforests and cloud forests of the Huon Peninsula, Papua New Guinea. It occurs on moist bark, and although these are not aquatic habitats, they have long moist periods. Pócs and Ninh (2005) found it (rarely) on streambed rocks in Vietnam. Logatec *et al*. (2019) found it along the trail to a mossy forest (almost always humid) in the Philippines.

Adaptations

In ***Lepidozia trichodes*** of the montane rainforest of Peninsular Malaya, the rhizoids are almost exclusive to the flagella (Pocock *et al*. 1984). Most of them exhibit terminal ramifications, a response to contact with the substratum.

Fungal Interactions

Lepidozia trichodes swollen tips, also on the flagellar axes, contain abundant fungal hyphae (Pocock *et al*. 1984).

Zoopsis argentea (Figure 93)

Distribution

Zoopsis argentea (Figure 93) has a relatively small distribution, occurring in Australia and southern Asia (ITIS 2020).

Aquatic and Wet Habitats

Only Ruttner (1955) seems to attribute it to a somewhat aquatic existence, describing it from acidic thermal spray in the tropics. Rather, it is typically a species of older logs, 33-67 years (Turner & Pharo 2005). In Tasmania, it occurs on the lowest levels of the buttress of ***Eucalyptus obliqua*** (Figure 94) (Kantvilas & Jarman 2004).

Figure 93. ***Zoopsis argentea***, a species of Australia and southern Asia. Photo by Peter de Lange, through Creative Commons.

Figure 94. ***Eucalyptus obliqua***, showing bases where one might find ***Zoopsis argentea***. Photo by Forest and Kim Starr, with limited online permission.

Adaptations

In ***Zoopsis argentea*** (Figure 93), the stem has totally taken over the photosynthetic role of the plant (Thiers 1988), forming deep green mats (Allison 1985). The stem is flattened and the leaves reduced (Figure 95), possibly an adaptation to its tropical habitats.

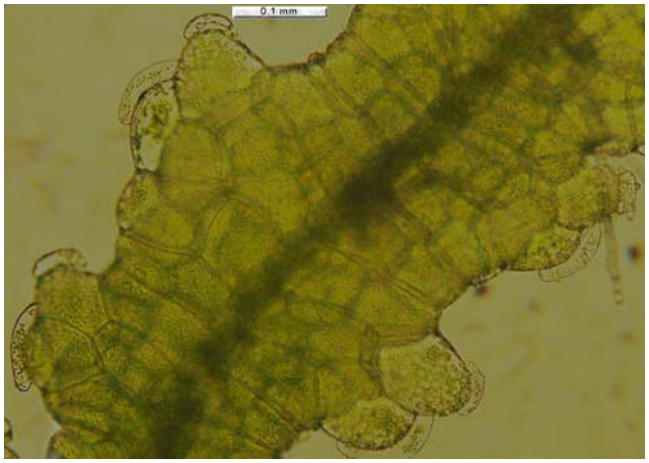

Figure 95. ***Zoopsis argentea*** showing the photosynthetic stem and reduced, flattened leaves. Photo by Tom Thekathyil, with permission.

Lophocoleaceae

Chiloscyphus (Figure 96-Figure 98, Figure 106-Figure 108)

Chiloscyphus (Figure 96-Figure 98, Figure 106-Figure 108) is a genus that in central France occurs in streams where it is embedded in basaltic rocks with elevated levels of Cu, Zn, Sr, V, Ba, Ni, and Co (Samecka-Cymerman & Kempers 1999). Aquatic varieties are almost black, whereas the typical variety ranges from deep yellow to pale green (Figure 104) to brownish green (Figure 96) (Salachna 2007). Submerged plants often lack rhizoids. It seems that common garden studies in a variety of habitat conditions would be helpful in understanding this genus.

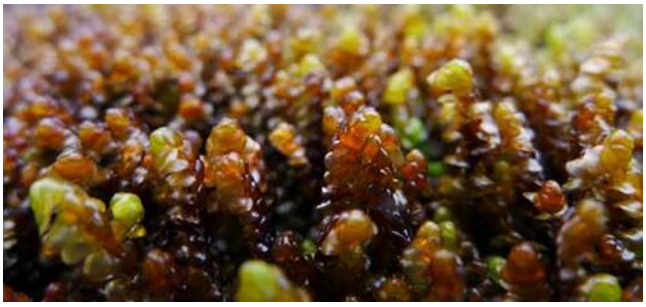

Figure 96. ***Chiloscyphus polyanthos*** brownish form. Photo by A. Neuman, through Creative Commons.

The species are autoicous or dioicous. Sporophytes (Figure 104) are produced in late winter and spring and can be abundant.

Chiloscyphus pallescens (Figure 97)

Järvinen (1983) considered ***Chiloscyphus*** to have three taxa in Europe. While she separated variety ***fragilis*** and variety ***rivularis*** from typical ***Chiloscyphus polyanthos*** (Figure 106-Figure 107), she considered ***Chiloscyphus pallescens*** (Figure 97) to be conspecific with ***Chiloscyphus polyanthos***. Nevertheless, in 2016 Söderström *et al*. considered these two to be separate species and placed variety ***fragilis*** in ***C. pallescens***. Factors related to the environment cause leaf variation that could account for the differences in interpretation.

Figure 97. ***Chiloscyphus pallescens***, a widespread species that is mostly aquatic, but also occurs above water. Photo by Hermann Schachner, through Creative Commons.

Distribution

Chiloscyphus pallescens (Figure 97) is a species in North America from Alaska to Mexico, Europe, Asia, and Africa (ITIS 2020).

Aquatic and Wet Habitats

In the Tatra National Park of Poland, ***Chiloscyphus polyanthos*** (Figure 106-Figure 108) grows mainly on rocks and stones in the stream bed and the lowest terrace of stream banks, whereas ***C. pallescens*** (Figure 97) prefers mires and springs where it most often occurs on the wet soil (Figure 98) and stones (Klama *et al*. 2008). There it prefers temperatures of 3.6-8.5ºC (5.12±1.56), *p*H 7.06. It is more common on north and northeastern slopes, often accompanied by ***Scapania undulata*** (Figure 99), ***Brachythecium rivulare*** (Figure 100), and ***Rhizomnium magnifolium*** (Figure 101).

Figure 98. ***Chiloscyphus pallescens***, forming a mat on a stream bank. Photo by Michael Lüth, with permission.

Figure 99. ***Scapania undulata***, a frequent associate of ***Chiloscyphus pallescens***. Photo by Janice Glime.

Figure 100. ***Brachythecium rivulare***, a frequent associate of ***Chiloscyphus pallescens***. Photo by David T. Holyoak, with permission.

Figure 101. ***Rhizomnium magnifolium***, a frequent associate of ***Chiloscyphus pallescens***. Photo by Hermann Schachner, through Creative Commons.

Elsewhere, ***Chiloscyphus pallescens*** (Figure 97) typically inhabits neutro-alkaline lakes, peat pits, ditches at *p*H 5.8-8.4, springs at *p*H ~7.1, calm water with low depth, streaming water at *p*H 7.2, weakly acid peat pits, lakes, ditches at *p*H 5.3-8.6 in Denmark (Sørensen 1948). It occurs in intermittent rivers (Dhien 1978), in the ***Platyhypnidium-Fontinalis antipyretica*** association (Figure 102, Figure 103) in Thuringia, Germany (Marstaller 1987), and in small lakes in southern Finland (Koponen *et al*. 1995; Toivonen & Huttunen 1995). It occurs in the Alsatian Rhine Valley streams (Vanderpoorten & Palm 1998) where it has oligotrophic status (Vanderpoorten & Palm 1998; Vanderpoorten *et al*. 1999), in streams in Polish and Czech Sudety Mountains (Samecka-Cymerman & Kempers 1998b), but is also characteristic in near-water or water environments of oligotrophic waters of the Iskur River, Bulgaria, where it is among the dominant bryophytes, and in its main tributaries (Papp *et al.* 2006a) and other Bulgarian rivers (Gecheva *et*

al. 2010, 2013a, b). In Montenegro, it occurs at the river in the Tara River Canyon and Durmitor area (Papp & Erzberger 2011).

Figure 102. ***Platyhypnidium riparioides***, a species common in the same streams as ***Chiloscyphus pallescens***. Photo by David T. Holyoak, with permission.

Figure 103. ***Fontinalis antipyretica***, a species common in the same stream as ***Chiloscyphus pallescens***. Photo by Hermann Schachner, through Creative Commons.

But this species can also occur above water in wet places. Madžule and Brūmelis (2008) found them growing epiphytically in Euro-Siberian alder swamps of Latvia. It also occurs there on mid-decay logs. And it occurs in Estonian transitional mires (Ingerpuu *et al*. 2014) and willow swamps and spring-fed areas of northern Sweden (Sjörs & Een 2000).

However, in the Hungarian beech forests, Ódor and van Hees (2004) found it to be restricted to well-decayed logs. In New York, USA, Burnham (1929) found it on old logs that extended into the water of Three Ponds.

The ***Chiloscyphus pallescens*** (Figure 97), along with ***Platyhypnidium riparioides*** (Figure 102) and ***Fontinalis antipyretica*** (Figure 103) remained unchanged in two years of study in the Ipel' River, a typical submontane river with regular winter/spring floods and with occasional summer floods, while tracheophyte cover fluctuated (Hrivnák *et al*. 2008). These bryophytes were not damaged by the summer flood, whereas the less-well attached tracheophytes were.

In the Alsacian Rhine River, France, ***Chiloscyphus pallescens*** (Figure 97) exhibited a very broad trophic range but occurred more often in eutrophic streams (Vanderpoorten *et al*. 1999). This was displayed in its relationship to ammonia vs. nitrate nitrogen and to phosphates. In the Laelatu wooded meadow in Estonia, ***Chiloscyphus pallescens*** was absent in control plots, but present in some fertilized plots (3.5 g m^{-2} N, 2.6 g m^{-2} P, and 5 g m^{-2} K annually) (Ingerpuu *et al.* 1998). In Polish and Czech Sudety Mountains, ***Chiloscyphus pallescens*** collects Au (gold) from the stream water (Samecka-Cymerman & Kempers 1998a). It also exhibited significantly more nickel, chromium, and barium, and significantly less zinc and mercury as compared to bryophyte samples from selected areas in the Swiss Alps (Samecka-Cymerman & Kempers 1998b).

Reproduction

Chiloscyphus pallescens (Figure 97) is **monoicous** (Crum 1991). It is among the few species in which the young spermatids are described in detail (Rushing *et al*. 1984). This study suggests that the Jungermannialian spermatids exhibit numerous variations and novel features. In Figure 104, one can see that many sperm are successful at fertilizing the eggs, and sporophytes can be abundant.

Figure 104. ***Chiloscyphus pallescens*** with capsules. Photo by Wayne Lampa, through Creative Commons.

Role

There are indications that the Great Crested Newt (***Triturus cristatus***, Figure 105) can serve as a dispersal agent for ***Chiloscyphus pallescens*** (Figure 97). Gustafson *et al*. (2006) found that when ponds with and without the newt were compared, those with the newt exhibited the largest populations of ***Chiloscyphus pallescens*** (Figure 97). On the other hand, the newt may simply be an indicator of the more suitable conditions that favor the liverwort.

Figure 105. ***Triturus cristatus***, a likely dispersal agent of ***Chiloscyphus pallescens***. Photo by Rainer Theuer, through public domain.

Biochemistry

With its widespread distribution, it is not surprising that studies have examined its biochemistry. Connolly *et al*. (1982) elucidated the structure of chiloscypholone, a sesquiterpenoid from this species.

Chiloscyphus pallescens var. *fragilis*

(syn. = *Chiloscyphus polyanthus* var. *fragilis*)

Distribution

Although there seem to be clear records for the variety ***Chiloscyphus pallescens* var. *fragilis*** in North America and Europe, more precise distributional information is difficult because of the taxonomic confusion of the variety. Several records place the variety in North America: in the Ozarks of Arkansas, USA (Redfearn 1979), in the Lake George region, New York, USA (Burnham 1929), and in Wyoming (Hong 1977).

Aquatic and Wet Habitats

Watson (1919), based on European experience, described the habitat as often on rocks just above fast streams, on banks with frequent submergence and slow water, sometimes completely submerged in fast streams. In North America, Redfearn (1979) found ***Chiloscyphus pallescens*** var. ***fragilis*** on rocks of a spring branch. Hong (1977) likewise reported it from submerged rocks. Burnham (1929), on the other hand, found it in a dried up streambed on rocks. Bakalin (2005) reported it from stream banks in rhododendron, sedge, and moss tundra and in shady crevices near streams on Bering Island in the northwest Pacific.

Chiloscyphus polyanthos (Figure 106-Figure 107)

Chiloscyphus polyanthos (Figure 106-Figure 107) has been considered by some to be conspecific with ***Chiloscyphus pallescens*** (Figure 97) (Järvinen 1983). Since researchers have not reached a consensus, I will report the information separately rather than try to judge the decisions of the individual researchers, but this has the caveat that some may not have been interpreted as I am listing them.

Figure 106. ***Chiloscyphus polyanthos***, a species widespread in the Northern Hemisphere, exhibiting the darkened color of aquatic forms. Photo by Barry Stewart, with permission.

Figure 107. ***Chiloscyphus polyanthos*** rhizoids. Photo by Paul Davison, with permission.

Distribution

Chiloscyphus polyanthos (Figure 106-Figure 107) is known from Europe, Asia, Africa, and North America (Damsholt 2002; ITIS 2020).

Aquatic and Wet Habitats

Watson (1919) described this species as one usually found on the margins of fast streams (Figure 1) or on wet ground associated with fast water, but it also occurs in rivers (Ferreira *et al*. 2008). It is typically oligotrophic (Tremp 2003).

The European ***Chiloscyphus polyanthos*** (Figure 108) is hygrophytic, growing mostly on soil or silt-covered rocks, tree roots, and more rarely on rotting wood along small streams and rivers (Salachna 2007). The variety ***polyanthos*** is more likely to be terrestrial, with the variety ***rivularis*** being submerged in running water. The species often is associated with ***Pellia epiphylla*** (Figure 109), ***P. neesiana*** (Figure 110), ***Marsupella emarginata*** (Figure 111), and ***Scapania undulata*** (Figure 112) (Damsholt 2002).

Figure 108. ***Chiloscyphus polyanthos*** var. ***polyanthos***. Photo by David T. Holyoak, with permission.

Figure 109. ***Pellia epiphylla***, a species commonly associated with ***Chiloscyphus polyanthos***. Photo by Jan-Peter Frahm, with permission.

Figure 110. ***Pellia neesiana***, a species commonly associated with ***Chiloscyphus polyanthos***. Photo by Michael Lüth, with permission.

In the Tatra National Park of Poland, Klama *et al*. (2008) reported that ***Chiloscyphus polyanthos*** (Figure 106-Figure 107) occurs mainly on rocks and stones of the streambed and close to the water on the streambanks (Figure 113). Nevertheless, it prefers mires and springs where it can occupy wet soil and stones (Figure 114). This species is among the commonest species in English and Welsh rivers (Scarlett & O'Hare 2006). It is occasionally abundant on wet shores and in pools in Scotland (West 1910). It is among the most common bryophytes in the River Tweed, UK (Holmes & Whitton 1975), is known from a river bank of the River Tees, UK (Holmes & Whitton 1977a), occurs upstream in the River Swale, Yorkshire, UK (Holmes & Whitton 1977b), but is mostly in the mid to lower River Tyne, UK, occurring above and below water (Holmes & Whitton 1981), and in northern England it occurs in both streams and rivers (Wehr 1983).

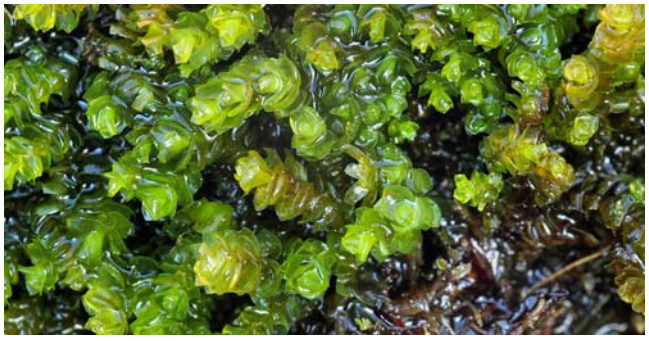

Figure 111. ***Marsupella emarginata***, a species commonly associated with ***Chiloscyphus polyanthos***. Photo by Barry Stewart, with permission.

Figure 112. ***Scapania undulata***, a species commonly associated with ***Chiloscyphus polyanthos***. Photo by Hermann Schachner, through Creative Commons.

Figure 113. ***Chiloscyphus polyanthos*** on rocks above and below the water of a stream. Photo from <www.aphotofauna.com>, with permission.

Figure 114. ***Chiloscyphus polyanthos*** habitat with brown colonies in the water. Photo by A. Neumann through Creative Commons.

Chiloscyphus polyanthos (Figure 106-Figure 107) occupies alpine streams in the Swiss Alps (Geissler 1976) as well as occurring beside small snowmelt streams in the arctic-alpine zone on granodioritic rocks in southern Europe (Casas & Peñuelas 1985). In Germany it occurs midstream, in unpolluted, upper and middle parts of streams in eastern Odenwald and southern Spessart, Germany (Philippi 1987), in middle and downstream reaches in Harz Mountains of Germany (Bley 1987), in the ***Platyhypnidium-Fontinalis antipyretica*** association (Figure 102, Figure 103), Thuringia, Germany (Marstaller 1987). It is aquatic in Finland (Koponen *et al*. 1995; Heino

& Virtanen 2006) or facultative aquatic in Finnish streams (Virtanen 1995). It occurs in streams in Greece (Papp 1998) and in mountain streams of northwest Portugal (Vieira *et al.* 2005). It occurs in mountainous streams on Madeira Island (Luis *et al*. 2015). In the Iskur River and its main tributaries in Bulgaria, it is characteristic in the near-water or water environment (Papp *et al.* 2006a) and is typically a hygrophyte in Bulgarian rivers (Gecheva *et al*. 2010, 2013)

North American records are less numerous. In Minnesota, USA, it occurs on boulders in 15-45 cm water of rivers (Moyle 1937). By contrast, it grows on very small rocks on the streambed of Adirondack Mountain streams (Slack & Glime 1985). In West Virginia, USA, mountain streams its preferred *p*H is 6.6 (Stephenson *et al.* 1995).

Vanderpoorten and Klein (1999) considered ***Chiloscyphus polyanthos*** (Figure 106-Figure 107) to be acid-sensitive in waterfalls of the Black Forest and the Vosges, Germany. It is able to tolerate low cation concentrations if the concentrations of protons is also low, hence being sensitive to low *p*H. This creates a fragile physico-chemical balance with low buffering capacity. Thus, only slight changes can cause a rapid reaction by the bryophyte flora, including ***C. polyanthos***. Pollution from human activity can increase the input of hydrogen ions, causing the disappearance of the sensitive ***C. polyanthos***.

Sossy Alaoui and Rossilon (2013) found that ***Chiloscyphus polyanthos*** (Figure 106-Figure 107) characterizes acidic and low-impacted streams and rivers in Belgium, an inconsistent behavior when compared to some earlier studies. Gil and Ruiz (1985) reported that it is found in calcareous water. But like other aquatic species, it is likely that local physiological races exist, so differences in *p*H preferences may indicate such races.

Reproduction

Chiloscyphus polyanthos (Figure 106-Figure 107) is **monoicous** (Crum 1991). It most likely reproduces by fragments.

Biochemistry

Chiloscyphus polyanthos (Figure 106-Figure 107) has a pungent odor (Asakawa *et al*. 1979). This odor, often helping in its identification, is due to a mixture of four sesquiterpene lactones, ent-5β-hydroxydiplophyllin, ent-3-oxodiplophyllin, diplophyllin, and diplophyllolide. Diplophylloides cause an intense numbness of the tongue. All the pungent sesquiterpene lactones exhibit inhibitory activity against the germination and root elongation of rice husks. Toyota *et al*. (1999) extracted and described the configuration of an eudesmane-type sesquiterpenoid. Azzollini *et al*. 2016) used ***Chiloscyphus polyanthos*** to develop an isolation strategy for purifying antifungal compounds. In this study they isolated seven sesquiterpene lactones, five of which were bioactive and one was a new compound.

Another biochemical aspect of importance is the production of UV-absorbing compounds. Arróniz-Crespo *et al*. (2004) reported that in mountain streams these are produced by ***Chiloscyphus polyanthos*** (Figure 106-Figure 107) and serve to protect them from the stronger UV-B radiation at the high elevations. Sclerophylly had little influence in protecting the ten mosses and four liverworts in the study. Among these, ***Chiloscyphus polyanthos*** was the least sclerophyllous species of the 14 species studied.

***Chiloscyphus polyanthos* var. *rivularis* (Figure 115)**

(syn. = *Chiloscyphus rivularis*)

Distribution

Chiloscyphus polyanthos* var. *rivularis (Figure 115) is a variety distributed in North America (ITIS 2020), but it has also been reported from Germany (Koppe 1945), Poland (Szweykowski 1951), and Finland (Heino & Virtanen 2006). Järvinen (1983) likewise considered it to be the aquatic variety of the species in Europe. Schuster (1980) likewise considers it to be abundant in Europe as well as North America.

Figure 115. ***Chiloscyphus polyanthos*** var. ***rivularis*** on wet mud. Photo by Jean Faubert, with permission.

Aquatic and Wet Habitats

Whereas ***Chiloscyphus polyanthos*** var. ***polyanthos*** (Figure 106-Figure 107) is common at many elevations in Europe and North America, ***C. polyanthos*** var. ***rivularis*** (Figure 115) is primarily restricted to the mountainous areas (Järvinen 1983). It differs from the typical variety in always having small leaf cells. It is sometimes completely submerged in fast streams, or submerged in slow water with poor mineral salts (Watson 1919). Fitzgerald and Fitzgerald (1967) describe it from rock in a stream in Ireland. In Westfalens, northwestern Germany, it is a strong hygrophil (Koppe 1945). It is likewise a hydroamphibiont in streams of Gory Stolowe Mountains, Poland, where it prefers neutral and basic (*p*H 6.4-6.6) water (Szweykowski 1951). It also occurs in streams in northeastern Finland (Heino & Virtanen 2006). In Muddus National Park, North Sweden, it occurs upstream of waterfalls (Sjörs & Een 2000). In the Vologda Region of Russia it occupies a somewhat different habitat on banks and in rapids of a darkwater stream with sandy-rocky ground, where it is rare (Dulin *et al*. 2009).

In North America, ***Chiloscyphus polyanthos* var. *rivularis*** is hydrophytic in rock ravines in Connecticut, USA (Nichols 1916). Likewise, it occurs on submerged

rocks in Rocky Mountain National Park, Colorado, USA, where it is often accompanied by ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 116) and ***Scapania undulata*** var. ***undulata*** (Figure 112) in running water (Hong 1980). It is relatively frequent in Adirondack and Appalachian Mountain streams in northeastern USA, but in their study Slack and Glime (1985) never observed a cover of more than 5%.

Figure 116. ***Jungermannia exsertifolia*** subsp. ***cordifolia***, a frequent associate of ***Chiloscyphus polyanthos*** var. ***rivularis***. Photo by Dick Haaksma, with permission.

Role

Not only do these leafy liverworts contribute to the productivity of the streams they occupy, but in the mountain springfed stream in Adamello-Brenta Regional Park of Northern Italy, they serve as considerable substrate area that is colonized by diatom communities (Cantonati 2001).

Biochemistry

As is often the case, Wu *et al*. (1997) found five new bioactive and other sesquiterpenes in this variety. And Zhang *et al*. (2016) added another seven new ent-eudesmane-type sesquiterpenoids to these, all from Chinese populations. One of these had weak inhibitory activity against a cancer cell line.

Hepatostolonophora paucistipula (Figure 117)

(syn. = *Clasmatocolea paucistipula*)

Distribution

Hepatostolonophora paucistipula (Figure 117) occurs in New Zealand (Suren & Winterbourn 1991), Antipodes, and Tasmania (Engel 1980). It is a species of uncertain taxonomic placement.

Aquatic and Wet Habitats

Suren and Winterbourn (1991) found that ***Hepatostolonophora paucistipula*** (Figure 117) dominates the bryoflora at shaded sites in an open, headwater tributary of the Otira River and shaded tributary of Bealy River, New Zealand. It was present in some of the 48 streams studied on South Island, New Zealand (Suran & Duncan 1999). It is one of the two most common liverworts on South Island (Suren 1996).

Figure 117. ***Hepatostolonophora paucistipula*** in its aquatic habitat, a New Zealand species that is one of the most common liverworts on South Island. Photo from Landcare Research, through Creative Commons.

Role

Hepatostolonophora paucistipula is particularly common in chutes, where it provides expanded invertebrate habitat by providing a refuge of reduced flow (Suren 1991). The species is particularly important in providing oviposition sites where young larvae are protected from the harsh flow.

In these New Zealand streams, ***Hepatostolonophora paucistipula*** (Figure 117) is an important food source for some invertebrates. But its use pales in comparison to that of the mosses, comprising only 2% of the gut contents of larvae of the cranefly ***Limonia hudsoni*** (Figure 118) compared to 57% mosses (Suren & Winterbourn 1991). They attributed this to the low nutritional quality of ***Hepatostolonophora paucistipula***: 2.8% lipids, 3.9% carbohydrates, 23.7 energy (kj/g), 1.1% starch, 1.1% N, 6.9% protein, 34.7% holocellulose, 27.7% fiber, 7.4% ash. Among the bryophytes, it trapped the lowest total organic matter biomass and lowest LPOM, FPOM, and UFPOM (Suren 1993). One reason for the invertebrate biomass may be the abundant periphyton growing there.

Figure 118. ***Limonia*** sp.; larvae of ***Limonia hudsoni*** live among branches of ***Hepatostolonophora paucistipula***, but the liverwort contributes little to its diet. Photo by Stephen Moore, Landcare Research, NZ, with online permission.

Biochemistry

Other deterrents to feeding may include the secondary compounds present in the liverwort. Baek *et al*. (2003) reported sesquiterpene lactones. Ludwiczuk and Asakawa (2019) found bioactive volatile terpenoids that are active against leukemia cells. Kim *et al*. (2009a) found a sesquiterpene lactone that is active against the fungus ***Trichophyton mentagrophytes*** (Figure 119) and a number of other medical conditions. They also isolated another compound with cytotoxic activity (Kim *et al*. 2009b). found that it is a rich source of sesquiterpenes that are very effective against P388 murine leukemia cells (Oh *et al*. 2004). It seems likely that some of these protect the liverwort by discouraging herbivory, but this remains to be tested.

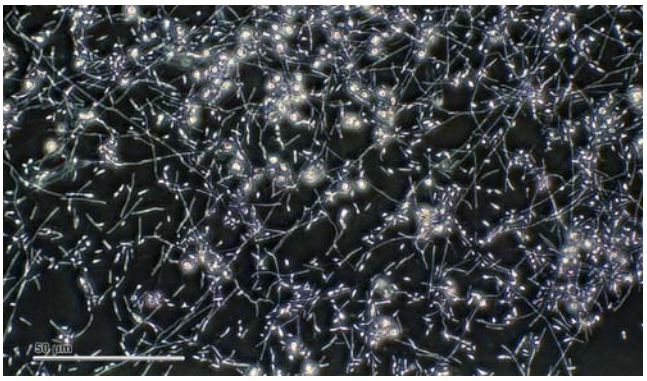

Figure 119. ***Trichophyton mentagrophytes*** in culture, a fungus that is inhibited by ***Hepatostolonophora paucistipula***. Photo by RNDr. Josef Reischig, CSc., through Creative Commons.

Heteroscyphus argutus (Figure 120-Figure 121)

(syn. = *Chiloscyphus argutus*)

Distribution

Heteroscyphus argutus (Figure 120-Figure 121) occurs in southern Asia and Australia (EOL 2020). Ruttner (1955) noted it from a tuff wall in the tropics. Satake (1983) reported it as aquatic from Kyushu, Japan. Srivastava and Srivastava (1989) found it in the western Himalayas, describing it as widespread in tropical Asia and south and central India. In 2011, Glenny *et al*. reported it from the Kermadec Islands (800-1,000 km northeast of New Zealand's North Island).

Figure 120. ***Heteroscyphus argutus***, a liverwort of southeastern Asia, Australia, and northern New Zealand. Photo by Lin Shanxiong, through Creative Commons.

Figure 121. ***Heteroscyphus argutus*** growing in moist, shady conditions, but starting to dry. Photo by Lin Shanxiong, through Creative Commons.

Aquatic and Wet Habitats

This is a species with a wide range of habitats, but mostly in moist, shady conditions on land (Alam *et al*. 2013). So and Zhu (1996) recorded it from Hong Kong, where it is locally common on moist soil and rock, typically associated with ***Calypogeia arguta*** (Figure 71), ***Pallavicinia subciliata*** (Figure 122), and ***Notoscyphus lutescens*** (Figure 123). Grolle and So (1999) also found ***Heteroscyphus argutus*** (Figure 121) mixed with ***Plagiochila*** species (Figure 18, Figure 70) on wet rocks in Hong Kong. In Guizhou, southern China, Bakalin *et al*. (2015) found it at 1200-1300 m asl on mesic to wet boulders, often near streams, as well as on decaying wood and tree trunk bases where there was partial shade. It occurred in both pure mats and in mixes with ***Syzygiella autumnalis*** (Figure 124), ***Lophocolea minor*** (Figure 161-Figure 162), ***Nowellia curvifolia*** (Figure 125), and other bryophytes. On Jeju (Cheju) Island, Korea, Song and Yamada (2006) found in on rocks in a stream. But on Luzon and Negros Islands in the Philippines, Hayashi and Yamada (2004) found it on branches, trunk, and roots of trees. In Sri Lanka, Samarakkody *et al*. (2018) found it mixed with ***Bazzania*** sp. (*e.g.* Figure 38) on a rock surface near a stream. In India Manjula *et al*. (2013) reported that it grows on bark, soil, and pure populations on soil-covered rocks or associated with other liverworts. It is widely distributed from low to high altitudes, although mostly low to medium altitudes. It furthermore occupies "all microhabitats" as pure populations or in association with bryophytes and ferns. But in their treatment of the genus, Srivastava and Srivastava (1989) treat it as a terrestrial species of soil, rock, or epiphytic in the tropics to warm temperate regions of the Eastern Hemisphere.

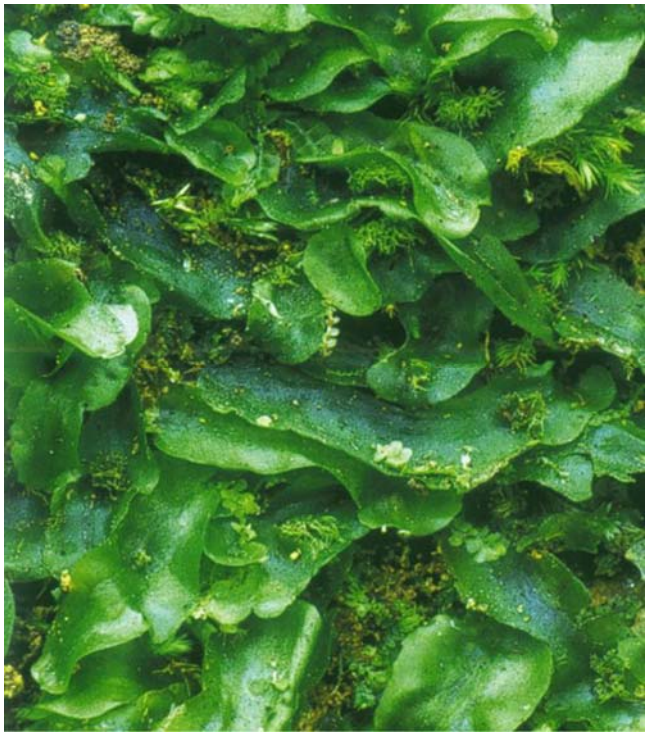

Figure 122. ***Pallavicinia subciliata***, a species often associated with ***Heteroscyphus argutus*** on wet soil and rock. Photo by Lin Shanxiong, through Creative Commons.

Reproduction

Heteroscyphus argutus (Figure 120-Figure 121) is dioicous, with short, lateral male branches (Srivastava & Srivastava 1989). Daniels (1998) observed the species in the Western Ghats and noted that its slime papillae helped it to absorb water quickly.

Figure 123. ***Notoscyphus lutescens***, a species often associated with ***Heteroscyphus argutus*** on wet soil and rock. Photo by David Tng, with permission.

Biochemistry

Chemical constituents in ***Heteroscyphus argutus*** (Figure 120-Figure 121) are effective in controlling wood rot in tea (Nepolean *et al*. 2014), but little work seems to have been done on the biochemistry of this species.

Figure 124. ***Syzygiella autumnalis***, a species often associated with ***Heteroscyphus argutus*** on wet soil and rock. Photo by Hugues Tinguy, with permission.

Figure 125. ***Nowellia curvifolia***, a species often associated with ***Heteroscyphus argutus*** on wet soil and rock. Photo by Botany Website, UBC, with permission.

Heteroscyphus coalitus (Figure 126-Figure 127)

(syn. = *Chiloscyphus coalitus*)

Distribution

Heteroscyphus coalitus (Figure 126-Figure 127) occurs in the Pacific – southwestern Asia, Australia, and Pacific islands (DiscoverLife.com 2020). Nair and Prajitha (2010) elaborated on these areas to include North-east India (Himalayas, Sikkim, Khasi Hills), Andaman Islands, Myanmar, Bhutan, China, Java, Sumatra, Borneo, Japan, New Guinea, Philippines, and Australia.

Figure 126. ***Heteroscyphus coalitus***, a species from southwestern Asia, Australia, and Pacific islands. Photo by David Tng, with permission.

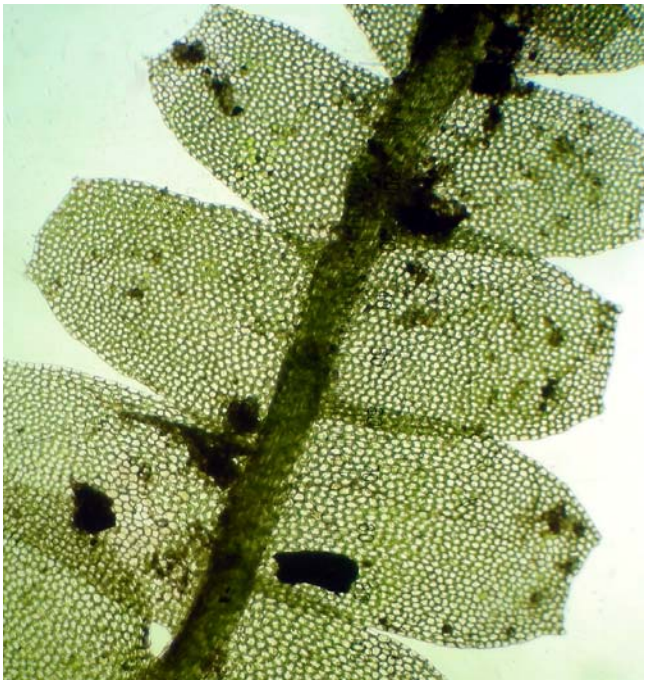

Figure 127. ***Heteroscyphus coalitus***, a moist habitat species from southwestern Asia, Australia, and Pacific islands. Photo by Kochibi, through Creative Commons.

Aquatic and Wet Habitats

Ruttner (1955) reported ***Heteroscyphus coalitus*** (Figure 128) at 10-20 cm above water level where it was kept moist by the acidic thermal spray. It is common in the cool and warm temperate regions of the Australian Rainforest streams (Carrigan 2008). Carrigan and Gibson (2004) described it as forming threadlike mats above waterlevel, downstream, upstream, and sides of rocks in a stream at Cement Creek Turntable, Victoria, Australia. Fleisch and Engel (2006) found it in Victorian rainforest streams that present a cool, strong current. Wilcox (2018) noted that in Craigavon Park, Auckland, New Zealand, where it inhabits the bases of old Monterey pine trees (***Pinus radiata***, Figure 129) and bases of old or dead silver fern trunks (***Cyathea dealbata***, Figure 130), its shaded colonies become especially conspicuous after rain.

Figure 128. ***Heteroscyphus coalitus***, a conspicuous species after rain. Photo by Yang Jia-Dong, through Creative Commons.

Figure 129. ***Pinus radiata***, a species where ***Heteroscyphus coalitus*** can grow on the tree bases. Photo by summitcheese, through Creative Commons.

Figure 130. ***Cyathea dealbata***, a species that can serve as substrate for ***Heteroscyphus coalitus*** on bases of old or dead fern trunks. Photo by Leon Perrie, through Creative Commons.

In Guizhou, China, ***Heteroscyphus coalitus*** (Figure 131) occurs at 1100-1300 m asl on moist to wet cliffs, boulders, and more rarely on decaying wood near streams and in waterfall spray zones, in partly shaded places (Bakalin *et al*. 2015).

Figure 131. ***Heteroscyphus coalitus*** with the fresh green seen after rain. Photo by Yang Jia-Dong, through Creative Commons.

Adaptations

Heteroscyphus coalitus (Figure 131) is present in pure **mats** or with ***Bazzania bidentula*** (Figure 132), ***Calypogeia angusta***, ***Calypogeia tosana*** (Figure 133), ***Isotachis indica/I. japonica*** (Figure 134), ***Kurzia gonyotricha***, ***Scapania undulata*** (Figure 112), and ***Schiffneria hyalina*** (Figure 135) (Bakalin *et al*. 2015). This growth habit uses the presence of other bryophytes to help maintain moisture.

Figure 132. ***Bazzania bidentula***, a species that occurs in mats with ***Heteroscyphus coalitus***. Photo by Lin Shanxiong, through Creative Commons.

Figure 133. ***Calypogeia tosana***, a species that occurs in mats with ***Heteroscyphus coalitus***. Photo from Hiroshima University Museum, with permission.

Figure 134. ***Isotachis japonica***, a species that occurs in mats with ***Heteroscyphus coalitus***. Photo by Jia-Dong Yang, with online permission.

Figure 135. ***Schiffneria hyalina***, a species that occurs in mats with ***Heteroscyphus coalitus***. Photo by Jia-Dong Yang, through Creative Commons.

Reproduction

In New Zealand, ***Heteroscyphus coalitus*** (Figure 128, Figure 131) us usually sterile and sporophytes are rare (Allison & Child 1975).

Biochemistry

Heteroscyphus coalitus (Figure 128, Figure 131) has been the subject of many biochemical studies. Zhu *et al*. (2006) determined that it was active against a number of bacteria. They further determined that there was no correlation between activity and size and number of oil bodies in the 38 liverworts tested. Toyota *et al*. (1996) identified two new diterpenoids and a new sesquiterpenoid from this species. Jong and Wu (2000) identified additional sesquiterpenoids and diterpenoids, with some being new compounds. Lin *et al*. (2012) reported a new dihydroisocoumarin derivative and three previously known terpenoid derivatives, demonstrating that they possessed moderate inhibitory activity against several human tumor cell lines. Wang *et al*. (2020) found 14 new terpenoids. They found that most of these were effective in blocking rhizoidal growth of the yeast ***Candida albicans*** (Figure 136). Among these, heteroscyphin D could suppress the

ability of ***C. albicans*** DSY654 to adhere to A549 cells and form biofilms and modulate the transcription of related genes in this yeast.

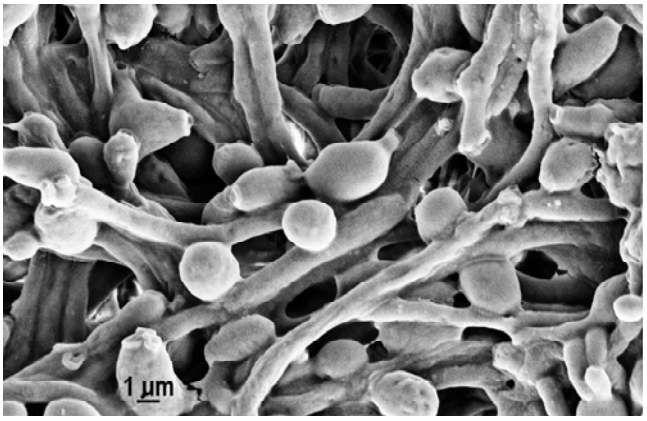

Figure 136. ***Candida albicans***; rhizoidal growth is blocked in this species by terpenoids from ***Heteroscyphus coalitus***. Photo from Vader 1941, through Wikipedia Creative Commons.

Heteroscyphus denticulatus (Figure 137-Figure 138)

Distribution

Heteroscyphus denticulatus (Figure 137-Figure 138) occurs in Spain and Tenerife (DiscoverLife.com 2020), and the Azores in Portugal (Gabriel & Bates 2005).

Figure 137. ***Heteroscyphus denticulatus***, a species known from Spain and nearby regions and South Africa. Photo by Pedro Cardoso, with permission through Azores Bioportal.

Aquatic and Wet Habitats

Heteroscyphus denticulatus (Figure 137-Figure 138) seems to be only marginally aquatic. Dirkse (1985) found the species on sheltered wet volcanic rocks in the laurel forest of the Canary Islands and Dirkse *et al*. (2018) found it on humid rocks in dark small ravine in Macaronesia. Luís *et al*. (2010) found it in riparian bryophyte communities on Madeira, a Portuguese island off the northwest coast of Africa. And in Cape Town, South Africa, Mitten (1877) found it on a stream bank. Sjögren (1997) found it to be epiphyllous in the Azores Islands, noting that it was among the few species to preferentially form associations in that habitat.

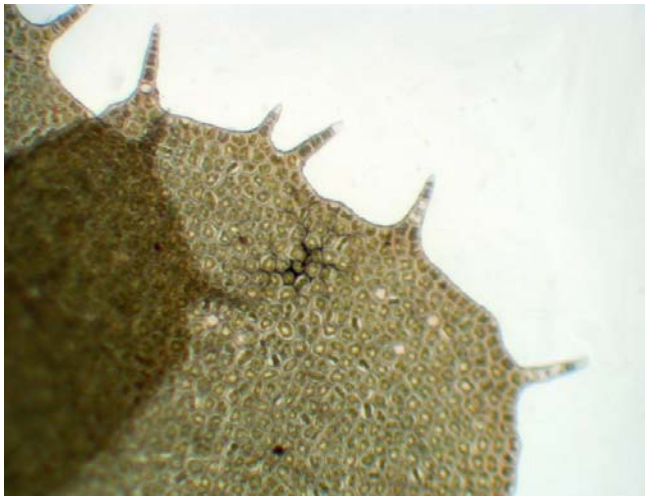

Figure 138. ***Heteroscyphus denticulatus*** leaf. Photo by Nidia Homen, with permission through Azores Bioportal.

Heteroscyphus planiusculus (Figure 139-Figure 140)

Distribution

Heteroscyphus planiusculus (Figure 139-Figure 140) is an Australian leafy liverwort, being dominant in the Australian Central Highlands (Carrigan 2008).

Figure 139. ***Heteroscyphus planiusculus***, an abundant liverwort in the Australian Central Highlands. Photo by Tom Thekathyil, with permission.

Aquatic and Wet Habitats

Little seems to be published about ***Heteroscyphus planiusculus*** (Figure 139-Figure 140), so I am unable to comment on the breadth of its habitats. In Cement Creek at Turntable, Victoria, Australia, it forms threadlike mats both above and below the water level (Carrigan & Gibson 2004). It had the greatest cover (17%) among the bryophytes. It occurred on all rocks, compared to most other species that occurred on only a few. And it was one of only four species occurring below the water level, but not restricted to it. It was the main species dominating the base of the rocks.

Adaptations

Heteroscyphus planiusculus (Figure 139-Figure 140) forms mats that permit it to live at the bases of rocks in a fast stream (Carrigan & Gibson 2004).

Biochemistry

Heteroscyphus planiusculus (Figure 139-Figure 140) has distinctive large oil bodies (Figure 140). Thus far, it does not seem to have any biochemical studies.

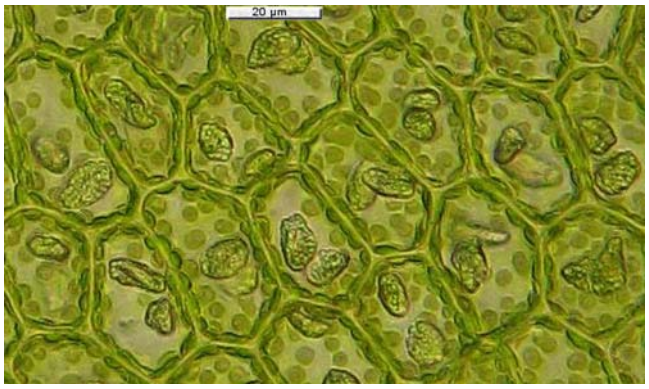

Figure 140. ***Heteroscyphus planiusculus*** leaf cells showing large oil bodies. Photo by Tom Thekathyil, with permission.

Heteroscyphus zollingeri (Figure 141)

(syn. = *Chiloscyphus zollingeri*)

Distribution

Heteroscyphus zollingeri (Figure 141) occurs mostly in the Pacific tropics.

Aquatic and Wet Habitats

There seems to be little information available on ***Heteroscyphus zollingeri*** (Figure 141). Ruttner (1955) reported ***Heteroscyphus zollingeri*** (Figure 141) from thermal acidic spray in the tropics. It is touted as a good aquarium plant, known as Pearl Moss (Aquascaper.org 2017). Although it is not usually an aquatic moss in nature, it is able to grow well as a submerged plant. It has no preference for hard or soft water, high or low light, or low or high CO_2. Its growth is faster than that of other bryophytes in the aquarium industry, sometimes being a desirable trait (and sometimes not!).

Figure 141. ***Heteroscyphus zollingeri*** from Guizhou, China. Photo courtesy of Li Zhang

Lophocolea (Figure 142-Figure 143, Figure 148-Figure 150, Figure 161-Figure 162, Figure 171-Figure 174)

Lophocolea (Figure 142-Figure 143, Figure 148-Figure 150, Figure 161-Figure 162, Figure 171-Figure 174) occurs in Himalayan streams (Suren & Ormerod 1998) and in central Southern Alps, Australia, in somewhat high rainfall area (Lepp 2012).

Lophocolea bidentata (Figure 142-Figure 143)

(syn. = *Lophocolea bidentata* fo. *latifolia*, *Lophocolea coadunata*, *Lophocolea cuspidata*)

Distribution

Lophocolea bidentata (Figure 142-Figure 143) is a common Northern Hemisphere species from the central parts of Europe and North America, becoming less common toward the north and south (Järvinen 1976). But it is also distributed in Asia, Africa, Australia, and South America, as well as some nearby islands, and in North America from Alaska to Mexico (ITIS 2020).

Figure 142. ***Lophocolea bidentata***, a common Northern Hemisphere species of moist locations, occasionally submersed. Photo by Des Callaghan, with permission.

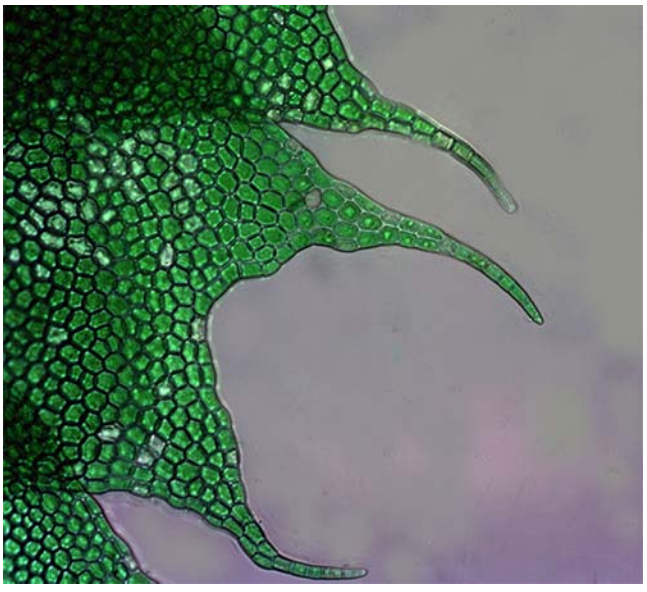

Figure 143. ***Lophocolea bidentata*** leaves. Photo by Aimon Niklasson, with permission.

Aquatic and Wet Habitats

Watson (1919) treated this species as occasionally submerged. This is consistent with its occurrence on moist rock surfaces or springy banks of ravines in Connecticut, USA (Nichols 1916). Similarly, Redfearn (1979) reported it from moist dolomite rocks in the Ozarks, Arkansas, USA. Glime *et al.* (1987) found it in Adirondack streams in northeastern USA. And Stephenson *et al*. (1995) reported it from mountain streams in West Virginia, USA, preferring a *p*H of 7.9.

Järvinen (1976) found it in moist places, including lake and river shores or near springs, considering it to be frequent in the central parts of Europe and North America, becoming rarer towards the north and south. It occurs on moist rock surfaces or springy banks of ravines in river bank of the River Tees, UK (Holmes & Whitton 1977a), but Ferreira *et al*. (2008) reported it from rivers. Wiltshire (1995) found it in dry stream beds in Ireland. Clapham (1940) reported it from the tops of high tussocks in calcareous fens of the Oxford District, UK. In Thuringia, Germany, it occurs in locations where one can find the submersed ***Platyhypnidium-Fontinalis antipyretica*** association (Figure 102, Figure 103), (Marstaller 1987). Also in Europe, it occurs in mountainous streams on Madeira Island (Luis *et al.* 2015).

On the subAntarctic Macquarie Island, Kirkpatrick and Scott (2002) found the species to be almost ubiquitous on the undisturbed coastal slopes.

Dulière *et al*. (2000) found no significant effect of liming on ***Lophocolea bidentata*** (Figure 142-Figure 143) compared to those on control stumps in a Norway spruce (***Picea abies***; Figure 89) forest in eastern Belgium.

Reproduction

Kent *et al*. (2005) studied the effects of long-term burial on bryophytes in the Outer Hebrides, Scotland. ***Lophocolea bidentata*** (Figure 142-Figure 143) occurred in the foredune turf and was among the plants experimentally buried to measure subsequent photosynthesis. They did not provide responses of individual species.

Sometimes ***Lophocolea bidentata*** (Figure 142-Figure 143) comes along for the ride. Fisk (2008) reported it as one of the species that travels with tree ferns [***Dicksonia fibrosa*** (Figure 144) and ***D. squarrosa*** (Figure 145)] in horticultural and botanical garden trade.

Figure 144. ***Dicksonia fibrosa***, a vector for spreading ***Lophocolea bidentata*** when it is planted in botanical gardens and other horticultural sites. Photo by Leon Perrie, through Creative Commons.

Figure 145. ***Dicksonia squarrosa***, a vector for spreading ***Lophocolea bidentata*** when planted in botanical gardens and other horticultural sites. Photo by Jeremy Rolfe, through Creative Commons.

Udar and Srivastava (1977) were able to describe the development of the sporeling. Rincón (1993) examined the growth responses to different light intensities, identifying shoot bending, growth rate, and chlorophyll content. Biomass and growth rates increased as light intensity increased. However, of the six bryophytes in the study, ***Lophocolea bidentata*** (Figure 142-Figure 143) was the only one that did not exhibit etiolation in decreased light. Chlorophyll concentrations were highest in low light, but the chlorophyll *a*:*b* ratio did not clearly change with light intensity. Suleiman *et al*. (1980) identified volemitol as a photosynthetic product in ***Lophocolea bidentata*** in addition to fructose and sucrose.

Role and Fungal Interactions

When ***Lophocolea bidentata*** (Figure 142-Figure 143) grows on very wet rocks, it often has a significant diatom community forming periphyton on its surface (Round 1957). A species, yet to be identified, of the **Ascomycota** fungus ***Octosporella*** is able to grow on the leaves (Eugenia Ron, Bryonet, 10 April 2021).

Figure 146. ***Octosporella*** sp. on ***Lophocolea bidentata***, a liverwort that also promotes conditions for the growth of diatoms. Photo by Tomás Sobota, with permission.

Rhizoids of ***Lophocolea bidentata*** (Figure 142-Figure 143), borne in tufts at the bases of the underleaves, penetrate the substratum and their ends becoming profusely branched, like the haustoria of many fungi. Cavers (1903) examined saprophytism and mycorrhizae in liverworts. He determined that in ***Lophocolea bidentata***, a species frequently occurring on decaying wood, the leafy gametophyte is entirely free from fungal hyphae. On the other hand, ***Lophocolea bidentata*** has been found growing on the fruiting body (basidiocarp) of ***Phellinus*** sp. – a fungus (Figure 147) (Vital *et al*. 2000).

Figure 147. ***Phellinus igniarius***; the genus ***Phellinus*** serves as substrate for several bryophytes, including ***Lophocolea bidentata***. Photo by George Chernilevsky, through Creative Commons.

Biochemistry

Mues *et al*. (1973) elucidated the carotenoids, identifying α-carotene, β-carotene, neo-β-carotene U, zeaxanthin, mono-cis-neoxanthin, trans-neoxanthin, poly-cis-neoxanthin, violaxanthin neo V, violaxanthin, antheraxanthin, lutein, and lutein-5,6-epoxide.

Biochemical studies that might help to explain why fungal relationships in ***Lophocolea bidentata*** (Figure 142-Figure 143) are rare. Rieck *et al*. (1995) identified an epoxy-trinoreudesmane sesquiterpene but did not include any antibiotic studies. It appears that little is known of the biochemistry of this species.

Lophocolea heterophylla (Figure 148-Figure 150)

(syn. = *Chiloscyphus profundus*)

Distribution

Lophocolea heterophylla (Figure 148-Figure 150) is widely distributed throughout the temperate and subarctic regions of North America, Europe, and Asia (Hatcher 1967; Järvinen 1976). It is even more common when one recognizes ***Chiloscyphus profundus*** (Figure 151) as conspecific with this species, adding Africa to its distribution.

Figure 148. ***Lophocolea heterophylla*** showing a form with only shallow leaf lobes. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 149. ***Lophocolea heterophylla*** showing a form with deep leaf lobes. Photo by Paul Davison, with permission.

Figure 150. ***Lophocolea heterophylla*** underleaves. Photo by Blanka Aguero, with permission.

Figure 151. ***Chiloscyphus profundus***, a former species now considered synonymous with ***Lophocolea heterophylla***. Photo by Hermann Schachner, through Creative Commons.

Figure 152. ***Lophocolea heterophylla*** in a common log habitat. Photo by Bob Klips, with permission.

Aquatic and Wet Habitats

Koponen *et al*. (1995) considered ***Lophocolea heterophylla*** (Figure 152) to be aquatic in Finland. However, in Michigan, USA, I have found it only on decorticated logs in the forest, not in water. Likewise, Ignatov *et al*. (2005) found it on rotten logs and stumps in Tatarstan in European Russia. Šoltés and Zubaľová (2015) considered it to be a species of decaying wood in the forests of the eastern Carpathians, Slovakia. Järvinen (1976) likewise reported it from decaying wood in moist places in eastern Fennoscandia and considered it to be widely distributed in Europe and Asia. as well as in both deciduous and coniferous forests in North America. Hatcher (1967) described its habitat as soil, decaying logs, tree bases, or on the vertical faces of sandstone bluffs.

Slack and Glime (1985) found it associated with Adirondack Mountain streams in northeastern USA, where it had a broad niche (Glime *et al*. 1987). In western Canada it was restricted to terrestrial locations in montane streams and on stream banks (Vitt *et al*. 1986; Glime & Vitt 1987).

But it can in fact occupy streams. Koponen *et al*. (1995) considered it to be aquatic in Finland, and Toivonen and Huttunen (1995) reported it from small lakes in southern Finland. Marstaller (1987) found it in locations with the ***Platyhypnidium-Fontinalis antipyretica*** association (Figure 102, Figure 103) in Thuringia, Germany.

Zehr (1977) investigated it in three sandstone canyons in southern Illinois. When he attempted to correlate presence with vapor pressure deficit, plant surface temperature, and radiant energy in the blue, red, and far red wavelengths, as well as substrate *p*H and exchangeable potassium and phosphorus ions, he found that ***Lophocolea heterophylla*** (Figure 152) has a wide ecological amplitude. Of these, moisture seemed to be the moist important in defining its microhabitat.

Hatcher (1967) also considered ***Lophocolea heterophylla*** (Figure 152) to be adapted to a wide range of environmental conditions, a fact that contributes to its morphological variability. Under adverse conditions, the plants maintain a prostrate growth, adhering closely to the substrate and attached by tufts of short rhizoids. These rhizoids arise from the lamina of the underleaves. When growing conditions are optimum, the stem tips instead are upright and the stems may attain a length of 3-4 cm. On the other hand, growing conditions seem to have no effect on the relationship of one character to another relating to cell dimensions. The male inflorescence occurs on the same stem as the female inflorescence in this monoicous species.

Some of this wide range of habitats includes decorticated logs. Jansová (2006) found it to be **epixylic** (logs with no bark) in Bohemia in the Czech Republic. She found that the 13 epixylic species in her study grew faster in winter (October-April) than in summer. Winter was also the season of extinction as well as of expansion. ***Lophocolea heterophylla*** (Figure 148-Figure 152) occurred in small, fragmented colonies.

Reproduction

Sporophyte development studies are lacking for most liverworts (Schertler 1979). A surprising number of studies have examined development of ***Lophocolea heterophylla***, particularly looking at the sporophyte (Figure 153-Figure 155). Schertler reported that in this species the hypobasal cell gives rise only to the **haustorium** (sporophyte tissue that penetrates gametophyte for transfer of substances). Thomas and Doyle (1976) learned that during seta elongation, the seta cell walls thin considerably, reaching a 25-fold increase in cell length and a accompanying 2-fold increase in cell wall carbohydrates. Starch diminishes during elongation, with the polyfructosans and sucrose being replaced by fructose and glucose. Is this what nourishes the developing spores (Figure 156)?

Figure 153. ***Lophocolea heterophylla*** with developing capsules. Photo by Michael Lüth, with permission.

Figure 154. ***Lophocolea heterophylla*** with a sporophyte near maturity. Photo by Paul Davison, with permission.

Figure 155. ***Lophocolea heterophylla*** with mature and dehiscing capsules. Photo by David Holyoak, with permission.

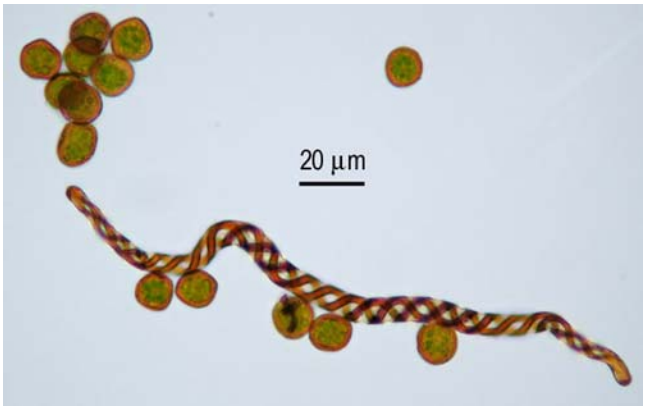

Figure 156. ***Lophocolea heterophylla*** spores and elater. Photo by Norbert Stapper, with permission.

Role

Lophocolea heterophylla can share its habitat with slime molds (Figure 157). Among these are species of the plasmodial slime mold ***Lycogala***. These occur on especially on decorticated log habitats as shown here by Allen Norcross.

Biochemistry

Thomas *et al*. (1970) demonstrated that exogenous IAA could elicit a two-phase growth response in setae, with lower concentrations stimulating growth and higher concentrations inhibiting it. Elongation in the seta cells is facilitated by the increase in osmotic potential to -6 bars, causing a 16-fold increase in both length and water content of the cells (Thomas 1977a). At the same time, there is a correlation between the protein content and cell elongation (Thomas 1976). The seta cells are qualitatively similar to primary cell walls in tracheophytes, with starch content increasing 1.8-fold at they mature (Thomas 1977b). There is no net loss of lipids during elongation, with the primary fatty acid components being arachidonic and eicosapentaenoic acids (Thomas 1975a). This extensive elongation, reaching 50-fold, is accomplished in 3-4 days (Thomas 1977b).

Taylor *et al*. (1972) determined that the young sporophyte exhibits the same basic pigments (chlorophyll *a*, chlorophyll *b*, neoxanthin, violaxanthin, lutein, zeaxanthin, and β-carotene). In fact, the total chlorophyll

concentration is significantly greater in the young sporophyte than it is in the leafy gametophyte. Nevertheless, the photosynthetic activity of the sporophytes is very low when compared to the associated uppermost leaves, perianth, and bracts (Proctor 1982). Rather, most of the carbon is translocated from the gametophyte to the sporophyte. And this is primarily from the leafy shoots, with little from the perianth, bracts, or even the uppermost leaves. It is interesting that the translocation from the gametophyte seems to be greatest when the capsule reaches full size but is still green. Once the capsule reaches its final stages of maturation, the translocation declines. This pattern would provide the greatest translocation of carbon during the spore development phase.

Figure 157. ***Lophocolea heterophylla*** and the plasmodial slime mold ***Lycogala epidendrum*** on decorticated log. Photo by Allen Norcross, with permission.

Konečný *et al*. (1982) described a number of sesquiterpenes from ***Lophocolea heterophylla*** (Figure 148-Figure 152). Herout (1985) considered the fragrance of ***Lophocolea heterophylla*** to be suitable for perfume, perhaps coming from the oil bodies (Figure 158). Toyota *et al*. (1990) isolated (−)-2-methylisoborneol as the source of its fragrance and described additional sesquiterpenoids. Tazaki *et al*. (1999) demonstrated the formation of lignans. Even the seta exhibits an array of sesquiterpenoids (Thomas 1975b). These vary before and during elongation. In 2002 Tazaki *et al*. isolated a caffeic acid derivative, subulatin, a compound known for its antitoxidic effects. (See also Pavletic & Stilinovic 1963; Wolters 1964).

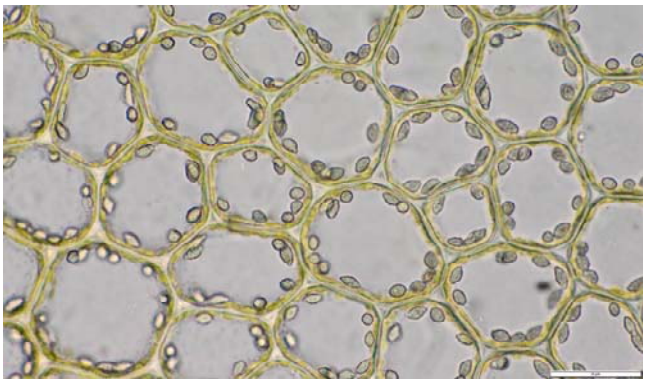

Figure 158. ***Lophocolea heterophylla*** leaf cells showing oil bodies, the site of at least some of the secondary compounds, especially aromatic ones. Photo by Blanka Aguero, with permission.

Nikolajeva *et al*. (2012) found that an extract of ***Lophocolea heterophylla*** (Figure 148-Figure 152) inhibited the growth of ***Bacillus cereus*** (Figure 159), but not the growth of ***Escherichia coli*** (Figure 160).

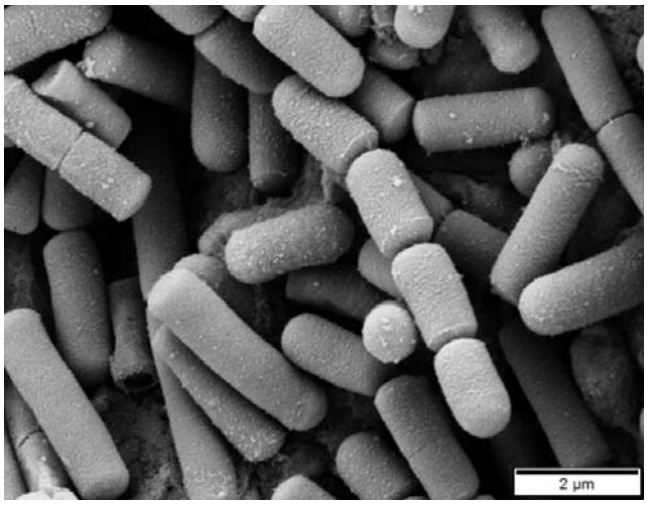

Figure 159. ***Bacillus cereus***, a bacterial species inhibited by extracts of ***Lophocolea heterophylla***. Photo by Mogana Das Murtey and Patchamuthu Ramasamy, through Creative Commons.

Figure 160. ***Escherichia coli***, a bacterial species not affected by extracts of ***Lophocolea heterophylla***. Photo by NIAID, through Creative Commons.

Lophocolea minor (Figure 161-Figure 162)

Distribution

Lophocolea minor (Figure 161-Figure 162) is sometimes included in ***Lophocolea heterophylla*** (Figure 148-Figure 152), but Söderström *et al*. (2016) maintain it as a separate species. It occurs across the Northern Hemisphere, from Alaska south to the continental USA and in the Eastern Hemisphere south to Spain (EOL.org 2020). Africa and South America also have records (ITIS 2020).

Figure 161. ***Lophocolea minor***, a species similar to ***Lophocolea heterophylla*** that occurs across the Northern Hemisphere. Photo from Earth.com, with permission.

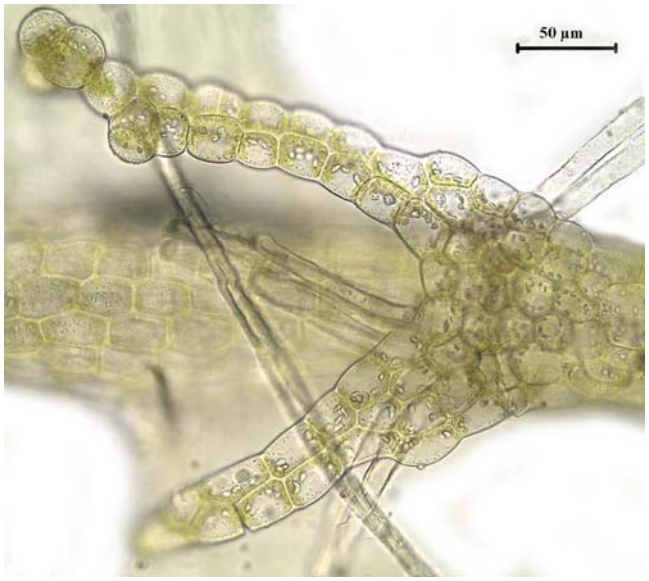

Figure 162. ***Lophocolea minor*** underleaf. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

Among the early records of wet habitats for this species, Nichols (1916) reported it along calcareous rivers in Connecticut, USA. It is a restricted terrestrial along montane streams and stream banks in western Canada (Vitt *et al.* 1986; Glime & Vitt 1987). It also occupies debarked rotting logs in Genesee Country, New York, USA (Lyman & Coleman 1966). In Quebec, Canada, it occurs on shaded rocks and banks (Evans 1916), habitats similar to those of the rock ledges and ground at the mouth of the Montreal River in the Upper Peninsula of Michigan, USA (Evans & Nichols 1935). Janssens and Glaser (1986) occasionally found it in the Red Lake peatlands of northern Minnesota, USA. Darlington (1938) found it on an earth bank at the south end of Glen Lake, Michigan, USA. In southern Michigan, USA, Nichols (1933) found this species on high banks of the Henton Creek. In Iowa USA, Conard (1940) attributed it to mesic woods and Cavanagh (1930) found it on moist, shady banks. However, Statler (1949) found that this species in Henry County, Iowa, preferred drier sites than those of ***Lophocolea heterophylla*** (Figure 152).

In Thuringia, Germany, it occurs along streams where one can find the ***Platyhypnidium-Fontinalis antipyretica*** association (Figure 102, Figure 103) (Marstaller 1987). Papp and Erzberger (2007) found it on soil among limestone rocks in Montenegro. In the Djerdap National Park of eastern Serbia, Papp *et al*. (2006b) found it on limestone rock. On the Spanish island of Minorca in the Mediterranean sea, ***Lophocolea minor*** (Figure 161-Figure 162) was associated with temporary ponds (Pericàs *et al*. 2009).

In the Eastern Caucasus of Russia, Konstantinova (2011) found it on decaying logs on a stream bank or in mats, mixed with other liverworts such as ***Conocephalum conicum*** (Figure 163), ***Pellia endiviifolia*** (Figure 164), ***Porella platyphylla*** (Figure 165), ***Plagiochila porelloides*** (Figure 18), ***Preissia quadrata*** (Figure 166), ***Reboulia hemisphaerica*** (Figure 167), and ***Scapania cuspiduligera*** (Figure 168). Dulin (2015) added greatly to these records through exploration in the Komi Republic of northwestern Russia. These included decaying wood, on fine grained soil of turned out wood roots, on wet, slightly matted soil, on trails in forests communities with soil surface covered with dead wood leaves, on tree butts in mires and boggy areas. It sometimes occurred in pure patches and other times associated with ***Blepharostoma trichophyllum*** (Figure 2-Figure 3), ***Cephalozia*** spp. (Figure 7, Figure 80), ***Chiloscyphus polyanthos*** (Figure 106-Figure 108), ***Geocalyx graveolens*** (Figure 169), ***Lophocolea heterophylla*** (Figure 148-Figure 150), ***Lophozia ventricosa*** *s.l.* (Figure 26), ***Plagiochila porelloides***, ***Scapania*** spp. (Figure 168) and other species.

Figure 163. ***Conocephalum conicum***, a species that sometimes accompanies ***Lophocolea minor*** on stream banks or decaying logs. Photo by Janice Glime.

Figure 164. ***Pellia endiviifolia***, a species that sometimes accompanies ***Lophocolea minor*** on stream banks or decaying logs. Photo by Michael Lüth, with permission.

Figure 165. ***Porella platyphylla***, a species that sometimes accompanies ***Lophocolea minor*** on stream banks or decaying logs. Photo by Hugues Tinguy, with permission.

Figure 166. ***Preissia quadrata*** on wet rock, a species that sometimes accompanies ***Lophocolea minor*** on stream banks. Photo by Andy Hodgson, with permission.

Figure 167. ***Reboulia hemisphaerica***, a species that sometimes accompanies ***Lophocolea minor*** on stream banks. Photo by Janice Glime.

Figure 168. ***Scapania cuspiduligera***, a species that sometimes accompanies ***Lophocolea minor*** on stream banks and mires or boggy areas. Photo by Hugues Tinguy, with permission.

Figure 169. ***Geocalyx graveolens***, a species that sometimes accompanies ***Lophocolea minor*** in mires and boggy areas. Photo by Hugues Tinguy, with permission.

Reproduction

Statler (1949) described the leaves of ***Lophocolea minor*** (Figure 161-Figure 162) in Iowa as sometimes being almost entirely composed of gemmae (Figure 170).

Sabovljević *et al*. (2001) considered ***Lophocolea minor*** to have a distinctive "mossy" smell.

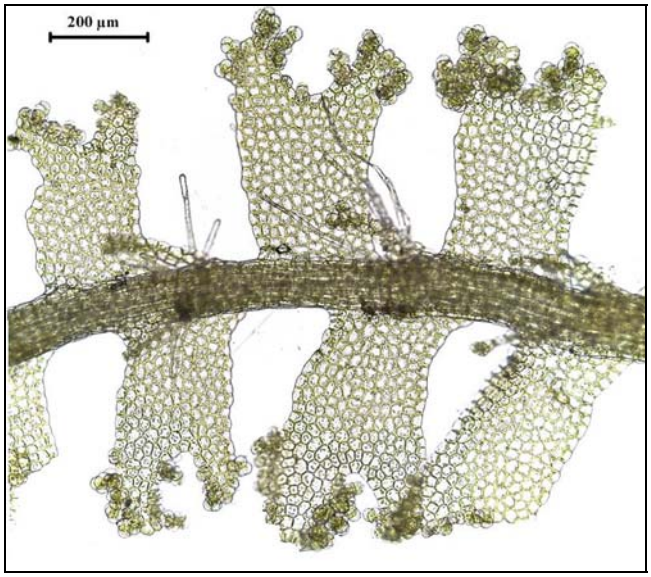

Figure 170. ***Lophocolea minor*** showing gemmae. Photo by Hugues Tinguy, with permission.

Lophocolea mollis

Ruttner (1955) found ***Lophocolea mollis*** in acidic thermal sprays in the tropics. Söderström *et al*. (2010) reported it from Java. Otherwise, there seems to be little published about this species.

Lophocolea semiteres (Figure 171-Figure 173)

(syn. = *Chiloscyphus semiteres*, *Jungermannia semiteres*)

Distribution

Lophocolea semiteres (Figure 171-Figure 173) has been recorded from South Africa, where it is relatively common, Australia, New Zealand, Vanuatu, Falkland Islands, Chile, Juan Fernández Islands, Scotland, Belgium, The Netherlands, Northern Ireland, and Marion Island (subAntarctic in Indian Ocean) (Váňa & Gremmen 2014). Barry Stewart has photographed its habitat and recorded its presence on Skomer Island, Wales (Figure 174).

Figure 171. ***Lophocolea semiteres***, a species of streams in New Zealand, but an invasive species in Europe. Photo by Des Callaghan, with permission.

Figure 172. ***Lophocolea semiteres*** showing underleaves. Photo from freenatureimages.eu, through Creative Commons.

Figure 173. ***Lophocolea semiteres***. Photo by Tom Thekathyil, with permission.

Figure 174. ***Lophocolea semiteres*** habitat on Skomer Island, Wales. Photo by Barry Stewart, with permission.

Paton (1965) identified this species from a woodland path in Tresco on the Isles of Scilly, a first record for the Northern Hemisphere. By 1982 it was well established in Argyll, Scotland, apparently introduced from New Zealand and occurring in gardens (Long 1982). But now, it is considered an invasive species in Belgium and The Netherlands (Stieperaere 1994). Where it invades a

pinewood forest in Belgium and The Netherlands, it becomes the dominant species of ***Lophocolea***, nearly excluding ***L. heterophylla*** (Figure 148-Figure 150) and diminishing the presence of ***L. bidentata*** (Figure 142-Figure 143) (Stieperaere *et al*. (1997).

Aquatic and Wet Habitats

Van Zanten (2003) reported its occurrence in The Netherlands on an open ditch wall in oak-birch forest with some spruces and beech and on coarse humus and twigs, sparingly occurring with ***Eurhynchium praelongum*** (Figure 175) and ***Plagiothecium laetum*** (Figure 176).

Figure 175. ***Eurhynchium praelongum***, a species that accompanies ***Lophocolea semiteres*** in the oak-birch forest in The Netherlands. Photo by David T. Holyoak, with permission.

Figure 176. ***Plagiothecium laetum***, a species that accompanies ***Lophocolea semiteres*** in the oak-birch forest in The Netherlands. Photo by Hermann Schachner, through Creative Commons.

In New Zealand, ***Lophocolea semiteres*** (Figure 171-Figure 173) occurs in some of the 48 studied streams on South Island (Suran & Duncan 1999). Fineran (1971) found it in a seepage area above the shore on one of the Auckland Islands off the coast of South Island, New Zealand. But at Pupu Springs (Figure 177), New Zealand, it seems to have its most aquatic habitat, submerged on boulders in water with a strong velocity (Mjchaelis 1977). In Australia it occurs in the Warm Temperate Victorian Rainforest streams (Carrigan 2008).

Figure 177. Pupu Springs, New Zealand, site of submerged populations of ***Lophocolea semiteres***. Photo by Kieron Norfield, through Creative Commons.

Elsewhere, ***Lophocolea semiteres*** (Figure 171-Figure 173) seems to have chosen other types of habitats. On Marion Island, Váňa and Gremmen (2014) found it on damp grassland in large **mats**, often with ***Marchantia berteroana*** (Figure 178), and growing on black lava rock in a small cave, where it formed large, loose mats.

Figure 178. ***Marchantia berteroana*** with archegoniophores, a species associated with ***Lophocolea semiteres*** in damp grassland on Marion Island. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

In northern Japan, on Mt. Hakkôda, this species occurs on the lower portion of various species of tree trunks (Figure 179) (Kitagawa 1978). Floyed and Gibson (2012) described them from urban industrial streetscapes in Victoria, Australia, where they were the most frequently occurring liverwort, forming **weft**-like growths (Figure 180) on gravel, cement, and soil. In addition, they frequently occurred among grass species in very wet, well shaded areas, providing protection from wind erosion.

Its Northern Hemisphere habitats seem drier than those in New Zealand (Figure 181 (Finch *et al*. 2000). Finch and collaborators were the first to find it in a swampy area, in addition to other more terrestrial habitats, in East Anglia, England.

Figure 179. ***Lophocolea semiteres*** on bark, a substrate where one might find it in northern Japan. Photo by Michael Lüth, with permission.

Figure 180. ***Lophocolea semiteres***, approaching a weft-like form. Photo by Brian Eversham, with permission.

Figure 181. ***Lophocolea semiteres***, dried. Photo by Barry Stewart, with permission.

Reproduction

Lophocolea semiteres is **dioicous** (Paton 1965). Nevertheless, it can be found with antheridia (Figure 182) capsules (Figure 183-Figure 184). Paton (1999) does not consider the structures on the leaf margins to be true **gemmae**, but rather are asexual reproductive structures that are regenerants – tiny buds which develop from a cell to form small plantlets. Engel (pers. comm. 20 August 2020) told me it does not produce gemmae.

Figure 182. ***Lophocolea semiteres***, showing swollen leaf bases where the antheridia reside. Photo by Dick Haaksma, with permission.

Figure 183. ***Lophocolea semiteres*** with mature capsules. Photo by David Tng, with permission.

Figure 184. ***Lophocolea semiteres*** dehisced capsule. Photo by Heino Lepp, Australian National Botanic Gardens, with online permission.

Biochemistry

Biochemical studies seem to be lacking. The species has large, hyaline oil bodies (Figure 185) that might yield interesting secondary compounds.

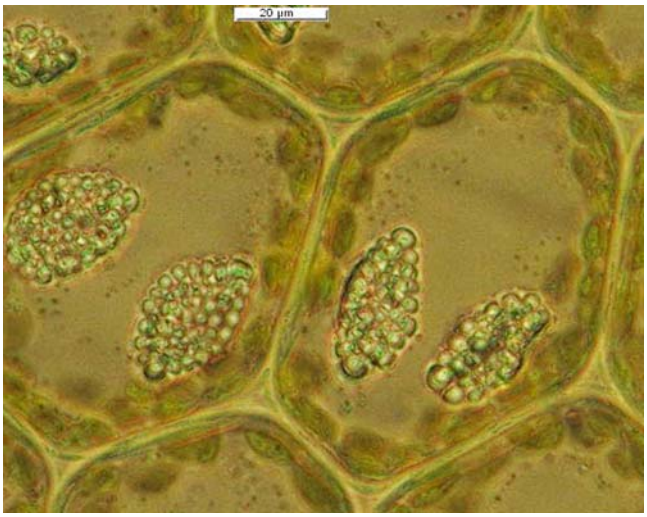

Figure 185. ***Lophocolea semiteres*** leaf cells with hyaline oil bodies. Photo by Tom Thekathyil, with permission.

Pachyglossa (Figure 186)

Pachyglossa (Figure 186) is a Southern Hemisphere genus with several species. In New Zealand, ***Pachyglossa*** is known from streams. ***Pachyglossa*** sp. is positively correlated with bankfull discharge in the studied 48 streams on South Island, New Zealand (Suran & Duncan 1999).

Pachyglossa austrigena subsp. *okaritana* (Figure 186)

Distribution

Pachyglossa austrigena **subsp.** ***okaritana*** (Figure 186) is an Australasian species (Engel 1992).

Figure 186. ***Pachyglossa austrigena*** **subsp.** ***okaritana***, an Australasian facultative aquatic species. Photo by Peter De Lange, through Creative Commons.

Aquatic and Wet Habitats

Pachyglossa austrigena **subsp.** ***okaritana*** (Figure 186) can be obligately or facultatively aquatic in South Island, New Zealand, streams (Suren 1996). It was one of the species that was positively correlated with bankfull discharge in 48 streams in South Island, New Zealand (Suran & Duncan 1999). In the Antipodes Island, New Zealand, it occurred on a wet cliff face (Godley 1989). It appears that its limited distribution has caused it to escape extensive study.

Pachyglossa dissitifolia

Distribution

Pachyglossa dissitifolia is a species of the extreme south. It occurs on Livingston Island in the South Shetland Islands (Bednarek-Ochyra *et al*. 2000). Engelskjøn (1986) noted that ***Pachyglossa dissitifolia*** occurs on the Antarctic Peninsula, but the distribution in Fuegia - Patagonia is also fairly extensive, reaching eastward to Bouvetøya and northward to Tristan da Cunha. Otero *et al*. (2008) collected ***Pachyglossa dissitifolia*** on Tierra del Fuego, Argentina.

Aquatic and Wet Habitats

On the South Shetland Islands ***Pachyglossa dissitifolia*** occurs in Midge Lake at about 1-2 m depth (Bednarek-Ochyra *et al*. 2000). There it is associated with ***Drepanocladus longifolius*** (Figure 187) and ***Warnstorfia sarmentosa*** (Figure 188).

Figure 187. ***Drepanocladus longifolius***, a species associated with ***Pachyglossa tenacifolia*** in the epilithic submerged bryoflora of Macquarie Island. Photo by John Game, through Creative Commons.

Figure 188. ***Warnstorfia sarmentosa***, a species associated with ***Pachyglossa tenacifolia*** in the epilithic submerged bryoflora of Macquarie Island. Photo by A. Neumann, Biopix.com, with online permission for educational use.

Otero *et al*. (2008) collected ***Pachyglossa dissitifolia*** from lakes on Tierra del Fuego, Argentina. They included it among a number of species they tested for range of maximum absorption of light. For this species, the maximum absorption was at 327 nm. It was in the second of two groups of bryophyte species, having lower concentrations of UV-absorbing compounds. This is to be expected for a species collected in the deeper water of lakes where the water serves as a filter of the UV radiation.

Pachyglossa tenacifolia

Distribution

On Macquarie Island in the sub-Antarctic, ***Pachyglossa tenacifolia*** is an indicator species, occurring in Scoble and Tulloch Lakes (Hughes 1986). Li *et al*. (2009) noted that ***Pachyglossa*** was the only liverwort reported from an Antarctic lake. They reported ***Pachyglossa tenacifolia*** was collected from relatively shallow waters at 1-2 m depth in Prion Lake, sub-Antarctic Macquarie Island.

Aquatic and Wet Habitats

Fife (2015) collected ***Pachyglossa tenacifolia*** among the submerged vegetation at the edge of a small lake at 110 m elevation on Macquarie Island. It was associated there with ***Blindia seppeltii***, ***Ditrichum strictum*** (Figure 189), and ***Riccardia aequicellularis*** (Figure 190). In the epilithic submerged bryoflora, it was associated with ***Blindia lewinskyae*** (Figure 191), ***Pachyglossa austrigena*** (Figure 192), and ***Hepatostolonophora rotata*** (see Figure 117).

Figure 189. ***Ditrichum strictum*** balls, a species that is associated with ***Pachyglossa tenacifolia*** submerged at the edge of a lake on Macquarie Island. Photo by Franek2, through Creative Commons.

Figure 190. ***Riccardia aequicellularis***, a species that is associated with ***Pachyglossa tenacifolia*** submerged at the edge of a lake on Macquarie Island. Photo by Tom Thekathyil, with permission.

Figure 191. ***Blindia lewinskyae***, a species associated with ***Pachyglossa tenacifolia*** in the epilithic submerged bryoflora of Macquarie Island. Photo by John Braggins, with permission.

Figure 192. ***Pachyglossa austrigena***, a species associated with ***Pachyglossa tenacifolia*** in the epilithic submerged bryoflora of Macquarie Island. Photo by Peter De Lange, through Creative Commons.

Mastigophoraceae

Mastigophora diclados (Figure 193)

Distribution

Mastigophora diclados (Figure 193) is Palaeotropical, distributed in African (including Madagascar), Asian, and Australian tropics, but not the Neotropics (Marline 2018). It is common in the Asiatic tropics (Inoue 1973) and is known from Hong Kong (So & Zhu 1996) and Reunion Island (Molnár *et al*. 2003). Daniels and Kariyappa (2012) reported it from Peninsular India; it was already known from the Eastern Himalaya and Nicobar Islands.

Figure 193. ***Mastigophora diclados***, a Palaeotropical species. Photo by Claudine Ah-Peng, with permission.

Aquatic and Wet Habitats

Ruttner (1955) reported that ***Mastigophora diclados*** (Figure 193) occurs in acidic thermal sprays in the tropics. But otherwise, it appears in moist habitats near water, but not in water, and even occurs on trees (Figure 194).

Figure 194. ***Mastigophora diclados*** on tree on São Tomé Island. Photo by César Garcia, through Creative Commons.

This is a tall species that is abundant at higher elevations (850-2050 m) (Marline 2018). In Taiwan, it occurs in the watershed of the acidic alpine Yuan-Yang Lake (Figure 195) (Wu *et al*. 2001). Similarly, it occurs on the ground in the Upper Montane zone in Tanzania, forming **cushions** (Doggart & Loserian 2007).

Figure 195. Yuan-Yang Lake Reserve in alpine, Taiwan, habitat for ***Mastigophora diclados***. Photo from Nature Reserve, through Creative Commons.

Adaptations

In the tropical mountainous rainforest it can be subjected to high light intensity, particularly in the UV-B range. Molnár *et al*. (2003) subjected ***Mastigophora***

diclados (Figure 193-Figure 194) from Reunion Island to three hours high light, causing a 50% drop in F_v/F_p (ratio of variable to maximum fluorescence in PS II) in shade plants, compared to a 20% drop in sun plants. This drop in sun plants was due to a pronounced inactivation of functional PS II reaction centers. The sun plants recovered completely in one hour, whereas the shade plants had reached only 70% recovery after three hours.

Biochemistry

Mastigophora diclados (Figure 193-Figure 194) has experienced its share of biochemical studies. Zaki (2014) reported that the oil bodies synthesize and store a variety of lipophilic acetogenins, terpenoids, and aromatic compounds, with ***Mastigophora diclados*** producing sesquiterpenoid herbertene compounds. Otari (2013) reported that the phenolic sesquiterpenes in this species are known to have cytotoxic, antioxidant, and antimicrobial properties. But in tests to evaluate the effect on glucose levels in rats, there was a 64% reduction by an n-hexane extract of the liverwort; the difference was not significantly different from the control using glibenclamide (medication used to treat diabetes mellitus type 2).

Komala *et al*. (2010) found that ***Mastigophora diclados*** (Figure 193-Figure 194) contained various volatile sesqui- and diterpenoids and aromatic compounds that presented cytotoxic activity against certain cancer cell lines, radical scavenging activity, and antimicrobial activity against ***Staphylococcus aureus*** (Figure 196) and ***Bacillus subtilis*** (Figure 197). Harinantenaina and Asakawa (2007) isolated unique sesquiterpenoids, mastigophorenes, known only from ***Mastigophora diclados***. Other studies have named more compounds or elucidated structures (Fukuyama & Asakawa 1991; Leong & Harrison 1997; Hashimoto *et al*. 2000; Harinantenaina & Asakawa 2004; Ludwiczuk *et al*. 2009; Komala *et al*. 2010; Ng *et al*. 2017). Some of these differed between populations and were considered taxonomic markers.

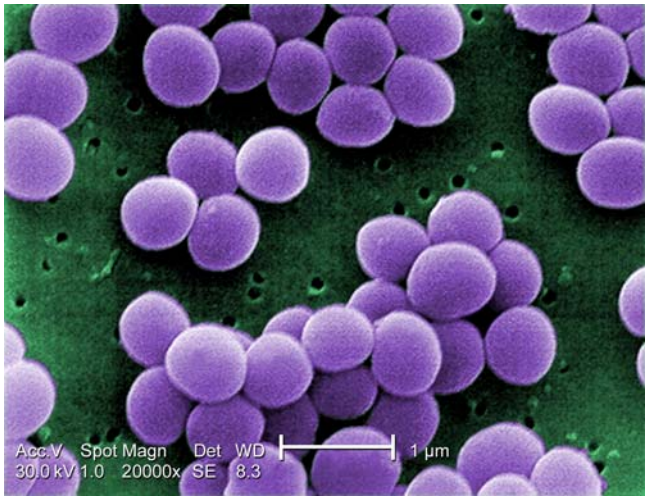

Figure 196. ***Staphylococcus aureus***; ***Mastigophora diclados*** exhibits antibiotic activity against this bacterium. Photo by Janice Haney Carr, CDC, through public domain.

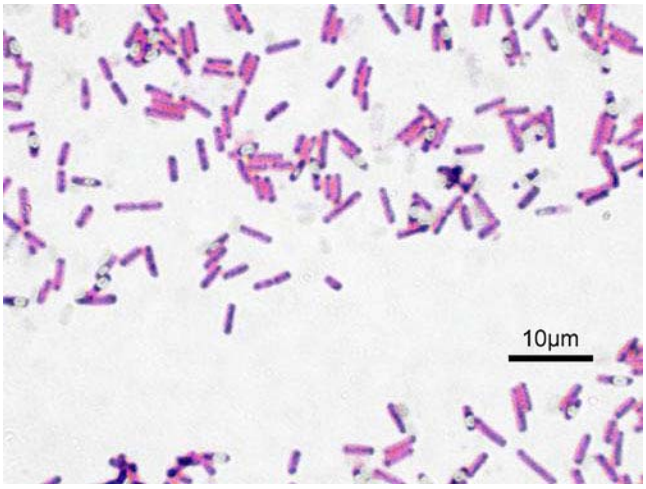

Figure 197. ***Bacillus subtilis*** with Gram stain; ***Mastigophora diclados*** exhibits antibiotic activity against this bacterium. Photo by Y. Tambe, through Creative Commons.

Summary

The **Lophocoleineae** occupy a wide range of habitats, many of which are wet, but few are truly aquatic. Among the species that are able to occur and thrive in submersed condition, ***Herbertus sendtneri*** occurs in a glacial lake in the Andes, but most of its reported habitats are never or rarely submersed. Others, like ***Kurzia makinoana***, are common on stream banks and in swamps and mires. ***Chiloscyphus polyanthos*** is typically submersed, whereas ***C. pallescens*** prefers mires and springs on wet soil, so both require a habitat that rarely leaves them dry. Theses two species don't typically develop rhizoids under water and are often dark-colored there. Some species of **Lophocoleineae** are amphibious, being submerged during flooding. Some, like ***Lophocolea heterophylla***, are aquatic in some parts of the world, but not in others. ***Lophocolea semiteres*** is aquatic at Pupu Springs on South Island, New Zealand, but is an invasive terrestrial species in Europe. In bog and other peaty habitats many **Lophocoleineae** survive and reproduce by stolons that penetrate the peat. Many have fungal associates, and probably all have secondary compounds that protect them from infections and herbivory. Even so, many have fungal inhabitants whose roles need further investigation.

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CHAPTER 1-6
AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES: LOPHOCOLEINEAE, PART 2, MYLIINEAE, PERSSONIELLINEAE

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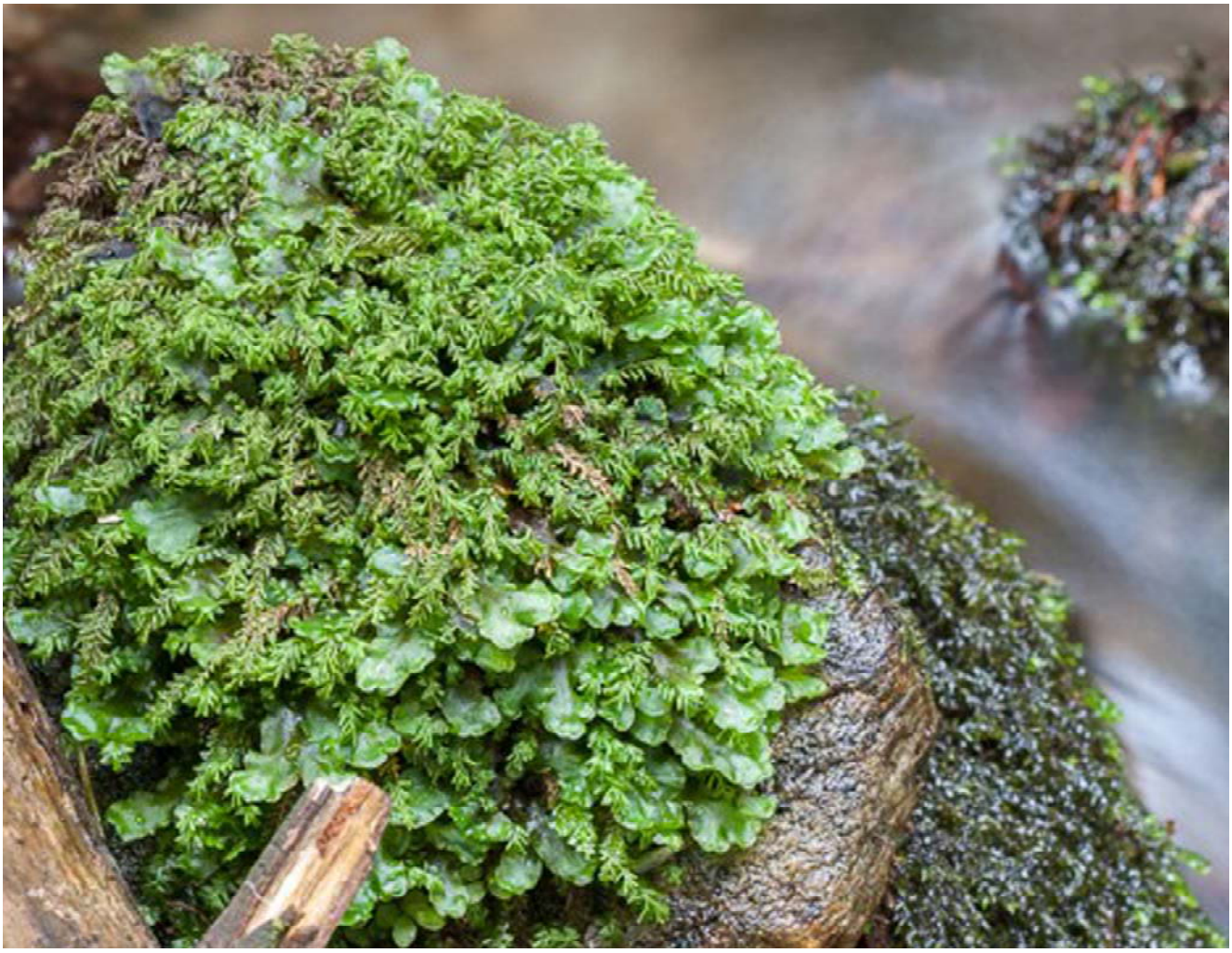

Figure 1. ***Plagiochila porelloides*** by stream, where it is overgrowing a patch of ***Pellia***. Photo by Štěpán Koval, with permission.

Suborder Lophocoleineae, cont.

Plagiochilaceae

Pedinophyllum interruptum (Figure 2-Figure 4)

Distribution

Pedinophyllum interruptum (Figure 2-Figure 4) is a Northern Hemisphere species, best known from Europe, but also with scattered records in North American and Japan (GBIF 2020). De Miguel and Indurain (1984) considered it to be circumboreal. Martinez-Abaigar and Ederra (1992) reported it from Spain and Sotiaux and Vanderpoorten (2017) from nearby Andora. There are records from Belgium (Sotiaux *et al*. 2007), Albania, where it was removed from the red list (Marka *et al*. 2012), and Iran (Frey & Kürschner 1983). It is relatively abundant in Croatia (Pandža & Milović 2015).

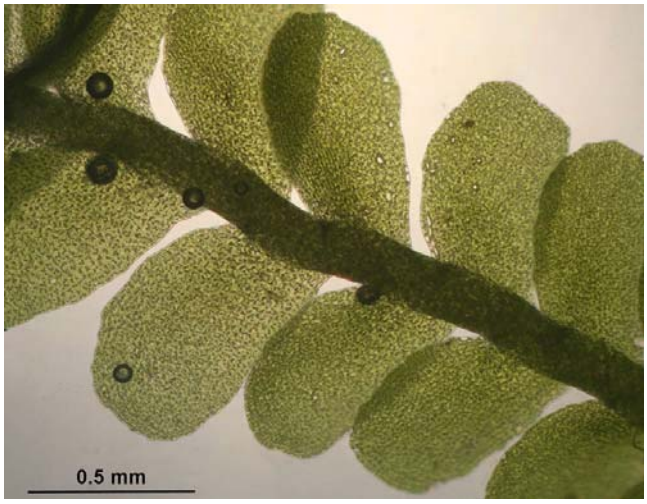

Figure 2. ***Pedinophyllum interruptum*** branch, a circumboreal species, occurring south into Europe, China, and Iran. Photo by Hermann Schachner, through Creative Commons.

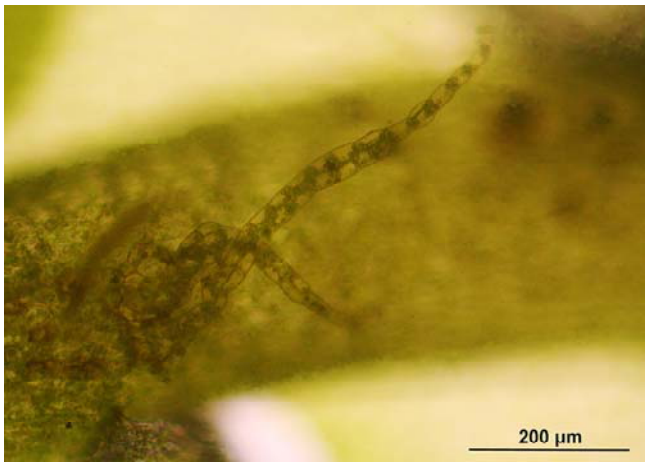

Figure 3. ***Pedinophyllum interruptum*** underleaf. Photo by Hermann Schachner, through Creative Commons.

Figure 4. ***Pedinophyllum interruptum*** forming mats. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Watson (1918) recognized the limestone association of ***Pedinophyllum interruptum*** (Figure 2-Figure 4) in East Somerset, UK. In the Tara River canyon, it occurs on limestone rock and at a spring in the Tara River canyon and the Durmitor area, Montenegro (Papp & Erzberger 2011). In the UK, it typically grows on or near Carboniferous or metamorphic limestone, occupying both rock and soil, or in wooded gorges or other very humid, sheltered upland sites (BBS 2020). It tolerates both open, bare limestone rock and deep shade. It likewise occupies shaded limestone in Croatia (Alegro *et al*. 2014), Macedonia (Papp *et al*. 2016), and Greece (Papp & Tsakiri 2017). Gerdol *et al*. (1991) found it to be frequent in moist carbonatic rocky habitats in the southern Italian Alps. De Miguel and Indurain (1984) considered it a saxicolous calcicole in La Foz de Arbayún, Spain.

Chytrý and Tichý (2003) termed the species **chasmophytic** (referring to plant growing in crevices of rocks) on shaded calcareous cliffs of the Czech Republic. In Bulgaria, Gecheva and Yurukova (2013) found it downstream from a karst spring. Veljié *et al*. (2001 similarly found it at well springs in a karst area of Serbia. Liu *et al*. (2019) found that it was rare outside karst sinkholes in Guizhou Province, Southwestern China, but could be found at the bottom of the sinkholes, a location they considered more suitable because of the greater presence of water and nutrition.

Pedinophyllum interruptum (Figure 2-Figure 4) occurs in Iskur River, Bulgaria, and its main tributaries (Papp *et al.* 2006). Choi *et al*. (2010) found it near streams or at the top of ridges on Mt. Deogyu in Korea. Tacchi *et al*. (2009) on rocks in ravines in the Apennines. In Thuringia, Germany, Marstaller (1987) found that ***Pedinophyllum interruptum*** occurs in streams with the ***Platyhypnidium*** (Figure 5) – ***Fontinalis antipyretica*** (Figure 6) association. But Frahm (1987) also found it in moist, shaded forests in Germany. In the UK, Preston *et al*. (2011) found that it is frequently associated with ***Scapania undulata*** (Figure 7).

Figure 5. ***Platyhypnidium riparioides***, often an indicator of suitable habit for ***Pedinophyllum interruptum***. Photo by Hermann Schachner, through Creative Commons.

Figure 6. ***Fontinalis antipyretica*** in Indian River, often an indicator of suitable habit for ***Pedinophyllum interruptum***. Photo by Matt Goff <www.sitkanature.org>, with permission.

Figure 7. ***Scapania undulata***, a species often associated with ***Pedinophyllum interruptum***. Photo by Hugues Tinguy, with permission.

In North America, ***Pedinophyllum interruptum*** (Figure 2-Figure 4) was found on dolomite rocks in a ravine in Brookfield, Connecticut, USA (Evans 1910). It is also known from Greenland, Labrador, a few additional locations in Canada, and Ohio, USA.

Reproduction

Pedinophyllum interruptum (Figure 2-Figure 4) is **monoicous** (Rycroft 2021).

Fungal Interactions

Bidartondo and Duckett (2010) examined 30 bryophyte species, represented by a total of 200 collections. Among these, only four species failed to present any fungal DNA sequences. One of these was ***Pedinophyllum interruptum*** (Figure 2-Figure 4). Perhaps ***Pedinophyllum interruptum*** is able to inhibit fungal growth through its extensive array of secondary compounds. Wang and Qiu (2006) likewise were unable to find any reference to a mycorrhizal relationship in this species.

But the species is not totally fungus free. Döbbeler (1998) reported ***Epibryon pedinophylli*** (see Figure 8) as a leaf-perforating ascomycete from ***Pedinophyllum interruptum*** (Figure 2-Figure 4). However, this fungus might not occur on aquatic populations (Peter Döbbeler, pers. comm. 8 September 2020).

Figure 8. ***Epibryon*** perithecia (arrows) on ***Sphagnum*** and surrounded by ***Botryococcus***. ***Epibryon pedinophylli*** is only known from ***Pedinophyllum interruptum***. Photo through Creative Commons.

Biochemistry

Pedinophyllum interruptum has oil bodies (Figure 9), where we might expect to find some of its secondary compounds. Feld *et al*. (2004) identified several secondary compounds in ***Pedinophyllum interruptum*** from Scotland. Liu *et al*. (2013) elucidated the structures of ten diterpenoids in Chinese populations of ***Pedinophyllum interruptum***. Seven of the pedinophyllols in this species inhibited seed germination and root growth of ***Arabidopsis thaliana*** (Figure 10) with a dose-dependent response (Wei *et al*. 2019). Do such compounds provide ***Pedinophyllum interruptum*** with a means to compete in its limestone habitats?

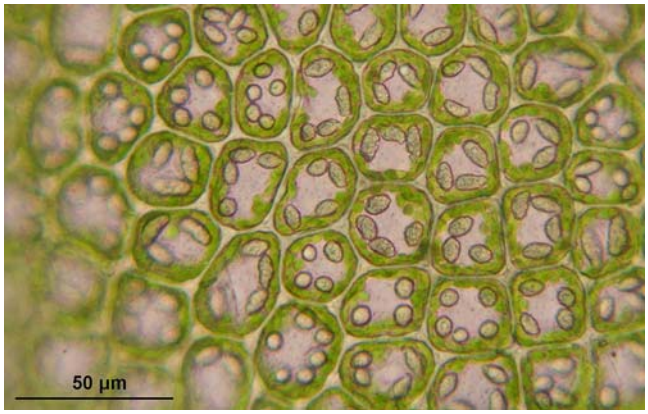

Figure 9. ***Pedinophyllum interruptum*** leaf cells showing oil bodies, a location of secondary compounds. Photo by Hermann Schachner, through Creative Commons.

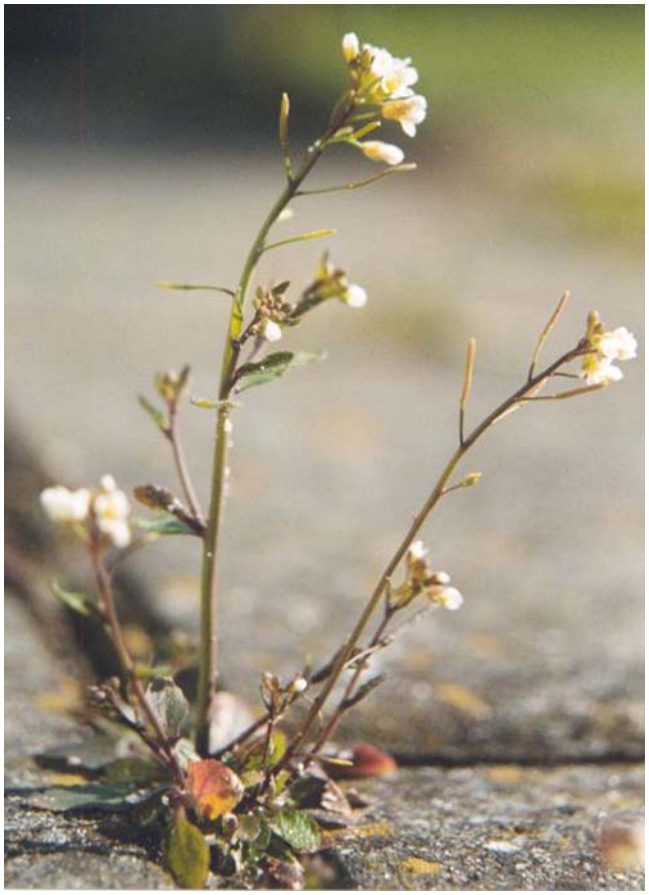

Figure 10. ***Arabidopsis thaliana***, a species for which root growth is inhibited by extracts from ***Pedinophyllum interruptum***. Photo through Creative Commons.

Plagiochila

The genus ***Plagiochila*** includes rheophytes in the wet tropics of SE Asia (Akiyama 1992) and west Africa (Shevock *et al*. 2017).

Other general characteristics of the genus include the documentation of surface wax in the family, including ***Plagiochilion mayebarae*** and five species of ***Plagiochila*** (Heinrichs *et al*. 2000). These waxes were previously unknown in the family and cannot be detected with a light microscope. I am aware of no evidence if these are present in aquatic populations, but it would be interesting to compare them in aquatic and terrestrial populations and through moisture gradients of streambank populations.

Plagiochila asplenioides (Figure 11, Figure 14)

(syn. = *Plagiochila maior*)

Plagiochila asplenioides (Figure 11, Figure 14) has been plagued by disagreements over the taxonomic level of ***Plagiochila porelloides*** (Figure 12). Schuster (1980) and Damsholt (2002) considered ***Plagiochila porelloides*** to be a subspecies of ***P. asplenioides***. Paton (1999) and Schumacker and Váňa (2000), however, consider them to be two separate species with different habitats. The species ***Plagiochila asplenioides*** *s.s.* is most common on herb-rich forest floors and moist depressions, whereas the closely related ***P. porelloides*** occurs at the bases of silicate boulders and in crevices. This taxonomic confusion creates difficulties in providing accurate descriptions of habitats. Some references attributed here to ***P. asplenioides*** might actually be for ***P. porelloides*** in areas where both species occur.

Figure 11. ***Plagiochila asplenioides*** ventral side. Photo by Ralf Wagner, with permission.

Figure 12. ***Plagiochila porelloides*** showing the succubous leaf arrangement. Photo by Hugues Tinguy, with permission.

Distribution

Using the two-species concept, in North America, ***Plagiochila asplenioides*** subsp. ***asplenioides*** (Figure 13) occurs only in western North America, on logs, rocks, and bases of trees (Hong 1992). It occurs in Europe (Schumacker & Váňa 2000). Marsh *et al*. (2010) reported it in Finland, Paton (1999) in the British Isles, Diekmann (1995) in Sweden, Pakalne and Čakare (2001) in Latvia, Grüll and Kvét (1976) in the Czech Republic. But in East and South Asia, So and Grolle (2000) specifically exclude this species from the flora based on their examination of herbarium material.

Figure 13. ***Plagiochila asplenioides*** subsp. ***asplenioides***, an endemic in western North America. Photo from Botany Website, UBC, with permission.

Aquatic and Wet Habitats

Typical of ***Plagiochila asplenioides*** (Figure 14), but not ***P. porelloides*** (Figure 12), the former occurs on decaying logs, leaf litter, and humus in Europe (Salachna 2007). Marsh *et al*. (2010) report ***Plagiochila asplenioides*** from herb-rich forest floors and moist depressions in Finland. It can tolerate slightly higher light levels than those in the forest, occurring among the tall turf (Gimingham & Birse 1957).

Figure 14. ***Plagiochila asplenioides***, a species of logs, litter and humus in Europe, but also near streams there. Photo by David T. Holyoak, with permission.

But other reports may represent what I am including as ***Plagiochila porelloides*** (Figure 12): ground, rock, spring, and water communities in or associated with streams near Lacko, Western Carpathians (Mamczarz 1970); not common in River Tweed, UK (Holmes & Whitton 1975a, b); in intermittent rivers (Dhien 1978); in the ***Platyhypnidium*** (Figure 5) – ***Fontinalis antipyretica*** (Figure 6) association, Thuringia, Germany (Marstaller 1987); at a spring in Tara River canyon and Durmitor area, Montenegro (Papp & Erzberger 2011).

Marstaller (2012), in his studies on **epilithic** (rock-dwelling) species, considered ***Plagiochila asplenioides*** (Figure 13-Figure 18) to be **hygrophytic** (referring to plant living in location with high moisture level, but not submersed). Similarly, in Latvia, Pakalne and Čakare (2001) found ***P. asplenioides*** at the foot of river ravine slopes and in forest springs – very wet but not submersed. Baláži *et al*. (2010) termed it a **macrophyte** (easily visible aquatic plant) in the Slovak Republic. Farr *et al*. (2019) report this as a species that occurs on slightly acidic soil of vertical stream banks in the UK at tufa-forming sites. Kelly (1981) found it to be typical of stream banks, but also on limestone rocks in the forest in Killarney, Ireland.

Figure 15. ***Plagiochila asplenioides*** in a forest habitat. Photo by Hermann Schachner, through Creative Commons.

Figure 16. ***Plagiochila asplenioides***, dry, showing a typical growth form on stream banks. Photo from <www.aphotofauna.com>, with permission.

Figure 17. ***Plagiochila asplenioides***, wet, showing a typical growth form on stream banks. Photo from <www.aphotofauna.com>, with permission.

Sotiaux and Vanderpoorten (2017) again separated the two species by habitat, reporting ***Plagiochila asplenioides*** (Figure 15-Figure 17) at 1840 m asl in the montane fir woodland. By comparison, they reported ***Plagiochila porelloides*** (Figure 1, Figure 12, Figure 45) from the sub-Mediterranean to the sub-Alpine belt up to 2250 m asl on montane, base-rich siliceous rocks, shaded, humid montane siliceous rock outcrops, sub-Mediterranean to Alpine siliceous, sometimes base-rich shaded north-facing outcrops, sub-Mediterranean to sub-Alpine limestone outcrops, shaded siliceous boulders in woodlands, base-rich ground along streams, forest floor, and limestone outcrops.

Puczko *et al*. (2018) indicated that ***Plagiochila asplenioides*** (Figure 15-Figure 17) serves as an indicator of good water quality in lowland spring niches. Papastergiadou (1995) reported this species from Greek wetlands.

Cappers *et al*. (1997) reported that fragments of this species were found as part of the caulking material in shipwrecks excavated in The Netherlands, but it was not used in any abundance.

Adaptations

Proctor (1982) examined the water movement in several bryophytes. He found that bryophytes with central strands had a sustained movement of water upward and outward through transpiration, similar to the transpirational movement in tracheophytes. However, in ***Plagiochila asplenioides*** (Figure 15-Figure 17), there is no central strand and this transpirational movement does not occur.

Gupta (1977) described the effects of moisture stress on ***Plagiochila asplenioides*** (Figure 18). He found the highest solute leakage of dried plants to occur in the first two minutes of rewetting, then slowing down. He considered this rapid stoppage to be the result of reassemblage of the membrane structure or to a rapid decrease of the solutes in the injured and dead tissues. The leached solutes are resorbed by the viable cells. This is not different from that found for terrestrial mosses, but may indicate the tools they have to survive in habitats that can dry out for weeks at a time.

Figure 18. ***Plagiochila asplenioides*** dry, but retaining its green color. Photo by J. C. Schou, through Creative Commons.

Reproduction

Plagiochila asplenioides is **dioicous** (Watson 1965), but sporophytes can be found (Figure 19).

Figure 19. ***Plagiochila asplenioides*** with capsules. Photo by Hermann Schachner, through Creative Commons.

Fungal Interactions

Stenroos *et al*. (2010) found that four genera of bryophytes (out of 19 checked) exhibited the highest diversity of fungal associates: ***Plagiochila***, ***Polytrichum***, ***Ptilidium***, and ***Sphagnum***.

Döbbeler (1997) considered the ascomycete fungus ***Epibryon plagiochilae*** (Figure 20-Figure 21) to be specific on ***Plagiochila asplenioides*** (Figure 15-Figure 17) and ***P. porelloides*** (Figure 12). ***Pedinophyllum interruptum*** (Figure 2-Figure 4), in the same family **Plagiochilaceae**, does not get infected by this fungus.

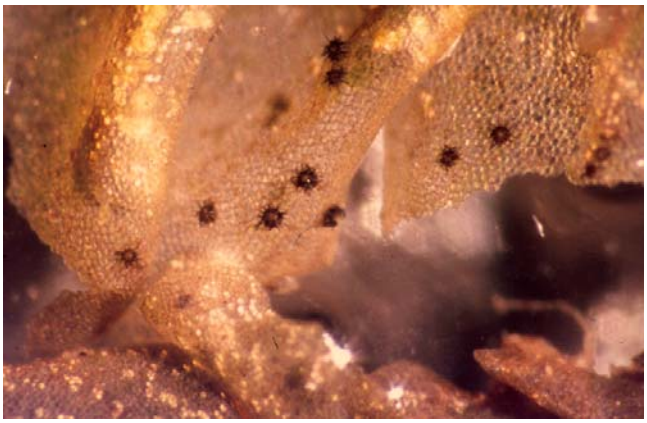

Figure 20. ***Epibryon plagiochilae*** (dark brown spots) on ***Plagiochila asplenioides*** leaves. Photo courtesy of Peter Döbbeler.

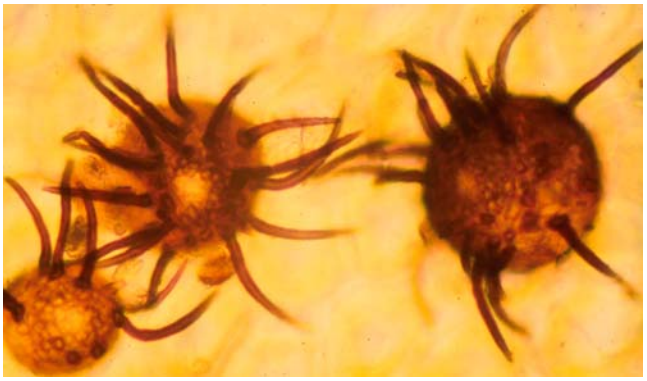

Figure 21. ***Epibryon plagiochilae*** on ***Plagiochila asplenioides*** showing the typical spider-like appearance. Photo courtesy of Peter Döbbeler.

Plagiochila asplenioides (Figure 15-Figure 17) serves as substrate for at least 7 genera and 13 species of fungi (Marsh *et al*. 2010). Out of more than 400 Finnish herbarium specimens of this species and ***P. porelloides*** (Figure 1, Figure 12, Figure 45), about 200 supported bryicolous species of fungi in the ascomycete genera ***Bryomyces*** (Figure 22-Figure 23), ***Dactylospora*** (Figure 24-Figure 25), ***Epibryon*** (Figure 8, Figure 20-Figure 21), ***Lichenopeltella*** (Figure 26), ***Octosporella*** (Figure 27-Figure 29), ***Pleostigma*** (Figure 30), and the **anamorphic** (unnatural grouping of fungi characterized by mitotic rather than meiotic production of spores – conidia) genus ***Epicoccum*** (Figure 31). ***Epibryon plagiochilae*** (Figure 20-Figure 21), a species that is apparently specific to ***P. asplenioides***, ***P. porelloides***, and ***P. britannica*** (Figure 32), shows a strong preference for the dorsal leaf border of its host liverwort, although ascomata can also occur on the stem or on female bracts and perianths. Bosanquet (2007) was delighted to discover ***E. plagiochilae*** on ***Plagiochila asplenioides*** and subsequently on ***P. porelloides*** and ***P. brittanica*** in Wales. In the next two months, he discovered this distinctive fungus on four of twelve colonies of ***P. asplenioides*** he examined and on two of three colonies of ***P. porelloides***. Many specimens of ***P. brittanica*** had the fungus, but the fungus was absent on all specimens of ***Pedinophyllum interruptum*** and all other species of ***Plagiochila***. Could it be that these species have the chemical ability to prevent the infection, or do the other **Plagiochilaceae** in Wales occur in habitats that are unsuitable for the fungus to become established?

Figure 22. ***Bryomyces velenovskyi***, in a genus known from ***Plagiochila asplenioides***, on moss leaves. Photo by George Greiff, with permission.

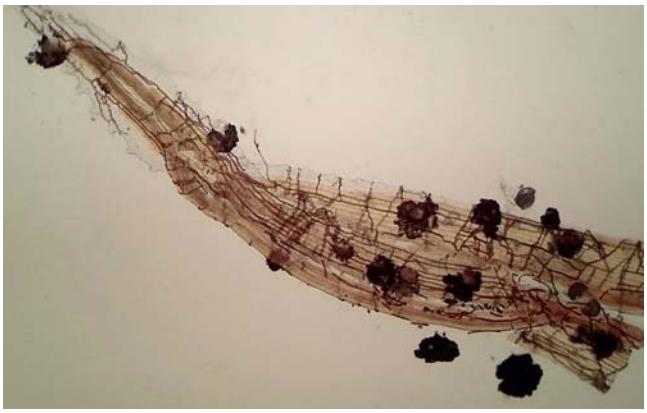

Figure 23. ***Bryomyces microcarpus*** var. ***rhacomitrii*** on moss leaf. Photo by George Greiff, with permission.

Figure 24. ***Dactylospora stygia*** on log; some members of the genus occur on ***Plagiochila asplenioides***. Photo by Milan Macalak, with permission.

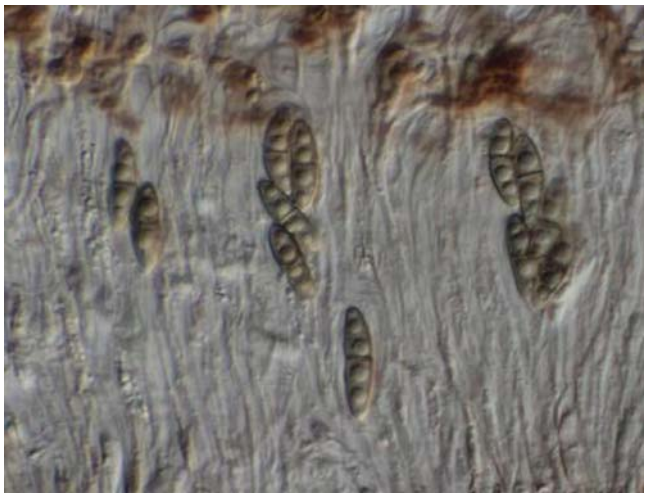

Figure 25. ***Dactylospora stygia*** asci. Photo through Creative Commons.

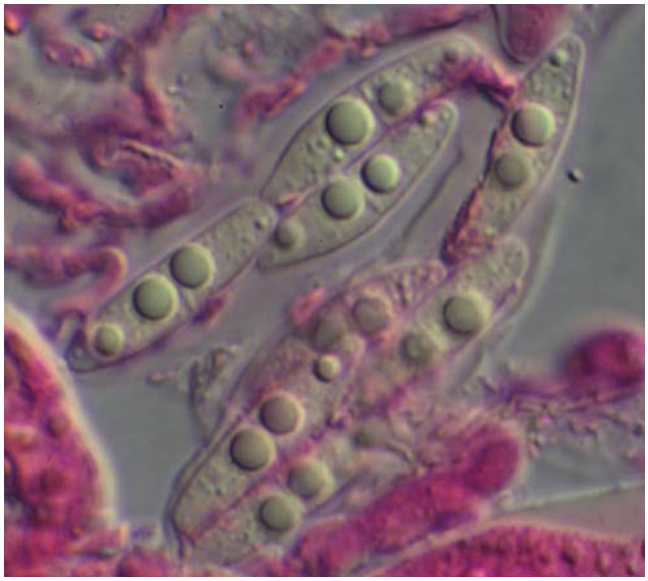

Figure 26. ***Lichenopeltella*** *santessonii* ascospores on dead *Peltigera membranacea*; some members of the genus ***Lichenopeltella*** occur on ***Plagiochila asplenioides*** leaves. Photo through Creative Commons.

Figure 27. ***Octosporella jungermanniarum*** probably, a species that occurs on ***Plagiochila asplenioides***, as shown here. Photo by Barry Stewart, with permission.

Figure 28. ***Octosporella jungermanniarum*** on ***Plagiochila asplenioides***. Photo courtesy of George Greiff.

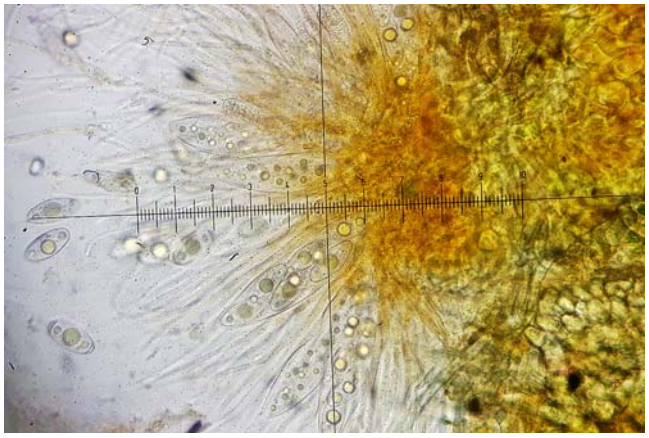

Figure 29. ***Octosporella jungermanniarum*** probably, showing ascospores. Photo by Barry Stewart, with permission.

Figure 30. ***Pleostigma jungermanniarum*** on ***Plagiochila porelloides***. Photo by courtesy of George Greiff.

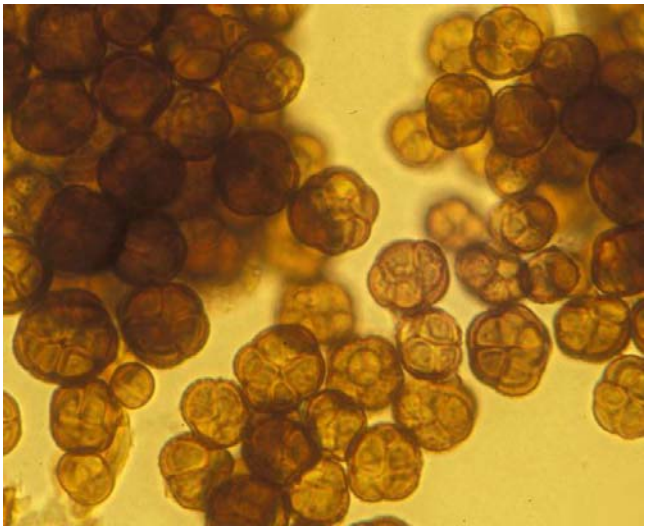

Figure 31. ***Epicoccum nigrum***; some members of this genus occur on ***Plagiochila asplenioides***. Photo by Gerald Holmes, through Creative Commons.

Figure 32. ***Plagiochila britannica***, a species that hosts the fungus ***Epibryon plagiochilae***. Photo by David S. Rycroft, with permission.

Epibryon endocarpum (see Figure 8) is another ascomycete that grows, and in this case fruits, within the cells of ***Plagiochila asplenioides*** (Döbbeler 1980). Among its adaptations is the small size of its ascomata (25-35 µm). In addition to these, George Greiff photographed ***Octosporella jungermanniarum*** (Figure 28), another ascomycete, on ***Plagiochila asplenioides***.

Biochemistry

When Suleiman and Lewis (1980) cultured ***Plagiochila asplenioides*** (Figure 15-Figure 17) in the dark for four months, the leafy plant rapidly lost starch, but little chlorophyll was lost. When revived, the tissues immediately became viable. The principal photosynthetic products were volemitol, sucrose, and starch, but the more abundant carbohydrates (fructans) were not among those most rapidly formed. Rather, conversion to fructans occurs in the prolonged four months of darkness. The starch turnover is rapid, but the volemitol and sucrose have a very slow turnover, even up to four months in the dark. This survival in the dark undoubtedly contributes to the plant's survival in the long winters in some of its more northerly locations.

Ultraviolet radiation can be a problem for bryophytes in exposed habitats. This can include wooded areas that lose the canopy leaves in winter. Whereas submersion in water reduces the effects of light, this species typically does not benefit from that habitat. Soriano *et al*. (2019) examined the role of phenolic compounds during these UV stress events. They found that the response of phenolic compounds was slow. They identified thirteen flavones in the methanol-soluble (mostly vacuolar) and two hydroxycinnamic acids in the insoluble (cell wall-bound) fractions. Only p-coumaric and ferulic acids, both from the insoluble fraction of ***Plagiochila asplenioides*** (Figure 15-Figure 17), exhibited a significant and rapid accumulation in response to UV radiation on the first day of exposure to elevated UV. This did not occur in the other leafy liverwort, the two thallose liverworts, or the two moss species. Six additional phenolic compounds accumulated during the 22 days of exposure, especially in the liverworts.

Plagiochila bifaria (Figure 33-Figure 35)

(syn. = *Plagiochila killarniensis*)

Distribution

Plagiochila bifaria (Figure 33-Figure 35) is widespread in the Neotropics, going by a variety of names (Grolle 1998; Gradstein 2015). Heinrichs *et al*. (1998a, b, 2004) argued for a broad species concept based on molecular, morphological, and phytochemical evidence. I have included here only the names I found in the aquatic literature. Heinrichs *et al*. (2004) reported it from the Western Hemisphere from Bolivia, Brazil, Costa Rica, Ecuador, Panama, and Mexico, as well as the British Isles and Tenerife on the eastern side of the Atlantic. Rycroft (2008) documented it from Venezuela and Peru. To these, Gradstein (2015) added Jamaica, Galapagos Islands, and the Barbados.

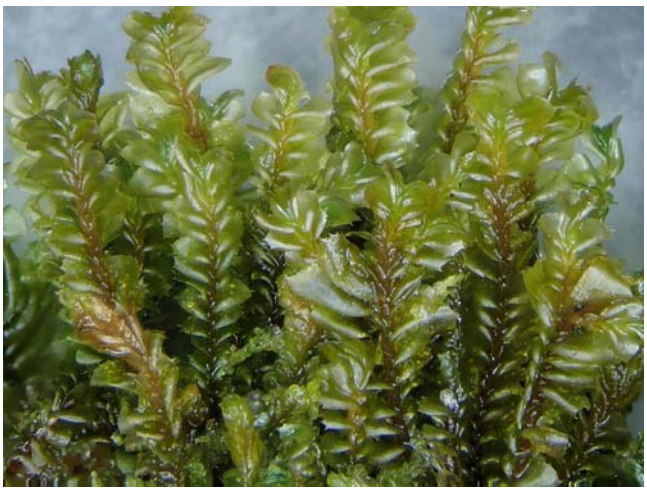

Figure 33. ***Plagiochila bifaria***, a Neotropical species, but extending into other hyperoceanic areas. Photo by Paul Bowyer, through Creative Commons.

Its range extends outside the tropics, including the Canary Islands (González M. *et al*. 2007), Madeira (Sim-Sim *et al*. 2005a), France (Hugonnot *et al*. 2013). Hugonnot *et al*. (2013) considered the species to be hyperoceanic.

Aquatic and Wet Habitats

Luis *et al*. (2015) described an aquatic habitat on Madeira Island, where it occurs at low altitudes in narrow streams and in mountainous streams with low flow. But Kürschner *et al*. (2007) found that the Madeira Island bryoflora was dominated by ***Plagiochila bifaria***, among others, that formed **tall turfs** (Figure 34-Figure 35).

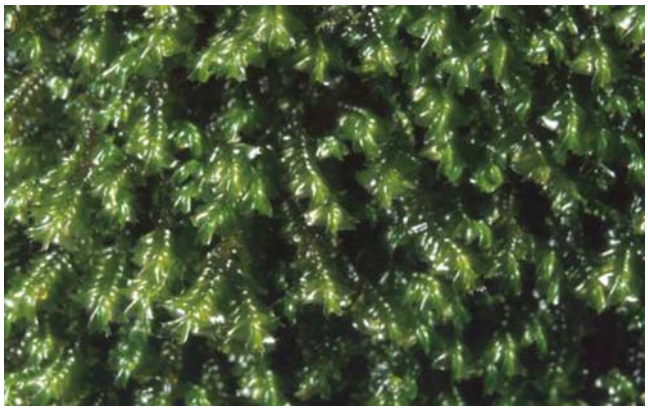

Figure 34. ***Plagiochila bifaria*** with green color, suggesting it grew in the shade. Photo by David S. Rycroft, with permission.

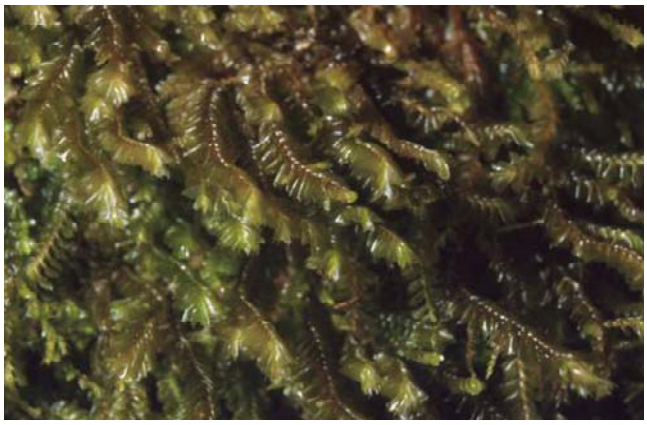

Figure 35. ***Plagiochila bifaria*** with olive-green color, suggesting sun exposure. Photo by David S. Rycroft, with permission.

In their studies on French populations, Hugonnot *et al*. (2013) reported ***Plagiochila bifaria*** (Figure 34-Figure 35) as a rock-dwelling forest species. Frahm (2013) reported it as relatively common in Italy, where it benefits from the high precipitation in the mountains. Holz *et al*. (2002) reported it as turfs on twigs and branches in Costa Rico in upper montane *Quercus* forests. On Madeira, it was the most frequent species in the Madeiran laurel forest. In the Azores, it was one of the ten most frequent species (Gabriel & Bates 2005). They found it in 88% of the bark samples and only 12% of the non-bark samples. At mid to high altitudes it is an indicator species of lower water availability and higher bark *p*H – not exactly what we would expect for an aquatic or wetland bryophyte.

Adaptations

Sim-Sim *et al*. (2005b) described the **rill-like** (upward folded, forming channel; Figure 36) leaf arrangement as an adaptation for condensing water vapor from fog and mist that is frequent at 1000-1299 m asl. This moisture permits

it to maintain a moisture status that is almost as consistent as being submersed.

Figure 36. ***Plagiochila bifaria***, from a population originally identified as ***Plagiochila killarniensis***, showing rill-like leaf arrangement. Photo by Barry Stewart, with permission.

Reproduction

Heinrichs *et al*. (1998a) noted that the perianths of ***P. bifaria*** (Figure 34-Figure 35) became rarer toward the northern limits of distribution. Most of the fertilized archegonia appear to be confined to Macaronesia, whereas descriptions of younger perianths with no fertilization led to conflicting descriptions that supported spurious species separations, especially that of ***Plagiochila killarniensis*** (Figure 36), now considered a synonym (TROPICOS 2020). The Macaronesian perianths match those occurring in the Neotropics. This is consistent with the formation of sporophytes in the Neotropics and Macaronesia, but not in continental Europe (Heinrichs *et al*. 2004).

Biochemistry

Plagiochila bifaria has distinct oil bodies (Figure 37), suggesting the presence of secondary compounds that could be adaptive. Although the ecological information on this species is relatively sparse, it has undergone several biochemical studies. Hackl *et al*. (2006) isolated and identified three eudesmane type sesquiterpenes from ***Plagiochila bifaria***. Rycroft (2008) described what appears to be the first example of a monocyclic 4-pyrone that has a polyketide origin. Heinrichs *et al*. (2004) used the biochemical composition of the species to delineate clades within the species, with indications that the basal clade is represented in Costa Rica, Brazil, and Bolivia, concluding that the differences among clades did not support differences at the species level. Rycroft *et al*. (1999) determined that certain minor components were common to both the European ***Plagiochila killarniensis*** (Figure 36) and the Neotropical populations treated as ***Plagiochila bifaria*** (Figure 34-Figure 35). Like Heinrichs and coworkers, they considered the biochemical differences between Scottish populations and those of the Azores to be minor.

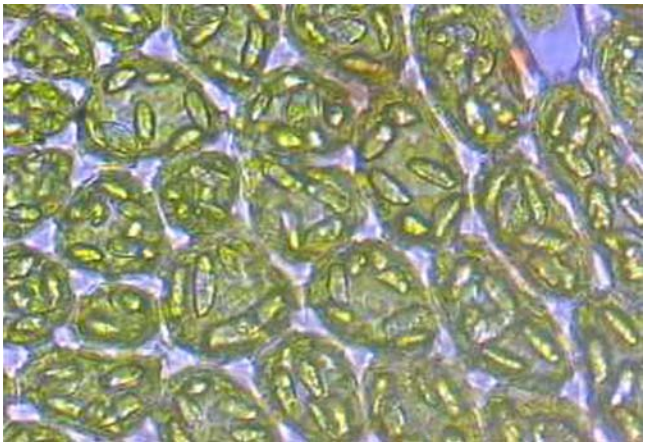

Figure 37. ***Plagiochila bifaria*** oil bodies (ovals in cells), a site of secondary compounds. Photo by David Rycroft, with permission.

Plagiochila porelloides (Figure 38-Figure 43)

(syn. = *Plagiochila asplenioides* var. *major*)

Distribution

In eastern North America, this species was for a long time interpreted as ***Plagiochila asplenioides***. Since it was later determined that these were instead ***Plagiochila porelloides***, I have herein included the eastern North American populations reported as ***P. asplenioides*** as ***P. porelloides***.

Plagiochila porelloides (Figure 38-Figure 43) is a circumboreal species (Sim-Sim *et al*. 2005a) distributed throughout Europe, including the Arctic, becoming submontane in the south (Hill *et al*. 1991). Ros *et al*. (2000) added it to Morocco in Africa. In Europe, it occurs in the Nordic countries (Schumacker & Váňa 2000; Damsholt 2002), in the British Isles (Paton 1999), in Greece and Poland (Cronberg 2000a, b), and in Germany in the forest (Marstaller 2007). Sim-Sim *et al*. (2005a) reported it as rare in the Madeiran laurel forests, but it occurred there in some sites that had high biodiversity and several rare species. In North America, it occurs from 82º32'N to the southeastern Coastal Plain in the east and California and Arizona in the west (Schuster 1980).

Figure 38. ***Plagiochila porelloides***, a species of stream banks in eastern and western North America and Europe. Photo by Hermann Schachner, through Creative Commons.

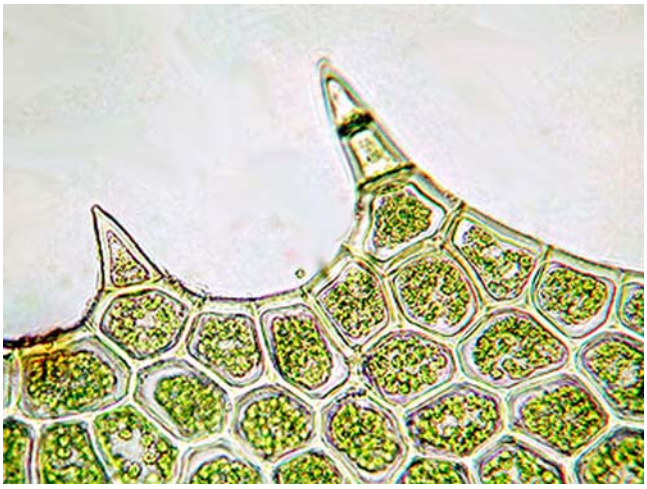

Figure 39. ***Plagiochila porelloides*** leaf teeth. Photo from Botany Website, UBC, with permission.

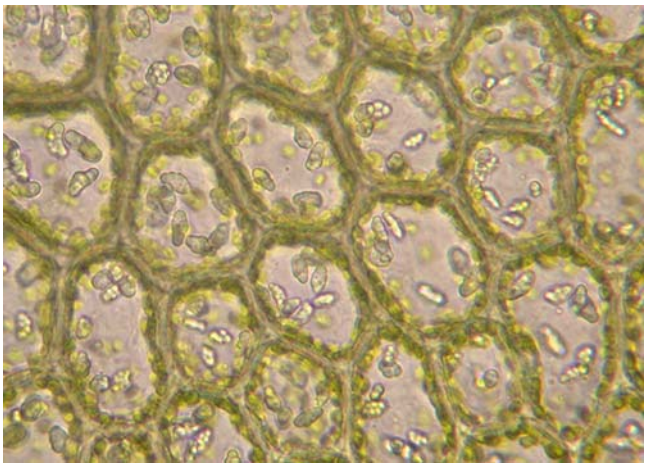

Figure 40. ***Plagiochila porelloides*** leaf cells showing oil bodies and peripheral chloroplasts. Photo from Botany Web Page, UBC, with permission.

Figure 41. ***Plagiochila porelloides*** in hydrated state. Photo by Štěpán Koval, with permission.

Figure 42. ***Plagiochila porelloides*** beginning to dry. Photo by Hermann Schachner, through Creative Commons.

Figure 43. ***Plagiochila porelloides*** showing leaves rolling as it dries out. Photo by Štěpán Koval, with permission.

Söderström *et al*. (1999) reported ***Plagiochila porelloides*** (Figure 38-Figure 43) from China in the Changbai Mountain, where it occurred on boulders, in the alpine heathland, and on decaying logs. Konstantinova, among others, (2011) documented it in the Eastern Caucasus of Russia, where it is often abundant.

Aquatic and Wet Habitats

Schuster (1980) comments that its wide variability in form is concurrent with a wide variability in habitat. It can, although rarely, be in xeric extremes at one end of its ecological spectrum to hydric, its most common form, at the other. It is very rarely submerged. Schuster considers it to be most common on moist rocks. And unlike most members of the genus, ***P. porelloides*** (Figure 38-Figure 43) tolerates high insolation when moisture is adequate. Because of its wide range of habitat conditions, it can be

found with nearly half the species of liverworts found in eastern North America. Its occurrence over such a wide north-south geographic range coincides with its wide temperature tolerance, more than is known for any other member of the genus.

In North America, Nichols (1918) reported ***Plagiochila asplenioides*** (Figure 15-Figure 17) from streambanks and wet rock cliffs associated with streams, Cape Breton Island, Canada, but in this location it was most probably ***Plagiochila porelloides*** (Figure 38-Figure 43). Elsewhere in North America, ***P. porelloides*** occurs on wet or moist cliffs of ravines and on moist rock surfaces or springy banks of ravines in Connecticut, USA (Nichols 1916); in Appalachian Mountain, USA, streams (Glime 1968); just above the water surface most of the year in a headwater stream in New Hampshire, USA (Glime 1970); on the wall in the Flume at Franconia Notch, New Hampshire, USA (Glime 1982); in Adirondack Mountain streams (Slack & Glime 1985; Glime *et al*. 1987); but it is a restricted terrestrial of montane streams and streambanks in western Canada (Vitt *et al*. 1986; Glime & Vitt 1987), perhaps due to the strong flow and spring flooding there. In Minnesota, it occurs in mesophytic calcareous communities, on peat-covered banks, much disintegrated decaying wood, and over wet to saturated humus in ***Thuja***-spruce-fir forests (Figure 44).

Figure 44. ***Thuja***-spruce-fir swamp in Michigan, USA, a suitable habitat for ***Plagiochila porelloides***. Photo from National Park Service, through public domain.

On Cygnes Mountain, Québec, Canada, it occurs on moist granitic rock in mid stream (Kucyniak 1947). In Quaker Run, New York, Matthews (1932) likewise found it on rocks midstream in a stream with a gentle gradient and numerous small waterfalls. It is not uncommon to find ***Plagiochila porelloides*** (Figure 38-Figure 43) just above the water level (Figure 45) in streams in the Appalachian Mountains of the eastern USA, above but close to the water surface (Figure 45), occasionally becoming submersed (Glime 1970). This keeps it moist most of the time, dry occasionally, and submersed in high water. Similarly, in Cataracts Provincial Park, Newfoundland, Canada, Weber and Brassard (Weber 1976; Weber & Brassard 1976) found it in the inundation zone where it is periodically submerged and exposed as the water level rises and falls along the river. It also occurred in the next higher zone on the river bank.

Plagiochila porelloides subsp. ***porelloides*** occurs on cliffs, damp soil banks, decayed wood, and bark of trees (Figure 1) in western North America from Alaska southward to California, USA and in damp, calcareous high Arctic tundra (Hong 1992).

Figure 45. ***Plagiochila porelloides*** just above water level and ***Fontinalis novae-angliae*** just below the water level, in a stream in New Hampshire, USA. Photo by Janice Glime.

In Europe, ***Plagiochila porelloides*** (Figure 1) occurs on rocks or soil of fast streams (Watson 1919); in the arctic-alpine zone of the UK (Watson 1925); in the ***Platyhypnidium*** (Figure 5) – ***Fontinalis antipyretica*** (Figure 6) association, in Thuringia, Germany (Marstaller 1987); submersed in low-buffered water of streams (Tremp & Kohler 1991); on stream boulders above mean water level, with low cover and high frequency in Finland (Virtanen 1995); springs in Finland (Heino *et al*. 2005); common in flood valleys of Upper Bureya River (Russian Far East) (Konstantinova *et al*. 2002); emerged and vertical stony streambanks or in waterfall margins, pure patches usually not extensive, associated with ***Thamnobryum alopecurum*** (Figure 46) and ***Lejeunea cavifolia*** (Figure 47) in mountain streams of northwest Portugal (Vieira *et al.* 2005); in irrigation ditches in Spain (Beaucourt *et al.* 1987); on montane, base-rich siliceous rocks, shaded, humid montane siliceous rock outcrops, sub-Mediterranean to Alpine siliceous, sometimes base-rich shaded north-facing outcrops, sub-Mediterranean to sub-Mediterranean to Alpine siliceous, sometimes base-rich shaded north-facing outcrops, sub-Mediterranean to sub-Alpine limestone outcrops, shaded siliceous boulders in woodland from the sub-Mediterranean to the sub-Alpine belt at 2550 m asl, on base-rich ground along streams, forest floor, and limestone outcrops from the Mediterranean to the sub-Alpine belt in Andorra (Sotiaux & Vanderpoorten 2017).

Figure 46. ***Thamnobryum alopecurum***, an associate of ***Plagiochila porelloides*** in wet, vertical habitats in Europe. Photo by Hugues Tinguy, with permission.

Figure 47. ***Lejeunea cavifolia***, an associate of ***Plagiochila porelloides*** in wet, vertical habitats in Europe. Photo by Hermann Schachner, through Creative Commons.

Plagiochila porelloides (Figure 38-Figure 43, Figure 53-Figure 55) can be found in the Iskur River, Bulgaria, and its main tributaries (Papp *et al.* 2006) and as a mesophyte in Bulgarian rivers (Gecheva *et al*. 2010, 2013). It occurs on limestone rock and on bark of ***Pinus*** (Figure 48) at a stream in the Tara river canyon and Durmitor area, Montenegro (Papp & Erzberger 2011); in the upper course in Maritsa River, Bulgaria (Gecheva *et al*. 2011). In the Madeiran laurel forests, ***Plagiochila porelloides*** grows on moist, shady rocks, forming isolated, small mats near populations of other bryophytes such as ***Andoa berthelotiana*** (Figure 49), ***Fissidens luisieri*** (Figure 50), ***Thamnobryum maderense*** (Figure 51), ***Porella canariensis*** (Figure 52), and ***Plagiochila bifaria*** (Figure 33-Figure 35) (Sim-Sim *et al*. 2005a).

Figure 48. ***Pinus*** bark, a substrate where ***Plagiochila porelloides*** can occur in Montenegro. Photo by SusquehannahMan, through Creative Commons.

Figure 49. ***Andoa berthelotiana*** with capsules, a species that often occurs near small mats of ***Plagiochila porelloides***. Photo by Michael Lüth, with permission.

Figure 50. ***Fissidens luisieri***, a species that often occurs near small mats of ***Plagiochila porelloides***. Photo by Jan-Peter Frahm, with permission.

Figure 51. ***Thamnobryum maderense***, a species that often occurs near small mats of ***Plagiochila porelloides***. Photo by Michael Lüth, with permission.

Figure 52. ***Porella canariensis***, a species that often occurs near small mats of ***Plagiochila porelloides***. Photo by Paulo A. G. Borges, with permission through Azoresbioportal.

For Portuguese streams, Vieira *et al*. (2004) reported that ***Plagiochila porelloides*** (Figure 53-Figure 55) was threatened. It occurs there in seasonally emerged locations on vertical stony stream banks (Figure 53) or at waterfall margins, both habitats where it remains wet most of the time and could be occasionally submerged. Its patches were extensive, often pure, but typically not well

developed. It was always found lacking sexual reproductive structures.

Figure 53. ***Plagiochila porelloides*** on a vertical substrate. Photo from Botany Web Page, UBC, with permission.

In Russia, ***Plagiochila porelloides*** (Figure 53-Figure 55) was recorded in some areas as ***P. asplenioides*** (Figure 13-Figure 18), but has since been determined to be ***P. porelloides*** (Konstantinova 2011). It occurs in a canyon with a rivulet, in deep ravines, on loamy and sandy soil on stream banks, but also on soil, rocks, decaying shaded wood, grasses and rocks in the mountain steppe, and in rock crevices, on ledges, and between boulders.

Adaptations

Color forms occur in response to solar radiation. In exposed sites, the plants are yellowish green (Figure 53-Figure 55); in the shade they can reach a deep green or dull olive green (Figure 41-Figure 43), but not brown (Schuster 1980).

Figure 54. ***Plagiochila porelloides***, showing a more yellowish green coloration of a species grown in an exposed site. Photo by Štěpán Koval, with permission.

Reproduction

The species is **dioicous**, with male plants slightly smaller than the females. Nevertheless, sporophytes (Figure 55) are present in at least part of the distribution, so some isozyme variability should be present in some areas.

Figure 55. ***Plagiochila porelloides*** with capsules. Štěpán Koval, with permission.

Cronberg (2000a,b) found a total absence of genetic variation in Greek and southern Scandinavian populations when comparing 16 isozyme loci. The study included areas that had been severely and mildly affected by the Pleistocene glaciations and supported an earlier study that found no variation among Polish populations. He suggested that the present-day populations may have passed through a severe bottleneck that reduced or eliminated the variability.

When Kowalczyk *et al.* (1997) cultured fragments of ten liverwort species, ***Plagiochila porelloides*** (Figure 54-Figure 55) was among them. The first problem in such studies is to obtain sterile material, which is difficult with wet and aquatic bryophytes where the surface is often replete with bacteria, algae, protozoa, and detritus, not to mention insects. They successfully sterilized this species with commercial bleach diluted 1:1 and 1:3 with distilled water with optimal time of 0.5-2.0 minutes. (I have found that longer exposures kill the bryophytes or at least destroy most of the chlorophyll.) The fragment should be no more than 3 mm long and should be obtained from a leafless branch or shoot tip.

Fungal Interactions

Marsh *et al*. (2010) compared the fungi on ***Plagiochila porelloides*** (Figure 54-Figure 55) and those (Figure 22-Figure 31) on ***P. asplenioides*** (Figure 13-Figure 18) in Finland. The former liverwort occurred on bases and crevices of shady silicate boulders, sometimes by brooks or on dead wood in shady forests, whereas the latter occurred mostly on herb-rich forest floors and in moist depressions. Thirteen species of bryicolous fungi are known to occur on one or both of these two species. Most of those found by Marsh and coworkers positioned their apothecia in leaf axils or perianths. The fungus ***Epibryon plagiochilae*** (Figure 20-Figure 21), however, strongly prefers the dorsal leaf border, although ascomata can occur on the stem or on female bracts and perianths. Although this fungus species has a strong preference for ***P. asplenioides***, it also occurs

on ***P. porelloides***, but much less frequently. ***Pleostigma jungermannianum*** likewise occurs on both ***P. porelloides*** and ***P. asplenioides*** (Figure 30).

Biochemistry

One can easily see oil bodies (Figure 56) in fresh cells, indicating the presence of secondary compounds. Toyota *et al*. (1994) verified the presence and established the structure of three sesquiterpene esters in ***Plagiochila porelloides*** (Figure 54-Figure 55). Asakawa *et al*. (1980) identified sesquiterpenoids from fourteen species of ***Plagiochila***, including ***P. porelloides***, identifying some that caused the distinctive odors.

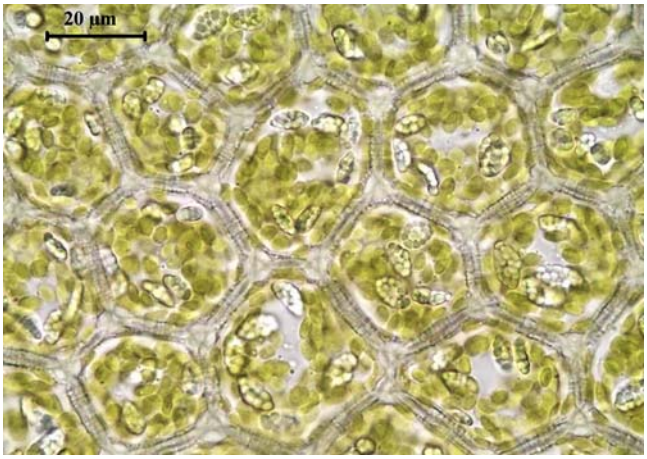

Figure 56. ***Plagiochila porelloides*** leaf cells showing oil bodies among the chloroplasts. Photo by Hugues Tinguy, with permission.

Plagiochila punctata (Figure 57-Figure 59)

(syn. = *Plagiochila stolonifera*, *Plagiochila choachina*, *Plagiochila patzschkei*, *Plagiochila subalpina*)

Distribution

Plagiochila punctata (Figure 57-Figure 59) is widespread in Neotropical mountains, but has, like so many tropical species, been known by a number of names now considered to be synonyms (Heinrichs *et al*. 2005). As a result of understanding its synonymy, it has been documented for Scotland, Spain, tropical Africa, Tanzania, Madagascar, Zaire, Karthala volcano (in Indian Ocean), Mexico, Venezuela, Ecuador, Colombia, Brazil, Bolivia, Costa Rica, and Dominican Republic. In 2006, Davison *et al*. added a record of ***Plagiochila punctata*** to the flora of Tennessee, USA.

Aquatic and Wet Habitats

Watson (1919) reported that ***Plagiochila punctata*** (Figure 58) is occasionally submerged. In the tropics, it is restricted to mountains, but it also occurs in Europe (Figure 58), where it occurs in the lowlands up to 1000 m asl. The feather-like habit is more common in the tropics than in Europe. But it is not always aquatic or in wetlands. It can also grow as an epiphyte (Figure 59).

Figure 57. ***Plagiochila punctata*** (larger plants with large teeth), a widespread and occasionally submerged species in Neotropical mountains. Photo by Paul Bowyer, through Creative Commons.

Figure 58. ***Plagiochila punctata*** growing on a vertical substrate. Photo by David Rycroft, with permission.

Figure 59. ***Plagiochila punctata*** growing as an epiphyte. Photo by Michael Lüth, with permission.

Reproduction

Plagiochila punctata (Figure 57-Figure 59) is **dioicous** (Gradstein *et al*. (2001).

Fungal Interactions

Plagiochila punctata (Figure 57-Figure 59) has several interesting interactions with other organisms. Döbbeler and Feuerer (2004) reported that ***Stenocybe***

nitida, an ascomycete, occurs on this liverwort species. Pilato *et al*. (2002) reported tardigrade specimens and eggs from ***Plagiochila punctata*** from the Otonga Forest in Ecuador and another two specimens from this liverwort in Alto Tambo, Ecuador.

Plagiochila renitens

Plagiochila renitens occurs in Australia and southern Asia (ITIS 2020). Its habitats are poorly reported. Ruttner (1955) reported it from acidic thermal spray in the tropics, but little else seems to connect it to aquatic or wetland habitats.

Plagiochila retrospectans (Figure 60) and *Plagiochila fuscella* (Figure 61)

Distribution

Engel and Merrill (2009) argued that ***Plagiochila retrospectans*** (Figure 60) does not occur in New Zealand, and specimens labelled with this name are actually ***Plagiochila fuscella*** (Figure 61), a New Zealand endemic. Nevertheless, ***Plagiochila retrospectans*** is known from Victorian rainforest streams in Australia (Carrigan & Gibson 2004; Fleisch & Engel 2006) and from the subAntarctic Macquarie Island (Hughes 1986), but the records of Suren (1988) from high alpine streams in New Zealand may actually be ***Plagiochila fuscella***, making that species one of the two dominant liverwort species in those streams.

Figure 60. ***Plagiochila retrospectans***, a Southern Hemisphere species that includes the subAntarctic. Photo by David Tng, with permission.

Figure 61. ***Plagiochila fuscella***, a segregate from ***Plagiochila retrospectans***, that occurs in New Zealand. Photo through Creative Commons.

Aquatic and Wet Habitats

In Cement Creek in Victoria, Australia, ***Plagiochila retrospectans*** (Figure 60) forms **cushions** on stream rocks (Carrigan and Gibson 2004). In New Zealand, ***P. fuscella*** (Figure 61) is especially common in chutes. On South Island, NZ, ***P. fuscella*** is in the group of species that prefer the highest number of days with low flow events, but also with the highest number of floods (Suren 1996). Wells *et al*. (1998) reported it from the 0-5 m sampling depth in a lake in New Zealand, but with low cover values.

Role

Plagiochila fuscella (Figure 61) is important for some aquatic invertebrates, especially insects. In the open headwater tributary of Otira River and shaded tributary of Bealy River, New Zealand, it occurred in 29% and 27% of the invertebrate guts, respectively (Suren & Winterbourn 1991). The liverworts provide habitat for the insects, substrate for periphyton, collector of detritus, and refuge from high flow (Suren 1991). This makes them ideal for oviposition and safe sites for small larvae and naiads while providing an abundant food source. Furthermore, ***P. fuscella*** contained the most CPOM, perhaps accounting for the greatest abundance of the stonefly ***Austroperla cyrene*** (Figure 62-Figure 63) and the mites **Oribatida** sp. B and ***Paratryssaturus*** sp. (Figure 64) occurring there compared to mosses.

Figure 62. ***Austroperla cyrene*** naiad, a resident on ***Plagiochila fuscella*** in New Zealand. Photo by James Cooper, through Creative Commons.

Figure 63. ***Austroperla cyrene*** adult on bryophytes. Photo by Jacob Littlejohn, through Creative Commons.

Figure 64. ***Paratryssaturus cantermus***, a mite that inhabits ***Plagiochila fuscella*** in New Zealand. Photo modified from TePapa website, through Creative Commons.

Biochemistry

Nagashima *et al*. (1994) reported a new sesquiterpenoid from ***Plagiochila fuscella*** (Figure 61) in New Zealand.

Plagiochila spinulosa (Figure 65-Figure 69)

Distribution

Plagiochila spinulosa (Figure 65-Figure 69) is predominantly an eastern Holarctic species, but it also occurs in Lesotho in southern Africa and both North and South Islands of New Zealand (Renner *et al*. 2017; Renner 2018). González-Mancebo *et al*. (2009) reported that records of this species from the Canary Islands were actually other species, but that it does occur on the more temperate Madeira (Sim-Sim *et al*. 2005a).

Figure 65. ***Plagiochila spinulosa***, a species distributed mostly in the eastern Holarctic. Photo by Michael Lüth, with permission.

Figure 66. ***Plagiochila spinulosa***, a species distributed mostly in the eastern Holarctic. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

Watson (1919) described ***Plagiochila spinulosa*** (Figure 65-Figure 69) as a species of waterfalls, occasionally becoming submerged. But in Scotland, it occurs in the Atlantic oakwood, forming large cushions or patches (Figure 67) on terrestrial rocks and tree trunks (Figure 68). Proctor (1980) found that this species in similar wooded habitats of the British Isles (Figure 69) received its peak irradiance in the spring before leaf expansion. On the Iberian Peninsula of northern Spain, Qlivan and Fuertes (2000) found it on wet acidic rocks and on quartzite rocks near the River Sobra. Renner (2018) reports that ***Plagiochila spinulosa*** occurs in a variety of habitats on South Island, New Zealand, including the low windswept broadleaf forest, tall ***Nothofagus***-dominated forest (Figure 70), waterfalls, cliff faces (Figure 71), and alpine herbfield. It also grows there as a lithophyte on cliff faces.

Figure 67. ***Plagiochila spinulosa*** habitat forming large cushion. Photo by Michael Lüth, with permission.

Figure 68. ***Plagiochila spinulosa*** on a birch log in Scotland. Photo by Michael Lüth, with permission.

Figure 69. ***Plagiochila spinulosa*** in a wooded habitat in England. Photo by Janice Glime.

Figure 70. ***Nothofagus*** forest, Western Ruahine Ranges, NZ. Photo courtesy of Marie-Claude Lariviere.

Figure 71. ***Plagiochila spinulosa*** on a vertical substrate. Photo by Barry Stewart, with permission.

One indication for the preference of ***Plagiochila spinulosa*** for moist sites is its sensitivity to desiccation. In their comparison of ten species of bryophytes regarding recovery from desiccation, Dilks and Proctor (1974) found that net assimilation and respiration of ***Plagiochila spinulosa*** and ***Hookeria lucens*** (Figure 72) showed the greatest sensitivity. Further details were added by Dilks and Proctor (1979), with indications of greater variability of water content in xeric species than in woodland species.

Figure 72. ***Hookeria lucens*** with capsules, a species that along with ***Plagiochila spinulosa*** showed the greatest sensitivity to drying. Photo by Michael Lüth, with permission.

Reproduction

Species in the group with ***Plagiochila spinulosa*** have **caducous** (easily detached; Figure 73-Figure 74) leaves that break at the base (Renner 2018) and permit them to reproduce asexually. These can account for both short- and long-distance dispersal.

Figure 73. ***Plagiochila spinulosa*** showing the portions of stems with lost leaves (caducous leaves). Photo by Paul Bowyer, through Creative Commons.

Figure 74. ***Plagiochila exiguua*** dispersing caducous leaves. Photo by Des Callaghan, with permission.

Fungal Interactions

Wang and Qiu (2006) found no references to document the presence of mycorrhizae in ***Plagiochila spinulosa*** (Figure 66-Figure 67, Figure 71-Figure 73).

Biochemistry

Rycroft *et al*. (2002) noted that one can distinguish between ***Plagiochila spinulosa*** (Figure 66-Figure 67, Figure 71-Figure 73) and ***P. stricta*** by the odors of the crushed plants. Hiroshi and Asakawa (1988) described oil body types and chemical constituents in ***P. spinulosa***, most of which are identical with those of ***P. exigua*** (Figure 75), a species that also has caducous leaves (Figure 74). Connolly *et al.* (1999) and Rycroft *et al*. (1999) identified some of the aromatic compounds in ***P. spinulosa***. Sim-Sim *et al*. (2005c) used the composition of the essential oils to verify the presence of ***P. spinulosa*** at elevations above the Madeira laurel forest where it is a hyper-humid zone.

Figure 75. ***Plagiochila exigua***, a species with secondary compounds like those of ***Plagiochila spinulosa***. Photo by Michael Lüth, with permission.

Plagiochila spinulosa (Figure 66-Figure 69, Figure 71-Figure 73) produces **volemitol** as one of its photosynthetic sugar products (Suleiman *et al*. 1980). It would be interesting to know if this product is in any way connected to its preference for moist habitats. In the intertidal brown alga *Pelvetia canaliculata*, concentrations of both mannitol and volemitol increased with increases in temperatures up to 27ºC (Pfetzing *et al*. 2000). Continuous emersion elicited no changes in concentrations of these two sugars at 10ºC for 7 days, but when the algae were emersed continuously for 8 or 12 days at 25ºC the volemitol concentrations exhibited significant decrease but mannitol concentrations did not change significantly. In its circumpolar distribution ***Plagiochila spinulosa*** is not likely to encounter such high temperatures in water, but above water it could encounter them for brief periods.

Rycroft (1990) identified two new bibenzyl-fusicoccane conjugates. Anton *et al*. (1997) identified hydroxy-4'-methoxy-bibenzyl in ***Plagiochila spinulosa*** (Figure 66-Figure 67, Figure 71-Figure 73).

One compound identified is **lunularic acid** (Rycroft *et al*. 1999), a hormone that has similar activity to that of abscisic acid and may help it to live in its wide range of habitats.

Plagiochilion oppositum (Figure 76)

Distribution

Plagiochilion oppositum (Figure 76) has a widespread distribution, including Australia, China, Fiji, India (West Bengal, southern Western Ghats, Eastern Himalaya, and Northeast India), Indonesia, Japan, Malaysia, Myanmar, New Caledonia, New Guinea, Philippines, Samoa, Solomon Islands, Sri Lanka, Taiwan, Thailand, Vanuatu, and Vietnam (Daniels & Kariyappa 2012). Renner *et al*. (2016) noted the variability of the species, but concluded that it "contains significant phylogenetic substructuring that is not necessarily the result of geographic isolation."

Figure 76. ***Plagiochilon oppositus***, Yunnan, China. Photo courtesy of Li Zhang.

Aquatic and Wet Habitats

Ruttner (1955) reported ***Plagiochilion oppositum*** (Figure 76) from waterfalls in the tropics. But it appears that this species is more typical of montane forests (Gradstein *et al*. 2010; Daniels 2020). In West Java, it occurs on bark at higher elevations. It is typical in tropical montane evergreen forests and wet evergreen forests (Daniels 2020). In Sulawesi it occurs in both lowland and montane forests (Nunik & Gradstein 2007).

Trichocoleaceae

Trichocolea tomentella (Figure 77-Figure 86)

Distribution

Trichocolea tomentella (Figure 77-Figure 86) is distributed in the temperate regions in the Northern Hemisphere, where it is mostly oceanic and suboceanic (Korpelainen *et al*. 2004). It occurs in Africa, Oceania, Australia, the Caribbean islands, Europe, Asia, Central America, and North America (ITIS 2020), with the largest number of known locations in Europe and North America. In New Zealand, there are four species of ***Trichocolea***, but not ***T. tomentella*** (Hatcher 1958). These are forest species, on the ground or as epiphytes.

Figure 77. ***Trichocolea tomentella*** leaf, a highly dissected structure. Photo by Hermann Schachner, through Creative Commons.

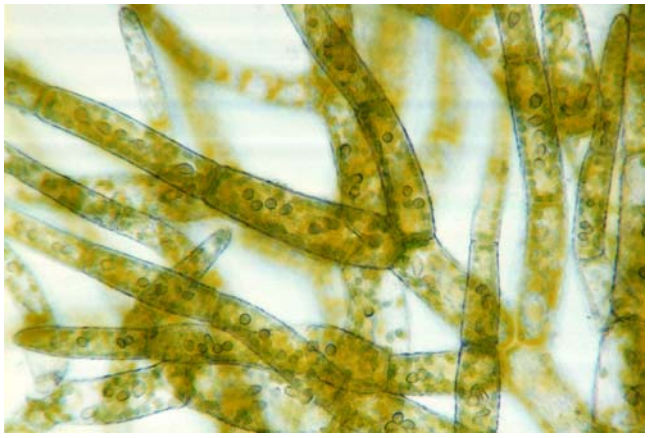

Figure 78. ***Trichocolea tomentella*** microscopic view showing chloroplasts and the very different arrangement of cells when compared to most leafy liverworts. Photo through Creative Commons.

Figure 79. ***Trichocolea tomentella*** forming clumps like one can find in a wetland. Photo by Hugues Tinguy, with permission.

Figure 80. ***Trichocolea tomentella*** with red pigmentation, suggesting it has been exposed to bright sunlight. Photo by Rick Ballard, through Creative Commons.

Aquatic and Wet Habitats

Because of its moisture requirements, ***Trichocolea tomentella*** (Figure 81-Figure 84) is habitat limited, occurring in springs and mesic habitats in woodlands.

Figure 81. ***Trichocolea tomentella*** showing its branching pattern. Note the whitish color of the dry form. Photo by Almantas Kulbis, through Creative Commons.

Figure 82. ***Trichocolea tomentella*** wet. Note the change in color to green in the wet form. This results from water filling in the spaces and probably activates the chloroplasts. The reflection of light waves by dry cells might account for the color change when water fills in the spaces. Photo by Li Zhang, with permission.

Figure 83. ***Trichocolea tomentella*** dry, showing the tight spacing of the leaf dissections. Photo by Erika Mitchell, through Creative Commons.

Figure 84. ***Trichocolea tomentella***, showing water clinging in the many capillary spaces, permitting it to remain hydrated longer. Photo by Hermann Schachner, through Creative Commons.

Trichocolea tomentella (Figure 77-Figure 86) grows in shaded and humid habitats in seminatural or natural forests (Korpelainen *et al*. 2004). It is a vulnerable species in Finland and rare in Lithuania, while declining in southern England due to habitat loss (Korpelainen *et al*. 2004). Likewise, in southern Norway it is becoming extinct in many localities due to logging and draining near streams, springs, and gullies (Rydgren *et al*. 2012).

In Norway and Sweden, ***Trichocolea tomentella*** (Figure 77-Figure 86) occurs mostly in moist, well-shaded places, especially in deciduous forests (Figure 85) (Rydgren *et al*. 2012). It is common near springs, streams (Figure 86), and gullies. In earlier studies, Watson (1919) reported it from ground associated with fast water. Mamczarz (1970) reported it from a spring community in streams near Lacko, Western Carpathians. Marstaller (1987) reported it as occurring with the ***Platyhypnidium*** (Figure 5) **–** ***Fontinalis antipyretica*** (Figure 6) association in Thuringia, Germany. In northwest Portugal, Vieira *et al*. (2005) reported it in dripping and steep granite slabs in fresh environments, associated with ***Sphagnum subsecundum* var. *auriculatum*** (Figure 87), ***Fissidens polyphyllus*** (Figure 88), and ***Radula holtii***, in mountain streams, and similarly, Vieira *et al*. (2004) found it on dripping and steep granite slabs in Portugal. In Latvia, it not only occurs in the swampy spruce and mixed forests, but also on brook banks and springs (Bambe 2004).

Figure 85. ***Trichocolea tomentella*** on a tree base, with melting snow. Photo by Ekaterina Rozantseva, through Creative Commons.

Figure 86. ***Trichocolea tomentella*** on a stream bank. Photo Erika Mitchell, through Creative Commons.

Figure 87. ***Sphagnum subsecundum*** var. ***auriculatum***, a species that associates with ***Trichocolea tomentella*** on dripping, steep granite slabs in Portugal. Photo by Hugues Tinguy, with permission.

Figure 88. ***Fissidens polyphyllus***, a species that associates with ***Trichocolea tomentella*** on dripping, steep granite slabs in Portugal. Photo by Michael Lüth, with permission.

These records adequately describe most of its habitat in North America and other locations as well (Schuster 1953). Slack and Glime (1985) found it associated with Adirondack Mountain, USA, forest streams. In their study

of 138 localities in the Polish Carpathians, Klama *et al*. (2019) concluded that ***Trichocolea tomentella*** (Figure 77-Figure 86) prefers wetland habitats, primarily in forests (Figure 89). These included areas in the vicinity of springs (34% stands), stream banks (32%; Figure 86), wet parts of the forest floor (20%), and mountain bogs (16%). The species is diminishing in frequency due to the loss of these habitats.

Figure 89. ***Trichocolea tomentella*** growing on a vertical bank. Photo by Bernd Haynold, through Creative Commons.

Vieira *et al*. (2004) reported that some populations of ***Trichocolea tomentella*** (Figure 77-Figure 86, Figure 89) in Portugal streams are threatened by human trampling in areas with easy access. They never found it fertile in the three years (2001-2004) that they studied it. It is a vulnerable species in Finland and rare in Lithuania, while declining in southern England due to habitat loss (Korpelainen *et al*. 2004). In Norway, this species has been lost from 23% of the localities where it occurred in 1950 (Rydgren *et al*. 2012). In southeastern Norway, losses are greater due to urbanization and logging and draining near streams, springs, and gullies.

Trichocolea tomentella (Figure 77-Figure 86, Figure 89) is a long-day plant, at least in southern Illinois (Zehr 1979). In southern Illinois it grows in restricted habitats, especially sandstone canyons with high moisture levels (Zehr 1977). It grows any time of the year that temperatures are above freezing (Zehr 1979). The finely divided leaves and paraphyllia seem to enable it to retain water. While it may cease growth during a drought, it resumes within 1-2 weeks upon rehydration. Zehr suggests that its lack of antheridia or sexual reproduction in southern Illinois may be due to the low irradiation in its habitats there. In more northern locations, more daylight reaches the plants in their habitats and sexual reproduction occurs at least occasionally. It is common for red light to be a stimulus for the production of gametangia.

Reproduction

Pohjamo *et al.* (2008) examined the genetic diversity, gene flow, and population structure in 18 populations of this species in Finland, Lithuania, UK, and Canada. This species is dioicous, so it is not surprising that gene flow between populations is limited. Spore production needed for longer dispersal distances requires sexual reproduction, a process that is difficult or impossible when only one sex is present in a population or the clones are disconnected. Rather, short-range dispersal of fragments is suggested by colonization within populations. Fortunately, this is promoted by the long life span of the species and its ramet productions that permit it to compete well in a suitable location with no disturbance. Nevertheless, the populations are small and becoming more and more fragmented, increasing the vulnerability of this dioicous species.

Although sporophytes (Figure 90) are rare in this **dioicous** species, most likely contributing to its increasing rarity, gametangia have been reported more frequently (Korpelainen *et al*. 2004). Nevertheless, the species exhibits a relatively high level of genetic diversity (Pohjamo *et al*. 2008), but gene flow between the disconnected populations is infrequent and suggests the occasional movement of fragments into new populations. The shoots have a long life span once they reach a suitable habitat. It expands its populations by efficient ramet production.

Figure 90. ***Trichocolea tomentella*** with capsule. Photo by Hermann Schachner, through Creative Commons.

Fungal Interactions

The fungus ***Penicillium chrysogenum*** (Figure 92) occurs on ***Trichocolea tomentella*** (Figure 77-Figure 86, Figure 89-Figure 90) (Rakotondraibe *et al*. 2015). Extracts from this fungus are known to be bioactive against the HT-29 colon cancer cell line. Ali (2017) and coworkers (Ali *et al*. 2017) found that ***Penicillium concentricum*** (see Figure 91-Figure 92) occurs as an endophyte in ***T. tomentella***. The interaction between the liverwort and its fungus induces the production of bioactive secondary metabolites by the fungus. Many of these are of medicinal value, including treatment for some types of cancer. Anaya-Eugenio *et al*. (2019) further elaborated on the medicinal compounds produced by endophytic ***P. concentricum***. Preziuso *et al*. (2018) explored the medicinal implications for the genus ***Trichocolea***.

Figure 91. ***Penicillium*** sp. on the moss ***Hylocomium splendens***. The genus ***Penicillium*** occurs on ***Trichocolea tomentella***. Photo courtesy of George Greiff.

Figure 92. ***Penicillium chrysogenum***, a species that is bioactive against the HT-29 colon cancer cell line, occurs on ***Trichocolea tomentella***. Photo by Crulina 98, through Creative Commons.

Biochemistry

Perry *et al*. (1996) identified structures of isoprenyl phenyl ethers and noted that these compounds were active as cytotoxic and antifungal agents. Nevertheless, fungi in the genus ***Penicillium*** (Figure 91-Figure 92) occur on and within ***Trichocolea tomentella*** (Figure 77-Figure 86, Figure 89). Barlow *et al*. (2001) described pathways of some of the isoprenyl phenyl ethers.

Asakawa *et al*. (1981) determined that isoprenyl benzoates serve as important chemical markers for ***Trichocolea tomentella*** (Figure 77-Figure 86, Figure 89) when compared to two other species in the **Jungermanniales**, supporting systematic classifications.

Suborder Myliineae

Myliaceae

Mylia anomala (Figure 93-Figure 102)

(syn. = *Leiomylia anomala*)

Distribution

Mylia anomala (Figure 93-Figure 102) occurs in the Northern Hemisphere, in Europe, Northern Asia, and North America. It has been recorded from Cape Breton Island, Canada (Nichols 1918), northern Alberta, Canada (Belland & Vitt 1995), Newfoundland, Canada (Weber 1976), New Hampshire, USA (Glime 1982), the Alps (Geissler & Selldorf 1986), Russia (Konstantinova *et al*. 2002; Shishkonakova *et al*. 2016), Finland (Pakarinen & Tolonen 1977; Pakarinen 1978; Väliranta *et al*. 2007), Sweden (Albinsson 1997), Spain (Reinoso & Rodríguez-Oubiña 1988), and UK (Duckett *et al.* 1991).

Figure 93. ***Mylia anomala***, a species that is widespread in the Northern Hemisphere. Photo by Hugues Tinguy, with permission.

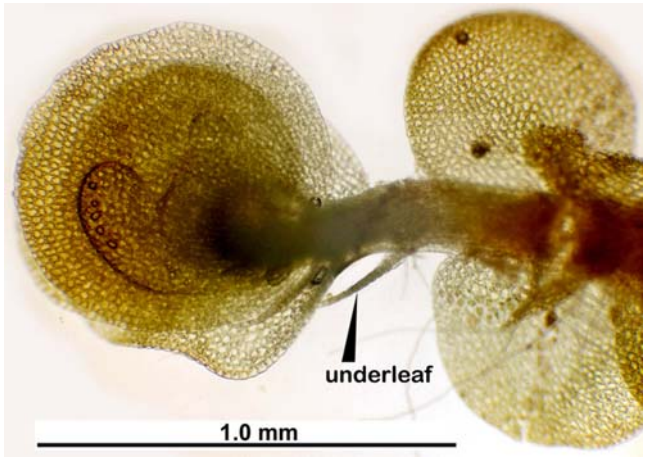

Figure 94. ***Mylia anomala*** branch. Photo modified from David H. Wagner, with permission.

Figure 95. ***Mylia anomala*** stem and leaf cross section. Photo by Kristian Peters, with permission.

Figure 98. ***Mylia anomala*** developing pigments in response to exposure. Photo by Michael Lüth, with permission.

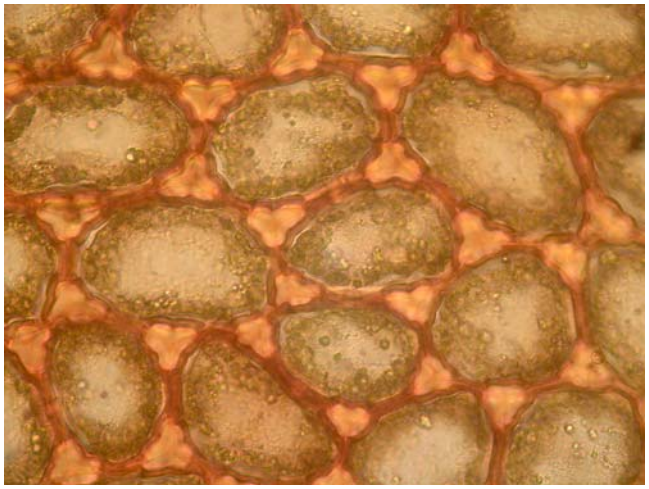

Figure 96. ***Mylia anomala*** cells showing trigones and wall pigmentation. Photo by Michael Lüth, with permission.

Figure 99. ***Mylia anomala*** forming a pigmented mat, indicative of exposure. Photo by Blanka Aguero, with permission.

Figure 97. ***Mylia anomala*** forming a tight mat on ***Sphagnum***. Photo by Michael Lüth, with permission.

Figure 100. ***Mylia anomala*** forming a green mat, indicative of shade. Photo by Jan-Peter Frahm, with permission.

Figure 101. ***Mylia anomala*** growing in an upright position. Photo by Des Callaghan, with permission.

Figure 102. ***Mylia anomala*** showing compact growth form. Photo by David Holyoak, with permission.

Aquatic and Wet Habitats

The habitats of this species typically are associated with ***Sphagnum*** (Figure 103). ***Mylia anomala*** (Figure 93-Figure 102) occurs in moist hollows between ***Sphagnum*** hummocks, Cape Breton Island, Canada (Nichols 1918). It occurs with ***Sphagnum*** at the edges of lakes (Figure 107) in New Hampshire (Lorenz 1908). Using macrofossil analysis, Väliranta *et al*. (2007) identified a wet lawn habitat in a southern Finnish boreal bog, based on the presence of ***Sphagnum rubellum*** (Figure 103) and ***Mylia anomala***.

Figure 103. ***Sphagnum rubellum***, species, along with ***Mylia anomala***, used to identify macrofossil wet lawn habitat in southern Finland. Photo by B. Gliwa, through Creative Commons.

Working in Finland, Pakarinen and Tolonen 1977) found that dead ***Sphagnum fuscum*** (Figure 104) could be covered by a thin layer of ***Mylia anomala*** (Figure 105). Pakarinen (1978) found that as the growth rate of ***Sphagnum fuscum*** decreases, liverworts, especially ***Mylia anomala*** (Figure 93-Figure 102), colonize the hummocks, increasing the volumetric density.

Figure 104. ***Sphagnum fuscum***; when this species dies, ***Mylia anomala*** can overgrow it. Photo by Hermann Schachner, through Creative Commons.

Figure 105. ***Mylia anomala*** overgrowing a hummock of ***Sphagnum fuscum***. Photo by Tuomo Kuitunen <luopioistenkasvisto.fi>, with permission.

In a study of peatland restoration Poulin *et al*. (2013) found that peatlands treatments differed in the responses they incurred after 8 years. Forest and ruderal species were more prominent in unrestored sites than in a reference site. Diversity and richness differed among sites. The peatland, forest, and wetland species were dominant in the restored sites. ***Mylia anomala*** (Figure 93-Figure 102), along with ***Sphagnum rubellum*** (Figure 103) and ***Pohlia nutans*** (Figure 106), were the main drivers of the revegetation.

Figure 106. ***Pohlia nutans*** with capsules, a species that, along with ***Mylia anomala*** and ***Sphagnum rubellum*** is a primary driver of revegetation in peatland restoration. Photo by Michael Lüth, with permission.

Shishkonakova *et al*. (2016) considered ***Mylia anomala*** (Figure 93-Figure 102), along with a number of lichen species, to be an indicator species for the soil subtype of destructive oligotrophic peat soils in the Russian classification of palso bogs. These are found in regressive bogs in the north taiga subzone of West Siberia. In Cataracts Provincial Park, Newfoundland, Canada, Weber (1976) considered ***Mylia anomala*** to be among the typical bog bryophytes. I should note here that at that time, North American botanists defined bogs as wetlands dominated by ***Sphagnum*** (Figure 103, Figure 104), thus not distinguishing them from poor fens.

In eastern Canadian bogs, the identification of early indicator species is a useful tool to indicate the need for intervention soon after restoration (González *et al*. 2013). Certain species are indicative when a site is not on a desired successional path. Important indicator species that signal a successful restoration are the bryophytes ***Sphagnum rubellum*** (Figure 103) and ***Mylia anomala*** (Figure 93-Figure 102), along with the black spruce tree ***Picea mariana*** (Figure 107-Figure 108).

Figure 107. ***Picea mariana*** "bog" forest in taiga (fen as described by Europeans), Quebec, Canada. Photo by Peupleloup, through Creative Commons.

Figure 108. ***Mylia anomala*** in a spruce fen. Photo by Michael Lüth, with permission.

In their study of boreal bog plants, Nordbakken *et al*. (2003) found that the lowest N percentages (0.8%) occurred in ***Mylia anomala*** (Figure 93-Figure 102). The N content increased in this species with experimental addition of N throughout the three years of the experiment. They suggested that the increases in the labelled N values in this species may represent an increasing importance of ammonium as the N source, or it could be due to its slow growth rate. Since this species grows between and over the top of the ***Sphagnum*** (Figure 103, Figure 104) shoots in the hummocks, the positive change in the N obtained may be due to its higher dependence on N in precipitation rather than that supplied by mycorrhizal relationships common in many tracheophytes of bogs. Prokaryotic endosymbionts are absent in these liverworts, so Duckett *et al*. (1991) considered the reports of nitrogen fixation by this and other liverworts to be due to associated **Cyanobacteria** (Figure 109).

Figure 109. ***Chroococcus*** sp. **(Cyanobacteria)** such as that one might find on ***Mylia anomala*** leaves. Photo by Jason Oyadomari, with permission.

Albinsson (1997) considered ***Mylia anomala*** (Figure 93-Figure 102) to have a narrow ecological amplitude in the mire habitat, particularly when compared to smaller species (Figure 110) like ***Cephalozia*** (Figure 111) or ***Kurzia*** (Figure 112) species. Gerdol (1995) determined that it likewise had a narrow nutrient niche. In the Swedish mires, it was among the most frequent of the 43 liverworts described by Albinsson (1997) and preferred poor mire

conditions, occupying hummocks (Figure 113-Figure 116). The adaptations of ***Mylia anomala*** to this elevated habitat include increased desiccation resistance, ability to overgrow ***Sphagnum*** (Figure 103, Figure 104, Figure 113-Figure 116), penetration of leaves by liverwort rhizoids, and a high reproductive output (Økland 1990), including gemmae (Figure 117-Figure 119). Albinsson considered this to be a compromise strategy.

Figure 110. ***Mylia anomala*** in association with smaller liverworts. Photo by Michael Lüth, with permission.

Figure 111. ***Cephalozia bicuspidata***, in a genus that has a wider ecological amplitude than ***Mylia anomala***. Photo by Hugues Tinguy, with permission.

Figure 112. ***Kurzia trichoclados***, in a genus that has a wider ecological amplitude than ***Mylia anomala***. Photo by David T. Holyoak, with permission.

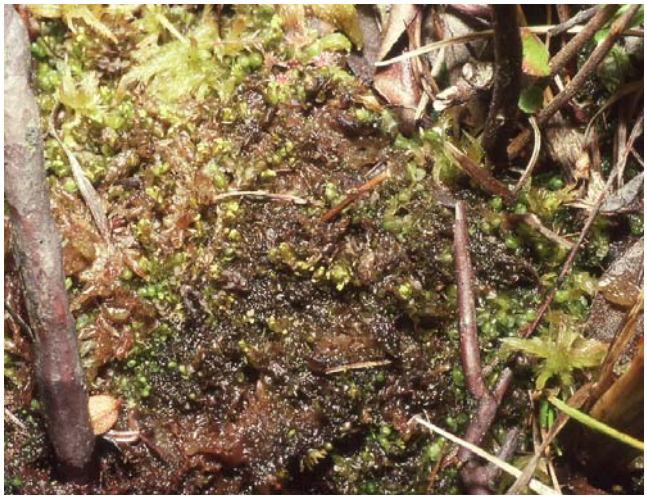

Figure 113. ***Mylia anomala*** overgrowing ***Sphagnum*** on a hummock in Perrault Fen, Upper Peninsula of Michigan, USA. Photo by Janice Glime.

Figure 114. ***Mylia anomala*** growing with cranberries on a hummock in a poor fen. Photo by Michael Lüth, with permission.

Figure 115. ***Mylia anomala*** growing with ***Sphagnum*** and ***Polytrichum***. Photo by Michael Lüth, with permission.

Figure 116. ***Mylia anomala*** with apical gemmae (yellow), growing with ***Sphagnum***. Photo by Michael Lüth, with permission.

Figure 117. ***Mylia anomala*** with gemmae on leaf tips. Photo by David Holyoak, with permission.

Figure 118. ***Mylia anomala*** with marginal and leaf-tip gemmae. Photo by Jan-Peter Frahm, with permission.

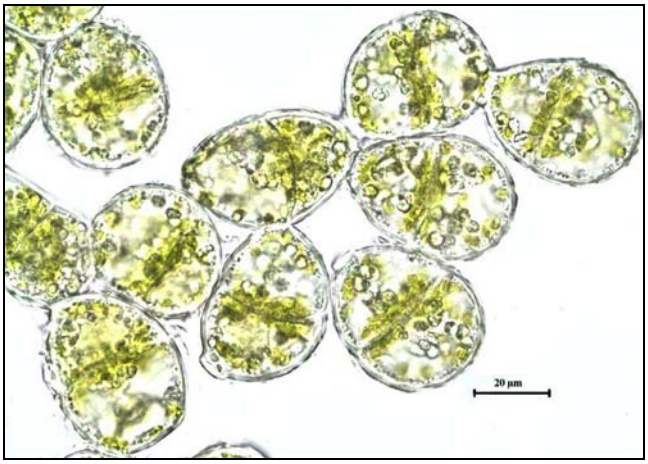

Figure 119. ***Mylia anomala*** gemmae. Photo by Hugues Tinguy, with permission.

But it is able to occupy other aquatic and wetland habitats as well; it appears on the walls in the flume (Figure 120) at Franconia Notch, New Hampshire, USA (Glime 1982). Some occur in moist moors (Figure 121). In the Alps, it is uncommon with ***Eleocharis quinqueflora*** (Figure 122) (Geissler & Selldorf 1986). In the Russian far east, it occurs on streambanks (Figure 123) at treeline of the Upper Bureya River (Konstantinova *et al*. 2002).

Figure 120. Flume at Franconia Notch, New Hampshire, USA, where one can find ***Mylia anomala*** on the walls. Photo by Janice Glime.

Figure 121. ***Mylia anomala*** with heather. Photo by Michael Lüth, with permission.

Figure 122. ***Eleocharis quinqueflora***, a wet habitat species in the Alps, but where ***Mylia anomala*** occurs uncommonly. Photo by Max Licher, through Creative Commons.

Figure 123. ***Mylia anomala*** habitat on streambank. Photo by Hermann Schachner, through Creative Commons.

Fungal Interactions

Duckett *et al*. (1991) found rhizoid-ascomycete fungi in ***Mylia anomala*** (Figure 93-Figure 102). In that liverwort, the fungi are restricted to the rhizoids (Figure 124) because this is one of the species that lacks flagelliform branches. They determined that the rhizoids swell in response to infection, with swelling being absent in sterile culture of the liverwort. It is in these swollen tips that most of the fungal hyphae reside.

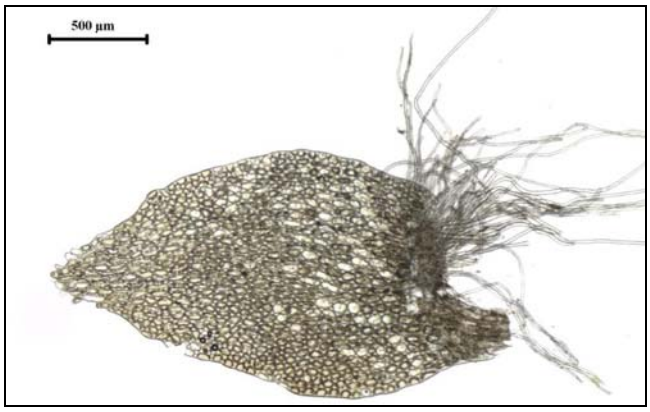

Figure 124. ***Mylia anomala*** underleaf with rhizoids, the site of ascomycete fungi. Photo by Hugues Tinguy, with permission.

Paul Davison has provided interesting images of the leaf cuticle of ***Mylia anomala*** (Figure 125). This cuticle may explain its ability to occupy habitats above water where it can become periodically dry. We know that the cuticle has a role in protecting tracheophytes from fungal invasions (Kolattukudy 1985). Could it serve any role in protection of these bryophytes against fungi?

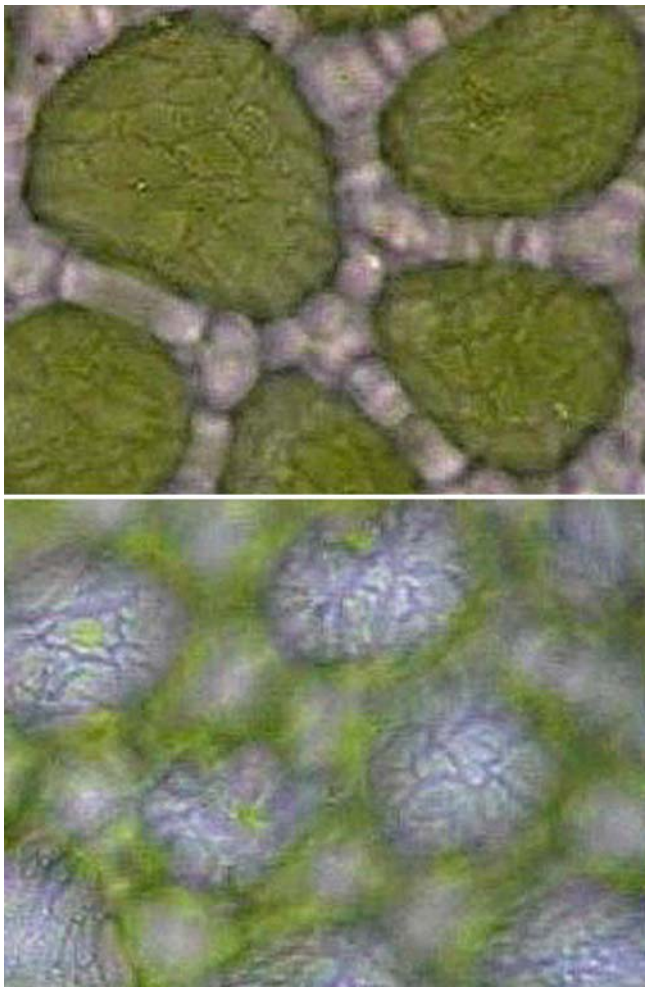

Figure 125. ***Mylia anomala*** showing cuticle. Photo by Paul G. Davison, with permission.

Biochemistry

Other potential protections against fungal presence are secondary compounds. Aromatic and other secondary compounds occur in oil bodies (Figure 126) of leaf cells. Ludwiczuk and Asakawa (2015) determined that ***Mylia anomala*** (Figure 93-Figure 102) produces mainly cyathane-type diterpenoids.

Figure 126. ***Mylia anomala*** cells with oil bodies, showing here mostly around the cell margins as oblong structures. Photo by Hermann Schachner, through Creative Commons.

Mylia taylorii (Figure 127-Figure 142)

Distribution

Mylia taylorii (Figure 127-Figure 142) is a circumboreal, mostly montane species with a suboceanic distribution (Engel & Braggins 2005). It occurs in mountainous districts of northern Europe, mountains of Continental Europe, Greenland, and eastern North America from Newfoundland to Tennessee (Wikipedia 2020). It is uncommon in western North America and eastern Asia, where it is known from Guizhou Province, China (Zhang & Chen 2006). It is best known from Great Britain and Scandinavia.

Figure 127. ***Mylia taylorii***, a circumboreal species. Photo by Tuomo Kuitunen <luopioistenkasvisto.fi.>, with permission.

Figure 128. ***Mylia taylorii*** with succubous leaves that help to conserve water. Photo by Martin Hutten, with permission.

Figure 129. ***Mylia taylorii*** showing the ability of the leaves to fold, reducing surface area for water loss. Photo by Kristian Peters, with permission.

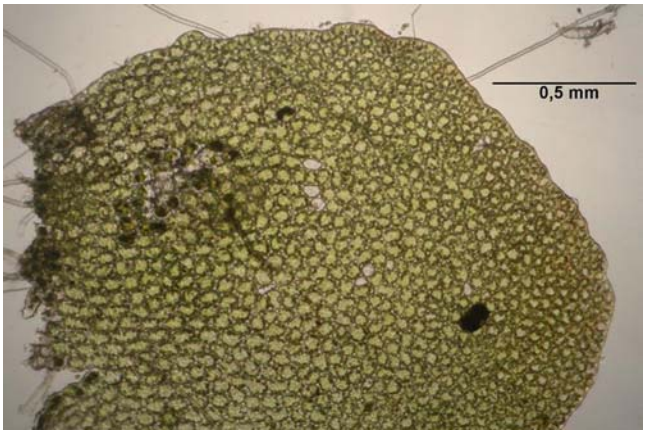

Figure 130. ***Mylia taylorii*** leaf. Photo by Snappy Goat, through public domain.

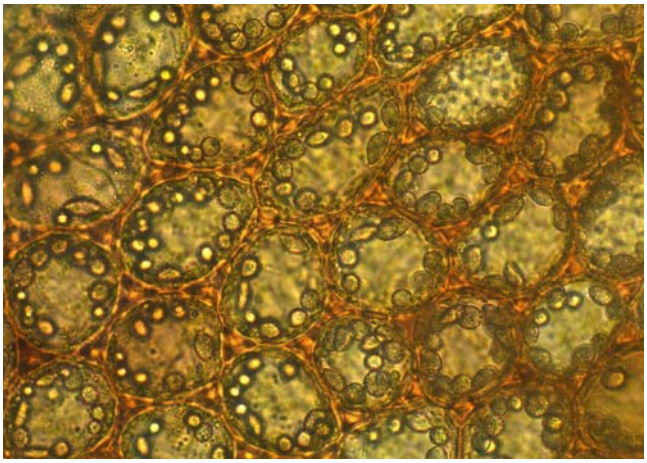

Figure 131. ***Mylia taylorii*** leaf cells showing trigones; the bright spots are oil bodies. Photo by Blanka Aguero, with permission.

Figure 132. ***Mylia taylorii*** forming a mat. Photo by Snappy Goat, through public domain.

Figure 133. ***Mylia taylorii*** green form that is typical of shade. Photo by Hermann Schachner, through Creative Commons.

Figure 134. ***Mylia taylorii*** red form that is typical of exposed sites. Photo by Hermann Schachner, through Creative Commons.

Figure 135. ***Mylia taylorii*** deep red form. Photo by Barry Stewart, with permission.

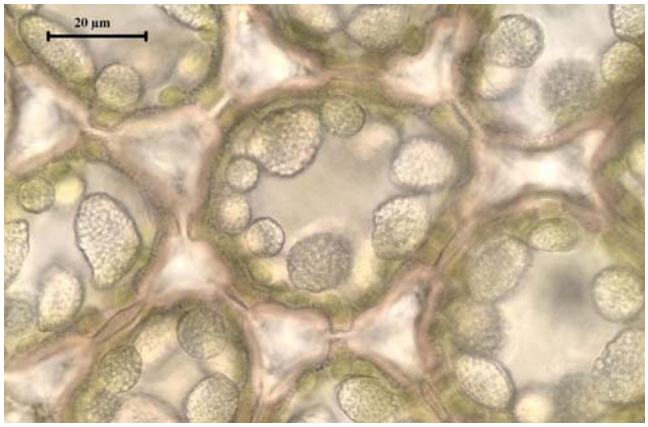

Figure 136. ***Mylia taylorii*** leaf cells showing oil bodies. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

Mylia taylorii (Figure 127-Figure 142) occurs on wet shore rocks and wet sandy shores in Scotland (West 1910), on wet rock cliffs associated with streams, Cape Breton Island, Canada (Nichols 1918), and in upstream reaches in the Harz Mountains of Germany (Bley 1987).

On the very wet Queen Charlotte Islands, British Columbia, Canada, Hong (2007) found it on shaded, decayed wood and moist soil. In the Bavarian Alps, Lotto

(1987) also found it on logs, humus, and the acidic forest floor.

In Germany, ***Mylia taylorii*** (Figure 127-Figure 142) forms large tufts that are easy to recognize on moist non-calcareous rocks, including sandstone, granite, and gneiss (Schnittler *et al*. 2010). It occupies sheltered conditions with high humidity and a cool climate, but it is rarely found on decaying wood, humus, or ***Sphagnum*** peat (Figure 137) there.

Figure 137. ***Mylia taylorii*** habitat in a seep with ***Sphagnum***. Photo by Michael Lüth, with permission.

Engel and Braggins (2005) consider ***Mylia taylorii*** (Figure 127-Figure 142) to be mostly restricted to acidic rocks never occurring on calcareous rocks. This makes moist siliceous rocks suitable, as well as vertical rock walls (Figure 138- Figure 141), but as just seen above, the species also finds suitable habitat on calcareous rocks and decaying logs.

Figure 138. ***Mylia taylorii*** habitat on rock. Photo by Richtid, with permission.

On the other hand, in Sakhalin, Russia, Bakalin *et al*. (2009) found ***Mylia taylorii*** (Figure 127-Figure 142) in wet moss mats on the seeping water in limestone cliff crevices. In these locations it can occur in pure mats (Figure 142) or with ***Sphenolobus minutus*** (Figure 143). It occurs on shady limestone cliffs and on decaying wood in ***Abies*** forests (Figure 144). In the tundra, it grows over moss mats on the seeping permafrost water and also in crevices of limestone cliffs. In addition to pure mats, it occurs with ***Bazzania denudata*** (Figure 145), ***Calypogeia integristipula*** (Figure 146), ***Eocalypogeia schusterana***, ***Douinia plicata*** (see Figure 147), ***Odontoschisma macounii*** (Figure 148), and ***Tritomaria exsecta*** (Figure 149).

Figure 139. ***Mylia taylorii*** habitat on rock. Photo by Richtid, with permission.

Figure 140. ***Mylia taylorii*** (red) habitat on rocks of an embankment. Photo by Michael Lüth, with permission.

Figure 141. ***Mylia taylorii*** showing growth form on a vertical substrate. Photo by Hugues Tinguy, with permission.

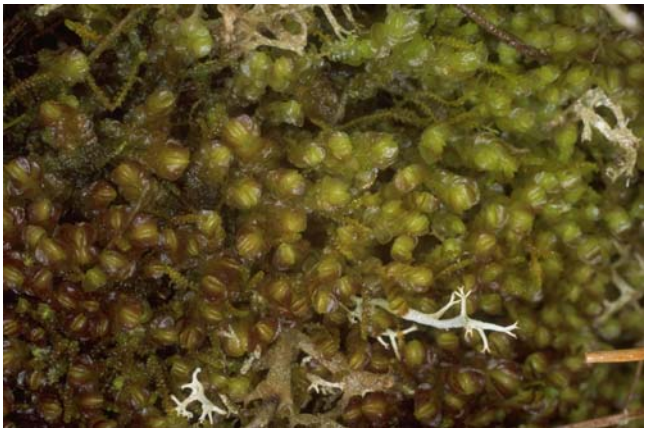

Figure 142. ***Mylia taylorii*** forming a pure wet mat (with occasional lichens), as one might find in seepage water of rock cliffs. Photo by Jan-Peter Frahm, with permission.

Figure 143. ***Sphenolobus minutus***, a species that occurs with ***Mylia taylorii*** in seeping water in limestone cliff crevices. Photo by Jan-Peter Frahm, with permission.

Figure 144. ***Abies sibirica*** forest, where ***Mylia taylorii*** can occur on shady limestone cliffs and decaying wood. Photo by Krasnoyarsk Territory, through Creative Commons.

Figure 145. ***Bazzania denudata***, a species that occurs with ***Mylia taylorii*** on limestone cliffs in the tundra. Photo from Botany Website, UBC, with permission.

Figure 146. ***Calypogeia integristipula***, a species that occurs with ***Mylia taylorii*** on limestone cliffs in the tundra. Photo by Hermann Schachner, through Creative Commons.

Figure 147. ***Douinia ovata***; ***Douinia plicata*** is a species that occurs with ***Mylia taylorii*** on limestone cliffs in the tundra. Photo by Des Callaghan, with permission.

Figure 148. ***Odontoschisma macounii***, a species that occurs with ***Mylia taylorii*** on limestone cliffs in the tundra. Photo from Earth.com, with permission.

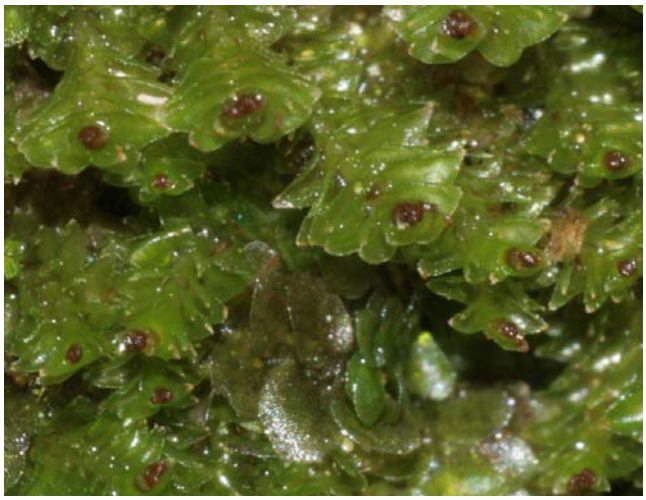

Figure 149. ***Tritomaria exsecta***, a species that occurs with ***Mylia taylorii*** on limestone cliffs in the tundra. Photo by Hermann Schachner, through Creative Commons.

Mylia taylorii (Figure 127-Figure 142) requires at least 120-140 wet days per year, a condition found in sessile oak (***Quercus petraea***; Figure 150) and downy birch (***Betula pubescens***; Figure 151) forests of the western UK (Ratcliffe 1968). It also occupies deep, wet bogs, but prefers sites where the ***Sphagnum*** (Figure 137) is unhealthy or has limited growth. It is interesting that Bakalin *et al*. (2009) found it in limestone habitats in Russia, whereas Ratcliffe and many other authors describe it as a calcifuge. Gaddy (2002) likewise reported ***Mylia taylorii*** from a montane acidic cliff, as well as on a spray cliff.

Figure 150. ***Quercus petraea*** forest, a habitat that typically provides the 120-140 wet days required by ***Mylia taylorii***. Photo by Gruban, through Creative Commons.

Figure 151. ***Betula pubescens*** forest, a habitat that typically provides the 120-140 wet days required by ***Mylia taylorii***. Photo by Dan Aamlid, through Creative Commons.

Juutinen *et al*. (2016) reported ***Mylia taylorii*** (Figure 127-Figure 142) from scree and stones at Kuusamo, Finland. Härtel *et al*. (2007) also considers this to be a liverwort of "rock cities."

Mylia taylorii (Figure 127-Figure 142) is a calcifuge, but it is able to live on rotten logs in calcareous areas (Olleck *et al*. 2020), finding there both acidic conditions and moisture. Perhaps there were mediating factors that provided acidic microhabitats with acidic conditions that could explain the report by Bakalin *et al*. (2009). Another possibility is that there are ecological races.

Its intolerance for desiccation explains the distribution of ***Mylia taylorii*** (Figure 127-Figure 142) in wet environments. At 85% relative humidity, about 75% of the cells remain alive (Clausen 1964). At 75% relative humidity, few cells remain alive. After 4-5 days at -10ºC in ice, only about 1/4 of the cells remain alive.

Adaptations

Many populations exhibit red coloration (Figure 152). Such coloration is usually an indication of stress, typically bright light or low temperatures or a combination of these. Nutrient stress could also be a factor. Research is needed to determine the stimulus for the coloration in this species.

Figure 152. ***Mylia taylorii*** exhibiting red coloration that typically is an indication of stress, including bright sunlight. Photo by Štěpán Koval, with permission.

Reproduction

In Finland where it grows on rock scree, ***Mylia taylorii*** (Figure 127-Figure 142) produces gemmae (Figure 153) on the margins of the upper leaves.

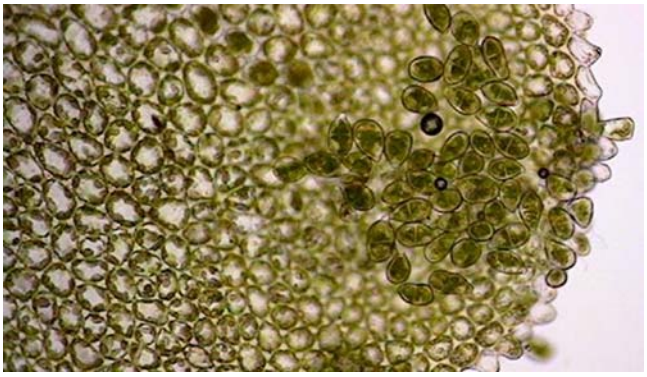

Figure 153. ***Mylia taylorii*** gemmae on leaf. Photo by Paul G. Davison, with permission.

Fungal Interactions

Mylia taylorii (Figure 127-Figure 142) is an indicator species for ravine myxomycetes, at least in parts of Germany (Schnittler *et al*. 2010). This liverwort was present in 64% of the myxomycete habitats in Saxonian Switzerland (Germany). And 96% of the records for the myxomycete ***Colloderma robustum*** (Figure 154) were associated with ***Mylia taylorii***. The liverwort turfs in this region are restricted to the deepest parts of the ravines where the climate is most uniform (Schnittler *et al*. 2010). The myxomycete plasmodium of ***Colloderma robustum*** lives in these turfs that are typically 2-5 cm thick. ***Colloderma robustum*** often has 500-1000 plasmodiocarps on a single ***Mylia taylorii*** turf of 10-20 cm diameter. The plasmodia are initially creamy-white, hiding within the turfs along with green algae. In about 2-3 weeks before fructification, these plasmodia emerge, later turning to a sulfur-yellow color. They then start to form their plasmodiocarps at the tips of the ***M. taylorii*** shoots and secrete a solid translucent slime sheath.

Figure 154. ***Colloderma robustum***, a common slime mold on ***Mylia taylorii*** in ravines. Photo by Sarah Lloyd, with permission.

Unlike ***Mylia anomala*** (Figure 93-Figure 102), ***Mylia taylorii*** (Figure 127-Figure 142) has normal rhizoids (Figure 155-Figure 156), indicating the absence of the ascomycete fungi that invade ***Mylia taylorii*** (Duckett *et al*. 1991).

Schnittler *et al*. (2010) observed that ***Mylia taylorii*** turfs (Figure 156) grow thicker each year. Eventually their weight causes them to drop from the rock and the growth cycle starts over. The result is that if a rock exceeds 60º inclination, it will not achieve more than 50% cover by this species due to this periodic loss.

Biochemistry

Matsuo *et al*. (1977) identified a new tetracyclic sesquiterpene ketone from ***Mylia taylorii*** (Figure 127-Figure 142). Later, the structure of another sesquiterpene ketone was described (Matsuo *et al*. 1979). Reuß *et al*. (2004) identified essential oils in this species.

Figure 155. ***Mylia taylorii*** rhizoids on ventral side of stem (**left**) and with underleaf (**right**). Photo by Paul G. Davison, with permission.

Figure 156. ***Mylia taylorii*** forming a turf, showing rhizoids along stem. Photo by Michael Lüth, with permission.

Suborder Perssoniellineae

Schistochilaceae

Schistochila aligera (Figure 157)

Distribution

Schistochila aligera (Figure 157) is distributed in Asia and Melanesia (So 2003a). It occurs in Indonesia, Java, Philippines, Fiji Islands, Samoa Islands, New Guinea, Tahiti, Cook Islands, New Caledonia, and Vanuatu (So 2003b). Daniels and Daniels (2008) have rediscovered it in India. More recently it has been reported from Thailand, where it is the most common species in the genus (Juengprayoon *et al*. 2015). Gao and Wu (2004) reported it from Taiwan and Hainan. But like so many tropical species, it is extremely variable and thus has been known by a number of names now considered synonyms.

Figure 157. ***Schistochila appendiculata***; ***Schistochila aligera*** occurs mostly in Asia and Ruttner (1955) listed it as aquatic in the tropics. Photo by Larry Jensen, with permission.

Aquatic and Wet Habitats

Ruttner (1955) reported this species as an aquatic species in the tropics. In Thailand it is epiphytic or lithophilic (Juengprayoon *et al*. 2015). Similarly, Gao and Wu (2004) described it from old trunks and decayed wood in Taiwan and Hainan. In Sulawesi, Indonesia, ***Schistochila aligera*** (Figure 157) forms one of three distinctive associations on bark (Gradstein & Culmsee 2010). We need to gather more information on its habitats and to determine just what sort of "aquatic" habitat it can occupy.

Reproduction

Schistochila aligera (Figure 157) can be **dioicous** or **autoicous** (Daniels & Daniels 2008), suggesting that it needs more biochemical and genetic studies to look for races and subspecies. Nagashima *et al*. (1991) identified diterpenoids in this species from Japan. Similarly Ludwiczuk and Asakawa (2008) reported pimarane-type diterpenoids from ***Schistochila aligera*** in Malaysia. Secondary compounds from ***Schistochila aligera*** from China and Mongolia have evidenced antibacterial activity against several species of bacteria (Zhu *et al*. 2006).

Fungal Interactions

An ***Octosporella***-like ascomycete (Figure 27-Figure 29) forms appressoria and haustoria on the leaves of ***Schistochila aligera*** (Figure 157) (Döbbeler 1978, 1997). However, there are no records of rhizoid infections on this liverwort (Pressel *et al*. 2008).

Summary

Members of the **Plagiochilaceae** and other families included here are mostly terrestrial, but some are restricted to or common in wet habitats, occupying stream banks, spray areas, and wetlands. The family is large, especially in the tropics, so the few presented here are only a small segment of the family.

Trichocolea tomentella occurs in fens, on streambanks, and in wet spots in forests.

Mylia anomala is predominantly a bog/poor fen species and other acidic habitats. ***Mylia taylorii*** seems to be restricted to non calcareous habitats in most of its range, but occupies limestone in Russia – a contrast that needs further study.

A number of the aquatic liverworts in these jungermannialian families have fungi on the surface or in the cells. The interactions of these fungi are not well known, but there is evidence that for some the bryophyte stimulates the fungus to produce antibiotic compounds that are active against some kinds of cancer cells.

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Lars Söderström provided me with the current acceptable names for a number of older taxa. Peter Döbbeler and George Greiff provided me with needed images and references. Many images came from the internet, and I thank all who have put their images in Creative Commons or given me permission to use their images.

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CHAPTER 1-7
AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA, ORDER PORELLALES: JUBULINEAE, PART 1

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CHAPTER 1-7
AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA, ORDER PORELLALES: JUBULINEAE, PART 1

Figure 1. ***Jubula hutchinsiae*** habitat. Photo by Michael Lüth, with permission.

Nomenclature for this chapter is based primarily on Söderström *et al*. (2016). In addition, Lars Söderström provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. These unverifiable taxa have been included in the species.

To develop this list, I used my own bibliography, collected over the past 56 years, and Google Scholar. These papers soon led me to others. I do not pretend that this is complete. It includes streams, lakes, and a wide range of other wetlands. It deliberately ignores bogs (especially ***Sphagnum***) and mostly ignores fens, but nevertheless includes some species from these habitats because they were found in a wetland study. Bogs and poor fens have been treated in whole books and provide an extensive literature; fens seem somewhat less studied. They would require considerably more review and time. Thus I felt that less-reviewed topics, particularly the aquatic habitats with which I am most familiar, should be given priority.

Many of the species in this subchapter are not typical wetland or aquatic species. They were, however, found in a wetland or aquatic study. Their relative frequency can be inferred based on the number of references cited.

Porellales – Suborder Jubulineae

Frullaniaceae

This family occurs predominantly on boulders and tree trunks and branches. However, a few taxa seem at least tolerant of more moist habitats and have been included here.

Frullania asagrayana (Figure 2)

(syn. = *Frullania tamarisci* subsp. *asagrayana*)

Although ***Frullania asagrayana*** (Figure 2) has been treated as a subspecies of ***Frullania tamarisci*** (Figure 3), Crandall-Stotler *et al*. (1987) found that both morphological and biochemical differences among these subspecies indicated a greater genetic distance than that expected for subspecies. This includes unique flavonoid profiles and a considerable level of terpenoid and phosphoglucoisomerase dissimilarity. Heinrichs *et al*. (2010) likewise supported its recognition as a separate species based on DNA markers, but found these were not as strongly supported by morphological differences. They considered this species complex to be "the most explicit example of a complex of semi-cryptic and cryptic liverwort species." Their findings "support frequent short-distance migration, rare successful long-distance dispersal events, extinction, and recolonization as an explanation for the range formation in these ***Frullania*** species."

Figure 2. ***Frullania asagrayana*** (reddish) with ***Drepanolejeunea appalachiana*** (green) growing on it. Photo by Ken McFarland and Paul Davison, with permission.

Figure 3. ***Frullania tamarisci*** (Tamarisk Scalewort); ***Frullania asagrayana*** was originally included as a subspecies of this species. Photo by Barry Stewart, with permission.

Distribution

Frullania asagrayana (Figure 2) is distributed broadly throughout eastern North America from Canada to the Gulf Coast (Ramaiya *et al*. 2010) and westward to the Ozarks (Schuster 1992). The leaves have **ocelli** (Figure 4-Figure 5), a character absent in many ***Frullania*** species.

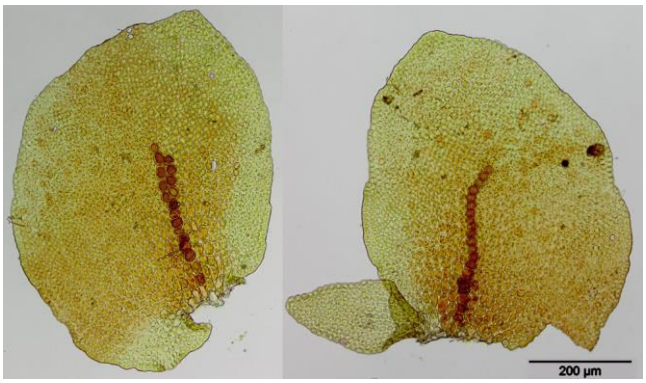

Figure 4. ***Frullania asagrayana*** leaf cells and ocelli (line of brown cells). Photo by Blanka Aguero, with permission.

Figure 5. ***Frullania asagrayana*** ocelli and leaf cells showing oil bodies where secondary compounds are stored. Photo by Blanka Aguero, with permission.

Aquatic and Wet Habitats

Frullania asagrayana (Figure 2) occurs in crevices or the surface of drier cliffs in a ravine in Connecticut, USA, but Nichols (1916) lists it in his study along rivers and streams from these habitats. Otherwise, it does not seem to be truly aquatic or wetland. More frequently, ***Frullania asagrayana*** (Figure 2) is epiphytic (Davison 1997).

Reproduction

Frullania asagrayana is **dioicous** (Figure 6), so one is not likely to see sporophytes often. It does, however, reproduce through regeneration. This permits leaves and leaf fragments to produce new plants.

Figure 6. ***Frullania asagrayana*** showing perianths on female plant. Photo by Blanka Shaw, with permission.

Fulford (1956) described regeneration from a leaf cell of ***Frullania asagrayana*** (Figure 2, Figure 6). First a cell dedifferentiates. Then it becomes swollen. The protonema pushes through the swollen area, creating a flap or lid that remains at the side of this new protonema and ultimately can appear at the base of the rhizoid of the developing plant. Fulford suggests that some cells that have been interpreted as gemmae are in fact these swollen regeneration cells.

Interactions

Cornejo and Scheidegger (2016) considered that cyanobacterial interactions with liverworts were important in the composition and dynamics in bryophyte and lichen-dominated epiphytic communities. They concluded that the liverwort ***Frullania asagrayana*** (Figure 2, Figure 6) serves as a reservoir for **Cyanobacteria** (Figure 7) that are partners for the lichens. The authors confirmed by DNA bar coding that strains of the cyanobacterial lichen partner ***Rhizonema*** were able to live on the surface of ***Frullania asagrayana***. Some of the strains of ***Rhizonema*** were very specific about the lichens that served as their partners, whereas others appeared to be generalists, a phenomenon also noted by Rikkinen (2013).

Figure 7. ***Nostoc***, a cyanobacterial genus that often occurs as a symbiont with leafy liverworts such as ***Frullania asagrayana*** and also as a symbiont in some lichens. Photo by Ralf Wagner, with permission.

Biochemistry

Asakawa *et al*. (1991) reported that the Type-T chemotype of ***Frullania moniliata*** (formerly *F. tamarisci* subsp. *ovata*; Figure 8) was similar to that of ***F. asagrayana*** (Figure 2). ***Frullania moniliata*** produces an intense mossy odor, but ***Frullania asagrayana*** lacks the two sesquiterpenoids that apparently are responsible for that odor.

Figure 8. ***Frullania moniliata***, a species with chemistry similar to that of ***F. asagrayana***, but with a mossy odor. Photo by Jia-dong Yang, through Creative Commons.

Frullania riparia (Figure 9-Figure 10)

Frullania riparia (Figure 9-Figure 10) is a rare species that occurs on both sides of the Atlantic in mostly middle latitudes (Schuster 1992). It is not part of the ***Frullania tamarisci*** (Figure 11, Figure 13-Figure 16) complex, but it has had its share of synonyms. Here, as elsewhere, I have only included those synonyms that occurred in the aquatic literature reported here.

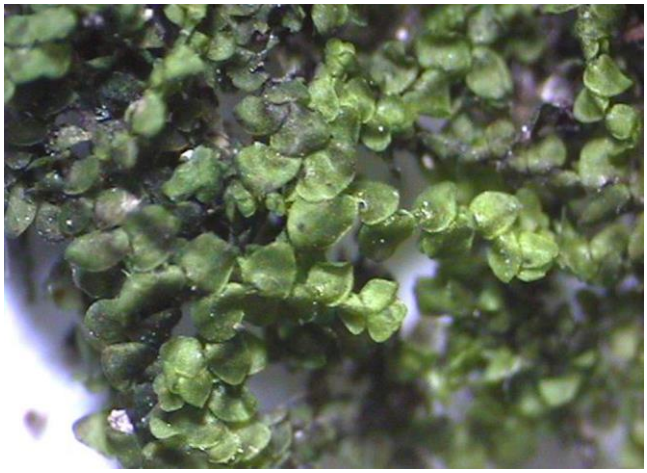

Figure 9. ***Frullania riparia*** exhibiting a hydrated shade form. Photo by Paul Davison, with permission.

Distribution and Habitats

Frullania riparia (Figure 9-Figure 10) occurs along calcareous rivers in Connecticut, USA (Nichols 1916). By

contrast, Schuster (1992) declares it "a pronounced xerophyte," colonizing vertical faces of shaded, dry rocks. He likewise considers it to be a calciphile, but not absolutely restricted to calcareous surfaces. On rare occasions it can be found on bark. Nevertheless, "riparian" means relating to or situated on the banks of a river, suggesting that early collections came from streamside habitats.

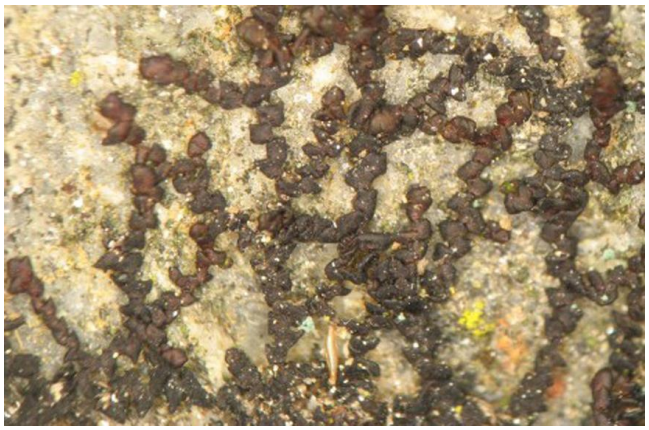

Figure 10. ***Frullania riparia*** on rock, exhibiting its xerophytic tendencies and the brown color expresses in sun exposure. Photo by Jan-Peter Frahm, with permission.

Frullania tamarisci (Figure 11-Figure 16)

Frullania tamarisci (Figure 11-Figure 16) now has a narrower concept than an earlier one. Heinrichs *et al*. (2010) reviewed the subspecies that had been described. It was once considered a polymorphic species with four allopatric subspecies [subsp. ***asagrayana*** (Figure 2), ***moniliata*** (Figure 6), ***nisquallensis*** (Figure 12), and ***tamarisci*** (Figure 11)]. Heinrichs *et al*. used sequences of the nuclear internal transcribed spacer region and the plastid trnL-trnF and atpB-rbcL regions to reveal at least eight main lineages within the ***Frullania tamarisci*** complex that can be considered as cryptic and semicryptic species, lacking morphological distinctions.

Figure 11. ***Frullania tamarisci***. Photo from Proyecto Musgo, through Creative Commons.

Figure 12. ***Frullania nisquallensis***, a member of the ***Frullania tamarisci*** complex. Photo by Dale Vitt, with permission.

Distribution

Schuster (1992) considered ***Frullania tamarisci*** (Figure 11-Figure 13) to be circumboreal and mostly suboceanic to oceanic, but its more recent separation into multiple species warrants a re-evaluation of its distribution.

Aquatic and Wet Habitats

West (1910) reported ***Frullania tamarisci*** (Figure 11-Figure 16) from damp rocks by lake shores in Scotland. Watson (1919) reported it as occasionally submerged (Watson 1919). Schuster (1992) considered it to be a species of tree bark, rock walls (Figure 14-Figure 16), and ledges. In Macaronesia, it is **epiphyllous** (growing on leaves) (von Konrat & Braggins 1999). My own experience suggests that it occurs in humid sites, such as stream canyons (Figure 17), but not in the water. It is able to grow in exposed sites and can form margins along grasses on rock where it is exposed to direct sunlight (Figure 18).

Figure 13. ***Frullania tamarisci*** forming a **smooth mat**. Photo by Hermann Schachner, through Creative Commons.

Figure 14. ***Frullania tamarisci*** on a canyon wall at Cwm Idwal National Nature Reserve, Wales. Photo by Janice Glime.

Figure 15. ***Frullania tamarisci*** on cliff at Cwm Idwal National Nature Reserve, Wales. Photo by Janice Glime.

Figure 16. ***Frullania tamarisci*** on a cliff. Photo by Michael Lüth, with permission.

Figure 17. Path between canyon walls with ***Frullania tamarisci*** in black patches on rock wall at left, Cwm Idwal National Nature Reserve, Wales. Photo by Janice Glime.

Figure 18. ***Frullania tamarisci*** showing zonation where it has the advantage of sun while benefitting from the moisture held by the adjoining grasses. Photo by Michael Lüth, with permission.

Adaptations

Like ***F. asagrayana*** (Figure 2), ***F. tamarisci*** (Figure 11) has lobules (Figure 19-Figure 20) that can retain water, permitting it to live in places that get dry. Nevertheless, it also lives in moist habitats near streams and in canyons, exhibiting a wide range of habitats. Its dark color protects it from the bright sunlight in exposed habitats.

Figure 19. ***Frullania tamarisci*** ventral side showing lobules. Photo by Snappy Goat, through public domain.

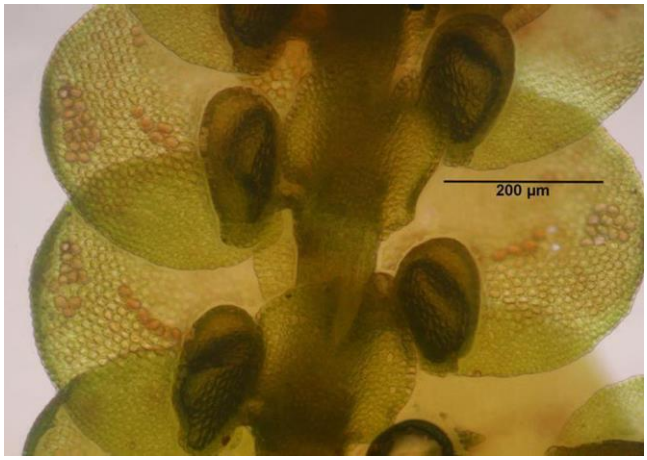

Figure 20. ***Frullania tamarisci*** showing lobules (that can hold water), ocelli, and underleaves. Photo from Snappy Goat, through public domain.

Reproduction

Frullania tamarisci is **dioicous** (Figure 21). Blackstock (2015) found that corticolous populations of ***Frullania tamarisci*** exhibited a very high sporophyte frequency when the colonies had both sexes. These colonies were highly fertile with male and female shoots (Figure 21), but fertilization nevertheless reduced the number of **gynoecia**. Exposed coastal populations, on the other hand, were sub-fertile with rare presentations of sporophytes. Furthermore, the coastal populations had a distinct female bias, with male scarcity limiting the production of sporophytes. Bisang (1987) defined the subspecies ***Frullania tamarisci*** ssp. ***tamarisci***. She described a globose, many-celled protonema that forms within the stretched spore.

Figure 21. ***Frullania tamarisci*** with perianths. Photo by Hermann Schachner, through Creative Commons.

Biochemistry

Connolly *et al*. (1984) reported **tamariscol** from ***Frullania tamarisci*** (Figure 21), a new sesquiterpenoid alcohol isolated from this population in Scotland. Asakawa *et al*. (1991) found evidence that ***Frullania tamarisci*** *s.l.* (Figure 21) has a Type T chemotype similar to that of ***F. asagrayana*** (Figure 2). Paul *et al*. (2001) identified tamariscene with a new sesquiterpene skeleton, in ***Frullania fragilifolia*** (*s.l.*?; Figure 22). Other research has been on subspecies that are now considered separate species, such as the finding of a new sesquiterpenoid in ***Frullania moniliata*** (formerly *F. tamarisci* subsp. *ovata*; Figure 8) (Toyota & Asakawa 1990).

Figure 22. ***Frullania fragilifolia***, a species that also has tamariscene. Photo by David T. Holyoak, with permission.

Frullania teneriffae (Figure 23, Figure 27-Figure 30)

Distribution

Frullania teneriffae (Figure 23, Figure 27-Figure 30) is distributed in Africa, Europe, and Asia (ITIS 2020). Its common name in the UK of sea scalewort suggests, along with the records I could find, that it is a coastal species, including islands.

Figure 23. ***Frullania teneriffae*** growing on rock. Photo by Stan Phillips, through public domain.

Aquatic and Wet Habitats

Frullania teneriffae (Figure 23, Figure 27-Figure 30) is recorded from mountainous streams on Madeira Island (Figure 24-Figure 25) (Luis *et al*. 2015). In Macaronesia it is also facultatively epiphyllous (von Konrat & Braggins 1999), a habitat it might invade from one of its epiphytic

locations (Figure 28). But on the islands of Canna and Sanday off the coast of Scotland, it occurs frequently on rocks near the sea (Figure 26) and on dry, rather exposed rock faces and boulders (Figure 27) (Birks *et al*. 1991).

Figure 24. Madeira Island at Ponta de São Lourenço (north side). Photo through Creative Commons.

Figure 25. Madeira Island 25 Fontes-waterfall during dry period. Photo by Bjørn Christian Tørrissen, through Creative Commons.

Figure 26. Shoreline where one can find ***Frullania teneriffae***. Photo by Michael Lüth, with permission.

Figure 27. ***Frullania teneriffae*** growing on exposed rock. Photo by Hugues Tinguy, with permission.

Figure 28. ***Frullania teneriffae*** dry on a branch. Photo by Jan-Peter Frahm, with permission.

Frullania teneriffae has small lobules (Figure 29-Figure 30) and is typically dark in color. The dark coloration gives it a shield from the bright sunlight in its exposed habitats.

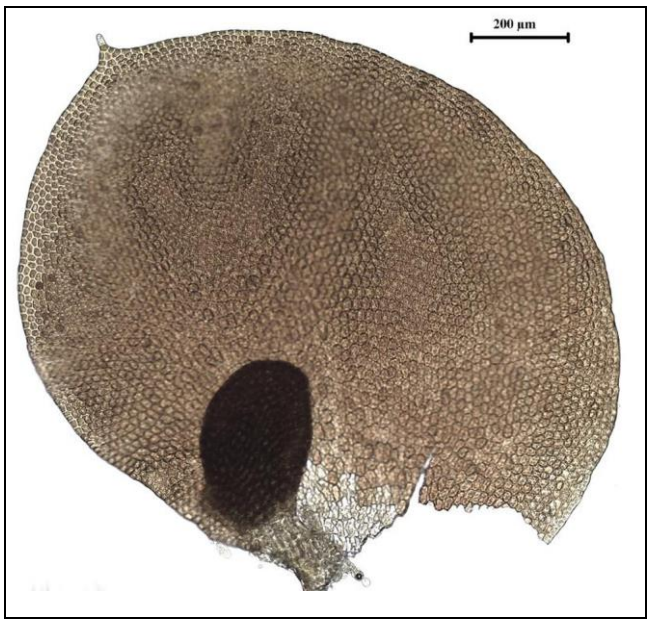

Figure 29. ***Frullania teneriffae*** leaf with lobule. Photo by Hugues Tinguy, with permission.

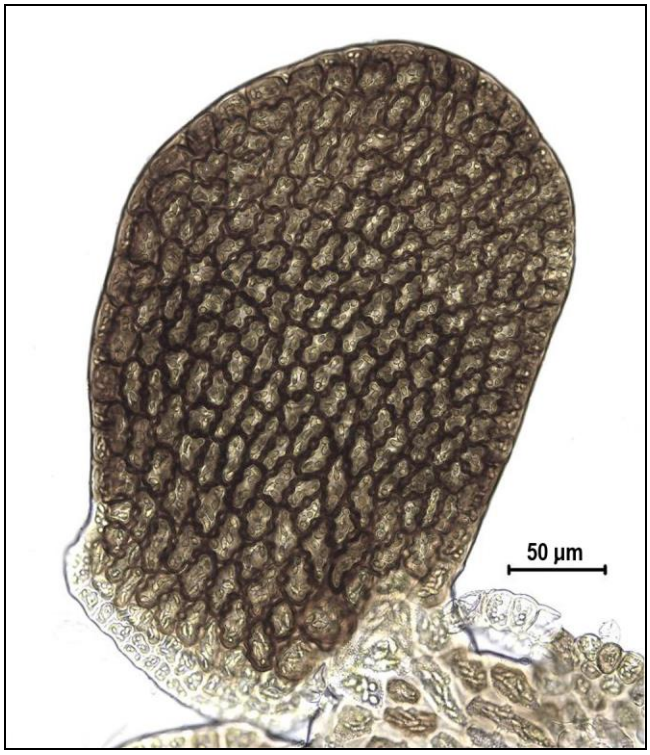

Figure 30. ***Frullania teneriffae*** leaf lobule. Photo by Hugues Tinguy, with permission.

Role

The ability of the lobules to hold water when the rest of the plant is drying is demonstrated by the presence of the aquatic invertebrates that can live there. Among these are the rotifers (Figure 31). The rotifers are able to go dormant when the leaves do dry out, surviving as resting eggs (Figure 32).

Figure 31. ***Frullania*** with rotifer "galls" in the lobules, showing the dormant egg stage of the rotifers. Photo courtesy of Puterbaugh, Skinner, and Miller.

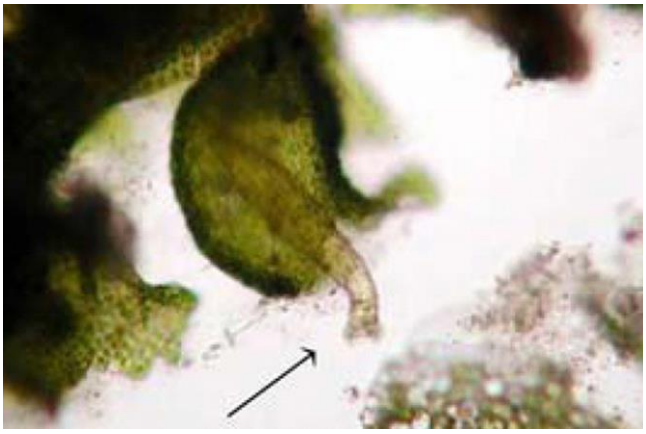

Figure 32. ***Frullania*** with rotifer. Photo courtesy of Andi Cairns.

Biochemistry

Biochemical studies on ***Frullania teneriffae*** (Figure 23, Figure 27-Figure 30) are lacking. Wang and Qiu (2006) found no references reporting mycorrhizal fungi on ***Frullania teneriffae***.

Jubulaceae

Schuster (1992) considered all members of ***Jubula*** (Figure 33-Figure 37, Figure 38, Figure 43, Figure 45-Figure 47) to be restricted to humid or damp sites, frequently occurring near flowing water. In North America it is almost entirely **saxicolous** (growing on rock), although it can be epiphyllous on ferns in the tropics or corticolous in humid rainforests.

Jubula hutchinsiae (Figure 1, Figure 33-Figure 38, Figure 43, Figure 45-Figure 47)

Like so many of the species of moist and wet habitats, ***Jubula hutchinsiae*** (Figure 33) is highly polymorphic (Sim-Sim *et al*. 2002). Pätsch *et al*. (2001) used nuclear and chloroplast DNA sequences to distinguish five subspecies: ***J. hutchinsiae* subsp. *bogotensis***, **subsp. *hutchinsiae*** (Figure 33), **subsp. *japonica*** (Figure 34-Figure 35), **subsp. *javanica***, and **subsp. *pennsylvanica*** (Figure 47).

Figure 33. ***Jubula hutchinsiae***. Photo by David T. Holyoak, with permission.

Figure 34. ***Jubula hutchinsiae*** ssp. ***japonica***. Photo by Jia-dong Yang, though Creative Commons.

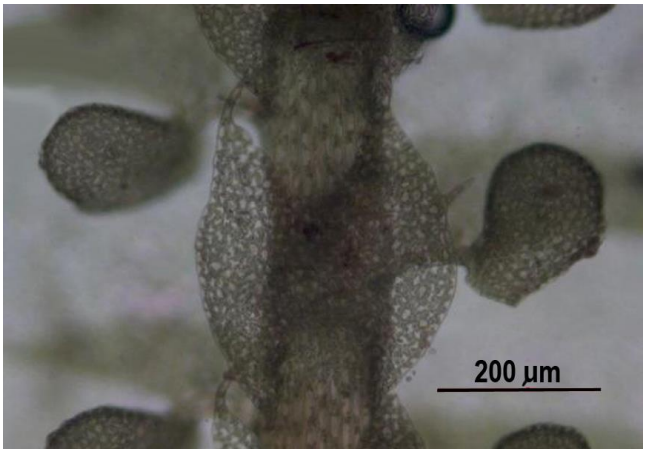

Figure 35. ***Jubula hutchinsiae*** ssp. ***japonica*** leaves and lobules. Photo by Jia-dong Yang, though Creative Commons.

Distribution

Jubula hutchinsiae (*s.l.* Figure 33-Figure 35) is known from Japan, Taiwan, and India in Asia, the Pacific Islands, Europe, and Macaronesia (Guerke 1978; Majumdar & Singh 2016). It is likely that all reports from Japan and Taiwan are the subspecies ***japonica*** (Figure 34-Figure 35). Pócs and Cairns (2008) added Australia to its distribution, but identified it as subspecies ***australiae***. Kürschner (2013) added subspecies ***caucasica*** to the flora of Turkey and Iran. Sukkharak (2017) added the subspecies ***javanica*** to the known flora of Thailand.

Aquatic and Wet Habitats

Jubula hutchinsiae (Figure 33) occurs on rocks in fast water (Figure 1), on rocks or in caves associated with fast water (Figure 36, Figure 37), and waterfalls (Watson 1919). Sim-Sim *et al*. (2002) likewise report it from waterfalls in the Canary Islands (Figure 38). In Thuringia, Germany, ***Jubula hutchinsiae*** is associated with streams that have the ***Platyhypnidium*** (Figure 39)-***Fontinalis antipyretica*** (Figure 40) association (Marstaller 1987). It is known in the UK from a ravine (Wallace 1952).

Figure 36. ***Jubula hutchinsiae*** forming mats on boulders in a common stream habitat. Photo by Michael Lüth, with permission.

Figure 37. ***Jubula hutchinsiae*** showing wet habitat at margin of fast stream. Photo by Michael Lüth, with permission.

Figure 38. ***Jubula hutchinsiae*** on Tenerife, Canary Islands, in the Macaronesian Islands. Photo by Jonathan Sleath, with permission.

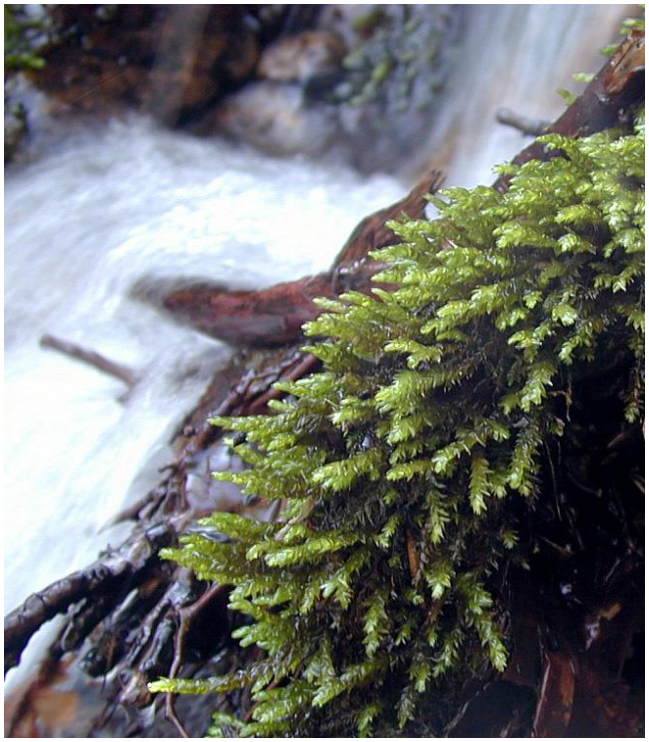

Figure 39. ***Platyhypnidium riparioides*** in Europe, a species that occurs in the same streams as ***Jubula hutchinsiae***. Photo by Michael Lüth, with permission.

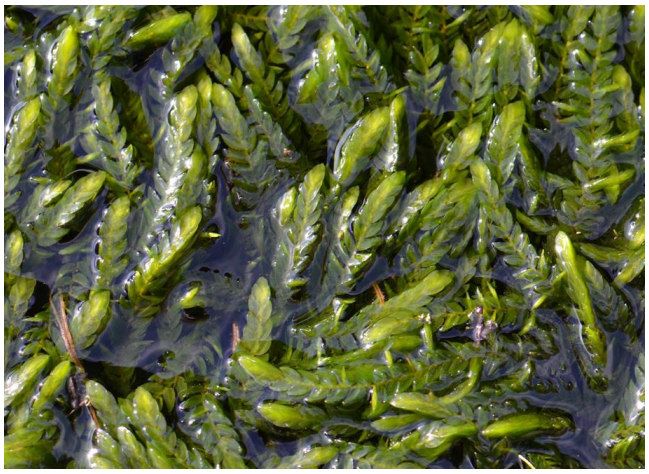

Figure 40. ***Fontinalis antipyretica***, a species that occurs in the same streams as ***Jubula hutchinsiae***. Photo by Tab Tannery, through Creative Commons.

The Australian subspecies ***australiae*** occurs in the tropical rainforest and the Wet Tropics (Pócs & Cairns 2008). In Macaronesia, Sim-Sim *et al*. (2002) found ***Jubula hutchinsiae*** (Figure 33) frequently in the native forests (Figure 38), as well as Atlantic Europe. In Thailand, it (subspecies ***javanica***?) occurred on the filmy fern ***Vandenboschia maxima*** (=*Crepidomanes maximum*; Figure 41-Figure 42) at the edge of a stream (Sukkharak 2017). On Achill Island off the west coast of Ireland, ***Jubula hutchinsiae*** occurs on wet rocks under an overhang by a stream (Warburg 1963). Proctor (1999) found it in Devon, UK, on dripping rocks in a shady stream gully. Averis *et al*. (2012) found it in Scotland on wet rocks beside a fast-water stream.

Figure 41. ***Vandenboschia maxima***, a fern where one can sometimes find ***Jubula hutchinsiae*** as an epiphyll in Thailand. CalPhotos, through Creative Commons.

Figure 42. ***Vandenboschia maxima*** leaf segments close-up – substrate where one can sometimes find ***Jubula hutchinsiae*** in Thailand. Photo from CalPhotos, through Creative Commons.

This species can also survive in humid habitats that are not subject to inundation (Figure 43). Gabriel *et al*. (2008) found that it occurs in cave (lava tube and volcanic pit) entrances (Figure 44) in the Azores, occupying particularly humid sites, where it is a frequent species.

In a main ravine in the UK, Callaghan *et al*. (2019) found large clumps of ***Jubula hutchinsiae*** (Figure 33); it often grew through, and upon, larger competitive species. It was among the three most frequent species in the study, but was also the most unevenly distributed. Following the development of hydroelectric power, it was one of two liverworts showing an increase, whereas the other three species declined. It appears to be a very stable species, occupying a position low down on the river bank where it experiences relatively frequent hydrological disturbance.

Figure 43. ***Jubula hutchinsiae*** forming shelves on vertical rock. Photo by Stan Phillips, through public domain.

Figure 44. Volcanic cave, Algar do Carvão, on Terceira Island, Portugal, the type of location where one might find ***Jubula hutchinsiae***. Photo by Vitor Oliveira, through Creative Commons.

Richards (1947) noted his surprise at finding no damage to ***Jubula hutchinsiae*** (Figure 33) after several days of being frozen solid, even though it seemed to be restricted to sheltered habitats.

Reproduction

Jubula hutchinsiae (Figure 33) is **autoicous**. It forms discoid gemmae from the lobe surfaces (Schuster 1992), a character also found in some species of **Lejeuneaceae** (Pócs 2012).

Biochemistry

Suire (2000) compared development of oil bodies (Figure 45-Figure 46) among liverworts. He found that ***Jubula hutchinsiae*** oil bodies (Figure 45) originate from the dilation of ER cisternae. Their membrane is thickened by an osmiophilic material. Each leaf cell contains several oil-bodies.

Biochemical studies seem to be lacking on this species. Wang and Qiu (2006) found no publications of mycorrhizal fungi on ***Jubula hutchinsiae***.

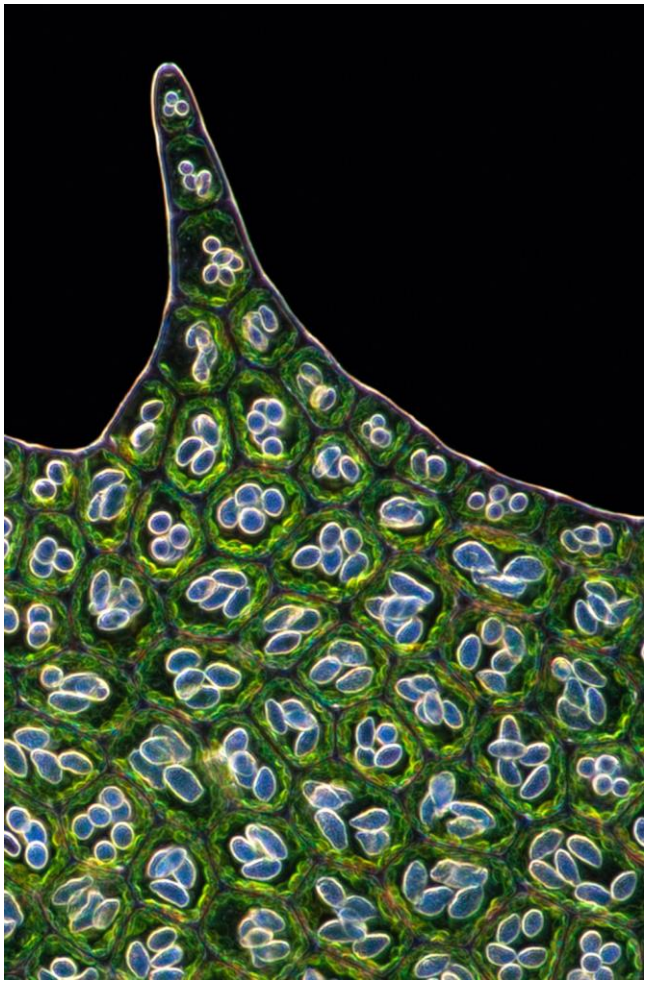

Figure 45. ***Jubula hutchinsiae*** leaf tip showing oil bodies. Photo by Des Callaghan, with permission.

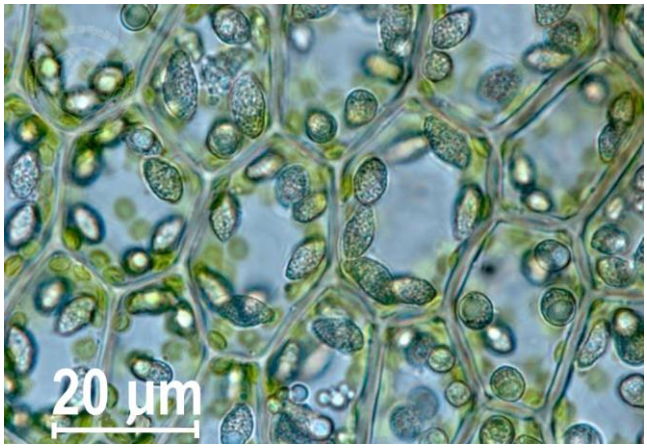

Figure 46. ***Jubula hutchinsiae*** ssp. ***japonica*** leaf cells and oil bodies. Photo by Jia-dong Yang, though Creative Commons.

***Jubula hutchinsiae* subsp. *pennsylvanica* (Figure 47)**

(syn. = *Jubula pennsylvanica*)

Distribution

Clark and Frye (1945) reported the distribution of ***Jubula hutchinsiae* subsp. *pennsylvanica*** (Figure 47) from Nova Scotia to Ohio, south to Oklahoma, Alabama,

and Georgia in North America, Bermuda, Azores, and Madeira (the latter two probably a different subspecies). Later, Schuster (1992) considered it to be an Appalachian (eastern North America) endemic (Schuster 1992). It ranges from Nova Scotia, south to Georgia, but also occurs in isolated locations in Ohio, west of the Appalachians.

Figure 47. ***Jubula hutchinsiae*** subsp. ***pennsylvanica***, a subspecies probably restricted to eastern North America, south to Bermuda. Photo by Wayne Lampa, through Creative Commons.

Aquatic and Wet Habitats

Jubula hutchinsiae **subsp.** ***pennsylvanica*** (Figure 47) has been found on moist rock surfaces or springy banks of ravines in Connecticut, USA (Nichols 1916); in streams in the Great Smoky Mountains National Park, Kentucky, USA (Knapp & Lowe 2009). It can be a rare species along rocky streams in the southern part of its range. In central New York, USA, ***Jubula hutchinsiae*** **subsp**. ***pennsylvanica*** lives in both large and small ravines on shady, permanently wet rock faces (Trigoboff 2013). Clark and Frye (1945) summarize the habitat for the eastern USA as occurring on rocks or soil in damp or wet situations or in deep shade.

Stephenson *et al.* (1995) found that ***Jubula hutchinsiae*** **subsp.** ***pennsylvanica*** (Figure 47) preferred a *p*H range of 5.95-6.6 in West Virginia, USA, mountain streams.

Reproduction

Jubula hutchinsiae subsp. ***pennsylvanica*** (Figure 47) is **monoicous** (having both sexes on the same plant) (Clark & Frye 1945) and often fertile, typically from April to early July (Schuster 1992). The capsule appears on a long stalk.

Jubula hutchinsiae var. *integrifolia*

Jubula hutchinsiae var. ***integrifolia***, the most frequent liverwort in the Madeira Archipelago, has questionable taxonomic status (Lars Söderström, pers. comm. 9 October 2020). Söderström suggests that it is probably a synonym of var. ***javanica*** or subsp. ***japonica*** (Figure 34-Figure 35), but some plants definitely do not belong to either. Accordingly, the record from Madeira is best referred to subsp. ***hutchinsiae***.

Distribution

Jubula hutchinsiae var. ***integrifolia*** occurs in mountainous streams in Madeira Island (Luis *et al.* 2015) and has been reported from the Canary Islands (Sim-Sim *et al*. 2002).

Aquatic and Wet Habitats

Sim-Sim *et al*. (2002) distinguished var. ***integrifolia*** as occurring completely submerged in waterfalls, whereas the typical variety occurs on humid slopes covered with soil along rivulets, not in waterfalls. These habitat differences may account for the morphological differences that led to the separation of the varieties. Perhaps they should be considered forms, but we need common garden experiments to be certain.

Lejeuneaceae

The **Lejeuneaceae** is represented by several species in Himalayan streams (Suren & Ormerod 1998).

Acanthocoleus aberrans

Distribution

Faria *et al.* (2012) report the distribution of ***Acanthocoleus aberrans*** as Neotropical and African. Schäfer-Verwimp (1999) considered it to be "rather rare" in the Neotropical region, noting only a few collections from Mexico, Costa Rica, Guatemala, Jamaica, French Guiana, and only once from Dominica. It occurs on the Guadaloupe archipelago in the French West Indies (Bernarda & Schäfer-Verwimp 2011).

Aquatic and Wet Habitats

Acanthocoleus aberrans occurs in mountainous streams on Madeira Island (Luis *et al*. 2015). But other than this report, it appears that this species is terrestrial and seldom occurs in wet areas.

Reproduction

There seems to be little information on reproduction of ***Acanthocoleus aberrans***. We know it is **dioicous** (dos Santos *et al*. 2017), perhaps accounting for its relative rarity.

Bromeliophila (Figure 52)

This is a unique genus with only two species [***Bromeliophila natans*** (Figure 52) and ***B. helenae***], both of which are restricted to the tanks made by leaves of **Bromeliaceae**, but may occur on many different bromeliad host species (Gradstein 1997). Heinrichs *et al*. (2014) used a three-marker dataset – chloroplast genome rbcL gene and trnL-F region, and nuclear ribosomal ITS1-5.8S-ITS-2 region – to determine relationships of this genus to ***Prionolejeunea*** (Figure 48) and ***Cyclolejeunea*** (Figure 49).

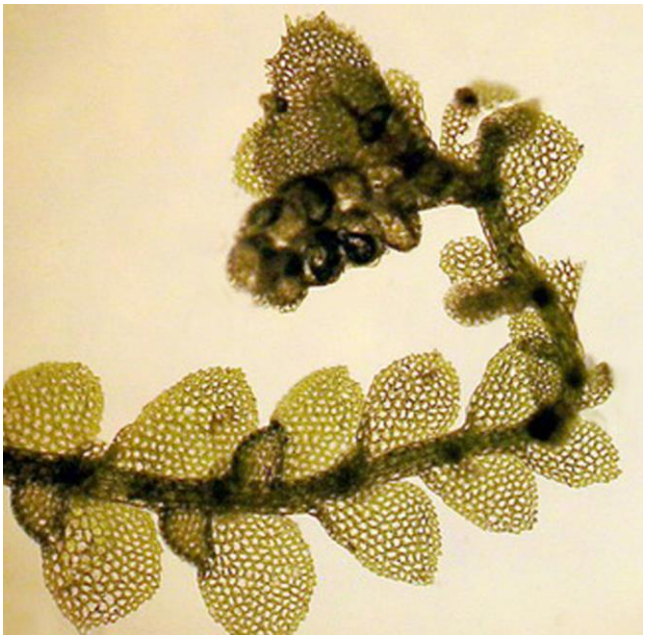

Figure 48. ***Prionolejeunea saccatiloba*** with perianth and male branch, in a genus that may be related to ***Bromeliophila***. Photo by Michaela Sonnleitner.

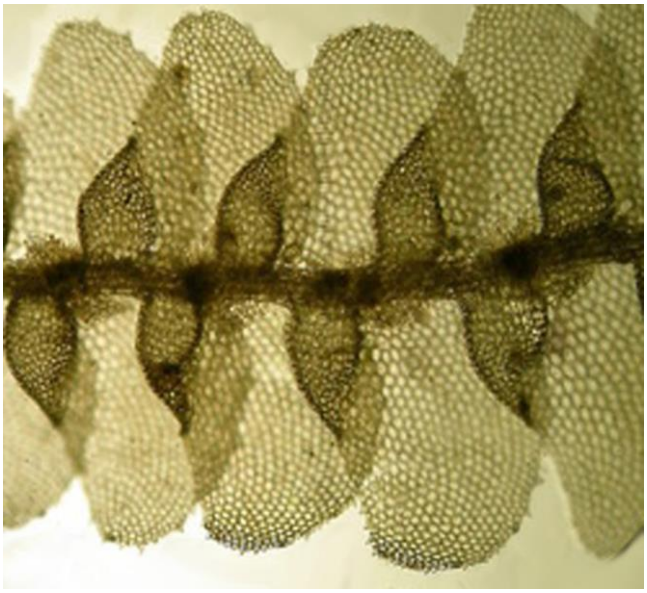

Figure 49. ***Cyclolejeunea peruviana***, in a genus that may be related to ***Bromeliophila***. Photo by Michaela Sonnleitner, with permission.

Because the **Bromeliaceae** hosts are restricted to the tropics and subtropics, ***Bromeliophila*** (Figure 52) is likewise (Gradstein *et al*. 2001). Its habitat is one in which the lower parts of the leafy gametophyte shoots are "often" submerged; only the upper parts extend above the water (Heinrichs *et al*. 2014).

Bromeliophila helenae

Distribution

Bromeliophila helenae is reported from Colombia (Gradstein 1997; Benavides & Callejas 2004; Campos & Uribe-M. 2006). ***Bromeliophila helenae*** also occurs in the Guayana Highland (Gradstein *et al*. 2001) and on Martinique in the Lesser Antilles (Bernard 2018).

Aquatic and Wet Habitats

The habitat for this species is in the water at the base of bromeliad leaves, including those of ***Brocchinia tatei*** (Figure 50-Figure 51) (Gradstein *et al*. 2001).

Figure 50. ***Brocchinia tatei***, home for ***Bromeliophila helenae*** in South America. Photo by Adalberto Jose Perez Lopez, through Creative Commons.

Figure 51. ***Brocchinia tatei*** showing the basin of water where ***Bromeliophila helenae*** lives. Photo by Imerú Alfonzo-Hernandez, through Creative Commons.

Bromeliophila natans (Figure 52)

Distribution

Bromeliophila natans (Figure 52), like ***Bromeliophila helenae***, occurs in bromeliad basins in South America (Gradstein 1997), particularly Neotropical countries (Heinrichs *et al*. 2014). Because it occurs only in these water-filled basins, Imbassahy *et al*. (2009) consider it to be "exclusively" aquatic.

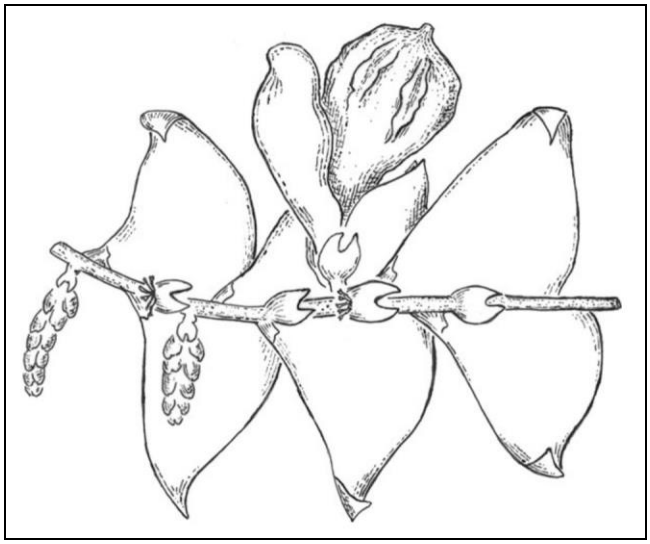

Figure 52. ***Bromeliophila natans*** with perianth, a species that lives in the water of bromeliad basins. Drawing from Heinrichs *et al*. 2014 through Rob Gradstein.

Visnadi (2010) considered ***Bromeliophila helenae*** to be restricted to the **restingas** of Brazil. This points to its dependence on water of the bromeliad basin. **Restingas** are a distinct type of coastal tropical and subtropical moist broadleaf forest in eastern Brazil. **Restingas** form on spits of sandy, acidic, nutrient-poor soil with trees and shrubs that are adapted to drier conditions with low nutrients.

Cephalantholejeunea temnanthoides

Distribution

Cephalantholejeunea temnanthoides is the only species in its genus (Shi *et al*. 2015), and it is a rare Amazonian **rheophyte** (aquatic plant that lives in fast-moving water currents in environment where few other organisms can survive) (da Costa 2003; Shi *et al*. 2015).

Aquatic and Wet Habitats

Cephalantholejeunea temnanthoides occurs on stems that are flooded by the Rio Negro (Reiner-Drehwald 2011). S. Robbert Gradstein (pers. comm. 3 November 2011) told me that he has found it in Andean streambeds. Daly *et al*. (2006) noted that it is characteristic of **salões** (lowland moist tropical environments in which virtually all plant diversity is accounted for by herbs). This unique habitat occurs along canalized portions of the Purus and Juruá river basins. As such, the available substrate is exposed parent materials with only a thin (<1 m) layer of soil. These **salões** are wetlands that remain constantly moist due to seepage. ***Cephalantholejeunea temnanthoides*** associates with ***Plagiochila martiana*** and ***Dumortiera hirsuta*** (Figure 53) in these habitats.

Reproduction

Cephalantholejeunea temnanthoides is **monoicous** (Schuster 1990; Reiner-Drehwald & Weis 2001). Thus its sexual condition does not explain its rarity. Reiner-Drehwald and Weis (2001) described sporophytes for the first time.

Figure 53. ***Dumortiera hirsuta***, an associate of ***Cephalantholejeunea temnanthoides*** in wetland areas. Photo by Michael Lüth, with permission.

Ceratolejeunea temnantha (Figure 56-Figure 55)

(syn. = *Lejeunea temnantha*)

Distribution

Ceratolejeunea temnantha (Figure 56-Figure 55) is another Amazonian endemic rheophyte (Sierra *et al*. 2018). Sierra and coworkers suggested that the evolution of rheophytes, including this species, in northern South America correlates with the expansion into novel ecological niches and dramatic landscape changes in the Miocene.

Aquatic and Wet Habitats

Ceratolejeunea temnantha (Figure 56-Figure 55) is a rheophyte of seasonally inundated black-water forests (Sierra *et al*. 2018). It was reported from a tree root (Figure 54) that is inundated at high water and likewise tree trunks that become inundated (Figure 55).

Figure 54. ***Ceratolejeunea temnantha*** on woody roots in an inundated area. Photo by Juan Carlos Villarreal, with permission.

Figure 55. ***Ceratolejeunea temnantha*** on inundated tree trunk. Photo by Juan Carlos Villarreal, with permission.

Reproduction

Ceratolejeunea temnantha is **monoicous** (Figure 56). It seems to lack any specialized asexual reproductive structures.

Figure 56. ***Ceratolejeunea temnantha*** with antheridial branches (hanging down) and perianth (upper left). Photo by Juan Carlos Villarreal, with permission.

Biochemistry

The oil bodies of this species are relatively large, with multiple bodies per cell (Figure 57). Descriptions of their chemical constituents remain unknown, partly due to the rarity of the species.

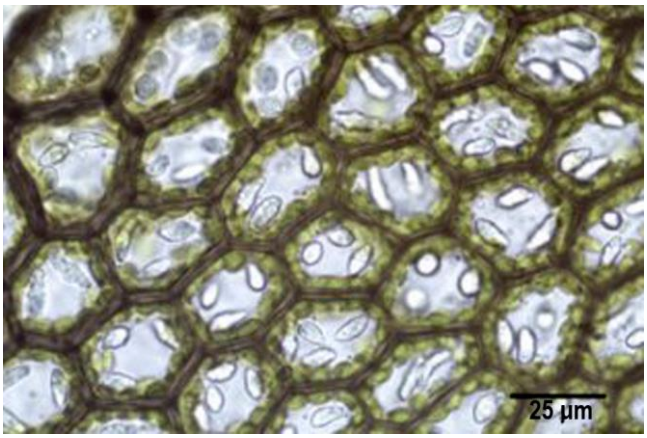

Figure 57. ***Ceratolejeunea temnantha*** leaf cells with oil bodies. Photo by Juan Carlos Villarreal, with permission.

Cheilolejeunea clypeata **(Figure 58-Figure 60, Figure 69)**

(syn.= *Leucolejeunea clypeata*)

Distribution

Ye and Zhu (2010) investigated synonyms in the genus ***Leucolejeunea***, contributing to the recognition of *Leucolejeunea clypeata* as a species of ***Cheilolejeunea***, ***Cheilolejeunea clypeata*** (Figure 58-Figure 60, Figure 69). ***Cheilolejeunea clypeata*** is endemic to eastern North America (New York to Florida), from sea level to 2000 m asl (Schuster 1980).

Figure 58. ***Cheilolejeunea clypeata***, an eastern North American endemic. Photo by Blanka Aguero, with permission.

Figure 59. ***Cheilolejeunea clypeata*** showing relatively small lobules. Photo by Blanka Aguero, with permission.

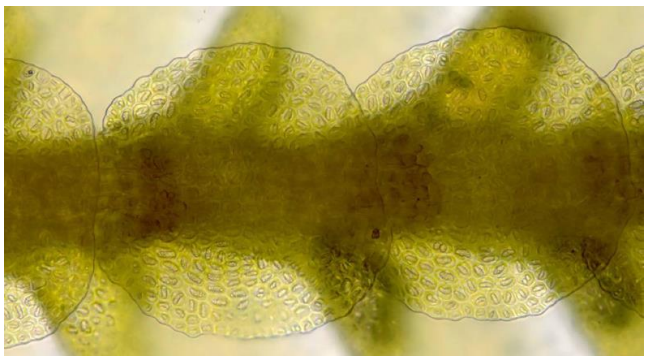

Figure 60. ***Cheilolejeunea clypeata*** showing underleaves. Photo by Blanka Aguero, with permission.

Aquatic and Wet Habitats

Nichols (1916) reported this from crevices or surfaces of drier cliffs in a ravine in Connecticut, USA. Schuster (1980) describes ***Cheilolejeunea clypeata*** (Figure 58-Figure 60, Figure 69) as having a highly diversified ecology. Its substrata are bark, rock walls, and boulders. It is on both calcareous and noncalcareous rocks, typically shaded, often moist, but sometimes dry. Its best habitats seem to be rich mesophytic forests and swamp forests, where it lives on bark of a variety of tree species. Its status as a wetland species is somewhat marginal.

Lendemer *et al*. (2016) discovered the lichen ***Catinaria brodoana*** (Figure 61) to occur most frequently on ***Cheilolejeunea clypeata*** (Figure 58-Figure 60, Figure 69) in swamp forests with ***Chamaecyparis*** (Figure 62), ***Taxodium*** (Figure 63), and mixed hardwoods [***Acer*** (Figure 64), ***Magnolia virginiana*** (Figure 65), ***Persea*** (Figure 66)] with an understory of ***Lyonia*** (Figure 67)***-Ilex glabra*** (Figure 68). The lichen has a much narrower distribution than its liverwort substrate.

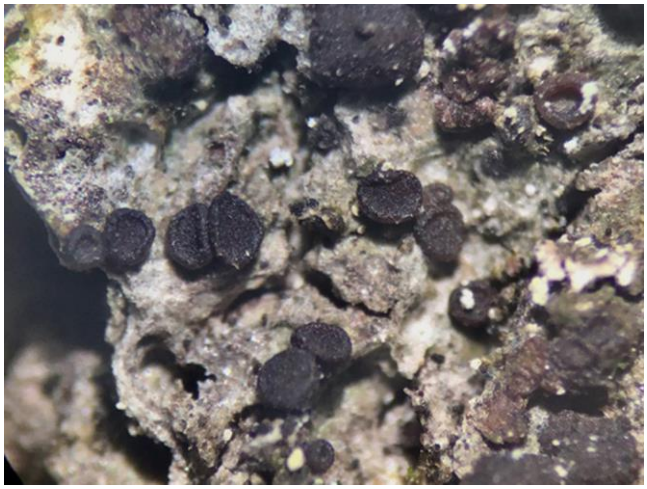

Figure 61. ***Catinaria atropurpurea***; the lichen ***Catinaria brodoana*** occurs most frequently on the liverwort ***Cheilolejeunea clypeata***. Photo by Tomás Curtis, through Creative Commons.

Figure 62. ***Chamaecyparis thyoides*** near edge of bog in Brendan T. Byrne State Forest, New Jersey, USA. Photo by Famarton, through Creative Commons.

Figure 63. ***Taxodium distichum*** (bald cypress) swamp, habitat for ***Cheilolejeunea clypeata***. Photo courtesy of Kim Barton.

Figure 64. ***Acer rubrum*** in forest, a common species in swamps where ***Cheilolejeunea clypeata*** lives. Photo by Digby Dalton, through Creative Commons.

Figure 65. ***Magnolia virginiana***, a common species in swamps where one can find ***Cheilolejeunea clypeata***. Photo courtesy Great Plant Picks, with online permission.

Figure 66. ***Persea americana*** with fruit, a common species in swamps where one can find ***Cheilolejeunea clypeata***. Photo by M. Clara Salviano, through Creative Commons.

Figure 67. ***Lyonia lucida*** with fruit; ***Lyonia*** is a common understory genus in swamps where ***Cheilolejeunea clypeata*** lives. Photo by Homer Edward Price, through Creative Commons.

Figure 68. ***Ilex glabra*** with flowers, a common understory species in swamps where ***Cheilolejeunea clypeata*** lives. Photo by Siddarth Machado, through Creative Commons.

Reproduction

The species is **autoicous** (Schuster 1980). This suggests that its narrow distribution is limited either by dispersal or narrow habitat requirements that do not occur frequently enough to provide stepping stones to any distant locations.

Biochemistry

Zhu and Gradstein (2003) described a single oil body per cell (Figure 69). There seem to be no biochemical studies to indicate what antibiotic/antiherbivore compounds might be secluded there.

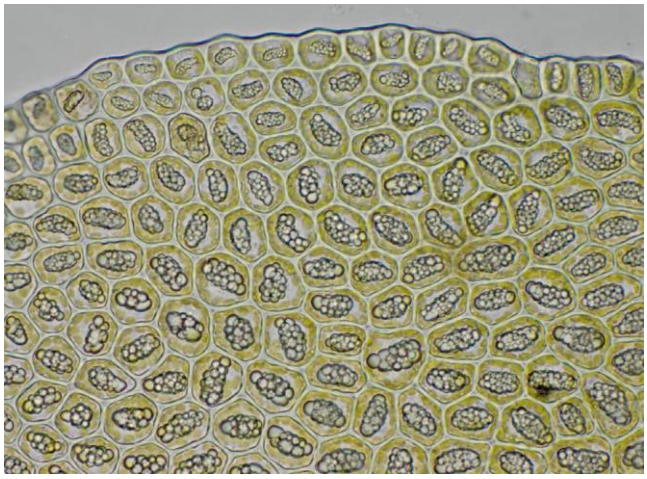

Figure 69. ***Cheilolejeunea clypeata*** leaf cells showing oil bodies. Photo by Blanka Aguero, with permission.

Cololejeunea biddlecomiae (Figure 70, Figure 74, Figure 78, Figure 81-Figure 85)

Distribution

Evans (1938) considered ***Cololejeunea biddlecomiae*** (Figure 70, Figure 74, Figure 78, Figure 81-Figure 85) to be the most widely distributed species of ***Cololejeunea***. It occurs from Nova Scotia, New Brunswick, and Ontario in Canada, south to Georgia and Oklahoma in the USA. Schuster (1956) described this as a species of temperate and sub-boreal North America, occurring in the southern half of the spruce-fir forest, throughout deciduous forests, and into the broad-leaved evergreen forests of the southeastern coastal plain.

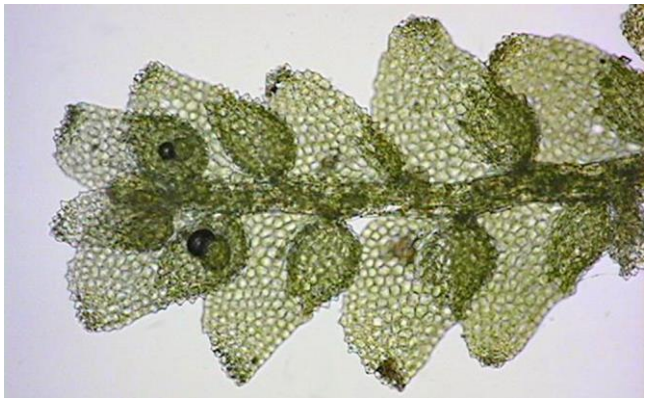

Figure 70. ***Cololejeunea biddlecomiae*** with lobules. Photo by Ken McFarland and Paul Davison, with permission.

Aquatic and Wet Habitats

Nichols (1916) reported ***Cololejeunea biddlecomiae*** (Figure 70, Figure 74, Figure 78, Figure 81-Figure 85) growing along calcareous rivers in Connecticut, USA. Wittlake (1950) reported that it occurs under and around springs along with ***Riccardia multifida*** (Figure 71), ***Aneura pinguis*** (Figure 72), ***Calypogeia sullivantii*** (Figure 73) in Spy Rock Hollow, Arkansas, USA. It occurs in Adirondack Mountain streams (Slack & Glime 1985). In central New York, it occurs in fine, yellow-green mats in ravines (Schuster 1956). In southern Illinois, Skorepa (1968) found it on sandstone in a creek bed.

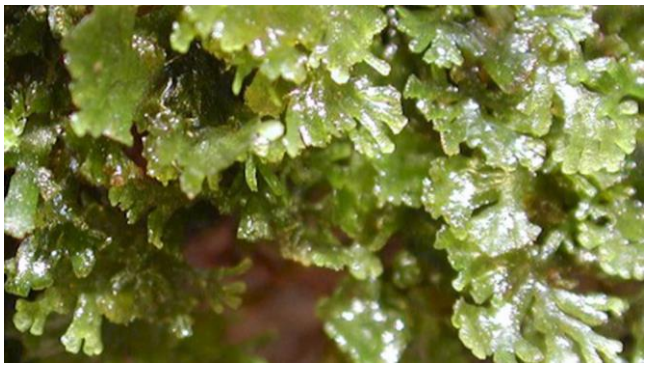

Figure 71. ***Riccardia multifida***, a species associated with ***Cololejeunea biddlecomiae*** at springs. Photo by Paul G. Davison, with permission.

Figure 72. ***Aneura pinguis***, a species associated with ***Cololejeunea biddlecomiae*** at springs. Photo by Hermann Schachner, through Creative Commons.

Figure 73. ***Calypogeia sullivantii***, a species associated with ***Cololejeunea biddlecomiae*** at springs. Photo by Paul Davison, with permission.

This species is not restricted to stream and riverine habitats. Schuster (1956) described a wide variation in its habitats. In his words, it is "almost indiscriminately corticolous (Figure 74) and saxicolous, occurring in shaded, relatively damp sites, especially moderately dry calcareous sandstone rocks." In New Jersey, USA, Barringer (2011) treated it as a tree bark species that rarely occurs on rocks in shaded ravines. Ammons (1933) found it in McKinney's Cave, West Virginia (Figure 75).

Figure 74. ***Cololejeunea biddlecomiae*** in its habitat on bark and wood. Photo by Ken McFarland and Paul Davison, with permission.

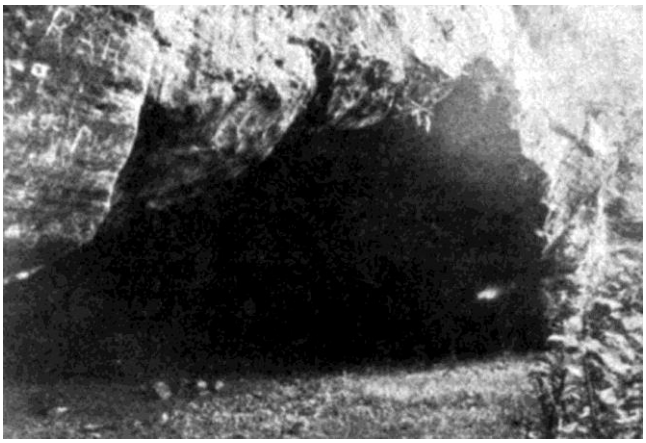

Figure 75. McKinney's cave, West Virginia, USA, entrance, where Ammons (1933) found ***Cololejeunea biddlecomiae***. Photo from Ammons 1933.

Interestingly, ***Cololejeunea biddlecomiae*** (Figure 70, Figure 74, Figure 78, Figure 81-Figure 85) is less calciphilic in the southernmost part of its range (Schuster 1956). Trigoboff (2013), reporting from central New York, considered ***Cololejeunea biddlecomiae*** (Figure 70, Figure 74, Figure 78, Figure 81-Figure 85) in his report of aquatic bryophytes, but mostly described it from shade and high humidity with a high frequency on trees. Brown (1948), also in New York, reported the species as occurring among other liverworts on the lower trunk and stumps in gorges and ***Thuja*** swamps (Figure 76) on both hardwoods and ***Thuja occidentalis*** (Figure 77), but not in the mountains.

Darlington (1938) found it in a slightly more humid environment on a rotten log (Figure 78) along the Crystal River in Leelanau County, Michigan, USA. Schuster and Patterson (1957) found it growing in Dismal Swamp, Virginia, USA, on tree trunks, along with ***Radula obconica*** (Figure 79) and ***R. australis*** (Figure 80).

Figure 76. ***Thuja occidentalis*** along stream – home for many bryophytes, including ***Cololejeunea biddlecomiae***. Photo by Peter M. Dziuk, with online permission.

Figure 77. ***Thuja occidentalis*** saplings, a species that can provide a substrate for ***Cololejeunea biddlecomiae***. Photo from Superior National Forest, through Creative Commons.

Figure 78. ***Cololejeunea biddlecomiae*** on log. Photo by Paul Davison, with permission.

Figure 79. ***Radula obconica*** with perianths, a species that accompanies ***Cololejeunea biddlecomiae*** on tree trunks in Dismal Swamp, Virginia, USA. Photo by Paul G. Davison, with permission.

Figure 80. ***Radula australis***, a species that accompanies ***Cololejeunea biddlecomiae*** on tree trunks in Dismal Swamp, Virginia, USA. Photo by Paul G. Davison, with permission.

Adaptations

Cololejeunea biddlecomiae (Figure 70) produces **styli** (Figure 81-Figure 82) that might help in moving water along the stem by providing capillary spaces.

Reproduction

Cololejeunea biddlecomiae (Figure 70, Figure 74, Figure 78, Figure 81-Figure 83) produces gemmae (Figure 84-Figure 85), mostly on the lower surface of the leaf lobes, but never on the lobules (Stevens 1910). But these are not numerous, typically with only a few and not more than five or six on an individual leaf. Even the numbers of gemmae-bearing branches in a population is only a relatively small proportion. Plants with large numbers of gemmae are typically closely associated with plants having none. As we might expect, plants with sexual organs have fewer gemmae, but gemma production is not completely inhibited in these plants. The gemmae sometimes occur on the bracts associated with the sexual organs, but they never seem to occur on perianths. These gemmae continue to increase in size after cell division ceases, resulting from cell growth (Figure 85). This increase continues until the time the gemmae are shed. The gemmae are shed by splitting of the cell wall between the stalk cell and gemma.

Figure 81. ***Cololejeunea biddlecomiae*** with **styli**. Photo by Paul Davison, with permission.

Figure 82. ***Cololejeunea biddlecomiae*** with **stylus** Notice the **tuberculate** (having protuberances) cells on the surface of the lobule. Photo by Paul Davison, with permission.

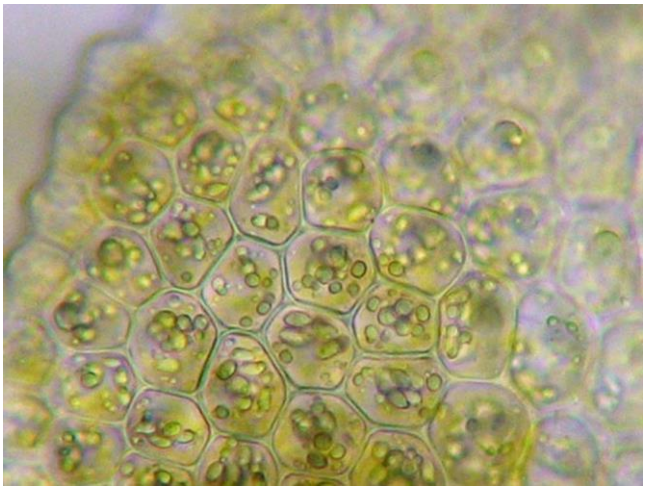

Figure 83. ***Cololejeunea biddlecomiae*** leaf cells showing oil bodies. Photo by Ken McFarland and Paul Davison, with permission.

Figure 84. ***Cololejeunea biddlecomiae*** with gemmae on the leaf surface. Photo by Ken McFarland and Paul Davison, with permission.

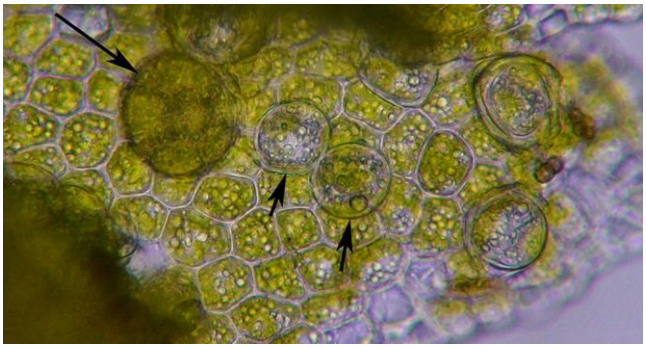

Figure 85. ***Cololejeunea biddlecomiae*** leaf gemmae showing various sizes and number of cells. Photo by Ken McFarland and Paul Davison, with permission.

Risk *et al*. (2011) found that leaves had been lost in a colony of epiphyllous ***Cololejeunea biddlecomiae***. This suggests a potential means of reproduction, whether it is by caducous leaves or transport by herbivores that have nibbled on the leaves. The species produces green, multicellular spores that can give a dispersed spore a good start when it arrives in a new location.

Hatcher (1965) reported difficulties in trying to establish a pure culture of ***Cololejeunea biddlecomiae*** (Figure 70, Figure 74, Figure 78, Figure 81-Figure 85), noting that it failed to differentiate stems and leaves, instead developing as an amorphous mass of cells. This suggests that it may need very specific environmental conditions for its early development.

Cololejeunea calcarea (Figure 86-Figure 90)

Distribution

Cololejeunea calcarea (Figure 86-Figure 90) occurs in Europe and northern Asia. Schuster (1955) considers it to be frequent in western Europe. Konstantinova (2011) reported it from the Eastern Caucasus, Russia.

Aquatic and Wet Habitats

Cololejeunea calcarea (Figure 86-Figure 90) is occasionally submerged (Watson 1919). It occurs on limestone rock in the Tara River canyon and Durmitor area, Montenegro (Papp & Erzberger 2011).

Figure 86. ***Cololejeunea calcarea***, showing imbricate leaves. Photo by Štěpán Koval, with permission.

Evans (1911) states that ***Cololejeunea calcarea*** (Figure 86-Figure 90) seems to be confined to rock (Figure 87). Watson (1918) attributed it to shaded limestone cliffs and skrees. Alegro *et al*. (2014), reporting from Croatia, likewise concluded that it occurs on shaded limestone rock. Blockeel (1991) provided more details on finding it on shaded limestone in a ravine at 200 m asl in the gorge of the River Akheron in Greece.

Figure 87. ***Cololejeunea calcarea*** habitat on rock wall in South Wales. Photo by Barry Stewart, with permission.

Figure 88. ***Cololejeunea calcarea*** showing large leaf lobules. Photo by Hermann Schachner, through Creative Commons.

Figure 89. ***Cololejeunea calcarea*** with perianths. Photo by Hermann Schachner, through Creative Commons.

Reproduction

This species has gemmae that it uses for asexual reproduction (Cavers 1903). These are produced on the leaf surfaces, mostly on the lower surface of the lobes but occasionally on the upper surface (Stevens 1910). These are small in numbers, not more than 5-6 on an individual leaf. Although the gemmae are relatively common in New England, USA, they only occur on a comparatively small proportion of the plants in any mat. One plant may have a "considerable number" while an adjacent plant has none. As in ***C. biddlecomiae***, fertile plants often have gemmae, but they are more abundant on sterile plants. They may even occur on the bracts, but never on the perianths. After cell division ceases, the gemmae continue to grow by cell expansion, not even stopping until sometime after the gemmae are shed. The gemma forms a flat disc that is one cell thick with no dorsi-ventral differentiation. The gemma is shed by splitting of the cell wall between the stalk cell and the gemma. ***Cololejeunea calcarea*** (Figure 86-Figure 90) is one of the species in southern Turkey that has frequent asexual reproduction (Kürschner 2014).

Figure 90. ***Cololejeunea calcarea*** showing perianths. Photo by Stan Phillips, through public domain.

Fungal Interactions

Wang and Qiu (2006) found no records of mycorrhizae associated with ***Cololejeunea calcarea*** (Figure 86-Figure 90).

Cololejeunea hodgsoniae

Distribution

Cololejeunea hodgsoniae is distributed in Australia (ITIS 2020) and New Zealand (de Lange *et al*. 2015), finding both warm temperate and cool temperate climates suitable.

Aquatic and Wet Habitats

One of the interesting habitats of ***Cololejeunea hodgsoniae*** in Australia is to grow on the leaves of the leafy liverwort ***Radula marginata*** (Figure 91) on rocks in streams (Renner 2003). In fact, Renner suggested that it might be muscicolous (bryicolous?).

Figure 91. ***Radula marginata***; ***Cololejeunea hodgsoniae*** grows on the leaves of ***R. marginata*** on rocks in Australian streams. Photo by Peter de Lange, through Creative Commons.

Reproduction

Cololejeunea hodgsoniae is **autoicous**, making spore production likely (de Lange *et al*. 2015).

Cololejeunea madothecoides

(syn. = *Hemilejeunea ruttneri*)

Distribution

Cololejeunea madothecoides ranges from India and Indochina to Japan and Borneo (Asthana & Srivastava 2003; Manju *et al*. 2012). Shu *et al.* (2016) later reported it from Vietnam.

Aquatic and Wet Habitats

Ruttner (1955) reported ***Cololejeunea madothecoides*** as a species that occurs in a zone less than 15 cm above water level in the tropics. Pócs and Ninh (2005) found it to be very abundant on streambed stones in parts of Vietnam and considered its subgenus to be especially adapted to riverine conditions. In the Western Ghats of India, the species is epiphyllous (Nair & Prajitha 2016; Manju *et al*. 2012). In northeastern India, Singh and Kumar (2106) reported it as epiphytic.

Adaptations

These adaptations include thick stems, rigid leaves, and adherence of large masses to temporarily inundated streambed rocks. Smets (2003) found it on very humid calcareous rocks in the western Carpathians in Romania.

Reproduction

Gradstein *et al*. (2011) reported that ***Cololejeunea madothecoides*** lacked gemmae in Ecuador.

Cololejeunea microscopica (Figure 92)

(syn. = *Aphanolejeunea microscopica*)

Distribution

Cololejeunea microscopica (Figure 92) occurs in India (Tripura), Africa, and Europe (Pócs 1984; Singh & Kumar 2017).

Aquatic and Wet Habitats

Cololejeunea microscopica (Figure 92) grows in shaded, humid places on damp or dry rocks, especially by streams and waterfalls (Hodgetts 2020). In India, it is epiphytic, growing on bark of trees in moist and shady places (Singh & Kumar 2017). It can even be epiphyllous on other bryophytes, as on ***Pyrrhobryum spiniforme*** in Brazil (Sierra *et al*. 2019).

Figure 92. ***Cololejeunea microscopica***, a sometimes epiphyllous species (as shown here) that grows near streams. Photo by Jan-Peter Frahm, with permission.

Figure 93. ***Pyrrhobryum spiniforme***, a moss on which ***Cololejeunea microscopica*** can be an epiphyll. Photo by John Brinda, through Creative Commons.

Cololejeunea rossettiana (Figure 94-Figure 97)

Distribution

Cololejeunea rossettiana (Figure 94-Figure 97) occurs in Africa, Europe, and Northern Asia (ITIS 2020). Kürschner and Erdağ (2005) reported it from Turkey.

Figure 94. ***Cololejeunea rossettiana***, a species found in Africa, Europe, and Northern Asia. Photo by Des Callaghan, with permission.

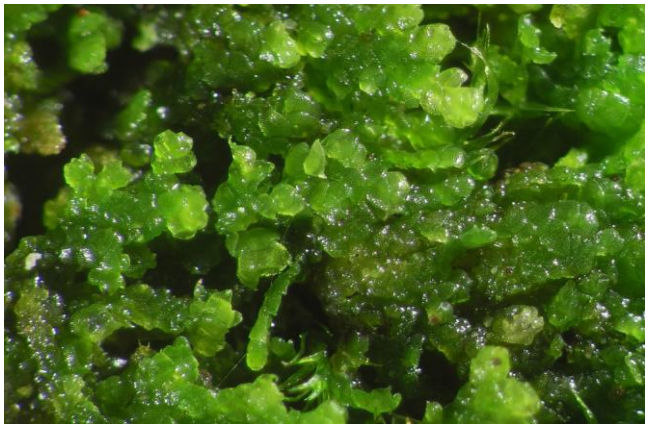

Figure 95. ***Cololejeunea rosettiana***, typically an epiphytic or saxicolous liverwort. Photo by Michael Lüth, with permission.

Figure 96. ***Cololejeunea rosettiana*** showing the bulging (trabeculate) cells. Photo by Michael Lüth, with permission.

Figure 97. ***Cololejeunea rosettiana*** showing trabeculate projections from cells. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Watson (1919) noted that ***Cololejeunea rossettiana*** (Figure 94-Figure 97) is occasionally submerged, but no other reports seem to consider it to be aquatic.

Although it occurs in most of the southeastern European countries, ***Cololejeunea rossettiana*** is nevertheless rare and occurs on many European Red Lists of bryophytes (Hodgetts 2015).

Reproduction

Cololejeunea rossettiana is **monoicous (**Figure 98-Figure 99**)** (Arnell 1953). That should make its sexual reproduction relatively easy. Part of its apparent rarity may be due to its very small size and inconspicuous appearance (Lawley 2010), causing it to be undercollected.

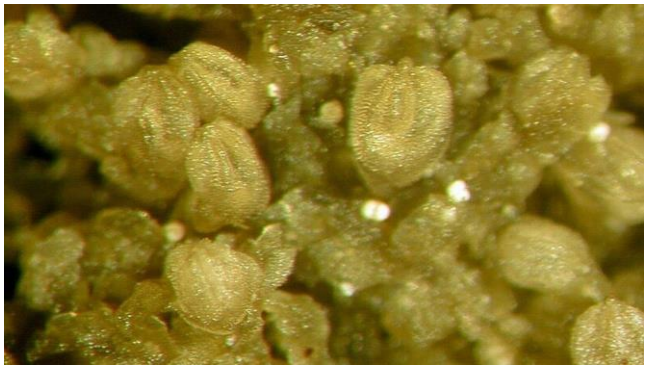

Figure 98. ***Cololejeunea rosettiana*** with perianths. Photo by Michael Lüth, with permission.

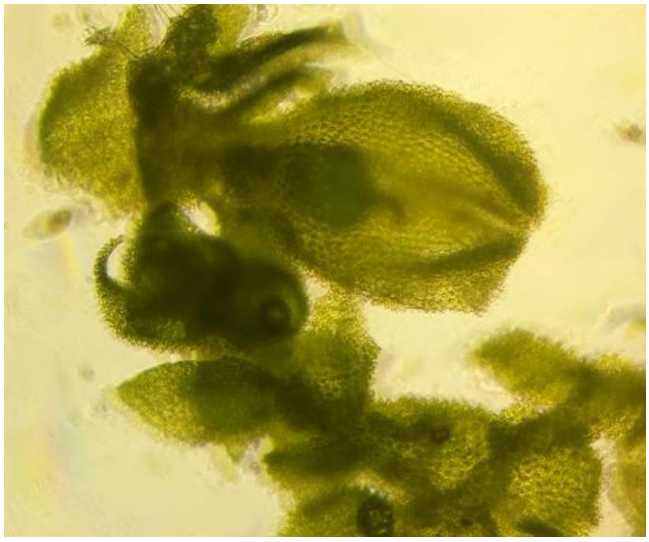

Figure 99. ***Cololejeunea rosettiana*** with perianth and swollen archegonium inside. Photo by Andy Hodgson, with permission.

Cololejeunea stotleriana (Figure 100-Figure 101)

Distribution

The rare ***Cololejeunea stotleriana*** (Figure 100-Figure 101) is known from South America (ITIS 2020) and was originally described from Ecuador (Gradstein *et al*. 2011).

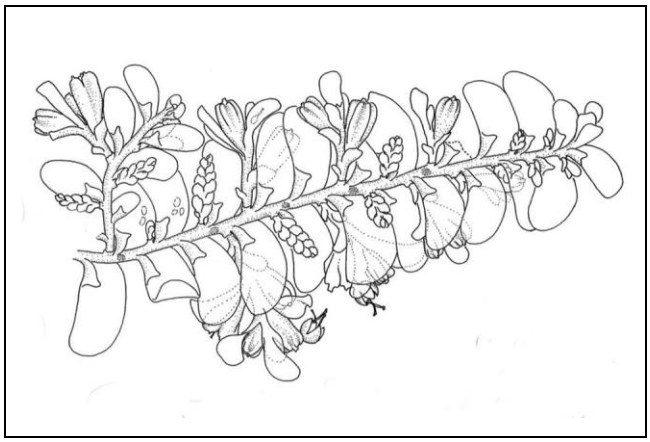

Figure 100. ***Cololejeunea stotleriana*** showing both perianths and antheridial branches (monoicous). Image from Gradstein *et al*. 2010, with permission.

Aquatic and Wet Habitats

Cololejeunea stotleriana (Figure 100) is rare, epiphyllous (Figure 101) or periodically submerged in streams at 950 m asl in Ecuador (Gradstein *et al*. 2011). It is the only common epiphyllous liverwort found in the flood zone of the river (Figure 102). But also in Ecuador, Gradstein *et al*. found this species on bark and rock.

In Ecuador, Gradstein *et al*. (2011) found that ***Cololejeunea stotleriana*** (Figure 100) grew in association with other rare bryophytes – the mosses ***Fissidens hydropogon*** (Figure 103) and ***Lepidopilum caviusculum*** (Figure 104).

Figure 101. ***Cololejeunea stotleriana*** growing as an epiphyll on a fern leaf in Ecuador. Photo by M. Richter, courtesy of Robbert Gradstein.

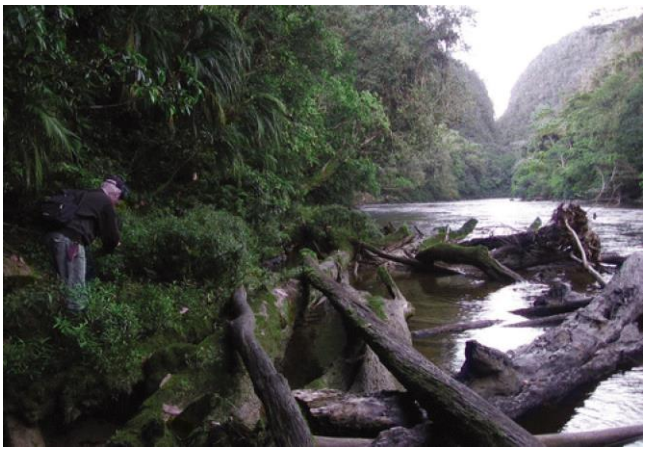

Figure 102. ***Cololejeunea stotleriana*** habitat in the Río Nangaritza, southern Ecuador. Photo by F. Werner, courtesy of S. Robbert Gradstein.

Figure 103. ***Fissidens hydropogon***, a rare moss that grows in association with ***Cololejeunea stotleriana*** in Ecuador. Photo from Earth.com, with permission.

Figure 104. ***Lepidopilum*** sp.; ***Lepidopilum caviusculum*** is a rare moss that grows in association with ***Cololejeunea stotleriana*** in Ecuador. Photo by Janice Glime.

Adaptations

Gradstein *et al*. (2011) found the new species ***Cololejeunea stotleriana*** (Figure 100-Figure 101) as rheophilous and epiphyllous (Figure 101) in Ecuador. It seemed well adapted to these habitats with its robust stem, flattened habit, triangular lobules, large rhizoid fields not produced near each leaf base, super fertility, and clustered gynoecia (Figure 100). Yu *et al*. (2014) likewise considered that the adaptations of this species (to extreme ephemeral substrate, smooth surfaces, limited access to water and nutrients, and light exposure) permit it to extend beyond the typical epiphyllous or epiphytic habitats of the genus.

Reproduction

In Ecuador, ***Cololejeunea stotleriana*** produces abundant gemmae (Figure 105).

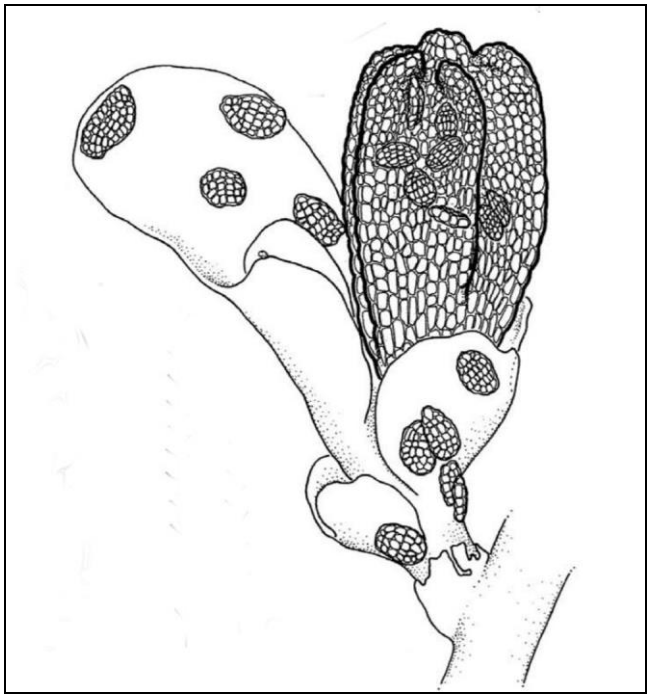

Figure 105. ***Cololejeunea stotleriana*** with perigynium and gemmae. From Gradstein *et al* 2010, with permission.

Biochemistry

Ludwiczuk and Asakawa (2014) used fingerprinting of secondary compounds in chemosystematics of ***Cololejeunea stotleriana*** (Figure 100-Figure 101) and were able to report only pinguisanes in this species.

Colura (Figure 109-Figure 110, Figure 121-Figure 122, Figure 124-Figure 125)

(syn. = *Myriocolea*)

The genus ***Colura*** (Figure 109-Figure 110, Figure 121-Figure 122, Figure 124-Figure 125) is represented by several species in Andean streambeds (S. Robbert Gradstein pers. comm. 3 November 2011).

One of the interesting discoveries about the genus ***Colura*** (Figure 109-Figure 110, Figure 121-Figure 122, Figure 124-Figure 125) is its ability to hold water in its leaf lobules (Figure 106) (Barthlott *et al*. 2000). The lobule has a complex opening with a movable lid that closes. Ciliate **Protozoa** (Figure 107-Figure 108) live in these lobules and feed on bacteria on the liverwort surface.

Figure 106. ***Colura*** showing water-holding lobule where protozoa live. Photo courtesy of Jan-Peter Frahm.

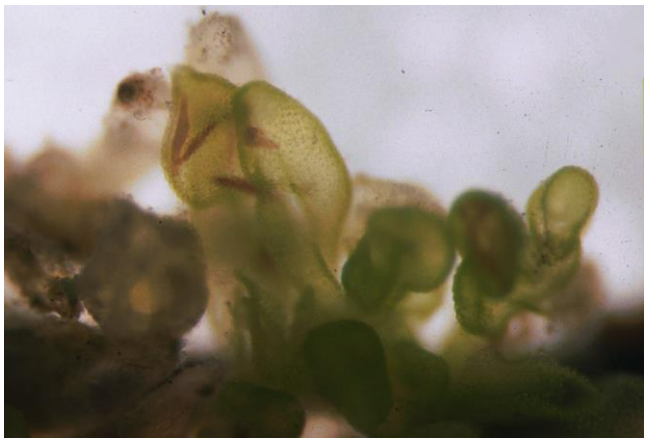

Figure 107. ***Colura*** with protozoa (stained pink). Photo courtesy of Jan-Peter Frahm.

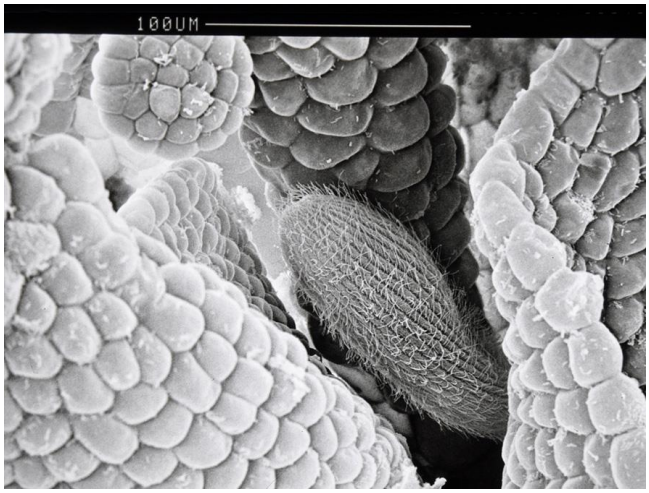

Figure 108. SEM of ***Colura*** with a ciliate (center). Photo by Wilhelm Barthlott, with permission.

Colura calyptrifolia (Figure 109-Figure 110)

(syn. = *Colurolejeunea calyptrifolia*)

Distribution

Colura calyptrifolia (Figure 109-Figure 110) is the only species of **Lejeuneaceae** that extends into the sub-Antarctic (Grolle 2002). Its distribution is oceanic-temperate Afro-American and European (Gradstein *et al*. 1983). Frahm (2005) reported it from the Azores. Zhu and Long (2003) reported its range as Africa, Europe, Central America, Sri Lanka, and Nepal, adding their own new collections from the Himalayas. It occurs in the Western Ghats of India as a tiny and rare species (Mufeed *et al*. 2018). An additional Asian record is from Taiwan (Yang *et al*. 2013). It has been reported several times from Brazil (Schäfer-Verwimp & Giancotti 1996; Bôas-Bastos & Bastos 2016). Gradstein *et al.* (2018) found it in the high Andes of Colombia, where it is rare. It is widely distributed in South America, from the Caribbean to southern Chile (Hassel *et al*. 2014). Newton (2004) considered it one of the most infrequent oceanic species in Britain, where it occurs mostly in the extreme west of Scotland and Ireland as well as Wales, requiring sustained high humidity. Bates and Preston (2011) contend that the range of this species is increasing in response to climate change.

Figure 109. ***Colura calyptrifolia***, an occasionally submersed species that grows in damp places. Photo by Michael Lüth, with permission.

Figure 110. ***Colura calyptrifolia*** showing the saccate leaves. Photo by Barry Stewart, with permission.

Aquatic and Wet Habitats

Colura calyptrifolia (Figure 109-Figure 110) is occasionally submerged (Watson 1919). Zhu and Long (2003) found it in a ravine in a dense forest in the Himalayas with ***Rhododendron*** (Figure 111), ***Betula*** (Figure 112), and ***Abies*** (Figure 113), where it occurred on a wet cliff face. Hassel *et al*. (2014) found it in Norway on a nearly vertical cliff wall about 5 m high, facing east to northeast with a small brook at the base of the cliff. There it grew at the base of the cliff in a zone 0.5-2 m above the brook.

Figure 111. ***Rhododendron*** in the Himalayas, a genus that can provide habitat for ***Colura calyptrifolia***. Photo by Nidhi Jamwal, through Creative Commons.

Figure 112. ***Betula utilis***, Himalayan birch in the Himalayas, a genus that can provide habitat for ***Colura calyptrifolia***. Photo by J. M. Garg, through Creative Commons.

Colura calyptrifolia (Figure 109-Figure 110) seems to have a rather wide habitat tolerance, and at most it is apparently facultatively aquatic. It tolerates some submersion, but does not grow continually submersed. ***Colura calyptrifolia*** occurs on heather stems in the dwarf shrub heaths of the western Scottish Highlands (Figure 114) (Averis 2007). In some heaths, it occurs as an epiphyll on the fronds of the fern ***Blechnum spicant*** (Figure 115). The long, very humid microclimate provides a long growing season on these fronds with only a 2-year life span.

Figure 113. ***Abies pindrow*** at Mt. Mukeshpuri, Pakistan. The genus ***Abies***, along with ***Betula*** and ***Rhododendron***, can provide habitat for ***Colura calyptrifolia***. Photo by Khalid Mahmood, through Creative Commons.

Figure 114. ***Calluna vulgaris*** (Scottish Heather), where ***Colura calyptrifolia*** grows on the stems of these shrubs. Photo by John McLeish, through Creative Commons.

Figure 115. ***Blechnum spicant***, a substrate for epiphyllous ***Colura calyptrifolia***. Photo by Robert Flogaus-Faust, through Creative Commons.

Reproduction

Colura calyptrifolia (Figure 109-Figure 110) is **autoicous** (Gradstein *et al*. 1983; Hassel *et al*. 2014). This permits it to have sexual reproduction and produce spores more easily than dioicous species. It produces large spores that give it a good start on new plants, but it also has fragmentation and produces abundant discoid gemmae that occur on the leaf tips (Figure 116).

Figure 116. ***Colura calyptrifolia*** with gemmae on tips of leaves at the upper left. Photo by David T. Holyoak, with permission.

With its ability to live on a wide range of inorganic substrates, along with its wide range of habitats, it is not surprising that Hill and Preston (2014) found significant increases in ***Colura calyptrifolia*** (Figure 109-Figure 110, Figure 116) between the 1960-1989 period and the 1990-2013 period.

Fungal Interactions

Thus far, there seem to be no records of mycorrhizae associated with ***Colura calyptrifolia*** (Figure 109-Figure 110, Figure 116) (Wang & Qiu 2006). Perhaps these have been missed because of the small size of the liverwort, but then, perhaps they just don't occur.

Biochemistry

The species is also lacking in biochemical studies, preventing us from developing good hypotheses regarding antifungal behavior.

Colura cataractarum (Figure 117-Figure 118)

Distribution

Colura cataractarum **(**Figure 117-Figure 118**)** is a new species, described in 2020 from Madagascar (Pócs 2020). Thus far, it has not been found elsewhere and is thus endemic to a small area at the Andringitra Massif.

Aquatic and Wet Habitats

Colura cataractarum **(**Figure 117-Figure 118**)** occurs on granite rocks in cataracts where it is steadily irrigated (Figure 119) (Pócs 2020). These cataracts are surrounded by mossy montane forest at 1,230 m asl.

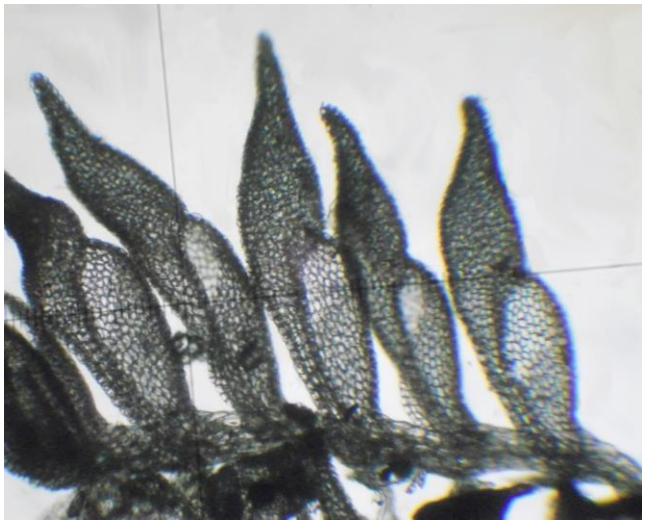

Figure 117. ***Colura cataractarum*** leaves. Photo courtesy of Tamás Pócs.

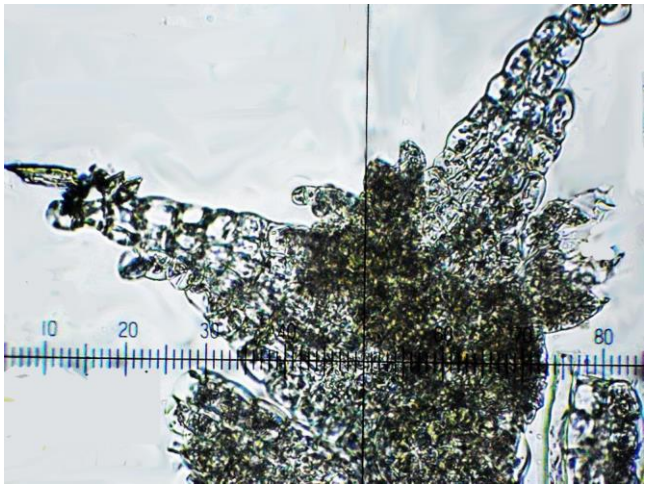

Figure 118. ***Colura cataractarum*** underleaf. Photo courtesy of Tamás Pócs.

Figure 119. ***Colura cataractarum*** being collected by András Szabó at its type locality in Madagascar, on irrigated granite rocks. Photo courtesy of Tamás Pócs.

Reproduction

Only female reproductive structures have been seen, so the species is presumably **dioicous** (Pócs 2020). Gemmae are produced at the perianth mouth.

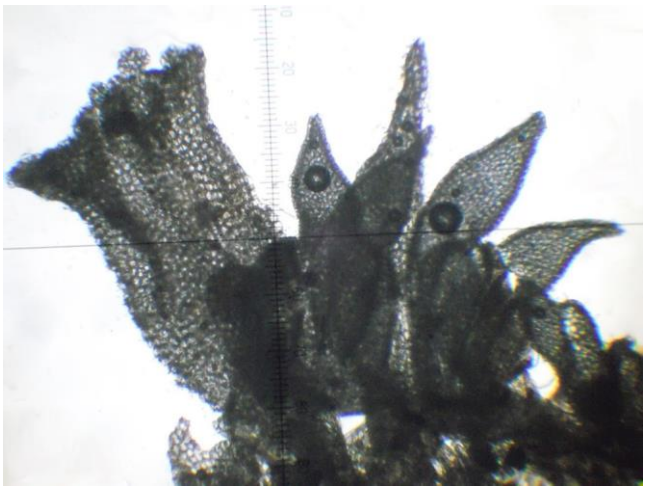

Figure 120. ***Colura cataractarum*** with perianths. Photo courtesy of Tamás Pócs.

Colura irrorata (Figure 121, Figure 124-Figure 125)

(syn. = *Myriocolea irrorata*)

Distribution

Colura irrorata (Figure 121, Figure 124-Figure 125) is known from the Andean Topo River in Ecuador (Gradstein & Jost 2004). It is rare and red-listed, being known from only a few localities (Figure 122) (Gradstein *et al*. 2004; Heinrichs *et al*. 2012).

Figure 121. ***Colura irrorata*** on stems of ***Cuphaea bombonasae*** along the Numpatakaima River in Ecuador at 1540 m asl. Photo by Lou Jost, EcoMinga, with permission.

Figure 122. ***Colura irrorata*** conservation site. Photo courtesy of S. Robbert Gradstein.

Aquatic and Wet Habitats

This tropical montane species occurs on small shrubs of ***Cuphea bombonasae*** (Figure 123) that are periodically submerged (Gradstein *et al*. 2004). Its submersion seems to be short-lived, but frequent, with floods causing water levels to rise and fall "dramatically" over just a few hours (Gradstein *et al*. 2004; Gradstein & Benitez 2014). It is threatened by the construction of a hydroelectric dam on the Rio Topo.

Figure 123. ***Cuphea bombonasae***, substrate for ***Colura irrorata*** in Ecuador. Photo from <swbiodiversity.org>, through Creative Commons.

Figure 124. ***Colura irrorata*** growing on ***Cuphea bombonasae*** in a location that becomes inundated. Photo courtesy of S. Robbert Gradstein.

Adaptations

Colura irrorata (Figure 121, Figure 124-Figure 125) exhibits long, robust stems, pinnate branching, and numerous small gametoecial branches, characteristics typical of other rheophytic members of **Lejeuneaceae** (Gradstein *et al*. 2004).

Reproduction

Colura irrorata (Figure 121, Figure 124-Figure 125) is **paroicous** and develops innovations between the gynoecia and male bracts. It produces numerous, but very tiny, sporophytes (Figure 125), but no vegetative reproduction has been found and its leaves decay while still on the shoots, suggesting they may not serve as propagules.

Figure 125. ***Colura irrorata*** with sporophytes (tiny grey structures seen at plant margins) on stems of ***Cuphaea bombonasae*** along the Numpatakaima River, Ecuador, at 1540 m asl. Photo by Lou Jost, EcoMinga, with permission.

Biochemistry

Despite its rarity and tiny size, ***Colura irrorata*** (Figure 121, Figure 124-Figure 125) has been subjected to several biochemical studies. Ludwiczuk *et al*. (2013) found only β-pinguisene in the species, contributing to the understanding of phylogenetic relationships. Coulerie *et al*. (2015) found only pinguisanes when testing for epidozanes, pinguisanes, fusicoccanes, monocyclofarnesanes. In further studies, Ludwiczuk and Asakawa (2014) tested for lepidozanes, pinguisanes, fusicoccanes, and monocyclofarnesanes; once again they found only pinguisanes.

Diplasiolejeunea cavifolia (Figure 126, Figure 128-Figure 129)

(syn. = *Lejeunea cavifolia*)

Schäfer-Verwimp and Reiner-Drehwald (2009) considered ***Diplasiolejeunea cavifolia*** Figure 126, Figure 128-Figure 129) a "somewhat variable" species. Dong *et al*. (2012) considered this pantropical species, along with ***D. rudolphiana***, to have a broader ecological amplitude than other members of the genus. This variety of habitats may help to explain its perceived variability.

Distribuition

The distribution of ***Diplasiolejeunea cavifolia*** (Figure 126, Figure 128-Figure 129) is pantropical. In the Neotropics it occurs in Mexico (in the Chiapas; Bourell 1992), Colombia (Benavides & Gutierrez 2011), Panama (common; Schäfer-Verwimp 2014), and the Guianas (Eggers *et al.* 2006; Gradstein 2006). Fuentes and Churchill (2005) also found it in Bolivia. Morales (2010) reported it from Venezuela.

Figure 126. ***Diplasiolejeunea cavifolia***, a sometimes submersed species that is usually in moist habitats. Photo by Hermann Schachner, through Creative Commons.

Tixier (1995) reported ***Diplasiolejeunea cavifolia*** (Figure 126, Figure 128-Figure 129) from San Thomé, Mt. Caffe, at 700 m asl, in the country of São Tomé and Príncipe, 4.5 km west of Trinidad off the northeastern coast of Brazil. Giancotti and Vital (1989) recorded it from Brazil, while noting that many **Lejeuneaceae** species seem to be disappearing; da Costa and Peralta (2015) reported it from the Atlantic Rainforest in Rio de Janeiro, Brazil. Dong *et al*. (2012) reported it from 3 m asl in Brazil, 1000 m asl in Dominica, 1540 m in Ecuador, 800 m in the Fiji Islands, 743-900 m in Graham *et al*. (2016) described its habitat in Peru. Guadeloupe, 970 m in Panama, and 370 m in Venezuela. Bernarda and Schäfer-Verwimp (2011) reported it from Guadeloupe archipelago and Martinique in the French West Indies. Mervin *et al*. (2001) found it in primary forests of Monteverde, Costa Rica.

In the old tropics, Ah-Peng *et al*. (2007) have reported ***Diplasiolejeunea cavifolia*** (Figure 126, Figure 128-Figure 129) on Réunion Island. Pócs *et al*. (2011) reported it from the Fiji Islands in the South Pacific. Wang *et al*. (2011) found it in Taiwan. Vanden Berghen (1960) reported it from Tanganyika (now Tanzania). Sánchez and Pérez (1998) reported it from the Republic of Equatorial Guinea (West Central Africa). Stam *et al*. (2020) reported it from a fog net in the lower montane forest in the Taita Hills in Kenya. But Tixier (1995) considered the genus ***Diplasiolejeunea*** to be "relatively depauperate" in Africa. Ariyati *et al*. (2009) reported it from Sulawesi, Indonesia. In 2016, Abay *et al*. included it in the flora of Rize, Northeast Turkey. It is telling that so many records for this species have occurred since 2000.

Dong *et al*. (2012) reported ***Diplasiolejeunea cavifolia*** (Figure 126, Figure 128-Figure 129) from 1580 m asl in Indonesia, 865-1015 m in Madagascar, 1280-1340 m in Malaysia, and 1030 m on Réunion Island. Long and Rubasinghe (2014) reported it from Sri Lanka. Yodphaka *et al*. (2018) found it in Thailand. Bakalin and van Sinh (2016) reported it from Vietnam.

Aquatic and Wet Habitats

Nichols (1916) found ***Diplasiolejeunea cavifolia*** (Figure 126, Figure 128-Figure 129) on wet or moist cliffs of ravines in Connecticut, USA, causing me to include it in this chapter. On Cape Breton Island, Canada, Nichols (1918) found it on rock cliffs associated with streams. Watson (1919) treated it as occasionally submerged. In the aquatic habitats of eastern Odenwald and southern Spessart, Philippi (1987) found it in association with ***Thamnobryum alopecurum*** (Figure 127). Vieira *et al*. (2005) found ***Diplasiolejeunea cavifolia*** in mountain streams of northwest Portugal.

Figure 127. ***Thamnobryum alopecurum***, a species that accompanies ***Diplasiolejeunea cavifolia*** in aquatic habitats in Germany. Photo by David T. Holyoak, with permission.

Benavides and Gutierrez (2011) reported ***Diplasiolejeunea cavifolia*** (Figure 126, Figure 128-Figure 129) from a cloud forest in the northern Andes of Colombia. In Bolivia, Fuentes and Churchill (2005) found it as an epiphyte. Schäfer-Verwimp (1992) found ***Diplasiolejeunea cavifolia*** (Figure 126, Figure 128-Figure 129) was not rare in Brazil, growing as an epiphyte in the restinga, on a rotting log, as an epiphyte in humid secondary shrub at the edge of banana plantations, in the rain forest, and as an epiphyll.

Siregar and Pasaribu (2020) found ***Diplasiolejeunea cavifolia*** (Figure 126, Figure 128-Figure 129) on bark in Indonesia. In Sabah of Malaysian Borneo, Pócs *et al*. (2020) found it in the epiphyllous communities on Mt. Silam, where it occurred in a lower montane rainforest at 600-740 m asl. In the Republic of Equatorial Guinea, Sánchez and Pérez (1998) found it in the most exposed places, occurring as epiphyllous and corticolous along river banks, in tree crowns, or rocky cliffs, between 75 and 1140 m asl. In fact, Alvarenga and Pôrto (2010) considered it to be a sun epiphyte in the Brazilian Atlantic forest.

On the other hand, one can find **mats** of ***Diplasiolejeunea cavifolia*** (Figure 126, Figure 128) growing as a corticolous species in the submontane rainforest and fallows in Bolivia (Acebey *et al*. 2003). ***Diplasiolejeunea cavifolia*** occurs not only in moist forests, but also in more mesic woods, plantations, and orchards. In Monteverde, Costa Rica, it is epiphytic in primary forests (Mervin *et al*. 2001) and occupies the wide range of 1-3000 m asl (Eggers 2001). Holz and Gradstein (2005) reported it from oak forests in the páramo of the Cordillera in Costa Rica; Holz *et al*. (2002) found it in **mats** on shrubs and trees in Costa Rican oak forests.

In Panama it can be epiphytic on shrubs, dead trees and branches in the canopy of a fallen tree, or epiphyllous, sometimes at riverside (Schäfer-Verwimp 2014). In the superhumid lowland tropical forest of Chocó, Colombia, Benavides and Sastre-De Jesús (2011) found it as an epiphyll on natural palms (frequency = 20, natural with no palms (14), secondary palm (10), and no palm (10) out of 240 leaf samples. In the eastern Andes of Peru, Graham *et al*. (2016) found it in a gallery forest on a sand substrate. In fact, Visnadi (2004) found it on sandy seashores in Brazil, where it was subjected to saline conditions due to waves and winds.

Figure 128. ***Diplasiolejeunea cavifolia*** with perianths and capsules. Photo by Hermann Schachner, through Creative Commons.

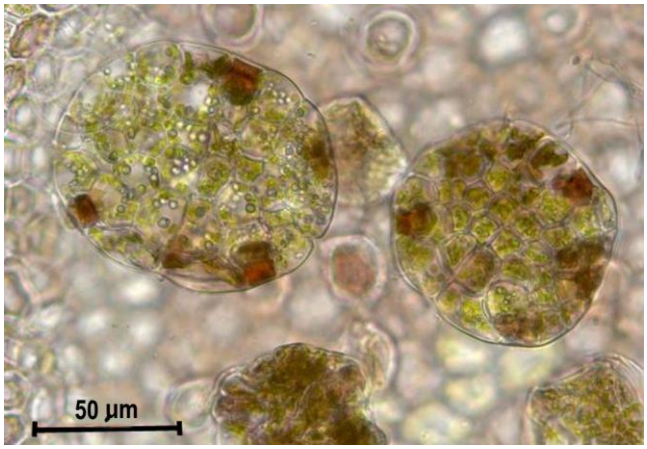

Figure 129. ***Diplasiolejeunea cavifolia*** showing gemmae developed on the leaf surface. Photo by Jia-ping Dong, through Creative Commons.

Adaptations

Zhu and So (2001) considered the small stem, imbricate leaves (Figure 126), absence of papillose cells, inflated lobules (hold water), neotenous habit, and asexual propagules (Figure 129) to adapt ***Diplasiolejeunea cavifolia*** (Figure 126, Figure 128-Figure 129) to the epiphyllous condition (see also Gradstein 2006; Kraichak 2012). These same characters could also be an advantage to a species that cliffs that are not always moist.

Reproduction

Zhu and So (2001) considered the **monoicous** condition of ***Diplasiolejeunea cavifolia*** (Figure 126, Figure 128-Figure 129) among its adaptations to its epiphyllous habitat. The same can be said for its epiphytic habitat (Figure 128), and for rock cliffs that are not always moist.

Kraichak (2012) considered asexual propagules such as gemmae (Figure 129) to be an adaptive trait for epiphylly among the tropical **Lejeuneaceae** and found that it was the only trait that was more likely to evolve among epiphyllic species. In ***Diplasiolejeunea cavifolia*** (Figure 126, Figure 128-Figure 129), the diaspores (gemmae) seem to be tolerant of both drought and frost, perhaps explaining the pantropical success (Dong *et al*. 2012).

Biochemistry

Kis and Pócs (1997) studied the oil bodies of this species from African populations. The species has smaller oil bodies (204 µm) than the average for members of the genus ***Diplasiolejeunea***. There seem to be no studies thus far on the biochemistry of this tiny species.

Summary

The **Jubulineae** are primarily terrestrial, but some also occur where they get wet or stay wet, sometimes getting submerged. The **Frullaniaceae** species here are **dioicous**; They are particularly adapted to xeric habitats with dark colors, mats, and water-holding leaf lobules. Most live on rocks or are epiphytes, but a few species of ***Frullania*** live in constantly moist habitats. Some serve as a reservoir for lichen-forming **Cyanobacteria**.

In the **Jubulaceae**, ***Jubula*** mostly occurs on rocks in humid or damp sites near or in flowing water and in waterfalls. However, thus far I have found only ***Jubula hutchinsiae*** and its subordinates in the aquatic literature. These are **monoicous**

The family **Lejeuneaceae** is a family of very small leafy liverworts, mostly **monoicous**. They can mix with other bryophytes or grow alone. Many, such as ***Acanthocoleus aberrans***, are facultative aquatic bryophytes, occurring sometimes in streams or becoming inundated during flooding, but usually

terrestrial. ***Bromeliophila*** is aquatic, restricted to bromeliad basins. ***Cephalantholejeunea temnanthoides*** is a rare species and is a rheophyte in Andean streambeds. ***Ceratolejeunea temnantha*** is likewise an endemic rheophyte, occurring in the Amazon region and being seasonally inundated. ***Cheilolejeunea clypeata*** occurs in mesic and swamp forests on a variety of substrates, but is not a true aquatic. ***Cololejeunea biddlecomiae*** often occurs along calcareous rivers and springs, but also occurs along the acidic Adirondack Mountain streams and becomes less of a calciphile in the southern part of its range. ***Cololejeunea calcarea*** is most frequent on limestone rock and may become submersed. ***Cololejeunea hodgsoniae*** can be found on the leaves of the leafy liverwort ***Radula marginata*** on rocks and streams of Australia and New Zealand. ***Cololejeunea madothecoides*** is adapted to riverine conditions with thick stems, rigid leaves, and adherence to its substrate. ***Cololejeunea microscopica*** is most frequent on rocks near streams and waterfalls, but can also be epiphytic or epiphyllous; it is also known to grow on the moss ***Pyrrhobryum spiniforme***. ***Cololejeunea rossettiana*** often grows on other bryophytes, but also occurs on shaded limestone and on trees; it is only occasionally submerged. ***Cololejeunea stotleriana***, like many of these species, is rare, but is a common epiphyll in the river flood zone. ***Colura calyptrifolia*** has been found in a ravine in the Himalayas and on a wet cliff face; it tolerates some submersion, but not continuous submersion. It accepts a wide range of substrates. including ***Polytrichastrum*** leaves, and can occur on rubbish! ***Colura irrorata*** is a rare epiphyte, growing on shrubs of ***Cuphea bombonasae*** in areas where it becomes inundated. ***Diplasiolejeunea cavifolia*** can occur on wet or moist cliffs or even be submerged, but it is more commonly epiphytic or epiphyllous.

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CHAPTER 1-8
AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA, ORDER PORELLALES: JUBULINEAE, PART 2

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CHAPTER 1-8
AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA, ORDER PORELLALES: JUBULINEAE, PART 2

Figure 1. ***Drepanolejeunea hamatifolia*** habitat on rocks by a rapid stream. Photo by Michael Lüth, with permission.

Many of the species in this chapter are not typical wetland or aquatic species. They were, however, found in a wetland or aquatic study. Their relative frequency can be inferred based on the number of references cited.

Porellales – Suborder Jubulineae

Lejeuneaceae, cont.

Drepanolejeunea hamatifolia (Figure 1-Figure 8)

Distribution

Drepanolejeunea hamatifolia (Figure 1-Figure 8) is an Atlantic species (Rhind 2010). It is, so far, restricted to the Atlantic coasts of Portugal (in laurel forests; Gutierres 2007), Spain (species of least concern; Sérgio *et al*. 2007), France (in Pyrénées; Dismier 1914), Ireland, England, Scotland (oceanic; Rothero 2003), and Macaronesia (Aleffi 2005). It is not known from Italy (Aleffi 2005), and it is known from only one site in continental Portugal (Cacciatori *et al*. 2015). To these records, Söderström and Pócs (2011) added South Africa. Sim-Sim *et al*. (2011) found it on Madeira Island.

Figure 2. ***Drepanolejeunea hamatifolia***, a species of eastern Atlantic coastal regions. Photo by Hugues Tinguy, with permission.

Figure 3. ***Drepanolejeunea hamatifolia*** showing overlapping leaves. Photo by Michaela Sonnleitner, with permission.

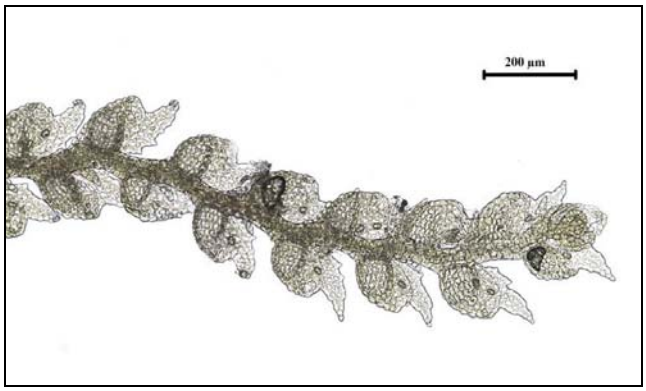

Figure 4. ***Drepanolejeunea hamatifolia***. Photo by Hugues Tinguy, with permission.

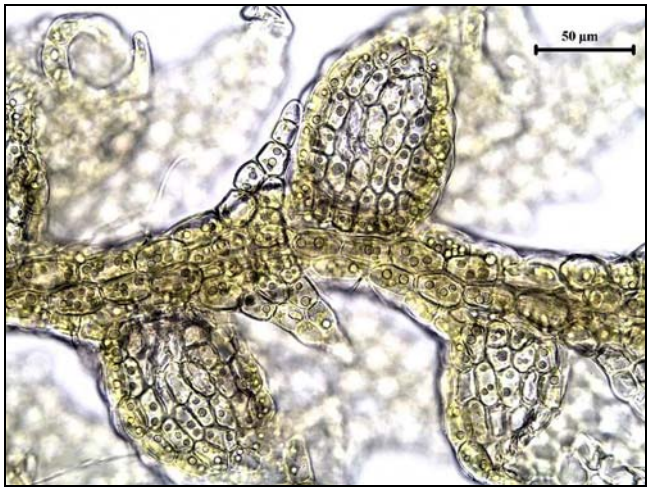

Figure 5. ***Drepanolejeunea hamatifolia*** showing underleaves. Photo by Hugues Tinguy, with permission.

Rothero (2003) considered ***Drepanolejeunea hamatifolia*** (Figure 2-Figure 8) to be rare in Europe, with the exception of Macaronesia and the Azores. In fact, Borges and Gabriel (2009) found it to be among the most common epiphyllous species in the Azores (see also Gabriel & Bates 2005).

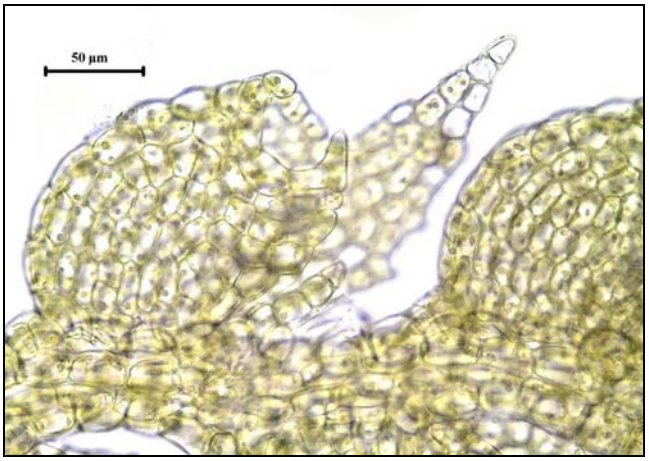

Figure 6. ***Drepanolejeunea hamatifolia*** leaf lobule. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

Watson (1919) considered ***Drepanolejeunea hamatifolia*** (Figure 2-Figure 8) to be occasionally submerged (Figure 1), thus justifying its inclusion here. Hodgetts *et al*. (1999) reported it from streamside rocks in a ravine woodland at 1750 m asl in Lesotho, the Natal Drakensberg and the Orange Free State in southern Africa. In the UK, Rothero (2010) reported that it occurs on steep granitic rock of a ravine at 300 m asl. In Ireland, Jones (1954) found that it was "not uncommon" on basalt in deep, shady stream ravines. In Scotland, Long (2016) located it along a ravine. Damsholt *et al.* (1980) reported it from a wooded ravine in NW Scotland, where it occurred on moist, shaded rock faces. Brown (1954) found it in northeast Ireland on basalt in deep, shady stream ravines, where it was "not uncommon."

Rothero (2005) found it on large rocks in ravines of the Atlantic oakwoods. These rocks were regularly inundated, but did not suffer scouring. ***Drepanolejeunea hamatifolia*** (Figure 1-Figure 8) formed a zone above the leafy liverwort ***Lejeunea patens*** (Figure 68-Figure 69) on these dark rocks (Figure 7-Figure 8).

Figure 7. ***Drepanolejeunea hamatifolia*** showing zonation patterns on boulder near a stream. Photo by Michael Lüth, with permission.

Figure 8. ***Drepanolejeunea hamatifolia*** on a wet rock. Photo by Barry Stewart, with permission.

Bosanquet (2015) discussed the effects of topography and rainfall on the distribution of Atlantic bryophytes in Wales. He recognized that rainfall in Wales ravines was not the sole driver of bryophyte diversity there. He considered that water courses and waterfalls were able to provide the mists that permitted the success of **hygrophilous** (humidity-demanding) bryophytes, in particular ***Drepanolejeunea hamatifolia*** (Figure 1-Figure 8). This species has a very patchy distribution due to its habitat restrictions. It is a desiccation-sensitive hyperoceanic species and is thus restricted to rocky cascades and other habitats that create a mist and moist environment.

Averis *et al*. (2012) found that those water courses that have the potential for electric power provide good habitats for ***Drepanolejeunea hamatifolia*** (Figure 1-Figure 8). Hence, if the construction of a power plant changes the mist and humidity of the area, the species is likely to become endangered there. Callaghan *et al*. (2019) found about 23% of colony losses following hydroelectric power development, including those changes to ***Drepanolejeunea hamatifolia***, were due to larger bryophytes multiplying or invading and excluding them. The most aggressive of these was the moss ***Ctenidium molluscum*** (Figure 9).

Figure 9. ***Ctenidium molluscum*** in rock canyon in Europe, a larger species that can overtake ***Drepanolejeunea hamatifolia***. Photo by Michael Lüth, with permission.

But it appears that the requirement of mist or high humidity is not always the case. Schwarz and Schumm (2019) reported ***Drepanolejeunea hamatifolia*** (Figure 1-Figure 8) from the Canary Islands on dry, shaded to half-shaded bark (Figure 10), stone, or leaves. Likewise, on Tenerife in the Canary Islands, Gónzalez-Mancebo *et al*. (2004a) reported it as a pioneer epiphyte on ***Laurus azorica*** (Figure 11), occurring only in the Pijaral area, and with a low frequency. But laurel forests are typically humid and shady (Kürschner *et al*. 2007a). They are dominated by bryophytes that form **mats** (Figure 8) or **fans** and are **perennial stayers** or **perennial shuttle** species. ***Drepanolejeunea hamatifolia*** occurs in the laurel forests of Madeira Island with a **thread** life form. In the Azores, it occurs on stem bases in dense stands of ***Persea*** (Figure 12), ***Pittosporum*** (Figure 13), and ***Acacia*** (Figure 14) (Sjögren 2003). It also occurs as an epiphyte in laurel forests on the Madeira archipelago (Gutierres 2007). Bates (2012) found it on ***Cryptomeria*** (Figure 15) on the higher hills of the Azores, where it joins acidophilic bryophytic epiphylls. Patiño and González-Mancebo (2011) reported it from subtropical cloud forests in the Canary Islands, growing on ericaceous shrubs. All of these habitats are moist.

Figure 10. ***Drepanolejeunea hamatifolia*** on bark in Bretagne. Photo by Michael Lüth, with permission.

Figure 11. Laurel forest (***Laurus azorica***), Macaronesia, on Flores Island. Photo by B. T. Varusko, through Creative Commons.

Figure 12. ***Persea americana*** with fruit; ***Persea*** can have ***Drepanolejeunea hamatifolia*** on bark at its base. Photo by M. Clara Salviano, through Creative Commons.

Figure 13. ***Pittosporum coriaceum***; species in this genus can have ***Drepanolejeunea hamatifolia*** on bark at the base. Photo by Krzystof Ziarnek, through Creative Commons.

The epiphyllous habitat of ***Drepanolejeunea hamatifolia*** (Figure 1-Figure 8) is not restricted to leaves of tracheophytes. It also occurs on other bryophytes, such as ***Thamnobryum alopecurum*** (Figure 16), another wet habitat species, in Killarney, Ireland (Kelly 1981). In the same woods, it grew on branches and upper parts of the trunk of yew trees, and Rose (1974) found it on oaks in Killarny. Similarly, Durfort (2015) found that this liverwort occurs as an epiphyte on mosses on tree trunks in Brittany, France. But it also occurs on rocks, old gorse, willows, birches, and larger trees in Brittany. Despite this variety of substrata, it is very rare in France.

Figure 14. ***Acacia saligna*** on Cyprus; ***Acacia*** can have ***Drepanolejeunea hamatifolia*** on bark at its base. Photo by Anna Anichkova, through Creative Commons.

Figure 15. ***Cryptomeria japonica*** in Azores, substrate for ***Drepanolejeunea hamatifolia***. Photo by Mary Anne Melo, through Creative Commons.

Figure 16. ***Thamnobryum alopecurum***, a substrate for ***Drepanolejeunea hamatifolia***. Photo by Michael Lüth, with permission.

Proctor (1980) measured the radiation for ***Drepanolejeunea hamatifolia*** (Figure 1-Figure 8) in several locations in the British Isles (North Wales and Yorkshire). In the wooded lowland habitats, peak irradiance occurred immediately before leaf expansion. Direct radiation was negligible in the ravine sites where ***Drepanolejeunea hamatifolia*** occurred.

Corley (1983) found ***Drepanolejeunea hamatifolia*** (Figure 1-Figure 8) in the Inner Hebrides, where it occurred on boulders in the stream and rocks at the edge, accompanied by ***Hyocomium armoricum*** (Figure 17), ***Thamnobryum alopecurum*** (Figure 16), ***Cololejeunea microscopica*** (Figure 18), ***Douinia ovata*** (Figure 19), and ***Colura calyptrifolia*** (Figure 20).

Figure 17. ***Hyocomium armoricum*** in its common habitat where it might be accompanied by ***Drepanolejeunea hamatifolia***. Photo by Dick Haaksma, with permission.

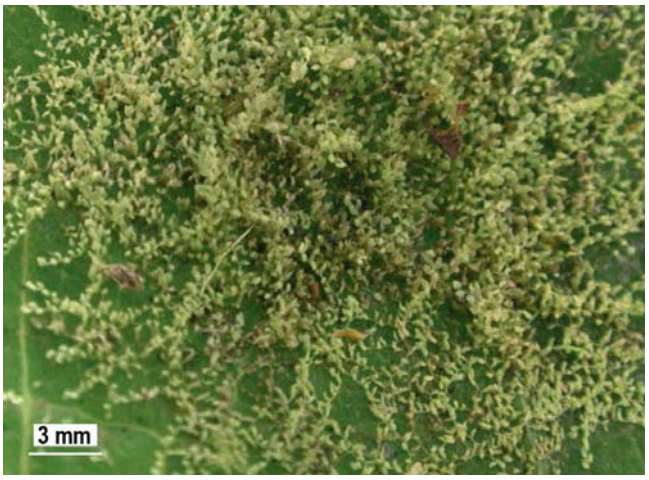

Figure 18. ***Cololejeunea microscopica***, a species that might be accompanied by ***Drepanolejeunea hamatifolia***. Photo by Jan-Peter Frahm, with permission.

But the reported habitats suggest that submersion is an unusual condition for the species. Instead, it occupies more terrestrial sites. Sim-Sim *et al*. (2011) report ***Drepanolejeunea hamatifolia*** (Figure 1-Figure 8) as an epiphyte on Madeira Island, where it is an indicator species for the high-altitude ***Erica*** habitat (Figure 21). Roden *et al*. (2007) found it in the oak woods in the valley of the Owendalulleegh River in Ireland.

Figure 19. ***Douinia ovata***, a species that might be accompanied by ***Drepanolejeunea hamatifolia***. Photo by Des Callaghan, with permission.

Figure 20. ***Colura calyptrifolia***, a species that might be accompanied by ***Drepanolejeunea hamatifolia***. Photo by Barry Stewart, with permission.

Figure 21. ***Erica maderensis***; ***Drepanolejeunea hamatifolia*** is an indicator species for the high altitude ***Erica*** habitat on Madeira Island. Photo by Thomas Dellinger, through Creative Commons.

Sjögren (1993) considered ***Drepanolejeunea hamatifolia*** (Figure 1-Figure 8) to be a species with no substrate preference on the island of Corvo in the Azores. He also considered it to be a pioneer on bark. The species was able to colonize with thin carpets that were frequently split up by areas almost nude of bark. To add further to

this lack of substrate preference, Schwarz and Schumm (2019) reported it from wet, shaded plastic pipe.

The invasive ***Rhododendron ponticum*** (Figure 22) in Atlantic oak woodlands impacted the oak woodland community (Maclean *et al*. 2017). However, ***Drepanolejeunea hamatifolia*** (Figure 1-Figure 8) seemed to have an affinity for these dense ***Rhododendron*** areas.

Figure 22. ***Rhododendron ponticum***, a species whose invasion seemed to have a favorable impact on ***Drepanolejeunea hamatifolia***. Photo by Rasbak, through Creative Commons.

Adaptations

Although it appears that ***Drepanolejeunea hamatifolia*** (Figure 1-Figure 8) seems to be most common in moist microclimates, it is nevertheless also adapted to drier conditions. **Lobules** (water sacs) in this species help it to survive in the sometimes dry epiphytic habitat (Sim-Sim *et al*. 2005a).

Unlike the report by Kürschner *et al*. (2007a) that considered ***Drepanolejeunea hamatifolia*** (Figure 1-Figure 8) to be a **perennial stayer** or **perennial shuttle species**, other researchers considered it to be a **short-lived shuttle** species in the Canary Islands (González-Mancebo *et al*. 2004b; Lloret & González-Mancebo 2011; Patiño & González-Mancebo 2011), with 2% cover and 2.98% frequency (González-Mancebo *et al*. 2004b).

Reproduction

Drepanolejeunea hamatifolia can be **autoicous** or **dioicous** (Paton 1999), probably accounting for some of its morphological variability. The perianth has various projections from the folds, suggesting they might attach to an animal or trap air bubbles that help them to float. This requires experimentation and would necessitate the disarticulation of the perianth.

In running water, fragmentation is a frequent form of asexual reproduction. I would assume that this is facilitated by the caducous branches (Paton 1999) in ***Drepanolejeunea hamatifolia*** (Figure 1-Figure 8). Paton reported frequent sporophytes, but did not report gemmae.

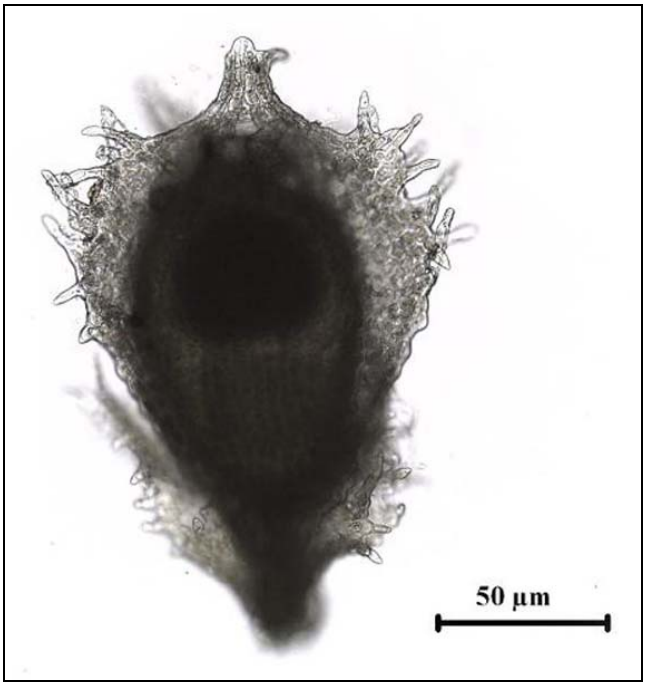

Figure 23. ***Drepanolejeunea hamatifolia*** perianth; note the spiny projections on the folds. Photo by Hugues Tinguy, with permission.

Fungal Interactions

Despite its association with ericaceous shrubs, known for the presence of mycorrhizae, there seem to be no records of mycorrhizal associations (Wang & Qiu 2006). Although the Ericaceae typically have mycorrhizae (Read & Stribley 1975; Specht 1979; Selosse *et al*. 2007), epiphytes such as this tiny liverwort usually do not.

Drepanolejeunea vandenberghenii

Distribution

Rwanda (Pócs 2021)

Aquatic and Wet Habitats

In Rwanda, ***Drepanolejeunea vandenberghenii*** occurs on dripping rocks, growing among ***Sphagnum*** and ***Breutelia***; not known in submerged condition (Pócs 2021).

Adaptations

Plants of ***Drepanolejeunea vandenberghenii*** are yellowish to light brownish-green (Pócs 2021). This is in contrast to the blackish appearance of ***D. vanderpoortenii*** and suggests a difference in light intensity or quality.

Drepanolejeunea vanderpoortenii

Distribution

Drepanolejeunea vanderpoortenii is known only in Madagascar (Pócs 2021).

Aquatic and Wet Habitats

Drepanolejeunea vanderpoortenii occurs on streambed stones, often under water (Pócs 2021). Such locations include on wet boulders in streams in submontane rainforest and on streambed stones of Mahavoho River, at 220 m asl.

Adaptations

Drepanolejeunea vanderpoortenii has blackish pigmentation, julaceous habit, thick-walled stems (Pócs 2021). The blackish color and thick-walled stems could be adaptations to its rheophytic habitat (Gradstein & Vital 1975, Pócs 2010). I would suggest that the julaceous habit is also an adaptation against the abrasion caused by flowing water. I would predict that it causes less turbulence than other forms, and certainly less subject to abrasion than are keeled leaves.

Reproduction

The sexual and vegetative reproduction are both unknown at this time (Pócs 2021). It is likely that it experiences vegetative reproduction with dispersal by water flow.

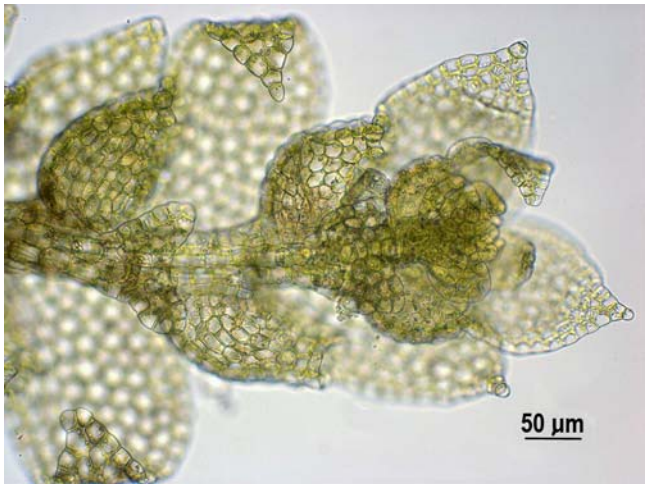

Figure 25. ***Harpalejeunea molleri*** underside. Photo by Blanka Aguero, with permission.

Harpalejeunea molleri (Figure 24-Figure 28, Figure 33-Figure 38)

(syn. = *Harpalejeunea ovata*; *Lejeunea molleri*)

Distribution

Harpalejeunea molleri (Figure 24-Figure 28, Figure 33-Figure 38) has had several synonyms (Grolle 1989) and there has been confusion about the use of some names (Schuster 1999). It is a widespread oceanic and suboceanic species from southern Norway south to Spain, Portugal, southern France, Tuscany, and Corsica (Sotiaux *et al*. 2007), the Canaries (Mancebo *et al*. 2007), and the Azores (Schuster 1980). In North America it extends from the Southern Appalachians from Virginia southward and outer Coastal Plain (Schuster 1980).

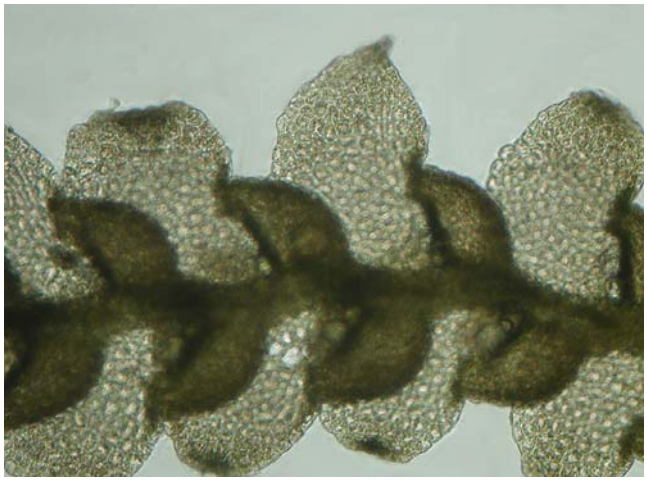

Figure 26. ***Harpalejeunea molleri*** showing leaf lobes that appear darker in this photo. Photo by Jan-Peter Frahm, with permission.

Figure 24. ***Harpalejeunea molleri***, a species from both sides of the Atlantic in oceanic and suboceanic regions. Photo by Stan Phillips, through public domain.

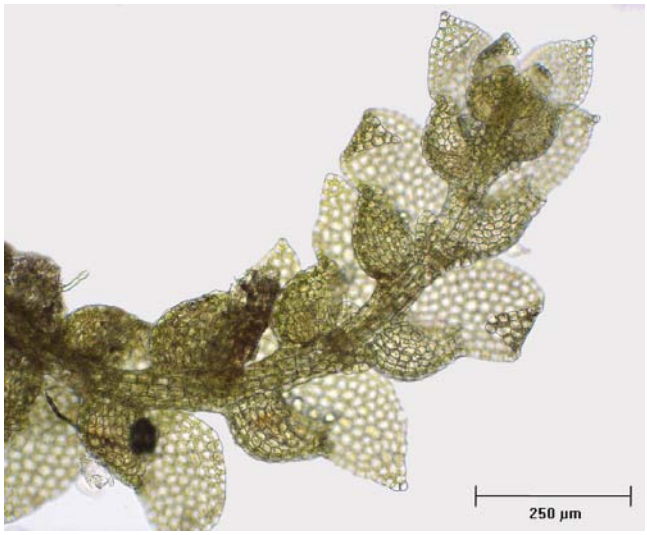

Figure 27. ***Harpalejeunea molleri*** subsp. ***integra***. Photo by Blanka Aguero, with permission.

Figure 28. ***Harpalejeunea molleri*** subsp. ***integra*** giving a view of leaf insertion and leaf cells. Photo by Blanka Aguero, with permission.

Aquatic and Wet Habitats

Schuster (1980) describes the wetter habitats of ***Harpalejeunea molleri*** as shaded humid rocks, in swamps, along black-water streams, or on damp rocks. Dirkse (1985) reported it from sheltered wet volcanic rocks in the laurel forests (Figure 11) of the Canary Islands. González-Mancebo *et al*. (2004b) found it growing in areas with high mist in the laurel forests of the Canary Islands. Sim-Sim *et al*. (2005a) found ***Harpalejeunea molleri*** (Figure 24-Figure 28, Figure 33-Figure 38) growing with ***Plagiochila exigua*** (Figure 29) on moist rock surfaces and slopes near water courses on Madeira, but it also occurred epiphytically, often with ***Frullania tamarisci*** (Figure 30) and other bryophytes.

Figure 29. ***Plagiochila exigua*** growing with smaller liverworts such as ***Harpalejeunea molleri***. Photo by Jan-Peter Frahm, with permission.

Figure 30. ***Frullania tamarisci***, a species that occurs epiphytically with ***Harpalejeunea molleri*** on Madeira. Photo by Proyecto Musgo, through Creative Commons.

Rothero (2005) reported ***Harpalejeunea molleri*** (Figure 24-Figure 28, Figure 33-Figure 38) as a very small liverwort making a delicate green pattern (Figure 24) against the dark stone of large rocks in ravines. These rocks were regularly inundated, but escaped scouring. Bosanquet (2015) described seven hotspots in Wales, noting that these are located away from high-rainfall areas. These typically are in woodland ravines in locations with mist zones and periodic inundation, usually governed by areas of high upstream rainfall. These habitats include waterfalls and rocky cascades. Such areas are suitable habitats for ***Harpalejeunea molleri***. Bosanquet considers this species to be desiccation intolerant. Pescott and Preston (2014) found that ***Harpalejeunea molleri*** in Britain and Ireland occurred with a group of species that experienced the most wet days. In hyperoceanic places in Scotland, Hodgetts *et al*. (2013) found it associated with ***Lejeunea mandonii*** (Figure 31) and other bryophytes on ash trees next to burns in ravines in a base-rich area. Denyer (2012) found it associated with crags that had calcareous seepage in the UK.

Figure 31. ***Lejeunea mandonii***, a species that can occur with ***Harpalejeunea molleri*** on ash bark. Photo by Jan-Peter Frahm, with permission.

In Nova Scotia, ***Harpalejeunea molleri*** (Figure 24-Figure 28, Figure 33-Figure 38) occurs on the bases of the eastern white cedar ***Thuja occidentalis*** (Figure 32) in a swamp (Haughian & Neily 2020).

Figure 32. ***Thuja occidentalis*** in snow; ***Harpalejeunea molleri*** grows on the bases of this species in Nova Scotia. Photo by Peter M. Dziuk, with online permission.

Averis *et al*. (2011, 2012) considered that watercourses with hydroelectric potential are an important habitat for ***Harpalejeunea molleri*** (Figure 24-Figure 28, Figure 33-Figure 38). Since their declaration of concern for this species, Callaghan *et al*. (2019) found that following disturbance in the flow regime caused by a new hydroelectric power development, ***Harpalejeunea molleri*** was one of the first species to be diminished. ***Harpalejeunea molleri*** can be overtaken by larger bryophytes, especially ***Ctenidium molluscum*** (Figure 9).

Like so many of the wet habitat **Lejeuneaceae**, ***Harpalejeunea molleri*** (Figure 24-Figure 28, Figure 33-Figure 38) can occur on dry bark or stone in half-shaded to shaded habitats of Madeira Island (Schwarz & Schumm (2019). In these habitats, other very small liverworts often grow on it.

Harpalejeunea molleri (Figure 24-Figure 28, Figure 33-Figure 38) occurs in small, yellowish-green patches (Schuster 1980). It can be found on bark and shaded humid rocks. In the North American Coastal Plain it is known only on bark, usually in swamps or deep, mesic, evergreen wood, often near or along black-water streams. But elsewhere it occurs on damp rocks, usually on shaded vertical sides of ledges or cliffs, less often on large boulders. It also occurs in relatively open xerophytic oak-hickory-chestnut forests.

Adaptations

González-Mancebo *et al*. (2004b) considered ***Harpalejeunea molleri*** (Figure 24-Figure 28, Figure 33-Figure 38) to be a **short-lived shuttle** species on the forest floor of the laurel forest (Figure 11) in the Canary Islands. Kürschner *et al*. (2007a) considered it to be a **thread** (Figure 38) on the Canary Islands. At its small size, the threads can form a **mat**.

Biodiversity, ecology, and morphology of bryophytes are related (Fontinha *et al*. 2010). In Madeira, Fontinha and coworkers measured the variables related to the distribution of bryophytes and found that temperature, precipitation, altitude, species cover, presence of snow, substrate *p*H, microaspect, and topography could be related to the morphological characters of underleaf (Figure 33) and lobule surfaces, lobule width, lobe length (Figure 34), lobe surface, and length of median cells of the lobe (Figure 35) in several liverwort species, including ***Harpalejeunea molleri*** (Figure 24-Figure 28, Figure 33-Figure 38). **Trigones** (cell wall thickenings, especially where three cells join; Figure 36-Figure 37) don't seem to be one of these characters. In these habitats, ***H. molleri*** was associated with other liverwort species (Figure 38), including ***Porella canariensis*** (Figure 39), ***P. inaequalis***, and ***P. obtusata*** (Figure 40).

Figure 33. ***Harpalejeunea molleri*** underleaf. Photo by Jan-Peter Frahm, with permission.

Figure 34. ***Harpalejeunea molleri*** subsp. ***integra*** showing lobes on ventral side. Photo by Blanka Aguero, with permission.

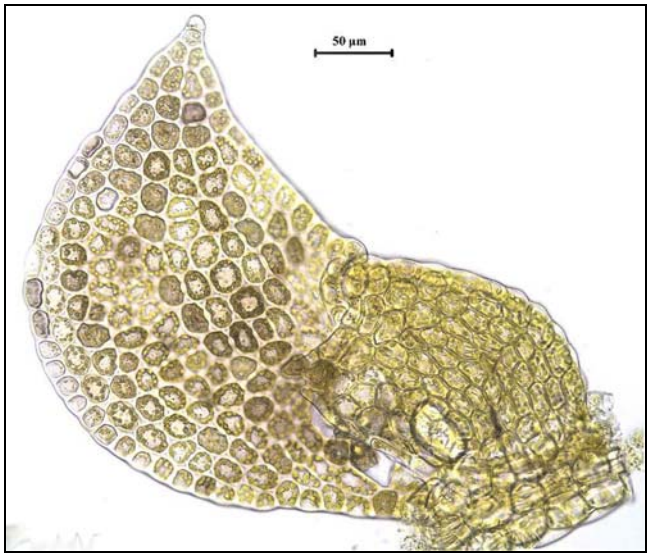

Figure 35. ***Harpalejeunea molleri*** leaf showing lobe. Photo by Hugues Tinguy, with permission.

Figure 36. ***Harpalejeunea molleri*** subsp. ***integra*** leaf and leaf lobe cells. Photo by Blanka Aguero, with permission.

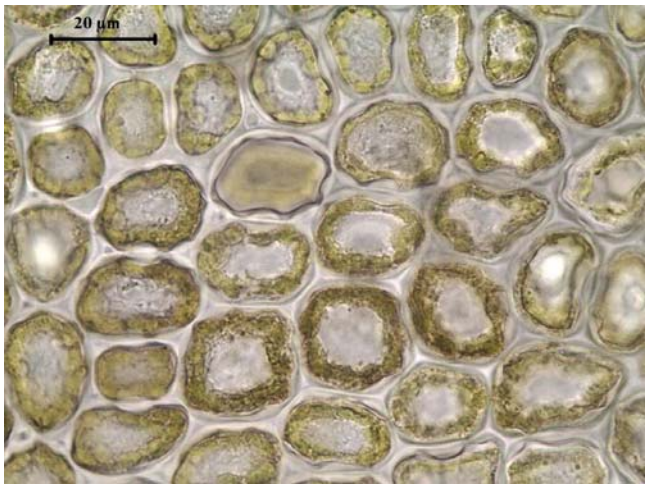

Figure 37. ***Harpalejeunea molleri*** leaf cells with trigones. Photo by Hugues Tinguy, with permission.

Figure 38. ***Harpalejeunea molleri*** growing as a thread on larger liverworts. Photo by Jan-Peter Frahm, with permission.

Figure 39. ***Porella canariensis***, a species that associates with ***Harpalejeunea molleri***. Photo by Jan-Peter Frahm, with permission.

Figure 40. ***Porella obtusata***, a species that associates with ***Harpalejeunea molleri***. Photo by Stan Phillips, through public domain.

Reproduction

Harpalejeunea molleri (Figure 24-Figure 28, Figure 33-Figure 38) is **dioicous**, usually sterile, usually without asexual reproduction.

Fungal Interactions

There seems to be little information about the interactions of ***Harpalejeunea molleri*** (Figure 24-Figure 28, Figure 33-Figure 38), although it seems to occur at least some of the time with other bryophytes (Figure 41). However, Vital *et al*. (2000) found that it can grow on the fungus ***Hyphodontia*** sp. (Figure 42), a capability of other liverworts as well.

Figure 41. ***Harpalejeunea molleri*** mixed with other bryophytes. Photo by Michael Lüth, with permission.

Figure 42. ***Hyphodontia sambuci*** overgrown by leafy liverworts, one of which can be ***Harpalejeunea molleri***. Photo by Roger Griffith, through public domain.

Lejeunea (Figure 43-Figure 44, Figure 47-Figure 51, Figure 61-Figure 71)

(syn. = *Neopotamolejeunea*)

S. Robbert Gradstein (November 2011) related to me that multiple species in the genus ***Lejeunea*** (Figure 43-Figure 44, Figure 47-Figure 51, Figure 61-Figure 71) are common in Andean streambeds. The genus has lobes that approach the structure of lobules. Both terms are used in the literature.

Lejeunea aloba

(syn. = *Eulejeunea aloba*, *Rectolejeunea aloba*, *Rectolejeunea submersa*)

Distribution

Lejeunea aloba occurs in the tropics. Records include Nilgiri Hills (Verma & Rawat 2013), Jog Falls (Schwarz 2013) and other locations in India (Shah & Gujar 2016; Singh & Singh 2016). It occurs in the African countries of Kenya (Chuah-Petiot & Pócs 2003; Enroth *et al*. 2019) and Rwanda (Biedinger & Fischer 1996). Söderström *et al*. (2014) included in the flora of Java.

Aquatic and Wet Habitats

Ruttner (1955) included ***Lejeunea aloba*** in his treatment of aquatic taxa of the tropics. But little seems to be known of its ecology. Biedinger and Fischer (1996) reported it in their epiphytic study in Rwanda. Malombe *et al*. (2016) found it growing as an epiphyll in the edges of Afromontane fragmented forests. Rashid *et al*. (2012) noted its altitudinal range in the Kashmir state of India to be 800-1100 m.

Lejeunea eckloniana (Figure 43-Figure 44)

Distribution

Lejeunea eckloniana (syn. = *Lejeunea holtii*; Figure 43-Figure 44) has been reported in South Africa (Jones 1974), Cape Verde Islands, Teneriffe, Sierra Leone and Angola to Kenya, Tanzania, Cape, and to the Mascarenes (widespread; Pócs 1993), Ethiopia (Hylander *et al*. 2010), Ghana (Hodgetts *et al*. 2016), Taita Hills region, Kenya (Enroth *et al*. 2019), Bioko Island in Equatorial Guinea (Müller & Pócs 2007), Réunion Island (Ah-Peng & Bardat 2005), India (Schwarz 2013; Singh & Pócs 2016; Kasiani *et al*. 2019), Portugal (Sérgio *et al*. 2012; Cacciatori *et al*. 2015), Azores (Gabriel & Bates 2005; Frahm 2006), Macaronesia (Sérgio 1978), Canary Islands (González-Mancebo & Hernández-García 1996), Pico Branco-Porto Santo Island, Madeira (rare; Lobo 2008; Ruas *et al*. 2015), Malaysia and Indonesia (Kasiani *et al*. 2019), UK (rare; Pescott 2016; Bosanquet *et al*. 2018), Ireland (endangered; Kingston 2012).

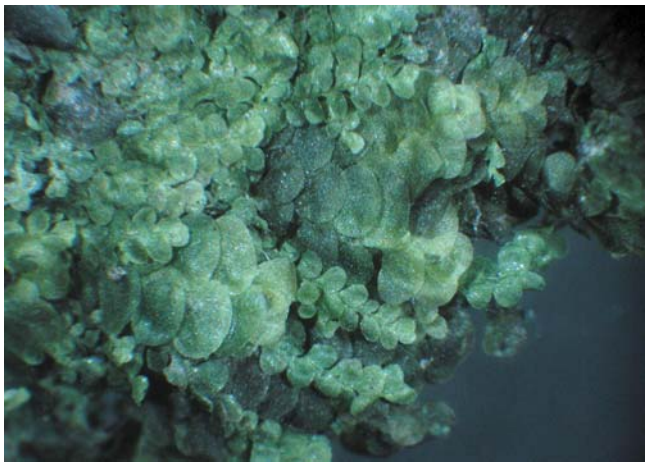

Figure 43. ***Lejeunea eckloniana***, a mostly tropical species in the Eastern Hemisphere and that can occur at waterfalls. Photo by Jan-Peter Frahm, with permission.

Aquatic and Wet Habitats

Lejeunea eckloniana (Figure 43-Figure 44) seldom occurs as a true aquatic, but it usually prefers damp habitats. Watson (1919) reported it from waterfalls in Europe. Dirkse (1985) found it on sheltered wet volcanic

rocks in the laurel forest (Figure 11) of the Canary Islands, Luís *et al*. (2015) found it in mountainous streams on Madeira Island. And Sim-Sim *et al*. (2005b) found it was a frequent part of the flora in the vicinity of temporary lagoons and swamps in the Madeira Archipelago. But Schwarz and Schumm (2019) reported it from wet to dry shaded stone or bark in the Madeira Island. In the Canary Islands, González-Mancebo and Hernández-García (1996) found it to be frequent in the laurel forest, but only occasional in the ***Erica-Myrica*** (Figure 45) woodland. On the other hand, in the Azores Gabriel and Bates (2005) found it to be a characteristic epiphyte, but it occurred where there was lower water availability and higher bark *p*H.

Figure 44. ***Lejeunea eckloniana***. Photo by Jan-Peter Frahm, with permission.

Figure 45. ***Myrica*** on Canary Islands. Photo through Creative Commons.

Bosanquet *et al*. (2018) considered ***Lejeunea eckloniana*** (Figure 43-Figure 44) to be a rare hyperoceanic species in British Atlantic woodlands. Crundwell *et al*. (1994) reported that it occurs on a ***Pittosporum*** (Figure 13) trunk near a stream, but also in small quantities among the moss ***Andoa berthelotiana*** (Figure 46) on rocks at a roadside in the UK. In the Iberian Peninsula, it is likewise quite rare except in the oceanic flora in semi-natural woodlands (Franco *et al*. 2003).

Figure 46. ***Andoa berthelotiana***, a moss that may have small quantities of ***Lejeunea eckloniana*** growing with it. Photo by Pedro Cardoso, with permission through Azoresbioportal.

Adaptations

Lejeunea eckloniana (Figure 43-Figure 44) seems to be best adapted to epiphylly, with small stems, imbricate leaves, and lobules, but no papillae (Kraichak 2012), perhaps reflecting its occurrence in both wet and dry habitats. Sim-Sim *et al*. (2005a) noted the use of water sacs to adapt the species to the variable water conditions. Its oil bodies are minute, with only 2-4 per cell (Kis & Pócs 1997). But the species is variable in other ways, with innovations in particular varying (Jones 1979).

Reproduction

Lejeunea eckloniana (Figure 43-Figure 44) is **monoicous** (Jones 1974).

Lejeunea juruana

(syn. = *Neopotamolejeunea uleana*, *Potamolejeunea ulena*)

Lejeunea juruana is endemic to Andean Brazil (Gradstein & Reiner-Drehwald 2007). It is a specialized rheophyte, occurring as rare in the rainforest on leaves of trees or shrubs in rivers (Bastos & Gradstein 2020). In this habitat it is periodically submerged. In the lowland rainforest, it is likewise periodically submerged, but can occur on rock and pendent on branches of shrubs in the rivers.

Lejeunea lamacerina (Figure 47-Figure 51)

Distribution

Lejeunea lamacerina (Figure 47-Figure 51) is a Holarctic species with a North American and a European/Macaronesian clade (Heinrichs *et al*. 2013; Lee *et al*. 2016; Bastos & Gradstein 2020), where it represents a euoceanic element (Vieira *et al*. 2005). Bastos and Gradstein (2020) reviewed the genus in Brazil and concluded that this species probably does not occur there. Although Schumacker and Váňa (2000) originally considered it to be a European/Macaronesian endemic, Cogoni *et al*. (2002) included North America, as well as Japan, Siberia, and Iceland in its distribution. They found it to be of limited occurrence in Italy. Blockeel (2004) expanded its known localities in Italy. Heinrichs *et al*. (2012) reported it from the Canary Islands. Vieira *et al*.

(2004) considered it to be a relic on Macaronesia due to its worldwide distribution. Özenoğlu and Gökler (2002) reported it from Turkey in the Dilek Peninsula National Park. In the Azores, it occurs on all nine islands (Frahm 2005).

Figure 47. ***Lejeunea lamacerina***, a Holarctic species often found in mountain streams. Photo by Andy Hodgson, with permission.

Figure 48. ***Lejeunea lamacerina***, a species often living in spray from rapids and waterfalls. Photo by David T. Holyoak, with permission.

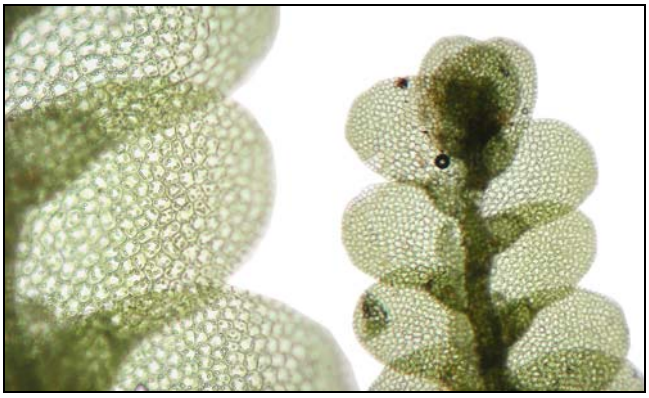

Figure 49. ***Lejeunea lamacerina***, showing lobes. Photo by Michael Lüth, with permission.

In North America, as subsp. ***gemminata*** (Figure 64), it is known from Newfoundland and Nova Scotia in Canada, south to Georgia, USA (Schuster 1980). Miller (1964) reported this subspecies from Hocking Co., Ohio. Schuette and Krayesky (2014) reported the subspecies from Wayne Co., Pennsylvania. Briscoe *et al*. (2009) reported it from Maine.

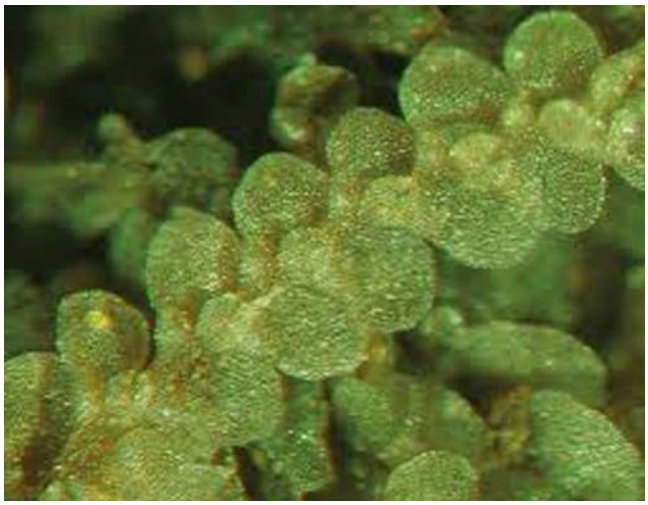

Figure 50. ***Lejeunea lamacerina*** showing underleaves. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

In Tuscany and Piedmont, Italy, ***Lejeunea lamacerina*** (Figure 47-Figure 51) grows on damp rocks along the Riu Rica Bianca (Cogoni *et al*. 2002) and is "not rare" on rocks in streams of the Apuanian Alps (Frahm 2013). Vieira *et al*. (2005) reported it as rare in the Portuguese mountain stream habitats, where it is either seasonally immersed or receives splash or spray (Figure 50-Figure 51). It also occurs in Portugal on dripping schistose wall (Vieira *et al*. 2004) and deeply shaded steep dripping granitic surfaces (Vieira *et al*. n.d.). On Madeira Island it occurs in mountain streams (Luís *et al*. 2015). Sim-Sim *et al*. (2005b) found it on Madeira Island on shaded rocks and rocky slopes near streams and ravines; it typically was associated with ***Plagiochila punctata*** (Figure 52). In the laurel forest (Figure 11) slope communities, it occurs along shaded rivulets, often with other liverworts. It had a 1.4% frequency in the stream, but a 27.1% frequency on the stream bank (Luís *et al*. 2010). Haury (1995) found it at a Breton (France) brook, a stream that also had ***Platyhypnidium riparioides*** (Figure 53) and ***Leptodictyum riparium*** (Figure 54). On Islay, the southernmost of the Inner Hebrides islands of Scotland, it occurs on wet, shaded rocks in a gully on the north coast (Birks & Adam 1978). In Turkey it occurs on tree roots and straight rocks, as well as damp shaded rocks, especially base-rich substrata, and not so often on the sheltered stream banks and tree trunks (Özenoğlu & Gökler 2002).

Figure 50. ***Lejeunea lamacerina***, showing a common stream habitat. Photo by Michael Lüth, with permission.

Figure 51. ***Lejeunea lamacerina*** on boulders in a stream – a common habitat for this species. Photo by Michael Lüth, with permission.

Figure 52. ***Plagiochila punctata***, a species often associated with ***Lejeunea lamacerina*** on shaded rocks and rocky slopes near streams and ravines on Madeira Island. Photo by Stan Phillips, through public domain.

Vieira *et al*. (2012) considered ***Lejeunea lamacerina*** (Figure 47-Figure 51) to be especially important in the northwestern streams of Portugal. These streams are their best habitat in the country, but these researchers considered them to be among the "most threatened" by a warming climate, thermal pollution, and changed hydrological regimes. Heras *et al*. (2002) reported it from humid, acidic conditions in the Botanical Garden of Madrid, Spain.

Figure 53. ***Platyhypnidium riparioides***, a species that often occurs in the same streams as ***Lejeunea lamacerina*** in Breton, France. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 54. ***Leptodictyum riparium***, a species that often occurs in the same streams as ***Lejeunea lamacerina*** in Breton, France. Photo by Štěpán Koval, with permission.

But like so many of the **Lejeuneaceae**, ***Lejeunea lamacerina*** (Figure 47-Figure 51) also occurs as an epiphyte. Kelly (1981) reported it to be frequent on epiphytic mosses in Killarney, southwest Ireland. Sim-Sim *et al*. (2011) found it on all the tree species on Madeira Island.

One of the habitats of ***Lejeunea lamacerina*** (Figure 47-Figure 51), at least in the Azores, is in lava tubes (Figure 55) and volcanic pits, where it is a frequent species (Gabriel *et al*. 2008). In central Spain, Luceño *et al*. (2017) occurs on the wet granites in the alder grove forest. Ravines with ***Prunus lusitanica*** (Figure 56) there serve as refugia for oceanic species such as this.

Figure 55. Volcanic cave (lava tube) at Algar do Carvão, on Terceira Island, Portugal. Photo by Vitor Oliveira, through Creative Commons.

Figure 56. ***Prunus lusitanica*** epiphytes, which can include ***Lejeunea lamacerina***, using these trees as refugia in ravines in the Azores. Photo by Krzysztof Ziarnek, through Creative Commons.

Pescott (2019) found it on drystone wall in the UK. Gökler (1998) found it on stones at 1200 m asl in the Altindere Valley National Park of Turkey. In Maine, USA, the subsp. ***gemminata*** (Figure 64) occurs on serpentine rock (Briscoe *et al*. 2009).

Like so many members of this family, ***Lejeunea lamacerina*** (Figure 47-Figure 51) occurs on a wide range of habitats. These include thin patches on rock and bark in damp to almost dry locations (Schuster 1980). Kürschner *et al*. (2007a, b) found that on Madeira Island it was among the dominant epiphytes in the laurel (Figure 11) and ericaceous forests (Figure 57). In the Canary Island subtropical cloud forests, it is the only species that is "distinctive" of the laurel forests (Patiño & González-Mancebo 2011). On Corvo in the Azores, Sjögren (1993) found that ***Lejeunea lamacerina*** is among the most frequent in the epiphyllous associations and also occurs in the epiphytic associations (Figure 56). It occurs as a primary invader in areas of almost nude bark on ***Erica*** (Figure 57) and ***Juniperus*** (Figure 58).

Kürschner *et al*. (2007b) found that ***Lejeunea lamacerina*** (Figure 47-Figure 51) is able to survive under minimal light in the Madeira laurel (Figure 11) and ericaceous forests (Figure 57). These forests exhibit deep shade and constantly humid conditions.

Figure 57. ***Erica azorica***, in a genus where ***Lejeunea lamacerina*** can be a primary invader in the Azores. Photo by Felix Gertz, through Creative Commons.

Figure 58. ***Juniperus cedrus***, in a genus where ***Lejeunea lamacerina*** can be a primary invader in the Azores. Photo by H. Zell, through Creative Commons.

In the Leyre valley of southwestern France, ***Lejeunea lamacerina*** (Figure 47-Figure 51) arrived after a mud wash with only a slight salt and nutrient enrichment (Hugonnot 2010). Mosses, particularly ***Dichelyma capillaceum***

(Figure 59), trapped and retained the mud, creating a suitable habitat for the ***L. lamacerina***.

Figure 59. ***Dichelyma capillaceum***, a species that traps mud during flooding, providing a suitable habitat for ***Lejeunea lamacerina*** in southwestern France. Photo by Michael Lüth, with permission.

In The Netherlands, van der Pluijm *et al*. (2015) reported that ***Lejeunea lamacerina*** (Figure 47-Figure 51) is usually found on rocks in or near streams that are sheltered by forests in lowland valleys. They suggested that this area is humid and provides protection from frost and drought. But their new find was epiphytic in a relatively open landscape, occurring at 1.5 m height on an oak (***Quercus robur***; Figure 60) stem.

Figure 60. ***Quercus robur*** in Dartmoor, UK; ***Lejeunea lamacerina*** grows on its trunks in The Netherlands. Photo by Alex Jane, through Creative Commons.

Adaptations

The life form of ***Lejeunea lamacerina*** is typically that of a **small mat** (Figure 61-Figure 62) (Sim-Sim *et al*. 2003, 2005b; Kürschner *et al*. 2007a; Patiño *et al*. 2009). Its life strategy in the Madeiran laurel (Figure 11) and ericaceous forests (Figure 57) is that of a **long-lived shuttle**, surviving in minimal light (Kürschner *et al*. 2007b). Schuster (1980) described these mats as thin, whitish to pale yellowish green, occurring in patches or scattered on rock or bark.

Figure 61. ***Lejeunea lamacerina*** (yellowish patches) forming mats on a rock. Photo by Michael Lüth, with permission.

Figure 62. ***Lejeunea lamacerina*** forming a mat. Photo by Michael Lüth, with permission.

Lejeunea lamacerina can exhibit modified form in some environments (Figure 63). This can be expressed as very slender stems with small leaves, and when shaded the leaves can be longer than usual (BAP 2001).

Figure 63. ***Lejeunea lamacerina*** exhibiting a shelf-like growth form. Photo by George G., through Creative Commons.

Kraichak (2012) describes its epiphyllous characteristics as being **monoicous** (facilitating sexual reproduction) and having imbricate leaves (Figure 65) and

lobules (Figure 66) to retain water, but at the same time it lacks the advantage of neoteny and asexual reproductive structures.

Reproduction

Lejeunea lamacerina (Figure 47-Figure 51) is **autoicous** and has no specialized asexual reproduction (Schuster 1980); the female perianth of subsp. ***gemminata*** is shown in Figure 64. Nevertheless, van der Pluijm *et al*. (2015) found buds of young plants on the margin or lamina of old weathered leaves. They suggested that these probably act as a means of vegetative propagation.

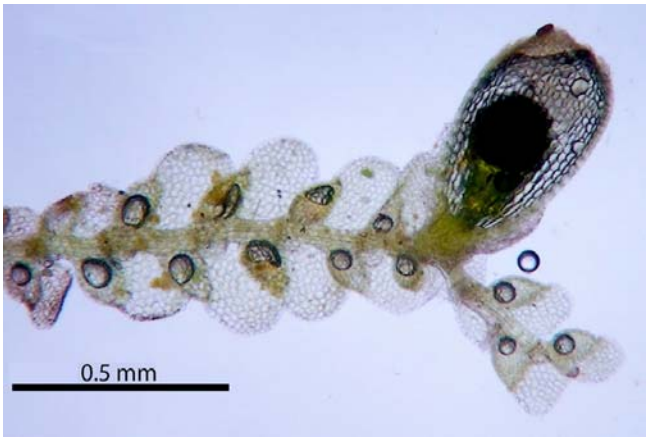

Figure 64. ***Lejeunea lamacerina*** subsp. ***gemminata***, with perianth. Photo by Ken McFarland and Paul Davison, with permission.

Figure 65. ***Lejeunea lamacerina*** showing imbricate leaves, lobules, and underleaves. Photo by Michael Lüth, with permission.

Figure 66. ***Lejeunea lamacerina*** showing underleaves and leaf lobes. Photo by David T. Holyoak, with permission.

Fungal Interactions

No studies have found any mycorrhizal relationships (Wang & Qiu 2006), but once more the small size may account for a lack of studies.

Biochemistry

Lejeunea lamacerina has a few small oil bodies per cell (Figure 67), indicating the presence of secondary compounds. Due to its small size, it is not surprising that biochemical studies are few. Asakawa *et al*. (2018) used chemical relationships of sesquiterpenoids to argue for its relationship among several Japanese species.

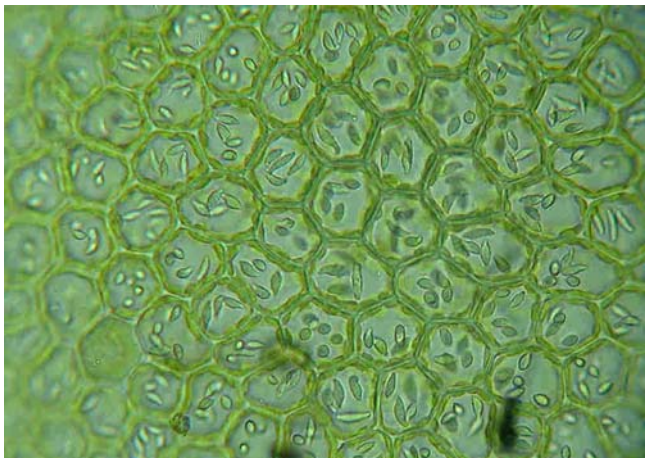

Figure 67. ***Lejeunea lamacerina*** leaf cells showing oil bodies. Photo by David T. Holyoak, with permission.

Lejeunea patens (Figure 68-Figure 69)

(syn. = *Crossotolejeunea polyantha*, *Neopotamolejeunea polyantha*, *Potamolejeunea polyantha*)

Lejeunea patens (Figure 68-Figure 69) has experienced misidentification in various geographic areas. Confusion between ***Lejeunea patens*** and other similar liverwort species and confusion in its synonymy in its various locations makes records of its occurrence

incomplete and sometimes misleading (see Söderström *et al.* 2007). For example, Miller (1964) considered ***Lejeunea patens*** Lindb. (Frye and Clark, 1947) to be the same as ***Lejeunea lamacerina*** Gott. ex. Steph. ssp. ***gemminata*** Schuster (Figure 64), but Söderström *et al.* 2016) consider both to be valid species.

Figure 68. ***Lejeunea patens*** on a boulder beside the river near Swallow Falls, Wales. Photo by Janice Glime.

Distribution

Lejeunea patens (Figure 68-Figure 69) has an Atlantic-Mediterranean distribution (Damsholt 2017). The species has been reported from Spain (Sérgio *et al*. 2007), Portugal (Sérgio *et al*. 2007; Cacciatori *et al*. 2015). Yamaguchi *et al.* (2005) found it in Indonesia in two unburned plots. Bakalin (2019) reported it from the Caucasus of western Russia. Bosanquet *et al*. (2018) reported it from the British Atlantic woodland. It is known in Britain and Norway (Barbour (1903; Frahm 2012), Ireland, Bretagne in France, the Iberian Peninsula, and the Faroe Islands (Frahm 2012). Hugonnot *et al*. (2013) reported it from the Massif Central in France.

Frahm (2005) reported it from eight of the nine Azorean islands, occurring in the Madeira laurel forests (Figure 11) (Sim-Sim *et al.* 2005a,b; Ruas *et al*. 2015). Gil and Guerra (1981) found it at Sierras de Algeciras in the Iberian Peninsula. Casas *et al*. (1983) found it at l'Alt Empordà in Spain. Poponessi and Aleffi (2016) listed it for the Sardinian region of Italy, Macaronesia, Spain, France, Madeira, Portugal, and Turkey. They termed it a Mediterranean-mountain hemiboreal species.

In North America, Barbour (1903) found that ***Lejeunea patens*** (Figure 68-Figure 69) occurs in Newfoundland and Nova Scotia and northern borders of the USA. Andrews (1921) reported it from several locations in North Carolina. Evans (1923) added Maine, New Hampshire, Vermont, Massachusetts, and Connecticut, USA.

Aquatic and Wet Habitats

Lejeunea patens (Figure 68-Figure 69) can be occasionally submerged (Watson 1919) and occurs in rivers (Ferreira *et al*. 2008). Cros (1982) found it on rocks in the Escalonada torrent of the Balearan Islands in the Mediterranean.

More likely one can find it on damp, shaded rocks in such locations as gorges (Poponessi & Aleffi 2016). Sim-Sim *et al*. (2003) reported it from rocks, boulders, and stone walls that were in either sheltered or exposed habitats (Figure 70) along water courses. These formed loose to dense patches, often with other bryophytes, on moist rock surfaces and slopes near the water (Figure 71). In the Faroe Islands, ***Lejeunea patens*** (Figure 68-Figure 69) occurs in rocky ravines or clefts where species richness is greater than in any other habitat in the Faroes (Damsholt 2017). In Turkey, Ezer *et al*. (2009) found it in humid locations.

In gorges in France, Hugonnot *et al*. (2016) report it from shaded and dry walls that have an accumulation of organic matter. They describe its habitat as having moderate shade with a "certain quantity" of light. In Bretagne, northern France, Durfort (2015) found it in ravines, wooded ridges, and mountainous areas with high atmospheric humidity.

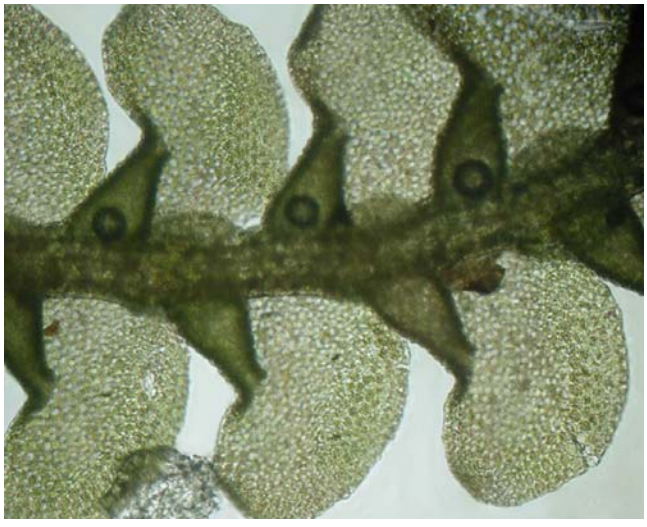

Figure 69. ***Lejeunea patens*** showing leaf lobes and underleaves. Photo by Jan-Peter Frahm, with permission.

Figure 70. ***Lejeunea patens*** habitat on vertical boulder surfaces. Photo by Michael Lüth, with permission.

Figure 71. ***Lejeunea patens*** on boulder near Swallow Falls, Wales, growing with ***Thamnobryum alopecurum*** in a humid environment. Photo by Janice Glime.

The habitat for ***Lejeunea patens*** (Figure 68-Figure 69) is clearly broadly defined, but usually in places with nearly constant humidity. It has even been found, but rarely, in a salt marsh in Britain (Adam 1976). In the Madeira Archipelago, Sim-Sim *et al*. (2005b) found it growing as an epiphyte where it was humid and shady in the laurel forest (Figure 11). It also often occurred with ***Plagiochila exigua*** (Figure 29) in **loose turfs** on moist rocks and slopes near water courses.

Long and Williams (2007) found that the intense shading of ***Rhododendron ponticum*** (Figure 22) causes the complete loss of a number riparian bryophytes. Only occasional patches of ***Lejeunea patens*** (Figure 68-Figure 69) on sheltered boulder faces are present. They assumed that this species could be washed in from stands living higher up on the rock face. Several reports mention that it tends to occur in brighter areas.

Lorenz (1924) found ***Lejeunea patens*** (Figure 68-Figure 69) on Mt. Desert Island, Maine, USA, on trees, rocks and the northern white cedar, ***Thuja occidentalis*** (Figure 32) – a swamp forest species.

Adaptations

The wide range of habitats is supported by the humidity and temperature tolerance of this species from the Faroes. In his experiments, Clausen (1964) found that at 43% and 51% relative humidity, half the cells of ***Lejeunea patens*** (Figure 68-Figure 69) were dead, but at 63% humidity, all cells remained alive. It did best between 70% and 100% rh with a temperature of ~35ºC and 60% relative humidity at 20ºC. All died at ~45ºC at all humidities and at 20ºC with 10% rh. These parameters placed it close to the middle among the liverwort species from various northern locations in the experiments. When maintained in ice at -10ºC for 2-5 days, about 3/4 of the cells remained alive, but the dead cells were mostly at the shoot apices. After 11-12 days, all cells were dead. However, if it was partly desiccated over sugar, all cells remained alive for 5 days. At -40ºC, all cells were dead in 1 day.

Lejeunea patens (Figure 68-Figure 69) can modify its form in different environments, sometimes having very slender stems with small leaves (BAP 2001). When so attenuated, shaded stems can produce leaves that are longer than usual.

Reproduction

Lejeunea patens (Figure 68-Figure 69) is **autoicous** (Evans 1902; Hugonnot *et al*. 2016). In the Faroe Islands, Damsholt (2017) found that perianths were frequent, but despite its autoicous sexuality, it only occasionally produces sporophytes there. Perhaps the climate is unsuitable for the antheridia or for sperm transfer for this species that extends southward to the Mediterranean. It is possible that the signals for antheridial and archegonial maturation are out of sync. On the other hand, even in Galicia in northwestern Spain, the species is frequent, but sporophytes are encountered only occasionally (Reinoso 1985). And in the gorges of the Rhue in France it does not produce sporophytes at the studied site, nor does it have any specialized vegetative propagation (Hugonnot *et al*. 2016).

Role

Des Callaghan (pers. comm.) has found rotifers (Figure 72) living among the mats of ***Lejeunea patens*** (Figure 68-Figure 69) in Wales (Figure 73).

Figure 72. ***Frullania***, showing how a rotifer can live in a lobule such as those found in ***Lejeunea patens***. Photo courtesy of Andi Cairns.

Figure 73. ***Lejeunea patens*** – home of rotifers near Swallow Falls, Wales, mixed with the moss ***Thamnobryum alopecurum***. Photo by Janice Glime.

Biochemistry

The species has larger oil bodies, usually 4-6 per cell, up to 10. Biochemical studies seem to be lacking. Wang and Qiu (2006) were unable to find any records of mycorrhizae associated with ***Lejeunea patens*** (Figure 68-Figure 69), but is this the result of biochemical inhibition, or just lack of study?

Lejeunea polyantha

Confusion quickly arises in finding information on this species because there are two taxa that have had this name (**homonyms**): ***Lejeunea polyantha*** Mont. and *Lejeunea polyantha* Mitt. – the homonym (TROPICOS 2020). At times like this I regret not including authors in the text of this book.

Distribution

(syn. = *Crossotolejeunea polyantha*, *Neopotamolejeunea polyantha*, *Potamolejeunea polyantha*)

Lejeunea polyantha occurs in South America (Reiner-Drehwald 1999), including Brazil and Venezuela (Gradstein & Reiner-Drehwald 2007; Bastos & Gradstein 2020).

Aquatic and Wet Habitat

I must admit that this species did not appear in my search for aquatic species. But, as I found information on other species, this one showed up as being a rheophyte, occurring in lowland rainforests and being periodically submerged on rock and pendent on branches of shrubs in rivers (Reiner-Drehwald 2000a, b; Bastos & Gradstein 2020).

Lejeunea subaquatica

Lejeunea subaquatica seems to be a barely known species, but it is still recognized by Söderström *et al*. (2016).

The only wet/aquatic record I have found thus far is for its occurrence in the tropics at 10-20 cm above water level (Ruttner 1955).

Lejeunea topoensis

Distribution

Lejeunea topoensis is a rare Andean species, occurring in Brazil and Ecuador (Gradstein & Reiner-Drehwald 2007; Bastos & Gradstein 2020). It has an interesting disjunction between the Andes and the Atlantic coastal region in Brazil (Gradstein & Reiner-Drehwald 2007).

Aquatic and Wet Habitats

Lejeunea topoensis is a rheophyte, occurring in fast water and often submerged (Gradstein & Reiner-Drehwald 2007). In Ecuador it grows on the dwarf shrub ***Cuphea bombonasae*** (Figure 74) where it forms large mats (Gradstein & Benitez 2014). In Brazil they found it in a spring bog, growing submerged in running water. Gradstein *et al*. (2011) found it in great abundance in torrential water currents of the Topo River in the Ecuadorian Andes.

Figure 74. ***Cuphea bombonasae***, substrate for ***Lejeunea topoensis***. Photo from <swbiodiversity.org>, through Creative Commons.

Adaptations

Lejeunea topoensis is green when fresh, forming large **mats** (Gradstein & Reiner-Drehwald 2007).

Reproduction

Lejeunea topoensis is very fertile, a benefit of its **autoicous** condition. The seta is **articulate** (having joint between two separable parts), probably contributing to its dispersal in running water. Its oil bodies are numerous (20-30 per cell) and thus small. The spores are green and germination is **precocious** (occurring early – germinating within capsule). The spores are irregular in shape with a surface covered with small granules and rosettes, perhaps giving the spores better flotation. Long-distance spore dispersal is quite possible, based on experiments by van Zanten and Gradstein (1988). This premise is supported by molecular phylogenetic studies in other species (Heinrichs *et al*. 2005, 2006).

Biochemistry

Ludwiczuk and Asakawa (2014) used fingerprinting of secondary metabolites to show that ***Lejeunea topoensis*** lacks isolepidozene, pingiusanes, fusicoccanes, and monocyclofarmesanes that are found in many of the genera of the **Lejeuneaceae**. No vegetative propagules were observed, but fragmentation remains a possibility.

Lopholejeunea nigricans (Figure 75-Figure 78)

(syn. = *Heterolejeunea javanica*)

Lopholejeunea nigricans Figure 75-Figure 78) has lots of synonyms (Staples & Imada 2006), an expected outcome for this species with lots of variation.

Figure 75. ***Lopholejeunea nigricans*** showing variation in leaf color. Photo by Jia-dong Yang, through Creative Commons.

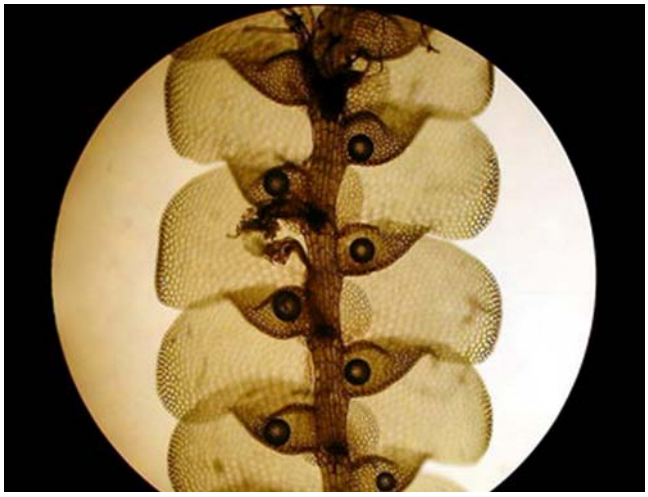

Figure 76. ***Lopholejeunea nigricans*** habit showing leaf lobes. Photo by Michaela Sonnleitner, with permission.

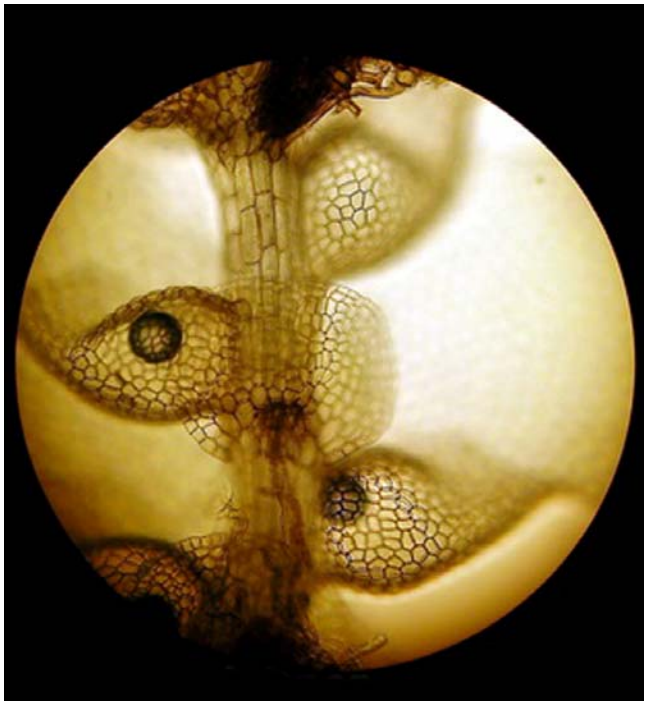

Figure 77. ***Lopholejeunea nigricans*** underleaves and lobes. Photo by Michaela Sonnleitner, with permission.

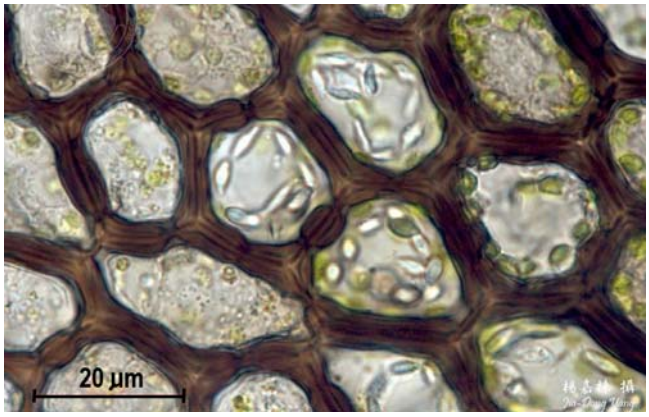

Figure 78. ***Lopholejeunea nigricans*** leaf cells showing oil bodies. Photo by Jia-dong Yang, through Creative Commons.

Distribution

Lopholejeunea nigricans (Figure 75-Figure 78) is a widespread pantropical species (Müller *et al*. 2011; Kornochalert *et al*. 2012; do Carmo & Peralta 2016). In Asia it is known from Bangladesh, Bhutan, Borneo, Cambodia, China, Hong Kong, India, Indonesia, Japan, Malaysia, Myanmar, Nepal, Papua New Guinea, Philippines, Taiwan, Thailand, Vietnam, and Yemen (Zhu & Gradstein 2005; Schwarz 2013). Kürschner and Ochyra (2003) found it in the Arabian Peninsula. Kornochalert *et al*. (2012) added much more information on the species in Thailand. Pócs and Chantanaorrapint (2016) reported it among non-epiphyllous species from several lowland areas in Thailand. Rajesh and Manju (2014) reported it from both lowlands and midlands in Kerala, India. In Sulawesi, an Indonesian island, Ariyanti and Gradstein (2007) found it in both lowland and montane regions. Zhu *et al*. (1998) added Zhejiang Province in China.

Haerida *et al*. (2010) found that ***Lopholejeunea nigricans*** (Figure 75-Figure 78) has a moderately wide distribution in West Java, occurring in both lowland and montane habitats (200-1700 m asl). Hodgetts *et al*. (2016) found it in the Eastern Region of Ghana. Hedderson *et al*. (2015) reported it from 1274 m asl in Mozambique and Wigginton (2001) from Malawi (up to 1635 m asl). It has been reported from Réunion Island off the eastern coast of Africa in the Indian Ocean (Ah-Peng & Bardat 2005) and the Central African island country of São Tomé and Príncipe. Carreon *et al.* (2016) added it to the Philippines. It also occurs in the Hawaiian Islands (Staples & Imada 2006).

In the Neotropics, ***Lopholejeunea nigricans*** (Figure 75-Figure 78) is known from Brazil (da Costa 2003; Peralta & Yano 2008; Visnadi 2009), Cocos Island in Costa Rica (Dauphin 1999), a tropical lowland cloud forest in central French Guiana (Gradstein 2006), Bolivia (Fuentes & Churchill 2005), and Peru (Drehwald 2003).

Aquatic and Wet Habitats

Lopholejeunea nigricans (Figure 75-Figure 78) occurred in a water spout of a tuff wall in the tropics (Ruttner 1955). Zhu and Gradstein (2005) reported that it occurs up to 1200 m asl in Asia, occasionally occurring on stones in running water. Hodgetts *et al*. (2016) reported it

from damp, shaded rocks by streams in Ghana, where it is locally abundant at 350-630 m asl. In India, Das and Sharma (2013) reported it from the bank of the River Boleswar at 70 m asl, as well as on loose moist soil of rock crevices. In Malawi, Wigginton (2001) found it on rocks beside rivers and streams. Müller *et al*. (2011) found it in the central African island country of São Tomé and Príncipe on exposed hardwood roots along a river. In Equatorial Guinea, Sánchez and Pérez (1998) found it both on rocks and bark near streams at 5-75 m asl.

The habitats of ***Lopholejeunea nigricans*** (Figure 75-Figure 78) are rather variable, including tree bases, roots, trunks, branches, shrubs, lianas, stumps, decaying logs, rocks, soil, occasionally on stones in running water, or on living leaves, from sea level to 2900 m asl (Zhu & Gradstein 2005). Hodgetts *et al*. (2016) found it forming small colonies in earthy rock crevices in the eastern region of Ghana.

Records for ***Lopholejeunea nigricans*** (Figure 75-Figure 78) on rock seem less frequent than epiphytic records except in or near water. Hedderson *et al*. (2015) found it on a small boulder in the ***Streptocarpus*** (Figure 80) forest on Mabu Mountain in Mozambique (Figure 81). Wigginton (2001) reported it from rocks, including granite, close to rivers. Müller *et al*. (2011) found it on soil and litter over volcanic rock where it received filtered light.

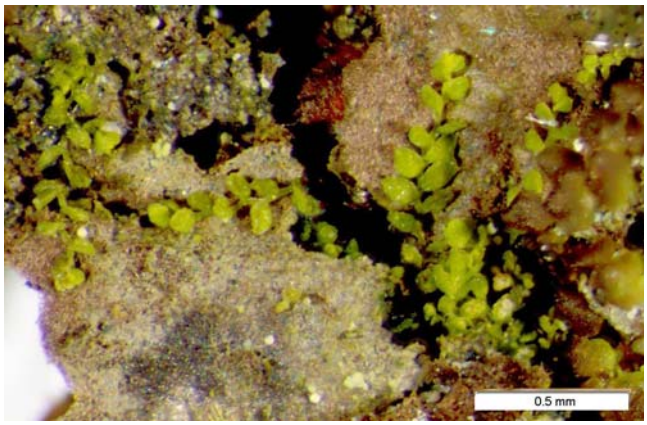

Figure 79. ***Myriocoleopsis minutissima***, a species that grows on ***Lopholejeunea nigricans***. Photo by Blanka Aguero, with permission.

Figure 80. ***Streptocarpus*** sp.; ***Lopholejeunea nigricans*** has been found in the ***Streptocarpus*** forest on Mabu Mountain in Mozambique. Photo by Mokkie, through Creative Commons.

Figure 81. Mount Mabu, Mozambique, where one can find ***Lopholejeunea nigricans*** on small boulders in the ***Streptocarpus*** forest. Photo by Conradie *et al*. 2016, through Creative Commons.

Adaptations

Sass-Gyarmati (2015) considered ***Lopholejeunea nigricans*** (Figure 75-Figure 78) to be the most variable species in the genus ***Lopholejeunea***. For example, in some cases the lobules may be reduced (Zhu & Gradstein 2005). In a moist environment these modifications include reduced female bract lobules, weakly laciniate perianths, and very small leaf lobules. These modifications have resulted in the description of several species that are now considered synonyms.

Lopholejeunea nigricans (Figure 75-Figure 78) forms mats (Figure 75) (Batista & Santos 2016) and has a dark pigmentation (de Oliveira 2018). De Oliveira found that the dark pigmentation was significantly more frequent among liverworts in the canopy and significantly less at the tree bases. This dark coloration (Figure 75) presumably protects the canopy liverworts from the bright light there.

Reproduction

Lopholejeunea nigricans (Figure 75-Figure 78) has both monoicous and dioicous sexuality, giving it the advantages of both ease of fertilization and diversity of cross fertilization. He and Zhu (2011) found that the spore output from ***Lopholejeunea nigricans*** was 936-1254 from a tree trunk population. But it lacks asexual reproduction. De Oliveira (2018) suggested that the absence of overrepresentation of asexual propagules in canopy liverworts challenges the current views of bryophyte strategy, especially in the canopy. But Zhu and Gradstein (2005) found that ***Lopholejeunea nigricans*** accomplishes asexual reproduction with **caducous** (falling off easily) or fragmenting leaves.

Myriocoleopsis (Figure 79, Figure 87-Figure 91)

Myriocoleopsis (Figure 79, Figure 87-Figure 91) can be found in Andean streambeds (S. Robbert Gradstein pers. comm. 3 November 2011). Discovery of the molecular relationship of *Cololejeunea vuquangensis* with ***Myriocoleopsis*** has also placed the genus in Asia from Vietnam as ***Myriocoleopsis vuquangensis*** (Pócs 2010). For a discussion of species and their affinities in this genus, see Pócs (2010).

In this genus, the development of robust stems seems to be an adaptation to the periodic submergence it

experiences (Reiner-Drehwald & Gradstein 1995). Gradstein *et al*. (2018) noted that it exhibits **neoteny** with perpendicular leaf segmentation, absence of underleaves, and stem with only one row of medullary cells.

But ***Myriocoleopsis*** (Figure 79, Figure 87-Figure 91) also is epiphyllous (Yu *et al*. 2013), a habitat much more subject to drying conditions. Yu and coworkers described the rheophytic relatives of these epiphyllous species, including ***Myriocoleopsis***. They found that the rheophytic taxa differed from epiphyllous species by having creeping stolons, robust stems, and long androecial spikes, and they considered these characters adaptive for running water. In addition to its epiphyllous substrata, the genus also occurs on rock (Gradstein *et al*. 2014), where these adaptations also could be beneficial, but especially on rocks in running water. Wilson *et al*. (2007) noted that rheophytes from unrelated taxonomic groups are driven to parallel development, resulting in similar adaptations to habitats of swiftly flowing water and regular flooding. These included long, robust stems with pinnate branching and numerous, small gametoecial branches on both sides of the stem.

Myriocoleopsis fluviatilis

(syn. = *Myriocoleopsis puiggarii*)

Distribution

Myriocoleopsis fluviatilis is endemic in Brazil (Gradstein & da Costa 2003; da Costa and dos Santos 2009), where it is classified as endangered (da Costa and dos Santos 2009; de Gasper *et al*. 2012), and thus threatened in the world (Hallingbäck and Hodgetts (2000).

Aquatic and Wet Habitats

Myriocoleopsis fluviatilis grows on rocks and shrubs that are periodically submerged in rivers (Gradstein & da Costa 2003). It is "very rare" and occurs at 150-1300 m asl in Brazil. It grows primarily on bare rocks or small rocky cliffs in the middle and along the edges of the River Pardo (Gradstein & Vital 1975). But it also grows on the bases of low shrubs, always in exposed places in or near running water, in or near a river with small waterfalls and rapids and a rocky bottom. The species is only found in exposed places in or near running water.

Myriocoleopsis fluviatilis colonizes bare rocks and small rocky cliffs in the middle and edges of the River Pardo (Gradstein & Vital 1975). The life form is a **mat**, which forms a dense, pale greenish growth. It has short, creeping, stoloniform primary stems and secondary stems that are ascending to erect, up to 3 cm long.

Continuous submergence is not suitable for the health of the plants. After a period of 5-15 days of submergence, leafy shoots die and only the stoloniferous stems survive (Gradstein & Vital 1975).

Adaptations

Gradstein *et al*. (2003a) ascribed the thicker stems with more numerous rows of cells to adaptations for the rheophytic habitat of ***Myriocoleopsis fluviatilis***. This species is also neotenous, but I know of no experimental study that shows any rheophytic advantage to this developmental strategy. It is common among epiphylls and among some aquatic **Lejeuneaceae**, as seen above.

Reproduction

Despite its autoicous sexuality, sporophytes develop only on plants that occur on emerged substrates, a phenomenon that has been noted for a number of other flowing-water bryophytes (Gradstein & Vital 1975). It has multicellular disciform gemmae that arise from the leaf surfaces, but these are rare.

Role

In the continuously wet habitat of this species, many diatoms find a suitable home on the liverworts: ***Melosira*** (in great number; Figure 82), ***Gomphonema*** (Figure 83), ***Synedra*** (Figure 84), ***Cymbella*** (Figure 85), and some **Naviculaceae** (Figure 86) (Gradstein & Vital 1975).

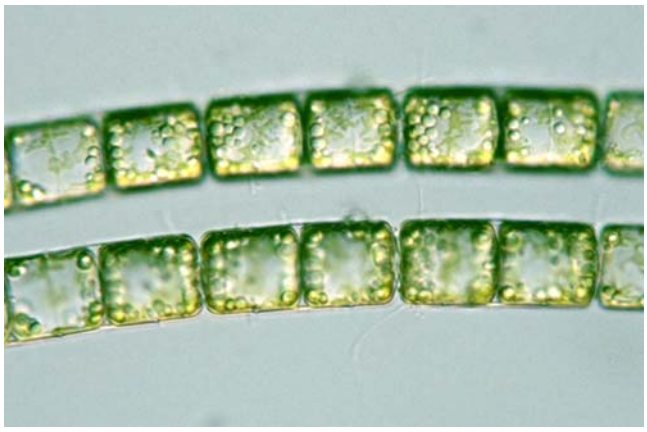

Figure 82. ***Melosira*** sp., a genus that can occur on ***Lopholejeunea nigricans*** in wet habitats. Photo by Yuuji Tsukii, with permission.

Figure 83. ***Gomphonema*** sp., a genus that can occur on ***Lopholejeunea nigricans*** in wet habitats. Photo by Yuuji Tsukii, with permission.

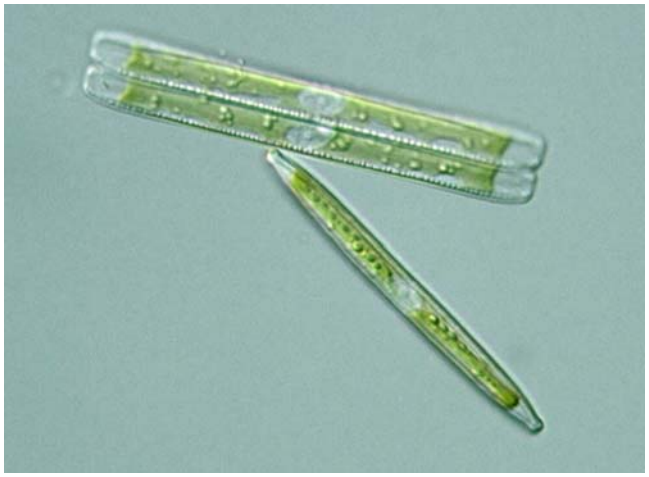

Figure 84. ***Synedra*** *cf.* ***ulna***, in a genus that can occur on ***Lopholejeunea nigricans*** in wet habitats. Photo by Yuuji Tsukii, with permission.

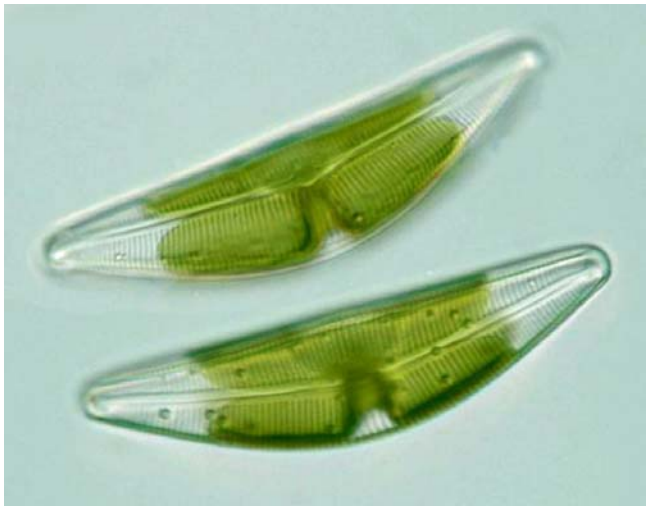

Figure 85. ***Cymbella*** *cf.* ***lanceolata***, in a genus that can occur on ***Lopholejeunea nigricans*** in wet habitats. Photo by Yuuji Tsukii, with permission.

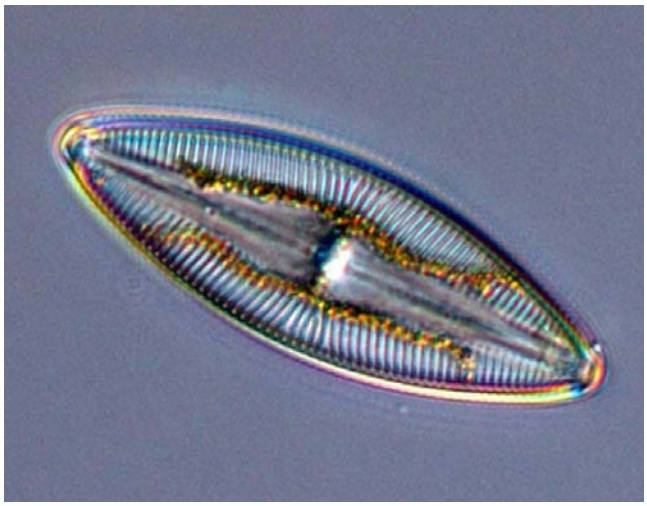

Figure 86. ***Navicula*** (**Naviculaceae**), in a genus that can occur on ***Lopholejeunea nigricans*** in wet habitats. Photo by Phyto'pedia – The Phytoplankton Encyclopaedia Project, through Creative Commons.

Myriocoleopsis gymnocolea

(syn. = *Myriocoleopsis riparia*)

Distribution

Myriocoleopsis gymnocolea is known from Argentina (Reiner-Drehwald & Gradstein 1995; Gradstein & da Costa 2003), Bolivia (Gradstein *et al*. 2003b), Brazil (Reiner-Drehwald & Gradstein 1995; Gradstein *et al*. 2003a; dos Santos & da Costa 2010; do Carmo *et al*. 2018), and Ecuador (Gradstein & da Costa 2003; Gradstein *et al*. 2004; Pócs 2010; Benitez & Gradstein 2011; Gradstein 2020).

In Ecuador ***Myriocoleopsis gymnocolea*** occurs at 500-1300 m asl (León-Yanez *et al*. 2006; Gradstein 2020), 100-1300 m asl in Brazil (Gradstein & da Costa 2003), 100-1300 m asl in Argentina (Reiner-Drehwald 1995).

Aquatic and Wet Habitats

Like ***Myriocoleopsis fluviatilis***, this species occupies periodically submerged rocks in rivers (Gradstein & da Costa 2003). Reiner-Drehwald (1995) found ***Myriocoleopsis gymnocolea*** above a waterfall, where it is sometimes submerged, but primarily on rocks that are periodically submerged. The species occurs in the center and on the banks of rivers, typically in rapid currents. The rapid currents provide splash that keep it moist in its emergent positions.

The species can occur as an epiphyte at the base of small shrubs and on river banks, occupying a niche similar to that of ***M. fluviatilis*** (Reiner-Drehwald 1995).

Adaptations

Myriocoleopsis gymnocolea exhibits traits that we have seen in previous rheophytic members of the **Lejeuneaceae**. It is **monoicous** and neotenous (Kraichak 2012), the latter a character that needs further investigation to determine its advantages in the aquatic environment. In fast water, this may permit it to remain small, thus creating little or no drag, while also permitting sexual structures to develop. The guarantee of a wet film over the plants at the right time would facilitate its ability to transfer sperm from antheridia to archegonia in this monoicous species.

Myriocoleopsis gymnocolea has thin stems with only 5 rows of cortical cells (Reiner-Drehwald & Gradstein 1995). Yu *et al*. (2014) considered certain remarkable characters to include its dimorphic stems with creeping stolons and erect leafy axes arising from them, reduced lobules, and long male spikes. The reduced lobules are often expressed in rheophytic species. In addition, they noted the absence of underleaves, another character that could be part of the neotenous development of many aquatic **Lejeuneaceae**. It might be interesting to examine the differences in **hydroxyproline** (component of plant hormones essential for growth, cell differentiation, and defense) concentrations surrounding the leaves in the aquatic environment (see Basile 1967). Could it be that the condition of immersion changes the concentrations of this component, thus affecting development? This could be accomplished by reduced diffusion in water.

Reproduction

Myriocoleopsis gymnocolea is **monoicous** (Kraichak 2012).

Role

Myriocoleopsis gymnocolea serves as a suitable substrate for diatoms (Figure 82-Figure 86) and other algae (Reiner-Drehwald 1995).

Biochemistry

Despite its small size, Ludwiczuk *et al*. (2013) examined chemical relationships in the **Lejeuneaceae**, including this species. ***Myriocoleopsis gymnocolea***, like a number of members of this family, has only pinguisanes and not isolepidozenes, fusicoccanes, or monocyclofarmesanes. The researchers considered this chemistry to be a marker of the subtribe **Cololejeuneinae**.

Like other members of the genus, ***Myriocoleopsis gymnocolea*** lacks lepidozanes, fusicoccanes, monocyclofarnesanes, having only pinguisanes (Coulerie *et al*. 2015), strengthening its relationship to those species of **Lejeuneaceae** not placed in ***Myriocoleopsis***.

Myriocoleopsis minutissima (Figure 79, Figure 87-Figure 91)

(syn. = *Cololejeunea minutissima*)

Distribution

Myriocoleopsis minutissima (Figure 79, Figure 87-Figure 91) was originally described as a species of ***Cololejeunea*** (see Chapt. 1-7 in this volume), but has been moved to ***Myriocoleopsis*** (Yu *et al*. 2014). It is a widespread pantropical species (Cañiza *et al*. 2016; Hodgetts *et al*. 2020) that is distributed in North America from Virginia and Tennessee to Florida and Texas (Stotler & Crandall-Stotler 2017). It is also known from Central America, South America, western and central Europe, central and eastern Asia, and Australia (Stotler & Crandall-Stotler 2017; Hugonnot (2019), southern Africa and South Indian Ocean islands (Bischler 2004; Hugonnot 2019).

Figure 88. ***Myriocoleopsis minutissima*** with perianth. Photo by Hugues Tinguy, through Creative Commons.

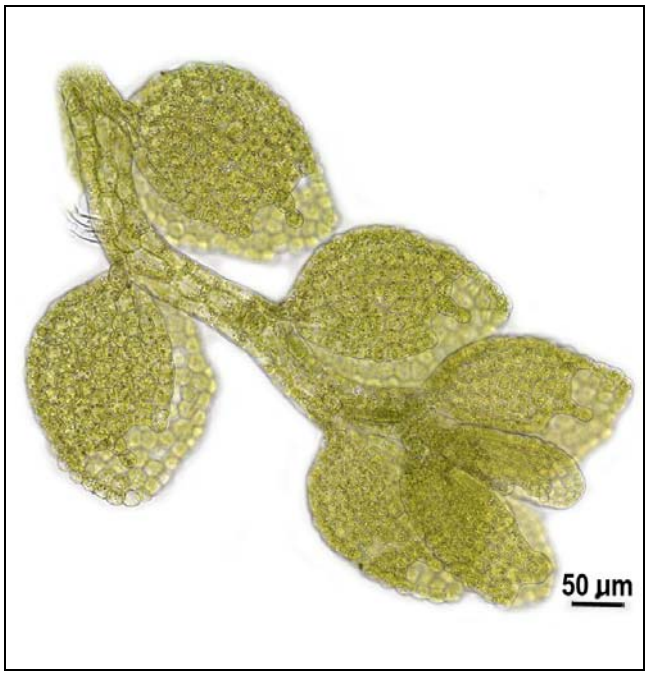

Figure 89. ***Myriocoleopsis minutissima***, showing large leaf lobes. Photo by Hugues Tinguy, through Creative Commons.

Figure 87. ***Myriocoleopsis minutissima*** in a large patch on rock. Photo by Hugues Tinguy, with permission.

Figure 90. ***Myriocoleopsis minutissima*** showing large lobes. Photo by Blanka Aguero, with permission.

Figure 91. ***Myriocoleopsis minutissima*** leaf cells with oil bodies. Photo by Blanka Aguero, with permission.

In Europe ***Myriocoleopsis minutissima*** (Figure 79, Figure 87-Figure 91) exhibits a Mediterranean-oceanic character (Düll 1983). European records include Madeira Island (Schwarz & Schumm 2019), Montseny massif in the Iberian Peninsula (very rare; Sáez *et al*. 2018), Corsica (Hugonnot 2019), Sicily (Dia *et al* 2017), and France (Hugonnot *et al*. 2017; Hugonnot & Simont 2018). It is rare in the Mediterranean region, occurring in the Azores, Canary Islands, Cape Verde Islands, Madeira, Croatia, Greece, Italy, Montenegro, Portugal, Serbia, and Spain (Hugonnot 2019).

In Asia ***Myriocoleopsis minutissima*** (Figure 79, Figure 87-Figure 91) is known from Vietnam (Shu *et al*. 2016), Singapore (Zhu *et al*. 2018), southern Thailand (Pócs and Chantanaorrapint 2016), Lebanon in south-western Asia (Hugonnot 2019), and Sabah in Malaysian Borneo (Pócs *et al*. 2020).

Wigginton (2018) found ***Myriocoleopsis minutissima*** (Figure 79, Figure 87-Figure 91) in the flora of Africa and the African islands. Enroth *et al*. (2019) included it in the checklist of the Taita Hills region of Kenya, noting that it is widely distributed in sub-Saharan Africa. Hugonnot (2019) included it in the flora of Algeria and Tunisia in northern Africa.

In Central and South America, Ristow *et al*. (2015) reported ***Myriocoleopsis minutissima*** (Figure 79, Figure 87-Figure 91) from Brazil. It occurs in Ecuador (Gradstein 2020) and Paraguay (Cañiza *et al*. 2016). Schäfer-Verwimp and van Melick (2016) reported it from Jamaica and Stotler and Crandall-Stotler (2017) from Bermuda.

Myriocoleopsis minutissima (Figure 79, Figure 87-Figure 91) has a varied altitudinal range. It has a known altitudinal range of 1500-2800 m asl in Ecuador (Gradstein 2020). In Malaysian Borneo, it occurs in the mossy cloud forest at 1900-1940 m asl (Pócs *et al*. 2020). On the Iberian Peninsula it occurs at 750 m. It is known from lowlands in Thailand, where it has expanded into the warm temperate, oceanic areas (Pócs & Chantanaorrapint 2016).

Aquatic and Wet Habitats

Myriocoleopsis minutissima (Figure 79, Figure 87-Figure 91) has little claim to the aquatic environment, but it is at least tolerant of a humid environment, living in "well preserved" humid riparian forests of Paraguay, where it is an epiphyte on the corky bark of ***Chloroleucon tenuiflorum*** (Figure 92) (Cañiza *et al*. 2016). Most records for ***Myriocoleopsis minutissima*** (Figure 79, Figure 87-Figure 91) present it as an epiphyte.

Figure 92. ***Chloroleucon tenuiflorum***, a species of humid riparian forests of Paraguay and substrate for ***Myriocoleopsis minutissima***. Photo by CECOAL, through Creative Commons.

Reproduction

Myriocoleopsis minutissima is **autoicous**. Images of perianths are in Figure 93-Figure 95. It produces large gemmae (Figure 96) with 16-48 cells, mostly on the lobes, but sometimes on the leaf periphery.

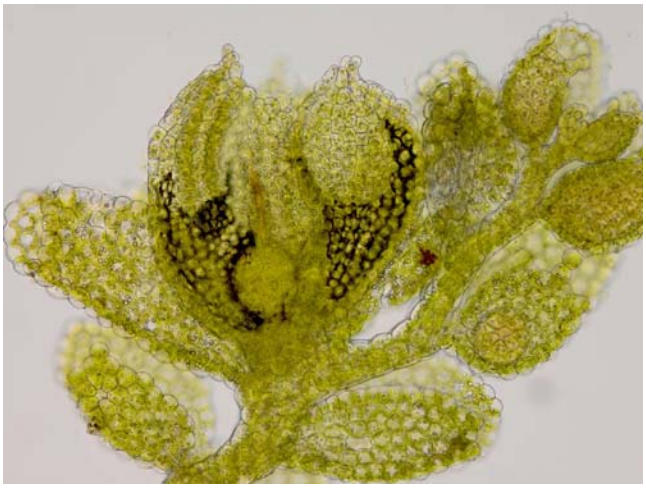

Figure 93. ***Myriocoleopsis minutissima*** with perianths and archegonia. Photo by Blanka Aguero, with permission.

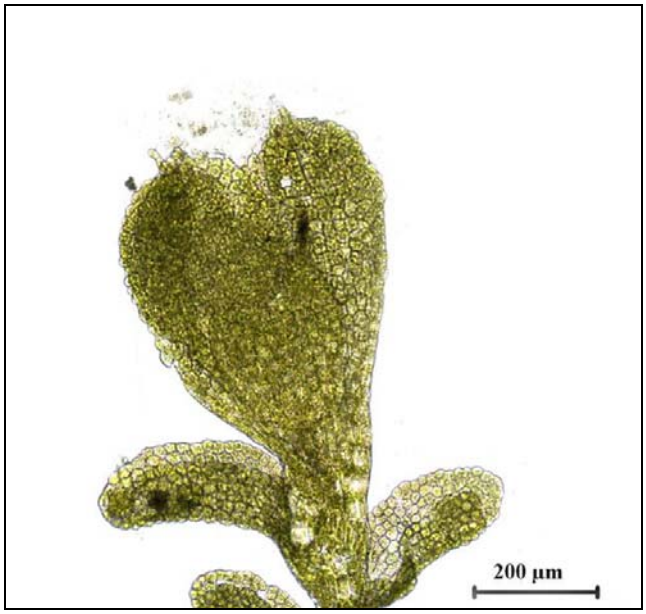

Figure 94. ***Myriocoleopsis minutissima*** perianth. Photo by Hugues Tinguy, through Creative Commons.

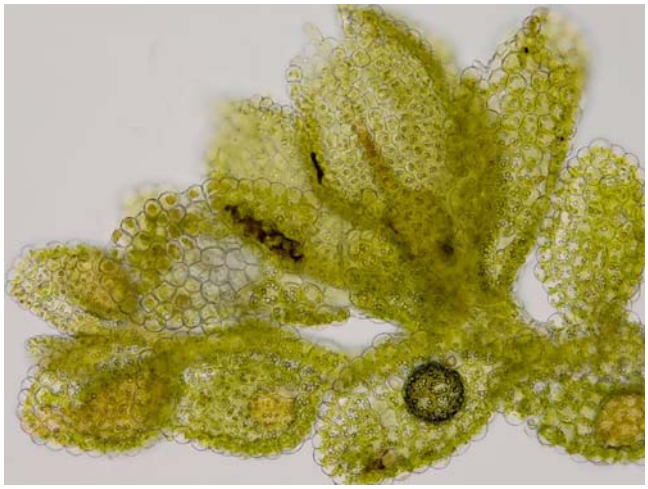

Figure 95. ***Myriocoleopsis minutissima*** with archegonium showing reddish neck. Photo by Blanka Aguero, with permission.

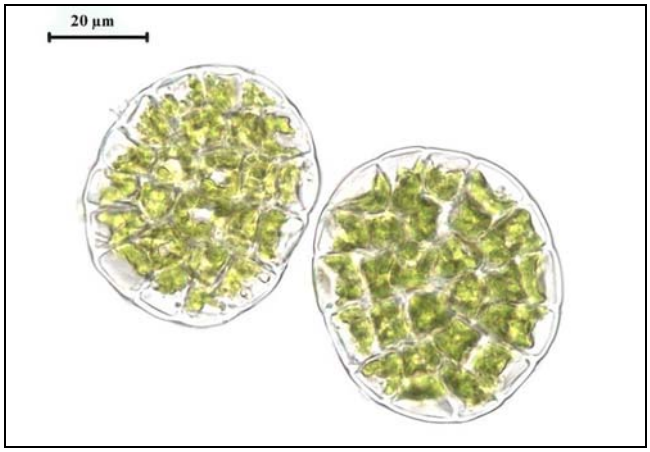

Figure 96. ***Myriocoleopsis minutissima*** gemmae. Photo by Hugues Tinguy, through Creative Commons.

Myriocoleopsis minutissima subsp. *myriocarpa*

Distribution

Like the subspecies ***minutissima*** (Figure 79, Figure 87-Figure 91), ***Myriocoleopsis minutissima* subsp. *myriocarpa*** is widespread in the tropics (Hodgetts *et al*. 2020). It is thus pantropical, with records in Europe, North America, and South America. Gradstein (2020) found it in Ecuador at 100-3000 m asl.

Aquatic and Wet Habitats

In Florida, USA, ***Myriocoleopsis minutissima* subsp. *myriocarpa*** occurs in mahogany (***Swietenia mahogani***) **hammocks** (Figure 97), in Everglades National Park (Schuster 1971; Zona & Sadle 2017). These are islands of trees in wetlands or on slopes between wetlands and uplands. Those serving as home for this species are low hammocks, surrounded by marshland (Schuster 1971).

Figure 97. ***Swietenia mahagoni*** hammock, Everglades. Photo by Miguel Vieira, through Creative Commons.

Myriocoleopsis vuquangensis

Distribution

Myriocoleopsis was considered a Neotropical genus until Pócs (2010) reported it from Vietnam in southeast Asia. Wilson *et al*. (2007) used molecular evidence to identify similarities of *Cololejeunea vuquangensis* to the Neotropical ***Myriocoleopsis*** (Figure 79, Figure 87-Figure 91), causing its transfer to ***Myriocoleopsis vuquangensis***. In the Neotropics it is known from the Nangaritza River in Ecuador (Pócs 2010).

Aquatic and Wet Habitats

This species has more qualifications as a wetland species, living as a rheophyte on twigs of the euphorbiaceous shrub ***Homonoia riparia*** (Figure 98) (Pócs 2010). In its known Asian home, this species of ***Myriocoleopsis*** (Figure 79, Figure 87-Figure 91) exists on the bush vegetation on riverbed shoals where it gets inundated twice a year during the monsoons. These shrubs occur in groups on river banks, rocky (fast-running) stream beds, and along the coast. Soil in these locations is usually

(temporarily) inundated, in some areas for months, creating a humid or wet environment.

Figure 98. ***Homonoia riparia***, a rheophyte that can support ***Myriocoleopsis vuquangensis*** on its twigs, where they are occasionally inundated. Flora of Peninsular India, through Creative Commons.

Adaptations

Like other ***Myriocoleopsis*** (Figure 79, Figure 87-Figure 91) species, ***Myriocoleopsis vuquangensis*** has both creeping stolons and erect leafy stems (Pócs 2010).

Reproduction

Myriocoleopsis vuquangensis is monoicous, with male branches and "very abundant" perianths (Pócs 2010).

Ptychanthus striatus var. *intermedius* (see Figure 99-Figure 101)

(syn. = *Ptychanthus intermedius*)

Although ***Ptychanthus striatus* var. *intermedius*** was described in 1934 by Verdoorn as *Ptychanthus intermedius*, I have not been able to find much ecological information on it under either name, so the information contained here is for the species ***Ptychanthus striatus*** (Figure 99-Figure 101).

Figure 99. ***Ptychanthus striatus***. Photo by Jia-dong Yang, through Creative Commons.

Figure 100. ***Ptychanthus striatus***, dry, growing on a vertical surface in Bhutan. Photo by David Long, with permission.

Figure 101. ***Ptychanthus striatus*** ventral side showing underleaves and perianths. Photo by Boon Chuan Ho, courtesy of Rob Gradstein.

Distribution

Ptychanthus striatus (Figure 99-Figure 101) is a variable species (Gradstein 1985). Singh and Singh (2016) noted that the species ***Ptychanthus striatus*** has many synonyms. He (1997) considered it to have worldwide distribution, especially in the Palaeotropics (Gradstein 1985), but it appears to be absent in the Western Hemisphere. It was considered to occur in warm temperate regions including South Africa, the Himalayas, Japan, and Australasia (Gradstein & Inoue 1980). Pócs *et al*. (2007) summed its distribution up as widespread in the whole Indopacific region.

Gradstein and Inoue (1980) also included Central Africa to the western Pacific, with several records indicating that ***Ptychanthus striatus*** (Figure 99-Figure 101) occurs in Africa (Bizot & Pócs 1974; Frahm 1994; Braun *et al*. 2004; Müller 2006). Müller (2006) even considered it to be widely distributed in tropical Africa. However, using both morphology and molecular characteristics, Ahonen *et al*. (2005) and Pócs and Luke (2007) considered all African records of ***Ptychanthus striatus*** to be the separate species ***Ptychanthus africanus***.

Thiers (1990) and Haerida *et al*. (2010) reported ***Ptychanthus striatus*** (Figure 99-Figure 101) from

Australia. It also has been found in Java and Sumatra (Verdoorn 1933), Peninsular Malaysia, Borneo, Sulawesi, Moluccas, Philippines, West Irian, New Zealand, Pacific Islands, India, Sri Lanka, Taiwan, Indochina, and China (Haerida *et al*. 2010). Kornochalert *et al.* (2012) reported its presence in Thailand. Additional Asian records include China (He 1997), including Sichuan (Piippo *et al*. 1997) and Yunnan (Han *et al*. 2010), Western Ghats in India (Pócs *et al*. 2007), and southern India (as *Spruceanthus wiggintonii*; Wang *et al*. 2014). The finding that ***Ptychanthus africanus*** replaces it in Africa and the Himalayas suggests that the remaining populations should be re-examined to determine whether they indeed all belong to ***Ptychanthus striatus*** (Figure 99-Figure 101).

Haerida *et al*. (2010) reported ***Ptychanthus striatus*** (Figure 99-Figure 101) in both lowlands and montane habitats at elevations ranging 1000-2400 m asl. Kornochalert *et al*. (2012) reported its range from 50-2480 m asl in Thailand. Frahm (1994) reported it at less than 1500 m on Mt. Kahuzi, Zaire. Pócs *et al*. (2007) found it at 2350 m asl in the Western Ghats in India. It even is considered common in the Himalayas at altitudes below 4000 m asl (Zhu & Long 2003), but those records might actually represent ***Ptychanthus africanus*** (see Singh & Singh 2008). Hence, the altitudinal ranges described here need to be verified following a more thorough assessment of the species.

Aquatic and Wet Habitats

It doesn't appear that ***Ptychanthus striatus*** (Figure 99-Figure 101) is particularly aquatic. Ruttner (1955) listed ***Ptychanthus striatus* var. *intermedius*** as aquatic in the tropics. Thiers (1990) reported ***Ptychanthus striatus*** (Figure 99-Figure 101) as growing especially near waterfalls (Figure 102) and steep escarpments in Australia, where the species forms large, "festooning" bodies in the mist that keeps these areas humid. In India, Singh and Singh (2008) reported the species ***Ptychanthus africanus*** as rare from moist places where it grew on rocks on a thin layer of soil.

Ptychanthus striatus also occurs in a variety of terrestrial habitats, including grassland (Gradstein & Inoue 1980), forest epiphytes (Müller 2006; Pócs *et al*. 2007), and on rocks (Kornochalert *et al*. 2012).

Several studies have examined the impact of heavy metals on ***Ptychanthus striatus*** (Figure 99-Figure 101). Shakya *et al*. (2008a, b) found that the metal accumulation in ***P. striatus*** increased with metal concentration in the water. Copper had a significant inhibition of both chlorophyll *a* and *b*. Similarly, zinc and lead accumulation caused a significant decrease in chlorophyll. They suggested that the greater loss of chlorophyll from ***P. striatus*** than from moss species in the experiments may have been caused by relatively more K^+ efflux in the leafy liverwort than in the mosses. However, there was no significant decrease in chlorophyll when the liverworts were exposed to copper, zinc, and lead together. The metals zinc and copper exhibited leaching in ***P. striatus***, indicating that they occur on exchange sites under hydrated conditions. Competition for these exchange sites might explain the lowered toxicity when the three metals were provided together. These results are consistent with the presence of the species only in clean sites, not those contaminated with heavy metals. This study has led to the use of ***P. striatus*** and other bryophytes in determining heavy metal loading near roads (Shakya *et al*. 2012).

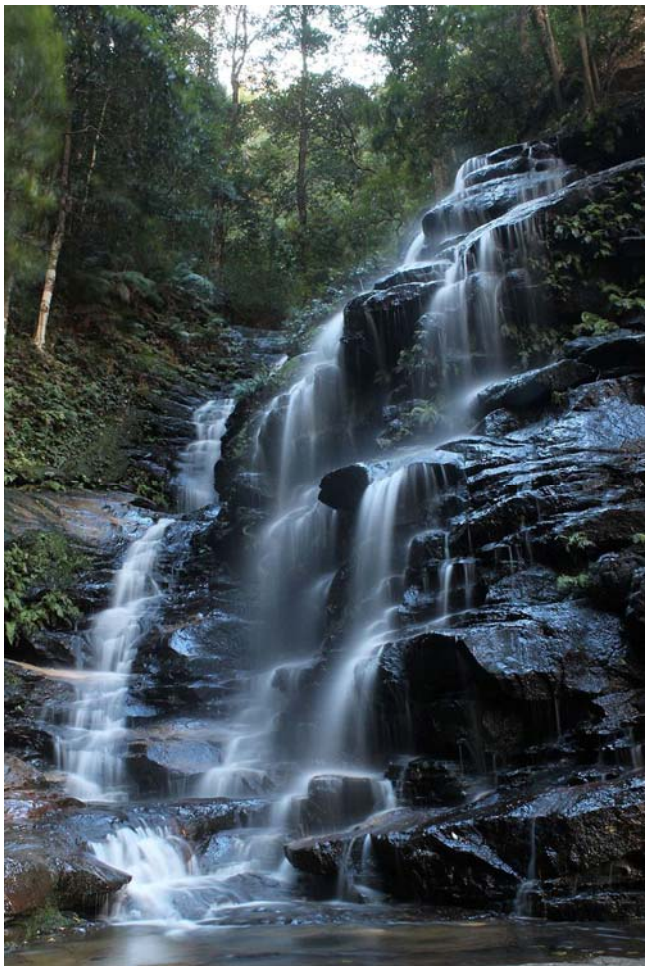

Figure 102. Waterfalls at Wentworth, Australia, a habitat where one might find ***Ptychanthus striatus***. Photo by Jack Brogan, through Creative Commons.

Adaptations

Ptychanthus striatus (Figure 99-Figure 101) is a robust species, up to 10 cm long, contrasting with the many tiny members of the **Lejeuneaceae**. These plants are either pendent or stand up away from their substrate.

Reproduction

Ptychanthus striatus is autoicous (see perianths in Figure 103) (Haerida *et al*. 2010), contrasting with its sister species, ***Ptychanthus africanus***, in which **dioicous** specimens "are not rare" (Bizot & Pócs 1974). The spore output of ***Ptychanthus striatus*** is high (up to 5750) among the Chinese **Lejeuneaceae** (He & Zhu 2011).

Biochemistry

Ptychanthus striatus (Figure 99-Figure 101) has 6-10 grayish-yellow oil bodies per cell (Figure 104) (Singh *et al*. 2008). These presumably are sites of concentrations of a number of secondary compounds. This species has one of the longest lists of biochemical studies. Such studies include the isolation and description of structures of a number of sesquiterpenoids (Takeda *et al*. 1982, 1983;

Nabeta *et al*. 1998, 2000; Wu *et al*. 2015), isolation and structure of diterpenoids such as ptychantins with elaboration of their synthetic pathway (Hashimoto *et al*. 1995, 1999; Hagiwara & Nozawa 2009; Wu *et al*. 2015). Like many of the **Lejeuneaceae**, it produces several pinguisane-type sesquiterpenes and striatene, but is poor in diterpenes (Gradstein *et al*. 1985).

Figure 103. ***Ptychanthus striatus*** with perianths. Photo by Jan-Peter Frahm, with permission.

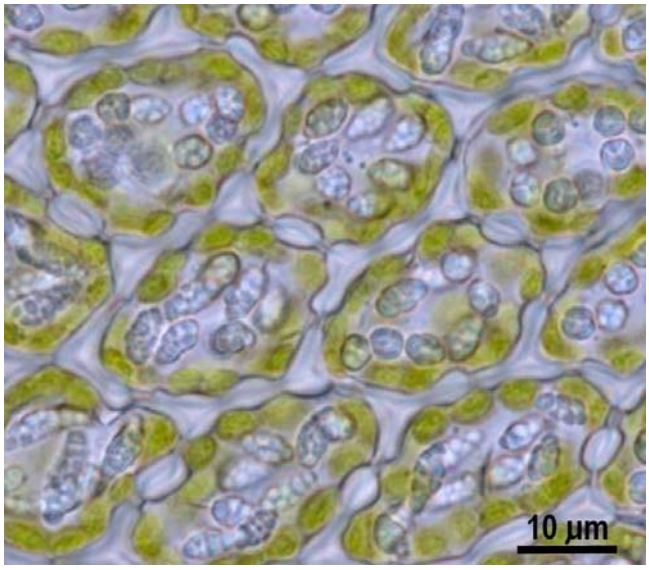

Figure 104. ***Ptychanthus striatus*** leaf cells with oil bodies. Photo by Jia-dong Yang, through Creative Commons.

In addition to the exploration of secondary compounds, other biological pathways were explored. Karunagoda *et al.* (Karunagoda *et al.* 2001, Karunagoda & Nabeta 2004) elucidated the biosynthesis of the phytyl side-chain of chlorophyll *a* using this species.

Ptychanthus striatus (Figure 99-Figure 101) is among the liverworts that have shown antidiabetic activity and antioxidant activity (Mukhia *et al*. 2015), as well as antigfungal activity against human pathogens (Dikshit *et al*. 1982). Other fungal interaction studies seem to be lacking.

Schusterolejeunea inundata

(syn. = *Cladocolea inundata*, *Lejeunea inundata*, *Potamolejeunea sprucei*)

Schusterolejeunea inundata is the only known species in ***Schusterolejeunea*** (Grolle 1980; Söderström *et al*. 2016).

Distribution

Schusterolejeunea inundata is a rare Amazonian endemic (Gradstein & Costa 2003; Gradstein & Costa 2003; Dauphin *et al.* 2008; Désamoré *et al*. 2014; Costa *et al.* 2017; Sierra *et al*. 2018). It was known only along the Rio Negro of Brazil (da Silva 2019) and Venezuela (Sierra *et al*. 2018). The latest records show it from Venezuela (Moreno 1992; Söderström *et al*. 2020), Brazil (Gradstein & da Costa 2003; da Silva 2019), the Guianas (Gradstein & Hekking 1985; Gradstein *et al.* 1990; Gradstein & da Costa 2003; Söderström *et al*. 2020), Surinam (Söderström *et al*. 2020), Guyana (Söderström *et al*. 2020), Ecuador (Gradstein *et al*. 2018), and Peru (Gradstein & da Costa 2003; Söderström *et al*. 2020).

Aquatic and Wet Habitats

Schusterolejeunea inundata occurs in Andean streambeds as a rheophyte on branches of trees, roots, and rocks that occur in these beds in undisturbed lowlands up to 100 m asl (Gradstein *et al*. 1990; Gradstein & da Costa 2003). Hallingbäck and Hodgetts (2000) considered it an indicator of undisturbed lowland rainforest.

Figure 105. ***Schusterolejeunea inundata*** with sediments imbedded in it from inundation. Photo from BioPortal, through Creative Commons.

Schusterolejeunea inundata occurs with ***Ceratolejeunea temnantha*** (Figure 106) in large **mats** in seasonal habits on rocks, lower portions of tree trunks, twigs, and roots in running water of seasonally inundated black-water forest habitats. It can also occur on river banks (Gradstein *et al*. 2011). Gradstein *et al*. (2001) described it as a liverwort of lakes and rivers in Amazonia.

Adaptations

Schuster (1990) considered the genus ***Schusterolejeunea*** to be among the most **apomorphic** (having novel evolutionary trait) of the liverwort genera (see also Vanderpoorten *et al*. 2010, 2012; Gradstein *et al.*

2011). This is among the **stenotypic** genera (those with 1-3 species) (Schuster 1990; Désamoré *et al*. 2014). Gradstein *et al*. (2011) contend that habitat specialization drives the evolution of unusual characters in such species as ***Schusterolejeunea inundata***. Such characters in this species are highly specialized for living in and out of water as the water level changes, permitting them to live on emergent vegetation and river banks.

Figure 106. ***Ceratolejeunea temnantha*** on tree roots, a habitat also occupied by ***Schusterolejeunea inundata***. Photo by Juan Carlos Villarreal, with permission.

Gradstein *et al*. (2001) describe the rheophytic adaptations of ***Schusterolejeunea inundata***. These include creeping rhizomes, thick stems, and "superfertility" (Thiers 1988). The species lacks **neoteny**, a common character of epiphylls, but one that seems to be mostly absent among species that become submersed.

Summary

Most of the **Lejeuneaceae** are not true aquatics, but many do occur in wetlands and very humid habitats. Splash from waterfalls and rapids in streams are often the source of such water. Many have wide substrate tolerances, particularly for both rocks and bark, and many also occur as epiphylls. And many, like ***Lejeunea lamacerina*** and ***L. patens***, have a wide moisture tolerance, from drying out to being submersed for short periods. This variety of habitat conditions leads to environmental forms that confound understanding of the taxonomy. Most **Lejeuneaceae** form mats, but some species are larger and have other growth forms. Many are dioicous, thus seldom producing sporophytes, but fragmentation and gemmae often provide an adaptive alternative. Their moisture retention allows many of them to provide suitable habitats for diatoms.

There seem to be almost no reports of these from polar regions, but they do often occur on mountains, some to relatively high elevations.

Drepanolejeunea hamatifolia is a desiccation-sensitive hyperoceanic species that is restricted to rocky cascades and similarly wet habitats. Humidity maintenance is sometimes achieved by growing on other bryophytes.

Harpalejeunea molleri is one of the species from moist habitats such as swamps, but not typically submerged. Many species, like ***Lejeunea lamacerina*** in mountain streams, are seasonally submersed.

Some ***Myriocoleopsis*** species can occupy rocks in streams that become inundated, but they occur more commonly as epiphytes in moist forests, mahogany hammocks, and other damp locations.

Ptychanthus striatus can form substrata suitable for nitrogen-fixing **Cyanobacteria**, as can a number of other moist-habitat bryophytes. Lobules/lobes in some, perhaps many, of the **Lejeuneaceae** can serve as watery habitats for rotifers.

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Lars Söderström provided me with the current acceptable names for a number of older taxa and helped me sort out some of the species, varieties, and subspecies.

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CHAPTER 1-9
AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA, ORDER PORELLALES: PORELLACEAE

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CHAPTER 1-9
AQUATIC MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA, ORDER PORELLALES: PORELLACEAE

Figure 1. ***Porella pinnata*** on ***Nyssa ogeche***, indicating the high water line. Many of the species of **Porellales** included here occur in this floodwater zone. Photo by Christine Davis, with permission.

Porellales – Suborder Porellineae

Porellaceae

Porella cordaeana (Figure 2-Figure 6)

(syn. = *Madotheca cordaeana*, *Madotheca rivularis*; Figure 2-Figure 6)

Porella cordaeana is a species with many more synonyms that I won't list here.

Distribution

It is a circumboreal species (Dia & Not 1991; Schofield *et al*. 2002), with a highly disjunctive distributionin the Northern Hemisphere. It occurs in Europe, northern Africa, Asia, and western North America from Alaska south to California and northern Mexico (Clark 1953; Piippo & Norris 1996). It has been reported from Finland (Sallantaus & Syrjänen 2005), Serbia (Sabovljević & Cvetić 2003; Cvetić & Sabovljević 2005; Papp *et al*. 2012), Yugoslavia (Sabovljević 2000; Cvetić & Sabovljević 2005), the Carpathians and Sudety Mountains of Poland (Górski *et al*. 2017), Estonia (protected; Vellak & Ingerpuu 2012), Bulgaria (Ganeva & Natcheva 2003), South Bohemia (Kučera *et al*. 2013), Montenegro (Dragićević *et al*. 2007), Switzerland (Meier *et al*. 2013), Croatia (Papp *et al*. 2013), France (Casas & Barrón 2003), Italy (Aleffi 2005; Düll 2006; Campisi *et al*. 2008; Aleffi *et*

al. 2009), Spain (Brugués *et al*. 2002; Casas & Barrón 2003; Elías *et al*. 2006); Portugal (Vieira *et al*. 2012), Greece (Blockeel 1991); Turkey (Gökler 1998; Kürschner 1999; Ursavaş & Abay 2009), Faeroe Isles (Damsholt 2017), and Madeira and Canary Islands (Ekstein 2010). In North America, it has been reported from British Columbia, Canada (Hong 1981; Schofield 1988), and Nevada, USA (Hong 1983).

Figure 2. ***Porella cordaeana***, a circumboreal leafy liverwort. Photo by Hugues Tinguy, with permission.

Figure 3. ***Porella cordaeana***, showing its bright green color. Photo by Jiří Kameníček, with permission.

Figure 4. ***Porella cordaeana*** in a moist condition. Photo by Hugues Tinguy, with permission.

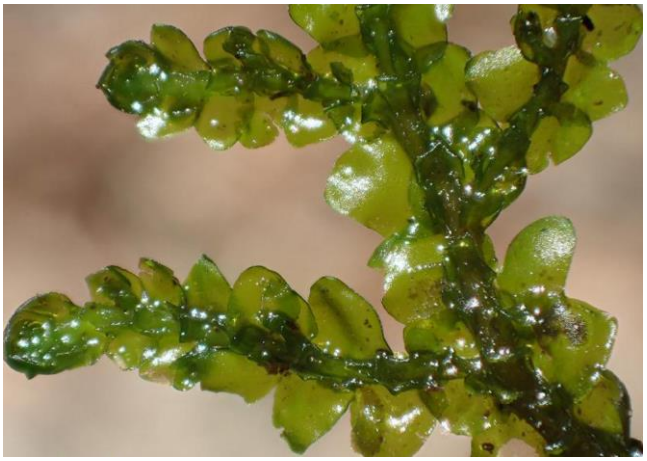

Figure 5. ***Porella cordaeana*** ventral side. Photo by Hugues Tinguy, with permission.

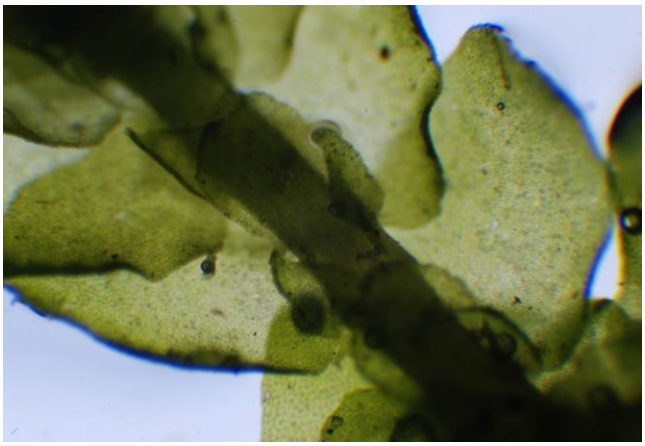

Figure 6. ***Porella cordaeana*** showing underleaves and lobes. Photo by J. C. Schou, with permission.

Aquatic and Wet Habitats

Porella cordaeana (Figure 2-Figure 6) is occasionally submerged, on rocks in fast water (Figure 7) (Watson 1919, as *Scapania madothca porella*). It occurs in the Danube around Ulm, Germany (Muhle *et al*. 1974-1979), and in the ***Platyhypnidium*** (Figure 8)-***Fontinalis antipyretica*** (Figure 9) association, Thuringia, Germany (Marstaller 1987). Similarly, Koponen *et al*. (1995) consider it to be aquatic in Finland. It occurs in the Iskur River, Bulgaria, and its main tributaries in Bulgaria (Papp *et al.* 2006b). In Montenegro, it is reported at a stream, on bark of ***Fagus*** (Figure 18) in the Tara River canyon and Durmitor area (Papp & Erzberger 2011).

Porella cordaeana (Figure 2-Figure 6) is among the bryophytes in Portuguese watercourses (Vieira *et al*. 2012). Sallantaus and Syrjänen (2005) similarly found it on stones in brooks in Finland, where one could also find ***Scapania undulata*** (Figure 10), ***Lejeunea cavifolia*** (Figure 11, and ***Dichelyma*** (Figure 12) species. In Central Europe, Jusik *et al.* (2015) found it in calcareous mountain and upland streams, accompanied by ***Chiloscyphus polyanthos*** (Figure 13) and ***Pellia endiviifolia*** (Figure 14).

Figure 7. ***Porella cordaeana*** on emergent rock in stream. Photo by Hugues Tinguy, with permission.

Figure 8. ***Platyhypnidium riparioides***, a species characteristic of some streams where one can find ***Porella cordaeana*** in Europe. Photo by Michael Lüth, with permission.

Figure 9. ***Fontinalis antipyretica***, a species characteristic of some streams where one can find ***Porella cordaeana*** in Europe. Photo by Chris Wagner, through Creative Commons.

Figure 10. ***Scapania undulata***, a species that accompanies ***Porella cordaeana*** in streams in Finland. Photo by Hermann Schachner, through Creative Commons.

Figure 11. ***Lejeunea cavifolia***, a species that accompanies ***Porella cordaeana*** in streams in Finland. Photo by Dick Haaksma, with permission.

Figure 12. ***Dichelyma pallescens***; ***Dichelyma*** sp. accompanies ***Porella cordaeana*** in streams in Finland. Photo by Blanka Aguero, with permission.

Figure 13. ***Chiloscyphus polyanthos***, a species that accompanies ***Porella cordaeana*** in calcareous mountain and upland streams of Central Europe. Photo by Hermann Schachner, through Creative Commons.

Figure 14. ***Pellia endiviifolia***, a species that accompanies ***Porella cordaeana*** in calcareous mountain and upland streams of Central Europe. Photo by David T. Holyoak, with permission.

In España, Brugués *et al*. (2002) reported ***Porella cordaeana*** (Figure 2-Figure 6) from stones in water courses, where it was among the most common bryophytes and one of the two most common liverworts. These were mostly, however, on the edge of the ravines on slopes with a mix of soil and rock. Aleffi *et al*. (2009) reported it from moist rocks in southeastern Italy. Papp and coworkers (Papp & Erzberger 2005; Papp *et al*. 2012) found it on siliceous stones in a stream in southwest Serbia, as well as on the streambank.

In somewhat less aquatic conditions in the UK, Rothero (2010) found ***Porella cordaeana*** (Figure 2-Figure 6) on the wall of old river "workings" in a flood plain. Papp *et al*. (2006b) reported it from the zone of water level fluctuations along the Iskur (Iskar) River.

In North America, Nichols (1938) reported it from submerged rocks in Cedar Creek in the Huron Mountain region of Michigan, USA.

Although ***Porella cordaeana*** (Figure 2-Figure 6) can be fully aquatic, it seems to be more a species of high moisture, tolerating occasional submersion. Kürschner (1999) even considered it to be an indicator of better moisture conditions when it occurred as an epiphyte in Mediterranean ***Pinus*** forests (Figure 15) and ***Platanus orientalis*** (Figure 16) alluvial forests of Turkey. Dia and Not (1991) considered it mesophytic. Papp *et al*. (2012, 2013) reported it "at" the stream, but also found it on bark of the beech (***Fagus***; Figure 18), on exposed as well as shaded siliceous rock, in limestone grassland, and on decaying wood. Papp and Erzberger (2007) similarly found it on bark of ***Salix***, as well as ***Fagus*** bark (Figure 17) in eastern Serbia. Dragićević *et al*. (2007) fount ***P. cordaeana*** on the bark of a decaying tree in the ***Abies-Fagus*** forest (Figure 19) of Montenegro.

Figure 15. ***Pinus pinea*** in Spain, the type of forest where ***Porella cordaeana*** can occur as an epiphyte in Mediterranean areas. Photo by Ori Fragman-Sapir, Board of Trustees, RBG Kew, through Creative Commons.

Figure 16. ***Platanus orientalis*** forest, the type of forest where ***Porella cordaeana*** can occur as an epiphyte in Turkey. Photo by Grecomara, through Creative Commons.

Figure 17. ***Salix pentandra***, where one can find ***Porella cordaeana*** on the bark in Serbia. Photo by MPF, through Creative Commons.

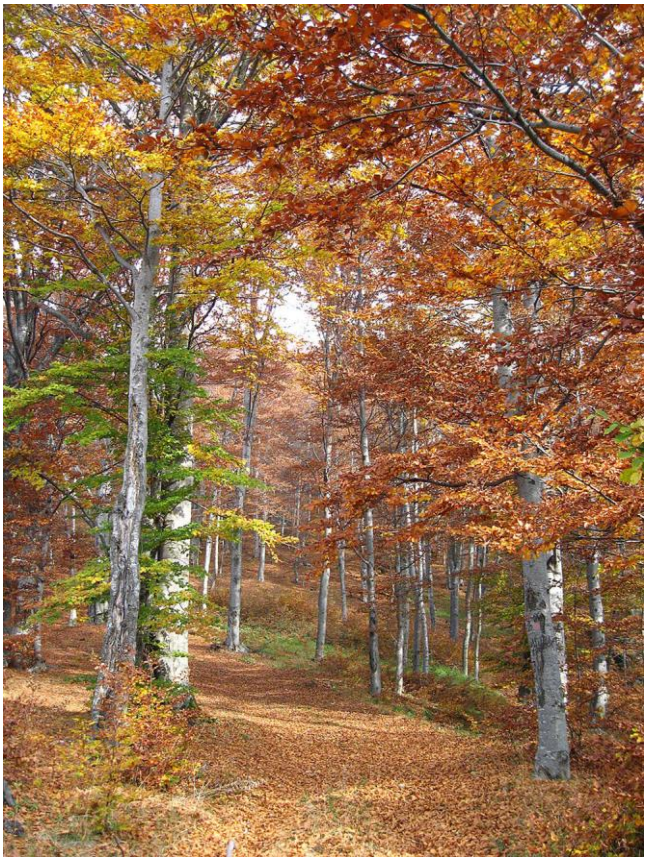

Figure 18. ***Fagus*** forest in Serbia, where one can find ***Porella cordaeana*** on the bark. Photo by Vladimir Pecikoza, through Creative Commons.

Figure 19. ***Abies bornmuelleriana***, ***Fagus orientalis***, and ***Populus tremula*** forest in Turkey, similar to the ***Abies-Fagus*** forest in Montenegro where one can find ***Porella cordaeana***. Photo by Marijn van den Brink, with permission.

Porella cordaeana (Figure 2-Figure 6) can also occur on soil, as observed by Campisi *et al*. (2008) in southern Italy. These occurred on slopes at 1400-1500 m asl. Similarly, in the Central Pyrenees of Spain and France, Casas and Barrón (2003) found this among the species on the humid soils of the forest, often associated with decomposed substrates. They considered the moisture and acidic conditions of the decomposing substrate to be suitable for these **saprolignous** (inhabiting dead wood) species. Piippo and Norris (1996) found it to be rare on logs and soil in California, USA.

In Louisiana, USA, ***Porella cordaeana*** (Figure 2-Figure 6) occupies cypress knees (indicative of a wet habitat), exposed roots, and small bushes and tree bases in swampy forests (Correll & Correll 1941). Vitt *et al*. (1973) found ***Porella cordaeana*** growing as epiphylls in the ***Thuja plicata*** forests (Figure 20) of western British Columbia, Canada.

Figure 20. ***Thuja plicata*** forest where one might find ***Porella cordaeana*** growing as an epiphyll. Photo by Crusier, through Creative Commons.

In Serbia and Yugoslavia, Sabovljević and Cvetić (2003) found that ***Porella cordaeana*** (Figure 2-Figure 6) occurs not only on roots and soil, but at tree bases by streams. Bijlsma *et al*. (2010) found it on the base of two poplars (***Populus***; Figure 18) along the river in The Netherlands.

In British Columbia, Canada, Schofield (1988) concluded that ***Porella cordaeana*** (Figure 2-Figure 6) is primarily restricted to areas with high precipitation, thus seemingly continuing its aquatic tolerances into its terrestrial habitats. As already noted, Kürschner (1999) considered it to be an indicator of better moisture conditions in the ***Pinus*** (Figure 15) and ***Platanus orientalis*** (Figure 16) forests in Turkey.

In northern Europe, Nordén *et al*. (2007) considered ***Porella cordaeana*** to be a **Signal species**. These are predominantly cryptogamic species that indicate Woodland Key Habitats. They signal the potential of finding **red-listed** (may be becoming extinct) species. Nordén and coworkers found that Signal species may be more useful for finding relatively valuable sites in a matrix of production forest. They furthermore concluded that Signal species can be useful surrogates for total cryptogam species richness.

Despite the commonness of the genus ***Porella*** on Madeira Island, the populations of ***Porella cordaeana*** (Figure 2-Figure 6) are small and fragile (Fontinha *et al*. 2010). ***Porella cordaeana*** is the rarest species in the genus there, being restricted to the central higher peaks of Madeira Island (mostly 1750-1800 m asl), where it occurs on rocks and stone walls in sheltered habitats. On Madeira in the Canary Islands, it occurs on wet volcanic rocks

(Ekstein 2010). In central Spain, it occurs on slopes and rocks that are near water (Elías *et al*. 2006). Gökler (1998) found it on stones by water in Turkey. In Greece, it occurs, but rarely, on moist rocks (Blockeel 2017). In the Lapland Nature Reserve in Murmansk Province, Russia, Borovichev and Koroleva (2015) found that it occurred mostly on stones and fine-grained soils.

Blockeel (1991) found ***Porella cordaeana*** (Figure 2-Figure 6) on limestone in the ***Abies cephalonica*** (Figure 21) forest. In Serbia and Montenegro, Papp *et al*. (2004) found it on limestone rock. But where more acidic rocks are available, it can inhabit them as well. Papp and Erzberger (2005) found it on soil and limestone rock, but also on siliceous stones in southwest Serbia. Papp *et al*. (2006a) found ***Porella cordaeana*** on both limestone rock and sandstone rock. These included rock crevices and wet sandstone (Papp & Erzberger 2007). Blockeel (2003) likewise found it in rock crevices as well as shaded boulders on a steep bank. In addition to limestone rock, it occurs in limestone grassland in Croatia (Papp *et al*. 2013).

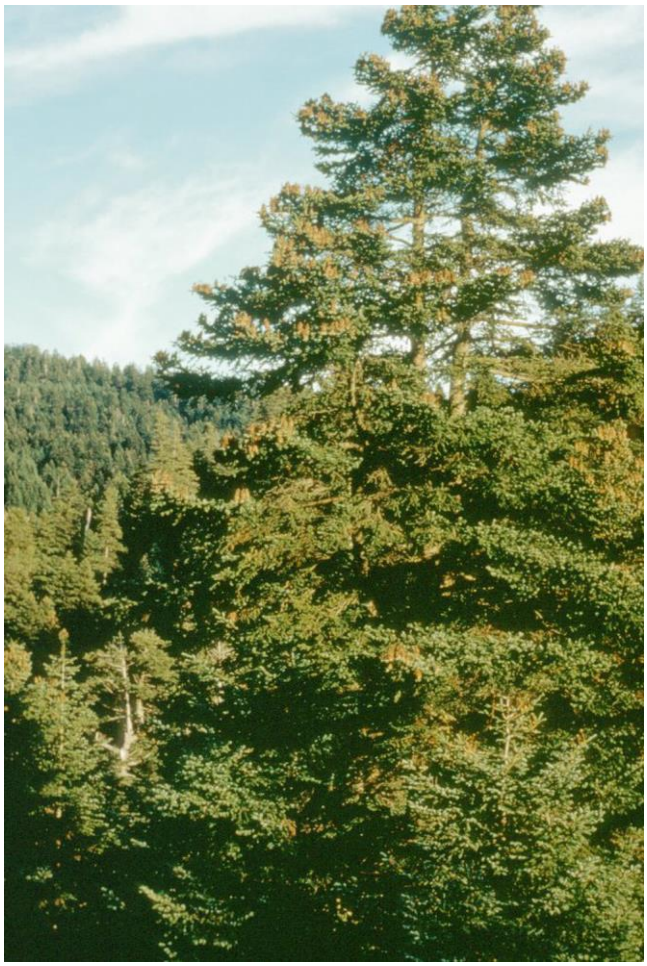

Figure 21. ***Abies cephalonica***, a forest type where ***Porella cordaeana*** can be found on limestone. Photo by W. H. Hodge, through Creative Commons.

As in several other studies, in Alaska Schofield *et al*. (2002) found ***Porella cordaeana*** (Figure 2-Figure 6) on shaded rock faces at lower elevations. Light does not seem to be an issue, as the species occurs on both exposed and shaded siliceous rock in Serbia (Papp *et al*. 2012). Furthermore, it seems to have a wide moisture tolerance as well (Figure 22-Figure 23) (Piippo & Norris 1996). It occurs on boulders and outcrops in both dry areas and along rivers. Sager and Wilson (2009) likewise found it in a semi-arid habitat in the Santa Monica Mountains, California, USA. In these locations, it required a suitable habitat that occupied at least 1 m^2.

Figure 22. ***Porella cordaeana*** in a drying condition. Photo by Jiří Kameníček, with permission.

Figure 23. ***Porella cordaeana***, showing underleaves and lobes in dry state. Photo by Jiří Kameníček, with permission.

Adaptations

Porella cordaeana (Figure 2-Figure 6) forms loose **mats** or **wefts** (Figure 24) (Piippo & Norris 1996). Its size and color vary, depending on the habitat. In wet conditions it is usually dark green, but the color varies from green to light brown (Figure 24) (Clark 1953; Piippo & Norris 1996).

Reproduction

Porella cordaeana (Figure 2-Figure 6) is a **dioicous** species (Clark 1953; Piippo & Norris 1996). This presents a problem for sexual reproduction because sperm might have a long distance to travel to a female. Not only that, but in their examination of specimens from Alaska, Schofield *et al*. (2002) found all specimens to be **sterile** (having no sexual structures). Fontinha *et al*. (2010) found no sexual reproduction or vegetative propagation for this

species on Madeira Island, most likely contributing to its rarity there, despite the genus being the most frequent liverwort genus on the island. This lack of both specialized vegetative reproduction and sexual reproduction also most likely is the cause for the lack of morphological variation. Most, and perhaps all, of the populations on this island could be the result of fragmentation from a single clone. Nevertheless, Uedo was able to photograph it with dehiscing sporophytes (Figure 24-Figure 25) in Japan.

Figure 24. ***Porella cordaeana*** with capsules, showing both green and brown color forms and a weft life form. Photo by Ken-Ichi Ueda, through Creative Commons.

Figure 25. ***Porella cordaeana*** with open capsules. Photo by Ken-Ichi Ueda, through Creative Commons.

Role

We know that many of the leafy liverworts have a close association with nitrogen-fixing **Cyanobacteria**, especially with ***Nostoc*** (Figure 26) (Dalton & Chatfield 1985). In the western United States, such associations occur with ***Porella cordaeana***, but these are not as common or abundant as on other ***Porella*** species.

Fungal Interactions

Wang and Qiu (2006) found no references to mycorrhizal associations in ***Porella cordaeana*** (Figure 2-Figure 6).

Figure 26. ***Nostoc***, a potential nitrogen fixer on liverworts like ***Porella cordaeana***. Photo by Ralf Wagner, with permission.

Biochemistry

Porella cordaeana (Figure 2-Figure 6) has numerous oil bodies (Figure 27) in each leaf cell. These can contribute compounds that are antifungal or that discourage herbivory. In 1998 Asakawa described the species as having an odor that is "dried seaweed-mossy like." Noting that this species is tasteless, Asakawa *et al*. (2012) found that it has drimane sesquiterpenoids. Toyota *et al*. (1989) identified three new pinguisane-type sesquiterpenoids in ***P. cordaeana*** in American populations.

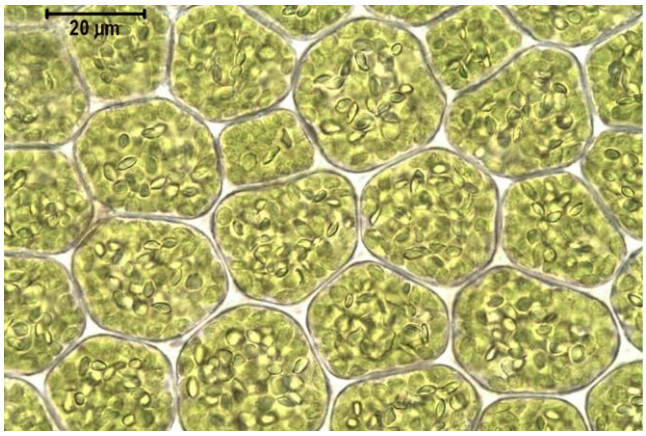

Figure 27. ***Porella cordaeana*** leaf cells with chloroplasts and oil bodies. Photo by Hugues Tinguy, with permission.

Bukvicki *et al*. (2012) identified a rich array of terpenoids in ***Porella cordaeana*** (Figure 2-Figure 6): sesquiterpene hydrocarbons (53.12%, 51.68%, 23.16%) and monoterpene hydrocarbons (22.83%, 18.90%, 23.36%), in methanol, ethanol, and ethyl acetate extracts, respectively. The dominant compounds in the extracts were β-phellandrene (15.54%, 13.66%, 12.10%) and β-caryophyllene (10.72%, 8.29%, 7.79%, respectively). All three extracts were highly active against tested yeast species; the activity against bacteria was somewhat less. The Gram-negative bacteria exhibited somewhat greater resistance than did the Gram-positive bacterium. The researchers expressed hope that these extracts may prove to be as potent and safer compared to the strong antibiotic cycloheximide. Furthermore, the ***P. cordaeana*** extracts exhibit significant antimicrobial potential against food

microorganisms. The researchers suggested that the high percentages of monoterpene and sesquiterpene hydrocarbons in ***P. cordaeana*** could be the agents responsible for its very effective antimicrobial activity.

Tan *et al*. (2017) demonstrated that ***Porella cordaeana*** (Figure 2-Figure 6) exhibits a weak anticancer activity against human breast cancer and human colorectal cancer. Tosun *et al*. (2013) found an inhibitory effect on **carrageenan-induced paw edema** (highly sensitive and reproducible test for nonsteroidal anti-inflammatory drugs), but the effect was rather small, ranging 25.4-29.4% inhibition. Its activity against p-benzoquinone-induced abdominal constriction animal models was move effective, ranging 27.6-41.1%. Nevertheless, ***P. cordaeana*** did not show any wound-healing effects (Tosun *et al*. 2016).

Porella pinnata (Figure 1, Figure 28-Figure 31)

Distribution

Porella pinnata (Figure 1, Figure 28-Figure 31) has a worldwide distribution (Garcia *et al*. 2010). In North America, it is abundant, and extends from Quebec (Evans 1916a), Nova Scotia, and Ontario in Canada (Evans 1916b), southward to Minnesota, Florida, Louisiana (Evans 1916b), and Arkansas (Redfearn 1964, 1979) in the USA, and Cuba in Central America (Evans 1916b). In Europe it is more restricted and rare, occurring in the British Isles and the western coast of France, with a possible occurrence in Portugal. Its presence in Portugal was confirmed in 2005 by Vieira *et al*. and again in 2010 by Garcia *et al*. In 2003, Ganeva and Natcheva added Bulgaria. Ekstein (2010) reported it from Madeira in the Canary Islands.

Figure 28. ***Porella pinnata***, a species mostly distributed in the Appalachian Deciduous Forest in eastern North America, but also occurs in Europe. Photo by Bob Klips, with permission.

Porella pinnata was also reported from China and South India, but when Bai *et al*. reviewed the Chinese ***Porella*** records, they found instead that these represented ***Porella chinensis***, ***P. densifolia***, ***P. gracillima***, ***P. japonica*** (Figure 32), ***P. oblongifolia***, and ***P. platyphylla*** (Figure 52-Figure 58), but not ***P. pinnata*** (Figure 28-Figure 31). Records from India may represent similar misidentifications and need to be confirmed.

Figure 29. ***Porella pinnata*** that is drying. Photo by David Holyoak, with permission.

Figure 30. ***Porella pinnata*** in a well-hydrated condition. Photo by Des Callaghan, with permission.

Figure 31. ***Porella pinnata*** showing a pale color. Photo by Hugues Tinguy, with permission.

Figure 32. ***Porella japonica*** ssp. ***appalachiana***; ***Porella japonica*** was once considered to be part of ***Porella pinnata***. Photo by Ken McFarland and Paul Davison, with permission.

Aquatic and Wet Habitats

Evans (1916a) reported ***Porella pinnata*** (Figure 1, Figure 28-Figure 31) from running water in Quebec. Brown (1929) found it on rocks in a streamlet in Nova Scotia. In Ontario, Cain and Fulford (1948) did not find it to be common, occurring on rocks or wood in small streams. It similarly occurs in rocky ravines in Connecticut, USA (Nichols 1916). Nichols (1918) considered ***Porella pinnata*** to be hydrophytic. Nichols (1935) found it attached to submerged rocks in Cliff Creek in the Huron Mountains of the Upper Peninsula of Michigan. Gilbert (1958) found ***Porella pinnata*** attached to submerged rocks in a stream in Iosco County, Michigan, USA, the first record for the Lower Peninsula of Michigan. Hall (1958) found it on moist sandstone adjacent to waterfalls in Ohio, where he considered it to be apparently rare. In Missouri, USA, Redfearn (1979) found it on shaded rocks in creeks and springs in the Ozark National Forest of Arkansas, USA. Solberg and Miller (1979) reported that it not only was frequent on rocks in a stream in North Carolina, but also occurred on trees along the stream. Conard (1946) reported it in a walled-in spring tributary, where it was plentiful along with ***Hygroamblystegium tenax*** (Figure 33).

Figure 33. ***Hygroamblystegium tenax***, a species that occurs with ***Porella pinnata*** in a walled-in spring tributary. Photo by Hermann Schachner, through Creative Commons.

Lanfear (1933) similarly found ***Porella pinnata*** (Figure 28-Figure 31) on emergent rocks in spring streams, where it was associated with ***Chiloscyphus polyanthos*** var. ***rivularis*** (Figure 34, ***C. pallescens*** var. ***fragilis*** (Figure 12, Figure 35), ***Riccardia multifida*** (Figure 36), ***Jubula hutchinsiae*** subsp. ***pennsylvanica*** (Figure 37), and ***Scapania*** (Figure 10), both above and below water. On the Appalachian Plateau in northern Georgia, USA, Carroll (1945) found it in abundance on submerged rocks and tree roots. In the Chapel Hill area of North Carolina, USA, Coker (1904) found it either immersed or on rocks close to the spray zone where humidity was high. In August in the Ozark springs of Missouri, USA, Drouet (1933) found dense growths of ***P. pinnata*** on rocks receiving spray from a spring.

Figure 34. ***Chiloscyphus polyanthos*** var. ***rivularis***, a species that associates with ***Porella pinnata*** in spring streams. Photo by Jean Faubert, with permission.

Figure 35. ***Chiloscyphus pallescens***, a species that associates with ***Porella pinnata*** in spring streams. Photo by Michael Lüth, with permission.

Figure 36. ***Riccardia multifida***, a species that associates with ***Porella pinnata*** in spring streams. Photo by Manju Nair, through Creative Commons.

Figure 37. ***Jubula hutchinsiae*** subsp. ***pennsylvanica***, a species that associates with ***Porella pinnata*** in spring streams. Photo by Wayne Lampa, through Creative Commons

In Walker Branch, Tennessee, USA, ***Porella pinnata*** (Figure 28-Figure 31) is the most abundant contributor to the biomass (Steinman & Boston 1993). It occurs in streams in the Great Smoky Mountains National Park, Kentucky, USA (Knapp & Lowe 2009). It is a common bryophyte on rocks and wood in seasonally inundated habitats in eastern North America, extending above and below the water line (Wood *et al*. 2016), and likewise occupies periodically inundated sites on river banks in Portugal (Garcia *et al*. 2010). Plitt (1908) found that in the Piedmont region of Maryland, USA, it was common on rocks that are frequently submerged. In the mid-order Middle Oconee River, Georgia, USA, it typically has a significantly higher density, organic matter, and invertebrate biomass than do the adjacent bare rock faces (Wood *et al*. 2016). Noble (2003) reported it as one of the dominant taxa on rocks in the east bank, center stream, and west bank of the riparian zone at Falls Branch Falls in Tennessee, USA.

Vieira *et al*. (2004, 2005) found that in northwest Portugal ***Porella pinnata*** (Figure 28-Figure 31) is seasonally emergent on stony streambanks and riparian tree roots along lowland rivers, including those that flow where agriculture and natural forest formations still co-exist. In the mountain stream locations it can be associated with ***Fontinalis squamosa*** (Figure 38). In some rivers it was frequently associated with ***Cinclidotus fontinaloides*** (Figure 39). Its distribution in Portugal was usually in medium to large rivers with moderate pollution, including river margins that were seasonally inundated. Ferreira *et al*. (2008) stated its habitat as simply rivers.

Figure 38. ***Fontinalis squamosa***, a species that is sometimes associated with ***Porella pinnata*** in Portugal. Photo by Janice Glime.

Figure 39. ***Cinclidotus fontinaloides***, a species that is sometimes associated with ***Porella pinnata*** in Portugal. Photo by Hermann Schachner, through Creative Commons.

Garcia *et al*. (2010) found that ***Porella pinnata*** (Figure 28-Figure 31) occurred along rivers with moderate water velocity and turbulence, where it experienced periodic inundation (Figure 40). These were typically well oxygenated waters in the middle and terminal portions of the river, but where the substrate was still rocky. In these reaches, the water typically has accumulated minerals from the soil, rocks, and leaf litter as it swelled onto the river banks. Garcia and coworkers have found it mostly in shaded conditions, created by overhanging vegetation or in granitic rock crevices, as well as on soil under the riparian

trees. Submerged populations of ***Porella pinnata*** (Figure 28-Figure 31) seem to prefer low conductivity with low concentrations of nitrogen and phosphorus.

Figure 40. ***Porella pinnata*** at high water line, ***Taxodium*** swamp near Tallahassee, Florida, USA. Photo by Janice Glime.

In North America, Howe (1897) likewise reported ***Porella pinnata*** (Figure 28-Figure 31) on the banks of shaded streams where it was subject to flooding (Figure 41). Barbour (1902) described its North American habitat as occurring at the base and on exposed roots of trees subject to flooding. Bakalin (2018) described its North American habitat as shaded stones and decaying wood along streams, where it occurred as a hygrophyte or hydrophyte, subject to submersion during high water. Evans (1916b) also considered it to occur most commonly on stones and logs both in the streams and on streambanks where it became submerged during part of the year. Although Sharp (1930) found it to be uncommon in southeastern Oklahoma, he also found it along stream margins on rocks and roots.

Figure 41. ***Porella pinnata*** habitat on roots in a flooding zone. Photo by Li Zhang, with permission.

Bosanquet (2010) described zonation along streambanks in the UK, reporting that ***Porella pinnata*** (Figure 28-Figure 31) dominates in a band along rivers and streams, with only occasional occurrences in the zone with ***Cinclidotus fontinaloides*** (Figure 39) and ***Schistidium rivulare*** (Figure 42) above it. In Bulgaria, Ganeva and Natcheva (2004) reported it from water sprayed rocks.

Figure 42. ***Schistidium rivulare***, a species that occurs in the streambank zone above the ***Porella pinnata*** zone in the UK. Photo by Janice Glime.

Vergouw and Siebel (1991) found it to be a "good acidophile" where it occurred in the water of the Chartreux source in Cahors, France.

Porella pinnata (Figure 28-Figure 31) appears to require nearness to water, thriving in places where it occasionally becomes submersed, but in most cases does not remain that way for long. Even in its terrestrial habitats, such as those growing on trees along Lake Superior in Michigan (Evans & Nichols 1935), are subject to high humidity and splash resulting from the activity of the lake. Similarly, Haynes (1927) reports it from river banks in Virginia, USA, but I have not found records of many truly terrestrial dry habitats. On trees, it can often exhibit a feather life form (Figure 43).

Figure 43. ***Porella pinnata***, showing its growth habit. Photo by Alan Cressler, with permission.

Adaptations

Hill *et al*. (2007) described ***Porella pinnata*** (Figure 28-Figure 31) as being attached to an aquatic substrate and trailing in the water, a description that suggests the **streamer** life form of Glime (1968). In terrestrial habitats, it can form shelves, a **feather** life form.

Howe (1897) described a southern USA form that dries out. When doing so, the leaves become closely wrapped around the stem or decurved; the branches are often sub-circinate (Figure 44-Figure 45). This could help to protect the liverwort from water loss, thus permitting it to live in somewhat drier habitats. This evidence suggests that it might be interesting to look for chemical evidence of cryptic species in ***Porella pinnata*** (Figure 28-Figure 31), separating the northern and southern populations.

Figure 44. ***Porella pinnata*** dry showing leaves rolling around the stem and sub-circinate branches. Photo by Li Zhang, with permission.

Figure 45. The same ***Porella pinnata*** wet. Photo by Li Zhang, with permission.

Reproduction

Porella pinnata (Figure 28-Figure 31) is **dioicous** (Howe 1897; So 2005; Garcia *et al*. 2010), with identifying male structures (Figure 46) unseen in Europe (Garcia *et al*. 2010). Garcia *et al*. (2010) reported that sporophytes (Figure 47-Figure 48) are unknown in Europe. Vieira *et al*. (n.d.) likewise reported that it was never found fertile in streams of northwest Portugal. Barbour (1902) reported that it is usually sterile in eastern North America. Howe (1897), however, reported that the "form" in the southeastern states (USA) produces sporophytes more commonly than the type, and that it grows in somewhat drier situations – more evidence there may be cryptic species. Evans (1916b), in his treatment of New England liverworts, may have shed some light on its sporophyte rarity; he reported that they only mature when the plants are exposed to air.

Figure 46. ***Porella pinnata*** with antheridial branch. Photo by Paul Davison, with permission.

Figure 47. ***Porella pinnata*** with capsules, near Tallahassee, FL. Photo by Janice Glime.

Figure 48. ***Porella pinnata*** with capsules. Photo by Janice Glime.

Guisen *et al*. (1996) examined the chromosomes of Chinese ***Porella pinnata*** (Figure 28-Figure 31) and determined n=8. This is the most common number for liverworts (see Volume 1, Chapter 2-7) and does not suggest any hybrid origin.

Fulford (1944) described vegetative reproduction in ***Porella pinnata*** (Figure 28-Figure 31). Plants of this species that had been kept in a moist chamber for a month became badly contaminated with a cottony fungus and filamentous green algae. The plants remained healthy and green, but showed no signs of regeneration. New cultures were set up in Petri dishes and supplied regularly with nutrient solution. After another month these plants showed numerous vegetative developments of bulging leaf cells and leafy shoots. These developing bulges were abundant, especially on older leaves, and were more common on the dorsal surface than on the ventral surface. These never formed on the leaf margins. When these brood bodies reached their approximate size, they formed rhizoids that branched at the tips and anchored the brood body to the leaf surface. A new leafy shoot developed from the tip of this globose brood body. Fulford provided a detailed description of the development of the new plant and noted that it was similar to development from spores in the genus.

Role

Roberts *et al*. (2007) monitored a forested headwater stream in eastern Tennessee, USA, to determine temporal differences in the stream metabolism. ***Porella pinnata*** (Figure 28-Figure 31) was the most abundant cover. Its cover increased during the study from 4.2% in May 2004 to 18.0% in January 2006.

In Walker Branch, Tennessee, ***Porella pinnata*** (Figure 28-Figure 31) is the most abundant bryophyte (Steinman & Boston 1993). The abundance peaked in late summer, then was reduced by a severe winter storm in the 13-month study. Stable substrate and water velocity were important in determining abundance, making bedrock steps and riffles good habitats. In this stream, the ***P. pinnata*** had significantly greater area-specific rates of photosynthesis and phosphorus uptake than did **periphyton** (freshwater organisms attached to plants) in all seasons. In the autumn, biomass-specific photosynthetic rates were also greater for ***P. pinnata***. But in winter and spring the periphyton on the cobble exceeded that of the liverwort. This was not the case on introduced cylinders. When translated to a year-round productivity and phosphorus uptake for the entire sampling area, the patchy distribution of the liverwort reduced its contribution, with rates similar to that of periphyton in late summer and autumn, but being exceeded by 3-5X greater rates by the periphyton in spring and early summer.

Steinman (1994) enriched Walker Branch with phosphorus to determine the effects on the dominant bryophyte, ***Porella pinnata*** (Figure 28-Figure 31). In a second-order reach of the stream, there was an N:P ratio of 3.5-1. The P:C ratio in ***P. pinnata*** was not significantly affected by the enrichment, but there was a significant increase in the P:N ratio. On the other hand, in Sludge Creek, which initially had an N:P ratio of 21.6:1 in the stream water, enrichment caused a significant increase in both the P:C and P:N ratios. To further complicate the results, the ***P. pinnata*** in Walker Branch actually had a significant decrease in phosphorus concentrations in its tissues after enrichment, whereas the same species in Sludge Creek had a significant increase in phosphorus in the enriched populations, but not in the controls. Steinman suggested that the increased P:N and P:C ratios could have resulted from either assimilation or adsorption.

Productivity in these streams increased by 15% following enrichment, but the increase was not significant (Steinman 1994). The periphyton did not increase significantly in either stream, but Steinman suggested that grazing by snails may have mitigated those results.

Bain and Proctor (1980) explored the requirement of aquatic bryophytes for free CO_2 for its carbon source. Results for ***Porella pinnata*** (Figure 28-Figure 31) were puzzling. Most of the species reached their photosynthetic compensation points at around *p*H 8.0-9.0. ***Anthoceros punctatus*** (Figure 49), now known to use the pyrenoid as a CO_2-concentrating mechanism, reached 9.5. ***Porella pinnata*** showed a similar, but less pronounced, anomaly. The researchers considered the ability to use bicarbonate, present in water instead of CO_2 at higher *p*H levels like this, was an unlikely source of CO_2 for the ***P. pinnata***. I am waiting for a micro *p*H probe that can measure the *p*H at the leaf cell surface. My hypothesis is that the bryophytes, possibly through cation exchange, lower the *p*H at the cell surface. This could permit the bicarbonate to convert to CO_2 for cellular uptake.

Figure 49. ***Anthoceros punctatus***, a species with pyrenoids and a high CO_2 compensation point. Photo by Jonathan Sleath, with permission.

Mulholland *et al*. (2000a) found the highest rates of ammonium uptake per unit area in a forest stream were accomplished by ***Porella pinnata*** (Figure 28-Figure 31), decomposing leaves, and fine benthic organic matter. The epilithon had the highest N uptake per unit biomass N. The ***Porella pinnata*** covered 19.1% of the stream, making it a major contributor to the nitrogen dynamics.

Wood *et al*. (2016) have demonstrated higher biomass and density of macroinvertebrates and greater organic matter content in patches of ***Porella pinnata*** (Figure 28-Figure 31) than that found on adjacent bare rocks in the Middle Oconee River, Georgia, USA. Average insect density was five times as great within the ***P. pinnata*** mats compared to the controls. Previously, these periodically submerged bryophytes were mostly ignored in aquatic food chains. In this case, they were submerged only when there was a substantial increase above the base flow level.

In cypress swamps, bryophytes can extend the oxygenated periods by growing on the cypress knees (***Taxodium distichum***; Figure 50) (Mehring *et al*. n.d.). ***Porella pinnata*** (Figure 28-Figure 31) is a common liverwort on these knees (Figure 1, Figure 50), and they generate enough oxygen to counteract significant portions of the oxygen used by the decomposing organic matter in the Little River in southern Georgia, USA. The highest levels of daily oxygen released by the liverworts occurred when the river was high enough to submerge them, while maximizing their light exposure. This provides a function for the cypress knees that adds to the theories that have been presented.

Figure 50. ***Porella pinnata*** on cypress (***Taxodium distichum***) knees. Photo by Paul Davison, with permission.

The role of bryophytes as a food source has been ignored until relatively recently. In the aquatic habitat, they not only are eaten themselves, but bryophytes can trap large quantities of detrital particles and provide homes for bacteria, fungi, protozoa, and numerous small invertebrates. Mulholland *et al*. (2000b) found that ***Porella pinnata*** (Figure 28-Figure 31) had similar values of labelled N to those of the epilithon. They suggested that the ***P. pinnata*** could be a possible food source for both ***Elimia*** (freshwater snail; Figure 51) and mayflies.

Figure 51. ***Elimia***, a snail that lives with ***Porella pinnata*** and could find food there. Photo through Creative Commons.

Fungal Interactions

Wang and Qiu (2006) were unable to find any records of mycorrhizal associations with ***Porella pinnata*** (Figure 28-Figure 31).

Biochemistry

The oil bodies in this species are small, but numerous (So 2005). With its widespread distribution and abundance in some locations, and its size extending up to 30 cm long (So 2005), it is surprising that it lacks biochemical studies to elaborate on what secondary compounds might be found in these oil bodies.

Porella platyphylla (Figure 52-Figure 58)

(syn. = *Madotheca platyphylla*; Figure 52-Figure 58)

Porella platyphylla is widespread in the temperate regions, especially in the deciduous forests, and reaching southward into the subtropics (Schuster 1980).

Figure 52. ***Porella platyphylla***, a widespread temperate leafy liverwort. Photo by Evan Raskin, through Creative Commons.

Figure 53. ***Porella platyphylla***, hydrated. Photo by Hugues Tinguy, with permission.

Figure 54. ***Porella platyphylla***. Photo by Malcolm Storey, DiscoverLife, with online permission.

Figure 55. ***Porella platyphylla*** showing hydrated form. Photo courtesy of Betsy St. Pierre.

Figure 56. ***Porella platyphylla*** dorsal surface. Photo by Paul Davison, with permission.

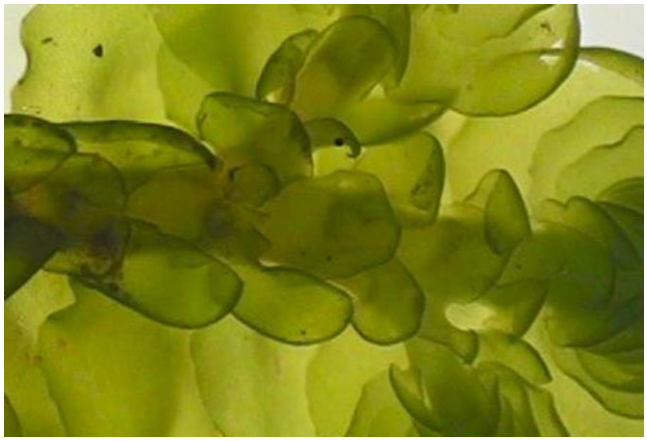

Figure 57. ***Porella platyphylla*** underleaves and lobes. Photo by Paul Davison, with permission.

Figure 58. ***Porella platyphylla*** wet. Photo by Tim Waters, through Creative Commons.

The status of ***Porella platyphylla*** (Figure 52-Figure 58) and that of ***P. platyphylloidea*** (Figure 91-Figure 93) has been debated for a long time. Evans (1916c) considered the double spirals of the elaters to separate them, with ***P. platyphylloidea*** apparently lacking elaters with two spirals throughout its entire length, whereas at least some are present in ***P. platyphylla***. With this understanding, he reported ***P. platyphylloidea*** to be the commonest species of ***Porella*** in eastern North America.

Barbour (1902) considered the American plants to be the "form" ***Porella thuja***, but acknowledged that the European ***P. platyphylla*** (Figure 52-Figure 58) also occurs. ***Porella thuja*** is no longer recognized as a legitimate taxon (Söderström *et al*. 2016).

But Boisselier-Dubayle *et al*. (1998) argued that ***Porella platyphylloidea*** (Figure 91-Figure 93), while being reported Europe, had never been confirmed there. Instead, they considered it to be restricted to North America. Furthermore, they considered the often cited ***P. platyphylla*** (Figure 52-Figure 58) to be absent in North America.

Therrien *et al*. (1998) used isozyme and morphometric analysis to attempt to clarify these two taxa. Based on 11 loci, they identified three discrete genotypes. They found no variation within populations, but each of the genotypes exhibited variation among populations. Each genotype possessed several unique alleles. Unfortunately, the

morphological characters for these two species had a continuous pattern rather than defining distinct entities. Furthermore, the two species type specimens fell into the same cluster. Unlike the report of Evans (1916c), they found that both single and double spiralled elaters occurred within identical genotypes. Therrien and coworkers concluded that instead of two species, ***P. platyphylla*** (Figure 52-Figure 58) and ***P. platyphylloidea*** (Figure 91-Figure 93) represented cryptic species of ***Porella platyphylla***.

Like Therrien *et al*. (1998), Hentschel *et al*. (2007) found that ***P. platyphylla*** (Figure 52-Figure 58) split into a European and a North American clade, with one tested North American population belonging with the European clade. Heinrichs *et al*. (2011) suggest that the North American ***P. platyphylloidea*** (Figure 91-Figure 93) might be an ancient hybrid between ***P. cordaeana*** (Figure 3-Figure 6) and ***P. platyphylla*** *s.str*. Based on their cladistic analysis, they likewise concluded that ***P. platyphylla*** *s.l.* has three main clades, with the nuclear and chloroplast loci providing incongruent phylogenetic signals. They considered ***P. platyphylla*** *s.l.* to consist of a North American main clade and a European clade, with the latter clade also present in North America and Asia. Blisard and Kleinman (2012) supported the conclusion that these two were cryptic species that cannot be separated based on morphological characters, requiring molecular studies for identification.

To illustrate the difficulty in defining this species, Wyatt *et al*. (2005) reported that ***Porella platyphylla*** (Figure 52-Figure 58) has high levels of genetic variation, contrasting with earlier studies suggesting that liverworts have little genetic variation. They found 26 multilocus genotypes and more than 80% of the enzyme loci to be polymorphic within a single population from southwestern North Carolina.

If I have not convinced you that ***P. platyphylloidea*** (Figure 91-Figure 93) is merely a cryptic species within ***P. platyphylla*** (Figure 52-Figure 58), you are not alone. In their 2016 list of accepted names of liverworts, Söderström *et al*. have listed both species as accepted.

Distribution

Shaw (2001) considered ***Porella platyphylla*** (Figure 52-Figure 58) to be widespread in North America and Europe. Bakalin (2018) listed ***Porella platyphylla*** from Alaska and British Columbia in the west, south to Texas, and in the east from Nova Scotia south to Florida in North America, and in Eurasia. Önder and Özenoğlu (2019) considered it to be the most common liverwort species in the Turkish flora, occupying a wide range of habitats (Özenoğlu & Gökler 2002; Ezer *et al*. 2009). Shaheen and Srivastava (1986) reported it from the western Himalayas in India.

Aquatic and Wet Habitats

Porella polyphylla (Figure 52-Figure 58) is not an aquatic bryophyte, but it is often associated with wet habitats. Dhien (1978) found it in intermittent rivers. But streambanks are more common than instream habitats for it. Önder and Özenoğlu (2019) found it on streambanks in Turkey; Özenoğlu and Gökler (2002) reported it from rocks and bark near a stream in Turkey.

Ezer *et al*. (2009) called ***Porella platyphylla*** (Figure 52-Figure 58) a **cortico-saxicolous** species in Turkey, a testimony to its broad niche. Özenoğlu and Gökler (2002) listed sheltered tree boles, walls, rocks, soil, stones on banks, rocks, and tree bark (Figure 59-Figure 60) as the habitats for ***Porella platyphylla*** in Turkey. Some of these were near streams, but the species was not restricted to nearness to streams.

Figure 59. ***Porella platyphylla*** with lichen on bark. Photo by Tim Waters through Creative Commons.

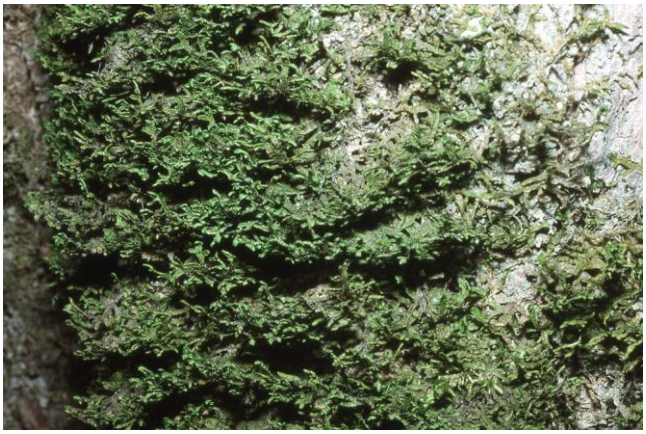

Figure 60. ***Porella platyphylla*** from the mid region of a tree trunk in the Hiawatha National Forest, Michigan, USA. Photo by Janice Glime.

A number of researchers (Barbour 1902; Plitt 1908; Özenoğlu & Gökler 2002; Heinrichs *et al*. 2011) have reported populations of ***Porella platyphylla*** (Figure 52-Figure 58) as sometimes occurring on rocks (Figure 61-Figure 63). Haynes (1927) considered damp rocks to be among its substrates in Virginia, USA. Redfearn (1964, 1979), in the Interior Highlands of North America in Arkansas, USA, found ***Porella platyphylla*** on shaded vertical limestone. Bakalin (2018) attributed its North American habitat to both dry and wet shaded rocks. Gustafsson *et al*. (1992) found it on shaded cliffs in Sweden. Özenoğlu and Gökler (2002) reported it from rocks, walls, stones on stream and river banks, and canyon rocks in Turkey.

Figure 61. ***Porella platyphylla*** on boulder. Photo by Owen C. Larkin, through Creative Commons.

Figure 62. ***Porella platyphylla*** on rock trail at Lost River Caverns, Poconos, Pennsylvania, USA. Photo by Janice Glime.

Callaghan and Ashton (2008) considered ***Porella platyphylla*** (Figure 52-Figure 58) to be a calciphile. Osadowski (2010) found it on calcareous tufas in Western Pomerania, noting that it prefers high concentrations of calcium. Proctor (2010) likewise found it on limestone rock.

Figure 63. ***Porella platyphylla*** on rock, Czech Republic. Photo by Vita Plasek, with permission.

Adaptations

Evans (1899) found ***Porella platyphylla*** forming pure **mats** (Figure 64) in the northeastern USA. The young plants grew prostate and adhered to the substrate. As they aged, they would form considerable mat size and hide the decayed portions under them (Figure 64). These often take on a **feather** life form on vertical substrata (Figure 65-Figure 66).

Figure 64. ***Porella platyphylla*** forming a **pure** mat on bark. Photo by Janice Glime.

Figure 65. ***Porella platyphylla*** forming shelves on tree in the Upper Peninsula of Michigan, USA, a **feather** life form. Photo by Janice Glime.

Figure 66. ***Porella platyphylla*** forming shelves, a **feather** life form. Photo by Suzanne Cadwell, through Creative Commons.

Proctor (2000a) defined desiccation-tolerant bryophytes as photosynthesizing and growing as long as water is readily available, but suspending metabolism when it is not. These, including ***Porella platyphylla*** (Figure 52-Figure 58), are typically ectohydric (moving water in external capillary spaces). The physical structure (Figure 67) of the bryophyte contributes to the rate at which a bryophyte loses water in drying conditions. ***Porella platyphylla***, along with the aquatic ***Palustriella commutata*** (Figure 68), required only five hours to reach an air-dried state (Deltoro *et al*. 1998). The other bryophytes in the experiments typically took 5-16.7 hours.

Figure 67. ***Porella platyphylla*** ventral side showing underleaves; the curling edges suggest it is drying. Photo by Hermann Schachner, through Creative Commons.

Figure 68. ***Palustriella commutata***, a species that, like ***Porella platyphylla***, dries in air in only 5 hours. Photo by Hermann Schachner, through Creative Commons.

Gupta (1977a) used ***Porella platyphylla*** (Figure 52-Figure 58) among the species in a study of photosynthesis and leakage in bryophytes. Decrease in photosynthesis is an indicator of desiccation injury. In this study, all the species reached the highest level of cell leakage in the first 2 minutes of rewetting, then slowed down. This reduction seems to be due to the reassemblage of the cell membranes or to a rapid decrease of solutes in damaged cells. Viable cells are able to reabsorb much of this lost leachate upon rehydration. Gupta (1977b) considered ***Porella platyphylla*** to be drought resistant, compared to the non-resistant ***Scapania undulata*** (Figure 10). In both species the relative water content dropped steadily for up to 50 hours at 96.5% relative humidity, then remained unchanged. Photosynthesis actually peaked after two hours of desiccation in ***P. platyphylla*** and six hours in ***Scapania undulata***. Proctor (2010) found wide variation in the half-recovery time, ranging from a few tens of seconds in ***Syntrichia ruralis*** (a xerophyte; Figure 69) and ***Porella platyphylla*** to an hour or more in **pteridophytes** (mostly club mosses and ferns).

Figure 69. ***Syntrichia ruralis***, a xerophytic species that has a half-recovery time from desiccation of several minutes, similar to that of ***Porella platyphylla***. Photo by Hermann Schachner, through Creative Commons.

Hinshiri and Proctor (1971) found that recovery from desiccation up to 60 days is normally completed within 3-4 hours upon rehydration. Longer periods of desiccation

cause an initial negative net assimilation, but it becomes positive as it increases progressively for several days. They attributed this to initial enhanced respiration and delayed recovery. ***Porella platyphylla*** (Figure 52-Figure 58) is desiccation tolerant (Figure 70) (Marschall & Proctor 1999; Marschall 2017). As such, it does not suffer photooxidative damage due to the coexistence of zeaxanthin-dependent **NPQ** (nonphotochemical chlorophyll fluorescence quenching) mechanisms and a desiccation-induced thermal energy dissipation.

Figure 70. ***Porella platyphylla*** dry. Photo courtesy of Betsy St. Pierre.

Proctor (2000b) found that ***Porella platyphylla*** (Figure 52-Figure 58) did not recover as rapidly as the xerophytic ***Syntrichia ruralis*** (Figure 69) or ***Grimmia pulvinata*** (Figure 71). In fact, although ***Porella platyphylla*** is among the more tolerant bryophytes, it had the worst performance at the lowest water potentials (Proctor 2001). But Proctor (2003) modified that description to call it moderately desiccation tolerant and found that it survived best in the highest humidity (74% r.h.) used. These experiments suggest that this species is adapted to the intermittent water conditions of streambanks and inundation areas as well as mesic forests, but not in conditions that remain dry for long periods of time.

Figure 71. ***Grimmia pulvinata***, a xerophyte that recovers more quickly from desiccation than does ***Porella platyphylla***. Photo by Darkone, through Creative Commons.

It is important to examine the effect of temperature on desiccation survival as our planet continues to warm. Hearnshaw and Proctor (1982) experimented with seven bryophytes kept dry in a range of 20-100ºC. The differences in chlorophyll content were largely in the time required for recovery. Survival times ranged from a few minutes or less for 50% loss of chlorophyll at 100ºC to weeks or even months at 20º and 37º for the more resistant species. ***Porella platyphylla*** (Figure 52-Figure 58) lost 50% of its chlorophyll content at 37ºC after 42.5 days, but at 60ºC, the same damage occurred in only 19.7 hours. This is consistent with the finding that the thylakoid membranes of the chloroplasts and the processes of PSII are sensitive to water stress (Marschall *et al*. 1998a). The species also survives freezing temperatures in winter (Figure 72-Figure 73). Because of its vertical position, snow cannot cover it completely to protect it, thus causing it to experience even sub-freezing temperatures.

Figure 72. ***Porella platyphylla*** with snow. Photo by Gergely Pápay, through Creative Commons.

Figure 73. ***Porella platyphylla*** with snow on bark in Europe. Photo by Michael Lüth, with permission.

Marschall *et al*. (1998a) demonstrated that drought in ***Porella platyphylla*** (Figure 52-Figure 58) leads to an accumulation of high-molecular-weight fructan. Marschall *et al*. (1998b) reported that the major soluble carbohydrates in ***Porella platyphylla*** (Figure 52-Figure 58) are sucrose and a homologous series of fructans (see also Marschall 2010). Adding glucose and fructose to the medium did not

affect the composition of the soluble carbohydrate pool, but sucrose caused the fructan pool to increase and inhibited photosynthetic oxygen evolution and respiration. In the dark, the fructan pool was amplified, and desiccation increased the proportion of the high-molecular-weight fructan. Marschall (2010) found that adding glucose, fructose, and sucrose to the medium, in light or dark, cause the down regulation of photosynthetic activity. Dark "starvation" of these sugars for one week does not cause a significant decrease in photosynthetic capacity.

Marschall (1998) found that in ***Porella platyphylla*** (Figure 52-Figure 58) the nitrogen reductase activity remained relatively constant, but at a low level, in the light, but increased in the dark. On the other hand, nitrogen reductase activity during the first hour of rehydration in the xerophyte ***Syntrichia ruralis*** (Figure 69) decreased considerably in both dark and light, although to a greater degree in the light. The nitrogen reductase activity of ***Porella platyphylla*** decreased to a low level after 4 days in the dark, but increased when sucrose was added to the medium. Thus, the behavior of ***Porella platyphylla*** is somewhat different from that of the xerophyte ***Syntrichia ruralis***.

Marschall and Proctor (1999) suggest that desiccation tolerance in ***Porella platyphylla*** (Figure 52-Figure 58) is essentially constitutive, *i.e.* always there and not requiring induction. Recovery of photoprotection in light is mostly complete within 24 hours. This strategy should work well for this species that grows epiphytically and thus experiences frequent wetting and drying cycles.

Sütő and Marschall (2016) looked for cell morphology changes in ***Porella platyphylla*** (Figure 52-Figure 58) following various abiotic stresses. They identified suitable stains for the best viewing of these changes, finding neutral red at *p*H 7.6 to be the best. Strong osmotic treatment (1 M KSCN) caused the central vacuole to fragment into small pieces, then rupture in 10 minutes. This osmotic shock caused irreversible damage to the chloroplasts. Oil bodies were the most resistant structures against the stresses tested (freezing, natural drying, heat, and osmotic stress). When plants were cold-hardened for 5 months, they were able to regenerate both cell structure and metabolism within 24 hours after a 24-hour natural drying regime.

Ezer *et al*. (2010) found that the highest chlorophyll *a*/*b* ratio occurred in the non-aquatic species, including ***Porella platyphylla*** (Figure 52-Figure 58), compared to such aquatic species as ***Cinclidotus aquaticus*** (Figure 74) and ***Platyhypnidium riparioides*** (Figure 8).

Aydin (2020) looked at free radical scavenging activities in ***Porella platyphylla*** (Figure 52-Figure 58). He found that the moss ***Dicranum scoparium*** (Figure 75) has significantly more scavenging activity than does ***P. platyphylla***. He noted that there is a strong relationship between phenolic content in methanol extracts and the DPPH (1, 1-diphenyl-2-picrylhydrazyl) radical scavenging efficiency. Fatty acid content was higher in ***P. platyphylla*** than in ***D. scoparium*** except for α-linolenic acid.

Reproduction

Porella platyphylla (Figure 52-Figure 58) is **dioicous** (Evans 1899; Heinrichs *et al*. 2011), with male plants that are more slender than the female plants (Evans 1899). Andrews (1908) described an abnormal archegonium in the species and observed branched elaters in the species. Manning (1914) observed similar abnormal archegonia and described a sporophyte surrounded by a cluster of broad leaves. Shaheen and Srivastava (1986) described the spores of the species using SEM.

Figure 74. ***Cinclidotus aquaticus***, a species with a lower chlorophyll *a*:*b* ratio than that of ***Porella platyphylla***. Photo by Hermann Schachner, through Creative Commons.

Figure 75. ***Dicranum scoparium***, a moss species with less fatty acid content than that of ***Porella platyphylla***, but significantly more free radical scavenging activity. Photo by Richard Orr, with permission.

Interactions

Dudka and Romanenko (2006) enumerated **Myxomycetes** and other organisms associated with ***Porella platyphylla*** (Figure 52-Figure 58) in Crimea. These included ***Arcyria cinerea*** (Figure 76), ***Echinostelium arboreum*** (Figure 77), ***E. minutum*** (Figure 78), ***Macbrideola cornea*** (Figure 79), ***Perichaena vermicularis*** (Figure 80), ***Physarum cinereum*** (Figure 81), and ***Symphytocarpus impexus*** (Figure 82-Figure 83). On the other hand, Wang and Qiu (2006) found no publications on mycorrhizal associations with ***Porella polyphylla***.

Figure 76. ***Arcyria cinerea***, a known associate of ***Porella platyphylla***. Photo by George Barron, with permission.

Figure 77. ***Echinostelium arboreum***, a species known to associate with ***Porella platyphylla***, with two sporocarps showing the persistent shiny peridium. Photo through Creative Commons.

Figure 78. ***Echinostelium minutum***, a species known to associate with ***Porella platyphylla***. Photo by Carlos de Mier and Carlos Lado, through Creative Commons.

Figure 79. ***Macbrideola cornea***, a species known to associate with ***Porella platyphylla***. Photo by Shirokikh125.

Figure 80. ***Perichaena vermicularis***, a species known to associate with ***Porella platyphylla***. Photo by Carlos de Mier and Carlos Lado, through Creative Commons.

Figure 81. ***Physarum cinereum***, a species known to associate with ***Porella platyphylla***. Photo by Bjorn S., though Creative Commons.

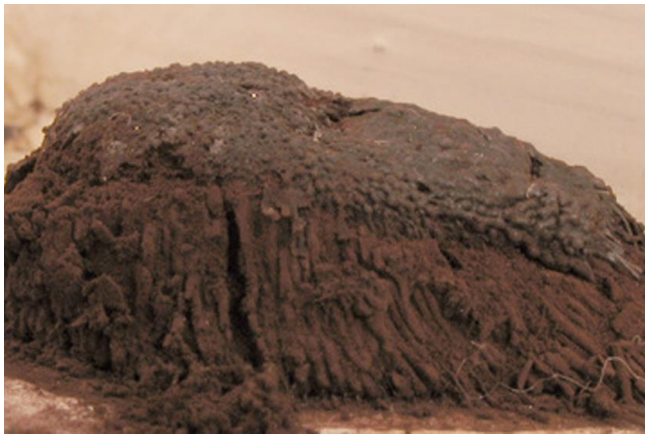

Figure 82. ***Symphytocarpus impexus***, a species known to associate with ***Porella platyphylla***. Photo from Eumycetozoan Project, www.discoverlife.org, with online permission.

Figure 83. ***Symphytocarpus impexus***, a species known to associate with ***Porella platyphylla***, showing capillitium and spores. Photo from Eumycetozoan Project, www.discoverlife.org, with online permission.

Smith (2000) contended that most plants in natural ecosystems form mycorrhizal relationships that facilitate acquisition of nutrients. Döbbeler (2004) reported that Ascomata were unknown on epiphytic ***Porella platyphylla*** (Figure 52-Figure 58) and several other epiphytes. However, he found ***Bryocentria metzgeriae*** (Figure 84) on this liverwort. This species regularly perforates the leaves of ***P. platyphylla***. The Ascomata develop on the protected lower side of the leaf and grow through the single layer of cells so that the ostiolar region is on the side away from the substrate. Occasionally single perithecia may develop in the perianths. Some leaves of ***Porella platyphylla*** may have several fruiting bodies of ***B. metzgeriae*** that do not perforate the leaves.

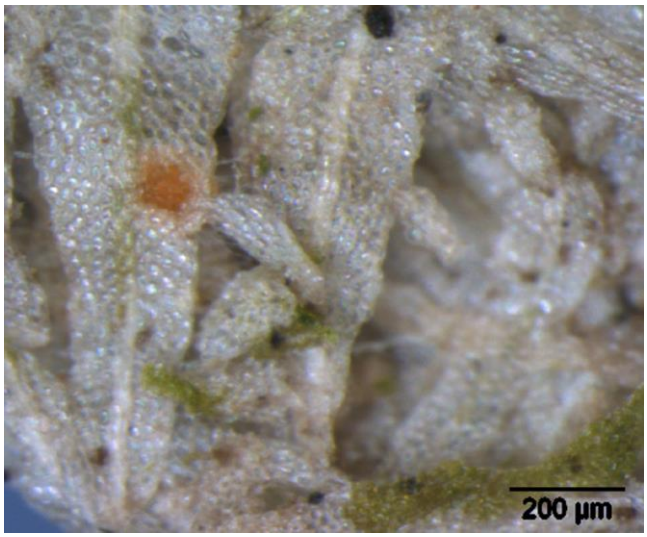

Figure 84. ***Bryocentria metzgeriae***, a species of **Ascomycetes** that penetrates leaves of ***Porella platyphylla***. Photo from Bold Systems, through Creative Commons.

Biochemistry

Schuster (1980) reported the oil bodies (Figure 85-Figure 86), a storage site for secondary compounds, to be minute to small. This can cause them to be difficult to notice (Figure 85-Figure 86).

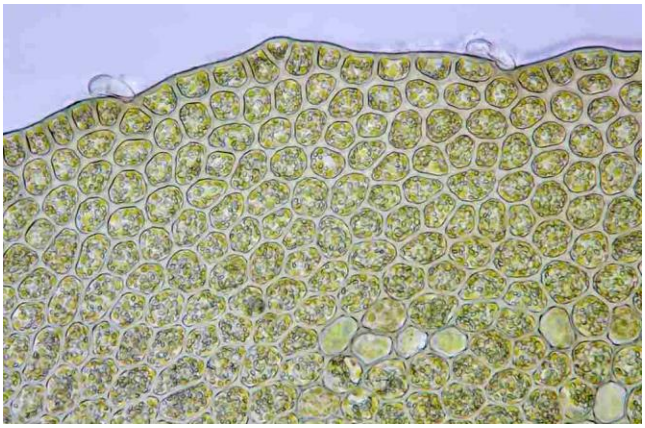

Figure 85. ***Porella platyphylla*** leaf cells showing numerous small oil bodies. Photo by Kristian Peters, with permission.

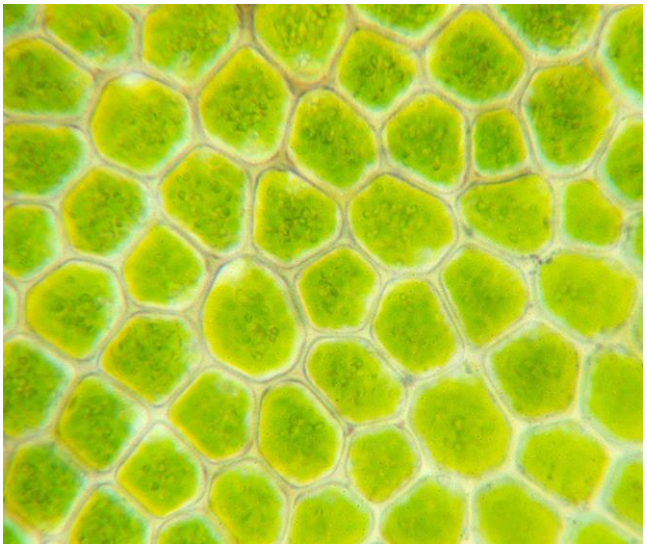

Figure 86. ***Porella platyphylla*** leaf cells with oil bodies not apparent. Photo by Malcolm Storey, with online permission.

Porella platyphylla (Figure 52-Figure 58) has a variety of color forms (*e.g.* Figure 87), but the cause of these color changes or forms does not seem to be documented. Nilsson (1969) described pigments in ***Porella platyphylla***, identifying the metabolite isovitexin-7-glucoside, a C-glycosyl compound. Nilsson (1973) later identified apigenin-6,8-di-C-glycoside from the same species.

Figure 87. ***Porella platyphylla*** golden brown form. Photo by Bob Klips, with permission.

Although there seem to be few discussions of the morphological adaptations of ***Porella platyphylla*** (Figure 52-Figure 58), there have been a number of studies that have used it to study physiology and biochemistry in bryophytes. Suleiman *et al*. (1980) found that polyols are not the primary assimilatory products in ***Porella platyphylla***, and they suggested that differences in these products among bryophytes could serve in classifying them.

Perhaps the secondary compounds in ***Porella platyphylla*** (Figure 52-Figure 58) can account for the scarcity of reports of fungal relationships. Suire and Borgeois (1977) reported monoterpenes in this species. Ludwiczuk *et al*. (2011) identified monoterpenoids, sesquiterpenoids, diterpenoids, flavonoids, and steroids in this species. Asakawa *et al*. (1979) identified three new pinguisane-type sesquiterpenes. Extracts of this species inhibited fungal growth, but only at higher concentrations (15 µL) compared to effective doses of ***Anomodon viticulosus*** (Figure 88) and ***Cinclidotus fontinaloides*** (Figure 39) (5 µL) (Latinovic *et al*. 2019). Mycelial growth of several fungal species was affected.

Figure 88. ***Anomodon viticulosus***, a species that is more effective at inhibiting fungal growth than is ***Porella platyphylla***. Photo by Hermann Schachner, through Public Domain.

In their study, Haas *et al*. (1978) found that the external alkane content of ***Porella platyphylla*** (Figure 52-Figure 58) was only 22.5%, whereas in the moss ***Polytrichum commune*** (Figure 89) it was up to 44.8%. More work needs to be done to see if this explains the more waxy leaves of ***Polytrichum***.

In addition to the antifungal activity, extracts of ***Porella platyphylla*** (Figure 52-Figure 58) exhibited antimicrobial activity against some gram-positive bacteria (Beike *et al*. 2010). And they inhibited the germination of cress seeds by 30% and lettuce seeds by 40% (Frahm *et al*. 2012).

Many bryophytes have demonstrated medicinal properties. The wound healing ability of ***Sphagnum*** (Figure 90) is well known. However, Tosun *et al*. (2016) were unable to demonstrate any wound-healing potential in Turkish populations of ***Porella platyphylla*** (Figure 52-Figure 58), although other liverworts in the study did improve healing.

Figure 89. ***Polytrichum commune***, a species with twice the external alkane content of ***Porella platyphylla***. Photo by Kristian Peters, through Creative Commons.

Figure 90. ***Sphagnum*** sp., a genus known for its wound-healing properties. Photo by Janice Glime.

Porella platyphylloidea (Figure 91-Figure 93)

The genus ***Porella*** is known for its high phenotypic plasticity (Bischler *et al*. 2006). This is further compounded by the presence of more than one clone within a single colony. Whereas the genetic component can differ between cryptic species, the morphological characters often do not. Evans (1916c) separated them by double-spiraled elaters, but others demonstrated that these could occur in both. And even chemical testing with IKI does not separate ***Porella platyphylla*** (Figure 52-Figure 58) and ***P. platyphylloidea*** (Figure 91-Figure 93), with both turning purple (Piippo & Norris 1996). The confusing complex that includes ***P. platyphylla*** and ***P. platyphylloidea*** is discussed above under ***P. platyphylla***. For this chapter, it is probably best to think of the information as referring to ***Porella platyphylla/platyphylloidea***. I have kept them separate based on the authors' and photographers' perspectives, but at different points in time, the concepts of these two species have changed.

Figure 91. ***Porella platyphylloidea***, part of the complex of cryptic species. Photo by C. Chapman, through Creative Commons.

Distribution

Based on more recent understanding of the species, ***Porella platyphylloidea*** (Figure 91-Figure 93) occurs from Ontario and Quebec in eastern Canada, south to Florida, and in western North America from British Columbia south to New Mexico and Arizona, USA (Bakalin 2018). It also occurs in Europe.

Figure 92. ***Porella platyphylloidea***, a common species in North America and Europe. Photo by KHA, through Creative Commons.

Aquatic and Wet Habitats

Porella platyphylloidea (Figure 91-Figure 93) is usually not a true aquatic, but it is often associated with damp or wet habitats. It occurs in crevices or on the surface of drier cliffs in a ravine in Connecticut, USA (Nichols 1916). Nichols (1918) also found it on rock cliffs associated with streams on Cape Breton Island, Canada. Iltis (1950) reported it from a moist side of a rock in a stream in Virginia, USA.

Figure 93. ***Porella platyphylloidea*** dry. Photo by Wayne Lampa, through Creative Commons.

Tree bark is probably the most common habitat for ***Porella platyphylloidea*** (Figure 94) (*e.g.* Burnham 1919; Nichols 1922; Fulford 1934; Little 1936a, b; Conard 1940, 1946; Schuster & Patterson 1957; Ehrle & Coleman 1963, 1968; Vitt 1967; Gunderson 1971). But even this habitat is frequently in wet forests. Schuster (1980) considered ***Porella platyphylloidea*** (Figure 91-Figure 93) to be widely distributed on bark of deciduous trees (Figure 94), frequently as a pioneer. It occurs mostly in open woods. Bakalin (2018) described mostly terrestrial habitats for ***Porella platyphylloidea*** in North America, noting that these ranged from wet to dry even on bark. Among its terrestrial habitats, Alteri and Coleman (1965) found it on a dead yellow birch (***Betula alleghaniensis***; Figure 95) log in a swamp forest in New York, USA. Darlington (1938) reported it as most common at the bases of trees in damp woods in the Glen Lake area of Michigan, USA.

Figure 94. ***Porella platyphylloidea*** on bark, the most common substrate for this species. Photo by Jan-Peter Frahm, with permission.

Figure 95. ***Betula alleghaniensis***, a substrate for ***Porella platyphylloidea*** on a dead tree in a swamp in New York, USA. Photo by Joseph OBrien, through Creative Commons.

Adaptations

Porella platyphylloidea (Figure 91-Figure 93) can dry (Figure 96) and rehydrate, then begin photosynthesis and growth again. When it dries, its leaves roll under (Figure 97), making small chambers on the ventral side (Figure 98-Figure 99). We need experiments to see how this structure affects water conservation and water absorption. I would hypothesize that the small spaces take advantage of the adhesion and cohesion of water to hold water droplets. At the same time, the underleaves, lobes, and dorsal leaves combine to reduce surface area and thus reduce the rate of evaporation.

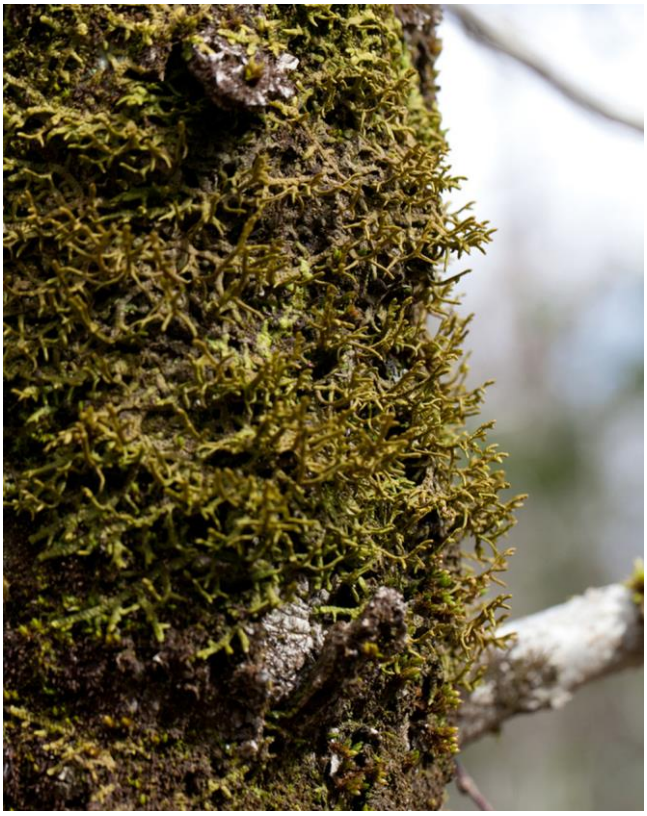

Figure 96. ***Porella platyphylloidea*** dry on a vertical substrate, showing the wiry appearance of dry plants. Photo by BKChallenge, through Creative Commons.

Figure 97. ***Porella platyphylloidea*** showing the reduction in surface area caused by the curling of the leaves around the stem. Photo by BKChallenge, through Creative Commons.

Figure 98. ***Porella platyphylloidea*** dry, showing leaves rolling to the under side of the stem. Photo by Bob Klips, with permission.

Figure 99. ***Porella platyphylloidea*** dry, showing overlapping leaves, lobes, and underleaves on the under side. Photo by Alex Graeff, through Creative Commons.

Reproduction

Schuster (1980) describes ***Porella platyphylloidea*** (Figure 91-Figure 93) as **dioicous** and usually fertile. The spores are large. It lacks any specialized asexual reproductive structures. Thus we must assume that its sexual reproduction is relatively successful because the species is widespread and relatively common (whether it is ***P. platyphylla*** or ***P. platyphylloidea***). Nevertheless, we cannot rule out dispersal of fragments, a feat that might be accomplished by birds gathering nesting materials or insects that carry very small fragments.

Biochemistry

Unlike those of ***Porella platyphylla*** (Figure 52-Figure 58), few studies have described the biochemistry of ***Porella platyphylloidea*** (Figure 91-Figure 93), at least by this name. Ludwiczuk *et al*. (2011) noted that it possessed flavonoids that might be useful as a taxonomic tool.

Summary

I found only four species in the **Porellaceae** that were associated with wet habitats. The most distinctive aquatic representative of these is ***Porella pinnata*** growing on cypress knees in swamps and marking a broad high water line. ***Porella cordaeana*** is occasionally submerged on rocks in fast water. ***Porella polyphylla*** is sometimes associated with intermittent streams and streambanks. ***Porella platyphylloidea*** is often growing epiphytically on trees in moist or wet habitats.

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Lars Söderström provided me with the current acceptable names for a number of older taxa.

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CHAPTER 1-10
AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA: RADULACEAE AND PTILIDIACEAE

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CHAPTER 1-10
AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA: RADULACEAE AND PTILIDIACEAE

Figure 1. ***Radula voluta*** on a rock, typical of its more aquatic habitat. This colony is likely to be submerged during times of increased flow. Photo by Stan Phillips, through public domain.

Porellales – Suborder Radulineae

Radulaceae

Radula aquilegia (Figure 2-Figure 3)

Distribution

Radula aquilegia (Figure 2-Figure 3) is distributed in Africa (Jones 1977), Australia, Europe, and Asia (ITIS 2020), including China and the Himalayas (Damsholt 2017). In Europe ***R. aquilegia*** occurs in Norway, the Faroes, British Isles, Iberian Peninsula, and Macaronesia (Söderström *et al*. 2002). In mainland Portugal it was considered extinct (Luís *et al*. 2005), but Cecília Sergio later rediscovered it there (Söderström *et al*. 2002; Luís *et al*. 2005). However, that appears to be a misidentification, once again making it absent in mainland Portugal (Luís *et al*. 2005).

Figure 2. ***Radula aquilegia***, a leafy liverwort distributed in Africa, Australia, Europe, and Asia. Photo by Michael Lüth, with permission.

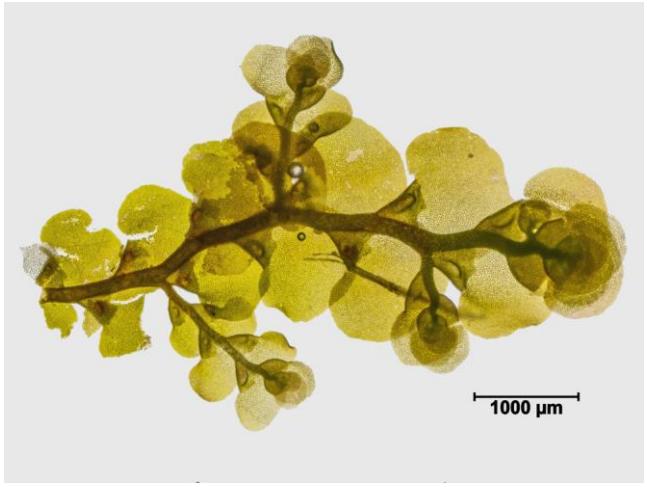

Figure 3. ***Radula aquilegia*** showing leaf lobes. Photo by Kristian Peters, with permission.

Aquatic and Wet Habitats

Watson (1919) reported that ***Radula aquilegia*** (Figure 2-Figure 3) is occasionally submerged, but that is not its primary habitat. Rothero (2005) reported that this species can occur in ravines in Scotland. Damsholt *et al*. (1980) similarly reported it from moist rock faces in a wooded ravine in Scotland, and Bosanquet (2015) found it in Wales in a humid area near a waterfall, but not in the direct splash.

For bryophytes that occur in the water, rocks are the typical substrate. Even the facultatively aquatic species ***Radula aquilegia*** (Figure 2-Figure 3) occurs frequently on rocks. In Scotland, it lives on shaded rocks (Rothero 2005). Heegaard (1997) reported it from small crevices in the Bergen area, Hordaland, Norway. Hassel *et al*. (2014) found it on a cliff wall in Norway where a stream at the base of the cliff maintained moisture. Ratcliffe (1968) likewise found indications of a preference for moist habitats, finding the species on rocks that were in damp, shady locations, especially in areas with the heaviest rainfall.

Radula aquilegia also occurs both as an epiphyte and an epiphyll. Frahm (2005) reported ***Radula aquilegia*** (Figure 2) from bark in the Azores. Luís *et al*. (2005) reported it from stems, trunks, and roots of ***Laurus azorica*** (Figure 4), ***Erica arborea*** (Figure 5-Figure 7), and ***E. cinerea*** (Figure 8) on Madeira. It sometimes even occurs on other bryophytes such as the wet-habitat moss ***Thamnobryum*** (Figure 9). It can even be epiphyllous on this moss (Sjögren 1975).

Figure 4. ***Laurus azorica***, a woody species where ***Radula aquilegia*** can grow on stems, trunks, and roots on Madeira. Photo by Ixitixel, through Creative Commons.

Figure 5. ***Erica arborea***, a woody species where ***Radula aquilegia*** can grow on stems, trunks, and roots on Madeira. Photo by Ehoarn Bidault, through Creative Commons.

Figure 6. ***Erica arborea*** showing flowers, leaves, and twigs; ***Radula aquilegia*** can grow on its stems, trunks, and roots. Photo by Ehoarn Bidault, through Creative Commons.

Figure 7. ***Erica arborea*** showing upright stems where ***Radula aquilegia*** can grow on Madeira. Photo by Ehoarn Bidault, through Creative Commons.

Figure 8. ***Erica cinerea***, a woody species where ***Radula aquilegia*** can grow on stems, trunks, and roots on Madeira. Photo by Dirk Hilbers, through Creative Commons.

Figure 9. ***Thamnobryum alopecurum***, a moss where one might find ***Radula aquilegia*** as an epiphyll. Photo by David T. Holyoak, with permission.

Adaptations

Clausen (1964) experimented with ***Radula aquilegia*** (Figure 2-Figure 3) from the Faroe Islands. At 15% relative humidity, only about 25% of the cells remained alive for 12 hours at 20ºC (Figure 10). At 35% humidity, all cells survived for 12 hours (Figure 10).

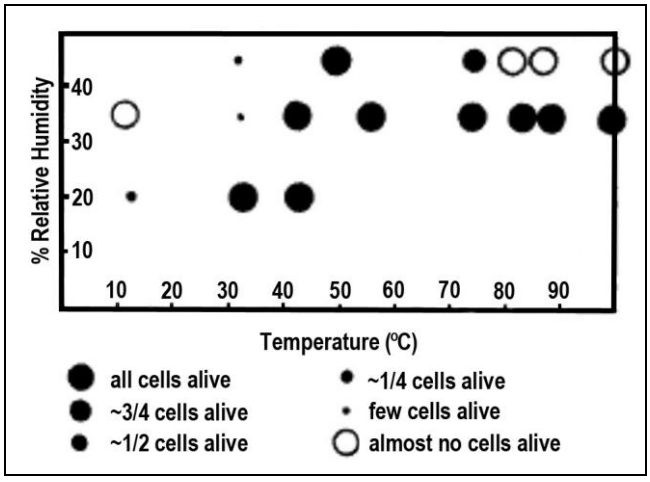

Figure 10. Relationship of temperature and relative humidity on the cell viability of ***Radula aquilegia*** after 12 hours of exposure. Redrawn from Clausen 1964.

Lloret and González-Mancebo (2011) considered ***Radula aquilegia*** (Figure 2-Figure 3) to be a **long-lived shuttle** species on the Canary Islands. Kürschner *et al*. (2007) noted that species on Madeira island benefitted from the humidity and shade of the undisturbed laurel forests, favoring **mat** (Figure 11) and **fan** (Figure 12) **perennial stayers** and **perennial shuttle** species. These species typically have moderately low sexual and asexual reproduction. In the ericaceous woodland, on the other hand, the habitat is more xeric and sunny, favoring **tall** and **short turf** but also **perennial stayers** and **perennial shuttle species**. These, however, have high levels of sexual reproduction. ***Radula aquilegia*** occurs in both woodland types. As an epiphyte it is typically **mat-forming** (Figure 11). Its sexual reproduction is limited.

Reproduction

Radula aquilegia is **dioicous** (Bouman & Dirkse 1990; Damsholt 2017). Damsholt found a male plant in the Faeroes, but no sporophytes have been found in the Faeroes. Sporophytes are rare in Great Britain. Lloret and González-Mancebo (2011) likewise noted limited sexual reproduction in the Canary Islands. Leaves never have gemmae (Bouman & Dirkse 1990).

Figure 11. ***Radula aquilegia*** forming a mat on bark. Photo by Gordon Rothero, with permission.

Figure 12. ***Radula aquilegia*** exhibiting the **fan** life form typical in high humidity habitats. Photo by Kristian Peters, with permission.

Fungal Interactions

Wang and Qiu (2006) were unable to find any records of mycorrhizae in ***Radula aquilegia*** (Figure 2-Figure 3). Apparently none of the oils from this species has been tested for antifungal or other activity.

Biochemistry

Figueiredo *et al*. (2009) extracted volatiles from seven species of ***Radula*** from the Azores and Madeira as well as mainland Portugal and Switzerland. One cluster of species, including ***R. aquilegia*** (Figure 2-Figure 3) from the Azores, exhibited large amounts of several sesquiterpenes from the oil bodies (Figure 13-Figure 14). Most of the species could be distinguished by their oil components, but in these tests, ***R. aquilegia*** could not be separated from ***R. complanata*** (Figure 18-Figure 20) or ***R. lindenbergiana*** (Figure 50-Figure 53).
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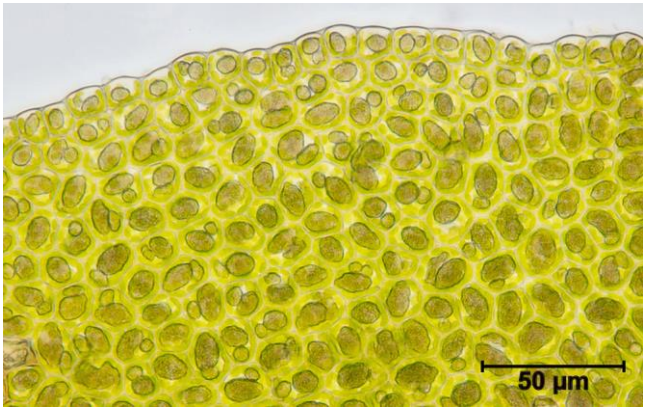


Figure 13. ***Radula aquilegia*** leaf cells with oil bodies. Photo by Kristian Peters, with permission.

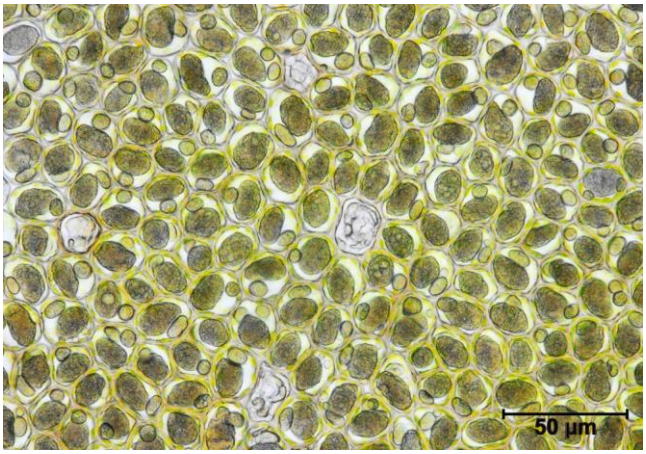


Figure 14. ***Radula aquilegia*** leaf cells with oil bodies. Photo by Kristian Peters, with permission.

Radula carringtonii (Figure 15-Figure 16)

Distribution

Radula carringtonii (Figure 15-Figure 16) has a narrow distribution in Scotland, Ireland, and Macaronesia (Bouman & Dirkse 1990). Later Yamada (1995) added Costa Rica, Central America, British Isles, and Spain. Yamada later (2000) reported it from Bolivia. Longton and Hedderson (2000) considered the species to be rare.

Figure 15. ***Radula carringtonii*** forming a **mat**, a species with known volatiles that are the same as those in ***Radula lindenbergiana***. Photo by David T. Holyoak, with permission.

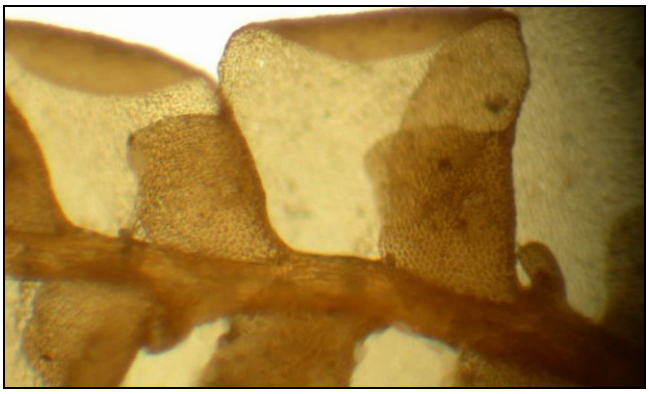


Figure 16. ***Radula carringtonii*** showing leaf lobes. Photo by Nidia Homem, with permission from Rosalina Gabriel.

Aquatic and Wet Habitats

Radula carringtonii (Figure 15-Figure 16) occurs on periodically wet rocks in the dense forests of Macaronesia (Bouman & Dirkse 1990).

Adaptations

The cell walls of ***Radula carringtonii*** (Figure 15-Figure 16) are thickened with trigones (Bouman & Dirkse 1990), a character that could add strength, but I don't know its value in this habitat, if any.

Reproduction

Radula carringtonii (Figure 15-Figure 16) is **dioicous** (Bouman & Dirkse 1990). The leaves never have gemmae. Therefore, we must assume it reproduces mostly by fragments. This limited reproduction can account for its narrow distribution.

Biochemistry

Mues (1984; Figueiredo 2009) reported flavone glycosides from ***Radula carringtonii*** (Figure 15-Figure 16). Stech *et al*. (2010) found that ***R. aquilegia*** (Figure 2-Figure 3), ***R. carringtonii***, ***R. complanata*** (Figure 18-Figure 20), ***R. holtii*** (Figure 43), ***R. jonesii***, ***R. lindenbergiana*** (Figure 50-Figure 53), ***R. nudicaulis*** (Figure 17), and ***R. wichurae*** (Figure 54) could be separated based on their chemistry.

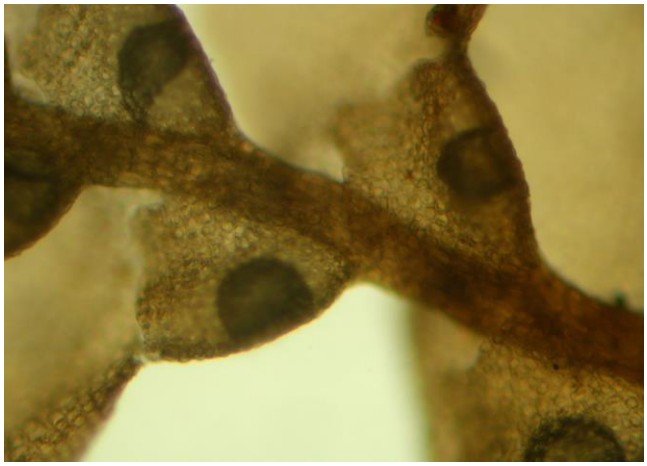


Figure 17. ***Radula nudicaulis***, a species that can be separated from ***Radula carringtonii*** by its chemistry. Photo by Nídia Homem, with permission from Rosalina Gabriel.

Radula complanata (Figure 18-Figure 20)

Distribution

Radula complanata (Figure 18-Figure 20) is widely distributed in North America, Europe, Asia, and northern Africa (Stevens 1910), Greenland, and South America (Krayesky *et al*. 2018). It seems to be nearly absent from the tundra and lowland tropics (Krayesky *et al*. 2018). On Mount Musa in Turkey, ***Radula complanata*** is one of the three most common species of liverworts (Ezer *et al*. 2009). In the coastal area of the Ukrina River, Bosnia and Herzegovina, ***Radula complanata*** is the only bryophyte present (Šarčević-Todosijević & Šarčević 2018).

Figure 18. ***Radula complanata***, a leafy liverwort widely distributed in North America, Europe, Asia, and northern Africa, Greenland, and South America. Photo by Allen Norcross, with permission.

Figure 19. ***Radula complanata*** showing leaf lobes. Photo by Sture Hermansson, with online permission.

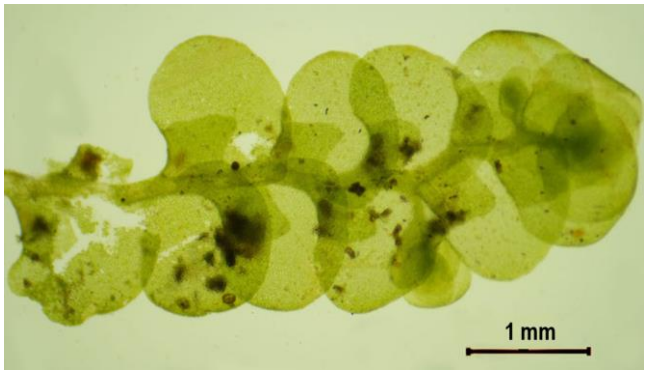


Figure 20. ***Radula complanata*** showing leaf lobes and collected detrital material. Photo courtesy of Norbert Ethan.

Aquatic and Wet Habitats

Krayesky *et al*. (2018) reported that ***Radula complanata*** (Figure 18-Figure 20) is **epicortic** (growing on bark), **epilithic** (growing on rock), and **terricolous** (living on ground), occurring in various habitats, including oceanside cliffs, peatlands, woodlands, waste places, riparian habitats, and subalpine crags. But it does indeed occupy wetter habitats such as wet or moist cliffs of ravines in Connecticut, USA (Nichols 1916); rock cliffs associated with streams, Cape Breton Island, Canada (Nichols 1918); streams characterized by the ***Platyhypnidium-Fontinalis antipyretica*** association, Thuringia, Germany (Marstaller 1987); aquatic and on vertical surfaces and moist habitats in Finland (Koponen *et al*. 1995; Virtanen 1995); on bark of ***Fagus*** and ***Fraxinus***, at a stream in Tara River canyon and Durmitor area, Montenegro (Papp & Erzberger 2011); in Ibar gorge, along the River Ibar (Papp *et al*. 2016). Alataş *et al*. (2017) considered it a hygrophyte in Turkey.

Coker (1993) reported ***Radula complanata*** (Figure 18-Figure 20) from branches that emerged above the winter water level. It occurred in **turloughs** (in Ireland, low-lying areas on limestone that become flooded in wet weather through welling up of groundwater) with their highest water level in winter.

There are few reports of ***Radula complanata*** (Figure 18-Figure 20) on rocks. Papp *et al*. (2016) reported it from shaded serpentine rock in the Ibar gorge of southwest Serbia. Hallingbäck and Holmåsen (1982) found it on rocks in Sweden. It occupies both acidic and basic substrates (Krayesky *et al*. 2018).

Adaptations

Šarčević-Todosijević and Šarčević (2018) considered ***Radula complanata*** (Figure 18-Figure 20) to be a **hemicryptophyte** (perennial plant having overwintering buds located at soil surface), a term usually reserved for tracheophytes. It nevertheless does describe the habit of this species to occur on the ground in the Ukrina River area of Bosnia and Herzegovina. Krayesky *et al*. (2018) described it as growing in **mats** (Figure 21) or among other bryophytes. On the other hand, Alataş *et al*. (2017) considered the species of epiphytes in Turkey to be mostly **weft** and **cushions** that are **perennial stayers**. That is consistent with the observations of Hazell *et al*. (1998) in Sweden, where ***Radula complanata*** forms **wefts** that adhere tightly to the bark surface.

Figure 21. ***Radula complanata*** forming a mat. Photo by Allen Norcross, with permission.

Reproduction

Radula complanata (Figure 18-Figure 20) has no **caducous** (falling off easily) leaves, but has asexual reproduction through discoid gemmae that are usually not only present, but numerous (Stevens 1910; Krayesky *et al*. 2018). Furthermore, gemma production is not suppressed by development of sexual structures (Stevens 1910), as is common in many bryophytes. At maturity, the gemmae are 2 cells thick throughout most of the gemma, presumably improving survivability during and after dispersal. The species is **paroicous** [having male (Figure 22) and female reproductive organs (Figure 23-Figure 25) beside or near each other] and often fertile (Krayesky *et al*. 2018), all of which suggest that it has a high reproductive potential (Figure 26-Figure 30) and may explain its wide distribution. Alataş *et al*. (2017) considered high sexual reproductive activity to be the dominant life strategy among the epiphytes at the Boraboy and Destek Forests in Turkey, an ideal location for the spread of windborne spores. This species produces copious spores (Arnell 1956; Nyholm 1954-1969; During 1992). On the other hand, Castle (1925) considered sexual structures to be rare in North America, especially when gemmae (Figure 31-Figure 36) were abundant.

Figure 22. ***Radula complanata*** antheridium in leaf axil. Photo courtesy of Norbert Ethan.

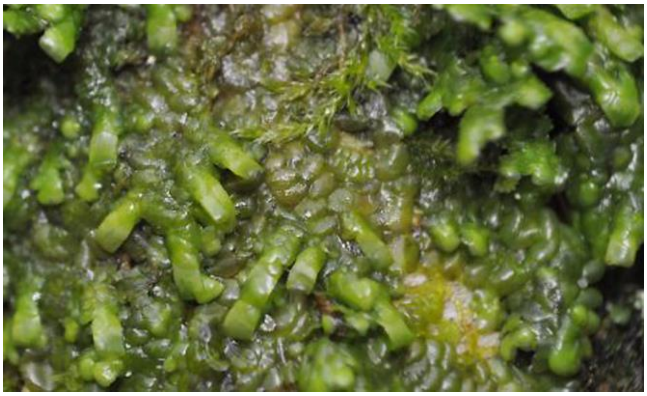


Figure 23. ***Radula complanata*** with numerous perianths. Photo by Andrew Hodgson, with permission.

Figure 24. ***Radula complanata*** with perianths. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 25. ***Radula complanata*** perianth. Photo courtesy of Norbert Ethan.

Figure 26. ***Radula complanata*** with capsules before seta elongation. Photo by Hermann Schachner, through Creative Commons.

Figure 27. ***Radula complanata*** with capsules and elongated seta. Photo by Andrew Hodgson, with permission.

Figure 28. ***Radula complanata*** with dehiscing capsules. Photo by Hermann Schachner, through Creative Commons.

Figure 31. ***Radula complanata*** with gemmae. Photo by J C. Schou, Biopix, through Creative Commons.

Figure 29. ***Radula complanata*** capsule dehiscing. Photo courtesy of Norbert Ethan.

Figure 32. ***Radula complanata*** with perianths, dorsal view. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

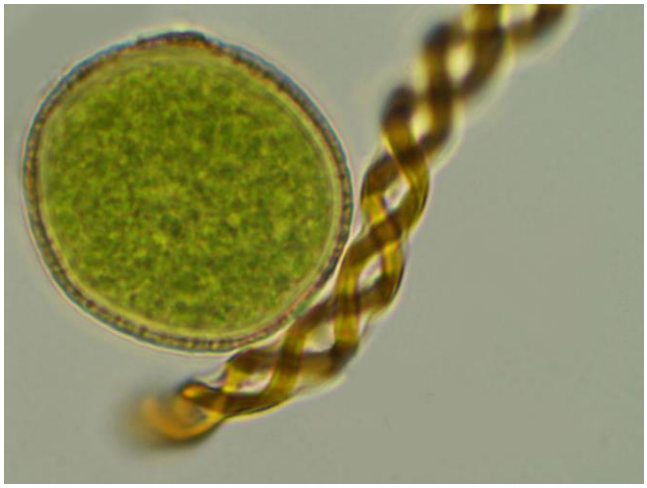


Figure 30. ***Radula complanata*** spore and elater. Photo courtesy of Norbert Ethan.

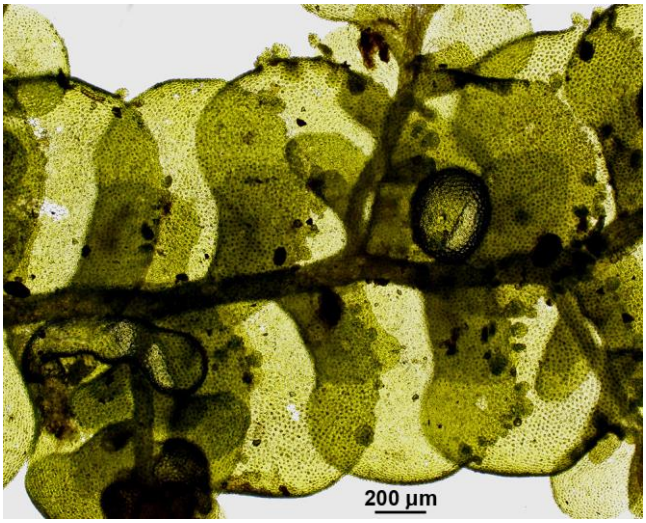


Figure 33. ***Radula complanata*** with gemmae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

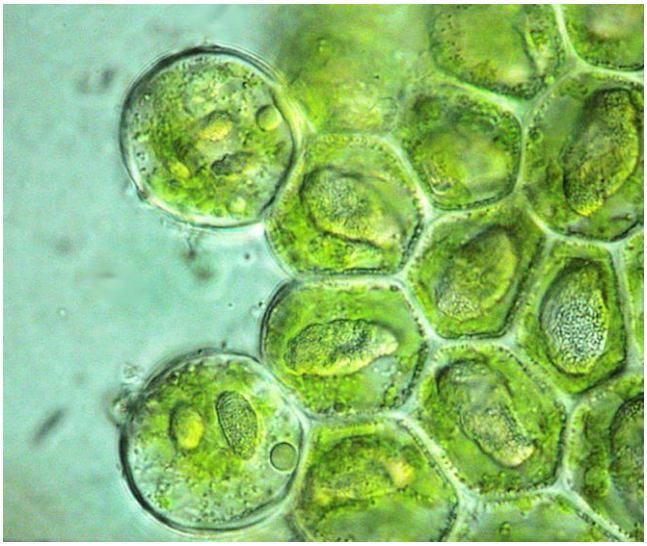


Figure 34. ***Radula complanata*** gemmae. Photo by Walter Obermayer, with permission.

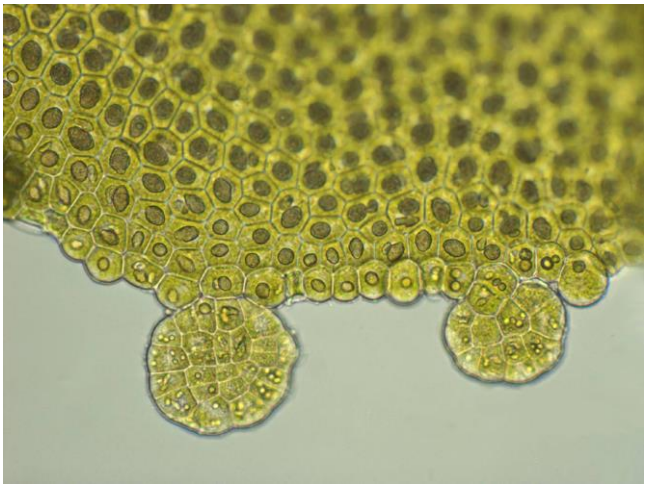


Figure 35. ***Radula complanata*** multicellular gemmae on leaf margin. Photo by Blanka Aguero, with permission.

Figure 36. ***Radula complanata*** gemmae. Photo by Walter Obermayer, with permission.

Heylen and Hermy (2008) implied that ***Radula complanata*** (Figure 18-Figure 20) might not be a good competitor. This species appears to be a good disperser, and thus is typically a pioneer on trees, reaching a maximum at 2-3 years, but then declining. They considered that its inability to colonize new patches at that stage was due to the presence of other bryophytes, particularly larger ones. Thus, good dispersal is definitely an advantage and a common adaptation for a pioneer.

Mehra and Pathania (1959) reported a chromosome number of *n*=6 for western Himalayan populations, noting that the diploid is present in the Himalayas. But Kapila (2016) reported the chromosome number as *n*=9 for some Indian populations.

Role

A number of bryophytes serve as habitat for testate amoebae (Davidova *et al.* 2016). ***Radula complanata*** (Figure 18-Figure 20) is among a group of bryophytes with protozoan species numbering 11-14, but it had the lowest number of dominants (three), compared to ***Brachythecium velutinum*** (Figure 37) with eight. ***Radula complanata*** did, however, have the most specific and different fauna of these testate amoebae. ***Euglypha ciliata glabra*** (Figure 38) was the dominant amoeba species on this liverwort.

Figure 37. ***Brachythecium velutinum*** with capsules, a species with more dominant protozoan species than found on ***Radula complanata***. Photo by Michael Lüth, with permission.

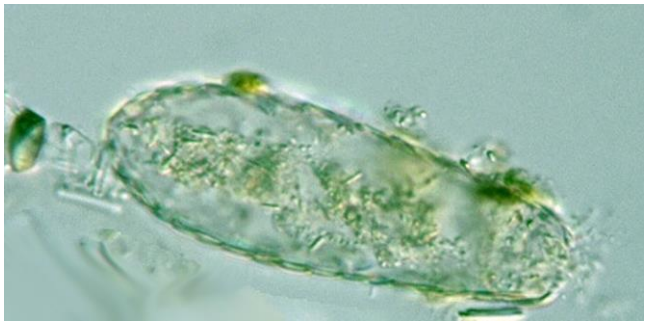


Figure 38. ***Euglypha ciliata***, a testate protozoan that inhabits ***Radula complanata***. Photo by Yuuki Tsujii, with permission.

In addition to protozoa, ***Radula complanata*** (Figure 18-Figure 20) is inhabited by **Mesostigmata** mites, at least in forests of Latvia (Salmane 2007). ***Holoparasitus excipuliger***, ***Pergamasus crassipes*** (Figure 39), ***Pergamasus parinteger***, and ***Pergamasus wasmanni*** inhabited ***R. complanata*** in the deciduous forest.

Figure 39. ***Pergamasus crassipes*** ventral side. Photo by Matthew Shepherd, through Creative Commons.

Fungal Interactions

Döbbeler (2004) reported the new **Ascomycetes** genus ***Bryocentria*** (Figure 40) from ***Radula complanata*** (Figure 18-Figure 20) as well as other bryophytes. It produces small, orange-colored perithecia and is parasitic on bryophytes. The presence of ***Bryocentria metzgeriae*** (Figure 40) on ***Radula complanata***, but not on ***Radula lindenbergiana*** (Figure 50-Figure 53) suggested to Döbbeler that corticolous hosts are preferred; ***R. complanata*** appeared to be an excellent host, but not the only host. Could it be a difference in secondary compounds?

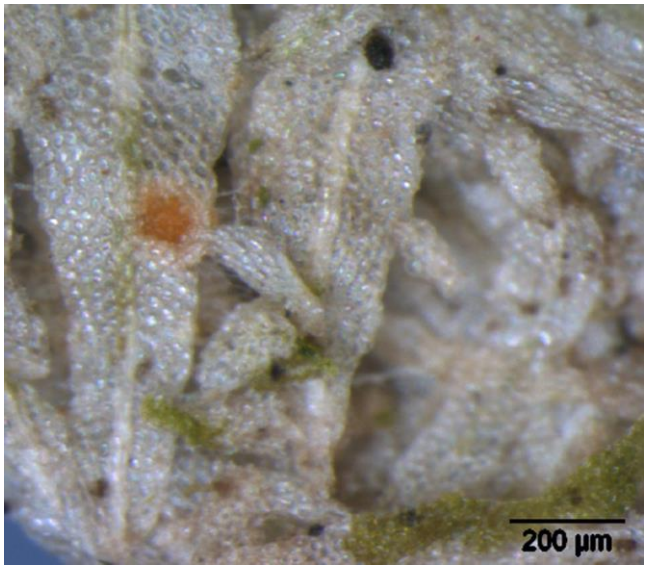


Figure 40. ***Bryocentria metzgeriae*** on ***Metzgeria***. Photo from Bold Systems, through Creative Commons.

Biochemistry

Rattray (1886) noted that ***Radula complanata*** (Figure 18-Figure 20) has oil bodies (Figure 41) that are embedded in a medium with a different refractive index. The oil bodies of ***Radula complanata*** are usually limited to one per cell and are conspicuous (Krayesky *et al*. (2018). Flegel and Becker (2000) characterized the contents of these oil bodies in ***Radula complanata*** and determined that 3-methoxybibenzyl is the main constituent.

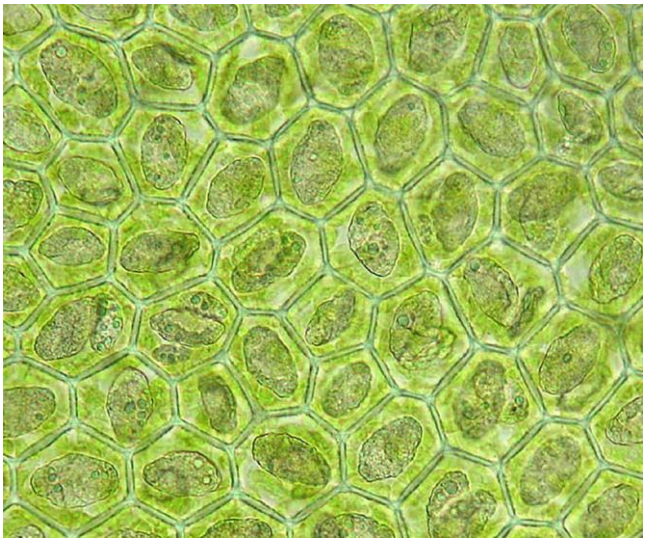


Figure 41. ***Radula complanata*** cells showing massive oil bodies. Photo by Walter Obermayer, with permission.

Figueiredo *et al*. (2009) reviewed the known volatile composition of ***Radula*** species from Portugal. Suire (1970) identified α-pinene, β-pinene, camphene, six sesquiterpenes (including b-caryophyllene), and 3-methoxybibenzyl in ***Radula complanata*** (Figure 18-Figure 20). In Japanese populations, Asakawa *et al*. (1978) identified methanol bibenzyls in ***Radula complanata***. Asakawa *et al*. (1982) reported ether + methanol extractions of bibenzyls and one sesquiterpene from French populations (see also Takikawa *et al*. 1989). Asakawa *et al*. (1991) reported prenyl bibenzyls from this species and identified Radulanin. Mues (1984) used an array of populations from Canada, Austria, France, Germany, Italy, Poland, Spain, and Switzerland, reporting on aqueous methanol flavone glycosides. Markham and Mues (1984) made aqueous extracts of flavone glycoside from Swiss populations.

Asakawa *et al*. (1991) provided an idea of the activity of some of these compounds. For example, some prenyl-containing bibenzyls exhibited 5-lipoxygenase and calmodulin inhibitory activity and vasopressin antagonist activity. Nikolajeva *et al*. (2012) were unable to demonstrate any antibacterial activity against the bacterium ***Staphylococcus aureus*** (Figure 42).

One of the roles of some secondary compounds is to inhibit the growth of fungi. But in many cases, fungi are common on bryophytes. The **Ascomycete** ***Belonioscyphella hypnorum*** uses ***Radula complanata*** (Figure 18-Figure 20) as one of its bryophyte hosts in calcareous areas of the Czech Republic (Egertová *et al*. 2016).

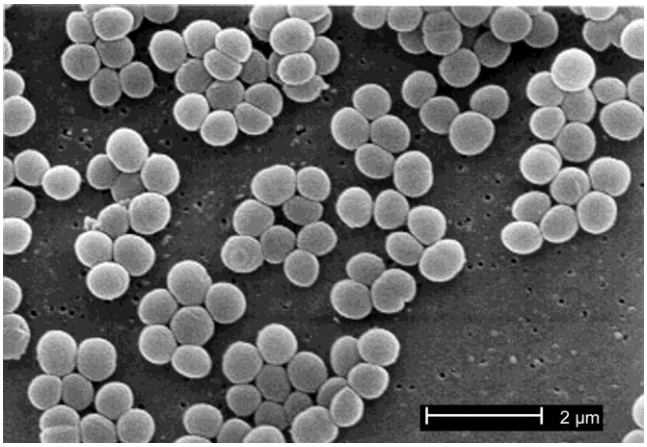


Figure 42. ***Staphylococcus aureus*** SEM. Photo from CDC - Matthew J. Arduino and Janice Carr, through public domain.

Radula holtii (Figure 43)

Figueiredo *et al*. (2009) used volatile compounds as chemotaxonomic characters to separate species of ***Radula*** from Portugal. They were able to differentiate geographic populations based on their chemistry, separating ***R. holtii*** (Figure 43) on the mainland from that of Madeira.

Distribution

Luís *et al.* (2005) reported that ***Radula holtii*** (Figure 43) was confined to Ireland, the Iberian Peninsula, and Macaronesia. Pescott (2016) reported it as new for Britain. Geissler *et al*. (1997) found that this species is rare wherever it occurs.

Aquatic and Wet Habitats

Radula holtii (Figure 43) occurs in water splash or steep, dripping granite surfaces deeply shaded by surrounding vegetation (Vieira *et al.* 2005). It is typically associated with ***Thamnobryum alopecurum*** (Figure 9), ***Dumortiera hirsuta*** (Figure 44-Figure 45), ***Pellia epiphylla*** (Figure 46), ***Plagiothecium nemorale*** (Figure 47), and ***Fissidens polyphyllus*** (Figure 48), in mountain streams of northwest Portugal. Ferreira *et al*. (2008) reported it from rivers. Geissler *et al*. (1997) reported it from wet rocks in southwest Ireland, Spain, Portugal, and Macaronesia.

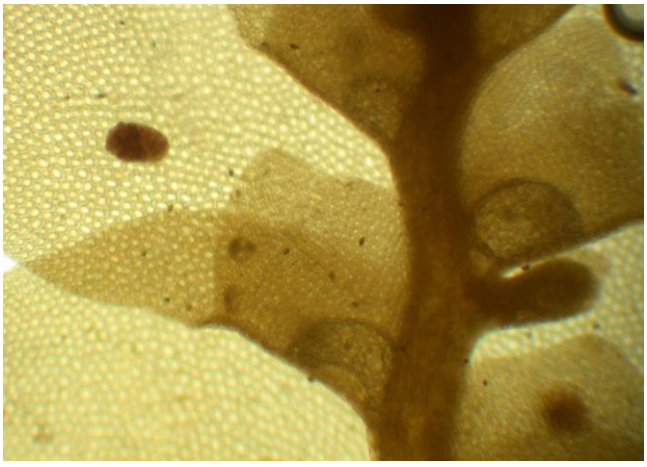


Figure 43. ***Radula holtii*** leaves and lobes. Photo by Nidia Homem, with permission from Rosalina Gabriel.

Figure 44. ***Dumortiera hirsuta*** showing a typical habitat; it is often associated with ***Radula holtii***. Photo by Michael Lüth, with permission.

Figure 45. ***Dumortiera hirsuta***, a species often associated with ***Radula holtii***. Photo by Michael Lüth, with permission.

Figure 46. ***Pellia endiviifolia***, a species often associated with ***Radula holtii***. Photo by David T. Holyoak, with permission.

Figure 47. ***Plagiothecium nemorale***, a species often associated with ***Radula holtii***. Photo by Hermann Schachner, through Creative Commons.

Figure 48. ***Fissidens polyphyllus***, a species often associated with ***Radula holtii***. Photo by David T. Holyoak, with permission.

Vieira *et al*. (2016) considered ***Radula holtii*** (Figure 43), a species already rare, to be vulnerable to hydrologic change such as that created by hydroelectric plants. This species prefers 1st to 3rd order mountain streams with permanent flow. In its localities in Ireland, Scotland, Iberian Peninsula, and Macaronesia these streams run through vertical granite surfaces where they create dripping rocks and spray zones in deeply shaded niches. It also occurs in drainage ditches of a thermal park. In these habitats they were often associated with a similar group of species as found in mountain streams: ***Thamnobryum alopecurum*** (Figure 9), ***Dumortiera hirsuta*** (Figure 44-Figure 45), ***Pellia epiphylla*** (Figure 46), ***Plagiothecium nemorale*** (Figure 47), ***Fissidens polyphyllus*** (Figure 48) (Vieira *et al*. 2005). It forms medium-sized pure patches near these and other hygrophilic and hydrophilic species. It also occurs on granite walls on river margins in northwestern Portugal (Vieira *et al*. 2007). Monteiro and Vieira (2017) likewise reported this vulnerable species from headwater streams in northwest and central west Portugal, being of "great interest" in waterfalls and on dripping walls. Vieira *et al*. (n.d.) found them in a *p*H range of 6.8 to 7.2 and clean to moderately polluted waters. They occupied slopes of 30-100%. O'Reilly (2020) summarized the habitat in Britain as growing where it is easily overlooked in deep shade on dripping rocks, in caves, by waterfalls, or in ravines.

Among the terrestrial habitats that suffice or encourage the development of bryophyte populations are cave entrances – habitats that can remain cooler and moister than the surrounding habitats. Among these cave-dwelling bryophytes is ***Radula holtii*** (Figure 43) (Gabriel *et al*. 2018). This species occurs at cave entrances in the Azores, but these habitats are threatened by climate change, severe weather, habitat change and degradation, and invasive plant species.

Adaptations

Radula holtii is green to olive-green, becoming more olive-green with age. The leaf cell walls are thin and lack trigones.

Reproduction

Radula holtii (Figure 43) is **paroicous** (Bouman & Dirkse 1990; O'Reilly 2020), but its sexual reproduction is apparently rare. O'Reilly (2020) stated that its perianths (Figure 49) are rarely produced, but when present they are of taxonomic importance. Furthermore, it "almost never has gemmae." Vieira *et al*. (n.d.) noted that it does sometimes produce perianths and sporophytes in the northwest Portugal populations. Leaf gemmae unknown (Bouman & Dirkse 1990).

Figure 49. ***Radula holtii*** with rarely occurring perianths. Photo by Rory Hodd, with permission.

Radula lindenbergiana (Figure 50-Figure 53)

(syn. = *Radula lindbergiana*)

Radula lindenbergiana (Figure 50-Figure 53) and ***R. complanata*** (Figure 18-Figure 20) are difficult to separate in the field when they lack reproductive structures (Kürschner *et al*. 2012). It has at times been considered a subspecies of ***Radula lindenbergiana*** (Stech *et al*. 2010).

Figure 50. ***Radula lindenbergiana***. Photo by Jan-Peter Frahm, with permission.

Figure 51. ***Radula lindenbergiana***. a species known from Macaronesia, Europe, Africa, and North America. Photo by Hermann Schachner, through Creative Commons.

Figure 52. ***Radula lindenbergiana*** in a wet condition. Photo by Michael Lüth, with permission.

Figueiredo *et al*. (2009) used volatiles to separate species in ***Radula*** from Portugal. However, they found no geographic separation for ***R. carringtonii*** (Figure 15-Figure 16), ***R. wichurae*** (Figure 54), and ***R. lindenbergiana*** (Figure 50-Figure 53). Laenen *et al*. (2011) considered Macaronesian populations to be a source of genetic diversity in the post-glacial recolonization of western Europe by ***R. lindenbergiana***. DNA results suggest that the mutation rate exceeds the dispersal rate in this species. Laenen and coworkers concluded that Macaronesia most likely served as a refugium during Quaternary glaciations.

Figure 53. ***Radula lindenbergiana***, Madeira. Michael Lüth, with permission.

Figure 54. ***Radula wichurae***, a species with known volatiles that are the same as those in ***Radula lindenbergiana***. Photo by Nídia Homem, with permission from Rosalina Gabriel.

Distribution

Laenen *et al*. (2011) sampled ***Radula lindenbergiana*** (Figure 50-Figure 53) in Macaronesia, Europe, and Africa. Gökler (1998) listed its known distribution from Turkey (Özenoğlu & Gökler 2002), Europe, Russia, Caucasus, Iran, Korea, Japan, Taiwan, Himalayas, Tunisia, Morocco, Algeria, Greenland, and S. Africa. To these, Figueiredo *et al*. (2009) added Austria, Azores, Portugal, Canary Islands, Spain, Crete, Germany, and Yugoslavia. Sotiaux and Sotiaux (2000) added Belgium, referring to the species as circumboreal. Krayesky *et al*. (2018) added Alaska and Tennessee (not a boreal state) in North America, and Atlantic Islands.

Aquatic and Wet Habitats

Gökler (1998) reported the habitat of ***Radula lindenbergiana*** (Figure 50-Figure 53) as wet rocks. Blockeel (2017) likewise treated it as a species of moist rocks in the Cyclades of Greece. Koponen *et al*. (1995)

described it as aquatic in Finland. In Flora North America, Krayesky *et al*. (2018) cited flooded rocks in streams among its habitats. Özenoğlu and Gökler (2002) considered it to be a species mainly of wet rocks in Turkey at the Dilek Peninsula National Park. Gabriel *et al*. (2019) reported it from coastal wetlands in the Azores.

Mogensen and Damsholt (1981) reported ***Radula lindenbergiana*** (Figure 50-Figure 53) from boulders in a river in Sweden. There it was accompanied by ***Hygroamblystegium tenax*** (Figure 55), ***Jungermannia pumila*** (Figure 56), and ***Platyhypnidium riparioides*** (Figure 57).

Rocks serve as suitable substrates for ***Radula lindenbergiana*** (Figure 50-Figure 53) on land as well as in the water. Papp (2004) found it on shaded volcanic rocks and on a rock wall. Krayesky *et al*. (2018) include dry to moist rocks among its habitats, but state that epilithic populations are found in forested localities and on sheltered rock faces. It occurs in low to high elevations.

It seems that most of the streambank and inundated species of liverworts also occur as epiphytes. This is likewise true for ***Radula lindenbergiana*** (Figure 50-Figure 53) – "very" occasionally on bark of trees (Krayesky *et al*. 2018).

Figure 55. ***Hygroamblystegium tenax***, a species that accompanies ***Radula lindenbergiana*** on boulders in Swedish rivers. Photo by Hermann Schachner, through Creative Commons.

Figure 56. ***Jungermannia pumila***, a species that accompanies ***Radula lindenbergiana*** on boulders in Swedish rivers. Photo from Earth.com, with permission.

Figure 57. ***Platyhypnidium riparioides***, a species that accompanies ***Radula lindenbergiana*** on boulders in Swedish rivers. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Adaptations

Radula lindenbergiana (Figure 50-Figure 53) usually grows in **mats** or singly among other bryophytes (Patiño *et al*. 2009; Krayesky *et al*. 2018).

Reproduction

Radula lindenbergiana (Figure 50-Figure 53) is **dioicous** and rarely fertile (Krayesky *et al*. 2018). Désamoré (2013) suggested that island populations lose their dispersal power, certainly a consequence of being dioicous, but noted that the Macaronesian Islands seem to have back-colonized the European mainland at least twice. Furthermore, the species exhibits its highest genetic diversity on Macaronesia. Like most of the liverworts the chromosome number for ***Radula lindenbergiana*** (Figure 50-Figure 53) is n=8 (Zheng & Zhu 2009).

Özenoğlu and Gökler (2002) reported that they frequently found abundant gemmae on the leaf margins of ***Radula lindenbergiana*** (Figure 50-Figure 53) in the Dilek Peninsula National Park, Turkey. Krayesky *et al*. (2018; see also Losada-Lima *et al*. 2001) likewise noted that the gemmae were usually "copious," but that **caducous** leaves were absent. The predominance of gemmae and limited sexual reproduction may explain the lack of diversity in populations of mainland Europe.

Fungal Interactions

Although many liverworts serve as host for Ascomycetes fungi, ***Radula lindenbergiana*** (Figure 50-Figure 53) seems not to be one of them. Döbbeler (2004) found that whereas ***Radula complanata*** (Figure 18-Figure 20) seemed to be an excellent host for the fungus ***Bryocentria*** (Figure 40), not a single record existed for ***R. lindenbergiana***. He suggested that this may be due to the substrate of siliceous rocks for ***R. lindenbergiana*** in his study.

Biochemistry

Oil bodies, usually only one per cell, are conspicuous (Krayeski *et al*. 2018) and may hold the secret to the apparent absence of fungi. Biochemical studies seem to be

lacking. These may explain further the absence of parasitic or epiphytic fungi on ***R. lindenbergiana***.

Radula obconica (Figure 58)

Distribution

Radula obconica (Figure 58) is a North American endemic (Risk *et al*. 2011). It occurs in eastern North America, from southern Quebec, south to Florida, west to Minnesota and Arkansas (Schuster 1980). Even in the southern Appalachians, it doesn't reach into the spruce-fir zone.

Aquatic and Wet Habitats

Nichols (1916) reported ***Radula obconica*** (Figure 58) as calciphobic along rivers in Connecticut, USA. Lorenz (1918) found it in moister situations, occurring on rocks in brooks, damp places near waterfalls, and on dripping rocks. Haynes (1927) reported it from wet river banks in Virginia, USA. Wittlake (1950) found it on open dripping ledges with ***Jubula hutchinsiae*** subsp. ***pennsylvanica*** (Figure 59), ***Amblystegium serpens*** (Figure 60), ***Rhizomnium punctatum*** (Figure 61), and ***Philonotis fontana*** (Figure 62). In a humid, but not constantly wet location in Missouri, USA, Redfearn (1964b) found it along a gulley on a north-facing wooded slope.

Figure 58. ***Radula obconica***, a leafy liverwort species endemic to eastern North America. Photo by Blanka Aguero, with permission.

Figure 59. ***Jubula hutchinsiae*** subsp. ***pennsylvanica***, a subspecies in eastern North America that accompanies ***Radula obconica*** on dripping ledges. Photo by Wayne Lampa, through Creative Commons.

Figure 60. ***Amblystegium serpens***, a species in eastern North America that accompanies ***Radula obconica*** on dripping ledges. Photo by Michael Lüth, with permission.

Figure 61. ***Rhizomnium punctatum*** with capsules, a species in eastern North America that accompanies ***Radula obconica*** on dripping ledges. Photo by Michael Lüth, with permission.

Figure 62. ***Philonotis fontana***, a species that accompanies ***Radula obconica*** on dripping ledges in eastern North America. Photo by Michael Lüth, with permission.

Typical water substrata for bryophytes are rocks. Redfearn (1964a) reported ***Radula obconica*** (Figure 58) from shaded sandstone in Arkansas, USA, and later (Redfearn 1979) on vertical sandstone. Lorenz (1918) reported it generally as occurring on both granitic and **trap rock** [any dark-colored, fine-grained, non-granitic intrusive or extrusive igneous rock, including basalt, peridotite,

diabase, and gabbro; also referring to flood (plateau) basalts]. Standley (1914) reported ***Radula obconica*** from moist, shaded rocks in North Carolina, USA. Solberg and Miller (1979) found it on rocks near streams in North Carolina. Gunderson (1971) found it on igneous rock in Wisconsin. In Minnesota it occurs on shaded, relatively humid, sheltered cliffs (Schuster 1957). Ammons (1933) found it in McKinney's Cave (Figure 63), a sandstone cave in West Virginia, on the rock wall.

Nichols (1916) considered ***Radula obconica*** (Figure 58) to be **calciphobous** (lime avoiding). But he went even farther in concluding that it was mostly restricted to **potassic rocks** (comprising $K_2O>Na_2O$ in percent weight and include compositional ranges from leucite-bearing basanites to K-enriched rock like leucitites, lamprophyres, orangeites, shoshonites, and lamproites).

Schuster and Patterson (1957) reported ***Radula obconica*** (Figure 58) from tree trunks in Dismal Swamp in Virginia, USA. McAvoy *et al*. (2011) reported it from the bark of trees in swamps in the Delmarva Peninsula (parts of Delaware, Maryland, and Virginia), and considered it rare. Lorenz (1918) noted that it occurs in moister habitats than does ***R. complanata*** (Figure 18-Figure 20), and reported it from bark, where it exhibited a dark olive-green color. Fulford (1934) reported it from trees in moist woods in Kentucky. In the Appalachian Plateau of Kentucky, USA, Risk *et al*. (2011) found it growing on ***Rhododendron maximum*** (Figure 64) as an epiphyll (Figure 65). ***Radula obconica*** did not appear on 1-year-old leaves, but increased in cover in the second and third years.

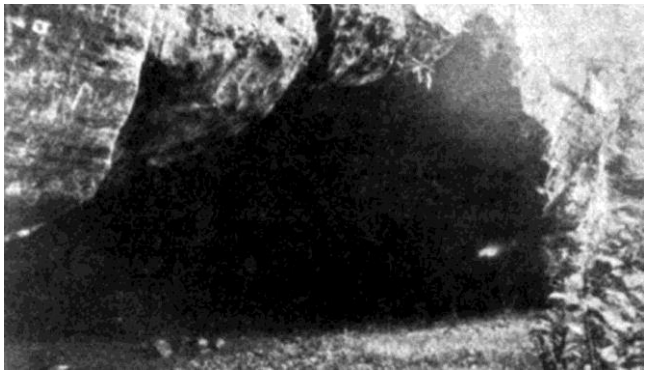


Figure 63. McKinney's cave, WV, entrance, showing the rock wall. Photo from Ammons 1933.

Figure 64. ***Rhododendron maximum*** leaves with small patches of epiphylls; in southern areas of the United States one can find ***Radula obconica*** on these leaves, but not commonly. Photo by Janice Glime.

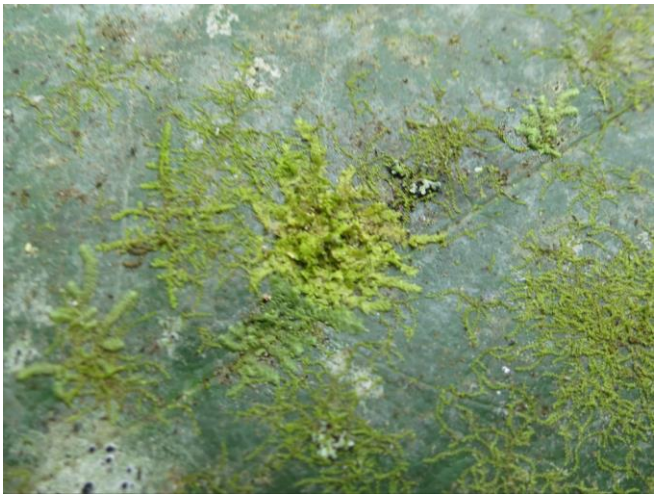


Figure 65. Epiphylls on ***Rhododendron*** in North Carolina, USA; the larger liverwort in the middle could be ***Radula obconica***. Photo courtesy of Jessica Nelson.

In the area of Athens, Ohio, Hall (1958) found ***Radula obconica*** (Figure 58) on moist sandstone, but also on rootlets and on other bryophytes. Hall reported it as "sometimes" occurring on tree trunks. In the Athens area the species is fairly common.

Carroll (1945) found it on moist soil in northern Georgia. Solberg and Miller (1979) likewise found it on soil in North Carolina.

Adaptations

Zhu and So (2001) suggested the leaf lobules of liverworts like ***Radula obconica*** (Figure 58) served as water reservoirs, an adaptation useful for their epiphytic and epiphyllous habitats and terrestrial rock substrates. This is probably not helpful in constantly moist or wet habitats, but for this species in swamp habitats, it is likely to have multiple drying events per year.

Reproduction

Radula obconica (Figure 58) is **monoicous** (Lorenz 1918), suggesting that it should produce frequent sporophytes. It appears to produce lots of perianths (Figure 66). However, Standley (1914) found only sterile plants in North Carolina.

Figure 66. ***Radula obconica*** with numerous perianths. Photo by Paul G. Davison, with permission.

Biochemistry

Crandall-Stotler (1971) described the development of oil bodies in ***Radula obconica*** (Figure 58). These develop in the youngest cells by fusing small, osmiophilic droplets that originate from chloroplasts. She suggested that these oil bodies function in storage of reserve photosynthate. Other researchers argue that the function is primarily ecological, performing such adaptive functions as frost protection, desiccation protection, or inhibiting insect attack (Crandall-Stotler 1971; Gradstein 1978). We now know that oil bodies serve as a reservoir of secondary compounds, and these have a wide range of ecological functions (Millar *et al*. 2007).

In experiments, Chen *et al.* (2018) found that ***Radula obconica*** plants grown in continuous darkness for 31 days lacked osmiophilic spherules in the matrix. Chen and coworkers concluded that this suggests a degradation of lipophilic contents in the dark.

Millar *et al*. (2007) examined the antimicrobial properties of this and a number of other North American species. ***Radula obconica*** (Figure 58) exhibited the greatest antibacterial activity, especially against the bacterium ***Bacillus subtilis*** (Figure 68). They concluded that antimicrobial activity is greater in taxa having oil bodies, such as this one. The most activity from the extracts was that of bibenzyls – widespread compounds in liverworts.

Figure 67. ***Radula obconica*** leaf cells with a single large, segmented oil body. Photo by Blanka Aguero, with permission.

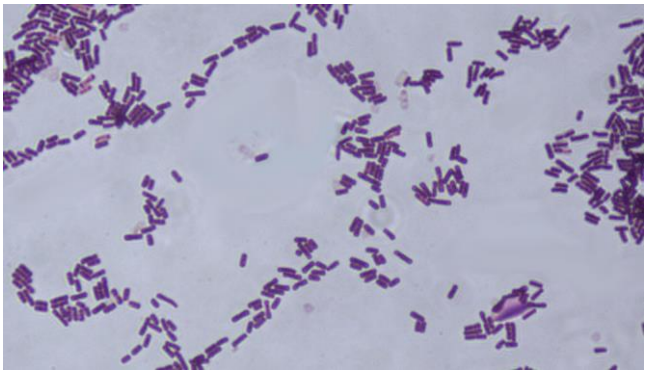


Figure 68. ***Bacillus subtilis*** with Gram stain, a species that is inhibited by ***Radula obconica*** extracts. Photo by Riraq25, with permission.

Radula prolifera (Figure 69)

Distribution

Radula prolifera (Figure 69) is a boreal species from Siberia, Alaska (Renner *et al.* 2010), Yukon, Northwest Territories, and British Columbia (Hong 1987; Godfrey & Schofield 1979).

Figure 69. ***Radula prolifera***, a mostly boreal species. Photo by Earth.com, with permission.

Aquatic and Wet Habitats

Records of ***Radula prolifera*** (Figure 69) are somewhat scanty. Its claim to aquatic and wetland habitats is its appearance on a south-facing wet cliff in the Upper Bureya River of the Russian Far East (Konstantinova *et al*. 2002). Fedosov *et al*. (2018) found it on dry clayish ground on a gentle slope in the Russian Arctic – not an aquatic habitat. Similarly, Köckinger (2016) found it in cold, wind-exposed habitats of the Siberian Arctic and Alaska, another terrestrial habitat. But Sofronova (2015) found it on soil, stones covered with soil, and on rock outcrops in wet and lichen tundra of northeastern Yakutia.

Adaptations

Radula prolifera (Figure 69) forms both large and small continuous **mats** in northeastern Yakutia (Sofronova 2015). It has extensive branching that enables it to spread through mosses and other plants that provide it with shelter

(Schuster & Steere 1958) and most likely help it to maintain hydration.

Reproduction

Castle, in 1950, described the species with little information on its reproduction. Perianths were unknown, as were any specialized means of asexual reproduction. Zheng and Zhu (2009) reported that the chromosome number of ***Radula prolifera*** (Figure 69) was *n*=6.

Radula voluta (Figure 70-Figure 72)

Distribution

Radula voluta (Figure 70-Figure 72) is widespread in the tropics. It occurs in Uganda (Sass-Gyarmati & Pócs 2014), Kenya (Enroth *et al*. 2019), Rwanda, and Zaire, (as *R. allamanoi*) (Yamada 1993). To these, Hylander *et al*. (2010, 2013) have added Ethiopia and noted that the species is widespread in Africa. Kürschner (2003) likewise considered it to be widespread in Africa and added Bioco, Madagascar, Malawi, Mauritius, Réunion, South Africa, and Tanzania to this list (Jones 1977; Wigginton 2002; Wigginton & Grolle 1996). Chuah-Petiot (2001) reported it from Kenya. In Europe it has been reported only from the British Isles (Yamada 1993). It is also known from North America (Mescal *et al*. 1980) – North Carolina and Tennessee (Schuster 1980), South America – Brazil and Peru (Schuster 1980), Costa Rica (Holz & Gradstein 2005), and the Galapagos Islands (Yamada & Gradstein 1991). In Bolivia it was known as both *Radula. appendiculata* and *Radula grandiloba* (Yamada 2000; Kürschner 2003).

Figure 70. ***Radula voluta***, a widespread tropical species. Photo by Paul G. Davison, with permission.

Bosanquet (2015) noted that the British Isles, and in particular Wales, were disjunct locations for ***Radula voluta*** (Figure 70-Figure 72). He noted the importance of humidity from a waterfall in creating a suitable habitat there for this tropical species.

Aquatic and Wet Habitats

Watson (1919) reported ***Radula voluta*** (Figure 70-Figure 72) as occasionally submerged. M'Ardle *et al*. (1898) found it at the Torc Waterfall in Killarney, Ireland. It occurred on rocks in the stream (Figure 1) and covered one boulder that they considered would be frequently submerged.

Figure 71. ***Radula voluta***. Photo by Paul G. Davison, with permission.

Figure 72. ***Radula voluta*** showing ventral lobes and underleaves. Photo by Paul G. Davison, with permission.

Callaghan *et al*. (2019) described ***Radula voluta*** (Figure 70-Figure 72) as a hyperoceanic liverwort having conservation interest. Since ravines are preferred sites for many bryophytes, the researchers were concerned with the potential loss of species due to hydroelectric power development. They were fortunate to mark population areas (Figure 74) and assess before and after populations with an interval of 4 years. They found that larger bryophytes, especially ***Ctenidium molluscum*** (Figure 73-Figure 75), increased in area, crowding out smaller species. ***Radula voluta***, however, was able to grow over and through these larger species. On the other hand, this species declined by the greatest cover (by 40%), due to loss of a small population on a single large rock.

In Kenya, Chuah-Petiot (2001) considered ***Radula voluta*** (Figure 70-Figure 72) to be **rupicolous** (living among, inhabiting, or growing on rocks; Figure 73). Pescott (2019) reported it among the rare bryophytes from calcareous rocks in the Galtee Mountains of Ireland. This most likely applies to both aquatic and terrestrial habitats.

Figure 73. ***Ctenidium molluscum*** in rock canyon in Europe, a species that crowds out other bryophytes following modification of the habitat for hydroelectric power; ***Radula voluta*** is able to grow over and among it. Photo by Michael Lüth, with permission.

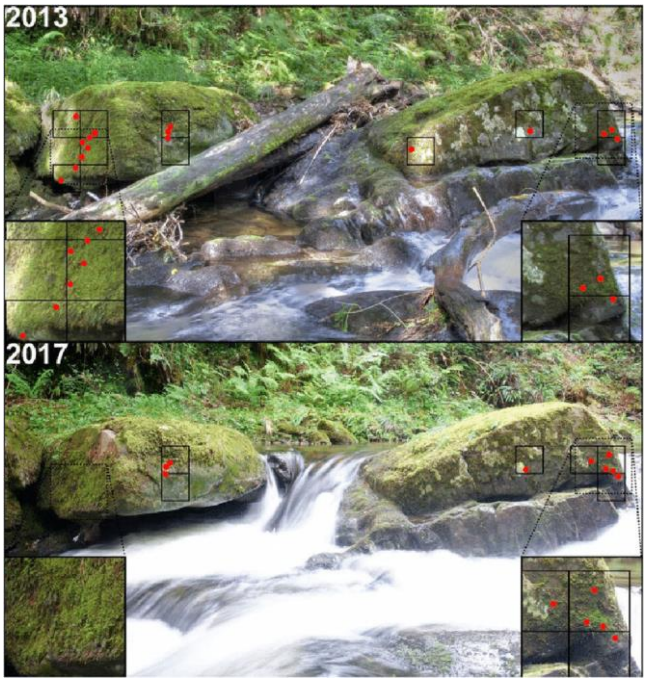


Figure 74. ***Radula voluta*** marked locations and occupied 25 cm grid cells of ***Radula voluta*** in Plot 4 at Period 1. From Callaghan *et al*. 2019, with permission.

Figure 75. ***Ctenidium molluscum***, a competitor of many bryophytes when the habitat is modified. Photo by Michael Lüth, with permission.

Adaptations

Gradstein and León-Yánez (2020) described ***Radula voluta*** (Figure 70-Figure 72) as a **smooth mat** (Figure 76**)** on ***Polylepis pauta*** (Figure 77-Figure 78) in Ecuador. They found that life forms of bryophytes differed based on moisture, with **smooth mats** predominating in the drier Mojanda and **rough mats** in the more moist páramo Papallacta. Holz *et al*. (2002) described their growth on shrubs in Costa Rica as **feathers** (Figure 79). In sharp contrast to the **smooth mats** in the ***Polylepis pauta*** forest, Homeier *et al*. (2008) reported ***Radula voluta*** as **pendent** in the Andean forests of southern Ecuador.

Figure 76. ***Radula voluta*** growing in a **smooth mat** life form. Photo by Paul G. Davison, with permission.

Figure 77. ***Polylepis pauta*** forest with numerous bryophyte cushions on the branches and trunks. Photo from Gradstein & León-Yánez 2020, with permission.

Figure 78. ***Polylepis pauta*** forest. Photo from Gradstein & León-Yánez 2020, with permission.

Figure 79. ***Radula voluta*** growing with a **feather** life form. Photo by Stan Phillips, through public domain.

Discussions of adaptations in ***Radula voluta*** (Figure 70-Figure 72) seem to be absent. The photo of the stem (Figure 80) by Paul Davison seem to indicate no adaptation there for drying out, with all cells thin-walled.

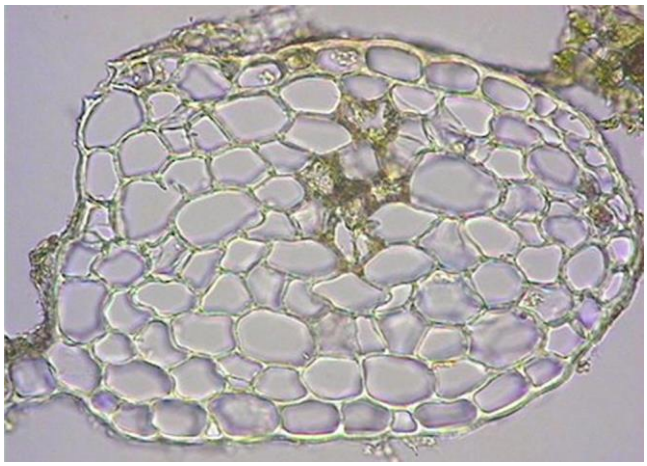


Figure 80. ***Radula voluta*** stem cross section showing no special adaptations for drying out. Photo by Paul G. Davison, with permission.

Reproduction

This species is **dioicous** and usually sterile (Figure 81) (Krayesky *et al*. 2018). Furthermore, sporophytes are unknown. It also lacks caducous leaves as a reproductive mechanism. It does, however, produce gemmae on the margins and median cells of the leaves, but these are produced rarely and often absent. Thus it is not surprising that this species is a poor disperser, at least in the British Isles where asexual propagules are unknown (Bosanquet & Dines 2011). However, in Rio de Janeiro, da Costa (2009) did find it with male branches and described it as a widespread species in southern Brazil.

Biochemistry

Kraut *et al*. (1997) verified the presence of two prenylated bibenzyl derivatives from ***Radula voluta*** (Figure 70-Figure 72). Nagashima and Asakawa (2011) isolated two known bibenzyls and elucidated their structure. Potential uses of bis-bibenzyls in liverworts include antimicrobial, antifungal, antiviral, cytotoxic, anti-oxidant, muscle relaxing, and antiobesity activity (Asakawa 2017).

Figure 81. ***Radula voluta*** with perianths but no indication of sporophytes. Photo by Jan-Peter Frahm, with permission.

Radula wichurae

Distribution

Radula wichurae occurs in the Azores, Madeira, and Canary Islands (Bouman & Dirkse 1990).

Aquatic and Wet Habitats

Radula wichurae is known from deep ravines and wet rocks in the Canary Islands (Bouman & Dirkse 1990).

Adaptations

Radula wichuraecis olive-green, becoming brown with age (Bouman & Dirkse 1990). The cell wals are typically thin, but can be thick and have trigones. This suggests variability, either genetic or induced by habitat conditions.

Reproduction

Radula wichurae is **dioicous** and leaf gemmae are unknown (Bouman & Dirkse 1990).

Ptilidiales: Ptilidiaceae

Ptilidium ciliare (Figure 82-Figure 85)

Ptilidium ciliare (Figure 82-Figure 85) is a bipolar species and was considered to be the progenitor of ***P. pulcherrimum*** (Figure 112-Figure 114) and ***P. californicum*** (Figure 86-Figure 88). However, using chloroplast DNA, Kreier *et al*. (2010) show that while this seemed to be a sound conclusion for ***P. pulcherrimum***, it was not for ***P. californicum***. They found indications that ***P. ciliare*** shared DNA with populations in Europe and the Southern Hemisphere; ***P. pulcherrimum*** shared DNA similarities with that in Europe. In New Zealand, it is sometimes recognized as a separate species, ***Ptilidium hodgsoniae***, a species not recognized by Söderström *et al*. (2016). Kreier and coauthors proposed that long-distance dispersal resulted in its bipolar distribution, including southern South America.

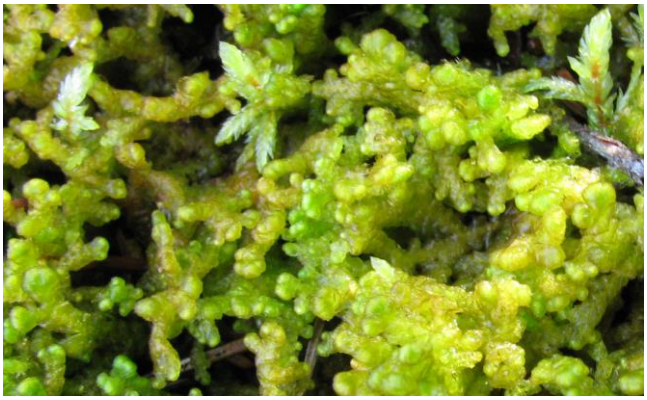


Figure 82. ***Ptilidium ciliare***, a bipolar species of leafy liverwort. Photo by Janice Glime.

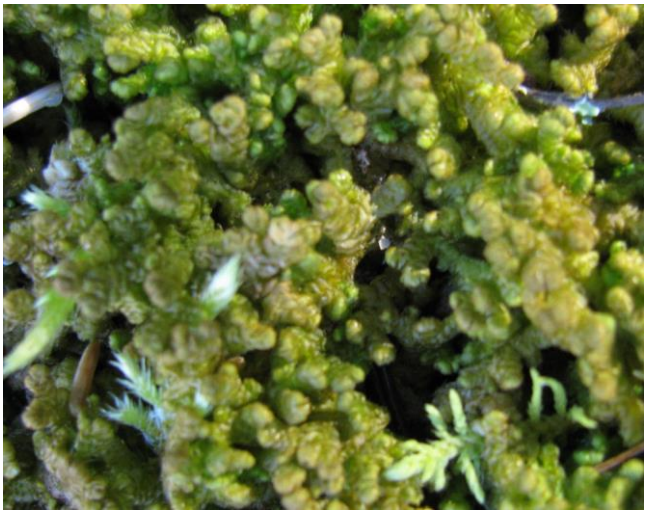


Figure 83. ***Ptilidium ciliare*** growing at Horseshoe Harbor, Copper Harbor, Michigan, USA. Photo by Janice Glime.

Figure 84. ***Ptilidium ciliare***, a mostly terrestrial species but that also occurs in poor fens and bogs. Photo by Hermann Schachner, through Creative Commons.

Figure 85. ***Ptilidium ciliare*** showing its finely divided leaves. Photo by Michael Lüth, with permission.

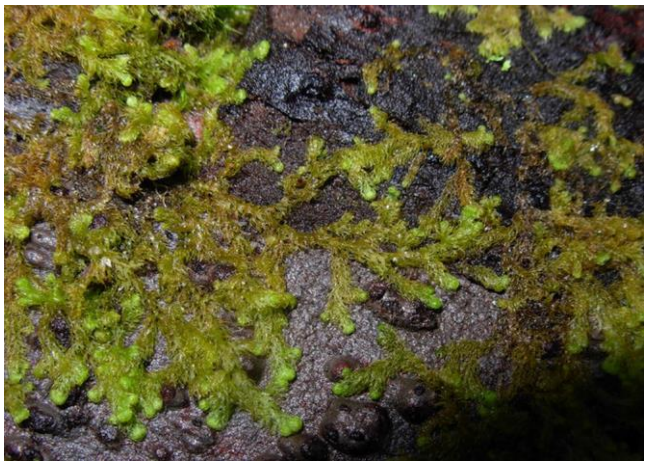


Figure 86. ***Ptilidium californicum***, a species once thought to be a derivative of ***Ptilidium ciliare***. Photo by Chris Wagner, through Creative Commons.

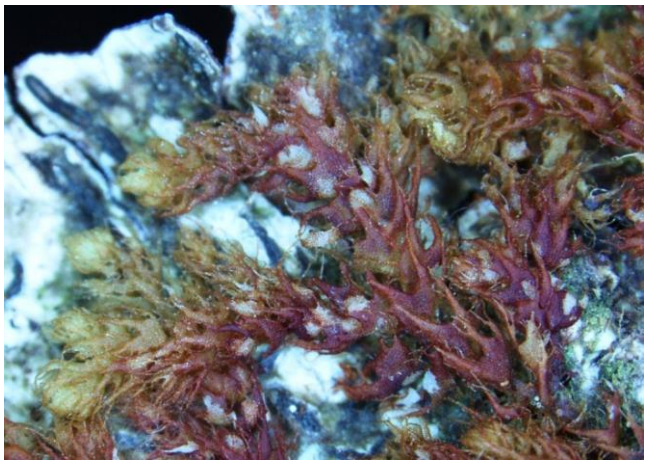


Figure 87. ***Ptilidium californicum*** showing divided leaves and red coloration except at growing tips. Photo from Botany Website, UBC, with permission.

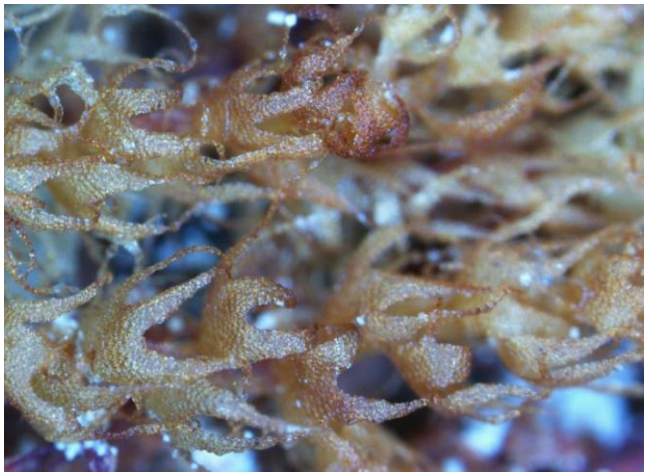


Figure 88. ***Ptilidium californicum*** close view of divided leaves. Photo from Botany Website, UBC, with permission.

Distribution

Ptilidium ciliare (Figure 82-Figure 85) occurs in the northeastern USA, south to Pennsylvania, where it is rare (Schuster 1966). More recently, Sass-Gyarmati *et al*. (2005) found it in the Metaliferi Mountains in Romania. It is distributed in Greenland, Scandinavia, south to Spain and Italy, and very rare in Japan. It is well adapted to cold climates, making it widespread in the boreal region (Schuster 1966).

Aquatic and Wet Habitats

I know this liverwort mostly from the overhanging cliffs along the Lake Superior shore. Nichols (1918) reported it from the moist hollows between ***Sphagnum*** hummocks (Figure 89) on Cape Breton Island, Canada. Schuster (1966) considered it to be rare in bog holes such as those in Minnesota. But in most cases, this is a terrestrial species (Elumeeva *et al*. 2011).

Figure 89. ***Sphagnum fuscum*** hummock; ***Ptilidium ciliare*** can be found in moist hollows between ***Sphagnum*** hummocks. Photo by Michael Lüth, with permission.

Boudreault *et al*. (2002) considered ***Ptilidium ciliare*** (Figure 82-Figure 85) to be a robust species in eastern boreal forests of Canada. They found that its importance value, along with that of ***Sphagnum fuscum*** (Figure 90), increased over time since fire, becoming maximal in forests more than 200 years old. Turetsky *et al*. (2012) found that late successional bryophyte species such as ***Ptilidium ciliare*** and the feather mosses diminish soon after fires in boreal forests and peatlands, being replaced by ***Polytrichum piliferum*** (Figure 91) and ***Polytrichum juniperinum*** (Figure 92). On the other hand, Nguyen-Xuan *et al*. (2000) found that ***Ptilidium ciliare*** tended to be more frequent after logging in black spruce (***Picea mariana*** - Figure 93) forests.

Figure 90. ***Sphagnum fuscum*** hummock, a species that increases following fire. Photo by Jutta Kapfer, with permission.

Figure 91. ***Ptilidium ciliare*** and ***Polytrichum piliferum*** on sand; ***Polytrichum piliferum*** can replace ***Ptilidium ciliare*** after a fire. Photo by Janice Glime.

Figure 92. ***Polytrichum juniperinum*** with capsules, a species that can replace ***Ptilidium ciliare*** after a fire. Photo by Paul Wilson, with permission.

Figure 93. ***Picea mariana*** forest, a habitat where the presence of ***Ptilidium pulcherrimum*** indicates a low *p*H. Photo from Western Arctic National Parklands, through Creative Commons.

In his North American treatment, Schuster (1966) described the habitat of ***Ptilidium ciliare*** (Figure 94) as mostly on thin soil over rock.

Figure 94. ***Ptilidium ciliare*** on rock, showing lack of a thick soil layer. Photo by Andy Hodgson, with permission.

Bryophytes are able to collect heavy-metal pollution and can thus be used in bioassays. Salemaa *et al*. (2001) assessed heavy-metal pollution along a gradient in southwest Finland and found the lichen ***Cladina*** spp. (Figure 95) could not be found within 2 km of the source, with some ***Cladina*** spp. not found within 3 km. ***Ptilidium ciliare*** (Figure 82-Figure 85), on the other hand, was found for the first time in the area, but only beyond 2 km. Al-Asheh and Duvnijak (1999) included ***Ptilidium ciliare*** in their assessment of sorption of heavy metals from synthetic metal solutions and industrial wastewater, but they did not separate the results by species.

Figure 95. ***Cladina*** spp., a genus less sensitive to heavy metal pollution than ***Radula ciliare*** in Tyresta. Photo by Peder Curman, through Creative Commons.

Jägerbrand *et al*. (2003) determined responses of various bryophytes to simulated environmental change in northern Sweden. The greatest response was by ***Rhytidium rugosum*** (Figure 96), which exhibited a significant decrease in abundance following treatment of increased temperature and fertilizer. ***Ptilidium ciliare*** (Figure 82-Figure 85) showed a similar but not significant trend.

Figure 96. ***Rhytidium rugosum***, a moss species that exhibits a significant decrease in abundance in response to increased temperature. Photo by Hermann Schachner, through Creative Commons.

Adaptations

In its tundra and boreal forest habitats, ***Ptilium ciliare*** (Figure 82-Figure 85) typically forms **cushions** (Figure 97) (Elumeeva *et al*. 2011; Soudzilovskaia *et al*. 2011), but Elumeeva and coworkers also referred to it as a **mat** (Figure 97). Similarly, Schuster (1966) described these growths as "deep, loose, often flocculent **mats** or **tufts**" (Figure 98). Soudzilovskaia *et al*. (2011) found that in these northern habitats, cushion thickness (Figure 99) was a good predictor of temperature and was species-specific.

Figure 97. ***Ptilidium ciliare*** forming a cushion or thick mat. Photo by Janice Glime.

Figure 98. ***Ptilidium ciliare*** showing thick mat or "tuft." Photo by Li Zhang, with permission.

Figure 99. ***Ptilidium ciliare*** exhibiting a life form that approaches a **cushion** or **weft**. Photo by David Holyoak, with permission.

A common adaptation in aquatic plants is dissected leaves. This often is manifest in divided underwater leaves and ovate or otherwise undivided leaves that develop above water. This adaptation does not seem to occur among aquatic bryophytes. We have assumed that the fine divisions facilitate CO_2 absorption and thus increase photosynthetic efficiency. With leaves only one cell thick, this is much less of a problem for liverworts. So we might ask why ***Ptilidium*** species have finely divided leaves (Figure 100). It is not a species that is commonly submersed. But it does permit parts of leaves to be exposed to the sun, including the ability of the sun to penetrate into the mat which can at times become quite thick. I am inclined to think that the fimbriate leaves of species like ***Ptilidium ciliare*** and ***Trichocolea tomentella*** might be an adaptation for rapid uptake and later retention of water by creating numerous capillary spaces – an advantage in their sometimes quite wet and other times quite dry habitats.

Figure 100. ***Ptilidium ciliare*** showing the finely divided leaves. Photo by Jan-Peter Frahm, with permission.

Water economy is important in the rocky habitats where ***Ptilidium ciliare*** (Figure 82-Figure 85) lives, due to the drying events (Figure 101). Elumeeva *et al*. (2011) described water economy traits of shoots and colonies for 22 subarctic species. They found that individual shoot properties (leaf cell wall properties, water retention capacity, and desiccation rate) did not correspond with colony water retention capacity. Rather, the colony desiccation rate depended on the density of the water-saturated colonies (Figure 102). It appears that ***Ptilidium ciliare*** acts much like a sponge, with its dissected leaves providing small capillary spaces that trap water and hold it by adhesion and cohesion.

Figure 101. ***Ptilidium ciliare*** in a dry state at Horseshoe Harbor, Copper Harbor, Michigan, USA. Photo by Janice Glime.

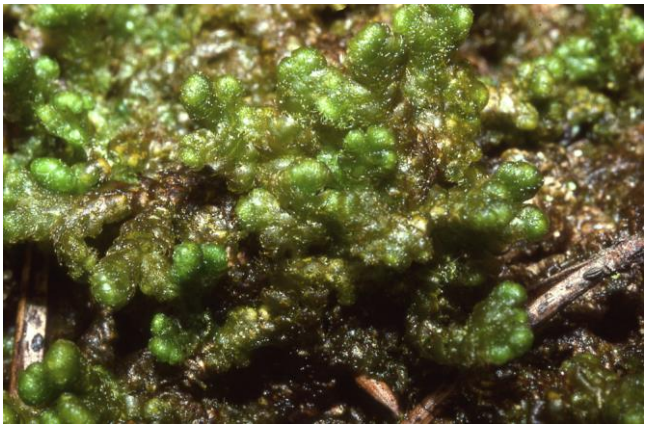


Figure 102. ***Ptilidium ciliare*** wet. Photo by Janice Glime.

Lang *et al*. (2012) conducted a 5-year experiment on the warming effect on tundra bryophytes on two continents. These showed no significant effect on ***Ptilidium ciliare*** (Figure 82-Figure 85), but I must caution that in this ecosystem with a short growing season and slow-growing organisms, it may take longer before any significant effect is rendered. In a longer experiment (9-16 years), bryophytes were less sensitive to warming than were lichens.

Street *et al*. (2018) tested the responses of the moss layer to increased nitrogen and phosphorus in a tundra environment. They found that individual bryophyte species responded differently. This included the increase of ***Ptilidium ciliare*** (Figure 82-Figure 85) in P-treated plots.

I have thus far not found studies on the effects of bright light, especially UV light, on ***Ptilidium ciliare***, but my own experience (Figure 103) and the pictures I have found (Figure 104-Figure 105) suggest that development of reddish to brown coloration may protect it from light damage. It could also be beneficial in absorbing sunlight and warming the liverwort on sub-freezing days with no snow cover.

Figure 103. ***Ptilidium ciliare*** showing the red coloration that can protect it from bright light, especially in cold weather that can occur before snow protects it or before leaves form a canopy (late April 1983) in Michigan, USA. Photo by Janice Glime.

Reproduction

Ptilidium ciliare (Figure 82-Figure 85) is **dioicous**, making sexual reproduction difficult, but it does sometimes occur (106). However, it is possible that fragments may play a role in its asexual reproduction and dispersal. Kowalczyk *et al*. (1997) cultured sterilized gametophyte fragments. Typically, for the ten species tested, including ***Ptilidium ciliare***, terminal portions and leafless shoots proved to be most suitable for culture of new shoots. They found that 50% commercial bleach (ACE) solution for 0.5-1 minute was the most effective way to sterilize this species.

Figure 104. ***Ptilidium ciliare*** exhibiting a dark coloration, presumably protecting it from high light intensity. Photo by Michael Lüth, with permission.

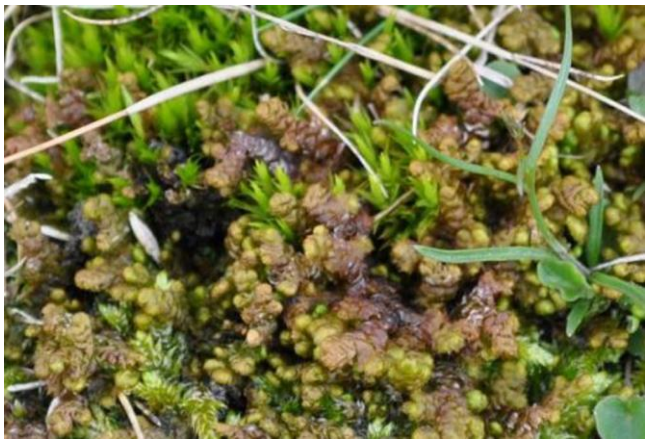
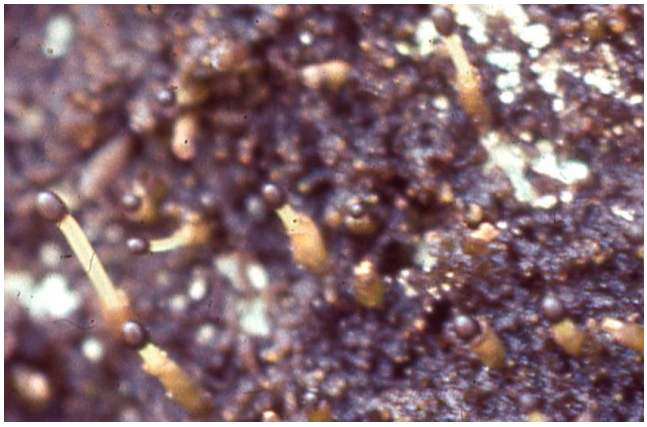


Figure 105. ***Ptilidium ciliare*** exhibiting reddish coloration among grasses and mosses that are typical sun species. Photo by Andrew Hodgson, with permission.



106. ***Ptilidium ciliare*** with capsules, Dollar Bay, Michigan, USA. Photo by Janice Glime.

Role

Bryophytes often serve as seed beds because they can alter the soil environment in ways that are often favorable for germination. Soudzilovskaia *et al*. (2011) assessed the role of six bryophyte species, including ***Ptilidium ciliare*** (Figure 82-Figure 85), in the germination of tracheophyte seeds. Temperature was modified by the thickness of the cushions of bryophytes and the specific temperatures created by each species was an important parameter in determining germination in these locations (Figure 107). The highest level of germination under bryophyte cover occurred under ***P. ciliare*** (Figure 107). Soil temperatures under ***Ptilidium ciliare*** had one of the top two highest amplitudes in monthly and growing season temperatures. The sums of temperatures in May were higher, but those in September were lower under ***P. ciliare*** than under most other species in the study.

In the tundra, bryophytes can be an important food source, especially during seasons with low productivity of tracheophytes. ***Ptilidium ciliare*** (Figure 82-Figure 85) is one of the common species there, so Olofsson *et al*. (2004) included it in their study of herbivore impacts. They found that large and small herbivores did indeed use ***P. ciliare*** as a food source. But at the same time, it was the only species in the study for which the exclosure led to a decrease in species abundance. Liverworts are considered to be weak competitors, succeeding only where herbivores or disturbance eliminate some of the competitive pressures. Size-dependent exclosures revealed that voles and lemmings have larger effects on the plant community structure than do reindeer at all four locations in the study.

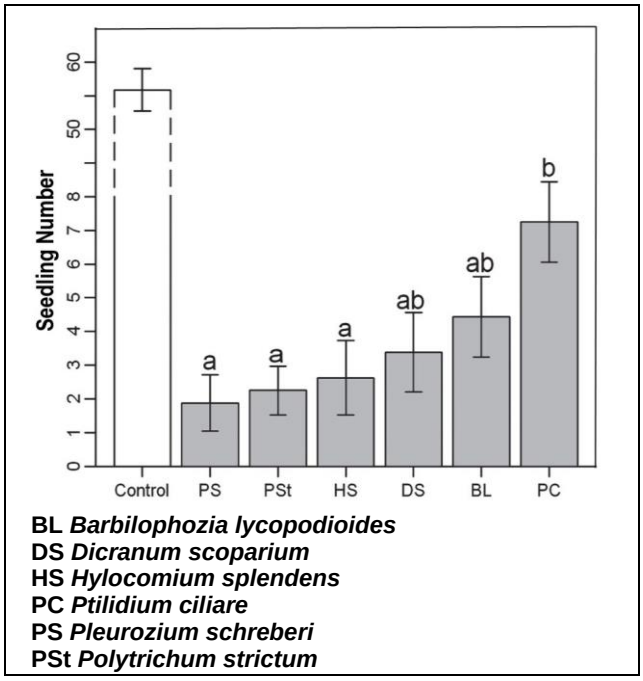


Figure 107. Number of tracheophyte plant seedlings (pooled) germinated in the field experiment by Soudzilovskaia *et al*. (2011) as affected by bryophyte species. Values are mean ± standard error; *n*=8. Different letters indicate significant differences in mean (Tukey *post hoc* test). Controls were not included in the statistical analysis in order to show the more subtle differences among bryophyte species. Modified from Soudzilovskaia *et al*. 2011.

Nitrogen fixation by Cyanobacteria in association with ***Ptilidium ciliare*** (Figure 82-Figure 85) appears to be absent in the Abisko region of Sweden (Gavazov *et al*. 2010). Testing locations included a nutrient-poor birch forest with ericaceous undergrowth, an oligotrophic bog dominated by ***Sphagnum fuscum*** hummock (Figure 90) communities, and a minerotrophic mire (fen).

Salemaa *et al*. (2019) found that low levels of nitrogen pollution suppressed N_2 fixation in the boreal forest, including that of ***P. ciliare***, but this species did show positive activity in a growth chamber. For it to register a positive nitrogen fixation, the colony had to acclimate to the high temperature of the growth chamber. These restrictions might account for the absence of N fixation for this species in the Gavazov *et al*. study. Rousk *et al*. (2017) found contrasting results in the High Arctic, where ***P. ciliare*** was also among the dominant bryophytes. They reported that all vegetation types exhibited a rapid transfer of fixed N_2 to other ecosystem components. On the other hand, hardly any ^{15}N was recovered in soil microbes in the bryophyte plots. Uptake was greater in the cottongrass-bryophyte plots, and the researchers suggested that the wetness of this bryophyte-dominant ecosystem could be responsible for the greater rate, or a difference in bryophyte species. Their data suggested that nitrogen fixation by bryophyte-Cyanobacteria associations provide a high contribution of N to the habitat where they occur.

Fungal Interactions

Döbbeler (1997) reported the **Ascomycetes** fungus ***Octosporella ptilidii*** (Figure 108) growing on ***Ptilidium ciliare*** (Figure 82-Figure 85). Later, Döbbeler *et al*. (2015) reported that 12 **Ascomycetes** have been recorded on both ***Ptilidium pulcherrimum*** (Figure 111-Figure 114) and ***P. ciliare.***

Figure 108. ***Octosporella fusispora***; ***Octosporella ptilidii*** is known from ***Ptilidium ciliare***. Photo by A. Gardiennet, through Creative Commons.

Biochemistry

The biochemistry is a little better known for this large liverwort species than for the tiny ones. Deoxopinguisone was isolated from ***Ptilidium ciliare*** (Figure 82-Figure 85) (Krutov *et al.* 1973). ***Ptilidium ciliare*** is known to have barbatane-, daucane- and pinguisane-type sesquiterpenoids

and dolabellane- and fusicoccane-type diterpenoids (Nagashima *et al.* 1999) .

Adamczak *et al*. (2005) used genetic markers to distinguish between ***Ptilidium ciliare*** (Figure 82-Figure 85) and ***P. pulcherrimum*** (Figure 111-Figure 114). Both species were polymorphic; ***P. ciliare*** exhibited alternative alleles at three loci; ***P. pulcherrimum*** exhibited alternative alleles at four. They furthermore found that asexually reproducing ***P. ciliare*** had lower total gene diversity than did the sexual plants of ***P. pulcherrimum***. ***Ptilidium ciliare*** further exhibited allele numbers and frequency differences between geographic regions.

Ptilidium pulcherrimum (Figure 109, Figure 111-Figure 114)

Ptilidium pulcherrimum (Figure 109) has the reputation of occurring in Eocene Baltic amber (Figure 110), but Heinrichs *et al*. (2015) challenge this identification. On re-investigation, they found that it was a better fit for the liverwort genus ***Tetralophozia***, renaming it ***Tetralophozia groehnii*** as a new species. A second specimen could not be located, but based on the description, they considered it to be morphologically similar to the North Pacific endemic ***Ptilidium californicum*** (Figure 86-Figure 88). DNA evidence from ***Ptilidium pulcherrimum*** supported the conclusion that the fossil did not represent ***P. pulcherrimum***.

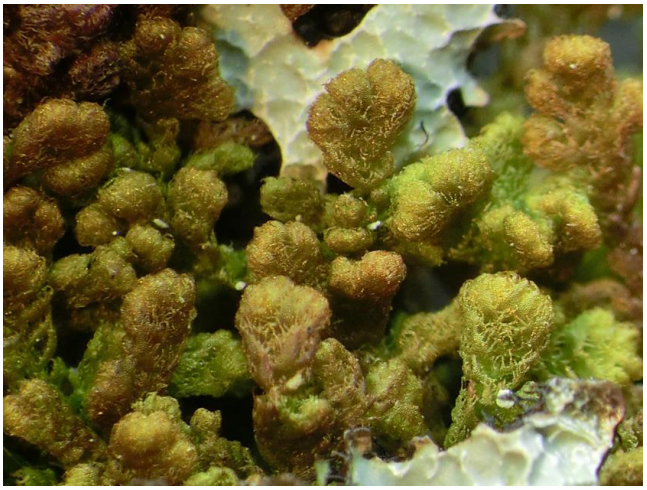


Figure 109. ***Ptilidium pulcherrimum*** a species once considered to be the same as one found in amber. Photo by Michael Lüth, with permission.

Distribution

Ptilidium pulcherrimum (Figure 111-Figure 114) has a Holarctic distribution, south to the deciduous forest. In Europe, it extends from Scandinavia to Italy and Bulgaria, England and Scotland, eastward to Siberia, China, and Japan (Schuster 1966). In North America, it occurs from Alaska southward to British Columbia, Alberta, Montana, Idaho, and Washington. In 2005, Keçeli and Çetin reported ***P. pulcherrimum*** as new from Turkey. In 2011, Singh and Singh reported it as new from India. But in Japan, it was already considered to be "not uncommon" in 1952 (Hattori 1952).

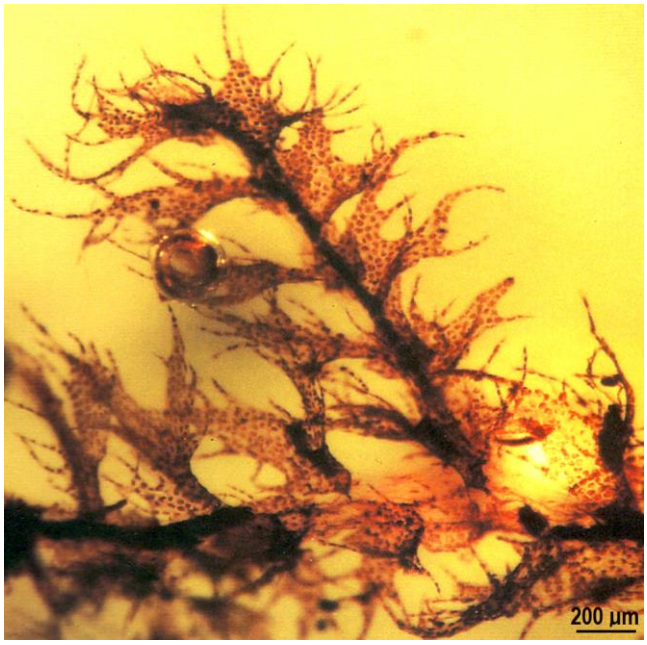


Figure 110. ***Tetralophozia groehnii*** (previously identified as ***Ptilidium pulcherrimum***) in amber. Photo from Heinrichs *et al*. 2015, through PLOS One Creative Commons.

Figure 111. ***Ptilidium pulcherrimum***, a Holarctic species with deeply divided leaves. Photo by Michael Lüth, with permission.

Figure 112. ***Ptilidium pulcherrimum*** branches. Photo by J. C. Schou, with permission.

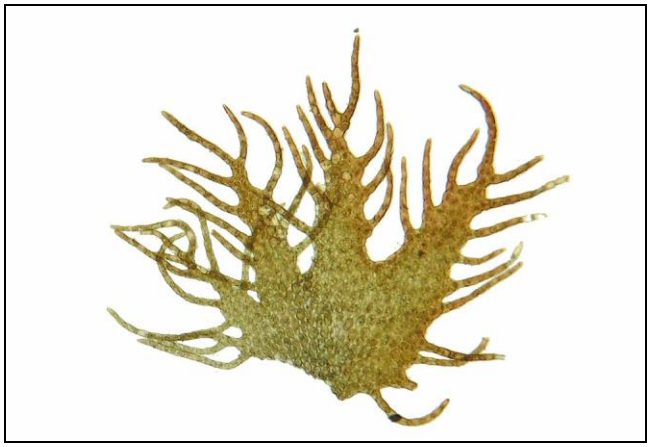


Figure 113. ***Ptilidium pulcherrimum*** showing the deeply divided leaf. Photo by Michael Lüth, with permission.

Figure 114. ***Ptilidium pulcherrimum*** showing leaves curling as they begin to dry. Photo by Martin Hutten, with permission.

Aquatic and Wet Habitats

Like ***Ptilidium ciliare*** (Figure 82-Figure 85), ***P. pulcherrimum*** (Figure 111-Figure 114) has little claim to the aquatic environment. For the eastern United States, Schuster (1966) reported as mostly restricted to trees in bogs (& poor fens) among its habitats, although I know it mostly from decorticated logs in that region. It was one of the bryophytes I found on the wall of the Flume, a damp habitat at Franconia Notch, New Hampshire, USA (Glime 1982).

Adaptations

In India, Singh and Singh (2011) found that ***Ptilidium pulcherrimum*** (Figure 111-Figure 114) grows prostrately or ascending in thin, straggling, or dense **mats**. It is yellowish-brown (Figure 115) to purplish-brown, becoming reddish-brown (Figure 116) when dry in the herbarium.

Clausen (1964) found evidence that ***Ptilidium pulcherrimum*** (Figure 111-Figure 114) is very desiccation tolerant. Using Danish populations, he showed that it retains 100% cell viability after 12 hours at 15% relative humidity at 20ºC. It also survived 11-12 days at -10ºC and in ice at -40ºC for 24-26 hours.

Figure 115. ***Ptilidium pulcherrimum*** exhibiting the brownish golden color that can be seen in locations with more light. Photo by Michael Lüth, with permission.

Figure 116. ***Ptilidium pulcherrimum*** in a dry state and showing its reddish-brown coloration in an exposed situation. Photo by Michael Lüth, with permission.

Reproduction

Söderström (1989) found sexually reproducing individuals at nearly all locations, despite the **dioicous** condition of this species (Schuster 1966). Its frequent fertility (Figure 117) has been reported multiple times (Schuster 1966; Söderström 1989; Singh & Singh 2011).

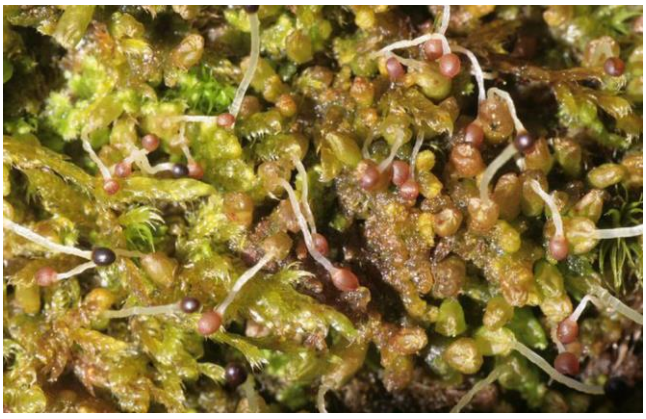


Figure 117. ***Ptilidium pulcherrimum*** with capsules, a relatively common appearance despite its dioicous condition. Photo from Snappy Goat, through public domain.

Söderström (1994) suggested that the size of spores may be important in limiting spore dispersal distance. In ***Ptilidium pulcherrimum*** (Figure 111-Figure 114) these are typically 25-27 µm, with most (52%) deposited within only a few meters. By comparison those of ***Bryum argenteum*** (Figure 118) has spores 8-14 µm, with only 2-5% landing within the same distance (Söderström & Johnson 1989). For ***Ptilidium pulcherrimum*** in a Swedish coastal spruce forest, the main substrate was rotting wood, accounting for 75% of its occurrences. Its annual spore production was 68,500 spores m^{-2} forest, 640,000 spores m^{-2} substrate, and 44,000,000 spores m^{-2} colony.

Figure 118. ***Bryum argenteum*** with capsules, a species with small spores that travel much farther than the larger ones of ***Ptilidium pulcherrimum***. Photo by Hermann Schachner, through Creative Commons.

Ptilidium pulcherrimum (Figure 111-Figure 114) has no known asexual reproductive structures (Söderström 1989.

Jonsson and Söderström (1988) studied the growth and reproduction of ***Ptilidium pulcherrimum*** (Figure 111-Figure 114) in northern Sweden. They found that the growth rate varied between years (4-year study), but that it was independent of colony size. The mean growth rate was 5.2 mm $year^{-1}$, range 3.5-6.3 mm $year^{-1}$. It has a strikingly long period to first reproduction – 9 years – at a size of about 68 cm^2. The capsules produce an average of 27,000 spores each, with a range of 18,000-44,000.

Jonsson and Söderström (1988) studied reproductive rate in 50 colonies of ***Ptilidium pulcherrimum*** (Figure 111-Figure 114) in northern Sweden. They found that antheridia were not produced until the third year. As the colony size increased, so did capsule density and spore production.

Fungal Interactions

Stenroos *et al*. (2009) described a new genus of lichen, ***Puttea*** (Figure 119), based on the previous lichen species known as *Fellhanera margaritella*. This new monospecific genus occurs almost exclusively on the liverwort ***Ptilidium pulcherrimum*** (Figure 111-Figure 114), but compared to its widespread host, it is relatively rare and has almost entirely a European distribution. It was thus far known from Austria, the Czech Republic, Finland, Norway, Russia, Slovakia, Sweden, and Switzerland. Since 2009, it has been reported from Quebec, Canada, in eastern North America (Buck & Lendemer 2012). ***Puttea margaritella*** (Figure 119) clearly harms the host, causing clearly visible infected areas. The ascomata, on the other hand, develop only on the decaying shoots of the host. Buck and Lendemer (2012) found the same restriction to dead and decaying plant parts. It appears that this lichen also occurs in western North America, but there it occurs on ***Ptilidium californicum*** (Figure 86-Figure 88).

Döbbeler *et al*. (2015) reported two new bryophilous **Ascomycetes**. One of these fungi, ***Trichosphaerella goniospora***, occurs on ***Ptilidium pulcherrimum*** (Figure 111-Figure 114) and was found in New Brunswick Canada. At that time, twelve species of **Ascomycetes** were known from ***P. pulcherrimum***.

Figure 119. ***Puttea margaritella*** (white spots), a species that occurs almost exclusively, but relatively rarely, on ***Ptilidium pulcherrimum***. Photo by Einar Timdal, Natural History Museum, University of Oslo, Norway, through Creative Commons.

Biochemistry

Ptilidium pulcherrimum (Figure 111-Figure 114) is one of the few bryophytes with complete sequencing of the chloroplast genome using NGS technology (Shanker 2012, 2014). Its plastid genome is 119,007 base pairs long, comprising 122 genes. Of these, 88 code for proteins, 4 for rRNAs, and 30 for tRNAs. Forrest *et al*. (2011) suggested that this sequencing could indicate an evolutionary stasis in the plastid genome structure of this liverwort.

Asakawa *et al*. (1981) reported pinguisane-type sesquiterpenes in ***Ptilidium pulcherrimum*** (Figure 111-Figure 114). Guo *et al*. (2009) reported a new trinortriterpenoid and a new diphenylmethane derivative, along with ten previously described pentacyclic triterpenoids and four aromatic compounds. They also evaluated toxicity and found moderate toxicity against PC3 cells. Asakawa *et al*. (2014) noted that liverworts rarely have triterpenoids. But ***Ptilidium pulcherrimum*** possesses several ursane triterpenoids that were active against the growth of PC3 human prostate cancer cells.

The presence of secondary compounds always raises the question of their antibiotic activity, whether it is to discourage herbivores or to be antimicrobial. Veljić *et al*. (2010) found that extracts of ***Ptilidium pulcherrimum*** (Figure 111-Figure 114) showed a stronger effect against tested Gram (+) than Gram (-) bacteria. A methanol extract exhibited a strong antifungal activity. When compared to the synthetic fungicide bifonazol, its best antifungal activity was against ***Trichoderma viride*** (**Ascomycota**; Figure 120) – a fungus that itself has antifungal activity. This fungus causes green mold rot of onions, dieback of ***Pinus nigra*** seedlings (Figure 121), and green mold disease of mushrooms. But it also has antifungal activity against pathogens on plants.

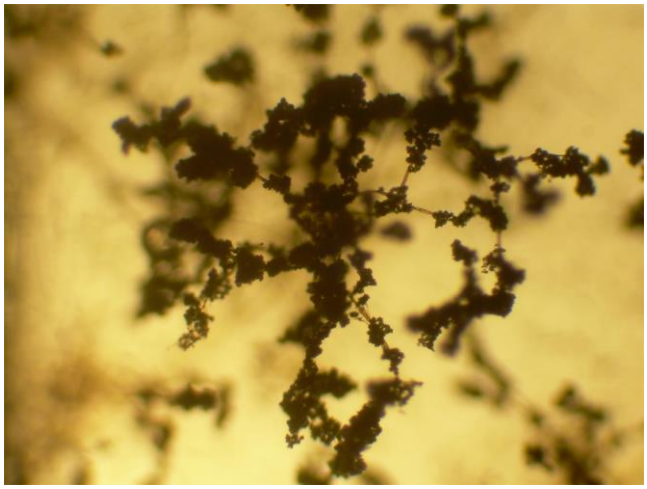


Figure 120. ***Trichoderma viride***, a species that occurs on ***Ptilidium pulcherrimum***, showing its conidiophores from an onion. Photo by Ninjatacoshell, through Creative Commons.

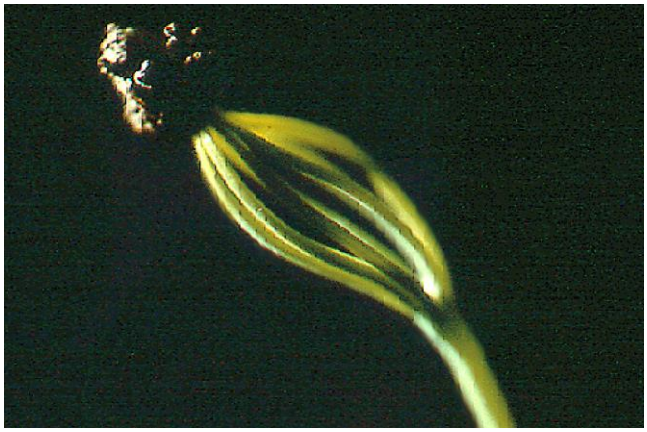


Figure 121. ***Pinus nigra*** seedling, a seedling that can suffer from infection by ***Trichoderma viride*** (**Ascomycota**). Photo by Janice Glime.

Summary

Both **Radulaceae** and **Ptilidiaceae** occur primarily in terrestrial habitats, especially logs and bark. ***Radula aquilegia*** is occasionally submersed or on wet rocks. ***Radula carringtonii*** occurs on rocks that occasionally are wet. ***Radula complanata*** seems to have a broader niche that includes wet cliffs and uncommonly submerged. ***Radula holtii*** occurs in splash zones, on wet rocks, and mountain streams. ***Radula lindenbergiana*** and ***Radula obconica*** likewise occur on wet rocks. ***Radula prolifera*** seems to only rarely be on wet rocks. ***Radula voluta*** is more tolerant of wet habitats, occurring on stream banks, in spray of waterfalls, and sometimes submerged. ***Radula wichurae*** occurs in deep ravines and on wet rocks. ***Ptilidium ciliare*** and ***Ptilidium pulcherrimum*** are predominantly terrestrial, sometimes occurring on cliffs that remain moist because of nearby water, but never submersed.

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Lars Söderström provided me with the current acceptable names for a number of older taxa.

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CHAPTER 1-11: AQUATIC AND WET MARCHANTIOPHYTA, ORDER METZGERIALES: ANEURACEAE

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CHAPTER 1-11: AQUATIC AND WET MARCHANTIOPHYTA, ORDER METZGERIALES: ANEURACEAE

Figure 1. ***Aneura pinguis*** growing in a zone that is just above and below the water surface, keeping it constantly wet. Photo by Michael Lüth, with permission.

As in the other chapters on liverworts in aquatic and wet habitats, nomenclature for this chapter is based primarily on Söderström *et al*. (2016). In addition, Lars Söderström has provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. Information on habitats of these unverifiable taxa has been included with the species.

Many of the species on this list are not typical wetland or aquatic species. They were, however, found in a wetland or aquatic study.

SUBCLASS METZGERIIDAE

Order Metzgeriales

Aneuraceae (Figure 1)

Aneura (Figure 2, Figure 3, Figure 7-Figure 10, Figure 18-Figure 26, Figure 29-Figure 32, Figure 52-Figure 57)

In a study of 48 streams on South Island, New Zealand, Suren and Duncan (1999) found that ***Aneura*** sp. was positively correlated with bankfull discharge. This genus has several species that are typically associated with water.

Bidartondo and Duckett (2010) found sebacinoid fungi in several species of ***Aneura***.

Aneura maxima (Figure 2, Figure 3, Figure 7-Figure 10; Figure 18-Figure 26)

The species ***Aneura maxima*** (Figure 2, Figure 3, Figure 7-Figure 10), ***A. pellioides*** (Figure 4), and ***A. pinguis*** (Figure 5-Figure 6) have created confusion in their identification (Frahm 2012). Frahm (2012) used water culture to determine if characters are modified by the culture conditions. This was done to understand the

distinctions among several ***Aneura*** species. The unilayered thallus margin was retained in ***Aneura maxima*** (Figure 3) and the multilayered thallus margin was retained in ***Aneura pinguis*** in common garden culture of aquatic and terrestrial conditions.

Figure 2. ***Aneura maxima***, one of three species that have been confused with each other. Photo by Jan-Peter Frahm, with permission.

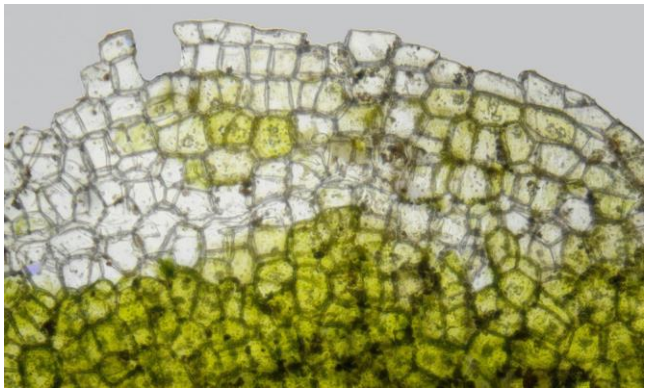

Figure 3 ***Aneura maxima*** showing 1-cell-thick thallus margin. Photo by Dick Haaksma, with permission.

Figure 4. ***Aneura cf pellioides***, one of three species that have been confused with each other. Photo by David Long, with permission.

Figure 5. ***Aneura pinguis***, one of three species that have been confused with each other. Photo by Hermann Schachner, through Creative Commons.

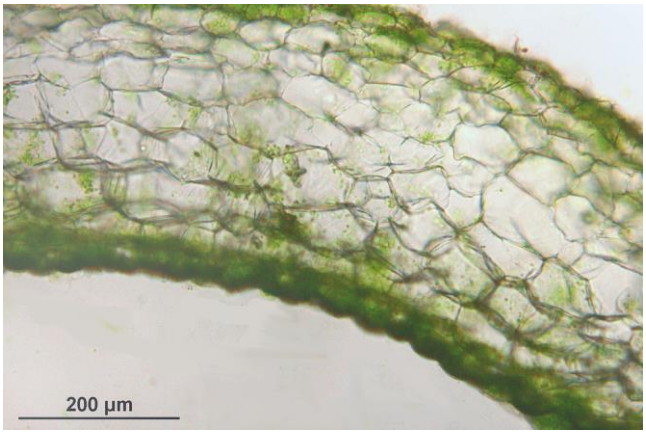

Figure 6. ***Aneura pinguis*** thallus cross section. Photo by Hermann Schachner, through Creative Commons.

Bączkiewicz *et al*. (2017) used DNA evidence to argue that ***Aneura pinguis*** (Figure 5-Figure 6) was comprised of many cryptic species, including ***Aneura maxima*** (Figure 2-Figure 3, Figure 7-Figure 10). I have treated the ones included here as separate species for two reasons. It is easy for the reader to combine the information to describe ***Aneura pinguis***, but once combined under one name it cannot be separated out without further research. Second, I have followed the nomenclature used by Söderström *et al*. (2016) throughout these wet habitat chapters, and they have listed it as a valid species. Furthermore, Buczkowska *et al*. (2016) demonstrated, using ISSR primers, that the ***Aneura maxima*** populations were genetically distinct from those of ***A. pinguis*** and these researchers maintained recognition of the species ***Aneura maxima***.

Distribution

Andriessen (1995) reported ***Aneura maxima*** (Figure 7-Figure 10) from Belgium in Europe, Asia (Indonesia, Japan, India), New Caledonia, and eastern North America. Miller (2002) noted its presence in Maine, and a number of other states in eastern USA. In 2006, Loskotová reported it from the Czech Republic and Slovakia. Later, Sérgio and Garcia (2009) reported it from the Iberian Peninsula, Frahm (2011) from Norway, Ştefănuţ (2012) from Romania, and Buczkowska and Byczkiewicz (2006) from Poland (see also Mierzeńska & Vončina 2010; Wawrzyniak *et al*.

2014). Frahm *et al*. (2009) reported it from Thailand. It is likely to have been collected elsewhere in Europe, hiding under a misidentified name.

Figure 7. ***Aneura maxima*** showing the wavy edge of the thallus. Photo by Hugues Tinguy, with permission.

Figure 8. ***Aneura maxima*** thallus. Photo by Dick Haaksma, with permission.

Figure 9. ***Aneura maxima*** showing new lobes. Photo by Jiří Kameníček, with permission.

Figure 10. ***Aneura maxima*** with upward-growing branching lobes. Photo by Jiří Kameníček, with permission.

Currently, neither TROPICOS nor Söderström *et al*. (2016) consider ***Aneura pellioides*** (Figure 4) a valid species, with the former listing it as a synonym of ***Aneura maxima*** (Figure 7-Figure 10).

Aquatic and Wet Habitats

Loskotová (2006) reported ***Aneura maxima*** (Figure 7-Figure 10) as most frequently occurring on wet mineral soil in spring habitats in Slovakia and the Czech Republic. The individual plants grow vertically upward (Figure 9-Figure 10) from the water, forming compact growths that resemble lettuce. It is a more robust species than common ***Aneura pinguis*** (Figure 5-Figure 6). It frequently occurs with ***Brachythecium rivulare*** (Figure 11), ***Chiloscyphus pallescens*** (Figure 12), ***Conocephalum conicum*** (Figure 13), ***Thuidium tamariscinum*** (Figure 14), and ***Trichocolea tomentella*** (Figure 15).

Figure 11. ***Brachythecium rivulare*** habitat, a species that sometimes accompanies ***Aneura maxima***. Photo by Michael Lüth, with permission.

Figure 12. ***Chiloscyphus pallescens***, a liverwort species that sometimes accompanies ***Aneura maxima***. Photo by Michael Lüth, with permission.

Figure 13. ***Conocephalum conicum*** by a stream from Poland where it can be associated with ***Aneura maxima***. Photo by Panek, through Creative Commons.

Figure 14. ***Thuidium tamariscinum***, a species that sometimes accompanies ***Aneura maxima***. Photo by David T. Holyoak, with permission.

In Poland, Buczkowska and Byczkiewicz (2006) found that ***Aneura maxima*** (Figure 7-Figure 10) was similarly associated with ***Conocephalum conicum*** (Figure 13) and ***Trichocolea tomentella*** (Figure 15). At other locations it occurred with ***Pellia epiphylla*** (Figure 16) or ***Pellia epiphylla*** subsp. ***borealis***. In all its locations, it was accompanied by cryptic species of ***A. pinguis*** (Figure 5-Figure 6). However, the substrata differed. ***Aneura maxima*** occurred on wet humus, peaty soil, a mire on river banks, and wet peaty soil of alder swamps. Jan-Peter Frahm photographed its habitat in a ravine near a lake (Figure 17)

Figure 15. ***Trichocolea tomentella***, a species that can be associated with ***Aneura maxima*** in Poland. Photo by Li Zhang, with permission.

Figure 16. ***Pellia epiphylla*** with developing sporophytes, a species that sometimes associates with ***Aneura maxima*** in Poland. Photo by Hermann Schachner, through public domain.

Figure 17. ***Aneura maxima*** habitat where a ravine enters a lake. Photo by Jan-Peter Frahm, with permission.

Schuster (1992) added habitats under waterfalls for some ***Aneura maxima*** (Figure 7-Figure 10) populations in North Carolina, USA. Furuki (2006) reported it from decaying logs in the mossy forest of the Philippines.

Vanderpoorten *et al*. (2006) developed a model to assess the rareness of ***Aneura maxima*** (Figure 7-Figure 10). They found that its localities in deep ravines on damp loamy soils (Figure 18-Figure 20) with light tree cover on the border between France and Belgium differed from conditions in other European localities. They considered this as evidence that it is not limited by a narrow ecological range. Rather, they considered it to be limited by poor dispersal ability. It is thus threatened by drainage of its preferred wet habitats.

Figure 18. ***Aneura maxima*** on a soil habitat. Photo by Dick Haaksma, with permission.

Figure 19. ***Aneura maxima*** in a habitat on soil. Photo by Dick Haaksma, with permission.

Figure 20. ***Aneura maxima*** in its habitat on soil. Photo by Dick Haaksma, with permission.

Adaptations

Aneura maxima has large, fleshy thalli that are deep green when fresh (Figure 21-Figure 22), pale brown when dry (Furuki 2006). These thalli sometimes grow upright (Figure 21), and they have pale margins that are one cell thick (Figure 23). The uppermost cells are lens-shaped and translucent (Figure 24-Figure 25), possibly focussing the light on the chloroplasts beneath.

Figure 21. ***Aneura maxima*** growing in upright clumps of fleshy thalli. Photo by Jiří Kameníček, with permission.

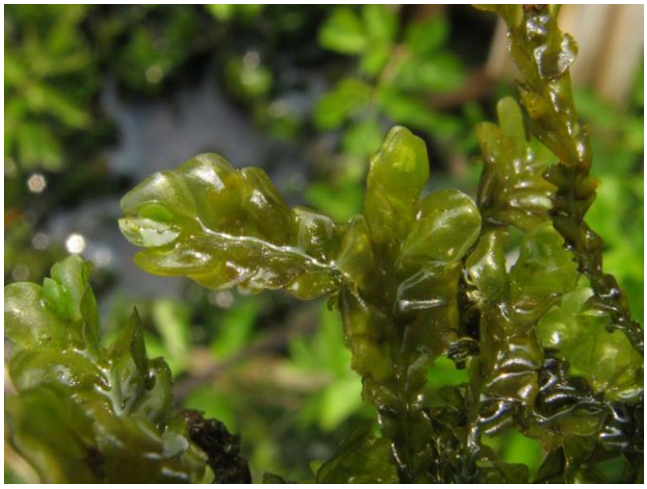

Figure 22. ***Aneura maxima*** showing its wavy margin and upright growth form. Photo by Jiří Kameníček, with permission.

Figure 23. ***Aneura maxima*** with translucent thallus wings. Photo by Jan-Peter Frahm, with permission.

Figure 24. ***Aneura maxima*** thallus showing lens-like upper cells. Photo by Dick Haaksma, with permission.

Figure 25. ***Aneura maxima*** showing lens-like upper cells that could focus light on the cells below. Photo by Dick Haaksma, with permission.

Reproduction

Aneura maxima (Figure 7-Figure 10) is **dioicous** and rarely fertile (Vanderpoorten *et al*. 2006). Gemmae are unknown (Preußing *et al*. 2010b). This combination seems to be responsible for its rarity. It is possible that the lobes (Figure 26) break off to form new plants and could even be dispersed short distances.

Figure 26. ***Aneura maxima*** with potentially reproductive branches. Photo by Jiří Kameníček, with permission.

Fungal Interactions

Duckett and Ligrone (2008) noted that whereas most species of ***Aneura*** have fungi, ***Aneura maxima*** (Figure 7-Figure 10) had never been investigated. Likewise, Bidartondo and Duckett (2010) were unable to find any associated with ***Aneura pellioides*** (Figure 4)/***maxima*** (Figure 7-Figure 10).

Biochemistry

Wawrzyniak *et al*. (2014) reported that volatile sesquiterpenoids, oxygenated sesquiterpenoids, and aliphatic hydrocarbons differed among the cryptic species within the ***Aneura pinguis*** (Figure 5-Figure 6) complex and ***Aneura maxima*** (Figure 7-Figure 10). They found that such compounds in all of the cryptic species within ***A. pinguis*** differed from those of ***A. maxima***.

Aneura mirabilis (Figure 29-Figure 32)

(syn. = *Cryptothallus mirabilis*)

This is perhaps the most unusual of all bryophytes because it is parasitic and totally lacking in chlorophyll.

Davis (2004) asserted that *Cryptothallus mirabilis* (Figure 27) was related to ***Aneura*** (Figure 7-Figure 10), a genus in the same family. Soon after that, Wickett *et al*. (2008a; Wickett & Goffinet 2008) used plastid genome sequencing to demonstrate the close relationships of the species to members of ***Aneura***. This **achlorophyllous** (lacking chlorophyll) species revealed loss of five chlororespiration (*ndh*) genes (Wickett *et al*. 2008a) compared to those of ***Marchantia polymorpha*** (Figure 28) (Wickett *et al*. 2008b), the only other liverwort with a completely sequenced chloroplast genome. Furthermore, six *ndh* genes that are subunits of PS I, PS II, and the cytochrome *b6f* complex were inferred to be **pseudogenes** (sections of chromosome that are imperfect copies of functional gene) (Wickett *et al*. 2008a). Bączkiewicz *et al*. (2017) used DNA barcoding to demonstrate the strong relationship between what was named *Cryptothallus mirabilis* and members of the genus ***Aneura***. Based on these studies, the species has been placed in ***Aneura*** as ***Aneura mirabilis*** (Figure 27, Figure 29-Figure 32).

Figure 27. ***Aneura mirabilis*** showing the many small branches typical of ***Aneura***, but totally lacking chlorophyll. Photo by Jan-Peter Frahm, with permission.

Figure 28. ***Marchantia polymorpha***, a thallose liverwort that has had its entire genome, including the chloroplast genome, sequenced. Photo by Holger Casselmann, through Creative Commons.

Distribution

Aneura mirabilis (Figure 29-Figure 32) is primarily a north oceanic species, but it is known as far south as Portugal (Sérgio *et al*. 2005). Its European distribution includes England, Germany, France, Portugal, Russia, Sweden, Norway, Scandinavia, and Greenland (Bates & Hodgetts 1995; Merckx 2013; Merckx *et al*. 2013). Temperature, precipitation, and degree of continentality can define its distribution pattern (Sérgio *et al*. 2005).

Figure 29. ***Aneura mirabilis*** that has been exposed from among mosses in a peatland. Photo by Jan-Peter Frahm, with permission.

Figure 30. ***Aneura mirabilis*** exposed amid peat. Photo by Jeff Duckett and Silvia Pressel, with permission.

Figure 31. ***Aneura mirabilis*** thalli that have been exposed. Photo courtesy of Martin Bidartondo.

Figure 32. ***Aneura mirabilis*** revealed in a peat mire. Photo by Jeff Duckett and Silvia Pressel with permission.

Aquatic and Wet Habitats

Aneura mirabilis (Figure 29-Figure 32) is not a submersed species, but it does seem to prefer moist habitats (Figure 33-Figure 34). In Welsh Marches, it grows underground under birch trees, hiding under ***Hyocomium armoricum*** (Figure 35) and ***Sphagnum quinquefarium*** (Figure 36) near a stream (Lawley 2012). Hill (1988) characterizes its habitat in North Wales as acid boggy woodland (see also Hill 1969). Boudier *et al*. (1999) found it on "the fringes of Tardais pond" in France. It also occurs in a Lakeland (UK) habitat where it was found in a steep, wooded gully on the north bank of a stream, 70-100 cm above the stream, growing in several places in a patch of ***Pellia*** (Figure 37) (Hopkins 1953). Sérgio *et al*. (2005) found that it was not rare in Portugal, where it occurred mainly in wet forests with an oceanic influence. Richards (1959) noted that it often lives in surface litter (Figure 38) beneath ***Molinia*** (grass; Figure 39) or large mosses such as ***Hylocomium splendens*** (Figure 40). Its association with birch trees can be explained by its need for a fungal association with species that are also attached to birch roots (Read *et al*. 2000). Its subterranean habitat means that it is likely to be easily overlooked.

Figure 33. ***Aneura mirabilis*** habitat in Bretagne. Photo by Michael Lüth, with permission.

Figure 34. ***Aneura mirabilis*** revealed in a ***Sphagnum*** mire. Photo by Michael Lüth, with permission.

Figure 35. ***Hyocomium armoricum***, a species that contributes to the habitat of ***Aneura mirabilis***. Photo by David T. Holyoak, with permission.

Figure 36. ***Sphagnum quinquefarium***, a species that contributes to the habitat of ***Aneura mirabilis***. Photo by Michael Lüth, with permission.

Figure 37. ***Pellia epiphylla***, a species that was associated with ***Aneura mirabilis*** in a wooded gully in the UK. Photo by Hermann Schachner, through public domain.

Figure 38. ***Aneura mirabilis*** in a wet litter habitat. Photo by Michael Lüth, with permission.

Figure 39. ***Molinia caerulea***, a species that can occur in the same habitats as ***Aneura mirabilis***, where the liverwort hides beneath the surface. Photo by James K. Lindsey, with permission.

Figure 40. ***Hylocomium splendens***, a species that may have ***Aneura mirabilis*** growing beneath it in peatland habitats. Photo by Hermann Schachner, through Creative Commons.

Aneura mirabilis (Figure 29-Figure 32) is acidophilic and occurs in locations with high bryophyte cover (Sérgio *et al*. 2005). Williams (1950) found it near an ant's nest. Could it be that the ants helped in its dispersal?

Adaptations

Aneura mirabilis (Figure 29-Figure 32) typically lives in dark habitats – deep forest, ravines, or otherwise well-shaded areas. This makes it difficult for a plant to supply enough carbohydrate through photosynthesis (Merckx 2013). But ***A. mirabilis*** has evolved a novel means of gaining its carbohydrate, unique among liverworts – it gets it from birch trees by way of a fungus (Hawksworth 2003), as discussed below under fungal interactions. It succeeds in this relationship, completely lacking chlorophyll in either generation (Hill 1969; Mårtensson & Nilsson 1974). Even the spores lack green color (Hill 1969; Mårtensson & Nilsson 1974), and Hill (1969) found no development of chlorophyll in spores that were cultured in light. The young thallus shows some evidence of plastid structure, but this never develops chlorophyll (Sigee 1969). In fact, Sigee found that proplastids, similar to those of normal green plants, developed in the apical cell and the surrounding cells. However, in more mature cells there was no evidence of development of a chloroplast. The early development of protoplasts and their subsequent changes occurred before any evidence of fungal invasion, but rather is similar to early stages in other mutant plant albinos wherein a genetic change causes the albino development.

Mårtensson and Nilsson (1974) noted that we do not know the extent to which precursors of chlorophyll are present, and I am not aware of any more recent studies on the topic, although the genes of the chloroplasts have been sequenced (Wickett *et al*. 2008b). On the other hand, Wickett *et al*. (2008b) found little reduction in the genome size. In this case, all the losses of genes and pseudogenes are also seen in the parasitic flowering plant ***Epifagus virginiana***, a forest plant connected through a fungus to beech (***Fagus***) roots. These gene losses are typical of early "decay" stages of the genes in consort with the relaxation of selection pressures. This would seem to imply that evolutionarily, the genes were lost after the mycorrhizal relationship developed.

Although ***Aneura mirabilis*** (Figure 29-Figure 32) lives below the surface in wet peatlands, these plants can dry out. Duckett *et al*. (1990) discovered that when ***Aneura mirabilis*** dries out over a period of 420 days, it develops a covering of multicellular hairs on the dorsal (upper) surface. These could serve to deflect excessive light as the peat shrinks upon drying, reduce water loss, and provide capillary spaces for water uptake. But we have no data to determine if any of these properties actually help it in the field.

Reproduction

Aneura mirabilis is **dioicous** (Figure 41), and in Portugal Sérgio *et al*. (2005) found that it is usually fertile with both male and female plants present (Figure 41). Female plants have a greater longevity than do male plants in this species (Benson-Evans 1960). Lewis and Benson-Evans (1960) suggested that this longevity difference might account for the **female-biased** (more females than males) sex ratio.

Induction of antheridia in ***Aneura mirabilis*** (Figure 29-Figure 32) responds to temperature, but not to photoperiod or light intensity (Benson-Evans 1961). When collected from the field in winter, the plants formed sex organs after 5 weeks at 21ºC. If kept continuously at 18ºC, they remained vegetative through winter and the following year. Benson-Evans interpreted this to mean that they must need a period of low temperatures before developing gametangia.

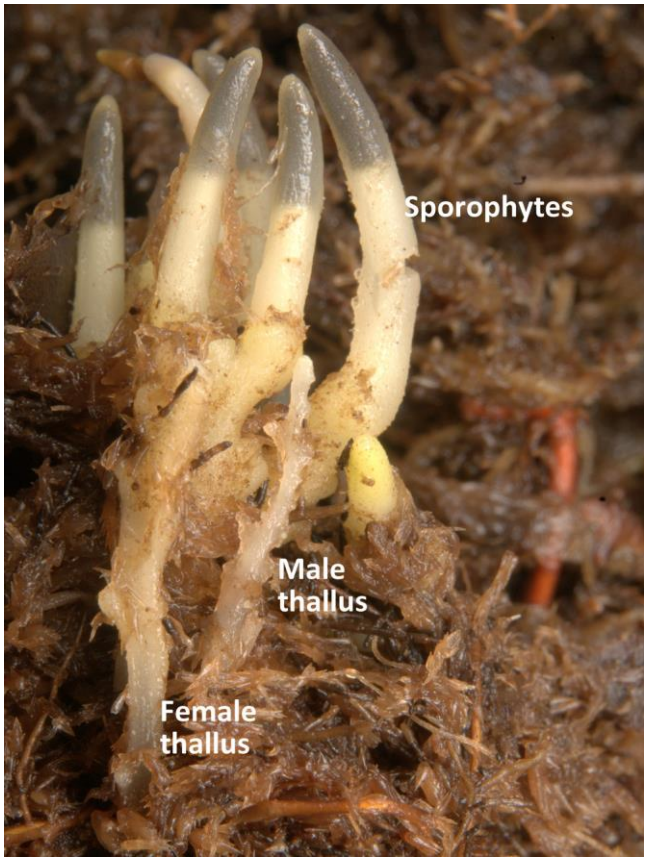

Figure 41. ***Aneura mirabilis***, showing male and female thalli and developing sporophytes *in situ* beneath ***Sphagnum*** among silver birch (***Betula pendula***). Photo by Brian Eversham, with permission.

Capsules of ***Aneura mirabilis*** (Figure 29-Figure 32) reach the surface of the moss layer through elongation of the seta (Figure 42-Figure 47) (Williams 1950), thus can be exposed to light at maturity (Benson-Evans 1960). Both Sjörs (1949) and Malmbörg (1933) found that at least some capsules reach the surface and dehisce there in the light. The large spores fall nearby and thus receive diffused light prior to germination.

Figure 42. ***Aneura mirabilis*** with developing sporophytes and exposed gametophyte thallus. Photo by David T. Holyoak, with permission.

Figure 43. ***Aneura mirabilis*** with peat and litter cleared away to expose the thallus and sporophytes protruding above the buried thallus. Photo by Hugues Tinguy, with permission.

Figure 44. ***Aneura mirabilis*** with sporophytes protruding. Photo by Hugues Tinguy, with permission.

Figure 45. ***Aneura mirabilis*** with sporophytes; exposed thallus is at the right, and evidence of the buried thallus is below the sporophytes in the image. Photo by David G. Long, through Creative Commons.

Figure 46. ***Anerua mirabilis*** under ***Hypnum cupressiforme***, showing mature capsules. Photo modified from Sérgio *et al*. 2005, with permission.

Figure 47. ***Anerua mirabilis*** dehiscing capsule. Photo modified from Sérgio *et al*. 2005, with permission.

In Portugal, the mature spores of ***Aneura mirabilis*** (Figure 29-Figure 32) are present in January to March, in France they are present in March, but farther north they appear in summer (Sérgio *et al*. 2005). The spores are large (30 µm) (Benson-Evans 1960). The spores remain in tetrads, even after dispersal. Upon germination, the tetrads separate and germination in culture occurs within a week. Keeping the tetrad intact until time for germination could explain the frequent presence of sporophytes – the male and female spores travel together and thus would germinate in proximity to each other.

Spores germinated on peat and peat extract agar, but not on Knop's agar or Voth's solutions (Benson-Evans 1960). Those cultured at -18ºC germinated within a few days. Germination was promoted by diffused daylight, but inhibited by strong light. In laboratory experiments, spores fail to germinate after 11-12 months, but they do remain viable throughout one season.

Young sporelings of ***Aneura mirabilis*** (Figure 29-Figure 32) may be washed to greater depths in the peat by rainwater (Benson-Evans 1960). Spores in culture never developed beyond the 20-30-cell stage, an indication that the developing gametophyte might be dependent on the fungus by that stage. The spores themselves seem to be free of fungal hyphae, so the fungal connection must be made at the site of germination for the ***Aneura mirabilis*** to succeed. It is therefore probably of little advantage for the species to have much long-distance dispersal as it has little chance of landing where it can find its partners. In the peatlands of the liverwort parents, the fungus is readily available nearby.

Hill (1969) notes that the achlorophyllous spores of ***Aneura mirabilis*** (Figure 29-Figure 32) nevertheless require light for germination, an accepted requirement for bryophyte spore germination (de Forest Heald 1898). But Benson-Evans (1960) found that reduced light was necessary even for germination of ***Aneura mirabilis*** spores.

Fungal Interactions

We are learning that most plant species are colonized by multiple species of mycorrhizal fungi, and in turn, the fungi are able to colonize many species of plants (Merckx 2013). Such is not the case for ***Aneura mirabilis*** (Figure 29-Figure 32) and associated fungi. In fact it seems that the **Metzgeriidae** often have specificity (Bidartondo & Duckett 2010). Thus far, only members of the **Aneuraceae** [***Cryptothallus*** (now in ***Aneura***), ***Aneura*** (Figure 7-Figure 10, Figure 18-Figure 26, Figure 29-Figure 32, Figure 52-Figure 57), and ***Riccardia*** (Figure 99-Figure 111, Figure 128-Figure 131, Figure 134, Figure 140-Figure 159, Figure 132-Figure 133)] are known to host **Basidiomycete** endophytes (Pocock & Duckett 1984). These form extensive hyphal coils in the cells of the liverworts, similar to those in orchid **endomycorrhizae** (close relationship between plant and root fungi in which hyphae of fungus actually penetrate cells of root, rather than just colonizing on its surface). Pocock and Duckett suggested that these fungi in ***Aneura mirabilis*** might be the same as those living as an ectotroph (fungus living on root surface) of ***Betula*** roots.

The interaction between ***Aneura mirabilis*** (Figure 48) and the fungus ***Tulasnella*** (Figure 49) is unique among the liverworts (Bidartondo *et al*. 2003; Hawksworth 2003;

Wickett & Goffinet 2008; Wickett *et al*. 2008b; Oberwinkler *et al*. 2017). ***Aneura mirabilis*** is the only **mycoheterotrophic** (having symbiotic relationship between plant and fungus, in which plant gets all or part of its carbohydrate from parasitism upon fungi rather than from photosynthesis) liverwort (Merckx 2013). This relationship has been referred to as "cheating" (Bidartondo *et al*. 2003). The plant, in this case ***Aneura mirabilis***, is able to exploit the existing mycorrhizal relationship that already exists between the **Basidiomycete** fungus ***Tulasnella*** and a tree (Read *et al*. 2000; Wickett *et al*. 2008b). Bidartondo *et al*. (2003) demonstrated, using ^{14}C in CO_2, that the carbon was transferred from ***Betula pendula*** seedlings (Figure 50) through a species of ***Tulasnella*** to this achlorophyllous liverwort. It appears that ***Aneura mirabilis*** is able to share ***Tulasnella*** with both ***Betula*** and ***Pinus*** (Figure 51) (Bidartondo *et al*. 2003; Davis & Shaw 2008), depending on an otherwise suitable habitat.

Figure 48. ***Aneura mirabilis*** with the fungal partner ***Tulasnella***. Photo by Martin Bidartondo, with permission.

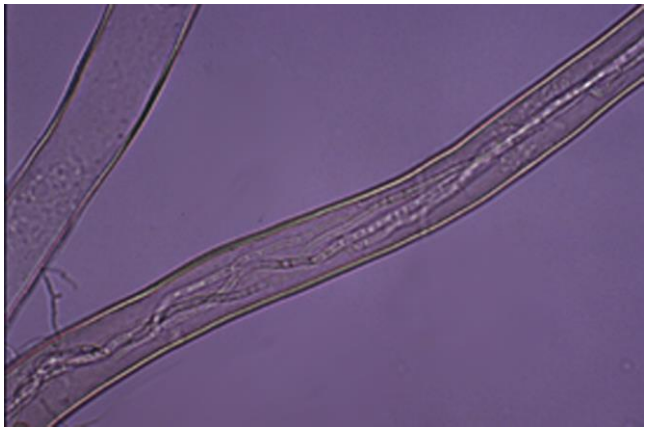

Figure 49. ***Aneura mirabilis*** rhizoid with ***Tulasnella*** inside. Photo by Martin Bidartondo, with permission.

When ***Aneura mirabilis*** (Figure 29-Figure 32) and ***A. pinguis*** (Figure 52-Figure 57) were collected from a variety of sites, the fungi were confined to specific regions of the gametophyte thallus in both liverwort species, and hyphal contact with the substratum occurred through the liverwort rhizoids (Ligrone *et al*. 1993). The colonization cycle presents a growth phase when the fungus forms large intracellular coils, host cytoplasm proliferates, and the starch content of the plastids decreases. This phase is followed by senescence in which the hyphae die back and aggregate into large masses. The fungus exhibits repeated colonization cycles. In ***Aneura mirabilis*** the young hyphae contain abundant glycogen and sometimes amyloid deposits. Despite these behavioral similarities, Ligrone *et al*. found that these two liverwort hosts did not share the same species of fungal partner. It seems that there is thus far no species name of the ***Tulasnella*** (Figure 48-Figure 49) species associated with ***Aneura mirabilis***.

Figure 50. ***Betula pendula*** seedling, a species that is able to share the fungus ***Tulasnella*** with ***Aneura mirabilis***. Photo by Krzysztof Ziarnek, through Creative Commons.

Figure 51. ***Pinus*** in peatlands, a habitat where the pines can share the fungus ***Tulasnella*** with ***Aneura mirabilis***. Photo by Runa S. Lindebjerg <Grida.no> with online permission.

Biochemistry

Although there have been a large number studies on the fungal partnership of ***Aneura mirabilis*** (Figure 29-Figure 32), the biochemical studies are relatively few. Rycroft (1998) reported that the new sesquiterpenoid 15-acetoxypinguisone was clearly the predominant compound in an extract of this species. But Rycroft and Cole (1998) noted that its relative abundance was much less in a second specimen. It would be interesting to determine to what degree the fungus alters the biochemical spectrum, and if the tree host plays any role in determining what secondary compounds are produced.

***Aneura pinguis* (Figure 52-Figure 57)**

(syn. = *Riccardia pinguis*)

Wachowiak *et al*. (2007) used chloroplast DNA sequence variation and polymerase chain reaction-restriction fragment length polymorphism to demonstrate cryptic species in the ***Aneura pinguis*** (Figure 52-Figure 57) complex. (See also Myszczyński *et al*. 2017). Interestingly, they found that lowland and mountain populations exhibited different tRNALeu types, with two types in the mountains and a third in the lowlands. Later, Wawrzyniak *et al*. (2018) demonstrated a number of cryptic species within ***Aneura pinguis***, using mostly differences in sesquiterpene hydrocarbons. What is even more interesting in our ecological context, Bączkiewicz *et al*. (2017) found that the cryptic species, based on DNA differences, clearly differed in habitat preferences.

Figure 52. ***Aneura pinguis*** habit. Photo by Bernd Haynold, through Creative Commons.

Figure 53. ***Aneura pinguis*** in a slightly dry condition. Photo by Chris Wagner, with permission.

Figure 54. ***Aneura pinguis*** habit. Photo by Hermann Schachner, through Creative Commons.

Figure 55. ***Aneura pinguis*** habit. Photo by Hermann Schachner, through Creative Commons.

Figure 56. ***Aneura pinguis*** growing over mosses. Photo by Hermann Schachner, through Creative Commons.

Figure 57. ***Aneura pinguis*** terrestrial form among mosses. Photo by Jan-Peter Frahm, with permission.

But perhaps the cryptic species are not so cryptic. Buczkowska *et al*. (2006a) found that 13 quantitative traits differed significantly among the cryptic species of ***Aneura pinguis*** (Figure 52-Figure 57). These were mostly in the area of dorsal epidermal cells, thickness and number of cells in the thallus cross section, size of inner cells in the thallus cross section, and thallus width. Furthermore, there were differences in sizes of various aspects of males vs. females as well as male:female ratios.

Different forms have been identified in nature (Figure 58), so we must ask if these are due to genetic differences or to habitat modification. Frahm (2012) reported ***Aneura pinguis*** (Figure 52-Figure 57) fo. ***rivularis*** growing under water in a mill pond in the Vosges Mountains. However, when the form ***rivularis*** is grown in the same conditions as the typical form, the form ***rivularis*** retains the unistratose borders (Figure 59), whereas ***Aneura pinguis*** (Figure 5-Figure 6, Figure 52-Figure 57) retains the multistratose margins (Figure 60). Frahm implies that ***Aneura pinguis*** fo. ***rivularis*** is actually ***Aneura maxima*** (Figure 2-Figure 3, Figure 7-Figure 10, Figure 17-Figure 25). But Schuster (1992) seems certain that ***Aneura maxima*** from North America is really the same as ***Aneura pellioides*** (Figure 4) from Japan, but ***A. pellioides*** in Europe may not be synonymous with ***A. maxima***.

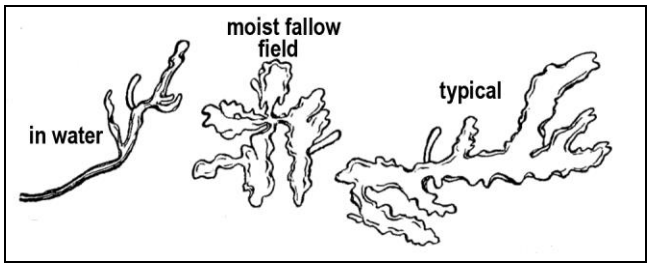

Figure 58. ***Aneura pinguis*** growing in water, in a moist fallow field, and in its typical growth form. Image modified from Watson 1915.

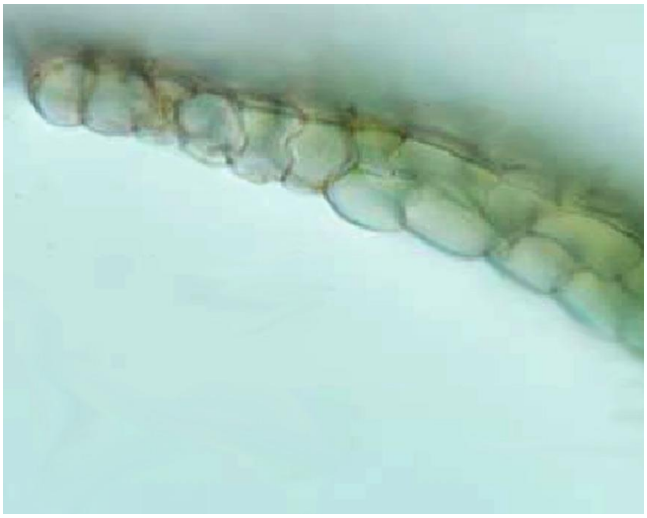

Figure 59. ***Aneura pinguis*** form ***rivularis*** thallus margin section after growing in water culture. Photo by Jan-Peter Frahm, with permission.

Figure 60. Typical form of ***Aneura pinguis*** thallus cultured in water for 4 months, showing its failure to develop thin margins. Photo by Jan-Peter Frahm, with permission.

Distribution

Aneura pinguis (Figure 52-Figure 57) is very cosmopolitan (Schuster 1992; Preußing *et al*. 2010a), extending from the High Arctic to the tropics (Schuster 1992). It occurs throughout most of Europe and North America, southward to the West Indies, South America, Africa, Asia, New Guinea, Australia, and New Zealand, south to Campbell Island (Schuster 1992), and in the Caribbean (Preußing *et al*. 2010b) and the Philippines (Furuki 2006).

Aquatic and Wet Habitats

Schuster (1992) refers to "enormous" habitat range for this species. Nevertheless, it seems to prefer basic conditions in moist habitats (Figure 61). Ceschin *et al*. (2012) considered the habitats of ***Aneura pinguis*** (Figure 52-Figure 57) to be so variable that it was an "invalid" indicator species.

Figure 61. ***Aneura pinguis*** on mud. Photo by Bas Kers, through Creative Commons.

Aneura pinguis (Figure 52-Figure 57) occurs on stream and river banks (Figure 62) with frequent submergence and slow water, often among wet rocks or soil, on rocks or soil in fast water, or submerged in slow water with poor mineral salts (Watson 1919). In Wales I found it near a stream and large waterfall (Figure 63). At Prudhoe Bay, Alaska, it is hydro-mesic or hydric (Rastorfer *et al*. 1973). It occurs in alpine streams (Figure 64) in the Swiss Alps (Geissler 1976). De Sloover and Goosens (1984) reported it from the travertine ***Cratoneuron*** (Figure 65) association of Lorraine River, Belgium. Geissler and Selldorf (1986) found that in their European studies it occurred with other wet habitat species (Figure 66), the moss ***Paludella squarrosa*** (Figure 67) and tracheophytes ***Eleocharis quinqueflora*** (Figure 68) and ***Trichophorum cespitosum*** (Figure 69), but was not common there. It occurs in streams in Belgium (Vanderpoorten & Tignon 2000), in mountain streams of northwest Portugal (Vieira *et al.* 2005), on European travertines (Pentecost & Zhang 2006), in rivers (Ferreira *et al*. 2008), and in poorly mineralized and basic waters in the Tiber River basin, Italy (Ceschin *et al*. 2012). On travertines, seepages and aspect are important and the liverworts are kept moist by capillarity (Pentecost & Zhang 2006).

Figure 62. ***Aneura pinguis*** in a streambank habitat at Cwm Idwal National Nature Reserve, Wales. Photo by Janice Glime.

Figure 63. ***Aneura pinguis*** at Cwm Idwal National Nature Reserve where it is kept moist by the nearby river and large waterfall. Photo by Janice Glime.

Figure 64. ***Aneura pinguis*** in water, where one can find it in alpine streams. Photo from Proyecto Musgo, through Creative Commons.

Figure 65. ***Cratoneuron filicinum***; ***Cratoneuron*** appears with ***Aneura pinguis*** on travertine rock in Belgium. Photo by Hugues Tinguy, with permission.

Figure 66. ***Aneura pinguis*** in wet habitat with other bryophytes. Photo by Kristian Peters, through Creative Commons.

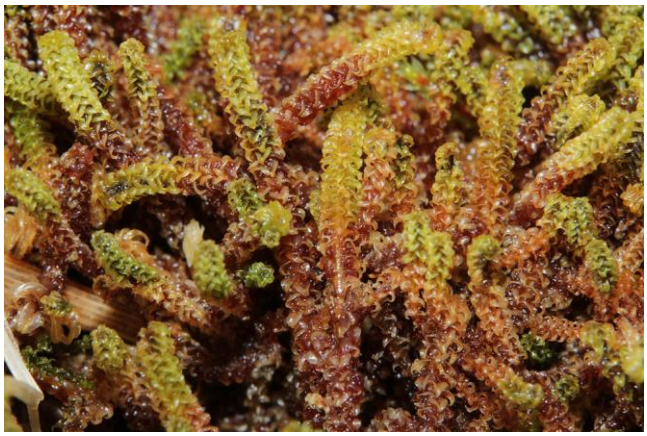

Figure 67. ***Paludella squarrosa***, a species that occurs with ***Aneura pinguis*** in wet habitats. Photo by Hermann Schachner, through Creative Commons.

Figure 68. ***Eleocharis quinqueflora***, a species that occurs with ***Aneura pinguis*** in wet habitats. Photo by Ed Stikvoort, Saxifraga, through Creative Commons.

In western Canadian montane streams, ***Aneura pinguis*** (Figure 52-Figure 57) is submerged and hemicalciphilous (Vitt *et al.* 1986) in some, but can also occur on streambanks (Glime & Vitt 1987). Vitt and Horton (1990) reported it from fens in Missouri, USA. At Mountain Lake, Virginia, USA, Sharp (1944) reported ***Aneura pinguis*** from wet soil at the edge of a stream.

Figure 69. ***Trichophorum cespitosum***, a species that occurs with ***Aneura pinguis*** in wet habitats. Photo by Elke Freese, through Creative Commons.

In a Somerset, UK, heath, zonation depends on the supply of fresh water (Watson 1915). The streams have ***Potamogeton polygonifolius*** (Figure 70), and immediately above that constantly submersed zone of deeper water one can find ***Aneura pinguis*** (Figure 52-Figure 57) along with ***Pellia epiphylla*** (Figure 71). If the water is present continuously, these two species are present, including also living in furrows that may be too shallow for ***Potamogeton polygonifolius***. In these submerged locations, ***Aneura pinguis*** usually becomes long and narrow (Figure 72). Above that liverwort zone, where the water supply is intermittent and the zone remains above water for some time, ***Riccardia multifida*** (Figure 71) occurs instead. In shallow boggy pools, ***Aneura pinguis*** is usually absent and the pools are occupied instead by ***Scorpidium scorpioides*** (Figure 73), whether by competition or by a habitat that is otherwise unsuitable for ***Aneura pinguis***.

Figure 70. ***Potamogeton polygonifolius***, a species found in deeper water of heathland streams and wet areas, just below the ***Aneura pinguis*** zone. Photo by Bert Lanjouw, through Creative Commons.

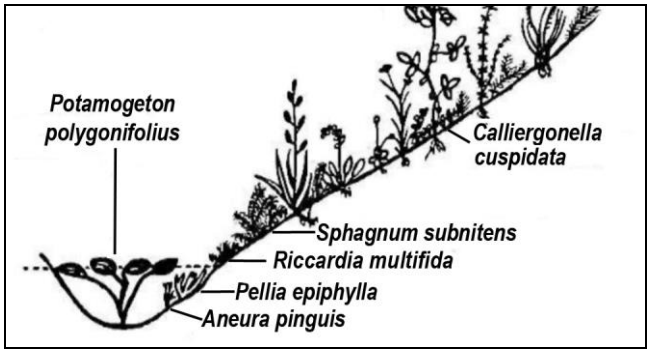

Figure 71. ***Aneura*** zonation in streams of wet heathland. Drawing modified from Watson 1915.

Figure 72. ***Aneura pinguis*** form ***rivularis*** thallus grown in water in a mill pond for 20 years. Photo by Jan-Peter Frahm, with permission.

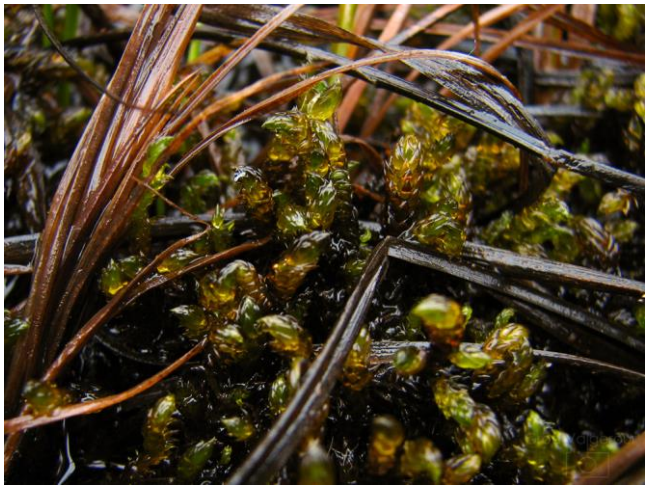

Figure 73. ***Scorpidium scorpioides***, a species that occurs in shallow pools that lack ***Aneura pinguis***. Photo by Gróa Valgerður Ingimunda, through Creative Commons.

Pentecost and Zhang (2006) examined effects of exposure and water availability on European travertine bryophytes, including ***Aneura pinguis*** (Figure 52-Figure 57). Only ***A. pinguis*** was significantly affected by aspect. It was also confined to seepages where moisture was ensured through capillarity.

The habitats of the various cryptic species of ***Aneura pinguis*** (Figure 52-Figure 57) differ. Gonera and Buczkowska (2016) reported that cryptic species A typically grows on humus over limestone rocks in the Western Carpathians, B is mainly on clay soil in Bieszczady Mts. and in clayish areas of lowlands, C grows both in lowlands and mountains and it occupies mostly wet sandy soils on the shores of oligotrophic lakes and river and mountain stream banks, E is associated with calcareous rocks in flowing water in mountains. Cryptic species A, B, and C differ somewhat in morphology, but the differences are subtle and relate mainly to thickness of the thallus and differences in thallus cells (Figure 74-Figure 76) (Buczkowska & Adamczak 2006).

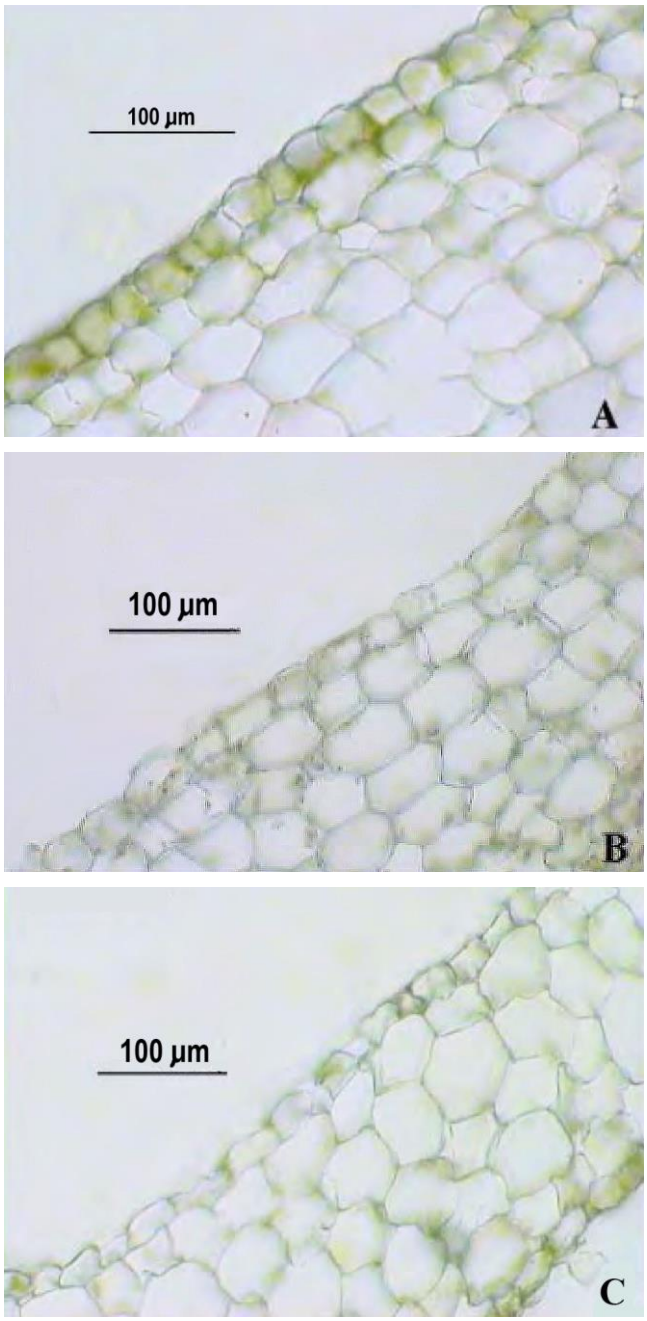

Figure 74. Cross sections of ***Aneura pinguis*** showing epidermis and median cells of cryptic species A, B, and C. Photo by Katarzyna Buczkowska, with permission.

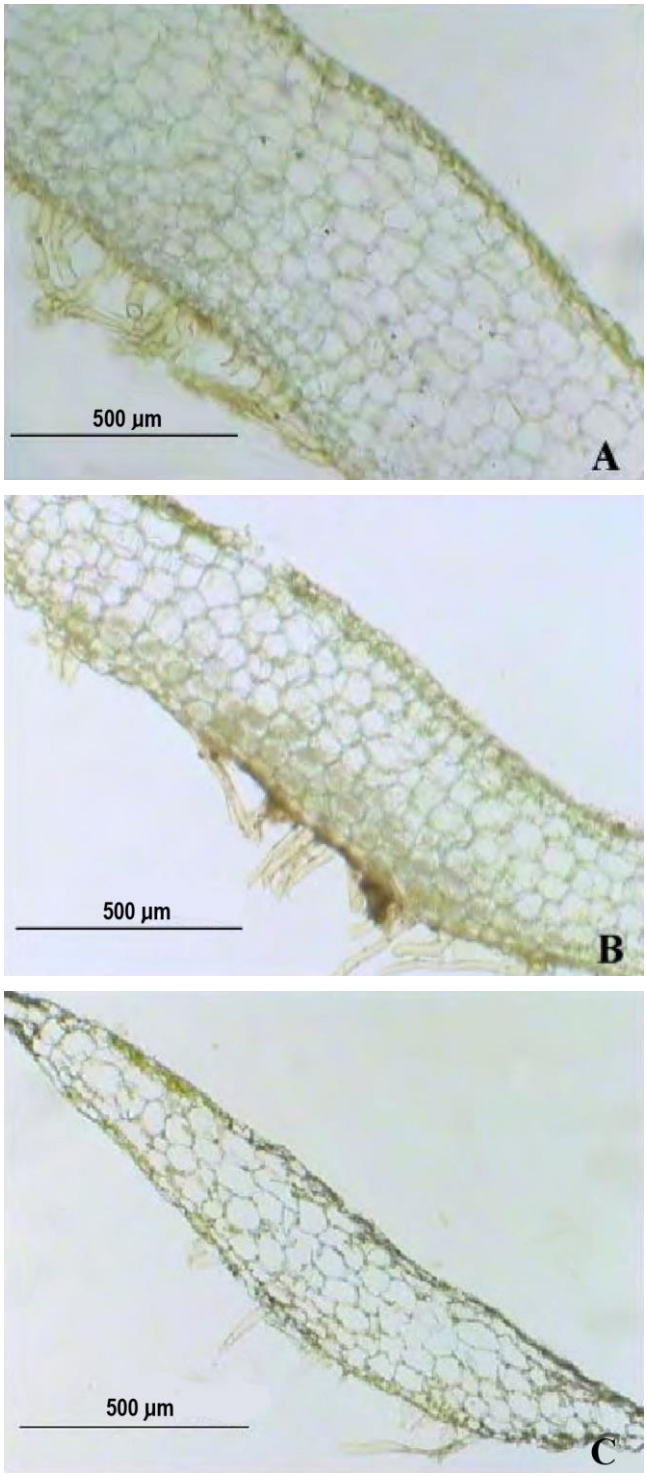

Figure 75. ***Aneura pinguis*** thallus cross section showing differences between cryptic species A, B, and C. Photo by Katarzyna Buczkowska, with permission.

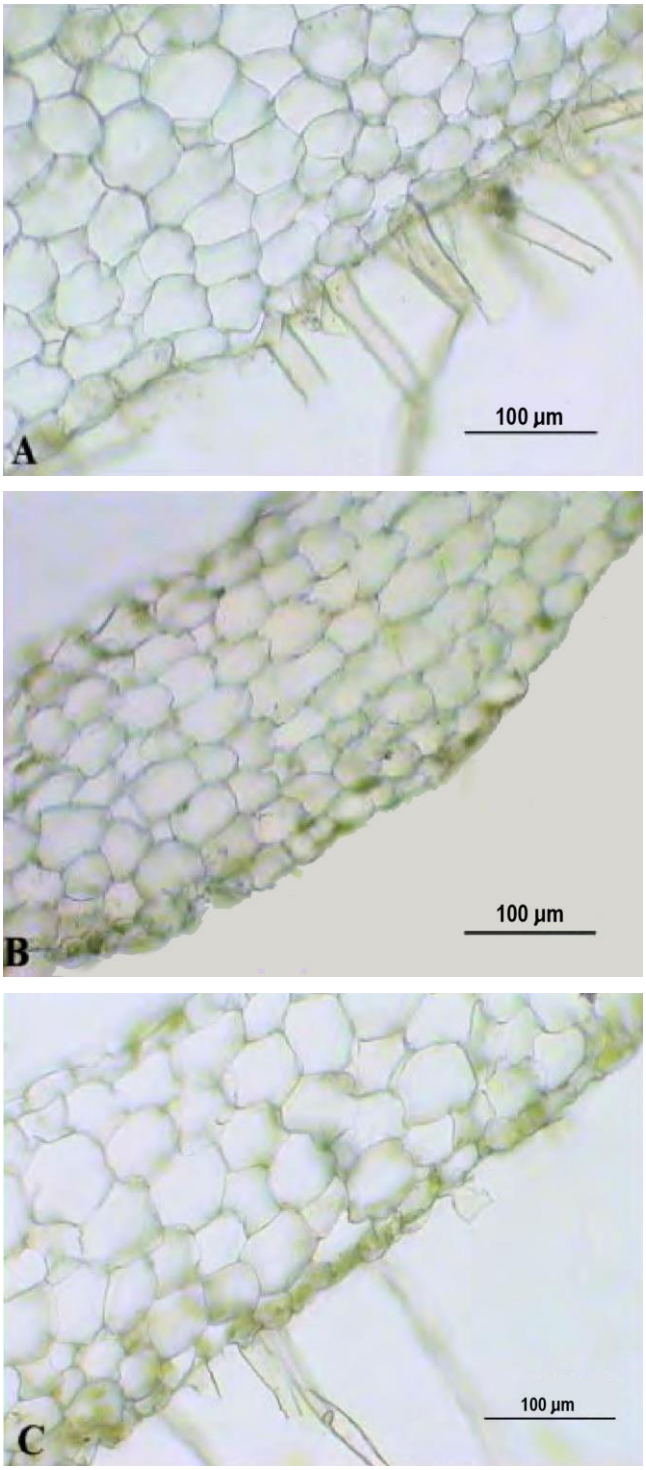

Figure 76. Cross section of ***Aneura pinguis*** showing ventral side of thallus in cryptic species A, B, and C. Photo by Katarzyna Buczkowska, with permission.

Váňa and Ignatov (1995) reported that they found ***Aneura pinguis*** (Figure 52-Figure 57) in two types of habitats: wet sandy banks and bars of creeks and rivers; on rotten logs in conifer woods (Figure 77). While both of these are moist habitats, the substrata are quite different, as well as the former having the possibility of submersion. Could these be cryptic species differences?

Foijt and Harding (1995) explored the effects of changes in Suffolk fens on the species composition of plants. Changes in the mires included lack of traditional management, changes in water regime, and increased fertility. In unmanaged areas, all of the fen associates and bryophytes were lost and replaced by non-fen species and ruderal tall herbs. When traditional management was maintained, small characteristic species of wet fens and semi-aquatic conditions still disappeared, but recruitment was not as evident. Those species that remained tended to

be species that are either quite common in fens or non-fen recruits. When the fens remained wet, but were derelict, some species remained, with ***Aneura pinguis*** (Figure 52-Figure 57) and ***Riccardia multifida*** (Figure 140-Figure 149) among them. The researchers concluded that stable hydrology is more important than extensive management in conserving these sites.

Figure 77. ***Aneura pinguis*** on bark; it can be found on decaying logs. Photo by Li Zhang, with permission.

Despite the ability of ***Aneura pinguis*** (Figure 52-Figure 57) to occupy a wide range of habitats, and to survive changes to its fen habitats, Albinsson (1997) determined that liverworts, including ***Aneura pinguis***, have a narrow ecological amplitude in mires, whereas smaller liverworts tend to have wider amplitudes. Albinsson used the term **compromise strategy** to describe those species that rely on habitats created by other living bryophytes. These include species that are frequently sterile.

In Japan, ***Aneura pinguis*** (Figure 52-Figure 57) also occurs on decaying logs (Figure 77) in the mossy forest (Furuki 2006), but once again in a constantly moist environment. Logs that are in advanced stages of decay, especially missing bark, hold more water.

Adaptations

Aneura pinguis (Figure 52-Figure 57) has light green thalli when fresh, turning brown as they dry (Furuki 2006). Could this color change protect the species against bright light in the dry condition, helping to prevent photo damage?

Proctor *et al*. (1992) measured stable carbon isotope discrimination of $\delta^{13}C$ in relation to different sites and heights above water level in a North Carolina, USA, lake, and from two Marchantialean and two Metzgerialean liverworts from various habitats. Among these bryophytes, ***Aneura pinguis*** (Figure 52-Figure 57) had a slightly more negative reading. The researchers suggested that ***A. pinguis*** might have some uptake of recycled CO_2. But where is it stored? Buczkowska *et al*. (2006a) compared the thallus morphology among various cryptic species of ***Aneura pinguis***. This liverwort does not have internal air chambers (Figure 60, Figure 74-Figure 76) (Clapp 1912), but the thickness differs (Figure 75) among the cryptic species (Buczkowska *et al*. 2006a). Could the distance required for CO_2 to travel to exit the plant cause retention that would permit nearby cells to benefit from its attempt to escape? This raises interesting questions that require more exploration. Could greater thickness of the thallus facilitate recycling of CO_2? Could larger cell size cause a longer retention of respired CO_2? Does cell wall thickness play any role in recycling respired CO_2 in photosynthesis?

One growth form of ***Aneura piguis*** is upright (Figure 78). This form is an advantage in wet habitats where there is little danger of drying out because it exposes more surface to gas exchange and sunlight.

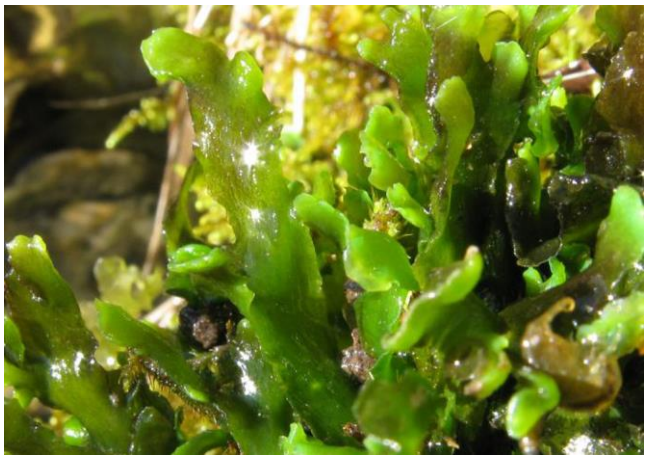

Figure 78. ***Aneura pinguis*** growing upright, a form that is possible in continuously wet habitats. Photo by Jiří Kameníček, with permission.

Reproduction

Aneura pinguis (Figure 52-Figure 57) is a thallose, **dioicous** species with sexual dimorphism (Buczkowska *et al*. 2006a). Male thalli are smaller and less branched than female thalli (Müller 1951-1958; Furuki 1991; Schuster 1992). d'Artenay and Renzaglia (2011) described the architecture of the spermatid in ***Aneura pinguis*** and provided high resolution images.

In cryptic species A of ***Aneura pinguis*** (Figure 52-Figure 57) only 55% of the gametophytes were fertile, compared to 80% (Figure 79) in B and almost 70% in C (Buczkowska *et al*. 2006a). Most colonies consisted of only one sex. Sex ratios differed among the three cryptospecies. Furthermore, the cryptic species are partly intersterile, differing in time of gametangial maturity (Showalter 1926, 1928; Buczkowska *et al*. 2006a).

Figure 79. ***Aneura pinguis*** perianths and young sporophytes. Photo by Dick Haaksma, with permission.

Clapp (1912) described the development of the capsules of ***Aneura pinguis*** (Figure 80-Figure 85) from first embryo cell to splitting of the capsule into four valves. The capsules are "highly specialized" (Clapp 1912). Horner *et al*. (1966) described the development of the spores (Figure 86). Showalter (1925) described the early stages of spore germination.

Figure 80. ***Aneura pinguis*** with sporophytes emerging from the perianth. Photo by Bernd Haynold, through Creative Commons.

Figure 81. ***Aneura pinguis*** perianths with embryonic capsules inside. Photo by Dick Haaksma, with permission.

Figure 82. ***Aneura pinguis*** perianth with embryonic sporophyte inside. Photo by Dick Haaksma, with permission.

Figure 83. ***Aneura pinguis*** with maturing sporophytes. Photo by Štěpán Koval, with permission.

Figure 84. ***Aneura pinguis*** with maturing capsules and elongating setae. Photo by Jan-Peter Frahm, with permission.

Figure 85. ***Aneura pinguis*** with dehisced sporophyte and perianths. Photo by Li Zhang, with permission.

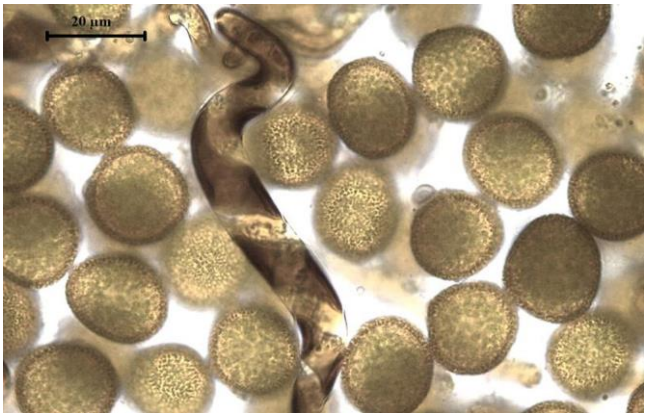

Figure 86. ***Aneura pinguis*** spores. Photo by Hugues Tinguy, with permission.

Gemmae are unknown in ***Aneura pinguis*** (Figure 52-Figure 57) (Clapp 1912; Preußing *et al*. 2010b). Vegetative reproduction occurs as older parts of the thallus die and apical portions become separated (Figure 87). This is facilitated by the production of lobes (Figure 88) that can break away. We do not know the degree to which these portions are dispersed, but we can assume that they are at least sometimes dispersed by flowing water. Waterfowl and insects might also contribute to dispersal.

Figure 87. ***Aneura pinguis*** showing older portions that are dying while tips are growing. Photo by Jouko Rikkinen, through Creative Commons.

Figure 88. ***Aneura pinguis*** showing vegetative lobes that can break off to form new plants. Photo by Hugues Tinguy, with permission.

Fungal Interactions

Aneura pinguis (Figure 52-Figure 57) is well known for its fungal interactions. In a study of symbiotic associations with liverworts, ***Aneura pinguis*** was associated with ***Tulasnella*** sp. (Figure 89; see also Figure 49), one of very few **Basidiomycetes** known to have a symbiotic relationship with liverworts (Kottke *et al*. 2003). These fungal interactions are typically highly species specific. Kottke *et al*. (2003) and Leake (2005) noted that the fungus in ***Aneura pinguis*** are closely related to those in ***Aneura mirabilis***. Liepiņa (2012) also demonstrated specificity between ***Fossombronia foveolata*** (Figure 90) and ***A. pinguis*** where thalli of the two species growing side-by-side housed different species of fungi.

Figure 89. ***Tulasnella violea*** on tree trunk, in a genus that is often associated with liverworts, including ***Aneura pinguis***. Photo by Esa Borén, through Creative Commons.

Figure 90. ***Fossombronia foveolata***, a species that can grow beside ***Aneura pinguis***, but that has different fungal associations. Photo by Hugues Tinguy, with permission.

Duckett *et al*. (2004) found different fungal endophytes in upland and lowland populations of ***Aneura pinguis*** (Figure 52-Figure 57) and likewise noted that the fungi had high host specificity. Bidartondo and Duckett (2010) considered the few overlaps of fungal species between ***Aneura pinguis*** and ***Aneura mirabilis*** (Figure 29-Figure 32) and the scattered occurrence of the fungus ***Sebacina*** (Figure 91-Figure 92) in ***Aneura pinguis*** may relate to the broad molecular diversity (cryptospecies) of this liverwort. Preußing *et al*. (2010a) determined that the composition of the communities of tulasnelloid fungi in ***A. pinguis*** differs between Ecuador and Europe, with a much higher diversity of tulasnelloid fungal partners at the Ecuadorian site, further supporting the hypothesis that the partnerships were related to cryptic species differences.

Figure 91. ***Sebacina sparassoidea*** with moss. Photo by Lloyd P. Roberts, through Creative Commons.

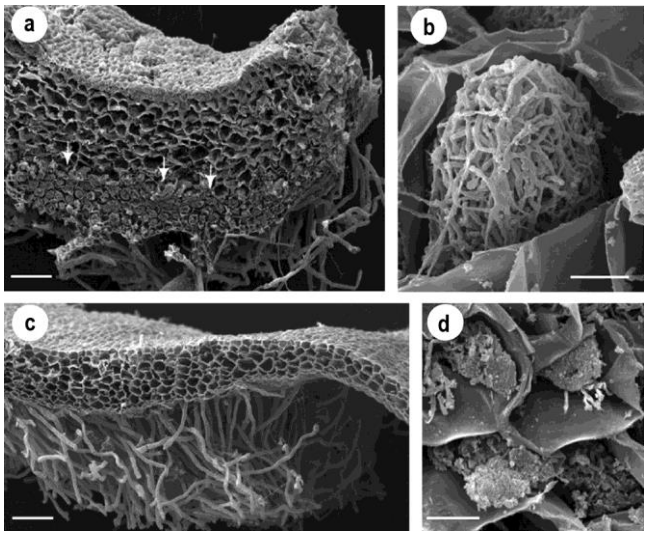

Figure 92. ***Sebacina*** infecting ***Aneura*** (a,b,d); ***Aneura pellioides*** hypha-free (c). Modified from Bidartondo and Duckett 2010, with permission.

Preußing *et al*. (2010b) consider the appearance of the mycothallus in the ***Aneura*** clade to be remarkably homogenous. Hyphae penetrate through living rhizoids; they colonize the parenchymal cells from the base of the rhizoid intracellularly by penetrating the cell walls, then forming dense coils of hyphae. Colonization of epidermal cells is rare (Brown & Braggins 1989) and intercellular infections are unknown (Preußing *et al*. 2010b).

Ligrone *et al*. (1993) learned through ultrastructural study that the interactions of endophytic Basidiomycetes were very similar in ***Aneura mirabilis*** (Figure 29-Figure 32) and ***Aneura pinguis*** (Figure 52-Figure 57). In both liverwort species, the fungus is confined to specific thallus regions. The fungus makes hyphal contact with its substrate through the rhizoids. Following the colonization phase, the fungus forms large intracellular coils. The liverwort cytoplasm then proliferates and starch content in the plastids diminishes. The fungal hyphae then senesce and die back, aggregating into large masses. A number of developmental characteristics of the ***A. mirabilis*** are identical to those of ***A. pinguis*** from alpine sites, but differ from those of ***A. pinguis*** from sand dunes and a chalk pit. These habitat differences further support the degree of differences among the cryptospecies. On the other hand, could the differences found among the cryptospecies be a result of different fungal epiphytes (see Damsholt 2002)?

Krause *et al*. (2011) followed the fungal colonization in ***Aneura pinguis*** (Figure 52-Figure 57) and a number of species of ***Riccardia*** (Figure 99-Figure 111, Figure 128-Figure 131, Figure 134, Figure 140-Figure 159, Figure 132-Figure 133). They found that the mode of colonization of tulasnelloid mycobionts differs in the species of these genera, despite having identical fungal sequences. Thus they suggested that the mode of colonization may be host-dependent.

Culturing

For many, **axenic** (sterile; culture with no living organisms but intended one) culturing bryophytes has been a challenge. Buczkowska *et al*. (2006b) developed a protocol for axenic culturing of ***Aneura pinguis*** (Figure 52-Figure 57) that permitted them to regenerate. The two most successful media were hormone-free: the special liverwort medium of Lukavsky *et al.* (1991) and the MS medium of Murashige and Skoog (1992).

Biochemistry

Duckett and Renzaglia (1987) noted the difficulty of preserving the oil bodies for TEM studies, but confirmed their presence in ***Aneura***. As you can see in the image of ***Aneura pinguis*** below (Figure 93), they can be difficult to discern even in fresh material.

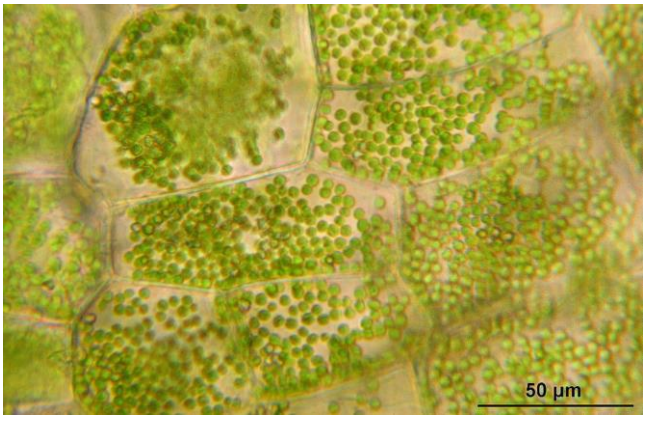

Figure 93. ***Aneura pinguis*** cells in which one cannot distinguish the oil bodies easily. Photo by Hermann Schachner, through Creative Commons.

In their study of cryptic species of ***Aneura pinguis*** (Figure 52-Figure 57), Wawrzyniak *et al*. (2018) found that the dominant compound among their samples was pinguisone, with deoxopinguisone being the second dominant. The differences among the samples were primarily due to genotype and little to habitat. Tazaki *et al*. (1995) reported that the concentrations of pinguisone were significantly high in the species. They were able to describe the structures of three new pinguisane-type sesquiterpenes (Tazaki *et al*. 1996).

Asakawa *et al*. (1981) demonstrated that the sesquiterpenes in ***Aneura pinguis*** (Figure 52-Figure 57) are chemically very different from those of two relatives that have been retained in ***Riccardia*** [***R. multifida*** (Figure 140-Figure 159), ***R. jackii***]. The pinguisones are not the dominant sesquiterpenes in the ***Riccardia*** (Figure 99-Figure 111, Figure 128-Figure 131, Figure 134, Figure 140-Figure 159, Figure 132-Figure 133) species.

Lobatiriccardia (Figure 94-Figure 95)

Lobatiriccardia is a Southern Hemisphere genus, mostly in Australia and New Zealand, but more recently reported from Ecuador in South America (Preußing *et al*. 2010b). Preußing *et al*. (2010b) suggested that the positioning of female gametangia on the lobe margins of ***Lobatiriccardia***, rather than in a central position, permits the development of more sporophytes, thus increasing reproduction.

Symbiotic fungi occur in parenchymal cells in this genus, inhabiting 3-10 layers on the ventral side, never occurring in epidermal cells or intercellular locations (Duckett & Ligrone 2008).

Lobatiriccardia alterniloba (Figure 94-Figure 95)

(syn. = *Aneura alterniloba*; *Riccardia alterniloba*)

Several varieties have been described for ***Lobatiriccardia alterniloba*** (Figure 94) (Nebel *et al*. 2013).

Distribution

Lobatiriccardia alterniloba (Figure 94) is known from New Zealand, Australia, Tasmania, and Vanuatu (Hewson 1970; Furuki 2002; Preußing *et al*. 2010b).

Figure 94. ***Lobatiriccardia alterniloba*** on a soil bank. Photo by Marley Ford, through Creative Commons.

Aquatic and Wet Habitats

Lobatiriccardia alterniloba (Figure 94) occurs in Cool Temperate Victorian Rainforest streams (Carrigan & Gibson 2004; Carrigan 2008). In Cement Creek, Victoria, Australia, it occurs below the water line, but can also occur above (Carrigan & Gibson 2004). It does not occur on upstream sides of rocks that receive the full force of the current, but can occupy downstream, top, and base locations that do not receive the full force of the current. It was one of the two dominant species at the bases of rocks and achieved 8% cover in the study area.

Preußing *et al*. (2010b) described its habitat as occurring on rock, or soil in damp to wet conditions, often in the spray of waterfalls, or in running water. Nebel *et al*. (2013) similarly reported ***Lobatiriccardia alterniloba*** (Figure 94) **var. *robusta*** from Russell Falls, in Tasmania.

Not all of the habitats of ***Lobatiriccardia alterniloba*** (Figure 94) are so wet. Wilcox (2018) reported it from exposed roots of a pine tree in a shaded forest, near a small stream in Craigavon Park, Auckland, New Zealand.

Adaptations

Lobatiriccardia alterniloba (Figure 94) forms tight, thin **mats** that reduce the force of the current at the base of the mat (Carrigan & Gibson 2004; Carrigan 2008).

Preußing *et al*. (2010b) suggested that the reduction of lateral thallus branches to short, gametangia-bearing branches may save resources. The ventral position of gametangia under thallus lobes could result in better protection of the young sporophyte from injury and stronger anchoring and direct nutrient uptake by the dense rhizoid coverage at the capsule foot.

Reproduction

Lobatiriccardia alterniloba is **dioicous** but does at least sometimes reach successful fertilization (Figure 95); gemmae are unknown (Preußing *et al*. 2010b).

Figure 95. ***Lobatiriccardia alterniloba*** with young capsule. Photo by Marley Ford, through Creative Commons.

Fungal Interactions

Duckett and Ligrone (2008) described the **Basidiomycota** endophyte in ***Lobatiriccardia alterniloba*** (Figure 94) as limited to five cell layers, contrasting with colonization of the entire thallus in ***Aneura mirabilis***.

Biochemistry

Oil bodies of ***Lobatiriccardia alterniloba*** (Figure 94) are typically 2-5 per cell (Preußing *et al*. 2010b). I found no studies on the biochemistry of the species.

Lobatiriccardia athertonensis

Distribution

Thus far, ***Lobatiriccardia athertonensis*** is only known from Australia (Preußing *et al*. 2010b) and New Guinea (Hewson 1970).

Aquatic and Wet Habitats

In disturbed rainforests, ***Lobatiriccardia athertonensis*** occurs with other bryophytes on basalt rocks on creek banks (Preußing *et al*. 2010b).

Reproduction

Lobatiriccardia athertonensis is **dioicous**; gemmae are unknown (Preußing *et al*. 2010b).

Biochemistry

Oil bodies are few, 1-3(4) per cell (Preußing *et al*. 2010b). No biochemical studies seem to be available for this species.

Lobatiriccardia coronopus

Distribution

Lobatiriccardia coronopus occurs in the Philippines, Malay Peninsula, Borneo, Sumatra, Java, Seram, and New Guinea (Furuki 1996, 2006)

Aquatic and Wet Habitats

Lobatiriccardia coronopus occurs on rocks and fallen logs at the waterside (Furuki 1996, 2006)

Lobatiriccardia oberwinkleri

Distribution

Lobatiriccardia oberwinkleri has a known distribution limited to South America, in Ecuador, at two locations in the same ravine (Preußing *et al*. 2010b). More recently, Schäfer-Verwimp and Nebel (2011) have added it to the flora of Brazil.

Aquatic and Wet Habitats

Lobatiriccardia oberwinkleri was found in a ravine in the upper mountain rainforest belt, where it occurs on steep, dripping rock faces beside two small cascades (Preußing *et al*. 2010b). It occurs there with ***Asterella macropoda***, ***Dumortiera hirsuta*** (Figure 96), and ***Riccardia*** (Figure 99-Figure 111, Figure 128-Figure 131, Figure 134, Figure 140-Figure 159, Figure 132-Figure 133) species. In southern Ecuador it occurs on shady, humid soil and on dripping cliffs of the lower to upper montane rainforest from 1760 to 2880 m asl (Gradstein & Reeb 2018).

Figure 96. ***Dumortiera hirsuta***, a species that occurs with ***Lobatiriccardia oberwinkleri***. Photo by Luis Funez, through Creative Commons.

Reproduction

Lobatiriccardia oberwinkleri is **dioicous**, with male plants unknown (Preußing *et al*. 2010b). Gemmae are unknown.

Lobatiriccardia verdoornioides

Distribution

Lobatiriccardia verdoornioides is thus far known only from Cuenca, El Cajas, and Quito, Pichincha, in Ecuador (Preußing *et al*. 2010b).

Aquatic and Wet Habitats

Lobatiriccardia verdoornioides was described as a new species from wet páramo-vegetation, where it was found in a bog on the bank of a small lake, embedded in cushions of flowering plants, together with other bryophytes [***Riccardia*** (Figure 99-Figure 111, Figure 128-Figure 131, Figure 134, Figure 140-Figure 159, Figure 132-Figure 133) and ***Campylopus*** (Figure 97) species], and in rivulets (Preußing *et al*. 2010b).

Figure 97. ***Campylopus atrovirens***; in the Páramo; ***Campylopus*** can occur with ***Lobatiriccardia verdoornioides***. Photo by Andrew Hodgson, with permission.

Schäfer-Verwimp *et al*. (2013) reported ***Lobatiriccardia verdoornioides*** from remnants of ***Polylepis***

(Figure 98) stands, where it occurred on very wet ground at 3995 m asl in Ecuador.

Figure 98. ***Polylepis rugulosa*** in Andes highland; ***Lobatiriccardia verdoornioides*** occurs in remnants of the ***Polylepis*** forest. Photo by Alexander Yates, through Creative Commons.

Adaptations

Thalli of ***Lobatiriccardia verdoornioides*** are very succulent and deeply embedded in the surrounding vegetation, which most likely protects them from the strong wind and sunlight (Preußing *et al*. 2010b).

Reproduction

Lobatiriccardia verdoornioides is **dioicous**; gemmae are unknown (Preußing *et al*. 2010b).

Lobatiriccardia yakusimensis

(syn. = *Riccardia lobata* var. *yakusimensis*)

Distribution

Lobatiriccardia yakusimensis is known only from the Ryukyu archipelago in southern Japan (Furuki 1991; Preußing *et al*. 2010b).

Aquatic and Wet Habitats

Lobatiriccardia yakusimensis occurs on wet rocks along streams, often submerged in running water (Preußing *et al*. 2010b).

Adaptations

The thallus of ***Lobatiriccardia yakusimensis*** is large and bluish-green when fresh (Preußing *et al*. 2010b). I don't know what this color indicates or if it is in any way adaptive.

Reproduction

Lobatiriccardia yakusimensis is **dioicous**; gemmae are unknown (Preußing *et al*. 2010b).

Biochemistry

Oil bodies occur in all epidermal and inner cells of ***Lobatiriccardia yakusimensis*** with 1-10 in each cell (Preußing *et al*. 2010b). Their biochemistry remains unknown.

Lobatiriccardia yunnanensis

Distribution

Lobatiriccardia yunnanensis is known only from Yunnan, China (Furuki & Long 2007; Preußing *et al*. 2010b). Unfortunately, a new road has been constructed, coming within a few meters of its only known location, accompanied with light deforestation, causing Furuki and Long (2007) to consider the species severely threatened.

Aquatic and Wet Habitats

Lobatiriccardia yunnanensis occurs on shady dripping cliffs of a river gorge in dense broadleaf evergreen forest in a humid subtropical valley at 1425 m asl (Furuki & Long 2007; Preußing *et al*. 2010b). In its single known location, it was associated with a number of other bryophytes (Furuki & Long 2007).

Adaptations

Plants of ***Lobatiriccardia yunnanensis*** form dense colonies with numerous rhizoids (Furuki & Long 2007), presumably facilitating their ability to persist on dripping cliffs. Is it possible that the translucent thallus permits light to penetrate to or focus on deeper layers in this low-light habitat?

Reproduction

Lobatiriccardia yunnanensis is **dioicous**, with its archegonia and sporophytes on the margins (Preußing *et al*. 2010b). As already suggested, this positioning permits more than one sporophyte to develop in a season on the same lobe, increasing the potential for reproduction. No gemmae are known.

Riccardia

Members of the genus ***Riccardia*** (Figure 99-Figure 111, Figure 128-Figure 131, Figure 134, Figure 140-Figure 159, Figure 132-Figure 133) are positively correlated with bankfull discharge in 48 streams in South Island, New Zealand (Suren & Duncan 1999). They are also among west African rheophytes (Shevock *et al*. 2017). Preußing *et al*. (2010b) suggested that the positioning of female gametangia on the lobe margins instead of the central position permits the development of more sporophytes, thus increasing reproduction. Furthermore, **endogenous** (formed within vegetative cells) gemmae are found regularly in ***Riccardia*** (Renzaglia, 1982), but are unknown in ***Aneura*** (Figure 7-Figure 10, Figure 18-Figure 26, Figure 29-Figure 32, Figure 52-Figure 57) or ***Lobatiriccardia*** (Figure 94-Figure 95).

Riccardia aequicellularis (Figure 99)

Distribution

Riccardia aequicellularis (Figure 99) occurs in Australia (English & Blyth 2000; Carrigan & Gibson 2004), Tasmania (Ratkowsky 1987; Jarman & Kantvilas 2001), and New Zealand (de Lange *et al*. 2020). Selkirk (2012) reported the species from the sub-Antarctic Macquarie Island.

Figure 99. ***Riccardia aequicellularis***, a species of the Eastern Southern Hemisphere. Photo by Tom Thekathyil, with permission.

Aquatic and Wet Habitats

Riccardia aequicellularis (Figure 99) occurs in Cool Temperate Victorian Rainforest streams (Carrigan & Gibson 2004; Carrigan 2008). In Cement Creek (Figure 100), Victoria, Australia, it occurs below the water line, but can also occur above. It is able to occupy upstream, downstream, and sides of rocks, but does not occupy the tops of rocks in the study stream. This is the only species in the studied area of Cement Creek that is able to withstand the force of the current on the upstream side of rocks. With these restrictions, it occupies less than 1% cover in the stream and occurs in only 2 of the 5 study locations.

Figure 100. Cement Creek, Yarra Ranges National Park, Victoria, Australia 1 98Octane, through Creative Commons.

Downes *et al*. (2003) listed ***Riccardia aequicellularis*** (Figure 99) as semi-aquatic. In two of the studied creeks in Australia it had a higher percentage cover on emergent than submerged rocks, but in another there was no difference; in a fourth the cover was greater on the submerged rocks. This is one of the species that seems to benefit from the additional habitats provided by splash zones above water.

Riccardia aequicellularis (Figure 99) occurs on peat mounds of tumulus springs (mound springs) in the Swan Coastal Plain of western Australia (English & Blyth 2000). Downing *et al*. (2007) found it in their study of a deep gully (Figure 101) in a closed canopy forest in the Blue Mountains of New South Wales, Australia.

Figure 101. Deep gully in Blue Mountains, Victoria, Australia, such as the ones where one might find ***Riccardia aequicellularis***. Photo by David Noble, with permission.

Adaptations

Riccardia aequicellularis (Figure 99) forms **threadlike mats** that permit it to reduce the rate of flow within the mat (Carrigan & Gibson 2004). At Deep Stream in New Zealand, it is a colonist (Michel *et al*. 2013).

Riccardia chamedryfolia (Figure 102-Figure 108)

(syn. = *Aneura sinuata*, *Aneura sinuata* fo. *submersa*, *Riccardia sinuata*)

Distribution

Riccardia chamedryfolia (Figure 102-Figure 108) is Holarctic, but is rare in the Arctic (Schuster 1992). It extends from Europe and the islands off the coast of Portugal, southward to northern Africa and eastward to China, Japan, Bonin, and Micronesia. In North America it extends along the western coastal states from Alaska to California and in some locations in the eastern USA states. Bakalin (2005) reported on its locations on the Kamchatka Peninsula, Russia.

Figure 102. ***Riccardia chamedryfolia*** (Jagged Germanderwort), a Holarctic species. Photo by Barry Stewart, with permission.

Figure 103. ***Riccardia chamedryfolia***. Photo by Des Callaghan, with permission.

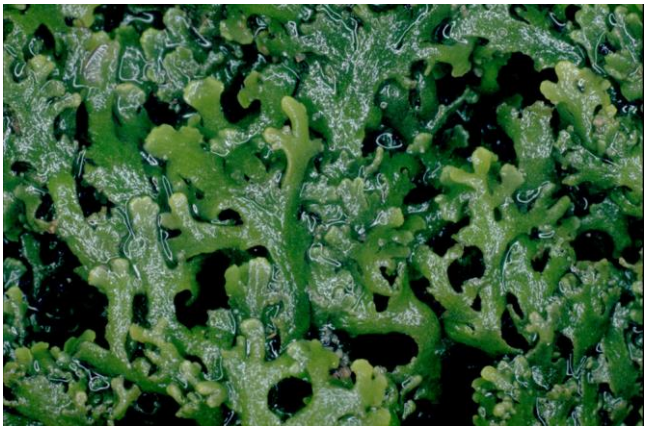

Figure 104. ***Riccardia chamedryfolia***. Photo by Jan-Peter Frahm, with permission.

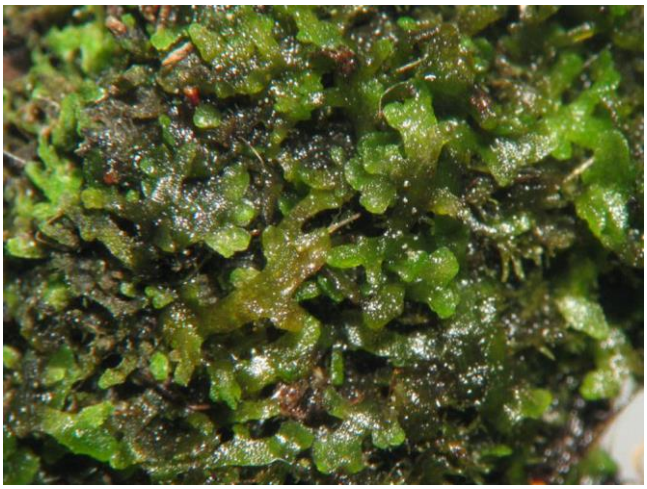

Figure 105. ***Riccardia chamedryfolia***. Photo by Kristian Peters, with permission.

Figure 106. ***Riccardia chamedryfolia***. Photo by Martin Hutten, with permission.

Figure 107. ***Riccardia chamedryfolia*** showing lush growth. Photo by Michael Lüth, with permission.

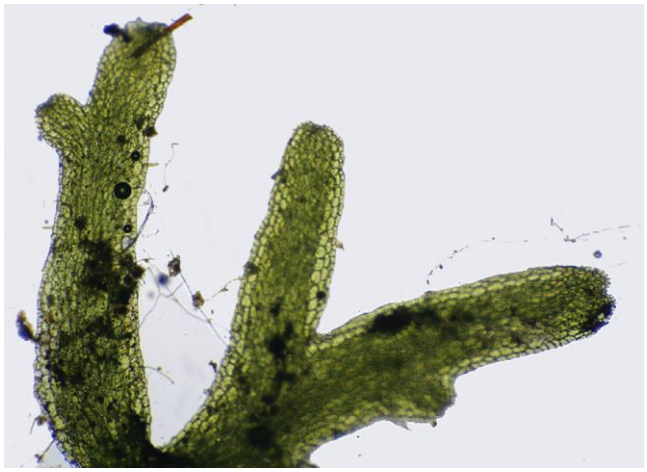

Figure 108. ***Riccardia chamedryfolia***. Photo by Malcolm Storey, DiscoverLife.com, with online permission.

Aquatic and Wet Habitats

Schuster (1992) described ***Riccardia chamedryfolia*** (Figure 102-Figure 108) as being typically associated with running water, but not always submersed. It is often kept wet by splash, or on damp to dripping rocks of ravines or gravelly bottoms of shallow springs.

Watson (1919) considered ***Riccardia chamedryfolia*** (Figure 102-Figure 108) to be the most hydrophilous of the "***Aneura***" species. It occurs on stony beds in fast water. It also occurs in rivers (Ferreira *et al*. 2008). In Westfalens, northwestern Germany, it occurs in water (Figure 109) and, less commonly, as a marsh plant (Koppe 1945). In Odenwald and southern Spessare, Philippi (1987) found it in spring areas in aquatic habitats; van Zanten and Colpa (2008) found it in seepage in North Gronigen, The

Netherlands. In southern Finland it occurs in small lakes (Toivonen & Huttunen 1995). It occurs in Portugal water courses (Vieira *et al.* 2012) and in northwest Portugal it can be found in mountain streams (Vieira *et al.* 2005). On Madeira Island, it occurs in upstream areas in mountainous streams (Luís *et al.* 2015). In the eastern USA, ***Riccardia chamedryfolia*** (Figure 102-Figure 108) occurs in Appalachian Mountain streams (Figure 110) (Glime 1968). Tremp (2003) considered the species to be oligo- to mesotrophic.

Figure 109. ***Riccardia chamedryfolia*** in water. Photo by Michael Lüth, with permission.

Figure 110. Appalachian Mountain stream, where some are inhabited by ***Riccardia chamedryfolia***. Photo by Janice Glime.

Barringer (2011) found ***Riccardia chamedryfolia*** (Figure 102-Figure 108) on dripping rocks near streams in New Jersey, USA. Vieira *et al*. (n.d.) found it at a mean of 8 cm above water that had velocities of 0-1.5 m s^{-1} in northwest Portugal. Daniel *et al*. (2006) found a negative correlation of depth with rheophilous bryophytes, including ***Riccardia chamedryfolia***, in the Scorff River and its tributaries, a salmon river system in southern Brittany of France. These studies support its description as living in habitats that stay wet (Figure 111), but not necessarily submerged.

Figure 111. ***Riccardia chamedryfolia*** above water, but wet on a wet rock. Photo by Bernd Haynold, through Creative Commons.

Bakalin (2007) found ***Riccardia chamedryfolia*** (Figure 102-Figure 108) in wet hollows in the southern Kuril Islands. Callaghan and Ashton (2007) found it locally in younger dune slacks in England. In Japan, Bakalin *et al*. (2013) found it on moist and wet boulders and cliffs along streams, in spray zones of waterfalls, but also on clayish road cuts in mesic conditions and partial shade of secondary forests.

Hugonnot (2011) reported ***Riccardia chamedryfolia*** (Figure 102-Figure 108) from fens in Aubrac, France. Vellak *et al*. (2015) listed ***Riccardia chamedryfolia*** as sporadic in Estonia. Ingerpuu *et al*. (2014) found it to be rare in fens, transitional mires, and bogs in Estonia. It is likewise rare in the southeastern Carpathians of Romania (Jakab 1999). Similarly, Albinsson (1997) reported it from only one location out of 67 mire sites in southern Sweden, despite its being considered a characteristic mire species.

Philippi (1987) described the aquatic vegetation of streams in the eastern Odenwald and southern Spessart, Germany. He described the ***Riccardia chamedryfolia*** (Figure 102-Figure 108) community and the ***Fontinalis antipyretica*** (Figure 112) community as the characteristic communities of the spring area. Both are sensitive to high water velocity. ***Riccardia chamedryfolia*** is one of the few species that characterize the source. In these locations, it forms fresh, olive-green to yellow-green lawns that are under water most of the year.

Schuster (1992) found that ***Riccardia chamedryfolia*** (Figure 102-Figure 108) was mostly in acidic sites, but was not confined to them. Gabriel and Bates (2005) found that in the Azores, the mean *p*H for this species was 5.0 and water availability was not the highest among the groups of bryophytes. On Madeira, ***Riccardia chamedryfolia*** occurs where there are low nutrient concentrations, preferring reaches with low temperatures and little turbulence (Luís *et al*. 2012). It is acidophilic, indicating low *p*H in summer.

It is related to low dissolved oxygen, low magnesium, and low calcium ions in summer, and low concentrations of phosphates and high ammonium in winter. These latter relationships may explain its occasional appearance in non-acidic habitats.

Figure 112. ***Fontinalis antipyretica***, a characteristic community in springs where ***Aneura chamedryfolia*** also characterizes one of the communities. Photo by Bernd Haynold, through Creative Commons.

Riccardia chamedryfolia (Figure 102-Figure 108) occurred in rock crevices near water leakage (Ivanova 2009). In river gorges in Norway, ***Ctenidium molluscum*** (Figure 113), ***Hylocomiastrum umbratum*** (Figure 114), and ***Trichocolea tomentella*** (Figure 115) are characteristic companion species of ***Riccardia chamedryfolia*** (Rydgren *et al*. 2012). Frahm (2005) reported ***R. chamedryfolia*** from the wet lava rocks in the dark interior of a crater in the Azores. ***Riccardia chamedryfolia*** fo. ***major*** (syn. = *Aneura major*) occurs on banks with frequent submergence and slow water (Watson 1919).

Figure 113. ***Ctenidium molluscum***, a species that occurs with ***Riccardia chamedryfolia*** in Norwegian gorges. Photo by David T. Holyoak, with permission.

Figure 114. ***Hylocomiastrum umbratum***, a species that occurs with ***Riccardia chamedryfolia*** in Norwegian gorges. Photo by Hermann Schachner, through Creative Commons.

Figure 115. ***Trichocolea tomentella***, a species that occurs with ***Riccardia chamedryfolia*** in Norwegian gorges. Photo by Li Zhang, with permission.

Riccardia chamedryfolia (Figure 102-Figure 108) is not entirely a wet habitat species. It is also known from trunks of the tree fern ***Cyathea delgadoi*** (Figure 116) in Brazil (Vital & Prado 2006). In Estonia, Kannukene *et al*. (1997) found it on the bank of a bomb crater on sand.

Adaptations

In the Tottori Prefecture of Japan, ***Riccardia chamedryfolia*** (Figure 102-Figure 108) can occur in pure **mats** (Figure 117), but it is more commonly mixed with other liverworts, such as ***Aneura maxima*** (Figure 2, Figure 3, Figure 7-Figure 10; Figure 18-Figure 26), ***Conocephalum salebrosum*** (Figure 118), ***Heteroscyphus coalitus*** (Figure 119), ***Jubula hutchinsiae*** (Figure 120), ***Lejeunea aquatica***, ***Makinoa crispata*** (Figure 121), ***Megaceros pellucidus*** (see Figure 122), ***Pallavicinia subciliata*** (Figure 123), ***Pellia neesiana*** (Figure 124), and ***Wiesnerella denudata*** (Figure 125) (Bakalin *et al*. 2013). Both the **mat** life form and the accompanying liverworts can help ***Riccardia chamedryfolia*** maintain hydration.

Figure 116. ***Cyathea delgadoi***, a species that sometimes has ***Riccardia chamedryfolia*** growing on its trunks. Photo from <powo.science.kew.org>, through Creative Commons.

Figure 118. ***Conocephalum salebrosum***, a species that can occur mixed with ***Riccardia chamedryfolia***. Photo by Paul Slichter, with permission.

Figure 119. ***Heteroscyphus coalitus***, a species that can occur mixed with ***Riccardia chamedryfolia***. Photo by Jia-Dong Yang, through Creative Commons.

Figure 117. ***Riccardia chamedryfolia*** forming a mat. Photo by Malcolm Storey, DiscoverLife.com, with online permission.

Figure 120. ***Jubula hutchinsiae***, a species that can occur mixed with ***Riccardia chamedryfolia***. Photo by Michael Lüth, with permission.

Figure 121. ***Makinoa crispata***, a species that can occur mixed with ***Riccardia chamedryfolia***. Photo through Creative Commons.

Figure 122. ***Megaceros*** sp.; ***Megaceros pellucidus*** can occur mixed with ***Riccardia chamedryfolia***. Photo by Scott Zona, through Creative Commons.

Figure 123. ***Pallavicinia subciliata***, a species that can occur mixed with ***Riccardia chamedryfolia***. Photo by Li Zhang, with permission.

Reproduction

Riccardia chamedryfolia (Figure 102-Figure 111) is **autoicous** (Schuster 1992). Gemmae can be present on the tips of the ultimate branches.

Figure 124. ***Pellia neesiana***, a species that can occur mixed with ***Riccardia chamedryfolia***. Photo from Botany Website, UBC, with permission.

Figure 125. ***Wiesnerella denudata***, a species that can occur mixed with ***Riccardia chamedryfolia***. Photo by David Long, with permission.

Fungal Interactions

Vital *et al*. (2000) reported the fungus ***Phellinus wahlbergii*** (**Basidiomycota**; Figure 126) in association with ***Riccardia chamedryfolia*** (Figure 102-Figure 111) in undisturbed Atlantic forest in Brazil.

Figure 126. ***Phellinus wahlbergii***, a bracket fungus with moss on it; it can also associate with ***Riccardia chamedryfolia***. Photo by Clive Shirley, Hidden Forest, with permission.

Bidartondo and Duckett (2010) noted that **Aneuraceae** typically have basidiomycete fungi, in particular species of ***Tulasnella*** (Figure 89; see also Figure 49), giving them the potential to form **ectomycorrhizae** (form of symbiotic relationship between fungal symbiont, or mycobiont, and roots or rhizoids of various plant species; mycobiont is often from **Basidiomycota** or **Ascomycota**, and more rarely from **Zygomycota**). Using fungal DNA sequence data, they did not detect fungi in ***Riccardia chamedryfolia*** (Figure 102-Figure 111).

Biochemistry

Riccardia chamedryfolia (Figure 102-Figure 111) has 1-2 oil bodies per cell (Figure 127).

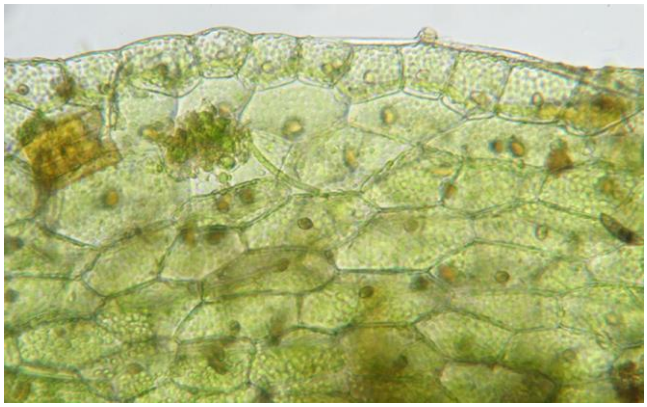

Figure 127. ***Riccardia chamedryfolia*** showing cells with 1-2 dark-colored oil bodies. Photo by Malcolm Storey, DiscoverLife.com, with online permission.

Some sesquiterpenoids have been isolated from ***Riccardia chamedryfolia*** (Figure 102-Figure 111) (Ge 2007).

Riccardia crassiretis

Distribution

Riccardia crassiretis is known from Sri Lanka, Philippines, Sumatra, Java, New Guinea, and New Caledonia (Furuki 2006).

Aquatic and Wet Habitats

In the Philippines, ***Riccardia crassiretis*** occurs on soil and rocks by water (Furuki 2006).

Adaptations

Although ***Riccardia crassiretis*** does not seem to live under water, its thick-walled thallus cells (Furuki 2006) could be of value if it is. On the other hand, they might be more important to prevent cell collapse when it dries out.

Reproduction

Riccardia crassiretis is **dioicous** (Furuki 2006). Capsules are described by Furuki (2001).

Riccardia crenulata

Distribution

Riccardia crenulata is known from Singapore, Philippines, Malaysia (Malay Peninsula and Borneo), and Indonesia (Java and Sumatra) (Furuki & Tan 2013). It is also reported from Taiwan (Buchanan *et al*. 1997; Lai & Wang-Yang 1976).

Aquatic and Wet Habitats

Riccardia crenulata (re-identified from *Riccardia tenuicostata*) occurs at <30 cm above water level in the tropics (Ruttner 1955). Furuki and Tan (2013) reported it from wet rocks in Singapore.

Reproduction

Riccardia crenulata is dioicous; its sporophytes are unknown (Furuki 2001).

Riccardia diminuta

Distribution

Furuki (2006) reported ***Riccardia diminuta*** from the Philippines, Sumatra, Java, and New Caledonia. Yin *et al.* (2016) listed it as one of the species on Hainan Island, China. Shu *et al*. (2016) added Vietnam and Horing (2017) added Malaysia.

Aquatic and Wet Habitats

Ruttner (1955) reported that ***Riccardia diminuta*** occurs in thermal acidic spray zones in the tropics (Ruttner 1955). Furuki (2006) reported that it occurs on soil and rocks by water in the Philippines.

Reproduction

Riccardia diminuta is **dioicous** (Furuki 2006).

Riccardia elata (Figure 128-Figure 131)

Distribution

Riccardia elata (Figure 128-Figure 131) is known from Singapore, Indonesia (Java, Sumatra). Malaysia (Malay Peninsula and Borneo) and the Philippines (Furuki & Tan 2013). Singh and Singh (2007) reported it from New Sikkim, India.

Figure 128. ***Riccardia elata*** showing its delicate branching. Photo by Li Zhang, with permission.

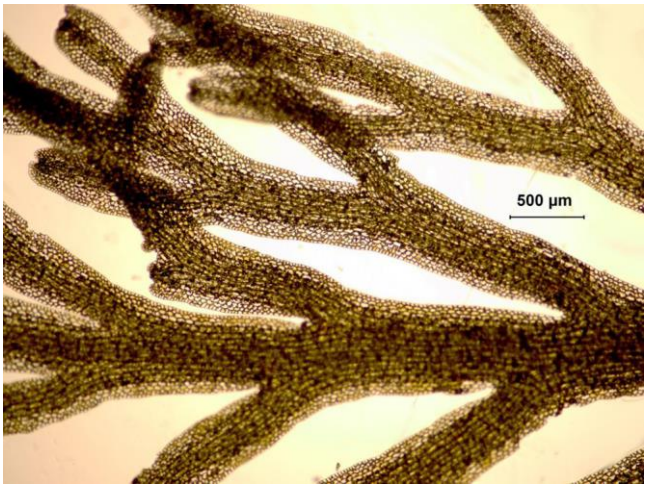

Figure 129. ***Riccardia elata*** showing the borders on the thalli. Photo by Li Zhang, with permission.

Aquatic and Wet Habitats

Ruttner (1955) included ***Riccardia elata*** (Figure 128-Figure 130) as an aquatic species in the tropics. In the Philippines, it is known from wet soil along a stream (Figure 130) (Furuki & Tan 2013). In Sikkim, India, it occurs in moist, shady locations under slowly dripping water (Singh & Singh 2007).

Figure 130. ***Riccardia elata*** in a wet habitat. Photo by Li Zhang, with permission.

Adaptations

Riccardia elata (Figure 128-Figure 130) is one of the larger (up to 10 cm) ***Riccardia*** species (Singh & Singh 2007). In the Philippines, ***Riccardia elata*** is deep green when fresh (Furuki & Tan 2013), but Singh and Singh (2007) described it as light green to yellowish green when fresh (Figure 130). This suggests that its color may depend on the environment, possibly light intensity or state of hydration, but also it could be a result of nutritional status.

Reproduction

Riccardia elata (Figure 128-Figure 130) is **dioicous**, with sporophytes mostly absent (Singh & Singh 2007; Furuki & Tan 2013). Finally, in 2017, Singh and Singh found and described capsules from the Himalayas in India. Furthermore, the 2-celled endogenous gemmae (Singh & Singh 2007) are rare, at least in the Philippines (Furuki & Tan 2013). Its chromosome number is *n*=9 m (Zheng & Zhu 2008).

Biochemistry

Biochemical studies on ***Riccardia elata*** (Figure 128-Figure 130) are rather limited. Figure 131 shows the cells with small oil bodies where one would expect secondary compounds to be stored.

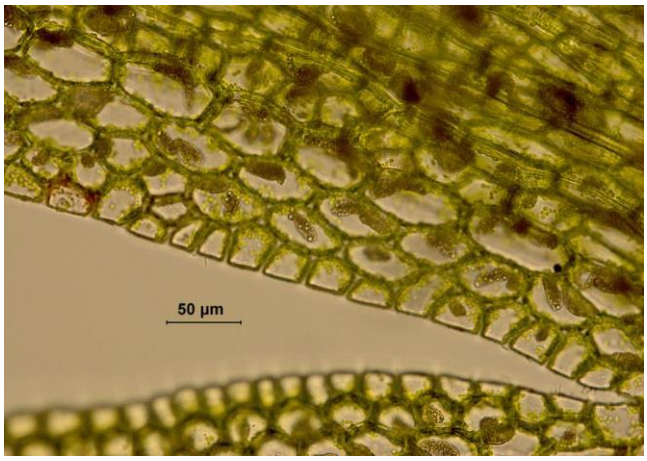

Figure 131. ***Riccardia elata*** showing cells with oil bodies (see cells near border) and a distinct border. Photo by Li Zhang, with permission.

From ***Riccardia elata*** (Figure 128-Figure 130) one stilbene and three flavonoids were isolated and their structures were determined (Ge 2007).

Riccardia graeffii (Figure 132-Figure 133)

(syn. = *Riccardia androgyna*, *Riccardia platyclada*)

In recent years, this species has gone by both *Riccardia platyclada* (Söderström *et al*. 2016) and ***Riccardia graeffei*** (Figure 132-Figure 133) (Furuki 1991; TROPICOS 2021). TROPICOS considers *Riccardia platyclada* to be a synonym of ***Riccardia graeffei***; The Plant List considers *Riccardia platyclada* an unresolved name, while accepting ***Riccardia graeffei***. In these chapters I am following the nomenclature used by Söderström *et al*. (2016) which recognizes ***Riccardia graeffei*** and not *Riccardia platyclada*. In any case, they are apparently accepted as the same species and I have treated them as such here.

Distribution

Riccardia graeffei (Figure 132-Figure 133) is widely distributed in tropical Asia, Australasia, and the Pacific (Furuki & Tan 2013). Its known records include India (Srivastava 1972; Sharma & Alam 2011; Gupta & Asthana 2016), Vietnam, Japan, Philippines, Malay Peninsula, Singapore, Borneo, Sumatra, Java, New Guinea, Caroline, New Caledonia, Vanuatu, Samoa, Fiji, Tonga, Tahiti, and Australia (del Rosario 1967; Furuki 2006). Singh and Singh (2015) recently reported it as new to Andaman and Nicobar Islands in the Bay of Bengal. To this list, Singh and Singh (2015) noted records from China, Indonesia, Malaysia, Taiwan, and Thailand.

Figure 132. ***Riccardia graeffei*** showing growth form, cs with multi-layered ells, and oil bodies in cells. Photos from MySpecies.info, through Creative Commons.

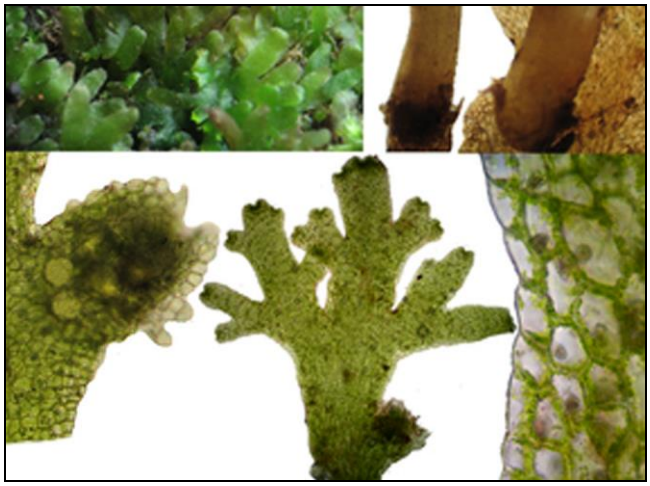

Figure 133. ***Riccardia graeffei***. Photos from MySpecies.info, through Creative Commons.

Aquatic and Wet Habitats

Ruttner (1955) reported ***Riccardia graeffei*** (Figure 132-Figure 133) from the wall of a bay, source of pond inflow, **tuff** (light, porous rock formed by consolidation of volcanic ash) wall, <30 cm above water level, on submerged tree trunk, and overhanging water in the tropics. Ruttner also listed ***Riccardia graeffei***) as an aquatic inhabitant in the tropics. Furuki reported it from wet rocks, fallen logs, and soil by water in lowland (Furuki 2006; Furuki & Tan 2013). Singh and Singh (2015) described it as terrestrial, lithophytic, or corticolous, growing in very moist places along a sheltered stream in dense tropical rainforest on the Andaman and Nicobar Islands, India. In India, Gupta and Asthana (2016) reported it from wet rocks and soil-overed rocks.

By contrast, Yamaguchi *et al*. (2005) identified ***Riccardia graeffei***; Figure 132-Figure 133) in plots that had been heavily burned in tropical lowland forest of East Kalimantan, Indonesia.

Adaptations

Riccardia graeffei (Figure 132-Figure 133) has yellowish green to green thalli when fresh (Furuki & Tan 2013). It lacks rhizoids, but possesses a smooth to granulose cuticle (Singh & Singh 2015). Its color suggests an adaptation to low light.

Reproduction

Riccardia graeffei exhibits the **heteroicous** condition with male, female, and paroicous branches (Furuki 2006; Furuki & Tan 2013; Singh & Singh 2015). The capsules are blackish brown (Singh & Singh 2015). Singh and Singh (2015) reported it with 2-celled endogenous gemmae. Its chromosome number is *n*=9 m (Zheng & Zhu 2008).

Biochemistry

Riccardia graeffei has numerous botryoidal oil bodies (bottom of Figure 132) in all cells of the thallus (Furuki & Tan 2013). Ge (2007) reported riccardiphenol C and two benzoic acids from ***Riccardia graeffei***.

Riccardia jackii

(syn. = *Riccardia jackii* fo. *submersa*)

Distribution

Riccardia jackii occurs in the Philippines and Java (Furuki 2006).

Aquatic and Wet Habitats

In the tropics ***Riccardia jackii*** is known from water spray and on volcanic tuff walls, in thermal acidic spray, and submersed in ponds (Ruttner 1955). But in the Philippines, Furuki (2006) found it on soil and humus.

Reproduction

Riccardia jackii is **dioicous** (Furuki 2006). Ono (1978) described the gemmalings of this species.

Biochemistry

Matsuo *et al*. (1982) isolated enantiomeric type sesquiterpenoids from ***Riccardia jackii***. It produces ent-selinane-, ent-aromadendrane and ent-bicyclogermacrane-type sesquiterpenes together with (R)-cuparene and α-barbatene (Asakawa *et al*. 1981; Ge 2007). In addition, 3,4-dimethoxy-5-hydroxy-9,1-dihydrophenanthrene is a rare dihydrophenanthrene derivative among liverworts and was first described in ***Riccardia jackii*** (Salamani 1978).

Riccardia marginata

(syn. = *Aneura marginata*, *Riccardia muscoides*)

Distribution

Riccardia marginata (Figure 134) occurs in New Zealand and the north coast of Australia (DiscoverLife 2008). To these locations, Furuki and Tamura (2015) have added Japan with ***Riccardia marginata*** var. ***pacifica***.

Figure 134. ***Riccardia marginata***, a species mostly of New Zealand and Australia. Photo by Shirley Kerr, with permission.

Aquatic and Wet Habitats

The liverwort ***Riccardia marginata*** (Figure 134) occurs on the wet banks of running water and grows on moist soil among rushes and introduced herbs in New Zealand reserves (Macmillan 1976). Tangney (1988) reported it from permanently wet open sites in New Zealand where ***Sphagnum cristatum*** (Figure 135) was one of the characteristic species.

Figure 135. ***Sphagnum cristatum***, a species that characterizes wet, open sites where ***Riccardia marginata*** occurs in New Zealand. Photo by Clive Shirley, The Hidden Forest, with permission.

Adaptations

Riccardia marginata (Figure 134) is small and brown (Pearson 1922). This coloration suggests protection against the damaging effects of high light intensity.

Reproduction

Riccardia marginata (Figure 134) is **dioicous** (Pearson 1922). Its spores are tiny, making them easily dispersed by wind, but providing it with limited resources with which to germinate and establish.

Fungal Interactions

I have seen no reports of fungi growing on or within ***Riccardia marginata*** (Figure 134). However, this may be a real absence based on its antibiotic activity, as discussed below, or a lack of study.

Biochemistry

It is interesting that this tiny species, ***Riccardia marginata*** (Figure 134), with so little ecological information has had a number of biochemical studies. Baek *et al*. (2004) isolated three new chlorinated bibenzyls from this species, the first time any simple chlorinated bibenzyl was reported from a natural source. These three compounds exhibited antimicrobial activity against ***Bacillus subtilis*** (bacterium; Figure 136), ***Candida albicans*** (yeast; Figure 137), and ***Trichophyton mentagrophytes*** (**Ascomycota**; Figure 138-Figure 139).

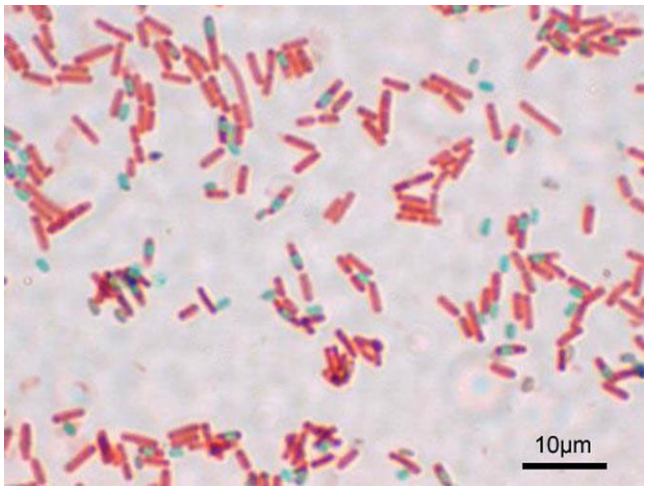

Figure 136. ***Bacillus subtilis*** spores, a species that is inhibited by extracts of ***Riccardia marginata***. Photo by Y. Tambe, through Creative Commons.

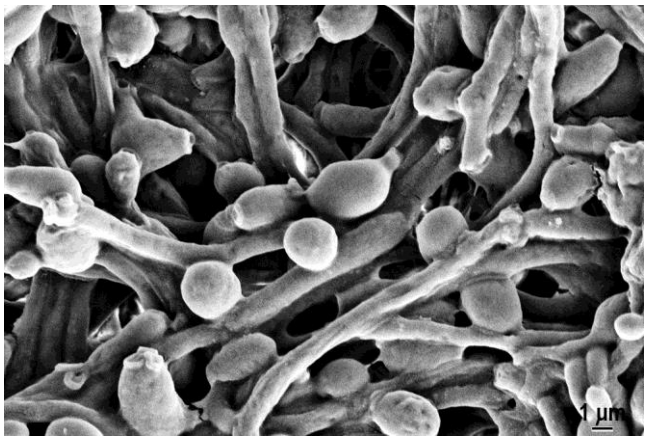

Figure 137. SEM of ***Candida albicans***, a species that is inhibited by extracts of ***Riccardia marginata***. Photo by Vader 1941, through Creative Commons.

Figure 138. ***Trichophyton mentagrophytes*** ringworm on arm, a species that is inhibited by extracts of ***Riccardia marginata***. Photo through Creative Commons.

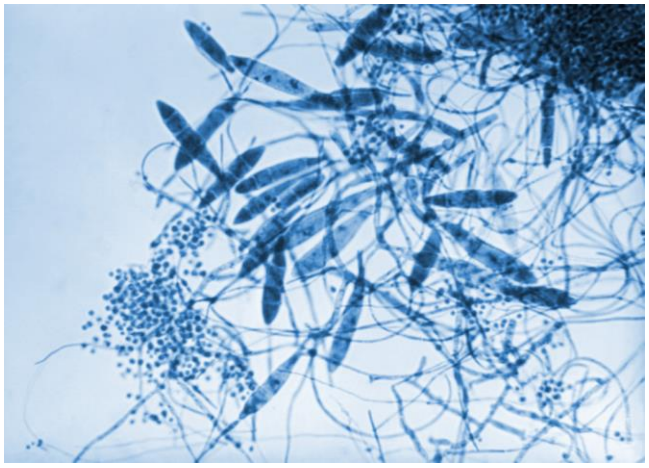

Figure 139. ***Trichophyton mentagrophytes*** as it appears stained under the microscope. Photo by Lucille K. Georg, through Creative Commons.

Unsinn *et al*. (2013) prepared an antimicrobial product (2,6-dichloro-3-phenethylphenol) from ***Riccardia marginata*** (Figure 134). Na *et al*. (2005a, b) likewise found that extracts of this species inhibited the Gram positive bacterium ***Bacillus subtilis*** (Figure 136), yeast (***Candida albicans***; Figure 137), and has strong action against the skin fungus ***Trichophyton mentagrophytes*** (Figure 138-Figure 139). It was ineffective against P388 murine leukemia cells.

Riccardia multifida (Figure 140-Figure 149)

Distribution

Riccardia multifida (Figure 140-Figure 149) has a wide distribution, known from India [Western Himalaya (Uttarakhand), Eastern Himalaya (Arunachal Pradesh, Assam, Sikkim, West Bengal), Western Ghats (Kerala, Maharashtra, Tamil Nadu), Central India (Madhya Pradesh)], China, Hawaii, Micronesia, Nepal, Russia, Sri Lanka, Taiwan, Turkey, Africa, Europe, and North America (Singh & Singh 2017). Damsholt (2017) listed it as known from the Faeroe Isles. Frey and Kurschner (1983) reported it from Iran.

In North America, it occurs in the northwestern part of the continent and in the east from Newfoundland southward (Perold 2001). Kruse and Davison (2012) reported it from Texas, USA. In Europe it is reported from Greenland, Iceland, and the British Isles. It occurs in both north and south Africa, Madagascar, and west Java. Furuki (1991) reported the subspecies ***R. multifida*** (Figure 140-Figure 149) subsp. ***decrescens*** from Japan. It is likely that many more records of this species exist in the USA and elsewhere.

Figure 140. ***Riccardia multifida***, a widespread species, forming a dense cushion. Photo by David T. Holyoak, with permission.

Figure 141. ***Riccardia multifida*** showing the branching pattern. Photo by Jan-Peter Frahm, with permission.

Figure 142. ***Riccardia multifida***. Photo by Manju Nair, through Creative Commons.

Figure 143. ***Riccardia multifida*** showing the pale color of a well hydrated colony. Photo by Hermann Schachner through Creative Commons.

Figure 144. ***Riccardia multifida*** showing a slightly darker phase. Photo by Jean Faubert, with permission.

Figure 145. ***Riccardia multifida***. Photo by Hermann Schachner, through Creative Commons.

Figure 146. ***Riccardia multifida***. Photo by Hermann Schachner, through Creative Commons.

Figure 147. ***Riccardia multifida*** growing on a vertical substrate. Photo by Michael Lüth, with permission.

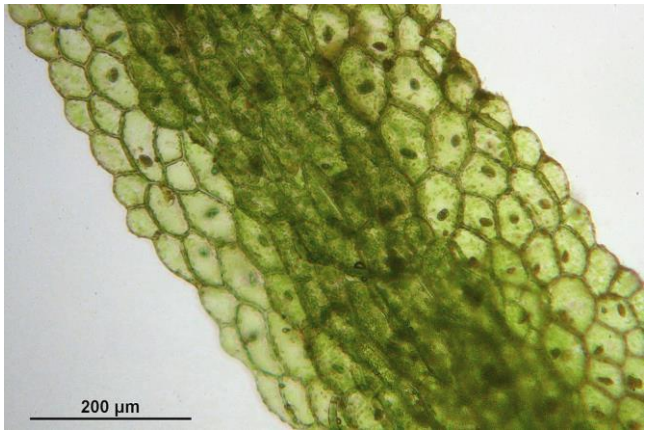

Figure 148. ***Riccardia multifida*** showing thallus with light-colored margins. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Riccardia multifida (Figure 140-Figure 149) occurs on streambanks with frequent submergence and slow water, wet rocks and soil near fast streams (Watson 1919), and may invade partially into the constantly submerged zone (Watson 1915). Konstantinova *et al*. (2002) found it on soil near brooks (Figure 150) in the forest of the Upper Bureya River (Russian Far East). In northwest Portugal, it occurs in mountain streams (Vieira *et al.* 2005).

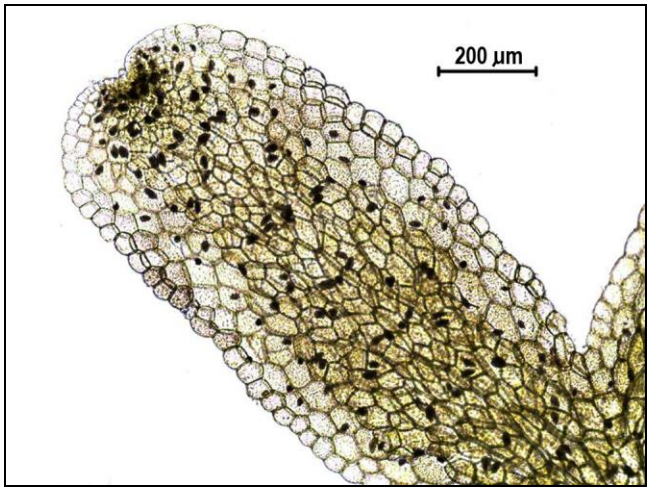

Figure 149. ***Riccardia multifida*** showing thallus with light-colored margins. Photo by Hugues Tinguy, with permission.

Figure 150. ***Riccardia multifida*** habitat. Photo by Hermann Schachner, through Creative Commons.

In the Himalayas, Singh and Singh (2017) report it from moist and shady places in dense mixed forest. Similarly, in Adjera, Georgia, on the coast of the Black Sea near the foot of the Lesser Caucasus Mountains, ***Riccardia multifida*** (Figure 140-Figure 149) occurs on stones and cliffs along streams in the broadleaved forest and in the waterfall spray zone, in partial shade, in broadleaved forests (Bakalin 2013).

In the Upper Peninsula of Michigan, USA, ***Riccardia multifida*** (Figure 140-Figure 149) occurs on gravelly bluffs along Lake Superior and on logs (Figure 151) in boggy woods (Evans & Nichols 1935). At Mountain Lake, Virginia, USA, it is "rather common" in wet sites (Sharp 1944). In West Virginia, it is one of the liverworts that occurs in McKinney's Cave (Ammons 1933). Burnham (1919) reported it from a "wet place" in the Lake George area, New York, USA. Trigoboff (2013) found that it could occur in massive clumps in Central New York on permanently wet creek rocks or dripping rocks at the sides of creeks, but nevertheless was never present at more than 2-3 spots along a creek. Fulford (1934) recorded it from shaded, swampy places in Kentucky, USA.

Figure 151. ***Riccardia multifida*** habitat where part of it is growing on decaying wood. Photo by Rick Ballard, through Creative Commons.

Few liverworts seem able to live in rich fens. In northwestern Europe, Kooijman and Westhoff (1995) found only two liverworts: ***Aneura pinguis*** (Figure 52-Figure 57) and ***Riccardia multifida*** (Figure 140-Figure 149), in these fens. Albinsson (1997) suggested that most liverworts require acidic, nutrient-poor sites.

Watson (1915) described zonation patterns in a Somerset heath (Figure 71). ***Riccardia multifida*** (Figure 140-Figure 149) occurs immediately above the zone of ***Aneura pinguis*** (Figure 52-Figure 57) and ***Pellia epiphylla*** (Figure 152). It sometimes extends downward into the latter zone. It also creates a definite zone in the furrows just at the water line.

Figure 152. ***Riccardia multifida*** on ***Pellia epiphylla***, an occurrence that can happen where it occurs adjacent to the ***Aneura pinguis*** and ***Pellia epiphylla*** zone in wet heath. Photo by Hermann Schachner, through Creative Commons.

In Arkansas, USA, Wittlake (1950) found it under and around the springs on the slope, accompanied by ***Aneura pinguis*** (Figure 52-Figure 57). On the Mahogany Hammocks, Everglades National Park, Florida, USA, ***Riccardia multifida*** (Figure 140-Figure 149) occurs on the low hammocks, but not on the high hammocks (Zona & Sadle 2017). These low hammocks have relatively continuous moisture in the soil. On the other hand, Haynes (1915) and McFarlin (1940) found ***Riccardia multifida*** on logs in wet places in Florida. Clebsch (1947) found it on a limestone face above Bellamy's Cave, Kentucky, USA.

In the Western Ghats, ***Riccardia multifida*** (Figure 140-Figure 149) occurs on tree buttresses near streams (Jyothilakshmi *et al*. 2016). Konstantinova *et al*. (2002) reported it from soil near a brook in the forest zone of the Upper Bureya River in the Russian Far East. Michael Lüth photographed it in a grass-sedge mire with other bryophytes (Figure 153-Figure 154).

Figure 153. ***Riccardia multifida*** occurring on soil amid grass. Photo by Michael Lüth, with permission.

Figure 154. ***Riccardia multifida*** with ***Scapania*** amid sedges. Photo by Michael Lüth, with permission.

Adaptations

In some wet habitats ***Riccardia multifida*** (Figure 140-Figure 149) forms dense **mats** (Figure 155-Figure 156). These seem to be able to change colors (Figure 155-Figure 156), but we need studies to show the environmental parameters that can cause these color changes and if they offer any advantage.

Riccardia multifida (Figure 140-Figure 149) does not seem to be well adapted to drying out. At 20ºC for 12 hours, only a few cells of ***R. multifida*** remained alive at 84% relative humidity (Clausen 1964). At 93% relative humidity about 3/4 of the cells remained alive.

Reproduction

Riccardia multifida (Figure 140-Figure 149) is **monoicous** (Singh & Singh 2017). The male and female branches are rarely **synoicous** (Perold 2001). Although Perold states that gemmae are unknown, Yang and Hsu had already described the germination of spores and gemmae of ***Riccardia multifida*** in 1967.

Figure 155. ***Riccardia multifida*** with pale green portions and pinkish portions. Photo by Michael Lüth, with permission.

Figure 156. ***Riccardia multifida*** showing two clumps with one brownish pink and one pale pink-green. Photo by Michael Lüth, with permission.

Benson-Evans (1964) found that gametangial production in ***Riccardia multifida*** (Figure 140-Figure 149) was a long-day response. Light intensities above 16 lux in the field also correlated with gametangial production.

Steil (1923) described the structure of the antherozoid in ***Riccardia multifida*** (Figure 140-Figure 149). Rushing *et al*. (1995) have described the blepharoplast of the spermatid.

Presence of sporophytes is known from a number of locations (Figure 157-Figure 159).

Figure 157. ***Riccardia multifida*** with young sporophyte. Photo by Paul G. Davison, with permission.

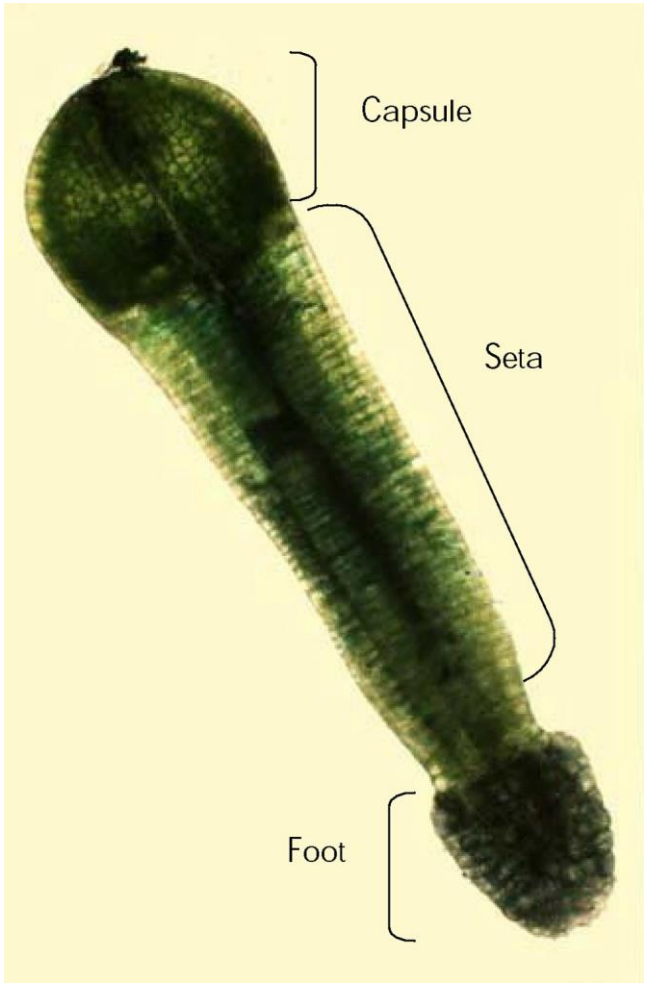

Figure 158. ***Riccardia multifida*** sporophyte before elongation. Image by Karen Renzaglia, with permission.

The chromosome number in the genus is n=9 + m (Zheng & Zhu 2008).

Fungal Interactions

In ***Riccardia multifida*** (Figure 140-Figure 149), Krause *et al*. (2011) were unable to find any fungal hyphae of tulasnelloid (**Basidiomycota**) fungi in living liverwort host cells. However, fungi had colonized dead cells. More commonly, the fungi occurred outside the thallus and on the adjacent substrate. In the liverwort, uncolonized living cells exhibited thick-walled cortical cells and ovoid, starch-filled chloroplasts. These chloroplasts were absent in the colonized cells. The hyphae on the dead cells proved to be those of **Ascomycetes**. Krause *et al*. (2011) found that the differences in colonization patterns among species in the genus differed from each other, supporting the hypothesis that the host regulates the pattern of colonization by the fungus.

Figure 159. ***Riccardia multifida*** with capsules and fully elongated setae. Photo from Botany Website, UBC, with permission.

Jiao *et al*. (2013) determined the chemical structures of compounds obtained from ***Penicillium*** sp. (Figure 160-Figure 161) that lived endophytically in ***Riccardia multifida*** (Figure 140-Figure 149). When tested, these compounds showed significant **allelopathic** effects (phenomena by which organisms produce one or more biochemicals that influence germination, growth, survival, and reproduction of other organisms) that retarded germination of ***Arabidopsis thaliana*** seeds (Figure 162-Figure 163). It would be interesting to test the allelopathic effects of this liverwort-fungus combination in nature. For a tiny plant this could provide a powerful competitive advantage against the larger tracheophytes.

Figure 160. ***Penicillium italicum*** and ***Penicillium digitatum*** growing on an orange. A species of ***Penicillium*** lives in cells of ***Riccardia multifida***. Compounds made by the fungus during this association can inhibit germination of ***Arabidopsis thaliana***. Photo by George Barron, with permission.

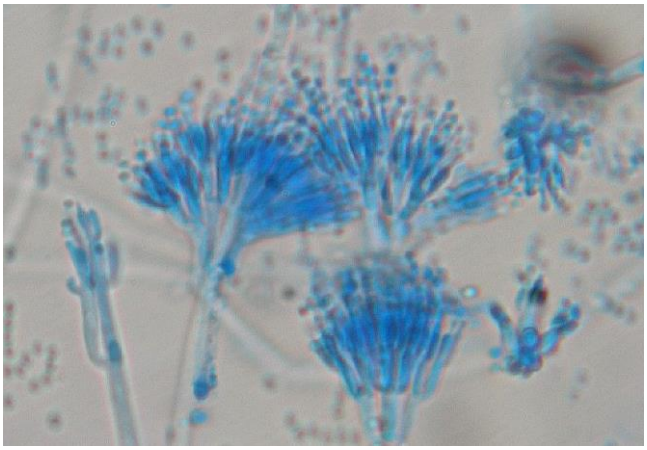

Figure 161. ***Penicillium*** sp. as seen under the microscope. Photo by Carlos de Paz, through Creative Commons.

Figure 162. ***Arabidopsis thaliana*** seeds, a species whose germination is inhibited by the ***Penicillium*** species that lives in cells of ***Riccardia multifida***. Photo by Stefan Lefnaer, through Creative Commons.

Figure 163. ***Arabidopsis thaliana***. Photo by Brona, through Creative Commons.

Biochemistry

The oil bodies are not evenly distributed, being absent or rare in the dorsal and ventral epidermal cells, absent in as much as 70% of the marginal cells, but present in internal cells (Perold 2001). They are mostly single, but occasionally two per cell.

Yoshida *et al*. (1997; Ge 2007) reported bisbibenzyls and other compounds from ***Riccardia multifida*** (Figure 140-Figure 149). They were able to isolate a new cyclic bisbibenzyl dimer from the variety ***decrescens***.

The aromatic ethers riccardin A and riccardin B have been isolated from ***Riccardia multifida*** (Figure 140-Figure 149) (Salamani 1978; Asakawa *et al*. 1983). These compounds, isolated from ***R. multifida***, have cytotoxic properties (Asakawa *et al*. 1983; Chandra *et al*. 2017).

Tori *et al*. (1985) used NMR spectra to identify new macrocyclic bis(bibenzyls) in ***Riccardia multifida*** (Figure 140-Figure 149).

Riccardia multifidoides

Distribution

Riccardia multifidoides is a tropical species that seems to be either rare or poorly known.

Aquatic and Wet Habitats

In the tropics, Ruttner (1955) reported ***Riccardia multifidoides*** as submersed in ponds and on the wall of a

bay. But in the Philippines, Furuki (2006) reported it only from fallen logs.

Reproduction

Riccardia multifidoides is **monoicous** (Furuki 2006).

Riccardia parvula

Distribution

Riccardia parvula is known from the Philippines, Malay Peninsula, Borneo, Sumatra, and Java.

Aquatic and Wet Habitats

Riccardia parvula occurs in waterfalls in the tropics (Ruttner 1955). In the Philippines, this species in known only from rotten logs (Furuki 2006). Nevertheless, rotten logs hold moisture longer than early stage logs, thus suggesting its preference for moisture.

On Mount Patuha, West Java, Indonesia, ***Riccardia parvula*** occurs on soil in disturbed forest adjacent to Situ (Lake) Patenggang, 1500 m asl (Gradstein *et al*. 2010).

Reproduction

Riccardia parvula is **dioicous** (Furuki 2006). Furuki (2001) has described the capsules and spores. The spores are 12.5-15 µm in diameter.

Riccardia singapurensis

The status of this species is controversial (Furuki & Tan 2013).

Distribution

Riccardia singapurensis occurs in Singapore (Zhu *et al*. 2018) and Australia (North Queensland) (Furuki & Tan 2013). It is rather common in Malesia and adjacent regions (Furuki & Tan 2013). Horing (2017) added it to the flora of Malaysia.

Aquatic and Wet Habitats

Riccardia singapurensis occurs on wet rocks and fallen logs in forests or along streams (Furuki & Tan 2013).

Adaptations

Thalli of ***Riccardia singapurensis*** are small, green to brownish green when fresh. Geotropic stolons give it a structure to survive unfavorable conditions and help the colony to spread (Furuki & Tan 2013). Rhizoids are scattered on the ventral surface of the prostrate thallus, providing a means of cementing itself to rocks.

Reproduction

Riccardia singapurensis is h**eteroicous** with male and **paroicous** branches, but male branches are rare and female branches are unknown (Furuki & Tan 2013). However paroicous branches are common. Gemmae are rare.

Biochemistry

Oil bodies of ***Riccardia singapurensis*** are pale brownish, composed of granules, globose to elliptical (Furuki & Tan 2013). The species lacks biochemical studies.

Riccardia subexalata

(syn. = *Aneura subexalata*)

Distribution

The only record I found for this species was the report by Ruttner (1955) that it occurs in the tropics.

Aquatic and Wet Habitats

This is one of those species listed as aquatic in the tropics by Ruttner (1955).

Riccardia tenuis

(syn. = *Aneura tenuis*)

Distribution

Riccardia tenuis is known from the tropics (Ruttner 1955). But otherwise, little seems to be known about it.

Aquatic and Wet Habitats

Riccardia tenuis occurs in waterfalls in the tropics (Ruttner 1955).

Riccardia tjibodensis

Distribution

Like the previous species, little is known about this species except the report by Ruttner (1955) that it occurs in the tropics.

Aquatic and Wet Habitats

Riccardia tjibodensis occurs in waterfalls in the tropics (Ruttner 1955).

Riccardia wettsteinii

Several varieties are known for this species.

Distribution

Riccardia wettsteinii is known from its type specimen from Java (Pócs 1976-77).

Aquatic and Wet Habitats

Riccardia wettsteinii occurs on the wall of a bay in the tropics (Ruttner 1955), presumably in Java.

Summary

The **Aneuraceae** has a number of members that live in wet habitats, but few that live submersed. The most remarkable member is ***Aneura mirabilis***, a completely parasitic species that partners with a fungus (***Tulasnella*** sp.) and a tree, especially birch trees. Other members of the genus can have fungal partners or epiphytc fungi, but ***Aneura mirabilis*** is the only liverwort that totally lacks chlorophyll.

Members of ***Aneura*** often differ in thickness of the thallus that within the species can represent different cryptic species.

Lobatiriccardia is a much less known genus, but its separation from ***Aneura*** seems justified. It occurs in the Southern Hemisphere and the tropics. Its wetland species are mostly not submersed, occurring in bogs, streambanks, decaying logs, but occasionally submersed.

Riccardia can be found from the tropics to both polar regions. Some species occur in cold alpine streams; others occur at stream margins and on emergent rocks. The genus occupies a wide range of wet habitats.

Acknowledgments

Lars Söderström helped me find the current acceptable names for a number of older taxa.

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CHAPTER 1-12: AQUATIC AND WET MARCHANTIOPHYTA, ORDER METZGERIALES: METZGERIACEAE AND CALYCULARIACEAE

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CHAPTER 1-12: AQUATIC AND WET MARCHANTIOPHYTA, ORDER METZGERIALES: METZGERIACEAE AND CALYCULARIACEAE

Figure 1. ***Metzgeria conjugata***, a widespread species that includes damp and humid locations such as gorges and ravines among its habitats. Photo by Bernd Haynold, through Creative Commons.

SUBCLASS METZGERIIDAE

Metzgeriales: Metzgeriaceae

Metzgeria (Figure 1-Figure 14; Figure 38-Figure 41; Figure 58, Figure 60-Figure 63)

Some members of the genus ***Metzgeria*** (Figure 1-Figure 14; Figure 38-Figure 41; Figure 58, Figure 60-Figure 63) can be submersed in the tropics (Ruttner 1955).

Figure 2. ***Metzgeria conjugata***, North American clade. Photo from UBC Botany Website, with permission.

Metzgeria conjugata (Figure 1-Figure 14)

Using molecular data, Fuselier *et al*. (2009) identified three morphologically cryptic clades of ***Metzgeria conjugata*** (Figure 1-Figure 14): northern North America (Figure 2), Europe (Figure 3), and south-eastern North America. These molecular differences, however, were not manifest in any morphological differences.

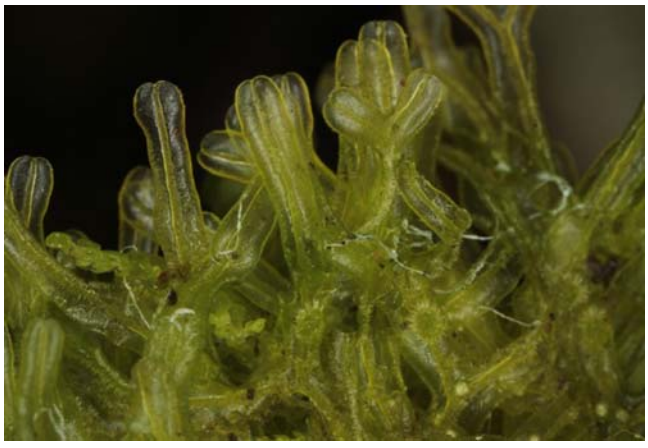

Figure 3. ***Metzgeria conjugata***, European clade. Photo by Jan-Peter Frahm, with permission.

Distribution

Distribution of ***Metzgeria conjugata*** (Figure 1-Figure 14) is a widespread amphi-Atlantic disjunct (Schofield, 1988). It occurs in most of Europe, eastward to the Caucasus, eastward in Asia to Japan, south to Burma, Java, Sumatra, and the Celebes, eastward to New Zealand, Africa from Mozambique to Natal, Tanganyika, and Madagascar. In North America it extends from Quebec and Ontario west to Alaska, southward to California, New Mexico, and in South America it is known from Brazil south to Colombia, Chile, and Argentina. Frey (1974) reported it from Iran.

Figure 4. ***Metzgeria conjugata***, a widespread amphi-Atlantic species. Photo by Jan-Peter Frahm, with permission.

Figure 5. ***Metzgeria conjugata*** showing a dense, pure colony. Photo by Štěpán Koval, with permission.

Figure 6. ***Metzgeria conjugata*** showing a growth form that extends away from the substrate. Photo by Michael Lüth, with permission.

Figure 7. ***Metzgeria conjugata*** showing the translucent nature of the hydrated thallus. Photo by Štěpán Koval, with permission.

Figure 8. ***Metzgeria conjugata*** growing flat in a wet habitat. Photo by Štěpán Koval, with permission.

Figure 9. ***Metzgeria conjugata*** showing the strong midrib and translucent (1 cell thick) thallus. Photo by Štěpán Koval, with permission.

Figure 10. ***Metzgeria conjugata*** showing 1-cell-thick thallus. Photo from UBC Botany Website, with permission.

Fuselier *et al*. (2009) considered that different forms of ***Metzgeria conjugata*** (Figure 1-Figure 14) may exhibit both Amphi-Atlantic and Western Europe-Western North America disjunctions.

Aquatic and Wet Habitats

Metzgeria conjugata (Figure 1-Figure 14) occurs in cool boreal forests worldwide (Schuster, 1992). Its habitats are as varied as its range, with both bark (Figure 11-Figure 12) and rocks serving as substrata, usually in damp and humid locations such as gorges and ravines (Figure 13). On rocks it usually occurs in large, pure mats. It seems to prefer calcareous sites, but it is not restricted to them.

Figure 11. ***Metzgeria conjugata*** on bark, Nara, Japan. Photo by Janice Glime.

Figure 12. ***Metzgeria conjugata*** on bark. Photo by Bernd Haynold, through Creative Commons.

Figure 13. ***Metzgeria conjugata*** stream bank habitat in Europe. Photo by Michael Lüth, with permission.

Metzgeria conjugata (Figure 1-Figure 14) occurs in crevices or surface of drier cliffs (Figure 14) in ravines in Connecticut, USA (Nichols 1916). It is occasionally

submerged (Watson 1919) or occurs on rock and in communities associated with streams near Lacko, Western Carpathians (Mamczarz 1970); it is rare in aquatic habitats of eastern Odenwald and southern Spessart (Philippi 1987); In Thuringia, Germany, it occurs in the ***Platyhypnidium-Fontinalis antipyretica*** association (Figure 15) (Marstaller 1987). Ferreira *et al.* (2008) described it from rivers; it occurs on limestone rock in the Tara River Canyon and Durmitor area, Montenegro (Papp & Erzberger 2011). In the eastern United States it occurs in Adirondack Mountain streams (Slack & Glime 1985).

Figure 14. ***Metzgeria conjugata*** on rock face. Photo by Michael Lüth, with permission.

Figure 15. ***Platyhypnidium riparioides*** on emergent rocks with ***Fontinalis antipyretica*** submerged. Photo by J. C. Schou, with permission.

In Brazil it usually occurs on shaded wet rocks and is rare on tree trunks (da Costa & Machado 1992).

In North Wales ***Metzgeria conjugata*** (Figure 1-Figure 14) grows on rocks (Figure 16) in the spray of waterfalls and on boulders by mountain streams (Rhodes 1916). In the Caucasus, Russia, this species occurs on soil, rocks, and cliffs along stream banks (Konstantinova *et al*. 2009). In Hungary, it is not rare and occurs in mountains in the western part in ravines and along streams on wet rocks (Ódor 2000).

Figure 16. ***Metzgeria conjugata*** on rock. Photo by Michael Lüth, with permission.

Philippi (1987) reported that ***Metzgeria conjugata*** (Figure 1-Figure 14) occurred occasionally in streams of eastern Odenwald and southern Spessart, where the streams are weakly acid, having little limestone, and the bryophyte substrate is red sandstone. Fulford (1934) reported it from moist sandstone cliffs in Kentucky, USA (Figure 17). Wagner (1952) suggested that its rarity in Indiana was the scarcity of deep canyons that provide the needed moist microclimate, and that light might also be a factor. Ódor (2000) supported this suggestion in Hungary, where in the Kékes North Forest Reserve in Mátra Mountains it occurs only in the wet fissures of high, shaded rock walls. In Hungary, it is not rare and occurs in mountains and in the western part in ravines and along streams on wet rocks (Ódor 2000). It also occurs on cavern ceilings – a habitat that is likely to have constant moisture levels (Norris 1967).

Figure 17. Red sandstone cliffs in Red River Gorge, Kentucky, USA, where one might find ***Metzgeria conjugata***. Photo by Jarekt, through Creative Commons.

In North Carolina, USA, ***Metzgeria conjugata*** (Figure 1-Figure 14) occurs on moist rocks, soil, and trees (Blomquist 1936). Šoltés and Zubaľová (2015) reported ***Metzgeria conjugata*** (Figure 1-Figure 14) from shaded limestone rocks in the Eastern Carpathians of Slovakia.

Metzgeria conjugata (Figure 1-Figure 14) is more typically not aquatic or in wetlands. In the Polish Carpathians, ***Metzgeria conjugata*** seems to occur primarily at 600-800 m asl on rocks or trees, rarely on wet soil (Zubel

et al. 2011). These mostly afforested places account for the lower percentage on trees. It rarely occurs on mineral soil and rotten wood. In Korea ***Metzgeria conjugata*** occurs in forests that have been protected by their owners, on both rocks and trees (Hong 1960). ***Metzgeria conjugata*** can be epiphyllous in India (Singh *et al*. 2007) and China (Luo 1990).

Adaptations

Metzgeria conjugata (Figure 1-Figure 14) can occur in pure **mats** (Figure 18) or with other bryophytes (Figure 19) (Konstantinova *et al*. 2009). Both of these habits help to conserve water in habitats that become periodically dry.

Figure 18. ***Metzgeria conjugata*** growing in a pure mat. Photo by Štěpán Koval, with permission.

Figure 19. ***Metzgeria conjugata*** occurring with other bryophytes. Photo by Štěpán Koval, with permission.

Metzgeria conjugata (Figure 1-Figure 14) is pale green (Figure 20) to green-yellowish (Figure 21) and prostrate (da Costa & Machado 1992). The cell walls are thickened with small trigones – a character that needs study to determine possible adaptive value. I am guessing it makes the thin thallus stronger while maintaining flexibility. The thallus is **hirsute** (hairy; Figure 22-Figure 23), a trait in liverworts that might help to take up and conserve water. Ono (1977) has described these hairs as well as rhizoids.

Figure 20. ***Metzgeria conjugata*** showing its pale green color form. Photo by Michael Lüth, with permission.

Figure 21. ***Metzgeria conjugata*** thallus showing its yellowish-green color form. Photo by Hugues Tinguy, through Creative Commons.

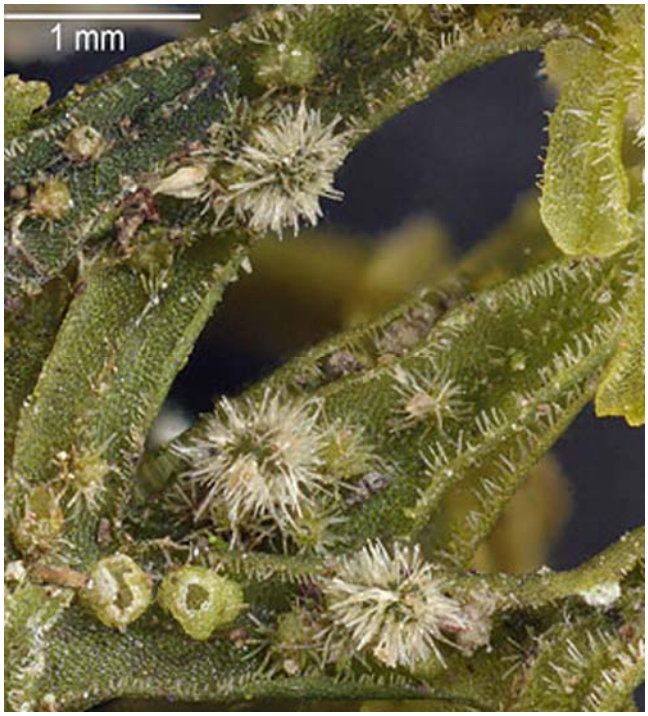

Figure 22. ***Metzgeria conjugata*** ventral view showing hirsute thallus. Photo by Norbert Stapper, with permission.

Figure 23. ***Metzgeria conjugata*** thallus hairs. Photo by Hugues Tinguy, through Creative Commons.

One of the characteristics I have surmised by looking at images of ***Metzgeria conjugata*** (Figure 1-Figure 14) from the web is that upon drying, the thallus margins curl under. The hydrated thallus is flat (Figure 18). The incurvation ultimately gives the thallus a tubular form (Figure 24-Figure 28) that reduces surface area and provides an internal chamber (Figure 28) that can help to maintain moisture.

Figure 24. ***Metzgeria conjugata*** fully hydrated. Photo from British Bryological Society, with permission per Barry Stewart.

Figure 25. ***Metzgeria conjugata*** beginning to dehydrate, showing the margins of the thallus beginning to curl under. Photo by David T. Holyoak, with permission.

Figure 26. ***Metzgeria conjugata*** showing a further stage of dehydration with thalli beginning to form tubes. Photo by Martin Hutten, with permission.

Figure 27. ***Metzgeria conjugata*** thallus dry, showing reduced surface area and tubular configuration of thalli. Photo by Hugues Tinguy, through Creative Commons.

Figure 28. ***Metzgeria conjugata*** showing hairs on the ventral surface. The margins are beginning to curl under, indicating that the thallus is drying. Photo by Hugues Tinguy, through Creative Commons.

Figure 30. ***Metzgeria conjugata*** with sporophyte. Photo from UBC Botany website, with permission.

Figure 31. ***Metzgeria conjugata*** with dehisced capsule. Photo by Hermann Schachner, through Creative Commons.

Reproduction

Metzgeria conjugata (Figure 1-Figure 14) is **monoicous** (Figure 29) and frequently fertile (Schuster 1992; Fuselier *et al*. 2009). Capsules are common (Figure 30-Figure 31) (Schuster 1992). Frye and Clark (1937) described gemmae, but Schuster (1992) described this species as lacking gemmae. Evans (1910) also considered reports of gemmae in ***Metzgeria conjugata*** to be in error. Rather, he considered these marginal gemmae to be normal outgrowths of the thallus (Figure 32). In the same year as Schuster described the absence of gemmae, da Costa and Machado (1992) described gemmae from populations in Brazil as lamellar at the thallus margin.

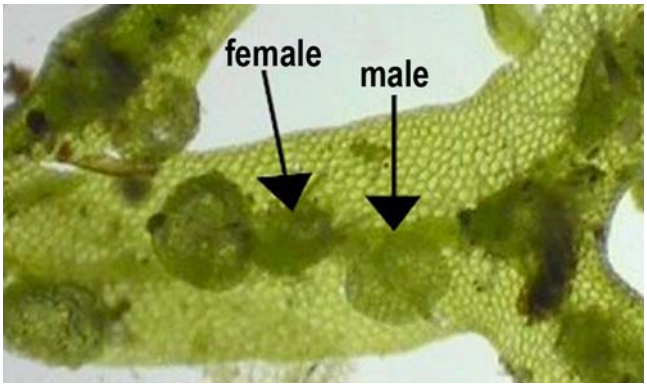

Figure 29. ***Metzgeria conjugata*** male and female. Modified from photo by Paul G. Davison, with permission.

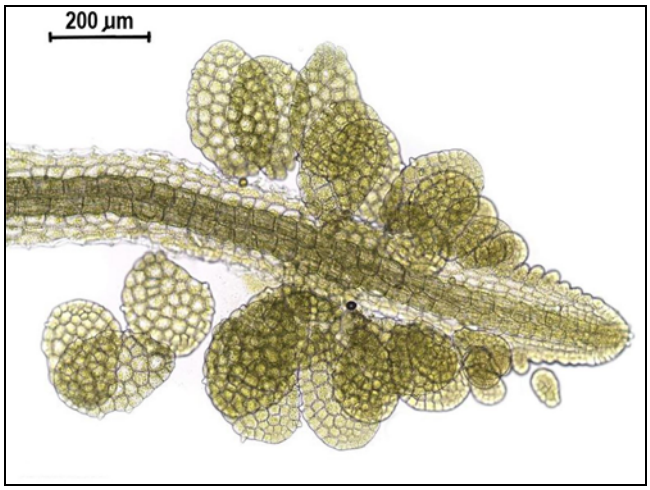

Figure 32. ***Metzgeria*** thallus with lobes that can serve as asexual reproductive structures. Photo by Hugues Tinguy, through Creative Commons.

Fungal Interactions

I have been unable to find any records of mycorrhizal or other fungal associations with ***Metzgeria conjugata***.

Biochemistry

Schuster (1992) reports that ***Metzgeria conjugata*** (Figure 1-Figure 14) lacks oil bodies. Suire (2000) affirmed this again in specimens from southwest France.

Metzgeria conjugata (Figure 1-Figure 14) is one of the species used to determine that RNA editing from genomic sequences in bryophytes is predictable, based on cDNA analysis (Steinhauser *et al*. 1999).

Theodor *et al*. (1981a) identified six already known tricin and apigenin di-c-glycosides, including 2″-o-ferulylisoschaftoside in the gametophyte thallus of ***Metzgeria conjugata*** (Figure 1-Figure 14).

Some of the compounds produced by ***Metzgeria conjugata*** (Figure 1-Figure 14) are effective against ***Paenibacillus larvae*** (Figure 33) isolates (Sevim *et al*. 2017). This bacterial species causes American foulbrood diseases in honeybee larvae. The newly hatched honey bee larvae are infected through ingestion of brood honey containing ***P. larvae*** spores (Figure 34). After germination and multiplication, the infected bee larvae die within a few days and decompose into a ropy mass (Figure 35). The bacteria release millions of spores after desiccation.

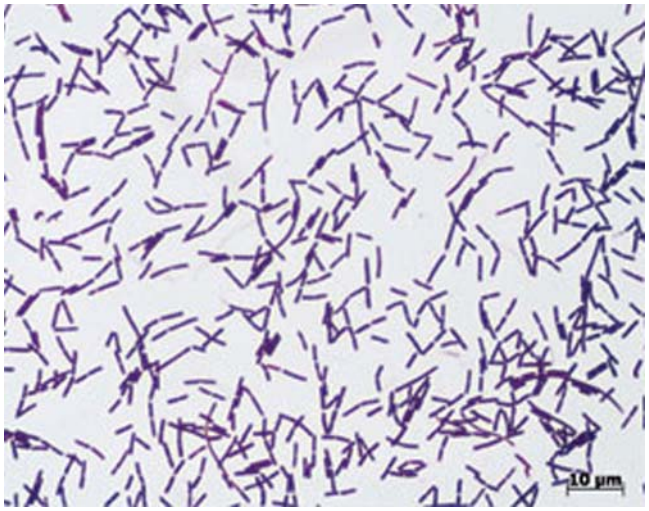

Figure 33. ***Paenibacillus larvae*** with Gram-positive stain, showing spore-forming, rod-shaped bacteria. Image modified from Sevim *et al*. 2017.

Figure 34. American-foulbrood-diseased bee larvae are beige or brown in color and have diminished segmentation. Image modified from Sevim *et al*. 2017.

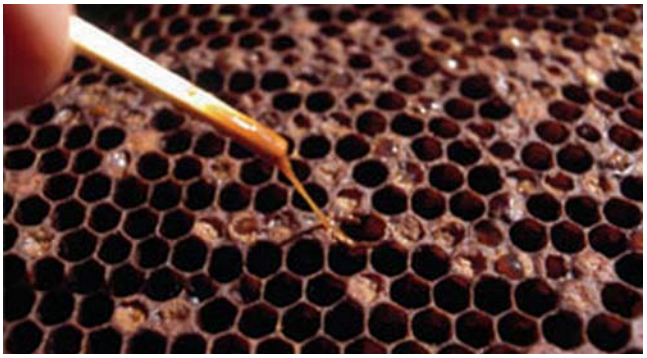

Figure 35. American foulbrood disease can be diagnosed by a matchstick test, demonstrating the viscous, glue-like larval remains adhering to the hive wall. Image modified from Sevim *et al*. 2017.

Metzgeria furcata/*Metzgeria setigera* (Figure 36, Figure 38-Figure 41)

Fuselier *et al.* (2009) demonstrated that within the broadly defined ***Metzgeria furcata*** (Figure 36), there are three very well-supported lineages, one from eastern North America and the other two widespread in Europe. Söderström *et al*. (2015) put the North American clade into ***Metzgeria setigera*** (Figure 37) as a new species.

Figure 36. ***Metzgeria furcata*** showing hairs on the thallus and long lobes. Photo by Shirley Kerr, with permission.

Figure 37. ***Metzgeria cf. setigera***, a representative of the North American clade that is now recognized as a separate species. Photo by Oskar Gran, through Creative Commons.

Distribution

The distribution of ***Metzgeria furcata*** (Figure 38-Figure 41) is worldwide (So 2002, 2004), but is mostly circumboreal (Schuster 1992). So (2002) listed countries from which specimens have been examined: Australia, Tasmania, Hawaii, Micronesia, New Caledonia, Papua New Guinea, New Zealand. Later So (2004) listed a number of African localities and Phephu and van Rooy (2015) reported it from southern Africa.

Figure 38. ***Metzgeria furcata*** growing in a tight, pure mat. Photo by Michael Lüth, with permission.

Figure 39. ***Metzgeria furcata*** with a somewhat more erect growth form. Photo by Michael Lüth, with permission.

Figure 40. ***Metzgeria furcata*** showing its translucent thallus. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

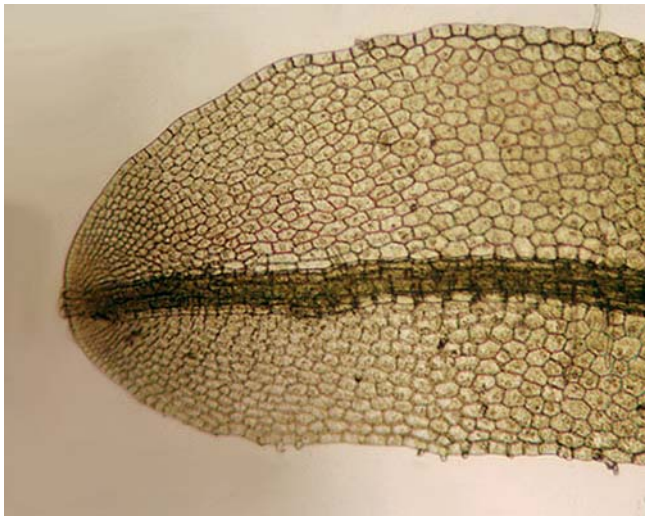

Figure 41. ***Metzgeria furcata*** thallus showing one-cell thickness. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Aquatic and Wet Habitats

Metzgeria furcata (Figure 38-Figure 41) occurs in rivers (Ferreira *et al*. 2008) and other aquatic habitats. It is part of the rock community in streams near Lacko, Western Carpathians (Mamczarz 1970). One of these is the ***Platyhypnidium-Fontinalis antipyretica*** association (Figure 15) in Thuringia, Germany (Marstaller 1987). In the Cool Temperate Victorian Rainforest it occurs in streams (Carrigan 2008).

Despite these aquatic records, Heylen and Hermy (2008) consider ***Metzgeria furcata*** (Figure 38-Figure 41) to be an obligate epiphyte. In the Tara River canyon and Durmitor area of Montenegro, it occurs on the bark of ***Fagus*** (Papp & Erzberger 2011). Although ***Metzgeria furcata*** is an epiphyte, it does often occur in wetlands and swamps, but still on typically bark (Schuster 1992).

Metzgeria furcata (Figure 38-Figure 41) var. ***ulvula*** is small and lives where there is high humidity, including along streams, but also 1-2 m high on tree trunks of older deciduous trees (Figure 42) or in the shade of rock faces or

steep banks along wooded creeks, and especially on big, steep ravines with high humidity and lots of rock face (Trigoboff 2013). It is especially common on rocks covered with ***Metzgeria conjugata*** (Figure 1-Figure 14). Newton (2012) reported ***Metzgeria furcata*** from bark of ***Sambucus*** spp. (Figure 43) and ***Salix*** sp. (Figure 44), species that often occur in wet habitats. ***Metzgeria furcata*** is useful as a biodiversity indicator (Heylen & Hermy 2008; Heylen & Hermy, in prep.).

Figure 42. ***Metzgeria furcata*** on bark. Photo by Michael Becker, through Creative Commons.

Figure 43. ***Sambucus nigra*** in Austria; ***Metzgeria furcata*** often occurs on the bark of ***Sambucus*** species. Photo by Franz Xaver, through Creative Commons.

In the Eurosiberian alder swamps of Latvia, ***Metzgeria furcata*** (Figure 38-Figure 41) occurs on decorticated logs (Madžule & Brūmelis 2008), a habitat that is typically moist longer than the surrounding habitat. On the other hand, in some areas ***Metzgeria furcata*** is an indicator species for logs in decay stage 1 (Madžule & Brūmelis 2008).

Metzgeria furcata (Figure 38-Figure 41) is typically an epiphyte in forests in a stream valley in the Carpathian Basin (Szövényi *et al*. 2004). In northwest Latvia it is one of the indicator species for old-growth forests, where it occurs as an epiphyte (Mežaka & Znotiņa 2006).

Figure 44. ***Salix alba***; ***Metzgeria furcata*** often occurs on the bark of ***Salix*** species. Photo by Willow, Creative Commons.

However, ***Metzgeria furcata*** (Figure 38-Figure 41) is not completely restricted to being an epiphyte. Dobrescu and Soare (2015) reported it among the saxicolous species in the Vâlsan Keys. It is of interest to note one unusual habitat for this widely distributed species: Koppe (1969) reported it from dry whale bones on Isle Borkum, in northwestern Germany.
(in South Africa) a steep-sided, wooded ravine or valley

Productivity

Photosynthesis of ***Metzgeria furcata*** (Figure 38-Figure 41) was measured as 4.2 ± 0.2 nmol CO_2 mg^{-1} Chl s^{-1} in air (Smith & Griffiths 2000).

Adaptations

Plants of ***Metzgeria furcata*** is yellowish green (Figure 45), thalli 1-2 cm long (So 2004). The thallus is one cell thick and translucent (Figure 45), perhaps adapting it to low light levels by permitting easy transmission of light.

Figure 45. ***Metzgeria furcata*** showing yellowish-green color and translucent thallus. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Metzgeria furcata (Figure 38-Figure 41) is quite desiccation tolerant (Schuster 1992). Clausen (1964) supported this concept with her experiments. At 20º C for

12 hours, all cells survived at 33% relative humidity; at 15% rh, only about 1/4 of the cells survived. All but undeveloped apical cells survived 2-4 days of freezing at -10ºC; after 30-34 days, only 3/4 of the apical cells survived. This tolerance explains its ability to live on the vertical trunks of trees, where it might have a **fan** form (Figure 46), giving it more exposed surface area, but possibly giving it more light exposure in forests. It can also grow with other bryophytes that could potentially help it to retain moisture (Figure 47).

Figure 46. ***Metzgeria furcata*** showing the shelf-like **fan** form. Photo by Michael Lüth, with permission.

Figure 47. ***Metzgeria furcata*** growing with other bryophytes, a potential way to maintain moisture longer. Photo by Shirley Kerr, with permission.

Reproduction

Schuster (1992) considered ***Metzgeria furcata*** (Figure 38-Figure 41) to be **dioicous**, but So (2002) described it as **autoicous**. Schuster notes that only gynoecia have been found in eastern North America (hence ***Metzgeria setigera***), and then only at higher elevations. Fuselier *et al.* (2011) likewise considered it to be dioicous. Perhaps it is **monoicous**, but conditions to stimulate production of antheridia do not occur in most of its locations. Yeates (1908) noted that typically one could only find females of ***Metzgeria furcata***. Plants that had developed calyptras had no embryos. Sporophytes were only found in colonies that also had male plants (Figure 48); antheridial abundance varied greatly even at the same location.

Figure 48. ***Metzgeria furcata*** with globular antheridia on midrib and potential propagules on the margin. Are these marginal structures gemmae or early stages of lobes? Photo by Tom Thekathyil, with permission.

Schuster (1992) describes ***Metzgeria furcata*** (Figure 38-Figure 41) as having plane, linear gemmae (maybe Figure 49), arising from the margin of the thallus (So 2004); in North America they are abundant (Schuster 1992). Gemma-bearing thalli (Figure 50) are typically more slender and less highly differentiated compared to non-gemma-bearing plants (Figure 45) (Evans 1910). Evans provides a detailed description of the development, separation, and subsequent germination of these structures.

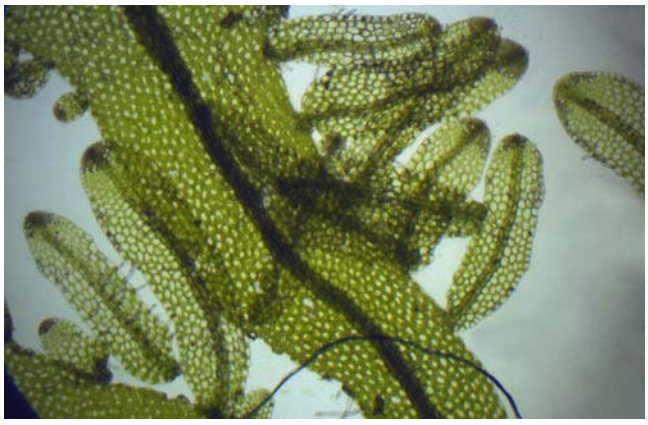

Figure 49. ***Metzgeria furcata*** showing lobes, possibly considered gemmae in some descriptions. Could these be the linear gemmae described by Schuster (1992)? Photo by Kristian Peters, with permission.

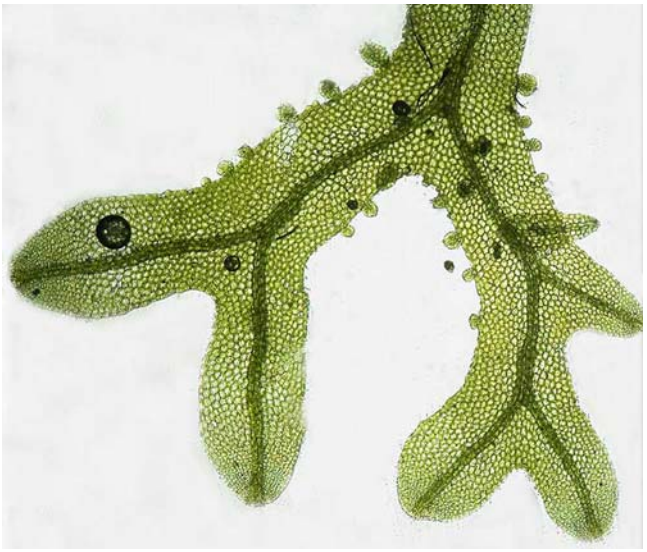

Figure 50. ***Metzgeria furcata*** with gemmae on margins and lobe arising from midrib. Photo by Walter Obermayer, with permission.

A discussion on Bryonet on 3 March 2021 did not really solve the problem of the definition of gemmae in ***Metzgeria furcata***. Dave Kofranek summarized a number of sources that defined gemmae as simply vegetative reproductive structures. Tom Thekathyil suggested that those structures on the margin in Figure 50 might be gemmae, whereas the one arising from the midrib might be just a thallus lobe. Sorin Stefanut challenged the gemma interpretation in ***Metzgeria furcata***, following the definition that gemmae are "uni- or multicellular, filamentous, globose, ellipsoidal, cylindrical, stellate, or discoid brood bodies, relatively undifferentiated, serving in vegetative reproduction," a definition found in the *Glossarium Polyglottum Bryologiae*. Stefanut contends that these are not true gemmae because they are only a small thallus having a midrib. Louis Thouvenot similarly suggested that the presence of a midrib would make them a thallus lobe. Jeff Duckett reminded us that in ***Metzgeria consanguinea*** and ***M. violacea*** the gemmae are endogenous and leave conspicuous holes in the thallus when they detach; such does not seem to be the case in ***M. furcata***. Arno van der Pluijm and Jacques van Rooy both considered ***Metzgeria*** to have both lobes and gemmae. In South African populations, gemmae occur as outgrowths along the margins of ***M. furcata*** (Phephu & van Rooy 2015). I have concluded that these outgrowths at the edge of the thallus are transitional structures that act like gemmae but retain the developmental pattern of thallus branching. Hence, I agree with Sean Edwards (Bryonet 5 March 2021) that gemmae don't evolve overnight, making this a semantic question. In the words of Sanna Laaka-Lindberg (Bryonet 5 March 2021), "we often look for evidence to categorize phenomena even in cases no clear limits perhaps exist."

Metzgeria furcata seems to be the great compromiser. In some cases the marginal bits of thalli fall off at an early stage, but others remain longer, developing into much larger lobes before falling off (Arno van der Pluijm, Bryonet 3 March 2021). In either case, these marginal structures can serve as propagules. Perhaps this is one of the places where bryophytes invented gemmae?

An additional potential means of reproduction in ***Metzgeria furcata*** (Figure 38-Figure 41) is the development of thalli from the female involucres (Kuwahara 1973). These are not rare occurrences in northwestern Europe, and they have been observed developing into thalli. These may be the same structures described by Yeates (1908) as thallidia; Yeates concluded that these seemed to provide most of the reproduction.

Heylen and Hermy (2008) suggested that the strongly aggregated distribution of ***Metzgeria furcata*** (Figure 38-Figure 41) indicates local dispersal (rather than regional dispersal). This is consistent with their apparent lack of sexual reproduction and spores, but instead the dispersal of larger bits of thalli.

Slime Molds and Fungal Interactions

Some slime molds are usually associated with ***Metzgeria furcata*** (Figure 38-Figure 41). Isabelle Mazaud photographed ***Diacheopsis synspora*** (Figure 51) with this species where it was growing on ***Quercus robur*** bark (Figure 52-Figure 53). Ing (1994) reported ***Hemitrichia minor*** (Figure 54-Figure 55) in association with this species.

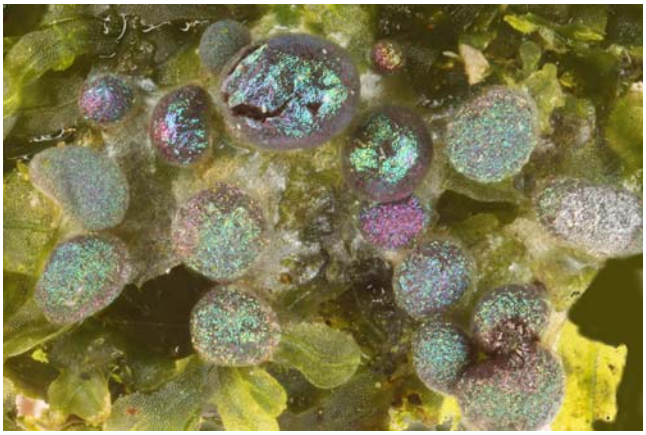

Figure 51. ***Diacheopsis synspora*** on ***Metzgeria*** in North Wales. Photo by Janet Graham, through Creative Commons.

Figure 52. ***Quercus robur*** in Devon, England, where one can find ***Metzgeria furcata***. Photo by Alex Jane, through Creative Commons.

Figure 53. ***Quercus robur*** bark, a suitable substrate for ***Metzgeria furcata*** in Essex, England. Photo by Acabashi, through public domain.

Figure 54. ***Hemitrichia minor***, a slime mold species known to associate with ***Metzgeria furcata***. Photo by G. Moreno and J. Francisco, micobotanicajaen.com, with online permission.

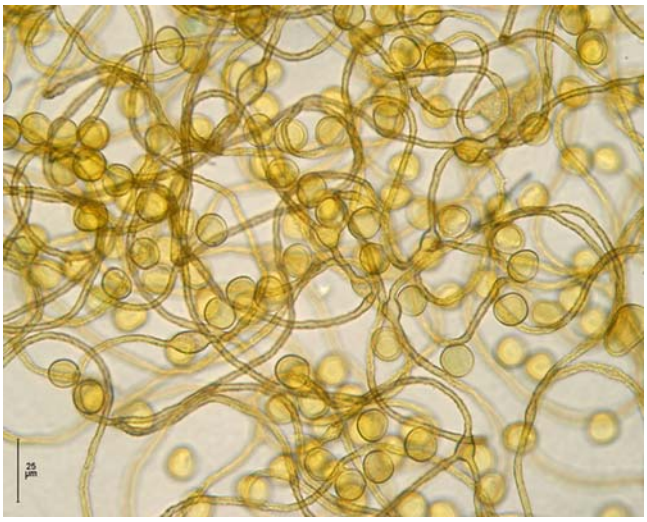

Figure 55. ***Hemitrichia minor*** microscopic view. Photo from Eumycetozoa Project, through DiscoverLife.org, with online permission.

Nordén *et al*. (2015) described the new **Ascomycete** fungus ***Bryocentria hypothallina*** from ***Metzgeria furcata*** (Figure 38-Figure 41). This fungus is indicated by bleached, necrotic patches on the liverwort. It produces ascomata on the under side of the thallus, perforating its surface. This parasitic fungus has a known distribution of France, Norway, and Spain – considerably less than the distribution of ***Metzgeria furcata***.

Biochemistry

Members of the genus ***Metzgeria*** lack oil bodies (Figure 56-Figure 57) (Suire 2000). Nevertheless, Theodor *et al*. (1983) identified 12 different flavone C-glycosides in ***Metzgeria furcata*** (Figure 38-Figure 41) and its variety ***ulvula***. Only four of these biochemicals are common to both the typical and the variety.

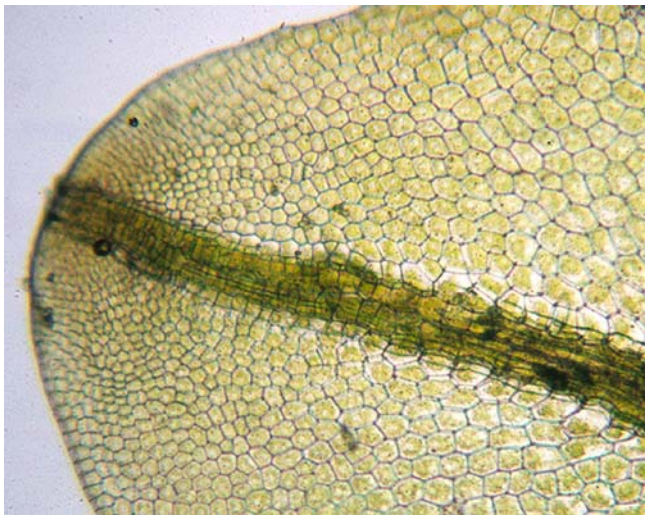

Figure 56. ***Metzgeria furcata*** showing absence of oil bodies in the thallus cells. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

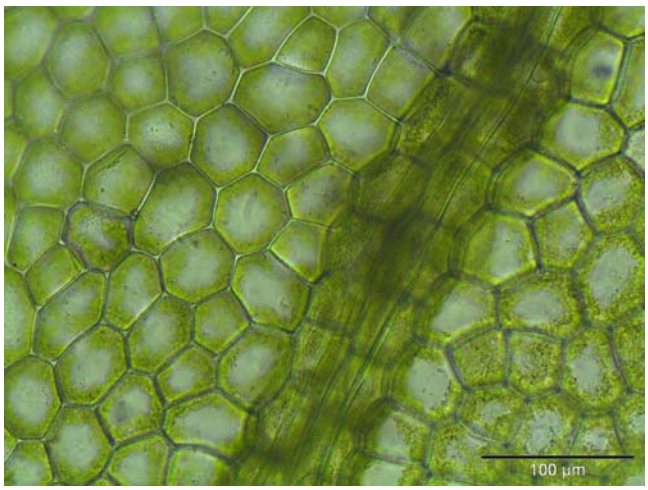

Figure 57. ***Metzgeria furcata*** lamina showing lack of oil bodies in thallus cells. Photo by Kristian Peters, with permission.

Werner *et al*. (2002) discovered that for ***Metzgeria furcata*** (Figure 38-Figure 41), thallus fragments longer than 1 mm inhibited the preparation of DNA for the polymerase chain reaction. They found that the optimal length was 0.5 mm. They suggested that the secondary

substances produced and stored in oil bodies might be responsible for this inhibition by bryophytes, but this does not explain the behavior in ***Metzgeria*** species because oil bodies are unknown.

The isolation of 6-C-a-L-rhamnopyranosylapigenin (isofurcatain) 7-0-/?-D-glucopyranoside, from ***Metzgeria furcata*** (Figure 38-Figure 41) var. ***ulvula***, the common variety reported in North America (Schuster 1992), is described and identified (Markham *et al*. 1982). This is a new natural product, as also is isofurcatain.

Metzgeria litoralis

Distribution

Metzgeria litoralis is known only from Chile in southern South America (Engel & Kuwahara 1973).

Aquatic and Wet Habitats

Metzgeria litoralis occurs on coastal rocks that are continuously exposed either to tidal action or ocean water spray (Engel & Kuwahara 1973). This is a highly unusual habitat for any bryophyte. The bryophytes have no mechanism for tolerating exposure to salt water. But Engel and Schuster (1973) suggest that in this case, drainage from forested areas directly above these beaches, along with high rainfall, provide sufficient fresh water for these liverworts to survive. They argue that these conditions do not allow for dispersal of bryophytes by tidal water along the shoreline.

Adaptations

Metzgeria litoralis has a yellow-green thallus that is convex, giving the appearance of a tube (Engel & Kuwahara 1973). But it is also flaccid, most likely due to the thin cell walls of the lamina.

Reproduction

Metzgeria litoralis is **dioicous** and lacks gemmae (Engel & Kuwahara 1973). However, females and sporophytes are unknown, so it is possible it is monoicous but has not experienced the environmental conditions necessary for female gametangia to develop.

Metzgeria pubescens (Figure 58, Figure 60-Figure 63)

(syn. = *Apometzgeria pubescens*)

The Southern Hemisphere populations are morphologically similar plants to the northern Holarctic ones but form a divergent lineage (often treated as ***Apometzgeria frontipilis***) in South America (Fuselier *et al*. 2011). But Engel and Kuwahara (1973) found both ***Metzgeria pubescens*** (Figure 58) and ***Metzgeria*** (***Apometzgeria***) ***frontipilis*** (Figure 59) growing together in southern South America. Thus, Fuselier *et al*. (2011) and others have considered ***Metzgeria pubescens*** to be bipolar, occurring throughout Europe, China, Russia, Korea, and North America (rather sparsely), as well as Chile (Engel 1978; Schuster 1992). In any case, it appears that there are distinct genetic differences in the species between the hemispheres, suggesting that there are new species in progress.

Figure 58. ***Metzgeria pubescens*** growing on bark. Photo by Štěpán Koval, with permission.

Figure 59. ***Metzgeria frontipilis***, a separate species that sometimes grows together with ***Metzgeria pubescens***. Photo by Blanka Aguero, with permission.

Results by Fuselier *et al*. (2011) indicate that ***Metzgeria pubescens*** (Figure 58) in South America forms a divergent lineage that shares a closer phylogenetic history with ***M. frontipilis***. As such, ***M. pubescens*** should be considered a Holarctic species.

Distribution

Metzgeria pubescens (Figure 60-Figure 63) occurs in Europe, Asia, and North America (So 2003). This known distribution has been expanded to a bipolar range with populations across the Holarctic and in southern South America (Fuselier *et al*. 2011). Blockeel (2020) reported it for the first time from Greece.

Figure 60. ***Metzgeria pubescens*** forming a nearly pure clump, but arranged to provide spaces between plants. Photo by Štěpán Koval, with permission.

Figure 62. ***Metzgeria pubescens*** showing the opaque thalli projecting away from the substrate. Photo by Štěpán Koval, with permission.

Figure 61. ***Metzgeria pubescens*** looking dry because of its covering of hairs. Photo by Štěpán Koval, with permission.

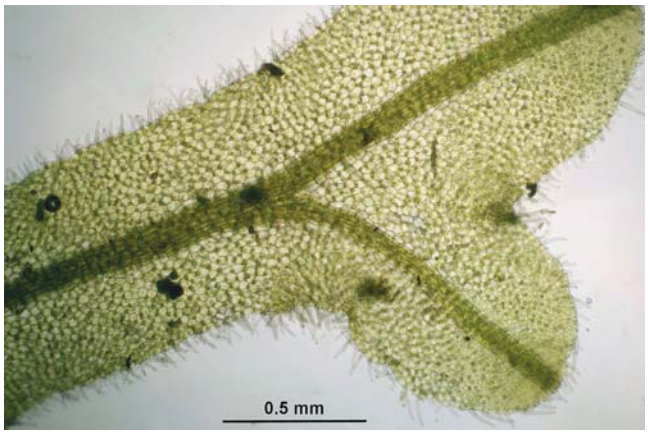

Figure 63. ***Metzgeria pubescens*** showing the thin (1-cell-thick) thallus and numerous hairs. Photo by Hermann Schachner, through Creative Commons.

For Romania (Ştefănuţ & Goia 2012) and Slovakia (Mišíková *et al*. 2021) ***Metzgeria pubescens*** (Figure 60-Figure 63) is listed as a liverwort of "Least Concern" in the Red List.

Aquatic and Wet Habitats

Metzgeria pubescens (Figure 60-Figure 63) is known from an intermittent stream (Dhien 1978). ***Metzgeria pubescens*** occurred on stones beside the water at Jumog Waterfall in Indonesia (Sidiq *et al*. 2019) and in Yakutia (Sofronova 2015). Chamberlain (1972) likewise reported it from **Breccia rock** (broken fragments of minerals or rock cemented together by fine-grained matrix; Figure 64) faces by the river and upstream on limestone. Lorenz (1910) similarly reported it from a limestone ravine in Switzerland, and Papp and Sabovljević (2002) in western Serbia.

Figure 64. Breccia rock at Titus Canyon Narrows, Death Valley National Park, California, USA. Photo from NPS, through public domain.

In the Vologda Region of Russia, ***Metzgeria pubescens*** (Figure 60-Figure 63) grew in the beds of mosses in a boggy spruce forest (Dulin *et al*. 2009). It is critically endangered in this region due to a scarcity of suitable habitats.

But ***Metzgeria pubescens*** (Figure 60-Figure 63) often occurs in habitats that would not be considered aquatic or wetland. In the Algama River basin of Yakutia, Russia, it occurs on stones, stones covered with humus, and rock outcrops in the forest belt (Sofronova 2013). Horikawa (1934) reported similar habitat in Japan, where it grew with mosses on rocky soil. Photographs also show that it can occur on bark (Figure 65).

Figure 65. ***Metzgeria pubescens*** on bark. Photo by Štěpán Koval, with permission.

One habitat that seems to be relatively common for bryophyte species tolerant of wetlands is that of wet, rotting logs. Such is the case also for ***Metzgeria pubescens*** (Figure 60-Figure 63) (Sofronova 2015).

Adaptations

Metzgeria pubescens (Figure 60-Figure 63), as indicated by its name, is a densely hairy species (Figure 66-Figure 68) on its ventral side, an uncommon character in the genus and used by some systematists to create a separate genus for it. This character would seem to protect it from drying out and also aid in providing capillary spaces that facilitate water uptake.

Figure 66. ***Metzgeria pubescens*** that is dry, but still green, with its hairs showing prominently. Photo by Štěpán Koval, with permission.

Figure 67. ***Metzgeria pubescens*** showing dense hairs. Photo by Štěpán Koval, with permission.

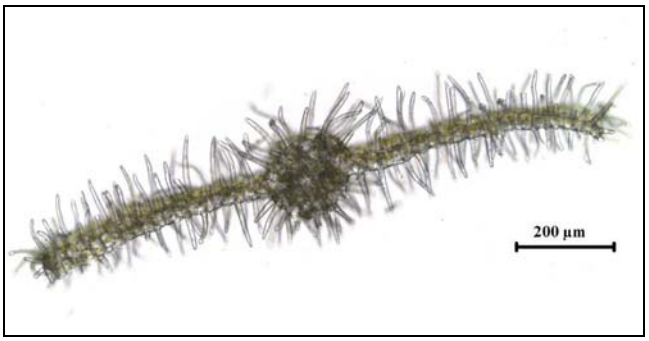

Figure 68. ***Metzgeria pubescens*** cs showing dense hairs. Photo by Hugues Tinguy, with permission.

Growth forms vary (Figure 69-Figure 70), presumably dependent on the habitat, but they could also represent different crypto species.

Figure 69. ***Metzgeria pubescens*** exhibiting a cluster growth form. Photo by Hugues Tinguy, with permission.

Figure 70. ***Metzgeria pubescens*** in a mat form. Photo by Štěpán Koval, with permission.

Reproduction

Metzgeria pubescens (Figure 60-Figure 63) is **dioicous** and rarely produces sporophytes. It furthermore apparently does not produce gemmae (Schuster 1992). Hence, it would be interesting to determine how it has become so widespread and common. These limiting reproductive strategies also help to explain the genetic divergence (Fuselier *et al*. 2011) seen for the species between the hemispheres.

M'Ardle (1896) suggested that ***Metzgeria pubescens*** (Figure 60-Figure 63), lacking females – at least in Ireland, was able to reproduce through a type of budding, adventitious branches that at some point could break away from the parent plant. I was unable to find any images that showed budding, at least not with the constricted bases of the branches seen in some of the above species (*e.g.* Figure 32, Figure 49).

Fungal Interactions

Glomeromycotean fungi are becoming well known in bryophytes. Ligrone *et al*. (2007) examined a large number of endophytic fungal associations in liverworts. They failed to discover any glomeromycotean fungi in ***Metzgeria pubescens*** (Figure 60-Figure 63).

Biochemistry

Markham *et al*. (1987) reported the existence of rotational isomerism in flavone-6,8-di-C-glycosides isolated from ***Metzgeria pubescens*** (Figure 60-Figure 63). Theodor *et al*. (1980, 1981b) reported five such flavone-C-glycosides.

Metzgeriales: Calyculariaceae

Calycularia crispula (Figure 71-Figure 72)

Distribution

Davison and Smith (1992) listed ***Calycularia crispula*** (Figure 71-Figure 72) from Asia (Himalaya, Burma, Thailand, Taiwan, Korea, Japan), Africa (Ethiopia, Tanzania, Malawi), and Mexico. When Daniels *et al*. (2014) reported it for the first time from the Western Ghats in India (see also Manju *et al*. 2015), they also included Bhutan, China, Myanmar, and Nepal. In 2010, Konstantinova and Mamontov (2010) excluded it from Russia, Canada, Japan, and Korea based on re-examination of the specimens. They instead contend that ***Calycularia crispula*** (Figure 71-Figure 72) is restricted to mountains of the tropics and subtropics, adding records from Zambia, China, and Costa Rica. They determined specimens from more northern collections to be ***Calycularia laxa***.

Figure 71. ***Calycularia crispula*** showing pale green and almost translucent thallus. Photo by Shanxiong Lin, Taiwan Mosses Color Illustrations, through Creative Commons.

Figure 72. ***Calycularia crispula*** in Sichuan, growing with mosses and exhibiting a medium green color with slightly reddish areas. Photo by David Long, with permission.

Figure 74. ***Plagiochila arbuscula*** as it would appear in a humid montane forest. Photo by Peter de Lange, through online permission.

Aquatic and Wet Habitats

Calycularia crispula (Figure 71-Figure 72) occurs in moist or foggy mountain locations on soil, tree bases, logs, stumps, and rocks (Davison & Smith 1992). Daniels *et al*. (2014) describe it as occurring in upland areas in the tropics of Asia, Africa, and Central America. The broad habitat descriptions may in some cases be based on the segregate northern species ***C. laxa***.

In the Western Ghats of India, ***Calycularia crispula*** (Figure 71-Figure 72) occurs at 1,540 m asl in montane wet temperate forests and also from 950 m asl in moist deciduous forest, attached to the bark of trees and on rocks; it also occurs on decaying logs, moist soil, in deep crevices and on shaded humus covered cliffs in river valleys.

In Thailand, ***Calycularia crispula*** (Figure 71-Figure 72) occurs on the bases of tree trunks, decaying wood, and humus rich rocks in humid montane forests at 1,200-2,550 m asl (Printarakul *et al*. 2019). ***Bazzania*** (Figure 73) and ***Plagiochila*** (Figure 74) often occur with it.

Figure 73. ***Bazzania tricrenata***; ***Calycularia crispula*** can occur with species of ***Bazzania*** in humid montane forests of Thailand. Photo by Hermann Schachner, through Creative Commons.

Adaptations

Daniels *et al*. (2014) describe ***Calycularia crispula*** (Figure 71-Figure 72) as translucent green (Figure 71). It is multilayered (Figure 75), thus not as translucent as the members of ***Metzgeria*** in this chapter. Konstantinova and Mamontov (2010) provide a more robust coloration, from "pale to yellowish (Figure 71) or deep green (Figure 72) often with secondary goldish, fuscous, reddish to purplish red or red-brown pigmentation." This broader description may be a better reflection of its pigmentation adaptations to various levels of light throughout its range and seasons.

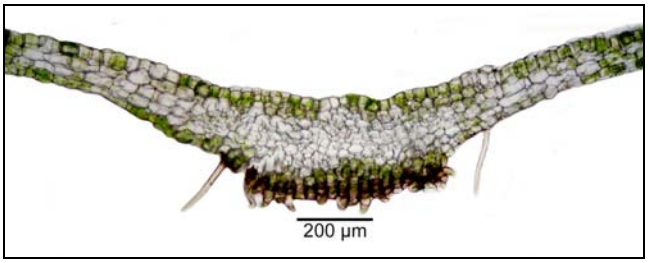

Figure 75. ***Calycularia crispula*** thallus cs. Photo by N. Printarakul, through Creative Commons.

Reproduction

Calycularia crispula (Figure 71-Figure 72) is **dioicous** (Konstantinova & Mamontov 2010). Both sexes are known and sporophytes are fairly common (Figure 76-Figure 77). Konstantinova and Mamontov suggest that the ventral shoots that arise from the midrib are likely to provide a means of vegetative propagation.

Figure 76. ***Calycularia crispula*** with capsules. Photo by N. Printarakul, through Creative Commons.

Figure 77. ***Calycularia crispula*** capsule in Sichuan. Photo by David Long, with permission.

The spores are endowed with large, somewhat cylindrical projections (Figure 78-Figure 79) (Konstantinova & Mamontov 2010). Experimentation is needed to determine if these facilitate flotation and subsequent dispersal of the spores.

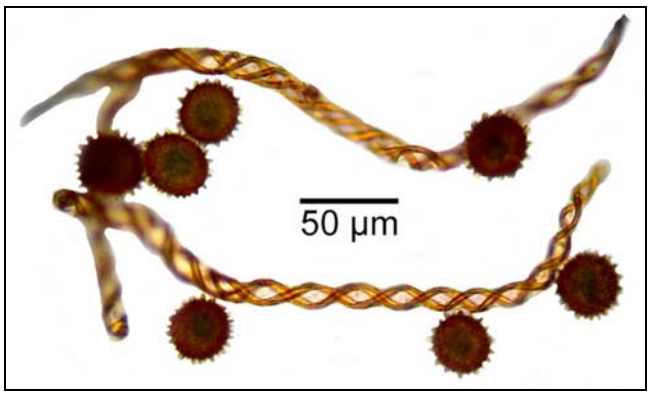

Figure 78. ***Calycularia crispula*** spores and elaters. Photo by N. Printarakul, through Creative Commons.

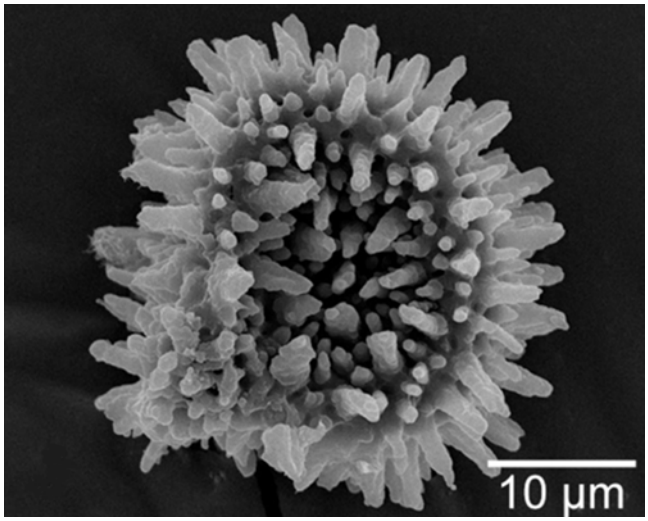

Figure 79. ***Calycularia crispula*** spore. Photo by N. Printarakul, through Creative Commons.

Biochemistry

Calycularia crispula (Figure 71-Figure 72) has 6-34 minute (1.5-4.9 µm) oil bodies per cell (Figure 80) that are presumably the source of the cedar-oil-like smell that is distinct when dried specimens are moistened (Konstantinova & Mamontov 2010).

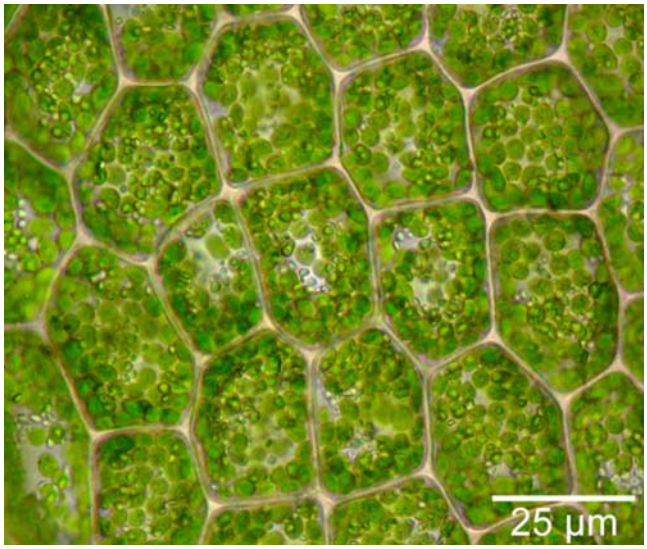

Figure 80. ***Calycularia crispula*** cells showing the numerous tiny oil bodies. Photo by N. Printarakul, through Creative Commons.

Calycularia laxa

Distribution

Apparently the report by Davison and Smith (1992) for ***Calycularia crispula*** from the Aleutian Islands and Pacific Northwest (British Columbia, SE Alaska) of North America is really ***Calycularia laxa***. When Konstantinova and Mamontov (2010) revised the genus, they excluded ***C. crispula*** from Russia, Canada, Japan, and Korea based on re-examination of the specimens and treated these collections as the northern species ***Calycularia laxa***. It is

widespread and relatively common in Siberia. It is more difficult to distinguish when sterile, so there may be a more widespread distribution in the North American tundra.

Daniels *et al*. (2014) further explained that the two species are separated by habitat and distribution. ***Calycularia crispula*** (Figure 71-Figure 72) occurs predominantly in upland areas of the tropics in Asia, Africa, and Central America, whereas ***Calycularia laxa*** occurs in temperate to Arctic regions in the Northern Hemisphere.

Aquatic and Wet Habitats

Calycularia laxa (originally reported as ***C. crispula***) occurs on wet cliffs of Upper Bureya River (Russian Far East) (Konstantinova *et al*. 2002). In northwestern North America it occurs on boulders and soil of moist banks of alpine streams (Davison & Smith 1992). Davison & Smith (1992) characterize its environment as having even moisture conditions and subdued light.

In the tundra zone ***Calycularia laxa*** occurs in moist habitats of river and lake valleys, where it grows on damp sandy soil, peat and humus-covered rocks along banks of streams, in dried river beds, in depressions between peat hillocks, in crevices of cliffs, or among boulders in rock fields (Konstantinova & Mamontov 2010). It also occurs on spots of bare soil in different types of tundra, on nival slopes, among boulders in rocky lichen tundra, on bare soil in sedge-lichen tundra, and occasionally in sedge-moss bogs. In mountains at the southern limit of its distribution the species is restricted to valleys of rivers on wet, often moss-covered, cliffs and rocks along streams in deep humid ravines, near waterfalls, on fine-grained and sandy soil or peat between rocks, in shaded crevices on wet cliffs, at the bottom of cliffs and rock outcrops, both in subalpine and forest zones, including broad-leaved forests, mixed and coniferous forests. It typically grows with other liverworts in these habitats.

Adaptations

The plants of ***Calycularia laxa*** are yellowish or deep green to reddish and purplish red and red-brown (Konstantinova & Mamontov 2010). Tundra plants are typically pigmented, exhibiting purple-reddish or green with "fuscous, reddish to purplish red or red-brown colored margins." This coloration is especially typical of the mouth of the pseudoperianth. This range of color potential may permit it to survive the often intense UV light in its northern locations. On the other hand, when plants occur in shaded depressions they often lack all secondary pigmentation.

Tundra plants of ***Calycularia laxa*** tend to be smaller, seldom exceeding 6 mm width and 15 mm length (Konstantinova & Mamontov 2010). This contrasts with plants from mountains in South Siberia, southern Alaska, and British Columbia, Canada, where plants can be as much as 12 mm wide and 50 mm long.

Calycularia laxa usually forms **mats** or grows as single plants among other bryophytes (Konstantinova & Mamontov 2010). Both of these characteristics can help to conserve moisture.

Reproduction

Calycularia laxa is **dioicous** (Konstantinova & Mamontov (2010). At least in North America, the two sexes have not been found in the same location, and females are much more common than males. ***Calycularia laxa*** lacks the ventral shoots that could potentially serve as a means of vegetative propagation (Konstantinova & Mamontov 2010). This combination bodes for poor reproduction.

Biochemistry

Oil bodies of ***Calycularia laxa*** are 1.0-3.7 µm long, numbering 12-58 per cell (Konstantinova & Mamontov 2010). These are presumably the source of an odor that is distinct when dried specimens are moistened.

Summary

Metzgeria (**Metzgeriaceae**) species are not true aquatic species, but some of them are occasionally submerged, and the one included here often occur in damp or wet places, especial riverine canyons. They often form mats, and with their ribbon-like thallus this can help to conserve moisture during drier periods. ***Metzgeria furcata*** is very desiccation tolerant. The thalli are often translucent, permitting light to reach greater depths. Hairs and curving under can help to retain moisture in some species. Thallus lobes contribute to asexual reproduction.

Slime molds are often associated with ***Metzgeria furcata***. While some species of ***Metzgeria*** have fungal partners, others have no known fungal associates (***Metzgeria conjugata***). ***Metzgeria furcata*** can have the **Ascomycete** fungal parasite ***Bryocentria hypothallina***. Some species have known antibiotic properties, perhaps accounting for a lack of fungi.

Calycularia crispula (**Calyculariaceae**) occurs in humid locations, but is not aquatic. The more northern ***Calycularia laxa*** occurs on wet cliffs and moist stream banks.

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Lars Söderström helped me find the current acceptable names for a number of older taxa.

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CHAPTER 1-13
AQUATIC AND WET MARCHANTIOPHYTA, ORDER FOSSOMBRONIALES, PART 1

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CHAPTER 1-13
AQUATIC AND WET MARCHANTIOPHYTA, ORDER FOSSOMBRONIALES, PART 1

Figure 1. ***Fossombronia caespitiformis* subsp. *multispira*** with capsules on bank. Photo by Michael Lüth, with permission.

Nomenclature for this chapter is based primarily on Söderström *et al*. (2016). In addition, Lars Söderström provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. Information on these unverifiable taxa has been included in the species.

To develop this list, I used my own bibliography, collected over the past 56 years, and Google Scholar. These papers soon led me to others. I do not pretend that this is complete. It includes streams, lakes, and other wetlands, but also other wet habitats such as waterfall spray and stream and river banks. I have not discussed or searched bog and fen habitats, but I nevertheless include a number of these species because they were found in a wetland study. Bogs and poor fens have been treated in whole books and provide an extensive literature; intermediate and rich fens seem somewhat less studied. They would require considerably more review and time. Thus I felt that less-reviewed topics, particularly the aquatic habitats with which I am most familiar, should be given priority.

SUBCLASS PELLIIDAE

Fossombroniales: Fossombroniaceae

Fossombronia (Figure 1)

Fossombronia has been a troublesome genus, and many parts remain so. For example, in her revision of the genus in Mexico, the Caribbean, Central and South America, Freire (2004) reduced the 30 species described to 13.

Many of the species of ***Fossombronia*** can live in wet or moist habitats. Some of these could even be considered aquatic. Toivonen and Huttunen (1995) reported species of ***Fossombronia*** in small lakes of southern Finland. The genus has a relatively wide range of habitats, including both terrestrial and aquatic.

Fossombronia angulosa (Figure 2-Figure 5)

The name ***Fossombronia angulosa*** (Figure 2-Figure 5) has met with confusion. Its use in publications appears frequently to be different from the species that was

originally described. Stotler *et al*. (2005) argued that the concept used for 200 years should be retained, following the basionym *Jungermannia angulosa*. It has become the type species for the split off genus ***Fossombronia***, based on the name ***Fossombronia angulosa***, and was conserved following the 200-year concept of the species.

Figure 2. ***Fossombronia angulosa***. Photo by Jan-Peter Frahm, with permission.

Figure 3. ***Fossombronia angulosa***. Photo by Jan-Peter Frahm, with permission.

Figure 4. ***Fossombronia angulosa*** in moist condition. Photo by Jan-Peter Frahm, with permission.

Figure 5. ***Fossombronia angulosa*** covering its substrate. Photo by Michael Lüth, with permission.

Distribution

Schuster (1992) considered all North American records to belong to *Fossombronia brasiliensis*, now considered to be ***Fossombronia porphyrorhiza*** (Figure 6), describing the distribution of ***Fossombronia angulosa*** (Figure 2-Figure 5) as European oceanic and Mediterranean. This included southern Ireland and southwestern England to coastal France, Spain, Portugal, southern Switzerland, Italy, eastward to Greece and Turkey, south to North Africa, the Canary Islands, Madeira, and the Azores.

Figure 6. ***Fossombronia porphyrorhiza***, considered by Schuster to be a North American species. Photo courtesy of Denilson Peralta.

Fossombronia angulosa (Figure 2-Figure 5) is a Northern Hemisphere species (Sabovljević & Natcheva 2006; Milner *et al*. 2011). Dia *et al*. (2007) consider it to be oceanic-Mediterranean and Jovet-Ast (1946) to be Mediterranean-Atlantic.

The 2019 edition of the Catalog of life reports ***Fossombronia angulosa*** (Figure 2-Figure 5) from Norway, Britain, Ireland, Netherlands (see also du Mortier 1874), Belgium, Switzerland (see also Meier *et al*. 2013), Czech Republic, France, Portugal (see also Sérgio 1974), Spain (see also Elias Rivas & Rupidera Giraldo 1991; Elías Rivas *et al*. 2001; Pericàs Mestre *et al*. 2010), Baleares, Corsica,

Sardinia, Sicily (see also Dia *et al*. 2007; Privitera *et al*. 2008), Italy (see also Puglisi & Privitera 2009; Pedrotti & Aleffi 2011), Croatia (see also Sabovljević 2003), Montenegro, Bulgaria, Albania, Greece, Crete, Turkey (see also Ezer *et al*. 2009; Oren *et al*. 2012) in Europe, Krasnodar, Morocco, Algeria, Tunisia, Azores (see also Frahm 2005), Madeira, Canary Islands, Cape Verde, South Africa, Azerbaydzhan, Turkey, Cyprus, Lebanon, Sinai, Palestine, Yemen, and Java. It most likely also includes Germany (du Mortier 1874). Ganeva (1997) notes that most of the Mediterranean-Atlantic liverworts in Bulgaria, including ***Fossombronia angulosa***, are mostly in the southern part of the country, along the Black Sea coast, but also in lowland areas in northern parts.

Despite the conclusions of Schuster (1992) regarding North American populations, a number of recent authors still recognize ***Fossombronia angulosa*** (Figure 2-Figure 5) as a species in the western hemisphere, including Söderström *et al*. (2020). Theirs and others include records in Canada: Ontario; USA: Rhode Island, New Jersey, Texas (see also Underwood 1896), South Carolina, Alabama (see also Underwood 1896), Louisiana, Florida (see also Underwood 1896; Redfearn 1952); Mexico; Cuba; Rio Grande do Sul; and Uruguay (Söderström *et al*. 2020), as well as Brazil (Bordin & Yano 2010).

Aquatic and Wet Habitats

Ezer *et al*. (2009) consider ***Fossombronia angulosa*** (Figure 2-Figure 5) to be a hygrophyte-mesophyte (Figure 7). Guerra (1982) likewise treats it as a mesophyte and earthbound. Saadi *et al*. (2020) describe it as terricolous, sub-aquatic, and aquatic in Morocco; along with ***Fontinalis antipyretica*** (Figure 8) and ***Cinclidotus riparius*** (Figure 9), it can be totally immersed, but it can also grow on a water-soaked forest floor. They consider ***Fossombronia angulosa*** to be very rare, at least in Morocco. But in Galicia, Reinoso (1985) considers it frequent, forming extensive mats.

Figure 7. ***Fossombronia angulosa*** in a terrestrial, mesic habitat. Photo by Michael Lüth, with permission.

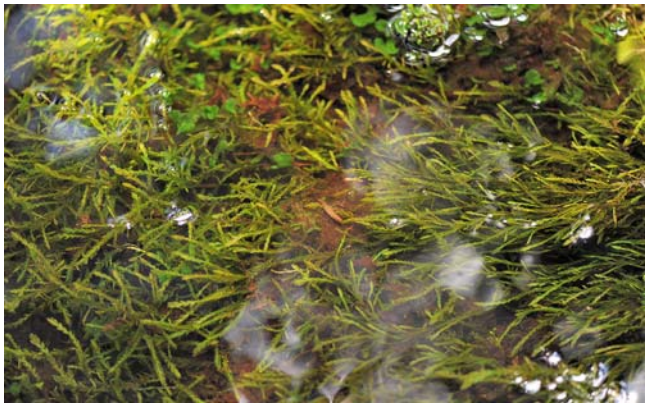

Figure 8. ***Fontinalis antipyretica***, a species that occurs under water in some of the same situations as ***Fossombronia angulosa*** in Morocco. Photo by Dick Haaksma, with permission.

Figure 9. ***Cinclidotus riparius***, a species that occurs under water in some of the same situations as Hermann Schachner, through Creative Commons.

Ferreira *et al*. (2008) reported ***Fossombronia angulosa*** (Figure 2-Figure 5) from rivers. Earlier, Armitage (1918) reported it from the wetter rocks and stones of streams in Madeira, but it was also found on bare earth, banks, and shady mountain ground. Özenoğlu Kiremit *et al*. (2007) found it on soil in the stream bed, but also on the soil of stream banks, frequently with other liverwort species. These habitats are consistent with what seems to be a more frequent habitat on stream banks.

In the Izarine Massif of Morocco, ***Fossombronia angulosa*** (Figure 2-Figure 5) occurs on wet clay soil next to a water gully and on small rocks (Laouzazni *et al*. 2021). On Tenerife in the Canary Islands, it frequents damp soil on the slopes of ravines and is again considered mesophilic (Losada Lima & Beltrán Tejera 1987). On Madeira, it occurs in the spray zone along stream margins, where it is often associated with the hygrophytic moss ***Brachythecium rivulare*** (Figure 10) and liverwort ***Scapania undulata*** (Figure 11) (Luís *et al*. 2008). In Spain it occurs on slopes close to a ravine (Figure 12) (Fuertes & Mendiola 1984; Gil Garcia & Castro 1987). Campisi *et al*. (2008) found it on soil slopes near water courses in Calabria, Italy. On the Greek Island of Crete, Blockeel (2012) found ***Fossombronia angulosa*** on the steep, heavily shaded banks of streams and gullies. In Ireland, where it is rare, M'Ardle (1894) found it on rocks at the mouth of the river at Pulleen Cove.

Figure 10. ***Brachythecium rivulare*** by stream, a common associate of ***Fossombronia angulosa*** in the spray zone on Madeira. Photo by Kim Nicole, through Creative Commons.

Figure 11. ***Scapania undulata*** with ***Marsupella emarginata*** surrounding it. ***Scapania undulata*** is a common associate of ***Fossombronia angulosa*** in the spray zone on Madeira. Photo by Jeremy Berker, through Creative Commons.

Figure 12. ***Fossombronia angulosa*** in a damp location by a stream. Photo by Michael Lüth, with permission.

Where the substrate is wet, ***Fossombronia angulosa*** (Figure 2-Figure 5) is able to venture away from streams and other water bodies. It occurs on humid soil (Cros *et al*. 1995), in humid areas of southeastern Spain (Casas *et al*. 1999) and on "shady slopes with a certain degree of humidity" (Jiménez *et al*. 1986). Likewise, it occurs on damp soil in the Küre Mountains in Turkey (Ören *et al*. 2012). In southern Europe it occurs on clayey moist shady soil and also lives in wetlands in Italy, England, and the Netherlands (du Mortier 1874). Sotiaux *et al*. (2008) listed it on the ground of a slope in Corsica, but made no reference to moisture.

Despite these wet sites, there is evidence that ***Fossombronia angulosa*** (Figure 2-Figure 5) is drought tolerant. It is able to live in temporary water courses (Jiménez *et al*. 1986; Mundo 1986). In Morocco, Fadel *et al*. (2020) found it on shale that is soaked with water in the winter, but is dry in summer. In Sierra del Calar, it also occurs in temporary water (Mundo 1986).

Puglisi *et al*. (2015) found ***Fossombronia angulosa*** (Figure 2-Figure 5) in Mediterranean temporary ponds in Italy. Puglisi and Privitera (2009) described the ***Fossombronia anglosae-Phaeocerotetum bulbiculosi***, now ***Phymatocerotetum bulbiculosi*** (Figure 13), from moist but not humified soil with a steep slope (60°-80°) on talus along the margin of a coastal lake in Italy. This association was previously only known from the Iberian Peninsula. In the British Isles, Preston *et al*. (2011) found a similar association of ***Fossombronia angulosa*** with ***Phaeoceros laevis*** (Figure 14) in locations that were very well-illuminated and relatively dry in summer.

Figure 13. ***Phymatoceros bulbiculosus***, a species that forms an association with ***Fossombronia angulosa*** in Italy. Photo by David H. Wagner, with permission.

Figure 14. ***Phaeoceros laevis***, a species that forms an association with ***Fossombronia angulosa*** in the British Isles. Tomás Curtis, through Creative Commons.

Pericàs Mestre *et al*. (2010) described its habitat in temporary ponds of Menorca. They considered that this habitat favored colonization, establishment, and succession of plant groups that have water requirements that are higher than in other environments.

Blockeel (2017) reported ***Fossombronia angulosa*** (Figure 2-Figure 5) from earthy rock crevices. Whereas rock is a common substrate for this species, it also occurs on soil (Losada Lima & Beltrán Tejera 1987) and bark (Özenoğlu & Gökler 2002), although the bark was covered with soil. It appears that the limiting factor for substrate is its *p*H because all the records that mention acidic or basic refer to it as acidic.

Fossombronia angulosa (Figure 2-Figure 5) occurs on sandstone rocks in Turkey (Papp & Sabovljevic 2003), a substrate that is typically acidic due to high silica content. Mundo (1986) reported that ***Fossombronia angulosa*** is often found with ***Epipterygium tozeri*** (Figure 15) and ***Anthoceros punctatus*** (Figure 16) on acidic vertical substrata. It occurs on acidic substrata in Spain (Fuertes & Mendiola 1984; Jiménez *et al*. 1986; Casas *et al*. 1999), and Guerra (1982) described it as acidophilic in Spain, as did Papp *et al*. 1999 in Greece and Puglisi and Privitera (2009) in Italy. In the Ibérican Peninsula the *p*H where it grew was 5.9 (Gil Garcia & Castro 1987).

Figure 15. ***Epipterygium tozeri***, a species that often occurs with ***Fossombronia angulosa***. Photo by David T. Holyoak, with permission.

Fossombronia angulosa (Figure 2-Figure 5) is one of the few bryophytes with any salt tolerance (Smith 1990; Perold 1999). Rilstone (1949) reported it from near the sea in Cornwall. Blockeel (1991) found it on a sandy coastal bank. While these are not immersed in salt water, salt in the air can accumulate on the bryophytes. Hill *et al*. (2007) reported that it occurs in both saline and non-saline situations in the British Isles. Perhaps its greatest salt tolerance is shown in salt marshes, where it can be found frequently in early spring in Kansas, USA (Smyth & Smyth 1911).

In almost all of these habitats, ***Fossombronia angulosa*** (Figure 2-Figure 5) appears to be **sciaphilous** (shade-loving or shade tolerant) (du Mortier 1874; Armitage 1918; Guerra 1982; Jiménez *et al*. 1986; Losasa Lima & Beltrán Tejera 1987; Puglisi & Privitera 2009; Blockeel 2012; Osman *et al*. 2019).

Figure 16. ***Anthoceros punctatus***, a species that often occurs with ***Fossombronia angulosa***. Photo from Proyecto Musgo through Creative Commons.

In surprising contrast, Preston *et al*. (2011) report the ***Fossombronia angulosa-Phaeoceros laevis*** (Figure 2-Figure 5; Figure 14) association from a "very well-illuminated" habitat in relatively dry places. These locations have higher January and July temperatures than those of any other species cluster, as well as experiencing relatively low annual precipitation. Some occur on waste by copper mines and in china-clay quarries.

Fossombronia angulosa (Figure 2-Figure 5) is rare in many countries. Pedrotti and Aleffi (2011) attributed its disappearance or threatened state to human activity and industrialization, especially exploitation of areas such as peatlands in the Alps.

Adaptations

Fossombronia angulosa has horizontal to patent leaves that are usually nearly plane (Figure 17) (Stotler *et al*. 2005). This form minimizes surface exposure and thus should contribute to reducing moisture loss.

Figure 17. ***Fossombronia angulosa*** growing horizontally. Photo by Jan-Peter Frahm, with permission.

Reproduction

Fossombronia angulosa (Figure 2-Figure 5) is a robust, **dioicous** plant (Stotler *et al*. 2005) with clearly visible antheridia (Figure 18). Reinoso (1985) reported that ***Fossombronia angulosa*** was a frequent species in parts of Galicia, where it formed extensive lawns that were fertile most of the times it was collected. It has been the subject of several studies related to its reproduction. Vian (1969, 1970) published observations on the evolution of intercellular substances during spermatogenesis. Bajon-Barbier (1997) made ultrastructural studies on the maturation of the egg cell.

Figure 18. ***Fossombronia angulosa*** with antheridia. Photo by Jan-Peter Frahm, with permission.

Showalter (1927) described cytology involved in fertilization. He gave detailed descriptions of the sexual organs and observed that sexual organs occurred in almost any season, but were most common in autumn and early winter. The egg is apparently viable for fertilization for "a considerable length of time." Following artificial insemination, several to 12 eggs were fertilized on a thallus. It required 6-9 days for the zygote to undergo its first division, following an increase in size. Sperm from the moss ***Funaria hygrometrica*** (Figure 19-Figure 20) were also able to penetrate the eggs, but these did not initiate development of an embryo. ***Sphaerocarpos donnellii*** (Figure 21) sperm were likewise able to penetrate and they were able to begin, but not complete, embryonic cell division. More than one ***Fossombronia angulosa*** (Figure 2-Figure 5) sperm can penetrate the same egg, but there is no evidence that more than one male nucleus ever penetrates the egg nucleus. Even in fully fertilized eggs, when multiple zygotes are formed on the same thallus, some of the zygotes do not undergo further development. Even so, 4-8 embryos may develop and become mature sporophytes (Figure 22-Figure 23) on one female thallus.

Figure 19. ***Funaria hygrometrica***, a species whose sperm can penetrate the eggs of ***Fossombronia angulosa***. Photo by Bob Klips, with permission.

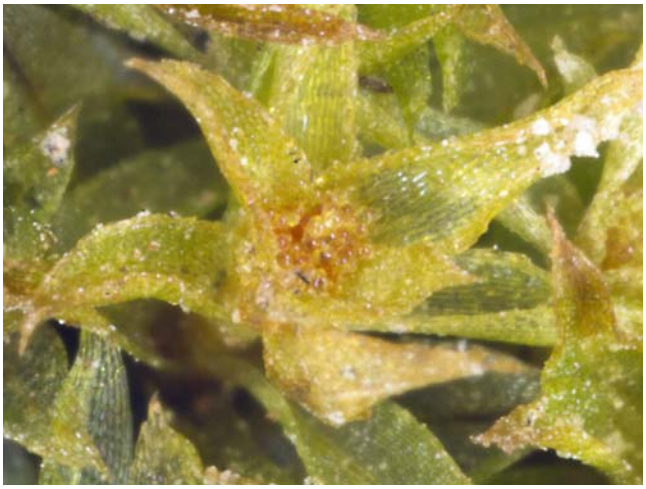

Figure 20. ***Funaria hygrometrica*** antheridia, source of sperm that can penetrate the eggs of ***Fossombronia angulosa***. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 21. ***Sphaerocarpos donnellii***, a species whose sperm can penetrate the eggs of ***Fossombronia angulosa*** and initiate embryo development. Photo by Belinda Lo through Creative Commons.

Figure 22. ***Fossombronia angulosa*** with capsule. Photo by Des Callaghan, with permission.

Figure 23. ***Fossombronia angulosa*** with capsules, some of which are dehiscing (brown). Photo by David T. Holyoak, with permission.

Leforestier (1975) described the spores (Figure 24) of ***Fossombronia angulosa*** (Figure 2-Figure 5) under both light and scanning microscopy and later described the germ tube (Figure 25-Figure 26) (Leforestier 1979). Castaldo-Cobianchi and Giordano (1986) further described the spore wall morphology. Gambardella (1987) described the surface features in detail, based on both SEM and TEM microscopy. Spores are produced in spring (Schuster 1992). Chromosome numbers have been reported as n = 9 (Mehra 1938; Newton 1975).

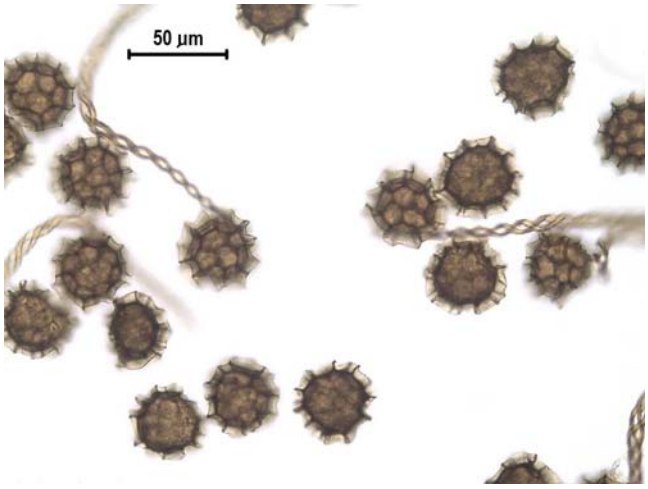

Figure 24. ***Fossombronia angulosa*** spores and elaters. Photo by Hugues Tinguy, with permission.

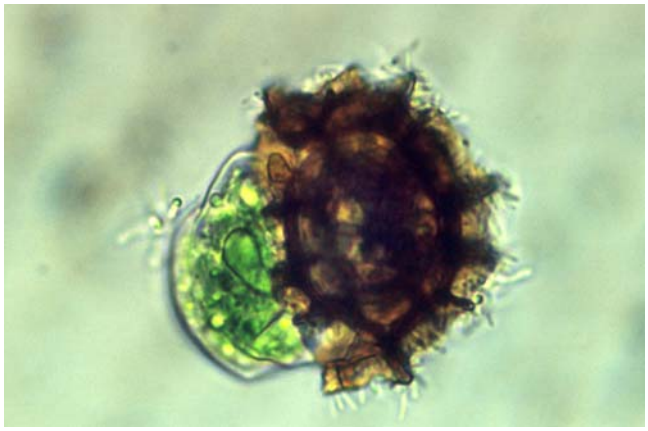

Figure 25. ***Fossombronia angulosa*** germinating spore. Photo from Plant Actions, with permission.

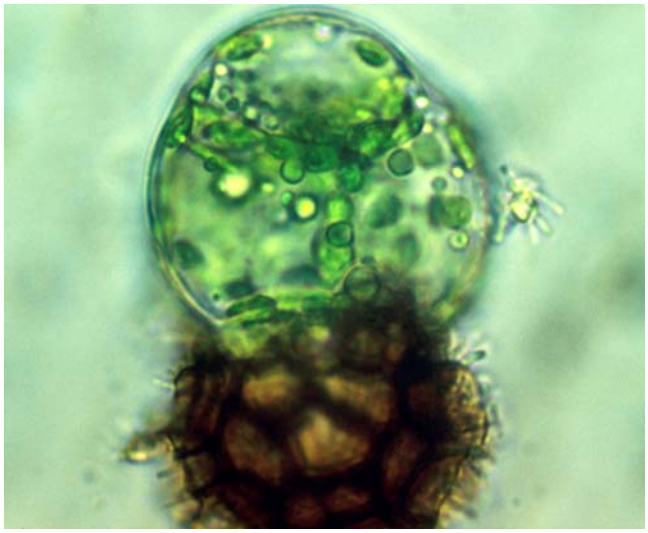

Figure 26. ***Fossombronia angulosa*** young protonema. Photo from Plant Actions, with permission.

Biochemistry

I have been unable to find any information on oil bodies in ***Fossombronia angulosa***. Figure 27 suggests that they might be tiny and diffuse, difficult to detect.

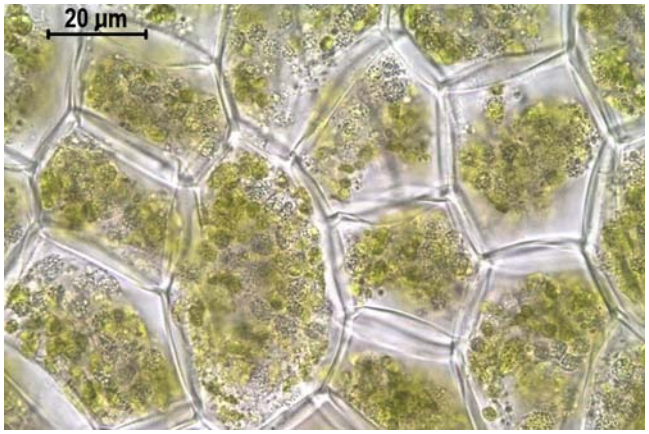

Figure 27. ***Fossombronia angulosa*** cells with what might be oil bodies. Photo by Hugues Tinguy, with permission.

Fossombronia angulosa (Figure 2-Figure 5) has been the subject of biochemical evolution. Based on the Greek populations studied, it has some of the same compounds [dictyotene, the main compound of the volatile fraction (14.1%), (Z)-multifidene, and dictyopterene] as that found in the brown algae (Ludwiczuk *et al*. 2008; Asakawa & Ludwiczuk 2017). Dictyotene is the major volatile compound (Asakawa & Ludwiczuk 2917). ***Fossombronia angulosa*** emits a seashore odor that is caused by dimethyl sulfide. Other identified compounds include biosynthesized cyathane-type diterpenoids, 2-tridecanone (13.0%), and β-sabinene (11.7%). Von Reuß (2009) found C11 hydrocarbons, dictyopterene A, ectocarpene, and dictyotene, compounds that are known as brown algal **pheromones** (chemical substances produced by organism and serves especially as stimulus to other individuals of the same species for one or more behavioral responses, often as attractants for opposite sex). Von Reuß also identified a new pentylbenzene.

Fossombronia australis (Figure 28-Figure 29)

Distribution

Fossombronia australis (Figure 28-Figure 29) occurs in Australia, New Zealand, and the sub-Antarctic Kerguelan and Prince Edward Islands (Crandall-Stotler & Gradstein 2017).

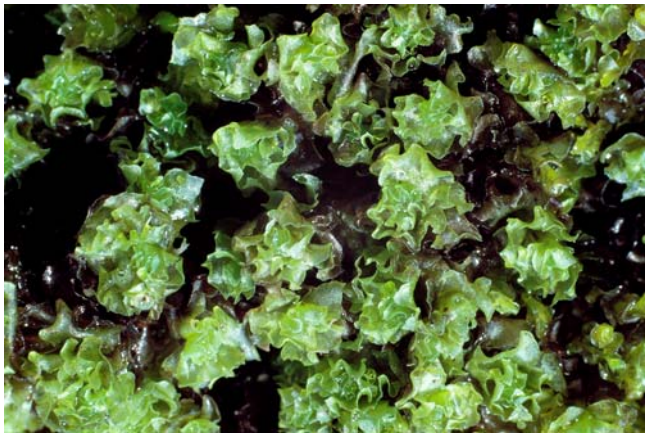

Figure 28. ***Fossombronia australis***. Photo by Bruce Fuhrer, ©CANBR (Centre for Australian National Biodiversity Research, <http://www.cpbr.gov.au/cpbr/>, with permission.

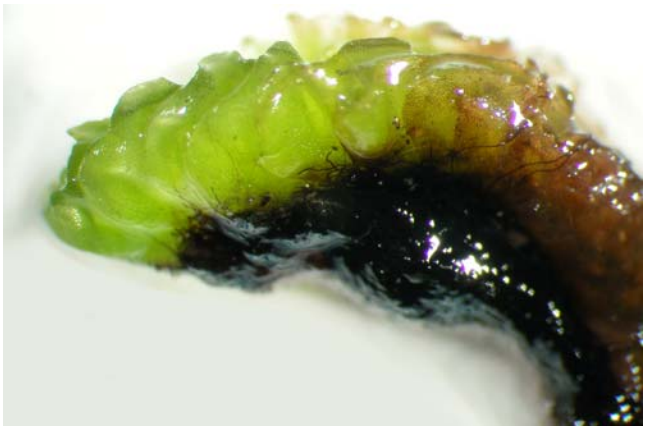

Figure 29. ***Fossombronia australis*** showing purple rhizoids. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <http://www.cpbr.gov.au/cpbr/>, with permission.

Aquatic and Wet Habitats

Fossombronia australis (Figure 28-Figure 29) occurs in low elevation wetlands in regions near the Antarctic (Crandall-Stotler & Gradstein 2017). Campbell (1988) considered its partial submersion to be sufficiently diagnostic to include the character in her key to Australian species. She reported it for wet, shady banks or as dense, partially submerged colonies in freshwater swamps and ***Sphagnum*** mires (Figure 30). Glenny (1995) reported it from a flush next to a stream in New Zealand.

Figure 30. ***Sphagnum cristatum*** mire in Australia. Photo by M. Fagg, ©ANBG (Australian National Botanic Gardens), <http://www.anbg.gov.au/photo/image-collection.html>, with online permission.

Carcaillet (1993) reported ***Fossombronia australis*** (Figure 28-Figure 29) with ***Azorella selago*** (Figure 31) in peat bogs of Crozet Island in the Southern Ocean. Váňa and Gremmen (2005) found it on all parts of nearby Heard Island, often associated with ***Azorella*** or ***Poa cookii*** (Figure 32). The area was influenced by birds and seals that are possible dispersal agents. On the same island, Bergstrom and Selkirk (2000) found it on gravel at the edge of ***Azorella selago*** cushions or growing between branches of ***A. selago***. Its rhizoids were anchored in a mixture of humic material typically consisting of abscised leaves and accumulated wind-blown sediment. At the margins of pools it grew with species of the moss ***Brachythecium***

(Figure 10) in moist or wet areas. They considered ***Fossombronia australis*** to be a species of wide ecological amplitude.

Figure 31. Cushions of ***Azorella selago*** in the Kerguelen Islands, a flowering plant species that may have ***Fossombronia angulosa*** growing with it in peat bogs of Crozet Island in the Southern Ocean. Photo from Creative Commons.

Figure 32. ***Poa cookii***, a grass species that may have ***Fossombronia angulosa*** growing with it in peat bogs of Crozet Island in the Southern Ocean. Photo M. Grun, through Creative Commons.

In the sub-Antarctic islands, Smith and Mucina (2006) found ***Fossombronia australis*** (Figure 28-Figure 29) among submerged and floating macrophytes in the lakes and tarns, as well as in fernbrakes.

Reproduction

Fossombronia australis (Figure 28-Figure 29) is **dioicous** (Campbell 1988), producing spherical antheridia on separate plants (Figure 33), perhaps explaining its lack of abundance despite being widespread within its distribution. Nevertheless, capsules are known (Figure 34), so dispersal by spores is possible (Figure 35).

Figure 33. ***Fossombronia australis*** antheridia. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <http://www.cpbr.gov.au/cpbr/>, with permission.

Figure 34. ***Fossombronia australis*** capsule. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <http://www.cpbr.gov.au/cpbr/>, with permission.

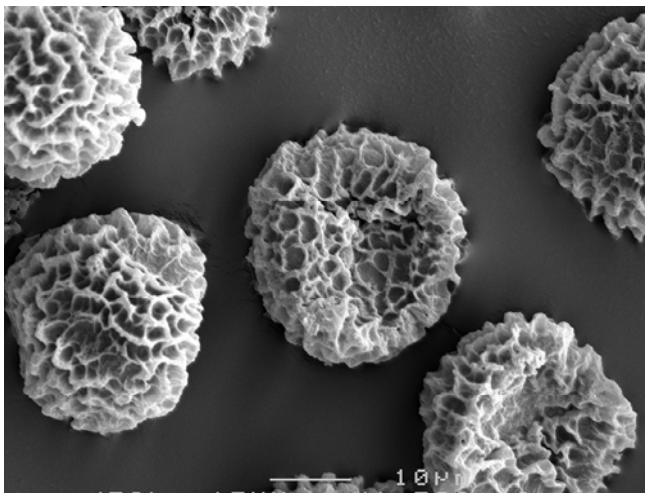

Figure 35. ***Fossombronia australis*** spores, SEM. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <http://www.cpbr.gov.au/cpbr/>, with permission.

Role

For such a little known species, it is surprising to learn that Chown and Scholtz (1989) have documented that ***Fossombronia australis*** (Figure 28-Figure 29) is consumed by the curculionid beetles ***Mesembriorrhinus brevis*** and ***Dusmoecetes marioni*** on the sub-Antarctic Prince Edward Islands. Few records of herbivory by specific insects are available on liverworts.

Fossombronia caespitiformis subsp. *multispira* (Figure 37-Figure 39)

(syn. = *Fossombronia husnotii*)

Fossombronia caespitiformis (Figure 36-Figure 39) is highly variable. Stotler *et al.* (2005) considered it to comprise two subspecies: ***F. caespitiformis* subsp. *caespitiformis*** (Figure 36) and **F. *caespitiformis* subsp. *multispira*** (Figure 37-Figure 39). I have found records of the latter from wet habitats.

Figure 36. ***Fossombronia caespitiformis***, a highly variable Mediterranean species. Photo by Des Callaghan, with permission.

Figure 37. ***Fossombronia caespitiformis* subsp. *multispira*** in Europe. Photo by Michael Lüth, with permission.

Figure 38. ***Fossombronia caespitiformis* subsp. *multispira***. Photo by Jan-Peter Frahm, with permission.

Figure 39. ***Fossombronia caespitiformis* subsp. *multispira***. Photo by Michael Lüth, with permission.

Distribution

Like so many of the liverworts, confusion in the taxonomy of ***Fossombronia caespitiformis* subsp. *multispira*** (Figure 37-Figure 39) (Lockhart *et al.* 2012) has made it difficult to describe the distribution of this variety (Poponessi *et al.* 2016). It is known from most of the Mediterranean countries as well as Madeira in the Canary Islands (González Mancebo *et al.* 2007; Ros *et al.* 2007), but is rare in Italy (Aleffi *et al.* 2008) and Critically Endangered there (Poponessi *et al.* 2916). Sérgio *et al.* (2011) recorded it from Portugal and Pericàs *et al.* (2016) as new from Minorca, Spain. Sotiaux *et al.* (2009) extended its known range to Belgium. It is also known from Ireland, but is listed as "data deficient" regarding its rarity (Kingston 2012). Blockeel (2020) verified its occurrence in Greece. But it is apparently even more widespread than indicated by these authors; Fischer (1993) reported it from Rwanda.

It is very rare in the cork oak forest of Morocco (El Harech *et al.* (2020) and on the Montseny Massif of the Iberian Peninsula (Sáez *et al.* 2018).

Aquatic and Wet Habitats

Although ***Fossombronia caespitiformis* subsp. *multispira*** (Figure 37-Figure 39) is quite rare in most of Italy, Poponessi *et al.* (2016) found it to be moderately abundant on water-logged soil (Figure 40-Figure 41) associated with temporary ponds in central Italy,

accompanied by ***Isoetes histrix*** (a lycopod; Figure 42). Puglisi *et al*. (2015) similarly found it associated with temporary ponds in Italy. In fact, Poponessi *et al*. (2018) found it to be one of the two bryophyte communities in these habitats. It was the dominant species in one, accompanied by ***Riccia sorocarpa*** (Figure 43) on waterlogged, clayey-sandy soil in heathland clearings (Figure 44). Hugonnot and Simont (2018) found a similar habitat for ***Fossombronia caespitiformis* subsp. *multispira*** in temporarily wet lawns in Corse-du-Sud, France, a habitat where grazing contributes to its ecology. It is also known from rivers (Ferreira et al. 2008). Cogoni *et al*. (2016) described the species as hygro-xerophytic, noting its presence in temporary ponds, where it had a frequency greater than 30%.

Figure 42. ***Isoetes histrix***, a species that accompanies ***Fossombronia caespitiformis* subsp. *multispira*** in temporary ponds. Photo by Ralph Mangelsdorff, through Creative Commons.

Figure 40. ***Fossombronia caespitiformis*** on mud. Photo by Michael Lüth, with permission.

Figure 43. ***Riccia sorocarpa***, a species that accompanies ***Fossombronia caespitiformis* subsp. *multispira*** in temporary ponds. Photo by Hugues Tinguy, with permission.

Figure 41. ***Fossombronia caespitiformis* subsp. *multispira*** on muddy soil in Europe. Photo by Michael Lüth, with permission.

Figure 44. Heathland, a habitat where one can find ***Fossombronia caespitiformis* subsp. *multispira*** in Italy. Photo from <mdpi.com>, through Creative Commons.

Substrata of ***Fossombronia caespitiformis* subsp. *multispira*** can include litter (Figure 45), as well as soil and rocky mixes. They also be a part of hummocks (Figure 46).

Figure 45. ***Fossombronia caespitiformis* subsp. *multispira*** on litter in Europe. Photo by Michael Lüth, with permission.

Figure 46. ***Fossombronia caespitiformis* subsp. *multispira*** in a hummock. Photo by Michael Lüth, with permission.

Sotiaux *et al*. (2009) found that ***Fossombronia caespitiformis* subsp. *multispira*** (Figure 37-Figure 39) is typical of intensive **arable** (describes land used or suitable for growing crops) fields (Figure 47). This habitat is often similar to that of temporary ponds, in particular requiring species with short life cycles.

Figure 47. ***Fossombronia caespitiformis* subsp. *multispira*** appearing as it could in arable fields. Photo by Michael Lüth, with permission.

Fossombronia caespitiformis* subsp. *multispira (Figure 37-Figure 39) is able to inhabit rocky areas (Figure 48). Blockeel (2012) reported it from schistose banks as well as thin soil in western Crete. Blockeel (2020) also found it on phyllite rocks on the sheltered gravelly track in a stream valley in Greece.

Figure 48. ***Fossombronia caespitiformis* subsp. *multispira*** on rocky bank. Photo by Michael Lüth, with permission.

As noted by Gabriel *et al*. (2011), approximately one-fourth of European bryophytes are under actual or potential threat. Gabriel and coworkers used geographical distribution, abundance, and habitat specificity to develop a list of such bryophytes in the Azores. ***Fossombronia caespitiformis* subsp. *multispira*** (Figure 37-Figure 39) is present in the Azores, where it grows in coastal wetlands (Gabriel *et al*. 2019), but its threat status was not listed by Gabriel *et al*. (2011), presumably due to insufficient data.

Adaptations

Cogoni *et al*. (2016) reported that ***Fossombronia caespitiformis* subsp. *multispira*** (Figure 37-Figure 39) is typically solitary and creeping. In the temporary ponds where it lives in parts of the Mediterranean, a **pauciennial/perennial** life strategy permits it to take advantage of the periods of adequate moisture (Puglisi *et al*. 2016). In the Mediterranean temporary ponds, it is a **short-lived shuttle** species. In that location, its sexual reproduction is abundant, but asexual reproduction is absent or rare. Despite its frequent sexual reproduction, its dispersal is short-range, most likely due to the large size of its spores, but assuring that most of the spores will fall on a suitable habitat. Furthermore, the somewhat large spores (32-35 µm) (Sotiaux *et al*. 2009) provide it with the resources to be more successful upon germination.

Fossombronia caespitiformis* subsp. *multispira (Figure 37-Figure 39) sometimes grows with other bryophytes (Figure 49), possibly benefitting from their presence to help in retaining moisture.

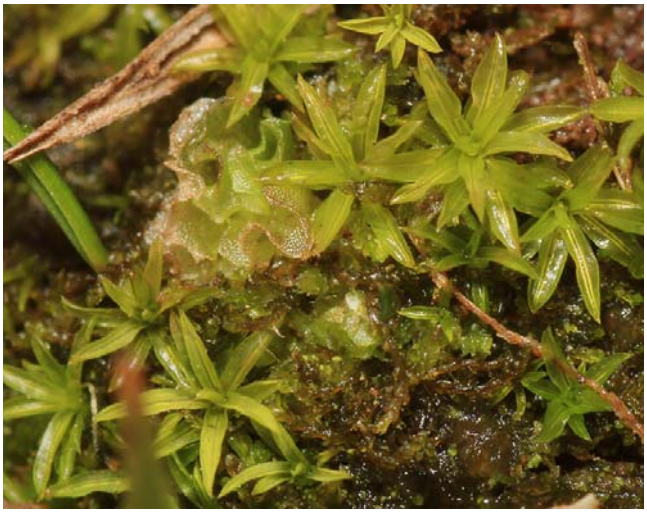

Figure 49. ***Fossombronia caespitiformis* subsp. *multispira*** growing with mosses. Photo by Barry Stewart, with permission.

Like many species of ***Fossombronia***, ***F. caespitiformis* subsp. *multispira*** (Figure 37-Figure 39) has violet rhizoids (Figure 50). It would be interesting to follow the evolutionary pathway to this unusual character, perhaps permitting us to determine why they have persisted in the genus.

Figure 50. ***Fossombronia caespitiformis*** with violet rhizoids. Photo by Tom Thekathyil, with permission.

Reproduction

Several authors (Mansion 1905; Puglisi *et al*. 2016) have noted that ***Fossombronia caespitiformis* subsp. *multispira*** (Figure 37-Figure 39) is abundantly fertile (Figure 51-Figure 60). Its spores (Figure 61) are relatively large (Sotiaux *et al*. 2009), partially compensating for the absence of specialized asexual reproduction by increasing the success of short-distance dispersal. The spores germinate to form a thalloid protonema (Figure 62).

Figure 51. ***Fossombronia caespitiformis*** developing sporophyte in archegonium. Photo by Tom Thekathyil, with permission.

Figure 52. ***Fossombronia caespitiformis*** in habitat showing nearly mature capsules before seta elongation. Photo by Michael Lüth, with permission.

Figure 53. ***Fossombronia caespitiformis*** showing capsules mostly before seta elongation. Photo by Michael Lüth, with permission.

Figure 56. ***Fossombronia caespitiformis*** with capsules and elongated setae. Photo by Jonathan Sleath, BBS, with permission.

Figure 54. ***Fossombronia caespitiformis*** before seta elongation. Photo by Andras Keszei, with permission.

Figure 55. ***Fossombronia caespitiformis*** as setae begin to elongate. Photo by Jan-Peter Frahm, with permission.

Figure 57. ***Fossombronia caesitiformis*** capsules with elongated seta. Photo by Andras Keszei, with permission.

Figure 58. ***Fossombronia caespitiformis*** capsule showing surface. Photo by Andras Keszei, with permission.

Figure 59. ***Fossombronia caespitiformis*** **subsp**. ***multispira*** with dehiscing capsules. Photo by Michael Lüth, with permission.

Figure 60. ***Fossombronia caespitiformis*** capsule opening, showing the irregular breakage of the capsule. Photo by Tom Thekathyil, with permission.

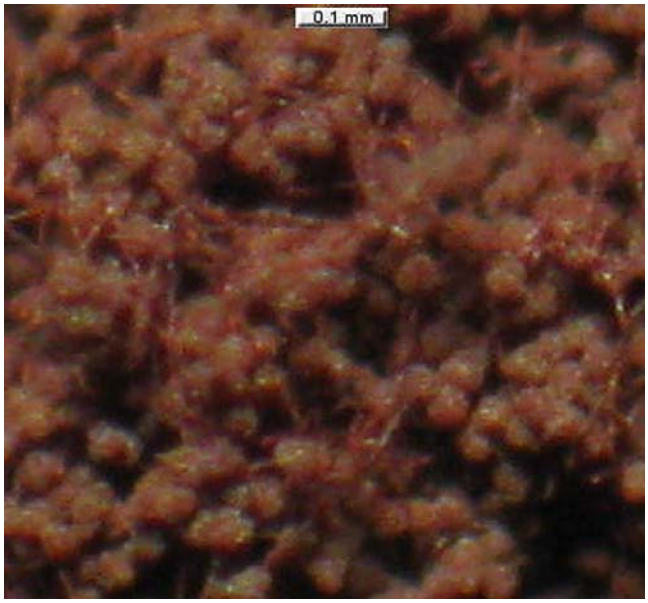

Figure 61. ***Fossombronia caespitiformis*** spores and elaters. Photo by Tom Thekathyil, with permission.

Figure 62. ***Fossombronia caespitiformis*** protonema. Photo from Plant Actions, with permission.

Fossombronia cristula (Figure 63-Figure 65)

Distribution

Fossombronia cristula (Figure 63-Figure 65) is endemic to the eastern United States and has been reported from Connecticut, Illinois, Indiana, Massachusetts, Maryland, Michigan, New Jersey, New York, North Carolina, Ohio, Tennessee, and West Virginia (Crandall-Stotler & Bray 2019).

Figure 63. ***Fossombronia cristula***, an endemic species in eastern USA. Photo by Kochibi, through Creative Commons.

Figure 64. ***Fossombronia cristula***. Photo by Kochibi, through Creative Commons.

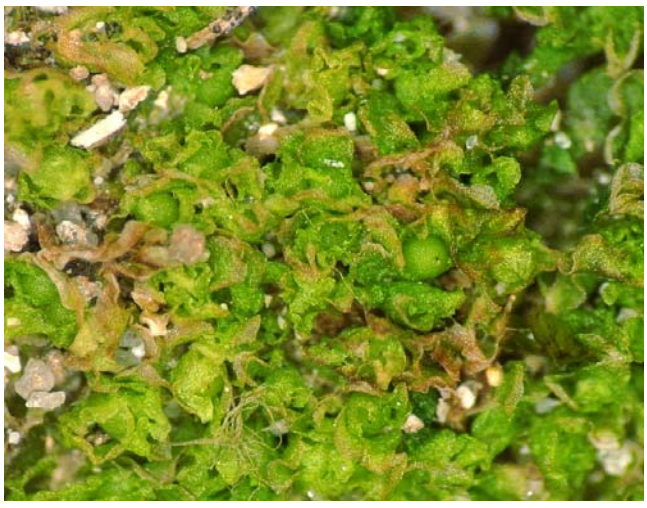

Figure 65. ***Fossombronia cristula***. Photo by Kochibi, through Creative Commons.

Aquatic and Wet Habitats

Fossombronia cristula (Figure 63-Figure 65) occurs on moist, denuded soils (Figure 66-Figure 68), often in disturbed habitats such as paths or ditches, and on lake or stream banks, typically at low to moderate elevations (Crandall-Stotler & Bray 2019).

Figure 66. ***Fossombronia cristula*** among graminoids. Photo by Kochibi, through Creative Commons.

Figure 67. ***Fossombronia cristula*** on disturbed soil. Photo by Kochibi, through Creative Commons.

Figure 68. ***Fossombronia cristula*** on disturbed soil. Photo by Kochibi, through Creative Commons.

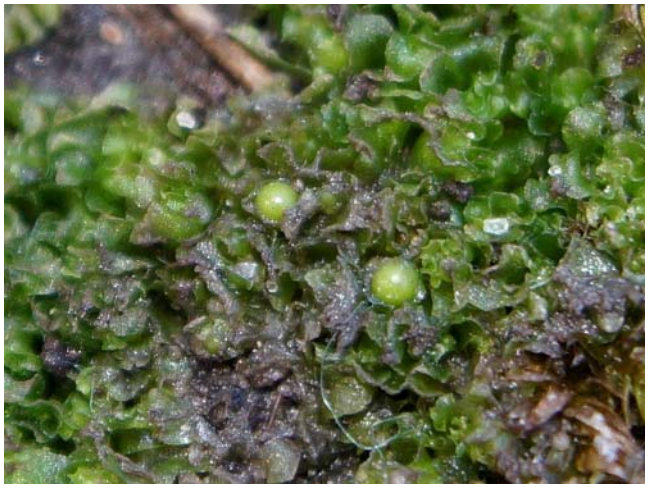

Figure 71. ***Fossombronia cristula*** with developing capsules before seta elongation. Photo by John Bunch, through Creative Commons.

Reproduction

Fossombronia cristula (Figure 63-Figure 65) is **monoicous** (Crandall-Stotler & Bray 2019). The antheridia (Figure 69-Figure 70) are intermixed with archegonia and develop simultaneously with them. The seta expands to about 3.4 mm and the capsule (Figure 71) "splits, expanding by depression" (Claassen 1904).

Spores (Figure 72) have a wide size range, tending on the large size (36-50 µm). Renzaglia and Bartholomew (1985) described sporeling development and its implications for phylogenetic relationships.

Figure 69. ***Fossombronia cristula*** with yellow antheridia. Photo by Kochibi, through Creative Commons.

Figure 72. ***Fossombronia cristula*** spores. Photo by Tom Wiebolt, through Creative Commons.

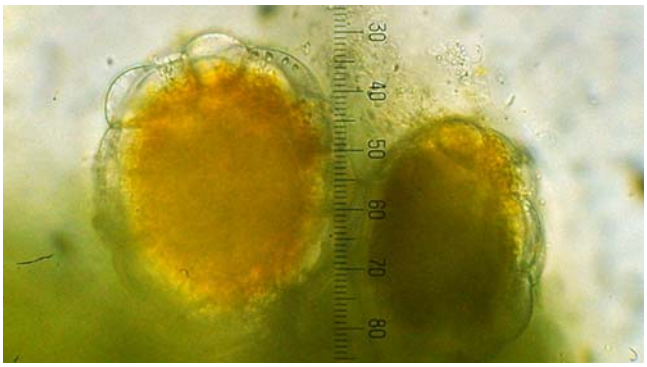

Figure 70. ***Fossombronia cristula*** antheridia. Photo by Kochibi, through Creative Commons.

Biochemistry

It appears that oil bodies have not been found in many species of ***Fossombronia***. Based on Figure 73, there appear to be small oil bodies in the cells of ***Fossombronia cristula*** (Figure 63-Figure 65).

Figure 73. ***Fossombronia cristula*** leaf cells, showing oil bodies. Photo by Kochibi, through Creative Commons.

Fossombronia delgadilloana (Figure 74-Figure 75)

Distribution

Fossombronia delgadilloana (Figure 74-Figure 75) is a recent species known only from the Latin American area – Mexico, high Andes of Venezuela, and Ecuador (Crandall-Stotler *et al*. 2019; Gradstein 2021).

Figure 74. ***Fossombronia delgadilloana***, a species of high elevations in Mexico, Venezuela, and Ecuador. Photo by Barbara Crandall-Stotler, with permission.

Figure 75. ***Fossombronia delgadilloana*** male with young antheridia. Photo by Barbara Crandall-Stotler, modified, with permission.

Aquatic and Wet Habitats

Fossombronia delgadilloana occurs submerged in high elevation mires of Latin America (Figure 76-Figure 78) (Crandall-Stotler *et al*. 2019). In Ecuador, it occurs in partly burned *Polylepis* forest, in streaming water, deeply shaded, at 3750 m (Gradstein 2021).

Figure 76. ***Fossombronia delgadilloana*** general habitat. Photo by Barbara Crandall-Stotler, with permission.

Figure 77. ***Fossombronia delgadilloana*** habitat. Photo by Barbara Crandall-Stotler, with permission.

Figure 78. ***Fossombronia delgadilloana*** habitat at high elevation in Andes. Photo by Barbara Crandall-Stotler, with permission.

Reproduction

Fossombronia delgadilloana (Figure 74-Figure 75) has "widely dispersed antheridia" (Figure 79-Figure 80) (Crandall-Stotler *et al*. 2019). Capsules are known (Figure 81); spores are > 40 µm in diameter (Figure 82-Figure 83).

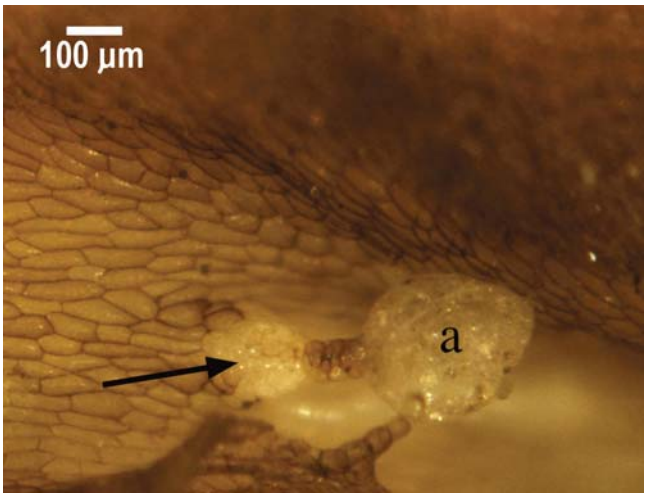

Figure 79. ***Fossombronia delgadilloana*** with young antheridia. Photo by Barbara Crandall-Stotler, modified, with permission.

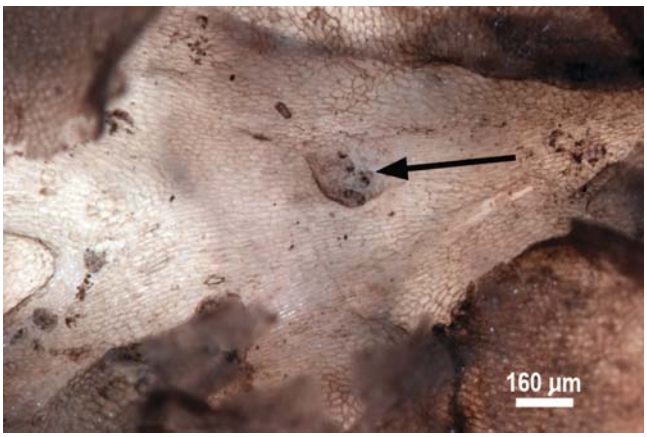

Figure 80. ***Fossombronia delgadilloana*** with dehisced antheridia (**at arrow**). Photo by Barbara Crandall-Stotler, modified, with permission.

Figure 81. ***Fossombronia delgadilloana*** with sporophyte, arrow at foot. Photo by Barbara Crandall-Stotler, modified, with permission.

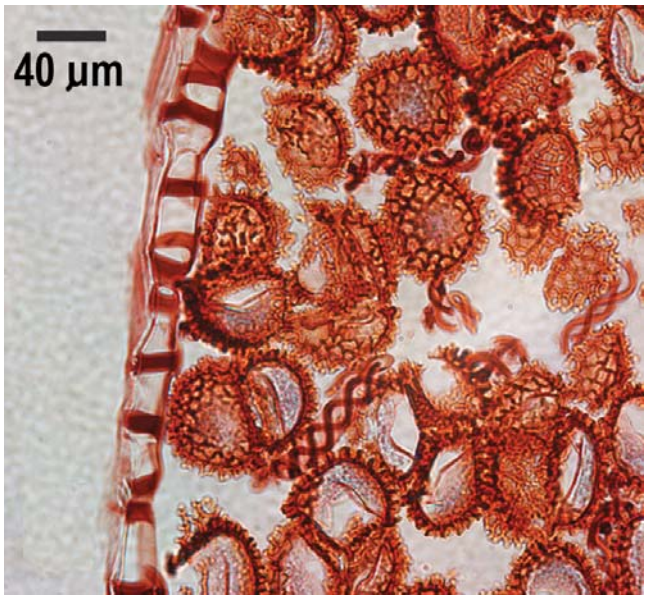

Figure 82. ***Fossombronia delgadilloana*** capsule and spores. Photo by Barbara Crandall-Stotler, with permission.

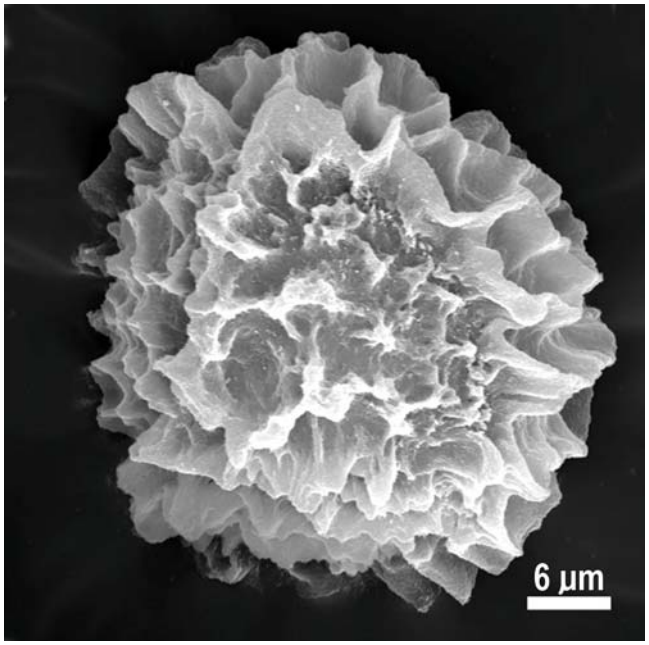

Figure 83. ***Fossombronia delgadilloana*** spore SEM. Photo by Barbara Crandall-Stotler, modified, with permission.

Biochemistry

Fossombronia delgadilloana has small (15-20 µm diameter) oil bodies (Figure 84). We can expect these to have secondary compounds that help to protect the plant from pathogens or herbivory, but no studies have been done on them.

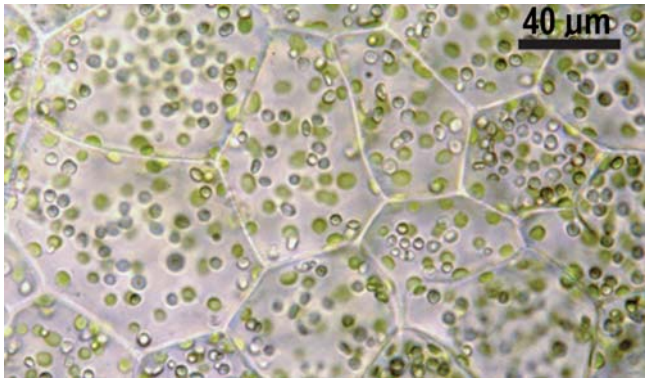

Figure 84. ***Fossombronia delgadilloana*** leaf cells showing small oil bodies and scattered chloroplasts. Photo by Barbara Crandall-Stotler, modified, with permission.

Fossombronia foveolata (Figure 85-Figure 90)

Fossombronia foveolata (Figure 85-Figure 90) has been variously considered and is perhaps best treated as a complex. Among the names I have encountered in aquatic and wet habitat studies, I here include ***Fossombronia salina***, a species that recent authors have placed in ***F. foveolata*** (Scott & Pike 1987). Species determination is often complicated by the absence of one or the other sexual organs in monoicous plants, causing some researchers to treat them dioicous and therefore not belonging to ***F. foveolata***.

Figure 85. ***Fossombronia foveolata***, a Holarctic species. Photo by Des Callaghan, with permission.

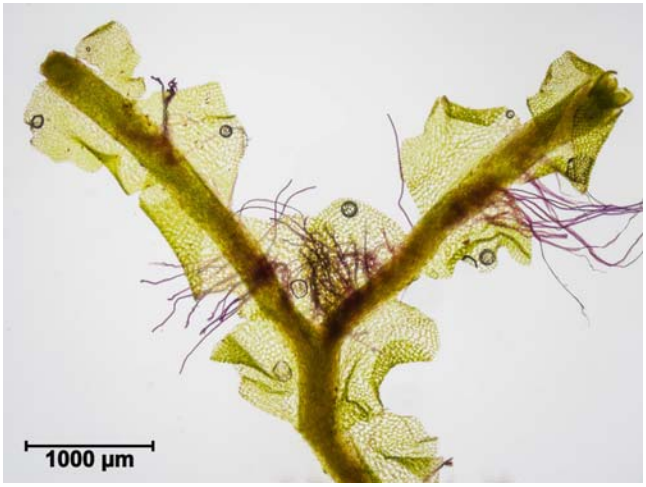

Figure 86. ***Fossombronia foveolata*** habit. Photo by Kristian Peters, with permission.

Figure 87. ***Fossombronia foveolata***. Photo by Jouko Rikkinen, through Creative Commons.

Figure 88. ***Fossombronia foveolata.*** Photo by Jouko Rikkinen, through Creative Commons.

Figure 89. ***Fossombronia foveolata*** forming a dense turf. Photo by Jouko Rikkinen, through Creative Commons.

Figure 90. ***Fossombronia foveolata***. Photo by Dick Haaksma, with permission.

Distribution

Schuster (1992) describes ***Fossombronia foveolata*** (Figure 85-Figure 90) as widespread temperate and cooler Holarctic in Europe and North America, but apparently absent from Asia, a content that is included in later reports. It is often a pioneer on bare soil, but also occurs on sandy or rocky margins of lakes and occasionally in bogs.

ITIS (2021) lists its distribution as Africa, Caribbean, Europe, Northern Asia, North America, Central America, and South America. Müller (2000) reported it from the East African Islands of Réunion and Mauritius.

Konstantinova (2000) considered ***Fossombronia foveolata*** (Figure 85-Figure 90) to be a North Holarctic liverwort. In Asia, it is known from Russia (Dulin 2015). In Europe, it is known from Estonia (rare) (Ingerpuu *et al*. 2014; Vellak *et al*. 2015), Romania (Ștefănuț & Maria 2018), Poland (vulnerable) (Staniaszek-Kik 2014; Klama & Górski 2018), and the British Isles (Smith 1978).

In North America it extends from Alaska southward to Mexico and the Caribbean islands. Evans (1916) reported ***Fossombronia foveolata*** (Figure 85-Figure 90) from Quebec, Canada. Crandall-Stotler and Bray (2019) added British Columbia, Newfoundland, Nova Scotia, and Ontario to its Canadian locations. Andrew (1931) reported it from New York, Sharp (1939) from Tennessee, and Miller (1964) found reports from Indiana, Michigan, New York, West Virginia, and Ohio in the USA. Spencer (1993) added Maine and Wheeler *et al*. (1983) added Minnesota. Crandall-Stotler and Bray (2019) added Arkansas, Connecticut, Delaware, Illinois, Kentucky, Louisiana, Maryland, Massachusetts, Mississippi, Missouri, New Hampshire, New Jersey, North Carolina, Oklahoma, Oregon, Pennsylvania, Rhode Island, South Carolina, Texas, Vermont, Washington, and Wisconsin, attesting to its widespread distribution. Yet, some states imbedded among these are missing, suggesting a lack of collecting in places like Pennsylvania.

In addition to North America, it is known from Europe and from the African locations of Azores, Madagascar, Morocco, South Africa, Tanzania, and Zaïre (Crandall-Stotler & Bray 2019).

Aquatic and Wet Habitats

Nichols (1918) reported ***Fossombronia foveolata*** (Figure 85-Figure 90) from rocks (Figure 91) on ravine streambanks (Figure 92), Cape Breton Island, Canada. Cain and Fulford (1948) similarly found it along river banks, but also on wet soil along lake shores in Ontario. Steere (1934) found it on the clay shore of Carp Lake in Michigan, USA. McFarlin (1940) found it in a low hammock along a creek in Florida. In Kentucky, USA, Norris (1967) found it on a grassy stream bank. Blomquist (1936) reported it from bare clayey soils in forests, stream edges, springs, and ponds. Andreas and Moosbrugger (2021) found it on moist clay soil in Ohio. Saadi *et al*. (2020) reported it from both aquatic and sub-aquatic soil in Morocco, occurring in the ravine of a river and from shady siliceous soil, and as in most places, it is very rare. Simons and Jansen (2018) found it in oligotrophic ponds in The Netherlands. Bosanquet *et al*. (2018) reported it from reservoirs, lakes, ponds, and lowland heath (Figure 44) in the British Isles.

Figure 91. ***Fossombronia foveolata*** on rock of a stream bank. Photo by Jouko Rikkinen, through Creative Commons.

Figure 92. ***Fossombronia foveolata*** habitat on a stream bank. Photo by Tom Neily, through Creative Commons.

Jacobs (1949) reported ***Fossombronia foveolata*** (Figure 85-Figure 90) from seasonally moist clay in locations that become periodically dry. Similarly, it is a species that finds the margins of ponds (Figure 93) to be a suitable habitat (Maine, USA – Taylor 1921; New York – Burnham 1929; Dorset – Aquilina 2010; France – Bardet & Douchin 2017). In such habitats, the liverworts can be immersed in winter, abruptly being exposed out of water again in the spring (Bardet & Douchin 2017). Such exposure also occurred at Sindor Lake in Russia (Dulin 2015) and at the wet edge of Aughnagurgan Lough in Ireland (Fitzgerald & Fitzgerald 1967). Rikkinen (1992) noted its presence on peat (Figure 94), mineral soil, and well-decayed wood on the periodically flooded margins of ponds in Finland.

Figure 93. ***Fossombronia foveolata*** on a pond margin. Photo by Dick Haaksma, with permission.

Figure 94. ***Fossombronia foveolata*** with ***Sphagnum***. Photo by Jouko Rikkinen, through Creative Commons.

Sharp (1939) described the habitat of ***Fossombronia foveolata*** (Figure 85-Figure 90) in Tennessee, USA, as moist open soil (Figure 95), where it was uncommon. Barringer (2011) noted that it prefers clay soils, occurring on exposed clay (Figure 96) and moist sand in New Jersey. Sabovljevic *et al*. (2010) reported it from mud in southeastern Europe. Preston *et al*. (2011) characterized it as preferring damp, acidic (see also Crandall-Stotler & Bray 2019) habitats as a pioneer in the British Isles. Its range of habitats also includes open, sloping sandstone among scrub oaks and very thin sandy soil mixed with woody debris (Wittlake 1954). It also seems able to inhabit ditches, as seen in Figure 97 by Kobichi.

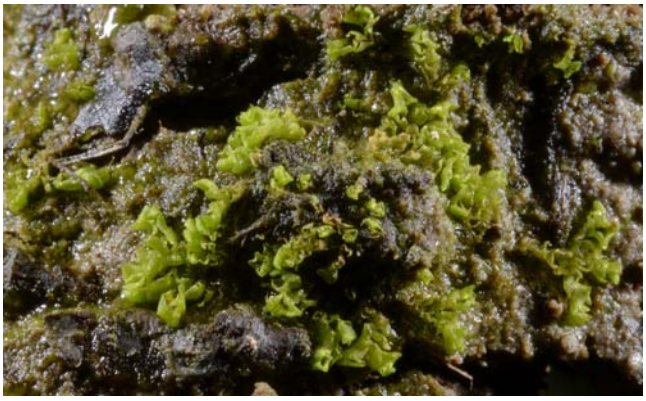

Figure 95. ***Fossombronia foveolata*** on moist soil. Photo by Jouko Rikkinen, through Creative Commons.

Figure 96. ***Fossombronia foveolata*** on open clay soil. Photo by Dick Haaksma, with permission.

Figure 97. ***Fossombronia foveolata*** habitat along ditch. Photo by Kochibi, through Creative Commons.

Its habitats include swamps, fens, and bogs. Ingerpuu *et al*. (2014) considered ***Fossombronia foveolata*** (Figure 85-Figure 90) to be a vulnerable species occurring rarely in Estonian fens. Staniaszek-Kik (2014) reported it from peat bogs and swamp forest depressions. In Minnesota, USA, it occurs in the Red Lake Peatland (Wheeler *et al*. 1983). Bradáčová *et al*. (2015) reported it from peaty and sandy soil along water-filled depressions in rich fens of Bohemia, as well as on bare soil of a wet, shaded path. In a somewhat similar habitat, Paton (1974) reported it from a dried out wet hollow on heath (Figure 44) in the British Isles. In Lithuania, ***Fossombronia foveolata*** occurred on bare peat in a swampy black alder forest (Jukonienė *et al*. 2013). In another seasonally wet habitat it occurs on the edges of snowbanks in the tundra of Alaska (Hermann 1973).

Fossombronia foveolata (Figure 85-Figure 90) also occurs in grasslands in the western Ghats of India (Manju & Rajesh 2009). Its occurrence in grassy cemeteries in the Interior Highlands of Arkansas might ensure that it is wet at times, perhaps seasonally, but we have no indication of that (Kyzer & Marsh 1999).

As noted earlier, *Fossombronia salina* may be a synonym of ***Fossombronia foveolata*** (Figure 85-Figure 90). This variant is known from saline situations, but it has also been collected from a swamp in Connecticut, USA (Evans 1901). Nevertheless, that location was less than 1 km from salt water.

Adaptations

Fossombronia foveolata (Figure 85-Figure 90) forms small patches (Figure 98-Figure 102) or tight **mats** (Figure 103-Figure 104), the latter helping to conserve water during dry periods (Crandall-Stotler & Bray 2019). This helps to extend the growing season long enough for reproduction.

Figure 98. ***Fossombronia foveolata*** patches on mud. Photo by Dick Haaksma, with permission.

Figure 99. ***Fossombronia foveolata*** patch on mud. Photo by Dick Haaksma, with permission.

Figure 100. ***Fossombronia foveolata*** in patches on mud. Photo by Dick Haaksma, with permission.

Figure 101. ***Fossombronia foveolata*** patches on mud. Photo by Dick Haaksma, with permission.

Figure 102. ***Fossombronia foveolata*** in patches on mud. Photo by Dick Haaksma, with permission.

Figure 103. ***Fossombronia foveolata*** forming a tight mat. Photo by Jouko Rikkinen, through Creative Commons.

Figure 104. ***Fossombronia foveolata*** dense turf. Photo by Jan-Peter Frahm, with permission.

Fossombronia foveolata (Figure 85-Figure 90) is pure green, but cell walls rarely become brown in the sun (Figure 105) (Schuster 1992). On the other hand, Evans (1901) observed that *Fossombronia salina*, considered by most to be synonymous with ***F. foveolata***, is dark green, becoming paler or brownish with age. The ***Fossombronia foveolata*** thallus is flat to strongly wavy, with purple rhizoids (Figure 106). This raises the question of the role of habitat in determining the degree of waviness – and the rhizoid coloration.

Figure 105. ***Fossombronia foveolata*** that is green, but older parts have become brown. Photo by Jouko Rikkinen, through Creative Commons.

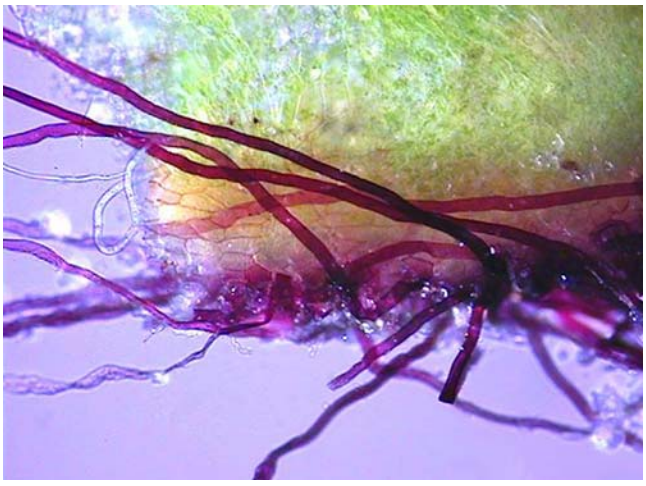

Figure 106. ***Fossombronia foveolata*** with purple rhizoids. Photo by Paul Davison, with permission.

Wood (2007) found that ***Fossombronia foveolata*** (Figure 85-Figure 90) is desiccation tolerant (Figure 107) down to 30% relative humidity. In Central Europe, it occurs in moderately low nutrient sites, with an Ellenberg (see Hill *et al*. 2007) nitrogen value of 3 (Simmel *et al*. (2021).

Figure 107. ***Fossombronia foveolata*** in dry state. Photo by Tim Faasen, with permission.

Figure 109. ***Fossombronia foveolata*** with yellow antheridia. Photo by J. C. Schou, with permission.

Figure 110. ***Fossombronia foveolata*** with young capsules. Photo by Kochibi, through Creative Commons.

Reproduction

Fossombronia foveolata (Figure 85-Figure 90) is an annual (Schuster 1992). It is **monoicous** [**paroicous** or **synoicous** (Scott & Pike 1987; Crandall-Stotler & Bray 2019)], usually producing predominantly archegonia with few antheridia (Figure 108-Figure 109) intermixed, but mostly spatially separated. Bray (1997) explored the life history and reproduction of ***F. foveolata*** for his doctoral dissertation. The species is **protandrous** (antheridia produced before archegonia) (Crandall-Stotler & Bray 2019). Sporophytes (Figure 110-Figure 117) are produced in summer and fall (Schuster 1992).

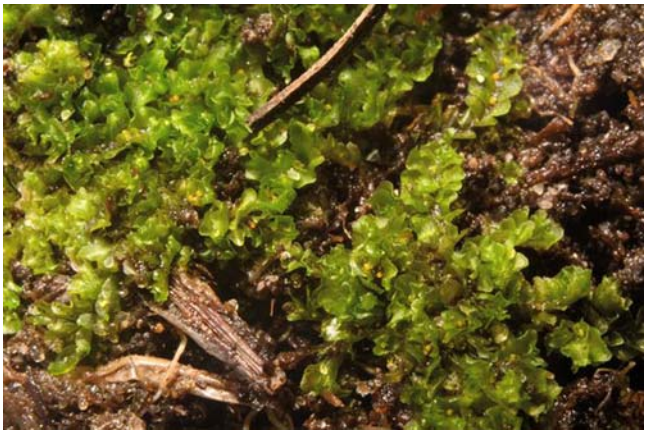

Figure 108. ***Fossombronia foveolata*** with a few yellow antheridia. Photo by J. C. Schou, with permission.

Figure 111. ***Fossombronia foveolata*** young capsule. Photo by J. C. Schou, with permission.

Figure 112. ***Fossombronia foveolata*** with young capsule. Photo by Manju Nair, through Creative Commons.

Figure 113. ***Fossombronia foveolata*** with capsule as seta begins to elongate. Photo by Hugues Tinguy, with permission.

Figure 114. ***Fossombronia foveolata*** with capsule with an elongating seta. Photo by Bob Klips, with permission.

Figure 115. ***Fossombronia foveolata*** with developing capsules among a few mature ones. Photo by J. C. Schou, with permission.

Figure 116. ***Fossombronia foveolata*** with elongated setae and mature capsules. Photo by J. C. Schou, with permission.

Figure 117. ***Fossombronia foveolata*** with maturing, mature, and dehiscing capsules. Photo by J. C. Schou, with permission

Evans (1901) found that the unusual *Fossombronia salina*, which is currently considered a likely form or variety of ***Fossombronia foveolata*** (Figure 85-Figure 90), had not yet produced mature sporophytes in late summer or early autumn in New Jersey, USA. On the other hand, numerous, somewhat immature, capsules were present in late May in a more northern coastal swamp population in Connecticut, USA. As further testament to the variability in sporophyte production, Suragina *et al*. (2002) reported

that few of the plants they found in the Volgograd Province in Russia had sporophytes with mature spores.

Scott and Crandall-Stotler (2002) demonstrated a high degree of homozygosity in the sporophytes of ***Fossombronia***. Within ***Fossombronia foveolata*** (Figure 85-Figure 90) in southern Illinois, the genetic differentiation exhibited low levels. This resulted in little polymorphism among the southern Illinois populations. The species furthermore exhibited short-distance sperm and spore dispersal, indicating that the populations there were probably the result of a single founder population that has spread through inbreeding and vegetative propagation.

Spores (Figure 118-Figure 120) of ***Fossombronia foveolata*** (Figure 85-Figure 90) are brown to dark brown, and relatively large (38-54 µm) (Crandall-Stotler & Bray 2019).

Figure 118. ***Fossombronia foveolata*** spores and elaters. Photo by David T. Holyoak, with permission.

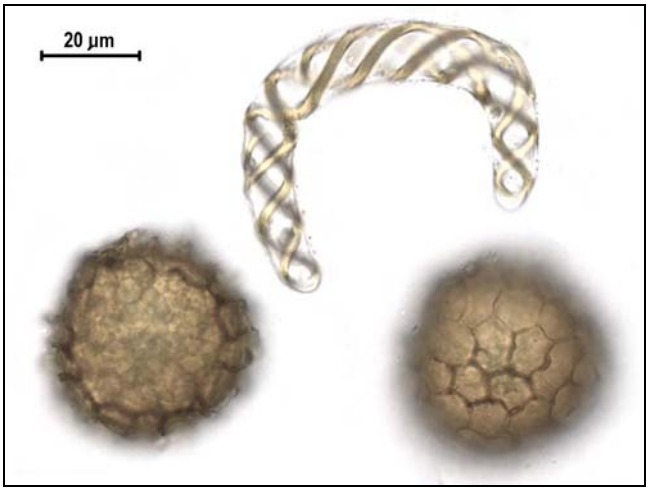

Figure 119. ***Fossombronia foveolata*** spores and elater. Photo by Hugues Tinguy, with permission.

Figure 120. ***Fossombronia foveolata*** SEM of spore. Photo by Barbara Crandall-Stotler, with permission.

Thomas *et al*. (1979) explored the sporophyte (Figure 110-Figure 117) nutrition in ***Fossombronia foveolata*** (Figure 85-Figure 90). They found that the sporophyte (separated from the gametophyte) was capable of fixing CO_2. In fact, the ratio of the ability to fix CO_2 per mg fresh weight ranged 0.13 to 0.39 in the five liverworts tested.

Fungal Interactions

Hoysted *et al*. (2019) reported that **Mucoromycotina** fungi colonized the gametophytes of ***Fossombronia foveolata*** (Figure 85-Figure 90). Field and Pressel (2018) reported that this liverwort has both **Glomeromycota** and **Mucoromycota** fungi (Figure 121). Rimington *et al*. (2018) determined at least some of these to be arbuscular mycorrhizal fungi.

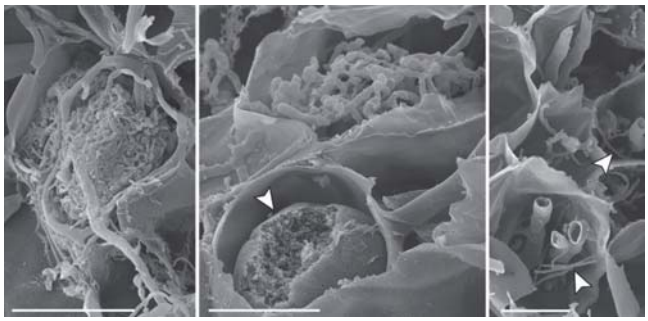

Figure 121. ***Fossombronia foveolata*** with **Mucoromycotina** and **Glomeromycotina**. Photo by Katie Field and Silvia Pressel, with permission.

Biochemistry

Fossombronia foveolata (Figure 85-Figure 90) typically has 6-9 oil bodies (Figure 122) per cell (Schuster 1992).

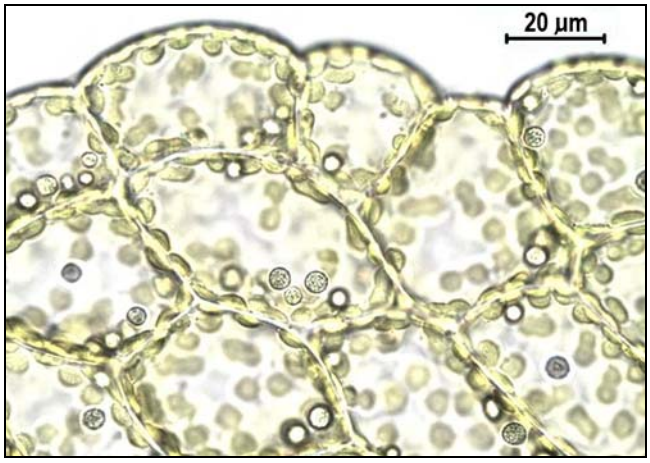

Figure 122. ***Fossombronia foveolata*** leaf cells and what appear to be oil bodies. Photo by Hugues Tinguy, with permission.

Basile and Basile (1987) demonstrated the presence of arabinogalactan-proteins (AGP's) in bryophytes, including ***Fossombronia foveolata*** (Figure 85-Figure 90) (see also Classen *et al*. 2019). These occur in the extracellular matrix of plants and are a class of hydroxyproline-containing glycoproteins. They suggested that AGP's are widespread in bryophytes. Their components and description help us understand the evolution of the plant cell wall.

Fossombronia foveolata (Figure 85-Figure 90) also is among the bryophytes for which the mitochondrial genome has been sequenced (Myszczyński *et al.* 2019).

Fossombronia incurva (Figure 123-Figure 124)

Distribution

Fossombronia incurva (Figure 123-Figure 124) occurs at low to moderate elevations in Oregon, USA, and in northwestern Europe (Britain, Ireland, Poland, Finland, Sweden) (Crandall-Stotler & Bray 2019). Despite its somewhat wide distribution, it is a rare species.

Figure 123. ***Fossombronia incurva***, a species with mostly northwestern European distribution. Photo by Dick Haaksma, with permission.

Figure 124. ***Fossombronia incurva*** growing in small clumps. Photo by Dick Haaksma, with permission.

Aquatic and Wet Habitats

Fossombronia incurva (Figure 123-Figure 124) occurs on moist sandy or gravelly soils, often along streams, lakes (Figure 125), or in dune slacks (Crandall-Stotler & Bray 2019). On a stream terrace along Sutton Creek in Oregon, USA, the species was growing with the also rare ***Haplomitrium hookeri*** (Figure 126), forming a community of mixed liverworts and hornworts.

Figure 125. ***Fossombronia incurva*** habitat. Photo by Barry Stewart, with permission.

Figure 126. ***Haplomitrium hookeri***, a leafy liverwort that sometimes grows with ***Fossombronia incurva*** in Oregon, USA. Photo by Des Callaghan, with permission.

Adaptations

Fossombronia incurva (Figure 123-Figure 124) can grow isolated or in small **tufts** (Figure 124) (Crandall-Stotler & Bray 2019). In some cases, it is surrounded by other bryophytes (Figure 127) that could help it to retain moisture. We need experimentation to see how these forms survive in their moist habitats, especially when they experience dry seasons.

Figure 127. ***Fossombronia incurva*** growing with other bryophytes. Photo by Barry Stewart, with permission.

Reproduction

Fossombronia incurva (Figure 123-Figure 124) is **dioicous**, with male plants smaller than females (Crandall-Stotler & Bray 2019). The antheridia are clustered near the shoot apices (Figure 128-Figure 129), protected in dorsal leaf axils. Capsules are black at maturity, with variable shape (obovoidal, ellipsoidal, to spheroidal) (Figure 130-Figure 132). Their dehiscence is irregular fracturing (Figure 133). The spores (Figure 134) are 20-24(-28) µm. These smaller spores, nevertheless, might limit their dispersal because they often remain in tetrads (Figure 134), thus being larger and dispersed shorter distances. This bet-hedging strategy should permit some (single) spores (Figure 135) to disperse long distances, while keeping others (tetrads) close to home in a known suitable habitat.

Figure 128. ***Fossombronia incurva*** males with yellow antheridia. Photo by David T. Holyoak, with permission.

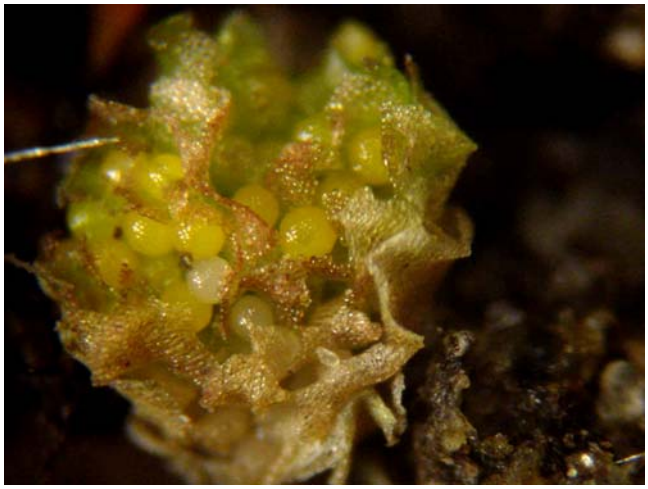

Figure 129. ***Fossombronia incurva*** with antheridia. Photo by Dick Haaksma, with permission.

Figure 130. ***Fossombronia incurva*** female plants with immature capsules. Photo by Dick Haaksma, with permission.

Figure 131. ***Fossombronia incurva*** with immature capsules. Photo by Dick Haaksma, with permission.

Figure 132. ***Fossombronia incurva*** with capsules and elongated setae. Photo by David T. Holyoak, with permission.

Figure 133. ***Fossombronia incurva*** dehiscing sporangium. Photo courtesy of David H. Wagner.

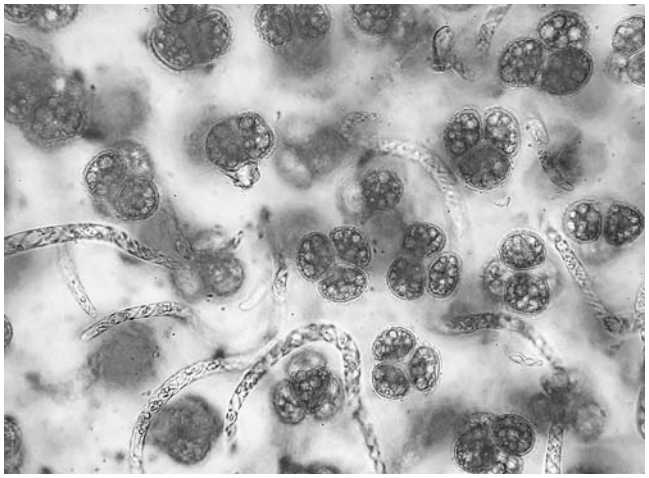

Figure 134. ***Fossombronia incurva*** spore tetrads and elaters. Photo by Barry Stewart, with permission.

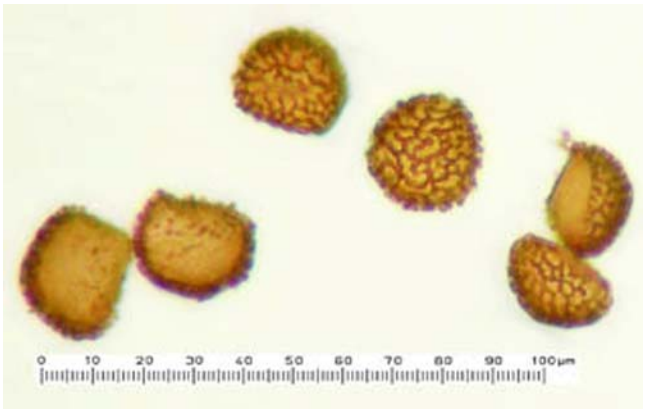

Figure 135. ***Fossombronia incurva*** spores. Photo courtesy of David H. Wagner.

Fossombronia incurva (Figure 123-Figure 124) apparently has no gemmae, and no other asexual structures seem to have been described, but it has a persistent, subterranean rhizome that can contribute to local spreading (Crandall-Stotler & Bray 2019).

Fossombronia isaloensis (Figure 136-Figure 138)

Distribution

Fossombronia isaloensis (Figure 136-Figure 138) is thus far endemic to Madagascar (Cargill *et al*. 2020).

Figure 136. ***Fossombronia isaloensis***. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <http://www.cpbr.gov.au/cpbr/>, with permission.

Figure 137. ***Fossombronia isaloensis*** in dry condition. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <http://www.cpbr.gov.au/cpbr/>, with permission.

Figure 138. ***Fossombronia isaloensis*** showing "maroon" margins. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <http://www.cpbr.gov.au/cpbr/>, with permission.

Figure 139. Massif where ***Fossombronia isaloensis*** type specimen was found. Photo by Des Callaghan, with permission.

Figure 140. Base of canyon habitat where ***Fossombronia isaloensis*** type specimen was found. Photo by Des Callaghan, with permission.

Figure 141. ***Fossombronia isaloensis*** at base of canyon where type specimen was found. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

Fossombronia isaloensis (Figure 136-Figure 138) occurs at 1010 m asl, on damp, soft, acidic sandstone beside a small stream (Figure 139-Figure 141) that is shaded by dry native scrub, growing with the tiny liverwort ***Cephaloziella*** (Figure 142) (Cargill *et al*. 2020).

Figure 142. ***Cephaloziella***; a member of this genus can grow with ***Fossombronia isaloensis***. Photo by Ken-Ichi Ueda, through Creative Commons.

Figure 144. ***Sphagnum magellanicum*** showing green color as seen in shade or immediately after snowmelt. Photo by Blanka Aguero, with permission.

Adaptations

Like many other ***Fossombronia*** species, ***Fossombronia isaloensis*** (Figure 136-Figure 138) has dark red-purple rhizoids (Cargill *et al*. 2020) – a character that is unusual in bryophytes (but not in ***Fossombronia***), but perhaps not adaptive. The margins of leaves and ventral surfaces of stems are maroon (Figure 138) (Cargill *et al*. 2020), but the color can extend into depths of the lobes, a character suggesting too much light, as seen on house plants that are placed outside on a sunny day after a winter indoors. This is seen in such species as ***Sphagnum magellanicum*** (Figure 143-Figure 144) that are red (Figure 143) in the sun but green (Figure 144) in the shade. The most intense purplish red coloring occurs when the sun is bright but the temperature is cold.

Reproduction

Fossombronia isaloensis (Figure 136-Figure 138) is **dioicous** (Figure 145-Figure 146) (Cargill *et al*. 2020), but at least produces some sporophytes (Figure 147). These are non-emergent or emergent on short setae. The spores (Figure 148-Figure 149) are medium to large [(37.5– 57.5 µm); Figure 148-Figure 149]. It does, however, produce tubers, formed as geotropic swollen apices.

Figure 143. ***Sphagnum magellanicum*** showing red color that is especially intense when it is cold and sunny. Photo by Michael Lüth, with permission/

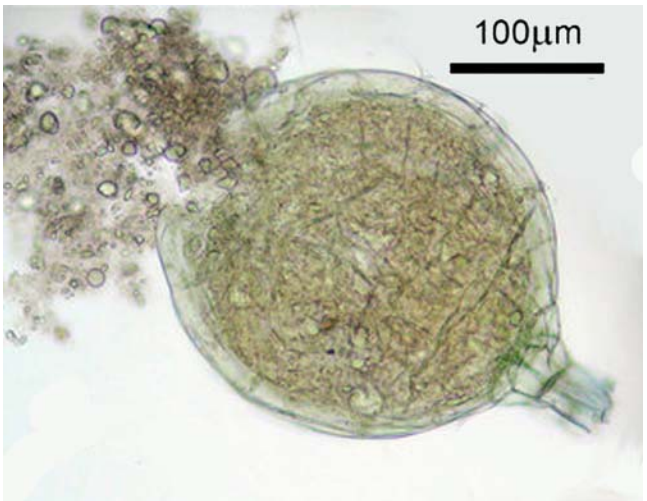

Figure 145. ***Fossombronia isaloensis*** antheridium. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <http://www.cpbr.gov.au/cpbr/>, with permission.

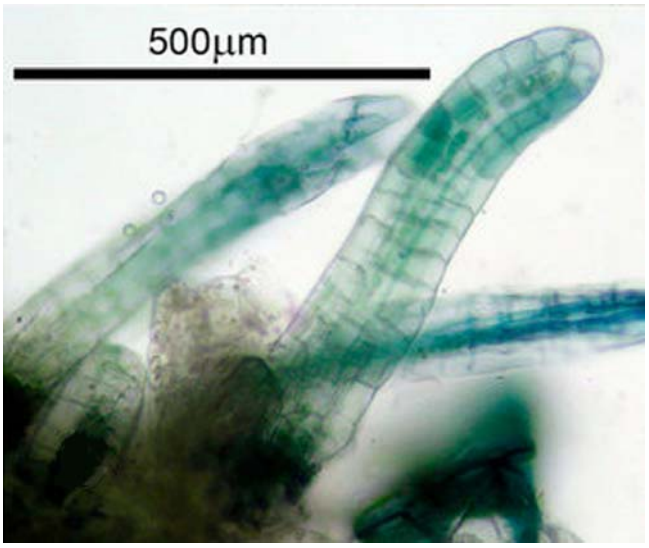

Figure 146. ***Fossombronia isaloensis*** archegonia. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <http://www.cpbr.gov.au/cpbr/>, with permission.

Figure 147. ***Fossombronia isaloensis*** sporophyte foot and seta. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <http://www.cpbr.gov.au/cpbr/>, with permission.

Figure 148. ***Fossombronia isaloensis*** spores. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <http://www.cpbr.gov.au/cpbr/>, with permission.

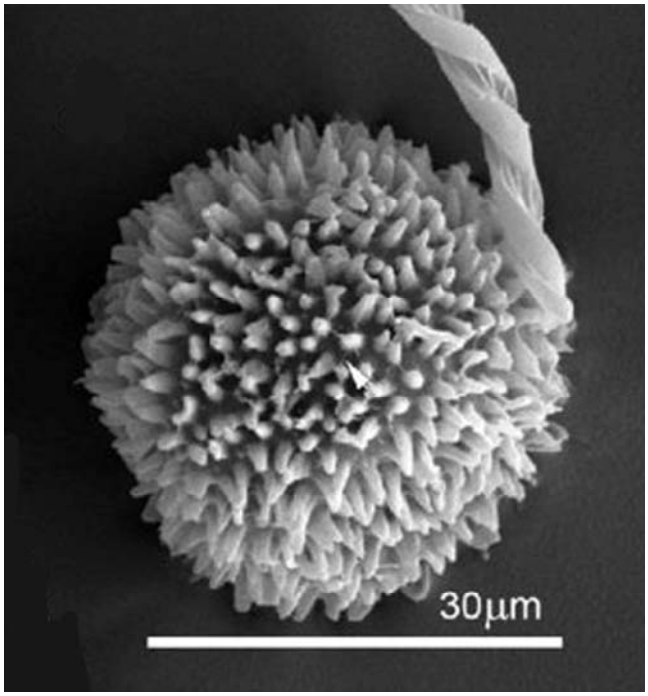

Figure 149. ***Fossombronia isaloensis*** spore and elater. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <http://www.cpbr.gov.au/cpbr/>, with permission.

Biochemistry

Thus far, oil bodies have not been observed in ***Fossombronia isaloensis*** (Figure 136-Figure 138) (Cargill *et al*. 2020). It also lacks biochemical studies.

Fossombronia jostii (Figure 150-Figure 151)

Distribution

Fossombronia jostii (Figure 150-Figure 151) is known only recently, from Ecuador (Crandall-Stotler & Gradstein 2017).

Figure 150. ***Fossombronia jostii***, a species endemic to Ecuador. Photo by Lou Jost, with permission from S. Robbert Gradstein.

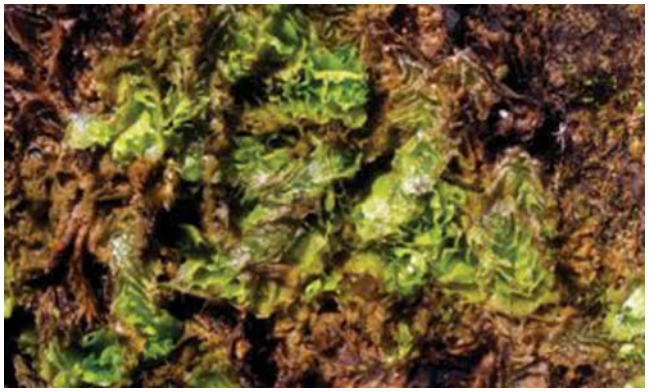

Figure 151. ***Fossombronia jostii*** in Rio Anzu Canyon, Ecuador. Photo by Lou Jost, with permission from S. Robbert Gradstein.

Aquatic and Wet Habitats

In Ecuador, ***Fossombronia jostii*** (Figure 150-Figure 151) occurs on limestone boulders along the Rio Anzu (Figure 152-Figure 153) where it flows though a narrow gorge (Crandall-Stotler & Gradstein 2017). The rocks are moist and periodically inundated in the riverbed. The Rio Anzu is periodically flooded and otherwise remains moist.

Figure 152. ***Fossombronia jostii*** on limestone rocks in Rio Anzu Canyon, Ecuador. Photo by S. Robbert Gradstein, with permission.

Figure 153. ***Fossombronia jostii*** in Rio Anzu Canyon, Ecuador, showing limestone rocks that serve as substrate. Photo by S. Robbert Gradstein, with permission.

Adaptations

Fossombronia jostii (Figure 150-Figure 151) forms large, light green, mats (Crandall-Stotler & Gradstein 2017).

Reproduction

Fossombronia jostii (Figure 150-Figure 151) is **dioicous** and sexually dimorphic (Crandall-Stotler & Gradstein 2017). Male plants are narrower, with smaller leaves, than the female. Antheridia occur at the apices of the male shoots. The spores (Figure 154-Figure 155) are relatively small (28-32 µm in diameter across distal face, 24-26 µm in polar diameter).

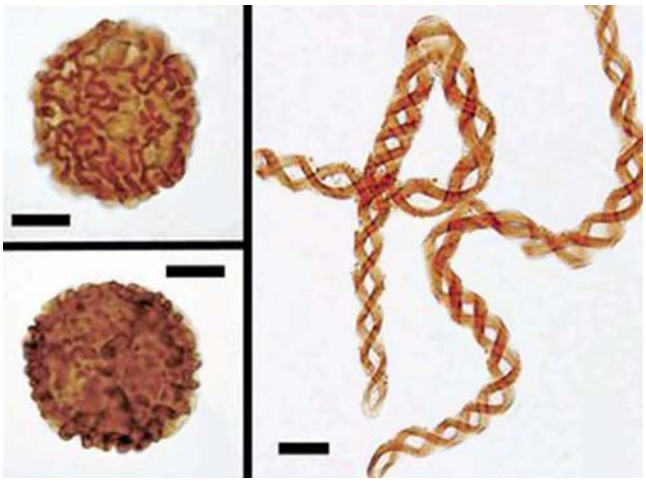

Figure 154. ***Fossombronia jostii*** spores (**left**) and elaters (**right**). Photo by Lou Jost, with permission from S. Robbert Gradstein.

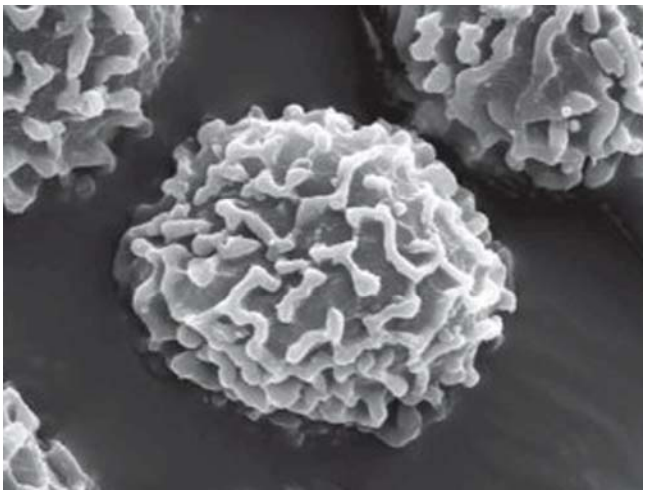

Figure 155. ***Fossombronia jostii*** SEM of spores. Photo by S. Robbert Gradstein, with permission.

It thus far is not known to produce any type of asexual reproductive or perennating structure, including a noted absence of tubers and gemmae (Crandall-Stotler & Gradstein 2017).

Summary

The wet habitat members of ***Fossombronia*** often occur in habitats that receive splash or that become inundated periodically, a habitat consistent with their presence in disturbed habitats. This suggests that they are poor competitors. Some are dioicous and others monoicous. Some produce abundant capsules. They quickly re-appear when disturbed conditions become favorable, some from spores, some from persistent tubers. Some benefit from moisture conservation derived by growing with other bryophytes, while others grow in solitary patches that look like green carnations. Some are annuals and others are perennials

Members of the genus ***Fossombronia*** were the subject of a number of early studies on development in liverworts. The presence of arabinogalactan-proteins (AGP's) was identified in bryophytes for the first time in ***Fossombronia foveolata***.

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CHAPTER 1-14
AQUATIC AND WET MARCHANTIOPHYTA, ORDER FOSSOMBRONIALES, PART 2

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CHAPTER 1-14
AQUATIC AND WET MARCHANTIOPHYTA, ORDER FOSSOMBRONIALES, PART 2

Figure 1. ***Fossombronia pusilla***, a cosmopolitan species of moist soil and temporary ponds. Photo by Hugues Tinguy, with permission.

SUBCLASS PELLIIDAE, Fossombroniales part 2

Fossombronia mylioides (Figure 2-Figure 3)

Distribution

Thus far, ***Fossombronia mylioides*** (Figure 2-Figure 3) is known only from Iriomote Island, Japan (Higuchi 2016; Crandall-Stotler & Gradstein 2017), making it a narrow endemic.

Figure 2. ***Fossombronia mylioides***, an endemic of Iriomote Island, Japan. Photo by Masanabu Higuchi, National Museum, Japan, with permission.

Figure 3. ***Fossombronia mylioides***. Photo by Masanabu Higuchi, National Museum, Japan, with permission.

Aquatic and Wet Habitats

Fossombronia mylioides (Figure 2-Figure 3) is a riverine species, growing on open boulders covered with sandy soil, along the Urauchi and Nakama Rivers of Japan (Krayesky *et al*. 2005; Higuchi 2016; Crandall-Stotler & Gradstein 2017).

Fossombronia mylioides (Figure 2-Figure 3) also grows directly on moist rocks and stones in river beds and along streams (Figure 4-Figure 5) (Krayesky *et al*. 2005; Higuchi 2016). In these habitats it is sometimes submerged. It can also grow on vertical rock faces near the streams. In areas that flood, it may be mixed with ***Riccardia*** (Figure 6) (Higuchi 2016).

Figure 4. ***Fossombronia mylioides*** on rock in Japan. Photo by Masanabu Higuchi, National Museum, Japan, with permission.

Figure 5. ***Fossombronia mylioides*** on rock in Japan. Photo by Masanabu Higuchi, National Museum, Japan, with permission.

Figure 6. ***Riccardia multifida***; ***Riccardia*** is mixed with ***Fossombronia mylioides*** in areas that flood in Japan. Photo by Hermann Schachner, through Creative Commons.

Adaptations

Fossombronia mylioides (Figure 2-Figure 3) is light green, with dense, deep purple rhizoids that attach it firmly to its substrate (Higuchi 2016). The color suggests bright sun, but there are no data to suggest protection from high light.

Reproduction

Fossombronia mylioides (Figure 2-Figure 3) is **monoicous**, with archegonia and antheridia scattered on the dorsal surface of the stem (Higuchi 2016). Setae are quite short (2-3 mm). Sporophytes mature in March (Krayesky *et al*. 2005; Higuchi 2016).

The capsule dehiscence is somewhat unusual among bryophytes. Once the capsules dry, they dehisce irregularly from apex downward, lacking sutures or other weakened area for splitting (Figure 7) (Higuchi 2016). Instead the capsule walls form irregular fragments. The spores and elaters tend to clump together and fall as a group. Higuchi observed that the time required from the beginning of dehiscence to the spore dispersal is about 22 minutes. If you are able to observe it, consider yourself lucky.

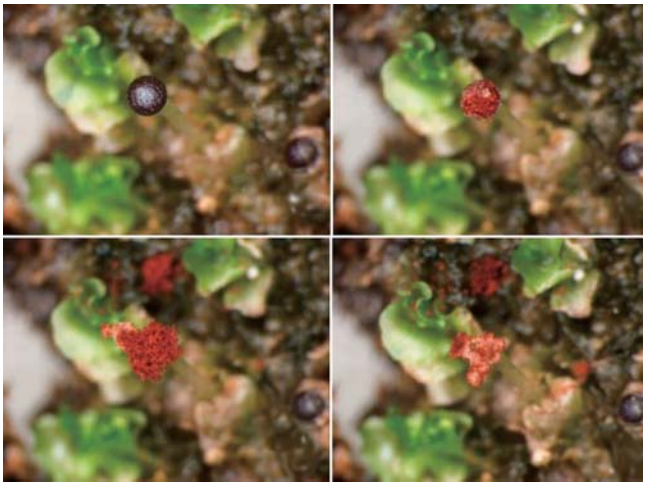

Figure 7. ***Fossombronia mylioides*** dehiscence and dispersal, shown here over 23 minutes. Photos by Masanabu Higuchi, National Museum, Japan, with permission.

Fossombronia peruviana

(syn. = *Fossombronia herzogii*; *Austrofossombronia peruviana*) (Crandall-Stotler *et al*. 1999)

Distribution

Fossombronia peruviana occurs in high elevation locations in the páramos and punas of the Andes (Crandall-Stotler & Gradstein 2017). Gradstein (2020) included it in the checklist for Ecuador; Müller (2016) reported it from Chile. Gradstein and Arbe (2003; Villagrán Moraga 2020) listed it for Bolivia and Villagrán Moraga (2020) for Venezuela and Peru.

Aquatic and Wet Habitats

Fossombronia peruviana occurs in consistently wet and aquatic habitats at high elevations in the Andean páramos and punas (Crandall-Stotler & Gradstein 2017), including high elevation mires in Latin America (Crandall-Stotler *et al*. 2019). Villagrán Moraga (2020) found it in the Chilean Altiplano wetlands. Gradstein and Pócs (2021) found the species to be characteristic of peaty soil along small streams and in mires of the páramo and puna, where it is sometimes submerged. Gradstein *et al*. (2016) reported it as usually submerged in pure, extensive mats in northern Chile. Although it is widespread, it is far from common.

Adaptations

Fossombronia peruviana is polymorphic, changing its form in response to its habitat (Crandall-Stotler *et al*. 2010). When submerged, it forms **mats**, but forms **turfs** rather than mats on soil. In the water they lack the purple rhizoids and are usually **sterile** (lacking reproductive organs).

Reproduction

Gradstein *et al*. (2016) found that most of the Chilean plants of ***Fossombronia peruviana*** were sterile. However, one plant was male with several groups of 10-12 naked antheridia on the midrib near the apex, where it is protected by strongly folded leaves. Capsules (Figure 8) are known, and the spores (Figure 9) resemble those of ***Fossombronia foveolata*** (Figure 10).

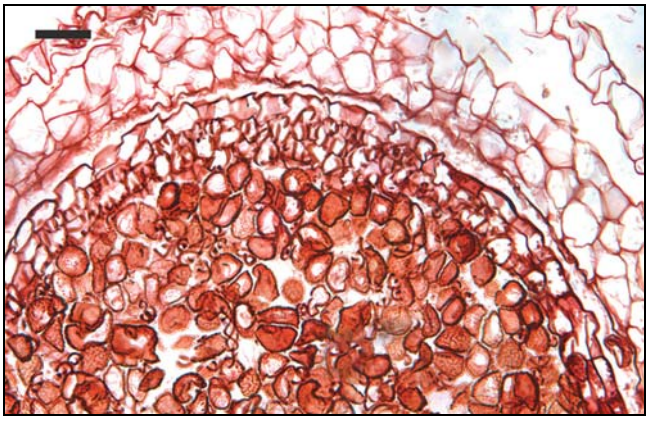

Figure 8. ***Fossombronia peruviana*** spore SEM. Photo by Barbara Crandall-Stotler, modified, with permission.

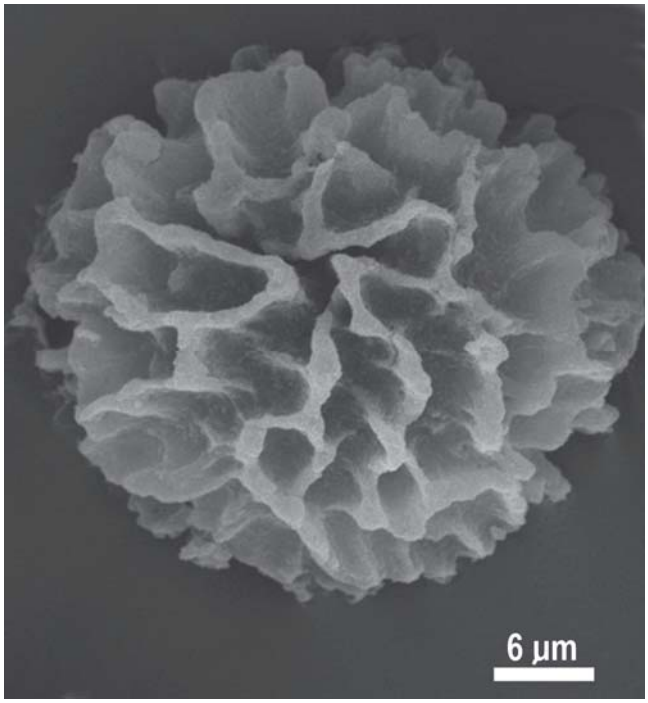

Figure 9. ***Fossombronia peruviana*** spore SEM. Photo by Barbara Crandall-Stotler, modified, with permission.

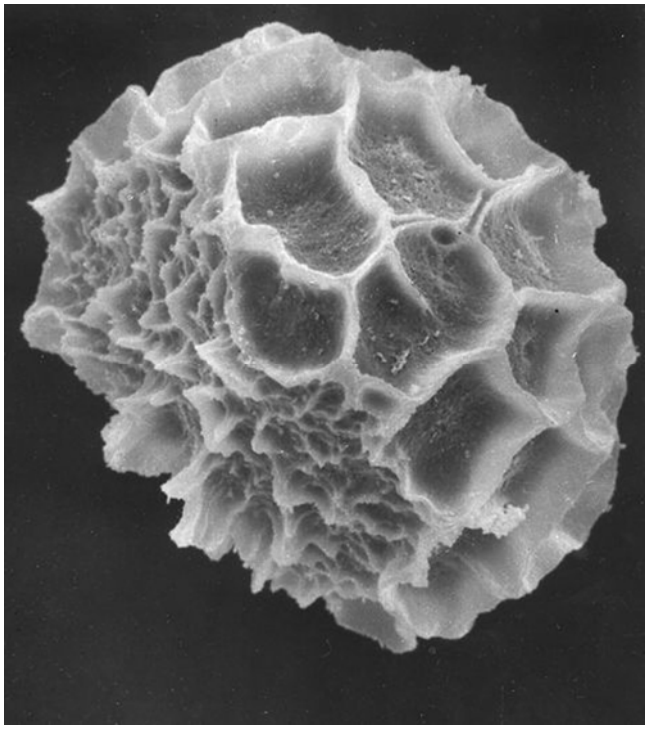

Figure 10. ***Fossombronia foveolata*** SEM of spore, showing its similarities to spores of ***Fossombronia peruviana***. Photo by Barbara Crandall-Stotler, with permission.

Fossombronia porphyrorhiza (Figure 11)

[syn. = *Fossombronia brasiliensis*, *Fossombronia salina*(?)]

With this species we suffer from confused taxonomy. My original introduction to it was through *Fossombronia salina* (Evans 1901), but that narrowly distributed species

was named as a synonym of ***F. brasiliensis*** (Evans 1914). Later, ***F. brasiliensis*** was considered a synonym of ***F. porphyrorhiza*** (Figure 11) (Schaefer-Verwimp 2010; TROPICOS 2021), but ***F. salina*** was considered more related to ***F. foveolata*** (Figure 12) by the Stotler's (Lars Söderström, pers. comm. March 2021). Hence I shall try to keep the published name intact as I discuss these three taxa under the umbrella of ***Fossombronia porphyrorhiza***.

Figure 11. ***Fossombronia porphyrorhiza***, Chapada dos Guimaraes, Brazil. Photo courtesy of Denilson Peralta.

Figure 12. ***Fossombronia foveolata***. Photo by Kochibi, through Creative Commons.

Distribution

Fossombronia porphyrorhiza (Figure 11) is both common and widespread in the Neotropics (Mexico, West Indies, Central America, South America) (Crandall-Stotler & Bray 2019). But it also extends into the southeastern United States. Other publications place it as far north as Rhode Island and Connecticut, USA.

Fossombronia porphyrorhiza (Figure 11) extends from coastal regions of Connecticut and Rhode Island, USA, southward to the southeastern US, Puerto Rico, Cuba, Haiti, Dominican Republic, Isle of Pines near Cuba, and Trinidad, through Mexico and Central America to Brazil (Schuster 1992). Schäfer-Verwimp (1999) reported this species (as *Fossombronia brasiliensis*) from Dominica, Gradstein and Hekking (1979) from Colombia, and Schäfer-Verwimp and Reiner-Drehwald (2009) from Guadeloupe, West Indies. Söderström *et al*. (2013) listed it from Paraguay.

Aquatic and Wet Habitats

Peralta and Yano (2008) considered ***Fossombronia porphyrorhiza*** (Figure 11) to be both **rupicolous** (living among, inhabiting, or growing on rocks) and **terricolous** (living on soil or ground). Pereira Correia *et al*. (2015) likewise considered it to be rupicolous. But those substrate classifications can place it in both terrestrial and aquatic habitats.

Schuster (1992) considers ***Fossombronia porphyrorhiza*** (as *F. brasiliensis*; Figure 11) to be one of wide ecological distribution It occurs on moist exposed soil along ditches, exposed sandy-clayey soil in broken ground of old fields. on moist rocks, and as is common among liverworts of such moist but not submersed habitats, it can occur on dead wood.

Guerke (1971) found ***Fossombronia porphyrorhiza*** (as *F. brasiliensis*; Figure 11) on moist ditch banks along a dirt road in Louisiana, USA, Pôrto *et al*. in a similar habitat in Brazil, and Schäfer-Verwimp (1999) in Dominica, West Indies. Hermann (1959) found it on the open clay bank of a pond in the eastern USA. Redfearn (1979) found it in the Ozarks of Arkansas, USA, on moist vertical sandstone along creek margins. Haupt (1942) found it on a moist humus bank along a road in Costa Rica. Yano and Bastos (2004) found it on a river bank in Brazil.

Sometimes ***Fossombronia porphyrorhiza*** (Figure 11) satisfies its moisture needs by living near waterfalls on shaded rocks (Schäfer-Verwimp 1999). Redfearn (1980) reported ***Fossombronia porphyrorhiza*** from calcareous cedar glades in Missouri, Tennessee, and Texas, USA.

Breil (1996) reported a greater variety of habitats in the Virginia Piedmont, USA. Here ***Fossombronia porphyrorhiza*** (Figure 11) occurred in swamps, along streams, and both single and as mats on moist, clayey, compact soil of old fields. It often accompanies other species of seasonal habitats such as ***Riccia*** (Figure 13) or ***Sphaerocarpos*** (Figure 14). Gradstein and Weber (1982) likewise reported it from terrestrial habitats in the Galapagos Islands, and Stotler *et al*. (1998) reported it from an exposed soil bank where it was intermixed with mowed grass in Panama.

Figure 13. ***Riccia sorocarpa*** on wet soil, a species that occurs in the same seasonal habitats as ***Fossombronia porphyrorhiza***. Photo by Hermann Schachner, through Creative Commons.

Figure 14. ***Sphaerocarpos donnellii***; ***Sphaerocarpos*** species of seasonal habitats often accompany ***Fossombronia porphyrorhiza*** there. Photo by Belinda Lo through Creative Commons.

Reproduction

Although the species has been confused with ***Fossombronia angulosa*** (Figure 15), ***F. porphyrorhiza*** (Figure 11) is **monoicous** (Breil 1996), contrasting with the dioicous condition of ***F. angulosa***. Despite this monoicous condition, Haupt (1942) reported that whereas it had numerous antheridia and archegonia on a roadside in Costa Rica, it had few sporophytes. On the other hand, Schäfer-Verwimp (1999) found it with mature sporophytes in Dominica, West Indies. Its brown to yellow-brown spores have a wide size range of 38-55 µm (Crandall-Stotler & Bray 2019).

Could this lack of sporophytes be due to the collecting season, or to the wrong photoperiod or other environmental conditions for fertilization? Chin *et al*. (1987) explored the influence of photoperiod, temperature, and inorganic nitrogen source on reproduction and growth in ***Fossombronia porphyrorhiza*** (Figure 11). They found that at 18ºC it behaved as a short-day plant, requiring 6-12 hours of night for development of archegonia and antheridia. At 10ºC it was a quantitative short-day plant, producing more female gametangia, whereas at 18ºC it produced more male gametangia. Nitrate was more favorable to the production of gametangia than was ammonium. This may explain incomplete development of the reproductive structures, but the scarcity of sporophytes in Haupt's (1942) collections remains without explanation.

Figure 15. ***Fossombronia angulosa***, a dioicous species often confused with ***Fossombronia porphyrorhiza***. Photo by Jan-Peter Frahm, with permission.

Fossombronia typically produces tubers for asexual reproduction (Paton 1974, Schuster 1992), with leafy propagules being rare (Pôrto *et al*. 1999). But in Brazil Pôrto and coworkers found that ***Fossombronia porphyrorhiza*** (Figure 11) produced numerous fleshy green propagules with small leaves on the dorsal sides of stems.

Fungal Interactions

There seem to be no records of fungal associations with ***Fossombronia porphyrorhiza*** (Figure 11).

Biochemistry

I found a surprising absence of biochemical information on this species.

Fossombronia pusilla (Figure 16-Figure 20)

Fossombronia pusilla (Figure 16-Figure 20) has been included in ***Fossombronia angulosa*** (Figure 15) by a number of authors (Stotler *et al*. 2005). I have maintained the two taxa separately here.

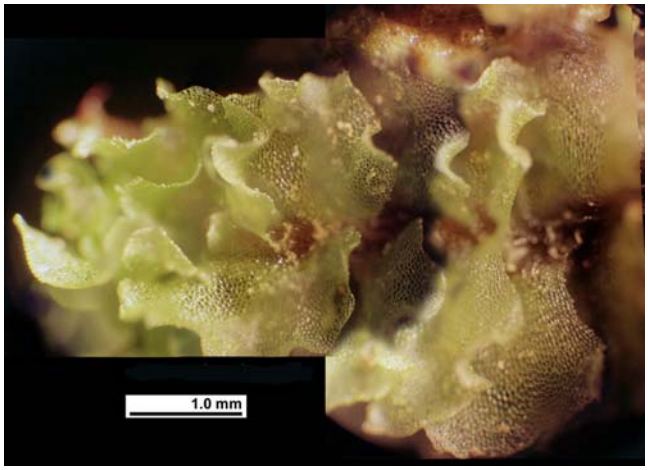

Figure 16. ***Fossombronia pusilla***. Photo by David H. Wagner, with permission.

Figure 17. ***Fossombronia pusilla* var. *pusilla*** whole plant. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 18. ***Fossombronia pusilla***. Photo by Štěpán Koval, with permission.

Figure 19. ***Fossombronia pusilla*** forming dense clumps. Photo by Andras Keszei, with permission.

Figure 20. ***Fossombronia pusilla* var. *pusilla***. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Distribution

Fossombronia pusilla (Figure 16-Figure 20) is a cosmopolitan species (Crandall-Stotler & Bray 2019). In North America it is restricted to the west coast (California and Oregon). But it also occurs in South America (Chile); Europe: Germany (Schultze-Motel 1968), England (Callaghan & Ashton 2008), Ireland, Denmark, Italy, France (Gökler 1998), Bulgaria, Croatia, Greece, Macedonia, Romania, Serbia, Slovenia, Turkey (Blockeel *et al*. 2002, Papp & Erzberger 2007), Belgium, Czech Republic, Portugal, Sicily, Spain, Switzerland (Sérgio 1974), Russia (Borovichev & Bakalin 2017), Maltese Islands (Gradstein 1972), Madeira (Sérgio 1974); Asia: Japan (Higuchi 2016), India (Singh & Singh 2007; Alam 2011 – at > 2100 m); and Africa: Algeria (Gökler 1998), Tunisia (Sérgio 1974). Frahm (2005) reported it from the Azores. It also occurs in Papua New Guinea (Krayesky *et al*. 2005).

Aquatic and Wet Habitats

Fossombronia pusilla (Figure 16-Figure 20) occupies a variety of habitats on open soil (Crandall-Stotler & Bray 2019). It frequently grows over moist soil (Çetin 1999),

remaining moist longer due to shade from nearby vegetation (Figure 21) (Crandall-Stotler & Bray 2019). Rilstone (1949) described it as frequent on bare, moist soil in Cornwall, UK. This is an apparent contrast with those colonies found by Osman *et al*. (2019) in Tunisia. They found that ***F. pusilla*** grew strictly on humus and litter there. Schultze-Motel (1968) found it on a loamy slope in Germany with ***Fissidens bryoides*** (Figure 22) and ***Brachythecium velutinum*** (Figure 23).

Figure 21. ***Fossombronia pusilla*** habitat in the shade of grass. Photo by Štěpán Koval, with permission.

Figure 22. ***Fissidens bryoides*** with capsules, a species that accompanies ***Fossombronia pusilla*** on loamy slopes in Germany. Photo by Dick Haaksma, with permission.

Figure 23. ***Brachythecium velutinum*** with capsules, a species that accompanies ***Fossombronia pusilla*** on loamy slopes in Germany. Photo by Michael Lüth, with permission.

Özenoğlu Kiremit *et al*. (2007) reported soil banks (Figure 24), stream banks, cave entrance, wet rocks, and stream beds as habitats for ***Fossombronia pusilla*** (Figure 16-Figure 20) in Antalya, Turkey. Casas *et al*. (1983) found it at the edges of a ravine in Spain.

Figure 24. ***Fossombronia pusilla*** habitat on a soil bank. Photo by Štěpán Koval, with permission.

In Italy, temporary ponds seem to be the best known habitat for ***Fossombronia pusilla*** (Figure 16Figure 17-Figure 20) (Puglisi *et al*. 2015 and others). In Sardinia, Italy, Cogoni *et al*. (2015) found it in temporary ponds, but it is critically endangered in Sardinia. In central Italy, Poponessi *et al*. (2016, 2018) found it associated with temporary ponds, where it was moderately abundant. It occurred on clayey-sandy waterlogged soil with ***Isoetes histrix*** (Figure 25) and in partially shaded pool systems along the borders of small ponds. It is, nevertheless, considered to be near threatened in Italy because of its scarcity in the country.

Figure 25. ***Isoetes histrix***, a species that accompanies ***Fossombronia pusilla*** on clayey-sandy, waterlogged soil in central Italy. Photo by Michel Garner, through Creative Commons.

In another study, Filippino (2018) reported ***Fossombronia pusilla*** (Figure 16-Figure 20) from Mediterranean temporary ponds, describing the ponds as small and shallow bodies of water isolated from permanent water bodies and undergoing periodic flooding and drought. ***Fossombronia pusilla*** is one of the bryophyte species found there, but it is considered critically endangered.

In Oregon, USA, it grows on moist soil in disturbed sites like road cuts, along trail cuts, but also in open natural habitats (Wagner 2006).

Fadel *et al*. (2020) found that in the Benslimane region of Morocco ***Fossombronia pusilla*** (Figure 16-Figure 20) was mostly present in wet crevices of limestone blocks, but also occurred in wetlands where the soil is humid (Figure 26) for a large part of the year and has a rich alluvium. In the Michlifen crater, they found it on shaded rock.

Gradstein (1972) similarly reported ***Fossombronia pusilla*** (Figure 16-Figure 20) from sheltered crevices in limestone rock of the Maltese Islands, where it was accompanied by ***Tortella inflexa*** (Figure 27). Papp and Erzberger (2007) found it on base-rich rock in Turkey. On the other hand, Hill *et al*. (2007) note that ***Fossombronia pusilla*** occurs on moderately acid soil that is constantly moist or damp, but not permanently waterlogged.

In addition to its wet habitats, it has been found on bark in Ohio, USA (Austin 1869).

Adaptations

Fossombronia pusilla (Figure 16-Figure 20) is a hygrophytic, solitary, creeping shuttle species (Filippino 2018). This life cycle strategy is suitable in particular for its temporary pond habitats. In Oregon, USA, it is a winter ephemeral that disappears in the summer (David H. Wagner, pers. comm. 18 April 2021).

In some cases it grows with other bryophytes (Figure 28) that may help it to hold moisture, but it is also possible that they can outcompete it.

Figure 26. ***Fossombronia pusilla* var. *pusilla*** on moist soil. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 27. ***Tortella inflexa***, a species that grows with ***Fossombronia pusilla*** in crevices of limestone rock on the Maltese Islands. Photo by Dick Haaksma, with permission.

Figure 28. ***Fossombronia pusilla* var. *pusilla*** mixed with other bryophytes. Photo by Malcolm Storey, <DiscoverLife.org>, with online permission.

It has purple rhizoids (Figure 29), but their adaptive value, if any, is unknown.

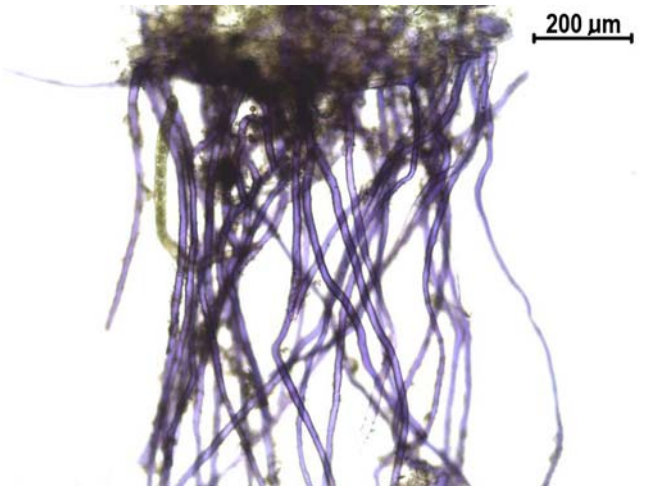

Figure 29. ***Fossombronia pusilla*** purple rhizoids. Photo by Hugues Tinguy, with permission.

Reproduction

Fossombronia pusilla (Figure 16-Figure 20) is **monoicous** (Crandall-Stotler & Bray 2019). The antheridia (Figure 30-Figure 32) and archegonia are intermixed. Wilson (1911) noted that the first mention of spermatozoids in plants was that of Schmiedel in 1747, for this species, accompanied by a description of their movement. The images I have found of the capsules show both immersed capsules and capsules with elongated setae. In both cases, one can find both brown (Figure 33-Figure 36) and black (Figure 37-Figure 43) capsules. Dehiscence is an irregular pattern of cell breakup (Figure 44-Figure 45). The spores (Figure 46-Figure 47) have a wide size range (38-58 µm) and are yellowish brown to dark brown (Crandall-Stotler & Bray 2019). The chromosome number is *n*=8 (Mehra 1938).

Figure 30. ***Fossombronia pusilla*** with small yellow antheridia showing. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 31. ***Fossombronia pusilla* var. *pusilla*** with antheridia. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

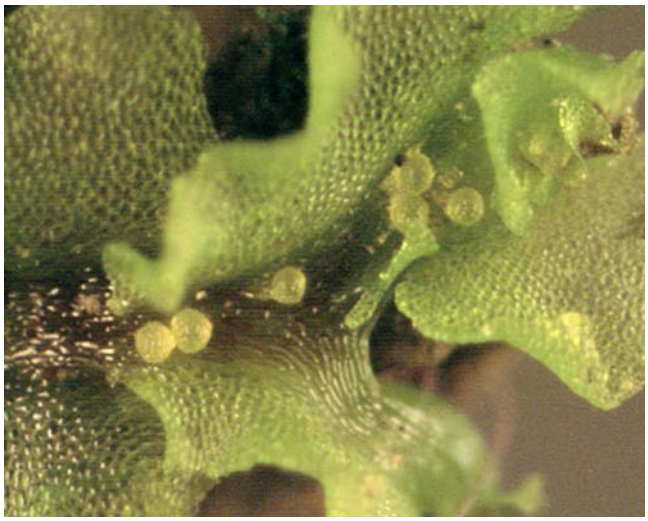

Figure 32. ***Fossombronia pusilla* var. *pusilla*** with antheridia. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 33. ***Fossombronia pusilla*** with capsules. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 34. ***Fossombronia pusilla* var. *pusilla*** with capsules. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 35. ***Fossombronia pusilla* var. *pusilla*** with capsules. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 36. ***Fossombronia pusilla* var. *pusilla*** with capsules. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 37. ***Fossombronia pusilla*** with capsules. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 38. ***Fossombronia pusilla*** with capsules. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 39. ***Fossombronia pusilla*** with capsules. Photo by David T. Holyoak, with permission.

Figure 40. ***Fossombronia pusilla*** with capsules, growing with ***Dicranella varia*** and ***Trichodon cylindrica***. Photo by Barry Stewart, with permission.

Figure 41. ***Fossombronia pusilla*** perianth and capsules. Photo by Štěpán Koval, with permission.

Figure 42. ***Fossombronia pusilla*** capsules with elongated seta. Photo by Štěpán Koval, with permission.

Figure 43. ***Fossombronia pusilla*** *var*. ***pusilla*** capsule. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 44. ***Fossombronia pusilla*** with dehiscing capsules. Photo by Heino Lepp, with online permission.

Figure 45. ***Fossombronia pusilla* var. *pusilla*** with dehisced capsules. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

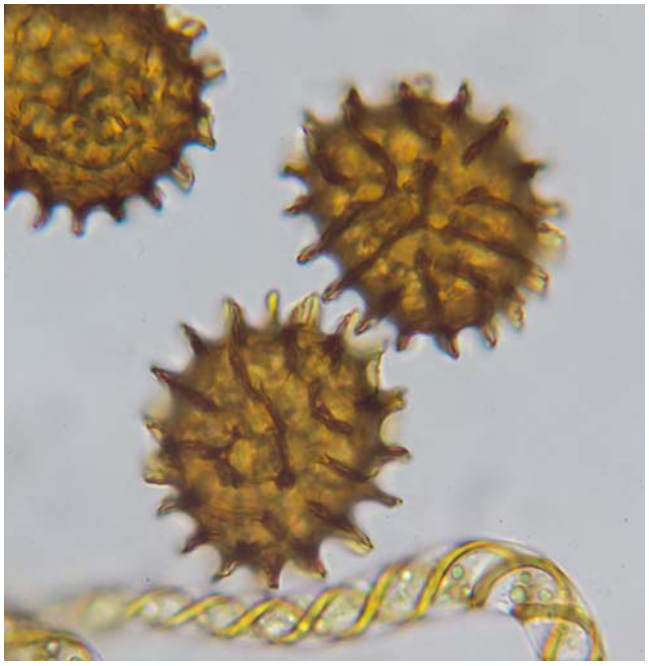

Figure 46. ***Fossombronia pusilla*** spores and elater. Photo by Štěpán Koval, with permission.

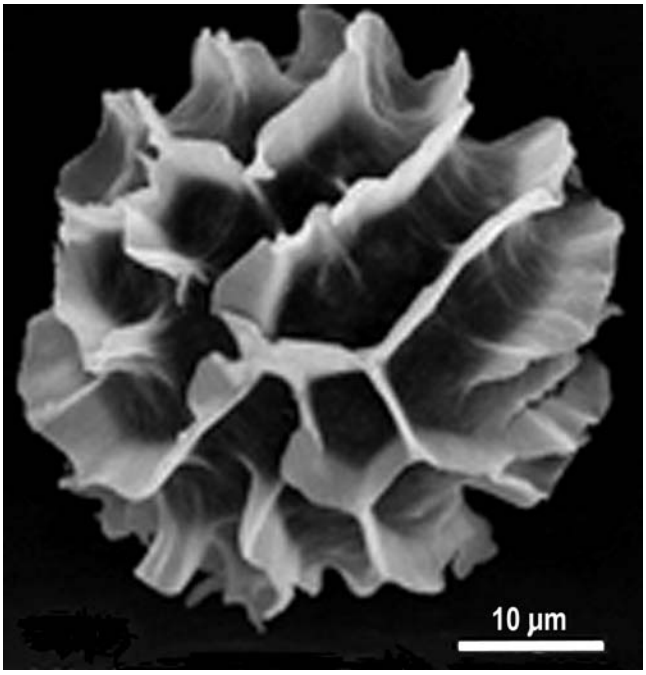

Figure 47. ***Fossombronia pusilla*** SEM of spore. Photo by Piyanart Suankeaw, through Creative Commons.

In California and Oregon, ***Fossombronia pusilla*** is **perennial** by means of fleshy, persistent tuberous stems (Figure 48) (Crandall-Stotler & Bray 2019). Otherwise, it appears that no specialized asexual reproductive structures exist.

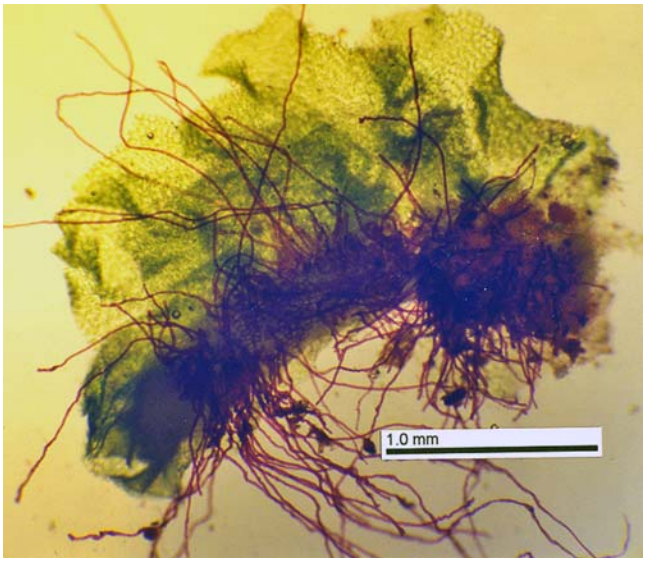

Figure 48. ***Fossombronia pusilla*** thallus showing purple rhizoids and perennial fleshy stem. Photo by David H. Wagner, with permission.

Ono (1973) reported the induction of callus formation in cultured ***Fossombronia pusilla***.

Fungal Interactions

Christie *et al*. (1985) used soluble carbohydrates of ten axenically cultured liverwort species to demonstrate that these are synthesized by the liverworts and not by fungal hyphae that are present with the field populations. They were unable to rule out the fungal production of hexitol by

fungal endophytes of the liverworts tested, but none was found in ***Fossombronia pusilla*** (Figure 16-Figure 20). Vesicular-arbuscular endophytic fungi were present in the field where ***F. pusilla*** was collected, but a symbiotic or parasitic relationship remained to be demonstrated.

Rimington *et al*. (2019) examined evolution and symbiotic networks in symbioses between **Mucoromycotina** fungi and liverworts. Network analysis permits us to visualize and quantify how network members interact, showing which plants interact with which fungi. The researchers found that these networks are dominated by specialists, not generalists. ***Fossombronia pusilla*** (Figure 16-Figure 20) was the only connector hub in all three networks and was the most important member of all three symbiotic networks. They suggested that many of the liverwort associations might be facultative.

Biochemistry

I have found no descriptions of the oil bodies, but Figure 49 has what appear to be spherical oil bodies.

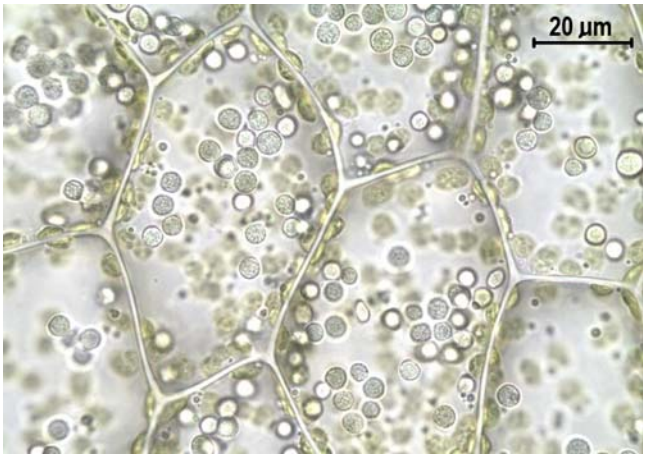

Figure 49. ***Fossombronia pusilla*** cells with what appear to be oil bodies. Photo by Hugues Tinguy, with permission.

Sauerwein *et al*. (1992) noted the difficulty in investigating secondary compounds in small liverworts such as ***Fossombronia pusilla*** (Figure 16-Figure 20). It is difficult to collect sufficient material, so they cultured it in the lab. They found that it grew well on Gamborg B5 solid medium, but the liverworts died in liquid media. When the researchers added vitamin B_{12} to the liquid media, growth was stimulated and the liverwort produced terpenes. These included diterpenedialdehydes perrottetianal A, B and 8-hydroxyperrottetianal A. They also reported santonin for the first time in a bryophyte. Grammes *et al*. (1994) identified three new terpenes, again using cultured gametophytes.

When Sauerwein and Becker (1990) cultured ***Fossombronia pusilla*** (Figure 16-Figure 20) from spores, they produced the same secondary substances as those measured in collected material. They identified perrottetianal A and B and α-(-)-santonin. They also identified seven terpenes and found that terpenes isolated from a petrol ether extract exhibited antibacterial activity.

Spiteller *et al*. (2002) found that whereas both the bacterium *Streptomyces* sp. and liverwort ***Fossombronia pusilla*** (Figure 16-Figure 20) produced geosmin, they used different pathways. Dickschat *et al*. (2005) also found that geosmin was manufactured by the Myxobacteria *Myxococcus xanthus* and *Stigmatella aurantiaca*. These likewise followed a different pathway from that used by ***Fossombronia pusilla***.

Fossombronia renateae

Distribution

Fossombronia renateae has a narrow distribution in southern Africa, where there are only two known locations (Perold 1999).

Aquatic and Wet Habitats

At Lone Creek Falls in southern Africa, ***Fossombronia renateae*** grows between rocks on soil that is kept moist by spray from the waterfalls (Perold 1999). It is accompanied there by ***Bryum alpinum*** (Figure 50) and ***Entosthodon limbatus*** (as *Funaria limbata*).

Figure 50. ***Bryum alpinum***, a species that accompanies ***Fossombronia renateae*** in the spray of waterfalls in southern Africa. Photo by David T. Holyoak, with permission.

Adaptations

Fossombronia renateae forms creeping, dense, crowded stands or is intimately to loosely mixed with mosses (Perold 1999). Both habits could help to conserve moisture during dry periods and permit slow drying that is more likely to prepare the liverwort for surviving the dry conditions.

Reproduction

Fossombronia renateae is **dioicous** (Perold 1999). Nevertheless, both sexes were seen and Perold was able to find a few dehisced capsules retained from the previous season.

Biochemistry

Oil bodies in ***Fossombronia renateae*** are few (4-6 per cell, 5 µm diameter) (Perold 1999).

Fossombronia texana (Figure 51)

(syn. = *Fossombronia mexicana*)

Distribution

Fossombronia texana (Figure 51) is known from Texas, Oklahoma, Missouri, and Arkansas (Timme & Redfearn 1997; Atwood & Brinda 2019), but its distribution is poorly known, causing its endangered status to be "no status rank" (NatureServe Explorer 2021). In addition to these USA sites, it occurs in Mexico, Cuba, and Bermuda (Crandall-Stotler & Bray 2019).

Aquatic and Wet Habitats

Atwood and Brinda (2019) reported ***Fossombronia texana*** (Figure 51) from a bridge over a creek. It also occurs on shaded dolomite ledges along the creek and generally is a calciphile on limestone near streams.

Fossombronia texana (Figure 51) forms loose to dense mats over calcareous boulders (limestone, marl, or travertine) in or next to rivers, where they are frequently inundated (Crandall-Stotler & Gradstein 2017). Crandall-Stotler and Bray (2019) consider it to be restricted to calcareous substrata. On loose marl it can form dense carpets. Its sites are often in shaded riverine habitats. Others are on drip walls of the Interior Highlands at low to moderate elevations.

Among north temperate ***Fossombronia*** species, only ***Fossombronia texana*** (Figure 51) forms mats directly on rocks along waterways, which at times become submerged (Bray 2001).

Figure 51. ***Fossombronia texana***. Photo by Bob O'Kennon, through Creative Commons.

Adaptations

The **mat** life form (Crandall-Stotler & Gradstein 2017) of ***Fossombronia texana*** (Figure 51) most likely helps it to conserve water in its streamside habitat where moisture can become less available in the summer. It may also help to reduce drag during times when it becomes inundated.

Reproduction

Fossombronia texana (Figure 51) is **monoicous** (Atwood & Brinda 2019) with antheridia scattered along with archegonia (Crandall-Stotler & Bray 2019). Therefore, production of capsules (Figure 52) is not limited by distance between the sexes. The spores are large (42-57 µm). It lacks tubers at the stem apices (Atwood & Brinda 2019), an asexual reproductive means known in some other species of ***Fossombronia***.

Figure 52. ***Fossombronia texana*** with capsules. Photo by Bob O'Kennon, through Creative Commons.

Fossombronia wondraczekii (Figure 53-Figure 54)

Distribution

Fossombronia wondraczekii (Figure 53-Figure 54) is widely circumboreal (Aleffi & Esposito 2005; Poponessi *et al*. 2015), scattered in North America (Crandall-Stotler & Bray 2019) and elsewhere, but widespread (Poponessi *et al*. 2015). It extends from eastern Greenland, south to the Appalachians, and west to Ohio and Indiana in North America. It is also present in Iceland, Europe, northern Africa, Australia, and New Zealand. Poponessi *et al*. (2015) added Cyprus, Mauritius, Réunion, Siberia, and Sri Lanka. Ştefănuţ and Goia (2012) listed it for Romania. It is usually not common, and in the Western Carpathians of Poland it is in the protected and threatened category (Stebel & Vončina 2017).

Figure 53. ***Fossombronia wondraczekii***, a species that occurs in both hemispheres. Photo by Hugues Tinguy, with permission.

Figure 54. ***Fossombronia wondraczekii*** with capsule before seta elongation. Photo by Dick Haaksma, with permission.

Aquatic and Wet Habitats

Aleffi and Esposito (2005) characterized ***Fossombronia wondraczekii*** as mesohygrophilous, photo-sciaphilous, and terricolous. ***Fossombronia wondraczekii*** (Figure 53-Figure 54) is mostly restricted to moist soil habitats in low to moderate elevations (Crandall-Stotler & Bray 2019). These are often disturbed habitats. It typically grows intermixed with other bryophytes or forms small rosettes on moist soil where it is shaded by nearby vegetation. Ştefănuţ and Maria (2018) found it with other bryophytes near a slow-flowing stream and Stebel (2015) found it on wet soil near a ditch, both in Poland. Sotiaux *et al*. (2007) reported it from ground along a streamlet in Corsica, France, growing with ***Bryum alpinum*** (Figure 50).

In the Nilgiri Hills of India, ***Fossombronia wondraczekii*** (Figure 53-Figure 54) grows in dense patches on moist and exposed rocks and soil-covered rocks along with other terrestrial mosses (Figure 55) (Alam 2011). ***Fossombronia wondraczekii*** occurs on calcareous stony soil (Figure 56) in the Balearic Islands (Sáez *et al*. 2006).

Figure 55. ***Fossombronia wondraczekii*** growing with mosses. Photo by Michael Lüth, with permission.

Figure 56. ***Fossombronia wondraczekii*** growing on stony soil. Photo by Tom Neily, through Creative Commons.

Like a number of other members of ***Fossombronia***, ***Fossombronia wondraczekii*** (Figure 53-Figure 54) occurs along the edge of ponds, especially in Italy, giving it a spotty and local distribution (Poponessi *et al*. 2016).

It is not unusual to find members of ***Fossombronia*** in temporary habitats. In the Western Carpathians, ***Fossombronia wondraczekii*** (Figure 53-Figure 54) occurs with other rare species in fallow fields (Armata 2005). Klama and Górski (2018) similarly found it in wet fields, stubble fields, and fallow fields (Figure 57) in Poland, as well as moderately used forest ground roads. Sotherton and Self (2000) reported it from lowland farmland in the UK. These records suggest that it benefits, for a short period of time at least, from the lack of competition in disturbed habitats. This suggestion is further supported by its ability to colonize burned soil in moist depressions in southern Italy (Aleffi & Esposito 2005). Its rapid maturation and high level of spore dispersal aid in its colonization of such disturbed areas.

Figure 57. ***Fossombronia wondraczekii*** on dry mud, typical of seasonally flooded habitats. Photo by Heino Lepp, Australian National Botanic Gardens, with online permission.

Adaptations

The habit of ***Fossombronia wondraczekii*** to grow among other bryophytes (Figure 58) (Crandall-Stotler & Bray 2019) most likely keeps this moisture-loving species moist longer, reducing both frequency and duration of desiccation.

Figure 58. ***Fossombronia wondraczekii*** habitat on soil, growing with mosses that may help to conserve moisture. Photo by Hugues Tinguy, with permission.

The dense patches are yellowish-green to green (Figure 59). In patches no bigger than a dime it grows "like a bunch of unkempt, light green, Victorian ruffles (Figure 60) with distinctive bright violet rhizoids growing from the undersides of horizontal stems" (Trigoboff 2012). Because of its small areas of growth, Hill *et al*. (2007) distinguish it as a "patch" rather than a mat.

Figure 59. ***Fossombronia wondraczekii***, showing yellowish-green color and small patch. Photo by Bernd Heynold, through Creative Commons.

Figure 60. ***Fossombronia wondrazeckii*** habitat on calcareous soil, showing patchy growth pattern. Photo by Bernd Heynold, through Creative Commons.

Reproduction

Fossombronia wondraczekii (Figure 53-Figure 54) is **monoicous** with its antheridia (Figure 61) scattered among and intermixed with the archegonia (Alam 2011; Crandall-Stotler & Bray 2019). It apparently lacks asexual reproductive structures and regenerates by spores (Figure 62-Figure 68) (Aleffi & Esposito 2005). One of its advantages toward arriving in disturbed habitats and in spreading somewhat rapidly is its high dispersal ability (Sotiaux *et al*. 2006). Brown and Lemmon (1993) described the development of the spores in detail.

Figure 61. ***Fossombronia wondraczekii*** with a few visible yellow antheridia. Photo by Štěpán Koval, with permission.

Figure 62. ***Fossombronia wondraczekii*** patch with capsules. Photo by Michael Lüth, with permission.

Figure 63. ***Fossombronia wondraczekii*** with nearly mature capsules. Photo by Michael Lüth, with permission.

Figure 64. ***Fossombronia wondraczekii*** with capsules in multiple stages of maturity and dehiscence. Photo by Bob Klips, through Creative Commons.

Figure 65. ***Fossombronia wondraczekii*** capsules with collapsed setae, showing how numerous they can be. Photo by Shaun Pogacnik, through Creative Commons.

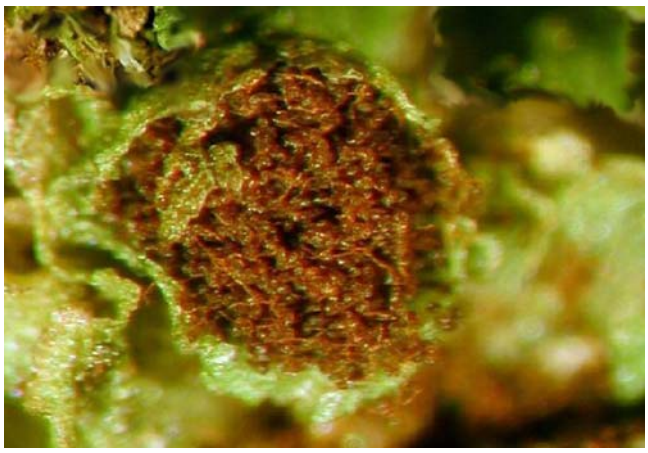

Figure 66. ***Fossombronia wondraczekii*** open sporangium exposing spores and elaters. Photo by Michael Lüth, with permission.

Figure 67. ***Fossombronia wondraczekii*** spores and elaters. Photo by Shaun Pogacnik, through Creative Commons.

Figure 68. ***Fossombronia wondraczekii*** spore and elater. Photo by Bob Klips, through Creative Commons.

Trigoboff (2012) reported ripe capsules on 5 December in Central New York, UA. There were shed spores, and many plants were bleached, with a "ghostly" appearance. On 10 January, he considered the plants to be "legally dead." Despite this unseemly condition, there were bits of green tissue, some unripe capsules, and a few unopened capsules with mature spores. The usual time for capsule (Figure 62-Figure 65) production of ***Fossombronia wondraczekii*** in central New York is 15 September to 15 October, with peak spore discharge 25 September to 5 October (Schuster 1949).

Srivastava and Sharma (1995) described the development and morphology of the ***Fossombronia wondraczekii*** sporelings. There were three types of development, with the most common one being filamentous, septate germ-tubes.

Biochemistry

Feld *et al*. (2005) identified five new sacculatane diterpenoids in ***Fossombronia wondraczekii*** (Figure 53-Figure 54).

Fossombronia wrightii (Figure 69)

Distribution

Fossombronia wrightii (Figure 69) occurs in the Carribean (ITIS 2021).

Aquatic and Wet Habitats

Like ***Fossombronia texana*** (Figure 51), ***Fossombronia wrightii*** (Figure 69) forms mats over calcareous boulders in or next to rivers, where they are frequently inundated (Crandall-Stotler & Gradstein 2017). Freire and Stotler (2007) reported it to be riparian on rocks in Cuba.

Adaptations

As do most of the wet habitat ***Fossombronia*** species included in this chapter, ***F. wrightii*** (Figure 69) forms **mats**, in this case on calcareous boulders. Once again, we can assume that it helps to conserve water during dry periods, but it would also reduce drag during periods of high water when it becomes inundated. At such times, the flow of rivers is likely to be rapid.

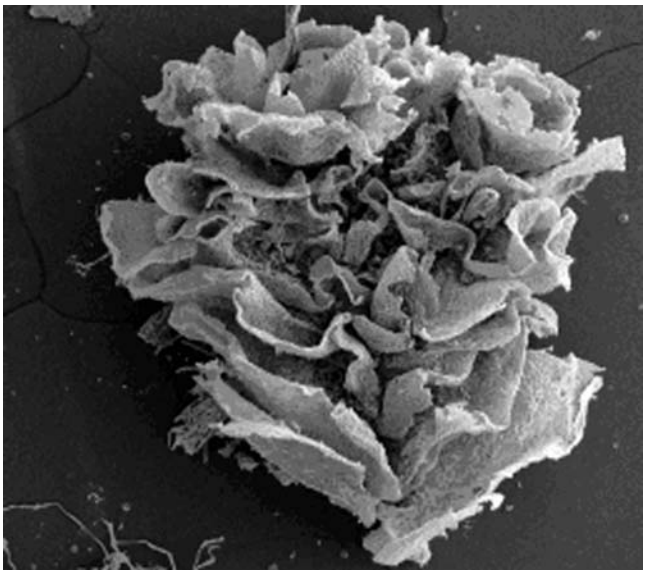

Figure 69. ***Fossombronia wrightii*** SEM, a riparian Carribean species. Photo courtesy of Virginia Freire.

Reproduction

Fossombronia wrightii (Figure 69) has known sporophytes (Figure 70) and produces spores without tubercles (Figure 71), but it is not known if it is **dioicous** or **monoicous** because no antheridia have been found (Virginia Freire, pers. comm. 24 April 2021). It forms fleshy tubers (Figure 72) that undoubtedly help it to spread where it has become established. They could also serve as dispersal agents at times of inundation, having a greater likelihood of survival than the leafy plant.

Figure 70. SEM of ***Fossombronia wrightii*** with sporophyte and tuber. Photo courtesy of Virginia Freire.

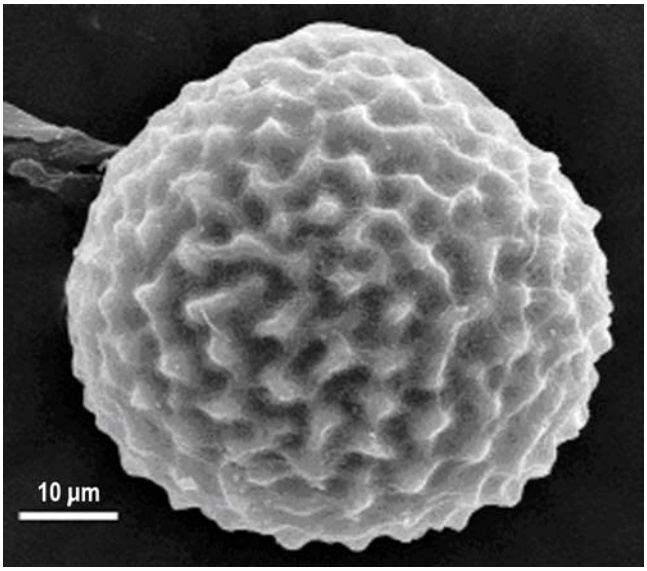

Figure 71. ***Fossombronia wrightii*** spore SEM. Photo courtesy of Virginia Freire.

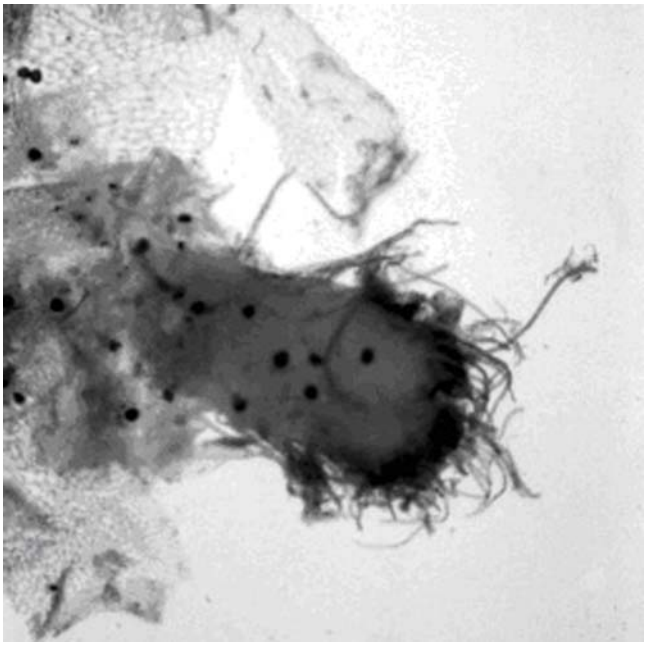

Figure 72. SEM of ***Fossombronia wrightii*** tuber. Photo courtesy of Virginia Freire.

Summary

Some of the species in this subchapter are at least periodically submerged (*e.g.* ***Fossombronia mylioides***), but most of the species can occur in wet habitats that can dry out. The adaptations seem to be physiological, permitting it to survive both submersion and drying out. For example, ***Fossombronia pusilla*** grows in temporary ponds. Some grow with other bryophytes, thus benefitting from reduced water loss; others benefit from forming large, closely overlapping mats. Some of the aquatic species are confined to high elevations in the Andes.

Acknowledgments

Thank you to Lars Söderström for his continued help in sorting out nomenclature changes.

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CHAPTER 1-15
AQUATIC AND WET MARCHANTIOPHYTA, PALLAVICINIALES

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CHAPTER 1-15
AQUATIC AND WET MARCHANTIOPHYTA, PALLAVICINIALES

Figure 1. Wetland habitat with ***Betula pubescens***, a habitat suitable for ***Pallavicinia lyellii***. Photo by Ingo2802, through Creative Commons.

Nomenclature for this subchapter is based primarily on Söderström *et al*. (2016). In addition, Lars Söderström provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. These unverifiable taxa have been included in the species.

SUBCLASS PELLIIDAE

Pallaviciniales: Hymenophytaceae

Hymenophyton flabellatum (Figure 2, Figure 4-Figure 6)

(syn. = *Symphyogyna flabellata*)

Hymenophyton flabellatum (Figure 2, Figure 4-Figure 6) has been treated variously by different researchers. Pfeiffer (2000) reviewed these differences in perspective and suggested that at least two distinct taxa of ***Hymenophyton*** exist in New Zealand and Tasmania. Pfeiffer *et al*. (2004) used molecular analysis to determine differences in populations and recognized four taxa in ***Hymenophyton***. Because of the differences in treatment through time, I have included all literature related to ***Hymenophyton flabellatum***, even if it has since been placed in a different species.

Figure 2. ***Hymenophyton flabellatum***, a species from Australia, New Zealand, and Tasmania. Photo by Ken Harris, EntSocVic, through Creative Commons.

Distribution

Hymenophyton flabellatum *s.l.* (Figure 2, Figure 4-Figure 6) has a Palaeoaustral distribution pattern, with populations known from Tasmania, New Zealand, and Australia. Pfeiffer (2000) recognized ***H. flabellatum*** and ***H. leptopodum*** (Figure 3) in New Zealand and ***H. mulleri*** collected from a river (Evans 1925) in Australia. ***Hymenophyton mulleri*** (*H. muelleri*) is not recognized by Söderström *et al.* (2016); TROPICOS (2021) includes it in ***Hymenophyton flabellatum***. The Tasmanian taxon might also be recognized as ***H. leptopodum***. The segregate ***Hymenophyton pedicellatum*** is known from South America (Pfeiffer *et al*. 2004). Segregates of ***H. flabellatum*** from New Caledonia, Fiji Islands, Colombia, and Chile (Evans 1925) have been variously treated as a member of ***H. flabellatum*** and as separate taxa (Pfeiffer 2000).

Figure 3. ***Hymenophyton leptopodum***, a segregate recognized in New Zealand. Photo by TePapa, through Creative Commons.

Figure 4. ***Hymenophyton flabellatum***. Photo by Niels Klazenga, with permission.

Figure 5. ***Hymenophyton flabellatum*** wet, growing on soil. Photo by Jan-Peter Frahm, with permission.

Figure 6. ***Hymenophyton flabellatum*** showing stipe and leafy plant. Photo by Jan-Peter Frahm, with permission.

Aquatic and Wet Habitats

Hymenophyton flabellatum (Figure 2, Figure 4-Figure 6) occurs in Cool Temperate Victorian Rainforest streams (Downes *et al*. 2003; Carrigan 2008) found it in an unregulated creek in Australia. In New Zealand, Frogley and Glenny (2020) found it in a small creek bed. Braggins (1987) found it in a Tasmanian stream on clay and humus. Suren (1996) considered it to be obligately or facultatively aquatic in streams.

But ***Hymenophyton flabellatum*** (Figure 2, Figure 4-Figure 6) is not restricted to streams. In their biochemical study, Asakawa *et al*. (2001) noted that ***Hymenophyton flabellatum*** occurred on shaded wet soil (Figure 7), humus, and old logs in forests, usually in shade, and on banks beside streams and waterfalls (Figure 8). In ***Eucalyptus regnans*** forest (Figure 9) at Wallaby Creek, Victoria, Australia, ***Hymenophyton flabellatum*** occurred on very wet, sodden, white-rot logs sheltered on south sides of logs (Ashton 1986). Gibson (2006) reported it to be common in wet forests in Australia.

Figure 7. ***Hymenophyton flabellatum*** growing on soil. Photo by Jan-Peter Frahm, with permission.

Figure 8. ***Hymenophyton flabellatum*** on a vertical substrate. Such growth forms of shelves can occur in the splash of waterfalls. Photo from Manaaki Whenua – Landcare Research, with online permission.

Figure 9. ***Eucalyptus regnans*** forest in Australia, where one can find ***Hymenophyton flabellatum*** on very wet logs. Photo by Patche99z, through Creative Commons.

Adaptations

It is interesting that ***Hymenophyton flabellatum*** (Figure 2, Figure 4-Figure 6) has water-conducting elements (Figure 10-Figure 11) in its gametophytes (Burr *et al*. 1974; Campbell *et al*. 1975). These are axially elongated cells with no living contents and numerous perforations in their walls, making them unique among land plants. Hébant (1978) identified endoplasmic-reticulum cisternae associated with the differentiating pores and compared them to developing sieve pores in phloem of tracheophytes.

Figure 10. ***Hymenophyton flabellatum*** showing ribs made of water-conducting elements. Photo by Arthur Chapman, through Creative Commons.

Figure 11. ***Hymenophyton flabellatum*** wet plants showing the prominent rib. Photo by Devaprayaga, through Creative Commons.

The plants of ***Hymenophyton flabellatum*** (Figure 2, Figure 4-Figure 6Figure 14) are olive-green with fan-shaped fronds (Figure 12), crowded chloroplasts, small cells, and thick cell walls. The aquatic and wet habitat affiliations of this species puzzle me because they would seem to be adapted to drier habitats with their small cells, thick walls, and conduction system. Nevertheless, the fan-

shaped fronds would most likely lose water easily (Figure 12-Figure 13), and they seem to handle both wet (Figure 11-Figure 12) and dry conditions (Figure 13).

Figure 12. ***Hymenophyton flabellatum*** showing signs of drying. Photo by Paul George, through Creative Commons.

Figure 13. ***Hymenophyton flabellatum*** dry plants. Photo by Robert Pergl, through Creative Commons.

Reproduction

The genus ***Hymenophyton*** (Figure 2, Figure 4-Figure 6Figure 14), as far as known, is **dioicous** (Figure 14) (Campbell *et al*. 1975; Crandall-Stotler *et al*. 2005). This image from Karen Renzaglia shows that at least sporophytes are known (Figure 15).

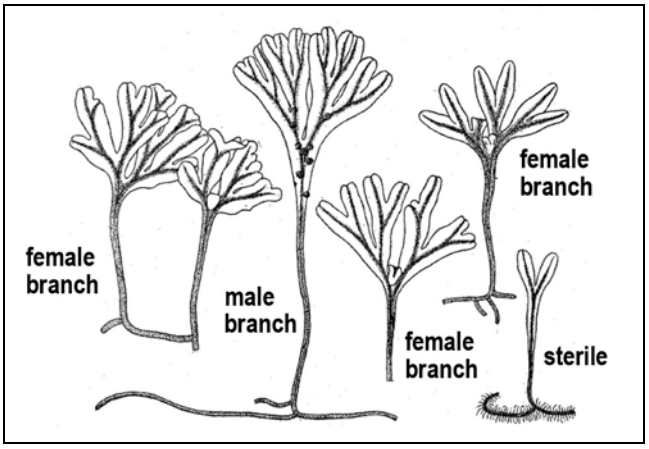

Figure 14. ***Hymenophyton flabellatum*** male, female, and sterile branches. Image modified from Evans 1925.

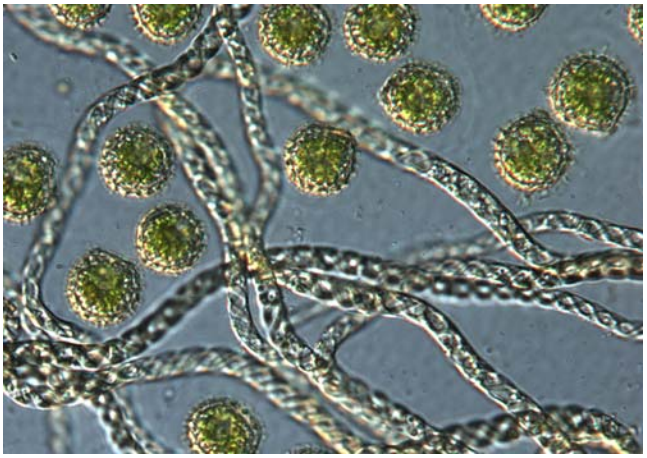

Figure 15. ***Hymenophyton*** spores and elaters. Photo by Karen Renzaglia, with permission.

Fungal Interactions

Johnson (1977) reported mycorrhizal infections of rhizoids in ***Hymenophyton flabellatum*** (Figure 2, Figure 4-Figure 6). Ligrone *et al*. (2007) identified **Glomeromycotean** endophytes in New Zealand specimens. They concluded that **Glomeromycota** (Figure 16) lineages that form arbuscular mycorrhizae in a wide range of liverwort taxa have been derived by "host-shifting" from tracheophyte taxa (Figure 17) to liverworts.

Figure 16. ***Glomus coremioides*** (**Glomeromycota**); some members of this phylum form arbuscular mycorrhizae in liverworts such as ***Hymenophyton flabellatum***. Photo by Damon Tighe, through Creative Commons.

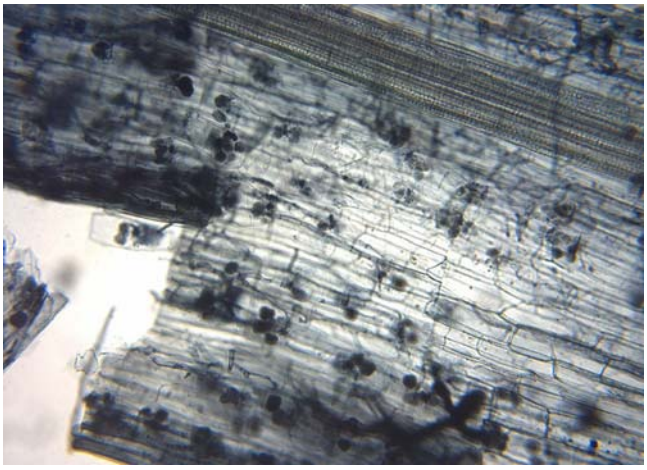

Figure 17. **Glomeromycota** arbuscular mycorrhiza in root of a tracheophyte. Photo by M. Sturmel, through public domain.

Figure 18. ***Eurema hecabe*** on ***Lespedeza bicolor***, a butterfly whose larvae are repelled by a compound that is present in ***Hymenophyton flabellatum***. Photo by Alpsdake, through Creative Commons.

Biochemistry

Campbell *et al*. (1975) used chemical constituents to distinguish between ***Hymenophyton flabellatum*** (Figure 2, Figure 4-Figure 6) and ***H. leptopodum*** (Figure 3), concluding that they were both valid species. One of these differences is the presence of kaempferols in the latter but not in ***H. flabellatum***. Both species have flavone C-glycosides. Markham *et al*. (1976) further supported this conclusion based on flavonoid constituents.

Classen *et al*. (2019) reported arabinogalactan-proteins, compounds found in the extracellular matrix of ***Hymenophyton flabellatum*** (Figure 2, Figure 4-Figure 6) plants. These proteins have a small protein moiety that is usually rich in **hydroxyproline** (found in plant cell walls; serve as attachment points for glycan chains which are added as post-translational modifications). ***Hydroxyproline*** seems to have a major evolutionary role in liverworts, by regulating leaf and branch development (Basile 1990).

Toyota *et al*. (2009) identified 1-(2, 4, 6-trimethoxy-phenyl)-but-2 (E)-en-1-one, a known compound, as the cause of the hot-tasting, strongly pungent substance released when fragments of ***Hymenophyton flabellatum*** (Figure 2, Figure 4-Figure 6) are chewed. It is possible that this compound serves to discourage herbivores, but do the likely herbivores – arthropods – taste things the same way we do? In fact, Numata *et al*. (1984) demonstrated that its compound 1-(2, 4, 6-trimethoxy-phenyl)-but-2 (E)-en-1-one has antifeedant activity against the larvae of the yellow butterfly ***Eurema hecabe mandarina*** (Figure 18), although for that test it was extracted from *Arachniodes standishii* (Figure 19), a fern (see also Asakawa *et al*. 2001; Asakawa 2015).

Asakawa (2004) considered ***Hymenophyton flabellatum*** (Figure 2, Figure 4-Figure 6) to be one of the most chemically isolated liverworts so far examined. It was the only liverwort known to contain phenyl butanone. phenyl butanone in some fruits is used in perfumery and cosmetics (PubChem 2021).

It is not surprising that a liverwort so well endowed with noxious chemicals should offer protection against infections. Earl (2010) reported that ***Hymenophyton flabellatum*** (Figure 2, Figure 4-Figure 6) is commonly used medicinally.

Figure 19. *Arachniodes standishii*, a fern that produces the same antifeedant 1-(2, 4, 6-trimethoxy-phenyl)-but-2 (E)-en-1-one as that in ***Hymenophyton flabellatum***. Photo by Ecelan, through Creative Commons.

Pallaviciniales: Pallaviciniaceae

Jensenia decipiens

(syn. = *Pallavicinia zollingeri*)

Schaumann *et al*. (2004) investigated DNA relationships in the genus ***Jensenia*** (Figure 20). They found a low level of variation both within and between taxa in the genus. On the other hand, the molecular data do support the separation of the genus ***Jensenia*** (Figure 20) from ***Pallavicinia*** (Figure 21-Figure 27). Forrest *et al*. (2005) further supported this separation and using cladistic methods concluded that ***Jensenia*** is monophyletic, thus a natural group. They considered its distribution to be the product of dispersal, not vicarious similarities.

Distribution

Jensenia decipiens is tropical, known from Sri Lanka (Farmer 1894; Long & Rubasinghe 2014), the Philippines, Malaysia (Grolle & Piippo 1986; Piippo & Tan 1992), Indonesia (Sumatra, Java, and Celebes) (Grolle & Piippo 1986; Piippo & Tan 1992; Gradstein *et al*. 2005), and

Papua New Guinea (Grolle & Piippo 1986; Enroth 1990; Piippo & Tan 1992), and more recently it has been reported from Malesia (Arianti & Gradstein 2007) and Japan (Schaumann *et al*. 2005).

Figure 20. ***Jensenia connivens***; ***Jensenia decipiens*** occurs on muddy stream banks. Photo by Bill Malcolm, with permission.

Aquatic and Wet Habitats

Jensenia decipiens in Ceylon occurs on muddy streambanks at 6200' (Farmer 1894). At lower elevations it outcompetes other plants with its profuse growth.

Ruttner (1955) reported ***Jensenia decipiens*** from the wall of a bay in the tropics. Piippo and Tan (1992) reported it from wet crevices of a trail in very deep shade in the Philippines.

Adaptations

Jensenia decipiens grows erect from a creeping rhizome. Its branches are thus tree-like (van der Gronde 1980). This would be a disadvantage in locations that dry, but in a moist environment it could provide greater access to CO_2 and possibly to light for photosynthesis.

Reproduction

Jensenia decipiens and all members of the genus thus far described are **dioicous** (van der Gronde 1980). Farmer (1894) described details of its development, including the gametophyte, archegonia, sporophyte, and spores.

Moore (1906) questioned the account of sporogenesis provided by Farmer (1894) and suggested that it was not unique, as suggested by the Farmer account, but was instead consistent with that known for other plants, including other liverworts.

The branching pattern of ***Jensenia decipiens*** is rather unusual. It appears to be dichotomous, but on closer inspection, the terminal bud occurs between the paired branches, and remains and grows, as in **monopodial** branching (having a central axis from which other branches arise, as in a spruce tree).

Pallavicinia

Pallavicinia can occur as a **rheophyte** (plant that lives in fast-moving water currents in environment where few other organisms can survive) in the wet tropics of SE Asia (Akiyama 1992).

Pallavicinia indica

Distribution

Pallavicinia indica is known from India, Java, Nepal, Sri Lanka, Sumatra, and Tahiti (Campbell 1908; Herzog 1942; Pradhan & Joshi 2009; Long & Rubasinghe 2014; Lavate *et al*. 2015; Manju *et al*. 2015). Specimens reported from China appear to belong to ***Pallavicinia levieri*** (Mamontov *et al.* 2015).

Aquatic and Wet Habitats

Pallavicinia indica occurs on **tuff** (porous volcanic rock) wall, waterfalls in tropics (Ruttner 1955). This species does not seem to prefer wet habitats. Nair and Prajitha (2016) reported the habitat of ***Pallavicinia indica*** as "land cuttings."

Pallavicinia levieri (Figure 21)

Distribution

Pallavicinia levieri (Figure 21) is an Asian temperate-tropical mountain species. It is known from Cambodia, China, Japan, Vietnam, Indonesia, Philippines, and Papua New Guinea (Grolle & Piippo 1984, 1986; Mamontov *et al*. 2015).

Figure 21. ***Pallavicinia levieri*** with leafy liverworts, from Guangdong, China. Photo by Li Zhang, with permission.

Aquatic and Wet Habitats

Ruttner (1955) reported ***Pallavicinia levieri*** (Figure 21) as aquatic from the tropics (Ruttner 1955). Mamontov

et al. (2015) reported that it occurs along river beds of primeval forests, along stream beds and slopes in secondary mixed evergreen forests, and in deep gorges. In Cambodia it occurs on wet cliffs near waterfalls.

Reproduction

Pallavicinia levieri (Figure 21) is **dioicous** (Figure 22-Figure 23) (Mamontov *et al*. 2015). Campbell and Williams (1914) provide a morphological study.

Figure 22. ***Pallavicinia levieri*** with perianths and young sporophytes, from Hainan, China. Photo by Rui-Liang Zhu, with permission.

Figure 23. ***Pallavicinia levieri*** with perianth and other bryophytes. Photo by Li Zhang, with permission.

Biochemistry

Hashimoto *et al*. (1993, 1995) repotted that the major component of ***Pallavicinia levieri*** (Figure 22-Figure 23) is sacculatal, a pungent diterpene dialdehyde (Asakawa 1982). It also produces pallavicinol and a rare chettaphanin-type diterpenoid. It has a pungent (-)-polygodial that is a strong piscicide (Asakawa 1990). Furthermore, killie-fish (*Oryzia latipes*) die within 2 hours when exposed to a solution of 0.4 ppm of sacculatal, and within 20 minutes at 1 ppm of sacculata and 1/3 1/3-hydroxysacculatal (Asakawa 1998).

Pallavicinia lyellii (Figure 24-Figure 27)

(syn. = *Pallavicinia radiculosa*)

Distribution

Pallavicinia lyellii (Figure 24-Figure 27) is a subcosmopolitan, temperate-tropical species (Stebel *et al*. 2018). It occurs in western and central parts of Europe, Asia, North, Central, and South America, northern and central Africa, and some areas in the Southern Hemisphere. Nevertheless, it is rare in Europe. Lavate *et al*. (2015) detailed its country locations, including Bermuda, Brazil, Cuba, England, Europe, Jamaica, Japan, Java, Kansaie, Moluccas, New Zealand, Philippines, Ryukya (Ryukyu?), Singapore, Sri Lanka, and West Indies.

Figure 24. ***Pallavicinia lyellii*** showing its typical life form. Photo by Jan-Peter Frahm, with permission.

Figure 25. ***Pallavicinia lyellii*** showing the ribbon-like life form. Photo by Jan-Peter Frahm, with permission.

Figure 26. ***Pallavicinia lyellii*** with narrow ribbons that suggest low light. Photo by Clive Shirley, Hidden Forest <hiddenforest.co.nz>, with permission.

Figure 28. Marshy habitat where ***Pallavicinia lyellii*** occurs. Photo by Des Callaghan, with permission.

Figure 27. ***Pallavicinia lyellii*** mat. Photo by Clive Shirley, Hidden Forest <hiddenforest.co.nz>, with permission.

Figure 29. ***Pallavicinia lyellii*** among grasses in marshy habitat. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

Pallavicinia lyellii (Figure 24-Figure 27) occurs in thermal acidic sprays in the tropics (Ruttner 1955). In northwest Portugal it occurs on steep, water-dripping schist surfaces or moist clayey streambanks between herbs, in shaded or moderately exposed places in low altitudes (Vieira *et al.* 2005). It can also occur in marshes, as photographed by Des Callaghan (Figure 28-Figure 29), where the grasses and sedges provide protection from moisture loss. It forms small patches mixed with other bryophytes such as ***Aneura pinguis*** (Figure 30), ***Solenostoma hyalinum*** (Figure 31), and ***Fissidens polyphyllus*** (Figure 32) in mountain streams.

Figure 30. ***Aneura pinguis***, a species that occurs with ***Pallavicinia lyellii*** in small patches in mountain streams. Photo by Hermann Schachner, through Creative Commons.

Figure 31. ***Solenostoma hyalinum***, a species that occurs with ***Pallavicinia lyellii*** in small patches in mountain streams. Photo by Michael Lüth, with permission.

Figure 32. ***Fissidens polyphyllus***, a species that occurs with ***Pallavicinia lyellii*** in small patches in mountain streams. Photo by David T. Holyoak, with permission.

Stebel *et al*. (2018) found that in Poland ***Pallavicinia lyellii*** (Figure 24-Figure 27) prefers damp or considerably wet habitats (Figure 33-Figure 37) and even grows in semi-aquatic conditions (Düll 1992). It grows on acidic to moderately acidic substrata and can live in moderately bright habitats (Stebel *et al*. 2018), but it is also very shade tolerant, as exemplified by its growth **under** a carpet of ***Sphagnum*** spp. (Figure 34) (Düll 1992; Dierβen 2001; Ellenberg & Leuschner 2010). Its light tolerance permits it to grow in open "bogs (Figure 35)," bog alder (***Alnus glutinosa***, Figure 36) or birch (***Betula pubescens***, Figure 37) forests, and beside wooded acid streams on moist soil (Figure 38), leaf litter, decaying wood (Figure 39), damp rocks (Figure 40), and rarely on exposed tree roots (Smith 1990; Dierβen 2001; Lavate *et al.* 2015; Mamontov *et al*. 2015). It doesn't seem to tolerate competition and thus is well-served by disturbed habitats with the right moisture.

Figure 33. ***Pallavicinia lyellii*** habitat at Cadnam Bog. Photo by Des Callaghan, with permission.

Figure 34. ***Pallavicinia lyellii*** under ***Sphagnum***. Photo by Gill Stevens, with permission from BBS website.

Figure 35. Bohemia bog with ***Sphagnum cuspidatum*** and ***S. denticulatum***. Photo by Jonathan Sleath, with permission.

Figure 36. ***Alnus glutinosa*** habitat where there is a suitable light level for ***Pallavicinia lyellii*** to grow. Photo by Sten Porse, through Creative Commons.

Figure 37. ***Betula pubescens*** habitat where there is a suitable light level for ***Pallavicinia lyellii*** to grow. Photo by Ingo2802, through Creative Commons.

Figure 38. ***Pallavicinia lyellii*** in a wet habitat. Photo by Michael Lüth, with permission.

Figure 39. ***Pallavicinia lyellii*** on wet, rotting log. Photo by Richard Orr, with permission.

Figure 40. ***Pallavicinia lyellii*** habitat. Photo by Michael Lüth, with permission.

Lavate *et al*. (2015) described the thallus of ***Pallavicinia lyellii*** (Figure 24-Figure 27) as **terricolous** (growing on soil or on ground) and **rupicolous** (growing on or among rocks), listing its habitats in India as moist soil on rocks, banks of freshwater streams (Figure 41), and cut surfaces as an associate with other liverworts. The relative humidity in these locations is typically 70-80%.

Figure 41. ***Pallavicinia lyellii*** growing streamside in Spain. Photo by Michael Lüth, with permission.

In Maryland, USA, ***Pallavicinia lyellii*** (Figure 24-Figure 27) occurs on soil, rotten wood (Figure 39), and tree bases in a stream valley (Glime 1966). In Florida, USA, White and Judd (1985) found it among the most conspicuous bryophytes at a ravine and adjacent uplands.

Sometimes ***Pallavicinia lyellii*** (Figure 24-Figure 27) seems to benefit from the shade of grasses, as observed by Gill Stevens at Wimbledon Downs (Figure 42-Figure 43).

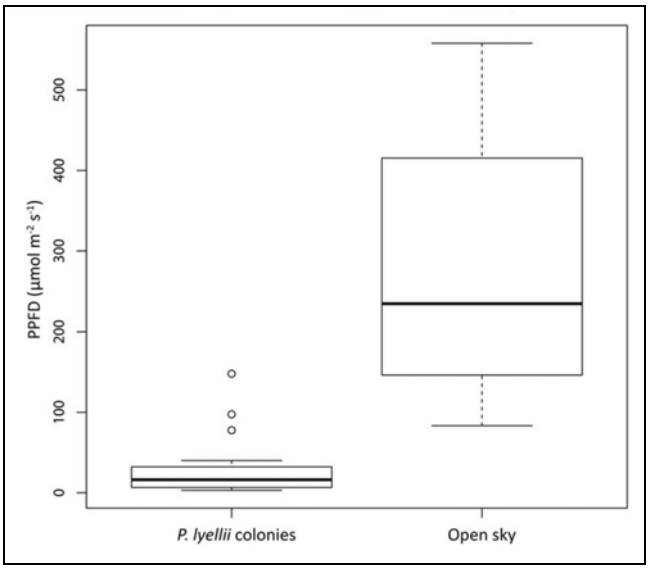

Figure 42. ***Pallavicinia lyellii*** photosynthetic photon flux density (PPFD), beneath canopies of ***Molinia caerulea*** and 1 m above (open sky), demonstrating the effect of cover on the liverwort. n = 20. Image by Des Callaghan, with permission.

Adaptations and Physiology

Pallavicinia lyellii (Figure 24-Figure 27) is a **short-lived shuttle** species (Smith 2006). This strategy permits it to inhabit the disturbed sites where it can enjoy the lack of competition.

Stebel *et al*. (2018) consider ***Pallavicinia lyellii*** (Figure 24-Figure 27) to be a **hemicryptophyte** (perennial plant having overwintering buds located at soil surface). It is sensitive to dehydration, but it has a prominent midrib that conducts water and that Stebel *et al*. and others (Dierβen 2001; Pence *et al*. 2005) suggest may serve as a buffer against the rapid loss of water. In some habitats it grows with other bryophytes (Figure 44) (Vieira *et al*. 2005; Lavate *et al*. 2015), another potential mechanism for conserving water (Stebel *et al*. 2018). But it can also grow in solitary, dense mats, as seen in Figure 45.

Figure 43. ***Pallavicinia lyellii*** at base of ***Molinia caerulea*** at Wimbledon Commons, UK. Photo by Gill Stevens, from BBS website, with permission.

Figure 44. ***Pallavicinia lyellii*** with mosses and other plants. Photo by Blanka Aguera, with permission.

Figure 45. ***Pallavicinia lyellii*** on stream bank, North Carolina. Photo by Janice Glime.

Charissou and Hugonnot (2020) note that ***Pallavicinia lyellii*** (Figure 24-Figure 27) pioneers moist clods but it is especially sensitive to desiccation. Pence *et al*. (2005) found that a pretreatment for one week with 10 µM ABA improved survival of desiccation in ***Pallavicinia lyellii***. ***Pallavicinia lyellii*** was less responsive to ABA treatment than the aquatic ***Riccia fluitans*** (Figure 46), but more responsive than the more terrestrial ***Marchantia polymorpha*** (Figure 47). Untreated ***Pallavicinia lyellii*** took 120 minutes to reach the same level of desiccation as that reached by ***Riccia fluitans*** in 45 minutes (11%). ABA did not change the rate of drying in these two species, but it slowed the drying rate significantly in ***Marchantia polymorpha***. Treated plants also exhibited an increase in total soluble carbohydrates.

Figure 46. ***Riccia fluitans***, a species that more commonly floats in ponds and other quiet waters. Photo by Christian Fischer, through Creative Commons.

Reproduction

Pallavicinia lyellii (Figure 24-Figure 27) is **dioicous** (Figure 48) (Stebel *et al*. 2018). Sex distribution varies between populations (Figure 49). Both males and females often occur together (Figure 48-Figure 57). Vieira *et al*. (2005) reported that the species was fertile in a Portuguese stream habitat in March. These plants had mature perigonia (Figure 52-Figure 57) and sporophytes (Figure 58-Figure 59).

Figure 47. ***Marchantia polymorpha***, a species that usually does not occur under water. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 48. ***Pallavicinia lyellii*** showing inter-mixed female (**red arrows**) and male (**white arrows**), **black** fertilized. Photo by Des Callaghan, with permission.

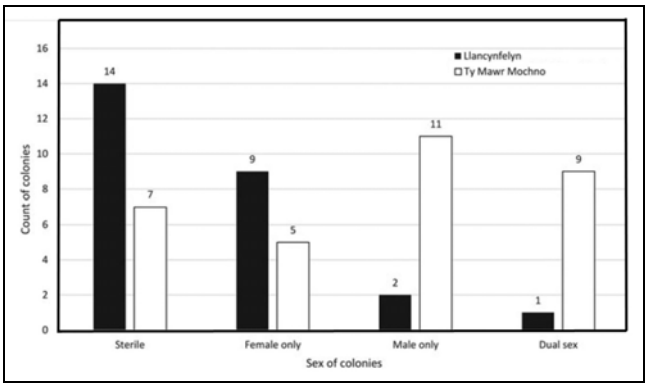

Figure 49. ***Pallavicinia lyellii*** sex distribution in 2 populations in Wales, showing differences in two locations. Modified from Des Callaghan, with permission.

Figure 50. ***Pallavicinia lyellii*** male. Photo by Blanka Aguera, with permission.

Figure 53. ***Pallavicinia lyellii*** female with laciniate scales that surround a group of archegonia. Photo by Des Callaghan, with permission.

Figure 51. ***Pallavicinia lyellii*** male with antheridia. Photo by Tom Thekathyil, with permission.

Figure 54. ***Pallavicinia lyellii*** with laciniate scales surrounding an emerging perianth. Photo by Jan-Peter Frahm, with permission.

Figure 52. ***Pallavicinia lyellii*** wet, with archegonia. Photo by Shyamal L, through Creative Commons.

Figure 55. ***Pallavicinia lyellii*** with senescing branches. Photo by Jeremy Collison, through Creative Commons.

Figure 56. ***Pallavicinia lyellii*** perianths. Photo by Blanka Aguero, with permission.

Figure 57. ***Pallavicinia lyellii*** young sporophyte still inside perianth (**arrow**). Photo courtesy of Des Callaghan.

Figure 58. ***Pallavicinia lyellii*** with emerging sporophytes. Photo by Jan-Peter Frahm, with permission.

Figure 59. ***Pallavicinia lyellii*** with dehisced capsule. Photo by John Bradford, with permission.

Biochemistry

The oil bodies (Figure 60) of ***Pallavicinia lyellii*** (Figure 24-Figure 27) are small, numerous per cell, and very variable in shape (Juslén *et al*. 2021). Ebner (2016) expressed surprise that despite the great variety of natural products in liverworts, he was only able to find already known compounds, including terpenes, fatty acids, and sterols in ***Pallavicinia lyellii***.

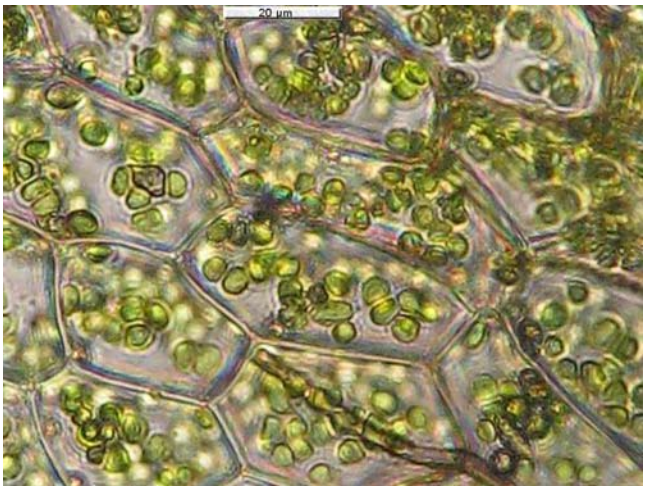

Figure 60. ***Pallavicinia lyellii*** thallus cells, showing the difficulty of observing oil bodies. Photo by Tom Thekathyil, with permission.

Adler (1983) identified the 4-desmethylsterol fraction in ***Pallavicinia lyellii*** (Figure 24-Figure 27). Rajan and Murugan (2010) extracted ascorbate peroxidase from

Pallavicinia lyellii. This enzyme performed optimally at 40ºC. The authors suggested that this pathway may contribute to desiccation tolerance in ***P. lyellii***.

Williams *et al*. (2016) found that ***Pallavicinia lyellii*** (Figure 24-Figure 27) has remarkable inhibitory activity against bacterial pathogens. Subhisha and Subramoniam (2005) reported antifungal activity by a steroid from this species. Extracts of ***Pallavicinia lyellii*** inhibited ***Pseudomonas aeruginosa*** (bacterium; Figure 61) and exhibited the greatest antibacterial activity against ***Escherichia coli*** (Figure 62) among the nine liverworts tested (Linde *et al*. (2016).

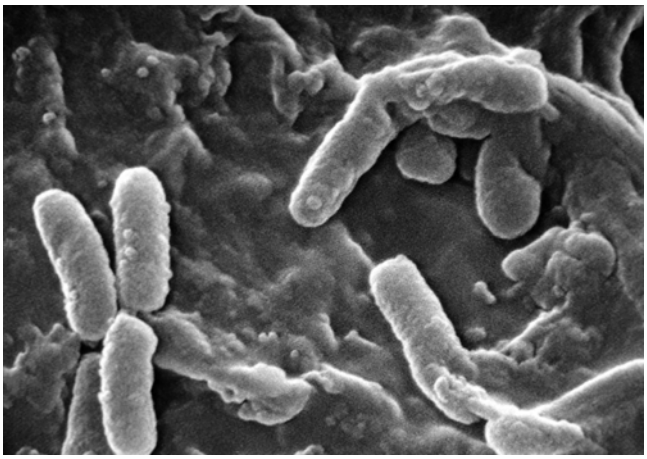

Figure 61. ***Pseudomonas aeruginosa*** SEM. Photo by Janice Haney Carr, CDC, through public domain.

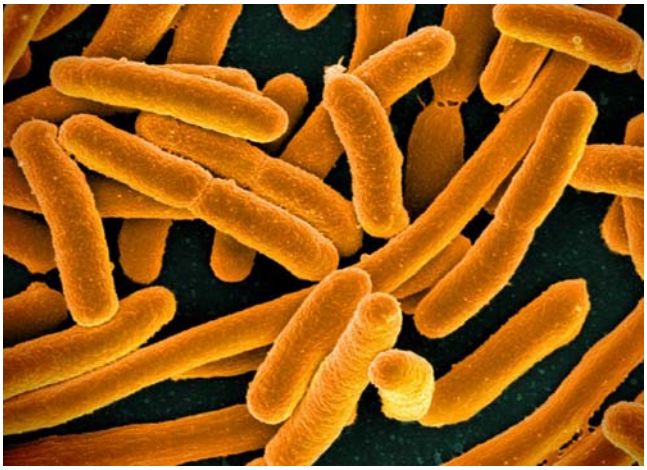

Figure 62. ***Escherichia coli*** SEM with color added. Photo by Niaid, through Creative Commons.

Summary

These members of the **Pallaviciniales** are at best facultatively aquatic. On the other hand, they like moist habitats such as stream banks, wet cliffs, and the spray of waterfalls. ***Hymenophyton flabellatum*** is able to form a mycorrhizal relationship with fungi in **Glomeromycota**. No fungal relationships seem to be known in the **Pallaviciniaceae** included here.

Acknowledgments

Thank you to Lars Söderström for his continued help in sorting out nomenclature changes.

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CHAPTER 1-16
AQUATIC AND WET MARCHANTIOPHYTA, PELLIALES

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CHAPTER 1-16
AQUATIC AND WET MARCHANTIOPHYTA, PELLIALES

Figure 1. ***Pellia endiviifolia*** by stream. Photo by J. Claude, through Creative Commons.

Nomenclature for this subchapter is based primarily on Söderström *et al*. (2016). In addition, Lars Söderström provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. These unverifiable taxa have been included in the species.

SUBCLASS PELLIIDAE

Pelliales: Pelliaceae

Pellia (Figure 1Figure 3-Figure 4, Figure 19-Figure 20, Figure 49-Figure 52, Figure 96-Figure 103)

Pellia sp. occurs at the base of the Flume wall and on ledges of the Flume at Franconia Notch, New Hampshire, USA (Figure 2) (Glime 1982), an environment that is always humid. In West Virginia, USA, mountain streams, members of this genus preferred *p*H 6.6 (Stephenson *et al*. 1995).

Figure 2. Flume, Franconia Notch, New Hampshire, USA, a habitat where one can find ***Pellia*** on the ledges and the base of the cliffs. Photo by Janice Glime.

Pellia appalachiana (Figure 3-Figure 4)

Distribution

Pellia appalachiana (Figure 3-Figure 4) is endemic to the southeastern USA (Alabama, Georgia, Kentucky, North Carolina, South Carolina, Tennessee) (Southern Appalachian Bryophytes 2019).

Figure 3. ***Pellia appalachiana*** female with involucres. Photo by Paul G. Davison, with permission.

Figure 4. ***Pellia appalachiana*** forming a large rosette, suggesting it originated from a single spore. **Arrows** indicate female with involucres. Photo by Paul G. Davison, with permission.

Aquatic and Wet Habitats

The species of ***Pellia*** included here have similar habitats. ***Pellia appalachiana*** (Figure 3-Figure 4) is intolerant of desiccation, so its habitats are ones that are constantly moist (Southern Appalachian Bryophytes 2019). It thrives where the habitat has periodic disturbance, especially stream banks (Figure 5-Figure 7) that experience episodes of scouring or muddy-rocky shelves associated with waterfalls. When it grows on vertical walls, mats may slough off, providing a bare surface for spores to germinate. Such habitats are available in **rockhouses** (shallow cave-like opening at the base of a bluff or cliff; Figure 8). Zartman and Pittilo (1998) found it in spray cliff communities of the Chattooga Basin in the southern Blue Ridge.

Figure 5. ***Pellia appalachiana*** on soil that is periodically inundated at edge of stream. Photo by Paul G. Davison, with permission.

Figure 6. ***Pellia appalachiana*** habitat at edge of stream. Photo by Paul G. Davison, with permission.

Figure 7. ***Pellia appalachiana*** habitat on stream bank. Photo by Paul G. Davison, with permission

Figure 8. ***Pellia appalachiana*** rock house habitat, Alabama. Photo by Paul G. Davison, with permission.

Adaptations

Pellia appalachiana (Figure 3-Figure 4) can grow with other bryophytes that are not too aggressive, most likely benefitting from greater moisture-holding ability. The ribbon-like structure also helps to minimize the effects of abrasion in their streamside habitat where inundation can bring mud and sand or small stones (Southern Appalachian Bryophytes 2019).

Figure 9. ***Pellia appalachianus*** growing with ***Pellia epiphylla, Pallavicinia lyellii***, ***Nardia lescurii***, and ***Sphagnum*** sp. Photo by Paul Davison, with permission.

Reproduction

Pellia appalachiana (Figure 3-Figure 4) is **dioicous** (Southern Appalachian Bryophytes 2019). Its antheridia (Figure 10- Figure 11) are sunken in dorsal pustules that are scattered along the midrib area. The archegonia (Figure 12-Figure 18) are at the base of a lobed involucre. The reproductive organs are typically absent on the new spring growth, but can often be located on older thalli hidden by the new growth.

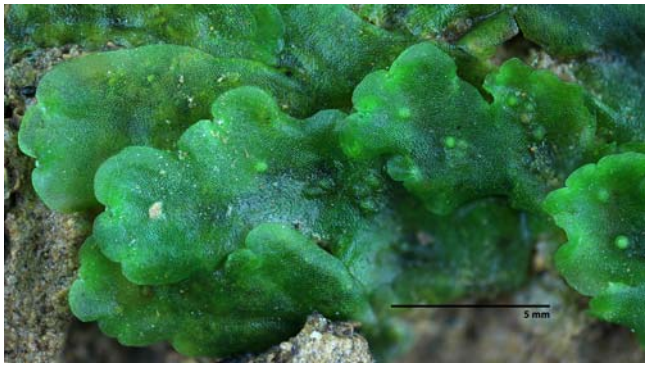

Figure 10. ***Pellia appalachiana*** with young antheridial pustules. Photo by Paul Davison, with permission.

Figure 11. ***Pellia appalachiana*** with maturing antheridia. Photo by Paul G. Davison, with permission.

Figure 12. ***Pellia appalachiana*** female showing involucres (**arrows**). Photo by Paul G. Davison, with permission.

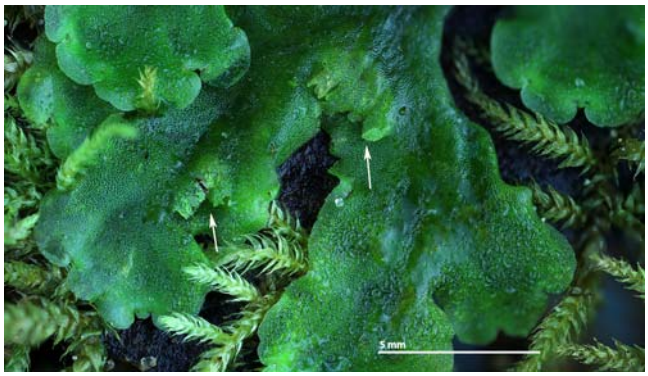

Figure 13. ***Pellia appalachiana*** female involucres (**arrows**). Photo by Paul G. Davison, with permission.

Figure 14. ***Pellia appalachiana*** female involucres (**arrows**). Photo by Paul G. Davison, with permission.

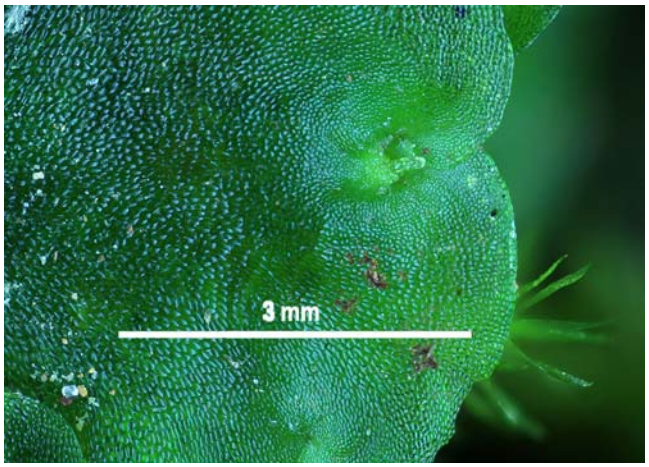

Figure 15. ***Pellia appalachiana*** female involucre with tip of archegonium protruding. Photo by Paul G. Davison, with permission.

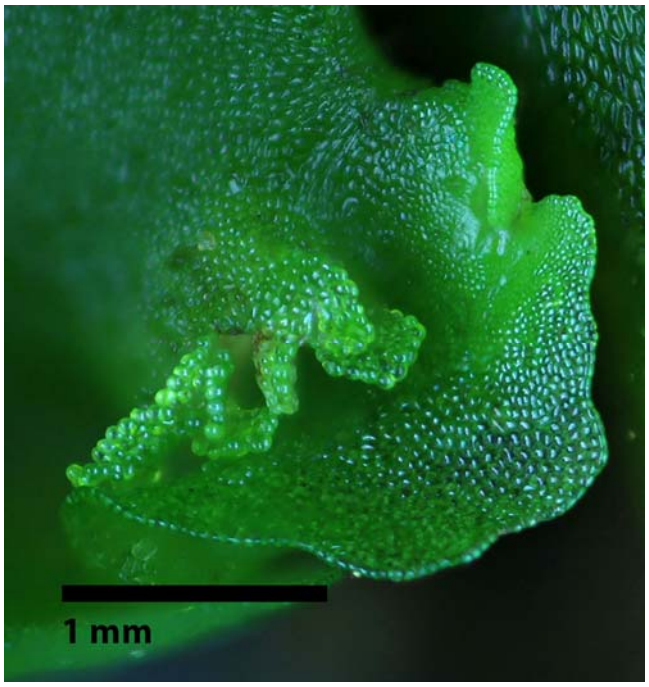

Figure 16. ***Pellia appalachiana*** female involucre showing lobes. Photo by Paul G. Davison, with permission.

Figure 17. ***Pellia appalachiana*** lobed female involucre. Photo by Paul G. Davison, with permission.

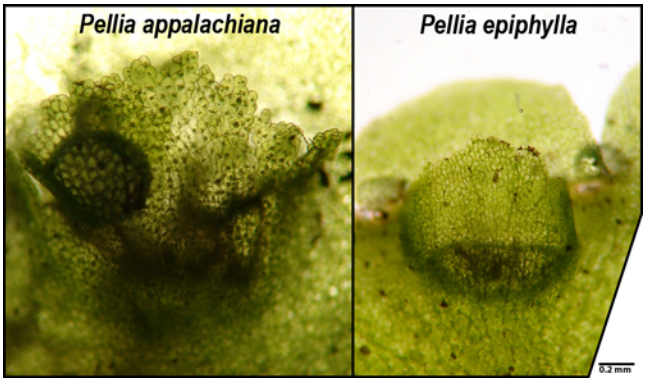

Figure 18. Comparison of the lobed involucre of ***Pellia appalachiana*** with the unlobed involucre of ***Pellia epiphylla***. Photo modified from Paul G. Davison, with permission.

Pellia endiviifolia (Figure 19-Figure 20)

(syn. = *Pellia calycina, Pellia endivifolia*, *Pellia fabroniana* var. *lorea*)

Distribution

Pellia endiviifolia (Figure 19-Figure 20) is widely distributed in the Northern Hemisphere (Parzych *et al*. 2018). Dhien (1983) considers it to be circumboreal. It occurs through a large portion of Europe from Denmark and Belgium, southward to Italy, Spain, and Portugal, and further to North Africa (Schuster 1992). In Asia it is known from Japan, Siberia, Taiwan, China, and possibly India. Schuster disallows reports from North America, instead considering these to be ***Pellia epiphylla*** (Figure 49-Figure 51), ***P. neesiana*** (Figure 96-Figure 103), and ***P. megaspora*** (Figure 21).

Figure 19. ***Pellia endiviifolia***. Photo from Snappy Goat, through public domain.

Figure 20. ***Pellia endiviifolia*** with dark coloration that suggests exposure to bright light. Photo by Des Callaghan, with permission.

Figure 21. ***Pellia megaspora***, one of the species Schuster accepted as occurring in North America. Photo by Jean Faubert, with permission.

Aquatic and Wet Habitats

Szoszkiewicz *et al*. (2006) listed ***Pellia endiviifolia*** (Figure 19-Figure 20) among the river species. It is among the most common bryophytes in the River Tweed, UK (Holmes & Whitton 1975). It is scattered in the River Swale, Yorkshire, UK (Holmes & Whitton 1977b). The species occurs on travertine in the ***Cratoneuron*** association of Lorraine River, Belgium (de Sloover & Goossens 1984) and in the ***Fissidens grandifrons*** (Figure 22) community in calcareous water (Gil & Ruiz 1985). In Thuringia, Germany, it can be found in the ***Platyhypnidium*** (Figure 23)-***Fontinalis antipyretica*** (Figure 24) association (Marstaller 1987). The streams are typically oligotrophic (Tremp 2003), as in the Alsatian Rhine valley (Vanderpoorten & Palm 1998; Vanderpoorten *et al*. 1999), in Belgian streams (Vanderpoorten & Tignon 2000), and in Iskur River and its main tributaries in Bulgaria (Papp *et al.* 2006).

Figure 22. ***Fissidens grandifrons*** wet at stream edge where it might occur with ***Pellia endiviifolia***. Photo by Scot Loring, through Creative Commons.

Figure 23. ***Platyhypnidium riparioides*** in water, inhabiting the type of stream where one might find ***Pellia endiviifolia***. Photo by Hermann Schachner, through Creative Commons.

Figure 24. ***Fontinalis antipyretica***, a species that may indicate habitat suitability for ***Pellia endiviifolia***. Photo by Matt Goff (www.sitkanature.org), with permission.

Papp (1998) found ***Pellia endiviifolia*** (Figure 19-Figure 20) to be common in streams (Figure 1) in Greece. Likewise, Scarlett and O'Hare (2006) reported that it is among the commonest species in English and Welsh rivers. It has a wide ecological amplitude, at times being exposed and other times inundated during periods of high flow (Pentecost & Zhang 2006; Pentecost & Zhaohui 2006).

Pellia endiviifolia (Figure 19-Figure 20) is among the most frequent species in Europe in association with rivers and streams, typically occurring on travertines (Pentecost & Zhang 2006). In Montenegro, it occurs at springs, rivers, and streams in Tara River canyon and the Durmitor area (Papp & Erzberger 2011). It occurs in poorly mineralized and basic waters in the Tiber River basin of Italy, where it does not seem to be influenced by phosphate concentrations (Ceschin *et al*. 2012)

In Ireland Weekes *et al*. (2018) found ***Pellia endiviifolia*** (Figure 19-Figure 20) in association with ***Fontinalis antipyretica*** (Figure 24) or ***Hygroamblystegium fluviatile*** (Figure 25), as described also by Bailly (2012). It typically was submerged or in the splash zone of shady, calcareous rivers, especially with overhanging trees or bridges. Although it has a high presence in these areas, it has low cover values. In Portugal, Vieira *et al*. (2005) included it among the threatened bryophytes.

Figure 25. ***Hygroamblystegium fluviatile***, an associate of ***Pellia endiviifolia***. Photo by Michael Lüth, with permission.

Some populations of ***Pellia endiviifolia*** (Figure 19-Figure 20) occur in river beds and brook beds, as reported by Konstantinova *et al*. (2009) for ***Pellia endiviifolia*** from the valley of the Bushujka River in the western Caucasus, Russia. It even occurs in artificial waterways with flowing water. Dhien (1983) reported it from canal water and on its banks.

But many populations of ***Pellia endiviifolia*** (Figure 19-Figure 20) seem to meet their needs out of the water (Figure 26), on stream banks and river banks. It occurs on the river bank of the River Tees, UK (Holmes & Whitton 1977b) and is similarly associated with the River Wear, England (Birch *et al*. 1988). In the Caucasus, it occurs on the bank of a Zakan River tributary and on rocks on stream banks, especially those rich in calcium and receiving splash (Konstantinova *et al*. 2009). Some of these bank locations are on soil on the banks of subalpine streams and the edges of forest streams. Weekes *et al.* (2018) similarly found it either submerged or in the splash zone of streams and rivers in Ireland, preferring calcareous conditions and shade. But in contrast to many studies, these researchers reported it from margins of fast-flowing **mesotrophic** water. In some locations it grew on clay banks in the shade of ***Petasites hybridus*** (Figure 27), the latter protecting it from competition.

Figure 26. ***Pellia endiviifolia*** habitat out of water in India. Photo by Michael Lüth, with permission.

Figure 27. ***Petasites hybridus*** along river, a plant that often occurs in dense patches that can provide shade for ***Pellia endiviifolia***. Photo through Creative Commons.

There seem to be few records of the association of ***Pellia endiviifolia*** (Figure 19-Figure 20) with lakes. It occurs in wet places around lakes in Scotland, especially in the shade (West 1910). In the Caucasus, Russia, it can occur on the banks of pools.

Watson (1919) reported ***Pellia endiviifolia*** (Figure 19-Figure 20) from waterfalls (Figure 28). Hazrat *et al*. (2020) found it in association with waterfalls in deep shade in Pakistan. Konstantinova *et al*. (2009) found that on streambanks in the Caucasus, it was especially associated with areas near waterfalls.

Figure 28. ***Pellia endiviifolia*** near Swallow Falls, Wales, where the habitat remains humid. Photo by Janice Glime.

In Ireland, Pilkington (2003) found it on wet rock faces that are continually irrigated by water trickling down, typically with large, mossy tufts.

Pakalne and Čakare (2001) documented the presence of ***Pellia endiviifolia*** (Figure 19-Figure 20) on steep river ravine slopes at the springs in the Gauja National Park, Latvia. This was often a marginal zone between the spring and mire vegetation. In the Netherlands it can be among the dominant bryophytes of cold springs (Sýkora 2006).

Some populations of ***Pellia endiviifolia*** (Figure 19-Figure 20) thrive in bogs and boggy habitats. In the Caucasus, Russia, it occurs in boggy meadows and bogs of subalpine meadows. Weekes *et al*. (2018) reported it from vertical peat banks associated with fast-flowing water in Ireland. Lewis (1976) described it as "creeping over the wet, peaty surfaces" in the northern isles of Shetland, where it can achieve high cover values.

Even moist cliffs can satisfy the needs of ***Pellia endiviifolia*** (Figure 19-Figure 20). Konstantinova *et al*. (2009) found it on moist cliffs in the western Caucasus, Russia, often associated with streams. Milliken and Pendry (2002) found it in cliff flushes where it occurs in continuous water flow on the rock face, usually in small patches.

Other occurrences take advantage of muddy soils, both wet and dry, and even on tree trunks (Figure 29) in Pakistan, but these don't seem to be preferred habitats (Hazrat *et al*. 2020). On Mount Boranja, West Serbia, ***Pellia endiviifolia*** (Figure 19-Figure 20) occurs on humid soil (Pantović & Sabovljević 2013).

Lo Giudice and Cristaudo (2004) note that in the mountains of Sicily ***Pellia endiviifolia*** (Figure 19-Figure 20) occurs on wet calcarenite rocks where it is mostly shaded by herbaceous plants. Boucard *et al*. (2013) noted that most of the low-shore bryophytes, including ***Pellia endiviifolia***, have been neglected in studies, whereas those associated with active tuffs, also including ***Pellia endiviifolia***, have been included in phytosociological surveys. It forms an association there with ***Cratoneuron filicinum*** (Figure 30).

Figure 29. ***Pellia endiviifolia*** on bark in a moist habitat. Photo by Martin Hutten, with permission.

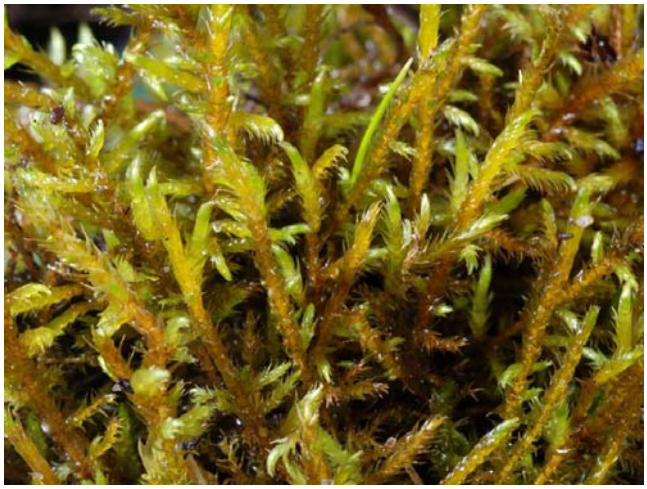

Figure 30. ***Cratoneuron filicinum***, a species that accompanies ***Pellia endiviifolia*** in low-shore environments. Photo by J. C. Schou, with permission.

Physiology

It has been difficult to understand how facultative aquatic bryophytes, such as ***Pellia endiviifolia*** (Figure 19-Figure 20), in calcareous waters are able to obtain sufficient CO_2 for photosynthesis and subsequent growth. In these high *p*H waters, CO_2 is readily converted to bicarbonates and carbonates. This understanding has been complicated by the assumption that all bryophytes are C_3 plants (Smith & Griffiths 1996), requiring free CO_2. For whatever reason, the pyrenoids that help many algae to concentrate CO_2 did not continue in any bryophyte lines except for the hornworts.

Pellia endiviifolia (Figure 19-Figure 20) lacks the internal ventilation (Figure 31) present in some thallose liverworts, such as ***Marchantia*** spp (Figure 32-Figure 33) (Meyer *et al*. 2008). This imposes limitations on the internal storage of free CO_2 needed for photosynthesis. Instead, species of ***Pellia*** are diffusion limited (Griffiths *et al*. 2004). ***Pellia*** has a simple thallus with no pores and a C_3 pathway of photosynthesis (Meyer *et al*. 2008). It is furthermore desiccation intolerant, thus requiring that CO_2 must enter the plants through water when it is submersed or in high humidity or splash. It in fact has "an extremely narrow" range of optimal water content" during maximal electron transport.

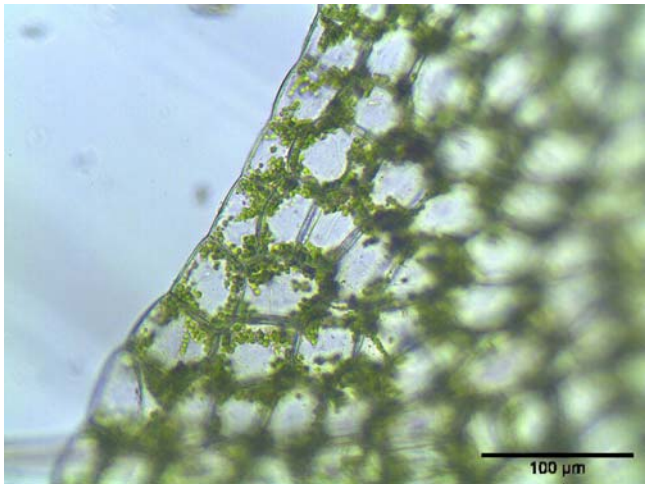

Figure 31. ***Pellia endiviifolia*** thallus showing lack of air chambers. Photo by Christian Fischer, through Creative Commons.

Figure 32. ***Marchantia polymorpha*** with isopod. Photo by Walter Obermayer, with permission.

Figure 33. ***Marchantia polymorpha*** thallus section through pore, showing internal chamber. Photo by Jennifer Steele, with permission through Botany Website.

Griffiths *et al*. (2004) suggested that understanding of the genes and regulatory processes related to pyrenoids and multiple plastids is necessary to understand the selective pressures that have shaped the evolutionary changes in bryophytes. For example, in the hornwort genus ***Megaceros*** (Figure 34), there is a gradual loss of the pyrenoid associated with the development of the multiplastidic condition. At the same time, it appears that the thalli of liverworts went from the simple, non-porous types like those of ***Pellia*** (Figure 19-Figure 20, Figure 31) to the chambered type in ***Marchantia*** (Figure 32-Figure 33) with access to the atmosphere through pores. But this advantage for CO_2 acquisition creates a more rapid loss of water from the thallus.

Figure 34. ***Megaceros*** with capsules, a genus in which pyrenoids diminished as multiplastidic species evolved. Photo by David Tng <www.davidtng.com>, with permission.

Because bryophytes take in water directly through the gametophyte tissues, in this case through the thallus, they tend to reflect the concentrations of minerals in the water. Satake *et al*. (1987) determined the elemental concentrations of selected nutrients and heavy metals in ***Pellia endiviifolia*** (Figure 19-Figure 20). The mean concentrations of major essential elements in the liverwort thalli were 49,600 µg g^{-1} K, 9,140 µg g^{-1} Na, 6,740 µg g^{-1} Ca, 3,840 µg g^{-1} P, and 3,060 µg g^{-1} Mg. When the field sites were polluted with the heavy metals Cu, Zn, and Pb, these appeared in high concentrations in the thalli of ***Pellia endiviifolia*** (maxima 0.88% Cu, 0.55% Zn, and 0.36% Pb in the older thalli).

Parzych *et al*. (2018) again assessed the accumulative possibilities of ***Pellia endiviifolia*** (Figure 19-Figure 20) for N, P, K, Mg, Ca, Zn, Fe, Cu, Ni, Mn, Al, and Sr. The nutrients normally considered to be macronutrients accounted for 96% of this pool. Nitrogen constituted 40% of this sum, phosphorus 4.9%, potassium 38%, magnesium 5%, calcium 12%, and trace elements 3.8% of this sum. Among the trace elements, iron was dominant (56.3%), manganese 24.8%, and aluminum 17%; other elements comprised less than 1%. ***Pellia endiviifolia*** accumulated high concentrations of iron and manganese, thus suggesting its usefulness as a bioaccumulator and a purification agent. Their research indicated that accumulation of Mg, Fe, and Cu was influenced by the environmental conditions, whereas N, P, K, Ca, Zn, Ni, Mn, Al, and Sr were determined by the species itself. Staniszewski (2001) used

Pellia endiviifolia as a bioindicator in the Kujawskie Lakeland, Poland.

Adaptations

Pellia endiviifolia (Figure 19-Figure 20) can form pure **mats** (Figure 1) (Konstantinova *et al*. 2009). These help to conserve water and to reduce drag during times of flooding. At other locations, it might exist with other liverworts, especially ***Conocephalum*** (Figure 35) and ***Chiloscyphus*** (Figure 36), or mosses (Figure 37), again having the potential to conserve moisture.

Figure 35. ***Conocephalum salebrosum***; ***Pellia endiviifolia*** sometimes grows with a member of this genus. Photo by Richard Draker, through Creative Commons.

Figure 36. ***Chiloscyphus polyanthos***, a species that often accompanies ***Pellia endiviifolia***. Photo by Hermann Schachner, through Creative Commons.

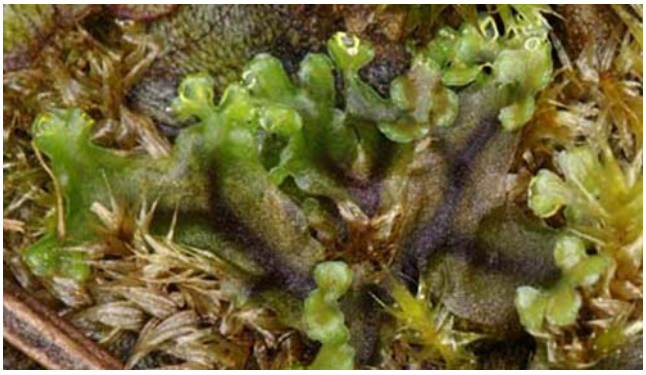

Figure 37. ***Pellia endiviifolia*** growing with mosses. Photo by Jean Faubert, with permission.

Reproduction

Pellia endiviifolia (Figure 19-Figure 20) is **dioicous** (Sierocka *et al*. 2014). Sierocka *et al*. identified a female-specific gene expression in ***Pellia endiviifolia*** (Figure 38) and determined its developmental regulation and connection to the production of archegonia. They recognized three genes that are expressed only in females. The archegonial tissue exhibited a 10-fold increase in transcript level for all three of these genes compared to the vegetative parts of the same female thalli. These genes appear to be developmentally regulated. Male plants are recognizable by their often red blisters scattered around the middle of the thallus (Figure 38-Figure 45). Female plants are recognizable by the collar-like involucre that surrounds the archegonia (Figure 38, Figure 46). Sporophytes are known (Figure 47).

Figure 38. ***Pellia endiviifolia*** **males** with reddish antheridial cavities and **females** in center. Photo by David T. Holyoak.

Figure 39. ***Pellia endiviifolia*** males. Photo by Hermann Schachner, through Creative Commons.

Figure 40. ***Pellia endiviifolia*** with antheridia. Photo by Hugues Tinguy, with permission.

Figure 41. ***Pellia endiviifolia*** with antheridia. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

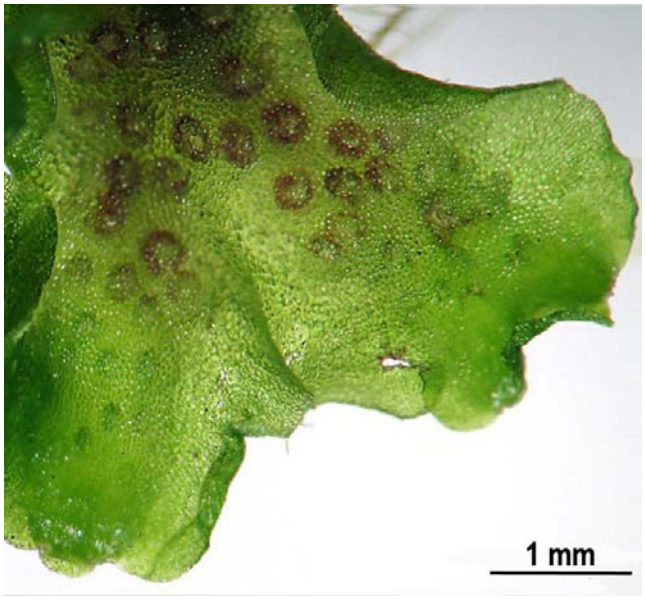

Figure 42. ***Pellia endiviifolia*** with antheridia. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 43. ***Pellia endiviifolia*** thallus cross section through antheridium. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 44. ***Pellia endiviifolia*** cross section with antheridium and escaping spermatocytes. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

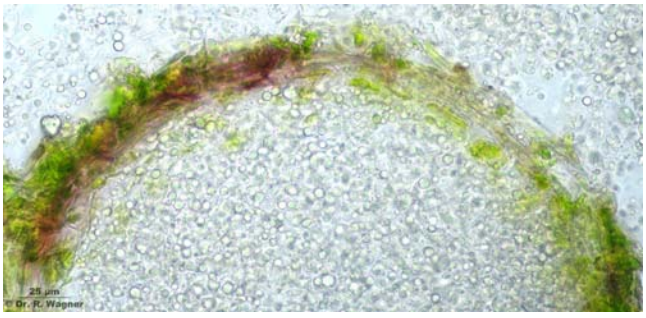

Figure 45. ***Pellia endiviifolia*** antheridium cross section and spermatocytes. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 46. ***Pellia endiviifolia*** females showing involucre. Photo by David T. Holyoak, with permission.

Figure 47. ***Pellia endiviifolia*** nearly mature capsules. Photo from Snappy Goat, through public domain.

Vojtkó (1993) described spore morphology in 29 liverwort species. The only elliptic spores in the study were in ***Pellia endiviifolia*** (Figure 19-Figure 20). At the same time, this was also the largest spore (80x65 µm). The spore also had "surprisingly" thin walls compared to the other spores studied.

Biochemistry

Ono *et al*. (1992) confirmed the presence of the pungent diterpene dialdehyde, sacculatal in ***Pellia endiviifolia*** (Figure 19-Figure 20). Later, Mehmeti (2009), using GCMS-GC, likewise found sacculatal and several derivatives to be the predominant components of the volatiles in this pungent liverwort in Tokushima, Japan. Asakawa (2004) suggested a lack of oil bodies in ***Pellia*** might explain the paucity of volatiles in the species tested. However other authors have noted the presence of oil bodies (Pihakaski 1972; Pihakaski & Pihakaski 1979, 1980), although at least in ***Pellia neesiana*** they are tiny (Figure 136) (Schuster 1992.

Hashimoto *et al*. (1995) found that the pungent l,β-hydroxysacculatal and sacculatal in ***Pellia endiviifolia*** (Figure 19-Figure 20) exhibit piscicidal activity by killing killie-fish in 20 min at 1 ppm.

Alaba *et al*. (2015) attempted to show microRNA relationships between green algae and liverworts, using the green alga ***Chlamydomonas reinhardtii*** (Figure 48) and liverwort ***Pellia endiviifolia*** (Figure 19-Figure 20). Until this study, no microRNA sequences were known from liverworts, but gene expression had only been studied in ***Marchantia polymorpha*** (Figure 32). They discovered an impressive array of 311 conserved microRNAs known from plant families in addition to 42 new liverwort-specific microRNAs. Nevertheless, degradome analysis revealed that target mRNAs of only three microRNAs (miR160, miR166, and miR408) have been conserved between liverworts and other land plants. Three of the liverwort microRNAs show high similarity to previously reported microRNAs from ***Chlamydomonas reinhardtii***.

Figure 48. ***Chlamydomonas reinhardtii***, a green alga species that shares three microRNAs with ***Pellia endiviifolia***. Photo by Yuuji Tsukii, with permission.

Pellia epiphylla (Figure 49-Figure 51)

(syn. = *Pellia fabbroniana*)

Distribution

Pellia epiphylla (Figure 49-Figure 51) is known from North America, Europe, North Africa, and nearby areas of Asia (Boll 2020).

Figure 49. ***Pellia epiphylla*** mat with a few mosses mixed in. Photo by Kristian Peters, with permission.

Figure 50. ***Pellia epiphylla*** forming tight layers that can help to conserve water. Photo by Michael Lüth, with permission.

Figure 52. ***Pellia epiphylla*** that is at least partially submersed. Photo by Ken McFarland and Paul Davison, with permission.

Figure 51. ***Pellia epiphylla*** on soil at Cwm Idwal National Nature Reserve 357 in Wales. Photo by Janice Glime.

Figure 53. ***Pellia epiphylla*** habitat under grass bank of flush at Cwm Idwal National Nature Reserve 39, Wales. Photo by Janice Glime.

Aquatic and Wet Habitats

Boll (2020) described ***Pellia epiphylla*** (Figure 49-Figure 51) as a liverwort that "loves very humid places," growing close to rivers and other watercourses (Figure 52). Watson (1919) described it from margins of fast streams, on banks with frequent submergence and slow water, submerged in slow water with poor mineral salts, waterfalls, wet rocks and soil near fast streams, and margins of fast streams on wet rocks or soil. Coroi *et al*. (2004) considered ***Pellia epiphylla*** to be a wetland indicator in streamside forests. Ferreira *et al*. (2008) attributed it to rivers. Marczonek (1984) investigated the ecology of ***Pellia epiphylla*** populations. In Wales, I found it growing on the sides of flushes, shaded by overhanging grasses (Figure 53).

In the British Isles, ***Pellia epiphylla*** (Figure 49-Figure 51) is among the most common bryophytes in the River Tweed (Holmes & Whitton 1975). It occurs on the river bank of the River Tees (Holmes & Whitton 1977a) and the upper to midstream of the River Swale (Holmes & Whitton 1977b). In the River Tyne, it occurs throughout (Holmes & Whitton 1981). Scarlett & O'Hare (2006) considered it to be among the commonest species in English and Welsh rivers.

Elsewhere in Europe, in the Sudeten Mountains of Poland and the Czech Republic, ***Pellia epiphylla*** (Figure 49-Figure 51) occurs in streams (Samecka-Cymerman & Kempers 1998), especially in waters affected by mineralization zones (Samecka-Cymerman & Kempers 1993). In Germany, it occurs in slow-flowing water in Westfalens, northwestern Germany (Koppe 1945), in the upper and middle reaches in the Harz Mountains (Bley 1987), and submersed or above water in the ***Platyhypnidium*** (Figure 23)-***Fontinalis antipyretica*** (Figure 24) association, Thuringia, Germany (Marstaller 1987). It often occurs just above ***Platyhypnidium riparioides*** (Figure 23) (Gimingham & Birse 1957). In northwest Portugal, it occurs in mountain streams (Vieira *et al.* 2005). It likewise occupies streams in the northeastern part of Finland (Heino & Virtanen 2006). On Madeira Island, it occurs at low altitudes, in a narrow stream, and where there is low flow in mountainous streams (Luís *et al.* 2015).

Most North American findings of ***Pellia epiphylla*** (Figure 49-Figure 51) have been above the water on stream banks rather than submersed, although the plants can be submersed for a short time in spring or other times when

the streams and rivers experience flooding. Steinman and Boston (1993) report only a small amount present at most of their research sites in Walker Branch, Tennessee.

Sørensen (1948) reported ***Pellia epiphylla*** (Figure 49-Figure 51) at a water *p*H of 7.7 in streaming water in Denmark. However, in West Virginia mountain streams its preferred *p*H was 4.17 (Stephenson *et al*. 1995).

Pellia epiphylla (Figure 49-Figure 51) can also occupy irrigation ditches (Beaucourt *et al*. 1987).

But ***Pellia epiphylla*** (Figure 49-Figure 51) seems to occur most commonly on stream banks, especially in North America. In the Western Carpathians near Lacko, Mamczarz (1970) attributed it to rocks and water communities associated with streams. In the Komi Republic of Russia it occurs on soil on river banks. Leclercq (1977) reported it from earthy and gravelly substrates of river banks in Haute Ardenne rivers, Belgium.

Greenwood (1911) commented that ***Pellia epiphylla*** (Figure 49-Figure 51) is common in some locations, growing on the ground in damp shaded places and preferring stream banks where it can be submerged or just above the water line, often extending a meter or more from the water's edge.

In North America, ***Pellia epiphylla*** (Figure 49-Figure 51) might be restricted to stream and river banks. In my own meanderings, I have never seen it submersed, but it is common on the banks immediately adjacent to streams. These locations can, of course, be submerged during high flows, but typically not for more than a few days.

In Connecticut, USA, Nichols (1916) reported ***Pellia epiphylla*** (Figure 49-Figure 51) from moist rock surfaces or springy banks of ravines, wet, sandy streambanks, and along calcareous rivers. Greenwood (1923) found it on moist, shaded banks, accompanied by ***Conocephalum conicum*** (Figure 54) and ***Bazzania trilobata*** (Figure 55) in Center County, Pennsylvania, USA.

Figure 54. ***Conocephalum conicum*** at a stream edge where it is often accompanied by ***Pellia epiphylla***. Photo by David Holyoak, with permission.

There seem to be few records of ***Pellia epiphylla*** (Figure 49-Figure 51) specifically from springs. Sørensen (1948) recorded it at *p*H 7.1 in springs in Denmark.

Figure 55. ***Bazzania trilobata***, a species that often accompanies ***Pellia epiphylla*** on stream banks. Photo by Bernd Haynold, through Creative Commons.

Similarly, it appears to be much less common in association with lakes than with streams and rivers. Toivonen and Huttunen (1995) reported ***Pellia epiphylla*** (Figure 49-Figure 51) from small lakes in southern Finland. It occurs in wet places around lakes, especially in shade, in Scotland (West 1910). Mallik and Wein (1986) reported that it could be found on the flooded side of a *Typha* marsh (Figure 56), but not on the drained side.

Figure 56. Flooded side of cattail (***Typha***) marsh, a potential site for ***Pellia epiphylla***. Photo by David Hoffman, through Creative Commons.

Some collectors have reported ***Pellia epiphylla*** (Figure 49-Figure 51) from wet cliffs and bluffs. Vitt (1967) reported finding it on the upper portions of sandstone bluffs in southeastern Missouri, USA, typically in wet, shaded areas (Figure 57).

Proctor *et al*. (1992) used ***Pellia epiphylla*** (Figure 49-Figure 51) from moist, shady clay banks near a stream gully to measure δ13C values from a wet heath in East Devon. Watson (1915) indicated zonation patterns of plants in a Somerset, UK, heath, noting that ***Pellia epiphylla*** occurred just above the water line of the channels

(Figure 58) in locations where it would remain constantly moist. Otherwise, I have found no reports of this species from peaty habitats.

Figure 57. Sandstone bluff in Missouri, USA, where ***Pellia epiphylla*** can be found in moist places. Photo by V. Smith, through Creative Commons.

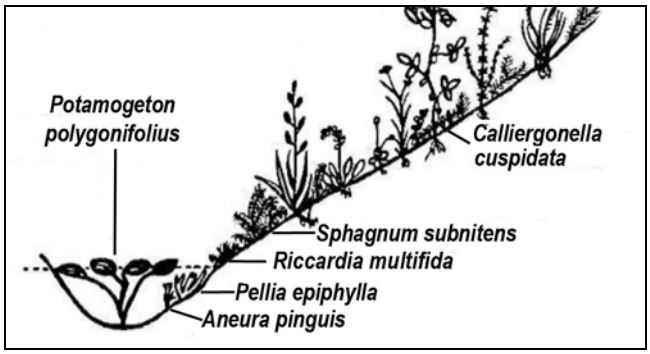

Figure 58. ***Pellia epiphylla*** zonation in a heathland water channel. Drawing modified from Watson 1915.

Clapham (1940) commented on the occurrence of the acidophilic ***Pellia epiphylla*** (Figure 49-Figure 51) in calcareous fens in the Oxford District of the UK. Clapham contended that the liverwort was able to grow there because of mats of fen mosses and the bases of woody plants that provided suitable substrata.

Physiology

Proctor *et al.* (1992) compared δ13C in nine ***Sphagnum*** species and several liverworts. That of ***Pellia epiphylla*** (Figure 49-Figure 51) was typical for that of the two Marchantialian liverworts.

One of the problems that aquatic bryophytes in particular must solve is obtaining CO_2 for photosynthesis. Evolutionarily, they have had the selective choice to concentrate it with such structures as pyrenoids, or to ventilate so that CO_2 can easily enter the plant and reach the photosynthetic tissue (Meyer *et al*. 2008). Tracheophytes have generally followed the latter evolutionary pathway. But ***Pellia*** lacks both pyrenoids and internal air chambers accessible through pores (Figure 31, Figure 59-Figure 60). In fact, ***Pellia*** has a simple thallus lacking pores and is diffusion limited. ***Pellia epiphylla*** (Figure 49-Figure 51) is more desiccation tolerant than ***Pellia endiviifolia*** (Figure 19-Figure 20). ***Pellia epiphylla*** exhibited a wider operating range of the mean total water content (88-142%) than did ***P. endiviifolia***. Meyer *et al*. concluded that it was this wider operating range that permitted ***Pellia epiphylla*** to maintain net gain in photosynthesis in drier habitats.

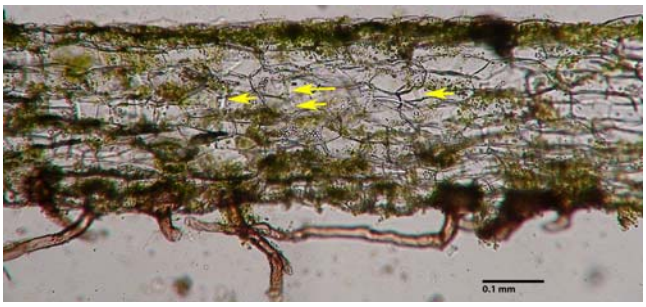

Figure 59. ***Pellia epiphylla*** longitudinal section, showing bands in some midrib cells (**arrows**) and rhizoids. Photo by Ken McFarland and Paul Davison, with permission.

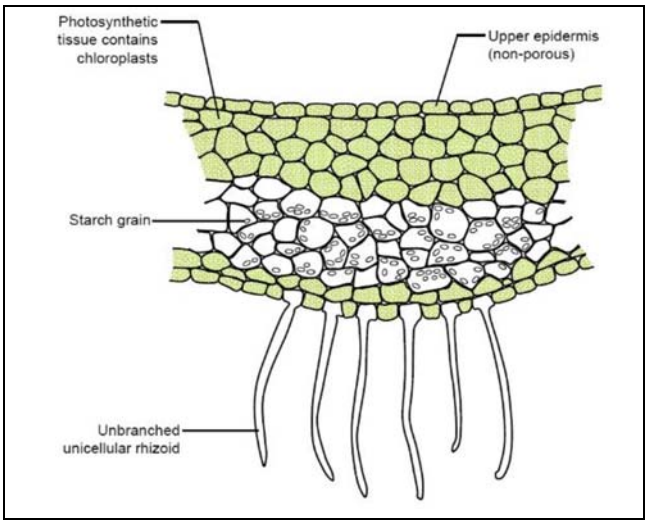

Figure 60. ***Pellia epiphylla*** cross section drawing. Photo from <Crondon.com>, with online permission for educational use.

Dilks and Proctor (1979) showed that species such as ***Pellia epiphylla*** (Figure 49-Figure 51) from moist habitats have increasing photosynthesis as water content increases in the range of 500 to 1000% of dry weight. Furthermore, its photosynthesis is affected at much lower water deficits than is respiration as the plant dries.

Proctor (1982) determined that the photosynthetic rate in the attached sporophyte of ***Pellia epiphylla*** (Figure 49-Figure 51) is very low when compared with that of its gametophyte. Using labelled CO_2, he found that the photosynthetic uptake of CO_2 by the sporophyte is only a few percent of the labelled C translocated from the gametophyte. It appears that this translocation from gametophyte to sporophyte is most active when the sporophyte has reached its full size but is still green, subsequently declining as the capsule matures through its final stages.

Samecka-Cymerman *et al*. (1997) investigated the ability of ***Pellia epiphylla*** (Figure 49-Figure 51) to serve as bioindicators of heavy metals in soil. They reported that in liverworts such as ***P. epiphylla*** the ionic balance is

disturbed by elevated concentrations of microelements, especially iron, copper, cobalt, and lead. Marczonek (1984) found a close correlation between the average thallus surface of ***Pellia epiphylla*** and the calcium to magnesium ratio in the soil, establishing the existence of relations between these liverworts and their substratum. For example, there is a significant relationship between lead and barium in the soil and that found in the liverwort (Samecka-Cymerman *et al*. 1997). But the relationships are not always simple. In ***Pellia epiphylla***, there is a negative correlation between manganese content of the soil and nitrogen, phosphorus, and potassium content in the liverworts. This relationship had already been established for tracheophytes and probably relates to competition for cation exchange sites on the liverwort surface. They suggested that the same competition probably applies to potassium. Mg^{++} can occupy two exchange sites, giving it a tighter hold, than can K^{+} that can occupy only one exchange site. On the other hand, ***Pellia epiphylla*** is a good biomonitor for nickel, chromium, copper, and barium.

Water in ***Pellia epiphylla*** (Figure 49-Figure 51) travels in capillary films between the rhizoids (Figure 59) and the lower surface, where it is partly absorbed (Clee 1939). What remains travels over the surface and is retained around the antheridia by the incurved and wavy thallus margins.

Those bryophytes, including most populations of ***Pellia epiphylla*** (Figure 49-Figure 51), that live out of the water must experience the freeze-thaw regimen of winter and early spring. Rütten and Santarius (1992) found that this species exhibits a distinct increase in cold tolerance from summer to winter. Nevertheless, compared to that of the mosses in the study, the hardening capacity of the liverwort was relatively low. All but one of the mosses experienced an increase in sucrose concentration in the cells, but no significant changes in glucose or fructose contents.

Pihakaski and Pihakaski (1979) examined the effects of chilling on the ultrastructure and net photosynthesis of ***Pellia epiphylla*** (Figure 49-Figure 51). Naturally frozen plants were thawed, revealing thallus margins that were brownish; cells were plasmolyzed. Chilling for 20 hours at -22ºC resulted in death of the thallus cells and disruption of the organelles. On the other hand, the apical growth region and the nerve with its surrounding cells were normal and green. Using various lengths of time at -22ºC, they determined that vacuoles of the dead cells were empty. Electron-dense particles appeared on the tonoplast and, in some cells, inside the vacuole; the nucleus also exhibited a granular appearance. Healthy cells that had been kept at 3ºC exhibited no granularity. At -22ºC lipid-like substances were apparent, but not at 3ºC. The oil bodies had either become more dense or were in various stages of disruption. Some appeared to have lost their contents.

Using ***Pellia epiphylla*** (Figure 49-Figure 51) that had been frost-hardened at 3ºC, Pihakaski and Pihakaski (1979) determined that both respiration and photosynthesis can continue below freezing (Figure 61). At -10ºC respiratory loss of CO_2 is greater than that gained by photosynthesis, but photosynthetic gain is greater in the range of -10 to -2ºC. As the plants thaw up to 5ºC, they reach a respiratory peak. At temperatures above 5ºC, photosynthesis increases slowly, then rapidly, then tapers off or decreases, approximating a sigmoid pattern as the temperature increases. Maximal photosynthesis in all plants occurs at 15-20ºC.

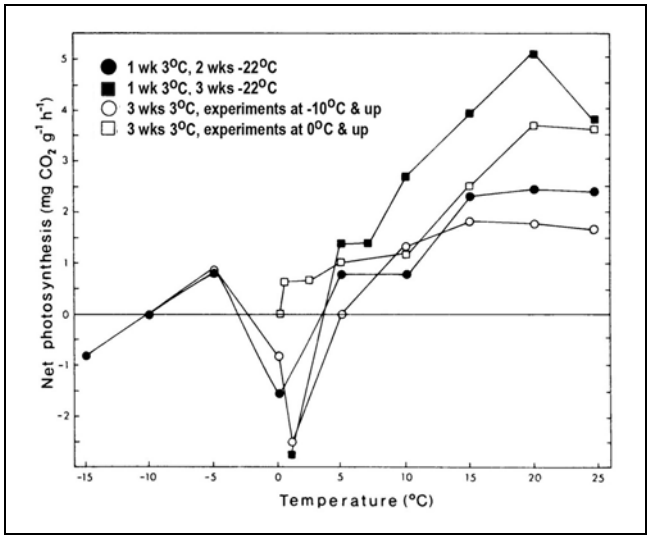

Figure 61. Net photosynthetic responses to temperature at 9000 lux for ***Pellia epiphylla***. Modified from Pihakaski and Pihakaski 1979.

Pihakaski and Pihakaski (1979) also noticed that the starch grains in the chloroplasts and the results of photosynthetic experiments indicate that chloroplasts of ***Pellia epiphylla*** (Figure 49-Figure 51) are able to photosynthesize at very low temperatures. Nevertheless, after 20 hours at -22ºC the starch-degrading is unable to perform and the plastids continue to contain large starch grains. In summary, cold-hardened ***Pellia epiphylla*** can recover very rapidly after a chilling period at -15ºC and even after long-term storage at -22ºC. Rapid chilling, however, is detrimental to CO_2 uptake. The researchers suggested that oil bodies may help in the survival of liverworts at low temperatures.

Dilks and Proctor (1975) noticed that leafy liverworts that withstood rapid cooling to -5ºC for 6 h are protected from intracellular freezing at normal rates of cooling by the withdrawal of water to form extracellular ice. On the other hand, they found that ***Pellia epiphylla*** (Figure 49-Figure 51) was killed by rapid cooling to -5ºC.

Adaptations

In the right circumstances. ***Pellia epiphylla*** (Figure 49-Figure 51) can achieve great masses and may cover a meter or more of soil (Greenwood 1911). One would expect such large clumps to provide more protection against desiccation than small patches.

The thalli of ***Pellia epiphylla*** (Figure 49-Figure 51) are typically completely green, but when they grow too far from water they can have a purplish or reddish tinge (Figure 62) along the middle (Greenwood 1911; Boll 2020). Their growth form changes from horizontal with close attachment to the substrate when the substrate is horizontal, but on vertical substrata they take on a more ruffled (Figure 63) habit (Boll 2020).

Figure 62. ***Pellia epiphylla*** with red coloration typical of populations growing too far from water. The mat habit and associated mosses can help it to retain water in these conditions. Photo by Michael Lüth, with permission.

Figure 63. ***Pellia epiphylla*** forming overlapping layers. Photo by Andrew Spink, with permission.

The ends of ***Pellia epiphylla*** (Figure 49-Figure 51), plants can overlap like shingles (Figure 63, Figure 66), providing at least some reduction in moisture loss. The gametophyte absorbs water primarily through its under surface (Figure 60, Figure 63) and the lower midrib is important in the retention of water (Boll 2020). Dry plants are thinner and have a more solid texture than that of plants from very moist locations (Greenwood 1911). The species furthermore produces more luxuriant growth near the water, which Greenwood attributes to having less compact cell structure in moist conditions.

It appears that ***Pellia epiphylla*** (Figure 49-Figure 51), lacks mechanisms to protect it from UV-B radiation. Takaćs *et al*. (1999) report that the protective mechanism is "rapidly exhausted" in this species, making it intolerant of increased UV-B.

Pellia epiphylla (Figure 49-Figure 51) does respond to light in another way. It exhibits positive phototropism of the sporophyte (Thomas *et al*. 1987). The entire length of the seta responded to 6 w m^{-2}. Curvature toward the light occurred within 10-15 minutes of continuous illumination. The growth rate of the shaded side of the seta increased significantly (from 0.50 to 0.96 mm hr^{-1}) and decreased on the lighted side (to 0.26 mm hr^{-1}).

Reproduction

Pellia epiphylla (Figure 49-Figure 51), is **monoicous** (Zielinski 1984). It was one of the first liverworts to have its development described. Hutchinson (1915) described development not only of growth, but also antheridia (Figure 64) and archegonia. As in most liverworts, fertilization requires that the plants be wet (Boll 2020).

Figure 64. ***Pellia epiphylla*** with antheridia. Photo by Des Callaghan, with permission.

Antheridia, archegonia, and sporangia are largely supplied with water from the exterior (Clee 1939). Capillary spaces retain the water in the narrow crevices between the antheridial cavity and antheridium, between the flaps of the involucre (Figure 66), and between these and the long necks of the archegonia. Antheridia absorb water until they burst, thus releasing the sperm cells that must swim to the archegonia for fertilization (Boll 2020). The antheridia absorb their water from the upper surface, probably ensuring that there is enough water to complete the fertilization process.

The water travels down the neck of the archegonium to the egg, thus facilitating entry of the sperm, and is there, available, for the developing embryo (Clee 1939). Films of water are retained between the sporophyte foot of the dividing embryo and the severed archegonium that now forms the calyptra. The sporophyte obtains water that is absorbed by the foot primarily from external sources. This water travels up the seta and eventually reaches the spores. Clee suggested that, therefore, the sporophyte is not very dependent on the gametophyte for its supplies of water or nutrients.

Walton (1943) described the sperm reaching the archegonium in greater detail. Noting that the archegonia are at the plant apex and that antheridia are 10-15 mm away on the dorsal surface, he questioned the feasibility of swimming between them. Showalter (1926) had found that it takes several hours for the sperm of a close relative, ***Aneura*** (Figure 65), to swim 10 mm. In fact, in many mosses and liverworts, it is the spermatocytes that are freed from the antheridia, and these are carried rapidly by water surface tension over the free water surface of the plants at ~20 mm per minute! When experimenting with ***Pellia epiphylla*** (Figure 49-Figure 51), Walton found that the spermatocytes broke loose from ripe antheridia, extruding in grey masses into the water. These masses quickly broke apart at the surface and dispersed rapidly across the wet

surface. It did not take hours, but only 15 seconds for the spermatocytes to reach the archegonial involucre (Figure 66). The free-swimming sperm required only 15 minutes to emerge from the spermatocytes and arrive at the archegonium.

Figure 65. ***Aneura pinguis***, in a genus in which sperm require several hours to swim 10 mm. Photo by Hugues Tinguy, with permission.

Figure 66. ***Pellia epiphylla*** with involucres (**arrow**) and overlapping lobes. Photo by Rob Cutis, through Creative Commons.

Various stages of capsule development of ***Pellia epiphylla*** (Figure 49-Figure 51) are shown in Figure 67 to Figure 82. Greenwood (1911) reported that plants of this species in moist conditions are more likely to be sterile than those in drier situations, with abundant capsules appearing in drier conditions (Figure 75-Figure 76). Interestingly, in April the maturity of capsules increases as plants occur nearer the water. New shoots were appearing at this time on the edges of the old plants (Figure 70-Figure 71), and antheridial beginnings were already visible as dots. Figure 84 shows a cross section of the capsule wall with spores inside.

Figure 67. ***Pellia epiphylla*** young capsules emerging from perianths. Photo from Biopix, through Creative Commons.

Figure 68. ***Pellia epiphylla*** young capsule emerging. Photo from Biopix, through Creative Commons.

Figure 69. ***Pellia epiphylla*** perianth inside involucre with seta extended. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 70. ***Pellia epiphylla*** from Illinois, USA, with senescing older parts and new green branches from the tips. Photo by Li Zhang, with permission.

Figure 71. ***Pellia epiphylla*** with emerging sporophyte. Note the old thalli that are brown and the new growth from the tips. Photo by Li Zhang, with permission.

Figure 72. ***Pellia epiphylla*** with nearly mature capsules. Photo by Michael Lüth, with permission.

Figure 73. ***Pellia epiphylla*** with elongating setae emerging from involucres at base. Photo by Malcolm Storey, <DiscoverLife.com>, with online permission.

Figure 74. ***Pellia epiphylla*** capsules nearing maturity. Photo by Allen Norcross, with permission.

Figure 75. ***Pellia epiphylla*** with abundant sporophytes in drier conditions. Photo by Michael Lüth, with permission.

Figure 76. ***Pellia epiphylla*** with numerous nearly mature capsules on elongated setae. Photo by Michael Lüth, with permission.

Despite the ease of having sperm reach the archegonia in this monoicous species, Zielinski (1984) found electrophoretic evidence of ***Pellia epiphylla*** (Figure 49-Figure 51) achieving cross-fertilization. In fact, Prus-Glowacki and Zielinski (1987) reported 93% cross fertilization, citing it as support of the hypothesis that this species might be self-incompatible. But it is also possible that a timing difference in maturity of antheridia and archegonia on the same plant might reduce self-fertilization. This needs further exploration.

Figure 77. ***Pellia epiphylla*** with both elongating setae and nearly dehiscing capsules. Photo by Jan-Peter Frahm, with permission.

Figure 78. ***Pellia epiphylla*** dehisced sporophytes. Photo by Kristian Peters, with permission.

Slade (1965) found that temperature and soil water tension affected both the rate of seta elongation and its final length in ***Pellia epiphylla*** (Figure 85). Daytime temperature is apparently more important than nighttime temperature. Day length has no effect, but low light intensity stimulates greater elongation, a seta version of etiolation.

Figure 79. ***Pellia epiphylla*** capsules with deliquescing setae after spores are shed. Photo by Jutta Kapfer, with permission.

Figure 80. ***Pellia epiphylla*** with numerous dehisced capsules. Photo by Allen Norcross, with permission.

Figure 81. ***Pellia epiphylla*** dehisced capsule. Photo by Allen Norcross, with permission.

Figure 82. ***Pellia epiphylla*** capsule dehisced. Photo by Ralf Wagner, <www.dr-ralf-wagner.de>, with permission.

Figure 83. ***Pellia epiphylla*** with dehisced capsule and mass of elaters. Photo by Malcolm Storey, <www.discoverlife.org>, with online permission.

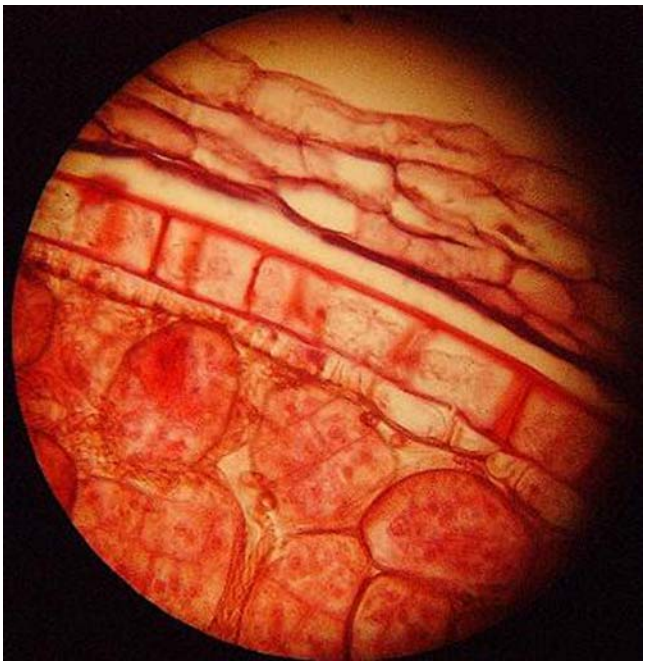

Figure 84. ***Pellia epiphylla*** capsule cross section showing capsule wall and spores. Photo from <Crondon.com>, with online permission for educational use.

Figure 85. ***Pellia epiphylla*** with emerging sporophytes. Photo by Michael Lüth, with permission.

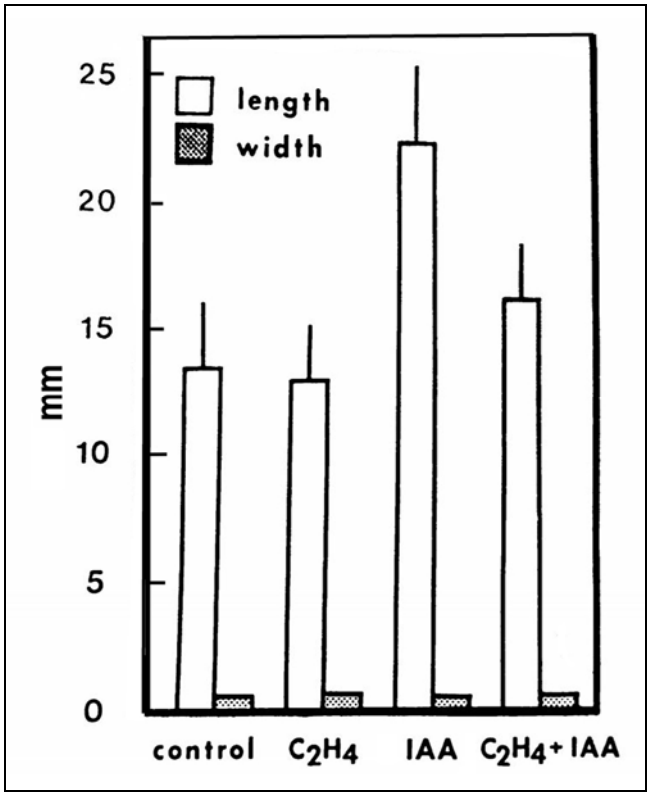

Figure 86. Effect of ethylene (C_2H_4 at 5 µl L^{-1}) and IAA (10 µM) on growth of ***Pellia epiphylla*** setae. Vertical line indicates standard error. Modified from Thomas *et al*. 1983.

Slade's observations are consistent with those of Asprey *et al*. (1958) for ***Pellia epiphylla*** (Figure 49-Figure 51). They reported that the sporangium, foot, and seta reach full differentiation by the end of September in Great Britain. However, in natural conditions, the seta does not elongate until the following year, usually starting in late February. Spores mature first, as indicated by the darkening of the capsule wall. The seta can elongate from 1 mm to as much as 80 mm in 3-4 days.

When capsules were treated with gibberellin (as 100 ppm potassium gibberellate) and maintained in culture at 18°C and natural daylight and day length in January, full seta elongation occurred in ***Pellia epiphylla*** (Figure 49-Figure 51) and reached an average length of 57 mm after 5 days (Asprey *et al*. 1958). The control capsules exhibited no elongation. When a solution of 1.0 ppm IAA was added to the gibberellic acid treatment, setae experienced full elongation. The researchers suggested that dormant setae of intact sporophytes may react to either potassium gibberellate or IAA to stimulate elongation of the seta. In isolated sporophytes, the potassium gibberellate produces only slight elongation (7-10 mm), whereas if that treatment is followed by IAA, full elongation (~63 mm) occurs. If only IAA is applied, elongation is attenuated at ~37 mm.

Thomas *et al*. (1983) demonstrated the presence of ~2.5-2.9 µg per gram fresh weight of putative free IAA in ***Pellia epiphylla*** (Figure 49-Figure 51) sporophytes. They also found that ethylene released by the setae increases during growth from 0.027 to 0.035 nanoliters per seta per hour (Figure 86). Applied ether (5 µL per liter) inhibits IAA-stimulated elongation of the seta. Thomas and coworkers postulated that IAA and ethylene act in tandem to modulate the elongation of the seta in this species. The further role of lunularic acid, a liverwort hormone similar to ABA, needs exploration.

Ellis and Thomas (1985) found that the shaded sides of sporophytes of ***Pellia epiphylla*** (Figure 49-Figure 51) became more acidic than the lighted sides. This change occurred before curvature occurred and could be produced also by the application of IAA or FC to one side of the seta. This response suggests that IAA mediates phototropism in ***Pellia epiphylla***.

Cromble and Paton (1958) found that there seems to be an age effect on sporophyte maturation. They suggest that a gradual change occurs during the winter months so that setae are ready for rapid elongation in spring when the temperature rises.

Schnepf *et al*. (1979) timed the growth of setae in ***Pellia epiphylla*** (Figure 49-Figure 51). The intact plants had a seta elongation rate of ~0.6 mm h^{-1}. Excised setae provided with 0.1 mM IAA exhibited a steady-state growth rate of 0.7-1.2 mm h^{-1}. A number of inhibitors altered the elongation rate. They interpreted the greater rate of elongation in excised sporophytes to indicate that this is not a passive thinning of auxin-loosened walls, but instead is dependent on maintenance of organized structure and macromolecule synthesis.

Poli *et al*. (2003) found that the IAA seems to move by simple diffusion in the liverworts, using ***Pellia epiphylla*** (Figure 49-Figure 51) as one of the model organisms. This contrasts with the bipolar transport that was operational in ***Polytrichum ohioense*** (Figure 87). Thomas *et al*. (2002) used radioactive labelling of IAA in ***Pellia epiphylla*** to trace the upward gravitropic curvature of horizontal sporophytes, showing response within 50-60 minutes. They furthermore showed that applied IAA moved preferentially to the lower side of the setae in horizontally oriented sporophytes. This mechanism provides a gravitropism that works to make sporophytes upright.

Figure 87. ***Polytrichum ohioense***, trail through virgin spruce, ***Picea rubra***, Gaudineer Park, WV. Photo by Janice Glime.

Farmer (1894b) found that the spores of ***Pellia epiphylla*** (Figure 49-Figure 51) don't germinate until after they leave the capsule, while noting that in some species of liverworts they germinate within the capsule. The ***P. epiphylla*** spores are "crowded" with starch grains. Willis (1957) described spore formation in the species.

Wolfson (1928) found that sporelings of ***Pellia epiphylla*** (Figure 49-Figure 51) have little capacity to resist desiccation, and they cannot resist drying for even one week. Wolfson describes early cell divisions in the sporelings.

Bartholomew-Began (1996) found the spores in ***Pellia epiphylla*** (Figure 49-Figure 51) to be **endosporic** (having 1 or more cell divisions within the spore wall; Figure 88) and **precocious** (developing early, sometimes within capsule). She describes the development of the protonema, noting that at the 23-24-cell stage rhizoid initiation occurs.

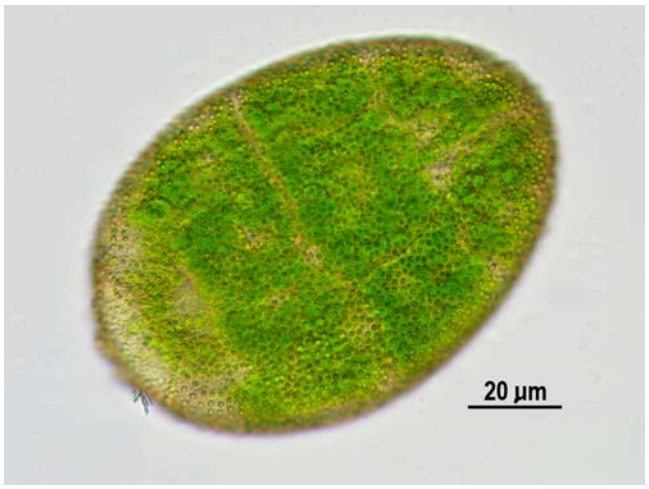

Figure 88. ***Pellia epiphylla*** spore showing divisions within the spore (**endosporic**). Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Interactions with Fungi and Slime Molds

Fungi have been observed in ***Pellia epiphylla*** (Figure 49-Figure 51) for more than a century. Ellis (1897) reported ***Trichoderma*** (Figure 89) as a parasite on the species. Ridler (1922) noted that every plant he inspected was infected with fungi. These appeared on both the gametophyte and sporophyte and the fungus seemed closest to a species of ***Phoma*** (Figure 90). Hadden (1921) reported the very rare ***Elaeomyxa cerifera*** (Figure 91), a slime mold, as occurring primarily on ***Pellia epiphylla*** (see also Ing 1994). But the role of fungi in the life of this and other liverworts have been largely ignored.

Figure 89. ***Trichoderma harzianum***, member of a fungal genus that is parasitic on ***Pellia epiphylla***. Photo from USDA, through public domain.

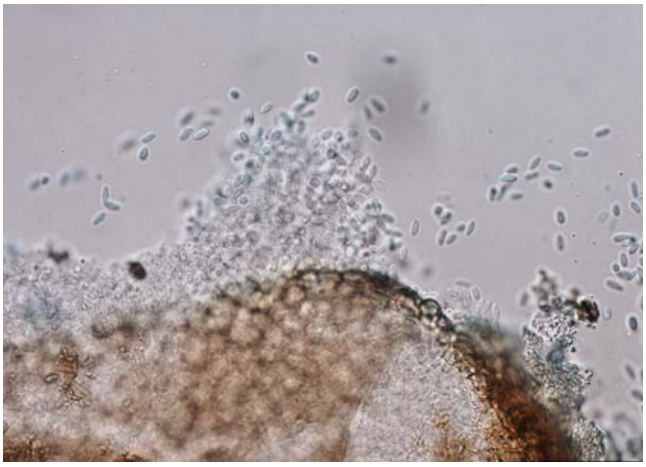

Figure 90. ***Phoma***, a genus that might be one that infects large numbers of ***Pellia epiphylla*** plants. Photo by Cesar Felderon, through Creative Commons.

Figure 91. ***Elaeomyxa cerifera***, a slime mold that occurs primarily on ***Pellia epiphylla***. Photo by Sarah Lloyd, with permission.

Magrou (1925) considered the relationship of fungi with ***Pellia epiphylla*** (Figure 49-Figure 51) to be **commensal** (describing relationship in which members of one species gain benefits while those of other species are neither benefitted nor harmed). Pressel *et al*. (2014) noted the use of molecular data and TEM (Figure 92-Figure 93) to understand the relationship between the two. Read *et al*. (2000) reported that glomalean fungi could form typical VA mycorrhizae in the flowering plant ***Plantago lanceolata*** (Figure 94), but also can colonize ***Pellia epiphylla***, where they produced arbuscules and vesicles in the thallus (Figure 92-Figure 93).

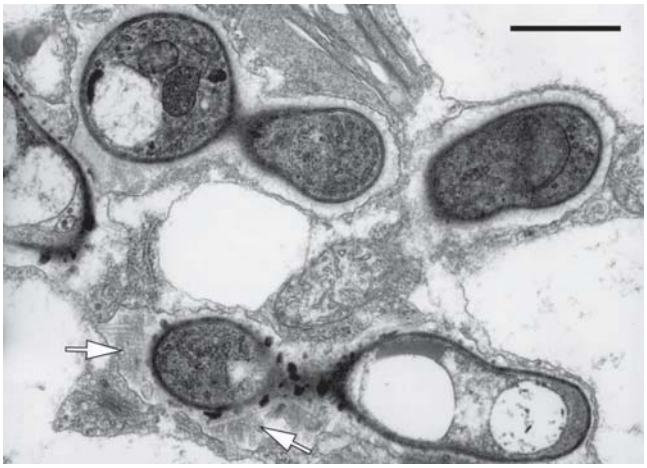

Figure 92. ***Pellia epiphylla*** cells with arbuscular fungi. Photo from Pressel *et al*. 2014, with permission.

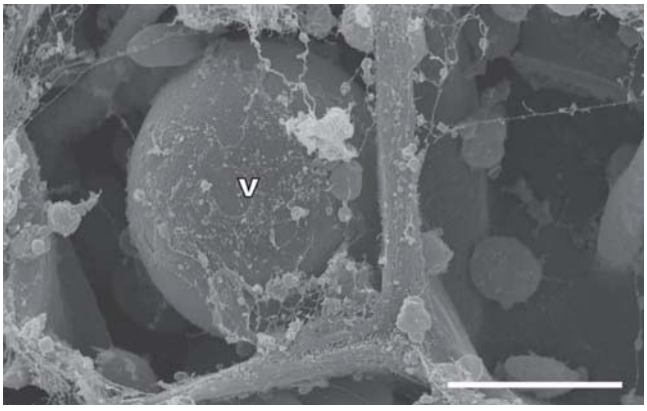

Figure 93. ***Pellia epiphylla*** with arbuscular fungi. Photo from Pressel *et al.* 2014, with permission.

Figure 94. ***Plantago lanceolata***, a species that has some of the same glomalean fungi as those in ***Pellia epiphylla***. Photo by Forest and Kim Starr, through Creative Commons.

Biochemistry

Pihakaski (1972) reported that proteins appeared to be present in the oil bodies (Figure 95) of ***Pellia epiphylla*** (Figure 49-Figure 51). Using electron microscope techniques, he showed that these proteins occur in the stroma, but not in the globules embedded in that stroma. Instead, the globules are comprised of unsaturated neutral lipids, forming the bulk of the total stainable lipids in the cell. These occur entirely in the oil bodies in ***Pellia epiphylla***.

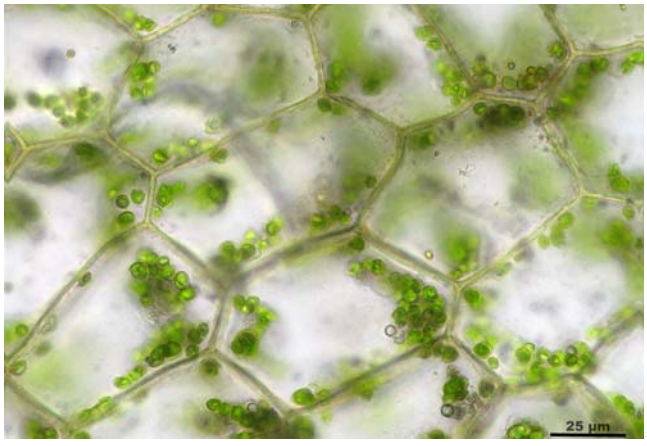

Figure 95. ***Pellia epiphylla*** lamina cells showing chloroplast and few small oil bodies. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Prus-Glowacki *et al*. (1998) found that two sibling species could be identified within ***Pellia epiphylla*** (Figure 49-Figure 51) based on differences in activity of malate dehydrogenase, esterase, and aspartate aminotransferase. Ono *et al.* (1992) demonstrated the closeness of ***P. epiphylla*** to ***P. neesiana*** (Figure 96-Figure 103) based on the presence of the pungent diterpene dialdehyde, sacculatal in both. Pacak *et al*. (1998) used RAPD to support the distinction between the northern and southern **allopatric** (having non-overlapping distributions) populations of ***Pellia epiphylla*** in Poland and that the polyploid ***Pellia borealis*** is a hybrid of these two.

Cullmann *et al*. (1996) isolated a new macrocycle of lignan, caffeic acid, and an aliphatic C_8 moiety from ***Pellia epiphylla*** (Figure 49-Figure 51). Cullmann *et al*. (1997) identified phenolic constituents, naming pellepiphyllin, 7-hydroxypellepiphyllin, perrottetin E, perrottetin E-11-methyl ether, 14′-hydroxyperrottetin E, 10′-hydroxyperrottetin E, 10′-hydroxyperrottetin E-11-methyl ether, 10,10′-dihydroxyperrottetin E and 13′, 13‴-bis (10′-hydroxyperrottetin E). Mukhia *et al*. (2015) confirmed the presence of the phenolic compounds coumarin, alkaloid, anthraglycoside, arbutin, phenol, and flavonoids and demonstrated significant anti-diabetic activity. Phenolic compounds often serve as herbivore deterrents, but to my knowledge this has not been tested in ***Pellia epiphylla***. Cullmann and Becker (1998a) extracted eight sesquiterpenoids from ***Pellia epiphylla***, three of which were new. Six diterpenes, several sterols, betulin, and δ-tocopherol were present. Pellialactone was present, and loliolide was shown in a liverwort for the first time. Rischmann *et al*. (1989) isolated a new naphthalene derivative from the gametophyte of ***Pellia epiphylla*** and defined its structure. Li *et al*. (2019) continued to isolate sacculatanes, describing eight that were not previously known from ***Pellia epiphylla***. Two of the epiphyllins exhibited antioxidant effects.

Cullmann and Becker (1998b) did an unusual study by examining secondary compounds in the sporophytes and spores of ***Pellia epiphylla*** (Figure 67-Figure 85). They identified five africanane-type sesquiterpenes, *epi*-swartzianin A, 9(15)-africanene, isoafricanol, leptographiol, and the new 10*β*-hydroxy isoafricanol, the new humulane derivative 1,8-humuladien-5-ol, caryophyllene oxide, phytol, and (1,2)-bis-nor-phytone. They also found palmitic acid, linolic acid methyl ester, 7, 10, 13-hexadecatriene acid methyl ester, octadecanol and three bisbibenzyls: perrottetin E, 10'-hydroxy perrottetin E, 10'-hydroxy perrottetin E-11-methyl ether, caffeic and ferulic acid methyl esters, and four flavones: luteolin, luteolin-7-methyl ether, luteolin-7,3'-dimethyl ether and the new luteolin-5,7,3'-trimethyl ether. In addition, spores contained isoafricanol and 1,8-humuladien-5-ol.

Pihakaski and Pihakaski (1980) demonstrated that in ***Pellia epiphylla*** (Figure 49-Figure 51) the herbicide glyphosate caused a rapid decrease in photosynthetic activity and also in its ability to react quickly to changes in light intensity. Nevertheless there appeared to be some sort of acclimation to the glyphosate. The net photosynthetic inhibition was strong for the week following exposure, but that reversed during the following weeks. After 4-5 weeks following glyphosate treatment, net photosynthesis increased again. On the day following treatment, a number of cytological changes occurred, including structural changes to the chloroplast surface, deterioration of oil bodies, endoplasmic reticulum, and ribosomes, increase of lipid spherules, and vacuolation of cytoplasm. After two weeks the grana formation was deteriorated, the plasmalemma was disconnected, and the length of mitochondrial cristae had decreased.

Pellia neesiana (Figure 96-Figure 103)

Distribution

Pellia neesiana (Figure 96-Figure 103) is widely distributed in the northern part of the Northern Hemisphere (Schütz *et al*. 2016). It occurs in Europe, Asia, North America, Greenland, and Iceland, particularly at higher elevations.

Figure 96. ***Pellia neesiana*** in a tight, single-species colony. Photo by C. and C. Johnson <www.ohbr.org.uk>, with permission.

Figure 97. ***Pellia neesiana*** showing a typical yellow-green thallus. Photo by David T. Holyoak, with permission.

Figure 98. ***Pellia neesiana*** thallus. Photo by Des Callaghan, with permission.

Figure 99. ***Pellia neesiana*** with scattered antheridia. Photo by J. C. Schou, with permission.

Figure 100. ***Pellia neesiana*** showing transparency of the thallus. Photo by Ken McFarland and Paul Davison, with permission.

Figure 101. ***Pellia neesiana*** female with involucre. Photo by Jan-Peter Frahm, with permission.

Figure 102. ***Pellia neesiana*** showing transparency of the thallus. Photo by Ken McFarland and Paul Davison, with permission.

Figure 103. ***Pellia neesiana*** in a wet habitat. Photo by J. C. Schou, with permission.

Aquatic and Wet Habitats

Pellia neesiana (Figure 96-Figure 103) occurs on grassy ground or on rocks by fast streams (Watson 1919). In the Alps, it is not common, with ***Trichophorum cespitosum*** (Figure 104) (Geissler & Selldorf 1986). It occurs on soil in the flood valley of the Upper Bureya River (Russian Far East) (Konstantinova *et al*. 2002). In northeastern Finland it occurs in streams (Heino & Virtanen 2006).

Figure 104. ***Trichophorum cespitosum***, a sedge species that is sometimes accompanied by ***Pellia neesiana*** in the Alps. Photo by Hermann Schachner, through Creative Commons.

Basile *et al*. (2017) considered ***Pellia neesiana*** (Figure 96-Figure 103) to be a species living submerged along the rivers in cool and temperate areas of the northern hemisphere. But based on the records I have found, ***Pellia neesiana*** is less of a river species, and the records suggest it might spend most of its life above water. Sharp (1944) reported that it could attain local abundance on boulders in a creek in Virginia, USA. Steere (1937) found it on a rotten log in a small stream in Michigan, USA. But it is not clear if these latter two finds were submersed.

Wet soil and habitats close to water are much more common for ***Pellia neesiana*** (Figure 105) than submersed habitats. Nichols (1922) reported that it was locally abundant along muddy river shores in Michigan, USA. Lepage (1953) reported a similar habitat in northern Québec, Canada. Hong (2007) reported it from moist soil near a stream in the Queen Charlotte Islands, British Columbia, Canada. Across the ocean in the Western Caucasus of Russia, ***Pellia neesiana*** occurs on dry river beds, on bare soil among grasses in wet areas (Figure 106), on rocks and soil on banks of streams in subalpine meadows, and at edges of streams in forests (Konstantinova *et al*. 2009). Dulin (2015) likewise found it on river banks in the Komi Republic of Russia. Schütz *et al*. (2016) included stream banks in their summary of its habitats.

Figure 105. ***Pellia neesiana*** at the edge of a stream. Photo by C. and C. Johnson <www.ohbr.org.uk>, with permission.

Figure 106. ***Pellia neesiana*** habitat on bank. Photo by Michael Lüth, with permission.

It appears that the best place to search for ***Pellia neesiana*** (Figure 96-Figure 103) might be on soil near pools and lakes (Figure 107). Bartholomew-Began (1999) found it on thin, fine soil over rocks at the edge of a pool in the Hawk Mountain Sanctuary, Pennsylvania, USA. Dulin (2015) reported it from the banks of lakes in the Komi Republic of Russia. Schütz *et al.* (2016) reported that it tolerates seasonal flooding, including along lake margins.

Figure 107. ***Pellia neesiana*** at the edge of water. Photo from Botany Website, UBC, with permission.

Haynes (1909) identified ***Pellia neesiana*** (Figure 96-Figure 103) from the side of a decaying log as well as on wet ground. The species occurs on moist, sandy soil in Kentucky, USA (Fulford 1934). Papp *et al*. (2013) reported it from a wet meadow in western Croatia. Dulin (2015) reported it from soil in hollows and on butts of trees in a grass-***Sphagnum*** (Figure 108) habitat as well as in birch forests (Figure 109). Schütz *et al*. (2016) considered it to prefer soils that were moderately acid to sub-neutral.

Schütz *et al*. (2016) included springs, marshes, ditches, and damp tracks among the habitats of ***Pellia neesiana*** (Figure 96-Figure 103). These are typically shaded, sub-neutral to moderately acid clayey to sandy loams with poor nutrient content.

Figure 108. Grass-***Sphagnum*** habitat where one might find ***Pellia neesiana*** in soil hollows. Photo by Janice Glime.

Figure 109. ***Pellia neesiana*** large patch on forest floor. Photo by Michael Lüth, with permission.

Wet cliffs (Figure 110) can at times be suitable for colonization. Bakalin (2015) reported ***Pellia neesiana*** (Figure 96-Figure 103) from moist crevices in cliffs, moist to wet cliffs, and gravelly barrens in open places, particularly in the alpine belt of the Tardoki-Yani Range in Pacific Russia.

Figure 110. Rock wall and waterfall on cliff that could be a habitat for ***Pellia neesiana***. Photo by Allen Norcross, with permission.

So far I have found only one report of boggy habitats. Konstantinova *et al*. (2009) report ***Pellia neesiana*** (Figure 96-Figure 103) on hillocks among ***Sphagnum*** and in grass-***Sphagnum*** bogs (Figure 108). Dulin (2015) similarly attributed it to grass-***Sphagnum*** and herb-***Sphagnum*** habitats. He also reported it in waterside boggy grass willow-birch communities.

Hugonnot (2011) described ***Pellia neesiana*** (Figure 96-Figure 103) fens (Figure 111) in the Massif of central France. Lenz (2011) found it in a sloping shrub fen of Bighorn National Forest in Wyoming, USA.

Figure 111. Fen habitat dominated by bryophytes. Photo through Creative Commons.

Although late snowbeds (Figure 112) are neither aquatic nor wetlands, they do provide an extended period of available water as they melt. ***Pellia neesiana*** (Figure 96-Figure 103) can be dominant in such areas (Górski 2015).

Figure 112. Alpine snowbed that can provide water well into summer, creating a habitat suitable for ***Pellia neesiana***. Photo by Alpandino, through Creative Commons.

Physiology

Like so many of the aquatic bryophytes, ***Pellia neesiana*** (Figure 96-Figure 103) has been the subject of the effects of pollution on bryophytes. Basile *et al*. (2017) examined the liverwort to determine the effect

contaminated water from the Sarno River in South Italy in consideration of its potential as a biomonitor. They floated the liverwort in the river in nylon bags for one week. They observed severe alterations to the chloroplasts and modified cell ultrastructure from samples exposed to the highest levels of Cd and Pb both in the lab and in the river. Interestingly, heat shock proteins (HSP70) increased as the pollution gradient increased. They attributed the ultrastructural changes to those heat shock proteins, noting that at the same time, histological changes were not evident after a 7-day exposure in the river.

Adaptations

Pellia neesiana (Figure 96-Figure 103) has an undifferentiated thallus (Figure 113-Figure 114) where photosynthesis occurs. Thus, it lacks air chambers and must exchange oxygen and CO_2 through its non-porous epidermis.

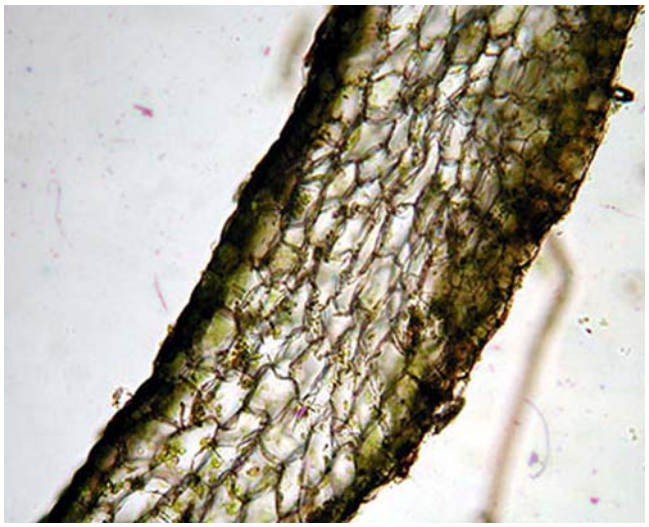

Figure 113. ***Pellia neesiana*** thallus cross section showing lack of internal air chambers. Photo from Botany Website, UBC, with permission.

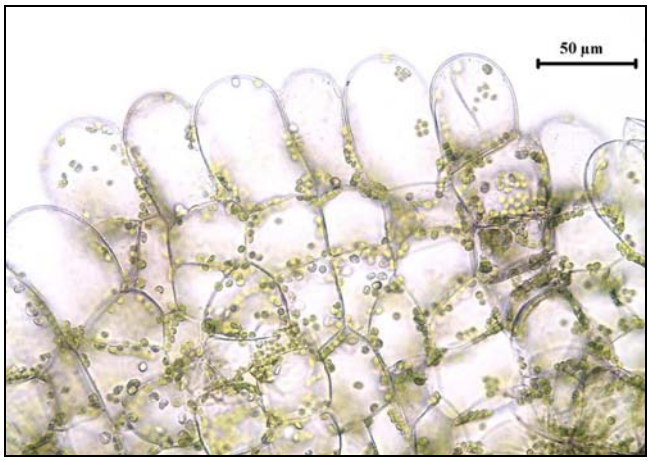

Figure 114. ***Pellia neesiana*** thallus cells, creating papillae on the margin. Photo by Hugues Tinguy, with permission.

Pellia neesiana (Figure 96-Figure 103) occurs in pure mats (Figure 115-Figure 116) or with ***Scapania spitsbergensis*** (Figure 117), ***Schistochilopsis opacifolia*** (Figure 118), ***Trilophozia quinquedentata*** (Figure 119) in the alpine belt of the Tardoki-Yani Range in Russia (Bakalin 2015).

Figure 115. ***Pellia neesiana*** forming a nearly pure mat with a few mosses. Photo by Bernd Haynold through Creative Commons.

Figure 116. ***Pellia neesiana*** showing dark-color form. Photo by Hermann Schachner, through Creative Commons.

Figure 117. ***Scapania spitsbergensis*** with pink coloration, species that occurs with ***Pellia neesiana*** in alpine belt of Russia. Photo by S. S. Choi <portal.kgilc.ru>, with online permission.

Figure 118. ***Schistochilopsis opacifolia***, species that occurs with ***Pellia neesiana*** in alpine belt of Russia. Photo by Hermann Schachner, through Creative Commons.

Figure 119. ***Trilophozia quinquedentata***, species that occurs with ***Pellia neesiana*** in alpine belt of Russia. Photo by Hermann Schachner, through Creative Commons.

Pellia neesiana is typically yellowish green (Figure 120), but it often develops red to reddish-purplish coloration (Figure 115) (Schütz *et al*. 2016). The color change could be a response to light exposure, but it can also be an indicator of other types of stress.

Reproduction

Pellia neesiana (Figure 96-Figure 103) is **dioicous** (Schuster 1992). Antheridia occur in the mid region of the thallus (Figure 120-Figure 125). Schütz *et al*. (2016) reported that ***Pellia neesiana*** can produce up to 30 archegonia from the vertical flat receptacle and the bottom of the gynoecium (Figure 126-Figure 127).

Figure 120. ***Pellia neesiana*** antheridia. Photo by C. and C. Johnson <www.ohbr.org.uk>, with permission.

Figure 121. ***Pellia neesiana*** with antheridia. Photo by Michael Lüth, with permission.

Figure 122. ***Pellia neesiana*** antheridia. Photo by Hugues Tinguy, with permission.

Figure 123. ***Pellia neesiana*** antheridia. Photo by Hugues Tinguy, with permission.

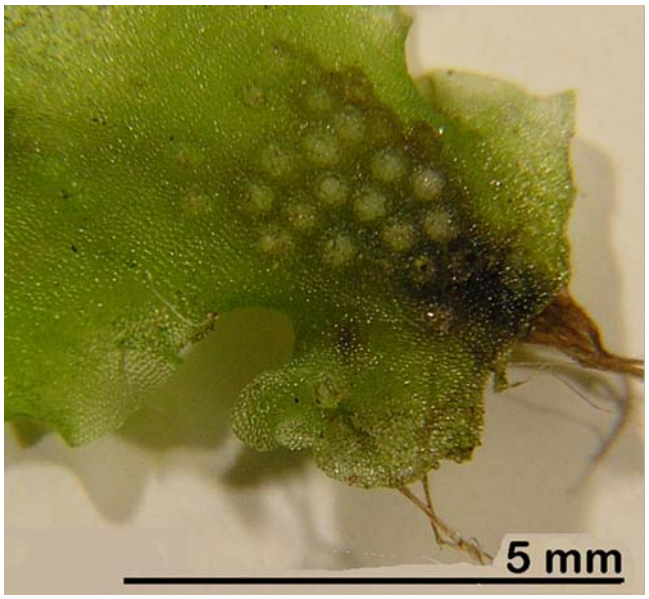

Figure 124. ***Pellia neesiana*** with opened antheridia. Photo courtesy of David H. Wagner.

Figure 125. ***Pellia neesiana*** antheridium. Photo by C. and C. Johnson <www.ohbr.org.uk>, with permission.

Figure 126. ***Pellia neesiana*** females, showing yellowish green color and involucres. Photo by David T. Holyoak, with permission.

Figure 127. ***Pellia neesiana*** with female involucre. Photo by Jan-Peter Frahm, with permission.

Despite its **dioicous** condition, ***Pellia neesiana*** (Figure 96-Figure 103) has produced enough sporophytes (Figure 128-Figure 131) for two researchers to study the germination and development of spores and sporelings. Wolfson (1928) described the cell division as the spore germinated and found that the sporelings have little tolerance for desiccation. Bartholomew-Began (1996) made further investigations into the divisions of the protonema, comparing them with those of ***Pellia epiphylla*** (Figure 49-Figure 51). Like ***P. epiphylla*** (Figure 49-Figure 50), ***Pellia neesiana*** is precocious and endosporic. Rhizoid initiation occurs after the protonema reaches 23 or 24 cells. The protonema develops into a thalloid form, but its pattern of division in both species differs from that of metzgerialian liverworts.

Figure 128. ***Pellia neesiana*** with young sporophyte. Photo from Botany Website, UBC, with permission.

Figure 129. ***Pellia neesiana*** with capsules and elongating setae. Photo by Janice Glime.

Figure 130. ***Pellia neesiana*** with nearly mature capsules and elongated setae. Photo by Dale Vitt, with permission.

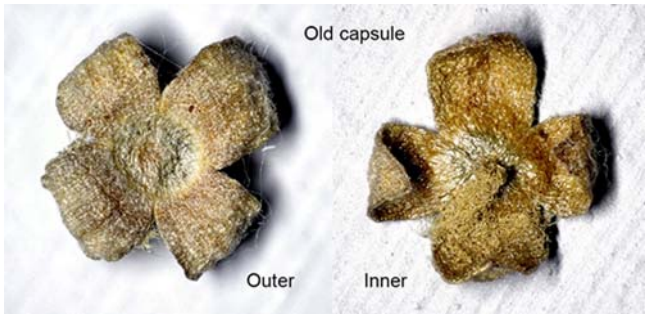

Figure 131. ***Pellia neesiana*** dehisced capsule. Photo by C. and C. Johnson <www.ohbr.org.uk>, with permission.

Role

Wilkinson *et al*. (2005) discovered that labelled nitrogen decreased in ***Pellia neesiana*** (Figure 96-Figure 103) with distance from the salmon stream into the forest. The researchers noted that bears catch fish, then transport them to land to consume them (Figure 132). This activity distributes the N from the salmon into the forest. ***Pellia neesiana*** also was in far greater abundance below the falls, and the researchers suggested that the liverwort was exploiting nutrients available from salmon carcasses and other wildlife activity.

Figure 132. ***Ursus americanus*** (black bear) carrying fish to land. Photo by Aaron Huelsman, through Creative Commons.

Pellia neesiana (Figure 96-Figure 103) has experienced several studies on its faunal relationships. However, Grimaldi (2018) reports that the leaf mining fly ***Spania nigra*** (Figure 133-Figure 135) uses ***Pellia neesiana*** as a home and food for its larvae and a place for pupation (see also (Mik 1896; Nartshuk 1995).

Figure 133. ***Spania*** sp. eggs (**arrows**) on ***Pellia endiviifolia***. Photo by Yume Imada and Makoto Kato, with permission.

Figure 134. ***Spania*** sp. first instar larva mining ***Pellia endiviifolia***. Photo by Yume Imada and Makoto Kato, with permission.

Figure 135. ***Spania*** sp. final instar larva and posterior spiracle closeup. Photo by Yume Imada and Makoto Kato, with permission.

Biochemistry

Pellia neesiana (Figure 96-Figure 103) has tiny oil bodies (3.6-6.5 µm across; Figure 136), numbering from 8 up to 32 (Schuster 1992).

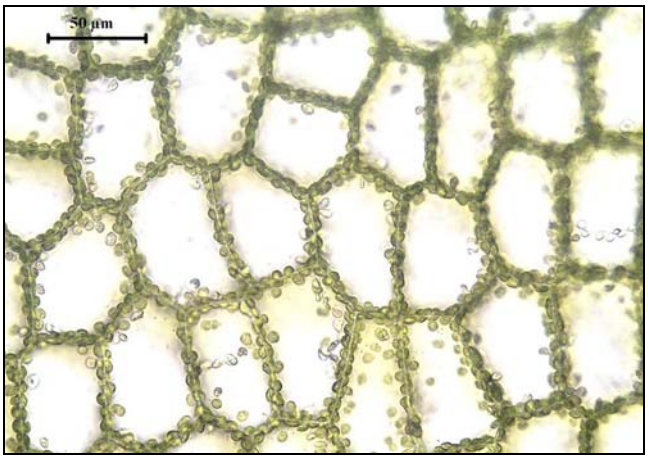

Figure 136. ***Pellia neesiana*** thallus cells. Chloroplasts confined to margins of cell indicate presence of large vacuole. Mostly colorless oil bodies are scattered. Photo by Hugues Tinguy, with permission.

Ono *et al*. (1992) detected the pungent diterpene dialdehyde, sacculatal in ***Pellia neesiana*** (Figure 96-Figure 103), suggesting its close relationship to ***P. endiviifolia*** (Figure 19-Figure 20).

Summary

These members of the **Pelliales** are at best facultatively aquatic. On the other hand, they like moist habitats and ***Pellia*** in particular can be found on stream banks, especially under overhanging grasses where it is moist and shaded. Others tolerate temporary ponds where they are submerged part of the year and out of water part of the year. ***Pellia epiphylla*** had both slime molds and fungi that find it a suitable place to live, whereas ***Pellia neesiana*** provides a home for the leaf-mining fly ***Spania***.

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Add *Blasia pusilla* slime papillae image

CHAPTER 1-17
AQUATIC AND WET MARCHANTIOPHYTA, ORDER BLASIALES

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CHAPTER 1-17
AQUATIC AND WET MARCHANTIOPHYTA, ORDER BLASIALES

Figure 1. ***Blasia pusilla*** forming a rosette on wet soil. Photo by Dale Vitt, with permission.

Nomenclature for this chapter is based primarily on Söderström *et al*. (2016). In addition, Lars Söderström provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. These unverifiable taxa have been included in the species.

To develop this list, I used my own bibliography, collected over the past 56 years, and Google Scholar. These papers soon led me to others. I do not pretend that this is complete. It includes streams, lakes, wetlands, and other wet substrata. It mostly ignores bogs and ignores fens, but nevertheless includes a few of these species because they were found in a wetland study. Bogs and poor fens have been treated in whole books and provide an extensive literature; fens seem somewhat less studied. They would require considerably more review and time. Thus I felt that less-reviewed topics, particularly the aquatic habitats with which I am most familiar, should be given priority.

The species in this subchapter are not typical wetland or aquatic species. They were, however, found in a wetland or aquatic study. Their relative frequency can be noted based on the number of references cited.

MARCHANTIOPSIDA

Blasiidae – Blasiales

Blasiaceae

Blasia pusilla

Distribution

Blasia pusilla is a boreal-montane species (Dia & Not 1991). It occurs in Europe, West Greenland, North America, Asia (India, Kamchatka, China, Korea, Japan) (Rohret 1916; Schuster 1992). Schuster (1992) considers the Australian records to be errors.

It tends to form rosettes on its substrate (Figure 1-Figure 3).

Figure 2. ***Blasia pusilla*** habit on soil. Photo by Štěpán Koval, with permission.

Figure 3. ***Blasia pusilla*** habit, Mt. Robson, BC, Canada, 26 July 1980. Photo by Janice Glime.

Figure 4. ***Blasia pusilla*** rosette on sand, showing conspicuous ribs. Photo by Štěpán Koval, with permission.

Figure 5. ***Blasia pusilla*** on sand, with stellate gemmae. Photo by Štěpán Koval, with permission.

Aquatic and Wet Habitats

Blasia pusilla (Figure 1-Figure 6) is not typically a submersed species. Holmes and Whitton (1975) considered it to be an "uncommon" member of the flora in the River Tweed. Jonsgard and Birks (1995) reported it from small streams in the Krakenes, Norway. In the Caucasian State Nature Reserve, Russia, it occurred in the dry river bed of the Bushujka River on silting rocks (Konstantinova *et al*. 2009).

Schuster (1992) comments that when ***Blasia pusilla*** (Figure 1-Figure 6) does occur in stream beds, it is almost always seasonal. Erosion and slippage seem to destroy most of the plants.

Nevertheless, the usual habitat of ***Blasia pusilla*** seems to be near water (Figure 6), occasionally submerged in some locations, but only facultatively aquatic.

Figure 6. ***Blasia pusilla*** on wet soil. Photo by Kristian Peters, with permission.

River and stream banks seem to be among the most suitable habitats for ***Blasia pusilla*** (Figure 1-Figure 6). Sampson (1905) reported it from the bank of the River Dee in the UK. Paton (1967, 1971) reported it from gravelly detritus by a river and a clay stream bank in the UK. Rilstone (1949) found it on wet banks (Figure 1) in Cornwall, UK, but considered it to be rare. Fitzgerald and Fitzgerald (1966) reported it from schist detritus on rocks by the Glenedra River in northeast Ireland. Similarly, M'Ardle (1909) noted that it occurred among wet rocks in Ireland. Schumacher and Sivertsen (1987) found it on the banks of rivers, brooks, and rivulets in Norway, and Damsholt *et al*. (1984) reported it from along rills, along with ***Scapania paludosa*** (Figure 7) and ***Pellia neesiana*** (Figure 8).

Figure 7. ***Scapania paludosa***, a species that occurs with ***Blasia pusilla*** along rills in Norway. Photo by Hermann Schachner, through Creative Commons.

Figure 8. ***Pellia neesiana***, a species that occurs with ***Blasia pusilla*** along rills in Norway. Photo from Botany Website, UBC, with permission.

Váňa and Ignatov (1995) reported ***Blasia pusilla*** (Figure 1-Figure 6) from ravine slopes and on logs covered by alluvium in flood valleys, as well as creek bars, in the Altai Mountains of Asia. In the Komi Republic, Dulin (2014) found ***Blasia pusilla*** on inundated soil along the river bank, in pure patches (Figure 9) or with other liverworts. Sofronova reported it from banks of water courses in the Upper Course of the Indigirka River, East Yakutia (Sofronova 2018), and on stones near the Timpton River as well as rock outcrops there, sustaining in both river and stream banks that experience occasional floods (Sofronova 2017). In South Siberia it can be found in willow thickets along river and stream banks, sometimes mixed with ***Jungermannia pumila*** (Figure 10) and ***Scapania mucronata*** (Figure 11) (Czernyadjeva *et al*. 2013).

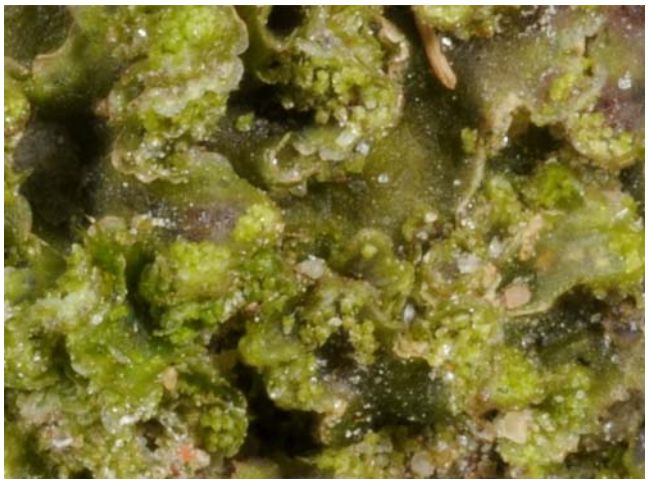

Figure 9. ***Blasia pusilla*** growing in pure patch on sand. Photo by Jouko Rikkinen, through Creative Commons.

Figure 10. ***Jungermannia pumila***, a species that occurs mixed with ***Blasia pusilla*** in South Siberia willow thickets. Photo by Michael Lüth, with permission.

Figure 11. ***Scapania mucronata***, a species that occurs mixed with ***Blasia pusilla*** in South Siberia willow thickets. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

In North America, Blomquist (1939) found ***Blasia pusilla*** (Figure 1-Figure 6) along the west branch of the New River in the Appalachian Mountains, USA. In the Arctic, it develops extensive cover, up to 75%, in the area flooded by glacial streams (Slack & Horton 2010). Skorepa (1968) found it on moist, shaded sandstone near a stream in southern Illinois, USA. Wagner (2009) reported it from moist sand (Figure 12-Figure 14) next to a creek in Oregon, USA, both solitary and mixed with other liverworts and with hornworts. It seems to like clay, occurring on clayey stream banks in Ohio, USA (Hall 1958). Hong (1978, 1980) reported it from wet rocks and soil in the North Cascades Range of Washington, USA.

Figure 12. ***Blasia pusilla*** in aging small, pure patches on sand. Photo by Jouko Rikkinen, through Creative Commons.

Figure 13. ***Blasia pusilla*** habit on sand. Photo by Jouko Rikkinen, through Creative Commons.

Figure 14. ***Blasia pusilla*** habit on sand with older thallus dying. Photo by Jouko Rikkinen, through Creative Commons.

Ditches (Figure 15) can offer similar conditions to streams, so the presence of ***Blasia pusilla*** (Figure 1-Figure 6) there might be expected. Taylor (1921) reported it from the sides of a ditch in Mount Desert, Maine, USA. Paton (1971) similarly found it on a ditch bank in the UK.

Figure 15. Drainage ditch in Germany, a habitat where one might find ***Blasia pusilla*** along the sides. Photo by Dirk Ingo Franke, through Creative Commons.

Waterfalls provide moist habitats where moisture-loving liverworts are able to survive (Figure 16). On Bering Island, Russia, ***Blasia pusilla*** (Figure 1-Figure 6) occurs on wet boulders in a waterfall canyon (Bakalin 2005). Gruber *et al*. (2005) found that in the area near Krimml Waterfalls of Austria, ***Blasia pusilla*** grows best in locations receiving spray from the waterfalls. Odland *et al*. (1991) found that following regulation of a river in Aurland, western Norway, cover by ***Blasia pusilla*** increased near the waterfall in the spray zone. The regulation reduced the spray precipitation by 98-100%, but there is still considerable spray near the waterfall.

Figure 16. Waterfalls such as these create a constantly moist environment suitable for liverworts such as ***Blasia pusilla***. Photo by Fabian Michelangeli, through public domain.

Slopes often provide moist, shaded habitats (Figure 17-Figure 18). Rose (1950) found that ***Blasia pusilla*** was "plentiful" on a damp, north-facing bank on clayey sand in the UK. Dulin (2014) found it on "slightly matted loamy soil at a slope ledge" and on the vertical surface of a ground wall in the Komi Republic. Bakalin *et al*. (2016) found it on the moist soil or mineral ground of eroded slopes, where it typically occurred with ***Anthelia juratzkana*** (Figure 19), ***Calypogeia muelleriana*** (Figure 20), and ***Solenostoma hyalinum*** (Figure 21).

Figure 17. ***Blasia pusilla*** habitat on slope. Photo by Hermann Schachner, through Creative Commons.

Figure 18. ***Blasia pusilla*** habitat on slope. Photo by Hermann Schachner, through Creative Commons.

Figure 19. ***Anthelia juratzkana***, a species that occurs with ***Blasia pusilla*** on slopes in Russia. Photo by Hermann Schachner, through Creative Commons.

Figure 20. ***Calypogeia muelleriana***, a species that occurs with ***Blasia pusilla*** on slopes in Russia. Photo by Hugues Tinguy, with permission.

Figure 21. ***Solenostoma hyalinum*** with capsule, a species that occurs with ***Blasia pusilla*** on slopes in Russia. Photo by Michael Lüth, with permission.

Figure 22. ***Blasia pusilla*** on wet soil. Photo by Bernd Haynold, through Creative Commons.

In the Mt. Greylock region of Massachusetts, USA, Andrews (1904) found only a small specimen on a wet bank in the Notch. Lanfear (1933) found ***Blasia pusilla*** (Figure 1-Figure 6) on clay banks and shale in western Pennsylvania, USA. Conard (1940) likewise reported it from moist, shaded clayey banks, where it was rare, in Iowa, USA. Breil (1996) found it on moist, eroding loamy slopes in the Virginia Piedmont, USA.

The suitable slopes include a number of records along trails. Váňa and Ignatov (1995) reported it from wet clayish soil along both trails and roads in the Altai Mountains of eastern Asia. Czernyadjeva *et al*. (2017) found it, albeit rare, on a railway embankment, as did Dulin (2014, 2015) in the Komi Republic. Bakalin *et al*. (2013) found it on a moist clayish road rut, occurring in pure mats, in Adjara, Georgia. Ören *et al*. (2015) found it on a damp, steep, roadside slope in Turkey, where it was the most common bryophyte on the slope. Rikkinen (1992) reported it from shaded roadside banks and other disturbed sites in Finland. Blomquist (1939) reported ***Blasia pusilla*** (Figure 1-Figure 6) from a moist clay road bank in North Carolina, USA. Greenwood (1915) found it on damp soil by roadsides in Massachusetts, USA.

Springs are not often mentioned as habitats for ***Blasia pusilla*** (Figure 1-Figure 6), but then springs are less common habitats. Paton (1961) found it in the UK on a sandy track that remained moist by water from small springs. Wittlake (1950) found it under and around springs on a slope in Arkansas, USA. Similarly, seepage areas sometimes provide suitable habitats. Blockeel (2020) reported it from moist soil by a seepage in Greece.

Damp or wet soil is suitable, but few reports seem to identify that habitat for ***Blasia pusilla*** (Figure 1-Figure 6) (Macvicar 1902; Lanfear 1933; Paton 1967; Hong 1977, 1978). In their survey of the upper course of the Indigirka River in East Yakutia, Sofronova (2018) reported it from soil in the horsetail, moss shrub post-ice community. Among its damp soil habitats (Figure 22-Figure 24), Rilstone (1949) found it on clayey moors in Cornwall, UK, but it is rare.

Figure 23. ***Blasia pusilla*** large population on soil. Photo by Hermann Schachner, through Creative Commons.

Figure 24. ***Blasia pusilla*** on soil. Photo by Bernd Haynold, through Creative Commons.

Bogs don't seem to be a usual habitat for ***Blasia pusilla*** (Figure 1-Figure 6). The only record I have seen is that of

Macvicar (1902) for Meiller Bog in the Ben Lawers District, UK (Figure 25).

Figure 25. View from summit of Ben Lawers, UK, where ***Blasia pusilla*** occurs in a "bog" habitat. Photo by Scott Holland, through public domain.

Some plants of ***Blasia pusilla*** (Figure 1-Figure 6) are able to inhabit dune slacks (Figure 26) (Swann 1982; Persson & Pleijel 2008). These habitats occur between foredunes in low-lying depressions (Geographyinaction 2021). In the winter the plants can be close to or below the water level. Organic matter is slow to develop in slacks, but there is usually an impervious layer. Mosses (and possibly some liverworts) help to retain moisture. Other dune slacks remain as pools (Wikipedia 2021).

Figure 26. Dune slack in UK, a habitat where ***Blasia pusilla*** can occur. Photo by Gary Rogers, through Creative Commons.

The ability of ***Blasia pusilla*** (Figure 1-Figure 6) to colonize disturbed substrata has made it a successful pioneer species. When a former peat moor became agricultural land, bryophytes were able to colonize. For example, ***Blasia pusilla*** was among the pioneers in a maize field (Figure 27) when it remained untilled due to extremely wet weather (van den Bosch & Kersten 2004).

Figure 27. Muddy field in the UK, a potential site for the occurrence of ***Blasia pusilla***. Photo by Ian Peterson, through Creative Commons.

Drawdown of a lake in western Norway exposed a floodplain system with artificial islands (Odland 1997). During the first three years following construction, ***Blasia pusilla*** (Figure 1-Figure 6) was among the dominants able to colonize, but they disappeared or were greatly reduced after 8 years. The colonization by ***B. pusilla*** was not immediate, as ***Subularia aquatica*** (Figure 28) and small acrocarpous mosses dominated after one month, but this soon shifted to one in which ***Blasia pusilla*** was one of the dominants (Odland 1997; Odland & del Moral 2002).

Figure 28. ***Subularia aquatica***, a species that is a primary colonizer in a drawdown lake, preceding the colonization by ***Blasia pusilla***. Photo by J. C. Schou, with permission.

Blasia pusilla (Figure 1-Figure 6) is also present as a pioneer in the early successional stages of the Arctic tundra (Figure 29, where it reaches 75% in areas flooded by a glacial stream (Slack & Horton 2010). In even harsher conditions of a gold mining area of northeast Yakutia, ***Blasia*** was the only liverwort present (Sofronova 2019).

Figure 29. Arctic tundra, a habitat where ***Blasia pusilla*** can cover 75% of the ground in glacial melt areas. Photo by A. Dialla, through Creative Commons.

Various Russian records indicate that ***Blasia pusilla*** (Figure 1Figure 2-Figure 6) is tolerant of more terrestrial, drier habitats as well (Figure 30). Sofronova found it on sand between rocks (Sofronova 2013), few plants on soil among ***Salix*** shrubs (Figure 31) (Sofronova 2015), and on decaying wood (Sofronova 2017), summarizing it as occurring in two main types of habitats in Yakutia: decaying wood and rocks. Dulin (2014) describes terrestrial habitats in the Komi Republic: matted loamy soil at slope ledge between inundated shrublet-moss spruce forest and pebbly bar; on slightly matted soil of roadside wall.

Figure 30. ***Blasia pusilla*** habitat on soil and roots. Photo by Michael Lüth, with permission.

Physiology

Nordhorn-Richter (1984) explored the presence of fluorescence in bryophytes, as seen with a compound microscope under UV light, including ***Blasia*** in her studies. She found that the receptacular gemmae (Figure 32) fluoresced yellow in UV light.

Smith (2002) examined rapid chlorophyll fluorescence induction in a number of bryophytes. ***Blasia pusilla*** (Figure 1-Figure 6) did not have outstanding values; its highest yield of PSII Fv/Fm was 0.78 ± 0.01.

Blasia pusilla (Figure 1-Figure 6) extends into the Arctic, surviving, for example, in the mountain tundra belt of Northeast Yakutia, Russia (Sofronova 2019). This area has permafrost, yet the liverwort is able to survive the long winters (Figure 33), probably mostly as gemmae.

Figure 31. ***Salix*** habitat, which can provide suitable habitat for ***Blasia pusilla***. Photo by Dennis Kalma, FEIS, through public domain.

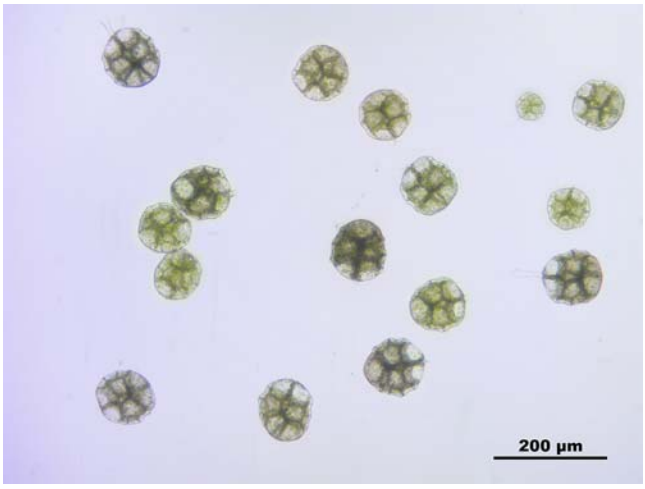

Figure 32. ***Blasia pusilla*** gemmae from flask. Photo by Hermann Schachner, through Creative Commons.

Figure 33. ***Blasia pusilla*** frozen. Photo by Bernd Haynold, through Creative Commons.

Adaptations

Blasia pusilla can dry out (Figure 34). This seems to be common at the end of the growing season, but gemmae are able to carry it over to the next spring. But it also has some adaptations to help it in its water relations.

Figure 34. ***Blasia pusilla*** with flasks, somewhat dry. Photo by Bob Klips, with permission.

Blasia pusilla (Figure 1-Figure 6) develops strands of thick-walled cells (Figure 35) that provide both mechanical support and conducting tissue (Rohret 1916). The plants can grow in pure mats (Figure 36) or with other liverworts (Wagner 2009; Dulin 2014; Sofronova 2017), both providing a reduction in water loss.

Figure 35. ***Blasia pusilla*** discolored, probably due to aging or sun exposure, and showing the strands that provide mechanical support and conduits for water. Photo by Štěpán Koval, with permission.

Figure 36. ***Blasia pusilla*** large population on soil. Photo by Hermann Schachner, through Creative Commons.

Reproduction

Allsopp and Ilahi (1971) described the morphology of ***Blasia pusilla*** (Figure 1-Figure 6). ***Blasia pusilla*** is typically seasonal, resulting from considerable dieback (Figure 37) in the winter months (Schuster 1992). This occurs both in submersed locations and out of water. Its reappearance in the spring results from its prolific production of gemmae (two types) and spores from its numerous sporophytes.

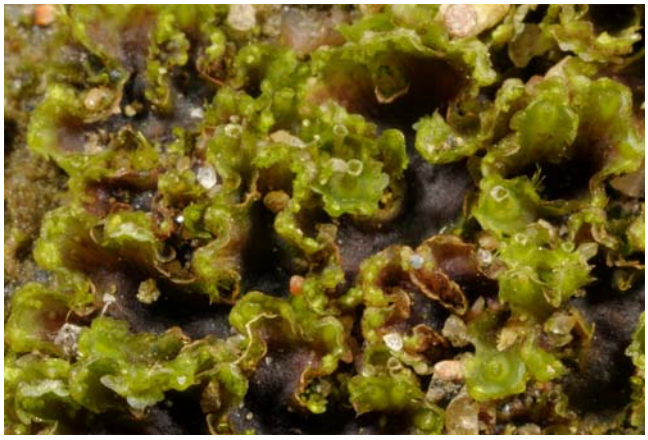

Figure 37. ***Blasia pusilla*** with older thallus dying. Photo by Jouko Rikkinen, through Creative Commons.

Blasia pusilla (Figure 1-Figure 6) is **dioicous**. Rohret (1916) describes the male plants as being more slender and deeply lobed than the female plants. Antheridia occur in a row on each side of the midrib in small lobes of the thallus (Figure 38). Ten to twelve archegonia (Figure 39) are produced near the tip, but the continued growth of the apex causes them to eventually reside near the middle of the thallus length. Ultimately, the sex organs are imbedded in the thallus (Figure 39) due to overgrowth by the thallus. Despite the numerous archegonia, typically only one sporophyte develops on a single thallus. Despite its dioicous condition, it can produce abundant sporophytes (Figure 40-Figure 46) in at least some locations (Rohret 1916; Schuster 1992; Breil 1996).

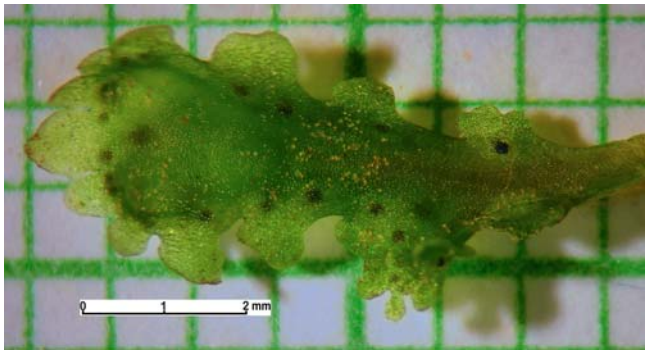

Figure 38. ***Blasia pusilla*** male thallus with small antheridial lobes at bottom. Photo courtesy of David H. Wagner.

Figure 39. ***Blasia pusilla*** archegonium imbedded in thallus. Photo courtesy of David H. Wagner.

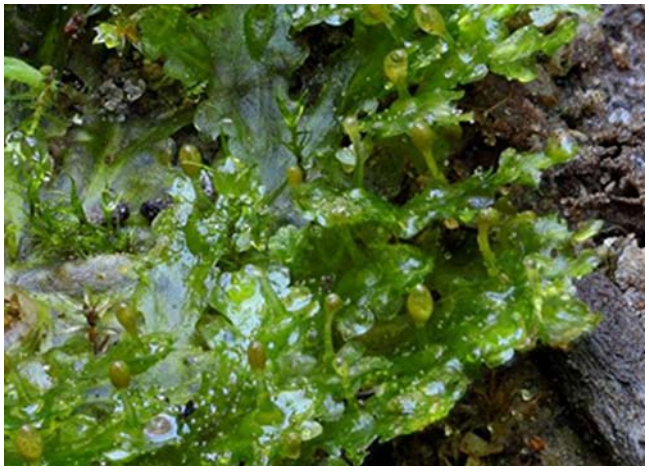

Figure 40. ***Blasia pusilla*** with emerging capsules. Photo by Kristian Peters, with permission.

Figure 41. ***Blasia pusilla*** capsules. Photo by Rafael Medina, with permission.

Figure 42. ***Blasia pusilla*** with mature capsules. Photo by Jouko Rikkinen, through Creative Commons.

Figure 43. ***Blasia pusilla*** with mature capsules. Photo by Jouko Rikkinen, through Creative Commons.

Figure 44. ***Blasia pusilla*** with mature and dehisced capsules. Photo by Jouko Rikkinen, through Creative Commons.

Figure 45. ***Blasia pusilla*** with dehisced capsules, showing tangled elaters. Photo by Jouko Rikkinen, through Creative Commons.

Figure 46. ***Blasia pusilla*** with open capsules. Photo by Rafael Medina, with permission.

Wagner (2009) reported the presence of male plants and females with sporophytes near Sutton Creek in Oregon, USA. Rohret (1916) reported that sex organs of ***Blasia pusilla*** are formed in the summer in Iowa, USA. But it appears that this timing differs by location, probably relating to factors associated with latitude. Fertilization of ***Blasia pusilla*** (Figure 1-Figure 6) occurs in the spring in England, Scotland, Wales, and North Carolina, USA (Duckett & Renzaglia 1993). Sporophytes develop during the summer months and the parent gametophytes die (Figure 42) (Duckett & Renzaglia 1993). Spores are shed in the spring, indicating that the sporophyte must overwinter on the dead gametophyte (Rohret 1916; Duckett & Renzaglia 1993; Shimamura *et al*. 2006). The death of the gametophyte before the sporophyte matures is unique to ***Blasia***. The cell division in the seta is completed by early autumn and the cells are packed with amylochloroplasts (Duckett & Renzaglia 1993). The capsule produces sporocytes with abundant protein bodies. These researchers suggest that day length probably controls the initiation of the sex organs in spring and dormancy of sporophytes in autumn. On the other hand, they suggest that it is higher temperatures that govern the sporophyte maturation. Both sporogenesis and seta elongation occur in early spring in Japan (Shimamura *et al*. 2006). Spores are large (35-50 µm). Udar and Srivastava (1983) provide SEM micrographs of the spores of ***Blasia*** and discuss the reproductive biology.

Van Zanten (2005) noted the rarity of sporophytes on ***Blasia pusilla*** (Figure 1-Figure 6) in The Netherlands. But when he was able to find ripe capsules, it was not spring, but November. He attributed the increase in plants with capsules to a greater search intensity. He also noted that the increase in capsules did not affect the production of gemmae.

Renzaglia and Duckett (1987) described the spermatogenesis of ***Blasia pusilla*** (Figure 1-Figure 6) in detail. Bartholomew (1986) described the sporeling development of ***Blasia pusilla***, noting that the spores are endosporic, but not precocious. Germination is initiated by imbibition of water, causing the spores to swell to 50-60 µm. Differences in temperature and light regimes (18ºC, 18:6 light dark & 3000-3500 lux; 18ºC, 12:12 light dark & 500 lux; 10ºC & 18:6 light dark, 1300 lux) had no effect on spore germination or development except to alter the rate. Bartholomew-Began (2009) explored the development of the sporeling in another member of Blasiales (***Cavicularia***; Figure 47) and found that the pattern of development is unique to ***Cavicularia*** and ***Blasia***.

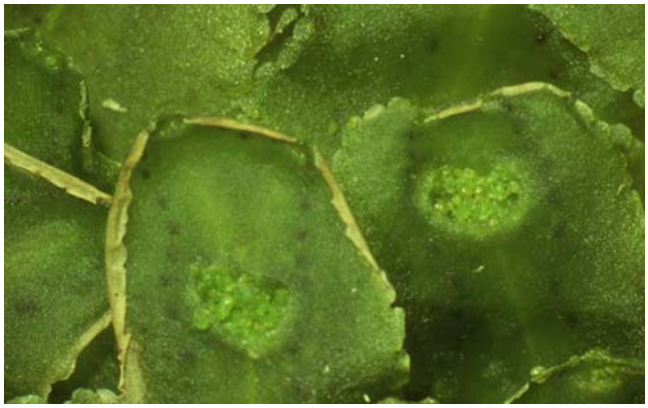

Figure 47. ***Cavicularia densa*** with ***Nostoc*** colonies forming a row on each side of the gemmae cups. Photo from Digital Museum Hiroshima University, with permission.

It is possible for ***Blasia pusilla*** (Figure 1-Figure 6) to reproduce aposporously in culture (Matzke & Raudzens 1968; Raudzens & Matzke 1968). Particular cells of the elongating seta can remain alive. After 3.5-6 weeks these can at times in the right conditions give rise to diploid gametophytes. These gametophytes develop in appearance like those with only one set of chromosomes. Normal gametophytes have *n*=9; the ones produced by apospory have *n*=18. They can produce archegonia, but not antheridia. Matzke and Raudzens consider that this type of apospory could not occur in the field.

Allsopp and Ilahi (1971) described regeneration in ***Blasia pusilla*** (Figure 1-Figure 6). An early description of the asexual reproduction in ***Blasia pusilla*** was provided by Buch in 1907. ***Blasia pusilla*** produces two types of gemmae in addition to spores (During 2001a). The stellate gemmae (Figure 48-Figure 55) form on the dorsal side of the thallus and the globose gemmae (Figure 56-Figure 68) are produced in receptacles (Buch 1907; Duckett & Renzaglia 1993; Paton 1999; Laaka-Lindberg *et al*. 2003). Those produced in the flask-like receptacles exhibit a yellow fluorescence in UV light (Nordhorn-Richter 1984)

Figure 48. ***Blasia pusilla*** with stellate gemmae. Photo by David T. Holyoak, with permission.

Figure 49. ***Blasia pusilla*** with stellate gemmae. Photo by Martin Hutten, with permission.

Figure 50. ***Blasia pusilla*** with stellate gemmae. Photo by Shaun Pogacnik, through Creative Commons.

Figure 51. ***Blasia pusilla*** with stellate gemmae. Photo by Jouko Rikkinen, through Creative Commons.

Figure 52. ***Blasia pusilla*** with stellate gemmae (**arrow**) on surface and ***Pellia*** on left (**arrow**). Photo by Paul Davison, with permission.

Figure 53. ***Blasia pusilla*** with stellate gemmae, habit on sand. Photo by Jouko Rikkinen, through Creative Commons.

Figure 54. ***Blasia pusilla*** showing stellate gemmae arranged on the thallus margins. Photo courtesy of David H. Wagner.

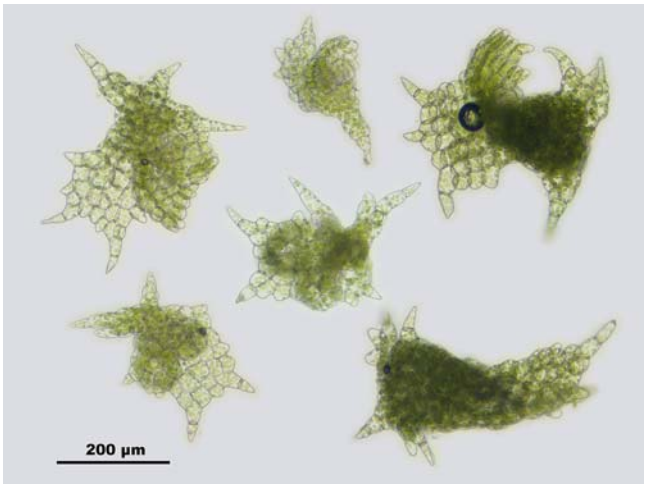

Figure 55. ***Blasia pusilla*** stellate gemmae. Photo by Hermann Schachner, through Creative Commons.

The globose gemmae (Figure 56-Figure 68) from the receptacles are able to persist in diaspore banks. Both kinds of gemmae of ***Blasia pusilla*** (Figure 1-Figure 6) are multicellular, with each cell containing a large nucleus and many oil bodies (Rohret 1916). I have been unable to find any other report of oil bodies in the gemmae of ***Blasia pusilla***.

Figure 56. ***Blasia pusilla*** with numerous flask-like receptacles containing gemmae. Photo by Dick Haaksma, with permission.

Figure 57. ***Blasia pusilla*** side view of gemmae flasks. Photo by Jouko Rikkinen, through Creative Commons.

Figure 58. ***Blasia pusilla*** side view of habit with gemmae flasks. Photo by Jouko Rikkinen, through Creative Commons.

Figure 59. ***Blasia pusilla*** showing numerous gemmae flasks. Photo by Hermann Schachner, through Creative Commons.

Figure 60. ***Blasia pusilla*** with flask-like gemmae receptacles and exuding gemmae. Photo by Tim Faasen, with permission.

Figure 61. ***Blasia pusilla*** habit with moisture. Photo by Jouko Rikkinen, through Creative Commons.

Figure 62. ***Blasia pusilla*** with flasks of gemmae and gemmae exuding from flask. Photo by Hermann Schachner, through Creative Commons.

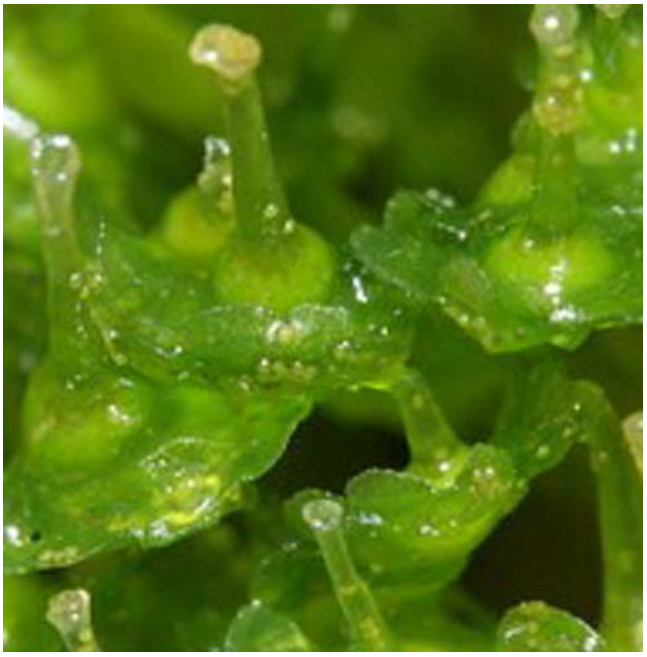

Figure 63. ***Blasia pusilla*** with gemmae in flask and mucilage exuding from tips. Photo by Hermann Schachner, through public domain.

Figure 64. ***Blasia pusilla*** gemmae on flask. Photo by Štěpán Koval, with permission.

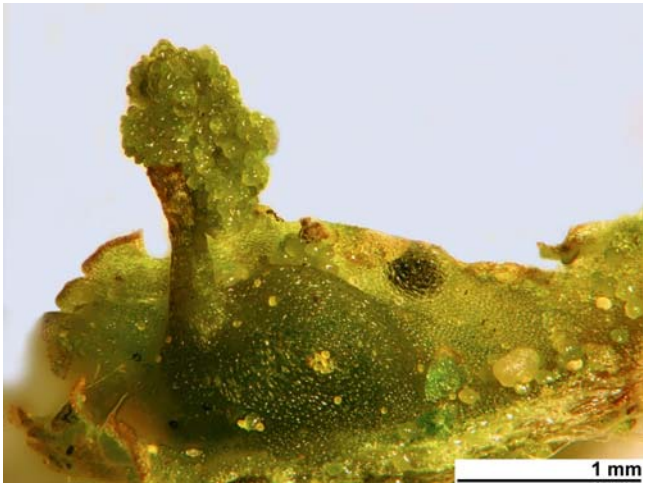

Figure 65. Gemmae flask of ***Blasia pusilla*** with gemmae exuding from the opening. Photo courtesy of David Wagner.

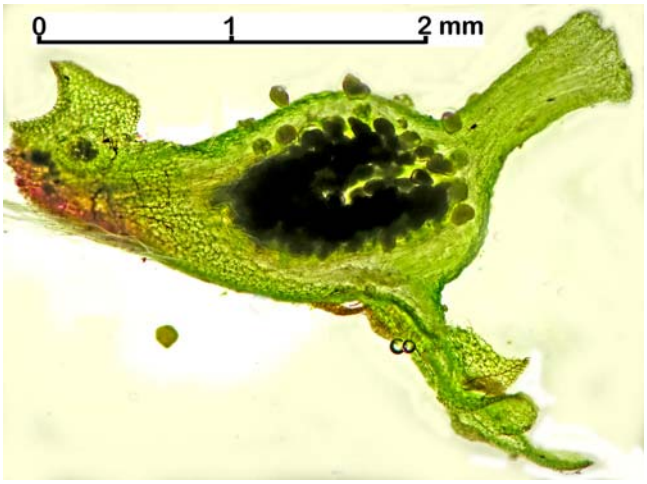

Figure 66. View of gemmae flask of ***Blasia pusilla***, showing globose gemmae inside and on its surface. Photo courtesy of David Wagner.

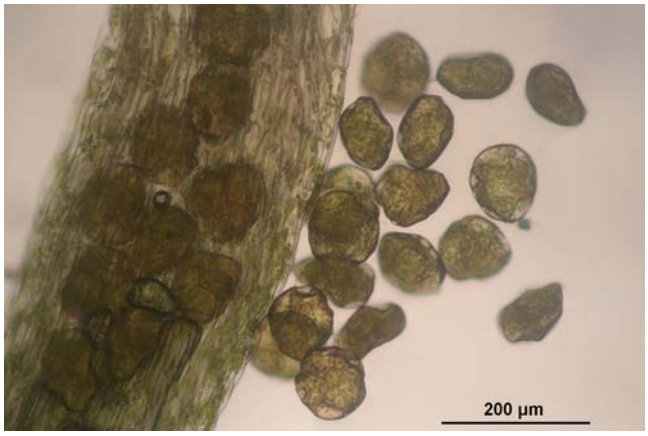

Figure 67. ***Blasia pusilla*** with gemmae in neck of flask. Photo by Hermann Schachner, through Creative Commons.

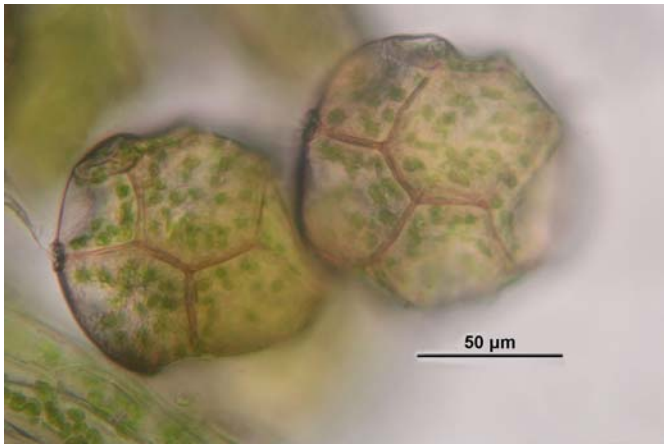

Figure 68. ***Blasia pusilla*** gemmae from flask. Photo by Hermann Schachner, through Creative Commons.

As the globose gemmae (Figure 56-Figure 68) in the flask-like receptacles of ***Blasia pusilla*** (Figure 1Figure 2-Figure 6) develop, the mucilage papillae secrete a slimy substance that enters the flask cavity (Rohret 1916). As the mature gemmae break from their stalks, they become imbedded in the viscid liquid. Pressure of the growing gemmae, and probably entrance of water into the flask, causes the mucilage to swell and exude from the flask neck (Figure 63-Figure 67). When the gemma begins to grow, the young plant benefits from the energy stored in the gemma (Figure 68). As the old thalli die, the gemmae and young plants are permitted to reach the soil. The gemmae can be shed during most of the year. These globose gemmae of ***Blasia pusilla*** have large oil droplets, and these may help the gemmae survive the winter to replace winter-damaged plants.

Bartholomew-Began and Jones (2005) described the receptacular gemma (Figure 56-Figure 68) development of ***Blasia pusilla*** (Figure 1Figure 2-Figure 6). These discoid to ellipsoid, stalked gemmae are produced within the flask-shaped receptacle. The gemma has distinct tiers of thick-walled cells with margins of lateral column of thin-walled cells. Germination does not occur until the gemmae are free from the receptacle. In fact, During (2001b) found that the disc-like gemmae do not seem to be able to germinate right away after they are dispersed, a condition that permits them to find their way into diaspore banks.

The globose receptacular gemmae (Figure 56-Figure 68) of ***Blasia pusilla*** (Figure 1-Figure 6) are present on both male and female plants (CRB 1908). However they are rare if the female is developing embryos. The apical brood-buds are common in summer; gemmae do not seem to germinate in summer or autumn, but instead are dormant until spring, when they can form new plants. Shoots arise from one side of the gemma, not both.

During (2001c) considers the production of two kinds of gemmae to be beneficial for ruderal species such as ***Blasia pusilla*** (Figure 1-Figure 6). The stellate gemmae (Figure 48-Figure 55) bring along their own nitrogen-fixing ***Nostoc*** symbiont in the two auricles (Duckett & Renzaglia 1993). These gemmae are also in possession of large amylochloroplasts (During 2001c). They are produced throughout the growing season, but are unable to survive the cold of winter. The more globose receptacular gemmae (Figure 56-Figure 68) are filled with starch, proteins, and lipids, but no ***Nostoc***. Unlike the stellate gemmae, they are not released until late summer or autumn, survive the winter, and germinate in spring. These cold-resistant gemmae are suitable for diaspore banks. When they are brought to the surface, they do not germinate right away. This could cause them to be missed in some diaspore studies since identification is usually based on germination. Perhaps they are waiting for the right combination of temperature, day length, and light intensity, or maybe requiring a cold period first.

Role

In the Mt. Kurikoma district of Japan, Chiba and Kato (1969) explored the testacean (protozoa) community associated with bryophytes. They found that these communities related to the habitat of the bryophytes, with ***Blasia pusilla*** (Figure 1Figure 2-Figure 6) among those that formed a suitable substrate for the protozoans.

Symbiotic Interactions

Most of the cyanobacterial symbiotic associations in the bryophytes are with the genus ***Nostoc*** (Watts *et al*. 1999). Although ***Nostoc*** partners are common in the **Anthocerotophyta**, this is not the case among the **Marchantiopsida**. Only two species of **Marchantiopsida** are known to harbor ***Nostoc*** (Figure 69) symbionts: ***Blasia pusilla*** (Figure 1Figure 2-Figure 6; Figure 70) and ***Cavicularia densa*** (Figure 47), both in **Blasiidae** (Rikkinen & Virtanen 2008). It is interesting that these species lack fungal symbionts (Adams & Duggan 2008; Rikkinen & Virtanen 2008; Liepiņa 2012), although they can have non-symbiotic fungal inhabitants.

Figure 69. ***Nostoc punctiforme***, a **Cyanobacterium** that can live symbiotically in ***Blasia pusilla***. Photo by Eduardo Zuñiga, through Creative Commons.

Figure 70. ***Blasia pusilla*** showing ***Nostoc*** colonies. Photo by Malcolm Storey, DiscoverLife.com, with online permission.

The ***Nostoc*** (Figure 69-Figure 70) of ***Blasia pusilla*** occurs extracellularly (Jackson *et al*. 2012) in auricles on the ventral surface (Figure 71-Figure 77) along the midrib (Adams 2002), thus receiving some protection from bright light and from desiccation. These ***Nostoc*** colonies cause areas of dark spots visible along the thallus (Adams *et al*. 2006). The assurance of transfer of these symbionts to the next generation is accomplished by the occurrence of the ***Nostoc*** in the lobes of the stellate gemmae (Figure 48-Figure 55) (Duckett & Renzaglia 1993; Rikkinen & Virtanen 2008). Rodgers and Stewart (1977) found that this symbiosis works well under moist conditions, but not in waterlogged or desiccated conditions. In their experiments, Rikkinen and Virtanen (2008) found that 95 out of 100 of the stellate gemmae produced cyanobacterial colonies within 3 months in culture.

Figure 71. ***Blasia pusilla*** side view of habit showing ***Nostoc*** colonies on ventral side. Photo by Jouko Rikkinen, through Creative Commons.

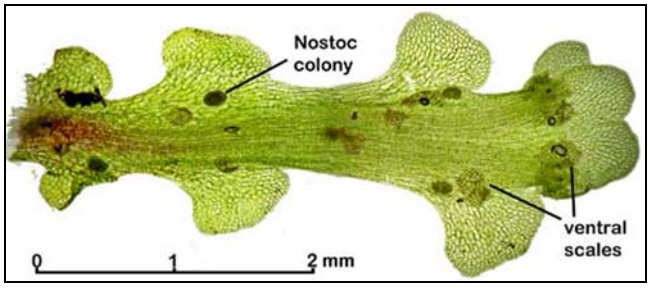

Figure 72. ***Blasia pusilla*** labelled to show location of ***Nostoc***. Photo by David H. Wagner, with permission.

Figure 73. ***Blasia pusilla*** showing ***Nostoc*** as darker patches on the lobes. Photo by Bernd Haynold, through Creative Commons.

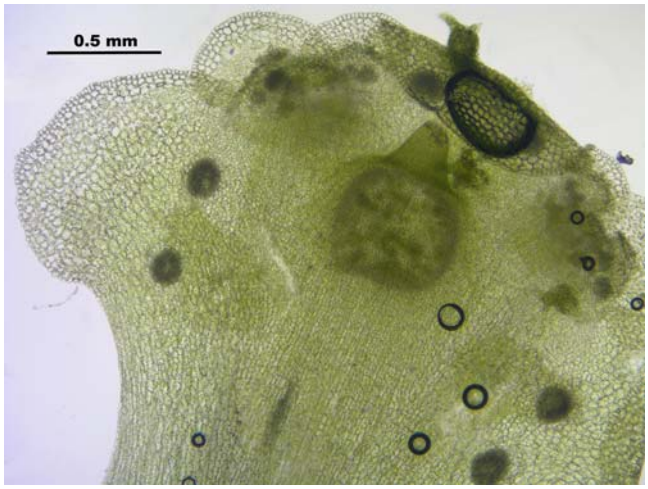

Figure 74. ***Blasia pusilla*** with ***Nostoc*** colonies. Photo by Hermann Schachner, through Creative Commons.

Duckett and Renzaglia (1993) found that viability differed between the non-symbiotic receptacular gemmae (Figure 78) and the symbiotic stellate gemmae (Figure 79). The stellate gemmae contain starch, but are short-lived. The receptacular gemmae, on the other hand, contain proteins and lipids and remain viable for a long time. The stellate gemmae, with their symbionts and starch, are able to secure their initial development and produce plants with symbiotic nitrogen fixation in a short time. The receptacular gemmae, by surviving longer, had more opportunity to obtain a ***Nostoc*** partner from the soil (Figure 80-Figure 82).

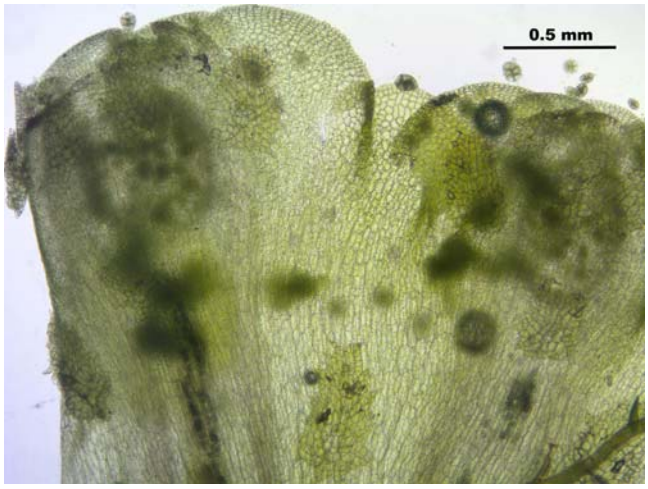

Figure 75. ***Blasia pusilla*** with ***Nostoc*** colonies and gemmae (globose especially at margins of thallus). Photo by Hermann Schachner, through Creative Commons.

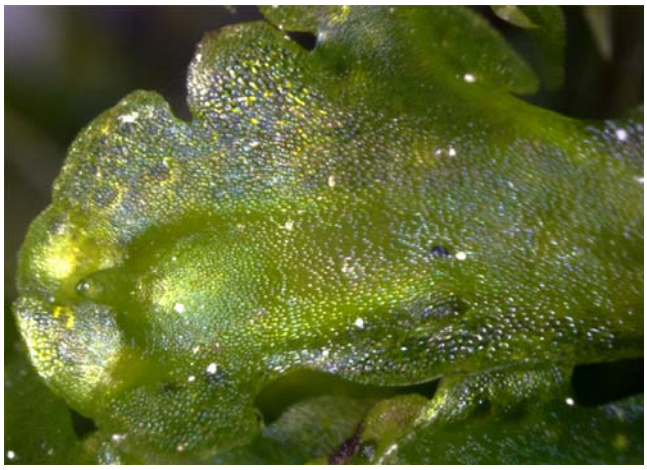

Figure 76. ***Blasia pusilla*** showing ***Nostoc*** in dark patches. Photo by Jouko Rikkinen, through Creative Commons.

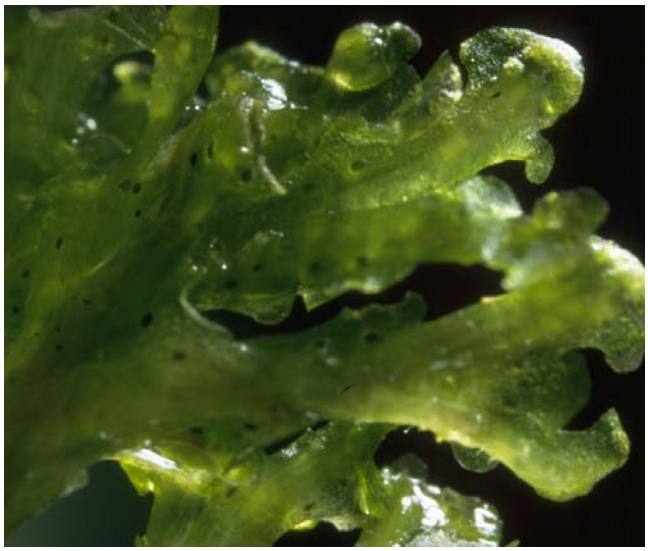

Figure 77. ***Blasia pusilla*** showing ***Nostoc*** colonies. Photo by Jan-Peter Frahm, with permission.

Figure 78. ***Blasia pusilla*** with flasks of gemmae. Photo by Hugues Tinguy, through Creative Commons.

Figure 79. ***Blasia pusilla*** with stellate gemmae. Photo by Jouko Rikkinen, through Creative Commons.

Figure 80. ***Nostoc commune*** on soil, a potential source for symbionts for ***Blasia pusilla***. Photo by Yamamaya, through Creative Commons.

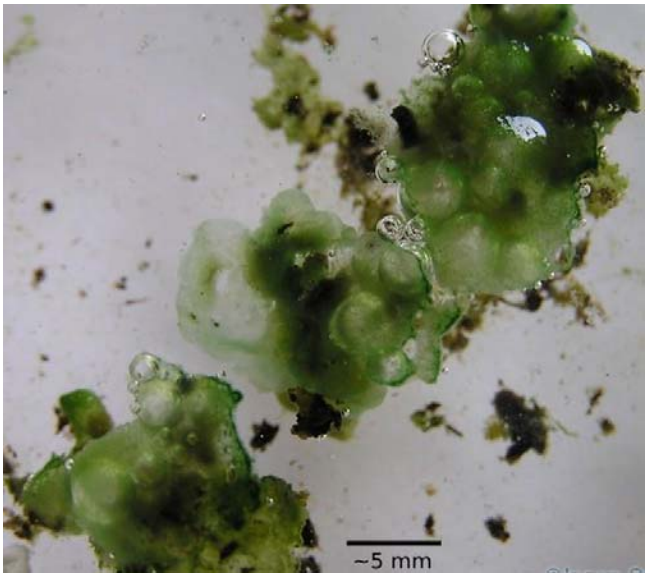

Figure 81. ***Nostoc*** free-living colonies. Photo by Jason Oyadomari, with permission.

Figure 82. Free-living ***Nostoc*** colonies. Photo by Jason Oyadomari, with permission.

Meeks (1990) described the colonization and establishment of ***Nostoc*** in ***Blasia pusilla*** (Figure 73-Figure 77), including both structural and metabolic changes that result from the symbiosis. There has been some controversy over the location of the ***Nostoc*** in pits (Davison 2009), attributing them to pits on the thallus. However, Davison argues that pits and open holes do not exist in ***Blasia pusilla***. The ***Nostoc*** actually occurs in the cavities formed by the slime papillae (Adams 2002; Solheim *et al*. 2004). These occur in auricles – as almost spherical structures.

Kimura and Nakano (1990) found that the ***Nostoc*** is only invasive when it is in its motile, hormogonial (describing mobile filaments) stage (Figure 83, Figure 84). Knight and Adams (1996; Adams 2002) found that when ***Blasia pusilla*** is deprived of N, it releases extracellular signals that trigger hormogonia to form; at the same time, these signals serve as a highly effective attractant to facilitate the hormogonia in finding the thallus. The ability of these shorter hormogonia to glide makes it possible for them to move to the sites where they can become symbionts (Adams 2002). This invasion induces morphological changes in the cavities it invades.

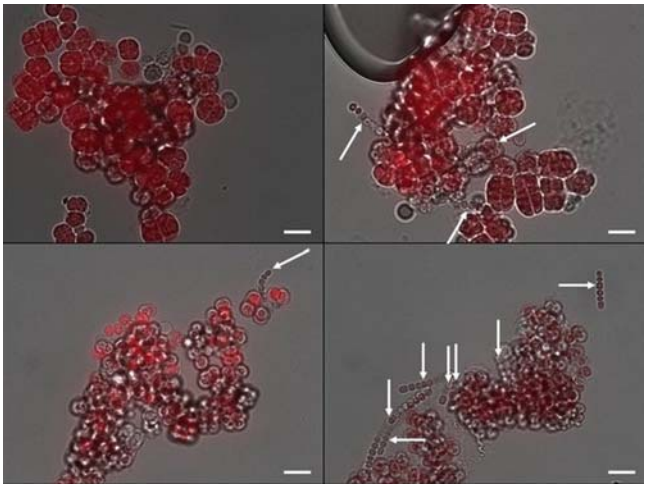

Figure 83. ***Chlorogloeopsis fritschii*** forming hormogonia, the mobile stage that is able to invade the thallus of liverworts such as ***Blasia pusilla***. Photo by Benjamin L. Springstein, Fabian Nies, and Tal Dag, through Creative Commons.

Nilsson *et al*. (2006) found that the extracts of both symbiotic plants such as ***Blasia pusilla*** (Figure 73-Figure 77) and non-symbiotic plants such as rice all elicited positive **chemotaxis** (directional movement in response to chemical) by the two ***Nostoc*** strains tested. The chemotaxis is reduced by increased temperature and darkness but stimulated by phosphorus and iron starvation or elevated salt concentrations. Sugars also stimulated chemotaxis, but flavonoids and amino acids had no effect. Díaz *et al*. (2011) suggested that **lectins** could be expected to promote the symbiont cellular dispersal. They demonstrated that it causes ***Nostoc*** to differentiate mobile cells that are attracted to the lectins. However, the ***Nostoc*** does not form filaments (Figure 82) before its chemotropic movement in response to lectins.

Once infection of the ***Blasia pusilla*** (Figure 73-Figure 77) thallus has occurred, the developmental pathway of the symbiont must switch from hormogonia development (Figure 83) to heterocyst (Figure 84) differentiation (Adams 2002). That means it must have a mechanism for repressing further hormogonia formation, which is genetically programmed. Once the symbiotic association has formed, the ***Nostoc*** produces **heterocysts (**Figure 84-Figure 85) (Herrero *et al*. 2004), which are the sites of the extensive nitrogen fixation. Gorelova *et al.* (1996) provided protocol that made it possible to study this symbiont development.

Figure 84. ***Nostoc*** with heterocysts (arrow). Photo by Jason Oyadomari, with permission.

Rodgers and Stewart (1977) reported that in ***Blasia pusilla*** (Figure 73-Figure 77) the 2-week-old colonies had a 20% heterocyst (Figure 84) frequency, whereas by six weeks this had increased to 48%. Production of heterocysts in symbiotic conditions can be 10-20 times that found free-living ***Nostoc*** (Adams 2002). Rodgers and Stewart (1977) found a heterocyst frequency of the free-living isolates to be 3-6%, but in their study this increased to 30% or more when they were symbiotic in ***Blasia***. ***Nostoc*** colonies develop in the slime cavities of the ***Blasia*** thallus within 72 hours. These colonies stretch the cells of the cavities. Filamentous protrusions develop on the liverwort cavity wall and penetrate the ***Nostoc*** colonies, forming a labyrinth of wall ingrowths in the ***Nostoc*** cells (Duckett *et al*. 1977), thus increasing the surface area of contact with the host by about 30% within 4 weeks (Rodgers & Stewart 1977), presumably facilitating transfer of the nitrogen compounds.

In ***Blasia pusilla*** (Figure 73-Figure 77), these specialized cells are formed as a response to limiting nitrogen conditions in the cell and are initiated by specialized genes (Herrero *et al*. 2004). In the ***Nostoc*** the **heterocysts**, as their name implies, are different from the other cells. They are able to reduce atmospheric nitrogen by providing an oxygen-free environment in which the nitrogenase enzyme can function (Wolk *et al*. 1994). This anoxic condition is achieved by both increased respiration and lack of photosynthesis in the heterocyst. The heterocyst loses the ability to fix CO_2, but products needing additional carbon can be supplied by the bryophyte (Duckett *et al*. 1977; Herrero *et al*. 2004). The heterocysts are unable to divide, but they perform an important function for the ***Nostoc***, and in turn, for the liverwort partner. They reduce N_2, readily available from the atmosphere, to ammonium (Figure 85) (Adams 2002) that is then incorporated into amino acids, particularly glutamine (Stewart & Rodgers 1978; Wolk *et al*. 1994). The symbiotic colonies of ***Nostoc*** in ***Blasia pusilla*** (Figure 73-Figure 77) are more effective at converting the nitrogen to a usable form (ammonia) than those that are free-living. This is rapidly transferred to the liverwort thallus, increasing the liverwort yield by 300-500% in 30 days.

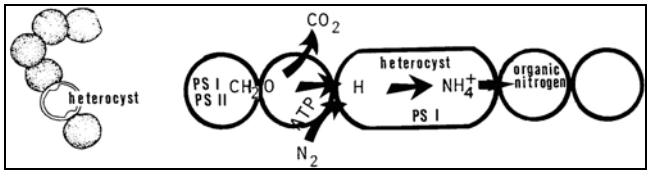

Figure 85. Heterocyst of ***Anabaena***, a member of the **Cyanobacteria,** showing the nitrogen fixation pathway. Drawing by Janice Glime.

Although ammonia (NH_3) is the immediate product of the nitrogen reduction, it is toxic and is quickly converted to harmless amino acids (Figure 85). It is unclear if the transfer to the photosynthetic cells of the ***Nostoc*** filaments (and probably the liverwort) is by ammonia or by glutamine (derived from the glutamate) and possibly other amino acids – or both (Stewart & Rodgers 1978; Wolk *et al*. 1994). It appears that the ***Nostoc*** is dependent on the ***Blasia*** for its fixed carbon. Stewart and Rodgers (1977) found that excised ***Nostoc*** colonies had only a negligible ability to fix CO_2, but that in the cavities of ***Blasia pusilla***

(Figure 73-Figure 77) they receive fixed carbon from the thallus of the liverwort. Further details of the biochemical pathway are provided by Chapman *et al*. (2008) and Duggan *et al*. (2013).

The mechanism of transfer of reduced nitrogen from the heterocyst is a source-sink relationship (Wolk *et al*. 1994; Meeks 2009). The carbohydrate serves as the reductant and the abundant reduced nitrogen (NH_4) is transferred to other cells due to a concentration gradient. Once the reduced nitrogen is incorporated into biological compounds, those compounds and the cells that contain them become sinks.

Rodgers (1978) described the conditions favorable to the ***Nostoc*** symbiosis in ***Blasia pusilla*** (Figure 73-Figure 77). As an endophyte, ***Nostoc*** has greater nitrogenase activity at lower *p*H levels than those suitable for the free-living form. On the other hand, the symbiont requires a higher light level than the free living form. Below 10ºC, the ***Nostoc*** has low activity in either growth condition, but the free-living form has high activity above 12ºC, whereas the endophyte requires 17ºC for such levels of activity. The free-living form is also more tolerant of desiccation, although both have protective mucilage.

Rodgers and Stewart (1977) identified ***Nostoc sphaericum*** (Figure 86) in the populations of ***Blasia pusilla*** (Figure 73-Figure 77) they examined. Although ***Nostoc punctiforme*** (Figure 69) is able to inhabit both ***Blasia pusilla*** and ***Anthoceros*** (Figure 87-Figure 89) species in the lab, different strains occupy ***Blasia*** and ***Anthoceros*** in the field (Leizerovich *et al*. 1990). In the lab, a strain of ***Nostoc punctiforme*** is able to colonize and form a symbiont with ***Blasia pusilla***, but the lab strain of this ***Nostoc*** species has not been identified from any of these liverworts in the field (Rikkinen & Virtanen 2008). Further studies indicate that there is a "moderate level of spatial and temporal continuity" by some of the ***Nostoc*** strains in the ***Blasia pusilla*-*Nostoc*** symbioses (Costa *et al*. 2001). Jackson *et al*. (2012) demonstrated that three arabinogalactan proteins (AGP) were common to widely diverse cyanobacterial partnerships.

Figure 86. ***Nostoc sphaericum***, "the caviar of the Andes" and also a symbiont of ***Blasia pusilla***. Antonio W. Salas, through Creative Commons.

Figure 87. ***Anthoceros***, NZ, showing bluish green color that suggests the presence of **Cyanobacteria**. Photo by Clive Shirley, Hidden Forest <hiddenforest.co.nz>, with permission.

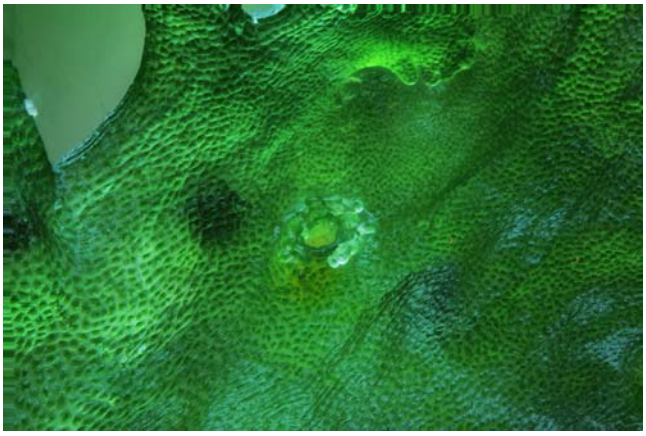

Figure 88. ***Anthoceros punctatus*** pore and ***Nostoc*** colony. Photo by Des Callaghan, with permission.

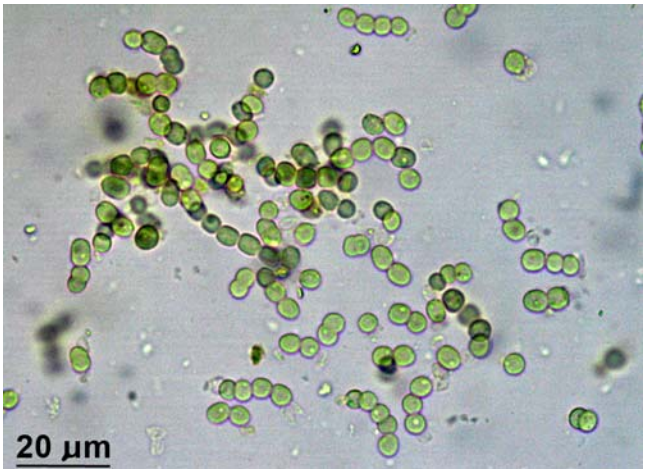

Figure 89. ***Nostoc*** from ***Anthoceros agrestis***, showing the breakup of hormogonia and scarcity of heterocysts during early colonization. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.

In axenic cultures, all but one of the free-living ***Calothrix*** spp. (Figure 90), ***Chlorogloeopsis*** spp. (Figure 83), and ***Nostoc*** spp. (Figure 69, Figure 84, Figure 86) (all **Cyanobacteria**) were able to join in a symbiotic relationship with both ***Blasia pusilla*** (Figure 73-Figure 77) and ***Phaeoceros*** sp. (Figure 91) (West & Adams 1997). By

contrast, the strains of **Cyanobacteria** found as symbionts in the field where not found free-living in those locations. Furthermore, none of the symbiotic strains were found at more than one sample site.

Figure 90. ***Calothrix parietina***, a **Cyanobacterium** in a genus that can inhabit ***Blasia pusilla***. Photo from Algae Base, through Creative Commons.

Figure 91. ***Phaeoceros laevis*** with a bluish-green color suggesting the presence of its ***Nostoc*** partner. Photo by Oliver S., through Creative Commons.

Liaimer *et al*. (2016) further elaborated on the diversity of **Cyanobacteria** strains. They claimed that ***Blasia pusilla*** (Figure 1Figure 2-Figure 6) recruits its symbiotic ***Nostoc*** partner from the soil nitrogen-fixing strains. They found that those from an agricultural community exhibited negative allelopathic interactions, but such was not the case in an undisturbed site. The **Cyanobacteria** did not exhibit antimicrobial activity, but four of the isolates were cytotoxic to human cells. Interestingly, the symbiotic recruits commonly produced microcystin, a toxic compound, but it was not commonly produced in the free-living community. Could this be an additional herbivore deterrent for the liverwort?

The bryophyte-**Cyanobacteria** symbiosis, by providing usable nitrogen compounds, is an important contributor to the environment (Solheim *et al*. 2004).

Interactions with Fungi

As already noted, ***Blasia pusilla*** (Figure 1Figure 2-Figure 6) is not known to have any fungal endophytes (Liepiņa 2012). On the other hand, they do have parasitic inhabitants. Redhead (1981) reported ***Blasiphalia pseudogrisella*** (**Basidiomycota**; Figure 92) from the rhizoids. Hallgrímsson (1981) found this fungus to be frequent on river banks in Iceland and concluded that it is probably always associated with ***Blasia pusilla***.

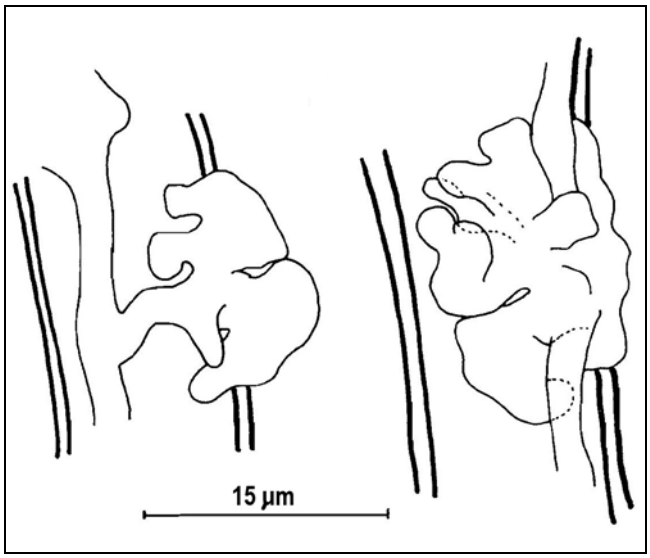

Figure 92. Appressoria of ***Blasiphalia pseudogrisella*** on rhizoids of ***Blasia pusilla***. Drawing modified from Scott Redhead 1981.

Persson and Pleijel (2008) reported the rare species ***Bryoscyphus marchantiae*** (discomycete; Figure 93) as a parasite on ***Blasia pusilla*** (Figure 1Figure 2-Figure 6) in dune slacks (Figure 26).

Figure 93. ***Bryoscyphus marchantiae*** on liverwort; this species is able to parasitize ***Blasia pusilla***. Photo by Iain Munro, through Creative Commons.

The mushroom ***Blasiphalia pseudogrisella*** (Figure 94) in the Arctic and alpine Northern Hemisphere is known only from ***Blasia pusilla*** (Figure 1Figure 2-Figure 6) (Antonin & Noordeloos 2001). Hyphae appearing to be identical to those of this mushroom formed clasping pads (**appresoria**) on the rhizoids of ***Blasia pusilla***.

Furthermore, gemmae of the liverwort had a sparse covering of fungal spores matching those of the mushroom. Some of these seemed to have infected the gemmae. In other cases, dispersed gemmae had short rhizoids covered with fungal appressoria. Antonin and Noordeloos suggested that the gemmae could be vectors for dispersing the fungus.

Figure 94. ***Blasiphalia pseudogrisella*** growing with bryophytes. Photo by Rénee Lebeuf, through public domain.

Biochemistry

Blasia pusilla (Figure 1Figure 2-Figure 6) is one of those liverworts that apparently lacks oil bodies (Figure 95-Figure 96) (Schuster 1992; Millar *et al*. 2007; He *et al*. 2013). On the other hand, Rohret (1916) reported numerous oil bodies from the gemmae. Whether they are in the oil bodies or not, a number of compounds have been recognized from this species, but their antibiotic activity is limited (Millar *et al*. 2007).

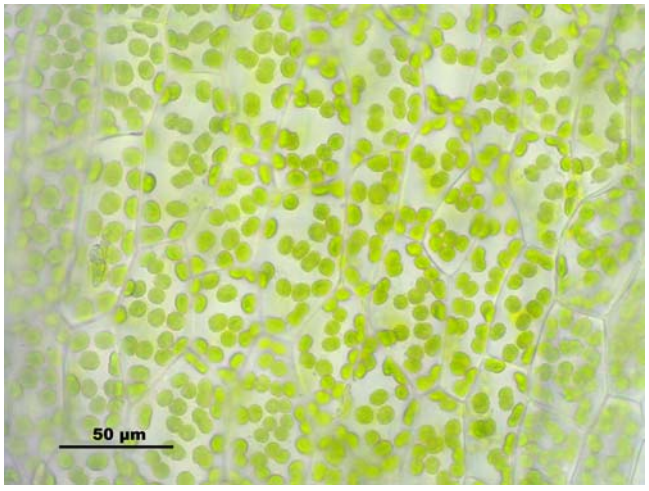

Figure 95. ***Blasia pusilla*** cells with chloroplasts, but lacking oil bodies. Photo by Hermann Schachner, through Creative Commons.

Hashimoto *et al*. (1993) reported riccardin C, riccardin F, and orsellinic acid methyl ester from ***Blasia pusilla*** (Figure 1-Figure 6). Viennois *et al*. (2011) found that riccardins from this species are natural antagonist compounds.

Four phenolic novel cyclic bisbibenzyl dimers, six bibenzyl derivatives, apigenin 7-O-β-d-glucoside, shikimic acid, and five orsellinic acid derivatives were isolated from ***Blasia pusilla*** (Figure 1Figure 2-Figure 6) (Hashimoto *et al*. 1994; Yoshida *et al*. 1996). Asakawa (1994) reported that the cyclic bis-bibenzyl dimers of this species exhibit inhibitory activity against plant growth. Could this help maintain a habitat with limited competition for this species that seems to thrive best in disturbed habitats and as a pioneer?

Axenic ***Blasia pusilla*** (Figure 1Figure 2-Figure 6) extract is able to produce bioactive compounds. These retard fungal sporulation, but thus far there is no indication that they are able to inhibit bacterial growth (Millar *et al*. 2007). Furthermore, Asakawa (2008) reported moderate cytotoxicity against KB cells and only weak activity against HIV-RT. Millar *et al*. (2007) suggest that antimicrobial activity is greater in taxa with oil bodies; this would limit the medicinal value of ***Blasia pusilla***.

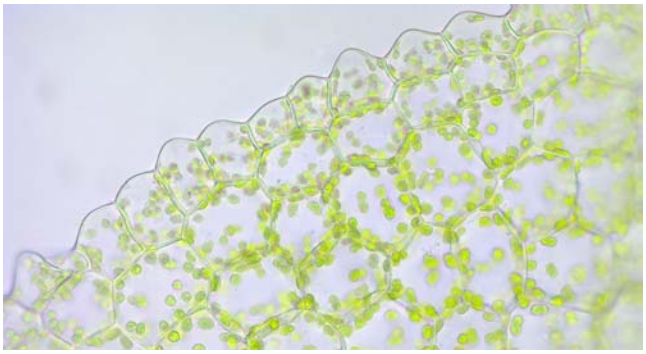

Figure 96. ***Blasia pusilla*** marginal cells with chloroplasts and no oil bodies. Photo by Hermann Schachner, through Creative Commons..

Summary

Blasia pusilla is the only species representing the **Blasiales** on wet substrates. It is rarely submerged, but can live in mires, streambanks, spray of waterfalls, fens, bogs, and similar wet habitats. It does well on disturbed substrata and is often an early pioneer. In these habitats, it benefits from persistent ovoid gemmae that can remain in the diaspore bank. Its ***Nostoc*** partner helps it to meet its fixed nitrogen needs. It is also able to spread through use of its stellate gemmae that get a head start with their own ***Nostoc*** colonies. The ovoid gemmae get their ***Nostoc*** partner from the soil.

Blasia pusilla is dormant through dieback in winter, the attached sporophyte is dormant in winter, and gemmae remain dormant while on the thallus. Both gemma germination and production of sexual structures are dependent on signals from the environment. Water triggers spore germination, but day length and temperature seem unimportant. Day length may affect initiation of sex organs and dormancy of sporophytes, but higher temperatures seem to affect sporophyte maturation.

Blasia pusilla has no symbiotic fungal partners, but they do harbor surface fungi and parasitic fungi. The absence of antibiotic effects against bacteria may be the result of lacking oil bodies.

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Lars Söderström helped me find the current acceptable names for a number of older taxa. I have also benefitted from discussions with him on conventions in naming of some structures. David Wagner provided me with important images of reproductive structures.

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CHAPTER 1-18
AQUATIC AND WET MARCHANTIOPHYTA, ORDER LUNULARIALES

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CHAPTER 1-18
AQUATIC AND WET MARCHANTIOPHYTA, ORDER LUNULARIALES

Figure 1. ***Lunularia cruciata*** with nearly mature gemmae cups, clearly showing the crescent shape of the cup. Photo by James Dickson, with permission.

MARCHANTIOPSIDA

Marchantiidae – Lunulariales

Lunulariaceae

Lunularia cruciata (Figure 1-Figure 13)

(syn. = *Lunularia thaxteri*)

Although ***Lunularia cruciata*** (Figure 1-Figure 13) and *L. thaxteri* can be morphologically distinct, these differences are due to environmental expressions (Bischler & Boisselier 1998). Their genetic markers indicate that they are the same species. Itouga *et al*. (2000) further described the genetic structure.

Distribution

Lunularia cruciata (Figure 1-Figure 13) is a common species in western Europe, being native around the Mediterranean (NBNatlas 2021). But it has spread through a wide range due to its propensity for growing in gardens and flower pots. It is easily spread by gemmae through horticultural watering regimes. Hence, one can also find it in California, USA (Whittemore 1982), in greenhouses in Australia, and in New Zealand (NBNatlas 2021). Not surprisingly, it is most common in urban areas and seems to be spreading northeastward in Europe with climate warming (Essl & Lambdon 2009; Skudnik *et al*. 2013a). Nevertheless, it is considered to be a rare liverwort away from the Mediterranean area. Skudnik *et al*. (2013b) reported that it had been considered rare or under threat in Slovenia, but their discovery of new locations suggested that instead it was a matter of under-recording.

Figure 2. ***Lunularia cruciata*** on soil. Photo from <www.aphotofauna.com>, with permission.

Figure 3. ***Lunularia cruciata*** habitat in Bhutan. Photo by David Long, with permission.

Figure 4. ***Lunularia cruciata*** with young gemmae cups. Photo by George Shepherd, through Creative Commons.

Figure 5. ***Lunularia cruciata*** showing numerous gemmae cups with gemmae beginning to disperse. Photo by Michael Lüth, with permission.

Figure 6. ***Lunularia cruciata***, almost entirely lacking gemmae cups. Photo from <www.aphotofauna.com>, with permission.

Figure 7. ***Lunularia cruciata*** in Europe. Photo by Michael Lüth, with permission.

Figure 8. ***Lunularia cruciata*** habitus. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 9. ***Lunularia cruciata*** in rock crevice, showing large pores in the thallus. Photo by Alexis Orion, through Creative Commons.

Figure 10. ***Lunularia cruciata*** with gemmae beginning to disperse. Photo by Hermann Schachner, through Creative Commons.

Figure 11. ***Lunularia cruciata*** with tiny gemmae cup sitting piggyback on another gemmae cup. Photo by Luis Nunes Alberto, through Creative Commons.

Figure 12. ***Lunularia cruciata*** with gemmae. Photo by Michael Lüth, with permission.

Figure 13. ***Lunularia cruciata*** with gemmae cups and lots of still-attached gemmae. Photo by Fotis Samaritakis, through Creative Commons.

This same horticultural transportation most likely accounts for the presence of ***Lunularia cruciata*** (Figure 1-

Figure 13) in Japan (Noguchi 1977; Taoda 1980). Taoda used it as a species indicating the degree of urbanization. It has also appeared in Kasmir of the Himalayas (Ismail *et al*. 2018). Other localities include Botswana and it is common in most of the southern African countries (Steel *et al*. 2004), Slovakia (Janovicova & Somogyi 1996), Germany (Frahm 1973), where it was fertile (Kirschner *et al*. 2010), Benslimane Region of Morocco where it is one of the two most common liverwort species (Elharech *et al*. 2018; Fadel *et al*. 2020), Nepal (Karki & Ghimire 2019), northeastern USA [Uva *et al*. (1997) considered it a weed], New York (Trigoboff 2000), British Columbia, Canada (Schofield 1997), and Central Chile (Gradstein & Cuvertino 2015).

Aquatic and Wet Habitats

Lunularia cruciata (Figure 1-Figure 13) has a relatively wide range of habitats (Yeates (1908). Ferreira *et al*. 2008) list it as a river species. It occurs midstream in the River Swale, Yorkshire, UK (Holmes & Whitton 1977a) and is mostly in the mid to lower River Tyne, UK (Holmes & Whitton 1981). It is among the commonest species in English and Welsh rivers (Scarlett & O'Hare 2006) In Thuringia, Germany, it is known in the ***Platyhypnidium*** (Figure 14)***-Fontinalis antipyretica*** (Figure 15) association, (Marstaller 1987). Özenoğlu Kiremit *et al*. (2007) found it on rocks and tree roots in a stream bed in Turkey. Konstantinova *et al*. (2009) found it on the bank of the Khosta River in the Caucasus of Russia. On Madeira Island, it occurs in mountain streams (Luis *et al*. 2015).

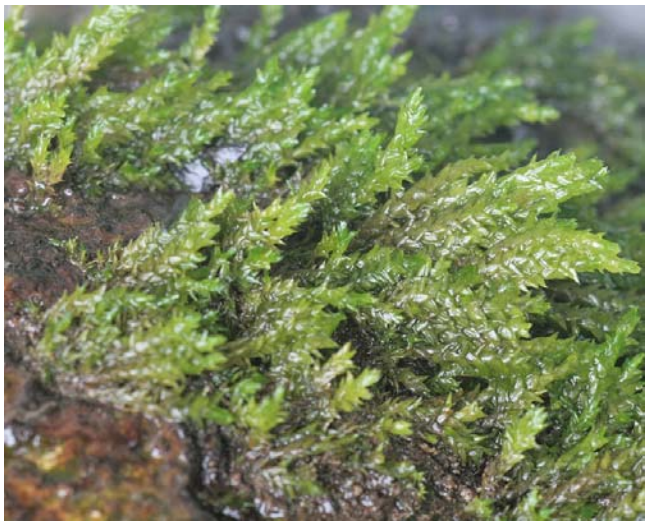

Figure 14. ***Platyhypnidium riparioides***, a species that is often an indicator of suitable habitat for ***Lunularia cruciata***. Photo by Hermann Schachner, through Creative Commons.

Figure 15. ***Fontinalis antipyretica***, an aquatic moss species that is often an indicator of suitable habitat for ***Lunularia cruciata***. Photo from Botany Website, UBC, with permission.

Yeates (1908) considers ***Lunularia cruciata*** (Figure 1-Figure 13) to be less hygrophilous than ***Marchantia polymorpha*** (Figure 16). The former is a suitable indicator of rich nutrients or eutrophic conditions in aquatic habitats (Werner 2001).

Figure 16. ***Marchantia polymorpha*** by water, a species that is more hygrophilous than ***Lunularia cruciata***. Photo by Hugues Tinguy, with permission.

But it is more likely that ***Lunularia cruciata*** (Figure 1-Figure 13) occurs near water, rather than in it, often wet or periodically inundated. It occurs on wet ground at the edge of waterfalls (Figure 17) in Morocco, as well as what Fadel *et al*. (2020) called small water surfaces.

Figure 17. Waterfall in Ireland, showing the effects of moisture from the falls that makes a suitable habitat for ***Lunularia cruciata***. Photo by Phil Armitage, through Wikimedia Commons.

Lunularia cruciata (Figure 1-Figure 13) occurs in damp places, on banks with frequent submergence and slow water (Figure 18-Figure 27) (Watson 1919), including the river bank of the River Tees, UK (Holmes & Whitton 1977b). In Germany it occurs increasingly in such natural habitats as brook banks (Borsdorf 1987; Bergl & Meinunger 1988). In Morocco, Saadi *et al*. (2020) found it both underwater and on soil and rocks near running water.

Figure 18. ***Lunularia cruciata*** on stream bank. Photo by Tom Kaye, through Creative Commons.

Figure 19. ***Lunularia cruciata*** forming shelves on rock by water. Photo by David Claro, through Creative Commons.

Figure 20. ***Lunularia cruciata*** on rock in stream. Photo by Andrew Melton, through Creative Commons.

Figure 21. ***Lunularia cruciata*** on stream bank. Photo by Gerrit Ohm, through Creative Commons.

Figure 22. ***Lunularia cruciata*** at base of log. Photo by Geerah, through Creative Commons.

Figure 23. ***Lunularia cruciata*** by water. Photo by S. Bushes, through Creative Commons.

Figure 24. ***Lunularia cruciata*** by water. Photo by Susan Marley, through Creative Commons.

Figure 25. ***Lunularia cruciata*** on rock by water. Photo by Thomas Koffel, through Creative Commons.

Figure 26. ***Lunularia cruciata*** by water. Photo by Ulysses M., through Creative Commons.

Figure 27. ***Lunularia cruciata*** on tree root near water. Photo by Maddi Song, through Creative Commons.

Figure 28. ***Lunularia cruciata*** with other bryophytes by water. Photo by Susan Marley, through Creative Commons.

Sometimes damp walls and slopes (Figure 29-Figure 31) provide suitable habitat. Armitage (1918) found ***Lunularia cruciata*** (Figure 1-Figure 13) on damp walls and bare earth banks on Madeira. Konstantinova *et al*. (2009) reported it at the base of limestone cliffs in the valley of the Khosta River, Caucasus, Russia. Garcia-Rowe and Saiz-Jimenez (1991) found it on vertical wet surfaces on Spanish cathedrals, where it could make it easier for tracheophytes to invade and damage the buildings with their roots.

Figure 29. ***Lunularia cruciata*** zone on slope. Photo by Stephen Thorpe, through Creative Commons.

Figure 30. ***Lunularia cruciata*** on clay bank. Photo by Susan Marley, through Creative Commons.

Figure 31. ***Lunularia cruciata*** habitat where it forms a zone on the substrate, probably related to water levels. Photo by Kate McCombs, through Creative Commons.

Springs are less common habitats. The only record I found was ***Lunularia cruciata*** (Figure 1-Figure 13) growing around a spring in Halstead, England (Lorenz 1910).

Wet soil in other locations is a more common habitat. Fadel *et al*. (2020) reported ***Lunularia cruciata*** (Figure 1-Figure 13) from rocky walls and wet soil (Figure 32-Figure 34) in Morocco. It was able to occupy limestone, schistose, and quartzite substrata. It was among the four most common species in wetlands. Salisbury (1962) considers it the commonest species on wet ground of gardens in the UK.

Figure 32. ***Lunularia cruciata*** with antheridial discs (dark brown) and gemmae cups, on wet soil. Photo by Michael Keogh, through Creative Commons.

Figure 33. ***Lunularia cruciata*** on clay. Photo by Mattia Manchetti, through Creative Commons.

Figure 34. ***Lunularia cruciata***, on soil, Waikite Pools Recreation Area, NZ, 16 July 1988. Photo by Janice Glime.

Karki and Ghimire (2019) reported ***Lunularia cruciata*** (Figure 1-Figure 13) as saxicolous (Figure 35-Figure 37) in Central Nepal, and locally rare. In some locations one can find it tucked into wet crevices (Figure 38-Figure 40) or on shale that is soaked with water (Figure 41) in the winter (Fadel *et al*. 2020).

Figure 35. ***Lunularia cruciata*** on rock. Photo by <www.aphotofauna.com>, with permission.

Figure 36. ***Lunularia cruciata*** on thin soil on rock. Photo by Zoltán Nagy, through Creative Commons.

Figure 37. ***Lunularia cruciata*** on thin soil on rock. Photo by Zoltán Nagy, through Creative Commons.

Figure 38. ***Lunularia cruciata*** with gemmae cups (**left**) + ***Marchantia polymorpha*** (**right**) among rocks. Photo by Michael Lüth in Europe, with permission.

Figure 39. ***Lunularia cruciata*** in rock crevice. Photo by Attila Oláh, through Creative Commons.

Figure 40. ***Lunularia cruciata*** in rock crevice. Photo by Alexis Orion, through Creative Commons.

Figure 41. ***Lunularia cruciata*** on wet rock. Photo by Loverworts, through Creative Commons.

Based on its other habitats, it is not surprising that ***Lunularia cruciata*** (Figure 1-Figure 13) is able to occupy the rich alluvium associated with temporary ponds (Fadel *et al*. 2020).

This opportunistic liverwort also lives by paths and roadsides. Skudnik *et al*. (2013b) found it on damp soil by paths and roadsides in Slovenia. Likewise, Yeates (1908) noted its presence on the banks of roadside water channels, but also on boulders in deep-seated valley beds, at the bottom of old walls and outhouses, and even on shaded banks where it was often hidden by brambles. Özenoğlu Kiremit *et al*. (2007) found it on soil banks along the road in Antalya, Turkey.

It appears that the most common habitat for the introduced populations is related to horticulture. ***Lunularia cruciata*** (Figure 1-Figure 13) is common in greenhouses (Figure 42) and gardens, where sprinkling systems and garden hose water facilitate dispersal of gemmae from the gemmae cups. Perold (1993) reported the species from old gardens, nurseries, and forested areas in southern Africa, where it is most likely introduced. Bergl and Meinunger (1988) reported that it was introduced to Central Europe through greenhouse cultures used to supply market gardens, churchyards, and parks (Frahm 1973). Schofield (1997) noted that in British Columbia, Canada, it occurs almost exclusively in gardens. Similarly, in Chile, it occurs in urban areas (Gradstein & Cuvertino 2015). A picture by Merav Vonshak suggests that it might occur in spruce forests (Figure 43).

Salisbury (1962) lists ***Lunularia cruciata*** (Figure 1-Figure 13) as a troublesome weed in gardens of the UK. Its frequency in such habitats is 40%! It does well in sunken paths and greenhouses as well (Augier 1966; Coudreuse *et al*. 2005).

Figure 42. ***Lunularia cruciata*** on soil in a flower pot in greenhouse in Ripley, Michigan, USA, with mosses. Photo by Janice Glime.

Figure 43. ***Lunularia cruciata*** amid spruce needles. Photo by Merav Vonshak, through Creative Commons.

Armitage (1918) found ***Lunularia cruciata*** (Figure 1-Figure 13) on open ground and bare earth banks as well as shady mountain ground, on Madeira. Gradstein (1972) reported it from the Maltese Islands on the thin soil layer of a sheltered floor enclosure of a temple. Steel *et al*. (2004) considered it to be one of the world's commonest liverworts and a common inhabitant of man-made and disturbed environments in Botswana. Lo Giudice *et al*. (1997) found it to be common in urban areas and relatively indifferent to substrate hardness. It can also occur on soil under shrubs and small trees (Özenoğlu Kiremit *et al*. 2007; Saadi *et al*. 2020).

Physiology

Lunularia cruciata (Figure 1-Figure 13) was the subject of a number of early physiological studies. Crocker (1912) evaluated its tropisms and concluded that, contrary to the conclusions of Weinert (1909), the rhizoids of growing gemmae are positively gravitropic, as are those of the thallus. Bischoff (1912) supported this argument by concluding that the absence of motile starch in the rhizoids does not negate the statolith theory and suggests that other bodies in the cell could accomplish this role of sensing the direction of gravity.

Temperature effects on ***Lunularia cruciata*** (Figure 1-Figure 13) could benefit from more study. It appears that not only is ***Lunularia cruciata*** spreading to more northern habitats, perhaps as a result of global warming, but it seems to be attaining more frost tolerance. Bergl and Meinunger (1988) contend that its expansion to the north is due to the establishment of frost-resistant types. In Japan, plants in cultivated locations are likewise frost-resistant (Fletcher 1982). Warming temperatures also can play a role in gemma germination (Schwabe 1990).

Lunularia cruciata has both rhizoids (Figure 44) and scales that contribute to its external capillary movement of water (McConaha 1941). This species has two types of rhizoids (Figure 45). The smooth rhizoids are partially enclosed by the ventral scales and may contact the substrate. The tuberculate rhizoids originate beneath the scales and create numerous connected capillary strands that parallel the thallus, creating a "rapid" distribution system for water uptake throughout the thallus.

Figure 44. ***Lunularia cruciata*** ventral side showing rhizoids clinging to soil. Photo by Pat Enright, through Creative Commons.

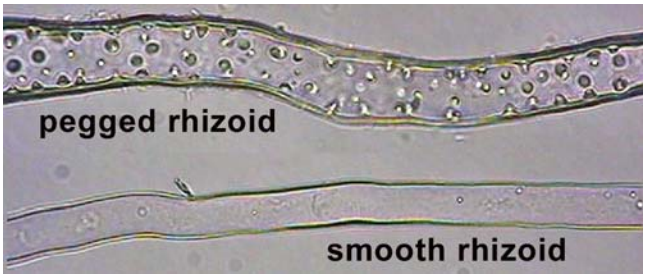

Figure 45. Pegged and smooth rhizoids of ***Conocephalum conicum***; ***Lunularia cruciata*** has the same two types. Photo by Paul Davison, with permission.

By contrast, the upper surface of ***Lunularia cruciata*** (Figure 1-Figure 13) is designed to keep water out, at least through the pores (Figure 46-Figure 47) (Schönherr & Ziegler 1975). The air pores are surrounded by hydrophobic ledges (Figure 48) that constrict the entrance. This permits only liquids with a contact angle of zero^{o} with the hydrophobic ledge to enter.

Figure 46. ***Lunularia cruciata*** showing pores. Photo by Steven Bodzin, through Creative Commons.

Figure 47. ***Lunularia cruciata*** showing pores. Photo by Mike, through Creative Commons.

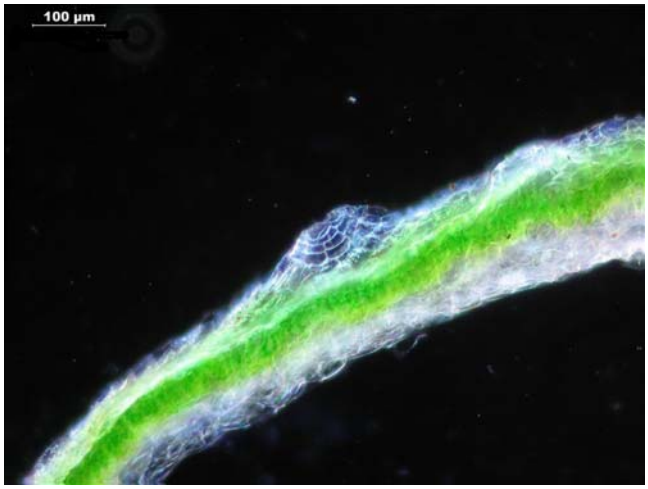

Figure 48. ***Lunularia cruciata*** thallus and pore longitudinal section. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Giordano *et al*. (1985, 1989) reported the presence of a hyaline parenchyma in the thallus of ***Lunularia cruciata*** (Figure 1-Figure 13). These have wall thickenings with large primary pit fields between them and numerous plasmodesmata-derived pores. These differ from the parenchymatous cells of the midrib, where the plasmodesmata-derived pores occur in small, sparse groups. The researchers suggest that the reticulate pattern has a role in the water-holding capacity and lateral distribution of water, using both **symplastic** (inside cell membrane) and **apoplastic** (space outside plasma membrane) pathways.

Deltoro *et al*. (1998) listed ***Lunularia cruciata*** (Figure 1-Figure 13, Figure 49) as a desiccation-intolerant bryophyte. At low water content they showed low efficiency of photosynthetic conversion, closed down their photosystem II reaction centers, and exhibited weak nonphotochemical quenching. They were unable to restore photochemical activity after desiccation. The large leakage of potassium suggests membrane damage.

Figure 49. ***Lunularia cruciata*** with gemmae, growing in a flower pot in a greenhouse where it gets watered regularly. Photo by Janice Glime.

Nevertheless, ***Lunularia cruciata*** (Figure 1-Figure 13) responds to long days by increasing its resistance to drought (Valio *et al*. 1969; Schwabe 1990, 2019). When moved from moist conditions to relative humidity levels of 90%, the liverwort dies (Figure 50). However, after long-day treatment, it can be dried for years and still survive. The rapidity of drying is likely to be important.

Figure 50. ***Lunularia cruciata*** dieback. It may still have some living tissue that will come back. Photo by Jon Sullivan, through Creative Commons.

Fredericq (1966) first examined the effects of photoperiod on growth in ***Lunularia cruciata*** (Figure 1-Figure 13). Lunularic acid increases with long-day treatment of ***Lunularia cruciata*** (Valio & Schwabe 1970). Its concentration changes rapidly in response to day-length change. The inhibition of growth in this species is linearly related to the concentration of the acid, with very high

concentrations being lethal. Sabovljević and Marka (2009) verified these day-length relationships in the field. Abscisic acid could not be detected in the species (Valio & Schwabe 1970), but lunularic acid appears to have the same functions (Yoshikawa *et al*. 2002).

Wilson and Schwabe (1964) found that red light induces dormancy and far-red reverses it. This suggests that phytochrome is involved in the response. But this is contradicted by the effect of short exposures (15 seconds) of far-red light that alone causes significant growth inhibition. They surmised that the far-red light could elicit the formation of some of the P 730 form of phytochrome. In experiments, ***Lunularia cruciata*** (Figure 1-Figure 13) exhibited photoreversibility like that in ***Marchantia polymorpha*** (Figure 16), but with a weaker response to far-red light than that of ***M. polymorpha*** (Fredericq 1966). Huault (1980) found that phytochrome was involved in the germination of propagules in ***Lunularia cruciata***.

The optimum day length for growth in ***Lunularia cruciata*** (Figure 1-Figure 13) is 8 hours (Schwabe & Valio 1970b). Continuous light causes growth to cease, with a rapid onset of dormancy. The effects of red vs far-red light depended on the duration and frequency and intervening light quality. Furthermore, growth promoters of tracheophytes generally inhibit ***Lunularia***, or have little effect.

Liverworts use lunularic acid where other plants use ABA as a dormancy hormone and, apparently, to help prepare them for drying, as shown in ***Lunularia cruciata*** (Figure 1-Figure 13) (Schwabe 1990). Schwabe and Nachmony-Bascomb (1963) found that long days induce dormancy and short days break it in this species. All parts of the thallus are able to register day length, including the young gemmae (Figure 51) in the cup. However, temperature interacts strongly with the photoperiod, making it difficult to determine the critical day length. High temperature (24ºC) in continuous light rapidly induces dormancy – within 6 days. During this dormancy, the plants have a greater capacity to resist drought; actively growing thalli die in a reduction to 80% relative humidity.

Figure 51. ***Lunularia cruciata*** with gemmae; the thallus and gemmae both respond to day length. Photo by Damon Tighe, through Creative Commons.

Thomas and Silcox (1983) explored the effects of various biological compounds on IAA effects and proton efflux in ***Lunularia cruciata*** (Figure 1-Figure 13). They suggested that **lysis** (breakage by rupture of cell wall or membrane) of cells may be caused by conversion of starch reserves to solutes that create greater osmosis, rather than protoplast swelling.

LaRue and Narayanaswami (1955, 1957; Narayanaswami 1957) determined that IAA inhibits the germination of gemmae of ***Lunularia cruciata*** (Figure 1-Figure 13) in the lab. They also demonstrated that if the gemmae remained in the thallus cups, they did not germinate (Figure 52), but if the thallus was cut close to the cup, germination could occur. Removal of the upper half of the thallus, above the gemma cup, caused the gemmae in the cups to germinate. Mutilations elsewhere on the thallus did not cause the gemmae to germinate. Hence, it appears that the apical growing region produces the growth inhibitors. This would be an ecologically advantageous trait, permitting resources to promote growth until unfavorable conditions stopped it. Lack of further production of the inhibitor would then permit the gemmae to germinate and provide a means of surviving such conditions as drying out.

Figure 52. ***Lunularia cruciata*** with dormant gemmae resting on thallus. Photo by Martin Hutten, with permission.

Schwabe and Valio (1970a) later demonstrated that the gemmae themselves exhibit self-inhibition through a substance produced in the growing tip. This inhibitor has greater production in short days compared to that in long-day dormancy conditions. Furthermore, the growing conditions determine how much inhibitor diffuses away. Dry conditions, for example, can elicit the morphological changes of incipient dormancy.

There are three life cycle stages that can become dormant in ***Lunularia cruciata*** (Figure 1-Figure 13): mature thallus, gemma, and spore. Plants from Israel that have dried in the air produce adventitious branches ventrally from the region immediately behind the meristem. That meristem fails to resume growth. Dormant gemmae, on the other hand, resume growth when removed from the cup.

Lunularia cruciata (Figure 1-Figure 13) succeeds and maintains growth at very low light intensities (Nachmony-Bascomb & Schwabe 1963). The gemmae are also able to grow at the same low light intensities. Initial growth of the gemmae is due only to the expansion of the cells. It would be interesting to learn whether they take advantage of sunflecks (Figure 53).

Figure 53. ***Lunularia cruciata*** with sunflecks that might give it bursts of photosynthesis. Photo by Siznax, through Creative Commons.

Gemmae cup production is markedly diminished by high temperatures above 12ºC (Nachmony-Bascomb & Schwabe 1963). Thallus growth is severely limited by lack of P; N can also restrict growth to a very low level.

The first sign of growth from dormant gemmae of ***Lunularia cruciata*** (Figure 1-Figure 13) is development of rhizoids (Valio & Schwabe 1969). Temperature and light are important in controlling this development. As long as the days are long, a wide range of temperatures is suitable. When gemmae have been illuminated for 2 hours in white light, then transferred to darkness, about 50% of the gemmae produce rhizoids, and only at 20-25ºC. No rhizoid production occurs in total darkness, but the gemmae remain alive for at least 6 months.

Fernández-Marín *et al*. (2009) found that darkness induced the xanthophyll cycle in ***Lunularia cruciata*** (Figure 1-Figure 13) as a response to dehydration.

Pollution

Lunularia cruciata (Figure 1-Figure 13) is known as a toxitolerant species (Daly 1970; Gilbert 1970). Gilbert (1971) found that it is SO_2-resistant. It has the advantage of being able to transform quickly from its more susceptible protonema stage to the more protected and resistant thallus stage (LeBlanc & Rao 1975).

Vieira *et al*. (n.d.) found that ***Lunularia cruciata*** (Figure 1-Figure 13) was among the most tolerant liverworts to water pollution and increased *p*H and conductivity. In their study, this species occurred at a mean height of 30 cm above the water. Basile *et al*. (2017) similarly found the species to be very tolerant of air pollution.

Other studies have examined the effects of heavy metals on ***Lunularia cruciata*** (Figure 1-Figure 13). Basile (1993) examined the localization of lead in the cells and tissues. Carginale *et al*. (2004) found that cadmium accumulation in this species was both dose and time dependent. This metal accumulated preferentially in hyaline parenchyma and at the base of the gemmae cups. In the cells, it accumulated in the vacuoles and cell walls. These accumulations were accompanied by an increase of sulfur in the vacuoles of the stressed cells. The researchers suggested that the excess sulfur in the vacuoles may have been facilitated by stress-induced phytochelatins. Ultrastructural changes also occurred at sublethal levels of cadmium: alteration of the fine structure of cells and induced alterations of the chloroplast structure. Both apical thallus growth and gemma germination were inhibited, following a dose-dependent response.

Basile *et al*. (2017) reported that in the Land of Fires, ***Lunularia cruciata*** (Figure 1-Figure 13) exhibited high values of Al, Cd, Cr, Cu, Hg, Ni, Pb in its tissues. Reactive Oxygen Species (ROS) were high and the plants exhibited antioxidant activity and DNA damage. Basile and coworkers likewise found that phytochelatins served as good biomarkers of metal pollution. Further exploration indicated that detrimental pollution was indicated by a significant increment in heat shock protein (Hsp70) expression and occurrence and modifications in the chloroplast ultrastructure. Basile *et al*. (2005) found that accumulation of cadmium, one of the most toxic metals in the environment, affected DNA expression. The enzyme cystathionine γ-synthase is upregulated by Cd. Three other genes are downregulated.

Nothing is ever simple in biology. Alam and Sharma (2012) found that responses could change. Nevertheless, the responses indicated an increase in heavy metal air pollutants in the summer, a change that could be missed by ordinary pollution monitoring.

Lower exposures to radiation elicited damage to gemmae apical cells (Miller 1968). Apical cells of gemmae of ***Lunularia cruciata*** (Figure 1-Figure 13) are larger than other cells. However, radiation exposure had no different effect on energy absorption per chromosome in gemmae apices than it did in vegetative cells.

Degola *et al*. (2014) questioned why the phytochelatin synthase enzyme evolved long before pollution became a problem. This pre-adaptive enzyme would seemingly not be needed in ancient organisms to sequester excess cadmium or arsenic. Therefore, they looked for essential functions. They hypothesized that there was a need to regulate trace element homeostasis and to minimize the risk of exposure to toxic concentrations of certain metals even in pre-plant organisms such as **Charophyta** (***Nitella mucronata***; Figure 54).

Figure 54. ***Nitella mucronata***, an alga species that is likely to regulate trace element homeostasis. Photo by Kristian Peters, through Creative Commons.

Adaptations

Thalli of ***Lunularia cruciata*** (Figure 1-Figure 13) are large and flat, forming overlying patches (Figure 55) or even extensive turfs (Perold 1993; Steel *et al*. 2004). Or they can grow with other mosses and liverworts (Figure 56-Figure 61) that help to maintain moisture. Such growth arrangements can help to conserve water. They have numerous rhizoids that help them remain attached in the disturbed habitats they frequent. As already noted the scales and rhizoids also move water to all locations on the thallus, and pores facilitate the movement of water between cells both apoplastically and symplastically.

Figure 55. ***Lunularia cruciata*** on soil, forming overlapping patches. Photo by George Shepherd, with permission.

Figure 56. ***Lunularia cruciata*** with mosses. Photo by Duarte Frade, through Creative Commons.

Figure 57. ***Lunularia cruciata*** with mosses on soil. Photo by Martin Hutten, with permission.

Figure 58. ***Lunularia cruciata*** with mosses. Photo from <www.aphotofauna.com>, with permission.

Figure 59. ***Lunularia cruciata*** with mosses. Photo from <www.aphotofauna.com>, with permission.

Figure 60. ***Lunularia cruciata*** with mosses. Photo from <www.aphotofauna.com>, with permission.

Figure 61. ***Lunularia cruciata*** with mosses. Photo from <www.aphotofauna.com>, with permission.

Reproduction

It appears that ***Lunularia cruciata*** (Figure 1-Figure 13) relies primarily on gemmae. It is a **dioicous** perennial (Perold 1993; Steel *et al*. 2004) and its spread through horticultural shipments seems to have created populations with only one sex. In fact, it rarely has sexual reproduction in the UK (Benson-Evans & Hughes 1955; Blackstock 2018). One factor seemed to be the cold winters, which were tolerable to female plants (Figure 62), but male-expressing plants (Figure 63-Figure 66), and consequently sporophytes (Figure 67), were restricted to the southern parts of England and Wales.

Figure 62. ***Lunularia cruciata*** developing archegoniophores. Photo by Fotis Samaritakis, through Creative Commons.

Figure 63. ***Lunularia cruciata*** male plants with antheridial discs (dark patches) and splash cups. Photo from <www.aphotofauna.com>, with permission.

Figure 64. ***Lunularia cruciata*** with antheridial discs. Photo by Rutger Barendse, Saxifraga, through Creative Commons.

Figure 65. ***Lunularia cruciata*** with antheridial discs. Photo by Ricardo Ferreiro Sanjurjo, through Creative Commons.

Figure 66. ***Lunularia cruciata*** with antheridial discs. Photo by Tricia Stewart, through Creative Commons.

Figure 67. ***Lunularia cruciata*** female plants with developing sporophytes in the archegoniophore receptacle lobes. Photo by Stavros Apostolou, through Creative Commons.

Benson-Evans and Hughes (1955) reported that ***Lunularia cruciata*** (Figure 1-Figure 13) requires a low temperature regime before the production of sexual organs, a physiological function similar to **vernalization** (cooling process that facilitates initiation of growth stage, such as initiation of sexual organs or gemma germination) in tracheophytes. Nevertheless, as Blackstock (2018) notes, both genders are known in more northern localities. Even sporophytes have a wider distribution than previously thought. The limited sporophyte production is in part due to the dioicous condition, but also to a female-biased sex ratio. Since warmer conditions have arrived, it appears that fertility has increased. In northwest Wales, sexual reproduction has benefitted from prolonged and synchronous production of archegonia and antheridia (Figure 63-Figure 66). Yeates noted in 1908 that it seems to reproduce best in the even temperatures of greenhouses, with most of its reproduction by gemmae. In fact, the thalli disappear in winter and reappear in spring, whereas the gemmae survive through winter, presumably accounting for most of the reappearance in spring.

But vernalization does not seem to be the only factor. Benson-Evans (1964) found that ***Lunularia cruciata*** (Figure 1-Figure 13) grew best and produced gametangia at 21ºC in long days (18 hours), but not at either 10ºC or in short days (6 hours).

Sporophyte production (Figure 67-Figure 80) in ***Lunularia cruciata*** (Figure 1-Figure 13) is so rare outside the Mediterranean that finding it is often considered worthy of publication. Such records include Chalaud (1931), Rousseau (1955), Goodman (1956) for South Wales, and Ahayoun *et al*. (2008) for Morocco. The sporophytes are elevated on an **archegoniophore** (stalk that elevates archegonia), with four occurring on each **receptacle** (expanded portion of archegoniophore bearing sporangia).

Figure 68. ***Lunularia cruciata*** with emerging archegoniophores and developing capsules. Photo by Ken-Ichi Ueda, with permission.

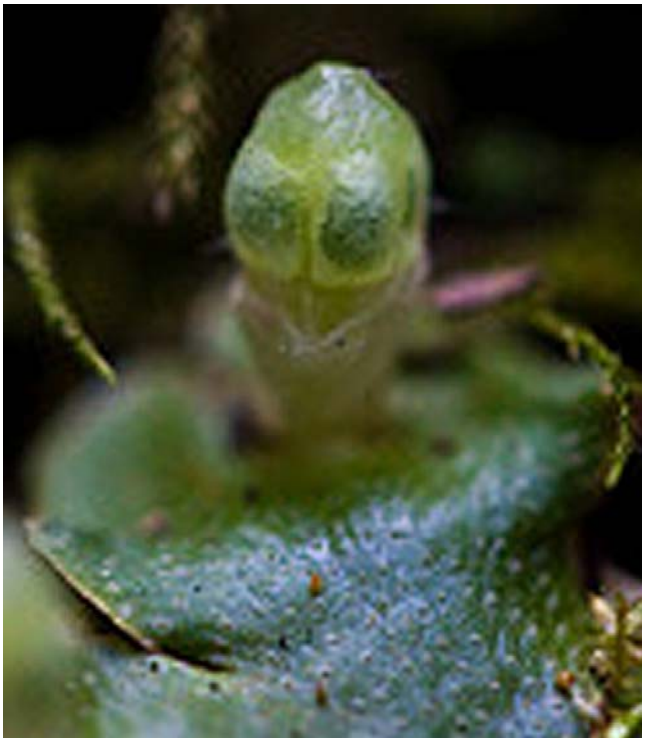

Figure 69. ***Lunularia cruciata*** with archegoniophore with developing sporophytes. Photo by Ken-Ichi Ueda, with permission.

Figure 70. ***Lunularia cruciata*** with archegoniophores, showing how common the archegoniophores can be in some locations. Photo by Stephen Thorpe, through Creative Commons.

Figure 71. ***Lunularia cruciata*** with mature archegoniophore. The few plants provide limited opportunity for fertilization. Photo by Loverworts, through Creative Commons.

Figure 72. ***Lunularia cruciata*** with fully elongated archegoniophore and nearly mature capsules. Photo by loverworts, through Creative Commons.

Figure 73. ***Lunularia cruciata*** with archegoniophores, in Israel. Photo by Jael Orgad, with online permission.

Figure 74. ***Lunularia cruciata*** with archegoniophores growing on vertical wall. Note the thallus dieback. Photo by Debbi Brusco, through Creative Commons.

Figure 75. ***Lunularia cruciata*** archegoniophore with four nearly mature capsules. Photo by loverworts, through Creative Commons.

Perold (1995) noted that ***Lunularia cruciata*** (Figure 1-Figure 13) responded to photoperiod in its native Israel, but this could not be determined in the field for New Zealand plants because of the much lower winter temperatures in New Zealand. On the other hand, Sérgio and Viana (1973) considered the availability of water as a possible limiting factor for development of sporophytes, based on the distribution of plants producing sporophytes. This would also explain the greater incidence of sexual reproduction in the Mediterranean climate.

Saxton (1931) described the archegoniophore and sporophyte (Figure 67-Figure 80) of ***Lunularia cruciata*** (Figure 1-Figure 13). I note here that many authors have avoided the term **archegoniophore** for this species, referring instead to the **receptacle**, which should be the expanded top portion of the archegoniophore. Kirschner *et al*. (2010) recorded the first sighting of sporophytes in Germany in the botanical garden in Main. They were able to observe all developmental stages, beginning with antheridial receptacles in early spring, followed by archegonial receptacles somewhat later in spring. Sporophytes developed in late summer.

Shinn (1902) presented a rather different picture of sexual reproduction of ***Lunularia cruciata*** (Figure 1-Figure 13) in California, USA. The first fertile plants appeared in April on the drier parts of shaded soil on the greenhouse floor. These bore many small, white, tuft-like sheaths (Figure 76) covering the young archegonial receptacles. Unlike most bryophytes (antheridia usually develop first), the antheridia developed two weeks later. These were on the same plants of this "**dioicous**" thallus! But they did occur on different divisions of the thallus. By 9 May, capsules appeared, while others were just beginning to emerge from the scales of the sheaths.

Figure 77. ***Lunularia cruciata*** with mature capsules, three of which are dehiscing. Photo by Fotis Samaritakis, through Creative Commons.

Figure 76. ***Lunularia cruciata*** with white sheaths where archegoniophores will emerge. Note the adjacent male plants. Carminda Santos, through Creative Commons.

Spores (Figure 77-Figure 80) of ***Lunularia cruciata*** (Figure 1-Figure 13) are "very small" (Perold 1993), a feature that should facilitate their long-distance dispersal but that would carry with it little reserved food to give the germaling a boost. They are either green or brown and smooth, so perhaps photosynthesis helps them to get a start. Kumar and Kapila (2003) reported a chromosome number of n=9.

Figure 78. ***Lunularia cruciata*** dehiscing capsules showing masses of spores and elaters. Photo by Fotis Samaritakis, through Creative Commons.

Figure 79. ***Lunularia cruciata*** dehisced capsules. Photo by Ken-Ichi Ueda, with permission.

Figure 80. ***Lunularia cruciata*** with sporophytes dispersing spores. Photo by Ken-Ichi Ueda, with permission.

The gemmae of ***Lunularia cruciata*** (Figure 1-Figure 13) occur in pocket-like gemmae cups (Figure 81) (Brodie 1951). The gemmae themselves are **lenticular** (lens-shaped; Figure 82), a common shape for gemmae in cups, and can be splashed for about 60 cm.

Yeates (1908) noted that gemmae are coated with an adhesive mucilage that could readily attach to the coats of animals, hence accomplishing dispersal. Furthermore, rats disperse them to gullies and sewers that further disperse them by moving water. They could also attach to bird's feet, but there are no data on their survival as the birds fly through the cooler atmosphere.

Sussman (1965) attributed the success of many bryophytes, especially ***Lunularia cruciata*** (Figure 1-Figure 13), to the resistant nature of their tissues and gemmae (Figure 83-Figure 96). Such bryophyte species have high regenerative capacity and gemmae have good desiccation resistance. This permits them to spread widely around the world without the production of spores. And for this species, they often spread as hitchhikers in horticultural shipments.

Figure 81. ***Lunularia cruciata*** with gemmae firmly tucked into the cups. Photo from Botany Website, UBC, with permission.

Figure 82. ***Lunularia cruciata*** showing the lenticular shape of the gemmae. Photo by Martin Hutten, with permission.

Figure 83. ***Lunularia cruciata*** with young gemmae cups, showing how quickly they can appear on a young thallus that is still small. Photo by Ken-ichi Ueda, through Creative Commons.

Figure 84. ***Lunularia cruciata*** with crescent-shaped gemmae cups. Photo by David T. Holyoak, with permission.

Figure 85. ***Lunularia cruciata*** gemmae tightly arranged in crescent-shaped cup. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 86. ***Lunularia cruciata*** gemmae cup with discoid gemmae. Photo by Andras Keszei, with permission.

Figure 87. ***Lunularia cruciata*** gemmae in cup, showing collected water and suggesting that the gemmae are not ready for dispersal. Photo by Bernard De Cuyper, with permission.

Figure 88. ***Lunularia cruciata*** thallus section through gemmae cup. Arrow indicates one of the gemmae. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

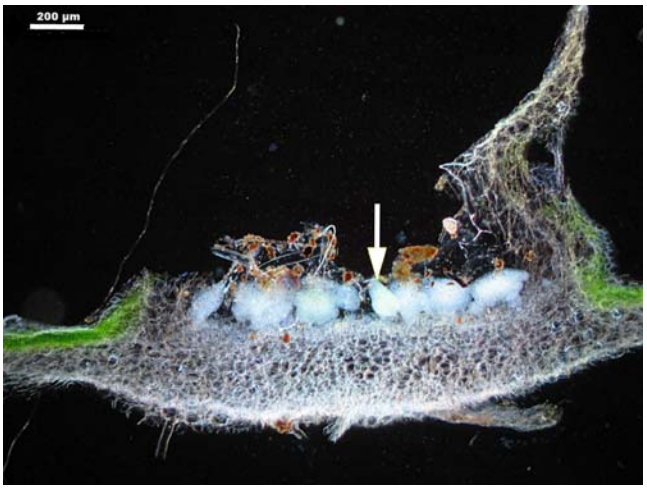

Figure 89. ***Lunularia cruciata*** gemmae cup cross section. **Arrow** indicates one of the gemmae. Note that the gemmae are attached and must break loose prior to dispersal. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 90. ***Lunularia cruciata*** with a few gemmae that have broken loose. Photo by Michael Lüth, with permission.

Figure 91. ***Lunularia cruciata*** gemmae cup with one escaped gemma. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 92. ***Lunularia cruciata*** with mature gemmae ready for dispersal. Those on the thallus will not germinate there. Photo by Jan-Peter Frahm, with permission.

Figure 93. ***Lunularia cruciata*** with some gemmae resting on the thallus, but not germinating. Photo by Michael Lüth, with permission.

Figure 94. ***Lunularia cruciata*** showing many dormant gemmae resting on the thallus, away from the gemmae cup. Photo by Jan-Peter Frahm, with permission.

Figure 95. ***Lunularia cruciata*** gemmae that have broken loose and are ready for dispersal. Photo by Walter Obermayer, with permission.

Figure 96. ***Lunularia cruciata*** and young plants, probably from gemmae. Photo by S. Bush, through Creative Commons.

Itouga *et al*. (2002) compared genetic differentiation in four species of East Asian liverworts. They found that the highest gene flow occurred in ***Conocephalum japonicum*** (Figure 97), a dioicous species that relies on spores, and was lowest in ***Lunularia cruciata*** (Figure 1-Figure 13), a dioicous species that relies on gemmae. ***Lunularia cruciata*** showed strong population differences, whereas ***Conocephalum japonicum*** showed little, further supporting the greater gene flow in the latter. In general, however, it was the monoicous species that exhibited the greatest population differences.

Following these, studies appeared on factors affecting the sexual cycle (Longton 1990) and morphology of the sporophyte of ***Lunularia cruciata*** (Figure 1-Figure 13) (Shimamura & Deguchi 2002).

Figure 97. ***Conocephalum japonicum*** with antheridial discs. Photo by David Long, with permission.

The persistence of gemmae permits the species to appear in disturbed areas. Biggs and Wittkuhn (2006) found diaspores of ***Lunularia cruciata*** (Figure 1-Figure 13) in litter samples, but not in soil samples. Disturbance can bring diaspores such as gemmae to the surface, where they can get light and germinate (Figure 98).

Figure 98. ***Lunularia cruciata*** germinating gemma. Photo from Plant Actions, with permission from Eugenia Ron Alvarez and Tomas Sobota.

Longton (1990) summarized the sexual reproduction problems in ***Lunularia cruciata*** (Figure 1-Figure 13). It readily produces both sexes and sporophytes in its native Mediterranean area. However, in areas where it has more recently become established, most likely by human dispersal through horticulture, sporophytes are rare. In Europe and California, USA, this is apparently due to insufficient moisture in summer to facilitate fertilization or sporophyte development. In temperate regions, it appears that climatic conditions are unsuitable for gametangial formation. Gametangia may occasionally appear in such temperate areas as southern Britain, but this may be due to aberrant weather that more closely resembles that of the Mediterranean area. It is also possible that the required long-day stimulation for gametangial development is not coupled with the right temperature (15-21ºC) or moisture availability. Based on observations, it appears that a warm period is needed to initiate antheridia in Britain, thus initiating them in late summer, followed by a cool period of winter when they become dormant. It also appears that the conditions needed to stimulate growth and reproduction differ geographically. In Israel, short days (winter) stimulate growth, during the more humid time of year, and the plants become dormant in the dry summer. But in Britain it is long days that stimulate growth. Clearly there are physiological races among these scattered populations. It appears that it has survived despite the mismatched timing because of its production of gemmae.

Uses

Aside from sometimes being welcome in a garden (but more likely considered a weed), ***Lunularia cruciata*** (Figure 1-Figure 13) has been used in making maize beer (Franquemont *et al.* 1990; Harris 2008).

Pande *et al*. (2004) found that extracts of ***Lunularia cruciata*** (Figure 1-Figure 13) inhibited germination of seeds of the legume ***Indigofera heterantha*** (Figure 99) and non-legume ***Impatiens scabrida*** (Figure 100). The inhibition was greater at lower concentrations than at higher ones. Initiation of germination was also delayed more in lower concentrations. Likewise, seedling growth was suppressed. As in most of these allelopathic studies, we need to demonstrate that the same inhibition occurs in the presence of whole plants of ***Lunularia cruciata*** and that the solvent alone does not contribute to the inhibition.

Or perhaps dying plants could leach the inhibitors in concentrations similar to those from the macerated plants. A further question is the ability of the soil to bind the inhibitor in the field, rendering it useless against these tracheophytes.

Figure 99. ***Indigofera heterantha***, a species whose seed germination is inhibited in the lab by extracts from ***Lunularia cruciata***. Photo by Dinesh Valke, through Creative Commons.

Figure 100. ***Impatiens scabrida***, a species whose seed germination is inhibited in the lab by extracts from ***Lunularia cruciata***. Photo by Paganum, through Creative Commons.

Schwabe (1990) found that an internal accumulation of lunularic acid could inhibit the growth of ***Lunularia cruciata*** (Figure 1-Figure 13). Schwabe also suggested that lunularic acid from the parent plant served to inhibit the germination of gemmae while still residing on the parent (Figure 101-Figure 102). As already noted, IAA could serve this function. On the other hand, despite leakage of lunularic acid to the soil, evidence suggests that it is not accumulated there, thus permitting gemmae to germinate once leaving the parent plant surface.

Figure 101. ***Lunularia cruciata*** with dormant gemmae on thallus. Photo by Martin Hutten, with permission.

Figure 102. ***Lunularia cruciata*** with dormant gemmae on thallus. Photo by Martin Hutten, with permission.

Herbivory

It is clear from some of the images posted that ***Lunularia cruciata*** (Figure 1-Figure 13) experiences herbivory (Figure 103). This could be from slugs, pillbugs, or insects. And perhaps even birds might nibble the edges.

Figure 103. ***Lunularia cruciata*** showing herbivory (**lower right**). Photo by Des Callaghan, with permission.

Interactions

Bacteria most likely play a larger role in bryophyte development than we have supposed. ***Methylobacterium*** (Figure 104) is able to inhabit the surfaces of plants, including ***Lunularia cruciata*** (Figure 1-Figure 13) (Kutschera & Koopmann (2005). While there, they secrete cytokinines that are able to promote growth of gemmae on agar plates. There seemed to be no effect on the seed plants tested, and Kutschera and Koopmann hypothesized that these bacteria have a role in normal development and regulation in ***Lunularia cruciata*** in nature.

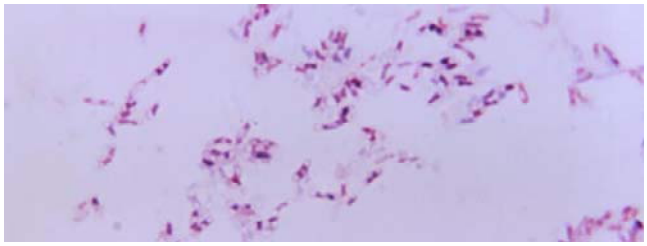

Figure 104. ***Methylobacterium***, a bacteria species that can live on the surfaces of ***Lunularia cruciata***. Photo by R. E. Weaver, CDC, through public domain.

Sahu *et al*. (2013) observed that the green alga ***Stichococcus bacillaris*** (Figure 105) occurred as a contaminant on laboratory cultures of ***Lunularia cruciata*** (Figure 1-Figure 13) on soil in growth chambers. They found that presence of the alga suppressed the growth of the liverwort, an example of algal allelopathy.

Figure 105. ***Stichococcus bacillaris*** on rotting wood, a green alga species that can be allelopathic to ***Lunularia cruciata***. Photo by James K. Lindsey, with permission.

Bukvicki *et al*. (2021) determined that bis-bibenzyl perrottetin F was isolated from ***Lunularia cruciata*** (Figure 1-Figure 13) by the fungus ***Aspergillus niger*** (Figure 106). This compound exhibits inhibitory activity against the bacteria ***Pseudomonas aeruginosa*** (Figure 107) PAO1 and ***Staphylococcus aureus*** (Figure 108) at concentrations of 100 µm to 450 µm. It also has "remarkable ability" to inhibit the synthesis of bacterial quorum-sensing signal molecules. These results suggest that this biological combination could provide a fast and effective way of producing bioactive substances.

Figure 106. ***Aspergillus niger***, a fungus that is able to isolate bis-bibenzyl perrottetin F from ***Lunularia cruciata***. Photo through public domain.

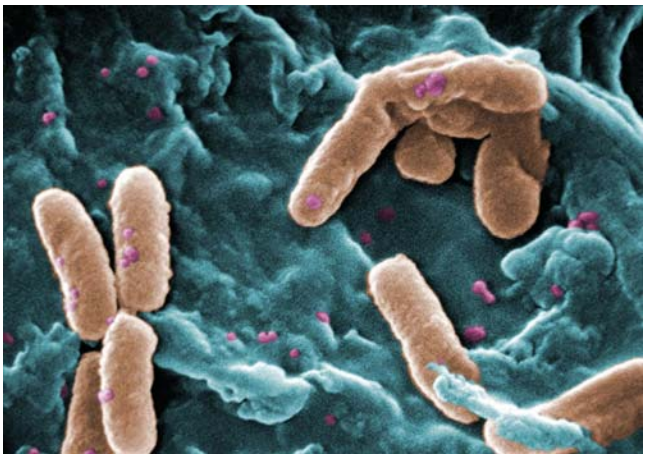

Figure 107. ***Pseudomonas aeruginosa***, colorized SEM. This is a bacterial species that is inhibited by bis-bibenzyl perrottetin F isolated by ***Aspergillus niger*** from ***Lunularia cruciata***. Photo by Janice Haney Carr, CDC, through public domain.

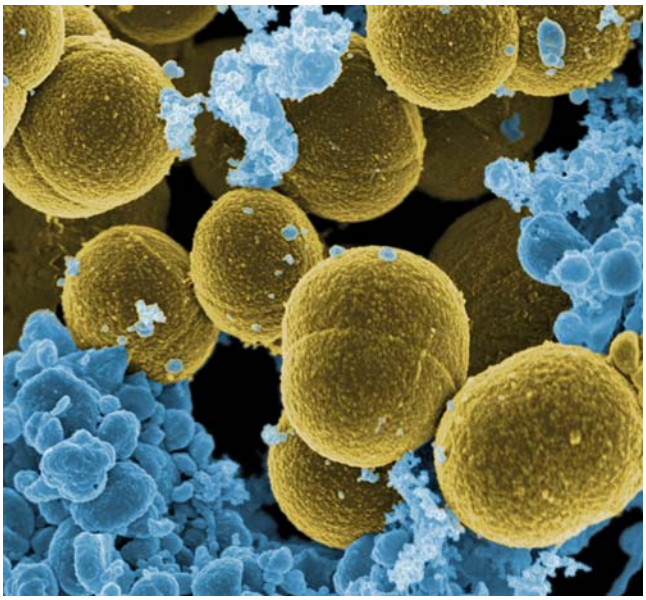

Figure 108. ***Staphylococcus aureus***, colorized SEM. This is a bacterial species that is inhibited by bis-bibenzyl perrottetin F isolated by ***Aspergillus niger*** from ***Lunularia cruciata***. Photo by Frank DeLeo, NIH, through public domain.

Lunularia cruciata (Figure 1-Figure 13) can be colonized by the oomycete pathogenic fungus ***Phytophthora palmivora*** (Figure 109) (Carella & Schornack 2018). The hyphae colonize the air chambers in the dorsal photosynthetic layer, and they may sometimes be associated with ventral epidermal cells and rhizoids (Figure 110). However, the fungus is never associated with the central storage region.

Figure 109. ***Phytophthora palmivora*** mycelia on papaya that has been damaged by herbivory. Photo by Scot Nelson, through Creative Commons.

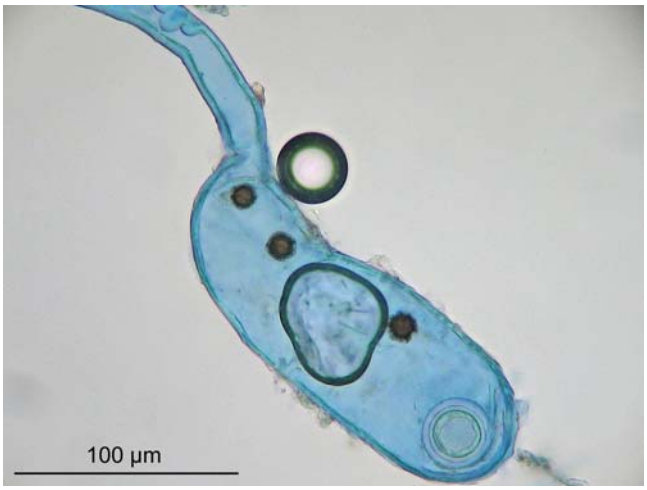

Figure 110. ***Lunularia cruciata*** inflated rhizoid. Photo by Jan Eckstein, with permission.

One of the most common groups of fungi in association with bryophytes is the **Glomeromycota**, a phylum of fungi that produce arbuscular mycorrhizal associations almost exclusively with bryophyte plants and tracheophyte roots. Among their habitats, they include wetlands and salt marshes.

Rhizophagus irregularis (Figure 111) is a symbiotic fungus in **Glomeromycota** that can colonize the thalli of ***Lunularia cruciata*** (Figure 1-Figure 13) (Carella & Schornack 2018). During the symbiosis, the fungus acts to up-regulate the transcriptome genes of the liverwort (Delaux *et al*. 2015). Delaux *et al*. conclude that the green alga ancestor of land plants was preadapted for symbiotic associations. This was followed in early land plants by gene duplication that permitted additional pathways, enabling a fully functional arbuscular mycorrhizal symbiosis.

Figure 111. ***Rhizophagus irregularis*** in the roots of the bean ***Vicia faba***; it is a symbiotic fungus that can colonize the thalli of ***Lunularia cruciata***. Photo by Mylène Durant, through Creative Commons.

Lunularia cruciata (Figure 1-Figure 13) is one of the bryophyte species in which the **Glomeromycota** mycorrhizae develop (Fonseca *et al*. 2006). Fonseca and coworkers cultured ***Rhizophagus irregularis*** (syn.=***Glomus intraradices***; Figure 111) and ***Glomus proliferum*** (see Figure 112), then introduced them to ***Lunularia cruciata***. The fungi produced external hyphae and spores similar to those found associated with roots.

Figure 112. ***Glomus*** sp.; ***Glomus*** species are all obligate arbuscular mycorrhizal (AM) fungi; ***G. proliferum*** forms this relationship with ***Lunularia cruciata***. Photo by Reiner Richter, through Creative Commons.

But that is not evidence of a symbiotic relationship, so Fonseca and Berbara (2008) used Koch's postulates to determine if they formed a symbiotic relationship. They found that fungi in cultured liverwort thalli were able to extend into a compartment of the Petri dish where they obtained phosphorus and to translocate that phosphorus

into the liverwort. The liverwort responded with increased dry weight, greater AM fungi spore production, and higher liverwort total phosphorus content. However, the researchers suggested that the energy requirements to maintain the symbiosis may limit its symbiotic advantage in the field. Fonseca and Berbara considered the relationship of endophytic ***Rhizophagus irregularis*** (Figure 111) and ***Glomus proliferum*** (see Figure 112) with ***Lunularia cruciata*** (Figure 1-Figure 13) to be a parasitic/opportunistic partnership rather than a mutualistic symbiosis.

The thalli of ***Lunularia cruciata*** (Figure 1-Figure 13) reveal major anatomical traits of mycorrhizal associations (arbuscules, coils, arbusculate coils and vesicles) when infected with ***Glomus proliferum*** (Figure 112) (Fonseca & Berbara 2008; Fonseca *et al*. 2009a). But colonized liverwort thalli exhibited a reduction in biomass in comparison with axenic thalli, supporting the conclusion that the relationship is parasitic (Fonseca *et al*. 2009a, b; Figueiredo 2010). Fonseca *et al*. 2009a) determined that those liverwort plants that did not fare well already had sufficient phosphorus, thus giving all the benefit to the fungus. This does not rule out the possibility of benefit to the liverwort in conditions where phosphorus is limiting because of the ability of the fungus to scavenge phosphorus from a much larger area than that available to the liverwort alone. Furthermore, significant reductions in growth of infected compared with uninfected cultured plants did not arise until 86 and 106 days of infection (Figueiredo 2010).

Fonseca *et al*. (2013) introduced laboratory methods for culturing ***Rhizophagus clarus*** (Figure 113) (syn.=***Glomus clarum***) and ***Gigaspora margarita*** (also in the **Glomeromycota**; Figure 114) with ***Lunularia cruciata*** (Figure 1Figure 4-Figure 13). *In vitro* cultures of ***Rhizophagus clarus*** and ***Gigaspora margarita*** were grown with ***Lunularia cruciata*** on macro and micronutrients with a layer of activated charcoal in the upper agar layer (Fonseca *et al*. 2014). Both fungal species reached maturity in less than 150 days and were still viable after more than 500 days. Container size was the only limiting factor for growth of the liverwort. Both fungal species colonized the midrib parenchyma. ***Gigaspora margarita*** developed relatively small, shallow colonies, apparently limited by its distribution within the plant. Penetration by this species occurs mainly through new entry points by its external hyphae from neighboring thalli and not by invasion from cell to cell. The higher level of colonization by ***Rhizophagus clarus*** most likely resulted from the internal growth of the fungi along the midrib parenchyma toward the thallus apical meristem. The production of spores occurred primarily among the rhizoids, developing between overlapping thalli and over the thalli (Fonseca *et al*. 2013). The pattern of development was similar to that seen in ***Rhizophagus irregularis*** (Figure 111) and ***Glomus proliferum*** (see Figure 112).

Nobre *et al.* (2013) found that inoculated thalli of ***Lunularia cruciata*** (Figure 1-Figure 13) achieved their peak absolute growth rate at 39 days after inoculation with ***Glomus proliferum*** (Figure 112), whereas those not inoculated required 42 days, suggesting a benefit to the liverwort under the growing conditions of the experiment. The liverwort exhibited a relative growth rate of 0.074 and 0.387 $cm^2\ cm^{-2}\ d^{-1}$, respectively. Addition of 20 and 80 mg carbon L^{-1} of humic acid had a positive influence on the growth of ***L. cruciata***.

Figure 113. ***Rhizophagus clarus***, a fungus that is able to colonize the midrib parenchyma of ***Lunularia cruciata***. Photo by Silvani Vanesa, Fernández Bidondo Laura, and Fracchia Sebastián, BGIV, through Creative Commons.

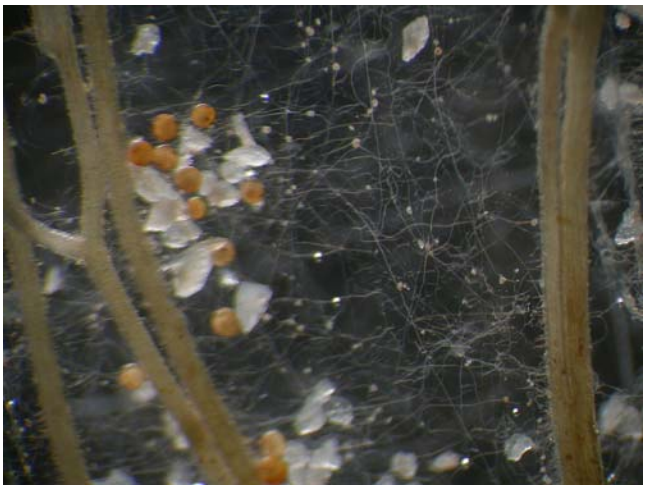

Figure 114. ***Gigaspora margarita***, a fungus that is able to form small colonies in the thallus of ***Lunularia cruciata***. Photo by Mike Geuther, through Creative Commons.

Desirò *et al*. (2013) renewed the story of big fleas have little fleas by demonstrating that the **Glomeromycota** inhabiting ***Lunularia cruciata*** (Figure 1-Figure 13) in a botanical garden were themselves inhabited by coccoid Gram-positive parasitic endobacterium related to the class **Mollicutes (**Figure 115**)**.

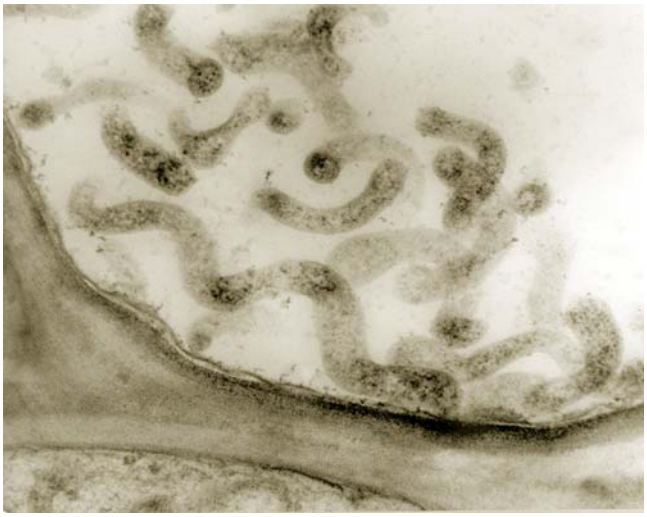

Figure 115. TEM image of ***Spiroplasma*** sp. (in class **Mollicutes**) from corn phloem. Photo through Creative Commons.

Auret (1930) first reported an endophytic fungus in ***Lunularia cruciata*** (Figure 1-Figure 13) in South Africa (only females were present). The fungi resided below the assimilating tissue and in the rhizoids. The mycelium exhibited branched, septate hyphae with granular contents, and they formed vesicles, arbuscules, and sporangioles, but none of the cells of the field-grown plants exhibited fructifications. However, when grown on glucose or protein agar, the fungus produced thin, hyaline hyphae that began to form pycnidia by the tenth day. These matured into flask-shaped structures with a beak or neck. Auret described this as a new species, ***Phoma lunulariicola*** (Figure 116-Figure 117). The relationship did not appear to harm the liverwort beyond the cells that were infected.

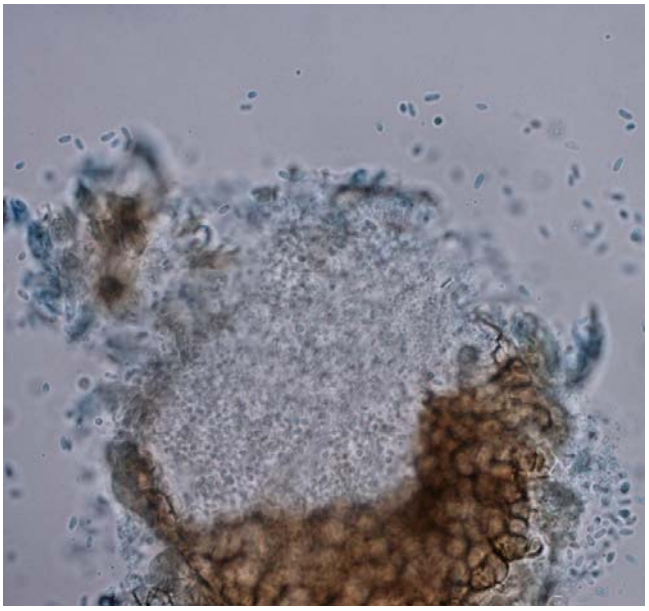

Figure 116. ***Phoma herbarum***; ***Phoma lunulariicola*** is an endophytic fungus in ***Lunularia cruciata***. Photo by Cesar Calderon, through Creative Commons.

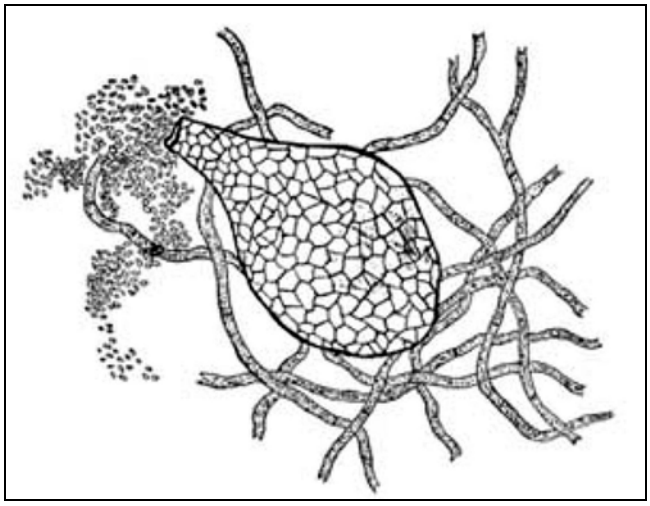

Figure 117. ***Phoma lunulariicola*** from ***Lunularia cruciata***, showing flask of spores. Modified from Auret 1930.

Ridler (1923) also observed the relationship. The fungus occurred in a single strand of cells along the thickened midrib area toward the surface of ***Lunularia cruciata*** (Figure 1-Figure 13). The liverwort partially digests the fungus, causing the fungus to form arbuscules and sporangioles. Its growth is restricted henceforth. The liverwort starch disappears after the fungus enters, benefitting the fungus. The liverwort does not seem to be harmed, agreeing with the description given by Auret (1930). Ridler also concluded that it was a species of ***Phoma*** (Figure 116-Figure 117).

Giordano *et al*. (1999) recorded the interactions between the lichen ***Cladonia foliacea*** (Figure 118) and ***Lunularia cruciata*** (Figure 1-Figure 13). The interaction by the lichen caused a delay in protonemal growth and reduction in the number of thallose plants produced. Internally, the cytoplasm obtained a granular appearance with many microvesicles in the protonema, enlarged periplasmic space, and changes in chloroplast shape.

Figure 118. ***Cladonia foliacea***, a lichen that causes a delay of protonemal growth and reduces the number of thalli produced in ***Lunularia cruciata***. Photo by J. C. Schou, with permission.

Basile *et al*. (2011) tested the effect of essential oils from the flowering plant ***Sideritis italica*** (**Lamiaceae**; Figure 119) on thallus and rhizoid growth and gemma development of ***Lunularia cruciata*** (Figure 1-Figure 13). Leaf oil was more active than was flowerhead oil, causing

inhibition of gemma development and browning, and inhibiting apical growth of the thallus of ***L. cruciata***.

Figure 119. ***Sideritis italica***, a species from which the essential oils inhibit gemma development and browning, and they inhibit apical growth in the thallus of ***Lunularia cruciata***. Photo by Andrea Moro, through Creative Commons.

Biochemistry

Lunularia cruciata (Figure 1-Figure 13) exhibits "conspicuous oil bodies" (Lepp & Lawson 1984). These are susceptible to damage from pollutants. In elevated vanadium levels, they change color from light brown to black.

Lunularia cruciata (Figure 1Figure 4-Figure 13) has been the subject of many physiological studies, so it is no surprise that it has been a subject of many biochemical studies as well. As early as 1940, Lugg determined that the amide tyrosine and tryptophan contents of the proteins of the main photosynthesizing tissues of ***Lunularia cruciata*** presented the same magnitude as those in seed plants.

Because of the micro-organisms that inhabit the surfaces of bryophytes, it is necessary to make certain that compounds identified actually were produced by the bryophyte and not the inhabitants. Christie *et al*. (1985) determined that the carbohydrates produced by axenically cultured ***Lunularia cruciata*** (Figure 1-Figure 13) were the same as those identified from field populations, especially alditols.

Lunularic acid, an ABA-like inhibitor and stress hormone, was named for its discovery in ***Lunularia cruciata*** (Figure 1-Figure 13) (Pryce & Kent 1971). Thus far, this hormone is almost unique to liverworts, and is notably absent from mosses (Pryce 1972). Yoshikawa *et al*. (2002) demonstrated the similarity of lunularic acid to ABA in both the physiological responses it elicits and in its apparent ability to bind to the same receptor in tracheophytes.

One of the early reports is the presence of sucrose phosphatase in ***Lunularia cruciata*** (Figure 1Figure 4-Figure 13) (Hawker & Smith 1984). This is evolutionarily significant because in all species tested it has been absent in red and brown algae and from fungi.

Markham and Porter (1974) identified luteolin 3′,4′-di-O-β-d-glucuronide as the major flavonoid in ***Lunularia cruciata*** (Figure 1-Figure 13) and at that time unique to this species. They also found luteolin 3′-O-β-d-glucuronide. James *et al*. (2020) reported the presence of carbohydrates, proteins, diterpenes, phytosterols, and anthocyanin, but flavonoids did not appear in the alcoholic or acetonic extracts.

Jocković *et al*. identified luteolin-7-O-glucoside and quercetin from extracts of ***Lunularia cruciata*** (Figure 1-Figure 13). Quercetin is a common plant flavonol in fruits, vegetables, leaves, seeds, and grains. It is reputed to bolster the immune system, to reduce hot flashes, and to serve as an antioxidant in humans. However, it is short-lived in humans, with a half life of only 1-2 hours, and the FDA warns that many of the claims for its beneficial effects to humans have not been validated.

Bryophytes present unique problems for biochemical analysis. Many species are quite small and it is difficult to get enough plants for analysis (Mukhia *et al*. 2019). Some are only available in a particular season; others have restricted geographic distribution or are rare. Hence, Mukhia *et al*. propagated ***Lunularia cruciata*** (Figure 1-Figure 13) for this purpose, using gemmae. This was a good choice because of its ability to grow in gardens over a large portion of the planet. They validated this approach by comparing its pharmacological properties with those of naturally grown plants. This endeavor revealed nine key compounds present in both lab-grown and field-grown plants. This verified that both *in vitro* and naturally grown plants produced antioxidant and anti-diabetic activity, thus making it feasible to culture this species for both experimental and clinical use.

The antibiotic activities of many liverworts against bacteria are well known. Joshi (1993) investigated antibacterial properties of ***Lunularia cruciata*** (Figure 1-Figure 13). Basile *et al*. (1993) explored the effects of a-D-oligogalacturonides on the production of antibiotic substances. Basile *et al*. (1998a) determined the minimum concentrations of extracts needed to illicit antibiotic activity against 13 bacterial strains and compared these with standard antipharmaceutical antibiotics. The extracts were effective against both Gram-positive and Gram-negative bacteria.

Sorbo *et al*. (2004) found significant antibacterial activity by ***Lunularia cruciata*** (Figure 1-Figure 13) extracts against the Gram-positive ***Staphylococcus aureus*** (Figure 108), ***Streptococcus*** sp. (Figure 120), and ***Enterococcus*** sp. (Figure 121) The activity against Gram-negative ***Proteus mirabilis*** (Figure 122), ***Pseudomonas aeruginosa*** (Figure 107), ***Escherichia coli*** (Figure 123), ***Salmonella*** sp. (Figure 124), and ***Klebsiella*** sp. (Figure 125) was especially good. The extracts also exhibited antioxidant activity, apparently due to A catechin and its derivatives. By contrast, Russell (2010) found no visible

antibiotic activity against the Gram-negative ***Escherichia coli*** (Figure 123) or ***Klebsiella pneumoniae*** (Figure 125). Nevertheless, ***Lunularia cruciata*** exhibited the most significant antibacterial activity among the 14 bryophyte species tested.

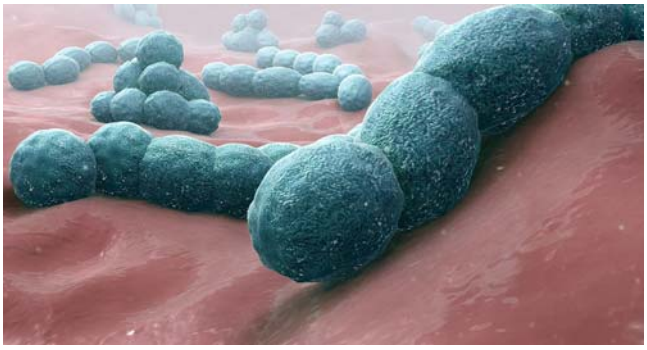

Figure 120. ***Streptococcus pneumoniae***; ***Lunularia cruciata*** exhibits significant antibacterial activity against ***Streptococcus*** sp. Photo from <www.scientificanimations.com>, through Creative Commons.

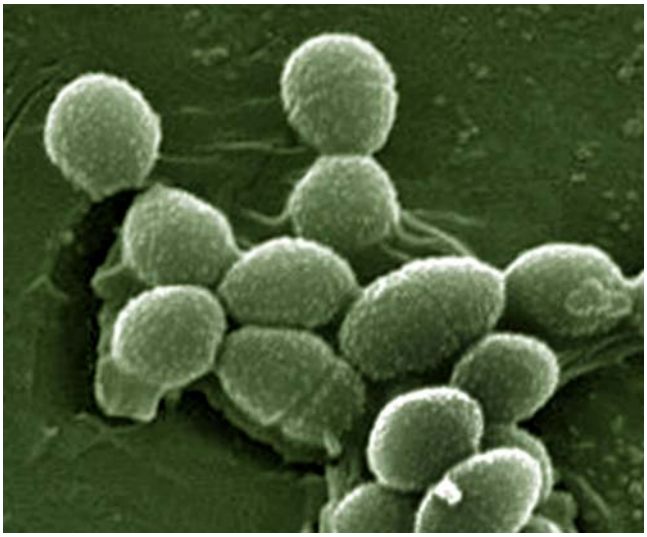

Figure 121. ***Enterococcus faecalis***; ***Lunularia cruciata*** exhibits significant antibacterial activity against ***Enterococcus*** sp. Photo by Janice Haney Carr, CDC, public domain.

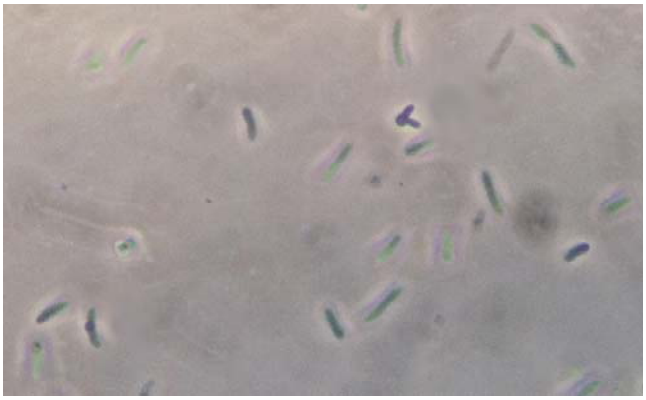

Figure 122. ***Proteus mirabilis*** suffering from Penicillin exposure. In early stages the bacteria are thickened in the middle (**lower left**). Later they fold into a V shape (**upper right**) just before lysis. Extracts from ***Lunularia cruciata*** are especially good at inhibiting the bacterium ***Proteus mirabilis***. Photo by Geoman3, through Creative Commons.

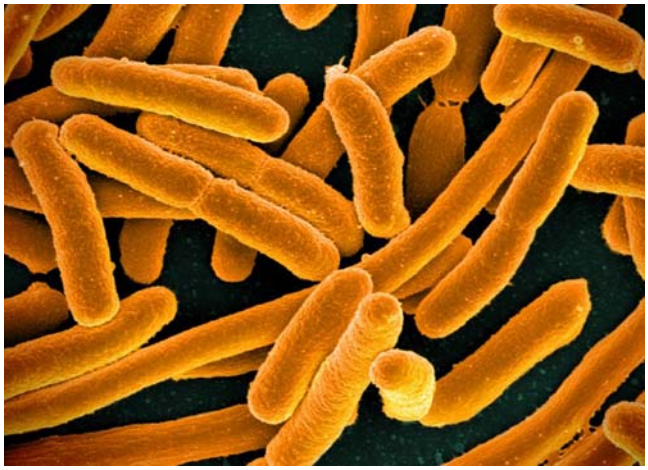

Figure 123. ***Escherichia coli*** colored SEM image, a species that does not seem to be affected by extracts from ***Lunularia cruciata***. Photo from NIAID, through Creative Commons.

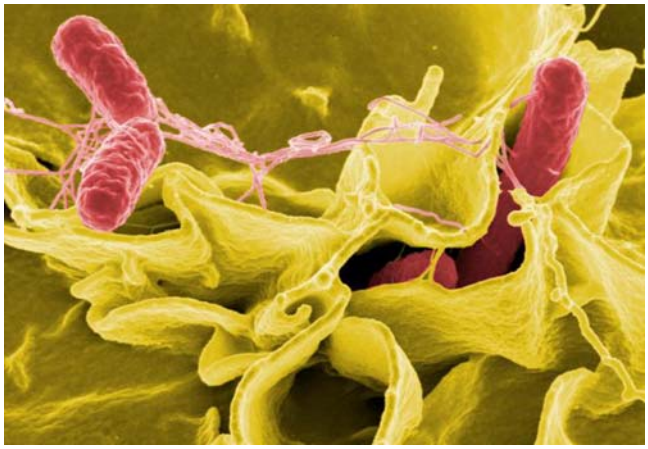

Figure 124. Colored SEM image of ***Salmonella*** invading cells; at least some members of this genus are unaffected by extracts from ***Lunularia cruciata***. Photo from NIAID, through Creative Commons.

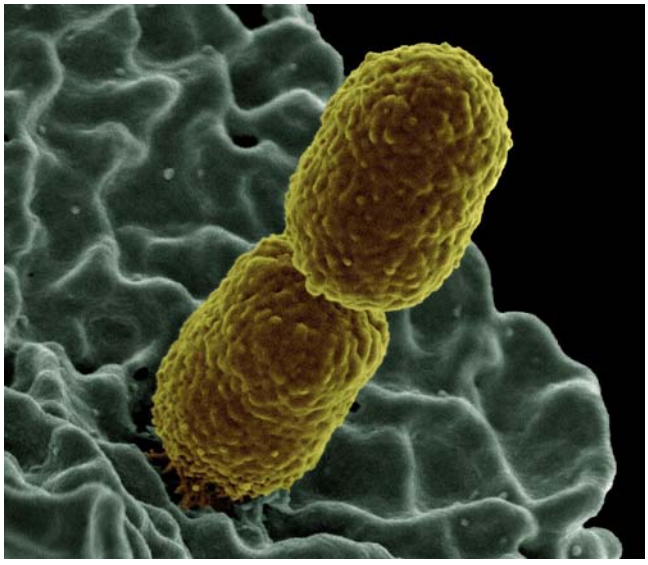

Figure 125. ***Klebsiella pneumoniae*** colored SEM image, a species that does not seem to be affected by extracts from ***Lunularia cruciata***. Photo from NIAID, through Creative Commons.

Dhondiyal *et al*. (2013) reported "substantial" antibiotic activity by ***Lunularia cruciata*** (Figure 1-Figure 13) extracts against five pathogenic species of bacteria [***Agrobacterium tumefaciens*** (Figure 126), ***Xanthomonas phaseoli*** (Figure 127), ***Escherichia coli*** (Figure 123), ***Bacillus subtilis*** (Figure 128), and ***Dickeya dadantii*** (Figure 129)]. This occurred in all four crude organic extracts against all five bacteria species. The extracts proved to be very effective against these bacteria when compared to the standard antibiotic ampicillin. But these results must be viewed with caution. While they provide evidence that the liverwort has medicinal properties, the aqueous extracts had no antibiotic effects, suggesting that the plants may not be protected by these natural compounds in nature. Furthermore, based on conflicting reports discussed above, we need to assess the role of the solvents as well as temperature, light, and nutrient conditions in altering the antibiotic effectiveness.

Figure 126. ***Agrobacterium tumefaciens*** causing a gall at the tree base. Photo by Jerzy Opioła, through Creative Commons.

Figure 127. ***Xanthomonas phaseoli*** infecting leaves of the bean ***Phaseolus vulgaris***; ***Lunularia cruciata*** exhibits significant antibiotic activity against this bacterial species. Photo by Howard F. Schwartz, through Creative Commons.

Lunularia cruciata (Figure 1-Figure 13) alcoholic and acetonic extracts are very active against ***Klebsiella pneumoniae*** (Figure 125) (James *et al*. 2020). ***Escherichia coli*** (Figure 123) is inhibited by both acetone and alcohol extracts. ***Staphylococcus aureus*** (Figure 108) is inhibited only by acetone extracts, whereas alcohol extracts elicit no inhibition. The researchers suggested that lunularic acid may be the reason for greater inhibitory responses to ***Lunularia cruciata*** extracts than to ***Marchantia emarginata*** (Figure 130) extracts.

Figure 128. ***Bacillus subtilis*** with Gram stain; ***Lunularia cruciata*** exhibits significant antibiotic activity against this species. Photo by W. D. Clark, CDC, through public domain.

Figure 129. ***Dickeya dadantii*** infecting ***Allium cepa*** (onion); ***Lunularia cruciata*** exhibits significant antibiotic activity against this bacterial species. Photo by Scot Nelson, through Creative Commons.

Figure 130. ***Marchantia emarginata***, a species that elicits less inhibitory response than does ***Lunularia cruciata***. Photo by Li Zhang, with permission.

Basile *et al*. (1998a) tested the minimum concentrations of extracts of ***Lunularia cruciata*** (Figure 1-Figure 13) needed to illicit antibiotic activity against 2 fungal species, but they found no antifungal activity among the strains tested.

Although extracts of ***Lunularia cruciata*** (Figure 1-Figure 13) in organic solvents proved to be very effective on the tested bacteria, none of the extracts had any effect against the three pathogenic fungi [***Alternaria alternata*** (Figure 131), ***Sclerotinia sclerotiorum*** (Figure 132), and ***Pyricularia oryzae*** (Figure 133)] tested (Dhondiyal *et al*. 2013).

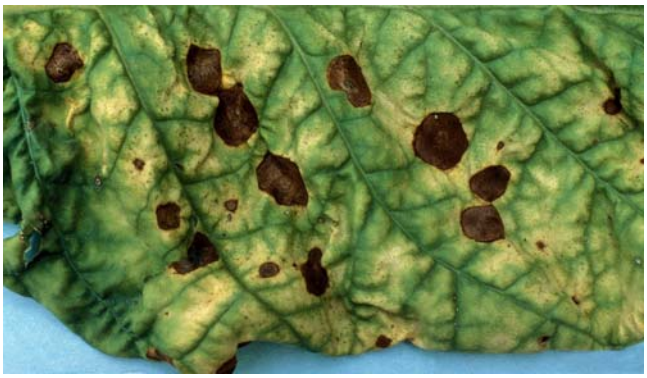

Figure 131. ***Alternaria alternata*** on tobacco leaf (***Nicotiana tabacum***), a species of fungi that is immune to extracts of ***Lunularia cruciata***. Photo by R. J. Reynolds Tobacco Company, through Creative Commons.

Figure 132. ***Sclerotinia sclerotiorum*** on bean, ***Phaseolus vulgaris***, a fungus species that is immune to extracts of ***Lunularia cruciata***. Photo by Jymm, through Creative Commons.

Figure 133. ***Pyricularia oryzae*** from rice, a fungus species that is immune to extracts of ***Lunularia cruciata***. Photo by Donald Groth, USDA Forest Service, through public domain.

Basile *et al*. (1991, 1993, 1998b) tested the ability of α-d-oligogalacturonides (OG) to induce antibiotic activity, using the fern ***Nephrolepis*** sp. (Figure 134) as a model system. This compound can occur naturally in the soil as a product of biological components. The experiments demonstrated that indeed the antibiotic activities can be induced, at least in the fern. Further testing indicated that extracts from wild-grown ***Lunularia cruciata*** (Figure 1-Figure 13) likewise inhibited the growth of all bacterial strains tested, whereas extracts from the axenically grown plants in the presence of α-d-oligogalacturonides were able to inhibit only three of the tested bacterial strains. Basile and coworkers concluded that the OG mixture induces the production of fewer antibiotic compounds compared to inducing compounds typically found in the soil. This does not rule out the possibility of more specific compounds being produced in response to OG.

Figure 134. ***Nephrolepis exaltata***, in a genus that produces the same α-d-oligogalacturonides (OG) as those of ***Lunularia cruciata***, compounds that can induce production of antibiotic compounds. Photo by Mokkie, through Creative Commons.

Sorbo *et al*. (2004) showed allelopathic activity by 7 pure flavonoids of ***Lunularia cruciata*** (Figure 1-Figure 13). In this case, they inhibited root development of the radish, ***Raphanus sativus*** (Figure 135). These same flavonoids presented severe allelopathic activity against spore germination and growth of the moss ***Tortula muralis*** (Figure 136).

Figure 135. ***Raphanus sativus*** (radish), a species whose roots are inhibited by flavonoids from ***Lunularia cruciata***. Photo by Rasbak, through Creative Commons.

Figure 136. ***Tortula muralis***, a moss species for which both spore germination and growth are severely inhibited by flavonoids from ***Lunularia cruciata***. Photo by Björn S., through Creative Commons.

Compounds from ***Lunularia cruciata*** (Figure 1-Figure 13) have other potential medical applications. An acetone extract is effective, causing significant changes in light emissions from whole blood phagocytes and polymorphonuclear leukocytes, providing inhibitory activity (Ielpo *et al*. 1998). The researchers postulated that the activity could be caused by compounds such as flavonoids or sesquiterpenes. In further experiments, Ielpo *et al*. (2000) demonstrated that both raw extracts and purified flavonoids exhibited activity against leukocytes.

Novakovic *et al*. (2019) isolated seven new bisbibenzyls from ***Lunularia cruciata*** (Figure 1-Figure 13), some of which are rare in nature. They demonstrated that riccardin G exhibited cytotoxic activity against the A549 cell line for lung cancer.

Summary

Lunularia cruciata is primarily a Mediterranean species, but it has spread to many places in the world through the horticulture trade. In many of these places sexual reproduction is rare or non-existent and gemmae provide the primary means of spread. It occurs in wet habitats, but is sometimes known from streams. Such moist habitats are provided by waterfalls, stream and river banks, moist slopes and dripping cliffs, springs, mires, seepage, wet soil, dune slacks, and roadside ditches. But it can in some circumstances venture farther from water, especially in gardens and greenhouses. It does especially well in greenhouses and gardens, perhaps due to dispersal gemmae by the watering regime.

Lunularia cruciata was the subject of a number of early physiological studies – finding positive gravitropism, conduction in midrib cells and between scales and rhizoids, hydrophobic pores, greater growth in response to short day length, desiccation hardening in long days, high temperatures and continuous light induce dormancy, lunularic acid protects against drought, inhibition of gemma germination by the thallus, and effects of higher temperatures on inhibiting gemmae.

Lunularia cruciata is highly resistant to pollution, but it can accumulate heavy metals and thus serves as a biological monitor. Flat, overlapping thalli and accompanying other bryophytes help to maintain moisture.

Various compounds in ***Lunularia cruciata*** are effective in inhibiting growth of bacteria. Fungi form various relationships from surface colonies to beneficial to parasitic. ***Lunularia cruciata*** has allelopathic properties against some seeds.

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CHAPTER 1-19
AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: AYTONIACEAE

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CHAPTER 1-19
AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: AYTONIACEAE

Figure 1. A steep stream bank where one might find liverworts in the **Aytoniaceae**. Photo by Michael Lüth, with permission.

Many of the species in this subchapter are not typical wetland or aquatic species. They were, however, found in a wetland or aquatic study or other wet habitat.

Marchantiidae – Marchantiales

Aytoniaceae

Asterella africana (Figure 2-Figure 3)

(syn. = *Fimbriaria africana*)

This species can exhibit a large variability in spore and elater dimensions, but other morphological characters seem to be relatively constant (Figueiredo *et al*. 2006).

Distribution

Asterella africana (Figure 2-Figure 3) is known from southern Europe, Macaronesia, and Africa (Long 2005), with widespread distribution in northern Macaronesia, but rare in Europe and North Africa (Blockeel 2012). Casas (1998) listed it for Spain and the Balearic Islands. Rupidera Giraldo and Elias Rivas (1996) reported it from the Ibérian Peninsula. Blockeel (2012) reported it from Crete as new to Greece. It occurs on Madeira and mainland Portugal (Sérgio *et al*. 2001; Figueiredo *et al*. 2006; Sim-Sim *et al*. 2010; Luís *et al*. 2015). Frahm (2005) found it on 5 of the 9 islands of the Azores. Van Dort and Nieuwkoop (2003) reported it from the laurel forests of the Canary Islands. Aleffi (2005) listed it from Italy.

Figure 2. ***Asterella africana*** thallus. Photo by Jan-Peter Frahm, with permission.

Figure 3. ***Asterella africana*** on soil. Photo by Jan-Peter Frahm, with permission.

Aquatic and Wet Habitats

Long (2005) considered ***Asterella africana*** (Figure 2-Figure 3) to have hygromorphic characters, but Losada Lima and Beltran Tejera (1987) considered it mesophytic in the Canary Islands. On the Iberian Peninsula Sérgio and García (2009) found that ***A. africana*** was associated with moderate temperatures and high humidity.

Luís *et al*. (2010) consider ***Asterella africana*** (Figure 2-Figure 3) to be riparian in Madeira (Figure 4), where it occurs in mountain streams (Luís *et al.* 2015). Luís and coworkers (2010) found that riparian bryophytes are affected by the habitat and position in the stream, but not by the main aspect (northern versus southern slope).

Figure 4. Fog among the mountains on Madeira Island. Photo courtesy of Michael Stech.

In the Adelantado Forest on Tenerife, wet habitats and shady areas permit the establishment of bryophytes that are scarce elsewhere (Cedrés-Perdomo *et al*. 2017). Among these, ***Asterella africana*** (Figure 2-Figure 3) occupies slopes near the ravine, taking advantage of the wet conditions. It is also frequent on shady humid slopes of ravines on Tenerife (Losada Lima & Beltran Tejera 1987). Patiño *et al*. (2010) considered anthropogenic disturbances such as water pollution and canalization to be a threat to this species along streams on the Canary Islands.

With these moisture requirements, it is not surprising to find ***Asterella africana*** (Figure 2-Figure 3) in association with waterfalls. González-Mancebo and Hernández-García (1996) found ***Asterella africana*** to be abundant on rocks and soil near continuously flowing springs and waterfalls in the Canary Islands. Capelo *et al*. (2005) reported a similar habitat on basalt in a waterfall on Madeira Island.

In Crete, one can find ***Asterella africana*** (Figure 2-Figure 3) on wet schistose rock ledges near a stream, where it seems to be always saturated (Blockeel 2012). Dirkse (1995) reported that on the Canary Islands it prefers sheltered rocks with dripping water, especially laurel and pine forests. Van Dort and Nieuwkoop (2003) similarly found it in the laurel forests of the Canary Islands. In particular, they found it at the foot of damp walls, where it was accompanied by ***Bryum donianum*** (Figure 5).

Figure 5. ***Bryum donnianum***, a species that accompanies ***Asterella africana*** at the base of damp walls in the Canary Islands. Photo by Michael Lüth, with permission.

Sérgio *et al*. (2010) found ***Asterella africana*** (Figure 2-Figure 3) on wet slopes on Macaronesia, again in laurel forests. Dirkse and Bouman (1996) found ***A. africana*** in the wettest and darkest places on the Canary Islands. Hernándes-García *et al*. (1995) considered it to be hydrophilic on the Islands, occurring in areas with low light and abundant drip.

Lava tube and pit cave entrances can provide interesting habitats for bryophytes. In the Azores, ***Asterella africana*** (Figure 2-Figure 3) seems to do well in such cave entrance habitats (Gabriel *et al*. 2008, 2011). It is possible that this habitat is a refugium because all recent records for ***Asterella africana*** are from cave entrances (Gabriel *et al*. 2008).

Physiology

Few studies discuss any aspect of the physiology of ***Asterella africana***. Pedrotti (1996) considers the species to have "thermophilic tendencies."

Adaptations

Long (2005) compared the hygromorphic ***Asterella africana*** (Figure 2-Figure 3) to the xeromorphic ***Asterella persica***. In ***A. africana***, the thallus is thin with large air chambers, whereas in the xeromorphic ***A. persica*** the thallus is thick and leathery with spongy assimilation tissue that has small, irregular air chambers. This is consistent

with the conclusion that air chambers in bryophytes provide for better gas exchange, but are a source of water loss.

On the Canary Islands, humidity conditions, substrate dynamics, and vegetation disturbance are important in influencing the life strategies present (González-Mancebo & Hernández-García 1996). These researchers report that ***Asterella africana*** (Figure 2-Figure 3) is a long-lived species, a strategy they consider typical around continuously flowing springs and waterfalls on both rocks and soil. In the Canary Islands, they found that the perennial life strategy is best represented in the more humid forests.

By contrast, Lloret and González-Mancebo (2011) considered ***Asterella africana*** (Figure 2-Figure 3) to be a short-lived shuttle species in the Canary Islands. These differences are likely the result of sampling two different habitat conditions, with the Lloret and González-Mancebo study being an altitudinal study.

Reproduction

On the Canary Islands, from which one can find many records of the presence of ***Asterella africana*** (Figure 2-Figure 3), the breeding systems, climatic conditions, and rarity can have considerable influence on the fertility of the species.

Asterella africana (Figure 2-Figure 3) is **monoicous** (Figure 6) (Long 1999, 2005). More specifically, it is **paroicous** (with archegonia and antheridia on same branch or stem) (Bischler-Causse & Long 1993). Losada Lima and Beltran Tejera (1987) found it fertile with archegonial heads (Figure 6-Figure 9) in the Canary Islands from February to July, and occasionally in November.

Figure 6. ***Asterella africana*** with young archegoniophores. Photo by Tim Waters, through Creative Commons.

Biochemistry

Although this species has a restricted distribution and is rare in many areas, the essential oils have been elucidated. The species of ***Asterella*** commonly produce intense scents (Ludwiczuk & Asakawa 2015). These odors are products of essential oils. Figueiredo *et al*. (2006) found that the essential oils were dominated by the monoterpene fraction (79-84%). These were predominantly myrtenyl acetate (30-42%) and α-pinene (10-17%). Sesquiterpene and non-terpenoid fractions amounted to only 1-2% and 4-8%, respectively (see also Asakawa *et al*. 2013).

Figure 7. ***Asterella africana*** on Tenerife with young archegoniophores. Photo by Jonathan Sleath, with permission.

Figure 8. ***Asterella africana*** archegonial heads. Photo by Jan-Peter Frahm, with permission.

Figure 9. ***Asterella africana*** archegonial head with capsules. Photo by Jan-Peter Frahm, with permission.

Asterella khasyana (Figure 10-Figure 15)

(syn. = *Fimbriaria khasyana*; *Rhacotheca azorica*)

Distribution

Asterella khasyana (Figure 10-Figure 15) is distributed in southeast Asia and tropical Africa (Long 2005). Its records include India, Pakistan, Nepal, Indochina, Indonesia, Bhutan, China, Philippines, and Thailand (Piippo 1990; Kaul *et al*. 1995; Piippo *et al*. 1997; Boonkerd *et al*. 2007; Singh & Singh 2008a; Daniels 2010; Piippo 2010; Singh *et al*. 2010; Piippo & Koponen 2013). It is common in the Great Himalayan National Park (Singh & Singh 2008a). Matcham (2000) found it in Uganda, Africa. Piippo and Koponen (2013) considered it to be present but very rare in Hunan Province, China.

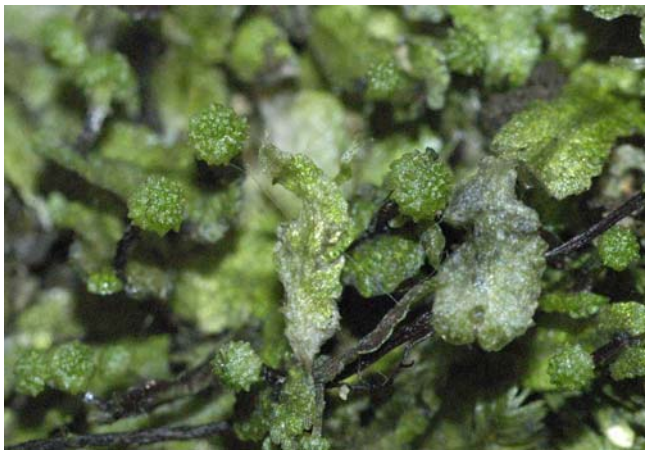

Figure 10. ***Asterella khasyana*** with archegoniophores and drying thalli. Photo by Manju Nair, through Creative Commons.

Figure 11. ***Asterella khasyana*** with archegoniophores. Photo by David Long, with permission.

Aquatic and Wet Habitats

Habitats for ***Asterella khasyana*** (Figure 10-Figure 11) vary. Karki and Ghimire (2019) consider it to be terricolous and saxicolous in Central Nepal, where it is locally rare. Dixit and Kerketta (2019) likewise consider it terricolous in the Lafa Hills, Chhattisgarh, India. But it seems to be predominantly reported from wet habitats.

Matcham (2000) reported ***Asterella khasyana*** from a very wet cliff in Uganda.

For bryophytes such as ***Asterella khasyana*** (Figure 10-Figure 11) that tend to be moisture loving, waterfalls offer a suitable habitat. Not many species can withstand being in the strong flow of the falls themselves, but the moist stream or river bank that is in the spray zone is a suitable habitat for many of these moisture loving species. Long (2006) reported ***Asterella khasyana*** from wet rocks by a waterfall in the Himalayas.

In the Himalayas, ***Asterella khasyana*** (Figure 10-Figure 11) occurs on damp rocky banks by the road (Long 2006). It has a sufficiently wide moisture tolerance to be found in dry habitats as well as wet ones. Long (2006) found it in a steep valley with patches of evergreen broad-leaved forest in the Himalayas in areas that are not wet. Singh and Singh (2008a) even classify it as terrestrial in the Great Himalayan National Park, where it is common, but state that it grows in moist and shady places.

For those species that are tolerant of higher humidity, stream and river banks are suitable and often preferred habitats. Piippo and Koponen (2013) reported ***Asterella khasyana*** (Figure 10-Figure 11) from sand on a wet brook side in Hunan Province, China. But also in China, in Hunan, Piippo and Koponen (2013) report ***A. khasyana*** from secondary forests and on sandy forest slopes. Piippo and Koponen (2013) also reported it from a cliff in China, where it has a humus substrate. Its rarity in the province may reflect a lack of suitable habitat, but it is more likely the result of not having arrived yet.

Boonkerd *et al*. (2007) reported ***Asterella khasyana*** (Figure 10-Figure 11) on moist, sandy soil slopes and rocks in exposed areas of the lower montane forests in Thailand. Paudel (2019) found it commonly in terrestrial habitats in Kailali in the Far West Nepal, where it was among the few species found in both acidic and basic *p*H.

Adaptations

Asterella khasyana (Figure 10-Figure 11) seems to cope with its somewhat wide range of habitats by several adaptive strategies. Long (2005) considers its thin, delicate thallus with large air chambers in overlapping layers to be hygromorphic characters. It lacks photosynthetic filaments in these chambers. It would be interesting to compare these characters among a large number of populations from varying degrees of moisture.

In some terricolous habitats ***A. khasyana*** grows in association with leafy liverworts (Dixit & Kerketta 2019), most likely affording it a greater water retention in its habitat. Sreenath and Rao (2020) found that in Andhra Pradesh, India, the species forms irregular rosettes that are often associated with ***Fissidens jungermannioides*** and other acrocarpous mosses, again a habit that is likely to conserve moisture.

Reproduction

Asterella khasyana (Figure 10-Figure 11) is **monoicous**, with its androecia on the main thallus just behind the base of the archegoniophore (**paroicous**) (Boonkerd *et al*. 2007). The archegonial heads (Figure 12-Figure 14) have distinct projections that may help in conservation of moisture, but we must also consider the possibility of light scattering to prevent damage to sporogenous tissue and developing spores.

Figure 12. ***Asterella khasyana*** with archegonial heads. Photo by David Long, with permission.

Figure 13. ***Asterella khasyana*** archegonial heads. Photo by Jan-Peter Frahm, with permission.

Figure 14. ***Asterella khasyana*** archegoniophores showing maturing sporangia looking like beaks. Photo by Jan-Peter Frahm, with permission.

The spores in ***Asterella khasyana*** (Figure 10-Figure 11) are large, ranging 65-78 µm in some Indian populations (Singh & Singh 2008b) and 80-90 µm in the Andhra Pradesh, India (Sreenath & Rao 2020). In Thailand, Boonkerd *et al*. (2007) reported a range of 75-90 µm. Alam *et al*. (2020) report spores that are 85-100 µm in southern India. Naveen *et al*. (2014) described the morphology spores of the species in India. It would be interesting to know how the spore size relates to habitat and to dispersal ability in this species.

No specialized asexual reproductive structures are known in ***Asterella*** (Schuster 1992), but Chaturvedi and Eshuo (2012) described abnormal asexual reproduction in ***Asterella khasyana*** (Figure 10-Figure 11). This was accomplished by the development of new thalli from the archegonial head (Figure 15), a type of regeneration.

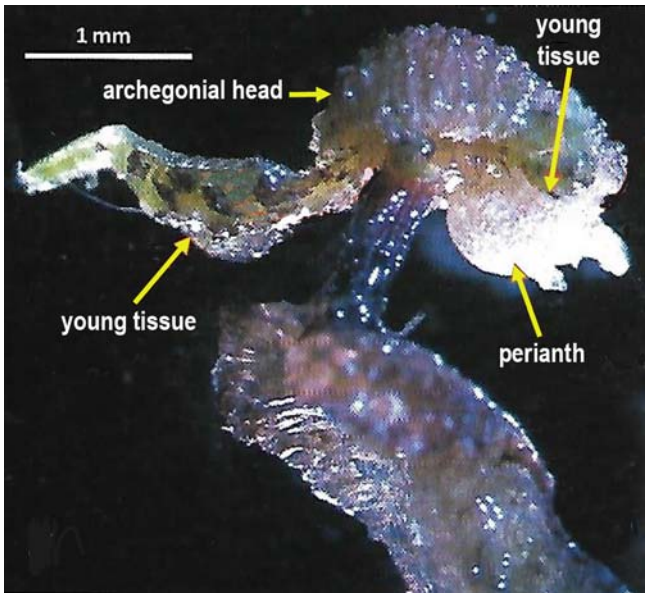

Figure 15. ***Asterella khasyana*** regeneration of archegonial head. Photo by Sunil Chaturvedi, with permission.

Mannia fragrans (Figure 16-Figure 18)

(syn. = *Grimaldia fragrans*)

Distribution

Mannia fragrans (Figure 16-Figure 18) is widely distributed, but its distribution is disjunct (Schuster 1992). Portions of its distribution are relict. It is known in Asia (Himalayan Mountains, Korea, China, Japan), Europe, and scattered locations in North America (Schuster 1992; Choi *et al*. 2020), but it is relatively rare, despite its widespread distribution.

Figure 16. ***Mannia fragrans*** thallus with scales. Photo by Martin Hutten, with permission.

Figure 17. ***Mannia fragrans*** growing on the ground. Photo by Michael Lüth, with permission.

Figure 18. ***Mannia fragrans*** showing curling dry thalli. Photo by Michael Lüth, with permission.

When Oesau (2010) investigated the current presence of ***Mannia fragrans*** (Figure 16-Figure 18) in the lower valley of the River Nahe, Germany, they were able to confirm its previously known locations in conservation areas, but they warned that it is nevertheless endangered due to natural succession and damage by game animals.

Aquatic and Wet Habitats

Schuster (1992) describes both xeromorphic and mesomorphic ecotypes for ***Mannia fragrans*** (Figure 16-Figure 20). Conard (1940) refers to Iowa, USA, populations as distinctly xerophytic, growing in wooded areas or on stony hills in the prairie, but it is also frequent on rocks in half shade. Oesau (2010) found it in the arid region of the River Nahe in Germany.

Nevertheless, ***Mannia fragrans*** (Figure 16-Figure 20) occurs along calcareous rivers in Connecticut, USA (Nichols 1916)**.**

Bakalin *et al*. (2019) reported a number of locations in Amur Province in Russia, but none of these was wet. Only mesic sandstone cliffs and crevices were somewhat moist.

In Poland ***Mannia fragrans*** (Figure 16-Figure 20) has been considered an endangered species (Piwowarczyk & Stebel 2012). Nevertheless, while it is threatened by succession of tracheophytes (Figure 21), it has been released from the damage due to former grazing. The researchers describe it as "almost all over the slope above the Kamienna River in the village of Podgrodzie."

Figure 19. ***Mannia fragrans*** soil habitat. Photo by Michael Lüth, with permission.

Figure 20. ***Mannia fragrans*** on bank. Photo from Gencat, with online permission.

Figure 21. ***Mannia fragrans*** showing competing tracheophytes and lichens. Photo by Michael Lüth, with permission.

One habitat that seems to favor ***Mannia fragrans*** (Figure 16-Figure 20) is wind holes (Figure 22). Choi *et al*. (2020) report its presence on shaded rocks near the wind hole in broad-leaved deciduous forests in Korea. Bakalin *et al*. (2017) describe these as formations where the wind enters large holes tens of meters above, then goes underground, where it passes among wet stones and cliffs in areas with much lower temperatures due to evaporation of water from the stones. Therefore, at the exit hole, the air temperature may be about 10ºC below that of the surrounding environment. This provides suitable habitat for several ***Mannia*** species.

Figure 22. Wind hole in Bihor Mts. in Transylvania, Romania. Note cryptogams growing on the interior walls. Photo courtesy of Tamás Pócs.

Physiology

In ***Mannia fragrans*** (Figure 23-Figure 24) all cells survived 12 hours at 20ºC and 15% humidity, making it the most desiccation-tolerant species among the 33 species reported (Clausen 1964). When in ice at -10ºC, it was unable to survive for even two days, but when partly desiccated it did survive 2 days at -10ºC. This suggests that when it is hydrated, there is likely to be membrane damage due to formation of crystals or cell expansion.

Figure 23. ***Mannia fragrans*** on soil in a dry state. Photo by Michael Lüth, with permission.

Figure 24. ***Mannia fragrans*** dry and curled. This might reduce moisture loss, but it could also reduce light damage in the dormant cells. Photo by Janice Glime. The dark color also helps to prevent light damage.

Adaptations

Sometimes ***Mannia fragrans*** grows with other bryophytes (Figure 25-Figure 26). This behavior can take advantage of the capillary water held by the adjoining bryophytes to maintain its own moisture longer.

Figure 25. ***Mannia fragrans*** with emerging archegoniophores and accompanying mosses. Photo by Angus Mossman, through Creative Commons.

Figure 26. ***Mannia fragrans*** with mosses, where it could benefit from their moisture retention. Michael Lüth, with permission.

In other cases, its own thalli tightly cover the ground (Figure 27), reducing evapotranspiration. This is probably useful in some habitats in preventing erosion and protecting soil organisms.

Figure 27. ***Mannia fragrans*** showing overlapping and tightly adhering thalli of a nearly pure colony. Photo by Michael Lüth, with permission.

One potential adaptation to obtaining and maintaining moisture is the presence of ventral scales (Figure 28). In other liverworts, these are known to provide capillary spaces that facilitate the uptake of water throughout the thallus.

Figure 28. ***Mannia fragrans*** ventral scale with transparent appendages. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Reproduction

The genus ***Mannia*** can be **dioicous** or **monoicous** (Choi *et al*. 2020). ***Mannia fragrans*** (Figure 29) is **polyoicous** (species being both monoicous and dioicous) (Schuster 1992). Hock *et al*. (2009) noted that colonizers that produce both sex organs are favored in selection because they ensure sexual reproduction when no partner is present. This is especially important for species like ***Mannia fragrans*** that have no specialized means of asexual reproduction.

Figure 29. ***Mannia fragrans*** with antheridial patches (dark brown) and young archegoniophores (pinkish red with scales, but it is hard to determine if they are on the same plant or on different plants. Photo by Jan-Peter Frahm, with permission.

The male branches or plants (Figure 30-Figure 31) produce patches of antheridia on the thallus surface. The phenology of these sexual structures, including the conditions that trigger their initiation, need to be studied.

Figure 30. ***Mannia fragrans*** on soil in NW Iowa, USA, with a few brown antheridial patches. Photo by Janice Glime.

Figure 31. ***Mannia fragrans*** with brown patches of antheridia. Photo by Janice Glime.

In ***Mannia fragrans*** (Figure 29), there is a strong female-biased sex ratio (Figure 32-Figure 35); sexual expression is high (Hock *et al*. (2008b). This high expression contributes to high fertilization rates and may account for its widespread distribution. But its relative rarity suggests that most arrival sites do not provide the conditions needed for establishment.

Figure 32. ***Mannia fragrans*** thalli with developing archegoniophores. Photo by Michael Lüth, with permission.

Figure 33. ***Mannia fragrans*** with beginning stages of archegoniophores and scales. Photo by Štěpán Koval, with permission.

Figure 34. ***Mannia fragrans*** showing archegoniophore scales. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 35. ***Mannia fragrans*** archegonial heads with scales. Note the browning thalli that can leave small apical portions for potential dispersal. Photo by Aaron Carlson, through Creative Commons.

The archegoniophore is surrounded by white scales (Figure 34-Figure 38) that remain at the base when it elongates. Perhaps these help to maintain the proper moisture levels at the time of fertilization. Following sexual reproduction, there is further growth in male plants, but not in female plants/branches (Hock *et al*. 2009).

Figure 36. ***Mannia fragrans*** young archegonial head with scales. Photo by Aaron Carlson, through Creative Commons.

Figure 37. ***Mannia fragrans*** archegonial head with scales as it emerges from the thallus. Photo by Botanicalwanderer, through Creative Commons.

Figure 38. ***Mannia fragrans*** female lobes with only small apical portions of the thallus remaining. Photo by Samuel Brinker, through Creative Commons.

Despite the elevation of the sporangia on the extended archegoniophore (Figure 39), the large spores [60.0-82.0 µm (Figure 40) (Choi *et al*. 2020)] will mostly fall back to the same population. This results in significant differences between distant populations and signals negligible gene flow between them. There are numerous rare alleles and unique recombinations, indicating that at least occasional recombination and mutation do occur (Hock *et al*. 2009). In Japan, mature spores occur in early winter (Furuki 1992).

Figure 39. ***Mannia fragrans*** mature archegonial heads with dehisced sporangia. Photo by Václav Dvořák, through Creative Commons.

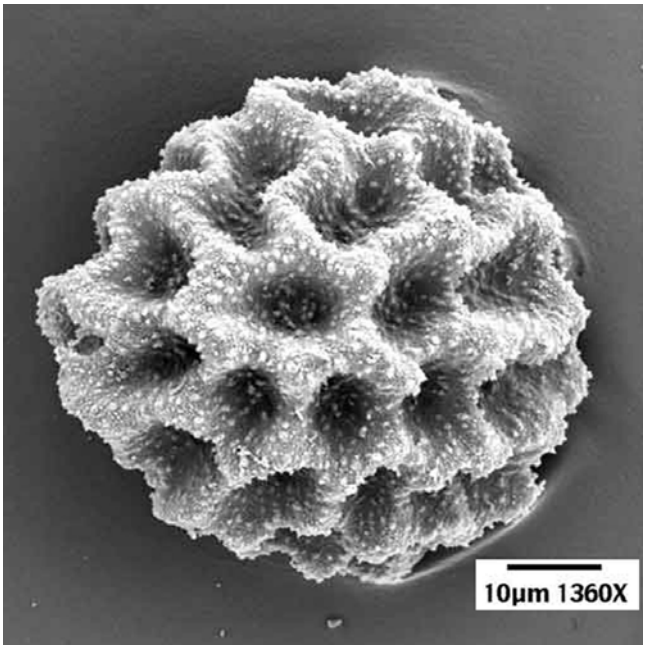

Figure 40. ***Mannia fragrans*** distal spore wall SEM. Photo by William T. Doyle, with permission.

Asexual reproduction in ***Mannia fragrans*** occurs commonly by fragmentation of thalli (Figure 41) (Hock *et al*. 2008b). But despite the high frequency of spore production, the genetic diversity within populations is low, suggesting that fragmentation is an important source of new plants (Hock *et al*. 2008b, 2009). Even when sexual reproduction occurs within the population, it is likely to occur between two identical genomes that have arisen through fragmentation.

Figure 41. ***Mannia fragrans*** with what appear to be dying older thalli with green apices and early stages of sexual structures. As these older parts of thalli die, they provide a means of fragmentation. During rain events, these smaller pieces of thalli could become dislodged, facilitating dispersal. This dispersal mechanism needs to be documented.

Hock *et al*. (2008a, b) used ***Mannia fragrans*** (Figure 41) to demonstrate that a diaspore bank can conserve genetic variability over generations and seasons. Propagules can remain in the soil for extended periods of time, then come to the surface following a disturbance, and grow, expressing the gene pool of previous points in time.

Fungal Interactions

De (2017) found that the **Glomeromycota** fungus ***Planticonsortium tenue*** (=*Glomus tenue*) grows in association with the gametophyte of ***Mannia fragrans*** (Figure 41). It primarily colonizes the smooth rhizoids, but can also live among the scales (Figure 28) and tuberculate rhizoids. From there, the fungus grows upward into the parenchyma cells of the thallus midrib and crosses the cell walls through the plasmodesmata. It is interesting that vesicles are able to develop in the smooth rhizoids and in the scales, but fail to develop in the tuberculate rhizoids. Within the thallus, the fungus occurs mostly intracellularly, forming vesicles and arbuscules in the midrib cells. Young cells are fungus free.

Biochemistry

As its name implies, ***Mannia fragrans*** (Figure 41) is usually aromatic, with the odor of cedar oil, although there seem to be some population variants (Choi *et al*. 2020). Schuster (1992) describes it as "oil cells frequent." Asakawa (2007) attributes the strong, sweet mossy odor to the cuparene-type sesquiterpene ketone, grimaldone.

Huneck *et al*. (1988a) reported pakynol as a macrocyclic bisbibenzyl diether from ***Mannia fragrans*** (Figure 41). Nogradi *et al*. (1990) later elaborated the synthesis of the compound in this species and Böcskei and Keserű (1994) described its crystal structure.

Huneck *et al*. (1988b) described the structure of the tricyclic sesquiterpenoid grimaldone in this species. Odrzykoski and Szweykowski (1981) found that ***Mannia fragrans*** (Figure 41) has only one form of glutamate dehydrogenase, but has two forms for glutamate-oxaloacetate transaminase.

Mannia triandra (Figure 42-Figure 43)

(syn. = *Mannia rupestris*)

There is a surprising number of publications on this species. Schill (2006) wrote a dissertation on the taxonomy and phylogeny of the genus ***Mannia***.

Distribution

Mannia triandra (Figure 42-Figure 43) is a disjunct, circumpolar, subcontinental species from subarctic and subalpine regions (Müller *et al*. 2014), *i.e.* **arctomontane** (Borovichev & Bakalin 2016). Its distribution includes Europe [Montenegro (Duda 1965) and Albania, Austria, Bosnia, Bulgaria, Croatia, Czech Republic, France, Germany, Hungary, Italy, Macedonia, Poland, Romania, Russia, Slovakia, Slovenia, Sweden, Switzerland, Ukraine (Hugonnot & Offerhaus 2005; Sabovljević & Natcheva 2006; Müller *et al*. 2014)], North America (Greenland, Canada, USA), and Asia (China, Japan, Russia) (Müller *et al*. 2014). Schuster (1992) questions the Japanese record as probably another species. Furthermore, there seemed to be no recent records in Bosnia, Macedonia, or Slovenia (Sabovljević & Natcheva 2006; Ros *et al*. 2007; Alegro *et al*. 2019). However, in 2017, Krajšek and Martinčič reported several localities for it in Slovenia and cautioned that it is only visible in spring due to its ephemeral life cycle. Records for Spain appear to be based on problems of incorrect synonymy and Brugués *et al*. (2011) therefore excluded it from the flora there.

Figure 42. ***Mannia triandra*** on soil in Europe. Photo by Michael Lüth, with permission.

Figure 43. ***Mannia triandra*** thalli amid other bryophytes. Photo by Michael Lüth, with permission.

Mannia triandra (Figure 42-Figure 43) is a calcicole, concentrated mostly at low elevations in the Alps (Schuster 1992). Shershen *et al*. (2018) reported ***M. triandra*** from the Loud Thunder Forest Preserve in Illinois, USA. Conard (1940) reported it as rare in Iowa, USA.

Mannia triandra (Figure 42-Figure 43) is red-listed (threatened or endangered) in many of the countries where it occurs (Schumacker & Matriny 1995; Kučera & Váňa 2003; Colacino & Sabovijevic 2006; Martinčič 2009; Németh & Papp 2011; Dulin 2013; Zechmeister & Köckinger 2014; Borovichev & Bakalin 2016; Hodgetts *et al*. 2019).

Aquatic and Wet Habitats

Mannia triandra (Figure 42-Figure 43) is a species that occurs on Ca-rich or other basic substrata (Borovichev & Bakalin 2016). Hugonnot (2010) considers it to be a temporary hygrophile. Philippe (2013) says it is "absolutely not rupicolous," *i.e.*, it does not grow on rocks. Conard (1940) states that it is strictly xeric in Iowa, USA.

But this xerophytic habit is not universally true. In Hungary, Németh (2011) found ***Mannia triandra*** (Figure 42-Figure 43) growing with ***Clevea*** (=***Athalamia***) ***hyalina*** (Figure 44), ***Myurella julacea*** (Figure 45), and ***Plagiobryum zieri*** (Figure 46) on north-facing slopes

where it is shaded, humid, and "rather cool" (see also Németh & Papp 2011). It is mesothermophilic (Dierßen 2001). Philippe (2013) describes its habitat of Bonneille, France, as one that has a misty escarpment with a high spring humidity and dry summer. But none of the colonies occurred in habitats that were even temporarily oozing.

Figure 44. ***Clevea hyalina***, a species that accompanies ***Mannia triandra*** in cavities of vertical rocks. Photo by Hugues Tinguy, with permission.

Figure 45. ***Myurella julacea***, a species that accompanies ***Mannia triandra*** in cavities of vertical rocks. Photo by Michael Lüth, with permission.

Figure 46. ***Plagiobryum zieri***, a species that accompanies ***Mannia triandra*** in cavities of vertical rocks. Photo by Tomas Hallingbäck, with permission.

Dürhammer (2017) finds ***Mannia triandra*** (Figure 42-Figure 43) on permanently humid substrata of calcareous rocks that are adequately lit. It is endangered in the damp cracks in the rock due to the rock climbers who tend to rest there or use them as footholds. It does especially well in humid rock overhangs, but that habitat is particularly fragile. Meinunger (1992) found that the same problems face populations in Germany. These habitats contrast with Philippe's (2013) assertion that it is not rupicolous, suggesting again that it may have population differences.

Borovichev and Andreeva (2009) found ***Mannia triandra*** (Figure 42-Figure 43) on limestone outcrops on the river bank in the Lapland Nature Reserve, Murmansk, Russia, where it was moist and shady.

Borovichev (2014) found that in the Murmansk Province of Russia, ***Mannia triandra*** (Figure 42-Figure 43) grows exclusively on calcareous substrates. Philippe (2013) describes ***M. triandra*** as **chasmophilic**, living in crevices of limestone escarpments. Alegro *et al*. (2019) reported it from small, earthy pits and cavities of vertical rocks, often accompanied by ***Preissia quadrata*** (Figure 47).

Figure 47. ***Preissia quadrata*** with archegoniophores, a species that often accompanies ***Mannia triandra*** in cavities on rocks. Photo by Oskar Gran, through Creative Commons.

Papp (1980) reported the only known location for ***Mannia triandra*** (Figure 42-Figure 43) in Hungary to be the base of a large limestone rock wall. Németh and Papp (2011) found it in cool, humid microhabitats of north-facing calcareous slopes in the Bükk Mountains of Hungary. Papp *et al.* (2007) reported it from limestone cliffs. In the Komi Republic of Russia, Dulin (2013) found it on ledges of southeast-facing outcrops (Figure 48-Figure 50).

Figure 48. ***Mannia triandra*** on rock in a large crevice. Photo by Renzo Salvo, through Creative Commons.

Figure 49. ***Mannia triandra*** in limestone rock crevice. Photo by Hugues Tinguy, with permission.

Figure 50. ***Mannia triandra*** on rock ledge. Photo by Oliver Dürhammer, through Creative Commons.

In the Korean Peninsula, ***Mannia triandra*** (Figure 42-Figure 43) occurs in wind holes (Figure 22) (Borovichev & Bakalin 2016). These cooler locations serve as refugia for rare alpine plants.

But often, ***Mannia triandra*** (Figure 42-Figure 43) occupies habitats that are not moist (Németh & Papp 2011). In the Bükk Mountains of Hungary, these include rock crevices on dolomite, soil (Figure 51) at the base of near vertical rock walls, and humus containing dolomite fragments between surface roots of small ***Fagus sylvatica*** (Figure 52) and ***Fraxinus ornus*** trees. Conard (1940) reported it from exposed dry rocks in wooded areas and on stony hills in the prairie in Iowa, USA.

Figure 51. ***Mannia triandra*** on soil. Photo by Hugues Tinguy, with permission.

Figure 52. ***Fagus sylvatica*** roots, providing a habitat where one might find ***Mannia triandra***. Photo by Vegetator, through Public Domain.

Physiology

Dierßen (2001) described the ecological amplitude of European bryophytes, including ***Mannia triandra*** (Figure 42-Figure 43). Simmel *et al*. (2021) assigned an Ellenberg Indicator Value (EIV) for N of only 3, an indicator that it occurs on sites that are more or less infertile.

The range of habitats known for ***Mannia triandra*** (Figure 42-Figure 43) suggest that it has a relatively wide moisture tolerance (Figure 53). Its presence on rock surfaces indicate that it will get dried out at times (Figure 53).

Figure 53. ***Mannia triandra*** in a dry condition. Photo by Hermann Schachner, through Creative Commons.

Adaptations

Mannia triandra (Figure 42-Figure 43) is a **short-lived shuttle species** (Orbán 1984; Németh & Papp 2011), permitting it to occupy transient habitats.

Mannia triandra (Figure 42-Figure 43) has well developed aerenchyma in the thallus (Figure 54), occupying 2-3 layers in the middle of the thallus and completely filling the wings (Borovichev & Bakalin 2016). These are, however, empty, having no photosynthetic filaments. Hence, they serve as reservoirs for CO_2, but can also increase evapotranspiration.

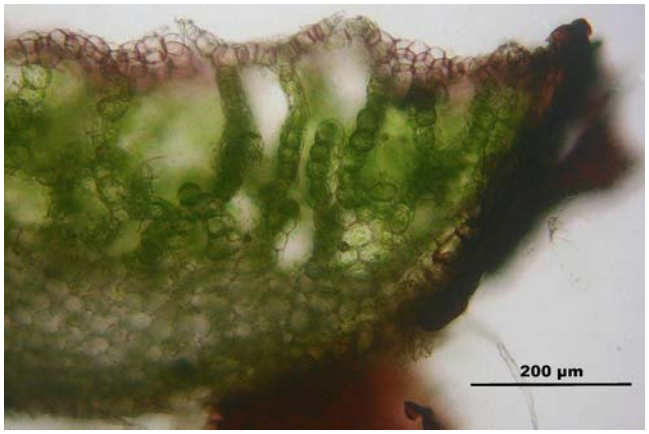

Figure 54. ***Mannia triandra*** thallus section showing air chambers and pores. Photo by Hermann Schachner, through Creative Commons.

Based on images I have seen, ***Mannia triandra*** (Figure 42-Figure 43) can grow with densely intermingled other bryophytes (Figure 55-Figure 56). Such a growth habit can help to maintain moisture for longer periods of time.

Figure 55. ***Mannia triandra*** with mosses, showing their dense growth that can help to retain water. Photo by Michael Lüth, with permission.

Figure 56. ***Mannia triandra*** with closely associated mosses and producing young archegoniophores. Photo by Michael Lüth, with permission.

Reproduction

Schuster (1992) describes ***Mannia triandra*** (Figure 42-Figure 43) as **dioicous**. However, Borovichev and Bakalin (2016) describe the androecia and gynoecia (Figure 57) as physically separated, with the androecia on the main thallus and not on the same branch as the female receptacle (Borovichev & Bakalin 2016).

Figure 57. ***Mannia triandra*** with brown androecia and a separate thallus or branch with one young archegoniophore (**lower left**). Photo by Štěpán Koval, with permission.

Hugonnot *et al*. (2017) found ***Mannia triandra*** fertile in May (Figure 57-Figure 60) in Saint-Maurin, France. Németh and Papp (2011) describe the life cycle of ***M. triandra*** in Hungary as thalli appearing in spring, producing spores in early spring, at which time its "small blue-green thalli" typically disappear during the dry season. The population size in any given year is very dependent on rainfall during its growing season. Müller *et al*. (2014) similarly found fluctuations in the population size from year to year. In 2008, one population occupied approximately 0.25 m². In 2009, it occupied only 5 dm². Then, in 2013, a rock was demolished and its area increased to at least 0.5 m². Similarly, Dürhammer (2017) found that the sporangia (Figure 61-Figure 67) numbers fluctuate considerably from year to year, perhaps driven by fluctuating weather conditions.

Figure 58. ***Mannia triandra*** with young archegoniophores showing the surrounding dense scales. Photo by Michael Lüth, with permission.

Figure 59. ***Mannia triandra*** with emergent archegoniophores and dead thalli. Photo by Štěpán Koval, with permission.

Figure 60. ***Mannia triandra*** young emergent archegoniophores and dying thallus. Photo by Hermann Schachner, through Creative Commons.

Figure 61. ***Mannia triandra*** archegoniophores with disintegrating thalli. Photo from Earth.com, with permission.

Figure 62. ***Mannia triandra*** archegoniophores with sporangia beginning to push scales surrounding them outward. Photo by Hugues Tinguy, with permission.

Figure 63. ***Mannia triandra*** archegoniophores beginning to elongate and sporangia beginning to emerge. Photo by Hugues Tinguy, with permission.

Figure 64. ***Mannia triandra*** with young capsules and elongated archegoniophores. Photo by Štěpán Koval, with permission.

Figure 65. ***Mannia triandra*** archegoniophores with mature capsules. Photo by Hermann Schachner, through Creative Commons.

Figure 66. ***Mannia triandra*** with mature sporangia. Photo by Paul G. Davison, with permission.

Figure 67. ***Mannia triandra*** underside of archegonial head showing mature sporangia. Photo by Paul G. Davison, with permission.

Spores (Figure 68) of ***Mannia triandra*** (Figure 42-Figure 43) are large [(55-)60-70(-75) µm] (Borovichev & Bakalin 2016). This is probably a major factor in its distribution. Since it is an annual species with no special asexual reproductive structures, it must rely on its spores, but being large, their dispersal is limited (Hugonnot & Celle 2012). As a result, it is not surprising that it is a poor competitor (Philippe 2013).

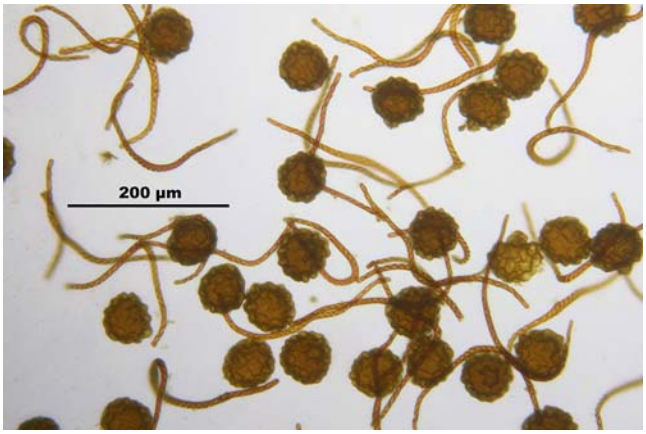

Figure 68. ***Mannia triandra*** spores and elaters. Photo by Hermann Schachner, through Creative Commons.

biochemistry

Mannia triandra (Figure 42-Figure 43) has numerous oil cells and has oil bodies that range 10-25 µm in diameter (Borovichev & Bakalin 2016). It nevertheless lacks the scent of cedar oil known in ***Mannia fragrans*** <http://e-ecodb.bas.bg/rdb/en/vol1/Mantrian.html>.

Reboulia hemisphaerica (Figure 69-Figure 76)

Stephani (1899) recognized ***Reboulia hemisphaerica*** (Figure 69-Figure 76) as a polymorphic species. It seems to have at least four genetically distinct races (Boisselier-Dubayle *et al*. 1998). Nevertheless, it exhibits less polymorphism than that generally attributed to mosses.

Hicks (1992) reported that three subspecies had been described for ***Reboulia hemisphaerica*** (Figure 69-Figure 76), differing in distribution of sex organs.

Figure 69. ***Reboulia hemisphaerica*** rosettes. Photo by Janice Glime.

Figure 70. ***Reboulia hemisphaerica*** in Europe. Photo by Michael Lüth, with permission.

Figure 71. ***Reboulia hemisphaerica***. Photo by Michael Lüth, with permission.

Figure 72. ***Reboulia hemisphaerica*** in Europe. Photo by Michael Lüth, with permission.

Figure 73. ***Reboulia hemisphaerica***. Photo by Janice Glime.

Figure 74. ***Reboulia hemisphaerica*** in Europe, with archegoniophores. Photo by Michael Lüth, with permission.

Figure 75. ***Reboulia hemisphaerica*** with purple edges. Photo by Allen Norcross, with permission.

Figure 76. ***Reboulia hemisphaerica*** in North America. Photo by Paul G. Davison, with permission.

Figure 77. ***Reboulia hemisphaerica*** with elongating archegoniophores on soil of a steep bank, Europe. Photo by Michael Lüth, with permission.

Figure 78. ***Reboulia hemisphaerica*** habitat on rocks. Photo by Michael Lüth, with permission.

Figure 79. ***Reboulia hemisphaerica*** on limestone cliff in Ohio, USA. Photo by Robert Klips, with permission.

Distribution

Reboulia hemisphaerica (Figure 69-Figure 76) is cosmopolitan (Piippo *et al*. 1997; Kürschner 2008) and is especially distributed in subtropical and temperate regions (Nieuwkoop 1996). ***Reboulia hemisphaerica*** is distributed in China, India, Japan, Korea, Nepal, Afghanistan, Pakistan, Java, Boning, New Zealand, Australia, Europe, Africa, Tahiti, North America, and South America (Singh & Singh 2002; Nair & Prajitha 2016).

Janovicová and Kubinská (2001) considered ***Reboulia hemisphaerica*** (Figure 69-Figure 76) to be both rare and threatened in the Biele Karpaty Mountains of Slovakia.

Aquatic and Wet Habitats

Reboulia hemisphaerica (Figure 69-Figure 76) is occasionally submerged (Watson 1919) and can occur in rivers (Ferreira *et al*. 2008). Konstantinova (2011) reported it from sandy soil between rocks in a dry stream bed in Dagestan, Russia. In the Uşak province of western Turkey it occurs on wet rocks (Gökler 2017). Hong (1977) found it on wet rocks in Montana, USA.

Reboulia hemisphaerica (Figure 69-Figure 76) occurs on the bank of the Banaz stream in the Uşak province of western Turkey (Gökler 2017). In the Izarene Massif of Rocco, it occurs on clayey soil on slopes (Figure 77) beside flowing water (Laouzazni *et al*. 2021). In Cyprus, it occurs under shrubs on the bank of a gully and on a steep bank by a stream in a deep valley (Blockeel 2003). Sharp (1939) found it on moist banks (Figure 1) in eastern Tennessee, USA. Konstantinova (2011) reported that ***Reboulia hemisphaerica*** subsp. ***australis*** occurs in Dagestan, Russia, in the gorge at the source of the Gunibka River on the bank. Some of its habitats on rocks and soil banks are shown in Figure 77-Figure 82.

Figure 80. ***Reboulia hemisphaerica*** on vertical face of rock. Photo by Michael Lüth, with permission.

Figure 81. ***Reboulia hemisphaerica*** habitat on steep soil bank with tree roots. Photo by Michael Lüth, with permission.

Figure 82. ***Reboulia hemisphaerica*** habitat on a soil bank. Photo by Michael Lüth, with permission.

Both streams and rivers can have floodplains. Many species have life cycles timed to take advantage of these ephemeral habitats. In the Virginia Piedmont, USA, the presence of ***Reboulia hemisphaerica*** (Figure 69-Figure 76) can indicate such a habitat where most of the species appear in late fall after leaf drop, regrowing from spores and dying soon after dispersing their spores (Breil 1977). These indicator species are sensitive to drying, yet typically require high light intensities.

Reboulia hemisphaerica (Figure 69-Figure 76) seems to have a preference for steep slopes (Figure 83-Figure 84). In the Netherlands, it is nearly always found on slopes up to 90º (Nieuwkoop 1996). Martin (1943) reported it from a cliff face in Ledges State Park, Iowa, USA. Miller and Thomson (1959) reported it from moist sandstone cliffs in Indiana, USA.

Figure 83. ***Reboulia hemisphaerica*** on a vertical face with soil over rock. Photo by Barry Stewart, with permission.

Figure 84. ***Reboulia hemisphaerica*** with archegoniophores on steep rocky slope. Photo by Michael Lüth, with permission.

Slopes and cliffs often have water trickling down them, or occur in canyons that remain humid. These provide suitable habitat for moisture-loving species of liverworts. In particular, cracks and crevices (Figure 85) provide protection and tend to remain moist longer than bare rock. ***Reboulia hemisphaerica*** (Figure 69-Figure 76) can occur in such locations (Sharp 1939; Crundwell & Nyholm 1979; Konstantinova 2011).

Figure 85. ***Reboulia hemisphaerica*** on rock ledge. Photo by Michael Lüth, with permission.

In the Netherlands, Nieuwkoop (1996) found that ***Reboulia hemisphaerica*** (Figure 69-Figure 76) preferred a loamy substrate (Figure 86), even if growing on a rock. These usually were on moist, loamy walls with light shade. Like the above members of the family **Aytoniaceae**, ***Reboulia hemisphaerica*** takes advantage of the cooler temperatures and greater moisture of wind holes (Figure 22) (Bakalin *et al*. 2017).

Figure 86. ***Reboulia hemisphaerica*** on soil. Photo by Štěpán Koval, with permission.

Reboulia hemisphaerica (Figure 69-Figure 76) exhibits a wide range of moisture tolerance, growing on slopes of ditches, on roadside banks, and along roads (Brown 1924). Jerath and Puja (2006) reported it as xeromorphic in the Shivalik Ecosystem of Punjab, India, but also growing in moist and exposed places. Nair and Prajitha (2016) found it on cut earth in the western Ghats of India. Singh and Singh (2002) found it on rocks in partially exposed places in India.

Province (2011) reported it in particular from basic schists and slate on rock outcrops among scrub vegetation in South-west Sichuan, China. Piippo and Koponen (2013) similarly found it in both primeval and secondary evergreen forests in northwestern Sichuan, China, in both open and shaded sites, on humus over rock (Figure 87) or stone, on cliffs, clay, and soil (Figure 88).

Figure 87. ***Reboulia hemisphaerica*** on soil over rock, Europe. Photo by Michael Lüth, with permission.

Figure 88. ***Reboulia hemisphaerica*** on soil. Photo by Jan-Peter Frahm, with permission.

Konstantinova *et al*. (2018) considered ***Reboulia hemisphaerica*** (Figure 69-Figure 76) to be a calcicole. It occurs in Russia on bare soil on mossy rock outcrops, on ledges (Figure 89-Figure 91) and in crevices, and even under rocks. Aleffi *et al*. (2005) listed it from rocks and escarpments in Italy. It finds similar habitats to be suitable in Morocco, including rock ledges with accumulated soil and bases of rocks (Ros *et al*. 2000), but Saadi *et al*. (2020) found it on siliceous soil in Morocco. Piippo and Tan (1992) found it on an abandoned wall in a shaded garden in the Philippines.

Figure 89. ***Reboulia hemisphaerica*** on rock ledges. Photo by Michael Lüth, with permission.

Figure 90. ***Reboulia hemisphaerica*** with archegoniophores on rock ledge. Photo by Michael Lüth, with permission.

Figure 91. ***Reboulia hemisphaerica*** with archegoniophores on rock ledge. Photo by Barry Stewart, with permission.

In Oklahoma, USA, ***Reboulia hemisphaerica*** (Figure 69-Figure 76) is the most frequent species of liverwort on dry rock outcrops (Little 1936) and also occurs on sandy soil (Sharp 1930). In Illinois, USA, it occurs on rocks, walls, and soil, including a sandstone wall (Spessard 1972; Simon 1977). Conard (1940) found it to be common on dry earth or rocks in Iowa, USA. At Mountain Lake, Virginia, USA, it similarly occurs on calcareous rocks and crevices (Sharp 1944).

In Myvatn, Iceland, ***Reboulia hemisphaerica*** (Figure 69-Figure 76) occurred as a pioneer on Krafla following the 1984 eruption (pers. obs. 1987). In just three years, it reached large populations (Figure 92-Figure 93).

Figure 92. ***Reboulia hemisphaerica*** in abundance during early succession on Krafla, Myvatn, Iceland, 3 years after 1984 eruption. Photo by Janice Glime.

Figure 93. ***Reboulia hemisphaerica*** succession on Krafla, Myvatn, Iceland, three years after the 1984 eruption. Photo by Janice Glime.

Physiology

Reboulia hemisphaerica (Figure 69-Figure 76) apparently has a wide moisture tolerance. Crundwell and Nyholm (1979) considered it to be one of the most drought-tolerant of the Turkish liverworts.

Reboulia hemisphaerica (Figure 69-Figure 76) exhibits growth and branching at moisture levels ranging 40-90%, with optimum growth at 70-80% (Vishvakarma & Kaul 1988a).

Xiang *et al.* (2010a) found that water stress affects the soluble sugar and proline, but has negligible effect on MDA. Calcium stress has even greater effects on sugar and proline. Low calcium results in a reduction in the accumulation of proline and soluble sugar, but as low calcium stress worsens their content gradually increases.

Hoffman and Gates (1970) demonstrated, using ***Reboulia hemisphaerica*** (Figure 69-Figure 76), that water loss proceeds rapidly in moist plants, with very low resistance. But as the water loss decreases, both convection and reradiation of energy become more important. At the same time, resistance increases in proportion to water loss. ***Reboulia hemisphaerica*** transpired for 2 hours under a radiation regime of 2.6 to 2.8 cal cm^{-2} min^{-1}.

Reboulia hemisphaerica (Figure 69-Figure 76) has a mean water conductive rate of ~0.5 mm s^{-1} (McConaha

1941). The areolation of its thallus greatly increases the surface through which water can be lost through the atmosphere by pores. A high phlobaphene content on the ventral surfaces helps to maintain a capillary film there among the tuberculate rhizoids and prevents water loss from the upturned thallus margins. McConaha demonstrated that a single water drop at one end of the thallus became distributed through the length of the thallus by its external capillary system. This water was immediately available to all absorptive surfaces. This external system provides a much more rapid transport than any known internal system. This seems to compensate successfully for the increased water loss due to areolation. In contrast to the description of McConaha, O'Hanlon (1928) describes the species with only a mere suggestion of air chambers and no air pores.

Takio *et al*. (1990) examined the chlorophyll content and photosynthetic rate in ***Reboulia hemisphaerica*** (Figure 69-Figure 76). They found that it possessed high levels of chlorophyll when cultured in light (4-34 µg mg^{-1} dry weight). These plants likewise had a high photosynthetic rate of 10-94 µmol O_2 mg^{-1} chlorophyll h^{-1}. Dark-grown cells exhibited these same high levels of chlorophyll and photosynthesis, contrasting sharply with the low chlorophyll levels in dark-grown ***Barbula unguiculata*** (Figure 94).

Figure 94. ***Barbula unguiculata***. Photo by Kristian Peters, through Creative Commons.

Rao *et al*. (1979) reported on the assimilation of labelled carbon into amino acids for ***R. hemisphaerica***. The CO_2 assimilation rate was lower than that of seed plants. The chlorophyll content of these populations (from moist locations in the Ooty Hills, India) was low, as was the chlorophyll *a*:*b* ratio, parameters that are typical of shade-loving species. Rao *et al*. (1979) reported that the Hill reaction rates of ***R. hemisphaerica*** was lower than that typically reported for seed plants.

Both dark-grown and light-grown cells of ***Reboulia hemisphaerica*** (Figure 69-Figure 76) exhibited high chlorophyll content (4-34 µg mg^{-1} dry weight) after one year of culture on 2% glucose medium (Takio *et al*. 1990). Photosynthetic activity was likewise high in both (10-84 µmol O_2 mg^{-1} chlorophyll h^{-1}).

Lei *et al*. (2010) explored the responses of photosystem II in ***Reboulia hemisphaerica*** (Figure 69-Figure 76) to nitrogen deposition. Increased N concentrations (40 and 60 kg h m^{-2} a^{-1}) caused changes in chlorophyll fluorescence and reduced the energy-trapping capacity per unit area. It furthermore changed the redox states, destroyed electron flow especially beyond the Q-A, disabling that energy absorption and necessitating its consumption by fluorescence and heat. Liu *et al*. (2009) also explored N effects on this species and found both photosynthetic rate and starch concentration were lower at N concentrations of 20 and 40 kg h^{-1} m^{-2} than at the control levels or at 60 kg h^{-1} m^{-2}. On the other hand, the total N in the tissue changed inversely. Both the inducible and constituted nitrate reductase activity were very low in all treatments, suggesting that it is unable to use nitrates. Potassium ion leakage increased significantly when the N addition increased to 60 kg N h^{-1} m^{-2}, suggesting membrane damage.

Vishvakarma and Kaul (1986) explored the temperature tolerance of ***Reboulia hemisphaerica*** (Figure 69-Figure 76). Morais and Becker (1991) cultured ***Reboulia hemisphaerica*** and found that it grew best on agar with 0.5% sucrose and an 18 h light: 6 h dark regime. Callus could be induced by phytohormones (2 mg L^{-1} a-naphthylacetic acid + 1 mg L^{-1} kinetin) or by 4% glucose. Once cultures differentiated, there was a tenfold increase in sesquiterpene production. No sesquiterpenes were produced in dark cultures, but 5-hydroxy-7,8,4'-trimethoxyflavone was present. In light cultures, apigenin n-7,4'-dim ethylether was the only flavonoid produced.

Xiang *et al*. (2010b) evaluated the effects of heavy metals on ***Riccardia hemisphaerica*** (Figure 69-Figure 76) from cavern rock and soil on walls. They found that ***R. hemisphaerica*** actually exhibited depletion levels of Ca in the Three Gorges karst region, whereas some mosses exhibited either strong or relative enrichment in their tissues. It exhibited no enrichment of Mg, whereas the moss ***Thuidium cymbifolium*** (Figure 95) did. ***Reboulia hemisphaerica*** did, however, show a strong enrichment by Zn.

Figure 95. ***Thuidium cymbifolium***, a species that can experience Mg enrichment. Photo by Chris Alice Kratzer, through Creative Commons.

Adaptations

One aspect that may account for the wide range of habitats for ***Reboulia hemisphaerica*** (Figure 69-Figure 76) is its ability to form pure mats or to grow with other bryophytes (Figure 96-Figure 97) (Konstantinova *et al*. 2018). The accompanying bryophytes can act like a sponge to retain moisture that could maintain suitable conditions for ***R. hemisphaerica***, whereas pure mats can completely cover the substrate and reduce evapotranspiration.

Figure 96. ***Reboulia hemisphaerica*** growing over mosses. Photo by Malcolm Storey <www.discoverlife.org>, with online permission.

Figure 97. ***Reboulia hemisphaerica*** with mosses and archegoniophores. Photo by Michael Lüth, with permission.

Reboulia hemisphaerica (Figure 69-Figure 76) has air chambers (Figure 98-Figure 100) that form an extensive system of air spaces separated by thin partitions (Dupler 1921; Haupt 1921a). These have air pores (Figure 99-Figure 101) on the upper surface, but no filaments, and thus serve primarily for gas exchange. Dupler (1921) describes them as very elongated air chambers that extend lengthwise along the midrib region. They radiate from there toward the thallus margins. They are in a single layer just below the surface and presumably facilitate CO_2 exchange in internal photosynthetic cells.

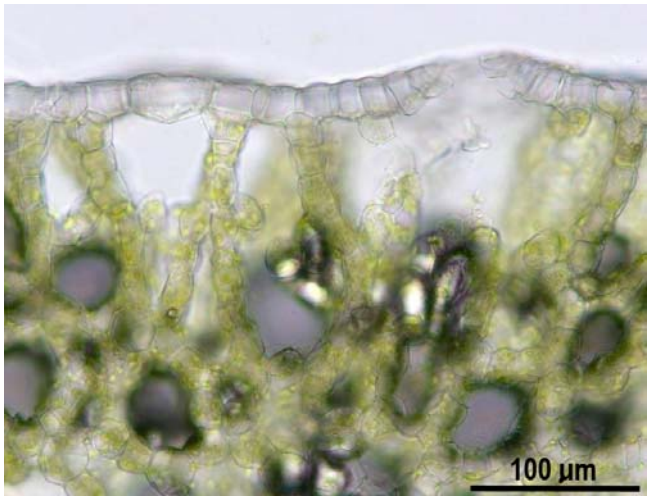

Figure 98. ***Reboulia hemisphaerica*** section showing air chambers. Photo by Jia-Dong Yang, through Creative Commons.

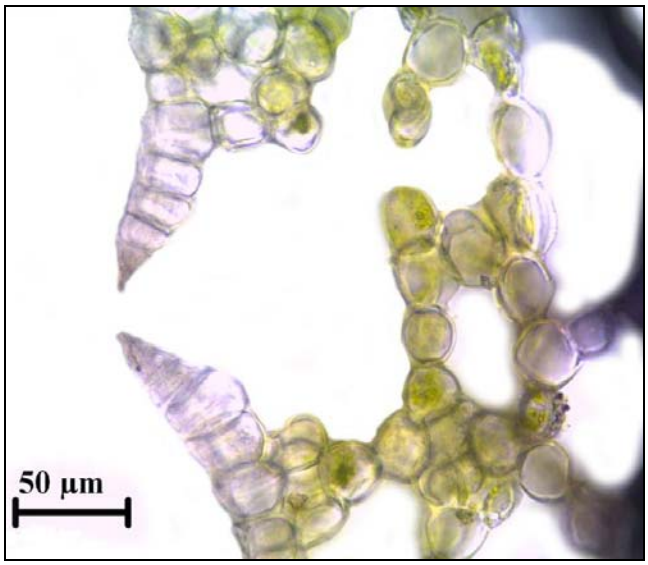

Figure 99. ***Reboulia hemisphaerica*** air chambers and pore. Photo by Hugues Tinguy, with permission.

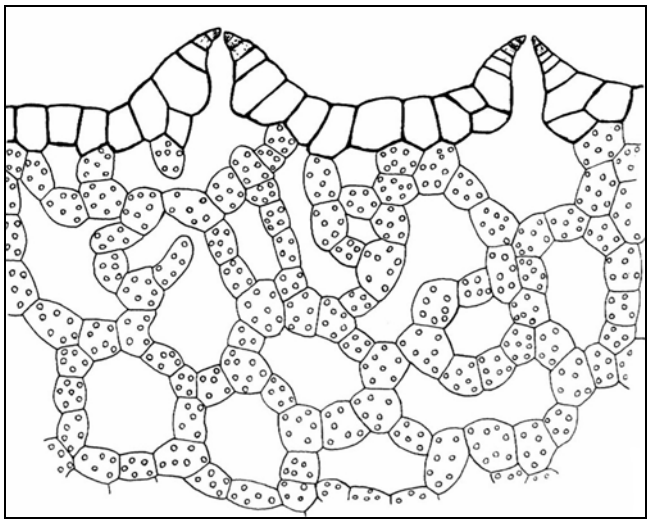

Figure 100. ***Reboulia hemisphaerica*** air chambers and pores. From Haupt 1921a.

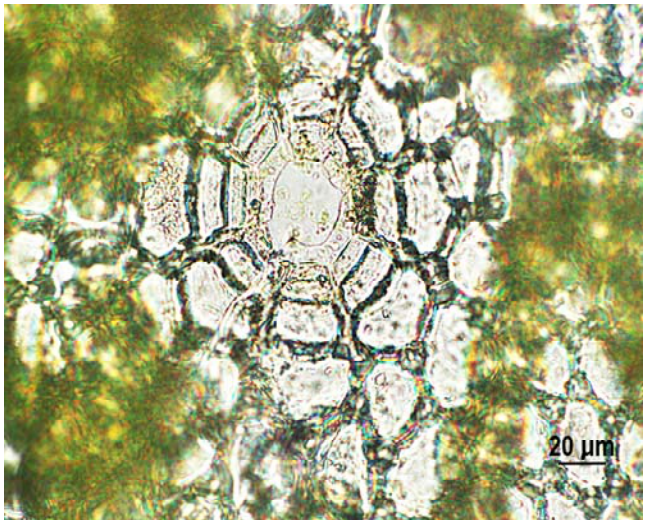

Figure 101. ***Reboulia hemisphaerica*** thallus pore. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Having pores (Figure 99-Figure 101) presents its own set of problems. They are advantageous for gas exchange, but not only do they allow water to leave the thallus, they also can allow water to enter. In species like ***Reboulia hemisphaerica*** (Figure 69-Figure 76), these pores have hydrophobic ledges that not only constrict the size of the pore, but that also repel water, preventing water from entering the plant during downpours or other water events Schönherr & Ziegler (1975). For water to enter, it must have a contact angle of 0º with the ledge. It would be interesting to see the difference in photosynthetic rate if these chambers were injected with water to fill the spaces.

Watson (1919) noted that when ***Reboulia hemisphaerica*** (Figure 69-Figure 76) grows on wet ground it has fewer rhizoids than when it grows in drier situations. This suggests that more rhizoids help to facilitate the movement and uptake of water, as noted above for other members of the family. Daniels (1998) cites the complex morphology along with tuberculate and smooth rhizoids, scale leaves (Figure 102), and well defined assimilatory and storage zones as xerophytic adaptations in ***R. hemisphaerica***.

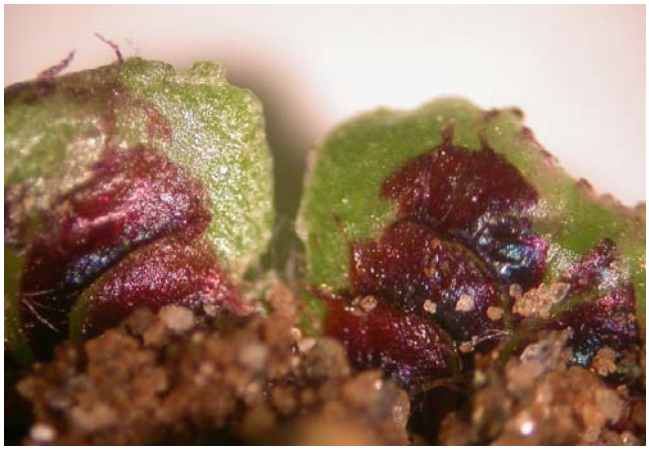

Figure 102. ***Reboulia hemisphaerica*** ventral side with scales (reddish). Photo by Blanka Aguero, through Creative Commons.

Reproduction

Haupt (1921a) described ***Reboulia hemisphaerica*** (Figure 69-Figure 76) as **monoicous** (Figure 103-Figure 107) in Midwestern USA. It is **protandrous** (antheridia develop before archegonia; Figure 105-Figure 106). Generally, 2-3 antheridial groupings develop in succession before the archegonia develop. The antheridia and archegonia occur in separate groups on the dorsal thallus surface.

Figure 103. ***Reboulia hemisphaerica*** male and female reproductive structures. Photo by Bob Klips, with permission.

Figure 104. ***Reboulia hemisphaerica*** with sexual structures. Photo by Ed Leathers, with permission.

Figure 105. ***Reboulia hemisphaerica*** with antheridia but no visible archegoniophores. Photo by Michael Lüth, with permission.

Figure 106. ***Reboulia hemisphaerica*** with male (**brown**) and female (**green**) sex organs. Photo by Ed Leathers, with permission.

Figure 107. ***Reboulia hemisphaerica*** with young archegoniophores and mosses that probably help in moisture retention. Photo by Barry Stewart, with permission.

Dupler (1922a) considered the male receptacle and antheridium to be plastic, including both primitive and advanced characteristics. It is typically dorsal and posterior to the female receptacle (Figure 108-Figure 118) that terminates the branch. It is sessile or on a very short stalk, a feature that places it close to the archegonial head before elongation of the latter on its stalk.

Figure 108. ***Reboulia hemisphaerica*** young archegoniophores in Europe. Photo by Michael Lüth, with permission.

Figure 109. ***Reboulia hemisphaerica*** young archegoniophores in Europe. Photo by Michael Lüth, with permission.

Figure 110. ***Reboulia hemisphaerica*** archegoniophores in Europe. Photo by Michael Lüth, with permission.

Figure 111. ***Reboulia hemisphaerica*** with young archegoniophores. Photo by Li Zhang, with permission.

Figure 112. ***Reboulia hemisphaerica*** archegonial heads. Photo by Heino Lepp, Australian National Botanic Gardens <www.anbg.gov.au>, with online permission.

Figure 113. ***Reboulia hemisphaerica*** archegonial heads. Photo by Malcolm Storey <www.discoverlife.org>, with online permission.

Figure 114. ***Reboulia hemisphaerica*** with emerged archegoniophores in Europe. Photo by Michael Lüth, with permission.

Figure 115. ***Reboulia hemisphaerica*** with elongated archegoniophores. Photo by Michael Lüth, with permission.

Figure 116. ***Reboulia hemisphaerica*** with emerging archegoniophores. Photo by Štěpán Koval, with permission.

Figure 117. ***Reboulia hemisphaerica*** with emerging archegoniophores and still green thalli. Photo by Malcolm Storey <www.discoverlife.org>, with online permission.

Figure 118. ***Reboulia hemisphaerica*** with archegoniophores and dying thalli. Photo by Štěpán Koval, with permission.

Udar and Chandra (1964) reported anomalous female receptacles in ***Reboulia hemisphaerica*** (Figure 69-Figure 76). One aberrant type produced branch stalks of the archegoniophores. A second aberrant type was just the opposite, producing no stalks or nearly sessile archegonial heads. Furthermore, Chandra (1963) reported compound female receptacles.

Miduno (1937) described the spermatozoids of ***Reboulia hemisphaerica*** (Figure 69-Figure 76). These typically had two cilia, although they also found five with three cilia. Other variations in size of the spermatozoid and relative length of the cilia were present.

Among the variations in the life cycle of ***Reboulia hemisphaerica*** (Figure 69-Figure 76) are differences in oicy. Since Haupt (1921a) published his descriptions of Midwestern, USA, populations, differences among populations have led to the description of subspecies. The subspecies of ***R. hemisphaerica*** differ in the distribution of their sexual organs (Hicks 1992). The typical variety is **paroicous**, whereas the three more recent subspecies are **dioicous** and two **autoicous** ones with differences in male receptacle size. Konstantinova (2011) reported that populations in the eastern Caucasus of Russia were **autoicous**. However in the entire country of Russia, one can find **paroicous**, **autoicous**, and **dioicous** populations (Bakalin 2008). Schuster (1992) considered all these to be one species, but Bakalin (2008) considers them to need further study. Itouga *et al.* (2005) noted that ***R. hemisphaerica*** had been subdivided into seven subspecies based on sexual condition, a strong indicator of genetic diversity. They recognized three subspecies in Japan, including the autoicous subsp. ***orientalis***, subsp. ***acrogyna***, and a new to Japan **paroicous** subsp. ***hemisphaerica***. In addition to differences in oicy, spore maturation times differed. In subsp. ***acrogyna*** spores matured in summer, whereas in subsp. ***hemisphaerica*** and subsp. ***orientalis***, they matured in spring.

The emergence of the archegoniophore of ***Reboulia hemisphaerica*** (Figure 69-Figure 76) does not occur until the sporophytes are nearly mature (Haupt 1921a). Archegonia appear in autumn and fertilization occurs then. The embryo develops immediately, but the sporophyte (Figure 119-Figure 123) does not mature until the following spring, necessitating survival through the winter.

Figure 119. ***Reboulia hemisphaerica*** with immature capsules. Photo by Jiří Kameníček (BioLib, Obázek), with permission.

Figure 120. ***Reboulia hemisphaerica*** with archegoniophores and emergng sporangia. Photo by Jan-Peter Frahm, with permission.

Figure 121. ***Reboulia hemisphaerica*** with mature black sporangia. Photo by Michael Lüth, with permission.

Figure 122. ***Reboulia hemisphaerica*** archegoniophores with young capsules and mature capsules. Photo by Adolf Ceska, with permission.

Figure 123. ***Reboulia hemisphaerica*** archegonial head with scales and capsules that have shed their spores. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Allsopp (1964) found that whereas male gametangiophores developed on media with 1% glucose, female gametangiophores developed on sugar-free media. Could these differences in energy needs serve to induce their formation at different times?

Rao and Das (1968) found a sharp rise in the respiratory rate and a doubling of the C:N ratio as ***Reboulia hemisphaerica*** (Figure 69-Figure 76) transformed from the vegetative to female reproductive phase. At that time, the plants exhibited enhanced levels of endogenous IAA (indole-3-acetic acid), RNA, and protein. During antheridial formation the plants exhibited a reverse trend and exhibited no appreciable change in the C:N ratio (see also Hartmann & Weber 1990).

As noted by Haupt (1921a), ***Reboulia hemisphaerica*** (Figure 69-Figure 76) is fertilized in autumn in southern Wisconsin and northern Illinois, USA (O'Hanlon 1928); Dupler (1922b) likewise reported fertilization in October. In early spring (8 March) the plants are still dormant (O'Hanlon 1928). Woodburn (1919) determined that both egg and sperm nuclei are in a resting condition in the early stages of fusion. When transplanted indoors on 29 October, ***R. hemisphaerica*** regenerated new branches but failed to exhibit elongation of the archegoniophore (O'Hanlon 1928). The plants exhibited an inverse relationship between amount of regeneration and development within the receptacle. Most thalli produce fewer than three mature sporophytes per head, but can produce up to nine.

As one might expect, ***Reboulia hemisphaerica*** (Figure 69-Figure 76) has a lower gene flow with increasing distance ($Nm=-0.0009 \times km^{1.1}$) (Itouga *et al*. 2002). The mean value for populations in East Asian populations was only 0.609. Thus, the genetic variation was high, as would be predicted for species that reproduce only by spores. Slatkin (1985) considers that Nm values <1 usually imply that genetic drift has been a major contributor to the distribution of genetic variation. Itouga and coworkers found that the break point for Nm values <1 was 125 km. Dispersal of spores beyond 100 km was negligible. Itouga and coworkers agree that the degree of genetic differentiation within monoicous marchantialean species is correlated with dispersal distances of sperm and rates of self-fertilization. Nevertheless, the dioicous ***Asterella wallichiana*** (Figure 124) and monoicous ***R. hemisphaerica*** showed similar levels of gene flow in this study.

Figure 124. ***Asterella wallichiana***, a dioicous liverwort with gene flow levels similar to those of the monoicous ***Reboulia hemisphaerica***. Photo by Forestowlet, through Creative Commons.

Woodburn (1919) described the union of egg and sperm and the early developmental stages of the ensuing sporophyte. Dupler (1922b) also described the early embryogeny of ***Reboulia hemisphaerica*** (Figure 69-Figure 76). The embryo begins immediate development following fertilization. There is considerable variation in the development of the early embryo, with accompanying variations in habitat, archegoniophore, and other morphological variations. By winter, the sporogenous tissue is becoming differentiated. However, the sporophyte does not mature until the following May or June. Brown found ***Reboulia hemisphaerica*** fruiting "profusely" in a variety of places in Georgia (in the Caucasus region).

Haupt (1921b) found that the archegoniophore begins to elongate in early spring (Figure 125), about the last week of March, in Indiana, USA. The sporogenous tissue resumes development, but there is no indication at that time as to which will become spores and which elaters. By the first part of May, these cells break apart from each other, form an abundance of mucilage, and spore mother cells and elaters are clearly distinguishable.

Figure 125. ***Reboulia hemisphaerica*** with developing archegoniophores and dying older thalli. Photo by Štěpán Koval, with permission.

Blair (1926) describes meiosis in ***Reboulia hemisphaerica*** (Figure 69-Figure 76). She notes only 16 chromosomes arriving at each pole. However, several authors (Sha *et al*. 2003; Itouga *et al*. 2005) have since determined the chromosome number for ***R. hemisphaerica*** to be n=9, a typical number in liverworts.

Patidar *et al*. (1987) reported 2410 spores (Figure 126-Figure 127) per capsule in ***Reboulia hemisphaerica*** (Figure 69-Figure 76). Schuster (1966) earlier reported 2500 per capsule (see also O'Hanlon 1930). These large (70-80 µm) spores germinate in about five days when in suitable conditions of fairly good light and plenty of moisture (O'Hanlon 1930). They remain completely viable for at least five months.

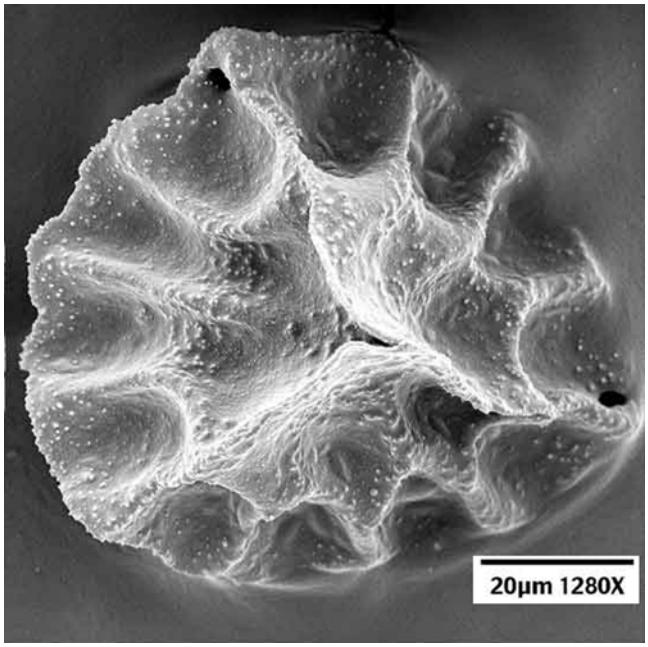

Figure 126. ***Reboulia hemisphaerica*** spore SEM. Photo by William T. Doyle, with permission.

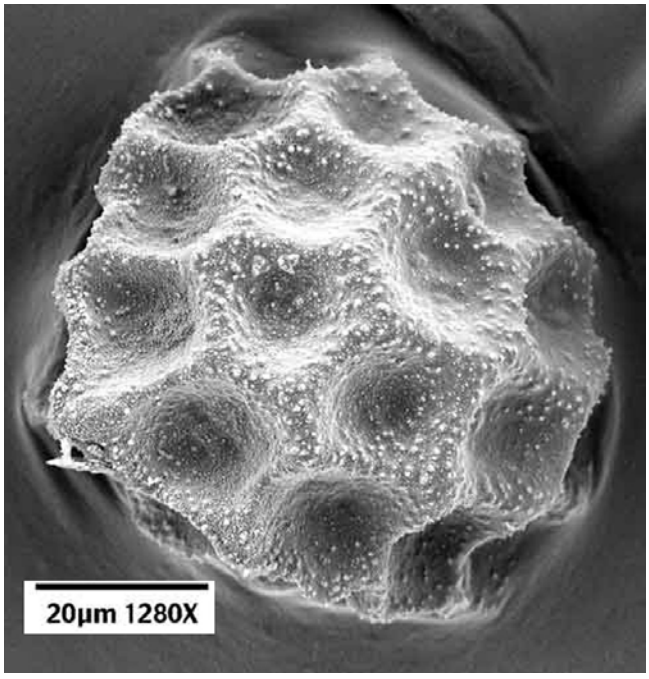

Figure 127. ***Reboulia hemisphaerica*** distal spore wall SEM. Photo by William T. Doyle, with permission.

Reboulia hemisphaerica (Figure 69-Figure 76) produces a tangle of white, sticky filaments (Figure 128) below the capsule (Frank 2015). These appear to aid in spore dispersal in a rather unusual way. They make a bryophyte version of masking tape. The springtail ***Bourletiella hortensis*** (Figure 129) peruses the capsule area and comes away with bits of the sticky filaments on its body. And to these, spores are attached. Frank suggests that not only do springtails aid dispersal through these adhered filaments, but that other animals could easily contribute as well.

Figure 128. ***Reboulia hemisphaerica*** archegoniophores with mature sporangia in Europe. Note the white filaments hanging below the capsules. Photo by Michael Lüth, with permission.

Figure 129. ***Bourletiella hortensis***, a springtail that facilitates spore dispersal in ***Reboulia hemisphaerica*** by getting sticky filaments with adhering spores stuck to its body. Photo by Andy Murray, through Creative Commons.

Vishvakarma and Kaul (1987) studied the effects of such conditions as duration, quality, and intensity of light on spore germination in ***Reboulia hemisphaerica*** (Figure 69-Figure 76). Inoue (1960) reported that blue and red light were the most effective in promoting rhizoid development, and far-red and green caused less activity. However, germ tube development was just the opposite of rhizoid development, being relatively short in blue and red light but elongating remarkably in far-red and green.

Vishvakarma and Kaul (1988b) found that the optimum *p*H for both germination and thallus growth was 6, but vegetative growth occurred in the range of 3.0-7.0. Germination was more restricted at *p*H 5-7. Differences between germination requirements and growth tolerances could explain the absences of species in some areas where we expect them.

O'Hanlon (1930) noted that the first stage in spore germination of ***Reboulia hemisphaerica*** (Figure 69-Figure 76) is the emergence of a germ tube and a single rhizoid. The author provides details of subsequent cell divisions leading up to bud formation. Rhizoids form on the ventral side of the protonema, establishing its dorsiventrality. Low intensity causes the germ tubes to be extremely long or to give rise to secondary and even tertiary germ tubes. Hartmann and Weber (1990) reviewed the literature on control of germination in this and other species of liverworts.

Vishvakarma *et al*. (1987) showed that percentage spore germination of ***Reboulia hemisphaerica*** (Figure 69-Figure 76) was enhanced by the addition of Mg in the liquid culture medium.

Not all bryophytes are known to produce callus tissue. Allsopp (1957) reported the first success in obtaining unlimited callus-like growth in liverworts, one of which was ***Reboulia hemisphaerica*** (Figure 69-Figure 76). This technique is often useful for mass producing desired chemical from bryophyte tissues.

Koevenig (1973) investigated reproductive physiology of ***Reboulia hemisphaerica*** (Figure 69-Figure 76). Archegoniophores elongate in late spring in Kansas. Under long days (12 hr light, 12 hr dark, or 16 hr light, 8 hr dark), pre-elongation archegoniophores elongated completely within two weeks at both 15 and 25ºC. But in short days (8 hr light, 16 hr dark) no elongation occurred. Cold temperature (5ºC) slowed elongation. Adding plant growth hormones (IAA, NAA, BA, GA) to heads failed to stimulate to normal lengths in short days. Koevenig suggested that perhaps the hormones could facilitate elongation but could not initiate it. (See also Sztein *et al*. 1997).

Brown and Lemmon (1990) elucidated the mitotic apparatus of ***Reboulia hemisphaerica*** (Figure 69-Figure 76). They concluded that the mitotic apparatus in this species demonstrates a transition between algae and land plants.

Nehira and Nakagoshi (1987) reported that after removal of bryophytes in an urban environment, the same community became re-established in 1-2 years. Pleurocarpous mosses and thalloid liverworts such as ***Reboulia hemisphaerica*** (Figure 69-Figure 76) regenerated faster than did acrocarpous mosses. This regrowth occurred primarily in spring and autumn, but there was little seasonal variation in the amount of available airborne diaspores.

Role

Bryophytes such as ***Reboulia hemisphaerica*** (Figure 69-Figure 76) often serve as substrates for algae, especially diatoms (Ando 1978). These algae and other micro-organisms provide food for visiting invertebrates. But the bryophytes themselves can serve as food (Konstantinov *et al*. 2019). The flea beetle ***Distigmoptera borealis*** (Figure 130) was recently discovered eating ***R. hemisphaerica***. Imada and Kato (2016) reported on larvae of the fly ***Litoleptis*** on bryophytes and described six new species, all thallus-miners of liverworts. ***Litoleptis kiiensis*** (Figure 131), ***L. niyodoensis***, ***L. himukaensis***, and ***L. izuensis*** are all thallus miners on ***Reboulia hemisphaerica*** and only that species.

Figure 130. ***Distigmoptera borealis***, a beetle that consumes ***Reboulia hemisphaerica*** thalli. Photo from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

Figure 131. ***Litoleptis kiiensis*** larva, an inhabitant of ***Reboulia hemisphaerica***. Photo courtesy of Yume Imada.

Biochemistry

Reboulia hemisphaerica (Figure 69-Figure 76) was an early subject of biochemical studies. Furusawa *et al*. (2006) isolated and described structures of new cyclomyltaylane and ent-chamigrane-type sesquiterpenoids from ***Reboulia hemisphaerica*** subsp. ***australis***. Morais *et al*. (1988, 1991) described a gymnomitrane-type sesquiterpenoid and two derivatives from cultures of this species. Keserű and Nogradi (1995) reported riccardins. Warmers and König (1999, 2000) reported gymnomitrone from plants in nature and described its synthesis. Wei *et al*. (1995) described five new sesquiterpenoids and three new marchantin-type compounds and elucidated their structures. Sakai *et al*. (1999) were able to describe the synthesis (+)-cyclomyltaylan-5α-ol from ***Reboulia hemisphaerica*** from Taiwan.

Toyota *et al*. (1999) found and described the structure of four new sesquiterpenes from ***Reboulia hemisphaerica*** (Figure 69-Figure 76), as well as isolating nine compounds that were already known. Warmers and König (2000) identified the biosynthesis of the gymnomitrane-type sesquiterpene in this species.

Reboulia hemisphaerica (Figure 69-Figure 76) has chemotypes (Ludwiczuk *et al*. (2008). The researchers found two "totally different chemical compositions" in two different locations in Tokushima, Japan, whereas those from the same location had very similar chemical composition, indicating genetic isolation of the two populations. They noted that ***R. hemisphaerica*** has sesquiterpenoids and acetogenins.

Asakawa and Matsuda (1982) isolated riccardin C from ***Reboulia hemisphaerica*** (Figure 69-Figure 76) – a secondary compound that appears to be widespread among thallose liverworts. Wang *et al*. (2011a) found four new phenolic glycosides in this species in China and described their structures as rebousides. Wang *et al*. (2011b) described the configuration of isoriccardin C and riccardin D isolated from this species.

Kwon *et al*. (2019) were able to describe the entire chloroplast genome of ***Reboulia hemisphaerica*** with its 122,596 base pairs with 87 protein-coding genes, eight rRNAs, and 36 tRNAs. These indicated a close relationship to ***Dumortiera hirsuta*** (Figure 132).

Figure 132. ***Dumortiera hirsuta***, a close relative of ***Reboulia hemisphaerica***, based on chlorophyll DNA. Photo by Lin Kyan, with permission.

There have been at least some traditional medical uses of bryophytes (Du 1997). Sabovljević *et al*. (2016) noted that ***Riccardia hemisphaerica*** (Figure 69-Figure 76) is sold in Chinese markets. It has been cited numerous times related to potential medicinal uses of its compounds. Belcik and Wiegner (1980) reported good antibacterial activity in culture, reinforcing the findings of Banerjee and Sen (1979), who considered it to be one of the most active bryophytes against bacteria.

Becker (1990) pointed out the need for *in vitro* plant cultures when the desired plant product has a high price or conventional production of the plant causes problems. Liverwort culture meets the second criterion, but the science is new and although many medicinally active compounds are known, development of their commercial use is negligible. Kandpal *et al*. (2016) further noted the need for new antibiotic compounds because of the increasing evolution of antibiotic-resistant bacterial strains.

While one extract may inhibit bacteria or have other medicinal properties, a different extract solvent of the same compound(s) may exhibit no activity (Zehr 1990). Although this is a serious consideration in making ecological interpretations, it is usually not a serious problem for medicinal applications. Furthermore, effectiveness differs among bacteria species. Zehr showed that ***Bacillus subtilis*** (Figure 133-Figure 134) and ***Escherichia coli*** (Figure 135) were the most susceptible bacteria tested while ***Enterococcus faecalis*** (Figure 136) experienced the least inhibition.

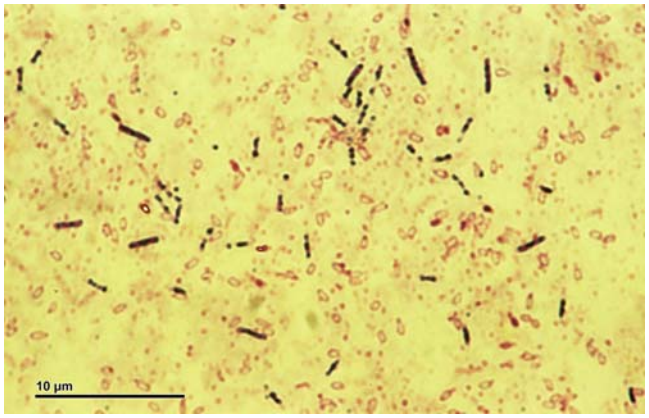

Figure 133. ***Bacillus subtilis***, a bacterial species that is inhibited by extracts of ***Reboulia hemisphaerica***. Photo by Josef Reischig, through Creative Commons.

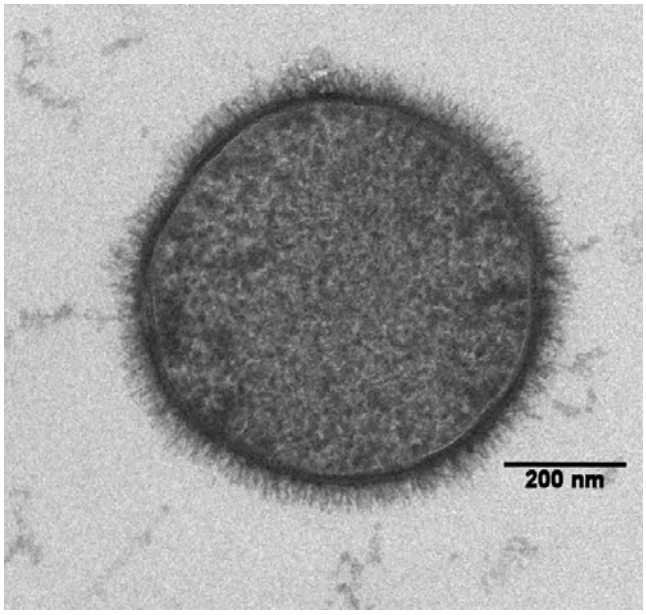

Figure 134. ***Bacillus subtilis***, a bacterial species that is inhibited by extracts of ***Reboulia hemisphaerica***. Photo by Allonweiner, through public domain.

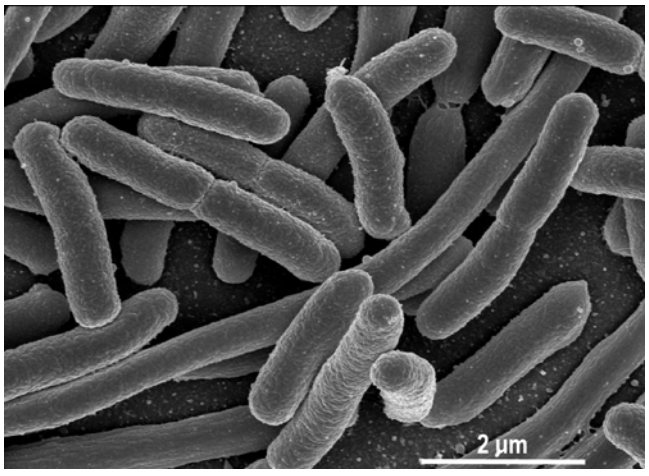

Figure 135. ***Escherichia coli***, a bacterial species that is inhibited by extracts of ***Reboulia hemisphaerica***. Photo from Rocky Mountain Laboratories, through public domain.

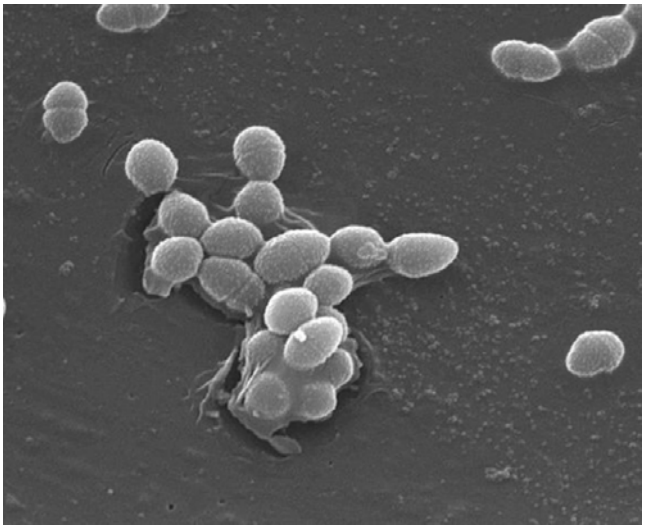

Figure 136. ***Enterococcus faecalis*** SEM, a species of bacteria that is more resistant than others in study to extracts of ***Reboulia hemisphaerica***. Photo from CDC, through public domain.

Following these early studies, a number of additional studies confirmed antibacterial and medicinal activity in ***Reboulia hemisphaerica*** (Figure 69-Figure 76) (Joshi 1995; Ko *et al*. 1995; Du 1997).

Ko *et al*. (1995) isolated marchantinquinone, from ***Reboulia hemisphaerica*** (Figure 69-Figure 76), a compound known to inhibit lipid peroxidation and to serve as a free radical scavenger. Liao *et al*. (2000) reported that marchantinquinone from ***R. hemisphaerica*** inhibited platelet aggregation and ATP release stimulated by thrombin. Harrowven *et al*. (2005) found that Riccardin C, manufactured by ***Reboulia hemisphaerica*** exhibited cytotoxicity against nasal epidermoid carcinoma cells in culture as well as inhibiting HIV-1 reverse transcriptase.

Asakawa (1998; 2007) cited a number of potential medical uses for ***Reboulia hemisphaerica*** (Figure 69-Figure 76), including treatment of blotches, external wounds, and bruises, and hemostasis. Tosun *et al*. (2016) and Chandra *et al*. (2017) expanded on this list, including uses to cure cuts, burns, wounds, bacteriosis, pulmonary tuberculosis, neurasthenia, fractures, convulsions, scalds, uropathy, inflammation, fever, and pneumonia. Tosun *et al*. (2016) further elaborated on the specific means of wound healing. Önder and Özenoğlu (2019) found that extracts of ***R. hemisphaerica*** were effective against three different cancer cell lines.

A variety of potential uses emerged in laboratory cultures of ***Reboulia hemisphaerica*** (Figure 69-Figure 76) (Gao *et al*. 2009; Asakawa 2013; Tosun *et al*. 2013). Harada *et al*. (2013) reported its potential for the treatment of cardio-vascular diseases, including arteriosclerosis. Even pet treatments are possible, with ***R. hemisphaerica*** inhibiting carrageenan-induced paw edema (Tosun *et al*. 2013).

Kandpal *et al*. (2016) found the extract of ***R. hemisphaerica*** (Figure 69-Figure 76) to be the most effective bryophyte species tested against ***Escherichia coli*** (Figure 135), ***Bacillus cereus*** (Figure 137), and ***Pseudomonas aeruginosa*** (Figure 138). The researchers found a correlation between total phenol and flavonoid contents and the antioxidant activity.

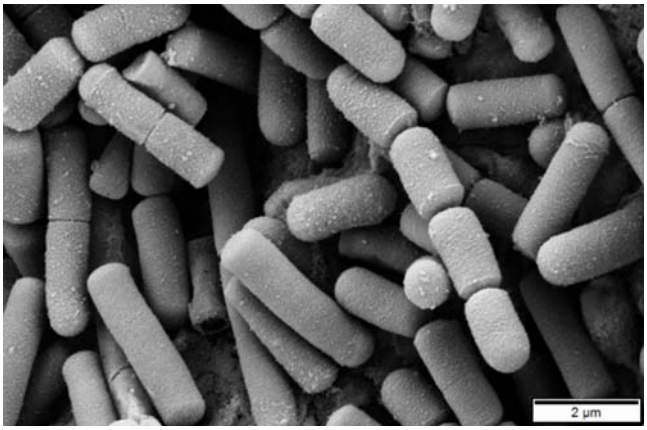

Figure 137. ***Bacillus cereus*** SEM, a bacterial species that is inhibited by extracts of ***Reboulia hemisphaerica***. Photo by Mogana Das Murtey and Patchamuthu Ramasamy, through Creative Commons.

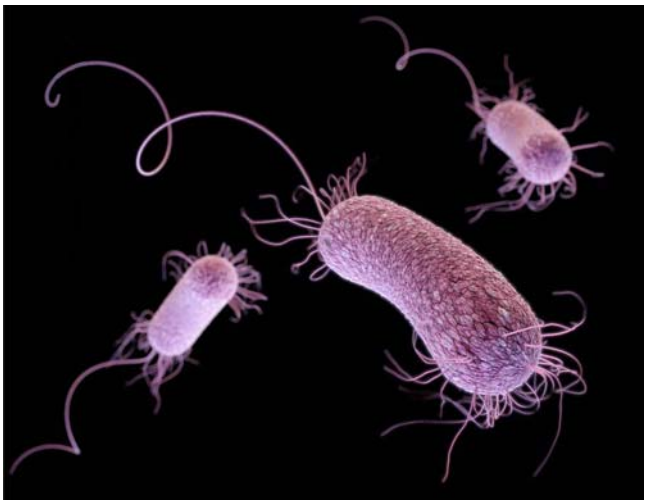

Figure 138. ***Pseudomonas aeruginosa***, a bacterial species that is inhibited by extracts of ***Reboulia hemisphaerica***. Photo from CDC, through public domain.

Summary

The Aytoniaceae does not have members that are typically submersed, but several species are at least tolerant of being constantly wet from water spray or other source of water. Their habitats include waterfall spray, streamside, dripping cliffs and ledges, wet soil and wind holes, but also various substrata in mesic forests. The latter habitat provides cool, moist air that permits Arctic species to survive in temperate regions. On the other hand, many of these species occur in the mountains, especially in Macaronesia.

The members of **Aytoniaceae** included here tend to endure a wide range of habitats, including a wide range of moisture conditions. They have air spaces that permit CO_2 exchange and rhizoids and scales that facilitate water uptake. Sexual condition varies, even within a species, but no gemmae or other specialized asexual reproductive structures are present. Most of the species die from the posterior end after fertilization, but grow from the apex.

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CHAPTER 1-20
AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: CONOCEPHALACEAE, PART 1

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AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: CONOCEPHALACEAE, PART 1

Figure 1. ***Conocephalum conicum*** *s.l.* habitat on emergent rock. Photo from <www.aphotofauna.com>, with permission.

Conocephalaceae

Conocephalum conicum (Figure 1-Figure 11)

Recently, genetic determinations and usable morphological characters have led to the division of ***Conocephalum conicum*** (Figure 1Figure 2-Figure 11) into several species (Szweykowski *et al*. 2005; Akiyama 2022). Therefore, one must read the research attributed to this species with caution because it might actually refer to ***Conocephalum salebrosum*** (Figure 12-Figure 13) in North America, or several species in Japan. When I can't be sure which species it is, I shall denote the species as ***Conocephalum conicum*** *s.l.* (the abbreviation *s.l.* refers to *sensu lato* and means in the broad sense; *s.s.* refers to *sensu stricto* and means in the narrow sense) (Figure 1Figure 2-Figure 11).

Conocephalum conicum *s.s.* (Figure 1-Figure 11) is a smaller plant than ***C. salebrosum*** (Figure 12); ***C. salebrosum*** plants are dull, with more conspicuous thallus grooves that are more conspicuous than the air pores (Figure 13) (Stotler & Crandall-Stotler 2017).

Figure 2. ***Conocephalum conicum*** showing conspicuous pores. Photo by Li Zhang, with permission.

Figure 3. ***Conocephalum conicum*** from Scotland, showing conspicuous pores. Photo courtesy of David Long.

Figure 4. ***Conocephalum conicum*** showing distinct pores and weaker thallus sections. Photo by Hermann Schachner, through Creative Commons.

Figure 5. ***Conocephalum conicum*** with conspicuous pores. Photo by Ralf Wagner, with permission.

Figure 6. ***Conocephalum conicum*** from Wales, showing distinct pores. Photo courtesy of Jonathan Sleath.

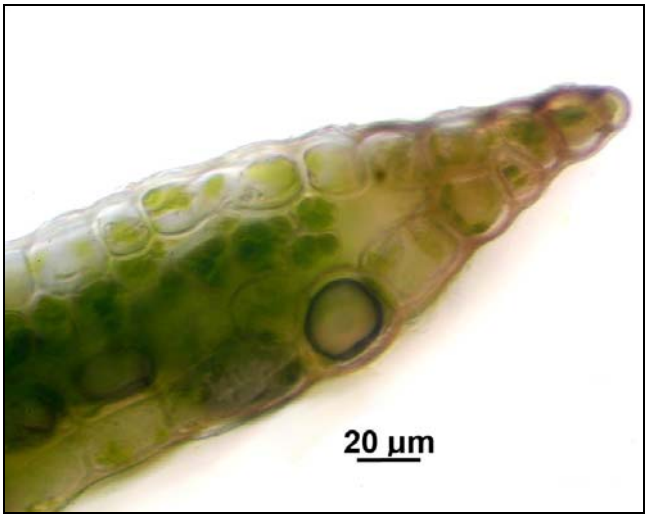

Figure 7. ***Conocephalum conicum*** thallus margin section, from Céret, France. Photo courtesy of Louis Thouvenot.

Figure 8. ***Conocephalum conicum*** *s.l.* showing conspicuous pores. Photo by Li Zhang, with permission.

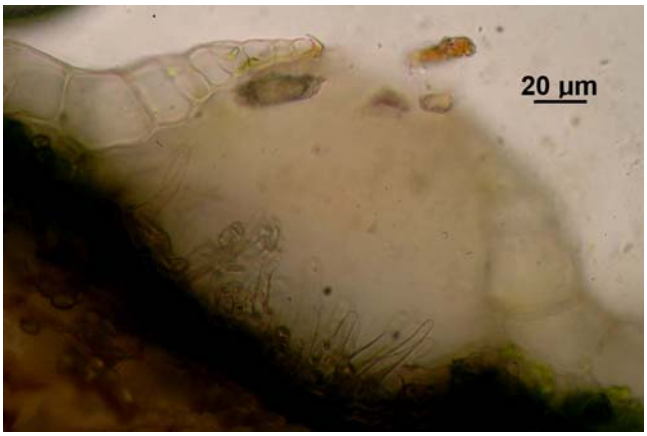

Figure 9. ***Conocephalum conicum*** from Céret, France, showing pore section. Photo courtesy of Louis Thouvenot.

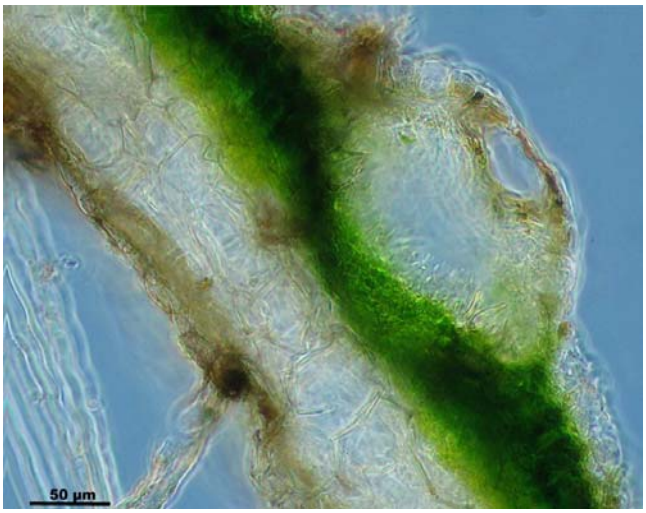

Figure 10. ***Conocephalum conicum*** showing pore section. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

Figure 11. ***Conocephalum conicum*** *s.l.* pore wall. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

Figure 12. ***Conocephalum salebrosum*** on **left** with conspicuous thallus grooves and dull thallus and ***C. conicum*** on **right** and **center** with conspicuous pores and shiny thallus. Photo courtesy of Jonathan Sleath.

Figure 13. ***Conocephalum salebrosum*** showing dull thallus, conspicuous grooves, and pores less conspicuous than thallus grooves. Photo by Jouko Rikkinen, through Creative Commons.

Distribution

Sérgio *et al*. (2011) surmised that ***Conocephalum salebrosum*** (Figure 12-Figure 13) has a more scattered and wider distribution than does ***C. conicum*** (Figure 1-Figure 11). Stotler and Crandall-Stotler (2017) concluded that ***Conocephalum conicum*** does not occur in North America and that all of the specimens previously identified as ***C. conicum*** are instead aligned with ***C. salebrosum***. In Russia Borovichev *et al*. (2009) found ***C. conicum*** to be more widespread than ***C. salebrosum***. The overall distribution of ***C. conicum*** appears to be restricted to Europe. The photos below illustrate its presence in a number of European countries (Figure 14-Figure 18).

Figure 14. ***Conocephalum conicum***, Wales. Photo courtesy of David Long.

Figure 15. ***Conocephalum conicum***, Scotland. Photo courtesy of David Long.

Figure 16. ***Conocephalum conicum***, Céret, France. Photo courtesy of Louis Thouvenot.

Figure 17. ***Conocephalum conicum***, Sardoa, Italy. Photo courtesy of Michael Lüth.

Figure 18. ***Conocephalum conicum***, Czech Republic. Photo by Vita Plasek, with permission.

Aquatic and Wet Habitats

Borovichev *et al*. (2009) found that ***Conocephalum conicum*** (Figure 1-Figure 11) and ***C. salebrosum*** (Figure 12-Figure 13) have similar ecological preferences and that they can even grow intermingled (Figure 19). Both form extensive mats on streambanks and at the bases of moist rocks and cliffs. ***Conocephalum conicum*** tends to be more hygrophytic than ***C. salebrosum***. Both species seem to specialize in colonizing spring and river micro-habitats close to running or standing water. The photographs below illustrate some of the habitats where ***Conocephalum conicum*** has been found in Europe (Figure 20-Figure 22).

Figure 19. ***Conocephalum conicum*** (**left**) and ***C. salebrosum*** (**right**). Photo courtesy of Michael Lüth.

Conocephalum conicum *s.l.* (Figure 1-Figure 11) occurs in wet places around lakes, especially in shade in Scotland (West 1910); in ground, rock, spring, and water communities associated with streams near Lacko, Western Carpathians (Mamczarz 1970); in association with the River Wear, England (Birch *et al*. 1988); associated with rivers (Ferreira *et al*. 2008). Its habitat seems to be primarily from rivers, streams, and stream banks (Figure 26). Nevertheless, it occurs often on rocky walls above streams (Figure 20) and in caves (Figure 21-Figure 22).

Figure 20. ***Conocephalum conicum*** growth habit on wall *s.l.* Photo by Allen Norcross, with permission.

Figure 21. ***Conocephalum conicum*** in wet limestone cave, Traeth Glaslyn Nature Reserve, Wales. Photo by Janice Glime.

Figure 22. ***Conocephalum conicum*** in wet, limestone cave, Traeth Glaslyn Nature Reserve, Wales. Photo by Janice Glime.

There are many reports of ***Conocephalum conicum*** (Figure 1-Figure 11) from streams and rivers. It is among the commonest species in English and Welsh rivers (Scarlett & O'Hare 2006). It is among the most common bryophytes in the River Tweed, UK (Holmes & Whitton 1975) and occurs throughout the River Swale, Yorkshire, UK (Holmes & Whitton 1977b). In the River Tyne, UK, it occurs mostly in mid to lower reaches (Holmes & Whitton 1981). It is part of the ***Platyhypnidium-Fontinalis antipyretica*** (Figure 23-Figure 24) association in Thuringia, Germany (Marstaller 1987). It occurs both in the Iskur River, Bulgaria, and its main tributaries (Papp *et al.* 2006). In Greece it is common in streams (Papp 1998). It occurs on moist stones and rocks in the streambed (Figure 1, Figure 25) in streams of Gory Stolowe Mountains, Poland (Szweykowski 1951). It is also found in mountain streams of northwestern Portugal (Vieira *et al.* 2005) and in mountainous streams on Madeira Island (Luis *et al.* 2015).

Figure 23. ***Platyhypnidium riparioides*** of the ***Platyhypnidium-Fontinalis antipyretica*** association that may also include ***Conocephalum conicum***. Photo by Hermann Schachner, through Creative Commons.

Figure 24. ***Fontinalis antipyretica*** of the ***Platyhypnidium-Fontinalis antipyretica*** association that may also include ***Conocephalum conicum***. Photo from Botany Website, UBC, with permission.

Figure 25. ***Conocephalum conicum*** *s.l.* on emergent rock in stream. Photo from <www.aphotofauna.com>, with permission.

Stream and River Banks

Conocephalum conicum (Figure 1-Figure 11) is able to live on banks with frequent submergence (Figure 26) and slow water, usually on rocks just above water (Figure 27-Figure 31) (Watson 1919). It occurs in a zone above ***Cratoneuron filicinum*** (Figure 32-Figure 33), up to 0.9 m above the water (Gimingham & Birse 1957). Holmes and Whitton (1977a) found it on the river bank of the River Tees, UK.

Figure 26. ***Conocephalum conicum*** habitat along a stream in France. Photo courtesy of courtesy of Leica Chavoutier.

Figure 27. ***Conocephalum conicum*** *s.l.* on rock wall at stream edge. Photo by Allen Norcross, with permission.

Figure 28. ***Conocephalum conicum*** *s.l.* on rock wall of stream. Photo by Allen Norcross, with permission.

Figure 29. ***Conocephalum conicum*** *s.l.* on rock at stream edge. Photo by Allen Norcross, with permission.

Figure 30. ***Conocephalum conicum*** on wet rock, Sardoa, Italy. Photo courtesy of Michael Lüth.

Figure 31. ***Conocephalum conicum*** *s.l.* on rock wall. Photo by Allen Norcross, with permission.

Figure 32. ***Cratoneuron filicinum***; ***Conocephalum conicum*** *s.l.* lives in a zone above this species in Europe. Photo by Claire Halpin, with permission.

Figure 33. ***Cratoneuron filicinum***, a species that lives in a zone closer to the water than that of ***Conocephalum conicum*** *s.l.* Photo by Tigerente, through Creative Commons.

Luis *et al*. (2008) reported ***Conocephalum conicum*** *s.s.* (Figure 1-Figure 11) along the lower reaches of Ribeira Brava in Madeira in disturbed areas dominated by the great

reed ***Arundo donax*** (Figure 34). It was associated there with the mosses ***Bryum dichotomum*** (Figure 35), ***Pohlia melanodon*** (Figure 36), ***Ptychostomum capillare*** (Figure 37), and ***Scorpiurium circinatum*** (Figure 38-Figure 39) and the liverwort ***Lunularia cruciata*** (Figure 40).

Figure 34. ***Arundo donax***, a grass that sometimes is accompanied by ***Conocephalum conicum*** *s.l.* along the lower reaches of the Ribeira Brava in Madeira. Photo by Forest and Kim Starr, through public domain.

Figure 35. ***Bryum dichotomum***, an associate of ***Conocephalum conicum*** along the Ribeira Brava in Madeira. Photo by David T. Holyoak, with permission.

Figure 36. ***Pohlia melanodon***, an associate of ***Conocephalum conicum*** along the Ribeira Brava in Madeira. Photo by David T. Holyoak, with permission.

Figure 37. ***Ptychostomum capillare***, an associate of ***Conocephalum conicum*** along the Ribeira Brava in Madeira. Photo by Michael Becker, through Creative Commons.

Figure 38. ***Scorpiurium circinatum*** moist, an associate of ***Conocephalum conicum*** along the Ribeira Brava in Madeira. Photo by Hugues Tinguy, with permission.

Figure 39. ***Scorpiurium circinatum*** dry. Photo by David T. Holyoak, with permission.

Figure 40. ***Lunularia cruciata***, an associate of ***Conocephalum conicum*** along the Ribeira Brava in Madeira. Photo by Michael Langeveld, through Creative Commons.

Springs

There seem to be few reports of ***Conocephalum conicum*** (Figure 1-Figure 11) in or around springs. It is known at a spring in the Tara river canyon and Durmitor area, Montenegro (Papp & Erzberger 2011).

Waterfalls

Watson (1919) reported ***Conocephalum conicum*** (Figure 1-Figure 11) from waterfalls, but others don't seem to attribute it to this habitat. This is often a lack of detail in reporting, with the splash zone of a waterfall included with "streambank."

Non-Aquatic Habitats

Although ***Conocephalum conicum*** (Figure 1-Figure 11) is usually associated closely with water, it can be found on slopes (Figure 41), perhaps getting water from seepage, or occurring on canyon walls where it is shaded and humid (Figure 42).

Figure 41. ***Conocephalum conicum*** *s.l.* habitat. Photo by Michael Lüth, with permission.

Figure 42. ***Conocephalum conicum*** *s.l.* on rock of stream canyon. Photo by Michael Lüth, with permission.

Physiology

Conocephalum conicum (Figure 1-Figure 11) is more easily stressed by **desiccation** than its sibling species ***C. salebrosum*** (Figure 12-Figure 13) (Szweykowski *et al*. 2005; Borovichev *et al*. 2009). This explains its more aquatic habitats.

Like ***C. salebrosum***, ***C. conicum*** (Figure 1-Figure 11) has scales (Figure 43-Figure 44) and rhizoids (Figure 45-Figure 46) that provide **capillary spaces** on the ventral surface. We can assume that like the case of ***C. salebrosum***, water moves through these spaces along the thallus and is delivered to all points on the thallus where it is taken in and distributed.

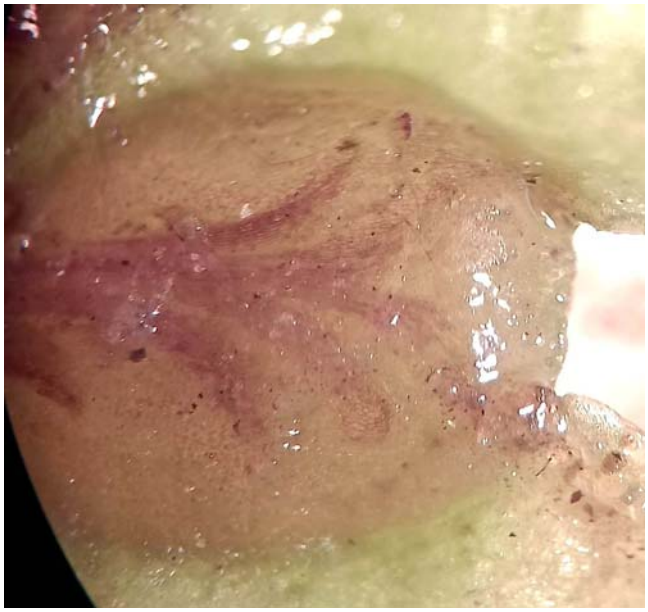

Figure 43. ***Conocephalum conicum*** s.l. from Italy showing scales on the ventral thallus surface. Photo courtesy of Anna di Palma.

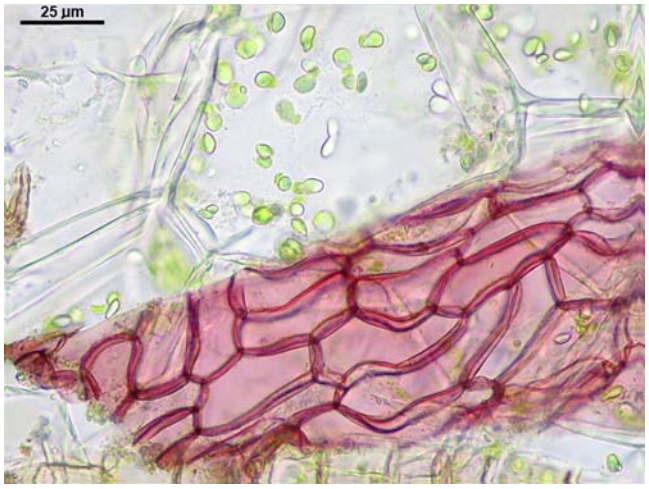

Figure 44. ***Conocephalum conicum*** *s.l.* ventral scale that aids in movement of water across the ventral side of thallus. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

Figure 45. ***Conocephalum conicum*** *s.l.* thallus with rhizoids and thallus; rhizoids help to move water across the ventral side of the thallus and facilitate uptake. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

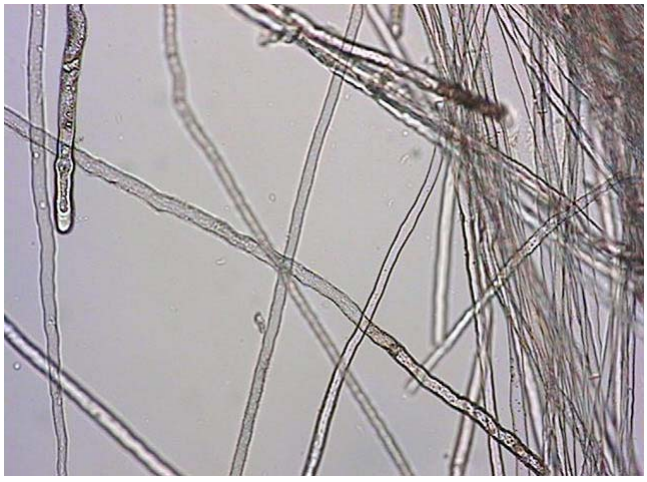

Figure 46. ***Conocephalum conicum*** rhizoids showing the capillary spaces where they are massed. Photo by Paul Davison, with permission.

The shade habitat of ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11) is supported by its reaction to supplemented **UV-B radiation** (Ihle & Laasch 1995; Ihle 1997). This radiation causes a drastic decrease in the reaction center proteins D1 and D2 as well as the outer light-harvesting antenna. Streptomycin inhibited the repair process of PS II, indicating that only chloroplastic protein synthesis is needed for recovery. A specimen from India suggests that under the right conditions this species can produce protective pigments (Figure 47).

Figure 47. ***Conocephalum conicum*** from India showing brown pigmentation. Photo courtesy of Muhammet Ören.

At the other end of the light intensity range, **low light** causes **etiolation**. Ken Adams (pers. comm.) demonstrated this by growing ***Conocephalum conicum*** in the dark (Figure 48).

Figure 48. ***Conocephalum conicum*** etiolation (3 weeks in dark). Photo by Ken Adams, with permission.

The ***p*H** seems to be important in the distribution of ***Conocephalum***, but most reports of preference can only be applied to ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11). Trębacz (1992) found that *p*H is also important within the cells of ***Conocephalum conicum*** *s.l.* It responds to the onset of **light** by decreasing its internal *p*H by about 0.15 units, followed by a slow increase. Respiration also can exhibit up to a 100% increase in response to excitation, but

the *p*H seems not to be involved. Dziubińska *et al*. (1989) found that cutting the thallus or providing an electrical stimulus elicited a transient rise in the rate of respiration. If the stimulation fails to produce any excitation, the respiration does not increase. The differences in response depend on the character of the excitation and the area of the thallus stimulated. Erdtmann and Mueller Stoll (1983) investigated the relationship between respiration and regeneration in ***Conocephalum conicum*** *s.l.*

Trębacz and Fensom (1989) found that in ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11) labelled carbon travelled cell to cell at a rate of ~2.0-1.7 µm 5^{-1}, a rate that is the same as that of cytoplasmic streaming. **Photosynthesis** occurs in the thallus cells (Figure 49); CO_2 is obtained from the air through the pores on the thallus surface (Figure 50-Figure 51) and oxygen is released there. Below these openings are chambers with chlorophyllous cells where photosynthesis occurs (Figure 51). Starch can be stored in the cells and can be densely clumped in the stalk portion of the archegoniophore (Figure 52).

Figure 49. ***Conocephalum conicum*** photosynthetic cells in thallus. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 50. ***Conocephalum conicum*** *s.l.* showing pore openings on the thallus surface in the UK. Photo by Dick Haaksma, with permission.

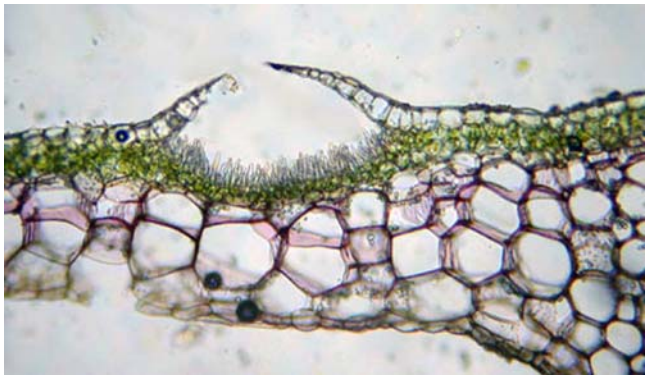

Figure 51. ***Conocephalum conicum*** *s.l.* showing longitudinal section of pore. Photo from Botany Website, UBC, with permission.

Figure 52. ***Conocephalum conicum*** *s.l.* archegoniophore stalk section showing stained dense starch grains. Photo from Botany Website, UBC, with permission.

In addition to whatever benefit may be derived from neighbors, ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11) has anatomical adaptations that may permit it to live where it can become inundated with water. The **air pores** (Figure 50), which are quite large in this genus, have hydrophobic cuticular ridges (Figure 51) surrounding them (Schönherr & Ziegler 1975). This allows only liquids with a contact angle of zero degrees with the ledges to enter the air pore. This presumably permits the internal air chambers of the species to maintain the air space needed to obtain CO_2. One would assume that this is necessary for rapid recovery once the water recedes and to allow continued photosynthesis when kept wet on the exterior by splash.

Dilks and Proctor (1975) found that ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11) was killed by **rapid cooling** to -5ºC, whereas many of the bryophytes tested could withstand such rapid cooling. Nevertheless, it certainly can survive freezing temperatures in caves, where the temperature is not likely to drop suddenly (Figure 53). Dilks and Proctor surmised that the ability to survive long periods at low temperatures, as exhibited by many species, seems to relate to desiccation resistance.

Figure 53. ***Conocephalum conicum*** *s.l.* on wet cave roof with ice. Photo by Allen Norcross, with permission.

Krol *et al.* (2003) found that ***Conocephalum conicum*** (Figure 1-Figure 11) *s.l.* exhibits all-or-none action potentials in response to **sudden temperature drops**. Calcium is important in these potentials, with its inhibition or decrease resulting in the inhibition of voltage transients. The researchers concluded that the temperature drop causes a change in membrane potential due to calcium influx from both internal and external stores.

Conocephalum conicum *s.l.* (Figure 1-Figure 11) produces **Heat Shock Protein 70** in response to atmospheric pollution (Basile *et al*. 2013). The **heavy metals** accumulate in cell walls, accompanied by a strong increment in the Heat Shock Protein 70. Cadmium and lead accumulate in the parenchyma and are absorbed to cell walls or concentrated in vacuoles. The pollutants result in severe alterations to the organelles. The researchers concluded that ***C. conicum*** *s.l.* is tolerant of heavy metals and can serve as a bioindicator (see also Maresca *et al*. 2020). Nevertheless, Iqbal *et al*. (2011b) expressed concern that it was threatened by changes in the environment in Bhaderwah as well as in the Kumaon Himalaya.

Trębacz *et al*. (1994) compared the activities of Ca^{2+}, K^+, Cl^-, and NO_3^- in ***Conocephalum conicum*** (Figure 1-Figure 11). The free cytosolic Ca^{2+} did not exhibit any light-dependent changes when no action potential was triggered. However, action potentials typically caused a 2-fold increase in free cytoplasmic Ca^{2+} concentration. Action potentials cause little change in K^+ activity. For both Cl^- and NO_3^- the vacuolar activity was 5 to 6 times that of the cytoplasmic activity. Changes in illumination had little effect on the concentrations of the two ions.

Samecka-Cymerman *et al*. (1997) found that the ecological differentiation between the liverwort species ***Conocephalum conicum*** (Figure 1-Figure 11), ***Marchantia polymorpha*** (Figure 54), and ***Pellia epiphylla*** (Figure 55) correlates closely with the soil chemistry. They found a high correlation between the soil concentrations of heavy metals as well as macroelements and the thalli of these liverworts. ***Conocephalum conicum*** *s.l.* proved to be a good biomonitor of chromium and cobalt.

Figure 54. ***Marchantia polymorpha*** with gemmae cups. Photo by Hermann Schachner, through Creative Commons.

Figure 55. ***Pellia epiphylla***, a species of similar locations near stream water, but differs in soil chemistry from that of ***Conocephalum conicum***. Photo by Hermann Schachner, with permission.

Adaptations

Gimingham and Birse (1957) concluded that thalloid mats such as those in ***Conocephalum*** occur at the most moist end of the spectrum. ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11) often occurs in **association** with other liverworts, such as ***Chiloscyphus kashyapii***, ***Dumortiera hirsuta*** (Figure 56), ***Marchantia*** spp. (Figure 54), ***Pellia endiviifolia*** (Figure 57), ***Preissia quadrata*** (Figure 58), ***Reboulia hemispherica*** (Figure 59), and occasionally with ***Aneura pinguis*** (Figure 60), ***Clevea hyalina*** (Figure 61), ***Mannia triandra*** (Figure 62), and as well as the mosses ***Myurella sibirica*** (Figure 63) and ***Thuidium delicatulum*** (Figure 64) (Iqbal *et al*. 2011a). ***Conocephalum conicum*** is also associated with fungi, ferns, flowering plants, and even insects. These associations might prove to be beneficial, perhaps by maintaining moisture or in helping the liverworts to obtain it. They could also result in competition.

Figure 56. ***Dumortiera hirsuta***, a liverwort that often occurs in association with ***Conocephalum conicum*** *s.l.* Photo by George Shepherd, through Creative Commons.

Figure 57. ***Pellia endiviifolia***, a liverwort that often occurs in association with ***Conocephalum conicum*** *s.l.* Photo by Hermann Schachner, through Creative Commons.

Figure 58. ***Preissia quadrata***, a liverwort that often occurs in association with ***Conocephalum conicum*** *s.l.* Photo by Bernd Haynold, through Creative Commons.

Figure 59. ***Reboulia hemisphaerica***, a liverwort that often occurs in association with ***Conocephalum conicum*** *s.l.* Photo by Michael Lüth, with permission.

Figure 60. ***Aneura pinguis***, a liverwort that often occurs in association with ***Conocephalum conicum*** *s.l.* Photo by Hermann Schachner, through Creative Commons.

Figure 61. ***Clevea hyalina***, a liverwort that sometimes occurs in association with ***Conocephalum conicum*** *s.l.* Photo by Hugues Tinguy, with permission.

Figure 62. ***Mannia triandra***, a liverwort that sometimes occurs in association with ***Conocephalum conicum*** *s.l.* Photo courtesy of Guido Brusa.

Figure 63. ***Myurella sibirica***, a moss that often occurs in association with ***Conocephalum conicum*** *s.l.* Photo by Dick Haaksma, with permission.

Figure 64. ***Thuidium delicatulum***, a moss that often occurs in association with ***Conocephalum conicum*** *s.l.* Photo by Blanka Aguero, with permission.

Levine (1999) explored the "indirect facilitation" in a riparian community where ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11) (see Shevock *et al*. 2021) was a member. "I**ndirect facilitation** occurs when the indirect positive effect of one species on another, via the suppression of a shared competitor, is stronger than the direct competitive effect." In a northern California, USA, riparian community, Levine conducted field experiments. Using a factorial design, he found three qualitatively different interactions between ***Carex nudata*** (Figure 65) and three target species. The ***Carex*** facilitated ***Conocephalum conicum*** *s.l.* in the presence of ***Mimulus guttatus*** (Figure 66) by suppressing the latter. On the other hand, when ***M. guttatus*** was absent, ***Carex nudata*** was a competitor with ***Conocephalum conicum*** *s.l.*

Figure 65. ***Carex nudata***, a species that interacts with ***Conocephalum conicum*** *s.l.* by suppressing ***Mimulus guttatus***, or to compete when ***M. guttatus*** is absent. Photo by Paul Slichter, with permission.

Figure 66. ***Mimulus guttatus***, a species that competes with ***Conocephalum conicum*** *s.l.* Photo by Christopher M. Luna, through Creative Commons.

Reproduction

Conocephalum conicum *s.l.* (Figure 1-Figure 11) has been of interest to bryologists in a number of studies related to reproduction. However, some of these have been done in North America, so I must assume they actually refer to ***Conocephalum salebrosum*** (Figure 12-Figure 13). Thus, I have discussed them under that species in the next subchapter.

One of the mechanisms of spread of ***Conocephalum*** species is its ability to **overwinter** and produce new growth in spring. The overwintering buds are protected by scales (Figure 67-Figure 69). But young plants (Figure 70-Figure 71) also arise with no apparent connection to plants from a previous year.

Figure 67. ***Conocephalum conicum*** *s.l.* overwintering bud scales. Photo from Botany Website, UBC, with permission.

Figure 68. ***Conocephalum conicum*** *s.l.* with scales covering winter buds. Photo by Allen Norcross, with permission.

Figure 69. ***Conocephalum conicum*** *s.l.* overwintering bud scales. Photo by Dick Haaksma, with permission.

Figure 70. ***Conocephalum conicum*** *s.l.* young. Photo by Dick Haaksma, with permission.

Figure 71. ***Conocephalum conicum*** *s.l.* young plants. Photo by Dick Haaksma, with permission.

Benson-Evans (1964) found that ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11) from Wales grew best and produced **gametangia** (Figure 72-Figure 75) at 21ºC, but not at 10ºC. It grew and produced gametangia best in long days (18 hours), but not in short days (6 hours).

Figure 72. ***Conocephalum conicum*** with immature antheridial receptacles, Sardoa, Italy. Photo courtesy of Michael Lüth.

Figure 73. ***Conocephalum conicum*** *s.l.* antheridial receptacles. Photo by Malcolm Storey through Creative Commons.

Figure 74. ***Conocephalum conicum*** *s.l.* males with mature antheridial receptacles, Nichinan, Japan, June 1983. Photo by Janice Glime.

Yamazaki (1981) discovered that even within a population of ***Conocephalum conicum*** (Figure 1-Figure 11) the **genetic variation** was abundant, a condition that suggests that sexual reproduction predominates in the natural populations. It is not unusual to see reproductive populations (Figure 76-Figure 78), and for the most part bryologists have not reported asexual structures. Since ***C. conicum*** can grow together with ***C. salebrosum*** (Figure 12-Figure 13), it is possible that some of the variation Yamazaki observed was really that of what we now consider to be two species.

Figure 75. ***Conocephalum conicum*** *s.l.* mature antheridial receptacle. Photo by Malcolm Storey, through Creative Commons.

Figure 76. ***Conocephalum conicum*** *s.l.* with developing archegoniophore. Photo by Li Zhang, with permission.

Figure 77. ***Conocephalum conicum*** *s.l.* mature sporangia in the cone-shaped archegonial head, a relatively frequent sight due to the frequent sexual reproduction. Photo by Hermann Schachner, through Creative Commons.

Figure 78. ***Conocephalum conicum*** *s.l.* sporangia ready to release spores. Photo from Botany Website, UBC, with permission.

More recently, **tubers** have been verified on ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11) in Sussex, England (Paton 1993). These were found so uncommonly that their presence was often omitted from descriptions of the species. They may, however, be more common than assumed because they are located on **moribund** (in terminal decline; lacking vitality or vigor; Figure 79) thalli – a part of the plant often overlooked or discarded in the preparation of specimens. Furthermore, they are on the ventral surface, hidden among the rhizoids. Nevertheless, when they become detached, they germinate to produce a new thallus.

Figure 79. ***Conocephalum*** *cf.* ***salebrosum*** dead and new growth on population at Hocking Hills, Ohio, USA. It is on the ventral side of such moribund tissues where tubers have been found in ***Conocephalum conicum*** *s.l.* Photo by Janice Glime.

Bhagat *et al*. (2012) suggested that sexual reproduction is a less important means of reproduction in ***Conocephalum*** than is asexual reproduction. They based this on the relatively constant ratio of spores to elaters (Figure 80) (0.40-0.43:1) over the past 54 years, a ratio that is much lower than that known in other **Marchantiales**.

Figure 80. ***Conocephalum conicum*** *s.l.* spores and elaters at maturity. Photo from Botany Website, UBC, with permission.

Fungal Interactions

Carré and Harrison (1961) reported a species of ***Pythium*** (Figure 81), a parasitic fungus, invading ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11). This endophyte invades the rhizoids (Figure 82) and then the thallus, but is limited to the area adjoining the midrib. A species of ***Pythium*** was consistently isolated from infected rhizoids and thalli. Other fungal species were in cultures with sterile thalli, but none was able to form the typical **vesicular-arbuscular** (Figure 83) condition. Some were, however, able to penetrate the rhizoids and lower cells of the thallus.

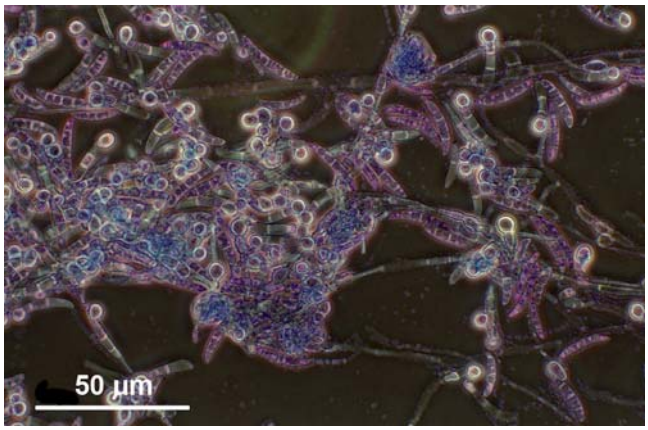

Figure 81. ***Pythium*** sp.; a species of ***Pythium*** is endophytic in ***Conocephalum conicum*** *s.l.* Photo by Josef Reischig, through Creative Commons.

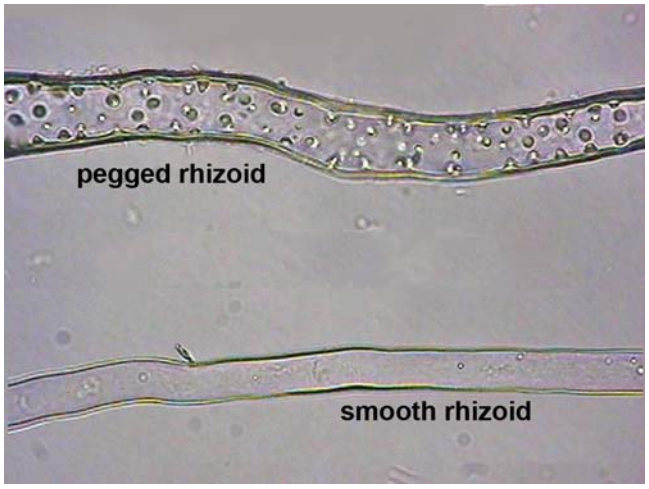

Figure 82. ***Conocephalum conicum*** *s.l.* two types of rhizoids. Photo by Paul Davison, with permission.

Figure 83. **Vesicular arbuscular mycorrhizae** in root cells, showing the form that might also show up in the thallus of ***Conocephalum conicum***. Photo by Rit Rajarshi, through Creative Commons.

Ligrone and Lopes (1989) reported a highly branched fungus that colonizes the smooth-walled rhizoids (Figure 82) of ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11). The fungus is able to enter the thallus through these rhizoids to the parenchyma of the midrib, where it is entirely intracellular. The fungus forms vesicles (see Figure 83) in the rhizoids and a few ventral layers of the parenchyma cells. The fungal hyphae spread from cell to cell. More internal cells have prominent arbuscules (Figure 83) formed by the infecting hyphae. The infected host cells experience proliferation of the ribosomes, plastids, and mitochondria. The arbuscules ultimately degenerate, leaving clumps of collapsed hyphae, and these cells have not been observed to become reinfected.

Later, Ligrone *et al.* (2007) reported **Glomeromycotean** associates in liverworts. ***Glomus mosseae*** (Figure 84) was identified in axenic thalli of both ***Conocephalum conicum*** (Figure 1-Figure 11) and ***C. salebrosum*** (Figure 12-Figure 13) and produced an association with these liverworts similar to that seen in the wild. These fungi suppressed cell wall autofluorescence in Marchantialean liverworts and triggered the deposition of a new wall layer that specifically bound the monoclonal antibody CCRC-M1 against fucosylated side groups associated with xyloglucan and rhamnogalacturonan I.

Figure 84. ***Glomus mosseae*** spores cultured with tomato root. Photo by Samson90, through Creative Commons.

Nevertheless, ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11) exhibited some antifungal activity. Asakawa (2007) reported antimicrobial, antifungal, antipyretic, and antidotal activity from ***Conocephalum conicum*** *s.l.*. It can be used to cure cuts, burns, scalds, fractures, swollen tissue, poisonous snake bites, and gallstones. We don't know which cryptospecies was used in the study.

Animal Interactions

Imada *et al.* (2011) found that there are ~25 East Asian endemic members of the micropterigid moths (Figure 85) that occur exclusively on ***Conocephalum*** (Figure 1-Figure 11, Figure 86). These moth species are separated by geographical isolation. It would be interesting to know if these moth species have any correlations with the chemical differences among cryptospecies of this liverwort.

Figure 85. ***Neomicropteryx nipponensis*** larva feeding on ***Conocephalum conicum*** *s.l.* Note the darkened necrotic areas where the outer cells have been removed. Photo by Yume Imada, with permission.

Figure 86. ***Conocephalum conicum*** *s.l.* that has been nibbled. Photo by Allen Norcross, with permission.

Biochemistry

Conocephalum conicum *s.l.* (Figure 1-Figure 11) has had more than its share of biochemical analyses. Only a few are included here. Unfortunately, most of these predate the breakup of the species into multiple species and cryptospecies.

Markham *et al*. (1976) found that flavonoids differed between a German sample and one from the USA. This difference might be the forerunner of our understanding that the North American populations are actually ***Conocephalum salebrosum*** (Figure 12-Figure 13). They also found that the flavonoids they identified did not change qualitatively with seasonal changes. Using 280 samples, Toyota *et al*. (1997) compared three chemotypes of ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11).

Ludwiczuk *et al*. (2013) identified cryptic species in ***Conocephalum conicum*** *s.l.* using volatile components. Using 13 samples, they identified four cryptic species of ***C. conicum*** and the species ***C. salebrosum*** (Figure 12-Figure 13). The chemical differences correlated with the geographic distribution of the samples.

Ghani *et al*. (2016) used Japanese material of Type-II ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11) to release a phenyl propanoid, trans-methyl cinnamate as a stress response. Although they used it to show that this type had this compound, only previously known from Type III, it is interesting ecologically to know that phenyl compounds can be released in response to stress. Are these similar to the herbivory responses known from many tree leaves?

Asakawa and Takemoto (1979) identified tulipinolide as the compound causing the pungency one can sense in the female gametophyte of ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11); the compound and the smell are absent in the males. The guaianolides were inhibitory toward germination and growth of roots of rice in the husk.

Castaldo-Cobianchi *et al*. (1988) reported antibiotic activity in ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11) against both Gram+ and Gram- bacteria.

Odrzykoski and Szweykowski (1991) described three new sesquiterpenoids from ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11) They found that the compounds varied in their cytotoxicity, but that they could exert immunosuppressive effects on rat splenocytes at lesser concentrations than those that were toxic. Melching and König (1999) identified three new sesquiterpenes from ***Conocephalum conicum*** *s.l.* in Germany.

Lu *et al*. (2006) identified four new monoterpene esters and elucidated a number of known compounds in ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11). Two compounds were moderately cytotoxic to human HepG2 cells and one of these also exhibited antibacterial activity against ***Pseudomonas aeruginosa*** (Figure 87).

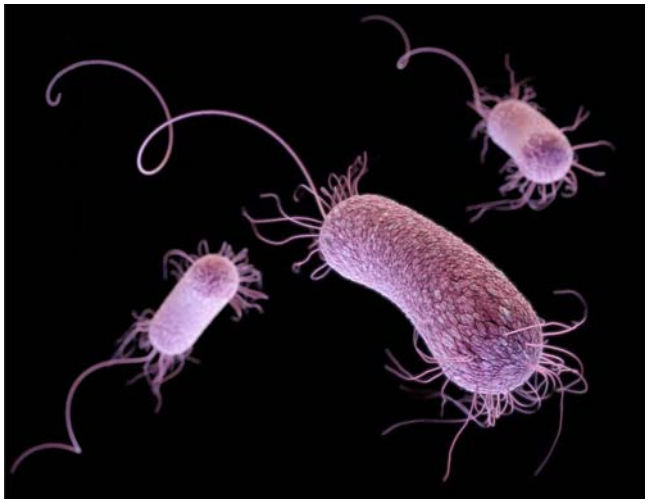

Figure 87. ***Pseudomonas aeruginosa***, a bacterium that is inhibited by compounds from ***Conocephalum conicum*** *s.l.* Photo from CDC, through public domain.

Himanshu *et al*. (2007) tested several bryophytes, including ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11) for activity against the human pathogens ***Escherichia coli*** (Figure 88) and ***Salmonella typhi*** (Figure 89) and two fungi, ***Aspergillus niger*** (Figure 90), ***Candida albicans*** (Figure 91). None of the water-soluble extracts was effective on the pathogens. However, the acetone-soluble extract was inhibitory against all the pathogens. ***Candida albicans*** was strongly inhibited by the extract from ***Conocephalum conicum*** *s.l.*

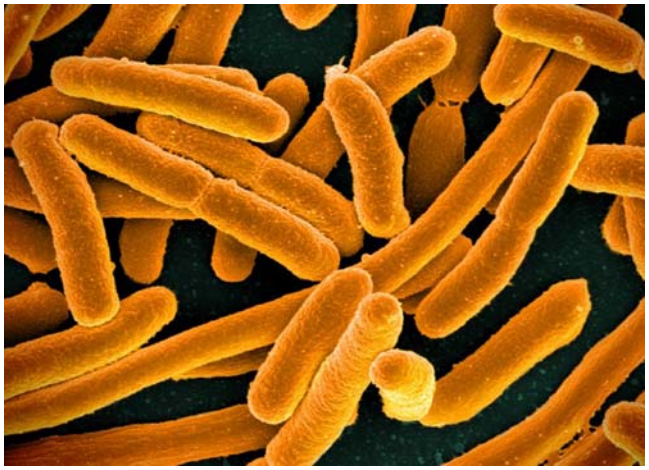

Figure 88. ***Escherichia coli***, a human pathogen that is inhibited by extracts of ***Conocephalum conicum*** *s.l.* Photo from NIAID, through Creative Commons.

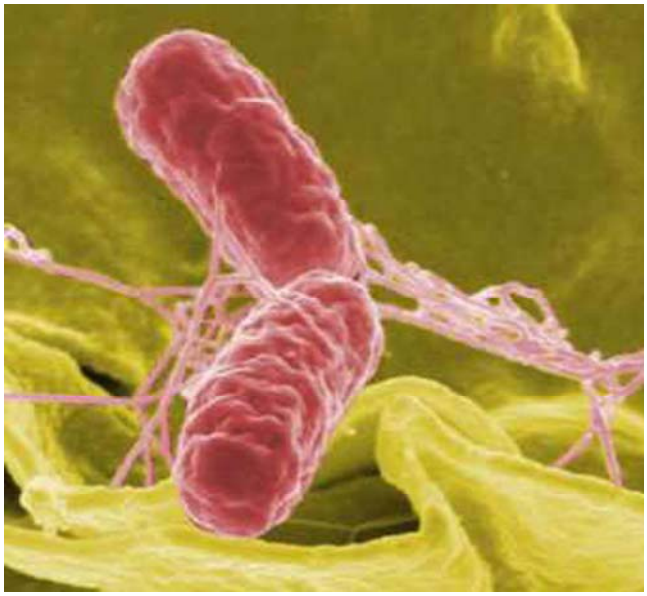

Figure 89. ***Salmonella*** sp., a human pathogen that is inhibited by extracts of ***Conocephalum conicum*** *s.l.* Photo by Elapied, through Creative Commons.

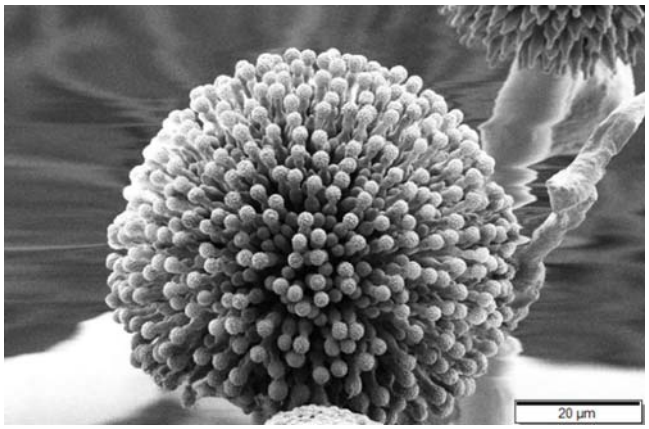

Figure 90. ***Aspergillus niger*** SEM, a pathogen that is inhibited by extracts of ***Conocephalum conicum*** *s.l.* Photo by Mogana Das Murtey and Patchamuthu Ramasamy, through Creative Commons.

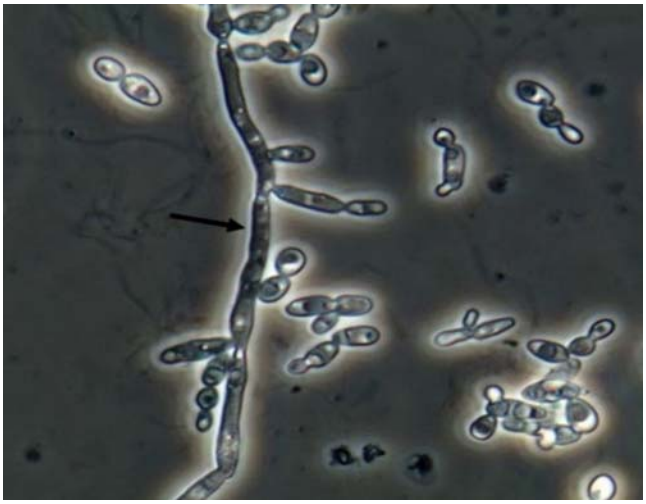

Figure 91. ***Candida albicans*** pseudohyphae in a fresh and unstained urine sediment. Photo from Controllab, through Creative Commons.

Ivković *et al*. (2021) found that methanol extracts of terpenes, oils, sugars and bis-bibenzyls were absent in ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11), whereas these are present in both ***Marchantia polymorpha*** (Figure 54) and ***Pellia endiviifolia*** (Figure 57).

Negi *et al*. (2020) found that ***Conocephalum conicum*** *s.l.* (Figure 1-Figure 11) acetone extracts were active against ***Aspergillus flavus*** (Figure 92) and ***A. parasiticus*** (Figure 93-Figure 94), with the highest activity coming from populations collected at Mukteshwar (2100 m asl). Negi and Chaturvedi (2021) further evaluated the usefulness of ***Conocephalum conicum*** *s.l.* and found that methanol extracts were highly effective against the fungal wilt disease caused by ***Fusarium oxysporum*** f. ***lycopersici*** (Figure 95-Figure 96), a disease that makes it unprofitable to grow tomatoes in the tropics. Since ***C. conicum*** is an "efficient" source of the Riccardin C that is active in inhibiting the fungi on tomatoes, it could be an eco-friendly alternative to the more conventional fungicides.

Figure 92. ***Aspergillus flavus***, a fungus that is inhibited by extracts of ***Conocephalum conicum*** *s.l.* Photo from Medmyco, through Creative Commons.

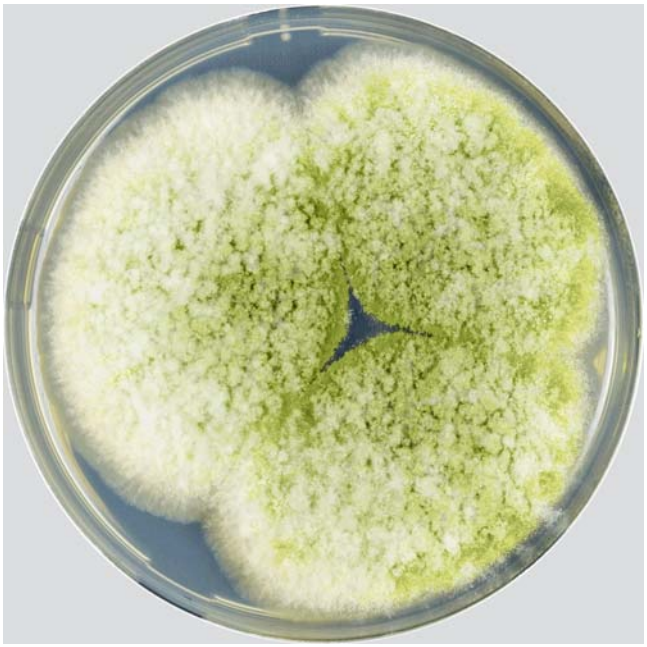

Figure 93. ***Aspergillus parasiticus***, a fungus that is inhibited by extracts of ***Conocephalum conicum*** *s.l.* Photo by Line Ledsgaard Jensen, Mikael Rørdam Andersen, Ellen Kirstine Lyhne, through public domain.

Figure 94. ***Aspergillus parasiticus***. Photo from Medmyco, through Creative Commons.

Figure 95. Tomato plant infected with ***Fusarium oxysporum*** f. ***lycopersici***. Photo by Gerald Holmes, Strawberry Center, Cal Poly San Luis Obispo, with permission.

Figure 96. Culture of ***Fusarium oxysporum***, a fungus that is devastating to tomato crops in the tropics; extracts of ***Conocephalum conicum*** *s.l.* inhibit its growth. Photo by Keith Weller, through public domain.

Conocephalum orientalis (Figure 97-Figure 100)

In 1994, Akiyama and Hiraoka (1994a, b) noted allozyme variation in the ***Conocephalum*** in Japan. This

led to later studies on the differences among the Japanese forms. In 2022 Akiyama has published several new species, some of which occur in wet habitats.

One of these new species is ***Conocephalum orientalis*** (Figure 97-Figure 100), a segregate of ***C. conicum*** (Figure 1-Figure 11) previously known as J type (Figure 97) (Akiyama 2022). The thallus of ***Conocephalum orientalis*** is shiny and light green (Figure 98-Figure 99), but becomes yellowish when growing in the shade; the air chambers (visible as polygons at the surface) increase in size toward the center of the thallus (Figure 100) The grooves are deep (Figure 101-Figure 102), like those of ***C. salebrosum*** (Figure 97). It forms the largest plant bodies of any ***Conocephalum*** species in Japan.

Figure 97. ***Conocephalum orientalis*** (**J**) and ***C. salebrosum*** (**S**). Photo courtesy of Hiroyuki Akiyama.

Figure 98. ***Conocephalum orientalis.*** Photo courtesy of Hiroyuki Akiyama.

Figure 99. ***Conocephalum orientalis*** showing thallus grooves and pores. Photo courtesy of Hiroyuki Akiyama.

Figure 100. ***Conocephalum orientalis*** showing thallus grooves and pores, with polygons larger toward the center. Photo courtesy of Hiroyuki Akiyama.

Thallus variation occurs within as well as between populations of ***Conocephalum orientalis*** (Figure 97-Figure 100) (Akiyama 2022). These can include differences in thallus size (Figure 101), degree of purplish pigments on ventral surface (Figure 102-Figure 104), wavy margins (type J2; Figure 105), and blackish thallus grooves (type J3; Figure 106-Figure 109).

Figure 101**.** ***Conocephalum orientalis*** showing variation in single population. Photo courtesy of Hiroyuki Akiyama.

Figure 102. ***Conocephalum orientalis*** young thallus that is still purplish. Photo courtesy of Hiroyuki Akiyama.

Figure 103. ***Conocephalum orientalis*** showing purplish midrib on underside. Photo courtesy of Hiroyuki Akiyama.

Figure 104. ***Conocephalum orientalis*** showing red underside of older tissues. Photo courtesy of Hiroyuki Akiyama.

Figure 105. ***Conocephalum orientalis*** type J2 with wavy margin. Photo courtesy of Hiroyuki Akiyama.

Figure 106. ***Conocephalum orientalis*** type J3 showing variation in purplish ventral side. Photo courtesy of Hiroyuki Akiyama.

Figure 107. ***Conocephalum orientalis*** type J3 with purplish ventral side and dark thallus grooves. Photo courtesy of Hiroyuki Akiyama.

Figure 108. ***Conocephalum orientalis*** type J3 showing blackish thallus grooves. Photo courtesy of Hiroyuki Akiyama.

Figure 109. ***Conocephalum orientalis*** type J3 with purplish ventral side and dark grooves. Photo courtesy of Hiroyuki Akiyama.

Although the separation of the species names is new, some natives of Japan have distinguished them for some time (Akiyama 2022). The plants now known as ***Conocephalum orientalis*** (Figure 97-Figure 100) are heated in oil and eaten like potato chips. The distinctive aroma is lost during heating. They taste similar to the dried seaweed **nori** (Figure 110).

Figure 110. Nori, a red alga used to wrap sushi; fried ***Conocephalum orientalis*** tastes much like this alga. Photo by Kropsoq, through Creative Commons.

Distribution

Conocephalum orientalis (Figure 97-Figure 100) is described as a segregate of ***C. salebrosum*** (Figure 111), another recent segregate from ***C. conicum*** (Akiyama 2022). ***Conocephalum orientalis*** is known from Japan and Taiwan, where it is the largest of the Japanese species and is the ***Conocephalum*** species most likely to be encountered on stream banks.

Figure 111. ***Conocephalum salebrosum*** from Japan. Photo courtesy of Hiroyuki Akiyama.

Aquatic and Wet Habitats

Conocephalum orientalis (Figure 97-Figure 100) forms large plants on streamsides (Figure 112) (Akiyama 2022). It occurs in slightly shaded places along streams and seepage slopes along forest trails.

Figure 112. ***Conocephalum orientalis*** on rock. Photo courtesy of Hiroyuki Akiyama.

Conocephalum orientalis (Figure 97-Figure 100) avoids rock surfaces with no soil, except where there is an extreme amount of rainfall (Akiyama 2022). It becomes quite succulent in areas with good moisture conditions. By contrast, populations in direct sunlight, such as concrete retaining walls along sunlit roadways, can become hard and yellowish. The J2 type becomes very thick with wavy margins in dry conditions (Figure 113). The J3 type is more common in mountain areas such as Hokkaido; these thalli can be orange to purplish on the ventral side, even in summer (Figure 114), most likely a response to higher UV light. Thalli in these mountainous areas are also larger than the streamside populations of lower elevations.

Figure 114. ***Conocephalum orientalis*** type J3 showing variation in orange to purplish ventral side. Photo courtesy of Hiroyuki Akiyama.

Physiology

Although there has not been time for separate physiological studies to be done on the newly named species ***Conocephalum orientalis***, we can infer some of its physiology from its structures and their known functions in other members of the ***C. conicum*** species complex. In other cases, Akiyama (2022) was able to link earlier studies with the new species through voucher specimens.

The color of ***Conocephalum orientalis*** (Figure 97-Figure 100) also changes with the seasons. The thallus is pale green in spring through autumn (see Figure 115), although there is a pale reddish purple coloration at the basal part of the midrib. In the shade the thallus can become dark green (Figure 116). However, in late autumn and through winter, the entire under surface becomes reddish purple.

Figure 113. ***Conocephalum orientalis*** type J2 with wavy margin. Photo courtesy of Hiroyuki Akiyama.

Figure 115. ***Conocephalum orientalis*** pale color at one location in the sun. Photo courtesy of Hiroyuki Akiyama.

Figure 116. ***Conocephalum orientalis*** dark color at one location in the shade. Photo courtesy of Hiroyuki Akiyama.

Akiyama (2022) found that plants of ***Conocephalum orientalis*** (Figure 97-Figure 100) grown in good moisture conditions become succulent and have clear slimy contents of polysaccharides flowing from the cut across mucilage canals (Figure 117). But it often lacks mucilage cells, suggesting that it is best adapted for a wet habitat (Akiyama 2022). It does, however, have abundant rhizoids (Figure 118-Figure 119) that form capillary spaces suitable for movement of water. We can surmise that its rhizoids and scales (Figure 118-Figure 119) move water along the ventral surface, as in other ***Conocephalum*** species, facilitating the uptake of water. In addition, it often has symbiotic fungi that can help in obtaining nutrients.

Figure 117. ***Conocephalum orientalis*** from Japan showing leak of mucilage from cross section of mucilage canals. Photo courtesy of Hiroyuki Akiyama.

Figure 118. ***Conocephalum orientalis*** from Taiwan, ventral side showing rhizoids. Photo courtesy of Hiroyuki Akiyama.

Figure 119. ***Conocephalum orientalis*** type J3 rhizoids and purplish ventral side. Photo courtesy of Hiroyuki Akiyama.

Adaptations

Plants of ***Conocephalum orientalis*** (Figure 97-Figure 100) seem to be quite plastic in nature. When plants grow in darker places, such as the entrance of a cave, thalli become very thin and yellowish (Figure 120), resembling Japanese forms of ***C. salebrosum*** (Akiyama 2022). Hard, leathery thalli can form in the sun, accompanied by dense ventral scales (Figure 119); their appendages are large and strongly colored reddish purple, a color that is also seen on the upper side of the thalli. These population differences can relate to altitude and shading, but the differences seem not to be linked to any genetic differences.

Figure 120. ***Conocephalum orientalis*** thin thalli produced under diffuse light. Photo courtesy of Hiroyuki Akiyama.

Akiyama (2022) described the thallus of ***Conocephalum orientalis*** (Figure 97-Figure 100) as having a light green ventral surface (Figure 118). However, this becomes reddish purple toward late autumn. This is a pattern seen in other bryophytes, including ***Sphagnum*** (Figure 121) species, presumably in response to the greater light intensity due to loss of canopy leaves, and to the cold nights. The cold nights and warm days are also responsible for the red colors seen on trees in the autumn (Kyne & Diver 2012).

Figure 121. ***Sphagnum capillifolium*** showing a color transition from green to red. Photo by Bernd Haynold, through Creative Commons.

Akiyama (2022) noticed that smaller plants of ***Conocephalum orientalis*** (Figure 97-Figure 100) tended to be the most common along the lower elevation streams, whereas at higher elevations they were larger, more "normal" plants.

Reproduction

Conocephalum orientalis (Figure 97-Figure 100) is **dioicous** (Figure 125-Figure 128) and **perennial** (Akiyama 2022). The antheridia appear as clusters in antheridial receptacles on the upper surface of the thallus at the tips of the thallus branches (Figure 122-Figure 124). In the spring, these receptacles appear at tips of newly formed lobes. These antheridial receptacles may appear on stalks created by the midrib because the thallus tissue ceases growth when the receptacle forms (Figure 125). These stalks differ from those of ***Marchantia*** in which the thallus folds and encloses the rhizoids.

Figure 122. ***Conocephalum orientalis*** male with antheridial receptacles. Photo courtesy of Hiroyuki Akiyama.

Figure 123. ***Conocephalum orientalis*** male with immature antheridial receptacle. Photo courtesy of Hiroyuki Akiyama.

Figure 124. ***Conocephalum orientalis*** male showing antheridial receptacle. Photo courtesy of Hiroyuki Akiyama.

Figure 125. ***Conocephalum orientalis*** male with stalked thallus, a condition that can sometimes be seen in new growth. Photo courtesy of Hiroyuki Akiyama.

Shimamura *et al*. (2008) described the dispersal of sperm (Figure 126) in ***Conocephalum conicum*** (Figure 1-Figure 11), providing photographs of their discovery in Japan. Shimamura now considers that the species is probably the newly described ***Conocephalum orientalis*** (Figure 97-Figure 100). Shimamura and coworkers found that as the sperm were discharged, they became airborne (Figure 126), a phenomenon they were able to verify in the field. They postulated that this explosive behavior, along with the elevated receptacles, would increase the efficiency of fertilization in this (and probably many other) liverwort species, particularly in a drought environment.

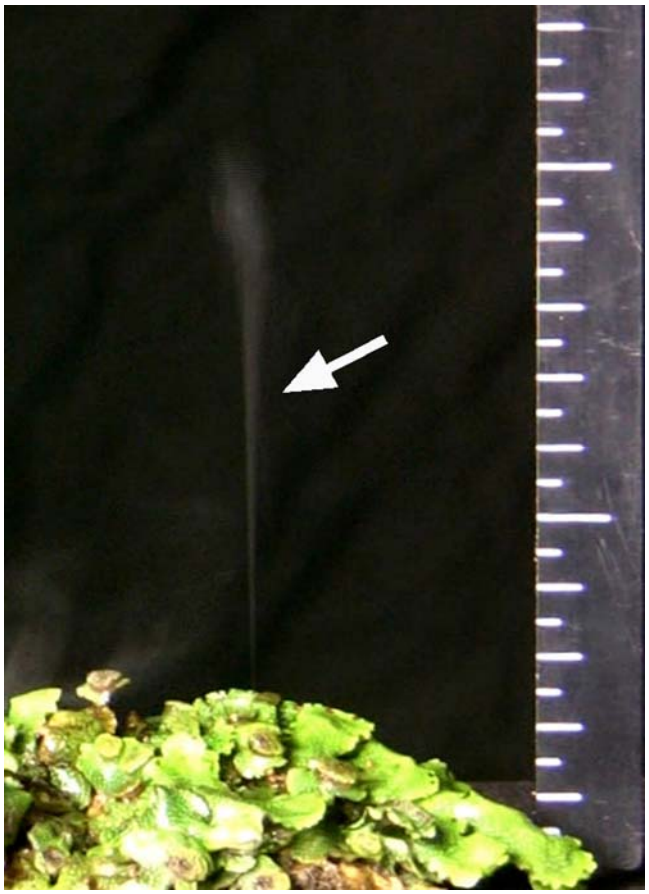

Figure 126. ***Conocephalum orientalis*** explosive sperm dispersal. Photo courtesy of Masaki Shimamura.

The archegonial heads begin growing near the growing tips (Figure 127). At maturity the archegonial heads are large and are perched on a stalk (Figure 128) up to 9 cm tall (Akiyama 2022).

Figure 127. ***Conocephalum orientalis*** with young archegoniophore. Photo courtesy of Hiroyuki Akiyama.

Figure 128. ***Conocephalum orientalis*** with mature archegoniophore. Photo courtesy of Hiroyuki Akiyama.

Conocephalum orientalis (Figure 97-Figure 100) produces spores that may be dispersed while small, or they may remain in the capsule, dividing into **endosporic** sporelings (Akiyama 2022). Spore germinability is 40-100% among the smaller spores. The remaining spores

divide within the spore walls (Figure 129) while still in the sporangium, thus increasing the number of chloroplasts. These larger spores lose their germinability within 30 days under room conditions (Inoue 1966 in Akiyama 2022). Such a two-size strategy permits immediate long distance dispersal of small spores, whereas the larger, short-lived spores have a size advantage that permits them to get a rapid start near the location of their parents. Spore sizes range 65-130 µm in longer diameter (Akiyama 2022).

Figure 129. ***Conocephalum conicum*** *s.l.* multicellular spores and elaters. Photo by Hugues Tinguy, with permission.

Conocephalum orientalis (Figure 97-Figure 100) has no known asexual reproductive structures (Akiyama 2022), but presumably it can reproduce by fragments. It is able to overwinter and produces bud scales (Figure 130-Figure 131) that protect the growing points. The thallus produces winter buds at the tip of the thallus in autumn, developing new shoots in the following spring. It can afford to lose some older cells, with other cells remaining viable, but cells that give rise to new tissue are few in number and vulnerable at the tip of the plant, so the bud scales help to protect them. These scales are absent in tropical populations, where the thallus grows throughout the winter, but a few populations in more northern locations of Japan also lack the buds, and these have been aligned with unique alleles (Isono *et al*. 1999; Akiyama 2022).

Figure 130. ***Conocephalum orientalis*** with young overwintering bud. Photo courtesy of Hiroyuki Akiyama.

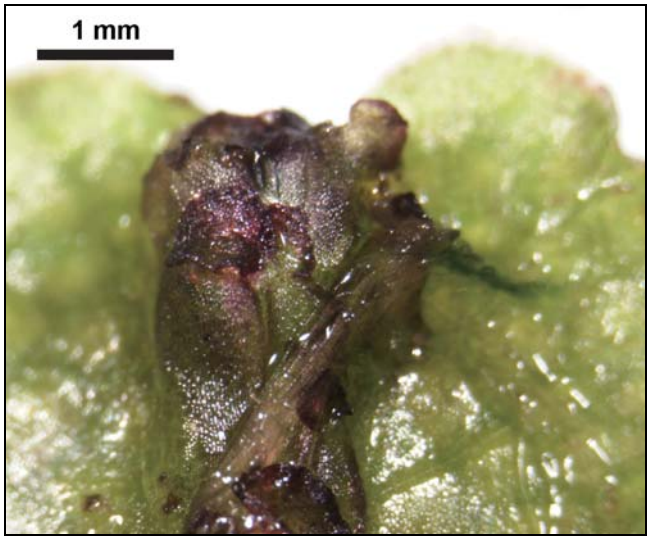

Figure 131. ***Conocephalum orientalis*** with overwintering bud. Photo courtesy of Hiroyuki Akiyama.

Biochemistry

Conocephalum orientalis (Figure 97-Figure 100) produces large amounts of methyl cinnamate, giving it a pleasant odor (Toyota *et al*. 1997; Toyota 2000; Ab Ghahi *et al*. 2016; Miyatake et al., 2018). It would be interesting to see if this compound has any role in discouraging herbivores.

Other biochemical studies on ***Conocephalum orientalis*** likely exist, but the task remains to link the studies with their current species concept.

Summary

Conocephalum conicum *s.l.* has recently been divided into multiple species in addition to several cryptospecies. Some studies indicate that ***Conocephalum*** *s.s.* does not exist in North America or Asia and is confined to Europe. This reconfiguration of the ***Conocephalum conicum*** complex has made it difficult to link many published studies with the modern species concepts.

Several of these newly defined species occur in wet habitats. ***Conocephalum conicum*** tends to be in wetter habitats than those of ***C. salebrosum***, a widespread species and possibly the only one in most of North America. Nevertheless, both of these species occur near water (streambanks, springs, splash of waterfalls, canyon walls) and can grow intermixed in Europe. ***Conocephalum conicum*** prefers shade and can grow in running water or on emergent rocks. It can also occur on slopes where it may get water from seepage.

Members of ***Conocephalum*** often occur in large mats or mixed with other bryophytes. They have scales and rhizoids on the ventral surface that aid in movement and uptake of water. Air pores have hydrophobic cuticular ridges that prevent water from entering to the internal air chambers through the pores. Rapid cooling kills the cells of ***C. conicum*** *s.l.*, but apical buds of members of the genus survive winter under the

protection of bud scales. Heat Shock Proteins help to protect the cells from heavy metals, where the latter can accumulate and serve as biomonitors.

Conocephalum conicum can experience **indirect facilitation** from other species, in some cases in which another species outcompetes a species that is a strong competitor to the ***C. conicum***.

Little is known about the tubers that grow among the rhizoids, but fragmentation occurs as new growth and branching occur and older parts die. Sexual reproduction is common. Gametangia of ***C. conicum*** *s.l.* are produced best at 21ºC in long days.

Conocephalum conicum *s.l.* is often infected by vesicular-arbuscular fungi and a species of ***Glomus***, but benefits and harmful effects need to be evaluated. The species does produce antifungal and antibacterial compounds, some of which could be used commercially.

There are ~25 East Asian micropterigid moths that occur exclusively on species of ***Conocephalum***.

Conocephalum orientalis is a newly described species from Japan that has deep grooves unlike those of ***C. conicum*** *s.s.* It is sometimes eaten in Japan, where it is the most common ***Conocephalum***, especially along streams. This species changes color with the seasons, becoming pale reddish purple in late autumn, and becoming dark green in the shade. It becomes succulent in good moisture conditions, but very thin in low light of caves.

Conocephalum orientalis expels its sperm explosively, presumably facilitating their dispersal to nearby female plants. Like other species of ***Conocephalum***, some spores are small and dispersed early, whereas others are larger due to **endosporic** development.

Acknowledgments

Bryonetters provided a wonderful array of images to illustrate this chapter. Thank you to Masaki Shimamura for providing me with the image of the explosive sperm dispersal in ***Conocephalum*** *cf.* ***orientalis***. And thank you to Hiroyuki Akiyama for sending me his 2022 paper on the new species in Japan and providing me with original images. I appreciate Guido Bursa's notification that one of my images was not the species indicated, and supplying me with a new, correct image.

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CHAPTER 1-21
AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: CONOCEPHALACEAE, PART 2

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CHAPTER 1-21
AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: CONOCEPHALACEAE, PART 2

Figure 1. ***Conocephalum*** *cf.* ***salebrosum*** at water's edge, Wahkeena Historical Preserve, Ohio, USA. Photo by Janice Glime.

Conocephalum purpureorubrum (Figure 2-Figure 14)

Conocephalum purpureorubrum (Figure 2-Figure 14) was previously designated as ***Conocephalum conicum*** F type (Akiyama 2022). The lower surface of the thallus is reddish purple (Figure 2-Figure 4) even in summer, although this coloration may be confined to the midrib (Figure 5). The upper surface of the thallus mat is yellowish green (Figure 6-Figure 9) in western Japan or slightly shiny and blackish green (Figure 10-Figure 11) in eastern Japan. Upper epidermal cells of thalli can have thin or thick walls. The grooves outlining the **areolae** (air chambers) are deep and distinct (Figure 12-Figure 13). These air chambers do not differ in size between the margins and central portions (Figure 14).

Figure 2. ***Conocephalum purpureorubrum*** from Japan, showing partially purple underside. Photo courtesy of Hiroyuki Akiyama.

Figure 3. ***Conocephalum purpureorubrum*** ventral side showing a large portion with purplish coloration. Photo courtesy of Hiroyuki Akiyama.

Figure 4. ***Conocephalum purpureorubrum*** from Toyama Prefecture, Japan, showing form with entire underside purplish in color. Photo courtesy of Hiroyuki Akiyama.

Figure 5. ***Conocephalum purpureorubrum*** ventral surface not purple except along midrib. Photo courtesy of Hiroyuki Akiyama.

Figure 6. ***Conocephalum purpureorubrum*** from Japan, showing thallus grooves and pores. Photo courtesy of Hiroyuki Akiyama.

Figure 7. ***Conocephalum purpureorubrum*** from Japan. Photo courtesy of Hiroyuki Akiyama.

Figure 8. ***Conocephalum purpureorubrum*** light form typical of western Japan. Photo courtesy of Hiroyuki Akiyama.

Figure 9. ***Conocephalum purpureorubrum*** pale form typical in western Japan. Photo courtesy of Hiroyuki Akiyama.

Figure 10. ***Conocephalum purpureorubrum*** showing dark green and blackish form typical of populations in eastern Japan. Photo courtesy of Hiroyuki Akiyama.

Figure 11. ***Conocephalum purpureorubrum*** showing dark thalli mixed with lighter ones. Photo courtesy of Hiroyuki Akiyama.

Figure 12. ***Conocephalum purpureorubrum*** from Japan, showing distinct polygons formed by thallus grooves and yellowish green color typical of populations in western Japan. Photo courtesy of Hiroyuki Akiyama.

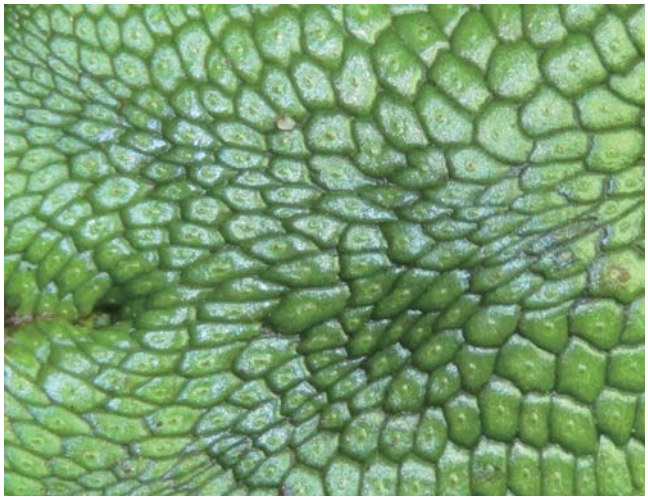

Figure 13. ***Conocephalum purpureorubrum*** from Japan, showing thallus grooves and pores. Photo courtesy of Hiroyuki Akiyama.

Figure 14. ***Conocephalum purpureorubrum*** from Japan, showing pores and distinct thallus grooves. Photo courtesy of Hiroyuki Akiyama.

Distribution

Conocephalum purpureorubrum (Figure 2-Figure 14) is known from southern China, South Korea, Taiwan, and Japan (Akiyama 2022).

Aquatic and Wet Habitats

Conocephalum purpureorubrum (Figure 2-Figure 14) can grow in drier habitats than those of ***C. orientalis*** (Figure 15), but it can also grow intermixed with that species (Figure 16). It occurs at some waterfall sites. It tends to grow in more humid habitats when it grows with ***C. salebrosum*** (Figure 1, Figure 30-Figure 49) (Akiyama 2022), a behavior suggesting possible **indirect facilitation** as discussed in the previous subchapter under ***C. conicum*** (Figure 17). It is also possible that these behavioral differences in habitat preference relate to differences in genetic races (see Akiyama & Hiraoka 1994).

Figure 17. ***Conocephalum conicum*** from Scotland, with distinct thallus grooves. Photo courtesy of David Long.

Figure 15. ***Conocephalum orientalis*** type J2 with wavy margin. Photo courtesy of Hiroyuki Akiyama.

Figure 16. ***Conocephalum purpureorubrum*** (**FW**) and ***C. orientalis*** (**J**) growing intermixed in Japan. Photo courtesy of Hiroyumi Akiyama.

Non-Aquatic

The eastern populations of ***Conocephalum purpureorubrum*** (Figure 2-Figure 14) usually occur on soil of valley slopes where they are far from water (Figure 18), but they can sometimes grow along streams (Akiyama 2022).

Figure 18. ***Conocephalum purpureorubrum*** from Mt. Takao, Japan, showing terrestrial habitat. Photo courtesy of Hiroyuki Akiyama.

Physiology

Plants of ***Conocephalum purpureorubrum*** (Figure 2-Figure 14) tend to be thick and pale in sunny conditions (Figure 19) and thin and dark in shaded conditions (Figure 20) (Akiyama 2022). The reddish ventral condition seems to persist all year, but does its intensity relate to low light? In some flowering plants on tropical forest floors this ventral purplish coloring helps in the back-scattering of sunlight to the photosynthetic tissue (Lee *et al*. 1979). Such a role has not been explored in bryophytes. It seems likely that it would mostly work in liverworts among the bryophytes because they have a dorsiventral orientation.

Figure 19. ***Conocephalum purpureorubrum*** pale form typical of populations in western Japan. Photo courtesy of Hiroyuki Akiyama.

Figure 20. ***Conocephalum purpureorubrum*** from Japan, showing dark form typical of shade, with deep thallus grooves. Photo courtesy of Hiroyuki Akiyama.

Rhizoids are abundant on the ventral surface of ***Conocephalum purpureorubrum*** (Figure 21-Figure 23) (Akiyama 2022). These undoubtedly facilitate the movement and uptake of water into the thallus.

Figure 21. ***Conocephalum purpureorubrum*** showing rhizoids along the midrib. Photo courtesy of Hiroyuki Akiyama.

Figure 22. ***Conocephalum purpureorubrum*** showing numerous rhizoids. Photo courtesy of Hiroyuki Akiyama.

Figure 23. ***Conocephalum purpureorubrum*** showing numerous rhizoids. Photo courtesy of Hiroyuki Akiyama.

Conocephalum purpureorubrum (Figure 2-Figure 14) may have mucilage canals (Figure 24), but mucilage cells are often absent (Akiyama 2022). The mucilage may help to keep the cells moist, but experiments are needed to verify this. They are often absent in populations in dry habitats.

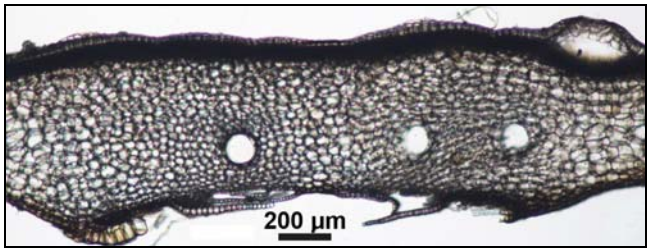

Figure 24. ***Conocephalum purpureorubrum*** from Japan, showing mucilage canals. Photo courtesy of Hiroyuki Akiyama.

Reproduction

Conocephalum purpureorubrum (Figure 2-Figure 14), like other species of ***Conocephalum***, is **dioicous**. The antheridial receptacles form at the apex of the male thallus (Figure 25-Figure 26). Bud scales can often be seen at their margins (Figure 25).

Figure 25. ***Conocephalum purpureorubrum*** young antheridial receptacle. Note the remaining reddish brown bud scales. Photo courtesy of Hiroyuki Akiyama.

Figure 26. ***Conocephalum purpureorubrum*** young antheridial receptacle. Photo courtesy of Hiroyuki Akiyama.

Female plants of ***Conocephalum purpureorubrum*** (Figure 2-Figure 14) form archegoniophores at the apex of the female plants (Figure 27-Figure 28). When sporangia mature, the stalks elongate to 3-6 cm with bluntly conical archegonial heads (Figure 28-Figure 29). The sporangia hang down from the archegonial heads.

Figure 27. ***Conocephalum purpureorubrum*** with young archegoniophore. Photo courtesy of Hiroyuki Akiyama.

Figure 28. ***Conocephalum purpureorubrum*** with young archegoniophores beginning to elongate. Note that the black sporangia are already visible. Photo courtesy of Hiroyuki Akiyama.

Figure 29. ***Conocephalum purpureorubrum*** with mature archegoniophores and sporangia. Photo courtesy of Hiroyuki Akiyama.

Biochemistry

Biochemical analysis may reveal some interesting compounds in ***Conocephalum purpureorubrum*** (Figure 2-

Figure 14). This species has a fresh, earthy odor, usually not a mushroom odor (Akiyama 2022).

Conocephalum salebrosum (Figure 1, Figure 30-Figure 49)

Conocephalum salebrosum (Figure 1, Figure 30-Figure 49) is a relatively recently described species and is a segregate of ***Conocephalum conicum*** (Figure 17) (Szweykowski *et al*. 2005). It appears that many of the North American records of ***Conocephalum conicum*** should be placed here (Stotler & Crandall-Stotler 2017), with populations in California (Figure 50) being potential exceptions (see Shevock *et al*. 2021). The latter, for now, are best designated as ***Conocephalum conicum*** *s.l.*

In Europe, the distinction of the species in older literature is not so simple, if even possible without checking voucher specimens. Both species occur there. For example, Poponessi *et al*. (2014) have reported ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) from Italy. Sérgio *et al*. (2011) reported it from Portugal and Madeira and Azores Islands. Other records are documented in Figure 30-Figure 36. Figure 37 shows the similarities of a British Columbia, Canada, population to ***Conocephalum salebrosum***.

Figure 30. ***Conocephalum salebrosum*** from Europe, showing distinct thallus grooves. Photo courtesy of Michael Lüth.

Figure 31. ***Conocephalum salebrosum*** showing distinct thallus divisions. Photo by Jouko Rikkinen, through Creative Commons.

Figure 32. ***Conocephalum salebrosum*** showing thallus section grooves, in Wales. Photo courtesy of Jonathan Sleath.

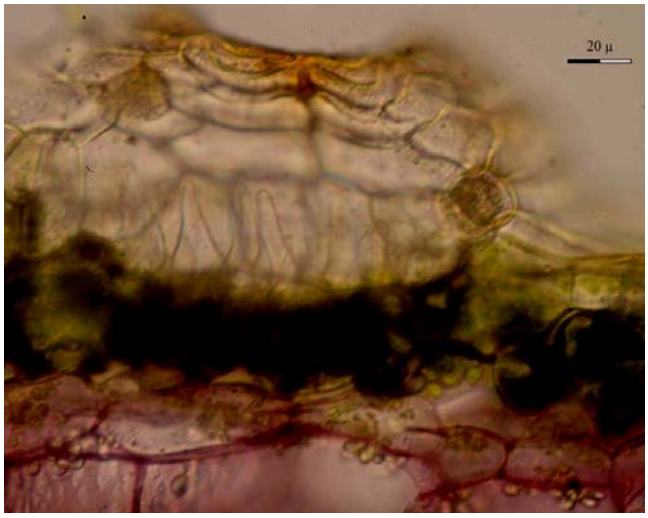

Figure 33. ***Conocephalum salebrosum*** from Corsavy, France, showing pore section. Photo courtesy of Louis Thouvenot.

Figure 34. ***Conocephalum salebrosum*** from Europe, showing pore section. Photo by Norbert J. Stapper, with permission.

Figure 35. ***Conocephalum salebrosum*** from Corsavy, France, showing thallus margin section. Photo courtesy of Louis Thouvenot.

Figure 36. ***Conocephalum salebrosum*** from Wales, showing distinct section grooves. Photo courtesy of Jonathan Sleath.

Figure 37. ***Conocephalum conicum*** *s.l.* showing distinct thallus grooves and less distinct pores. These thallus grooves of a western North American population fit more closely with those of ***C. salebrosum***. Photo from Botany Website, UBC, with permission.

Distribution

The distribution of ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) remains sketchy because of the long treatment of the species as part of ***Conocephalum conicum*** (Figure 17) (Szweykowski *et al*. 2005). It is definitely known from North America (Figure 38-Figure 41), but can also be found in Europe (Figure 42-Figure 43) (*e.g.* Tacchi *et al*. 2009) and eastern Asia (Figure 44-Figure 49) (Sérgio *et al*. 2011). Sérgio and coworkers consider it to be Holarctic.

Figure 38. ***Conocephalum*** *cf.* ***salebrosum*** habitat in Quebec, Canada. Photo by Martine Lapointe, with permission.

Figure 39. ***Conocephalum salebrosum*** in New York, USA. Photo courtesy of Jerry Jenkins.

Figure 40. ***Conocephalum*** *cf.* ***salebrosum*** from Ohio, USA. Photo by Bob Klips, with permission.

Figure 41. ***Conocephalum*** *cf.* ***salebrosum***, Grand Ledge Park, Michigan, USA. Photo by Janice Glime.

Figure 42. ***Conocephalum salebrosum*** from the UK. Photo by Barry Stewart, with permission.

Figure 43. ***Conocephalum salebrosum*** from Chauderon, France. Photo courtesy of David Long.

Figure 44. ***Conocephalum salebrosum*** in Yunnan, China. Photo by David Long, with permission.

Figure 45. ***Conocephalum salebrosum*** from Sichuan, China. Photo courtesy of David Long.

Figure 46. ***Conocephalum salebrosum*** from Japan. Photo courtesy of Hiroyuki Akiyama.

Figure 47. ***Conocephalum*** males, Mt. Hiei, Japan. The prominent thallus grooves suggest this is now in the species ***Conocephalum salebrosum***. The thallus sections do not get larger in the center of the thallus, as they do in ***Conocephalum orientalis***. Photo by Janice Glime.

Figure 48. ***Conocephalum salebrosum*** thallus from Japan, showing grooves and pores. Photo courtesy of Hiroyuki Akiyama.

Figure 49. ***Conocephalum salebrosum*** thallus from Japan, showing pores and distinct grooves. Photo courtesy of Hiroyuki Akiyama.

Populations in California (Figure 50), however, are similar, but not identical, to ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) (Shevock *et al*. 2021).

Figure 50. **Conocephalum conicum** *s.l.* from California, USA. Photo by R. L. Fleming, Jr., courtesy of David Wagner.

Aquatic and Wet Habitats

Conocephalum, presumably ***C. salebrosum*** (Figure 1, Figure 30-Figure 49), occurs on wet, sandy streambanks and on moist rock surfaces (Figure 51-Figure 53) or springy banks of ravines in Connecticut, USA (Nichols 1916). On Cape Breton Island, Canada it also occurs on streambanks (Nichols 1918).

Figure 51. ***Conocephalum cf. salebrosum*** with archegoniophores on canyon wall at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 52. ***Conocephalum cf. salebrosum*** at Scott Falls, Michigan, USA. Photo by Janice Glime.

Figure 53. ***Conocephalum*** *cf.* ***salebrosum*** habitat in Quebec, Canada. Photo by Martine Lapointe, with permission.

Figure 54. ***Conocephalum*** *cf.* ***salebrosum*** on canyon wall at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Conocephalum salebrosum (Figure 1, Figure 30-Figure 49) can be found along stream banks in the Appalachian Mountain, USA, streams (Glime 1968). In another humid environment, it is known from the base of the Flume wall and ledges in the flume at Franconia Notch, New Hampshire, USA (Glime 1982). It is likely the species that is a restricted terrestrial species in montane streams and on streambanks in western Canada (Vitt *et al.* 1986; Glime & Vitt 1987). It seems to avoid the submersion that is common for ***C. conicum*** (Figure 17).

Stephenson *et al*. (1995) reported its preferred *p*H as 7.9 in West Virginia, USA, mountain streams. Sérgio *et al*. (2011) considered ***Conocephalum conicum*** (Figure 17) to be less hygrophytic than ***C. salebrosum*** (Figure 1, Figure 30-Figure 49), being more tolerant of desiccation and preferring limestone areas.

Figure 55. ***Conocephalum*** *cf.* ***salebrosum*** habitat near top of canyon at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Stream and River Banks

In North America, Porter (1933) reported ***Conocephalum*** (now probably ***C. salebrosum*** – Figure 1, Figure 30-Figure 49) from shady streambanks on soil in Wyoming, USA. Little (1936) described its habitat as constantly moist, shaded rock outcrops within a few feet of water in Oklahoma, USA. There it is one of the commonest species on moist, shaded bases of walls near water, occurring on both sandstone and limestone, as well as chert bluffs near water and especially in canyons and by springs.

In Europe, Tacchi *et al*. (2009) found it in ravines in the Apennines of Italy. Antkowiak *et al*. (2008) reported ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) synusia overgrowing high escarpments below the headstream at the River Kamionka in eastern Poland. Borovichev *et al*. (2009) found that ***C. salebrosum*** formed extensive mats on stream banks as well as on the bases of moist rocks and cliffs.

Figure 56. ***Conocephalum*** *cf.* ***salebrosum*** on canyon wall at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Canyon Walls

I have found ***Conocephalum*** *cf.* ***salebrosum*** (Figure 1, Figure 30-Figure 49) in extensive mats on canyon walls (Figure 54-Figure 67). These canyons were sandstone and humid.

Figure 57. ***Conocephalum cf. salebrosum*** on canyon walls Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 58. ***Conocephalum cf. salebrosum*** between ledges in damp canyon wall, Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 59. ***Conocephalum cf. salebrosum*** on canyon walls at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 60. ***Conocephalum cf. salebrosum*** and ferns on canyon walls at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 61. ***Conocephalum cf. salebrosum*** and ferns on canyon walls at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 62. ***Conocephalum cf. salebrosum*** and ferns on canyon walls at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 63. ***Conocephalum*** *cf.* ***salebrosum*** on canyon walls at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 64. ***Conocephalum*** *cf.* ***salebrosum*** new growth in rock shadow in the canyon at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 65. ***Conocephalum*** *cf.* ***salebrosum*** with new growth on canyon walls, Hocking Hills, Ohio, USA, on 26 April 2015. Photo by Janice Glime.

Figure 66. ***Conocephalum*** *cf.* ***salebrosum*** new growth at apices of old thalli on canyon walls, Hocking Hills, Ohio, USA, on 26 April 2015. Photo by Janice Glime.

Figure 67. ***Conocephalum*** *cf.* ***salebrosum*** young plants on canyon wall at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Floodplains

Because of its need for high humidity and tolerance of submersion, ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) commonly occurs in floodplains of streams and rivers (Figure 69-Figure 68), including periodically flooded bases of canyons (Figure 70-Figure 71).

Figure 68. ***Conocephalum*** *cf.* ***salebrosum***, floodplain, Rose Lake, Michigan, USA, where the products of sexual reproduction are readily visible (8 May). Photo by Janice Glime.

Figure 69. ***Conocephalum cf. salebrosum***, growing on floodplain, Rose Lake, Michigan, USA. Photo by Janice Glime.

Figure 70. ***Conocephalum cf. salebrosum*** on mud in the canyon at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 71. ***Conocephalum cf. salebrosum*** at base of canyon rock where it is flooded during high water, Hocking Hills, Ohio, USA. Photo by Janice Glime.

Waterfalls

Among its moist habitats, ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) can form large, dense patches on dripping rocks and wet soil where it is in close contact with water (Sérgio *et al*. 2011), including those areas wet by the splash of waterfalls (Figure 72) (personal observation).

Figure 72. ***Conocephalum cf. salebrosum*** beside Hungarian Falls at Tamarack City, Michigan, USA. Photo by Janice Glime.

Conocephalum salebrosum (Figure 1, Figure 30-Figure 49) was locally abundant at the entrance to Grotta degli Innamorati in central Italy at the Marmore Waterfalls Regional Park (Poponessi *et al*. 2020). I have seen the species in several locations in Michigan, USA, growing on a rock wall behind a waterfall (Figure 73).

Figure 73. ***Conocephalum salebrosum*** behind waterfall at Scott Cave, Michigan, USA. Photo by Janice Glime.

Non-Aquatic Habitats

Akiyama (2022) considered rather dry habitats (Figure 74) to be included among those of ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49). This fits with my own experience in North America. Other somewhat dry habitats are shown in Figure 75-Figure 79.

Figure 74. ***Conocephalum salebrosum*** from Japan, on limestone boulder. Photo courtesy of Hiroyuki Akiyama.

Figure 75. ***Conocephalum salebrosum*** from Japan, on limestone boulder. Photo courtesy of Hiroyuki Akiyama.

Figure 76. ***Conocephalum salebrosum*** from Japan, dry on thin soil on boulder. Photo courtesy of Hiroyuki Akiyama.

Figure 77. ***Conocephalum salebrosum*** from Japan, on moist limestone soil. Photo courtesy of Hiroyuki Akiyama.

Figure 78. ***Conocephalum salebrosum*** from Japan, on rock. Photo courtesy of Hiroyuki Akiyama.

Figure 79. ***Conocephalum salebrosum*** from Japan, small plants from moist, shaded site. Photo courtesy of Hiroyuki Akiyama.

Physiology

McConaha (1939) determined that the water absorption of ***Conocephalum salebrosum*** is limited to the ventral appendages, which are restricted to the underside of the midrib (Figure 80). The scales (Figure 80) increase the surface area by ~380% and the rhizoids (Figure 80-Figure 83) increase it by 5100%. The rhizoid strands and scales create an extensive capillary system (that is able to move water ventrally along the entire length of the thallus.

Figure 80. ***Conocephalum salebrosum*** showing rhizoids and scales that move water along ventral surfaces by capillarity. Photo by Jouko Rikkinen, through Creative Commons.

Figure 81. ***Conocephalum salebrosum*** from Japan showing rhizoids and purplish coloring restricted to the midrib. Photo courtesy of Hiroyuki Akiyama.

Figure 82. ***Conocephalum salebrosum*** from Japan showing rhizoids and purplish color extending beyond midrib. Photo courtesy of Hiroyuki Akiyama.

Figure 83. ***Conocephalum conicum*** *s.l.* showing **pegged** (**upper**) and **smooth** (**lower**) rhizoids. Photo from Botany Website, UBC, with permission.

Schott *et al*. (2021) found that ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) from west Germany had ice-nucleating proteins that differed in ice-nucleating temperature and seasonal concentration from those of ***Marchantia polymorpha*** subsp. ***ruderalis*** (Figure 84). Ice formed in the air chambers of both species, and crystals grew out of the air chamber pores (Figure 85). Crystals also formed in various locations on the ventral side of the thallus. This crystal formation resulted in dehydration of the thallus cells and permitted survival of low temperatures and frost (Figure 86). Presumably, this is a means of preventing crystal formation within the cells where it can damage membranes.

Figure 84. ***Marchantia polymorpha*** subsp. ***ruderalis***. Photo by Michel Langeveld, through Creative Commons.

Figure 85. ***Conocephalum*** *cf.* ***salebrosum*** with ice crystals emanating from the thallus. Photo by Allen Norcross, with permission.

Figure 86. ***Conocephalum salebrosum*** and icicles, showing a habitat where it is able to survive the cold of winter with its ice-nucleating proteins, but without sudden cooling. Photo by Allen Norcross, with permission

Adaptations

Although no specific adaptations have been attributed to ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49), it is likely that many are similar to those of ***Conocephalum conicum*** (Figure 17). However, ***C. salebrosum*** does have more conspicuous pores (Akiyama 2022) that could be an advantage is gas exchange and hence, photosynthesis.

Conocephalum salebrosum (Figure 87-Figure 88) from Japan has more mucilage canals and mucilage cells than most other members of the ***Conocephalum conicum*** complex there (Akiyama 2022). These most likely help it to conserve moisture in its drier habitats.

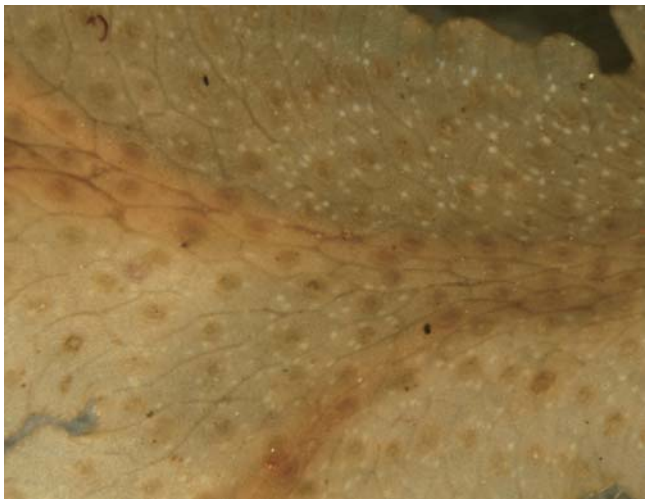

Figure 87. ***Conocephalum salebrosum*** from Japan, showing mucilage cells and canals. Photo courtesy of Hiroyuki Akiyama.

Figure 88. ***Conocephalum salebrosum*** from Japan, showing mucilage cells and canals in thallus cross section. Photo courtesy of Hiroyuki Akiyama.

In addition to its rhizoids and scales (Figure 80-Figure 83) for water movement and uptake, ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) often occurs in large mats (Figure 1) or mixed with other bryophytes (Figure 89-Figure 90) (Akiyama 2022). These closely intermingled plants can help to maintain moisture on the lower side of the plant where uptake occurs.

Figure 89. ***Conocephalum*** *cf.* ***salebrosum*** in Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 90. ***Conocephalum cf. salebrosum***, ***Mnium hornum***, and ***Atrichum undulatum***. Photo by Bob Klips, with permission.

Reproduction

Showalter (1921) determined that the male and female chromosomes of ***Conocephalum cf. salebrosum*** (Figure 1, Figure 30-Figure 49) in Wisconsin and New York, USA, and in Copenhagen, Denmark, did not differ as they do in some **dioicous** liverworts, but that 1 of the 9 chromosomes was considerably smaller, a condition that apparently led to some earlier researchers finding only 8.

Antheridia in ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) are borne in receptacles on the thallus surface (Figure 91-Figure 94) and apparently not elevated by an elongated midrib as they are in ***C. orientalis*** (Figure 15) (see Conocephalaceae part 1 subchapter).

Figure 91. ***Conocephalum cf. salebrosum*** males. Photo by John Hribljan, with permission

Figure 92. ***Conocephalum salebrosum*** males from Canada. Photo by Jean Faubert, with permission.

Figure 93. ***Conocephalum salebrosum*** antheridial receptacle with bud scales at edge. Photo courtesy of Hiroyuki Akiyama.

Figure 94. ***Conocephalum salebrosum*** antheridial receptacle from Japan. Photo courtesy of Hiroyuki Akiyama.

Graham (1909) described the development of both the gametophyte and sporophyte of ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49). In New York, USA, the gametangiophore (Figure 95-Figure 105) begins development early in June. Archegonia are mature by the first of July. The development of the sporangia (Figure 104-Figure 105) is rather slow, with spores and elaters

maturing by the onset of winter. At that time, growth ceases. The stalk of the gametangiophore is still very short, with the conical head appearing to be sessile on the thallus. In the warmth of the following May, this archegoniophore elongates rapidly, lifting the receptacle well above the thallus surface (Figure 100-Figure 103). When the stalk of the sporangium elongates, the spores are released when the capsule ruptures. A surrounding sheath may protect the overwintering capsule from excessive radiation and transpiration.

Figure 95. ***Conocephalum salebrosum*** from Japan, with beginning of archegoniophore. Photo courtesy of Hiroyuki Akiyama.

Figure 96. ***Conocephalum salebrosum*** with young archegoniophore. Photo by Jouko Rikkinen, through Creative Commons.

Figure 97. ***Conocephalum salebrosum*** with beginning archegoniophore, from Pfälzer Wald, Germany. Photo courtesy of Michael Lüth.

Figure 98. ***Conocephalum*** *cf.* ***salebrosum*** developing archegoniophore. Photo from Botany Website, UBC, with permission.

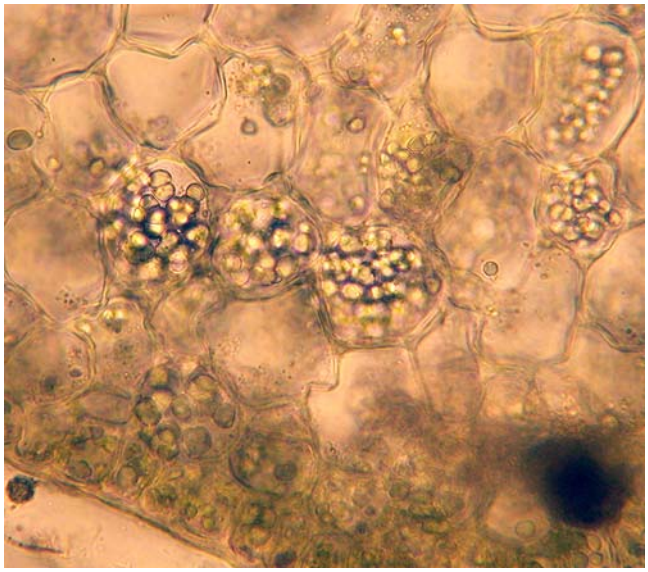

Figure 99. ***Conocephalum salebrosum*** archegoniophore stalk cs showing starch grains. Photo from Botany Website, UBC, with permission.

Figure 100. ***Conocephalum cf. salebrosum*** with elongating archegoniophores, floodplain, Rose Lake, Michigan, USA. Photo by Janice Glime.

Figure 101. ***Conocephalum salebrosum*** with mature archegoniophores, in Merthyr Tidfil, Wales. Photo by Des Callahan, with permission.

Figure 102. ***Conocephalum c.f. salebrosum*** with archegoniophores on canyon wall, Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 103. ***Conocephalum cf. salebrosum*** with mature archegoniophores. Photo from Botany Website, UBC, with permission.

Figure 104. ***Conocephalum salebrosum*** archegoniophores with capsules.. Photo by Hermann Schachner through Wikimedia Commons.

Figure 105. ***Conocephalum salebrosum*** archegonial receptacle showing black sporangia, from Europe. Photo by Barry Stewart, with permission.

Taylor and Hollensen (1984) elaborated on this cycle for plants of ***Conocephalum cf. salebrosum*** (Figure 1, Figure 30-Figure 49) in Michigan, USA. Growth is initiated in March. The full reproductive cycle requires 21 months. Archegonia are initiated in August and fertilized the following June. The sporophyte matures in that autumn and spores are shed in the next spring. The thalli are under snow and dormant from December through February.

Ellen (1920) described the germination of the spores of ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) in Sinsinawa, Wisconsin, USA. Here, the spore mother cells are well developed before the beginning of September and the spores are freed from the mother cell walls about mid September. In Early October, growth and a heavy deposit of starch precede the cell division. Each sporeling has up to eight cells that remain in the spore wall (Figure 106). Before winter, the partition cell walls thicken, starch is deposited, and growth occurs by division of the spores. These multicellular sporelings remain through the winter. When warm weather returns, cell division resumes and continues until the stored food is gone. Cell division pauses and the cells expand, accompanied by a rapid development of chlorophyll and starch. This is followed by a second series of cell divisions until the sporelings become a spherical mass of 30-40 cells. As this mass matures, the archegoniophore elongates rapidly in 4-5 days to attain a height of 5-6 cm. At the same time, the seta on each capsule elongates and the capsule emerges through the calyptra and sheath. The capsule wall ruptures and sporelings and elaters are dispersed. Most of the sporelings are short-lived, but some survive up to 38 days of desiccation.

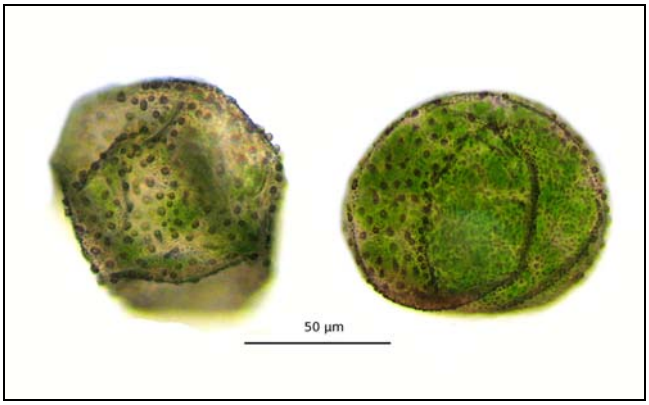

Figure 106. ***Conocephalum salebrosum*** multicellular spores resulting from endosporic development. Photo courtesy of Leica Chavoutier.

It appears that some spores of ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) might be dispersed while they are still small – one-celled (Ellen 1920). This strategy of multicellular spore spheres (sporelings) and single-celled spores would permit achieving a good start in the nearby habitat by dispersed spheres while permitting long-distance dispersal of the one-celled spores.

At the end of the growing season, apical buds form and older portions become moribund (Figure 107). In the spring, these buds expand and develop new plants (Figure 107-Figure 114), increasing the area covered due to branching.

Figure 107. ***Conocephalum salebrosum*** dead (moribund) and new growth at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 108. ***Conocephalum cf. salebrosum*** showing new growth at tips of older thalli, from Europe. Photo by Michael Lüth, with permission.

Figure 109. ***Conocephalum cf. salebrosum*** showing new growth and moribund older thalli, from Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 110. ***Conocephalum cf. salebrosum*** new growth, from Hocking Hills, Ohio, USA. Photo by Janice Glime.

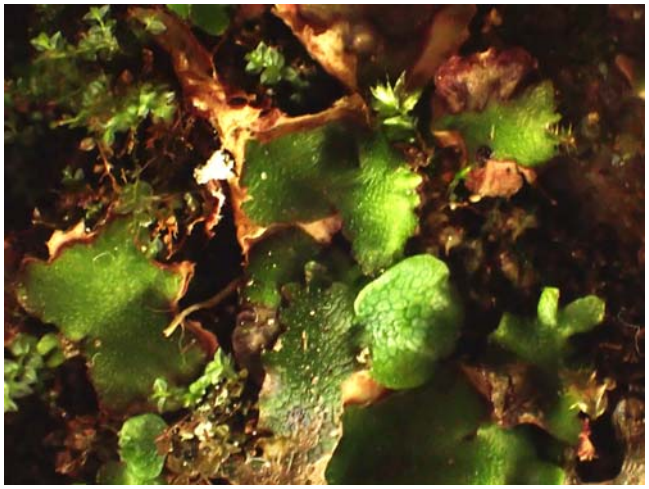

Figure 111. ***Conocephalum cf. salebrosum*** new growth on canyon walls, Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 112. ***Conocephalum cf. salebrosum*** new growth on canyon walls at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 113. ***Conocephalum cf. salebrosum*** new growth and dead thalli at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 114. ***Conocephalum salebrosum*** dead with new growth at Hocking Hills, Ohio, USA, Photo by Janice Glime.

By whatever mechanism, when ***Conocephalum cf. salebrosum*** (Figure 1, Figure 30-Figure 49) was growing in my garden room, it managed to appear in new locations around the room. It never had sexual structures. I attributed its dispersal to the movement of my box turtle, but I have no real proof. Unfortunately, I never caught anybody in the act.

Ainsworth (1965) reported bulbils in ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) from New York, USA, that had been kept in the dark for 28 days. These occur anywhere on the ventral surface, but when the midrib has bulbils still attached, these seem to inhibit the production of bulbils elsewhere on the thallus. An average of ~1.3 bulbils can occur in 1 mm² of thallus. This is not the first report of these structures. Karsten (1887) found them on thalli of ***Conocephalum conicum*** *s.l.* (Figure 17) that had been so completely overgrown by other thalli that they too, were in complete darkness.

These "bulbils" have been somewhat controversial. Paton (1993) referred to the tubers of ***Conocephalum conicum*** *s.l* (Figure 17). that occur on the ventral surface of the midrib and become detached to form new plants, as described by MacVicar (1926) and again by Paton from Sussex, England. These likewise occurred on moribund

thalli (Figure 107). Paton noted that these dark-produced structures, termed bulbils by Ainsworth (1965), germinated in ~5 days when placed in moist conditions in the light.

Animal Interactions

When growing in my garden room, ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) had nibbles around its edges. These were triangular and best fit the hypothesis that they were eaten by the Society Finches or the Canary in the room.

In the field I have found evidence of herbivory, but in these cases the removal was not triangular. Instead, it occurred not only on the margins but also mid thallus and the eaten areas were of irregular shape (Figure 115-Figure 117). These could be the product of insects, isopods, or possibly snails.

Figure 115. ***Conocephalum salebrosum*** herbivory in the Upper Peninsula of Michigan. Photo courtesy of John Hribljan.

Figure 116. ***Conocephalum*** *cf.* ***salebrosum*** eaten in Houghton County, Michigan, USA, 6 August 2009. Photo by Janice Glime.

Figure 117. ***Conocephalum*** *cf.* ***salebrosum*** eaten in Houghton County, Michigan, USA. Nibbling on the edges suggests a large arthropod, perhaps an isopod. Photo by Janice Glime.

Fungal Interactions

Liepiņa (2012) reported that both ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49) and ***C. conicum*** (Figure 17) were "moderately" mycorrhizal. Both liverworts have Glomeromycotean endophytes and these fungi form nonseptate hyphae, vesicles, and arbuscules (see Figure 118), indicating that they created a functional symbiosis with the liverworts. The hyphae entered through the rhizoids and passed directly through the cell walls of the liverworts.

Figure 118. **Vesicular arbuscular mycorrhizae** in root cells, showing the form that might also show up in the thallus of ***Conocephalum salebrosum***. Photo by Rit Rajarshi, through Creative Commons.

Biochemistry

It is likely that some of the biochemical work attributed to ***Conocephalum conicum*** (Figure 17) actually applies to ***C. salebrosum*** (Figure 1, Figure 30-Figure 49), but unless it is recent or in North America, voucher specimens from the study would need to be verified. Even then, since the two liverworts grow together, the assays might have included both species without having both represented in the voucher specimens.

Craft *et al*. (2016) attempted to demonstrate chemotypes in the ***Conocephalum*** complex in the southern Appalachian Mountains, USA. They used a common garden experiment, but found that the experiment became a common stress experiment that significantly altered the compositions of volatile compounds in ***Conocephalum salebrosum*** (Figure 1, Figure 30-Figure 49). This phenomenon might provide antiherbivory compounds in response to herbivory, as already known from tree leaves (see, for example, Moreira *et al*. 2012). It would also be interesting to know the cost of producing such compounds relative to the cost of herbivory.

Summary

When chemical and genetic analyses were done on the ***Conocephalum conicum*** complex, the researchers decided that division into multiple species was warranted. From that division, ***C. salebrosum*** was identified and determined to be holarctic, seemingly replacing what was known as ***C. conicum*** in North America. Then, in 2022, several Japanese species were segregated from ***C. conicum***, including ***C. purpureorubrum***.

Ecological information on ***Conocephalum purpureorubrum*** is scant due to its recent consideration as a different species. It occurs in both damp habitats and dry ones, sometimes occurring streamside or on steep slopes. Its life cycle seems to be the same as that of ***C. conicum***, with no asexual structures known. It is unusual in always having at least some purplish color present on the ventral surface. It has mucilage canals, but it often lacks mucilage cells.

Conocephalum salebrosum occurs near water, but extends into drier habitats than those typical of ***C. conicum***. Most of the North American populations may belong to this species, often occurring on rock in canyons, near waterfalls, and along stream margins. Scales and rhizoids facilitate water movement and uptake along the ventral surface. The species can suffer from herbivory, but it contains compounds that are potentially antiherbivorous. It also frequently has vesicular arbuscular mycorrhizae.

Acknowledgments

Bryonetters provided a wonderful array of images to illustrate this chapter. Thank you to Masaki Shimamura for providing me with the image of the explosive sperm dispersal in ***Conocephalum*** *cf*. ***orientalis***. And thank you to Hiroyuki Akiyama for sending me his 2022 paper on the new species in Japan and providing me with original images.

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CHAPTER 1-22
AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: CYATHODIACEAE, DUMORTIERACEAE

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CHAPTER 1-22
AQUATIC AND WETLAND MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA – CYATHODIACEAE, DUMORTIERACEAE

Figure 1. ***Dumortiera hirsuta*** habitat in Europe. Photo by Michael Lüth, with permission

Marchantiidae – Marchantiales

Cyathodiaceae

There have been several taxonomic considerations of the genus ***Cyathodium*** (Schiffner 1938; Srivastava & Dixit 1996; Salazar Allen & Korpelainen 2006).

This family often occurs in moist habitats such as caves and stream banks. ***Cyathodium*** habitats are typically shaded and include river banks on soil or rocks, in waterfalls, caves, cement floors, stairs, and flowerpots, with some occurring as epiphytes (Salazar Allen & Korpelainen 2006). Large communities can occur on unstable river banks where they can become submerged and sometimes become detached by flooding or drying. They are often associated with filamentous **Cyanobacteria** (Figure 32), but these are not endophytic. Endophytic fungi are known from wild populations of ***C. spruceanum*** (Figure 2) and ***C. cavernarum*** (Figure 3) in Panama (Salazar Allen unpublished data). Riverbank plants often provide substrate for diatoms, including ***Surirella*** (Figure 4), ***Nitzschia*** (Figure 5), ***Amphora*** (Figure 6), ***Rhopalodia*** (Figure 7), ***Eunotia*** (Figure 8), and possibly ***Diploneis*** (Figure 9) (Allen & Korpelainen 2006). The most aquatic of ***Cyathodium*** species is ***Cyathodium bischlerianum*** (Figure 10).

Figure 2. ***Cyathodium spruceanum*** males. Photo by José Gudiño L., courtesy of Noris Salazar Allen.

Figure 3. ***Cyathodium cavernarum***, a species that grows on river and streambanks with ***Cyathodium bischlerianum***. Photo by Renjusplace, through Creative Commons.

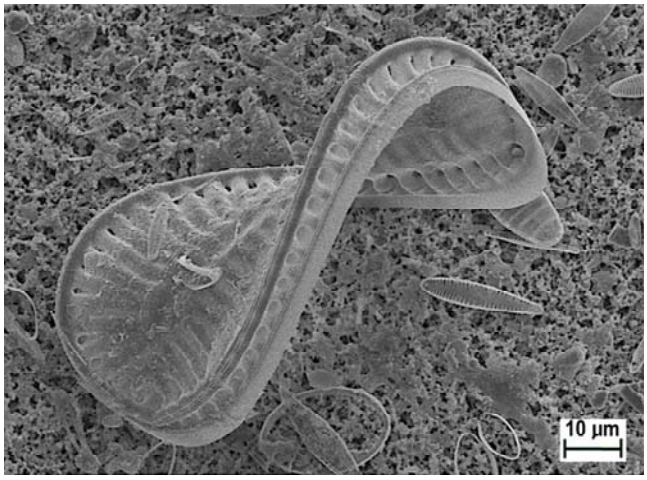

Figure 4. ***Surirella spiralis***, in a genus of diatoms that often grows on species of ***Cyathodium***. Photo by Nicola Angeli, through Creative Commons.

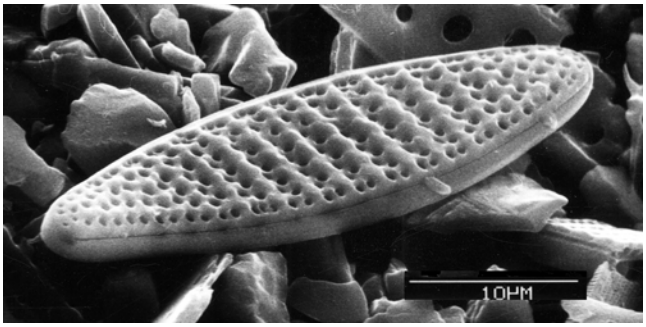

Figure 5. ***Nitzschia kerguelensis***, in a genus of diatoms that often grows on species of ***Cyathodium***. Photo by Hans Grobe, through Creative Commons.

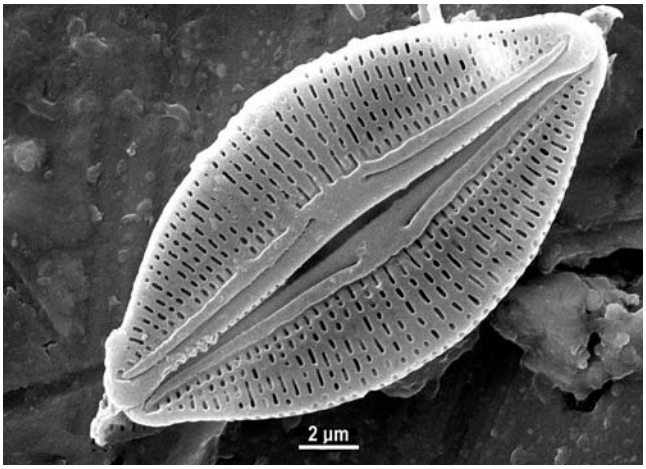

Figure 6. ***Amphora*** sp, in a genus of diatoms that often grows on species of ***Cyathodium***. Photo by Berezovska, through Creative Commons.

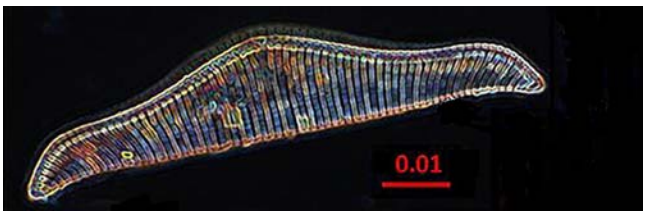

Figure 7. ***Rhopalodia gibba***, in a genus of diatoms that often grows on species of ***Cyathodium***. Photo by Leena Virta and Alf Norkko, through Creative Commons.

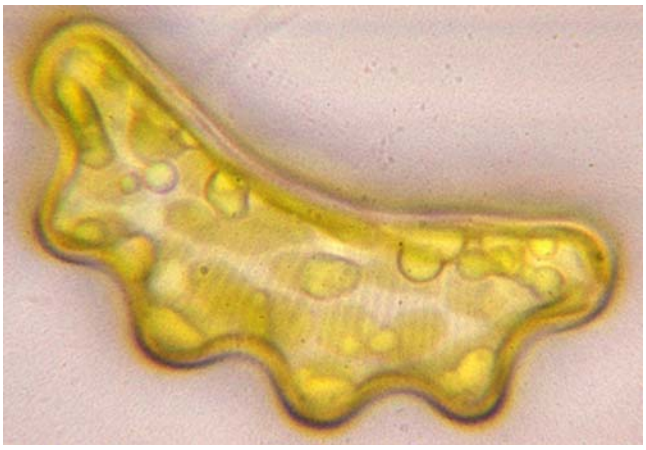

Figure 8. ***Eunotia***, in a genus of diatoms that often grows on species of ***Cyathodium***. Photo by National Museum of Natural History, through Creative Commons.

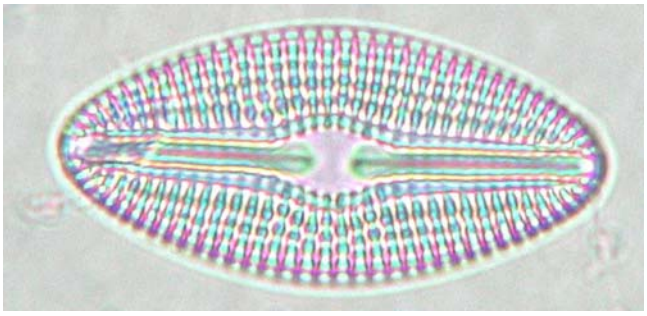

Figure 9. ***Diploneis ovalis***, in a genus of diatoms that often grows on species of ***Cyathodium***. Photo by Kristian Peters, through Creative Commons.

Members of ***Cyathodium*** prefer moist, shady habitats (Daniels 1998). Large communities of ***Cyathodium*** occur on unstable river banks in Costa Rica and Panama, and here they often experience submergence or become detached by floods. In other locations they are subject to drying on soil along cement road ditches in humid areas (Salazar Allen & Korpelainen 2006). The genus endures weak light intensities where it is able to grow on rock, soil, or in two species on bark. ***Cyathodium*** sp. (Figure 10) occurs over (overhanging?) water and in waterfalls in the tropics (Ruttner 1955). Although there are several semi-aquatic species in ***Cyathodium***, Cavers (1910), citing Lang (1905) regarded it as a genus primarily adapted to shade, rather than as a hygrophyte.

Daniels (1998) noted that ***Cyathodium*** species lack the complex structure of many thallose liverworts, such as well-defined assimilatory and storage zones or scales.

Tiwari (1929a,b, 1935) studied the spore germination of ***Cyathodium*** spores. Crum (1976) noted that some of the species have spores that emit a yellowish luminescence. There are few spores in ***Cyathodium*** species, numbering 20-100 per capsule (Bischler-Causse *et al*. 2005).

Cyathodium bischlerianum (Figure 10)

Distribution

Cyathodium bischlerianum (Figure 10) is a Neotropical species known only from Panama (Salazar Allen 2001). Because of its small size and association with other ***Cyathodium*** species, it can easily be overlooked, and Salazar Allen suspects that it is more widely distributed in the Neotropics. For these reasons, information on it is also rather scant.

Figure 10. ***Cyathodium bischlerianum*** habit on tree near water. Photo by José Gudiño L., courtesy of Noris Salazar Allen.

Members of ***Cyathodium*** have a simple, slender, dichotomously branched thallus with no purple coloring (Figure 2-Figure 3). The pores are simple with a single ring of cells and no hyaline inner ring (Salazar Allen 2001; Bischler-Causse *et al*. 2005). The air chambers are empty. Most rhizoids are smooth, but some may be tuberculate. It has 2 rows of ventral scales, often restricted to the apex. Its asexual reproduction includes fragmentation of thallus segments and ventral tubers in some.

Aquatic and Wet Habitats

Cyathodium bischlerianum (Figure 10) is one of two species that can be corticolous (Salazar Allen & Korpelainen 2006). It typically grows mixed with other species of ***Cyathodium*** in very moist, shaded locations, particularly on rocks near or even in creeks, along eroding river banks, and in other locations subject to partial submergence during high water levels (Bischler-Causse *et al*. 2005). It is more mesic than ***C. spruceanum*** (Figure 2).

Cyathodium bischlerianum (Figure 10) occurs on stream and river banks, along with ***C. cavernarum*** (Figure 3), in the shaded, more moist habitats close to the rivers and seepage, whereas ***C. spruceanum*** (Figure 2) occurs on more upper slopes (Salazar Allen & Korpelainen 2006). ***Cyathodium bischlerianum*** also can occur on bark (Figure 11-Figure 12) near streams and rivers and in seepages and on moist rocks.

Figure 11. ***Cyathodium bischlerianum*** habit on bark. Photo by José Gudiño L., courtesy of Noris Salazar Allen.

Figure 12. ***Cyathodium bischlerianum*** on bark. Photo by José Gudiño L., courtesy of Noris Salazar Allen.

Reproduction

Cyathodium bischlerianum (Figure 10) is **monoicous** (Salazar Allen 2001; Bischler-Causse *et al.* 2005). The involucre can have 1 or 2 archegonia and sporophytes (Figure 13); male receptacles occur on the sides of the thallus. The species lacks any specialized asexual reproductive structures, with no tumors as found in dioicous members of the genus (Salazar Allen & Korpelainen 2006).

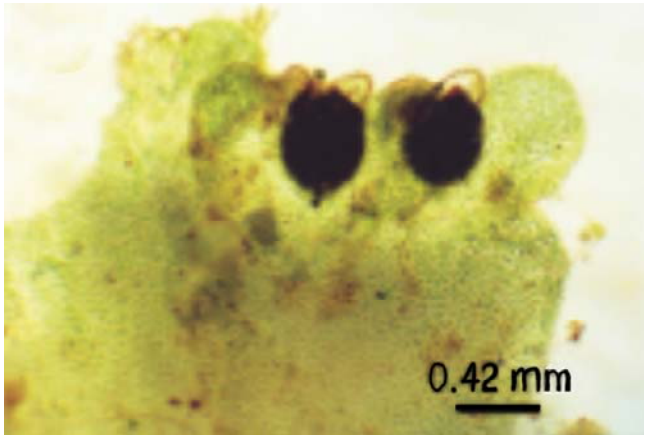

Figure 13. ***Cyathodium bischleriana*** thallus with sporangia. Photo by Noris Salazar Allen, with permission.

Cyathodium bischlerianum (Figure 10) is an **r-selected** species (Salazar Allen & Korpelainen 2006). This means that it has a high reproductive rate, its population size varies through time, and recolonization occurs every year, creating competition with itself and other species (Pianka 1970).

Biochemistry

Despite the newness of the species and its limited distribution, the biochemistry of ***Cyathodium bischlerianum*** (Figure 10) has been evaluated. It is unique among the ***Cyathodium*** species, containing mostly aromatic monoterpenes (Salazar Allen *et al*. 2017). It has less than 3% of the sesquiterpenes germacrene D and bicyclogermacrene.

Nerolidol is the main compound among these (Salazar Allen *et al*. 2017). This compound has a floral and woody fragrance (Padalia *et al*. 2015). Already known from other plants, it has been approved for use in fine fragrances, cosmetics, shampoo, soaps, detergents, and cleaning products (Padalia *et al*. 2015; Boskabady *et al.* 2014). The industry level consumption is 10-100 tons per year (Queiroga *et al*. 2014).

Cyathodium cavernarum (Figure 14-Figure 15)

syn. = *Cyathodium africanum*, *C. barodae*, *C. mexicanum*

Distribution

Cyathodium cavernarum (Figure 14-Figure 15) is a widespread pantropical species (Lye & Pócs 1997) and is the most widespread species in the genus (Bischler-Causse *et al*. 2005). It is known from China (Zhang *et al*. 2004a), Japan (Furuki *et al*. 2012), India, Java, Africa, Madagascar (Srivastava & Dixit 1996; Reeb *et al*. 2018), western Australia (Meagher 2002), and the American tropics in Colombia (Winkler 1976), Mexico, Costa Rica, Panama, Cuba, and Brazil (Srivastava & Dixit 1996; Salazar Allen 2005; Salazar Allen & Korpelainen 2006; Gradstein *et al*. 2016; Reeb *et al*. 2018). Shah and Gujar (2016) reported that ***Cyathodium cavernarum*** was the most widely distributed liverwort species in Gujarat, India.

Figure 14. ***Cyathodium cavernarum*** on roof of cave. Photo by Célio Moura Neto, through Creative Commons.

Figure 15. ***Cyathodium cavernarum*** showing young and old thalli. Photo by Eric Hough, through Creative Commons.

Aquatic and Wet Habitats

Lye and Pócs (1997) reported ***Cyathodium cavernarum*** (Figure 14-Figure 15) growing on overhanging, dripping, or sprayed rocks as well as temporarily inundated muddy forest floor low areas of Uganda. On river banks, it occupies lower positions than does ***C. spruceanum*** (Figure 2), preferring more shaded, damper sites or those with seepage (Bischler-Causse *et al*. 2005; Salazar Allen & Korpelainen 2006). In the Northern Western Ghats it is usually found in low altitudes where there is human habitation or shaded disturbed areas (Nair & Prajitha 2016). Glenny (2002) similarly reported it from stream and river banks in Australia.

Cyathodium cavernarum (Figure 14-Figure 15) usually occurs on calcareous substrata but it can also occupy slightly acidic substrates with underlying calcareous bedrock (Bischler-Causse *et al*. 2005). Its substrata include soil, wet rocks, walls, and termite mounds in moist deciduous, semi-evergreen, or evergreen forests (Nair & Prajitha 2016). In exposed habitats it is typically associated with members of the **Pottiaceae** (Figure 16); in ravines and river banks with species of ***Philonotis*** (Figure 17), ***Fissidens*** (Figure 18), ***Notothylas*** (Figure 19), ***Racopilum tomentosum*** (Figure 20), ***Cyathodium spruceanum*** (Figure 2), and **Lejeuneaceae** (Figure 21) (Bischler-Causse *et al*. 2005).

Figure 16. ***Syntrichia ruralis***, a member of the **Pottiaceae**, a family that often occurs with ***Cyathodium cavernarum***. Photo by Alexis Orion, through Creative Commons.

Figure 17. ***Philonotis***, member of a genus that is often associated with ***Cyathodium cavernarum***. Photo by A. Neuman, through Creative Commons.

Figure 18. ***Fissidens fontanus***, member of a genus that is often associated with ***Cyathodium cavernarum***. Photo by Bob Klips, with permission.

Figure 19. ***Notothylas orbicularis***, member of a genus that is often associated with ***Cyathodium cavernarum***. Photo by Christian , through Creative Commons.

Figure 20. ***Racopilum tomentosum***, a species that is often associated with ***Cyathodium cavernarum***. Photo by David Tng, with permission.

Figure 21. ***Lejeunea flava***, member of a family that is often associated with ***Cyathodium cavernarum***. Photo by Scott Zona, through Creative Commons.

Although caves are not aquatic habitats, they are often wet and at least damp, providing suitable habitat for ***Cyathodium cavernarum*** (Figure 22-Figure 25) including the Birds'-Nest Cave near Niah, Sarawak, Borneo (Holttum 1938). Reeb *et al*. (2018) likewise found this species at cave entrances in Madagascar, occupying naked, compact soils that were shady. And Furuki *et al*. (2012) found it on soil of a limestone cave in Japan and Zhang *et al*. (2004a,b) in karst caves of China.

Figure 22. ***Cyathodium cavernarum*** iridescence on wall of ruins in Bombay. Photo ©Patrick Blanc, with permission.

Figure 23. ***Cyathodium cavernarum*** on rock in cave. Photo by Cédric de Foucault, through Creative Commons.

Figure 24. ***Cyathodium cavernarum*** in cave. Photo by Cédric de Foucault, through Creative Commons.

Figure 25. ***Cyathodium cavernarum*** on cave ceiling. Photo by Célio Moura Neto, through Creative Commons.

Adaptations

Cyathodium cavernarum (Figure 14-Figure 15) exhibits a bright metallic-green color (Figure 26-Figure 27) (Bischler-Causse *et al*. 2005). Reeb *et al*. (2018) described it as iridescent, with colors that change when viewed from various angles. Zhang *et al*. (2004b) described it as luminous with a "peculiar light-reflecting power which produces a kind of starry effect, so that the plants seem to flood the dark caves where they grow with a luminous, golden-green light."

Figure 26. ***Cyathodium cavernarum*** iridescence in Bombay. Photo ©Patrick Blanc, with permission.

Figure 27. ***Cyathodium cavernarum*** showing iridescent colors. Photo by Jan-Peter Frahm, with permission.

But what does this peculiar light reflection mean for the liverwort? Does it increase the ability to capture light for photosynthesis? Does it attract some sort of invertebrate that henceforth carries sperm or fragments, thus aiding in dispersal? This is a mystery that needs to be investigated.

Water can collect on the thallus and remain there for some time (Figure 28), helping the plant to remain hydrated. This may be the mechanism that permits it to live in caves where it doesn't rain.

Figure 28. ***Cyathodium cavernarum*** with accumulated water droplets. Photo from Idlegrraphics, through Creative Commons.

Cyathodium cavernarum has pores in the thallus that increase the loss of water (Figure 29). As with many liverworts, ***C. cavernarum*** (Figure 14-Figure 15) often benefits from the added water retention of living among mosses (Figure 30).

Reproduction

Cyathodium cavernarum (Figure 14-Figure 15) is **monoicous** (Srivastava & Dixit 1996; Bischler-Causse *et al*. 2005). Salazar Allen and Korpelainen (2006) demonstrated that ***C. cavernarum*** and ***C. spruceanum*** (Figure 2) have more similar genetics from nearby geographic areas than those from more distant areas, suggesting a role of sexual reproduction. Sporelings in culture develop initial filamentous growth followed by apical development into the thallus.

In addition to sexual reproduction, it can reproduce by fragments and spread by branching (Figure 31) (Bischler-Causse *et al*. 2005). Tubers are unknown in this and other monoicous species (Salazar Allen & Korpelainen 2006).

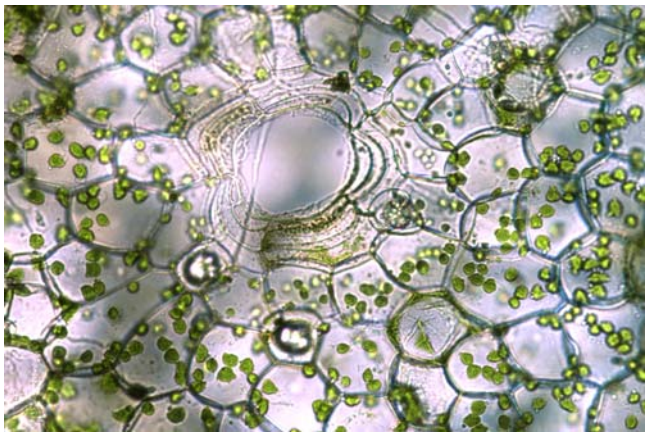

Figure 29. ***Cyathodium cavernarum*** pore showing layers of cells surrounding it. Photo courtesy of Noris Salazar Allen.

Figure 30. ***Cyathodium cavernarum*** growing among mosses. Photo by Célio Moura Neto, through Creative Commons.

Figure 31. ***Cyathodium cavernarum*** showing young thalli mixed with old ones. Some show branching. Others may be derived from fragments or spores. Photo by Eric Hough, through Creative Commons.

Interactions

Cyanobacteria (Figure 32) are common associates of ***Cyathodium cavernarum*** (Figure 14-Figure 15) (Bischler-Causse *et al*. 2005). Fungal endophytes are known from ***Cyathodium cavernarum*** in Panama (Salazar Allen & Korpelainen 2006).

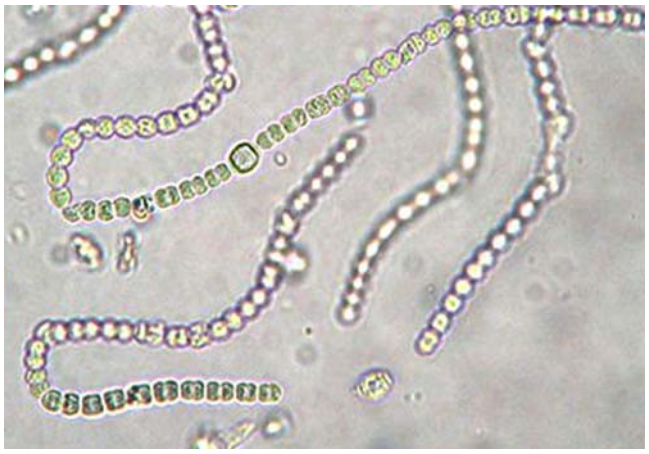

Figure 32. ***Nostoc commune***, one of the **Cyanobacteria** often associated with bryophytes. Photo by Kristian Peters, through Creative Commons.

Biochemistry

Salazar Allen *et al*. (2017) found that ***Cyathodium cavernarum*** (Figure 14-Figure 15) has a distinct chemical composition with an octane derivative as its major compound, suggesting that this could be used as a chemical marker for the species. Nevertheless, Ulka and Karadge (2010) found little antimicrobial activity by extracts of ***Cyathodium cavernarum***. Furthermore, Surendra Kumar *et al*. (2014-15) found that extracts of ***C. cavernarum*** were ineffective, compared to a standard drug, in causing paralysis or death in the Indian earthworm ***Pheretima posthuma*** (see Figure 33. It is interesting that this widespread species seems to lack the usual liverwort ability to inhibit potentially deadly organisms. Could it be that these other organisms seldom occur where it lives? Or does it have associated bacteria or fungi that accomplish this purpose?

Figure 33. *Pheretima praepinguis* from China; ***P. posthuma*** is unaffected by extracts of ***Cyathodium cavernarum***. Photo by Panzer VI-II , through Creative Commons.

Cyathodium foetidissimum (Figure 34)

Cyathodium foetidissimum (Figure 34) is the largest of the ***Cyathodium*** species (Lang 1905).

Figure 34. ***Cyathodium foetidissimum***. Photo by Philippe Birnbaum, with permission.

Distribution

Cyathodium foetidissimum (Figure 34) is Asiatic with limited records in the Neotropics (Salazar Allen *et al*. 2004). It is known from Java, Sumatra, Tahiti, Nukahiva (Srivastava & Dixit 1996), Cameroon (Wigginton 2002; Wigginton & Grolle 1996), Costa Rica (Salazar Allen *et al*. 2004), Ecuador (Bischler-Causse *et al*. 2005), and Colombia (Gradstein *et al*. 2016). The specimens from Ecuador might represent an error in identification. They have tubers (otherwise unknown in ***C. foetidissimum***) and the uppermost thallus cells exceed the size of those found in specimens from Costa Rica (Bischler-Causse *et al*. 2005).

Duckett and Ligrone (2006a) reported the first record of ***Cyathodium*** in Europe. This they identified as ***Cyathodium foetidissimum*** (Figure 34). It was located in southern Italy, outside its normal tropical range. They suggested that it was probably a pre-glacial relic rather than a recent arrival from sub-Saharan Africa.

Aquatic and Wet Habitats

Lang (1905) described the habitat of ***Cyathodium foetidissimum*** (Figure 34) in Perak, Malaysia, as one on rocks in deep forest shade, especially on vertical faces of damp rocks. Salazar Allen and Korpelainen (2006) found that it is more mesic than is ***C. spruceanum*** (Figure 2). Lang (1905) considers it to be more adapted to shade conditions, rather than being a **hygrophyte** (plant that grows in wet conditions). Angeles *et al*. (2020) described the species as rupestrian, occurring as **chasmophytes** (plants growing in fissures and cracks of limestone) on rock.

In Costa Rica this species forms small patches in depressions in very shady conditions on sandy limestone rock (Bischler-Causse *et al*. 2005); it also occurred in a limestone valley in Italy (Duckett & Ligrone 2006a). Its common associates include ***Dumortiera hirsuta*** (Figure 35), ***Marchantia*** (Figure 36), ***Fissidens flaccidus*** (Figure

37), ***Taxiphyllum taxirameum*** (Figure 38), and **Lejeuneaceae** (Figure 21).

Figure 35. ***Dumortiera hirsuta***, a common associate of ***Cyathodium foetidissimum*** in Costa Rica. Photo by David T. Holyoak, with permission.

Figure 36. ***Marchantia polymorpha* ssp. *montivagans***, in a genus that is a common associate of ***Cyathodium foetidissimum*** in Costa Rica. Photo by Claire Halpin, with permission.

Figure 37. ***Fissidens flaccidus*** a common associate of ***Cyathodium foetidissimum*** in Costa Rica. Photo by Vinod Deora and Deora G.S., through Creative Commons.

Figure 38. ***Taxiphyllum taxirameum***, a common associate of ***Cyathodium foetidissimum*** in Costa Rica. Photo by Bob Klips, with permission.

In Mali, Philippe found it in small caves on rocks (Figure 39-Figure 41).

Figure 39. ***Cyathodium foetidissimum*** in cave in Mali. Photo by Philippe Birnbaum, with permission.

Figure 40. ***Cyathodium foetidissimum*** in Mali. Photo by Philippe Birnbaum, with permission.

Figure 41. ***Cyathodium foetidissimum*** in small cave in Mali. Photo by Philippe Birnbaum, with permission.

Adaptations

Cyathodium foetidissimum (Figure 40) has a multistratose region of cells in the mid region of the thallus (Salazar Allen *et al*. 2004). These could give the thallus greater strength or act as a storage region, but the function needs to be explored. The oil cells have a single oil body. Unlike some species in the genus, this one has strongly dimorphic rhizoids (smooth and pegged) and large ventral scales, both adaptations that could facilitate water movement and uptake.

Srivastava and Dixit (1996) described the thalli as brownish-green and delicate, but usually larger than those of other species in ***Cyathodium***. They likewise described large ventral scales, occurring just behind the involucre.

When Duckett and Ligrone (2006a) found this species in Italy, they discovered internal cells in the air chambers, the only report of such internal cells in the genus.

Cyathodium foetidissimum (Figure 40) has a phosphorescent appearance (Figure 42) – another mystery (Lang 1905; Salazar Allen *et al*. 2004). Duckett and Ligrone (2006a) suggested that this might enhance its light interception.

Figure 42. ***Cyathodium foetidissimum*** in cave in Mali. Photo by Philippe Birnbaum, with permission.

Reproduction

Cyathodium foetidissimum (Figure 40) is **monoicous**, but can also produce unisexual male plants in the same population (Salazar Allen *et al*. 2004). The male receptacle is apical with archegonia, wrapped in undulate laminar involucres, flanking it. It is **protandrous** (antheridia appear before archegonia).

The antheridia occur on short, disc-shaped antheridiophores (Srivastava & Dixit 1996). Archegonia are enclosed by an involucre that sits below the apex at the base of a sinus. Like those in ***Targionia hypophylla*** (Figure 43), antheridial receptacles occur not only on ventral shoots, but also on the main shoot along the midrib (Kashyap 1914).

Figure 43. ***Targionia hypophylla***, a species that, like ***Cyathodium foetidissimum***, has antheridial receptacles arising from both ventral shoots and main shoots. Photo by Ken-Ichi Ueda, through Creative Commons.

The capsule has an operculum of only 12 cells. Spores are verrucose (Salazar Allen *et al*. 2004). The spores initially germinate into a filamentous phase in culture (Salazar Allen & Korpelainen 2006). This is followed by apical development of thalli.

Cyathodium foetidissimum (Figure 40) grows in the rainy season, dying back when the dry season begins (Salazar Allen & Korpelainen 2006). Where the habitat is wetter and shaded on the banks of creeks and rivers, it is able to persist for more than one year.

Interactions

Cyanobacteria (Figure 32) are known associates of all species of ***Cyathodium*** (Salazar Allen & Korpelainen 2006).

Fungi are known to associate with ***Cyathodium foetidissimum*** (Figure 40) in the Malay Peninsula (Lang 1905) and in Italy (Duckett & Ligrone 2006a).

Biochemistry

Many liverworts have distinctive odors. As its name suggests, ***Cyathodium foetidissimum*** (Figure 40) is recognizable by its bad small (Gradstein 2011). Sakurai *et al*. (2018) described it as the smell of an old person or old chest of drawers, but also called it a nostalgic odor. Collections from Tahiti were described as having a pleasant odor, whereas those in the Marquesas Islands smelled like urine and feces.

Ludwiczuk *et al*. (2009) found skatole, a well known compound produced by biodegradation of tryptophan and responsible for the fecal odor of ***Cyathodium foetidissimum*** (Figure 40). This species also biosynthesized izolepidozene (3.1%) and lunularin (2.4%). Izopepidozene is the main volatile component of ***Conocephalum japonicum*** (Figure 44) and ***Marchantia emarginata*** **ssp**. ***tosana*** (Figure 45). Among the six species of Polynesian liverworts tested, Ludwiczuk *et al*. (2010) found that each had a unique combination of volatile compounds.

Figure 44. ***Conocephalum japonicum***, a species that, like ***Cyathodium foetidissimum***, has the compound izolepidozene. Photo by David Long, with permission.

Figure 45. ***Marchantia emarginata*** **ssp**. ***tosana***, a species that, like ***Cyathodium foetidissimum***, has the compound izolepidozene. Photo by Lin Shanxiong, through Creative Commons.

Sakurai *et al*. (2018) identified three volatile components [4-methoxystyrene (24.4%), 3,4-dimethoxystyrene (28.7%), and skatole (15.9%)], as well as several aliphatic aldehydes [n-octanal, n-nonanal, and n-decanal] from Tahitian specimens. However, they did not find (E)-2-nonenal, a recognized compound causing an aged foul odor. Sakurai *et al*. (2018) found that a methanol extract (100 μg mL^{-1}) showed no activity against *Bacillus subtilis* (Figure 46), *Staphylococcus aureus* (Figure 47), *Escherichia coli* (Figure 48), or *Klebsiella pneumoniae* (Figure 49), although a number of bryophytes do show activity against these. Perhaps the volatile compounds have a role in antiherbivory?

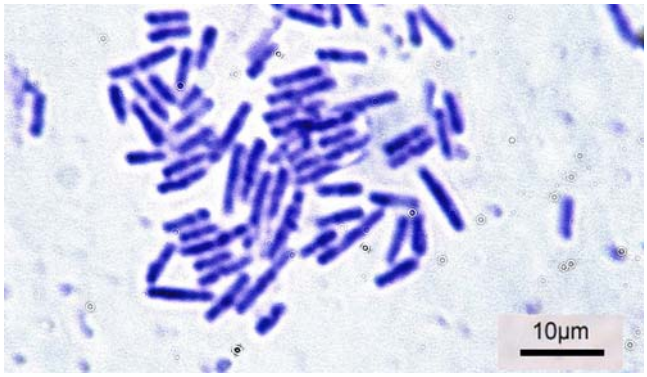

Figure 46. ***Bacillus subtilis***, a bacterium that is not inhibited by methanol extracts of ***Cyathodium spruceanum***. Photo by Graham Beards, through Creative Commons.

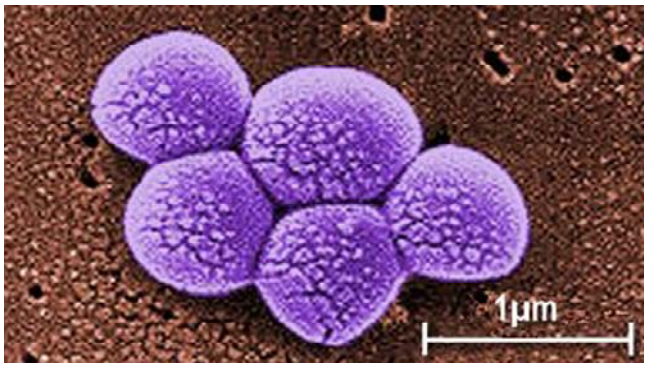

Figure 47. ***Staphylococcus aureus***, a bacterium that is not inhibited by methanol extracts of ***Cyathodium spruceanum***. Photo by Janice Haney Carr, through public domain.

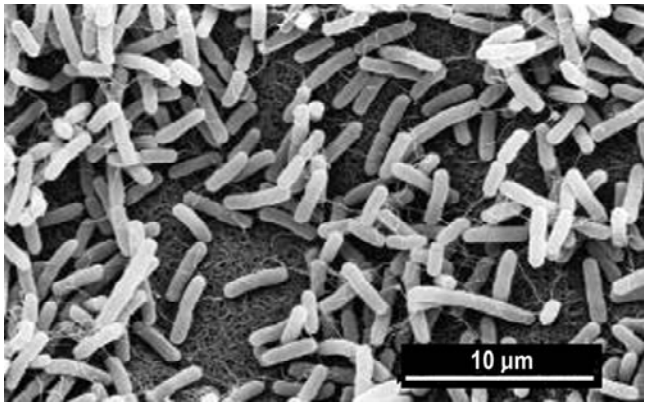

Figure 48. ***Escherichia coli***, a bacterium that is not inhibited by methanol extracts of ***Cyathodium spruceanum***. Photo by David Gregory & Debbie Marshall, through Creative Commons.

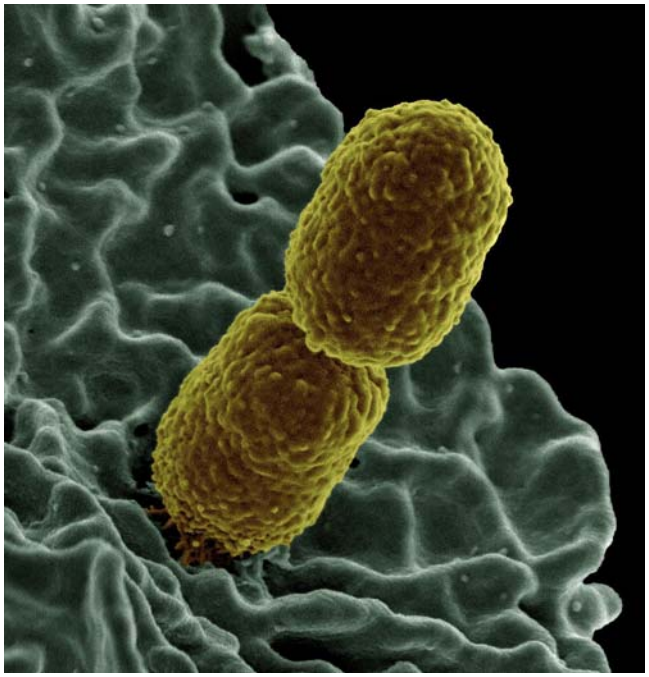

Figure 49. ***Klebsiella pneumoniae***, a bacterium that is not inhibited by methanol extracts of ***Cyathodium spruceanum***. Photo by NIAID, through Creative Commons.

Of four species of ***Cyathodium***, Salazar Allen *et al*. (2017) found indole compounds only in ***C. foetidissimum***. The researchers suggested that indole compounds could be used as species markers.

Cyathodium spruceanum (Figure 50)

Among four Neotropical species they examined, Salazar Allen and Korpelainen (2006) found the greatest genetic differences between ***Cyathodium foetidissimum*** and ***C. spruceanum*** (Figure 50).

Figure 50. ***Cyathodium spruceanum***. Photo by Jose De Gracia, through Creative Commons.

Distribution

Cyathodium spruceanum (Figure 50) is endemic to South America (Srivastava & Dixit 1996) in the Neotropics (Salazar Allen & Korpelainen 2006).

Aquatic and Wet Habitats

Cyathodium spruceanum (Figure 50) typically grows in homogeneous patches on exposed places (Salazar Allen & Korpelainen 2006). Proskauer (1951) reported the original ***C. spruceanum*** at the edge of a forest stream. The populations are usually rather large in years experiencing high rainfall. The species is less mesic than ***C. cavernarum*** (Figure 3) or ***C. bischlerianum*** (Figure 10), with ***C. spruceanum*** growing farther up the banks in less shaded, less damp habitats that are less mesic. At the Ratu Boko temple in Java, ***Cyathodium spruceanum*** occurs on limestone (Aryani 2014).

Adaptations

Cyathodium spruceanum (Figure 50) has a thallus that is light-green to whitish-green (Srivastava & Dixit 1996). However, Proskauer (1951) described it as iridescent with light-reflecting lens cells in the roofs of the air chambers. Other than the dark colors that protect against bright sun, little seems to be known about the adaptive values, if any, of some of the colors in bryophytes.

The thalli are overlapping (Srivastava & Dixit 1996), potentially helping to conserve water. Scales provide protection of the growing points (Proskauer 1951).

This species has numerous rhizoids, but the straight, smooth ones predominate (Proskauer 1951; Srivastava & Dixit 1996).

Reproduction

Cyathodium spruceanum (Figure 50) is **dioicous** (Srivastava & Dixit 1996). The female receptacles are ventral pouches. Male (Figure 51) and female plants can grow close to each other, permitting frequent fertilization success (Salazar Allen & Korpelainen 2006). Salazar Allen *et al*. (2017) found that the chemical composition of males and females was very similar, with three compounds found only in females [12-norcyercene-B, longifolenaldehyde and 1(5)-3-aromadenedraidene were found only in female plants].

Figure 51. ***Cyathodium spruceanum*** males. Photo by José Gudiño L., courtesy of Noris Salazar Allen.

Sporophytes are produced in abundance (Salazar Allen & Korpelainen 2006). Spores are numerous (>400 in a capsule). In culture, these can produce males and female gametophytes in the same year as produced, but there are no field observations to demonstrate germination in the same year as production. Salazar Allen and Korpelainen suggested that this delay in germination is due to soil dryness when the spores are released, a phenomenon that occurs because they are released at the onset of the dry season.

Figure 52. ***Cyathodium spruceanum*** with sporangia (**S**). Photo courtesy of Noris Salazar Allen.

The species of ***Cyathodium*** are **r-selected species** (Salazar Allen & Korpelainen 2006). **R-selected species** generally have high growth rates, produce many offspring, but have a low probability of survival to adulthood. The numerous offspring are able to exploit niches that are less crowded. The abundant sporophytes and spores permit ***C. spruceanum*** (Figure 50) to be among the better of the ***Cyathodium*** species at achieving high levels of reproduction. Long-term studies on individual populations are lacking.

The spores of ***Cyathodium spruceanum*** (Figure 50) are lamellate-reticulate (Salazar Allen *et al*. 2004). The sporeling initially produces a budlike protonema (Salazar Allen & Korpelainen 2006). From this structure, a thallus develops.

Cyathodium spruceanum (Figure 50) is one of the species in the genus to produce ventral tubers (Salazar Allen & Korpelainen 2006). These generally develop in the middle of the rainy season and remain attached to the parent thallus until the thallus decays. In culture, tubers are produced in abundance when nutrients are depleted. The tubers produce numerous rhizoids on their distal portion. They germinate on agar, but germination in the field has thus far not been observed. Salazar Allen and Korpelainen suggest that when the tubers are covered by mud, they may remain dormant until the next season or become part of the diaspore bank to recolonize if the population is destroyed or if the growing season is extended with plentiful water.

Fungal Interactions

In Panama, fungal endophytes are known from ***Cyathodium spruceanum*** (Figure 50) (Salazar Allen & Korpelainen 2006). These interactions have barely been explored by bryologists, but mycological literature is not so scarce.

Biochemistry

As in ***Cyathodium bischlerianum*** (Figure 10), ***C. spruceanum*** (Figure 50) has less than 3% of the sesquiterpenes germacrene D and bicyclogermacrene (Salazar Allen *et al*. 2017). Oil bodies are present in all cells with the chloroplasts in this species, but the odor is not as offensive as that of ***C. foetidissimum***. Nevertheless, the researchers identified far more volatile compounds in ***C. spruceanum*** than in the other four ***Cyathodium*** species assessed. Salazar Allen and coworkers identified 12-norcyercene B (70.2%), germacrene D (1.6%), and longifolenaldehyde (1.4%).

Dumortieraceae

Dumortiera hirsuta (Figure 53-Figure 55)

Most bryologists seem to recognize only one species of ***Dumortiera*** (Figure 53-Figure 55). However, Forrest *et al*. (2011) found two very distinct lineages, represented by ssp ***hirsuta*** (Figure 53-Figure 55) and ssp ***nepalensis*** (Figure 102-Figure 103). One (ssp. ***hirsuta***) is restricted to Central America and the other (ssp. ***nepalensis***) is more widely distributed throughout the range of the genus. See also the discussion of Taiwan populations (Akiyama *et al*. 2003). Forrest and coworkers concluded that there are at least two distinct species, a conclusion reached by O'Hanlon in 1934, but that the molecular basis for naming these is not known for much of the distribution. Therefore, in this chapter I will treat all as ***Dumortiera hirsuta*** (Figure 53-Figure 55) since most of the publications cited here do not distinguish these.

Figure 53. ***Dumortiera hirsuta*** mature colony. Photo through Creative Commons.

Figure 54. ***Dumortiera hirsuta*** *s.l.* Photo by Nicola van Berkel, through Creative Commons.

Figure 55. ***Dumortiera hirsuta*** on soil. Photo by Cheong Weei Gan, through Creative Commons.

More recently, the chloroplasts (Kwon *et al.* 2019a) and mitochondria (Kwon *et al*. 2019b) of Korean populations of this liverwort have been sequenced.

Distribution

Dumortiera hirsuta (Figure 53-Figure 55) is widely distributed in tropical and subtropical regions, extending into some temperate regions (O'Hanlon 1934; Forrest *et al*. 2011). It is rare in Europe (Aleffi *et al*. 1998), reaching its northernmost distribution in the UK (Callaghan 2020). In the same year Gaston (2020) found it in France.

This distribution includes more humid and warmer regions of the temperate zones of India, Nepal, Japan, Brazil, México, Jamaica, North and South America, Europe, British Isles, New Zealand, Hawaii, and Africa (O'Hanlon 1934; Nair *et al*. 2005). In the USA it is found in southeastern states, including Arkansas (Timme & Redfearn 1997).

Aquatic and Wet Habitats

Reeb *et al*. (2018) describe the habitat of ***Dumortiera hirsuta*** (Figure 53-Figure 55) as a shady, humid environment. Tosun *et al*. (2015) considered it to be a large thalloid on wet rocks. Gaston (2020) described it as a pantropical hydrophile.

Dumortiera hirsuta (Figure 53-Figure 55) occurs on dripping rocks (Watson 1919). Ruttner (1955) reported it in water spray, tuff wall, <40 cm above water level, and waterfalls (Figure 1) in the tropics. McAllister *et al*. (2019) found it to be common on rocks in deep canyons, in riparian habitats, on seepy hillsides, and abundant on shale near seepages. It could occur near tributaries, on slopes near or on the underside of sandstone ravines, and at springs (Figure 56-Figure 60).

Figure 56. ***Dumortiera hirsuta*** in a wet habitat in the UK. Photo by David T. Holyoak, with permission.

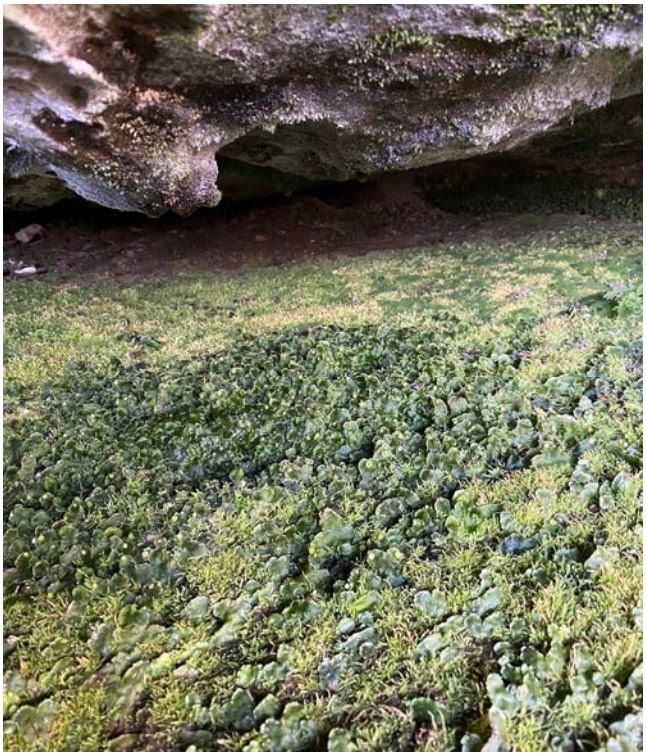

Figure 57. ***Dumortiera hirsuta*** habitat. Photo by Abel Kinser, through Creative Commons.

Figure 58. ***Dumortiera hirsuta*** on sandstone. Photo by Vitaly Charny, through Creative Commons.

Figure 59. ***Dumortiera hirsuta*** where the liverwort can be found on the wet stream banks. Photo by Michael Lüth, with permission.

Figure 60. ***Dumortiera hirsuta*** habitat on wet soil among rocks. Photo by Luis Funez, through Creative Commons.

Vieira *et al*. (2005) found that in Portugal it was not extensive but seemed stable in steep, water-dripping granite surfaces next to waterfalls. It was also found at the margin of fast flow in a streambed, where it was submerged for long periods and grew associated with ***Plagiothecium nemorale*** (Figure 61), ***Aneura pinguis*** (Figure 62), ***Pellia epiphylla*** (Figure 63), and ***Riccardia multifida*** (Figure 64), in mountain streams of northwest Portugal (Vieira *et al.* 2005).

Figure 61. ***Plagiothecium nemorale***, an associate of ***Dumortiera hirsuta*** in Portugal. Photo by Hermann Schachner, through Creative Commons.

Figure 62. ***Aneura pinguis***, an associate of ***Dumortiera hirsuta*** in Portugal. Photo by Proyecto Musgo, through Creative Commons.

Figure 63. ***Pellia epiphylla***, an associate of ***Dumortiera hirsuta*** in Portugal. Photo by Bernd Haynold, through Creative Commons.

Figure 64. ***Riccardia multifida***, an associate of ***Dumortiera hirsuta*** in Portugal. Photo by Hermann Schachner, through Creative Commons.

In the UK, Callaghan (2020) found all colonies in close association with flowing and moderately alkaline water, including springs, flushes and streams (Figure 56-Figure 60). It never occurred within the **spate zone** (zone suddenly flooded) of larger rivers. It occurs almost entirely on rocks (mudstone, sandstone, slate), predominantly in deciduous woodland and only in lowland sites. In these locations, it occurs with ***Thamnobryum alopecurum*** (most frequent associate; Figure 65), and ***Conocephalum conicum*** (Figure 66), as well as ***Chrysosplenium oppositifolium*** (flowering plant; Figure 67). Ottley (2014) reported a "strong colony" from dripping rocks at Rolvenden in the UK.

Figure 65. ***Thamnobryum alopecurum***, the most frequent associate with ***Dumortiera hirsuta*** in the UK. Photo by Claire Halpin, with permission.

Figure 66. ***Conocephalum conicum*** on wet rock, a desiccation-intolerant liverwort and frequent associate of ***Dumortiera hirsuta*** in the UK. Photo by Samaritakis, through Creative Commons.

Figure 67. ***Chrysosplenium oppositifolium***, a frequent associate of ***Dumortiera hirsuta*** in the UK. Photo by Richtid, through Creative Commons.

In the western Himalayas, Pant and Tewari (1984) found ***Dumortiera hirsuta*** (Figure 53-Figure 55) in tufaceous aquatic habitats, perennial springs, **Gadheras** (small river tributaries; active only during rainy season and stay wet and damp throughout year for growth of bryophytes), and the muddy banks of **Gadhs** (broad rivulets that never dry, resulting from joining of Gadheras). Srinivasan (1968) reported that in India it is often seen in very wet, shady situations where the flow is continuous or at least dripping

In Java, Indonesia, Nadhifah *et al*. (2018) reported that in the Cibodas Botanical Garden this liverwort occurred on soil in wet areas such as rivers, waterfalls, and ponds. Gradstein (2006) reported that ***Dumortiera*** sp. was successfully cultivated in association with a small river and pond at the Cibodas Botanical Garden.

In China, ***Dumortiera hirsuta*** (Figure 53-Figure 55) occurs on brook sides, valleys, or slopes, in wet, mesic, or moist localities, usually in partial or full shade of forested habitats in **orotemperate** (temperate mountain climate) of deciduous and warm temperate evergreen primeval or secondary forests (Piippo & Koponen 2013).

Colon (2000) found it in limestone sinkholes in the karst zone of Puerto Rico, where it had the highest importance value among species in the Empalme Sink.

Not all of its habitats are aquatic. It occurs in oak-hickory forests with shale and sandstone, but still near streams (McAllister *et al*. 2019).

Physiology

Dumortiera hirsuta (Figure 53-Figure 55) is shade adapted (Callaghan 2020). The linear flow of electrons in photosystem II experiences a sharp decline when the photon flux density is greater than 200 µmol m^{-2} s^{-2}. The chlorophyll *a*:*b* ratio was 1.61, contrasting with that of 2.04 in ***Phaeoceros carolinianus*** (Figure 68), a species of somewhat sunny habitats (Zhang *et al*. 2018). This means that the ***D. hirsuta*** has more chlorophyll *b*, an adaptation to low light. Duckett and Ligrone (1993, 2006b) reported massive grana and stromal crystals in the chloroplasts and considered it to be a species of extreme shade. The thylakoids in the grana often exceeded 100 (Duckett & Ligrone 2006b). All of these characteristics are consistent with adaptations to shade conditions.

Figure 68. ***Phaeoceros carolinianus***, a somewhat sunny species with a higher Chlorophyll *a*:*b* ratio. Photo by Hermann Schachner, through Creative Commons.

Devi *et al*. (2015) found seasonal variation in the photosynthetic pigments of ***Dumortiera hirsuta*** (Figure 53-Figure 55). They found that chlorophyll *a* remained higher than chlorophyll *b* in ***Dumortiera hirsuta*** in all seasons. Chlorophyll *a* is at its lowest levels in winter, whereas there was no seasonal pattern for chlorophyll *b*. Total chlorophyll reaches it greatest levels at the end of the growing season. The carotenoid content was much lower in winter (0.06 ± 0.005 mg g^{-1} fresh weight) than in the rainy season (0.16 ± 0.005 mg g^{-1} fw) or the end of the growing season (0.15 ± 0.005 mg g^{-1} fw).

Bold (1938) demonstrated that the sporophyte is strongly photosynthetic during development in ***Dumortiera hirsuta*** (Figure 53-Figure 55), exhibiting chloroplasts in the immature foot cells, seta cells, capsule wall cells, and elaters. This photosynthetic ability would provide greater energy for developing spores.

Beckett (1993) found that the turgor of ***Dumortiera hirsuta*** (Figure 53-Figure 55) correlates well with the other indicators of water stress damage, including photosynthesis, respiration, and potassium loss. The rate of respiration dropped to zero following desiccation and the plants did not recover. This was similar to results of other desiccation-intolerant liverworts such as ***Conocephalum conicum*** *s.l.* (Figure 66) (Slavik 1965). However, such measures of intolerance must be reviewed because we now know that the rate of desiccation can have a profound effect on the survival and recovery from desiccation. He developed a successful method, using a thermocouple psychrometer, to correct for apoplastic water. Nevertheless, he found that the error introduced by apoplastic water was negligible.

Loo (2005) noted the difficulties in studying the cytology of ***Dumortiera hirsuta*** (Figure 53-Figure 55). Nevertheless, Loo *et al*. (2005a) presented a cytological study on this species. In a separate publication (2005b), they reported that ***Dumortiera hirsuta*** survived at 47-1511 lux, 15-27ºC, and relative humidity of 60-95% on Mt. Kinabalu. Frahm *et al*. (1996) considered the minimum light level for photosynthesis to be 400 lux. The numbers presented by Loo and coworkers suggest that this species has a good tolerance range of the physical parameters of the environment.

Proctor *et al*. (1998) found that the full-turgor water content reached 1400% in ***Dumortiera hirsuta*** (Figure 53-Figure 55). In a different study it was 1636% (Proctor 1999). These are much higher figures than those in the mosses ***Syntrichia ruralis*** (Figure 16) or ***Andreaea alpina*** (Figure 69) (Proctor *et al*. 1998). Beckett (1993) found that ***D. hirsuta*** was very sensitive to desiccation. The cells lost potassium, and during drying the thallus continued respiration while shutting down photosynthesis, causing the thalli to lose weight. He used this species to show that turgor loss correlated with other indicators of stress-induced damage.

Figure 69. ***Andreaea alpina***, a species with a much lower full-turgor water content than that of ***Dumortiera hirsuta***. Photo by Stephen Moores, through Creative Commons.

Marschall and Beckett (2005) found that ABA and partial dehydration hardening can increase desiccation tolerance, with ***Dumortiera hirsuta*** (Figure 53-Figure 55) being much more responsive to ABA treatment than was ***Atrichum androgynum*** (Figure 70). Furthermore, unlike ***A. androgynum***, ***D. hirsuta*** did not exhibit increased **NPQ** (non-photochemical quenching) or decreased PSII efficiency with dehydration hardening. It also had little change with partial dehydration hardening before the onset of stress, but following rehydration it displayed a 22% improvement in PSII activity within an hour.

Figure 70. ***Atrichum androgynum***, a species that is more resistant to cadmium damage than is ***Dumortiera hirsuta***. Photo by Niels Klazenga, through Creative Commons.

Many bryophytes are now known to produce superoxide during rehydration. ***Dumortiera hirsuta*** (Figure 53-Figure 55) is among those that produce extracellular superoxide rapidly, even when not stressed (Beckett *et al*. 2004). Nevertheless, the production of superoxide increases greatly in this species during rehydration even after a mild desiccation stress. There are indications that this production provides an important protection against invasion of bacteria and fungi during the period of membrane repair. (See Chapter 19 in Volume 2.)

Li *et al*. (2010) determined that cell wall peroxidases are responsible for the extracellular burst of superoxide in ***Dumortiera hirsuta*** (Figure 53-Figure 55). They also found that this oxidative burst may have roles in formation of protective substances such as suberin, melanin, and lignin, supporting the hypothesis that the burst of superoxide enhances protection against pathogens. These peroxidases might also have a role in signal transduction and protection against abiotic stress and Yadav *et al*. (2022) looked at seasonal changes in chemical constituents of ***Dumortiera hirsuta*** (Figure 53-Figure 55), particularly changes in oxidative stress responses. In the fruiting season, the plants had their highest level of malondialdehyde (MDA) and H_2O_2, with the lowest levels occurring during the premonsoon and monsoon seasons. Protein content and pigment concentrations were maximal during the monsoon season and minimal during the fruiting season. On the other hand, the enzymatic activity and content of superoxide dismutase, catalase, and glutathione reductase and non-enzymatic antioxidants were higher during the fruiting season and low during the pre-monsoon and monsoon seasons. During the fruiting season, the temperature is very low and nutrient availability is diminished. Hence these activities provide a defense in neutralizing or suppressing the increased **ROS** (reactive oxygen species) during the fruiting season The researchers suggested that the antioxidative defence system may have a role in the adaptation of the species against oxidative stress, mediated by seasonal changes.

Heavy metals are often a component in aquatic and semi-aquatic environments. These are often toxic to plants, including bryophytes, but the latter seem to have at least some coping mechanisms. Heavy metals can interact to provide varying responses in ***Dumortiera hirsuta*** (Figure 53-Figure 55). It exhibits both internal and external cadmium uptake (Mautsoe & Beckett 1996). The intracellular uptake is linear with time, displaying Michaelis-Menten kinetics, whereas the extracellular uptake exhibits saturation kinetics [K(m) and V(max) 149 ± 19 μM & 11.0 ± 0.8 μM g^{-1} h^{-1} respectively]. Both are temperature dependent and intracellular uptake is light stimulated, increasing by about 15. Incubation with Cd and equimolar concentrations of Ca, Mg, or Zn reduced both intracellular and extracellular uptake. Pretreating the thalli with KNO_3 stimulated Cd uptake, most likely due to the ability of the K to remove competing ions from the cell walls, a technique used to measure cation exchange. All of this suggests the involvement of cation exchange in the uptake of cadmium. The researchers suggested that such exchange sites might protect the liverworts by securing the heavy metal ions outside the cell.

When Mautsoe and Beckett (1996) explored the effects of Cd on ***Dumortiera hirsuta*** (Figure 53-Figure 55), they found that intracellular Cd uptake was linear, but extracellular uptake exhibited saturation kinetics. These uptake processes were temperature dependent. Light also stimulated intracellular uptake, but storage for 20 days in the dark did not affect it. Uptake decreased when the plants were incubated with additional Mg, Zn, or Cd, whereas pretreatment with KNO increased uptake, indicating cation exchange with the KNO clearing the exchange sites of cations. Such exchange sites might protect the liverworts by securing the heavy metal ions outside the cell.

Mautsoe (1997) found that photosynthesis of ***Dumortiera hirsuta*** (Figure 53-Figure 55) was more sensitive to Cd than it was in ***Atrichum androgynum*** (Figure 70), with differences directly related to intracellular Cd concentrations. These concentrations were considerably higher in ***D. hirsuta***. Furthermore, in ***D. hirsuta*** the Cd caused K loss, but this did not occur in ***A. androgynum***. Intracellular uptake in ***D. hirsuta*** was affected by thallus age, K pretreatment, and site characteristics.

Loo *et al*. (2005b) described the tolerance range of ***Dumortiera hirsuta*** (Figure 53-Figure 55) to occur within the 480-1740 m asl on Mt. Kinabalu. Here it experienced ranges of 47-1511 lux, 15-27ºC, and 60-95% humidity. Hence we should expect it to be adapted to stresses within these ranges.

Adaptations

Butt and Anima (2011) found that ***Dumortiera hirsuta*** (Figure 53-Figure 55) in Bhaderwah, northwest Himalayas, exhibits great diversity of habitat, *p*H, and altitude, with accompanying diversity of morpho-anatomical characters of both gametophyte and sporophyte. Piippo and Koponen (2013) noted that this species is likely to include many cryptic taxa.

Although ***Dumortiera hirsuta*** (Figure 53-Figure 55) occurs in moist habitats, those are not always moist (Figure 71). Thus, the plants need mechanisms to protect vulnerable life cycle stages that coincide with less favorable seasons. Perhaps one such adaptation is that the archegonial head is covered with hairlike appendages (O'Hanlon 1934), suggesting an adaptation that protects the critical archegonia and developing sporophytes from drying out. The adult thallus has no **lacunae** (unfilled space or interval; gap) and no definite demarcation between the chlorophyllous and colorless cells, the latter being mostly in the central part of the thallus. Does the lack of lacunae suggest faster drying, or does the absence of these air spaces slow it down? Based on movement of water through stomata of tracheophytes, we can hypothesize that the absence of lacunae would slow down water loss. Researchers have demonstrated that stomatal-derived water loss from plants is ~50% of the total terrestrial evaporation and 80-90% of the continental evaporation (Hetherington & Woodward 2003; Jasechko *et al*. 2013).

There are only vestigial ventral scales (Figure 72) (McAllister *et al*. 2019) – structures that usually help in water movement, uptake, and conservation, perhaps causing the restriction of ***Dumortiera hirsuta*** to moist habitats. Watson (1919) considered that having few or no ventral scales is an adaptation or characteristic of a species from an aquatic habitat.

Figure 71. ***Dumortiera hirsuta*** with thallus showing signs of drying. Photo by Blanka Aguero, with permission.

Figure 72. ***Dumortiera hirsuta*** ventral side showing absence of or vestigial scales. Photo by Nicola van Berkel, through Creative Commons.

Adaptations may differ between lineages. The Central American lineage has plants with a light green velvety appearance, caused by abundant papillae on the upper surface (Forrest *et al*. 2011). The role of papillae has been controversial and unproven, including movement of water into cells in some species, scattering light, and reducing water loss. The more widespread lineage is dark green and papillae range from absent to dense; marginal hairs are usually abundant. It appears that these two lineages might have different adaptations to surviving periods of drought and receding water.

Dumortiera hirsuta (Figure 53-Figure 55) is polyploid, with populations exhibiting monoploid or diploid gametophytes (Tatuno 1938, 1939). It is likely that the differences between monoploid and diploid gametophytes of ***Dumortiera hirsuta*** might confer some differences in adaptations. In some cases, some alleles of diploids were missing among monoploids, but both types shared the character of upright, short hairs scattered on the dorsal surface (Akiyama *et al*. 2003). In Taiwan populations, Akiyama and coworkers found that monoploids could grow on non-calcareous substrata, a single population could have different levels of ploidy, heterozygosity is fixed in diploids, and there are at least four monoploid lineages ("species" according to Akiyama *et al*.). The evidence suggests that these diploids are **allopolyploids** (two or more chromosome sets originating as complete sets from different species or lineages). The presence of multiple chromosome sets and lineages would provide greater variation, thus permitting the species to survive a wider range of conditions.

Storage compounds can vary with seasons. Kapila *et al*. (2014) compared three liverworts and found that the more hydric ***Dumortiera hirsuta*** (Figure 53-Figure 55), with a habitat near streams or other hydric locations, exhibits higher carbohydrate and protein content with little seasonal change compared to ***Marchantia emarginata*** (Figure 73) and ***M. paleacea*** (Figure 74), both of mesic habitats. All three species experienced a decrease in α-amylase, β-amylase, and invertase near the end of the primary growth season due to carbohydrate accumulation in their tissues. There was an inverse relationship between protein and free amino acids. Protease activity, associated with protein metabolism, peaked in the rainy season.

Figure 73. ***Marchantia emarginata***, a species with lower carbohydrate and protein content and more seasonal change compared with ***Dumortiera hirsuta***. Photo by Li Zhang, with permission.

Figure 74. ***Marchantia paleacea***, a species with lower carbohydrate and protein content and more seasonal change compared with ***Dumortiera hirsuta***. Photo by Jan-Peter Frahm, with permission.

Reproduction

Mcallister *et al*. (2019) considered ***Dumortiera hirsuta*** (Figure 53-Figure 55) to be **monoicous**. But Bischler-Causse *et al*. (2005) considered it to be **monoicous** or **dioicous** (Figure 75-Figure 77). It has no known asexual propagules.

Figure 75. ***Dumortiera hirsuta***, with emerging archegoniophores. Photo by Cheng-Tao Lin, through Creative Commons.

Figure 76. ***Dumortiera hirsuta*** with archegoniophores. Photo by Luis Funez, through Creative Commons.

Shimamura (2015) reported that the sperm possessed four flagella and experienced aerial dispersal. This species was the first to be documented with explosive sperm dispersal. Small droplets with sperm cells are expelled several centimeters into the air from the antheridial disk. Even in monoicous plants, this explosive dispersal facilitates the cross-fertilization between male and female reproductive structures on different individuals.

From South Carolina, USA, Patterson (1933) reported that male receptacles were initiated 11-19 August, with female receptacles (Figure 77) appearing 5-12 September. Fertilization occurred primarily 25 September to 5 October. Young embryos appeared 5 October to 15 October. Sporophytes developed in November and December, with meiosis occurring 26 January to 4 February. Meanwhile, the antheridial branches withered 20 December to 20 January. Spores matured in February. In March, the capsules blackened, fertile thalli were dying, and the receptacles elongated. In April the setae elongated and the spores were dispersed. Precipitation modified this schedule from year to year. Patterson detailed the development of the reproductive structures. One unusual character is that some receptacles have both male and female gametangia, but these do not occur on the same radii, with radii of the same sex grouped together. These receptacles with both sexes were relatively common in populations from Jamaica, but were rare in the North Carolina populations.

Figure 77. ***Dumortiera hirsuta*** young archegoniophores. Photo by Lin Kyan, with permission.

All the archegonia within an involucre may experience fertilization, but only one will get beyond the 2-8 cell stage (Patterson 1933).

In the UK the production of sporophytes is rare (Callaghan 2020). Since the seasons there are quite different from those in the tropics, temperature, day length, and rainy season might modify the reproductive timing so that it is unlikely to be successful.

Patterson (1933) reported the species producing sporophytes (Figure 78-Figure 80) on the bank of a small stream near Columbia, South Carolina, USA. O'Hanlon (1934) found that only one or two sporophytes (Figure 81) in each of the typically eight groups of archegonia are able to reach maturity. In Florida, USA, O'Hanlon found ripe spores (Figure 82-Figure 83) in the middle of April. They remain viable for only a short time after dehiscence. In the lab they germinate within 6-7 days on a liquid medium.

Figure 78. ***Dumortiera hirsuta*** with archegoniophores. Photo by buggi, through Creative Commons.

Figure 79. ***Dumortiera hirsuta*** with mature sporangia. Photo by Chris Wagner, through Creative Commons.

Figure 80. ***Dumortiera hirsuta*** with maturing sporangia. Photo by Chris Wagner, through Creative Commons.

Figure 81. ***Dumortiera hirsuta*** with mature sporangia, showing only 1-3 mature sporangia per archegonial head. Photo by tigris 8, through Creative Commons.

Figure 82. ***Dumortiera hirsuta*** archegonial head with dehiscing sporangia, in this case with four sporangia. Photo courtesy of Zen Iwatsuki.

Figure 83. ***Dumortiera hirsuta*** with sporangia and ripe spores. Photo by Luis Funez, through Creative Commons.

The young sporocyte has a single large plastid, but the plastid divides before the nucleus divides, resulting in four plastids (Shimamura *et al*. 2000). These often continue to divide before nuclear division. The cytoplasm forms lobes around the four plastid domains, enclosing at least one plastid. This monoplastidic meiosis is rare among liverworts.

O'Hanlon (1934) found that ***Dumortiera hirsuta*** (Figure 53-Figure 55) produces 1-2 sporophytes (Figure 82) that reach maturity among the eight groups of archegonia. Spores reach maturity in mid April in Florida, USA. They remain viable only a short time after the capsule dehisces. These spores germinate within 6-7 days after culturing in a liquid medium. The spore first produces a rhizoid; then a bud forms from the spore.

The young sporocyte has a single large plastid, but the plastid divides before the nucleus divides, resulting in four plastids (Shimamura *et al*. 2000). These often continue to divide before nuclear division. The cytoplasm forms lobes around the four plastid domains, enclosing at least one plastid. This monoplastidic meiosis is rare among liverworts.

Miyoshi (1973) described the spore wall structure of ***Dumortiera hirsuta*** (Figure 53-Figure 55). Kamimura (1973) used the electron microscope to help describe the

fine structure of the spore walls. Pyramidal or rectangular planks or columnar protuberances have irregular patterns on the surfaces of the spore walls. Two-three of these protuberances frequently form lamellae. The foundation of the spore wall is nearly smooth.

Role

This species surely plays a greater role in housing invertebrates than the examples we know (Figure 84). And what might its role be in stabilizing the banks of streams during high water? The ecosystem role of ***Dumortiera hirsuta*** (Figure 53-Figure 55) remains mostly unexplored.

Figure 84. ***Dumortiera hirsuta*** with snail, a potential herbivore on this species. Photo by Chaturvedi, with permission.

Interactions

Iqbal *et al*. (2011) enumerated the wide array of organisms associated with ***Dumortiera hirsuta*** (Figure 85), including fungi, other bryophytes, pteridophytes, gymnosperms, angiosperms, and insects. In Bhaderway in the Doda district of Jammu, India, in the range of 1230-2600 asl ***Conocephalum conicum*** (Figure 66) formed the most frequent associations, but these researchers found 12 species of plants and one insect that were frequently associated with ***D. hirsuta***.

Figure 85. ***Dumortiera hirsuta*** with the moss ***Sematophyllum*** sp. in India. Photo by Syamal L, through Creative Commons.

Fungal Interactions

The fungi associated with ***Dumortiera hirsuta*** (Figure 53-Figure 55) remain unexplored. The species has antifungal properties (Alam *et al.* 2011), but that is not usually enough to deter all fungi. And are those antifungal compounds produced by the liverwort, or by associated bacteria?

Alam *et al*. (2011) found that treatment of ***Aspergillus niger*** (Figure 86) by extracts from ***Dumortiera hirsuta*** (Figure 53-Figure 55) caused distinct morphological changes in the fungus. These included anomalies in the hyphae, flaccid cell wall, and cytoplasm leaking through cell wall and becoming granulated.

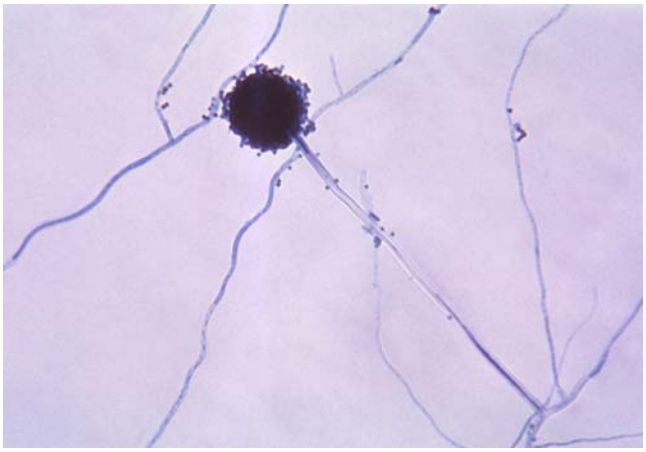

Figure 86. ***Aspergillus niger***, a species that exhibits morphological aberrations after exposure to extracts of ***Dumortiera hirsuta***. Photo from CDC, through public domain.

Egertová *et al*. (2018) described a new species of Ascomycetes growing on ***Dumortiera hirsuta*** (Figure 53-Figure 55). ***Octosporopsis erinacea*** (Figure 87) parasitizes the thallus, exhibiting tiny, light yellow, rimless apothecia. The hyphae develop both on and within the cells of the thallus, especially near a waterfall.

Figure 87. ***Octosporopsis erinacea***, a species of Ascomycetes that parasitizes the thallus of ***Dumortiera hirsuta***. Photo by Z. Egertová, through Creative Commons.

Animal Interactions

Among the inhabitants of ***Dumortiera hirsuta*** (Figure 53-Figure 55) is the odonate ***Epiophlebia superstes*** (Figure

88) (Asahina & Sugimura 1981). This odonate is intermediate between dragonflies and damselflies. It injects its eggs into the thallus of ***D. hirsuta***. Later, Carle (2012) described the new species ***Epiophlebia diana*** from naiads in China. However, Büsse and Ware (2022) have considered it to be a synonym of ***Epiophlebia laidlawi*** (Figure 89), occurring in Nepal, India, Bhutan, and Vietnam. Members of this genus in China typically choose plants growing in wet and mostly shaded areas less than a meter from a stream.

Figure 88. ***Epiophlebia superstes*** on bryophytes. Photo by Tom Kompier, with online non-commercial permission.

Figure 89. ***Epiophlebia laidlawi*** naiad, an inhabitant of ***Dumortiera hirsuta*** in China. Photo modified from Robert John Tillyard, through public domain.

Lien (1989) suggested that species of biting midges (**Ceratopogonidae: *Lasiohelea***) that rest on ***Dumortiera hirsuta*** (Figure 53-Figure 55) and other bryophytes are likely to be feeding on the **Cyanobacteria** (Figure 32) that are growing there. Lien found that ***Anabaena*** sp. (Figure 90) is especially beneficial for ***Forcipomyia anabaenae*** (see Figure 91), in a closely related genus.

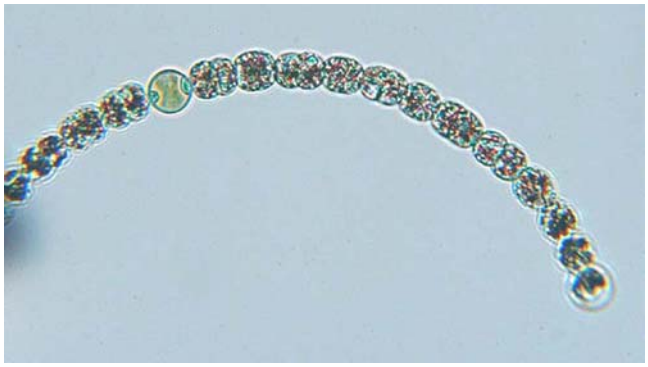

Figure 90. ***Anabaena circinalis***; the genus ***Anabaena*** is a beneficial food for some biting midges that visit bryophytes. Photo by B D Carl, through Creative Commons.

Figure 91. ***Forcipomyia*** sp., a genus wherein some members seem to benefit from eating ***Anabaena*** associated with bryophytes. Photo by XPDA, through Creative Commons.

The fly family **Agromyzidae** (Figure 92-Figure 94) occurs on liverworts throughout the world (Spencer 1990). It is a miner on ***Dumortiera hirsuta*** in Mexico.

Figure 92. ***Phytoliriomyza dorsata*** (**Agromyzidae**), in a family that mines thallose liverworts. Photo by Mardon Erbland, through Creative Commons.

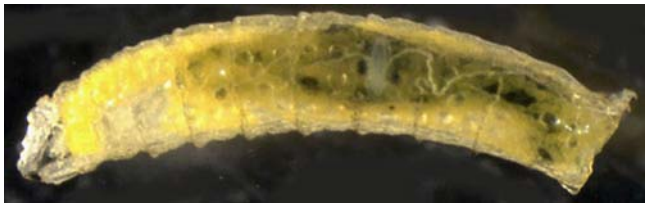

Figure 93. ***Phytoliriomyza melampyga*** larva (**Agromyzidae**), in a family that mines thallose liverworts. Photo by W. N. Ellis, through Creative Commons.

Figure 94. ***Phytomyza*** sp. leaf mining (**Agromyzidae**), in a family that mines thallose liverworts. Photo by Beatriz Moisset, through Creative Commons.

Biochemistry

Dumortiera hirsuta (Figure 53-Figure 55) has been the subject of a number of biochemical studies. Matsuo *et al*. (1976) reported 10 sesquiterpene hydrocarbons from ***Dumortiera hirsuta***. Toyota *et al*. (1997a,b) reported on a new sesquiterpene compound and 13 additional known compounds from the species and described their structures. Saritas *et al*. (1998) added additional sesquiterpenes to this list, some of which were rare or unusual. To these, Lu *et al*. (2006) added more compounds (terpenoids and bisbibenzyls from Chinese populations, including riccardin D) and described their structure. Some of these were cytotoxic to the human HepG2 cells. One was also active against ***Pseudomonas aeruginosa*** (Figure 95).

Liu *et al*. (2012) found that riccardin D (a macrocyclic bisbibenzyl compound), a product of ***Dumortiera hirsuta*** and other liverworts, was effective at inhibiting intestinal adenoma from forming in mice. Its effectiveness is through multiple mechanisms, including anti-proliferative, apoptotic, anti-angiogenic, and anti-inflammatory activity. Xue *et al*. (2012) found that the riccardin D also induces apoptosis of human leukemia cells.

Xie and Lou (2008) identified two calamenane-type sesquiterpenoids (5,7-dihydroxycalamenene and 7-hydroxycalamenene) from ***Dumortiera hirsuta*** (Figure 53-Figure 55). Bardón *et al*. (1999) isolated dumortane sesquiterpenes, four new, from Argentine populations of ***Dumortiera hirsuta*** (Figure 53-Figure 55). Linde *et al*. (2016) considered that the presence of dumortane-type sesquiterpenoids in ***D. hirsuta*** from South Africa indicated that this species is similar in chemistry to an Argentinean sample.

Xie *et al*. (2007) reported an unusual phenylethyl cyclohexadienone (dumhirone A) from Chinese populations of ***Dumortiera hirsuta*** (Figure 53-Figure 55).

Alam *et al*. (2011) found that aqueous extracts of ***Dumortiera hirsuta*** (Figure 53-Figure 55) were effective against seven plant pathogens. Six of seven plant pathogenic fungi were completely inhibited by the extract at 550-600 ppm. Joshi (1993) also found extracts to be effective against bacteria. Kumar *et al*. (2007) likewise found that extracts of this liverwort in Indian Himalayas were effective in enhancing wound healing due to its antibacterial properties.

Setyati *et al*. (2021) found that extracts from ***Dumortiera hirsuta*** (Figure 53-Figure 55) were able to prevent infection by pathogenic bacteria, including flavonoids, alkaloids, and steroids. These were able to inhibit the bacteria ***Escherichia coli*** (Figure 48), ***Staphylococcus aureus*** (Figure 47), and ***Salmonella typhi*** (Figure 96), causing weak to moderate responses (see also Luthfiah *et al*. 2021). Junairiah *et al*. (2015) similarly found that ethylacetate extracts of ***D. hirsuta*** from Indonesia contained flavonoids, alkaloids, and steroids that can inhibit the pathogenic bacteria ***Staphylococcus aureus*** and ***Escherichia coli*** and the yeast ***Candida albicans*** (Figure 97).

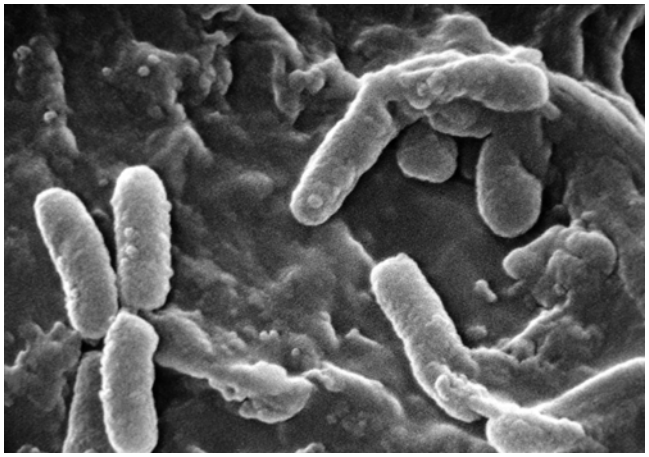

Figure 95. ***Pseudomonas aeruginosa***, a species that experiences toxicity from one of the compounds produced by ***Dumortiera hirsuta***. Photo by Janice Haney Carr, CDC, through public domain.

Figure 96. ***Salmonella typhi***, a species that is inhibited by extracts from ***Dumortiera hirsuta***. Photo by CDC, through public domain.

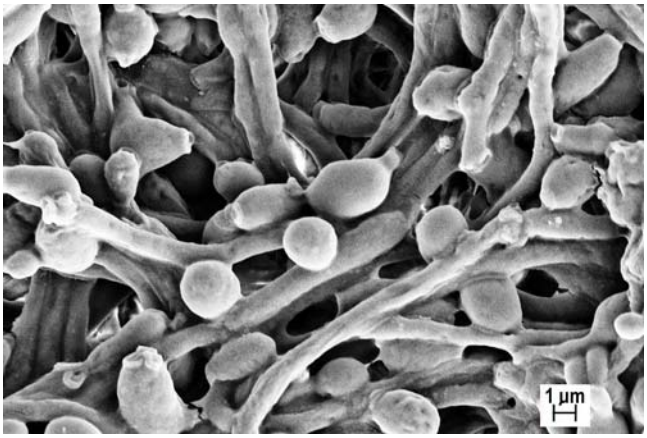

Figure 97. ***Candida albicans*** SEM, a yeast species that is inhibited by extracts from ***Dumortiera hirsuta***. Photo by Vader1941, through Creative Commons.

An aqueous extract from ***Dumortiera hirsuta*** (Figure 53-Figure 55) exhibited fungitoxicity against seven plant pathogenic fungi, inhibiting their ability to produce germinable spores (Alam *et al*. 2011). Morphological aberrations were present in ***Aspergillus niger*** (Figure 86) treated with extracts of ***Dumortiera hirsuta***.

Mukherjee *et al*. (2012) examined antibacterial activity of ***Dumortiera hirsuta*** (Figure 53-Figure 55) against ***Serratia marcescens*** (Figure 98) from various altitudes in the Himalayas. Those plants from higher altitudes exhibited slightly less antibacterial activity than those from lower altitudes. The reproductive thallus extracts exhibited less antibacterial activity than did the vegetative thallus.

Figure 98. ***Serratia marcescens*** on bread, a bacterial species that is inhibited less by populations of ***Dumortiera hirsuta*** from higher elevations than by those at lower elevations. Photo by DBM, through Creative Commons.

Noting that ***Dumortiera hirsuta*** contains the bioactive alkaloids, terpenoids, flavonoids, and saponin, Sari (2014) explored its usefulness in the treatment of malaria. It was effective in treating parasitemia caused by ***Plasmodium berghei*** (Figure 99) in mice, so its usefulness against ***Plasmodium malariae*** (Figure 100) was worth exploration. Unfortunately, in their further experiments against ***P. berghei*** in mice, they found that it damaged microanatomical structures in the liver and kidneys at levels of 300 mg kg^{-1} BW and above.

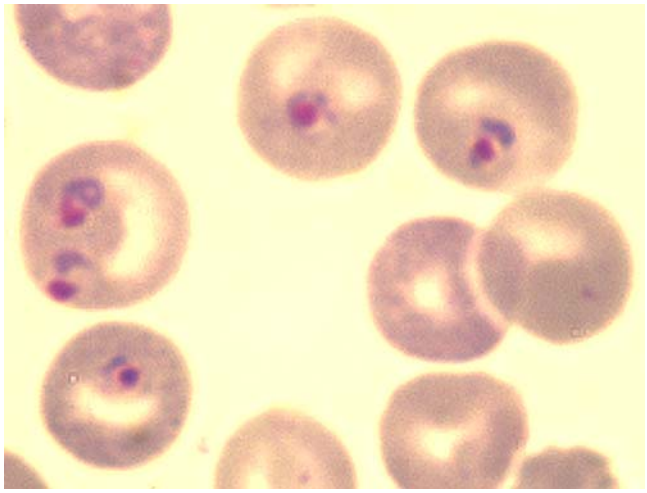

Figure 99. ***Plasmodium berghei***, a species that can be inhibited successfully by extracts of ***Dumortiera hirsuta***. Photo by C. J. Janse, through Creative Commons.

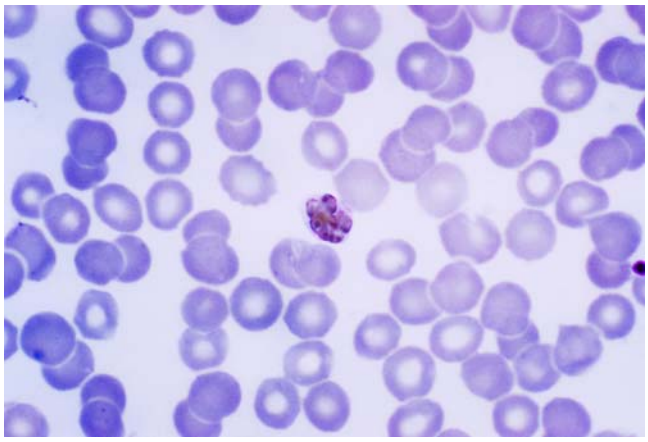

Figure 100. ***Plasmodium malariae***, a species that might be inhibited by extracts of ***Dumortiera hirsuta***. Photo by Mae Melvin, CDC, through public domain.

Shirzadian *et al*. (2009) found that ethanolic extracts of ***Dumortiera hirsuta*** (Figure 53-Figure 55) exhibited one of the broadest spectra of antifungal activities shown by the 23 bryophytes tested. Luthfiah *et al*. (2021) noted that this species can be used medically to prevent bacterial infection.

Asakawa (1982) used the terpenoids and aromatic compound differences to argue for separation of ***Wiesnerella denudata*** (Figure 101) and ***Dumortiera hirsuta*** (Figure 53-Figure 55) into different families. Those sesquiterpene lactones and monoterpenoids occurring in ***W. denudata*** appear to be absent in ***D. hirsuta***. This supports the morphological differences also known between these two species. Kraut *et al*. (1996) reported several carboxylated α-pyrone derivatives and flavonoids from ***Dumortiera hirsuta*** and elucidated structures.

In their attempts to distinguish differences in secondary compounds between ***D. hirsuta*** ssp. ***hirsuta*** (Figure 53-Figure 55) and ***D. hirsuta*** ssp. ***nepalensis*** (Figure 102-Figure 103). Durant-Archibold *et al*. (2018) reported 34 compounds for the first time in the species ***Dumortiera hirsuta***. They found that the two subspecies differed biochemically.

Figure 101. ***Wiesnerella denudata*** in Bhutan, a species wherein chemical differences separate it from ***Dumortiera hirsuta***. Photo by David Long, with permission.

Dumortiera hirsuta ssp. *nepalensis* (Figure 102-Figure 103)

(syn. = *Dumortiera trichocephala*)

Figure 102. ***Dumortiera hirsuta* ssp. *nepalensis***. Photo courtesy of David Wagner.

Figure 103. ***Dumortiera hirsuta* ssp. *nepalensis*** from Bhutan. Photo courtesy of David Long.

In most cases, the subspecies ***nepalensis*** is considered as part of ***Dumortiera hirsuta***, but it has been classified as a variety, a subspecies, and even a species. In the foregoing discussion I have considered ***Dumortiera hirsuta*** *sensu lato*. However, since I did find some separate information on it, I shall comment on that with the anticipation that it might be officially removed from ***D. hirsuta*** in the future.

Distribution

In 1919, Evans considered this to be the separate species ***Dumortiera nepalensis*** (Figure 102-Figure 103). He described its distribution as close to that of ***D. hirsuta*** (Figure 53-Figure 55), but absent in Europe and Africa. But it is rare in much of its range, especially the southern United States and West Indies, and David Long (pers. comm. 26 June 2022) considers these populations to belong to ***Dumortiera hirsuta* ssp. *hirsuta*** (Figure 53-Figure 55). ***Dumortiera hirsuta* ssp. *nepalensis*** (Figure 102-Figure 103) is most abundant in southeastern Asia.

Aquatic and Wet Habitats

Dumortiera hirsuta* ssp. *nepalensis (Figure 102-Figure 103) occurs submersed under water jets, above the water level, and in waterfalls in the tropics (Ruttner 1955). David Long (pers. comm. 26 June 2022) reports the subspecies from the slope of dry rocky side valley and under overhanging dripping rocks by roads in the Tashigang districts south of Tashi Yangtse, Bhutan.

Biochemistry

Durant-Archibold *et al*. (2018) found that the major volatile compounds in ***Dumortiera hirsuta* ssp. *nepalensis*** (Figure 102-Figure 103) from Panama were ledene, α-gurjunene, β-caryophyllene, and α-guaiene, differing from those of the subspecies ***hirsuta***.

Summary

Cyathodium is **r-selected**. It has several species that occupy wet habitats in mostly tropical areas. Several species occur on stream and river banks, with ***C. bischlerianum*** and ***C. cavernarum*** typically closer to the water than is ***C. spruceanum***. Species often have pungent odors, attesting to their unique secondary compounds. Others, such as ***Cyathodium bischlerianum***, have pleasant odors suitable for cosmetics and soaps. Some species, such as ***Cyathodium cavernarum***, have iridescent colors, but the function of those, if any, is unknown.

Dumortiera hirsuta has a similar distribution and occurs in splash zones of streams and waterfalls and on otherwise wet rocks. It is a shade-adapted species that otherwise occupies a wide range of habitat conditions, *p*H, and altitude. There are flies in **Agromyzidae** and **Ceratopogonidae** that are specialists on it. In some cases, the invertebrates occur there to consume associated **Cyanobacteria**. The secondary compounds of ***D. hirsuta*** possess antibiotic and medicinal properties.

Acknowledgments

Lars Söderström helped me find the current acceptable names for a number of older taxa.

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AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: MARCHANTIACEAE, PART 1

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CHAPTER 1-23
AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: MARCHANTIACEAE, PART 1

Figure 1. ***Marchantia debilis*** on emergent rocks in Madagascar. Photo courtesy of Catherine Reeb.

Marchantiaceae

Marchantia

Marchantia is widespread in the world. In the western Cascade Mountains, Oregon, USA, it is a pioneer **riparian** (relating to wetlands adjacent to rivers and streams) genus (Campbell & Franklin 1979). Several species in this genus are associated with wet habitats, with some occasionally becoming submersed.

ike most of the older taxa, this genus has a history of species synonyms (Bischler-Causse 1993). For example, of the 28 species described in Africa, Bischler-Causse reduced them to only 6, although another 8 remained unresolved.

Zheng *et al*. (2020a) have suggested that the morphology of the gemmae can be used to help in separation of the taxa, and that molecular analyses support these separations.

Bischler-Causse (1993) suggested that dispersal of at least some of the species seems to be limited by temperature extremes, but the species also require water throughout the year, free space, and light, thus limiting their success in much of the dry parts of the African continent. This distribution is further limited by the low level of sexual reproduction, relying on vegetative multiplication – a means that is more limited in dispersal distance.

Although ***Marchantia polymorpha*** (Figure 2) is by far the liverwort of choice, other species have been important

in unravelling the genetic and evolutionary history of liverworts. Marks *et al*. (2019a,b) presented the genome assembly for ***Marchantia inflexa*** (Figure 3-Figure 4) and found evidence suggesting that dehydration tolerance may be related to sex-specific genes in ***Marchantia***. They found that the genes on the sex chromosomes experience greater diversifying selection than do the autosomal and organellar genes.

Figure 2. ***Marchantia polymorpha*** at tree base on bank of small river in Pfaelzer Wald, Germany. Photo courtesy of Michael Lüth.

Figure 3. ***Marchantia inflexa*** females, a species where dehydration tolerance may be related to sex-specific genes. Photo by Amelia Merced, with permission.

Figure 4. ***Marchantia inflexa*** with gemmae. Photo by Alan R. Franck, through Creative Commons.

Ahmad (1981) described the historical studies on spore germination and gametophyte development in ***Marchantia***.

Marchantia berteroana (Figure 5-Figure 7)

(syn. = *Marchantia cephaloscypha*, *Marchantia tabularis*)

Campbell (1965) reviewed some of the history of the nomenclature for this species. Another species recorded for New Zealand and described by Stephani (1883), namely *M. cephaloscypha*, is considered by Evans after examination of an original specimen to correspond with ***M. berteroana*** (Evans 1917). In Columbia, Herzog (1934) described the variety *polylepida*, but that is now considered to be ***M. berteroana*** as well.

Distribution

Marchantia berteroana (Figure 5-Figure 7) is known in Australia, New Zealand (Campbell 1965; Wikipedia 2021), Southern Africa (Perold 1995; Lüth & Schafer-Verwimp 2004; Phephu 2012a,b), South America (Costa Rica to the Antarctic Peninsula) (Hassel de Menendez 1962; Campbell 1965; Lüth & Schafer-Verwimp 2004), Antarctica (Davey 1997), and non-continental locations such as Papua New Guinea, Java, New Caledonia, and various smaller islands (Driessen 2009; Wikipedia 2021). Phephu (2012a) noted that this species is prevalent in the winter-rainfall region of South Africa, but it also grows in regions that receive summer rain in KwaZulu-Natal, Mpumalanga and Limpopo provinces.

Figure 5. ***Marchantia berteroana*** thallus. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 6. ***Marchantia berteroana*** thallus. Photo by Sarah Lloyd, with permission.

Figure 7. ***Marchantia berteroana*** vegetative thallus with gemmae cups. Photo by Clive Shirley, Hidden Forest, with permission.

Aquatic and Wet Habitats

Marchantia berteroana (Figure 5-Figure 7) lives in constantly damp, shaded areas (Figure 8) (Wikipedia 2021), including fresh water, waterfall splash zones, forest floors, and streambanks (Phephu 2012a,b). The species is widespread in New Zealand, especially near hot springs, and in southern Africa in swampy areas, **kloofs** (steep-sided wooded ravine or valley in Africa), gorges, and burned areas (Campbell 1965; Perold 1995). Li Zhang (pers. comm. 4 August 2022) found it growing in peatlands in Chile (Figure 9). In also occurs in peatlands in Colombia (Campos 2014). On the Juan Fernández Islands, it grows in expansive colonies on the mountain tops (Figure 10-Figure 11) where clouds most likely maintain its needed moisture levels.

Figure 8. ***Marchantia berteroana*** thallus growing on a damp soil bank. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 9. ***Marchantia berteroana*** in peatland in Puerto Williams, Chile. Photo courtesy of Li Zhang.

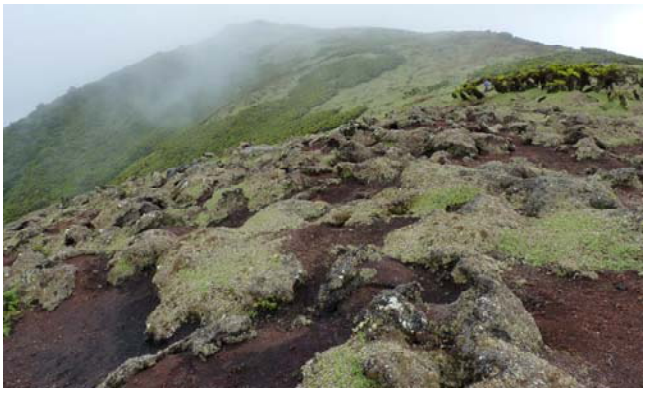

Figure 10. ***Marchantia berteroana*** soil habitat on Alejandro Selkirk Island, Juan Fernández Archipelago, Chile. Photo by Pato Novoa, through Creative Commons.

Figure 11. ***Marchantia berteroana*** habitat on Alejandro Selkirk Island, Juan Fernández Archipelago, Chile. Photo by Pato Novoa, through Creative Commons.

In geothermal areas in the Antarctic, ***M. berteroana*** (Figure 5-Figure 7) can occur at surface temperatures of 25-35ºC and subsurface temperatures of 50-60ºC, although these underground temperatures have no direct effect on the bryophytes (Convey & Lewis Smith 2006). Lewis Smith (2005a,b) found that on Deception Island in the South Shetland Islands, a geothermal gully included ***Marchantia berteroana*** (Figure 5-Figure 7) as one of the colonizers, forming a peripheral zone at the margin of the primary moss vegetation, living on fine moist compacted clay. He attributed its abundance to the "copiously produced and widely dispersed gemmae."

Halloy (1991) reported ***Marchantia berteroana*** (Figure 5-Figure 7) from heated areas (Figure 12) in the Andes, at 6000 m asl. These communities comprised the highest elevation of the known autotrophic communities on the planet.

Figure 12. Geothermal fissure and ***Sphagnum***; heated areas in the Andes can be suitable habitats for ***Marchantia berteroana***. Photo from a geothermal vent in Iceland, by Janice Glime.

Despite its seeming preference for wet habitats, it is a colonizer on soil following fire in Tasmanian mixed forests (Duncan & Dalton 1982) and also in southern Africa (Perold 1995). The rapid germination of the spores and rapid development of the gametophyte gives the species an advantage in this habitat. Brasell and Mattay (1984) found it as a colonizer in burned *Eucalyptus* forest (Figure 13) in Tasmania, where it accumulated a high concentration of potassium. In these forests, N, P, K, and Ca, but not Mg, all decreased with time following the fire. Brasell *et al*. (1986) found that ***Marchantia berteroana*** contributed significantly to nitrogen fixation in burned sites of southern Tasmania, greatly exceeding rates of bryophytes in unburned forests.

Figure 13. *Eucalyptus* forest at Sherbrooke, Victoria, Australia – fire-adapted forest where ***Marchantia berteroana*** often appears after fire. Photo by Patche99z, through public domain.

Duncan and Dalton (1982) showed that ***Marchantia berteroana*** spores germinated well on burned ground. The protonemal growth is more rapid than that of the non-colonizing species, giving the ***M. berteroana*** a chance to establish before other, more competitive species arrive.

Phephu (2012a) considers ***Marchantia berteroana*** to be important in nutrient cycles and erosion control, thus stabilizing the soil.

Physiology

Davey (1997) used measurements of respiration, photosynthesis, irradiance, and temperature to model the year-round net productivity of ***Marchantia berteroana*** (Figure 5-Figure 7), estimating a yearly net productivity of 823±75 mg C g^{-1} ash-free dry weight. Desiccation was highly adverse to the thalli (Figure 14). Below a water content of 12 g g^{-1} ash-free dry weight the photosynthetic capacity was reduced. Recovery was only ca. 10% after dehydration and rehydration. Freezing also caused great photosynthetic reduction, although the model indicated that this species should be able to photosynthesize at sub-zero temperatures. Davey suggested that the photosynthetic capacity and freezing tolerance were likely to be seasonal.

Figure 14. ***Marchantia berteroana*** showing dying edges, suggesting drought damage. Note its low-lying habit on the mosses. Photo by Andrew Hodgson, with permission.

Despite that fact that the model indicates that freezing causes a great reduction in photosynthesis, the model suggests that photosynthesis at sub-zero temperatures is, nevertheless, likely (Davey 1997). It is suggested that seasonality in the photosynthetic capacity and the survival of these plants subjected to sub-zero temperatures might be important. However, their distribution is likely to be limited by available moisture.

Green and Lange (1995) found that the CO_2 compensation point is much lower for ***Marchantia berteroana*** (Figure 5-Figure 7) in 2% oxygen than for the other bryophytes they tested, and that the compensation points rise with a rise in temperature, resulting in inhibition (Figure 15). Photosynthesis at 21% oxygen [usual atmospheric oxygen concentration on Earth (National Geographic 2022)] is depressed compared to that at 2% oxygen (Figure 16), with the depression increasing at higher temperatures.

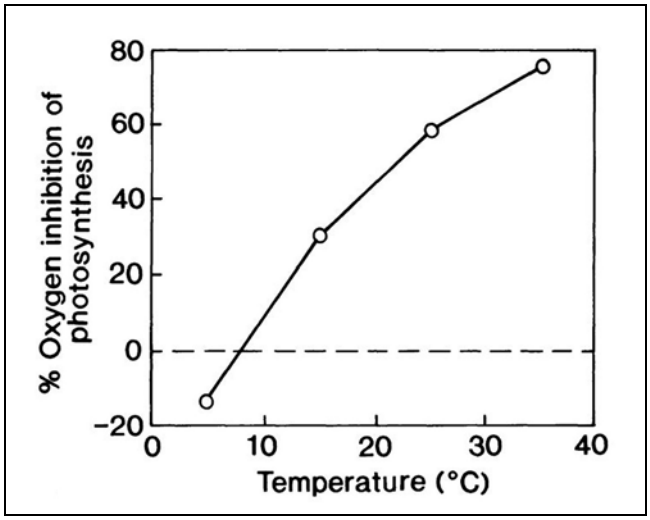

Figure 15. Temperature effect on oxygen inhibition in ***Marchantia berteroana***. Modified from Green & Lange 1995.

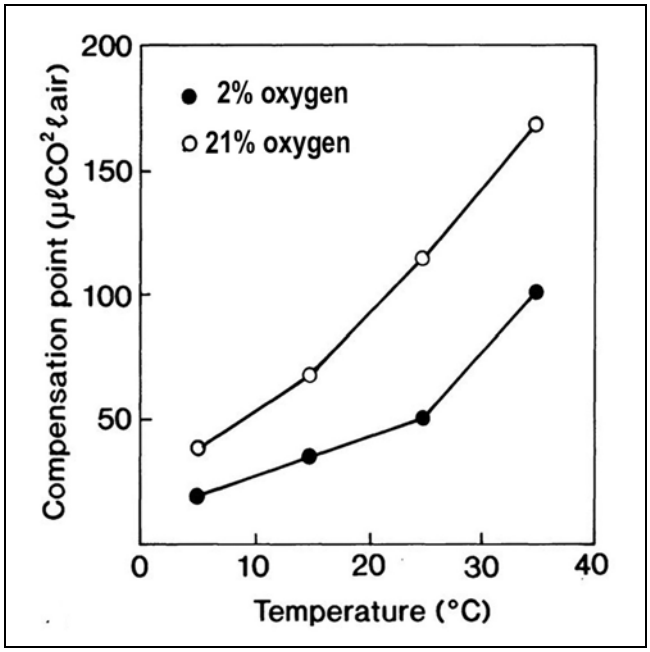

Figure 16. Temperature effect on CO_2 compensation point in ***Marchantia berteroana***. Modified from Green & Lange 1995.

Adaptations

Marchantia berteroana (Figure 5-Figure 7) has scales on the lower surface, a common feature of the genus, but in this case they extend nearly to the margins (Phephu 2012a, b). These may be hyaline or colored reddish-brown (Campbell 1965). The thallus itself helps to maintain its moisture by its low-lying habit (Figure 14) that keeps it closer to the water in the soil and by reducing evaporation from the soil.

Like other members of ***Marchantia***, the thalli have apical growing tips that are covered by scales (Figure 17). Presumably, these protect the important growing region from desiccation. When the older thallus dries out and dies, these apical areas can still retain living cells that can resume growth when favorable conditions return.

Figure 17. ***Marchantia berteroana*** thallus showing apical growing regions with apical scales covering them. Photo by Jan-Peter Frahm, with permission.

Reproduction

Marchantia berteroana (Figure 5-Figure 7) is **dioicous**, with a chromosome number of n=9 (Perold 1995; Phephu 2012a).

Males (Figure 18) are a bit larger than females (Figure 19-Figure 23) (Campbell 1965). In New Zealand, the antheridiophores (Figure 18) appear in August, followed in September by the archegoniophores (Figure 19-Figure 23).

Figure 18. ***Marchantia berteroana*** antheridiophore heads. Photo by Tom Thekathyil, with permission.

Figure 19. ***Marchantia berteroana*** with young archegoniophores. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 20. ***Marchantia berteroana*** with young archegoniophores before elongation. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 21. ***Marchantia berteroana*** with developing archegoniophores. Photo by Pato Novoa, through Creative Commons.

Figure 22. ***Marchantia berteroana*** mature archegonial head before sporangia are mature. Photo by Andrew Hodgson, with permission.

Figure 23. ***Marchantia berteroana*** with elongated archegoniophores, demonstrating how large a population can become. Photo by Pato Novoa, through Creative Commons.

Markham *et al*. (1978) found that there is a "dramatic" change in flavonoid pattern of ***Marchantia berteroana*** (Figure 5-Figure 7) that accompanies sexual reproduction. Is this a consequence or an adaptation? It would be interesting to know the role of the change in compounds in reproduction. Markham and Porter (1975, 1978) found that the aurone aureusidin 6-O-glucuronide occurs in antheridiophores (Figure 18) of at least two species of ***Marchantia***, one of which is ***M. berteroana***. It is unknown from any other organ of the liverworts. In flowering plants it gives brighter yellow colors to the flowers (Nakayama 2022). Markham and Porter suggested parallel evolution in bryophytes and flowering plants, although the compound is not common even in flowering plants.

The sporophyte begins development the following spring, continuing through the summer (Phephu 2012a). Once it matures, its stalk elongates by absorbing water, causing the cells to stretch. This causes the sporangia to protrude from the archegonial head (Figure 24-Figure 25). When the sporangium breaks open, it exposes the spores and elaters (Figure 25). Wiggling of the elaters in response to humidity changes helps to disperse the spores. Once the spores are dispersed, the fragile stalk disintegrates.

Figure 24. ***Marchantia berteroana*** archegoniophore heads with emerging open sporangia. Photo by Tom Thekathyil, with permission.

Figure 25. ***Marchantia berteroana*** mature sporangia with elaters protruding. Photo by Tom Thekathyil, with permission.

On the Falkland Islands, ***Marchantia berteroana*** (Figure 5-Figure 7) forms extensive patches several meters in diameter, from sea level to mountain tops (Duckett *et al*. 2012). Although it seems typical for females of this species to dominate elsewhere (Garcia-Ramos *et al*. 2007; Groen *et al*. 2010a), these populations produced males and females in about equal proportion. Perhaps this sex ratio is regulated by environmental/climatic conditions?

We know that gemmae (Figure 26-Figure 27) are produced when the sexual reproduction is inactive. High humidity suppresses the production of these gemmae cups, but high temperatures (ca. 15ºC) promote greater production of the cups (Chopra & Kumra 1988). Gemmae, and probably at times spores, are dispersed by water (Phephu 2012a).

Figure 26. ***Marchantia berteroana*** thallus forming a rosette, with gemmae cups. Photo by Tom Thekathyil, with permission.

Scott (1963) observed that plants of ***Marchantia berteroana*** (Figure 5-Figure 7) failed to produce gemmae cups (Figure 26-Figure 27) in New Zealand when pots were covered with glass or polyethylene sheets. He experimented with plants growing in a saturated atmosphere and demonstrated that it was indeed moisture that inhibited the development of gemmae cups. This behavior permits the liverwort to divert its resources to sexual reproduction at a time when conditions are most favorable for that type of reproduction.

Figure 27. ***Marchantia berteroana*** thallus showing distinct pores and gemma cups. Photo by Tom Thekathyil, with permission.

Interactions

Marchantia berteroana (Figure 5-Figure 7) has close associations with at least several other organisms. Meeks (2018) reported associations with **Cyanobacteria**. Brasell *et al.* (1986) found that ***Marchantia berteroana*** exhibited high rates of acetylene reduction, indicating a high rate of nitrogen fixation, in populations from burned sites in southern Tasmania. **Cyanobacteria** are important contributors to nitrogen fixation. Activity was considerably greater than that for the same species when they occurred in the adjacent undisturbed forest. There was no significant relationship with temperature, moisture, organic matter, nitrogen, or phosphorus in these associations. I found no studies regarding nitrogen fixation association in wet habitat populations, but I would expect it to occur there as well.

Fungal Interactions

Baylis (1970) found that ***Marchantia berteroana*** (Figure 5-Figure 7) formed mycorrhizal associations on unsteamed phosphorus-deficient soil. Baylis suggested that the fungi entered through the rhizoids. Johnson (1977) demonstrated that infection by members of the **Enogonaceae** in a New Zealand forest occurred in the lower part of the thallus and in rhizoids in ***Marchantia berteroana***. These endophytes seemed to lack specificity, occurring in a variety of the tracheophytes tested. It is likely that many associations remain to be identified.

Biochemistry

This species does not have the large number of biochemical studies reported for some of the other ***Marchantia*** species. Markham and Porter (1975) provided early reports on the flavones isoscutellarein and hypolaetin 8-glucuronides in ***Marchantia berteroana*** (Figure 5-Figure 7). The composition and concentration of these change in response to seasonal changes and reproductive stage of the plant. Acacetin and its glycosides are absent when

gametangia are present (Markham *et al*. 1978). Instead, during the sexually active stage, the predominant flavonoids are 8-hydroxyapigenin and 8-hydroxyluteolin glycosiduronic acids. These latter flavonoids are absent during the stage of asexual reproduction when the acacetin and its glycosides achieve their most active concentrations.

Asakawa and Campbell (1982) found that the major components of terpenoids and bibenzyls in ***M. berteroana*** (Figure 5-Figure 7) are cuparene and (−)-2-hydroxycuparene. Cuvertino-Santoni *et al*. (2017) described a number of the volatile constituents.

Marchantia debilis (Figure 1, Figure 28-Figure 32)

(syn. = *Marchantia chevalieri*)

Distribution

Marchantia debilis (Figure 28-Figure 32) is widespread in tropical Africa (Pócs & Lye 1999), where it is common north to south in the drier areas (Reeb *et al*. 2018).

Figure 28. ***Marchantia debilis*** on rock near water in Madagascar. Photo courtesy of Catherine Reeb.

Figure 29. ***Marchantia debilis*** in Madagascar, with archegoniophore. Photo courtesy of Catherine Reeb.

Figure 30. ***Marchantia debilis*** in Madagascar, showing dieback at the base of the thallus while the tips continue to grow. Photo courtesy of Catherine Reeb.

Figure 31. ***Marchantia debilis*** in Madagascar, showing numerous, overlapping thalli that help to conserve water. Photo courtesy of Catherine Reeb.

Figure 32. ***Marchantia debilis*** in Madagascar, growing on wet soil and rocks. Photo courtesy of Catherine Reeb.

Aquatic and Wet Habitats

Marchantia debilis (Figure 28-Figure 32) is more closely associated with water than some of the other species of ***Marchantia*** included here. It occurs on the edges of water in habitats like waterfalls, slow rivers (Figure 33-Figure 34), and ponds, on damp soil or rocks,

and sometimes experiences flooding, but it also occurs on terrestrial banks in both shaded and exposed areas (Reeb *et al*. 2018).

Figure 33. ***Marchantia debilis*** habitat on the riverbank in Madagascar. Photo courtesy of Catherine Reeb.

Figure 34. ***Marchantia debilis*** with ***Riccia*** on a riverbank in Madagascar. Photo courtesy of Catherine Reeb.

Hodgetts *et al*. (1999) similarly reported ***Marchantia debilis*** (Figure 28-Figure 32) from flushed rocks (Figure 35-Figure 36) in southern Africa. They are joined in this environment by the liverwort ***Asterella bachmannii*** (Figure 37), the mosses ***Bryum alpinum*** (Figure 38) and ***Philonotis*** spp. (Figure 39), and the hornworts ***Anthoceros*** spp. (Figure 40) and ***Phaeoceros carolinianus*** (Figure 41). ***Marchantia debilis*** also occurs on the soil and mud on river- and streambanks.

Figure 35. ***Marchantia debilis*** on rocks along riverbank in Madagascar. Photo courtesy of Catherine Reeb.

Figure 36. ***Marchantia debilis*** on rocks along riverbank in Madagascar. Photo courtesy of Catherine Reeb.

Figure 37. ***Asterella bachmannii***, an associate of ***Marchantia debilis*** on flushed rocks in southern Africa. Photo by Ricky Taylor, through Creative Commons.

Figure 38. ***Bryum alpinum***, an associate of ***Marchantia debilis*** on flushed rocks in southern Africa. Photo by Claire Halpin, with permission.

Figure 39. ***Philonotis fontana***; several species of ***Philonotis*** associate with ***Marchantia debilis*** on flushed rocks in southern Africa. Photo by Claire Halpin, with permission.

Figure 40. ***Anthoceros*** sp., an associate of ***Marchantia debilis*** on flushed rocks in southern Africa. Photo by Bramadi Arya, through Creative Commons.

Figure 41. ***Phaeoceros carolinianus***, an associate of ***Marchantia debilis*** on flushed rocks in southern Africa. Photo by Hermann Schachner, through Creative Commons.

Leonard (1994) found that ***Marchantia debilis*** (Figure 28-Figure 32) occurred on the periodically flooded parts of sandstone cliffs near Yanonge, Zaire, typically with ***Garckea flexuosa*** (Figure 42).

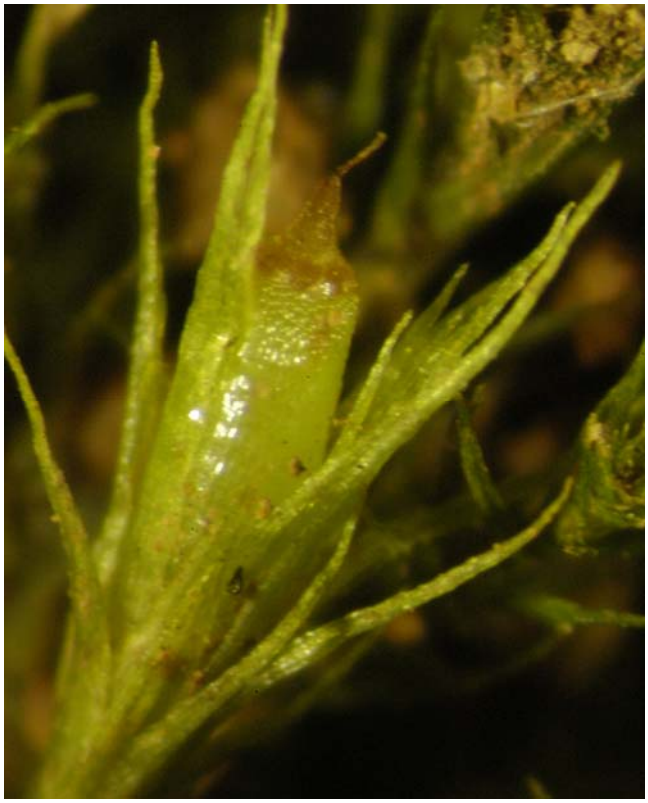

Figure 42. ***Garckea flexuosa***, an associate of ***Marchantia debilis*** in the flooded parts of sandstone cliffs in Zaire. Photo by Manju C. Nair, through Creative Commons.

Adaptations

The adaptations of ***Marchantia debilis*** (Figure 28-Figure 32) involve the same structures as in other species of ***Marchantia***. They have large air pores bordered with 5-8 rings of cells, with half projecting above the epidermis and half below into the photosynthetic air space (Reeb *et al*. 2018). The ventral scales occur in four rows and do not cover more than 30-50% of the thallus. These are purple, at least in the median portion of the thallus.

The thalli can grow over mosses (Figure 43), providing them with a water-retaining sponge that keeps them moist longer than just soil.

Figure 43. ***Marchantia debilis*** in Madagascar, growing with mosses that can help to retain moisture. Photo courtesy of Catherine Reeb.

Reproduction

As is typical for species of ***Marchantia***, ***Marchantia debilis*** (Figure 28-Figure 32) is **dioicous** (Reeb *et al*. 2018). I have not found information on stimuli needed to produce archegoniophores (Figure 44-Figure 45) or antheridiophores or what their seasonal behavior is. Gemmae (Figure 46) serve as effective means of asexual reproduction.

Figure 44. ***Marchantia debilis*** with an archegoniophore, in Madagascar. Photo courtesy of Catherine Reeb.

Figure 45. ***Marchantia debilis*** archegoniophore in Madagascar, showing large pores. Photo courtesy of Catherine Reeb.

Figure 46. ***Marchantia debilis*** with gemmae cups, in Madagascar. Photo courtesy of Catherine Reeb.

Biochemistry

Anchang *et al*. (2016) reported a new methanol extract, marchantinquinone-l'-methyl ether, from ***Marchantia debilis*** (Figure 28-Figure 32). In addition it had three known bis-bibenzyls. Asakawa (2021) noted that ***Marchantia debilis*** produces large quantities of marchantin-type bis-bibenzyls. Anchang and Simonsen (2019) reported that extracts from both wet and dry liverworts were able to inhibit the bacteria ***Staphylococcus aureus*** and ***Dermatophilus congolensis***, and the fungus ***Aspergillus flavus***. On the other hand, the bacteria ***Pseudomonas aeruginosa*** and ***Bacillus*** spp. were inhibited by extracts from dry, but not wet, ***Marchantia debilis***. This suggests that at least one of the inhibitory substances must be produced in response to desiccation.

Yongabi *et al*. (2016) reported that petroleum extracts from ***Marchantia debilis*** (Figure 28-Figure 32) could be used to treat at least some of the bacteria responsible for diabetic bacterial foot infections. This product has been marketed as BryoCream™. It had a 90% cure rate in three weeks.

Marchantia emarginata (Figure 47-Figure 53)

(syn. = *Marchantia palmata*, *Marchantia sumatrana*)

The taxonomic relationships of ***Marchantia emarginata*** (Figure 47-Figure 53) have recently been evaluated in India (Singh & Singh 2013) and Japan (Zheng & Shimamura 2021, 2022a).

Figure 47. ***Marchantia emarginata*** with enlarged terminal buds. Photo by Taiwan Mosses, through Creative Commons.

Distribution

Marchantia emarginata (Figure 47-Figure 53) is widespread, occurring in the Northern Hemisphere in Asiatic and Oceanic regions (Bischler-Causse 1989). Its distribution includes Borneo, China, Guam, Hong Kong, India, Indonesia Japan, Korea, Malaysia, Marianas, New Britain, New Caledonia, New Guinea, Philippines, Solomon Island, Sri Lanka, and Thailand (Bischler-Causse 1989; Siregar *et al*. 2020). In Malesia, it occurs from sea level to 1500 m asl, and Lu and Huang (2017) reported that it occurs below 1800 m asl, adding Taiwan to its distribution. Singh and Singh (2013) reported it for the first time in the Indian Himalayas. It is threatened in Singapore (Ho 2013).

Aquatic and Wet Habitats

Marchantia emarginata (Figure 47-Figure 53) occurs on walls of bays, in side brooks, on a large block in pouring water, in waterfalls, and in thermal acidic spray in the tropics (Ruttner 1955). In Sumatra, Siregar *et al*. (2020) found it on soil (Figure 48) and rocks (moist, damp or wet, shaded, semi-exposed places, riversides, creeks; Figure 49-Figure 50). Lu and Huang (2017) reported similar habitats in Taiwan, including damp soils up to 1800 m asl. As seen in the images, it occurs on the sides of drainage ditches (Figure 51-Figure 52) as well.

Figure 48. ***Marchantia emarginata*** male on soil. Photo by Ellen8355, through Creative Commons.

Figure 49. ***Marchantia emarginata*** on rocks in and beside stream. Photo courtesy of Tian-Xiong Zheng (NICH).

Figure 50. ***Marchantia emarginata*** on rocks along stream. Photo courtesy of Tian-Xiong Zheng (NICH).

Figure 51. ***Marchantia emarginata*** on rocks and concrete along ditch. Photo courtesy of Tian-Xiong Zheng (NICH).

Figure 52. ***Marchantia emarginata*** on rocks along ditch. Photo courtesy of Tian-Xiong Zheng (NICH).

But it can also occur on soil banks (Figure 53) if there is enough moisture. In southern China, this species is found frequently with ***Dumortiera hirsuta*** (Figure 54) on soil banks beside roads (Figure 55) (Li Zhang, pers. comm. 12 August 2022).

Figure 53. ***Marchantia emarginata*** ssp. ***cuneiloba*** on soil bank beside road. Photo courtesy of Tian-Xiong Zheng (NICH).

Figure 54. ***Dumortiera hirsuta***, associate of ***Marchantia emarginata*** on roadside soil banks. Photo ©mutolisp, through Creative Commons.

Figure 55. ***Marchantia emarginata*** ssp. ***tosana*** with ***Dumortiera hirsuta*** (larger, hairy thalli). Photo courtesy of Li Zhang.

Tewari and Pant (1996) reported that ***Marchantia emarginata*** (Figure 47-Figure 53) grew along the borders of warm springs in hot spring areas of the Kumaon Himalaya, but was unable to grow in the hot, sulfurous springs.

Adaptations

This is not a truly aquatic bryophyte, but lives in habitats that can be wet part or most of the time, then experience drought when water levels recede. Hence we should expect adaptations that mediate these drier conditions.

Marchantia emarginata (Figure 47-Figure 53) has scales that are purple or pale-purple (see Figure 56) (Lu & Huang 2017). These contribute to water movement, absorption, and maintenance of hydration. One can only speculate about the advantages of the color. We have seen, in the chapter on light in Volume 1, that red pigments can be in higher concentrations in shade plants than in full sunlight (Melati *et al*. 2019). Furthermore, in the extreme shade of the rainforest, some forest floor tracheophytes have red or purple on the lower leaf surface, increasing the absorption of light at the upper end of the photosynthetic action spectrum (Lee & Graham 1986). Hence, we can speculate that such a function might be operating in liverworts with purple scales. We need data to determine if the intensity of the color relates to the level of light in the habitat. I see no value to having this pigmentation on the ventral surface as a protection in high light. Do these scales somehow reflect light back to the photosynthetic tissue under low light conditions?

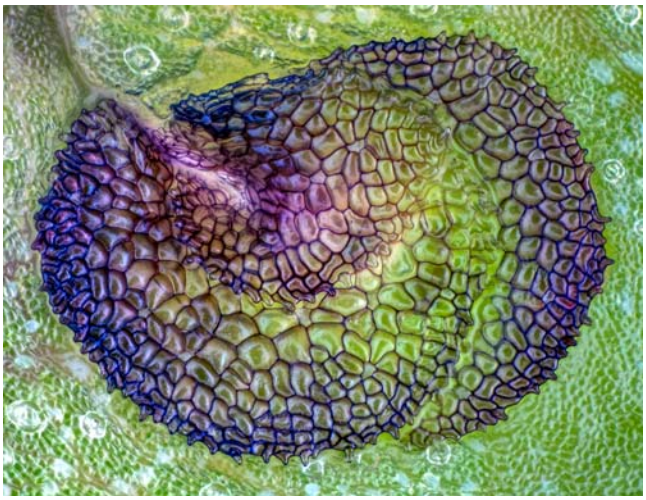

Figure 56. ***Marchantia polymorpha*** ssp. ***ruderalis*** scales showing purplish color of some ***Marchantia*** species. Photo by Des Callaghan, with permission.

Like other members of ***Marchantia***, ***M. emarginata*** (Figure 47-Figure 53) has pores in the epidermis. These provide entry of CO_2 into the chamber beneath where photosynthetic filaments reside. And cuticular ridges around the pores are hydrophobic, preventing the entry of water that would greatly reduce the ability of CO_2 to enter the photosynthetic filaments.

Like many thallose liverworts, the thallus of ***Marchantia emarginata*** (Figure 47-Figure 53) often grows over mosses (Figure 57, Figure 61). These mosses provide a sponge-like base that helps to retain water longer than soil or pebbles alone, thus widening the habitat range of the liverwort.

Figure 57. ***Marchantia emarginata*** subsp. ***tosana*** growing on mosses. Photo from Taiwan Mosses, through Creative Commons.

Reproduction

Reproduction in ***Marchantia emarginata*** (Figure 47-Figure 53) follows that of other species in the genus. It is **dioicous** (Lu & Huang 2017). Cutting (1910) described the antheridial receptacles (Figure 58-Figure 59) of the species. A later description by Srinivasan (1939) suggests that it could actually be **protogynous** (female parts develop before male parts), with archegonial receptacles (Figure 60) developing first, then antheridial receptacles developing, a rather unusual order for bryophytes (see Vol. 1, Chapt. 3-2). Srinivasan describes the species as having receptacles that start as purely female, but soon one or more of the proliferations bear antheridia that grow out from the ventral surface. However, these proliferations once again become active lobes of the female receptacle. Srinivasan describes them as intermediate between an archegonium and an antheridium, later becoming typical antheridia. This observation leads him to the suggestion that the two reproductive structures are homologous. Nevertheless, the species is generally accepted as **dioicous**.

Figure 58. ***Marchantia emarginata*** males with antheridiophores. Photo by Ellen8355, through Creative Commons.

Figure 59. ***Marchantia emarginata*** males showing antheridial receptacles. Photo by Li Zhang, with permission.

Figure 60. ***Marchantia emarginata*** ssp. ***tosana*** females with archegonial heads. Photo courtesy of Li Zhang.

Asexual reproduction occurs by **gemmae** in cups (**cupules**) (Figure 61) (Ho 2013). In Singapore, these gemmae appear to be the primary means of reproduction, along with fragmentation and branching (see also Johnson 1958). On the other hand, Singh and Singh (2013) found no gemmae cups in the Himalayan material they studied, suggesting perhaps a climatic or photoperiod problem. We know that production of ***Marchantia polymorpha*** (Figure 2) gemmae are favored by short days (Carter & Romine 1969). If these conditions are coupled with the wrong temperatures, then the hormonal stimulus to produce gemmae might be absent.

Figure 61. ***Marchantia emarginata*** with gemmae. Photo by 楊玉鳳, through Creative Commons.

Kumra and Chopra (1989a,b) found that cytokinins (2iP, BAP, kinetin and zeatin) increased both growth and gemma cup formation in ***Marchantia emarginata*** (Figure 47-Figure 53) and were of decreasing effectiveness in that order. However, BAP is the most effective in increasing the number of gemmae. They also found (1989b) that vegetative growth and gemmae cup production were greatest in continuous light at 4500 lux, but were inhibited by applied auxins at most concentrations.

Li Zhang (pers. comm. 6 August 2022) sent me images of very unusual ***Marchantia emarginata*** ssp. ***tosana*** with

gemmalings growing on the antheridiophore and archegoniophore (Figure 62-Figure 63). He concluded that the gemmae landed on these reproductive structures when the latter were young and the stalks had not yet elongated. These gemmae then were elevated as the antheridiophore and archegoniophore elongated. These two images represent two different populations in the same area. He considered that the high humidity in that location could make this unusual substrate possible. It also suggests that the inhibitor(s) to gemmae germination present in the thallus are absent in the archegoniophore and antheridiophore. But really, on the ends of the fingers of the antheridial head? It is interesting that the antheridial head does not have the typical shape seen in Figure 58.

Figure 62. ***Marchantia emarginata*** ssp. ***tosana***, in Guangdong, S. China, with germinated gemmae and gemmae cups growing on male receptacle arms. Photo courtesy of Li Zhang.

Figure 63. ***Marchantia emarginata*** ssp. ***tosana*** with gemmaling on archegoniophore stalk, Guangdong, S. China. Photo courtesy of Li Zhang.

Fungal Interactions

Although I found little on fungal interactions for this species, Srinivasan (1939) reported fungal-forming **pycnidia** (flask-shaped fruiting body bearing conidiophores and conidia on interior and occurring in various imperfect fungi and Ascomycetes; Figure 64) in ***Marchantia emarginata*** (Figure 47-Figure 53). Srinivasan further suggested that the fungal attack might cause a change in the sex of the receptacle. This remains to be demonstrated experimentally, but with what we currently know about hormones from bacteria and fungi, and their influence on the development of bryophytes, this would be a worthwhile experiment.

Figure 64. ***Phoma*** (**Coelomycetes**) pycnidium. Some fungi have pycnidia that appear on ***Marchantia emarginata***. Photo by Brawlings, through Creative Commons.

Iqbal *et al*. (1988) described vesicular-arbuscular mycorrhizal fungi from both rhizoids and the ventral thallus parenchyma of ***Marchantia emarginata*** (Figure 47-Figure 53).

Fatma (2018) determined an endophytic mold in ***Marchantia emarginata*** (Figure 47-Figure 53) to be ***Daldinia eschscholtzii***. (Figure 65-Figure 66).

Figure 65. ***Daldinia eschscholzii***, an endophytic fungal species that can occur in ***Marchantia emarginata***. Photo by Petra White, through Creative Commons.

Figure 66. ***Daldinia eschscholzii*** ventral view. Photo by Byrain, through Creative Commons.

Biochemistry

Many biochemical studies have described the biochemical properties and potential uses of secondary compounds in the genus ***Marchantia***. See Jantwal *et al*. (2019) for a review. The species ***Marchantia emarginata*** (Figure 47-Figure 53) may be less well known than the widespread ***M. polymorpha*** (Figure 67), but its biochemical studies are nevertheless numerous. Only a sampling will be presented here to suggest their ecological importance.

Figure 67. ***Marchantia polymorpha*** female with archegoniophores; this species is the typical example used for teaching about liverworts. Image copyright Stuart Dunlop <www.donegal-wildlife.blogspot.com>, with permission.

Yuan *et al*. (2021) demonstrated the presence of uridine diphosphate-dependent glycosyl transferases (UGTs) in ***Marchantia emarginata*** (Figure 47-Figure 53), noting the importance of flavonoid glycosides for their pharmaceutical activities. The value of pharmaceutical compounds to the liverworts needs much experimental study. Are they merely a consequence of some other function or pathway, or do they defend the bryophytes against pathogens or herbivores?

Huang *et al*. (2010) isolated marchantin A, a bibenzyl ether, from ***Marchantia emarginata*** subsp. ***tosana*** (Figure 68). This secondary compound is able to induce **apoptosis** (death of cells which occurs as normal and controlled part of organism's growth or development) in human MCF-7 breast cancer cells. It furthermore has good anti-oxidant activity. Fatma (2018) likewise demonstrated anti-oxidant activity in this species. Antioxidants can be important in rehydration of bryophytes, countering the oxidative burst that often occurs (see for example Minibayeva & Beckett 2001).

Figure 68. ***Marchantia emarginata*** ssp. ***tosana*** females, a source of marchantin A. Photo from Taiwan Mosses, through Creative Commons.

Kumar *et al*. (2007) found that ***Marchantia emarginata*** could be used against tumors.

Wang *et al*. (2017) described the chemistry of the cuticle of ***Marchantia emarginata*** (Figure 47-Figure 53). They isolated the fatty ω-hydroxyacid/fatty alcohol hydroxycinnamoyl transferase (HFT) from the species and, based on a species of tobacco, suggested that its occurrence in the cells indicate that the **feruloylation** (subclass of carboxylic acid esterases that hydrolyze ester bonds between hydroxycinnamic acids and sugars present in plant cell walls) of the cutin monomers takes place in the cytoplasm. Bryophytes are often described as lacking cuticle, but **cutin** (insoluble polyester of C_{16} and C_{18} hydroxy fatty acids and main component of cuticle) is becoming well known in bryophytes. It appears that in bryophytes the cuticle is simply thinner than in tracheophytes.

Toyota *et al*. (2004) described the **sesquiterpene** alcohol 1,6-Humuladien-10-ol from ***Marchantia emarginata*** subsp. ***tosana*** (Figure 68). These **sesquiterpenes** are C_{15}-terpenoids comprised of three isoprene units. They are especially common in tracheophytes, but also are becoming well known in bryophytes (Awouafack *et al*. 2013). We know that sesquiterpenes can include essential oils and aromatic constituents; others are antimicrobial or provide protection against oxidative damage.

Alcoholic and acetonic extracts of ***Marchantia emarginata*** (Figure 47-Figure 53) indicated the presence of

carbohydrates, proteins, diterpenes, phytosterols, and anthocyanin, whereas flavonoids were present only in the alcoholic extract and phenol only in the acetonic extract (James *et al*. 2020). Alcohol extracts exhibited activity against the bacterium ***Escherichia coli*** (Figure 69) and both alcohol and acetone extracts against ***Klebsiella pneumoniae*** (Figure 70). However, neither alcohol nor acetone extracts exhibited activity against ***Staphylococcus aureus*** (Figure 71). This is unfortunate because this hospital scourge has become methicillin-resistant (Solberg 2000) and a new treatment is needed.

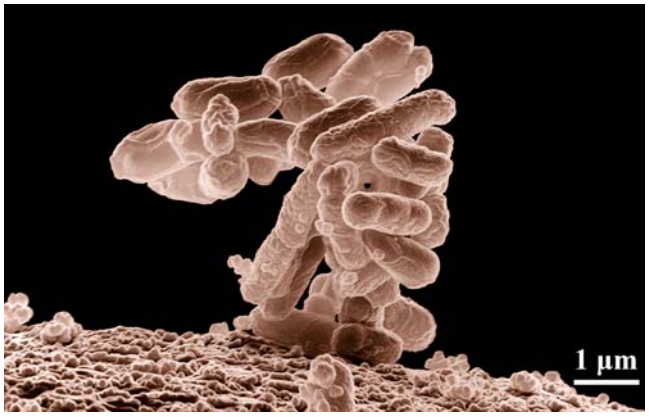

Figure 69. ***Escherichia coli***, a bacterial species that is inhibited by alcohol extracts of ***Marchantia emarginata***. Photo by USDA, through public domain.

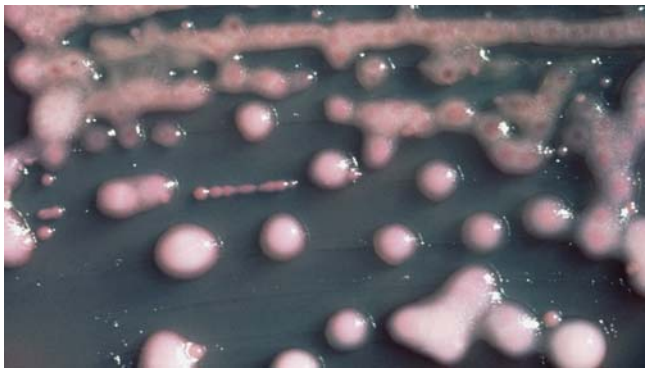

Figure 70. ***Klebsiella pneumoniae***, a bacterial species that is inhibited by both alcohol and acetone extracts of ***Marchantia emarginata***. Photo from CDC, through public domain.

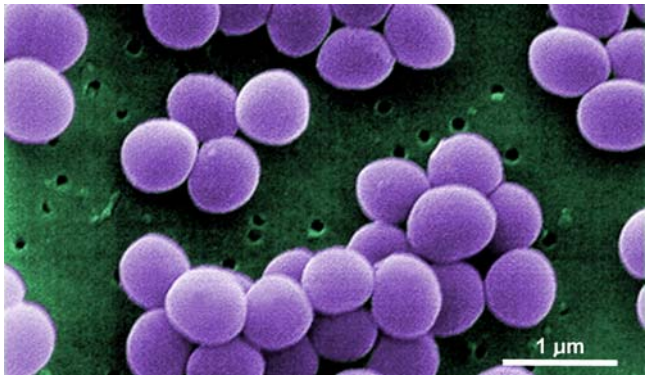

Figure 71. Colorized SEM of ***Staphylococcus aureus***, a species that is not inhibited by alcohol or acetone extracts of ***Marchantia emarginata***. Photo by Janice Haney Carr, CDC, through public domain.

Spermine is a polyamine in all **eukaryotic** (having nucleus with nuclear membrane) cells and is involved in cellular metabolism. The amino acid ornithine is its precursor. It is an essential growth factor in some bacteria as well.

Culturing

Chopra and Dhingra-Babbar (1986) studied the effects of various amino acids, complex organic substances, and active charcoal on the growth and development of ***Marchantia emarginata*** (Figure 47-Figure 53). The amino acid response was dependent on the concentration, with lower concentrations enhancing growth and higher ones inhibiting it. Glutamic acid, histidine, and methionine stimulated callus growth, whereas tryptophan induced thallus differentiation. Activated charcoal delayed callus formation and growth was extremely reduced. Coconut milk stimulated callus growth at 15% (v/v) and inhibited it at 25%.

Marchantia inflexa (Figure 72-Figure 74)

Despite its somewhat narrow tropical distribution, ***Marchantia inflexa*** (Figure 72-Figure 74) has received considerable attention regarding its sexual expression and the role of the environment in this expression. Marks *et al*. (2019a,b) revealed that those genes on sex chromosomes are subject to greater diversifying selection than those on autosomal (non-sexual) and organellar genes. This diversification occurs mostly among male-specific genes, whereas divergence of other sex-linked genes differs little from that of autosomal genes.

Distribution

Marchantia inflexa (Figure 72-Figure 74) is restricted to the Neotropics and bordering regions, from Central America and the Caribbean and from northern Venezuela to the southern United States (Marks *et al*. 2019a).

Figure 72. ***Marchantia inflexa*** thalli with brown scales covering apical growth regions. Photo by Scott Zona, with permission.

Figure 73. ***Marchantia inflexa*** with gemmae cups. Note brown scales covering the apical growth region. Photo by Alan R. Frank, through Creative Commons.

Figure 74. ***Marchantia inflexa*** showing large population of overlapping thalli. Photo by Alan R. Frank, through Creative Commons.

Aquatic and Wet Habitats

Marchantia inflexa (Figure 72-Figure 74) occurs mostly on streambank rocks (Figure 75-Figure 76) and soil (Figure 77-Figure 78) (Marks *et al*. 2019a).

Figure 75. ***Marchantia inflexa*** on rock. Note the meristematic tips on the branches, with brown scales covering them. Photo by Alan R Frank, through Creative Commons.

Figure 76. ***Marchantia inflexa*** on streambank. Photo by Karen and Philip, through Creative Commons.

Figure 77. ***Marchantia inflexa*** on soil bank. Photo by Jeff Garner, through Creative Commons.

Figure 78. ***Marchantia inflexa*** on soil bank. Photo by Jeff Garner, through Creative Commons.

Figure 79. ***Marchantia inflexa*** population on soil bank where mosses can help it to maintain moisture. Photo by Alan R. Frank, through Creative Commons.

Physiology

water relations

Marks *et al*. (2019a,b) investigated dehydration tolerance, emphasizing differences between genetic lines, that allowed them to identify multiple dehydration-associated genes, two of which were sex-linked, suggesting that dehydration tolerance may be impacted by sex-specific genes. Identification of these genes permits the identification of gender when sexual expression is not present. Although the more common habitat for ***Marchantia inflexa*** (Figure 72-Figure 74) is on rock and soil surfaces along streambanks (Figure 79) in tropical forests, it can also colonize more exposed sites such as disturbed sites along roads.

Marks *et al*. (2019ab) explored the relationships to drought in five populations of ***Marchantia inflexa*** (Figure 72-Figure 74) in northern Trinidad and Tobago in the Republic of Trinidad. When grown in a common garden, the responses maintained the differences they had exhibited in their original habitats, indicating that they were genetically determined. They also found that males (Figure 86-Figure 87) had a lower desiccation tolerance than did females (Figure 88-Figure 89) in less exposed sites, but not in more exposed sites. The males furthermore exhibited more variation in morphology than did females, while females exhibited similar desiccation tolerance across the five sites.

Marks *et al*. (2021) identified stress responses to dehydration in ***Marchantia inflexa*** (Figure 72-Figure 74), including expression of LEA and ELIP genes and evidence of cell wall remodelling. They found, however, that there was little temporal synchronization of the responses across six genotypes. The researchers suggested that differences in timing of the transcriptional adjustments contribute to the variation seen among genotypes. Furthermore, developmental differences affect the relative tolerance of meristematic and differentiated tissues.

electrical responses

Measuring electrical responses in bryophytes is not a common activity, but such measures can be used to assess a plant's response to injury or environmental stimuli. Several studies have used ***Marchantia inflexa*** (Figure 72-Figure 74) as a subject. Cooper *et al*. (2022a) commented that the KCl-filled glass electrodes placed into plant tissues is subject to artifacts and is less reliable than the impedance method. Using the impedance method, one can detect plant injury and exposure to environmental compounds such as glutamate. This method was used successfully in ***M. inflexa*** by placing two impedance leads 2 cm apart into the thallus tissue, with a cut made to a third thallus between the two leads. Cooper *et al*. (2022b) found that the liverwort showed no electrical response to glutamate exposure, whereas *Arabidopsis thaliana* (Figure 80) and *Pisum sativum* (Figure 81) (both flowering plants) produced rapid depolarization upon exposure.

Figure 80. ***Arabidopsis thaliana***, a species that, unlike ***Marchantia inflexa***, experiences rapid depolarization upon exposure to glutamate. Photo by Stefan Lefnaer, through Creative Commons.

Figure 81. ***Pisum sativum*** var. ***sativum***, a species that, unlike ***Marchantia inflexa***, experiences rapid depolarization upon exposure to glutamate. Photo by Stefan Lefnaer, through Creative Commons.

Adaptations

Among the common adaptations is their ability to form dense mats that help to maintain moisture in the soil (Figure 82-Figure 83). But this ability to form mats brings its own problems of self-competition.

Figure 82. ***Marchantia inflexa*** with overlapping thalli that can help to conserve soil moisture. Photo by Scott Zona, with permission.

Figure 83. ***Marchantia inflexa*** with gemmae cups, showing closely contacting and overlapping thalli. Photo by Jamie Newman, through Creative Commons.

Crowley *et al*. (2005a) described three mechanisms for competition for space (Figure 82-Figure 83): **expansion** (spreading to unoccupied habitat), **lottery** (replacing dead competitors), and **overgrowth** (encroaching on competitors along zones of contact). For ***Marchantia inflexa*** (Figure 72-Figure 74), a local stable coexistence of the sexes requires the avoidance of this self-competition. This stable coexistence of the sexes seems to be possible in a narrow range of disturbance intensities, explaining ambiguous results in simulation studies (McLetchie *et al*.. 2002). Crowley *et al*. noted the importance of **contact inhibition** in this species. They considered that the improbability that a disturbance regime could maintain death rates within the high and restricted range is consistent with stable coexistence and that it indicates that long-term coexistence of the two genders may be dependent on processes operating at the scale of the metapopulation (Garcia-Ramos *et al*. 2002, 2007). Garcia-Ramos *et al*. (2002, 2007) indicated that single-sex populations were common and that males were rare. In the tropics the two sexes often co-existed in a single patch; in the USA only all-male or all-female populations were known. The spores were able to colonize disturbed sites, and large disturbed areas permitted

the colonization and coexistence by both sexes, with fertilization typically occurring between patches.

Reproduction

For a species that has few publications describing habitats, ***Marchantia inflexa*** (Figure 72-Figure 74) has an abundance of published reproductive studies, particularly related to the environmental conditions. Like the genus, the species is **dioicous**. Prominent among the studies are those related to environmental effects on sex ratio.

McLetchie and Puterbaugh (2000) noted that unisexual populations and female- or male-biased populations were common in this **dioicous** liverwort. Garcia-Ramos *et al*. (2002) found that whereas both sexes could coexist in a single patch in the tropics, in the USA only all-male or all-female populations are known. McLetchie and Puterbaugh (2000) found that sex-ratio patterns could be related to growth rates, number of meristematic regions (Figure 72-Figure 73), and asexual reproduction in the riverside populations they studied in Trinidad. Of the 209 patches they observed, 83% contained no sex-expressing thalli. Only 9% contained thalli of both sexes. The remainder were either entirely female-expressing (4%) or male-expressing (4%). Small patches were less likely to be expressing sexual reproductive structures. Shade (less canopy openness) also correlated with lower sexual expression. In those populations with expression of both sexes, the ratios of male (Figure 86-Figure 87) to female (Figure 88-Figure 89) ranged 0.22-0.80.

But what causes this variation? McLetchie and Puterbaugh (2000) found that females (Figure 88-Figure 89) of ***Marchantia inflexa*** (Figure 72-Figure 74) grew faster, produced more meristematic tips (Figure 73), and had lower levels of asexual reproduction (Figure 83-Figure 85) than did males (Figure 86-Figure 87). Furthermore, the number of meristematic tips exhibited a negative correlation with both asexual reproduction and growth rate. Hence, these factors could lead to female sex bias in reproductive colonies. A further factor in shifting toward female dominance is that populations that reproduce better asexually (*i.e.* males) are less likely to succeed under stressful conditions. These relationships position the species to produce more spores under stressful conditions and thus have a means to arrive at a different location where the stress might not be present.

McLetchie *et al*. (2002) followed with a study on the local sex-ratio dynamics using ***Marchantia inflexa*** (Figure 72-Figure 74) from rock surfaces and bark in Trinidad. These populations differed widely in their population sex ratios at the study site in the rainforest. They followed seven life history stages In some stages the thalli became more abundant and extend over the substrate and each other in their quest for space (Figure 84-Figure 85). The sex ratio within a patch was not stable: at low to moderate disturbance levels, females gradually eliminated males. At high disturbance levels, males (Figure 86-Figure 87) eliminated females (Figure 88-Figure 89). This pattern was not dependent on whether sexual propagules (spores) could germinate within the patch, but germination of gemmae (Figure 84-Figure 85) within the patch had an important role. Hence, sexual reproduction, while unimportant within patches, is critical in spatial landscapes (Garcia-Ramos *et al*. 2002).

Figure 84. ***Marchantia inflexa*** with gemmae. Photo by Jeff Garner, through Creative Commons.

Figure 85. ***Marchantia inflexa*** with gemmae cups. Photo by Jamie Newman, through Creative Commons.

However, spores may be the primary means for recolonizing patches eliminated by large-scale disturbances (McLetchie *et al*. 2002). Once a patch became fully occupied, the production of the wind-dispersed spores was maximized. Once the colony became re-established, spore production declined and the sex ratio became increasingly more biased toward one or the other sex. Such scenarios support the concept that the sex ratio is determined at the **metapopulation** (group of spatially separated populations of same species which interact at some level; regional group of connected populations of species) level.

One question that arises is how does a species maintain sexually dimorphic pre-adult traits (Fuselier & McLetchie 2002). Fuselier and McLetchie noted that sexual dimorphism can influence the distribution of the sexes, the population sex ratios, the maintenance of the sex in populations, and the evolutionary potential of the species. Hence, in species like ***Marchantia inflexa*** (Figure 72-Figure 74), where sexual dimorphism results in greater growth and reproduction in females, the population could develop a female-biased sex ratio. Fuselier and McLetchie found that the sexes overlapped in habitat use. Furthermore, different populations exhibited differences in growth, asexual reproductive rates (Figure 84-Figure 85), degrees of sexual dimorphism, and the strength of their

among-trait correlations. The investment in growth and in asexual reproduction differed in single-sex and mixed-sex populations, but the degree of sexual dimorphism did not. The researchers concluded that the local environment may exert more influence than does the presence of the opposite sex in maintaining sexual dimorphism. Furthermore, between-sex correlations were not significant in the greenhouse common garden, but were significant in the field. Garcia-Ramos *et al*. (2002) found that males were able to persist longer in local populations due to minor disturbances such as drought.

Females (Figure 88-Figure 89) exhibited a cost for plasticity, whereas males (Figure 86-Figure 87) did not (Fuselier & McLetchie 2002). Among females, early sex-expressing individuals produced fewer gemmae cups than did late-expressing plants, supporting the concept that there is a tradeoff between the two modes of reproduction. These observations suggest that events during the life of the plant can influence its success at the local population level. These events can differ among the years of its life, making the success of a given population a somewhat random process dependent upon the changing conditions in the environment.

Figure 86. ***Marchantia inflexa*** males. Photo by Jeff Garner, through Creative Commons.

Fuselier and McLetchie (2004) explored several environmental parameters to determine if the two sexes exhibited different preferences. Using two populations in Trinidad and ten in the USA, they found no differences in preference for substrate, humidity, wind speed, or exposure among or within populations. However, in the USA, male populations (Figure 86-Figure 87) tended to occur under more open canopies and in a wider light range than did females (Figure 88-Figure 89).

Figure 87. ***Marchantia inflexa*** males. Photo by Scott Zona, with permission.

Figure 88. ***Marchantia inflexa*** females. Photo by Jeff Garner, through Creative Commons.

Figure 89. ***Marchantia inflexa*** females. Photo by Jeff Garner, through Creative Commons.

Crowley *et al*. (2005b) postulated that the long-term coexistence of the sexes in ***Marchantia inflexa*** (Figure 72-

Figure 74) might be only temporary. They found that fragmentation is important in overgrowth competition. Stanley (2019) hypothesized that females (Figure 88-Figure 89) in bryophytes would show a greater competitive ability, thus at least in part accounting for the frequent female (Figure 88-Figure 89) bias in bryophyte sex ratio. In their greenhouse cultures of ***M. inflexa***, they found that both sexes averaged 41% more growth if accompanied by the opposite sex than that of single-sex cultures. Their model predicted coexistence between the sexes, but that males (Figure 86-Figure 87), not females, would be in greater numbers, with a ratio of 3.2 males to 1 female.

Groen *et al*. (2010a) were surprised to find that males (Figure 86-Figure 87) of ***Marchantia inflexa*** (Figure 72-Figure 74), the gender that occurs in more tree-canopy openness, have lower chlorophyll *a*:*b* ratios than do females. Generally, a low chlorophyll *a*:*b* ratio, caused by more chlorophyll *b*, is an adaptation to shade. But both sexes had lower edge pore density in greater canopy openness; males had a weak positive correlation between edge pore density and light intensity (Groen *et al*. 2010b). Thus it appears that light intensity and canopy openness have opposing effects on edge pore density in males (Figure 86-Figure 87). The researchers suggest that males might be more responsive to water stress than are females (Figure 88-Figure 89). Females, on the other hand, have more support tissue, providing greater storage, and providing the resources needed for the female plants to support their sexual role.

Garcia-Ramos *et al*. (2007) noted that as a patch of ***Marchantia inflexa*** (Figure 72-Figure 74) persists through time, it is more likely to lose males (Figure 86-Figure 87) than females (Figure 88-Figure 89). This is due, at least in part, to the faster tissue growth of females. On the other hand, both sexes generally persist in the metapopulation, but with females predominating. Males had the advantage during patch filling, with their more abundant gemmae (Figure 84-Figure 85) providing an effective colonization strategy. Since males kept colonizing these available patches, they were maintained in the metapopulation. Similar maintenance of both sexes, particularly in small, highly disturbed populations where life-history traits and mortality differ between sexes, is likely to be a widespread phenomenon, particularly among dioicous bryophytes.

Using methods described by Chang *et al.* (2006), Fuselier (2008) found that geographically separated populations were significantly different. Single-sex populations of ***M. inflexa*** (Figure 72-Figure 74) in Oklahoma and Florida, USA form a distinct phenotypic group and it would be worthwhile to study physiological and developmental differences as well. Plants from single-sex and both-sex populations differed in their life history strategies. Those in single-sex populations invested more in growth than in asexual (gemmae; Figure 84-Figure 85) reproduction. While they produced as many sexual structures, they produced fewer gametangia per gametophore than did plants from both-sex populations, suggesting a possible chemical interaction among the plants. Characters of female plants (Figure 88-Figure 89) were positively correlated with geographic, nearest-neighbor distance. Characters of male plants (Figure 86-Figure 87) showed no relationship to geographic distance.

Dispersal is a logical choice for differences in population genders. Male plants produce more gemmae (Figure 84-Figure 85) and therefore should propagate more new plants near the parent colony. Female plants (Figure 88-Figure 89) produce spores and can therefore colonize areas at greater distances. But the gemmae, mostly falling within 1 m of the parent, have a greater chance of landing on a suitable substrate with suitable environmental conditions. To further complicate the picture, gemmae from males (Figure 86-Figure 87) (producing more males) have lower survivability yhan female gemmae due to desiccation (Stieha *et al*. (2014).

Brzyski *et al*. (2014) collected male and female plants from two strikingly different habitats within the same region: along natural sites (rivers) and along novel human-modified sites (roadsides). They used a common garden to demonstrate a strong sex by habitat interaction: male (Figure 86-Figure 87) and female (Figure 88-Figure 89) responses differed significantly by their source habitat. Road-collected females had higher growth and asexual reproduction compared to females from riverside habitats. In males, the pattern was not significant, but tended to be opposite to that of the females. The researchers found significant genetic differentiation between plants of the two habitats and found no evidence of individual differences in growth plasticity. However, there was a genotype effect for gemmae production. Although males and females did not differ genetically, river-collected plants with lower sexual potential were more diverse than roadside-collected plants. Could this be due to founder events, or are there selection pressures yet to be discovered? Nevertheless, these populations show that individual variation in reproduction is controlled by the interaction of genetics and environment.

Moore *et al*. (2016) questioned the selection for gamete dispersal and capture in clump water-holding capacity. In ***Marchantia inflexa*** (Figure 72-Figure 74), a dense tomentum-like mass of scales surrounds the archegonia (Figure 88-Figure 89), presumably retaining sperm-laden water. The male receptacle (Figure 86-Figure 87), on the other hand, has no scales and may serve as a dispersal splash platform (Figure 86).

Stieha *et al*. (2014) observed the productivity and dispersal of gemmae in ***Marchantia inflexa*** (Figure 72-Figure 74). Male plants produce more gemmae and more quickly than do female plants, but male plants have lower desiccation tolerance, leading to lower gemmae survival rates. They found that gemmae in this species can move up to 20 cm per minute in a light rain, permitting them to reach locations unoccupied by their parents. Models demonstrated that long-distance dispersal of gemmae is possible and they are likely to be successful if they stay moist. They warned that measurements of different stages to dispersal can be misleading about the survival of the sexes. Nevertheless, the gemmae are critical to the maintenance of both sexes.

Stieha *et al*. (2017) summarized the known mechanisms for maintaining both sexes to be "semi-independent dynamics of populations within a metapopulation. These semi-independent dynamics are influenced by dispersal and recolonization rates, which are affected by the spatial arrangement of populations." Using a mathematical model, Stieha and coworkers demonstrated

that at intermediate distances between populations, metapopulations maintained both sexes, and the spatial arrangement of populations changed the threshold at which one sex was lost. However, when populations were close to one another, one sex was eliminated and the single-sex metapopulation persisted through dispersal of asexual propagules. When populations were far apart, one sex was eliminated, and the metapopulation either went extinct due to lack of recolonization by asexual propagules or persisted because clumped populations facilitated recolonization. Hence, spatial arrangements are important in the maintenance or elimination of sexes in clonal organisms. This helps to explain the persistence of geographic parthenogenesis and the continuance of asexual species such as founder populations of dioicous species.

With so much known about the sexual behavior of ***Marchantia inflexa*** (Figure 72-Figure 74) populations, Walter (2015) set out to detect genetic evidence of sexual reproduction in sexual and asexual populations. She predicted that genetic variation would be higher in sexually reproducing populations when compared to asexually reproducing populations. In these haploid organisms, there is rapid selection for advantageous traits and rapid removal of deleterious ones. Sexual reproduction permits recombinations among the genes on different chromosomes, creating variability among offspring. Asexual reproduction such as gemmae produces a carbon copy of the parent. The results, using ***Marchantia inflexa*** (Figure 72-Figure 74), are fascinating. Bisexual populations are becoming more female biased (Figure 88-Figure 89), suggesting some mechanism of competition. The all-female populations have a low level of genetic diversity, implying that they have arisen mostly from asexual reproduction.

Brzyski *et al*. (2018) noted that sexual reproduction requires close proximity to potential mates. Clonal growth can increase this distance by carrying the reproductive structures farther from a neighboring plant of the opposite sex, thus reducing the probability of mating. The researchers calculated the spatial distributions as the likelihood that pairs of individuals were the same sex or genotype of ***Marchantia inflexa*** (Figure 72-Figure 74) and determined how the likelihood was affected by habitat patch size. In this species, asexual reproduction dominates within patches but could also occur between populations. Males (Figure 86-Figure 87) were more likely to occur near other males than the likelihood of females (Figure 88-Figure 89) being near other females, presumably reflecting the greater gemma production by males in ***M. inflexa***. In small patches the likelihood of both sexes being near members of the same sex was greater than in large patches. In the large habitat patches, male genotypes were nearly 15% more likely to be near their own clone mates than were female plants. This difference is most likely due to differential survival or colonization. Thus, male plants were more likely to be aggregated clones than were females, particularly in large patches.

Based on earlier studies on differences in light preference, Lay *et al* (2022) experimented with the effects of light intensity and quality on phytochromes in germination of gemmae of ***Marchantia inflexa*** (Figure 72-Figure 74). The germination responses of both sexual (spores) and asexual (gemmae) offspring were consistent with a phytochrome-mediated event. This contrasts with germination in ***M. polymorpha*** (Figure 90) wherein photosynthesis mediates the event.

Figure 90. ***Marchantia polymorpha*** with gemmae in cups. Photo by Brenda Dobbs, through Creative Commons.

Stanley (2019) likewise found that in single-sex cultures, males had more asexual structures (gemmae) than in the mixed-sex cultures, with the reverse relationship for growth rate. Such an increase of asexual structures in single-sex cultures would increase the probability of encountering females. The reduction in growth is a tradeoff in resource allocation. The same pattern did not occur in the females.

These differences in behavior of males (Figure 86-Figure 87) in single- vs mixed-sex cultures suggest an interaction, perhaps hormonal, based on density of plants and presence of females (Figure 88-Figure 89). Stanley (2019) suggested that in this case there could be a change in sex ratio before the plants allocate their resources to sexual reproduction; this could also be caused by environmental conditions.

Such changes in sex ratio due to environmental conditions have been known in monoecious seed plants for some time. Freeman *et al*. (1981) found that in xeric conditions the males (Figure 86-Figure 87) were more prominent, whereas female (Figure 88-Figure 89) functions were more abundant on mesic sites. Similar results were found by Dawson and Elheringer (1993) for *Acer negundo* (box elder, Figure 91) in the Intermountain West, USA. In drought-prone habitats, the male:female ratio is 1.62:1, whereas in moist-streamside habitats (Figure 76) it is female (Figure 88-Figure 89) biased (0.65 male:1 female). By reviewing many publications, Golenberg and West (2013) indicated that environmental conditions could affect ethylene concentrations, which in turn affected other hormones in flowering plants, ultimately affecting the expression of sexual structures.

Blake-Mahmud and Struwe (2020) even found that sexual expression as male in the sexually plastic *Acer pensylvanicum* (striped maple, Figure 92-Figure 93) could be completely suppressed by wounding, with increasing likelihood of the sex changing to female as the severity of damage increased. Understanding such responses of bryophytes to environmental stresses is important to our

understanding of the changes we might expect as the climate becomes more stressful, particularly as drought increases and more severe weather events occur.

Figure 91. ***Acer negundo*** male flowers. Photo by Krzysztof Ziarnek, Kenraiz, through Creative Commons.

Figure 92. ***Acer pensylvanicum*** female flowers. Photo by Crosier, through Creative Commons.

Figure 93. ***Acer pensylvanicum*** male flowers. Photo by Ashley Bradford, through Creative Commons.

Interactions

Like many, probably most, other bryophytes, ***Marchantia inflexa*** (Figure 72-Figure 74) consorts with bacteria. The bacterial communities associated with bryophytes contribute to nutrient cycling, community interactions, and cost-benefit relationships of the individual organisms involved (Marks *et al.* 2018). There is evidence of nitrogen fixation by these associated bacteria from the early invasion of bryophytes on land (Knack *et al*. 2015).

Marks *et al*. (2018) compared the bacterial community between males (Figure 86-Figure 87) and females (Figure 88-Figure 89) of ***Marchantia inflexa*** (Figure 72-Figure 74) across habitats. They found an abundant and diverse community, even when grown in a common garden. Differences were present among habitats as well as between sexes. Marks and coworkers suggested that differences in communities between males and females may contribute to "subtle differences in both physiology and form," possibly contributing to their acclimation to the local environment. Females differed from males in having higher abundances of the bacterial order **Rhizobiales**, (Figure 142-Figure 143) an order known to have species that are able to fix nitrogen. At the same time, females had a lower abundance of nitrogen-fixing **Cyanobacteria** (Figure 94) compared to males.

Figure 94. ***Cylindrospermum*** sp., a nitrogen-fixing member of **Cyanobacteria**. Photo from CSIRO ScienceImage, through Creative Commons.

Graham *et al*. (2018) noted that some bacterial associations with ***Marchantia inflexa*** (Figure 72-Figure 74) growing on streambanks (Figure 75) appear to have methane oxidation capabilities. Since streams are known sources of methane, albeit heterogeneous within the stream (Crawford *et al.* 2017), the bryophytes might have an important role in reducing this greenhouse gas.

Marchantia miqueliana

(syn. = *Marchantia cataractarum*)

Distribution

Marchantia miqueliana appears to be endemic to Java. Because of this narrow distribution, little has been published about it. Siregar *et al*. (2013) were unable to relocate it in Sumatra, a location that had been reported by Bischler-Causse (1989). Instead they found what they

considered to be a new species on soil in a wet place around the Dwi Warna waterfall at 1100 m asl.

Aquatic and Wet Habitats

Marchantia miqueliana occurs on the walls of bays and in the spray of waterfalls in the tropics (Ruttner 1955). Campbell (1908) likewise reported it from near a waterfall in Java.

Adaptations

Biochemistry

Despite its rarity, Campbell *et al*. (1979) listed flavonoids from ***Marchantia miqueliana***. These included apogenin and flavone.

Marchantia paleacea (Figure 97-Figure 99)

(syn. = *Marchantia nitida, Marchantia nepalensis*)

Bischler (1986) sank a number of species into this one, based on type material, but warned that other records of these species do not necessarily belong to ***Marchantia paleacea*** (Figure 98-Figure 100).

Marchantia paleacea (Figure 97-Figure 99) usually is considered to have two subspecies, ssp. ***paleacea*** and ssp. ***diptera*** (Figure 95-Figure 96) (Zheng & Shimamura 2019; Zheng *et al*. 2020b). In China and Japan, ***Marchantia paleacea*** subsp. ***paleacea*** tends to be distributed in higher altitudes and latitudes compared to subsp. ***diptera*** (Zheng & Shimamura 2019). Zheng and coworkers (2020b) found that the two subspecies overlap in western Japan and may be able to interbreed there.

Figure 95. ***Marchantia paleacea*** ssp. ***diptera*** in Japan. Photo by Janice Glime.

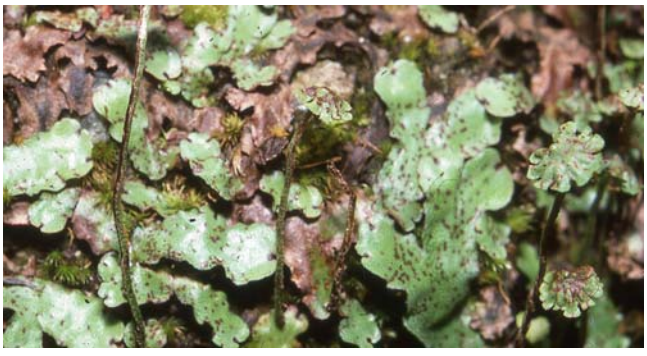

Figure 96. ***Marchantia paleacea*** ssp. ***diptera*** females with capsules, Arimma, Japan. Photo by Janice Glime.

Distribution

Marchantia paleacea (Figure 97-Figure 99) is a widely distributed tropical and subtropical species, ranging through the West Indies, Mexico, Guatemala, Asia, Europe, Azores, and Africa (Svihla 1940). Country records include Andaman Islands, China, India, Japan, New Guinea, Ryukyus, southeastern Asia, Sri Lanka, and Taiwan (Lu & Huang 2017; Bischler-Causse 1989). Borovichev and Bakalin (2014) added it to the known Russian flora, stating that it is poorly known there. It is considered vulnerable in Italy (Poponessi *et al*. 2020) and rare in southern Africa (Perold 1995). In the Americas, it is known from the southern states of the USA, Mexico, and Central America (Bischler 1988).

Figure 97. ***Marchantia paleacea*** thallus growing in Europe. Photo by Jan-Peter Frahm, with permission.

Figure 98. ***Marchantia paleacea*** in Europe, showing reddening of margins. Photo by Michael Lüth, with permission.

Figure 99. ***Marchantia paleacea*** with red bases and distinct dichotomous branching. Photo by Dmitry Ivanov, through Creative Commons.

Figure 101. ***Marchantia paleacea*** with gemmae on rock wall at edge of subtropical laurel forest, Madeira. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

Marchantia paleacea (Figure 97-Figure 99) can occur submersed in small pools, on the walls of bays, and in waterfalls in the tropics (Ruttner 1955). Lu and Huang (2017) reported subspecies ***paleacea*** to occur on damp soil from 300 to 2500 m asl in Taiwan. It can occur on wet rocks beside rivers and streams (Figure 100). Des Callaghan photographed it on a rock wall at the edge of a subtropical laurel forest in Madeira (Figure 101). Zheng and Shimamura (2022b) described this subspecies in Japan as growing on boulders, soil, concrete, or limestone walls in wet or shaded places. They provided a similar but slightly different habitat description of ***Marchantia paleacea*** ssp. ***diptera*** (Figure 95-Figure 96) on stones or soil in shaded or semi-shaded areas, anthropogenic regions, or near streams.

Bischler (1986) reported that ***Marchantia paleacea*** (Figure 97-Figure 99) had a high environmental tolerance, *i.e.* a wide niche, for soil factors, but that its climate tolerance was narrower.

In Oklahoma, USA, ***Marchantia paleacea*** (Figure 97-Figure 99) occurs on constantly moist, shaded rock outcrops within a few feet of water, on travertine deposits along streams (Figure 102-Figure 106), and on moist, shaded bluffs (Figure 107) (Little 1936). Images provided by members of Bryonet indicate that in some parts of the world it can occur elsewhere on wet banks (Figure 108-Figure 109), on the sides of drainage ditches (Figure 109-Figure 110), and in the splash of spring water (Figure 111-Figure 112) used for drinking.

Figure 100. ***Marchantia paleacea*** wet by river. Photo by Rafael Medina, through Creative Commons.

Figure 102. ***Marchantia paleacea*** on emergent rocks in stream. Photo courtesy of Tian-Xiong Zheng (NICH).

Figure 103. ***Marchantia paleacea*** on emergent rocks in stream. Photo courtesy of Tian-Xiong Zheng (NICH).

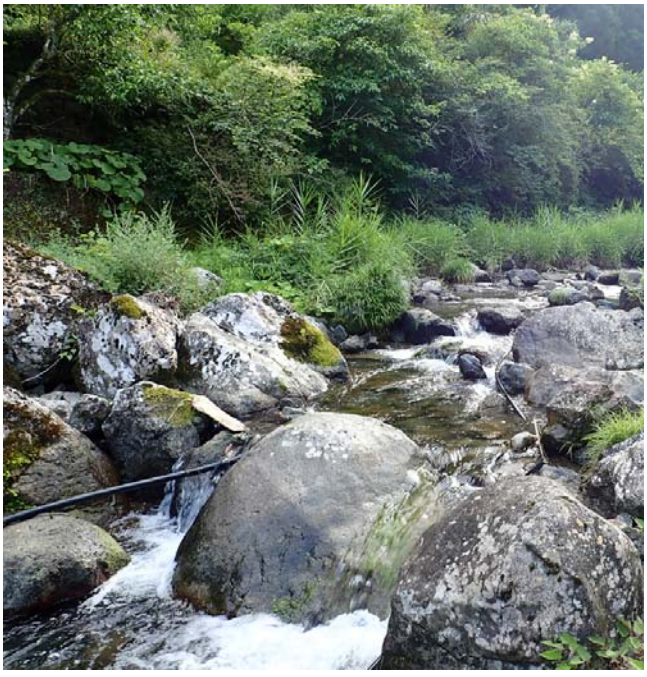

Figure 104. ***Marchantia paleacea*** on rocks at edge of stream. Photo courtesy of Tian-Xiong Zheng.

Figure 105. ***Marchantia paleacea*** on rocks in open stream. Photo courtesy of Tian-Xiong Zheng (NICH).

Figure 106. ***Marchantia paleacea*** on soil bank beside dry stream. Photo courtesy of Tian-Xiong Zheng (NICH).

Figure 107. ***Marchantia paleacea*** habitat on rocky bank in India. Michael Lüth, with permission.

Figure 108. ***Marchantia paleacea*** on a wet bank. Photo by Michael Lüth, with permission.

Figure 109. ***Marchantia paleacea*** on concrete wall of ditch. Photo courtesy of Tian-Xiong Zheng (NICH).

Figure 110. ***Marchantia paleacea*** on concrete wall of ditch. Photo courtesy of Tian-Xiong Zheng (NICH).

Figure 111. ***Marchantia paleacea*** on rocks near spring water pipe. Photo courtesy of Tian-Xiong Zheng (NICH).

Figure 112. ***Marchantia paleacea*** on rocks at spring. Photo courtesy of Tian-Xiong Zheng (NICH).

Physiology

Kaul *et al*. (1962) found that regenerating thalli of ***Marchantia paleacea*** (Figure 97-Figure 99) did not form protonemata, contrasting with regenerants of mosses. Liquid culture caused the production of more gemmae cups. Those gemmae germinated on solid media produced rhizoids, but those in liquid cultures did not, suggesting that these would not be able to attach if they germinated in water in nature. However, that might be remedied if the water level receded. Unlike observations for most ***Marchantia***, gemmae frequently germinated within the cups.

Takio *et al*. (1988) demonstrated that ***Marchantia paleacea*** ssp. ***diptera*** (Figure 95-Figure 96) could synthesize chlorophyll in the dark as well as in the light in cell suspension culture. This ability continued for the one year of experiments. Doubling time (dry weight) required 1.2 days in the light, but 1.5 days in the dark. Could this behavior permit the species to survive and even grow while temporarily covered by litter or snow? Ngumi *et al*. (1990) further found that when the dark-grown cells were placed in the light, there was no lag phase before they were able to grow photoautotrophically. Their optimum light was 6 W m^{-2} or higher in an atmosphere of 2.5% CO_2. Using ***Marchantia paleacea*** ssp. ***diptera***, Taya *et al*. (1995) obtained "good growth" at 1% CO_2. They demonstrated both stimulatory and inhibitory light levels. At levels of 5.4-60 W m^{-2} growth rate increased with light intensity; above 60 W m^{-2} the rate decreased as the light intensity increased.

One has to ask what advantages a thallose liverwort has when it is able to grow heterotrophically in the dark. This would seem like a suitable trait for those in areas with snow, but this is a species (***Marchantia paleacea*** ssp. ***diptera***; Figure 95-Figure 96) that is mostly distributed in areas that do not see snow. Ngumi *et al*. (1990) grew it heterotrophically for two years, in the dark, then transferred it to light. The cells started to grow immediately, photoautotrophically, with no lag phase. Optimum growth occurred at 6 W m^{-2} and above in an atmosphere of 25% (v/v) CO_2. The growth cycle exhibited high photosynthetic activity (7-88 mol O_2 per kg chlorophyll h^{-1}) with a high chlorophyll content of 17-25 g per kg dry weight. The cells once again returned to heterotrophic growth when placed in the dark.

Eguchi *et al*. (2002) investigated further and found that transfer of ***Marchantia paleacea*** var. ***diptera*** (Figure 95-Figure 96) to darkness resulted in a reversible repression in the gene coding for NADPH: protochloride oxidoreductase (EC 1.3.1.33). Further investigation suggested that the photosynthetic electron transport was involved in regulation of the stability of the por transcript involved in the reactions.

Nitrogen processing is also affected by light. Harada *et al*. (1993) found that when dark-grown cells were transferred to the light, the levels of activity of NaR and NiR activities decreased to about half those of cells remaining in the dark. When ammonium was the only nitrogen source supplied, activities of NiR, GS, and NADH-GOGAT were greatly reduced. Fd-GOGAT and GDH activities were not affected as greatly. But all this still begs the question how the dark production of chlorophyll is able to benefit the plant enough for the genes to remain in the population.

Many bryophytes are known for their ability to accumulate heavy metals. Concentrations of Pb, Cu, Ni, and Zn were higher in plant samples of ***Marchantia palacea*** (Figure 97-Figure 99) from disturbed sites as compared to less disturbed sites in the Kumaon Hills, India (Sahu *et al*. 2014). Mn concentration, on the other hand, was higher in soil samples as compared to plant samples. Correlation analysis (r) was also performed to investigate the relationship between the soil samples and accumulation of metals in the plant. At the Bhowali taxi stand (Nainital), Sahu and coworkers recorded significant accumulation (P<0.01) of Pb, Cu, and Ni.

It appears that activation of enzymes might help to protect ***Marchantia paleacea*** ssp. ***diptera*** (Figure 95-Figure 96) from some heavy metals (Tanaka *et al*. 1995, 1996, 1998). The cytosolic Cu/Zn-superoxide dismutase is inactivated when the cells are copper deficient and reactivated when copper is added (Tanaka *et al*. 1995). The conversion from the active form to the inactive form of Cu/Zn-SOD by release of copper is the first step in the process of its degradation. Furthermore, a copper chelator causes transformation to the inactive form. Shiono *et al*. (2003) further found that the presence of copper decreases the accumulation of gene transcripts for Fe-SOD, but increases that for CuZn-SOD in a moss, whereas it produces little effect on the gene for Fe-SOD in the liverwort ***Marchantia paleacea*** ssp. ***diptera***.

Shiono *et al*. (2003) found that whereas copper represses the expression of Fe-superoxide dismutase (Fe-SOD) in chloroplasts of the moss ***Barbula unguiculata*** (Figure 113), this is not the case in ***Marchantia paleacea*** ssp. ***diptera*** (Figure 95-Figure 96). Both are typical chloroplastic SODs, comparable to those in tracheophytes. The difference in ***M. paleacea*** var. ***diptera*** is that the copper has little effect on the gene for the Fe-SOD in the liverwort. Sakaguchi *et al*. (2004) found that instead the photosynthetic electron transport system differentially regulates the expression of the SOD genes in ***M. paleacea*** var. ***diptera***.

Figure 113. ***Barbula unguiculata,*** a species in which copper represses the expression of Fe-superoxide dismutase (Fe-SOD) in chloroplasts. Photo by Michael Lüth, with permission.

Suzuki *et al*. (2001) explored the role of **phytochrome** (photoreceptor in plants; sensitive to light in red and far-red region of visible spectrum) and red/far-red reversibility in ***Marchantia paleacea*** ssp. ***diptera*** (Figure 95-Figure 96). Hata *et al*. (1997) found that the cell growth rate related so well to the light intensity that it could be used to calculate the light intensity. Chlorophyll content was inversely related to the light intensity.

Siregar *et al*. (2021) demonstrated strong antioxidant activity (LC50=25.25 µm mL^{-1}) for ***Marchantia paleacea*** (Figure 97-Figure 99). This is important during rehydration, when most bryophytes experience an oxidative

burst. It appears that the oxidative burst prevents bacteria from entering the cells, whereas the antioxidant prevents the high oxygen levels from harming the cells.

Marchantia paleacea (Figure 97-Figure 99) is one of the species that has been used as an indicator of heavy metals (Afroz & Srivastava 2009). Alfroz and Srivastava found that it is a good accumulator, and therefore can be useful as an indicator species of heavy metals in the soil.

Sahu *et al*. (2014) similarly touted the use of ***Marchantia paleacea*** (Figure 97-Figure 99) as a bioindicator. Among their sites in the Kumaon Hills, they found that Pb, Cu, Ni, and Zn concentrations were higher from disturbed sites. Mn, on the other hand, was higher in soil samples than in the liverwort. Lead (Pb) exhibited a significantly higher concentration in the liverworts at a taxi stand.

Adaptations

Marchantia paleacea (Figure 97-Figure 99) requires a somewhat humid environment and can suffer from desiccation (Figure 114). Therefore, it survives with adaptations that permit it to live in places that are wet or sometimes submersed, but that also can become dry for days at a time.

Figure 114. ***Marchantia paleacea*** in a partially dry condition. Note that the terminal portions, where growth occurs, are still alive. Photo by Jan-Peter Frahm, with permission.

Marchantia paleacea (Figure 97-Figure 99), like other members of the genus, has pores (Figure 115) in the upper epidermis of the thallus, overlying air chambers that have photosynthetic filaments (Apostolakos *et al*. 1982). As noted earlier by Schönherr and Ziegler (1975), the cuticular ledges around the air pores prevent the entry of water into the thallus, thus permitting gas exchange without the interference of water within the thallus. The ledge has a surface of methyl and methylene groups and is covered by a layer of cutin. Schönherr and Ziegler considered these ridges to be "perfect" structures to protect against the entry of water.

Figure 115. ***Marchantia paleacea*** with gemmae cups, showing thallus pores. Photo by Efrain DeLuna, through Creative Commons.

Apostolakos and coworkers (Galatis *et al.* 1978b; Apostolakos *et al*. 1982; Apostolakos & Galatis 1985a,b,c) have provided us with a detailed study of the development of the air pores and air chambers in ***Marchantia paleacea*** (Figure 97-Figure 99).

Oil bodies can have multiple benefits to the liverwort plants. Oil bodies nearly fill the thallus cells they occupy in ***Marchantia paleacea*** (Figure 97-Figure 990) (Galatis *et al*. 1978c). The role of oil bodies was the subject of speculation for some time. Galatis *et al*. (1978a) provided an early assessment of the contents of oil bodies in ***Marchantia paleacea***. They observed that the polysaccharidic material is first elaborated in the dictyosomes, then transferred into the oil bodies by their vesicles. Proteins appear to be absent in the oil bodies. However, phenolics and other aromatic compounds seem to be present, at least in the inner oil bodies. These observations suggest as the oil bodies serve as energy reserves and as sites of protective compounds such as phenolics.

One means of conserving water is to grow with overlapping thalli that reduce evaporation (Figure 116-Figure 118). Others grow on a mat of mosses (Figure 119). These mosses provide a sponge that keeps the water in proximity to the rhizoids and that further reduce evaporation from the soil.

Figure 116. ***Marchantia paleacea*** showing dense, overlapping thalli. Photo by Jan-Peter Frahm, with permission.

Figure 117. ***Marchantia paleacea*** with gemmae cup and overlapping thalli that reduce evaporation from the soil. Photo by Michael Lüth, with permission.

Figure 118. Overlapping thalli of ***Marchantia paleacea*** ssp. ***diptera***. Photo courtesy of Tian-Xiong Zheng (NICH).

Figure 119. ***Marchantia paleacea*** growing over mosses in India. Photo by Michael Lüth, with permission.

Zheng and Shimamura (2019) suggested that the inward bent receptacle (Figure 120) of ***Marchantia paleacea*** ssp. ***diptera*** might help it to withstand the high temperatures and desiccation it experiences in its southern Japan distribution.

Figure 120. Females of ***Marchantia paleacea*** ssp. ***diptera*** showing inward bent margins of the female receptacle. Photo courtesy of Tian-Xiong Zheng (NICH).

Reproduction

Marchantia paleacea (Figure 97-Figure 99) is considered to be **dioicous** (Bischler 1986; Perold 1995; Lu & Huang 2017). Like other ***Marchantia*** species it develops antheridiophores (Figure 121-Figure 122) and archegoniophores (Figure 123-Figure 129). Other than these reproductive branches, the two sexes look the same (Bischler 1986). The life cycle is typical for species of ***Marchantia***.

Figure 121. ***Marchantia paleacea*** male plants with antheridiophores. The two lower receptacles, at this stage looking like females, appear to be young male receptacles. Photo by Naufal Urfi Dhiya'ulhaq, through Creative Commons.

Figure 122. ***Marchantia paleacea*** males with antheridiophores. Note rows of antheridia on the fingers of the antheridial head. Photo by Naufal Urfi Dhiya'ulhaq, through Creative Commons.

Figure 123. ***Marchantia paleacea*** females showing archegonial heads. Photo by Jan-Peter Frahm, with permission.

Figure 124. ***Marchantia paleacea*** females, Nichinan, Japan. Photo by Janice Glime.

Figure 125. Receptacles of ***Marchantia paleacea*** ssp. ***diptera***, showing how dense these structures can be in the colony. Photo courtesy of Tian-Xiong Zheng (NICH).

Figure 126. ***Marchantia paleacea*** females with archegoniophores. Photo by Efrain DeLuna, through Creative Commons.

Figure 127. ***Marchantia paleacea*** archegonial receptacle. Photo by Efrain DeLuna, through Creative Commons.

Figure 128. Receptacle of ***Marchantia paleacea*** ssp. ***diptera*** with inward bent margins of the receptacle. Photo courtesy of Tian-Xiong Zheng (NICH).

Figure 129. ***Marchantia paleacea*** females with mature archegoniophores. Photo by 楊玉鳳, through Creative Commons.

Populations are usually small and do not increase in size rapidly (Bischler 1986). Growth seems to be limited by water availability. The lack of outcrossing may account for the limited variability of the species, the absence of ecotypes, and division into only two subspecies.

Male plants in nature are less frequent than female plants (Evans 1917; Bischler 1986). Near the borders of the range, males are almost completely absent (Bischler 1986).

Sporophytes can be found on the Azores islands and in the Caucasus mountains at fairly high elevations (Bischler 1986). Thus, male plants are present along with the females. Is it temperature that controls males, or do they have a dispersal limitation?

But even when both males and females are growing intermixed, only 25-42% of the females produce sporangia (Bischler 1986). Nevertheless, Bischler wondered why it was so high when both sperm and archegonia were elevated on stalked structures. But evidence presented in this chapter demonstrates that sperm, easily splashed, swim directly to the archegoniophore and may even be carried upward by the same means that water moves upward.

With so few males, especially in some areas, ***Marchantia paleacea*** (Figure 97-Figure 99), relies to a great degree on gemmae (Figure 130-Figure 135) for local spread. As the gemmae age, the gemmae cups may disintegrate (Figure 136-Figure 138).

Figure 130. ***Marchantia paleacea*** with gemmae cups. Photo through Creative Commons.

Figure 131. ***Marchantia paleacea*** with gemmae cups in India. Note the conspicuous pores. Photo by Michael Lüth, with permission.

Figure 132. ***Marchantia paleacea*** with purple margins (suggesting stress) and gemmae cups. Photo by Maria Emília Martins, through Creative Commons

Figure 133. ***Marchantia paleacea*** with gemmae. Photo by Jan-Peter Frahm, with permission.

Figure 134. ***Marchantia paleacea*** with gemmae cups. Photo by Jan-Peter Frahm, with permission.

Figure 135. ***Marchantia paleacea*** gemmae cup. Photo by 楊玉鳳, through Creative Commons.

Figure 136. ***Marchantia paleacea*** with deteriorating and nearly empty gemmae cups in Europe. Photo by Michael Lüth, with permission.

Figure 137. ***Marchantia paleacea*** in Bhutan, with disintegrating gemmae cups. Photo by David Long, with permission.

Figure 138. ***Marchantia paleacea*** from India showing reddening of borders and disintegrating gemmae. Photo by Michael Lüth, with permission.

Interactions

Bacterial Interactions

Using cultures from gemmae of ***Marchantia paleacea*** (Figure 97-Figure 99), Alcaraz *et al*. (2018) isolated members of ***Bryobacter***, ***Lysobacter*** (Figure 139),

Methylobacterium (Figure 140), ***Paenibacillus*** (Figure 141), ***Pirellula***, ***Rhizobium*** (Figure 142-Figure 143), and ***Steroidobacter*** from the thalli. These bacteria are known to promote plant growth, degrade complex exudates, fix nitrogen, use and convert methylene, and suppress disease.

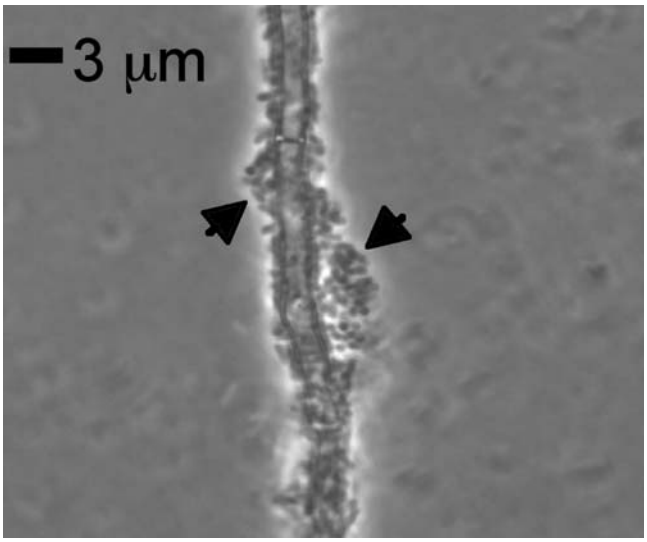

Figure 139. ***Lysobacter*** sp. hyphae, a genus associated with ***Marchantia paleacea***. Photo by Don Kobayashi, through Creative Commons.

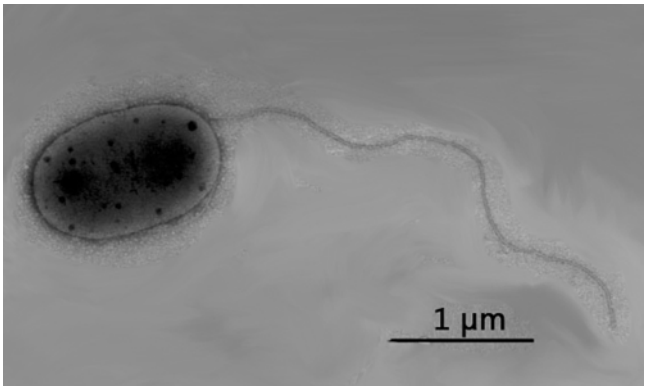

Figure 140. ***Methylobacterium jeotgali***, member of a genus associated with ***Marchantia paleacea***. Photo from Aslam *et al*. 2007, through Creative Commons.

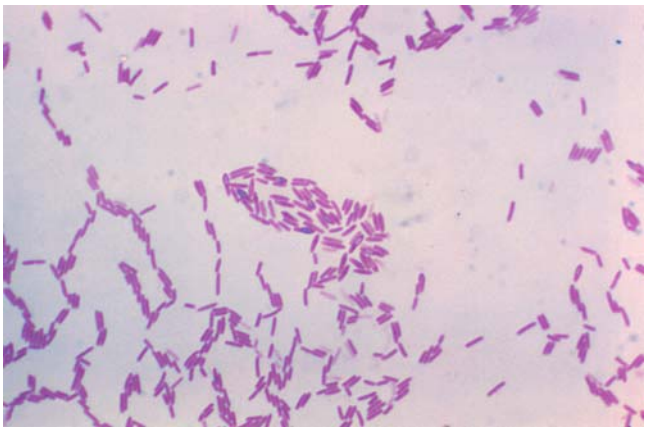

Figure 141. ***Paenibacillus*** *polymyxa*; some members of this genus are associated with ***Marchantia paleacea***. Photo from CDC, through public domain.

Figure 142. ***Rhizobium*** root nodule on *Vicia faba* roots; ***Rhizobium*** is a known associate of ***Marchantia paleacea***. Photo by Whitney Cranshaw, through Creative Commons.

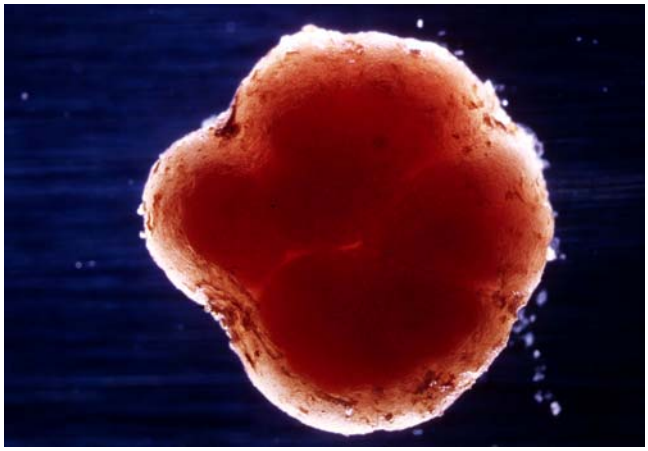

Figure 143. ***Rhizobium*** showing typical red color of nodules. Photo from CSIRO, through Creative Commons.

On the other hand, as in many liverworts, Pinfang *et al*. (2001) found that ***Marchantia paleacea*** (Figure 97-Figure 99) alcohol extracts were active against the Gram-positive bacterium ***Bacillus subtilis*** (Figure 144).

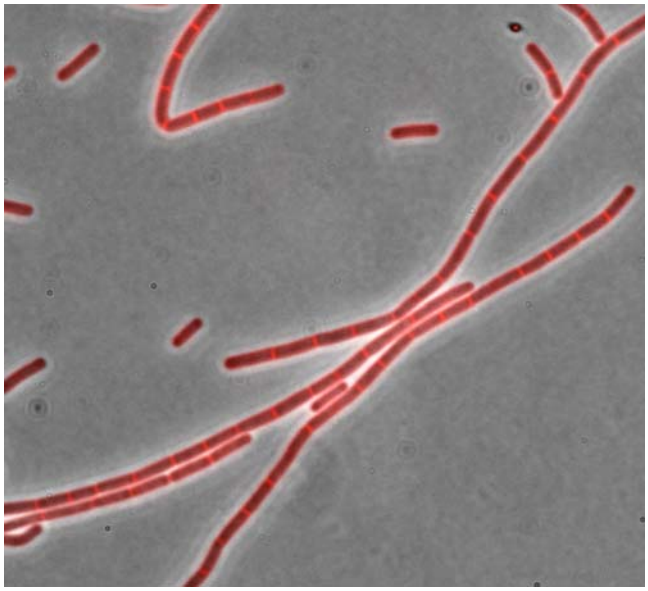

Figure 144. ***Bacillus subtilis*** stained with Nile Red, a species that is inhibited by alcohol extracts of ***Marchantia paleacea***. Photo by EditorInTheRye, through Creative Commons.

In their study of 52 bryophyte species, Banerjee and Sen (1979) found that ***Marchantia paleacea*** (Figure 97-Figure 99) exhibited the broadest spectrum of antibiotic activity against the 12 microorganisms tested.

Fungal Interactions

Fungi have played a major role in the nutrition of land plants, and ***Marchantia paleacea*** (Figure 98-Figure 100) is no exception to these benefits. But they also contribute to this relationship. Rich *et al*. (2021) found that in the relationship between this species and its arbuscular mycorrhizal fungi, lipids are transferred from the liverwort to the fungus. Bouwmeester (2021) likewise found that liverwort lipids served to "entice" fungi into the mutualism and were essential to its establishment.

When gemmae (Figure 130-Figure 138) from this liverwort were cultured with tracheophyte roots, it took only 18 days for the liverwort to exhibit arbuscules, indicating fungal colonization (Kobae *et al*. 2019). These arbuscular mycorrhizal fungi entered through the rhizoids.

Field *et al*. (2019) identified the presence of both **Glomeromycotina** and **Mucoromycotina** fungal groups in ***Marchantia paleacea*** (Figure 97-Figure 99). They found that dual partnerships, hosting two different fungal species, provided complementarity both in greater nutrient pool use and greater allocation of photosynthate to the fungal partners. The partners seemed to provide different functions and the researchers argue for this complementarity as a reason for the success of multiple fungal partners in the plant kingdom. In this case, only the **Mucoromycotina** provided liverworts with substantial access to algal N, unrelated to atmospheric CO_2 concentration. Both fungal symbionts increased P uptake, but **Glomeromycotina** were often more effective.

Kodama *et al*. (2021) identified carotenoid-derived strigolactones in ***Marchantia paleacea*** (Figure 97-Figure 99). These compounds are known to both serve as hormones to regulate growth and development and to serve as rhizosphere-signalling molecules that induce a symbiotic relationship with arbuscular mycorrhizal fungi. However evidence suggests that in ***Marchantia paleacea*** the receptor needed for it to serve as a hormone is absent. It does, on the other hand, seem to serve as a mycorrhizal signalling device.

Other Interactions

It appears that ***Marchantia paleacea*** (Figure 97-Figure 99) might even have allelopathic effects on tracheophytes. Wang *et al*. (2013) found that secondary metabolites, in particular bibenzyls, from callus cultures of this species could inhibit seedling growth of the flowering plant ***Arabidopsis thaliana*** (Figure 80), with a dose-dependent response.

Biochemistry

Takio *et al*. (1998) found that expression of the cDNA that encodes the NADPH:protochlorophyllide oxidoreductase in ***Marchantia paleacea*** ssp. ***diptera*** (Figure 95-Figure 96) is light-dependent, whereas in most tracheophytes it is light-independent.

So *et al*. (2002) verified the presence of marchantin C, isoriccardin C, and the phenanthrene derivative, 2-hydroxy-3,7-dimethoxyphenanthrene in ***Marchantia paleacea*** (Figure 97-Figure 99). They also described the structures of two novel cyclic bis (bibenzyls), isoriccardinquinone A and B.

Yuan *et al*. (2021) characterized three genes for uridine diphosphate-dependent glycosyl transferases (DBRs) in this species. Wu *et al*. (2018) isolated and characterized two double bond reductases (DBRs). These enzymes are capable of catalyzing the NADPH-dependent reduction of the α,β-unsaturated double bond. The two reductases differed in their behavior and temperature optima. This was the first report of a microbial type of DBR in any plant. Both enzymes are important in protection against environmental stress in liverworts.

Mukhia *et al*. (2014) demonstrated that ***Marchantia paleacea*** (Figure 97-Figure 99) exhibited potential antioxidant activity and the existence of a variety of phytochemicals involved in scavenging activities.

Sakurai *et al*. (2016) identified the monocyclic monoterpene aldehyde, perillaldehyde, as the major component of volatiles, comprising about 50% of the volatiles in ***Marchantia paleacea*** subsp. ***diptera*** (Figure 95-Figure 96). This represents the first report of a perillaldehyde in a liverwort. Minor volatiles included α-selinene, β-selinene, β-caryophyllene, β-pinene, and limonene. But what do they do for the liverwort?

We have named a number of secondary compounds here, but in many cases their role for the liverwort is unclear. It is presumed that most of these serve in protection against pathogens and herbivores, but some might simply be intermediates in a pathway toward another needed compound. Others are apparently part of the ability to survive drought.

The antimicrobial properties (Xia *et al*. 2001) of many of these compounds may be of use to them. Examples include action against the Gram-positive bacterium ***Bacillus subtilis*** (Figure 144). Xia *et al*. (2001) isolated 2-hydroxy-3, 7-dimethoxyphenanthrene, marchantin C, and isoriccardin C from ***Marchantia paleacea*** (Figure 97-Figure 99).

Culturing

Awasthi *et al*. (2012) compared sterilization techniques in culturing ***Marchantia paleacea*** (Figure 97-Figure 99) and several other thallose liverworts. They found the best results with 1% sodium hypochlorite solution for 8-10 seconds. They used repeated sub-culturing to ultimately achieve aseptic cultures. All of these species grew well in half strength Knop's macronutrients + Nitsch's trace elements with 10 ppm freshly prepared ferric citrate under the continuous illumination of 4,500-5,000 lux at 20 ± 2ºC.

Marchantia pappeana (Figure 147)

Distribution

Marchantia pappeana (Figure 145) is widely distributed in tropical Africa. Bischler-Causse (1993) reported it from the Cape Verde Islands to Ethiopia and south to southern Africa, generally at an elevational range of 1000-2500 m. Its distribution in southern Africa

includes the Northern Province, Northern Transvaal, and Eastern Transvaal, Gauteng [PWV], Swaziland. Kwazulu-Natal, eastern [Orange] Free State, and Lesotho (Perold 1995). Müller (1995) recorded it for Zaire. Manyanga and Perold (2004) listed it for Zimbabwe. Enroth *et al*. (2019) recorded it from the Mwatate River in Kenya (see also Chuah-Petiot 2001). The World Flora Online (2022) simply describes the distribution as tropical Africa.

Figure 145. ***Marchantia pappeana*** along ditch in Ranomafana National Park, Madagascar. Photo courtesy of Catherine Reeb.

Aquatic and Wet Habitats

Marchantia pappeana (Figure 145) often grows in the same localities as ***M. debilis*** (Figure 28-Figure 36), including vertical soil banks of streams (Figure 146-Figure 148), at waterfalls, at sluice canals, rarely on rotting wood or on rocks, in open grassland, or in forests, sometimes in deep shade (Perold 1995; World Flora Online 2022).

Figure 146. ***Marchantia pappeana*** habitat on Zahamean riverbanks, Madagascar. Photo courtesy of Catherine Reeb.

Figure 147. ***Marchantia pappeana*** habitat on Zahamean riverbanks, Madagascar. Photo courtesy of Catherine Reeb.

Figure 148. ***Marchantia pappeana*** habitat on Zahamean riverbanks, Madagascar. Photo courtesy of Catherine Reeb.

Wigginton (2013) considered ***Marchantia pappeana*** (Figure 145) on Ascension Island to be a plant that grows mostly on rocks and soil (Figure 146-Figure 149), rarely on tree roots. Catherine Reeb (pers. comm. August 2022) has found it on the walls of ditches (Figure 149).

Figure 149. ***Marchantia pappeana*** along ditch in Ranomafana National Park, Madagascar. Photo courtesy of Catherine Reeb.

Reproduction

Marchantia pappeana (Figure 145) is **dioicous** (Perold 1995). Male plants produce antheridiophores; females produce archegoniophores (Figure 150). But sometimes male branches appear on the female receptacle (World Flora Online 2022).

Figure 150. ***Marchantia pappeana*** with archegoniophores along ditch in Ranomafana National Park, Madagascar. Photo courtesy of Catherine Reeb.

Sporangia are elevated on the archegoniophore (Figure 151). These disperse spores that are aided by wiggling elaters (Figure 152) as moisture changes occur.

Figure 151. ***Marchantia pappeana*** habitat on Zahamena riverbanks, Madagascar. Photo courtesy of Catherine Reeb.

Figure 152. ***Marchantia pappeana*** with mature sporangia dispersing spores, along ditch in Ranomafana National Park, Madagascar. Photo courtesy of Catherine Reeb.

Like other species of ***Marchantia***, gemmae (Figure 153-Figure 154) are important means of asexual reproduction. Their hormone system curtails production of gemmae cups when sexual development begins. Of the 50 specimens Perold (1995) examined, 62% had cupules, 20% had antheridiophores, and 34% had archegoniophores; only 6% had both cupules and sexual structures.

Figure 153. ***Marchantia pappeana*** with gemmae cups, in river in Zahamena, Madagascar. Photo courtesy of Catherine Reeb.

Figure 154. ***Marchantia pappeana*** with gemmae cups and distinct pores in river in Zahamena, Madagascar. Photo courtesy of Catherine Reeb.

Fungal Interactions

Strullu-Derrien *et al*. (2014) indicated that the fungal associations in ***Horneophyton ligneri*** from Rhynie Chert closely resemble the **Glomeromycota** symbionts in ***Marchantia pappeana***. Field *et al*. (2015) found that the **Glomeromycota** found in ***Marchantia pappeana*** (Figure 155-Figure 156) were similar to the structures of the typical arbuscular mycorrhizae occurring in flowering plants. This species lacks studies on the benefits to ***Marchantia pappeana*** and its partner(s) in this association.

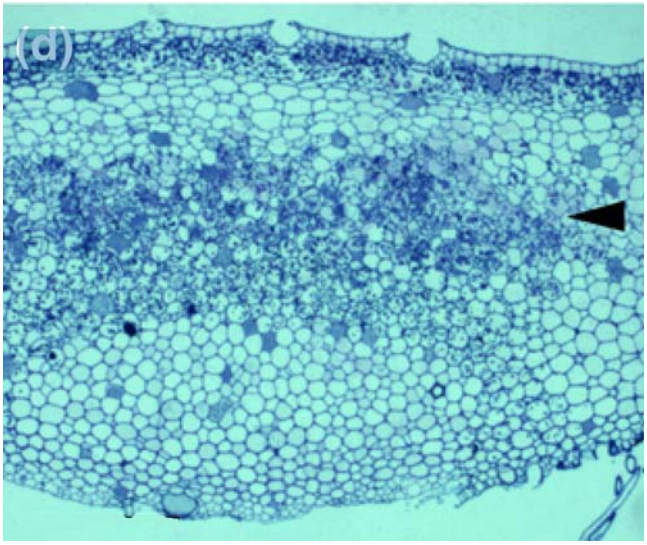

Figure 155. ***Marchantia pappeana*** mid thallus colonized by **Glomeromycota**. Modified from Strullu-Derrien *et al*. 2014, with permission from Jeff Duckett.

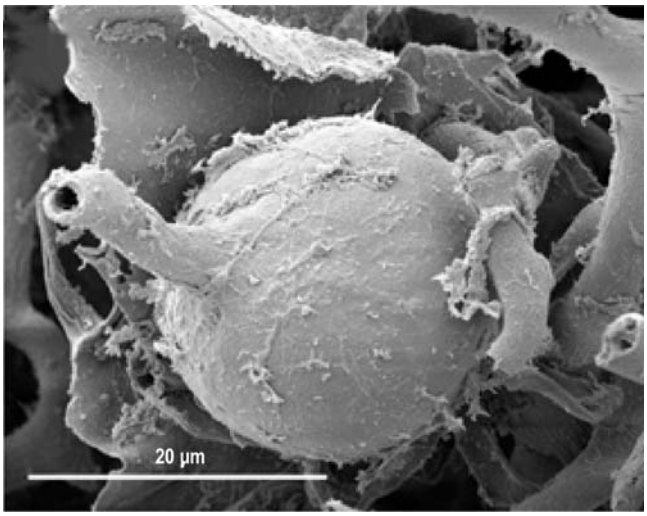

Figure 156. ***Marchantia pappeana*** colonized by **Glomeromycota** with detail of large vesicle. Modified from Strullu-Derrien *et al*. 2014, with permission from Jeff Duckett.

Biochemistry

Despite its somewhat narrow distribution, ***Marchantia pappeana*** (Figure 146) has experienced several biochemical studies. Linde *et al*. (2016) reported that sesquiterpene hydrocarbons are characteristic of this species (see also Combrinck *et al*. 2015). Linde *et al*. (2016) found that crude extracts of ***M. pappeana*** from South Africa (as well as ***Pallavicinia lyellii***) had the highest level of antibacterial activity against ***Escherichia coli*** among the nine liverworts tested. Much remains for us to learn about the role of these sesquiterpenes for the liverwort.

Summary

The species of ***Marchantia*** covered in this subchapter are those of wet habitats. They may become submersed occasionally during flooding events, but they do not normally live submersed. To survive in these habitats, they are protected by a thick thallus with air chambers to permit CO_2 entry. Oil bodies serve as a storage organ for polysaccharides and for secondary compounds that help prevent herbivory and protect the thallus from pathogens. A ridge of cutin around the pore prevents water entry. Scales on the lower surface help to move water to the thallus and to retain it in capillary spaces. Some rhizoids anchor the thallus while others help in directing water to the thallus on the lower surface.

They all have gemmae, which seem to be their primary means of reproduction. Yet some are able to colonize rapidly after a fire, suggesting that they are also dispersed by spores. The longevity of spores and gemmae has not been tested.

Secondary compounds, mostly sesquiterpenes and flavonoids, help to protect the plants from herbivory and pathogens.

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Lars Söderström helped me with puzzling nomenclature. Masaki Shimamura alerted me to nomenclature problems in ***Marchantia paleacea*** *vs.* ***M. polymorpha*** in some important publications. Li Zhang sent me a variety of papers and reviewed my treatment of ***Marchantia emarginata***. Catherine Reeb introduced me to ***Marchantia debilis*** and ***M. pappeana*** as species of wet habitats and provided me with many images and habitat information. Thank you to Tian-Xiong Zheng and for sending me much needed images. And thank you to the many photographers who have given me blanket permission to use their images or who have put them in Creative Commons.

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CHAPTER 1-24
AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: MARCHANTIACEAE, PART 2

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CHAPTER 1-24
AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: MARCHANTIACEAE, PART 2

Figure 1. ***Marchantia polymorpha*** in a typical waterside habitat. Photo by Michael Lüth, with permission.

Marchantiaceae, cont.

Marchantia polymorpha (Figure 1-Figure 12)

(syn. = *Marchantia alpestris*; *Marchantia aquatica*; *Marchantia coarctata*) – see Long (1995) for a discussion of the history of older naming of the species and subspecies.

Boisselier-Dubayle *et al.* (1995) elaborated on the genetic variability in the three subspecies of ***Marchantia polymorpha*** (Figure 1-Figure 12). The three subspecies [***montivagans*** (Figure 2-Figure 4), ***polymorpha*** (Figure 5), ***ruderalis*** (Figure 6-Figure 8)] had high genetic similarity within each subspecies over a wide geographic area, but the similarity was low between subspecies. These differences indicate that speciation included adaptation to different ecological niches, followed by reproductive isolation.

Figure 2. ***Marchantia polymorpha*** ssp. ***montivagans*** with antheridiophores. Photo by Jan-Peter Frahm, with permission.

Figure 3. ***Marchantia polymorpha*** ssp. ***montivagans*** with archegoniophores. Photo by Hugues Tinguy, with permission.

Figure 4. ***Marchantia polymorpha*** ssp. ***montivagans*** with gemmae cups. Photo by Hugues Tinguy, with permission.

Figure 5. ***Marchantia polymorpha*** ssp. ***polymorpha***. Photo by Jan-Peter Frahm, with permission.

Figure 6. ***Marchantia polymorpha*** ssp. ***ruderalis*** with gemmae cups. Photo by Jiří Kameníček, with permission.

Figure 7. ***Marchantia polymorpha*** ssp. ***ruderalis*** antheridial receptacles. Photo by Malcolm Storey, DiscoverLife, with online permission.

Figure 8. ***Marchantia polymorpha*** ssp ***ruderalis*** females with receptacles. Note smaller archegoniophores on the outer (younger) thalli. Photo by Malcolm Storey, DiscoverLife, with online permission.

The variety ***aquatica*** (Figure 9) (Campbell 1968; Hollensen & Taylor 1981; Kitagawa 1987) is not recognized by Söderström *et al*. (2016). Instead, it is considered within the species ***Marchantia polymorpha*** as ssp. ***polymorpha***. Nevertheless, it appears that those thalli that develop underwater can be distinguished by a black

midrib (Michael Lüth, pers. comm.). Recognition of this distinction can give us an ecological history of plants we find and deserves some experimental attention.

Figure 9. ***Marchantia polymorpha*** ssp. ***polymorpha*** with distinct black midribs, typical of aquatic forms, in Europe. Photo by Michael Lüth, with permission.

Google Scholar found 20,500 references in a search for ***Marchantia polymorpha*** (Figure 1-Figure 12). ***Marchantia polymorpha*** has been a subject of intensive study for nearly 200 years (Shimamura 2016). The species offers many benefits for research, including its short life cycle, ease of propagation and crossing, high frequency of transformation, haploidy, and small genome size (approximately 280 Mb).

Figure 10. ***Marchantia polymorpha*** with overlapping thalli. Photo by Sanja through Wikimedia Commons.

Berrie and Webster (1982) elaborated on the ultrastructure of the plastids and mitochondria of the ***Marchantia polymorpha*** gemmae (Figure 4). They found that division among plastids and maturing vegetative cells differed from that of developing oil body cells and rhizoid initials. Bopp and Vicktor (1988) developed methods for following protoplast development, determining that cell wall formation requires light.

Figure 11. ***Marchantia polymorpha*** thallus. Photo from Botany Website, UBC, with permission.

A Liverwort Model

genetics and sequencing

The species has served as a model organism in many biological studies (Chiyoda *et al*. 2008), including the discovery of sex in cryptogams and more recently the elucidation of the V chromosome (term for male chromosome in haploid organism), understanding the plant life cycle, and origins of polarity in development. The use of ***Marchantia polymorpha*** *s.l.* (Figure 1-Figure 12) as a plant model system continues (Durand 1908; Alam & Pandey 2016; Shimamura 2016), with its dominant haploid generation being a benefit for genetic studies and gene expression as well as details of evolutionary and developmental biology.

Marchantia polymorpha (Figure 1-Figure 12) has been used to demonstrate the presence of "X" and "Y" chromosomes in bryophytes, now referred to as U and V chromosomes, respectively (Renner *et al*. 2017). I shall continue this discussion using the designation of U for female and V for male. This early discovery of sex chromosomes was followed by the sequencing of the male and female genomes (Ohyama 2001). Ohyama found that some of the genes on the V chromosome were unique, whereas those on the U chromosome were also on somatic chromosomes or even on the V chromosome. Since these are haploid organisms, the males have a very small V chromosome with no U chromosome and females have one U chromosome with no second U or any V (Lorbeer 1934; Tanurdzic & Banks 2004). Sporophytes are UV.

Yamato *et al*. (2007) reported that these V chromosomes differ from other chromosomes in lacking recombination. They reported the gene organization of the V chromosome of ***Marchantia polymorpha*** (Figure 1-Figure 12) and identified 64 genes on the V chromosome. Of these, 14 are found only in the male genome and are expressed only in male reproductive organs. Another 40 are expressed in thalli and reproductive organs. Interestingly, at least 6 of these have U-linked counterparts that are expressed in both thalli and sex organs of females. Yamato and coworkers suggested that these sex chromosomes share ancestral autosomal genes, and they predict that essential genes on sex chromosomes of haploid organisms are more likely to persist than those in diploid organisms.

As in many other studies, ***Marchantia polymorpha*** (Figure 1-Figure 12) was the choice for studying the divergence of land plant chloroplast (Figure 12) genes (Morton 1994). Bischler (1986) analyzed the karyotype. In ***Marchantia polymorpha*** the genes with the highest codon adaptation index correspond to the ones that are expressed at the highest levels (Morton 1994). This relationship is weaker in *Nicotiana tabacum* (Figure 13).

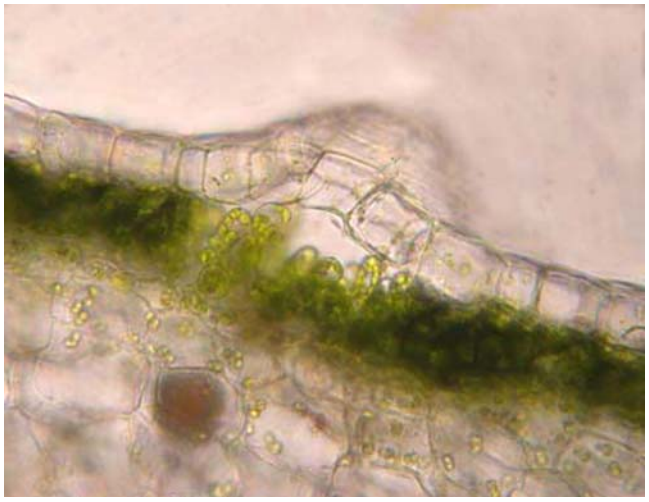

Figure 12. ***Marchantia polymorpha*** thallus section through pore, showing location of photosynthetic filaments with chloroplasts. Photo from Botany Website, UBC, with permission.

Figure 13. *Nicotiana tabacum*, a species that demonstrates the conservation of ***Marchantia*** genes in flowering plants. Photo through Creative Commons

One interesting finding is that chloroplast ribosomal protein rpl 21 in ***Marchantia polymorpha*** (Figure 1-Figure 12) is encoded by the plastid gene, but in tobacco and rice this is a nuclear gene (Smooker *et al*. 1990). Sone *et al*. (1999) reported for the first time a co-localization of repeat rDNA in land plants. These researchers suggested that the structural re-organization of rDNAs occurred after the evolutionary divergence of bryophytes from other plants.

Marchantia polymorpha (Figure 1-Figure 12) appeared to be one of the first organisms to have its chloroplast and mitochondrial DNA sequenced (Ohyama *et al*. 1986; Oda *et al*. 1992a; Kisiel *et al*. 2011; Lin *et al*. 2016). But unfortunately, the species used in early studies (Ohyama *et al*. 1986; Oda *et al*. 1992a,b,c,d) was a mis-identified ***Marchantia paleacea*** (Figure 14) (Kijak *et al*. 2013, 2016; Masaki Shimamura, pers. comm. 10 July 2022). Hence, this first sequencing cannot be attributed to ***Marchantia polymorpha***.

Figure 14. ***Marchantia paleacea*** with archegoniophores. Photo by Jan-Peter Frahm, with permission.

Posno *et al*. (1986) showed that there was "substantial" conservation in the chloroplast genome sequences between ***Marchantia polymorpha*** (Figure 1-Figure 12) and those of the aquatic flowering plant ***Landoltia punctata*** (Figure 15). Umesono and Ozeki (1987) found that the chloroplast genome sequence of ***Marchantia polymorpha*** differs little in gene makeup and function from that of flowering plants, despite flowering plants one that is 25%.

Figure 15. *Landoltia punctata*, a species with considerable conservation of the chloroplast genome sequences found in ***Marchantia polymorpha***. Photo from US Dept. Interior, through Creative Commons.

Kohchi *et al.* (1988) characterized parts of the chloroplast DNA in presumably ***Marchantia paleacea*** (Figure 14), under the name of ***M. polymorpha***. Raubeson and Jansen (1992) further explored what these DNA sequences had in common with later plants.

Takemura *et al.* (1992) elaborated on ribosomal proteins that are coded in the mitochondrial genome of ***Marchantia polymorpha*** (possibly ***M. paleacea***), and these differ substantially in size from their counterparts in the bacterium ***Escherichia coli*** (Figure 16). In the same year, Oda *et al*. (1992a,b,c) found that the mitochondrial DNA of ***Marchantia paleacea*** (Figure 14; misidentified as ***M. polymorpha***) is a single circular form that exhibits no incorporation of chloroplast DNA. Whichever species was actually used, Ohyama *et al*. (1982, 1983, 1986, 1988a,b,c; Ozeki *et al*. 1987; Los & Semenenko 1991) showed that many (most?) chloroplast genes in such liverworts as ***Marchantia*** have been conserved in tobacco, *Nicotiana tabacum* (Figure 13).

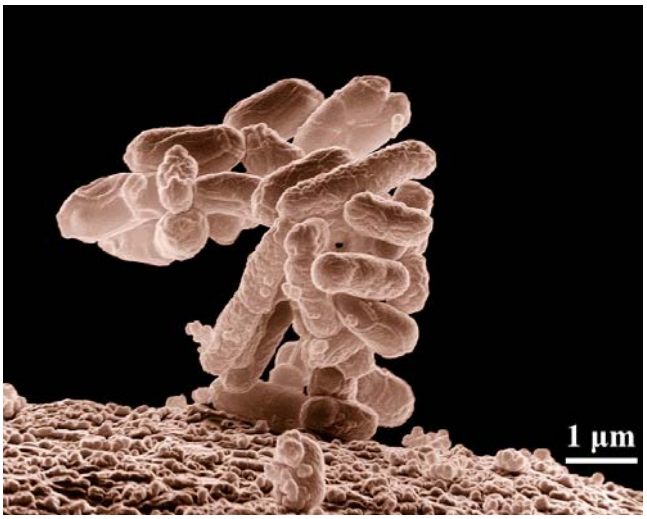

Figure 16. ***Escherichia coli***, a bacterium that exhibits very different ribosomal proteins from those of ***Marchantia polymorpha***/***paleacea***. Photo from USDA, through public domain.

Takemura *et al.* (1992) elaborated on ribosomal proteins that are coded in the mitochondrial genome of ***Marchantia polymorpha*** (possibly ***M. paleacea***), and these differ substantially in size from their counterparts in the bacterium ***Escherichia coli*** (Figure 16).

Downie *et al*. (1991) and Sibbald (1988) subsequently compared chloroplast DNA of dicotyledonous flowering plants with those attributed to ***Marchantia polymorpha***. Comparisons between mosses and liverworts with hornworts indicated that the two former groups were more closely related to each other than either was to hornworts (Katoh *et al*. 1983).

The entire gene sequence was not known until 2017, using ***Marchantia polymorpha*** ssp. ***ruderalis*** (Figure 17-Figure 19) (Bowman *et al.* 2017). Since then, the subspecies have been sequenced and their evolutionary relationships elucidated (Linde *et al*. 2020). The results supported the hypothesis that ***M. polymorpha*** ssp. ***ruderalis*** is not a hybrid of the other two subspecies, as some researchers had thought.

Figure 17. ***Marchantia polymorpha*** ssp. ***ruderalis*** gemmae cups. Photo by David T. Holyoak, with permission.

Figure 18. ***Marchantia polymorpha*** ssp. ***ruderalis*** with archegoniophore. Photo by Jiří Kameníček, with permission.

Figure 19. ***Marchantia polymorpha*** ssp. ***ruderalis*** with archegonial head showing numerous scales. Photo by Jiří Kameníček, with permission.

Marchantia polymorpha (Figure 1-Figure 12) has likewise been used as a model organism in understanding development in thallose liverworts (Suzuki *et al*. 2020).

But the scientific study of this species, especially regarding development, has been occurring for at least 200 years (Shimamura 2016). Suzuki and coworkers described merophyte lineages and elaborated on the derivation of growth from stem cells in the apical notch (Figure 20).

Figure 20. ***Marchantia polymorpha*** showing apical notch with brown covering scale. Photo by Li Zhang, with permission.

Linde *et al*. (2021) compared rates of mutations among the major plant groups and found that the gymnosperms had the fewest synonymous mutations, flowering plants the most, and bryophytes were located between those two. In this regard, the silent site substitution rate (neutral evolution) is lower for the liverwort compared to flowering plants, but not as low as that of gymnosperms. They found the same selective constraints on the haploid-specific genes as those on the diploid-specific genes. However, in the haploid generation the new mutations experience immediate and direct selection, hence quickly being lost if they are maladaptive. The nonsynonymous to synonymous substitution rate ratio (dN/dS) represents selective evolution. This silent site substitution rate is lower for liverworts as compared to flowering plants, but again not as low as for gymnosperms. The selection pressure, measured as dN/dS, is not remarkably lower for bryophytes when compared to diploid dominant plants as we might expect based on the **masking hypothesis** (predicts more efficient selection in haploids than in diploids, because dominant alleles can mask deleterious effects of recessive alleles in diploids; however, gene expression breadth and noise can potentially counteract the effect of masking on the rate at which genes evolve), indicating that other factors are more important than ploidy.

Liu *et al.* (2019) noted that the dN/dS for nuclear genes was more than three times higher for bryophytes when compared to seed plants. However, the sets of genes compared were not the same genes in both groups. Linde and coworkers (2021) compared the same 42 genes in both groups and found that the dN/dS rates were much more similar. This raises the question of why bryophytes, given their long history, are less diverse and appear to have less morphological diversity than tracheophytes, especially flowering plants. But as I have argued elsewhere, they are confined to being small due to their lack of lignin. They furthermore, because of this small size, are at greater risk of disappearance due to herbivory and pathogens. If one considers their biochemical diversity, affording them protection from herbivores and pathogens, are they really less diverse?

Fang *et al*. (2014) reported for the first time the presence of oleosin genes in liverworts, using ***Marchantia polymorpha*** (Figure 1-Figure 12). The liverworts tested exhibited only M-oleosins, whereas three types are known from various plant lineages. This seems to be a precursor to the other two oleosins, suggesting another piece of the evolutionary story.

With all of our knowledge about molecular similarities and differences, molecular/genetic studies have become the driving force in plant systematics. Using the **Marchantiales**, Boisselier-Dubayle *et al*. (1997) were among the early researchers to point out that there can be an incongruence between morphological characters and molecular data, complicating our systematic efforts.

Understanding the genome, coupled with the greater ease of working with haploid organisms, has contributed to the use of ***Marchantia polymorpha*** (Figure 1-Figure 12) in transferring genes to determine their functions.

teaching

The genus ***Marchantia*** is notable in the pre-Renaissance literature, with illustrations of ***M. polymorpha*** (Figure 1-Figure 12) appearing as early as the mid-15th Century (Bowman 2016). Notable early treatments are those of Schmidel (1762) and Hedwig (1783). It has been used for centuries in nearly every textbook and classroom that teaches about bryophytes or life cycles (Cutting 1910; Inoue & Asakawa 1966; Register & West 1971; Une 1998; Bowman 2016).

Marchantia polymorpha (Figure 1-Figure 12) has also been used as a pedagogical model to teach the bioindicator concept to seventh graders (Pedroza-Manrique & Arévalo 2009). This was part of a study on comparison of learning strategies. Results demonstrated that "learning must be related to the environment of the students and must also represent a challenge for them, this allowed for significant learning."

Durand (1908), in preparing material for teaching a course in embryology, selected ***Marchantia polymorpha*** (Figure 1-Figure 12) to represent development in liverworts. He wrote that he "naturally selected ***Marchantia polymorpha***" because of its accessibility and ease of study. And it is illustrated in practically every textbook that treats liverworts.

Distribution

Marchantia polymorpha (Figure 1-Figure 12) has a worldwide distribution (Figure 21), especially in the Northern Hemisphere (Bischler-Causse 1989; Lu & Huang 2017). It is known from Afghanistan, Bhutan, China, India, Indonesia (Java, Sumatra), Iran, Iraq, Israel, Japan, Korea, Lebanon, Malaysia, Nepal, New Guinea, New Zealand, Pakistan, Philippines, Russia, Sri Lanka, Syria, Tadzhikistan, Taiwan, Tasmania, Thailand, Turkey, USSR, Uzbekistan, and Vietnam (Bischler-Causse 1989; Söderström *et al*. 2010; Ginting & Batubara 2019). As seen in Figure 21, it is also extensively reported throughout North America. ***Marchantia polymorpha*** has three subspecies. In South Africa, ***M. polymorpha*** ssp. ***ruderalis*** (Figure 6-Figure 8, Figure 17-Figure 19) only occurs in

nurseries (Figure 22-Figure 23), indicating that it has been introduced (Ginting & Batubara 2019).

Figure 21. ***Marchantia polymorpha*** distribution. Image from DiscoverLife, with online permission.

Figure 22. ***Marchantia polymorpha*** ssp. ***ruderalis*** in flower pot in nursery, the only place it occurs in South Africa. Photo courtesy of Javier Martínez-Abaigar.

Figure 23. ***Marchantia polymorpha*** ssp. ***ruderalis*** in flower pot intended for growing a tree. Photo courtesy of Javier Martínez-Abaigar.

Aquatic and Wet Habitats

Boisselier-Dubayle and Bischler (1989) described the electrophoretic biochemistry of ***Marchantia polymorpha*** (Figure 1-Figure 12) as having a good correlation with the habitats. They identified two ecotypes: domestic with a spread over a wide geographic area (possibly corresponding with ***M. polymorpha*** ssp. ***ruderalis*** – Figure 6-Figure 8, Figure 17-Figure 19), and a wet-habitat-restricted ecotype that exhibited two biotypes [corresponding with ***M. polymorpha*** ssp. ***polymorpha*** (Figure 5) and possibly ***M. polymorpha*** ssp. ***montivagans*** (Figure 2-Figure 4)].

In their recent publication on ***Marchantia*** in Japan, Zheng and Shimamura (2022) described the habitat of ***Marchantia polymorpha*** ssp. ***polymorpha*** (Figure 5) as growing on wet soil in marshland or stone near streams, seldom on wet concrete. They described ***Marchantia polymorpha*** ssp. ***ruderalis*** (Figure 6-Figure 8, Figure 17-Figure 19) as often on soil, stone, gravel, or walls of drainage channels in anthropogenic regions, supporting the conclusions of Long (1995). But Zheng and Shimamura (2022) also found that when the latter subspecies grows in dripping wet habitats, "plants often have an erect and robust thallus with a distinct and continuous blackish median band on the thallus and are sometimes difficult to distinguish from ssp. ***polymorpha*** based on these characters." However, they consider that the discontinuous blackish median band and prostrate thallus of ssp. ***polymorpha*** will distinguish them. I would like to see common garden experiments on the effects of wet vs drier habitats on the expression of the black median band (midrib) in each of the subspecies.

Subspecies ***montivagans*** (Figure 2-Figure 4) in Britain and Ireland is a species occurring in springs, marshes, and flushes, in somewhat calcareous areas, and occurs mostly in subalpine or montane habitats (Long 1995). It can also be found on damp calcareous mossy banks and rocks beside streams and ravines. However, in their studies Boisselier-Dubayle and Bischler (1989) found it in some locations together with ***M. polymorpha*** ssp. ***polymorpha*** (Figure 5).

Frye (1928) found that ***Marchantia polymorpha*** (Figure 1-Figure 12) was sometimes submersed in winter. This, presumably, was ssp. ***polymorpha*** (Figure 5).

Darigo (2004) reported the aquatic form of ***Marchantia polymorpha*** (as *Marchantia aquatica*; now ***M. polymorpha*** ssp. ***polymorpha***; Figure 5) as new to Missouri, USA, noting its distinctive black midrib. He found it in dense mats on shaded moist soil and limestone bedrock at the base of a small waterfall. It was associated with ***Fissidens grandifrons*** (Figure 24), ***Rhizomnium punctatum*** (Figure 25), and ***Leptodictyum riparium*** var. ***laxirete*** (Figure 26).

Marchantia polymorpha *s.l.* (Figure 1-Figure 12) occurs in wet places around lakes, especially in shade, and in bog water in Scotland (West 1910). In Denmark it can be found on terrestrial soil or submerged (Sørensen 1948). It is uncommon with the graminoid ***Eleocharis quinqueflora*** (Figure 27) and the moss ***Paludella squarrosa*** (Figure 28) Geissler & Selldorf 1986).

Figure 24. ***Fissidens grandifrons***, an associate of ***Marchantia polymorpha*** on limestone in wet habitats. Photo by Brad Von Blon, through Creative Commons.

Figure 25. ***Rhizomnium punctatum***, an associate of ***Marchantia polymorpha*** on limestone in wet habitats. Photo by Sharon Pilkington, with permission.

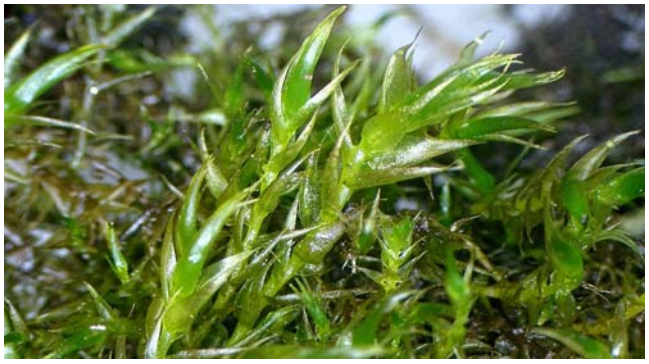

Figure 26. ***Leptodictyum riparium***; var. ***laxirete*** is an associate of ***Marchantia polymorpha*** on limestone in wet habitats. Photo by William Lampa, through Creative Commons.

Figure 27. ***Eleocharis quinqueflora***, an occasional associate of ***Marchantia polymorpha*** in Denmark. Photo by Kristian Peters, through Creative Commons.

Figure 28. ***Paludella squarrosa***, an occasional associate of ***Marchantia polymorpha*** in Denmark. Photo by Hermann Schachner, through Creative Commons.

Marchantia polymorpha (Figure 1-Figure 12) occurs in shady areas with high humidity and exhibits a low tolerance to desiccation (Lagos-López 2008). In such areas it can develop extensive cover (Linares 1986; Churchill & Linares 1995; Uribe & Aguirre 1995; Lagos-López 2008). But perhaps one of the most extensive covers develops in burned over areas (Durand 1908; Janet Marr, pers. obs. 2022), usually not an aquatic habitat.

streams and rivers

Watson (1919) described the habitat of ***Marchantia polymorpha*** (Figure 1-Figure 12) as often on boulders in streams, on banks with frequent submergence and slow water. In the Western Carpathians it occurs in the rock community in streams near Lacko (Mamczarz 1970). It

occurs in streams in Greece (Papp 1998) and in streams in northeastern Finland (Heino & Virtanen 2006). It is among the most common species in the River Tweed, UK (Holmes & Whitton 1975) and is among the commonest species in English and Welsh rivers (Scarlett & O'Hare 2006).

It can also be common in rivers (Ferreira *et al*. 2008), such as the Iskur River, Bulgaria, and its main tributaries (Papp *et al.* 2006), as a hygrophyte in Bulgarian rivers (Gecheva *et al*. 2010, 2013), and in the Iregua River of Spain (Martínez-Abaigar & Ederra 1992).

It is often a mountain species, occurring in alpine streams in the Swiss Alps (Geissler 1976) and in mountain streams of northwest Portugal (Vieira *et al.* 2005) as well as mountainous streams on Madeira Island (Luis *et al.* 2015). Frye (1928) reported it from western Washington, USA, in burned sites, but also in submersed sites. It is interesting that several ***Marchantia*** species occur in both aquatic habitats and as pioneers after fire.

stream and river banks

Perhaps the most common wet habitat for ***Marchantia polymorpha*** (Figure 1-Figure 12) is the damp banks of streams and rivers (Figure 29-Figure 32). In the Haute Ardenne rivers in Belgium, it occurs on earthy and gravelly substrates of river banks (Leclerq 1977) and in the UK it occurs on the riverbank of the River Tees (Holmes & Whitton 1977a). It can be found throughout the River Swale, Yorkshire, UK (Holmes & Whitton 1977b), and mostly in the mid to lower River Tyne, UK (Holmes & Whitton 1981b). It is similarly associated with the River Wear in England (Birch *et al*. 1988). In Germany it occurs in the middle and lower reaches in the Harz Mountains (Bley 1987). Ginting and Batubara (2019) similarly describe it from rocks of a creek wall in exposed places (Figure 33), at 1500 m altitude in Indonesia. In western Canada, it is restricted to terrestrial habitats of montane streambanks (Vitt *et al*. 1986; Glime & Vitt 1987).

Figure 29. ***Marchantia polymorpha*** ssp. ***polymorpha*** on the bank of a small stream, showing partially upright branches. Photo by Vladimir Bryukhov, through Creative Commons.

Figure 30. ***Marchantia polymorpha*** on steep stream bank. Photo by Olga Chernyagina, through Creative Commons.

Figure 31. ***Marchantia polymorpha*** ssp. ***polymorpha*** wet beside stream. Note the rhizoids hanging from the lower side of the thallus. Photo by Penny Anderson, with online permission.

Figure 32. ***Marchantia polymorpha*** with gemmae cups on moist soil by stream. Photo by Rudolf Macek, with permission.

In Denmark ***Marchantia polymorpha*** (Figure 1-Figure 12) can be found in ditches at *p*H 6.2-8.5 and in neutro-alkaline lakes, peat pits of spring bogs (Figure 34) at *p*H 6.2-8.0, on terrestrial soil or submerged (Sørensen 1948; Clausen 1952). Alfasane *et al*. (2013) recorded environmental conditions in Lake Rainkhyongkain, where it grew in masses in the shallow littoral zone of the lake. These included mean values (n = 4) of dissolved oxygen

content (7.93 ± 0.78 mg L^{-1}), alkalinity (1.70 ± 0.12 meq L^{-1}), soluble reactive phosphorus (17.25 ± 0.62 µg L^{-1}), soluble reactive silicate (10.44 ± 0.72 mg L^{-1}), and NO_3-N (34.00 ± 4.00 µg L^{-1}). The mean temperature on the sampling date was 33.5°C and *p*H was 7.39.

Figure 33. ***Marchantia polymorpha*** with ***Thuidium delicatulum*** growing over flagstone at Mountain Moss Enterprise, demonstrating the breadth of its habitat. Photo by Annie Martin, with permission.

In the high moor transition areas of Denmark ***Marchantia polymorpha*** (Figure 1-Figure 12) can be found at *p*H 5.0-6.09 (Sørensen 1948). O'Toole and Synnott (1971) found that ***Marchantia polymorpha***, along with ***Funaria hygrometrica*** (Figure 35), was an early indicator of increased calcium carbonate and phosphorus levels on blanket peat following fertilization of the peat. However, these two bryophytes are suited to other environmental conditions, with ***M. polymorpha*** preferring wet, unsheltered plots with no iron or copper, whereas ***F. hygrometrica*** prefers dry, sheltered locations with iron (Synnott 1987). Li Zhang (pers. comm. 4 August 2022) has found ***Marchantia polymorpha*** in peatlands (Figure 34) in China.

Figure 34. ***Marchantia polymorpha*** ssp. ***montivagans*** in a spring, Sierra Nevada near Merida, Venezuela. Photo courtesy of Javier Martínez-Abaigar.

Figure 35. ***Funaria hygrometrica***, an indicator, along with ***Marchantia poymorpha***, of increased calcium carbonate and phosphorus levels in blanket peat. Photo by Bonnie Nickel, through Creative Commons.

In Taiwan, Lu and Huang (2017) found ***Marchantia polymorpha*** (Figure 1-Figure 12) on damp soils from 300-2500 m asl, a habitat similar to that on Mt. Edith Cavell in Canada (Figure 36).

In high moors in Denmark it occurs in the transition areas at *p*H 5.0-6.0 (Sørensen 1948). In the Caucasas it is in watery and swampy lands (Alijev & Babajev 1976).

Figure 36. ***Marchantia polymorpha*** with gemmae, on damp soil with mosses on the mountainside of Mt. Edith Cavell, Jasper, Canada. Photo by Janice Glime.

Other damp soil habitats are also suitable, including open areas (Figure 37), moist slopes (Figure 38), marshy areas (Figure 39), and other wetlands (Figure 40). Thatcher (1949) found it in an artificially illuminated cave.

Figure 37. ***Marchantia polymorpha*** on soil, with gemmae cups, in Europe. Photo by Michael Lüth, with permission.

Figure 38. ***Marchantia polymorpha*** on a damp soil bank. Photo by Michael Lüth, with permission.

Figure 39. ***Marchantia polymorpha*** in a marshy habitat near a stream. Photo by Michael Lüth, with permission.

One of the more interesting habitats for ***Marchantia polymorpha*** (Figure 1-Figure 12) is on a **desalinating wadden-polder** (tract of low land reclaimed from the sea; Figure 41) (Joenje & During 1977). Although it was able to colonize, it was unable to compete after 2-3 years. It was especially common on mussel banks. Joenje and During suggested that its small spores contribute to its rapid arrival on newly available substrata.

Figure 40. ***Marchantia polymorpha*** ssp. ***montivagans*** with ***Calliergon cordifolium*** in a wetland. Photo by Des Callaghan, through Creative Commons.

Figure 41. Gradual transition from recently deposited salt marshes and the Wadden sea on a desalinating wadden-polder. This stage is too salty, due to manipulation, and the only bryophyte able to live here is ***Hennediella heimii***. Photo courtesy of Bart van Tooren.

Another unusual habitat where ***Marchantia polymorpha*** (Figure 1-Figure 12) can thrive is in geothermal areas (Figure 42). These can have some similarities to saline areas because of sulfur and other salts. In the Antarctic, they provide a warm haven for species from warmer climes, including ***M. polymorpha*** (Kennedy 1996). Takaki (1967) found it on an active volcano in Japan. Takaoki and Mitani (1986) used ***Marchantia polymorpha*** in experiments to develop a method for measuring the effects of SO_2 on photosynthesis in bryophytes and lichens. They found that illumination during the exposure to SO_2 caused the SO_2 to have greater inhibition of photosynthesis in ***M. polymorpha*** than did SO_2 alone. In this species, the photosynthetic system was more sensitive than the respiratory system. In concentrations less than 4 ppm, the thalli were able to partially recover.

Figure 42. Geothermal fissure with ***Sphagnum***, Geyser, Iceland, a potential habitat for ***Marchantia polymorpha***. Photo by Janice Glime.

Figure 43. Mt. Hood Riverside, Oregon, USA, post-fire, at a stage where ***Marchantia polymorpha*** can be a pioneer. Photo from U.S. Department of Agriculture, through public domain.

after fire

It is interesting that several species of ***Marchantia*** are post-fire colonizers (Figure 43). This is true for ***Marchantia polymorpha*** (Figure 1-Figure 12) (Benson & Blackwell 1926; Torrey 1932; Bradbury 2006). Frye (1928) and Hoffman (1966) both reported it on burned sites in Washington, USA, and Graff (1936) similarly found that the species invaded after forest fires. Adámek *et al*. (2016) studied post-fire vegetation in central Europe and again found that ***Marchantia polymorpha*** was among the first invaders, but it typically disappeared after a few years. Froment (1975) found it to be among the pioneer dominants in a Belgian high fen post-fire site. Heras-Ibáñez *et al.* (1991) recorded it in post burn sites in SE Spain, where it had diminished numbers after 6 years. They noted that some of the species, including ***M. polymorpha***, were known to fix nitrogen (through bacterial partners) on such sites. Duckett *et al*. (2008) noted that ***M. polymorpha*** is common after fires in Canada and explored post-fire invasion at Thursley Common, UK. Once again, ***M. polymorpha*** was a common invader. In fact, they noted that thalli had abundant reproductive structures in the first year following the fire. They attributed the rapid colonization to the tiny (10-16 μm) spores. Subspecies. ***ruderalis*** and ssp. ***polymorpha*** were present side by side. The species formed patches reaching up to 12 m in diameter, with individual colonies of 5-20 cm diameter (Duckett & Pressel 2009). Rather that naming tracheophyte competition, they attributed the later decline to nutrient leaching (Duckett *et al*. 2008). Its presence is so common after fire that Rees and Juday (2002), when reporting it from Alaskan burned sites, considered it to be a fire specialist.

The succession of species following fire is a fairly constant one, as noted already by Skutch (1929). Typically, the pioneer stage with ***M. polymorpha*** (Figure 1-Figure 12) is succeeded by ***Polytrichum*** (Figure 44).

These habitats would seem to be quite different from the wet ones already discussed. But one thing they have in common is reduced competition, giving the liverworts time to become established.

Figure 44. ***Polytrichum juniperinum***, a post-fire species that succeeds ***Marchantia polymorpha***. Photo by James K. Lindsey, with permission.

Having said that, how then do we explain that in East Anglia ***Marchantia polymorpha*** (Figure 1-Figure 12) is more common in town than in the countryside (Stevenson & Hill 2008)? Is the subspecies ***ruderalis*** more tolerant of competition, or do the spores manage to find spots with limited competition?

Physiology

It is not surprising that the anatomy and physiology of this well known species were among the early bryological studies (Mirbel 1835). Since that time, a long period of mostly taxonomic activity ignored the physiology of most bryophytes. However, ***Marchantia polymorpha*** (Figure 1-Figure 12) was frequently the subject of those studies that did address bryophyte physiology.

hormones - IAA

Among the many studies on ***Marchantia polymorpha*** (Figure 1-Figure 12), it often served as the model organism for understanding physiology of thallose liverworts, or bryophytes in general. Maravolo and Voth (1966) reported the actions of various concentrations of indoleacetic acid (IAA), naphthalene acetic acid (NAA), and maleic hydrazide on development of sterile gemmae (Figure 45) of ***Marchantia polymorpha***. They found that the two auxins

(IAA and NAA) promoted similar responses, often resembling those of tracheophytes. In ***M. polymorpha***, rhizoids elongated on the dorsal surface; the growing region became dormant, and cells became strongly elongated. When apical growth (Figure 20, Figure 46) was inhibited, the thallus became winged. The maleic hydrazide likewise elicited responses similar to those in tracheophytes, including inactivation of meristematic regions, deterioration of chloroplasts, inhibition of rhizoid production, and **hyperplasia** (enlargement of organ or tissue caused by increased reproduction rate of its cells).

Figure 45. ***Marchantia polymorpha*** with gemmae in gemmae cups. Photo by Holger Casselmann, through Creative Commons.

But at that time, the production of IAA by bryophytes was still unknown. Schneider *et al*. (1967) reported for the first time that IAA (indoleacetic acid) occurs in bryophytes, using ***Marchantia polymorpha*** (Figure 1-Figure 12) as one the test organisms. Furthermore, Sheldrake (1971) reported auxin in the substrata of bryophytes, so its effect on them is relevant. However, concentrations of the IAA in substrata with no bryophytes were the same in those that had them. Hence, it is questionable whether these substrate sources were of importance to the development of the bryophytes. Nevertheless, they could play a role in the induction of rhizoids as they do for roots. And they might have more effect on some bryophytes not included in the tests.

Following up on the possible functions, Otto and Halbsguth (1976) examined the effects of light and the auxin IAA on the formation of the primary rhizoids of gemmae in ***Marchantia polymorpha*** (Figure 1-Figure 12). They found that the number of rhizoid-forming gemmae depends on the wavelength of irradiation. Following a 1-hour exposure to 10^{-4} M IAA, rhizoids developed as they would if exposed to red irradiation for one hour. They concluded that this relationship suggests a role of the phytochrome system in membrane permeability for IAA.

Transport of the auxin 11C-indoleacetic acid occurs basipetally in the thallus, where it is localized in the midrib (Figure 46-Figure 47) (Maravolo 1976; Gaal *et al*. 1982).

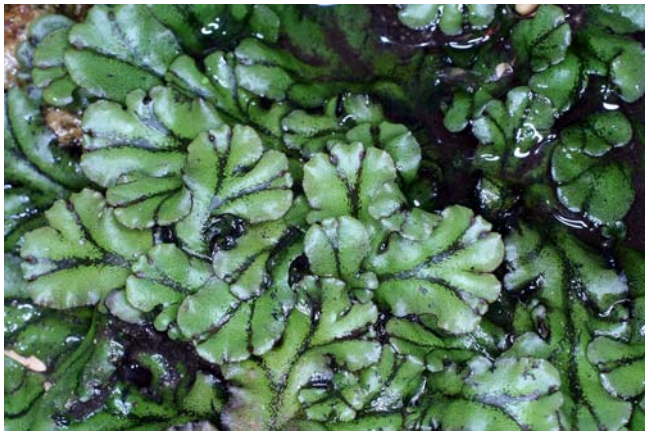

Figure 46. ***Marchantia polymorpha*** with strong midrib on older thalli; this character is common in aquatic forms. In several branches you can see apical dominance where a single branch is dominant and the other is shorter or has an unbranched midrib (*e.g.* **center left**). Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 47. ***Marchantia polymorpha*** with only hints of midrib on young thallus tissue, probably ssp. ***ruderalis***. Photo by Janice Glime.

Reynolds and Maravolo (1973) determined that extracts of ***Marchantia polymorpha*** (Figure 1-Figure 12) contain substances that in the lab can enhance or inhibit IAA oxidation. These extracts contained four unknown phenolic compounds. Two of these enhanced the oxidase activity and two inhibited it. Although the inhibitors were present throughout the thallus, they were slightly more concentrated in basal and apical areas. In other words, there was an **acropetal** (movement of dissolved substances outward toward shoot and basal apices) gradient of increase in this cofactor concentration. In this case IAA moves away from the growing tips.

Gaal *et al*. (1982) used tracer experiments to determine that ^{14}C IAA transport is localized in the cells of the midrib of the thallus (Figure 46). It occurs both acropetally and basipetally, with a far greater intensity basipetally. In anaerobic conditions, basipetal transport was reduced by 40-50%. Centrifugation also disrupted it, reducing basipetal transport by 30-40%. Hence, in the parameters measured, transport of IAA in ***Marchantia polymorpha*** (Figure 1-Figure 12) is essentially the same as that in seed plants.

Davidonis and Munroe (1972) described apical dominance (Figure 46) in ***Marchantia polymorpha*** (Figure 1-Figure 12), a function known from tracheophytes. The species dichotomous branching and its apical dominance is exhibited by one of those branch lobes having greater growth than the other (Figure 46). They demonstrated that if the lobes are separated by a cut, the dominance is lost. IAA is needed to maintain this dominance. If it is applied to the smaller lobe after the cut, that lobe is again inhibited. It also exhibits greater inhibition of the smaller lobe when applied to the intact plant. Interestingly, the dominant lobe is neither inhibited nor enhanced by application of IAA to it. They suggested that this behavior indicates that the two lobes have a different sensitivity to the auxin. This is somewhat reminiscent of apical dominance in plants like snapdragons. IAA produced in the apex of the plant migrates downward and inhibits the development of side branches. If the apex is removed, a lower branch becomes dominant.

Hormones can both activate and suppress pathways in ***Marchantia polymorpha*** (Figure 1-Figure 12). Binns and Maravolo (1972) found that cytokinin suppressed the normal germination of gemmae (Figure 45), instead stimulating nodular, callus-like growths. Responses were time-dependent on the cytokinin-enriched medium. Auxin, on the other hand, had no effect on the regeneration of normal thallus growth. Auxin could, however, reverse the suppression caused by inhibiting compounds such as transcinnamic acid. Auxin exhibited a basipetal gradient and this gradient is essential to normal growth and regeneration. These two hormones interact, with high levels of cytokinin destroying the polarity by increasing the auxin-synthesizing capacity. Maintaining the right balance permits the liverwort to maintain its apical dominance (Figure 20, Figure 46).

Flores-Sandoval *et al*. (2015) characterized the functions of the auxin transcriptional response in ***Marchantia polymorpha*** (Figure 1-Figure 12). It acts to facilitate branching, differentiation, and growth, but it does not determine specific tissues.

Eklund *et al*. (2015) found that the auxin IAA regulates the dormancy of gemmae (Figure 48) on the ***Marchantia polymorpha*** (Figure 1-Figure 12) thallus. Kato *et al*. (2015) found that auxin repression could cause severe defects in the development of ***Marchantia polymorpha***, including gemmaling development, dorsiventrality, organogenesis, and tropic responses, noting the interactions of hormones. Billhardt (2021) further discussed the interactions, and using these was able to explain the long-known observation that gemmae typically do not germinate while still on the parent thallus (Figure 48). This dormancy mechanism is controlled by high levels of abscisic acid (ABA) in the cup (see also Tougane *et al*. 2010). But gemmae are not attached to the thallus while they reside in the cup. Therefore, it appears that the actual signal is a gas. Billhardt found that when the regulators of the ethylene signalling pathway were mutated, it affected the dormancy, suggesting that ethylene regulates dormancy through ABA. Müller (2021) notes that ABA and ethylene commonly act antagonistically, possibly explaining these observations.

Ishizaki *et al*. (2012) used transgenic plants to monitor the effects of auxin-mediated transcriptional activation in plants. This demonstrated that IAA had a role in the transcription of some genes. These genes were demonstrated at the bottom of the gemmae cups. Additional activity occurred at the gametophyte-sporophyte junction and in the developing sporophyte.

Figure 48. Gemmae cups with loose dormant gemmae on thallus of ***Marchantia polymorpha***, demonstrating their continued dormancy while associated with the parent tissue. Photo by Hermann Schachner, through Creative Commons.

hormones - gibberellins

Melstrom *et al*. (1974) found that ***Marchantia polymorpha*** (Figure 1-Figure 12) exhibits gibberellin activity and was responsive to photoperiod. When they increased the photoperiod from 12 to 18 hours of light the activity of the gibberellins increased and thallus elongation and **orthogeotropic** (directly in line with gravitational pull; Figure 49) growth increased.

Figure 49. ***Marchantia polymorpha*** ssp. ***polymorpha*** growing upright in water. Photo by Oleg Kosterin, through Creative Commons.

Maravolo (1980) applied both auxins (IAA) and gibberellin to bryophytes, including ***Marchantia polymorpha*** (Figure 1-Figure 12). In this case, the applied auxin stimulated rhizoid growth, cell proliferation, and elongation. Gibberellin, on the other hand, promotes cell enlargement, chloroplast development, and starch degradation. Under the right photoperiod, it also influences the geotropic curvature and causes ultrastructural changes in starch granules and thylakoids.

Loomis and Maravolo (1985) found that exogenous gibberellin increases the amylolytic activity of two protein fractions from ***Marchantia polymorpha*** (Figure 1-Figure 12).

hormones - ethylene

Little information has been available on ethylene presence and physiology in bryophytes. Ethylene is a gaseous hormone and therefore can be used to communicate between plants. Katayose *et al*. (2021) noted that genes for ethylene have been conserved from the algae, but that the function and biosynthesis of this hormone remain unknown in the bryophytes. They found that ***Marchantia polymorpha*** (Figure 1-Figure 12) synthesizes ethylene. However, treatment with the precursor ACC only slightly promoted the production of ethylene. On the other hand, ACC "remarkably" suppressed thallus growth and rhizoids, contrasting with the slight promotion of thallus growth when external ethylene was applied. These experiments indicate that ethylene functions independently of ACC and that ACC is not essential to its production in ***Marchantia polymorpha***.

Li *et al*. (2020) similarly found that ACC (ethylene precursor) and ethylene can induce different responses in ***Marchantia polymorpha*** (Figure 1-Figure 12). Ethylene causes larger gemmae, induces more gemmae cups, and promotes the dormancy of the gemmae. ACC, on the other hand, inhibits gemma growth and development by suppressing cell division. This suggests that the pathway might be different from that tracheophytes.

In ***Marchantia polymorpha*** (Figure 1-Figure 12), more ethylene is produced in the light than after prolonged darkness (Fredericq *et al*. 1977; Rethy *et al*. 1977). Veroustraete *et al*. (1982) further elaborated on ethylene physiology in the species. They found involvement of the low energy red:far-red reversible type of phytochrome action for both the light-induced ethylene production and the control of **epinasty** (nastic movement in which plant part such as flower petal or thallus branch is bent outward and often downward; Figure 50) in the species. They found that CO_2 had no effect on the production of ethylene when the thallus was irradiated with terminal far-red light, but in controls without the light treatment, there was a clear CO_2 dependency. This behavior suggests the involvement of phytochrome. De Greef *et al*. (1979) studied environmental effects on ethylene production in ***M. polymorpha*** and concluded that ethylene production requires energy and depends on either cyclic photophorylation or oxidative phosphorylation.

Figure 50. ***Marchantia polymorpha*** showing an unusual margin formation that exhibits **epinasty**. Photo by Steve Trynoski, with permission.

hormones - cytokinins

Binns and Maravolo (1972) found that cytokinin suppressed germination of gemmae (Figure 45) in ***Marchantia polymorpha*** (Figure 1-Figure 12). Externally applied auxins had no effect on regeneration from thallus discs.

Aki *et al*. (2019a,b) noted that cytokinins regulate a variety of physiological events in plants. They found that the cytokinin signalling pathway in ***Marchantia polymorpha*** (Figure 1-Figure 12) controls the formation of both gemmae cups (Figure 45, Figure 48) and rhizoids (Figure 53-Figure 54) during the development of the thallus. It is further implicated in the distribution of air pores (Figure 51) and the shape of the thallus margin (compare Figure 49 and Figure 50), suggesting that cytokinins regulate cell division or differentiation of precursor cells, thereby coordinating development.

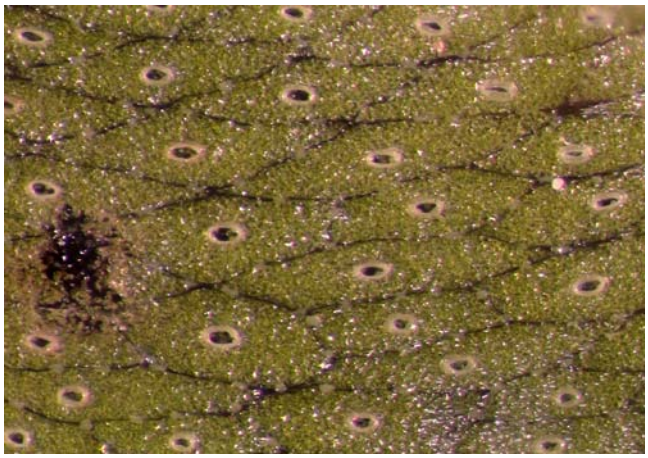

Figure 51. ***Marchantia polymorpha*** epidermis with air pores, showing green layer beneath. Photo by Walter Obermayer, with permission.

hormones – ABA and lunularic acid

In 1979, Weiler used a radioimmunoassay in an attempt identify the presence of ABA in ***Marchantia polymorpha*** (Figure 1-Figure 12). At that time, using that sensitive technique, ABA appeared to be absent. Fortunately, that result was not accepted by everyone. Li *et al*. (1994) announced, for the first time, the presence of abscisic acid (ABA) in liverworts, using ***Marchantia polymorpha*** as the model organism. In fact, the concentrations were similar to those of tracheophytes.

Akter *et al*. (2014) found that pretreatment with ABA and sucrose increases the survival rate after both freezing and desiccation of gemmalings in ***Marchantia polymorpha*** (Figure 1-Figure 12). ABA also increases the accumulation of soluble sugars. Furthermore, ABA induces the accumulation of transcripts for proteins that are similar to late embryogenesis abundant (LEA) proteins, proteins that accumulate in maturing seeds as they acquire desiccation tolerance. ABA also causes the vacuoles to fragment, causing an increase in the cytosolic volume and increasing the volume and density of chloroplast distribution.

Eklund *et al*. (2018) also found that ABA delays the germination of gemmae (Figure 48) in ***Marchantia polymorpha*** (Figure 1-Figure 12).

Ghosh *et al*. (2016) was the first to report on the regulation of ABA in the liverwort ***Marchantia polymorpha*** (Figure 1-Figure 12). Previously, a hormone with similar functions, **lunularic acid**, was known from some liverworts. Ghosh and co-workers found that the expression of ABA-induced β-glucoronidase (GUS) reporter gene was less in older, mature thalli than in young gemmalings of this species This change corresponded with reduction in the sensitivity to exogenous ABA. Lunularic acid, on the other hand, had no effect on GUS expression.

Nevertheless, it appears that ***Marchantia polymorpha*** (Figure 1-Figure 12) has **lunularic acid** (Gorham 1977; Abe & Ohta 1983), a hormone with functions similar to those of ABA. However, it appears that in ***M. polymorpha***, the prelunularic acid greatly exceeds the lunularic acid (Abe & Ohta 1984). Gorham found it in all parts of ***M. polymorpha***. In continuous light, both lunularic acid and fresh weight increased relative to that in interrupted light periods. It appears that the lunularic acid either was not inhibited by continuous light or that the photosynthetic products overrode the inhibition.

Imoto and Ohta (1985) found that lunularic acid compounds were equally distributed in vacuoles and cytoplasm, but they were absent in plastids, mitochondria, and peroxisomes.

hormones - brassinosteroids

Brassinosteroids occur in a wide range of organisms, including early land plants (Bajguz & Hayat 2009). These steroidal plant hormones affect the promotion of plant growth and development. Metabolism of these steroids is altered when plants respond to abiotic stresses as well as bacterial, fungal, and viral pathogens. Ko *et al*. (1995) characterized five 4-demethylsterols that seem to be potent biosynthetic precursors of brassinosteroids in suspension cell cultures of ***Marchantia polymorpha*** (Figure 1-Figure 12).

cell growth

Fries (1964) explored the effects of growth inhibitors on growth and elongation in ***Marchantia polymorpha*** (Figure 1-Figure 12).

Matsui *et al*. (1991) detected the activity of lipoxygenase in ***Marchantia polymorpha*** (Figure 1-Figure 12) in culture. Most of this activity occurred in the **cytosol** (aqueous component of cytoplasm of cell). The activity increases rapidly during the lag phase of cell growth (Matsui *et al.* 1996). This activity decreased in the logarithmic phase, then increased again in the stationary phase. This series of changes in lipogenase activity is caused by *de novo* synthesis and degradation of the same lipoxygenase. They also found enzyme activity that degrades fatty acid hydroperoxides – products of lipoxygenase.

circadian rhythm

Lagercrantz *et al.* (2020) examined the circadian clock in ***Marchantia polymorpha*** (Figure 1-Figure 12). They found that this clock coordinates the **nyctinastic** (periodic movement plant parts, especially flowers or leaves, caused by nightly changes in light intensity or temperature) thallus movement of the species and suggested it is controlled by auxin (IAA). The thalli "wave" up and down on a 24-hour cycle in 12 hours light: 12 hours dark. These movements in gemmalings are maintained in continuous light. The auxin, produced in the apical region (Figure 20), travels basipetally through the midrib region, creating a gradient. The circadian rhythm regulates the IAA levels. At low doses (10-100 nM) the angle of growth is reduced, creating a more flattened thallus. These experiments support the observations of Went and Thimann (1937) that the response to auxin depends on the time of day.

Marchantia polymorpha (Figure 1-Figure 12) has often been a model for evolution in land plants. Linde *et al*. (2017) found homologues of core clock genes in *Arabidopsis* (Figure 52), bryophytes, and charophytes, with fewer copies in the latter. The data supported the hypothesis that adaptation to terrestrial life occurred earlier than that supposed by current theory, particularly occurring in the charophytes. The bryophytes exhibit not only duplication and acquisition of new genes, but also loss of genes in development of their circadian clock.

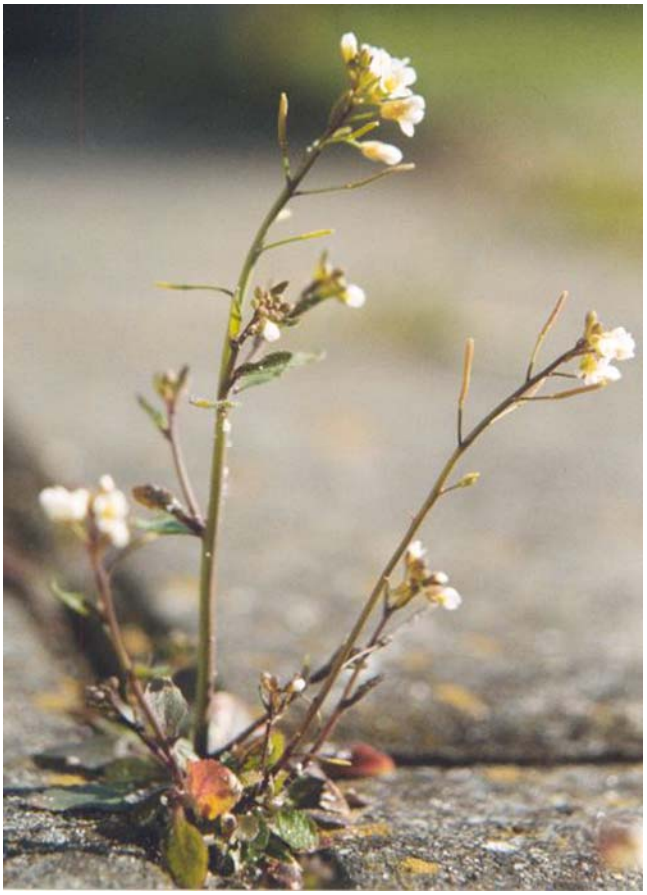

Figure 52. *Arabidopsis thaliana*, in a genus that has homolog genes with early land plants and is frequently used for evolutionary comparisons. Photo by Roepers, through Creative Commons.

Cuitun-Coronado *et al*. (2022) noted that photosynthesis is a circadian process in some flowering plants and Cyanobacteria. They reported the first record of circadian regulation of the photosynthetic pathway in a liverwort, ***Marchantia polymorpha*** (Figure 1-Figure 12). They determined that the light:dark cycle synchronized the 14-hour photosynthetic cycle, but that the phases of different thalli desynchronize under free-running

conditions. They suggested that chloroplast translation might be necessary for the clock to control the light-harvesting process in this plant.

Lagercrantz *et al*. (2021) used sequencing to identify the genes involved in circadian rhythms in ***Marchantia polymorpha*** (Figure 1-Figure 12). They identified a homolog of the *Arabidopsis* (Figure 52) gene DE-ETIOLATE1 as having a high amplitude and morning phase. The circadian rhythm resulting from Mp*DETl* expression is disrupted when core clock genes lose their function in mutants. In knock-down experiments with this gene, the circadian rhythm of nyctinastic thallus movement is altered. But the researchers were unable to detect any effect in response to light, leaving us with no explanation of the function of the Mp*DEP1* gene in ***M. polymorpha***.

water relations

Ghosh *et al*. (2021) explored the drought tolerance in this model organism. They desiccated gemmae in various desiccating solutions and found that these led to extreme growth inhibition, disruption of membrane stability, and reduction in chlorophyll content. At the same time, the accumulation of hydrogen peroxide and malondialdehyde increased and electrolyte leaked from the gemmalings, creating oxidative stress. Activities of antioxidant enzymes, including superoxide dismutase, catalase, ascorbate peroxidase, dehydroascorbate reductase, and glutathione S-transferase increased, while total antioxidant activity also increased in response to increased oxidative stress. When they applied exogenous ABA, it reduced drought-induced tissue damage and improved the activities of antioxidant enzymes and accumulation of proline.

Godinez-Vidal *et al*. (2020) noted that both water deficit and ABA cause osmotic adjustment in ***Marchantia polymorpha*** (Figure 1-Figure 12). This species increases its ABA levels under water deficit. Like Ghosh and coworkers, they found decreased growth and morphological changes in response to water deficits. Cell organelles changed locations, largely due to the volume change of the central vacuole, a consequence of the change in osmotic potential.

Hatanaka and Sugawara (2010) found that after exposure to drying below 0.1 g H_2O g^{-1} dry weight the desiccation tolerance level of ***Marchantia polymorpha*** (Figure 1-Figure 12) was very low, with a survival rate of less than 10%. When cells were pretreated in 0.5 M sucrose, the survival rate rose to 87%, even at lower water levels. This treatment caused cell alteration and the accumulation of a large amount of sucrose and newly made proteins.

Duckett and Ligrone (2003) found that rhizoids (Figure 53) in the bryophytes, particularly the **Marchantiales**, contribute to their water movement. They also contribute to movement of food. The smooth rhizoids (Figure 53-Figure 54) are living cells and often contain fungal hyphae. The pegged rhizoids (Figure 53-Figure 54) are dead, but they nevertheless contribute to the movement of water in the grooves of the archegoniophores. They also help to prevent the collapse when the thalli dry out and they facilitate recovery upon rehydration.

Figure 53. ***Marchantia polymorpha*** ventral surface of thallus showing pattern of horizontal pegged rhizoids that are close to the thallus and that facilitate water movement and uptake. The pinkish rhizoids toward the base are the perpendicular smooth rhizoids that adhere to the thallus. Photo by Larry Jensen, with permission.

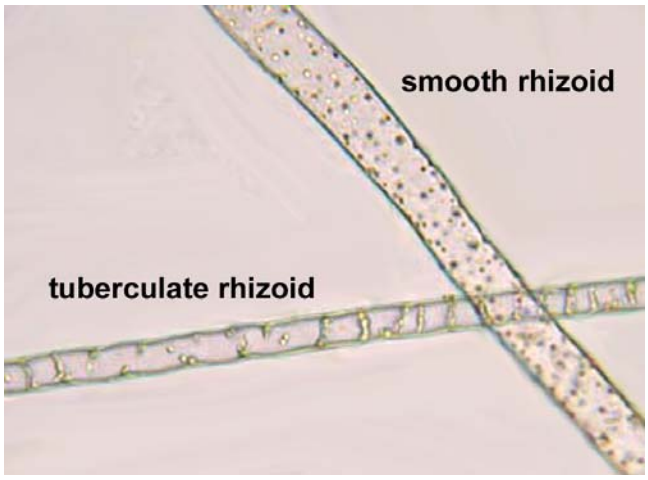

Figure 54. ***Marchantia polymorpha*** smooth and tuberculate (pegged) rhizoids. Photo from Botany Website, UBC, with permission.

Marchantia polymorpha ssp. ***ruderalis*** (Figure 6-Figure 8, Figure 17-Figure 19, Figure 56) was among the first plants to use extracellular ice formation (Figure 55) as a dehydrating agent, a mechanism to provide freezing avoidance (Schott *et al*. 2021). During exposure to freezing temperatures, ice crystals formed in the air chambers and grew out the pores. These hygroscopic crystals, along with other ice on the outside of the thallus, drew ice out of the cells and caused their dehydration. This ice removal can prevent the formation of crystals within the cells, where the crystals can cause membrane and structural damage. The thallose liverwort ***Conocephalum salebrosum*** (Figure 57) proved to be more resistant to frost than did ***Marchantia polymorpha*** ssp. ***ruderalis*** (Figure 56).

Figure 55. Extracellular ice crystals on ***Marchantia polymorpha***, a mechanism for causing dehydration and preventing freezing damage to membranes. Photo by David Taylor, with permission.

Figure 56. ***Marchantia polymorpha*** ssp. ***ruderalis*** with gemmae. Photo by Malcolm Storey, DiscoverLife, with online permission.

Figure 57. ***Conocephalum salebrosum***, a species that is more frost resistant than is ***Marchantia polymorpha*** ssp. ***ruderalis***. Photo by Hermann Schachner, through Creative Commons.

translocation

Rota and Maravolo (1975) traced the translocation of ^{14}C sucrose in ***Marchantia polymorpha*** (Figure 1-Figure 12). They found that during regeneration, higher levels of ^{14}C-sucrose moved to the apical region than during normal growth. The auxin IAA inhibited the transport and thallus regeneration.

desiccation

Pence (1998) found that for successful cryopreservation, ***Marchantia polymorpha*** (Figure 1-Figure 12) required both ABA and encapsulation in alginate beads, differing from ***Riccia fluitans*** (Figure 58) and ***Helicodontium capillare*** (Figure 59) that only required one of these. Without ABA and encapsulation, ***M. polymorpha*** was killed upon drying in liquid nitrogen. I found that interesting because ***R. fluitans*** is more aquatic than is ***M. polymorpha***, but perhaps it is because it is structurally smaller.

Figure 58. ***Riccia fluitans***, a species requiring only one of the two cryopreservation treatments (ABA and encapsulation in alginate beads) required by ***Marchantia polymorpha***. Photo by Kerry Wixted, through Creative Commons.

Figure 59. ***Helicodontium capillare***, a species requiring only one of the two (ABA and encapsulation in alginate beads) cryopreservation treatments required by ***Marchantia polymorpha***. Photo by D. Peralta, MNHN, through Creative Commons.

nutrients

Voth and Hamner (1940) described some of the symptoms of nutrient deficiency as expressed in ***Marchantia polymorpha*** (Figure 1-Figure 12). They found that cultures that lacked Ca ions but contained ions of K and Mg were able to regenerate new thalli, primarily from adventitious buds that arose from ventral cells in the midrib region. When NO_3 and PO_4 were absent, the ventral layers of cells developed a red-violet color in the walls, reminiscent of the phosphate deficiency in seed plants. Nevertheless, phosphate was needed in very small quantities in ***Marchantia polymorpha***. Increasing levels of nitrate increased growth, provided all essential nutrients were present.

Rico-Reséndiz *et al*. (2020a) unravelled the responses to low phosphate in ***Marchantia polymorpha*** (Figure 1-Figure 12). They found that phosphate starvation elicited the induction of phosphatase activity, acidification of the media, reduction of the internal phosphate concentration, and developmental changes in the rhizoids. Lipid turnover enzymes led to the synthesis of **auronidins** (see below). Up-regulation of certain genes led to changes in organic acid biosynthesis and transport, favoring citric acid exudation. The genes involved in the synthesis of cytokinin are repressed and those involved in auxin and ethylene signalling are upregulated (Rico-Reséndiz *et al*. 2020b). Genes involved in jasmonate synthesis were highly upregulated, but those involved in jasmonate signalling did not change their expression. It appears that auxin and ethylene act as positive regulators in rhizoid development when phosphate is limited, possibly increasing surface area for potential phosphate absorption. Cytokinin, on the other hand, may act as a negative regulator. These observations revealed diverse strategies that contribute to the ability to cope with low phosphate levels.

Voth (1941, 1943) compared various nutrient solutions on ***Marchantia polymorpha*** (Figure 1-Figure 12) growth. It is interesting that vegetative growth was favored by different concentrations than were gemmae cups. Furthermore, gemmae cups are in greater number on male plants compared to female plants, with a ratio of 1.44 to 1.0. High salt concentrations caused the growing tips to die and the thalli to become translucent. In low salt concentrations, "anthocyanin" (probably auronidin; see Albert *et al*. 2018; Kubo *et al.* 2018) was produced, along with numerous rhizoids and a sturdy plant body with thicker cell walls. Presumably the assumption of anthocyanin was due to a red coloration.

Absence of K (potassium) in the medium causes development of tan-colored bases on the plants and narrower tips (Voth 1941). Absence of Ca causes nearly immediate death of the growing tips. Both nitrate and phosphate deficiency cause reddening of the scales (Figure 60-Figure 61), rhizoids, and lower epidermis.

Miller *et al*. (1962a) developed methods to obtain nutritionally deficient mutants of ***Marchantia polymorpha*** (Figure 1-Figure 12). At that time, even few mutants of tracheophytes had been created for that purpose. Nevertheless, little has been published on nutrient deficiency symptoms in bryophytes.

Takio (1987) reported nitrate reductase activities in extracts from cultured cells of ***Marchantia polymorpha*** (Figure 1-Figure 12) growing in a medium with only nitrate as a nitrogen source. They found that the liverworts differed from the mosses in using NADPH as the electron donor, whereas the mosses used NADH. The coenzyme requirement also differed from that known for the other green plants.

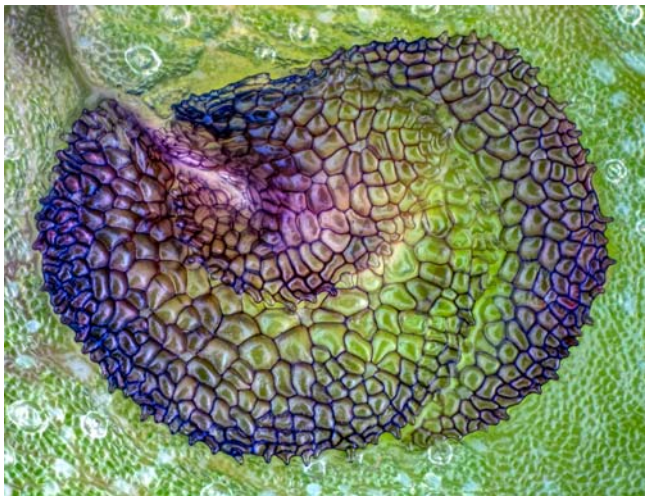

Figure 60. ***Marchantia polymorpha*** ssp. ***ruderalis*** scales showing purplish color that could develop as a deficiency symptom or possibly help to reflect the green light back to the chloroplasts. Photo by Des Callaghan, with permission.

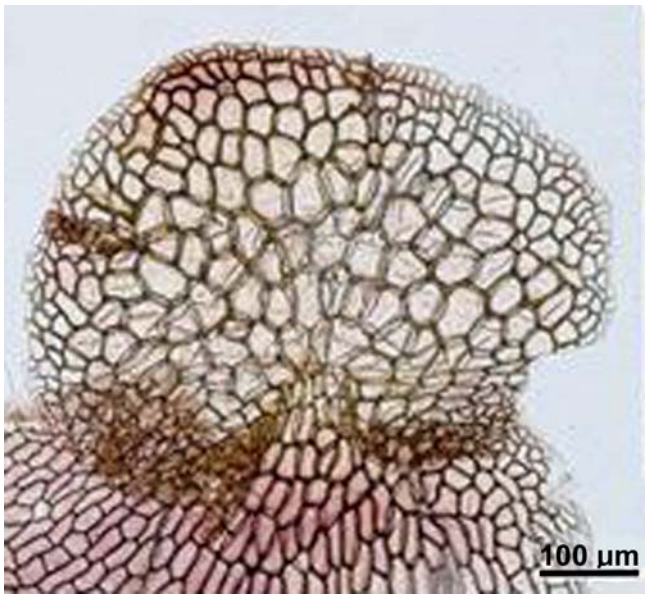

Figure 61. ***Marchantia polymorpha*** ventral scale and epidermis showing reddening that is typical of phosphate or nitrate deficiency. Photo by Masaki Shimamura, with permission.

Not all nutrients are inorganic compounds. Some of these are organic. Dunham and Bryan (1968) found that ***Marchantia polymorpha*** (Figure 1-Figure 12) is able to use a number of different nitrogenous compounds. They tested 24 compounds and found that nine of these had any effect on normal development. Among these, l-isoleucine, l-leucine, l-methionine, and l-threonine caused a disruption of the apical regions at concentrations of 10^{-3} M. At even lower concentrations, l-arginine, l-histidine, l-hydroxyproline, l-lysine, and l-tryptophan each caused morphological irregularities that were highly specific to the

amino acid. The modifications ranged from lack of development of the air chambers to complete thallus disorganization. The effects were dependent on the concentrations of the amino acids. This negative interaction raises questions about the role of compounds released by the decomposition of leaf litter in the environment in interfering with the growth of at least some bryophytes.

Effects of nutrients can differ between males and females of ***Marchantia polymorpha*** (Figure 1-Figure 12). Males with abundant nitrates produce many gemmae cups, narrower thalli, and incurved margins Female plants in these conditions produce fewer cups, have broader thalli, and plant surfaces remain flat.

Bryophytes grow in strange places and on strange substrata. Walkinshaw *et al*. (1970) tested ***Marchantia polymorpha*** (Figure 1-Figure 12) among the plants used to see the effects of lunar rocks on plant growth. They found that this liverwort grew several times larger than normal and had enhanced pigmentation when grown on media enriched with lunar rocks. Hoffman (1974) tested the effects of finely ground ilmenite basalt and loam-textured C-horizon substrate that was rich in volcanic ash, mixtures that closely resemble lunar samples from the Apollo 11 mission, on the growth of ***Marchantia polymorpha***. The moon rock was already known to stimulate the growth of ***M. polymorpha***. Analyses of the two Earth volcanic soil types suggested that the growth stimulus resulted from additional nutrients present in the basalt or volcanic ash.

heavy metals and pollution

For most nutrients, high concentrations become lethal. This is particularly true for heavy metals (Wu & Bradshaw 1972; Ares *et al*. 2018). These are often needed in small quantities in enzymes, but soon become toxic at higher quantities.

For this reason, bryophytes, including ***Marchantia polymorpha*** (Figure 1-Figure 12Figure 23), are suitable organisms to indicate heavy metal pollution (Maschke 1981). Coombes and Lepp (1974) examined the effects of zinc and copper on gemmalings of ***Marchantia polymorpha***. Copper proved to be more toxic than zinc, inhibiting gemmaling growth at levels above 8 ppm. Zinc actually had little effect on the gemmalings.

Ares *et al*. (2018) examined the physiological responses of ***Marchantia polymorpha*** (Figure 1-Figure 12) to Cd, Cu, Pb, and Zn. Under high concentrations, there was a significant enrichment and translocation of Cu, Zn, and especially Cd, achieving a concentration of 1800 $\mu g\ g^{-1}$ in three weeks. On the other hand, Pb achieved the lowest concentration (50 $\mu g\ g^{-1}$), with 90% of the total concentration in the rhizoids. Ozkem *et al*. (2019) further found that when ***Marchantia polymorpha*** was exposed to elevated levels of $CuCl_2$, $ZnCl_2$, and $Pb(NO_3)_2$ it experienced a significant reduction in chlorophyll content.

Both zinc and copper are toxic to the gemmalings of ***Marchantia polymorpha*** (Figure 1-Figure 12), with copper being more effective (Coombes & Lepp 1974). At levels of copper above 8 ppm ***M. polymorpha*** gemmalings exhibited greatly reduced growth. Other morphological changes also occurred.

Lepp and Roberts (1977) found that cadmium at levels above 5 ppm had negative impacts on gemmaling growth of ***M. polymorpha*** (Figure 1-Figure 12). Furthermore, respiration rates diminished with increasing Cd levels. Gekeler *et al*. (1989) found that ***M. polymorpha*** produces two phytochelatins when exposed to cadmium.

Samecka-Cymerman *et al*. (1997) summarized previous studies on heavy metals, noting that the concentrations of elements in the liverworts they studied, including ***Marchantia polymorpha*** (Figure 1-Figure 12), correlate positively with the concentrations of elements in the soil. Some, such as cobalt, surpass the background values found in most bryophytes, indicating the ability of the bryophytes to accumulate them. Some elements, such as Fe, Co, Pb, and Cu, caused an ionic imbalance in this liverwort and others.

Iron is sometimes considered a micronutrient and sometimes a macro nutrient. ***Marchantia polymorpha*** (Figure 1-Figure 12) uses reduction-based iron acquisition. Under deficiency conditions, growth of this species is reduced. Activity of ferric chelate reductase is increased and proton ATPase becomes active (Lo *et al*. 2016).

Manganese is needed in photosynthesis where it catalyzes the water-splitting reaction, but excess Mn creates metal stress. In ***Marchantia polymorpha*** (Figure 1-Figure 12) excess Mn causes a strong accumulation of N-methylalanine, a response differing from that of tracheophytes (Messant *et al*. 2022). When the concentrations of Mn were not optimal, the ratio of photosystem I to PSII changed and the organization of the thylakoid membranes was altered. This is important in photoprotection. The deficiency of Mn favors cyclic electron flow around PSI, thus protecting PSII against photoinhibition.

As demonstrated by the **bryometer** (air bags holding bryophytes), pollutants such as SO_2, oxidants, NO, and NO_2 can cause severe toxicity to ***Marchantia polymorpha*** (Figure 1-Figure 12) on the leeward side of a pollution source, resulting in the lowest growth rate in the area (78%) (Yokobori 1978; Yokobori & Taoda 1980).

responses to abiotic stress

Fujita *et al*. (2006) pointed out that much of the research on molecular mechanisms that cope with stress in plants have been carried out independently. Hence, our understanding of the evolutionary relationships and convergence points between biotic and abiotic stress signaling pathways remains very incomplete. More recently, evidence is emerging that suggests that hormone signaling pathways regulated by abscisic acid, ethylene, jasmonic acid, and salicylic acid, in addition to ROS-signaling pathways, play important roles in the crosstalk between biotic and abiotic stress signaling.

Marchantia polymorpha (Figure 1-Figure 12) has a large repertoire of responses to environmental changes (Spinedi *et al*. 2021). In response to anthracene, they found an increase in the activity of main ROS-detoxifying enzymes of 34.09% of peroxidase and 692% of ascorbate peroxidase, supported at transcriptional level with the up-regulation of ROS-related detoxifying responses. The net result was the activation of antioxidant mechanisms and the accumulation of the anthracene pollutant within the plant tissues.

Hirata *et al*. (2000) used bornyl acetate as a chemical stressor of ***Marchantia polymorpha*** (Figure 1-Figure 12).

In response, the liverwort produced peroxidase. This is a glycoprotein that is stable at temperatures as high as 50ºC for up to one hour, suggesting that the liverwort might have protection against the increasing temperatures of climate change. Its optimum *p*H is 6.5, which does not bode well for the dangers of acid rain. The peroxidase appears to be unlike any of those known from tracheophytes.

Hydrogen peroxide (H_2O_2) often has a protective role in plants. It forms in ***Marchantia polymorpha*** (Figure 1-Figure 12) in the presence of $MnCl_2$. Its production is also stimulated by phenols such as 2,4-dichlorophenol (a 2,4-D precursor) or *p*-coumarate, both processes similar to the last step in lignification, suggesting that while bryophytes apparently lack lignin, they already had a large part of the process required for its production. Phenols are important substances in antiherbivory in bryophytes.

Bryophytes are often resistant to stresses that can kill tracheophytes. Merwin (2003) found that herbicides designed for long-term use on tracheophytes actually promoted the growth of ***Marchantia polymorpha*** (Figure 1-Figure 12). They furthermore were resistant to the human traffic in the orchard.

Measurements of impedance can be a tool to determine health of small plants like ***Marchantia polymorpha*** (Figure 1-Figure 12). Bulanda (1980) Researchers have used this species to develop and test the efficacy of a method for measuring the resistance and capacity of the thallus, based on previous methods for measuring these in cell suspensions (Bulanda 1980; Paszewski *et al*. 1982).

radiation damage

A need to understand radiation damage arose as we began to explore space and to use radiation for energy. Typically, the effects on the nucleus were used to assess such damage (Miller & Sparrow 1964). One generalization that arose indicated that cells with smaller nuclei had more resistance to the radiation than did those with large nuclei. Using ***Marchantia polymorpha*** (Figure 1-Figure 12) Miller and Sparrow found that a more accurate indicator was the nuclear volume (at interphase) divided by the chromosome number. Miller *et al*. (1965) found that larger nuclei in gemmae exhibited inhibition at lower levels of radiation than did smaller nuclei.

Sarosiek and Wozakowska-Natkaniec (1967) demonstrated that chronic gamma radiation caused inhibition of the development of sex organs in ***Marchantia polymorpha*** (Figure 1-Figure 12).

One of the tools used in assessing effects of such things as X-rays is to use mutants (Miller *et al*. 1962a, b). Bryophytes, particularly ***Marchantia polymorpha*** (Figure 1-Figure 12), are particularly suitable for this because of their haploid condition. Miller and coworkers used the method to obtain nutritionally deficient mutants, a condition that could affect the response to radiation.

CO_2

The current atmosphere has a CO_2 concentration of about 0.0415% (415 ppm) (Climate.gov, accessed 21 September 2022). But it seems that most of the studies on CO_2 effects on the physiology of ***Marchantia polymorpha*** have been done at much higher levels.

Katoh *et al*. (1979) found that in 1% CO_2 ***Marchantia polymorpha*** (Figure 1-Figure 12) had a dry-weight doubling time of 1.76 days. The increase rate of chlorophyll was 1.6 times that of the growth rate. In the exponential phase of growth, the photosynthetic activity was at least 60 µmol mg^{-1} chl h^{-1}. The highest chlorophyll content they recorded was 24 mg g^{-1} dry weight.

Bockers *et al*. (1997) compared responses of ***Marchantia polymorpha*** (Figure 1-Figure 12) to two levels of CO_2. At the higher concentration (2.0%), the chloroplast shape seemed modified and there were 70% more chloroplasts per cell than at 0.4%. However, the chlorophyll content per cell indicated a reduction in chlorophyll per chloroplast. Furthermore, the cell size was about 37% lower in the higher CO_2 concentration. The net result was that the photosynthetic oxygen evolution was about the same under both conditions.

Marchantia polymorpha (Figure 1-Figure 12) has a C_3 pathway (Hanson *et al*. 2002), as do all bryophytes. Its growth form is a thallus, similar to that of hornworts. Its **CO_2 compensation point** (CO_2 concentration at which photosynthetic rate = respiration rate) was 64 ppm (Hanson *et al*. 2002), whereas the hornwort ***Megaceros*** (Figure 62), a genus lacking pyrenoids (Villarreal & Renner 2012), had a compensation point of 31 ppm (Hanson *et al*. 2002). On the other hand, ***Notothylas*** (Figure 63) and ***Phaeoceros*** (Figure 64), both with pyrenoids, had compensation points of 11-13 ppm CO_2. Those species lacking **pyrenoids** had more **RuBisCo** content, permitting them to increase their carboxylation catalytic rate (***Marchantia***, 2.6 s^{-1}; ***Megaceros***, 3.3 s^{-1}; ***Phaeoceros***, 4.2 s^{-1}; ***Notothylas*** 4.3 s^{-1}). ***Marchantia polymorpha*** had the highest percentage of RuBisCo per soluble protein (8%), ***Megaceros*** followed (4%), and the pyrenoid-containing species had only 3%.

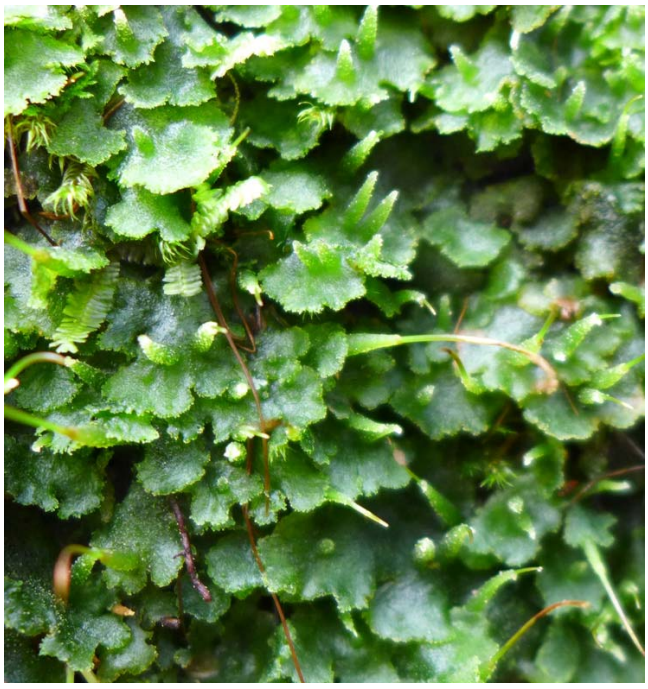

Figure 62. ***Megaceros flagellaris***, a hornwort species that lacks pyrenoids and has a lower CO_2 compensation point than does ***Marchantia polymorpha***. Photo by Scott Zona, through Creative Commons.

Figure 63. ***Notothylas orbicularis***, a hornwort species that has pyrenoids and has a CO_2 compensation point that is lower than that of ***Marchantia polymorpha*** (liverwort) or ***Megaceros*** (hornwort with no pyrenoids). Photo from One Thousand Plant Transcriptomes Initiative, through Creative Commons.

Figure 64. ***Phaeoceros carolinianus*** with capsules, a species that has pyrenoids and has a CO_2 compensation point that is lower than that of ***Marchantia polymorpha*** or ***Megaceros*** (with no pyrenoids). Photo by Hermann Schachner, through Creative Commons.

photosynthesis

Katoh (1983a) grew a cell line of ***Marchantia polymorpha*** (Figure 1-Figure 12) in suspension culture, using 1% CO_2. He found a growth rate in the exponential phase of 0.171 and a doubling time of 1.76 days. The rate of chlorophyll increase was 1.6 times higher than the growth rate. The cells reached their highest chlorophyll content at 24 mg g^{-1} dry weight in their exponential phase, with at least 60 µmol mg^{-1} chlorophyll h^{-1}.

Katoh (1983b) considered the inability of cells of ***Marchantia polymorpha*** (Figure 1-Figure 12) in suspension culture to grow in the dark to be the result of low respiration. In the light, the respiration increased to four times that in the dark. The compensation ratio (photosynthetic rate/respiration rate) was less than 1.0 during the growth period. Furthermore, these cells are unable to grow anaerobically in light in the absence of CO_2. Addition of 1% CO_2 permitted the liverwort to sustain growth. They found that at least one-third of the cellular carbon came from atmospheric CO_2.

light

Fredericq (1964) tested the influence of far-red light on thallus development in ***Marchantia polymorpha*** (Figure 1-Figure 12). Rethy *et al*. (1976) explored the effects of different light treatments on chlorophyll content in ***Marchantia polymorpha***.

Courtoy (1965-1966) experimented with light regimes on the germination and development of gemmae of ***Marchantia polymorpha*** (Figure 1-Figure 12). In artificial light of 4000 lux and 16-hour photoperiod, there were two distinct phases of growth. In the **juvenile phase**, requiring at least 15 days, light quality was unimportant. Adding sucrose in the juvenile phase reduces the phase to 5 days. In the **inductive phase**, when primordia appear, incandescent light permits development, suggesting the importance of red wavelengths.

Mache and Loiseaux (1973) found that the maximum growth rate of ***Marchantia polymorpha*** (Figure 1-Figure 12) in low light was at 2-3 x 10^3 lux, its saturation level. In optimal conditions, photosynthetic rates reach as high as 35 µM CO_2 h^{-1} mg^{-1}. High light inhibited the photosynthetic rate, with small grana in the chloroplasts and fret membranes being replaced by continuous grana.

Carter and Nickell (1967) experimented with the effects of wavelengths of light on both thallus growth and gemmae cup production. Using 16-hr light:8 hr dark at 21ºC day:13ºC night, they incubated 4 gemmae per Petri dish. After 11 weeks the controls with no colored acetate had produced a mean of 32.7 cm^2 of thalli and 83.3 gemmae cups per dish. Dishes with single-wrapped red acetate produced only 16.11 cm^2 of thalli (Figure 65) and 19.83 gemmae cups per dish (Figure 66). On the other hand, double-wrapped red dishes produced 17.5 cm^2 of thalli and 8.25 gemmae cups, suggesting that the lower light inhibited production of gemmae cups, putting more of the available resources into thalli. Those in single-layered green dishes produced 14.8 cm^2 of thalli and 8.16 gemmae cups per dish, a response consistent with the greater activity of photosynthesis in the red range. The double green, single blue, and double blue produced a mean of 10.5, 11.5, and 1.2 cm^2 of thalli respectively, but produced no gemmae cups, again supporting the importance of red light.

Aro (1982) used ***Marchantia polymorpha*** (Figure 1-Figure 12) to show that bryophytes had more chlorophyll associated with their light-harvesting protein complexes and less with reaction center complexes than did tracheophytes. Furthermore, the tracheophytes had a chlorophyll *a*:*b* ratio of 3, whereas it was only 2 in the bryophytes. These figures indicate that the bryophytes are shade plants, having proportionally more chlorophyll *b* when compared to that of tracheophyte sun plants.

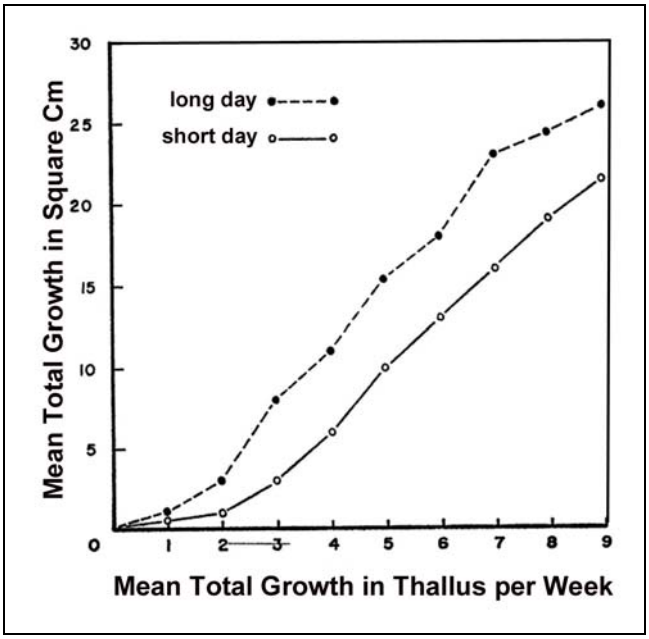

Figure 65. ***Marchantia polymorpha*** growth in long and short photoperiods. Image modified from Carter & Romine 1969.

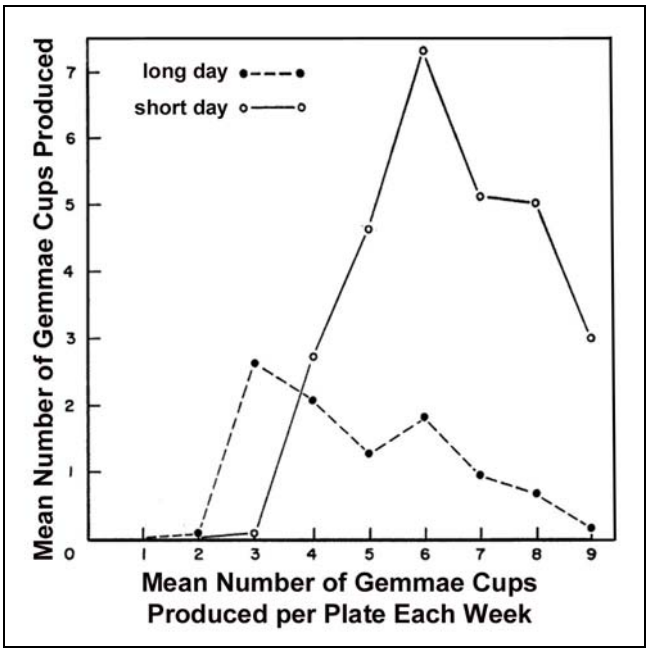

Figure 66. ***Marchantia polymorpha*** gemmae cups per week in long and short days. Modified from Carter & Romine 1969.

In further studies, Aro *et al*. (1981) determined that the plastid ultrastructure of the sun species ***Ceratodon purpureus*** (Figure 67) was characteristic of a sun plant, whereas in ***Marchantia polymorpha*** (Figure 1-Figure 12) it was characteristic of a shade plant. Nevertheless, both species exhibited photosynthetic kinetics typical of shade plants.

Figure 67. ***Ceratodon purpureus*** with young sporophytes, a sun species with plastid ultrastructure of a sun plant, but with photosynthetic kinetics of a shade plant. Photo by Claire Halpin, with permission.

Shinmen *et al*. (1991) determined that ***Marchantia polymorpha*** (Figure 1-Figure 12) produced arachidonic acid (ARA) and eicosapentaenoic acid (EPA) in cell culture. During high growth rate conditions the cells produced high quantities of both acids, with 98 mg L^{-1} of arachidonic acid and 48 mg L^{-1} of eicosapentaenoic acid. Kajikawa *et al*. (2004) isolated and characterized the genes behind the production of these acids in ***Marchantia polymorpha***. The role of arachidonic acids in cold weather has already been discussed. Eicosapentaenoic acids are known for their antifungal effects against plant pathogens (Bajpai *et al*. 2008). Both of these compounds seem to be essential in the wounding response forming volatiles in ***Marchantia polymorpha*** (Kihara *et al*. 2014). Eight-carbon volatiles form rapidly (within 40 minutes) of wounding.

Kajikawa *et al*. (2008) reported that ***Marchantia polymorpha*** (Figure 1-Figure 12) synthesizes arachidonic acid and eicosapentaenoic acid. By causing the overexpression of the involved genes, they produced 3-fold and 2-fold accumulation of these two acids, respectively. They were able to transplant these genes to tobacco and soybean, a feat that suggests that ***M. polymorpha*** can provide genes for transplantation to tracheophytes and provide them with desirable traits.

Later, Takemura *et al*. (2011) elucidated some of the physiological mechanisms involved in the observed effects of light quality and intensity on these acids. They noted that ***Marchantia polymorpha*** (Figure 1-Figure 12) synthesized both arachidonic acid (AA) and eicosapentaenoic acid (EPA), polyunsaturated fatty acids that are not known in tracheophytes. They found that the relative content of EPA to total fatty acid was highest under blue light, but that of AA did not vary. EPA content also increased under higher intensity white light. They found that 80 photon flux density μmol m^{-2} s^{-1} was the optimum intensity for both AA and EPA accumulation.

Harrer (2003) demonstrated that ***Marchantia polymorpha*** (Figure 1-Figure 12) has the same structure of the PS II-light-harvesting assembly as that of seed plants. They provided the first 3-d structure for such a large assembly by using this liverwort.

Marchantia polymorpha (Figure 1-Figure 12) was used in a study to describe the polyphasic rise of chlorophyll fluorescence at the onset of strong continuous light. Neubauer and Schreiber (1987) described the saturation characteristics and partial control by photosystem II.

In low light, bryophytes can exhibit etiolation. Ninnemann and Halbsguth (1965) elucidated the role of phytochrome in etiolation of ***Marchantia polymorpha*** (Figure 1-Figure 12). Ninnemann (1967) then described the growth substances, phytochrome, nucleic acid, and protein synthesis involved in the etiolation of the gemmae of ***Marchantia polymorpha***.

Rao *et al*. (1979) described the Hill reaction rates of three members of the Marchantiales, including ***Marchantia polymorpha*** (Figure 1-Figure 12). Using three different measures of the Hill reaction activity, they determined that the rate was lower in the three liverworts than in the seed plants tested. Furthermore, they also found lower total chlorophyll content and chlorophyll *a*:*b* ratio, all supporting the shade adaptation of these plants. They found that the greatest labelled ^{14}C occurred in the amino acids aspartate and alanine. ***Marchantia polymorpha*** exhibited higher photosynthetic rates than the other species in the test.

Maximum polyunsaturated fatty acids (PUFA) productivity is attained in ***Marchantia polymorpha*** (Figure 1-Figure 12) under low light intensity, with a photon flux density ca. 20 μmol m^{-2} s^{-1} (Chiou *et al*. 2001). Optimal inoculum size and glucose concentration for PUFA production are 8-12% and 2030 g L^{-1}, respectively. Ferrous ions, necessary components of many enzymes, promote PUFA productivity by increasing the intracellular lipid content. The highest productivities measured for PUFA were 35.0±2.1, for arachidonic acid 6.7±0.4, and for eicosapentaenoic acid 6.6±0.4 mg L^{-1} day^{-1}.

High light has different effects on ***Marchantia polymorpha*** (Figure 1-Figure 12) from those of low light (Volchenkova *et al*. 2001). It affects the area occupied by the lipid molecule. The digalactosyl diacylglycerol and phosphatidyl glycerol fractions increase significantly after high light stress, increasing from 0.50 to 0.80 nm^2 and from 0.47 to 0.63 nm^2 respectively.

red/far-red

Fredericq and de Greef (1966) examined the red:far-red control on growth and chlorophyll content in thalli of ***Marchantia polymorpha*** (Figure 1-Figure 12) grown in the light. Fredericq and de Greef (1968) followed up on these experiments by subjecting the plants to daily far-red (FR)-irradiations at the end of photoperiods of white fluorescent light. Following the first sequence, at the end of the night, the chlorophyll content of the tips of the thalli was significantly lower that that of the controls lacking the far-red treatment. Instead, upward growth (Figure 68) was beginning.

By the end of the night following the first FR-exposure, the chlorophyll content of the tips was already significantly lower than that of the controls, and there was a beginning of upward growth (Fredericq & de Greef 1968). After 8 hours in white light, those effects had become much more pronounced. After one week, a 5-minute far-red treatment at the end of the photoperiod cause a 20-30% lower chlorophyll content in the tips after the 8-hour photoperiod in white light. Following a 16-hour photoperiod, the chlorophyll was decreased by ±10%. Morphogenic effects also were less pronounced after 16 hours compared to 8 hours of white light. Basal parts of the thalli were less affected than the tips. On the other hand, a 1-hour photoperiod following far-red treatment caused much greater effects on the basal portions than on the tips. If the daily light period was diminished to 5 minutes, it caused drastic bleaching of 60-70% chlorophyll *a* loss compared to controls. Of relevance to the aquatic habitat, de Greef and Fredericq (1969) found that when the incandescent light was filtered through water for 10 minutes, it caused a somewhat weak effect. These responses are similar to those of tracheophytes and indicate that high levels of the PFR form of phytochrome are needed to maintain the horizontal growth and optimal chlorophyll content in these thalli.

Figure 68. ***Marchantia polymorpha*** exhibiting upward growth as it would occur under far-red light at the end of a period of white light. Photo by Vladimir Bryukhov, through Creative Commons.

Among the photoreceptors in ***Marchantia polymorpha*** (Figure 1-Figure 12) and other bryophytes are the phytochromes (Inoue *et al*. 2019). Phytochromes are the only known receptors for red light and far-red light and are therefore important in controlling various developmental processes. The phytochrome Mpphy regulates the formation of gametangiophores, similar to the far-red response of flowering plants. Inoue and coworkers identified the genes responsible for this regulation and demonstrated that the production of Mpphy increases when the gene is multiplied, while disappearing when the gene is deleted.

Another effect of far-red light is to accelerate senescence in ***Marchantia polymorpha*** (Figure 1-Figure 12) (de Greef & Fredericq 1972). Once again, the reversibility indicates the involvement of phytochrome. A daily exposure of only 5 minutes of red light will prevent this aging; photosynthesis plays no direct part in this response.

UV light

When photosynthetic organisms first invaded land, one of the new problems they had to deal with was their introduction to UV light (Jordan *et al*. 2016; Sancha 2017). The levels of UV reaching the Earth's surface at that time were higher than now due to the less-well developed ozone

layer. Therefore, it stands to reason that the surviving bryophytes, previously as early invaders of land, should have mechanisms to protect them from UV radiation. In seed plants, flavonoids are important in this role.

Khetwal (1985) demonstrated the presence of the flavonoid glucuronides apigenin, apigenin-7-O-glucuronide, luteolin, and luteolin-7-O-glucuronide in ***Marchantia polymorpha*** (Figure 1-Figure 12).

There has been much activity in recent years to determine the effects of increased UV light on bryophytes. Markham *et al*. (1998) found that as they increased UV-B levels, the growth rate of ***Marchantia polymorpha*** (Figure 1-Figure 12) decreased, the production of gemmae cups (Figure 69) decreased, and the proportion of dead thallus increased. Total flavonoid levels had no statistically significant change, but the ratio of luteolin to apigenin glycosides did increase (Figure 69-Figure 71). The researchers did not consider this to be a means of filtering and protecting the plants from the UV-B, but instead they experienced an improved level of antioxidant defense.

Figure 69. ***Marchantia polymorpha*** with red edges, perhaps in response to stress. Photo by Brenda Dobbs, through Creative Commons.

Figure 70. ***Marchantia polymorpha*** with red archegoniophores, perhaps responding to the stress of a cold climate in Laxarbakki, Myvatn, Iceland. Photo by Janice Glime.

Figure 71. ***Marchantia polymorpha*** with red archegoniophores, from Laxarbakki, Myvatn, Iceland, 26 July 1987. Photo by Janice Glime.

Clayton (2017) looked specifically at flavonoids in ***Marchantia polymorpha*** (Figure 1-Figure 12) exposed to UV-B radiation and determined that the flavonoids increased when UV-B radiation was enhanced. Flavones were the most predominant, with apigenin-based flavones in highest amounts and luteolin-based flavones second. The ratio shifted toward luteolin-based flavones at the higher UV-B levels. At these UV-B levels, reactive oxygen species (ROS) are produced, and the liverwort may require the luteolin flavones to scavenge these. Under low UV-B exposure, the flavone compounds accumulated in high concentrations in the epidermal layers, suggesting that they might participate in screening the UV-B. When flavone concentrations were lower, greater damage to the thallus occurred. Higher levels of flavones corresponded with greater protection and reduced thallus damage. When flavones were suppressed completely the plants became severely stunted under the UV-B treatment.

Sancha (2017) noted that bryophytes have "remarkable tolerance to UV radiation." Sancha subjected various bryophytes to enhanced UV radiation and found that all, including ***Marchantia polymorpha*** (Figure 1-Figure 12), showed increased levels of CARUVs (UV-radiation-absorbing compounds), with all being significant except for ***Anthoceros agrestis*** (Figure 72)**.**

Figure 72. ***Anthoceros agrestis***, a hornwort species with increasing, but not significant, UV-radiation-absorbing compounds with increasing of UV intensities. Photo by Hermann Schachner, through Creative Commons.

Soriano *et al*. (2019a) further examined UV damage in ***Marchantia polymorpha*** ssp. ***ruderalis*** (Figure 56, Figure 60, Figure 73). They found that liverworts subjected to low photosynthetically active radiation (PAR), low PAR+ UV-A, low PAR + UV-B, low PAR + UV-A + UV-B, and high PAR exhibited no significant difference in the maximum quantum yield of PSII after 35 days. There were no changes in the chl *a*/*b* ratio and only slight changes in growth. But both chlorophylls and carotenoids decreased in content in the UV radiation treatments and even more strongly in the high-PAR treatment. The xanthophyll index (antheraxanthin + zeaxanthin) / (violaxanthin + antheraxanthin + zeaxanthin) increased only in the high-PAR (Figure 73). On the other hand, the **sclerophylly index** (ratio between thallus dry mass and surface area) increased in the UV-B-exposed treatments, suggesting a UV-induced structural protection. Only the UV-B treated liverworts exhibited DNA damage.

Figure 73. ***Marchantia polymorpha*** ssp. ***ruderalis*** showing red bases, perhaps in response to high UV levels. Photo by Malcolm Storey <www.DiscoverLife.com>, with online permission.

In further studies, Soriano *et al*. (2021) found that the developmental stage was important in determining the accumulation of UV-absorbing compounds in ***Marchantia polymorpha*** ssp. ***ruderalis*** (Figure 56, Figure 60, Figure 73). They compared gemmae (Figure 69), one-month thalli, and two-month thalli after 38 days of exposure or non-exposure to UV radiation. They found that the UV responsiveness decreased with thallus age, with gemmae being the most responsive. Older thalli became progressively tougher in UV due to decreasing water content, possibly providing structural protection. Most phenolic compounds decreased with thallus age, but di-glucuronide derivatives were highest in the 1-month thalli.

Close and McArthur (2002) contend that phenolics have the primary function of protecting plants from photodamage, not from herbivores as originally thought.

Kondou *et al*. (2019) reported that MpUVR8 provides physiological benefits in UV-B resistance in ***Marchantia polymorpha*** (Figure 1-Figure 12). It is highly expressed in the apical notch (Figure 20) of the thalli and gametangiophores, including the antheridial and archegonial heads. In this species, citrine-fused MpUVR8 was translocated from the cytosol into the nucleus when exposed to increased UV-B radiation.

Ultraviolet light was a major stress to be overcome when plants first invaded land (Clayton *et al*. 2018). The ***Marchantia polymorpha*** (Figure 1-Figure 12) UVB response included many components already known from *Arabidopsis* (Figure 52), including production of UVB-absorbing flavonoids, the central activator role of ELONGATED HYPOCOTYL5 (HY5), and negative feedback regulation by REPRESSOR OF UV-B PHOTOMORPHOGENESIS1 (RUP1). Important differences included a greater importance for CHALCONE ISOMERASE-LIKE (CHIL). Mutants that disrupted the response pathway or flavonoid production were more easily damaged by UV-B than normal plants, whereas mutants that increased the flavonoid content exhibited increased UV-B tolerance.

Kondou *et al*. (2019) determined that UV-B resistance and the translocation of the UVR8 from the cytosol to the nucleus was operational in ***Marchantia polymorpha*** (Figure 1-Figure 12) in response to UV-B radiation. This series of events is highly expressed in the apical notch of the thalli and in the gametangiophores and receptacles.

fluorescence

It is widely known that chlorophyll fluoresces. The degree of fluorescence is a measure of the health of the plant. Shi *et al*. (1992) described two categories of fluorescence emission from bryophytes. ***Marchantia polymorpha*** (Figure 1-Figure 12) exhibits maximum emission around 725 nm. The fluorescence kinetics of primitive bryophyte photosynthesis, including ***M. polymorpha***, exhibited lower PS II activity, lower efficiency of primary photoconversion in PS II, and lower photosynthetic C assimilation and efficiency than did the advanced bryophyte species.

photoperiod

Photoperiod is known to control various events in the life of a plant. Differences in response to photoperiod can keep closely related species from interbreeding by bringing reproductive parts to maturity at different times (see Reproduction section below), while taking advantage of the climatic conditions at the optimum time for the event.

Marchantia polymorpha (Figure 1-Figure 12) grown in a long photoperiod (18 hours daylight) are larger and have greater dry weight than those grown in a short photoperiod (9 hours daylight) (Voth & Hamner 1940; Carter & Romine 1969). Short photoperiods favor production of gemmae (Figure 69, Figure 153-Figure 170), whereas long photoperiods favor the production of gametangiophores.

Benson-Evans (1961) found that photoperiod influences the number of gametophores, and like Carter and Romine, found that longer days (16 hrs light) result in greater thallus size and fewer gemmae cups, but a faster production of the cups.

tropisms

A little-studied area of bryophyte physiology is tropisms. Yet the ability to grow in response to the

direction of light and gravity is of considerable adaptive importance to most bryophytes.

There is a long history of studies on rhizoid tropisms in ***Marchantia polymorpha*** (Figure 1-Figure 12). Haberlandt (1889) noted **positive gravitropism** (originally known as geotropism; growing toward the gravitational pull) in the apical rhizoids of ***Marchantia polymorpha***. Weinert (1909) investigated rhizoid tropisms and growth in liverworts, including ***Marchantia***. Rawitscher (1932) reviewed the tropisms in this species. Douin (1936) reported that the thallus exhibited photogravitropism. But Miller and Voth (1962) experimented with various orientations of the thalli and found that the rhizoids would securely anchor the thalli no matter what position the plant held, contrasting with the view held by Haberlandt (1889). Perhaps this is explained by the behavior I observed in ***Fontinalis***. The rhizoids initially grow away from the plant and use a spiral growth pattern. However, once a rhizoid contacts a substrate, it branches and secures the plant to the substrate. I am not aware that this behavior has been observed in ***Marchantia polymorpha***, but such behavior has not been disproved either.

So what does a gemma cup do when its parent plant is attached to a vertical surface? Miller and Voth (1962) observed that initially the cup exhibits no tropism, growing in a perpendicular alignment with its thallus. But when it develops the achlorophyllous scale-like rim of the cup, this is negatively gravitropic, permitting the cup to become upright with respect to gravity.

Rethy *et al*. (1990) described the role of far-red illumination in tropisms of ***Marchantia polymorpha*** (Figure 1-Figure 12). It causes greater cell elongation on the ventral side of the thallus just below the apical notch, causing upward growth, whereas red light reverses the reaction.

Komatsu *et al*. (2019) demonstrated that under low light both sporelings and thalli of ***Marchantia polymorpha*** (Figure 1-Figure 12) develop narrow shapes and their apices grow toward the light source. These responses are blue-light dependent and respond to **phototropin** (photoreceptor protein; flavoproteins).

temperature

Somehow, this fleshy liverwort manages to survive winter, even when covered by snow (Figure 74). Exact responses to temperature at the cellular level have been a puzzle. ***Marchantia polymorpha*** (Figure 1-Figure 12) serves as a model system to unravel these responses (Hirano *et al*. 2022). Chloroplasts respond to cold by changing positions, optimizing photosynthesis. This response is triggered by the blue-light photoreceptor phototropin, the cold-sensing molecule. This sensor is present in the plasma membrane, cytosol, Golgi apparatus, and periphery of the chloroplast. By using genetic variants, Hirano and coworkers demonstrated that the cold response originates with the phototropin in the plasma membrane, at least in this liverwort.

Antropova (1974) included ***Marchantia*** in studies on temperature adaptations in bryophytes. He incubated the bryophytes at 10 and 20ºC for 72 hours. But this period of time does not influence either thermostability or cold resistance. A treatment of 3 hours at superoptimal temperatures does cause an increase in thermostability, but no change in cold resistance. The behavior of the bryophytes was similar to that of flowering plants but differed from the temperature acclimation of algae.

Figure 74. ***Marchantia polymorpha*** in snow; note how dry the thallus appears, a condition that reduces damage from interior ice crystals. Photo by Vladimir Teplouhov, through Creative Commons.

But experiments by Weis *et al*. (1986) differed. Using ***Marchantia polymorpha*** (Figure 1-Figure 12) and other thallose liverworts, they found that high temperature treatment elicited a reversible depression of photosynthesis. The time required to achieve complete recovery depended on the extent of the heat damage. With severe heat treatment, PS II was damaged and inactivation of photosynthesis was irreversible. Unlike Antropova, Weis and coworkers found that exposure of these thallose liverworts to high sublethal temperatures did not result in the significant increase in heat stability of the photosynthetic apparatus as had been seen in seed plants. They interpreted this to mean that the heat hardening capacity of water-loving liverworts was extremely low.

Fletcher (1982) found no frost damage to ***Marchantia polymorpha*** (Figure 1-Figure 12) in cultivation in New Zealand populations. Some of the other species of thallose liverworts became severely bleached or blackened in greenhouse cultivation down to -5.5ºC. The ***M. polymorpha***, on the other hand, remained a healthy green all winter.

Response to heat appears to be more complicated. It involves several subcellular compartments as well as multi-level regulatory networks (Marchetti *et al*. 2021). Studies on ***Marchantia polymorpha*** (Figure 1-Figure 12) indicate that the core components of the response are conserved from bryophytes to flowering plants.

Temperature affects the relative production of fatty acids in ***Marchantia polymorpha*** (Figure 1-Figure 12) (Saruwatari *et al*. 1999). At 25°C this liverwort contained approximately 18% linolenic acid (18:3ω3), 11% arachidonic acid (20:4ω6) and 3% eicosapentaenoic acid (20:5ω3) as percentages of total fatty acids. At 15ºC, the ratios of linolenic acid and arachidonic acid increased greatly, with less effect on the other acids. Arachidonic acid and eicosapentaenoic acid increased in the chloroplast but not elsewhere in the cell. Linolenic acid increased in

both fractions. Various galactolipids were present in one or the other or both compartments, but only monogalactosyldiacylglycerol and chloroplastic phosphatidylcholine increased in low temperatures. Gellerman *et al.* (1972) found that ***Marchantia polymorpha*** had arachidonic acid in all tissues, ranging 10-30% of the total fatty acids.

Takemura *et al*. (2012) likewise reported the production of arachidonic acid and eicosapentaenoic acid in ***Marchantia polymorpha*** (Figure 1-Figure 12), noting that neither is produced in tracheophytes. The accumulation of ω-3 polyunsaturated fatty acids increased significantly as the temperature decreased. At 5ºC the concentration was approximately 3x that at 15ºC. ω-6 polyunsaturated fatty acids, on the other hand, decreased at low temperatures.

Akter *et al*. (2011) acknowledged the role of ABA in both desiccation tolerance and freezing. This dual role is not surprising since one of the dangers of freezing is desiccation as ice crystals draw water out of the cell or make the water unavailable as ice. Akter and coworkers found that isolated gemmae (Figure 153-Figure 170) of ***Marchantia polymorpha*** (Figure 1-Figure 12) responded to increased ABA by increasing the sucrose concentration. These treated gemmae survived freezing, whereas most of the controls did not. The best survival occurred with 5% sucrose and 19 µM ABA.

Takeuchi *et al*. (1980) even found a successful method for freezing ***Marchantia polymorpha*** (Figure 1-Figure 12) for cryopreservation.

The movement of organelles in response to stress is seldom discussed. In response to a cold treatment, ***Marchantia polymorpha*** (Figure 1-Figure 12) sporelings and gemmalings nuclei and peroxisomes relocated from the **periclinal cell wall** (wall parallel to surface of meristem or surface of organ; Figure 75) to the **anticlinal cell wall** (wall arranged perpendicular to surface of plant body; anticlinal division results in formation of anticlinal walls between daughter cells, enabling tissue to increase circumference, thus keeping pace with any increase in girth of organ; Figure 75) (Ogasawara *et al*. 2013). Mitochondria, on the other hand, did not relocate.

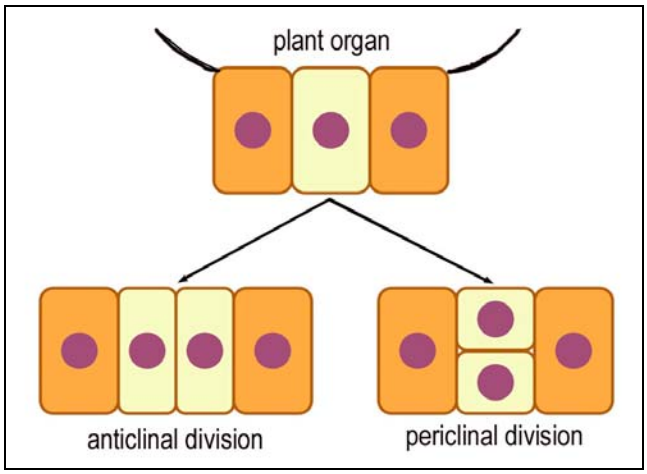

Figure 75. Comparison of anticlinal and periclinal divisions. Drawing modified from The Science of Plants, Meristem Morphology, Open Library <open.lib.umn.edu>.

senescence

Sometimes it seems like bryophytes never die. They just keep growing at the top while lower portions remain and may even decay. But **senescence** (process of aging) does indeed occur. Stanislaus and Maravolo (1994) examined cell factors that influenced senescence. They found light-induced senescence in young, middle-aged, and old tissues of ***Marchantia polymorpha*** (Figure 1-Figure 12) all exhibited suppressed senescence in treatments with spermine, spermidine, and putrescine. Not surprisingly, ethylene induced senescence in these tissue ages, an effect that could be retarded by putrescine, a compound they tentatively identified in ***M. polymorpha*** extracts.

LaBelle *et al*. (1997) identified two isophosphatases in senescing ***Marchantia polymorpha*** (Figure 1-Figure 12) thalli. They found that spermine reduced total phosphatase activity by 135-175%. Ethylene, on the other hand, reduced it by 133-155%. When ethylene and spermine were added together, they decreased the activity by 120-163% compared to the levels with the ethylene treatment alone. LaBelle and coworkers interpreted these findings to indicate that phosphatase and ethylene are associated with senescence. Spermine, on the other hand, functions in preventing senescence.

It may seem inconceivable to a bryologist, but ***Marchantia polymorpha*** (Figure 1-Figure 12) is not always a welcome visitor in a garden (Figure 76). Altland *et al*. (2008) found that quinoclamine can serve as both a PRE and POST activity herbicide at 4-6 mg L^{-1}. It could inhibit PRE germination in gemmae (Figure 153-Figure 170), but its ability to stay on the substrate made it increase the efficacy of other kinds of treatments.

Aging brings a variety of responses in plants. Maravolo (1976) found that transport, a function especially of the midrib, was inhibited by aging, cinnamic acid, and ethylene in ***Marchantia polymorpha*** (Figure 1-Figure 12).

Seaman *et al*. (2005) examined the role of spermine in programmed cell death of ***Marchantia polymorpha*** (Figure 1-Figure 12). They found that **PKC** (protein kinase C) concentrations in untreated young thalli were higher than those of older tissues. **PKC** refers to a family of protein kinase enzymes involved in a variety of signal transduction pathways (Blumberg 1991). PKC enzymes play important roles in several signal transduction cascades. When Seaman and coworkers treated older tissues with spermine, they also had higher cytosolic putative PKC concentrations than even the young untreated thalli. The spermine also resulted in higher total protein levels than untreated tissues. Hence, it appears that the spermine causes both qualitative and quantitative decreases in senescence.

One of the consequences of spermine is to reduce DNA fragmentation, as demonstrated in ***Marchantia polymorpha*** (Figure 1-Figure 12) (Pagoria & Maravolo 2005). The fragmentation is localized near the lower epidermis of the apical meristem. From there it progresses into the mesophyll cells. However, when these plants were treated with 100 µM spermine, they exhibited significantly lower (p<0.001) levels of DNA fragmentation in aged (2-5 cm) tissues.

Figure 76. ***Marchantia polymorpha*** females in garden in Houghton, Michigan, USA. So far we have been unable to find any males. This illustrates the density it can reach. Fortunately, the owners find these plants fascinating, permitting their invasion. The yellow patches are ***Brachythecium*** cf. ***salebrosum***. Photo courtesy of Craig Waddell.

genetics

Marchantia polymorpha (Figure 1-Figure 12) is typically considered a model for the early terrestrial colonizing plants. With this in mind, Bowman *et al*. (2017) characterized the genome of this species as having low genetic redundancy in most of its regulatory pathways. This species differs from its purported charophycean ancestors by encoding novel biochemical pathways, new phytohormone signalling pathways (especially auxin), expanded repertoires of signalling pathways, and increased diversity of transcription factor families. It sheds light on the evolution of haploid sex chromosomes as they occur in a dioicous plant. The haploid condition makes gene transfer and subsequent study easier than in the diploid tracheophytes (Chiyoda *et al*. 2008).

Ikeuchi and Inoue (1988) used a computer-assisted homology search to identify the D1-D2-cytochrome b-559 complex protein region in the chloroplast genome of ***Marchantia polymorpha*** (Figure 1-Figure 12).

Takenaka *et al*. (2000) found that ***Marchantia polymorpha*** (Figure 1-Figure 12) had at least 1-4 copies of the hpt gene, an example of gene redundancy in early land plants.

Chung *et al*. (2006a) compared two bryophytes and *Arabidopsis thaliana* (Figure 52) to determine the number of genes in common. They found 79% of the genes expressed by ***Marchantia polymorpha*** (Figure 1-Figure 12) were also expressed in the moss ***Physcomitrium patens*** (Figure 77). They found 763 genes expressed not only in both bryophytes, but also in *Arabidopsis thaliana*. Another 363 genes were found in the bryophytes, but not in *Arabidopsis*.

Figure 77. ***Physcomitrium patens***, a species that expresses 79% of the same genes as in ***Marchantia polymorpha***. Photo through public domain.

Chung *et al*. (2006b) contrasted gene expression in ***Marchantia polymorpha*** (Figure 1-Figure 12) with that of *Arabidopsis thaliana* (Figure 52 In the latter tracheophyte species, ~50% of the expressed genes exhibited cell-type-specific expression patterns. On the other hand, in ***M. polymorpha*** the expression in cultured cells did not differ from those of the thalli. Instead, 110 genes were expressed in cultured cells of ***M. polymorpha***, but not in those of *A. thaliana*, whereas in the 10 *A. thaliana* genes checked, they were expressed in whole plants of both species, but not in cultured cells of *A. thaliana*. Thus, ***Marchantia polymorpha*** with transplanted genes can be used more easily to determine the expression of tracheophyte genes.

Lin and Bowman (2018) identified micro RNAs in ***Marchantia polymorpha*** (Figure 1-Figure 12). Tsuboyama *et al*. (2018) elaborated on methods of using the model liverwort ***Marchantia polymorpha*** in AgarTrap transformation for studying genetic transformation, achieving a 97% transformation efficiency.

Schmid *et al*. (2018) found that methylation pattern of DNA changes in cytosines varies significantly during the life cycle. These coincide with four major epigenetic states, corresponding to the states of vegetative gametophytes, antherozoids, archegonia, and sporophytes. They concluded that epigenetic reprogramming occurs in at least two events during the life cycle, once in each generation. These events occur in parallel with the differences in the gene expression involved in DNA methylation.

Ishizaki *et al*. (2008) used ***Agrobacterium*** (Figure 20)-mediated transformations on immature thalli of ***Marchantia polymorpha*** (Figure 1-Figure 12) that had developed from spores. Plants grown from gemmae (Figure 153-Figure 170) of these plants all expressed the introduced gene GUS. Because of the haploid state of the

thallus, these plants offer a very useful system for such transformations.

Marchantia polymorpha (Figure 1-Figure 12) has become a model organism for using promoters in overexpression studies to determine gene functions (Althoff *et al*. 2014). The protocol developed has the potential to screen large numbers of transgenic plants, including the use of knock-down mutants.

These studies have shown the usefulness of ***Marchantia polymorpha*** to test the function of genes.

One of the applications of our genetic knowledge of this species is to determine its susceptibility to radiation damage. Using Co^{60} gamma rays, Miller and Sparrow (1965) determined that the ability of the two apical cells to reproduce was inhibited at doses less than the lethality dosage. The thallus exhibits different radiosensitivity from that of the gemmae (Figure 153-Figure 170) when based on energy absorption; the thallus is 4.3 times as sensitive as the gemmae.

Adaptations

Halbsguth (1953) explored the development of dorsiventrality in ***Marchantia polymorpha*** (Figure 1-Figure 12). We can assume that this body form has advantages, particularly in habitats that can at times be very wet and at other times can dry out. The overlapping thalli of the colony help to retain water in the soil (Figure 78). This same advantage can be accomplished by growing with mosses (Figure 79).

Figure 78. ***Marchantia polymorpha*** in Houghton, Michigan, showing overlapping thalli. Photo by Matt Tianen, with permission.

Bischler and Jovet-Ast (1981) commented that members of the **Marchantiales** seem to have some characters that are not essential for survival, reproduction, or dispersal. Others seem to be disadvantageous, but they have not prevented the continued existence of these traits. Instead, they concluded, the adaptations to their niches are linked primarily to biochemical and biophysical properties of the cell content rather than to morphological expressions.

Since wet habitat species typically experience dry seasons, among the most common adaptations are those that conserve water. McConaha (1941) described the ventral structures that affect water uptake and conservation. In the Marchantiales, these include smooth and tuberculate rhizoids (Figure 80-Figure 84) and ventral scales (Figure 83-Figure 86). Using several members of the order, including ***Marchantia polymorpha*** (Figure 1-Figure 12), McConaha reported that the **smooth rhizoids** (Figure 80) emerge from the scales and can make contact with the substrate (Figure 81-Figure 82). **Tuberculate (pegged) rhizoids** (Figure 53, Figure 83) serve a different purpose. They originate beneath the scales, forming numerous connected capillary strands that lie parallel to the thallus (Figure 53, Figure 83). This arrangement provides a rapid capillary distribution of water to all the absorptive areas of the thallus. The efficiency in water balance depends on the form and imbrication of the scales (Figure 84-Figure 86), as well as with the length and number of these rhizoids.

Figure 79. ***Marchantia polymorpha*** with gemmae cups, overgrowing mosses that can help to retain moisture in the soil and the liverwort thallus. Photo by Janice Glime.

Figure 80. ***Marchantia polymorpha*** ventral side showing smooth rhizoids along midrib. Photo from Botany Website, UBC, with permission.

Figure 81. ***Marchantia polymorpha*** archegoniophores and thallus showing brown, perpendicular rhizoids. Photo by Janice Glime.

Figure 82. ***Marchantia polymorpha*** ventral smooth rhizoids at midregion of thallus, along the midrib. Photo by Larry Jensen, with permission.

Figure 83. ***Marchantia polymorpha*** bundles of pegged rhizoids terminating in marginal scales. Photo by Larry Jensen, with permission.

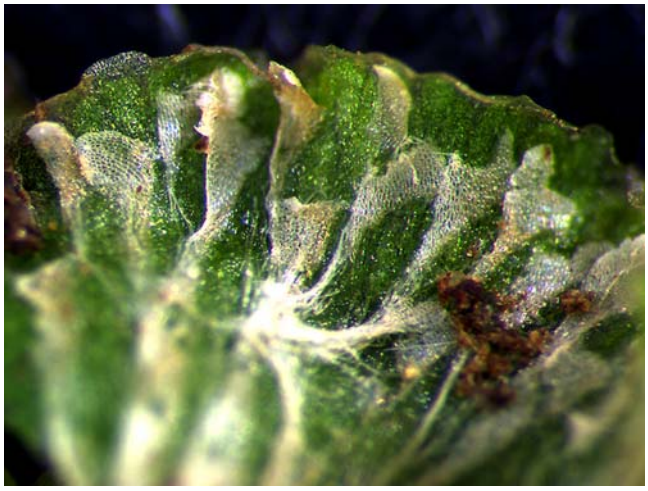

Figure 84. ***Marchantia polymorpha*** ventral growing tip of thallus with marginal scales. Photo by Larry Jensen, with permission.

Figure 85. ***Marchantia polymorpha*** ssp. ***ruderalis*** scales showing purple coloring. Photo by Des Callaghan, with permission.

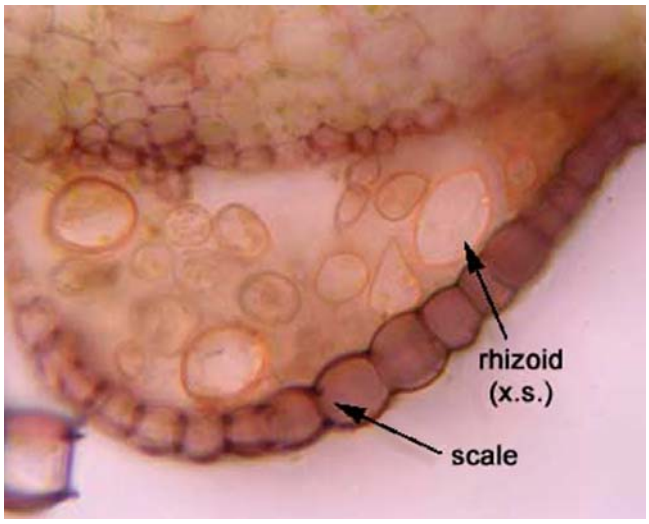

Figure 86. ***Marchantia polymorpha*** section showing scale and rhizoids on ventral surface. Photo from Botany Website, UBC, with permission.

Cao *et al*. (2014) further described the rhizoids (Figure 80-Figure 84) in ***Marchantia polymorpha*** (Figure 1-Figure 12). These researchers noted that the tuberculate (pegged) rhizoids converge toward the midrib (Figure 83-Figure 84). The smooth rhizoids occur in clusters in the free portions near the midrib at the thallus posterior (Figure 80, Figure 82). Unlike the tuberculate rhizoids, these lie perpendicular to the thallus, always growing toward the moist soil (Figure 81-Figure 82).

Many botany textbooks still claim that bryophytes lack cuticles. But we now know that this is not the case, at least for many bryophytes. Many species develop a thin cuticle that is not easily noticed. Brockington *et al*. (2013) and Xu *et al*. (2021) noted that even in flowering plants we lack understanding of the cuticle genetics and the role of the cuticle in evolution. Hence, these researchers have provided a detailed description of the cuticle and its genetic origins in ***Marchantia polymorpha*** (Figure 1-Figure 12). The cuticle is hydrophobic and is generally considered to be a barrier between the plant and the atmosphere wherein it helps to maintain internal moisture levels and to prevent entry of potentially pathogenic organisms. It is also a filter of UV radiation and barrier against mechanical damage. Because of these important roles in the terrestrial environment, it has been considered to be one of the key innovations needed for colonization of land (Corner 1964).

Xu *et al*. (2021) analyzed the role of the cuticle in preventing water loss in ***M. polymorpha*** (Figure 1-Figure 12). Using mutant plants, they found no change in morphology of the thallus for plants without a cuticle. However, they found more effects of desiccation in mutant plants with no cuticle. These plants frequently exhibited brownish tissues at the flank and tip of the thallus after five days with no cover and no added water. Most significantly, water content declined to about 70%, compared to 90% in non-mutant plants (Figure 87), the latter being only a 5% decrease in water content following the drying regime. Wu and coworkers were unable to detect any waxes in the cuticle of the lab-grown ***M. polymorpha***. Rather, the cuticle of ***M. polymorpha*** in these experiments consisted only of cutin, except for the waxy cuticle surrounding the pores (Figure 88). We know that environmental conditions affect the manufacture of cuticle waxes in flowering plants and could have been a cause for suppression of these waxes in the lab populations of ***M. polymorpha***.

While the plants with the addition of cuticles solved the problem of water loss, they had created another problem. An epidermis with a cuticle also interferes with gas exchange, impeding photosynthesis by the underlying photosynthetic tissue. In a thallose liverwort like ***Marchantia polymorpha*** (Figure 1-Figure 12) chloroplasts are buried (Figure 89, Figure 91-Figure 92) below the epidermis where light is reduced and it would be difficult to exchange CO_2 and O_2 if they did not have air pores (Figure 89-Figure 90). These openings permit the entry of air into the chambers (Figure 89, Figure 91-Figure 92) beneath them and the escape of the photosynthetic O_2. But these air pores present another problem. When the thallus becomes submersed or even when raindrops land in the pores, there is the danger that the water could enter the thallus and prevent the gas exchange. ***Marchantia polymorpha*** protects itself from this internal drowning by having cuticular ridges (Figure 90-Figure 94) around the opening of the pores (Schönherr & Ziegler 1975). The hydrophobic waxes, helped by the cohesive properties of water, repel the water and prevent its entry. Schönherr and Ziegler considered them to be "perfect structures."

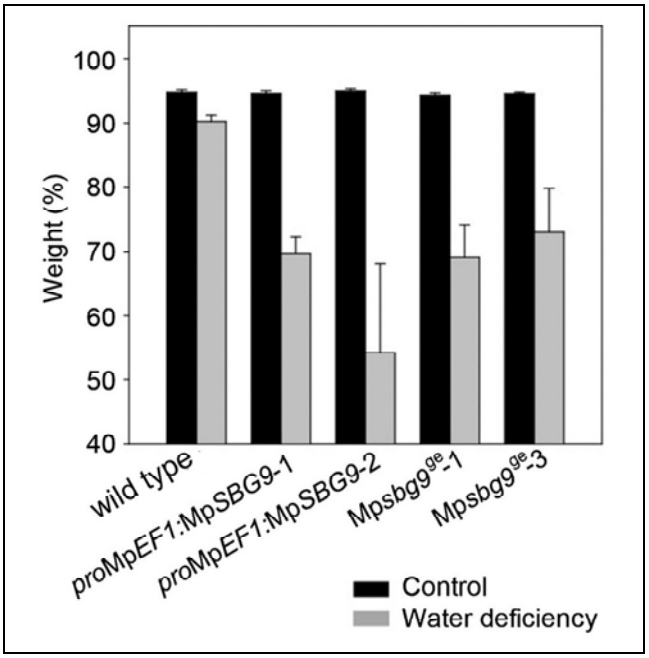

Figure 87. Cuticle water loss as percent weight in ***Marchantia polymorpha*** in wild type and four different mutants that reduce cuticle formation. Modified from Xu *et al*. 2021.

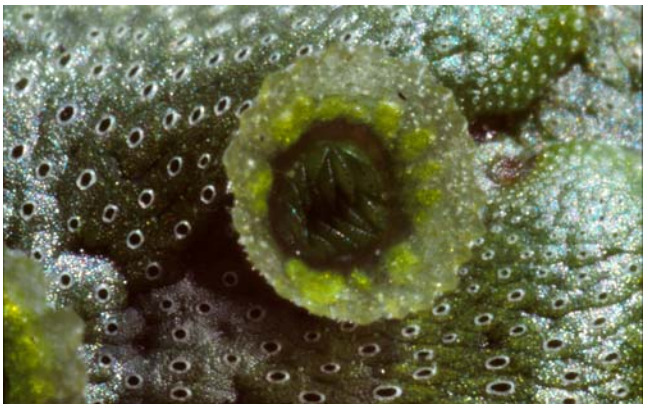

Figure 88. ***Marchantia polymorpha*** gemma cup and distinct air pores surrounded by white cuticle on thallus. Photo by John Forlonge, through Flickr.

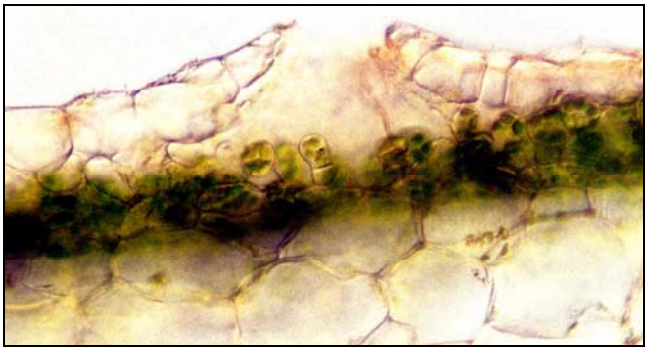

Figure 89. ***Marchantia*** thallus section showing pore opening and layer of chlorophyllous filaments. Photo by George Shepherd, with permission.

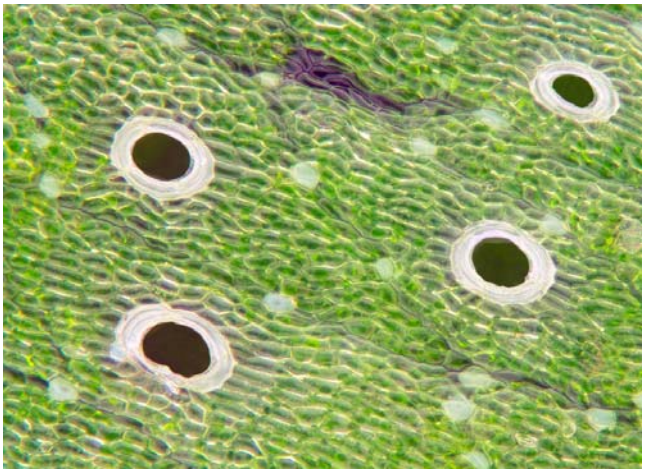

Figure 90. ***Marchantia polymorpha*** air pores and green layers showing through surface. Note the donut-shaped cuticular ridges. Photo by Des Callaghan, through Creative Commons.

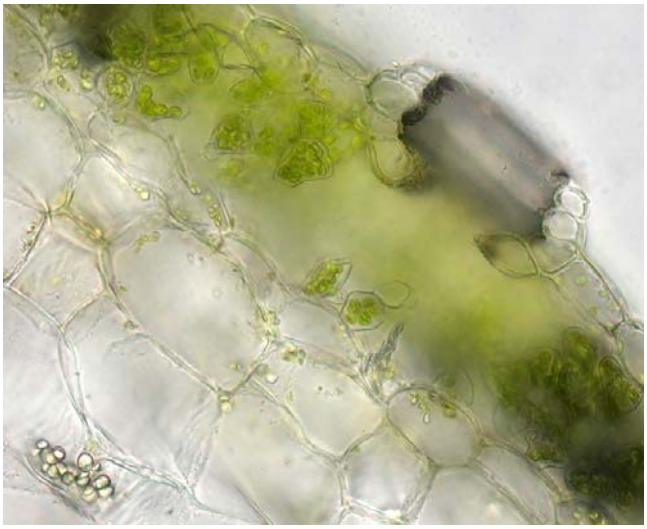

Figure 91. ***Marchantia polymorpha*** section through pore opening. Note the photosynthetic cells beneath the pore. Photo by Walter Obermayer, with permission.

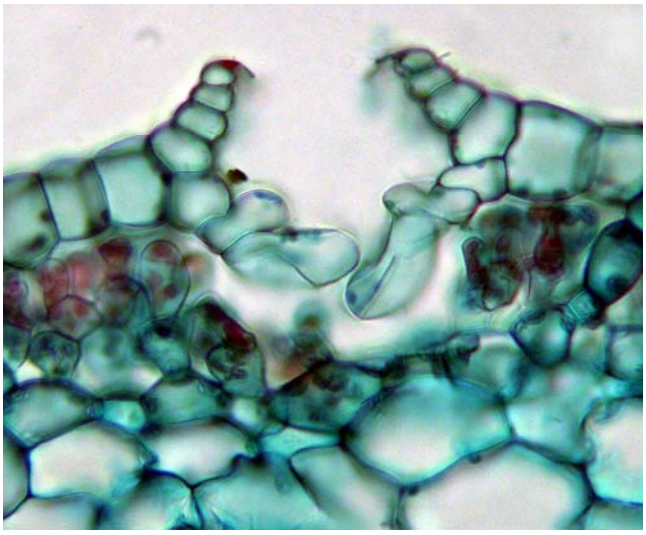

Figure 92. ***Marchantia*** thallus section showing pore opening. Photo by George Shepherd, with permission.

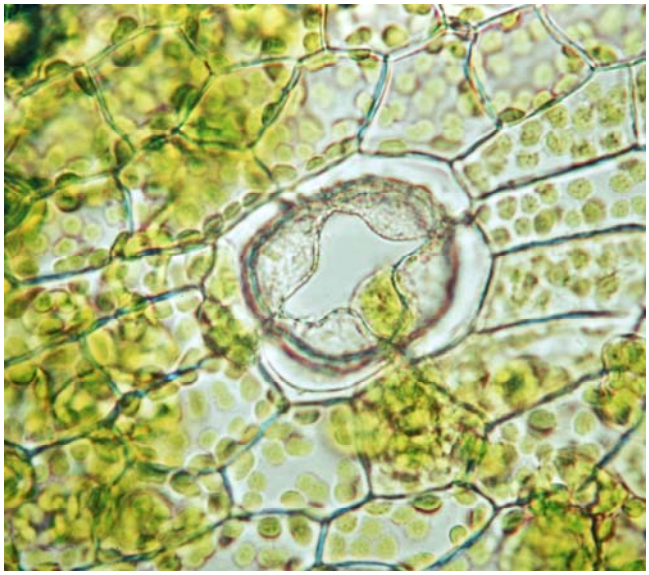

Figure 93. ***Marchantia polymorpha*** pore opening as seen from thallus surface, showing cuticular ridge surrounding the opening. Photo by Wilhelm Barthlott, with permission.

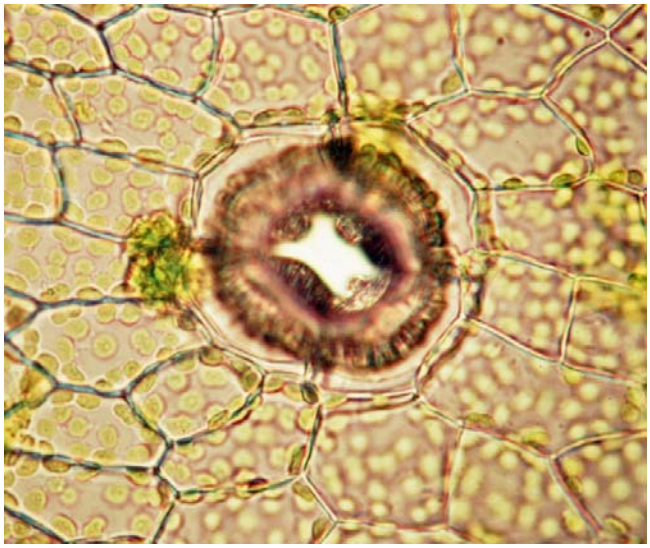

Figure 94. ***Marchantia polymorpha*** pore opening with cuticular ridge and small opening. Photo by Wilhelm Barthlott, with permission.

The adaptive value of oil bodies puzzled bryologists for a long time. Galatis and Apostolakos (1976) described the association of the microbodies with the cytoplasmic tubules of oil body cells in ***Marchantia***. They found that the tubules increase in number at the stage when the cells are actively synthesizing oil.

One of the protections exhibited by liverworts is the ability to store sesquiterpenes and bisbibenzyls in oil bodies (Figure 95). Suire *et al*. (2000) isolated a number of isoprenoid biosynthetic enzymes from oil bodies (Figure 95-Figure 96) in ***Marchantia polymorpha*** (Figure 1-Figure 12). In ***Marchantia polymorpha*** these oil bodies are localized in oil body cells (Tanaka *et al*. 2016). Tanaka *et al*. (2016) reported that oil bodies served as sites of accumulation of sesquiterpenoids and marchantin A. They also observed that the number of oil body cells increased in thalli grown in low-mineral conditions.

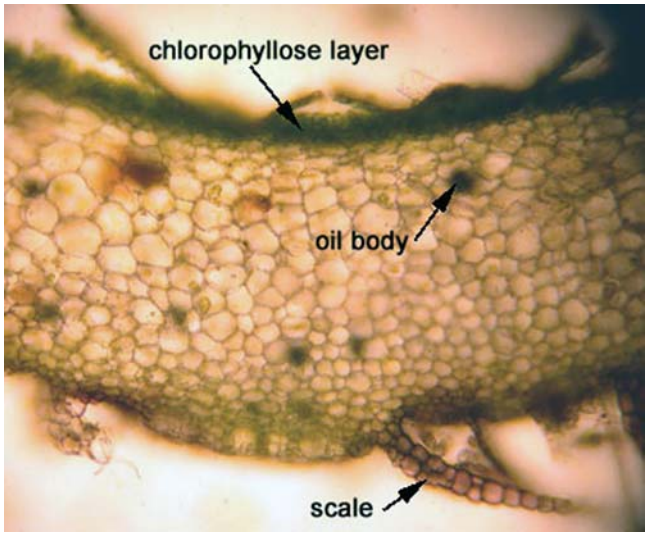

Figure 95. ***Marchantia polymorpha*** section showing scales and oil bodies. Photo from Botany Website, UBC, with permission.

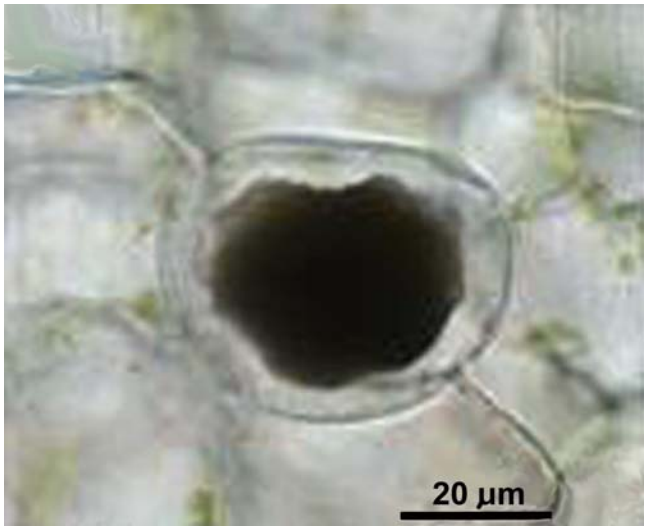

Figure 96. ***Marchantia polymorpha*** oil body in oil cell. Photo by Masaki Shimamura, with permission.

He *et al*. (2013) described the liverwort oil bodies (Figure 95-Figure 96) as "intracellular organelles bounded by a single unit membrane containing lipophilic globules suspended in a proteinaceous matrix." Oil bodies are unique to liverworts. In ***Marchantia polymorpha*** (Figure 1-Figure 12), we know that they contain protein complex that is immunologically related to the plastid and cytosolic enzymes of the isoprenoid synthesis. They are known as sites of essential oil accumulation and sequestration. Although they are known to contain compounds useful for medical purposes, their full function in liverworts remains unknown. What are the advantages of size and morphology – characters that differ sufficiently among species to be of taxonomic value?

By suppressing the genes controlling this sesquiterpenoid production, Romani *et al*. (2020) found that the terpenoid-rich oil bodies (Figure 95-Figure 96) are responsible for protecting ***Marchantia polymorpha*** (Figure 1-Figure 12) from arthropod herbivores, but that unlike those in tracheophytes, these oil bodies seem to have no role in abiotic stress response, including desiccation. Takizawa *et al*. (2021) found that when ***Marchantia polymorpha*** was exposed to non-axenic conditions the number of oil bodies increased, as did the amounts of sesquiterpenes. They likewise demonstrated that the bacterium ***Escherichia coli*** (Figure 16) elicited the same response.

Kihara *et al*. 2014) found that ***Marchantia polymorpha*** (Figure 1-Figure 12) emitted C8 volatiles following mechanical wounding. Induction of these emissions occurred within 40 minutes of the wounding. When transgenic plants lacking arachidonic acid and eicosapentaenoic acid were wounded, only minimal C8 volatiles were detectable. Octan-3-one was produced only minimally when thalli were completely disrupted, but was the most abundant product in only partially disrupted thalli.

Yoshikawa *et al*. (2018) traced the wounding response in ***Marchantia polymorpha*** (Figure 1-Figure 12). Wounding of the thallus resulted in the synthesis of phenylpropanoids, including luteolin, apigenin, and isoriccardin C.

Watson (1919) suggests that reduced pores in ***Marchantia*** species might be an advantage in a wet habitat. Due to cohesion of the water molecules, water is unable to enter the smaller openings.

Among the advantages that bryophytes have are their plasticity and adaptability. Plasticity is exhibited by the various biochemical responses to different pathogens and environmental conditions. Adaptability is enhanced by the haploid condition. Selection on gametophyte plants is more rapid than in tracheophytes because there is only one set of chromosomes, permitting rapid removal of non-adapted genes in the population. This mechanism is evident in adaptations to heavy metals. Briggs (1972) demonstrated this in the response of ***Marchantia polymorpha*** (Figure 1-Figure 12) to lead contamination. When Briggs compared plants from areas with high levels of lead in the soil to those from an area with low levels of lead pollution, those from highly contaminated soil were highly tolerant of lead, whereas those from areas with less lead contamination are more sensitive. Krupinska (1976) found that lead tetraethyl causes distorted growth patterns in ***Marchantia polymorpha***. The thalli become "profusely" branched, a reversible phenomenon. The chloroplasts degenerate and growth of the spores and gemmae is inhibited.

Reproduction

sexual

Marchantia polymorpha has been used in a number of studies on sexual expression in plants, particularly to demonstrate that expression in early plants. Nagai *et al*. (1999) generated 970 expressed sequence tag (EST) clones from an immature female sexual organ (Figure 112-Figure 128) of the liverwort ***Marchantia polymorpha*** (Figure 1-Figure 12). In 376 ESTs they found 123 redundant groups, reducing the unique sequences to 717.

Marchantia polymorpha (Figure 1-Figure 12) is a **dioicous** species with easily recognizable differences between **antheridiophores** (Figure 98-Figure 110) and **archegoniophores** (Figure 110-Figure 128). Durand (1908) described these as well as the sporangium. The

stages of the sexual life cycle can be seen in Figure 98-Figure 146.

As noted earlier, sex in ***Marchantia*** is determined by a **small V chromosome** in males and no U chromosome, whereas the female has a **single U chromosome** and no V chromosome (Lorbeer 1934). But the designation of the gender is not perfectly genetic. Naidu (1973) reported abnormal receptacles that bore both archegonia and antheridia, based on specimens from a population in India. The V chromosome (Figure 97) has several chromosome-specific sequence elements (Okada *et al*. 2001; Ishizaki *et al*. 2002). Okada *et al*. (2000) identified 70 male-specific PAC clones and verified that the V chromosome exhibits unique sequences that are not present on the U chromosome or any non-sex chromosomes. These repeat sequences contribute 2-3 Mb on the V chromosome. Okada and coworkers introduced us to the first active V chromosome-specific gene known in plants. Fujisawa *et al*. (2001) isolated two female-specific and six male-specific DNA fragments that originated from these U and V chromosomes. Okada *et al*. (2000) suggested that this liverwort was a suitable model for identifying roles of sex genes in sexual differentiation. Bisang *et al*. (2010) noted that molecular sex markers have thus far only been described for a few bryophytes, one of which is ***Marchantia polymorpha***.

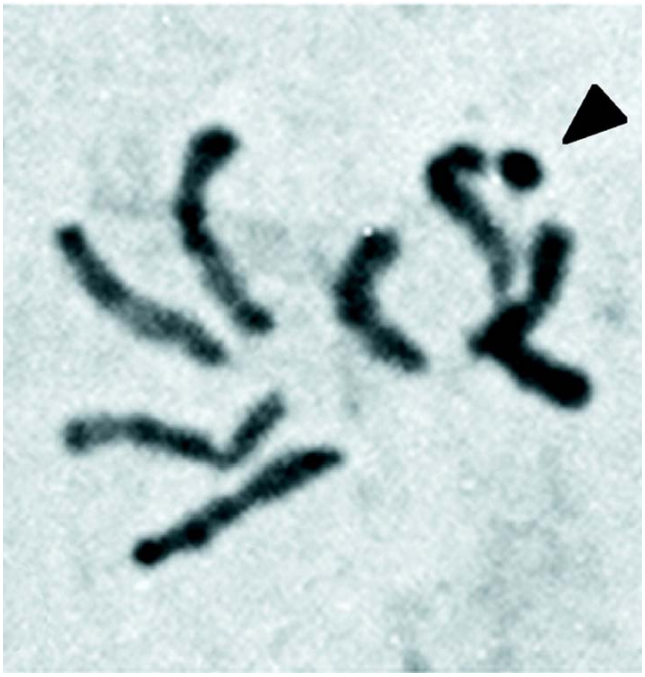

Figure 97. ***Marchantia polymorpha*** male chromosomes, with tiny V chromosome indicated by arrow. Photo from Okada *et al.* 2001, through Creative Commons.

Wann (1925) determined that photoperiod was important in initiating sexual branches in ***Marchantia polymorpha*** (Figure 1-Figure 12). In long days, males produce mature antheridiophores in 3-4 weeks. Females seem to respond to the same stimulus, but require 6-8 weeks for archegoniophores to reach maturity. The role of temperature remained unknown. High humidity hastens the sexual branches, but low humidity retards them and may completely inhibit their production, particularly for archegoniophores. And as in some of the algae, low nitrogen relative to carbohydrate may initiate sexual branches. These nutrient relationships in algae signal the end of the growing season and the beginning of the unfavorable conditions of winter. The same could be likely for the bryophytes as the tracheophytes use up the nitrogen during the growing season. Hence, forming a sexual reproductive structure that can remain dormant until favorable conditions return is adaptive.

Lloyd and Steinmetz (1937) found that high temperatures (above 30ºC) at least temporarily suppress development of archegoniophores and antheridiophores in ***Marchantia polymorpha*** (Figure 1-Figure 12). Low temperatures, on the other hand, promote development of these reproductive structures during short days. But during late autumn, plants moved to a warm greenhouse from the cool outdoors would also produce more archegoniophores and antheridiophores compared to plants that had remained in the greenhouse continuously. Furthermore, plants brought to the greenhouse in late autumn developed these sexual structures more quickly than those brought into the greenhouse earlier in the autumn. Greenhouse-grown plants could be induced to develop archegoniophores and antheridiophores during short days if they were exposed to natural autumn conditions found at Orono, Maine, USA. Nevertheless, a long photoperiod is important in inducing this sexual response.

Benson-Evans (1964) found that ***Marchantia polymorpha*** (Figure 1-Figure 12) produced gametangia at 21ºC in long days (18 hours), but lowering the temperature to 10ºC or the photoperiod to 6 hours resulted in no gametangia production.

Yamaoka *et al*. (2021) summarized that initiation of the development of gametangia depends on environmental factors such as light, but they considered that these factors are still elusive. They recognized recent studies that considered their development to use conserved regulatory modules that are involved in light signalling.

Maravolo *et al*. (1967) explored activity of 12 enzyme systems in various parts of ***Marchantia polymorpha*** (Figure 1-Figure 12). Of these, only phosphatases, esterases, and peroxidases were found in extracts of uninduced thalli, induced thalli, stalks, and antheridiophore and archegoniophore disks. They found an amplification of esterases in the antheridia (Figure 105-Figure 109). These esterases can hydrolyze particular esters into acids and alcohols or phenols. Gorska-Brylass (1970) reported increased esterase activity in the early stages of spermatogenesis in ***Marchantia polymorpha***, an activity that declines near the end of that cellular division. Could these be important in protecting the antheridia against stresses, especially desiccation?

Markham and Porter (1978) isolated an aurone (known for making flowers yellow) from ***Marchantia polymorpha*** (Figure 1-Figure 12) during its sexual phase. The aurone aureusidin 6-O-glucuronide is present only in the antheridiophores (Figure 98-Figure 110).

Figure 98. ***Marchantia polymorpha*** males with antheridial receptacles (antheridial heads). Photo by Li Zhang, with permission.

Figure 99. ***Marchantia polymorpha*** with expanding antheridiophores, showing development of the antheridial receptacle before elongation of the stalk. Photo by Des Callahan, with permission.

Figure 100. ***Marchantia polymorpha*** ssp. ***polymorpha*** male with antheridiophores that look healthy, despite the curling of the thallus. Photo by David Holyoak, with permission.

Figure 101. ***Marchantia polymorpha*** antheridiophores reaching full elongation. Photo by Walter Obermayer, with permission.

Figure 102. ***Marchantia polymorpha*** mature antheridial heads, showing how dense they can be. The presence of only one gender suggests that this is a clone. Photo by Steve Juntikka, with permission.

Figure 103, ***Marchantia polymorpha*** antheridial head in side view, with rhizoids and scales hanging from the head. Photo from Botany Website, UBC, with permission.

Figure 104. ***Marchantia polymorpha*** antheridial head that is not quite mature. Photo by Walter Obermayer, with permission.

Figure 105. ***Marchantia polymorpha*** mature antheridial receptacle showing yellow antheridia. Photo by Larry Jensen, with permission.

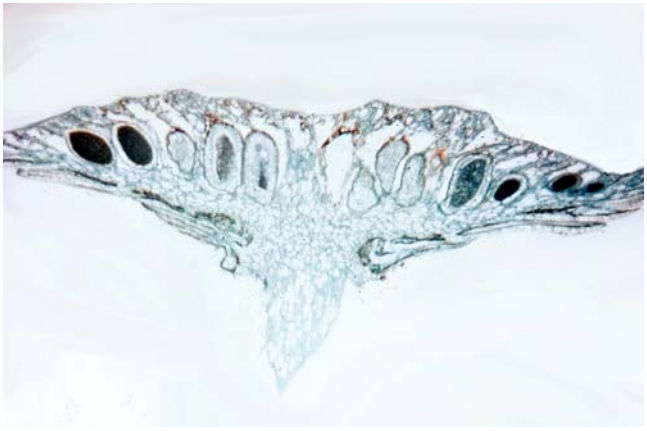

Figure 106. ***Marchantia polymorpha*** antheridial receptacle section showing arrangement of antheridia. Photo by Janice Glime.

Figure 107. ***Marchantia polymorpha*** antheridium section with developing sperm cells. Photo by Janice Glime.

Michelot-Gernez (1984) described the nuclear condensation during spermatogenesis in ***Marchantia polymorpha*** (Figure 1-Figure 12). Reynolds and Wolfe (1984) identified protamines in plant sperm, using ***Marchantia polymorpha*** as one of the representative organisms. These are small, arginine-rich proteins that replace histones near the end of the haploid phase of spermatogenesis; they are considered essential for sperm head condensation and DNA stabilization.

Carothers and Kreitner (1968) described the blepharoplast of the **spermatid** (developing spermatozoid) of ***Marchantia polymorpha*** (Figure 1-Figure 12). Bajon *et al*. (1995) described the nucleus of the **spermatozoid** (male gamete; sperm). They found that RNAs remain scattered in the spermatozoid throughout differentiation. They are closely associated with chromatin strands that fuse in the mature gamete. They found that mRNAs associated with the mature spermatozoid genome are stored mRNAs. They permit the transfer of paternal information to the zygote during fertilization. Using a high-speed video technique, Inouye and Hori (1991) described the movement of the sperm (spermatozoid) of ***Marchantia polymorpha*** as a breast stroke. Miyamura *et al*. (2002) further described the flagellar movement of the sperm, using high-speed video.

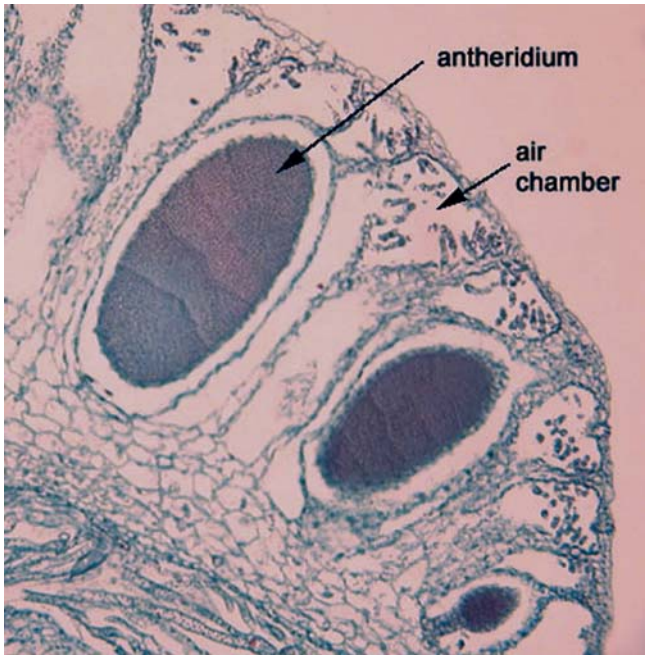

Figure 108. ***Marchantia polymorpha*** section of antheridial head. Photo from Botany website, UBC, with permission.

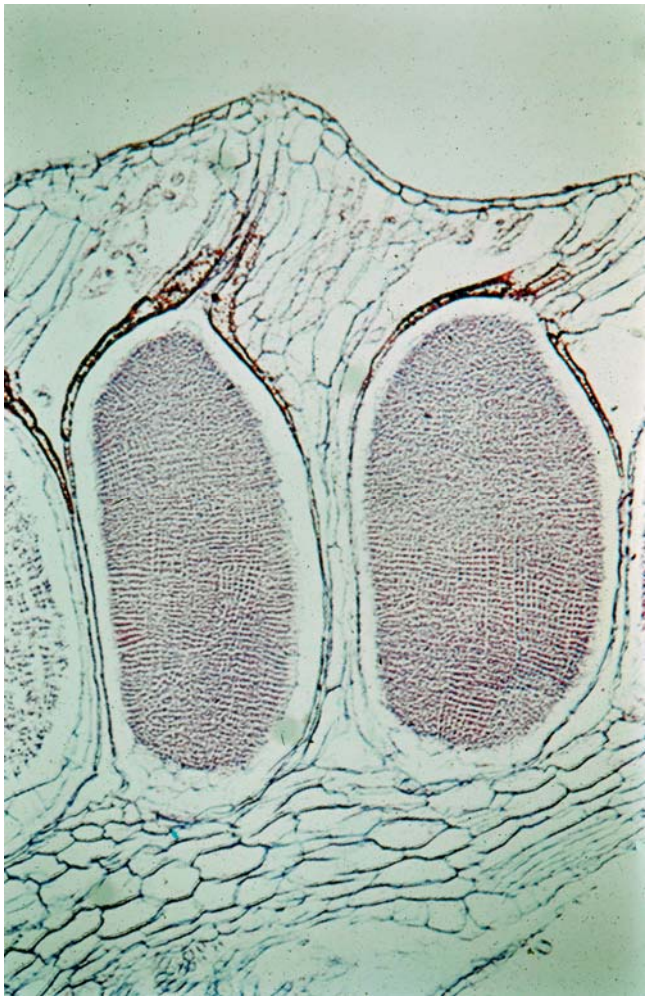

Figure 109. ***Marchantia polymorpha*** section of antheridia at maturity. Photo by Wilhelm Barthlott, with permission.

Figure 110. ***Marchantia polymorpha*** antheridiophores and archegoniophores, occurring on separate thalli. Photo by Robert Klips, with permission.

Une (1984) observed that female plants produce sexual branches more frequently than do male plants (Figure 111). Archegoniophores, in particular, may be inhibited by low humidity (Wann 1925). As in many algae, a low nitrogen:high carbohydrate ratio can stimulate the formation of sexual branches. This nutrient relationship often serves as a signal that growing conditions are declining and the formation of spores provides a mechanism for surviving until favorable conditions return or the spores land in a suitable habitat.

Figure 111. ***Marchantia polymorpha*** females in July 1982, in Rydhave, Denmark, showing how dense the population can become.

The archegoniophores (Figure 112-Figure 121) arise from a separate thallus from that of the antheridiophores. The archegoniophores are formed by an infolding and rolling of the thallus, trapping rhizoids and scales inside the stalk that is thus formed (Figure 118-Figure 121). The rhizoids, in particular, aid in the movement of water to the receptacle head at the top of the stalk.

Figure 112. ***Marchantia polymorpha*** archegonial heads before the elongation of the stalk. Photo by Rudolf Macek, with permission.

Figure 113. ***Marchantia polymorpha*** nearly mature archegoniophores before the arms of the receptacle spread. Photo from <www.aphotofauna.com>, with permission.

Figure 114. ***Marchantia polymorpha*** archegoniophores before the fingers spread. Photo from <www.aphotofauna.com>, with permission.

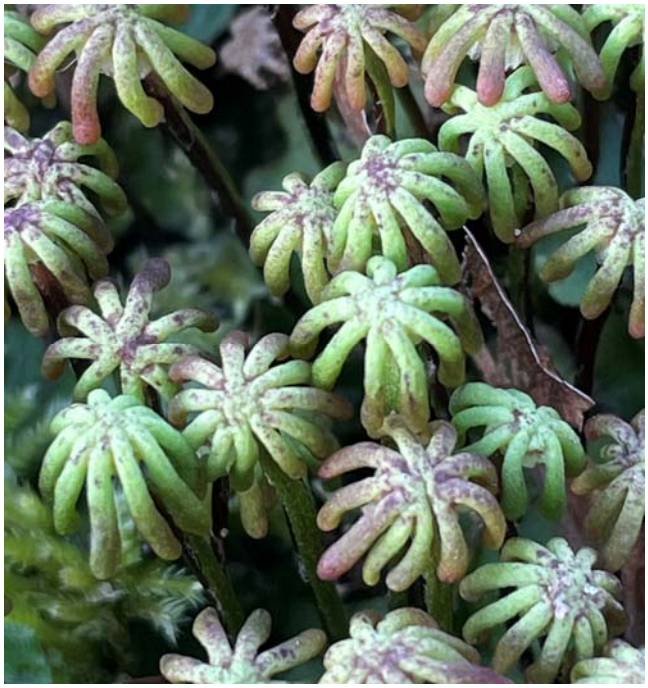

Figure 115. ***Marchantia polymorpha*** females before the fingers are uplifted. Photo by Craig Waddell, with permission.

Figure 116. ***Marchantia polymorpha*** archegoniophores with fully expanded fingers on the receptacle on 1 July 2009 in Michigan, USA. Photo by Janice Glime.

Figure 117. ***Marchantia polymorpha*** females in what appears to be a purely female clone in Houghton, Michigan, USA. Note the different stages of old and young archegoniophores. Photo courtesy of Craig Waddell.

The archegonial head, at maturity, is filled with scales that protrude from the fingers of the structure (Figure 118-Figure 122). These scales help to conserve water in the head and offer protection to the developing sporophyte.

Figure 118. Newly emerging and maturing archegoniophores of ***Marchantia polymorpha***. Note the rhizoids along the stalk and the scales protruding from under the receptacle head. Photo copyright Stuart Dunlop <www.donegal-wildlife.blogspot.com>, with permission.

Figure 119. ***Marchantia polymorpha*** mature archegoniophores 1 July 2009 in Michigan, USA. Photo by Janice Glime.

Figure 120. ***Marchantia polymorpha*** archegoniophores showing numerous scales hanging from the receptacle and groove in stalk where the rolled edges meet. Photo by Janice Glime.

Figure 121. ***Marchantia polymorpha*** archegoniophores nearing maturity. Note the rhizoids at the left. Photo by Rudolf Macek, with permission.

Figure 122. ***Marchantia polymorpha*** archegoniophore showing rhizoids along stalk, from Tahquamenon Falls, MI. Photo by Janice Glime.

The archegonia form on the fingers with the oldest near the stalk (Figure 123-Figure 129). Maintenance of dormancy by the egg (Figure 124-Figure 125, Figure 130) can prolong the period of time in which fertilization is possible. In ***Marchantia polymorpha*** (Figure 1-Figure 12), MpRKD regulates gametophyte development and keeps the egg cell dormant until fertilization occurs (Rövekamp *et al*. 2016). By doing this, it also prevents **parthenogenesis** (development of a zygote without fertilization).

In 1974, Zinsmeister and Carothers (1974) elucidated details of the fine structure changes involved in egg (Figure 124-Figure 125, Figure 130) formation. An amorphous substance surrounds the egg, perhaps preventing desiccation and protecting the egg.

Figure 123. ***Marchantia polymorpha*** archegoniophore with developing archegonia; showing thallus nature of the receptacle. Photo by George Shepherd, through Creative Commons.

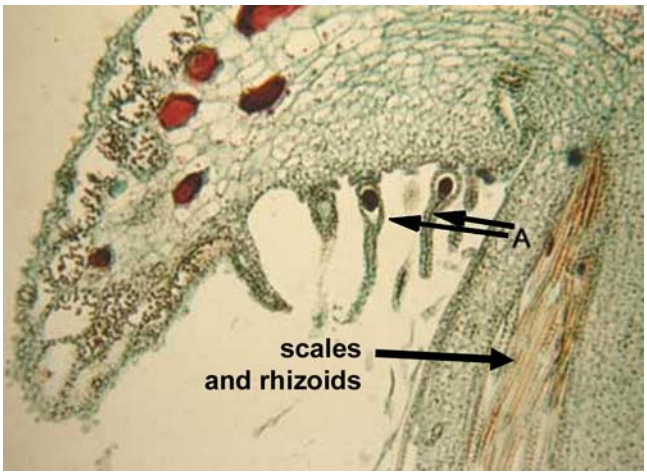

Figure 124. ***Marchantia polymorpha*** archegonial head longitudinal section showing archegonia (**A**) and scales and rhizoids in stalk. Image modified from Botany Website, UBC, with permission.

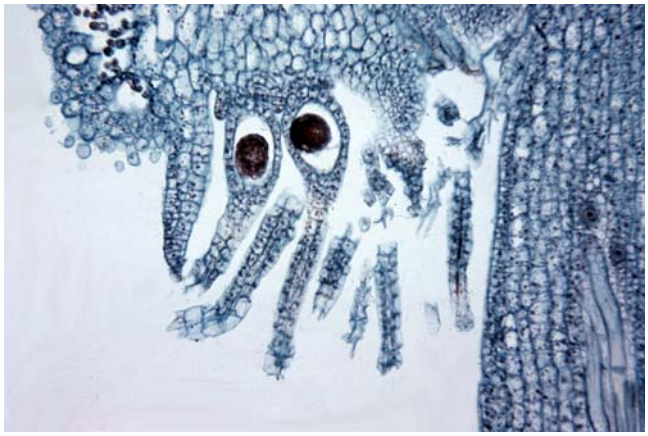

Figure 125. ***Marchantia polymorpha*** archegonia with what appear to be zygotes. Note the rhizoids within the stalk. Photo by Janice Glime.

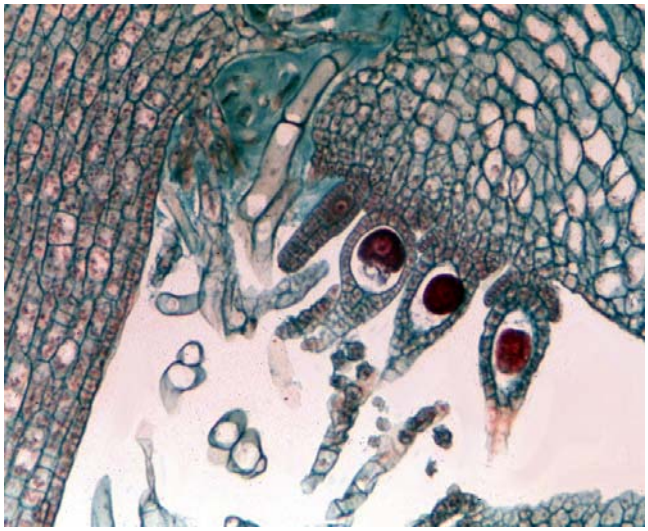

Figure 126. ***Marchantia polymorpha*** archegonia in various stages of development with least mature being closest to the stalk; the one furthest away has a zygote. Photo by Janice Glime.

Figure 127. ***Marchantia polymorpha*** with very young archegoniophores before stalk has expanded fully, mixed with mature archegoniophores showing yellow sporangia and elaters. Photo by Janice Glime.

Figure 128. ***Marchantia polymorpha*** unfertilized archegonium before neck canal cells disintegrate. Photo by Wilhelm Barthlott, with permission.

Figure 129. ***Marchantia polymorpha*** archegoniophores in a female clone on 6 July 2018 in Houghton, Michigan, USA; males were nearby in a separate clone. Photo by Janice Glime.

Part of this curiosity was to understand how the sperm could reach the egg in these dioicous plants. Kitagawa (1985) noted that due to the dioicous nature of ***Marchantia polymorpha*** (Figure 1-Figure 12), the male and female must be near each other (Figure 110) for fertilization to occur (Figure 130). But just how near is near?

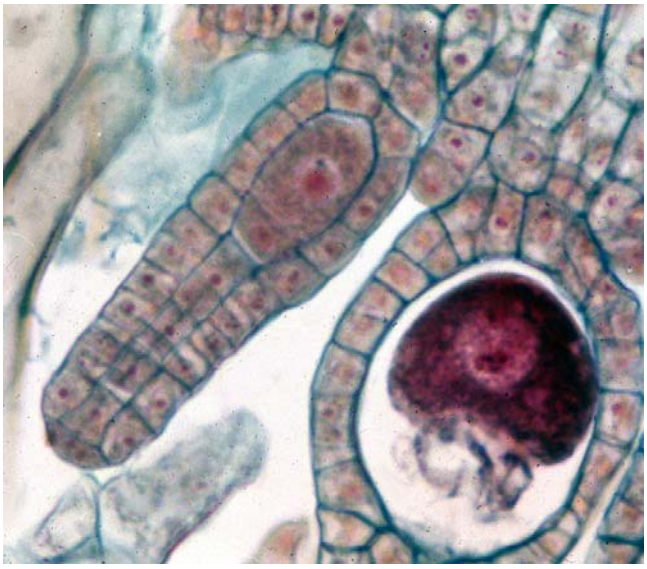

Figure 130. ***Marchantia polymorpha*** archegonia; one on left is immature with neck canal cells still in place; one on right has neck canal cells disintegrated (not shown) and the sperm is uniting with the egg. Photo by Janice Glime.

Strasburger (1869, in Parihar 1961) described the splashing of **sperm** (=male gamete, antherozoid, or spermatozoid; Figure 131-Figure 132) from the surface of the antheridial receptacle to the surface of the archegonial receptacle at a time when the antheridiophore was taller than the archegoniophore, thus permitting the water droplets to travel downward to the archegonial receptacles. He considered the splashing to extend to about 65 cm. By this time archegonia would have developed on the lower surface and the water would flow over the edge of the archegonial receptacle to reach them.

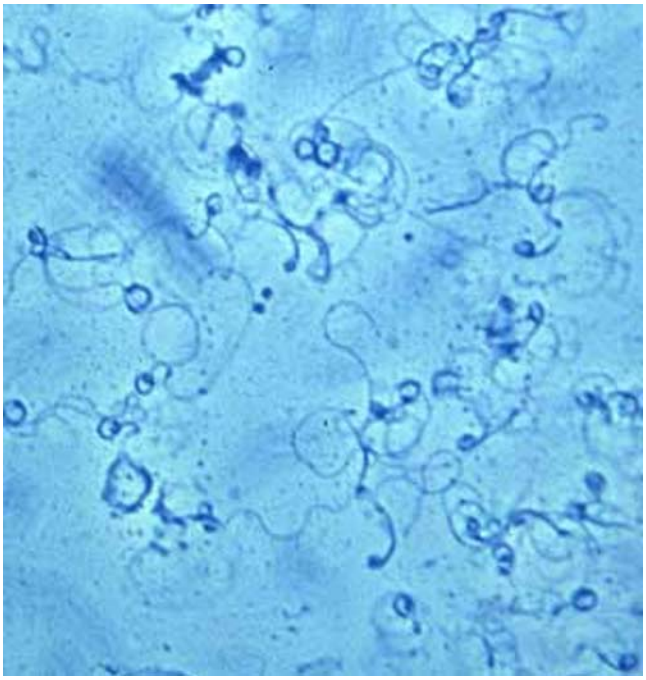

Figure 131. ***Marchantia polymorpha*** sperm. Photo from Botany Website, UBC, with permission.

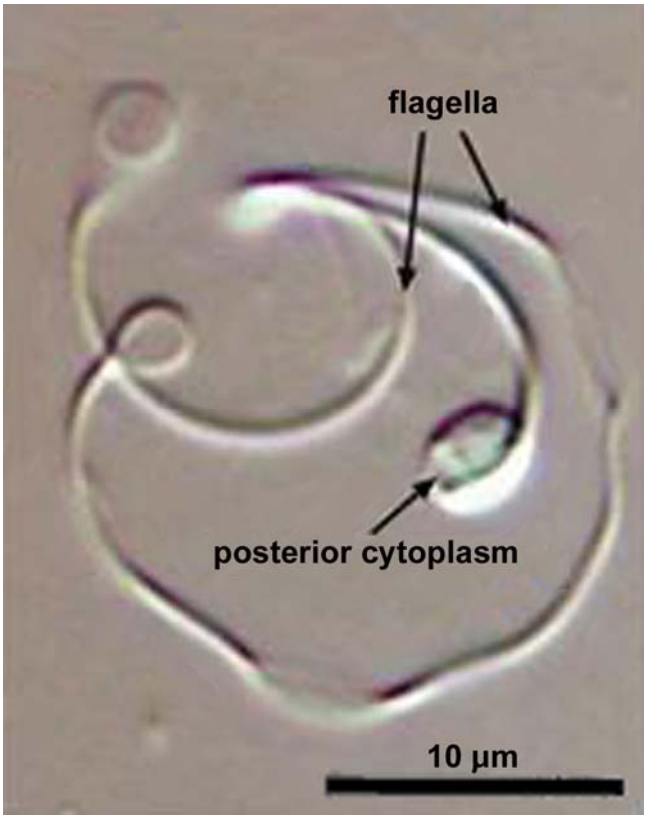

Figure 132. ***Marchantia polymorpha*** sperm. Photo by Masaki Shimamura, with permission.

One of the puzzles in fertilization of plants is how the sperm find the eggs, or at least the archegonium. Lidforss (1904) was among the early researchers on this question. Again using ***Marchantia polymorpha*** (Figure 1-Figure 12), Lidforss found the proteins albumin, hemoglobin, and diastase could each attract the sperm into the capillary tube that held them.

Åkerman (1910) experimented with various salts as attractants or repellants of sperm (Figure 131-Figure 132) in ***Marchantia***, possibly ***M. polymorpha*** (Figure 1-Figure 12). Some salts had positive effects on chemotaxis, whereas others, especially heavy metals, had negative effects.

Furuichi and Matsuura (2016) found time-dependent changes in sperm motility (Figure 131-Figure 132) from high to low motility states in ***Marchantia polymorpha*** (Figure 1-Figure 12). Based on the average lifetime of the high motility state and the speed of movement, they estimated that these sperm would travel less than 3 cm. Hence, they concluded that other factors were needed to explain apparent travel distances greater than this, and that the motility of the sperm itself most likely only was important in the final fertilization step.

Alvarez (2017) described the movement of the sperm (Figure 131-Figure 132) in ***Marchantia polymorpha*** (Figure 1-Figure 12), based on the publication of Myamura *et al*. (2002). The movement caused by these biflagellated sperm is waveform and differs between the two flagella. This permits the sperm to adjust both steering and propulsion. The beat of the posterior flagellum is more 3-d than that of the anterior flagellum. When the sperm collides with an obstacle, it does not exhibit backward swimming.

Shimamura (2016) reported that water droplets could splash sperm cells (Figure 131-Figure 132) 30 cm or farther from the male plants of ***Marchantia polymorpha*** (Figure 1-Figure 12), as previously demonstrated experimentally (Burgeff 1943; Brodie 1951; Duckett & Pressel 2009). Drops of dye-containing water dropped onto the antheridia did limited splashing and most of the dye (>90%) was absorbed by the ventral side of the antheridial receptacles. But the dye also quickly moved to the ground level and managed to spread throughout the entire colony within an hour. This was facilitated by the bundles of rhizoids in the archegoniophore. When encountering a female plant, the dye moved up the archegoniophore stalk to the archegonial receptacle through the bundles of rhizoids enclosed by the stalk. This movement upward required 30-60 minutes. Furthermore, Duckett and Pressel (2009) observed that the youngest sporophytes are located near the stalk and the older ones are located near the periphery, indicating that fertilization continues after stalk elongation.

But Pressel and Duckett (2019) also measured the distances travelled by the sperm (Figure 131-Figure 132) of ***Marchantia polymorpha*** (Figure 1-Figure 12) to achieve fertilization. They followed more than 80,000 males and females for two years after a major fire and recorded the number of sporophytes. While these numbers seem high, they found the astounding number of more than 200,000 sperm in individual antheridia of ***Marchantia polymorpha*** (Figure 1-Figure 12). This is a greater number than in most bryophytes, but it is coupled with very effective sperm dispersal. They found that distances could exceed 20 m and that dispersal resulted in 100% fertilization of the female plants. The dehiscing antheridia release lipids that help to move the sperm in the surface water films both along the antheridiophores and across the surface water films to the archegoniophores. In a single flooding event, a male thallus with 10-12 antheridiophores can release more than 50 million sperm. This high fertilization success, coupled with the numerous tiny spores, can account for the ease with which the species seems to arrive after disturbances such as fire.

sporangia

Fertilization occurs in the archegonia, making possible a number of sporangia on the same archegonial head. The embryos (Figure 133-Figure 134) remain in the arms of the archegonial head where they are protected by many scales. The maturing embryo forms a foot, seta, and capsule inside the archegonium (Figure 135-Figure 136). The scales protrude more as the embryo matures (Figure 137-Figure 146), thus helping to maintain moisture.

Figure 133. ***Marchantia polymorpha*** archegonium with young sporophyte embryo. Photo by Janice Glime.

Figure 134. ***Marchantia polymorpha*** archegonium with young embryo. Photo by Janice Glime.

Figure 135. ***Marchantia polymorpha*** archegonium with young sporophyte showing foot, seta, and capsule (sporangium). Photo by Janice Glime.

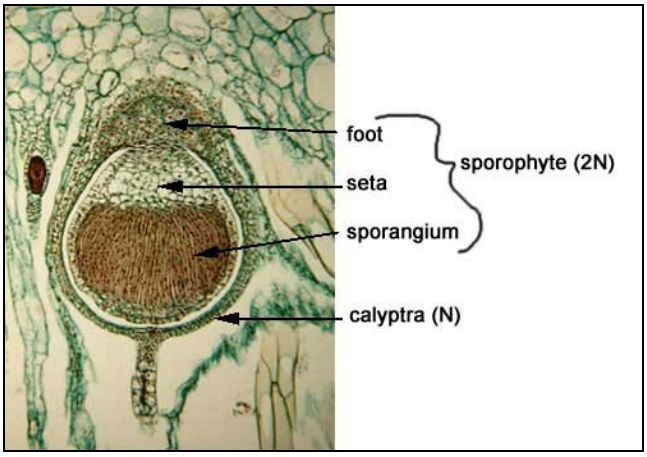

Figure 136. ***Marchantia polymorpha*** capsule longitudinal section. Image modified from Botany Website, UBC, with permission.

Figure 137. ***Marchantia polymorpha*** females with sporophytes, forming a female clone in Myvatn, Iceland, 8 August 1987. Photo by Janice Glime.

Figure 138. ***Marchantia polymorpha*** mature archegoniophores, Keweenaw Peninsula, Michigan, USA. Photo by Janice Glime.

Wann (1925) found that sporophytes (Figure 139-Figure 145) became mature in 10-12 weeks. This rate can be increased by high humidity and retarded by relatively low humidity.

Figure 139. ***Marchantia polymorpha*** archegonial heads showing a bluish green variant. Sporangia are just beginning to emerge from the scales. Photo by Felipe Osorio-Zúñiga, with permission.

Figure 140. ***Marchantia polymorpha*** archegoniophores showing population with bluish-green coloring and purple scales with capsules emerging. Photo from BlueRidgeKitties, through Creative Commons.

Figure 141. ***Marchantia polymorpha*** ripe, unopened sporangia. Photo by Felix Riegel, through Creative Commons.

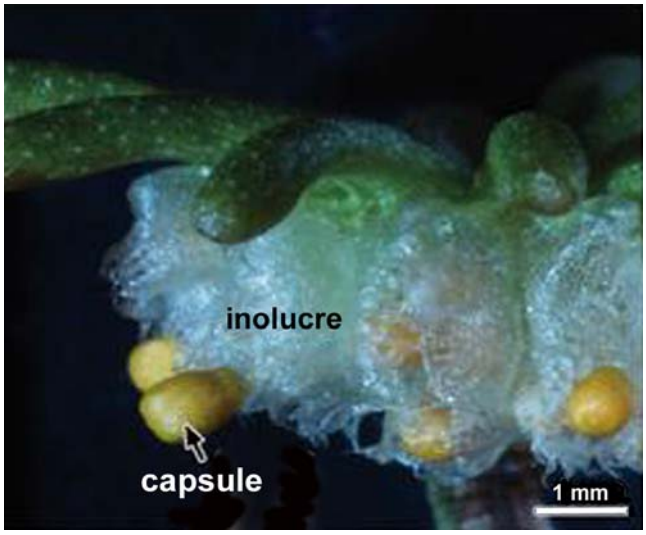

Figure 142. ***Marchantia polymorpha*** sporangia (capsules) emerging from the involucre. Photo by Masaki Shimamura, with permission.

Figure 143. ***Marchantia polymorpha*** archegonial head with elaters emerging on left, an empty capsule in center, and a capsule ready to open on right. Note the protective scales from which they are emerging. Photo by George Shepherd, through Creative Commons.

Figure 144. ***Marchantia polymorpha*** with mature sporangia dispersing spores, Laxarbakki, Myvatn, Iceland, 8 August 1987. Photo by Janice Glime.

Figure 145. ***Marchantia polymorpha*** archegoniophore with several unopened capsules on left and numerous elaters extended elsewhere. Note the purplish fringes on the scales of this specimen. Photo by Janice Glime.

Dörken (2012) described the sporophytes (Figure 139-Figure 145) of ***Marchantia polymorpha*** as short-lived, dying back after releasing the spores (Figure 146). A capsule typically contains several hundred thousand spores of similar size and shape, helping to account for the ability of this species to colonize newly disturbed areas such as those after fire.

Figure 146. ***Marchantia polymorpha*** archegonial head with empty sporangia among the scales and with sporangia beginning to die back. Photo by Janice Glime.

spores

O'Hanlon (1926) reported that in the Midwest of the USA, spores of ***Marchantia polymorpha*** (Figure 1-Figure 12) were "available" from early July to the middle of September. The sporophyte (Figure 147) produces an elater to spore (Figure 148-Figure 149) ratio of 1:128. A single capsule (Figure 141-Figure 142) of ***Marchantia polymorpha*** holds about 300,000 spores. Based on the typical number of capsules per archegonial head (~24), this would yield >7,000,000 spores per receptacle. But under favorable conditions, ~100 sporophytes are produced on one receptacle during a single growing season, suggesting that the total number of spores per individual archegonial receptacle is probably much greater (Duckett & Pressel 2009). The spores can be available for dispersal from early July to mid September, depending on latitude and altitude (O'Hanlon 1926). The spores remain viable for about one year.

Figure 147. ***Marchantia polymorpha*** archegonial head with dispersing sporangia having exserted elaters (yellow). Note the rhizoids on the rolled stalk. Photo by George Shepherd, through Creative Commons.

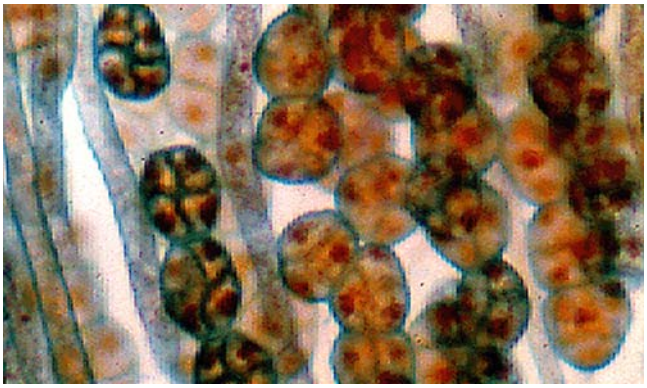

Figure 148. ***Marchantia polymorpha*** spore tetrads and immature elaters in capsule. Photo by Janice Glime.

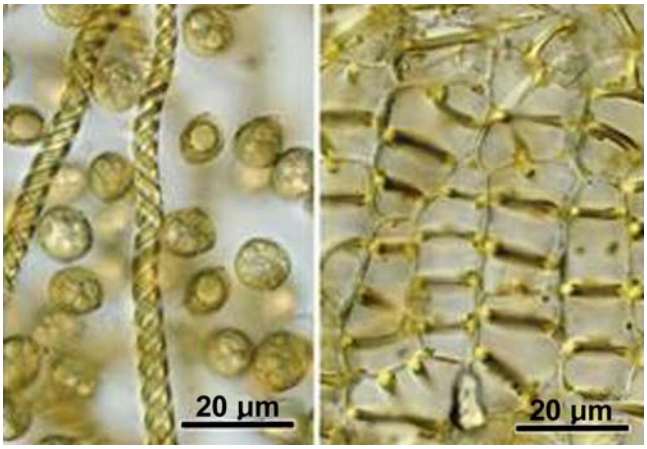

Figure 149. ***Marchantia polymorpha*** spores and elaters on **left** with closer view of thickenings of elaters on **right**. Photo by Masaki Shimamura, with permission.

Young and Kläy (1971) found ***Marchantia polymorpha*** (Figure 1-Figure 12) on the crater of a volcano on Deception Island, Antarctica, following the 1969 eruption. This rapid colonization of newly exposed substrata is itself remarkable, but the closest known source of propagules is 1,000 km away in South America! They assumed that numerous propagules must have arrived on just a small area to produce the colony pattern observed. Hence, the dispersal potential of this species is great, a factor that relates to the small size of its spores.

O'Hanlon (1925) detailed the germination of spores (Figure 150) and the early gametophyte stages in ***Marchantia polymorpha*** (Figure 1-Figure 12). Inoue (1960) studied the spore germination and early gametophyte development in the Marchantiales. Bischler (1984) examined spore morphology and germination in ***Marchantia***.

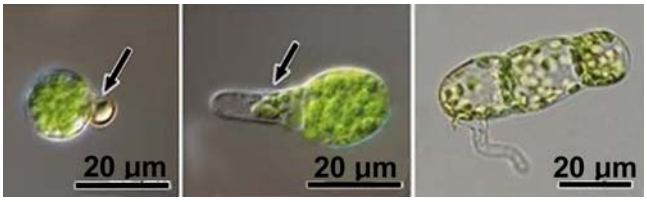

Figure 150. ***Marchantia polymorpha*** spore germination stages to a 3-celled protonema. Photo by Masaki Shimamura, with permission.

When the spore germinates (Figure 150), it typically produces a single primary rhizoid (Figure 151) after the spore has expanded and produced chlorophyll (O'Hanlon 1926). The spore first produces a very short filament. This is followed by division in a second cell, resulting in the thalloid structure that describes the mature protonema. Branching of the young thallus is common and can begin at an early stage. Rather than having a single apical cell dividing, it produces a marginal row of meristematic cells that continue to produce the mature thallus. At a stage of 30-40 cells, a notch develops in the apical region (Figure 151). Rhizoids develop behind this notch, anchoring the thallus and establishing its dorsiventrality. Mucilage cells arise on the lower side of the apex. In early stages, diminished light seems favorable, but by this stage 13-15 hours of light per day is optimum, with an optimum temperature of 18-22ºC. However, the optimum for "fruiting" is lower at 10-15ºC. They also germinate and grow better on a solid substrate than in a liquid medium.

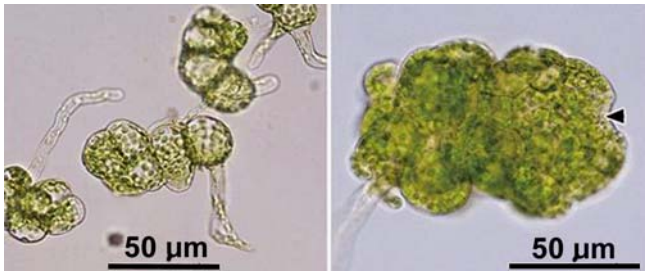

Figure 151. ***Marchantia polymorpha*** protonema development. Apical notch is shown at arrow on right. Photo by Masaki Shimamura, with permission.

Nakazato *et al*. (1999) were able to induce spore germination in ***Marchantia polymorpha*** (Figure 1-Figure 12) with intermittent irradiation with 15-min red light pulses given every 1 or 2 h for 24 h. Germination could also be induced by the addition of glucose to spores in total darkness. Their experiments indicate that photosynthesis is involved in the photoinduction of spore germination in this species, supporting the conclusion of Inoue (1960).

In the right conditions, the spores swell and gain chlorophyll (Figure 150) (Shimamura 2016). Once swollen they shed the primary spore walls and germinate within a few days. This germination is light-dependent (Heald 1898), suggesting a need for additional energy resources. The light requirement is 10 hours or longer (Nakazato *et al*. 1999). It seems to require a brighter light for protonema and thallus development than that required by other liverworts (Inoue 1960).

Red and far-red light affect both cell division and elongation in ***Marchantia polymorpha*** (Figure 1-Figure 12) sporelings (Figure 150) (Nishihama *et al*. 2015). Thus, it is likely that phytochromes are involved in development of sporelings.

Gemmrich (1976) found that both Fe and $Ca(NO_3)_2$ induce germination of the spores (Figure 150) of ***Marchantia polymorpha*** (Figure 1-Figure 12). Optimal germination also requires KNO_3 and $MgSO_4$. Gibberellic acid had no effect on induction of spore germination in dark cultures.

Initial spore germination (Figure 150) is dependent on light (Hartmann & Weber 1990). As shown in ***Marchantia***

polymorpha (Figure 1-Figure 12), following the initial series of reactions that ultimately result in the swelling of the spore, polarity develops (Figure 150). This becomes obvious when the protonema protrudes from the spore as a filamentous germ tube (Figure 150).

Spore germination (Figure 150) of ***Marchantia polymorpha*** (Figure 1-Figure 12) requires 10 hours or longer (Nakazato *et al*. 1999). The entire light spectrum is effective for germination, but red light is the most effective. The effect of red light is not reversed by subsequent far-red light.

Shibaya *et al*. (2005) demonstrated that AGPs (arabinogalactan proteins) differed before and after protonema development, suggesting that they are involved in differentiation and development. Furthermore, binding of the AGPs inhibits protonema development in ***Marchantia polymorpha*** (Figure 1-Figure 12), causing disturbances at the cell surface and inhibiting cell-wall synthesis.

Upon germination, one primary rhizoid appears (Figure 150) following the growth of the spore and chlorophyll development (O'Hanlon 1926). At a stage of about 30-40 cells a notch appears in the apical region of the young gametophyte (Figure 151-Figure 152). Although germination seems to benefit from more moderate light, growth is best at 12-15 hours of "good intensity light," with the best temperatures in the range of 18º-22ºC. However optimum temperatures for sporophyte development are 10º-15ºC. It is interesting that chlorophyll can form in the spores as they imbibe water in the dark. Furthermore, with glucose in the medium spore germination can occur in the dark, further supporting the conclusion that photosynthesis, hence the production of sugar, is necessary for germination.

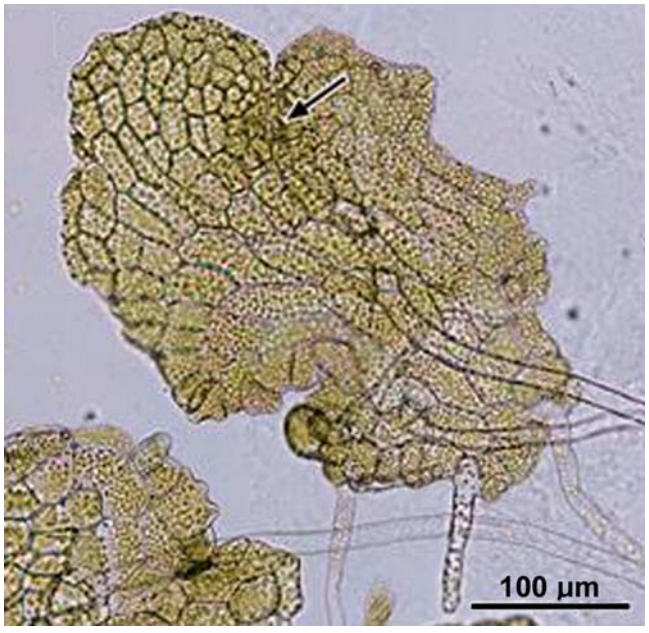

Figure 152. ***Marchantia polymorpha*** mature thalloid protonema with rhizoids. **Arrow** indicates apical notch. Photo by Masaki Shimamura, with permission.

gemmae (Figure 153-Figure 170)

Hallier (1966) experimented with germination of gemmae in ***Marchantia polymorpha*** (Figure 1-Figure 12). He examined the effect of 2,4-mononitrophenol on respiration and induction of germination.

Terui (1981) reported that archegoniophore production in ***Marchantia polymorpha*** (Figure 1-Figure 12) occurs under long-day conditions, conditions that at the same time suppress the formation of gemmae cups. The gemmae cup suppression occurs about 20 days before the archegoniophore protrudes. High sucrose, on the other hand, induces gemmae cup development. When low light was provided for a prolonged time, it stimulated gemmae cup formation.

Une (1984) confirmed the negative correlation between gemmae cup (Figure 153-Figure 170) production and initiation of sexual structures. The gemmae cups occur more frequently on the margins of the colony, decreasing in number as sexual branches arise toward the inner part of that colony. This seems to relate to the age of the thalli and consequent change in the nutrient condition of the soil beneath the colony, with younger thalli occurring at the margins. Une also found that female plants produce sexual structures more frequently than do males.

Benson-Evans (1964) cultured ***Marchantia polymorpha*** (Figure 1-Figure 12) that produced gemmae (Figure 153-Figure 170) at 10ºC in short days (6 hrs), the opposite conditions of those that resulted in archegoniophore production. On the other hand, Hedger *et al*. (1972) found that long days were needed to maintain the development of gemmalings of this species on an inorganic medium. Carbon additions did not affect the growth rate under long-day or short-day photoperiods.

Figure 153. ***Marchantia polymorpha***; note the arrangement of the gemmae cups along the midrib in these older thalli. Photo by Jan-Peter Frahm, with permission.

Figure 154. ***Marchantia polymorpha*** gemmae cups arranged on midrib. Photo by Robert Klips, with permission.

Figure 155. ***Marchantia polymorpha*** showing gemmae cups along the midrib. Photo by Walter Obermayer, with permission.

Figure 156. ***Marchantia polymorpha*** with red edges; note the rim within the gemmae cup, holding young gemmae within it. Photo by Brenda Dobbs, through Creative Commons.

Figure 157. ***Marchantia polymorpha*** gemmae cup with lenticular gemmae and thallus showing pores. Photo by Walter Obermayer, with permission.

Figure 158. ***Marchantia polymorpha*** gemmae cup. Photo by Bernard de Cuyper, with permission.

Figure 159. ***Marchantia polymorpha*** gemmae in red cups that may indicate high light or other stress. Photo by Dick Haaksma, with permission.

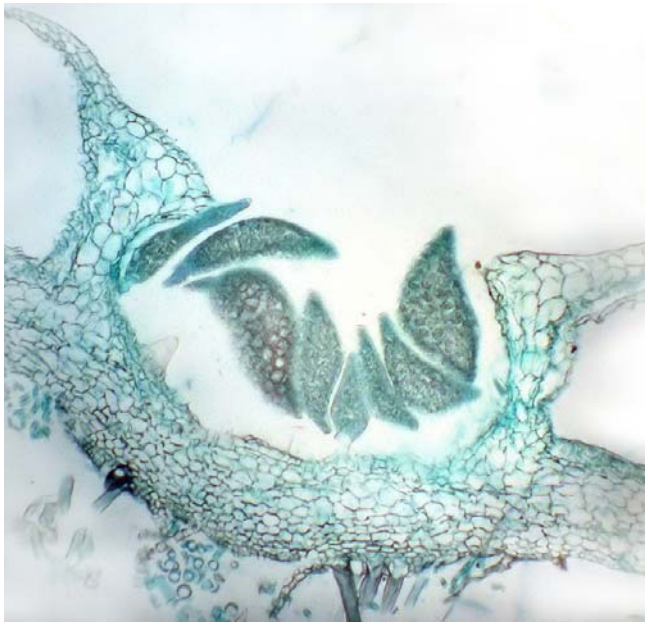

Figure 160. ***Marchantia polymorpha*** section of gemmae cup; note stalk on middle gemma. Photo by George Shepherd, with permission.

Figure 161. ***Marchantia polymorpha*** gemmae cup section. Note the inner rim that confines the young gemmae in the cup. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 162. ***Marchantia polymorpha*** gemmae cups; note that some of the cups have disintegrated, permitting gemmae to escape easily, but mostly onto the thallus. Photo by Andrew Spink, with permission.

Figure 163. ***Marchantia polymorpha*** gemmae cups as the mature gemmae begin to leave the cup. Photo by Walter Obermayer, with permission.

Figure 164. ***Marchantia polymorpha*** gemmae cups with a fringe; some gemmae are on the thallus, ungerminated. Photo from BlueRidgeKitties, through Creative Commons.

Figure 165. ***Marchantia polymorpha*** gemma. Photo by Des Callaghan, through Creative Commons.

Figure 166. ***Marchantia polymorpha*** females showing gemmae cups on younger thalli and mature archegoniophores on older parts. Photo courtesy of Craig Waddell.

Tarén (1958) described the gemmae (Figure 165) as growing on stalks in the cup (Figure 160, Figure 167),

where they are surrounded by hairs that excrete slime (Figure 161). They have two growing regions and branches develop from both.

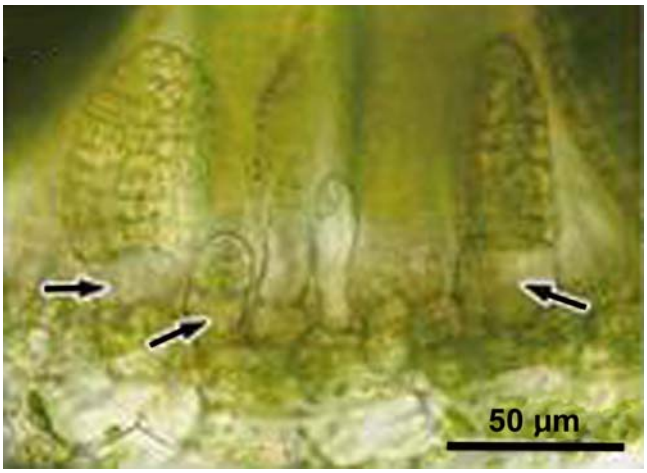

Figure 167. ***Marchantia polymorpha*** gemmae with arrows indicating stalks. Photo by Masaki Shimamura, with permission.

Hiwatashi *et al*. (2019) and Yasui *et al*. (2019) explored the genetic encoding for the genes that are involved in the regulation and formation of gemmae (Figure 153-Figure 165).

Gemmae cups (Figure 153-Figure 164) need nutrients to develop. Plants lacking nitrate become light green and have few gemmae cups and infrequent forking (Voth 1941). By contrast, those lacking phosphate become dark green and produce gemmae cups. They also have frequent dichotomies that cause the plants to form rosettes.

The mechanism of dispersal of the gemmae (Figure 153-Figure 165) has been a favorite example for textbooks. In fact, Laplaud *et al.* (2022) even presented their work at a meeting of the American Physical Society.

The splash cup (Figure 168) a dispersal mechanism served as the topic for an entire book (Brodie 1951). Brodie noted that splash cups commonly form 60-70º angles with their horizontal surface. These cups have a broad basal attachment and the propagules are **lenticular** (lens-shaped). He suggested that such cups could facilitate splashing of their contents for about 60 cm in ***Marchantia polymorpha*** (Figure 1-Figure 12). Equihua (1987) conducted further experiments, finding that raindrops could splash the gemmae up to 120 cm from the parent cup.

Figure 168. ***Marchantia polymorpha*** with gemmae cups. Note the bird's nest fungus (*Nidularia*) beside the thallus, a larger splash cup. Photo by Martin Hutten, with permission.

The ease of dispersal of the gemmae (Figure 153-Figure 165) has been a point of consternation for nursery growers, inspiring research on the mechanism. England and Jeger (2005) experimented with an overhead sprinkler system to determine various nozzle differences and their effects on dispersal. They demonstrated the effectiveness of the dispersal by using red dye in the cups in place of gemmae. At extreme water pressures of 1.5 and 3 bars, fewer gemmae were dispersed at all nozzle sizes. When the flow rate was adjusted to 160 L h^{-1} dispersal number increased with height of the nozzle. At the other flow rates tested the nozzle height lacked any clear effect on number dispersed. The maximum distance travelled was 1.6 m.

The gemmae cup (Figure 153-Figure 164) has a decorated border and is cone-shaped (Figure 169). The cup-shaped container permits a raindrop to splash the gemmae to some distance from the cups (Laplaud *et al*. 2022). When a raindrop is non-centered when it lands, it creates a jet of water splash that carries a few gemmae with it. Laplaud and coworkers found that this propulsion can carry gemmae up to a meter from the cup. They are continuing their research to determine the effects of cone angle and the presence of decorations on its border (Figure 169).

Figure 169. ***Marchantia polymorpha*** gemma cup showing decorated border. Photo by John Forlonge through Flickr.

The climatic conditions can be right for germination, but the gemmae (Figure 153-Figure 164) could be in the wrong place. To determine if a substrate surface is present, ethylene is the most likely hormone to carry out this function. Because it is a gas, it is able to accumulate between a gemma and its substrate. Duarte (2020) used constant ethylene-signalling mutants to search for such a response. She found that the hormone ethylene could be part of the process of dormancy establishment, maintenance, and release of gemmae (Figure 153-Figure 165) in ***Marchantia polymorpha*** (Figure 1-Figure 12).

But experiments by Thullen (1965) suggest that the substrate is not important in the orientation of the rhizoids (Figure 82-Figure 54) of ***Marchantia polymorpha*** (Figure 1-Figure 12) gemmae (Figure 153-Figure 165). When the light source is above, surface gemmae produced 92% of their rhizoids on the side away from the light; those gemmae submersed in the agar produced only 85% on the side away from light. When the light source is beneath the gemmae, only 50 and 45% of the rhizoids, respectively,

appeared on the side opposite the light. When light was provided from beneath the gemmae it changed the percentage of rhizoids arising from the upper surface, but did not change the total number of rhizoids. Gemmae grown in total darkness produced rhizoids only on the lower side. Thullen concluded that both gravity and direction of light are important in rhizoid production. Light intensities seemed to have no effect. Temperature appears to be an important determinant in gemma germination of ***Marchantia polymorpha*** gemmae. Thullen found a sharp decrease in the number of rhizoids produced by gemmae at temperatures of 26ºC and above.

Otto (1976) also demonstrated that the orientation of the gemma (Figure 153-Figure 165) determines where rhizoids form, with the gravitational force assuring their development on the lower side of the gemma. If that side is in contact with the substrate, more rhizoids are produced than if that surface is exposed to air. In the dark, only ~20% of the gemmae produce rhizoids. If the gravitational direction is alternated and no illumination is provided, no rhizoids form. The direction of light source influences the location of rhizoids only when the gravitational direction is not constant, with more rhizoids formed on the darker side.

As already noted, Otto and Halbsguth (1976) found that 350 nm light was the most effective wavelength to induce rhizoids in the gemmae of ***Marchantia polymorpha*** (Figure 1-Figure 12). Wavelengths below 550 or above 670 nm failed to stimulate rhizoid formation. The responses exhibited red far-red reversibility, suggesting that phytochrome was involved. IAA at 10^{-4} M causes the same effect as 1 hour of red radiation. They suggested that the wavelength of light might affect the influence of the phytochrome system on permeability of the membrane to IAA.

Rousseau (1952, 1953, 1954a) explored the influence of heteroauxins (IAA) on the growth of gemmae cups (Figure 169) in ***Marchantia polymorpha*** (Figure 1-Figure 12). Rousseau (1954b) further showed that coumarin inhibited the growth of the gemmae.

Prior and Brown (1970) attempted to identify the hormone(s) involved in initiation of rhizoids. They found no influence on germination or initial intercalary growth of gemmae (Figure 153-Figure 165) by 2,4-D, maleic acid hydrazide, gibberellic acid, or 2-furanacrylic acid (β-2-furylacrylic acid) in a range of concentrations Gibberellic acid delayed development. But none of them caused a difference in number of rhizoids. They did, however, find that apical cell activity and cell elongation were suppressed. Both 2,4-D and maleic hydrazide suppressed internal differentiation They did find that increasing age of the thallus caused greater sensitivity to both type and concentration of the regulator.

Dunham and Bryan (1968) explored the effects of amino acids on the development of the gemmalings in ***Marchantia polymorpha*** (Figure 1-Figure 12). At concentrations of 10^{-3}, l-isoleucine, l-leucine, l-methionine, or l-threonine resulted in a disruption of the apical regions. At lower concentrations, l-arginine, l-histidine, l-hydroxyproline, l-lysine, or l-tryptophan caused morphological irregularities. The irregularities were amino acid specific.

Gemmalings can reach reproductive maturity relatively quickly. Miller and Colaiace (1969) found that within 3-6 weeks the gemmalings of ***Marchantia polymorpha*** (Figure 1-Figure 12) responded to a 1% agar medium in a 24-hour photoperiod at 23ºC by producing antheridiophores and archegoniophores.

During (2001) hypothesized that the tradeoff between dispersability and longevity in soil diaspore banks could result in the scarcity of weedy species such as ***Marchantia polymorpha*** (Figure 1-Figure 12) in the soil bank. But in fact, the opposite appears to be the case. Species with large spores (*i.e.* limited dispersal distances) tend to be more persistent in the soil diaspore bank. Presumably, this larger diaspore would include the large gemmae of ***M. polymorpha***. This is also in sharp contrast to seeds, wherein small seeds predominate in the diaspore bank. During suggests that there is more predation on larger seeds. Furthermore, bryophytes have much more representation of asexual diaspores than do seed plants. Such asexual diaspores as gemmae are generally produced through a greater part of the growing season than the very seasonal seeds or most kinds of bryophyte spores. The spores of ***M. polymorpha*** might be an exception to that spore seasonality, however. And certainly, its spores greatly exceed gemmae in number.

Miller and Alvarez (1965) emphasized that in gemmae both notches with apical cells are capable of growing. In their experiments with ^{60}Co they found that both cells had to be damaged to eliminate the survival of the gemma.

Miller (1966) described the gemmae of ***Marchantia polymorpha*** (Figure 1-Figure 12) as discoidal with two apical notches 180º from each other. Each notch has two apical cells. These apical cells, however, are not the only locations where growth, as cell proliferation, can occur. In irradiated gemmae, the nuclear volume is important in the cell survival, with larger nuclei having greater survival.

Nehira (1973, 1977) explored the development of the rhizoids of the gemmae of ***Marchantia polymorpha*** (Figure 1-Figure 12) and the adsorption of Ca on the rhizoids of the gemmae and its role in their differentiation.

One surprising effect on germination of the gemmae is that of nickel (Ni). Lepp and Hockenhull (1983) found that $NiSO_4$ served as a significant growth stimulus at 0.15 ppm Ni, but at concentrations above 0.25 ppm the gemmalings exhibited a toxic response. On the other hand, $NiCl_2$ stimulated growth of the gemmalings at 0.25 ppm Ni, and they could tolerate $Ni(NO_3)_2$ up to 0.5 ppm. Furthermore, they observed different toxicity depending on the environment of the gemmalings, with those from an urban area being more tolerant than those grown in the glasshouse.

regeneration and growth

Perhaps the earliest form of reproduction is **regeneration**. This ability to grow new plants from fragments is known from the **Cyanobacteria** and algae and permits them to survive from parts when most of the whole has died. It is particularly useful in aquatic organisms that can be moved rather easily to new locations by the water.

Vöchting (1885) noted the regeneration capability of the **Marchantiales** and in 1887 (Vöchting 1887) reported that that every living cell in ***Marchantia polymorpha*** (Figure 1-Figure 12) was capable of regenerating an entire plant. Frye (1928) determined the age of a population of ***Marchantia polymorpha*** in western Washington, USA, to

be four years old. Only three of these yearly growth segments was alive. The growth habit of ***Marchantia polymorpha*** to die at the postical end while growing at the bifurcating apical end permits the population to expand.

Giles (1971) discussed the mechanism that governed the stability of differentiation in ***Marchantia***. These included a possible mechanism intrinsic to the to the cell, presumably in more highly differentiated species. However, in other bryophytes this control might be more affected by factors in the environment. But the factors affecting cellular dedifferentiation of an isolated fragment remained unknown. Giles suggested that these factors must be biochemical, probably involving RNA metabolism, and should be investigated.

Barner (1990) found that only the rhizoids from subcultured explants were able to regenerate thalli. The cultures required a directional light source.

Light is critical in regeneration of bryophytes (Nishihama *et al*. 2015). These researchers demonstrated that ***Marchantia polymorpha*** (Figure 1-Figure 12) has a single phytochrome gene and that phytochrome regulates re-entry into the cell cycle and control of cell shape in newly regenerating tissues. Nevertheless, light is not essential for regeneration, but it exhibits considerable control over the process. But, sugar can cause normal regeneration in the dark, suggesting the importance of photosynthesis to supply the energy.

Li (1990) described the difficulties of culturing gemmae and gametophytes of ***Marchantia polymorpha*** (Figure 1-Figure 12). They found that in their cultures it required dedifferentiation and redifferentiation, with rather specific cultural conditions and media. They used 2,4D and 3% sucrose to encourage the tissue development. This process could require as long as 10 months. Nevertheless, they found the process to be easier than in tracheophytes.

Bryophytes are known for their "extraordinary competency of regeneration" (Nishihama *et al*. 2015). This is possible due to their high level of developmental plasticity, permitting them to regenerate from cells, tissue fragments, branches, and even reproductive organs. Gardeners in Japan and elsewhere take advantage of this ability to propagate many plants from just a few by drying and fragmenting them (see Horticulture chapter in Volume 5).

Yoshikawa *et al*. (2018) found that the stress caused by wounding (Figure 170) induces phenylalanine ammonia lyases. These lyases initiate the accumulation of phenylpropanoids in ***Marchantia polymorpha*** (Figure 1-Figure 12). Wounding induces the biosynthesis of luteolin, apigenin, and isoriccardin C, all of which are biosynthesized through the phenylpropanoid pathway.

Ishida *et al*. (2022) found that diminished auxin signalling triggers the cellular reprogramming needed for regeneration in ***Marchantia polymorpha*** (Figure 1-Figure 12). Auxin is produced in apical cells, and removal of the apex enhances regeneration. Addition of auxin inhibits regeneration. They were able to identify the gene responsible for the cell proliferation needed for regeneration.

Mechanisms that control regeneration are also at play in controlling apical dominance (Figure 20) in ***Marchantia polymorpha*** (Figure 1-Figure 12). Davidonis and Munroe (1972) found that the larger lobe in this dichotomously branching plant is always the one closest to the midrib. If these two lobes are separated by a cut while still in an early stage of lobe growth, the smaller lobe is no longer inhibited and is able to grow to equal size. Adding the auxin IAA to the smaller lobe after cutting will re-establish the dominance of the other lobe. The researchers suggested "that the type of neighbor lobe dominance in ***Marchantia*** resulting in its typical fan-shaped growth habit is maintained by auxin through a differential sensitivity of the two neighbors to auxin inhibition."

Figure 170. ***Marchantia polymorpha*** gemmae cups and antheridiophores in Europe; note the dead thalli and the red gemmae cups that indicate stress. At the same time, the apical portions continue to grow. Photo by Michael Lüth, with permission.

Maravolo *et al*. (1975) traced the transport of labelled IAA in the thallus of ***Marchantia polymorpha*** (Figure 1-Figure 12). There was a marked dominance of the hormone in the primary lobe. Movement to the secondary lobe could be enhanced by disruption of the conductive tissue or by removing the primary apex. Gibberellin and cytokinin also increased the activity of the IAA in the subdominant lobe, indicating that gradients of these three hormones might serve as growth regulators and these could be established independently at each apex.

Bhargava and Chauhan (1978) reported a dichotomously branched vegetative thallus at the tip of a gametophore stalk. I have to wonder if this is a germinated gemma, such as that observed by Li Zhang for ***Marchantia emarginata*** (Figure 171) rather than a branch.

Figure 171. ***Marchantia emarginata*** ssp. ***tosana***, in Guangdong, S. China, with germinated gemmae and young thalli with gemmae cups growing on male receptacle arms. Photo courtesy of Li Zhang.

Kubota *et al*. (2013) were successful in achieving ***Agrobacterium***-mediated (Figure 172) transformation in regenerating thalli of ***Marchantia polymorpha*** (Figure 1-Figure 12). Developmental timing is important to the success of this transformation. Previously, efficient ***Agrobacterium***-mediated transformation had only been accomplished with sporelings. Iwakawa *et al*. (2021) further described a protocol useful for using this method in ***M. polymorpha***. GUS (β-glucuronidase) activity was detected 2 days after infection and became saturated after 3 days.

Figure 172. SEM of ***Agrobacterium tumefaciens***; the genus ***Agrobacterium*** is used for genetic transformation and has been developed as a tool in ***Marchantia polymorpha***. Photo from CDC, through public domain.

Shibaya and Sugawara (2007) found that the protoplasts of ***Marchantia polymorpha*** (Figure 1-Figure 12) could regenerate new cell walls in the initial culture, but the survival rate then decreased rapidly. β-glucosyl Yariv reagent (βglcY) could suppress this reduction in the survival rate. This substance binds to arabinogalactan proteins (AGPs) and does not increase survival except when added during the incipient cell wall regeneration. The researchers suggested that AGPs were involved in cell wall regeneration. Adding activated charcoal to the medium also permitted the cells to divide vigorously. It appears that AGPs and β-1,3-glucan are important in the survival and subsequent cell division of regenerated cells of ***M. polymorpha*** protoplast cultures.

Harashima and Ono (1991) tested the long-term culturing of ***Marchantia polymorpha*** (Figure 1-Figure 12). They found that after years of suspended culture they regained regeneration potential. The loss of morphogenetic potential in some was correlated with chromosome aberrations. They were able to maintain gemmae cultures for 213 months and spore cultures for 64 months.

Takenaka *et al*. (2000) used ***Marchantia polymorpha*** (Figure 1-Figure 12) for direct particle bombardment with plasmid pMT. They produced hygromycin-resistant cell masses that developed into hygromycin-resistant thalli. These modified thalli transmitted the genetic modification to their gemmae for three generations. Hence, this could be a valuable tool for molecular analysis of this species and others.

Role

The role of aquatic bryophytes in accumulating pollutants is well known. Even ***Marchantia polymorpha*** (Figure 1-Figure 12) has been tested for its ability to purify water (Baltazar Pereda & Rebaza 2021). The researchers were concerned that there is no treatment for the wastewater for a sewage system in La Libertad. The water is used to irrigate stem crops, but it causes bad odors and endangers the health of those living around the canal. Both the water hyacinth (***Eichhornia crassipes*** – Figure 173) and duckweed (***Lemna minor*** – Figure 174) showed an excellent removal efficiency, improving oxygen and diminishing coliforms. However, the ***Marchantia polymorpha*** failed to make significant changes in water quality.

Figure 173. ***Eichhornia crassipes*** (water hyacinth), a species that is much more efficient at removing pollutants than is ***Marchantia polymorpha***. Photo by Wouter Hagens, through public domain.

Figure 174. ***Lemna minor*** (duckweed), a species that is much more efficient at removing pollutants than is ***Marchantia polymorpha***. Photo by Barbarossa, through Creative Commons.

Briggs (1972) reported that this species contains higher levels of lead than bryophytes that had been used in previous studies. Large quantities of plants could be grown quickly from gemmae, then exposed in a lead-polluted atmosphere to determine levels in the plants, and by extrapolation, the environment.

Accumulation of heavy metals characterizes many bryophytes (Cahuana & Aduvire 2019). Sharma (2007) placed ***Marchantia polymorpha*** (Figure 1-Figure 12) in moss bags to monitor pollution in several areas to compare pollutants. Plants accumulated the highest levels (2276 µg g^{-1} dry weight) of lead in summer. But ***Marchantia*** lacks the high level of surface area seen in most mosses, making Sharma conclude that it a less useful accumulator than we might find in mosses and leafy liverworts.

Perhaps the most useful role of ***Marchantia polymorpha*** (Figure 1-Figure 12) is its use in the laboratory. The gemmae (Figure 153-Figure 165) of liverworts such as ***M. polymorpha*** represent isogenic progeny that can be used to experiment with gene expression (Kubota *et al*. 2013). The most common system used is to supply ***Agrobacterium*** (Figure 20) to regenerating thalli produced from these gemmae. These bacteria are able to transfer genes into the liverwort.

Interactions

Seed plants have an array of structural defenses as well as biochemical defenses against herbivores. Bryophytes, on the other hand, generally lack structural defenses, at least the elaborate ones such as spines, thick cuticle, and dense, lignified tissues. But the bryophytes, instead, are endowed with an extremely varied array of biochemical defenses.

Despite knowing about the wide diversity of secondary compounds in bryophytes, especially in liverworts, the research on their functions in the ecosystem and their sources, particularly in cooperation with microorganisms, has been rather neglected until recently (Stelmasiewicz *et al*. (2021). Noting that bryophytes produce many compounds unique to bryophytes, Stelmasiewicz and coworkers used a volatile extract to isolate the volatile compounds produced by the ***Marchantia polymorpha*** (Figure 1-Figure 12)-microorganism symbiosis. They isolated cuparane-, chamigrane-, acorane-, and thujopsane-type sesquiterpenoids from ***Marchantia polymorpha***. These compounds proved to be active against some types of human cancer. But what do they do for the liverwort?

Poveda (2020a) touted the use of ***Marchantia polymorpha*** (Figure 1-Figure 12) as a model organism in studies of plant-microorganism interactions. He reviewed the published literature on these interactions.

Bacterial Interactions

As new studies are emerging, we are learning of the great dependence of bryophytes on other organisms. Bacteria are among these partners. Kutschera and Koopmann (2005) found that epiphytic methylobacteria promote the growth of ***Marchantia polymorpha*** (Figure 1-Figure 12). While living on the surfaces of plants these bacteria secrete cytokinins. The bacterial extracts had no effect on seeds of maize or sunflower, but did promote the growth of isolated ***M. polymorpha*** gemmae (Figure 153-Figure 165) on agar plates.

Alcaraz *et al*. (2018) identified ***Bryobacter, Lysobacter*** (Figure 175), ***Methylobacterium*** (Figure 176), ***Paenibacillus*** (Figure 177), ***Pirellula***, ***Rhizobium*** (Figure 178-Figure 179), and ***Steroidobacter*** from ***Marchantia polymorpha*** (Figure 1-Figure 12) as well as from ***M. paleacea*** (Figure 14; see part 1 of this chapter). These plant symbionts are known for plant-growth promotion, complex exudate degradation, nitrogen fixation, methylotrophs, are disease-suppressive bacteria, and are hosted within the plant thallus.

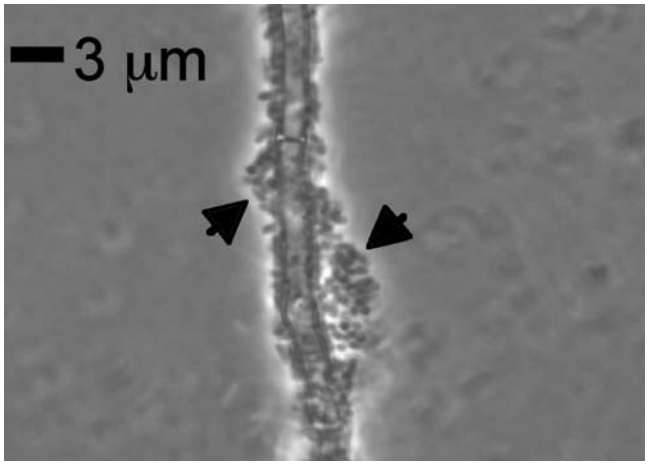

Figure 175. ***Lysobacter*** hyphae, a genus that is sometimes associated with ***Marchantia polymorpha***. Photo by Don Kobayashi, through Creative Commons.

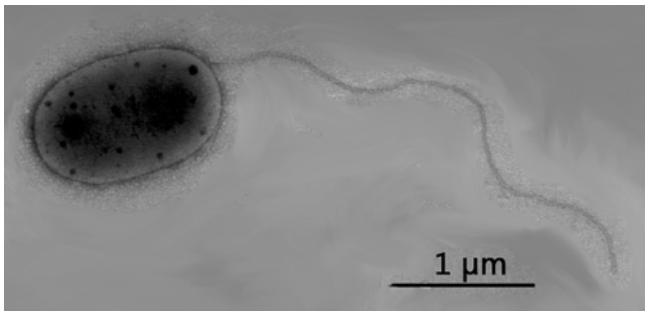

Figure 176. ***Methylobacterium jeotgali***; ***Methylobacterium*** is a genus that is sometimes associated with ***Marchantia polymorpha***. Photo from Aslam *et al*. 2007, through Creative Commons.

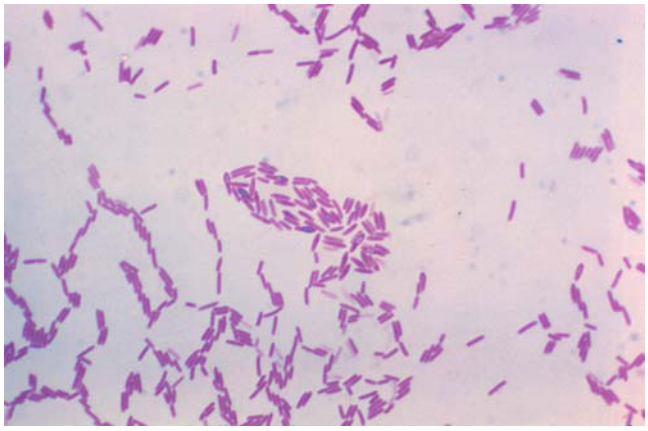

Figure 177. ***Paenibacillus polymyxa***; ***Paenibacillus*** is a genus that is sometimes associated with ***Marchantia polymorpha***. Photo from CDC, through public domain.

Figure 178. ***Rhizobium*** root nodule on *Vicia faba* (broad bean) roots; ***Rhizobium*** is a nitrogen fixer and known associate of ***Marchantia polymorpha***. Photo by Whitney Cranshaw, through Creative Commons.

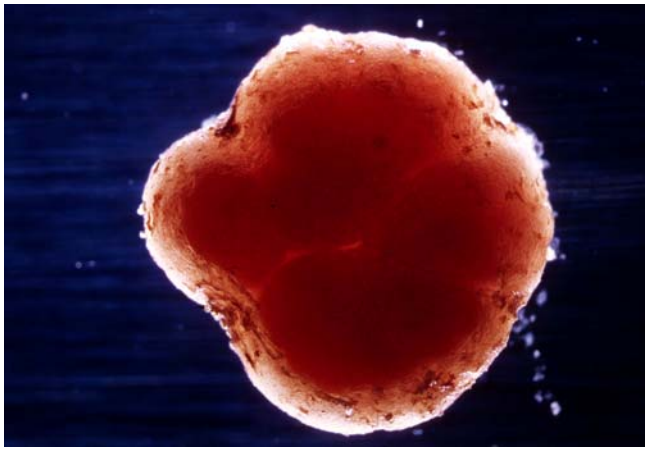

Figure 179. ***Rhizobium*** nodule, showing typical red color. Photo from CSIRO, through Creative Commons.

Bryophytes are used in some cultures as medicinal plants. Some groups of Indonesian people use ***Marchantia polymorpha*** (Figure 1-Figure 12) as a traditional medicine to treat skin infections (Ramadhan & Agustien 2019). The species has flavones and flavone glycosides as well as simple terpenoids that are able to inhibit the multiplication of bacteria. These researchers chose to isolate endophytic bacteria from ***Marchantia polymorpha.*** Six species of endophytic bacteria that have the potential to produce antibiotics were successfully isolated from the thallus; these bacteria were successful against ***Staphylococcus aureus*** (Figure 180).

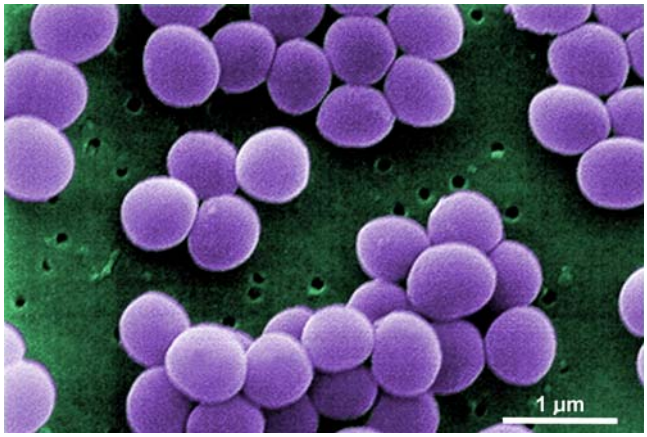

Figure 180. Colorized SEM of bacterium ***Staphylococcus aureus***, a species that is inhibited by antibiotics produced by other bacteria endophytic in ***Marchantia polymorpha***. Photo by Janice Haney Carr, CDC, through public domain.

Himanshu *et al*. (2007) found that acetone-soluble extracts of ***Marchantia polymorpha*** (Figure 1-Figure 12) had antibiotic activity against the Gram negative bacteria ***Escherichia coli*** (Figure 16) and ***Salmonella typhi*** (Figure 181) and two fungi ***Aspergillus niger*** (Figure 182) and ***Candida albicans*** (Figure 183-Figure 184), all human pathogens. Such antibiotic activity makes this species of interest for finding applications to replace the ever-growing number of antibiotics that are helping to create "super bugs" with antibiotic resistance. But do they help the bryophyte? One indication that they might not, at least as antibacterial agents, is that the water soluble extracts did not show any inhibitory effects on the pathogens tested.

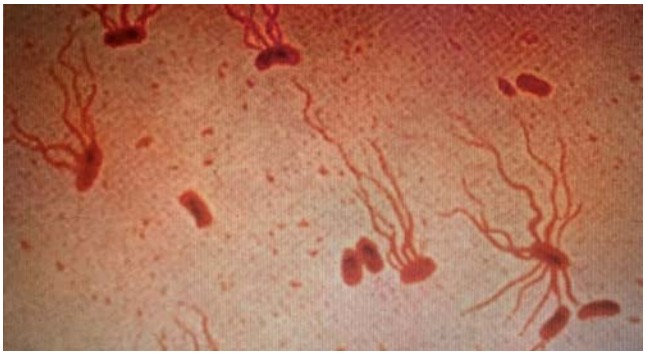

Figure 181. ***Salmonella typhi*** with flagellar stain, a species of bacteria that experiences antibiotic activity from acetone-soluble extracts of ***Marchantia polymorpha***. Photo by Microbewriter, through Creative Commons.

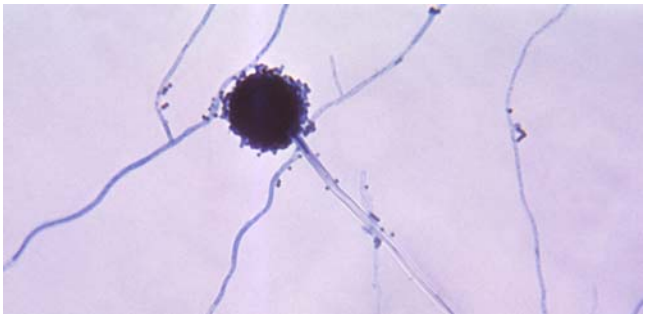

Figure 182. ***Aspergillus niger***, a species of fungus that experiences antibiotic activity from acetone-soluble extracts of ***Marchantia polymorpha***. Photo from CDC, through Creative Commons.

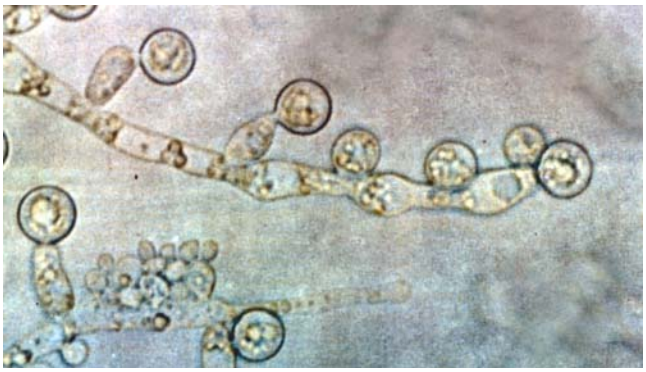

Figure 183. ***Candida albicans***, fungus that experiences antibiotic activity from acetone-soluble extracts of ***Marchantia polymorpha***. Photo by Graham Colm, through Creative Commons.

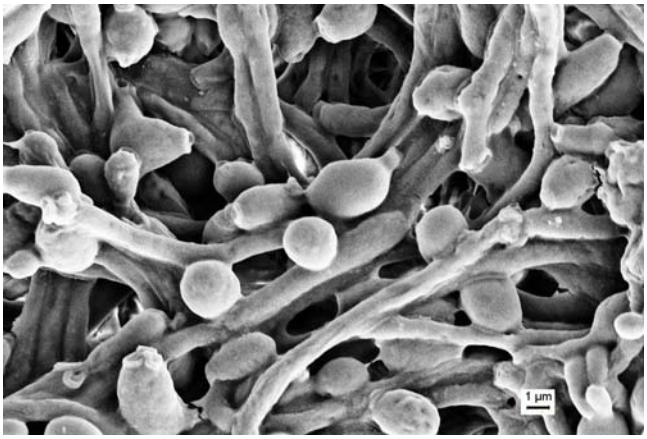

Figure 184. SEM of ***Candida albicans***. Photo by Vader1941, through Creative Commons.

Using specimens from Vietnam, Son *et al*. (2020) isolated lunularin, marchantin A, isoriccardin C, luteolin, and apigenin from ***Marchantia polymorpha*** (Figure 1-Figure 12). Isoriccardin C had "remarkable" antibacterial activity against ***Staphylococcus epidermidis*** (Figure 185). Several extracts exhibited anticancer activity.

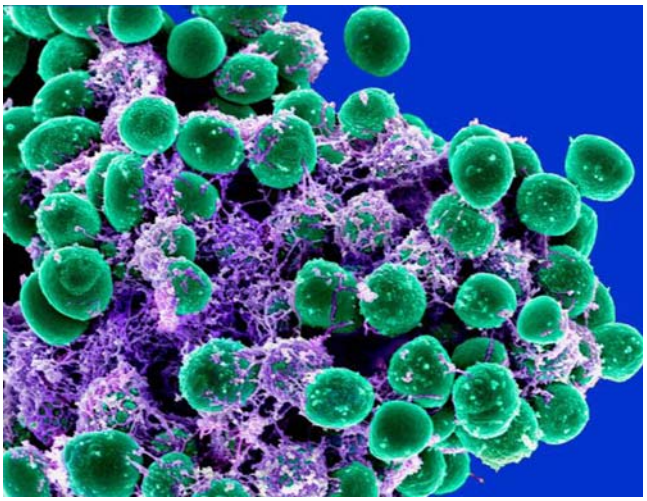

Figure 185. ***Staphylococcus epidermidis***, a species that experiences strong negative effects from isoriccardin C from ***Marchantia polymorpha***. Photo from NIAID, through Creative Commons.

Ivković *et al*. (2021) identified terpenes, oils, sugars, and bis-bibenzyls in methanol extracts of ***Marchantia polymorpha*** (Figure 1-Figure 12). These extracts were effective in inhibiting Gram-positive bacteria but had no effect on Gram-negative bacteria.

Mewari and Kumar (2008) tested antibacterial activity using crude methanol and flavonoid extracts of ***Marchantia polymorpha*** (Figure 1-Figure 12) against three strains of bacteria [***Escherichia coli*** (Figure 16), ***Proteus mirabilis*** (Gram negative; Figure 186), and ***Staphylococcus aureus*** (Figure 180) (Gram positive)] and four of fungi [***Aspergillus flavus*** (Figure 187), ***A. niger*** (Figure 182), ***Candida albicans*** (Figure 183-Figure 184), and ***Trychophyton mentagrophytes*** (Figure 188)]. All the microorganisms proved to be sensitive to all of the extracts, suggesting that ***M. polymorpha*** had a good potential as a source of antimicrobial drugs.

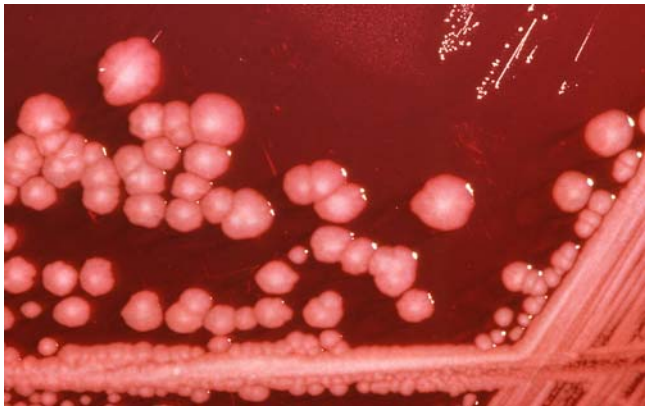

Figure 186. ***Proteus mirabilis***, a bacterial species that is sensitive to crude methanol and flavonoid extracts of ***Marchantia polymorpha***. Photo from CDC, through public domain.

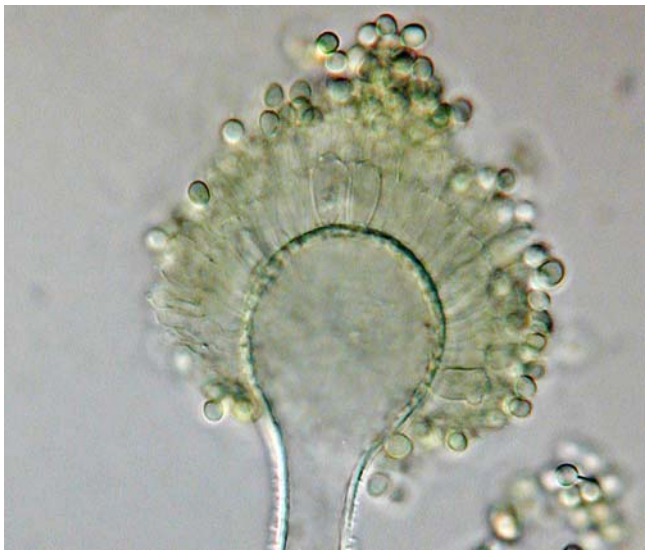

Figure 187. ***Aspergillus flavus***, fungal species that is sensitive to crude methanol and flavonoid extracts of ***Marchantia polymorpha***. Photo from Medmyco, through Creative Commons.

Figure 188. ***Trichophyton mentagrophytes***, fungal species that is sensitive to crude methanol and flavonoid extracts of ***Marchantia polymorpha***. Photo by Dr. Libero Ajello, CDC, through public domain.

Wang *et al*. (2016) found that the total flavonoid content of the archegoniophore was ten times that of the thallose gametophyte. This correlated with greater bio-activity in the archegoniophore, potentially protecting the reproductive structure from bacteria, fungi, and perhaps even herbivory.

Most of the work on antibacterial activity by secondary compounds in bryophytes has been done on human pathogens. The question remains, what can they do for bryophytes? De *et al*. (2015) noted that bryophytes lack the mechanical protections available to tracheophytes and that instead use secondary metabolites as protectants. If such is the case, then we should see greater selection for higher concentrations in bryophytes from habitats where there are more herbivores or pathogens present. However, few studies have attempted to address this hypothesis. De and coworkers compared secondary compounds from ***Marchantia polymorpha*** (Figure 1-Figure 12) from five different altitudes in Darjeeling Himalayas. To my surprise, they found higher antibacterial activity at higher altitudes. This suggests to me that their antibacterial activity is not the most important factor operating in selection for these secondary compounds.

Protozoa Interactions

Protozoa are also inhibited by extracts from ***Marchantia polymorpha*** (Figure 1-Figure 12). Jensen *et al*. (2012) found that marchantin A extracted from this liverwort inhibited the proliferation of the protozoan ***Plasmodium falciparum*** (Figure 189). ***Trypanosoma brucei rhodesiense*** (Figure 190), ***T. cruzi*** (Figure 191), and ***Leishmania donovani*** (Figure 192), all human pathogens, likewise experienced inhibition by marchantin A.

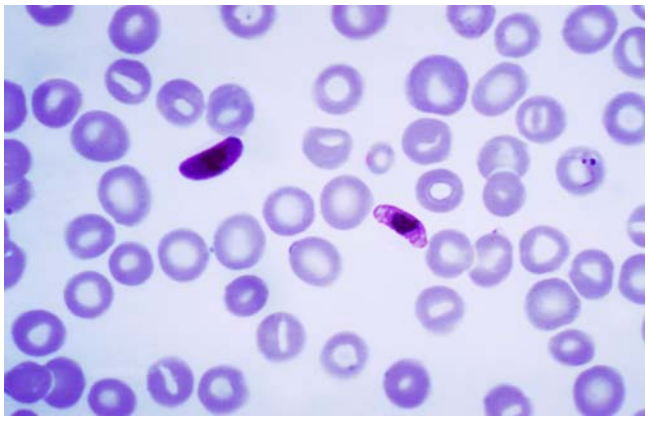

Figure 189. ***Plasmodium falciparum***, protozoan inhibited by marchantin A extracted from ***Marchantia polymorpha***. Photo from CDC, through public domain.

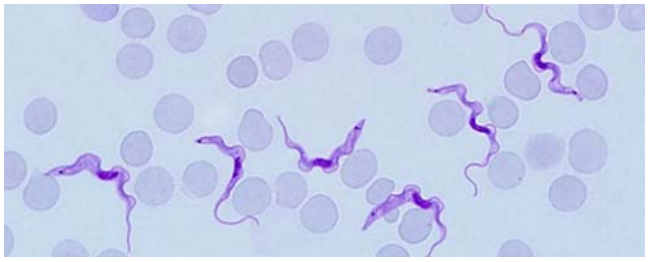

Figure 190. ***Trypanosoma brucei***, protozoan inhibited by marchantin A extracted from ***Marchantia polymorpha***. Photo from CDC, through public domain.

Figure 191. ***Trypanosoma cruzi***, protozoan inhibited by marchantin A extracted from ***Marchantia polymorpha***. Photo by Dr. Myron G. Schultz, CDC, through public domain.

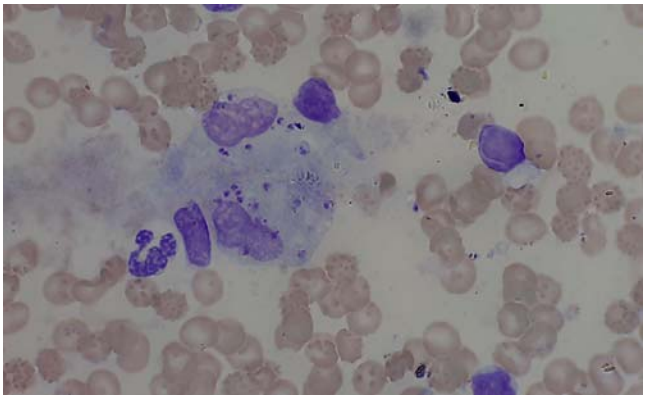

Figure 192. ***Leishmania donovani***, protozoan inhibited by marchantin A extracted from ***Marchantia polymorpha***. Photo by Ajay Kumar Chaurasiya, through Creative Commons.

Fungal Interactions

The associations of fungi with bryophytes was a long-neglected topic in bryology. In fact, many seemed to assume that fungi could not live with bryophytes, or that the bryophytes had too low a nutrient concentration to be of value to the fungi. But this view has now been disproved.

endophytes

Döbbeler (1979) found fungal infections in the rhizoids of ***Marchantia polymorpha*** (Figure 1-Figure 12). Duckett and Ligrone (2003) further reported that the living smooth rhizoids of **Marchantiales** contained the hyphae of fungal endophytes (Figure 193). Benkert (1998) reported a fungus (***Octospora inthacaensis***) growing on ***M. polymorpha***. But what does this relationship mean for the bryophyte?

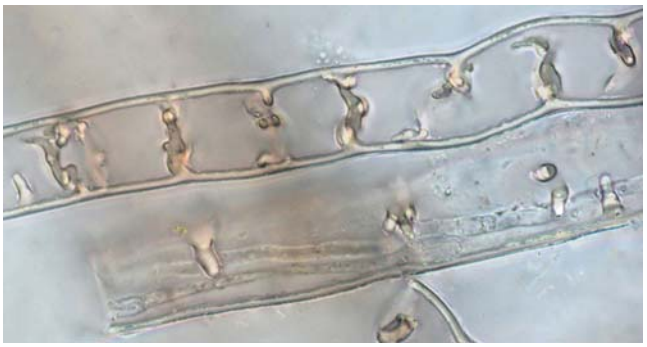

Figure 193. Rhizoids of ***Marchantia polymorpha*** with fungus in lower rhizoid. Photo by Walter Obermayer, with permission.

Döbbeler (2002) reported that the Ascomycetes (fungi) growing on the gametophytes of bryophytes typically did not form ascomata on general locations on their bryophyte hosts, but instead occupied distinct locations that were specific for the host species. These microsites usually offered protection against rapid water loss by the fungus and permitted enough exposure to permit unhindered spore dispersal of the fungus by air currents. Among the thallose liverworts, the ascomata were typically immersed in the spongy thalli. But what do they do to or for the liverwort?

Fungal actions may be subtle, and certainly fungi can inhabit ***Marchantia polymorpha*** (Figure 1-Figure 12). Guminska and Mierzenska (1992) reported that the fungus ***Loreleia marchantiae*** (=*Gerronema marchantiae*; Figure 194) was associated with this species and with ***Nostoc*** sp. (**Cyanobacteria**).

Figure 194. ***Loreleia marchantiae*** growing with ***Marchantia polymorpha***. Photo by Alexey Sergeev, with permission.

Nelson and Shaw (2019) found a very diverse fungal community that was distinct between patches of ***Marchantia polymorpha*** (Figure 1-Figure 12). Only a few core fungi were the same across widely separated populations across the USA. However, they found that the two methods used detected different species.

symbiosis?

Trees are usually dependent on fungal partners in their roots as a means of scavenging nutrients from a much larger soil volume than that available to roots. Hanke and Rensing (2010) considered that ***Marchantia polymorpha*** (Figure 1-Figure 12), with what is now a sequenced genome, provided many genetic tools by which to establish the association of fungi such as ***Glomus intraradices*** with gametophyte plants, including culturing, infection strategies, and staining procedures.

Marchantia species, including ***M. polymorpha*** ssp. ***montivagans*** (Figure 34) (Ligrone *et al*. 2007), often form mycorrhizal associations (Bowman *et al*. 2016). However, such associations are not known in ***M. polymorpha*** ssp. ***polymorpha*** or ssp. ***ruderalis*** (Figure 6-Figure 8, Figure 17-Figure 19). Bowman and coworkers (Bowman *et al*. 2017) attribute this independence to increased transport capacity in the subspecies, permitting them to be weedy colonizers of newly disturbed habitats.

pathogens

Certainly not all fungi have a friendly relationship with the bryophytes. Verkley *et al*. (1997) reported the ascomycete ***Bryoscyphus atromarginatus*** (Figure 195) as a new species parasitizing the thallus of ***Marchantia polymorpha*** (Figure 1-Figure 12) in the Netherlands. The type specimen of the species named as ***Bryoscyphus marchantiae*** (Figure 196) was actually collected from ***Reboulia haemisphaerica*** (Figure 197). The description given by Naumov (1964) of the collection he reported as ***Hymenoscyphus marchantiae*** (Figure 198) on ***M. polymorpha*** agrees well with the new species described by Verkley *et al*. Naumov commented that it appeared that this could be a new species.

Figure 195. ***Bryoscyphus atromarginatus*** growing on thallus of ***Marchantia***. Photo ©Michel Hairaud, through Creative Commons.

Figure 196. ***Bryoscyphus marchantiae*** on ***Marchantia***. Photo ©Iain Munro, through Creative Commons.

Figure 197. ***Reboulia hemisphaerica***, apparently also another host substrate for ***Bryoscyphus atromarginatus***. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 198. ***Hymenoscyphus kathiae*** on submerged twig of *Alnus glutinosa*; ***Hymenoscyphus marchantiae*** can inhabit ***Marchantia polymorpha***. Photo ©Nick Aplin, through Creative Commons.

Fraiture and Ertz (2007) reported that the fungus ***Didymosphaeria marchantiae*** (Figure 199) was a parasite on ***Marchantia polymorpha*** (Figure 1-Figure 12).

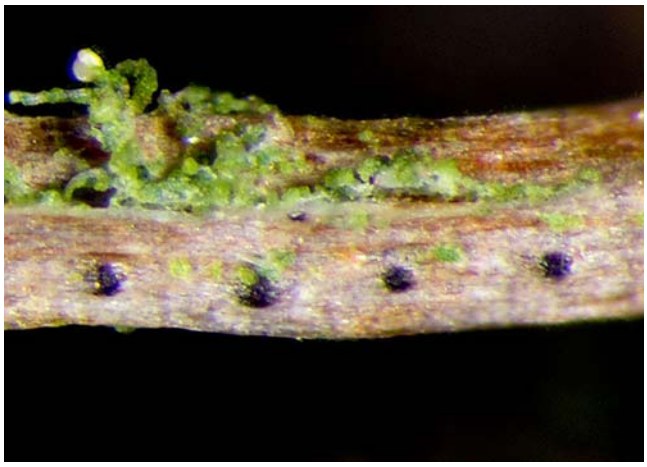

Figure 199. ***Didymosphaeria marchantiae*** infecting leafy liverwort, but also known to be a parasite on ***Marchantia polymorpha***. Photo by Dragiša Savić, with permission.

Nelson (2017; Nelson *et al*. 2018) noted the lack of studies on fungal endophyte interactions with bryophytes while at the same time realizing that the reactions of the plants to these organisms is quite varied. They found that such fungi in ***Marchantia polymorpha*** (Figure 1-Figure 12) ranged from "aggressively pathogenic to strongly growth-promoting." Nevertheless, most of them seemed to cause no change in host growth. Furthermore, those that promoted growth were dependent on nutrient concentrations and their effects on growth were inhibited by inoculation of the liverwort with multiple fungi. Some of the fungi that are known as pathogens in tracheophytes were actually beneficial to the liverworts.

With the large arsenal of secondary compounds, we should consider it to be likely that some of these are effective against fungal pathogens. Takikawa *et al*. (2014) inoculated several powdery mildews on the thallus and gemmae (Figure 153-Figure 165) of ***Marchantia polymorpha*** (Figure 1-Figure 12). The conidia and germ tubes of ***Erysiphe trifoliorum*** (Figure 200) were destroyed. The germ tube tip was destroyed in four hours when it reached the gemma leaf surface. After six hours the conidial bodies were destroyed as well. On the other hand, ***Oidium neolycopersici*** (see Figure 201) continued growth with no destruction of conidia and produced normal appressoria on the surface of the gemmae.

Figure 200. ***Erysiphe trifoliorum*** on ***Trifolium pratense*** leaves; this fungus is destroyed when inoculated on thallus or gemmae of ***Marchantia polymorpha***. Photo by John Plischke, through Creative Commons.

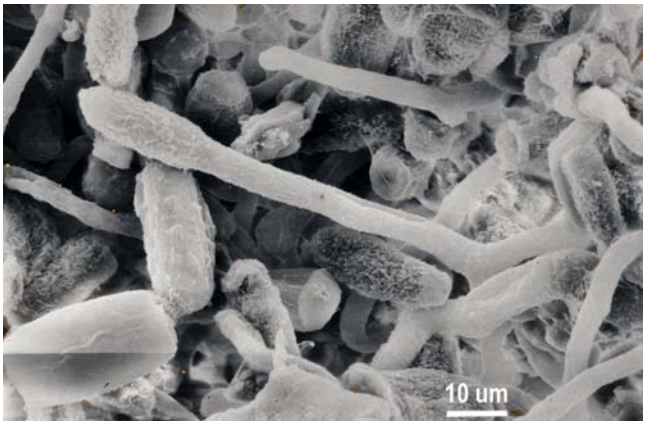

Figure 201. SEM of ***Oidium*** sp; ***Oidium neolycopersici*** continued growth with no destruction of conidia and produced normal appressoria on surface of gemmae of ***Marchantia polymorpha***. Photo by Gerald Holmes, through Creative Commons.

Peumans *et al*. (2007) found the surprising result that a **lectin** (protein that binds to carbohydrates – features that lectins use to defend plants in nature may cause problems during human digestion; lectins resist being broken down in gut and are stable in acidic environments, features that protect lectin-containing plants in nature) identified in ***Marchantia polymorpha*** (Figure 1-Figure 12) had never been found in any plant, but that instead it closely resembles one from the common edible mushroom ***Agaricus bisporus*** (Figure 202), *i.e.*, it is a lectin that was hitherto considered to be exclusive to fungi. It was also confirmed in the moss ***Syntrichia ruralis*** (Figure 203).

Figure 202. ***Agaricus bisporus***, common edible mushroom that has lectin similar to one found in ***Marchantia polymorpha***. Photo by Мыць Денис, through Creative Commons.

Figure 203. ***Syntrichia ruralis***, species that shares same lectin as that found in ***Marchantia polymorpha***. Photo by Alexis Orion, through Creative Commons.

Carella *et al*. (2019) explored the molecular response of ***Marchantia polymorpha*** (Figure 1-Figure 12) to oomycete infection. These early land plants necessarily had to defend against pathogens with their new exposure to land. We know of many pathogens and defenses in tracheophytes, but we know little about the plant-pathogen interactions in these early land plants. Whereas we have explored their medical use and even uses as fungicides for tracheophytes, we know relatively little about their functions in the bryophytes that produce them. Carella and coworkers traced the response of this liverwort to the oomycete pathogen ***Phytophthora palmivora*** (Figure 204). They found that the liverwort shared a set of orthologous microbe-responsive genes with tracheophytes. These include members of the phenylpropanoid metabolic pathway. Using both knockout and induction techniques, they determined that MpMyb14 leads to the accumulation of anthocyanin-like pigments (**auronidin**) while greatly enhancing the resistance of ***Marchantia polymorpha*** to ***Phytophthora palmivora*** infection. The auroidin prevented the penetration of the fungal hyphae into the pigmented portions of the liverwort.

Figure 204. ***Phytophthora palmivora*** infecting papaya; ***Marchantia polymorpha*** was used to identify the mechanism of resistance to this plant pathogen. Photo by Scot Nelson, through Creative Commons.

Gahtori and Chaturvedi (2011) used methanol and chloroform extracts to test the activity of ***Marchantia polymorpha*** (Figure 1-Figure 12) against three bacterial and four fungal species. The extracts exhibited antimicrobial activity with potency that differed among organisms that were pathogenic to both plants and animals. Some were inhibitory toward multiple organisms, and others showed potential.

In other experiments, Mewari and Kumar (2011) made similar tests and found that ***Marchantia polymorpha*** (Figure 1-Figure 12) completely inhibited the mycelial growth of the fungal pathogen ***Rhizoctonia solani*** (Figure 205). Furthermore, most extracts also caused 100% inhibition of spore germination of fungal pathogens ***Alternaria solani*** (Figure 206) and ***Fusarium oxysporum*** (Figure 207).

Figure 205. ***Rhizoctonia solani***, fungal species that is completely inhibited by extracts of ***Marchantia polymorpha***. Photo by Gerald Holmes, through Creative Commons.

Figure 206. ***Alternaria solani*** on tomato leaf. Extracts of ***Marchantia polymorpha*** completely inhibit spore germination of this fungal pathogen. Photo from USDA Cooperative Extension, through Creative Commons.

Figure 207. ***Fusarium oxysporum*** on *Cucumis sativa*; extracts of ***Marchantia polymorpha*** completely inhibit spore germination of this fungal pathogen. Photo by Jerzy Opioła, through Creative Commons.

In China, Niu *et al*. (2006) isolated seven bis[bibenzyl]-type macrocycles, including three new ones. They assessed their antifungal activities against ***Candida albicans*** (Figure 183-Figure 184), using TLC bioautography. This fungal species is an opportunistic pathogenic yeast that is the most prevalent cause of fungal infections in humans. Several of the compounds proved to be active against this fungus.

Purkon *et al.* (2022) reported the medicinal use of ***Marchantia*** in China, North America, Ancient Greece, and Indonesia for treatment of open wounds, burns, hepatotoxicity (damage to liver caused by medicine, chemical, or herbal or dietary supplement), and infection prevention.

Matsui *et al*. (2020) found antagonism between salicylic acid and jasmonate in the fungal pathogen interaction with ***Marchantia polymorpha*** (Figure 1-Figure 12). They isolated ***Bjerkandera adusta*** (Figure 208), ***Irpex lacteus*** (Figure 209), and ***Phaeophlebiopsis peniophoroides*** (Figure 210) from diseased ***M. polymorpha***. They found that salicylic acid promotes infection by ***I. lacteus***, but this action is suppressed when jasmonate is treated at the same time.

Figure 208. ***Bjerkandera adusta***, species that has been isolated from diseased ***Marchantia polymorpha***. Photo by James K. Lindsey, with permission.

Figure 209. ***Irpex lacteus***, species that has been isolated from diseased ***Marchantia polymorpha***. Jasmonate can stop the infection. Photo by Otto Miettinen, through Creative Commons.

Figure 210. *Phaeophlebiopsis ravenelii*; ***Phaeophlebiopsis peniophoroides*** is a species that has been isolated from diseased ***Marchantia polymorpha***. Photo by James K. Lindsey, with permission.

Hipol and Broñola-Hipol (2016) screened 22 fungal associates of ***Marchantia polymorpha*** (Figure 1-Figure 12) for their carboxyl esterase activity. Half were endophytes and half were epiphytes on the liverwort. All of the isolates produced this enzyme, with the fungus ***Colletotrichum boninense*** (see Figure 211) producing the lowest levels of the enzyme and ***Nodulisporium*** sp. (Figure 212) produced the highest levels.

Figure 211. *Colletotrichum lindemuthianum*; ***Colletotrichum boninense*** produced lowest levels of carboxyl esterase activity among 22 fungi isolated from association with ***Marchantia polymorpha***. Photo by David B. Langston, through Creative Commons.

Figure 212. ***Nodulisporium cecidiogenes*** on rotten wood; species of ***Nodulisporium*** produced highest levels of carboxyl esterase activity among 22 fungi isolated from association with ***Marchantia polymorpha***. Photo by Alexey Sergeev, with permission.

Poveda (2020b) asked if the arbuscular-mycorrhizal fungal (AMF) association with ***Marchantia polymorpha*** ssp. ***ruderalis*** (Figure 6-Figure 8) was beneficial or harmful. Despite all the studies on this species, this is one of the many questions remaining unanswered. They found that *in vitro*, the interaction is detrimental, causing reduced growth and tissue viability, with only those elements involved in plant defenses increasing in nutritional content. These changes were coupled with increases in reactive oxygen species (ROS) content. One such fungus is ***Rhizophagus fasciculatus*** (Figure 213) – a species present only when there is evidence of thallus damage. Hence, this fungus appears to be a pathogen to ***Marchantia polymorpha*** ssp. ***ruderalis***. Further examination of fungi with bryophytes could reveal interesting symbiotic relationships, modes of infection, and defenses against fungi. ***Marchantia polymorpha*** (Figure 1-Figure 12) is large enough, cultures easily, and is known to respond in a variety of ways to fungal invaders. Hence, it would be a good initial test organism to help us understand these relationships and their effects in their ecosystem.

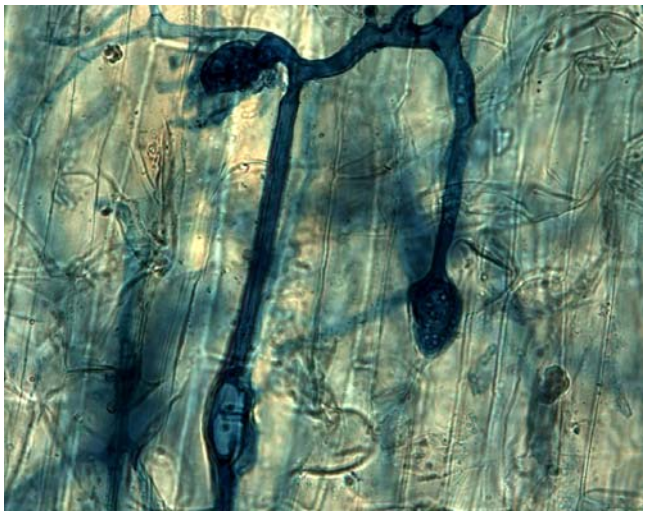

Figure 213. *Rhizophagus irregularis*; ***Rhizophagus fasciculatus*** is fungal pathogen on ***Marchantia polymorpha*** ssp. ***ruderalis***. Photo by Mylène Durant, through Creative Commons.

Invertebrate Interactions

Herbivory (Figure 214) on liverworts seemed to be a blind spot in older bryological studies, but recent reports tell us it is real. Sawangproh *et al*. (2016) reported the feeding of ***Scatopsciara cunicularius*** (**Diptera**: **Sciaridae**) larvae on ***Marchantia polymorpha*** (Figure 1-Figure 12). They found that larvae fed at 12ºC fed more slowly than those at 22ºC, but those at the lower temperature fed over a longer period of time, ultimately causing more damage to the liverwort. The researchers suggested using these larvae to control the invasion of the liverwort in plant nurseries and greenhouses. I wonder what other plants they eat?

Figure 214. ***Marchantia polymorpha*** female eaten on one of the receptacle fingers. Photo by Li Zhang, with permission.

Koeduka *et al*. (2022) found that allene oxide synthase (AOS) from ***Marchantia polymorpha*** (Figure 1-Figure 12) is important in inhibiting the survival rate and oviposition of the spider mite ***Tetranychus urticae*** (see Figure 215). When mutants lacking the AOS gene were subjected to these spider mites, survival of the mites was greater than in the wild type. Their research indicated that defense system signalling pathways respond to spider mite presence.

Figure 215. ***Marchantia polymorpha*** gemmae cups with mite, possibly spider mite. Photo By Bernard de Cuyper, with permission.

Some invertebrates commonly live among bryophytes, ***Marchantia polymorpha*** (Figure 1-Figure 12) included. A common bryophyte inhabitant is the isopod (Figure 216). In some cases these might actually eat the bryophytes. In other cases, there is no evidence of herbivory. Spiders also build webs (Figure 217), perhaps catching some of the other inhabitants of the thallus community.

Figure 216. ***Marchantia polymorpha*** and isopod; there does not seem to be any evidence of herbivory – yet. Photo by Walter Obermayer, with permission.

Figure 217. ***Marchantia polymorpha*** males with gemmae cups and spider web. Photo by Nancy Leonard, with permission.

The importance of bryophyte herbivory in the ecosystem is virtually unknown. This seems to be particularly true for ***Marchantia polymorpha*** (Figure 1-Figure 12). As the climate shifts and herbaceous plant communities change, it is possible some herbivores could shift to consumption of bryophytes. Few studies have addressed the effects of temperature or precipitation patterns on the interaction of invertebrates with bryophytes.

Tracheophyte Interactions

Little has been written about the interaction between bryophytes and tracheophytes. Bryophytes are not good competitors with tracheophytes because of the small size of

the bryophytes. How, then, do the tiny bryophytes survive in habitats dominated by tracheophytes?

Whittemore (1991) suggested that bryophytes such as those in the **Marchantiales** might be toxic not only to herbivores and pathogens, but also to competing plants such as tracheophytes. On the other hand, Asakawa *et al*. (1982) found that compounds from the tracheophyte family Apiaceae could inhibit the growth of ***Marchantia polymorpha*** (Figure 1-Figure 12).

Nakayama *et al*. (1996) tested the inhibitory effects of lunularic acid and its analogs on the growth of ***Marchantia polymorpha*** (Figure 1-Figure 12), ***Rorippa nasturtium-aquaticum*** (watercress; Figure 218), and ***Phleum pratense*** (timothy grass; Figure 219). The analogs proved to be more inhibitory than lunularic acid, suggesting that the liverworts that produce this hormone might have less growth inhibitory activity than tracheophytes, or they are somehow protected from its inhibitory effects.

Figure 218. ***Rorippa nasturtium-aquaticum***, plant that has less inhibition by lunularic acid than more advanced analogs. Photo by Matt Lavin, through Creative Commons.

Figure 219. ***Phleum pratense***, species that has less inhibition by lunularic acid than more advanced analogs. Photo through Creative Commons.

Sharma *et al*. (2009) used ***Marchantia polymorpha*** (Figure 1-Figure 12) water extracts as one of the bryophyte species they tested for allelopathic effects on the flowering plant ***Bidens biternata*** (Figure 220). Although there was 100% inhibition of seed germination in the lipophilic extract, germination was not delayed significantly in water extracts. Sharma and coworkers reasoned that hydrophilic allelochemicals would be released more easily into the environment, but that these would also leach from the soil more quickly, thus favoring hydrophobic allelopathic compounds as a better defense.

Figure 220. ***Bidens biternata***, species for which seed germination is 100% inhibited by lipophilic extracts of ***Marchantia polymorpha***, but not by water extracts. Photo by J. M. Barg, through Creative Commons.

Kaihara and Takimoto (1990) found that a water extract of ***Marchantia polymorpha*** (Figure 1-Figure 12) could inhibit the flower-inducing activity of L-pipecolic acid. This L-pipecolic behaved synergistically with water extracts of ***Lemna aequinoctialis*** (duckweed; Figure 221) and ***Ipomoea hederacea*** (ivy-leaved morning glory; Figure 222) to enhance flowering, but all other tested plants suppressed it. This flowering inhibition is a sneaky way for the liverwort to compete with tracheophytes, but we have no field assessment of its effectiveness.

Figure 221. ***Lemna aequinoctialis***, plant for which its water extracts work synergistically with L-pipecolic to enhance flowering. Photo by Kevin Thiele, through Creative Commons.

Figure 222. ***Ipomoea hederacea***, plant for which its water extracts work synergistically with L-pipecolic to enhance flowering. Photo by Bobby Hattaway <www.discoverlife.org>, with online permission.

Marchantia polymorpha (Figure 1-Figure 12) can even become a pest in domestic gardens. The need to control weeds can provide new spaces where this liverwort can easily invade through gemmae or spores brought to the surface by the disturbance or as companions when new plants are introduced. Callaghan (2009) assessed domestic gardens in Britain and found that more than 80% of them included six moss species, but that ***Marchantia polymorpha*** was present in only 30% of the gardens. Nevertheless, Caron (1972) emphasized the need to fight such bryophytes as ***Marchantia polymorpha*** in arboriculture.

At least some herbicides tend to have different effects on different groups of plants. Bryophytes are no exception. Balcerkiewicz and Rusinska (1987) found that ***Marchantia*** actually expanded its populations in areas treated with herbicides. This may be due to the elimination of the competing tracheophytes, but the possibility existed that the herbicides could actually promote the growth of the liverworts. Iwata *et al*. (1992) subsequently suggested that ***Marchantia polymorpha*** (Figure 1-Figure 12) suspension cultures would be an excellent system for herbicide assays because of the rich chlorophyll content of the liverwort and its ability to grow in both **mixotrophic** (deriving nourishment from both autotrophic and heterotrophic mechanisms) and **autotrophic** (producing complex organic compounds using carbon from simple substances such as carbon dioxide) conditions.

Biochemistry

In a species that has been fundamental in so many studies to represent bryophytes, it is not surprising that there have been many biochemical studies as well. Those included here are only representative of the many publications.

Konno *et al*. (1987) isolated three classes of pectic polysaccharides from ***Marchantia polymorpha*** (Figure 1-Figure 12): rhamnogalacturonan polymer class, glucose rich polymer class, and galacturonan core. The cell walls are low in arabinosyl residues, unlike those of flowering plants.

Boisselíer-Dubayle and Bishler (1989) reported on the presence of esterases, peroxidases, acid phosphatases, and glutamate-oxaloacetate transaminase as revealed by their electrophoretic studies on ***Marchantia polymorpha***. Izumi *et al*. (1995) identified esterase secreted from suspension cell culture of ***Marchantia polymorpha***.

flavonoids

Singh *et al*. (1987) confirmed the presence of saponins, tannins, and flavonoids in ***Marchantia polymorpha*** (Figure 1-Figure 12). However all tests for alkaloids were negative, thus eliminating one of the chemical groups used in antiherbivory in some tracheophytes.

Markham and Porter (1974) identified major flavonoids of ***Marchantia polymorpha*** ssp. ***polymorpha***. Flavonoids exhibit properties of antiherbivory and UV filters (Johnson 1983; Treutter 2006). Treutter (2006) reviewed the literature on their roles in plants and found that they act as stress protecting agents, attractants, or feeding deterrents, and have a significant role in plant resistance.

Flavonoids are important compounds that enabled the first land plants to interact with their environment (Davies *et al*. 2020). Hence, it is hypothesized that the flavonoid pathway must have evolved during the colonization of land by early plants, about 450 million years ago, providing essential protection against abiotic stress (Albert *et al*. 2018). The flavonoids are important reactants that permitted early plants to tolerate both abiotic and biotic stresses. Their production in plants can be induced by cold, UV-B light, strong white light, nutrient deficiency, desiccation, salinity, metal toxicity, senescence, and attack by pests and pathogens (Agati & Tattini 2010; Cheynier *et al*. 2013; Landi *et al*. 2015; Davies *et al*. 2018, 2020). They provide signals to microbes, serve as **allelochemicals** (chemical produced by living organism, exerting detrimental physiological effect on individuals of another species when released into environment), and can be important **nutraceuticals** (any food substance that provides medical or health benefits, including prevention and treatment of disease) in the animal diet (Taylor & Grotewold 2005).

Kubo *et al*. (2018) demonstrated that the regulation of gene expression as a stress response was already present in ***Marchantia polymorpha*** (Figure 1-Figure 12). They found that overexpression of one regulatory gene greatly increased the amount of riccionidins, a flavonoid. The gene was up-regulated by UV-B irradiation, nitrogen deficiency, and NaCl treatment.

Clayton *et al*. (2018) monitored the biosynthesis of flavonoids in ***Marchantia polymorpha*** (Figure 1-Figure 12), using three different UV-B regimes and mutant cultures. They found that the **chalcone** isomerase-like compound was one of greater importance. Mutants with a disrupted pathway for this enzyme were more easily damaged by UV-B. Those mutants with increased flavonoid content demonstrated greater UV-B tolerance.

The flavonoid pathway starts with **chalcones** as the first flavonoids (Davies *et al*. 2020) Since their origin, more than 8,000 different flavonoid structures have been reported (Andersen & Markham 2006). The major flavonoid classes are the flavones, flavonols, isoflavonoids, aurones, 3-deoxyanthocyanins, anthocyanins, proanthocyanidins (condensed tannins), and auronidins (Davies *et al*. 2020). Most flavonoids go to the vacuoles as water-soluble glycosides, but in some species they are

transported to the cell wall or are released to the environment.

Many flavonoids can absorb UV light, but the colored anthocyanins and auronidins can screen visible light (Lee & Gould 2002; Landi *et al.* 2015; Berland *et al.* 2019). Thus far, flavonoids have not been found in hornworts. They seem to have no role in development in bryophytes; a mutant of ***Marchantia polymorpha*** (Figure 1-Figure 12) lacking flavonoids has normal developmental patterns (Clayton *et al*. 2018).

In ***Marchantia polymorpha*** (Figure 1-Figure 12), nitrogen deprivation and increased white light exposure both induce the accumulation of auronidin (Albert *et al*. 2018; Kubo *et al.* 2018), a phenomenon similar to that of seed plants for anthocyanin accumulation in *Arabidopsis* and apples (Rubin *et al.* 2009; Wang *et al.* 2018). But in ***M. polymorpha*** auronidin also greatly increases the resistance of the plants to infections by ***Phytophthora palmivora*** (Figure 204), with hyphae apparently unable to penetrate into highly pigmented regions of the plant (Carella *et al*. 2019). Thus their roles are widespread.

Berland *et al*. (2019) reported **auronidins** for the first time. These flavonoid pigments seem to be important in protecting the plants from such environmental stresses as high light, drought, and nutrient deprivation. We initially thought that the red pigments bound in the cell walls of the early land plants were anthocyanins, but recent studies have revealed that they are in fact a group of phenylpropanoids that Berland and coworkers named **auronidins**. Their colors are similar to those of anthocyanins, but they are synthesized differently and have different optical properties. It appears that they contribute to the ability of ***Marchantia polymorpha*** (Figure 1-Figure 12) to survive extreme environments.

Excess light of any quality enhances the biosynthesis of flavonoids in plants, performing multiple functions at the expense of the antioxidant flavonoids and hydroxycinnamates (Agati & Tattini 2010). Several research groups have provided indications that common oxidative signal components may up-regulate flavonoid biosynthesis, regardless of their origins (Taylor & Grotewold 2005; Fujita *et al.* 2006; Quattrocchio *et al.* 2006) and may link the REDOX potential of the cell to the control of flavonoid accumulation (Taylor & Grotewold 2005). It appears that the main purpose of the flavonols is their involvement in responses to abiotic and biotic stresses (Roberts & Paul 2006; Kilian *et al*. 2007; Mellway *et al*. 2009). More research is needed on their involvement in reducing oxidative stress.

Using knockout genes, Albert *et al*. (2018) determined that all pigmentation was lost from the flavonoid riccionidin A in ***Marchantia polymorpha*** (Figure 1-Figure 12), but when overexpression was used these plants produced large amounts of flavones and riccionidin A and exhibited red pigmentation. Light- and nutrient-deprivation stress induced flavonoid pigmentation in the thallus, as these stresses do for the anthocyanins in flowering plants.

In evolutionary theory, red leaves represent a signal of the health status of a tree, providing a signal to insects to migrate when trees change color in autumn (Cheynier *et al* 2013). Could similar signals be active in bryophytes, with red plants signalling nutrient deficiency or other poor health condition? Red can also signal toxicity and is known as **warning coloration**.

phenolics

From the beginning of my interest in antiherbivory, I understood that phenolics were the important antiherbivore compounds in plants. But Close and McArthur (2002) challenged that thinking. They contend that it is not antiherbivory, but photoprotection, that makes these compounds so important for plants. They suggest that phenolics accomplish this role by acting as antioxidants and that their levels may vary with environmental conditions to provide this protection. Thus, their level of phenolics in the plants is dependent on the risk of photodamage and not on resources in the environment.

Cheynier *et al*. (2013) noted that for the successful colonization of land plants needed UV light screens. These were apparently achieved by phenolic compounds. These compounds play no role in the developmental and growth processes, but they are vital for survival in the interaction of the plants with their environment, for their reproductive strategy, and reputedly, for their defense. These survival mechanisms are controlled by plant phenolics that respond to potentially overlapping regulatory signals. Some of these effects are likewise associated with the growth hormone auxin.

Soriano *et al*. (2019b) found that bryophytes rarely exhibited a quick response to UV radiation in their production of UV-absorbing compounds. They experimented with ***Marchantia polymorpha*** (Figure 1-Figure 12) and measured the phenolic content under three realistic UV levels on day 1 and day 22 (Figure 223). The levels of UV-absorbing compounds mostly responded with linear or hyperbolic relationships with the UV level (Figure 224). They identified thirteen flavones (apigenin and luteolin derivatives) and two hydroxycinnamic acids (p-coumaric and ferulic acids) in the soluble and insoluble fractions, respectively. The speed of response depended on the compound, but those identified in ***M. polymorpha*** were slow responders.

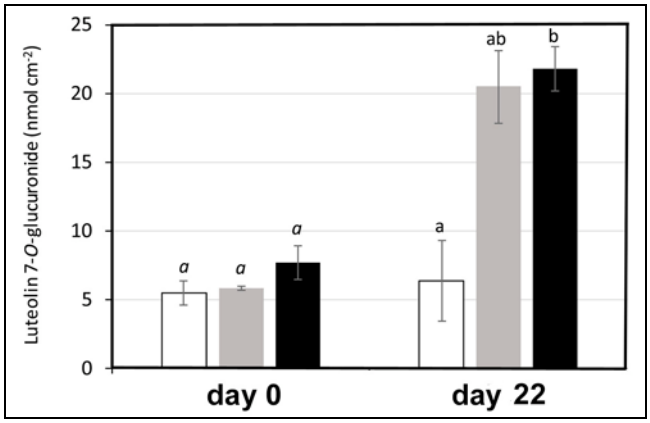

Figure 223. UV-absorbing compounds and time. White bars = UVBE low; grey bars = medium; black bars = high. Letters that are same represent means that are not significantly different from each other. Image modified from Soriano *et al*. 2019b.

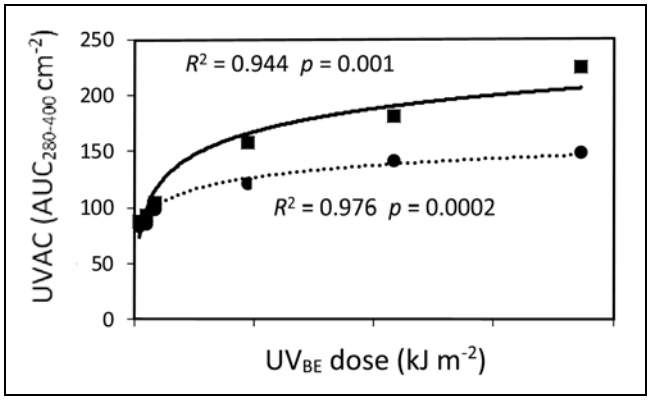

Figure 224. ***Marchantia polymorpha*** phenolics produced with increasing levels of UV-B. Photo modified from Soriano *et al*. 2019b.

light effects

Roberts and Paul (2006) introduced the concept that light serves to modulate plant defenses, in some cases being essential for the development of that resistance. They suggest that this interaction is multifaceted, extending across both temporal and biological scales. This needs further exploration in bryophytes and might explain our (false?) assumption that phenolic compounds have antiherbivore properties. Perhaps they accomplish both light protection and antiherbivory.

phenolics - phrenanthenes

Adam and Becker (1993a) reported phenanthrenes and other phenolics from cultured ***Marchantia polymorpha*** (Figure 1-Figure 12). Phenolics are secondary compounds that were widely considered to be antiherbivory compounds, but now the their importance in antiherbivory is questionable. Phenathrenes, on the other hand, have been used in traditional medicine, including usefulness in cytotoxicity, antimicrobial, spasmolytic, anti-inflammatory, antiplatelet aggregation, antiallergic activities, and phytotoxicity (Kovács *et al*. 2008), suggesting that they could serve as antiherbivore compounds as well as antibiotics. But perhaps their role in allelopathy toward tracheophytes is also feasible.

Anton *et al*. (1997) also found phenanthrene in the leafy liverwort ***Plagiochila*** (Figure 225), suggesting that it might be somewhat widespread in liverworts. Phenanthrene seems to have an interesting relationship with plants. It is one of the PAHs – phenols that occur naturally in coal, crude oil, and gasoline. PAHs are released from burning coal, oil, gas, wood, garbage, and tobacco and are toxic to both plants and animals (Wei *et al*. 2014). For example, phenanthrene inhibits seed germination and affects growth and chlorophyll levels of wheat seedlings. They also decrease the effects of antioxidants. Dupuy *et al*. (2016) also found that phenanthrene exposure causes developmental perturbation in maize roots. In the environment, they are degraded by bacteria (Anton *et al*. 1997). Corgié *et al*. (2003) demonstrated that root exudates are able to stimulate the degradation of PAHs in soil. In fact, it appears that the presence of the phenanthrene stimulates the release of more of these exudates, thus increasing the bacterial populations that accomplish the breakdown of the phenanthrene (Muratova *et al*. 2009). Thomas *et al*. (2019) also noted that plants can stimulate microbial degradation of PAHs, using phenanthrene as the test compound. The soil bacteria **Proteobacteria** (**Pseudomonadota**; Figure 16), **Actinobacteria** (Figure 226), and **Firmicutes** (bacterial groups that are also common on bryophytes; Figure 227) are phenanthrene degraders. Plant root exudates enhanced the development of these phenanthrene-degrading bacteria.

Figure 225. ***Plagiochila strombifolia***; phenanthrene occurs in at least some members of this genus. Photo by John Walter, through Creative Commons.

Figure 226. ***Actinomyces israelii***, member of **Actinobacteria**, group often associated with bryophytes and soil; some are phenanthrene degraders. Photo by Graham Beards, through Creative Commons.

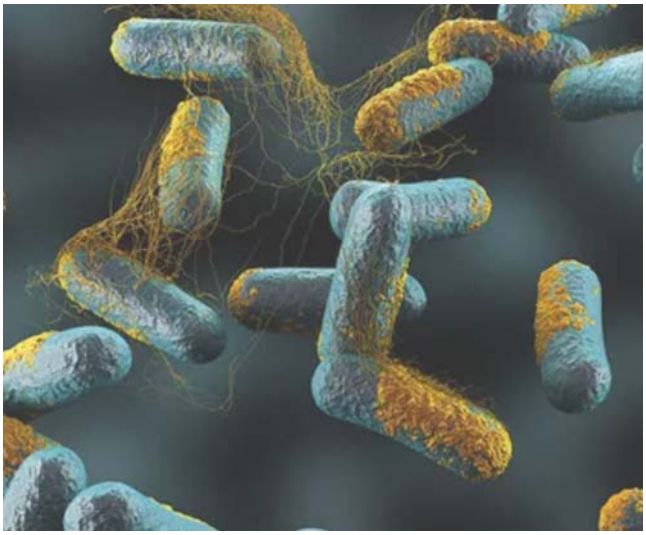

Figure 227. A member of **Firmicutes**, group often associated with bryophytes and soil; some are phenanthrene degraders. Photo by Argonne National Laboratories, through Creative Commons.

This raises the question of the presence of phenanthrenes in liverworts. Does it help, harm, or have a neutral action on them? Or like many of these compounds, might it have multiple roles? Perhaps the work with grassland plants might suggest a possible interaction. Chiapusio *et al*. (2007) found that in grasslands the phenanthrene did not generally affect plant biomass. In fact, red clover biomass was enhanced by it. This apparently resulted by a stimulation of its *Rhizobium* partner, a nitrogen-fixing bacterium. On the other hand, phenanthrene had a drastic negative effect on the mycorrhizal colonization of both ryegrass and red clover. As in other studies, the phenanthrene stimulated the PAH degraders in the soil.

This raises a possibility for ***Marchantia polymorpha*** (Figure 1-Figure 12) and its production of phenanthrene. It could stimulate the bacterial partners that are so common among the bryophytes (see Volume 2 chapter on bacterial interactions). In this role, it could play a critical role in their development. This won't be discovered in a sterile lab culture.

sesquiterpenoids and terpenes

Matsuo *et al*. (1985) isolated a series of ent-sesquiterpenoids that were stereoisomers of those compounds known in the tracheophytes, supporting the ancient origin of many of the defense compounds.

In 1990, Asakawa *et al*. described three new ent-sesquiterpenoids from German populations of ***Marchantia polymorpha*** (Figure 1-Figure 12). The chemistry of this species, including other isolates in this study, suggest that the German populations are close to the Japanese ***M. polymorpha*** and ***M. paleacea*** ssp. ***diptera*** (Figure 228).

Figure 228. ***Marchantia paleacea*** ssp. ***diptera*** females with capsules, Arima, Japan, 7 August 1988 – subspecies that has chemistry similar to that of ***M. polymorpha*** from Germany. Photo by Janice Glime.

Terpenes are volatile unsaturated hydrocarbons that constitute the essential oils and are aromatic compounds found in plants. Kumar *et al*. (2016) noted that despite their ability to accumulate structurally diverse terpenes that are "believed" to serve in deterring disease and herbivory, the genes and enzymes responsible for this chemical diversity of terpenes in ***Marchantia polymorpha*** have never been described. They were able to identify four diterpene synthase genes by function that were related phylogenetically to those in diverged plants. However, there were also nine "rather unusual" monoterpene and sesquiterpene synthase-like genes.

lectins

Adam and Becker (1993b) tested ***Marchantia polymorpha*** (Figure 1-Figure 12) for **lectins**. **Lectins** are proteins that bind to carbohydrates. They are defense compounds in plants, but can cause problems in human digestion because they are able to resist being broken down in the gut and remain stable in acidic environments. In some cases they interfere with the absorption of other nutrients. These capabilities make them good antiherbivore compounds. They are in many human foods, especially dried beans, and those extracted from ***Marchantia polymorpha*** agglutinate the erythrocytes of various mammals and exhibit carbohydrate specificity against complex carbohydrate structures. This was the first report of lectins in liverworts. On the other hand, they are important in attracting specific ***Rhizobium*** species toward roots of host plants, suggesting they could possibly have a similar role in bryophytes.

bibenzyls

Asakawa *et al*. (1987) isolated two new cyclic bis[bibenzyls] from Indian populations of ***Marchantia polymorpha*** (Figure 1-Figure 12). Bis[bibenzyls] are rare products of plants, but more than 125 types have been discovered among liverworts (Asakawa *et al*. 2021). They are biosynthesized from lunularic acid, perhaps explaining why this compound has remained in even those liverworts such as ***Marchantia*** that also have ABA. The known biological activities of cyclic bis[bibenzyls] include antimicrobial, antifungal, cytotoxic, muscle relaxation, antioxidant, tubulin polymerization inhibitory, and antitrypanosomal activities.

Niu *et al*. (2006) isolated and identified seven bis[bibenzyl]-type macrocycles from Chinese populations of ***Marchantia polymorpha*** (Figure 1-Figure 12). Several of these compounds exhibited antifungal activities against ***Candida albicans*** (Figure 183).

The **marchantins** are bis[bibenzyls]. As far as we know, these are unique to bryophytes and are cytotoxic, having cancer treatment applications (Kodama *et al*. 1988). Kámory *et al*. (1995) isolated marchantin A from ***Marchantia polymorpha*** (Figure 1-Figure 12). This was followed later by isolation of a number of different marchantins. At least some of these have proven antibacterial activity.

Fang *et al*. (2007) described three new bibenzyl (=1,1′-(ethane-1,2-diyl)bisbenzene) derivatives from Chinese populations of ***Marchantia polymorpha*** (Figure 1-Figure 12). Its polymorphin A was a new type of bis[bibenzyl] and one compound was described as the first discovery of a bibenzyl that is oxidatively coupled to a phenylmethanol.

Friederich *et al*. (1999) elaborated on the pathway from lunularic acid to formation of marchantin C and CO_2 and the hydroxylation of marchantin C to marchantin A. Both of these reactions depend on the presence of O_2 and NADPH. Both are also inhibited by CO in the dark.

Marchantins are another example in which Kubo *et al*. (2018) demonstrated that the regulation of gene expression as a stress response was already present in ***Marchantia polymorpha***. They found that overexpression of one

regulatory gene greatly increased the amount of several marchantins. The gene was down-regulated by NaCl.

antibacterial

Zehr (1990) found that ether extracts of ***Marchantia polymorpha*** (Figure 1-Figure 12) inhibited bacteria at 84.4%, whereas the ethanol extract lacks inhibitory ability. Those most affected were ***Bacillus subtilis*** (Figure 229) and ***Escherichia coli*** (Figure 16), whereas ***Enterococcus faecalis*** (Figure 230) was least inhibited. Zhu *et al*. (2006) noted that the antibacterial activity of ***Marchantia*** was "particularly prominent." As in many antibacterial studies with bryophytes ***Staphylococcus aureus*** (Figure 180) was the most resistant of the seven bacterial species tested. ***Bacillus subtilis*** was the most sensitive species to liverwort extracts.

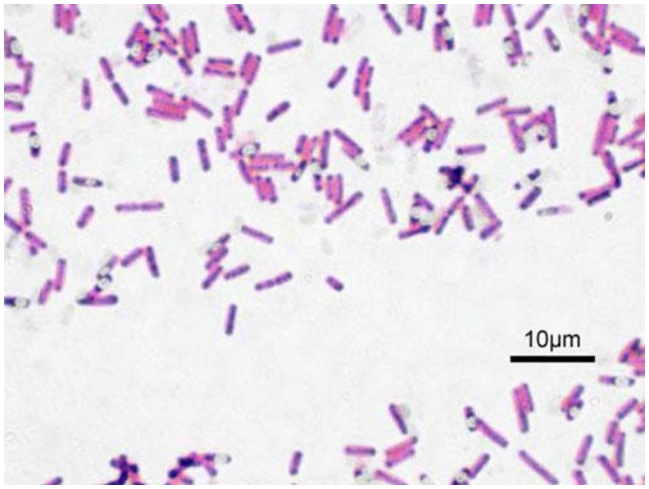

Figure 229. ***Bacillus subtilis*** Gram stained, one of bacteria most affected by extracts of ***Marchantia polymorpha***. Photo by Y. Tambe, through Creative Commons.

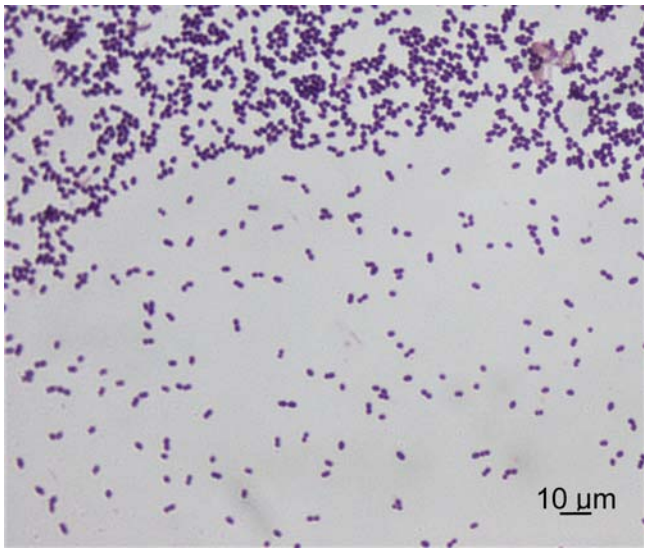

Figure 230. ***Enterococcus faecalis***, one of bacteria least affected by extracts of ***Marchantia polymorpha***. Photo by Dr. Sahay, through Creative Commons.

Gahtori and Chaturvedi (2011) likewise touted the usefulness of extracts of ***Marchantia polymorpha*** (Figure 1-Figure 12) as antimicrobial agents, some killing the organisms and others simply arresting growth. Among those affected were the Gram-negative bacterial strains ***Pasteurella multocida*** (Figure 231), ***Salmonella enterica*** (Figure 232), and ***Xanthomonas oryzae*** pv. ***oryzae*** (Figure 233), and the four fungal strains ***Fusarium oxysporum*** f. sp. ***lini*** (Figure 207), ***Rhizoctonia solani*** (Figure 205), ***Sclerotium rolfsii*** (Figure 234), and ***Tilletia indica*** (Figure 235). They found a unique activity against ***X. oryzae*** and ***P. multocida***. They also acted against the fungi ***S. rolfsii*** and ***F. oxysporum***. ***Marchantia polymorpha*** showed different potencies against micro-organisms that are pathogenic to both plants and animals.

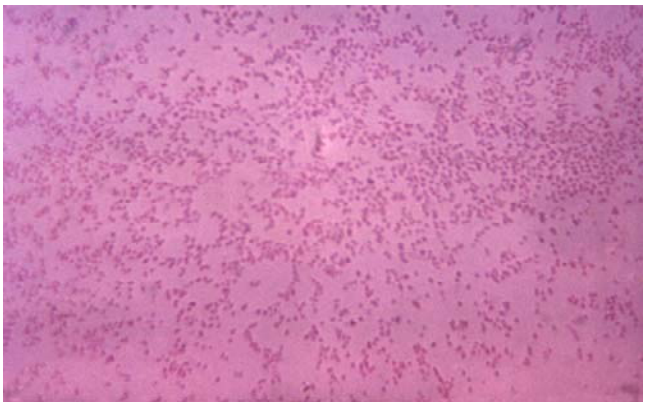

Figure 231. ***Pasteurella multocida*** bacteria, causative agent of fowl cholera, and species that is negatively affected by extracts of ***Marchantia polymorpha***. Photo by Dr. R. Weaver, CDC, through public domain.

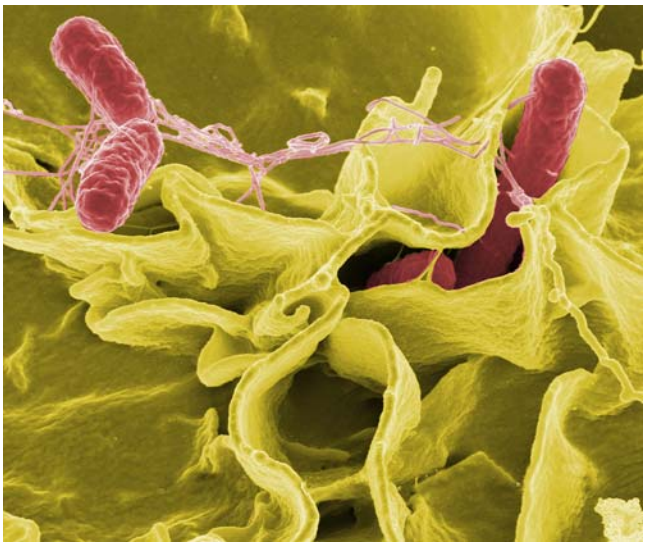

Figure 232. ***Salmonella*** in human tissue, and species that is negatively affected by extracts of ***Marchantia polymorpha***. Photo by NIH, HHS, through public domain.

Figure 233. ***Xanthomonas oryzae***, species that is negatively affected by extracts of ***Marchantia polymorpha***. Photo by Rui map Zheng at <Bugwood.org>, through Creative Commons.

Figure 234. ***Sclerotium rolfsii***, fungal species that is negatively affected by extracts of ***Marchantia polymorpha***. Photo by Bridget Lassiter, NCDA&CS <Bugwood.org>, with online permission.

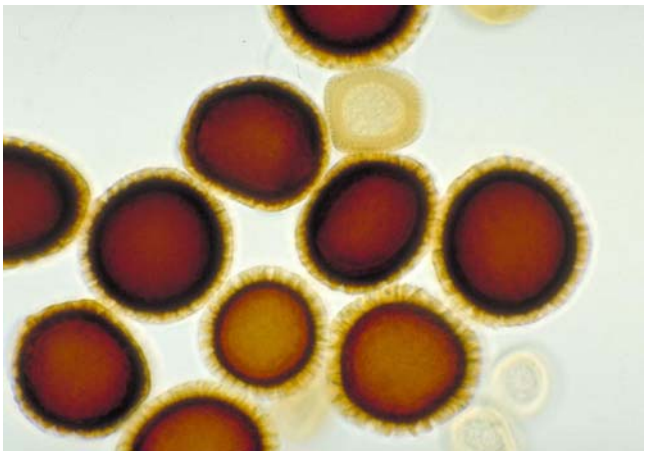

Figure 235. ***Tilletia indica***, fungal species that is negatively affected by extracts of ***Marchantia polymorpha***. Photo by Ruben Durán, through public domain.

antifungal

Hamashima *et al*. (2019) noted the development of many techniques using ***Marchantia polymorpha*** (Figure 1-Figure 12). They used S-Agar Trap to genetically transform the species, using spores. They were able to insert a T-DNA mutant and isolate and characterize a gain-of-function mutant. This mutant hyper-accumulates the flavonoid riccionidin A, verifying that this technique is a powerful tool in the genetic tool library, including production of antibiotics.

In a comprehensive study on published antifungal activities of bryophytes, Miranda *et al*. (2022) found that in the period of 2000 to 2019 ***Marchantia polymorpha*** (Figure 1-Figure 12) was included in the most publications.

glycosides

Qu *et al*. (2007) isolated four new glycosides and three known aromatic glycosides from ***Marchantia polymorpha*** (Figure 1-Figure 12) and described their structures. Many drugs and poisons derived from plants are glycosides, such as the several cyanogenic glucosides used by the Heliconius butterfly that incorporate these plant compounds in their tissues as a defense against predators (Nahrstedt & Davis 1983). I wonder if anything eats bryophytes to gain their secondary compounds for their own defense.

medicinal uses

Dioscorides (De Materia Medica, 50-70 AD) extolled the value of ***Marchantia polymorpha*** (Figure 1-Figure 12) for treating liver ailments, based on its liver form (Doctrine of Signatures; in Schuster 1966). In Yunnan and Sichuan this liverwort is available in street markets (Wu & Yu 2003). It is used to cover the skin for curing jaundice and as an antipyretic. Asakawa (1981, 1982) reported that this species contains sesquiterpenoids that have anti-tumor activity. Hartwell (1982) referred to its use against cancer, referring to Pliny the Elder.

Fischer *et al*. (1995) verified the presence of chalcone synthase activity in ***Marchantia polymorpha*** (Figure 1-Figure 12), and the subsequent presence of naringenin. Chalcones are used medicinally in treatment of viral disorders, cardiovascular diseases, parasitic infections, pain, gastritis, and stomach cancer. **Naringenin** has strong anti-inflammatory and antioxidant activities and seems to be beneficial in treating obesity, diabetes, hypertension, and metabolic syndrome in humans.

Kumar *et al*. (2007) reported that ***Marchantia polymorpha*** (Figure 1-Figure 12) was among those liverworts useful for treating tumors and that it was among the traditional herbal medicines in India.

Culturing and Cultivating

With so many studies being performed on the species ***Marchantia polymorpha*** (Figure 1-Figure 12), the methods of culturing have been worked out well (Figure 236). Voth and Hamner (1940) grew ***Marchantia polymorpha*** on glass cloth in an open moist chamber. They tested 56 nutrient solutions to develop suitable conditions for culturing the species in the lab. Voth (1941) indicated that the omission of K, Ca, NO_3, or PO_4 ions caused differences in the gross appearance of the species. Mg and SO_4 are not indicated by any characteristic symptoms. Effects of calcium appear to be dose dependent. Almost immediate death occurs in its absence, whereas in 0.3 mM of calcium per liter of solution the thallus apices die and degenerate.

Figure 236. ***Marchantia polymorpha*** ssp. ***ruderalis*** in peat disc culture. Photo courtesy of Javier Martínez-Abaigar.

Molar concentrations that are adequate for good growth, based on Voth (1941) are:

K 0.0012 M L^{-1}
Ca 0.0007 M L^{-1}
Mg 0.0014 M L^{-1}
NO_3 0.0034 M L^{-1}
PO_4 0.0004 M L^{-1}
SO_4 0.0008 M L^{-1}

These can be provided in a 1 L, 0.5 M solution of the following forms:

KNO_3 1.6 cc
$Ca(NO_3)_2$ 1.4 cc
$Mg(NO_3)_2$ 1.2 cc
KH_2PO_4 0.8 cc
$MgSO_4$ 1.6 cc

Minor variations of the concentrations do not cause growth problems.

Voth (1943) contributed additional experiments on nutrient concentrations, finding that some were better for production of gemmae cups than others. High salt concentrations often killed the growing tips and thalli became translucent.

Schneider *et al*. (1967) further developed culture methods that attempted to standardize them and address some of the inconveniences of past methods. They found that five substrates worked well, including vermiculite, perlite, glass cloth, nutrient agar, and nutrient solution. These are compared for their maintenance, yields, and usefulness for particular experimentation.

Miller (1964) contributed to the culturing protocol by defining procedures for harvesting, surface sterilizing, and culturing of gemmae. He also described conditions for a high production of gemmae and large numbers of gemmae cups in stock plants. He described methods for culturing the gemmae axenically, noting that they did not fare well at temperatures above 25ºC, but that they were tolerant of high light. Miller *et al*. (1962b) used five different photoperiods to determine the best photoperiod for developing gemmalings. The greatest size and weight were achieved in an 18-hour photoperiod. They experimented with X-rays, light intensity, various nutrients, amino acids, vitamins, and other supplements to determine their effects and ability to prevent damage to the plants.

Miller and Colaiace (1969) cultured gemmae to ultimately produce antheridiophores and archegoniophores, structures that developed after 3-6 weeks on 1% agar medium in 24-hour photoperiods at 23ºC.

In his attempts to grow gemmae of ***Marchantia polymorpha*** (Figure 1-Figure 12), Gemmrich (1976) found that Fe and $Ca(NO_3)_2$ induced germination, but optimal germination occurred on $Ca(NO_3)_2$, KNO_3, and $MgSO_4$. Gibberellic acid failed to induce germination in the dark.

Sugawara *et al*. (1983) found that activated charcoal in the culture medium increases cell wall regeneration and subsequent cell division, suggesting that something in the medium is too strong for he plant, or that the plant's own by-product(s) become inhibitory. Charcoal is usually used to bid things, thus removing them from availability to plants.

Pedroza-Manrique and Caballero Arévalo (2009) recognized that bryophytes typically require lower nutrients than do tracheophytes and algae. They successfully grew ***Marchantia polymorpha*** (Figure 1-Figure 12) propagules in 25% Murashige and Skoog (1962) mineral salt concentration, incubated at 25°C ± 1°C. They warned that when transplanting such cultures to their natural environment or other conditions, one should provide gradual adjustment to new humidity, temperature, and substrate conditions.

Katoh *et al*. (1980) used a modified Murashige and Skoog's medium to culture ***Marchantia polymorpha*** (Figure 1-Figure 12). They improved the medium for use with the liverwort, including only eight of the 24 original micro-organic constituents. This new medium resulted in richer chlorophyll and a higher growth rate in the exponential phase.

Xu *et al*. (2021) found that they could induce reproductive organs in ***Marchantia polymorpha*** (Figure 1-Figure 12) on agar plates. Cultures from gemmae were transplanted after 10 days onto soil at 22ºC with a 16h:8h photoperiod using white light. After 14 days, they supplemented the cultures with far red light.

Gradstein (2006) reported the successful cultivation of ***Marchantia*** in the bryophyte garden of the Cibodas Botanical Garden, Java, Indonesia. Supplementary spray is needed during the dry season.

Control

Marchantia polymorpha (Figure 1-Figure 12) can be a serious weed in some types of gardens, especially in nurseries, and in greenhouses. Jin and Pyon (2007) noted the need to control it in ginseng gardens. Uva *et al*. (1997) even listed it in their publication on the weeds of the northeastern USA. Schofield (1997) listed the species as one obviously spread by human activity in British Columbia, Canada.

Sato *et al*. (1991), working in Japan, used Cyclohexanedione derivatives on ***Marchantia***, causing photosynthetic inhibition in cultured cells. They suggest that indicated the usefulness of the liverwort in herbicide assays.

Fausey (2003) considered ***Marchantia polymorpha*** (Figure 1-Figure 12) to be highly invasive and difficult to control, becoming a concerning pest in ornamental containers. They compared pre-emergence and postemergence herbicides, using chlorothalonil, captan, ammonium chlorides, hydrogen dioxide, flumioxazin, oxyfluorfen, pelargonic acid, acetic acid (vinegar), Cu sulfate, cinnamaldehyde, prodiamine, and oxadiazon. Of these, only flumioxazin, oxyfluorfen, pelargonic acid, acetic acid, and oxadiazon elicited acceptable control. Sprayable preparations were more effective than were granular ones.

Newby *et al*. (2007) experimented with various herbicides as a means of controlling ***Marchantia polymorpha*** (Figure 1-Figure 12) in nursery containers. The effectiveness differed by location, with flumioxazin and oxadiazon being the most effective for control in Alabama, whereas flumioxazin and oxyfluorfen + oryzalin were the most effective for control in Oregon.

Since ***Marchantia polymorpha*** (Figure 1-Figure 12) benefits from the same high humidity and shading as that needed in most nurseries for growing native tree seedlings, it quickly becomes a pest species there (Navas *et al*. 2014). Navas and coworkers used a variety of treatments,

including sterilizing the soil, using three concentrations of acetic acid, using two concentrations of oxygenated water, and using the herbicides glyphosate and fomesafen. They also used pre-emergence application of diuron and trifluralina. Only the two pre-emergence applications caused a 100% control of ***Marchantia polymorpha***.

Särkkä and Tahvonen (2020) suggested several means of control of ***Marchantia polymorpha*** (Figure 1-Figure 12) in nurseries where it appeared as a weed. In pots with growing horticultural plants it can reduce access to water and nutrients (Figure 237). Growth of the liverwort can be minimized with mulches. Särkkä and Tahvonen used ***Sphagnum*** (Figure 238) and 1-cm blackcurrant stem pieces. Highbush blueberry and blackcurrant controlled the liverwort for two years, whereas rhododendron controlled it for only one year. Blueberry and rhododendron require an acid medium that is beneficial for the liverwort. Blackcurrant mulch was nearly 100% effective, whereas other treatments ranged 78-99%.

Figure 237. ***Marchantia polymorpha*** with splash cups, in nursery flower pot. Photo by Janice Glime.

Figure 238. ***Sphagnum capillifolium***; ***Sphagnum*** can be used in layers to discourage growth of ***Marchantia polymorpha*** in pots. Photo by Bernd Haynold, through Creative Commons.

Khamarea *et al*. (2021) used a method of substrate stratification and fertilizer to control ***Marchantia polymorpha*** (Figure 1-Figure 12) growth. They used pine bark and other layers with different physical properties to manipulate the soil moisture dynamics and improve irrigation and fertilizer efficiency. This proved to also work as a tool of weed management. Each of the stratified techniques reduced the liverwort coverage by nearly 100%.

Summary

Marchantia polymorpha is perhaps the most studied bryophyte on the planet. It is a teaching model for liverworts, has had its genome sequenced, and is common in both wet habitats and as an invader after fires. It has been the subject of many physiological studies, including hormone effects and capillary movement of water among rhizoids. Growth hormones such as IAA elicit responses like those in tracheophytes. The thalli exhibit circadian rhythms that regulate the IAA levels. Lipoxygenase also contributes to control of cell growth. Gibberellins respond to photoperiod. Ethylene causes larger gemmae, induces more gemmae cups, and promotes the dormancy of the gemmae, whereas the precursor ACC inhibits gemma growth and development by suppressing cell division. Cytokinins control formation of both gemmae cups and rhizoids during thallus development and seem to influence distribution of air pores and shape of thallus margin, implicating control of cell division. Desiccation causes oxidative stress. ***Marchantia polymorpha*** has both lunularic acid and ABA, important hormones in desiccation tolerance. Light affects senescence, but spermine, spermidine, and putrescine reduce it. Ethylene induces senescence. Nitrate and phosphate deficiency cause the ventral layers of cells to develop a red-violet color. Thalli can grow on vertical surfaces, but gemmae cups exhibit gravitropisms.

Adaptations are a coordinated set of resistance to effects of drying. These include rhizoids, scales, thick thallus, thin cuticle, air pores with a waxy ring, and oil bodies, as well as a suite of biochemical adaptations.

It is dioicous and prolifically produces sexual structures. However, gemmae are usually the most important means of reproduction and enable it to colonize rapidly after a disturbance. Short photoperiods favor production of gemmae, whereas long photoperiods favor the production of gametangiophores and greater growth. Developmental stage is important in determining the accumulation of UV-absorbing compounds in ***Marchantia polymorpha*** ssp. ***ruderalis***. High temperatures can change the ratios of fatty acids and cause a reversible depression of photosynthesis; there seems to be limited thermostability. They are much more cold tolerant and don't suffer frost damage. The ω-3 polyunsaturated fatty acids increase as the temperature decreases and ABA seems to play a role in cold survival.

Marchantia polymorpha produces sesquiterpenoids that are active against some fungi and bacteria. Some methylobacteria promote the growth of gemmae. Other bacteria promote thallus growth, fix nitrogen, and inhibit pathogens. Extracts of the liverwort have antibiotic properties. The

archegoniophore is particularly well protected, with a flavonoid content ten times that of the thallose gametophyte. Antibacterial properties increase with altitude. The antibacterial compounds also inhibit protozoa. Fungi can occur as endophytes and pathogens, but others might contribute to symbiosis. The subspecies ***montivagans*** develops mycorrhizal associations with some fungi, but this relationship is not known in subspecies ***polymorpha***. The liverwort protects the fungi from water loss and can have a number of species living in association with it.

We have a meager understanding of the invertebrates that depend on ***Marchantia polymorpha***. At least one fly (***Scatopsciara cunicularius***) feeds on it as larvae. Extracts of allene oxide synthase inhibits oviposition and survival rate of the spider mite ***Tetranychus urticae***. Spiders and isopods inhabit them, but herbivory needs to be studied.

Some members of the **Apiaceae** can inhibit growth of ***Marchantia polymorpha***, whereas the liverwort can inhibit seed germination in ***Bidens biternata***.

It appears that the species has evolved numerous biochemical adaptations. Anthocyanins and auronidins can screen visible light, protecting it from strong sunlight. Auronidins seem to be important in protecting the liverwort in the extremes of its environmental conditions. Flavonoids protect against UV light and herbivory. They may provide antibiotics benefitting animals in nature. Their phenolic compounds are important in UV protection and might not have the importance in antiherbivory we once thought.

Large increases in CO_2 cause a number of changes in the ***Marchantia polymorpha*** photosynthetic system, but the net result is that there is little change in photosynthetic rate. High light intensity inhibits photosynthesis. Light quality can affect growth and gemma production. The red:far red ratio affects chlorophyll concentration and senescence and is mediated by phytochromes.

The species accumulates heavy metals, but not in large quantities like mosses do, due to lower surface area. Its best role seems to be in the laboratory. It is easy to culture, so easy that in greenhouses it is necessary to find ways to discourage its growth in pots for trees and other plants. Chronic gamma radiation causes inhibition of the development of sex organs in ***Marchantia polymorpha*** and its responses can be used to monitor radiation effects. Rapid and easy growth and haploid condition make the species useful to test the function of plant genes.

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CHAPTER 1-25
AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: MARCHANTIACEAE, PART 3

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CHAPTER 1-25
AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: MARCHANTIACEAE, PART 3

Figure 1. ***Marchantia quadrata*** on dripping cliff, a wet habitat with a more constant set of conditions than open areas. Photo courtesy of Keir Wefferling.

Marchantiaceae, cont.

Marchantia quadrata (Figure 1-Figure 5)

(= *Preissia quadrata*)

Most readers may be more familiar with the synonym ***Preissia quadrata***. However, Stotler and Crandall-Stotler (2017) have moved it to the genus ***Marchantia*** and this seems to be the name the bryological community has accepted. But Zheng & Shimamura (2022) just published a paper that once again offers support for the separation of this species into the genus ***Preissia***. And they have added another species to that genus, ***Preissia platycarpa***. This conclusion on their part is based on several differences in morphology, including the absence of gemmae cups and the presence of only one archegonium and sporophyte per arm in the female receptacle. This genus argument among bryologists seems to depend on the degree of difference accepted, both morphological and genetic, to define a different genus.

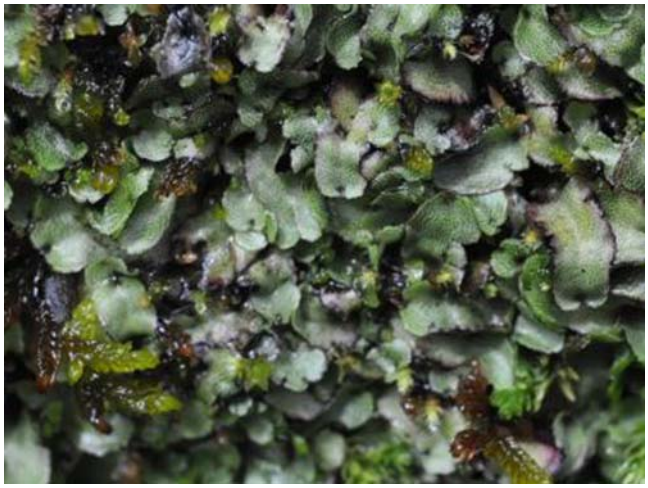

Figure 2. ***Marchantia quadrata*** showing frequent character of purple edges. Photo by Andy Hodgson, with permission.

Figure 3. ***Marchantia quadrata*** with young archegonial heads and distinct red-purple margins. Photo by Hermann Schachner, through Creative Commons.

Figure 4. ***Marchantia quadrata*** with expanded archegoniophores. Photo by Janice Glime.

Figure 5. ***Marchantia quadrata*** thallus. Photo from Snappy Goat, through public domain.

Boisselier-Dubayle *et al*. (1997) reported that there was an incongruence between molecular data and morphological characters in the **Marchantiales**. They recommended a weighting of the morphological character data and were able to resolve the contradictions by so doing. They suggested that this might mean that the molecular sampling is too limited.

Distribution

Marchantia quadrata (Figure 1-Figure 5) is known from Australia, Europe, Northern and Southern Asia, Central America, North America, Oceania, and South America (ITIS 2022). It was recently reported as new to Turkey (Şimşek *et al*. 2014).

Aquatic and Wet Habitats

In North America, ***Marchantia quadrata*** (Figure 1-Figure 5) occurs along calcareous rivers in Connecticut, USA (Nichols 1916). I have seen it at the top of a waterfall in shallow water on bedrock (Figure 6) in the Keweenaw Peninsula, Michigan, USA. Forrest (2018) found it at the edge of a stream at the top of Snowbird Mountain in Utah, USA. McNeilus and Sharp (1975) reported it from limestone bluffs with dripping water in Tennessee, USA. Nichols (1918) reported it along a rock ravine streambank, Cape Breton Island, Canada. In western Canada, it occurs submerged, in hemicalciphilous montane streams (Vitt *et al*. 1986) and also on streambanks (Figure 7) (Glime & Vitt 1987).

Figure 6. ***Marchantia quadrata*** habitat in river gorge at top of falls, Keweenaw County, Michigan, USA. Photo by Janice Glime.

Figure 7. ***Marchantia quadrata*** growing with mosses beside water. Photo by Claire Halpin, with permission.

Watson (1919), in his discussion of aquatic bryophytes, reported that ***Marchantia quadrata*** (Figure 1-Figure 5) usually occurs on rocks (Figure 8-Figure 9) (Watson 1919). Near Lacko in the Western Carpathians, it is part of the ground community in streams (Figure 10) (Mamczarz 1970). In the River Tweed, UK, it is not common (Holmes & Whitton 1975), but occurs on the river bank of River Tees, UK (Holmes & Whitton 1977a) and occurs in the upper upstream of River Swale, Yorkshire, UK (Holmes & Whitton 1977b). It is again infrequent in River Tyne, UK (Holmes & Whitton 1981).

Figure 8. ***Marchantia quadrata*** on wet rock at edge of stream. Photo by Andy Hodgson, with permission.

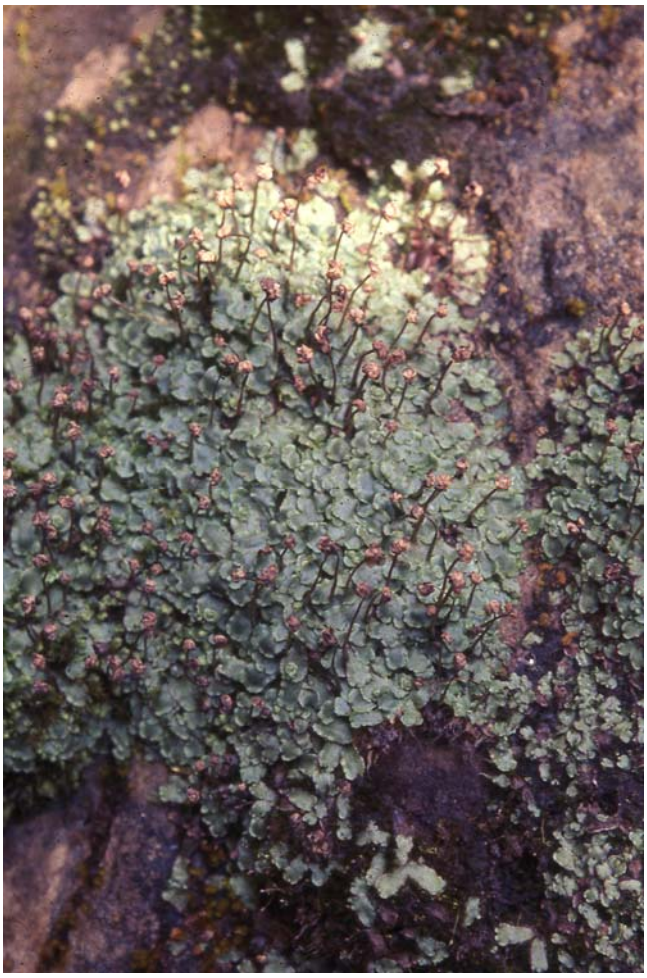

Figure 9. ***Marchantia quadrata*** on rock at waterfall, Michigan, USA. Photo by Janice Glime.

Figure 10. ***Marchantia quadrata*** with archegoniophores, growing on soil. Photo by Hermann Schachner, through Creative Commons.

Lee and Greenwood (1976) reported that ***Marchantia quadrata*** (Figure 1-Figure 5) was able to occupy calcareous waste deposits in the UK in areas where there were no natural calcareous substrata.

Marchantia quadrata (Figure 1-Figure 5) occurs in the travertine ***Cratoneuron*** (Figure 11) association in the Lorraine River, Belgium, (de Sloover & Goossens 1984), in streams in Greece (Papp 1998), and at springs in the Tara river canyon and Durmitor area, Montenegro (Papp & Erzberger 2011).

Figure 11. ***Cratoneuron filicinum***, a species associated with ***Marchantia quadrata*** on travertine rock. Photo by Hermann Schachner, through Creative Commons.

Contrasting with these limestone habitats, Haupt (1926) reported ***Marchantia quadrata*** (Figure 1-Figure 5) on thin soil (Figure 10) over granitic rocks, particularly along stream banks. It tends to occur in drier situations than ***Marchantia polymorpha*** (Figure 12) or ***Conocephalum*** (Figure 13-Figure 14), but they can occur intermixed. Nevertheless, it can occur close to the water (Figure 15-Figure 17).

Figure 12. ***Marchantia polymorpha*** gemmae cups in Europe; ***Marchantia quadrata*** prefers drier conditions than does ***M. polymorpha***. Photo by Michael Lüth, with permission.

Figure 13. ***Marchantia quadrata*** with archegoniophores on wet canyon wall by stream at Hocking Hills, Ohio, USA. Note the ***Conocephalum cf. salebrosum*** at the bottom of the view, illustrating the presence of ***Marchantia quadrata*** in a higher zone above the water. Photo by Janice Glime.

Figure 14. ***Marchantia quadrata*** with archegoniophores stacked on canyon wall at Hocking Hills, Ohio, USA, growing next to ***Conocephalum salebrosum***. Photo by Janice Glime.

Figure 15. ***Marchantia quadrata*** on stream bank. Photo by Scot Loring, through Creative Commons.

Figure 16. ***Marchantia quadrata*** on wet rock. Photo by Andy Hodgson, with permission.

Figure 17. Wet ***Marchantia quadrata*** near falls at Tahquamenon Falls, Michigan, USA. Photo by Janice Glime.

In the Netherlands, ***Marchantia quadrata*** (Figure 1-Figure 5) occurs on the **trilveen** (Kooijman & During 1989). The **trilveen** (Figure 18) is a bog that is a rare, with thin, extremely soft "soil" and vegetation type with sedges

and grass roots. It floats on water or soft mud and occurs in low moor areas such as peat meadows.

Figure 18. Trilveens in The Netherlands. Note the person pushing one across the water surface. Photo from Wikiwand, through Creative Commons.

Keir Wefferling found it growing on dripping sandstone cliffs in Wisconsin, USA (Figure 1-Figure 5, Figure 19).

Figure 19. ***Marchantia quadrata*** (**bottom**) forming a zone above the base of a dripping cliff in Wisconsin, USA. Photo courtesy of Keir Wefferling.

In Turkey ***Marchantia quadrata*** (Figure 1-Figure 5) occurs on moist calcareous rocks (Figure 20) of the subalpine zone (Şimşek *et al*. 2014).

Figure 20. ***Marchantia quadrata*** growing among calcareous rocks. Photo by Michael Lüth, with permission.

I have also seen the species on a rock ledge of a cliff in New York, USA (Figure 21). It can occur on rock and cavern walls (Figure 22-Figure 26).

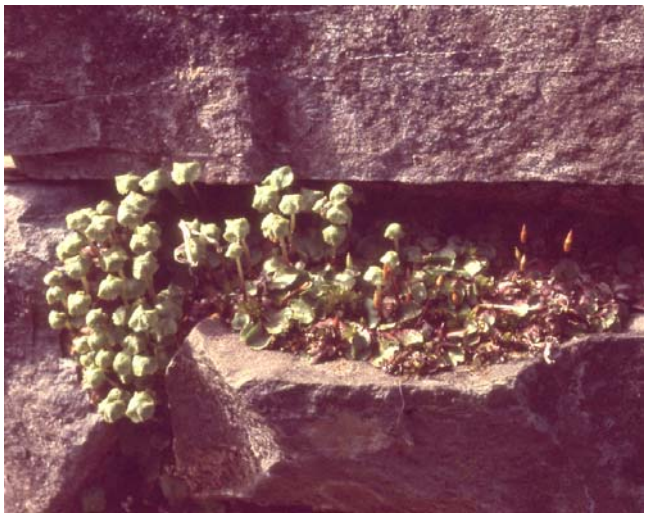

Figure 21. ***Marchantia quadrata*** on ledge in New York, USA. Photo by Janice Glime.

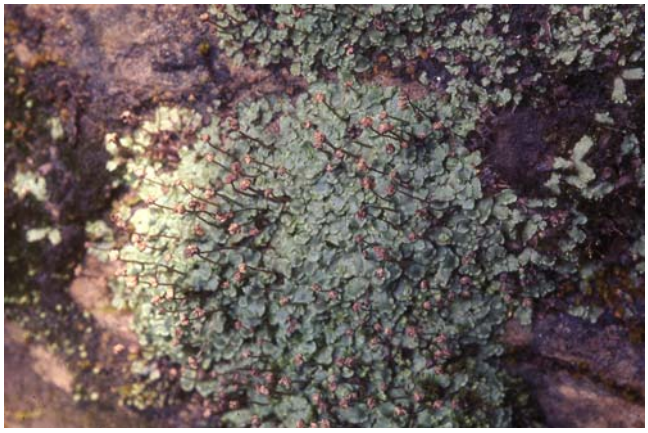

Figure 22. ***Marchantia quadrata*** on rocky bank at Tahquamenon Falls, Michigan, USA. Photo by Janice Glime.

Figure 23. ***Marchantia quadrata*** on calcareous rock. Photo by Michael Lüth, with permission.

Figure 24. ***Marchantia quadrata*** on rock in NW Iowa, USA. Associated mosses can help it to retain moisture. Photo by Janice Glime.

Figure 25. ***Marchantia quadrata*** with archegoniophores on rock. Photo by Michael Lüth, with permission.

Figure 26. ***Marchantia quadrata*** on a rock depression – a common habitat for the species. Photo by Oskar Gran, through Creative Commons.

Others have found it in open areas on soil, as seen in these pictures by Michael Lüth (Figure 27-Figure 28).

Figure 27. ***Marchantia quadrata*** with archegoniophores, growing on open soil. Photo by Michael Lüth, with permission.

Figure 28. ***Marchantia quadrata*** with archegoniophores, growing on soil in the location shown above. Photo by Michael Lüth, with permission.

Physiology

Tyler *et al*. (1995) found that soluble phosphate was important to the occurrence of ***Marchantia quadrata*** (Figure 1-Figure 5) on limestone soil. It produced 7 times as much biomass when phosphate was added to the soil. Perhaps this is due to the ability of the calcium carbonate of the limestone to be an effective binder of phosphate (Yanamadala 2005). Furthermore, the liverwort is likely to be phosphate limited without the high levels of phosphate. The mix of $CaCO_3$ and phosphate could also encourage certain bacteria, particularly nitrogen-fixing bacteria, that are beneficial to the liverwort. The reaction with limestone further releases water and CO_2, the latter being a limiting factor in submersed plants:

$$2\ H_3PO_4 + 3\ CaCO_{3(aq)} \rightarrow Ca_3(PO_4)_{2(s)} + 3\ CO_3^{-2} + H^+$$

$$2\ H^+ + CO_3^{-2} \rightarrow H_2O_{(l)} + CO_{2(d)}$$

Fletcher (1982) reported that ***Marchantia quadrata*** (Figure 1-Figure 5) was among the ***Marchantia*** species from several areas that sustained no frost damage when other bryophytes suffered blackening, bleaching, or growth cessation in cultivation down to -5.5ºC. In nature, it can survive winter under the snow and ice in the 5-6 months of snow cover in the Keweenaw Peninsula, Michigan, USA (Figure 29).

Figure 29. Snow covering ***Marchantia quadrata*** habitat at top of Manganese Falls, Keweenaw County, Michigan, USA. Photo by Janice Glime.

Heat is less kind, but it can have reversible damage effects on ***Marchantia quadrata*** (Figure 1-Figure 5) (Weis *et al*. 1986). Mild heat treatment suppresses photosynthesis. More severe heat causes irreversible damage of PSII similar to that known in tracheophytes. Exposure to high but sublethal temperatures does not increase the heat stability of these liverworts, indicating an extremely low heat-hardening capacity.

Adaptations

Marchantia quadrata (Figure 1-Figure 5) has a thallus that is multiple cells in thickness (Figure 30-Figure 31). The upper layer and the epidermis cells (Figure 32) contain chloroplasts, but these are absent in the cells surrounding the pores (Walker & Pennington 1939). The thickness is likely to aid in moisture retention during drought periods.

Figure 30. ***Marchantia quadrata*** thallus section showing photosynthetic cells on top and scales hanging from the ventral side. Photo by Hermann Schachner, through Creative Commons.

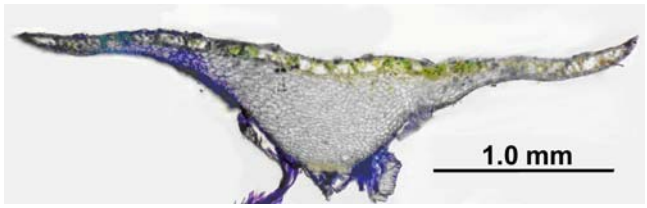

Figure 31. ***Marchantia quadrata*** section showing distinctive photosynthetic layer on top. Rhizoids hang from the ventral surface. Photo by David Wagner, with permission.

Figure 32. ***Marchantia quadrata*** thallus showing epidermis with pores. Photo from Bioimages, through Creative Commons.

Rhizoids (Figure 33) are known to create capillary spaces that conduct water in the **Marchantiales**. McConaha (1941) suggests that the more numerous rhizoids present in ***Marchantia quadrata*** (Figure 1-Figure 5) compensate for its less compact arrangement of the capillary system. It also does not have its capillary system over the wings of the thallus to the extent seen in ***Marchantia*** *s.s.* Thallus areolation in ***M. quadrata*** exposes a greater surface to water loss despite having pores that are able to achieve partial closure; there is little regulation of the transpiration.

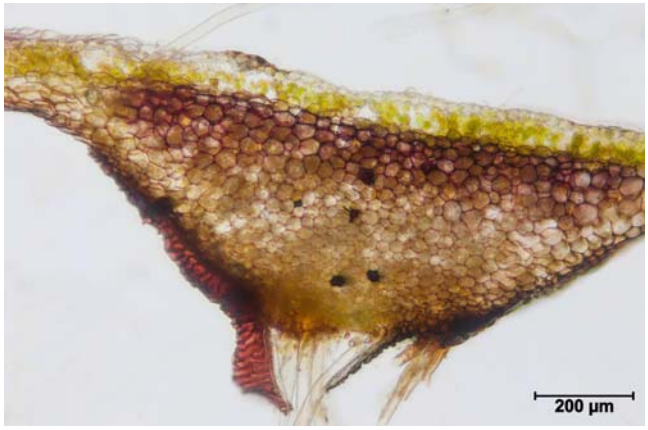

Figure 33. ***Marchantia quadrata*** thallus cross section with scales and rhizoids projecting from the lower surface. Photo by Kristian Peters, with permission.

Like other ***Marchantia*** species, ***M. quadrata*** (Figure 1-Figure 5) has both smooth and pegged rhizoids (Figure 33) as well as appendaged scales (Figure 33-Figure 34) on the lower surface (Cavers 1904). Presumably, these serve the same functions in conduction as those of ***M. polymorpha*** (Figure 12).

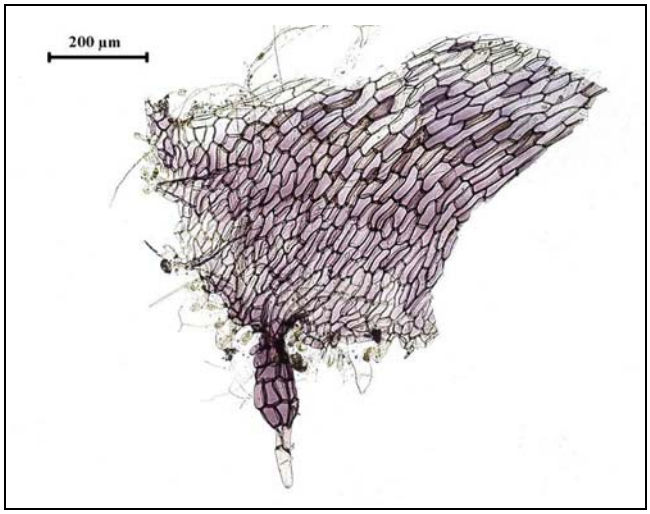

Figure 34. ***Marchantia quadrata*** ventral scale. Photo by Hugues Tinguy, with permission.

Like other species of ***Marchantia***, ***M. quadrata*** (Figure 1-Figure 5) has air pores (Figure 35-Figure 43) in the thallus that permit more rapid gas exchange than the thallus epidermis does (Haupt 1926). In this species, the pore is barrel-shaped with cells in four or five tiers (Figure 38, Figure 40, Figure 43) (Walker & Pennington 1939). The upper opening is always wide open (Figure 40, Figure 41, Figure 43), but the inner part is narrower and can be closed (Figure 41-Figure 43). Each cell of the basal tier, referred to by Walker and Pennington as **motor cells**, has a papilla which projects freely inward. The papilla has a thinner wall than the remainder of the motor cell. Movements of the papillae are responsible for changes in the size of the opening.

Figure 35. ***Marchantia quadrata*** showing epidermis with pores. Photo by Jan-Peter Frahm, with permission.

Figure 36. ***Marchantia quadrata*** thallus portion showing pores. Photo by Kristian Peters.

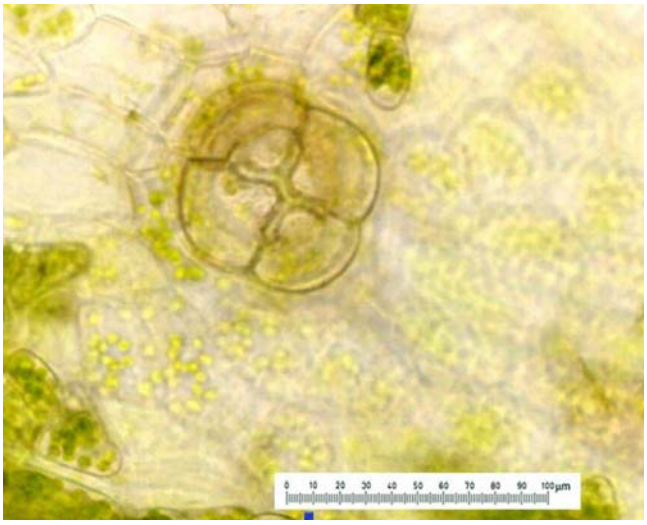

Figure 37. ***Marchantia quadrata*** thallus showing pore viewed from ventral surface. Photo by David Wagner, with permission.

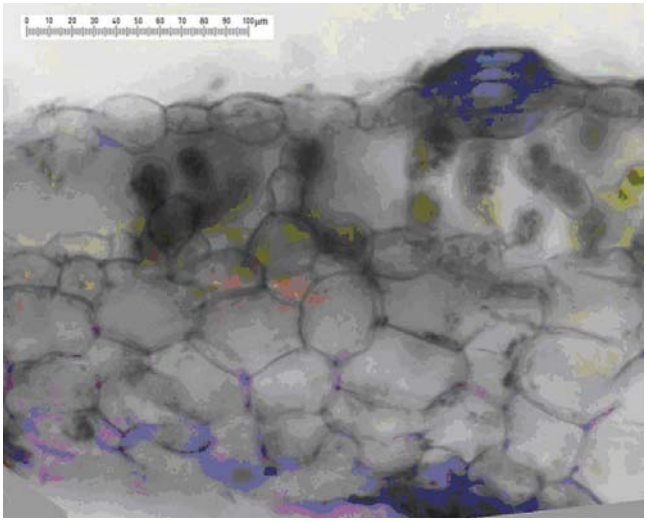

Figure 38. ***Marchantia quadrata*** thallus section showing air spaces, photosynthetic cells, and pore. Photo by David Wagner, with permission.

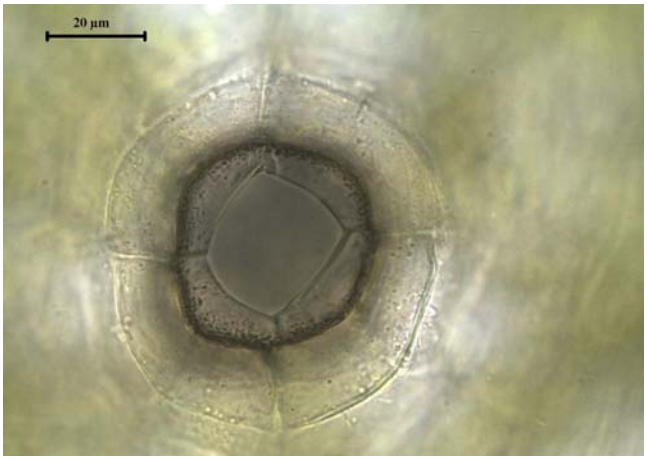

Figure 39. ***Marchantia quadrata*** pore showing cuticular ridge (grey). Photo by Hugues Tinguy, with permission.

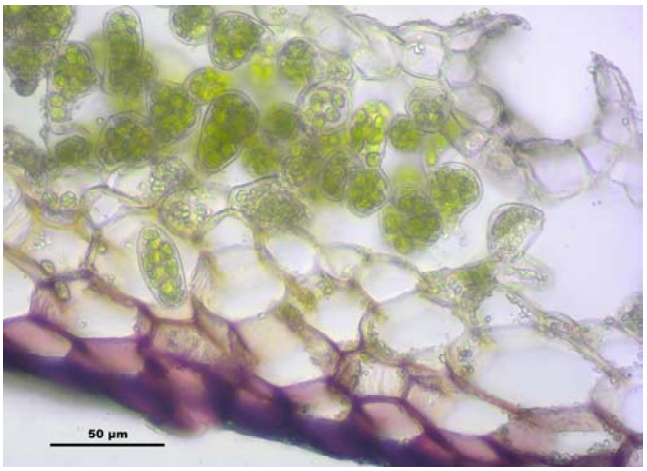

Figure 40. ***Marchantia quadrata*** thallus section showing closed pore, photosynthetic layer, and purple ventral side. Photo by Hermann Schachner, through Creative Commons.

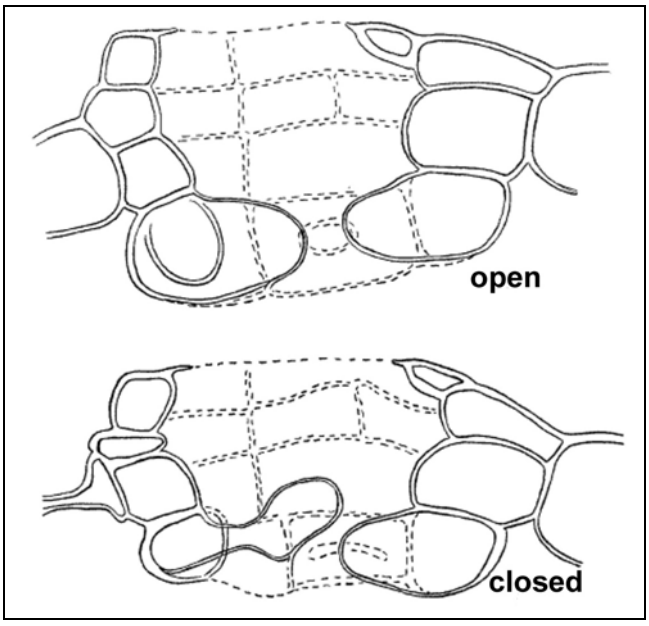

Figure 41. ***Marchantia quadrata*** pore closing. Note that the motor cell on the right is not functioning, presumably due to injury. Image modified from Walker & Pennington 1939.

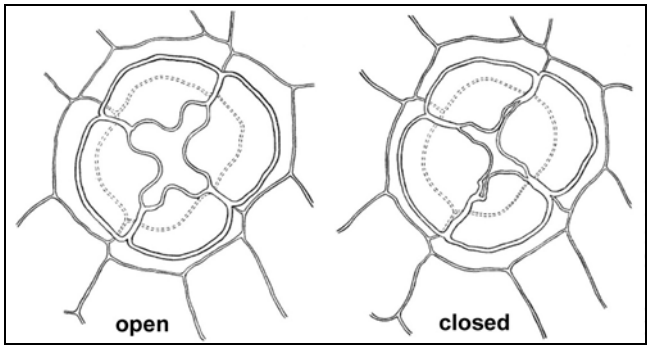

Figure 42. ***Marchantia quadrata*** pore closing. Image modified from Walker & Pennington 1939.

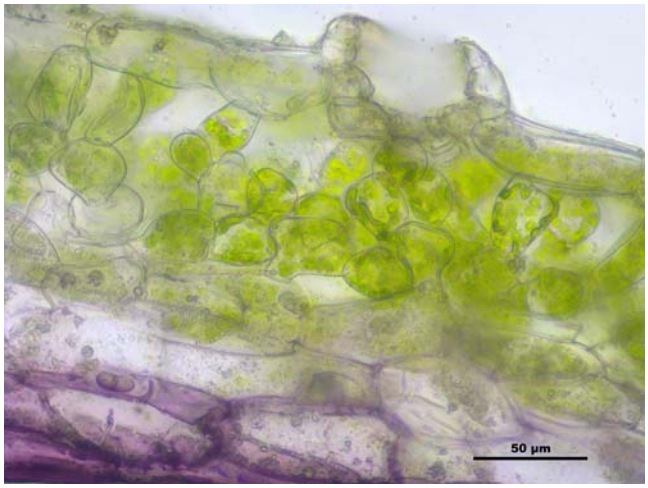

Figure 43. ***Marchantia quadrata*** thallus section showing pore and chamber beneath it with photosynthetic filaments. Photo by Hermann Schachner, through Creative Commons.

Growth occurs at the apical notch, which is covered by a small scale that is usually purplish (Figure 44-Figure 45). The thallus can dry out or senesce while the reproductive branches continue to grow (Figure 46). Red coloration on the thallus margins (Figure 47) is common in this species and could indicate that it has experienced stress.

Figure 44. ***Marchantia quadrata*** in Europe, showing purple covers of the apical growing region. Photo by Michael Lüth, with permission.

Figure 45. ***Marchantia quadrata*** in Europe, showing purple covers of the apical growing region. Photo by Michael Lüth, with permission.

Figure 46. ***Marchantia quadrata*** archegoniophores and dying thallus, showing the ability of archegoniophores to persist even when the thallus is senescing or dying. Photo by Jiří Kameníček (BioLib, Obázek), with permission.

Figure 47. ***Marchantia quadrata*** with red margins, indicating stress. Photo by Allen Norcross, with permission.

One feature that seems to lack documentation for liverworts, but present in ***Marchantia quadrata*** (Figure 1-Figure 5), is the presence of scattered sclerotic cells in the ventral part of the thallus (Haupt 1926). These are elongated, thick-walled, dark brown, fiber-like cells with pointed ends. Their significance is not clear. Cavers (1904) suggests that their primary function is conduction and storage of water. These fibers are absent in the plants that grow in a moist atmosphere (Haupt 1926).

Isolated mucilage cells can be found in all parts of the thallus, but mucilage canals are absent (Haupt 1926). Starch grains seem only to accumulate in the older female receptacles where they presumably are available to the growing sporophytes. Oil globules occur in the apical region, particularly in the epidermal cells, and in the epidermis of the receptacles.

Reproduction

Marchantia quadrata (Figure 1-Figure 5) is usually considered to be **dioicous** (Haupt 1926). However, Haupt (1926) also found a few **monoicous** plants, comprising about 1% of the material studied. Zheng and Shimamura (2022) furthermore noted that dioicous plants are known to be widely distributed in the temperate boreal region and monoicous plants are usually found in the Arctic (Schuster 1972, 1985, 1992; Long & Crandall-Stotler 2020). Are these different races, or different expression of genes in the cold Arctic with its long summer days?

However, all the Japanese ***M. quadrata*** plants that Zheng and Shimamura (2022) examined and found during fieldwork were **monoicous**. Because the growing season of archegoniophores and antheridiophores is different and the archegoniophores do not grow unless fertilization is successful (Haupt 1926) it is easy to falsely conclude that one sex is absent in the population.

In spring in Japan, thalli with young antheridiophores arise from the apex of the ventral side of previous thalli with a well-stalked female receptacle bearing sporophytes Zheng and Shimamura (2022). In summer, a new thallus with a new archegoniophore occurs in the same way from the underside of the apex of the previous thalli with a well-stalked male receptacle and the oldest archegoniophore withers after spore dispersal. That is, each time a new branch is formed, the sexuality alternates. Only by following the same population throughout the year can the true sexuality condition be determined.

Usually the antheridia are produced on a separate stalk, the **antheridiophore** (Figure 48-Figure 50), and archegonia are produced on **archegoniophores** (Figure 51-Figure 58). When the plants are **monoicous**, antheridia occur on the upper surface of the anterior portion of the receptacle and the archegonia occur on the under side of the posterior portion (Haupt 1926). Haupt, presumably in North America, found that antheridia begin to appear in late spring, with archegonia developing somewhat later in early summer.

Figure 48. ***Marchantia quadrata*** antheridiophores. Photo from Bioimages, through Creative Commons.

Figure 49. ***Marchantia quadrata*** antheridiophores. Photo from Bioimages, through Creative Commons.

Figure 50. ***Marchantia quadrata*** antheridiophores. Photo from Bioimages, through Creative Commons.

Benson-Evans (1964) reported that in the UK ***Marchantia quadrata*** (Figure 1-Figure 5) is a long-day plant for sexual reproduction. In 16 hours of light, 66% of the plants expressed sexual structures; in 18 hours of light this increased to 80%. Light of 16.1-87.6 lux was suitable for gametangia development. However, when the temperature was dropped to 10ºC in 18 hours light, the plants exhibited few sexual structures and had slow growth. These were even more limited at both 10ºC and 21ºC in 6 hours light. This species is, however, mostly influenced by photoperiod, operative within a somewhat broad temperature range (Longton 1990).

Both sexual organs continue to form during the entire growing season, with young archegonial receptacles in northern New York, USA, appearing as late as the end of September (Haupt 1926). On 24 September, Haupt observed that nearly all of the plants had the same sexual condition. The male nucleus was within the egg and in contact with the egg nucleus, but not yet fused. These archegonial receptacles overwinter with sporogenous tissue that has just differentiated. In the spring, growth of the sporophytes continues and the female receptacle stalk continues growth. In this location, the spores mature in June.

Figure 51. ***Marchantia quadrata*** with developing archegoniophores. Photo by Hermann Schachner, through Creative Commons.

Figure 52. ***Marchantia quadrata*** with developing archegoniophores. Photo by Claire Halpin, with permission.

Figure 53. ***Marchantia quadrata*** with developing archegoniophore. Photo by Hermann Schachner, through Creative Commons.

Figure 54. ***Marchantia quadrata*** with expanding archegoniophores. Photo by Jan-Peter Frahm, with permission.

Figure 55. ***Marchantia quadrata***, showing numerous fertile plants at Pictured Rocks, Michigan, USA. Photo by Janice Glime.

Figure 56. ***Marchantia quadrata*** young (at tip) and older archegoniophores in Europe. Photo by Michael Lüth, with permission.

Figure 57, ***Marchantia quadrata*** with extended archegoniophores. Note white scales showing at the margins. Photo by Hermann Schachner, through Creative Commons.

Figure 58. ***Marchantia quadrata*** with mature archegoniophores, showing how numerous they can be. Photo by Michael Lüth, with permission.

When the sporangia mature, they protrude from the archegonial head (Figure 59-Figure 63). They burst and elaters wiggle among the spores (Figure 64-Figure 65) in response to moisture changes, in some cases helping the spores to exit the capsule, but in others entangling them in clusters of tangled elaters.

Figure 59. ***Marchantia quadrata*** with mature archegoniophores. Photo by Michael Lüth, with permission.

Figure 60. ***Marchantia quadrata*** mature archegoniophores with green thalli in Europe. Photo by Michael Lüth, with permission.

Figure 61. ***Marchantia quadrata*** archegoniophores with emerging sporangia. Photo by Michael Lüth, with permission.

Figure 62. ***Marchantia quadrata*** mature archegonial head with sporangia. Photo by Des Callaghan, with permission.

Figure 63. ***Marchantia quadrata*** archegoniophore with emerging sporangia and elaters. Photo by Bob Klips, with permission.

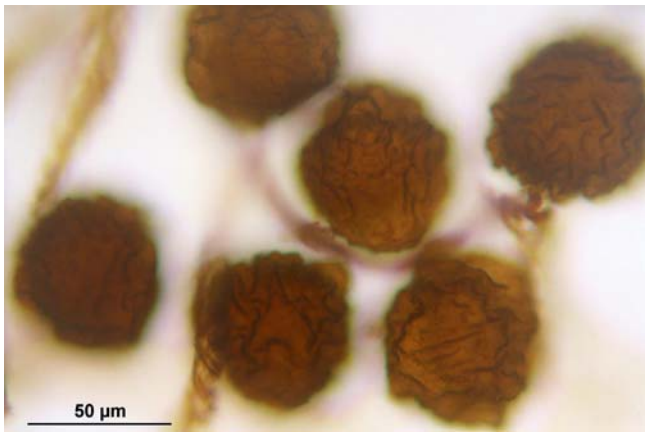

Figure 64. ***Marchantia quadrata*** spores and elaters. Photo by Hermann Schachner, through Creative Commons.

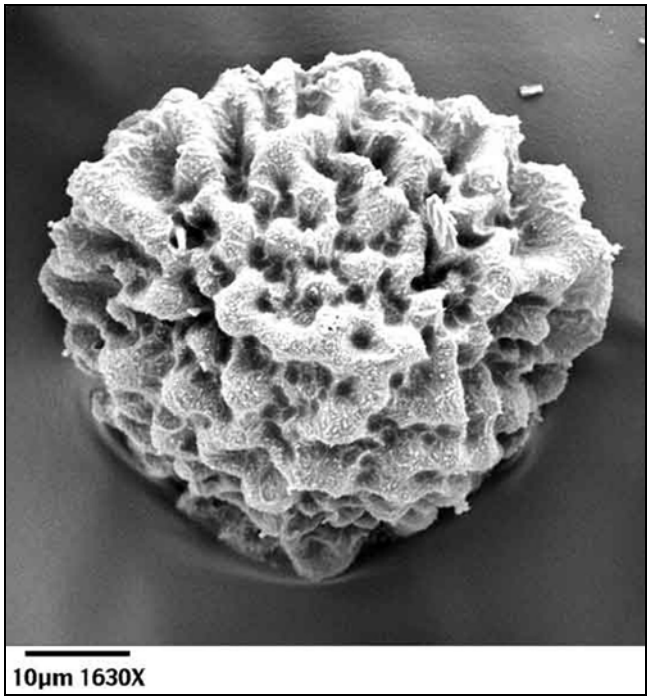

Figure 65. SEM of ***Marchantia quadrata*** distal spore wall. Photo by William T. Doyle, with permission.

Unlike other members of the **Marchantiaceae**, ***M. quadrata*** (Figure 1-Figure 5) has no gemmae (Boisselier-Dubayle & Bischler 1997; Zheng *et al*. 2020). Nevertheless, members of an individual colony were genetically identical, suggesting vegetative reproduction was important, achieved by growth and division of the thalli. There was little indication of any genetic exchange between colonies growing in proximity.

Fungal Interactions

Haupt (1926) reported intracellular fungi in the lower part of the ***Marchantia quadrata*** (Figure 1-Figure 5) thallus (see also Golenkin 1902). These occur mostly along the median line and are more abundant in older tissues. This fungal zone frequently occupies one-half to two-thirds the thickness of the thallus, sometimes reaching the air chambers. In the ventral region, the hyphae form parallel strands that extend longitudinally. Above this area they form compact tangled masses inside the shorter thallus cells.

Biochemistry

Gorham (1977) reported the presence of lunularic acid in all parts of ***Marchantia quadrata*** (Figure 1-Figure 5). This presence was greatest in continuous light. Gorham suggested that either the lunularic acid was not inhibited in continuous light or the inhibition was overcome by products of photosynthesis.

König *et al*. (1996) reported that the main constituent of a southern German chemotype of ***Marchantia quadrata*** (Figure 1-Figure 5) is the labile sesquiterpene hydrocarbon germacrene C. These researchers also observed several rare ent-sesquiterpenes as major constituents.

Asakawa *et al*. (1997) reported a number of sesquiterpenes and the cyclic bis(bibenzyls) riccardin B and neomarchantin A from ***Marchantia quadrata*** (Figure 1-Figure 5).

Marchantia treubii

(syn. = *Marchantia sciaphila*)

Distribution

Siregar *et al*. (2013) reported on ***Marchantia treubii*** from Sumatra. This species is among the most common ***Marchantia*** species on Mount Sibayak, found from lowland to high altitude. It is relatively widespread in Indonesia (Sumatra, Java, Lesser Sunda Island), Borneo, and Malaysia (Bischler-Causse 1989; Chuah-Petiot 2011).

Aquatic and Wet Habitats

Marchantia treubii occurs in the spray of waterfalls in the tropics (Ruttner 1955). ***Marchantia treubii*** occurs on soil and rocks in open places and semi-shaded places in Indonesia (Siregar *et al*. 2013; Haerida 2017). Raihan *et al*. (2018) reported that this liverwort occurs almost everywhere on rocks at their study area at Peucari Bueng Jantho Waterfall in the Aceh Besar District of Indonesia.

Azwir *et al*. (2022) reported its environmental parameters from Mesjid Raya in Indonesia. The site was humid, with *p*H ranging 4.9-7.3 (mean 6.3) and a low light intensity of 0.07-0.09 lux, mean of 0.08 lux. Since the light intensity also affects the temperature and humidity, this indicates lower temperatures and higher humidity in its habitat.

Adaptations

Most of the adaptations described for other species of ***Marchantia*** apply here. ***Marchantia treubii*** from Indonesia had purplish lines on the thallus and fine hair at the edge (Raihan *et al.* 2018). I was unable to find much specific information on this species.

Reproduction

Fritsch (1991) reported a chromosome count of n=9 for ***Marchantia treubii***. It is **dioicous** (Siregar *et al*. 2013). Raihan *et al.* (2018) found ***Marchantia treubii*** with gemmae cups as well as sporophytes in Indonesia, exhibiting female receptacles with 3-5 lobes.

Summary

Marchantia quadrata was classified in the genus ***Preissia*** and might return there. It lacks gemmae, but occurs in similar habitats to some of the ***Marchantia*** species. Its distribution is similar (Australia, Europe, Northern and Southern Asia, Central America, North America, Oceania, and South America). It occurs on wet rocks and soil of stream banks, waterfalls, and dripping cliffs, including limestone. It benefits from phosphates, especially on limestone. It survives winter under the snow, but does not do well in high temperatures. Its adaptations are similar to those of other ***Marchantia*** species, with thick thallus, pores, photosynthetic chambers, rhizoids that either anchor or provide capillary spaces for conduction, and scales that help move and conserve water.

Marchantia treubii occurs in a small, tropical portion of Asia. It is best known from waterfalls, but in some areas of Indonesia it is the most common liverwort on the mountain. It is dioicous and has gemmae.

Acknowledgments

I appreciate the email discussions with T. Zheng and M. Shimamura on the classification of *Marchantia quadrata*.

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CHAPTER 2-5
STREAMS: LIFE AND GROWTH FORMS AND LIFE STRATEGIES

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CHAPTER 2-5
STREAMS: LIFE AND GROWTH FORMS AND LIFE STRATEGIES

Figure 1. ***Fontinalis novae-angliae*** with capsules, exemplifying the **streamer** life form in a mountain stream. Photo by Janice Glime.

Life and Growth Forms

Definitions and Habitats

In bryophytes, **growth forms** are genetically determined forms of adult individual gametophyte plants (Meusel 1935; Mägdefrau 1982). **Life forms** are the environmental expressions of those plants and refer to the growth pattern of the colony. But for many species, perhaps most, a single protonema, developing from a single spore, develops multiple buds that develop into stems and thus form a colony from the onset, giving rise to a **life form** as that colony develops.

A number of bryologists have stressed the importance of life forms as adaptations to habitat conditions. Bryophyte growth forms and life forms can be used to indicate conditions of hydrologic permanence in non-polluted mountain streams (Fritz *et al.* 2009; Vieira *et al.* 2012a). In 165 locations in Portuguese water courses, Vieira *et al.* (2012a) found 11 life forms, with a mean of 2.7 per sample. There was a clear dominance of **smooth mats** (Figure 2; 37%), **tall turfs** (Figure 3; 25%), **fans** (Figure 4; 10%), and **short turfs** (Figure 5; 10%). As habitat zones were less frequently submersed, the number of life forms increased. The deepest or most permanently submersed regions had **mats** and **streamers** [Figure 1; long, dangling stems (Glime 1968)].

Figure 2. ***Frullania tamarisci*** **smooth mat**, a common species near water on canyon walls. Photo by Hermann Schachner, through Creative Commons.

Figure 3. ***Drepanocladus aduncus***, a **tall turf**; this species produces sporophytes when out of water. Photo by Heike Hofmann © swissbryophytes <swissbryophytes.ch>, with permission.

Figure 4. ***Neckera crispa*** **fans**, in this case growing terrestrially. Photo by Malcolm Storey, with online permission.

Figure 5. ***Marsupella emarginata***, an aquatic liverwort that forms a **short turf**. Photo by Hermann Schachner, through Creative Commons.

When Vieira *et al*. (2012b) assessed life forms in mountain streams of Portugal, they found that **thallose liverworts** (Figure 6) typically avoided the flowing water, occurring in shaded locations where they were only seasonally submersed or splashed. These forms were easily damaged by submersion and drag forces. On the other hand, some leafy liverworts that formed **smooth mats** (Figure 2) occurred submersed. Those permanently submersed bryophytes tended to be **streamers** (Figure 1) and **smooth mats**, found up to 30 cm of depth in streams. The **streamers** tended to occur mostly in slower currents of the streambed in full sunlight, whereas **smooth mats** seemed to prefer the torrential water zones in deep shade. Bryophytes subject to frequent water level fluctuations, *i.e.* close to the water, were characterized by a more 3-dimensional life form, but one that was resistant to desiccation and drag forces. These included well anchored **fans** (Figure 4), **dendroids** (Figure 7), and **short turfs** (Figure 5), often occupying vertical surfaces of rocks short distances from the water, but able to benefit from the splash.

Figure 6. ***Pellia epiphylla***, a thallose liverwort that is common on stream banks. Photo by David Holyoak, with permission.

Figure 7. ***Climacium dendroides*** exhibiting the **dendroid** life form. This species can occupy stream banks that get submersed during snowmelt flooding. Photo by Stan Phillips, through public domain.

In the seasonally flooded habitats Vieira *et al*. (2012b) found **tall** and **open turfs** (Figure 8) that have stiff texture, multi-layered tissues, and thick cell walls (Figure 9). These permit them to resist both desiccation and water abrasion. On the upper zones of stones where strong currents are less frequent and in exposed streambeds, bryophytes are represented by **smooth densely-packed cushions** (Figure 10) and **short turfs** (Figure 5) that can resist drought stress (Gimingham & Birse 1957; Muotka & Virtanen 1995; Barrat-Segretain 1996; Vieira *et al*. 2012b). Here and at higher zones on boulders, but in the shade, smooth **mats** (Figure 2) and **fans** (Figure 4) develop (Vieira *et al*. 2012b). Above the level of maximum flooding annuals join the bryophytes, displaying **loose rough mats** (Figure 11) or **wefts** (Figure 12).

Figure 8. ***Tomentypnum nitens***, a wetland **tall turf** species that occurs in fens. Photo by Michael Lüth, with permission.

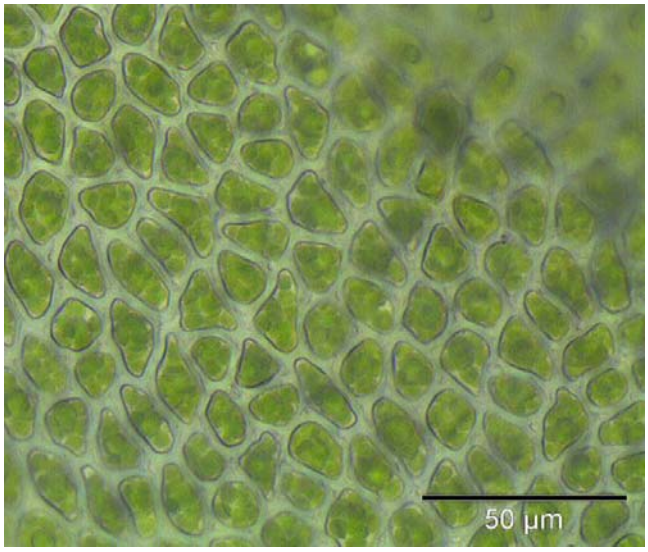

Figure 9. ***Aulacomnium palustre*** leaf lamina showing thick-walled cells. Photo by Kristian Peters through Creative Commons.

Figure 10. ***Andreaea alpina*** **cushion**, a species that can be found on rocks that are occasionally inundated on crags near lakes and streams. Photo by Michael Lüth, with permission.

Figure 11. ***Brachythecium rivulare*** **rough mat**, a species that occurs on stream margins, and in springs and marshes. Photo by Hugues Tinguy, with permission.

Figure 12. ***Trichocolea tomentella*** **wefts**, a species of fens and low areas that can become submersed. Photo by Li Zhang, with permission.

In this same top or higher zones of the boulders, if shaded conditions prevailed for most of the year, **smooth mats** (Figure 2) along with **fans** (Figure 4) developed. Additionally, microhabitats higher than the normal level of maximum floods could be recognized by the co-existence of **annuals** (must grow new plants every year), loose **rough mats** (Figure 11) or **wefts** (Figure 12) that developed mostly associated with deposited sediments.

Birse (1958) related life form to habitat. She found that **wefts** (Figure 12) were typical in freely drained habitats and conditions of intermediate moisture. **Tall turfs** (Figure 3) were more common when water was close to the soil surface. **Wefts** (Figure 12) and **dendroid** (Figure 7) life forms occupied habitats with moisture available from the water table in summer. The semi-aquatic emergents are more likely to be **tall turfs**. Truly aquatic mosses are rarely **tall turfs**, but may be **streamers** (Figure 1, Figure 15), a term introduced by Glime (1968).

Jenkins and Proctor (1985) considered aquatic bryophytes to have two main life forms: **turfs** of densely-set shoots such as those of ***Scapania undulata*** (Figure 13) and ***Hygrohypnum luridum*** (Figure 14) that cling to boulders experiencing turbulent, fast-flowing water; **streamers** (Figure 1, Figure 15) such as ***Fontinalis*** more typical of slower, more streamlined flow. On the other hand, ***F. dalecarlica*** (Figure 15) can occur on boulders in rapids, defending itself with numerous rhizoids and wire-like strong stems.

Thalloid liverworts (Figure 6) grow in zones that are rarely submersed. These liverworts are intolerant of the physiologic stress of continuous submersion or drought and the mechanical stress of mechanical scouring (Gimingham & Birse 1957; Kimmerer & Allen 1982; Martinez-Abaigar & Núñez-Olivera 1991). Rather, they develop in abundance in a more humid and shaded environment above the upper limit of flood-water impact.

Vieira *et al*. (2012b) found that **colonial** growth often occurred through shoot innovations that were firmly attached to the substrate (Figure 16), permitting them to remain in place during heavy flow (During 1990; Grime *et al*. 1990; Muotka & Virtanen 1995). **Ephemeral colonists**, on the other hand, indicate stream zones that are submerged by shifting currents that create abrasive events (Vieira *et al*. 2012b). They survive in tiny rock crevices where they are protected from the torrential currents (Muotka & Virtanen 1995). **Colonists** and **pioneer colonists** are positively correlated with a moderate distance to water and its impact, *i.e.*, in zones that are seasonally flooded with strong discharges (During 1979; Kimmerer & Allen 1982; Vieira *et al*. 2012b). Some **fugitives**, **annual shuttles**, and **stress-tolerant perennials** are able to tolerate slight and infrequent submergence.

Figure 13. ***Scapania undulata***, a **mat**-forming liverwort that can reduce drag in fast water. Photo by Hermann Schachner, through Creative Commons.

Figure 14. ***Hygrohypnum luridum*** with capsule. Photo by Michael Lüth, with permission.

Figure 15. ***Fontinalis dalecarlica***, a **streamer** species that uses numerous rhizoids to maintain its position in rapid water. Photo by Jean Faubert, with permission.

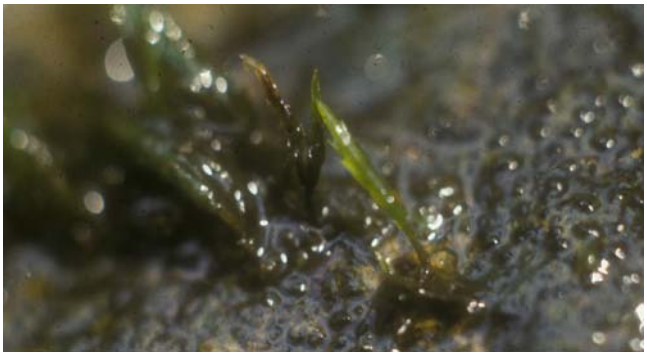

Figure 16. ***Fontinalis novae-angliae*** with new shoots beginning where a stem has been scoured and broken, forming a new colony. Photo by Janice Glime.

Although mountain streams are very different habitats from slow-moving lowland streams, it appears that the life forms defined by Gimingham and Robertson (1950) for English mountain streams can be broadly applied. They identified **large cushions**, **small cushions** (Figure 10), **large turfs** (Figure 3, Figure 8), **small turfs** (Figure 5), **dendroids** (Figure 7), **compact mats** (Figure 2), **thalloid mats** (Figure 6), and **wefts** (Figure 12). As noted, Glime (1968) added **streamers** (Figure 1).

In terrestrial situations, unstable environments are often characterized by acrocarpous mosses such as ***Bryum*** (Figure 17), ***Pottia*** (mostly now in ***Tortula***; Figure 18), and ***Gigaspermum*** (Figure 19) (Ramsay 2006). Pleurocarpous taxa such as ***Hypnum*** (Figure 20) and ***Thuidiopsis*** (Figure 21) seem to require more stable environments. Similar relationships hold in streams, where small, acrocarpous mosses such as ***Blindia acuta*** (Figure 22) live in disturbed areas with movable substrata, whereas the large, pleurocarpous moss ***Fontinalis*** spp. (Figure 23) is characteristic of stable boulders (Muotka & Virtanen 1995). Furthermore, the large **streamers** (***Fontinalis***; Figure 1) occur on the lower parts of stream rocks where they are continuously submersed, whereas the tops of the boulders support growths of low, but not mat-forming, mosses (Virtanen *et al*. 2001).

Figure 17. ***Bryum ruderale***, an **acrocarpous** moss of unstable habitats. Photo by Štěpán Koval, with permission.

Figure 18. ***Tortula lanceolata*** with capsules, an **acrocarpous** moss suitable for terrestrial unstable environments. Photo by Michael Lüth, with permission.

Figure 19. ***Gigaspermum repens***, an **acrocarpous** moss suitable for terrestrial unstable environments. Photo by David Tng, with permission.

Figure 20. ***Hypnum chrysogaster***, a **pleurocarpous** moss requiring a stable environment. Photo by Larry Jensen, with permission.

Figure 21. ***Thuidiopsis furfurosa***, a **pleurocarpous** moss requiring a stable environment. Photo by David Tng, with permission.

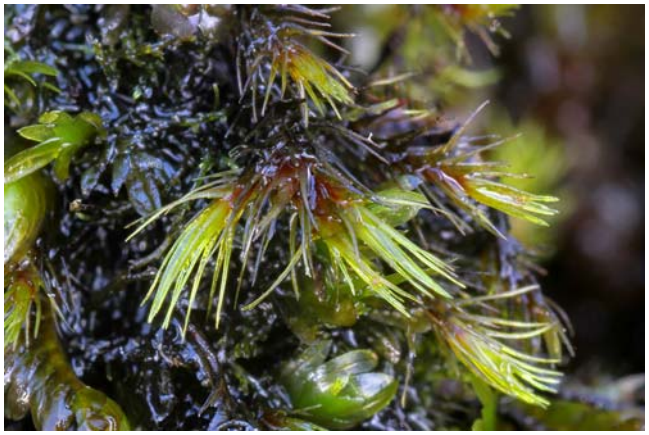

Figure 22. ***Blindia acuta***, an **acrocarpous** species that can live in small crevices in streams. Photo by Barry Stewart, with permission.

Figure 23. ***Fontinalis novae-angliae*** below the water surface and the leafy liverwort ***Plagiochila porelloides*** above. Photo by Janice Glime.

In the Victorian temperate rainforest streams of Australia, all seven of the Gimingham and Robertson (1950) life forms were represented, but not **streamers** (Carrigan 2008), **pendants**, or **tails** (Mägdefrau 1982). However, only two species were of the **cushion** (Figure 10) life form. **Mats** (Figure 2, Figure 11) and **turfs** (Figure 8) were the most represented, with 36 and 32 species, respectively. Wood and sediment had approximately the same distribution of life forms. No life forms stand out on the various sizes of rocks, with approximately the same distribution of life forms on each as for the total set. **Turf** was the only life form that appeared to have significant differences among the rock sizes, with the greatest representation on the medium-sized rocks.

Functional Groups

Monteiro *et al*. (2019) determined the functional structure of bryophytes in headwater streams in Portugal, as represented by life forms. The rock dwellers are typically **rough mats** (Figure 11). Truly aquatic species are mostly perennial, pleurocarpous mosses in **smooth mats** (Figure 24); they rarely produce capsules, and those are typically submerged. The very dynamic mountain flushes, springs, and ephemeral streams support pioneer colonists and **turfs**. Streamsides support **dendroid** (Figure 7) mosses and **thalloid liverwort mats** (Figure 6). At high altitudes, leafy liverworts and competitive perennials predominate. Basic substrates typically have **tufts** and **colonists** of **basophilous** (living or thriving in alkaline habitats) species.

Figure 24. ***Hypnum cupressiforme***, **pleurocarpous** moss forming a **smooth mat**. Photo by Michael Lüth, with permission.

Fernández-Martínez *et al*. (2019) noted the importance of structure and function of bryophytes in the ecosystem. However, the authors lamented that knowledge of these roles is far behind that for other plants. To help in alleviating this lack of knowledge, they investigated 303 moss assemblages in aquatic and semi-aquatic habitats of natural springs in the northeastern Iberian Peninsula. The study encompased 30 moss species and 17 traits using phylogenetic comparative methods and an extended RLQ analysis. They found that **life forms** (results of life conditions, including growth form, influence of environment, and assemblage of individuals) and, especially, morphological traits were well preserved

phylogenetically and responsive to water chemistry and climate. "That combined with spatial autocorrelation in environmental variables resulted in a clustered distribution of phylogenetically closely related mosses in space."

Mosses living in springs with a warm, dry climate and hard water were dominated by species with needle-like leaves, were denser, and had lower water absorption capacity (Fernández-Martínez *et al*. 2019). In cold, humid, soft-water springs, the opposite characters were present. The researchers concluded that among the springs in their study, climate and water chemistry are the main determinants of both traits of hygrophytic mosses and of species distributions. They suggested that their data indicate a potential **sclerophylly** (leaf hardness) continuum in moss traits, and they hypothesize that these may be mainly related to physical and physiological constraints produced by water chemistry. The gradient of the moss sclerophylly in a gradient of water conductivity is similar to that in tracheophytes relative to water availability and temperature. The researchers emphasize that more research is needed before we can make generalities for bryophytes.

Factors Influencing Life Forms

Life forms are important in determining the drag coefficient and in attenuating the flow velocity, especially within the clump. Dodds and Biggs (2002) showed that even **periphyton** (freshwater organisms attached or clinging to plants and other objects) attenuated the flow velocity with depth. In fact, dense colonies of diatoms (primarily ***Cymbella***; Figure 25) had more effect than did filamentous green algae or red algae. Macrophytes also attenuated the flow rates, but less than the periphyton, and their attenuation was more variable.

Figure 25. ***Cymbella***, a member of the periphyton that can attenuate the flow velocity. Photo by Janice Glime.

One of the factors that influences successful life forms is the **diffusion resistance** to CO_2 uptake. Jenkins and Proctor (1985) measured this resistance in the mat-forming leafy liverworts ***Nardia compressa*** (Figure 26) and ***Scapania undulata*** (Figure 13), both species typical of headwaters. The researchers suggested that the high leaf-area index compensates for the diffusion resistance and permits these mats to effectively exploit low boundary-layer resistance at high velocities while at the same time protecting the liverworts from drag. In the **mats**, boundary-layer resistance limits photosynthesis at flow rates less than ~0.1 m s^{-1}. ***Fontinalis antipyretica*** (Figure 27), on the other hand, is not limited until rates slow to 0.01 m s^{-1}. They attribute this to the **streamer** (Figure 1, Figure 15) life form of ***Fontinalis***.

Figure 26. ***Nardia compressa***, a mat-forming liverwort that can reduce drag. Photo by Barry Stewart, with permission.

Figure 27. ***Fontinalis antipyretica***, having a **streamer** life form that permits it to live in both relatively fast and almost still water. Photo by Hermann Schachner, through Creative Commons.

Proctor (1984) summarized both physiological and structural adaptations of bryophytes for the aquatic habitat. Priddle (1979) reported that bryophytes of still or slow-flowing water had open, slender, elongated life forms. Fast-flowing streams favor tight **mats** (Figure 13) or **cushions** (Figure 10) that mimic or even reduce the drag coefficient of the rocks (Jenkins 1982; Proctor 1984; Jenkins & Proctor 1985). ***Nardia compressa*** (Figure 28) and ***Scapania undulata*** (Figure 29) provide such **compact mats** (Proctor 1984). These two species show reductions in photosynthesis in flow rates below 10 cm s^{-1}; this is most likely due to the need for turbulence to penetrate the spaces between the leaves. But by contrast, as will be seen below, ***Fontinalis*** species typically have trailing shoots (**streamers**; Figure 1, Figure 15) that are able to move easily with the water flow, permitting water to enter the clump. ***Fontinalis antipyretica*** (Figure 30) shows little change in the rate of photosynthesis with flow reduction down to 1 cm s^{-1}.

Figure 28. ***Nardia compressa*** showing **compact mat**. Photo by Hermann Schachner, through Creative Commons.

Figure 29. ***Scapania undulata*** showing **compact mat**. Photo by Michael Kesl, through Creative Commons.

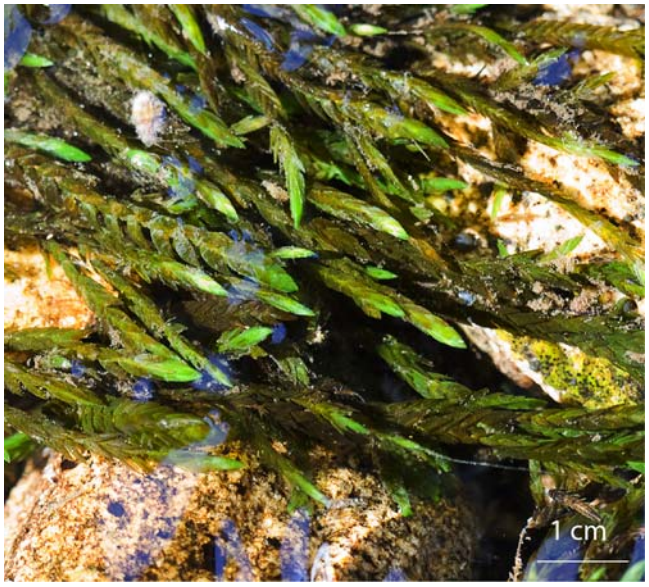

Figure 30. ***Fontinalis antipyretica*** showing a **streamer** life form. Photo from Projecto Musgo, through Creative Commons.

Morphological Plasticity of Life Form

Life forms can differ for a species when its habitats vary. ***Climacium dendroides*** (Figure 31) changes from an upright **dendroid** plant to a **creeping**, non-dendroid plant after a long submergence. The Southern Hemisphere species of ***Hypnodendron*** (Figure 32) and ***Hypopterygium*** (Figure 33) behave similarly.

Figure 31. ***Climacium dendroides***, in a genus that changes from an upright **dendroid** plant to a **creeping**, non-dendroid plant after a long submergence. Photo by Li Zhang, with permission.

Bates (1998) reminded us that life forms "minimize evaporative water loss and maximize primary production." Many species show plasticity of life form according to environmental conditions. One of the common characteristics of aquatic bryophytes is the ability to express different life forms when being grown in different conditions. This can be sufficient to cause erroneous descriptions of new species.

Figure 32. ***Hypnodendron menziesii*** from New Zealand, in a genus that changes from an upright **dendroid** plant to a **creeping**, non-dendroid plant after a long submergence. Photo by Jan-Peter Frahm, with permission.

Figure 33. ***Hypopterygium novae-seelandiae***, Saddle Mtn. Rd., NZ, in a genus that changes from an upright **dendroid** plant to a **creeping**, non-dendroid plant after a long submergence. Photo by Janice Glime.

Scapania undulata (Figure 13) occupies a range of habitats from full submersion to rocky ledges in streams of Poland (Samecka-Cymerman 1990). The ledge populations typically are 2-3 cm long, whereas the stream populations are usually 5-10 cm, up to 20 cm. Samecka-Cymerman suggested that low nitrogen might account for the smaller plants on the ledges, a phenomenon known from tracheophytes (Czerwiński (1976; Gumiński 1976). It exhibits a range of morphology that has caused at least one of its forms to be described as separate species (*e.g.* ***Scapania dentata***) (Hiesey 1940), now considered a synonym (Hiesey 1940).

Higuchi *et al*. (2003) reported **mat**-forming green plants from acidic rivers in Japan. When cultured, these produced bryophyte gametophyte buds, indicating that the filaments were protonemata (Figure 34). The large subunit of ribulose-1, 5- bisphosphate carboxylase/oxygenase indicated the moss was 98% similar to ***Dicranella heteromalla*** (Figure 35). This species is common in acidic habitats, including woodland banks, tree stumps, tree roots, hedge banks, dry peaty banks, and sheltered soil of crevices on crags and gullies in the mountains (Royal Botanic Garden, Edinburgh 2019). In Illinois, it occurs also on sandstone walls along streams (Hilty 2017). Its protonemal growth in the water may be a habitat response that inhibits gametophore development.

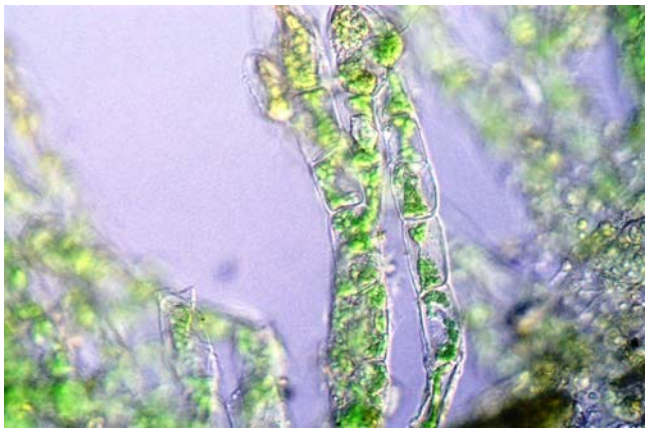

Figure 34. ***Dicranella heteromalla*** protonema, a stage that seems to stop development in very acidic rivers. Photo by Jiri Váňa, permission pending.

Figure 35. ***Dicranella heteromalla*** with capsules, a species with attenuated development in very acid water. Photo from Botany Website, UBC, with permission.

Life Strategies and Reproduction

I was surprised at how few studies appeared when I searched Google for aquatic bryophyte reproduction. But at least some studies exist. Field observations have suggested that production of capsules in submersed bryophytes is relatively rare (Carrigan & Gibson 2004; Ares *et al*. 2014). Instead, fragmentation has seemed to be a major strategy.

Like the life forms, the number of life strategies increases as the frequency of submergence decreases for bryophytes associated with Portuguese streams (Vieira *et al*. 2012a, b). Water velocity and hydrologic zone are the primary influences on the life strategies present (During 1979; Lloret 1986; Vieira *et al*. 2012b). The communities that were mostly submersed were characterized by **perennials** and **ephemeral colonists** (Vieira *et al*. 2012b). Those communities that were more frequently emergent had more diversity of life strategies. At higher altitudes, **perennials** seemed to be favored. Hence, **perennials** are more likely in permanent fast-flowing currents, whereas **pioneer colonists** and **colonists** are more common in the lower currents or emergent positions. In those habitats emerged for brief periods each season, **fugitives**, **annual shuttle species**, and **stress-tolerant perennials** were able to colonize deposited sediments.

In their study of environmental drivers for stream bryophytes, Lang and Murphy (2012) concluded that bryophyte abundance in high-latitude streams was typically a function of predominant growth morphology and life strategy. Ock (2014) included life cycle strategies among the adaptations to rheophytic conditions in bryophytes. He described them as mostly **dioicous** (having separate male and female plants) with rare or uncommon sporophytes. This results from the difficulty of travel for the sperm from the **antheridium** (Figure 36) as it attempts to overcome water flow on its way to the **archegonium** (Figure 37-Figure 38) that is located on a different plant.

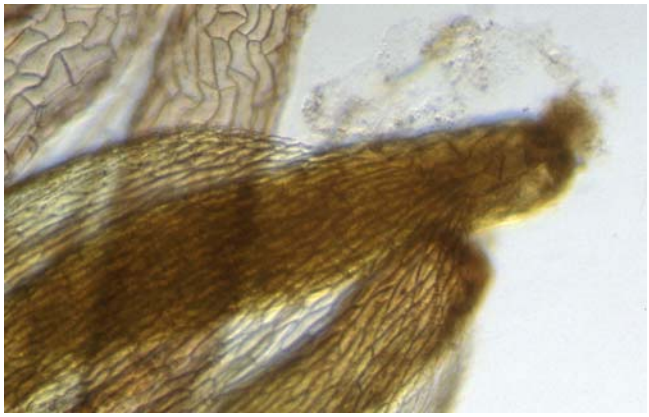

Figure 36. ***Fontinalis duriaei*** antheridia on 13 September 1979 in Coles Creek, Houghton County, Michigan, USA, cultured at 20ºC in artificial stream. Photo by Janice Glime.

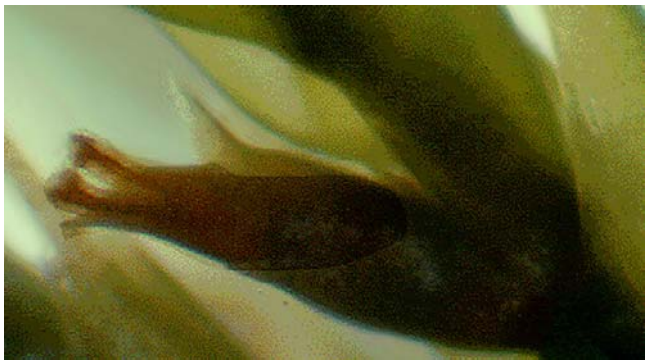

Figure 37. Archegonia of ***Fontinalis*** sp. showing red neck canal cells. Photo by Janice Glime.

Figure 38. ***Fontinalis*** archegonia, with the enlarged one indicating it has been fertilized. Photo by Janice Glime.

Thamnobryum alopecurum (Figure 39) is **dioicous**. During (1978b) found the largest numbers of inflorescences in places with constantly high air humidity. These places also tend to have greater mixing of male and female plants. In drier air, the plants remain mostly sterile. Instead, they develop into large sprouting systems that have little contact between each other. Some even form moss balls in these conditions.

Figure 39. ***Thamnobryum alopecurum*** with capsules, a **dioicous** species with more reproductive inflorescences in places with constantly high humidity. Photo by Snappy Goat, through public domain.

Sexual Strategies and Gametangia

Leitgeb (1868) found antheridia on ***Fontinalis antipyretica*** (Figure 27) from spring until fall, a pattern similar to that which I found in several ***Fontinalis*** species in the Keweenaw Peninsula of Michigan, USA and the long period of development for antheridia is typical of antheridia (see Volume 1, Chapter 5-8). Degree of **apical dominance** (physiological behavior in which the main axis grows more strongly than side branches) is important in determining the location of antheridia and archegonia in ***Fontinalis*** (Berthier 1968). With weak apical dominance, the sexual shoots occur at the axils of the first leaves on side branches. By contrast, when there is strong apical dominance, the main stem forms narrow leaves and these have densely branched first-order sexual shoots in their axils. These first-order shoots occur naturally when the free CO_2 decreases rapidly in the water of late spring, a phenomenon repeated at 8ºC in the laboratory. Apical dominance of the vegetative stem can be increased by cutting off some of the leaves or by using weak illumination.

Carrigan and Gibson (2003) compared the sexuality of species that occurred both streamside and on stream rocks at Cement Creek in the Yarra Ranges National Park, Victoria, Australia. They found that streamside populations had higher numbers of stems, inflorescences, and **gametangia** [archegonia (Figure 37-Figure 38) and antheridia (Figure 36)] than did the same species on stream rocks. The streamside populations of species tested produced more sporophytes than those species on stream rocks. ***Cyathophorum bulbosum*** (Figure 40), however, produced more sporophytes on the stream rocks than did its

populations on streamside locations. The gender was generally female-biased for stem numbers and numbers of inflorescences.

Figure 40. ***Cyathophorum bulbosum***, a species that can produce more sporophytes on the stream rocks than do its populations on streamside locations. Photo by John Braggins, with permission.

Berthier (1966) explored the role of light in initiation and development of the sexual organs in ***Fontinalis*** (Figure 27). He found that light influenced both the density and development of buds, with antheridia forming on branches. A low growth rate enabled formation of these antheridial branches. Increased light intensity increased both the density and initiation of these antheridial branch buds.

Fertilization

Goebel (1913, 1915-1918) illustrated development in some of the water mosses, including ***Fissidens*** (Figure 41), ***Fontinalis*** (Figure 27), ***Hygroamblystegium*** (Figure 42), and ***Thamnobryum*** (Figure 39). His drawings included details of archegonia and antheridia. I translated one of his statements to mean that fertilization in ***Fontinalis*** took place in a "glass" of water. A better translation is that the gametangia are suppressed but can be richly formed. The sperm are easily swept away in flowing water. If both archegonia and antheridia are in small water volumes, the ***Fontinalis*** fruits richly. If the sporophytes are not under water, the spores perish. These observations of Goebel emphasize the importance of timing as part of the life strategies. For example, fertilization is likely to be more successful when the water level is low and they can swim without being washed away. In other cases, fast water might be required to splash sperm from males to females. This might mean that only emergent females get fertilized, but at least some should receive sperm.

Scapania undulata (Figure 13) is among the widely distributed species of aquatic bryophytes. It grows in shallow streams from boreal regions to subtropical zones (Holá *et al*. 2014). It is dioicous, making fertilization difficult, particularly in its typical submersion in rapid water. But Holá *et al*. (2014) found that it had an "overproduction" of males in 10 streams in southern Finland (100 plots) and suggested that this might be a strategy to overcome sperm dilution in the flowing water, "ensuring" fertilization over longer distances in the water. This male bias contrasts with most dioicous species and seems to relate to its flowing-water habitat. The males and females differ in branching pattern, but no size difference exists. They found few females sex-expressing in the female-only plots and female plants had only one sexual branch per female shoot. The low number of sex-expressing shoots in female-only plots, no co-occurrence of gemmae and female sex organs on a single branch, large number of male plants, and only one sexual branch per female shoot suggest a trade-off between sexual and asexual reproduction and a higher cost for female reproduction.

Figure 41. ***Fissidens fontanus***, a species that develops sporophytes above and below water, but the operculum does not dehisce. Photo by Matt Keevil, through Creative Commons.

Figure 42. ***Hygroamblystegium fluviatile***, in one of the genera for which fertilization was described by Goebel. Photo by Hermann Schachner, through Creative Commons.

Belkengren (1962) further learned that sexual reproduction in ***Leptodictyum riparium*** (Figure 43) was induced by a CO_2-free period, followed by addition of CO_2 or sugar. It is a little more difficult to suggest how this might apply in nature, but it could be a change from high temperatures, hence low CO_2, followed by cooler temperatures in which more CO_2 can dissolve in water. Subsequently, it appears that senescence of the plants may induce the formation of sporophytes, perhaps by stopping

the production of some inhibitory substance or reduction of photosynthesis.

Figure 43. ***Leptodictyum riparium*** with capsules, a species in which yeast inhibits development from protonemata to the next stage. Photo by Michael Lüth, with permission.

Sporophytes

Aquatic moss sporophytes can be divided into two groups (Vitt 1981). In one group, the gametophytes are aquatic, but the sporophytes are not, often being produced during periods of low water. This includes such taxa as ***Scorpidium*** (Figure 44), ***Hygrohypnum*** (Figure 14), ***Platylomella*** (Figure 45), ***Platyhypnidium riparioides*** (Figure 46), and ***Drepanocladus*** *s.l.* (Figure 3). The other group produces sporophytes that are adapted to the aquatic habitat. This group of species includes ***Blindia*** (Figure 47), ***Fontinalis*** (Figure 27, Figure 50), ***Scouleria*** (Figure 48), ***Wardia*** (Figure 49), and others with reduced or absence of peristomes, ovate or oblong, smooth, immersed capsules, enlarged perichaetial leaves, and pachydermal exothecial cells.

Figure 45. ***Platylomella lescurii***, a species that produces sporophytes while the plant is above water. Photo by Northern Forest Atlas, with permission from Jerry Jenkins.

Figure 44. ***Scorpidium scorpioides*** with capsules, a species that produces these sporophytes while the plant is above water. Photo by Michael Lüth, with permission.

Figure 46. ***Platyhypnidium riparioides*** with capsules, a species that develops sporophytes above and below water, but the operculum does not dehisce. Photo by J. C. Schou, with permission.

Figure 47. ***Blindia acuta***, a species that produces sporophytes while the plant is below water. Photo by Barry Stewart, with permission.

Figure 48. ***Scouleria aquatica*** with capsules, a species that typically produces sporophytes while the plant is below water. Photo by Matt Goff, with permission.

Carrigan and Gibson (2004) followed 9 mosses and 7 liverworts, representing 8 and 6 families respectively. They found sexual reproduction, but not in all species. As in the 2003 study, they found that sexual reproduction was lower on stream rocks than in more terrestrial habitats. Asexual reproduction was most important in maintaining colonies compared to sexual reproduction, with all species exhibiting asexual reproduction. There was a female sex bias in all but 2 species. There seemed to be no synchrony of phenological stages.

Landry (1973) collected field-grown capsules of ***Fontinalis dalecarlica*** (Figure 15) in June, 1973, in Plymouth, New Hampshire, USA. These immature capsules were permitted to develop in culture until 27 July 1973, but they remained green and did not appear to be completely mature. Capsules were sterilized, opened, and spores spread on a Chlorophyta medium with 3 ppm tannic acid added. There was still no germination on 10 August when it became necessary to terminate the experiment. This was an unusually late date for capsule maturation compared to what had been observed in prior years, and the sterilization process with 0.1N potassium permanganate may have damaged the spores. The other problem is that the capsules had been transported from New Hampshire to Houghton, Michigan and may have experienced excessive temperatures during the trip.

Figure 49. ***Wardia hygrometrica*** with capsules, a species that typically produces sporophytes while the plant is below water. Photo by Sanbi, with online permission.

Kortselius (2003) found that ***Fontinalis antipyretica*** (Figure 27) produces capsules when it is submerged (Figure 50), but he considered dry conditions to be necessary for dehiscence (Figure 51). When desiccation occurs, the operculum is torn loose and lifted off by the hygroscopic movements of the exostome teeth (Figure 52). Spores are released during reversible shape changes in the capsule (Figure 53). It seems that this would require careful timing so that capsules were still pliable when they were desiccated. old capsules have thick walls and are quite hard, seemingly unable to change shape significantly.

During (1978a) found capsules on ***Fontinalis antipyretica*** (Figure 27) 30 April-2 May, but his short note did not indicate the degree of maturity. In my own studies I did not find this species with capsules, but this species was not nearly as common as other ***Fontinalis*** species in the areas that I studied.

Figure 50. ***Fontinalis dalecarlica*** submersed capsules on 26 November 1979 in Fox Run, Plymouth, New Hampshire, USA. Note that the operculum is still intact in the upper mature capsule, but missing in th lower one. Photo by Janice Glime.

Figure 51. ***Fontinalis*** capsule that is shedding its operculum out of water. Photo by Janice Glime.

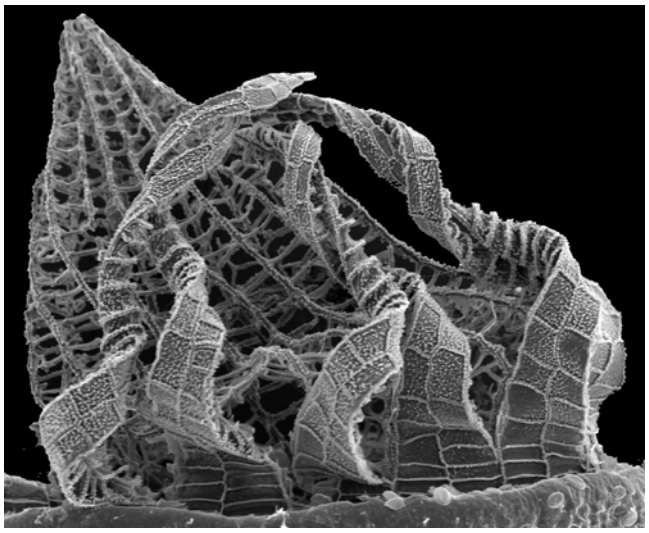

Figure 52. SEM of ***Fontinalis*** peristome showing inner trellis endostome and outer twisted teeth of exostome. Photo by Misha Ignatov, with permission.

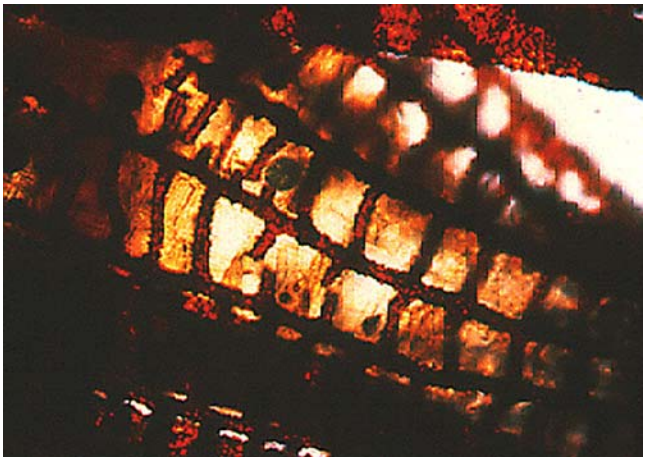

Figure 53. Trellis peristome of ***Fontinalis*** showing green spores among the teeth. Photo by Janice Glime.

Although ***Fissidens fontanus*** (Figure 41) produces capsules in the USA and Europe, capsules were unknown in Mexico. Pursell (1992) reported these in Mexico for the first time. However, no data were available on timing of capsule production. The capsules were illustrated, demonstrating the short seta compared to some species of ***Fissidens***. The capsule likewise was quite small, with an urn only about 0.2-0.3 mm long in the one illustrated.

Lawton (1966) reported capsule production in ***Hygrohypnum bestii*** (Figure 54). This was the first time that the sex organs and capsule had been described in this dioicous species. The species occurs in montane streams, typically at 1500-3000 m elevation, on wet rocks that are often covered with silt.

Figure 54. ***Hygrohypnum bestii***, a **dioicous** species that rarely produces capsules. Photo by Robin Bovey, with permission through Dale Vitt.

One of the reasons for the lack of capsule observations may be the timing of their presence (Glime 2014). In a stream in New Hampshire, USA, both ***Fontinalis dalecarlica*** (Figure 15) and ***F. novae-angliae*** (Figure 23) produce their capsules in the freezing waters of winter. The capsules are badly eroded by the spring runoff, and it seems likely that this is a major vehicle for spore dispersal. By the time the snow is gone, most of the capsules have disappeared, and only a few damaged capsules remain. Their appearance at that time suggests that it is abrasion, not loss of operculum, that permits spore dispersal.

The timing in Finland does not seem to fit this pattern. Kotilainen (1927) found capsules on ***Fontinalis dalecarlica*** (Figure 15) on 6 July 1925 in Finland.

Dispersal

Few studies have addressed dispersal in aquatic bryophytes. Miller (1985) examined subfossils of a number of bryophyte fragments in late Pleistocene deposits buried in sediments in the northeastern United States. These suggested that the fragments had served as propagules dispersed by wind and melting glaciers. Many of the fragments had shoots extending from them, supporting the notion that these were serving as propagules.

Elssmann (1923-1925) commented on the fact that capsules of ***Fontinalis antipyretica*** (Figure 27) retained their lids (Figure 51). He noted that Grimme had mentioned that the shedding of the operculum may be delayed until April of the next year, attributing this to the fact that the plants remain submersed. Rather, at least in culture, the capsules themselves were eventually shed several months after maturity, falling to the bottom of the culture dish. There they gradually died, as did the spores inside. Grimme had reported capsule ripening in August, so Elssmann harvested capsules from his cultures at the beginning of July and found them to contain spores with abundant chlorophyll. When the spores were then cultured, nearly all had germinated within 18 days. Elssmann also cultured capsules on moist sand starting in April. These drier capsules likewise failed to lose the operculum. But the spores developed as they had in the submersed capsules. The same behavior occurred in ***Cinclidotus fontanus*** (***C. fontinaloides***?; Figure 55), ***Fissidens fontanus*** (Figure 41), and ***Platyhypnidium riparioides*** (Figure 46). This begs the question, then, how do the spores escape the capsule? The image in suggests that they do indeed dehisce in nature.

Figure 55. ***Cinclidotus fontinaloides*** with capsules that have lost their opercula. Photo by Hermann Schachner, through Creative Commons.

Hydrochory

Hutsemekers *et al*. (2013) addressed the question of dispersal somewhat indirectly by examining gene flow in ***Platyhypnidium riparioides*** (Figure 46). They summarized the assumed effects of **hydrochory** (dispersal by water): decreases or erases patterns of isolation by distance, increases outbreeding, and results in downstream increase in genetic diversity. They found that the geographical partitioning of genetic variation was "substantial" in the river basin. Using this as indirect measurement of dispersal, they found that the overall dispersal ability of moss diaspores, including fragments, was weaker than that of pollen or windborne seeds. Thus, these spore-producing plants suffer from the severe limitations of clonal dispersal and establishment. Hydrochory does not enhance dispersal and fertilization, at least in ***P. riparioides***. Instead, the genetic structure suggests clonality and discrete events of spore migration, with the **unidirectional diversity/dispersal hypothesis** (downstream hydrochoric spread of propagules of aquatic and riparian plant species, without upstream compensation, can be expected to result in downstream accumulation of population genetic diversity) being unsupported by this species. Rather, **metapopulation** (group of populations separated by space but are same species) processes apply to this aquatic moss. As the concept of metapopulation implies, such spatially separated populations interact as individual members move from one population to another. This can occur through spores, fragments, or specialized vegetative propagules.

Certainly ***Fontinalis*** species benefit from downstream dispersal in flow. This is possible because vegetative propagation is usually successful in these species (Welch 1948). In fact, biologists with the Burley Irrigation District in Cassin County, Idaho, USA, complained that it (***Fontinalis duriaei*** – Figure 56-Figure 57) "catches on almost anything and holds silt, forming mounds in the canals. It is hard to kill, and costs considerable to keep it out." When wounded, stems of ***Fontinalis*** will produce protonemata at the site of a broken stem (Figure 58). Removal of the stem tip can result in new branches below the apex in several ***Fontinalis*** species (Figure 59-Figure 61).

Figure 56. ***Fontinalis duriaei***, a species that is rejected by Rainbow Trout, but that passes through the digestive tract mostly without physical damage. Photo by Michael Lüth, with permission.

Figure 57. Detached ***Fontinalis duriaei*** caught on wood in Gardner's Creek, Michigan, USA. Photo by Janice Glime.

Figure 58. Protonemata growing from broken tip of ***Fontinalis hypnoides***. Photo by Janice Glime.

Figure 59. ***Fontinalis antipyretica*** wound rhizoids and a new branch just below the broken tip. Photo by Janice Glime.

Figure 60. ***Fontinalis squamosa*** branch below broken tip, exhibiting phototropism to a light source at the left. Photo by Janice Glime.

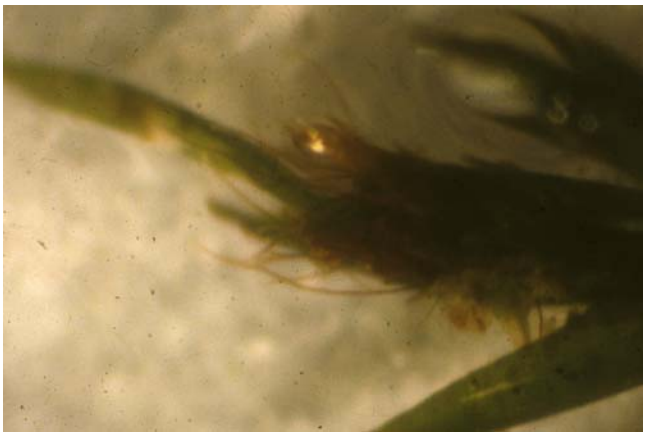

Figure 61. ***Fontinalis squamosa*** with broken tip and a new branch initiating just below that break. Photo by Janice Glime.

Welch (1948) noted that ***Fontinalis sphagnifolia*** (Figure 62) produces "rhizomes" with numerous rhizoids. This permits it to spread, but also provides a base ready for establishment in a new site when it gets carried downstream by water flow. The effectiveness of flow dispersal is suggested by observations of ***Fontinalis*** in a series of connected moraine ponds (Sayre 1945).

Figure 62. ***Fontinalis sphagnifolia***, a species that produces rhizomes with numerous rhizoids. Photo by Will Van Hemessen, through Creative Commons.

Korpelainen *et al*. (2013) used genetic markers in three clonal aquatic moss species in a connected lake system. They found a mean genetic diversity per population of 0.138 for ***Calliergon megalophyllum*** (a quiet water species; Figure 63), of 0.247 for ***Fontinalis antipyretica*** (slow to moderately rapid water; Figure 27, Figure 30), and of 0.271 for ***Fontinalis hypnoides*** (moderately rapid water; Figure 64). The total diversity of their populations in the connected lake system was 0.223, 0.385, and 0.421, respectively. Although the differences were significant, there was evidence of a moderate amount of gene flow within this system. The researchers suggested that both water flow and animal vectors, including water flow, dispersed these three bryophytes. Furthermore, the genetic structure suggests that fragments are the major contributors to this dispersal.

Figure 63. ***Calliergon megalophyllum***, a species that might be dispersed by both water flow and animal vectors. Photo from Earth.com, with permission.

Figure 64. ***Fontinalis hypnoides***, a species that can regenerate from broken stem tips. Photo by Ivanov, with permission.

Adaptations for Hydrochory

Boedeltje *et al*. (2019) assessed the floating ability, shoot length, and abundance as drivers to facilitate hydrochorus dispersal of bryophyte fragments. Using a 200 µm net they followed dispersal of viable bryophyte fragments for one year in a navigation canal in the Netherlands. They examined the relationship of dispersal to fragment buoyancy, shoot length, growth form, abundance in the vegetation, and discharge. They found that 77% of their 144 samples contained bryophyte fragments, comprising 54,514 fragments and 18 species of bryophytes. ***Riccia fluitans*** (Figure 69), a floating liverwort, was the most abundant species, followed by ***Brachythecium rutabulum*** (Figure 65). Variation for most (total of 55% of variation) of attached species could be explained by abundance in the vegetation, buoyancy, and shoot length. Among those sessile species, mean floating time was 5.9 days and mean shoot length 79 mm. Species that occurred in the canal but were poorly represented or absent in the net collections had a significantly lower buoyancy and shoot length.

Figure 65. ***Brachythecium rutabulum***, an attached streambank species that is common in drift water. Photo by Robert Klips, with permission.

Dispersal Vectors

One of the problems of dispersal in aquatic habitats is isolation (Figuerola & Green 2002). While streams can carry propagules downstream, they cannot carry them to a different stream or disconnected lake. Many rarely produce spores that could be transported by wind to a different water body. But recent studies have indicated that waterbirds can facilitate dispersal. Fortunately, even small fragments of leaves can develop new plants, and these can easily be transported by feathers and feet. And some may survive gut transport.

Lazarenko (1958) considered long-distance dispersal of moss spores unlikely, considering their dispersal to follow patterns like those of tracheophytes. Rather, he considered there to be polytopic origins to account for disjunctive species. While the dispersal of spores in ***Fontinalis*** (Figure 56-Figure 62) seems to be facilitated by abrasion and flowing water (Glime *et al*. 1979), the lack of dehiscence in most capsules would seem to support Lazarenko's suggestion. On the other hand, fragments can travel relatively long distances in the flow, and water birds

might carry the moss fragments in their feathers. It is likely that bears and other mammals can carry the fragments in their fur and claws.

Proctor (1961) demonstrated that the liverwort ***Riella*** (Figure 66-Figure 67) spores can be dispersed by waterfowl. Mallard ducks were placed in a pen with ***Riella*** having mature spores. The ducks consumed the liverworts immediately. Feces were collected 50 minutes later and examined. Many individual spores were present, but there were no intact sporophytes and all the fragments were dead. Spores subsequently stored in water at 24ºC germinated after 60 days.

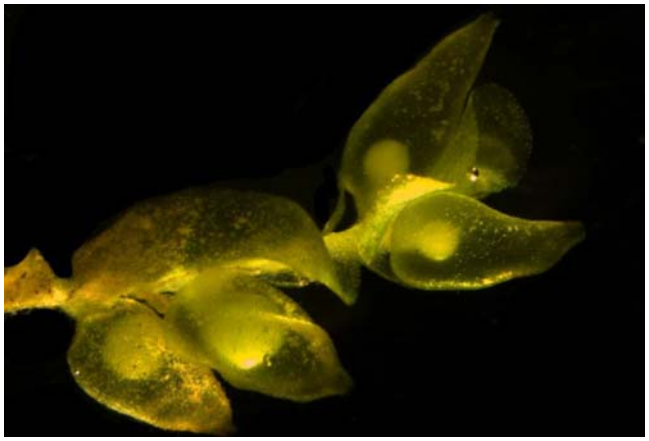

Figure 66. ***Riella helicophylla*** showing capsules. Photo by NACICCA through Creative Commons.

Figure 67. ***Riella cossoniana*** showing spores that can be dispersed by ducks. Photo by Jan-Peter Frahm, with permission.

Laaka-Lindberg *et al*. (2003) reviewed dispersal of asexual propagules in bryophytes. They also noted that migrating birds, especially waterfowl, can carry vegetative attached to the mud on their feet (see also Davison 1976). Such a possibility for the floating liverworts ***Ricciocarpos natans*** (Figure 68) and ***Riccia fluitans*** (Figure 69) was suggested by Buch (1954). It would be interesting to see if these two species are eaten by waterfowl, especially as they accompany duckweed, and if they can germinate from the feces. Frahm (2007) also assumed that the worldwide distribution of ***Ricciocarpos natans*** had been facilitated by waterfowl.

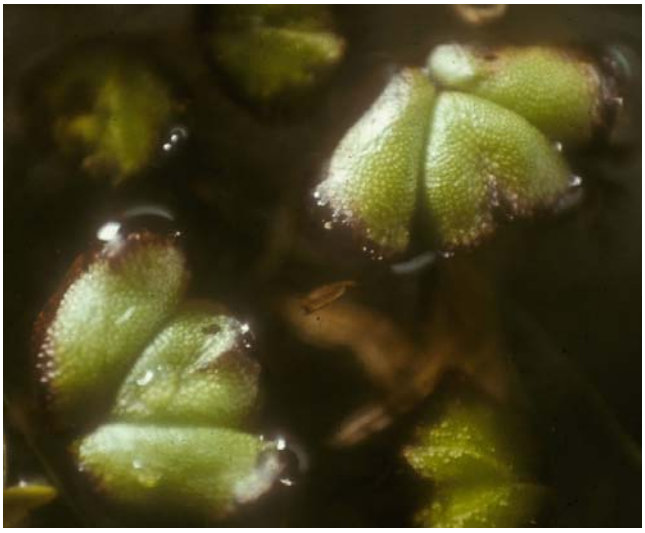

Figure 68. ***Ricciocarpos natans***, a floating liverwort with the potential of dispersal by waterfowl. Photo by Janice Glime.

Figure 69. ***Riccia fluitans***, a floating liverwort with the potential of dispersal by waterfowl. Photo by Štěpán Koval, with permission.

Lewis *et al*. (2014) brought further credence to these suggestions by showing correlations between transhemispherical migratory routes of shorebirds and the bipolar disjunctions in bryophytes. They then examined a number of birds in their Arctic breeding grounds, finding bryophyte propagules, among other propagules, clinging to the feathers. Eight species of these migrant waders had bryophyte diaspores among their feathers. The propagules were so common among the feathers that they suggested the entire population could potentially carry viable plant parts during migration.

It is possible that fish aid in the dispersal of aquatic mosses. Since the mosses provide cover for a number of aquatic insect species (Glime 1994; see Volume 2), they are a good site for foraging by fish. It is likely that at least occasionally the fish may ingest bits of mosses. Paulson (1980) collected a "packet" of feces (Figure 70) from

Rainbow Trout (*Oncorhynchus mykiss*) that was comprised mostly of ***Fontinalis duriaei*** (Figure 56). The moss was bright green when it was expelled. It was placed in a baby food jar in the artificial stream, but by the second day it had lost its green color. If it had been deposited in a stream instead of such a confined space, the associated gut contents would have been diluted and might not have the same effect on the moss, perhaps permitting its survival. If so, this would be a potential mechanism for moving the mosses upstream as well as downstream for dispersal. However, I must point out that the moss had to be force-fed to the fish, so I suspect this mode of dispersal is rare.

Figure 70. ***Fontinalis duriaei*** in feces from force-fed Rainbow Trout. Photo by Janice Glime.

Boch *et al*. (2013) reasoned that slugs might be good dispersal agents for bryophyte spores since they often eat spores (Figure 71). But could the spores survive the digestive tract? They fed capsules of several bryophyte species to three species of slugs. They found an overall germination rate of 51.3% of bryophyte spores from the 117 samples. Among these was the streambank species ***Apopellia endiviifolia*** (Figure 72). There was little difference evident among the bryophyte species, but there was strong variation among the spores from the three slug species (Figure 73): ***Arion vulgaris*** (Figure 74), ***Arion rufus*** (Figure 75), ***Limax cinereoniger*** (Figure 76).

Figure 71. ***Ariolimax cf. californicus*** feeding on ***Asterella*** archegonial head and possibly the spores. Photo by Tom Voltz, with permission.

Figure 72. ***Apopellia endiviifolia*** with capsules. The spores can survive slug guts, a possible dispersal means. Photo by Janice Glime.

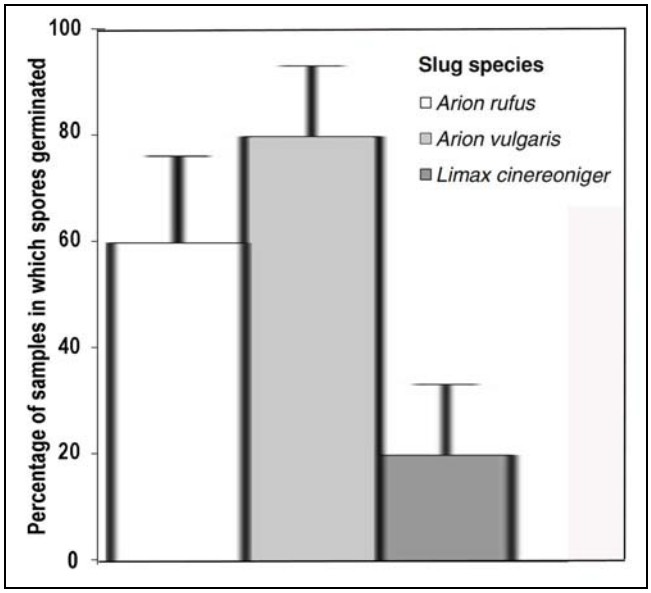

Figure 73. Slug gut dispersal of ***Apopellia endiviifolia*** spores. Modified from Boch *et al*. 2013.

Figure 74. ***Arion vulgaris*** on bryophytes, a slug that can potentially disperse spores of streamside bryophytes. Photo by F. Welter-Schultes, animalbase.uni-goettingen.de, through public domain.

Figure 75. ***Arion rufus*** on ***Sphagnum***, a potential endochorous bryophyte spore disperser. Photo by Walter Siegmund, through Creative Commons.

Figure 76. ***Limax cinereoniger*** feeding on lichen, a potential endochorous bryophyte spore disperser. Photo by H. Krisp, through Creative Commons.

Not only do bryophyte fragments get dispersed by wind and water, but so do their inhabitants. Bitušík *et al*. (2017) demonstrated that larvae of the chironomid (midge) ***Micropsectra uliginosa*** (Figure 77) travel in fragments of aquatic mosses, including ***Hygrohypnum*** sp. (*e.g.* Figure 14, Figure 54). This facilitates short-distance dispersal of the species, including the flightless males, albeit in their larval stage. They found detached moss tufts with chironomid larvae in their pan traps and assumed that these mosses had been flushed first by water, then trapped behind rocks or other obstructions in shallow water. Subsequently strong winds and gusts could lift the mosses and their inhabitants to mossy habitats above water nearby.

Figure 77. ***Micropsectra*** sp. larva; ***Microspectra uliginosa*** can be dispersed by blowing moss fragments. Photo by Aina Maerk Aspaas, NTNU University Museum, through Creative Commons.

Changes in Distribution

Frahm and Abts (1993) demonstrated the rapidity of dispersal of a number of aquatic species in the lower Rhine, Germany. From 1972 until 1992, the initial eight species were joined by ten more. The greater number of species in 1992 was attributed to improvement in water quality.

Frahm (1997) documented the distributional increase of aquatic mosses in the Rhein, Germany. ***Cinclidotus danubicus*** (Figure 78) has spread from its 1911 location to the Upper Rhine and Netherlands in 1997. ***Cinclidotus riparius*** (Figure 79) has spread northward. ***Fissidens arnoldii*** (Figure 80) spread from the Upper Rhine to the Lower Rhine in 70 years. ***Fissidens fontanus*** (Figure 41) was first recorded in the Upper Rhine in 1968 and by 1997 it had spread extensively along rivers in Central Europe. ***Hyophila involuta*** (Figure 81) spread 100 km northward along the Upper Rhine from 1927 to 1964. ***Fissidens rivularis*** (Figure 82) and ***Orthotrichum sprucei*** (Figure 83), both previously known only from British Isles, Belgium, and The Netherlands, have spread to the Rhine and its tributaries.

Figure 78. ***Cinclidotus danubicus***, a species that has spread in the Rhein (Rhine) since 1911. Photo by Michael Lüth, with permission.

Figure 79. ***Cinclidotus riparius***, a species that has spread northward in Germany. Photo by Hermann Schachner, through Creative Commons.

Figure 80. ***Fissidens arnoldii***, a species that spread from the upper to the lower Rhein (Rhine) within 70 years. Photo by Michael Lüth, with permission.

Figure 81. ***Hyophila involuta***, a species that has spread rapidly among rivers in Central Europe. Photo by Bob Klips, with permission.

Figure 82. ***Fissidens rivularis***, a species that has spread rapidly and recently in Europe. Photo by David T. Holyoak, with permission.

Figure 83. ***Orthotrichum sprucei***, a species that has spread rapidly and recently in Europe. Photo by Michael Lüth, with permission.

Small Dispersal Units and Long-distance Dispersal

Heino *et al*. (2012) concluded that organisms with small propagules such as ferns and bryophytes may have weak geographical variation over broad areas due to unlimited dispersal. They found that environmental factors were most important in boreal headwater streams. The

bryophyte data seemed to be better explained by environmental variables than by spatial characters.

Finlay (2002) contended that organisms less than 1 mm in size generally occur worldwide (the "everything is everywhere" hypothesis; see Vol. 1, Chapt. 4-8), whereas larger organisms are more restricted. He supported this with data on 1278 species of freshwater pond eukaryotic organisms showing that they were cosmopolitan. It follows that if the propagules are less than 1 mm, like bryophyte spores, they should follow the same principle. Kyrkjeeide *et al*. (2014) demonstrated a negative correlation of range with spore size of bryophytes in Europe based on spores up to 40 µm in diameter. In this case, those bryophytes reproducing (producing spores) less frequently had greater genetic differentiation than did bryophytes with frequent reproduction (p=0.04). Van Zanten (1978a, b) supported the possibility of long-distance travel of at least some species by placing the spores on airplane wings for trans-oceanic travel. Among these were the aquatic ***Warnstorfia fluitans*** (Figure 84) and ***Leptodictyum riparium*** (Figure 43), which could survive desiccation up to 13 months.

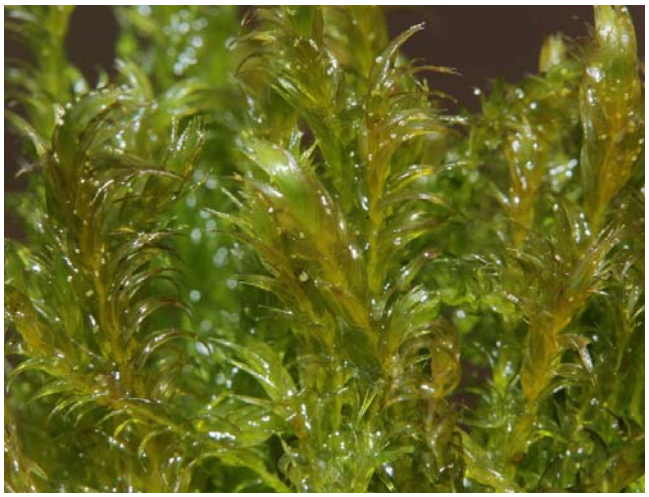

Figure 84. ***Warnstorfia fluitans***, a species in which spores can survive conditions necessary for long distance travel. Photo by Hermann Schachner, with permission.

Santos *et al*. (1996) collected airborne spores and other propagules on agar in Petri dishes. Once germinated, the collections revealed the presence of the bryophytes ***Fossombronia angulosa*** (Figure 85), ***Pellia epiphylla*** (Figure 6), ***Leptodictyum riparium*** (Figure 43), ***Bryum dunense*** (Figure 86), ***Ditrichum*** sp. (Figure 87), ***Gymnostomum calcareum*** (Figure 88), ***Pottia*** sp. (probably now in ***Tortula***; Figure 18), and ***Trichostomum brachydontium*** (Figure 89). Of these, ***Pellia epiphylla*** is a common streambank species and ***Leptodictyum riparium*** lives submersed in quiet water. It is also notable that a number of **Cyanobacteria** (Figure 90) arrived, providing potential nitrogen-fixers to associate with the bryophytes. Of the taxa collected, 75% were spores <25 µm. These successful spores suggest that diaspore banks can be important sources to recolonize a stream when it is disturbed or changes channel location.

Figure 85. ***Fossombronia angulosa***, a species that grew from collected spores. Photo by Jan-Peter Frahm, with permission.

Figure 86. ***Bryum dunense***, a species that grew from collected spores. Photo by Michael Lüth, with permission.

Figure 87. ***Ditrichum gracile***; ***Ditrichum*** sp. grew from collected spores. Photo from Snappy Goat, through public domain.

Figure 88. ***Gymnostomum calcareum***, a species that grew from collected airborne spores. Photo by Larry Jensen, with permission.

Figure 89. ***Trichostomum brachydontium***, a species that grew from collected airborne spores. Photo by David T. Holyoak, with permission.

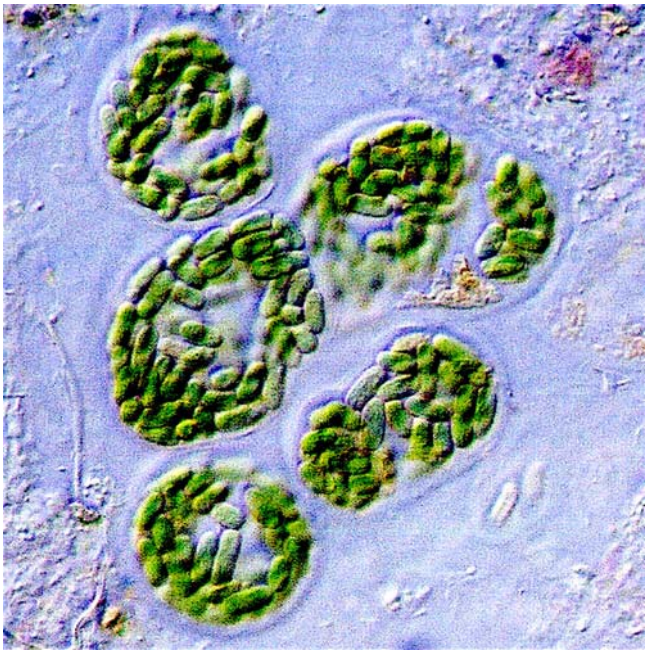

Figure 90. Cyanobacterial mat. **Cyanobacteria** germinated from airborne collections. Photo from NASA, through public domain.

Spore Germination and Protonema Development

Spore germination and protonema development have been studied in a number of bryophytes, including aquatic species (Kanda & Nehira 1976). These are illustrated and early stages following germination are described for the aquatic mosses ***Leptodictyum riparium*** (Figure 43) and ***Cratoneuron filicinum*** (Figure 91).

Figure 91. ***Cratoneuron filicinum***, one of the aquatic species for which protonema development was described by Kanda and Nehira (1976). Photo by J. C. Schou, with permission.

Glime and Knoop (1986; Glime 2014) concluded that ***Fontinalis squamosa*** (Figure 92) is an opportunist that releases spores (Figure 93) from multiple capsules over a relatively long period. This extended period of spore release may be the result of having fertilization over an extended time. Glime (1984) demonstrated that ***F. dalecarlica*** (Figure 15) produces mature archegonia over several months. A single collection of ***F. squamosa*** likewise provided both antheridia (Figure 36) and archegonia (Figure 37-Figure 38) in various stages of development. Capsules were also present in this single collection and similarly were in various stages of development. This spread of maturation could provide spores at different conditions of flow, and increase opportunities for at least some spores to meet favorable conditions. Elssmann (1923-1925) found that spores in capsules exposed to air ripened several weeks earlier than those that were submersed, providing further variability in response to changing water levels.

Figure 92. ***Fontinalis squamosa***, a species that produces both chloronemata and caulonemata. Photo from <www.aphotofauna.com>, with permission.

Figure 93. Longitudinal section of ***Fontinalis squamosa*** capsule showing green spores. Photo by Janice Glime.

Fontinalis squamosa (Figure 92) exhibits another potentially adaptive trait. Its spores within a single capsule (Figure 93) do not all mature at the same time. As the spores develop, some abort (Figure 94) (Glime 1983; Glime & Knoop 1986; Glime 2014). Others enlarge and are bright green, while some remain smaller and may be only partially green. Both can germinate, but the larger ones germinate more quickly (5 days) and have a higher germination success than the small ones (18 days). The protonemata in this species are also negatively **phototropic** (Figure 95) (Glime 2014). This habit of growing away from the light source may be adaptive in keeping them under water. It would be interesting to see if there is a threshold light level that elicits this phototropic response.

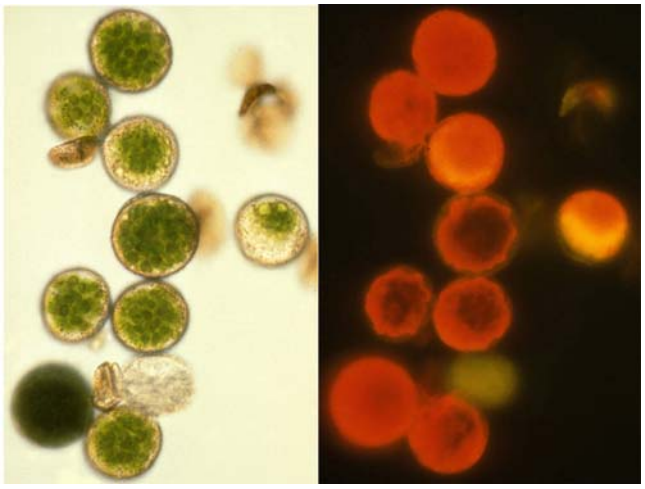

Figure 94. ***Fontinalis squamosa*** spores; those with clear areas on the left and yellow areas on the right are abortive. Those on the right are indicating chlorophyll fluorescence, showing red. Photos by Janice Glime.

Figure 95. ***Fontinalis squamosa*** protonemata singles typical of those grown at 3ºC. Light is coming from the lower right corner, indicating these protonemata are negatively phototropic. Photo by Janice Glime.

Glime and Knoop (1986) described the spore germination and development of ***Fontinalis squamosa*** (Figure 92). This moss develops both **chloronemata** (Figure 96) (protonemal filaments with many well developed chloroplasts and perpendicular cross walls) and **caulonemata** (protonemal filaments with fewer, less well developed chloroplasts and oblique crosswalls; portion of protonema that generates buds when both protonemal types are present). They can grow straight with no branches or have multiple branches, depending on lighting conditions. But buds failed to develop in the laboratory cultures until some of the abandoned plates became contaminated with fungi, suggesting that some developmental hormone might be supplied by the fungi.

Figure 96. ***Fontinalis squamosa*** branched protonema, with **caulonemata** forming at the tips of the branches, exhibiting lighter coloring due to fewer chloroplasts. This growth form was typical of cultures at 20ºC. Photo by Janice Glime.

Physiological conditions and environmental signals that are important to the developmental stages of aquatic bryophytes are poorly known. Belkengren (1962) experimented with ***Leptodictyum riparium*** (Figure 43) under a variety of conditions. Yeast inhibits its shoot growth in culture. But protonemal growth is not affected. Yeast causes death to shoot buds. As a result, the moss grows in the presence of yeast and never reaches another stage. Could this be the sort of interaction that maintains ***Dicranella heteromalla*** (Figure 35) in a protonema stage in

the water (Higuchi *et al*. 2003)? The acid environment would be favorable to growth of fungi. Or is it some nutrient level?

Temperature can play a role in both germination success and form of the protonemata (Glime & Knoop 1986). At 3ºC, no spores germinated in culture, although distention occurred. At 20ºC, the protonemata grew aerially away from the agar and toward the light source, subsequently forming balls of irregular filaments with rounded cells.. The best growth was exhibited by cultures at 14ºC, with greater growth on the unshaded side of the plate. Growth forms differed with temperature (Figure 95-Figure 97). Nishida and Iwatsuki (1982) considered the protonema type to be adaptive, reflecting habitat more than its taxonomic affinity. Bud development did not occur until 3 months after the cultures were started, and the presence of buds was restricted to contaminated cultures, suggesting that the fungus might provide a needed stimulant to the bud development (Glime & Knoop 1986). Rhizoids formed before leaves at about an 8-cell stage.

Figure 97. ***Fontinalis squamosa*** protonemata with mostly 2 branches from the spore, typical of protonemata grown at 14ºC. Photo by Janice Glime.

Asexual Reproduction

Carrigan and Gibson (2003) concluded that reproduction of stream bryophytes is primarily asexual. This is supported by evidence that most fragments of these bryophytes seem able to develop new plants in nature. For example, Glime (1970) found a fragment of ***Scapania undulata*** (Figure 13, Figure 98) leaf with a new plant growing from the center of the leaf, even though this species is also able to produce gemmae. I don't know if it was able to develop rhizoids to attach, but as the new shoot got larger, I would expect it to be able to develop rhizoids at the leaf nodes.

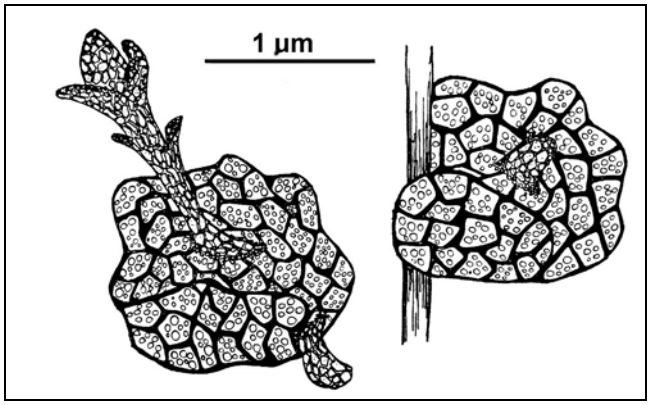

Figure 98. ***Scapania undulata*** plantlets from detached leaves of ***S. undulata*** in March 1969 in a stream near Plymouth, NH, USA. Drawings by Flora Mace.

It is likely that aquatic species are more successful at making new colonies from fragments because of their aquatic habitat. If a fragment arrives in a new location, it most likely arrived with flowing water and lodged somewhere that was wet. This would permit it to develop a new plant while it remains wet, whereas in the terrestrial environment new arrivals have a much greater chance of drying out and losing vigor before a new plant can begin growth or become established.

Regeneration

With the difficulty of accomplishing sexual reproduction and spore dispersal, fragmentation becomes more important. For this to succeed, these fragments must be able to dedifferentiate and regenerate new branches and whole colonies.

Regeneration is common among bryophytes. Giles 1971) describes the dedifferentiation and regeneration. Kreh (1909 in Giles 1971) demonstrated that every part of a liverwort except the antheridia could be induced to regenerate. Even diploid gametophytes can develop from pieces of a seta. In ***Plagiomnium affine*** (Figure 99), if a leaf remains on the stem it does not dedifferentiate. However, if it is removed from the stem in appropriate light, the leaf will dedifferentiate and redifferentiate to form **secondary protonemata**.

Figure 99. ***Plagiomnium affine***, a species that can regenerate from a detached leaf. Photo by Hermann Schachner, through Creative Commons.

Gimeno and Puche (1998) followed the responses of ***Platyhypnidium riparioides*** (Figure 100) in a polluted stream to assess damage to the moss and regeneration. They found that it produces caulonemata at the leaf bases of apical branches. Buds form while these filaments are still attached. When these sets of leaves become detached following **necrosis** (cell death), they can disperse. Rhizoids eventually develop, permitting these fragments to attach in a new location. In the lab, newly cut fragments developed the caulonema in only 5 days and buds arose in 11 days. Rhizoids developed in 21 days. Fragments and damaged leaves were common in the stream and the researchers suggested that in the apparent absence of sporophytes this was the major means of reproduction.

Figure 100. ***Platyhypnidium riparioides***, a species that can form new buds and rhizoids on detached pieces. Photo by Hermann Schachner, through Creative Commons.

Heald (1898) was unsuccessful in his attempts to regenerate ***Fontinalis antipyretica*** (Figure 27). He cultured leaves and stems in water, on earth, and with varying amounts of moisture with no success. On the other hand, I have successfully cultured broken stems of ***Fontinalis squamosa*** (Figure 60), ***F. hypnoides*** (Figure 64), and observed protonemata growing at the broken tips (Figure 58) of the latter. ***Fontinalis dalecarlica*** instead produced rhizoids from detached terminal buds (Figure 101) and leaves (Figure 102). I was also able to grow 2-cm pieces of ***F. antipyretica*** in artificial streams.

Figure 101. Unattached tip of ***Fontinalis dalecarlica*** developing rhizoids, hence serving as a propagule. Photo by Janice Glime.

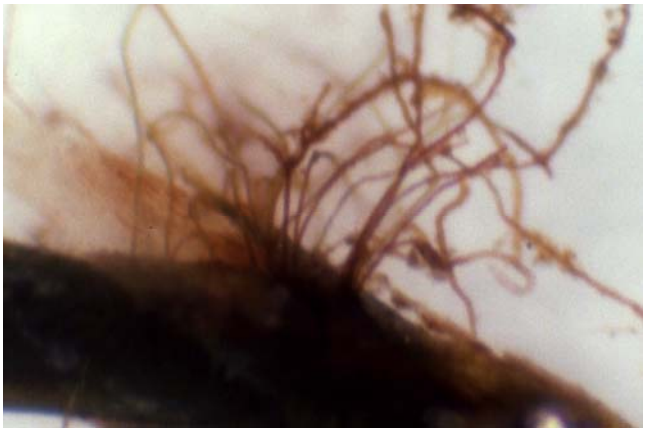

Figure 102. Rhizoids on detached leaf of ***Fontinalis dalecarlica***. Photo by Janice Glime.

The aquatic moss ***Fontinalis antipyretica*** (Figure 27) is capable of regeneration from nearly every part of the gametophyte (Ares *et al*. 2014). She was able to regenerate plants from cortical cells in the bases of detached shoots, margins and abaxial surfaces of leaves, stems with leaves removed, and laminae of detached leaves. These plant parts produce a variety of filament systems, including protonemata with short rectangular cells with transverse crosswalls, and unbranched rhizoids.

Fissidens fontanus (Figure 41) can regenerate even from its calyptra (Figure 103, Britton 1902). The capsules fall from the plants before they mature and the calyptra is still retained. Both the capsule and calyptra can float, so both can act as dispersal units. Goebel (1915-1918) also reported such a capsule of ***Fissidens fontanus*** with a young shoot emerging from beneath the calyptra (Figure 103); it even is producing an archegonium.

Figure 103. ***Fissidens fontanus*** calyptra exhibiting germination of a new shoot. Photo courtesy of Hans Kruijer.

Gemmae and Bulbils

Little has been written about gemmae and bulbils in truly aquatic bryophytes, especially in mosses. One study

of interest is the induction of vegetative propagules in ***Porella pinnata*** (Figure 104). The leafy liverwort ***Porella pinnata*** did not fare well when cultured in moist chambers, with fungi and algae developing (Fulford 1944). However, when two cultures were transferred to nutrient media and given regular nutrient treatments and dim light, they developed vegetative propagules, ranging from bulging leaf cells to leafy shoots.

Figure 104. ***Porella pinnata***, a floodplain species that develops growths of fungi and algae when cultured in moist chambers. Photo by Alan Cressler, with permission.

Ares *et al*. (2014) discovered that the aquatic moss ***Fontinalis antipyretica*** produces gemmae. Filamentous gemmae are freed by **schizolysis** (splitting and breaking apart). Spherical brood cells are produced in ageing and desiccating cultures. Ares and coworkers suggested that these asexual propagules may occur in response to falling water levels in nature. These previously unknown means of reproduction may be important in spread and spatial genetic structure. These researchers also suggested that differences between axenic and contaminated cultures may be due to positive associations between the moss and bacterial or fungal contaminants.

Could there be other protonematal gemmae from other aquatic species hiding in the ecosystem, undiscovered because the protonemata are so difficult to find in nature?

Longevity

For many bryophytes that are not securely attached to the substrate, the living portion may only reflect a few years, whereas older basal portions are senescing or dying at the same rate. However, for a stream bryophyte, attachment makes decomposition of the basal portions a bigger problem. It is not unusual, however, to find basal portions that have lost their leaves, but the apical portions are vibrant, living plants. Therefore, **longevity** of the whole plant is an important part of a successful strategy, especially for **streamer** life forms.

Estimating the age of aquatic bryophytes can be challenging. Frye (1928) estimated the ages of a number of bryophytes based on apical regions that survived the winters, but none of these was submersed. These terrestrial bryophytes, including several streambank species, ranged up to 6 years of age present. I would estimate that ***Fontinalis*** (Figure 27) lives considerably longer than that, although the basal portions may be devoid of leaves. I grew a number of species in the lab and found that they could rebranch 1-2 times in just 15 weeks, so it does not appear that counting branches would be a useful indicator.

Life Cycle Strategy

All of these life cycle strategies work together to make a successful life cycle (Figure 105). Spore germination in the field is unknown for most aquatic species, but for ***Fontinalis novae-angliae*** and ***F. dalecarlica*** the capsules are produced in the winter and can release spores during early spring runoff. At the same time, the plants experience scouring and dispersal of fragments. In the later spring, when there is good sunlight and the trees do not yet form a canopy, growth and branching are at their best. In the summer, when temperatures rise and water levels drop, the rhizoids have their greatest growth. By fall, water levels rise again, temperatures cool, and days are shorter. Archegonia mature, reaching maturity as the longer-developing antheridia also mature. If the water level permits some branches to be wet, but above water, sperm can be splashed to new plants and accomplish fertilization.

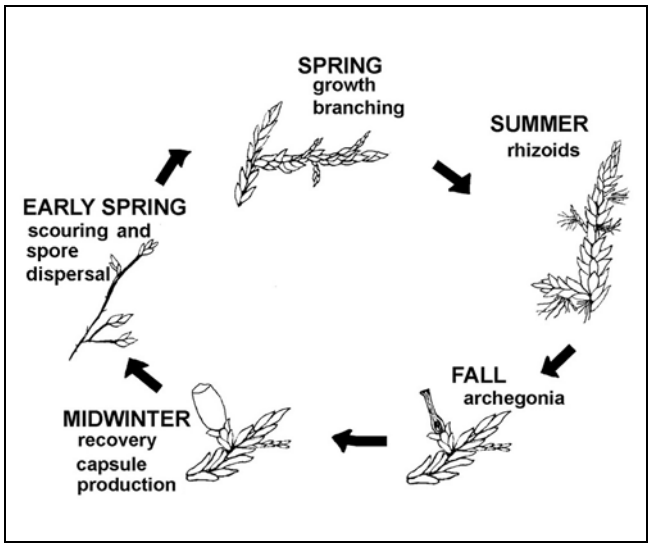

Figure 105. ***Fontinalis novae-angliae*** (Figure 23) and ***F. dalecarlica*** (Figure 15) seasonal life cycle. Diagram by Janice Glime.

Heino and Virtanen (2006) provide a good summary of the interrelationship of life strategies and stream bryophyte success. They considered that bryophytes could be divided into dominants and transients/subordinates. These two groups had sharp differences in life-history strategies and growth/life forms. They concluded that the abundance-occupancy relationships suggest that dispersal limitation and metapopulation processes may be the governing factors for the dynamics of the aquatic bryophytes, whereas in the semi-aquatic habitat, habitat availability may be more important in contributing to regional species occupancy.

The next subchapter will further discuss the physiological factors relating to the reproductive cycle. These will include temperature and light effects on the induction of reproductive structures.

Summary

Life forms are environmental expressions, whereas **growth forms** are genetically controlled. Both help to determine the suitability of the species for survival in streams. In fast water, these life forms include **streamers**, especially in permanently submersed sites. Other dominant forms include **smooth mats**, **tall turfs**, **fans,** and **short turfs**. Plasticity of life forms permits a species to occupy a wider range of moisture habitats, with stem elongation typically occurring in submersed conditions.

Asexual reproduction predominates; fertilization is difficult under water, particularly for dioicous species. Sporophytes are often emergent, even if the leafy portion is under water. For those submersed capsules, there is evidence that dehiscence might only occur when the capsule becomes emergent, or not at all. Fragments are particularly common as propagules. These can be dispersed by flowing water and animals, and once on land some might be dispersed by wind. Waterfowl might be especially important vectors for long-distance dispersal. The life cycle strategy seems to optimize energy and take advantages of the changing conditions with seasons. For example, in several ***Fontinalis*** species, spring is important for growth, summer for rhizoids, fall for sexual reproduction, early spring for scouring and dispersal, and capsule production depending on whether it can take advantage of emergence or must disperse under water.

Acknowledgments

Many bryonetters have contributed to these aquatic chapters, permitting me to expand my world view of the taxa. My permission for the ***Agriolimax*** feeding on ***Asterella*** required finding the email address for Tom Voltz. I started with Brent Mishler, who sent it to Amanda Heinrich, who sent it to Ken Kellman, who sent it to someone with the initials JJ, who sent it to Tom Voltz. And I got permission the same day this chain of emails started! Thank you to all of these people for their help!

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CHAPTER 8-1
TROPICS: GENERAL ECOLOGY

JANICE M. GLIME AND S. ROBBERT GRADSTEIN

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CHAPTER 8-1
TROPICS: GENERAL ECOLOGY

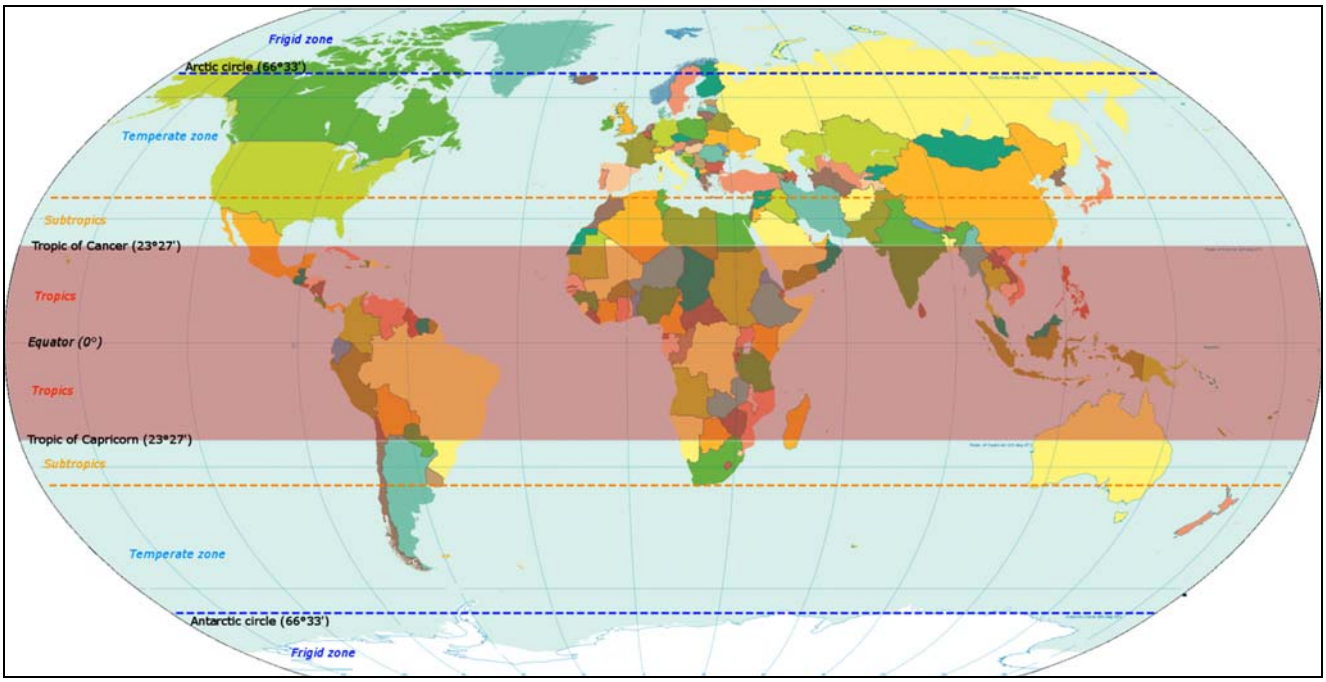

Figure 1. World map indicating tropics in pink band, subtropics in orange dotted line. Photo from KVDP, through Creative Commons.

General Ecology

Occupying the area between the Tropic of Cancer and the Tropic of Capricorn, the tropics comprise the most complex ecosystems of the world (Figure 1), extending 23º27' north and south of the Equator. The tropical land mass is nearly one-third of the land on the planet (Schuster 1988). Complex ecosystems provide multiple niches (Figure 2), and the tropics undoubtedly provide the highest number of niches anywhere with their multi-storied forests (Figure 3).

Figure 2. Tropical forest and waterfalls at Quebrada Cataguana, Honduras. Photo by Josiah Townsend, with permission.

Bryophytes in the tropics were largely ignored in early botanical studies. Resident botanists, lacking training by bryologists and preceding the development of taxonomic aids, largely ignored the bryophytes (Moreno 1992). Although bryophytes have been recorded from the tropics since the 18th century, tropical bryophyte ecology started to emerge only rather recently because keys to identify tropical bryophytes were long lacking. Early fieldwork in the tropics was done by foreign bryologists, *e.g.* Goebel (1888), Schiffner (1900), Fleischer (1904-1923) and Giesenhagen (1910) in Asia, and by Spruce (1884-1885) and Spruce and Wallace (1908) in tropical America. Spruce collected extensively in the Amazon regions and the Andes of Ecuador and Peru, and identified the liverworts himself, but gave his moss collections to William Mitten, who subsequently published them in *Musci Austro-Americani* (Mitten 1869).

Early studies on the ecology of tropical bryophytes has been summarized by Pócs (1982) and Richards (1984a). Some of the earliest studies were on **epiphyllous** (growing on leaves of other plants) bryophytes and will be discussed in the subchapter on epiphylls.

In Puerto Rico, Fulford *et al*. (1970, 1971) described liverwort communities in the elfin (cloud) forest (Figure 4). Griffin *et al*. (1974; Griffin 1979) reported on altimontane (Figure 5) bryophytes. Steere (1970) took advantage of the haploid condition of bryophytes to report on the effects of ionizing cesium radiation in Puerto Rico.

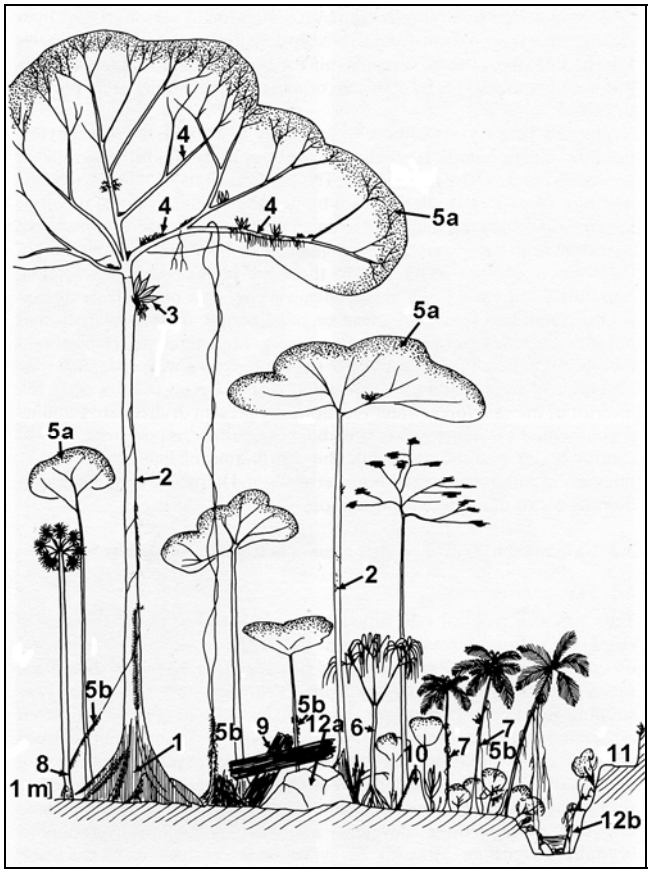

Figure 3. Microhabitats in tropical forests. **1:** Bases of large trees; **2:** upper parts of trunks; **3:** macro-epiphyte nests; **4:** bark of main branches; **5a:** terminal twigs and leaves; **5b:** bark of lianas, shrub branches, and thin trunks; **6:** *Pandanus* stems; **7:** tree fern stems; **8:** palm trunks and basal prop roots; **9:** rotting logs and decaying wood; **10:** soil surface and termite mounds; **11:** roadside banks and cuttings; **12a:** rocks and stones; **12b:** submerged or emergent rocks in streams. Image modified from Pócs 1982.

Figure 4. Elfin cloud forest fog, Luquillo Mountain, Puerto Rico, USA. Photo by Janice Glime.

Once the bryophytes were better known, bryologists began asking ecological questions (*e.g.* Frahm & Gradstein 1990). Based on the results of elevational transect analyses throughout the tropics, Frahm & Gradstein (1991) recognized five tropical rainforest belts using bryophytes as indicators: lowland rainforests (Figure 6-Figure 7), submontane rainforests (=premontane rainforest; Figure 8), lower montane rainforests (Figure 9), upper montane rainforests (Figure 10), subalpine rainforests (Figure 11).

Figure 5. Drakensberg, South Africa, altimontane region. Photo by Diriye Amey, through Creative Commons.

Figure 6. Lowland rainforest tree in Colombian Amazon. Photo by Laura Campos, courtesy of Robbert Gradstein.

Figure 7. Canopy in lowland rainforest in Colombian Amazon. Photo by Laura Campos, courtesy of Robbert Gradstein.

Figure 8. Submontane rainforest, Peruvian Andes. Photo by Robbert Gradstein, with permission.

Figure 9. Lower montane forest in Colombia, rich in lignified vascular epiphytes. Photo by A. M. Cleef, courtesy of Robbert Gradstein.

To further complicate our ecological understanding, early differences in methodology made ecological comparisons nearly impossible, while poor understanding of the taxonomy gave that area of study priority and limited the kinds of ecological studies that were feasible. The earliest limited ecological studies have included the relationships among climate, mountain topography, vegetation zones (Pócs 1976), ecology, reproductive biology, and dispersal trends (Schuster 1988), biomass (Frahm 1990b), water relations, and CO_2 exchange (Zotz *et al*. 1997).

Figure 10. Upper montane forest, Pui-Pui Protection Forest, Peru. Photo by E. Lehr and R. von May, through Creative Commons.

Figure 11. Subalpine dwarf mossy ***Polylepis*** forest in Ecuador. Photo by K. Romoleroux, courtesy of Robbert Gradstein.

Richards (1984a) provided a very useful overview of the ecology of tropical forest bryophytes, making it clear that studies at that time were limited and his coverage was superficial. One of the things that quickly becomes obvious is that most of the known ecological information relates to **epiphytes** (growing on other plants). This is because most of the tropical bryophytes are epiphytes, limited by low light levels and leaf burial on the forest floor.

In the Luquillo Mountains of Puerto Rico (Figure 12), three environmental factors cause contrasting communities of leafy liverworts (Bryant *et al*. 1973). Using area x area (**Q-mode**) analysis, they demonstrated that high-altitude liverwort communities contrast with those of low altitudes, shaded, moist habitats contrast with open, exposed habitats of all elevations, and disturbed low-elevation habitats contrast with less disturbed habitats of all elevations. **R-mode** analysis (species x species) produced nearly identical results to those of Q-mode.

Figure 12. Luquillo Mountains, Puerto Rico. Photo by Stan Shebs, through Creative Commons.

For recent species lists of tropical studies, see Gradstein *et al*. (2001) for tropical America, Churchill *et al*. (2010) on Bolivia, and many others. For additional older studies and reviews of tropical bryophyte species lists and ecology, see Delgadillo (1976) on Mexico; Lisboa (1976) on the Amazon; Egunyomi (1978) on distribution of pantropical ***Octoblepharum albidum*** (Figure 13) in Africa; Pócs (1982) on tropical forests; Gradstein *et al*. (1983) on Neotropical-African liverwort disjunction; Richards (1984a, b, 1988) on tropical forest ecology; Linares (1986) on the high Andes; Gradstein & Pócs (1989) on tropical rainforest bryophytes; Frahm & Gradstein (1990, 1991) on bryophytes as indicators of tropical rainforests; Frahm & Kürschner (1992) on tropical rainforests in general; Frangi & Lugo (1992) on biomass and nutrients in a Puerto Rico floodplain; Delgadillo (1993) on Neotropical-African disjunction; Miehe & Miehe (1994) on ecology in East Africa; Lösch *et al.* (1999) on Central African photosynthesis; Merwin & Nadkarni (2002) on tropical ecology, and others.

Figure 13. ***Octoblepharum albidum***, a species that produces most of its juvenile, immature, and mature gametangia during the rainy season in tropical Brazil. Photo by Niels Klazenga, with permission.

Water Relations

In general, tropical adaptations reflect moisture conditions, with light and other factors being secondary (Frahm 1990a). Hence, we find that lowland forests are dominated by **mats**, and montane and cloud forests by **wefts** (loosely interwoven, often ascending growth form). Thiers (1988) reported the leafy liverworts ***Radula*** (Figure 111), ***Frullania*** (Figure 14), and various **Lejeuneaceae** (Figure 130-Figure 131) to exhibit the mat growth form on their bark substrate; these taxa tend to lack dominance in the main axis. Where they form extensive mats on tree boles, they are able to trap water as it runs down the tree.

Figure 14. ***Frullania*** sp. from the Neotropics, demonstrating mat growth habit. Photo by Michael Lüth, with permission.

Studies on water relations seem to have been more common than other areas of tropical bryophyte ecology. Pócs (1980) studied the water interception and retention by bryophytic cover (biomass) in different types of tropical forest, forming the basis for all other studies on the subject. He found a positive correlation between the amount of "surplus" rainfall (rainfall above 100 mm/month) and the epiphytic biomass in rainforest climates. Rainfall and epiphytes will be discussed in Chapter 8-3 of this volume.

When working on disturbance, Norris (1990) suggested four aspects of water relations that required consideration: hydration/dehydration frequency; hydration duration; dehydration duration; degree of water loss. We have since learned that rate of dehydration is important (Greenwood & Stark 2014). As Norris (1990) further surmised, these are all biomass-dependent functions, wherein large colonies typically maintain hydration longer than smaller colonies. Lateral branching of the colony allows lateral movement of capillary water. This spread of the water extends to clones that are in contact with each other. On the other hand, when tufts and cushions are separated, they contribute little to lateral spread of the water over the substrate.

Johnson and Kokila (1970) experimented with ten species of tropical mosses to determine their resistance to desiccation. These were exposed to relative humidities ranging 10-76% for four hours. After a recovery period of 24 hours, the researchers found the mosses could be divided into high and low resistance groups. Those species in the high resistance group occur in tropical forests with low humidity.

Pócs (1980) found a positive correlation between the amount of "surplus" rainfall (rainfall above 100 mm/month) and the epiphytic bryophyte biomass in rainforest climates. As demonstrated by Larson (1981) mosses with a large surface area to weight ratio are able to absorb water very rapidly.

Thompson *et al*. (1994) calculated the bryophyte cover on a single tree of ***Sloanea woollsii*** (Figure 15-Figure 16) in a notophyll forest of southeast Queensland, Australia (subtropical), to be 66 sq m. Water collected by the bryophytes in a single rainfall event exceeded that of the maximum daily transpirational loss from the host tree. Hence, bryophytes can contribute significantly to the relative humidity of the forest through evaporation. This is also a typical role in the tropics.

Figure 15. ***Sloanea woollsii***, a species known for a large cover of bryophytes. Photo by Peter Woodard, through public domain.

Figure 16. ***Sloanea woollsii*** forest, where many bryophytes grow. Photo by Pete the Poet, through Creative Commons.

Frey *et al*. (1990) recognized three principles of water conduction and storage by plants. In the wet season, it is necessary to drain off surplus water. In the dry season, storage and use of condensation of water vapor are important. Above 1700 m, structures that encourage condensation from water vapor aid in water capture. They felt that leaves with grooves could permit support as well as a means of draining off excess water, an adaptation that seems to reach its maximum in the cloud forest and subalpine zone. In the lowland forest, water sacs, mats, and smooth bark combine to preserve water during short dry periods.

Karger *et al*. (2012) considered air humidity to be one of the most difficult and time-consuming climatic measurements to obtain. Thus, they tested the use of bryophyte cover as a proxy, a suggestion proposed by van Reenen and Gradstein (1983), van Reenen (1987), and Frahm and Gradstein (1991). Using 26 study sites in tropical forests, these researchers considered the possibility of using bryophyte cover as a surrogate for relative humidity as a climatic measurement. They found only a weak correlation between bryophyte cover and relative humidity across all the sites. However, when the highland (1,800-3,500 m asl) data were separated from that of the lowland (<1,800 m asl) sites, relative air humidity had a significant and distinct relationship to bryophyte cover (R^2 = 0.36-0.62). Temperature, on the other hand, was related to bryophyte cover only in the lowlands (R^2 = 0.36). The researchers concluded that epiphytic bryophyte cover can be used as a proxy for air humidity if both temperature and altitude are considered, but cover might not be a good proxy across extensive elevational gradients or wide temperature differences.

Proctor (1990) has demonstrated the reasons for bryophyte distributions through the use of physiological experiments. Whereas many bryophytes tolerate drying, even down as low as 5% water by dry weight, their photosynthesis declines rapidly as water is lost. Regaining photosynthesis can be rapid or slow upon remoistening, depending on the species and the drying conditions. In the tropics, it is important to know that most bryophytes are shade plants, even when they grow in habitats with lots of sunlight, due to their low chlorophyll *a*:*b* ratios. This means that they become light-saturated at relatively low light levels and do not benefit when the canopy opens up, admitting more light. But it also means that photosynthesis does not occur at a high rate, so having moist conditions provides them with a longer period of photosynthetic activity.

Both moisture and light relationships can be seen easily within a single tree as well as between habitats. For example, when Sillett and coworkers (1995) compared bryophyte diversity in a cloud forest and pasture in Costa Rica, they found 127 species of bryophytes (50 mosses, 76 liverworts, 1 hornwort) in the crowns of just 6 ***Ficus tuerckheimii*** (Figure 17) trees in the lower montane wet forest. Of these, 109 species were on 3 intact forest trees and only 76 on 3 isolated trees, the isolated trees having more macrolichen cover. The isolated trees were more subject to drought conditions, with higher evaporation in the inner crowns and more exposure to sunlight. The higher moisture of the intact forest supported not only a greater bryophyte species richness and cover, but also a

greater frequency of **pendants**, **tall turfs**, **tails**, and **fans**. Furthermore, 52 species were found only on the intact forest trees, whereas only 18 were exclusive to the three isolated trees.

Figure 17. ***Ficus tuerckheimii***, a strangler fig, substrate for significant bryophyte cover in Costa Rica. Photo by Dick Culbert, through Creative Commons.

Cardosa (2012) described the hydrological cycle and the implications of climate change, using data from a La Réunion cloud forest. As already noted, the bryophytes intercept both fog and rainfall over their entire surface. This ability is important in the hydrological cycle of their ecosystems. Using two liverwort species, ***Mastigophora diclados*** (Figure 18-Figure 19) and ***Bazzania decrescens*** (see Figure 20), they determined biomass, water storage capacity, atmospheric and cloud water interception, and photosynthetic response to desiccation. Compared to ***M. diclados***, ***B. decrescens*** stored water at approximately double the mean and maximum per hectare while at the same time occupying less than half the bryophyte volume of ***M. diclados***. On the other hand, ***M. diclados*** had a greater ability to intercept the atmospheric moisture. Both species showed a significant relationship between photosynthesis and water content, with both species losing photosynthetic capacity at both low and high water contents. If the clouds lift, as they are predicted to do by the global climate change models, these bryophytes will most likely not survive and their role in the water cycle will be lost.

Figure 18. ***Mastigophora diclados*** habitat. Photo by Claudine Ah-Peng, with permission.

Figure 19. ***Mastigophora diclados***, a species that stores only half the water stored by ***Bazzania decrescens***. Photo by Claudine Ah-Peng, with permission.

Figure 20. ***Bazzania*** sp. from the Neotropics. Photo by Michael Lüth, with permission.

In addition to decreasing diversity, tropical bryophyte productivity is already being impacted by global climate change (Zotz & Bader 2008; Jácome *et al*. 2011; Song *et al*. 2012; Pardow & Lakatos 2013). Jácome and coworkers

used transplanted communities to determine potential climate change effects on the ecology of these bryophyte species.

As a result of climate change, periods of drought are becoming longer and microclimatic conditions are drier (Pardow & Lakatos 2013). Unfortunately, few physiological studies are available on tropical bryophytes, and even less is known about community responses. Pardow and Lakatos, in the first pilot study for effects of climate change on bryophyte ecology in the tropics, used chlorophyll fluorescence to indicate recovery of bryophytes from a tropical lowland forest in French Guiana (Figure 21). They found that canopy species were well adapted to desiccation events, with 13 of the 18 species maintaining more than 75% of their photosynthetic capacity after recovery from 9 days of desiccation at 43% relative humidity. Understory species were sensitive and could recover only if the relative humidity did not go below 75%. Water vapor, as one might find in fog, was sufficient to rehydrate and reactivate photosynthesis in all of these bryophytes.

Figure 21. Top of lowland rainforest canopy, French Guiana. Photo by Renske Ek, courtesy of Robbert Gradstein.

Additional discussions of water relations as they relate to habitat can be found in the following subchapters.

Light

Although moisture is the overriding factor in bryophyte distribution in most of the tropics, light is limiting near the forest floor in well-developed multi-story rainforests (Richards 1984a; Cornelissen & ter Steege 1989). Cornelissen and ter Steege demonstrated that true sun epiphytes increase in photosynthetic rates with increasing light intensity, even when that intensity is very high and atmospheric humidity is low. Hosokawa *et al.* (1964) found that the vertical gradient of bryophyte and other cryptogamic species and growth forms is somewhat related to light and atmospheric humidity, with the lowermost canopy species being more limited by illumination and the uppermost occurrences of trunk species being limited by insufficient atmospheric humidity.

Although high temperatures may be detrimental to some species, Barkman (1958) considered that these are probably not damaging to the bryophytes, but rather that direct solar radiation may be harmful. He cited examples of adaptive coloration exhibited by some bryophytes. Cornelissen and ter Steege (1989) found red to black pigmentation represented in many sun epiphytic species, including **Orthotrichaceae**, ***Frullania*** spp., and several members of holostipous **Lejeuneaceae**. The upper canopy species ***Frullania apiculata*** (Figure 22), ***F. kunzei*** (Figure 23), and ***F. nodulosa*** (Figure 24) are always dark red I these locations. By contrast, ***F. mucronata*** from zones 3 and 4 is dark olive green and ***F. obcordata*** (Figure 25), a generalist, is more strongly pigmented with red color in zones 5 and 6 than in zone 4. Krinsky (1968) described photochemical pathways that can be used by colored pigments that protect plants.

Figure 22. ***Frullania apiculata*** stem, SEM, a species that is dark red in sunny locations. Photo by Matt von Konrat, with permission.

Figure 23. ***Frullania kunzei***, a species that is dark red in sunny locations. Photo by Juan Larrain, with permission.

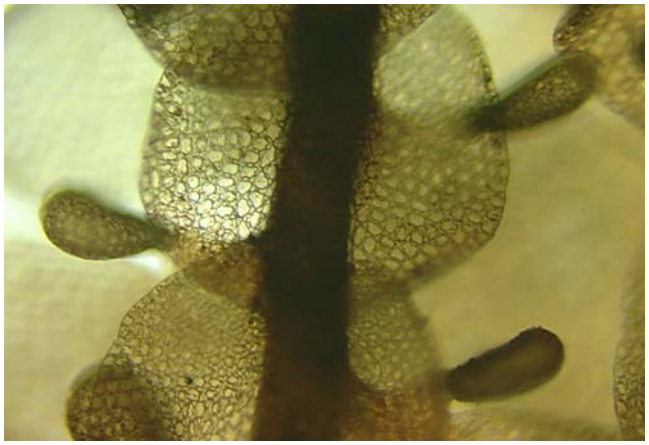

Figure 24. ***Frullania nodulosa*** stem ventral view, a species that is dark red in sunny locations. Photo by Matt von Konrat, with permission.

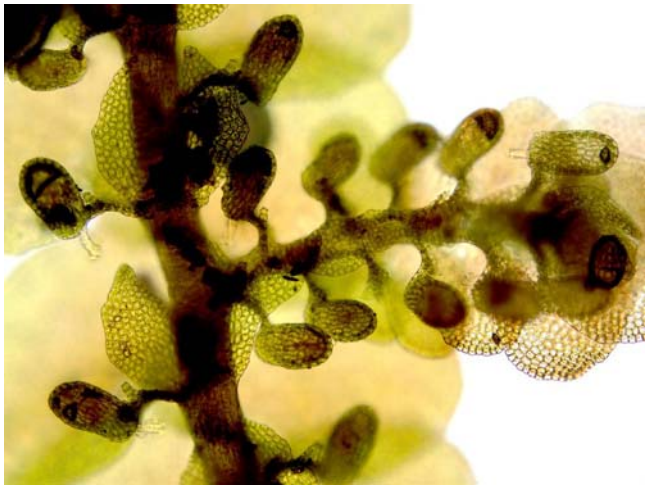

Figure 25. ***Frullania obcordata***, a generalist species that is more strongly pigmented in tree zones that receive more light. Photo by Blanka Aguero, with permission.

Life and Growth Forms

Bryophyte life and growth forms reflect the habitat conditions, particularly that of available moisture. Life forms of tropical bryophytes were described in detail by Mägdefrau (1982). Aceby *et al*. (2003) found that 4-15-year-old fallows have a significantly decreased diversity of bryophyte families and mosses in Bolivia (Figure 26). Liverworts, on the other hand, have nearly as much diversity in the fallows as in the submontane rainforest. The life form is ~72% **smooth mat**, a much higher percentage than that found in the forest.

Pardow *et al*. (2012) used life forms as an indicator of high diversity in a tropical lowland cloud forest of the Guianas (Figure 27-Figure 28). These lowland cloud forests are hotspots of bryophyte diversity in tropical lowland areas compared to the common lowland rainforest, as shown in detail by Gradstein (2006) and Gehrig-Downie *et al*. (2011, 2013). The cloud forest benefits from the frequent early morning fog in the valleys. Pardow *et al*. compared the distribution of the functional groups of epiphytes across height zones in the lowland cloud forest and lowland rainforest and found a higher diversity of life forms of bryophytes in the cloud forest. In the cloud forest, **tail**, **weft**, and **pendants** are common, whereas in the rainforest they are almost absent. The researchers suggested that identification of life forms could be used as a rapid method for identifying lowland cloud forests for conservation.

Figure 26. Bolivian old field at 600 m, surrounded by secondary forest with submontane rainforest in the background. Photo by Thorsten Krömer, courtesy of Robbert Gradstein.

Figure 27. Lowland cloud forest of French Guiana. Photo courtesy of Robbert Gradstein.

Figure 28. Canopy of lowland cloud forest in French Guiana. Photo by Renske Ek, courtesy of Robbert Gradstein.

In our study (Li *et al.* 1989) of ***Frullania*** (Figure 14, Figure 22-Figure 25) in Papua New Guinea (Figure 29), moisture and elevation gradients were important in determining taxa assemblages. Although we suspected that light and temperature were likewise important, we had no data to test these directly. Pócs (1982) and Richards (1984a, b) and a review by Thiers (1988) likewise report that the most important influences on tropical rain forest liverwort (**Jungermanniales**) growth are relative humidity, rainfall, light, and temperature (Thiers 1988). Frahm (1990a) found compensation points for two mosses in controlled temperature regimes, relating these to the tropical temperature regimes. Within this group, growth habit and stem anatomy are often modified, but perhaps the most adaptive features are the development of both simple and complex saccate leaf lobules in liverworts such as ***Frullania*** (Figure 22-Figure 25), presumably for retention of water, and elongate, thin-walled leaf cells.

Figure 29. Papua New Guinea. Photo from eGuide Travel, through Creative Commons.

On the other hand, excess water can be a problem because it reduces diffusion of CO_2 and can encourage fungal growth (Frey *et al*. 1990). Trees in the tropics often have leaves with prolonged (**acuminate**) tips. This has been considered by some to be an adaptation that permits water to run off the leaf, thus reducing the colonization by fungi on leaves that are subjected to daily rains. **Pendent** bryophytes in rainforests have a somewhat similar adaptation, but the interpretation has been more debatable. For example, in north temperate forests, ***Frullania*** (Figure 30) is recognized as a liverwort that closely adheres to its bark substrate (**mats**). However, in the rainforest, several **pendent** species of ***Frullania*** (Figure 31) exist (Li *et al.* 1989). One interpretation of this is again the possibility of the water to be shed by running down the rope-like plant body. However, an alternate interpretation seems to be just the opposite. The **pendent** form is actually a response to the weight of water, first in weighing down taller plants with weak stems, and then in collecting the water at the tips of the branches where the dividing cells are. Thus, the tip of the moss, during the rainy season, may be bathed in water nearly all the time, giving it a nearly aquatic environment. This continual supply of water permits the cells to divide uninterrupted by periods of drought during the rainy season. Such bryophytes can be found not only in tropical and subtropical forests such as those of southern Japan, but also in the rainforests of the Pacific Northwest in North America.

Figure 30. ***Frullania bolanderi***, an adnate species in the North Temperate Zone. Photo by Janice Glime.

Figure 31. Pendent ***Frullania*** from the Neotropics. Photo by Michael Lüth, with permission.

Proctor (2002) found that the **pendent** mosses ***Floribundaria floribunda*** (Figure 32) and ***Pilotrichella ampullacea*** (Figure 33) hold large amounts of external capillary water. Nevertheless, both species are able to recover from 11 months of dry storage at 5°C (not a very likely temperature in lowland tropics, but possible at some higher elevations). Both require several days to recover, with ***F. floribunda*** taking somewhat longer. Short desiccation periods elicit rapid recovery, with ***P. ampullacea*** reaching a positive carbon balance after only 30-60 minutes following 20 hours of air drying. After six days, they require 2-5 hours, suggesting that they are adapted to the short periods of desiccation found in the humid tropical forests, but not to longer, frequent periods. ***Floribundaria floribunda***, on the other hand, is best adapted for more shady and continuously moist forests.

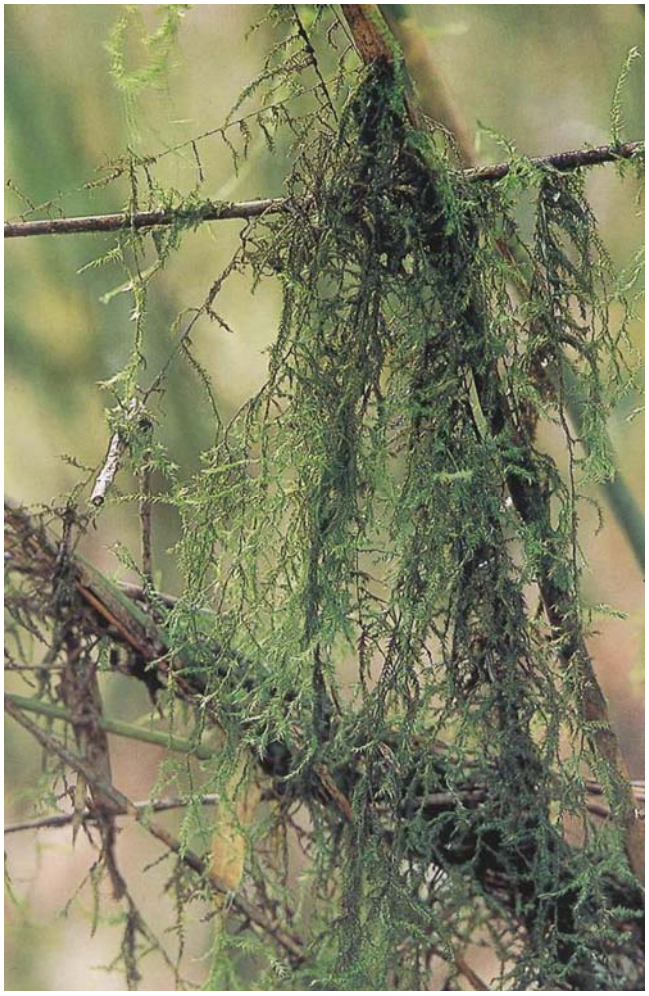

Figure 32. ***Floribundaria floribunda***, a species that holds large amounts of external capillary water. Photo from Taiwan Biodiversity website, through Creative Commons.

Figure 33. ***Pilotrichella ampullacea***, a species that holds large amounts of external capillary water. Photo by Jan-Peter Frahm, with permission.

In the leafy liverworts, Thiers (1988) recognized stem characters such as growth habit (projecting, prostrate, rheophytic) and anatomical characters such epidermal thickenings, stem reduction, and stem flattening (often present in **mats**) as conserving moisture during dry periods. The flattened stems, such as those in ***Pteropsiella frondiformis*** (**Lepidoziaceae**), do most of the photosynthesizing, and accompanied by reduced leaves, the reduced life form would most likely conserve water during dry periods. Other leaf modifications include development of simple and complex saccate leaf lobules [*e.g.* ***Pleurozia*** (Figure 34-Figure 35) and ***Colura*** (Figure 36-Figure 37)] and presence of elongate, thin-walled, hyaline cells in the leaf margins [*e.g.* ***Cololejeunea marginata*** (Figure 38), ***C. cardiocarpa*** (Figure 39)], all of which help to hold or absorb water.

Further descriptions of life forms and growth forms as they relate to habitat can be found in the following subchapters. For an introduction to the topic, see Volume 1, subchapter 4-5.

Figure 34. ***Pleurozia purpurea***, a species with lobules. Photo by Matt von Konrat, through public domain.

Figure 35. ***Pleurozia purpurea*** showing lobules with the protozoan ***Blepharisma*** living in them. Photo courtesy of Hess and Jan-Peter Frahm.

Figure 36. ***Colura vitiensis*** on leaf, Fiji Islands, a species with leaf lobules. Photo courtesy of Tamás Pócs.

Figure 37. ***Colura*** leaf showing lobule. Photo courtesy of Jan-Peter Frahm, with permission.

Figure 38. ***Cololejeunea marginata***, a leafy liverwort species with thin-walled hyaline cells on the leaf margins. Photo by Jan-Peter Frahm, with permission.

Figure 39. ***Cololejeunea cardiocarpa***, a leafy liverwort species with thin-walled hyaline cells on the leaf margins; it also has lobules. Photo by Blanka Aguero, with permission.

Nutrient Relations

Nutrients are also affected by the rainy and dry seasons. Nutrient pulses occur as bryophytes dry and rewet. Damaged membranes leak nutrients and other substances such as sugars and polyols. Rainfall leaches these nutrients from the bryophytes, including their surfaces, and carries them to the forest floor (Lodge *et al.*). These pulses synchronize nutrient availability that maintains higher rates of nutrient mineralization, plant uptake, and forest productivity. It provides nutrients at the beginning of the growing seasons, a time at which they should be most beneficial to forest species. Thus the bryophytes serve as storage units that provide nutrients at the most critical time.

Coxson and coworkers (Coxson 1991; Coxson *et al.* 1992) noted the importance of wetting/drying cycles for the accumulation of sugars and polyols to more than 950 kg ha^{-1} in the epiphytic bryophytes of the cloud forest canopy of Guadeloupe (French West Indies). These sugars can stimulate the growth of microbes and thus facilitate the breakdown of litter. These relationships suggest some of the importances of these wet to dry changes in nutrient release from the epiphytic bryophytes (and for some, probably ground-dwelling species as well) and their role in the forest dynamics.

Further support for these responses comes from differences between upper and lower canopy bryophytes. Coxson and coworkers (1992) found that the upper canopy leafy liverwort ***Frullania atrata*** (Figure 40) holds 17% of its dry weight as sugar and polyol reserves. [Note that the name ***F. atrata*** has been misapplied to a number of tropical ***Frullania*** specimens, so information regarding the species may actually belong to one of its look-alikes (pers. comm. Robbert Gradstein).] By contrast the lower canopy moss ***Phyllogonium fulgens*** (Figure 41) holds these reserves as less than 6% of its dry weight. The upper canopy bryophytes seem better adapted at retaining these, with ***F. atrata*** releasing only 0.3 g m^{-2} compared to 0.9 g m^{-2} for ***P. fulgens***. This relationship was supported by similar relationships of bryophytes under field conditions in the tropical montane cloud forest of Guadeloupe, French West Indies.

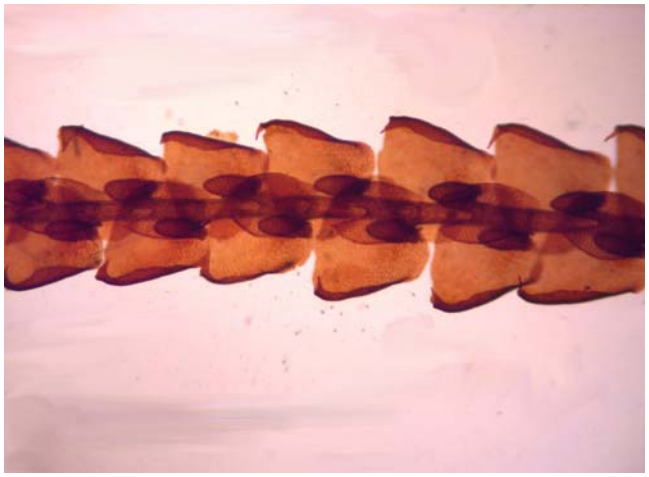

Figure 40. ***Frullania atrata***, an upper canopy liverwort and a species that can hold 17% of its dry weight as sugar and polyol reserves. Photo by Juan Larrain, with permission.

Figure 41. ***Phyllogonium fulgens***, a lower canopy moss in the Neotropics, where it holds less than 6% of its dry weight as sugar and polyol reserves. Photo by Michael Lüth, with permission.

Frangi and Lugo (1992) studied the biomass and nutrient accumulation in ten-year-old communities in a flood plain at the Luquillo Experimental Forest, Puerto Rico. They found a higher bryophyte cover on streambanks where flooding was frequent but of short duration. The cover decreased toward the longer-lasting flood plain, with the minimum cover occurring in depressions where water remained and became stagnant. They measured nutrient accumulations in ash-free biomass of bryophytes. These accumulations in kg ha^{-1} were 14.5 for N, 0.8 for P, 5.3 for K, 2.7 for Ca, 2.7 for Mg, 0.5 for Mn, 18.5 for Fe, and 22 for Al. These numbers were similar to those found in fine litter. Nevertheless, these values were low compared to that of other bryophyte communities. Both biomass and nutrients were greater in streambank slope communities and slopes of tree mounds than that in depressions that remained wet for a long time. The bryophytes in these tropical flood plain communities appear to retain nutrients and serve as filters during flooding in these communities.

In the coastal forests of Kenya, some bryophytes specialize on acid or alkaline substrates (Wilding *et al.* 2016). For example, ***Tortella tortuosa*** (Figure 42) is strongly associated with calcareous substrates, whereas ***Racomitrium lanuginosum*** (Figure 43) only occurs on acid ground. These preferences most likely relate to their ability to obtain their needed nutrients, without getting them in excess.

Figure 42. ***Tortella tortuosa***, a species of calcareous substrates. Photo by Michael Lüth, with permission.

Figure 43. ***Racomitrium lanuginosum***, a species of acid substrates. Photo by Janice Glime.

Further discussion of nutrient relations of tropical bryophytes is in the subchapters on Epiphytes.

Productivity

Productivity studies, in particular, are difficult to compare because of differences in methodology. Moreover, few exist.

Pócs (1987) was among the early productivity researchers, examining the changes in biomass among bryophytes in the East African rainforests. As we might expect from temperate studies (Proctor 1982), physiological and experimental studies indicate that net productivity drops rapidly as temperatures rise above 25ºC (Frahm 1990b). Add low light levels to the high temperatures and the bryophytes are hindered by high

respiration rates and low photosynthetic rates, resulting in low or negative net assimilation. Due to differences in precipitation, humidity, temperature, and desiccation (Frahm 1990a, b), it is generally true that biomass of epiphytic bryophytes in equatorial latitudes increases from the tropical lowlands to the treeline. Thus, high temperatures, combined with low light intensities, can account for the low diversity of bryophytes in the lowlands. Richards (1952) found data indicating that during the wet, and thus cloudy, season, the maximum temperatures in the ground layer are lower than those in the dry season when the sun shines a greater proportion of the time.

This raises the question of how the limited numbers of species in the lowlands survive. Frahm (1990b) suggested this could involve a specialized phytochrome system or more effective storage of the photosynthetic products. Perhaps more realistically, the relatively high nutrient supply that arrives through abundant precipitation could support a positive net photosynthesis. Another factor that could contribute is that the forest floor can have high CO_2 concentrations due to enhanced decomposition of leaves in a hot, moist environment, but increased CO_2 levels are most beneficial in high light levels.

Zotz *et al*. (1997) provided further information on the CO_2 and water relations for net photosynthesis. Using six tropical bryophytes, these researchers measured the daily changes in water status and net CO_2 exchange in a submontane tropical rainforest in Panama (Figure 44). Daily variation of water content was "pronounced." Both high and low water content limited carbon gain. Low light during rainstorms was less important in limiting CO_2 exchange compared to water content. More than half the carbon gain was lost at night to respiration.

Figure 44. Panamanian submontane and montane forests. Photo by S. B. Matherson, through Creative Commons.

In a more recent publication, Chen *et al*. (2016) examined photosynthetic properties of epiphytes in Southwest China. These adaptations include higher total chlorophyll concentrations, specific leaf area, and chlorophyll per unit leaf N (Chl/N), lower ratio of chlorophyll *a*:*b*, and greater photosynthetic nitrogen-use efficiency. Measurements, in μmol m^{-2} s^{-1}, showed means for light-saturated net photosynthetic rate (0.55), light saturation point (106.72), light compensation point (4.17) and dark respiration rate (0.25). They demonstrated photosynthetic down-regulation under high light conditions for these low-light epiphytes. These trunk-dwelling epiphytes are adapted for high resource retention rather than high resource gain. This is accomplished by low respiration rates and low light compensation points in shady habitats.

Waite and Sack (2010) hypothesized that leaf trait values would "reflect the distinctive growth form and slow growth of mosses, but also that trait correlations would be analogous to those of tracheophytes." Using ten species from Hawaii (Figure 45), they quantified 35 physiological and morphological traits of cell, leaf, and canopy level of bryophytes growing on the ground, trunk, and canopy. These bryophytes had low leaf mass per area ($\mathbf{A_{mass}}$) and low gas exchange rates. Perhaps not surprisingly, but in contrast to that of tracheophytes, the moss light-saturated photosynthetic rate per mass did not correlate with habitat irradiance. However, leaf area, cell size, cell wall thickness, and moss canopy density all correlated with microhabitat irradiance. Waite and Sack furthermore found that costa size, canopy height, and A_{mass} were coordinated traits linked with structural allocation.

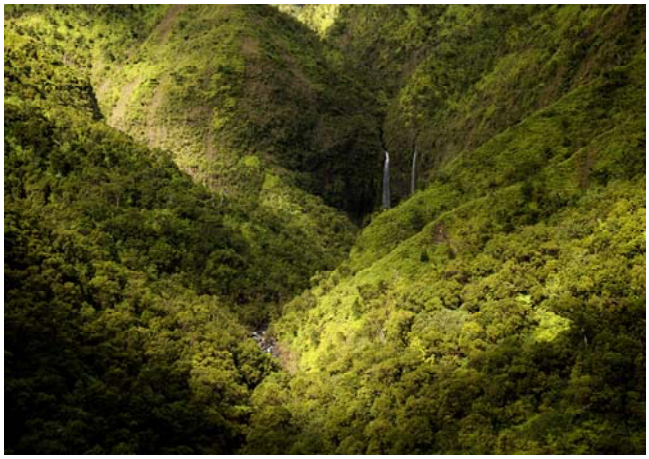

Figure 45. Hawaiian forest near Hanalei Bay, Kauai. Photo by Lukas, through Creative Commons.

Wagner *et al*. (2014) sought to explain the distribution of tropical bryophytes based on their physiological ecology. They noted the increase in bryophyte biomass with altitude in rain and cloud forests. They suggested that the low bryophyte abundance in the lowland rainforests is a result of the limitation of net carbon gain during fast drying and low light levels during daytime, coupled with the moist, warm nights. These moist, warm nights promote respiration and the daytime photosynthesis can be insufficient to balance the nighttime CO_2 loss. Wagner and coworkers concluded that the timing of hydration is crucial for net photosynthetic gain.

Datta Munshi (1974) studied seasonal changes in standing crop (chlorophyll) and annual net production of two moss communities at Varanasi, India. The mean bryomass in a perennial ***Hydrogonium*** (Figure 46) community was 95 g m^{-2} and in the seasonal community of ***Physcomitrium*** (Figure 47) it was only 11 g m^{-2}. These values represent the first on non-epiphytic bryophytes in the tropics and were lower than those typical of bryophytes in temperate forests, being more like those in Arctic ecosystems.

Figure 46. ***Hydrogonium ehrenbergii***, member of a perennial genus in the Indian tropics. Photo by Jan-Peter Frahm, with permission.

Figure 47. ***Physcomitrium eurystomum*** capsules; this genus is a member of seasonal community in the Indian tropics. Photo by Dick Haaksma, with permission.

Tropical forests generally have a larger biomass of epiphytic bryophytes than do temperate forests (Norris 1990). However, when trees are widely spaced or occur as lone trees, the greater penetration of wind can quickly desiccate the adhering bryophytes.

Overall, bryophytes comprised 40% of the epiphytic biomass in a Neotropical lower montane cloud forest at *ca*. 1600 m in Costa Rica (Nadkarni 1984) compared to 6% in the leeward rainforest (Ingram & Nadkarni 1993). In both forests, bryophytes were most abundant among the smallest branches. The gnarled, windblown trees and the frequent mist in the elfin forest provide extremely favorable conditions for bryophytic growth (see Lawton & Dryer 1980).

In an upper montane cloud forest at 3700 m in the Andes of Colombia (near the forest line), the bryophyte contribution to total epiphyte biomass was much higher, almost 70% (Hofstede *et al*. 1993) and total epiphytic biomass (including suspended soil) was a staggering 44 tons per hectare, the highest value ever reported.

Light is an important limiting factor for photosynthesis in the tropics. For three species of ***Pogonatum***, chlorophyll content and chloroplast size differed with light intensities where they predominated (Nasrulhaq-Boyce *et al*. 2011). For ***P. cirratum*** subsp. ***macrophyllum*** (Figure 48) and ***P. subtortile***, the total chlorophyll and beta-carotene content are higher than that in ***P. neesii*** (Figure 49). The latter lives in the areas with much higher light intensities (751±45 W m^{-2}), compared to 28±4 and 230±39 W m^{-2}, respectively. The sun species, ***P. neesii***, had a higher soluble protein content, likewise having a higher soluble protein to total chlorophyll ratio. ***Pogonatum cirratum*** subsp. ***macrophyllum***, the species from the lowest light, had significantly larger chloroplasts as well as more grana and thylakoids per chloroplast than did the other two species. And the two species from the lowest light had more than double the numbers of starch grains. On the other hand, the leaf **lamellae** (vertical stack of cells on leaf; Figure 50) were shortest in the species receiving the lowest light levels. Nevertheless, the CO_2 assimilation rates were highest in ***P. neesii*** even when light intensities were low. Lamellae can provide more surface area for photosynthesis and capillary spaces to hold water longer. In low-light ***P. cirratum*** subsp. ***macrophyllum***, these are rudimentary, whereas those of ***P. subtortile*** are 5-7 cells high.

Figure 48. ***Pogonatum cirratum***, a species of low light and large chlorophyll. Photo by Li Zhang, with permission.

Figure 49. ***Pogonatum neesii***, a species of higher light intensity and less chlorophyll than that in ***P. cirratum*** subsp. ***macrophyllum***. Photo by Yang Jia-dong, through Creative Commons.

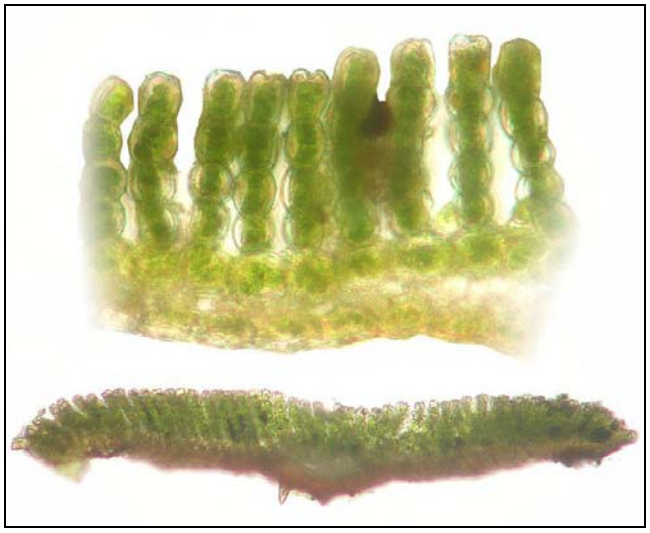

Figure 50. ***Pogonatum*** leaf cs showing leaf lamellae at two different magnifications. Photo by Michael Lüth, with permission.

Further discussions of productivity and biomass will be provided in the succeeding subchapters as they pertain to particular habitats.

Climate Effects

As noted above, moisture and temperature are important determinants of the types of bryophyte vegetation that survive. And precipitation events and cloud cover will diminish the light intensity. Among the early studies on the effects of these climate parameters on tropical bryophytes is a study by Biebel (1964, 1967). He examined temperature resistance of jungle mosses. Weber (1985) examined the effects of El Niño on bryophytes of the Galápagos. Furthermore, hurricanes can be devastating to epiphytes, ripping them from the trees or breaking branches and even toppling trees.

Rainy "seasons" are common in the tropics, punctuated by dry periods. If there are two periods in the year when the sun is overhead in the tropics, two wet seasons will occur (Richards 1952). If the two periods of overhead sun are close together, the two wet seasons will merge, but two maxima will still occur.

In the winters of many parts of the tropics, a dry season turns the area into near desert conditions. Akande (1984, 1985) attempted to understand the desiccation tolerance, or lack of it, among several tropical African bryophytes. Using the leafy liverwort ***Mastigolejeunea florea*** (now called ***Spruceanthus floreus*** according to Robbert Gradstein; see Figure 51) and the mosses ***Calymperes palisotii*** (Figure 52) and ***Entodontopsis nitens***, he concluded that these mosses were more desiccation-tolerant than the liverwort. It is interesting that bryophytes maintained at 0% relative humidity for one week and one month at 28°C were able to resume respiration more quickly than those kept at 32 and 54% relative humidity. He considered this ability to recover from 0% humidity so easily to be a case of **anhydrobiosis** (living state without water).

Figure 51. ***Spruceanthus planiusculus*** in a genus where some of the tropical African species are less desiccation tolerant than mosses. Photo by Claudine Ah-Peng, courtesy of Robbert Gradstein.

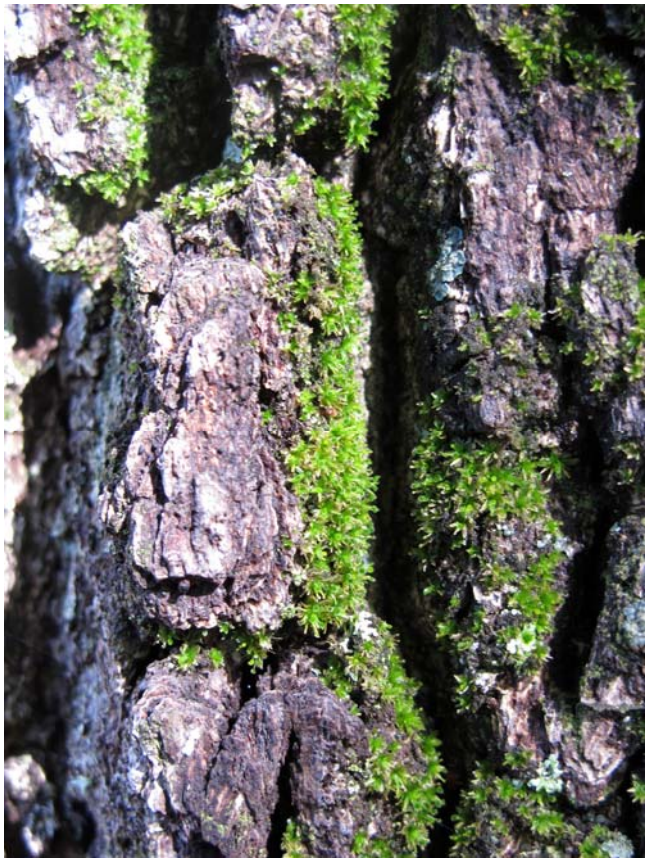

Figure 52. ***Calymperes palisotii*** on bark, a species that seems to be capable of anhydrobiosis in tropical Africa. Photo by Scott Zona, with permission.

Reproductive Biology and Phenology

As discussed earlier, the timing of reproduction must coincide with conditions favorable for dispersal. For example, both ***Sematophyllum subpinnatum*** (Figure 53) and ***Octoblepharum albidum*** (Figure 13) in the tropical Brazilian lowland forest have considerably more juvenile, immature, and mature gametangia during the rainy season than during the dry season, and that corresponds with an increase in the number of fertilized eggs in the archegonia

(Oliveira & Pôrto 2001; Pôrto & Oliveira 2002). One must keep in mind that unlike the desert, the dry season is subject to occasional, but short, rainfall events. In contrast to gametes, spores benefit from dry air for dispersal, and these two species derived that advantage by beginning sporophyte development during the rainy season, but completing it during the dry season.

Figure 53. ***Sematophyllum subpinnatum***, a species that produces most of its juvenile, immature, and mature gametangia during the rainy season in tropical Brazil. Photo by Michael Lüth, with permission.

Despite our limited taxonomic knowledge, there have been several studies on the reproduction of tropical bryophytes. By their very nature, individual studies are limited to one or few species (*e.g.* Fatoba 1998). Nevertheless, Kürschner and Parolly (1998a, b), Kürschner *et al*. (1999), and Kürschner (2004) were able to review the life strategies and adaptations of bryophytes, noting that functional types are "important for the establishment, habitat maintenance, and dispersal of species," indicating relationships among site ecology, niche differentiation, and species evolution.

Bryophytes in tropical regions seem to have relatively fast population dynamics when compared to those of temperate species (Monge-Nájera 1989; Coley *et al*. 1993; Zartman 2004). This is often an adaptation to the ephemeral nature of many of their substrates.

Cerqueira *et al*. (2016) studied the seasonality of reproduction of epiphytic bryophytes in the flooded forests of the eastern Amazon. Of 54 species, 34 were fertile. They were unable to identify a pattern in the seven studied species when comparing those in dry vs rainy conditions. Two species, however, were associated with the seasonality. They concluded that some bryophytes may maintain constant fertility as an adaptation to these tropical forests.

Batista *et al*. (2018) found that in a humid forest in northeastern Brazil, with seasonal rainfall and dry season, the 76 bryophyte species were predominantly monoicous (67%) and exhibited reproductive traits that tolerated adverse conditions, permitting them to persist under the seasonal water availability of the forest. A total of 80% of the species had sporophytes, mostly among the monoicous species. Only 21% exhibited asexual reproduction, including gemmae, regenerating fragments, and caducous leaves. Of these with asexual means, 75% were dioicous.

Life Cycle Strategies

Tropical forest substrata are usually rather temporary (Richards 1988), whether it be due to rapid decay, exfoliation, or soil erosion. In fact, Richards considers all substrata available to bryophytes in the tropics to be impermanent. Hence efficient short-distance dispersal is important. Epiphyllous species are frequently **colonists** with a short life span and production of numerous propagules. Species of ***Fissidens*** (Figure 71) and others that grow on termite mounds have a short-lived strategy. Richards (1988) carefully stated that the **perennial shuttle** with its relatively long life span and only moderate sexual or asexual reproduction is probably the commonest life strategy in the tropics, but that epiphylls are likely to be colonists because of the short duration of their substrate. **Fugitives** are rare, exceptions being the thallose liverwort ***Riccia*** (Figure 54) and the moss ***Micromitrium*** (Figure 55), as seen in West Africa.

Figure 54. ***Riccia cavernosa***, a thallose liverwort; members of this genus are fugitives in West Africa. Photo by Des Callaghan, with permission.

Figure 55. ***Micromitrium tenerum***; members of ***Micromitrium*** are fugitives in West Africa. Photo by Amelia Merced, with permission.

Mosses

The earliest of the tropical reproductive studies I could locate were those of Odu (1979, 1981). Studies on the mosses ***Racopilum*** (Figure 56) and ***Fissidens*** (Figure 71), indicate the importance of temperature in early life stages, with germination occurring at 30ºC and protonema growth at 25ºC (Odu 1979). This temperature requirement coincides with the maturation and dispersal of spores in the dry season, favoring the establishment of new shoots.

Figure 56. ***Racopilum africanum***, a tropical species that relies on the rainy season for sexual reproduction. Photo by Jan-Peter Frahm, with permission.

Where seasons alternate between rainy and dry seasons, the rainy season is critical for completion of reproduction in species that rely on sexual reproduction. Odu (1981) demonstrated this for four species in southwest Nigeria, showing that release of spores was timed to take advantage of the dry season. The reproductive phenology of several tropical African mosses (***Racopilum africanum*** (Figure 56), ***Fissidens weirii*** (see Figure 71; syn.=*F. glauculus*), ***Pelekium gratum*** (Figure 57; syn.=*Thuidium gratum*), ***Stereophyllum*** sp. (Figure 58) illustrate this. Using populations in southwestern Nigeria, Odu found that gametangia develop at the onset of the rainy season (March-April), whereas the development of sporophytes occurs later, with capsule maturation occurring at the end of the same rainy season (October-December). This permits dispersal of spores during and after the dry season (November-April). Thus the entire reproductive cycle is completed within one year. A similar relationship occurred among four species in a savannah in southwestern Nigeria (Makinde & Odu 1994).

Figure 57. ***Pelekium gratum***, a tropical moss species that relies on the rainy season for sexual reproduction. Photo by Manju Nair, through Creative Commons.

Figure 58. ***Stereophyllum radiculosum***, a tropical moss species that relies on the rainy season for sexual reproduction. Photo by Juan David Parra, through Creative Commons.

Both Olarinmoye (1974) and Egunyomi (1979a) determined that in studied bryophytes of west tropical Africa moisture is the regulatory factor for both growth and sporophyte production. Nevertheless, differences between species exist (Odu 1982). Odu found that ***Fissidens weirii*** (see Figure 71) and ***Racopilum africanum*** (Figure 56) have the shortest fertilization period, occurring in May. This fertilization period is earlier in ***Pelekium gratum*** (Figure 57) and much later in ***Octoblepharum albidum*** (Figure 13; Figure 59) (July-September). Nevertheless, the sporophytes of all four species mature toward the end of the rainy season (October-November). Herbarium specimens of these mosses collected over an 11-year period support this pattern.

Maciel-Silva and Oliveira (2016) examined the seasonal relationships of ***Octoblepharum albidum*** (Figure 13; Figure 59) in Brazil. Among 100 sporophyte-bearing plants, representing ten populations, the development was clearly seasonal, relating principally to rainfall. The early stages (immature to post-meiotic) occurred primarily during the dry season. Dehiscence, on the other hand, occurred mostly during the rainy season. This seems to be the opposite of that found for the species in Africa.

Octoblepharum albidum (Figure 59) is an autoicous pantropical species. Thus, its handling of various climatic regimes can help us to understand adaptations of reproductive strategies. Maciel-Silva *et al.* (2013) compared reproductive traits of this species in two Atlantic rainforests and two coastal sites in northeastern Brazil. This species not only produces spores frequently (Figure 59), but also produces gemmae at the leaf tips (Figure 60). In the coastal sites, the shoots had higher numbers of sporophytes, male and female branches per shoot, male gametangia per sexual branch, and longer setae than in the forest sites. Numbers of female gametangia per sexual branch did not differ between the two habitats and the male-biased sex ratio was present at all sites. Longer shoots produced more sporophytes, protonemata, and/or buds than did shorter ones, compared to production of gemmae, but only in the forest sites. The researchers suggested that the longer setae could favor spore dispersal, aiding colonization in coastal sites.

Figure 59. ***Octoblepharum albidum*** with capsules, a pantropical species that adjusts its reproductive strategies based on habitat climate. Photo by John Bradford, with permission.

Figure 60. ***Octoblepharum albidum*** with gemmae on the leaf tips. Photo by Li Zhang, with permission.

Oliveira and Pôrto (2005) examined sporophyte production and population structure of two moss species in the **Pottiaceae** in Brazil. Both ***Hyophila involuta*** (Figure 61) and ***Hyophiladelphus agrarius*** (Figure 62) produce capsules in the Atlantic forest at Recife, Pernambuco, Brazil (see Figure 63). Both species had a significantly female-biased sex ratio. The ratio of sterile to fertile shoots was close to 1:1. ***Hyophila involuta*** had a mean shoot density of 19 cm^{-2}, whereas it was 27 for ***Hyophiladelphus agrarius***. Furthermore, ***H. involuta*** had only 48% sporophyte production, whereas ***H. agrarius*** had 55%. Neither species seemed to change its sporophyte production based on any of the environmental parameters measured. The males and females do not clump by sex, favoring sporophyte production.

Figure 61. ***Hyophila involuta*** with capsules. Photo by M. C. Nair, K. P. Rajesh, and Madhusoodanan, through Creative Commons.

Figure 62. ***Hyophiladelphus agrarius*** with capsules. Photo by Fred Essig, with permission.

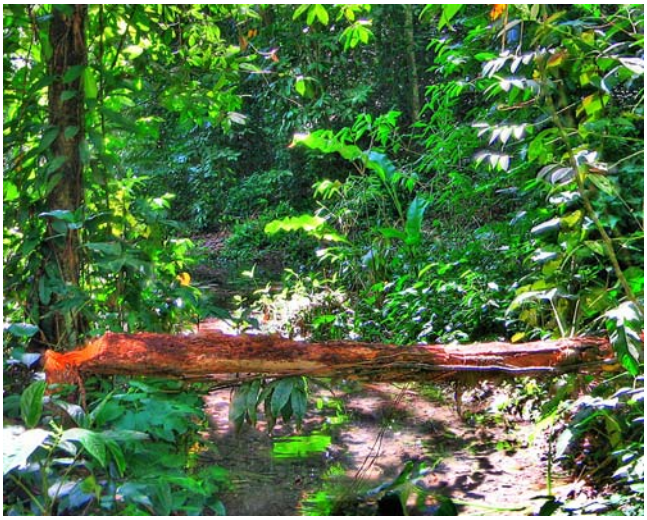

Figure 63. Atlantic forest, Pernambuco coastal habitat, Camarigibe, Brazil. Photo by Leonardo Brito Uniemelk, through Creative Commons.

Antheridia and Archegonia

Pôrto and Oliveira (2002) did a more intensive study on the reproductive **phenology** (study of cyclic and seasonal natural phenomena) of ***Octoblepharum albidum*** (Figure 59) in the Atlantic Forest in Brazil. In this 2-year study, they found an average of 13.4 antheridia per **perigonium** (envelope of modified leaves surrounding antheridia) and 6.7 archegonia per **perichaetium** (ensheathing cluster of modified leaves surrounding archegonia). All stages of gametangia were much greater in the rainy season, with a concomitant increase in fertilized eggs in archegonia. The sporophytes began development during the rainy season and matured in the dry season, at which time spores were dispersed.

Even in the moss ***Sematophyllum subpinnatum*** (Figure 53), in which antheridia and archegonia initiate, mature, and achieve fertilization throughout the year, the frequency increases in the rainy season (Oliveira & Pôrto 2001). Sporophytes (see Figure 64) initiate primarily in June through September, indicating that the rainy season is the most favorable time for fertilization.

Figure 64. ***Sematophyllum substrumulosum*** with capsules; capsules in ***Sematophyllum subpinnatum*** initiate in June through September in tropical Brazil, following fertilization in the rainy season. Photo by Michael Lüth, with permission.

Maciel-Silva and Valio (2011) found that in two different sites in the Brazilian rainforest, the phenology was somewhat different. Examination of eleven species of bryophytes indicates that the reproductive organs are active year-round. Female gametangia often mature before the onset of the rainy season. Male gametangia, however, tend to mature at the end of the dry season. Furthermore, at sea level, the highest production of immature male gametangia occurs at the start of the rainy season, whereas in the montane region, the highest production of immature male gametangia is at the end of the dry season. The researchers suggested that high temperatures could damage the development of male gametangia during the rainy season. Sporophytes dehisce before the rainy season begins, a time when spores can be dispersed farther by dry winds.

In summary, tropical gametangia mature primarily at the end of the dry season or beginning of the rainy season, most fertilizations occurs during the rainy season, and spore dispersal occurs during the dry season.

The pantropical moss ***Sematophyllum subpinnatum*** (Figure 53) is **autoicous** (having both sex organs on same plant but different branches) (Oliveira & Pôrto 2001). Sampling of two populations for two years in northeastern Brazil revealed that the average number of antheridia per perigonium ranges 9-20; archegonia per perichaetium ranges 3-26.

Monoicous vs Dioicous

As one might expect, **monoicous** (having both sexes on same plant) species have the highest levels of sporophyte production compared to **dioicous** (having sexes on separate plants) (Maciel-Silva *et al*. 2012a). Nevertheless, in the tropics, as elsewhere among mosses, the dioicous condition prevails in the tropical north Queensland, Australia, and most likely elsewhere in the tropics (Ramsay 1987).

Gradstein (1975, p. 29) found the highest level of sporophyte production in the autoicous ***Acrolejeunea fertilis*** (Figure 65) and ***A. pycnoclada***, with 15% presence of sporophytes in 100 collections of each of the two species studied. In other ***Acrolejeunea*** species mature sporophytes were present in less than 10% of collections studied, and sporophytes were not seen in two dioicous species. In their study of fertilizations in 11 species from a Brazilian Atlantic rainforest, Maciel-Silva and coworkers found that female-biased sex ratios and low rates of fertilization are typically balanced by high production of reproductive structures at the beginning of the reproductive cycle.

These same 11 species expressed sexual organs continuously over the 15-month period of study (Maciel-Silva & Valio 2011). Nevertheless, male gametangia are typically mature by the end of the dry season, with fertilization occurring during the wettest months. Female gametangia, on the other hand, are receptive over the entire period, with many maturing before the rainy season begins. Male gametangia experience a high abortion rate and take longer to develop. This pattern of male gametangia taking longer to develop is typical of bryophytes in many parts of the world. Sporophytes subsequently develop during the dry season, dispersing their spores toward the end of the season. Although the patterns of gametangia and sporophyte development differ among the species, it does not differ between the sea level and montane sites.

Figure 65. ***Acrolejeunea fertilis***, an autoicous species with good sporophyte production. Photo by Heino Lepp, Australian National Botanic Gardens, with online permission for non-commercial use.

In Mexico, two dioicous species of ***Syntrichia*** [***S. fragilis*** (Figure 66), ***S. amphidiacea*** (Figure 67)] are abundant (Mishler 1988). Both produce sporophytes only in limited circumstances within their range. Nevertheless, they are just as abundant in areas where sporophytes are rare or absent. This suggests that they must rely heavily on asexual reproduction in these areas.

Figure 66. ***Syntrichia fragilis*** dry, an abundant dioicous species in Mexico, but seldom producing capsules. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 67. ***Syntrichia amphidiacea*** dry, with gemmae, an abundant dioicous species in Mexico, but seldom producing capsules. Photo by Claudio Delgadillo Moya, with permission.

Dwarf Males

The genus ***Macromitrium*** is well known not only for its two sizes of spores (see below), but also for its dwarf males. Having tiny males (<1 mm tall) permits the spores to germinate and the tiny plants to reach maturity on the female plants, often very close to the archegonia of the female. This does present a serious inbreeding probability, but the great advantage of having many more sperm be successful in reaching a female seems to outweigh the disadvantages, particularly for epiphytes (Ando 1977) where sperm dispersal is especially difficult.

Ramsay (1987) reported that at least 23 genera of mosses in tropical north Queensland, Australia, have dwarf males. Some are facultative (physiologically determined), being dwarf only when the spore germinates on a female plant. Others are obligate (genetically determined), always forming dwarf males from the male spore. Both types are present in among species of ***Macromitrium*** (Ramsay 1979; Une 1985).

Propagules and Regrowth

Some widespread tropical bryophytes do not produce capsules and spores, usually due to absence of the opposite sex, poor gamete dispersal, or unsuccessful development of the sporophyte. Olarinmoye (1986) examined survival strategies of the mosses ***Hyophila crenulata*** (see Figure 68), ***Barbula lambarenensis*** (see Figure 69-Figure 70), and ***Fissidens asplenioides*** (Figure 71) in Ibadan, Nigeria. He established that survival strategies during unfavorable periods of drought could be as spores (only in ***Hyophila crenulata***), gemmae, and regrowth from the gametophores, as well as regrowth from rhizoids, shoot bases, apices, and the main stem. Rhizoids produce more regrowth than do shoot apices and main stems. He considered the production of spores in ***H. crenulata*** to give it a competitive advantage. Nevertheless, the gemma production and success of the other two species seems to more than compensate for lack of spores, as witnessed by their abundance and widespread distribution there.

Figure 68. ***Hyophila involuta*** (**Pottiaceae**) with capsules; ***Hyophila crenulata*** survives dry periods by spores, gemmae, and regrowth from any of its gametophore parts. Photo by Michael Lüth, with permission.

Figure 69. ***Barbula horrinervis*** (**Pottiaceae**) with bulbils in leaf axils; ***B. lambarenensis*** survives dry periods by gemmae that serve the same function as bulbils. Photo by Michael Lüth, with permission.

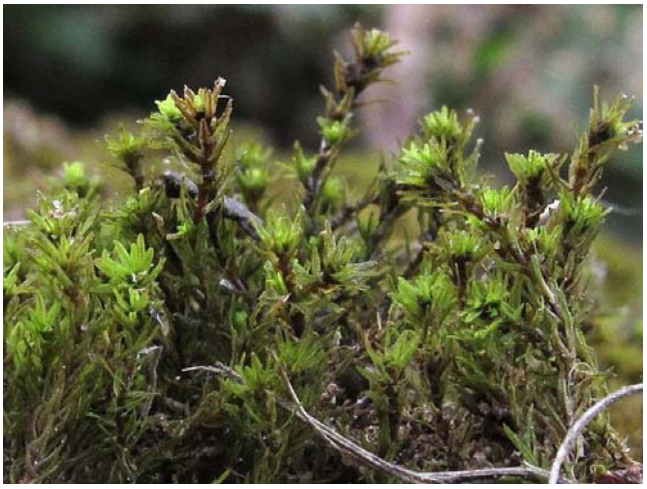

Figure 70. ***Barbula tenuirostris*** (**Pottiaceae**) showing broken leaves that could regenerate; ***B. lambarenensis*** uses such fragments to regrow following drying out. Photo by Michael Lüth, with permission.

Figure 71. ***Fissidens asplenioides***, a species that survives following drought through regrowth from various plant parts. Photo by Jan-Peter Frahm, with permission.

Propagule Forms

Tropical moss gemmae do not seem to have the same limited number of forms as do liverwort gemmae. Odu (1987) found a "great multiplicity of forms" among the gemmae in tropical West African mosses. These occur in a variety of locations, including leaf and leaf axils, and sometimes occur in more than one type of location. Odu concluded that gemmae are of "immense ecological importance" to the tropical mosses. This is facilitated in **Calymperaceae** (Figure 52) by rapid germination – within 1-2 days after becoming dislodged from the leaves. In **Bryaceae**, asexual propagules are often produced as multicellular rhizoidal tubers (Figure 72). In addition to these, there may be gemmae in leaf axils and on rhizoids. As in **Calymperaceae**, gemma germination is rapid, within 2-3 days. In southern Nigeria, some species of **Pottiaceae** (Figure 68-Figure 70) have few male plants and hence rely on gemmae.

Figure 72. ***Bryum dichotomum*** rhizoidal tuber, a common means of reproduction in West Tropical Africa. Photo by Des Callaghan, with permission.

Calymperes (Figure 52) is one of the prominent gemmiferous mosses in the tropics. When examining ***C. afzelii*** (Figure 73) and ***C. erosum*** (Figure 74) Odu and Owotomo (1982) found that the shoots are **dimorphic** (having two forms). That is, the first leaves to develop do not produce gemmae. Later leaves are gemmiferous (Figure 74), and these alternate in coordination with the dry and rainy seasons.

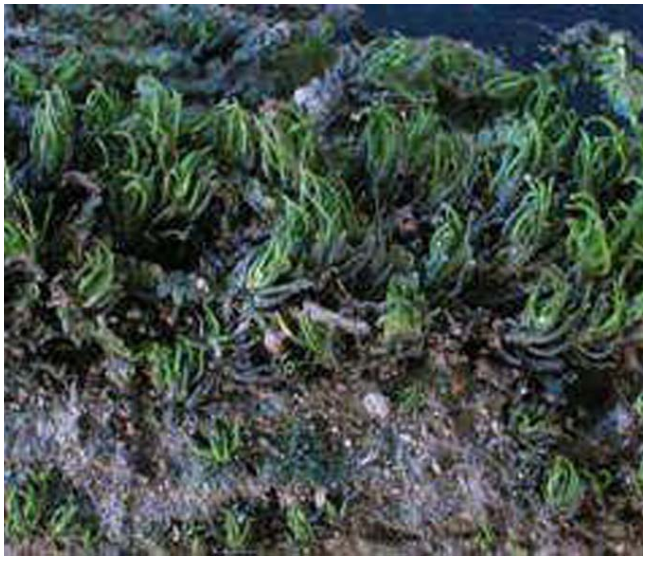

Figure 73. ***Calymperes afzelii***, a species that produces protonemata and single-layered gemmae in leaf axils. Photo by Piers Majestyk, through Creative Commons.

Figure 74. ***Calymperes erosum*** with gemmae; this species does not produce gemmae on its first shoots. Photo by Li Zhang, with permission.

Egunyomi (1984) surveyed the asexual **diaspores** (propagule; any structure that functions in plant dispersal) of mosses in Nigeria. He recognized two major categories: caducous shoots and gemmae. Species with one or more of these asexual diaspores comprise 15% of the Nigerian moss flora. He considered this means of reproduction to be especially important for mosses that do not produce sporophytes in all or part of their range. Seven of these species are sexually sterile.

The miniature **caducous** (can break away from the stem) shoots are often found with rhizoids (Egunyomi (1984). Species with this type of diaspore include ***Trachycarpidium tisseranti*** (see Figure 75), ***Archidium*** sp. (Figure 76), ***Bryum argenteum*** (Figure 77), ***B. coronatum*** (Figure 78), ***Bryum nitens***, and ***Campylopus*** (Figure 79) species. The latter two are strongly caducous.

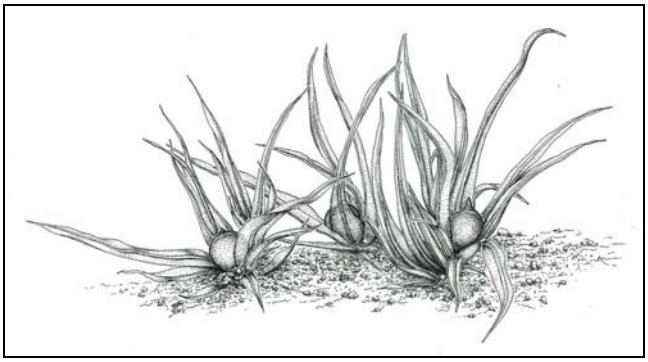

Figure 75. ***Trachycarpidium brisbanicum***; ***Trachycarpidium tisseranti*** has caducous shoots that aid its dispersal in tropical Africa. Drawing by Rod Seppelt, with permission.

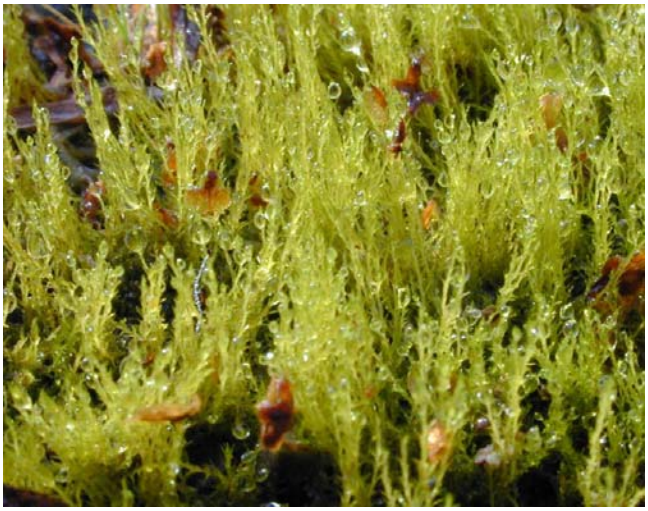

Figure 76. ***Archidium alternifolium***, a species with caducous shoots. Photo by Jan-Peter Frahm, with permission.

Figure 77. ***Bryum argenteum***, a species with caducous shoots. Photo by Tushar Wankhede, through Creative Commons.

Figure 78. ***Bryum coronatum***, a species with caducous shoots. Photo by Michael Lüth, with permission.

Figure 79. ***Campylopus subulatus*** with broken tips that become dispersal units. Photo by David T. Holyoak, with permission.

The second type is the **gemma** (Egunyomi 1984). In some, these are **uniseriate** (having only one cell layer) and produced from protonemata in leaf axils. This type includes ***Splachnobryum gracile*** (see Figure 80), ***Jaegerina scariosa*** (Figure 81), ***Henicodium geniculatum*** (Figure 82), and ***Bryum argenteum*** (Figure 77). Production of rhizoidal gemmae in ***Splachnobryum gracile*** and ***B. argenteum*** seems to be related to the high humidity where they were collected. Another type of gemma is borne on **excurrent** (extending beyond leaf tip) **costae** (leaf rib) and is **clavate** (club-shaped, like a baseball bat). Species with these include ***Calymperes erosum*** (Figure 74), ***C. afzelii*** (Figure 73), ***C. palisotii*** (Figure 52), and ***C. rabenhorstii***. ***Calymperopsis martinicensis*** produces filamentous gemmae that occur in splash cups at the shoot apex. In ***Octoblepharum albidum*** (Figure 13), the gemmae occur at leaf apices and along the margins. Multiseriate gemmae occur in ***Semibarbula lambarenenis*** and ***Hyophila crenulata*** (see Figure 61). ***Gemmabryum apiculatum*** (see Figure 83-Figure 85), and ***Anoectangium spathulatum*** (see Figure 86) produce **tubers** (Figure 85). These tubers are present on rhizoids in the soil and can germinate when the soil is disturbed. This can occur when wet season rains first disturb the soil. Tubers are able to remain viable 9-12 months after collection.

Figure 80. ***Splachnobryum obtusum***; ***Splachnobryum gracile*** produces rhizoidal gemmae in the tropics. Photo from British Bryological Society, with permission.

Figure 81. ***Jaegerina scariosa***, a species that produces protonemata and single-layered gemmae in leaf axils. Photo courtesy of Lucas Matheus da Rocha.

Figure 82. ***Henicodium geniculatum***, a species that produces protonemata and single-layered gemmae in leaf axils. Photo by Piers Majestyk, through Creative Commons.

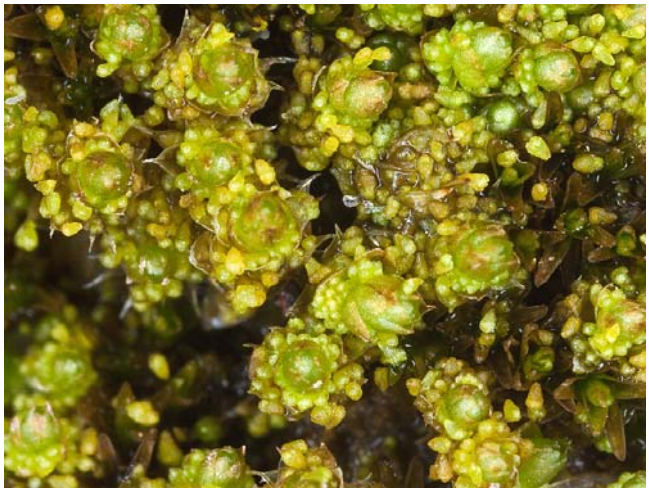

Figure 83. ***Gemmabryum dichotomum***; ***Gemmabryum apiculatum*** is a species with both bulbils and tubers. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

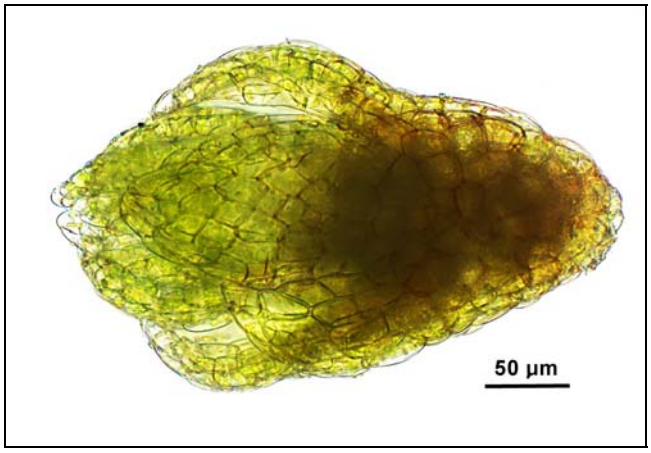

Figure 84. ***Gemmabryum dichotomum*** bulbil. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

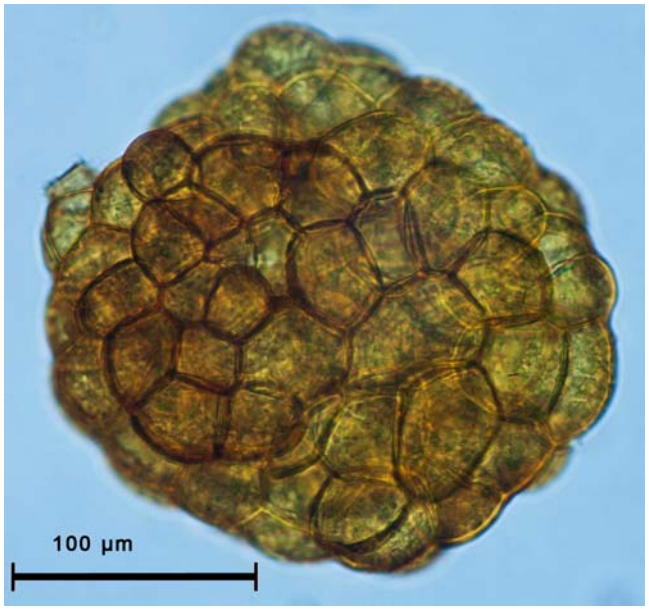

Figure 85. ***Gemmabryum apiculatum*** tuber. Photo by Jan Janssens, with permission.

Figure 86. ***Anoectangium aestivum***; ***Anoectangium spathulatum*** produces tubers in the tropics. Photo by Hermann Schachner, through Creative Commons.

In Australia, Ramsay (1987) reported a variety of asexual reproductive types from the tropical north Queensland mosses. These include plantlets on leaf tips (***Octoblepharum albidum***), fragile leaf apices (***Groutiella tomentosa***), gemmae on leaf surfaces (***Macromitrium brevicaule, Syrrhopodon*** sp., ***Calymperes tenerum***, ***Clastobryella***), gemmae on leafless stem apices (***Trachyloma diversinerve***), or axillary toward stem apex (***Trachyloma wattsii***), Flagellate julaceous shoots (***Taxithelium wattsii***, ***Wijkia extenuata***); shedding of whole leaves (***Arthrocormus*** sp).

Fragments

In many cases throughout the world, fragments of bryophytes are important in producing new colonies [see, for example, ***Octoblepharum albidum*** (Figure 13) Egunyomi *et al*. 1980]. Nadkarni *et al*. (2000) tested the interception and retention of bryophyte fragments on branches in a tropical montane cloud forest in Costa Rica. They found that for canopy-dwelling tracheophytes, establishment of bryophytes frequently occurs first. Most fragments don't succeed in becoming established, but about 1% do adhere and become established when dropped from above. On the other hand, 24% were retained among undisturbed bryophytic epiphytes during the 6-month study and 5% were retained on stripped branches.

One of the more uncommon means of dispersal is through specialized branches that can break off easily. In the epiphytic, dioicous ***Meteoriopsis undulata*** (Figure 87), a recent addition to the Australian Wet Tropics flora, Meagher and Cairns (2016) found flagellate branches that break off when dry. Sexual reproduction is unknown in ***M. undulata***. ***Floribundaria walkeri*** (Figure 88) is a relatively uncommon species in these Wet Tropics and also has flagellate branches. But in this case, the branches are not specialized, but rather are extensions of normal branches.

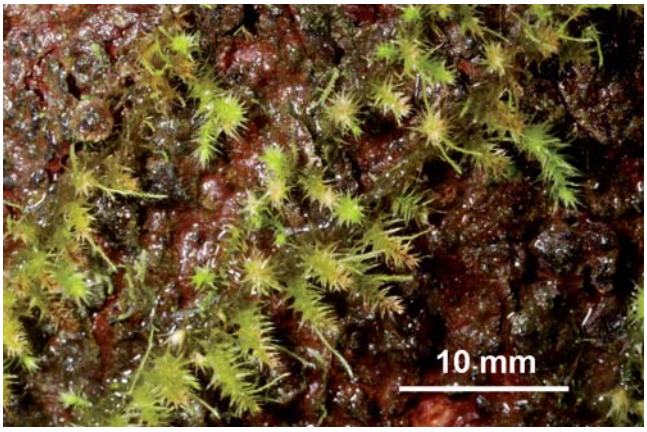

Figure 87. ***Meteoriopsis undulata*** on tree trunk in North Queensland, showing flagelliform branches. Photo from Meagher & Cairns 2016, with permission.

Figure 88. ***Floribundaria walkeri***, a species that produces flagelliform ends on its branches. Photo by Manju Nair, through Creative Commons.

Spore Size

Richards (1984a) found that sun epiphytic mosses usually have larger spores than do shade epiphytes. This would provide a better energy source for establishment of sun mosses, whereas shade mosses would more opportunity for dispersal. Spore size seemed to be unimportant among liverworts, but van Zanten and Gradstein (1988) determined that some shade liverwort epiphytes had spores with much less drought resistance, failing germination after only a few days of desiccation. This lack of drought resistance greatly limits dispersal range.

Diaspore Banks

Diaspore (structure that functions in plant dispersal; propagule) banks provide temporary refuge for spores, gemmae, and sometimes fragments, particularly in habitats that are frequently dry (During & Moyo 1999).

Egunyomi (1979b) tested longevity of spores from Nigeria by keeping them at room temperature and humidity for 1-3.5 years. Subsequent germination ranged from 0 to 92%. Fifteen of 21 species had no germination after that time. Only four species [***Weisiopsis nigeriana, Microcampylopus nanus*** (see Figure 89), ***Mittenothamnium overlaetii*** (see Figure 90), ***Weissia papillosa*** (see Figure 91)] had at least 50% germination after two years. ***Calymperes erosum*** (Figure 74) survived at least 1 year with 71% germination. ***Microcampylopus nanus*** and ***Weissia papillosa*** had 75 and 76% survival, respectively, of alternate wetting and air drying every 24 hours for four weeks following two years of desiccation. None of the four species with 50% germination listed above survived 4 weeks at -2º following 2 years of desiccation. All four species had at least 43% survival for 4 weeks at 8ºC following 2 years of desiccation, with ***Microcampylopus nanus*** having 80% and ***Weissia papillosa*** having 81%. Continuous submersion in water was as detrimental as freezing, with none of the four species surviving up to 3 weeks and the highest survival after one week was only 31% (***Weissia papillosa***). Egunyomi suggested that the submersion led to deterioration of the spores due to fungal attack.

Figure 89. ***Microcampylopus laevigatus***; ***M. nana*** can germinate from spores after two years of storage. Photo by Jan-Peter Frahm, with permission.

Figure 90. ***Mittenothamnium reptans*** from the Neotropics; ***M. overlaetii*** can germinate from spores after two years of storage. Photo by Michael Lüth, with permission.

Figure 91. ***Weissia rutilans*** with capsules; ***Weissia papillosa*** can germinate from spores after two years of storage. Photo by Michael Lüth, with permission.

Zander and During (1999) noted that diaspore banks often harbor the small species with a short life cycle that make them difficult to find above ground. They found ***Uleobryum occultum*** (Figure 92) (new to Africa, a moss species formerly known only from Brazil and Australia) and ***Bryoceuthospora aethiopica*** (Figure 93) (new to Zimbabwe). They also described a new species of the moss family **Pottiaceae – *Neophoenix matoposensis*** (Figure 94) from the diaspore bank of an experimental fire plot in Zimbabwe.

Figure 92. ***Uleobryum occultum***, a species known from diaspore banks in Zimbabwe. Photo by Claudio Delgadillo Moya, with permission.

Figure 93. ***Bryoceuthospora aethiopica*** with capsules, a species known from diaspore banks in Zimbabwe. Photo by Claudio Delgadillo Moya, with permission.

Figure 94. ***Neophoenix matoposensis***, a new species discovered from a diaspore bank in Zimbabwe. Image modified from drawing by Patricia Eckel in Zander & During 1999.

Maciel-Silva *et al*. (2012b) examined the properties of diaspore species in diaspore banks in the tropical rainforests. They compared species from the Atlantic rain forest (montane and sea level) in Brazil. Of the species identified, 68 were from bark, 55 from decaying wood, and 22 from soil. These species numbers differed little between sites. Mosses predominated, and monoicous species were more numerous than dioicous species. There was little *p*H effect on shoot emergence. The extant vegetation was well represented, with gemmae and spores making a high contribution. The researchers postulated that the diaspore banks contribute to fast establishment of species after disturbance of the tropical rainforests, as well as contributing to succession there. This is particularly true for species that produce lots of gemmae or monoicous mosses with a large commitment to sexual reproduction.

Bisang *et al*. (2003) germinated diaspores from Malaysian soil. Many of the germinated plants could not be identified and lived only a short time. Two moss species germinated from stem fragments – ***Isopterygium*** (Figure 95) and possibly ***Ectropothecium*** (Figure 96). The diaspore origin of the third identifiable moss, ***Calymperes*** (Figure 52), could not be determined.

Figure 95. ***Isopterygium tenerum***; the genus ***Isopterygium*** was among those that germinated from diaspore banks in the Malaysian mountain rainforest. Photo by Scott Zona, with online permission.

Figure 96. ***Ectropothecium*** sp., a genus tentatively identified among those that germinated from diaspore banks in the Malaysian mountain rainforest. Photo by Niels Klazenga, with permission.

Diaspore banks can be especially important after a major disturbance such as a fire (During 1998, 2007). In his study in southern Zimbabwe, During found emergence of 2 hornworts, 10 liverworts, and 22 mosses from surface soil samples of the savannah Matopos Sandveld Fire Plots. Annual burning did not seem to harm the diaspores hidden in the soil.

Conditions are not good for sexual reproduction in the tropics. Even if the plant has successful fertilization, sporophyte maturation and dispersal might not be successful. For example, in ***Bryum coronatum*** (Figure 78), sporophytes are common in Nigeria (Egunyomi 1982). Nevertheless, Egunyomi found 42% of the capsules remained undehisced even in the dry season. Furthermore, 41% of the setae had no capsules. On the other hand, spore germination was successful 65-88% of the time, but the protonemata exhibited abnormal growth. Egunyomi suggested that the numerous axillary propagules were important in dispersal in this species.

Prolonged Protonemal Stage

One adaptation to the short growth period is to prolong the duration of the protonema. As Gradstein and Wilson (2009) put it, this can be interpreted as a short-cut in the life cycle that permits rapid maturation and reproduction, both providing benefits in unstable, impermanent habitats. In this extreme, it is known as **neoteny**. The most extreme of these are in bryophytes that produce capsules directly on the protonema. The thalloid type occurs only among epiphyllous bryophytes. In the tropics, the epiphytic moss ***Ephemeropsis*** (Figure 97-Figure 98) produces persistent thalloid protonemata.

Figure 97. ***Ephemeropsis trentepohlioides*** with capsules and neotenous gametophyte. Photo by David Tng, with permission.

Figure 98. ***Ephemeropsis tjibodensis*** protonematal mat on palm in Fiji. Photo by Tamás Pócs, with permission.

Liverworts

Liverworts in general produce gemmae more commonly than do mosses. And many of them are more sensitive to desiccation and low humidity. This leads to some differences in their adaptations to living in the tropics.

Monoicous vs Dioicous

Schuster (1988) surmised that sexuality of liverworts shifts to **monoicous** (both sexes on same plant) in the tropics, with ***Plagiochila*** (Figure 99) being a notable exception as entirely **dioicous** (sexes on separate plants). Schuster considers the ability of monoicous taxa to easily achieve fertilization to be an advantage on impermanent substrata such as leaf surfaces, twigs, and even tree trunks.

Figure 99. ***Plagiochila*** sp., a dioicous tropical leafy liverwort. Photo by Lin Kyan, with permission.

Figure 101. ***Cololejeunea minutissima***; members of ***Cololejeunea*** exhibit neoteny in the tropics. Photo by Michael Lüth, with permission.

Neoteny

The monoicous property is further enhanced by multiple examples of **neoteny** (ability of juvenile plants to reproduce, *e.g*. species of ***Cololejeunea*** (Figure 100-Figure 102), a condition known for liverworts only in the tropics (Schuster 1988; Gradstein *et al*. 2006). Gradstein and Wilson (2009) note that botanists have interpreted neoteny as a short-cut in the life cycle because it permits rapid maturation and reproduction, an advantage in unstable, impermanent habitats. This is especially important for those species, like ***Cololejeunea*** species, that live on such temporary substrata as leaves (Schuster 1988; Gradstein *et al*. 2006). The high level of reproduction, especially sexual reproduction, coupled with the high diversity of niches in tropical forests, has resulted in a large number of liverwort taxa. In some cases, the leafy liverwort gametophyte is replaced by a large and persistent protonema (Figure 102) (Gradstein & Wilson 2009).

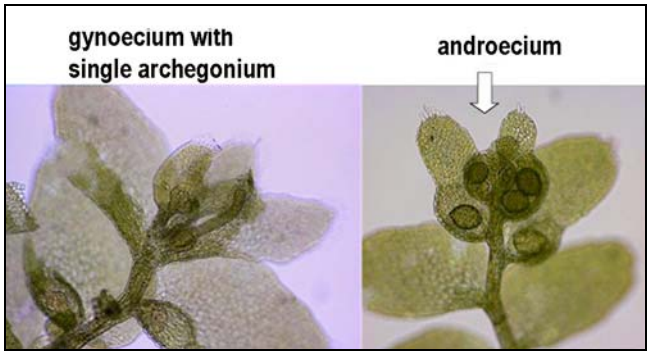

Figure 100. ***Cololejeunea cardiocarpa*** archegonium and antheridia exhibiting neoteny. Photo by Paul Davison, with permission.

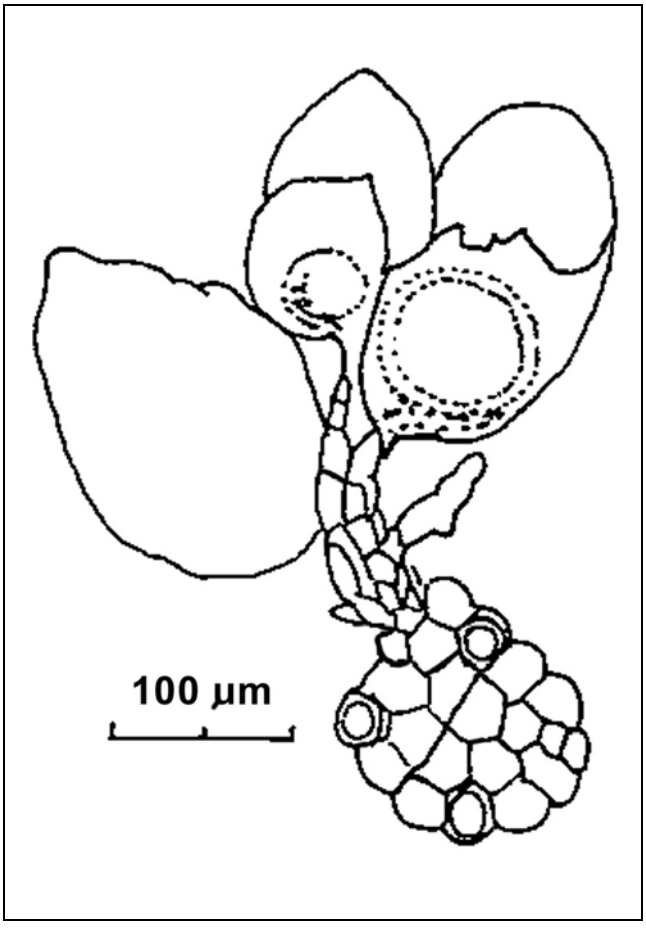

Figure 102. ***Cololejeunea borhidiana*** dwarf male, an extreme case of neoteny. Image by Tamás Pócs, slightly modified, with permission.

Reduced Numbers of Antheridia and Archegonia

Many temperate liverwort taxa produce numerous antheridia (5-16) and archegonia (12-25) (Schuster 1988). This is wasteful since only one archegonium on a branch can successfully produce a sporophyte. In tropical liverworts, these numbers are reduced to a more typical 1-4 archegonia and 1-2 antheridia per set of bracts (Figure 100). Furthermore, the size of gametangial branches is reduced (Figure 102) in many tropical taxa. Since gametes are typically released during the wet season, the danger of their drying out without achieving fertilization is reduced.

One rather unusual tropical leafy liverwort is ***Colura irrorata*** (Figure 103), a **rheophilous** (thrives in running water) member of **Lejeuneaceae** that grows part of the year submerged in torrential water (Figure 103). It was long known only from the banks of the Rio Topo in the Pastaza province of Ecuador (Thiers 1988) where it was discovered by Richard Spruce in 1857. It was long considered extinct until it was rediscovered there by Gradstein *et al.* (2004). A second locality of the rare species, in the same type of habitat, was recently found several hundreds of km further to the south in Ecuador (Gradstein & Benitez 2014). The species is more robust and has a more complex structure than other members of the **Lejeuneaceae**, but its most outstanding feature is its reproduction. Thiers (1988) estimated that a 2-cm section of stem could produce as many as 1600 **gynoecia** (archegonia and surrounding bracts, *i.e.* female reproductive structures).

Figure 103. ***Colura irrorata***, a species that produces up to 800 gynoecia per cm. Photo by Lou Jost, through Robbert Gradstein.

Short Life Cycles

These tropical liverworts enjoy short life cycles (spore to spore), with epiphyllous species completing a full cycle in one year and those on other substrata in 2-3 years (Schuster 1988; Piippo 1992). This is enhanced by green spores (Figure 104) that are able to germinate immediately, and that predominantly germinate within the capsule (Schuster 1988). Despite these indicators that long-distance dispersals are unlikely, there is ample evidence that at least some of them are successful.

One example of the spore germination for a common tropical species is that of the leafy liverwort ***Frullania ericoides*** (Figure 104-Figure 105) (Silva-e-Costa *et al.* 2017). This species is **endosporic** (spores divide within spore wall), producing a globular protonema within the spore wall. By the fourth week, the protonema breaks through the spore wall and produces tightly concave primordial leaves. This germination occurs at 1/4, 1/2, full, and 1 1/2 strength Knop's nutrient solution, but fails to occur at double strength solution. This suggests nutrient requirements for successful germination are relatively low (compared to that of tracheophytes) and that nutrient-rich substrates would be detrimental to these liverworts.

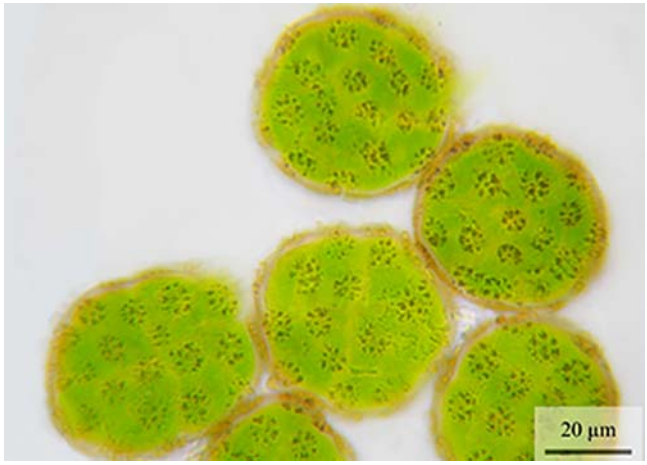

Figure 104. ***Frullania ericoides*** endospores, demonstrating their green color and germination within the spore. Photo from da Costa Silva-e-Costa *et al*. 2017, through Creative Commons.

Figure 105. ***Frullania ericoides***, a common tropical leafy liverwort. Photo by Blanka Aguero, with permission.

Alfayate *et al*. (2013) examined the spores of four pleurocarpous mosses in the Canary Islands, islands with a subtropical climate. They found that two of these were **isosporic** (all spores same size), but ***Leucodon canariensis*** (Figure 106) had two size classes of spores: medium-sized 1-celled spores and large multicellular spores. Furthermore, ***Cryptoleptodon longisetus*** (see Figure 107-Figure 108) has two sizes of spores, small spores and medium-sized spores. Spores germinate within the capsules in three of these species: ***Leucodon canariensis***, ***Cryptoleptodon longisetus***, and ***Neckera intermedia*** (Figure 109). ***Neckera cephalonica*** (Figure 110) spores do not germinate in the capsule. The perine wall of the spores of these species is papillose, an uncommon character for spores. The spores contain abundant lipid-like structures and chloroplasts with well-developed thylakoids.

Figure 106. ***Leucodon canariense***, a species with two spore sizes: medium-sized 1-celled spores and large multicellular spores. Photo from BBS website, with permission from Barry Stewart.

Figure 107. ***Cryptoleptodon*** sp. in its habitat in India. Photo by Michael Lüth, with permission.

Figure 108. ***Cryptoleptodon*** sp. ***Cryptoleptodon longisetus*** is a species with two sizes of spores. Photo by Michael Lüth, with permission.

Figure 109. ***Neckera intermedia***, a species with spores that germinate in the capsule. Photo by Jan-Peter Frahm, with permission.

Figure 110. ***Neckera cephalonica***, a species with spores that do not germinate in the capsule. Photo by Jan-Peter Frahm, with permission.

Short Spore Longevity

Tropical liverwort spores have a short longevity and are unable to survive desiccation (Schuster 1988). Rather, they have several adaptations for rapid germination. They are typically **endosporic** (germinating and beginning development within spore wall; Figure 104), spores germinate within the capsule, and spores have elastic walls to facilitate development.

Prolonged Protonemal Stage

Several liverworts have remarkably prolonged protonemal stages, as in ***Radula yanoella*** (Figure 111) from the Amazonian rainforest (Thiers 1988; Gradstein & Wilson 2009). This species has since been found in French Guyana, Ecuador, and Costa Rica (Gradstein & Ilkiu-Borges 2009). In ***Protocephalozia ephemeroides*** (Figure 112) and ***Cololejeunea metzgeriopsis*** (Figure 113-Figure 114; syn.=***Metzgeriopsis pusilla***), the protonemal stage

replaces the leafy gametophyte except in association with the reproductive structures (Gradstein *et al*. 2006). ***Metzgeriopsis pusilla*** was formerly considered the only species in its genus, but has since been placed in ***Cololejeunea*** as ***C. metzgeriopsis*** (Gradstein & Wilson 2009). It lives in humid montane forests of tropical southeast Asia, growing as an epiphyll on living leaves. Its thallus is unistratose with minute, leafy sexual branches arising from the margins. ***Protocephalozia ephemeroides*** is a very rare liverwort, known only from two localities in southern Venezuela, near the border with Brazil, where it was collected by Richard Spruce. There it was growing on moist earth in shade and on little mounds "thrown up by mud worms." Thiers (1988) suggests that the normally short-lived liverwort protonemal stage has been lost in these taxa, replaced by a long one, because of the always abundant moisture. The protonemal stage of most bryophytes is typically subject to damage from rapid drying. This protonema can be thalloid, as in the liverworts ***Cololejeunea metzgeriopsis*** (Figure 114) and ***Radula yanoella*** (Figure 111), or filamentous, as in the leafy liverwort ***Protocephalozia*** (Figure 112) (Gradstein & Wilson 2009).

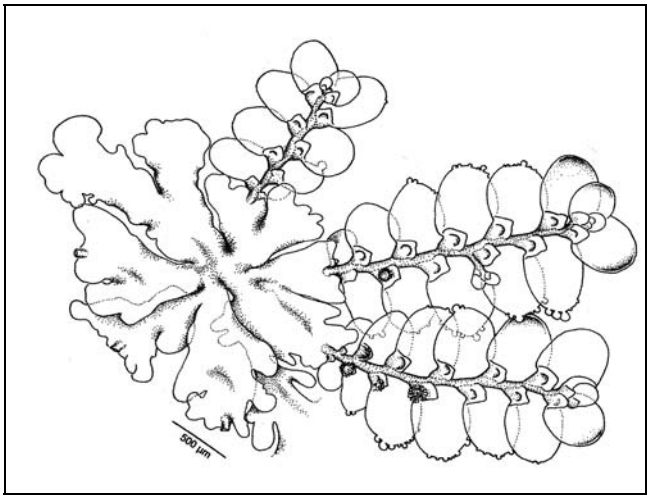

Figure 111. ***Radula yanoella***, a leafy liverwort with a remarkably prolonged thalloid protonema. Drawing courtesy of Robbert Gradstein, from Gradstein and Ilkiu-Borges 2009.

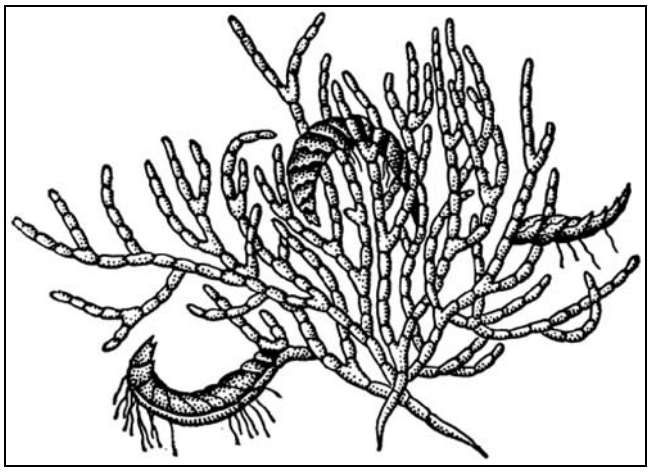

Figure 112. ***Protocephalozia ephemeroides*** with protonema and male gametophores. Image from Plantlife.ru, with implied online permission.

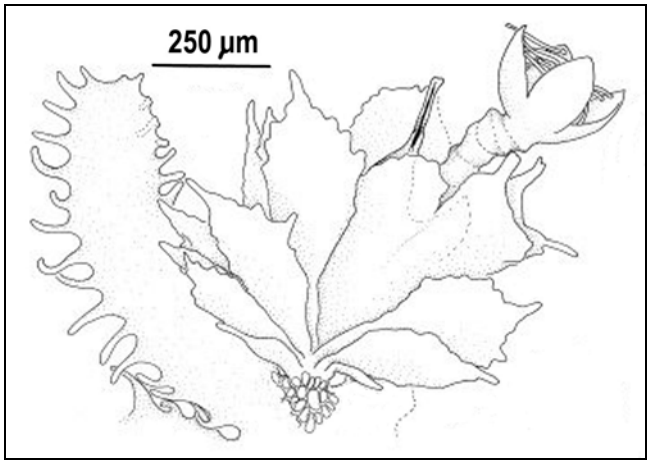

Figure 113. ***Cololejeunea metzgeriopsis*** plant with female organ. Drawing modified from Gradstein *et al*. 2006, with permission.

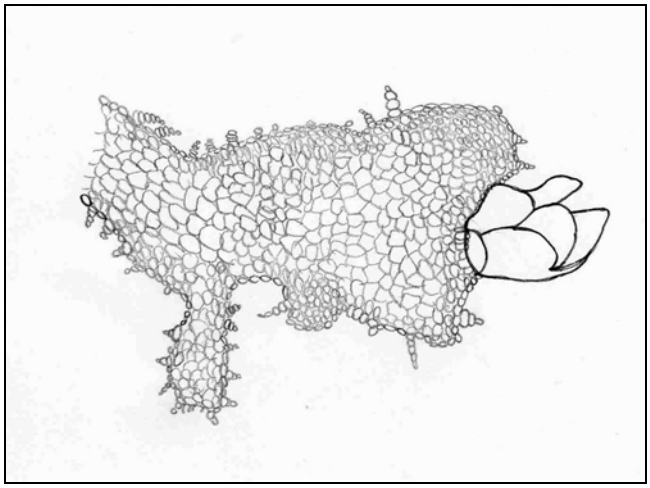

Figure 114. ***Cololejeunea metzgeriopsis*** protonema. Drawing by Žofie Juřičková, through Creative Commons.

Types of Gemmae

Even gemmae differ between the tropics and temperate zones (Schuster 1988). In temperate zones, the commonest types of gemmae are 1-2 cells and occur in branching chains (Figure 115). As such, they are easily dispersed, much like spores. These small gemmae occur in the **Jungermanniales** [*e.g.* **Cephaloziaceae** (Figure 116), **Calypogeiaceae** (Figure 117-Figure 118), **Scapaniaceae** (Figure 119-Figure 121), **Lophoziaceae** (Figure 122-Figure 124), **Cephaloziellaceae** (Figure 125-Figure 126)]. A single shoot can produce thousands of gemmae in a single growing season. This type of gemma is not so common in the tropics, where the more common **Porellales** (including **Lejeuneaceae**; Figure 127-Figure 128) have large gemmae. Instead, many tropical species tend to have discoid and single-layered gemmae, permitting easy dispersal to "considerable distances." The number of types is more limited, including discoid gemmae (Figure 128) and **caducous** (deciduous) branches (Figure 129). Even fragmenting branches are rare in the tropics. Gemmae are in general less common and less important among sexually reproducing tropical liverworts, even though many liverworts may produce both gemmae and sexual organs.

Figure 115. ***Nowellia curvifolia*** leaf gemmae, demonstrating the branching chains of 1-2-celled gemmae. Photo by Paul Davison, with permission.

Figure 116. ***Odontoschisma longiflorum*** (**Cephaloziaceae**) from the Neotropics, showing the small, branched chains of gemmae. Photo by Michael Lüth, with permission.

Figure 117. ***Calypogeia muelleriana***, with clusters of gemmae. Photo by David T. Holyoak, with permission.

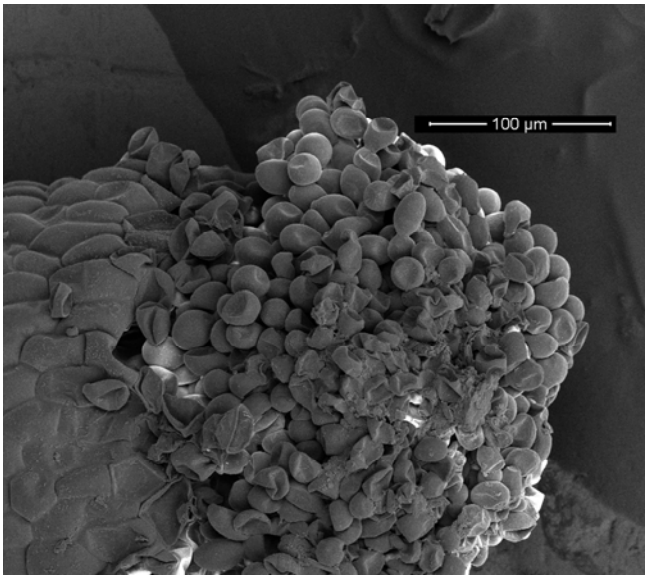

Figure 118. SEM of ***Calypogeia muelleriana*** leaf with gemmae. Photo courtesy of Jeff Duckett and Silvia Pressel.

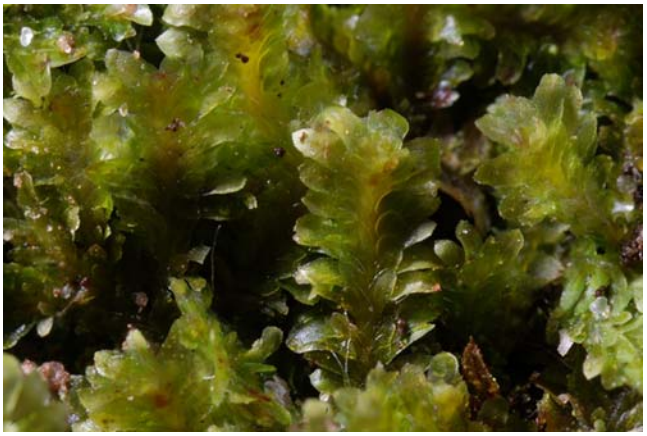

Figure 119. ***Diplophyllum albicans*** (**Scapaniaceae**), a species with worldwide distribution that includes the tropics. Photo by J. C. Schou, with permission.

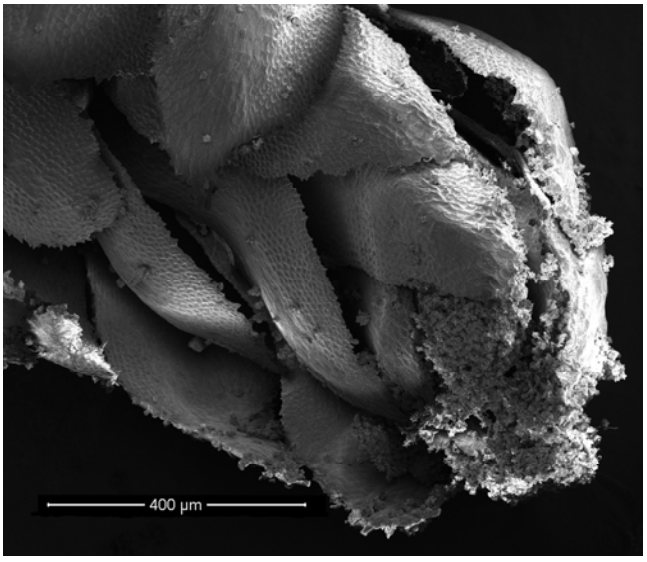

Figure 120. SEM of ***Diplophyllum albicans*** leaves with gemmae. Photo courtesy of Jeff Duckett and Silvia Pressel.

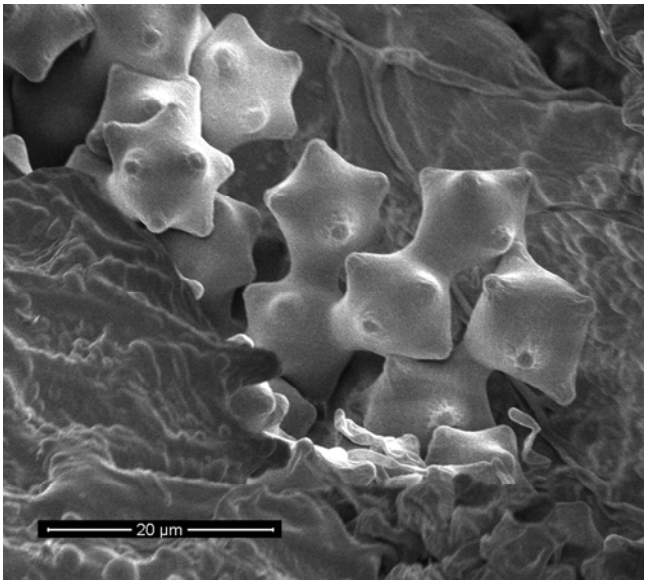

Figure 121. SEM of ***Diplophyllum albicans*** gemmae. Photo courtesy of Jeff Duckett and Silvia Pressel.

Figure 122. ***Lophozia ventricosa***, a widespread species that occurs in the Neotropics. Photo by Hermann Schachner, through Creative Commons.

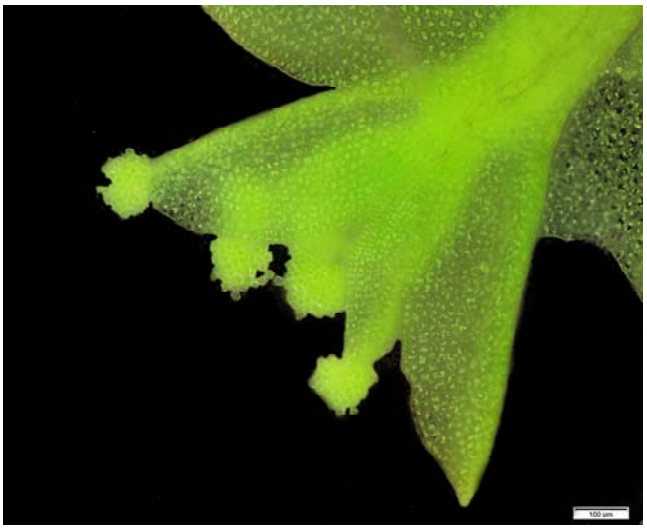

Figure 123. ***Lophozia ventricosa*** with gemmae on the leaf tips, a species found in the Neotropics. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

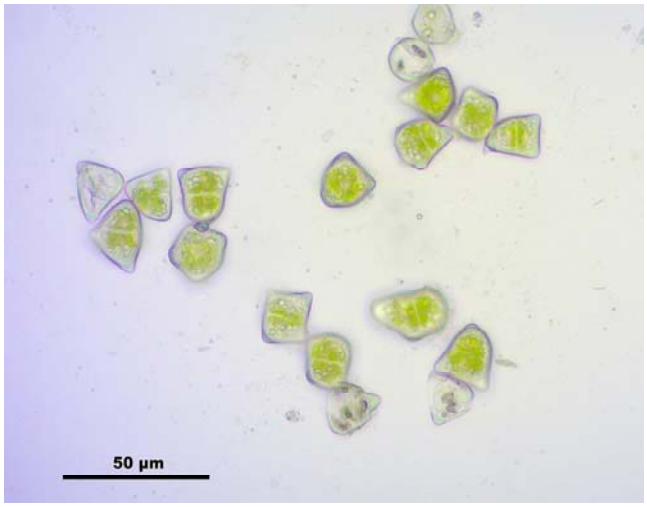

Figure 124. ***Lophozia ventricosa*** gemmae. Photo by Hermann Schachner, through Creative Commons.

Figure 125. ***Cephaloziella bicuspidata*** (**Cephaloziellaceae**). Photo by Botany Website, UBC, with permission.

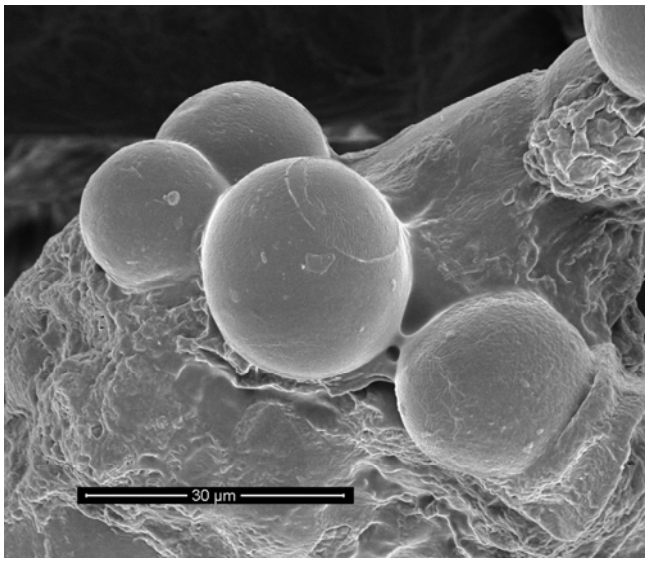

Figure 126. SEM of ***Cephaloziella bicuspidata*** gemmae, demonstrating the small gemma size of the **Cephaloziellaceae**. Photo courtesy of Jeff Duckett and Silvia Pressel.

Figure 127. ***Cololejeunea cardiocarpa*** (**Lejeuneaceae**), a leafy liverwort that occurs in the tropics and has large gemmae. Photo by Blanka Aguero, with permission.

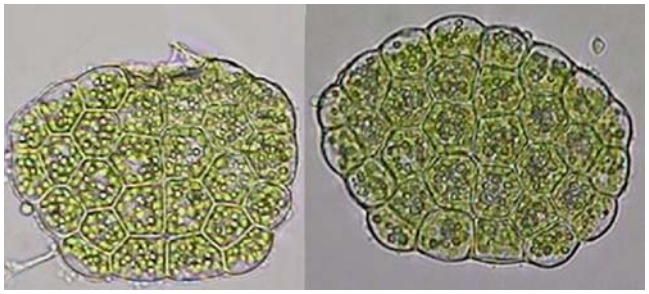

Figure 128. ***Cololejeunea cardiocarpa*** gemmae, showing the large gemma size typical of the **Lejeuneaceae**. Photo by Paul Davison, with permission.

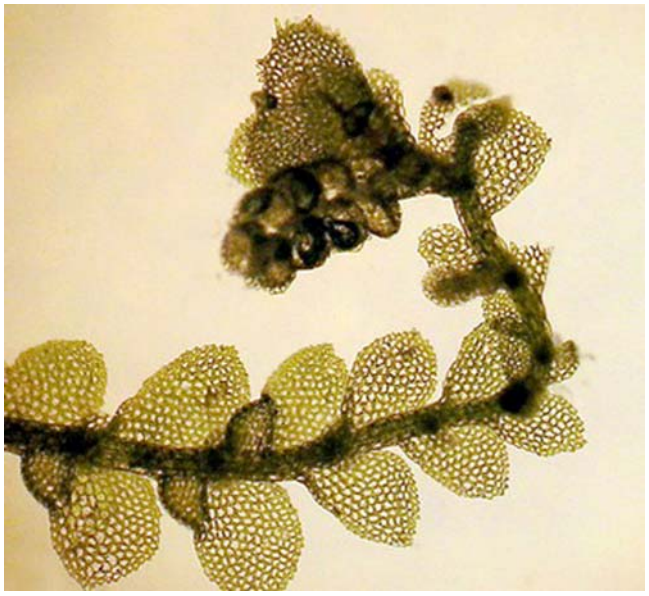

Figure 129. ***Prionolejeunea saccatiloba*** showing small, caducous branch that can fall off for asexual reproduction. Photo by Michaela Sonnleitner, with permission.

Another anomaly among tropical liverworts is that gemmae and sexual organs can be produced at the same time, as in many species of ***Cololejeunea*** (Figure 127-Figure 128, Figure 130-Figure 131) (Schuster 1988). By contrast, in temperate regions many species of **Lophoziaceae** and **Scapaniaceae** (Figure 132) may produce gemmae and sex organs at the same time. Their gemmae are typically produced in response to submarginal growth conditions that would often suppress production of sex organs.

Figure 130. ***Cololejeunea minutissima***; many species in this large genus produce gemmae and sexual organs at the same time. Photo by David T. Holyoak, with permission.

Figure 131. ***Cololejeunea truncatifolia*** from Uganda; many species in this genus produce gemmae and sexual organs at the same time. Photo by Martin Wigginton, with permission.

Figure 132. A temperate one ***Scapania nemorea*** with gemmae. Some temperate populations of ***Scapania*** can at times produce sexual structures and gemmae at the same time. Photo by Dick Haaksma, with permission.

Van Zanten and Gradstein (1987) found that spores of endemic liverwort species had less resistance to drying and freezing than did the transoceanic species of Colombian liverworts. When subjected to intercontinental transport on the wing tips of a jet airplane, spores of 60 out of 61 species became inviable, presumably due to high UV levels

at jet stream levels. Only spores of two species growing at high elevation (ca. 4000 m) were able to germinate after the flight. Probably they were well-adapted to UV radiation. On the other hand, van Zanten and Gradstein found that wet freezing permitted survival. They suggested that liverworts from high altitudes had a "good possibility" for aerial long-distance dispersal through hurricanes and tropical storms.

Diaspore Banks

Bisang *et al*. (2003) cultured diaspores from three Malaysian mountain rainforests. They found that more liverworts than mosses germinated in the samples, especially those from lower altitudes. Samples from higher elevations produced twice the species diversity compared to those from lower elevations. They were able to identify the liverworts ***Calypogeia arguta*** (Figure 133), ***C. fusca***, ***Lepidozia wallichiana*** (Figure 134), and ***Zoopsis liukiuensis*** (Figure 135), all common taxa in the collection area. The diaspore origin of the liverworts could not be determined.

Figure 133. ***Calypogeia arguta***, a species that survives in diaspore banks in Malaysian mountain rainforests. Photo by Jan-Peter Frahm, with permission.

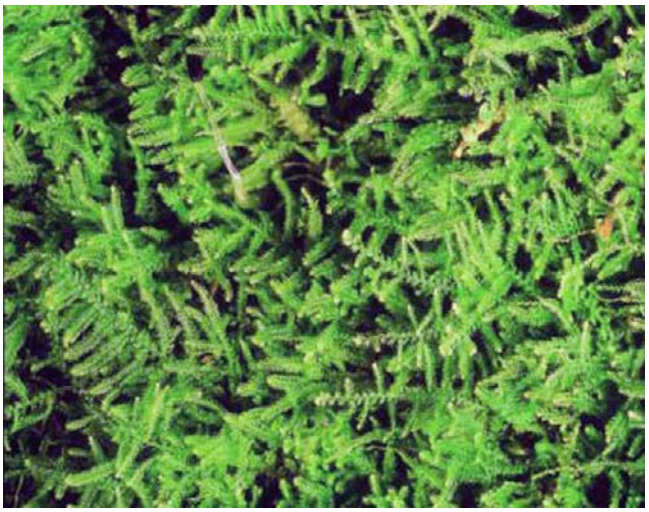

Figure 134. ***Lepidozia wallichiana***, a species that survives in diaspore banks in Malaysian mountain rainforests. Photo by Jia-dong Yang, through Creative Commons.

Figure 135. ***Zoopsis liukiuensis***, a species that survives in diaspore banks in Malaysian mountain rainforests. Photo by Rui-Liang Zhu, with permission.

Rheophilic Adaptations

River banks present problems unique to that habitat. The leafy liverwort ***Cololejeunea stotleriana*** (Figure 136) from Ecuador presents a highly specialized morphology and represents adaptations to that habitat (Figure 137) where little study has occurred (Gradstein *et al*. 2011). This species is both rheophilous and epiphyllous. Its adaptations include a robust stem, flatness, triangular lobules, large rhizoid fields not produced near each leaf base, super fertility, and clustered gynoecia. It was growing with the rare mosses ***Fissidens hydropogon*** (Figure 138) and ***Lepidopilum caviusculum*** (Figure 139).

Figure 136. ***Cololejeunea stotleriana*** on a fern frond. Photo by F. Werner, courtesy of Robbert Gradstein.

Figure 137. Habitat of the rheophilous ***Cololejeunea stotleriana***, ***Fissidens hydropogon***, and ***Lepidopilum caviusculum***. Photo by F. Werner, courtesy of Robbert Gradstein.

Figure 138. Herbarium specimen of ***Fissidens hydropogon***, a rare rheophilic moss from Ecuador. Photo from Alchetron.com, through Creative Commons.

Figure 139. Herbarium specimen of ***Lepidopilum caviusculum***, a rare rheophilic moss from Ecuador. Photo from the Natural History Museum, London, through Creative Commons.

Dispersal

Norhazrina *et al*. (2016) considered bryophytes to be very good dispersers, especially in contrast to flowering plants. This superior dispersal of bryophytes may lead to similar species richness patterns among the tropical regions, although tropical Africa has significantly fewer species than tropical America and tropical Asia. They found a slight but significantly higher beta diversity within tropical regions than among them. For many locations, oceans act as a barrier to "routine" dispersal, causing large-scale floristic patterns.

Suitable dispersal differs among regions and habitats. The tropics is in some places remote, separated from propagule sources by a wide expanse of ocean, and in others a mountain-valley topography likewise provides an expanse of unsuitable habitats. Thus, in discussing an area as expansive as the tropics, dispersal considerations are important for both biogeography and ecology.

With no experimental evidence but with vast ecological experience in the tropics and other regions, Richards (1988) ventured to apply his experience to hypothesize about dispersal of bryophytes in the tropics. First, he noted the impermanent nature of tropical substrates and suggested that these conditions would require efficient short-distance dispersal. He furthermore noted that each microhabitat has a distinct synusia of bryophytes that are characterized by particular life forms and life strategies. The swampy or oft-flooded sites are usually richer in species than sites that are well drained. The undergrowth probably has less effective wind dispersal than does the canopy.

For various asexual diaspores, splash is probably important (Richards 1988). For example, ***Calymperopsis*** species in Africa, as noted above, have their gemmae in splash cups. And discoid **Lejeuneaceae** (Figure 130-Figure 131) gemmae are probably dispersed by splashing rainfall. Richards also considered it likely that birds disperse fragments, particularly of **Meteoriaceae** (Figure 32-Figure 33), when they gather the mosses for nest building.

Baas-Becking (1934) introduced the concept that "everything is everywhere" for small things that can be dispersed by wind. The tropics seem like a good place to test this concept for bryophytes. Shaw *et al*. (2005) considered global patterns of moss diversity, patterns that must to some degree reflect dispersal patterns. Based on 86 globally distributed taxonomic checklists, they concluded that mosses are not more species-rich in the tropics than elsewhere. On the other hand, analysis of only North, Central, and South American samples demonstrate that a latitudinal gradient is apparent. Molecular diversity suggests that moss diversity is highest in the Southern Hemisphere, thus lowest in the Northern Hemisphere. The tropics are intermediate. These differences, however, are small, and essentially all moss lineages are represented in all three latitudinal zones. Hence, their data support the "everything is everywhere" hypothesis (Baas-Becking 1934) that is evident among many organisms with small

propagules. (See Chapter 4-8 for more information on the topic of "everything is everywhere.")

But liverworts seem to exhibit a somewhat different pattern, more closely mimicking the distribution patterns of the tracheophytes (Schuster 1969). Schuster cites as evidence their patterns of endemism and disjunction, as well as their having highly specific, restricted ranges. He cites further support from the high number of species of liverworts in the Arctic. Nevertheless, some taxa, especially the **monoicous** (both sexes on same plant) ones, seem to have wide spore dispersal, as suggested by their presence on islands in the Mid-Atlantic and Indian Ocean ridges. Interpretation is complicated by our inability to distinguish between ancient "overland" dispersal and more recent dispersal by spores. But in 1969, tropical liverworts were poorly known. Can we still support Schuster's (1969) distributional conclusions today?

Based on analysis of a large, world-wide data set of species distributions, Wang *et al*. (2016) found a clearcut latitudinal diversity gradient in liverworts and hornworts. The highest species richness was found in the tropics, which they explained by the explosive diversification of some of the most speciose liverwort lineages, such as **Lejeuneaceae** (Figure 36-Figure 39, Figure 65, Figure 101-Figure 103, Figure 113-Figure 114, Figure 127-Figure 131, Figure 136), **Plagiochilaceae** (Figure 99), and **Frullaniaceae** (Figure 14, Figure 105) in the humid tropical forests. But they also noted that there is much evidence to suggest that dispersal is not limiting, and that long-distance dispersal is common among bryophytes. In fact, bryophytes exhibit a much lower global turnover of **beta diversity** (ratio between regional and local species diversity) than do flowering plants and maintain relatively constant levels of **alpha diversity** (local species richness) on a gradient of geographical isolation (Patiño *et al*. 2015).

New ideas are emerging suggesting that islands, including tropical islands, are sources of diversity instead of the previously thought evolutionary dead ends and diversity sinks (Patiño *et al*. 2015). The dead end concept was based on "perceived low levels of genetic diversity, poor interspecific competitive and defensive ability, and loss of dispersal capacities." But bryophytes do not fit well into this model. They have high dispersal capabilities compared to most tracheophytes, and when genetic diversity was examined, it proved to be higher in island populations than in continental populations. Patiño and coworkers suggest that rather than being evolutionary dead ends for such organisms as bryophytes, islands become sources of diversity for bryophytes that subsequently disperse to continents. They also found that species richness of islands correlates by habitat diversity, not by size or age of the islands or distance to the continent, hence is not driven by dispersal.

Karlin *et al*. (2012) examined genetic diversity on the remote Hawaiian Islands in the Neotropics. Because of this remoteness, the popular opinion was that long-distance dispersal to the islands was rare. In their investigation into the population genetic diversity, the researchers concluded that the peat moss ***Sphagnum palustre*** (Figure 140) most likely arrived with a single dispersal event. This species lacks sporophytes on the Hawaiian Islands and most likely lacks sexual reproduction. Further evidence to support a single dispersal event is that all samples share a rare genetic trait. They concluded that the original Hawaiian dispersal event was from vegetative propagation.

Figure 140. ***Sphagnum palustre***, a species that apparently arrived on the Hawaiian Islands as a single dispersal event. Photo by Bernd Haynold, through Creative Commons.

Bryophytes exhibit a high capacity for transoceanic dispersal (Lewis *et al*. 2014) when compared to flowering plants (Patiño *et al*. 2014). This thinking is further supported by the low levels of competition among bryophytes compared to that among flowering plants (Rydin *et al*. 2009). This low competition suggests that the niche preemption hypothesis (Whittaker & Fernández-Palacios 2007) does not apply to bryophytes and thus makes it easier for them to succeed when they arrive on an island or subsequently on a new continent. The clonal nature of bryophytes (Cronberg *et al*. 2006; Hutsemékers *et al*. 2010, 2013; Karlin *et al*. 2011; Patiño *et al*. 2013), and their ability to disperse viable fragments means that the minimum population size is quite small (Bengtsson & Cronberg 2009) and further enables them to succeed when they colonize. Thus, as indicated by a compilation of data, island populations of bryophytes are not necessarily genetically depauperate (Fernández-Mazuecos & Vargas 2011; Laenen *et al*. 2011; Désamoré *et al*. 2012; García-Verdugo *et al*. 2015). Even seed plants can have a larger genetic diversity on islands than in associated continents (Désamoré *et al*. 2012). Based on these studies, and particularly that of Patiño *et al*. (2015), it is likely that the Macaronesian archipelagos, including the tropical portion, have provided a stepping stone for trans-continental bryophyte immigration to other tropical regions in new continental locations. Hence, islands may help to explain the **pantropical** (distribution covers tropical regions of both hemispheres) distribution of many bryophytes.

Another possibility, potentially as an additional scenario rather than a preferred one, is that islands can serve as refugia during times when the continent becomes uninhabitable. Such seems to be the case for the leafy

liverwort ***Radula lindenbergiana*** (Figure 141) in Macaronesia (Laenen *et al*. 2011). It appears that a number of European plants, including ***R. lindenbergiana***, share a Macaronesian common ancestor and that these species may have back-colonized Europe. The widespread (including tropical Africa and tropical America) aquatic moss ***Platyhypnidium riparioides*** (Figure 142-Figure 143) likewise supports the concept that oceanic islands serve as major sources of biodiversity for recolonization of continents following glaciation (Hutsemékers *et al*. 2011). The lack of morphological diversity among the bryophytes, but presence of high genetic diversity, reflects the simple structure of the bryophytes.

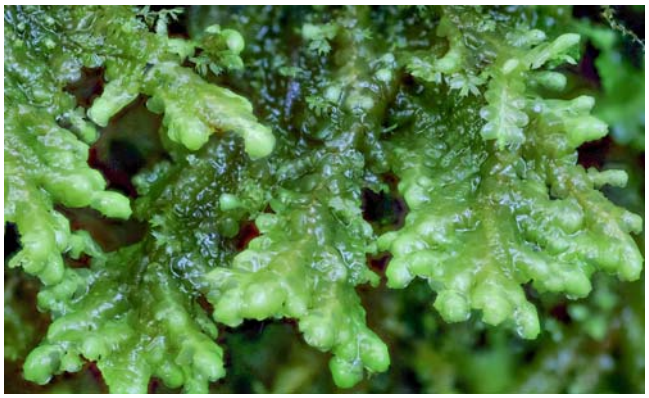

Figure 141. ***Radula lindenbergiana***, a species that seems to have used Macaronesia as a refugium. Photo by Dick Haaksma, with permission.

Figure 142. ***Platyhypnidium riparioides*** in its usual habitat. Photo by Hermann Schachner, through Creative Commons.

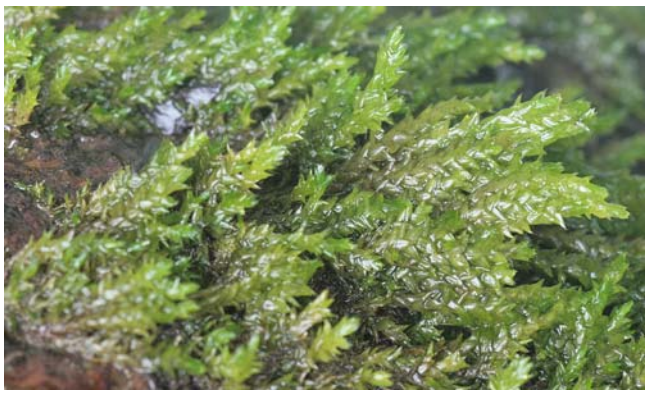

Figure 143. ***Platyhypnidium riparioides***, a species that exhibits some genetic variation along its river course, using mostly fragments as dispersal units. Photo by Hermann Schachner, through Creative Commons.

For the moss ***Platyhypnidium riparioides*** (Figure 142-Figure 143), Hutsemékers *et al*. (2013) found that some genetic variation occurs along the river basin and indicates that this widespread aquatic moss has weaker dispersal than that expected for pollen or wind-dispersed seeds. Rather, it appears that fragments are more important than spores for local dispersal of this moss, thus explaining the low levels of genetic diversity.

Even the dispersal-limited dung moss ***Tetraplodon*** (Figure 144) has **amphitropical** (distributed on both sides of the tropics) and bipolar (distributed in cold temperate regions) disjunctions that seem to require long-distance dispersal (Lewis *et al*. 2014). Lewis and coworkers suggested that the disjunct distribution in the Western Hemisphere may have been accomplished through stepwise migration along the Neotropical Andes. But ***Tetraplodon*** is typically dispersed by flies that provide only short dispersal ranges. Furthermore, experiments indicate that the spores of ***Tetraplodon*** cannot survive long-distance dispersal by wind. The researchers suggest that instead, birds might provide the dispersal vector necessary to account for the widespread but disjunctive distribution of the species in South America.

Figure 144. ***Tetraplodon mnioides***, an amphitropic moss, with the toad ***Nannophryne variegata*** in South America. Photo by Filipe Osorio, with permission.

In examining bryophytes on oceanic islands, Patiño *et al*. (2013) concluded that even bryophytes exhibit an island syndrome. They exhibit genetic drift, indicating relatively slow migration rates between the oceanic islands and continents. This suggests that the ocean does impede migration. This period of isolation seems to lead to an increase in production of specialized asexual diaspores and a decrease in sporophyte production on the oceanic islands.

To demonstrate the relatively large number of Afro-American distributions in bryophytes, Gradstein (2013) examined records of liverworts in tropical regions of both Old World and New World tropics. Based on the disjunctions of 74 liverworts in 13 genera with Afro-American ranges, he estimated that about 5% of the

Neotropical and 8% of the African liverwort species had Afro-American disjunct distributions. This number is doubled when pantropical species are included. Gradstein cited spore dispersal experiments and molecular-phylogenetic studies to conclude that for the majority of these genera, long-distance dispersal was the reason for the disjunction.

Ah-Peng *et al*. (2010) demonstrated the high bryophyte diversity on the small, oceanic La Reunion Island. In only 2512 km^2, 776 taxa are known. This island is near East Africa and Madagascar. The high diversity is fostered by its subtropical climate, a high altitudinal range (to 3070 m asl), and high rainfall.

Much of our understanding of long-range dispersal comes from van Zanten (1978; van Zanten & Pócs 1981; van Zanten and Gradstein 1987). In their laboratory experiments using 86 Colombian liverwort species, van Zanten & Gradstein (1987) found that spores of transoceanic species were more durable than those of endemic species. Survival was also greater in wet air-currents at high altitudes than in dry air currents. When they placed the spores on airplane wing tips during flights at jet stream elevation from Amsterdam to Los Angeles and back, however, only two species, the endemic ***Marchantia chenopoda*** (Figure 145) and the transoceanic ***Gymnocoleopsis cylindriformis***, could survive. All others were dead, probably due to exposure to UV radiation. Presumably ***G. multiflora*** spores survive because this species grows in the high Andes above 4000 m, where UV radiation is high. Van Zanten and Pócs (1981) concluded that tropical lowland moss species are much less drought tolerant than are temperate species. These tropical species are, however, resistant to wet-freezing and can be dispersed over short distances by rain showers and typhoons. They concluded that north-south dispersal across the equator was the most difficult and occurred rarely, if at all.

Figure 145. ***Marchantia chenopoda*** archegoniophores, a species whose spores can survive flight on the wings of a jet plane. Photo by Janice Glime.

Dispersal by wind is considered limited in forests, except in the canopy (Richards 1988). Some species, such as African moss species of ***Syrrhopodon*** (Figure 146) subsect. ***Calymperopsis***, produce gemmae in splash cups similar to those of the moss ***Tetraphis pellucida*** (Figure 147). Although experimental dispersal studies are lacking for tropical species, but Richards suggests that the discoid gemmae (Figure 128) of many of the **Lejeuneaceae** (Figure 130-Figure 131) are probably dispersed by splashing rain. Hanging mosses get dispersed by birds through dropped fragments when they are collected for nest making.

Figure 146. ***Syrrhopodon albovaginatus***; some species of this genus produce gemmae in cups in the tropics. Photo from Natural History Museum, London, through Creative Commons.

Figure 147. ***Tetraphis pellucida*** with gemmae cup and discoid gemmae – similar to those of African species of ***Syrrhopodon***. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Dispersal adaptations reflect moisture relationships. The secretion of sticky mucilage (Thiers 1988) can aid in the attachment to vertical surfaces and prevent being washed away during rainstorms. Gemmae and the precocious development of spores permit more rapid development and thus greater chance for establishment. The prolongation of the protonemal stage may also aid in insuring attachment, whereas the **neotenous life cycle** (see under Liverworts above) permits early maturity, providing greater likelihood of completion of the life cycle before host leaves are shed during the rainy season.

I must re-emphasize the strategies of the **Lejeuneaceae** (Figure 36-Figure 39, Figure 130-Figure 131), a large pantropical family of considerable importance among the liverworts. This family has many monoicous species, and many species have intercontinental ranges, but all have large, multicellular spores – an atypical character for taxa with transoceanic distributions (Gradstein *et al.*

1983; Gradstein & Pócs 1989). Nevertheless, the multicellular large spores should permit the species to become established more easily once they arrive because of greater food reserves to permit a quick start. And the monoicous character facilitates sexual reproduction.

Although I have discussed the flying fox in volume 1, a discussion of dispersal in the tropics cannot be complete without the recalling this unique mechanism for some bryophytes in the Wet Tropics of northeastern Australia. Parsons *et al*. (2007) found that the spectacled flying fox ***Pteropus conspicillatus*** (Figure 148) spreads bryophyte fragments in its feces (Figure 149). When the researchers cultured the feces, they found that the fragments were viable (Figure 150). Not only were there bryophyte fragments, but also live invertebrates and other organisms.

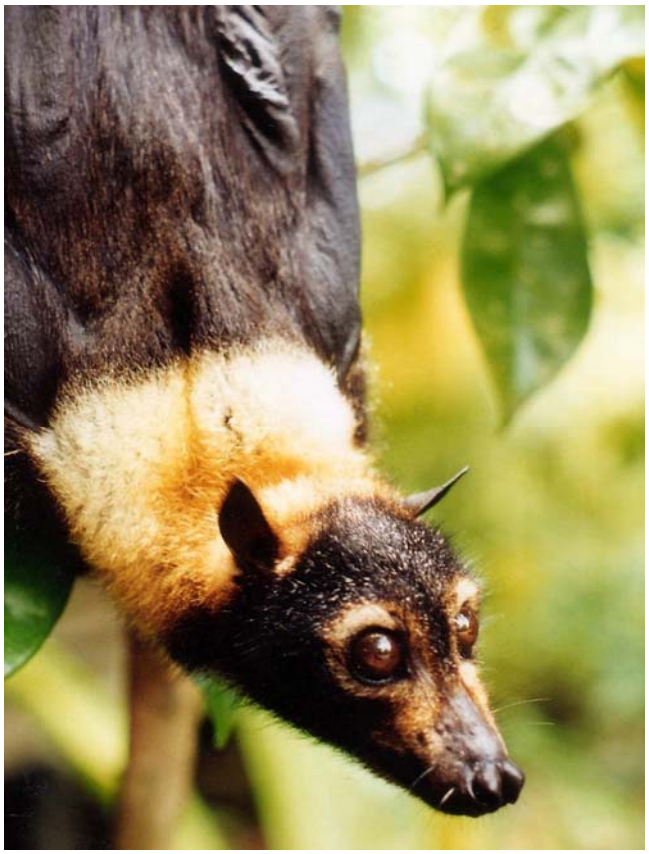

Figure 148. Spectacled flying fox (***Pteropus conspicillatus***), a possible disperser of bryophytes in the Wet Tropics of Australia. Photo courtesy of Jennifer Parsons.

Figure 149. Bat splat (feces) of the spectacled flying fox. Photo by Jennifer Parsons, with permission.

Figure 150. ***Racopilum*** sp. from flying fox splat. Photo courtesy of Andi Cairns.

Sampling

Sampling in the tropics can present problems that are less important elsewhere – such difficulties as canopy height and excessive moisture. Mountainous areas may be remote, with some available only by foot paths. Tall trees make small branches of the canopy almost impossible to sample; methods to overcome this obstacle are in the subchapter on epiphytes. Several researchers have addressed the problems unique to bryological collecting in the tropics (Mori & Holm-Nielson 1981; Edwards 1986; Delgadillo 1987; O'Shea 1989; see Frahm *et al*. 2003 for a comprehensive review).

One important consideration when collecting in tropical countries is that researchers there are often struggling with inadequate herbarium materials, particularly ones that can be used for checking their own collections. Duplicate specimens should always be provided to an accessible herbarium in the country – one that has a curator and can loan specimens. And of course one should be aware of local collection laws, obtain proper collecting permits, and determine in advance what restrictions there might be by customs and plant control in both the country of collection and in the receiving country.

Delgadillo (1987) and Frahm *et al.* (2003) detail many things to consider before departing for the tropical country, behavior during the visit, and how to treat specimens from another country upon return home. He suggests researching the geography, customs, and language of the country and contacting one or more resident bryologists for suggestions on places to stay and places to sample. Obtain collecting permits in advance for each country you plan to visit. Be sure you have health insurance to cover you in the places you will visit. Follow the routines of the local herbaria and institutions you visit and take their advice on food, roads, and other items of local knowledge. Remember that appointment times are not as rigid in some countries, so be patient, especially with local natives who might help you. Be sure you provide the local herbaria or national herbarium with a set of identified specimens. If possible, use their herbarium specimens in their herbarium so you don't have to borrow from their typically small number of specimens. To get both loans and your own specimens back to your own country, use registered mail.

Be sure you understand the quarantine regulations in both countries. Avoid travelling in the field alone; taking a local student along can benefit both of you. Carry a first-aid kit and a letter of introduction from the local university or herbarium in case it is needed to satisfy local authorities. Upon returning home, return loaned specimens as soon as possible, being sure to meet quarantine requirements. Send a set of duplicate specimens from your own identified collections for any species you have not already deposited in a herbarium in the country visited.

Braun-Blanquet Sampling Method

While sampling may be more difficult in a tropical jungle, methods used elsewhere often work well. A common method of sampling vegetation, particularly in Europe, is the **Braun-Blanquet method**. This method uses a cover-abundance scale to describe the vegetation. These levels are divided into cover classes, typically using 5-7 categories:

1 <1
2 1-5
3 5-10
4 10-25
5 25-50
6 50-75
7 75-100

The levels are estimated through the use of **relevés**. This system has been applied originally to tracheophytes, but many bryologists have adapted it for a more efficient means of quantitative sampling. Poore (1955) criticized the system, but Moore (1962) countered those criticisms, stating that Poore had misapplied the method. Damgaard (2014) determined that despite its bias to over-estimate abundance, the Braun-Blanquet method gave results comparable to those of other methods of estimating plant cover. It has the added advantage of providing comparisons to the many studies that have used it, permitting data comparisons over time.

Wikum and Shanholtzer (1978) noted that most methods of measuring vegetation density are time-consuming and costly. The Braun-Blanquet method requires only about one-third to one-fifth the amount of field time, giving comparable results. I am unaware of any studies comparing the Braun-Blanquet system with other cover estimates for bryophytes, but it has been used in tropical studies and provides a relatively rapid method that is helpful when time is often quite limited.

A discussion of the unique methods for sampling epiphytes is in the subchapters on epiphytes and epiphylls in this chapter.

Drying Specimens

Because of periods of daily rain, there isn't enough time for anything to get dry, and that includes your clothes and your bryophytes. And both damp clothing and bryophytes can soon become a garden for molds. Molds make the bryophytes difficult to identify, and certainly make them unsightly, not to mention a health hazard. They introduce molds to the herbarium, and their spores can cause allergic reactions and asthma. They will also make it more difficult to get the bryophytes through plant protection agencies when you enter another country. Frahm and Gradstein (1986) note these difficulties in the tropics, making several suggestions to overcome them.

One method that is used is to place the bryophytes in paper bags on a dry floor of a tent with open flaps (Frahm & Gradstein 1986). The opening is covered with mosquito netting to permit air movement. But during the rainy season, the dry periods are often insufficient for the bryophytes to dry. Some bryologists have resorted to putting a professional plant dryer in the back of a truck, using butane to provide the heat. But this method is not practical when only foot paths are available to the campsite. And most budgets can't afford such equipment. A less expensive approach is to suspend the bryophytes near a campfire, but the fire might get too hot and thus requires close watching. It can heat the bryophytes too much and thus damage them, particularly for those who might later want to use them for chemical analysis.

Frahm and Gradstein (1986) suggest an inexpensive, lightweight apparatus for drying bryophytes (Figure 151). It is constructed of L-shaped aluminum pieces with a frame that supports a wire mesh. Nylon should not be used because of its flammability. The heat source is two kerosene camping stoves (see also Croat 1979). The structure should then be surrounded with cotton cloth, as shown in the inset, again avoiding the more flammable nylon. The frames are about 1 m high, but the level of the screen can be adjusted to change the heat level. The apparatus should be monitored until you learn how much flame you need to avoid toasting the bryophytes or causing a forest fire. Once the ideal flame size is determined, the apparatus can be left unguarded overnight.

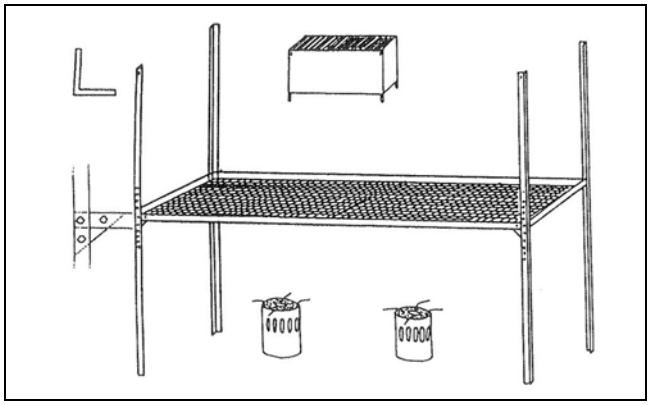

Figure 151. Light-weight drying apparatus for bryophytes in the field. From Frahm & Gradstein 1986.

Greene (1986) used chicken wire instead of wire screening. He suggested a method for keeping the specimens dry once getting them that way. They should immediately be put into large, heavy-duty plastic bags with silica gel to absorb moisture and sealed. [The plastic bags can be sealed by folding in the top corners, then folding down the top several times and fastening it with several large paper clips. – JG.] The specimens themselves can be kept in paper bags or packets. Greene transported the silica gel containers to the site in cotton bags. When they were needed, the silica gel containers were put into paper specimen bags and heated along with the specimens so that they were dry and ready when the specimens were stored.

Summary

Bryophytes in the tropics undoubtedly have a crucial role in water and nutrient retention, releasing nutrients during re-wetting, but filtering them from the lower branches and ground during rain events. Because of their sponge-like behavior, they can maintain moisture and nutrients for other members of the ecosystem. Nutrients can be released slowly, providing nutrients to the forest floor at critical times.

The primary environmental drivers determining the types of bryophyte communities are moisture, temperature, and light intensity. Life and growth forms differ among the habitats, with such forms as **pendants**, **fans**, and **tails** in moist habitats and **mats** and short acrocarpous mosses in dry conditions. Likewise, productivity differs with habitat, with dense growths in wet cloud forests and little biomass on the rainforest floor where there is little light penetration. Furthermore, growth periods and reproduction coincide with rainy periods, whereas the bryophytes are typically dormant in dry seasons.

Moss reproduction varies with habitat, but antheridia and archegonia are typically produced during the rainy season. **Monoicous** species have the most sexual reproduction. Many species lack sexual reproduction and spread through gemmae and regrowth. Sun species typically have larger spores than do shade species. Protonemal development is often prolonged.

Some liverworts and a few mosses may exhibit **neoteny**. Liverworts often have shortened life cycles, fewer antheridia and archegonia, longer spore lives, longer protonemal stages, and few types of gemmae in the tropics. Both mosses and liverworts can survive as spores, vegetative propagules, or fragments in diaspore banks, but liverwort spores typically have short longevity in the tropics. Liverworts have a limited number of propagule types, whereas the mosses have many.

Dispersal is mostly by wind and occurs in most cases in the dry season. Long distance dispersal is often important between mountains, and some species exhibit disjunct distributions between Africa and the Neotropics.

Rheophilic species probably have similar adaptations to the stream habitat, but few tropical studies have occurred.

Sampling brings special problems of getting mosses dry in the cloud forest or in the rainy season, often necessitating drying racks and a heat source. Investigators need to gain permission and should leave a set of herbarium specimens with a notable herbarium in the host country.

Acknowledgments

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CHAPTER 8-2
TROPICS: GEOGRAPHIC DIVERSITY DIFFERENCES

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CHAPTER 8-2
TROPICS: GEOGRAPHIC DIVERSITY DIFFERENCES

Figure 1. Rainforest in Borneo. Photo by Duke Abruzzi, through Creative Commons.

Diversity – Geographic Differences

Only in the 21st century are we seeing publications with keys that cover broad areas or a wide range of taxa in the tropics, especially the Neotropics. This lack of taxonomic understanding has hindered our understanding of diversity and geographic differences.

Among these recent publications, the publication by Gradstein *et al*. (2001) dealing with all bryophytes of the Neotropics (mosses, liverworts, hornworts) is notable. In addition, there is a large series of floras dealing with Neotropical mosses (for a list see Gradstein et al. 2001), fewer on liverworts (Gradstein & Costa 2003; Gradstein & Ilkiu-Borges 2009). For Africa, a broad spectrum moss key has been translated from 1978, lacking modern familial classifications, but is somewhat comprehensive (Petit 1992). More recent treatments on liverworts and hornworts was published for West Africa by Jones *et al*. (2004), based on an unpublished flora manuscript of the specialist of African liverworts E. W. Jones, and for Rwanda by Fischer (2013), including keys to genera and species and many color photos. For the southwestern part of Asia (Arabia) one can use the treatise by Kürschner and Frey (2011), for Singapore mosses by Tan *et al*. (2008) and for liverworts and hornworts of Java by Gradstein (2011). Other treatments are available for China and Japan, where bryology has long been studied, but publications were mostly in the native languages until recently. Recent publications include dozens of good floristic papers by young bryologists from the tropical countries, for example

from Brazil, Bolivia, Venezuela, Costa Rica, Puerto Rico, Guadeloupe, but also West Africa, Reunion, Madagascar and Malaysia.

Hedenäs (2007) used checklists from 78 countries to determine the global diversity patterns of pleurocarpous mosses. He found that most of this moss diversity occurred outside the Holarctic area. Rather, the tropics have an especially diverse pleurocarpous moss flora. Furthermore, species turnover among pleurocarpous mosses is higher in the tropics than in the temperate zone.

It is not surprising that the greatest number of bryophyte species occurs in the tropics, with one-third of the Earth's flora occurring in the tropical Americas alone (Gradstein 1995a, b; Gradstein *et al*. 2001). Nevertheless, there are fewer species of mosses in the tropics than in the temperate zone; it is the liverworts and hornworts that reach their peak of species here. Delgadillo (1998) reported 3,900 species of mosses recorded from the Neotropics but considered that the real number, taking into account taxonomic revisions, might be considerably lower. Gradstein *et al*. (2001) accepted about 2,600 species of mosses, 1,350 of liverworts, and 30 of hornworts in the region, and this number may further fluctuate due to synonymy and new discoveries. This number is commensurate with the high diversity of flowering plants (90,000) in the Neotropics, compared to 250,000 species of flowering plants worldwide (Churchill *et al*. 1995a). Frahm (1995) compared the European, tropical African, and Neotropical moss floras, a task that provides the knowledge base for many kinds of ecological studies.

On the other hand, estimates of the number of bryophyte species in the tropics is compromised by the large number of synonyms in the literature. For example, ***Frullania atrata*** (Figure 2) has been widely misinterpreted in the literature and has been confused with other ***Frullania*** species, whereas the true ***F. atrata*** is rare (Uribe & Gradstein 2003; Gradstein, pers. comm. 9 September 2018). The common Neotropical ***Marchantia chenopoda*** (Figure 3-Figure 4) has 15 synonyms (Bischler 1984) and the common pantropical moss ***Leucomium strumosum*** (Figure 5) has almost 30 synonyms from all over the tropics (Allen 1987). Such synonymy is mostly the result of researchers in different parts of the world naming a species as new because of inadequate knowledge of or access to bryophytes in other locations.

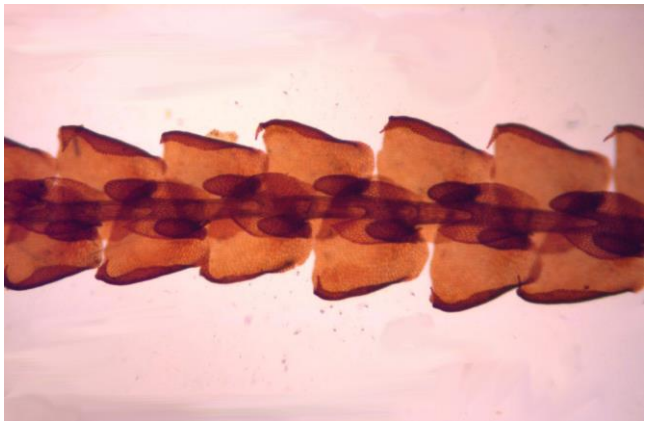

Figure 2. ***Frullania atrata***, a species name that has been used for many similar ***Frullania*** species. Photo by Juan Larrain, with permission.

Figure 3. ***Marchantia chenopoda*** with antheridiophores, a Neotropical species in a genus with many tropical synonyms. Photo by Janice Glime.

Figure 4. ***Marchantia chenopoda*** females. Photo by Martin Nebel, courtesy of Robbert Gradstein.

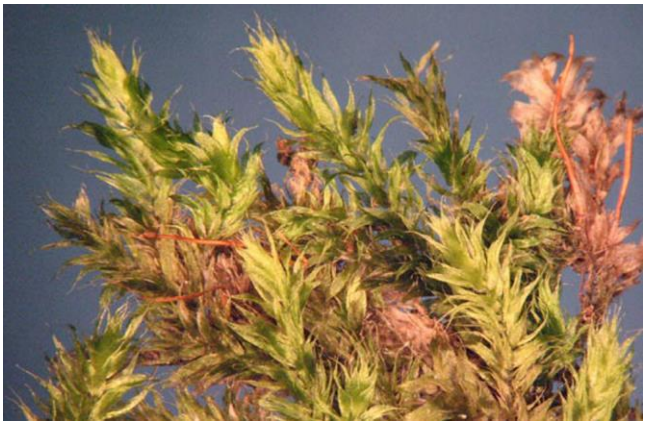

Figure 5. ***Leucomium strumosum***, a tropical species with almost 30 synonyms. Photo by Claudio Delgadillo Moya, with permission.

Tropical liverworts in the families **Lejeuneaceae** (Figure 6), **Frullaniaceae** (Figure 7-Figure 8), **Radulaceae** (Figure 9-Figure 10), **Plagiochilaceae** (Figure 11), and **Lepidoziaceae** (Figure 12) predominate among the liverworts, with lesser numbers in **Metzgeriaceae** (Figure 13) and **Aneuraceae** (Figure 14) (Schuster 1988). Gradstein (1995a) suggests that the liverwort genus ***Plagiochila*** (Figure 11), with hundreds of species in tropical montane forests, is generally considered the most

diverse liverwort genus. Pendent taxa are common on branches and tree trunks of the montane forests.

Figure 6. ***Cololejeunea truncatifolia*** (**Lejeuneaceae**) from Uganda. Photo by Martin Wigginton, with permission.

Figure 7. ***Frullania*** (**Frullaniaceae**) in the Neotropics. Photo by Michael Lüth, with permission.

Figure 8. ***Frullania*** (**Frullaniaceae**) in the Neotropics. Photo by Michael Lüth, with permission.

Figure 9. ***Radula buccinifera*** on a tree in the Asian tropics. Photo by David Tng <www.davidtng.com>, with permission.

Figure 10. ***Radula cf. voluta*** (**Radulaceae**) from the Neotropics. Photo by Michael Lüth, with permission.

Figure 11. ***Plagiochila adianthoides*** (**Plagiochilaceae**) from the Neotropics. Photo by Michael Lüth, with permission.

Figure 12. ***Lepidozia*** sp. (**Lepidoziaceae**), a common tropical family of leafy liverworts. Photo by Ken-ichi Uedo, through Creative Commons.

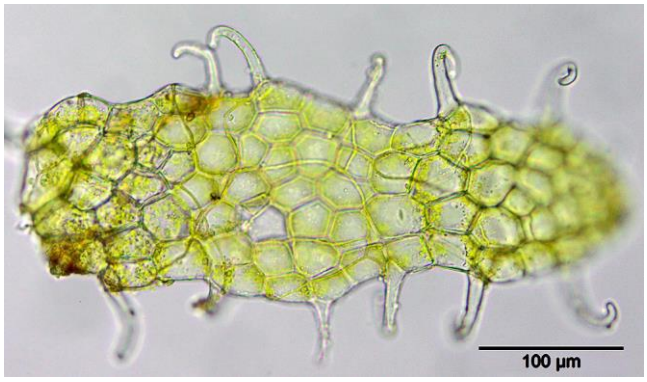

Figure 13. ***Metzgeria uncigera*** (**Metzgeriaceae**), a common tropical family of liverworts. Photo by Blanka Aguero, with permission.

Figure 14. ***Riccardia multifida*** (**Aneuraceae**), representing a common tropical family. Photo by Hermann Schachner, through Creative Commons.

Despite all these cautions about conspecific taxa that have been given multiple names in multiple locations, DNA genetics may once again expand the species number. For example, Dong *et al*. (2012) analyzed molecular data from the epiphyllous liverwort ***Diplasiolejeunea*** (Figure 15-Figure 16). This is a pantropical genus that occurs from lowlands to more than 4,000 m altitude. This indicated that the evolutionary diversity of the genus based on morphology alone has been underestimated. The molecular data indicate a distinct split between the Neotropical and **Palaeotropical** (Old World) clade, with two predominantly Neotropical subgenera [***Austrolejeuneopsis*** and ***Diplasiolejeunea*** (Figure 15) with the former containing mainly epiphytic species, the latter mainly epiphylls] and one predominantly Palaeotropical subgenus, ***Physolejeunea*** (Figure 16), an epiphytic montane subgenus.

Figure 15. ***Diplasiolejeunea brunnea*** (subgenus ***Diplasiolejeunea***) in Ecuador on leaf. Photo courtesy of Tamás Pócs.

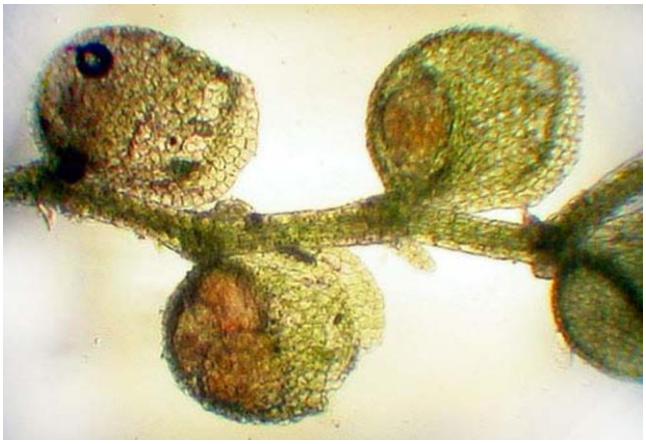

Figure 16. ***Diplasiolejeunea plicatilobula***, in the epiphytic montane subgenus ***Physolejeunea***. Photo by David Tng, with permission.

Checklists of the tropics are listed in Frahm *et al*. (2003). For the geographic areas treated in this chapter, the number of references given are probably less than representative, but are listed to help researchers get started on the areas. More recent references have been included only as I have discovered them, with much help from Robbert Gradstein.

Frahm *et al*. (2003) estimated that about 8,000 species of bryophytes occur in the tropics, comprising half to two-thirds of all the bryophyte species in the world. The European flora has only about 1,600 species that one can find in 32 floras. For the tropics, as of 2003, only 16 floras existed. As will be seen in the following subchapters, the liverworts and hornworts are much more abundant and occupy a much higher percentage of the bryophyte flora in the tropics compared to other regions of the world. Nevertheless, many areas remain unexplored or poorly explored, so numbers of species and numbers of **endemics**

(known only from a limited area) should be compared with caution.

Norhazrina *et al*. (2016) considered the **beta diversity** [ratio between gamma (regional) and alpha (local) diversities] of bryophytes in the tropics. They examined the beta diversity of 7485 tropical moss species and 3276 tropical liverwort and hornwort species in 164 and 154 operational geographical units, respectively. They found a "slight but significantly higher beta diversity among than within tropical regions." They concluded that oceans provide a significant barrier to the routine dispersal, even for the easily dispersed bryophytes, causing large-scale floristic patterns.

The following sections on diversity and endemism are mostly historic. Hence, numbers are likely to be out-dated. They are designed to provide the background and explain why ecological studies in the tropics are occurring only recently.

Africa

Africa is a continent with a wide range of tropical habitats, from dry desert of the Sahara to the 5,895 m summit of Mt. Kilimanjaro. The climate ranges from tropical to subarctic, but much of the land is desert, particularly the northern half.

One of the earliest recorded observations relating to ecology of the African desert is that of Mungo Park. As quoted in Crum (1983), Park was crossing 3220 km of unknown land and African desert when he reported "I considered my fate as certain, and that I had no alternative but to lie down and perish… At this moment, painful as my reflections were, the extraordinary beauty of a small moss in fructification irresistibly caught my eye." Stark (1860) captured the story in this poem (author not specified):

Sad, faint, and weary on the sand
Our traveller sat him down; his hand
Cover'd his burning head.
Above, beneath, behind, around,
No resting for the eye he found;
All nature see'd as dead.

One tiny tuft of moss alone
Mantling with freshest green a stone
Fix'd his delighted gaze;
Through bursting tears of joy he smiled
And while he raised the tendril wild
His lips o'erflowed with praise

O! shall not He who keeps thee green,
Here in the waste, unknown, unseen,
Thy fellow-exile save?
He who commands the dew to feed
Thy gentle flower, can surely lead
Me from a scorching grave.

Mungo Park lived to tell the tale and a specimen of this lowly moss was later identified as a species of ***Fissidens*** in the ***F. bryoides*** (Figure 17) group. This genus is particularly common in Africa, with ~90 known species out of 450 worldwide (Bruggeman-Nannenga, 2013a, b), with a new one soon to be published from termite mounds (Bruggeman-Nannenga in press; Ezukanma *et al*. in prep.).

Figure 17. ***Fissidens bryoides***, possibly the moss found by Mungo Park, or one of its close relatives. Photo by Hermann Schachner, through Creative Commons.

O'Shea (1995) provided an early checklist of the mosses of sub-Saharan Africa (Figure 18), listing 2939 species, based on the literature, and indicating distribution by country. While he updated some of the nomenclature, naming new combinations, much remained to straighten out the duplication in names around the continent.

Figure 18. Sub-Sahara Africa. Photo from CIFOR, through Creative Commons.

Ros *et al*. (1999) provided a checklist of northern Africa. It is striking that only 171 liverwort species were known, compared to 706 of mosses. It is likewise remarkable that only 4 taxa were known from the Republic of Mali or Niger. Wigginton (2001b) noted that ***Eucladium verticillatum*** is widespread in Mali, where it is encrusted with **tufa** (variety of limestone formed when carbonate minerals precipitate out of ambient temperature water).

Pócs, with his coworkers, has been a lifelong contributor to the bryophyte flora of Africa. Among his earlier contributions was a joint paper (Bizot & Pócs 1974) on bryophytes of East Africa, based on collections from a number of bryologists, himself included. This included 441 species, of which 115 were new for East Africa and 4

for all of tropical Africa and 30 were new for all of continental Africa. Other studies reporting on African bryophytes include Arnell (1956 – East African Mountains – liverworts), Bizot & Pócs (1974, 1979, 1982 – East Africa), Pócs (1990, 2011 – East Africa), Kürschner & Onraedt (1990 – Republic of Djibouti), Grolle [1993 – Zaire and Rwanda – **Pallaviciniaceae** (Figure 19), **Haplomitriaceae** (Figure 20)], and Miehe & Miehe (1994 – Ethiopia).

Figure 19. ***Symphogyna brasiliensis*** female from the Neotropics. This family **Pallaviciniaceae** also occurs in Africa. Photo by George Shepherd, through Creative Commons.

Figure 20. ***Haplomitrium hookeri***; **Haplomitriaceae** are among the liverworts known from Zaire and Rwanda. Photo by Des Callaghan, with permission.

In an update of his earlier checklist, O'Shea (1997a, b) reported 3,048 taxa from sub-Saharan Africa (Figure 18), but suggested that it will probably be reduced to ~1300 species by revisions. Based on an expedition of the British Bryological Society to the Mulanje Mountain (Figure 21), Wigginton (2001a) reported 64 taxa in the single leafy liverwort family of **Lejeuneaceae** (Figure 6, Figure 15-Figure 16). This report acknowledged 47 species new to Malawi, emphasizing how poorly we knew the bryophyte flora in so many tropical areas. Frahm (2003) bemoaned the lack of studies in Africa and the likely number of synonyms. Such taxonomic and floristic studies and compilations as these laid the foundation that permitted ecological work to begin.

Figure 21. Mount Mulanje, Africa. Photo by David Davies, through Creative Commons.

Not all of the African tropics have a high bryophyte diversity. In three locations in the Ekiti State, Nigeria (Figure 22), 69 samples yielded only 8 species of mosses (Adebiyi & Oyeyemi (2013), two of which were among those studied by Odu (1981, 1982) in Nigeria for their reproductive phenology: ***Pelekium gratum*** (syn.=*Thuidium gratum*; Figure 23) and ***Racopilum africanum*** (Figure 24). A study of bryophytes in the Eastern Nigerian Highlands yielded only 27 bryophyte taxa – 22 mosses, 5 liverworts (Ezukanma *et al*. 2017).

Oyesiku (2012) reviewed the Nigerian bryophytes, including a discussion of uses. His was one of the few attempts to assess the importance of bryophytes to agriculture and the effects that agriculture is having on the bryophytes. He expressed concern that so few people are working on Nigerian bryophytes.

Figure 22. Ikole Town, Ekiti State. Photo by Tijae07, through Creative Commons.

Figure 23. ***Pelekium gratum***, a tropical Nigerian moss. Photo by Shyamal L., through Creative Commons.

Figure 24. ***Racopilum africanum*** with capsules, a tropical Nigerian moss. Photo by Jan-Peter Frahm, with permission.

Few studies seem to be available from Ghana. Hodgetts *et al*. (2016) reported on the bryophytes of the Atewa Forest in eastern Ghana. The region is highly threatened by farming, hunting, and illegal mining. Hodgetts and coworkers explored the swamp forest and upland evergreen forest where they expected the greatest bryophyte richness. They identified 164 species, 58 of which were new to Ghana.

The cover of bryophytes differs markedly, dependent on light availability, litter cover, and climate. Petit and Symons (1974) found that in the planted woods of ***Cupressus*** (Figure 25) and ***Acacia*** (Figure 26) in Burundi (an east African country with an equatorial climate), the ground surface is mostly covered with bryophytes. Nevertheless, in 17 woods, only 28 species were found, and only 15 of these were typical for that habitat.

Figure 25. ***Cupressus macrocarpa***. Photo by Ames, through Creative Commons.

Figure 26. ***Acacia***; forest floors of ***Acacia*** are covered by bryophytes in Burundi. Photo from pxhere, through Creative Commons.

To demonstrate just how poorly some African floras are known (Hylander *et al*. 2010), we need only look at the new records from the biosphere reserve of Kafa in Ethiopia (Figure 27). A team of 29 experts, but no bryologists, spent 10 days collecting plants (Müller & Flügel 2016). They did, however, bring some bryophyte specimens back. While this yielded only 13 liverwort and 24 moss species, it revealed 5 mosses not previously known from Ethiopia!

Hylander *et al*. (2010) found 89 species of liverworts, of which 41 were new to Ethiopia (Figure 27), further emphasizing that bryological explorations have been inadequate there. Among these are many epiphyllous species that are typically sensitive to drought. These are mostly along streams where humidity remains higher. The family **Lejeuneaceae** (Figure 6, Figure 15-Figure 16) is the most common family, with several representatives in other families, including **Frullaniaceae** (Figure 2, Figure 7-Figure 8), **Plagiochilaceae** (Figure 11), and **Radulaceae** (Figure 9-Figure 10).

In a more recent study, Hylander *et al*. (2017) found 139 moss species in montane forests of Ethiopia (Figure 28), of which 53 are newly reported for the country. ***Meteoriopsis reclinata*** (Figure 29) is a new record for Africa.

Figure 27. Forest with native carrying firewood in Kafa, Ethiopia. Photo by Rod Waddington, through Creative Commons.

Figure 28. Semien Mountains, Ethiopia. Photo by Hulivili, through Creative Commons.

Hedderson *et al*. (2015) added to the list of bryophytes from Mabu Mountain in Mozambique, based on collections from non-bryologists. They were able to identify 56 species, of which 43 were new records for the country. The authors considered this small sampling of the country to be indicative of its bryophyte diversity and the need for more study.

Marline *et al*. (2012) provided an updated checklist of Madagascar bryophytes. This updated list revealed 751 moss, 390 liverwort, and 3 hornwort taxa. Of these, ~29% are endemic.

Reunion Island provides an interesting ecological site. It has diverse habitats of lava flows and large topographic relief. Ah-Peng *et al*. (2010) brought the total number of species and infraspecific taxa to 776 in 2010 with the addition of 123 taxa. They considered the presence of a high altitudinal gradient and high rainfall regime, coupled with relatively short distance to East Africa, to account for the large number of species on an island with only 2512 km^2.

Figure 29. ***Meteoriopsis reclinata*** was a new record for Africa in 2017. Photo by Niels Klazenga, with permission.

Several studies have compared the bryophyte floras of parts of Africa with other parts of the tropics (Frahm 1995), including Asia (Pócs 1976), and Madagascar (Pócs 1975). Oyesiku (2012) noted the "moribund" state of bryology in Africa.

Asia

The earliest studies on tropical Asian bryophytes are those in Java. Dozy and Molkenboer produced *Bryologia Javanica* (1856 – vol. 1, 1867 – vol. 2) on the Java mosses. Later Max Fleischer produced a three volume set, the *Moss Flora of Java* (1900-1922). For liverworts, Reinwardt *et al*. (1824) and Nees von Esenbeck (1830) provided the first species lists. These were followed later by the floras of vander Sande Lacoste (1857, 1864) and Schiffner (1900) (in Gradstein 2011). The latter work remained unfinished. Most recently, Gradstein (2011) has presented the Guide to the Liverworts and Hornworts of Java, covering nearly 200 years of bryological studies in Java. Approximately 1000 species of bryophytes are now known from Java (Robbert Gradstein, pers. comm. 9 September 2018). The presence of a biological research station at Cibodas (Figure 30) in Indonesia, founded by the Dutch around 1890 in the montane rainforest belt, has been of enormous help in accomplishing these bryological studies, including also work by Schiffner, Goebel, Giesenhagen, Verdoorn, and others.

Figure 30. Botanical garden in Cibodas, Indonesia. Photo by Hullie, through Creative Commons.

One of the early Asian studies was that of Dixon (1935) who reported on the moss flora of Borneo (Figure 1). Other studies on Asian tropics in China and Japan have been unavailable to people from other countries because they were published in the native languages and not understood by others. In some cases political boundaries and cultural differences complicated the ability of bryophyte ecologists to conduct studies. Redfearn (1990) points out that many of the early studies in China have been lost during the Cultural Revolution. And isolationism led to much synonymy, even within China. At that time he noted that much study was needed. Now there are many bryologists in China, but work is still needed on the many diverse habitats that define the country.

Asia has the most generic and familial diversity in the tropics, with many taxa that occur only in the Asian tropics. Africa, on the other hand, has few taxa of its own and little liverwort diversity, as we currently understand the flora. In the Americas, there are fewer unique moss taxa, but the liverworts are more diverse, with cover of liverworts in montane forests exceeding that of the mosses.

Asia is the center for distribution of a number of tropical taxa in a variety of families and is home to the **epiphyllous** (living on leaves) moss ***Ephemeropsis*** (Figure 31) and liverwort ***Metzgeriopsis*** (Figure 32) (Gradstein & Pócs 1989). Again, members of **Lejeuneaceae** (Figure 6, Figure 15-Figure 16) dominate liverworts, but with a number of different genera. The African flora is less rich and has few elements of its own. Typical mosses in the Asian rainforest (Figure 33) are ***Leucoloma*** (**Dicranaceae**; Figure 34), **Cryphaeaceae** (Figure 35), **Rutenbergiaceae**, ***Hildebrandtiella*** (Figure 36) and ***Renauldia*** (**Pterobryaceae –** see Figure 183), and in both lowlands and montane regions, ***Fissidens*** (Figure 37). Among liverworts, ***Lepidozia*** (Figure 12; subgen ***Sprucella***) is most common (vanden Berghen 1983; Gradstein & Pócs 1989).

Figure 31. ***Ephemeropsis trentepohlioides*** with capsules, a species from the Asian tropics, but also from Tasmania and New Zealand. Photo by David Tng, with permission.

Figure 32. ***Metzgeriopsis*** sp. growing on a palm leaf on Bukit Larut, Malaysia, 1100-1200 m, with Malaysian bryologist Kien Tai Yong (right). Photo courtesy of Robbert Gradstein.

Figure 33. Misty forest at Emei Shan, China. Photo by McKay Savage, through Creative Commons.

Figure 34. ***Leucoloma*** sp., a typical rainforest species. Photo by Shyamal L., through Creative Commons.

Figure 35. ***Cryphaea heteromalla***, a typical rainforest species. Photo by Tim Waters, through Creative Commons.

Figure 36. ***Hildebrandtiella guyanense*** from the Neotropics, in a typical rainforest genus. Photo by Michael Lüth, with permission.

Figure 37. ***Fissidens asplenioides***, in a genus that is found in both lowlands and montane regions. Photo by L. Jensen, University of Auckland, with online permission.

Gradstein (1991) summarized the known Asian **Ptychanthoideae** (Figure 38) in the leafy liverwort family **Lejeuneaceae** (Figure 6, Figure 15-Figure 16). This group was represented by 88 species in 17 genera, having fewer genera but more species than this group in the Neotropics. Gradstein suggested that the greater number of species in Asia might be the result of the greater latitudinal extension of the rainforest in the Far East. That region has 22% non-tropical species of **Ptychanthoideae** compared to less than 2% in the Neotropics. It could also represent greater early exploration.

Figure 38. The tropical leafy liverwort ***Ptychanthus striatus***. Photo by Li Zhang, with permission.

In Malaysia (Figure 39-Figure 40), the diverse vegetation consists of swampy mangroves, extensive river floodplains, dipterocarp forests, and montane forests (Chuah-Petiot 2011). **Altimontane** (montane grasslands, shrublands, and woodlands; Figure 40) communities occur on Mt. Kinabalu in Sabah above 3300 m asl, with average temperatures from 6º to 10ºC. The tropical climate of Malaysia ranges in temperature from 21º to 32ºC; annual rainfall is from 2000 mm to 3500 mm.

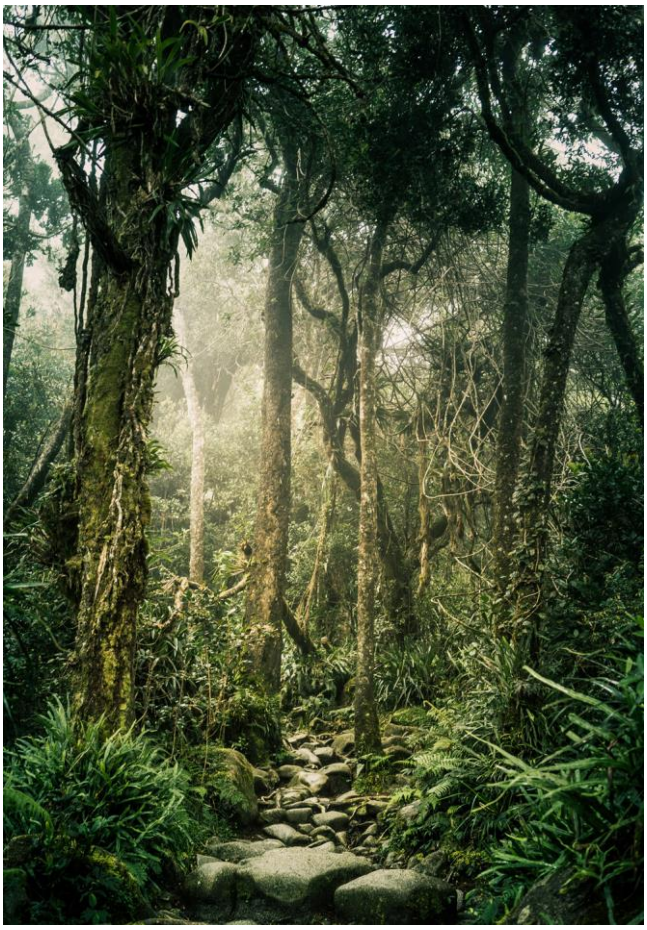

Figure 39. Malaysian Pathway to Mount Kinabalu. Photo by Arto Marttinen <Wandervisions.com>, through Creative Commons.

Figure 40. Mt. Kinabalu altimontane zone. Photo through Creative Commons.

Malaysian (Figure 41) liverwort studies can be traced to the year 1838 (Lee *et al*. 2018). Most of the collections have been made from 1950 to 2000, with many new taxa described. In a recent paper, Chuah-Petiot (2011) published a checklist of liverwort and hornwort species and infra-specific taxa, citing 758 liverworts and 6 hornworts. The **Lejeuneaceae** (Figure 6, Figure 15-Figure 16) far outnumber the other liverwort families (282 taxa), as found also in the study by Pócs and Chantanaorrapint (2016) in Thailand, where 30 out of 38 liverworts were in the **Lejeuneaceae**. In Malaysia, Chuah-Petiot found that species richness of the **Lejeuneaceae** was followed by **Lepidoziaceae** (110, Figure 12), **Frullaniaceae** (67; Figure 2, Figure 7-Figure 8), **Plagiochilaceae** (52; Figure 11), **Geocalycaceae** (36; Figure 42), **Lophoziaceae** (35; Figure 43), and **Radulaceae** (35; Figure 9-Figure 10). As in many areas of the tropics, the genera with the most Malaysian species are ***Cololejeunea*** (84; Figure 44), ***Frullania*** (67; Figure 2, Figure 7-Figure 8), ***Bazzania*** (53; Figure 45, Figure 149), ***Plagiochila*** (47; Figure 11), and ***Radula*** (35, Figure 9-Figure 10). More recently, Lee *et al*. (2018) reported 747 liverwort species from Malaysia, occupying nearly 15% of the liverwort diversity in the world.

Figure 41. Dermakot Forest Reserve in Malaysia. Photo by Angela Sevin, through Creative Commons.

Figure 42. ***Heteroscyphus coalitus***, a member of the **Geocalycaceae**; this family is one of those present in the Atlantic Forest. Photo by Yang Jia-dong, through Creative Commons.

Figure 43. ***Lophozia incisa*** (**Lophoziaceae**) with perianth. Photo by J. C. Schou, with permission.

Figure 44. ***Cololejeunea calcarea***, among the genera with the most species in Malaysia. Photo by Hermann Schachner, through Creative Commons.

Figure 45. ***Bazzania*** in the Neotropics, among the genera with the most species in Malaysia. Photo by Michael Lüth, with permission.

Among the older studies including mosses of Malaysia (Figure 41) are those of Tixier (1980), Mohamed and Tan (1988), Frahm *et al*. (1990), Inoue (1989), and Akiyama *et al*. (2001). Mohamed and Tan (1988) reported 475 taxa of mosses, a number that has changed with further studies and nomenclatural synonymies. More recently, Suleiman *et al*. (2006) enumerated 582 moss taxa from Sabah, Borneo. Tan and Iwatsuki (1999) considered Mt. Kinabalu (Figure 40, Figure 46) to be one of four diversity hotspots for mosses in Malesia, an area that includes the Malay Peninsula, the Malay Archipelago, New Guinea, and the Bismarck Archipelago. Vitt *et al*. (1995) characterized the **Orthotrichaceae** flora of the Huon Peninsula of Papua New Guinea. Higuchi *et al*. (2008) found 97 species of mosses, exclusive of pleurocarpous species, on Mt. Kinabalu. Among the rare species there is the moss ***Takakia lepidozioides*** (Figure 47) near Paka Cave. Higuchi and Lin (2005) found that the size and life form of ***Takakia lepidozioides*** in Taiwan differ between sheltered and exposed sites. Higuchi and coworkers (2008) found that plants in their open sites on Mt. Kinabalu were larger, forming loose mats, compared to those from sheltered places.

Figure 46. Mount Kinabalu, Borneo. Photo by Nep Grower, through Creative Commons.

Figure 47. ***Takakia lepidozioides***, a rare species of moss that occurs on Mt. Kinabalu. Photo through Creative Commons.

In 2019, Pócs *et al.* added a number of new records to the known liverwort (**Lejeuneaceae**) flora of the Huon Peninsula, Papua New Guinea. They brought the number of ***Cheilolejeunea*** (Figure 48-Figure 49) species to 21 and the number of ***Drepanolejeunea*** (Figure 50) to 26. In this publication they summarized altitudinal ranges for the Peninsula, noting that most of the species are in the wet montane rainforests at 1000-3000 m asl. Most of these liverworts were epiphyllous on trees and shrubs with few on tree trunks, twigs, or logs.

Figure 48. ***Cheilolejeunea*** sp., a species-rich genus on the Huon Peninsula, Papua New Guinea. Photo from the Auckland Museum, through Creative Commons.

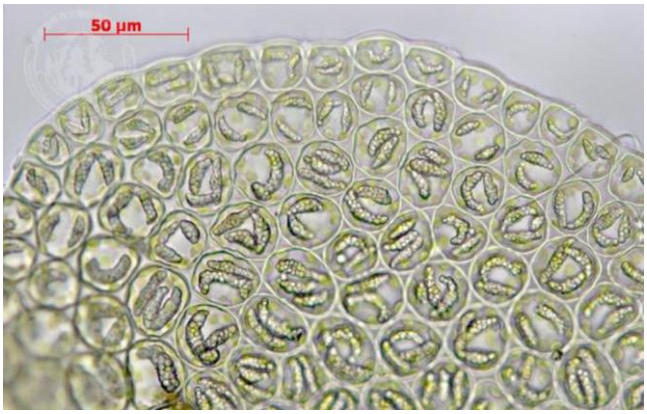

Figure 49. ***Cheilolejeunea trifaria*** leaf cells showing oil bodies; this is one of the ***Cheilolejeunea*** species occurring on the Huon Peninsula, Papua New Guinea. Photo from taibif.tw, through Creative Commons.

Figure 50. ***Drepanolejeunea*** sp., a species-rich genus on the Huon Peninsula, Papua New Guinea. Photo from the Auckland Museum, through Creative Commons.

Kürschner (2003a) is among the more recent of the Asian researchers. He studied epiphytes in the Asir Mountains of Saudi Arabia and Yemen (see Tropics subchapters on epiphytes). In a second study (Kürschner 2003b), he examined the xeric bryophyte community in Yemen. He described a new association of ***Riccia jovet-astiae*** with ***R. argenteolimbata*** and ***Barbula unguiculata*** (Figure 51). This association occurs typically on the shallow soils overlying volcanic rock outcrops in the *Sterculia africana* (Figure 54) woodland. This area is beset with monsoons. It supports a number of **Ricciaceae** (Figure 52-Figure 53) and **Marchantiaceae** (Figure 3-Figure 4) that are typical or xerotropical Africa. ***Riccia atromarginata*** var. ***jovet-astiae*** (see Figure 52) and ***R. albolimbata*** (Figure 53) are characteristic of this habitat. The life strategies are characterized by shuttle species with large spores, providing for a good diaspore bank.

Figure 51. ***Barbula unguiculata***, a species of the xeric community in Yemen. Photo by Bob Klips, with permission.

Figure 52. ***Riccia atromarginata***, a species found on the thin soils of the ***Sterculia africana*** woodland. Photo by Jan-Peter Frahm, with permission.

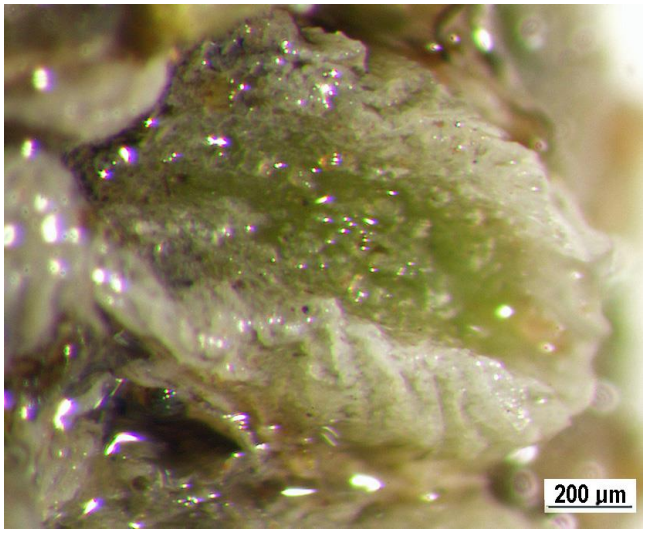

Figure 53. ***Riccia albolimbata***, a species found on the thin soils of the ***Sterculia africana*** woodland. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

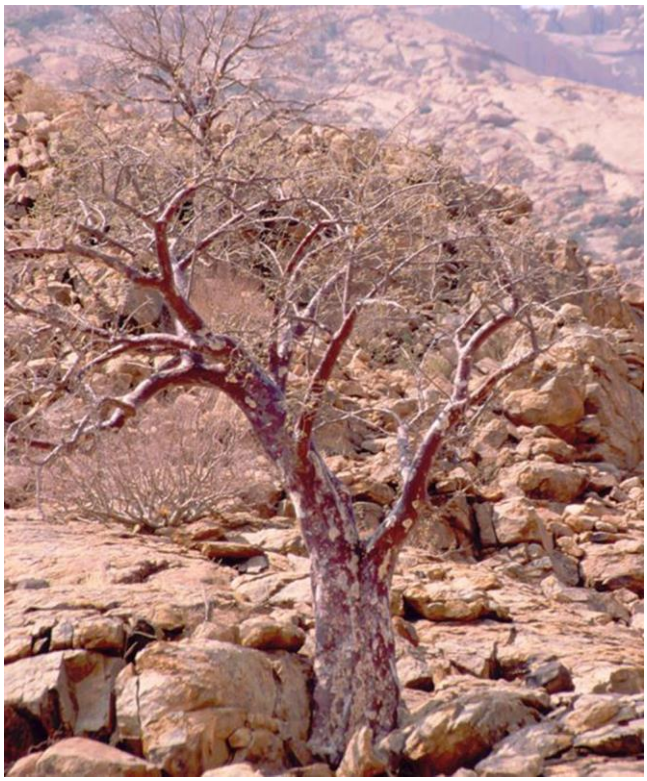

Figure 54. ***Sterculia africana*** woodland, where shallow soils support xeric bryophytes such as **Ricciaceae** and **Marchantiaceae**. Photo by Joachim Beyenbach, through Creative Commons.

Sukkharak and Chantanaorrapint (2014) summarized the bryophyte studies that have occurred in Thailand (Figure 55). They indicated two periods in bryological studies. In the first period (1899-1977), foreign bryologists were the contributors. In the second period (1977 to present), bryologists from Thailand conducted the studies. These studies resulted in 2 new species of hornworts, 20 of liverworts, and 63 of mosses. Based on studies elsewhere, 48 remain unique to Thailand and may therefore be considered endemic.

Figure 55. Thai rainforest. Photo by Michael Cory, through Creative Commons.

Many areas of the Asian tropics remain poorly explored for bryophytes. Sulawesi, Indonesia (Figure 56), is among such locations. Steep mountains with dense vegetation make exploration difficult (Rowe *et al*. 2016). In their exploration of the island, Gradstein *et al*. (2005) found 476 species of bryophytes. Four moss species and one liverwort species appear to be **endemic** to the island. But several large genera are unknown from Sulawesi, suggesting that sufficient exploration may be lacking.

Figure 56. South Sulawesi, Indonesia, Mountains. Photo by Achmad Rabin Taim, through Creative Commons.

Few studies seem to be available on Viet Nam (Figure 57) bryophytes. Pócs (1969) surveyed the leafy liverwort genus ***Bazzania*** (Figure 45, Figure 149). A more comprehensive study by Ninh (1993) recorded 178 taxa. Much more comprehensive work is needed in that country, and ecological work seems to be absent.

Sri Lanka (Figure 58) is likewise an understudied country bryologically. Rubasinghe and Long (2014) reviewed the history of bryological work in the country and remarked on the goal to produce a comprehensive bryophyte flora for Sri Lanka, the first of its kind for the country.

Figure 57. Vietnamese valley. Photo by Ottre, through Creative Commons.

Figure 58. Rainforest in Sri Lanka. Photo by Dan Lundberg, through Creative Commons.

Australia

Scott (1985) provided a basis for bryophyte studies in the late 20th century. While the nomenclature is largely out-dated now, one can still use the reference for its keys and figures, keeping a good modern checklist or database at hand.

There are around 13 different rainforest types in northeastern Australia (Figure 59), including inland "dry rainforest" (Andi Cairns, pers. comm. 23 October 2019). Among the somewhat earlier studies on Australian tropics, Fensham and Streimann (1997) described the moss flora from the inland dry rainforest in north Queensland. They found that moss species richness correlated strongly with several parameters: patch area, mean annual rainfall, and tracheophyte species richness. Volcanic craters create areas with increased moisture, supporting greater species richness. Their analyses suggested that large closed canopy patches create a humid microclimate where more species are preserved. What seems to be most unusual is that a high proportion of rare species were associated with the soil – a substrate that in most tropical forests has few species due to low light and heavy litter.

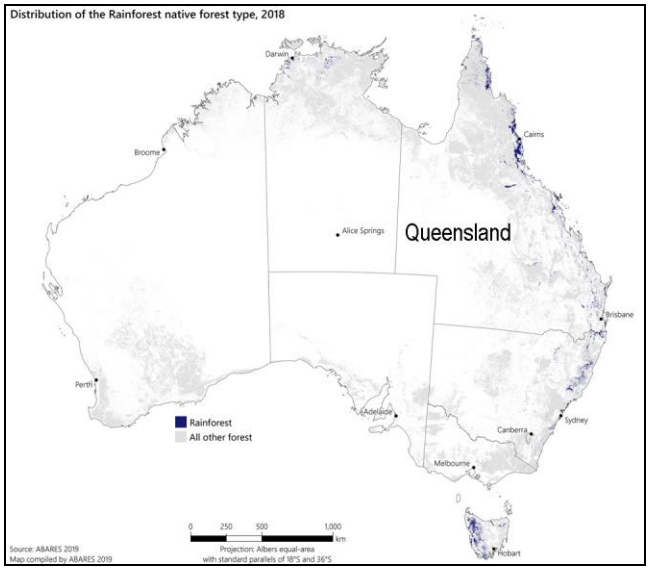

Figure 59. Australian rainforest locations. Image from Department of Agriculture, Australian Government (ABARES), with permission.

The Wet Tropics bioregion of Australia exists along the seaboard of northeastern Queensland for about 500 km (Goosem *et al.* 1999). The Wet Tropics climate usually has two seasons, a wet season in December-April, with a summer monsoon season and occasional tropical cyclones, and then a nearly dry season in May-November when there are occasional showers. Mean annual temperatures range from 30ºC in the lowland to less than 10ºC in the montane areas (Webb 1968). The rainfall is highly variable, being strongly influenced by the local topography, and declining both northward and southward (Adam 1994).

Monographic studies on genera and families contributed to the possibilities for more accurate floristic studies [*e.g.* Reese & Stone 1995 – **Calymperaceae** (Figure 64-Figure 65); Streimann 1991 – **Meteoriaceae** (Figure 60); 1997, 2000 – **Hookeriaceae** *s.l.* (Figure 61)]. Other studies have specifically compared the rainforests, of which many are not in tropical parts of Australia (Ramsay *et al.* 1987).

Figure 60. ***Papillaria crocea*** (**Meteoriaceae**), a tropical epiphyte. Photo courtesy of Andi Cairns.

Figure 61. ***Achrophyllum dentatum*** (**Hookeriaceae**), a species known from the Wet Tropics of Australia. Photo by Niels Klazenga, with permission.

Even now, studies in the Wet Tropics of Queensland are revealing new records and range extensions (Cairns & Meagher 2017). Both ***Pleuridium nervosum*** (Figure 62) and ***Pseudotaxiphyllum pohliaecarpum*** (Figure 63) were new to this region, among a number of other new records.

Figure 62. ***Pleuridium nervosum*** growing with ***Wilsoniella karsteniana*** in the Wet Tropics of Australia. Photo from Cairns & Meagher 2017, with permission.

Ramsay and Cairns (2004) found the greatest species richness in the rainforests of high mountain peaks and on the Atherton Tableland of the Wet Tropics bioregion. They found that the **mats**, **cushions**, and **pendents** are able to harvest water on their surfaces. These droplets of water can store nutrient exudates and insect droppings, releasing them slowly over time as leachates. The bryophytes are able to reduce runoff and maintain forest humidity.

The mangroves, in contrast to the high diversity in other parts of the Wet Tropics, have very little diversity, with only ***Calymperes*** (Figure 64-Figure 65) species present on the mangrove trees (Ramsay & Cairns 2004). The terrestrial ***Taxithelium leptosigmatum*** (Figure 66-Figure 67) forms extensive mats on mud and exposed mangrove roots, especially if there is a high input of fresh water.

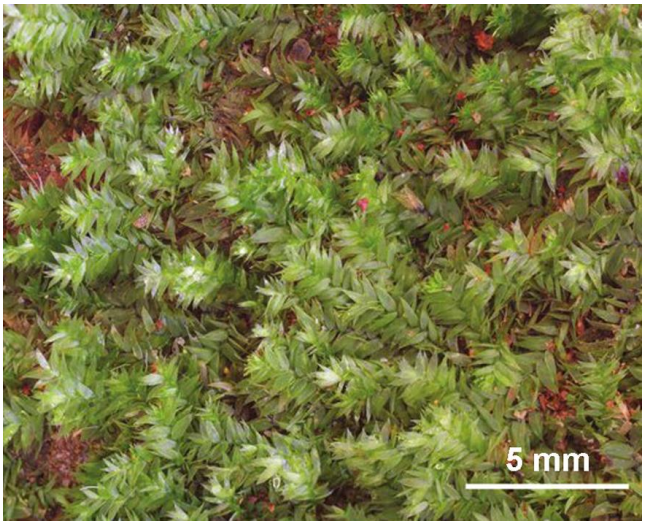

Figure 63. ***Pseudotaxiphyllum pohliaecarpum*** in the Wet Tropics of Australia. Photo from Cairns & Meagher 2017, with permission.

Figure 64. ***Calymperes motleyi*** with gemmae on leaf tips; species of ***Calymperes*** are the only known species on the mangrove trees in the Wet Tropics, but this area is poorly explored. Photo by Niels Klazenga, with permission.

Figure 65. ***Calymperes tenerum*** with gemmae on leaf tips; species of ***Calymperes*** are the only ones on the mangrove trees. Photo from Auckland Museum through Creative Commons.

Figure 66. ***Taxithelium leptosigmatum*** on mangrove mud in the Wet Tropics of Australia. Photo by Andi Cairns, with permission.

Figure 67. ***Taxithelium leptosigmatum*** on mangrove root in Australian Wet Tropics. Photo courtesy of Andi Cairns.

On the forest floor one can find ***Pogonatum*** (Figure 68) and ***Dawsonia*** (Figure 84-Figure 85) where they gain more exposure from road cuts (Ramsay & Cairns 2004). ***Dicranella*** (Figure 69) and the rarer ***Garckea*** (Figure 70) occur in more protected cuttings. Shaded earth banks and forest tracks typically have colonizing species of ***Fissidens*** such as ***F. crispulus*** (Figure 71) and ***F. perobtusus*** in coastal areas or ***F. dietrichiae*** and ***F. pallidus*** (Figure 72) at higher altitudes. The tiny earth mosses [***Archidium*** (Figure 73), ***Erpodium*** [now in ***Solmsiella*** (Figure 74) and ***Venturiella*** (Figure 75)], and ***Gigaspermum*** (Figure 76) are frequent, but difficult to locate. No specific study has addressed epiphytes or epiphylls, but one can find ***Distichophyllum mittenii*** (Figure 77) on leaves of filmy ferns. ***Calyptrochaeta brassii*** (see Figure 78) is present on Mt. Finnigan and ***Clastobryum cuculligerun*** var. ***dimorphum*** (see Figure 79) on many high peaks in the Australian Wet Tropics.

Figure 68. ***Pogonatum neesii***, a soil bryophyte in the Wet Tropics. Photo by Yang Jia-dong, through Creative Commons.

Figure 69. ***Dicranella*** sp., a forest floor species in more protected cuttings. Photo by Tisrel, through Creative Commons.

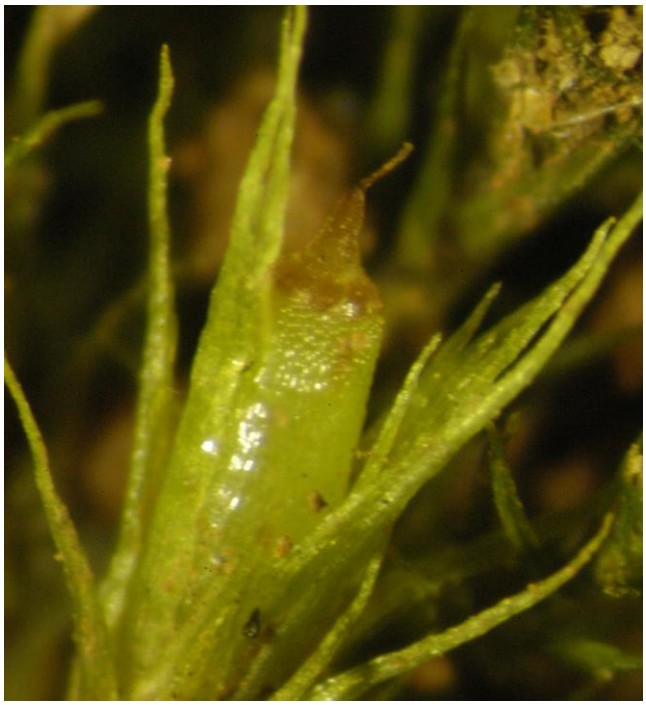

Figure 70. ***Garckea flexuosa*** with capsule, a forest floor species in more protected cuttings. Photo by Manju Nair, K. P. Rajesh, and P. V. Madhusoodanan, through Creative Commons.

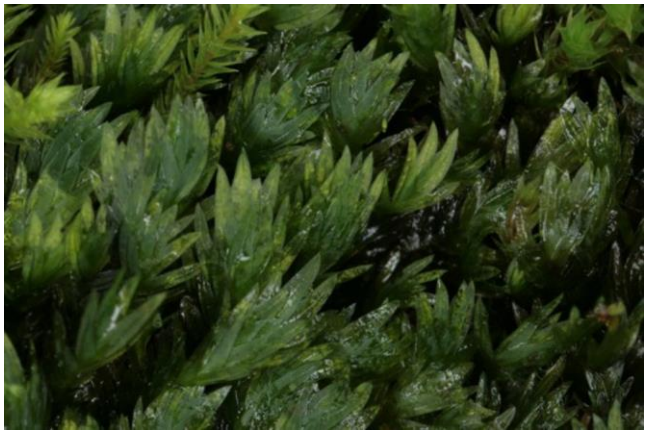

Figure 71. ***Fissidens crispulus***, a colonizer on shaded earth banks and forest tracks in the coastal areas of the Wet Tropics. Photo by Jan-Peter Frahm, with permission.

Figure 72. ***Fissidens pallidus***, a colonizer on shaded earth banks and forest tracks in the higher altitudes of the Wet Tropics. Photo by Tom Thekathyil, with permission.

Figure 73. ***Archidium ohioense*** with capsules, one of the tiny earth mosses in the Wet Tropics of Australia. Photo by Li Zhang, with permission.

Figure 74. ***Solmsiella biseriata*** leaves and rhizoids, a moss that grows on trunks and branches of trees and sometimes on boulders in the Wet Tropics of Australia. Photo by Heino Lepp, Australian National Botanic Gardens, with online permission.

Figure 75. ***Venturiella coronatum*** with capsules, one of the tiny mosses in the Wet Tropics of northern Queensland, Australia. Photo courtesy of Andi Cairns.

Figure 76. ***Gigaspermum repens*** with capsules, one of the tiny earth mosses in the Wet Tropics of Australia. Photo by David Tng, with permission.

Figure 77. ***Distichophyllum mittenii***, a species found on the stem of a tree fern in tropical Australia. Photo by Cairns & Meagher 2017.

Figure 79. ***Clastobryum*** habit, a genus in the Wet Tropics of Australia. Photo courtesy of Andi Cairns.

We once thought that the larger mosses (*e.g.* ***Dawsonia***) in **Polytrichaceae** (Figure 80), **Garovagliaceae** (Figure 81), **Hypnodendraceae** (Figure 82), and **Spiridentaceae** (Figure 83) were unique to Asia (Gradstein & Pócs 1989). However, we now know that most of these families also occur in the Australian tropics. ***Dawsonia longiseta*** (Figure 84) and ***D. polytrichoides*** (Figure 85) occur in the Wet Tropics (Cairns *et al.* 2019)]. In the **Hypnodendraceae**, ***Hypnodendron vitiense*** (Figure 87) subsp. ***australe*** and ***H. vitiense*** subsp. ***vitiense*** both occur in tropical Australia, as does ***H. spininervium*** (Figure 86). Also in the Wet Tropics of Australia we find ***Ephemeropsis tjibodensis*** (Figure 88), an epiphyllous moss. ***Garovaglia*** (Figure 81) has since been moved to the **Pterobryaceae** (see TROPICOS) and along with several other species in this family or closely related ones occurs in the Wet Tropics of Australia: ***Euptychium setigerum*** subsp. ***setigerum***, ***Garovaglia elegans*** (Figure 81) subsp. ***dietrichiae***, ***Garovaglia powellii*** (Figure 89) var. ***muelleri***. ***Hampeella concavifolia*** (Figure 90), ***Hampeella pallens*** (Figure 91-Figure 92), and ***Ptychomnion aciculare*** (Figure 93) are also in the Australian Wet Tropics**.** ***Spiridens*** (Figure 94), considered by Bell *et al*. (2007; Catcheside & Meagher 2016) to be in the **Hypnodendraceae**, is only known in Australia from Lord Howe Island. It is still unknown in the Australian tropics, although it occurs elsewhere in Eastern Hemisphere tropics.

Figure 78. ***Calyptrochaeta*** sp. from New Zealand; ***C. brassii*** is an endemic species in the Australian tropics. Photo by Jan-Peter Frahm, with permission.

Figure 80. ***Dawsonia superba***, a species in the common Asian tropical family **Polytrichaceae** (or **Dawsoniaceae**). Photo by Phil Bendle, permission through John Grehan.

Figure 81. ***Garovaglia elegans***, a species in the common Asian tropical family **Garovagliaceae** (now in **Pterobryaceae**; see TROPICOS). Photo by Zen Iwatsuki, with permission.

Figure 82. ***Hypnodendron vitiense*** with capsules, a species in the common Asian tropical family **Hypnodendraceae**. ***Hypnodendron vitiense*** subsp. ***vitiense*** and ***H. vitiense*** subsp. ***australe*** both occur in tropical Queensland. Photo by Marshall Simon, through Creative Commons.

Figure 83. ***Spiridens reinwardtii***, a species in the common Asian tropical family **Spiridentaceae** (or **Hypnodendraceae**). Photo by Daniel L. Nikrent, with online permission for non-commercial use.

Figure 84. ***Dawsonia longiseta*** (**Polytrichaceae**) with capsules, a species that occurs in the Wet Tropics of Australia. Photo by Niels Klazenga, with permission.

Figure 85. ***Dawsonia polytrichoides*** (**Polytrichaceae**) with capsules, a species that occurs in the Wet Tropics of Australia. Photo from Naturemapr, through Creative Commons.

Figure 86. ***Hypnodendron spininervium*** (**Hypnodendraceae**), a species that occurs in the Wet Tropics of Australia. Photo through Creative Commons.

Figure 87. ***Hypnodendron vitiense*** (**Hypnodendraceae**), a species that occurs in the Wet Tropics of Australia. Photo by David Tng, with permission.

Figure 88. ***Ephemeropsis tjibodensis*** protonematal mat on palm leaf, an epiphyllous species in the wet tropics. Photo by Tamás Pócs, with permission.

Figure 89. ***Garovaglia powellii*** var. ***tahitensis***; var. ***muelleri*** occurs in the Wet Tropics of Australia. Photo by Claudine Ah-Peng, with permission.

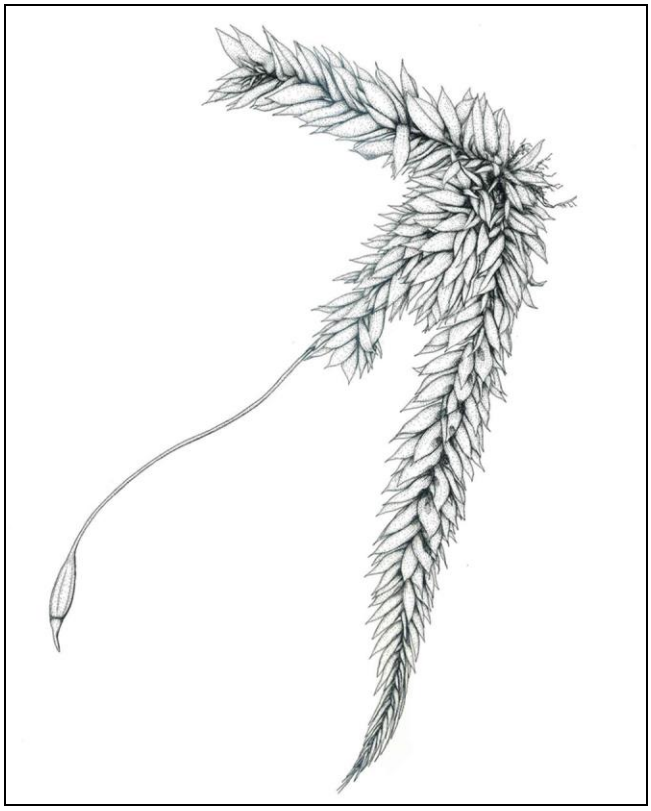

Figure 90. ***Hampeella concavifolia***, a species that occurs in the Wet Tropics of Australia. Drawing by Rod Seppelt, with permission.

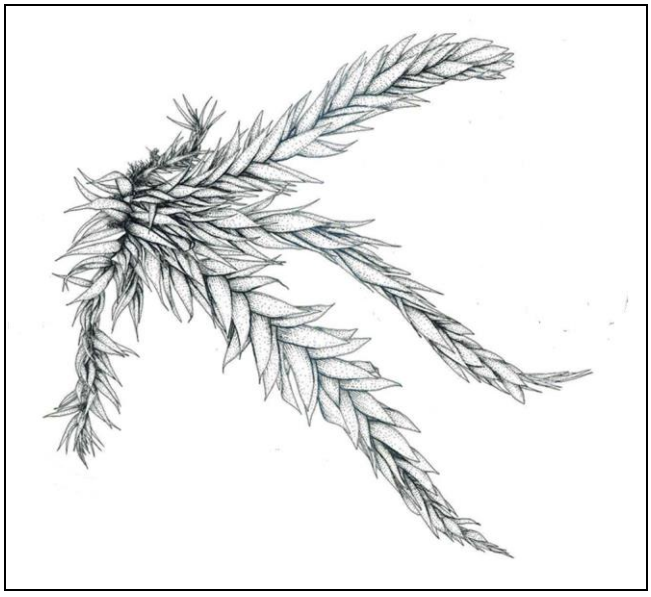

Figure 91. ***Hampeella pallens***, a species that occurs in the Wet Tropics of Australia. Drawing by Rod Seppelt, with permission.

Figure 92. ***Hampeella pallens***, an epiphytic species in the Wet Tropics of Australia. Photo courtesy of Andi Cairns.

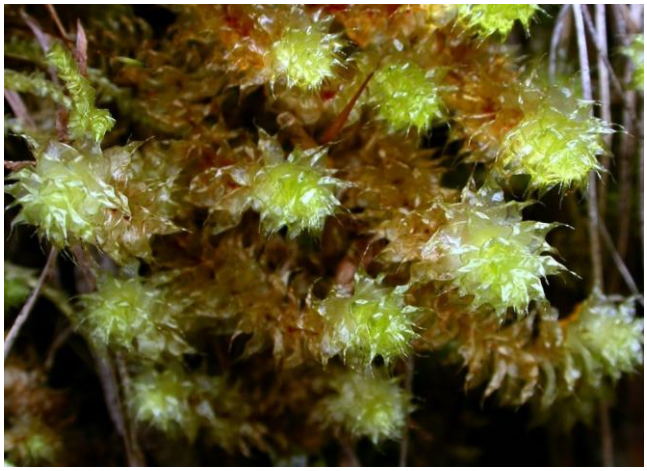

Figure 93. ***Ptychomnion aciculare***, a species that occurs in the Wet Tropics of Australia. Photo by David Tng, with permission.

Figure 94. ***Spiridens muelleri***, an endemic species on Lord Howe Island, but the genus has not yet been found in tropical Australia. Photo by Peter Woodard, through Creative Commons.

Dixon (1938) considered the bryophyte flora of tropical Queensland as one of special interest to botanists, considering both what had already been found and what was yet to be discovered. It is currently considered a hotspot for bryophyte diversity (Cairns *et al*. 2019).

More than 80 years later, new records of bryophyte species are still being added regularly to the tropical Queensland flora (Cairns *et al*. 2019). For example, family or generic treatments of the Australian tropical moss flora include the **Brachytheciaceae** – especially ***Rhynchostegium*** / ***Platyhypnidium*** (Figure 95) (Huttunen & Ignatov 2010), **Stereophyllaceae** – ***Entodontopsis*** (Figure 96) (Meagher & Cairns 2014), **Sematophyllaceae** – ***Clastobryophilum balansaeanum*** (Figure 97), a species previously known only in New Caledonia, on bark with the leafy liverwort ***Heteroscyphus aselliformis*** (Figure 97) (Cairns & Meagher 2014) and ***Entodontopsis pygmaea*** (Figure 96), a paroicous epiphytic species (Meagher & Cairns 2014), **Meteoriaceae** (Figure 98) (Meagher & Cairns 2016), and **Orthotrichaceae** – especially ***Macromitrium*** (Figure 99) (Vitt & Ramsay 1985). Comprehensive treatments of the liverwort flora include the **Lejeuneaceae** (Figure 100) (Renner 2011), **Radulaceae** (Figure 101) (Renner 2014, Renner *et al.* 2014), and **Lepidoziaceae** (Figure 102) (Brown & Renner 2014; Renner & Wilson 2018). Meagher (2019 reports 28 species of ***Bazzania*** (**Lepidoziaceae**; Figure 103) in the Australian Wet Tropics bioregion, representing the highest species richness of the genus in Australia. These Wet Tropics ***Bazzania*** species occur on trees, tree ferns, logs, soil, rocks, rocks on stream banks, but are not epiphyllous (Meagher 2019). In the **Plagiochilaceae** 8 species were newly named from the Wet Tropics (Figure 104), occupying the diverse substrates of forest floor saturated humic soil, granite boulders, decaying wood, tree trunks, branches, and twigs (Renner 2018).

Figure 95. ***Rhynchostegium tenuifolium***, a species in the tropical Queensland moss flora. Photo from Naturmapr.org, through Creative Commons.

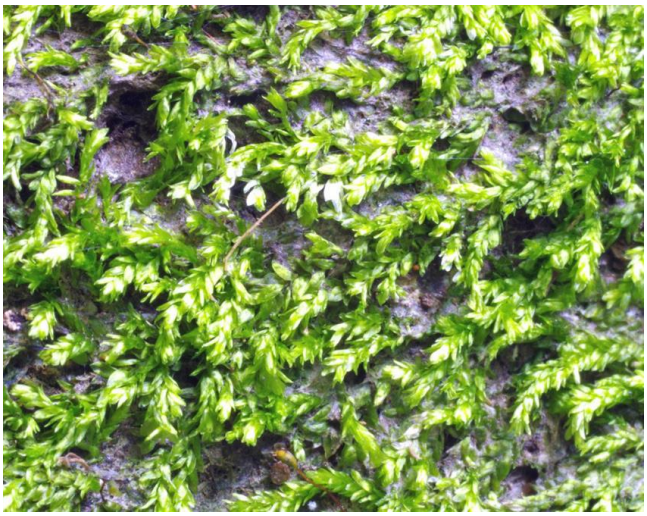

Figure 96. ***Entodontopsis pygmaea***, a species in the tropical Queensland moss flora. Photo from Meagher & Cairns 2014, with permission.

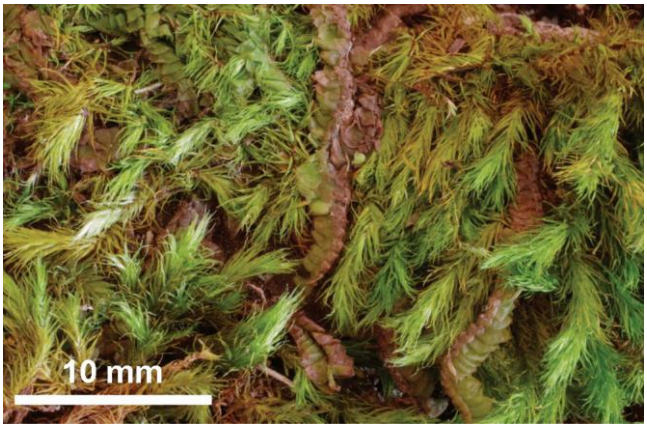

Figure 97. ***Clastobryophilum balansaeanum*** with leafy liverwort ***Heteroscyphus aselliformis*** (reddish) in Wet Tropics, northern Queensland. Photo from Cairns & Meagher 2014, with permission.

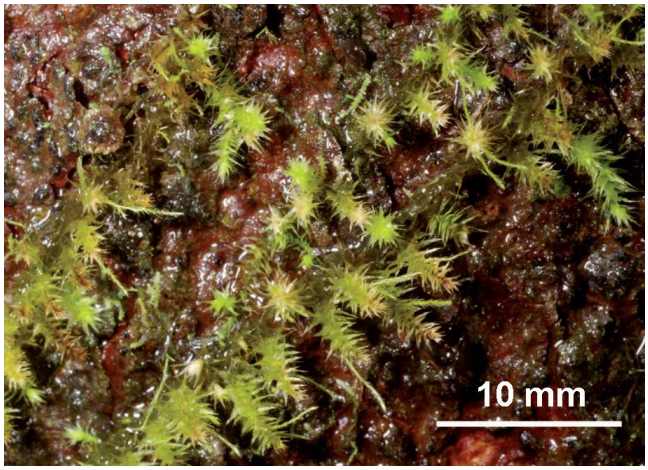

Figure 98. ***Meteoriopsis undulata*** on tree trunk in North Queensland. Photo from Meagher & Cairns 2016, with permission.

Figure 99. ***Macromitrium erythrocomum*** (**Orthotrichaceae**), an endemic species in the Wet Tropics of Australia. Photo from Ramsay *et al*. 2017, with permission.

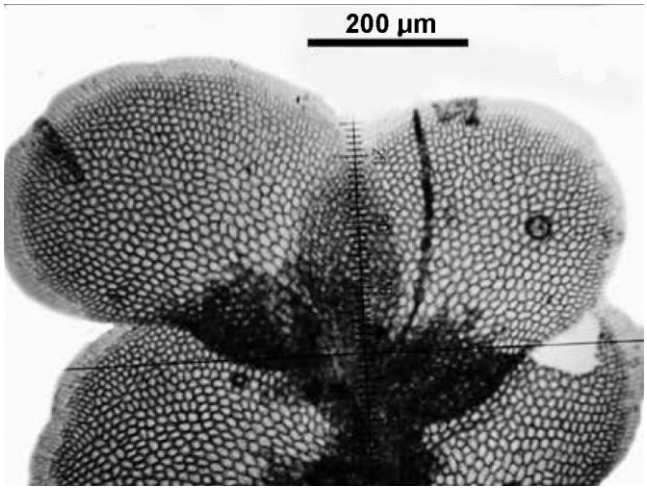

Figure 100. ***Cololejeunea triapiculata***, a species occurring in the Australian Wet Tropics. Photo by Tamás Pócs, with permission.

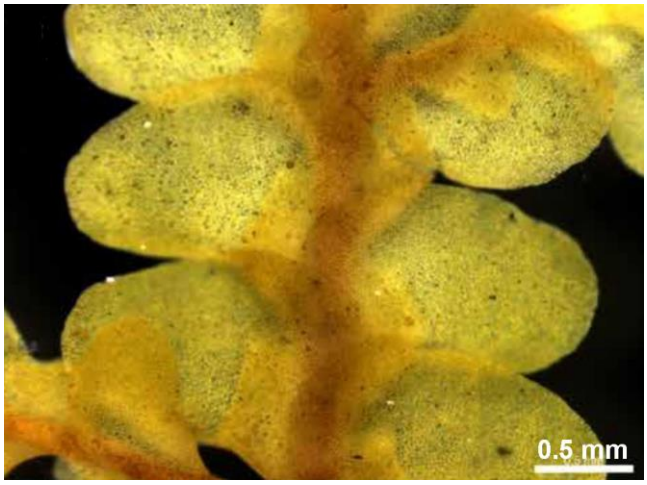

Figure 101. ***Radula oreopsis***, a species occurring in the Australian Wet Tropics. Photo modified from one by Matt Renner, with permission.

Figure 102. ***Acromastigum implexum*** (**Lepidoziaceae**) from the Wet Tropics, northern Queensland. Photo from Renner & Wilson 2018, permission pending.

Figure 103. ***Bazzania adnexa***, a widespread ***Bazzania*** in Australia, including the tropical region. Photo by Jan-Peter Frahm, with permission.

Figure 104. ***Plagiochila obtusa***, a tropical species from northern Queensland. Photo by Leon Perry, through Creative Commons.

Australia appears to have received much more attention (at least in English publications) than many of the Asian countries. This has permitted ecological and physiological studies to take place. Nevertheless, as already noted, the tropical regions remain under-explored. In 2004, Ramsay and Cairns contributed a checklist for the Wet Tropics bioregion in northeastern Queensland (Figure 105), listing 397 species. This permitted them to determine the families represented by the most species (Table 1). They elaborated on habitat, distribution, and bryogeographical affinities for the Wet Tropics. These areas of study have been possible due to the strong taxonomic background that is available online via the Australian Mosses Online website. In 2019, Cairns *et al*. released a new checklist that updated the nomenclature and included new finds, bringing the total number of species of mosses to 410, including 170 genera in 60 families. This number is somewhat misleading because some families decreased in number of species due to realization of synonymy, while others increased (Table 1); the total of new moss species was 55. Nevertheless, most of the bryological studies in Australia have been in the southern part where bryophyte-friendly habitats are more common and accessible, but not tropical. The epiphytes and epiphylls in the Australian tropical forests remain unexplored in any comprehensive way.

Figure 105. Tropical rainforest in northeastern Australia. Photo by Thomas Schoch, through Creative Commons.

Table 1. Families of mosses exhibiting the highest species richness in the Wet Tropics of Australia. The first line of each family is based on Ramsay and Cairns 2004. The second line is based on Cairns *et al*. 2019.

Family	Number of genera	Number of species
Bryaceae	5	23
	9	32
Calymperaceae	7	47
	7	48
Dicranaceae	7	29
	8	19
Meteoriaceae	8	13
	9	16
Sematophyllaceae	16	32
Sematophyllaceae	11	23
Pylaisiadelphaceae	7	13
Additional Species-Rich Families		
Orthotrichaceae	4	24
Fissidentaceae	1	44

This history is representative of the background necessary to carry out ecological studies on species dominance, community structure, comparative diversity, biomass comparisons, and many other aspects of ecology. It demonstrates the long process needed before ecologists can begin many kinds of studies and it helps to explain the paucity of ecological studies in many parts of the tropics, especially in Australia.

Neotropics

The **Neotropics** (Figure 106) is synonymous with New World Tropics. It includes areas of Mexico, Central America, the West Indies, Chocó, Northern Andes, Central Andes, Amazonia, Guyana Highland, Planalto, and Southeastern Brazil (Gradstein *et al.* 2001).

Until relatively recently, any comprehensive guide to the bryophytes of the Neotropics was lacking. Researchers had to find the scattered treatments among individual papers, making comprehensive ecological studies, especially community studies, difficult to impossible. The publication by Gradstein *et al*. (2001) made it possible to expand the types of ecological studies that are feasible.

Figure 106. Neotropics map. The dashed lines mark the borders of the tropics, with Tropic of Cancer in the north and Tropic of Capricorn in the south; the solid straight line is the Equator. Photo from Ökologix, through Creative Commons.

Most studies have been exclusive to either mosses or liverworts. Various studies contributing to these records include, for mosses, Steere 1948 – Ecuador, Pursell 1973 – Venezuela, Bowers 1974 – Costa Rica, Hermann 1976 – Bolivia, Yano 1981, 2011 – Brazil, Florschütz Waard 1990 – Guianas, Menzel 1992 – El Salvador, Moreno 1992a, b – Venezuela, Sharp *et al*. 1994 – Mexico, and Churchill & Linares 1995 – Colombia. For liverworts, these include Gradstein & Hekking 1989 – Guianas and Bolivia; Gradstein 2006 – French Guiana, Gradstein *et al*. 2007 – Ecuador, Gradstein 2016 – Colombia, Gradstein & León-Yánez 2018 – Ecuador, Gradstein *et al*. 2018 – Colombia. But these provided primarily checklists and descriptions. Those publishing the lists of species often did not have access to specimens collected elsewhere. Hence, many species from multiple countries were named more than once, creating synonyms and inaccurate estimates of species numbers and distributions. It was not until keys became available that an ecologist had the tools needed to conduct ecological studies that included species information.

To illustrate the problems caused by synonyms among the bryophytes of the Neotropics, we need only examine a few studies. Delgadillo *et al*. (1995) indicated 4,103 species and varieties of mosses recorded from the Neotropics. Within five years, subsequent taxonomic revisions reduced the number to 3,869 species and varieties (Delgadillo 2000). Only one year later, Gradstein *et al.* (2001, Table 2, page 3) estimated 3,980 species of all bryophytes in the Neotropics, including only 2,600 mosses, 1,350 liverworts, and 30 hornworts, based on systematic studies that found many synonyms.

Based on the 1996 expedition in the Chagos Archipelago (Neotropics; Figure 107), Seaward *et al*. (2006) found a good correlation of bryophyte diversity with island size. But only 19 taxa were recorded on the 25 islands (out of 55) that they explored. They attributed the low diversity to the remoteness and young age of the islands, as well as their small size. Nevertheless, where the bryophytes are found on these islands, they tend to be in abundance and play "significant" ecological roles. They found no evidence of host specificity of epiphytes and no epiphyllous species were found by the expedition.

Figure 107. Salomons Atoll in the Chagos Islands in the Indian Ocean. Photo by Charles and Anne Sheppard, through Creative Commons.

Bryophytes are advantageous as indicators of biodiversity and can be useful in broader conservation efforts in the Neotropics (Salazar Allen *et al.* 1996). Hence, the presentation of the treatise of Gradstein *et al*. (2001) is of tremendous value to all Neotropical bryophyte researchers. The two volumes present 200 genera of liverworts and 400 of mosses. They provide not only taxonomic aids, but also ecological attributes such as habitat indicators.

The rainforest of the Americas (**Neotropics**) is quite different from that in the African or Asian tropics (Gradstein & Pócs 1989). The New World Americas are characterized by **Pilotrichaceae** (Figure 108), **Phyllogoniaceae** (Figure 109), ***Porotrichodendron*** (Figure 110; **Lembophyllaceae**), ***Chorisodontium*** (Figure 111; **Dicranaceae**), ***Octoblepharum*** (Figure 112; lowland; **Octoblepharaceae**), and ***Phyllodrepanium*** (Figure 113; **Phyllodrepaniaceae**) among the mosses, and **Monocleaceae** (Figure 114) and numerous **Lejeuneaceae** (Figure 6, Figure 15-Figure 16) among the liverworts. In the Asian **Lejeuneaceae**, the subfamily **Ptychanthoideae** (Figure 38) predominates, whereas in the Neotropics the **Brachiolejeuneae** (Figure 115-Figure 116) predominate (Gradstein 1991, 1994).

Figure 108. ***Cyclodictyon*** sp. (**Pilotrichaceae**) from the Neotropics. Photo by Michael Lüth, with permission.

Figure 109. ***Phyllogonium viride*** (**Phyllogoniaceae**), a genus characteristic of the Neotropics. Photo by Michael Lüth, with permission.

Figure 110. ***Porotrichodendron superbum***, a characteristic species of the Neotropics. Photo by Juan David Parra, through Creative Commons.

Figure 111. ***Chorisodontium mittenii***; ***Chorisodontium*** is a characteristic genus in the Neotropics. Photo by Jan-Peter Frahm, with permission.

Figure 112. ***Octoblepharum albidum***; ***Octoblepharum*** is a characteristic genus in the Neotropics. Photo by Niels Klazenga, with permission.

Figure 113. ***Phyllodrepanium falcifolium***, a moss characteristic of the Neotropics. Photo by Juan David Parra, through Creative Commons.

Figure 114. ***Monoclea gottschei*** (**Monocleaceae**), a thallose liverwort characteristic of the Neotropics, shown here with two sporophytes. Photo by Martin Nebel, courtesy of Robbert Gradstein.

Figure 115. ***Dicranolejeunea axillaris*** (**Brachiolejeuneae**) in abundance in the pampa of the Galapagos Islands. Photo courtesy of Robbert Gradstein.

Figure 116. ***Lindigianthus cipaconeus*** (**Brachiolejeuneae**) growing on tree fern in the Colombian Andes at 3000 m. Photo courtesy of Robbert Gradstein.

Nevertheless, disjunctions among the liverworts between the **Neotropics** (American tropics) and Africa are well known (Pócs 1976, 1992; Gradstein *et al*. 1983; Delgadillo 1993; Frahm 1995). Records in 1983 indicate 35 Afro-American shared species (see examples in Figure 117-Figure 118) (Gradstein *et al*. 1983). Most of these liverwort disjuncts are in the **Jungermanniales** (leafy liverworts) (Gradstein *et al*. 1983). By 1993, records indicated the Neotropics shared 334 bryophyte species and infraspecific taxa with the African tropics (Delgadillo 1993). This might be the result of an ancient land connection or long-distance dispersal. These are just hypotheses as experimental data on longevity of liverwort spores is greatly lacking (Gradstein *et al*. 1983). Another possibility is dispersal from Gondwanaland.

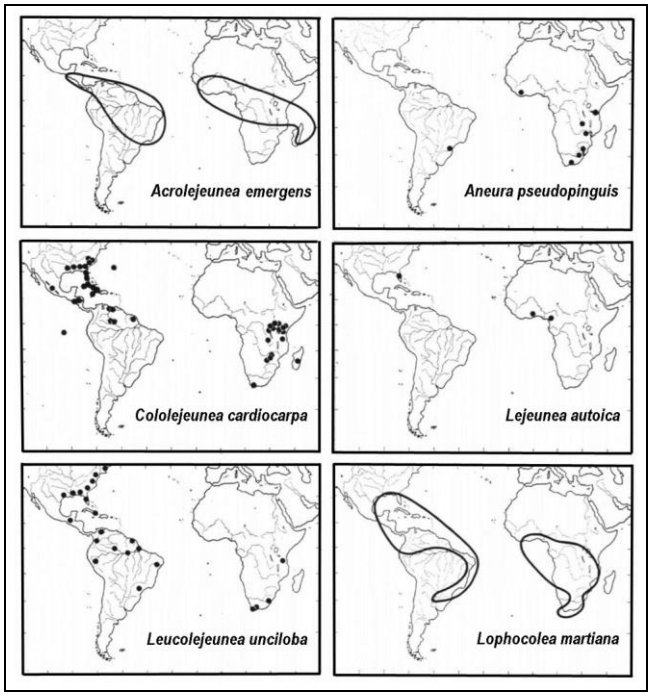

Figure 117. New and old tropical lowland disjunct species between Africa and the Americas. Modified from Gradstein *et al.* 1983.

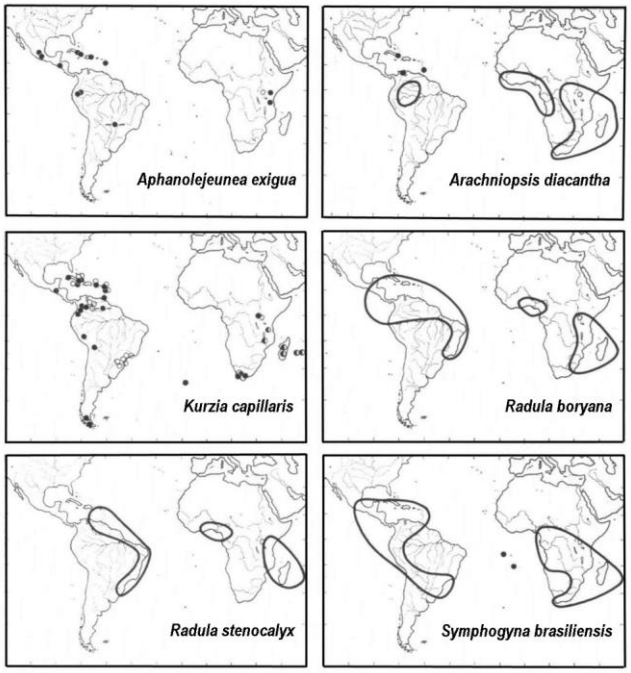

Figure 118. New and old tropical montane disjunct species between Africa and the Americas. Modified from Gradstein *et al.* 1983.

North and South America seem to have more species in common, sharing about 675 species (Delgadillo 1992, 1995). These include those with a continuous range and those with a disjunct distribution. Migration seems to have been stepwise, but some of these occurrences may have resulted from the breakup of previous distributions. Others arrived by long-distance dispersal. Other connections of the bryophyte flora to other parts of the Americas is through elevational distributions (Delgadillo & Cárdenas 1989). For example, the highlands of Chiapas, Mexico (Figure 119), are suitable for growth of species that may be found at lower elevations farther from the equator. The Chiapas have 155 taxa of mosses that fit into five phytogeographical elements. Mexico and Colombia alone share 371 moss species (Delgadillo 1992). Of these, 25 have a disjunct distribution that suggests long-distance dispersal. The Central American bridge facilitates the exchange of species, but the northern Andes in Colombia and the Neovolcanic Belt of Mexico form barriers that limit that exchange.

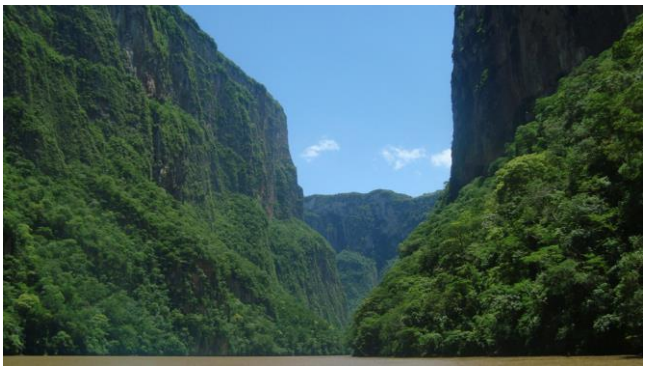

Figure 119. Sumidero Canyon, Chiapas, Mexico. Photo by Srplattano, through Creative Commons.

Delgadillo (1984) reported on mosses of the Mexican part of the Yucatan Peninsula (Figure 120). He identified 69 moss species and varieties and noted the similarities to the flora of the West Indies. There are virtually no endemics, perhaps due to the close connections with the Mexico mainland and the West Indies.

Figure 120. Yucatan moist forest, Mexico. Photo by Carlos Delgado, through Creative Commons.

In the ***Liquidambar*** forest (Figure 121) of Mexico, 194 species of mosses were known in 1979 (Delgadillo 1979). Of these, 70% are strictly American. This flora exhibits both a wide altitudinal and latitudinal range in Mexico and represents both tropical and temperate species.

Figure 121. ***Liquidambar*** forest canopy, through Creative Commons.

Herrera-Paniagua *et al*. (2008) reported 212 moss species for the Mexican state of Querétaro. As indicated by endemism, this state has three distinct regions: the conifer-cloud-temperate forests in the northeast (Sierra Madre Oriental), the more xeric parts in the center and southeast (Mexican Plateau and ecotone areas of the Transmexican Volcanic Belt), and the almost temperate areas in the south (Transmexican Volcanic Belt). The Sierra Madre Oriental province has the highest species richness.

The Trans-Mexican Volcanic Belt spans Central-Southern Mexico from the Pacific Ocean to the Gulf of Mexico between 18°30'N and 21°30'N. Villaseñor *et al*. (2006) reported diversity hotspots for mosses in this tropical region, finding 596 moss species out of 980 known for Mexico at the time. The tropical region of Oaxaca had 459 recorded species in 2011 (Delgadillo & Cárdenas 2011).

It seems that almost any expedition even now is likely to reveal new records for the region. In 2001, Equihua *et al*. reported nine new moss records for Mexico from the Lacandona rainforest. The authors noted that these and other records continue to corroborate the continuity of bryophytes from North America to South America through the Central American bridge.

In a study of only 6 hectares (about 6 rugby fields or 10 American football fields) in a Costa Rican upper montane ***Quercus*** (oak) forest (Figure 122), Holz *et al*. (2002) found 100 species of mosses, 105 of liverworts, and 1 hornwort. In the oak forests and páramo of the Cordillera de Talamanca, Costa Rica, Holz and Gradstein (2005) found 401 species of bryophytes. In both studies, the number of mosses and liverworts was almost equal, with Holz and Gradstein finding 209 mosses, 191 liverworts, and 1 hornwort. To illustrate the limitations that early ground-based studies imposed, studies in the lowland rainforest found 50% of the bryophyte species only in the crowns and upper trunks, >10 m above the ground (Cornelissen & Gradstein 1990).

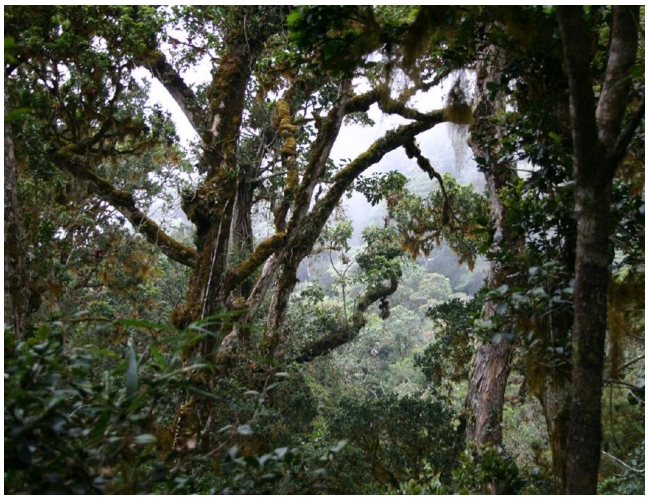

Figure 122. ***Quercus*** (oak) tropical montane forest. Photo by Cody Hinchliff, through Creative Commons.

Acebey *et al*. (2003) found similar high numbers of species in Bolivia (Figure 123). In a submontane rainforest there, they found 80 species on just six trees, 48 liverwort and 32 moss species. But they are quick to point out that finding nearly all the species in the forest requires only a small sample size. They estimate that these six trees had floras that represented 95% of the total bryophyte flora of the forest. Churchill *et al*. (2010) published a catalog of the bryophytes of Bolivia with discussions of diversity, distribution, and ecology.

In Cuba (Figure 124), an island in the Greater Antilles, 383 taxa were reported, mainly from mountain areas (Motito *et al*. 1992). However, more recent studies seem to be lacking, preventing an evaluation of Cuban species compared to those of other localities.

Figure 123. Santa Cruz, Bolivia. Photo by Vincent Raalvia, through Creative Commons.

Figure 124. Montane moist forest on the slopes of Pico Turquino, Santiago de Cuba, Cuba. Photo by Male Gringo, through Creative Commons.

The tropical Andes (Figure 125) has by far the highest bryophyte diversity in the tropical Americas. For a general review on liverwort diversity in the Andes see Gradstein (1995b). Gradstein *et al*. (1977) compared oil body structures and examined the ecological distributions of selected species of the leafy liverworts in the Andes of Colombia. Churchill and co-workers listed 2,058 moss species names but suggested the actual number was probably closer to 1,500-1,700 because of likely synonyms (Churchill *et al*. 1995b).

The extraordinary biological richness of the Andean region is due to the great climatic and elevational variation of the area as well as historical factors. The authors concluded that an "increase in species diversity from the poles to the equator does not apply to mosses" (Churchill *et al*. 1995b). The latitudinal gradient has recently been studied by Shaw *et al*. (2005) for mosses and by Wang *et al*. (2016) for liverworts. These papers indicate that moss diversity is highest in the Southern Hemisphere and lowest in the Northern Hemisphere, with the tropics having an intermediate level. Liverwort diversity, in contrast, is highest in the tropics.

Figure 125. Andes, Ausangate hillside, Peru. Photo by Marturius, through Creative Commons.

In the El Sira Communal Reserve of the Peruvian Andes, Graham *et al*. (2016) found 171 liverwort species, representing 51 genera and 18 families. This flora flourishes in the high humidity, with sometimes more than 7500 mm in a year. Climate, soils, and microhabitat delineated diverse distributional patterns along the 2000-m elevational range.

An example of the high diversity is the San Francisco Biological Reserve in the Andes of southern Ecuador (Figure 126) (Gradstein *et al*. 2007). The reserve ranges from 1,800 to 3,100 m asl and consists of about 1,000 ha of pristine montane forest and páramo. Almost 570 species of bryophytes (357 liverworts, 206 mosses, 3 hornworts), including more than half the total number of liverwort species known from Ecuador, have been recorded from the reserve and the number is still rising (Schäfer-Verwimp *et al*. 2013; Gradstein & Benitez 2017). One reason for the high number of species recorded is probably the large number of bryologists who conducted fieldwork in the reserve and studied the collections. As Churchill *et al.* (2009) remarked: "One could readily predict similar diversity numbers throughout the montane forest of the tropical Andes employing such expertise. This study provides a basis for comparing other localities of similar vegetation and elevational range."

Figure 126. Reserva Biológica San Francisco, southern Ecuador. Photo courtesy of Robbert Gradstein.

In contrast, lowland habitats are usually less rich in bryophytes and do not provide for the same diversity seen by the rest of the flora and fauna (Churchill *et al.* 2009). While the number of niches in the multi-layered rainforest is relatively high, much of the tropical lowland is inhospitable to bryophytes, being too dry, too hot, or too dark. Whereas Churchill (1991) suggested that there is no strong latitudinal gradient of species richness from the temperate zone to the tropics, Hallingbäck (1992) further asserted that the temperate regions have a much higher diversity of mosses than is known in the tropics.

But "known" may be the operative word. On the one hand, many species have been described as different species multiple times; Ireland (1992) reduced the number of Latin American species of ***Isopterygium*** (Figure 127) from 92 to 8, Edwards (1980) accepted only 6 of the 93 species of ***Calymperes*** (Figure 128) from West Africa, and Bischler (1984) only 9 of 69 previously described New World ***Marchantia*** (Figure 3) species. Many taxa have been viewed as different simply because they were from a new place (O'Shea 2002). On the other hand, we are just beginning to explore the bryophytes high in the canopy through the use of a number of somewhat recent techniques (McClure 1966; Grison 1978; Perry 1978; Whitacre 1981; Parker *et al*. 1992; Gradstein 1996; Zotz & Vollrath 2003). Cornelissen and Gradstein (1990) report that about 50% of the lowland rainforest bryophyte species of Guyana occur in the crowns and upper bole, typically missed by early bryological studies. Bryologists are beginning to find that the canopy of these primary forests may support many more species than the more-readily studied understory (Cornelissen & ter Steege 1989; Wolf 1993a, b). Bryophytes in the tropics find their dominance in different places from those in the temperate forests.

Figure 127. ***Isopterygium tenerum***; the genus ***Isopterygium*** has had many of the same species named by different names in the tropics, creating many synonyms. Photo by John Bradford, with permission.

Figure 128. ***Calymperes*** sp. (**Calymperaceae**), one of the families that dominate in tropical Guyana. Photo by Niels Klazenga, with permission.

In the lowland rainforests of Mabura Hill, Guyana (Figure 129), South America, Cornelissen and Gradstein (1990) found 134 bryophyte species. The dominant bryophyte family is the leafy liverwort family **Lejeuneaceae** (Figure 6, Figure 15-Figure 16), comprising about 30% of the cryptogamic flora (including bryophytes and lichens). As seems to be typical, the canopy accounted for 50% of the species. The humid mixed forest on loamy soil sports the richest liverwort flora.

Figure 129. Rainforest in Guyana. Photo through Creative Commons.

In Guyana (Figure 129), **Calymperaceae** (Figure 128), **Hookeriaceae** (Figure 182), **Hypnaceae** (Figure 130), **Orthotrichaceae** (Figure 99), and **Sematophyllaceae** (Figure 131) dominate the mosses. **Lepidoziaceae** (Figure 12), **Plagiochilaceae** (Figure 11), and **Frullaniaceae** (Figure 2, Figure 7-Figure 8), in addition to the species-rich **Lejeuneaceae** (Figure 6, Figure 15-Figure 16), are the predominant liverworts (Gradstein 1992). As will be discussed in another subchapter of this chapter, **epiphylls** (those algae, plants, and fungi living on leaves of other

plants) are common in the lowland and lower montane rainforests.

Figure 130. ***Mittenothamnium reptans***, in the family **Hypnaceae**, one of the dominant families from Guyana. Photo by Michael Lüth, with permission.

Montfoort and Ek (1990) have provided us with a detailed study in French Guiana (Figure 132), reporting 154 bryophyte species from only 28 mature trees (22 species) in a lowland rainforest by sampling from tree base to top of the canopy. Of these, 88 were liverworts, with 71 of these in the **Lejeuneaceae** (Figure 6, Figure 15-Figure 16).

Figure 131. ***Sematophyllum*** sp. (**Sematophyllaceae**), one of the families that dominates in tropical Guyana. Photo by Michael Lüth, with permission.

Figure 132. Cataratas de Kaieteur, Guiana. Photo through Creative Commons.

In Kartabo, Co-operative Republic of Guiana (Figure 132), Graham (1933) also found the most diverse family to be the leafy liverwort family **Lejeuneaceae** (Figure 6, Figure 15-Figure 16). The most abundant moss here, by far, is ***Rhaphidorrhynchium subsimplex*** (see Figure 133), a species that is likewise abundant in Trinidad. Gradstein and Ilkiu-Borges (2009) compiled a guide to the liverworts and hornworts of Central French Guiana, including descriptions of habitats, especially the lowland cloud forest. This guide included 175 species of liverworts and 2 of hornworts, with the **Lejeuneaceae** again being the most species rich with 117 species. This guide recognized new combinations, providing updated nomenclature.

Figure 133. ***Rhaphidorrhynchium callidum***; ***R. subsimplex*** is abundant in Kartabo in the Co-operative Republic of Guiana and in Trinidad. Photo by Juan Larrain, with permission.

In Moraballi Creek rainforest in the Co-operative Republic of Guyana (Figure 132), few species are very frequent (Richards 1954). ***Calymperes lonchophyllum*** (see Figure 134) and ***Octoblepharum albidum*** (Figure 135) occur in all synusiae (high canopy epiphytes, shade epiphytes, dead wood) except epiphyllous ones. Like most of the moist rainforests, the stream area is characterized by absence of ground-dwelling bryophytes, abundance of epiphyllous bryophytes, and dominance of the leafy liverwort family **Lejeuneaceae** (Figure 6, Figure 15-Figure 16).

Figure 134. ***Calymperes tenerum*** showing gemmae on leaf tips. ***Calymperes lonchophyllum*** is a frequent species, occurring in all synusiae except epiphylls at Moraballi Creek, Guyana. Photo by P. J. de Lange, through Creative Commons.

Figure 135. ***Octoblepharum albidum***, a frequent species occurring in all synusiae except epiphylls at Moraballi Creek, Guyana. Photo by Janice Glime.

The Chocó region (Figure 136) of Colombia has the highest precipitation level in the Neotropical rainforests (Frahm 2012) and one of the wettest rainforests in the world (Frahm 1994), with an annual rainfall up to 12,000 mm, in some places even up to 15,000 mm. As a result, the bryophyte flora differs from elsewhere and the mosses do not serve as adequate indicators of the vegetational zones. Rather, this location permits us to observe the effects of high humidity on bryophytes.

Figure 136. Everwet lowland rainforest of the Chocó, Pacific coast of Colombia. Photo by Jan-Peter Frahm, with permission.

Frahm (1994, 2012) worked on the moss flora of the Chocó region. Although it has a high level of endemism in flowering plants, birds, and butterflies, the moss flora was too poorly known to assess endemism. Frahm found 125 species of mosses on a transect from sea level to 1600 m elevation, using 10-hectare plots and different altitudes. In contrast, liverwort diversity in the same area was much higher, more than 200 species were reported, including 13 endemic taxa (Gradstein & Reiner-Drehwald 2017). In fact, Frahm (2012) found that mosses comprise only ~10% of the bryophyte cover, whereas elsewhere at the same elevational vegetation zone in the rainforest they comprise 40-50%. Gradstein (pers. comm.) commented that Frahm was able to finish his moss identifications quickly and get them published because there were rather few species only, whereas it took years to complete the many more liverwort identifications.

Some of the endemic liverworts of the Chocó region (Figure 136), such as ***Fulfordianthus pterobryoides*** (Figure 137), ***Luteolejeunea herzogii***, and ***Symbiezidium dentatum***, all members of **Lejeuneaceae** (Figure 6, Figure 15-Figure 16), are surprisingly common and widespread in the Chocó despite their absence elsewhere (Frahm 1994).

The higher liverwort diversity in the Chocó is probably due to the exceedingly high humidity in the area.

Figure 137. The endemic ***Fulfordianthus pterobryoides*** on a twig in Chocó, Colombia. Photo by Jan-Peter Frahm, with permission.

When Vital and Visnadi (1994) surveyed the bryophyte flora of the Rio Branco Municipality in Brazil, they found only 76 species of bryophytes; 66 of these were new records for the State of Acre and 2 were new records for Brazil. The only hornwort was ***Notothylas vitalii*** (Figure 138). We now know that there are at least 12 species of hornworts in Brazil (Felipe *et al*. 2016).

Figure 138. ***Notothylas*** sp.; ***N. vitalii*** was the only hornwort known to Vital and Visnadi from Rio Branco Municipality in Brazil in 1994. Photo by Blanka Aguero, with permission.

Costa (2003) studied the Amazonian rainforest bryophytes in Acre, Brazil. She revealed 514 species, with two field trips increasing the known bryoflora by 50%. She concluded that the diversity is still poorly known for the Brazilian Amazon.

In their study in the Chapada Diamantina region of Brazil, Valente *et al*. (2013) identified 400 bryophyte taxa, with the forests and **campos rupestres** (Figure 139; dry, rocky grasslands) accounting for 51% and 40%, respectively. The **caatinga** (Figure 140; shrub and thorn desert vegetation in interior northeastern Brazil) and **cerrado** (Figure 141; savanna) accounted for only 5% and 4%, respectively.

Figure 139. Campos Rupestres da Serra da Canastra, Brazil. Photo by Antonio José Maia Guimarães, through Creative Commons.

Figure 140. Caatinga – sertão nordestino, Brazil. Photo by Maria Hsu, through Creative Commons.

Figure 141. Cerrado, Campo Sujo, Brazil. Photo by Andreza Oliveira Borges, through Creative Commons.

Recent studies mostly support the earlier ones, but changes in nomenclature are reducing the numbers of endemic species. Costa and Peralta (2015) reported 1,524 species of bryophytes in Brazil, including 11 hornwort, 733 liverwort, and 880 moss species. As has been typical, the **Lejeuneaceae** (Figure 6, Figure 15-Figure 16) are the most abundant (285 species!). Following that record high are **Lepidoziaceae** (Figure 12) (48), **Frullaniaceae** (Figure 7-Figure 8) (37), **Ricciaceae** (Figure 52-Figure 53) (36), **Plagiochilaceae** (Figure 11) (27), **Radulaceae** (Figure 9-Figure 10) and **Metzgeriaceae** (Figure 13) (26 each), **Lophocoleaceae** (Figure 142) (18), **Aneuraceae** (Figure 14) (15), and **Calypogeiaceae** (Figure 143) (13). Surprisingly, **Sphagnaceae** (Figure 144) sets the record for mosses with 83 species, followed by **Fissidentaceae** (Figure 145) (65), **Pottiaceae** (Figure 146) (63), **Dicranaceae** (Figure 34, Figure 111) (54), **Bryaceae** (Figure 147) and **Sematophyllaceae** (Figure 131, Figure 184) (53 each), **Orthotrichaceae** (Figure 99) and **Pilotrichaceae** (Figure 148, Figure 182) (51 each), **Calymperaceae** (Figure 128, Figure 134) (48), and **Hypnaceae** (Figure 130) (28). Together, these account for 71% of the known bryophyte species in Brazil.

Figure 142. ***Lophocolea cf polychaeta*** (**Lophocoleaceae**) from the Neotropics; **Lophocoleaceae** is one of the common liverwort families in Brazil. Photo by Michael Lüth, with permission.

Figure 143. ***Calypogeia*** (**Calypogeiaceae**) from the Neotropics; **Calypogeiaceae** is one of the common liverwort families in Brazil. Photo by Michael Lüth, with permission.

Figure 144. ***Sphagnum cuspidatum*** (**Sphagnaceae**); **Sphagnaceae** is the moss common moss family in Brazil. Photo by Michael Lüth, with permission.

Figure 145. ***Fissidens asplenioides*** (**Fissidentaceae**) from the Neotropics; **Fissidentaceae** is one of the common moss families in Brazil. Photo by Michael Lüth, with permission.

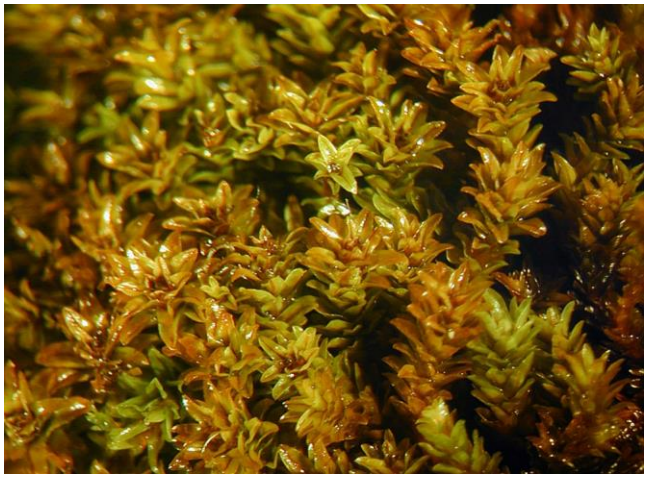

Figure 146. ***Leptodontium stellatifolium*** (**Pottiaceae**) from the Neotropics; **Pottiaceae** is one of the common moss families in Brazil. Photo by Michael Lüth, with permission.

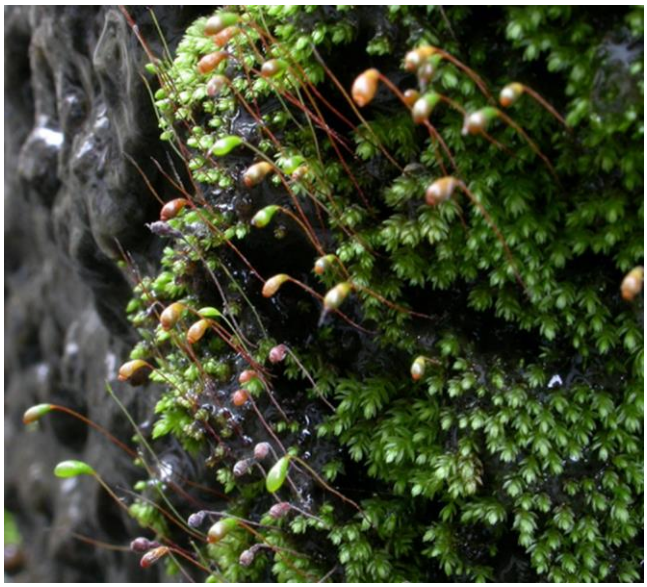

Figure 147. ***Bryum cellulare*** (**Bryaceae**); **Bryaceae** is one of the common moss families in Brazil. Photo by Li Zhang, with permission.

Figure 148. ***Crossomitrium patrisiae*** (**Pilotrichaceae**) from the Neotropics; **Pilotrichaceae** is one of the common moss families in Brazil. Photo by Michael Lüth, with permission.

Other new records include those of Oliveira and Alves (2007) for the State of Ceará, Brazil. Even at this recent date, 35 of the 81 species they identified were new for the state, and one was new for Brazil. In the Parque Ecológico de Gunma, Pará, Brazil, Fagundes *et al*. (2016) found 103 species, with the liverworts exhibiting the greater diversity (59). Of course the **Lejeuneaceae** again had the predominant representation of species (42). The rare species predominated with 62 species, whereas generalists were represented with only 47 species. Five new records were uncovered.

Oliveira and Bastos (2009) contributed to the knowledge of **Anthocerotophyta** and **Marchantiophyta** from Chapada da Ibiapaba, Ceará, Brazil. Of the 10 thallose liverwort species found, this study revealed 3 species of thallose liverworts for the first time in northeastern Brazil.

Florschütz-de Waard and Bekker (1987) compared the bryophyte flora in different forest types in West Suriname. They found the highest species richness in the marsh forest and the lowest in the savannah and **xeromorphic** (having structural adaptations to dry conditions) scrub forests. Based on their microclimatic data, they considered liverworts to have a greater ecological amplitude in these forests than that of mosses, a conclusion different from that in many ecosystems.

Although the Neotropics have not been studied to the degree of the temperate systems, most areas have had at least some studies. Spruce (1884-1885), Fulford (1963, 1966, 1968, 1976) and Gradstein (numerous papers, *e.g.* Liverwort Flora of Brazil by Gradstein & Costa 2003 and Liverwort Flora of French Guiana by Gradstein & Ilkiu-Borges 2009) studied liverworts. Very little work, however, has been done on the hornworts, a problem that Villarreal (2007) and others are attempting to rectify.

A number of additional general Neotropical floristic studies are available, but nomenclature should be reviewed to find more recent revisions: Delgadillo (1976) on bryophyte ecology in Veracruz, Mexico, Mägdefrau (1983 – forests and páramos of Venezuela and Colombia), van Reenen and Gradstein (1983, 1984), Timme (1985 – Peru), Buck & Thiers (1989), Gradstein *et al*. (1990 – Guianas, especially lowland forest), Richards (1991 – Co-operative Republic of Guiana and West Indies), Sastre de Jesus & Santiago-Valentín [1996 – Puerto Rico, managed forests of ***Cupressus*** (Figure 25) and ***Acacia*** (Figure 26)], Churchill (1996 – Andes), Gradstein (1998 – páramos), Benavides *et al*. (2006) in the Colombian Amazon, Gradstein *et al.* (2016) on bryophytes of Sierra Nevada de Santa Marta, Colombia among others.

More recently, Delgadillo-Moya *et al*. 2017) have studied mosses in the cloud forests of Veracruz, Mexico. They suggested that the terminology of **Humid Mountain Forest** provided the broadest conceptual and geographical term. Nevertheless, using the most restrictive definition of the cloud forest, they found 323 species and varieties through literature searches, field, and herbarium records.

A few have ventured into ecological studies such as the vegetative variability of liverworts as demonstrated by ***Bazzania*** (Figure 149) (Bernecker 1990) or the differences among physiognomies in species richness and distribution (Valente *et al*. 2013). Others have sought to make broader statements regarding the ecology and biogeography

(Gradstein & Pócs 1989). More recent studies, particularly on epiphytes, epiphylls, altitude, and rock outcrops, will be covered in more detail in subsequent subchapters of this chapter. These studies point to the need for more studies in order to gain a clear understanding of tropical bryophyte ecology.

Figure 149. ***Bazzania*** sp., a genus with vegetative variability from the Neotropics. Photo by Michael Lüth, with permission.

Endemism

Endemism (condition of species being unique to defined geographic location) has in the past been considered high in the tropics. In 1994 Delgadillo reported 48% endemism for mosses in the Neotropics. He suggested that endemism for mosses is higher in Bolivia, Costa Rica, and Ecuador than in other Neotropical areas. But he also considered that low numbers in some areas may be due to insufficient study. In others, low numbers result from strong connections with adjacent land masses having suitable habitat. I would also caution that high numbers may be the result of synonymy.

Frahm (2003) concluded that the rate of endemism is much higher in the tropics than outside the tropics but it is always much lower than that of tracheophytes (Table 2). Furthermore, we must consider these earlier numbers of endemics with skepticism. Throughout the tropics, many researchers worked independently of each other. They encountered bryophytes that were new to them and gave them new names. But researchers in other locations encountered these same bryophytes and gave them different names. There were no comprehensive keys to species from the tropics, and it was difficult to know that a species had already been named by someone else in a different location.

Schuster (1982) explained the high degree of endemism in the liverwort flora of Gondwanaland (Figure 150) as a result of the break up and dispersal of Gondwanaland. The resulting isolation permitted speciation that led to endemism. This was further enhanced by extinctions in the Antarctic, leaving behind an isolated flora in New Zealand. Schuster attributes the current degree of endemism seen in the Antipodes (Australia and New Zealand) to the climate changes and breakup of Gondwanaland.

Table 2. Percent of endemism in tracheophytes and bryophytes in tropical countries. From Frahm 2003.

	Tracheophytes	Bryophytes
Galapagos Islands	50%	10%
Cuba	50%	12%
Kilimanjaro		6%
Usambara Mtns.		3%
Réunion		9%
Mauritius		6%

Figure 150. Gondwana Box Log Falls; Gondwanaland has a high degree of liverwort endemism. Photo by Malcolm Jacobson, through Creative Commons.

In Australia (Figure 105), endemism in the Wet Tropics is among the highest in the country (Stevenson *et al*. 2012). That area likewise had the highest number of species. Areas having high numbers of species were not necessarily the areas with endemism.

Schuster (1982) contended that only two areas had high levels of endemic genera: Australasia and South America. India (Figure 151) has few endemic groups, most likely reflecting wide-spread extinction of cool-adapted taxa. By contrast, Schuster listed 39 genera and 11 subgenera of leafy liverworts that were endemic to tropical America. All but two of these endemic genera are in the families **Acrobolbaceae** (Figure 152), **Cephaloziellaceae** (Figure 151, Figure 155-Figure 156), **Gymnomitriaceae** (Figure 153), **Jungermanniaceae** (Figure 154), and **Plagiochilaceae** (Figure 11), or the very specialized **Lejeuneaceae** (Figure 6, Figure 15-Figure 16). (Note that family classification may be different now.) The endemic

species, furthermore, are usually highly specialized. One common feature of the liverwort genera ***Pteropsiella*** and ***Protocephalozia*** in the **Lepidoziaceae** (Figure 12) and ***Phycolepidozia*** (Figure 151, Figure 155-Figure 156) in the **Cephaloziellaceae** is that they develop either a thalloid or **confervoid** (loosely interwoven) gametophyte (Figure 156).

Figure 151. ***Phycolepidozia indica*** growing on rock in a forest fragment at Mt. Tandiandamol at 1600 m in the Western Ghats, India. Photo by Uwe Schwarz, courtesy of Robbert Gradstein.

Figure 152. ***Acrobolbus ciliatus***, in the **Acrobolbaceae**, a family with several endemic species in the Neotropics. Photo by Blanka Aguero, with permission.

Figure 153. ***Gymnomitrion concinnatum***, in the **Gymnomitriaceae**, a family with several endemic species in the Neotropics. Photo by Herman Schachner, through Creative Commons.

Figure 154. ***Jungermannia rubra*** with perianth, in the family **Jungermanniaceae**, a family with a number of Neotropical endemic species. Photo by Ken-ichi Ueda, through Creative Commons.

Figure 155. ***Phycolepidozia indica*** habitat in forest fragments on Mt Tandiandamol, Western Ghats, at 1600 m. Photo by Uwe Schwarz, courtesy of Robbert Gradstein.

Figure 156. ***Phycolepidozia indica***, a species that can develop either a thalloid or **confervoid** (loosely interwoven) gametophyte. Photo by Uwe Schwarz, courtesy of Robbert Gradstein.

In Australia (Figure 105), at least four endemic species of the moss ***Macromitrium*** (Figure 99) occur in higher elevation rainforests dominated by *Nothofagus moorei* (Figure 157; not tropical) (Ramsay *et al*. 1987). Of these, the tropical rainforests have three endemic ***Macromitrium*** species: ***M. erythrocomum*** (Figure 99), ***M. dielsii***, and ***M. funiforme*** (Andi Cairns, pers. comm. 7 October 2019).

Figure 157. *Nothofagus moorei* forest. Photo by David, through Creative Commons.

Karlin *et al*. (2012) used ***Sphagnum palustre*** (Figure 158) in Hawaii to explore the viability of a species from a single propagule. They concluded that this species currently has significant genetic diversity in Hawaii and that vegetative propagation does not preclude evolutionary success. This species is not known to produce sporophytes in Hawaii, although it does in other parts of the world (Figure 159).

Figure 158. ***Sphagnum palustre***, a species with significant genetic diversity in Hawaii. Photo by Bernd Haynold, through Creative Commons.

Figure 159. ***Sphagnum palustre*** with capsules in Sweden. Photo by Oskar Gran, through Creative Commons.

Africa

In sub-Saharan Africa (Figure 160), O'Shea (1997b) reported 77% of the 3,000 taxa to be endemic. However, he warned that this figure may be misleading because the bryophyte flora of Africa was (and still is) so poorly known (and many may turn out to be synonyms).

Figure 160. Sub-Saharan Ruwenzori moss. Photo by Albert Backer, through Creative Commons.

Pócs (1998) found a high species diversity (~700 species known in 1998) along the Eastern Arc Mountains of Africa (Kenya and Tanzania; Figure 161), with only 32 (4.5%) endemic species, a low number even when compared to that of tracheophytes in the area.

Figure 161. Usambara Mountains, Eastern Arc Mountains, Tanzania. Photo by Joachim Huber, through Creative Commons.

Asia

In 2003, O'Shea reported 11% bryophyte endemism in Sri Lanka. The bryophyte flora of Sri Lanka is relatively rich, with 561 taxa. In fact, Gunawardene *et al*. (2007) considered the Western Ghats and Sri Lanka to be biodiversity hotspots.

In the Azores (Figure 162), of the 89 epiphyllous bryophyte species, 14 were considered endemic to the Azores or to Macaronesia (Sjögren 1997). These are somewhat frequent members of the endemic epiphyllous (Figure 163) association, the ***Cololejeuneo-Colurion***: ***Cololejeuneetum azoricae*** (see Figure 44, Figure 163, Figure 164).

Figure 162. Island of Ponta Delgada, Azores. Photo by Laragheast, through public domain.

The Asian endemics of the **Ptychanthoideae** (Figure 38) in the **Lejeuneaceae** (Figure 6, Figure 15-Figure 16) tend to be restricted to subtropical and temperate regions, with the majority also known from Eocene fossils (Gradstein 1991). They are largely **relicts** (something that has survived from earlier period). The **Lejeuneoideae** (Figure 165-Figure 166) are mainly in the tropical rainforests of the Malesian archipelago, are frequently highly specialized, and have no fossil records.

Figure 163. ***Cololejeunea diaphana*** and ***Lejeunea floridana***, common epiphylls. Photo by Scott Zona, through Creative Commons.

Figure 164. ***Colura leratii*** in Fiji. Photo courtesy of Tamás Pócs.

Figure 165. ***Lejeunea flava*** (**Lejeuneoideae**) growing as an epiphyte. The **Lejeuneoideae** are common in tropical rainforests of the Malesian archipelago. Photo by Linda Phillips, through Creative Commons.

Figure 166. ***Lejeunea flava*** (**Lejeuneoideae**), growing as an epiphyll. Photo by Yang Jia-dong, through Creative Commons.

In 1987 Piippo *et al*. reported 48% endemism among the liverworts of New Guinea; 23% of the moss species seemed to be endemic. Most of these occur between 1500 and 3500 m elevation. The researchers found a high degree of endemism in the Frieda River Area and concluded that this is due to the high levels of metals in the area. The leafy liverworts ***Bazzania*** (Figure 149), ***Frullania*** (Figure 2, Figure 7-Figure 8), ***Plagiochila*** (Figure 11), and ***Radula*** (Figure 9-Figure 10) have a high degree of species endemism. The highest percentages of endemics among liverworts were in the **Plagiochilaceae** (Figure 11) (78%) and **Schistochilaceae** (Figure 167) (74%). Among the mosses, the number of species is much smaller, so the percentages may not be meaningful. The most notable may be the **Bryaceae** (Figure 168) with 35 species, 12 of which were considered endemic. The researchers cautioned that many of the families had not been studied well, so these numbers for both mosses and liverworts should be considered preliminary. All of these numbers will need revision after eliminating synonymy.

Figure 167. ***Schistochila*** sp., in the family **Schistochilaceae**, a family with many endemics in New Guinea. Photo by Li Zhang, with permission.

Figure 168. ***Bryum billardieri***; ***Bryum*** is a genus with 12 endemic species in New Guinea. Photo by Jan-Peter Frahm, with permission.

Piippo (1994a) reported 38.2% endemism in Western Melanesia among the 440 species there. The highest reported endemism occurs in **Frullaniaceae** (Figure 2, Figure 7-Figure 8) and **Plagiochilaceae** (Figure 11). Although this is a slightly more recent study, synonyms again create a problem in determining endemism.

Piippo (1994b) also studied the liverwort family **Lejeuneaceae** (Figure 6, Figure 15-Figure 16) of Western Melanesia and reported that only 20.5% of these species were endemic. She attributed this to the large number of epiphyllous species in the family, a group that is widespread throughout the tropics.

Australia

Ramsay *et al*. (1987) considered about 50-60 of the mosses to be endemic to the Wet Tropics bioregion in northeast Queensland (Ramsay & Cairns 2004). This number is most likely no longer accurate due to new discoveries and synonymy of old ones. One might expect a high number here; the next closest known population is 5400 km away (Figure 169) from the Australian populations (Meagher & Cairns 2016).

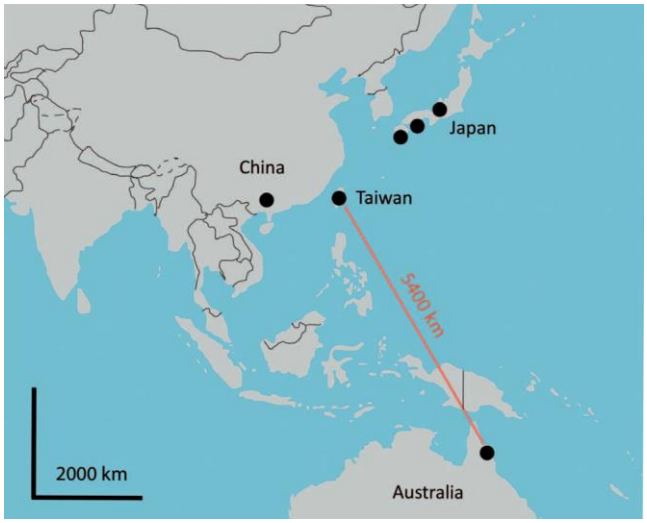

Figure 169. Australian tropical distance map. From Meagher & Cairns 2016.

In his report to the IUCN on areas and bryophytes to be protected, Streimann (2000) noted that "a reasonable number of endemics and restricted species are generally found in higher, more moist ranges in north Queensland." This area includes several high peaks with high levels of rainfall and cloud cover. Such endemics as ***Calyptrochaeta brassii*** (see Figure 78) (Streimann 2001) and ***Dicranoloma braunii*** (Figure 170) occur on Mt. Finnigan. On the Bellenden-Ker Range, ***Clastobryum dimorphum***, once considered an endemic to the Wet Tropics, has been reduced to a variety of the more widespread ***Clastobryum cuculligerum*** (see Figure 79), now as var. ***dimorphum*** (Cairns *et al*. 2019). ***Mniodendron comatulum*** (Figure 171; treated as ***Hypnodendron comatulum*** in TROPICOS) is another endemic to the Australian tropics. Because of many nomenclatural changes and synonymies, the number of endemics is most likely different from that suggested by Ramsay *et al*. (1987), and it is likely that more endemics will be discovered in the future in this relatively underexplored part of Australia.

Figure 170. ***Dicranoloma billarderii***, a species common in southern Australia; ***D. braunii*** is known only from Mt Finnigan in the Wet Tropics of Australia, but is widespread in continental SE Asia, Malesia and Oceania (Klazenga 2012). Photo by Niels Klazenga, with permission.

Figure 171. ***Mniodendron*** (syn.=***Hypnodendron***) ***comatulum***, endemic to the Australian Wet Tropics. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Neotropics

Holz and Gradstein (2005) found more endemics in the oak (***Quercus***) forests of Central America than in the páramo. They considered that the high percentages of endemic bryophytes in oak forests in Central America reflected the importance of climatic changes associated with Pleistocene glaciations. In an older publication, Delgadillo (1998) likewise reported a high endemic element, with *ca*. 47% endemics. At that time, he reported 2,900 species of mosses, a number that decreases when systematic studies uncover synonymy. He considered isolation as the major contributor to endemism.

Delgadillo *et al*. (2003) compared endemism in the mosses, grasses, and Asteraceae. Of the 2,373 endemic taxa known among these groups, 86 are mosses; 2030 are Asteraceae. In an earlier study, Delgadillo and Cárdenas (2002) reported no endemic taxa from the Monies Azules Biosphere Reserve, where they identified 136 species and varieties, plus 8 more from published records. In the Chiapas, Mexico, Delgadillo and Cárdenas (2002) found that endemic taxa are "virtually absent." Nevertheless, they considered the area to be unique in harboring life-forms and structural diversity of mosses that have been lost in other tropical areas of Mexico.

As suggested by earlier studies, when Delgadillo-Moya *et al*. reported on moss endemism in the entire Mexican flora, they were only able to verify 77 endemic species out of the nearly 1000 species. They identified three main areas of endemism in Mexico: lowland areas in various states, the mountain area along 19020ºN lat., and the highlands in Oaxaca and Chiapas. Their data suggest that the highest numbers of endemic species occur in the Trans-Mexican Volcanic Belt, Sierra Madre Oriental, Chihuahuan Desert, and Sierra Madre del Sur. Although many areas have not been explored, they do not anticipate many additions to the endemic list. It is likely that more species will reveal a wider distribution as other areas of the Neotropics are explored.

Fortunately, there are now good Neotropical bryologists who are increasing our knowledge of that bryoflora. Costa *et al*. (2015) examined the species richness and floristic composition on an elevation gradient in the Itatiaia National Park in Brazil. They reported 519 taxa, representing 10 elevations, using literature, herbarium samples, and data banks. These represented 34% of the total Brazilian bryoflora.

In southeastern Brazil, the endemic ***Bromeliophila natans*** (Figure 172) is difficult to distinguish from ***Lejeunea*** (Figure 173) (Gradstein 1997). It was so-named because it lives in the basins of bromeliads (Figure 174) (Heinrichs *et al*. 2014). The Neotropical moss ***Philophyllum tenuifolium*** (**Leucomiaceae**; Figure 175) is also restricted to this unusual habitat.

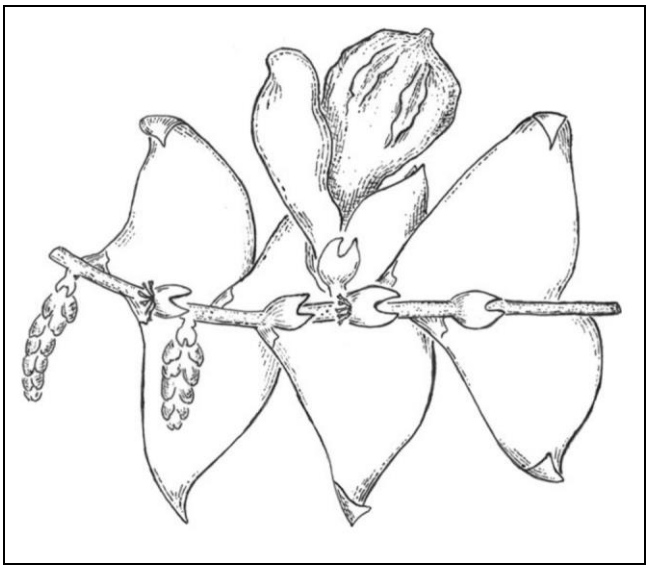

Figure 172. ***Bromeliophila natans***, an endemic species that lives in bromeliad basins. Drawing from Heinrichs *et al*. 2014, slightly modified, through Robbert Gradstein.

Figure 173. ***Lejeunea floridana*** and ***Cololejeunea cardiocarpa*** on leaves. Photo by Scott Zona, with permission.

Figure 174. Bromeliads in the trees, showing basins where bryophytes can grow. Photo by Gail Hampshire, through Creative Commons.

Figure 175. ***Philophyllum tenuifolium*** herbarium specimen. Photo from Natural History Museum, London, through Creative Commons.

It is interesting that ***Spruceanthus theobromae*** (Figure 176) is endemic to the ***Cacao*** (source of cocoa) plantations (Figure 177) of western Ecuador (Gradstein 1999). Kautz and Gradstein (2001) concluded that because of its host specificity on ***Cacao*** and its exclusive occurrence in plantations, it should be removed from the World Red List of Bryophytes and its status changed to that of a near threatened species. Its survival depends on the low management intensity of plantations such as those in western Ecuador.

Figure 176. ***Spruceanthus theobromae***, a species endemic to **Cacao** plantations in western Ecuador. Photo by Robbert Gradstein, with permission.

Figure 177. Cacao plantation in Cameroon. Photo by Barada-nikto, through Creative Commons.

Due to the efforts of a number of bryologists, the flora of Brazil is reasonably well known. Endemism in the Atlantic rainforest of Brazil reaches 242 endemic species out of the 1,337 species present (Costa & Peralta 2015). The dense **ombrophilous** (tolerant of wet conditions) forest here has 73% of these species represented, 62% of which are endemic. The southeastern region, with 1,228 species in total, has 219 endemic species. But the Atlantic rainforest in southeastern Brazil has most of the endangered species. Further monographic, worldwide or continent-wide studies may reduce the number of endemic species, but numbers are starting to approach reality.

Pócs (2019) recently reported a large number of liverworts new to Peru, two of which are endemic: ***Colura ochyrana*** (Figure 178) and ***Drepanolejeunea halinae*** (Figure 179), both restricted to the Andes.

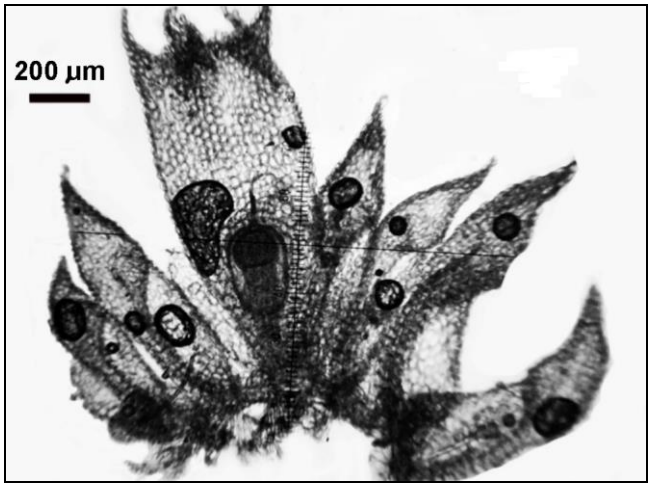

Figure 178. ***Colura ochyrana***, a new endemic species from the Peruvian Andes. Photo modified from Pócs (2019), with permission.

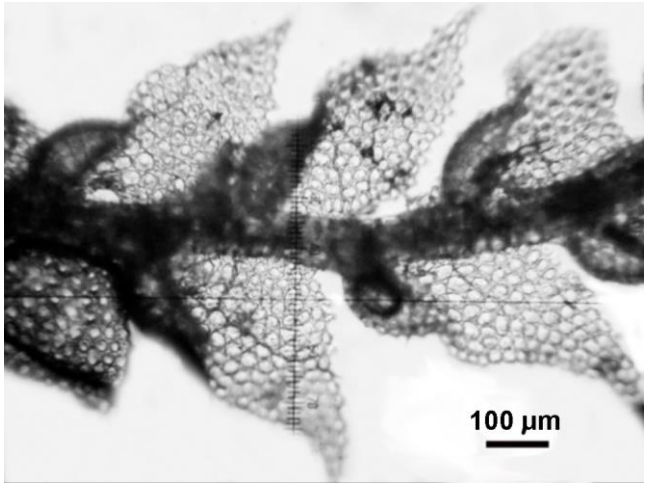

Figure 179. ***Drepanolejeunea halinae***, a new endemic species from the Peruvian Andes. Photo modified from Pócs (2019), with permission.

Visnadi (2015) likewise reported on the Atlantic Forest of southeastern Brail, at Mata Atlântica. This research revealed 199 species newly known for the area, bringing the total for the area to 220 species. This added two new records for Brazil and revealed locations of 13 Brazilian endemic species.

Causes of Endemism

Merckx *et al*. (2015) surmise that tropical mountains are diversity hot spots, but also exhibit a high degree of endemism. They point out that researchers have debated whether these mountain endemics originate more from local lowland taxa or from long-range dispersal from cool localities elsewhere. The latter could be similar to the separation of many frog species on different mountain tops, as discussed in the interaction chapter on amphibians in volume 2. This would presume that the species arrived, but was separated from interbreeding with the original species for a long enough period of time that a new species evolved. On the other hand, if the population originated from lower elevations, it might have become a new species through the **founder principle** (loss of genetic variation that occurs when new population is established by very small number of individuals from larger population), followed by natural selection for characters that suited their mountain habitat.

To try to answer this question, Merckx *et al*. (2015) examined the species on Mount Kinabalu, a 4,095 m high mountain in Sabah, East Malaysia. They found that most of the unique species of the mountain are younger than the mountain (6 million years). This mountain exhibits a mix of pre-adapted immigrant lineages and descendants from local lowland ancestors, suggesting that the species did not arrive by long distance. Nevertheless, substantial shifts from lower to higher vegetation zones in these lowland groups were rare. The presence of sibling pairs of ***Frullania*** (Figure 2, Figure 7-Figure 8) with each member of the pair at a different elevation range of the same mountain (Figure 180) would tend to support the latter (Glime *et al*. 1990). Is there any reason to think that both processes could not occur? Is one of them the dominant cause?

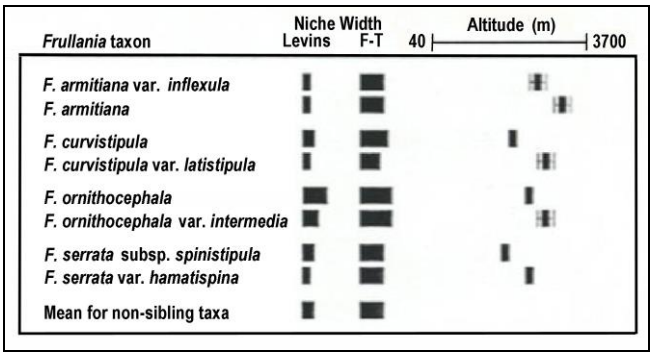

Figure 180. Levins and Freeman-Tukey niche width and elevational range of sibling pairs of ***Frullania*** on Mount Albert Edward, Papua New Guinea. Redrawn from Glime *et al*. 1990.

Patiño *et al*. (2014) attempted to explain the emergence of endemism by questioning why some genera diversify and others do not. Speciation on islands through gradual change from a founder population has been termed **anagenetic speciation**. They challenge this approach, saying that this process does not lead to "rapid and extensive speciation within lineages." Using surveys of the endemic bryophyte, fern, and seed plant floras of nine oceanic archipelagos, they showed that **anagenesis** (species formation without branching of evolutionary line of descent) was highest in bryophytes (73%), as measured by the proportion of genera with a single endemic species. Ferns had 65% and seed plants 55%. They concluded that "the dominance of anagenesis in island bryophytes and pteridophytes [ferns] is a result of a mixture of intrinsic factors, notably their strong preference for (sub)tropical forest environments, and extrinsic factors, including the long-term macro-ecological stability of these habitats and the associated strong phylogenetic niche conservatism of their floras."

Dangers to Endemics

Silva *et al*. (2014) raised concerns about conserving key species of bryophytes. They created potential distribution models for ten species that had been classified as bio-indicators of environmental quality and/or were endemic to the Atlantic Forest or to Brazil. Distributions of nine of the species could be explained by the Mean Diurnal Temperature Range. They raised concern that these species were not known in all the potentially suitable areas and that only 27% of the potentially suitable areas overlapped with Conservation Units. While these species were not specifically endemic, this approach could be used for determining the need for areas to protect endemic species.

Like Silva and coworkers (2014), Raxworthy *et al*. (2008) found that temperature was important in shifting altitudinal distributions of plants and animals, with increasing temperature likely to surpass a warming threshold for some species. Of three endemic species in the tropical montane of Madagascar, two could not be relocated after 10 years. In addition, out of nine species analyzed, seven species had shifted their distributions to higher elevational means. In the 10 years of study, the mean lower elevation limit had shifted upward 29-114 m.

Tropical Rainforests

Whitmore (1998) provided an introduction to the tropical rainforest. These forests are evergreen, and the precipitation occurs more or less equally throughout the year, exceeding *ca*. 2000 mm per year. Under the umbrella of **rainforests** (Figure 181), Frahm and Gradstein (1991) recognized elevational rainforest types (see Chapter 8-1). The elevations of the different types of rain forest are lower on islands than on the continent. In areas with prolonged dry periods (>3 months), these forests are replaced with deciduous forests, seasonal forests, and savannahs. These types of forests will be discussed more specifically in the subchapters on Altitude.

Figure 181. Hawaiian tropical rainforest. Photo from Photoeverywhere, through Creative Commons.

Early researchers in the tropics considered the tropics to be an "inexhaustible" source of new bryophyte species (Pócs 1982). Richards (1954) bemoaned the scantiness of studies on the species and their ecology in tropical rainforests.

As one moves from the temperate zone into the tropics, there will be an increase in members of the moss families **Calymperaceae** (Figure 128, Figure 134) and **Sematophyllaceae** (Figure 131, Figure 184), in particular, as well as **Fissidentaceae** (Figure 17, Figure 37), **Leucobryaceae** (including ***Octoblepharum***; Figure 112), **Pilotrichaceae** (Figure 182), and **Pterobryaceae** (Figure 183) (Pócs 1982). The **Calymperaceae** are distributed primarily in the humid lowland tropical and subtropical forests (Reese 1993). These primarily epiphytic taxa are usually dioicous but produce numerous gemmae at their leaf tips, facilitating short-distance dispersal (Gradstein & Pócs 1989). Whereas ***Calymperes*** (Figure 128) is restricted to the lowlands, another tropical member of **Calymperaceae**, ***Syrrhopodon*** (Figure 185), extends up to more than 2,000 m elevation. Both are primarily **corticolous** (growing on bark), but occur also on logs in the first stages of decomposition. In the **Sematophyllaceae**, ***Taxithelium planum*** (Figure 184) is abundant enough to be termed a weed in the lowland tropical forests of the Americas (Buck 1985; Churchill & Salazar Allen 2001).

Figure 182. ***Cyclodictyon*** sp., representing **Pilotrichaceae**, a family that increases in representation as one goes toward the tropics. Photo by Michael Lüth, with permission.

Figure 183. ***Pireella pohlii***, representing **Pterobryaceae**, a family that increases in numbers as one goes toward the tropics. Photo by Michael Lüth, with permission.

Figure 184. ***Taxithelium planum***, a common moss species in lowland Neotropical forests. Photo by Michael Lüth, with permission.

Figure 185. ***Syrrhopodon gaudichaudi*** from the Neotropics, where the genus is known up to 2000 m asl. Photo by Michael Lüth, with permission.

Ramsay *et al*. (1987) stressed the importance of learning the role of bryophytes in the rainforest ecosystem in order to encourage more study of rainforest bryophytes. Jordan *et al*. (1980) could only hypothesize on the role of epiphytes in scavenging nutrients and moderating the flux of nutrients in the throughfall. Since then, Nadkarni and her students have greatly increased our knowledge of the role of bryophytes in nutrient relationships in the tropics (see Nutrient Relations in Chapter 8-1 of this volume).

Elevation and waterways are major contributors in determining the flora. Dixon (1935) described that below the Borneo ridgetop, cushions of the moss family **Dicranaceae** (Figure 34, Figure 111) are relatively common on both the ground and on logs, but liverworts remain more abundant. Near the stream, the large, pendent moss ***Spiridens reinwardtii*** (Figure 83) might be found on tall tree ferns. Dixon also reported abundant ***Macromitrium ochraceum*** (Figure 99) under the thin cover of *Dacrydium* (Figure 186; Podocarpaceae) and *Leptospermum* (Figure 187; Myrtaceae).

Figure 186. ***Dacrydium cupressinum***; the genus ***Dacrydium*** provides cover for ***Macromitrium ochraceum*** near streams in Borneo. Photo by James Shook, through Creative Commons.

Figure 187. ***Leptospermum trinervium***, in the genus that provides cover for ***Macromitrium ochraceum*** near streams in Borneo. Photo by John Tann, through Creative Commons.

Several additional studies are helpful in understanding the rainforest bryophyte communities. Giesenhagen (1910) described moss species of the rainforest. Pócs (1987) reported the changes in the biomass and productivity of bryophytes in east African rainforests. Gradstein and Pócs (1989) discussed tropical rainforest ecosystems and biogeography. Equihua and Gradstein (1995) compared the bryophyte communities of a rainforest with those of an old field. A more recent comprehensive study is that of Gradstein and Sporn (2010) on land use gradients.

Pantropical Distributions

Although liverworts seem to reach particularly high diversity in the tropics, moss richness estimates, based on 86 taxonomic checklists, do not support the hypothesis of a richer moss flora in the tropics compared to that of other latitudes (Shaw *et al*. 2005). Nevertheless, the latitudinal gradient for just North, Central, and South America was significant. Molecular data suggest that the Southern Hemisphere exhibits a higher diversity than does the Northern Hemisphere. The tropics are intermediate. Furthermore, virtually all the moss lineages are represented in all three latitudinal zones. Hence, it should be no

surprise that mosses have travelled long distances and that many tropical mosses, particularly above the species level, are pantropical. This reasoning fits the Baas-Becking Hypothesis that everything is everywhere, a principle that seems to apply well to organism with small, resistant propagules such as spores (see Volume 2, Chapter 2-6; Pisa *et al*. 2013).

By examining tropical bryophyte communities in both Old World and New World tropics, Kürschner and Parolly (1999) could compare the differences. They concluded that although communities may be similar among the Americas, Africa, and Asia, there is not a **pantropical** (in tropics of both Eastern and Western Hemispheres) bryophyte flora. Could this be a result of too many bryologists giving different names to the same species in different places? In any case, there are clear similarities among the bryophyte communities of the three continents and a pantropical class of epiphyte communities can be recognized. Earlier, similarities and differences among the bryofloras of the tropical Americas, Africa, and Asia have been described by Theodor Herzog (1926) in his classical treatise *Geographie der Moose*. Recent studies such as that of Dauphin L. and Grayum (2005) support the relatively large number of pantropical species, with 16% of their 55 collected species of bryophytes from the dry lowland forests and moist montane forests of the Santa Elena Peninsula and Islas Murciélago, Guanacaste Province, Costa Rica, being pantropical.

While most of the species are not pantropical, many families and genera are, and certain general community characters are present. For example, Germano and Pôrto (2006) examined bryophytes in Pernambuco, Brazil (Figure 188), and found that the community distribution patterns and growth forms were similar to those of other humid tropical forests, but in Pernambuco the richness was somewhat less. In their study, the most diverse bryophyte flora was that of **corticolous** (living on bark) bryophytes (33% of species). **Epixylic** (growing on wood, *i.e.*, trunks without bark, mostly logs) bryophytes were next (23%). With this high diversity, it is somewhat surprising that communities share 75% of the species. Liverwort diversity is higher than that of mosses, with a ratio of 23:1 among the **epiphyllous** (living on leaves) and 2:1 among corticolous species. However, **terricolous** (living on ground) species exhibited a 1:3 ratio of liverworts to mosses. The researchers also found that epixylic species were not specific for degree of decomposition, nor did richness vary with degree of decomposition.

Figure 188. National Park of Catimbau, Pernambuco, Brazil. Photo by Guilherme Jófili, through Creative Commons.

The mangroves, in contrast to the high diversity in other parts of the Wet Tropics, have very little diversity, with only ***Calymperes*** (Figure 64-Figure 65) species present on the mangrove trees (Ramsay & Cairns 2004). The terrestrial ***Taxithelium leptosigmatum*** (Figure 66-Figure 67) forms extensive mats on mud and exposed mangrove roots, especially if there is a high input of fresh water.

Substrate Specificity

Usable substrates in the understory of mature lowland forests are somewhat limited. The forest floor is typically covered with leaf litter that buries bryophytes. Rock surfaces may be available, especially vertical surfaces, if there is sufficient light. The forest itself provides trunk, branches, and leaf surfaces as substrates. At higher elevations, the soil and rock surfaces provide suitable surfaces. Soil in disturbed areas and other areas with sufficient light provides an available substrate. Bien (1982) examined substrate specificity of the leafy liverworts in a rainforest in Costa Rica. A later subchapter will be devoted to the leaf as a substrate for epiphyllous liverworts.

In a study in the Ecological Reserve of Gurjaú, Pernambuco, Brazil, Germano and Pôrto (2005) found few species that have substrate specificity. Rather, they typically occurred on two or three types of substrates. Some, however, were exclusively **corticolous** (bark-dwelling): ***Archilejeunea fuscescens*** (see Figure 189), ***Cheilolejeunea rigidula*** (see Figure 190), ***Lejeunea monimiae*** (Figure 191), some species of ***Frullania*** (Figure 2, Figure 7-Figure 8), and additional members of the **Lejeuneaceae** (Figure 6, Figure 15-Figure 16, Figure 191-Figure 192). Few epiphyllous species were restricted to leaves, including several species of ***Cololejeunea*** (Figure 163) and ***Leptolejeunea elliptica*** (Figure 192). Only ***Neckeropsis disticha*** (Figure 193) was restricted to rocks (**rupicolous**). On the ground the typical bryophytes were **Fissidentaceae** (Figure 17, Figure 37), thallose liverworts, and the hornwort ***Notothylas vitalii*** (see Figure 194).

Figure 189. ***Archilejeunea olivacea***; ***Archilejeunea fuscescens*** is a species that grows exclusively on bark at Pernambuco, Brazil. Photo by John Braggins, through Creative Commons.

Figure 190. ***Cheilolejeunea imbricata***; ***Cheilolejeunea rigidula*** is a species that grows very commonly on bark at Pernambuco, Brazil. Photo by Yang Jia-dong, through Creative Commons.

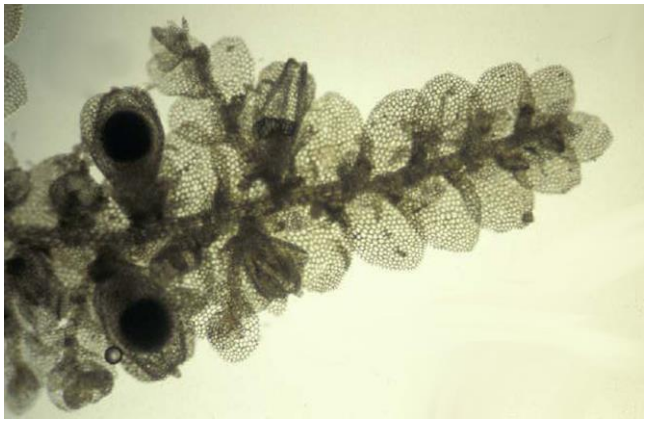

Figure 191. ***Lejeunea monimiae***, a species that is strictly corticolous in the Pernambuco study site in Brazil. Photo by Elena Reiner-Drehwald, with permission.

Figure 192. ***Leptolejeunea elliptica***, a species restricted to leaves at the Pernambuco study site in Brazil. Photo by Yang Jia-dong through Creative Commons.

Figure 193. ***Neckeropsis undulata***, a family (**Neckeraceae**) that indicates very shady, wet habitats in the tropics. Photo by Michael Lüth, with permission.

Figure 194. ***Notothylas javanica***; ***N. vitalii*** is a similar common hornwort on the ground in the Ecological Reserve of Gurjaú, Brazil. Photo by Li Zhang, with permission.

Forest Floor

The forest floor of the lowland rainforest is nearly devoid of bryophytes, suffering from the same leaf burial found in temperate deciduous forests (Richards 1954), but also suffering from the multi-layered canopy that blocks a large percentage of the sunlight.

But decaying logs, stumps, and branches here can host a number of taxa. It is here, in the low light and high humidity, that one finds ***Leucobryum*** (Figure 195) and mosses in the **Hookeriaceae** (Figure 182), **Hypnaceae** (Figure 130), and **Sematophyllaceae** (Figure 131, Figure 184) (Gradstein & Pócs 1989). Liverworts of the **Lepidoziaceae** and **Lophocoleaceae** (Figure 196), rather than the seemingly ever-present **Lejeuneaceae** (Figure 6, Figure 15-Figure 16, Figure 191-Figure 192), thrive here. Generally, only on road cuts, termite mounds, and other disturbed soil can one find bryophytes, including many ***Fissidens*** (Figure 17, Figure 37) species.

Figure 195. ***Leucobryum juniperoideum***; ***Leucobryum*** occurs on stumps, logs, and branches in the tropics. Photo by Hermann Schachner, through Creative Commons.

Figure 196. ***Leptoscyphus*** sp., a tropical representative of the **Lophocoleaceae**, where the family is common on logs. Photo by Paul Davison, with permission.

Rockhouses

Outside the tropics, **rockhouses** can mimic the conditions prevailing in some tropical habitats. These rockhouse cliffs, occurring as geologic formations in the eastern United States, are sufficiently deep holes among the rocks to buffer both temperature and moisture extremes. Added to this are very low light conditions, thus in several ways mimicking conditions deep under the tropical rainforest canopy. These caves house a group of endemic species whose closest relatives are tropical, as well as disjunct species with a primarily tropical range (Farrar 1998). Although the ferns are the most conspicuous of these plants, the bryophytes are the most numerous (Figure 197). Farrar suggests that their vegetative reproduction and adaptation to net photosynthetic gain in very low light makes their existence in these unusual habitats possible. Evidence of morphology, physiology, genetics, and geology suggest that they have persisted in these relict habitats since the pre-Pleistocene when the eastern U.S. experienced tropical and subtropical climates.

Figure 197. ***Trichomanes petersii*** and bryophytes. Rockhouses have collections of plants similar to these. Photo by Robbin Moran, with permission through Dale Vitt.

Summary

Although some bryophytes are pantropical or have disjunct distributions on both sides of the Atlantic, their specialized habitats often restrict their distributions. This is indicated by a higher **beta diversity** among than within tropical regions. Nonetheless, the greatest number of bryophyte species occurs in the tropics. But many publications represent synonyms and many areas remain to be explored. Furthermore, it appears that increase in species diversity from the poles to the equator does not apply to mosses.

Tropical liverwort families are dominated by **Lejeuneaceae**, **Frullaniaceae**, **Radulaceae**, **Plagiochilaceae**, and **Lepidoziaceae**, with lesser numbers in **Metzgeriaceae** and **Aneuraceae**. The moss ***Fissidens*** has ~90 species in Africa. In tropical Asia and Australia, common mosses include the large species in **Dawsoniaceae**, **Pterobryaceae**, **Ptychomniaceae**, and **Hypnodendraceae**. The liverwort family **Lejeuneaceae** is particularly species-rich in Asian tropics.

In the Australian Wet Tropics, moss species richness correlates strongly with patch area, mean annual rainfall, and tracheophyte species richness. The greatest species richness occurs in the rainforests of high mountain peaks and on the Atherton Tableland of the Wet Tropics bioregion. The tropical mangroves have little diversity, with only ***Calymperes*** species as epiphytes. Road cuts and downed forests permit the growth of such large mosses as those in **Polytrichaceae**. Several liverwort families are very species rich.

In the **Neotropics**, typical moss families are **Pilotrichaceae**, **Phyllogoniaceae**, **Lembophyllaceae**, **Dicranaceae**, **Octoblepharaceae**, and **Phyllodrepaniaceae**. Dominant liverwort families include **Monocleaceae** and **Lejeuneaceae**, with the subfamily **Ptychantheae** mainly in Asia and subfamily **Brachiolejeuneae** mainly in the Neotropics.

An inordinate number of endemic species has been reported from the tropics, but this number has been

steadily decreasing as synonyms are determined. Furthermore, the rate of bryophytic endemism is much lower than that of tracheophytes. O'Shea reported that 77% of the sub-Saharan bryophyte flora was endemic, but warned that this large number probably represented many synonyms. Some of the liverwort families in Asia reach such high numbers, but mostly the endemism reported there is notably lower. Records in the Neotropics are similar to those of Asia. Tropical mountains are often diversity hot spots, and distance from similar habitats can lead to endemism, but these also are a source of many synonyms. Nevertheless, differences in selection pressures with elevation can cause speciation. But endemic species, by their very nature of having a restricted distribution, increase their probability of extinction. Only 27% of the areas deemed suitable for them occur in protected areas. Much exploration is still needed in areas of little or no collecting, hinting at more new species and endemic species on the horizon. The Australian Wet Tropics are still underexplored. There is a greater chance for discovery of new endemic species there because of the distance from other tropical areas of the world.

The tropical rainforest provides a wide range of niches due to its multiple levels of vegetation heights. To the usual substrata of rocks, logs, trunks, and branches, the tree and shrub leaves add a highly diverse assemblage of liverworts. The soil, however, typically has too many leaves and not enough light penetration for bryophytes to survive. As one goes from the temperate zone to the tropics, the moss families **Calymperaceae**, **Sematophyllaceae**, **Fissidentaceae**, **Leucobryaceae/Octoblepharaceae**, **Pilotrichaceae**, and **Pterobryaceae** increase in representation. Liverworts are typically more species-rich than mosses.

In the eastern United States, **rockhouses** created on mountainsides and slopes provide a tempered environment where a number of tropical species are able to survive.

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CHAPTER 8-3
TROPICS: EPIPHYTE ECOLOGY, PART 1

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CHAPTER 8-3
TROPICS: EPIPHYTE ECOLOGY, PART 1

Figure 1. Celaque cloud forest in tropical Honduras. Photo by Josiah Townsend, with permission.

Barkman (1958) has contributed the definitive work on cryptogamic epiphytes (bryophytes, lichens) in 628 pages. It provides an account of the ecology and adaptations as they were known at the time and is the "bible" on cryptogamic epiphyte ecology. The work is restricted to temperate regions and does not treat tropical epiphytic bryophytes, which were very little known at the time. Nevertheless, much of the ecological information provided in this book is also valid for the tropics.

I was surprised to learn that approximately 10% of the tracheophytes are epiphytes (Prosperi & Michaloud 2001). It was not a surprise to learn that these are almost exclusively tropical, where they represent up to 25% of the tracheophytes. Overall, bryophytes comprised 40% of the epiphytic biomass in a neotropical cloud forest in Costa Rica (Nadkarni 1984) compared to 6% in the leeward cloud forest (Ingram & Nadkarni 1993). In both forests, bryophytes were most abundant among the smallest branches. The gnarled, windblown trees and the frequent mist in the elfin forest provide extremely favorable conditions for bryophytic growth (see Lawton & Dryer 1980).

The epiphytic habitat (Figure 1) is the most diverse one for tropical rainforest bryophytes, with 14 of the 15 main bryophyte families being predominantly epiphytic (Figure 1) (Gradstein & Pócs 1989). This is where the greatest bryophytic biomass of the rainforests occurs (Hofstede *et al*. 1993). Not surprisingly, the dry weight of epiphytes in the tropics is generally less than that shown in a New Zealand study (Hofstede *et al*. 2001), where lower temperatures and shorter dry periods are more favorable for bryophytes. In a New Zealand lowland, a single tree supported 61 tracheophyte species compared to 94 non-tracheophytes (lichens included). Pócs (1980) found a positive correlation between the amount of "surplus" rainfall (rainfall above 100 mm/month) and the epiphytic biomass in rainforest climates.

Among the early studies on bryophytic epiphytes, one must note the Japanese studies (Horikawa 1932, 1939, 1948, 1950; Kamimura 1939; Horikawa & Nakanishi 1954; Hattori & Noguchi 1954; Hattori & Kanno 1956; Hattori *et al*. 1956; Hattori 1966; Hattori & Iwatsuki 1970; Iwatsuki 1960, 1961, 1962, 1963a, b; Iwatsuki & Hattori 1955, 1956a, b, c, d, e, f, 1957, 1959a, b, 1965a, 1965b, 1966,

1968, 1970, 1987; Mizutani 1966). Hosokawa (1950, 1951, 1953, 1954) and coworkers (Hosokawa & Kubota 1957; Hosokawa & Odani 1957; Hosokawa & Omura 1959; Hosokawa *et al*. 1954, 1957, 1964) pioneered in describing epiphytic communities. Another important early study from Asia is the work by Tixier (1966) on epiphytic communities in Vietnam. Went (1940) discussed the sociology of tracheophytic epiphytes of Java.

Gradstein *et al*. (2007) compared the species richness on various substrates in southern Ecuador. This study demonstrated the preponderance of epiphytes there (Figure 2).

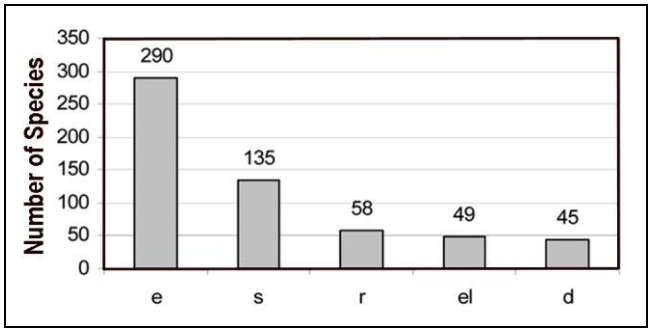

Figure 2. Substrate types of liverworts and hornworts at Reserva Biológica San Francisco, southern Ecuador. Number above each bar is number of species on that substrate type; e = epiphytic (bark); s = soil (incl. humus); r = rock; el = epiphyllous (living leaves); d = decaying wood. From Gradstein *et al*. 2007.

Frahm (1990a, 1994) found that in Borneo lowland and montane rainforests, even bark texture (smooth, fissured, flaky, or striped) made a difference in the epiphytic communities that developed. All bryophytes were considered to be acidophilic, with epiphytic bryophytes having no significant correlation with *p*H. On the other hand, rich concentrations of Na, K, and Mg seemed to be important in the substrate.

Akiyama *et al*. (2001) contributed to the knowledge of the Borneo bryophyte flora through two expeditions to the Kinabalu National Park in Malaysia. They reported 203 moss species and 31 liverwort species, with 25 species added to the checklist for the park and 17 new to Borneo.

Kürschner and Parolly (1998a) examined **pantropical** (tropical regions of both Eastern & Western Hemispheres) features that determined distribution of the epiphytic bryophytes. They found that distribution is correlated with structural parameters of the tree stands and with temperature zone intervals. Using only **supraspecific** taxa (*i.e.*, above the species level) they concluded that communities at low altitudes and those at high altitudes, respectively, resemble each other more pantropically than do lowland and montane communities on the same continent. Kürschner and coworkers were instrumental in elucidating epiphytic bryophyte communities in Africa (Kürschner 1995a, b).

Kürschner and Parolly (1999) sought to derive a consistent system for classifying the tropical epiphytes on a pantropical basis. Instead of using species, they used higher classification levels. For the lowland and submontane tropics they recognized the **Coeno-Ptychanthetalia** (Figure 3), whereas in the montane zones they recognized the **Coeno-Bazzanio-Herbertetalia** (Figure 4-Figure 5). Using this thinking, they found that the low-altitudinal and high-altitudinal communities are more silimar to each other pantropically than the communities of lowland and montane vegetation units occurring on the same continent.

Figure 3. ***Ptychanthus striatus***; the ***Pychanthalia*** synusia is typical in the lowland and submontane tropics, with pantropic distribution. Photo by Li Zhang, with permission.

Figure 4. ***Bazzania*** sp. from the Neotropics, a genus characteristic of the **Coeno-Bazzanio-Herbertetalia** in the montane zone. Photo by Michael Luth, with permission.

Figure 5. ***Herbertus aduncus***, in a genus characteristic of the **Coeno-Bazzanio-Herbertetalia** in the montane zone. Photo by Barry Stewart, with permission.

Much remains to be found among the tropical bryophytes. Lee and Pócs (2018) have recently added to our knowledge of the distribution of the large genus ***Lejeunea*** (Figure 6), describing the new species ***Lejeunea konratii*** from Fiji.

Figure 6. ***Lejeunea flava***; ***L. konratii*** was a new species in Java in 2018. Photo by Jia-dong Yang, through Creative Commons.

Some epiphytic bryophytes are **facultative**, growing on other types of substrate. Ando (1969) reported that the epiphytic bryophytes on ***Buxus microphylla*** var. ***insularis*** (=*B. sinica* var. *insularis*; Figure 7) also grew on limestone ridges in Taishaku.

Figure 7. ***Buxus microphylla***. Epiphytic mosses of this species also grow on limestone ridges. Photo by Sage Ross, through Creative Commons.

Frahm and Kürschner (1989) investigated factors related to bryophyte success on trees. Rhoades (1995) provided an extensive review on the nontracheophyte epiphytes of the canopy, including distribution, abundance, and ecological roles, but this paper mainly focuses on temperate forests.

Water Relations

The distribution of epiphytic bryophytes in the tropics seems to be all about water. The bryophytes in the crowns of the trees generally are more desiccation-resistant than are those at the tree base (Hosokawa & Kubota 1957; Hosokawa *et al*. 1964).

Water is always a primary limiting factor for epiphytes, and in the tropics the daily change from wet to dry can be particularly problematic (Johnson & Kokila 1970). For some species in the saturated rainforests, as little as 4 hours of exposure to a relative humidity of 63% or less can result in damage. Thus, such sensitive species often live on the wettest sides of the trees. Within a range of 10-76% humidity for four hours, two groups of mosses emerged. One group had low resistance, but the other had a high resistance to desiccation. This latter group of species grew in microhabitats of the forest with low humidity.

Löbs *et al*. (2019) opined that our understanding of the role of the extensive epiphytic bryophyte cover was largely unknown, noting their potential importance in biosphere-atmosphere exchange, climate processes, and nutrient cycling. Their water content could have important impact on local, regional, and even global biogeochemical processes. The researchers measured a vertical gradient from the Amazon Tall Tower Observatory in the Amazonian rainforest and determined that only minor variations occurred in the monthly average ambient light intensity above the canopy, but that different patterns emerged at different heights. At 1.5 m, the values were extremely low, exceeding 5 µmol m^{-2} photosynthetic photon flux density only 8% of the time. These values differed little throughout the year. The temperatures likewise showed only minor variation throughout the year, with larger values and more height dependence during the dry season. Water levels, on the other hand showed more variability. At higher levels they were affected by the frequency of wetting and drying; at low levels near the forest floor they retained water over a longer time period. They concluded that water content is the deciding factor for overall physiological activity, with light intensity determining whether net photosynthesis or dark respiration occurs. Temperature was of only minor importance. Light was limiting on the forest floor; in the canopy the bryophytes had to withstand a larger variation in microclimatic conditions.

Water Content

Klinge (1963) reported on the epiphyte humus from El Salvador. Their role in forest water and nutrient dynamics, however, seemed to attract little attention. Water content of bryophytic epiphytes in an old-growth forest in Costa Rican cloud forest reached maximum values of 418% of dry weight, with a minimum of 36% (Köhler *et al*. 2007). The epiphytic bryophytes experienced more dynamic wetting and drying cycles than did the canopy humus. The maximum water loss from bryophytes through evaporation was 251% (dry weight), whereas it was only 117% from the canopy humus, following three days of sunny weather with no intervening precipitation.

Pócs (1989) estimated that high altitude epiphytic bryophytes in Tanzania can absorb up to 30,000 L ha^{-1} of water during one rainstorm. When high humidity and high

temperatures occur at the same time, as they often do, they cause respiratory losses that cannot be balanced by photosynthesis in these C_3 plants, thus limiting their productivity, especially in the lowland forests (Richards 1984, Frahm 1990b).

Karger *et al*. (2012) measured the relationship of bryophyte cover to air humidity at two elevation ranges in the tropics. When the highland site (1800-3500 m asl) was considered separately from the lowland site (<1800 m asl) there was a significant relationship between bryophyte cover and relative air humidity. Temperature related to cover in the lowlands only. They confirmed that bryophyte cover is a good proxy for relative air humidity along the elevational gradient in the tropics, proposed earlier by van Reenen and Gradstein (1983).

Müller and Frahm (1998) compared the water-holding capacity of epiphytes in a montane rainforest in the Andes of Ecuador. They found an average of 0.57 L m-2 on the trunks, 19.51 L m-2 on branches, and 4.16 L m-2 on twigs. This is ten times the dry weight on branches, but only three times on twigs. Using a representative tree of 27 m height, which has an average of 65.4 kg dry weight of epiphytes, , they calculated that the epiphytic bryophytes on one such tree could store 669 liters of water.

Growth Forms and Life Forms

Several life forms and their role in water relations have already been discussed in an earlier chapter. For definitions, illustrations, and examples, see Chapter 4-5 in the Physiology volume.

Kürschner (1990) looked at the distribution of life forms and water-bearing and water-storing structures in epiphytic moss communities on Mt. Kinabalu, North Borneo. Norris (1990) concluded that water relations must be understood along at least four dimensions: hydration/dehydration frequency; duration of hydration; duration of dehydration; degree of water loss. More recent studies of xerophytic bryophytes suggest that the rate of drying is also important (Greenwood & Stark 2014). Norris further concluded that **large colonies** generally maintain hydration longer than do smaller colonies. Water can be conducted laterally among contiguous clones. Separated **tufts** and **cushions**, on the other hand, may store more water, but they contribute little to transfer of water over the surface of the host tree. In the tropical rainforests, the mass of the bryophytic epiphytes is typically larger than that found in temperate forests. The biomass is reduced as a result of disturbance, probably due to increased opportunity for desiccation with increased isolation and wind movement. This further results in the loss of water transfer and reduction in both water and mineral retention. Norris cited the ***Braunfelsia*** (moss; Figure 8) community in Papua New Guinea as an example of sensitivity to deforestation and resulting increase in dehydration frequency of adult plants.

Working in the tropical montane oak-bamboo forest of Costa Rica, Romero *et al*. (2006) conducted investigations on four **pendent** bryophyte species, listed from most protected to most exposed: ***Phyllogonium viscosum*** (Figure 9), ***Pilotrichella flexilis*** (Figure 10), ***Dendropogonella rufescens*** (Figure 11), and ***Frullania convoluta*** (Figure 12). They found that the most exposed species had higher light saturation and compensation points, higher dark respiration rates, more chlorophyll, higher chlorophyll *a*:*b* ratios, and higher N concentrations. Contrary to expectations, the most exposed species had the lowest water content at full saturation. Rate of water loss differed little among the species. The rather exposed moss ***Dendropogonella rufescens*** had a substantially higher moisture compensation point for carbon uptake than did the other three species. The researchers concluded that density, size, and arrangement of leaves, as well as clump architecture, defined the physiological patterns of water storage and transport they observed.

Figure 8. ***Braunfelsia dicranoides***. The ***Braunfelsia*** community is especially sensitive to deforestation in Papua New Guinea. Photo from the Natural History Museum, London, through Creative Commons.

Figure 9. ***Phyllogonium viscosum***, a **pendent** species requiring the most protected part of the tree in the tropical montane oak-bamboo forest of Costa Rica. Photo by Jan-Peter Frahm, with permission.

Figure 10. ***Pilotrichella flexilis nudiramulosaa***, a **pendent** species requiring a protected part of the tree in the tropical montane oak-bamboo forest of Costa Rica. Photo by Claudio Delgadillo Moya, with permission.

Figure 11. ***Dendropogonella*** sp.; ***D. rufescens*** has a substantially higher moisture compensation point for carbon uptake than the other three tropical species tested. Photo by Claudio Delgadillo Moya, with permission.

Kürschner and Parolly (1998b) discussed adaptations to water conduction and storing. The **mat** life form that is typical of lowland habitats correlates with such water-holding structures as leaf lobules (Figure 13) [especially **Lejeuneaceae** (Figure 6)] and water sacs as well as rhizoids that can act like sponges to hold and move water in capillary spaces. In addition to these, Frey *et al*. (1990) included **alar cells** (Figure 14), **vittae** (row of elongated cells down center of leaf, only one cell deep; Figure 15), and **ocelli** (darkened cells in row in leafy liverwort leaf; Figure 13, Figure 16) as characteristic of epiphytic bryophytes in the lowland forest of Mt. Kinabalu, North Borneo. Rhizoid discs (Figure 17) maintain attachment. In areas with high humidity in the montane belt, the **mat** form is replaced by **fan** (Figure 21), **weft**, and **pendant** (Figure 9-Figure 12, Figure 34-Figure 35) life forms that are able to obtain water from fog and mist (**fog-stripping**). Fine leaves (Figure 10) or deeply divided leaves are able to capture this water.

Figure 12. ***Frullania convoluta***, a **pendent** species requiring the least protection by the tree in the tropical montane oak-bamboo forest of Costa Rica. Photo by Jan-Peter Frahm, with permission.

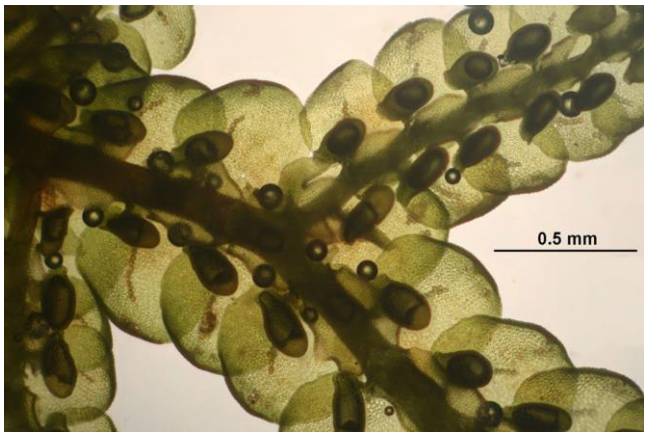

Figure 13. ***Frullania tamarisci*** with **ocelli** (dark lines of leaf cells) and leaf **lobules**. Photo by Hermann Schachner, through Creative Commons.

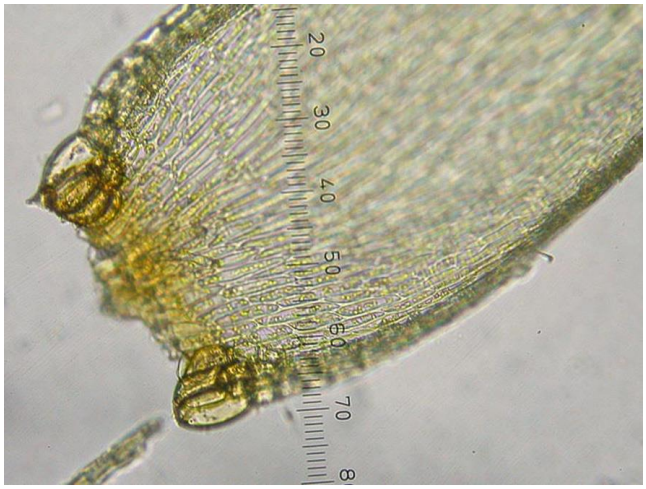

Figure 14. ***Pylaisiadelpha tenuirostris*** with inflated alar cells. Photo by Bob Klips, with permission.

Figure 15. ***Herbertus aduncus*** leaf vittae (note longer cells running down midleaf. Photo from Botany Website, UBC, with permission.

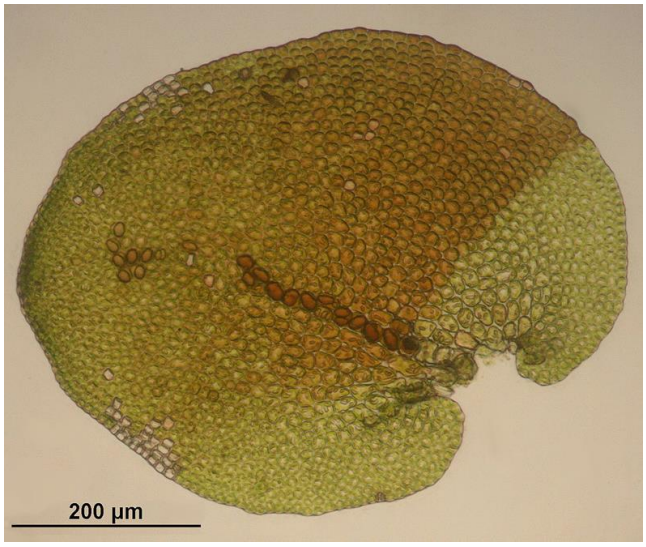

Figure 16. ***Frullania tamarisci*** with **ocelli** (row of brown cells). Photo by Hermann Schachner, through Creative Commons.

Figure 17. ***Frullania*** rhizoids. Photo courtesy of Andi Cairns.

Frey *et al*. (1990) suggested three principles of water conduction and storing mechanisms: draining surplus water, storing water in dry seasons, and condensing water vapor. They cited the "groovelike" arrangement of leaves as a mechanism to permit water support as well as drainage of water surplus. They found a significant correlation between water sacs (Figure 13), **mat** life form, and smooth bark in the epiphytic bryophyte communities of the lowland forest, facilitating water availability during short periods of dryness.

Parolly and Kürschner (2004) noted that the adaptive trends of functional types (life forms, life strategies, water conduction, and water storage) among the **oreal** (pertaining to mountains) trunk epiphytes at various elevations of southern Ecuador were distinct. They further concluded that these trends occur worldwide among tropical trunk epiphytes.

Kürschner (2003) conduted a phytosociological analysis on the epiphytic Afromontane bryophytes of southwestern Arabia. These epiphytes are affected by monsoons, but at the same time must be drought-tolerant. ***Orthotrichum diaphanum*** (Figure 18) and ***Syntrichia laevipila*** (Figure 19) provide "character species" that define alliances. As in other studies, life forms and life strategies correlate with the ecological site conditions. The ***Orthotricho*** (Figure 18) – ***Fabronietum socotranae*** (see Figure 20) is a drought-tolerant, light-tolerant, and xerophytic alliance. It is dominated by cushions, short turfs, and mats of perennial stayers that regularly produce sporophytes. In contrast, the alliance in the shaded, subhumid habitats are described as the ***Leptodonto*** (Figure 21) – ***Leucodontetum schweinfurthii*** (see Figure 22) association. This association is comprised of **tail** or **fan**-forming **pleurocarpous perennial shuttles** that have large spores. This life strategy adapts them for short-range dispersal and moderately limited reproduction, with large spores more likely to survive and germinate than would smaller ones. Furthermore, this more humid atmosphere supports a much higher diversity in life forms and life strategies.

Figure 18. ***Orthotrichum diaphanum***, member of a drought-tolerant, light-tolerant, and xerophytic alliance. Photo by Michael Lüth, with permission.

Figure 19. ***Syntrichia laevipila*** with capsules, a character species that defines an alliance of epiphytic Afromontane bryophytes in southwestern Arabia. Photo by Michael Luth, with permission.

Figure 20. ***Fabronia pusilla***; ***Fabronia*** forms a drought-tolerant, light-tolerant, and xerophytic epiphytic alliance with species of ***Orthotrichum*** in Afromontane regions of southwestern Arabia. Photo by Michael Luth, with permission.

Figure 21. ***Leptodon smithii***; ***Leptodon*** forms an epiphytic alliance with ***Leucodon schweinfurthii*** in the shaded, subhumid habitats of the Afromontane in southwestern Arabia. Note the **tail** or **fan**-forming **pleurocarpous** habit. Photo by Michael Luth, with permission.

Figure 22. ***Leucodon sciuroides***; ***Leucodon schweinfurthii*** forms an epiphytic alliance with ***Leptodon*** in the shaded, subhumid habitats of the Afromontane in southwestern Arabia. Photo from Elurikkus, through Creative Commons.

In a similar study on Socotra Island, Yemen, Kürschner (2004) described the epiphytic ***Lejeuneo rhodesiae*** (see Figure 23) – ***Sematophylletum socotrensis*** (see Figure 24) from the upper parts of Haghier Mountains. This association characterizes the evergreen Afromontane forests where heavy fogs and mists are typical. Kürschner identified three subassociations [*typicum*, ***Hyophiletosum involutae*** (drought-tolerant; Figure 25), and ***Papillarietosum croceae*** (shade-loving humid; Figure 26).

These subassociations are dependent on altitude, forest structure, life conditions, and humidity. Both the *typicum* and ***Hyophiletosum involutae*** subassociations are characterized by **perennial stayers** or **perennial shuttle** species that form **mats** and **short turfs**. They regularly produce sporophytes. The ***Papillarietosum croceae*** subassociation is likewise characterized by **perennial stayers** and **perennial shuttle** species that are **pendant** or **mat**-forming, but these have large spores with moderate-low reproductive rates. As seen in the more humid areas in the 2003 study, the ***Papillarietosum croceae*** subassociation has a much higher species richness with more diverse life forms and life strategies.

Figure 23. ***Lejeunea*** sp. growing as an epiphyll; ***L. rhodesiae*** forms an epiphytic alliance with ***Sematophyllum socotrense*** from the upper parts of Haghier Mountains, Yemen. Photo by Bramadi Arya, through Creative Commons.

Figure 24. ***Sematophyllum substrumulosum***; ***S. socotrense*** forms an epiphytic alliance with ***Lejeunea rhodesiae***. Photo by Johathan Sleath, with permission.

For a comparative discussion of life strategies in bryophytes as functional types, see Kürschner and Frey (2013). This treatise addresses vegetation types and their associated bryophyte life strategies for both temperate and tropical systems, based on more than 140 bryophyte communities and 1,300 taxa for corticolous, saxicolous, and terrestrial bryophytes. Sporn (2009) compared life forms of bryophytes in various height zones in the forests of Central Sulawesi, Indonesia (Figure 27).

Figure 25. ***Hyophila involuta***, in the drought-tolerant subassociation ***Hyophiletosum involutae***, drying. Photo by Bob Klips, with permission.

Figure 26. ***Papillaria crocea*** in cloud forest – a species that prefers humid shade, found in the ***Papillarietosum croceae*** subassociation. Photo by Peter Woodard through Creative Commons.

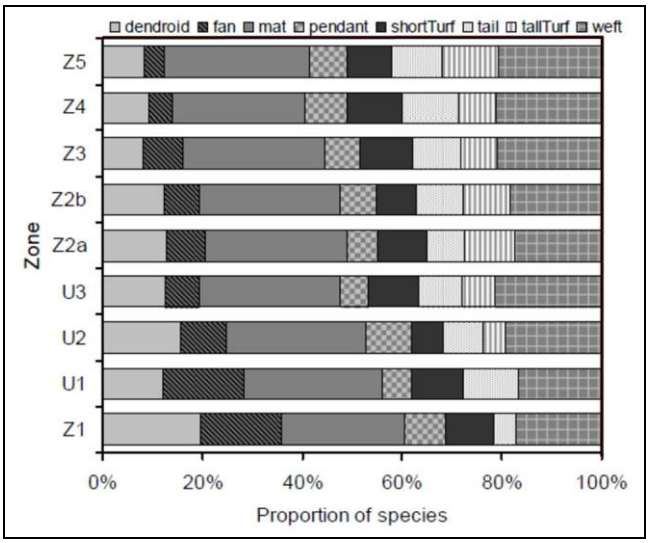

Figure 27. Comparison of eight life forms of bryophytes among five zones (Z1-Z5) of canopy trees and 3 zones of understory trees (U1-U3) in southwestern Nigeria. See Figure 28 for location of zones. From Sporn 2009.

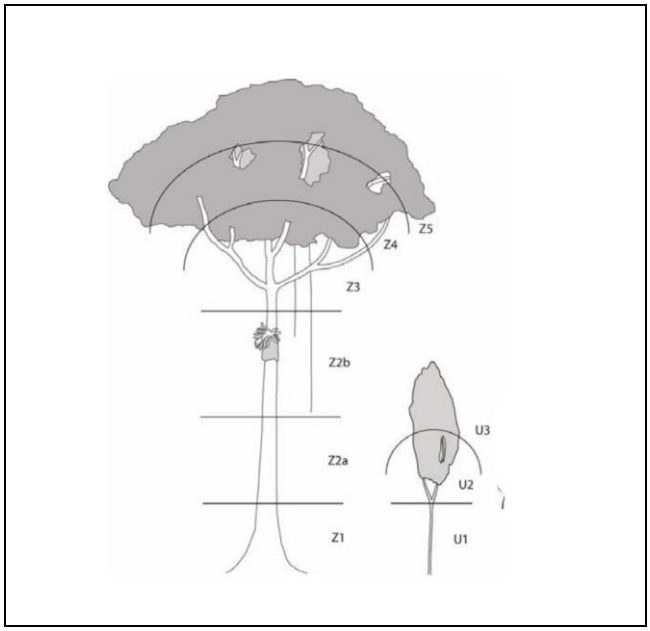

Figure 28. Epiphyte zones from Sporn 2009.

Osmotic Potential

Experimental studies on tropical bryophytes are still rare. However, several have looked at **osmotic potential**. This is the potential of water molecules to move from a **hypotonic** solution (more water, less solutes) to a **hypertonic** solution (less water, more solutes) across a semi permeable membrane. The osmotic potential becomes more negative as solutions become more concentrated.

Hosokawa and Kubota (1957) discussed the resistance to desiccation of epiphytic mosses from a beech forest in southwest Japan and related this to osmotic pressure. They found that the amount of time adult bryophytes could tolerate desiccation varied by species, but also by season of collection.

Akande (1984) looked at the use of **anhydrobiosis** (strategy that permits organisms to survive severe dry and/or extreme cold or hot conditions they often encounter) by corticolous tropical bryophytes as a means of surviving dry periods. Akande (1985b) also demonstrated the importance of **osmotic potential** (measure of tendency of solution with dissolved salts to withdraw water from pure water by osmosis, across differentially permeable membrane) as a factor in resistance to water stress in four Nigerian corticolous species. Using the mosses ***Stereophyllum nitens*** (see Figure 29-Figure 30) and ***Calymperes palisotii*** (Figure 31-Figure 32) and the leafy liverworts ***Spruceanthus floreus*** (syn. = ***Mastigolejeunea florea***; see Figure 33) and ***Frullania spongiosa*** (see Figure 12) he found that the osmotic potentials of the corticolous mosses are higher than those of the tested liverworts. These osmotic potentials increase from wet to dry season. ***Spruceanthus floreus*** is less desiccation tolerant than the two mosses, but all three of these taxa could survive desiccation of 0%, 32%, and 54% relative humidities for six months at room temperature.

Figure 29. ***Stereophyllum radiculosum.*** In Nigeria, ***Stereophyllum nitens*** is a moss in which osmotic potential increases from wet to dry season. Photo by Juan David Parra, through Creative Commons.

Figure 30. ***Stereophyllum nitens*** herbarium specimen. Photo from Natural History Museum, London, through Creative Commons.

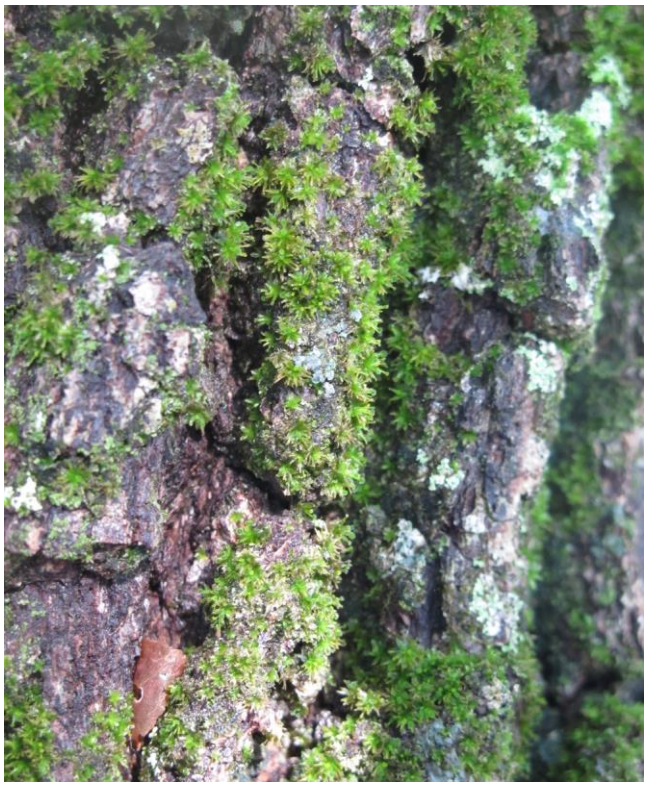

Figure 31. ***Calymperes palisotii*** on bark, a species with high osmotic potential. Photo by Scott Zona, through Creative Commons.

Figure 32. ***Calymperes palisotii***, a species with high osmotic potential. Photo by Scott Zona, through Creative Commons.

Figure 33. ***Spruceanthus planiusculus*** in a genus where some of the tropical African species are less desiccation tolerant than mosses. ***Sprutheanthus floreus*** has a demonstrated low osmotic potential. Photo by Claudine Ah-Peng, courtesy of Robbert Gradstein.

Proctor (2002) measured water relationships in two **pendent** mosses [***Pilotrichella ampullacea*** (Figure 34), ***Floribundaria floribunda*** (Figure 35)] in Uganda. The estimated osmotic potential at full turgor in ***P. ampullacea*** was -1.82 MPa and in ***F. floribunda*** it was -1.43 MPa. Based on the definition above, net diffusion of water occurs from regions of less negative potential to ones of more negative (or lower) potential. Hence, in this case, more water would move into ***P. ampullacea***. Both species are able to hold large quantities of external capillary water, up to *ca*. 12 in ***P. ampullacea*** and *ca*. 6 in ***F. floribunda***. ***Pilotrichella ampullacea*** has a very rapid initial recovery (30-60 minutes after 20 h air drying at -37 MPa), but as desiccation time increased from 20 hours to 12 days recovery became less complete and full recovery time was slower. This osmotic relationship is well suited to its humid tropical forest environment. ***Floribundaria floribunda*** requires more continuously moist conditions.

Figure 34. ***Pilotrichella ampullacea***, a species in Uganda that holds large quantities of external water. Photo by Jan-Peter Frahm, with permission.

Figure 35, ***Floribundaria floribunda***, a species in Uganda that holds large quantities of external water, but requires nearly continuously moist conditions. Photo through Creative Commons.

Desiccation Recovery

One advantage that bryophytes have following desiccation is that liverworts and some mosses recover their full photosynthetic capacity within hours of rehydration, whereas resurrectable ferns such as *Polypodium* (Figure 36) need at least a full day (Peterson *et al*. 1994). On the other hand, liverworts and most mosses lose water very quickly, whereas orchids, bromeliads, and other succulent tracheophytes lose water slowly. But some mosses also are able to retain their water for a longer time, as, for example, ***Leucobryum*** (Figure 37). ***Leucobryum*** has several adaptations that facilitate its water storage. It has a tight, compact cushion life form (Figure 37); its leaves are several cells thick (Figure 38); and it has **hyaline** (colorless – lacking chloroplasts; Figure 38) cells that permit water storage. Peterson and co-workers found that plants in the understory and gaps dried more slowly than did plants in their box treatment that simulated the canopy. Those in the gap dried slightly faster than did those in the understory.

Figure 36. ***Polypodium polypodioides***, a resurrection fern that requires a full day to recover from desiccation. Photo by Korall, through Creative Commons.

Figure 37. ***Leucobryum boninense***, showing the cushion life form. Photo by Tomio Yamaguchi, through Creative Commons.

Figure 38. ***Leucobryum glaucum*** leaf cs showing the outer hyaline cells surrounding the green chlorophyllous cells, typical of ***Leucobryum*** leaves. Photo by Walter Obermayer, with permission.

In French Guiana (Figure 39), 13 of 18 tested bryophyte species were able to maintain more than 75% of their photosynthetic capacity, as indicated by chlorophyll fluorescence, after 9 days of desiccation at 43% relative humidity (Pardow & Lakatos 2012). However, species from the understory required maintenance at 75% or higher relative humidity in order to recover. The researchers reactivated these bryophytes with water vapor only, a condition that is common in many tropical habitats, but which has been largely ignored in physiological ecology studies. The researchers concluded that tolerance to desiccation is of utmost importance as climatic changes occur (see also Wagner *et al.* 2013 and pertaining discussions in the subchapters on Tropics: Altitude).

Figure 39. French Guiana tropical forest. Photo by Cayambe, through Creative Commons.

Rainfall Interception

Frahm (2003a) compared the microhabitats of epiphytic bryophytes and lichens to determine why some trees were covered by lichens and others by bryophytes

(Figure 40) or others where lichens were in the crowns and bryophytes were on the trunks. Using humidity data loggers for one year, he used periods when the plants were wet and the relative humidity was at least 80%. He found that bryophytes typically thrive where there is a 20-30% longer duration of the wet period than where the lichens thrive. He cautioned that when doing pollution studies, such humidity differences should be considered.

Figure 40. Moss forest Mt. Ruwenzori Africa. Photo by G. Miehe, courtesy of Robbert Gradstein.

Pócs (1980) in the Uluguru Mountains, Tanzania (Figure 41), East Africa, examined the effect that epiphytic biomass (all kinds of epiphytes) had on the water balance of two rainforest types. With 2,130 kg ha^{-1} dry matter in the submontane rainforest, the rain interception capacity was approximately 15,000 L ha^{-1}. By contrast, the mossy **elfin forest** (cloud forest; Figure 42) at 2,120 m altitude had approximately 14,000 kg ha^{-1} with an interception capacity of 50,000 L ha^{-1} during a single rainfall. Aerial humus accounts for a large portion of the interception capacity of the elfin forest, with ca 4,700 kg ha^{-1} compared to ca 375 kg ha^{-1} in the submontane rainforest.

Figure 41. Uluguru Mountains, Tanzania. Photo by Aleksip, through Creative Commons.

Figure 42. Tanzania forest in fog. Photo by pxhere, through public domain.

Hölscher *et al*. (2004) examined the importance of epiphytes to rainfall interception in a tropical montane rainforest of Costa Rica. These canopy epiphyte masses are comprised mostly of mosses, liverworts, and lichens, all known for their ability to intercept rainfall. Biomass of all epiphytes was 1.9 t ha^{-1} dry weight in the studied 35-m-tall old-growth oak (*Quercus*) forest. The monthly moss water contents measured *in situ* ranged 24-406% of moss dry weight. This contrasts with sums of observed throughfall, stemflow, and interception measurements of 70, 2, and 28%, respectively, of the associated 2,150 mm of rain. Cloud water was not a factor in this ecosystem. This study suggested that mosses contributed only about 6% to the interception total, making the bryophytes much less important than in many rainforest ecosystems.

In central Veracruz, Mexico, Holwerda *et al*. (2010) assessed rainfall and cloud-water interception in a mature forest (Figure 43) and a 19-year-old secondary lower montane cloud forest. The researchers used separate calculations for events with rainfall only. They estimated cloud-water interception at 6% of dry-season rainfall (640 mm on average) for the secondary forest and 8% for the mature forest. On the other hand, annual values of cloudwater interception were less than 2% of the total rainfall (3,180 mm). The researchers considered the higher

loss in the mature forest to be the result of a higher canopy storage capacity, reflected in the greater tree leaf area and more epiphyte biomass.

Figure 43. Cloud forest, Bosque Comaltepec, Mexico. Photo by Prsjl, through Creative Commons.

In Colombia, Veneklaas and van Ek (1990) found that rainfall interception was 262 mm (12.4%) of the 2,115 mm of annual precipitation at 2,550 m elevation and 265 mm (18.3%) of the 1,453 mm precipitation at 3,370 m elevation. They found no evidence of fog precipitation. Most of this rainfall interception was accomplished by the epiphytic bryophytes. They attributed the higher rainfall retention at 3,370 m to differences in rainfall distribution and canopy storage capacities. They considered epiphytes to have an important role in this retention. The total epiphyte mass was approximately 12 **tonnes** (metric ton = 1,000 kg) dry weight per hectare, with most of it consisting of bryophytes and dead organic matter. In experiments, Veneklaas *et al*. (1990) found that epiphyte-covered branches were efficient in capturing rainfall. Most of this capture was accomplished by bryophytes. Release of this rainwater was very gradual, as was loss by evaporation.

In southeast Queensland, Ford (1994) found that epiphytes could absorb water 6-7 times their dry weight. This absorption affects stemflow and throughfall. The increased weight can cause outer, thin branches to break.

Other sources may prove helpful in understanding the water relations of tropical bryophytes. Pócs (1976) elaborated on the role of epiphytic bryophytes and other plants in the water balance of rainforests in the Uluguru Mountains, East Africa. Thompson *et al*. (1994) described the water-holding capacity of subtropical epiphytic bryophytes. Bergstrom and Tweedie (1995) described the hydrologic properties of epiphytic bryophytes. Kürschner and Parolly (1998b) described life forms and adaptations to water conduction and storage in North Peruvian epiphytic bryophytes. Other studies that pertain to rainfall interception are those of Kürschner & Parolly (2004) and Fleischbein *et al*. (2002).

Fog Interception

Some areas that receive little rainfall do experience fog on a regular basis (Lakatos *et al*. 2012). Fine wires and thin leaves are able to collect this fog water (Figure 44). Lakatos and coworkers measured dew formation on bark and lichens to be 0.29-0.69 mm d^{-1}. This water aids in cooling and provides enough moisture to prolong photosynthetic activity.

Figure 44. Spider web with fog drops; a similar appearance of water drops occurs on spider webs, fine wires, bryophyte leaf awns, and other thin structures in fog. For mosses, this is a source of water. Photo by Janice Glime.

Fog is able to provide sufficient water to many kinds of bryophytes in areas with low rainfall. Santon and Horn (2013) demonstrated this in lichens in a shrubland of northern Chile. They compared the ability to harvest fog water to the biomechanical mechanisms of filter-feeding aquatic invertebrates. Greater branchiness, as measured by fractal dimensionality, indicates greater fog-harvesting ability. Fractal dimension of the foliose and fruticose lichens increased significantly as fog availability increased.

Fog (Figure 45) is an important contributor to the cloud forest (elfin forest) (Camilo *et al*. 2008). The abundant epiphytes in these forests benefit from this fog input, especially during periods of lower rainfall. Camilo and coworkers suggested that it is especially important when wind speed is high and leaf water content has intermediate values, but that at both low and high leaf water content the interception of fog water is constrained.

Figure 45. Cloud forest showing fog, Ella, Sri Lanka. Photo by Kenny OMG, through Creative Commons.

In a subtropical montane forest in northern Taiwan, Chang *et al*. (2002) estimated fog deposition rate on epiphytic bryophytes by measuring the increase in plant weight when exposed to fog. Fog duration in this forest averaged 4.7 hours per day in summer months and 11.0 hours per day in other months. The maximum duration was 14.9 hours per day in November. The bryophytes experienced an average fog deposition rate of 0.63 g water g^{-1} dw h^{-1}.

Many bryophytes in the cloud forest and some tropical rainforests are **pendent** (Figure 34-Figure 35). Renner (1932) referred to these as dripping liquid water under various conditions in Javanese forests. León-Vargas *et al*. (2006) demonstrated the humidity stratification in the lowland Amazonian forest in upper Orioco (Figure 46). They found that all six species of **pendent** bryophytes in their Venezuelan cloud forests could survive at least a few days of desiccation. High humidities supported more recovery than low humidities. They considered droplets of cloudwater to be important sources of water for **pendant** and other bryophyte life forms, particularly during periods of low rainfall.

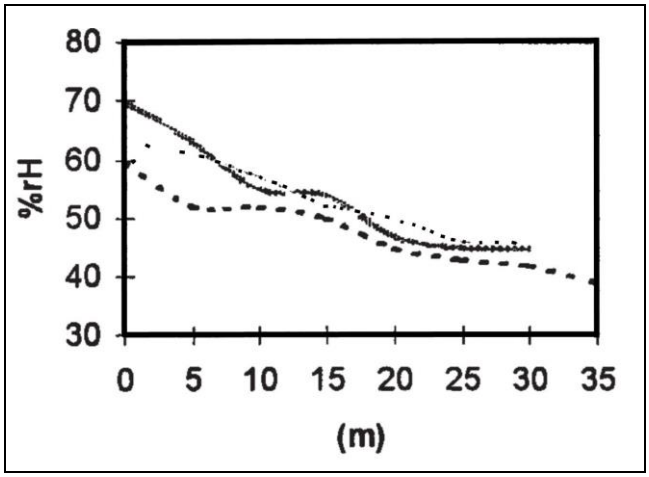

Figure 46. Relative humidity profile in meters above the ground in an Amazonian lowland forest of Surumoni, upper Orinoco. Modified from León-Vargas *et al*. 2006.

Pardow *et al*. (2012) described a recently discovered tropical lowland cloud forest type in the Guianas (Figure 47), originally discovered by Gradstein (2006) (see Gradstein *et al.* 2010; Obregón *et al*. 2011; Gehrig-Downie *et al.* 2013). This habitat is created by frequent early morning fog events in the valleys, providing suitable habitat for a richer epiphytic species diversity compared to the common lowland rainforest. In the French Guiana (Figure 39) they compared the distribution of functional groups of epiphytes by height zone in the lowland cloud forest and lowland rainforest. These forests differed in composition of epiphytes in the canopy, especially in the mid and outer canopy, with the cloud forest exhibiting both a higher biomass and cover of both bryophytes and tracheophytes. Furthermore, the cloud forest had a richer bryophyte life-form composition. The cloud forest frequently exhibited tails, wefts, and pendants, life-forms that were nearly absent in the canopies of the common rainforest.

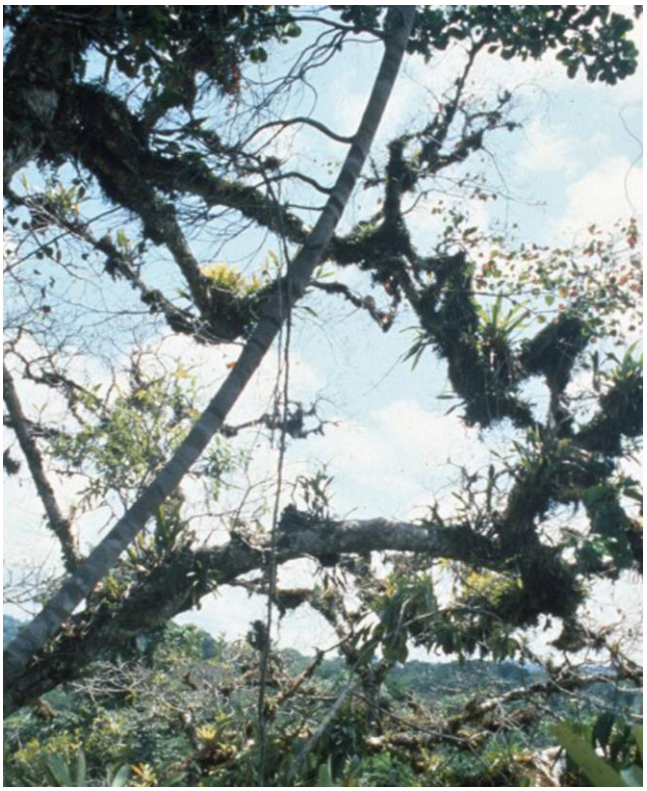

Figure 47. Canopy of a lowland cloud forest, French Guiana. Photo by Renske Ek, courtesy of Robbert Gradstein.

Microclimate

In any ecosystem, a diversity of microclimates can increase the diversity of species. These provide differences in substrate, temperature, light, and moisture availability. With their many layers of canopy, the tropical forests provide a wide range of microclimates and niches.

One might expect that gradients in light and humidity would affect species diversity and richness. In a Brazilian Atlantic Forest remnant, Silva and Pôrto (2013) found the highest diversity and richness in the trunk zone. But they found no significant difference of bryophyte total richness or diversity along edge distance or vertical zonation gradients. However, at the species level, they found that shade epiphytes decreased significantly along vertical gradients, while sun epiphytes increased. They concluded that the bryophyte distribution in the forest is more related

to the microenvironmental gradation than to such landscape characteristics as edge distance.

Early studies by Biebl (1964, 1967) attempted to relate success of the tropical species to water and temperature. Wolf (1993a) recognized that some species from the Colombian lower montane rainforest were able to occupy the more exposed habitats in the warmer lowland rainforest of Guyana where they could receive more radiant energy. Furthermore, the epiphytes in the northern Andes tropical montane rainforests were divided by height on the tree, occupying a gradation of microhabitats characterized by differences in moisture (Figure 46) and light (Figure 48).

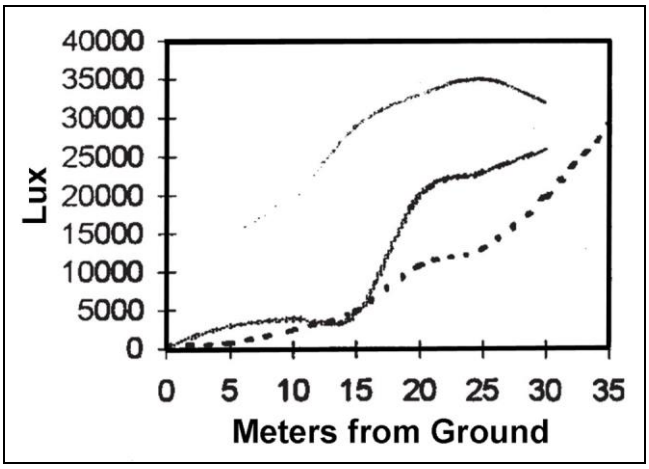

Figure 48. Light gradation from ground to canopy in an Amazonian lowland forest. Modified from León-Vargas 2001.

Temperature is one of the important aspects of microclimate. As noted by Wagner *et al*. (2013), bryophyte biomass and diversity both decrease dramatically as one goes from high to low altitudes in the tropics. They surmise that high respiration rates at high temperatures may at least in part explain this decrease. They transplanted two bryophyte species from 1,200 and 500 m asl to 500 m and sea level, respectively, in Panama and studied the short-term temperature acclimation of CO_2 exchange for 2.5 months. They also compared survival and growth for 21 months. Mortality was highest and growth lowest in transplanted samples, with no evidence of short-term acclimation.

Whereas the Wagner *et al.* (2013) study implies that temperature is important in altitudinal distribution of species, Wolf (1993c) suggests that it is a moisture gradient that accounts for epiphyte community differences in the northern Andes. Nevertheless, in a study in Panama, Zotz *et al*. (1997) found a strong diurnal variation in water content of tropical bryophytes in a lower montane rainforest. Both low and high water content limited carbon gain. More than half of the daily carbon gain was lost during the night as respiration, suggesting that temperature also was important.

Hosokawa and Odani (1957) tied the limits on the period of assimilation to the loss of carbon from respiration. They found that those species at the tree base (***Thuidium cymbifolium*** (Figure 49), ***Loeskeobryum cavifolium*** (Figure 50), ***Thamnobryum subseriatum*** (Figure 51), ***Homaliodendron scalpellifolium*** (Figure 52) had a minimum light requirement of 400 lux, whereas those species higher in the trunk had a higher **light compensation point** (light level at which photosynthetic gain = respiration loss on daily basis). On cloudy days, only the mosses at the tree base could reach their compensation point.

Figure 49. ***Thuidium cymbifolium*** with capsules, a tree base species with minimum light requirements. Photo by Li Zhang, with permission.

Figure 50. ***Loeskeobryum cavifolium***, a tree base species with minimum light requirements. Photo by Digital Museum Hiroshima, with permission.

Figure 51. ***Thamnobryum subseriatum***, a tree base species with minimum light requirements. Photo by Michael Luth, with permission.

Figure 52. ***Homaliodendron scalpellifolium***, a tree base species with minimum light requirements. Photo by Taiwan Biodiversity, through Creative Commons.

The CO_2 levels differ throughout the canopy. In a subalpine forest of Taiwan, higher CO_2 levels occur in the lower canopy (Kao *et al*. 2000). Low CO_2 levels can limit photosynthesis, but higher levels can help to compensate for limited light.

Cao *et al*. (2005) found a correlation between epiphylls and light, moisture, habitat, and disturbance due to human activities. They found that the number of epiphytes increased from the center of the city to the outer suburbs. In the city, 67.4% of the epiphytes had a Levin's niche width of less than 0.1.

Gehrig-Downie *et al*. (20110 found that the lowland cloud forest had significantly more epiphytic biomass than did the lowland rainforest without fog in French Guiana (Figure 39). The lowland cloud forest is characterized by the high air humidity and morning fog that characterize river valleys in hilly areas, explaining the higher epiphytic bryophyte biomass.

Some of our understanding of microhabitat differences can be derived from studies on the effects of disturbance. For example, Werner and Gradstein (2009) conducted the first study comparing tracheophytic epiphytes and bryophytes along a disturbance gradient in a dry forest. They compared various degrees of disturbance in closed-canopy mixed acacia forest (old secondary), pure acacia forest (old secondary), forest edge, young semi-closed secondary woodland, and isolated trees in grassland (Figure 53). They found that density of bryophytic epiphytes on 100 trees of ***Acacia macracantha*** (in northern Ecuador; Figure 54) was significantly lower in edge habitat and on isolated trees than in closed forest. Forest edge was more impoverished than semi-closed woodland and had similar floristic affinity to isolated trees and to closed forest types. The microhabitats among these habitat types varied, contributing to the diversity. As they pointed out, "Assemblages were significantly nested; habitat types with major disturbance held only subsets of the closed forest assemblages, indicating a gradual reduction in niche availability." They found no diversity effect from distance to the forest for epiphytes on isolated trees. Species density was closely correlated with crown closure. They concluded that microclimate, not dispersal constraints, determined most of the epiphyte assemblage. Their most important conclusion is that in these dry environments, tracheophytic epiphyte diversity is not affected by disturbance, whereas bryophyte diversity is clearly affected. They attribute this to the poikilohydric bryophyte condition that is more sensitive to changes in microclimate as compared to that of the homoiohydric tracheophytic epiphytes. The importance of microclimate for niche assembly of epiphytic bryophytes and absence of dispersal constraints is further supported by Oliveira *et al*. (2009) in the Guianas.

Figure 53. ***Acacia koaia***. Degree of disturbance affects density of bryophytic epiphytes in forests of ***Acacia macracantha***. Photo by Forest and Kim Starr, through Creative Commons.

Figure 54. ***Acacia macracantha***, an Ecuadorian species with lower density of bryophytes at forest edges and on isolated trees. Photo by Vladeq, through Creative Commons.

Oliveira (2018) noted that the major differences from base to outer canopy are those of relative abundance. She then tested character traits of 104 species of epiphytic **Lejeuneaceae** (Figure 6, Figure 23) in the Amazonian terra firme forests. She examined dispersal ability, dark pigmentation of leaves, ability to convolute leaves when

drying, possession of thickened cell walls, monoicous vs dioicous reproduction, and facultative epiphyllous habit. Four of these six traits proved useful in separating canopy and/or understory communities. Interestingly, high dispersal ability did not vary much along the height gradient. She further noted that asexual propagules were not over-represented in the dynamic environment of the canopy, seemingly challenging the bryophyte life strategy theory.

Oliveira (2018) found that facultative epiphylls were over-represented on the tree bases. Dark pigmentation and convolute leaves were significantly more common in the canopy and less common at the base. These two traits can protect against high light intensity and prolong periods of hydration, respectively. The paucity of these species at the bases of trees may be the result of high temperatures and low light, made lower by the pigmentation, while the prolonged hydration in these conditions would add to a high rate of respiration relative to photosynthesis.

Stuntz *et al*. (2002) noted that microclimate goes two directions. Bryophytes not only respond to the microclimate around them, but they can have a major impact on the microclimate of the forest around them. To put it in the descriptive wording of the researchers, they "air-condition the forest."

Although their study included only two orchids and a bromeliad, Stuntz *et al*. (2002) showed that the space around these epiphytes had significantly lower temperatures than did areas of the same tree with no epiphytes. Evapotranspiration was reduced almost 20% compared to microsites with no epiphytes. This study would suggest that the effect of bryophytes on the microclimate in tropical forests could likewise be significant.

Understanding of the microclimate is important in management strategies if one wants to protect the bryophytes (Sporn 2009; Sporn *et al*. 2009). These researchers sampled understory trees in a natural forest and in two types (natural shade trees and planted shade trees) of ***Theobroma cacao*** (cacao; Figure 55) agroforests in Central Sulawesi, Indonesia. The two agroforests had low air humidity and high afternoon temperatures. Although bryophyte species richness differed little among the habitats, the species composition was markedly different between the natural forest and the agroforests. These differences were most likely the result of microclimate differences.

Nutrient Dynamics

Akande *et al*. (1985a) found that the nutrients in the tested corticolous bryophytes increased from the dry season to the wet season. The nutrient fluctuations were more pronounced in mosses than in the liverworts tested. They concluded that bryophytes must be significant in the nutrient cycling of tropical ecosystems.

We are beginning to understand now how bryophytes play a major role in nutrient dynamics in the tropical forest. Their ability to sequester rain and fog water consequently means that they can sequester the nutrients dissolved in this water. When they dry out, damaged membranes release the nutrients, and the early stages of precipitation dissolve these released nutrients and carry them downward.

Figure 55. Cacao plantation in Sulawesi, showing trunk epiphytes. Photo courtesy of Robbert Gradstein.

Vitousek (1984) summarized known nutrient relationships in lowland tropical forests, based on published studies from 62 tropical forests. He found that these forests and higher nitrogen levels lower ratios of dry mass to nitrogen in the litterfall compared to that ratio in most temperate forests. Nevertheless, the nitrogen return is comparable to that of temperate forests. Phosphorus return is very low in many of these tropical forests, whereas calcium return is high. The phosphorus cycling seems to be very efficient.

Sometimes the nutrients in the host affect the colonization by epiphytes. Benner (2011) found that epiphytes in the unfertilized Hawaiian montane forests (Figure 56) colonized high-phosphorus (fertilized) host trees more frequently than they did unfertilized trees. Mosses were less responsive to the fertilization than the cyanolichens. The cyanolichens were good predictors of chlorolichen and bryophyte abundance at three out of four Kauai, Hawaii, sites, indicating high bark and leaf phosphorus. Benner and Vitousek (2007) found that after 15 years of P fertilization in the forest, there was a "dramatic increase" in both abundance and species richness of the canopy epiphytes. There was, on the other hand, no response to fertilization with nitrogen or other nutrients.

Figure 56. Spring rainforest stream with mosses, Hawaii. Photo by Jcklyn Baltazar, through Creative Commons.

Nadkarni (1983, 1986) noted the importance of epiphytes in making a significant contribution to the overall nutrient cycling in both temperate forests and tropical rainforests. In both forest types they absorb nutrients collected from the atmosphere during the dry season. The net release from branches with epiphytes during the wet season is greater than that from branches stripped of their epiphytes. Chang *et al*. (2002) measured ion input in a subtropical montane forest in Taiwan and found that more than 50% of the ecosystem input arrived in fog deposition, suggesting that fog is an important nutrient contributor in some tropical ecosystems.

Nadkarni *et al*. (2004) found that the primary forest canopy of a cloud forest in costa Rica had 63% of its organic matter as dead organic matter (DOM). Bryophytes comprised 12%. By contrast, the canopy organic matter of the secondary forest was 95% bryophytes, with only 3% DOM. Different locations within the primary canopy varied, with branch junctions having only dead organic matter and roots. Rather, bryophytes were the only organic matter at branch tips, subcanopy, and understory substrates. The trunks had diverse organic matter, but were dominated by tracheophytes and bryophytes; little dead organic matter was present. The secondary forest differed in having little difference in organic matter between trunks and branches. Canopy organic matter was high because of the strong presence of bryophytes. One surprise was that bryophytes were absent in branch junctions, although that is a likely place for them in other ecosystems. The researchers recommended transplant studies to try to determine the causes of the bryophyte distribution on the trees.

Rainfall vs Throughfall

Not all nutrients respond to their trip through the bryophyte sponges in the same way. Clark *et al*. (1998b) assessed net retention of ions by the canopy in a tropical montane forest, Monteverde, Costa Rica. They found that phosphate, potassium, calcium, and magnesium were leached from the canopy, but nitrogen compounds were retained.

Hölscher *et al*. (2003) determined that differences in the canopy structure of predominately ***Quercus copeyensis*** (Figure 57) forests and epiphyte (mosses, liverworts, and lichens) abundance in old growth vs two ages of secondary growth in Cordillera Talamanca, Costa Rica, resulted in large differences in the way nutrient transport was divided into stemflow and throughfall. Nevertheless, the nutrient transfers reaching the soil were similar. Significantly higher litterfall of non-tracheophyte epiphytes indicated the higher epiphyte load in the old-growth forest.

In seeming contrast to the findings of Clark *et al*. (1998b), in a Venezuelan rainforest with a low-nutrient forest floor, the fluxes in calcium, sulfur, and phosphorus in the rainfall were greater than those in the throughfall (Jordan *et al*. 1980). Other elements occasionally had greater fluxes in the rainfall than in throughfall. Jordan and coworkers suggested that the canopy epiphylls (algae, lichens) intercepted and modulated the nutrients, resulting in their conservation in the canopy. Phosphate, potassium, calcium, and magnesium were at sometime later leached from the canopy. Seasonal data suggest that biomass burning increased concentrations of NO_3^- and NH_4^+ in cloud water and precipitation at the end of the dry season. Regardless, a large majority of the inorganic N in atmospheric deposition was retained by the canopy at this site.

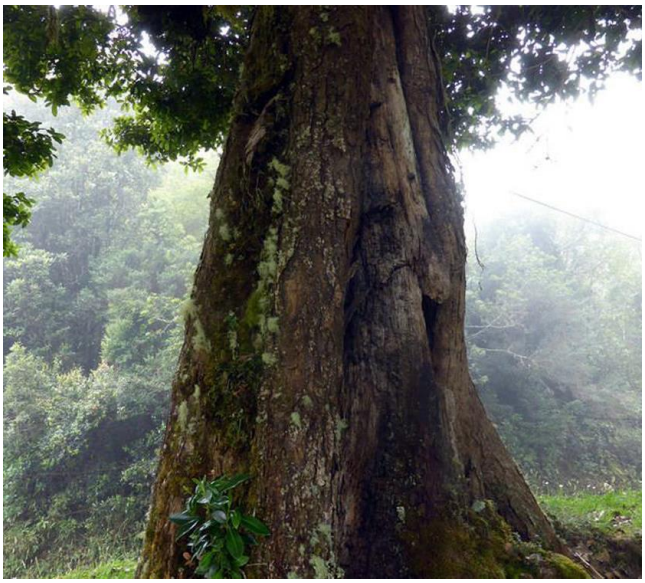

Figure 57. ***Quercus copeyensis*** with trunk epiphytes. Photo through Creative Commons.

To help us understand the effects the rainforest has on the nutrients, Wilcke *et al*. (2001) established five 20-m transects on the lower slope of a tropical lower montane rainforest in Ecuador. In the soil, they found the total Ca (6.3-19.3 mg kg^{-1}) and Mg concentrations (1.4-5.4) in the O horizon were significantly different between the transects. The throughfall ranged 43-91% of the rainfall; cloudwater inputs were less than 3.3 mm yr^{-1} except for one of the five transects where it was 203. Even the *p*H was affected by filtering through the canopy and associated epiphytes, increasing from a mean of 5.3 in the rainfall to 6.1-6.7 in the throughfall.

The leaves in this rainforest increase the element (Al, TOC, Ca, K, Mg) concentrations in the throughfall due to leaching from the leaves and washing off the dry deposition (TOC, Cu, Cl^-, $NH4^+$-N) (Wilcke *et al*. 2001). This could be an advantage for inner canopy bryophytes that receive these nutrients from the top of the canopy. Only Mn, Na, and Zn escape enhancement as a result of throughfall contacts. However, in high flow events, even Mn and Zn are elevated in the throughfall.

The nutrient input to forest bryophytes is higher at 2,250 m than at 3,370 m asl in two montane tropical rainforests of Colombia (Veneklaas 1990) attributed this to the greater precipitation volume at the lower altitude. The losses of nutrients from the canopy were likewise higher at 2,550 m. Veneklaas considered the differences between forests to be related to differences in precipitation, geographical situation, and soil nutrient availability.

Bryophytes can alter the nutrient dynamics of the forest in a variety of ways. They act as sponges, absorbing rainfall, and with it the nutrients carried by that rainwater. Epiphytes furthermore trap water and nutrients as they flow down branches and tree boles, retaining nutrients leached from bark, leaves, and other kinds of epiphytes or collected in their dust. They host a variety of nitrogen-fixing bacteria, most notably the **Cyanobacteria (**Figure 58**)**.

Figure 58. ***Scytonema***, a genus that performs nitrogen fixation in the phyllosphere. Photo by Yuuji Tsukii, with permission.

Nitrogen Dynamics

Bergstrom and Tweedie (1998) found that epiphytes were able to access at least three sources of nitrogen, including atmospheric, the phorophyte through decomposed litter, and a source of nitrogen fixation. The ^{15}N exhibited considerable spatial heterogeneity within the tree.

Clark and coworkers (Clark 1994; Clark *et al*. 2005) reminded us of the large role bryophytes can have in nitrogen dynamics of a tropical forest. The assemblages of epiphytic bryophytes, vascular epiphytes, litter, and associated humus harbor ~80% of the inorganic nitrogen retained in the canopy (Clark 1994). The forest canopies are able to trap and retain inorganic nitrogen from rainfall, dry deposition of gasses, vapors, and particles, and nitrogen previously trapped by clouds. Because they form much of the surface area in the canopy and lack a thick cuticle (many, perhaps all, bryophytes have a waxy cuticle, but it is very thin) and epidermis, they are able to trap and retain this nutrient much more effectively than the tree leaves. Clark and coworkers compared nitrogen retention of field samples of epiphytic bryophytes, epiphytic assemblages, epiphytic tracheophyte foliage, and host tree foliage to cloud water and precipitation in a tropical montane forest canopy in Costa Rica. They estimated, using models and field data, that epiphytic bryophytes and epiphyte assemblages retained 33-67% of the nitrogen deposited by cloud water and precipitation. The model predicted an annual retention of 50% of the inorganic nitrogen that arrived through atmospheric deposition. The bryophytes are important in the transformation of inorganic nitrogen such as nitrates to less mobile forms such as ammonia, but also deposit some of it in **recalcitrant** (unresponsive to treatment; resistant, *i.e.*, it doesn't break down easily, if at all) forms of biomass, litter, and humus.

The collected nitrogen that is added to the epiphytic biomass, litter, and canopy humus (Vance & Nadkarni 1990, 1992) is eventually added to the very large pool of nitrogen in the soil organic matter (Edwards & Grubb 1977; Grieve *et al.* 1990; Bruijnzeel & Proctor 1995). Clark *et al*. (1998b) found that the net nitrogen accumulation was ~8-13 kg ha^{-1}.

Cloud loadings can contribute to nutrient availability. Clark and Nadkarni (1992) experimented with excised epiphytes from Monteverde, Costa Rica, by subjecting them to NO_3^- loadings; from 0% to 90% of that NO_3^- is retained by the epiphytes. Ammonium (NH_4^+) is considerably more variable, ranging from a 200% loss to a 90% gain. These bryophytic epiphytes retain ca. 85% of the nitrate N from the atmospheric deposition to the canopy.

Wania *et al*. (2002) used ^{15}N levels to compare nitrogen in various positions within the forest canopy of a lowland rainforest in Costa Rica. The ^{15}N levels of canopy soils did not vary significantly, but the content in the epiphytes (including bryophytes) in different canopy layers did. The researchers concluded that epiphytes in different levels exhibited different ^{15}N during nitrogen acquisition.

Wanek and Pörtl (2008) examined nitrogen (NO_3^-, NH_4^+, and glycine) uptake in bryophytes of a lowland rainforest of Costa Rica. They found no significant differences between the epiphyllous and epiphytic bryophytes. The mean uptake rates for these bryophytes are 1.8 µmol g^{-1} dw h^{-1} for nitrate, 3.6 µmol g^{-1} dw h^{-1} for ammonium, and 3.4 µmol g^{-1} dw h^{-1} for glycine, suggesting that amino acids such as glycine significantly contribute to bryophyte nutrition in these epiphytes.

Most of the nitrogen fixation probably occurs on leaves with epiphylls. In any case, it is an important contributor to the tropical forest nitrogen dynamics. Matzek and Vitousek (2002) found that the total nitrogen fixation in a Hawaiian montane rainforest (Figure 59) was highest in sites having low N:P ratios in the leaves and stemwood. They suggested that epiphytic bryophytes and lichens depend on canopy leachate for their mineral nutrients, but the heterotrophic nitrogen fixation is controlled by the nutrient supply in the decomposing substrate. Differences in substrate cover had a larger effect on total N input from fixation than did fixation rates, a conclusion consistent with the low fixation rates observed in young forests. Nitrogen fixation in the **phyllosphere** (space surrounding a leaf) will be discussed under epiphylls.

Figure 59. Hawaiian tropical wet montane forest. Photo by Djzanni, through Creative Commons.

In 1998, Clark *et al*. (1998a) used epiphytic bryophyte samples in enclosures to estimate rates of growth, net production, and nitrogen (N) accumulation by shoots in the canopy in a tropical montane forest in Monteverde, Costa Rica. They also used litterbags to estimate rates of decomposition and N dynamics of epiphytic bryophyte litter in the canopy and on the forest floor. They estimated N accumulation at 1.8-3.0 g N m^{-2} yr^{-1}. The cumulative mass loss from litterbags in the canopy after one year was 17±2% (mean ± 1 SE) and after two years 19±2 % of initial sample mass. Mass loss from litter in litterbags after one year on the forest floor was 29±2%, and from green shoots 45±3%. On the forest floor, ca 47% of the initial N mass was lost within the first three months. The N that remained in the litter was apparently **recalcitrant** (resistant to microbial decomposition), although there was no evidence for net immobilization by either litter or green shoots. The annual net accumulation of N by epiphytic bryophytes was ca 0.8-1.3 g N m^{-2} yr^{-1}.

Akande and coworkers (Akande 1985a; Akande *et al*. 1985) concluded that the role of bryophytes in nutrient cycling of African tropics is significant and requires study. Nutrient contents of bryophytes fluctuate with season, and in three forests at Ibidan, Nigeria, the highest mean monthly nutrient composition of the bryophytes is in June to July, with the lowest in November to January. Magnesium is an exception, reaching its peak in October when the other nutrients are diminishing. There are considerable differences between species, although the phenological patterns are very similar, with mosses accumulating more than liverworts. Relationships of bryophyte concentrations to those of bark suggest that the bryophyte obtains its nutrients from stemflow containing leachates not only from the canopy leaves, branches, and canopy dust, but also from the bark, and that bryophytes do not get nutrients directly from the bark, but rather get them only from those leached out by rain. Akande *et al*. concluded that the predominant source of these nutrients was from dust and other pollutants such as smoke and sulfur dioxide.

Base cation and fluxes increase in throughfall, but NH_4^+-N and NO_3^--N decrease relative to that in rainfall in a subtropical montane moist forest in Yunnan, southwest China (Liu *et al*. 2002). The throughfall inputs of N, P, Ca, and S come primarily from precipitation, whereas most of the potassium and 2/3 of the magnesium in throughfall come from canopy leaching. The cycling rates for mineral elements are generally low compared to other tropical forests. Epiphytes are abundant on the bole and affect the chemical composition of the stemflow through selective uptake or release of elements. The total N, NH_4^+-N, Mg, Na, and SO_4^{2-}-S are enhanced, while NO_3^--N, K, P, and Ca are depleted in stemflow. Nitrogen from nitrogen-fixing organisms is low, most likely due to constraints by low temperatures.

In a study in the subtropical forest of northeastern Taiwan (Figure 60), Hsu *et al*. (2002) noted that nutrients in epiphytes and tree foliage are more readily available than those in the woody parts of the tree, making the tiny bryophytes proportionally more important than their size would suggest.

Figure 60. Taiwan blue magpie in subtropical rainforest of Taiwan. Photo by Gulumeemee, through Creative Commons.

Pulse Release

One mechanism by which the bryophytes help the forest floor plants is through pulse release of nutrients. This burst of nutrients occurs when dry bryophytes with damaged membranes first get water that wets them. This pulse is especially important for nutrients that are typically held in nutrient pools within the cells. The damaged membranes resulting from drying permits the rain to leach these nutrients from their otherwise safe interior locations. Coxson (1991) estimated the efflux of these solutes from stem segments of canopy bryophytes in tropical montane rainforest in Gaudeloupe (Figure 61). These reached 80.1 kg ha^{-1} yr^{-1} for potassium, 1.4 kg ha^{-1} yr^{-1} for phosphorus, and 11.8 kg ha^{-1} yr^{-1} for nitrogen in these rewetting episodes. On the other hand, estimates using intact bryophyte mats during natural field rewetting episodes were smaller, causing release of 28.7 kg ha^{-1} yr^{-1} for potassium and 0.2 kg ha^{-1} yr^{-1} for phosphorus. The lower numbers most likely result from internal recycling of released ions within the bryophyte mats.

Within the cloud forest canopy, and most likely elsewhere in the tropics, bryophytes accumulate considerable quantities of sugars (Coxson *et al*. 1992). In Guadeloupe, French West Indies (Figure 61), more than 950 kg ha^{-1} of sugars and polyols are released by epiphytic bryophytes per year as a result of wetting and drying cycles. The sugars come as a pulse during re-wetting, contributing to growth of the microbial flora both within and beneath the canopy. These sugars and polyols account for 17% of the dry weight of the upper canopy liverwort ***Frullania atrata*** (Figure 62), while providing less than 6% of the dry weight of the lower canopy moss ***Phyllogonium fulgens*** (Figure 63). (The name ***Frullania atrata*** may be incorrect as many species have incorrectly been identified as this one.)

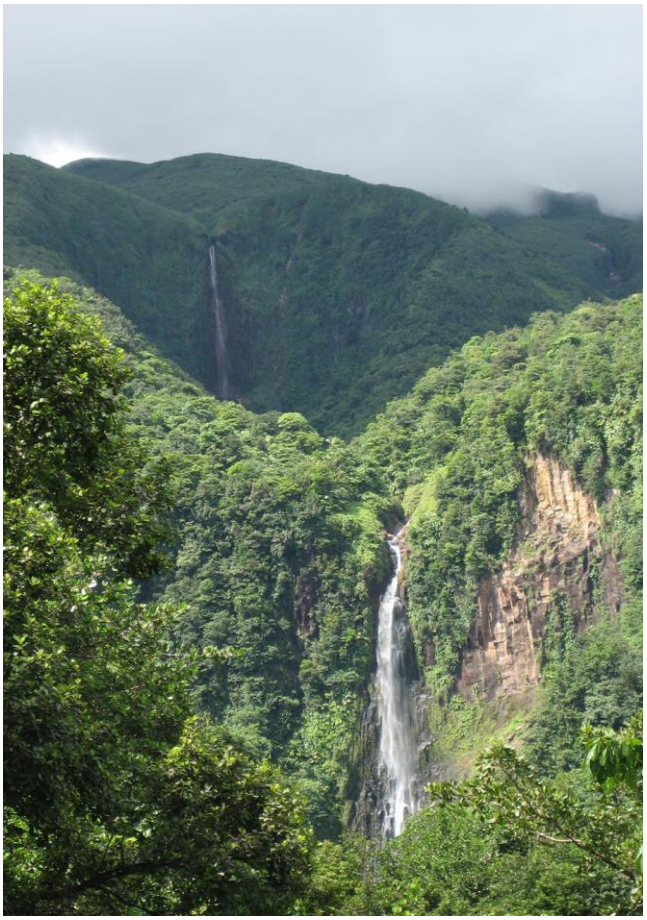

Figure 61. Montane rainforest, Guadeloupe. Photo by Bobyfume, through Creative Commons.

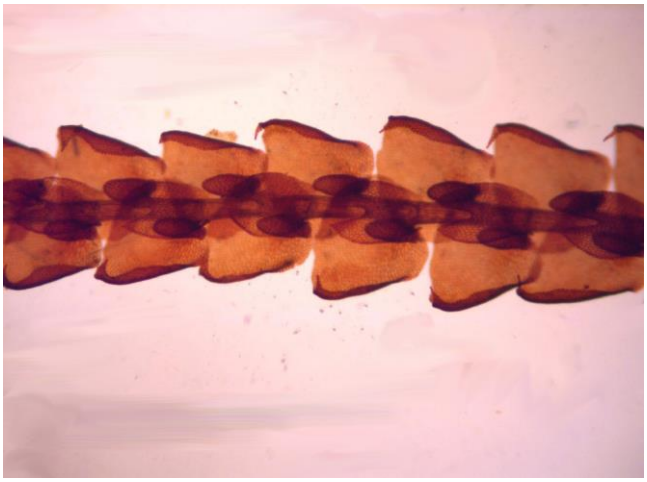

Figure 62. ***Frullania atrata***, an upper canopy liverwort. Photo by Juan Larrain, with permission.

Keystone Resource

Nadkarni (1994a) attributed to the canopy epiphytes the role of **keystone** resource in the nutrient cycling of tropical forest ecosystems. That is, this is a resource that is critical to the structure and function of the ecosystem, without which the system would cease to function as it does. The epiphytic bryophytes may have a key role in the nutrient dynamics of these forests.

Figure 63. ***Phyllogonium fulgens***, a lower canopy **pendent** moss. Photo by Yelitza Leon, Venezuelan Flora, through Creative Commons.

In a subtropical forest of the Ailao Mountains in Yunnan, southwest China, Liu *et al.* (2002) found that bryophytes enhance the annual amounts of total N, NH_4^+-N, Mg, Na, and SO_4^{-2}-S but deplete NO_3^--N, K, P, and Ca in the stemflow. Although many kinds of N-fixing organisms often are associated with epiphytic bryophytes, their contribution to total N in the mountains of Yunnan is most likely constrained by low temperatures. In a montane rainforest of the warmer Hawaii, on the other hand, Matzek and Vitousek (2003) found that the potential nitrogen fixation ranges from ~0.2 kg ha^{-1} yr^{-1} in a 300-year-old site to ~1 kg ha^{-1} yr^{-1} in a 150,000-year-old site. They felt that the dependence of epiphytic bryophytes and lichens on nutrients leached from the canopy might account for the fact that the highest fixation rates occurred in sites with low N:P ratios in the leaves and stemwood of the trees. For heterotrophic fixation, the nutrient supply offered by the decomposing substrate is also important in controlling the fixation rate. Thus, older substrata with more epiphytes are likely to contribute more nutrients to these N fixers, and indeed Matzek and Vitousek did find that the fixation rates relate to substrate cover.

With an epiphyte biomass and associated soil of 44 tons ha^{-1}, the epiphytes form a significant contribution to the Colombian upper montane rainforests (Hofstede *et al.* 1993). The 20 kg of epiphytes exceeded the biomass of the

part of the tree that supported them. In this epiphytic community, the researchers found 2,360 g N, 215 g P, 1,350 g K, and 99 g Ca. The epiphytes create large accumulations of bryophytes, favored by low temperatures, continuous high humidity, low air turbulence, and the structure of the forest. The water-soluble phosphorus stored in the epiphytic biomass is higher than that of the forest floor soil.

Pentecost (1998) assessed the cryptogamic epiphytes in the upper montane forest of the Rwenzori Mountains of Uganda (Figure 64). He found that the lichens contain ~2% of the total above ground nutrients, whereas 8% occurs in the bryophytes. The concentrations of the three "fertilizer" nutrients were N (10 kg ha^{-1}), P (1 kg ha^{-1}), and K (3 kg ha^{-1}).

Figure 64. Rwenzori Mountains, western Uganda. Photo by Agripio, through Creative Commons.

Nadkarni (1984) reported 141.9 kg of epiphytes on a single ***Clusia alata*** (Figure 65) in a Costa Rican cloud forest. The nutrients in these epiphytes were estimated as 1062 g N, 97 g P, 678 g K, 460 g Ca, 126 g Mg, and 207 g Na. This is significant because this relatively small component (less than 2%) of the forest biomass holds up to 45% of the nutrients found in the foliage of similar forests and stresses the importance of epiphytes as keystone resources in the nutrient dynamics of these forests.

Canopy Roots

To me, the most intriguing relationship is the relationship of bryophytes with canopy roots, first discovered and described by Nalini Nadkarni in her classical paper in Science (1981). Laman (1995) reported the improved germination of ***Ficus stupenda*** in moss beds associated with canopy knotholes, attributing their survival to good moisture retention. However, seed harvesting ants (*Pheidole* sp.; Figure 66) killed many of the seedlings later in development.

Figure 65. ***Clusia alata,*** a common epiphyte host in Costa Rica. Photo by Evaristo Garcia Foundation, through Creative Commons.

Figure 66. ***Pheidole pilifera*** minor (**left**) and major (**right**) workers. Some species of ***Pheidole*** kill ***Ficus stupenda*** seedlings in epiphytic moss beds. Photo by M. L. Muscedere and J. F. A. Traniello, through Creative Commons.

Epiphytic bryophytes also provide a rooting medium for **adventitious roots** (roots that arise from stem tissue; Figure 67) of trees. In fact, a dynamic interaction may occur in which the bryophytes help the tree, and the tree roots likewise help the establishment of the epiphytic community (Nadkarni 1994b). The bryophyte mat traps inorganic nutrients (Nadkarni 1986) and organic nutrients (Coxson *et al*. 1992) that are leached from members of the epiphyte community. These nutrients nourish the roots of the tree (Nadkarni & Primack 1989). The two appear to grow in mutual benefit, with the roots benefitting from the nutrients and providing a larger anchoring system for the epiphytes as they grow (Nadkarni 1994b). As the bryophytes and organic matter increase, they provide more leachates, causing the tree roots to increase.

Figure 67. Adventitious roots of banyan tree (*Ficus benghalensis*). Photo through Creative Commons.

Nadkarni (1981) found that epiphytes, including bryophytes, stimulate the growth of adventitious roots. The bryophytes serve to trap nutrients for them, and the relationship is so strong that Nadkarni argues that evolution has selected for it.

In ***Senecio cooperi*** (Figure 68), a species in the tropical cloud forest, Nadkarni (1994b) experimented with epiphytes air-layered on stem segments. For comparisons, she used wet epiphytes or dry epiphytes plus associated humus, sponges wetted with either water or nutrient solutions, dry sponges, and controls with no added layering. The wet epiphyte-humus mix and sponges with nutrient solutions were most successful in producing roots. Nadkarni suggested that the epiphytes intercept nutrients that they retain and provide the "cue" for the host tissue to produce the roots.

Some adventitious roots take advantage of the microenvironment created by epiphytic bryophytes (Sanford 1987). The roots are able to grow upward, and can do this in as rapidly as 5.6 cm in 72 hours. The roots are less than 2 mm in diameter and grow on the exposed bark surfaces, in bark fissures, and beneath attached epiphytic mosses, ferns, and vines.

Epiphytes decompose in the canopy to form soil on the large branches (Hietz *et al*. 2002). Epiphyte groups differ, in part relating to uptake of N through mycorrhizae or nitrogen fixation. These different sources affect the highly variable quantity of epiphytes, often depending on the systematic group and canopy position.

Figure 68. ***Senecio cooperi*** , a species that produces aerial roots in wet epiphytes. Photo by Dick Culbert, through Creative Commons.

In Hawaii, the koa tree (***Acacia koa***; Figure 69) takes advantage of the bryophyte mats for moisture and other favorable conditions (Leary *et al*. 2004). The roots of this tree actually grow upward and form **nodules** (Figure 70) with the bacterium ***Bradyrhizobium*** (Figure 71) in pockets of organic soils within the canopy. These organic soils in the tree contain significantly higher levels of exchangeable cations and total nitrogen, and significantly lower aluminum levels than the ground soils. Some of these mats have significant bryophyte presence.

Figure 69. ***Acacia koa***, Maui, Hawaii, a species that forms adventitious roots in moss clumps on the trunk. Photo by Forest and Kim Starr, through Creative Commons.

Figure 70. ***Acacia koa*** nodules in a bed of mosses. Photo courtesy of Leary *et al*. 2004.

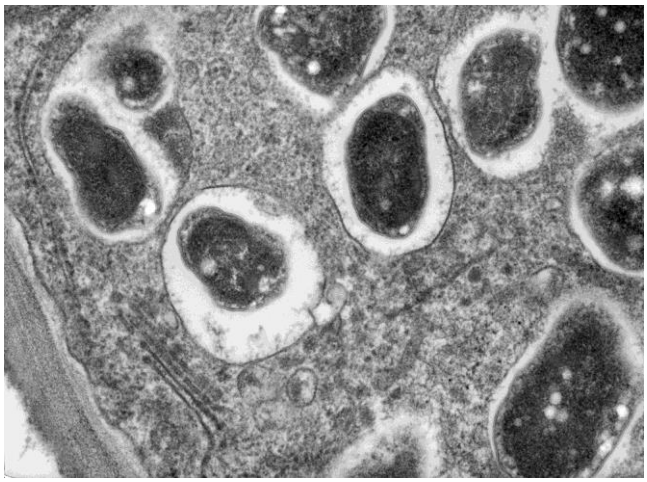

Figure 71. ***Bradyrhizobium*** from root nodule. Photo by Louisa Howard, through public domain.

Herwitz (1991) examined the aboveground adventitious roots of ***Ceratopetalum virchowii*** (see Figure 72) in an Australian montane tropical rainforest. These roots developed from stems and branches of this canopy species. In this case, Herwitz could find no evidence that this tree requires the epiphyte mats to stimulate its root growth. Instead, it appears that the stemflow of this species is particularly rich in Ca^{2+}, Mg^{2+}, and Na^{+} compared to the soil. The bark of this species remains moist for a long period of time, providing a suitable environment for the adventitious root.

Productivity and Biomass

Studies on productivity in the tropics are rare. Jacobsen (1978) published one of the earliest studies. Most seem to be simply reports of standing crops. Several look at the effects of temperature on net carbon storage (see above under Microclimate).

Köhler *et al*. (2007) reported that bryophytes dominate the epiphytic vegetation in both an old-growth cloud forest and a 30-year-old secondary forest on slopes of the Cordillera in northern Costa Rica. The combined epiphyte biomass and canopy humus was 16,215 kg ha^{-1} in the old-growth forest and 1,035 kg ha^{-1} in the secondary forest.

Figure 72. *Ceratopetalum apetalum*; *C. virchowii* forms adventitious roots but shows no evidence of influence by epiphytic bryophyte mats. Photo by John Tann, through Creative Commons.

Van Dunne and Kappelle (1998) studied epiphytic bryophytes on five small stems of ***Quercus copeyensis*** (Figure 57) in a Costa Rican montane cloud forest (Figure 73). They found 22 species of mosses and 22 species of liverworts. Biomass of the bryophytes correlates with their frequency, with bryophytes contributing 54-99% of the biomass. Nearly 90% of the biomass is contributed by only 14% of the species, with the predominant contributors being the mosses ***Pilotrichella flexilis*** (Figure 10), ***Rigodium*** sp. (Figure 74), ***Porotrichodendron superbum*** (Figure 75), ***Prionodon densus*** (Figure 76), ***Neckera chilensis*** (see Figure 77), and the leafy liverwort ***Plagiochila*** (Figure 78).

Figure 73. Cloud forest, Monteverde, Costa Rica. Photo by R. K. Booth, through Creative Commons.

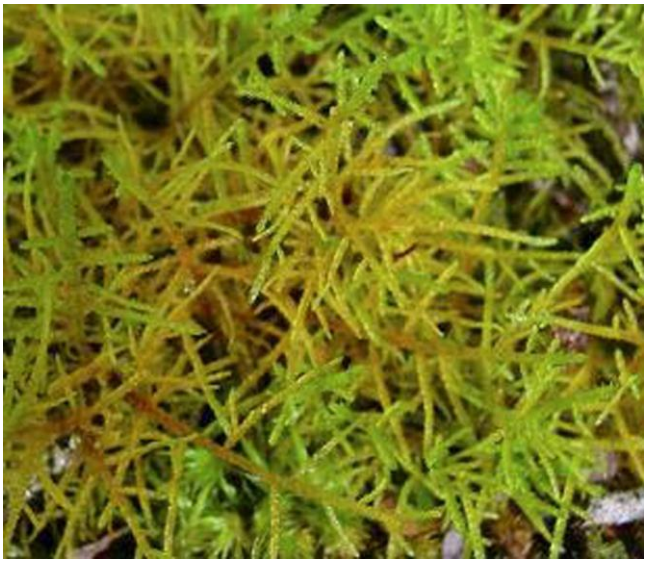

Figure 74. ***Rigodium pseudo-thuidium***, in a genus that is a major biomass contributor to Costa Rican epiphytes. Photo by Juan Larrain, with permission.

Figure 75. ***Porotrichodendron superbum*** with capsules, a species that is a major biomass contributor to Costa Rican epiphytes. Photo Paris Cryptogamic Herbarium, through Creative Commons.

Figure 76. ***Prionodon densus***, a major biomass contributor to Costa Rican epiphytes. Photo by E. Lavocat Bernard, with permission.

Figure 77. ***Neckera scabridens***; ***N. chilensis*** is a major biomass contributor to Costa Rican epiphytes. Photo by Juan Larrain, with permission.

Figure 78. ***Plagiochila*** sp., in a genus that is a major biomass contributor to Costa Rican epiphytes. Photo by Jan-Peter Frahm, with permission.

Frahm (1987) raised the question of how altitude affected the biomass and productivity of epiphytes in the tropics. Researchers had typically assumed that it related to greater light and lower temperatures at higher altitudes, permitting greater photosynthesis, but no physiological studies had been used to support this hypothesis. In his study, he used a transect with sampling at 200-m intervals from 200 to 3,200 m asl in Peru. He determined biomass in the field and measured CO_2 gas exchange in a series of light and temperature combinations in the lab. The lab experiments used specimens from 2,300 m asl collected in Colombia in October. These were 150 cm^2 specimens of the mosses ***Neckera*** sp. (Figure 77), ***Heterophyllium affine*** (Figure 79), ***Porotrichum*** sp. (Figure 80), and the liverwort ***Metzgeria*** (Figure 81). These experiments support the

hypothesis that it is a combination of high temperatures and low light that limits most of these tropical bryophytes at lower elevations. They are unable to store enough carbon in the low light to balance that lost to respiration at the high temperatures of the lowland forest. This is supported by experiments with temperature on the moss ***Plagiomnium rhynchophorum*** (Figure 82-Figure 83), but unfortunately, no methods were provided.

Figure 79. ***Heterophyllium affine***, a species in which high temperatures and low light limits these tropical bryophytes. Photo by Blanka Shaw, with permission.

Figure 80. ***Porotrichum bigelovii***; a species in this genus has high temperature and low light limits in tropical habitats. Photo by Ken-ichi Ueda, with online permission.

Figure 81. ***Metzgeria***, a genus that has high temperature and low light limits in tropical habitats. Photo by Michael Lüth, with permission.

Figure 82. ***Plagiomnium rhynchophorum*** with capsules, a mostly Asian tropical moss that has no net photosynthetic gain at 25ºC and above. Photo by Germaine A. Parada, through Creative Commons.

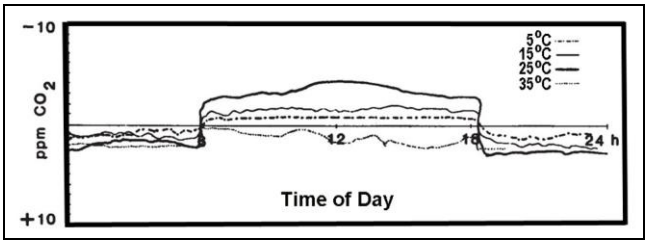

Figure 83. Photosynthesis of ***Plagiomnium rhynchophorum*** (Figure 82) under various temperature conditions at 1500 lux. The montane forest conditions of 5° and 15°C yield sufficient net photosynthesis; the lowland condition of 25°C permits photosynthesis throughout the day but no net photosynthetic gain. At 35°C no net photosynthesis occurs during the day. Graph modified from Frahm 2003b.

Wolf (1993b) found that altitude explains most of the variation in the epiphytic bryophytes and lichens on selected bark types of canopy trees, using 15 sites on an altitudinal transect from 1,000 to 4,130 m asl in the Central Cordillera of Colombia (Figure 84). Species richness varies among the three groups (mosses, liverworts, and lichens). Liverworts reach their greatest species richness (ca 100 taxa) at mid-elevational sites (2,550-3,190 m asl). In this case, biomass of bryophytes and lichens increases with altitude, coinciding with an increase in humidity.

Figure 84. Cordillera in central Colombia. Photo by Samual Rengifo, through Creative Commons.

Hofstede *et al*. (1993) examined the relationship between the epiphytic biomass and the nutrient status in a Colombian upper montane forest near the treeline at 3,700 m asl with a massive presence of epiphytes. The amount of accumulated epiphytic mass, suspended soil, and living plants on a full-grown tree was 32.7 g dry weight per dm^2 surface area, the highest documented value ever. This high value is attributed to a combination of low temperatures, high humidity, low wind velocities, and structural characteristics of the tree.

Müller and Frahm (1998) sampled epiphytic bryophytes in a montane rainforest in the Andes of Ecuador at about 2,000 m asl. They measured the dry weight on various parts of the trees and found that on trunks it was 80 g m^{-2}, on branches 1,873 g m^{-2}, and on twigs 1,230 g m^{-2}.

Clark *et al*. (1998a) conducted one of the few studies on retention of carbon by the tropical epiphytic bryophytes. They found an annual net accumulation of carbon to be approximately 37-64 g C m^{-2} yr^{-1} in their study in a tropical montane forest in Monteverde, Costa Rica. Net production of epiphytic bryophytes in the forest was 122-203 g m^{-2} yr^{-1}.

In the upper montane forest of the Rwenzori Mountains of Uganda, Pentecost (1998) found that large cushion-forming liverworts are dominant in the lower canopy. These are predominately ***Chandonanthus*** (Figure 85), ***Herbertus*** (Figure 86-Figure 87), and ***Plagiochila*** (Figure 88) species. Their productivity is controlled by light intensity and substrate tree age. In total, he found 14 species of bryophytic epiphytes. The total epiphytic biomass, including bryophytes, lichens, and algae, contribute nearly 1 ton ha^{-1} standing crop, a figure that is approximately 10% of the above-ground standing crop.

Figure 85. ***Chandonanthus birmensis***, in a genus that forms large cushions in the lower canopy of the Rwenzori Mountains of Uganda. Photo by Manju Nair, through Creative Commons.

Figure 86. ***Herbertus aduncus*** in BC, showing large "muffs" around branches. This genus forms large cushions in the lower canopy of the Rwenzori Mountains of Uganda. Photo by Botany Website, UBC, with permission.

Figure 87. ***Herbertus aduncus*** showing dense cushions formed by this genus in the lower canopy of the Rwenzori Mountains of Uganda. Photo from Botany Website, UBC, with permission.

Figure 88. ***Plagiochila cristata*** showing dense cushions like those formed by other members of this genus in the lower canopy of the Rwenzori Mountains of Uganda. Photo by Michael Lüth, with permission.

Lösch *et al*. (1994) describe differences in environmental conditions and photosynthetic rates for bryophytes in a rainforest (800 m asl), a bamboo forest, and a tree-heath (2,200-3,200 m asl) in east central Africa. In the lowland rainforest, the climatic conditions are a nearly constant 24°C, 100% relative humidity, and PAR below 100 µmol photons m^{-2} sec^{-1}. The mountain bryophytes exhibit approximately 6 times those daily sums of PAR while experiencing temperatures of 10-25°C and relative humidities of 60-100%. In the bamboo forest, the epiphytic mosses experience water loss down to less than 70% of their water content, but become saturated again from the vapor-saturated air at night. In these habitats, the photosynthesis peaks between 22 and 30ºC. The lowland species exhibit higher optima than do those of the mountain sites. The light saturation points for all species are below 400 µmol photons m^{-2} s^{-1}, but the slopes differ. Those bryophytes from the lowland have a smaller light compensation point (3-12 µmol photons m^{-2} s^{-1}), accompanied by a steeper slope in the low-light range. In the highland, the compensation point is 8-20 µmol photons m^{-2} s^{-1}.

Waite and Sack (2010) considered the relationship of moss photosynthesis to leaf and canopy structure. These include ground-dwelling species as well as branch and trunk dwellers: ***Acroporium fuscoflavum*** (Figure 89), ***Campylopus hawaiicus*** (Figure 90), ***Distichophyllum freycinetii*** (Figure 91), ***Fissidens pacificus*** (Figure 92), ***Holomitrium seticalycinum*** (see Figure 93), ***Hookeria acutifolia*** (Figure 94), ***Leucobryum*** cf. ***seemannii*** (Figure 95), ***Macromitrium microstomum*** (Figure 96), ***M. piliferum*** (Figure 97), and ***Pyrrhobryum pungens*** (see Figure 98) (all mosses). Interestingly, they did not find any correlation between light saturation for photosynthesis and habitat irradiance. The bryophytes have low leaf mass per area and a low gas exchange rate. The nitrogen concentration, as well as $\mathbf{A_{mass}}$, (maximum assimilation per unit leaf mass) has a negative correlation with the canopy mass per area. ***Campylopus pyriformis*** (Figure 99) exhibits a high $\mathbf{A_{max}}$ (maximum assimilation) that could be the result of its high leaf area index. Anatomical factors such as smaller cells, thicker cell walls, or physiological adaptations such as higher osmotic adjustment could lower the potential for a higher A_{max} in sun mosses.

Figure 89. ***Acroporium fuscoflavum***, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Jan-Peter Frahm, with permission.

Figure 90. ***Campylopus hawaiicus***, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Jan-Peter Frahm, with permission.

Figure 91. ***Distichophyllum freycinetii***, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by John Game, through Creative Commons.

Figure 92. ***Fissidens pacificus***, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Jan-Peter Frahm, with permission.

Figure 93. ***Holomitrium trichopodum***; ***Holomitrium seticalycinum*** is a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Niels Klazenga, with permission.

Figure 94. ***Hookeria acutifolia***, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Michael Lüth, with permission.

Figure 95. ***Leucobryum seemannii***, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Jan-Peter Frahm, with permission.

Figure 96. ***Macromitrium microstomum***, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Janice Glime.

Figure 97. ***Macromitrium piliferum***, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Jan-Peter Frahm, with permission.

Figure 98. ***Pyrrhobryum*** sp.; ***Pyrrhobryum pungens*** is a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Niels Klazenga, with permission.

Figure 99. ***Campylopus pyriformis***, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Michael Lüth, with permission.

Epiphyte Litterfall

Both bryophyte and tracheophyte litter can fall from the trees, especially during severe storms. This is a loss of canopy productivity, but provides a new source of nutrients for the soil, and in some cases these plants may continue growth on the ground.

Matelson *et al*. (1993) considered the rate of nutrient release from bryophytic and other epiphytic litter fall. They determined that it varies with microhabitat and suggested that both spatial and temporal distribution should be studied at the species level as they relate to microhabitat characteristics.

Köhler (2002) investigated total epiphytes in 10-15-year-old early secondary forest, a 40-year-old later-stage secondary forest, and an old-growth (primary) forest in Costa Rican mountain rainforests. Succession resulted in an increase in epiphytic litterfall. They estimated 4.8 g m^{-2} in early secondary forests (160 kg ha^{-1} at stand level), 12.0 g m^{-2} in later secondary forest (520 kg ha^{-1} at stand level), and 78.5 g m^{-2} in the old-growth forest (3400 kg ha^{-1} at stand level). Nevertheless, epiphytes constitute only a small part of the litter.

In a Neotropical cloud forest in Monteverde (Figure 100), Costa Rica, Nadkarni and Matelson (1992) found that epiphyte litter (bryophytes, lichens, and tracheophytes) comprises 5-10% of the total fine litter at that site. This litterfall contributes to the nutrients of the forest, with measurements (in kg ha^{-1} yr^{-1}) of N (7.5), P (0.5), Ca (4.2), Mg (0.8), and K (0.1). These epiphytic litter components have a higher annual rate than does the litter from plants rooted in the ground. On the other hand, the turnover time of all nutrients except potassium is 4-6 times slower in the fallen epiphytic litter. Potassium turnover is ten times as fast. In a later study, Nadkarni (2000) determined that epiphyte litterfall in a lower montane cloud forest in Monteverde, Costa Rica, occurs at a rate of 50 g dry wt m^{-2} yr^{-1}. This slow turnover of most bryophyte litter is most likely due to the high phenolic content that protects the bryophytes from herbivory and attack by fungi and bacteria.

When branches make contact with each other, by wind or storm, the impact can cause tiny branches at the tips to break, a phenomenon known as **crown shyness** (Figure 101) (Franco 1986). This can occur between the same species of tree, or among different species. The exact cause is not clearly known, but at least in some cases it appears that it is the result of **reciprocal pruning** as trees contact each other. It appears that lateral branch growth is usually not influenced by the neighbors until such mechanical abrasions occur. One such tree is *Clusia alata* (Figure 65). This branch breakage can cause any adhering bryophytes to lost from the canopy as the branch tips fall away.

Figure 100. Cloud forest, Monteverde, Costa Rica. Photo by R. K. Booth, through Creative Commons.

Figure 101. Crown shyness in Buenos Aires, Argentina; branches break when they contact in wind events. Refractor, through Creative Commons.

Summary

Bryophytes in the tropics, particularly epiphytes, undoubtedly have a crucial role in water and nutrient retention, releasing nutrients during re-wetting, but filtering them from the lower branches and ground during rain events. They are adapted by their life forms and physiology to withstand desiccation. **Anhydrobiosis** and **osmotic potential** are typically used as means of surviving dry periods. Dry areas typically have **mats**; in areas with high humidity these are replaced by **fans**, **wefts**, and **pendants** that are able to obtain water from fog and mist (**fog-stripping**). Many are **perennial stayers** or **perennial shuttle** species.

Species of highly exposed locations have higher light saturation and compensation points, higher dark respiration rates, more chlorophyll, higher chlorophyll *a*:*b* ratios, and higher N concentrations than those of shade species. Some are able to retain water and nutrients in **hyaline** cells that hold water and surround photosynthetic cells. But most lose water easily and survive by their ability to recover quickly from desiccation, without the need to make new chlorophyll.

Substrate, temperature, light, and moisture availability are the microclimate variables that drive the community structure of epiphytic bryophytes. Their biggest physiological problem is the need to store more carbon than they lose to respiration.

Nutrients are obtained from the atmosphere, rain, and the bark and collected on the bryophyte surface until it becomes moist and can absorb them. Hence, nutrients in the bryophytes increase from the dry season to the wet season. **Cyanobacteria** living in the microenvironment of the bryophytes contribute to the usable nitrogen of the ecosystem. The ability of the bryophytes to leak nutrients but retain them on their surfaces permits external nutrient storage until rainfall returns, but releases them to the ecosystem as heavy rains carry them away. Light rains and fog permit the bryophytes to hydrate and absorb the nutrients. This makes the epiphytic bryophytes a keystone resource for the forest. These nutrient-rich, wet bryophytes furthermore provide a suitable substrate for canopy roots for some species.

Biomass of the bryophytes correlates with their frequency, with bryophytes contributing 54-99% of the biomass at higher elevations. Biomass increases with altitude, coinciding with an increase in humidity. At lower elevations, the combination of high temperatures and low light severely limit bryophyte productivity. Epiphyte litter (bryophytes, lichens, and tracheophytes) comprises 5-10% of the total fine litter in the cloud forests and only a small amount in the lowland forest. Whereas leaf litter decays rapidly in the tropics, bryophyte litter is slow to decay due to its many phenolic compounds that inhibit insects, bacteria, and fungi.

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CHAPTER 8-4
TROPICS: EPIPHYTE ECOLOGY, PART 2

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CHAPTER 8-4
TROPICS: EPIPHYTE ECOLOGY, PART 2

Figure 1. Mossy forest in rainy season on Reunion Island. Bryophytes surround the branches like a muff. Photo Courtesy of Min Chuah-Petiot.

Adaptations

Living on trees often puts the bryophytes at the mercy of rainfall (where there is no fog), either as throughfall or stemflow. Thus, special adaptations are necessary for those times when it is not raining, for the substrate is unlikely to do much to maintain the humidity (Frahm & Kürschner 1989). Gradstein and Pócs (1989) suggest a number of adaptations that permit these taxa to be so successful in this living habitat:

1. **Green, multicellular spores** with **endosporous** development (Figure 2) [*e.g.* **Dicnemonaceae** (Figure 3), **Lejeuneaceae** (Figure 6, Figure 8-Figure 9)] (Nehira 1983), permitting the protonema to get a quick start. **Anisomorphic** spores in ***Macromitrium erythrocomum*** (Figure 4) (Ramsay *et al*. 2017) could increase chances of dispersal at different times.
2. **Sexual dimorphism** and **phyllodioicy** (having dwarf males that live on leaves or tomentum of females; Figure 5), possibly increasing gene flow by ensuring that males are close to females. [*e.g*. dwarf males in ***Macromitrium erythrocomum*** (Ramsay *et al*. 2017)].
3. Numerous means of **asexual reproduction**, **monoicous** condition, and **neoteny** (sexual maturity at early developmental stage; Figure 6), permitting movement from place to place among **ephemeral** (short-lived) substrata [*e.g.* **Lejeuneaceae** (Figure 6, Figure 8-Figure 9)] (Schuster 1984; Richards 1984).
4. **Rhizoid discs** (Figure 7) for anchorage and adhesion (Winkler 1967).
5. **Lobules** [**Frullaniaceae** (Figure 70), **Lejeuneaceae** (Figure 6, Figure 8-Figure 9)] and **hyaline leaf**

margins for absorption and retention of water; ***Colura*** (Figure 8-Figure 9) even has a closing apparatus at the entrance of its lobule (Jovet-Ast 1953). Many **Calymperaceae** (Figure 10) have **hyaline cells** (Figure 11) in their leaves (Richards 1984).

6. **Cushion** life form (Figure 28) on branches of open montane forests (Pócs 1982).

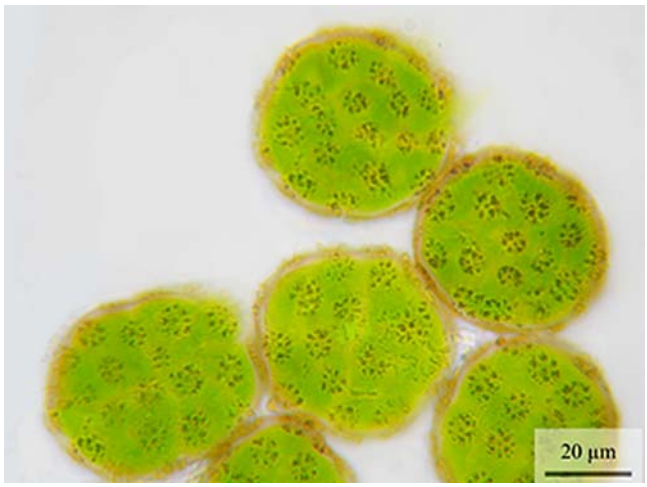

Figure 2. ***Frullania ericoides*** multicellular green endospores, demonstrating their germination within the spore. Photo modified from Silva-e-Costa *et al*. 2017, through Creative Commons.

Figure 3. ***Dicnemon*** sp., a genus with endosporic development. Photo by Vita Plášek, with permission.

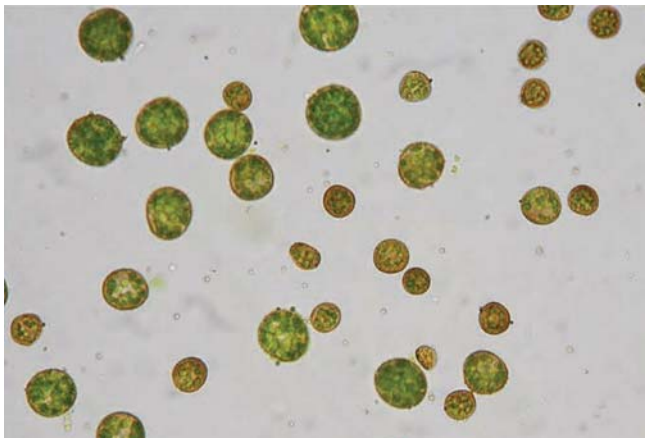

Figure 4. ***Macromitrium erythrocomum*** anisomorphic spores. Photo from Ramsay *et al.* 2017, with permission.

Figure 5. ***Leucobryum candidum*** with dwarf males, showing **phyllodioicy**. Photo by Paddy Dalton, with permission.

Figure 6. ***Drepanolejeunea inchoata*** with perianth, an example of **neoteny** in the **Lejeuneaceae**. Photo by Michaela Sonnleitner, with permission.

Figure 7. ***Frullania*** rhizoids. Photo courtesy of Andi Cairns.

Figure 8. ***Colura calyptrifolia*** on willow, with lobules showing. Photo by Stan Phillips, through public domain.

Figure 9. ***Colura*** leaf showing lobule. Photo courtesy of Jan-Peter Frahm.

Figure 10. ***Leucophanes molleri*** (**Calymperaceae**). Some members of this family have hyaline cells in their leaves. Photo courtesy of Noris Salazar Allen.

Figure 11. ***Leucophanes molleri*** (**Calymperaceae**) leaf cross section showing hyaline cells surrounding photosynthetic cells. Photo courtesy of Noris Salazar Allen.

Frey *et al*. (1990) studied the epiphytes in Mt. Kinabalu (Figure 12) in North Borneo. They examined distribution patterns of life forms and the water-storing structures in epiphytes. They also looked at their role in water leaching, an important aspect in tropical forest nutrient cycling. Other useful studies on adaptations include those of Thiers (1988 – **Jungermanniales**, *i.e.* leafy liverworts; Figure 6, Figure 8) and Kürschner (2000 – adaptations in the tropical rainforest).

Figure 12. Mt. Kinabalu in Borneo. Photo through Creative Commons.

Pigmentation

In their study of ***Macromitrium*** in the Wet Tropics bioregion of Queensland, Australia, Ramsay *et al*. (2017) questioned the appearance of red species there. This was particularly striking in the epiphyte ***M. erythrocomum*** (Figure 13). Although some bryophyte species have been studied for their use of pigmentation as protection against high light (*e.g.*, Marshall & Proctor 2004), no tropical species has thus far been used in such experimentation. In ***Macromitrium*** species, red, orange, and yellow pigments are likewise most pronounced in species adapted for high light (Vitt 1994). In mosses, these accessory pigments occur mostly in cell walls. For ***M. erythrocomum***, the function of these pigments is elusive. These mosses grow in dense shade where protection from high light intensities is unnecessary. Ramsay *et al*. suggested that the pigmentation could be a genetic leftover from an ancestor adapted to high light.

Figure 13. ***Macromitrium erythrocomium*** from northern Queensland. Note young, green leaves at the bottom and mature yellow to reddish leaves on the mature plants with sporophytes. Photo from Ramsay *et al.* 2017, with permission.

This species also presents an interesting progression of leaf color in its life cycle (Ramsay *et al*. 2017). Young leaves are light green, having cells packed with chloroplasts and walls not colored (Figure 13). At this stage, the costa is already bright red. As the leaf ages, it loses its chloroplasts, making the cell lumen yellowish while retaining the red costa (Figure 13-Figure 14). It continues to develop red pigments, eventually filling the cells, and the walls also become colored, making the entire leaf red.

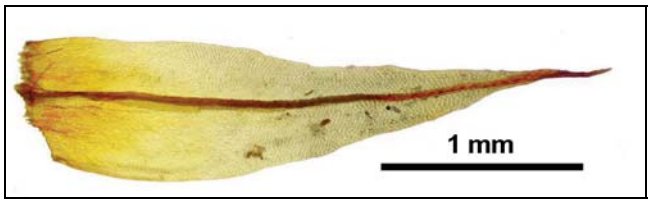

Figure 14. ***Macromitrium erythrocomum*** leaf with red costa. Photo from Ramsay *et al.* 2017, with permission.

Growth Forms and Life Forms

Growth forms, life forms, and life cycle strategies interact with other adaptations to provide the bryophytes with the best strategy for a particular environment. The main reference for growth or life forms of bryophytes is Mägdefrau 1982 and for life strategies During 1979. See also Volume 1, Chapter 4, of this series on Bryophyte Ecology for details on these.

Based on a number of pilot studies in the tropics (Frahm 1990; Frey *et al*. 1990, 1995; Frey & Kürschner 1991; Kürschner & Seifert 1995; Kürschner & Parolly 1998b; Kürschner *et al*. 1998), Kürschner *et al*. (1999) described generalizations of tropical growth forms, life forms, and life strategies for the epiphyte habitat. **Perennial stayers** and **perennial shuttle** species (see During 1979) are important life cycle strategies in most of the tropics. They dominate in the tropical lowland and submontane belt as well as in the cooler and more humid montane rainforest. However, in the former two they are **mat formers**, whereas in the montane rainforest they are mostly **fans** and **wefts** that rely on propagules and clonal growth. Some species have ciliate leaves that are able to collect water from fog. In the more xeric conditions of the open, upper montane forests, **short turfs**, **tall turfs**, and **cushions** predominate, but are also **perennial stayers** and **perennial shuttle** species. **Colonists**, by contrast, occur almost exclusively in secondary forests. Kürschner and coworkers considered these relationships to apply throughout the tropics.

In the Sulawesi rainforest (Figure 15) in Indonesia, the understory has a preponderance of **dendroid** and **fan-like** species of bryophytes, whereas the crowns of the trees have more **tuft** species than other types (Sporn *et al*. 2010). Like many other factors, this reflects the differences in microclimate between the upper canopy and the understory, but it also reflects differences in substrate provided by understory trees vs canopy trees.

Figure 15. Mountains of South Sulawesi, Indonesia. Photo by Achmad Rabin Taim, through Creative Commons.

Kürschner and Seifert (1995) described epiphytic communities in the eastern Congo basin (Figure 16) and nearby mountain ranges. These included consideration of life forms and water storage.

Figure 16. Forests in the Democratic Republic of the Congo. Photo from Bobulix, through Creative Commons.

Bryophyte life forms in flooded and non-flooded habitats in the Colombian Amazon (Figure 17-Figure 18) reflect the differences in humidity (Benavides *et al*. (2004). In the floodplains, the **fan** and **mat** forms predominate,

whereas more epiphytic liverworts occur in the non-flooded forest.

Leerdam *et al*. (1990) described the epiphytes of a Colombian cloud forest (Figure 19). Bryophytes comprise most of the biomass. They found a sequence of life forms along the canopy branches, creating two groups: inner canopy and outer canopy. These are mostly **tall turfs** and **smooth mats**, respectively. The life forms corresponded with microclimatological factors, water and nutrient availability, and substratum age. The phorophyte species also influence the type of growth and life forms that grow there.

Figure 17. Amazon rainforest. Photo by Phil Harris, through Creative Commons.

Figure 18. Colombian Amazon. Photo by Actorsuarez, through Creative Commons.

Figure 19. Colombian cloud forest with White Yarumo. Photo by Alejandro Bayer Tamayo, through Creative Commons.

Some striking life forms that are almost exclusively tropical are the **feather**, **bracket**, and **pendent** (Figure 20) forms. These seem to reflect the high atmospheric humidity around the first few meters of the tree bole, where little air stirs to carry away the moisture quickly.

Pendent (Figure 20) bryophytes are common in areas with high humidity. Proctor (2004) examined the light and desiccation responses of two of these **pendent** taxa [***Weymouthia mollis*** (Figure 21) and ***W. cochlearifolia*** (Figure 22)]. ***Weymouthia cochlearifolia*** is more typical forming patches on the trunk and branches, but it can grow as a **pendent** form. ***Weymouthia mollis*** typically grows as a **pendent** form. ***Weymouthia cochlearifolia*** reached 95% saturation at 160 µmol m^{-2} s^{-1} PPFD, whereas ***W. mollis*** ranged 176-307 µmol m^{-2} s^{-1} PPFD or even more. They demonstrated the primary needs of **pendent** forms: high levels and reasonably regular precipitation, shelter from wind, and moderate shade. From this they surmised that exposure and the high evaporation rate that accompanies it will favor **small cushions** or **smooth mat** life forms. Proctor reasoned that exposure would minimize the boundary-layer resistance to CO_2 uptake and maximize the mechanical effects of wind. **Tight cushions** and **smooth mats** can more easily resist these. On the other hand, the more open life forms are more exposed for efficient light interception and CO_2 uptake.

Figure 20. ***Cheilolejeunea jackii*** **pendent** liverwort on the Galapagos Islands. Photo courtesy of Robbert Gradstein.

Figure 21. ***Weymouthia mollis***, a species that is typically **pendent**, in Chile. Photo by Juan Larrain, with permission.

Figure 22. ***Weymouthia cochlearifolia***, a species that can form both **mats** and **pendent** forms. Photo by Niels Klazenga, with permission.

Some bryophyte species develop different life forms based on their habitat (Ford 1994). For example in Queensland ***Papillaria*** (Figure 23) spp. on ***Sloanea woollsii*** (Figure 25) exhibit forms ranging from **long pendent** forms in the canopy branches to **creeping mats** on lower branches and the upper trunk. **Dendroid** forms are especially common on tree trunks. Stumps have mosses such as the dominant ***Camptochaete vaga*** (see Figure 24), but also can have ***Dicranum*** spp. (see Figure 26)

Figure 23. ***Papillaria crocea***, a species of the Wet Tropics in Australia. Photo courtesy of Andi Cairns.

Figure 24. ***Camptochaete*** sp. from New Zealand. Photo by Jan-Peter Frahm, with permission.

Figure 25. ***Sloanea woollsii*** with epiphytes on the base and trunk. Photo by Peter Woodard, through public domain.

Figure 26. ***Dicranum*** sp., a cushion former from the Neotropics. Photo by Michael Lüth, with permission.

Additional references on tropical bryophyte life forms include those of Kürschner and Parolly (1998a, 2005, 2007).

Life Cycle Strategies

One of the most important adaptations to tropical climates is that of life cycle strategies. These must be timed to coordinate with wet and dry periods. Sperm require at least some water for transfer. Spores are dispersed best by dry winds.

Furthermore, life strategies of epiphytic bryophytes change with altitude. Frey *et al*. (1995) compared these strategies in the eastern Congo basin (Figure 27), a tropical lowland. In the primary rainforests of the tropical lowland and lower montane, the epiphytes were generally **perennial shuttle** species and **perennial stayers**. These had low to moderate sexual and asexual reproduction. This strategy combination is well suited for the high temperature and humidity regime, particularly for the leafy liverworts that dominate these communities. In the montane rainforests and cloud forests the perennial shuttle species have high asexual reproduction, with both propagules and clonal growth contributing. In **secondary woodlands** (areas of regrowth), ericaceous woodlands, and subpáramo of African volcanoes, the perennial shuttle and perennial stayers with high levels of sexual reproduction reach their greatest numbers. This is facilitated by the regular production of sporophytes in the **xeric** (dry) conditions with a strong **diurnal** (daily) climate. This reproductive strategy is typical of epiphytes in xeric woodlands.

Figure 27. Lowland rainforest, Congo Basin, Cameroon. Photo by Mauri Rautkari, through Creative Commons.

Kürschner (2003) described the life strategies of two epiphytic bryophyte associations in southwestern Arabia. The species are mostly drought tolerant. Their life strategies are distinctly correlated with their ecological site conditions. The ***Orthotricho*** (Figure 28)***-Fabronietum socotranae*** (Figure 29) is a drought-tolerant association dominated by **cushions**, **short turf**, and **mats** – **perennial stayers** with regular sporophyte formation. By contrast, in the sub-humid ***Leptodonto*** (Figure 30)***-Leucodontetum schweinfurthii*** (Figure 31) association, the typical life forms are **tails** and **fans**. These are **pleurocarpous perennial shuttle** species that have large spores. These large spores limit them to short-range dispersal, relatively low reproductive rates, and generative reproduction. This association has a much higher diversity of life forms and life strategies, including liverworts.

Figure 28. ***Orthotrichum tasmanicum*** with capsules. Photo by David Tng, with permission.

Figure 29. ***Fabronia pusilla***; in Arabia ***Orthotricho-Fabronietum socotranae*** is a common association. Photo by Michael Lüth, with permission.

Figure 30. ***Leptodon longisetus*** from Tenerife; this genus forms the ***Leptodonto-Leucodontetum schweinfurthii*** association in humid Arabia. Photo by Jonathan Sleath, with permission.

Figure 31. ***Leucodon julaceus***; this genus forms the ***Leptodonto-Leucodontetum schweinfurthii*** association in humid Arabia. Photo by Bob Klips, with permission.

Spore size is an adaptive trait wherein small spores have a good chance for long-distance dispersal and large spores do not, but have a greater chance for successful germination and establishment (Kürschner & Parolly 1998a). Few bryophytes are able to use both strategies. However, one notable exception is an epiphytic **heterosporous** (having two sizes of spores) moss of the Andes of northern Peru – ***Leptodontium viticulosoides*** (Figure 32). More recently, this was reported in ***Macromitrium erythrocomum*** (Figure 4, Figure 13) from the Australian Wet Tropics (Ramsay *et al*. 2017).

Figure 32. ***Leptodontium viticulosoides***, a heterosporous species that uses both long-distance dispersal of small spores and more successful establishment of large spores. Photo by Claudio Delgadillo Moya, with permission.

Having similar adaptive traits in similar conditions is common among bryophytic epiphytes (Kürschner 2003, 2004a) – a product of convergent evolution. This convergence is common among life strategies of tropical bryophytes.

Additional studies on life strategies include Egunyomi and Olarinmoye (1983), Kürschner (2004b), Kürschner and Parolly (2005, 2007), and Kürschner *et al*. (2006, 2007).

Dispersal and Colonization

Colonization must be preceded by dispersal. Thus, to examine colonization rates, we must necessarily understand the limitations to dispersal.

Yeaton and Gladstone (1982) examined colonization patterns of epiphytic orchids on calabash trees (***Crescentia alata***; Figure 33) in Costa Rica. They hypothesized that the number of propagules produced by the species determined the colonization pattern. The same hypothesis can be considered for bryophytes.

Figure 33. ***Crescentia alata*** in Guanacaste dry forest. Photo by Daniel H. Janzen, through Creative Commons.

Wolf (1994) examined the factors that control the distribution of bryophytes and lichens in the northern Andes (Figure 34). He concluded that randomness of propagule supply appears to be the most important factor in determining the epiphyte composition on branch and trunk segments.

Figure 34. Northern Andes in Colombia. Photo by Conocer, through public domain.

But Mari *et al*. (2016) reached a somewhat different conclusion. They avoided the differences among **phorophytes** (plants on which epiphytes grow) by sampling only one tree species, ***Aldina heterophylla*** (a legume). This is a dominant species in the Amazonian white-sand habitats and sports heavy loads of epiphytes. Mari and coworkers attempted to quantify the importance of the tree zone in colonization by comparing geographic distances at scales of 100 m^2 and 2,500 km^2. At the larger, regional scale, the tree zone explained approximately two-thirds of the primary compositional gradient – a factor more than double that accounted for by site differences.

On the other hand, spatial effects were absent at the fine scale of 100 m^2, with more dissimilarity than expected by chance when compared to communities on neighboring phorophytes. The researchers concluded that microsite availability, not dispersal limitation, is the most important factor in structuring the epiphytic communities of this forest type.

The **phorophyte** itself can play a role in the colonization (Olarinmoye 1977). Such factors as bark roughness and smoothness determine whether a propagule is able to adhere once it arrives. Leachates from the host leaves could inhibit growth, but for the leafy liverwort ***Radula flaccida*** (Figure 35), it was only extracts, not leachates, that inhibited growth (Olarinmoye 1981, 1982).

Figure 35. ***Radula flaccida*** habit with gemmae. Extracts, but not leachates, from tree leaves inhibited growth on the phorophyte host. Photo by Michaela Sonnleitner, with permission.

Oliveira *et al*. (2009) noted the gradient of bryophyte species communities from the base of the tree to the top of the canopy in the Guianas (Figure 36), highlighting the role of niche assembly in defining these communities. They set out to test whether niche assembly, rather than dispersal limitation, drives species composition of epiphytic bryophyte communities on a large spatial scale. Using three lowland forests, they sampled six different height zones of several trees in each. They tested whether specialists maintain a preferred height zone across the Guianas. They found that 57% of the species had a preferred height zone throughout the localities. In fact, the communities were more similar across 640 km at the same height zone than they were among the heights on any single tree. Hence, they concluded that niche assembly was a stronger determinant of the communities than were dispersal factors on both local and regional scales.

While the similarity within a zone is greater even at 640 km than among height zones of a tree, the similarity within the same locality is greater than that with greater distances (Oliveira & ter Steege 2015). Using nine localities across 2800 km from east to west in the Amazon forest (Figure 17), these researchers again demonstrated that height zone explains most of the variation among communities. The outer canopy communities exhibit the greatest similarity between trees and localities. The variation at the geographic scale could be explained primarily by elevation and temperature.

Figure 36. French Guiana tropical forest. Photo by Cayambe, through Creative Commons.

Oliveira and ter Steege (2015) furthermore found that establishment limitation is strongest at the extremes of the vertical gradient. Communities of the tree base and the outer canopy draw individuals from outside the habitat species pool at a rate of 0.28 and 0.22, respectively, in contrast with values between 0.55 and 0.76 of other height zones, contrasting with the hypothesis that species inhabiting the canopy have higher chances of engaging in long-distance dispersal events (see *e.g.* Gradstein 2006, p. 17). Whereas the canopy may have a greater exposure to propagules that are in the air currents, they are also subject to winds that can dislodge the propagules. They might also be limited by propagule availability as those propagules might be constrained by their canopy of origin, preventing them from entering the air currents. Oliveira and ter Steege suggested that bryophytes in these two extreme zones (outer canopy and tree base) might be, through time, subjected to stronger selection.

Hietz (1997) studied the population dynamics of epiphytes in a Mexican humid montane forest. He used repeated photographs to follow 5,124 individuals (44 species) for more than two years. This study demonstrated the importance of branch loss as a contributor to the mortality of epiphytic flowering plants and ferns.

Nadkarni (2000) performed one of the few experimental studies on colonization by epiphytes. She stripped branch surfaces of their epiphytes in a lower montane cloud forest, then tracked what landed where and whether it was able to remain where it landed. Epiphytes are lost from the canopy due to sloughing, branch breakage, and treefalls, typically caused by wind or heavy rainfall. Most of our understanding of colonization patterns has been from studying forests of a series of ages and comparing their floras. In the temperate forest, colonization is rapid, with up to 6 cm elongation in the first year. Furthermore, the composition is similar to that of the original community. But in the tropical forest, colonization is very slow, exhibiting no colonization in the first five years! The new colonization furthermore differs markedly from the original communities. Instead of the dead organic matter, bryophytes, and tracheophytes of the mature branch community, the new community begins with crustose and foliose lichens. Even more surprising is that instead of encroachment from the sides, the colonizers enter the bare areas from the bottom up. In the sixth year, algae and

bryophytes begin to colonize the lower sides of branches. This appears to be related to the greater moisture on that side of the branch.

Nadkarni (2000) concluded that bare branches, typically with smooth bark, retain little moisture and are unsuitable for the developing epiphytes. Once early lichens become established, more water is retained, permitting growth of species adapted to frequent drying. As colonization increases, nutrients as well as water are retained, permitting larger and less xerophytic species to survive. She further surmised that at the branch tips, where colonization is much more rapid, the small branches are more able to trap and hold propagules, and they are more exposed to fog and mist, thus having more available moisture. In both cases, once the bryophytes become established, the better retention of water and nutrients facilitates a more rapid continuation of the colonization.

In a separate study, Nadkarni *et al*. (2000) experimented with artificially dispersing bryophyte fragments in a tropical montane cloud forest of Costa Rica, using quadrats above branches of saplings and mature trees of ***Ocotea tonduzii*** (see Figure 37). Only 1% of the dispersed fragments were retained by the sapling crowns for the six months of the study. On the other hand, branches in the forest canopy, already possessing intact epiphyte communities, retained 24% of the dropped bryophytes. Branches that had been stripped of their epiphytes retained only 5%.

Figure 37. *Ocotea minarum*; ***Ocotea tonduzii*** was used to study adherence of bryophyte fragments in Costa Rica. Photo by Denise Sasaki, through Creative Commons.

Colonization of bryophytes can be important to establish a suitable habitat for larger epiphytes such as orchids. Zotz and Vollrath (2003) found that epiphytes on the palm ***Socratea exorrhiza*** (Figure 38-Figure 39) become established in bryophyte clumps (Figure 39) more often than could be expected from randomness, but they nevertheless do not seem to depend on them 100%. This enhancement of the habitat by bryophytes most likely accounts for the delay in tracheophyte colonization until the trees are at least 20 years old.

Figure 38. ***Socratea exorrhiza*** in Brazil. Photo by Andrew J. Henderson, Palmweb, through Creative Commons.

Figure 39. ***Socratea exorrhiza*** with various tracheophyte epiphytes established in bryophytic epiphytes. Photo by David J. Stang, through Creative Commons.

A number of ant species live in the trees in the tropics and some even build nests using tracheophytes (Longino & Nadkarni 1990; Blüthgen *et al*. 2001). In Costa Rica, these ants often make nests in arboreal litter, mosses, and humus that accumulate under the canopy epiphytic tracheophytes. The species in the canopy are rarely found on the ground and their travels among the canopy branches are likely to contribute to the dispersal of bryophyte fragments, gemmae, and spores. Their role in dispersal needs to be explored quantitatively.

In contrast with the experimental colonization study by Nadkarni (2000), Frahm *et al*. (2000) observed that crustose lichens seemed to inhibit epiphytic bryophyte growth. They tested extracts of these lichens and bark samples on spore germination of the soil bryophytes ***Ceratodon purpureus*** (Figure 40) and ***Funaria hygrometrica*** (Figure 41). These extracts inhibit spore germination of these two species. They also tested the extracts on seeds of the bromeliad *Vriesea splendens* (Figure 42) and the soil-dwelling mustard *Lepidium sativum* (Figure 43). The extracts reduce the germination of seeds of *Vriesea*, but they actually promote germination of *Lepidium*. Thus we cannot conclude from this study of soil species whether the crustose lichens actually inhibit growth of bryophytes that are normally epiphytes, but the results suggest that such interaction needs to be tested.

Figure 40. ***Ceratodon purpureus*** with young sporophytes, a soil-dwelling species whose spore germination is inhibited by at least some lichen extracts. Photo by Hermann Schachner, through Creative Commons.

Barkman (1958) and Pócs (1980) suggested that bryophytes may cause their own displacement by retaining water that makes tracheophytic epiphyte presence possible. They furthermore form humus, accelerate bark decay (Barkman 1958), and facilitate anchorage of seeds and other propagules.

Figure 41. ***Funaria hygrometrica*** with young sporophytes, a soil-dwelling species whose spore germination is inhibited by some lichen extracts. Photo by Hermann Schachner, through Creative Commons.

Figure 42. *Vriesea splendens*; germination of seeds in this species are inhibited by lichen extracts. Photo by Bernard Dupont, through Creative Commons.

Figure 43. *Lepidium sativum*, a species in which seed germination is enhanced by lichen extracts. Photo by Dinesh Valke, through Creative Commons.

Host Trees

Specific bryophyte-host relationships have been reported a number of times in temperate regions where tree species richness is very low, as for example those found by Slack (1976). As is often the case, she found strong preferences among eastern North American trees, but none of the bryophytes occurred exclusively on one tree sp.

Wolf (1995) summarized the forces leading to presence and abundance of species in epiphytic bryophyte communities in the canopy of an Upper Montane Rain Forest, Central Cordillera, Colombia. He considered two ways to look at these communities: emphasis on quality or quantity of preceding propagule supply; within community interactions such as competition. For the first of these, researchers have placed great importance on observed distribution patterns and high variability between epiphyte communities in seemingly identical habitats. But the great cover and biomass in these tropical montane rainforests suggests that competitive interactions may also be important. In his own study, Wolf found 120 bryophyte taxa (and 61 macrolichens). He recognized four community types from outer to inner canopy. Nevertheless, these four communities share many species and exhibit a species richness of about 100 taxa each. The inner canopy, with thick branches (21-80 cm diameter) had significantly fewer taxa per unit surface area, with an average of 1.72 taxa per dm^2 compared to 3.2 from the thinner middle canopy branches. Richness was even higher in the outer canopy, with 7.8 taxa per dm^2. If time were the most important factor, then the inner crown should have the highest number of species. Instead, one finds that the thick inner branches and trunks carry large patches of individual clones, suggesting competition through horizontal growth.

In the subtropical Tenerife, Canary Islands, González-Mancebo *et al*. (2003) described epiphytic bryophyte communities from five tree species in a laurel forest (Figure 44). Most of these bryophytes (37 species total) are **facultative epiphytes**, living on other substrates as well. And many are found on several tree species, with five being found on all five tree species. They further supported the observations that the species composition varies with bark characteristics, leeward vs windward exposure, height on tree, tree size, and degree of uprightness. Growth and life forms also relate to the moisture conditions of the bark.

Figure 44. Laurel forest on Tenerife, Canary Islands. Photo by Inkaroad, through Creative Commons

In tropical forests that have high tree species richness, such host-tree relationships are absent; at the same height, one can expect to find mostly the same bryophytes in the same forest. However, in tropical forests with low tree species diversity, clear host-tree relationships may be observed. The best example is demonstrated by Cornelissen and ter Steege (1989; ter Steege and Cornelissen 1989) on dry evergreen forest in Guyana dominated by two tree species (***Eperua grandiflora*** (rough-barked) or ***E. falcata***) (wallaba, smooth-barked; Figure 45-Figure 46). Not surprisingly, the two tree species host different epiphytic bryophyte assemblages, with the rough bark of ***E. grandiflora*** supporting more epiphytes.

Figure 45. ***Eperua falcata***, Guyana, showing smooth bark. Photo by Bernard Dupont, through Creative Commons.

Figure 46. ***Eperua falcata***, a species that has smooth bark and inhabits dry sites. Photo by Hiobson, through Creative Commons.

Rudolph *et al.* (1998) examined host tree characteristics in a western Andean rainforest in Ecuador (Figure 47). Müller and Frahm (1998) elaborated on the epiphytic mosses in an Ecuadorian montane rainforest in the Andes. They found 65 species (24 mosses, 41 liverworts) on the ten trees they examined. They found no significant correlation between species number and branch diameter, branch exposure, or elevation. However, as bark *p*H increased, the number of epiphytic bryophyte species decreased.

Figure 47. Ecuador tropical rainforest in middle of Rio Tiguiono at Bataburo Lodge. Photo by Andreas and Christel Nöllert, with permission.

Thus, even in cases where host specificity is absent, certain characteristics seem to encourage or discourage bryophytes. As noted earlier, bark differences in the tropics can be important for some bryophyte species, but have little effect on bryophyte communities or species richness.

Host "trees" can also include tree ferns. Jaag (1943) examined the foliage renewal rate, leaf life, and epiphyte "involvement" on tropical tree ferns. Frahm (2003) described the meager studies on epiphytes on tree ferns. In Southeastern Brazil, he identified 142 species on ***Cyathea*** (Figure 48-Figure 49) and ***Dicksonia*** (Figure 50) trunks. Most of these seem to be chance occurrences, with only 20 species occurring on more than 10% of the fern trunks in the study. Vital and Prado (2006) found a species new to Brazil (***Ceratolejeunea dentatocornuta***; see genus in Figure 51) occurring on ***Cyathea delgadii*** (Figure 52-Figure 53). These were in a fragment of the Atlantic forest in the state of Sao Paulo. In total, the researchers found 35 bryophyte species, 12 of mosses and 23 of liverworts. Medeiros *et al*. (1993) reported epiphytes on ***Cibotium*** species (Figure 54) and ***Sphaeropteris cooperi*** (=***Cyathea cooperi***; Figure 55), both tree ferns, in a Hawaiian rainforest (Figure 56).

Figure 48. ***Cyathea arborea*** in Guadeloupe. In Brazil and elsewhere, this genus serves as substrate for epiphytic bryophytes. Photo by Patrice, through Creative Commons.

Figure 49. ***Cyathea arborea***. In Brazil, trunks of this genus serve as substrates for epiphytic bryophytes. Photo by Xemenendura, through Creative Commons.

Figure 50. ***Dicksonia antarctica***. In Brazil, this genus serves as substrate for epiphytic bryophytes. Photo by Fir0002-Flagstaffotos, with online permission.

Figure 51. ***Ceratolejeunea cubensis***; ***C. dentacornuta*** was found as a new species on ***Cyathea delgadii*** in Brazil. Photo by Scott Zona, with permission.

Figure 52. ***Cyathea delgadii***, host of the new species of liverwort ***Ceratolejeunea dentacornuta***. Photo by Alcatron, through Creative Commons.

Figure 53. ***Cyathea delgadii***, host of the new species of liverwort ***Ceratolejeunea dentacornuta***. Photo by Alcatron, through Creative Commons.

Figure 54. ***Cibotium menziesii***; some members of this genus host bryophytic epiphytes in Hawaii. Photo by Forest and Kim Starr, through Creative Commons.

Figure 55. ***Sphaeropteris cooperi***, host of bryophytic epiphytes in Hawaii. Photo through Creative Commons.

Figure 56. Spring rainforest stream with mosses, Hawaii. Photo by Jcklyn Baltazar, through Creative Commons.

Using a line-intercept method, Batista and Santos (2016) studied the epiphytic bryophytes in the Atlantic Forest of southeastern Brazil (Figure 57). They identified 71 taxa. The mean coverage did not vary significantly among the various phytophysiognomies. Nevertheless, the species compositions were distinct among these phytophysiognomies, but no cohesive or isolated groups emerged. There was, however, a correlation between bryophyte cover and tree DBH. Bark *p*H of the palm ***Euterpe edulis*** (Figure 58) and bark roughness of members of the tree fern family **Cyatheaceae** (Figure 52-Figure 53, Figure 55) also affected species composition.

Figure 57. Atlantic forest, Pernambuco coastal habitat, Camarigibe, Brazil. Photo by Leonardo Brito Uniemelk, through Creative Commons.

Figure 58. ***Euterpe edulis*** in Brazil. Bark *p*H of this species affects species composition of bryophytic epiphytes. Photo by Alex Popovkin, through Creative Commons.

In areas with many plantations and more than one host species, more specificity may present itself. For example, in Nigeria over 60% of ***Octoblepharum albidum*** (Figure 59) collections were from ***Elaeis guineensis*** (Egunyomi 1975, 1978), whereas ***Calymperes palisotii*** (Figure 60) prefers ***Albizia saman*** (Figure 61-Figure 62) over the relatively smooth, non-fissured bark of ***Lagerstroemia*** sp. (Figure 63-Figure 64) (Egunyomi & Olarinmonye 1983). Different agroforests [mango (Figure 65) and *Citrus* (Figure 66)] house unique bryophyte communities. Ezukanma *et al*. (2019) found that each of these two communities had 12 bryophyte species, but only five were common to both.

Figure 59. ***Octoblepharum albidum***, one of the eight most common bryophytic epiphytes in the Amazon basin. Photo by Portioid, through Creative Commons.

Figure 60. ***Calymperes palisotii*** showing gemmae on leaf tips. Photo from Wilding *et al*. 2016, with permission.

Figure 61. ***Albizia saman***, substrate for ***Calymperes palisotii***. Photo by A. Gentry, MBG, through Creative Commons.

Figure 62. ***Albizia saman*** rough bark suitable for ***Calymperes palisotii***. Photo by David Stang, through Creative Commons.

Figure 63. ***Lagerstroemia speciosa*** from India. The smooth bark of species of ***Lagerstroemia*** in Nigeria is not suitable for the moss ***Calymperes palisotii***. Photo by Raju Kasambe, through Creative Commons.

Figure 64. ***Lagerstroemia speciosa*** bark from Hawaii, USA; smooth bark in this genus is not a preferred substrate for the moss ***Calymperes palisotii*** in Nigeria. Photo by Kim and Forest Starr, through Creative Commons.

Figure 65. Mango agroforest in India, a forest type that supports unique bryophyte communities in Nigeria. Photo from Bioversity International, through Creative Commons.

Figure 66, ***Citrus*** (orange plantation), a forest type that supports unique bryophyte communities in Nigeria. Photo by Hans Braxmeier, through Creative Commons.

Height on Tree

Andersohn (2004), working in central Guatemala, asked the question "Does tree height determine epiphyte diversity?" He listed the epiphytes, including the bryophytes. Many other studies have provided insight into this question.

Like epiphytes in other parts of the world, communities at the base, trunk, and crown differ due to light, moisture, and nutrients [Cornelissen & ter Steege 1986; Montfoort & Ek 1990; Kürschner 1990 (studied only base and trunk)]. In some forests, the tree bases receive so little light that even bryophytes are unable to grow there. The branches, on the other hand, can have complex, dense growths that sometimes surround the entire branch like a winter muff (Figure 1) for warming one's hands. In the crown, high light intensity and dryness become limiting. For example, in the dry evergreen (wallaba – ***Eperua falcata***; Figure 45-Figure 46) forest of Guyana, bryophytes and lichens on the canopy twigs of mature ***Eperua*** trees are predominantly of two types, the sun-tolerants and the pioneers (facultative epiphylls) (Cornelissen & ter Steege 1989). Many researchers follow the zones as described by Johansson (1974) (Figure 67-Figure 68).

Campos *et al.* (2019) evaluated The bryophyte epiphytes in six height zones of four forests in the northwestern Amazon. Among the 64 trees sampled, they found 63 species that they considered indicator species for their zones. The tree base (zone 1) exhibited the highest number of species, followed by the outer canopy (zone 6). There was a gradual change in bryophyte communities with height zone, and these indicated the importance of the environmental differences encountered in the vertical gradient of a single tree.

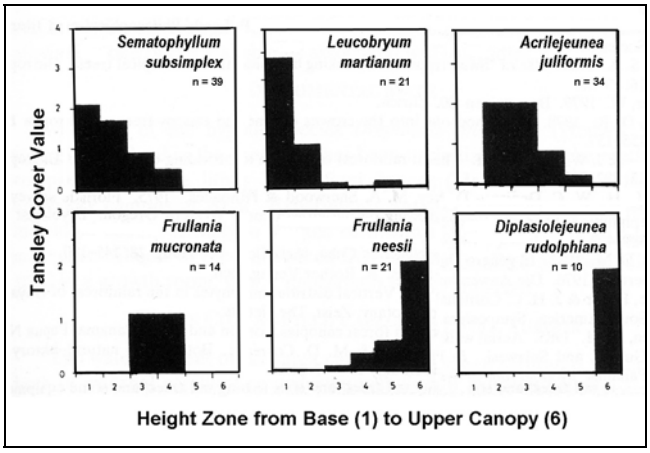

Figure 67. Vertical distribution (see Figure 68) of four moss and two leafy liverwort species in Guyana. Height zones are in Figure 68. Modified from Cornelissen & ter Steege 1989.

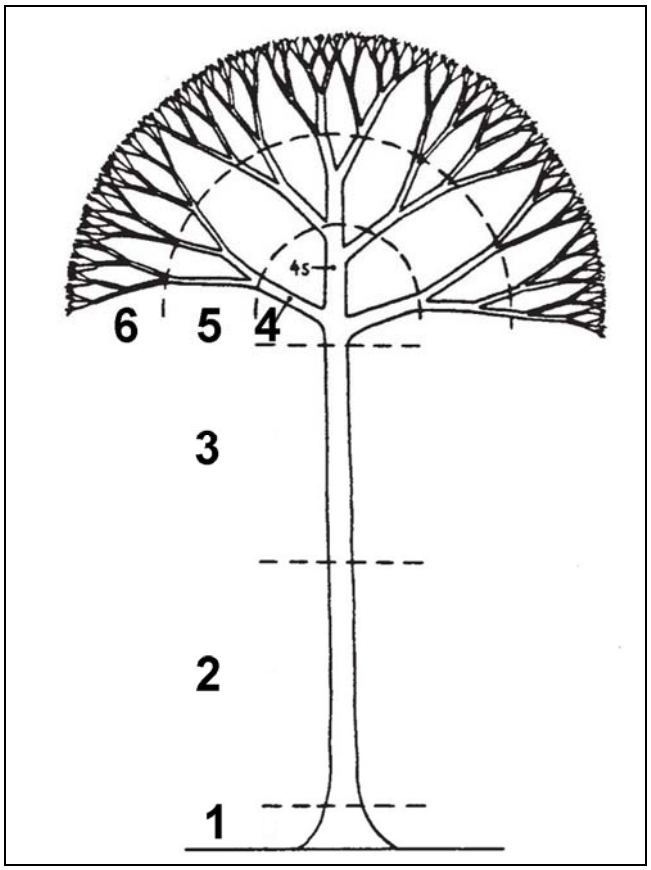

Figure 68. Epiphyte zones on a tree. Modified from Johansson 1974.

Zonation patterns occur from branch tips to center of the crown as well. Freiberg and Freiberg (2000) found that in the two lowland and two montane forests they studied in Ecuador (Figure 69), the epiphytic biomass per branch surface decreases from the center of the crown to the periphery.

Figure 69. Montane forests, Ecuador. Photo by Martin Zeise, through Creative Commons.

Pócs (1982) found that mosses dominate the base of the trunk, but leafy liverworts, especially the ever-present ***Frullania*** (Figure 70) and **Lejeuneaceae** (Figure 6, Figure 8-Figure 9), dominate the branches.

Figure 70. ***Frullania*** sp., a genus that dominates branches of tropical trees. Photo by George Shepherd, through Creative Commons.

In French Guiana (Figure 37), Gehrig-Downie *et al.* (2013) compared the diversity and vertical distribution of epiphytic liverworts between the lowland rainforest and the lowland cloud forest. These lowland cloud forests occur in river valleys with high air humidity and morning fog. This combination creates ideal conditions for epiphytic leafy liverworts. The researchers found a significantly higher species richness of these liverworts in the cloud forest and

the species composition differed (Figure 71) in all six height zones (Figure 68).

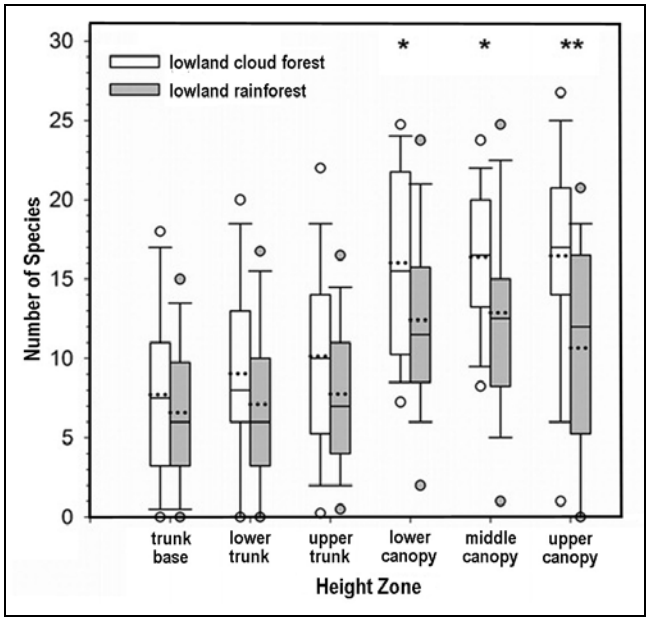

Figure 71. Number of epiphytic liverwort species in each tree height zone (see Figure 68) in the lowland cloud forest and lowland rainforest. n=24 trees per forest type. Boxes are upper and lower quartile, unbroken lines are medians, dotted lines are means, whiskers are 95 percentile, and circles are max and min. **P*<0.05, ***P*<0.01 for t-test differences. Modified from Gehrig-Downie *et al*. 2013.

The lowland cloud forests included more indicator species, particularly shade epiphytes and generalists that also occur in the montane forests (Gehrig-Downie *et al*. 2013). The lowland rainforest exhibited sun epiphyte indicators that characterize dry, open sites. At least in this case, liverwort species richness differs more between forest types than it does among elevation types. Furthermore, the lowland cloud forest may be more species-rich than are the montane rainforests. As is typical throughout most tropical habitats, the **Lejeuneaceae** (Figure 6, Figure 9, Figure 20, Figure 51) represents the largest family, with 95 species. This was followed by **Plagiochilaceae** (9 spp.; Figure 72) and **Frullaniaceae** (7spp.; Figure 70). In the **Lejeuneaceae**, ***Lejeunea*** (Figure 73) had 14 species; ***Ceratolejeunea*** (Figure 51), ***Cololejeunea*** (Figure 74), and ***Plagiochila*** (Figure 72) each had nine species there.

Figure 72. ***Plagiochila*** sp. in the Neotropics. Photo by Michael Lüth, with permission.

Figure 73. Epiphyllous ***Lejeunea*** sp., a species-rich genus in the Neotropics. Photo by Bramadi Arya, through Creative Commons.

Figure 74. ***Cololejeunea gracilis*** var. ***linearifolia*** from Guadeloupe on leaf; ***Cololejeunea*** is a species-rich genus in the Neotropics. Photo by Tamás Pócs, with permission.

Jarman and Kantvilas (1995), working on epiphytes of an old Huon pine (***Lagarostrobos franklinii***; Figure 75) in Tasmania, found 76 species of lichens, 55 of bryophytes, and 16 tracheophytes on that single tree. One factor accounting for the high diversity is that there is little

overlap in species between the base and canopy taxa. Bryophytes dominate at the base, but lichens dominate in the more exposed crown. The bryophytes and lichens on these older trees build sufficient biomass peat on the branches that terrestrial tracheophytes are able to become established in the peat.

Oliveira and ter Steege (2013) used a standardized sampling method across the Amazon Basin (Figure 76) to describe the epiphytic bryophytes in five height zones from the forest floor to the canopy. They sampled eight canopy trees per locality, generating 3,104 records. They were able to identify 222 species and 39 morphospecies. As expected, the leafy liverwort family **Lejeuneaceae** (Figure 6, Figure 9, Figure 20, Figure 51) was the most common (55%), followed by the moss families **Calymperaceae** (Figure 10) (8%), **Leucobryaceae** (Figure 5) (4%), and **Sematophyllaceae** (Figure 102) (4%). Among these, 155 species occur in more than one locality, with 57 species considered to be specialists. In the canopy they found 29 species that are exclusive to the canopy.

Figure 75. ***Lagarostrobos franklinii***, a species that hosts lots of bryophytic epiphytes in Tasmania. Photo by Krzysztof Ziarnek, through Creative Commons.

Sporn *et al*. (2010) reported a record number of 146 epiphytic bryophyte species on eight canopy trees and eight trees from the understory of a submontane rainforest in Central Sulawesi, Indonesia (Figure 77). The trunks of canopy trees have significantly different species composition from that of the understory trees. Furthermore, 45% of the species are restricted to canopy tree crowns, whereas only 12% are restricted to the understory. This study emphasized that inventories of epiphytic bryophytes in a tropical forest should not only focus on canopy trees but also include the small understory treelets and shrubs, which may add at least 10% more species. A similar conclusion was reached by Krömer *et al.* (2007) in a study on tracheophytic epiphyte diversity in tropical submontane and montane forests.

Krömer *et al*. (2007) found that 90% of the tracheophytic epiphytes in the submontane and montane forests of the Bolivian Andes were represented in tree zones Z1-Z2 in the Johansson tree zones (Figure 68). Canopy tracheophytes were primarily orchids and ferns that had special adaptations to the frequent drought conditions. This vertical distribution responds to microenvironmental gradients of the tree, including light intensity, wind speed, and air temperature that increase with height, and moisture that decreases with height. But just what role do bryophytes have in their success?

Figure 76. Amazon rainforest aerial view in Brazil. Photo by Lubasia, through Creative Commons.

Figure 77. Sulawesi forest. Photo by T. R. Shankar Raman, through Creative Commons.

In lowland rainforests around Mabura Hill (Figure 78), Guyana, South America, Cornelissen and Gradstein (1990) reported 134 (52 mosses, 82 liverworts) bryophytes species. Of these, ~30% are **Lejeuneaceae** (Figure 6,

Figure 9, Figure 20, Figure 51). Mountaineering techniques permit study of the forest canopy. There, 50% of the bryophyte species are exclusive to the canopy. The mixed forest has more exclusive species than does the dry evergreen forest, largely because of the outer canopy effect where xerophytic species occur. The canopy species in the dry evergreen forest have wider vertical distributions than do those in the mixed forest, a difference the researchers attribute to the more open canopy foliage in the dry evergreen forest.

Wolf (1994) examined epiphytic vegetation in the northern Andes (Figure 34). He restricted the bark type and sampled four full-grown forest trees at altitudinal intervals of ca 200 m from 1,000 to 4,130 m asl. The variation he found did not seem to relate to any environmental factor. Rather, as noted above, it seemed to relate to randomness in propagule supply. Nevertheless, ordination indicates that distribution patterns relate to altitude and height within the host tree. Interestingly, Oliveira and ter Steege (2015) found the same relationship in Amazonian lowland rainforest (Figure 76). Unlike many other studies, Wolf also found a relationship between the epiphytic vegetation and the host species, particularly for the host ***Brunellia occidentalis*** (see Figure 79-Figure 80), a high altitude species with rapid growth. There is no indication of a relationship with chemical characteristics of suspended soil.

Figure 78. ***Eperua rubiginosa*** seedlings, Mabura Hill Forest Reserve, Guyana. Photo by Hans ter Steege, through Creative Commons.

Figure 79. *Brunellia comocladifolia*; ***B. occidentalis*** is an epiphyte host at high altitudes in the Andes. Photo by Yolanda Leon, through Creative Commons.

Figure 80. *Brunellia goudotii* in Colombia; ***B. occidentalis*** is an epiphyte host at high altitudes in the Andes. Photo by Alvaro Neira, through Creative Commons.

Oliveira *et al*. (2010) noted that, like tracheophytes, bryophytes demonstrate a species gradient from the base to the upper canopy of the host trees. They set out to test the role of niche assembly on a regional scale. They sampled six height zones on several trees in each of three lowland forests of the Guianas (Figure 37) and found that height zone was relatively consistent in the three localities, despite distances up to 640 km, and that that consistency was greater than among communities within the height zones of a single tree (30-50 m in height). More than half (57%) of the species exhibited a height zone preference.

Overall, Oliveira (2010) identified 225 species and 38 morphospecies of Amazonian basin epiphytic bryophytes. As we might expect, the leafy liverwort family **Lejeuneaceae** was the most species-rich family (55% of species). Among the mosses, the most common families were **Calymperaceae** (8%), **Leucobryaceae** (4%), and **Sematophyllaceae** (4%). All four of these families occurred in all 9 sampling locations. The most common species was the leafy liverwort ***Cheilolejeunea rigidulus*** (see Figure 81), followed by ***Ceratolejeunea cornuted*** (Figure 82), ***Octoblepharum pulvinatum*** (Figure 83), ***Octoblepharum albidum*** (Figure 59), ***Archilejeunea fuscescens*** (see Figure 84), ***Sematophyllum sub simplex*** (Figure 85), ***Lopholejeunea subfuscus*** (Figure 86), and ***Symbiezidium barbiflorum*** (see Figure 87). These eight species accounted for 21% of the known species in the study.

Figure 81. ***Cheilolejeunea*** sp. from the Neotropics; ***C. rigidula*** is the most common epiphytic bryophyte in the Amazon basin. Photo by Michael Lüth, with permission.

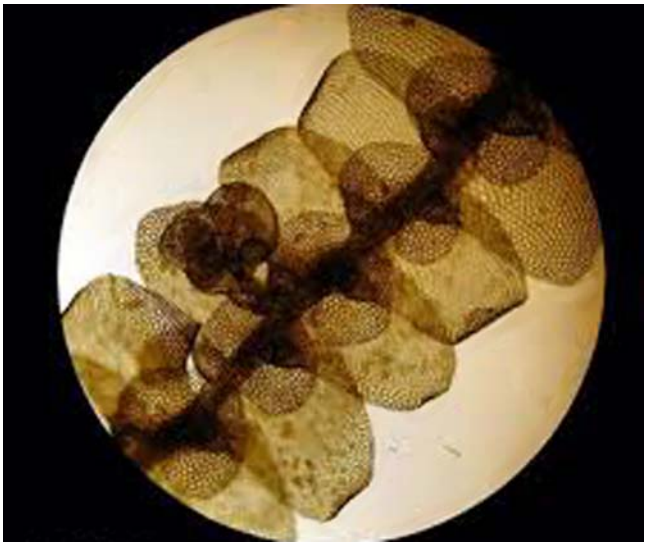

Figure 82. ***Ceratolejeunea cornuta***, one of the eight most common bryophytic epiphytes in the Amazon Basin. Photo by Michaela Sonnleitner, with permission.

Figure 83. ***Octoblepharum pulvinatum*** (light green), one of the eight most common bryophytic epiphytes in the Amazon basin, and ***Syrropodon*** on tree bark in the Luquillo Mountains, Puerto Rico. Photo by Janice Glime.

Figure 84. ***Archilejeunea olivacea***; ***A. fuscescens*** is one of the eight most common bryophytic epiphytes in the Amazon Basin. Photo by John Braggins, through Creative Commons.

Figure 85. ***Sematophyllum subsimplex***, one of the eight most common bryophytic epiphytes in the Amazon Basin. Photo by Yelitza Leon, through Creative Commons.

Figure 86. ***Lopholejeunea subfusca***, one of the eight most common bryophytic epiphytes in the Amazon Basin. Photo by Yang Jiadong, through Creative Commons.

Figure 87. ***Symbiezidium*** sp.; ***S. barbiflorum*** is one of the eight most common bryophytic epiphytes in the Amazon Basin. Photo by Hermann Schachner, through Creative Commons.

Oliveira (2010) found that a total of 155 species occurred in more than one locality, and of these 57 were considered to be specialists (37%), whereas 98 (63%) were considered generalists. The specialists were typically found at the extremes of the gradient, either in zone 1 or zone 6. Only 8 seemed to be specialists in other tree zones. Oliveira concluded that the structure of the communities fit the Neutral Model of Biodiversity and Biogeography, *i.e.*, being there by random recruitment from the local environment. The distribution of the species appears to be influenced by two processes. On a local scale, the interaction between the environment and local abundance provide the greatest influence. Within the Amazon basin, the abundance of the species in the **metacommunity** (sum of all communities sampled in localities and linked by dispersal) are the primary influence. Furthermore, the frequency of long-distance dispersal increased with the height of the zone in the tree. What seems strange is that the greatest genetic distance occurs between the canopy and subcanopy.

In the constant clouds of the dense montane **ombrophilous** (capable of withstanding or thriving in presence of high rainfall) forest (1,000 to 1,500 m asl) in southern Brazil (Figure 88), Santos *et al*. (2018) characterized six vertical zones on 28 trees and identified 96 species of bryophytes in 31 families. The leafy liverwort family **Lejeuneaceae** (Figure 6, Figure 8-Figure 9) was the most species-rich family, followed by **Frullaniaceae** (Figure 70). Liverworts predominated. Species diversity was high, ranging from H'=2.6 to H'=4.1, with high abundances. Of the 28 trees sampled, across this elevation range, the species composition was similar, with only two differing by more than 50%. Bryophyte cover ranged from 3.04% (2 m high to first branches; epiphylls) to 8.97% (0.0-0.5m) in the six phorophyte zones.

Tree Base

In the rainforests, the least light reaches the bases of the great trees (Pócs 1982). At the same time, the bases have the highest humidity in the forest. The bole height of dense bryophyte growth is limited by humidity and the physical condition of the bark, but where it is extremely wet it can reach as high as the first main branches, which may reach 8-10 m high (Richards 1954; Pócs 1982). More typically, it reaches up to 1-3 m, being limited by humidity that sinks to 60% during dry periods (Pócs 1974).

Figure 88. Brazilian southern highlands. Photo by Cecicilio, through Creative Commons.

On tropical tree bases one is likely to find **mats** and **wefts** of various ***Thuidium*** (Figure 89) species, intermixed ***Fissidens*** (Figure 90), and the leafy liverworts in **Lejeuneaceae** (Figure 6, Figure 9, Figure 20, Figure 51) and small turfs of mosses in **Orthotrichaceae** (Figure 28) (Gradstein & Pócs 1989). More suitable, porous bark often supports growths of the mosses ***Leucobryum*** (Figure 5), ***Leucophanes*** (Figure 10), and ***Calymperes*** (Figure 91). Farther up one might find **turfs** of the mosses **Dicranaceae** such as ***Leucoloma*** (Figure 92). As the **wefts** and **turfs** grade away from the base, one can find the **feather** type forming horizontal shelves on the bole (Figure 93) (Gradstein & Pócs 1989). The **dendroid**, **feather**, and **bracket** forms are specialists on the more narrow stems of small trees and branches of shrubs in this low-light zone, but they can also be found at the base (Pócs 1982). These include the mosses ***Lopidium*** (Figure 94) and ***Pinnatella*** (Figure 95) on all continents with tropical forests.

Figure 89. ***Thuidium cymbifolium*** with capsules, in a genus that can be found on some tree bases in tropical rainforests. Photo by Li Zhang, with permission.

Figure 90. ***Fissidens serratulus***, in a genus that occurs on tree bases in tropical rainforests. Photo by Jonathan Sleath, with permission.

Figure 91. ***Calymperes tenerum***, in a genus that occurs on porous bark of tree bases. Photo from the Auckland Museum, through Creative Commons.

Figure 92. ***Leucoloma*** sp. in the Neotropics, a genus that occurs above the tree base in tropical rainforests. Photo by Michael Lüth, with permission.

Figure 93. ***Neckera pennata***, demonstrating shelf formation. Photo by Janice Glime.

Figure 94. ***Lopidium concinnum***. Photo by David Tng, with permission.

Figure 95. ***Pinnatella*** sp. in Bhutan. Photo by David Long, with permission.

In the lowland rainforest of Guyana (Figure 96), Cornelissen and ter Steege (1989) found that the tree base community is characterized by the abundance of pleurocarpous mosses. In the wet, very shady habitats of tree bases these pleurocarpous species include **pendent** and **dendroid** mosses in the **Neckeraceae** (Figure 97-Figure 98) and **Pterobryaceae** (Figure 116) (Pócs 1982). In Asia and northern Australia, these include the mosses ***Homaliodendron*** (Figure 99) and ***Neckeropsis*** (Figure 97-Figure 98), both in **Neckeraceae**; in Africa one finds the mosses ***Renauldia*** and ***Hildebrandtiella*** (Figure 100) in the **Pterobryaceae** and ***Porotrichum*** (**Neckeraceae**; Figure 101). In the Neotropics, ***Neckeropsis disticha*** (Figure 97) and ***N. undulata*** (Figure 98) are ubiquitous. The mosses ***Sematophyllum*** (Figure 102) and ***Taxithelium*** (Figure 117) are likewise common in this zone. The number of species seems to vary in this synusia, with ~100 species in Vietnam, 60 in East Africa, and 50 in Cuba.

Figure 96. Forest at Angoulême, French Guiana (Guyana). Photo by M. Wilkinson, E. Sherratt, F. Starace, and D. J. Gower, through Creative Commons.

Figure 97. ***Neckeropsis disticha***, a species that occurs on tree bases of wet, shady Neotropical habitats. Photo by Piers Majestyk, through Creative Commons.

Figure 98. ***Neckeropsis undulata***, a species that occurs on tree bases of wet, shady Neotropical habitats. Photo by Scott Zona, with permission.

Figure 99. ***Homaliodendron flabellatum***, in a genus that occurs on tree bases of wet, shady tropical habitats in Asia and in tropical Australia, in densely shaded, lowland to montane habitats, epiphytic or on boulders. Photo by Yao, through Creative Commons

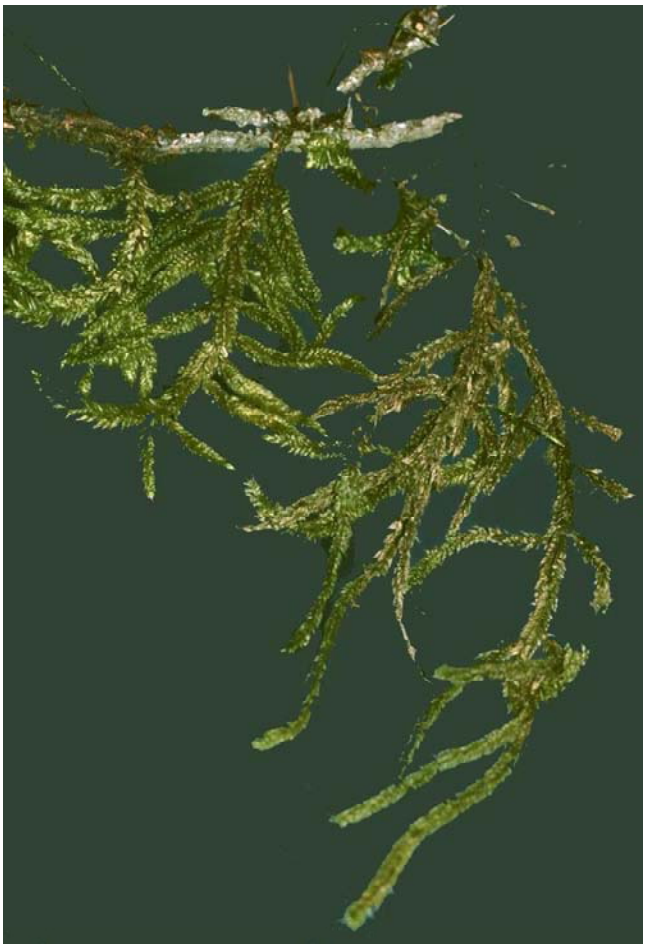

Figure 100. ***Hildebrandtiella guyanensis***, in a genus that occurs on tree bases of wet, shady tropical habitats in Africa. Photo by Claudio Delgadillo Moya, with permission.

Figure 101. ***Porotrichum bigelovii***, in a genus that occurs on tree bases of wet, shady tropical habitats in Africa. Photo from Calbryos, with permission through Paul Wilson.

Figure 102. ***Sematophyllum substrumulosum***, in a genus that occurs on tree bases of wet, shady Neotropical habitats. Photo by James K. Lindsey, with permission.

In Costa Rica, Holz *et al*. (2002) documented the diversity, microhabitat differentiation, and distribution of life forms in the tropical upper montane ***Quercus*** forest [***Q. copeyensis*** (Figure 103), ***Q. costaricensis*** (Figure 104)], using seven freshly fallen trees. They were surprised to find that not only is the tree base bryophyte community distinct from that of the rest of the tree, it is fundamentally the same as that of the forest floor! They also noted the importance of the understory as bryophyte habitat. On **lianas** (vines), poles, twigs on shrubs, ferns, and palms they found 65 species. More details of the Holz *et al*. study are in the subchapter Tropics – Altitude.

Figure 103. ***Quercus copeyensis***, a species whose tree base bryophytes match those of the forest floor. Photo through Creative Commons.

Figure 104. ***Quercus costaricensis***, a species whose tree base bryophytes match those of the forest floor. Photo by Stan Shebs, through Creative Commons.

Further descriptions of the epiphyte bryophyte habitat can be found in Richards (1954) from Guiana (Figure 37), Iwatsuki (1960) from southern Japan, and Tixier (1966) from South Vietnam.

Equihua and Equihua (2007) examined spatial distributions of ***Bryopteris filicina*** (**Lejeuneaceae**; Figure 105) on tree trunks in Chiapas, Mexico (Figure 106). They found it to be over-represented on ***Ampelocera hottlei*** (Figure 107), ***Brosimum alicastrum*** (Figure 108), and ***Guarea glabra*** (Figure 109), all species with smooth bark. Its distribution was determined by height on the tree, bark texture, and orientation, preferring smooth texture and a north-facing orientation.

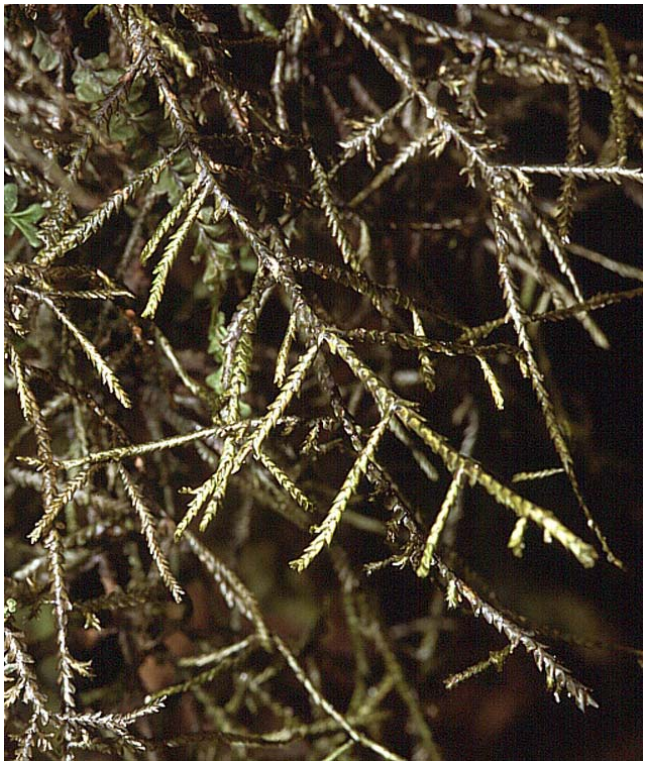

Figure 105. ***Bryopteris filicina*** in the Neotropics. Photo by Michael Lüth, with permission.

Figure 106. Selva Lacandona in Chiapas, Mexico. Photo by Marrovi, modified, through Creative Commons.

Figure 107. ***Ampelocera hottlei*** bole showing smooth bark, a tree preferred by bryophytes. Photo by Indiana Coronado, through Creative Commons.

Figure 108. ***Brosimum alicastrum*** tree base showing smooth bark, a tree preferred by bryophytes. Photo by David Stang, through Creative Commons.

Figure 109. ***Guarea glabra*** showing smooth bark, a tree preferred by bryophytes. Photo from Smithsonian Institution, through public domain.

Upper Trunk

The upper trunks have mostly appressed species (Schofield 1985, pp. 313-314). These are most commonly leafy liverworts such as ***Frullania*** (Figure 70) and **Lejeuneaceae** (Figure 6, Figure 9, Figure 20, Figure 51) (Pócs 1982). Among the mosses one can find **smooth mats** and thread-like **Sematophyllaceae** (Figure 102) again, as well as **Hypnaceae** (Figure 110) and ***Mitthyridium*** (Figure 111), again being appressed.

Figure 110. ***Hypnum cupressiforme*** var. ***heseleri***, a smooth mat former. Photo by Robin Stevenson, with permission.

Kürschner and Parolly (1998c) used the **Braun-Blanquet method** (system using cover-abundance classes; Poore 1955) to describe the various associations on tropical rainforest tree boles. The distribution patterns of the trunk-epiphytic vegetation can be generalized pantropically. Three alliances fall into two orders. Their distribution is correlated to structural parameters of the phorophyte stands and to **isothermic** (equal temperature) intervals: tropical lowland and submontane alliances (20-27°C mean annual temperature); subtropical and montane alliances of the montane rain- and cloud forests (12-20°C); temperate, boreal to subalpine alliances of elfin forests and ericaceous woodlands ((5)8-12°C). A fourth unit (<8°C) includes the Afro-subalpine ***Syntrichion cavallii*** (see Figure 112), mostly known outside the moist tropics and typical of the subpáramo vegetation.

Figure 111. ***Mitthyridium micro-undulatum***, among the genera one can find on the upper trunks. Photo by Jan-Peter Frahm, with permission.

Figure 112. ***Syntrichia*** sp., ***Syntrichia cavallii*** is part of an Afro-subalpine association that lives in elfin forests with low temperatures. Photo by J. C. Schou, with permission.

Lower Branches

The lower, thick canopy branches are typically inhabited by large **mats** of robust epiphytic bryophytes such as ***Plagiochila*** (Figure 72), ***Bazzania*** (Figure 105, Figure 113), ***Macromitrium*** (Figure 114), and others (Cornelissen & ter Steege 1989). Using mountaineering techniques, Cornelissen and ter Steege sampled the ***Eperua*** trees [***Eperua grandiflora*** and ***E. falcata*** (Figure 45-Figure 46)] in the dry evergreen forest of Guyana (Figure 45) from the base to the highest canopy twigs. This revealed a clear vertical distribution pattern of species and life forms for bryophytes. The upper canopy twigs are particularly species rich with both sun epiphytes and pioneers (facultative epiphylls).

Figure 113. ***Bazzania*** from the Neotropics. Photo by Michael Lüth, with permission.

Figure 114. ***Macromitrium*** sp. from the Neotropics. Photo by Michael Lüth, with permission.

Epiphyllous bryophytes, predominantly leafy liverworts in the **Lejeuneaceae** (Figure 6, Figure 9, Figure 20, Figure 51), abound in this lower branch zone, but also occur in abundance in the forest understory (Gradstein & Pócs 1989), in both cases living out of the damaging and desiccating reaches of the sun. The general trend observed for epiphylls is a reduction of species richness from the understory to the canopy (see Montfoort & Ek 1990), while species richness of epiphytes usually increases. These epiphyllous communities are discussed in the subchapter Tropics: Epiphylls.

Twigs

Wolf (1993a, b, c, 1995) described the changes in epiphytic bryophyte community structure of the montane forest, from the canopy twigs to the thickest lower canopy branches, in admirable detail. The lower branches and terminal twigs (Figure 115) of lowland forests support the **pendent Meteoriaceae** (Figure 115) and **Pterobryaceae** (Figure 116), provided it is sufficiently humid, and also the ever-present leafy liverworts ***Frullania*** (Figure 70) and **Lejeuneaceae** (Figure 6, Figure 9, Figure 20, Figure 51) (Pócs 1989). Here one finds **Neckeraceae** (Figure 97-Figure 98) and **Pterobryaceae** such as ***Lopidium*** (Figure 94) or ***Pinnatella*** (Figure 95), or others that are more specific to certain continents (Pócs 1982). ***Sematophyllum*** (Figure 102) and ***Taxithelium*** (Figure 117) reach their peak here. Farther up on the main branches, bryophytes must withstand high light and desiccation. There, dense mats occur, including the mosses **Cryphaeaceae** (Figure 118), **Erpodiaceae** (Figure 119-Figure 120), **Orthotrichaceae** (Figure 28), and **Sematophyllaceae** (Figure 102), as well as the liverworts ***Frullania*** and **Lejeuneaceae** (Figure 6, Figure 9, Figure 20, Figure 51). For those of us from the north temperate and boreal zones, only **Orthotrichaceae** and a few ***Frullania*** and **Lejeuneaceae** taxa are familiar.

Figure 115. ***Pseudobarbella mollissima***, a **pendent** moss in Japan. Photo by Janice Glime.

Figure 116. ***Hildebrandtiella guyanensis*** (**Pterobryaceae**) in the Neotropics. Photo by Michael Lüth, with permission.

Figure 117. ***Taxithelium planum***. Photo by Scott Zona, with permission.

Figure 118. ***Cryphaea jamesonii*** (**Cryphaeaceae**) from the Neotropics. Photo by Michael Lüth, with permission.

Figure 119. ***Aulacopilum abbreviatum*** forming **mats** on a tree in Bareilly India. Photo by Michael Lüth, with permission.

Figure 120. ***Aulacopilum abbreviatum*** forming a dense **mat** in Bareilly India. Photo by Michael Lüth, with permission.

Several species found on the fine canopy twigs are not restricted to this habitat but also occur lower down in the forest on the upper trunks or on living leaves in the forest understory (Cornelissen & ter Steege 1989). These species are considered pioneer species of the rainforest, well adapted to growth on open, unstable substrates. Most of them are small **Lejeuneaceae** (Figure 6, Figure 9, Figure 20, Figure 51) and copiously reproduce by vegetative propagules.

Romero (1999) found the most abundant **pendent** bryophytes on the thin branches (<1 cm diameter). The highest biomass per unit substrate occurred on branches of shade-tolerant species.

Canopy

The canopy, especially the outer canopy, can be a very different and stressful habitat in the forest. It is exposed to the full force of the wind. But based on turbulence analysis of two Amazon rainforest canopies (Figure 17, Figure 76), Kruijt *et al*. (2000) reported a sharp daytime attenuation of turbulence in the top third of the canopies. Thus, within the canopy there is very little air movement. Their hypothesis is that "the upper canopy air behaves as a plane mixing layer." This suggests that tropical rainforest canopies differ from other forests where there are rapid, coherent downward sweeps that penetrate the lower canopy. This penetration does not occur in these Amazonian rainforests. Rather, there is strong heat absorption by the canopy leaves near the top. The weak turbulence is unable to destroy the temperature gradient that is present through the large canopy depth. The inversion is likely to be maintained by strong heat absorption in the leaves concentrated near the canopy top, with the generally weak turbulence being unable to destroy the temperature gradients over the large canopy depth.

Sillett (1991) studied canopy bryophyte communities of six mature ***Ficus aurea*** (Figure 121-Figure 122) trees to elucidate the canopy bryophyte community and compare microhabitats. He divided these into three intact cloud forest and three isolated trees in Costa Rica. He used hemispherical canopy photography to compare light in the crowns, determining that the interior crowns of isolated trees were twice as bright as those in the intact forest. Isolated trees had lower species richness and life-form

diversity. He found 41 species of mosses on the intact forest trees compared to only 29 on the isolated trees, with 50 species in total. The bryophytes on the forest trees are dominated by **pendants**, **fans**, **wefts**, and **tall turfs**, whereas the isolated trees have more **short turfs**. As in other studies, variation of bryophyte communities is greater within a single tree than among trees. Furthermore, the among-tree variation is greater in the forest than among isolated trees.

Figure 121. ***Ficus aurea***, a species that supports many more epiphytes when in the forest than when isolated in the open. Photo by Forest and Kim Starr, through Creative Commons.

Gradstein (2006) described the lowland cloud forest of French Guiana (Figure 123) (in moist river valleys below 400 m asl) where the climate differs from that of the mixed lowland rainforest, but differs by the frequent presence of fog and a large presence of epiphytes, especially liverworts. This forest has species richness of epiphytic liverworts that is similar to that at 2,000 m asl in the Andes and exhibits three times the richness of the Amazonian lowland forest (Figure 17, Figure 76). The moisture counterbalances the high temperatures, permitting the large diversity. The taxonomic composition and abundance differ from those in the tropical montane cloud forest. In the lowland cloud forest, asexual reproduction and dispersal are significantly more common in the canopy than in the forest understory. These canopy species have significantly wider ranges than that found among understory species. Gradstein suggested that these wider ranges are due to long-range dispersal by spores.

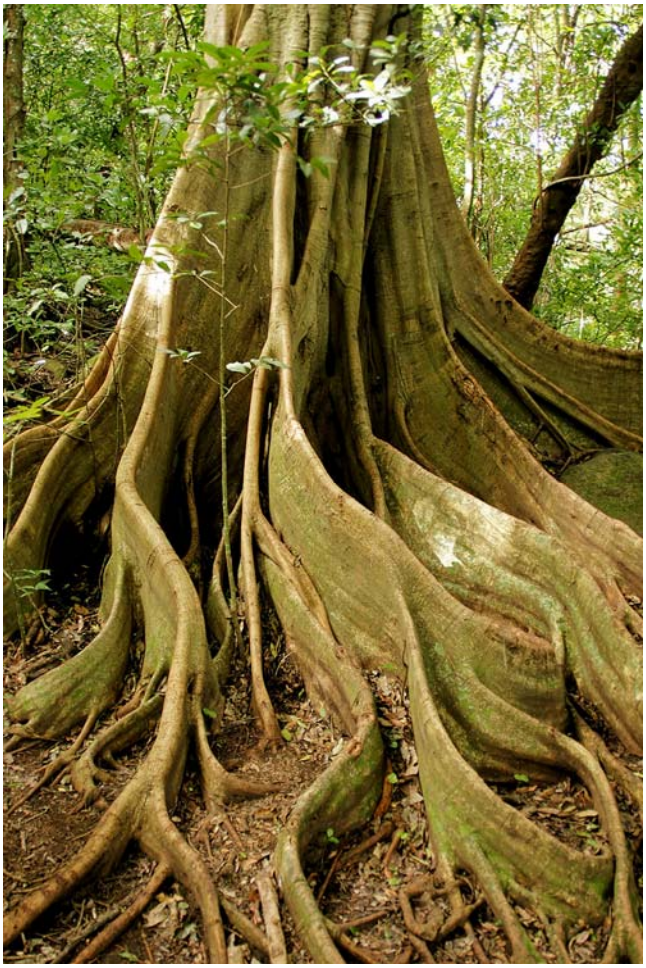

Figure 122. ***Ficus aurea*** in Costa Rica, showing epiphytes on the buttresses. Photo by Has Hillewaert, through Creative Commons.

Figure 123. Canopy in a lowland cloud forest of French Guiana. Photo by Renske Ek, courtesy of Robbert Gradstein.

Logs and Rotten Wood

Where lumbering or wind and hurricane disturbances occur, logs become a visible feature of the landscape (Figure 124). They also result from the normal aging and death of a tree. These logs provide a different habitat, especially in the **epixylic stage** (after bark is lost; Figure 125), than that of tree trunks.

Figure 124. Illegal export of rosewood logs from Madagascar. Photo by Erik Patel, through Creative Commons.

Figure 125. Decorticated log with epixylic bryophytes. Photo from UuMUfQ, through Creative Commons.

Winkler (1976) conducted some of the earliest studies of tropical bryophytes on rotten wood. Frahm (2003) compared the taxa on rotten wood in the tropics. This is the primary available substrate in lowland forests due to the heavy cover of leaf litter elsewhere on the forest floor. Logs usually are inhabited by **Sematophyllaceae** (Figure 102), **Hookeriaceae** (Figure 134), and **Leucobryaceae** (Figure 5) among the mosses. At Monteverde, one can also find ***Pyrrhobryum spiniforme*** (Figure 126) (Gradstein *et al*. 2001). In the cloud forest of Monteverde, Costa Rica (Figure 127), one can find the bryophytes on logs that can differ from these (see subchapter Tropics: Altitude, part 2).

Figure 126. ***Pyrrhobryum spiniforme*** in Hawaii. Photo by Alan Cressler, with permission.

Figure 127. Monteverde cloud forest, Costa Rica. Photo by Haakon S. Krohn, through Creative Commons.

The rotten wood of moist tropical montane forests supports a rich bryophyte flora. Such logs on Mt. Meru and the Usambara Mountains in Tanzania (Figure 128) supported 102 taxa of bryophytes on logs (86 mosses, 16 liverworts), including 71 taxa in 51 20x20 cm plots. (Mattila & Koponen 1999). Cornelissen and Karssemeijer (1987) presented a scale to determine the decomposition stage of the wood: 1 – knife does not penetrate, 2 – penetrates one centimeter, 3 – penetrates several centimeters, 4 – penetrates to the handle. (See also Frahm 2003 for its use in the tropics.)

In Neotropical Puerto Rico, Sastre-de Jesús (1992) found that **Lejeuneaceae** (Figure 6, Figure 8-Figure 9) and **Calymperaceae** (Figure 10, Figure 91) dominated the logs with bark intact. Softwood logs frequently had ***Taxithelium planum*** (Figure 117) and ***Isopterygium tenerum*** (Figure 129). Bryophytes on heavily decayed logs tended to have species with higher water requirements, presumably due to the relatively constant water content of these logs.

Figure 128. Western Usambara Mountains, Tanzania. Photo by David Ashby, through Creative Commons.

Figure 129. ***Isopterygium tenerum***, a species that occupies softwood logs in Puerto Rico. Photo by Scott Zona, through Creative Commons.

Rotten logs and rotting wood with bryophytes are able to retain good moisture (Laman 1995). This in turn provides a suitable and important substrate for the germination of seeds such as ***Ficus crassiramea* subsp. *stupenda*** (Figure 130-Figure 131).

Figure 130. ***Ficus crassiramea*** subsp. ***stupenda***, a species that germinates on bryophyte-covered logs in the tropics. Photo by Pia Tan, through Creative Commons.

Figure 131. ***Ficus crassiramea*** subsp. ***stupenda***, a species that germinates on bryophyte-covered logs in the tropical rainforest. Photo by Reuben C. J. Lim, through Creative Commons.

Parolly and Kürschner (2005) reported that under the relatively stable climatic conditions of tropical montane forests, the decay process is predictable. These conditions favor the **weft** and **mat** life form, following **perennial stayers**, a succession similar to that of the trunk epiphytic communities. Flood disturbance is more likely to favor species that are **dendroid** and **mat**-forming **shuttle species** that utilize a diaspore bank to return after flooding. In dry conditions, species are more likely to be **short-turf**-forming colonists. Shady sites are most suitable for **wefts**, giving them greater exposed surface area to take advantage of the low light conditions.

In the remnant Atlantic forest (seasonal coastal deciduous forest; Figure 132) of Brazil, Germano and Pôrto (1996, 1997) found 35 epixylic species of bryophytes. These comprised 11 families of mosses [**Calymperaceae** (Figure 10, Figure 91), **Pilotrichaceae** (Figure 133), **Fissidentaceae** (Figure 90), **Hookeriaceae** (Figure 134), **Hypnaceae** (Figure 135), **Leucobryaceae** (Figure 5), **Leucomiaceae** (Figure 136), **Orthotrichaceae** (Figure 28), **Plagiotheciaceae** (Figure 137), **Sematophyllaceae** (Figure 102), **Thuidiaceae** (Figure 138)] and 5 families of liverworts [**Aneuraceae** (Figure 139), **Frullaniaceae** (Figure 70), **Geocalycaceae** (Figure 140), **Plagiochilaceae** (Figure 72), **Radulaceae** (Figure 35)]. Note the absence of **Lejeuneaceae**. They related the species composition to the decomposition stage of the substrate (Germano & Pôrto 1997).

Figure 132. Remnant Atlantic forest, Brazil. Photo by Leandro Pereira Chagas, through Creative Commons.

Figure 133. ***Pilotrichella ampullacea*** (**Pilotrichaceae**), in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Jan-Peter Frahm, with permission.

Figure 134. ***Cyathophorum bulbosum*** (**Hookeriaceae**), in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Peter Woodard, through Creative Commons.

Figure 135. ***Hypnum curvifolium*** (**Hypnaceae**) with capsules on rock, in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Bob Klips, with permission.

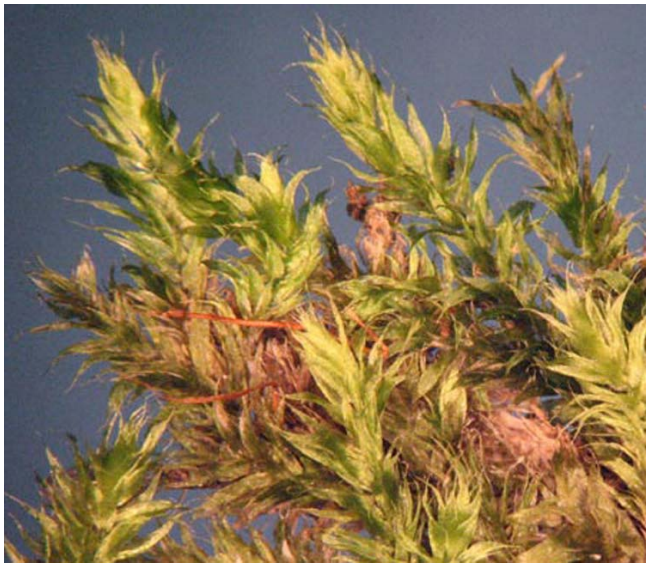

Figure 136. ***Leucomium strumosum*** (**Leucomiaceae**), in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Claudio Delgadillo Moya, with permission.

Figure 137. ***Plagiothecium undulatum***; the **Plagiotheciaceae**, a family represented in a remnant of the Atlantic Forest. Photo by J. C. Schou, with permission.

Figure 138. ***Pelekium cf. gratum***. Photo by Shyamal L., through Creative Commons.

Figure 139. ***Riccardia multifida*** (**Aneuraceae**), in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Hermann Schachner, through Creative Commons.

Figure 140. ***Geocalyx graveolens*** (**Geocalycaceae**), in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Michael Lüth, with permission.

In forest fragments in the Atlantic forest (Figure 132) of northeastern Brazil, Silva and Pôrto (2009) used 100 m transects and small (<100 ha), medium (100-500 ha), and large (>500 ha) fragments to examine fragmentation and edge effects on bryophytes growing on decaying wood. They identified 99 species of epixylic bryophytes (52 liverworts, 47 mosses); liverworts barely predominated here. They found that fragment size was important in determining composition, richness, diversity, and abundance on epixylic substrata. Furthermore, species richness, coverage, and shade tolerance did not correlate with the distance from forest edge. Rather, edge effects seemed to be non-linear, extending beyond 100 m from the forest edge.

In Pernambuco, Brazil, Germano and Pôrto (1996) described the dominant bryophytes in several community types. They found that ***Cololejeunea sicaefolia*** (see Figure 141), ***Lejeunea quinque-umbonata*** (Figure 142), both in the **Lejeuneaceae**, and ***Riccardia*** spp. (Figure 139) are exclusively **epixylic** in their study area.

Figure 141. ***Cololejeunea subcristata***; ***C. sicaefolia***, a leafy liverwort that occurs exclusively on decaying wood in the Pernambuco, Brazil, study area. Photo by Scott Zona, through Creative Commons.

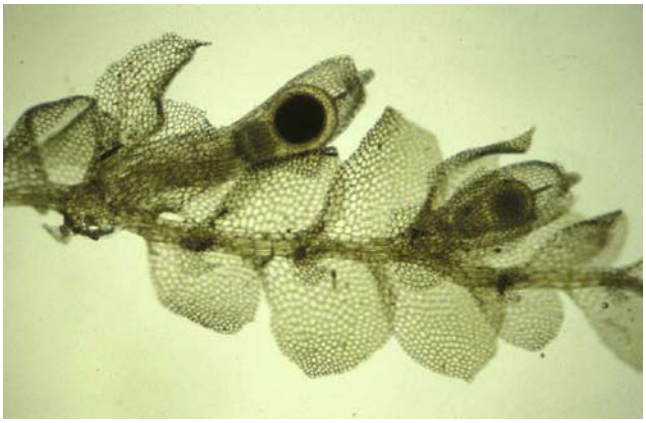

Figure 142. ***Lejeunea quinque-umbonata***, a leafy liverwort that occurs exclusively on decaying wood in the Pernambuco, Brazil, study area. Photo by Elena Reiner-Drehwald.

Sampling

Many bryophytes grow high in the canopy and this provides a particular challenge for collection. Popular recent methods include rope-climbing (Figure 143) (Perry 1978; Whitacre 1981; Cornelissen & ter Steege 1986) and bow-and-arrow techniques (Dial & Tobin 1994). These methods can even be used to collect the tiny leafy liverworts that hide among the larger bryophytes and tracheophytes. Tweedie and Bergstrom (1995) developed a

hierarchical approach for bryophytic epiphytes that could handle their spatially complex ecosystems.

Figure 143. Rope-climbing to sample the canopy of a lowland rainforest in the Colombian Amazon. Photo by Laura Campos, courtesy of Robbert Gradstein.

Pardow *et al*. (2012) concluded that bryophyte life-form analysis of the canopy can be accomplished from the ground in the lowland rainforest of French Guiana (Figure 37). When this is the case, life forms could be used easily to indicate functional diversity.

Several sampling techniques for estimating abundance of non-vascular epiphytes, including bryophytes, have been developed over the past decade. The efficacy of those techniques, however, has never been investigated. Lovai *et al*. (2012) compared three protocols for sampling epiphytic bryophytes in tropical montane rainforests. They examined ladder quadrats, 10 x 10 cm quadrats at intervals of 40 cm, and a 10-cm-wide strip around the stem. The use of 10 x 10 cm quadrats at intervals of 40 cm proved to be the most effective and efficient sampling method for quantifying bryophyte cover and demonstrated a typical species-area curve (Figure 144).

Bryant *et al.* (1973) used **R-mode analysis** (species x species) and **Q-mode analysis** (principal component analysis for linear discriminant analysis) (Lee *et al*. 2017) of area x area to compare the distributional patterns of 155 species of leafy liverworts in the Luquillo Mountains of Puerto Rico (Figure 145. They compared high altitude with low-altitude areas, shaded, moist habitats with open, more exposed habitats, and disturbed, low-elevation habitats with less disturbed habitats at all elevations. R-mode and Q-mode produced nearly identical distribution patterns. Therefore, either method can be used to determine which species are the best indicators of habitat differences.

A technique that has been used in ecological studies in several ecosystems is that of recording **morphospecies** (species forms). This permits the researchers to use a team of novices and accomplish a wide survey in a short time (Gradstein *et al*. 2003). Using the technique for bryophytes, lichens, and tracheophytes, but not epiphylls, they estimated that they could inventory one hectare of tropical rainforest in two weeks. No identifications were attempted, enabling a team of six with three specialists (bryophytes, lichens, tracheophytes) and three assistants to accomplish the survey.

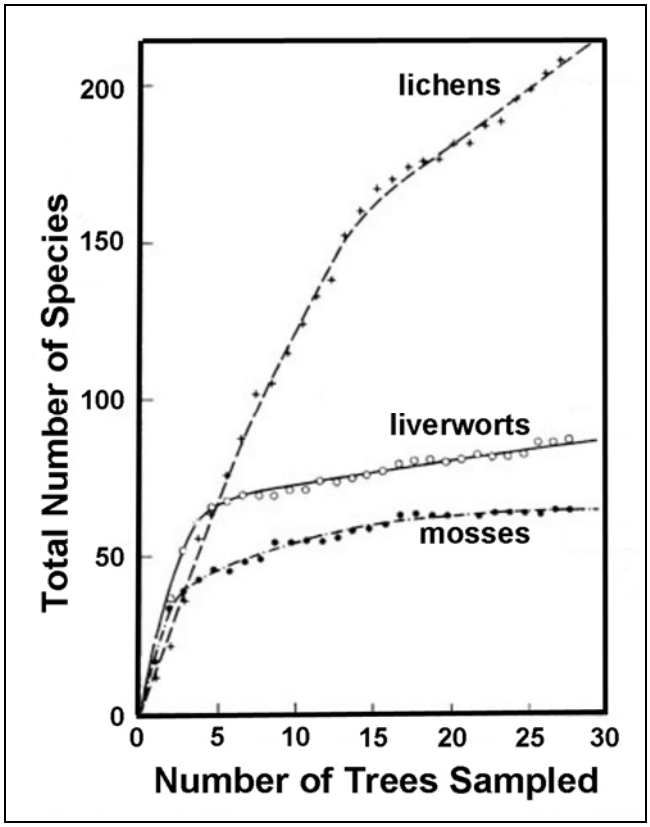

Figure 144. Species-area curve for epiphytic bryophytes and lichens in a lowland rainforest of French Guiana, based on Montfoort & Ek 1990.

Figure 145. El Yunque National Forest, Luquillo Mountains, Puerto Rico. Photo by Kai Griebenow, through Creative Commons.

Gradstein *et al.* (2003) developed a standard protocol of recording morphospecies (species forms) for rapid and representative sampling of epiphyte diversity of one hectare of tropical rainforest. Based on species-accumulation curves they found that inventories of 5 whole trees, using standard plots in all height zones, may be sufficient to sample 70-80% of the diversity of the epiphytic bryophytes of the forest. For vascular epiphytes and epiphytic lichens, however, more trees must be sampled. Using the protocol, the bryophyte inventory of one hectare can be

accomplished in two weeks by a team of one specialist and one field assistant. The results obtained by means of the standard protocol have been used for making comparisons of bryophyte species richness along elevational gradients (Gehrig-Downie *et al.* 2013) and along disturbance gradients (Gradstein & Sporn 2010). A standardized technique also permits comparisons between locations (countries) and hopefully even among researchers.

Quadrats

Nadkarni (2000) established "cylindrats" that she used to track colonization. In a lower montane cloud forest, Monteverde, Costa Rica, she used photography to track the colonization in these epiphytic plots. She also wrapped a clear acetate sheet around the branch, then placed a second clear sheet with a matrix of 100 dots (10x10). Using five random locations around the branch segment she counted the number of dots that touched epiphytes. These counts were converted to percent cover.

Affeld *et al*. (2008) used single samples (30 x 25 cm) from 96 epiphyte assemblages located on inner branches of 40 northern rata (***Metrosideros robusta***; Figure 146-Figure 147) trees to show that epiphytes are important in determining community structure on South Island, NZ.

Figure 146. ***Metrosideros robusta*** with epiphytes. Photo by Phil Bendle, through Creative Commons.

Wolf (1993d) used **relevés** (visual descriptions of vegetation of area plus habit and habitat data) to study epiphytes in the tropical montane rainforest in the northern Andes (Figure 34). This usually involves examining all the microhabitats and niches to find all possible species. They used rope-climbing techniques to reach the bryophytes.

Figure 147. ***Metrosideros robusta*** showing inner branches. Photo by Phil Bendle, through Creative Commons.

Rope Climbing

Early tropical researchers, in an attempt to get better representation of the canopy bryophytes, frequently used ropes to help them climb the trees (Wolf 1993a, b, c, 1995; Gradstein *et al*. 1996; Nadkarni 2000).

Sillett (1991) set out to develop a quantitative method for sampling tropical canopy bryophytes. He used hemispherical canopy photography to learn that interior crowns of isolated trees (Figure 148) are twice as bright as the interior crowns of intact forest trees of the same species (***Ficus tuerckheimii***; Figure 149). He climbed the trees to sample them. Sillett used a cost-benefit analysis that indicated more branches per tree and fewer plots per branch minimizes time but provides similar information.

Figure 148. Tree climbing on tropical montane isolated tree, showing the brightness of the canopy. Photo by F. Werner, courtesy of Robbert Gradstein.

Figure 149. ***Ficus tuerckheimii***, a species used by Sillett to develop methods for sampling the canopy. Photo by Dick Culbert, with online permission.

Older techniques such as tree climbing for collecting canopy bryophytes can present several problems. Many twigs and small branches cannot be reached from those branches that are strong enough to support the climber. Pole-climbing techniques require using a harness and the climbing spikes used can dislodge bryophytes and other epiphytes and put holes in the tree trunks, providing entry sites for pathogenic fungi and insects (Perry 1978). Inspired by Perry (1978), Cornelissen and ter Steege (1989) developed a rope-climbing technique that has been used by many researchers, including Dimitri Montfoort, Renske Ek, Jan Wolf, Ingo Holz, Nicole Nöske, Simone Sporn, Sylvia Mota de Oliveira, Laura Campos, and Angel Benitez, among others.

Using this method, Lücking *et al*. (1996) and Gradstein *et al*. (1996) reported that trees can be prepared for rope climbing in an hour, permitting the researcher to climb to 30 m in 5-10 minutes. Unfortunately, the outer branches are too fragile for climbing and must be sawed off.

Non-bryologists who collect may be fascinated by the epiphyllous species and usually do not provide representative sampling of the branch species. They furthermore often fail to provide the necessary data, such as substrate, that helps the taxonomist to identify the samples. While their collections are valuable to increase our knowledge of the species in an area, they can miss whole groups of taxa and should be used with caution for quantitative conclusions or ecological inferences.

Bow and Arrow

Perry (1978) modified the pole climbing techniques by adding ropes to the equipment. Once the rope is thrown over a sturdy branch, it can be used to help hoist the climber to the level of the branches. The placement of the rope is facilitated by use of an 80-pound pull crossbow and weighted arrow tied to 30-pound test monofilament. The weight of the arrow insures that the arrow will fall to the ground. A spool can be wrapped around the line to prevent tangling.

This is only the first step. Next, a 120-240 pound test braided line is attached to the first, smaller line (Perry 1978). The line that can support the climber is too heavy for the bow and arrow. The heavier (240 pound test) line is needed if there are many large branches because abrasion by the branches can break the lighter-weight line. Safety is a foremost concern.

Ter Steege and Cornelissen (1988) described rope techniques (Figure 150-Figure 153) to climb trees to capture epiphytic bryophytes. These were based on previous use by Day (1962), Pike *et al*. (1975), Perry (1978), Perry and Williams (1981), Whitacre (1981), Hoi (1984). Ter Steege and Cornelissen (1986) used a rope technique in Guyana (Figure 96), Wolf (1986) in Colombia, Montfoort & Ek (1990) in French Guiana (Figure 143).

Ter Steege and Cornelissen (1988) emphasized safety aspects: making sure the branch is strong enough and has an angle of less than 45º; using a proper, strong knot; avoiding branches infected by parasites and hemiparasites. The technique requires shooting an arrow over the selected branch (Figure 150), carrying with it a strong nylon fishing line (50-60/100). Tangles are prevented by keeping the line on a fishing reel, preferably a sea-fishing reel, attached to the bow. The arrow head is weighted with lead to help it return to the ground through the branches. The arrow is then removed and a 3-mm cord is tied to the fishing line using a double sheet bend knot (Figure 150). Winding the reel helps to pull the line and attached cord over the branch. An 11-mm speleocord is attached to the 3-mm cord using a double sheet bend knot (see Figure 150 for knots). This 11-mm cord is hauled over the limb by hand power. Construct a lasso with a figure of eight knot and pull it against the limb. The 3-mm cord is attached to the free end of the knot to facilitate pulling the knot down after use. Test the strength of the branch by having **two** people hang onto it with their full weight. Be prepared to get out of the way if the branch breaks! Hang two ascenders or jumars (Figure 151) on the rope to facilitate ascent. Attach one ascender to a seat belt and the other to the climber's feet (Figure 151). Always use locking karabiners to link the ascenders (Figure 152-Figure 153). Another rope can be tossed over desired branches higher up, using a load attached to a 3-mm cord. The procedure of hanging a rope is then repeated. I recommend reading the original article for details. And if this vocabulary is unfamiliar to you, you might not have enough experience to use this method safely.

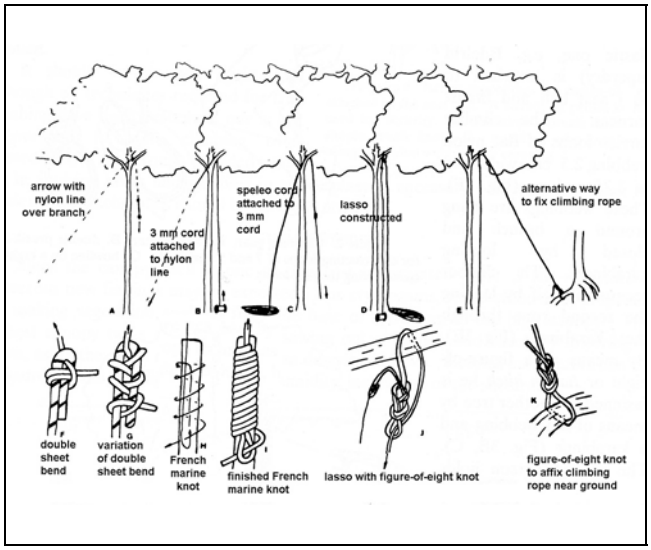

Figure 150. Knots used for rope climbing of trees. Modified from ter Steege & Cornelissen 1988.

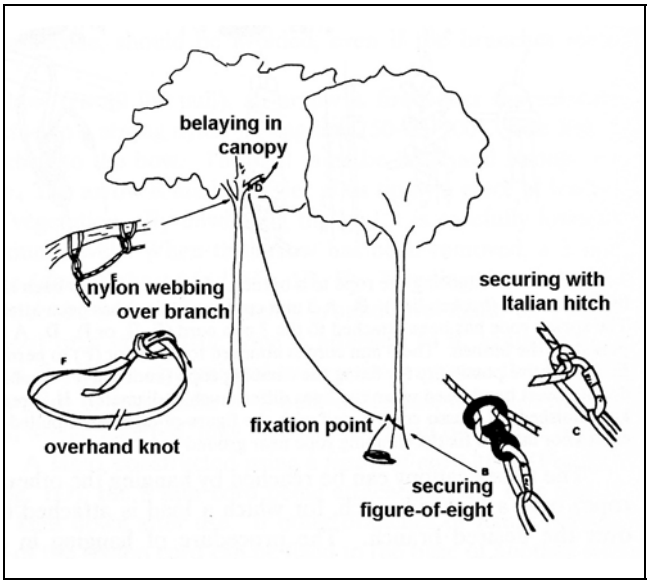

Figure 152. Free-climbing technique. Modified from ter Steege & Cornelissen 1988.

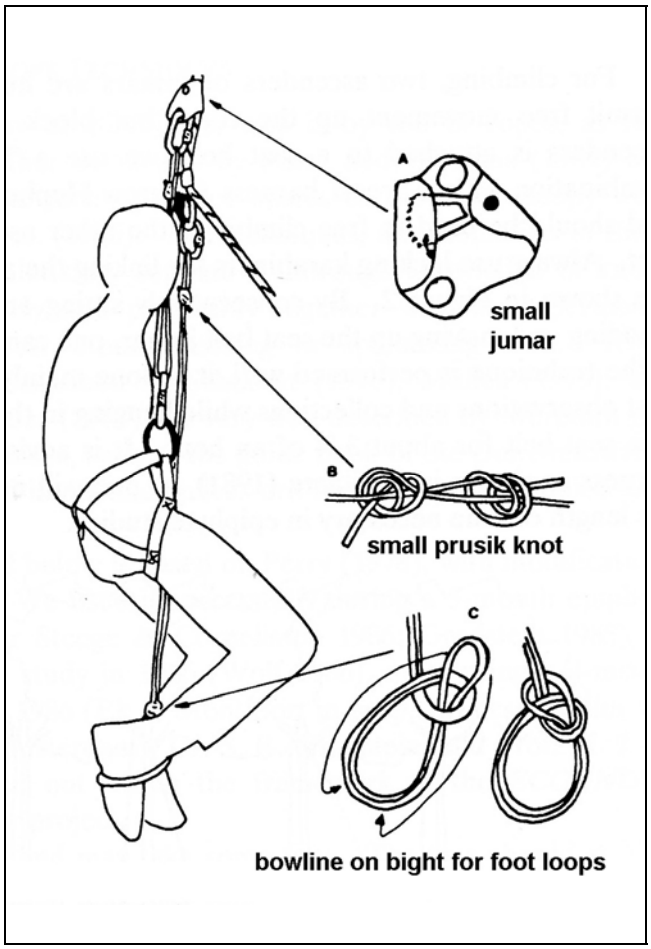

Figure 151. Climbing gear. Modified from ter Steege & Cornelissen 1988.

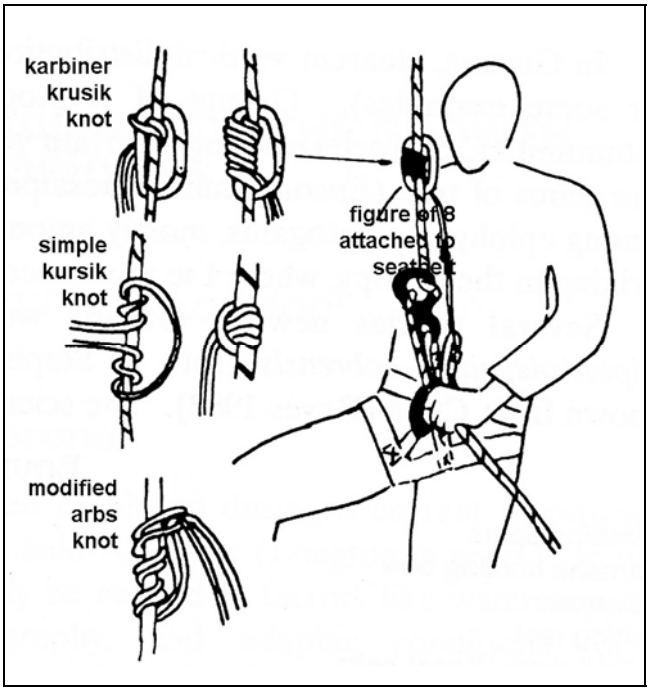

Figure 153. Rappelling knots. Modified from ter Steege & Cornelissen 1988.

Other Canopy Access

Hallé (1990) used an inflatable raft carried by a hot-air dirigible to gain access to canopy epiphytes. Other methods include the use of cranes (Figure 154-Figure 155) (Parker *et al*. 1992; Zotz & Vollrath 2003) and special platforms and walkways (Figure 156) (McClure 1966; Grison 1978; Perry 1978). Lowman *et al*. (2012) provide the standard modern reference on canopy research methods.

Figure 154. Canopy crane at Surumoni, Venezuela. Photo courtesy of Robbert Gradstein.

Figure 155. Canopy crane with gondola in Panama. Photo courtesy of Robbert Gradstein.

Figure 156. Costa Rica skywalk. Photo by Dirk van der Made, through Creative Commons.

Role

Gotsch *et al*. (2016) emphasized the importance of epiphytic material in tropical montane cloud forests (Figure 156). As noted earlier, they intercept both nutrients and moisture from the atmosphere and contribute these over an extended period of time to the forest floor. The amounts of these contributions vary with stand age and microclimate. This epiphytic biomass provides food sources for both birds and mammals, and birds use bryophytic biomass for nest building. Gotsch and coworkers state that more than 200 species of birds use the epiphytes. Wilding *et al*. (2016) cited a number of pendent genera of mosses and liverworts that are used in nest building. These included the mosses ***Papillaria***, ***Floribundaria***, ***Meteorium***, and ***Squamidium*** and the liverworts ***Frullania*** and ***Plagiochila***.

Barkman (1958) and Pócs (1980) suggested that bryophytes may cause their own displacement by retaining water that makes tracheophytic epiphyte presence possible. They furthermore form humus, accelerate bark decay (Barkman 1958), and facilitate anchorage of seeds and other propagules.

Adventitious Roots

Herwitz (1991) found that adventitious roots of the montane tropical rainforest canopy tree species ***Ceratopetalum virchowii*** (see Figure 157) take advantage of the nutrient-rich stemflow, whereas the stemflow of other canopy tree species is nutrient-poor. Such observations as this raise the question of the role of bryophytes in the development of adventitious roots.

Figure 157. *Ceratopetalum apetalum*; ***Ceratopetalum virchowii*** is a canopy tree in the tropical montane rainforest and uses adventitious roots to gain nutrients from stemflow. Photo by John Tann, through Creative Commons.

Nadkarni (1994) found that epiphytic bryophytes do provide a rooting medium for adventitious roots of trees. In fact, a dynamic interaction may occur in which the bryophytes help the tree, and the tree roots likewise help the establishment of the epiphytic community. The bryophyte mat traps inorganic nutrients (Nadkarni 1986) and organic nutrients (Coxson *et al*. 1992) that are leached from members of the epiphyte community. These nutrients nourish the roots of the tree (Nadkarni & Primack 1989). The two appear to grow in mutual benefit, with the roots benefitting from the nutrients and providing a larger anchoring system for the epiphytes as they grow (Nadkarni 1994). As the bryophytes and organic matter increase, they provide more leachates, causing the tree roots to increase.

Leary *et al*. (2004) found that nodulation of the legume ***Acacia koa*** (Figure 158) occurred in the canopy in Hawaii. These nodules contain the bacterium ***Bradyrhizobium*** (Figure 159) in pockets within the canopy. These pockets provide organic soils with trapped nutrients and often form among bryophytes. They even have lower aluminum levels than the terrestrial soils.

Figure 158. ***Acacia koa***, Maui, Hawaii, a species that forms nodules in epiphytic organic soils, including among bryophytes. Photo by Forest and Kim Starr, through Creative Commons.

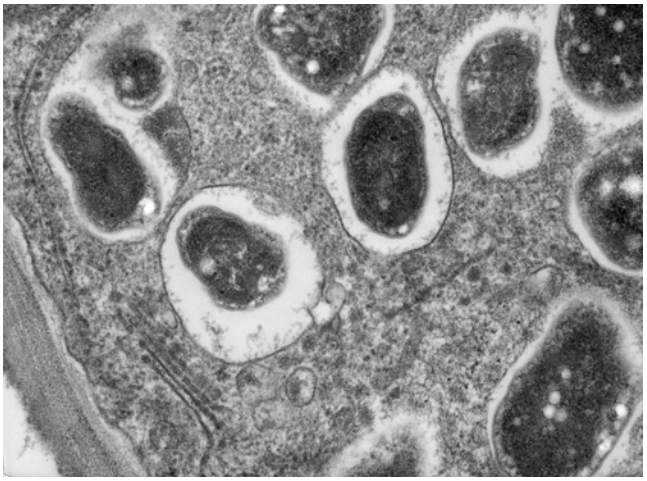

Figure 159. ***Bradyrhizobium japonicum*** from soybean root nodule. A species of ***Bradyrhizobium*** occurs in nodules among mosses on ***Acacia koa***. Photo by Louisa Howard, through public domain.

Substrata for Tracheophytes

Zotz and Vollrath (2003) used a canopy crane (Figure 154-Figure 155) to explore the epiphyte flora of the palm ***Socratea exorrhiza*** (Figure 38-Figure 39) in a primary lowland rainforest of Panama. They examined each palm in a 0.9 hectare and identified 701 tracheophyte epiphytes and hemi-epiphytes on 118 palm trees, identifying 66 species. The tracheophytes usually do not colonize trees less than 20 years old. These tracheophytic epiphytes are significantly associated with bryophytes, but the researchers could find no species that seemed to depend on the bryophytes. On the other hand, one must wonder if the bryophytes are important in maintaining moisture for the roots and storing nutrients trapped during precipitation events, as well as providing a suitable anchor for germinating seeds.

In Madagascar, orchids commonly grow in beds of ***Leucoloma*** (Figure 160) on tree trunks (Pócs 1982; Catherine La Farge, Bryonet September 2004). The bryophytes trap nutrients that make them a suitable substrate for epiphytes.

Figure 160. ***Leucoloma*** sp, India, common substrate for orchids on tree trunks. Photo by Shyamal L., through Creative Commons.

But finding orchids among bryophytes does not indicate any necessary role for the bryophytes. Tremblay (2008) relocated a rare epiphytic orchid after its dislocation from Hurricane Georges. He found that the orchid population size did not correlate with the percent of moss cover on the standing trees. Nevertheless, the orchids seemed to be more frequent when the tree bole had 40-90% moss cover. We need studies to determine the role in bryophytes in trapping and holding seeds and seedlings until the orchids and other plants are able to attach to the tree.

Probably the best example of a moss-dwelling epiphyte is the neotropical fern genus ***Melpomene*** (Figure 161). Almost all species in this genus grow in dense epiphytic bryophyte mats (Lehnert 2007). Sylvester *et al*. (2014) noted that the highest epiphyte elevation known for a tracheophyte was from the southern Peruvian Andes. They reported three species of the fern ***Melpomene*** from ***Polylepis pepei*** (see Figure 162) forests above 4,250 m, with ***Melpomene peruviana*** reaching close to 4,550 m asl. Could it be that bryophytes contribute in some way to their ability to live at these high elevations?

Ferns often inhabit bryophyte mats, where the bryophytes may support the heavy weight of the rhizome on vertical surfaces. Kelly *et al*. (2004) reported that ***Elaphoglossum hoffmannii*** was typically associated with mosses, specifically with ***Syrrhopodon gaudichaudii*** (Figure 163). ***Elaphoglossum wawrae*** (Figure 164) is a Hawaiian epiphytic endemic that occurs in moss mats, and is among the tracheophyte species that characterize the montane zone (Higashino *et al*. 1988; Kitayama and Mueller-Dombois 1992). ***Elaphoglossum glabellum*** growing on ***Epeura falcata*** (Figure 45-Figure 46) is restricted to small moss mats that occur around forks and knots found only in the lower canopy in the lowland rainforest of Guyana (Figure 96) (ter Steege & Cornelissen 1989). On ***Epeura grandiflora***, this species occurs on bryophyte mats from the lower trunk to the middle canopy. The bryophyte mats provide a longer supply of water. But bark differences may account for the differences in bryophyte cover, with ***E. grandiflora*** having rougher bark than that of ***E. falcata***. They may also provide a chemical buffer against toxins in the bark (Frei 1973).

Figure 161. ***Melpomene firma*** and ***M. monoliformis*** – grammitid ferns, both species that grow in dense bryophyte mats in trees. Photo by Marcus Lehnert, courtesy of Robbert Gradstein.

Figure 163. ***Syrrhopodon gaudichaudii***, a species that typically is found with ***Elaphoglossum hoffmannii***. Photo by Michael Lüth, with permission.

Figure 162. ***Polylepis rugulosa*** in the Andes; ***Polylepis pepei*** is host to ***Melpomene*** species in the Andes. Photo by Alexander Yates, through Creative Commons.

Figure 164. ***Elaphoglossum wawrae*** among mosses, a fern endemic to Hawaii that seems to benefit from an association with bryophytes. Photo from USDA, through public domain.

On the other hand, Werner and Gradstein (2008) studied the factors important for seedling establishment of tracheophytic epiphytes in the Andes and found no relationship to bryophyte cover. Rather, isolated trees closer to the forest had significantly greater colonization by these plants, but colonization did not correlate with greater canopy or bryophyte cover.

Friend or Foe?

Cacao plantation owners had concerns over the epiphytes on the leaves, removing them in an effort to improve productivity of the fruit crop (Sporn *et al*. 2007). Removal of epiphytes from cacao had no notable effect on the harvest size of the cacao trees.

But sometimes the bryophytes seem to have negative effects on these trees. Akinfenwa (1989) reported that the epiphytic moss ***Erythrodontium barteri*** (Figure 165) reduced yield of the ***Theobroma cacao*** (Figure 166) trees. They cause a "dressing" effect on palms wherein the leaf bases collect soil in the leaf axils. This soil supports an epiphytic community with microbial activities in the soil. The result is decay of leaf bases, causing the joints to weaken. They can no longer support the epiphytic community, causing it to fall gradually along with the remains of the leaf bases. This process continues as the trees age and grow taller, resulting in smooth boles and consequently fewer leaves for photosynthesis.

Figure 165. ***Erythrodontium squarrosum*** from the Neotropics; ***E. barteri*** is known to reduce yield in the cocoa tree, ***Theobroma cacao***. Photo by Michael Lüth, with permission.

Faunal Habitat

The epiphytes provide a suitable habitat for a number of arthropods in the Neotropical cloud forest (Yanoviak *et al*. 2004). The arthropod morphospecies are similar between green and brown portions of the epiphyte mats, but relative abundances often differ. The most common of these arthropods was an oribatid mite; these preferred the brown portion in laboratory trials.

Bryophytes are home to a variety of frogs and salamanders and are even used by chimpanzees to gather water. Birds use them for nesting material. These interesting interactions are discussed in the volume on Interactions.

Figure 166. ***Theobroma cacao*** in the Dominican Republic, host of epiphytic bryophytes. Photo by C. T. Cooper, through public domain.

Summary

Bryophytes exhibit a number of adaptations to the epiphyte living style. Many of these relate to the usually dry habitat and short duration of available water. The adaptations include green, multicellular spores, sexual dimorphism, asexual reproduction, monoicous condition, rhizoid discs, hyaline leaf margins, and cushion life forms. Their life strategies are typically **perennial stayers** and **perennial shuttle species**. In humid lowland areas **mats** are typical, contrasting with the **fans** and **wefts** that rely on propagules and clonal growth in the montane rainforest. Ciliate leaves collect water. In the xeric open, upper montane forests, **short turfs**, **tall turfs**, and **cushions** predominate. The understory often has **dendroids** and fans while the crowns have more **tufts**. In other cases, the inner branches have **tall turfs** and the outer ones have **smooth mats**. **Fans** and **mats** predominate in floodplains. **Colonists** occur almost exclusively in secondary forests.

The large spores facilitate short-distance dispersal and rapid development when water is available. Arrival on the tree bark appears to be a random event. Succession begins with crustose and foliose lichens and typically proceeds from the underside of the branch upward, although some observers conclude that the lichens inhibit the bryophytes. Ants may sometimes help in the dispersal. Rough bark is more easily colonized and holds more water for growth.

Host specificity is less important than tree characteristics. These relate to bark characteristics, leeward vs windward exposure, height on tree, tree size, and degree of uprightness. The inner canopy has thick branches and fewer bryophyte taxa compared to the thinner middle canopy branches, with greatest richness in the outer canopy. Many species are **facultative** epiphytes. Increasing bark *p*H seems to result in decreased bryophyte richness. Tree base, trunk, and crown differ due to light, moisture, and nutrients. Approximately 45-50% of the species occur in the crowns of rainforest trees.

Tropical forests have an array of vertical niches, but on a horizontal scale, 4-5 trees are adequate to find 95% of the diversity. The **Lejeuneaceae** are common in the canopy as branch epiphytes and as epiphylls. Tree bases often have **mats** and **wefts** of ***Thuidium*** spp., with ***Fissidens*** spp., **Lejeuneaceae**, and **Orthotrichaceae**. Farther up the trunk are **feather** types. **Dendroids**, **feathers**, and **brackets** occur on narrow stems of small trees and branches of shrubs in the understory. Species on the upper trunk are more appressed and correlate with structure of the phorophyte stands and to temperature zones. The lower branches and thick canopy branches typically have large **mats**; epiphyllous **Lejeuneaceae** abound. In moist forests, twigs support **pendent Meteoriaceae**, **Pterobryaceae**, ***Frullania***, and **Lejeuneaceae**. On drier twigs one can find **Cryphaeaceae**, **Erpodiaceae**, **Orthotrichaceae**, **Sematophyllaceae**, ***Frullania***, and **Lejeuneaceae**. The outer canopy contrasts with the inner canopy by having more light and less moisture, creating a stressful environment.

Logs and decaying wood are the primary substrate on the forest floor, raised above the thick litter layer. Dominant bryophytes are in the **Sematophyllaceae**, **Hookeriaceae**, and **Leucobryaceae**. Under stable climatic conditions, **perennial stayers** precede **wefts** and **mat**, a succession similar to that of the trunk epiphytic communities. Flood disturbance favors **dendroid** and **mat**-forming **shuttle species** that utilize a diaspore bank. In dry conditions, species are more likely to be **short-turf**-forming colonists. Shady sites are most suitable for **wefts**.

Epiphyte sampling is best done with ropes or bow and arrow, unless cranes or skywalks are available, minimizing damage to the trees and their flora. Quadrats in all tree zones can permit quantitative sampling. **Life forms** are suitable for assessing functional ecology.

Bryophyte clumps can provide moist rooting media for adventitious roots, and rooting media for ferns and orchids. They retain water, and store nutrients that can be released in pulses. Numerous invertebrate and amphibian species live among them.

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CHAPTER 8-5
TROPICS: EPIPHYTE GEOGRAPHIC DIVERSITY

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CHAPTER 8-5
TROPICS: EPIPHYTE GEOGRAPHIC DIVERSITY

Figure 1. Wet forest of Kohala Mountain, Hawaii, with abundant epiphytes. Photo by Melora Purell, through Creative Commons.

Diversity

As is generally true in the tropics, many species have been named multiple times under different names in different countries (Pócs 1984). Hence, understanding the diversity is difficult, as is understanding the bryogeography. As herbaria have become established in more tropical locations, comprehensive studies of various genera and families is untangling some of these taxonomic problems (see, for example, the revision of African **Lepidoziaceae** (Figure 2) by Pócs 1984).

Figure 2. ***Bazzania hookeri*** (**Lepidoziaceae**) from the Neotropics. Photo by Michael Lüth, with permission.

The **Pterobryaceae** (Figure 21), a family restricted to the tropics, is almost exclusively epiphytic and mostly large, including **dendroid** and **pendent** forms (Churchill & Salazar Allen 2001). Consequently, that family, along with **Neckeraceae** (Figure 3), ***Sematophyllum*** (Figure 10), and ***Taxithelium*** (Figure 4), indicates very shady, wet habitats (Pócs 1982). Typically, mosses dominate the base of the trunk, but leafy liverworts, especially the ever-present ***Frullania*** (Figure 48-Figure 49) and **Lejeuneaceae** (Figure 14), dominate the branches (Pócs 1982; Gradstein 1992).

Figure 3. **Neckeraceae** (***Neckera cephalonica***), a family that indicates very shady, wet habitats in the tropics. Photo by Jan-Peter Frahm, with permission.

Figure 4. ***Taxithelium planum***; ***Taxithelium*** indicates very shady, wet habitats in the tropics. Photo by Scott Zona, with permission.

Australia

The largest number of tropical and subtropical species in the world occur as epiphytes (Ramsay *et al*. 2017). Australia is no exception, where more than 85% of the epiphytic bryophytes occur in the Wet Tropics of north Queensland (Ramsay & Cairns 2004). Of the 21 species of **Orthotrichaceae** reported by Vitt and Ramsay (1985) reported 21 species of **Orthotrichaceae** in all of Australia, but now we know there are at least 24 in tropical Queensland alone (Cairns *et al*. 2019). Many of these Queensland **Orthotrichaceae** species occur above 1200 m, including ***Macromitrium dielsii***, ***M. funiforme***, and ***M. erythrocomum***, all endemic to the Australian Wet Tropics (Ramsay *et al*. 2017). In the **Orthotrichaceae**, 17 taxa are endemic (Ramsay *et al*. 2012). Vitt *et al*. (1995) suggested that such high-elevation taxa are often narrow endemics.

Ramsay *et al*. (1987) found seven genera of mosses that occur in all the major rainforest types in Australia (not all Australian rainforests are tropical): ***Macromitrium*** (Figure 5), ***Racopilum*** (Figure 6), ***Hymenodon*** (Figure 7; not in tropical Australia), ***Rhizogonium*** (Figure 8), ***Pyrrhobryum*** (Figure 9), ***Sematophyllum*** (Figure 10), and ***Thuidium*** (***Pelekium***?; Figure 11). Epiphyte succession there can occur rapidly in the right microclimate. In the crown, species change from prostrate or small upright plants to large cushion mosses such as ***Leptostomum inclinans*** (Figure 12; not in tropical Australia). These large mosses occur only on the upper surfaces of branches. But large cushions become unstable, falling to create new habitats. Bark furrows create niches where mosses can become established.

Figure 5. ***Macromitrium archeri***, member of a genus of mosses that is in all major rainforests in Australia, forming mats. Photo by David Tng, with permission.

Figure 6. ***Racopilum*** cf. ***cuspidigerum***; ***Racopilum*** is a genus of mosses that is in all major rainforests in Australia. Photo by Peter Woodard, through Creative Commons.

Figure 7. ***Hymenodon pilifer***, member of a genus of mosses that is in all major rainforests in Australia, but this species is not in the Australian Wet Tropics. Photo by Niels Klazenga, with permission.

Figure 8. ***Rhizogonium*** sp., member of a genus of mosses that is in all major rainforests in Australia. Photo by Andras Keszei, with permission.

Figure 9. ***Pyrrhobryum paramattense***, member of a genus of mosses that is in all major rainforests in Australia. Photo by David Tng, with permission.

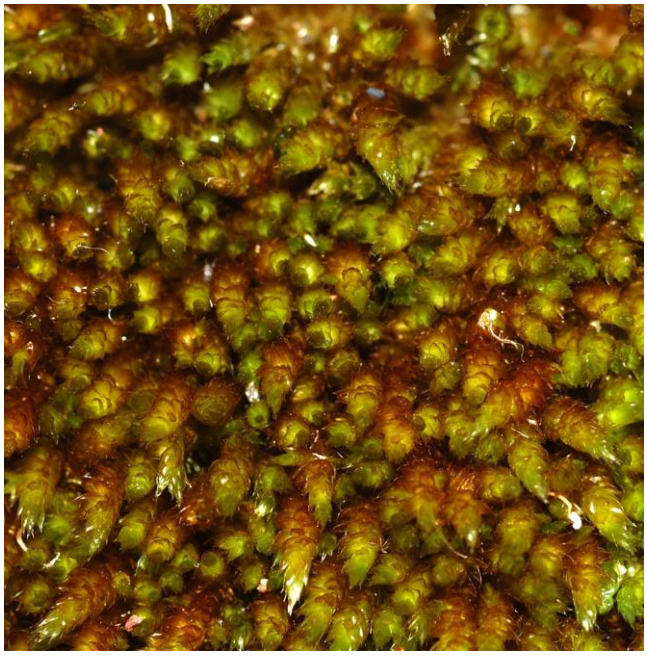

Figure 10. ***Sematophyllum homomallum***, representing a genus of mosses that is in all major rainforests in Australia; in the Wet Tropics. Photo by David Tng, with permission.

Figure 11. ***Pelekium** cf. **gratum***, member of a genus of mosses that is in all major rainforests in Australia, forming **wefts**. Photo by Shyamma L., through Creative Commons.

Figure 12. ***Leptostomum inclinans*** with capsules, a species that forms cushions in the crowns of Australian rainforests, but not in tropical rainforests of Australia. Photo by Clive Shirley, Hidden Forest, with permission.

Asia

The **Lejeuneaceae** (Figure 14, Figure 51) is the most abundant and diverse tropical family. In Asia, Gradstein (1991) found 88 species in 17 genera of **Lejeuneaceae**, subfamily **Ptychanthoideae**. This subfamily has more species but fewer genera in Asia than in the Neotropics, and the species in these two floras are very different. Asia is the center of diversity for the tribe **Ptychantheae** (Figure 13); the Neotropics, on the other hand, has its greatest number of species of **Ptychanthoideae** in the tribe **Brachiolejeuneae** (Figure 14). The two floras (Asia vs Neotropics) are distinctly different taxonomically. Gradstein considered the higher species diversity in Asia to be related to the greater latitudinal extension of the rainforest in the Far East. In the Far East, 22% of the **Ptychanthoideae** are non-tropical species, whereas in the Neotropics the non-tropical species are less than 2%.

Figure 13. ***Ptychanthus striatus***, tribe **Ptychantheae**, in Thailand. Photo by Soonthree Kornochalert, courtesy of Robbert Gradstein.

Figure 14. ***Drepanolejeunea hamatifolia*** (**Brachiolejeuneae** in the **Lejeuneaceae**), a genus represented in the Neotropics. Photo by Barry Stewart, with permission.

Gradstein and Culmsee (2010) reported 150 bryophyte species on tree bases of only eight canopy trees in montane Sulawesi (Figure 15), Indonesia. Using only tree bases, they compared bryophyte communities based on tree diameter and bark roughness at a series of elevations. Low elevation bryophytes were characterized by the mosses in **Calymperaceae** (Figure 52-Figure 53), **Fissidentaceae** (Figure 16), **Hypopterygiaceae** (Figure 17-Figure 18), **Leucobryaceae** (Figure 19), **Meteoriaceae** (Figure 20), **Neckeraceae** (Figure 3), **Pterobryaceae** (Figure 21), and

Thuidiaceae (Figure 11), and the leafy liverworts **in Lejeuneaceae** (Figure 14, Figure 51)**, Lophocoleaceae** (Figure 22), **Porellaceae** (Figure 23), and **Radulaceae** (Figure 24).

Figure 15. Tangkoko National Park, North Sulawesi, Indonesia. Photo by Lip Kee Yap, through Creative Commons.

Figure 16. ***Fissidens pacificus*** (**Fissidentaceae**), in a family that characterizes low-elevation bryophytes. Photo by Jan-Peter Frahm, with permission.

Figure 17. ***Hypopterygium didictyon*** (**Hypopterygiaceae**) on tree, in a family that characterizes low-elevation bryophytes. Photo by Juan Larrain, with permission.

Figure 18. ***Hypopterygium didictyon*** (**Hypopterygiaceae**), a dendroid moss, in a family that characterizes low-elevation bryophytes. Photo by Felipe Osorio-Zúñiga, with permission.

Figure 19. ***Leucobryum boninense*** (**Leucobryaceae**), an epiphytic species in Asia, in a family that characterizes low-elevation bryophytes. Photo by Tomio Yamaguchi, through Creative Commons.

Figure 20. ***Floribundaria plumaria*** (**Meteoriaceae**), in a family that characterizes low-elevation bryophytes. Photo by Michael Lüth, with permission.

Figure 21. ***Calyptothecium duplicatum*** (**Pterobryaceae**), a low elevation genus in Sulawesi, shown here from the Neotropics. Photo by Michael Lüth, with permission.

Figure 22. ***Lophocolea cf polychaeta*** (**Lophocoleaceae**) from the Neotropics, in a low-elevation genus in Sulawesi. Photo by Michael Lüth, with permission.

Figure 23. ***Porella canariensis*** (**Porellaceae**), a low elevation tropical genus in Sulawesi. Photo by Michael Lüth, with permission.

Figure 24. ***Radula flaccida*** (**Radulaceae**) habit with gemmae, in a family that characterizes low-elevation bryophytes. Photo by Michaela Sonnleitner, with permission.

By contrast, bryophytes at higher elevations in Sulawesi (Figure 25) were predominately in the leafy liverwort families **Herbertaceae** (Figure 26), **Lepidoziaceae** (Figure 2), **Mastigophoraceae** (Figure 27-Figure 28), **Scapaniaceae** (Figure 29), **Schistochilaceae** (Figure 30), and **Trichocoleaceae** (Figure 31-Figure 32) (Gradstein & Culmsee 2010). In the submontane and lower montane, **Lejeuneaceae** (Figure 14, Figure 51) has the most species; **Plagiochilaceae** (Figure 33) is also important in the lower montane forest. In the upper montane forest that high diversity is found in the **Lepidoziaceae** (Figure 2). Rough bark is preferred by some species, but none prefer smooth bark. A few species correlate with trunk diameter, but species composition and richness do not. As elevation increases, liverwort species richness generally increases and moss richness decreases. This is a common trend in the tropics. Differences between communities on tree trunks increase with distance, reaching only about 25% similarity between Sulawesi and Borneo. At continental distances, similarity is nearly zero.

Figure 25. Montane mossy cloud forest in Sulawesi, 2300 m at summit of Mt Lokilalaki. Photo courtesy of Robbert Gradstein.

Figure 26. ***Herbertus aduncus*** (l**Herbertaceae**), member of a family that predominates at high elevations in Sulawesi. Photo from Botany Website, UBC, with permission.

Figure 27. ***Mastigophora diclados*** (**Mastigophoraceae**), member of a family that predominates at high elevations in Sulawesi. Photo by Jan-Peter Frahm, with permission.

Figure 28. ***Mastigophora flagellifera*** (**Mastigophoraceae**), member of a family that predominates at high elevations in Sulawesi. Photo by Jan-Peter Frahm, with permission.

Figure 29. ***Scapania cuspiduligera*** (**Scapaniaceae**) with gemmae, member of a family that predominates at high elevations in Sulawesi. Photo by Michael Lüth, with permission.

Figure 30. ***Schistochila*** sp. (**Schistochilaceae**) in China, member of a family that predominates at high elevations in Sulawesi. Photo by Li Zhang, with permission.

Figure 31. ***Trichocolea*** sp. from the Neotropics, member of a family that predominates at high elevations in Sulawesi. Photo by Michael Lüth, with permission.

Figure 32. ***Trichocolea*** sp. from the Neotropics, member of a family that predominates at high elevations in Sulawesi. Photo by Michael Lüth, with permission.

Figure 33. ***Plagiochila dendroides*** (**Plagiochilaceae**), member of a family that predominates at high elevations in Sulawesi. Photo from Taiwan mosses color illustrations, through Creative Commons.

Ariyanti *et al*. (2008) considered that forest disturbance and land use altered for agriculture was changing the landscape in Central Sulawesi, Indonesia (Figure 34), at a drastic rate. Nevertheless, total bryophyte richness did not differ among forest types. But mosses and liverworts reacted differently. Moss richness was lowest in the cacao **agroforests** (Figure 34); liverwort richness was equal in all forest types. But in contrast, moss cover was unaffected, whereas liverwort cover decreased significantly in the agroforest. These differences resulted because species composition changed in the cacao agroforests. The more open agroforests were populated by drought-tolerant species. The species composition also differed markedly between large and small trees in the agroforests, but not in the natural forests. The authors suggested that these effects of tree size were due to changes in stemflow of precipitation water.

Figure 34. Cacao plantation in Sulawesi. Photo courtesy of Robbert Gradstein.

Kürshner (2008) identified six floral elements in southwest Asia, creating a heterogeneous flora. This included endemics with various origins. There is a very strong tropical influence on the bryophyte flora, particularly of the **Palaeotropical** and **Afromontane** elements. Nevertheless, nearly 10% (>95 taxa) are of xero-tropical origin. Many are unique relicts of a formerly more widely distributed flora and are concentrated primarily in the escarpment mountains of the Arabian Peninsula and Socotra Island.

Magdum *et al*. (2017) colleted nine species of corticolous mosses in Panhalgad in the Western Ghats, India, in different seasons, providing the first record of the mosses from the Kolhapur District. These mosses were ***Pogonatum microstomum***, ***Campylopus flexuosus*** (Figure 35), ***Leucobryum bowringii*** (Figure 36), ***Fissidens bryoides*** (Figure 37), ***Fissidens macrosporoides***, ***Loiseaubryum nutans***, ***Anomobryum auratum*** (Figure 38), ***Bryum capillare*** (Figure 39), and ***Bryum uliginosum*** (Figure 40).

Figure 35. ***Campylopus flexuosus***, an epiphyte in Panhalgad of the Western Ghats. Photo by Štěpán Koval, with permission.

Figure 36. ***Leucobryum bowringii***, an epiphyte in Panhalgad of the Western Ghats. Photo through Creative Commons.

Figure 37. ***Fissidens bryoides***, an epiphyte in Panhalgad of the Western Ghats. Photo by Janice Glime.

Figure 38. ***Anomobryum auratum*** in India, an epiphyte in Panhalgad of the Western Ghats. Photo by Michael Lüth, with permission.

Figure 39. ***Bryum capillare***, an epiphyte in Panhalgad of the Western Ghats. Photo by Michael Lüth, with permission.

Figure 40. ***Bryum uliginosum***, an epiphyte in Panhalgad of the Western Ghats. Photo by Štěpán Koval, with permission.

Kürschner (2003) conducted a phytosociological analysis in southwestern Arabia in the Asir Mountains. The characteristic species are drought-tolerant Afromontane mosses, with ***Orthotrichum diaphanum*** (Figure 41) and ***Syntrichia laevipila*** (Figure 42) being most prominent. Life forms and life strategies correlate with the environment. The ***Orthotricho-Fabronietum socotranae*** (see Figure 43) is a drought-tolerant association that is both xerophytic and tolerant of high light. This formation is dominated by **cushion**, **short-turf**, and **mat-forming perennial stayers** that have regular sporophyte production. The ***Leptodonto*** (Figure 44)***-Leucodontetum schweinfurthii*** (see Figure 45) association is typical of sub-humid areas with **sciophytic** (shade-loving) vegetation. Its bryophytes are liverworts in addition to the mosses that are predominantly tails or fan-forming pleurocarpous perennial shuttle species. The mosses typically have large spores, adapting them for short-range dispersal that is either passive (with moderately low reproduction) or generative reproduction. This sciophytic group has a much higher diversity of life forms and life strategies than the xerophytic group.

Figure 41. ***Orthotrichum diaphanum***, a species of dry locations in the Asir Mountains of southwestern Arabia. Photo by Michael Lüth, with permission.

Figure 42. ***Syntrichia laevipila*** with capsules, a prominent species in the Asir Mountains in southwestern Arabia. Photo by Michael Lüth, with permission.

Figure 43. ***Fabronia*** sp.; ***Fabronia socotrana*** is a prominent epiphytic species in the Asir Mountains in southwestern Arabia. Photo by Michael Lüth, with permission.

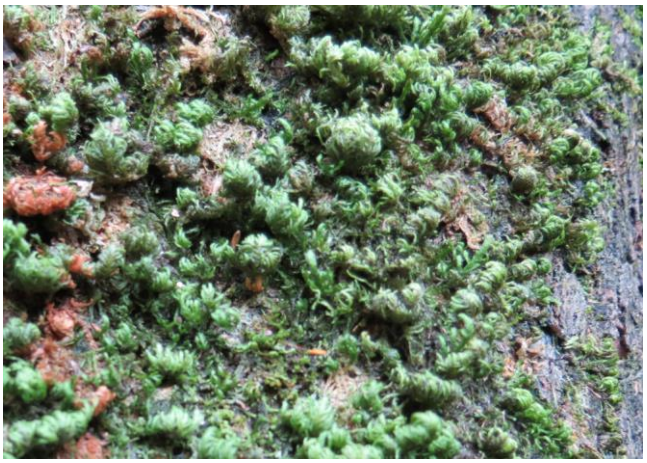

Figure 44. ***Leptodon smithii***; the ***Leptodon*** community is typical of the sub-humid area in the Asir Mountains in southwestern Arabia. Photo courtesy of Jeff Duckett and Silvia Pressel.

Figure 45. ***Leucodon treleasii***; the ***Leptodonto-Leucodontetum schweinfurthii*** community is typical of the sub-humid area of the Asir Mountains in southwestern Arabia. Photo by Jan-Peter Frahm, with permission.

Additional references that may be useful regarding tropical epiphyte diversity in the Asian region include Frahm (1990 – Malaysia), Tixier (1966 – Indonesia), Osada & Amakawa (1956 – Tsushima Islands, Japan).

African Region

Exploration of tropical African bryophytes is relatively new. Augier (1974) listed **corticolous** (growing on bark) bryophytes in the submontane forest of western Cameroon (Figure 46). Akande *et al*. (1982) examined **corticolous** bryophytes in Ibadan, Nigeria. On the 8 phorophytes on two sites they examined, they identified 20 bryophyte species. ***Entodontopsis nitens*** (Figure 47) is common and present on both sites. They considered ***Frullania dilatata*** (Figure 48-Figure 49) and ***Entodontopsis tenuinervis*** to be accidental species. They found the *p*H of the bryophytes to be similar to that of their bark substrate. In 28 comparisons, 11 bryophyte species combinations have a similarity of 50% or more. ***Entodontopsis nitens*** and ***Pelekium gratum*** (Figure 50) have a high degree of association, as do ***E. nitens*** and ***Mastigolejeunea florea*** (see Figure 51), ***Entodontopsis nitens*** and ***Erythrodontium barteri***, ***Entodontopsis nitens*** and ***Calymperes palisotii*** (Figure 52-Figure 53), and ***Erythrodontium barteri*** and ***M. florea***. Light is important in determining the height of the bryophytes on the trees. There seems to be no indication of preference for tree species, but the number of trees sampled was limited.

Figure 47. ***Entodontopsis nitens***, a common epiphytic species in Ibadan, Nigeria. Photo from Wilding *et al.* 2016, with permission.

Figure 48. ***Frullania dilatata*** on smooth bark, a species considered to be accidental in this habitat in Ibadan, Nigeria. Photo by Bernd Haynold, through Creative Commons.

Figure 46. Menchum Falls, NW Province, Cameroon. Photo by Nick Annejohn and family, through public domain.

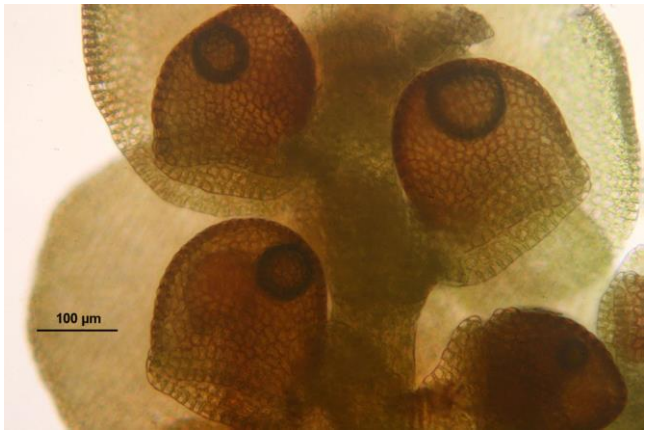

Figure 49. ***Frullania dilatata*** lobules. Photo by Hermann Schachner, through Creative Commons.

Figure 50. ***Pelekium cf. gratum***, a species that shares a 50% similarity index with ***Entodontopsis nitens***. Photo by Shyamma L., through Creative Commons.

Figure 51. ***Mastigolejeunea repleta***; ***M. florea*** shares a 50% similarity index with ***Entodontopsis nitens***. Photo by Y. M. Wei, courtesy of Robbert Gradstein.

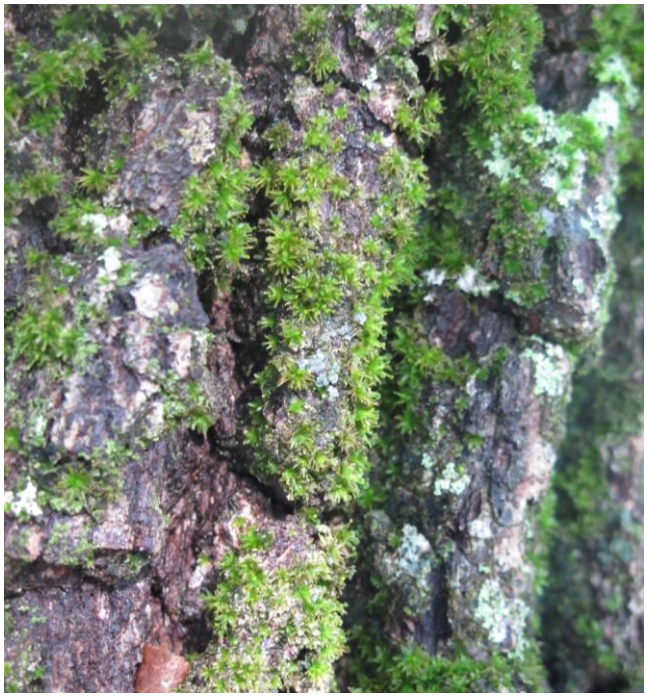

Figure 52. ***Calymperes palisotii*** on bark. Photo by Scott Zona, through Creative Commons.

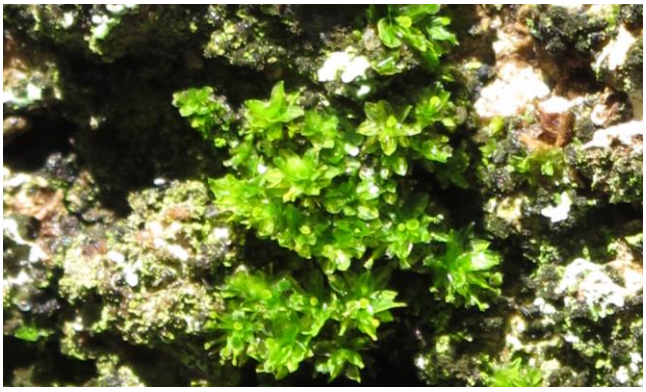

Figure 53. ***Calymperes palisotii***, a species that shares a 50% similarity index with ***Entodontopsis nitens***. Photo by Scott Zona, through Creative Commons.

Odu (1985) found a greater species richness of epiphytic bryophytes in lowland and freshwater forests than in the mangrove forests of the Niger Delta in Nigeria (Figure 54). He suggested that atmospheric humidity and air impurities may be influencing the bryophytes found. ***Calymperes*** (Figure 52-Figure 53, Figure 55) and ***Octoblepharum*** (Figure 56) occur all over the Niger Delta, whereas others are restricted to the lowland freshwater forests. Those in the mangrove forests require adaptations that permit their tolerance of salt water. Further discussion of the mangrove forest is in the Tropics subchapter Hydric and Xeric Habitats.

Figure 54. Mangrove roots in the Niger Delta, Nigeria. Photo through Creative Commons.

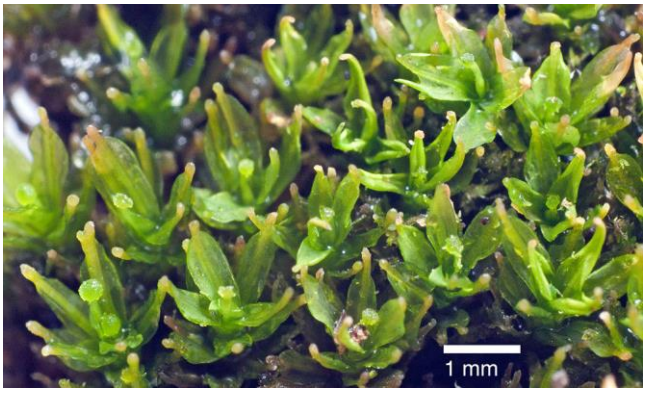

Figure 55. ***Calymperes tenerum***, a common species in the mangrove forests of Thailand. Photo from the Auckland Museum, through Creative Commons.

Figure 56. ***Octoblepharum albidum***, a common species in the mangrove forests of Thailand. Photo by M. C. Nair, K. P. Rajesh, and P. V. Madhusoodanan, through Creative Commons.

Akinsoji (1991) reported 26 tracheophytic epiphytes from a tropical rainforest in southwestern Nigeria. As noted elsewhere regarding bryophytes, bark texture makes a difference. Akinsoji found that rough bark is able to collect soil, nutrients, and moisture for epiphytic growth, all features that could benefit bryophytes as well. Trees with smooth bark lacked debris and dust accumulation or moisture retention and had only one or two epiphytes.

More recently, Ezukanma *et al*. (2019a, in review) examined corticolous bryophytes in agroforests of southwestern Nigeria. Only 14 bryophytes were identified. Seven leafy liverwort species were present, but in only two families – **Lejeuneaceae** (Figure 14, Figure 51) and **Radulaceae** (Figure 24). Similarly, seven moss species were found, but they were distributed in five families – **Calymperaceae** (Figure 52-Figure 53), **Entodontaceae** (Figure 57), **Fissidentaceae** (Figure 16), **Hypnaceae** (Figure 58), and **Leucomiaceae** (Figure 59) with one species each, and **Plagiotheciaceae** (Figure 60) with two species. Cashew forests (Figure 61) had eight species, kola (Figure 62) had seven, and cocoa (Figure 63) had six. Only the liverworts ***Thysananthus nigrus*** (see Figure 64) and ***Mastigolejeunea auriculata*** (Figure 65) were found in all three forest types. ***Entodontopsis nitens*** (Figure 47) was the most frequent species, occurring in the kola forest and having a frequency of 27.6%. Next in frequency were ***Mastigolejeunea auriculata*** (23.65%) and ***Entodontopsis nitens*** (18.92%) in the cocoa agroforest.

Figure 57. ***Entodon*** sp. (**Entodontaceae**); this family is frequent on trees in the agroforests of Nigeria. Photo by Cindy Hough, through Creative Commons.

Figure 58. ***Chryso-hypnum diminutivum*** (**Hypnaceae**) from the Neotropics; this family is frequent on trees in the agroforests of Nigeria. Photo by Michael Lüth, with permission.

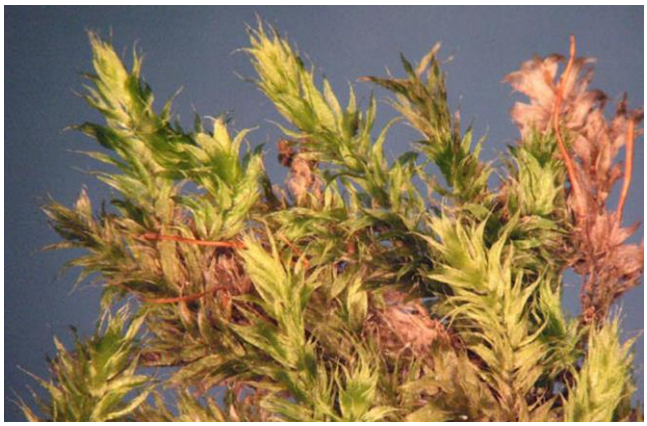

Figure 59. ***Leucomium strumosum*** (**Leucomiaceae**), a family that occurs on trees in agroforests in Nigeria. Photo by Claudio Delgadillo Moya, with permission.

Figure 60. ***Plagiothecium undulatum*** (**Plagiotheciaceae**), a family that occurs on trees in agroforests in Nigeria. Photo from Proyecto Musgo, through Creative Commons.

Figure 61. Cashew trees in Brazil. Photo by Ben Tavener, through Creative Commons.

Figure 62. Kola (***Cola nitida***) plantation in Malaysia. Photo by Michael Hermann, through Creative Commons.

Figure 63. ***Cacao*** plantation in Cameroon. Photo by Barada-Nikto, through Creative Commons.

Figure 64. ***Thysananthus repletus*** (= *Mastigolejeunea repleta*) from China; ***Thysananthus nigrus*** is present in all three forest types in southwestern Nigeria. Photo by Y. M. Wei, courtesy of Robbert Gradstein.

Figure 65. ***Mastigolejeunea auriculata***, a liverwort found in all three of these types of agroforests in Nigeria. Photo by Paul Davison, with permission.

Ezukanma *et al*. (2019b, in press) also assessed the epiphytic bryophytes in the urban agroforests of Ibadan, Nigeria. They studied the corticolous bryophytes up to 2m on the phorophytes of 30 trees in ***Citrus*** (Figure 66) and ***Mangifera*** (Figure 67) plantations. Here they identified 19 species, 13 leafy liverworts and 6 mosses. Five species

were in both forest types. The mango forests had higher bryophyte diversity and more even distribution of species. The researchers suggested that this might relate to the frequent pruning of the crowns in the mango agroforest. The moss ***Calymperes palisotii*** (Figure 52-Figure 53) was the most abundant species, especially in the ***Citrus*** plantations. Corticolous species were generally absent at the base of the phorophyte, occurring with a mean height of 1.39 m (range of 1.17-1.60) on ***Mangifera*** and 1.11 m (range of 0.48-1.8) on ***Citrus***. The moss ***Rhacopilopsis trinitensis*** (Figure 68) had the highest mean height, extending up to 1.8 m. ***Ceratolejeunea beninensis*** (see Figure 80-Figure 81) was second in abundance, likewise in the ***Citrus*** forest. As in the cashew, kola, and cacao forests, ***Mastigolejeunea auriculata*** (Figure 65; in the ***Mangifera*** forests) and ***Entodontopsis nitens*** (in the ***Citrus*** forests; Figure 47) were species with high frequencies. There were 13 liverwort species, 12 in **Lejeuneaceae** (Figure 14, Figure 51) and 1 in **Jubulaceae** (Figure 69). The six moss species were in four families, with 3 in **Stereophyllaceae** (Figure 47) and 1 each in **Calymperaceae** (Figure 52-Figure 55, Figure 82), **Hypnaceae** (Figure 58), and **Leucomiaceae** (Figure 59). Twelve species occurred in both forest types.

Figure 66. ***Citrus*** (orange) plantation. Photo by Hans Braxmeier, through Creative Commons.

Figure 67. ***Mangifera*** (mango) picking, Réunion Island. Photo by B. Navez, through Creative Commons.

Figure 68. ***Rhacopilopsis trinitensis***, the species that reaches the greatest heights on ***Mangifer*** and ***Citrus*** phorophytes. Photo by Juan David Parra, through Creative Commons.

Figure 69. ***Jubula hutchinsiae*** (**Jubulaceae**), a family that occurs on ***Citrus*** trees in Nigeria. Photo by Jonathan Sleath, with permission.

Biedinger and Fischer (1996) compared the diversity of epiphytic tracheophytes, bryophytes, and lichens in the montane rainforests and dry forests of Rwanda and Zaïre They identified 167 species of tracheophytes, 45 of mosses, 82 of liverworts, 78 corticolous lichens, and 57 epiphyllous lichens. While the numbers may be replaced with more recent studies, the proportions are likely to be more accurate.

In South Africa, Dilg and Frahm (1997) explored the epiphytic flora in southern Drakensberg. They found only 38 species, 12 of which were liverworts and 26 were mosses. The ***Podocarpus*** (Figure 70) forest provides a habitat with high humidity and fire protection; it has the highest number of bryophyte species.

Figure 70. ***Podocarpus cunninghamii*** trunk with epiphytic bryophytes. Photo by Rudolph89, through Creative Commons.

In addition to these studies, Frahm (1994) reported on ecology of epiphytic bryophytes on Mt. Kahuzi in Zaire. Additional references that may be useful regarding epiphytic diversity in the African tropics include Kürschner (1984 – Saudi Arabia; 1990a – moss societies on Mt. Kinabalu, North Borneo; 1995 – Eastern Congo), Pócs & Szabo (1993 – Mt Elgon, Kenya), Gill & Onyibe (1986 – phytosociology of epiphytes on oil palm in Benin City, Nigeria), Ezukanma (2012 – agroecological corticolous species in southwestern Nigeria). A number of references by Ah-Peng and coworkers will be addressed in other appropriate subchapters of this chapter.

Neotropics

The Neotropics are rich in bryophyte species. In a six-hectare upper montane ***Quercus*** forest (Figure 71) in Costa Rica, Holz *et al*. (2002) found 206 species, comprised of 100 moss species, 105 liverwort species, and 1 hornwort. They found three main groups of microhabitats in the forest: forest floor, including the tree base; the **phyllosphere** (space surrounding the leaf); other epiphytic habitats. Life forms differ with the humidity and light levels, as discussed in earlier subchapters. Van Reenen (1987) noted that the epiphytic cover of bryophytes in the Andes of Colombia increases with altitude. Wolf (2003) found that the greatest liverwort diversity occurs in the transition zone where two distinct floras are in contact.

Sillett *et al*. (1995) examined the bryophyte communities of six ***Ficus tuerckheimii*** (Figure 72) trees in a Costa Rican lower montane wet forest. They found 109 species on the three intact forest trees and only 76 on the three isolated trees. Of these, 52 species occurred only on the intact forest trees; 18 were only on the isolated trees. Species richness, cover, and frequency of **pendants**, **tall turfs**, **tails**, and **fans** were significantly higher on the trees in the intact forest. Isolated trees had higher rates of evaporation from the inner crowns, more macrolichen cover, and higher levels of sunlight compared to the intact forest trees. Ordination analysis revealed a desiccation gradient ranging from the sheltered intact forest trees to the exposed isolated trees.

Figure 71. ***Quercus copeyensis***; in Costa Rica; the ***Quercus*** forest is home to more than 200 bryophyte species. Photo through Creative Commons.

Delia *et al*. (2015) reported 34 epiphytic moss species from El Zancudo, Honduras. They concluded that the montane rainforest that borders Honduras and El Salvador is bryologically diverse, but is largely unexplored.

Figure 72. ***Ficus tuerckheimii***, Costa Rica. Photo by Dick Culbert, with online permission.

Richards (1954) considered the Moraballi Creek in Co-operative Republic of Guyana to have four main bryophyte **synusiae** (structural units of major ecological community characterized by relative uniformity of life form or height): high epiphytes, shade epiphytes, epiphylls, dead wood communities. Although these communities are very distinct in both structure and composition, several species, such as ***Calymperes lonchophyllum*** (see Figure 52-Figure 55) and ***Octoblepharum albidum*** (Figure 56), occur in all but the epiphyllous synusiae. The epiphyllous species are highly specialized, as will be discussed in a later subchapter. Korpelainen and Salazar Allen (1999) demonstrated genetic variation in three species of ***Octoblepharum***, perhaps explaining their ability to occur in multiple community types. Richards (1954) found that Moraballi Creek synusiae differ in their growth (and life) forms of the species, creating differences in community structure. This results in differences between the very dry habitat of the high epiphyte synusiae and the more moderated shade epiphyte synusiae. The latter is characterized by freely projecting or dangling shoots and large thin-walled cells. The Moraballi Creek rainforest bryophyte synusiae differ markedly from those of temperate forests by the absence of ground-dwelling bryophyte synusiae, the presence of epiphyllous bryophytes, and the preponderance of liverworts, especially **Lejeuneaceae** (Figure 14, Figure 51).

In a semi-deciduous tropical forest of southern Guyana (Figure 73), Sipman (1997) found 100 species of lichens, with 8 out of 14 trees lacking lichens on leaves completely, whereas 3 had 34-46 taxa! Instead, the foliicolous lichens are most likely to grow close to the ground. In contrast to the 34-46 species of lichens on a single tree, they were able to find only 18 bryophyte taxa on canopy leaves.

Figure 73. Guyana waterfall and forest near Paramakatoi. Photo by Kevin Gabbert, through public domain.

Large trees support more species than small ones, with a typical logistic curve of increasing numbers of species related to both plot size and tree **DBH** (diameter at breast height) (Figure 74) (Gradstein *et al*. 1996).

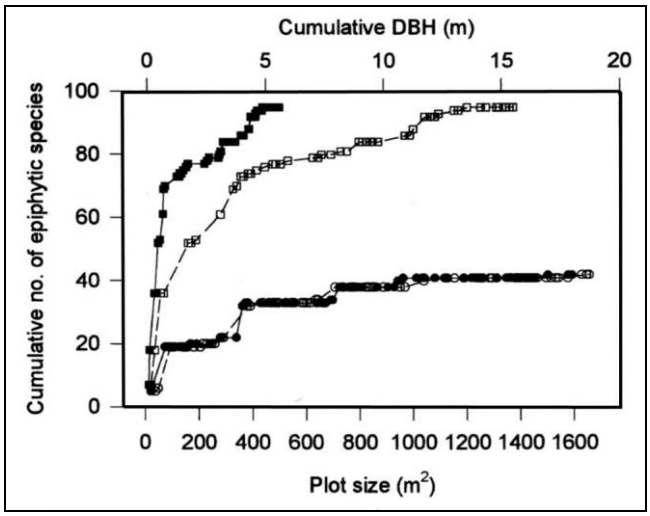

Figure 74. Relationship between number of epiphyte species and plot size and tree DBH in Mexico. Species-area curves are **solid** symbols, cumulative number of species vs cumulative diameter of all trees sampled are **open** symbols. **Squares** represent humid montane cloud forest; **circles** represent humid lowland forest. Modified from Gradstein *et al*. 1996.

Gradstein *et al.* (1990) investigated the epiphytic bryophytes in the dry evergreen forest and mixed forest of the Guianas (Figure 73) using mountaineering techniques. They discovered that the lowland rainforest is not as poor in species as had been thought, once the bryophytes of the canopy are included in the exploration. More than 50% of the local species may occur in the canopy. The mixed forest has the most species. A single tree can support up to 67 species, with 50 species being an average number. The 28 trees sampled supported 154 species of bryophytes. Only a few trees are needed to find most of the species of the local area. Most of the species in this area are rather common, with 80% being widespread in the Neotropics.

In the Colombian Amazon (Figure 75), Campos *et al*. (2015) established 384 plots on 64 trees in four localities.

These exhibited 160 species of epiphytic bryophytes, with a preponderance of liverworts (116 species; 44 species of mosses). These included collections from the base to the outer canopy, including 16 trees at each locality. The highest representation of families (Figure 76) included the leafy liverworts **Lejeuneaceae** (Figure 14, Figure 51) (55%) and **Lepidoziaceae** (Figure 2) (8%), and the mosses **Calymperaceae** (Figure 52-Figure 55) (10%), **Octoblepharaceae** (Figure 56) (6%), and **Sematophyllaceae** (Figure 10) (5%). The most common genera were members of **Lejeuneaceae** – ***Cheilolejeunea*** (Figure 77) (11%), ***Pycnolejeunea*** (Figure 78) (8%), ***Archilejeunea*** (Figure 79) (8%), and ***Ceratolejeunea*** (Figure 80-Figure 81) (8%) – and the moss ***Syrrhopodon*** (**Calymperaceae**; Figure 82) (7%).

Figure 75. Lowland rainforest in Colombian Amazon. Photo by Laura Campos, courtesy of Robbert Gradstein.

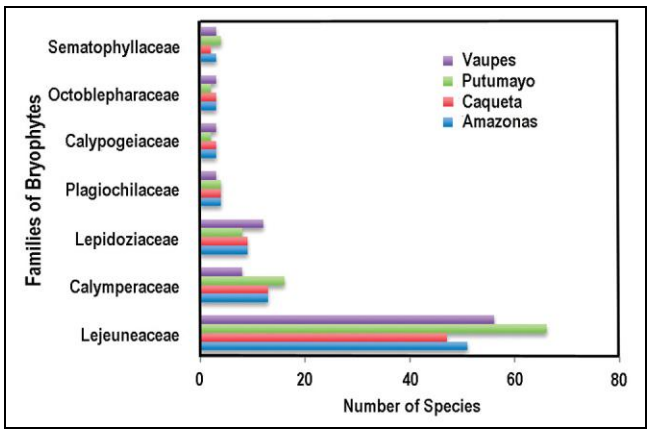

Figure 76. Species richness per family in 4 locations of Colombian Amazon. Modified from Campos *et al*. 2015.

Figure 77. ***Cheilolejeunea frangrantissima***, in one of the most common genera of **Lejeuneaceae** in the Colombian Amazon. Photo by Scott Zona, with permission.

Figure 78. ***Pycnolejeunea pilifera***, member of a common leafy liverwort genus in the mangrove forests of Thailand. Photo by MNHN – Paris, Muséum National d'Histoire Naturelle, MB, through Creative Commons.

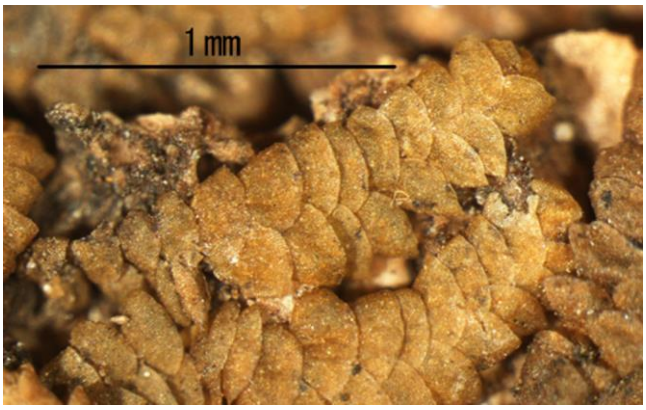

Figure 79. ***Archilejeunea japonica***, in one of the most common genera of **Lejeuneaceae** in the Colombian Amazon. Photo from Digital Museum, Hiroshima University, with permission.

Figure 80. ***Ceratolejeunea cubensis***, in one of the most common genera of **Lejeuneaceae** in the Colombian Amazon. Photo by Scott Zona, with permission.

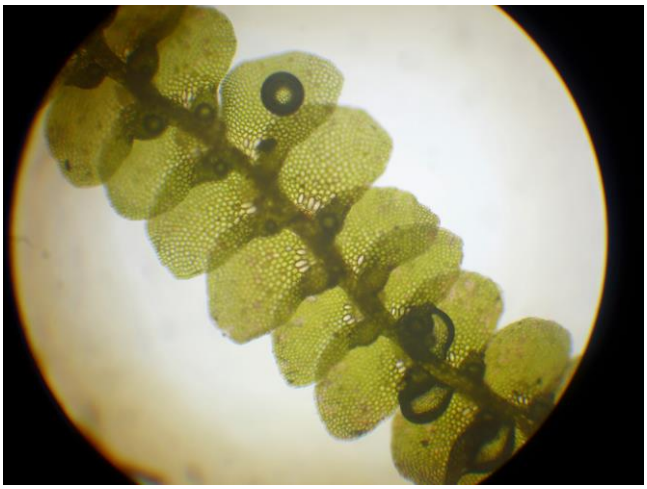

Figure 81. ***Ceratolejeunea cubensis***, showing lobules at leaf insertions. Photo by Scott Zona, with permission.

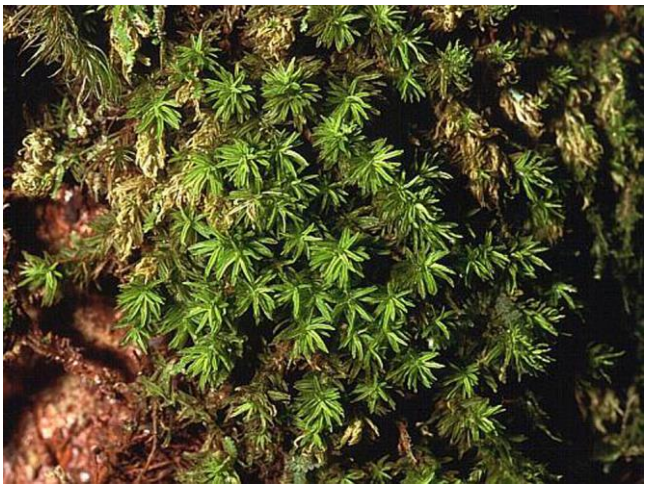

Figure 82. ***Syrrhopodon gaudichaudii***, in one of the most common genera in the Colombian Amazon. Photo from Michael Lüth, with permission

Wolf *et al*. (2003) found that the richness per surface area decreases significantly with branch diameter (Figure 83) in the upper montane rainforest of the Cordillera in Colombia. Diversity is highest when the standing crop is at intermediate levels and is negatively correlated with the area of the largest species. On the other hand, **evenness** (similarity of frequencies of different units making up population or sample) is less on older branches. The inner canopy species have the smallest niche widths. When only branch segments are sampled, the vegetation is highly variable, whereas that on whole trees is more uniform. The species follow a species area curve that approaches a flat line after sampling only four trees. The liverworts have the greatest richness in the contact transition zone between two distinct floras. Wolf and coworkers suggested that the arrival time of aggressive competitors such as those that form large patches may be "crucial." Many accidental species maintain a high richness and suggest that dispersal of propagules is important in creating richness.

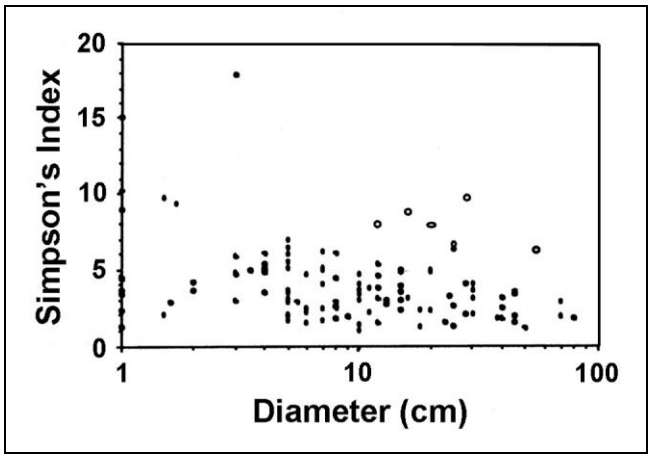

Figure 83. Branch or trunk diameter in the canopy of the upper montane rainforest and Simpson's index of diversity. **Open circles** indicate a group of seven samples that do not adhere to increasing dominance with diameter. Modified from Wolf *et al*. 2003.

In flooded (Figure 84) and "tierra firme" (upland habitat where elevation does not allow water, even during high water season, to inundate forest; Figure 85) forests of the Colombian Amazon, Benavides *et al*. (2004) found 109 bryophyte species on 14 0.2-ha plots. Mosses and liverworts had opposite responses to moisture, with many more liverworts than moss species in the **tierra firme**, but total richness (mosses + liverworts) differed little between the flooded and non-flooded habitats (Figure 86). The use of the habitat differed between the two forest types, with differences in humidity being the major factor in determining bryophyte communities. Nevertheless, soil was a little-used substrate for both groups in both habitats (Figure 86). Epiphyll species assemblages (*e.g*. Figure 87) were not strongly affected by floodplain vs tierra firme. Life forms differed between the two habitat types, with more **fan** and **mat** bryophyte species in the floodplains, and more epiphytic liverworts (hence, almost no **wefts**) in the tierra firme forest (Figure 88).

Figure 84. Várzea forest with açaí palms, the flooded forest of the Amazon. Photo by Frank Krämer through Creative Commons.

Figure 85. Amazon rainforest, Brazil. Photo by Phil P. Harris, through Creative Commons.

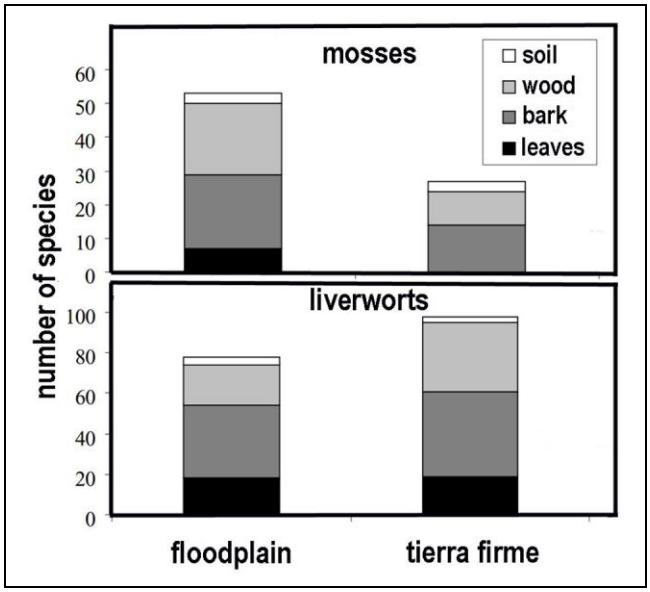

Figure 86. Distribution of bryophyte substrates in tierra firme and floodplain in the Aracuara region of Colombia. Modified from Benavides *et al*. 2004.

Figure 87. Epiphylls on leaf. Photo by Jessica M. Budke, with permission.

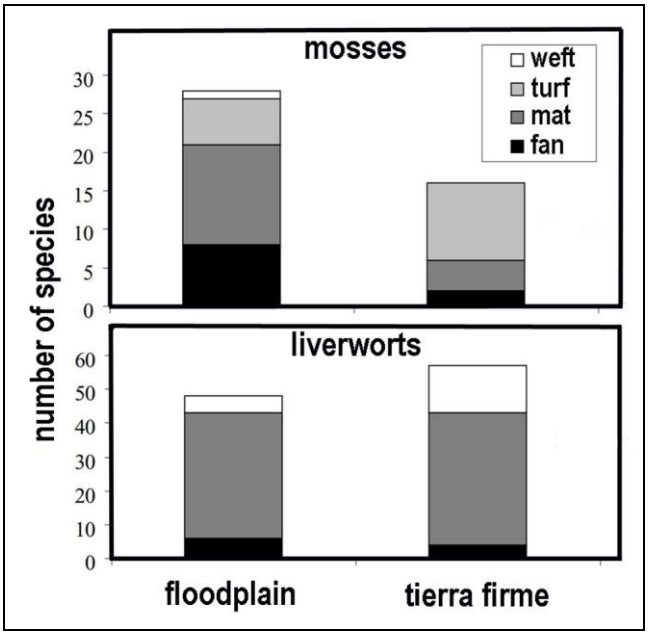

Figure 88. Distribution of bryophyte life forms in tierra firme and floodplain in the Aracuara region of Colombia. Modified from Benavides *et al*. 2004.

Oliveira and ter Steege (2013) determined that epiphytic bryophytes in the tierra firme forests of the Amazon Basin exhibited a typical species abundance distribution (Figure 89).

Kelly *et al*. (2004) described the epiphytic communities of a montane rainforest in the Venezuelan Andes (Figure 90). They surveyed 20 trees, all in a site of only 1.5 ha at 2600 m asl. The non-tracheophyte epiphytes were recorded in 95 sample plots and yielded 22 moss and 66 liverwort species, as well as 46 species of macrolichens. Few of the bryophytes in these communities are **endemic** (native distribution restricted to a certain country or area), although they are mostly restricted to the Neotropics. The dominant bryophyte on the lower trunks is ***Syrrhopodon gaudichaudii*** (Figure 91), along with the fern ***Elaphoglossum hoffmannii*** (Figure 92). The intermediate levels are dominated by the leafy liverwort ***Omphalanthus filiformis*** (**Lejeuneaceae**; Figure 93) and the orchid *Maxillaria miniata* (see Figure 94). The upper crowns are dominated by the lichens *Usnea* (Figure 95) and *Parmotrema* (Figure 96). Diversity of non-tracheophytes is

greatest in the upper crowns; tracheophyte diversity is greatest at the intermediate levels. As noted in a number of other studies cited herein, similarity is low among plots of the same community, but between-tree and between-stand similarities are relatively high.

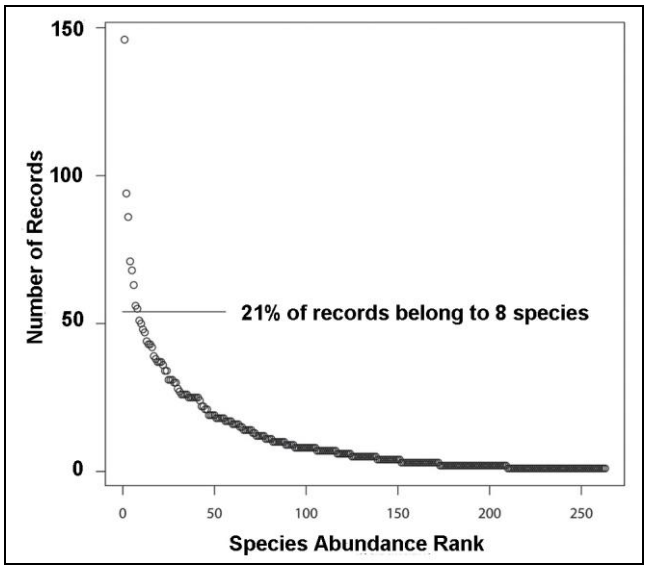

Figure 89. Species abundance distribution based on the complete dataset. Axis x is species ranked by number of records. Modified from Mota de Oliveira and ter Steege 2013.

Figure 90. Montane rainforest in Venezuelan Andes. Photo by Jorge Paparoni, through Creative Commons.

Figure 91. ***Syrrhopodon gaudichaudii***, the dominant bryophyte on the lower trunks in a montane rainforest in the Venezuelan Andes. Photo by Michael Lüth, with permission.

Figure 92. ***Elaphoglossum hoffmannii***, a fern that typically accompanies ***Syrrhopodon gaudichaudii*** on lower trunks in montane rainforests in the Venezuelan Andes. Photo by Robbin Moran, with permission.

Figure 93. ***Omphalanthus filiformis***, a dominant leafy liverwort at intermediate levels of tree trunks in a montane rainforest in the Venezuelan Andes. Photo by Michael Lüth, with permission.

Figure 94. ***Maxillaria molitor***; ***Maxillaria miniata*** is the dominant flowering plant species, along with the leafy liverwort ***Omphalanthus filiformis***, at intermediate levels in the montane rainforest of the Venezuelan Andes. Photo from Megadiverso, through Creative Commons.

Figure 95. *Usnea* from Cumbre Vieja, Canary Islands. Members of this genus dominate the crowns of the montane rainforest in the Venezuelan Andes. Photo by Fährtenleser, through Creative Commons.

Figure 96. *Parmotrema perlatum*. Members of this lichen genus dominate the crowns of the montane rainforest in the Venezuelan Andes. Photo by Alan J. Silverside, with permission.

By comparison, Costa (1999) studied the epiphytic bryophyte diversity of both primary and secondary lowland rainforests in southeastern Brazil, a subtropical region. Unlike many earlier studies, hers included the forest canopy. She found 75 bryophyte species, 39 mosses and 36 liverworts. The highest species richness is exhibited by the mature secondary hillside rainforest, with 43 species. The highly degraded hillside rainforest has the lowest diversity, with only 6 species, and the hillside secondary rainforest with only 5 species. As in so many other studies, the leafy liverwort family **Lejeuneaceae** (Figure 14, Figure 51) is the "most important" with 23 species (30 %) and the moss family **Sematophyllaceae** (Figure 10) with 7 species (10%). Demonstrating the importance of the canopy species in understanding species diversity, Costa found that 45% of the bryophyte species occurred exclusively in the canopy. The most common life form is the **mat**, describing 45% of the species. Forest destruction is more detrimental to shade species than to sun species. Even after 20-45 years, many bryophytes had not returned, but after 80 years the communities were similar to those of primary forest.

In 2017, Gradstein and Benitez added 15 liverwort species to the known flora of Ecuador. They furthermore described two species new to science.

One might not think of looking in a savannah for epiphytes because of the high exposure to sunlight and low moisture. Nevertheless, bryophytic epiphytes do grow there in an Amazonian savanna in Brazil (Figure 97). Gottsberger and Morawetz (1993) found that lichens dominate on the young trees, typically becoming less abundant as the tree ages. Bryophytes are most abundant on older trees and seem to suppress the lichen growth.

Figure 97. Amazonian savannah (Cerrado) in Brazil. Photo by Paulo Q Maio, through Creative Commons.

Additional references that may be useful regarding tropical diversity in the Neotropical epiphytes include Chung (1996 – Panama), Wolf (1993 – Colombia); Jovet-Ast (1949 – groupings of epiphytic mosses in the French West Indies); Frahm (1987a, b – composition of moss vegetation in Peruvian rainforests); Frahm (1987a, c – composition of moss vegetation in Peruvian rainforests).

Summary

Full understanding of the bryogeography of epiphytes is still hampered by our need for comprehensive systematic studies that identify synonyms and demonstrated genetic relatedness.

In Australian tropical rainforests, epiphyte succession is usually rapid, with seven genera occurring in all the major rainforest types (including non-tropical ones): ***Macromitrium***, ***Racopilum***, ***Hymenodon***, ***Pyrrhobryum***, ***Rhizogonium***, ***Sematophyllum***, and ***Thuidium*** (***Pelekium***?).

In general, the mosses in **Pterobryaceae** and **Neckeraceae** occur as epiphytes throughout the tropics, along with ***Sematophyllum*** and ***Taxithelium***. The liverworts ***Frullania*** and **Lejeuneaceae** dominate the branches. The tribe **Ptychantheae** is predominant among Asian **Lejeuneaceae**, whereas the tribe **Brachiolejeuneae** predominates in the Neotropics. In Indonesia, the characteristic low-elevation tree-base moss families are **Calymperaceae**, **Fissidentaceae**, **Hypopterygiaceae**, **Leucobryaceae**, **Meteoriaceae**, **Neckeraceae**, **Pterobryaceae**, and **Thuidiaceae**, and the leafy liverwort families **Lejeuneaceae**, **Lophocoleaceae**, **Porellaceae**, and **Radulaceae**. By

contrast the higher elevations have mostly leafy liverworts in **Herbertaceae**, **Lepidoziaceae**, **Mastigophoraceae**, **Scapaniaceae**, **Schistochilaceae**, and **Trichocoleaceae**. In Africa, ***Calymperes*** and ***Octoblepharum*** species occur all over the Niger Delta, whereas in agroforests Ezukanma *et al*. (2019 in review) found only **Lejeuneaceae** and **Radulaceae** among the liverworts, but found five families of mosses. African studies are limited and promise many more species on future expeditions. Bryophyte diversity in the Neotropics is particularly rich and increases with altitude. Intact forests typically have **pendants**, **tall turfs**, **tails**, and **fans**. ***Calymperes lonchophyllum*** and ***Octoblepharum albidum*** are common in all communities except as epiphylls. Larger trees support more species than do small ones by providing more niches. For the Neotropics in general, the **Lejeuneaceae** are again the most species-rich family; the most highly represented moss families are **Calymperaceae**, **Octoblepharaceae**, and **Sematophyllaceae**. Fewer endemics occur here compared to those of the flowering plants, and as more systematic studies occur, the number is diminishing.

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CHAPTER 8-6
TROPICS: EPIPHYLLS

JANICE M. GLIME AND TAMÁS PÓCS

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CHAPTER 8-6
TROPICS: EPIPHYLLS

JANICE M. GLIME AND TAMÁS PÓCS

Figure 1. Epiphyllous ***Lejeunea floridana*** and ***Cololejeunea cardiocarpa***. Photo by Scott Zona, with permission.

Epiphyllous Communities

A unique community occurs in the tropics, especially in the wet rainforests, the **epiphyllous** community (Figure 1), *i.e.* those bryophytes, lichens, algae, fungi, and bacteria that live on the leaves of higher plants. Among these, bryophytes contribute most of the biomass (Bentley 1987). A discussion of tropical epiphytes would not be complete without considering these bryophytes that spend their lives on leaves.

Some of the earliest bryophyte studies in the tropics were on epiphyllous species, typically on trees and shrubs. These included studies by Goebel (1888, 1889), Massart (1898), Busse (1905), Pessin (1922), Richards (1932), Allorge *et al*. (1938), and Allorge & Allorge (1939). Later, Winkler (1967, 1970) reported on epiphyllous communities of both upland and lowland rainforests of tropical Americas.

Foliicolous bryophytes occur predominantly on the upper surface of leaves (**epiphyllous**), but some do occur on the lower surface (**hypophyllous**) (Santesson 1952). This leaf habitat is termed the **phyllosphere** (Ruinen 1961). These communities are mostly restricted to the rainforests of the humid tropics and subtropics, but some have been reported, albeit not well-developed, in wet temperate regions as well: Japan (Schiffner 1929), the Appalachian Mountains, USA (Schuster 1959; Ellis 1971), British Columbia (Vitt *et al*. 1973), the Caucasus (Pócs 1982b; Vězda 1983), Macaronesia (Sjögren 1975, 1978) and the Pyrenees (Vězda & Vivant 1972).

In equatorial regions, these foliicolous communities occur from sea level to about 3000 m asl, where they become limited by lack of forest substrate. Pócs (1976a, 1982a) concluded that the upper limit is determined by the frequency of night frosts and the degree of oceanity. Optimal conditions, on the other hand, occur in the lower montane rainforest belt. In East Africa this occurs at ~1500-2000 m.

Luo (1990) noted the need for very moist air in the habitats of epiphyllous liverworts. This defines the primary distribution of epiphyllous liverworts in the tropical or subtropical regions of IndoMalay, Central and South America, central Africa, and the Asian-Pacific regions of South Korea and southern Japan south to Australia.

Among the early studies, Jaag (1943) investigated epiphytes and epiphylls on ferns (Figure 2-Figure 3), examining these as they related to the leaf renewal rate and leaf life.

Figure 2. ***Blechnum loxense*** tree fern at treeline in the Ecuadorian Andes at 3500 m asl, with Jan Peter Frahm. Members of this genus often have epiphylls. Photo courtesy of Robbert Gradstein.

Figure 3. ***Lejeunea*** *cf.* ***epiphylla*** on ***Blechnum wattsii***. Photo by Tom Thekathyil, with permission.

Richards (1952) has written one of the definitive treatises on tropical plant ecology. In it, he describes the epiphyllous community as common in tropical, montane, and subtropical rainforests, particularly in wet forests. The epiphylls occur mostly on the upper surfaces of evergreen leaves. In tropical forests that are seasonally dry, they usually occur only near streams and in swampy areas. Exceptionally, they can occur also in dry woodlands if they are affected by mist/cloud formation regularly (Pócs.1976b).

The long-lived, somewhat leathery leaves of tropical forest trees make it predominantly possible for bryophytes to become established there, particularly in the more humid sites. But they can also occur on bamboo (Doei 1990) and palm leaves as well (Schuster & Anderson 1955), even on fern and other herbaceous plant leaves and exceptionally on succulents.

In western Nigeria, for example, as many as 1200 shoots/colonies can occur on one 58x35 mm leaf of ***Citrus sinensis*** (Figure 4) (Olarinmoye 1975c).

Figure 4. ***Citrus sinensis***, a species that can house as many as 1200 epiphytic shoots on a 6 x 3 cm leaf section. Photo by Antandrus, through Creative Commons.

Filmy fern leaves usually have a special epiphyllous community formed by tiny ***Cololejeunea*** (Figure 5-Figure 6) and hookerioid moss species (Pócs 1978).

Figure 5. ***Cololejeunea minutissima***, in a genus that is among the epiphylls in the world. Photo by Michael Lüth, with permission.

Figure 6. ***Cololejeunea magnilobula***, in a genus that is among the epiphylls in the world. Photo by Yang Jia-dong, through Creative Commons.

In the 1990's Pócs (1996, 1997) reported 1,000 epiphyllous species of liverworts worldwide. Although this includes epiphyllous species that are not exclusively tropical, most are in the tropics (Figure 7). Among these, Asia had the highest reported number of any continent at 504 species, with 224 in the Malesian archipelago alone. These worldwide epiphylls are divided among the **Lejeuneaceae** genera ***Cololejeunea*** (389 species; Figure 5-Figure 6), ***Ceratolejeunea*** (114 spp.; Figure 8), ***Drepanolejeunea*** (98 spp.; Figure 9), ***Colura*** (76 spp.; Figure 10), ***Diplasiolejeunea*** (68 spp.; Figure 11), ***Prionolejeunea*** (59 spp.; Figure 12), ***Aphanolejeunea*** (54 spp.; Figure 13; this genus is now included in ***Cololejeunea***), ***Leptolejeunea*** (48 spp.; Figure 14), and ***Microlejeunea*** (34 spp.; Figure 15), the **Radulaceae** genus ***Radula*** (13 spp.; Figure 16), and another 12 genera with fewer than 10 species each. This distribution of genera and numbers of species is likely to have changed since that time as synonyms have been identified and genera have been split or unified and new species have been described. For example, TROPICOS lists only 29 currently accepted species names in ***Diplasiolejeunea***, listed above as having 68 in the tropics, but the World Checklist of liverworts and Hornworts (Söderström *et al.* 2016) lists more than 90! These epiphyllous genera are susceptible to losses whenever the forest is disturbed.

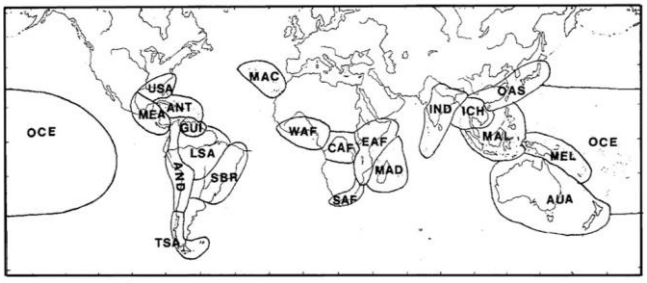

Figure 7. Epiphyll floristic regions of the world. Modified from Pócs 1996.

Figure 8. ***Ceratolejeunea cubensis***, in a genus that is among the epiphylls in the world. Photo by Scott Zona, with permission.

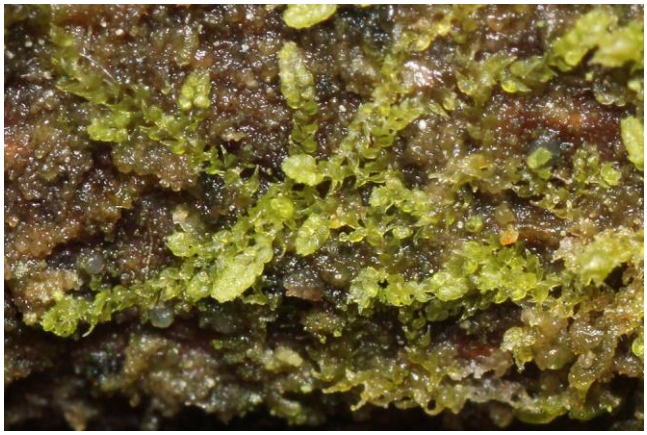

Figure 9. ***Drepanolejeunea hamatifolia***, in a genus that is among the epiphylls in the world. Photo by Barry Stewart, with permission.

Figure 10. ***Colura calyptrifolia***, a species that is among the epiphylls in the world. Photo by David T. Holyoak, with permission.

Figure 11. ***Diplasiolejeunea cavifolia***, a pantropical epiphyllous liverwort species that is among the epiphylls in the world. Photo by Hermann Schachner, through Creative Commons.

Figure 12. ***Prionolejeunea saccatiloba*** with perianth and androecium, in a genus that is among the epiphylls in the world. Photo by Michaela Sonnleitner, with permission.

Figure 13. ***Cololejeunea sintenisii***, in a genus that is among the epiphylls in the world; ***Cololejeunea sicifolia*** dominates communities in dry microsites of Central America, but is rare in wet microsites. Photo by Pedro Cardosa, Biodiversidad, with permission.

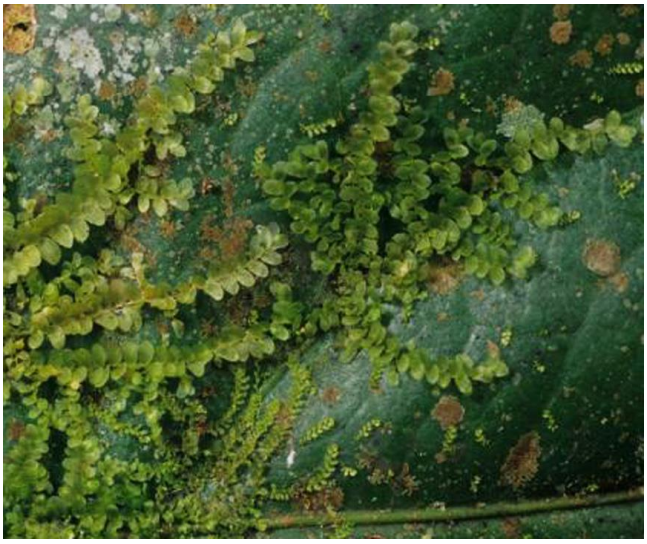

Figure 14. ***Leptolejeunea elliptica***, in a genus that is among the epiphylls in the world. Photo by Yang Jia-dang, through Creative Commons.

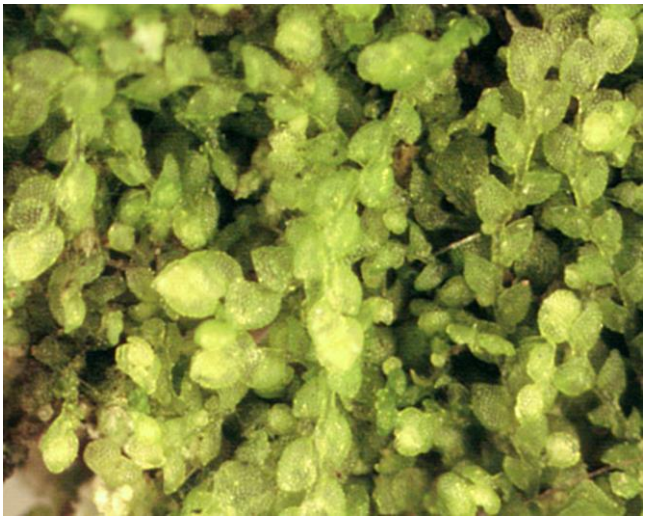

Figure 15. ***Microlejeunea ulicina***, in a genus that is among the epiphylls in the world. Photo by Malcolm Storey, <DiscoverLife.org>, with online permission.

Figure 16. ***Radula complanata***, in a genus that is among the epiphylls in the world. Photo by Malcolm Storey, <DiscoverLife.org>, with online permission.

In 1997 Lücking estimated the number of epiphyllous bryophyte species to be only about 535 worldwide. He found 83 species of epiphyllous bryophytes in a Costa Rican tropical rainforest. A single leaf of the palm ***Welfia georgii*** (Figure 17; see also Figure 18) had 24 species. Nearly all the epiphylls were liverworts, with 78 species in the family **Lejeuneaceae** (Figure 6-Figure 15). The others were ***Radula*** (**Radulaceae**; Figure 16), ***Metzgeria*** (**Metzgeriaceae**; Figure 19, Figure 127), and ***Frullania*** (**Frullaniaceae**; Figure 20). ***Crossomitrium patrisiae*** (Figure 21) was the only epiphyllous moss species. Only 17% of the bryophytes are widely distributed on more than one continent in the tropics; the others in this study are Neotropical, with 11% known only from Costa Rica.

Figure 17. Everwet lowland rainforest of the Chocó with dominance of ***Welfia georgii***. Photo by Jan-Peter Frahm, with permission.

Figure 18. The palm ***Welfia regia*** with epiphytes on its leaf bases. ***Welfia georgii*** (Figure 17) can have 24 bryophytic epiphylls on a single leaf. Photo by David J. Stang, through Creative Commons.

Figure 19. ***Metzgeria furcata***. Members of this genus are epiphyllous on the palm ***Welfia georgii*** (Figure 17). Photo by Malcolm Storey, <DiscoverLife.org>, with online permission.

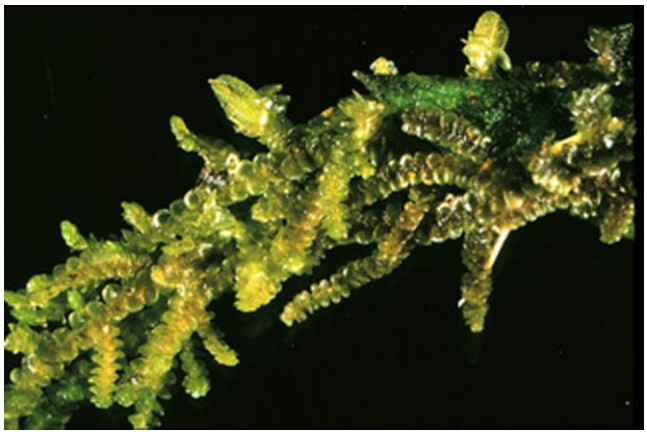

Figure 20. ***Frullania pycnantha***; some members of this genus are epiphyllous on the palm ***Welfia georgii*** (Figure 17). Photo by John Braggins, with permission.

Figure 21. ***Crossomitrium patrisiae***, a species that is epiphyllous on the palm ***Welfia georgii*** (Figure 17). Photo by Jan-Peter Frahm, with permission.

Epiphylls can include rare and endangered species, not to mention many species yet to be discovered. For example, Reiner-Drehwald and Drehwald (2002) discovered the extremely rare and critically endangered epiphyllous ***Lejeunea drehwaldii*** (Figure 22) in northern Peru. It exhibits some of the more common adaptations of epiphyllous species: leaf lobes that are bordered by hyaline cells, strongly inflated lobules, and cylindrical perianths, characters that are common to its family, **Lejeuneaceae** (Figure 6-Figure 15).

Figure 22. ***Lejeunea drehwaldii*** on leaf. Photo by Elena Reiner-Drehwald and Uwe Drehwald, with permission.

Identification problems have made ecological studies difficult. On the one hand, many species have multiple names in various places throughout the tropics. Others have never been described and some important epiphyllous genera do not yet have an up-to-date revision. And some species that have been described represent multiple cryptic species that cannot be distinguished morphologically, as demonstrated in the epiphyllous genus ***Diplasiolejeunea*** (**Lejeuneaceae**; Figure 11, Figure 23) (Dong *et al*. 2012).

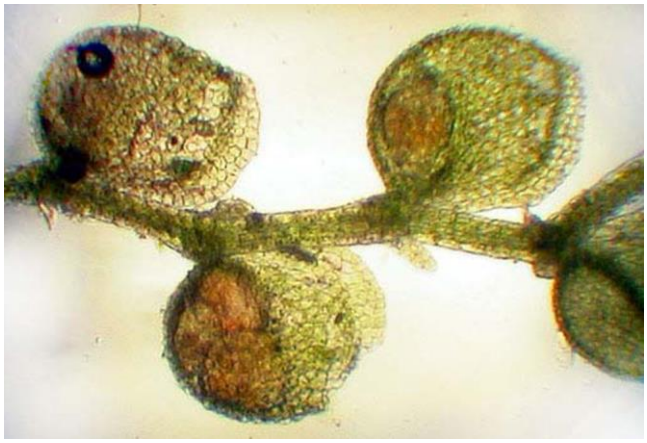

Figure 23. ***Diplasiolejeunea plicatiloba***, in a genus with cryptic species. Photo by David Tng, <www.davidtng.com>, with permission.

Because of the need for a stable substrate that lasts several years and maintains sufficient humidity, these associations are almost entirely restricted to tropical and subtropical regions with few notable exceptions, such as those living on the leaves of ***Thuja*** (Figure 24) species (Vitt *et al*. 1973). One of the northernmost records of non-***Thuja*** epiphylls in North America is in Louisiana, where leafy liverworts have been found on ***Rhododendron maximum*** (Figure 25), ***Leucothoe editorum*** (Figure 26) (both in **Ericaceae**) (Schuster 1959), and ***Magnolia grandiflora*** (Figure 27) (Guerke 1973). The moss ***Taxithelium planum*** (Figure 28) occurs on Sabal palmetto (***Serenoa repens***; Figure 29) (Schuster & Anderson 1955). On ***Buxus colchicus*** leaves at the foot of the Caucasus Mountains five liverwort species occur that are growing otherwise on different substrates (Pócs 1982b). All these host species have leathery, persistent leaves. Even in the boreal coniferous zone a few epiphyllous lichens occur on needle-like gymnosperm leaves.

Figure 24. ***Thuja occidentalis***, in a northern genus that gets epiphylls. Photo by Raul654, Longwood Gardens, through Creative Commons.

Figure 25. ***Rhododendron maximum***, an evergreen species outside the tropics that get epiphylls. Photo by S. B. Johnny, through Creative Commons.

Figure 26. ***Leucothoe editorum*** is known to have epiphylls in non-tropical regions. Photo by David Stang, through Creative Commons.

Figure 27. ***Magnolia grandiflora***, an evergreen species that gets epiphylls outside the tropics. Photo by Andrew Butko, through Creative Commons.

Figure 28. ***Taxithelium planum*** in the Neotropics, a moss that occurs on Sabal palmetto (***Serenoa repens***). Photo by Michael Lüth, with permission.

Figure 29. ***Serenoa repens*** (Saw Palmetto); leaves of this species can have growths of the moss ***Taxithelium planum***. Photo by Homer Edward Price, through Creative Commons.

The success of many epiphylls may reflect the fact that the tiny leafy liverworts have leaves in two rows that look as if they were ironed to the substrate (Figure 22). Such a flattened conformation provides the least exposure to the drying atmosphere (Figure 30).

Figure 30. **Lejeuneaceae** epiphylls showing their flattened habit. Photo by Janice Glime.

Some epiphylls are **facultative** (capable of functioning under various environmental conditions). Geissler (1997) considered five populations (4 species) of the leafy liverwort ***Marchesinia*** subgenus ***Marchesiniopsis*** (Figure 31) to be "accidentally **foliicolous**" (accidentally growing on leaves), *i.e.*, facultative. She considered their rainforest habitat to correspond with optimal conditions in equatorial primary forest in Latin America and Africa.

Figure 31. ***Marchesinia*** subg. ***Marchesiniopsis***; ***M. brachiata*** from St. Helena, a species growing here on bark, but that can be an accidental epiphyll. Photo By M. Wigginton, courtesy of Robbert Gradstein.

Alvarenga and Pôrto (2007) found that species richness and abundance of epiphytic bryophytes increased with altitude in lowland and submontane areas of Pernambuco, Brazil. However, fragmentation can negate that effect. Fragment size and isolation are important factors, with isolation having a negative effect for epiphylls in particular. Furthermore, species with smaller niches were more affected than those with large niches.

Sipman (1997) studied the lichens and bryophytes in the crowns of semi-deciduous trees in southern Guyana.

Whereas the lichens grew preferentially close to the ground, the bryophytes could be found in the crowns. He found 18 taxa of bryophytes associated with canopy leaves. These seemed to follow a distribution pattern similar to that of the lichens.

Other studies that describe this fascinating group of communities include those of Kiew (1982) on leaf color, epiphyll cover, and damage on ***Iguanura wallichiana*** (Figure 32) in Malaya. Lücking (1995a, b) described the diversity, ecology, and interactions of epiphylls in a tropical rainforest in Costa Rica; Lücking and Lücking (1998) examined adaptations and convergences of organisms living in the **phyllosphere** (space surrounding the leaf, where epiphylls are found). Baudoin (1985) analyzed the distribution patterns of epiphyllous bryophytes on the Soufrière of Guadeloupe. Pócs (1978) reported on the distribution of epiphyllous communities in East Africa, and Reynolds (1972) reported on stratification of tropical epiphylls. Farkas and Pócs (1997) reported on systematics, distribution, ecology, and uses. Winkler (1967, 1970) reported on the epiphyllous bryophytes in cloud forests of El Salvador and Colombia. Olarinmoye (1977) examined the relationship of the epiphylls to the host tree. Gradstein and Lücking (1997) summarized a symposium on epiphyllous bryophytes. The symposium emphasized floristics and ecology, including diversity analyses and the role of these bryophytes in the tropical rainforest.

Figure 32. ***Iguanura wallichiana*** var. ***major***, a species that appears to be harmed by epiphylls. Photo by David J. Stang, through Creative Commons.

Fossil Records

The oldest evidence of bryophytes is a fossil record from the Middle Carboniferous period, 330 million years ago. But fossil records of bryophytic epiphylls have been lacking (Barclay *et al*. 2013). Barclay *et al*. (2013) described an epiphyllous moss, ***Bryiidites utahensis***, from a single fossil leaf specimen from the middle Cretaceous, at least 95 million years ago. The moss presence was only 450 µm long, represented by a spore and protonema. This fossil suggests that central North America had a tropical maritime climate at that time.

Biomass Contributions

Pócs (unpublished) has found the foliicolous biomass in tropical montane rainforest (mossy forest) with well-developed foliicolous communities to be 0.139 g 100 cm^{-2} of host leaf area, or 0.216 g g^{-1} of host leaf dry mass. This figure can be extrapolated to 69.5 kg foliicolous biomass ha^{-1} forest (assuming that leaves occupied by foliicolous communities cover at least half the ground area at these localities). The interceptive capacity of this foliicolous biomass is 2.357 g 100 cm^{-2} host leaf area, or 1175 L ha^{-1} according to experiments by Pócs (unpublished). These figures include the entire community of algae, bacteria, lichens, fungi, and bryophytes. They are valid only where conditions are optimal, such as condensation zones (van Reenen & Gradstein 1983). Under less favorable conditions, foliicolous communities are restricted to certain moist habits such as streamside and near waterfalls, to certain forest layers such as leaves of the lower shrubs, or are lacking entirely. By comparison, Carroll (1979) found the biomass of foliicolous communities in oceanic temperate regions to be ~50 kg ha^{-1}, of which 30 kg is composed of fungi and 20 kg of algal cells.

Microclimate

Epiphyllous species require shade and high humidity, thus confining them mostly to the understory and lower parts of the canopy (Gradstein 1992). On the other hand, in lowland cloud forests they can also occur in higher parts of the canopy (Gradstein *et al.* 2010). An average of 3-13 species of bryophytes can occur on a single leaf.

Light and available moisture appear to play the most important roles in the distribution of epiphyllous bryophytes within the tropical evergreen forests. In Costa Rica, Reynolds (1972) found that bryophytic epiphylls existed up to about 10 m under a 24-m canopy, where they disappeared, but lichens persisted nearly to the top of the canopy. Reynolds attributed this limited bryophyte distribution to availability of continuous moisture.

In the subtropical evergreen forests of southeast China (Figure 33) the light intensity in the open can be 632 times as great as that in some forested areas supporting epiphyllous liverworts (Wu *et al*. 1987). For these liverworts to thrive through the winter, they require about two hours of direct light and ten hours of diffuse light. In general, it seems that shade and moisture promote growth while high light and drought hinder it. Heavy rains hinder colonization (Busse 1905), most likely contributing to the greater biomass found on lower branches than on upper ones.

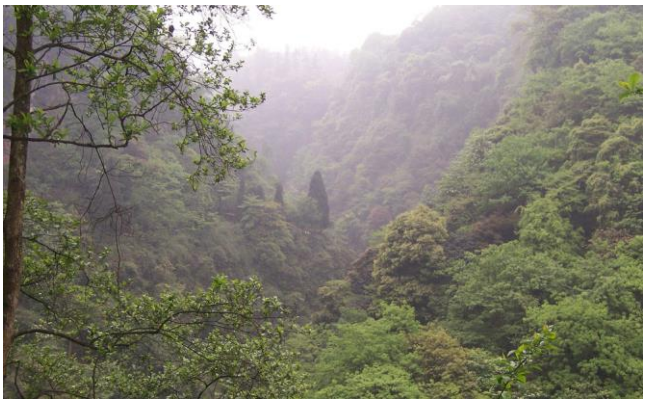

Figure 33. China – Emei Shan lush misty forest in the Sichuan Basin, China. Photo by McKay Savage, through Creative Commons.

Wu *et al*. (1987) found that temperature and humidity, in addition to light, are the main factors influencing communities of epiphyllous liverworts in subtropical evergreen forests of southeast China. They observed that these liverworts did not occur in very shady or dark forests. They studied the light intensities in a subtropical evergreen forest beside streams where the dominant epiphyllous liverworts were ***Cololejeunea ocelloides*** (Figure 34), ***Leptolejeunea elliptica*** (Figure 14) (both **Lejeuneaceae**), ***Radula acuminata*** (Figure 35; **Radulaceae**), and ***Frullania moniliata*** (Figure 36; **Frullaniaceae**). They sampled at 0.5 m intervals in the range of 0.5-2 m. There was no discernible difference in species composition in the heights sampled, but 10 m from the streams the epiphyllous liverworts were rare.

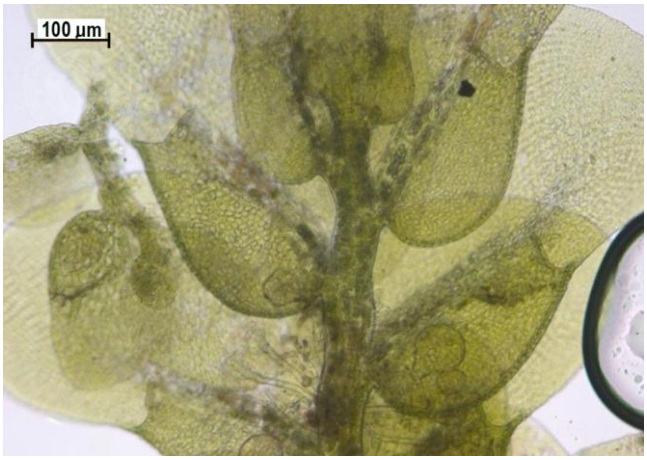

Figure 34. ***Cololejeunea ocelloides***, a dominant epiphyll beside streams in subtropical evergreen forests in China. Photo by Yang Jia-dong, through Creative Commons.

Figure 35. ***Radula acuminata***, a common epiphyllous species in broad-leaved forests of Guangdong, China. Photo by Yang Jia-dang, through Creative Commons.

Figure 36. ***Frullania moniliata***, a dominant epiphyll beside streams in subtropical evergreen forests in China. Photo by Yang Jia-dong, through Creative Commons.

Jiang *et al*. (2014) noted that epiphyllous liverworts usually grow in areas that are constantly moist with evergreen forest trees in the tropical and subtropical regions. They also considered them to be species that are very sensitive to both pollution and climate change. They also found that humidity, temperature, and light are important limiting factors for these epiphylls. The researchers used the Area Under the receiver operating characteristic Curve (AUC) and True Skill Statistic (TSS) and the Wilcoxon paired test in comparing model performances. These tests indicated that climatic and remotely sensed vegetation variables were the best predictors of bryophyte composition on a macrohabitat scale. The researchers concluded that epiphyllous liverworts could be useful indicators of forest degradation at broad spatial scales.

Reyes (1981) has shown that epiphylls are very good indicators of air pollution. In Cuba, in a large area around the Nicaro nickel metallurgical works, epiphylls do not occur even among favorable macro-climatic conditions. Pócs (1989) has found that epiphylls disappear when the forest canopy is partly loosened by invasive tree species, due to the decreasing air moisture.

Marino and Salazar Allen (1991) compared the tropical epiphyllous communities (all liverworts) on two shrub species on Barro Colorado Island, Panama. They used five randomly selected shrubs in each site (dry light, dry shade, wet light, wet shade) for each of *Hybanthus prunifolius* (Figure 37) and *Psychotria horizontalis* (Figure 38). To determine cover, they used leaf transects (midrib and 2 parallel to midrib) to determine the epiphyll cover. The small gaps with greater light clearly had more cover than did the shaded sites. Interestingly, the dry ridges had significantly more cover than did the wet creek area. There was little difference in epiphytic communities (15 species overall) between the two shrub species in the same environmental conditions. The dry site epiphylls were dominated by ***Cololejeunea sicifolia*** (see Figure 120); in the wet sites, ***Leptolejeunea elliptica*** (Figure 14) dominated. They suggested that ***C. sicifolia*** was rare in the wet site due to competition from ***L. elliptica***. On the other hand, ***L. elliptica*** was limited by insufficient moisture on the dry sites.

Figure 37. *Hybanthus prunifolius*, a species that supports epiphyllous bryophytes on Barro Colorado Island, Panama. Photo by Barry Hammel, through Creative Commons.

Figure 39. ***Scytonema hofmannii*** (**Cyanobacteria**); ***Scytonema javanicum*** and ***S. hofmannii*** grow as epiphylls on Barro Colorado Island, Panama. Photo from Utex, through Creative Commons.

Figure 38. ***Psychotria horizontalis***, a species that supports epiphyllous bryophytes on Barro Colorado Island, Panama. Photo by Daniel H. Janzen, through Creative Commons.

Figure 40. ***Spathacanthus hoffmannii***, a host for epiphyllous bryophytes and **Cyanobacteria**. Photo by Armando Astrados, with online permission.

Freiberg (1999) looked at microclimate as it affects the **Cyanobacteria** (Figure 39) on leaves in a premontane rainforest of Costa Rica. He found seven species of **Cyanobacteria**, with the two most frequent being ***Scytonema javanicum*** and ***Scytonema hofmannii*** (Figure 39). He found that air humidity is more important than light in determining their relative abundance, a factor that also determined abundance of the epiphyllous bryophytes. On moist sites, these two **Cyanobacteria** species and the bryophytes appeared nearly simultaneously on leaves that were 6-9 months old. However, on drier sites, the **Cyanobacteria** did not appear until 6-9 months after the bryophytes became established. When ***Spathacanthus hoffmannii*** (Figure 40) leaves were 2-5 years old, the average leaf cover of bryophytes was 20-30%, that of ***Scytonema javanicum*** 2-3%, and that of ***Scytonema hofmannii*** 0.1-0.2%. When bryophytes were present, the ***Scytonema hofmannii*** was more frequent, whereas ***Scytonema javanicum*** did not seem to be influenced by bryophyte presence.

Kraichak (2014) found that the **beta diversity** (ratio between regional and local species diversity) of epiphyllous bryophyte communities on Moorea, French Polynesia (Figure 129), fluctuated with the microclimate. The beta diversity among these epiphylls on different host types tended to increase as the daily range of vapor pressure deficit increased at that site. Kraichak suggested that the high fluctuations in these microclimatic conditions might augment the habitat quality differences among the host types, causing greater dissimilarities among these epiphyllous communities. However, Kraichak detected no change in niche breadth.

In western Nigeria, Olarinmoye (1974) followed the growth of four epiphyllous liverworts [***Radula flaccida*** (Figure 41), ***Caudalejeunea hanningtonii*** (see Figure 42), ***Leptolejeunea astroidea*** (see Figure 14), and ***Cololejeunea obtusifolia*** (Figure 43)] for ~18 months. Growth of larger species always exhibited faster growth. The wet and dry seasons caused a growth periodicity, but there was no dormancy. However, growth was reduced considerably during the dry season.

Figure 41. ***Radula flaccida*** habit with gemmae, a common epiphyllous liverwort in tropical Africa, with a parasitic bryophilous **Ascomycetes** on its left-most leaf. Photo by Michaela Sonnleitner, with permission.

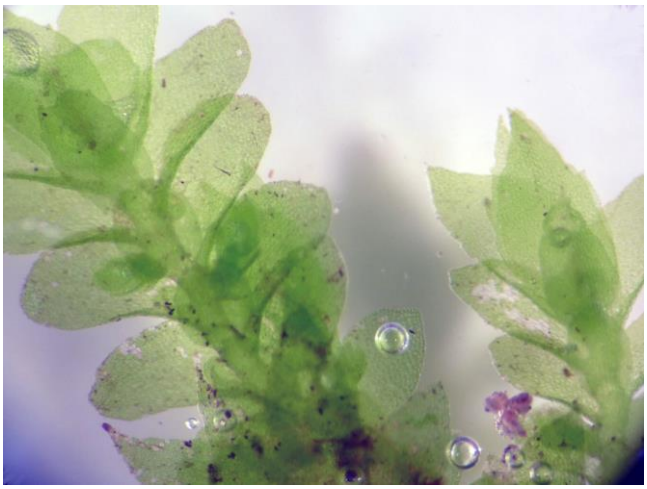

Figure 42. ***Caudalejeunea lehmanniana***; ***Caudalejeunea hanningtonii*** is an epiphyllous species with no dormancy, but with seasonal growth in Nigeria. Photo by Scott Zona, with permission.

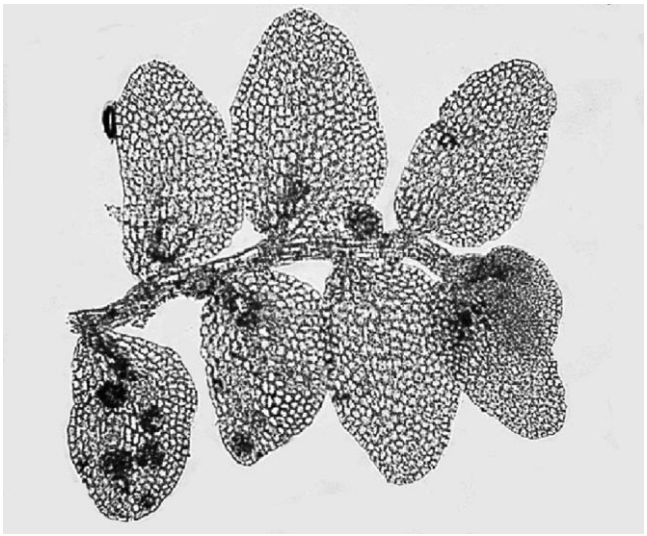

Figure 43. ***Cololejeunea obtusifolia***, an epiphyllous species with no dormancy, but with seasonal growth in Nigeria. Photo by Tamás Pócs, with permission.

Sonnleitner *et al*. (2009; Sonnleitner 2008) explored microclimatic effects by sampling epiphyllous bryophytes on two leaves per tree of 57 individual trees in a tropical lowland rainforest in Costa Rica. They sampled from three adjacent sites that had different microclimates and found that pronounced daily humidity fluctuations placed considerable restraints on the epiphyll distribution and colonization. Phorophyte species, air temperature, and light availability were only weakly correlated with epiphyll cover and diversity. Nevertheless, all of these factors influenced the species composition of the epiphyll communities. The ability of the forest to buffer the microclimate seems to be important to the success of these epiphylls. Lücking (1995a) provides additional information on microhabitat preferences of epiphylls in a tropical rainforest in Costa Rica.

Monoculture affects epiphyll establishment and success differently from the natural forests. Arnold and Fonseca (2011) examined the effects of monoculture that replaced the ***Araucaria*** forest (Figure 44) in southern Brazil. The natural ***Araucaria*** forest (Figure 44) has a larger percentage of leaves with epiphylls than does the ***Eucalyptus*** plantation (Figure 45), a fact the researchers attribute to the shadier and moister microclimate of the natural forest. Nevertheless, monocultures help to maintain epiphylls in areas that might otherwise be devoid of forest.

Figure 44. ***Araucaria*** forest, an epiphyll host that is being replaced by monoculture plantations such as ***Eucalyptus*** in southern Brazil. Photo by Jason Hollinger, through Creative Commons.

Figure 45. ***Eucalyptus*** plantation in Nilgiris, India. Such plantations have fewer epiphyll species than native ***Araucaria*** forest in southern Brazil. Photo by Shyamal, through Creative Commons.

Monge-Nájera (1989) found that both absolute and relative cover by epiphylls are higher in forest clearings than in the understory at Monte Verde, Costa Rica. They suggested this was due to the high atmospheric humidity in the area and the presence of **heliophilic** (sun-loving) bryophyte species.

Colonization

Kursar *et al*. (1988) determined rates of leaf colonization by epiphylls in Panama. Coley and Kursar (1996) found that epiphylls have both positive and negative effects on the host leaves. Conversely, the host leaf can affect the rate of epiphyll colonization.

For epiphylls, establishment on the host leaves is the most difficult step, requiring adherence of a spore or gemma and protonema through rainstorms that would attempt to wash them off. Young leaves are usually first colonized by lichens, then by liverworts, and perhaps mosses (Richardson 1981). Mosses seldom become established on the leaves, but more often grow onto them from neighboring twigs. Colonization can be rapid and dynamic, as demonstrated for a leaf from El Salvador that was colonized by 7 species in the period from May to December (Figure 46) (Winkler 1967). Winkler found that young leaves were colonized by liverworts within three months in the montane rainforest of San Salvador. Nevertheless, these could die during subsequent dry weather.

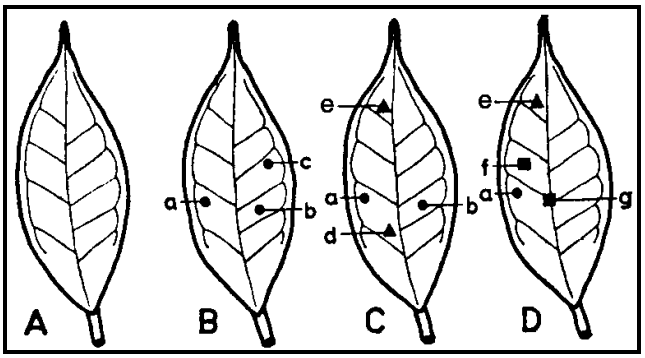

Figure 46. Progression of epiphyllous species on a leaf in El Salvador from May to December. **A**. May 1962. **B**. August 1962, with 3 colonies. **C**. October 1962, with 2 additional colonies and 2 lost. **D**. December 1962, with 2 new colonies and 2 colonies lost. From Winkler 1967.

Succession

There is a succession in leaf colonization. There are pioneer species (like members of the genus ***Leptolejeunea*** – Figure 14), which can appear even on short-lived (*e.g.* banana – Figure 47) leaves, and those which occur only in a well-established epiphyllous community on perennial leaves.

Richards (1932) made the first observations of succession in foliicolous communities, using leaf pairs of different ages in the Guyana rainforest. Harrington (1967) in West Africa and Winkler (1967) in Central America made careful studies on colonization and growth of foliicolous communities by observations on host leaves in sample plots for periods of over 200 days. All authors concluded that foliicolous growth in bryophytes and lichens does not exceed 3-7 mm annually, hence does not differ significantly from the growth rate of non-foliicolous species (*cf.* Hawksworth & Chater 1979). According to Winkler (1967) and Olarinmoye (1975c), colonization and growth rate of foliicolous liverworts coincide with climatic periods and are greatest during rainy seasons when atmospheric humidity is high. The host leaves are colonized first by **eufoliicolous** (true leaf-dwelling) taxa possessing an adhesive apparatus (***Aphanolejeunea*** – Figure 13, ***Cololejeunea*** – Figure 5-Figure 6, ***Drepanolejeunea*** – Figure 9, ***Leptolejeunea*** – Figure 14, and others) and by hemiepiphyllous taxa. Many of the early colonizers are soon overgrown by others that lack special devices to adhere to the leaf surface (Pócs 1978).

Figure 47. ***Musa*** sp. (banana), substrate for some ***Leptolejeunea*** species. Photo by Jean-Pol Grandmont, through Creative Commons.

Daniels (1998) conducted an extensive study on establishment and succession of epiphyllous bryophytes on the understory palm ***Geonoma seleri*** (see Figure 48) in Costa Rica. Using 914 pinnae from 100 individual palms, he inferred chronology based on the position of the frond on the palm. He also selected 50 pinnae and examined them repeatedly from frond emergence to abscission. Daniels concluded that there is no succession in the classical sense. Rather, the composition of species is highly variable. However, as expected, the cover values of individual species does change significantly over time. But no stable climax community emerges. Furthermore, the bryophyte assemblage development is not influenced by the season of emergence of the frond. It is somewhat

surprising that canopy closure and height of palm tree have no significant effect on total cover of epiphyllous bryophytes.

Figure 48. ***Geonoma seleri***, a host of epiphyllous bryophytes in Costa Rica. Photo from INaturalist, through Creative Commons.

Kiew (1986) studied epiphyll colonization in a Malayan rainforest. Leaves on the shrub ***Thottea dependens*** (see Figure 49) live up to 70 months and become completely covered with epiphylls. The longest-living leaves were those of the palm ***Iguanura wallichiana*** (Figure 50). These leaves had no epiphyll colonists in the first 6 months. Bryophytes didn't colonize until approximately 2 years, but they then covered half the leaf surface in another 6 months.

Figure 49. ***Thottea sivarajanii***; ***Thottea dependens*** leaves live up to 70 months and can become completely covered with epiphylls. Photo by Vinayaraj, through Creative Commons.

Figure 50. ***Iguanura wallichiana*** var. ***major***, a species that is not colonized by epiphylls in the first 6 months, but bryophytes can cover half the leaf surface by 30 months. Photo by David J. Stang, through Creative Commons.

Olarinmoye (1975c) reports no orderly successional colonization or phenological rhythm in order of species establishment in his western Nigerian study. Rather, colonization depends on nearness of propagules, number produced, and their ability to become established. Subsequent succession, however, does at some locations seem dependent on competition and seasonal changes. Lichens are common cohabitants with the bryophytes, and liverworts seem always able to overgrow the crustose lichens, but the foliose lichens are able to overgrow even the large, fast-growing ***Radula flaccida*** (Figure 41). On the other hand, the large ***Caudalejeunea hanningtonii*** (see Figure 42) seems to be able to overgrow all types of lichens and algae, at least at Alkenne and Gambari, Nigeria. But even some of the algae can overgrow the small, slow-growing liverworts. The large, tufted or shelf-forming ***Trentepohlia*** (Figure 51-Figure 52) is one such alga, whereas the **Cyanobacteria** (Figure 39) tend to live in association with the liverworts without overtaking them. Despite all this competition, the ultimate winner seems to be ***Radula flaccida***, which eventually occupies the entire leaf surface. That is, until the dry season in Erin-Odo, when only ***Leptolejeunea astroidea*** (see Figure 14) remains, mixed with scattered shoots of ***Cololejeunea nigerica***. And at Ojo Rocks, where ***Caudalejeunea hanningtonii*** predominates in the wet season, it likewise disappears in the dry season, being replaced by thick felts of ***Leptolejeunea astroidea***. It appears quite clear that the large ***Radula flaccida*** and ***Caudalejeunea hanningtonii*** are unable to prosper during the dry season.

Richards (1996) stated that epiphyllous species do not also occur on bark, but in fact, there are a number of examples where both substrates are occupied. He cites only one example for this, the genus ***Floribundaria*** (Figure 55), that establishes on twigs, then expands onto the leaves. He suggests that such species are not able to establish directly on a leaf.

Figure 51. ***Trentepohlia aurea*** on cypress in California, USA; some ***Trentepohlia*** species can overgrow epiphyllous liverworts. Photo by Jason Hollinger, through Creative Commons.

Figure 52. ***Trentepohlia abietina*** with akinetes, in an alga genus with some members that can overgrow epiphyllous liverworts. Photo by A. J. Silversides, with permission.

Coley and Kursar (1996) examined the causes and consequences of epiphyll colonization in tropical forests. Coley *et al*. (1993) found that while lichen cover changed little among their sites in Panama, liverwort cover increased with rainfall. In their experimental plots, liverwort cover increased from 1.7% in the controls to 20.5% in irrigated plots, whereas lichen cover decreased in response to the same watering regime. Surprisingly, liverworts at one site grew more quickly in high light compared to shade, and Coley and coworkers suggested that the liverworts were competitively superior to the lichens, resulting in the negative association between them. Contrasting sharply with the conclusion that bryophytic epiphytes require long-lived leaves, the short-lived leaves of ***Alseis*** (Figure 53) had 27% cover whereas the long-lived ones of ***Ouratea*** (Figure 54) had only 2% one year after removal of epiphytes. Within one year, the liverworts had colonized 45% of the leaves that had a lifetime of only one year, whereas they had colonized only 5% of the leaves of those with longer lives. This is, however, consistent with the known presence of chemical defenses of long-lived leaves against herbivores and pathogens. These defenses could affect the liverworts directly or by preventing growth of **Cyanobacteria** (Figure 39) or fungi that might benefit them.

Figure 53. ***Alseis costaricensis***, in a genus with short-lived leaves that can have extensive cover of epiphylls, in Guanacaste dry forest. Photo by Daniel H. Janzen, through Creative Commons.

Figure 54. ***Ouratea brevicalyx***, in a genus with long-lived leaves that develop poor epiphyll cover, in Venezuela. Photo by Vojtěch Zavadil, through Creative Commons.

Figure 55. ***Floribundaria floribunda*** (**Meteoriaceae**), a species that colonizes leaves only after becoming established on twigs. Photo through Creative Commons.

Figure 56. ***Distichophyllum***; ***Distichophyllum mniifolium*** occurs primarily on filmy fern leaves. Photo by Phil Bendle, through Creative Commons.

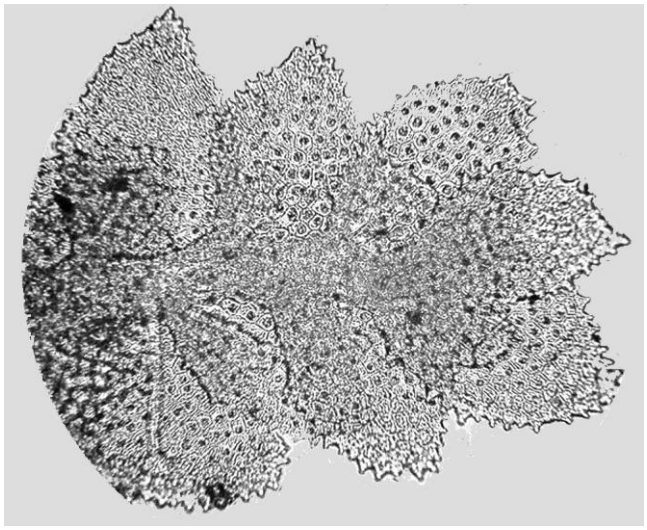

Figure 57. ***Cololejeunea mocambiquensis***, a species that is epiphyllous on filmy fern leaves. Photo modified from Tomas Pocs, with permission.

Host Preference

There seems to be little preference by the foliicolous communities for a particular host species. Rather, their occurrence seems to depend primarily on microclimatic conditions and availability of suitable leaf surfaces (Santesson 1952; Tavares 1953; Richards 1984b).

Nevertheless, some species do seem to have preferences. Members of the **Hookeriaceae** (*e.g.* ***Distichophyllidium africanum***, ***Distichophyllum mniifolium*** – see Figure 56), and certain liverworts (*e.g.* ***Cololejeunea mocambiquensis*** – Figure 57, ***C. tanneri***, ***Lejeunea gradsteiniana*** – Figure 58, ***L. lyratiflora***) occur primarily on filmy fern leaves, whereas others (***Diplasiolejeunea cavifolia*** – Figure 11, ***Cheilolejeunea xanthocarpa*** – Figure 59) prefer hard, smooth, leathery leaf surfaces (Pócs 1978, 1985). Overall, the epiphylls have a relationship with size, age, and texture of phorophyte leaves.

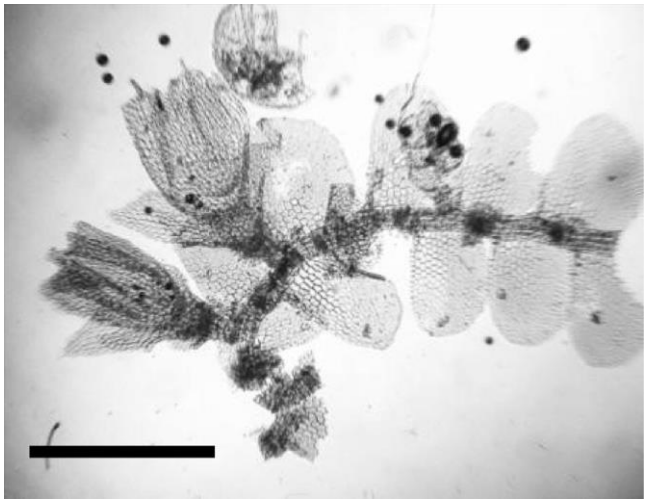

Figure 58. ***Lejeunea gradsteiniana*** with perianths and antheridia, a species that is epiphyllous on filmy fern leaves. Photo by Tamas Pocs, with permission.

Figure 59. ***Cheilolejeunia xanthocarpa***, a species that prefers hard, smooth, leathery leaf surfaces. Photo source unknown.

Winkler (1967) considered leaf hair density and quality of phorophyte leaves to be important. He pointed out that a stellate hair cover may inhibit foliicolous growth. Foliicolous species also seem to avoid waxy, water-repelling leaf surfaces (Richards 1932), but may be abundant on other surfaces, *e.g.* on leaves of planted citrus trees (Figure 4) in rainforest clearings. Pócs (pers. comm. May 2019) suggested that it was the sugary, sticky exudates of the citrus leaves that discouraged the epiphylls. A long life for the host leaf is also important, although some leaves with only a 3-4-month life span are occasionally colonized. In Cuba, Pócs observed a large vegetation of ***Leptolejeunea*** sp. (Figure 14) on smooth banana leaves (Figure 47). In habitats that were relatively dry, but affected by mist, foliicolous species occurred only on evergreen leaves such as the succulent ***Agave*** (Figure 60), ***Aloe*** (Figure 61), ***Sansevieria*** (Figure 62), **Bromeliaceae** (Figure 143), and **Cactaceae** (Figure 63) leaves or **phyllocladia** (branches that look like leaves).

Figure 60. ***Agave americana***, a substrate for epiphylls in dry communities. Photo by Marc Ryckaert, through Creative Commons.

Figure 61. ***Aloe vera***; ***Aloe*** species provide a substrate for epiphylls in dry communities. Photo by Biology Big Brother, through Creative Commons.

Figure 62. ***Sansevieria trifasciata***; ***Sansevieria*** species provide a substrate for epiphylls in dry communities. Photo by Mokkie, through Creative Commons.

Figure 63. ***Macrocoma tenue*** on cactus. Photo courtesy of Tatiany Oliveira da Silva.

It appears that substrate preference diminishes further with increasing air humidity. In an everwet rainforest, foliicolous species occur on many kinds of host leaves. Several species tend to occur on other substrates as well (**elective foliicolous species**). On the other hand, **terricolous** (soil-dwelling), **rupicolous** (rock-dwelling), or

corticolous (bark-dwelling) species may occur on leaf surfaces in this kind of wet forest (**accidental foliicolous species** such as certain species of ***Bazzania*** – Figure 64).

Figure 64. ***Bazzania peruviana***; some species of ***Bazzania*** become accidental epiphylls. Photo by Felipe Osorio-Zúñiga, with permission.

Growth Structure

Fitting (1910) considered three groups to classify foliicolous lichens on leaves:

1. species penetrating the leaf tissue
2. species growing subcuticularly on the epidermis
3. species growing supracuticularly

Fünstück (1926) considered that most foliicolous lichens penetrate into the mesophyll, others (Santesson 1952; Brodo 1973; Margot 1977) disagreed with this concept. Nevertheless, even some liverworts do this and can take nutrients from the leaf tissue (Berrie & Eze 1975).

One can also distinguish between the **obligately foliicolous species** (those unable to grow elsewhere) and the **facultative foliicolous species** (those able to also grow on other plant parts and even on rocks). Sérusiaux (1977) divided this even further:

1. **strictly foliicolous**: never occurring on substrata other than leaves
   locally eufoliicolous: restricted to the phyllosphere in a definite geographical area, while occurring on other substrata elsewhere
2. **pseudofoliicolous taxa**: not restricted to living leaves and occurring also on other substrata
   elective pseudofoliicolous: showing highest vitality and abundance on living leaves
   indifferent pseudofoliicolous: occurring both on living and other substrata and not showing any preference
   accidental foliicolous species: normally corticolous, saxicolous, or terricolous, and occurring on leaves only accidentally (*e.g.* the leafy liverwort ***Bazzania*** – Figure 64; mosses in the **Meteoriaceae** (Figure 55).

To these, Pócs (1982b) added the bryophyte category of **hemiepiphyllous** – those species that start their lives on branches, but subsequently grow from the twig to the leaf blade via the petiole, subsequently forming a community there.

Bryophyte Adaptations

Epiphytic life forms in general are considered late results of evolution. Among phanerogams, almost all epiphytic groups are at the tips of phylogenetic tree branches (Emberger, cited by Tixier 1980) and this seems also to be true for bryophytes (Vitt 1984). Hence, we should expect that special adaptations exist.

In the tropical rainforest, epiphytism among bryophytes is probably the result of coevolution since the Cretaceous (Gradstein & Pócs 1989). Most of the foliicolous bryophytes are in the leafy liverwort family **Lejeuneaceae**, a family that is diversified most strongly in the rainforest, especially the subfamilies **Lejeuneoideae** and **Cololejeuneoideae**. The **Lejeuneaceae** has several morphological adaptations, as noted below, but its most significant evolutionary trend in the phyllosphere is its shortened life cycle. Several taxa may reach reproductive maturity in an early stage of development (**neoteny**).

Gradstein (1997b) pointed out that many epiphyllous species are **facultative –** also able to grow on bark or other substrates. He described the **typical epiphyllous species** (those growing exclusively or almost exclusively on leaves) as shade epiphytes of the understory. These are small, pale-colored, appressed (Figure 65), with rhizoids in bundles that form large adhesive discs. They sometimes are **neotenous** (condition in which juvenile characters remain in adults). Gemmae (Figure 66), used in short-distance dispersal, are common.

Figure 65. Epiphylls on leaf, demonstrating their small size, pale color, and appression to leaf. Photo by Jessica M. Budke, with permission.

Figure 66. ***Radula australis*** with gemmae on leaves. Photo by Paul Davison, with permission.

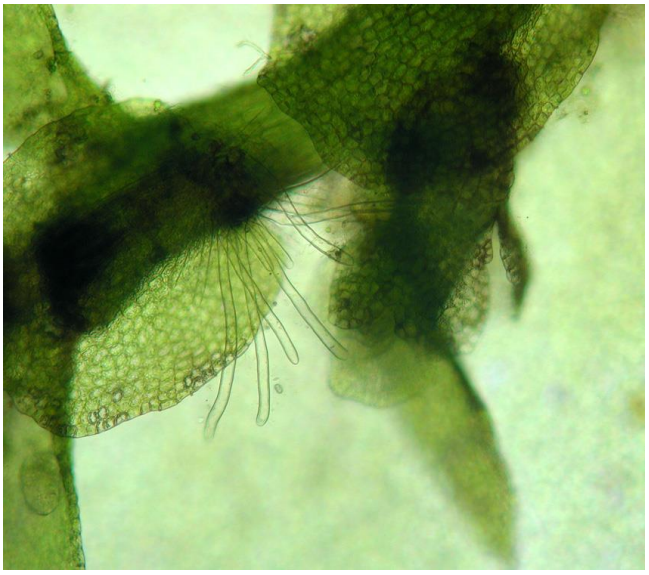

Figure 68. Rhizoids at base of underleaf on leafy liverwort. Photo courtesy of Andi Cairns.

Morphology

There must be some advantage in being a small, flattened, leafy liverwort when inhabiting a leaf surface, as nearly all the epiphyllous bryophytes fall in this category, mostly in the family **Lejeuneaceae** (Figure 6-Figure 15). Many of these adaptations have been described for liverworts (Massart 1898; Evans 1904, 1935; Schiffner 1929; Renner 1933; Jovet-Ast 1949; Winkler1967, 1970; Bischler 1968).

Some thallose liverworts, *e.g*. species of ***Metzgeria*** (Figure 67), are anchored to the leaf surface by rhizoids that arise randomly from the ventral thallus surface (Figure 67). In most of the foliicolous liverworts, these anchoring rhizoids develop at a definite place (Figure 68), such as the main axis, on the lobule in ***Radula***, or at the base of underleaves in **Lejeuneaceae** (Figure 68, Figure 69).

Figure 69. ***Microlejeunea ulicina*** showing rhizoids near leaf bases. Note the rotifer peering out from the middle leaf. Photo by Blanka Shaw.

Figure 67. ***Metzgeria conjugata*** ventral view showing rhizoid clusters. Photo by N. J. Stapper, with permission.

In the **Lejeuneaceae** the rhizoids are usually fused together to form an adhesive disc that enhances the attachment to the leaf surface. The attachment of rhizoids is strengthened by a glutinous mucus secreted by the rhizoid disc. Winkler (1967) tested this attachment experimentally and found that adhesion is stronger on smooth leaf surfaces than on rough ones.

Perhaps ***Chiloscyphus koponenii*** (see Figure 70) in the **Geocalycaceae** can provide some clues as to the important structures contributing to success in this habitat. This leafy epiphyllous liverwort from Papua New Guinea possesses many characteristics similar to those of some genera of epiphyllous **Lejeuneaceae**, including its tiny size, ability to fragment and grow from fragments, two-lobed and often toothed leaves, thin-walled cells, small **trigones** (cell wall swellings), very shallow but wide underleaves with two lobes, two teeth, and numerous rhizoids (Piippo 1998), which many times fuse into a firm rhizoid plate. It is likely that the small size, the saccate lobules, and close adherence to the leaf surface (often with aid of a hyaline margin) are especially adaptive to maintaining moisture.

Figure 70. ***Chiloscyphus pallescens*** branch (**left**) and leaf cells with small trigones (**right**). Photo by Paul Davison, with permission.

Bernecker-Lücking and Morales (1999) considered the flattened stem and reduced lobule of ***Cololejeunea sigmoidea*** (Figure 71) to be adaptations to being a closely appressed epiphyll. But Olarinmoye (1975c) considered that for western Nigerian epiphylls the small size and closely appressed shoots were a disadvantage in competition with other species not so appressed. Instead, he considered ***Radula flaccida*** (Figure 41) and ***Caudalejeunea hanningtonii*** (see Figure 42) to be at a competitive advantage due to their larger size and faster growth, while he considered the small, appressed form to have a possible advantage in competing with erect species of smaller size. Fragmentation is useful for short-distance dispersal and spreading, and Olarinmoye considered the production of "copious propagules" of more than one type to provide a competitive advantage over those with only one type. For example, ***Radula flaccida*** produces numerous gemmae, but it can also produce as many as 10,000 spores in a single capsule, with 90% viability in the first few hours, dropping to about 40% after three weeks out of the capsule. And these capsules are produced only occasionally. Numerous rhizoids would aid in maintaining the position on a waxy leaf surface during a torrential onslaught, and some leafy liverworts have rhizoids or other parts with adhesive secretions that aid in maintaining attachment (Winkler 1967; Berrie & Eze 1975).

Figure 71. ***Cololejeunea sigmoidea*** growing as an epiphyll. Photo by Yang Jia-dong, through Creative Commons.

Eze and Berrie (1977) found that under the extreme drying conditions of sodium chloride solution or silica gel, liverwort leaf cells did not plasmolyze, but instead the cell walls folded inward and became contorted. The **oil bodies** (Figure 72) lost their shape, and after rehydration they all coalesced into one, indicating that the membrane of the oil body had been destroyed. The oil body content of these liverworts is high, comprising 17% of the dry cell, whereas liverworts from more moist habitats (***Plagiochila praemorsa*** and ***P. integerrima***; see Figure 73) exhibit oil body contents of about 5%. Although the role of the oil bodies is still largely speculative, their large volume helps to reduce the loss of cell volume as the cell dries, thus somewhat preserving the cell shape. The oil body itself is unaffected by water loss. It could also be a potential source of energy upon rehydration.

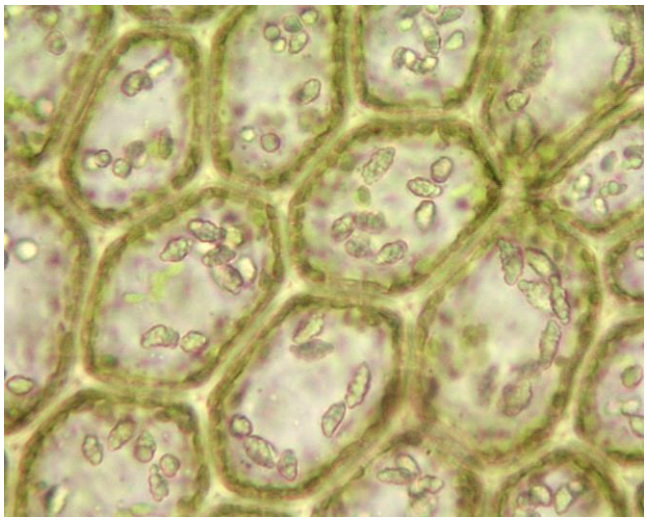

Figure 72. ***Plagiochila asplenioides*** showing leaf cells with **oil bodies** (bright, oblong structures in cells). Photo by Malcolm Storey, <DiscoverLife.org>, with online permission.

Figure 73. ***Plagiochila asplenioides***; ***Plagiochila praemorsa*** and ***P. integerrima*** have only about 5% content of oil bodies. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Water Relations

Bryophytes in general act like sponges to absorb water. Epiphylls are no exception. The bryophytes are also able to

hold water for a greater period of time than the leaf surface. This moist environment permits colonization by nitrogen-fixing **Cyanobacteria** (see Figure 39**)**.

Pócs (pers. comm. May 2019) concluded that the most effective method to ensure continuous water saturation seems to be **subcuticular growth**, a method used by about 6% of the foliicolous lichen species. Among liverworts, this method seems to be lacking. Instead, for many success seems to be a leaf lobule that retains water, as found in **Radulaceae** (Figure 74), **Jubulaceae** (Figure 75), and **Lejeuneaceae** (Figure 76). This lobule, in many cases among epiphylls, develops into a watersack, with the most sophisticated ones in ***Colura*** (Figure 77; **Lejeuneaceae**). This genus has a special closure apparatus. Other epiphyllous liverworts have hyaline leaf margins (*e.g.* species of ***Cololejeunea*** – Figure 78 and ***Diplasiolejeunea*** – Figure 11). These hyaline margins consist of dead cells, which may absorb water, adhere quite close to the substrate, and retain water below the leaf surface. They apparently form a capillary system that promotes the distribution of available water (*e.g.* a raindrop) along the liverwort shoot.

Figure 74. ***Radula*** from the Neotropics, showing lobule at arrow. Photo by Michael Lüth, with permission.

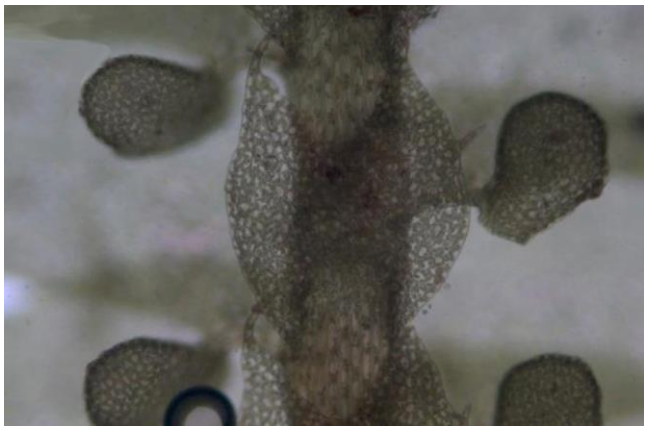

Figure 75. ***Jubula japonica*** leaves and lobules. Photo by Yang Jia-dong, though Creative Commons.

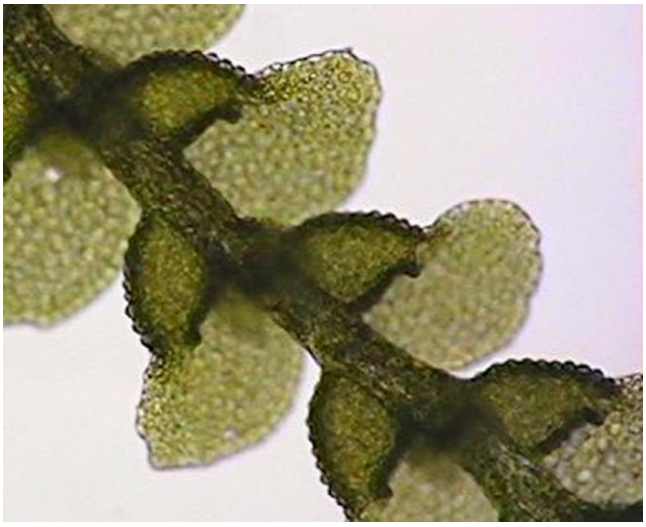

Figure 76. ***Cheilolejeunea evansii*** branch showing leaf lobules. Photo by Paul Davison, with permission.

Figure 77. ***Colura*** leaf showing well-developed lobule. Photo courtesy of Jan-Peter Frahm.

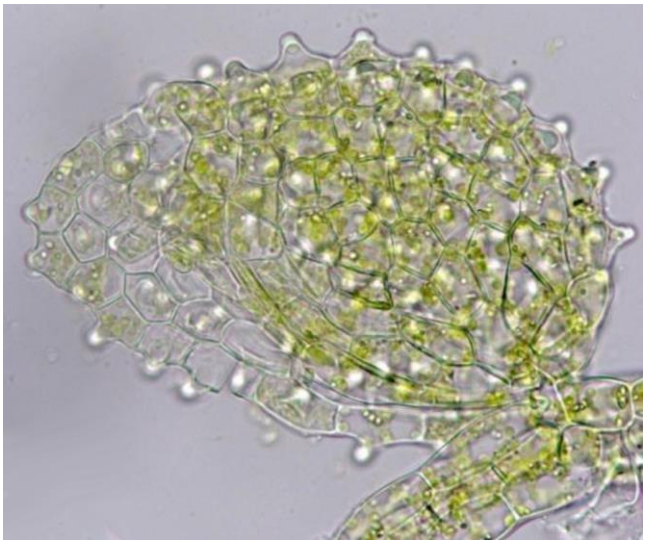

Figure 78. ***Cololejeunea grossepapillosa*** leaf showing hyaline marginal cells. Photo by Yang Jia-dong, through Creative Commons.

Dietz *et al*. (2007) examined surface wetness in an old-growth tropical montane forest in central Sulawesi, Indonesia. The canopy remained wet 25-30% of the time in the May-August study. The lower canopy surface

wetness is continuous for up to 22 hours per day or more. During dry periods, wetness is contributed by dewfall in the second half of the night, affecting primarily the uppermost canopy. This causes radiative heat loss and under-cooling of the leaves. The researchers suggest that epiphyll colonization might take advantage of this surface water.

Epiphylls may also steal water from the host leaves as drying commences. Barkman (1958) reported osmotic potentials as low as -90 bars in epiphytes, and Berrie and Eze (1975) have shown transfer of both water and phosphate from host to epiphyll. In the leafy liverwort ***Radula flaccida*** (Figure 41) in Nigeria, the osmotic potential can reach -30 to -35 bars while the potential in leaf cells of two species of their hosts are only down to -10 to -12 bars (Eze & Berrie 1977). This osmotic differential could facilitate transfer of host leaf water to the epiphyll.

Larson (1981) compared the morphologies of various lichens and bryophytes to determine their water relations. Water uptake to saturation required only three minutes in ***Polytrichum juniperinum*** (Figure 79-Figure 80) to more than 300 minutes in the lichen *Stereocaulon saxatile* (Figure 82). The large surface area to weight ratio was the major contributor to rapid uptake in ***P. juniperinum*** and other species with a high ratio. It is likely that the lamellae on leaves (Figure 81-Figure 80) of ***P. juniperinum*** contribute to this rapid uptake, but this species also has internal conduction to contribute to water movement. Nevertheless, this suggests that species with small capillary spaces have an advantage in both uptake and holding of water.

Figure 79. ***Polytrichum juniperinum***, a species with very rapid water uptake. Photo by Bob Klips, with permission.

Figure 80. ***Polytrichum juniperinum*** leaf lamellae in cross section, providing extensive capillary space. Photo courtesy of John Hribljan.

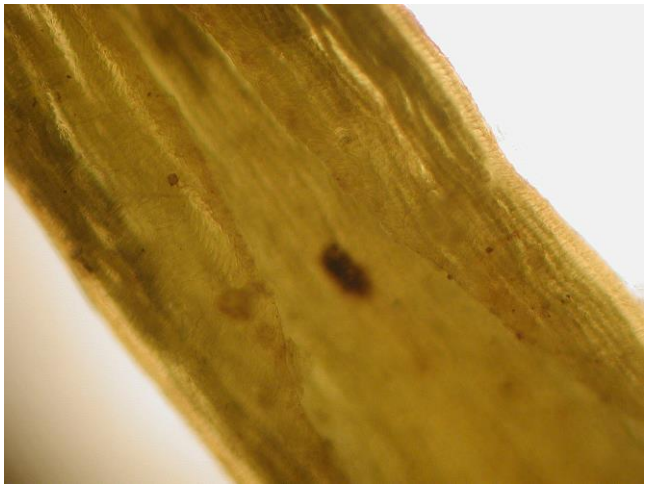

Figure 81. ***Polytrichum juniperinum*** leaf showing tops of lamellae. Photo courtesy of John Hribljan.

Figure 82. ***Stereocaulon saxatile***, a lichen with a very slow water absorption rate. Photo by Ed Uebel, through Creative Commons.

The host may reap some advantage from the association of drying epiphylls. In some cases, the thick growth of bryophytes and other epiphylls may aid in evaporative cooling as they release the water retained during a rainstorm (Olarinmoye 1976). And this water may also be absorbed by some tracheophyte leaves, thus contributing to their health.

Nutrient Budget

The foliicolous species seem to have a low nutrient budget and are very effective at using nutrients. They depend on rainwater for most of their nutrients, including leachates from canopy throughfall. Some epiphyllous liverworts, however, are able to take up nutrients from the mesophyll tissue of the host leaves (Berrie & Eze 1975), using rhizoids that penetrate the cuticle. Water-soluble salts could pass from the host leaf tissue into the epiphylls in this way. Thus, we could consider the epiphyllous liverworts to be semiparasitic. On the other hand, the **Cyanobacteria** (Figure 39) that inhabit many of these liverworts can carry out nitrogen fixation. Harrelson (1969) and Edmisten (1970a) demonstrated that N fixation in leaves having foliicolous bryophytes was higher than that of leaves with no epiphylls. The interaction of the

epiphylls and nitrogen fixation is discussed further below under Interactions.

Life Cycles

Reproductive strategies are usually important in habitat limitation, and this appears to be true for epiphyllous liverworts as well (Zartman *et al*. 2015). Unfortunately for most vegetation studies, the life cycle is slow and makes it difficult to predict long-term survival. Epiphyllous species, on the other hand, must complete their life cycles in a relatively short period of time because their leaf substrate is short-lived. In fact, they have some of the shortest generation times known for terrestrial plants.

The most common type of life strategy among foliicolous bryophytes appears to be that of the **perennial shuttle** (During 1979). A shortened life span is characteristic, permitting them to complete the cycle before the leaf falls and the habitat becomes unfavorable. This makes us wonder if any species has taken advantage of this programmed change in the microhabitat, perhaps producing capsules or gemmae only after the leaf substrate falls to the ground.

Zartman and coworkers (2015) investigated the relationship of the leafy liverwort ***Radula flaccida*** (Figure 41) in a central Amazonian rainforest to the seasonal precipitation. By marking 154 colonies, the researchers followed colony growth, extinction, recolonization, and rates of sexual and asexual expression. They found that the dry season increased mortality due to both increased leaf fall and ***R. flaccida*** colony mortality. Asexual reproduction decreased significantly in the dry months, but sporophyte density seemed unrelated to rainy season or dry season. Sporophyte density did, however, relate to a threshold colony size.

Kraichak (2012) considered asexual propagules to be adaptive among tropical leafy liverworts in the **Lejeuneaceae** (Figure 6-Figure 15). He tested several potentially adaptive traits and only asexual reproduction seemed to be evolved in the presence of epiphylly. Other traits associated with epiphylly appeared to result from shared evolutionary history, not adaptive evolution.

Epiphyllous mosses are much rarer than epiphyllous leafy liverworts. The epiphyllous moss ***Crossomitrium patrisiae*** (Figure 21) is **dioicous** (having male and female organs on separate plants), presenting a particularly challenging reproductive mode for this habitat. Alvarenga *et al*. (2013) set out to determine what permitted its success as an epiphyll. To do this, they examined 797 **ramets** (**ramet** – individual in a clone) for total length, presence, number of **gametoecia** (sexual reproductive structures and surrounding bracts), and number of fertilized **perichaetia** (modified leaves enclosing female reproductive structures and later the seta). They found high rates of sexual expression (76%). They unexpectedly found a highly male-biased population (0.43 females to 1 male) at the ramet level, n=604. Despite the isolation, with only 36.7% of the shrubs and 12.8% of the colonies having co-occurring sexes, the species nevertheless has one of the highest rates of fertilization known for any dioicous bryophyte. Nearly 90% of the mixed colonies produced sporophytes, with 40% of the female-only ramets producing sporophytes. Individual female ramets exhibited 74% sporophyte production. The researchers suggested that the species invests in the success of the sporophyte rather in the number of perichaetia in a species that demonstrates low levels of abortion. To further elucidate this unusual reproductive strategy, Alvarenga *et al*. (2016) experimented with threshold colony sizes and alternative reproductive strategies. They followed growth, reproduction, and fate of 2101 colonies of ***C. patrisiae*** for two years and found that asexual expression, but not sexual onset, was limited by a threshold colony size. Age and threshold size did not correlate. Colonies with brood bodies survived nearly twice as long as did sterile or solely sporophytic colonies. Nevertheless, reproductive strategy had no effect on colony growth rate.

He and Zhu (2011) compared the spore output of 26 selected species, representing 11 genera in the **Lejeuneaceae**. The mean spore output for these species ranges from 257 in ***Cololejeunea magnilobula*** (Figure 83) to 5038 in ***Ptychanthus striatus*** (Figure 84). The **Lejeuneaceae** has a much lower but more stable spore output than other leafy liverwort families. However, among eight species of **Ptychanthoideae**, ***Acrolejeunea pusilla*** (Figure 85) is the only species with a mean spore output of less than 1000 spores per capsule.

Figure 83. ***Cololejeunea magnilobula***, a species that produced a mean of only 257 spores in a Chinese population. Photo by Yang Jia-dong, through Creative Commons.

Figure 84. ***Ptychanthus striatus***, a species that produced a mean of 5,038 spores in a Chinese population. Photo by Yang Jia-dong, through Creative Commons.

Figure 85. ***Acrolejeunea pusilla***, the only species in **Ptychanthoideae** with a mean spore output of less than 1000 spores per capsule. Photo by Li Zhang, with permission.

The moss ***Ephemeropsis trentepohlioides*** (Figure 86) has globose gemmae and spores that can germinate in the capsule, and protonemata can extend out of the capsule (Bartlett & Iwatsuki 1985). Like ***E. tijbodensis***, this species can cover an entire leaf by expansion of its persistent protonemata (Figure 87). The bunches of erect filaments increase its surface area for adsorbing water. Nevertheless, this species has seldom been reported from leaves – it usually grows on twigs.

Figure 86. ***Ephemeropsis trentepohlioides*** with capsules, a species with spores that can germinate in the capsule. Photo by David Tng <www.davidtng.com>, with permission.

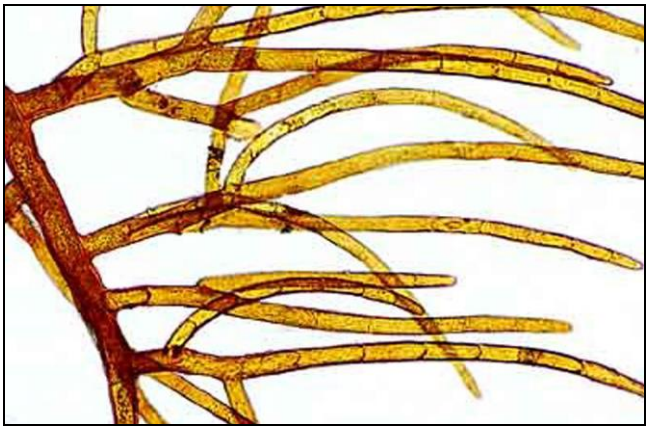

Figure 87. ***Ephemeropsis trentepohlioides*** mature growth form of protonema that can cover a leaf. Photo by Bill and Nancy Malcolm, with permission.

Lücking and Lücking (1998) looked for adaptations and convergences in the phyllosphere, using mosses, lichens, and insects. Sierra *et al*. (2018) looked at the mechanisms of species assembly in epiphyllous bryophytes. These small organisms have the advantage of a short period of assembly that must be completed during the life of the host leaf. Sierra and coworkers studied the frequency and distribution of 55 species of epiphyllous bryophytes inhabiting 5 leaf-age classes on the understory shrub ***Piper grande*** (Figure 88) in a Panama premontane tropical forest. They found that dispersal was an important contributor to the assembly pattern, particularly for early arrivals. These early arrivals also had greater probabilities of sexual and specialized asexual reproduction. They concluded that interspecific variation in dispersal capacity, combined with various indirect effects, are the prerequisites for the high **alpha diversity** (average species diversity in habitat or specific area) of these epiphyllous communities.

Figure 88. ***Piper colubrinum***; ***P. grande*** is an understory tree that hosts 55 species of epiphylls in the Panamanian premontane forest**.** Photo by Vinayaraj, through Creative Commons.

Neoteny

Pócs (1980) observed that young gemmalings of **Lejeuneaceae** with 2-3 pairs of leaves produced gametangia. Gemmae also apparently are important in the life cycle of foliicolous liverworts (Schiffner 1929) and gemmae production together with sexual reproduction may significantly accelerate their propagation (see also Schuster in Richards 1984b, p. 1270). In some foliicolous taxa sexual organs are produced "directly" on an expanded, persistent protonema which is thallose in ***Metzgeriopsis pusilla*** (see Figure 127) and ***Radula yanoella*** (Figure 89) (Schuster 1980) and filamentous in the moss genus ***Ephemeropsis*** (Figure 86-Figure 87) (Fleischer 1929; Tixier 1974). The vegetative leafy gametophore in these plants has almost completely become suppressed as the result of neotenic evolution. The neotenic life-cycle of foliicolous taxa may be seen as an adaptation to the relatively short life span of the "evergreen" host leaves and represents a striking example of an evolutionary strategy to survive the hazards of life in the tropical rainforest.

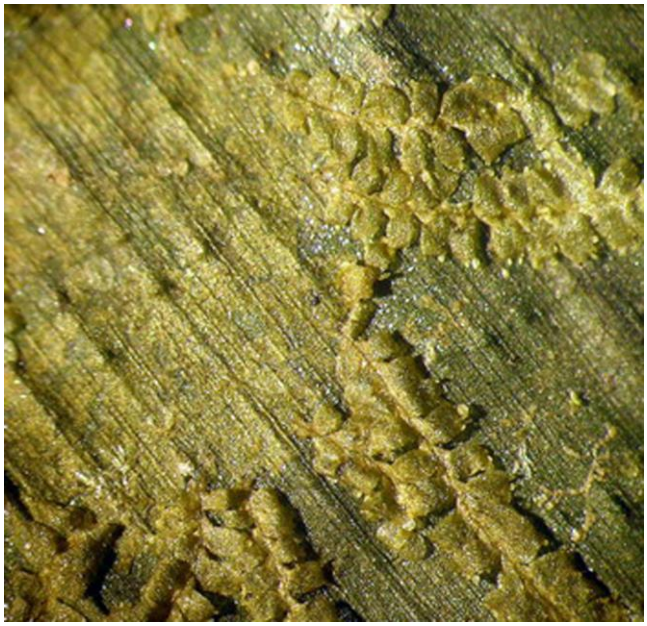

Figure 89. ***Radula yanoella***, a leafy liverwort with a thallose protonema. Photo by Michaela Sonnleitner, with permission.

Life Strategy Types

Colonizers (primary colonists of Winkler 1967)	Adhesive apparatus or hemiepiphyllous growth, abundant gemmae and spores
temporary	Small size, short life cycle (*e.g.* ***Aphanolejeunea***)
resistant	Appressed or subcuticular growth, or ciliae, setae, perpendicular structures, or size preventing overgrowth (***Cololejeunea*** with hyaline margin, ***Colura***)
Occupants (secondary colonists)	
overrunner and overgrower (see Kiss 1982)	Fast growth rate, loose, creeping habit or robust size (***Radula flaccida***, ***Diplasiolejeunea***, ***Cheilolejeunea*** spp.)
squeezer (line contact of Kiss 1982)	Physical or chemical pressure against another species (latter by ***Frullania***)
Explerents (*sensu* Ramensky 1938, tertiary colonists)	
space economizer	Utilizing space between other species, *e.g.* by hypophyllous growth, pendulous from leaf margin, *e.g.* **Meteoriaceae**)
replacer	Settling in the debris of dead, decomposing plants (*e.g.* ***Syrrhopodon*** on leaf surface) or occupying over-mature center of round colonies (window contact of Kiss 1982)
Accidental (non-adapted) settlers that cannot reach maturity after germination (non-epiphyllous bryophytes like ***Bazzania*** or ***Leucoloma***)	

Host Adaptations

While epiphylls are not parasitic (Olarinmoye 1976), they can reduce photosynthesis and in some cases may encourage the growth of fungi by maintaining a higher humidity on the leaf surface. They can also block stomatal openings, hampering gas exchange. Hence, we might expect some trees to have evolved adaptations that discourage the growth of epiphylls.

Drip Tips

Some leaves have special adaptations that permit them to slough off the cuticle on a regular basis, getting rid of the epiphytes at the same time (Attenborough 1995). Some tropical biologists have attributed the success of some leaves in preventing epiphyte colonization to the presence of a **drip tip** (Figure 90) that increases the flow of water from the leaf, thus making the habitat less hospitable for colonization (Briscoe 1994). For example, O'Brien (1994) asked if drip tips can affect the population dynamics of fungal pathogens and epiphyllous organisms such as bryophytes. Junger (1891) found fewer epiphylls on leaves with drip tips and believed that the tip was an adaptation to avoid interference with assimilation that could handicap the plant. He contended that taxa with rounded or cordate bases and rounded apices lacked any special adaptation for getting rid of water and appeared to support larger populations of epiphyllous plants (Junger, in Howard 1969).

Figure 90. Drip tips on sacred fig leaves. Photo by Challiyil Eswaramangalath Vipin, through Creative Commons.

However, recent experiments have shown that the tip does not increase the drying speed and thus the adaptive value in warding off epiphyllous taxa is doubtful. Monge-Nájera and Blanco (1995) noted that leaf substrates vary in both biochemistry and morphology. Using plastic ribbon

tape as artificial leaves the researchers found that the epiphyll cover differed little after nine months of exposure on five shapes and two sizes. Furthermore drip tips did not affect the epiphyll cover. But cover was four times higher in a clearing than in a shaded understory.

Panditharathna *et al*. (2008) noted that drip tip (Figure 90) lengths were greatest in seedlings and least in canopy trees, an observation that would seem to negate likely benefits for epiphylls or for preventing their establishment on leaves. Lücking and Bernecker-Lücking (2005) found no significant difference in the development of lichen colonies on leaves with drip trips and those without. On the other hand, leaves lacking drip tips accumulated more debris in the apex and concomitantly few lichens in this region. It might be the same for bryophytes. The drip tips cause a difference in accumulated drop size and residence time on the leaf. On those leaves with drip tips, the water forms smaller drops that run off more frequently.

Ivey and DeSilva (2001) experimented with drip tips (Figure 90) in Costa Rica (Figure 91) from 23 November to 2 December during the rainy season to see if having a drip tip reduces colonization. With a sample of 28 saplings and three leaves per tree for each treatment, they were unable to show any effect on the bryophytic epiphylls. However, fungi had greater cover on the leaves that were missing their drip tips. They found instead that the bryophytes tended to be on the drier parts of the leaves, away from bases, midveins, and tips. Fungi, on the other hand, tended to be in those very regions. Nonetheless, 9 days is much too short to expect much effect on colonization rate by bryophytes. Their experiment did demonstrate that the drip tip had little effect on helping the leaf to shed debris, but those with drip tips intact had significantly less water retention (about half) compared to those with the tip cut off. Ivey and DeSilva suggested that prevention of fungi might be the important adaptation and that epiphylls may not be a significant factor in reducing photosynthesis by the host leaves because of their slow growth. By the time they have achieved significant cover, the leaf is ready to senesce. But Ellenberg (1985) has argued that the tip is an environmental response to high humidity, not an adaptation to it, whereas Edmisten (1970b) has argued that it might reduce nutrient leaching. The latter might even be of some benefit to bryophytes if it means that more nutrients remain on the leaf and might help explain their greater abundance near the drier margins.

Figure 91. Montane oak forest in Costa Rica. Photo by Jorge Antonio Leoni de León, through Creative Commons.

Ellenberg (1985) discussed the drip tips found on many tropical leaves. They occur mostly in humid areas of warmer zones. The prevailing hypothesis was that these tips would facilitate drainage of water from the leaves, thus preventing growth of epiphyllic algae, lichens, and bryophytes. But this hypothesis was not supported by field observations or by experiments with leaves and leaf models. These tips typically develop before the leaf expansion and rarely develop after the leaf has expanded fully. Those tips that develop before the leaf expands expose the tips to the environment outside the buds. Their role, if any, in preventing epiphyll colonization remained a matter of conjecture.

Leaf Size and Shape

Monge-Nájera and Blanco (1995), also working in Costa Rica (Figure 91), likewise found that leaf shape had little or no influence on epiphyll cover. What did matter in their study was light. The epiphyllous cover in a clearing was four times that found in the dark understory of the tropical forest, regardless of leaf size or shape. However, in an earlier Costa Rican study, while finding a similar relationship between clearings and epiphyllous cover, Monge-Nájera (1989) found that epiphyllous cover increases more rapidly than the size of the leaves. This is somewhat offset by an increasing rate of herbivory on the epiphylls as the tree leaves increase in size.

Epiphyllic cover is generally higher on larger leaves, as demonstrated by epiphyllous liverworts in Monteverde, Costa Rica (Figure 91) (Monge-Nájera 1989). Perhaps this is because the growth of the epiphylls increases more rapidly than does the leaf area. Once again, degree of epiphylly does not correlate with leaf shape. Surprisingly, both absolute and relative epiphyllic cover are higher in the forest clearing than in the understory. Monge-Nájera attributed this to the greater light in a region with overall high atmospheric humidity.

The ratio of bryophytes to lichens in these communities depends on environmental conditions. Drier, more open habitats seem to favor lichens and are usually poor in bryophytes. The number of foliicolous species in one locality varies between 20-50 for lichens and 30-90 for bryophytes. A single leaf will average 5-25 lichen species and 3-13 bryophyte species, with a maximum of 45 and 20, respectively (Jovet-Ast 1949; Santesson 1952; Tixier 1966; Pócs 1978). The number of species increases with leaf area, to a maximum at 5-8 cm^2 and remains more or less constant above that (Sjögren 1975; Pócs unpublished). Leaflets of compound leaves should in this respect be treated as separate leaves because the composition of the foliicolous communities often varies among the leaflets of one leaf.

Leaf Age

The number of species and individuals is also determined by the age of the host leaves. Richards (1932) observed a decrease of species number and increase in number of individuals with leaf age. However, Olarinmoye (1975c) and Pócs (1978) observed an increase in number of both species and individuals. On ***Marattia*** (Figure 92) fern leaflets Pócs observed an increase of the average plantlet number from 588 to 1754 per 100 cm^2 within 1-2 years. One explanation for the observed differences in number of

species is that as the colonies increase in size, competition may eliminate some of the species.

Figure 92. ***Marattia fraxinea***; the genus ***Marattia*** serves as a substrate for epiphylls. Photo by Vassia Atanassova, through Creative Commons.

Leaf Longevity

Coley *et al*. (1993) questioned whether long-lived leaves may attain a higher epiphyll cover as suggested by Richards (1954), Pócs (1982a), and Bentley (1987). This hypothesis had never been tested before. Coley and coworkers found that rather than having higher cover, these long-lived leaves actually have both lower colonization rates and lower accumulated cover throughout the life of the leaf. They suggest that characters that protect the leaves from herbivory and environmental events might also protect them from epiphylls. But they also suggest that there may also have been selection for leaf characters that specifically protect them from epiphyll colonization. They suggest that the rapid colonization on short-lived leaves would cause detrimental effects when persistent over long periods of long-lived leaves.

One of the limiting factors that prevents bryophytes from making leaves their home is that the leaf is short lived and the bryophyte is slow growing. This generally limits colonization to those leaves that endure for more than one year and that live in regions where the atmospheric moisture or frequency of rain is ample for growth on a substrate that doesn't hold water.

Leaf Chemistry

On the other side of the story is the co-adaptation of the host leaf. Coley *et al*. (1993) found that longer-lived leaves actually had greatly reduced rates of epiphyll accumulation, suggesting that these leaves have some sort of defense against the epiphylls. Liverworts colonized 45% of the leaves with one-year lifetimes, but only 5% of longer-lived leaves. If this is indeed an adaptation against epiphylls rather than just an adaptation against pathogens (longer-lived leaves are known to have good defenses against pathogens), then it implies that epiphylls present a problem for their host leaves. On the other hand, liverworts may actually protect the host leaves from herbivory – see below, and may encourage the development of nitrogen-fixing **Cyanobacteria** (Figure 39).

Voglgruber (2011) reported that up to 80% of a leaf may be covered by epiphylls, where they can have a significant effect of reducing photosynthesis of the host leaf. Voglgruber studied the relationship in the humid tropical rainforest of Piedras Blancas National Park, Costa Rica. The rates of colonization were host specific. The fastest colonization was on ***Costus laevis*** (Figure 93) leaves; the slowest were on ***Asplundia pittieri*** (Figure 94) leaves, among the six species studied. Voglgruber tested the cuticles and identified long-chained alkanes, alkanols, sterols, and unidentifiable compounds. The species and leaf ages differed in wax composition. The data support the hypothesis that epicuticular wax chemistry has an effect on the growth of the epiphylls.

Figure 93. ***Costus laevis***, a species whose leaves are colonized quickly by epiphylls. Photo by Dick Culbert, through Creative Commons.

Figure 94. ***Asplundia pittieri*** with epiphylls, one of the species with the slowest epiphyll colonization rates. Photo from Earth.com, with permission.

Interactions

We might well ask if there is any advantage to the liverwort, or disadvantage to the host, resulting from this close association. Bentley (1987) reported that leafy liverworts, especially **Lejeuneaceae** (Figure 6-Figure 15), form dense coverage on leaves in the rainforest. Suitable leaves can be completely covered in only two years (Coley *et al*. 1993).

Cornelissen and ter Steege (1986) suggest that the ecological and evolutionary effects of epiphylls on their host leaves may be significant. Working in a rainforest of Guiana, they examined the liverworts and lichens that formed the dominant epiphylls and demonstrated both positive and negative effects by the epiphylls. They also found that host leaf characteristics can influence the colonization rates of epiphylls.

Nutrient Exchanges

Host Leaf Leachates

The role of leachates from the host leaf in the success of the epiphylls should not be ignored. Olarinmoye (1981, 1982) found that leachates and extracts of various tracheophyte leaves greatly increase extension growth of gemmaling shoots, leaf size, and rhizoid production of the leafy liverwort ***Radula flaccida*** (Figure 41), although they have no effect on the initiation of gemma growth. Rhizoid branching differs, depending on availability of the leachate, with long, straight and little-branched rhizoids when grown in leachates, but short, much-branched, and crooked rhizoids in some extracts. Extracts from ***Averrhoa carambola*** (Figure 95) killed all the cultures within four weeks. But are the liverworts ever exposed to the cell contents? We need tracer studies to determine if these extractable substances ever contact the liverworts. The leachates are available to them and have an important role in promoting the successful establishment and growth of these epiphylls, particularly in tropical areas with abundant annual rainfall. Often they provide nearly all of the nutrient supply.

Figure 95. ***Averrhoa carambola*** leaves and fruits. Extracts from these leaves kill cultures of the leafy liverwort epiphyll ***Radula flaccida***. Photo by Dinesh Valke, through Creative Commons.

Pócs (pers. comm.) observed that leaves of planted orange trees at Amani Station (Tanzania) with mass occurrence of aphids were covered by a sticky, sugar-containing exudate that promoted copious colonization by epiphylls, mostly ***Leptolejeunea*** (Figure 14) sp. and also some specimens of ***Diplasiolejeunea cornuta***.

Bryophyte Leachates

Montagnini *et al*. (1984) gathered indirect evidence that minerals are transferred from epiphylls to host leaves. They found that the concentrations of Cd, Pb, Ni, and Cr were higher in leaves that had epiphylls than in leaves that lacked them. The tropical Amazonian bryophytes usually have lower concentrations of heavy metals than in those from temperate zones, suggesting that long-range transport of these air pollutants is limited.

It seems logical that if heavy metals in leaves increase as the result of epiphyll colonization, other nutrients might increase as well. Epiphylls live and die on the leaves where they live. Hietz *et al.* (2002) found a correlation in leaf delta ^{15}N with that of epiphylls, suggesting that there was at least some exchange of nitrogen between the epiphylls and the host leaves (or that leaves with epiphylls might have more **Cyanobacteria**).

Jordan *et al*. (1980) examined the role of bryophytes in scavenging nutrients from rainfall and subsequent nutrients in the throughfall in Venezuela. They hypothesized that nutrients were intercepted by epiphylls in the canopy, conserving nutrients in the forest. They supported this by demonstrating that nutrient flux of calcium, sulfur, and phosphorus in rainfall was greater than that in the throughfall.

Ruinen (1965) reported that epiphylls on coffee leaves (Figure 96) can increase the coffee leaf nitrogen content by up to 60% in about one week due to the ability of the epiphylls to retain the nitrogen. These bryophyte (mostly liverwort) assemblages most likely help to maintain the necessary humidity and nutrient retention for the included micro-organisms to survive.

Figure 96. Coffee plantations with dwarf trees in the distance, in Colombia. Photo courtesy of Robbert Gradstein.

Witkamp (1970) used paired leaf discs to compare retention of added elements by epiphylls from a tropical rainforest at El Verde, in El Yunque, Puerto Rico (Figure 97). He found that the epiphylls increased ^{137}cesium by 6.7-20 times that of the cleaned leaf discs. For phosphorus it was 4.7-18.3, for manganese 1.7-4.7, and for strontium

1.9-2.9. These numbers indicate the significant role that epiphylls can play in mineral nutrient retention.

Figure 97. El Yunque forest, Puerto Rico. Photo by Matt Shiffle, through Creative Commons.

Volcanic activity can be a major contributor to bryophyte nutrients. Baudoin (1985) reported that epiphyllous bryophytes can be used satisfactorily as indicators of volcanic air pollution and nutrient contributions. Similarly, Witkamp (1970) used epiphyllous bryophytes in studies of irradiation at El Verde, Puerto Rico (Figure 97) by measuring mineral retention. According to Pócs (1990) near the Great African Rift Valley with active soda volcanoes, leafy epiphylls do not occur at all, even in wet rainforests, due to the alkaline-containing dust accumulated in the soil, air, and on the bryophyte substrates including leaf surfaces, and their components accumulate even in the epiphytic mosses.

Seed Beds

In some cases, old leaves have such a dense covering of bryophytes (Figure 98) that seeds of epiphytic flowering plants germinate there (Richards 1932) or spores of ferns – a disadvantage to the host plant, no doubt, but possibly an advantage to that tracheophyte.

Figure 98. Dense covering of bryophytic epiphylls on a palm in Guyana. Photo copyright Patrick Blanc, with implied online permission.

Nitrogen Fixation

Zhou *et al*. (2009) noted that epiphylls obtain their nutrients independently. However, there are indications that substances can be exchanged between epiphylls and host plants. They report that **nitrogen fixation** within the epiphyll community provides 10-25% of the nitrogen for the understory forest in tropical ecosystems. **Nitrogen fixation** is the process of converting atmospheric nitrogen into a form that is usable by plants, typically to NH_4^+.

The most important contribution of epiphylls to leaves is most likely through the nitrogen-fixing organisms they harbor. Nitrogen-fixing **Cyanobacteria** (Figure 39), particularly ***Scytonema*** (Figure 39) (Basilier 1979), are often associated with the epiphyllae, and this added nitrogen could be of benefit to the host leaf as well. Bentley (1987) suggested that epiphyllous bryophytes, especially liverworts in the **Lejeuneaceae** (Figure 6-Figure 15), enhance moisture levels, permitting nitrogen-fixing bacteria to subsist. Bentley and Carpenter (1980) found that epiphyllous liverworts improve the microenvironment for **Cyanobacteria** and other nitrogen-fixing bacteria by increasing the leaf moisture. Using radioactive tracers, Bentley and Carpenter (1984) were able to show a direct transfer of fixed N from the epiphyllous micro-organisms to the host leaf on the palm ***Welfia georgii*** (Figure 17) and estimated that such transfer could account for 10-25% of the host leaf N content. Most of the N fixation appeared to occur among filamentous **Cyanobacteria** associated with leafy liverworts, as well as within a thick layer of coccoid **Cyanobacteria** immediately above the leaf cuticle (Carpenter 1992). Nitrogenase activity, indicating nitrogen fixation, in the ***W. georgii*** association produces about 270 mg N per ha daily. Furthermore, this association may benefit the forest as water dripping from these leaves is enriched in nitrogen compared to rainwater (Richards 1984a).

Bentley and Carpenter (1980) examined the effects of desiccation on nitrogen fixation rates among epiphylls. Fixation on leaves that had been dried for 12 hours was only 0.66 ng N per 10 cm^2 h^{-1}, whereas that on continuously hydrated leaves was 18.69 ng N per 10 cm^2 h^{-1}. Intermediate rates occurred after 2 and 4 hours of rehydration. The bryophytic epiphytes helped to maintain moisture on the leaf surface, prolonging the duration of fixation.

In general, **Cyanobacteria** (Figure 39) are the typical contributors of nitrogen fixation on leaves. Bentley (1987) considered glucose and mineral nutrients leached from host leaves, light intensity, and desiccation to be the major influences on the co-occurrence of the **Cyanobacteria** and epiphyllous bryophytes. Bentley found that a significant portion of the fixed nitrogen is transferred to the host leaf and may contribute 10-25% of the total nitrogen in the leaf. The bryophytes most likely contribute to the fixation rates by maintaining moisture longer than leaves with no epiphylls. Although desiccation has a dramatic effect on fixation, recovery is quite rapid, reaching the levels of moist controls within 4 hours. Berrie and Eze (1975) contend that the bryophytes are also able to draw water from the host leaves, contributing further to maintaining moisture for the fixation. Low light reduces the rate of fixation. The water flowing on a leaf actually has less

nitrogen than rainfall collected in the open, suggesting very efficient uptake mechanisms on the leaf surface. High N fixation rates are associated with dense cover of epiphyllous bryophytes, especially for leafy liverworts in the **Lejeuneaceae** (Figure 6-Figure 15). Bentley suggested that the bryophytes enhance the moisture levels on the leaf, encouraging microbial growth. One can observe that a few hours after rain, when the naked leaf surface is already dry, under the cover of epiphylls a still good amount of moisture is preserved.

Roskoski (1980) measured nitrogen fixation by epiphylls on coffee (***Coffea arabica***; Figure 99). The C_2H_2 reduction (a measure of N fixation) was similar at all sites in Vera Cruz, Mexico, despite differences in shade, averaging 3.21 nmoles C_2H_2 reduced per leaf with epiphylls per day. This suggests that the shading/light intensity within the range encountered was unimportant in the fixation rate. Furthermore, he found no correlation between percent epiphyll cover and magnitude of nitrogen-fixing activity. Roskoski concluded that the nitrogen fixation associated with epiphylls is not an important N source for that coffee ecosystem.

Figure 99. ***Coffea arabica***, a species that commonly hosts bryophytic epiphytes, with fruit, in Hawaii. Photo by Forest and Kim Star, with permission.

For the epiphyllous liverworts living on leaves of the undergrowth, as opposed to higher levels of the canopy, these **Cyanobacteria** (Figure 39) may even be a necessity. Canopy leaves and epiphytes remove so much of the nutrients before the rainfall reaches the lower branches that liverworts like ***Radula flaccida*** (Figure 41) are likely to be nutrient limited (Olarinmoye 1975a). In support of this suggestion, Olarinmoye found that the standard bryophyte media used by other researchers (Diller *et al*. 1955; Basile 1965; Bennecke in Schuster 1966) caused aberrant plants, and he was forced to reduce the concentration to 10-20% of the standard. The greatest percent of buds producing leafy shoots occurred in the 10% solution; growth was highest in the 10 and 20% media as well. Even in distilled water the gemmalings exhibited appreciable growth extension, although they were not as healthy as in the diluted nutrient media.

Wanek and Pörtl (2005) acknowledged the role of free-living nitrogen-fixing organisms and throughfall to provide nutrients to epiphyllous bryophytes, but added that the bryophytes also obtained nutrients from leachates of the host leaf. On the other hand, bryophytic epiphylls lose quantities of nutrients after drying events, and these can be absorbed by host leaves. However, when the researchers measured the nitrogen leachates from the epiphylls of four species in a lowland tropical wet forest in Costa Rica, they contributed less than 2.5% of the lost leaf N after 14 days. Nevertheless, 180 days of observations demonstrated that the nitrogen in the phyllosphere was highly dynamic, with the bryophytes at times being sinks and other times being sources.

Freiberg (1994, 1998, 1999) measured nitrogen fixation on leaves in a premontane rainforest in Costa Rica. He found maximum rates on 26 ng N cm^{-2} leaf area h^{-1} and determined that two species of ***Scytonema*** (***Sc. javanicum***, ***Sc. hofmannii*** – Figure 39; **Cyanobacteria**) contributed most of that. The rates of fixation correlated with the leaf area covered by ***Scytonema***. This fixation was dependent on rainfall and ceased completely in 2-3 days with no precipitation. Liquid water was necessary – fog and mist were not helpful. Light and temperature both influenced the rate. In a follow-up study, Freiberg (1999) identified seven species of epiphyllous **Cyanobacteria** in a primary premontane rainforest in Costa Rica.

Harrelson (1969) further discussed the epiphyllae of tropical leaves and their relationship to nitrogen fixation, noting that nitrogen fixation was greater in leaves with epiphylls. Goosen and Lamb (1986) measured nitrogen fixation associated with leaves in one tropical and two sub-tropical rainforests.

Herbivore Protection

Coley *et al*. (1993) found that ***Cololejeunea*** (Figure 13), ***Leptolejeunea*** (Figure 14), and ***Lejeunea*** (Figure 3) (all **Lejeuneaceae**) were common epiphylls. They hypothesized that the liverworts might protect their host leaves from herbivores. Liverworts are known for their rich terpenoids, and experiments show that leaf cutter ants (Figure 100) prefer leaves with no epiphylls. On the other hand, the epiphylls hold moisture that may increase pathogenic infection. The epiphylls also block light, reducing photosynthesis, possibly making the leaves a less desirable food source.

Figure 100. ***Atta cephalotes*** carrying a cut piece of a leaf. Photo by Jim Webber, through Creative Commons.

Epiphylls have a little more direct relationship with the leafcutter ants (***Atta cephalotes***; Figure 100), albeit a

negative one. These ants are known for their attacks on leaves. When Wetterer (2003) removed the epiphylls from the base and two side branches of a grapefruit (***Citrus paradisi***; Figure 101), the ants chose to cut leaves from the cleaned branches nine out of ten times. This behavior suggests that the epiphylls provide protect the host leaves from the leafcutter ants.

Figure 101. ***Citrus paradisi***, a species on which epiphylls seem to provide protection from leafcutter ants that would eat the leaves. Photo by Amada44, through Creative Commons.

For some leaves, the antiherbivore role may be significant. For example, in Costa Rica, leafcutter ants (***Atta cephalotes***; Figure 100) preferentially clipped leaves of ***Citrus paradisi*** (Figure 101) and ***Cyclanthus bipartitus*** (Figure 102) from which epiphylls had been removed (Figure 103-Figure 104) (Mueller & Wolf-Mueller 1991). This benefit may be derived from the greater processing effort required of the ants when epiphylls cover the leaves or from decreased palatability due to secondary compounds found in epiphyllous lichens and bryophytes. In particular, liverworts are rich in terpenoids that are toxic to both the leafcutter ants and the fungus they cultivate (Hubbell *et al*. 1983; Howard *et al*. 1988; Coley *et al*. 1993). Citrus leaves with epiphylls are less preferred by leaf cutter ants, most likely due to these terpenoids (Coley *et al.* 1993).

Figure 102. ***Cyclanthus bipartitus***, having leaves that are eaten by leafcutter ants. Photo by David J. Stang, through Creative Commons.

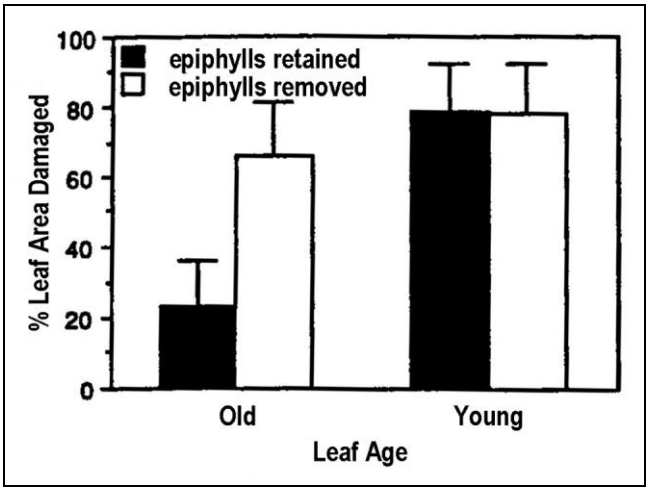

Figure 103. Leaf cutter ant consumption on old and young leaves of ***Citrus paradisi*** with epiphylls undisturbed and epiphylls removed. Error bars represent one standard error. Modified from Mueller & Wolf-Mueller 1991.

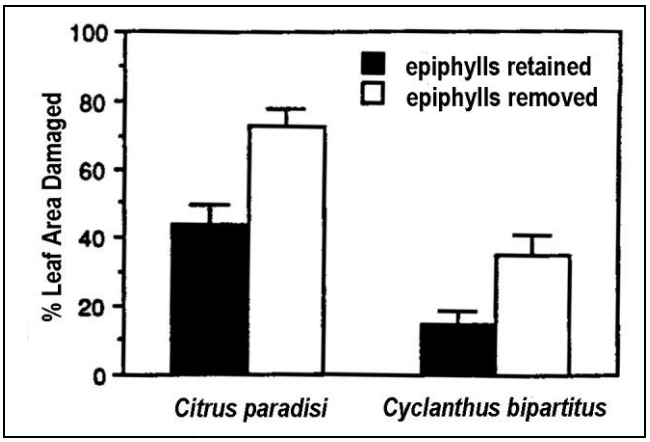

Figure 104. Leaf cutter ant damage on leaves of two species of tropical plants; leaves have epiphylls retained and epiphylls removed. Error bars represent one standard error. Modified from Mueller & Wolf-Mueller 1991.

In a southern Ecuadorian montane rainforest, Bodner *et al*. (2015) found many caterpillars (**Lepidoptera**) that were not feeding on leaves as might be expected. Instead, they feed on lichens, dead leaves, and epiphylls, including bryophytes. Bodner *et al*. (2011) conducted feeding trials with caterpillars in the Montane Forest Zone in Southern Ecuador. They found that more than 22% of the caterpillars did not eat the leaves, but rather ate dead leaves and epiphylls. In some cases, up to 80% were epiphyll consumers.

Similarly, Callaghan (1992) found that the butterfly ***Pentila picena cydaria*** (Figure 105) laid its eggs singly on live trees that were covered with lichens and mosses in a Nigerian cola forest. The initially white eggs soon became dark brown (within a day). The caterpillars subsequently fed on the epiphylls.

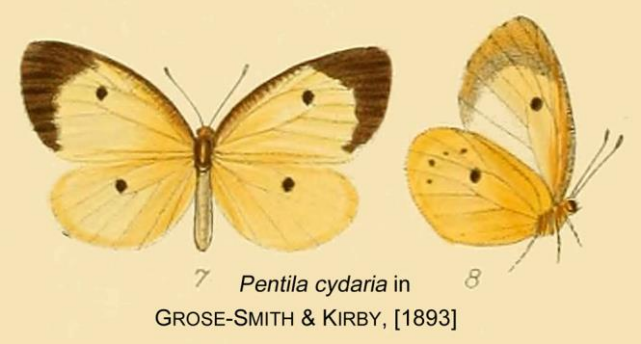

Figure 105. ***Pentila picena cydaria,*** a species whose caterpillars feed on epiphylls. Photo by Grose-Smith and Kirby, through public domain.

Yet another butterfly, ***Sarota gyas*** (Figure 106), uses the epiphylls (DeVries 1988). The larvae of this species rest on the upper surfaces of leaves and feed on the epiphylls, where they blend in. The epiphylls are primarily **Cyanobacteria** (Figure 39) and leafy liverworts in the **Lejeuneaceae** (Figure 6-Figure 15). Others (Lycaenidae: Lipteninae) in the Nigerian cola forest feed on epiphyllic lichens and fungi as larvae (Callaghan 1992).

Figure 106. ***Sarota gyas*** in Ecuador, a species whose larvae feed on the epiphylls. Photo by Harold Greeney, through Creative Commons.

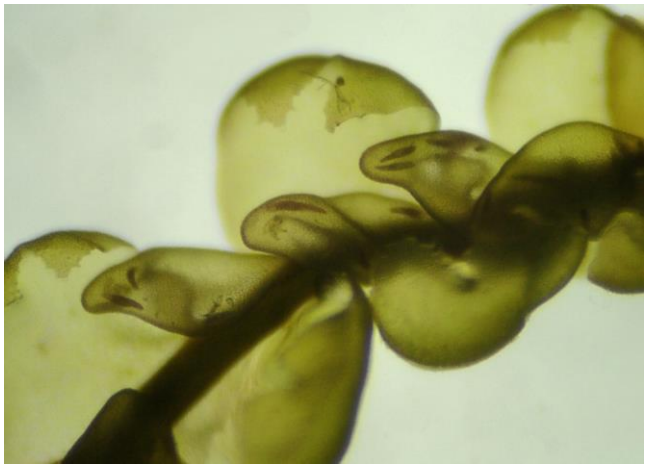

Figure 107. ***Pleurozia purpurea*** showing lobules with several of the protozoan ***Blepharisma*** living in them. Photo courtesy of Hess.

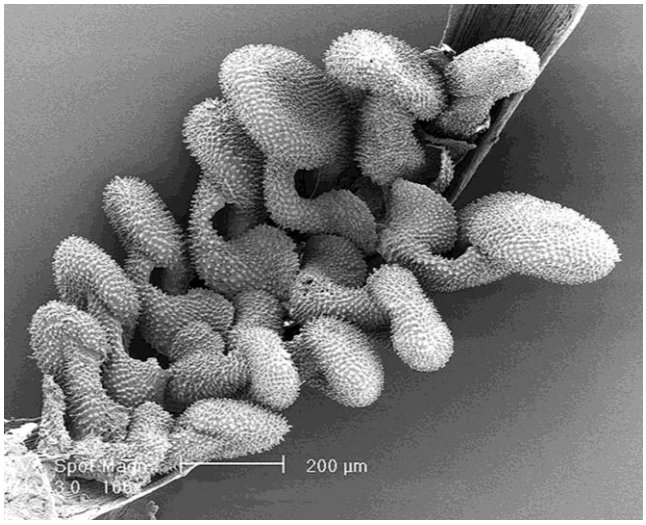

Figure 108. ***Colura saccophylla*** SEM showing lobules. Photo by John Braggins, with permission.

Micro-organisms

The same lobules that hold water for the leaves of many epiphyllous liverworts also serve as the habitat for some species of protozoa (Barthlott *et al*. 2000). In the liverworts ***Pleurozia*** (Figure 107) and ***Colura*** (Figure 108), the openings of these sacs can be closed by a movable lid. This caused some researchers to hypothesize that sacs could trap small animals, a theory that they supported by finding ciliate protozoa in them. These protozoa feed on bacteria on the surface of the plants, but there seems to be no evidence that there is any mechanism to attract the protozoa to the liverwort. Hence, there is thus far no evidence that the protozoa provide any useful function for the liverwort leaves.

Epiphyllous bryophytes can provide a suitable habitat for a number of kinds of micro-organisms, and the role of these micro-organisms in affecting the health of the host is largely unknown. Leafy liverworts in Ecuador, Costa Rica, and Puerto Rico support the growth of at least eleven species of slime molds (**Myxomycetes**), especially in lowland rainforests with high annual rainfall (Schnittler 2001). Among these, ***Arcyria cinerea*** (Figure 109), ***Didymium iridis*** (Figure 110), and ***D. squamulosum*** (Figure 111) have the most common (frequency of 59-66%). While these produce visible sporocarps in culture, it is likely that they exist in their amoeboid stage among the epiphylls, in which case they may contribute to controlling bacteria.

Figure 109. ***Arcyria cinerea***, a species that often occurs on leafy liverworts in the Central American tropics. Photo by Malcolm Storey, through Creative Commons.

Figure 110. ***Didymium iridis***, a species that often occurs on leafy liverworts in the Central American tropics. Photo by Sava Kristic, through Creative Commons.

Figure 111. ***Didymium squamulosum***, a species that often occurs on leafy liverworts in the Central American tropics. Photo by BioImages, the Virtual Field Guide, through Creative Commons.

A number of ascomycetous fungi parasitize epiphyllous liverworts. According to Döbbeler (1997) and Döbbeler and Hertel (2013) more than 400 known fruit-body-forming species of **Ascomycetes** (Figure 41) occur obligately on the gametophytes of mosses and hepatics. A good portion of them is specialized to epiphyllous liverwort hosts.

Küttner (2005) used 4x4 cm leaf squares to investigate parameters that controlled epiphyllous micro-organisms in a tropical humid lowland rainforest in Costa Rica. The size of these microbial communities was influenced by both species and leaf age of the host leaf. On the other hand, site had little or no effect on the composition or size of the epiphyllous microbial community. This microbial community has experienced few studies, and more information is needed to asses how it affects the epiphyllous bryophytes and *vice versa*.

Negative Impacts on Leaves

Most of the impacts of epiphylls on their host leaves seem to be positive. However, epiphyll rhizoids may actually penetrate the epidermal cells of the host, presumably serving as a means of anchorage (Berrie & Eze 1975). This can result in the death of some leaf epidermal cells, permitting more rhizoids to enter. It appears that this penetration contributes to water loss, as leaves with extensive epiphyllous colonies and those stripped of their epiphyllae both have a high evaporative loss compared to uninhabited leaves of the same age. Further detriment to the leaf may occur if the sites of penetration serve as entry points for leaf pathogens. So far, this has not been demonstrated, except for senescent leaves. (But could it be that the penetration has contributed to the senescence?)

Light Interference

In some areas, the bryophytes become so abundant that they can seriously interfere with photosynthesis by intercepting the light (Attenborough 1995). In other cases, light interference is scant; Eze and Berrie (1977) found that even under the heaviest colonization of ***Radula flaccida*** (Figure 41), only 2% of the light was intercepted by that liverwort. They found no difference in the chlorophyll content of colonized and uncolonized parts of the host leaf. Furthermore, they found no loss of photosynthetic product from the host to the epiphyll, or from epiphyll to host. Coley *et al*. (1993) found that epiphyllous liverworts in several locations in Panama transmitted 44% of the light through liverworts in a single layer and that transmission did not differ between saturated and blotted dry liverworts.

Conflicting reports on the effects of epiphylls on ***Cacao*** trees have been discussed above. Roskoski (1981) found that the number of leaves with epiphylls is lowest on ***Coffea arabica*** (Figure 99) in a shadeless site. The percent cover of epiphylls is inversely related to the number of young coffee leaves, making them highest in February and lowest in May. Height strata have no significant effects on number of leaves with epiphylls. Epiphylls do affect the host leaves by reducing the photosynthetic area of the trees, with shading ranging 0.5-19.7%. Nevertheless, the epiphylls do not seem to cause any detrimental effects on the coffee productivity.

Zhou *et al*. (2014) compared the effects of lichens vs liverworts on host leaf traits in the tropical montane rainforest, Hainan Island, China. They studied effects of epiphyllous lichens, liverworts, and uncolonized leaves on leaf characters of ***Photinia prunifolia*** (Figure 112). Colonization by lichens significantly decreases leaf water content, chlorophyll *a* and *a* + *b* content, whereas liverworts have no effect on these. Furthermore, lichens have more effect on net photosynthesis than do liverworts. Lichens caused an increase in leaf light compensation point by 21% and a decrease of the light saturation point by 54%, whereas liverworts exhibited contrary effects. This study suggests that the type of epiphyll is important in assessing potential decreases in productivity of the host plant.

Figure 112. ***Photinia prunifolia***, a species of the moist tropical forest. Photo by Caroline Léna Becker, through Creative Commons.

Composition and Distribution of Communities

Based on studies through the 20th century, Pócs (unpublished) considered indications that some genera or species are typical for certain geographic or vegetational units or altitudinal belts. In Africa, for example, ***Radula flaccida*** (Figure 41), ***Cololejeunea auriculata***, ***C. jonesii***, and all species of ***Leptolejeunea*** (Figure 14) seem to be typical of lowland rainforest, whereas ***Radula stenocalyx***, ***Cololejeunea jamesii***, ***C. malanjae***, ***C. tanzaniae***, ***C. zenkeri***, and all species of ***Drepanolejeunea*** (Figure 9) seem to be restricted to submontane and montane forest habitats. Ericaceous heaths have endemic species of ***Colura*** (***C. berghenii***, ***C. hedbergiana***, ***C. ornithocephala***, and ***C. saroltae***) that are apparently restricted to ericaceous leaves and twigs.

Within the montane rainforest habitat Tixier (1966) was able to distinguish the lower and upper strata by their characteristic foliicolous communities. Winkler (1970) found a significant correlation between certain groups of species within the same geographic area. Host preference allows two different foliicolous communities to occur at close distances, *e.g.* on evergreen shrubs and on filmy ferns within the same forest habitat (Pócs 1978).

Species Richness

As already noted, the most common of the **epiphyllous** species are in the leafy liverwort family **Lejeuneaceae** (Figure 6-Figure 15), a dominant member of the epiphyllous bryophyte flora in lowland rainforests (Piippo 1994). Many of these species are endemic, for example 20.5% in Western Melanesia [Papua New Guinea, Papua (West Irian), and the Solomon Islands].

The family **Lejeuneaceae** (Figure 6-Figure 15) is repeatedly considered the most diverse and abundant family among the epiphylls. However, the species and even the tribes differ by continent and between the Old World and Neotropics. Many of the epiphyllous species extend outside the tropics into the Macaronesian Azores, Madeira, and the Canary Islands. Even in these sub-tropical locations, several of the species belong to typical tropical families of **Lejeuneaceae** and **Radulaceae** (Figure 16) (Sjögren 1997). These islands had 89 epiphyllous species reported, 14 of which were endemic to the Azores or to Macaronesia. Nan and Zhu (2007) reported a much smaller number of species (19 epiphyllous liverworts) in the Maoershan Nature Reserve, Guangxi, China. Boecker *et al*. (1993) reported on epiphylls of the Canary Islands.

Table 1. Number of epiphyllous liverwort species known in genera having pantropical distribution, based on Pócs 1978. These constitute 60% of the ~1000 foliicolous liverwort species described at the time. Revisions have eliminated some of these species.

	Neotropics	Africa incl islands	Asia, Oceania, Australia
Aphanolejeunea	24	9	8
Colojeunea	40	72	41
Colura	14	18	41
Diplasiolejeunea	19	28	8
Drepanolejeunea	34	18	37
Leptolejeunea	11	5	24
Microlejeunea	12	6	11
Radula sec *epiphyllae*	6	5	8

The epiphyll richness varies with altitude differently in the different parts of continents or islands. In continental East Africa the highest epiphyllous diversity occurs at 1500-1800 m near the coast and at 1800-2500 m inside the continent (Pócs 1978, 1994), while in more oceanic conditions, like in the Indian Ocean islands (Mascarenes, Seychelles) we can observe the highest epiphyllous diversity already from 600 m above the sea level.

Asia

In India, the epiphyllous species of liverworts are restricted to the Eastern Himalayas, South India, and Andaman and Nicobar Islands (Lal 2003). By 2003, only a small number of epiphyllous species were known; 39 species in 14 genera were all that had been identified. These were in only three families: **Lejeuneaceae** *s.l.* (Figure 6-Figure 15), **Radulaceae** (Figure 16), and **Metzgeriaceae** (Figure 19). But Dey and Singh (2012) soon reported 89 taxa of epiphyllous liverworts from the Eastern Himalayas, of which 66 species belong to **Lejeuneaceae**.

Gao and Be (1988) identified 12 species of epiphyllous liverworts from Daiwa Shan, Jiulong, China. Despite the small number of species, these represented 10 genera and 5 families, occurring at 650 m asl. As has been common when exploring these small organisms, these researchers found that five of the genera and six of the species were new to China.

Ji and Wu (1996) reported only 10 species in 1 family and 4 genera from Jinggangshan Nature Reservation, Jiangxi Province. Nevertheless, one species was new for China.

When Li and Wu (1992) assessed epiphyllous liverworts from Heishiding Natural Reserve, Guangdong Province, China, they reported only 13 species in two families and 7 genera. The most common species among these were ***Leptolejeunea elliptica*** (Figure 14) and ***Radula acuminata*** (Figure 35). ***Leptolejeunea hainanensis*** and ***Cololejeunea floccosa*** (Figure 113) occur in the broad-leaved forests in ravines at 350-600 m asl.

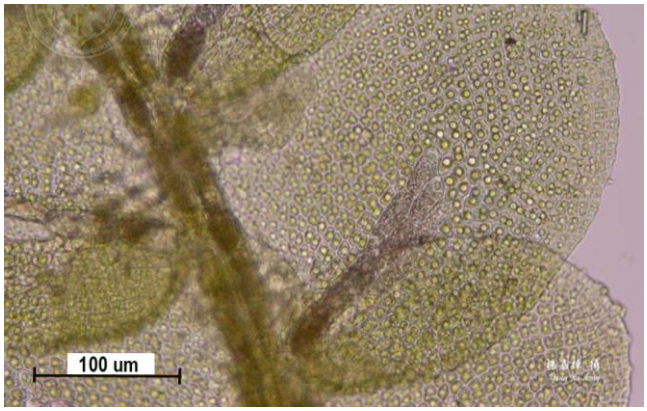

Figure 113. ***Cololejeunea floccosa***, an epiphyllous liverwort species that occurs in the broad-leafed forests in ravines at 350-600 m asl in Guangdong Province, China. Photo by Yang Jia-dong, through Creative Commons.

Liu *et al*. (1988) found slightly more species (17 species) when investigating the epiphyllous liverworts from southern parts of Anhui Province, East China. Nevertheless, these occurred in only 10 genera and 4 families. Not surprisingly, 11 of these species were new for the province. Only one was new for China. The researchers were unable to show any obligate relationship between the epiphyllous liverworts and the host species. They did determine that leaves that were thin, soft, and/or rough were less suitable for these liverworts than those that were thick, rigid, and smooth. They surmised that the distribution of these liverworts is currently much narrower than it was in the distant past.

Zhu *et al*. (1994) found a greater species richness at the Fengyangshan Nature Reserve, Zhejiang Province, China. They identified 33 species of epiphyllous liverworts. These researchers found two species new to China.

Among the more diverse assemblages of epiphyllous bryophytes in China, the Wuyanling of Zhejiang Province supports 18 species, in 3 families and 13 genera (Zhang & Hu 1991). ***Rhaphidolejeunea foliicola*** (Figure 114) and ***Leptolejeunea elliptica*** (Figure 14) are the dominant epiphyllous liverworts in the region. Most of the epiphyllous species occur on leaves of ***Ilex latifolia*** (Figure 115), ***Symplocos sumuntia*** (see Figure 116), ***Trachelospermum jasminoides*** (Figure 117), and ***Rhododendron ovatum*** (Figure 118).

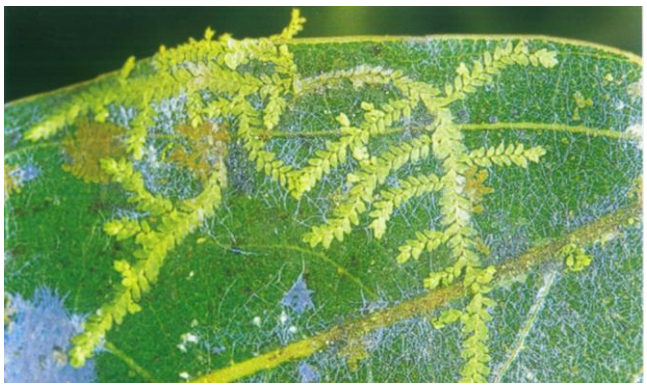

Figure 114. ***Raphidolejeunea foliicola***, a dominant epiphyll of the Wuyanling of Zhejiang Province, China. Photo from <subject.forest.gov.tw>, permission unknown.

Figure 115. ***Ilex latifolia***, a host for epiphyllous bryophytes in China. Photo by Kristine Paulus, through Creative Commons.

Figure 116. ***Symplocos cochinchinensis*** with a variety of epiphylls, including leafy liverworts; ***Symplocos sumuntia*** is a host for epiphyllous bryophytes in China. Photo by Vinayaraj, through Creative Commons.

Figure 117. ***Trachelospermum jasminoides***, a host for epiphyllous bryophytes in China. Photo by Ανώνυμος Βικιπαιδιστής, through Creative Commons.

Figure 118. ***Rhododendron ovatum***, a host for epiphyllous bryophytes in China. Photo from Horticultural Society of London, through public domain.

Ji *et al*. (2001) found 14 epiphyllous species in the Matoushan Nature reserve of Jiangxi Province, China. These occur at 450-950 m asl in evergreen broad-leaved forests. They are distributed in 5 families and 10 genera. ***Leptolejeunea elliptica*** (Figure 14) and ***Lejeunea flava*** (Figure 119) are the most common of these species.

Figure 119. ***Lejeunea flava***, a common facultative epiphyllous species in the evergreen broad-leaved forest of Jiangxi Province, China. Photo by Scott Zona, with permission.

Zhu *et al*. (1992) found 27 epiphyllous liverworts in Babaoshan, Guangdong, China. Even this larger number is only distributed in 6 families. The dominant epiphyllous species are ***Radula acuminata*** (Figure 35), ***Leptolejeunea elliptica*** (Figure 14), and ***Cololejeunea spinosa*** (Figure 120).

Figure 120. ***Cololejeunea spinosa*** epiphyllous on a fern. Photo by Ying Jia-dong, through Creative Commons.

But *et al*. (2000) examined the epiphyllous liverworts on rosette leaves of ***Ardisia*** (Figure 121) species in China. This species in China, including Hong Kong, hosts only 12 species of epiphyllous liverworts, but these include 9 genera. There is no apparent species-specific relationship to the hosts.

Figure 121. ***Ardisia crenata***. In China members of this species host only 12 species of epiphyllous liverworts. Photo by Kenpei, through Creative Commons.

But and Gao (1991) identified 28 species of epiphyllous liverworts from 25 sites in the Kowloon Peninsula, Hong Kong. These are mostly located at 30-200 m asl.

Summarizing the epiphyllous liverworts known in China up to the year 1990, Luo reported 102 species, in 11 families and 32 genera (Luo 1990). Of these, the largest family is the **Lejeuneaceae** (Figure 6-Figure 15) with 21 genera and 85 species. ***Cololejeunea*** (Figure 6, Figure 13, Figure 113) is the largest genus, which has altogether 48 epiphyllous species in China according to Zhu and So (2001).

Some of the Chinese epiphyllous liverworts are **facultative**, occurring on soil rocks, and tree trunks. These include ***Calypogeia*** (Figure 122), ***Cephaloziella*** (Figure 123), ***Frullania*** (Figure 20), ***Lepidozia*** (Figure 124), ***Metzgeria*** (Figure 19, Figure 127), ***Plagiochila*** (Figure 73), ***Porella*** (Figure 125), and ***Radula*** (Figure 16, Figure 35). In China, the epiphyllous species extend to 31º N. Most of the Chinese species occur in the South Yangtzi River areas at 200-2,800 m asl, where warm, moist air currents come from the Pacific and Indian Oceans, there is considerable geographical relief, and several large rivers add to the moisture.

Figure 122. ***Calypogeia tosana***; the genus ***Calypogeia*** is a facultative epiphyll in China. Photo by Yang Jia-dong, through Creative Commons.

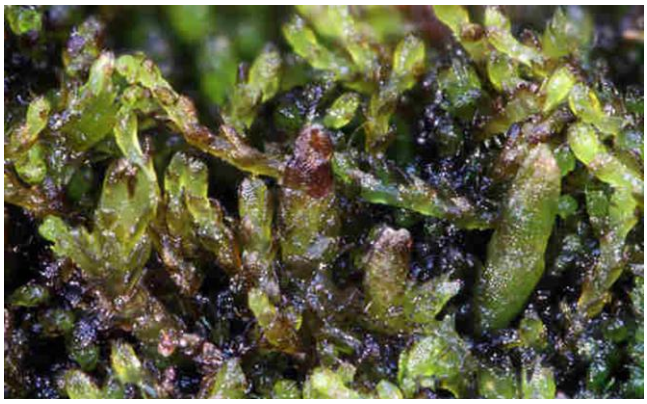

Figure 123. ***Cephaloziella integerrima***; the genus ***Cephaloziella*** is a facultative epiphyll in China. Photo by David T. Holyoak, with permission.

Figure 124. ***Lepidozia reptans***; the genus ***Lepidozia*** is a facultative epiphyll in China. Photo by Yang Jia-dong, through Creative Commons.

Figure 125. ***Porella perrottetiana***; the genus ***Porella*** is a facultative epiphyll in China. Photo by Yang Jia-dong, through Creative Commons.

More recently, Zhu and So (2001) studied the epiphyllous liverworts of China, recording 168 species. Of these, 14 are endemic. They recognize obligate, common facultative, and occasional epiphylls. In China, the epiphylls prefer tropical and subtropical forests with evergreen, thick, hard, smooth leaves. These epiphylls are most common in Yunnan, Hainan, and Taiwan, where they are highly frequent in the cloud-zone forests at 800-1500 m asl.

Jiang *et al*. (2014) identified six core distribution areas for the epiphyllous liverworts of China, concluding that it was the macrohabitat factors that most affected their distribution.

The genera of Chinese epiphylls tend to be pantropical in their distribution. In subtropical evergreen forests of southeast China, Wu *et al*. (1987) found four leafy liverworts to be dominant, each in a genus that is common throughout the tropics [***Leptolejeunea*** (Figure 14), ***Radula*** (Figure 16), ***Cololejeunea*** (Figure 6), and ***Frullania*** (Figure 20)].

The genus ***Cololejeunea*** (Figure 6, Figure 13, Figure 113) preferentially lives on leaf surfaces or other aerial parts of tracheophytes in wet forests (Yu *et al*. 2014). Among 70 species of ***Cololejeunea*** in their study, Yu and coworkers found that there were only weak correlations between morphological variations and species diversity. These differences were not linked to epiphytism, although some characters did show positive or negative relationships. ***Cololejeunea*** is described by its small gametophyte size and the occurrence of adaptive features such as compressed, thin stems, lack of underleaves, inflated lobules, and asexual propagules (Gradstein 1997b; Gradstein *et al*. 2006; Kraichak 2012). It is able to live on substrates that are extremely ephemeral, smooth, have limited access to nutrients and water, and may have exposure to light (Yu *et al.* 2014).

Diplasiolejeunea (Figure 11, Figure 23, Figure 126) is an epiphyllous genus with a pantropical distribution (Dong *et al*. 2012). It ranges from lowlands to more than 4,000 m asl. In contrast to ***Cololejeunea*** (Figure 6), these species prefer to live on leathery, harder leaves. Their morphological diversity hides their genetic diversity, with four morphologically semi-cryptic species. Based on

molecular data, the genus exhibits a deep split into a **Palaeotropical** (relating to phytogeographical kingdom comprising Africa, tropical Asia, New Guinea, and many Pacific islands, excluding Australia and New Zealand; Old World tropics) clade and a Neotropical (North, South, and Central American tropics) clade. Nevertheless, ***D. cavifolia*** (Figure 11) and ***D. rudolphiana*** (Figure 126) remain valid pantropical species, providing evidence for transcontinental dispersal from the Neotropics to the Palaeotropics. The molecular data support the subgenus ***Physolejeunea*** (Figure 23) as Palaeotropical and the subgenera ***Austrolejeuneopsis*** (Figure 126) and ***Diplasiolejeunea*** (Figure 11) as Neotropical. The subgenus ***Physolejeunea*** is primarily epiphytic, whereas ***Austrolejeuneopsis*** and ***Diplasiolejeunea*** are primarily epiphyllous. But these disjunct subgenera also separate on ocelli, which are present in ***Diplasiolejeunea*** and absent in ***Physolejeunea*** and ***Austrolejeuneopsis***.

Figure 126. ***Diplasiolejeunia rudolphiana*** (subgenus ***Austrolejeunepsis***) from the Neotropics. Photo by Michael Lüth, with permission.

A number of other Chinese studies on epiphylls have been published: Chen & Wu 1964; Wu & Lou 1978; Wu *et al*. 1983; Wu & Guo 1986; Dengke & Wu 1988; Li & Wu 1988; Li 1990, 1997; Ji & Liu 1998; Ji *et al*. 1998a, b, 1999, 2001; Peng *et al*. 2002.

Asia and the Pacific are home to the epiphyllous liverwort ***Metzgeriopsis*** (Figure 127). One unusual epiphyllous moss species, ***Ephemeropsis tjibodensis*** (Figure 128), forms horizontal protonemata on monocots, whereas it grows on lawyer vines and broad-leaved trees in Malaya and Queensland, Australia (Goebel 1888; Győrffy 1916; Richardson 1981). These protonemata have photosynthetic side branches that grow upwards and end in long bristles. The basal protonemata have holdfasts that attach the moss to the leaf surface. The leafy gametophore and capsule, on the other hand, are both quite small (Bower 1935). Meijer (1972) found only one location in West Sumatra where the moss had capsules, and suggested that we need to include studies on all the epiphyllous liverworts associated with this moss to get clues as to the long-distance recent dispersal versus the ancient distribution of this unusual moss.

Figure 127. ***Metzgeriopsis*** growing on a palm leaf on Bukit Larut, Malaysia, 1100-1200 m, with bryologist Kien Tai Yong left. Photo courtesy of Robbert Gradstein.

Figure 128. ***Ephemeropsis tjibodensis*** protonematal mat on a palm leaf in Fiji. Photo by Tamás Pócs, with permission.

In southern Thailand, the most recent study reports that epiphylls number 54 liverwort species and 1 moss species (Pócs & Podani 2015).

Additional studies on epiphylls include those of Japanese researchers Horikawa (1932, 1939, 1948), Kamimura (1939), Tixier (1966), and Mizutani (1966, 1975).

South Pacific Islands

Kraichak (2013) studied the epiphyllous bryophytes on the island of Moorea, French Polynesia (Figure 129). As leaves age and epiphyll succession occurs, there are significant changes in abundance, species richness, and composition. These successional changes in epiphylls on ***Inocarpus fagifer*** (Figure 130) do not follow any single trajectory, causing older leaves to have divergent communities.

Figure 129. Polynesia – Moorea Island. Photo by Anne Caillaud, through Creative Commons.

Figure 130. ***Inocarpus edulis***, an epiphyll host. Photo by Tau'olunga, through Creative Commons.

Piippo (1994) found that 20.5% of the western Melanesian and Malaysian **Lejeuneaceae** (Figure 6-Figure 15) were endemic, but this is actually somewhat lower than the figure for liverworts in general (38.2%). She attributed the smaller number of endemic **Lejeuneaceae** to the many epiphyllous taxa. The epiphyllous taxa tend to be particularly widespread in the lowland rainforests.

Eggers and Pócs (2010) added 13 new epiphyllous liverwort species new to the flora of Samoa (Figure 131) in the South Pacific islands. Söderström *et al*. (2011) reported more than 70 epiphyllous liverwort and hornwort species from Fiji Islands. Our understanding of dispersal patterns and mechanisms, as well as the ecology, will remain poor until we have a better understanding of the distribution of the species in these poorly studied areas.

Figure 131. American Samoa forest. Photo from US Department of Agriculture, through public domain.

Africa

In Africa, epiphyllous bryophytes have not been studied in many areas. Busse (1905) was among the first to become intrigued with identifying these bryophytes in Africa He wrote eight pages on the occurrence of these epiphylls in the rainforest of Cameroon.

Pócs has been one of the early explorers of the African epiphylls (*e.g.* Pócs 1975). In 1978 Pócs reported 185 species of epiphyllous bryophytes for the entire continent of Africa. In a country where many areas have not been explored, this number is likely to be a very low estimate. Pócs and Tóthmérész (1997) found an average of 8-9 species per leaf in epiphyllous communities in East Africa (Figure 132) and the nearby Indian Ocean islands. Degraded habitats are more likely to have only 3-4 species. The number of species within habitats varies from 14 to 25. Nevertheless, this total number does not correlate with habitat degradation due to increased **beta diversity** (ratio between regional and local species diversity).

Figure 132. Uganda – Murchison Falls, Nile River, in East Africa. Photo by Rod Waddington, through Creative Commons.

On Bioko Island in Equatorial Guinea, Müller and Pócs (2007) found 57 species of epiphyllous bryophytes, of which 55 were liverworts and 2 were mosses. One of these, ***Cololejeunea papilliloba*** (Figure 133) was new to Africa. Only 24 of the liverworts were previously known to the island.

Figure 133. ***Cololejeunea papilliloba***, a species unknown in Africa until 2007. Photo by Barbara Thiers, NY Botanical Garden, through Creative Commons.

As in most of the tropics, in Malawi (Figure 134) the **Lejeuneaceae** (Figure 6-Figure 15) are abundant, with 64 taxa found during a single collecting trip of the BBS (Wigginton 2001) of which 45 were epiphylls. As has been common in tropical collecting trips, 51 species of the 64 taxa were new to the Malawi bryoflora.

Figure 134. Nyika miombo, Malawi, showing diminishing forests in the background. Photo by Dr. Thomas Wagner, through Creative Commons.

Host leaf size, age, and texture play important roles in the distribution of East African (Figure 132) epiphylls (Pócs 1978). Pessin (1922) found that some types of leaves are preferred and others avoided. Host specificity may play a role based on longevity of the leaf, water-holding capacity, overgrowth by mold, and other factors. Wetability is important – essential – but it is the **glabrous** (smooth) and leathery leaves that are usually colonized. This most likely is because these are the persistent leaves, and that longevity is necessary for the bryophytes to become established. But in many rainforests, it seems that host specificity is of little importance. Olarinmoye (1971, 1975a) found similar growth of ***Radula flaccida*** (Figure 41) on leaves of eight different taxa in a laboratory experiment. And in western Nigeria (Olarinmoye 1975b), he found no specificity among the bryophytes for any particular tree species.

Neotropics

Central America

Like Olarinmoye (1975b) in Africa, Marino and Salazar Allen (1991) likewise found that it is light and microsite, not shrub species, that determines the epiphyllous communities on ***Hybanthus*** (Figure 37) and ***Psychotria*** (Figure 38) in the Neotropics. In this case, the epiphylls grow poorly in the shade but as expected are very sensitive to quite small differences in moisture. For example, ***Cololejeunea sicifolia*** (see Figure 13) dominates communities in dry microsites but is rare in wet microsites, whereas ***Leptolejeunea elliptica*** (Figure 14) dominates in wet microsites and is relatively rare in dry microsites. When the two shrubs grow together in the same microsites, their epiphyllous communities are similar.

Equihua and Pócs (1999) reported 26 liverwort and 1 moss species growing as epiphylls in the Lacandon Forest in Chiapas, Mexico. Nine were new for the country, all members of the **Lejeuneaceae** (Figure 6-Figure 15).

It is interesting that the epiphylls worldwide are nearly all liverworts, especially in the family **Lejeuneaceae** (Figure 6-Figure 15), suggesting that this family has some special adaptations for this habitat. For example, in El Salvador Winkler (1967) found 66 species of liverworts, but only 12 species of mosses on leaves, a number that is actually quite high. In the rainforest on Bioko Island of

Guinea, Müller and Pócs (2007) found 57 species of epiphyllous bryophytes, of which only two were mosses and the remainder were liverworts.

Dauphin (1999) reported 98 liverwort, 54 moss, and 1 hornwort species among epiphytes from Cocos Island, Costa Rica (Figure 135). In this study, more than 60% of the species have a Neotropical or Pantropical distribution. Less than 5% are endemic. The **Lejeuneaceae** (Figure 6-Figure 15; many as epiphylls) and **Lepidoziaceae** (Figure 136) comprised most of the taxa. Few thallose liverworts or moss taxa were found. Dauphin attributed the greater bryophyte species count in the Galapagos Archipelago to greater habitat variety, particularly wet and dry habitats. But most of the bryophytes in this Cocos Island study area are corticolous (46%), with only 25% epiphyllous.

Figure 135. Cocos Island beach and forest, Costa Rica. Photo by J. Rawls, through Creative Commons.

Figure 136. ***Lepidozia cupressina*** (**Lepidoziaceae**) from the Neotropics where this family is occasionally one of the epiphylls. Photo by Michael Lüth, with permission.

By contrast, Bernecker-Lücking (2000) reported 56 mosses and 106 liverworts growing on Cocos Island, Costa Rica. Of these, 45 were epiphyllous. Like the study of Lücking (1997) and Dauphin (1999), these had primarily Neotropical affinities. One surprising result of their study was the discovery of epiphylls growing on the undersides of leaves in the mountainous area, perhaps due to the high light intensity there. Most of the epiphyllous species are in the liverwort family **Lejeuneaceae** (Figure 6-Figure 15). Other epiphyllous liverworts include ***Metzgeria*** (Figure 19, Figure 127) and ***Radula*** (Figure 16). Of the few species of mosses, most are in the genus ***Crossomitrium*** (Figure 21). In this study, the diversity, distribution, and density were related to microclimate, especially humidity, but they also related to differences in the vegetation.

South America

In a superhumid tropical lowland forest of Chocó, Colombia, epiphyllous bryophytes have had little study, leading to an assumption of rarity that might not be justified (Benavides & Sastre de Jesús 2011). Among these poorly known or rare species are ***Cololejeunea gracilis*** (Figure 137), ***Leptolejeunea tridentata*** (see Figure 14), and ***Otolejeunea schnellii***. The researchers found that the diversity and composition of epiphyll species differs little between the palm and non-palm leaves. Disturbance affects epiphyll cover, species richness, and diversity of rare species negatively. The rare species do not agree well with the global or national red lists, again reinforcing the need for more studies.

Figure 137. ***Cololejeunea gracilis*** var. ***linearifolia*** on leaf. Photo courtesy of Tamás Pócs.

In the Colombian Amazonia, Benavides *et al*. (2004) found a total of 109 bryophyte species in a non-flooded and a floodplain forest. The life forms differed little in the two forest types, but the species of mosses and liverworts were different. On the other hand, the floodplain had more fan and mat species, whereas the non-floodplain had more epiphytic liverworts. The epiphyll species seemed to differ little between the habitats. Benavides and coworkers suggested that the epiphyll habitat is stressful enough that the habitat differences have little effect.

One of the common genera of leafy liverworts among the epiphylls is ***Frullania*** (Figure 20), although none of its species is typically epiphyllous. Von Konrat and Braggins (1999) reported eleven epiphyllous species in New Zealand, New Caledonia, and Colombia, with 29 more that had been listed previously as epiphylls in other regions of the world. Epiphyllous species of ***Frullania*** range from sea level to 2,500 m and can be considered facultative or accidental on the leaf substrate. The genus also occurs on rocks and bark. The largest number of epiphyllous ***Frullania*** species occurs in the floristic regions of New Zealand, New Caledonia, Macaronesia, and Madagascar (Braggins & von Konrat 1999).

Pócs (2002) explored the Neotropical species of ***Cololejeunea*** (Figure 6) from Ecuador and Brazil and found two new species: ***Cololejeunea ecuadoriensis*** and ***C. schusteri***. In fact, it is unusual to find a tropical study that does not include new species. In 2018, Pócs found the epiphyllous liverwort ***Reinerantha foliicola*** (**Lejeuneaceae**; Figure 138) in Venezuela, in a genus previously described from Ecuador by Gradstein *et al*. (2018) as a new genus.

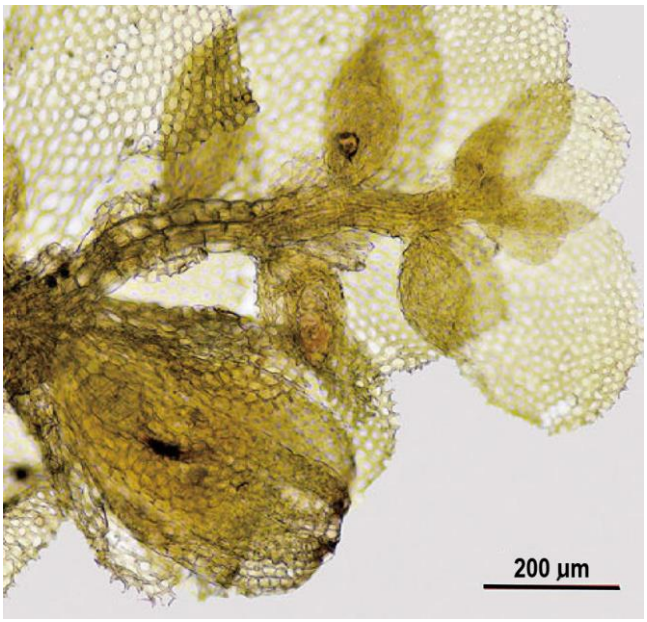

Figure 138. ***Reinerantha foliicola***, an epiphyllous lefy liverwort from Ecuador and Venezuela. Photo modified from Gradstein *et al*. 2018, with permission.

Campelo and Pôrto (2007) provided a checklist including both epiphyllous and epiphytic bryophytes of Frei Caneca RPPN, Jaqueira, Pernambuco State, Northeastern Brazil. This was a remnant Atlantic forest at 750 m alt. They found 21 families, with the liverworts in **Lejeuneaceae** (Figure 6-Figure 15; 31 species) and the mosses in **Calymperaceae** (Figure 139-Figure 142; 7 species) predominating in species number. Most of the species (67%) are Neotropical, but 15% are pantropical. Orbán (1997) has shown that different genera of **Calymperaceae** prefer to colonize different parts of the leaves, like ***Mitthyridium*** (Figure 139) mostly the petiole, ***Calymperes*** (Figure 140), ***Leucophanes*** (Figure 141), and some ***Syrrhopodon*** (Figure 142) the midrib, while other ***Syrrhopodon*** species grow on the margin.

Zartman and Ilkiu-Borges (2007) have provided a key, descriptions, and illustrations for the epiphyllous bryophytes of Central Amazonia. To facilitate bryological work in both English and Spanish, the keys and descriptions are provided in both languages.

Figure 139. ***Mitthyridium micro-undulatum***; some members of ***Mitthyridium*** prefer leaf petioles. Photo by Jan-Peter Frahm, with permission.

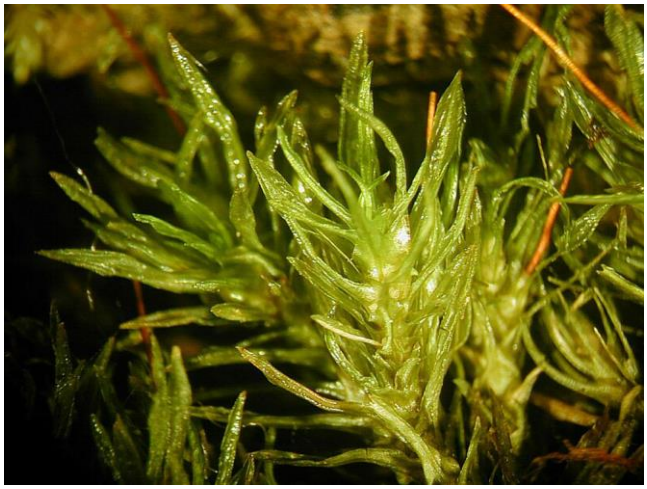

Figure 140. ***Calymperes nicaraguense***; its family, the **Calymperaceae**, is common among epiphytes in the Neotropics; some species prefer midribs. Photo by Michael Lüth, with permission.

Figure 141. ***Leucophanes*** sp., a genus that prefers the midribs of leaves. Photo by Niels Klazenga, with permission.

Figure 142. ***Syrrhopodon*** *cf.* ***platycerii***; some members of this genus may prefer the leaf midrib or the margin. Photo by Niels Klazenga, with permission.

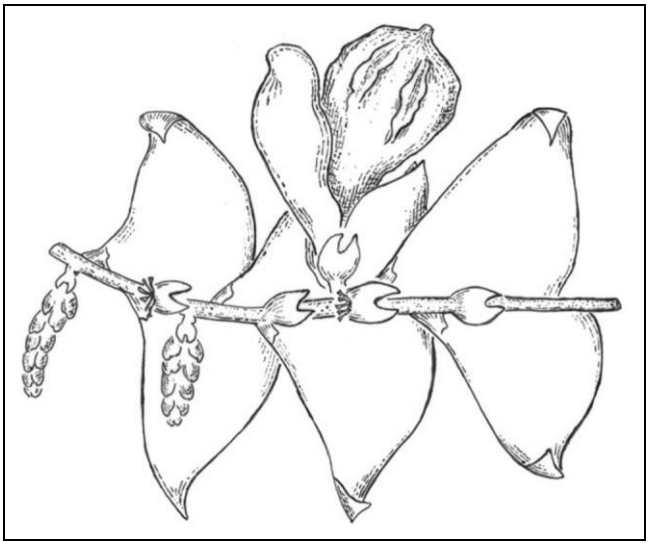

Figure 144. ***Bromeliophila natans***, a species that occurs in bromeliad basins. Drawing from Heinrichs *et al*. 2014; courtesy of Robbert Gradstein.

Bromeliad Basins

Some bryophytes live on bromeliad leaves (Figure 143) and in the basins of water provided by them. ***Bromeliophila helenae*** and ***B. natans*** (Figure 144) grow exclusively in the leaf axils of bromeliads (Gradstein 1997a; Gradstein *et al*. 2001; Benavides & Callejas 2004; Heinrichs *et al*. 2014). ***Bromeliophila natans***, which like its sister species is barely distinguishable from ***Lejeunea*** (Figure 3), is apparently endemic to southeastern Brazil (Gradstein 1997a). It occurs, often submerged, in terrestrial bromeliads such as ***Vriesea glutinosa*** (Figure 145), ***Aechmea nudicaulis*** (Figure 146), and ***Quesnelia arvensis*** (Figure 147), mostly on open sites in the coastal rainforest. ***Bromeliophila helenae***, a montane species, is known from the Guayana Highland of Venezuela and on the island of Dominica in the central Lesser Antilles. It grows in the basins of both terrestrial and epiphytic bromeliads such as the terrestrial ***Brocchinia hechtioides*** (see Figure 148-Figure 149).

Figure 143. Epiphyllous liverwort on bromeliad leaf. Photo by Jessica M. Budke, with permission.

Figure 145. ***Vriesea glutinosa***, one of the bromeliads with basins in which ***Bromeliophila natans*** sometimes occurs. Photo by BotBin, through Creative Commons.

Figure 146. ***Aechmea nudicaulis***, Brazil, one of the bromeliads with basins in which ***Bromeliophila natans*** sometimes occurs. Photo by Marcia Stefani, through Creative Commons.

Figure 147. ***Quesnelia arvensis***, one of the bromeliads with basins in which ***Bromeliophila natans*** sometimes occurs. Photo by John Thagard, through Creative Commons.

Figure 148. ***Brocchinia tatei*** on the north ridge of Mt Roraima, Guyana, at 2000 m asl; the liverwort ***Bromeliophila helenae*** grows in the basins of ***Brocchinia hechtioides***. Photo courtesy of Robbert Gradstein.

Figure 149. Insectivorous plant ***Utricularia humboldtii*** growing in leaf axils of the bromeliad ***Brocchinia tatei*** at Mt. Roraima north ridge at 2000 m. Photo courtesy of Robbert Gradstein.

In Puerto Rico, 13 out of 65 bromeliads sampled near the radiation center in 1965 had bryophytes in their basins (Maguire 1970). Mosses in these aerial basins are rare, with the only known species being ***Philophyllum tenuifolium*** in the **Leucomiaceae**, occurring submerged or emergent in ***Vriesia*** (Figure 145) and ***Nidularium*** (Figure 150) of Guatemala, SE Brazil, and Peru (Gradstein *et al*. 2001). The basin of water created in the middle of the youngest leaves is available to keep the bromeliad hydrated and thus provides an aquatic habitat for bryophytes.

Figure 150. ***Nidularium procerum***. ***Nidularium*** is one of the bromeliads with basins in which the moss ***Philophyllum tenuifolium*** sometimes occurs. Photo by Bocabroms, through Creative Commons.

Fragmented Habitats

Deforestation is creating forest fragments in many areas of the tropics. Oliveira *et al*. (2011) reported that they could detect no edge effect on epiphytic bryophytes in a fragmented landscape of an Atlantic forest in northeast Brazil. Furthermore, canopy openness was not correlated with bryophyte richness. Here we explore if this absence of edge effect holds as well for the epiphyllous bryophytes in the Neotropics.

Zartman (2003) discussed the effects of this habitat fragmentation on epiphyllous bryophyte communities in central Amazonia. He found that regionally common taxa were often reduced in epiphyll diversity in small forest fragments. On the other hand, rare taxa were often more abundant in fragments than in continuous forest habitat. Larger fragments (100 ha) exhibited higher species richness, abundance, and among-site variation than did the smaller fragments (1 & 10 ha).

Like Daniels (1998), Zartman and Nascimento (2006) took advantage of the accelerated life cycles, high rates of local extinction, and naturally patchy substrates of epiphyllous bryophytes to look at the effects of habitat fragmentation. They examined both local abundance and regional distribution of 67 epiphyllous bryophyte species in Amazonia. The landscape was experimentally fragmented and demonstrated that changes in local abundance caused by habitat fragmentation can be explained by fragment size rather than nearness to the forest edge. The simultaneous inter-specific decline in epiphyll local abundance and regional distribution in small (1-10 ha) forest fragments support metapopulation predictions of the importance of immigration in ameliorating risk of patch extinction (*i.e.* the **rescue effect**). They concluded that their results provide indirect evidence that dispersal limitation, not compromised habitat quality due to edge effects, can account for species loss from small tropical forest fragments. They further concluded that preservations of rainforest areas of at least 100 ha are necessary for the long-term persistence of these epiphyllous communities.

Alvarenga and Pôrto (2007) explored eight Atlantic forest fragments in Pernambuco, Brazil, ranging in size from 7 to 500 ha to determine the effects on epiphytes and epiphylls. Habitat fragmentation existed in the lowland and submontane forests (Alvarenga & Pôrto 2007). Despite the increase in richness, diversity, and abundance with altitude, clear evidence exists that fragment size and isolation are more important as determinants of these community parameters. Isolation is the most important factor, emphasizing the importance of dispersal. Furthermore, the greatest proportion of shade species occurs in larger fragments with lower degrees of isolation. Fragments also increase the number of species with larger niches (**generalists**) while decreasing the number with smaller niches that were likely to specialize on shady or sunny areas.

In the Eastern Arc Mountains of Kenya, Malombe *et al.* (2016a) investigated fragmentation and its effect on the sensitive epiphylls. Using a disturbance gradient up to 200 m from the forest edge in three moist forest fragments, they collected at least four leaves from each host species. They found 96 epiphyllous bryophyte species. No correlation was evident between the environmental variables (relative humidity, temperature) and the forest edge gradient. Nevertheless, epiphyll diversity differs with site-specific characteristics. Forest edge distance does not have a significant influence on richness or distribution of the epiphyllous bryophyte species. Instead, these parameters depend on microhabitat variables such as tree species composition, sunlight exposure, and spatial and dimensional canopy structure.

Malombe *et al*. (2016b) also examined fragmentation effects on the composition, abundance, and species richness of epiphyllous bryophytes in fragments of tropical cloud forests in the Eastern Arc Mountains of Kenya. Again using a disturbance gradient extending 200 m out from the forest edge, they collected four leaves from each phorophyte at three sites, totalling 1,387 leaves from 489 phorophytes. This revealed 95 species of bryophytic epiphylls. Once again, richness did not change with distance from the forest edge. And as in their moist forest fragment study, richness depended on the tree species composition and microhabitat, including exposure to sunlight and canopy structure.

Hylander *et al*. (2013) studied fragmentation effects in the moist Afromontane forests of Ethiopia. This study differed from most in that the forest margins were still in heavy use by local farmers, creating a mosaic landscape. Going into the forest instead of away from it, they found strong edge effects on canopy cover and number of stumps. Heavy usage by humans was indicated by paths, beehives in trees, and timber harvesting, and perennial crops such as coffee and spices. The number of epiphyllous bryophytes increased from 20 m to 75 m inward from the edge. They concluded that the edge effects on epiphyllous bryophytes do not get worse over time.

Silva and Pôrto (2010) similarly studied the species richness and diversity of both epiphytic and epiphyllous bryophytes on an edge to interior gradient in a large remnant of the Atlantic forest in Northeast Brazil. The researchers estimated light differences using hemispherical photographs. They found no significant difference in species richness or diversity based on distance from forest edge up to 1084 m inside. Altitude, however, causes an increase in bryophyte diversity, especially for epiphylls and shade-tolerant bryophytes. Canopy cover is somewhat less important than altitude. Differences within the forests are more important than distance from the edge.

Alvarenga *et al*. (2009) also studied bryophytic epiphylls in fragmented forests of northeastern Brazil, from forest edge to 100 m within the fragment. They found decreasing abundance both locally and regionally resulting from habitat loss. They concluded that this is related to both sexual and asexual expression. Frequently-fertile species are more frequent in forest fragments than infertile species. Nevertheless, the landscape and habitat quality are more important in epiphyll richness and presence than distance from forest edge. As in the above studies, habitat modification is less important than forest characteristics, but they nevertheless play a role. They concluded that fragmentation results in negative and long-term effects in fragmented landscapes. Connectivity between patches is important in successful conservation.

Zartman *et al*. (2012) experimented with recolonization rates by stripping bryophytes from their branches. When both local and neighboring phorophytes within 400 m^2 plots were experimentally denuded, the extinction events increased, along with a reduction in colonization. When no denuding occurred, losses of the epiphylls were subject to rescue effects from neighboring leaves. The researchers suggest that negative density-dependent growth in within-leaf populations indicates resource limitation or intraspecific competition.

Zartman and Shaw (2006) considered the demographic mechanisms causing species loss in the tropics to be greatly underexplored. To contribute to the understanding of the impact of fragmentation, they chose the epiphyllic leafy liverworts ***Radula flaccida*** (Figure 41) and ***Cololejeunea surinamensis*** (see Figure 71). They transplanted these two species to study sites with areas ranging 1, 10, 100, up to 110,000 ha. All the transplants exhibited significantly positive local growth with a nearly constant per-generation extinction probability of 15%. In reserves of 100 ha or greater, the colonization rate nearly doubled (to 48%) compared to small reserves (27%). They considered this an indication that epiphyll loss in small fragments was due to reduced colonization.

Pócs (1996) emphasized that conservation of epiphytes "can only be achieved through the rigorous protection of the forests."

Sampling Epiphylls

Collection of the epiphyllous bryophytes requires the same techniques as for bryophytes on branches at the same level in the forest, including use of ropes, bow and arrow, or climbing. Ecological methods, however, may be somewhat different.

In a study of epiphylls in Colombia, Benavides and Sastre de Jesús (2011) used 10 x 10 cm quadrats in 30 plots, totalling 240 samples. They recommend the Floristic Habitat Sampling, a method that focuses on mesohabitats as the sampling unit. Unfortunately, that does not provide the randomness required for statistical comparisons. They therefore recommend a combination of a systematic grid of 1-several km^2 with Floristic Habitat Sampling within the plots.

Vanderpoorten *et al*. (2010) emphasized that many bryophytes are annual or identifiable during only part of the year. They claimed that completely random plot sampling or systematic sampling are both likely to miss species and variation within the sampling area unless the sampling effort is very high (number of plots, large number of sampling dates).

The IUCN uses the Area of Occupancy for recording rare species. This is defined as the area calculated by summing all 2x2 km grid squares that actually have the taxon. But Vanderpoorten and coworkers recommend reducing the mesh size because the Area of Occupancy values decline sharply with a reduction in scale. This occurs because the bryophyte species have a more linear and fragmented distribution.

Collection is necessary to identify or verify most bryophytes and to permit DNA analysis now or later. For epiphyllous bryophytes, it is necessary to collect entire leaves that host them and to put them in new papers in a plant press so that the host leaf remains flat. They should be lightly pressed until they are dry.

Bryophytes living on leaves are typically collected by collecting host leaves. These are preserved by pressing and drying. Pócs and coworkers (Pócs 1978; Pócs & Podani 2015) found that 30 (50 preferred) randomly collected leaves from a hectare are usually representative of most species occurring there. Each leaf can be considered as a separate stand which can be studied and compared by the methods generally used in phytosociology. These should be examined microscopically. Pócs (1978, 1982b) counted the number of foliicolous plantlets on each leaf and related that number to leaf area. Frequency is used to represent the presence of a certain species on different leaves among the samples collected.

To determine cover values, one can use a celluloidin film solution spread over the leaf (Tamás Pócs, unpublished). Once this has hardened, it can be removed, together with the foliicolous community, and examined under a microscope at low magnification using a square grid ocular micrometer. This can provide the data to determine cover values.

Carroll (1979) developed another method when surveying the epiphyllous organisms on Douglas fir needles (***Pseudotsuga menziesii***). He used photographs of random sections of needles and extrapolated these to total needle area. This method is especially useful where collecting is not allowed or sampling would be too destructive.

Benavides and Sastre de Jesús (2009) similarly used digitized images for estimating bryophyte cover. They compared accuracy, efficiency, and objectivity among three methods: Braun-Blanquet cover classes, grid percentage, and digital image processing. Two observers used clay tiles that had been planted with ***Neckeropsis disticha*** (Figure 151) and estimated cover by the three methods. Accuracy was determined by comparing cover values with the dry weights. Efficiency was a measure of time and data

variability. Objectivity was compared between observers. The digital method was the most efficient in time in the field (p<0.001) and furthermore had the least variation among the data (p=0.01). This method is especially useful when repeated measures through time are needed and is more accurate when the cover is small, as in epiphylls.

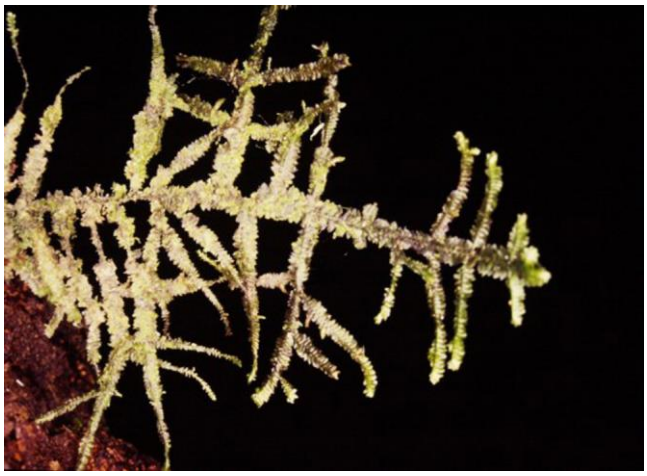

Figure 151. ***Neckeropsis disticha***, an epiphyll. Photo by Jan-Peter Frahm, with permission.

Epiphylls typically have associated **Cyanobacteria** that fix nitrogen, benefitting both the epiphylls and the leaf. Some leaf leachates benefit the epiphylls. Bryophytes may accumulate heavy metals, causing the host leaf to have greater concentrations of these. The epiphylls also seem to protect the host leaves from at least some kinds of herbivory. But sometimes rhizoids penetrate the epidermal cells, permitting the entry of leaf pathogens. They can also interfere with light, but the leaves seem to be able to compensate for this. Bromeliads growing in the trees can provide a unique habitat for bryophytes.

Species richness varies with habitat, but not as much as one might expect. Moisture is the main limiting factor, with light and temperature also being important. Disturbance and pollution decrease species richness. Comparison of geographic areas is still in its infancy, with many undescribed species and nomenclatural problems. Nevertheless, it is clear that the family **Lejeuneaceae** is the most species rich family of epiphylls.

Fragmented habitats may limit dispersal, thus reducing frequency and diversity.

Sampling requires some of the sampling techniques for epiphytes in general. They can be quantified using quadrats. Digitized images of marked quadrats are useful for quantifying growth.

Summary

Bryophytic epiphylls are almost entirely leafy liverworts. Epiphylls are common on leathery, persistent leaves, but colonize more rapidly on short-lived leaves, most likely due to antibiotic compounds in the persistent leaves. Close adherence to the leaf, numerous rhizoids, adhesive secretions, sacs and grooves to hold and transport water all help epiphylls survive on the alternately wet and dry leaves of their hosts. Crustose lichens often colonize as epiphylls first, then liverworts, then foliose lichens that may overgrow the liverworts. In other cases, the liverworts are first to colonize.

Liverworts hold water on the leaf surface and may make it more suitable for fungi. On the other hand, they might provide secondary compounds that inhibit fungal growth. The bryophytes can provide evaporative cooling as they lose water over a longer period of time than do the uncolonized leaves.

Epiphylls necessarily have short life cycles that can be completed before the leaf falls. Epiphyllous **Lejeuneaceae** have protonematal spores that adhere to the leaf surface and are able to germinate quickly. Asexual reproduction is particularly common but is limited by colony size. Asexual reproduction may decrease in dry months, whereas sporophyte density may be unrelated to the rainy season.

Host leaves may have drip tips, but their role is controversial. Leaf longevity is important, and evergreen leaves may even have epiphylls in moist forests outside the tropics. Epicuticular wax chemistry seems to affect epiphyll growth.

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CHAPTER 8-7
TROPICS: LOWLAND RAINFORESTS

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CHAPTER 8-7
TROPICS: LOWLAND RAINFORESTS

Figure 1. Amazon rainforest near Manaus, Brazil aerial view. Photo by Neil Palmer, through Creative Commons.

Lowland Rainforests

Undeveloped areas of the humid tropics are characterized by tropical rainforest. As shown by Frahm and Gradstein (1991) there are five tropical rainforest belts and their elevational limits are higher on continents than on islands due to the "mass elevation effect." On the continent the forest line is normally ca. 4,000 m asl but has been lowered to ca. 3,200 m in many places due to human impact, reaching as high as 1,500 m asl near the Equator and up to 700 m at the upper and lower tropical borders (Pócs 1982). The area covered, originally at 12% of Earth's surface, is estimated at only about 5% of Earth's surface now (Butler 2006), and it is still rapidly diminishing.

The lowland tropical rainforests (up to 500 m asl) are characterized by their great height, up to 60 m tall (Pócs 1982), with many evergreen species, particularly in areas that have a dry season. With annual rainfall greater than 1500 mm and an average temperature of 20-27°C (Pócs 1982), with little seasonal change, the trees flourish and the canopy is dense. Thus, the forest floor is characterized by limited light, even for a bryophyte. This unfavorable light level, in particular in the lowland rainforest, is made more unfavorable to bryophytes by the heavy leaf litter (Gradstein 1992; Delgadillo & Cardenas 2002). The result is that the tropical rainforest floor has lower moss species diversity than in temperate regions (Hallingbäck 1992).

Richards (1954) was among the first to attempt a description of these lowland forests. He recognized four main bryophyte synusiae in the Moraballi Creek rainforest of British Guiana: high epiphytes, shade epiphytes, epiphyllae, dead wood, noting their distinctness in both structure and floristic composition. Nevertheless, few species are very frequent. Exceptions to this are ***Calymperes lonchophyllum*** (see Figure 2) and ***Octoblepharum albidum*** (Figure 3); with the exception of the epiphyllous habitat, these two species occur in all the other synusiae. The epiphylls are almost entirely highly specialized species exclusive to the phyllosphere. Richards noted that growth/life forms differ among the synusiae. He further remarked on the absence of bryophyte synusiae on the ground at Moraballi Creek, the presence of an epiphyllous community, and the distinct dominance of liverworts, especially **Lejeuneaceae** (Figure 62-Figure 64). Although he noted that the forest was probably poorer in species than many temperate forests, his basis for this statement did not include knowledge of the diverse canopy bryophytes. Richards further claimed that these

comparisons would likewise apply to the lowland rainforests in Africa or the Indo-Malayan region. They would not, however, apply to the montane forests.

Figure 2, ***Calymperes*** sp.; ***C. lonchophyllum*** is a species found in all synusiae except epiphyllous at Moraballi Creek rainforest of British Guiana. Photo by Niels Klazenga, with permission.

Figure 3. ***Octoblepharum albidum***, a species found in all synusiae except epiphyllous at Moraballi Creek rainforest of British Guiana. Photo by Portioid, through Creative Commons.

In lower elevations, below 1500 m, the forest typically has a complex canopy. Trees have a variety of heights, some of which may reach 50-60 m tall. Levels in these forests can be classified as emergent, canopy, understory, and forest floor. This provides a variety of conditions for bryophytes, and often the within-tree diversity is greater than that between trees.

The canopy buffers and protects the lower strata of the forest. It reduces turbulence by absorbing wind energy; in one Costa Rican study, canopy (10 m) wind speeds were 11.3 m sec^{-1} while those on the forest floor (2 m) were 4.0 m sec^{-1} (Lawton 1980). The canopy modifies the temperature by absorbing heat and radiation (Nadkarni 1994). Its leaf surfaces absorb CO_2 and emit water vapor. It modifies the light quality by absorbing red and transmitting green, and it can reduce light intensity by as much as 98% before it reaches the forest floor (Cachan 1963). But for the canopy dwellers, being near the upper surface means intense sunlight, more temperature and humidity extremes, higher water stress, and a nutrient supply dependent on that in rainfall (Nadkarni 1994).

Although irradiation and desiccation are high in the canopy, the inner canopy affords some protection (Gradstein & Pócs 1989). Hence, dense mats or cushions are able to develop here, including the liverwort ***Frullania*** (Figure 4) and the moss ***Macromitrium*** (Figure 5). When it is very humid, **pendent** bryophytes and epiphyllous lichens and liverworts become established. In Bolivia (Figure 6), Acebey *et al*. (2003) found that rough mats appeared almost exclusively in the canopy, apparently requiring the high light intensity. This same restriction of rough mats to the high light zone of the upper canopy occurs in Guyana (Cornelissen & ter Steege 1989), and undoubtedly other areas of the tropics.

Figure 4. ***Frullania*** sp. in the Neotropics, where it can form dense cushions in the lowland rainforest inner canopy. Photo by Michael Lüth, with permission.

Figure 5. ***Macromitrium*** sp. (**Orthotrichaceae**) in the Neotropics, where it can form dense cushions in the lowland rainforest inner canopy. Photo by Michael Lüth, with permission.

Figure 6. Los Yungas La Paz, Bolivia. Photo by Elial Bizannes, through Creative Commons.

Costa (1999) studied the rainforest epiphytes in six forest types in the lowland rainforest of Rio de Janeiro, southeastern Brazil (Figure 7). She found 39 moss species and 36 liverwort species. The highest species richness occurred in the mature secondary hillside rainforest (43 species) whereas the lowest diversity was in the highly degraded hillside rainforest (6 species) and hillside secondary rainforest (5 species). As in Guyana (Cornelissen & Gradstein 1990), Costa found that the **Lejeuneaceae** (Figure 62-Figure 64) was one of the most important families (30% of species), with the moss family **Sematophyllaceae** (Figure 41) being second with 7 species (10%). In this case, 45% of the species were exclusively in the canopy. Mats were the most common life form of the six found there. Shade epiphytes are more susceptible to deforestation damage than are sun epiphytes, with many species not returning after 20-45 years. However, after 80 years, the bryophyte flora has recovered to that of the primary forest.

Figure 7. Rainforest canopy, Brazil. Photo by Ben Sutherland, through Creative Commons.

The Tropical Atlantic Rainforest in southeastern Brazil (Figure 7) has the high diversity of 338 taxa, with 49 families and 129 genera represented, with the altitudinal zones accounting for the richness (Costa & Lima 2005). As expected, the lowest diversity was in the Lowland Atlantic Rainforest; the highest was in the Montane Atlantic Rainforest. The moss family **Sematophyllaceae** (Figure 41) had 19% of the taxa in the lowland forest, **Meteoriaceae** (Figure 8) had 10% in the montane forests, and **Dicranaceae** (Figure 9) had 18% in the upper montane forests. Taxa with wide distributions in the Neotropics accounted for 40% of the total taxa and were important in all the forests. The taxa restricted to Brazil were second most important in the upper montane and montane forests.

Figure 8. ***Papillaria*** (**Meteoriaceae**), a common family of pendant mosses in the montane forests of Brazil. Photo by Pete the Poet, with online permission.

Figure 9. ***Campylopus pilifer*** (**Dicranaceae**), a family having 18% of the taxa in the upper montane forests of southern Brazil. Photo by Michael Lüth, with permission.

In Australian rainforests (Figure 10), liverworts usually dominate the bryophytes in lowland vine forests (Ramsay *et al.* 1987). Mosses are the more common bryophytes in wet higher altitudes or valley forests. Such bryophytes as ***Chandonanthus*** (Figure 11), ***Dicnemon*** (Figure 12), and ***Leptostomum*** (Figure 13) can be so heavy when they are wet that they become important in pruning the upper and dead branches.

Figure 10. Rainforest at Daintree, Australia. Photo by Thomas Schoch, through Creative Commons.

Figure 11. ***Chandonanthus squarrosus***, representative of a genus that gets so heavy from collected water in the tropics that it contributes to loss of canopy and dead branches. Photo by Tom Thekathyil, with permission.

Figure 12. ***Dicnemon*** sp. from NZ, representative of a genus that gets so heavy from collected water in the tropics that it contributes to loss of canopy and dead branches. Photo by Jan-Peter Frahm, with permission.

Figure 13. ***Leptostomum*** sp. Seno Courtenay Cape Horn, representative of a genus that gets so heavy from collected water in the tropics that it contributes to loss of canopy and dead branches. Photo by Blanka Shaw, with permission.

In Australia, members of the epiphytic and **saxicolous** (growing on or among rocks) moss genus ***Macromitrium*** (Figure 5) are found primarily in the rainforest (Figure 10) (Ramsay *et al*. 1987). These reach their greatest diversity in the lower elevation ravine rainforests. These habitats form an archipelago of refugia where the remnant patches of forest occur along the eastern and northern coast of the continent.

Streams often create a habitat suitable for a rich bryophyte flora (Dixon 1935; Shevock *et al*. 2017). At Tenompok in Borneo, smaller shrub and tree vegetation is adorned with thin pendulous mosses and liverworts. Tree trunks are thinly covered, but cushions are nearly absent. However, on the more exposed steeper slopes the small trees have moss and liverwort cushions. At higher elevations, these cushions are dominated by liverworts. Above ~2,000 m, up to ~3,000 m asl, the liverwort ***Mastigophora*** (Figure 14) and other liverworts provide most of the ground cover in the open ridge forest. In more sheltered places, different liverworts occur. Mosses, while present, are not abundant in the ridge forest. ***Sphagnum*** (Figure 15) cushions can be found, but not abundantly.

Figure 14. ***Mastigophora diclados***; in Borneo, this genus, along with other liverworts, provides most of the ground cover in the open ridge forest. Photo by Cesar Garcia, through Creative Commons.

Figure 15. ***Sphagnum junghuhnianum***; ***Sphagnum*** cushions are present but uncommon in the ridge forests of Borneo. Photo from Taibif, through Creative Commons.

In the Guianas, Pardow *et al*. (2012) described a new type of tropical lowland forest, the tropical lowland cloud forest. This forest type has a high epiphytic bryophyte species richness. This diversity is facilitated by frequent early morning fog in valley locations. Lowland cloud forests and lowland rainforests differed in the functional composition of bryophytes in the canopy, especially the mid and outer canopy. The cloud forest reached a higher biomass and cover of both bryophytic and tracheophytic epiphytes. It similarly had a greater diversity of bryophyte life forms. the typical cloud forest life forms of **tail**, **weft** and **pendants** were almost completely absent in the lowland rainforests, making life forms an easy way to characterize differences in these two forest types.

Figure 16. Top of lowland rainforest canopy in French Guiana. Photo by Renske Ek, courtesy of Robbert Gradstein.

Obregón *et al*. (2011) studied the fog frequency in tropical lowland forests. Its occurrence is frequent in the lowland valleys of central French Guiana (Figure 17). It reaches its maximum before sunrise, with a duration of about 4.6 hours. This fog forms when rain saturates the soil, creating greater evapotranspiration. This morning fog follows an increase in temperature differences between the valleys and hill sites after the sun sets. This increase in fog provides an early morning moisture that provides suitable conditions for photosynthesis while the day is still somewhat cooler, supporting a higher epiphyte diversity in the lowland cloud forest compared to the hills. This fog even makes photosynthesis possible in the early mornings of the dry season.

Figure 17. Lowland fog, French Guiana. Photo by Delome, through Wikimedia Commons.

Amazonia Lowlands

Prance (1980) decried the mixed terminology being used to describe the Amazonian floodlands. Hence, reading older literature and comparing vegetation types can be challenging and lead to misconceptions. Prance recommended creating terminology based on vegetation cover type, water type, and duration of flooding.

The Amazonian lowlands (Figure 1, Figure 18) include both the dry land (**terra firme**) and the wetlands, including mangrove (Figure 19) forests and estuaries. The latter two are saltwater habitats that are not hospitable for bryophytes. Kürschner and Parolly (1998) reported on the shade epiphytes of the Amazonian lowlands of Peru. Since then a number of studies have contributed to our understanding of the bryoflora of Amazonia.

Figure 18. Canopy of lowland rainforest in Colombian Amazon. Photo by Laura Campos, courtesy Robbert Gradstein.

Figure 19. Mangroves in Dominican Republic. Photo by Rachel Doherty, through Creative Commons.

In 1985, Amazonia occupied nearly 6,000,000 km^2 of South America (Pires & Prance 1985). Since then, deforestation for agriculture, cattle ranching, and logging has greatly reduced its size (Fearnside 2005; Heckenberger *et al*. 2007; Nepstad *et al*. 2008; Clement *et al*. 2015; Butler 2017). Some of the sub-basins have lost up to 33% since 1970 (RAISG 2015). In 2018, the Amazon Basin of 7,000,000 km^2 had only 5,500,000 km^2 covered by the rainforest (Wikipedia 2018). Although these numbers do not seem to agree, they nevertheless indicate that considerable loss of Amazonian lowland rainforest is disappearing.

The Amazonian lowland occurs mostly below 100 m asl and rarely rises above 200 m asl. Classification of the vegetation is based primarily on the topography. Two main types of forest vegetation occur: the **terra firme** (dry land) and the inundated formations [**igapó** (Figure 20) and **várzea** (Figure 21)], terms exclusive to Amazonia and all of which are primarily forest land. In addition, some areas have savannah vegetation, but this is a much smaller percentage of the land. Additional more specialized wetland vegetation types are mangrove swamps, **restinga** (spit and distinct type of coastal tropical and subtropical moist broadleaf forest in eastern Brazil), **buritizal** (periodically inundated palm thicket characterized by buriti – the palm *Mauritia flexuosa*), and **pirizal** (cariazal – extensive, emergent vegetation of small, stagnant lakes and puddles). The terra firme forest occupies the largest percentage of the area in Amazonia.

Figure 20. Igapó in Brazil. Photo by Lisa Cyr, through Creative Commons.

Figure 21. Várzea forest, Marajó, Brazil. Photo by Dayse Ferreira, through Creative Commons.

The lowland forests typically have a strong gradient of humidity and light, with humidity decreasing and light intensity increasing from the ground to the upper canopy (Figure 22-Figure 23) (Leon-Vargas 2001).

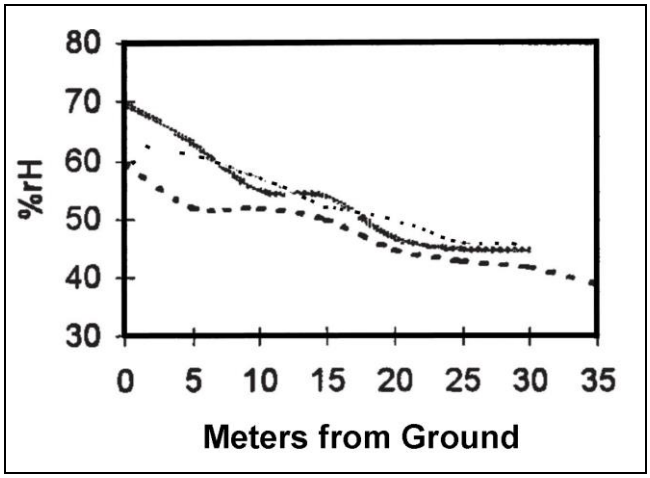

Figure 22. Humidity in ascending heights in the Amazon lowland forest. Modified from Leon-Vargas 2001.

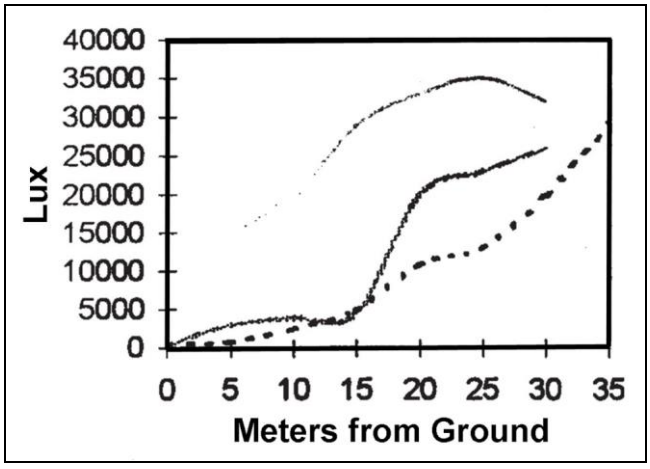

Figure 23. Light intensity at ascending heights in a Neotropical lowland forest. Modified from Leon-Vargas 2001.

Amorim *et al*. (2017) compared bryophyte distribution in southeastern Brazil. They considered two distinct groupings, the inland areas and the coastal areas, with annual precipitation and temperature influencing the floristic similarity among the coastal areas. Distance from the ocean and altitude were the dominant factors influencing the bryophyte composition of the inland areas.

Lisboa (1976) characterized the Amazonian plain as having poor soil nutrients. Unlike many rainforests, the light intensity can in some areas be very high, resulting in high air (38ºC) and soil (42.3ºC) temperatures. This combination of high light and high temperatures restricts the bryophyte community. Nevertheless, they found 34 bryophyte species, representing the moss families **Calymperaceae** (Figure 2), **Leucobryaceae** (Figure 40), **Leucodontaceae** (Figure 24), **Plagiotheciaceae** (Figure 25), **Sematophyllaceae** (Figure 41), and liverwort families **Frullaniaceae** (Figure 4, Figure 26), **Lepidoziaceae** (Figure 53), **Lejeuneaceae** (Figure 62-Figure 64), **Odontoschismaceae** (currently included in **Cephaloziaceae**; Figure 27), **Plagiochilaceae** (Figure 28), **Radulaceae** (Figure 73), and **Zoopsidaceae** (currently included in **Lepidoziaceae**; Figure 29). The liverwort ***Frullania nodulosa*** (Figure 26) stood out as the most frequent species, a species with wide ecological amplitude. Bark of the tree ***Aldina heterophylla*** (**Rubiaceae**) proved to be a preferred substrate, providing old age, thick bark, and otherwise good conditions for bryophyte community development.

Figure 24. ***Antitrichia curtipendula*** a member of the **Leucodontaceae**. Photo from Proyecto Musgo through Creative Commons.

Figure 25. ***Plagiothecium undulatum***, a member of the **Plagiotheciaceae**. Photo by Christian Peters, with permission.

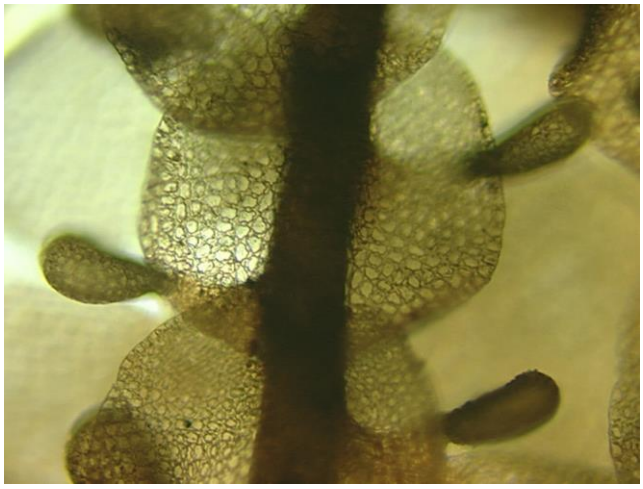

Figure 26. ***Frullania nodulosa*** underside, the most frequent species in the Amazonian plain. Photo by Matt von Konrat, with permission.

Figure 27. ***Odontoschisma longiflorum*** (**Cephaloziaceae**) from the Neotropics. Photo by Michael Lüth, with permission.

Figure 28. ***Plagiochila adianthoides*** (**Plagiochilaceae**) from the Neotropics. Photo by Michael Lüth, with permission.

Figure 29. ***Zoopsis liukuensis*** (**Lepidoziaceae**, formerly **Zoopsidaceae**). Members of the **Zoopsidaceae** are common in the Amazonian lowland rainforests. Photo by Rui-Liang Zhu, with permission.

Benavides *et al*. (2006) claimed the first bryophyte surveys from the Colombian Amazon. They divided the bryophytes into mosses and liverworts and into four life-form classes to describe floodplains, swamps, terra firme forests, and white-sand areas. They identified 50, 45, 45, and 32 species respectively. The higher number of species in the floodplains and swamps suggested the importance of moisture in delimiting communities. **Fan** life forms in the floodplains (Figure 30) further attested to the higher humidity there. Liverworts were more likely to form **mats** in both floodplain and terra firme habitats. And liverworts had greater species richness in the white-sand plots, suggesting a greater importance of light intensity than humidity for these species. Tree bark was the most important substrate for both bryophytes and liverworts in both floodplain and terra firme (Figure 31) (Benavides *et al.* 2004). The floodplain (várzea – Figure 21) differed markedly in species from the other three habitats.

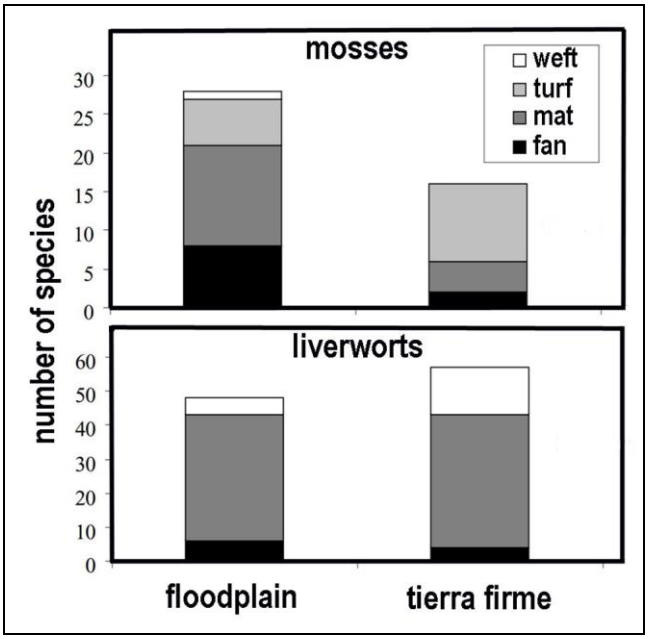

Figure 30. Bryophyte life forms in Tierra Firme vs Floodplain. Modified from Benavides *et al.* 2004.

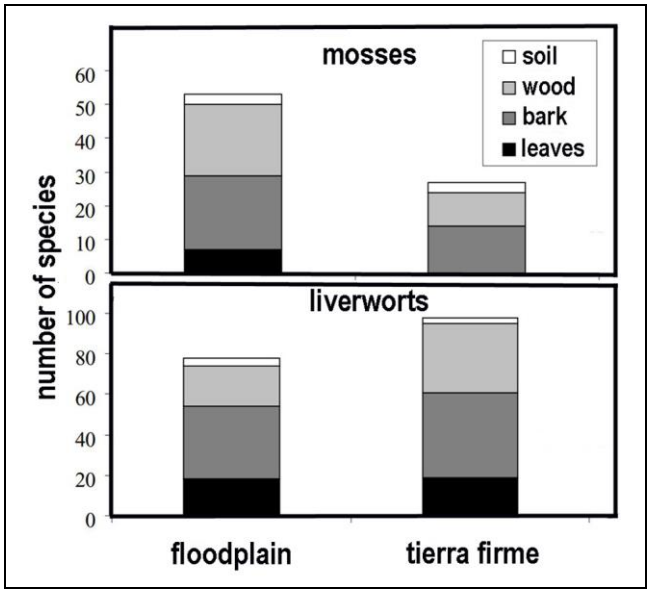

Figure 31. Bryophyte substrates in tierra firme vs floodplain. Modified from Benavides *et al.* 2004.

Leal *et al*. (2010) considered the possibility of using bryophytes (and other taxa groups) as surrogate taxa to indicate species richness in the Brazilian Atlantic forest and caatinga. But they did not include the bryophytes in their sampling of the caatinga. They found that the species richness of the various taxa groups (bryophytes, pteridophytes, trees, ants, euglosine bees, birds, and mammals; total of 768 species) were significantly correlated with each other. Only two taxa (trees and ants) were required to have excellent surrogacy for species richness of all groups. Bryophytes did not seem to be good surrogates for the richness of the other taxa groupings.

Valente *et al*. (2009) described the mosses in a segment of the Atlantic forest in Bahia State, Brazil. They found 61 moss species, distributed in 23 families. The most species-rich family was **Sematophyllaceae** (7 spp.; Figure 41), followed by **Orthotrichaceae** (6 spp.; Figure 5), **Pilotrichaceae** (5 spp.; Figure 32), **Calymperaceae** (5 spp.; *e.g*. Figure 2), **Leucobryaceae** (5 spp.; *e.g.* Figure 40), and **Meteoriaceae** (4 spp.; Figure 8). Corticolous species predominated, with 70% of the species, followed by **epixylous** (on wood with no bark) having 23% of the species. The area was species-rich, with 24% of the bryophytes in the Bahia State represented there.

Epixylic bryophytes (living on logs with no bark) in the Atlantic forest of Brazil supported 35 species of bryophytes, not counting the **Lejeuneaceae** (Figure 62-Figure 64) (Germano & Pôrto 1996, 1997). These comprise 11 families of mosses: **Calymperaceae** (Figure 2), **Pilotrichaceae (**Figure 32), **Fissidentaceae** (Figure 71, Figure 91-Figure 93), **Hookeriaceae** (Figure 33), **Hypnaceae** (Figure 34), **Leucobryaceae** (Figure 40), **Leucomiaceae** (Figure 35), **Orthotrichaceae** (Figure 5), **Plagiotheciaceae** (Figure 28), **Sematophyllaceae** (Figure 41), and **Thuidiaceae** (Figure 36), and 5 families of liverworts: **Aneuraceae** (Figure 55), **Frullaniaceae** (Figure 4), **Geocalycaceae** (Figure 37), **Plagiochilaceae** (Figure 28), and **Radulaceae** (Figure 73). These included 8 species new for northeastern Brazil.

Figure 32. ***Cyclodictyon*** sp. (**Pilotrichaceae**) in the Neotropics. Photo by Michael Lüth, with permission.

Figure 33. ***Hookeria acutifolia*** (**Hookeriaceae**), a family that occurs on logs in the Atlantic forest in Brazil. Photo by John Game, through Creative Commons.

Figure 34. ***Chryso-hypnum diminutivum*** (**Hypnaceae**), a family that occurs on logs in the Atlantic forest in Brazil. Photo by Michael Lüth, with permission.

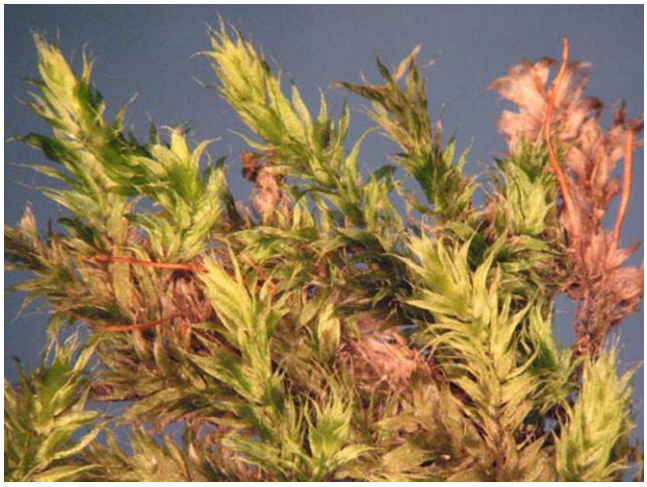

Figure 35. ***Leucomium strumosum*** (**Leucomiaceae**), a family that occurs on logs in the Atlantic forest in Brazil. Photo by Claudio Delgadillo Moya, with permission.

Figure 36. ***Cyrto-hypnum involvens*** (**Thuidiaceae**) on a log in the Neotropics. Photo by Michael Lüth, with permission.

Figure 37. ***Geocalyx graveolens*** (**Geocalycaceae**), a widespread species in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Michael Lüth, with permission.

Pires and Prance (1985) considered the dense tropical forests of the Amazon to be fireproof. These dense forests create many niches, permitting the occurrence of many species. Costa (2003) reported 514 species in the Amazonian rainforest. Nevertheless, only 106 species are known from the state of Acre, Brazil, suggesting that the area has been understudied. After only two field trips, Costa was able to increase the known flora by 50%. These trips yielded 50 species that were new for the state and 10 more that were "interesting." In an earlier study, Vital and Visnadi (1994) reported only 76 species, and at that time 66 were new records for the state of Acre. This report included one hornwort, ***Notothylas vitalii*** (see Figure 38).

Figure 38. ***Notothylas orbicularis***; ***Notothylas vitalii*** is the only species of ***Notothylas*** known to Costa in 1985 for the Amazonian lowland rainforest. Michael Lüth, with permission.

New species most likely await us in these forests. Moura *et al*. (2012) noted the abundance of ***Lejeunea*** (Figure 39) species in the low várzea (Figure 21) forest in lower Amazon, Pará, Brazil, and reported the new species ***Lejeunea combuensis***.

Figure 39. ***Lejeunea*** from the Neotropics, an abundant species in the low várzea of the Amazon. Photo by Michael Lüth, with permission.

Terra Firme

Oliveira and ter Steege (2013) used standardized sampling methods for epiphytic bryophytes in nine localities in the Amazon basin terra firme forests. They sampled five height zones from forest floor to canopy on

eight canopy trees at each locality, generating 3,014 records and 222 species plus 39 morphospecies. As is typical in the tropics, the most common family was **Lejeuneaceae** (Figure 62-Figure 64) (55% frequency), along with the mosses **Calymperaceae** (Figure 2) (8%), **Leucobryaceae** (Figure 40) (4%), and **Sematophyllaceae** (Figure 41) (4%). No geographical gradient was evident in species richness or composition. Nevertheless, richness differences were evident, with the greatest richness in Saül of French Guiana and Tiputini of Ecuador, compared to other localities. Of the 155 species occurring in more than one locality, 57 were specialists. A total of 29 species were found only in the canopy.

Figure 40. ***Leucobryum martianum***. Members of its family, **Leucobryaceae,** are common on trees in the Amazon basin. Photo by Jan-Peter Frahm, with permission.

Figure 41. ***Sematophyllum*** sp. (**Sematophyllaceae**), a well-represented family from the Amazon lowlands. Photo by Michael Lüth, with permission.

Alvarenga and Lisboa (2009) reported 120 species of bryophytes from the Amazon lowlands. Among these, the **Lejeuneaceae** (Figure 62-Figure 64) species are by far the most abundant with 58 species, followed by **Calymperaceae** (Figure 2) (13 spp.), **Sematophyllaceae** (Figure 41) (9 spp.), and **Plagiochilaceae** (Figure 42). Of these 120 species, 97 are epiphytic; 65 are **epixylic** (growing on wood that has lost its bark). Only 27 species are epiphyllous and only 15 occur on the ground. The most diverse ecosystem is the terra firme forest. The liverworts are strong dominants on leaves, with dominance gradually shifting among the habitats. Liverworts are only slightly dominant on live and dead trunks, and mosses are dominant on the other substrates.

Figure 42. ***Plagiochila*** sp. from the Neotropics; **Plagiochilaceae** is a common family in the Amazon lowlands. Photo by Michael Lüth, with permission.

Sierra *et al*. (2018) provided a more comprehensive study on the Amazon lowlands, listing 150 species from 712 collections. These were comprised of 109 liverworts and 41 mosses. Of these 104 species lived as epiphytes and 38 as **epiphylls** (species living on leaves). Another 31 species occurred on decaying logs, 16 on rocks, and 24 on soil. But of these species, 68 occurred in only one or two samples. As is obvious from the numbers in each habitat, many were not exclusive to one habitat.

As in many other communities, the most species-rich liverwort families in the studied Amazon lowlands were **Lejeuneaceae** (81 species) and **Lepidoziaceae** (11 species) (Sierra *et al*. 2018). The three most species-rich genera were ***Cheilolejeunea*** (15 spp.; Figure 43), ***Cololejeunea*** (12 spp.; Figure 60-Figure 61), and ***Ceratolejeunea*** (6 spp.; Figure 63), all in the **Lejeuneaceae**. The most common liverwort species were ***Cheilolejeunea aneogyna*** (see Figure 43), ***Pycnolejeunea contigua*** (see Figure 44), ***Cheilolejeunea neblinensis***, ***Cololejeunea surinamensis*** (see Figure 60-Figure 61), ***Archilejeunea fuscescens*** (see Figure 45), ***Acrolejeunea torulosa*** (see Figure 46), and ***Vitalianthus aphanellus***, all in the **Lejeuneaceae**.

Figure 43. ***Cheilolejeunea*** sp., a species-rich genus in the Amazon lowlands. Photo by Michael Lüth, with permission.

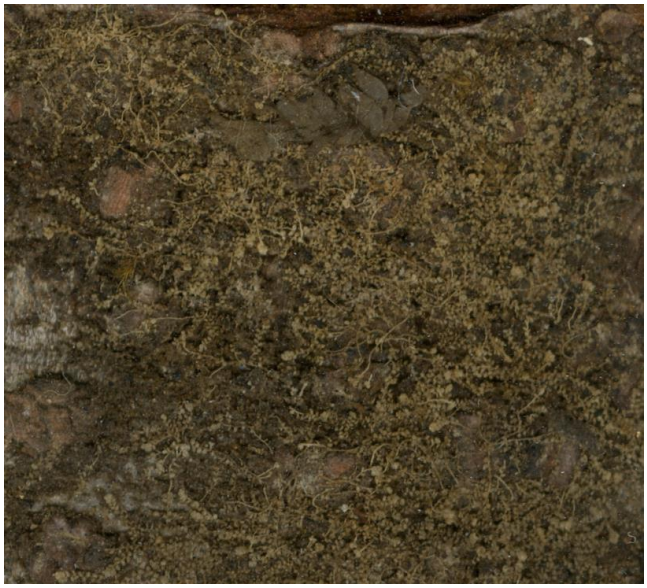

Figure 44. ***Pycnolejeunea pilifera***; ***Pycnolejeunea contigua*** is one of the common species in Amazonian lowlands. Photo from the Paris, Muséum National d'Histoire Naturelle, MB, through Creative Commons.

Figure 45. ***Archilejeunea olivacea***; ***Archilejeunea fuscescens*** is one of the common species in Amazonian lowlands. Photo by John Braggins, through Creative Commons.

Figure 46. ***Acrolejeunea*** sp.; ***Acrolejeunea torulosa*** is one of the common species in Amazonian lowlands. Photo by Peter de Lange, through Creative Commons.

The most species-rich moss families in the studied Amazon lowlands were **Calymperaceae** (16 species), and **Sematophyllaceae** (9 species), again being common families throughout the Neotropics (Sierra *et al*. 2018). The most species-rich genus of mosses was ***Syrrhopodon*** (12 spp.) in the **Calymperaceae**. The most common moss species were ***Leucobryum martianum*** (**Leucobryaceae**; Figure 40) and ***Syrrhopodon xanthophyllus*** (see Figure 47).

Figure 47. ***Syrrhopodon lycopodioides*** from the Neotropics; ***Syrrhopodon xanthophyllus*** is one of the two most common moss species in the Amazon lowlands. Photo by Michael Lüth, with permission.

Benavides *et al*. (2006) suggested that the periodic flooding added nutrients to the tree trunks, possibly contributing to the high diversity of bryophytes there compared to the swamps, terra firme forests, and white-sand habitats.

Most of the studies in the Amazon lowlands seem to be floristic with little ecological information on bryophytes. The following habitats can be identified, but few seem to have been described bryophytically, giving us little or no information on dominant species.

Dense Forest

This forest has the greatest biomass of the terra firme forests (Pires & Prance 1985). The understory is distinct, occurring where environmental conditions are optimal. Water is not limiting, having neither too much nor too little.

Open Forest without Palms

This forest has considerably less biomass and trees typically have a basal area of only slightly more than 20 m^2 per hectare (Pires & Prance 1985). The trees are lower, permitting a greater penetration of light. This allows shrubs and lianas to develop well. Large trees are only occasional. This vegetation type may be limited by a lower water table, impermeability of the soil, poor drainage, poor root penetration, somewhat long dry seasons, or lower relative humidity. Epiphytes are fewer due to the drier habitat. This forest type is not affected by fire and is predominantly not deciduous.

Open Forest with Palms

This forest has a similar physiognomy to that of the open forest without palms, but it has palm trees, especially ***Attalea maripa*** (Figure 48), ***Attalea speciosa*** (Figure 49), ***Euterpe precatoria*** (Figure 50), ***Jessenia bataua*** (Figure 51), and ***Oenocarpus distichus*** (Figure 52) (Pires & Prance 1985).

Figure 49. ***Attalea speciosa***, one of the palms found in the open forest of the Amazonian lowlands. Photo by Marcelo Cavallari, through Creative Commons.

Figure 48. ***Attalea maripa***, a palm of the open forest in the Amazonian lowland. Photo by Arria Belli, through Creative Commons.

Figure 50. ***Euterpe precatoria***, one of the palms found in the open forest of the Amazonian lowlands. Photo by Dick Culbert, through Creative Commons.

Figure 51. ***Jessenia bataua***, a palm of the open forest in the Amazonian lowland. Photo by Jean-Christophe Pintaud, through Creative Commons.

Figure 52. ***Oenocarpus*** sp., one of the palms found in the open forest of the Amazonian lowlands. Photo from Kew.org, through Creative Commons.

Van Dunne *et al*. (2001) sampled the epiphytes on the palm ***Jessenia bataua*** (Figure 51) at 1, 3, and 5 m heights. They found greater similarity among species of bryophytes on the same trunks than they did between palms. Of the 42 species identified, only 3 showed a spatial dependence. The biomass ratio of mosses to liverworts increased with height on the tree, but total bryophyte biomass showed no significant differences with height. The number of species increased with height sampled. They concluded that short-distance dispersal was less important than long-distance dispersal in determining the species composition. The most abundant families in this palm tree trunk habitat were **Lejeuneaceae** (Figure 62-Figure 64) (13 spp.) and **Lepidoziaceae** (Figure 53) (9 spp.), both leafy liverwort families. The moss family **Leucobryaceae** (Figure 40) was represented by 6 species. The lower and middle tiers of the trunk had mosses in addition to the leafy liverwort families **Calypogeiaceae** (Figure 54) and **Lepidoziaceae**. Only the family **Lejeuneaceae** was typically higher in the higher tiers. In addition, the only other families represented on this palm species were the mosses **Calymperaceae** (Figure 2) and **Sematophyllaceae** (Figure 41) and the thallose liverworts **Aneuraceae** (Figure 55) and **Pallaviciniaceae** (Figure 56).

Figure 53. ***Lepidozia cupressina*** from the Neotropics; members of the **Lepidoziaceae** occur on the palm ***Jessenia bataua*** (Figure 51). Photo by Michael Lüth, with permission.

Figure 54. ***Calypogeia peruviana*** (**Calypogeiaceae**), a family that occurs on the palm ***Jessenia bataua*** (Figure 51). Photo by Paul Davison, with permission.

Figure 55. ***Riccardia fucoidea*** (**Aneuraceae**) from the Neotropics; some members of this family occur on the palm ***Jessenia bataua*** (Figure 51). Photo by Michael Lüth, with permission.

Figure 56. ***Symphyogyna podophylla*** (**Pallaviciniaceae**) with sporophytes; some members of this family occur on the palm ***Jessenia bataua*** (Figure 51). Photo by Andras Keszei, with permission.

Liana Forest

Lianas occur in the open forest where one might typically find Brazil nut trees (*Bertholletia excelsa*; Figure 57) and *Attalea speciosa* (Figure 49) (Pires & Prance 1985). These forests are usually discontinuous, intermeshed with dense forests lacking lianas. These forests usually are somewhat elevated and have rich deposits of such minerals as iron, aluminium, manganese, nickel, gold, and others. Some bryophytes are able to live on these woody lianas.

Figure 57. ***Bertholletia excelsa***, a dominant tree in the liana forest of Amazonian lowlands. Photo by Vihelik, through public domain.

Dry Forest

The **dry forests** (Figure 58) are transitional forests and are seasonal and drier than rainforests (Pires & Prance 1985). The trees are at least partially deciduous except along the rivers and streams where flooding occurs. These forests do not occupy large areas.

Figure 58. Caatinga rich dry forest. Photo by Duarte, through Creative Commons.

Restinga

The **restinga** is the vegetation of coastal sand dunes. This vegetation type has few species in Amazonia.

Figure 59. Restinga forest at Itaguare beach in Bertioga State Park, Brazil. Photo by Miguel Rangel Jr., through Creative Commons.

The restinga has received at least some attention regarding its bryophytes. Working in the Setiba State Park, Espírito Santo, Brazil, Visnadi and Vital (1995) found 25 liverwort and 9 moss species, reporting the fewest species in the low and sparse restinga, with the most in the high and sandy restinga. Some of the bryophytes are specific, with the liverworts ***Cololejeunea*** (syn.=***Aphanolejeunea***) ***subdiaphana*** (see Figure 60), ***Chonecolea doellingeri***, and ***Cololejeunea cardiocarpa*** (Figure 61) occurring only in the low and sparse restinga. ***Leucolejeunea conchifolia*** (Figure 62) occurs only in the medium restinga. ***Ceratolejeunea laete-fusca*** (see Figure 63) was only found in the high restinga; ***Taxilejeunea pterigonia*** (see Figure 64) only appeared in the high and sandy restinga. The mosses ***Bryum capillare*** (Figure 65) and ***Campylopus pilifer*** (Figure 9) only occur in low and sparse restinga; ***Groutiella apiculata*** (Figure 66) and ***Schlotheimia rugifolia*** (Figure 67) occur only in the high restinga. In other areas, the restinga bryophyte vegetation can be very different, with few species in common with this one. This is especially true when comparing the northwestern Amazonian restinga bryophyte vegetation with that in the southern Amazonian lowlands.

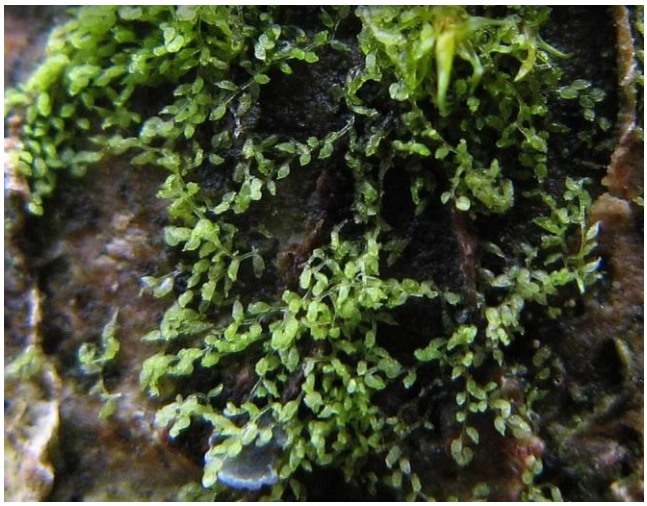

Figure 60. ***Cololejeunea microscopica***; ***C. subdiaphana*** is found only in the low and sparse restinga in Setiba State Park, Espírito Santo, Brazil. Photo by Stan Phillips, through public domain.

Figure 61. ***Cololejeunea cardiocarpa***, a species found only in the low and sparse restinga in Setiba State Park, Espírito Santo, Brazil. Photo by Paul Davison, with permission.

Figure 62. ***Leucolejeunea conchifolia***, a species from the medium restinga. Photo by Paul Davison, with permission.

Figure 63. ***Ceratolejeunea cubensis***; ***C. laete-fusca*** occurs only in the high restinga. Photo by Scott Zona, with permission.

Figure 64. ***Taxilejeunea*** from the Neotropics; ***T. pterigonia*** occurs only in the high and sandy restinga. Photo by Michael Lüth, with permission.

Figure 65. ***Bryum capillare*** with young sporophytes, a species that occurs only in low and sparse restinga. Photo by Michael Lüth, with permission.

Figure 66. ***Groutiella apiculata*** with capsules, a species that occurs only in the high restinga in Brazil. Photo by Frank Bungartz, through Creative Commons.

Figure 67. ***Schlotheimia rugifolia***, a species that occurs only in the high restinga in Brazil. Photo by Juan David Parra, through Creative Commons.

In the Parque Nacional da Restinga de Jurubatiba, RJ, Brazil, Imbassahy *et al*. (2009) reported 61 taxa. As is typical in the tropics, the **Lejeuneaceae** (Figure 62-Figure 64) had the most species (25), greatly exceeding other high-species families of **Jubulaceae** (Figure 68-Figure 69) (7), **Calymperaceae** (Figure 2) (4), and **Sphagnaceae** (Figure 70) (4). Most of the taxa are **corticolous** (on bark) and most are of Neotropical distribution (35%). The most common life form is the **mat**.

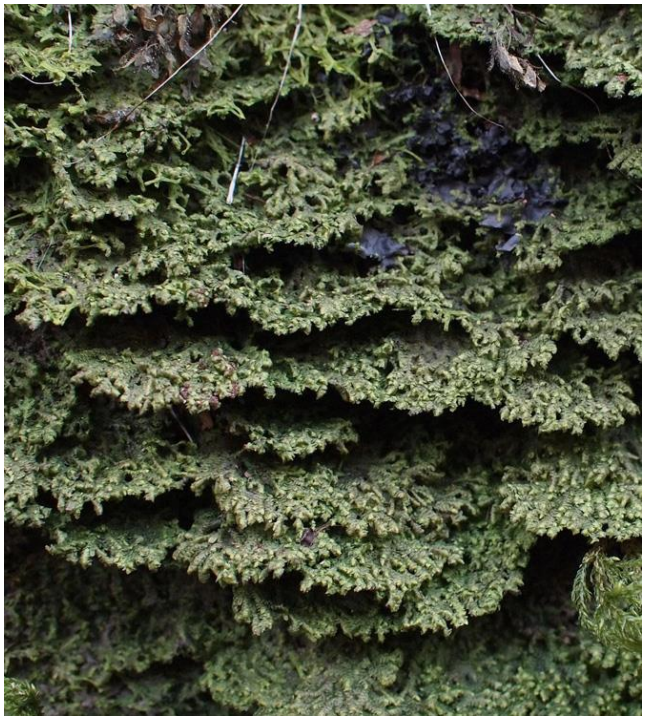

Figure 68. ***Jubula hutchinsiae*** in **Jubulaceae**, one of the families with high species richness in Parque Nacional da Restinga de Jurubatiba, RJ, Brazil. Photo by Stan Phillips, through public domain.

Figure 69. ***Jubula hutchinsiae***, representing the **Jubulaceae**, one of the families with high species richness in Parque Nacional da Restinga de Jurubatiba, RJ, Brazil. Photo by Jonathan Sleath, with permission.

Figure 70. ***Sphagnum*** sp. from the Neotropics, one of the families with high species richness in Parque Nacional da Restinga de Jurubatiba, Brazil. Photo by Michael Lüth, with permission.

In the restingas of Northeastern Brazil, the soils have a low capacity to retain water, a low nutrient content, and a high salt concentration, coupled with occasions of high temperatures (Silva *et al*. 2016). In the seven areas studied, 55 species were identified. These exhibit intermediate desiccation tolerance and occupy corticolous and ground habitats. This number of species is low compared to other Brazilian restingas. The dominant families are **Lejeuneaceae** (Figure 62-Figure 64) (24 spp.), **Fissidentaceae** (Figure 71) (8 spp.), and **Calymperaceae** (Figure 2) (6 spp.). The families **Metzgeriaceae** (Figure 72), **Plagiochilaceae** (Figure 42), and **Radulaceae** (Figure 73) are absent, whereas they are common in the southeastern restingas. Life forms facilitate their success, with high (**tuft** and **cushion**) or intermediate (**mat** and **carpet**) tolerance to desiccation; the former colonize soil or live trunks, and the latter colonize live trunks and/or, more rarely, decaying trunks. Sun-tolerant species are mostly those with intermediate desiccation that colonize live trunks and decayed logs. There are fewer shade-tolerant species and these are represented by ***Fissidens*** spp. (Figure 71), which form tufts and have a terrestrial habitat, and by the **pendent** and corticolous ***Squamidium nigricans*** (Figure 74).

Figure 71. ***Fissidens asplenioides***, a common Neotropical species. Photo by Janice Glime.

Figure 72. ***Metzgeria conjugata*** (**Metzgeriaceae**) British Bryological Society, with permission per Barry Stewart.

Figure 73. ***Radula*** (**Radulaceae**) in the Neotropics. Photo by Michael Lüth, with permission.

Figure 74. ***Squamidium*** sp.; ***S. nigricans*** is a **pendent** moss on bark in the restingas of northeastern Brazil.

Caatinga

This vegetation type of **caatinga** (shrubland; Figure 75) is also known as **campina**, **campinarana**, **chavascal**, and **charravascal** (Pires & Prance 1985). The vegetation grouping grows over leached white sand. This habitat is suitable for forest vegetation, but is limited by the nutrient-poor soil and seasonality of flooding and extreme drought due to the soil (sand) porosity. Diversity is low in a given area, but great variability exists between areas, making the caatingas overall rich in diversity. The caatinga vegetation is **xeromorphic** (having forms adapted to dry habitats). This is exhibited in thick leaves and thick bark. Nevertheless, lichens and mosses are abundant on the branches and soil surface.

Figure 75. Caatinga Biosphere Reserve, Brazil. Photo by Diego Rego Monteiro, through Creative Commons.

When comparing the elevational zones of the **caatinga** (Figure 75) biome in Brazil, Valente *et al*. (2013) found the highest numbers of exclusive bryophyte taxa in the forests and **campos rupestres** (dry, rocky grasslands; Figure 76), accounting for 51% and 40% of the taxa, respectively The caatinga and cerrado (savanna) had only 5% and 4% respectively. The lower and upper montane zones had the highest species richness and numbers of exclusive taxa. The number of disjunct species was significant between Brazil and the Andes.

Figure 76. Campos rupestres, Brazil, showing dry, rocky grassland. Photo by Antonio José Maia Guimarães, through Creative Commons.

The low elevation Amazon caatinga forest (Figure 77) is an evergreen sclerophyllous forest (Klinge & Herrara 1983). It forms small "islands" in the tall Amazon caatinga. These "islands" are surrounded by a 20-m wide band of vegetation with trees over 10 m tall (**tall bana**). This band resembles the vegetation of the **tall Amazon caatinga**. The low Amazon caatinga is known as **bana**. Klinge and Herrera describe it as an evergreen sclerophyllous woodland with bleached quartz sands in the lowlands of southwestern Venezuela. It occurs as small islands within the tall Amazon caatinga. The outer vegetation belt is about 20 m wide with trees over 10 m tall and this is known as the **tall bana**. Its floristic composition is similar to that of the tall Amazon caatinga. The **low bana** has a maximum tree height that is typically less than 5 m. The central part is occupied by **open bana** where trees are even shorter and very widely spaced.

Figure 77. Caatinga in Brazil. Photo by Glauco Umbelino, through Creative Commons.

Bastos *et al*. (2000) found 65 taxa in the campos rupestres at Estado da Bahia, Brazil. Of these, 41 were mosses and 24 genera were liverworts. Six of the moss species were ***Sphagnum*** (Figure 70). Consistent with the argument for the need of more studies, 23 of these species are new records for this state.

The first study of bryophytes in Bahia, Brazil, was as recent as 1998 (Bastos *et al*. 1998). In this initial study in the state of Bahia, only 18 species were discovered, 15 mosses and 3 liverworts. These are mainly generalists and **xerophilous** (preferring dry habitat conditions). However, some **hygrophilous** (preferring moist habitats) species occur here. The generalists are represented by ***Hyophiladelphus agrarius*** (Figure 78-Figure 79), ***Hyophila involuta*** (Figure 80-Figure 81), ***Calymperes palisotii*** subsp. ***richardii*** (Figure 82), ***Bryum argenteum*** (Figure 83), ***Entodontopsis leucostega*** (see Figure 84), ***Octoblepharum albidum*** (Figure 3), ***Frullania ericoides*** (Figure 85). ***Helicophyllum torquatum*** (Figure 86-Figure 87) and ***Riccia vitalii*** (Figure 88) and others are restricted to this type of vegetation. Unlike most of the epiphytic flora, most of these species are erect, acrocarpous species with **short turf** life forms. The leafy liverworts present are **incubous** (leaves overlap from base of stem to tip like shingles of a roof from peak to edge).

Figure 80. ***Hyophila involuta*** drying, a xerophilous generalist that occurs in Bahia, Brazil. Photo by Bob Klips, with permission.

Figure 78. ***Hyophiladelphus agrarius***, a xerophilous generalist in Bahia, Brazil. Photo by Frederick B. Essig, with permission.

Figure 81. ***Hyophila involuta*** with capsules. Photo by Michael Lüth, with permission.

Figure 79. ***Hyophiladelphus agrarius*** dry, with capsules. Photo by Frederick B. Essig, with permission.

Figure 82. ***Calymperes palisotii***, a xerophilous generalist that occurs in Bahia, Brazil. Photo by Jan-Peter Frahm, with permission.

Figure 83. ***Bryum argenteum***, a xerophilous generalist that occurs in Bahia, Brazil. Photo by Michael Lüth, with permission.

Figure 84. ***Entodontopsis nitens***; ***Entodontopsis leucostega*** is a generalist in Brazil. Photo from Wilding *et al*. 2016, with permission.

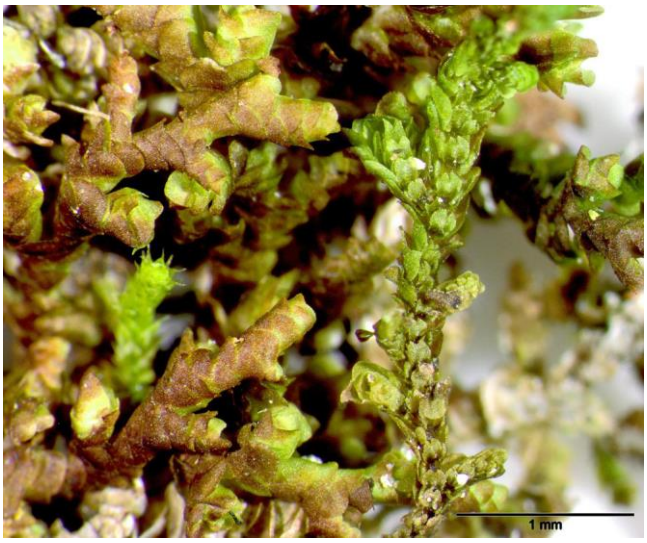

Figure 85. ***Frullania ericoides***, a xerophilous generalist that occurs in Bahia, Brazil. Photo by Blanka Aguero, with permission.

Figure 86. ***Helicophyllum torquatum*** growing on a rock in tropical Mexico. Photo courtesy of Claudio Delgadillo

Figure 87. ***Helicophyllum torquatum***, a xerophilous generalist that occurs in Bahia, Brazil. Photo by George Shepherd, through Creative Commons.

Figure 88. ***Riccia vitalii***, a xerophilous generalist that occurs in Bahia, Brazil. Photo courtesy of Tatiany Oliveira da Silva.

Silva and Pôrto (2016) used mosses to determine if stem growth can be used to indicate changes in local climate change in the caatinga. But the gametophyte length is highly variable in the test moss, ***Campylopus pilifer***. They concluded that stem length in this species is a poor indicator of local conditions in harsh environments. On the other hand, soil islands seemed to account for longer stems than typical values for this species.

Savannah Vegetation

Non-forested vegetation in Amazonian Brazil is also known as **campo** (Pires & Prance 1985). These savannahs may have trees or be treeless and are dominated by grasses. The savannahs on terra firme occupy 3-4% of Brazilian Amazonia. The littoral savannahs occur on coastal areas and have frequent lakes. The most common grass is *Paratheria prostrata* (Figure 89). **Roraima savannahs** (Figure 90) are usually open with few trees. **Campos rupestres** (Figure 76) are open formations on rocks and are often confused with open savannahs. These formations suffer drought and are unable to retain water. Lichens are common on the rocks.

Some savannahs are inundated. These are created where sediments are deposited by muddy rivers. Grasses colonize these areas as the rivers recede.

Figure 89. ***Paratheria prostrata***, the most common grass in the littoral savannahs. Photo by Ehoarn Bidault, through Creative Commons.

Figure 90. Roraima savannah in Gran Sabana, Venezuela. Photo by Paolo Costa Baldi, through Creative Commons.

South Atlantic Islands

The most recent studies describe the small Brazilian islands in the South Atlantic, Fernando de Noronha and Trinidade (Câmara & Carvalho-Silva 2018; Costa *et al*. 2018). Noronha is primarily a caatinga vegetation, but presents some interesting differences in species composition (Costa *et al*. 2018). Like the island of Trindade, there is a lack of endemism on Fernando de Noronha, compared to St. Helena (29 of 110 species), Tristan da Cunha (18 of 160 species), and Ascension (16 of 87 species). Nevertheless, ***Riccia ridleyi***, which occurred at just one location, is critically endangered, but during the rainy season, extensive populations can appear (Pereira & Câmara 2015). ***Fissidens*** (Figure 91-Figure 93) is the most species-rich genus with 12 species. On the other hand, the only member of the **Lejeuneaceae** present is ***Lejeunea laetevirens*** (Figure 94)! On Trinidade, there are 11 species of **Lejeuneaceae**, with a total of 33 bryophyte species. Fernando de Noronha also has more species of mosses (23) compared to liverworts (3) (Costa *et al*. 2018), whereas Trinidade has more liverworts (20) compared to mosses (12). Fernando de Noronha island has **Notothyladaceae** (Figure 95), **Ricciaceae** (Figure 88), **Bryaceae** (Figure 96), **Dicranaceae** (***Dicranella varia***; Figure 97), **Fissidentaceae** (Figure 91-Figure 93), **Pottiaceae** (Figure 79), **Splachnobryaceae** (***Splachnobryum obtusum***; Figure 98), with very low numbers of corticolous species [***Calymperes palisotii*** (Figure 82), ***Frullania ericoides*** (Figure 85), and ***Lejeunea laetevirens***]. Many (39%) of the species on this island have worldwide distribution, including ***Bryum coronatum*** (Figure 96), ***Entodontopsis leucostega*** (see Figure 84; the only pleurocarpous moss on the island), and ***Hyophiladelphus agrarius*** (Figure 79). But be careful what you do to preserve species. It is only on a disturbed site with engineering activity that one can find new populations of ***Notothylas*** (Figure 95), ***Fissidens*** spp. (*e.g.* Figure 91-Figure 93), and ***Philonotis cernua*** (see Figure 99), with the most extensive populations of ***Notothylas*** occurring there.

Figure 91. ***Fissidens bryoides***, a widespread species and one of the 12 species in this genus on Fernando de Noronha. Photo by Dick Haaksma, with permission.

Figure 92. ***Fissidens crispus***, a pantropical species and one of the 12 species in this genus on Fernando de Noronha. Photo by Michael Lüth, with permission.

Figure 93. ***Fissidens curvatus***, a Neotropical species and one of the 12 species in this genus on Fernando de Noronha. Photo by Des Callaghan, with permission.

Figure 94. ***Lejeunea laetivirens***, the only member of **Lejeuneaceae** present on Fernando de Noronha in the South Atlantic. Photo by Scott Zona, through Creative Commons.

Figure 95. ***Notothylas orbicularis***, a species that does well on disturbed habitats on Fernando de Noronha. Photo by Štěpán Koval, with permission.

Figure 96. ***Bryum coronatum***, a widespread species that occurs on Fernando de Noronha. Photo by Paul Siri Wilson, with permission.

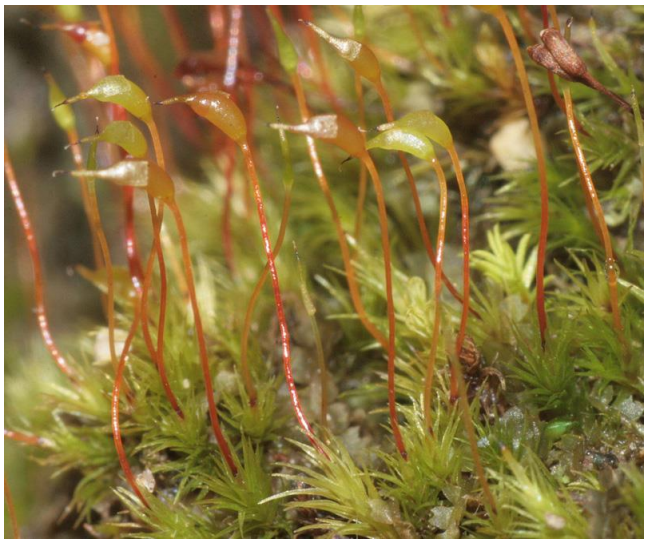

Figure 97. ***Dicranella varia*** with capsules, a widespread species that occurs on Fernando de Noronha. Photo by Hermann Schachner, through Creative Commons.

Figure 98. ***Splachnobryum obtusum***, a widespread species in the **Splachnobryaceae** and present on Fernando de Noronha. Photo from BBS website, with permission from Barry Stewart.

Figure 99. ***Philonotis*** sp. from the Neotropics; ***Philonotis cernua*** occurs on disturbed sites on Fernando de Noronha. Photo by Michael Lüth, with permission.

Summary

Many names are used for lowland rainforests and Amazon rainforests. Some are local names, whereas others are general. Terra (tierra) firme refers to the dryland habitats, thus not including mangroves and other wetlands. It includes dense forest, open forest without palms, open forest with palms, liana forest, dry forest, restinga, caatinga, and savannah, with classification based primarily on topography.

High light intensity and high temperatures limit the bryophyte vegetation in parts of terra firme, but it includes some members of the moss families **Calymperaceae**, **Leucobryaceae**, **Leucodontaceae**, **Plagiotheciaceae**, and **Sematophyllaceae**, and liverwort families **Frullaniaceae**, **Lepidoziaceae**, **Lejeuneaceae**, **Odontoschismaceae** (currently included in **Cephaloziaceae**), **Plagiochilaceae**, **Radulaceae**, and **Zoopsidaceae** (currently included in **Lepidoziaceae**). Logs are an important substrate on terra firme. Otherwise, the most common bryophyte families on terra firme are **Lejeuneaceae**, along with mosses **Calymperaceae**, **Leucobryaceae**, and **Sematophyllaceae**. Other important families are **Calypogeiaceae** and **Lepidoziaceae**, both leafy liverworts. In the drier restinga, the **Lejeuneaceae** predominates among the liverworts, with ***Bryum argenteum*** and ***Campylopus pilifer*** among the mosses. In the caatinga, erect generalist, acrocarpous species forming s**hort turfs** are the most common.

In places with a protracted dry season, like the South Atlantic Islands, **Ricciaceae** are common, going dormant and all but disappearing in the dry season.

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My appreciation goes to Noris Salazar Allen for her efforts to make this chapter reliable and up-to-date. Her helpful discussions kept me going on this part of the world I know so little about. Tatiany Oliveira da Silva was a tremendous help on this subchapter, providing me with references and constructive feedback and helping me to understand the various habitats. S. Robbert Gradstein was invaluable in providing me with papers, images, and constructive criticism.

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CHAPTER 8-8
TROPICS: ELEVATION

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CHAPTER 8-8
TROPICS: ELEVATION

Figure 1. Elevational vegetation differences at Tangkoko National Park, North Sulawesi, Indonesia. Photo by Lip Kee Yap, through Creative Commons.

Elevation

First, a definition. Merriam-Webster defines elevation as "the vertical elevation of an object above a surface (such as sea level or land) of a planet."

Although most of us use altitude and elevation interchangeably, for clarity in science we need to be precise and consistent. In fact, in Italian, they have the opposite meanings from usage in English. Hence, I shall try to use them based on the publication in Oecologia by McVicar and Körner (2013). "**Elevation** is the vertical distance between a point on the land surface and a reference point, usually taken to be the mean sea level. **Altitude** is the vertical distance between an object (e.g., a bird, aircraft, or parcel of air) and a reference point or stratum, where the object is not in direct contact with the reference point/stratum. The reference point/stratum is usually either the mean sea level (e.g., as often used by commercial airlines) or the land surface (at whatever elevation), which is often used when describing the altitude of a parcel of air, for example. **Height** is the vertical distance between (usually) the top of an object (e.g., a tree, building, person, or Stevenson screen) and the land surface, where the object is in direct contact with the ground. It is therefore a measure of how far something vertically protrudes above the land surface."

The changes with elevation are multifold (Figure 1, leading to various hypotheses on the identity of the controlling factors for vegetation. These differences include distinct elevational thermal zones, differences in floristic composition and functional forms with both elevation and windward versus leeward slopes, differences in seasonal monsoon wind systems, and isolation of montane forests that cause them to behave like islands (Ohsawa 1995). In addition to these, we will soon see that available moisture is a significant factor. Troll (1948) diagrammed the vegetation zones as they relate to latitude and elevation (Figure 2).

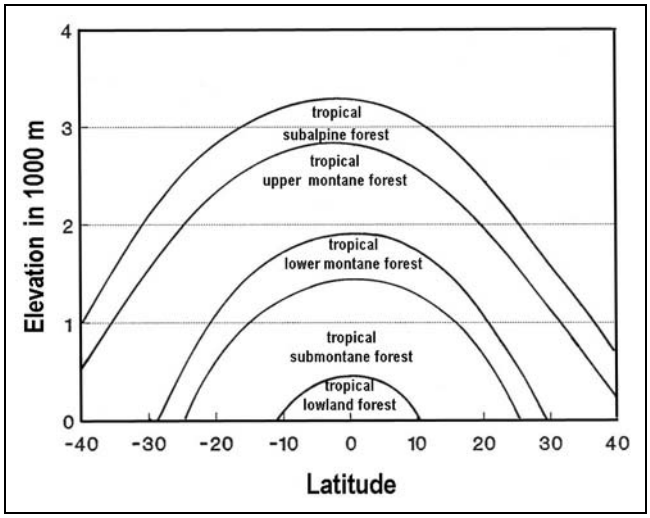

Figure 2. Elevation vs. latitude of vegetational zones. Modified from Troll 1948.

Santos *et al*. (2014) considered the possibility of using liverworts to indicate elevational zonation in the Brazilian Atlantic Forest. Among those species found, 34 appeared to be good indicators of the Atlantic Forest groups. Among the 26 localities in the study, the **beta diversity** [ratio between gamma (regional) and alpha (local) diversities, *i.e.* effective number of distinct compositional units in the region] shows a deterministic distribution along the Atlantic coast in southeastern Brazil. Elevation has a significant role in determining the species, with five floristic groups emerging. The important variables are elevation, temperature, and precipitation. But in regions such as oceanic islands and coastal mountains, geographic distance is important.

Santos *et al*. (2017) used a short elevational gradient from 10 m to 1170 m asl in southeastern Brazil to assess changes in bryophyte communities. Using six elevational belts, they sampled ten 10 x 10 m subplots located randomly in a 1-ha forest plot at each elevation in the survey. This revealed 253 species. Richness did not vary significantly with elevation and floristic similarities among the elevations were all greater than 50% except the mountaintop forest, which had a similarity of less than 35%. **Endemism** (ecological state of species being unique to defined geographic location) increased with elevation and amplitudes of the phytogeographical patterns of species decreased as the elevation increased. It is interesting that **dioicous** (sexes on separate plants) species predominated in all elevations sampled and that the smallest dioicous:monoicous ratio was at mid elevations.

At an early date, Seifriz (1924) showed differences in elevational distributions of mosses on Mt. Gedeh, Java (Figure 3). Frahm *et al*. (2003) contended that bryophytes were good indicators of elevational zones in rainforests. Based on the reaction of bryophytes to climatic factors, Frahm and coworkers considered the bryophytes to be especially good as indicators of climatic changes. In the tropical rainforests, they have several advantages over flowering plants. The bryophytes are less numerous, have considerably fewer species worldwide, with no more than 5000 species in the Neotropics. Many of the species occur throughout the Neotropics. Recent studies verify the latitudinal diversity gradient in liverworts and hornworts (Figure 4) (Wang *et al*. 2016).

Figure 3. Mount Gede, Java. Photo by Afrogindahood, through Creative Commons.

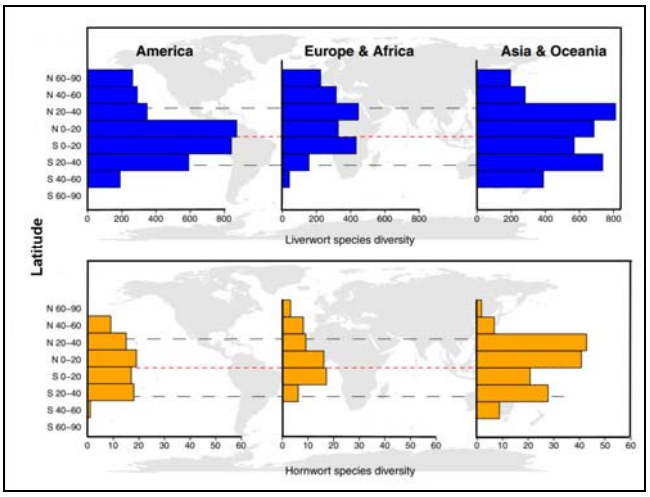

Figure 4. Latitudinal distribution of liverwort and hornwort species richness. Modified from Wang *et al*. (2016).

We find that at greater latitudes the bryophyte communities become more like those at greater elevations near the Equator (Gradstein & Pócs 1989). Comparing high mountains in Colombia, Peru, Borneo, and Papua New Guinea, Gradstein and Frahm (Gradstein & Frahm 1987; Frahm 1990c, d; Frahm & Gradstein 1991) identified similar elevational zonations of bryophytes indicating **lowland forest** (Figure 5), **submontane forest**, **upper lower montane forest**, **montane forest** (Figure 6), and **subalpine forest**. These zones seem to be correlated primarily with climate (precipitation, air temperature), rather than with substrate (van Reenen & Gradstein 1983). Bryophyte diversity and abundance both increase from lowlands to montane regions (Figure 7) (van Reenen & Gradstein 1983; Gradstein & Pócs 1989; Frahm 1990b). A similar pattern occurs in Madagascar (Figure 8) (Lewis *et al*. 1996) and Brazil (Pôrto 1992), with an increase in bryophyte and lichen cover and diversity as elevation increases. The distribution patterns of bryophytes through the elevational zones of the humid tropics mimics that of the ferns, which similarly have their highest species numbers in the lower montane forests (Kessler 2000 – Andes, Bolivia & Colombia; Hemp 2002 – Mt. Kilimanjaro, Tanzania).

Figure 5. Lowland rainforest, Rio Dantas, Costa Rico. Photo by Natox, through Creative Commons.

Figure 6. Montane and upper montane forests, Parque Nacional de Itatiaiae, Brazil. Photo by Gabriel R. Vallim.

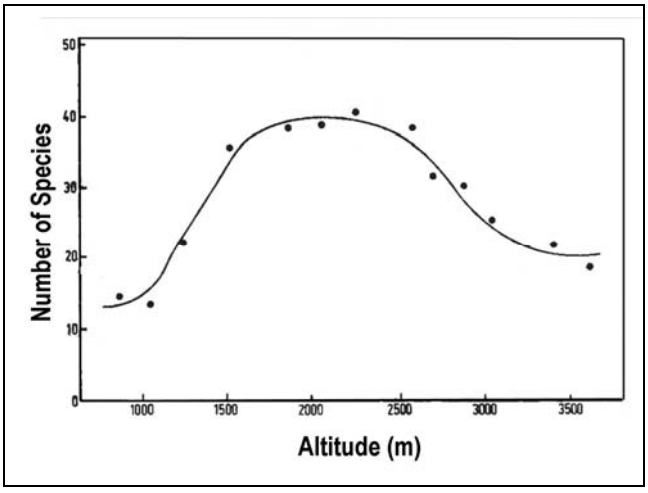

Figure 7. Species curve along an elevational transect in Colombia. Modified from van Reenen & Gradstein 1983.

Figure 8. Mountains of Tsingy de Bemaraha, Madagascar. Photo from Travel Tuesdays to Madagascar, through Creative Commons.

Another important observation for the tropical distributions of species with elevation is that for most species the habitat preferences are comparable to those at higher latitudes (Gradstein & Vána 1987). Nevertheless, some occupy quite different habitats in the tropics, such as ***Diplophyllum obtusatum*** (Figure 9), ***Solenostoma sphaerocarpum*** (Figure 10), and ***Schistochilopsis incisa*** (Figure 11). Whereas these may be found in pristine habitats at higher latitudes, they are colonizers of man-made habitats in the tropics. Some species that are especially common (and typically have relatively wide niches and/or distributions) extend from tropical elevations to northern habitats. From peat bogs, ***Sphagnum magellanicum*** (Figure 12) and ***S. cuspidatum*** (Figure 13) fit this description. Rock outcrops in both latitudinal and elevational extremes can have ***Racomitrium lanuginosum*** (Figure 14) and ***Andreaea rupestris*** (Figure 15) as well as ***Racomitrium crispulum*** (Figure 16) and ***Rhacocarpus purpurascens*** (Figure 17) from southern latitudes. Mires typically have ***Calliergonella cuspidata*** (Figure 18), and ***Scorpidium scorpioides*** (Figure 19), whereas less boggy ground may have ***Pleurozium schreberi*** (Figure 20). Tropical roadsides often have ***Schistochilopsis incisa*** and ***Solenostoma sphaerocarpum***. On periodically submerged rocks one can find the ubiquitous ***Platyhypnidium riparioides*** (Figure 21), ***Brachythecium plumosum*** (Figure 22), and ***Schistidium rivulare*** (Figure 23), along with the southern latitude ***Clasmatocolea vermicularis*** (Figure 24) and ***Cryptochila grandiflora*** (Figure 25).

Figure 9. ***Diplophyllum obtusatum***, a species that occurs in the tropics as well as at higher latitudes, but with a different habitat. Photo by Paul Davison, with permission.

Figure 10. ***Solenostoma sphaerocarpa***, a species that occurs in the tropics as well as at higher latitudes, but with a different habitat. Photo by Michael Lüth, with permission.

Figure 11. ***Schistochilopsis incisa***, a species that occurs in the tropics as well as at higher latitudes, but with a different habitat. Photo by Michael Lüth, with permission.

Figure 12. ***Sphagnum magellanicum***, a species that occurs in the tropics as well as at higher latitudes, in bogs and poor fens. Photo by Michael Lüth, with permission.

Figure 13. ***Sphagnum cuspidatum***, a species that occurs in the tropics as well as at higher latitudes, in bogs and poor fens. Photo by Michael Lüth, with permission.

Figure 14. ***Racomitrium lanuginosum***, a species that occurs on rock outcrops in both latitudinal extremes, as well as the tropics. Photo by Janice Glime.

Figure 15. ***Andreaea rupestris***, a species that occurs on rock outcrops in both latitudinal extremes, as well as the tropics. Photo by Michael Lüth, with permission.

Figure 16. ***Racomitrium crispulum***, a species that occurs on rock outcrops in both latitudinal extremes, as well as the tropics. Photo by Jan-Peter Frahm, with permission.

Figure 17. ***Rhacocarpus purpurascens***, a species that occurs on rock outcrops in both latitudinal extremes, as well as the tropics. Photo by Michael Lüth, with permission.

Figure 18. ***Calliergonella cuspidata***, a typical mire species that occurs at high latitudes as well as the tropics. Photo by Des Callaghan, with permission.

Figure 19. ***Scorpidium scorpioides***, a typical mire species that occurs at high latitudes as well as the tropics. Photo by Janice Glime.

Figure 20. ***Pleurozium schreberi***, a typical mire species that occurs at high latitudes as well as the tropics and elsewhere. Photo by Janice Glime.

Figure 21. ***Platyhypnidium riparioides***, a rock-dwelling species that is periodically submerged in both high latitudes and the tropics. Photo by Michael Lüth, with permission.

Figure 22. ***Brachythecium plumosum***, a rock-dwelling species that is periodically submerged in both high latitudes and the tropics. Photo by Michael Lüth, with permission.

Figure 23. ***Schistidium rivulare*** with capsules, a rock-dwelling species that is periodically submerged in both high latitudes and the tropics. Photo by Michael Lüth, with permission.

Figure 24. ***Clasmatocolea vermicularis***, a rock-dwelling species that is periodically submerged in both high southern latitudes and the tropics. Photo by John Engel, through Creative Commons.

Figure 25. ***Cryptochila grandiflora***, a rock-dwelling species that is periodically submerged in both high southern latitudes and the tropics. Photo by Felipe Osorio-Zúñiga, with permission.

Ah-Peng *et al*. (2007) demonstrated elevational gradients in bryophyte diversity on a 19-year-old lava flow in La Réunion. Because the lava flow is a uniform substrate, it provides an ideal opportunity for studying elevational effects without interference by substrate differences. Using quadrats in the range of 250-850 m asl, they determined that diversity increases with elevation, a pattern that occurs in many studies cited in this chapter. Nevertheless, a variety of available host plants seems to be important in fostering diversity (70 species) of epiphytic bryophytes on the lava flow.

In the Andes of Peru and Colombia, Kessler (2000) found floristically discrete communities that corresponded with elevational belts. He found that the floristic boundaries related to strong changes in **orography** (topographic relief of hills and mountains). These included the transition from the hilly lowland to the steep mountains, a co-occurring change in geological substrate at 400 m, a strong humidity gradient at 1,000 m on the Bolivian transect and at 1,250-1,980 on the Colombian transect, and the transition from mixed cloud forests to forests

dominated by ***Polylepis*** (**Rosaceae**; Figure 26) or ***Podocarpus*** (a broad-leafed evergreen conifer; Figure 27). In relatively species-poor forest communities, the presence or absence of a few tree species influences the whole ecosystem. By contrast, in species-rich communities such as the forests at low to mid elevations, the elevational belts are ill-defined.

Figure 26. ***Polylepis tarapacana***, a dominant tree in the cloud forest in Colombia. Photo by Rodrisan, through Creative Commons.

Figure 27. ***Podocarpus***, a broad-leaved evergreen conifer in the mixed cloud forests of Colombia. Photo by Koppchen, through Creative Commons.

In 2017, von Konrat stated that his study of elevational bryophyte communities in the Fiji Islands was the first of its kind for Fiji. Von Konrat assessed presence/absence on the lower stems of the ***Calophyllum*** spp. (Figure 28) trees and on tree ferns at three elevations (~160 m, 590 m, and 1,260 m). Unlike the Uganda study of Tusiime *et al*. (2007 – see below), this one revealed a hump-shaped diversity distribution (Figure 7), with the greatest species richness in the mid elevation or upland forest. Liverworts dominated at all three elevations. The bryophyte communities were distinctly different at both the host tree level and among the three elevations.

Figure 28. ***Calophyllum brasiliense***, a bryophyte host in the Fiji Islands. Photo by Mauro Halpern, through public domain.

Churchill *et al*. (1995) reported a moss diversity for the tropical Andes of 2,058 species comprised of 343 genera and 75 families. However, they considered that once the systematics are understood, and superfluous species are reduced to synonymy, this number is likely to drop to 1,500-1,700. The tropical Andes have a moss flora that is approximately eight times as rich in species as that of the Amazon basin. While **α diversity** (site diversity) may be similar, **β diversity** (differences in species composition among sites) and **γ diversity** (landscape diversity) in the Andes are much greater. These differences are largely due to **orographic** factors (relating to mountains, especially regarding position and form) (see also Pócs 1976). Nevertheless, the mosses do not seem to follow the latitudinal species gradient shown by other species groups. That is, there is no increase in number of species from the poles to the equator.

Despite these high numbers, one habitat had typically been overlooked in the early studies: the canopy. Particularly in the lowland rainforest, the canopy (Figure 29) houses a rich diversity with many species that are unique to the high canopy (Gradstein *et al*. 1990). In fact, these canopies can house more than 50% of the local species, as discussed in the sub-chapter on epiphytes.

Figure 29. Lowland rainforest tree, Colombian Amazon. Photo by Laura Campos, through Robbert Gradstein.

Campylopus pilifer (Figure 30) is broadly distributed and drought-tolerant and is found at high elevations in the tropics (Gradstein & Sipman 1978; Stech & Wagner 2005).

Figure 30. ***Campylopus pilifer*** (**Dicranaceae**), a broadly distributed species that occurs at high elevations in the tropics. Photo by Michael Lüth, with permission.

Westerners tend to think of Africa as the land of elephants and camels. But Africa has a remarkable topography and wide diversity of habitats. Tusiime *et al*. (2007) compared species richness among the habitats along an elevational range as well as along streamsides and trails in the forests of Bwindi Impenetrable National Park, Uganda, using 1000-m transects with 1x1 m quadrats at 50 m intervals. In contrast with some of the Neotropical studies, richness of bryophyte species was negatively correlated with elevation. The exception to this was the thalloid liverworts, which increased with elevation. Streamside diversity was the highest, compared to that along trails. The evergreen forest had the greatest bryophyte richness, followed by the mature mixed and bamboo forests.

Additional studies discuss the effects of elevation on the bryophyte vegetation. Hedberg (1951) examined bryophytes in vegetation belts in the East African mountains and Pócs (1984) on Kilimanjaro. Bryant *et al*. (1973) demonstrated habitat differences among liverworts in ten areas of the Luquillo Mountains of Puerto Rico. Van Reenen and Gradstein (1983, 1984) investigated distribution and ecology on an elevational gradient in the Andes and on the Sierra Nevada de Santa Marta of Colombia; van Reenen (1987) reported on elevational zonation. Wolf (1989) reported on abundance of epiphytic communities along an elevational transect in the Cordillera Central, Colombia.

In some cases, soils may play a role in determining differences in bryophyte communities. Grieve *et al*. (1990) compared soils in six primary forest plots at 100 m, 500 m, 1,000 m, 1,500 m, 2,000 m, and 2,600 m asl on Volcán Barva, Costa Rica. As elevation increased, there was less evidence of intensity of weathering and organic matter decomposition. Simultaneously, subsoil clay content decreased from 80% at 100 m to less than 10% at 2000 m. Other soil factors likewise changed, with the ratio of free to total iron decreasing while surface organic matter increased. In fact, most nutrients at high elevations did not seem to be less than at low elevations.

On Mt. Kinabalu and the Himalaya of Bhutan, Ashton (2003) considered the floristic relationships to be complicated. He observed that the elevational level at which changes occur has only minor differences between the Equator and the tropical area. Rather, Ashton concluded that soil changes may play a more direct and important role than previously considered. The important soil factors are the increase in organic content in lower montane soils when compared to those of the lowland. This is accompanied by a change from termite-dominance to earthworm-dominance and frequency of dense moss layers and mor humus in the upper montane soils. But the question remains, do these soil differences make any differences in the composition of bryophyte communities?

Defining Zones

Enroth (1990) recognized five elevational zones in Papua New Guinea: 0-300 m, 300-1,200 m, 1,200-2,200(-2,300) m, 2,200(-2,300)-2,800(-2,900) m, and 2,800(-2,900)-3400 m asl. These zones are recognized by their distinct changes in the bryophyte flora. These zones also correspond well with previous studies on seed-plant flora. At the highest elevations, species from the Northern Hemisphere occur. The high elevations generally have New Guinean or Western Melanesian and Malesian endemics. At low to moderate elevations, the flora is representative of Asian-Oceanian and Asian-Oceanian-Australian taxa, particularly among the mosses.

Cosmopolitan species have either wide vertical ranges or occur only at high elevations.

Van Reenen and Gradstein (1983) recognized five elevational bryophyte zones in the Sierra Nevadas of Colombia in the range of 500-4,100 m asl. Four zones are forest zones and one is **páramo** (high treeless plateau). They based their classification of these zones on relevés that included species presence, substrate preference, and percentage cover of bryophytes. The zones are correlated with precipitation and air temperature. Species presence and percent cover seem to be of equal importance in distinguishing the bryophyte zones in the forests. These are highest in the **condensation zones** (zones where water vapor in atmosphere condenses and becomes liquid).

Frahm and Gradstein (1991) examined the cover, biomass, and turnover rates of bryophytes in rainforests of Colombia, Peru, Borneo, and Papua New Guinea. From these, they concluded that elevational zonation is similar in different parts of the humid tropics.

In Hawaii, Kitayama and Mueller-Dumbois (1992) studied the community organization on the windward slope of Haleakala. On a transect from 350 m asl to the summit at 3,055 m asl they used a Braun-Blanquet approach to record species. They found hierarchical arrangements that were correlated with elevation. The low to mid-elevational climate is wet, changing abruptly to an arid high-elevation climate. This climatic distinction created three broad zones with elevation: lowland, montane, and high-elevation zones. Further distinctions partitioned these into seven plant communities, six based on elevation and one dieback zone.

Zone Limitations

In Ecuador, the montane and lowland rainforests both have a cooler, wetter season from April to July (Grubb & Whitmore 1966). The montane site has fog-bound and fog-free days. On the fog-free days, sunshine may be present for a prolonged period. These sunny periods are longest in the dry season, lasting 1-2 weeks. On fog-bound days, there is little diel (within a period of 24 hours) temperature change and the relative humidity typically remains at 95% or higher. On fog-free days, the temperature range and minimum relative humidity are similar to those on an average day in the lowland forest. These fog conditions are absent in the lowland rainforest. Nevertheless, on the fog-bound days in the montane forests, the conditions are similar to those of the lowland forests in the wet season. The forest types correlate with the frequency of fog, not the temperature regime. The success and greater abundance of epiphytes in the montane forest compared to the lowland forest seems to result from the frequency of wetting by fog, not to a constantly higher humidity.

On a worldwide basis, Ashton (2003) is right; the causes of zonation with elevation are complicated. In Costa Rica, Kluge *et al*. (2006) studied the pteridophyte richness at 10-2800 m asl and at 2,700-3,400 m on the Atlantic slope of Costa Rica. They analyzed species richness in 156 plots of 20x20 m. They regressed species richness against temperature, humidity, precipitation, and actual evapotranspiration. As in many other studies, the species richness distribution of the 484 species was a hump-shaped one (Figure 7) typical of many elevational distributions in the tropics. And as is typical, it peaked at the mid-elevations. Nonetheless, the distribution correlated with the climatic variables of humidity and temperature. The mid-elevations have the highest humidity and offer moderate temperatures; high elevations have a reduced richness that the researchers attribute to the low temperatures. At low elevations, reduced water availability, coupled with high temperatures, reduce the species richness.

Low elevation bryophytes are limited by high temperatures and low light intensity (Richards 1984a; Frahm 1990a). In fact, the light intensity barely exceeds the **light compensation point** (intensity at which CO_2 lost by respiration = that fixed by photosynthesis). By contrast, montane bryophytes experience low temperatures and higher light intensities, with nearly horizontal rainfall and constant humidity, providing "suitable" conditions for a rich bryophyte flora (Pócs 1982; Richards 1984a; Stadtmüller 1987). The characteristics of the host plant for the predominantly epiphytic flora seem to be of minor importance.

Traditional assumptions have been that temperature, light intensity, and water availability determine the distribution of tropical bryophytes. Chantanaorrapint (2010) determined that in a slightly disturbed tropical forest in Thailand (Figure 31), it was a complex set of factors that affected the distributions of the epiphytic bryophytes. These related to these same elevational gradient factors of light intensity, air temperatures, and relative humidity working together.

Figure 31. Thailand rainforest. Photo courtesy of Ochin Nuchitprasitchai.

Kürschner (1995) demonstrated a strong correlation between known elevational zonation, forest zones, and plant sociological units in the tropics of the Democratic Republic of Congo and Rwanda (Figure 32). Because of their broad geographic distribution, relatively small number of species (compared to seed plants), sensitivity to climate, and prominence in tropical rainforests, bryophytes are good indicators of the elevational zonation pattern that is characteristic of the humid tropics.

There are a number of changes in the environment from lowland to montane, and these may work in consort, as noted by Chantanaorrapint (2010), to provide more favorable habitats in the mountains. Richards (1984b) suggested that lowland temperatures are too hot for most

bryophytes. We can expect that these C_3 plants generally have their photosynthetic optimum around 20°C; mean annual temperatures in the montane rainforests are generally 10-20°C (Gradstein & Pócs 1989). As already noted, Frahm (1990b) found that the rate of net assimilation of tropical montane bryophytes decreases radically above 25°C. Biebl (1964) showed that most of the bryophytes of the montane forest at El Yunque, Puerto Rico, could not survive at temperatures above 35°C. Light intensity in the lowlands is low, respiration (including photorespiration) is high, and moisture is often limiting, making it difficult for lowland bryophytes to assimilate more by photosynthesis than they lose to respiration. In fact, Frahm (1987) experimented in the laboratory with montane rainforest bryophytes from Peru and demonstrated just that – they cannot photosynthesize enough under the conditions of the tropical lowland rainforest. In such lowlands, one is most likely to find pantropical families such as **Calymperaceae** (Figure 134), **Hookeriaceae** (Figure 33), and **Lejeuneaceae** (Figure 76-Figure 94) (Gradstein & Pócs 1989).

Figure 32. Mount Mikeno, DR Congo, and Mount Karisimbi, Rwanda. Photo by Abel Kavanagh, through Creative Commons.

Figure 33. ***Hookeria acutifolia*** (**Hookeriaceae**); **Hookeriaceae** is a pantropical family found in Peruvian lowlands. Photo by John Game, through Creative Commons.

These dry conditions of the lowlands, however, do not persist throughout the other climatic zones of the tropics. In the lower montane rainforest in Panama (Figure 34), the daily water content of liverwort thalli is pronounced, and both the low and the high water content place considerable limitation on the CO_2 exchange (Zotz *et al*. 1997). However, between those values is a range where a net carbon gain is possible. Even so, half of the mean daytime carbon gain is lost during the night due to respiration at the relatively high temperatures. Enough carbon is stored and not subsequently released to account for a net annual gain of approximately 45% of the initial carbon content of the thallus.

Figure 34. Panamanian montane forests. Photo by S. B. Matherson, through Creative Commons.

Additional studies include those by Grubb (1974) on the factors that control the distribution of forest types on tropical mountains in Malesia. Frahm (1990c) examined the elevational zonation of bryophytes on Mt. Kinabalu, Malaysia.

Transplant Studies

Experimental studies are few, but can provide a clearer picture of elevational relationships. Stam *et al*. (2017) transplanted 558 pendent epiphytes in the Afromontane forests of Taita Hills, Kenya (Figure 35). Several of the four pendent mosses grew very well in the upper montane forest where it was cool and humid, more than doubling their biomass in the year of study. By contrast, all of the transplanted mosses performed poorly in the humidity, heat, and low light of the lower canopy in the dense lower montane forests.

Latitude vs Elevation

Delgadillo and Cardenas (1989) found that the highlands in the Chiapas of Mexico have moss floras similar to those of temperate regions. Truly tropical taxa are mostly confined to the lowland moist sites. The Meso-American species and species with wide distributions are the most numerous in species.

Churchill (1991) suggested that latitude does not play a major role in distinguishing moss diversity from high to low latitudes in the temperate and tropical regions. Rather, in Colombia (Figure 36), bryophyte species richness increases with elevation up to treeline (Figure 37). It is on

the high mountains that the tropical bryophytes reach their zenith in diversity. A similar curve is seen for Yunnan, China (Figure 38) (Song *et al*. 2015). The hump shape (Figure 37-Figure 38) is typical of the diversity distribution.

Figure 35. Taita Mountains, Kenya. Photo by Ina96, through Creative Commons.

Figure 36. Páramo in Colombia, showing vegetation above treeline. Photo by Friedrich Kircher, through Creative Commons.

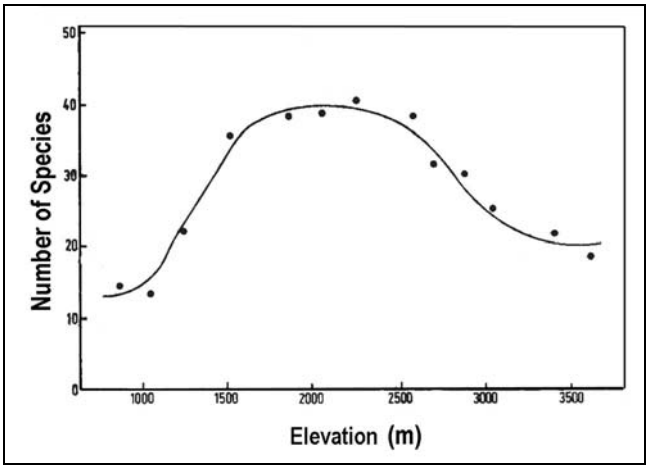

Figure 37. Species-elevation curve in Colombia. Modified from van Reenen & Gradstein 1983.

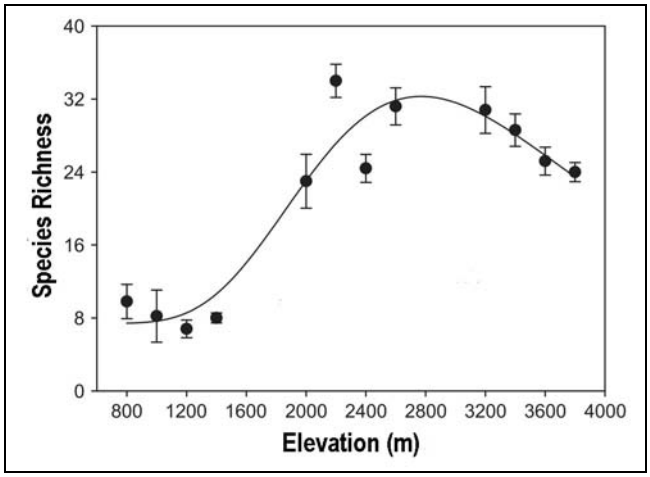

Figure 38. Mean (±SE) species richness for bole bryophytic epiphytes along elevational gradients in Yunnan, China. Modified from Song *et al*. 2015.

Churchill (1991) reported that ~93% of total species richness for mosses (900 spp.) in Colombia occurs within the 20-25% of land surface occupied by the Andes. Within that area, ~50% of diversity occurs at 2,600-3,300 m asl, the high montane zone. Among tropical bryophyte families, 60% are primarily montane while less than 5% are primarily lowland taxa. Freiberg and Freiberg (2000) also found higher bryophyte biomass in the montane zone of Ecuador (Figure 39) compared to the lowland forests, with a corresponding increase in dead organic matter. Similarly, in the Andes of Colombia (Figure 40), montane areas may produce at least ten times the epiphytic bryophyte biomass of lowland forests (van Reenen & Gradstein 1983). Frahm (1987) obtained similar biomass relationships in Peru (Figure 41). Lowlands and submontane regions also are deprived of endemics, sporting a number of transoceanic and pantropical taxa, especially liverworts in **Lejeuneaceae** (Figure 76-Figure 94) and mosses ***Fissidens asplenioides*** (Figure 42), ***Floribundaria floribunda*** (Figure 43), and ***Neckeropsis disticha*** (Figure 44), whereas endemics increase in number in alpine areas, causing the tropics to have a high number of endemic bryophytes (Gradstein *et al*. 2001a). Nöske *et al*. (2003) reported that in Ecuadorian Andes species range sizes decrease toward higher elevations, refuting **Rapoport's elevational rule** (prediction of trends of increased elevational ranges of plants with increase in elevation). It does suggest that more endemics might be expected at higher elevations. Nevertheless, endemism overall was very low (1%).

Figure 39. Alpine zone and snowline on Chimborazo volcano, Ecuadorian Andes. Photo by Bernard Gagnon, through Creative Commons.

Figure 40. Nevado del Ruiz, Andes, Colombia. Photo by Edgar, through Creative Commons.

Figure 41. Peruvian lowland forest. Photo by Irvin Calicut, through Creative Commons.

Figure 42. ***Fissidens asplenioides***, a pantropical moss. Photo by David Tng, with permission.

Figure 43. ***Floribundaria floribunda***, a pantropical moss. Photo through Creative Commons.

Figure 44. ***Neckeropsis disticha***, a pantropical moss. Photo by Piers Majestyk, with permission.

Using only bole bryophytes to assess elevational differences eliminates most of the soil influences. Song *et*

al. (2015) compared bole bryophytes in three protected forest areas in tropical sub-montane (800-1400 m asl), montane (2000-2600 m asl) and sub-alpine (3200-3800 m asl) in Yunnan, SW China (Figure 45). They used 60 20x20 sampling plots, with five plots at each of 12 elevations with 200 m elevational intervals. They used 540 subplots, each with an area of 400 cm^2. These revealed 226 epiphytic bryophyte species. Life forms included smooth mat, fan, and turf as dominants in the sub-montane, montane, and sub-alpine forests, respectively (Figure 46). The sub-montane forest had significantly lower bryophyte species richness, a response they attributed to higher temperature, limited water availability, and more frequent human disturbance. As in many other studies cited here, the distribution of species richness was a hump-shaped curve with elevation (Figure 7), reaching its highest richness where the moisture levels were highest at ~2,600 m asl. Liverworts had the greatest species richness at all three sites (Figure 47).

Figure 45. Mountains at Yunnan, China. Photo by Ariel Steiner, through Creative Commons.

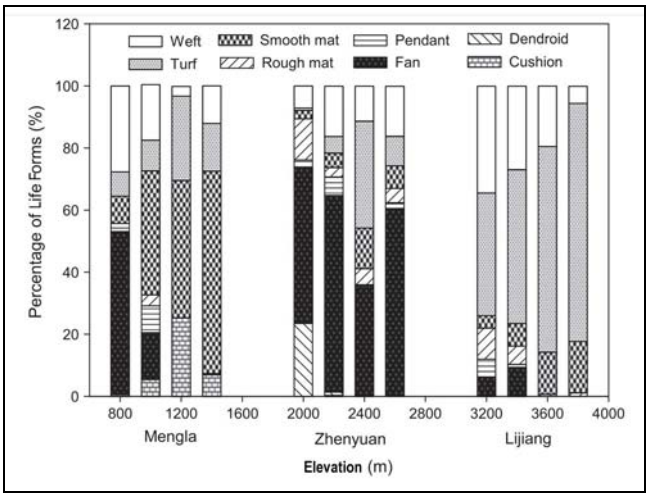

Figure 46. Comparison of life forms on three mountains in Yunnan, China. Modified from Song *et al*. 2015.

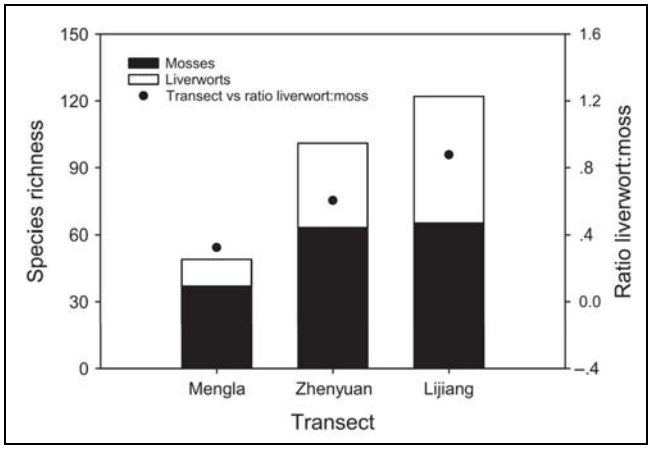

Figure 47. Species richness of mosses vs liverworts on three elevational transects in Yunnan, China. Species richness represents twenty 20 x 20 m plots on each mountain. Modified from Song *et al*. 2015.

Using data on more than 840 mosses and liverworts from the Himalayas in Nepal (actually subtropics; Figure 48), Grau *et al*. (2007) determined the known maximum and minimum elevations of the species. They found strong correlations in species richness among the ferns, flowering plants, mosses, and liverworts and elevational relationships. Maximum richness of liverworts occurred at 2,800 m, for mosses at 2,500 m asl. The endemic liverworts reached maximum richness at 3300 m; non-endemic liverworts at 2,700 m. Nevertheless, the mosses again did not support **Rapoport's elevational rule** (prediction of trends of increased elevational ranges of plants with increase in elevation). For liverworts, the relationship is not clear. Grau and coworkers (2007) suggest that differences in importance of climatic variables such as available energy and water might explain the differences among the four plant groups.

Figure 48. Himalaya Mountains at sunset, Nepal. Photo by Jules Air, through Creative Commons.

Records of Elevation

One might expect the highest known elevation for bryophytes to be in the tropics, where the climate will be the warmest at high elevations compared to the same elevation elsewhere. Grolle (1966) reported records up to 5100-5200 m asl in Nepal (subtropics). Alexey Potemkin (Bryonet 11 February 2016) noted that these were liverworts from a wide variety of genera: ***Scapania***

ornithopodioides (Figure 49), ***Lophozia incisa*** (Figure 50), ***Chandonanthus filiformis*** (see Figure 51), ***Gymnomitrion sinense*** (see Figure 52), ***Marsupella commutata*** (Figure 53), ***M. revoluta*** (Figure 54), ***Plagiochila carringtonii*** subsp. ***lobuchensis*** (Figure 55), ***Herbertus sendtneri*** (Figure 56), ***Anthelia julacea*** (Figure 57), ***Bazzania tricrenata*** (Figure 58), ***Metacalypogeia alternifolia*** (Figure 59).

Figure 49. ***Scapania ornithopodioides***, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Michael Lüth, with permission.

Figure 50. ***Lophozia incisa***, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Michael Lüth, with permission.

Figure 51. ***Chandonanthus***, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Blanka Aguero, with permission.

Figure 52. ***Gymnomitrion concinnatum***, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Hermann Schachner, through Creative Commons.

Figure 53. ***Marsupella commutata***, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Michael Lüth, with permission.

Figure 54. ***Marsupella revoluta***, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Michael Lüth, with permission.

Figure 55. ***Plagiochila carringtonii***, Scotland, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Michael Lüth, with permission.

Figure 56. ***Herbertus sendtneri***, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Michael Lüth, with permission.

Figure 57. ***Anthelia julacea***, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Michael Lüth, with permission.

Figure 58. ***Bazzania tricrenata***, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Michael Lüth, with permission.

Figure 59. ***Metacalypogeia alternifolia***, a leafy liverwort that is among those at the highest elevations on the planet. Photo through Creative Commons.

Schiavone and Suárez (2009) reported the moss ***Globulinella halloyi*** (**Pottiaceae**; see Figure 60) as a new species from Volcán Socompa, Argentina. It has the distinction of occurring at 6,000 m asl, 280-590 m higher than any known record for a bryophyte. It forms large, dense patches in communities with dense clumps of ***Pohlia papillosa*** (see Figure 63-Figure 64) on warm soil with moist conditions.

Figure 60. ***Globulinella globulifera***; ***G. halloyi*** is a new species that occurs at 6000 m asl in Volcán Socompa, Argentina, making it the bryophyte at the highest elevation on the planet. Photo by Claudio Delgadillo Moya, with permission.

Volcanoes are particularly likely to have high-elevation bryophytes. Areas near geothermal vents have heated soil and sufficient moisture to maintain a suitable bryophyte habitat. Potemkin *et al*. (2018) reported two liverwort and two moss species from the top of Elbrus (5,590 m asl) in the Caucasus. They occupied an area free of snow and ice. The liverworts are ***Marsupella boeckii*** (see Figure 61) and ***M. cf. funckii*** (Figure 61). The mosses are ***Atrichum cf. angustatum*** (Figure 62) and ***Pohlia nutans*** (Figure 63-Figure 64), both widespread species. These are not tropical locations, and thus the high elevation is more remarkable, but the heat and moisture from the geothermal vent makes this habitat livable for these species. ***Pohlia nutans*** is also recorded from 3,000-4,000 m asl in China (Zhang *et al*. 2007). ***Atrichum angustatum*** is reported in Europe, Macaronesia, Turkey, Iran, eastern and central North America, and China. ***Marsupella boeckii*** is an infrequent Holarctic species; ***M. funckii*** is a European species.

Figure 61. ***Marsupella funckii***, a species that occurs at 5,590 m asl in the Caucasus. Photo by Hermann Schachner, through Creative Commons.

Figure 62. ***Atrichum angustatum*** with ice crystals, a widespread species that occurs at 5,590 m asl in the Caucasus. Photo by Bob Klips, with permission.

Figure 63. ***Pohlia nutans*** below old mine on Svalbard. Photo by Michael Lüth, with permission.

Figure 64. ***Pohlia nutans*** in Khibiny Mountains, Apatity, Murmansk, a species that occurs at 5,590 m asl in the Caucasus. Photo by Michael Lüth, with permission.

Rodriguez (2015) reports the first known symbiosis in a high elevation (6480 m asl, Mt. Everest) population of mosses. The moss ***Gymnostomum aeruginosum*** (Figure 65) has a symbiotic fungus living completely within the tissues, making it the first documentation of a high elevation symbiosis. Rodriguez has continued testing to see if fungi confer any low temperature or high UV tolerance on the moss. Potemkin *et al*. (2018) have reported the Mt. Everest location of this species, based on a photograph, as hidden in a crevice in cold snow.

Figure 65. ***Gymnostomum aeruginosum***, a moss with a symbiotic fungus at 6,480 m on Mt. Everest, possibly the highest elevation for a bryophyte. Photo by Hermann Schachner, through Wikipedia Commons.

Frey *et al*. (2012) listed the highest records for bryophytes in the Cordillera Real in Bolivia. The liverworts ***Stephaniella paraphyllina*** (Figure 66) and ***Gymnocoleopsis multiflora*** occur at 5,000 m asl. The moss ***Grimmia longirostris*** (Figure 67) occurs at 5,800 m asl. Thus it appears that the highest elevation record thus far goes to ***Gymnostomum aeruginosum*** on Mt. Everest.

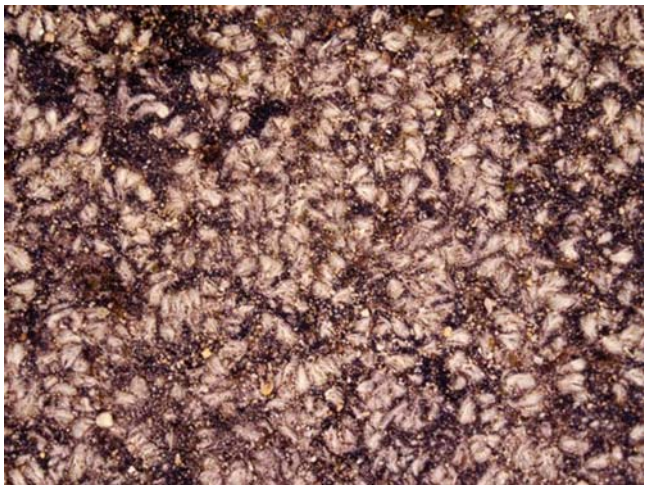

Figure 66. ***Stephaniella paraphyllina***, a leafy liverwort species that occurs at 5,000 m asl in Bolivia. Photo by Jan-Peter Frahm, with permission.

Figure 67. ***Grimmia longirostris*** with capsules, a moss species that occurs at 5,800 m asl in Bolivia. Photo by Hermann Schachner, through Creative Commons.

Diversity-Richness Changes

Early studies recognized differences in the bands of vegetation as elevation increased. Bryologists naturally became curious about the co-occurring changes in the bryophyte vegetation.

Pócs (1984) used four transects on the SSW slope of Mt. Kilimanjaro to show bryophyte species changes in each 100-m elevational section. On this mountain they found that the number of species increased "rapidly" from 1,800 m asl upward. They found two peaks in species diversity, one at 2,200 m, where the structure of the montane rainforest is most complex, and one at 2,700 m in the cloud belt, where the precipitation is greatest. At timberline (3,000 m), there is a rapid decrease in species diversity, but this remains relatively constant until 3,800 m, where the vegetation is subalpine heath and it is more open and dry with less rainfall. Above this level, the number of bryophyte species reach their minimum level on the mountain. The uppermost known species occurs at 5,050 m asl. These conditions created six bryophyte zones, each with characteristic species combinations, and these parallel the established zones of tracheophyte vegetation.

In Southwest Nigeria, Oyesiku (2013) conducted one of the rare ecological studies in a tropical rainforest biome in Africa. He found 138 bryophyte species, with 70% mosses and 30% liverworts. Unlike other studies, this one found the species distribution to be relatively homogeneous along the elevational trail (**Gini coefficient**=2.54%). A Gini coefficient of zero expresses perfect equality, where all values (species) are the same; 100% indicates that all values (species) are different. Nevertheless, there was a significant correlation between number of bryophyte species (for both mosses and liverworts separately) and elevation.

Frahm (1990c) investigated the elevational zonation of Bryophytes on Mt. Kinabalu in Borneo. Later, Frahm (1994a) summarized the results of the BRYOTROP Expedition to the Democratic Republic of Congo (previously Zaire) and Rwanda, which examined the elevational zonation of bryophytes on Mt. Kahuzi in the Democratic Republic of Congo. Based on bryophyte parameters such as species per hectare plot and elevational ranges of species, they identified four bryophyte vegetation zones: submontane forest (<1,500 m), lower tropical montane forest (1,500-2,000 m), upper tropical montane forest (2,100-2,800 m), and subalpine forest (2,900-3,200 m). These zones correlate with those previously named for the general tracheophyte vegetation.

Gradstein *et al*. (1983) compared liverworts between the Neotropics and Africa to determine the level of disjunction. Early researchers tended to name species on a new continent as new, but as more in-depth studies occur, many of these emerge as synonyms. Among 35 known Afro-American species, there are three distribution types one can recognize. These are Tropical Afro-American (lowland, montane, and the alpine element), Subtropical-Mediterranean (southern, wide element) and Temperate-SubAntarctic (southern, wide element). Most of these disjuncts occur in the leafy liverwort order **Jungermanniales** (Figure 10). The subtropical disjuncts are an exception, being thallose liverworts. The researchers suggest that the species disjunctions are due to long-distance dispersal, but experimental evidence to support this is totally lacking. On the other hand, it is possible that generic disjunctions and species vicariance might be the result of ancient land connections through Gondwanaland.

Although the bamboo forest (Figure 68) is low in bryophyte species diversity, it nevertheless exclusively hosted 17.6% of the collected bryophytes in the Bwindi Impenetrable National Park, Uganda (Tusiime *et al*. 2007).

Zhang (2001) demonstrated that the number of species per plot increases linearly with elevation in Hong Kong. Sun *et al*. (2013) found that the species richness of ground bryophytes on Gongga Mountain, China, shows no elevational trend. Cover, on the other hand, increases with elevation, with the maximum occurring at ~3,758 m asl,

with biomass averaging 700 g m^{-2} and maximum thickness reaching 8 cm. For these ground dwellers, litter, air temperature, and precipitation seem to control distribution.

Figure 68. Uganda bamboo forest. Photo by A. M. Doughty, through Creative Commons.

Nekesa (2015) used a transect from 2,400 m to 4,800 m asl, sampling at 200-m intervals to examine the distribution of both bryophytes and tracheophytes on Mt. Kenya. Tracheophytes were sampled in 10 x 10 m quadrats with 10 x 5 cm bryophyte quadrats nested within them. Bryophytes had the highest diversity, followed by flowering plants. Diversity overall decreased from 2400 m asl to 460 m asl, with the optimum occurring at 2400 and 3000 m asl (over 350 species each). The most diverse bryophytes were humicolous and corticolous (80%) with only 0.001% in the aquatic habitat. Nekesa concluded that elevation is the major factor affecting the distribution of both groups, with microhabitats of bogs, rocks, and tracheophytes themselves being the secondary factors.

Glime *et al.* (1990) demonstrated a change in associations among ***Frullania*** (Figure 72) species with elevation on Mount Albert Edward, Papua New Guinea (Figure 69). The species diversity of this genus is greatest in the middle elevations, least in the dry lowlands. Sibling taxa show elevational differences within pairs, thus occupying different niches. It is likely that we will find multiple environmental races among at least some species when we compare them among elevations.

Figure 69. Mount Albert Edward, Papua New Guinea. Satellite image through Creative Commons.

On Mount Albert Edward, Papua New Guinea (Figure 69), there are more than 50 taxa of the leafy liverwort genus ***Frullania*** (Figure 72) (Glime *et al.* 1990). These taxa form many associations, often with other members of the same genus. The associations and the major taxa differ with elevation, and the species richness likewise differs. The most taxa occur at the middle elevations, especially the cloud forests, and the least in the dry lowlands and high alpine areas. Furthermore, many clumps of single ***Frullania*** species occur in the latter two regions, whereas at the other elevations collections are rarely pure. In fact, at 2,000-2,500 m asl associations between ***Frullania*** taxa are so common between repeating species pairs or groups (*i.e.* high fidelity) that we (Glime *et al.* 1990) suggested that some benefit might be derived from the association. We suggested that these untested benefits might include:

1. high light intensity protection for small liverworts that live among larger ones in the forest canopy or in exposed alpine areas
2. protection from drying out by reducing the amount of free space among the branches and leaves
3. gain in water availability by species that have a poor ability to move water from the substrate or surface of the clump to their own branches but that can take advantage of the water moved by an associated species.

Although few authors describe such commensal water relationships in plants, except by use of mycorrhizae, Rydin (1985) has suggested that they exist among ***Sphagnum*** (Figure 70) species with differential abilities to absorb water in one circumstance and to retain it in another. His conclusions are further supported by the experimental studies of Li *et al*. (1992) on two additional species of ***Sphagnum***.

Figure 70. ***Sphagnum capillifolium*** with capsules, in Chile. Photo by Juan Larrain, with permission.

Ah-Peng *et al*. (2012) compared elevational bryophyte species variation on the Reunion Island (summit 2,069 m asl) to that of the Colombia high volcano (5,321 m asl) on

the South American continent. Species richness was similar between the two locations, with 265 on Reunion Island and 295 on the Colombian volcano. On Reunion Island, species with small range sizes dominated, with mean elevational range increasing with elevation (perhaps Rapoport's elevational rule is right for bryophytes sometimes), and with species richness decreasing with elevation. The island's cloud forest has a high bryophyte species richness as well as a large number of rare species. The continental elevational gradient, by contrast, was dominated by large-ranged species.

The elevational gradient seems also to be reflected in the niche width (Figure 71) of the ***Frullania*** (Figure 72) taxa (Glime *et al* 1990). At both the low and the high elevations, the niche widths are narrower (not supporting Rapoport's elevation rule), at least for the parameters tested, further restricting the taxa that are there to well-defined habitats. For example, ***Frullania papillata*** has 95% of its observations expected between 2,368 and 2,575 m asl and occurs only between 2,500 and 3,500 m. Similarly restricted taxa, elevationally, include ***F. apiculata***, ***F. attenuata***, ***F. gracilis*** (Figure 72), ***F. ornithocephala***, and ***F. ornithocephala*** var. ***intermedia***. On the other hand, the middle elevations have the highest number of species pairs with non-overlapping distributions (Figure 73).

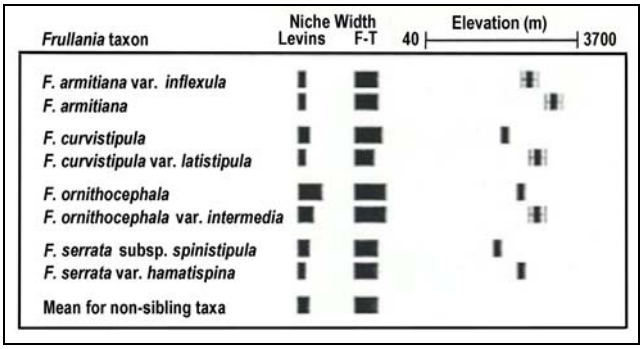

Figure 71. Levins and Freeman-Tukey niche width and elevational range of sibling pairs of ***Frullania*** on Mount Albert Edward, Papua New Guinea. Redrawn from Glime *et al*. 1990.

Figure 72. ***Frullania gracilis***. Photo from Bryophyte Flora of Doi Suthep-Pui National Park, Chiang Mai, Thailand, through Creative Commons.

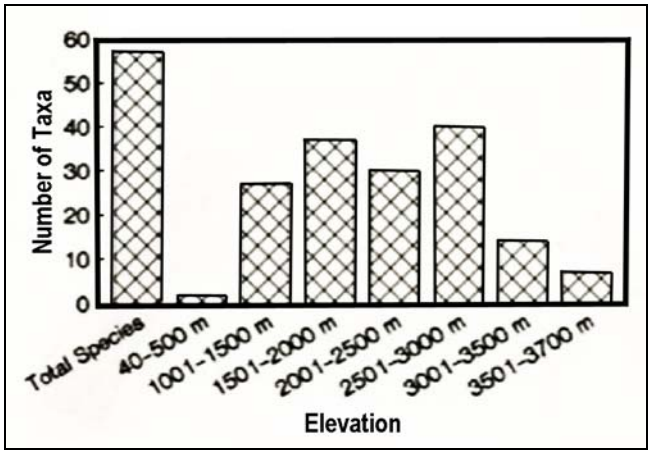

Figure 73. Elevational distribution of species richness of ***Frullania*** on Mount Albert Edward, Papua New Guinea. Redrawn from Glime *et al*. 1990.

Four sibling taxa pairs of ***Frullania*** occur (Figure 71, but among the ones examined, each member of the pair exhibits distinct elevational niches, suggesting that while they may have remained morphologically similar, they may have diverged physiologically (Glime *et al*. 1990).

The canopy typically has more species than the ground in a lowland rainforest. Cornelissen and Gradstein (1990), working in Guyana, reported that 50% of the species were restricted to the canopy; only 14% corticolous species were restricted to the understory. However, in Monteverde, Costa Rica (Figure 74), when rotten logs and living leaves are added to the understory percentage, about 20% of the species are exclusive to the understory (Figure 75) (Gradstein *et al*. 2001b). Gradstein and coworkers suggested that the percentage of species restricted to the canopy may be the same in lowland and montane rainforests, despite large differences in both species abundance and composition (see also Gradstein 1995).

Figure 74. Monteverde, Costa Rica, canopy. Photo by Cephas, through Creative Commons.

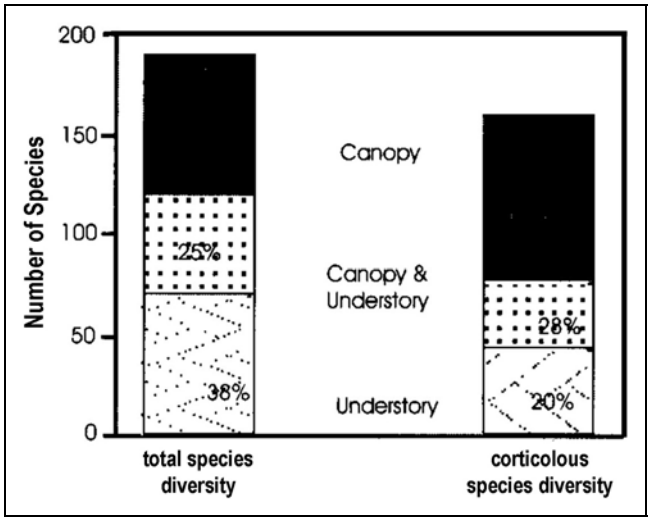

Figure 75. Diversity of canopy vs understory in the cloud forest at Monteverde, Costa Rica. Modified from Gradstein *et al*. 2001b.

Figure 77. ***Cololejeunea cardiocarpa***, a leafy liverwort species that occurs from 1 to 1,600 m asl in Costa Rica. Photo by Paul Davison, with permission.

Eggers (2001) described the groupings of epiphyllous **Lejeuneaceae** (Figure 76-Figure 94) in Costa Rica based on their elevational distribution:

only <500 m:

Cololejeunea setiloba (see Figure 77)

1-1,600 m:

Cololejeunea (syn.=***Aphanolejeunea***) ***costaricensis*** (see Figure 76), ***Cololejeunea moralesiae*** (see Figure 76), ***Cololejeunea cardiocarpa*** (Figure 77), ***C. guadeloupensis*** (see Figure 77), ***C. linopteroides*** (see Figure 77), ***C. obliqua*** (see Figure 77), ***C. minutilobula*** (see Figure 77), ***C. standleyi*** (see Figure 77), ***Colura verdoornii*** (see Figure 78), ***Cyclolejeunea chitonia*** (see Figure 79), ***C. peruviana*** (Figure 79), ***Diplasiolejeunea brunnea*** (Figure 80), ***Microlejeunea epiphylla*** (see Figure 81), ***Rectolejeunea berteroana*** (Figure 82), ***R.*** *cf.* ***emarginuliflora*** (see Figure 82), ***Stictolejeunea squamata***.

Figure 78. ***Colura tenuicornis***; ***C. verdoornii*** is a leafy liverwort species that occurs from 1 to 1,600 m asl in Costa Rica. Photo by Jan-Peter Frahm, with permission.

Figure 76. ***Cololejeunea microscopica***; ***Cololejeunea costaricensis*** and ***C. moralesiae*** occur from 1 to 1,600 m asl in Costa Rica. Photo by Stan Phillips, through public domain.

Figure 79. ***Cyclolejeunea peruviana***, a leafy liverwort species (as well as ***C. chitonia***) that occurs from 1 to 1,600 m asl in Costa Rica. Photo by Jan-Peter Frahm, with permission.

Figure 80. ***Diplasiolejeunea brunnea*** in Ecuador on leaf, a leafy liverwort species that occurs from 1 to 1,600 m asl in Costa Rica. Photo by Tamás Pócs, with permission.

Figure 81. ***Microlejeunea*** sp.; ***M. epiphylla*** is a leafy liverwort species that occurs from 1 to 1,600 m asl in Costa Rica. Photo by Tangatawhenua, through Creative Commons.

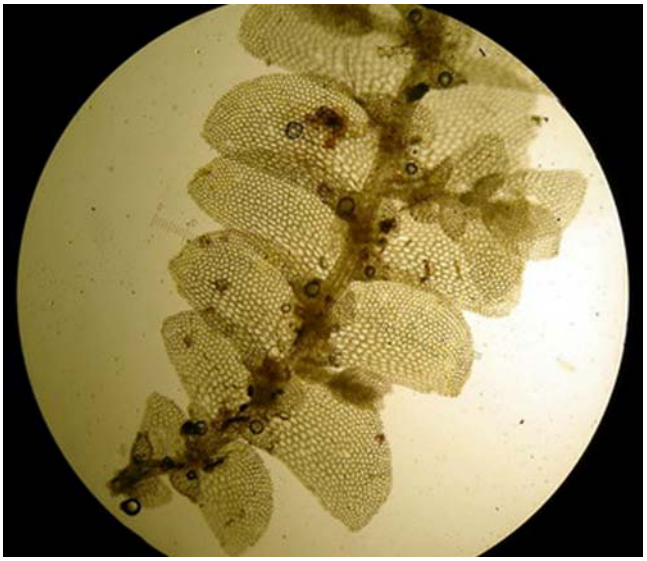

Figure 82. ***Rectolejeunea berteroana***, a leafy liverwort species (as well as ***R.*** *cf.* ***emarginuliflora***) that occurs from 1 to 1,600 m asl in Costa Rica. Photo by Michaela Sonnleitner, with permission.

1-3,000 m:

Cololejeunea (syn.=***Aphanolejeunea***) ***angustissima*** (see Figure 76), ***Colura tortifolia*** (Figure 83), ***Diplasiolejeunea cavifolia*** (Figure 80, Figure 84), ***D. pellucida*** (Figure 84), ***Drepanolejeunea inchoata*** (Figure 85), ***Dr. lichenicola*** (see Figure 85), ***Lejeunea laetevirens*** (Figure 86), ***Odontolejeunea lunulata*** (Figure 87).

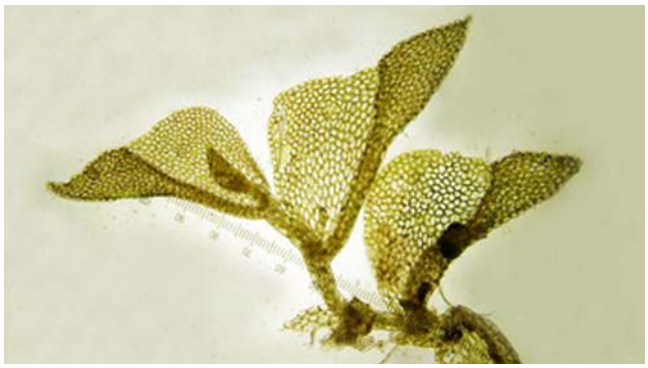

Figure 83. ***Colura tortifolia***, a leafy liverwort species that occurs from 1 to 3,000 m asl in Costa Rica. Photo by Michaela Sonnleitner, with permission.

Figure 84. ***Diplasiolejeunea pellucida***, a leafy liverwort species that occurs from 1 to 3,000 m asl in Costa Rica. Photo by Michaela Sonnleitner, with permission.

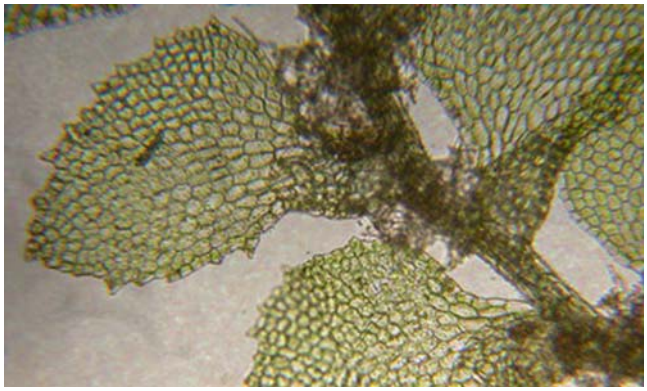

Figure 85. ***Drepanolejeunea inchoata*** (as well as ***Dr. lichenicola***), a leafy liverwort species that occurs from 1 to 3,000 m asl in Costa Rica. Photo by Michaela Sonnleitner, with permission.

Figure 86. ***Lejeunea laetevirens***, a leafy liverwort species that occurs from 1 to 3,000 m asl in Costa Rica. Photo by Scott Zona, through Creative Commons.

Figure 88. ***Cololejeunea longifolia***, a species that occurs only from 500 to 1,600 m asl in Costa Rica. Photo by Yang Jia-dong, through Creative Commons.

Figure 87. ***Odontolejeunea lunulata*** with perianth, a leafy liverwort species that occurs from 1 to 3,000 m asl in Costa Rica. Photo by Michaela Sonnleitner, with permission.

only 500-1,600 m:

Cololejeunea (syn.=***Aphanolejeunea***) ***cingens*** (see Figure 76), ***Cololejeunea*** (syn.=***Aphanolejeunea***) ***longifolia*** (Figure 88), ***Cololejeunea*** (syn.=***Aphanolejeunea***) ***pustulosa*** (see Figure 76), ***Cyclolejeunea accedens*** (see Figure 79), ***C. convexistipa*** (see Figure 79), ***Diplasiolejeunea grolleana*** (see Figure 80, Figure 84), ***D. unidentata*** (see Figure 80, Figure 84), ***Harpalejeunea uncinata*** (see Figure 89), ***Lejeunea filipes*** (Figure 90), ***Odontolejeunea decemdentata*** (Figure 91).

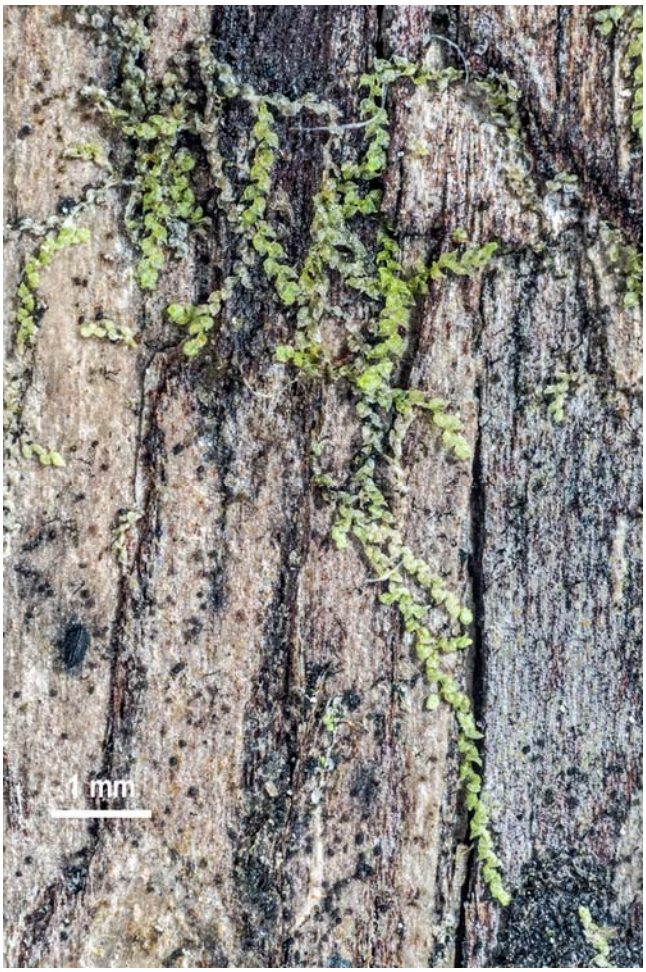

Figure 89. ***Harpalejeunea latitrans***; ***H. uncinata*** occurs only from 500 to 1,600 m asl in Costa Rica. Photo by Jeremy Rolfe, through Creative Commons.

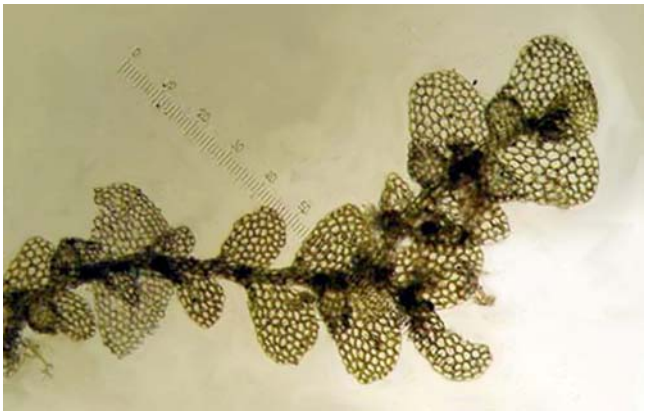

Figure 90. ***Lejeunea filipes***, a leafy liverwort species that occurs only from 500 to 1,600 m asl in Costa Rica. Photo by Michaela Sonnleitner, with permission.

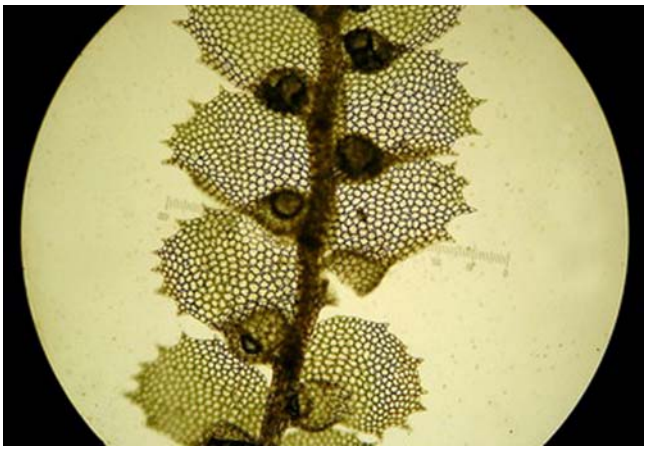

Figure 91. ***Odontolejeunea decemdentata***, a leafy liverwort species that occurs only from 500 to 1,600 m asl in Costa Rica. Photo by Michaela Sonnleitner, with permission.

500-3,000 m:

Anoplolejeunea conferta, ***Cololejeunea*** (syn.=***Aphanolejeunea***) ***crenata*** (see Figure 76), ***Cololejeunea*** (syn.=***Aphanolejeunea***) ***ephemeroides*** (see Figure 76), ***Colura tenuicornis*** (Figure 78), ***Diplasiolejeunea alata*** (see Figure 80, Figure 84), ***Drepanolejeunea infundibulata*** (see Figure 85), ***Dr. mosenii*** (see Figure 85), ***Lejeunea flava*** (Figure 92-Figure 93), ***Omphalanthus filiformis*** (Figure 94).

Figure 92. ***Lejeunea flava***, a leafy liverwort species that occurs from 500 to 3,000 m asl in Costa Rica. Photo by Linda Phillips, through Creative Commons.

Figure 93. ***Lejeunea flava*** on a leaf, a leafy liverwort species that occurs from 500 to 3,000 m asl in Costa Rica. Photo by Yang Jia-dong, through Creative Commons.

Figure 94. ***Omphalanthus filiformis*** in the Neotropics, a leafy liverwort species that occurs from 500 to 3,000 m asl in Costa Rica. Photo by Michael Lüth, with permission.

only >1,600-3,000 m:

Cololejeunea (syn.=***Aphanolejeunea***) ***camillii*** (see Figure 76), ***Cololejeunea fefeana*** (see Figure 77), ***Diplasiolejeunea costaricensis*** *sp. nov*. (see Figure 80, Figure 84), ***D. involuta*** (see Figure 80, Figure 84).

In Panama, Gradstein and Salazar Allen (1992) assessed the bryophytes along an elevational gradient on Cerro Pirre (1,200 m asl). As shown in the other studies above, they found very different species assemblages along the gradient from inundated lowland, to hillside lowland, to submontane, to montane elfin forest. Among these, they found the greatest species richness in the submontane forest. The greatest number of exclusive species, however, occurred in the montane elfin (cloud) forest, along with the greatest bryophyte biomass. The mountain proved to have a number of rare liverworts, and this one study produced 40 liverwort species new for Panama.

Wolf (1989, 1992) elaborated on the species richness of epiphytic bryophytes on an elevational gradient in the northern Andes (Figure 95). This study included 187 liverworts and 108 mosses. Wolf (1993a, b) also examined the diversity patterns and biomass of epiphytic bryophytes along this gradient in the Central Cordillera of Colombia

(Figure 96) from 1,000 to 4,130 m asl. Elevation emerged as a complex factor in explaining the variation in species composition. Species area curves for each sampling site indicated that sampling was adequate. α and β diversity patterns along the elevational gradient differed between mosses and liverworts. Liverwort richness was maximum (~100 taxa) in the range of 2,550-3,100 m. This high level corresponds with the contact transition zone between vegetation zones. This supports the prediction that the highest species diversity will occur in a transition zone, indicating that between community interactions are more important in determining diversity than within community relationships (*i.e.* niche relationships). This is further supported by the fact that only 20.5% of the liverwort taxa are exclusive to this belt of greatest richness. Humidity appears to be an important limiting factor, with biomass increase of bryophytes corresponding with a humidity increase with elevation. Bryophyte species turnover also appears to be greater in this mountain system than that known for the temperate mountains in North America.

Figure 95. Nevado del Ruiz, northern Andes, Colombia. Photo by Edgar, through Creative Commons.

Figure 96. Western Cordillera of Colombia bordering Chocó, very rich montane cloud forests on a sunny day at 1,600 m in 1992. Photo courtesy of S. Robbert Gradstein.

The ECOANDES project has contributed greatly to our understanding of Neotropical elevational effects on bryophytes (Gradstein *et al*. 1989). Gradstein and coworkers compared the wet, foggy western slope (1,000-4,500 m) with the drier eastern slope (500-4,500 m) of the Colombian Central Cordillera at the Parque de los Nevados. Again, the species richness increases with elevation to the upper montane forest, where the greatest bryophyte diversity occurs. Liverworts demonstrate their greater preference for moisture by outnumbering mosses in the upper submontane and montane forests on the wet western slope, but in the drier environments they are less diverse than the mosses. At lower elevations (<3000 m), the species are wide-ranging tropical species, whereas in the higher elevations the species are those with narrow ranges (Andean and endemics). Few temperate species occur, with less than 10% in the upper montane forest and ~20% in the páramo. We can assume they have arrived in Colombia relatively recently (last 5 million years) after the Cordilleras arose.

Germano and Pôrto (2006) reported on bryophyte communities in the remnant Atlantic forests in Pernambuco, Brazil. In the Atlantic Forest of Rio de Janeiro, southeastern Brazil, Santos and Costa (2010) reported 360 liverwort taxa. In addition to having floristic differences among the different formations, there were elevational differences. The montane forest has the highest species richness (238) with 63 exclusive taxa and 27 endemics, as of the year 2010. The upper montane is next with 173 species, 58 exclusive taxa, and 21 endemics. The leafy liverwort family **Lejeuneaceae** (Figure 76-Figure 94) is the most species-rich family in all formations, whereas other families may be restricted to certain formations.

In the Itatiana National Park (Figure 6) of Brazil, three vegetation zones are clearly defined: montane forest (Figure 97), upper montane forest (Figure 97), and high-elevation fields (Figure 98) (Costa *et al*. 2015). Sampling at 10 representative elevations revealed 519 taxa, 57% of the total known bryophyte flora in the Rio de Janeiro State and 34% of that of Brazil. The montane forest had the highest species richness (296). The most endemic species (47) occurred in the upper montane zone. The researchers attributed the richness in these locations to their diversity of climate, soil, and physiographic parameters. As is typical in the tropics, especially the Neotropics, the highest diversity occurs at the mid-elevational range of 2,100-2,200 m asl. As the elevation increases, so does the number of threatened species.

Figure 97. Montane and upper montane forests, Parque Nacional de Itatiaiae, Brazil. Photo by Gabriel R. Vallim, through Creative Commons.

Figure 98. High-elevation field, Parque Nacional do Itatiaia, Rio de Janeiro, Brazil. Photo by Pedro Luz, through Creative Commons.

On Mt. Kitanglad (up to 2,938 m asl) in the Philippines (Figure 99), Azuelo *et al*. (2010) examined the diversity and ecology of bryophytes. They report 428 species, with mosses predominating. Of these, 326 species are mosses; only 98 of these species are liverworts and 4 are hornworts. The mosses occur in 70 genera and 29 families. The highest diversity occurs in the lower montane forest (112 species), followed by the mossy (cloud) forest (108 species) and upper montane forest (87 species). Nevertheless, the highest bryophyte cover occurs in the mossy forest. A major substrate choice is epiphytic (40% of mosses, 15% of liverworts, and 1 hornwort). But, the highest richness is on the rotten logs and decaying litter, with 43% of the mosses and 42% of the liverwort species occurring there, including **Lepidoziaceae** (Figure 100), **Plagiochilaceae** (Figure 55), **Schistochilaceae** (Figure 11), and **Trichocoleaceae** (Figure 101). The moss families **Meteoriaceae** (44 species; Figure 43) and **Dicranaceae** (43 species; Figure 30) are the most species-rich families, contrasting with the prominence of the liverwort family **Lejeuneaceae** (Figure 76-Figure 94) in most areas of the tropics. Rather, the **Plagiochilaceae** (26 species) and **Lepidoziaceae** (20 species) are the most species-rich liverwort families. Among the species on the mountain, 11 moss and 6 liverwort species are considered to be medicinal.

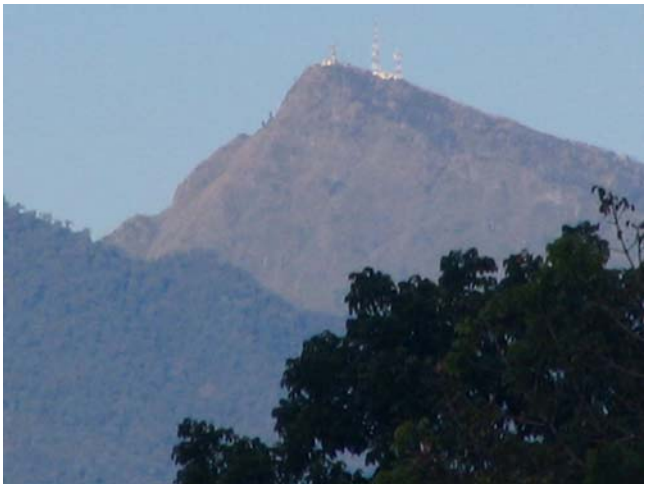

Figure 99. Mt. Kitanglad, Philippines. Photo by Kleomarlo, through public domain.

Figure 100. ***Bazzania tridens***, in the family **Lepidoziaceae**, one of the common families of liverworts on logs and decaying matter in the Philippines. Photo by Li Zhang, with permission.

Figure 101. ***Trichocolea tomentella***; **Trichocoleaceae** is a common family on rotten logs and decaying litter in the Philippines. Photo by Dick Haaksma, with permission.

Santos *et al*. (2017) compared the numbers of species in families at six elevations at the Serra do Mar State Park, Brazil (Figure 102)

In an attempt to determine the usefulness of liverworts as bioindicators, Santos *et al*. (2014) sampled 26 localities to determine β diversity relationships. They found a significant association of the first CCA axis with a floristic gradient from lowland forests to high montane forests. They found 34 species that could serve as bioindicators. The species groupings could be explained by elevation, temperature, and precipitation.

Churchill (pers. comm. 29 November 2011) has observed that diversity relationships with elevation are basically true throughout the tropical Andes.

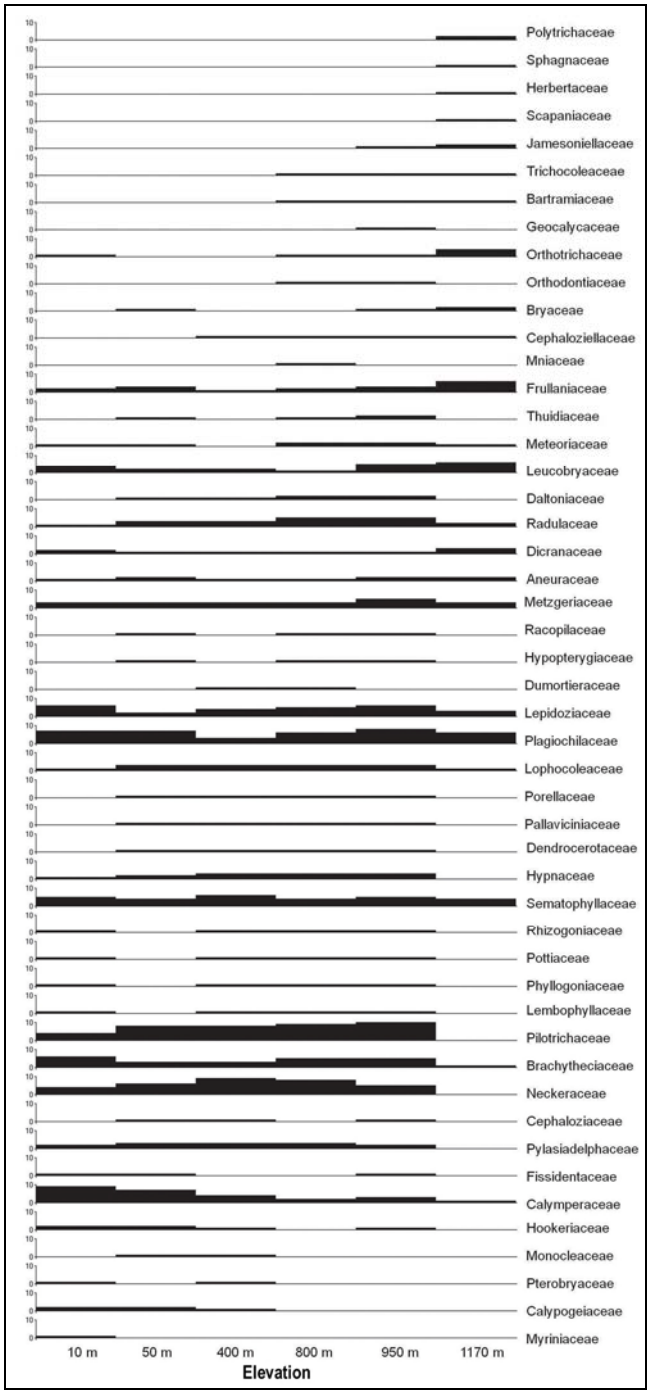

Figure 102. Abundance of species in families by elevation in Serra do Mar State Park, Brazil. Height of bar denotes number of species. **Lejeuneaceae** are not included. Modified from Santos *et al.* 2017.

Dominance Changes

As the elevation increases, the dominant species change. Santos *et al*. (2017) illustrated this clearly in the Atlantic Forest in Serra do Mar State Park, Brazil (Table 1).

Table 1. Indicator species of bryophytes with a *p* value ≤0.03 from five vegetation types in the Atlantic Forest in Serra do Mar State Park, Brazil, demonstrating the change in dominance with elevation.

RESTINGA FOREST	
Bazzania phyllobola	
Leptolejeunea elliptica	Figure 103
Cololejeunea obliqua	Figure 104
Syrrhopodon incompletus	Figure 105
Plagiochila disticha	Figure 106
Harpalejeunea oxyphylla	
LOWLAND FOREST	
Crossomitrium patrisiae	Figure 107
SUBMONTANE FOREST	
Bryopteris filicina	Figure 108
Homalia glabella	Figure 109
Ceratolejeunea rubiginosa	
Tortella sp.	Figure 110
Homaliodendron piniforme	
MONTANE FOREST	
Porotrichum longirostre	
Radula nudicaulis	
Racopilum tomentosum	Figure 111
Thamniopsis langsdorffii	Figure 112
Bazzania stolonifera	Figure 113
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Schlotheimia tecta	Figure 115
Cheilolejeunea xanthocarpa	Figure 116
Frullania atrata	Figure 117
Frullania kunzei	Figure 118
Campylopus heterostachys	Figure 119
Frullania apiculata	
Herbertus juniperoideus subsp. *bivittatus*	Figure 120
Macromitrium cirrosum	Figure 121
Plagiochila bifaria	Figure 122
Campylopus griseus	Figure 123
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Figure 103. ***Leptolejeunea elliptica***, an indicator species of the Restinga Forest. Photo by Yan Jia-dang through Creative Commons.

Figure 104. ***Cololejeunea obliqua***, an indicator species of the Restinga Forest. Photo by Jan-Peter Frahm, with permission.

Figure 105. ***Syrrhopodon incompletus*** with capsules, an indicator species of the Restinga Forest. Photo by John Bradford, with permission.

Figure 106. ***Plagiochila disticha***, an indicator species of the Restinga Forest. Photo by Michael Lüth, with permission.

Figure 107. ***Crossomitrium patrisiae***, an indicator species of the Lowland Forest. Photo by Michael Lüth, with permission.

Figure 108. ***Bryopteris filicina***, an indicator species of the Submontane Forest. Photo by Michael Lüth, with permission.

Figure 109. ***Homalia glabella***, an indicator species of the Submontane Forest. Photo by Claudio Delgadillo Moya, with permission.

Figure 110. ***Tortella humilis***, an indicator species of the Submontane Forest. Photo by Michael Lüth, with permission.

Figure 111. ***Racopilum tomentosum***, an indicator species of the Montane Forest. Photo by Michael Lüth, with permission.

Figure 112. ***Thamniopsis langsdorffii***, an indicator species of the Montane Forest. Photo by Michael Lüth, with permission.

Figure 113. ***Bazzania stolonifera***, an indicator species of the Montane Forest. Photo by Michael Lüth, with permission.

Figure 114. ***Jamesoniella rubricaulis***, an indicator species of the Mountaintop Forest. Photo by Jan-Peter Frahm, with permission.

Figure 115. ***Schlotheimia tecta***, an indicator species of the Mountaintop Forest. Photo by Michael Lüth, with permission.

Figure 116. ***Cheilolejeunea xanthocarpa***, an indicator species of the Mountaintop Forest. Photo by Michael Lüth, with permission.

Figure 117. ***Frullania atrata***, an indicator species of the Mountaintop Forest. Photo by Jan-Peter Frahm, with permission.

Figure 118. ***Frullania kunzei***, an indicator species of the Mountaintop Forest. Photo by Blanka Aguero, with permission.

Figure 119. ***Campylopus heterostachys***, an indicator species of the Mountaintop Forest. Photo by Germaine Parada, through Creative Commons.

Figure 120. ***Herbertus juniperoideus***, an indicator species of the Mountaintop Forest. Photo by Jan-Peter Frahm, with permission.

Figure 121. ***Macromitrium cirrosum***, an indicator species of the Mountaintop Forest. Photo by Michael Lüth, with permission.

Figure 122. ***Plagiochila bifaria***, an indicator species of the Mountaintop Forest. Photo by Jan-Peter Frahm, with permission.

Figure 123. ***Campylopus griseus***, an indicator species of the Mountaintop Forest. Photo by Michael Lüth, with permission.

Figure 124. ***Polytrichum juniperinum***, an indicator species of the Mountaintop Forest. Photo by Janice Glime.

Productivity

Zotz (1999) found a distinct increase in abundance of mosses and liverworts with elevation. They are especially important in tree crowns in montane regions and are inconspicuous in the lowlands. This study demonstrates that drying in the daytime in the lowlands limits photosynthesis, whereas hot, moist nights cause excessive respiration that exceeds photosynthetic gain.

Based on studies in Borneo, Tanzania, Transvaal, Venezuela, and Peru, Frahm (1990b) concluded that the biomass of epiphytic bryophytes in the tropics increases from the lowlands to the **treeline** (elevation above which trees cannot grow). Like the conclusions of Zotz (1999), he attributed this gradient to combinations of precipitation, humidity, temperature, and desiccation. This was supported by experiments showing that net assimilation decreases rapidly above 25ºC. The high temperatures and low light result in higher respiratory losses compared to photosynthetic gains. This problem is further exacerbated by problems of desiccation in lowlands. At higher elevations, on the other hand, the abundant precipitation carrying a relatively high nutrient supply enhances growth in the tropical montane forests.

In this study, Frahm (1990b) compared the monthly and yearly production and chlorophyll content of the perennial moss ***Hydrogonium*** (Figure 125) and the seasonal moss ***Physcomitrium*** (Figure 126) and their associated communities in 10 x 10 cm quadrats. For ***Hydrogonium***, the mean biomass was 95 g m^{-2} and for ***Physcomitrium*** 11 g m^{-2}. These values are both lower than many measures of bryophytic biomass in temperate forests.

Bader *et al*. (2013) found a similar increase in biomass from lowlands to highlands in Panama, with increases to "extreme richness" in some montane cloud forests. Using gas-exchange measurements before and after transplanting bryophytes to lower elevations, these researchers determined that temperature alone could not explain the lack of success of high elevation species in the lowlands. Nevertheless, a few samples of nearly every species survived for at least 20 months. Hydration patterns proved to be important in the survival. Sunny mornings cause rapid desiccation, a regime that can be deadly to many species. This is further complicated by afternoon rains that hydrate the mosses, renewing their activity and causing high respiratory losses at night.

Figure 125. ***Hydrogonium ehrenbergii***; in the tropics this genus has lower biomass than in the temperate zone. Photo by Jan-Peter Frahm, with permission.

Figure 126. ***Physcomitrium eurystomum***; the genus ***Physcomitrium*** in the tropics seems to have lower productivity than populations in the temperate zone. Photo by Show-Ryu, through Creative Commons.

Wagner *et al*. (2012) noted that **poikilohydric** organisms (those with predominantly external control over water content, including bryophytes) increase with elevation in the tropics. In the lowlands, low light and high temperatures cause a high respiration to photosynthesis ratio, often causing bryophytes to have negative net productivity. Among 18 tropical bryophytes in the study, from three elevations (sea level, 500 m, 1,200 m) in Panama, the optimum temperatures of net photosynthesis closely matched the mean temperatures of the habitats where the species grew. This adaptation resulted in a lack of differences in the ratio of dark respiration to net photosynthesis with elevation. As one might surmise from this, responses of individual species to water, light, and CO_2 did differ, but not systematically with elevation. Water relations seemed to be important, with higher temperatures increasing the evaporation rates. This, in turn, decreased the time available for photosynthesis each day, while nighttime respiration rates did not necessarily increase.

Chantanaorrapint (2010) compared biomass of epiphytes along three elevational transects in southern Thailand, ranging from 25 m asl to 1,500 m asl. The dry weight of epiphytic bryophytes increased with elevation, with 1.15 g m^{-2} in the lowland to 199 g m^{-2} in the montane forests. The dry weight increased with elevation from 2.4 kg per hectare to 620 kg per hectare. These bryophytes were important in water storage, holding 1.2 to 2.4 times their dry weight. This storage was typically higher in the montane region (up to 1,500 L ha^{-1}) than in the lowland forests. Bark *p*H also varies with elevation, ranging from 3.19 to 6.84, decreasing with elevation. Air temperature decreases about 0.6ºC per 100 m increase in elevation.

Zotz *et al.* (1997) measured CO_2 exchange in six tropical bryophytes in a lower montane forest in Panama. The **diel** water content varied greatly. Both low and high water content were severely limiting for photosynthesis. Low photon flux density (a measure of light intensity), as occurs during rain storms, was less limiting for CO_2 exchange than water availability. More than half of the daily carbon gain of 2.9 mg C g^{-1} was lost at night to respiration. This suggests an estimate of 45% carbon gain for the bryophytes per year.

Adaptations

There appear to be distinct adaptations that characterize forest epiphytes in elevational zones throughout the tropical regions of Southeast Asia, Africa, and South America (Kürschner *et al*. 1999). In the tropical lowlands and submontane regions, **perennial stayer** and **perennial shuttle species** dominate the life forms. In the cooler and more humid montane rainforests, **fan** and **weft** forms of **perennial stayers** and **perennial shuttle** species are prominent, relying on propagules and clonal growth to achieve the large biomass found there. These **fan**-forms and other structures such as ciliate leaves are effective at trapping fog water through rapid condensation and facilitating conduction and storage. In the upper montane forests, conditions are more open and xeric and the diurnal fluctuations are more extreme. Here the bryophytes tend to form **cushions** or **short** and **tall turfs** of **perennial stayers** and **perennial shuttle** species. They often conserve water through an abundant rhizoid tomentum and a more developed central strand in the stem.

Frahm (1994b), as part of the BRYOTROP Expedition, reported on life forms from various elevations on Mt. Kahuzi (Democratic Republic of the Congo), using a transect from 900 to 3,300 m asl. From 900 to 2,300 m elevation, the **dendroid** life form is characteristic. He interprets this as an adaptation for better gas exchange in conditions of low light and high air humidity. **Cushions** predominate above 2,500 m asl. These are typically 2-5 cm high, but some reach 50 cm at treeline. **Moss balls** can form, reaching up to 1 m in diameter. Bryophyte cover on soil is less than 5% below 2,700 m asl, but in the subalpine ericaceous belt it is 90%. Similarly, cover on bark is as low as 5% or less in the low elevations, increasing to 80% at high elevations. This gradation corresponds with light intensities from <1% to up to 50%. Temperature, on the other hand, decreases from 10.6ºC at 900 m to 1.5ºC at 4,500 m. The bark *p*H is in a relatively narrow range of 4.1-6.2.

In the Amazonian Andes in northern Peru (Figure 127), Kürschner and Parolly (1998a, b) were able to define apparent adaptations based on relative biomass of morphological types. They found three dominant life strategy categories: **colonists**, **perennial shuttle species**, and **perennial stayers**. However, the **colonists** were confined to disturbed sites and were not typical of the elevational zones. Lowland bryophytes exhibit **mat** forms with water lobules, water sacs, and rhizoid discs. The balance of high temperatures with the humidity of both the lowlands and submontane belt seem to favor the passive reproduction (having low or moderately low sexual and asexual reproduction) of **perennial shuttle** and **perennial stayer species**. In the more humid and often foggy montane zone, the **mat** forms of the lowlands disappear and **dendroid** and **pendent** forms join the more universal **fan** and **weft** forms – all forms that are able to condense water from the fog and mist (**fog-stripping**). The leaves are often ciliate or deeply fissured and frequently have a **rill-like** arrangement (like series of small, narrow valleys), all characteristics that facilitate water uptake, conduction, and storage. High vegetative reproduction through propagules and clonal growth predominates here. In the upper montane zone near timberline, the bryophytes of the

Peruvian Andes likewise exhibit **short** and **tall turfs** of other upper montane forests but also "**tails**." They retain the rill-like leaf arrangement seen in the humid montane zone and commonly have a central strand, as seen in bryophytes of other upper montane forests. These bryophytes put forth a high sexual reproductive effort, producing numerous sporophytes on a regular basis, a pattern of change toward timberline also seen in Southeast Asia and Central Africa.

Figure 127. Andes at Huandoy, Peru. Photo by Clarquitecto, through Creative Commons.

It is noteworthy that the development of **anisospory** (in bryophytes refers to a bimodal size difference between spores produced in the same sporangium) and **heterospory** (having spores of two sizes) occurs within the tropical Andean forests (Figure 128) (Kürschner & Parolly 1998a), although it can be argued that bryophytes lack true heterospory (see Volume 1, Chapter 3-3 on Sexuality: Size and Sex Differences). Anisosporous bryophytes in the **perennial shuttle** category exhibit the development of **dwarf males** (small males epiphytic on females) with no size differentiation visible among the spores. In other cases, true size differences occur, where small male spores and large female spores occur in the same capsule, for example, in ***Macromitrium*** spp. (Figure 129) and ***Phyllogonium fulgens*** (Figure 130). ***Leptodontium viticulosoides*** (Figure 131) exhibits a functional heterospory in which small spores are able to travel long distances, whereas the larger spores are more adaptive for short distances and a quick start for the protonema upon germination – an ideal shuttle strategy.

Figure 128. Tropical Andean forest. Photo by Samuel Rengifo, through Creative Commons.

Figure 129. ***Macromitrium sulcatum***, in a genus with two spore sizes, on ***Careya arborea***. Photo by Shyamal L., through Creative Commons.

Figure 130. ***Phyllogonium fulgens***, a species that has two spore sizes and genders. Photo by Michael Lüth, with permission.

Figure 131. ***Leptodontium viticulosoides***, a species with small and large spores that are not separated by gender. Photo by Claudio Delgadillo Moya, with permission.

Physiological adaptations necessarily include tolerance to desiccation and in some cases resistance to drying. Akande (1985) found that the corticolous liverworts ***Frullania spongiosa*** (see Figure 72) and ***Mastigolejeunea***

florea (see Figure 132) had higher osmotic potentials than the mosses ***Stereophyllum nitens*** (see Figure 133) and ***Calymperes palisotii*** (Figure 134) in his Nigerian study. This potential increased from wet to dry season, presumably making it easier for them to extract water from dew and fog.

Figure 132. ***Mastigolejeunea auriculata***; ***M. florea*** is a leafy liverwort that uses high osmotic potentials to maintain hydration. Photo by Blanka Aguero, with permission.

Figure 133. ***Stereophyllum wightii***; ***S. nitens*** has a low osmotic potential when compared with ***Mastigolejeunea florea***. Photo by Michael Lüth, with permission.

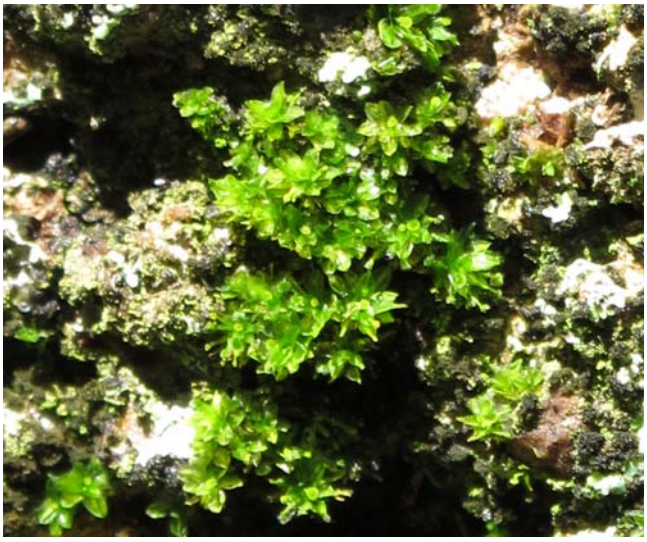

Figure 134. ***Calymperes palisotii***, a species with a low osmotic potential when compared with ***Mastigolejeunea florea***. Photo by Scott Zona, with permission.

Life Cycle Strategies

Understanding the climate and soil parameters that define the bryophyte distributions is just a beginning of our understanding of the limitations of distribution. The physiology and reproductive biology of the bryophytes are likely to be major factors in their distribution. Maciel-Silva *et al*. (2012) examined reproductive performance as influenced by elevation in both monoicous and dioicous bryophytes in the Brazilian Atlantic rainforest. They sought to separate effects of reproductive strategy from effects of habitat. Using 11 species of bryophytes, they measured reproductive performance of sexual branches, sex organs, fertilization, and sporophyte production at sites from sea level to the montane region during 15 months. As is typical, monoicous bryophytes had the highest reproductive performance, with more sexual branches, fertilized eggs, and capsule production. At sea level, bryophytes produced more sexual branches and had more female-biased sex ratios than did those in the montane site. Nevertheless, the sporophyte frequency was similar between sea level and montane zones. Fertilization occurred mostly during periods of heavy rains (October to December). But habitat is also important in influencing life-history differences. The high production of reproductive structures early in the reproductive phase seems to compensate for the female-biased sex ratios and low fertilization rates. Maciel-Silva and Valio (2011) found similar phenological characteristics in the reproduction of bryophytes from sea level and the montane region of Brazil.

Santos *et al*. compared monoicous vs dioicous species numbers at five elevations at Serra do Mar State Park, Brazil. The pattern is interesting because the ratio of dioicous to monoicous is highest at sea level, then drops, and again rises at 1200 m (. This ratio is even more pronounced for liverworts than for mosses. The monoicous condition increased with elevation except on the mountaintop (1200 m). The researchers suggested that asexual reproduction may permit species to live in conditions that are unfavorable to fertilization, particularly for dioicous taxa.

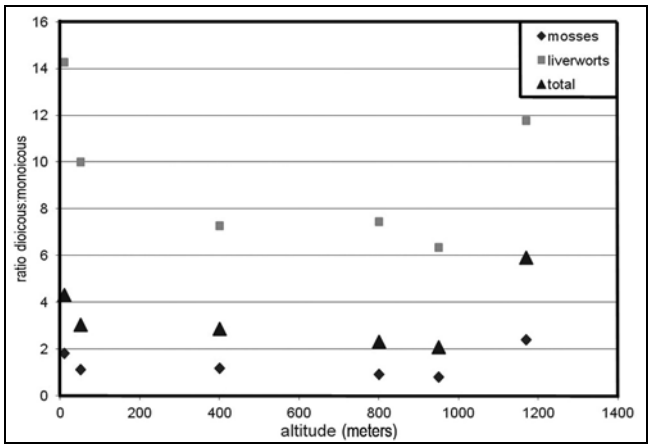

Figure 135. Dioicous-monoicous comparison for bryophytes at five elevations at Serra do Mar State Park, Brazil. Modified fom Santos *et al*. 2017.

Frey *et al*. (1995) examined the life strategies of epiphytic bryophytes on an elevational gradient from tropical lowland and montane forest, ericaceous woodlands, and the ***Dendrosenecio*** (Figure 136-Figure 137) subpáramo of the eastern Congo basin and adjacent mountains as part of the BRYOTROP expedition. They identified three strategies: **colonists**, **perennial shuttle species**, and **perennial stayers**. But only the **perennial stayers** seem to be important, an indication of the more constant ecological conditions and long-lasting microsites for epiphytes. These conclusions were based on both sociological investigations and determination of mean percentage cover values in each of the life strategy categories. In the tropical lowland and lower montane zone forests the **perennial shuttle** species and **perennial stayers** with moderately low or low sexual and asexual reproductive effort are most common. This strategy is suitable for the high temperatures and humidity levels in these zones. In the montane rainforests and cloud forests of the upper montane zone, the **perennial shuttle** species is still dominant, but has high asexual reproductive activity using propagules and clonal growth. In the secondary forests of this zone and in the ericaceous woodlands and subpáramo of African volcanoes (Figure 138), the **perennial shuttle** and **perennial stayers** are dominant, using high levels of sexual reproduction and producing sporophytes regularly here and in the subalpine-alpine zone. Such a strategy is typical for epiphytes under xeric conditions. Thus, life cycle strategy seems to be important as an adaptation to the changing conditions that arise with elevational change.

Figure 136. ***Dendrosenecio***, a genus typical of the subpáramo of the eastern Congo basin, Rwenzori Mountains National Park, Africa. Photo by Agripio, through Creative Commons.

In the Neotropics, Batista *et al*. (2018) studied life forms in the humid forest of Chapada do Araripe, Ceará State, Brazil. This region experiences seasonal rainfall. The predominant life forms are the desiccation-tolerant **turfs** and intermediate **mat** and **weft** (67%) life forms (Figure 139). Few low-tolerance species (3%) were present. Turfs were further divided into **turf** and **sparse turf**. **Mats** also included **thallose mats**. The monoicous life strategy predominated (67%), with 75 % of those with asexual reproductive means (gemmae, regenerating fragments, and caducous leaves) being dioicous species (Figure 140).

Figure 137. ***Dendrosenecio***, a genus in the subpáramo of the eastern Congo basin. Photo through Creative Commons.

Figure 138. Páramo on Mt. Cameroon old lava flows. Photo by Amcaja, through Creative Commons.

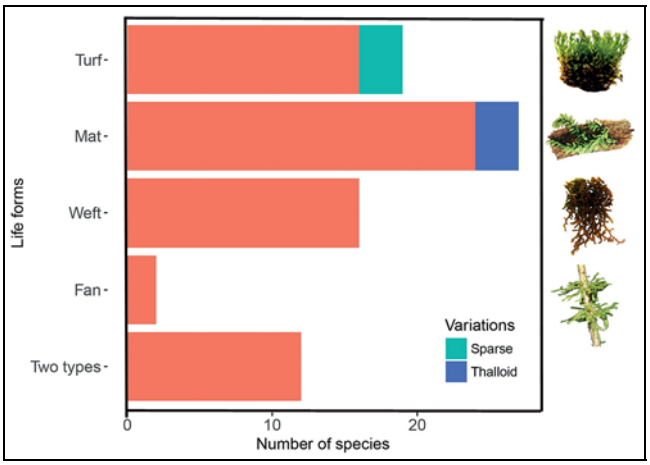

Figure 139. Number of species in the represented life forms in the humid portion of northeastern Brazil. Modified from Batista *et al*. 2018.

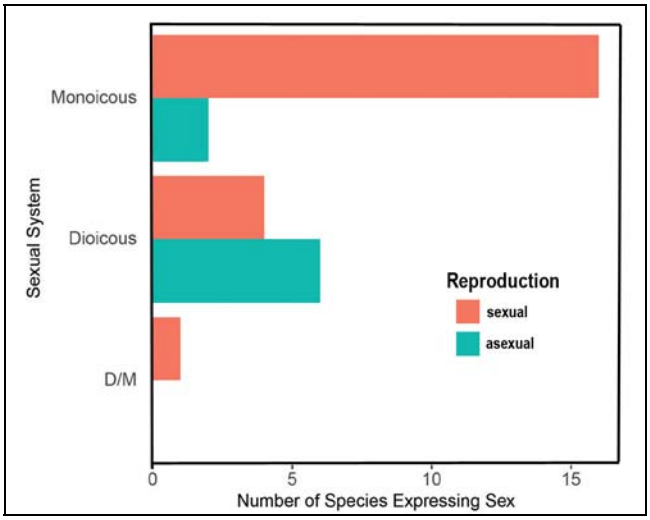

Figure 140. Sexual vs asexual reproductive strategies in the humid portion of northeastern Brazil. Modified from Batista *et al.* 2018.

Batista *et al*. (2018) also examined substrate preferences. Bark epiphytes were by far the most species rich (Figure 141). Some preferred rocks or soil, but the number without any substrate preference was large, exceeded only by bark species.

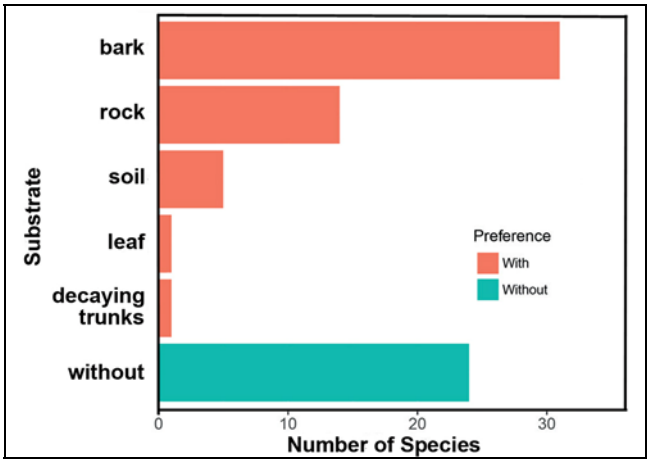

Figure 141. Numbers of species **with** substrate preferences, on tree bark, rocks, soil, leaves, and on decaying tree trunks in the humid portion of northeastern Brazil. Species that colonize more than one type of substrate (two types) and those that do not demonstrate any preference (**without**). Modified from Batista *et al*. 2018.

Silva *et al*. (2014) found that mean dirunal temperature range explained habitat suitability for 9 of the 10 indicator species they used from the Brazilian Atlantic Forest. This can explain the elevational distribution of bryophytes.

Summary

High elevations near the equator have similar bryophytes to those at lower elevations farther from the equator. Tropical bryophyte diversity and abundance both increase from lowlands to montane regions. Bryophytes throughout most of the humid tropics have the same elevational zonation patterns: lowland forest, submontane forest, upper lower montane forest, montane forest, and subalpine forest, mimicking the zonation patterns of tracheophytes and correlating with temperature and available moisture. Bryophytes, therefore, serve as good indicators of the zones.

In southeastern Brazil, **dioicous** species predominate in all elevations, with the smallest dioicous:monoicous ratio at mid elevations. **Endemism** increases with elevation, but in some locations, endemism can be very low. The highest elevation records of bryophytes are mostly in the tropics. The greatest species richness typically occurs below the alpine zone. The **α diversity** in the Andes is typically similar, but **β diversity** and **γ diversity** in the Andes are much greater.

Species presence and percent cover seem to be of equal importance in distinguishing bryophyte zones. These are highest in the **condensation zones**. Higher elevations tend to have more moisture and greater species richness. At low elevations, light intensity barely exceeds the **light compensation point**, greatly limiting productivity. This problem is exacerbated by the high temperatures, as supported by transplant studies. Mosses do not support **Rapoport's elevational rule** (prediction of trends of increased elevational ranges of plants with increase in elevation). It is likely that genetic races will emerge as we examine molecular data for the species that occur in multiple zones.

Both abundance and biomass of epiphytic bryophytes increase from the lowlands to the **treeline.** Both low and high water content severely limit photosynthesis. **Perennial stayers** and **perennial shuttle species** predominate throughout the elevations, but life forms change from **mat** forms of the lowlands to **dendroid**, **pendent, fan**, and **weft** forms that can extract moisture from fog in higher elevations of the montane. **Cushions** become common in the alpine zone. Sea level bryophytes may produce more sexual branches and have more female-biased sex ratios than do those in the montane zone. The **perennial shuttle** species is still dominant in the montane zone, but has high asexual reproductive activity using propagules and clonal growth.

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CHAPTER 8-9
TROPICS: SUBMONTANE AND MONTANE

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CHAPTER 8-9
TROPICS: SUBMONTANE AND MONTANE

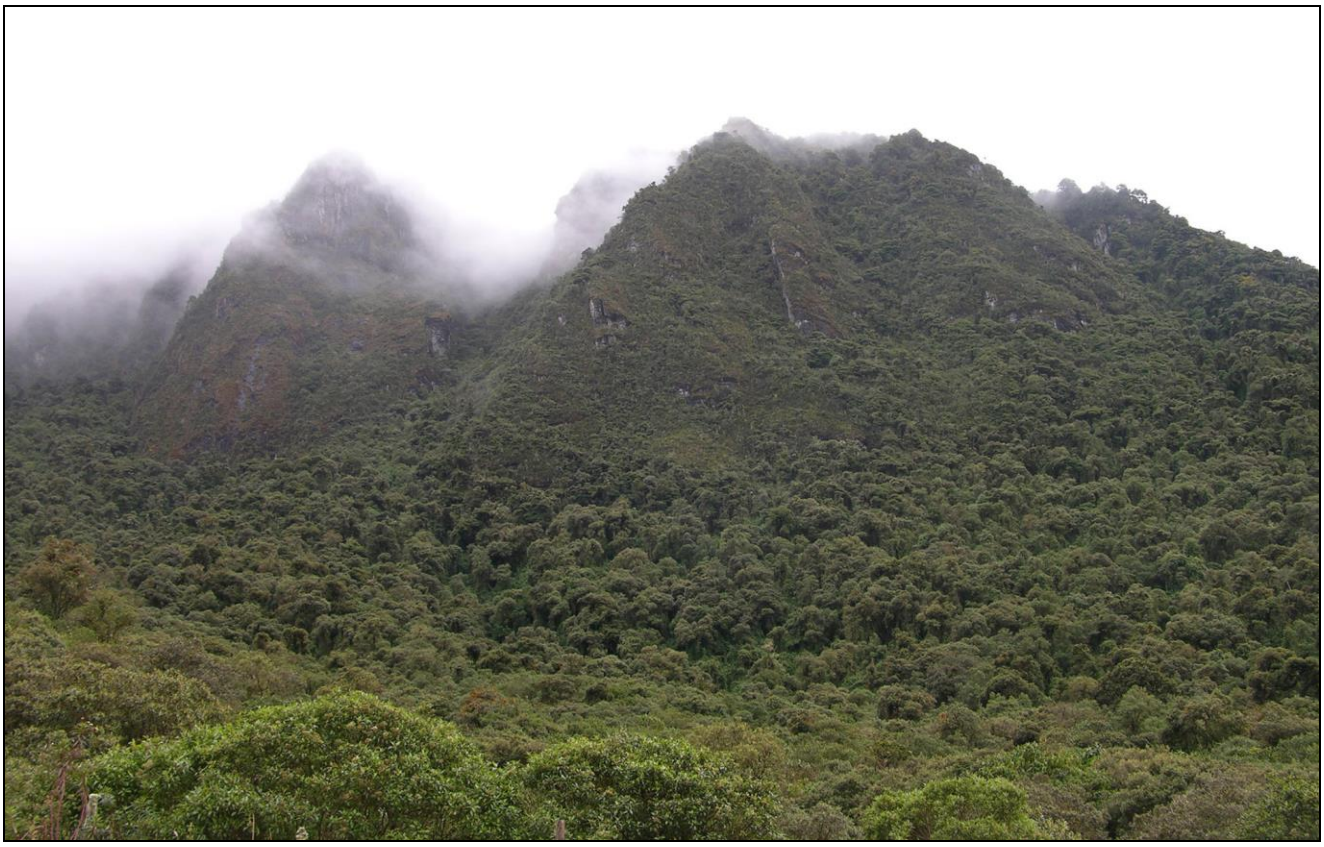

Figure 1. Ecuadorian mountains and cloud forest. Photo by Arthur Anker, with permission.

Altitudinal zonation of bryophytes in the humid tropics are similar throughout the world (Frahm & Gradstein 1991). This subchapter will discuss zonation of the submontane and montane zones.

Submontane

The submontane region in Dominica are influenced primarily by the presence or absence of the canopy tree *Amanoa caribaea* (DeWalt *et al*. 2016). But in addition to that, hurricane disturbance is a major factor.

Aceby *et al*. (2003) compared bryophyte species richness in the submontane rainforest and fallows of Bolivia. The fallows exhibited a significantly decreased diversity of moss species, but the liverwort diversity showed little reduction in species except in the very young fallows. **Smooth mats** were significantly greater in presence in the fallows (72%), probably due to the warmer, drier climate there. Generalists and sun species were the more common members of the fallow communities, with about half of the submontane species occurring there. The specialists are slower to become re-established. The submontane exhibits the highest species richness in the canopy, whereas the fallows reaches its highest diversity in the understory. This was in part due to the shifting of typical **rough mats**, **fans**, and **tails** to the lower heights in the fallows where the air temperature and humidity were more similar to those of the montane forest.

In central Sulawesi (Figure 2), Sporn *et al*. (2010) found 146 epiphytic species. They noted that this was among the highest number of epiphytic bryophyte species reported for any tropical forests, suggesting that the Malesian region is a global biodiversity hotspot. Among these bryophytes, 45% of the species were restricted to the tree crowns. The **dendroid** and **fan**-like species were in the understory; **tufts** dominated in the tree crowns.

Valdevino *et al*. (2002) reported on the pleurocarpous mosses (*e.g.* Figure 21-Figure 22) from a submontane rainforest in Pernambuco State, Brazil. They found only 23 pleurocarpous moss species in the 700 ha of their study of valleys and hills at 900-1,120 m asl.

Sonnleitner *et al*. (2009) found that even the smallest disturbance of the forest canopy could alter the microclimate and have a negative impact on the epiphyll community in the tropical lowland rainforest in Costa Rica (Figure 3).

Figure 2. Rice field with coffee and cacao plantations and submontane rainforest in the background, Sulawesi. Photo courtesy of S. Robbert Gradstein.

Figure 3. Submontane rainforest Costa Rica. Photo courtesy of S. Robbert Gradstein.

The strong response of epiphyllous (Figure 4) bryophytes to even subtle microclimatic variations suggests that undisturbed forest canopies and their control on microclimate may be essential for the development of epiphyll communities.

Figure 4. Epiphylls on a leaf. Photo by Rafael Medina, with online permission.

In a submontane tropical rainforest in Panama (Figure 5), Zotz *et al*. (1997) found that water relations were important. Both low and high water contents reduced carbon gain. Low light levels such as those found during a rainstorm were less important. They found a net carbon gain for the year for the mosses and liverworts to be 45%.

Figure 5. Panamanian sub-montane and montane rainforests. Photo by S. B. Matherson, through Creative Commons.

One of the factors that can affect productivity is nitrogen availability. Bryophytes can't use atmospheric nitrogen, but nitrogen fixation by associated organisms contributes to their nitrogen supply. Matzek and Vitousek (2003) found that when leaves had low N:P ratios, the N fixation was greater.

In the Colombian Andes (Figure 6), Gradstein *et al*. (1989) found that liverworts outnumber the mosses in both upper submontane and montane forests on the western slopes, but in drier environments their species numbers are lower than those of mosses. Species richness increases with altitude to the upper montane forest. Furthermore, at the lower altitudes, the wide-ranging tropical species are most prevalent.

Figure 6. Ritacuba Blanco, in the Andes of Colombia. Photo by 2005biggar, through Creative Commons.

Kürschner *et al*. (1999) described, for the first time, the pantropical patterns of life forms, life strategies, and ecomorphological structures of bryophytes inhabiting tree trunks. These represented altitudinal variations in transects in Southeast Asia, Africa, and South America. They considered the **mat**-forming **perennial stayers** and **perennial shuttle** species to characterize the tropical lowlands and submontane belt. In Ecuador, Kürschner and Parolly (2005) compared life forms in submontane and montane epiphytic bryophyte communities. The life forms are actually functional types and can provide considerable information (humidity, water supply, desiccation risk, light climate) about an ecosystem without necessitating species identification. In the submontane region, **mat**-forming **perennial stayers** and **perennial shuttle species** are the dominant forms, forming the ***Symbiezidio transversalis*** (Figure 7)-***Ceratolejeunion cubensis*** (Figure 8) alliance. These are replaced by **fan** and **weft** life forms of **perennial stayers** and **perennial shuttle species** in the more montane regions, where they can take advantage of the cooler, more humid climate.

Figure 7. ***Symbiezidium*** sp.; ***S. transversalis*** is a species indicative of the submontane zone. Photo by Hermann Schachner, through Creative Commons.

Parolly and Kürschner (2004) found that bryophytes in the submontane and montane regions of southern Ecuador fall into two zonal groups. The submontane ***Symbiezidio transversalis*** (Figure 7)-***Ceratolejeunion cubensis*** (Figure 8) has two communities, whereas the montane ***Omphalantho filiformis*** (***Cheilolejeunea filiformis***; see Figure 9)-***Plagiochilion apicedentis*** (***Plagiochila longiramea***; see Figure 10) has six. There is a slight deviation from the species in these associations in Peru (Figure 11). The epiphytic bryophyte communities correspond "perfectly to the supporting forest types" and thus are useful in defining the vegetation zones.

Figure 8. ***Ceratolejeunea cubensis***, a species indicative of the submontane zone. Photo by Scott Zona, with permission.

Figure 9. ***Cheilolejeunea*** (**Lejeuneaceae**) from the Neotropics; ***Cheilolejeunea filiformis*** forms an association with ***Plagiochila longiramea*** in the Neotropical montane zone. Photo by Michael Lüth, with permission.

Figure 10. ***Plagiochila adianthoides*** from the Neotropics; ***Plagiochila longiramea*** forms an association with ***Cheilolejeunea filiformis*** in the Neotropical montane zone. Photo by Michael Lüth, with permission.

Figure 11. Submontane rainforest in the Peruvian Andes. Photo courtesy of S. Robbert Gradstein.

Montane Forests

Even countries like Ethiopia (Figure 12) and Kenya (Figure 13) that we picture as dry can have distinctive montane bryophyte communities (Hylander *et al*. 2010). In their first collecting trip to the southwestern Ethiopian montane forests (Figure 12), Hylander and coworkers recorded 89 species of liverworts, with 51 of these species new for Ethiopia.

Figure 12. Harenna Forest and Bale Mountains, southeastern Ethiopia. Photo by Sabine's Sunbird, through Creative Commons.

Figure 13. Montane rainforest around Mt Kenya. Photo by Chris 73, through Creative Commons.

These forests not only have a higher altitude, but also have rocky soil types (Pires & Prance 1985). The rocky substrate can create extreme drought, particularly during the short dry periods. At higher elevations there is greater humidity. The air can be saturated, providing a constant mist that is available to the bryophytes. Mosses, lichens, and small ferns form carpets over the rocks, tree trunks, and branches. Where the slopes are not steep, the forest is dense. Trees become smaller with altitude, with the treeline at Serra Neblina, Brazil (Figure 14), at about 2,600 m asl. The flowering plant family Theaceae (Figure 15) becomes prominent at higher altitudes and insectivorous Sarraceniaceae (*Heliamphora*; Figure 16) occur here. Fire is more likely here, but in Guayana the humidity is high and fires are uncommon.

Figure 14. Serra Neblina, where the **Theaceae** is common. Photo by Michellblind, through Creative Commons.

Figure 15. ***Gordonia fruticosa*** (**Theaceae**) with bryophytes on the bark. **Theaceae** becomes prominent at higher altitudes at Serra Neblina, Brazil. Photo by David J. Stang, through Creative Commons.

Figure 16. ***Heliamphora chimantensis***, an insectivorous plant in the Serra Neblina in Peru. Photo by Andreas Eils, through Creative Commons.

In the Neotropics, the upper montane rainforest (Figure 17) can be distinguished from the lower montane rainforest by the greater percentage of temperate vegetation in the upper one (Churchill *et al*. 1995). The lower montane cloud forests, typically between 1,000 and 2,000 m asl, are characterized by a high percentage of epiphytes and tropical taxa.

Figure 17. Upper montane forest, Pui-Pui, Junín, Peru. Photo by E. Lehr and R. von May, through Creative Commons.

Montane forests have a simpler structure than the lowland forest with a much more luxuriant epiphytic vegetation (Gradstein 1992). The forest floor is often covered with dense carpets of bryophytes, in contrast to the lowland forests. Low temperatures and higher light levels than in the lowland forests support a luxuriant growth of bryophytes up to 15-20 cm thick. These growths may be **tall turfs**, **feather** types, and **pendent** life forms.

The montane forest ecosystems are the most diverse of the highland habitats. In Bolivia, 88% of the liverworts and 74% of the mosses known in the country occur in the montane forest, yet this forest type occupies only 8% of the land (Churchill *et al*. 2009).

Within the highlands the 226 montane forest ecosystems are the most diverse. In Bolivia, for example, montane forests (Yungas and Tucuman-Bolivian) occupy only 8% of the land surface of the country, but contains 88% of the liverworts and 74% of the mosses recorded from the country (Churchill *et al.* 2009).

In the Ecuadorian montane (Figure 18) and lowland rainforest (Figure 19), Grubb *et al*. (1963) found an "exceedingly high" diversity of mosses (2,058 species), suggesting that the tropical Andes might be the richest in species of any tropical region of the world. The tropical Andes have approximately eight times as many species as the Amazon basin. The moss flora supports the vegetation zonation concept, with strong differences between the montane-páramo/puna ground species and the montane forest where epiphytes predominate.

Figure 18. Montane region, El Cajas National Park, Ecuador. Photo by Kate, through Creative Commons.

Figure 19. Ecuador tropical rainforest in middle of Rio Tiguiono at Bataburo Lodge. Photo by Andreas & Christel Noellert, with permission.

In the montane rainforest of Peru, at 2,400 m asl in the Peruvian Yungas, a single tree of ***Weinmannia*** (Figure 20) sp. was substrate for 110 bryophyte species – 77 liverworts, 32 mosses, and 1 hornwort, a remarkably high species richness (Romanski *et al*. 2011). Using the Johansson zones (lower trunk, upper trunk, mid-crown, mid-outer crown, and outer crown), the researchers found that the upper trunk and large branches of the mid-crown had the highest species richness and abundance. Liverworts, especially **Lejeuneaceae** (Figure 9), dominated all five Johansson zones. (See Gradstein 1995 for additional discussion of the liverwort diversity in the montane forests of the tropical Andes.) The mid-crown enjoys a higher light intensity than the darkness surrounding the lower trunk, coupled with a high relative humidity. Romanski *et al*. distinguished four communities: outer crown, mid to mid-outer crown, upper trunk, and lower trunk. The outer crown had a remarkable 35 liverwort species, joined by only 2 moss species. Of these, 17 of the liverworts had a high light tolerance. This suggests that overall these liverworts have a higher tolerance to high light and exposure.

Costa and Lima (2005) supported previous studies by finding that the moss flora is not uniform in the tropical rainforests of Rio de Janeiro, southeastern Brazil. The lowland, montane, submontane, and upper montane Atlantic rainforests have very different moss floras. The highest number of exclusive species and greatest species richness occur in the montane Atlantic rainforest. The intermediate level of species richness is in the sub-montane Atlantic rainforest. The lowland Atlantic rainforest has the smallest number of species. The high diversity seen in the montane forest is most likely a consequence of the diversity of climatic, edaphic, and physiographic changes present in the macrophytic vegetation. The moss family **Sematophyllaceae** (Figure 21) comprises 19% of the taxa in the lowland forest, the **pendent** mosses of **Meteoriaceae** (Figure 22) 10% of the montane forests, and **Dicranaceae** (Figure 26) 18% of the upper montane forests. Those taxa having broad Neotropical distributions are important in all these forests. These comprise 40% of the bryophyte taxa. Grubb (1977) contributed additional information on the mineral nutrition in wet tropical mountains.

Figure 20. ***Weinmannia trichosperma*** trunk with epiphytes. Photo by Lin Linao, through Creative Commons.

Figure 21. ***Sematophyllum*** sp. from the Neotropics; **Sematophyllaceae** comprise 19% of the lowland forest bryophyte taxa. Photo by Michael Lüth, with permission.

Figure 22. ***Meteorium nigrescens*** (**Meteoriaceae**) from the Neotropics. Photo by Michael Lüth, with permission.

Gradstein and Vána (1994) noted the similarity of the bryophyte community of tropical montane forests of Mexico to that of the boreal community. For example, in the central highlands of the Chiapas, the ***Nowellia curvifolia*** (Figure 23) community is common on rotten logs and is rich in boreal liverworts. Among these, ***Cephalozia catenulata*** (Figure 24), ***Nowellia curvifolia***, ***Campylopodiella stenocarpa*** (Figure 25), and ***Dicranum frigidum*** (Figure 26) were the most abundant. The humid flanks of logs typically had ***Syzygiella autumnalis*** (Figure 27), ***Leptoscyphus amphibolius*** (see Figure 28), and ***Lophozia longiflora*** (Figure 29), with ***Anastrophyllum hellerianum*** (Figure 30-Figure 31) also being frequent. In addition to these locations on logs, ***Nowellia curvifolia*** is very abundant on logs that have already lost their bark (**decorticated** logs).

Figure 23. ***Nowellia curvifolia***, a common species on rotten logs in the Chiapas. Photo by Štěpán Koval, with permission.

Figure 24. ***Cephalozia catenulata***, a common species on rotten logs in the Chiapas. Photo by Michael Lüth, with permission.

Figure 25. ***Campylopodiella ditrichoides*** with capsules; ***C. stenocarpa*** is a common species on rotten logs in the Chiapas. Photo by Michael Lüth, with permission.

Figure 26. ***Dicranum frigidum***, a common species on rotten logs in the Chiapas. Photo by Jan-Peter Frahm, with permission.

Figure 27. ***Syzygiella autumnalis***, a common species on rotten logs in the Chiapas. Photo by Michael Lüth, with permission.

Figure 28. ***Leptoscyphus azoricus***; ***L. amphibolius*** is a common species on rotten logs in the Chiapas. Photo by Jan-Peter Frahm, with permission.

Figure 29. ***Lophozia longiflora***, a common species on rotten logs in the Chiapas. Photo by Michael Lüth, with permission.

Figure 30. ***Anastrophyllum hellerianum*** on log. Photo by Michael Lüth, with permission.

Figure 31. ***Anastrophyllum hellerianum***, a common species on rotten logs in the Chiapas. Photo by Michael Lüth, with permission.

Among the early south American bryophyte studies was that of Linares (1986). This researcher studied the taxonomic and ecological aspects of the high Andean strip of the El Tabalzo, Cundinamarca, Colombia.

As already noted for epiphytes in earlier subchapters, Veneklaas (1990) reported that the bryophytic epiphytes in the montane rainforests can play a major role in the nutrient dynamics of the rainforest. Veneklass found that in two epiphyte-rich Andean rainforests of the Central Cordillera of Colombia, the elevation of 2,550 m exhibited a higher nutrient input to the forest through bulk precipitation, at least in part because this elevation has higher total precipitation. At the same time, losses of nutrients from the canopy were also higher, both in total amounts and per unit of precipitation. Bryophytes are able to capture and hold nutrients, often releasing pulses in the first rainfall after a drying period.

Concerned with the role of bryophytes in maintaining water balance and contributing to nutrient cycling in tropical montane forests, Benítez *et al*. (2015) assessed bryophytes and lichens on tree bases of 240 trees in both primary and secondary forests in southern Ecuador (Figure 19). As expected, diversity was higher in primary forests than in monospecific secondary forests. The reduction of canopy diminished bryophyte species. Shade epiphytes were intolerant of the increased light penetration and were replaced by sun epiphytes in the secondary forests.

Bisang *et al*. (2003) explored the diaspore banks in three Malaysian mountain rainforests (Figure 32). They

incubated soil samples from 0-5 cm depth for 15 hours of light daily and mean daily temperature of 19ºC with radiation of 3-5 µE m^{-2} s^{-1}. These were kept moist with sterilized water as needed. After 5 months the cultures were gently disturbed with forceps. After 4 and 5 months they were placed under a bright light intensity of 100 µE m^{-2} s^{-1}. Liverwort emergence exceeded that of mosses, especially from soils from lower altitudes. Consistent with living bryophytes, the species diversity was twice as high in samples from higher elevations compared to those from lower ones.

Figure 32. Montane rainforest in tropics on Gunung Batu Brinchang, Malaysia. Photo by Peter Coxhead, through Creative Commons.

In Costa Rica, Dauphin L. and Grayum (2005) collected from dry lowland forests and moist montane forests in Guanacaste Province, Costa Rica (Figure 33). In the moist montane forests, **corticolous** (growing on bark) bryophytes predominate. This is in contrast to the soil, log, and rock substrates that are most important in the lowland dry forests. The submontane zone had significantly less species richness. The researchers considered higher temperatures, limiting water availability, and human disturbance as factors limiting the diversity of the submontane zone. Rare species occurred on the tree boles, with 99% of the locally rare species occurring on the tree boles.

Figure 33. Guanacaste, Costa Rica, montane forests. Photo by Jason Folt, with permission.

Song *et al*. (2015) compared bole bryophytes in three protected forests, one in sub-montane, one in montane, and one in subalpine regions in Yunnan, China (Figure 34). Five plots were established at each of 12 altitudes, using 200 m intervals, totalling 594 subplots. The total number of species identified was 226. Life forms differed among the forest types, with **smooth mat** dominating the sub-montane, **fan** in the montane, and **turf** in the subalpine.

Figure 34. Lowland forest, Guangnan, Yunnan, China. Photo by Anders Johnson, through Creative Commons.

The Itatiaia National Park in Brazil (Figure 35) has well-defined climatic bands of montane, upper montane, and high-altitude fields. Costa *et al*. (2015) used literature, herbarium material, and data banks in addition to examining 10 representative elevations. These sources revealed 519 taxa. As in many other studies, the mid-altitudinal range (2,100-2,200 m asl) had the highest species richness. The number of threatened species increased with elevation. Furthermore, the upper montane forest had the most endemic species (47).

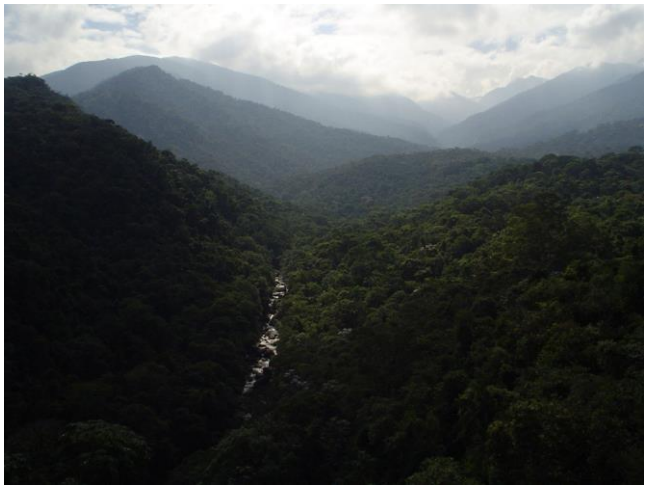

Figure 35. Mountains in Itatiaia National Park, Brazil. Photo by Pedroivan, through Creative Commons.

In Indonesia (Figure 36), submontane forests are known to have a very rich bryophyte flora (Gradstein & Culmsee 2010). On only eight canopy trees, 150 species were present. The researchers found that the lower

montane and upper montane forests of Sulawesi have very different bryophytes that characterize them. The low elevations have mostly mosses in **Calymperaceae** (Figure 37), **Fissidentaceae** (Figure 38), **Hypopterygiaceae** (Figure 93), **Leucobryaceae** (Figure 39), **Meteoriaceae** (Figure 40), **Neckeraceae** (Figure 41), **Pterobryaceae** (Figure 42), and **Thuidiaceae** (Figure 43), and liverworts in **Lejeuneaceae** (Figure 8-Figure 9), **Lophocoleaceae** (Figure 100), **Porellaceae** (Figure 60), **Radulaceae** (Figure 56). By contrast, the high elevations are characterized by the leafy liverworts **Herbertaceae** (Figure 44), **Lepidoziaceae** (Figure 97-Figure 99), **Mastigophoraceae** (Figure 45), **Scapaniaceae** (Figure 46), **Schistochilaceae** (Figure 47), and **Trichocoleaceae** (Figure 102). As is typical, the liverwort family **Lejeuneaceae** has the most species in the submontane and lower montane forests, whereas the leafy liverwort family **Lepidoziaceae** has the most in the upper montane forest. Moss dominance decreases while liverwort dominance increases with elevation. Some of these species prefer rough bark, but none shows a preference for smooth bark. Trunk diameter is important for some species, but communities don't seem to be affected by it.

Figure 36. Tangkoko National Park, North Sulawesi, Indonesia, showing mountains in the background. Photo by Lip Kee Yap, through Creative Commons.

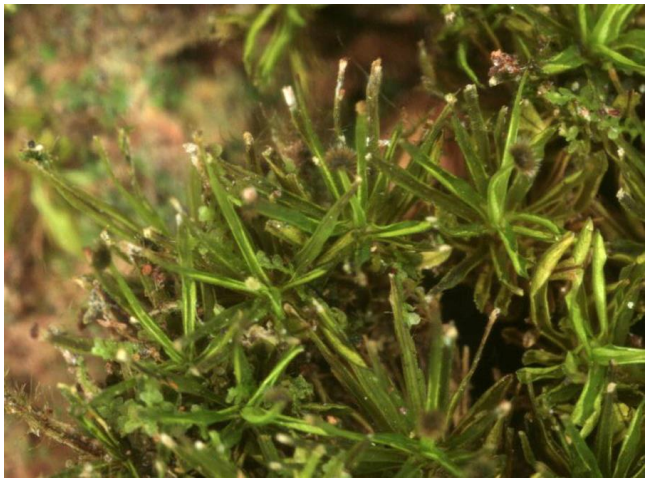

Figure 37. ***Calymperes afzelii***, one of the representatives of **Calymperaceae** in Indonesia. Photo by Jan-Peter Frahm, with permission.

Figure 38. ***Fissidens nobilis***; ***Fissidens*** species are common at low elevations in Indonesia. Photo by Janice Glime.

Figure 39. ***Leucobryum juniperoideum***, one of the representatives of **Leucobryaceae** in Indonesia. Photo by Jan-Peter Frahm, with permission.

Figure 40. ***Aerobryopsis wallichii***, one of the representatives of **Meteoriaceae** in Indonesia. Photo by Jan-Peter Frahm, with permission.

Figure 41. ***Neckeropsis lepineana***, one of the representatives of **Neckeraceae** in Indonesia. Photo by Colin Meurk, through Creative Commons.

Figure 42. ***Pterobryon*** sp. (**Pterobryaceae**), a genus with the more robust species found in drier forests of tropical Asia. Photo by Efraín de Luna, with permission.

Figure 43. ***Thuidium cymbifolium*** with capsules, one of the representatives of **Thuidiaceae** in Indonesia. Photo by Li Zhang, with permission.

Figure 44. ***Herbertus bivittatus*** from the Neotropics. The family **Herbertaceae** is known in Indonesia. Photo by Michael Lüth, with permission.

Figure 45. ***Mastigophora woodsii***. The family **Mastigophoraceae** is known in Indonesia. Photo by Blanka Aguero, with permission.

Figure 46. ***Scapania compacta***; ***S. javanica*** represents the family **Scapaniaceae** in Indonesia. Photo by Michael Lüth, with permission.

Figure 47. ***Gottschelia schizopleura***, one of the representatives of **Schistochilaceae** in Indonesia. Photo by Li Zhang, with permission.

Based on investigations in Southeast Asia, Africa, and South America, as the mountain vegetation zones shift from submontane to lower montane, the bryophyte life forms also shift (Kürschner *et al*. 1999). The **mats** are replaced by **fan** and **weft** formers that are able to take advantage of the cooler air with higher humidity. **Perennial stayers** and **perennial shuttle species** have a greater reliance on asexual propagules and clonal growth. The plants furthermore have a structure that permits them to take advantage of water vapor from fog, to conduct water internally, and to store water.

Lower Montane

In the lowland forest and the lower montane rainforest of Colombia (Figure 48), Wolf (1993a) identified four main bryophyte community groupings, primarily related to position within the host tree:

1. Communities of the lowland forest at 1,000 m (valley floor)
2. Communities of the lower montane rainforest, 1,250 m to ca. 2,130 (2,550) m
3. Communities of the upper montane rainforest, ranging from ~2,460 m to the treeline at 3,700 m.
4. Communities of ***Polylepis*** (Figure 49-Figure 50) dwarf forest at 4,130 m.

Figure 48. Lower montane forest in Colombia, rich in tracheophytic epiphytes. Photo by A. M. Cleef, courtesy of S. Robbert Gradstein.

Figure 49. Páramo of Ecuador with remnant subalpine ***Polylepis*** dwarf forest in the back at skyline. Photo courtesy of S. Robbert Gradstein.

Figure 50. Subalpine dwarf mossy ***Polylepis pauta*** forest in Ecuador. Photo by K. Romoleroux, courtesy of S. Robbert Gradstein.

The ***Polylepis pauta*** (Figure 49-Figure 50) forests have dominated in many humid environments of the high Andes of Ecuador, Peru, and Bolivia (3,500-4,500 m asl) (Gradstein & León-Yánez 2018). However, now these forests are greatly diminished due to replacement with grasslands for grazing. They have become one of the most threatened ecosystems in South America. Gradstein and León-Yánez have documented the liverwort flora in the remnant forests in the páramo of Papallacta, Ecuador, finding 51 liverwort species. The forest floor and tree bases were nearly completely covered with bryophytes, in particular ***Lepidozia auriculata*** (see Figure 99) and the robust ***Plagiochila*** species ***P. dependula***, ***P. ensiformis***, ***P. fuscolutea*** (Figure 51), and ***P. ovata***. The branches had abundant growths of ***Frullania paradoxa*** (see Figure 55), ***Leptoscyphus hexagonus*** (see Figure 28), ***Plagiochila bifaria*** (Figure 52), and ***P. punctata*** (Figure 53).

Figure 51. ***Plagiochila fuscolutea***, a species of the forest floor in the high Andes. Photo by Jan-Peter Frahm, with permission.

Figure 52. ***Plagiochila bifaria***, a species from the Azores and also of the forest floor in the high Andes. Photo by Jan-Peter Frahm, with permission.

Figure 53. ***Plagiochila punctata***, a species of the forest floor in the high Andes. Photo by Stan Phillips, through public domain.

The secondary, semi-deciduous lowland forest is dominated by ***Machaerium capote*** (Figure 54) (Wolf 1993a). The epiphytes are characterized by the leafy liverworts ***Frullania ericoides*** (Figure 55) and ***Radula tectiloba*** (Figure 56), as well as various **Lejeuneaceae** (Figure 9). ***Frullania ericoides*** is a pantropical xerophytic species. The canopy is characterized by a lichen community of *Heterodermia albicans* (Figure 57)-*Trypethelium eluteriae* (Figure 58). The trunk, by contrast, is dominated by the **pendent** moss ***Meteorium nigrescens*** (Figure 22) and the leafy liverwort ***Radula caldana*** (see Figure 56). Exclusive taxa in this association are ***Papillaria nigrescens***, ***Radula caldana***, ***Mastigolejeunea auriculata*** (Figure 59), ***Porella brasiliensis*** (see Figure 60), and ***Sematophyllum subpinnatum*** (see Figure 21). This community occurs from the tree base up to the inner crown. Epiphytes are absent on the twiglets of the outer canopy.

Figure 54. ***Machaerium capote***, the dominant species in the secondary, semi-deciduous lowland forest. Photo by Damon Salveo, through Creative Commons.

Figure 55. ***Frullania ericoides***, an epiphyte in secondary, semi-deciduous lowland forests of the Neotropics. Photo by Blanka Aguero, with permission.

Figure 56. ***Radula***; ***R. tectiloba*** is an epiphyte in secondary, semi-deciduous lowland forests and ***R. caldana*** is a species of the trunk in the lowland forests of the Neotropics. Photo by Michael Lüth, with permission.

Figure 57. ***Heterodermia albicans***, part of the lichen community that dominates the canopy of the secondary, semi-deciduous lowland forest. Photo by Bobby Hattaway, with online permission through DiscoverLife.

Figure 58. ***Trypethelium eluteriae***, part of the lichen community that dominates the canopy of the secondary, semi-deciduous lowland forest. Photo by Harrie Sipman, through Creative Commons.

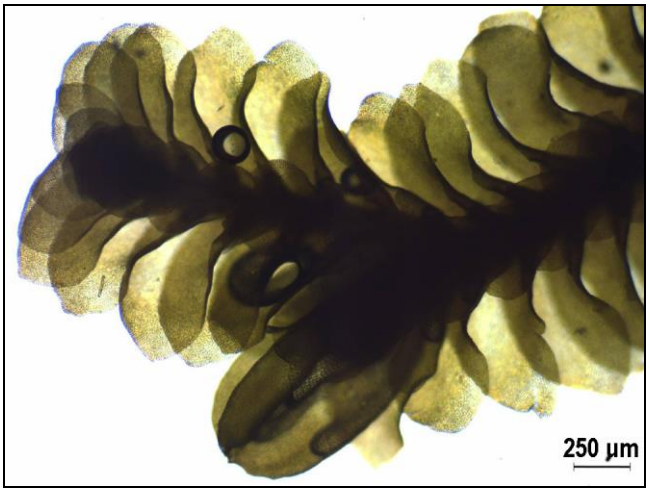

Figure 59. ***Mastigolejeunea auriculata***, a species on tree trunks in secondary, semi-deciduous lowland forests in the Neotropics. Photo by Blanka Aguero, with permission.

Figure 60. ***Porella navicularis*** on tree; ***P. brasiliensis*** is a species **pendent** on tree trunks in secondary, semi-deciduous lowland forests in the Neotropics. Photo from Botany website, UBC, with permission.

Because of the high humidity, every surface is potentially a bryophyte substrate. But these are also suitable substrata for other types of plants. Ingram and Nadkarni (1993) reported that the bryophytes formed only 5% of the epiphytic organic matter in a Neotropical lower montane forest where the dominant host was ***Ocotea tonduzii*** (see Figure 61). Flowering plants formed only 10% of the species biomass, with dead organic matter being the dominant portion at 60%.

Figure 61. ***Ocotea*** *cf* ***leucoxylon***, a species that is dominant in a Neotropical lower montane forest where bryophytes comprise only 5% of the epiphytic organic matter. Photo by Jens G. Rohwer, through Creative Commons.

The lower montane rainforest communities differ from those of the lowland forest (Wolf 1993a). Exclusive species include the leafy liverwort ***Lejeunea flava*** (Figure 62-Figure 63), the **pendent** moss ***Squamidium nigricans*** (see Figure 116), and the foliose lichen ***Parmotrema subsumptum*** (Figure 64). Three of the six identified communities of epiphytes [***Bryopteris filicina*** (Figure 65) tree bole community, ***Cheilolejeunea trifaria*** (Figure 66) **-** ***Schlotheimia acutifolia*** var. ***angustifolia*** (see Figure 67) community, ***Plagiochila fragilis*** (see Figure 51-Figure 53) community from tree crowns] share the liverwort species ***Cheilolejeunea rigidula*** (see Figure 66), ***Frullania caulisequa*** (Figure 68), ***Lejeunea laetevirens*** (Figure 69), and the moss ***Sematophyllum subpinnatum*** (see Figure 21). Furthermore, ***Cheilolejeunea rigidula*** and ***Lejeunea laetevirens*** are exclusive to these three communities. In other communities, exclusive species include ***Diplasiolejeunea pauckertii*** (see Figure 70) in the ***Diplasiolejeunea pauckertii*** - ***Brachiolejeunea laxifolia*** community and ***Squamidium nigricans*** in the ***Frullania arecae*** (Figure 71) – ***Frullanoides densifolia*** (Figure 72) – ***Squamidium nigricans*** community. In the ***Bryopteris filicina*** (Figure 65) community, present in the range of 1,210 and 1,980 m asl on the lower parts of tree trunks and less commonly on steep inner branches in the lower canopy, ***B. filicina*** is exclusive, accompanied by the liverworts ***Cheilolejeunea rigidula*** and ***Lejeunea laetevirens***. The liverworts are closely appressed and grow intermixed with feather-shaped dendroid genera such as ***Bryopteris***, ***Neckeropsis*** (Figure 41), and ***Porotrichum*** (Figure 114) that stand out for several centimeters as horizontal shelves. The ***Cheilolejeunea trifaria*** **–** ***Schlotheimia acutifolia*** var. ***angustifolia*** community occurs in the inner crowns of trees in the range of 1,210 to 1,980 m asl. This Columbian community shares ***C. trifaria*** and ***Lopholejeunea subfusca*** (Figure 73) with a lower trunk community of open secondary forests at 1,300 m asl in Malaysia (Kürschner 1990). The ***Diplasiolejeunea pauckertii*** - ***Brachiolejeunea laxifolia*** community occurs in the outer canopy at elevations primarily from 2,460 to 2,550 m asl.

Figure 62. ***Lejeunea flava***, a species exclusively in the lower montane rainforest. Photo by Linda Phillips, through Creative Commons.

Figure 63. ***Lejeunea flava*** growing as an epiphyll and typical in the lower montane rainforest. Photo by Yang Jia-dong, through Creative Commons.

Figure 64. ***Parmotrema subsumptum***, a lichen exclusively in the lower Neotropical montane rainforest. Photo through Creative Commons.

Figure 65. ***Bryopteris filicina***, a species that forms a tree bole community of the Neotropical lower montane rainforest. Photo by Eliana Calzadilla, through Creative Commons.

Figure 66. ***Cheilolejeunea trifaria***, part of the bryophyte community in tree crowns in the Neotropical lower montane rainforest. ***Cheilolejeunea rigidula*** also occurs in the crowns. Photo by Michael Lüth, with permission.

Figure 67. ***Schlotheimia*** sp., part of the bryophyte community in tree crowns in the Neotropical lower montane rainforest. Photo by Michael Lüth, with permission.

Figure 68. ***Frullania caulisequa***, part of the bryophyte community in tree crowns in the Neotropical lower montane rainforest. Photo by Blanka Aguero, with permission.

Figure 69. ***Lejeunea laetevirens***, part of the bryophyte community in tree crowns in the Neotropical lower montane rainforest. Photo by Scott Zona, through Creative Commons.

Figure 70. ***Diplasiolejeunea brunnea*** in Ecuador on leaf. Photo by Tamás Pócs, with permission.

Figure 71. ***Frullania arecae***, a species exclusive to the ***Frullania arecae*** - ***Frullanoides densifolia*** - ***Squamidium nigricans*** community in the lower montane tropical rainforest. Photo by Juan Larrain, with permission.

Figure 72. ***Frullanoides densifolia***, a species exclusive to the ***Frullania arecae*** - ***Frullanoides densifolia*** - ***Squamidium nigricans*** community in the lower montane tropical rainforest. Photo by Jan-Peter Frahm, with permission.

Figure 73. ***Lopholejeunea subfusca*** epiphyllous on palm in Fiji. This species occurs in the lower trunk community of open secondary forests in Malaysia. Photo by Tamás Pócs, with permission.

In the lower montane rainforest of Panama, water content of bryophytes experiences pronounced daily flux (Zotz *et al*. 1997). These low and high levels are more important in limiting CO_2 exchange than the low photon flux density (light level) during rainstorms. More than half of the fixed carbon was lost to respiration during the night. Lösch *et al*. (1994) contributed an additional study on the photosynthetic gas exchange of bryophytes from the tropical lowlands and mountain forests of Central Africa.

In a lower montane rainforest of New Guinea, Edwards and Grubb (1977) estimated the epiphytic biomass to be 2 t ha^{-1}. Unfortunately, the bryophyte component of this was not measured separately, but the role of the epiphytes and accumulated "soil" in the crowns contribute ca. 1 t ha^{-1} of soil. Minerals are released slowly from this epiphytic mass accumulation, providing a reservoir of nutrients for the soils.

Upper Montane

As the lower montane transitions into the upper montane, the proportion of **cushion**, **short**, and **tall turf** life forms of **perennial stayers** and **perennial shuttle species** begin to predominate (Kürschner & Parolly 2005). And as the habitat becomes more open, the bryophytes often have a dense rhizoid tomentum and a central conducting strand, aiding in rapid water conduction.

In the ericaceous forest of the upper montane of the Rwenzori Mountains of Uganda (Figure 74), Pentecost (1998) studied the epiphytes on mature trees of ***Phillipia*** (**Ericaceae**). ***Usnea*** spp. (Figure 75) and other macrolichens dominate the upper canopy. In the lower canopy, large cushion-forming liverworts such as ***Chandonanthus*** (Figure 76), ***Herbertus*** (Figure 44, Figure 77), and ***Plagiochila*** (Figure 10, Figure 51-Figure 53) dominate. Pentecost concluded that light intensity and age of host tree controlled the distribution of the bryophytes and lichens. Using fallen trees, Pentecost identified 14 bryophyte species, along with 2 algae, 22 lichens, and 2 ferns. The biomass of these organisms was nearly 1 ton ha^{-1} and comprised 10% of the above-ground standing crop. Bryophytes held 8% of the above ground nutrients, with concentrations of 10 kg ha^{-1} of N, 1 of P, and 3 of K. This

forest was cool, with the temperature below the canopy ranging 4-9.5ºC during the 10-day study period. The temperature increased slightly with canopy height. Evaporation below the canopy decreased significantly with increasing altitude from 2,300 to 3,600 m asl.

Figure 74. Rwenzori Mountains with *Denrosenecio adnivalis*. Photo by Agripio, through Creative Commons.

Figure 75. ***Usnea***, a genus that occurs in the upper canopy of the ericaceous forest of the upper montane of the Rwenzori Mountains of Uganda. Photo through Creative Commons.

Figure 76. ***Chandonanthus squarrosus***; ***Chandonanthus*** forms cushions in the lower canopy in Rwenzori Mountains of Uganda. Photo by David Tng, with permission.

Figure 77. ***Herbertus aduncus***, in a genus that forms cushions in the lower canopy in Rwenzori Mountains of Uganda. Photo by Adolf Ceska, with permission.

Bizot *et al*. (1978) conducted one of the early studies on East African bryophytes, sampling in Ethiopia, Kenya, and the United Republic of Tanzania. They identified 96 liverwort and 211 moss species. They concluded that the Ethiopian Highlands are a part of the Afromontane vegetation group. Here they found disjunct populations of ***Garckea comosa*** (see Figure 78) and ***Aongstroemia julacea*** (Figure 79).

Figure 78. ***Garckea flexuosa***; ***G. comosa*** occurs as a disjunct in the Afromontane region. Photo by Manju C. Nair, through Creative Commons.

Figure 79. ***Aongstroemia julacea***, a disjunct in the Afromontane region. Photo by Jan-Peter Frahm, with permission.

Kürschner (2003) expanded his studies of epiphytic bryophytes to Arabia. He described the associations ***Leptodonto*** (Figure 80) - ***Leucodonetetum schweinfurthii*** (see Figure 81) and ***Orthotricho*** (Figure 82)-***Fabronietum socotranae*** (see Figure 83) from the Yemen escarpment mountains. These associations are typical in the monsoon-impacted ***Juniperus procera*** (Figure 84) and ***Acacia origena*** (Figure 85) woodland. The species of bryophytes are typically drought-tolerant Afromontane mosses, with ***Orthotrichum diaphanum*** (Figure 82) and ***Syntrichia laevipila*** (Figure 86) typifying the synusiae. The drought-tolerant ***Orthotricho-Fabronietum socotranae*** (see Figure 83) is dominated by **cushions**, **short turf**, and **mat**-forming **perennial stayers** that regularly produce capsules. The sunny sites, by contrast, have **tail** or **fan** pleurocarpous **perennial shuttle species** with large spores and either moderately low reproduction or more "generative" reproduction, in addition to liverworts. This grouping forms the subhumid ***Leptodonto*** (Figure 80) – ***Leucodonetetum schweinfurthii*** (see Figure 81).

Figure 80. ***Leptodon smithii***; ***Leptodon*** is a characteristic epiphyte in sunny sites in Arabia. Photo by Michael Lüth, with permission.

Figure 81. ***Leucodon sciuroides***; ***L. schweinfurthii*** is a characteristic epiphyte in sunny sites in Arabia. Photo by Hermann Schachner, through Creative Commons.

Figure 82. ***Orthotrichum diaphanum***, a drought-tolerant Afromontane moss in Arabian ***Acacia*** and ***Juniperus*** woodland. Photo by Michael Lüth, with permission.

Figure 83. ***Fabronia pusilla***; ***F. sacrotrana*** is a drought-tolerant Afromontane moss in Arabian ***Acacia*** and ***Juniperus*** woodland. Photo by Michael Lüth, with permission.

Figure 84. ***Juniperus procera***, a species that is habitat for bryophytes in monsoon regions of Arabia. Photo by Plantsman, through Creative Commons.

Figure 85. ***Acacia abyssinica*** in Tanzania; ***A. origena*** is habitat for bryophytes in monsoon regions of Arabia. Photo by Guenther Eichhorn, through Creative Commons.

Figure 86. ***Syntrichia laevipila***, a drought-tolerant Afromontane moss in Arabian ***Acacia*** and ***Juniperus*** woodland. Photo by Jonathan Sleath, with permission.

In the upper montane oak forests in the Cordillera de Talamanca of Costa Rica, Holz *et al*. (2002) found a large diversification of microhabitats and a high diversity of bryophytes. Liverworts (106 species) were slightly more numerous than mosses (100), with 1 hornwort in only 6 ha of forest. The researchers identified three main groups of microhabitats: forest floor, including tree bases, phyllosphere, and other epiphytic habitats. The forest floor was much richer in bryophyte species than in forests of lower elevation zones. These were distributed among tree bases (69 species), rotten logs (70), and soil (69) as the most species-rich habitats (Figure 87), heralding the greater light than that in lowland forests. Trunks (61 species), branches of the inner canopy (35), twigs of the outer canopy (14), and leaves of the understory (14) supported somewhat fewer species (Figure 87).

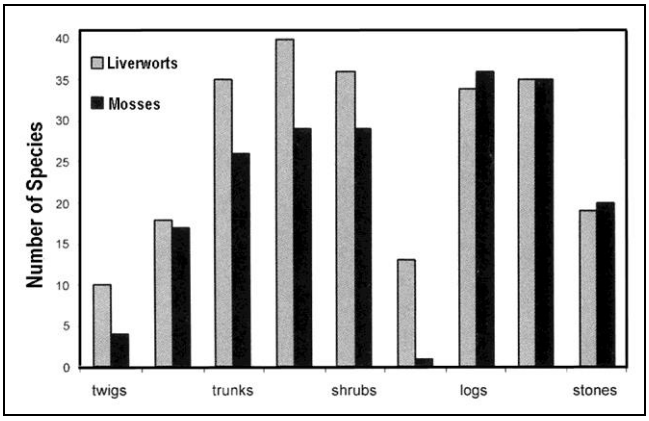

Figure 87. Number of species on each of the major microhabitats at Los Robles, Costa Rica, in the upper montane forest. Modified from Holz *et al*. 2002.

Holz and coworkers (2002) once again found that **Lejeuneaceae** (Figure 9) was by far the family represented by the most species, reaching ~60 at Monteverde, Costa Rica. The distribution of species among the major families is shown in Figure 88. The life forms are quite varied, with **turfs** and **mats** being the most common strategies (Figure 89). The "pronounced" dry season and host tree characters (tree height, stratification, number of host tree species)

modified this upper montane zone compared to more humid lower altitudes.

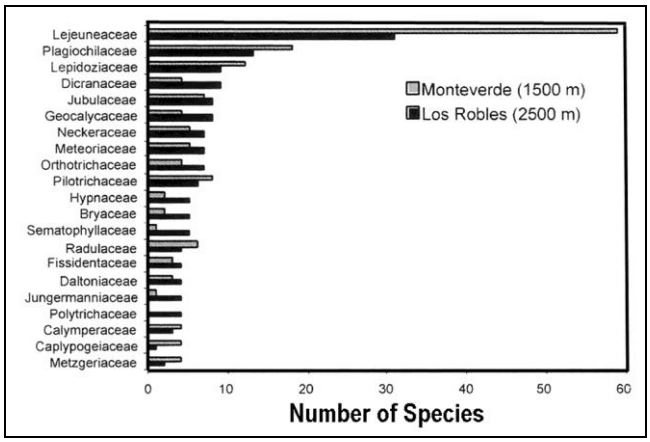

Figure 88. Numbers of species in the major bryophyte families in the upper montane forest at two sites in Costa Rica. Modified from Holz *et al*. 2002.

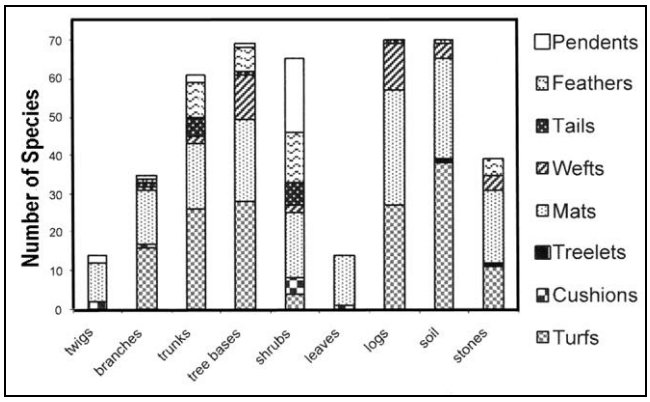

Figure 89. Proportions of species in each of the life forms in the major microhabitats at Los Robles, Costa Rica, in the upper montane forest. Modified from Holz *et al*. 2002.

Holz and Gradstein (2005) compared cryptogamic epiphytes in early and late secondary oak (***Quercus copeyensis***; Figure 90-Figure 91) forests and in primary forest in Cordillera de Talamanca, Costa Rica. They found little difference in species richness between the secondary and primary forests. They concluded that the closed canopy of the secondary forests explained the high diversity there, resulting at least in part from the high atmospheric humidity. Nevertheless, even after 40 years one-third of the primary forest species were still absent in the secondary forest. Furthermore, while diversity was similar, the community composition differed markedly between primary and secondary forest, with 40% of all the species restricted to the secondary forests.

Figure 90. ***Quercus copeyensis*** forest like those in Cordillera de Talamanca, Costa Rica. Photo through Creative Commons.

Figure 91. ***Quercus copeyensis***, a bryophyte host in Cordillera de Talamanca, Costa Rica. Photo through Creative Commons.

In the upper montane in the Central Cordillera of Colombia, rope-climbing techniques permitted assessment of the upper canopy (Wolf 1993b). Using the Braun-Blanquet method, Wolf sampled 15 sites at 200 m intervals on an altitudinal gradient. Wolf sampled four canopy trees, avoiding those with smooth, scaling, or hard bark. As in other studies, location within the host tree and altitude are the most influential characters on the epiphytic vegetation. Based on 59 host trees, Wolf found 187 liverwort and 108 moss species. There is great variability between relevés in

a single community, with a community of ~16%. A rapid change in community structure of the epiphytic vegetation occurs between 2,130 and 2,460 m asl. This is the elevation range where there is a rapid increase in air humidity. As in the Cordillera de Talamanca, *Usnea* (Figure 92) is very abundant in the outer canopy. *p*H values were somewhat wide-ranging and may have played a role in community composition. For example, at *p*H 7.1, the dominant community is that of the moss ***Hypopterygium tamariscinum*** (Figure 93) whereas at *p*H 3.2 the community of ***Scapania portoricensis*** (see Figure 46) – ***Plagiothecium novogranatense*** (see Figure 94-Figure 95) is prominent. The suspended soils of the lower montane rainforest and the upper montane rainforest differ significantly, with the latter having more organic matter and lower nutrient contents. Soils at tree bases in the lower montane rainforest have higher nutrient content than do the canopy soils. The opposite is the case in the upper montane rainforest. Exclusive epiphytic taxa in the upper montane rainforest are the liverworts ***Adelanthus pittieri*** (see Figure 96), ***Bazzania breuteliana*** (see Figure 97), ***B. hookeri*** (Figure 97), ***Lepicolea pruinosa*** (see Figure 98), ***Lepidozia*** spp. (Figure 99), ***Lophocolea trapezoides*** (see Figure 100), ***Plagiochila bursata*** (see Figure 10, Figure 51-Figure 53), ***Riccardia*** spp. (Figure 101), and ***Trichocolea tomentosa*** (Figure 102), and the moss ***Sematophyllum insularum*** (see Figure 21). In the canopy, the most common exclusive taxa are ***Anoplolejeunea conferta***, ***Jamesoniella rubricaulis*** (Figure 103), ***Leptoscyphus jackii*** (see Figure 28), ***L. porphyrius*** (see Figure 28), ***Plagiochila echinella***/***P. hansmeyeri***/***P. paludosa*** (see Figure 10, Figure 51-Figure 53), ***Prionodon fuscolutescens*** (Figure 104), ***Trachylejeunea dominicensis***, and the lichen ***Hypotrachyna laevigata*** (Figure 105)/***H. producta***. On tree bases, exclusive taxa for all five tree base communities include ***Calypogeia peruviana*** (Figure 106), ***Cephalozia crassifolia*** (Figure 107), ***Lophocolea*** aff. ***connata*** (see Figure 100), and ***Telaranea nematodes*** (Figure 108).

Figure 93. ***Hypopterygium tamariscinum***, the dominant epiphytic community at *p*H 7.1 at Cordillera de Talamanca, Costa Rica. Photo by Efrain de Luna, with permission.

Figure 92. *Usnea* hanging on pine, an abundant species in the outer canopy at Cordillera de Talamanca, Costa Rica. Photo by Fährtenleser, through Creative Commons.

Figure 94. ***Plagiothecium undulatum*** on a rotting log. Photo from Botany Website, UBC, with permission.

Figure 95. ***Plagiothecium dentatum***; some members of this genus occur at *p*H 3.2 on trees in Colombia. Photo by Janice Glime.

Figure 96. ***Adelanthus decipiens***; ***A. pitteiri*** occurs exclusively as an epiphyte in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Des Callaghan, through Creative Commons.

Figure 97. ***Bazzania hookeri***, a species that occurs exclusively as an epiphyte in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Michael Lüth, with permission.

Figure 98. ***Lepicolea ochroleuca***; ***L. pruinosa*** occurs exclusively as an epiphyte in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Jan-Peter Frahm, with permission.

Figure 99. ***Lepidozia cupressina***; some species in this genus occur exclusively as epiphytes in the upper montane rainforest of the Central Cordillera of Colombia. Photo from British Bryological Society, with permission per Barry Stewart.

Figure 100. ***Lophocolea*** *cf* ***polychaeta***; ***L. trapezoides*** occurs exclusively as an epiphyte in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Michael Lüth, with permission.

Figure 101. ***Riccardia fucoidea*** from the Neotropics; several species of ***Riccardia*** occur exclusively as epiphytes in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Michael Lüth, with permission.

Figure 102. ***Trichocolea tomentella***, a widespread species that occurs exclusively as an epiphyte in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Michael Lüth, with permission.

Figure 103. ***Jamesoniella rubricaulis***, a species that occurs exclusively in the canopy in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Jan-Peter Frahm, with permission.

Figure 104. ***Prionodon fuscolutescens***, a species that occurs exclusively in the canopy in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Juan David Parra, through Creative Commons.

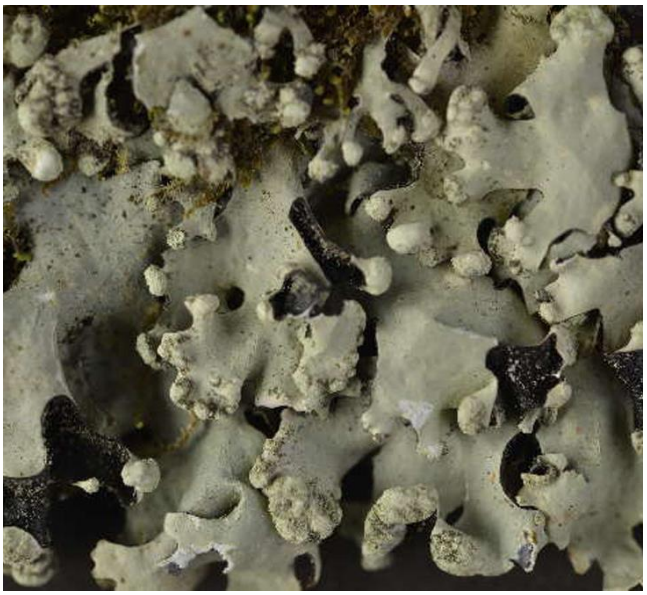

Figure 105. ***Hypotrachyna laevigata***, a lichen that occurs exclusively in the canopy in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Siri Synnøve Høle, through Creative Commons.

Figure 106. ***Calypogeia peruviana***, one of the exclusive liverwort taxa for tree bases in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Paul Davison, with permission.

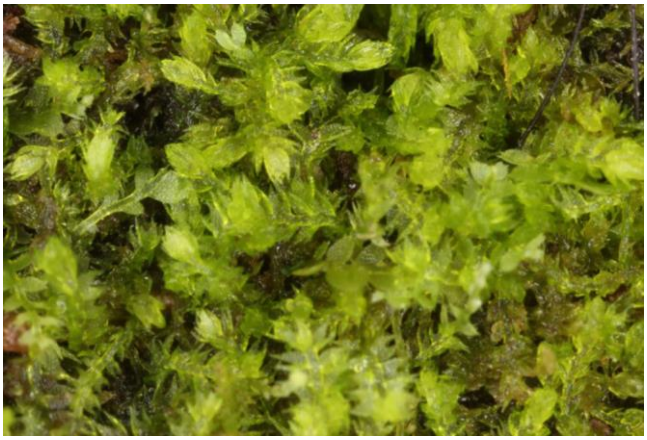

Figure 107. ***Cephalozia crassifolia***, one of the exclusive liverwort taxa on tree bases in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Jan-Peter Frahm, with permission.

Figure 108. ***Telaranea nematodes***, one of the exclusive liverwort taxa on tree bases in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Michael Lüth, with permission.

The most common taxa exclusive for the canopy communities of the upper montane rainforest of the Central Cordillera of Colombia are ***Anoplolejeunea conferta***, ***Jamesoniella rubricaulis*** (Figure 103), ***Leptoscyphus jackii*** (see Figure 28), ***L. porphyrius*** (see Figure 28), ***Plagiochila echinella*** *sensu lato* (incl. ***P. hansmeyeri*** and ***P. paludosa***; see Figure 10, Figure 51-Figure 53), ***Prionodon fuscolutescens*** (Figure 104), ***Trachylejeunea dominicensis***, and ***Hypotrachyna laevigata*** (not separated from ***H. producta***; Figure 105).

In Tanzania (Figure 109), the upper montane forest bryophytes capture 50% of the yearly precipitation (Gradstein 1992). That amount is 2.5 times the capture of the lower montane forest. Interception values in the Colombian montane forests were much less, reaching only 18.3% capture in the upper montane forest (Veneklaas & van Ek 1991). This difference is likely to be related to the differences in the forest types, with the Colombian mossy forest being much higher and much more open (Gradstein 1992). Furthermore, bryophytes in the Colombian forest formed discontinuous cover on the branches and usually were in clumps, contrasting with nearly continuous bryophyte cover on the branches in Tanzania.

Figure 109. Kilimanjaro at Amboseli National Park, Tanzania. Photo by Ninara, through Creative Commons.

The leafy liverwort genera ***Plagiochila*** (Figure 10, Figure 51-Figure 53), ***Bazzania*** (Figure 97), ***Herbertus*** (Figure 44, Figure 77), ***Lepidozia*** (Figure 99), ***Lepicolea*** (Figure 98), and ***Trichocolea*** (Figure 102) are the dominant liverworts in the wetter tropical montane forests (Gradstein 1992). In drier forests, mosses are more common. These include ***Macromitrium*** (Figure 110), ***Meteoridium*** (Figure 111), ***Mittenothamnium*** (Figure 112), ***Papillaria*** (Figure 113), ***Porotrichum*** (Figure 114), ***Porotrichodendron***, ***Prionodon densus*** (Figure 115), and ***Squamidium*** (Figure 116). In Asia, one might find more robust mosses such as ***Dicranoloma*** (Figure 117), ***Hypnodendron*** (Figure 118), ***Braunfelsia***, ***Dicnemon*** (Figure 119), and various members of the **Pterobryaceae** (Figure 42).

Figure 110. ***Macromitrium sulcatum***; some members of ***Macromitrium*** occur in dry tropical forests on ***Careya arborea***. Photo by Shyamal L., through Creative Commons.

Figure 111. ***Meteoridium remotifolium***; the genus ***Meteoridium*** is among the dominant liverworts in the drier montane forests of the Neotropics. Photo by Michael Lüth, with permission.

Figure 112. ***Mittenothamnium reptans*** from the Neotropics; the genus ***Mittenothamnium*** is among the dominant liverworts in the drier montane forests of the Neotropics. Photo by Michael Lüth, with permission.

Figure 113. ***Papillaria flavolimbata***; the genus ***Papillaria*** is among the dominant liverworts in the drier montane forests of the Neotropics. Photo by Lorraine Phelan, through Creative Commons.

Figure 114. ***Porotrichum bigelowii***; the genus ***Papillaria*** is among the dominant liverworts in the drier montane forests of the Neotropics. Photo by Michael Lüth, with permission.

Figure 115. ***Prionodon densus***, a species among the dominant liverworts in the drier montane forests of the Neotropics. Photo by Jan-Peter Frahm, with permission.

Figure 116. ***Squamidium*** sp., a genus that is among the dominant liverworts in the drier montane forests of the Neotropics. Photo by Janice Glime.

Figure 117. ***Dicranoloma billardierei***, in a genus with the more robust species found in drier forests of tropical Asia. Photo by Juan Larrain, with permission.

Figure 118. ***Hypnodendron menziesii***, in a genus with the more robust species found in drier forests of tropical Asia. Photo by Jan-Peter Frahm, with permission.

Upper montane forests can have epiphytic bryophyte biomass reaching as much as 44 tons dry weight per hectare (Gradstein 1992), compared to only ~2 tons in the submontane rainforest (Pócs 1982).

Gradstein and Vána (1994) reported that rotten logs in the pine forests in the central highlands of Chiapas, Mexico, exhibited a ***Nowellia curvifolia*** (Figure 23) community that had many species of boreal liverworts. They found eight species of liverworts and two of mosses. The most abundant of these, forming dense mats, were the leafy liverworts ***Fuscocephaloziopsis catenulata*** (Figure 120) and ***Nowellia curvifolia*** and the mosses ***Campylopodiella stenocarpa*** and ***Dicranum frigidum*** (Figure 26), Other common species were the liverworts ***Syzygiella autumnalis*** (Figure 121), ***Leptoscyphus amphibolius*** (see Figure 122), and ***Lophozia ventricosa*** (Figure 123), with ***Crossocalyx hellerianus*** (Figure 124) often occurring on the very humid flanks of the logs. The species were all pioneers on the logs except for ***Dicranum frigidum***. Six of the liverwort species are characteristic of boreal forest conifer logs. The researchers concluded that this community is probably limited in the tropics to occurrences of conifer forests in the northern parts of Central America.

Figure 119. ***Dicnemon calycinum*** with capsules, in a genus with the more robust species found in drier forests of tropical Asia. Photo by Janice Glime.

Figure 120. ***Fuscocephaloziopsis catenula***, a species that forms dense mats on rotten logs in the pine forests in the central highlands of Chiapas, Mexico. Photo by H. Tinguy, National Museum of Natural History, with online permission.

Figure 121. ***Syzygiella autumnalis***, a species that forms dense mats on rotten logs in the pine forests in the central highlands of Chiapas, Mexico. Photo by H. Tinguy, French National Museum of Natural History, with online permission.

Figure 122. ***Leptoscyphus azoricus***; ***L. amphibolius*** is a common species on rotten logs in the pine forests in the central highlands of Chiapas, Mexico. Photo by Jan-Peter Frahm, with permission.

Figure 123. ***Lophozia ventricosa***, a common species on rotten logs in the pine forests in the central highlands of Chiapas, Mexico. Photo by Hermann Schachner, through Creative Commons.

Figure 124. ***Crossocalyx hellerianus***, a common species on the flanks of rotten logs in the pine forests in the central highlands of Chiapas, Mexico. Photo by Štěpán Koval, with permission.

Corrales *et al*. (2010) surveyed secondary montane forest, ***Cupressus lusitanica*** (Figure 125) plantations, and ***Pinus patula*** (Figure 126) plantations in the Central Cordillera of Colombia. They used 1 m^2 random plots along 40 transects. They identified 151 species of bryophytes. Species richness, weighted based on number of samples, was higher in the secondary montane forests and cypress plantations than in the pine plantations. The greatest abundance was in the cypress plantations. Nevertheless, DCA indicated a high degree of floristic similarity. Soil *p*H, slope, and light availability were the primary factors in determining bryophyte distribution, suggesting that habitat specialization is the main mechanism governing species distribution within a forest type. The similarity of the three forest types suggests that propagule dispersal is also important.

Figure 125. ***Cupressus lusitanica***; the greatest diversity of bryophytes is in the plantations of these species. Photo by Sergio Kasusky, through Creative Commons.

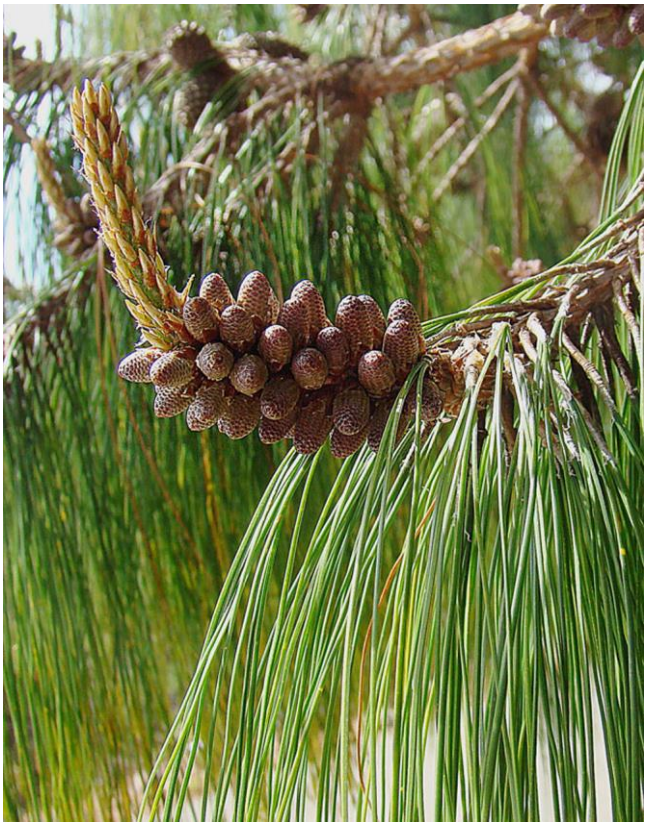

Figure 126. ***Pinus patula***; plantations of this species have fewer bryophyte species than those of the cypress (***Cupressus lusitanica***). Photo by Dick Culbert, through Creative Commons.

Veneklaas *et al*. (1990) investigated the effects of epiphytic vegetation in rainfall interception in an upper montane rainforest at 3,370 m asl in the Central Cordillera of the Colombian Andes. This site had ~12 tons dry weight of epiphytes per hectare, comprised mostly of bryophytes and dead organic matter. They learned that the epiphytes were efficient at rainfall capture, gradually releasing the excess. Furthermore, loss through evaporation was slow.

Summary

High mountains throughout the tropics have similar zonation patterns. Canopy tree presence or absence are important determinants of the bryophyte vegetation. Water relations are important, and trees affect the relative humidity. Nitrogen is made available by associated **Cyanobacteria** species. Submontane species are primarily **mat**-forming **perennial stayers** and **perennial shuttle species**. Liverworts outnumber mosses in humid areas, but the reverse is true in dry areas. Montane regions often have rocky substrata as well as soil, contributing to niche diversity. The montane is also likely to have more temperate plants than the submontane. These regions contrast sharply with the lowland forests by having dense carpets of bryophytes on the forest floor. Trees often support **pendent** bryophytes, and **tall turfs** and **feathers** are common. These more favorable growing conditions support some of the richest diversity of bryophytes in the world and the most exclusive species. **Lejeuneaceae** can dominate in all the epiphytic zones. **Meteoriaceae** dominates in montane forests, with **Dicranaceae** typically dominant in the upper montane. The bryophyte communities of the montane have considerable similarity to those of the boreal zones. Bryophytes on logs are predominately liverworts.

Bryophytes lost through disturbances can be replaced through diaspore banks, with liverworts more common than mosses. In the lower montane, water content experiences pronounced daily fluxes. Much carbon is still lost due to respiration at night. Soils at tree bases in the lower montane have higher nutrient content than do the canopy soils. The upper montane bryophytes of Tanzania capture 50% of the precipitation, 2.5 times that captured in the lower montane, but Neotropical bryophytes can be in discontinuous clumps and capture much less water. Upper montane forests can have as much as 44 tons of bryophyte biomass, compared to only 2 in submontane forests. In the upper montane, **cushion**, **short**, and **tall turf** life forms increase in proportion among the typically **perennial stayers** and **perennial shuttle species**.

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CHAPTER 8-10
TROPICS: CLOUD FORESTS, SUBALPINE, AND ALPINE

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CHAPTER 8-10
TROPICS: CLOUD FORESTS, SUBALPINE, AND ALPINE

Figure 1. Ecuadorian mountains and cloud forest. Photo by Arthur Anker, with permission.

Cloud Forests

Neotropical **cloud forests** (Figure 2, often known as **elfin forests** or **mossy forests**, extend from 23ºN to 25ºS (Churchill *et al*. 1995). These researchers suggested that the cloud forests of the Neotropics are a subset of the montane rainforest. They are isolated in Mexico on the north by xeric vegetation and on the south in Chile and Argentina by temperate rainforest. These cloud forests generally occur at 1000-3000 m asl. But the seasonal variation in precipitation is low and there are no months in which the evapotranspiration exceeds the rainfall. Rather, cloud cover is nearly continuous, with 2,000-4,000 mm precipitation per year. The temperature decreases from 18-22ºC at 1,000 m to less than 10ºC at 3,000 m asl. The taxa of these cloud forests are strongly influenced by their connections with both North and South America. The low generic level of endemism and high species endemism suggest recent and rapid speciation.

Figure 2. Cloud forest at Parque Nacional Montana de Santa Barbara at 2,180 m asl in Honduras. Photo by Josiah Townsend, with permission.

Cloud forests carry an intrigue that matches their names. Generally perched atop high mountains where they are blanketed in the fog of low-lying clouds or recipients of moisture-laden air that results in a mist zone most of the time (Vitt 1991), these forests must survive the harsh, uninterrupted winds and the continuous moisture that accompanies such a lofty abode. (See also Lawton 1980, 1982.) Consequently, trees there tend to be short compared to forests at lower elevations. For example, in Taveuni, Fiji, the forest trees on top of Mt. Koroturanga at 1,210 m asl were about 3-7 m tall, increasing to 10 m at 1,140 m elevation, and to 30 m at sea level (Ash 1987). Sadly, these dwarfed forests are rapidly disappearing from the face of the Earth before we can begin to understand a fraction of their complexity. In the northern Andes alone, 90% of these remarkable forests have disappeared, compared with 20% loss of the Amazon rainforest (Wuethrich 1993). In Peru alone, the mountainous areas house more than 25,000 plant species.

One problem that keeps these elfin forests out of the public eye is their relative lack of trees. Instead, they are dominated by herbs, shrubs, epiphytic ferns and seed plants, and mosses, with the diversity of all of these increasing with altitude (Wuethrich 1993). Nevertheless, they are the source of more than 3,000 species of plants that are used by the local people and house the ancestors of some of the most important world food crops.

Gotsch *et al*. (2017) showed that vapor pressure deficit could predict the epiphyte abundance in a tropical elevational gradient where the montane cloud forests occupy only a narrow band of microclimate and are thus vulnerable to climate change that changes the heights of the clouds and brings drought to the area. Their predictions are supported by their data showing that epiphyte abundance increases with elevation and leaf wetness and that it decreases as vapor pressure deficit (VPD) increases. VPD differences, however, are not always correlated with elevation and thus serve as better predictors of the epiphyte abundance.

In cloud forests of the Amazon, a high density of 21,900 trees per hectare belies the low tree species richness of 15 species, whereas the lower elevation tabonuco has 170 species with only 1750 trees per hectare (Gorchov & Cornejo 1993). The area behaves as an **ombrotrophic** (low-nutrient) wetland with its 5000 mm rainfall per year and another 10% moisture contributed by clouds. Poor soil oxygenation due to water logging results in most roots being above the soil. These buttress roots are usually covered by numerous bryophytes, and one might suppose that these bryophytes steal most of the nutrients returned by stemflow. Research has begun only recently on the ecological role of these cloud forest bryophytes.

Terrestrial bryophyte cover in the elfin forest is strikingly different from that of the lowland rainforest. The bryophytes are less specialized, with many of the same taxa occurring on the soil and on the trees. And the higher moisture permits bryophytes to grow higher on the bole, often reaching the canopy (Richards 1984).

Russell and Miller (1977) found that at Pico del Oeste in Puerto Rico, 55% of their collections of ***Campylopus*** (Figure 3) also contained the moss ***Hemiragis*** (Figure 4), but ***Hemiragis*** never occurred with ***Leucoloma*** (Figure 5). As in the submontane rainforest, the leafy liverworts dominated the upper branches (Russell & Miller 1977). This high humidity no doubt accounts for the high percentage of leafy liverworts, estimated up to 90% of the bryophyte flora (Fulford *et al*. 1970). Yet at Monteverde, Costa Rica, Gradstein *et al*. (2001b) found that 36% of the 190 bryophyte species occurred exclusively in the canopy. The thick, lower branches had the highest diversity, with 99 species, presenting a sharp delineation of communities (Figure 6).

Figure 3. ***Campylopus introflexus***, in a genus that occurs in the Pico del Oeste cloud forest in Puerto Rico. Photo by Paul Wilson, with permission.

Figure 4. ***Hemiragis aurea***, in a genus that occurs in the Pico del Oeste cloud forest in Puerto Rico. Photo by Elisabeth Lavocat Bernard, with permission.

Figure 5. ***Leucoloma*** from the Neotropics, a genus that never occurs with ***Hemiragis*** in the cloud forest. Photo by Michael Lüth, with permission.

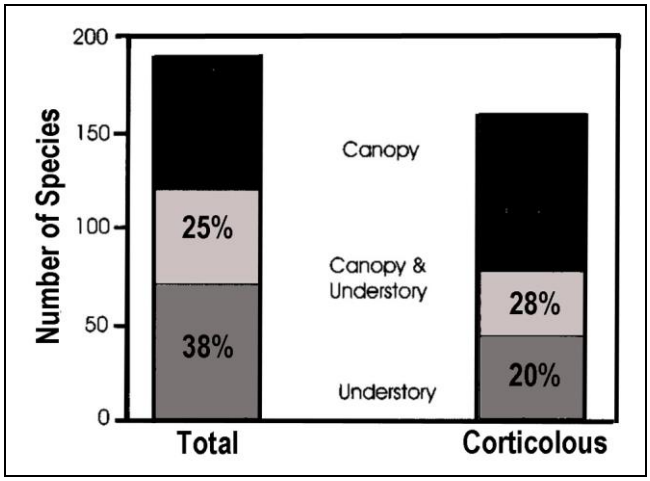

Figure 6. Total bryophyte species richness vs corticolous bryophyte species diversity in the canopy vs the understory in a cloud forest at Monteverde, Costa Rica. Species of rotten logs and epiphylls are not included in the corticolous counts. Redrawn from Gradstein *et al*. 2001b.

Merwin *et al*. (2001) reported 198 epiphytic bryophyte taxa in the Monteverde Cloud Forest Preserve. As is typical, the liverwort species (120) considerably out-numbered the moss species (77), with only 1 hornwort. Of these bryophyte species, 63 occurred in secondary forest and 84 in pastureland, whereas 178 species occurred in the primary forest.

These forests have such dense bryophyte growths on every trunk, branch, and twig that the forests appear "furry" (Gradstein & Pócs 1989). Biomass is high, with 11,000 kg ha^{-1} dry weight in a Tanzanian elfin forest (80% of total canopy biomass), compared to the lower submontane rainforest with 1,773 kg (Pócs 1982). By comparison, an oak forest in Atlantic Europe had 355 kg (Schnock 1972) and a continental European oak forest had only 41 kg (Simon 1974).

One can find accumulations of organic matter in the crowns of trees of tropical wet forests such as the cloud forests. Bohlman *et al*. (1995) investigated the moisture and temperature patterns of these organic soils in the canopy and on the ground in Costa Rica. These two soil groupings ranged in temperature from 11.5ºC to 21.0ºC throughout the 42-month study period, but the soil from the two locations generally were within 1ºC of each other. Both soils remained moist (>70% water content) during the wet and misty seasons. Nevertheless during dry periods the canopy soils dropped to a water content of 20-40%) while the forest floor soils retained 60-70% water content.

Gotsch *et al*. (2016) considered that a shift in the heights of the cloud base or precipitation due to climate change would make a huge impact on the cloud forest epiphyte community.

For a more general understanding of cloud forests one can consult such publications as that of Stadtmüller (1987).

Adaptations and Water Relations

In two Venezuelan cloud forests (Figure 7) in the northern Andes at 2000-2400 m, rainfall in January and February is typically 20 mm or less, but in August to October it can be 200 mm or more (León-Vargas *et al*. 2006). Nevertheless, it is quite variable in all seasons. The longest record for a dry period is only 143 hours. Humidity typically rises to more than 90% relative humidity at night, with one night in two typically reaching 100%. Six **pendent** (Figure 16) bryophytes were all able to survive at least a few days of desiccation; their recover was, however, better from high humidities. Their ability to reach light-saturation reached 95% at 110-256 µmol m^{-2} s^{-1}, levels only slightly higher than that of typical field levels. The **pendent** and other diffuse life forms are especially able to intercept cloudwater droplets, a feature the permits them to maximise conditions during periods of low rainfall.

Figure 7. Cloud forests, Venezuelan Andes. Photo by Gianfranco Cardogna, through Creative Commons.

The horizontal plane of a **fan** provides maximum surface area to capture light for photosynthesis as well as intercepting water from the moving air (Song *et al*. 2015). In three of the common **fan** bryophytes [moss ***Homaliodendron flabellatum*** (Figure 8), liverworts ***Plagiochila arbuscula*** (Figure 9), ***P. assamica***] in an Asian subtropical montane cloud forest, the plants experienced high relative humidity coupled with low light and temperatures in the understory. Fog is a major source of water. Data suggest that photosynthetically active periods for these bryophyte are short because they lose most of their free water within an hour. These **fan** bryophytes are further adapted to their low-light understory position by having low light saturation and compensation points for photosynthesis. The researchers expressed concern that these **fan** bryophytes would experience a net carbon loss if the frequency and severity of dry periods increase.

Figure 8. ***Homaliodendron flabellatum***, a **fan** form found in the Asian subtropical montane cloud forest. Photo by Jiang Zhenyu, Mou Shanjie, Xu Zawen, Chen Jianzhi, through Creative Commons.

Figure 9. ***Plagiochila arbuscula***, a **fan** life form found in the Asian subtropical montane cloud forest. Photo by Peter de Lange, through public domain.

In the Asian subtropical montane cloud forest, there is high relative humidity accompanied by low light levels and temperatures in the understory (Song *et al*. 2015). Fog provides good water availability for the bryophytes. In this habitat, **fan** life forms (Figure 8-Figure 9) thrive. This life form loses its free water within one hour. Without sufficient water content, net photosynthesis can become negative. Song *et al*. (2015b) considered the **fan** life form to be especially suited to the cloud forest regime. The **fan** life form, extending outward from the vertical surfaces of trees (or rocks), is able to capture water from fog efficiently (Song *et al*. 2015). Furthermore, the cell walls have a high elasticity and osmoregulatory capacity that permit these life forms to tolerate desiccation. Additionally, these **fan** species have low light saturation and low compensation points for photosynthesis, all providing shade tolerance. While these characteristics provide ideal adaptations to the humid, low-light conditions of the cloud forest, the inability to tolerate and succeed under desiccating conditions puts these **fan** species at risk under changing climatic conditions that increase both the frequency and severity of droughts.

Biomass

Van Dunne and Kappelle (1998) estimated biomass of epiphytic bryophytes on ***Quercus copeyensis*** (Figure 10) in a Costa Rican montane cloud forest. They found 22 species each of mosses and liverworts. Biomass of bryophytes was correlated with frequency, with mosses contributing 54-99% of that biomass. Of these, 14% of the species accounted for 90% of the biomass. These bryophytes are important in controlling water flow. Dominant taxa include ***Pilotrichella flexilis*** (Figure 11), ***Rigodium*** sp. (Figure 12), ***Porotrichodendron superbum*** (Figure 13), ***Prionodon densus*** (Figure 14), ***Neckera chilensis*** (see Figure 15), and ***Plagiochila*** (Figure 16).

Figure 10. ***Quercus copeyensis***, a good bryophyte substrate in a Costa Rican montane cloud forest. Photo through Creative Commons.

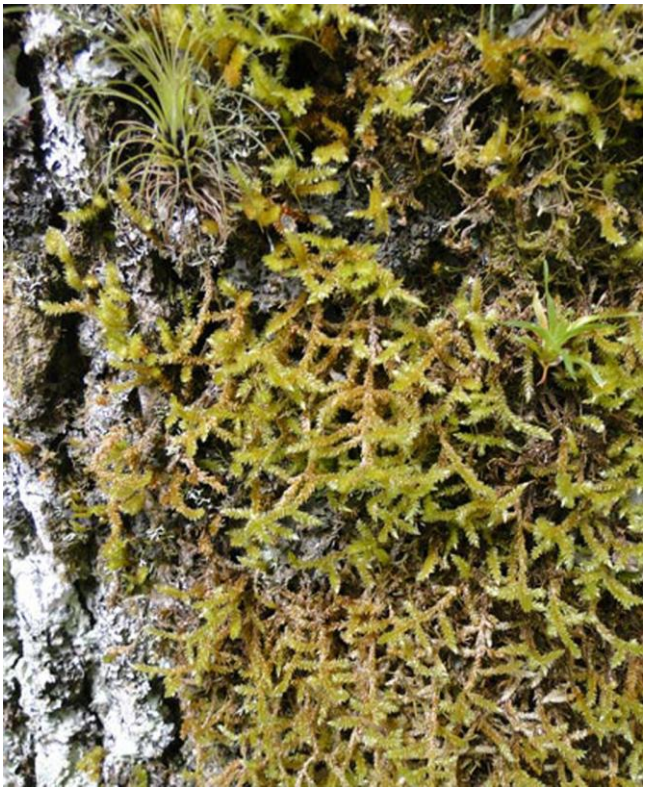

Figure 11. ***Pilotrichella flexilis***, a species that occurs on ***Quercus copeyensis*** (Figure 10) in a Costa Rican montane cloud forest. Photo by Claudio Delgadillo Moya, with permission.

Figure 12. ***Rigodium pseudo-thuidium***, a species that occurs on ***Quercus copeyensis*** (Figure 10) in a Costa Rican montane cloud forest. Photo by Juan Larrain, through Creative Commons.

Figure 13. ***Porotrichodendron superbum***, a species that occurs on ***Quercus copeyensis*** (Figure 10) in a Costa Rican montane cloud forest. Photo by Jan-Peter Frahm, with permission.

Figure 14. ***Prionodon densus***, a species that occurs on ***Quercus copeyensis*** (Figure 10) in a Costa Rican montane cloud forest. Photo by Jan-Peter Frahm, with permission.

Figure 15. ***Neckera cephalonica***; ***N. chilensis*** occurs on ***Quercus copeyensis*** (Figure 10) in a Costa Rican montane cloud forest. Photo by Jan-Peter Frahm, with permission.

Figure 16. ***Plagiochila adianthoides*** from the Neotropics, in a genus that occurs on ***Quercus copeyensis*** (Figure 10) in a Costa Rican montane cloud forest. Here it is showing a **pendent** life form. Photo by Michael Lüth, with permission.

Nadkarni (1984) was among the early Neotropical researchers who investigated ecology of the epiphytes. Unfortunately for us, these typically included the bryophytes, lichens, and tracheophytes together. Nevertheless, we can generally consider that most of the dead epiphyte biomass that accumulates is comprised of bryophytes. On a single large tree (***Clusia alata***), the standing crop was 141.9 kg, with the nutrient concentrations of N 3062 g, P 97 g, K 678 g, ca 460 g, Mg 126 g, and Na 207 g. Despite contributing only 2% to the biomass of the elfin forest dry weight, they contribute approximately 45% of the nutrients. This gives them a considerable role in the nutrient cycling of the cloud forest.

In a later study, Nadkarni *et al*. (2004) distinguished the role of bryophytes. The canopy organic matter in a primary montane cloud forest of Monteverde, Costa Rica, was 63% dead organic matter. Bryophytes comprised 12% of this. However, in the secondary cloud forest, bryophytes provided 95% of the biomass, with only 3% as dead organic matter. Branch junctions in the primary forest supported only dead organic matter and roots, whereas branch tips, subcanopy, and understory substrates supported only bryophytes. Trunks had diverse organic matter components, but little associated dead organic matter. The secondary forest, on the other hand, exhibited little differentiation between trunks and branches due to the dominance of bryophytes. The absence of bryophytes in branch junctions of both forest types is in stark contrast to their common appearance in these location in temperate forests.

Colonization and Life Strategies

A major problem for tropical bryophytes is that those with the common epiphytic life style must get dispersed and then become established on a vertical or otherwise elevated substrate. It is likely to be even more difficult for seeds of larger plants to become so established, so the bryophytes have an important role in providing a catchment for these propagules. Hence, the establishment of the bryophyte biomass is crucial to the cloud forest ecosystem. Nadkarni and coworkers (2000) attempted to determine how successful the bryophytes were in becoming established from macroscopic fragments onto branches in a tropical cloud forest in Costa Rica (Figure 17). Not surprisingly, only 1% of the bryophyte fragments managed to land and remain on saplings for the six months of study. However, those dropped on the canopy were more successful. Those branches with intact epiphytes retained 24% of the fragments, whereas stripped branches in the same area retained only 5%. This suggests that larger-diameter branches are more successful at retaining the fragments, as are other epiphytes. After 10 years, the bryophytes showed good recovery (Figure 18) (Nadkarni 2000).

Figure 17. Cloud forest fog at Monte Verde, Costa Rica. Photo courtesy of David Fenlon.

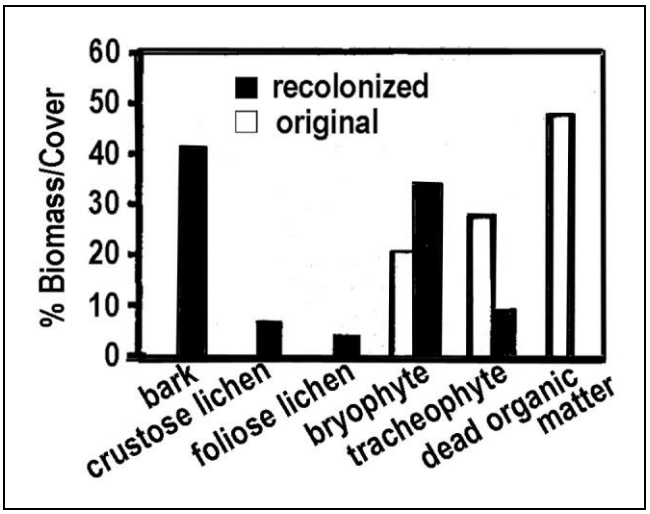

Figure 18. Comparison of component abundance in percent biomass of **original** epiphytic vegetation and percent total cover of **recolonizing** vegetation after 10 years on 75 m segments of inner canopy branches of mature trees at Monteverde, Costa Rica. Redrawn from Nadkarni 2000.

Life forms such as **feather**, **dendroid**, and **large cushions**, and **pendent** forms of **Meteoriaceae** (Figure 72-Figure 73), **Phyllogoniaceae** (Figure 40), ***Frullania*** (Figure 54), and ***Taxilejeunea*** (Figure 19) on horizontal branches of small trees and shrubs are often dominant and much more common than in lowland forests (Gradstein & Pócs 1989). Among the cloud forest species is ***Fissidens polypodioides*** (Figure 20), a member of a very large genus

with more than 500 species (Pursell 1994). In Central America, this is the largest ***Fissidens*** species, reaching 8 cm. In a Colombian cloud forest (Figure 21), van Leerdam and coworkers (1990) found **tall turfs** and **smooth mats** to predominate in the crowns, with forms differing between the inner and outer canopy. While **smooth mats** are common forms in the higher branches of temperate forests, the **tall turf** would seem to be possible only where moisture is abundant. Surprisingly, they found that growth and life forms differed dependent upon phorophyte species. Epiphyllous forms seem to be limited by frost, occurring up to only about 3,000 m (Pócs 1982).

Figure 19. ***Taxilejeunea***, a genus that occurs on horizontal branches of small trees and shrubs in the Neotropics. Photo by Michael Lüth, with permission.

Figure 20. ***Fissidens polypodioides***, a cloud forest species that is the largest ***Fissidens*** species in Central America. Photo by Janice Glime.

The **perennial shuttle species** take advantage of vegetative reproduction to become very important in the epiphytic communities on Mt. Kanabalu, North Borneo, whereas **perennial stayers** take advantage of the spores ultimately resulting from sexual reproduction or the occasional successful fragment to reach a new substrate, where they can persist for a long time (Frey & Kürschner 1991).

Figure 21. Montane cloud forest of Colombia. Photo courtesy of S. Robbert Gradstein.

Species Diversity

The humid cloud forests are important habitats for the leafy liverworts that typically exceed the mosses in number of species. For example, Russell and Miller (1977) found 60 species of epiphytic liverworts, but only 23 of mosses, in an elfin forest in Puerto Rico.

Mandl *et al*. (2010) questioned whether certain species groups could be used as surrogates for diversity in Neotropical montane forests in Ecuador (Figure 22). To test this, they surveyed 28 plots (400 m^2 each) of both terrestrial and epiphytic species in the ridge and slope forests in three locations in southern Ecuador. The epiphytic habitat had significantly more liverworts than the ground habitat. Mosses, on the other hand, were predominantly ground dwellers. Liverwort diversity proved to be a good indicator of fern α diversity. Moss α diversity was similar to that of ferns and liverworts only in epiphytic habitats. β diversity of ferns, mosses, and liverworts was similar among ground species, but not among epiphytic species. Thus, α diversity is not a good surrogate for β diversity in these cloud forests.

Figure 22. Montane cloud forest in Ecuador. Photo by Nils Köster, courtesy of S. Robbert Gradstein.

In a lower montane cloud forest at Monteverde, Costa Rica, Gradstein *et al*. (2001b) identified 133 liverwort, 56 moss, and 1 hornwort species. The thick branches of the lower canopy were the most species rich, with 99 species,

whereas trunks 1 m and above supported only 65 species. The lianas, shrubs, saplings, and understory leaves had only 36-46 species. Rotten logs were even more limited, with only 16 species. Roughly 36% of the species were exclusively in the canopy, with half the corticolous ones occurring there. In this case, the percentage of bryophyte species restricted to the canopy differs little from that of lowland and montane rainforests.

The Monteverde cloud forest has many rotting logs and fallen branches (Gradstein *et al*. 2001b). These serve as important habitats for the thallose liverworts ***Monoclea gottschei*** (Figure 23) and ***Riccardia*** spp. (Figure 24) and the mosses ***Trachyxiphium guadalupense*** (Figure 25) (**Pilotrichaceae**), ***Mittenothamnium reptans*** (**Hypnaceae**; Figure 26-Figure 27), ***Plagiomnium rhynchophorum*** (**Mniaceae**; Figure 28), and ***Pyrrhobryum spiniforme*** (**Rhizogoniaceae**; Figure 29). Only one hornwort (***Nothoceros vincentianus***; Figure 30) was found in the study, and this could be found on rotten logs. The rotten log species were also frequently encountered on tree bases, especially rotten humus ones.

Figure 23. ***Monoclea gottschei***, a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. Photo by Jan-Peter Frahm, with permission.

Figure 24. ***Riccardia fucoidea*** from the Neotropics; the genus ***Riccardia*** is a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. Photo by Michael Lüth, with permission.

Figure 25. ***Trachyxiphium guadalupense***, a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. Photo by Michael Lüth, with permission.

Figure 26. ***Mittenothamnium reptans***, a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. Photo by Michael Lüth, with permission.

Figure 27. ***Mittenothamnium reptans*** from the Neotropics. Photo by Michael Lüth, with permission.

Figure 28. ***Plagiomnium rhynchophorum***, a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. Photo by Michael Lüth, with permission.

Figure 29. ***Pyrrhobryum spiniforme***, a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. Photo by Jan-Peter Frahm, with permission.

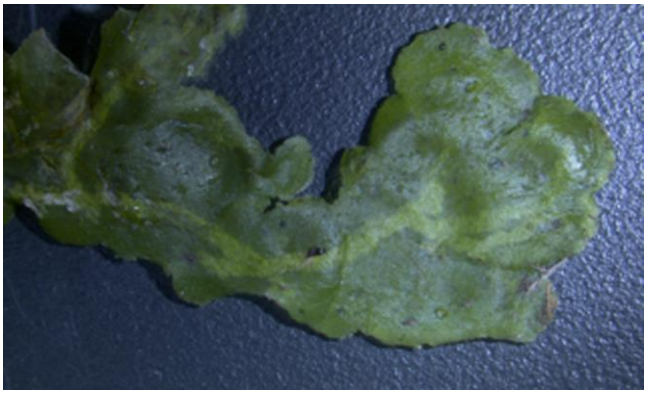

Figure 30. ***Nothoceros vincentianus***, a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. This one is inhabited by a leaf-miner that has made the lighter green paths. Photo courtesy of Juan Carlos Villareal.

Gradstein *et al*. (2001b) elaborated on the species found in the various levels of this Monteverde cloud forest, where they identified 190 species. Unlike some wet forests where ***Lejeunea*** (Figure 31) presents the most species, in this case that role belonged to ***Plagiochila*** (Figure 16). In the understory, the most frequent bryophytes on trunks, shrubs, lianas *etc*. were the moss ***Porotrichum korthalsianum*** (see Figure 32) and the leafy liverworts ***Plagiochila*** spp. and ***Radula antillana*** (see Figure 33), with other common taxa including ***Lepidopilum muelleri*** (see Figure 34-Figure 35), ***Metzgeria leptoneura*** (Figure 36), ***Omphalanthus filiformis*** (Figure 37), ***Taxilejeunea pterigonia*** (see Figure 38), and ***Trichocolea tomentosa*** (Figure 39). The well-lit sites were largely characterized by the **pendent** mosses ***Phyllogonium fulgens*** (Figure 40) in particular and various **Meteoriaceae** (Figure 54; Figure 72-Figure 73). These often occurred together with the robust liverworts ***Porella swartziana*** (see Figure 41), ***Bryopteris filicina*** (Figure 42), ***Plagiochila*** spp. (Figure 9, Figure 16), and ***Radula gottscheana*** (see Figure 33).

Figure 31. ***Lejeunea flava*** on a leaf; ***Lejeunea*** is common in wet forests, but not in the cloud forests of Monteverde. Photo by Yang Jia-dong, through Creative Commons.

Figure 32. ***Porotrichum madagassum***; in a Montverde cloud forest, ***Porotrichum korthalsianum*** is common on trunks, shrubs, lianas *etc*. Photo by Nicola van Berkel, through Creative Commons.

Figure 33. ***Radula*** from the Neotropics, a genus that is frequent in the understory on trunks, shrubs, and lianas in the cloud forests of Monteverde. Photo by Michael Lüth, with permission.

Figure 34. ***Lepidopilum*** from the Neotropics; ***Lepidopilum muelleri*** is common on trunks, shrubs, lianas *etc*. in the Montverde cloud forest. Photo by Michael Lüth, with permission.

Figure 35. ***Lepidopilum*** from the Neotropics. Photo by Michael Lüth, with permission.

Figure 36. ***Metzgeria*** from the Neotropics; in a Montverde cloud forest, ***M. leptoneura*** is common on trunks, shrubs, lianas *etc*. Photo by Michael Lüth, with permission.

Figure 37. ***Omphalanthus filiformis***, an understory species in the Monteverde cloud forest. Photo by Jan-Peter Frahm, with permission.

Figure 38. ***Taxilejeunea*** Neotropics; ***T. pterigonia*** is common on trunks, shrubs, lianas *etc*. in the Montverde cloud forest. Photo by Michael Lüth, with permission.

Figure 39. ***Trichocolea*** sp.; ***T. tomentosa*** is common on trunks, shrubs, lianas *etc*. in the Montverde cloud forest. Photo by George Shepherd, through Creative Commons.

Figure 40. ***Phyllogonium fulgens*** from the Neotropics, a species common on trunks, shrubs, lianas *etc*. in the Montverde cloud forest. Photo by Michael Lüth, with permission.

Figure 41. ***Porella obtusata***; ***P. swartziana*** is a species common on trunks, shrubs, lianas *etc*. in the Montverde cloud forest. Photo by Kristian Hassel, through Creative Commons.

Figure 42. ***Bryopteris filicina***, a species common on trunks, shrubs, lianas *etc*. in the Montverde cloud forest. Photo by Eliana Calzadilla, through Creative Commons.

Trunk bases at Monteverde (Figure 44) typically had the liverworts ***Cephalozia crassifolia*** (Figure 43), ***Lophocolea connata*** (see Figure 45), ***Telaranea nematodes*** (Figure 46), and various species of ***Lejeunea*** (Figure 31). Mosses here included ***Fissidens*** spp. (Figure 20) and ***Hypopterygium tamariscinum*** (Figure 47) (Gradstein *et al*. 2001b). Less common, but nevertheless characteristic trunk base species, were the leafy liverworts ***Calypogeia*** spp. and the thallose liverwort ***Pallavicinia lyellii*** (Figure 48), and the mosses ***Cyrto-hypnum schistocalyx*** (Figure 49), ***Leskeodon andicola*** (Figure 50), ***Octoblepharum erectifolium*** (Figure 51), and ***Syrrhopodon*** spp. (Figure 52). Species of the liverwort ***Bazzania*** (Figure 53) could also be found, but these are much more common in the forest canopy.

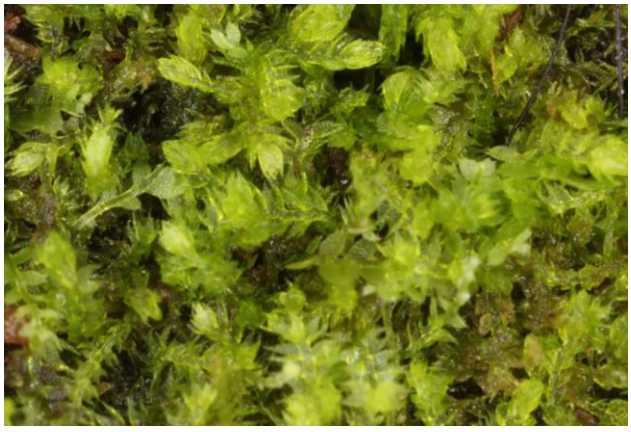

Figure 43. ***Cephalozia crassifolia***, a species found on trunk bases at Monteverde, Costa Rica. Photo by Jan-Peter Frahm, with permission.

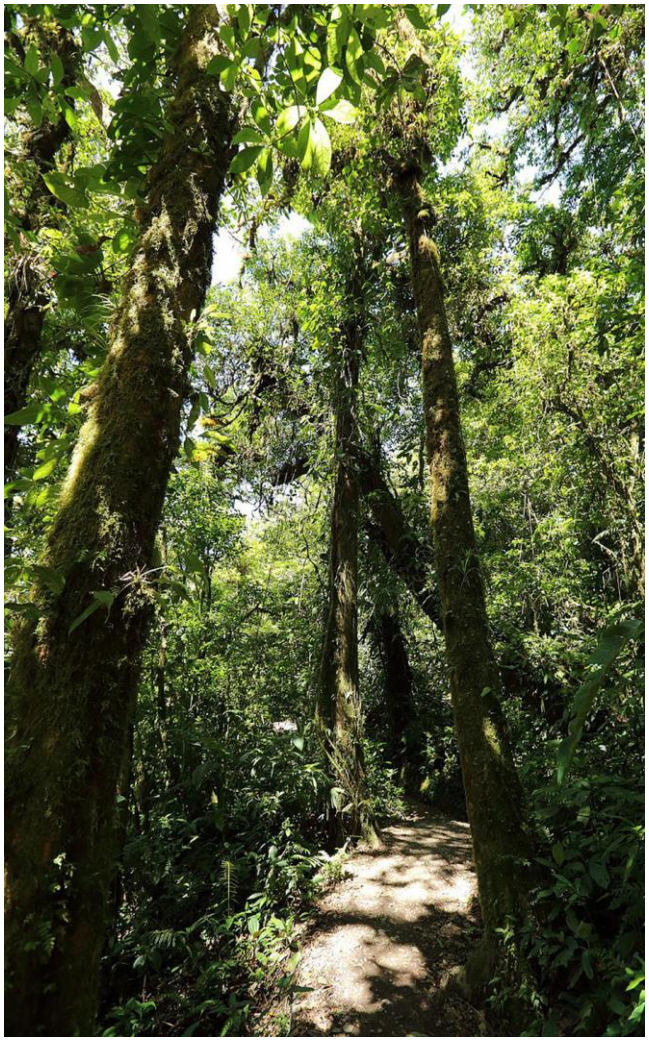

Figure 44. Cloud forest, Monteverde Reserve, Costa Rica. Photo by Cephas, through Creative Commons.

Figure 46. ***Telaranea nematodes***, a species found on trunk bases at Monteverde, Costa Rica. Photo by Michael Lüth, with permission.

Figure 47. ***Hypopterygium tamariscinum***, a species found on trunk bases at Monteverde, Costa Rica. Photo by Efrain de Luna, with permission.

Figure 45. ***Lophocolea*** *cf* ***polychaeta*** from the Neotropics; ***L. connata*** is a species found on trunk bases at Monteverde, Costa Rica. Photo by Michael Lüth, with permission.

Figure 48. ***Pallavicinia lyellii*** with sporophytes, a tree base species in the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.

Figure 49. ***Cyrto-hypnum schistocalyx***, a tree base species in the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.

Figure 50. ***Leskeodon andicola***, a tree base species in the Monteverde cloud forest, Costa Rica. Photo from Natural History Museum, London, through Creative Commons.

Figure 51. ***Octoblepharum albidum***; ***O. erectifolium*** is a tree base species in the Monteverde, Costa Rica, cloud forest. Photo by Javier Alejandro, through Creative Commons.

Figure 52. ***Syrrhopodon gaudichaudii*** from the Neotropics; there are several ***Syrrhopodon*** tree base species in the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.

Figure 53. ***Bazzania*** from the Neotropics; a tree base genus in the Monteverde, Costa Rica, cloud forest. Photo by 3 Michael Lüth, with permission.

The canopy in the Monteverde cloud forest (Figure 44) demonstrated different communities (Gradstein *et al*. 2001 b). The nearly horizontal branches of the lower canopy displayed these mats of bryophytes. These included the leafy liverworts ***Bazzania*** (Figure 53), ***Frullania convoluta*** (Figure 54), ***Herbertus*** (Figure 55-Figure 56), ***Lepidozia*** (Figure 57), and ***Plagiochila*** (Figure 16), and the moss ***Macromitrium*** (Figure 58). Thick canopy branches added more ***Frullania*** plus the leafy liverworts ***Adelanthus*** (Figure 59), ***Ceratolejeunea*** (Figure 60), ***Kurzia capillaris*** (Figure 61), ***Leptoscyphus porphyrius*** (see Figure 62), ***Syzygiella pectiniformis*** (see Figure 63), and ***Acrobolbus laxus*** (Figure 64.

Figure 54. ***Frullania convoluta***, a canopy species in the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.

Figure 55. ***Herbertus aduncus*** forming deep cushions on branches, a typical sight to be found in the Monteverde, Costa Rica, cloud forest. Botany Website, UBC, with permission.

Figure 56. ***Herbertus runcinatus*** from Chile. Photo by Blanka Aguero, with permission.

Figure 57. ***Lepidozia cupressina*** from the Neotropics; ***Lepidozia*** is a common genus on the horizontal branches in the cloud forest at Monteverde, Costa Rica. Photo by Michael Lüth, with permission.

Figure 58. ***Macromitrium microstomum*** on rock; ***Macromitrium*** is frequent on lower branches in the Monteverde, Costa Rica, cloud forest. Photo by Tom Thekathyil, Blue Tier, with permission.

Figure 59. ***Adelanthus decipiens***; the genus ***Adelanthus*** occurs on thick canopy branches in the cloud forest of Monteverde, Costa Rica. Photo by Michael Lüth, with permission.

Figure 60. ***Ceratolejeunea cubensis***; thick canopy branches support mats of members of ***Ceratolejeunea*** in the cloud forest of Monteverde, Costa Rica and in the lowland cloud forest in French Guiana. Photo by Scott Zona, through Creative Commons.

Figure 61. ***Kurzia capillaris*** from the Neotropics, a species that occupies thick branches in the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.

Figure 62. ***Leptoscyphus azoricus***; thick canopy branches support mats of members of ***Leptoscyphus*** in the cloud forest of Monteverde, Costa Rica. Photo by Jan-Peter Frahm, with permission.

Figure 63. ***Syzygiella autumnalis***; thick canopy branches support mats of members of ***Syzygiella*** in the cloud forest of Monteverde, Costa Rica. Photo by H. Tinguy, French National Museum of Natural History, with online permission.

Figure 64. ***Acrobolbus laxus***, a species that occupies thick branches in the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.

Mosses of the canopy included ***Acroporium pungens*** (Figure 65), ***Bryum capillare*** (Figure 66), ***Campylopus arctocarpus*** (Figure 67), ***Leucobryum giganteum*** (Figure 68), ***Leucoloma cruegerianum*** (Figure 69), ***Pilotrichella flexilis*** (Figure 11), ***Squamidium nigricans*** (see Figure 70), and ***Syrrhopodon lycopodioides*** (Figure 71) (Gradstein *et al*. 2001). Some moss species were generalists: ***Toloxis imponderosa*** (Figure 72-Figure 73), the **pendent *Phyllogonium*** (Figure 40), and ***Cheilolejeunea filiformis*** (see Figure 74), occurring in both the canopy and the understory. The fine twigs in the outer canopy supported communities of the moss ***Daltonia gracilis*** (see Figure 75) and many small species of the leafy liverwort family **Lejeuneaceae** (Figure 31, Figure 74). And of course the **Lejeuneaceae** predominated on leaves, especially in the understory. These **Lejeuneaceae** included ***Cololejeunea*** (Figure 76), ***Cyclolejeunea convexistipa*** (Figure 77), ***C. peruviana*** (Figure 78), ***Drepanolejeunea*** (Figure 79), and ***Odontolejeunea lunulata*** (Figure 80). Overall, 52% of the species are exclusive to the canopy and 20% to the forest understory.

Figure 65. ***Acroporium pungens*** in the cloud forest of the Luquillo Mountains, Puerto Rico. Photo by Janice Glime.

Figure 66. ***Bryum capillare*** with capsules, a species that occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo from Northern Defences, through Creative Commons.

Figure 67. ***Campylopus arctocarpus***, a species that occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.

Figure 68. ***Leucobryum giganteum***, a species that occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.

Figure 69. ***Leucoloma cf cruegeriana***, a species that occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.

Figure 70. ***Squamidium*** from Toro Negro, Puerto Rico; ***S. nigricans*** occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Janice Glime.

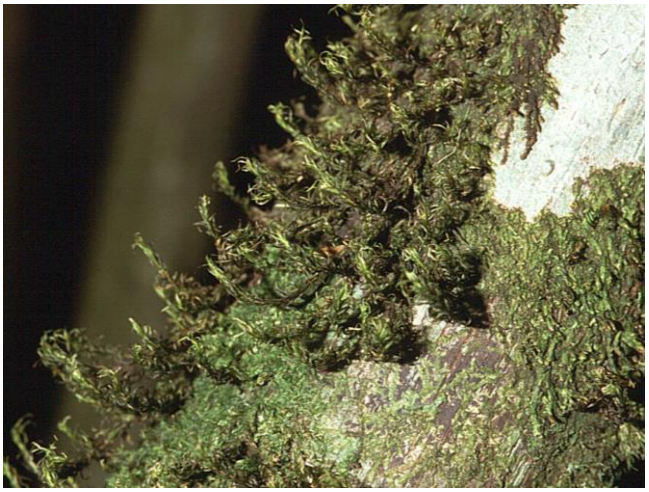

Figure 71. ***Syrrhopodon lycopodioides*** from the Neotropics, a species that occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.

Figure 72. ***Toloxis imponderosa*** from the Neotropics, a species that occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.

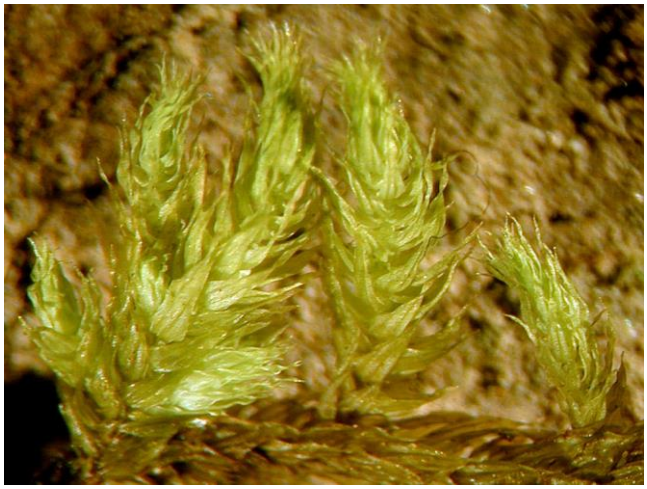

Figure 73. ***Toloxis imponderosa*** from the Neotropics, where it is a generalist in the canopy. Photo by Michael Lüth, with permission.

Figure 74. ***Cheilolejeunea*** from the Neotropics; ***Cheilolejeunea filiformis*** is a **pendent** generalist species in the canopy and understory of the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.

Figure 75. ***Daltonia*** *cf* ***longifolia*** with capsules; ***D. gracilis*** occurs on the fine twigs of the outer canopy in the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.

Figure 76. ***Cololejeunea cardiocarpa***; the genus ***Cololejeunea*** occurs on leaves in the Monteverde, Costa Rica, cloud forest. Photo by Paul Davison, with permission.

Figure 79. ***Drepanolejeunea mosenii***; the genus ***Drepanolejeunea*** occurs on leaves, especially in the understory of the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.

Figure 77. ***Cyclolejeunea convexistipula***; this species occurs on leaves of the understory in the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.

Figure 80. ***Odontolejeunea lunifolia***; this species occurs on leaves of the understory in the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.

Figure 78. ***Cyclolejeunea peruviana***; this species occurs on leaves in the understory of the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.

The epiphytic biomass and the associated canopy humus and canopy water storage capacity vary greatly among old-growth tropical montane cloud forests (Köhler *et al*. 2007). Köhler and coworkers compared the epiphytes in an old-growth cloud forest and a 30-year-old secondary forest on wind-exposed slopes in the Cordillera de Tilarán (Figure 81) in northern Costa Rica where bryophytes were the dominant epiphytes. Epiphyte biomass and canopy humus of the old-growth forest (16,215 kg ha-1) greatly exceeded that of the secondary forest (1,035 kg ha^{-1}). These old-growth forests held water contents of 36%-418% of their dry weights. Stand water storage of the non-tracheophyte epiphytes in the secondary forest was only 0.36 mm, compared to 4.95 mm in the old-growth forest. The bryophytes experienced more dynamic wetting and drying cycles when compared to canopy humus.

Figure 81. Monteverde, Costa Rica, cloud forest, Cordillera de Tilarán. Photo by Peter Andersen, through Creative Commons.

Bubb *et al*. (2004) suggested that bryophytes could serve as indicator species to map the distribution of cloud forests. Because the cloud forest bryophyte species are so sensitive to levels of atmospheric humidity, many have very restricted habitat requirements.

In the Pacific region, many tropical montane cloud forests occur as isolated patches on peaks of volcanoes or rugged upland ridges (Merlin & Juvik 1995). These typically have high rainfall, but also receive "horizontal precipitation" from wind-driven cloud water.

Nadkarni and Solano (2002) expressed concern that climate change models predict reduced cloud water in the tropical montane forests. This could greatly reduce the number of cloud forests in the world. They tested the effects of reduced cloud water on epiphytes by transplanting them, along with their arboreal soil, from the upper cloud forest trees to trees at slightly lower elevation where less cloud water was available. There were no transplantation effects among the controls that remained in the cloud forest. However, those transplanted to the lower elevations had significantly higher leaf mortality, lower leaf production, and reduced longevity. Although these were predominately tracheophytes, it raises the question of survivability of bryophytic epiphytes as well.

Sillett *et al*. (1995) demonstrated a reduction in species when comparing bryophytes in inner tree crowns of ***Ficus tuerckheimii*** (Figure 82) isolated in a pasture (76 species) with those from an intact cloud forest (109 species) in Costa Rica. Of these, 52 species occurred only on the intact forest trees, whereas only 18 were exclusive to the pasture trees. The intact forest similarly had significantly higher bryophyte species richness, cover, and frequency of **pendants**, **tall turfs**, **tails**, and **fans**. The isolated pasture tree epiphytes experienced higher rates of evaporation and more sunlight compared to those on forest trees. This corresponded with a desiccation gradient from the intact forest to the isolated trees.

Figure 82. ***Ficus tuerckheimii***, a species that has more inner crown epiphytes in the forest than when the tree is in the open. Photo by Dick Culbert, with online permission.

Additional studies include those on the microclimate and ecology (Baynton 1968) and ecology of leafy liverworts (Fulford *et al*. 1971a, b) of Puerto Rican cloud forests.

As in so many other studies, Gradstein *et al*. (1977) found "numerous" species of **Lejeuneaceae** (Figure 31, Figure 74), as well as **Plagiochilaceae** (Figure 16). Characteristic species were ***Lepicolea pruinosa*** (see Figure 83), ***Riccardia fucoidea*** (Figure 24), and ***Scapania portoricensis*** (see Figure 84), as well as multiple species of ***Bazzania*** (Figure 53), ***Frullania*** (especially **pendulous** species of the section ***Meteoriopsis***; Figure 54), ***Herbertus*** (Figure 55-Figure 56), ***Lepidozia*** (*e.g.* ***L. wallisiana***; see Figure 57), ***Lophocolea*** (Figure 45), ***Metzgeria*** (Figure 36), and ***Radula*** (Figure 33).

Figure 83. ***Lepicolea ochroleuca***; ***L. pruinosa*** is a characteristic cloud forest species in the tropics. Photo by Jan-Peter Frahm, with permission.

Figure 84. ***Scapania ornithopodioides***; ***Scapania portoricensis*** is a characteristic cloud forest species in the tropics. Photo by Michael Lüth, with permission.

Mount Kenya

Mount Kenya (Figure 85-Figure 86) is the highest mountain in Kenya (5,199 m), exceeded in Africa only by Mount Kilimanjaro (Figure 87). The wettest climate on the mountain is the lower southeastern slopes where the predominating weather system comes from the Indian Ocean (Wikipedia 2018b). This area is dominated by very dense montane forest. The mountain experiences two distinct wet seasons and two distinct dry seasons. Hedberg (1969) described the mountain as having winter every night and summer every day – a challenging climate for most organisms. See also Chamberlin and Okoola (2003) for a discussion of the rainy and dry seasons in eastern Africa.

Figure 85. Mt. Kenya at sunrise. Photo by Alpsdake, through public domain.

Figure 86. Near timberline forest with mosses, Mt. Kenya. Photo by Mehmet Karatay, through Creative Commons.

Figure 87. Mt. Kilimanjaro at Amboseli National Park, Tanzania. Photo by Ninara, through Creative Commons.

The mountain straddles the equator, so in the northern summer the sun shines on the north side of the mountain and in the southern summer it shines on the south side (Wikipedia 2018b). There is only a one-minute difference between the shortest and longest day of the year, a phenomenon that eliminates the possibility of photoperiod as a trigger for life cycle events or preparation for seasonal changes.

The summit of the mountain is alpine, with most of the precipitation occurring as snow (Figure 85). However, frost serves as the primary water source. Between 2,400 m and 3,000 m asl (the lower part of the mountain), moist air rising from Lake Victoria forms clouds over the western forest zone (Clemens *et al*. 1991). Winds carry these clouds to the summit, where they protect the glaciers from melting by screening out direct sun (Hastenrath 1984).

Karlén *et al.* (1999) provide an historic climate perspective based on fluctuations in the glacier on Mount Kenya (Figure 85). Coe (1967) discusses the ecology of the alpine zone of Mt. Kenya. A somewhat recent expedition to Mt. Kenya revealed 10 new taxa, with two being new to all of Africa (Chuah-Petiot & Pócs 2003). These researchers found many protozoa living in the lobules of the leafy liverwort ***Colura kilimanjarica*** (see Figure 88).

Figure 88. ***Colura leratii*** from Fiji; ***C. kilimanjarica*** houses protozoa on Mt. Kilimanjaro in Africa. Photo courtesy of Tamás Pócs.

Lowland Cloud Forest

Following the lead of Gradstein (2006) in French Guiana, Gehrig-Downie *et al*. (2011) defined this new type of cloud forest in northern South America, the lowland cloud forest (Figure 89). This type of forest occurs in river valleys in hilly areas where high air humidity and morning fog occur (Gradstein *et al*. 2010; Gehrig-Downie *et al*. 2011). The area is a rich epiphyte habitat in central French Guiana (Gehrig-Downie *et al*. 2011). This is most likely a result of the much longer periods of high relative humidity after sunrise. These researchers found significantly more epiphytic biomass in the lowland cloud forest (59 g m^{-2}) than in the lowland rainforest that lacked fog (35 g m^{-2}). Furthermore, epiphyte cover in the lowland cloud forest exceeded that of the lowland rainforest in all forest height zones (Figure 90).

Figure 89. Lowland fog in French Guiana. Photo by Delome, through Wikimedia Commons.

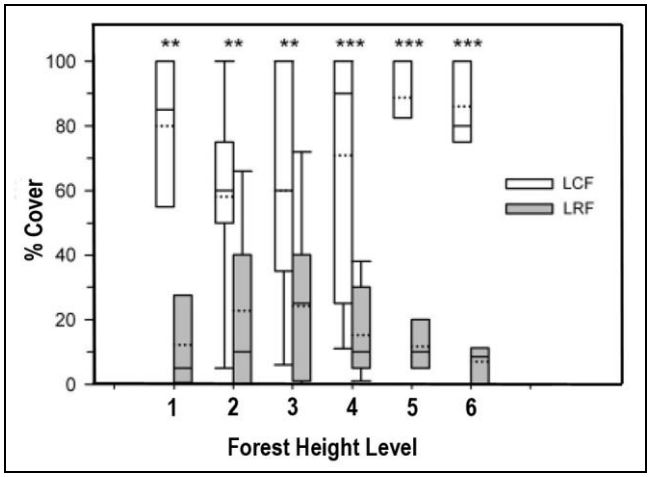

Figure 90. Abundance of all epiphytes as percentage of bark coverage in lowland cloud forest (LCF - white) and lowland rainforest (LRF - grey) in different height zones (1-6) on the tree; N=24 trees per forest type. Boxes indicate upper and lower quartile of data, unbroken line gives the median, dotted line the mean, and whiskers 95th percentile. Levels of significance with unpaired Student t-tests are shown by asterisks, * P<0.05, ** P<0.01, ***P<0.001. Modified from Gehrig-Downie *et al*. 2011.

Gradstein (2006) referred to the lowland cloud forest (400 m) of French Guiana (Figure 89) as a "liverwort hotspot." The species richness here is three times that of the Amazonian lowland forest. He found the species richness of epiphytic liverworts to be similar to that at 2,000 m asl in the Andes. Daytime fog prevents desiccation, permitting a positive net photosynthesis despite the high temperatures. About 30% of the liverwort species are restricted to the canopy and several are obligate epiphylls. Asexual reproduction in the understory is significantly more common than in the canopy. The greater dispersal ability of canopy species, particularly by spores, may explain the greater distributional ranges of species that occur there.

Following up on their earlier studies, Gehrig-Downie *et al*. (2013) described the species differences between lowland cloud forests (Figure 89) and lowland rainforests (Figure 91) in French Guiana. The species composition differs in all height zones, with three times as many indicator species in the lowland cloud forest. The liverwort richness differs more strongly between these two forest types than among the sampled elevations, with lowland cloud forests sometimes being richer in species than even the montane rainforests. Species restricted to the lowland cloud forest and occurring on more than one tree include ***Bazzania hookeri*** (Figure 92), ***Ceratolejeunea coarina*** (Figure 93), ***Cyclolejeunea chitonia*** (see Figure 77-Figure 78), ***Metzgeria leptoneura*** (see Figure 36), ***Pictolejeunea picta***, ***Plagiochila*** *cf.* ***gymnocalycina*** (see Figure 16, Figure 94), ***P. raddiana*** (Figure 94), ***P. rutilans*** (see Figure 16, Figure 94), and ***Radula flaccida*** (Figure 95). ***Ceratolejeunea cubensis*** (Figure 60) is the commonest species, occurring in more than 50% of the plots. In the lowland rainforest and collected on more than one tree, the exclusive species are ***Anoplolejeunea conferta***, ***Diplasiolejeunea*** *cf.* ***cavifolia***, and ***D. rudolphiana*** (Figure 96). ***Cheilolejeunea adnata*** (see Figure 74) was present in 80% of lowland rainforest samples, but only in 40% of the lowland cloud forest samples. Liverwort species richness increased with height zone in both forest types. However, in the lowland cloud forest it was the middle and outer crowns where most species occurred, whereas it was highest only in the middle crowns in the lowland rainforest.

Figure 91. French Guiana tropical lowland forest. Photo by Cayambe, through Creative Commons.

Figure 92. ***Bazzania hookeri*** from the Neotropics, where in French Guiana it is restricted to the lowland rainforests. Photo by Michael Lüth, with permission.

Figure 93. ***Ceratolejeunea coarina*** perianth, a species that in French Guiana is restricted to the lowland cloud forest. Photo by Michaela Sonnleitner, with permission.

Figure 94. ***Plagiochila raddiana*** from the Neotropics, where in French Guiana it is restricted to the lowland rainforests. Photo by Michael Lüth, with permission.

Figure 95. ***Radula flaccida*** habit with gemmae, a species restricted to the lowland cloud forest in French Guiana. Photo by Michaela Sonnleitner, with permission.

Figure 96. ***Diplasiolejeunea rudolphiana*** from the Neotropics, a species exclusive to the lowland rainforest in French Guiana. Photo by Michael Lüth, with permission.

Cloud forest life forms are benefitted if they are able to take advantage of the moisture in the clouds. Even in lowland rainforests, such as those found in French Guiana, the clouds increase the diversity of epiphytic bryophytes. Compared to other lowland rainforests, the lowland cloud forest exhibits higher biomass and cover of bryophytes, especially in the mid and outer canopy. These bryophytes likewise exhibit a greater diversity of life forms. Typical cloud forest life forms such as **tail**, **weft**, and **pendants** are nearly absent in the canopies of the lowland rainforest, but these are frequent in the lowland cloud forests.

Role

Bryophytes have another important role in these cloud forests. Bruijnzeel and Proctor (1995) emphasized the importance of the tropical montane cloud forest in the water cycle, even in headwater areas. This role is especially important during dry periods, supplying water to downstream areas. Nevertheless, they are often neglected in vegetation studies.

While interception of rainfall in the submontane rainforest is high, that in the elfin forest is about 2.5 times higher and accounts for intercepting over 50% of the annual rainfall (Pócs 1980). The most effective of these receptive bryophytes were the leafy liverworts ***Bazzania***

(Figure 92), ***Plagiochila*** (Figure 94), ***Frullania*** (Figure 54), ***Lepidozia*** (Figure 57), and ***Trichocolea*** (Figure 39). These bryophytes maintain a humid environment beneath by nearly continuous dripping (Lyford 1969 – Puerto Rico; Pócs 1980 – Tanzania) and this seems to create the necessary conditions for terrestrial bryophyte growth. In montane rainforests of the Colombian Andes, at 3370 m, the epiphyte mass, primarily of bryophytes, was 12 tonnes of dry weight per hectare and held considerable rainfall (Figure 97), which was likewise released very gradually through drainage as well as slow evaporation (Veneklaas *et al*. 1990).

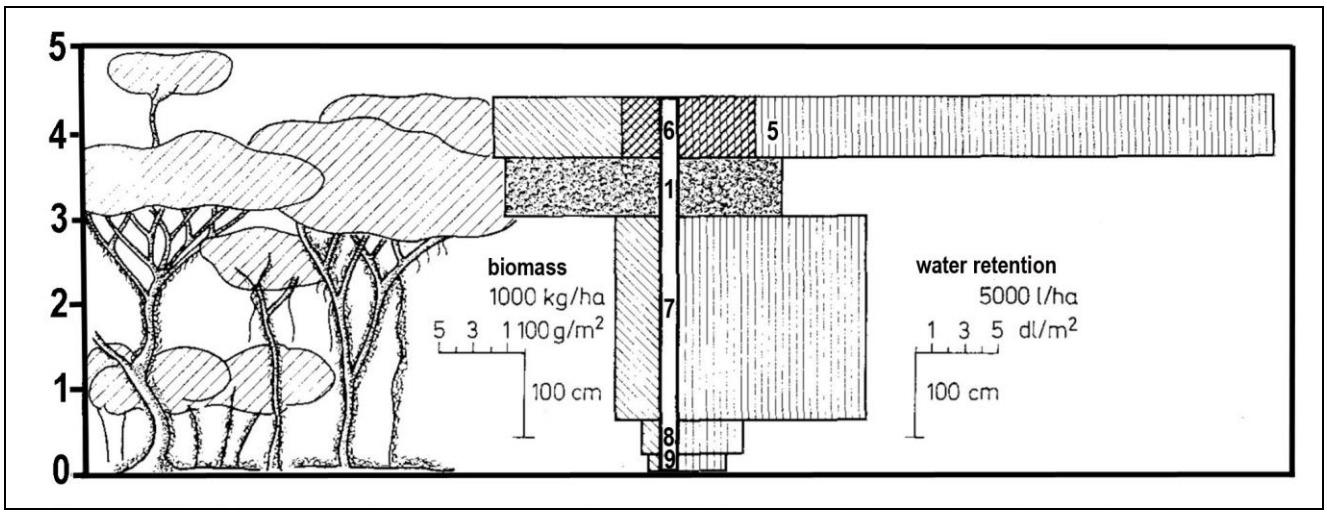

Figure 97. The biomass and interception of water by epiphytes, including bryophytes, and tree leaves in the cloud forest, showing their positions in the forest layers in Tanzania. Modified from Pócs 1980.

Martin *et al*. (2011) remind us that the moisture in a cloud forest reduces fire risk. This same cloud immersion fosters the growth of epiphytic bryophytes (Proctor 1982; Frahm & Gradstein 1991). These bryophytes, in turn, serve as sponges that strip moisture from the air and retain it, further lowering the flammability (Bruijnzeel & Proctor 1995).

Ah-Peng *et al*. (2017) reported excellent cloud water interception ability by the bryophytes in the cloud forest on Reunion Island, using ***Bazzania decrescens*** (Figure 98) and ***Mastigophora diclados*** (Figure 99) as study organisms. ***Mastigophora diclados*** had the greater ability to intercept water, but ***Bazzania decrescens*** had a far greater water storage capacity. Despite having less than half the abundance of ***M. diclados***, ***B. decrescens*** stored more than twice the water per hectare. The two species combined stored approximately 34,500 L ha^{-1}, the equivalent of 3.46 mm rainfall.

Figure 98. ***Bazzania decrescens***, one of the bryophytes that intercepts cloud water in cloud forests on Reunion Island. Photo by Jan-Peter Frahm, with permission.

Figure 99. ***Mastigophora diclados***, one of the bryophytes that intercepts cloud water in cloud forests on Reunion Island. Photo by Claudine Ah-Peng, with permission.

In the cloud forests of Papua New Guinea, Norris (1990) found that disturbance could cause serious reduction in the moisture within an epiphytic bryophyte colony. The epiphytes in these tropical cloud forests and rain forests have a much larger biomass than those of temperate forests. He suggested that larger **colonies** might maintain moisture longer than small **colonies**. Furthermore, contiguous clones will allow lateral conduction of water, whereas separated **tufts** result in little if any transfer across the host surface.

That water trapping is not always beneficial to the trees. In places where there are trees, the bryophytes can contribute to their demise. Encircling and hanging from branches, the bryophytes often capture 25% of the precipitation and absorb up to four times their own weight

(Schofield 1985). With this added weight, they can break the branches upon which they rest.

Epiphytes have another interesting role as well in the development of some forest trees. Bryophytes, along with other components (filmy ferns, dead organic matter) of the humus on the branches, provide the moisture and nutrients needed to stimulate adventitious roots, that is, roots that develop from locations other than the base of the stem, in this case from the trunk or branches (Nadkarni 1994b). Using the shrub-tree ***Jessea cooperi*** (Figure 100), an inhabitant of landslides, she determined that wet epiphytes or nutrient solutions with foam sponges would stimulate the production and growth of adventitious roots, whereas dry epiphytes, distilled water with foam sponges, and dry sponges would not.

Figure 100. ***Jessea cooperi***, a species that responds to wet sponges to form adventitious roots, suggesting a possible role for epiphytic bryophytes. Photo by Dick Culbert, through Creative Commons.

As with epiphytes in general, the epiphytes in the cloud forest can provide substrate, water reserves, and nutrient release that are available to tracheophytes. Orchids frequently become established in these mats (Frei 1973).

As with any thick bryophyte mat, the tropical bryophyte assemblages are home for numerous invertebrates. In the cloud forest of Costa Rica, these are likely to include amphipods, isopods, mites, Collembola, larvae, adult beetles, and ants (Nadkarni & Longino 1990). Interestingly, Nadkarni and Longino found that the composition of the fauna was basically the same in the canopy as that on the forest floor, but the ground had a mean density that was 2.6 times as great as that in the canopy, with the exception of ants, which were similar in both.

Subalpine

The sub-alpine (Figure 101) can act like an island, presenting a temperature regime that is more like the Arctic than the tropics. This makes mountaintop extinctions and a loss of biodiversity a danger under the influence of global climate change (Ah-Peng *et al*. 2014). On Réunion Island, Ah-Peng and coworkers found a relatively high species richness for bryophytes in the subalpine habitats, with diversity peaking at 2750 m asl for the ground-dwellers. They found that the functional richness with elevation differed between ground-dwellers and epiphytes, suggesting differences in the processes that structure these two community types. The ground-dwellers have a higher functional redundancy; the researchers interpreted this to indicate that the ground-dwellers may be more robust than the epiphytes when disturbances occur in this subalpine system.

Figure 101. Tropical subalpine dwarf forest in Peru at 3,200 m asl with Jan-Peter Frahm among the epiphytes. Photo courtesy of S. Robbert Gradstein.

Alpine

Luteyn *et al*. (1999, p. 1; see also Smith & Young 1987) list the different local names applied to the band of vegetation between the upper limit of continuous, closed-canopy forest (**timberline**; Figure 102) and the upper limit of plant life (**snowline**; Figure 103). In tropical regions of Mexico, Central and South America, Africa, Malesia including New Guinea, and Hawaii, this zone typically has tussock grasses, large rosette plants, evergreen shrubs, and cushion plants. These areas have different local names, including ***zacatonales*** (Mexico, Guatemala; Figure 104), ***páramo*** (Central and northern South America; Figure 105), ***jalca*** (northern Peru; Figure 115), ***puna*** (drier areas of the

altiplane of central Andes; Figure 106), ***Afro-alpine*** or ***moorland*** (East Africa; Figure 107), and ***tropical-alpine*** (Malesia; Figure 108-Figure 109).

Figure 102. **Treeline** (timberline) in Tararuas, North Island of New Zealand. Photo by William Demchick, through Creative Commons.

Figure 103. Snowline on Chimborazo volcano, Ecuadorian Andes. Photo by Bernard Gagnon, through Creative Commons.

Figure 104. Zacotolal, Nevado de Toluca, Mexico. Photo by Mainau, through public domain.

Figure 105. Páramo in Colombia. Photo by Friedrich Kircher, through Creative Commons.

Figure 106. Central Andean wet puna. Photo by Idobi, through Creative Commons.

Figure 107. Afro-alpine, at Lascar, northern Chile. Photo by Jorge Lásca, through Creative Commons.

Figure 108. Mount Kinabalu, Malaysia, showing tropical alpine region in the distance. Photo by Nep Grower, through Creative Commons.

Figure 109. Mount Kinabalu summit plateau (Afro-alpine). Photo by Ariel Steiner, through Creative Commons.

Bader *et al*. (2007) examined the role of bryophytes in tree regeneration above treeline in Ecuador (Figure 110). It is difficult for tree seedlings to become established there, and the researchers hypothesized that bryophytes could facilitate that establishment. First, they found that the number of naturally occurring tree sprouts (seedlings, saplings, and ramets) was highest just outside the forest, and decreased with distance to the forest edge. They transplanted seedlings ino the alpine vegetation. The forest floor is totally covered with mosses, including species of ***Sphagnum*** (Figure 111), especially at the forest edge, and has a peaty organic layer of 30-100 cm on top of he dark mineral soil. The transplanted seedlings had negligible growth after 2.5 years, and some decreased in size due to damage ot upper parts. Others seemed to be shorter due to the growth of fast-growing forest floor mosses that served as the measurement base. The seedlings that were planted in the mosses were sometimes overgrown by the mosses. The researchers concluded that seedlings can grow among mosses in the forest where that is the only available substrate, but that they are not favored by mosses.

Figure 110. ***Blechnum loxense*** tree fern at treeline in the Ecuadorian Andes at 3,500 m asl, showing tropical researcher Jan-Peter Frahm. Photo courtesy of S. Robbert Gradstein.

Figure 111. ***Sphagnum magellanicum***; the genus ***Sphagnum*** occurs on the forest floor near treeline in Ecuador. Photo by Michael Lüth, with permission.

In the Neotropics, Gradstein *et al*. (2001a) recognized páramo, Puna, and Zacatonal as the alpine habitats. Smith and Young (1987) noted how few studies existed on tropical alpine bryophytes and emphasized their importance in tropical mountain communities.

Páramo

The **páramo** (sparsely vegetated alpine zone on tops of high mountains of Andes and other high-elevation South American mountains; Figure 112-Figure 114) is generally considered to occur in Venezuela, Colombia, and northern Ecuador, with a pocket in Costa Rica (Luteyn 1999; Daniel Stanton, pers. comm. 4 December 2011). In northern Peru, wetter grasslands are known as **jalcas** (Figure 115). As pointed out by Daniel Stanton (pers. comm. 4 December 2011), the differences in naming may be more political or cultural than a reflection of real differences.

Figure 112. Páramo Sumapaz, Colombia. Photo by Yuri Romero Picon, through public domain.

Figure 113. Páramo in Colombia. Photo by Friedrich Kircher, through Creative Commons.

Figure 114. Páramo of Rabanal, Colombia. Photo by Patricio Mena Vásconez, through public domain.

Figure 115. **Jalca** district, Chachapoyas, Peruvian Amazon Region. Photo by Pitxiquni, through Creative Commons.

There is a striking shift in the substrate of bryophytes as one goes up in elevation in many parts of the tropics. Lower elevations, ranging up through the condensation zone and only slightly into the **páramo**, one can find most of the bryophyte cover as epiphytes on trees and shrubs. However, beginning at in the lower montane and increasing dramatically in the páramo, the major bryophytic cover is found on soil and rock for both mosses and liverworts (van Reenen & Gradstein 1983).

Central America enjoys the interesting flora that is a product of influence from both North and South America. In the Cordillera de Talamanca of Costa Rica, Holz (2003) and Holz and Gradstein (2005) identified 191 liverworts, 209 mosses, and 1 hornwort. Of these, 128 liverworts, 122 mosses, and 1 hornwort occur in the oak (*Quercus*) forests. The bryophytes are represented by proportionally more tropical species than are the tracheophytes. In the páramo, by contrast, the bryophyte flora is more similar to that of temperate regions. There are fewer endemics than are found in the oak forests.

Table 1. Ten largest families and genera of páramo mosses and liverworts. From Holz & Gradstein 2005.

Family (no. genera/spp.)	Genus (family) (no. spp.)
Mosses (prepared by Steve Churchill and Dana Griffin III)	
Dicranaceae (17/67) – Figure 3	***Sphagnum*** (**Sphagnaceae**) (37) – Figure 111
Bryaceae (10/65) – Figure 121, Figure 123	***Zygodon*** (**Orthotrichaceae**) (21) – Figure 116
Pottiaceae (19/63) – Figure 159	***Bryum*** (**Bryaceae**) (18) – Figure 121
Bartramiaceae (7/40) – Figure 120	***Leptodontium*** (**Pottiaceae**) (16) – Figure 140
Orthotrichaceae (3/36) – Figure 116, Figure 117	***Orthotrichum*** (**Orthotrichaceae**) (14) – Figure 117
Sphagnaceae (1/27) – Figure 111	***Breutelia*** (**Bartramiaceae**) (13) – Figure 120
Amblystegiaceae (9/19) – Figure 118-Figure 119	***Daltonia*** (**Daltoniaceae**) (13) – Figure 122
Brachytheciaceae (7/18) – Figure 141	***Macromitrium*** (**Macromitriaceae**/**Orthotrichaceae**) – Figure 58
Polytrichaceae (6/16) – Figure 158	***Schizymenium*** (**Bryaceae**) (11) – Figure 123
Grimmiaceae (4/17) – Figure 132-Figure 133	
Liverworts (prepared by Robbert Gradstein)	
Lejeuneaceae (16/38) – (Figure 31, Figure 74)	***Riccardia*** (**Aneuraceae**) (20) – (Figure 24)
Jungermanniaceae (11/31) – Figure 149	***Metzgeria*** (**Metzgeriaceae**) (20) – Figure 124
Lepidoziaceae (6/20) – Figure 57	***Plagiochila*** (**Plagiochilaceae**) (18) – Figure 16, Figure 94
Aneuraceae (2/21) – (Figure 24)	***Frullania*** (**Jubulaceae**/**Frullaniaceae**) (13) – Figure 54
Metzgeriaceae (1/20) – Figure 124	***Bazzania*** (Lepidoziaceae (13) – Figure 98
Plagiochilaceae (2/19) – Figure 16, Figure 94	***Anastrophyllum*** (**Jungermanniaceae**/**Anastrophyllaceae**) (8) – Figure 149
Geocalycaceae (7/18) – Figure 62	***Lepidozia*** (**Lepidoziaceae**) (8) – Figure 57
Gymnomitriaceae (5/14) – Figure 129-Figure 130	***Leptoscyphus*** (**Geocalycaceae**) (7) – Figure 62
Jubulaceae/**Frullaniaceae** (1/13) – Figure 54	***Isotachis*** (**Balantiopsidaceae**) (6) – Figure 125
Balantiopsaceae (2/7) – Figure 125	***Cephaloziella*** (**Cephaloziellaceae**) (6) – Figure 126
	Marsupella (**Gymnomitriaceae**) (6) – Figure 129-Figure 130
	Radula (**Radulaceae**) (6) – Figure 33

Figure 116. ***Zygodon conoideus***, with capsules, representing one of the 10 largest families in the páramo. Photo by Proyecto Musgo through Creative Commons.

Figure 117. ***Orthotrichum rupestre*** from the Neotropics, representing one of the 10 largest families in the páramo. Photo by Michael Lüth, with permission.

Figure 118. ***Vittia pachyloma*** habitat in Chile, representing one of the 10 largest families in the páramo. Photo by Juan Larrain, with permission.

Figure 121. ***Bryum apiculatum*** from the Neotropics, representing one of the 10 largest families in the páramo. Photo by Michael Lüth, with permission.

Figure 119. ***Vittia pachyloma***, representing one of the 10 largest families in the páramo. Photo from NYBG, through public domain.

Figure 122. ***Daltonia cf longifolia*** from the Neotropics, representing one of the 10 largest families in the páramo. Photo by Michael Lüth, with permission.

Figure 120. ***Breutelia wainioi*** from the Neotropics, representing one of the 10 largest families in the páramo. Photo by Michael Lüth, with permission.

Figure 123. ***Schizymenium pontevedrense*** with capsules, in a genus that is common in the páramo in the Neotropics. Photo by Michael Lüth, with permission.

Figure 124. ***Metzgeria*** in the Neotropics, representing one of the 10 largest families (**Metzgeriaceae**) in the páramo. Photo by Michael Lüth, with permission.

Figure 125. ***Isotachis aubertii*** in the Neotropics, representing one of the 10 largest families (**Balantiopsidaceae**) in the páramo. Photo by Michael Lüth, with permission.

Figure 126. ***Cephaloziella exiliflora***, in a genus that is common in the páramo of the Neotropics. Photo by Tom Thekathyil, with permission.

One reason for the low number of bryophyte taxa at lower elevations might be due to nighttime respiratory losses. High nighttime temperatures in the lowlands elevate the loss of CO_2 and prevent the bryophytes from attaining a net positive carbon balance (Proctor 1982; Richards 1984; Frahm 1987, 1990, 1994; Zotz *et al*. 1997; Zotz 1999). This is consistent with observations that the distribution correlates with increased moisture and lower temperatures at higher elevations (Pôrto 1992), permitting more time per day for photosynthetic gain.

Other studies on the páramo include liverwort diversity in the Neotropics (Gradstein 1998) and bryophytes and lichens of the páramo (Griffin 1979). Cleef (1978) described the Neotropical páramo vegetation and its relationship to that of the subAntarctic. Mägdefrau (1983) described bryophyte vegetation in the páramo of Venezuela and Colombia.

Moss Balls

Moss balls, also known as **vagrant plants**, erratic, solifluction floaters, and errant cryptogams (Pérez 1997b), are unattached plants that are blown about by the wind or moved by water or frost-heaving. Because of their movement, they frequently change their upward direction and consequently begin growth in a different direction (Shacklette 1966). This, and the tumbling that can break off extruding parts, forms them into balls. These are somewhat common on bare soils where climate conditions are subarctic, creating lenticular to spherical moss balls that are completely unattached and free to blow about on the snow and ice (Beck *et al*. 1986). These moss balls are particularly abundant in the alpine zone of high mountains of tropical Africa, especially on Mt. Kenya. In that location, the balls are formed by ***Grimmia ovalis*** (Figure 127-Figure 128). These are formed by continual motion of fragments of cushions that have been broken by frost or by single plants or small aggregations that occur on bare soil. These vulnerable bryophytes can be moved by wind and solifluction that occurs due to nocturnal needle-ice formation and subsequent thawing in the daytime. The outer layer of the balls that are formed is the living part; next is a layer of dead plant sections, whereas the core is a peaty material of disintegrated leaflets, rhizoids, stems, and minute soil particles.

Figure 127. ***Grimmia ovalis***, a species that is able to form moss balls. Photo by Michael Lüth, with permission.

Figure 128. ***Grimmia ovalis*** forming balls that can break away to form moss balls. Photo by Barry Stewart, with permission.

Others, in particular ***Marsupella*** (Figure 129-Figure 130), occur on small soil buds and nubbins that are common on the ground surface in the high páramo (Pérez 1994). The moss balls are known in many biomes where wind or water create them. In the superpáramo zone, frost-heaving creates such moss balls, as also seen in the fruticose lichen *Thamnolia vermicularis* (Figure 131) and the acrocarpous moss ***Grimmia longirostris*** (Figure 132) (Pérez 1991, 1994). Members of **Grimmiaceae** seem to be suited to making vagrant populations. Shacklette (1966) reported unattached polsters (known as glacier moss) of ***Schistidium apocarpum*** (Figure 133) on sandy soil on Amchitka Island, Alaska, where they become detached by wind erosion.

Figure 129. ***Marsupella emarginata*** var ***pearsonii***; ***Marsupella*** occurs on small soil buds and nubbins that are common on the ground surface in the high páramo. Photo by Michael Lüth, with permission.

Figure 130. ***Marsupella emarginata***, a species that can form bryophyte balls. Photo by Michael Lüth, with permission.

Figure 131. ***Thamnolia vermicularis***, a species that forms balls in the superpáramo. Photo by Schaude, through Creative Commons.

Figure 132. ***Grimmia longirostris*** moss balls created by solifluction. Photo by Henk Greven, with permission.

Figure 133. Glacier mice – moss balls, probably ***Schistidium apocarpum***. Photo from Wondergressive, through Creative Commons.

Afro-alpine

In most people's minds, the combination of African and alpine (Figure 134) seems like an oxymoron. Nevertheless, **Afro-alpine** (high mountains of Ethiopia and tropical East Africa, which represent biological 'sky islands' with high level of endemism) zones exist and present unique communities (Hedberg 1964). The ***Dendrosenecio*** (Figure 135) woodlands present ***Breutelia diffracta*** (Figure 136), ***B. stuhlmannii*** (Figure 137), ***Brachythecium ramicola***, ***Campylopus nivalis*** (Figure 138), ***Sanionia uncinata*** (Figure 139), and ***Leptodontium viticulosoides*** (Figure 140). The bottom layer is characterized by the mosses ***Brachythecium ruderale*** (Figure 141), ***B. spectabile***, and ***Hypnum bizotii***, and the liverworts ***Chiloscyphus cuspidatus*** (Figure 142), ***Lophocolea martiana*** (see Figure 45), ***Metzgeria hamata*** (Figure 143), ***M. hedbergii***, ***Mylia hedbergii*** (see Figure 144), and ***Plagiochila haumanii*** (see Figure 16, Figure 94).

Figure 134. Mt. Kenya. Photo by Elizabeth Kiragu Wanjugu and Tobias Schonwetter, through Creative Commons.

Figure 135. ***Dendrosenecio***, a tree found in the Afromontane zone. Photo through Creative Commons.

Figure 136. ***Breutelia diffracta***, a species in the ***Dendrosenecio*** woodlands of the Afromontane region. Photo by Jan-Peter Frahm, with permission.

Figure 137. ***Breutelia stuhlmannii***, a species in the ***Dendrosenecio*** woodlands of the Afromontane region. Photo by Jan-Peter Frahm, with permission.

Figure 138. ***Campylopus nivalis***, a species in the ***Dendrosenecio*** woodlands of the Afromontane region. Photo by Jan-Peter Frahm, with permission.

Figure 139. ***Sanionia uncinata***, a species in the ***Dendrosenecio*** woodlands of the Afromontane region. Photo by Michael Lüth, with permission.

Figure 140. ***Leptodontium viticulosoides***, a species of ***Dendrosenecio*** woodlands in the Afro-alpine zones. Photo by Li Zhang, with permission.

Figure 141. ***Brachythecium ruderale***, a species of the bottom layer in the ***Dendrosenecio*** woodlands in the Afro-alpine zones. Photo by Claudio Delgadillo Moya, with permission.

Figure 142. ***Chiloscyphus cuspidatus***, a species of the bottom layer in the ***Dendrosenecio*** woodlands in the Afro-alpine zones. Photo from the TePapa collection, through Creative Commons.

Figure 143. ***Metzgeria hamata***, a species of the bottom layer in the ***Dendrosenecio*** woodlands in the Afro-alpine zones. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 144. ***Mylia anomala***; ***M. hedbergii*** is a species of the bottom layer in the ***Dendrosenecio*** woodlands in the Afro-alpine zones. Photo by David T. Holyoak, with permission.

Older stems of the ***Dendrosenecio*** (Figure 135) commonly support thick cushions of moss, with lichens being relatively rare (Hedberg 1964). These include numerous bryophyte species, but the moss ***Antitrichia curtipendula*** (Figure 145-Figure 146) is the most abundant.

Accompanying species include the moss ***Hypnum cupressiforme*** (Figure 147-Figure 148) and the leafy liverworts ***Anastrophyllum auritum*** (see Figure 149), ***Lophocolea molleri*** (see Figure 150), ***Plagiochila colorans*** (Figure 16, Figure 94), and ***Radula boryana*** (see Figure 151) (Hedberg 1964). These moss mats support several tracheophytes, including ***Polypodium moniliforme*** var. ***rigescens*** (see Figure 152), ***Poa schimperiana*** (see Figure 153), ***Cardamine obliqua*** (see Figure 154), ***Arabis pterosperma*** (Figure 155), and juvenile ***Senecio*** sp. The ground layer has a nearly continuous carpet of mosses that also cover boulders and decaying stems of ***Senecio***/***Dendrosenecio*** and ***Lobelia*** (Figure 156). The important bryophytes in these carpets include the mosses ***Brachythecium spectabile*** (see Figure 141), ***Breutelia diffracta*** (Figure 136), ***Hylocomium splendens*** (common in boreal forests; Figure 157), ***Pogonatum urnigerum*** (Figure 158), ***Syntrichia cavallii*** (see Figure 159), and the liverwort ***Metzgeria hamata*** (Figure 143). Stones typically had a thin cover of ***Homalothecium sericeum*** (Figure 160). Many additional species were identified on the ***Dendrosenecio***. The dominant ***Sphagnum*** species in the sedge (***Carex***) peatland was ***S. strictum*** subsp. ***pappeanum*** (Figure 161), with additional species on and among the grass tussocks.

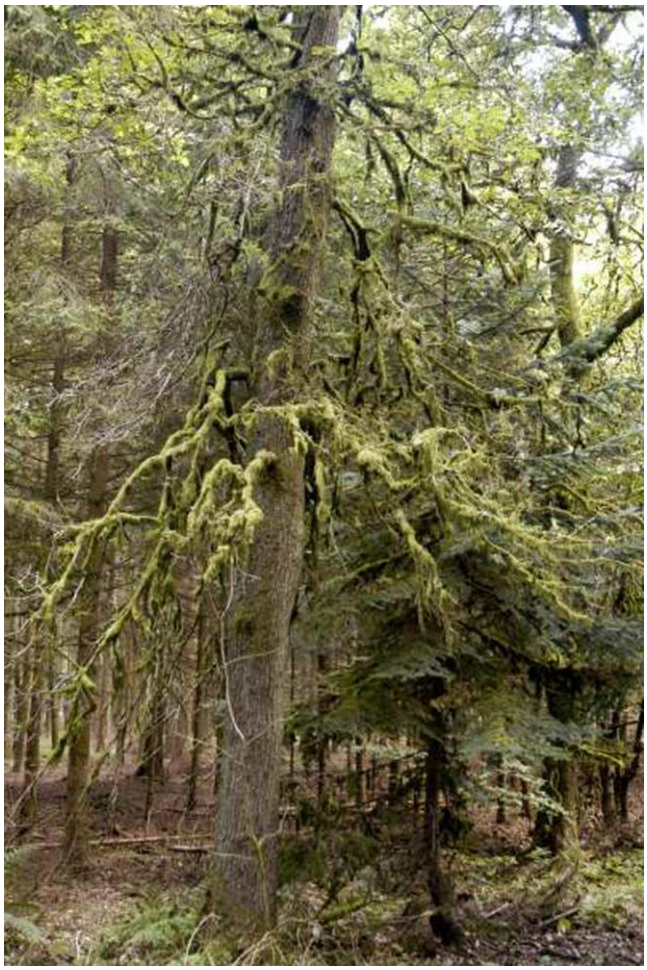

Figure 145. ***Antitrichia curtipendula*** habitat. This species is the most abundant on ***Dendrosenecio*** in the Afromontane. Photo by James K. Lindsey, with permission.

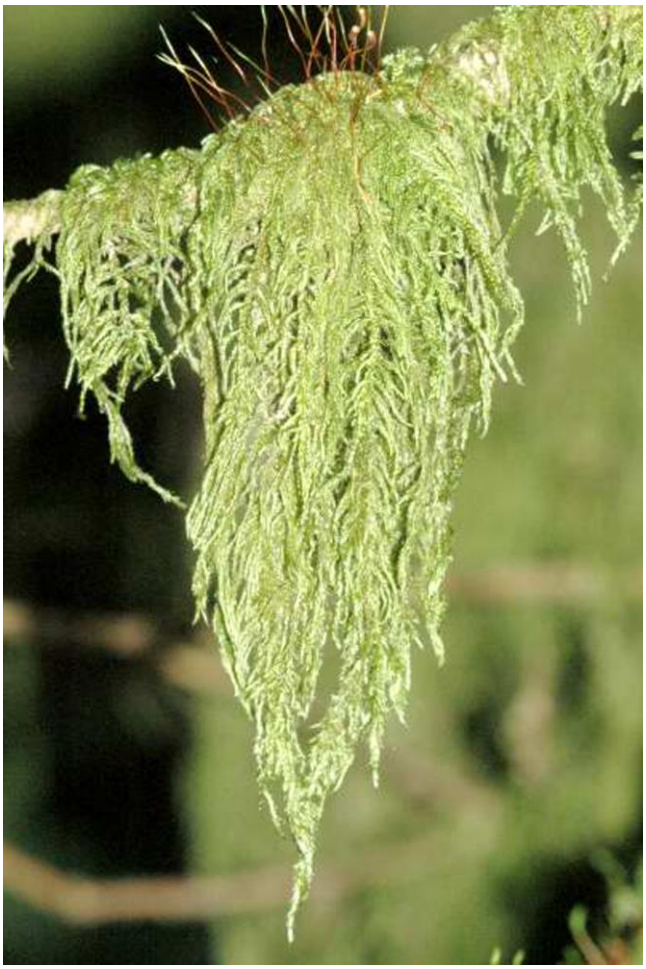

Figure 146. ***Antitrichia curtipendula***, the most abundant species on ***Dendrosenecio*** in the Afromontane. Photo by James K. Lindsey, with permission.

Figure 147. ***Hypnum cupressiforme***, a worldwide species that occurs on ***Dendrosenecio*** in the Afromontane. Photo by Michael Lüth, with permission.

Figure 148. ***Hypnum cupressiforme***, a species that occurs on ***Dendrosenecio*** in the Afromontane. Photo by Michael Lüth, with permission.

Figure 149. ***Anastrophyllum donnianum***; ***Anastrophyllum auritum*** occurs on ***Dendrosenecio*** in the Afromontane. Photo by Michael Lüth, with permission.

Figure 150. ***Lophocolea semiteres***; ***Lophocolea molleri*** occurs on ***Dendrosenecio*** in the Afromontane. Photo by David T. Holyoak, with permission.

Figure 151. ***Radula bolanderi***; ***R. boryana*** occurs on ***Dendrosenecio*** in the Afromontane. Photo by Ken-ichi Ueda through Creative Commons.

Figure 152. ***Polypodium glycyrrhiza*** growing among mosses; ***P. moniliforme*** var. ***rigescens*** grows among mosses on ***Dendrosenecio***. Photo by J. Brew, through Creative Commons.

Figure 153. ***Poa annua***; ***P. schimperiana*** is supported by moss mats on older stems of ***Dendrosenecio***. Photo by Rasbak, through Creative Commons.

Figure 154. ***Cardamine*** sp.; ***Cardamine obliqua*** grows in moss mats on ***Dendrosenecio*** in the Afromontane. Photo through Creative Commons.

Figure 155. ***Arabis pterosperma***, a species that grows in moss mats on ***Dendrosenecio*** in the Afromontane. Photo by B. R. Kailash, through Creative Commons.

Figure 156. Giant lobelia (***Lobelia deckenii***) on Mt. Kenya; juvenile lobelias can establish in moss mats. Photo by Mehmet Karatay, through Creative Commons.

Figure 157. ***Hylocomium splendens***, a common boreal forest species that occurs in the Afromontane zone. Photo by Michael Lüth, with permission.

Figure 158. ***Pogonatum urnigerum***, a species that forms carpets on the forest floor in the Afro-alpine zones. Photo by Michael Lüth, with permission.

Figure 159. ***Syntrichia ruralis***; ***S. cavallii*** forms carpets on the forest floor in the Afro-alpine zones. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University with permission from Russ & Karen Blisard.

Figure 160. ***Homalothecium sericeum***, a species that forms a thin layer on rocks in the Afro-alpine zones. Photo Kristian Peters, through Creative Commons.

Figure 161. ***Sphagnum strictum***; ***S. strictum*** subsp. ***pappeanum*** is the dominant ***Sphagnum*** species in the Afromontane ***Carex*** peatlands. Photo by Blanka Aguero, with permission.

Summary

The cloud forests have dwarfed trees that are typically covered with bryophytes. Seasonal variation in rainfall in cloud forests can be low or high. **Pendent** bryophytes and **fans** effectively trap water droplets and expose maximum surface area to the light; bryophytes can intercept over 50% of the annual rainfall in cloud forests. Water conservation within the bryophytes is facilitated by elastic cell walls. **Fan** species have low light saturation and low compensation points. Because of the high moisture requirements, the bryophyte species are often restricted to these cloud forests.

Liverworts typically outnumber mosses, but mosses can contribute 54-99% of the biomass. Whereas this biomass is relatively low compared to woody biomass, the bryophytes can contribute 45% of the nutrients through nitrogen fixation and entrapment of nutrients from the air, fog, and precipitation.

Dispersal may occur by fragments, and these are more successful when landing among epiphytes. **Tall turfs** and **smooth mats** predominate in crowns. **Meteoriaceae**, **Phyllogoniaceae**, ***Frullania***, and ***Taxilejeunea*** are the most common taxa on horizontal branches of small trees and shrubs. These are among the typically **perennial shuttles** and **perennial stayers** that dominate the life strategies. Mosses predominate on the ground, liverworts as epiphytes. Instead of the typical ***Lejeunea***, ***Plagiochila*** predominates among the epiphytes at Monteverde, Costa Rica. Nevertheless, the **Lejeuneaceae** is common. Thallose liverworts are common on logs.

Lowland cloud forests are a recent discovery and have a similar high humidity to mountain cloud forests and a species richness often exceeding them. Life forms such as **tail**, **weft**, and **pendants** are nearly absent in the canopies of the lowland rainforest, but these are frequent in the lowland cloud forests. Bryophytes play a major role in the water cycle, with ***Bazzania***, ***Plagiochila***, ***Frullania***, ***Lepidozia***, and ***Trichocolea*** maintaining a humid environment beneath by nearly continuous dripping.

The canopy bryophytes serve to trap dust and contained nutrients, hold moisture, and in some cases provide rooting media. Their cushions hold massive amounts of water, thus maintaining a humid environment long after rainfall ceases. This minimizes fire danger. Unfortunately, their weight sometimes causes the branches to break. The bryophytes also provide habitat for a number of invertebrates.

The subalpine and alpine areas can act as islands because most of their species cannot grow at lower elevations. As one goes up into the alpine region, bryophytes are increasingly found on the soil and rocks. Glaciers and windy alpine tundra provide conditions that create moss balls that blow about on the substrate. Other moss balls are created by and carried by **solifluction** – movement by water. Members of **Grimmiaceae** are particularly common among these moss balls.

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CHAPTER 8-11
TROPICS: HYDRIC AND XERIC HABITATS

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CHAPTER 8-11
TROPICS: HYDRIC AND XERIC HABITATS

Figure 1. Várzea in Brazil. Photo by D. N. Santos, through Creative Commons.

Inundated Forests

The classification of inundated forests has been inconsistent even by botanists, particularly in different regions (Prance 1980), making descriptions of the vegetation based on literature difficult and confusing. Prance divided these forests into periodically inundated (seasonal várzea, seasonal igapó, mangrove, tidal várzea, flood plain forest) and permanently waterlogged (permanent white water swamp forest, permanent igapó).

Inundated forests are forests that are constantly or periodically in water and include the **igapós** (Figure 2-Figure 3) and **várzeas** (Figure 1, Figure 7) (Pires & Prance 1985). These flood forests cover 2% or more of Brazilian Amazonia, excluding the rivers themselves. For example, the palm ***Astrocaryum jauari*** is, in various places, flooded 30-340 daya a year (Piedale *et al.* 2005, 2006). The **igapós** are black and clearwater areas, whereas the **várzeas** are muddy waters. In the black and clearwater areas, the **igapó** gives the water a golden appearance (Figure 4) (Pires & Prance 1985). In flood season, the igapó trees are flooded so that their trunks are completely submerged (Figure 5), permitting one to canoe through the canopy (Figure 6).

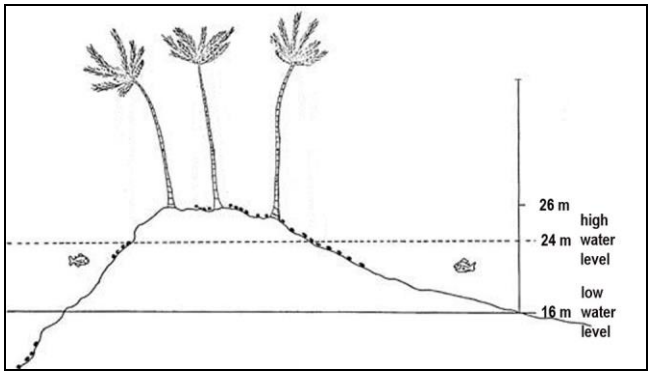

Figure 2. Diagram of igapó showing water level fluctuation for a mound of trees. Modified from Piedade *et al*. 2006.

Figure 3. Flooded igapó forest in Black River of Anavilhana, Brazil, in 2014. Photo courtesy of Tatiany Oliveira da Silva.

Figure 4. Golden water in flooded igapó forest in Black River of Novo Airão, state of Amazonas, Brazil, in 2014. Photo courtesy of Tatiany Oliveira da Silva.

Figure 5. Flooded igapó forest in Black River of Anavilhana, Brazil, in 2014. Photo courtesy of Tatiany Oliveira da Silva.

Figure 6. Canoeing through canopy of flooded igapó forest in Black River of Anavilhana, Brazil, in 2014. Photo courtesy of Tatiany Oliveira da Silva.

Várzea and Igapó Forests

The classification of Amazonian floodplains is based on water and vegetation types (Ferreira *et al*. 2005, 2013). The **igapó** (Figure 8) and **várzea** (Figure 1, Figure 7) are the most common of these. The **várzea** is a seasonally whitewater-flooded forest growing along rivers in the Amazon. The **igapó** forests are seasonally inundated with freshwater and typically occur along the lower reaches of rivers and around freshwater lakes, whereas the **permanent igapó** forest is in water year-round, but with fluctuating water levels.

Using 100 plots, each of 20 x 20 m, within 4 hectares, Ferreira and coworkers (2013) identified all trees and lianas greater than 10 cm diameter at breast height. They identified a total of 97 species, with 75 in igapó and 48 in várzea forests. Only 26 species occurred in both forests, indicating that these are distinct forests. The várzea forests have more soil nutrients, more light availability, and greater natural disturbance, perhaps helping to explain the plant diversity differences.

Figure 7. Várzea forest, Marajó, Brazil. Photo by Dayse Ferreira, through Creative Commons.

Figure 8. Igapó in Brazil. Photo by Lisa Cyr, through Creative Commons.

Cerqueira *et al*. (2017) studied the epiphytic bryophytes on ***Virola surinamensis*** (baboonwood; Figure 9) in igapó (Figure 8) and várzea (Figure 7) forests in the Caxiuanã National Forest. They found a greater richness in the igapó forest (44 species) compared to that of the várzea forest (38 species) (Figure 10). Furthermore, the composition of the bryophyte communities differed between the várzea and the igapó, but did not differ between dry and rainy periods. Although Cerqueira *et al*. (2016) studied only seven species in detail, two species were associated with the forest type and two species to the seasonality of flooding. They identified 54 bryophyte species in 502 samples; 34 were fertile. Sexual reproduction predominated over asexual (Figure 10).

Figure 9. ***Virola surinamensis***, an igapó substrate for bryophytes. Photo by Reinaldo Aguilar, through Creative Commons.

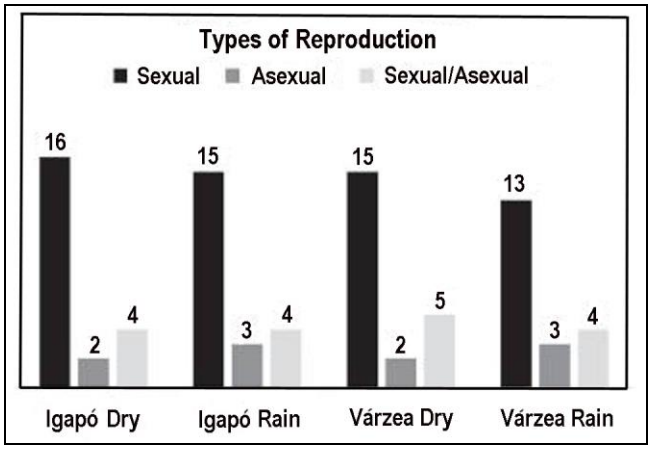

Figure 10. Reproduction of bryophytes in inundated forests. Numbers refer to number of species. Modified from Cerqueira *et al*. 2016.

Lopes *et al*. (2016) compared the bryophyte communities as they relate to degrees of flooding in the igapó and várzea. They sampled eighteen transects each in the igapó and várzea forests of São Domingos do Capim, Pará State, Brazil. As in many rainforest studies, they found that the leafy liverwort family **Lejeuneaceae** (Figure 28) was the predominant family, with 63 species. Among the mosses, the **Calymperaceae** (Figure 11, Figure 30) had the most species, with 8 species. In total, they reported 118 bryophyte species, 82 liverworts and 37 mosses. Live bark was the most colonized substrate, with 45 species exclusive to it, but 101 species in total on bark. Decomposing bark followed, with 66 species, 16 of which were exclusive to it.

Floodplains and Mangrove Forests

Mangrove forests and floodplains are subject to inundation by salt water (Pires & Prance 1985). They are species-poor and typically quite uniform. Among the primary tree species is the mangrove, ***Rhizophora mangle*** (Figure 12).

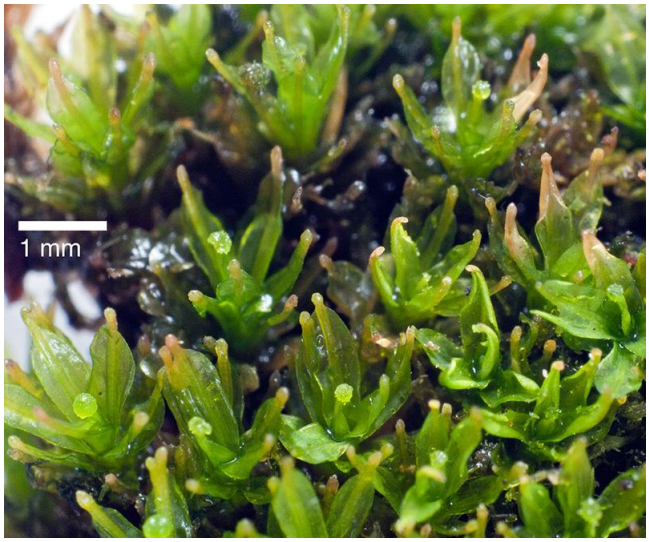

Figure 11. ***Calymperes tenerum***, one of the common species on mangroves in eastern Thailand. Photo from Auckland Museum, through Creative Commons.

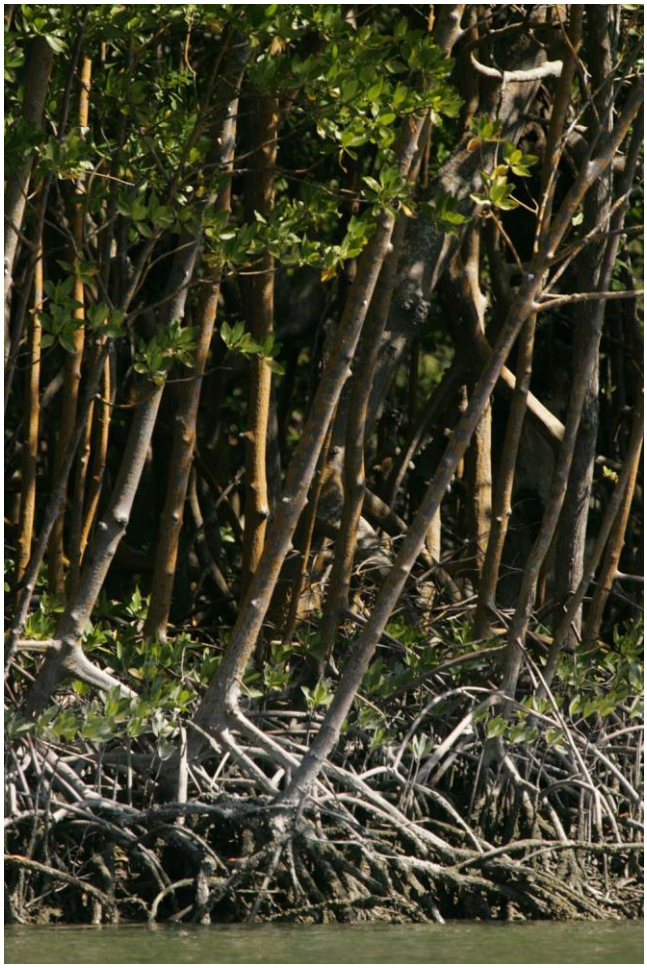

Figure 12. ***Rhizophora mangle***, a primary species of the mangrove forest. Photo by Steve Hillebrand, through public domain.

In Thailand there are about 40 tree species in the mangrove forests (Thaithong 1984). Among these, only 10 species support epiphytic bryophytes. Thaithong found only 5 species of mosses and 21 species of leafy liverworts. ***Rhizophora apiculata*** (Figure 13) was the most favorable phorophyte for bryophyte species richness, with 23 bryophyte species found on this host. She found 22 of the 111 specimens of bryophytes belong to only 5 species of mosses [***Calymperes tenerum*** (Figure 11), ***Calymperes hampei***, ***Octoblepharum albidum*** (Figure 14), ***Leucophanes albescens*** (see Figure 15), and ***Dixonia orientalis***]. The remaining 89 specimens were represented by 21 species of leafy liverworts in the genera ***Frullania*** (Figure 26), ***Lejeunea*** (Figure 16), ***Acrolejeunea*** (Figure 17-Figure 18), ***Mastigolejeunea*** (Figure 19), ***Lopholejeunea*** (Figure 20), ***Pycnolejeunea*** (Figure 21), ***Thysananthus*** (Figure 22), ***Schiffneriolejeunea*** (Figure 23), ***Caudalejeunea*** (Figure 24), and ***Cololejeunea*** (Figure 25). The most common bryophytes, occurring in both the eastern and western mangrove forests, were ***Frullania meyeniana*** (Figure 26), ***Acrolejeunea fertilis*** (Figure 27), ***Cheilolejeunea intertexta*** (Figure 28), and ***Lopholejeunea subfusca*** (Figure 29), all leafy liverworts and all but ***Frullania*** in the **Lejeuneaceae**. In the eastern mangrove forests, the moss ***Calymperes tenerum*** (Figure 11) is also common, whereas in the western mangroves ***Calymperes erosum*** (Figure 30) is common.

Figure 13. Mangrove of ***Rhizophora apiculata***, a favorable host for bryophytes in Thailand. Photo by Bernard Dupont, through Creative Commons.

Figure 14. ***Octoblepharum albidum***, a common species in the mangrove forests of Thailand. Photo by Bramadi Arya, through Creative Commons.

Figure 15. ***Leucophanes*** sp.; ***Leucophanes albescens*** is one of five species of mosses in the mangrove forests of Thailand. Photo by Neils Klazenga, with permission.

Figure 16. ***Lejeunea flava***, member of a common leafy liverwort genus in the mangrove forests of Thailand. Photo by Scott Zona, through Creative Commons.

Figure 17. ***Acrolejeunea fertilis***, member of a common leafy liverwort genus in the mangrove forests of Thailand. Photo by Heino Lepp, Australian National Botanic Gardens, with online permission for non-commercial use.

Figure 18, ***Acrolejeunea fertilis***, in a common leafy liverwort genus in the mangrove forests of Thailand. Photo by Heino Lepp, Australian National Botanic Gardens, with permission only for non-commercial use.

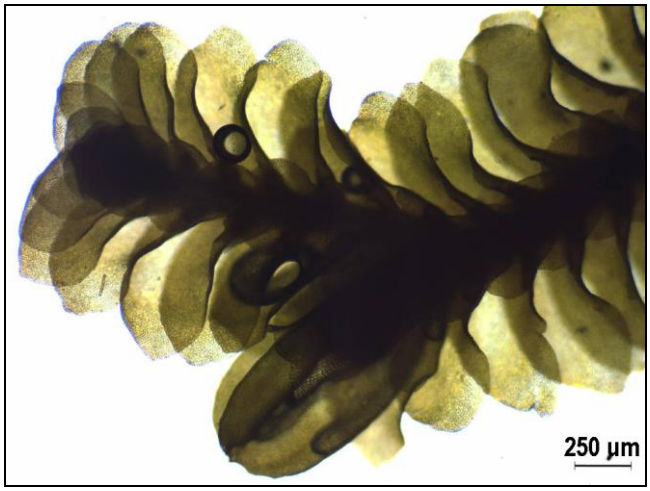

Figure 19. ***Mastigolejeunea auriculata***, member of a common leafy liverwort genus in the mangrove forests of Thailand. Photo by Blanka Aguero, with permission.

Figure 20. ***Lopholejeunea subfusca***, member of a common leafy liverwort genus in the mangrove forests of Thailand. Photo by Yang Jia-dong, through Creative Commons.

Figure 21. ***Pycnolejeunea pilifera***, member of a common leafy liverwort genus in the mangrove forests of Thailand. Photo by Paris, Muséum National d'Histoire Naturelle, MB, through Creative Commons.

Figure 22. ***Thysananthus repletus*** from China, in a common leafy liverwort genus in the mangrove forests of Thailand. Photo by Y. M. Wei, courtesy of Robbert Gradstein.

Figure 23. ***Schiffneriolejeunea polycarpa***, in a common leafy liverwort genus in the mangrove forests of Thailand. Photo from <docencia.udea.edu.co>, with implied permission.

Figure 24. ***Caudalejeunea lehmanniana***, member of a common leafy liverwort genus in the mangrove forests of Thailand. Photo by Scott Zona, with permission.

Figure 25. ***Cololejeunea cardiocarpa***, member of a common leafy liverwort genus in the mangrove forests of Thailand. Photo by Paul Davison, with permission.

Figure 26. ***Frullania meyeniana***, one of common species on ***Rhizophora apiculata***. Photo by Scott Zona, through Creative Commons.

Figure 27. ***Acrolejeunea fertilis***, one of common species on ***Rhizophora apiculata***. Photo by Heino Lepp, Australian National Botanic Gardens, with online permission.

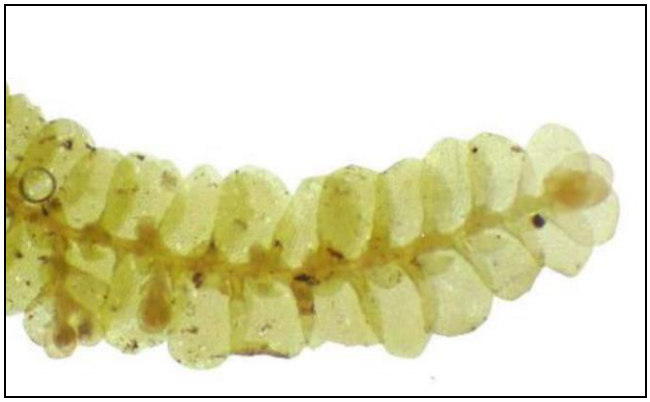

Figure 28. ***Cheilolejeunea intertexta***, a species common on ***Rhizophora apiculata*** in Malaysia. Photo from Wilding *et al.* 2016, with permission.

Figure 29. ***Lopholejeunea subfusca***, one of the common species on ***Rhizophora apiculata***. Photo by Yang Jia-dong, through Creative Commons.

Figure 30. ***Calymperes erosum***, one of the common species on mangroves in western Thailand. Photo by Li Zhang, with permission.

Frangi and Lugo (1992) used 10-year-old wooden stakes to examine bryophytes on the microtopographic gradient of a floodplain forest in the Luquillo Experimental Forest, Puerto Rico. They assessed biomass and nutrients, finding 210-1400 kg ha^{-1} of ash-free biomass. Nutrient levels for bryophytes in the floodplain floor in kg ha^{-1} were N (9.1), P (0.5), K (3.3), Ca (1.7), Mg (1.7), Mn (0.33), Fe (11.6), and Al (13.8). These accumulations are in the same order of magnitude as those of the fine litter, suggesting passive accumulation. On streambank slopes or slopes of tree mounds, the biomass and nutrient accumulation were greater than in other microhabitats. Frangi and Lugo concluded that the floodplain bryophytes serve as biotic filters of flood waters, helping in retention of nutrients in these habitats.

Studies on bryophytes of tropical floodplains and mangrove forests seem to be minimal. Yamaguchi *et al.* (1987) listed the terrestrial bryophytes in mangrove forests of Japan. Windolf (1989) analyzed the bryophyte species in sub-tropical mangroves in southern Queensland, Australia. Windolf made 337 collections and described the host-substrate relationship, comparing bryophyte occurrences to those on the adjacent non-mangrove trees. There seems to be an absence of ecological studies for this habitat.

Hydropogon fontinaloides occurs in periodically inundated locations in the Orinoco and Amazon River floodplains (Mägdefrau 1973).

Pirizal

The **pirizal** vegetation occurs only in small, restricted areas. These are shallow lakes or puddles and the water is stagnant, dark, and transparent. This tropical habitat is not typically a habitat for bryophytes.

Peatlands

Gates (1915) reported on ***Sphagnum*** (Figure 31-Figure 33) bogs in the tropics, noting that these had only been described from higher altitudes. Eddy (1977) provided a treatment of the ***Sphagnum*** species of tropical Asia.

McQueen (1991) considered the ***Sphagnum***-dominated peatlands in southern Ecuador to be similar to the intermediate or transitional poor fens in the Northern Hemisphere, based on levels of *p*H, conductivity, and concentrations of Fe, K, Mg, Mn, Na, and P. Species included ***S. magellanicum*** (Figure 31), ***S. recurvum*** (Figure 32), ***S. sancto-josephense***, and ***S. denticulatum*** (Figure 33).

Figure 31. ***Sphagnum magellanicum***, a species found in ***Sphagnum***-dominated peatlands in southern Ecuador. Photo by Michael Lüth, with permission.

Figure 32. ***Sphagnum recurvum***, a species found in ***Sphagnum***-dominated peatlands in southern Ecuador. Photo by Malcolm Storey, <www.discoverlife.com> through Creative Commons.

Figure 33. ***Sphagnum denticulatum***, a species found in ***Sphagnum***-dominated peatlands in southern Ecuador. Photo by Michael Lüth, with permission.

Wolfe and McQueen (1992) noted that few tropical studies of ***Sphagnum*** (Figure 31-Figure 33) habitats had been published and that these were restricted to the páramo in the northwestern part of South America. Cleef (1981) distinguished four kinds of ***Sphagnum*** bogs in the Cordillera Oriental of Colombia, distinguished on the basis of vegetation, *p*H, altitude, and peat depth. In addition, Cleef described ***Sphagnum*** habitats including wet seeps, peaty lake shores, floating mats, and boggy glacial valleys at 3,600-3,850 m asl.

Peatlands are not always ***Sphagnum*** (Figure 31-Figure 33) habitats. In the high elevation tropical Andes of Colombia, similar conditions to those of ***Sphagnum*** bogs prevail, but these peatlands are *Distichia muscoides* (Juncaceae – rushes; Figure 34) cushion bogs. These cushions provide similar function and structure to those of ***Sphagnum*** in boreal and austral regions (Cleef 1981; Fritz *et al*. 2011). Even the dead parts of these cushions fall to the bottom of the pool and are converted to turf, as does ***Sphagnum*** (Cuatrecasas 1968). In the high Andes, such cushion plants are restricted to areas with poor drainage or that have a positive water balance (Cleef 1981; Kleinebecker *et al*. 2010). Benavides *et al.* (2013) concluded that cushion plants are "capable of reducing methane emission on an ecosystem scale by thorough soil and methane oxidation," whereas ***Sphagnum*** lawns had substantial methane emissions. These mountaintop peatland habitats are in danger of extinction under most climate change scenarios (Colwell *et al*. 2008; Ruiz *et al*. 2008).

Figure 34. *Distichia muscoides*, a member of the rush family Juncaceae that resembles moss cushions and is forming a cushion bog like those found in the Andes. Photo by Sergejf – Bofedal, through Creative Commons.

Likewise, despite geographic differences, the niche width and overlap values of ***Sphagnum*** (Figure 31, Figure 35) species in tropical Costa Rica are similar to those for ***Sphagnum*** species in North America (McQueen 1995). In Costa Rica, ***S. magellanicum*** (Figure 31) and ***S. sparsum*** have the broadest niche widths. Despite its relatively narrow niche with, ***S. sancto-josephense*** is one of the most common ***Sphagnum*** species accompanying the other two. The niche overlap values are high, except for that of ***S. platyphyllum*** (Figure 35). This species occurs in habitats rich in iron. The *p*H, conductivity, and concentrations of Ca, Fe, K, Mg, Mn, Na, and P in these peatlands are similar to those of the páramo habitats in South America.

Figure 35. ***Sphagnum platyphyllum***, a species with small niche overlap in Costa Rica. Photo by Michael Lüth, with permission.

In Bolivia, McQueen (1997) determined that, based on *p*H, conductivity, and concentrations of Ca, K, Mg, Na, and P, the ***Sphagnum*** habitats in páramo and cloud forests of Bolivian Andes are ombrotrophic. In these habitats, the ***Sphagnum*** forms small, scattered carpets. The species include those from Ecuador and Costa Rica. Common species are ***S. alegrense***, ***S. boliviae***, ***S. cuspidatum*** (Figure 36), ***S. magellanicum*** (Figure 31), ***S. oxyphyllum***, ***S. recurvum*** (Figure 32), ***S. sancto-josephense***, and ***S. sparsum***.

Figure 36. ***Sphagnum cuspidatum***, a common species in the páramo and cloud forests of the Bolivian Andes. Photo by Michael Lüth, with permission.

Bosnian *et al*. (1993) described cushion mires in the páramo. Two types are dominated by tracheophytes, with ***Campylopus reflexisetus*** (Figure 37) occurring on the cushions. Two are dominated by bryophytes. The mosses ***Sphagnum sparsum***, ***Breutelia*** sp. (Figure 38), and ***Campylopus cuspidatus*** var. ***dicnemoides*** (Figure 39) dominate one of these, and the leafy liverwort ***Lophonardia laxifolia*** along with the tracheophyte *Cortaderia sericantha* (Figure 40) dominate the other. The ***Sphagnum sparsum*** type requires higher conductivity of ground water, higher NO_3 and PO_4 levels, and lower Fe levels. The ***Lophonardia laxifolia*** type requires lower levels of K and Al. A fifth type is dominated by submerged ***Sphagnum cyclophyllum*** (Figure 41), whereas the sixth has only the aquatic vegetation of *Equisetum bogotense* (Figure 42) and algae. Moss cover is low in the water-filled depressions among the cushions.

Figure 37. ***Campylopus reflexisetus***, a species that occurs on tracheophyte cushions in cushion mires of the South American páramo. Photo by Michael Lüth, with permission.

Figure 38. ***Breutelia***, one of the dominant mosses in one type of cushion mire in the páramo. Photo through Creative Commons.

Figure 39. ***Campylopus cuspidatus***, one of the dominant mosses in one type of cushion mire in the páramo. Photo by Michael Lüth, with permission.

Figure 40. ***Cortaderia selloana*** in Brazil; ***Cortaderia sericantha***, along with the liverwort ***Lophonardia laxifolia***, dominates one of the moss-dominated cushion mires in the páramo. Photo by H. M. Longhi-Wagner, through Creative Commons.

Figure 41. ***Sphagnum cyclophyllum***, the dominant species in one type of cushion mire in the páramo. Photo by Blanka Aguero, with permission.

Figure 42. ***Equisetum bogotense***, the dominant plant in one type of cushion mire in the páramo. Photo by Penarc, through public domain.

Liu *et al*. (2014) examined population structure of ***Sphagnum tumidulum*** (Figure 43) on tropical Reunion Island. Using genotypes at 10 microsatellite loci, they determined the species to be highly variable. They identified 31 multilocus genotypes. This variability suggests that sexual reproduction is successful on the island, although capsules have not been found. On the other hand, gene flow among populations appears to be very limited.

Figure 43. ***Sphagnum tumidulum***, a common species on tropical Reunion Island. Photo by courtesy of Jacques Bardat.

Oxygen deficiency is important for the survival of ***Sphagnum*** spores (Figure 44) (Feng *et al*. 2018). After 60 days of storage, those spores that experienced oxygen injection had lower germinability than those that lacked it. High *p*H further diminished the germinability. These requirements make ***Sphagnum*** peat suitable substrate for retaining viable spores.

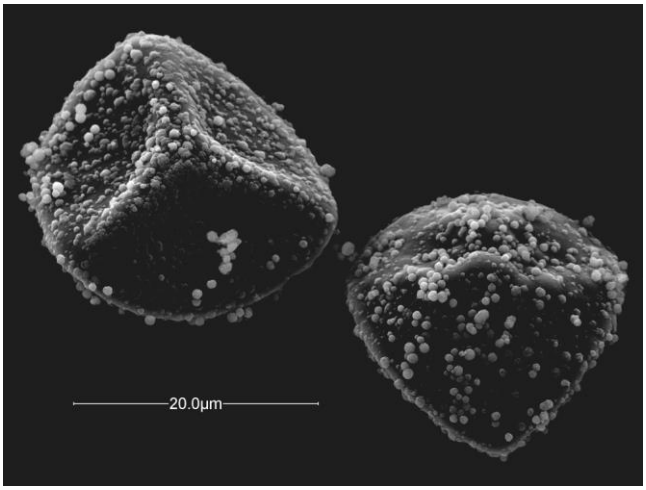

Figure 44. ***Sphagnum*** spores SEM. Photo from Whitaker & Edwards 2010, with permission from Diane Edwards.

Aquatic

In the tropics, aquatic bryophytes grow in periodically inundated habitats such as river beds, marshes, and waterfalls (Gradstein *et al*. 2018). Permanently submerged bryophytes are rare, occurring primarily at high altitudes. Their modifications of morphological traits (de Winton & Beever 2004; Rankin *et al*. 2017), sometimes induced by changing water conditions, make identification difficult.

Lowland tropical habitats are especially challenging for bryophytes. Because the bryophytes are continuously hydrated, they continue respiration even when the temperatures are high. This results in net carbon loss as respiration exceeds photosynthesis, especially in low light conditions.

The red-listed liverwort ***Colura irrorata*** (Figure 45) was known only from its type collection from the Ecuadorian Andes in 1857 (Gradstein *et al*. 2004). But Gradstein and coworkers found the species along two tributaries of the Rio Pastaza, Ecuador. It is in fact abundant along the Rio Topo, where it lives on the periodically submerged ***Cuphea bombonasae*** (Figure 45) shrubs along with the rare ***Myriocoleopsis gymnocolea*** (see Figure 46). In the Ecuadorian Andes, ***Colura irrorata*** occurs almost exclusively on the small, woody subshrub ***Cuphea bombonasae*** where it is very close to torrential water (Gradstein & Benitez 2014). Three other rare rheophytic bryophytes [***Lejeunea topoensis*** (see Figure 47), ***Myriocoleopsis gymnocolea***, and ***Sematophyllum steyermarkii*** (see Figure 48)] typically occur with it. The species ***Colura irrorata*** is distinguished by a very high number of clustered gynoecia as well as numerous antheridia per male bract (Gradstein *et al*. 2004).

Figure 45. ***Colura irrorata***, showing numerous gynoecia, growing on stems of ***Cuphea bombonasae*** along the Numpatakaima river at 1,540 m asl. Photo by Lou Jost, EcoMinga, with permission.

Figure 46. ***Myriocoleopsis minutissima***; ***Myriocoleopsis gymnocolea*** is one of the rare rheophytic liverworts in the Ecuadorian Andes. Photo by Hugues Tinguy, through Creative Commons.

Figure 47. ***Lejeunea cavifolia***; ***Lejeunea topoensis*** is one of the rare rheophytic liverworts in the Ecuadorian Andes. Photo by Hermann Schachner, through Creative Commons.

Figure 48. ***Sematophyllum*** sp. from the Neotropics; ***Sematophyllum steyermarkii*** is one of the rare rheophytic liverworts in the Ecuadorian Andes. Photo by Michael Lüth, with permission.

Rheophytes

Our knowledge of bryophytic **rheophytes** (aquatic plant that lives in fast moving water currents) in the tropics is somewhat limited. It is greater for Asia than for Africa or South America (Shevock *et al.* 2017). In Malesia, studies of floristic works have elaborated the bryophytes of such habitats (Koponen & Norris 1983; Eddy 1988, 1990, 1996). In Borneo Island, bryophytes are species rich above 1,000 m asl. In lower elevations, heavy deposits of sediments can be detrimental to rheophytic bryophytes.

The seemingly ever-present **Lejeuneaceae** even ventures into rheophytic habitats. Reiner-Drehwald (1999) reported ***Potamolejeunea polyantha*** [now considered to be a subgenus of ***Lejeunea*** (Gradstein & Reiner-Drehwald 2007)] as a rheophyte from South America, noting that it was poorly known.

At higher elevations, one can find ***Neckeropsis beccariana*** (see Figure 49), ***Thamnobryum ellipticum*** (see Figure 50), and ***Fissidens beccarii*** (see Figure 51) on boulders; ***Calymperes tahitense*** (see Figure 52) occurs on hardwood branches or exposed tree roots; and ***Sclerohypnum littorale*** on branches of rheophytic shrubs (Akiyama 1992a). In a separate paper, Akiyama (1992b) described the morphology and ecology of these rheophytes. Along the river and streambanks, one can find carpets of bryophytes that are actually rheophytic, surviving high water levels and rapid flow (Ma *et al.* 2014). Above this flooding zone, the same shrub species lack these rheophytic bryophytes. In many areas of the tropics, these bryophytes are submerged multiple times through the year, especially during monsoon season.

Figure 49. ***Neckeropsis lepineana***; ***Neckeropsis beccariana*** occurs at higher elevations on boulders. Photo by Li Zhang, with permission.

Figure 50. ***Thamnobryum neckeroides***; ***Thamnobryum ellipticum*** occurs at higher elevations on boulders. Photo by Blanka Aguero, with permission.

Figure 51. ***Fissidens marthae***; ***Fissidens beccarii*** occurs at higher elevations on boulders. Photo by Jan-Peter Frahm, with permission.

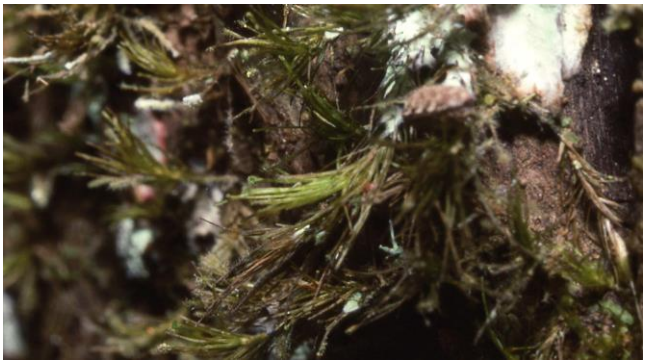

Figure 52. ***Calymperes*** sp. from Toro Negro, Puerto Rico. ***Calymperes tahitense*** occurs on hardwood branches or exposed tree roots. Photo by Janice Glime.

Despite the cosmopolitan nature of many rheophytes in the temperate zone, new tropical species are still awaiting exploration. For example, Shevock *et al*. (2011) named ***Yunnanobryon*** as a new genus of rheophytic moss from southwest China. ***Yunnanobryon rhyacophilum*** (Figure 53-Figure 54) occurs in fast-flowing rivers. As is typical of mosses in fast-flowing water, it is pleurocarpous. It is slender with stoloniform primary stems and intricately much-branched secondary stems that become flagellate-attenuate at the tips.

Figure 53. ***Yunnanobryon rhyacophilum*** with developing young leaves in a stream in Yunnan, China. Photo by Jim Shevock, with permission.

Figure 54. ***Yunnanobryon rhyacophilum*** from a stream in Yunnan, China. Photo by Li Zhang, with permission.

Neotropical bryophyte families with at least some species that can be found as rheophytes include the mosses **Amblystegiaceae** (Figure 78, Figure 81), **Andreaeaceae** (Figure 55), **Brachytheciaceae** (Figure 56), **Fissidentaceae** (Figure 51), **Hydropogonaceae**, **Leucomiaceae** (Figure 57), **Pilotrichaceae** (Figure 58), **Pottiaceae** (Figure 86-Figure 87), **Seligeriaceae** (Figure 76), **Sematophyllaceae** (Figure 48), **Sphagnaceae** (Figure 31-Figure 33, Figure 35-Figure 36), and the liverworts **Aneuraceae** (Figure 73), **Balantiopsidaceae** (Figure 70), **Cephaloziellaceae** (Figure 59), **Fossombroniaceae** (Figure 62-Figure 63), **Jungermanniaceae** (Figure 75), **Lejeuneaceae** (Figure 27-Figure 29), **Lophocoleaceae** (Figure 60), and **Pelliaceae** (Figure 61) (see Mägdefrau 1973; Griffin *et al*. 1982; Bartlett & Vitt 1986; Gradstein & Váňa 1999; Reiner-Drehwald 1999; Gradstein *et al.* 2001a, 2004, 2011; Gradstein & Reiner-Drehwald 2007; Hedenäs 2003; Crandall-Stotler & Gradstein 2017). Permanent submergence is less common in the tropics compared to temperate and Arctic zones (Gradstein *et al*. 2018).

Figure 55. ***Andreaea nivalis*** (**Andreaeaceae**). Some members of this family are among the Neotropical rheophytes. Photo by Michael Lüth, with permission.

Figure 56. ***Platyhypnidium riparioides*** (**Brachytheciaceae**). Some members of this family are among the Neotropical rheophytes. Photo from Proyecto Musgo through Creative Commons.

Figure 57. ***Leucomium strumosum*** (**Leucomiaceae**). Some members of this family are among the Neotropical rheophytes. Photo by Claudio Delgadillo Moya, with permission.

Figure 58. ***Cyclodictyon laetevirens*** (**Pilotrichaceae**). Some members of this family are among the Neotropical rheophytes. Photo by Jan-Peter Frahm, with permission.

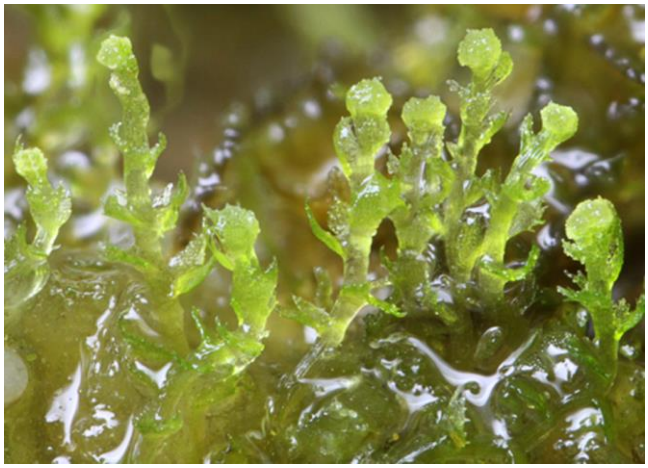

Figure 59. ***Cephaloziella dentata*** (**Cephaloziellaceae**). Some members of this family are among the Neotropical rheophytes. Photo by Des Callaghan, with permission.

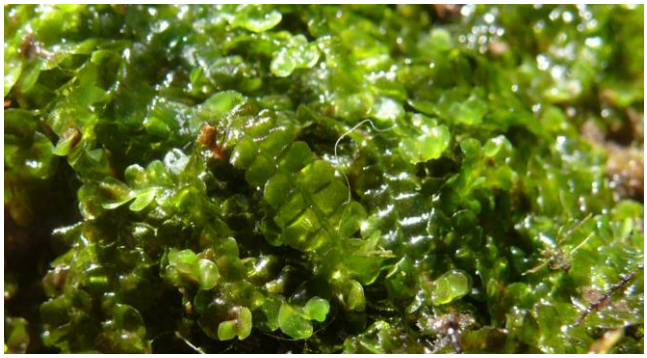

Figure 60. ***Chiloscyphus polyanthos*** (**Lophocoleaceae**). Some members of this family are among the Neotropical rheophytes. Photo by Bernd Haynold through Creative Commons.

Figure 61. ***Pellia endiviifolia*** (**Pelliaceae**). Some members of this family are among the Neotropical rheophytes. Photo by Janice Glime.

Gradstein and Reiner-Drehwald (2007) described a new rheophytic liverwort, ***Lejeunea topoensis*** (Figure 16), from the Andes in Ecuador and southern Brazil. Crandall-Stotler and Gradstein (2017) found a new riverine species in Ecuador, ***Fossombronia jostii*** (Figure 62). It seems to be restricted to limestone boulders, where one can also find ***F. texana*** (Figure 63) and ***F. wrightii***. These species experience major flooding events that appear to wipe out the entire population, but given a little time, these species return, regenerating from remaining shoot apices of plants that have otherwise been killed by the flooding.

Figure 62. ***Fossombronia jostii*** resprouting on limestone rocks in Ecuador after flooding. Photo by Lou Jost, EcoMinga, with permission.

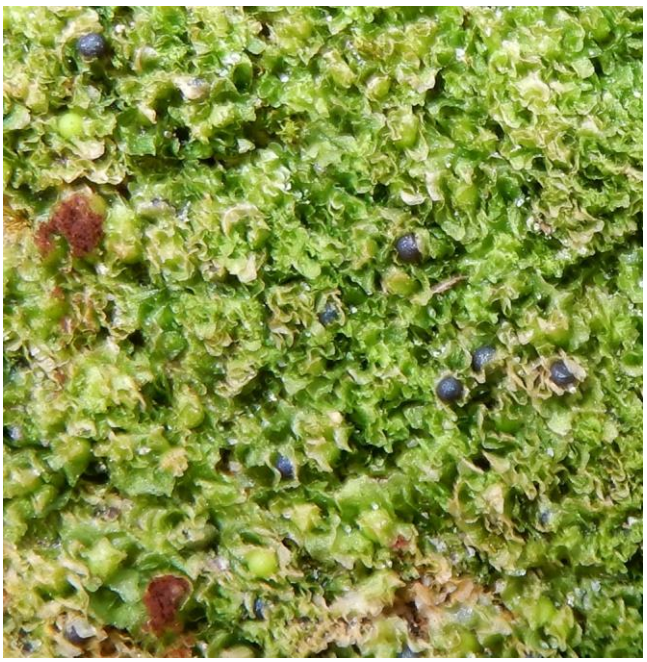

Figure 63. ***Fossombronia texana***, one of the species on the limestone rocks in Ecuador. Photo by Bob O'Kennon, through Creative Commons.

Racomitrium lamprocarpum (=***Bucklandiella lamprocarpa***; Figure 64) is a rheophytic moss from the central and northern Andean countries (Bednarek-Ochyra 2015). Ochyra concluded that ***Racomitrium bartramii*** should be included within this species. ***Racomitrium lamprocarpum*** is an austral cool-adapted species that has spread deep into the tropics, where it finds suitable habitat at high elevations in the Neotropics and in East and Central Africa.

Figure 64. ***Racomitrium lamprocarpum***, Cape Horn, a rheophyte in both Africa and the Neotropics. Photo by Juan Larrain, through Creative Commons.

Ochyra *et al*. (1998) reported a new moss species from subtropical Tenerife as ***Gradsteinia torrenticola***, considering it to be most closely related to the Andean ***Gradsteinia andicola*** from Colombia. But instead it was later placed in ***Platyhypnidium*** (***P. torrenticola***; Figure 65) (Ochyra & Bednarek-Ochyra 1999). In the Neotropics, ***Platyhypnidium torrenticola*** is known only from a single waterfall.

Figure 65. ***Platyhypnidium torrenticola***, a species from waterfall habitats in Colombian Andes. Photo by BBS website, with permission from Barry Stewart.

So why are we seeing so many new species in a relatively restrictive habitat? Gradstein *et al*. (2011) attributed the unusual morphology of river bank species to habitat specialization and isolation. Such is the case for ***Cololejeunea stotleriana*** (Figure 66) from Ecuador. This species is both rheophilous and epiphytic. It was the first member of the subgenus ***Chlorolejeunea*** to be found in the Neotropics, with the other known member occurring in Asia. Furthermore, it occurs with the rare mosses ***Fissidens hydropogon*** (Figure 67) and ***Lepidopilum caviusculum*** (Figure 68), both previously known only from their type collections 150 years ago. But rarity and new species are probably products of the isolation between mountaintops, with unsuitable habitat in between.

Figure 66. ***Cololejeunea stotleriana*** on a fern frond. Photo by F. Werner, courtesy of Robbert Gradstein.

Figure 67. Herbarium specimen of ***Fissidens hydropogon***, a rare rheophilic moss from Ecuador. Photo from Alchetron.com, through Creative Commons.

Figure 68. Herbarium specimen of ***Lepidopilum caviusculum***, a rare rheophilic moss from Ecuador. Photo Natural History Museum, London, through Creative Commons.

Lakes

Like the rheophytic habitat, Andean and other high-altitude lakes are isolated from those on surrounding mountains by inhospitable habitat surrounding them. Since aquatic bryophytes are transported mostly by fragments, this effectively isolates them.

In high altitude lakes in the Neotropics, one can find the liverworts ***Clasmatocolea vermicularis*** (Figure 69), ***Gymnocoleopsis cylindriformis***, ***Herbertus sendtneri*** (Figure 83), ***Isotachis obtusa*** (Figure 70), ***Jensenia spinosa*** (Figure 71), ***Lophonardia laxifolia***, ***Marchantia plicata*** (Figure 72), ***Riccardia cataractarum*** (see Figure 73), ***Ricciocarpos natans*** (Figure 74), and ***Syzygiella***

sonderi (see Figure 75) (Gradstein *et al*. 2018; see also Cleef 1981; Gradstein *et al*. 2001b; Hedenäs 2003; Churchill 2018). Mosses include ***Blindia gradsteinii*** (see Figure 76), ***Ditrichum submersum*** (see Figure 77), ***Drepanocladus*** spp. (Figure 78), ***Fontinalis bogotensis*** (see Figure 79), ***Gradsteinia andicola***, ***Philonotis andina*** (see Figure 80), ***Pseudocalliergon*** spp. (Figure 81), ***Scorpidium*** spp. (Figure 82), and ***Sphagnum*** spp. (Figure 31-Figure 33). Most of the mosses and all of the liverworts also can grow out of water in wet situations. Only the mosses ***Blindia gradsteinii***, ***Ditrichum submersum***, ***Fontinalis bogotensis***, and possibly some ***Sphagnum*** species are restricted to submergence. ***Blindia gradsteinii*** is known from only one locality, a small pond at 4,090 m asl in the páramo de Sumapaz in Colombia (Churchill 2016). ***Gradsteinia andicola*** has been found only once, in a dried-up lake at 3,650 in the same páramo (Gradstein *et al*. 2018). These two rare species suggest that they are restricted by temperature.

Figure 69. ***Clasmatocolea vermicularis***, a leafy liverwort from high altitude lakes in the Neotropics. Photo by John Engel, through Creative Commons.

Figure 70. ***Isotachis*** sp. from the Neotropics. ***Isotachis obtusa*** occurs in high-altitude lakes in the Neotropics. Photo by Michael Lüth, with permission.

Figure 71. ***Jensenia spinosa***, a liverwort from high altitude lakes in the Neotropics. Photo by Jan-Peter Frahm, with permission.

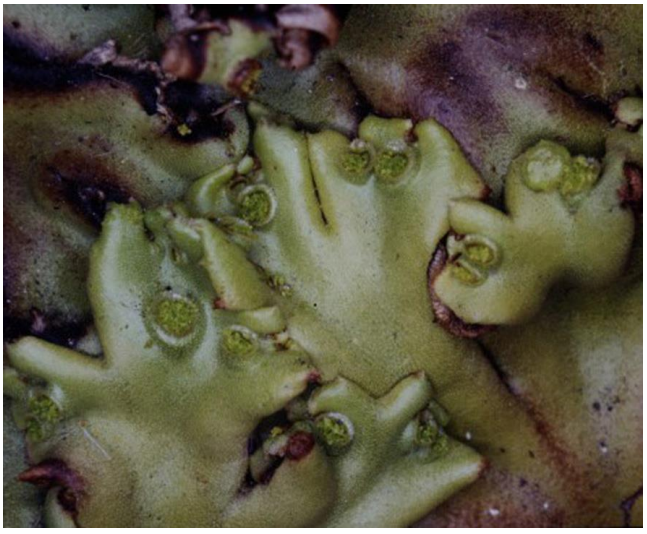

Figure 72. ***Marchantia plicata***, a liverwort from high altitude lakes in the Neotropics. Photo by Jan-Peter Frahm, with permission.

Figure 73. ***Riccardia*** sp. from the Neotropics. ***Riccardia cataractarum*** is a liverwort from high altitude lakes in the Neotropics. Photo by Michael Lüth, with permission.

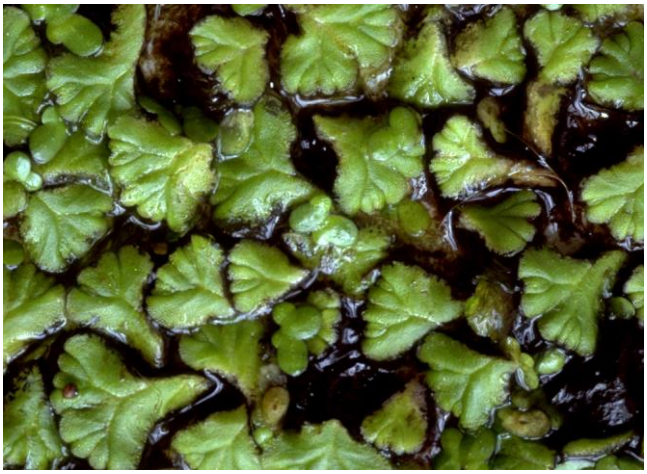

Figure 74. ***Ricciocarpos natans***, a liverwort from high altitude lakes in the Neotropics. Photo by Jan-Peter Frahm, with permission.

Figure 75. ***Syzygiella autumnalis***; ***Syzygiella sonderi*** is a liverwort from high altitude lakes in the Neotropics. Photo by Hermann Schachner, through Creative Commons.

Figure 76. ***Blindia acuta***; ***Blindia gradsteinii*** is a moss from high altitude lakes in the Neotropics. Photo by Hermann Schachner, through Creative Commons.

Figure 77. ***Ditrichum gracile***; ***Ditrichum submersum*** is a moss from high altitude lakes in the Neotropics. Photo by Hermann Schachner, through Creative Commons.

Figure 78. ***Drepanocladus aduncus***; several species of ***Drepanocladus*** *s.l.* occur in high altitude lakes in the Neotropics. Photo by Hermann Schachner, through Creative Commons.

Figure 79. ***Fontinalis antipyretica***; ***Fontinalis bogotensis*** is a moss from high altitude lakes in the Neotropics. Photo by Malcolm Storey <DiscoverLife.com>, through online permission.

Figure 80. ***Philonotis*** sp. from the Neotropics; ***Philonotis andina*** is a moss from high altitude lakes in the Neotropics. Photo by Michael Lüth, with permission.

Figure 81. ***Pseudocalliergon trifarium***; members of this genus occur in high altitude lakes in the Neotropics. Photo by Blanka Aguero, with permission.

Figure 82. ***Scorpidium scorpioides***; members of this genus occur in high altitude lakes in the Neotropics. Photo by David T. Holyoak, with permission.

In the Andes of Colombia, at 4,120 m asl, Gradstein *et al*. (2018) found a large population of ***Herbertus sendtneri*** (Figure 83) in a glacial lake. The researchers speculated that a rock-inhabiting population had washed into the lake by vegetative branches or other fragments.

Figure 83. ***Herbertus sendtneri***, a species found in a glacial lake of the Colombian Andes. Photo by Michael Lüth, with permission.

In seven páramo lakes above 3,800 m asl on Volcán Chiles, Ecuador, Terneus (2001) found that moss species (not including ***Sphagnum***) were the most abundant and most frequent vegetation, exhibiting a 71.4% frequency among the lakes and a 70% frequency among the transects. They provided a mean cover of 26.7% and occupied maximum depths greater than 100 m. They had a wide depth range (>100 m) compared to other vegetation types.

In Lake Titicaca in the Andes on the border of Peru and Bolivia, ***Drepanocladus longifolius*** (Figure 84) is another deep-water moss (Richards 1984). It is not as deep as the moss occurrences reported by Terneus (2001), but reaches depths to 29 m and dominates one of the submerged vegetation zones in the lake.

Figure 84. ***Drepanocladus longifolius***, a deep-water moss in the Andes in Lake Titicaca. Photo by Juan David Parra, MBG, through Creative Commons.

Seepage Areas

Volk (1979) reported ***Riccia cavernosa*** (Figure 85) (a nitrophilous species), ***R. runssorensis***, and ***R. volkii*** from seepage areas around dams in southwest Africa. Similarly, Pettet (1967) reported several species of ***Riccia*** from seepage areas in the Sudan. In addition, Pettet found ***Tortula bogosica*** (see Figure 86), ***Barbula unguiculata*** (Figure 87), ***Physcomitrium niloticum*** (Figure 88), ***Funaria*** (Figure 89), and ***Bryum*** (Figure 90) from such areas.

Figure 85. ***Riccia cavernosa***, a species from seepage areas around dams in southwest Africa. Photo by Des Callaghan, with permission.

Figure 86. ***Tortula hoppeana***; ***Tortula bogosica*** occurs in seepage areas in southwest Africa. Photo by Bryophyte CNPS, through Creative Commons.

Figure 87. ***Barbula unguiculata***, a species of seepage areas in southwest Africa. Photo by Michael Lüth, with permission.

Figure 88. ***Physcomitrium collenchymatum*** from pond edge; ***Physcomitrium niloticum*** occurs in seepage areas of southwest Africa. Photo by Fred Essig, with permission.

Figure 89. ***Funaria hygrometrica*** with capsules, a species that occurs in seepage areas of southwest Africa. Photo by Li Zhang, with permission.

Figure 90. ***Bryum pseudotriquetrum*** by stream; species of ***Bryum*** occur in seepage areas in southwest Africa. Photo by Michael Lüth, with permission.

Xeric Habitats

Subtropical Israel provides us with a glimpse of the importance of climate, particularly water availability. Distribution of bryophytes there depends on climate, altitude, other vegetation, and shelter (Bischler 2002). Israel is one of the drier sites on the Mediterranean, and the low liverwort species richness reflects this fact. Within Israel, species richness of liverworts is lowest in the arid region and highest in the Mediterranean zone. Those liverworts that are able to grow in the arid zone are also able to grow under less severe conditions and have a wide geographic distribution, whereas many of the Mediterranean species are absent in the arid zone, but otherwise widely distributed. The flora of the country tends to be cosmopolitan and no endemics are known.

To succeed in habitats that have long dry periods interrupted by short periods of moisture, bryophytes must be able to recover quickly from desiccation. Di Nola *et al*. (1983) found that the **Pottiaceae** mosses ***Tortula brevissima*** (Figure 91) and ***Trichostomopsis aaronis*** (see Figure 92) are able to resume photosynthesis and respiration rapidly after prolonged desiccation. Furthermore, they suffer little high light intensity damage. The chlorophyll is ready to resume photosynthesis without additional chlorophyll synthesis first. This is true for some temperate species as well, as seen in the Mediterranean moss ***Didymodon fallax*** (Figure 93), whereas ***Homalothecium aureum*** (Figure 94) has a slower recovery and is more sensitive to desiccation. But the temperate ***Pohlia*** (subgenus ***Mniobryum***; Figure 95) sp. was unable to survive prolonged desiccation, exhibiting a lack of drought tolerance.

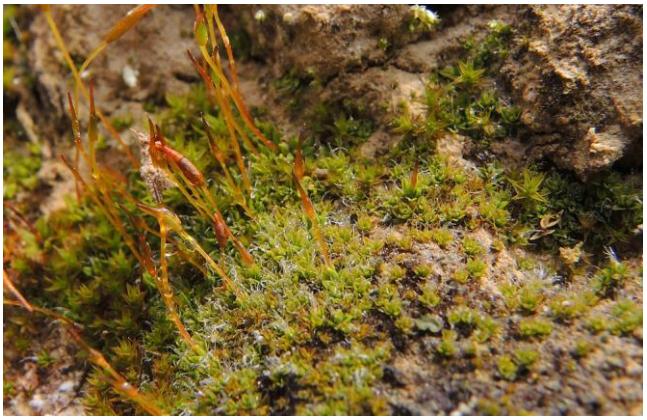

Figure 91. ***Tortula brevissima*** with capsules, a species that is able to resume photosynthesis and respiration rapidly after prolonged desiccation. Photo by Michael Lüth, with permission.

Figure 92. ***Trichostomopsis umbrosa***; ***Trichostomopsis aaronis*** is a species that is able to resume photosynthesis and respiration rapidly after prolonged desiccation. Photo by Jan-Peter Frahm, with permission.

Figure 93. ***Didymodon fallax***, a temperate species that is ready to resume photosynthesis without additional chlorophyll synthesis. Photo by Michael Lüth, with permission.

Figure 94. ***Homalothecium aureum***, a temperate species with a slower recovery from desiccation and greater sensitivity to desiccation. Photo by Michael Lüth, with permission.

Figure 95. ***Pohlia melanodon***; temperate species in this subgenus (***Mniobryum***) are unable to survive desiccation. Photo by Jan-Peter Frahm, with permission.

Frey (1986) noted the large percentage of endemic species in the arid parts of southwest Asia. Notable genera with endemic species include ***Tortula*** (Figure 86, Figure 91), ***Crossidium*** (Figure 122), and ***Targionia*** (Figure 102).

Pócs *et al*. (2007) reported on dry-land communities in Kenya. They described a community of ***Mannia capensis*** (Figure 96) that was accompanied by ***Exormotheca pustulosa*** (Figure 97), ***Gongylanthus ericetorum*** (Figure 98), ***Plagiochasma rupestre*** (Figure 99), ***Riccia congoana*** (Figure 100), ***Riccia crinita*** (Figure 101), and ***Targionia hypophylla*** (Figure 102), all liverworts. They identified several other associations in the dry lands. ***Plagiochasma microcephalum*** (see Figure 99) was accompanied by ***Asterella cf. linearis*** (see Figure 103), ***Exormotheca pustulosa***, and ***Riccia albolimbata*** (Figure 104-Figure 105). ***Riccia lanceolata*** is widespread in tropical Africa, where it reaches a high diversity. This genus is particularly adapted to the seasonal rain, going dormant, then springing to growth when the rain arises. Other important ***Riccia*** species include ***Riccia microciliata*** (Figure 106), accompanied by ***Riccia congoana***, ***Riccia crinita***, and ***Riccia okahandjana*** (Figure 107). Widespread species include ***Riccia congoana*** and ***Riccia atropurpurea*** (Figure 108), accompanied by ***Exormotheca pustulosa***, ***Riccia crinita***, ***Targionia hypophylla***.

Figure 96. ***Mannia capensis***, a species forming a dry-land community in Kenya. Photo by Tony Benn, through Creative Commons.

Figure 97. ***Exormotheca pustulosa***, a species in the ***Mannia capensis*** dry-land community in Kenya. Photo by Michael Lüth, with permission.

Figure 98. ***Gongylanthus ericetorum***, a species in the ***Mannia capensis*** dry-land community in Kenya. Photo by Jan-Peter Frahm, with permission.

Figure 99. ***Plagiochasma rupestre***, a species in the ***Mannia capensis*** dry-land community in Kenya. Photo by Alan Rockefeller, through Creative Commons.

Figure 100. ***Riccia congoana***, a species in the ***Mannia capensis*** dry-land community in Kenya. Photo by Catherine Reeb, through Creative Commons.

Figure 101. ***Riccia crinita***, a species in the ***Mannia capensis*** dry-land community in Kenya. Photo by Štěpán Koval, with permission.

Figure 102. ***Targionia hypophylla***, a species of vertical volcanic cliffs in Kenya. Photo by Catherine Reeb, through Creative Commons.

Figure 103. ***Asterella africana***; ***Asterella*** *cf.* ***linearis*** is a species in the ***Mannia capensis*** dry-land community in Kenya. Photo by Jonathan Sleath, with permission.

Figure 104. ***Riccia albolimbata*** dry, a species in the ***Plagiochasma microcephalum*** dry-land community in Kenya. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

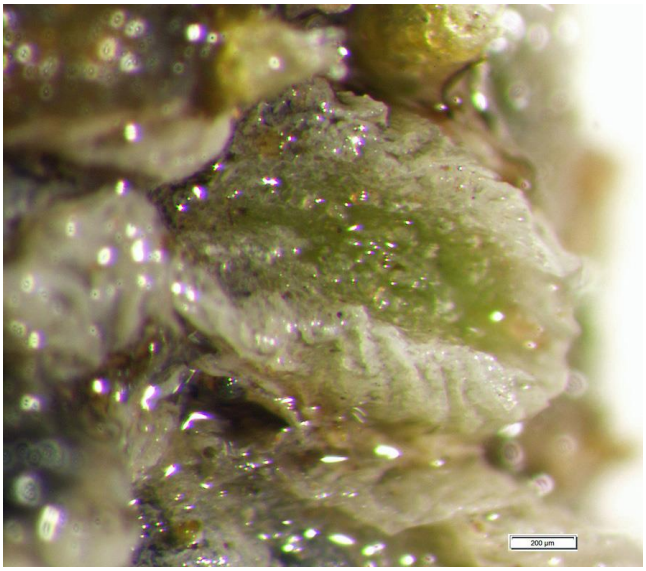

Figure 105. ***Riccia albolimbata*** wet; the ability to rehydrate and resume growth permits this species to live in dry-land areas with seasonal rainfall in Kenya. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 106. ***Riccia microciliata***, a species in the ***Plagiochasma microcephalum*** dry-land community in Kenya. Photo by Catherine Reeb, through Creative Commons.

Figure 107. ***Riccia okahandjana***, an important ***Riccia*** species in the dry-land communities in Kenya. Photo by A. A. Dreyer, permission pending.

Figure 108. ***Riccia atropurpurea*** on sandstone. a widespread species in southwest Asia. Photo by Catherine Reeb, through Creative Commons.

Savannahs

In their study of savannah bryophytes in southwest Nigeria, Makinde and Odu (1994) found little bryophyte diversity. Liverworts were rare.

Oyesiku and Egunyomi (2001, 2002) have explored savannah bryophytes in southwestern Nigeria. They likewise found that mosses were far more common than liverworts in the dry savannah. The intense dryness is unfavorable to liverworts. Tree bark, however, provides some protection, permitting corticolous bryophytes to live in areas with bush burning. On the trees in relatively closed stands, bryophytes, particularly **mat**-forming species, are able to spread from the base to locations under 3 m height. Some of these bryophytes [***Hyophila*** (Figure 109), ***Erythrodontium*** (Figure 110), ***Riccia*** (Figure 85)] are specialists at specific heights. Generalists with no height preference include the mosses ***Fissidens*** (Figure 51, Figure 67), ***Calymperes*** (Figure 11, Figure 30), ***Thuidium*** (Figure 111), and the leafy liverwort ***Lejeunea*** (Figure 47). Among these epiphytes, 60% of the mat species are dominant on host trees; the co-dominant tuft species comprise 34%.

Figure 109. ***Hyophila involuta***; members of this genus are specialists at specific heights in the savannahs. Photo by Michael Lüth, with permission.

Figure 110. ***Erythrodontium squarrosum*** from the Neotropics; members of this genus are specialists at specific heights in the savannahs. Photo by Michael Lüth, with permission.

Figure 111. ***Thuidium peruvianum*** from the Neotropics; members of this genus are specialists at specific heights above ground in the savannahs. Photo by Michael Lüth, with permission.

Silva Bonfim *et al*. (2018) collected bryophytes from a Cerrado fragment in Caxias, Maranhão, Brazil. This area is mostly savannah. They identified 175 bryophyte samples in 12 families (10 mosses, 2 liverworts), 17 genera (15 mosses, 2 liverworts), and 23 species (21 mosses, 2 liverworts. The **Sematophyllaceae** was best represented (***Trichosteleum subdemissum***, ***Sematophyllum subsimplex*** (Figure 113), ***Sematophyllum subpinnatum*** (Figure 114), and ***Taxithelium planum*** (Figure 115). **Dicranaceae**, **Fissidentaceae** (Figure 51, Figure 67), and **Pottiaceae** (Figure 86-Figure 87, Figure 91-Figure 93) followed with three species each.

Figure 112. Cerrado savannah in Brazil. Photo by Conrado, through Creative Commons.

Figure 113. ***Sematophyllum subsimplex***, a savannah species in Corrado, Brazil. Photo by Yelitza Leon, through Creative Commons.

Figure 114. ***Sematophyllum subpinnatum***, a savannah moss in the Cerrado, Brazil. Photo by Michael Luth, with permission.

Figure 115. ***Taxithelium planum***, a savannah moss in the Cerrado, Brazil. Photo by Scott Zona, with permission.

Succession

In their study of epiphytes in an Amazonian savannah in Brazil, Gottsberger and Morawetz (1993) noted that lichens and bryophytes have a successional relationship with their host trees. Young trees have lichen dominants. These lichens usually are diminished in older trees and bryophytes assume abundance, apparently supressing the lichens.

Life Cycle Strategies

Makinde and Odu (1994) followed the reproductive cycles of four species [***Archidium ohioense*** (Figure 116), ***Bryum coronatum*** (Figure 117), ***Fissidens minutifolius*** (see Figure 51, Figure 67), ***Trachycarpidium tisserantii***] that reproduce predominately sexually. They found that the protonemata and gametophytes are produced in the field in March-April. Capsule dehiscence and spore dispersal occurs in September-October. The development of gametangia through the completion of dispersal all occur within the rainy season. **Cleistocarpous capsules** (capsules with no operculum and that open irregularly) of ***A. ohioense*** and ***T. tisserantii*** do not disperse their spores easily. All species experience only a short period between the formation of sex organs and the dehiscence of the capsule.

Figure 116. ***Archidium ohioense***, a species with cleistocarpous capsules and a short period between fertilization and ripe capsules. Photo by Li Zhang, with permission.

Figure 117. ***Bryum coronatum***; in the Nigerian savannah, development of gametangia through the completion of dispersal all occur within the rainy season in this species. Photo by Jan-Peter Frahm, with permission.

When long periods of drought are a regular part of the environment, reproduction can be challenging. Spore longevity would help to solve this problem. However, when Egunyomi (1979) tested spore viability of 20 tropical moss species, only 7 germinated after more than two years of storage, and only 4 species had as much as 50% germination. Freezing for 1 week or more was detrimental to all 20 species. ***Microcampylopus nanus*** (see Figure 118) had the highest spore longevity and germination after desiccation. Other species that survived desiccation for at least two years were ***Weissia papillosa*** (see Figure 119), ***Mittenothamnium overlaetii*** (Figure 120), and ***Weisiopsis nigeriana***. What is interesting is that these four species are from a locality that is persistently wet.

Figure 118. ***Microcampylopus laevigatus***; ***Microcampylopus nanus*** has high spore longevity and germination after desiccation. Photo by Jan-Peter Frahm, with permission.

Figure 119. ***Weissia multicapsularis***; ***Weissia papillosa*** survives desiccation for at least two years. Photo by David T. Holyoak, with permission.

Figure 120. ***Mittenothamnium reptans***; ***Mittenothamnium overlaetii*** can survive desiccation for at least two years. Photo by Michael Lüth, with permission.

Although we cannot rule out spore longevity, we need to find other means to explain reproductive success in these dry-habitat mosses. During and coworkers (During 1998, 2007; During & Moyo 1999) examined the diaspore bank in a savannah in Zimbabwe. They determined at least 2 hornworts, 10 liverworts, and 22 mosses that emerge from these soil samples. Some of these were in large numbers. Some of these species, such as ***Micromitrium tenerum*** (Figure 121), were rare or previously unknown in Africa or Zimbabwe. An added advantage for these diaspores is that they are able to survive above-ground burning.

Figure 121. ***Micromitrium tenerum***, a species that can survive desiccation for at least two years. Photo by Jan-Peter Frahm, with permission.

Tropical Deserts

Deserts are not very friendly to bryophytes, and this habitat is likewise unfriendly for bryologists. Tropical deserts are often among the worst of these due to their even higher temperatures. Hence, systematic studies of bryophytes in these habitats are rare. Nevertheless, the guileless bryophytes and their adventurous observers can occur in these inhospitable places.

O'Shea (1997) reported over 3000 taxa of mosses in sub-Saharan Africa. Of these, 77% were considered endemic at the time. Because of the small number of bryologists exploring the vast area of Africa, it may still be a long time before we understand the African flora well enough to know how many of these are truly endemic.

The moss ***Crossidium laevipilum*** (Figure 122) occurs in semidesert conditions in Kenya, where it is associated with many xeric species (Pócs *et al*. 2007). ***Didymodon revolutus*** (Figure 123) occurs on vertical volcanic cliffs. This species has both axillary and rhizoidal gemmae, contrasting with American plants that are only known to have axillary gemmae. This species is known as a xerophyte in the desert and semidesert of southern United States, Mexico, Guatemala, and Ecuador.

Figure 122. ***Crossidium laevipilum***, a species of semi-desert conditions in Kenya. Photo by Michael Lüth, with permission.

Figure 123. ***Didymodon revolutus*** dry, a species of vertical volcanic cliffs in Kenya. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

At the edge of the Tunisian Sahara, Pócs (2007) found the community of ***Crossidium laevipilum*** (Figure 122)-***Tortula atrovirens*** (Figure 124) to be dominant. Only the tips of the plants and apical hair points, if present, extended above the sand. The hair points can protect against UV light and collect moisture. Most of the bryophytes, like these two, are in the **Pottiaceae**. The rock cliffs can support a community dominated by ***Grimmia capillata*** (Figure 125)-***Tortula revolvens*** (Figure 126). The association of ***Eucladium verticillatum*** (Figure 127-Figure 128) and ***Didymodon tophaceus*** (Figure 129) occurs only near waterfalls of the Tamerza oasis. North-facing cliff bases provide enough shelter to support ***Bryum funckii*** (Figure 130)-***Didymodon australasiae*** (Figure 131) associations. On the exposed limestone gravel scree and loess cliffs one can find the pioneer community of ***Crossidium squamiferum*** (Figure 132) and ***Aloina bifrons*** (Figure 133). The northern part is less extreme in climatic conditions and one can find the ***Didymodon australasiae-Tortula revolvens*** community.

Figure 124. ***Tortula atrovirens***, part of the dominant ***Crossidium laevipilum-Tortula atrovirens*** community at the edge of the Tunisian Sahara. Photo by John Game, through Creative Commons.

Figure 125. ***Grimmia capillata*** with capsules, dry – part of the ***Grimmia capillata-Tortula revolvens*** association on rock cliffs at the edge of the Tunisian Sahara. Photo by Hank Greven, with permission.

Figure 126. ***Tortula revolvens*** – part of the ***Grimmia capillata-Tortula revolvens*** association on rock cliffs at the edge of the Tunisian Sahara. Photo from Proyecto Musgo, through Creative Commons.

Figure 127. ***Eucladium verticillatum***, part of the waterfall association of ***Eucladium verticillatum*** and ***Didymodon tophaceus*** at the edge of the Tunisian Sahara. Photo by Michael Lüth, with permission.

Figure 128. ***Eucladium verticillatum***, showing individual plants. Photo by Hermann Schachner, through Creative Commons.

Figure 129. ***Didymodon tophaceus*** with capsules, part of the waterfall association of ***Eucladium verticillatum*** and ***Didymodon tophaceus*** at the edge of the Tunisian Sahara. Photo by David T. Holyoak, with permission

Figure 130. ***Bryum funckii***, a species of the ***Bryum funckii-Didymodon australasiae*** association on north-facing cliff bases that provide enough shelter for them to survive at the edge of the Tunisian Sahara. Photo by Michael Lüth, with permission.

Figure 131. ***Didymodon australasiae***, a species of the ***Bryum funckii-Didymodon australasiae*** association on north-facing cliff bases that provide enough shelter for their survival at the edge of the Tunisian Sahara. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

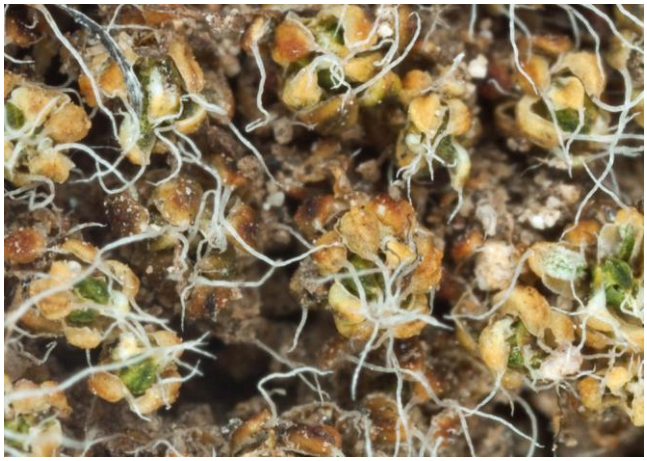

Figure 132. ***Crossidium squamiferum***, a member of the ***Crossidium squamiferum*** and ***Aloina bifrons*** association – a pioneer community on the exposed limestone gravel scree and loess cliffs at the edge of the Tunisian Sahara. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

Figure 133. ***Aloina bifrons*** with capsules, a member of the ***Crossidium squamiferum*** and ***Aloina bifrons*** association – a pioneer community on the exposed limestone gravel scree and loess cliffs at the edge of the Tunisian Sahara. Photo by Ben Carter, through Creative Commons.

Figure 134. ***Aloina bifrons***, showing the thickened leaves that are able to maintain water and hair points that collect water. Photo by Martin Hutten, with permission.

The thallose liverworts in such dry areas are "tiny" and become practically invisible during the dry season, reappearing when the rains arrive. This ability is particularly common in the **Ricciaceae** (Pócs *et al*. 2007). The ***Riccia*** species (Figure 100-Figure 101, Figure 104-Figure 106) in these dry habitats exhibit 20% endemism while another 20% are widespread, often cosmopolitan xerophytes. Most of the mosses are in the **Pottiaceae** (Figure 122-Figure 123). These xerophytic mosses have crispate, often contorted leaves with inrolled or recurved margins (Kürschner 2004).

Kürschner (2000) described the bryophyte flora of the Arabian Peninsula (Figure 135) and Socotra (Figure 136), much of which is desert. Prior to 1980, no bryophytes were known from the entire peninsula. The bryological flora is characteristic for the monsoon-influenced peninsula, including 1 hornwort, 50 liverworts, and 173 mosses, with many Palaeotropical and Afro-montane taxa. On the other hand, the arid and semi-arid regions, with winter rainfall, are dominated by species that are drought adapted and drought tolerant. These include many **Pottiaceae** and thalloid liverworts that go dormant during the drought.

Figure 135. Arabian Peninsula desert and oasis in Oman. Photo by Hendrik Dacquin aka loufi, through Creative Commons.

Figure 136. Desert community of Dixam canyon, Socotra. Photo by Gerry and Bonni, through Creative Commons.

Later, Kürschner (2003) conducted a phytosociological analysis of the ***Riccietum jovet-astii-argenteolimbatae*** association as a new association found in the Jabal Arays area of Yemen. This association consists predominantly of ***Riccia jovet-astiae*** and ***Riccia*** *cf.* ***albolimbata*** (Figure 104-Figure 105). Kürschner identified this association as being grouped within the alliance of ***Mannia androgyna*** (Figure 137) with ***Barbula unguiculata*** (Figure 87). The new association typically occurs on shallow soils that overly volcanic rock outcrops, where it occurs in the understory of *Sterculia africana arabica* (Figure 138) woodland in monsoon-affected areas. The life strategy here is that of a shuttle species with large spores. Thus dispersal is short range. Spores in a diaspore bank help to maintain the presence of these liverworts. Of minor importance is their colonist strategy and they live on the soil where they can go dormant until monsoon season.

Figure 137. ***Mannia androgyna***, a member of the ***Mannia androgyna-Barbula unguiculata*** alliance; the ***Riccietum jovet-astii-argenteolimbatae*** association is in this alliance. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

Figure 138. ***Sterculia africana***, a species that occurs on shallow soils that overly volcanic rock outcrops in monsoon-affected areas of Yemen. Photo by Peter B. Phillipson, through Creative Commons.

Summary

Neotropical floodplains include the **igapó** and **várzea** habitats, seasonally inundated, and supporting different bryophyte communities. Sexual reproduction predominates among the bryophytes. The leafy liverwort family **Lejeuneaceae** predominates in species richness, while the family **Calymperaceae** has the most moss species.

Mangrove forests are limited in bryophyte species because of saltwater. Nevertheless, **Calymperaceae** are among the few moss species present, with **Lejeuneaceae** being the most species-rich among the liverworts. Bryophytes in these floodplains are passive accumulators of nutrients and help to retain them within the floodplain.

Tropical peatlands are effectively restricted to higher altitudes and include some of the well-known high latitude species such as ***Sphagnum magellanicum*** and ***S. recurvum***. ***Sphagnum platyphyllum*** is common in peatlands rich in iron. Two mire types are dominated by tracheophytes, with the moss ***Campylopus reflexisetus*** occurring on the cushions. Two are dominated by bryophytes, differing in vegetation with differences in conductivity and nutrients. Genetic variation within species may be highly variable, as seen in ***Sphagnum tumidulum*** from Reunion Island. At least some ***Sphagnum*** spores have greater longevity in the absence of oxygen, permitting them to survive in the peat.

Few tropical bryophytes live permanently submerged except at high elevations. In low elevations, high temperatures, low CO_2 levels, and low light intensities result in negative carbon gain. But in the Andes, several rare species are associated with torrential waters.

In **rheophytic** habitats, one can find leafy liverworts in the **Lejeuneaceae**, with a number of moss species on rheophytic shrubs, roots, and rocks where they are seasonally submerged. The absence of tropical studies on rheophytes leaves species awaiting discovery. Nevertheless, a number of families with rheophytic representatives are known.

Glacial lakes may have such species as ***Herbertus sendtneri***. These lakes and other high-altitude tropical lakes are isolated by the hot valleys that are unsuitable as vegetative dispersal avenues for bryophytes.

Seepage areas often have species of ***Riccia*** and mosses that are typical of disturbed areas such as ***Barbula unguiculata***, ***Funaria***, and ***Bryum***.

The tropics create a number of xeric habitats. These have low liverwort diversity but are able to support desiccation-tolerant mosses, particularly members of the **Pottiaceae**. These mosses are able to resume photosynthesis quickly upon rewetting. Among the liverworts, ***Riccia*** species can become dormant for prolonged periods of time, then expand and resume growth. Among these xeric habitats are savannahs, where liverworts are rare and little diversity is common. Nevertheless, the liverworts ***Riccia*** and **Lejeuneaceae** can occur as epiphytes. The meager evidence on life cycle strategies suggests that the sexual cycle takes advantage of the short wet periods, with spore dispersal likewise occurring in wet periods. Some mosses have **cleistocarpous** capsules. Spores in 20 tested species exhibit limited longevity. However, spores seem to survive better in diaspore banks. Deserts, as might be expected, have their highest bryophyte diversity in the **Pottiaceae** and **Ricciaceae**. Canyon and shaded cliffs have a higher diversity.

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CHAPTER 8-12
TROPICS: ROCKS AND INSELBERGS

JANICE M. GLIME AND TATIANY OLIVEIRA DA SILVA

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CHAPTER 8-12
TROPICS: ROCK OUTCROPS AND INSELBERGS

JANICE M. GLIME AND TATIANY OLIVEIRA DA SILVA

Figure 1. Inselbergs in Mozambique, Africa. Photo by Ton Rulkens, through Creative Commons.

Rock outcrops and inselbergs provide unique habitats, usually being more xeric than surrounding habitats. An **inselberg** (Figure 1) is distinguished as "those isolated rock outcrops that stand out abruptly from surrounding plains" (Potembski & Barthlott 2012). The term appears to have been introduced by Bornhardt (1900). Both outcrops and inselbergs can differ in rock types, and this can promote different vegetation groupings. Potembski and Barthlott noted that study of the widespread granite inselbergs has been neglected, yet it is "remarkably" rich in plant life. Porembski (2007) identified the three hot spots of inselberg plant diversity on a global scale as southeastern Brazil, Madagascar, and southwestern Australia; the first two of these are tropical.

Barthlott *et al.* (1993) note that the flora of the inselbergs differs almost completely from that of the surrounding area, behaving like islands. They concluded that the bare rock is covered almost completely by **Cyanobacteria** in French Guyana, but by lichens in the Ivory Coast. Nevertheless, the life forms are similar in the Palaeotropics and Neotropics. It would be interesting to make these same comparisons for bryophytes.

It is interesting that tracheophytes in such dry habitats may mimic some of the traits of bryophytes. These adaptations include forming **mats** and **poikilochlorophyllous** (lose chlorophyll and cease photosynthesis and transpiration when dry) behavior (Porembski & Barthlott 2000). It is incredible that of the approximately 330 species (in only 13 families) of tracheophytes that are desiccation-tolerant, close to 90% occur on inselbergs.

In Brazil, ironstone rock outcrops provide an adverse environment where daily temperatures vary widely, UV exposure is elevated, constant winds are present, and soils

are impermeable and have low water retention with high levels of iron (Peñaloza-Bojacá *et al*. 2018b). Such conditions favor a very rich and endemic community where xerophilic plants thrive.

Rock outcrops are not just bare rock, even in their earliest stages. These topographic differences include shallow depressions that can fill with water (Figure 2), drainage channels (Figure 3), vertical faces with directional N-S exposures (Figure 4), and horizontal plains (Figure 5). In Guinea, mats of ***Afrotrilepis pilosa*** (Figure 6) create protected habitats, habitats with extremes (*e.g*. Figure 5) that support ephemeral plants, and areas experiencing flushes that have their own distinct vegetation (Porembski *et al*. 1994). Sandstone outcrops of Fouta Djalon in Guinea (Figure 7) are species-rich and have a large number of endemics. Porembski and coworkers suggested this may be due to the combination of vertical differentiation, large area, long-term climate stability, and isolation. The granite inselbergs and **ferricretes** (hard, erosion-resistant layer of sedimentary rock, usually conglomerate or breccia, cemented into a duricrust by iron oxides), on the other hand, lack local endemics and have a lower species richness. The greatest diversity of inselberg vegetation of tropical Africa seems to occur in Tanzania, Malawi, Mozambique, Zambia, Zimbabwe, and Angola.

Figure 4. Colonizing plants on vertical surface of rock outcrop at Pedra do Cachorro, northeast Brazil. Photo courtesy of Tatiany Oliveira da Silva.

Figure 2. Rock outcrop at Pico do Papagaio, Brazil, showing shallow pool in rock in the foreground. Photo courtesy of Tatiany Oliveira da Silva.

Figure 5. Fully exposed horizontal rock outcrop at Pedra, Brazil. This dark-colored rock is even more formidable because it absorbs heat. Photo courtesy of Tatiany Oliveira da Silva.

Figure 3. Rock outcrop, Pedra da Massa, Brazil, showing drainage channels descending from its crest. Photo courtesy of Tatiany Oliveira da Silva.

Figure 6. ***Afrotrilepis pilosa*** (grass) on an inselberg in West Africa. Photo by Stefan Porembski, through Creative Commons.

Figure 7. Sandstone rock outcrop at Fouta Djallon, Guinea. Photo by Maarten van der Bent, through Creative Commons.

Inuthail and Sridith (2010) examined the structure of plant communities on the granitic inselberg in Songkhla Province in Peninsular Thailand. They identified seven microhabitat types: rock crevices and clefts (Figure 8), rock falls (Figure 7), shallow depressions (Figure 2), deep depressions, exposed rock slopes (Figure 4), shady flat rocky slopes (Figure 3, Figure 9), and rock platform fringes. They recorded 73 species of tracheophytes, with Orchidaceae, Rubiaceae, and Poaceae predominating. The highest number of plant species occurred on the fringes of the rock platforms where soil conditions and light intensities vary.

Figure 8. Mosses in fissure of rock outcrop, Brazil. Photo courtesy of Tatiany Oliveira da Silva.

Figure 9. Rock outcrop with shade provided by tracheophytes at Sítio Pedra das Moças, Brazil. Photo courtesy of Tatiany Oliveira da Silva.

Although some researchers disagree about which formations belong to the inselberg category, Porembski *et al*. (1997) considered granitic inselbergs to be present in all the climatic and vegetational zones of the tropics. Because of the harsh edaphic and microclimatic conditions, the vegetation of inselbergs differs greatly from that of their surroundings. The habitats on these rocks can be defined by vegetation groups including cryptogamic crusts, rock pools, monocot mats, and ephemeral flush vegetation. **Stochastic** (randomly determined) environmental disturbances promote greater species richness due to prevention of competitive exclusion. Other processes are deterministic, creating high temperatures and light levels and extended periods of drought. Moss cushions are able to take advantage of seepage water. In West Africa, ***Bryum arachnoideum*** (Figure 10) is able to take advantage of such wet areas (Frahm & Porembski 1994).

Figure 10. ***Bryum arachnoideum***, a moss that colonizes wet seepage areas on rock outcrops in West Africa. Photo by Jan-Peter Frahm, with permission.

Sarthou *et al*. (2009, 2017) described tropical inselbergs as rocky outcrops protruding from a plain landscape. These are hot spots of plant and animal biodiversity that result from the igh turnover of species between sites and the presence of organisms mostly

restricted to the inselberg habitat. Thus they are isolated patches of tracheophytic vegtation surrounded by bare rock or cryptogamic vegetation (algae, lichens, and bryophytes).

Sarthou and Villiers (1998) remind us that tropical inselbergs are surrounded by rainforest, but that they have their own special vegetation. They describe six such associations on French Guianan inselbergs. These respond to different environmental characteristics, including local relief, insolation, water availability, and soil depth. Species diversity is low in all of these associations. They found striking similarities in the vegetation units when comparing those of South American and African inselbergs.

It is only recently that ecological studies of bryophytes on inselbergs have emerged. Ribeiro *et al*. (2007) provided a comprehensive summary of vegetation on rock outcrops in Brazil and outlined the three needs they considered most urgent for study:

1. inselbergs and high mountains in the Amazon and the Brazilian northeast
2. long-term studies, which are almost totally unavailable, hindering global change monitoring and assessment
3. national and international networking to speed up scientific production about such habitats.

Frahm (2000) summarized early studies in the volume by Barthlott and Porembski on inselbergs. Valente and Pôrto (2006) described the bryophytes from a rocky outcrop in Bahia, Brazil. Even in 2018, Peñaloza-Bojacá *et al*. (2018a, b) commented on the paucity of bryophyte studies on rock outcrops and inselbergs.

To elucidate outcrop vegetation in the northeastern Brazil, Silva *et al*. (2014a, b) looked at both tracheophytes and bryophytes on rocky outcrops there. They noted that for these small plants, the large outcrops served as islands amid a "sea" of soil, resulting in a floristic composition that results from **stochastic processes** (unpredictable events) at a regional scale. However, such stochastic processes did not show any clear relationship with the communities on a local scale.

Figure 11. ***Frullania gibbosa*** on rock outcrop in Brazil. Photo courtesy of Tatiany Oliveira da Silva.

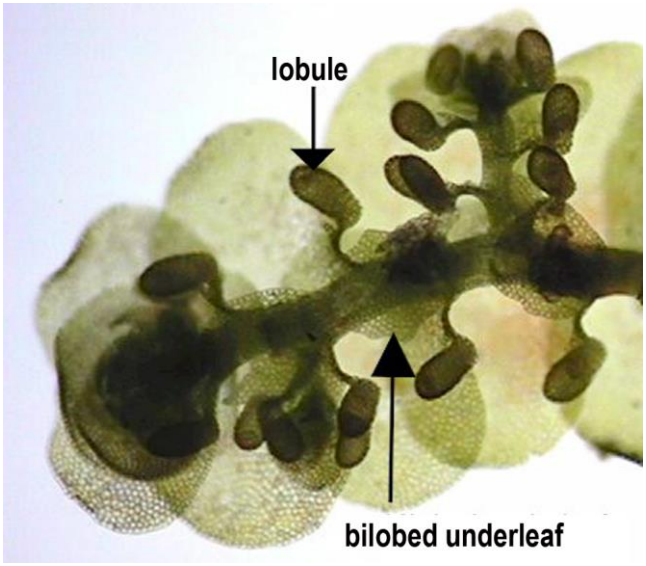

Figure 12. Underside of a ***Frullania*** branch, showing lobules. Photo by Paul Davison, with permission.

Adaptations

Watson (1933) gave an early view of adaptations to terrestrial adaptations of bryophytes. He suggested that these included **cushion** life forms, the arrangement of the leaves to be imbricated or twisted upon drying, hair points or hyaline leaf apices, leaf borders, infolded leaf margins, thickened cell walls, cell size, and papillae. Some store water and others prevent evaporation. Capillarity was accomplished by spaces between leaves, at leaf axils, between leaf folds, and specialized water folds (lobules as in ***Frullania***; Figure 11-Figure 12) and storage cells as in ***Leucobryum*** (Figure 13). Although at that time there was little experimental evidence to support his suggestions, we now find that these traits often describe adaptations of bryophytes of rock outcrops and inselbergs.

Figure 13. ***Leucobryum*** *cf* ***giganteum*** on rock in the Neotropics. Photo by Michael Lüth, with permission.

Life Cycle Strategies

Life cycle strategies can be particularly important in these severe environments. As noted by Benassi *et al*. (2011) for the desert moss ***Syntrichia caninervis*** (Figure 14), those in the most extreme environments have lower frequencies of sexual expression, fewer sexual branches per individual, and a lower male:female ratio. Sexual reproduction is infrequent. They suggested that male rarity may be due to a lower desiccation tolerance in males. Males have a higher energetic requirement for their sex expression, and this may make them less tolerant to repeated cycles of hydration and desiccation. While rock outcrops and inselbergs are not deserts, many of their microclimate characteristics are similar, so we might expect similar life cycle restrictions.

Figure 14. ***Syntrichia caninervis*** (**Pottiaceae**), a xerophytic moss that has lower frequencies of sexual expression, fewer sexual branches per individual, and a lower male:female ratio. Photo by John Game, through Creative Commons.

Frahm (1996) found that bryophytes from the inselbergs he examined in the Ivory Coast and Zimbabwe had a conspicuous lack of both sexual and vegetative propagules. They lacked both the animal and wind dispersal found in inselberg tracheophytes.

Kürschner (2003) found that the life strategy for the ***Riccia*** liverwort association on thin soil over volcanic rock in Yemen was that of a **shuttle** species. These liverworts produce large spores with short-range dispersal. Disturbances could result in exposure of these spores that have been stored in the diaspore bank. **Geophytes** (plants with short, seasonal lifestyle and some form of underground storage organ) and colonists also occur, but are of only minor importance.

Kürschner (2006) elucidated the ecology of the **saxicolous** (growing on rocks) ***Grimmia ovalis*** (Figure 15)-***G. laevigata*** (Figure 16-Figure 17)-***G. longirostris*** (Figure 18) association on Socotra Island of Yemen. The bryophytes on these sun-exposed, acidic rock formations appear to be mostly endemic and are dominated by ***Schlotheimia balfourii*** (see Figure 19). The life strategy is that of drought-tolerant **cushions**, **short turf**-forming generative **perennial shuttle species**, **perennial stayers**, and **pauciennial** (short-lived) **colonists**.

Figure 15. ***Grimmia ovalis*** with capsules, a rock dweller on Socotra Island. Photo by Michael Lüth, with permission.

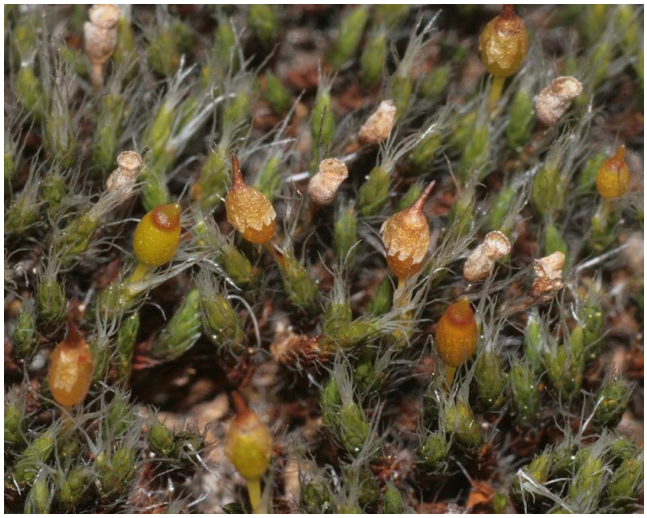

Figure 16. ***Grimmia laevigata*** with capsules, a rock dweller on Socotra Island. Photo by Hermann Schachner, through Creative Commons.

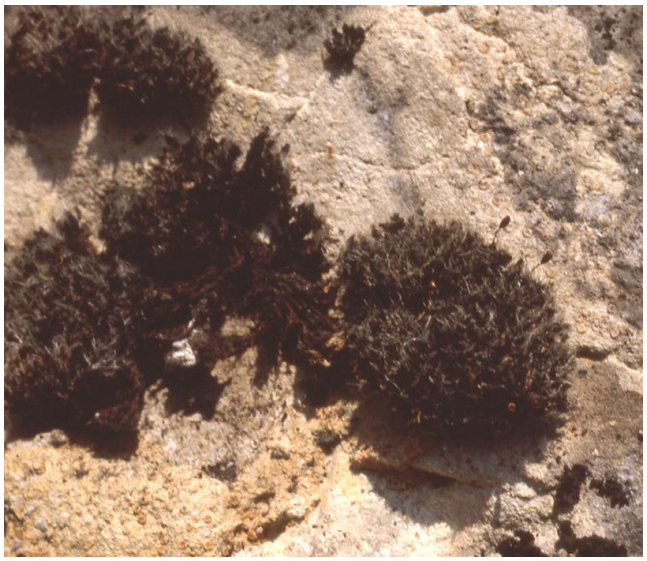

Figure 17. ***Grimmia laevigata***, dry, a rock dweller on Socotra Island. Photo by Janice Glime.

Figure 18. ***Grimmia longirostris*** with capsules, a rock dweller on Socotra Island. Photo by Hermann Schachner, through Creative Commons.

Figure 19. ***Schlotheimia*** sp. from the Neotropics; ***Schlotheimia balfourii*** is a rock dweller on Socotra Island. Photo by Michael Lüth, with permission.

In her study of bryophytes on rock outcrops in Brazil, Silva found that most species were monoicous (26 spp. compared to 20 dioicous species) (Silva 2012; Silva *et al*. 2014b). Nevertheless, the three most frequent species were dioicous. But of these three, two rarely produced sporophytes and one had them only occasionally.

Peñaloza-Bojacá *et al*. (2018a) found that asexual reproduction was important for several of the key species of mosses on Brazilian ironstone outcrops. Surprisingly, dioicous mosses had the highest sexual expression and reproductive success, with most of these species having a female bias. Of the 108 species, 70% were reproducing. A total of 50% of the specimens were reproducing either sexually or asexually. Mosses exhibited mostly asexual reproduction, whereas liverworts mostly exhibited sexual reproduction. Of the asexually reproducing species, 31% had gemmae and 69% had other deciduous propagules. Among the dioicous species, the majority had a female bias.

Pôrto *et al*. (2017) specifically studied the life cycle strategies of the widespread moss ***Bryum argenteum*** (Figure 20) from a rock outcrop in northeastern Brazil. They noted that despite the severe water constraints of the inselbergs, dioicous mosses are able to colonize rock outcrops and inselbergs. Previous researchers had found that in northeastern Brazilian rock outcrops, only ***Bryum argenteum*** frequently had sporophytes (Valente & Pôrto 2006; Silva & Germano 2013; Silva *et al*. 2014a, b). This dioicous species has several asexual strategies – axillary bulbils, rhizoidal gemmae (tubers), and caducous shoot apices (Frey & Kürschner 2011), complemented with numerous small spores when it reproduces sexually (Söderström 1994). Despite its asexual options, 93% of the rock outcrop colonies were expressing sex (Pôrto *et al*. 2017). Although there was a slight female bias, the ratio was only 56:44 female to male. The relationship of number of sporophytes to male:female sex ratio is shown in Figure 21.

Figure 20. ***Bryum argenteum*** with capsules on rock outcrop in Brazil. Photo of Tatiany Oliveira da Silva.

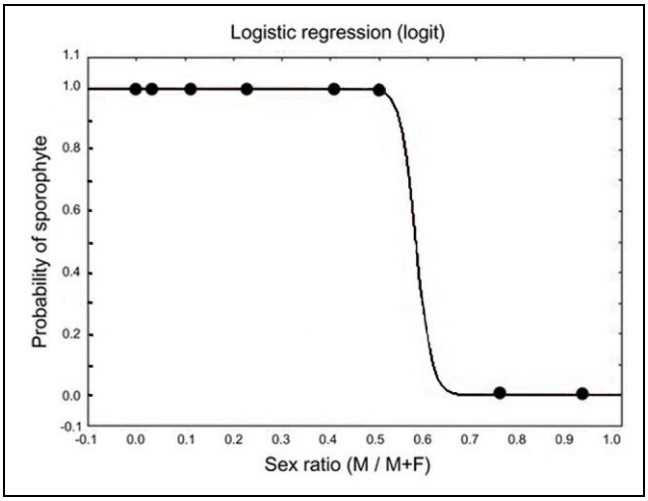

Figure 21. Probability of sporophytes based on sex ratio in ***Bryum argenteum***. Modified from Pôrto *et al*. 2017.

So why is ***Bryum argenteum*** (Figure 20) so productive with sporophytes on the rocks when most other dioicous species are unable to succeed on these rocks? Cronberg *et al*. (2006, 2008) may have the answer. They found that mites are able to disperse the asexual propagules and that springtails (**Collembola**; Figure 22) and possibly mites as well facilitate fertilization. Another factor that may contribute to the success of ***B. argenteum*** on the rocks and

elsewhere is the ability of antheridia to survive desiccation and rehydration, then to release viable sperm (Shortlidge *et al*. 2012; Stark *et al*. 2016).

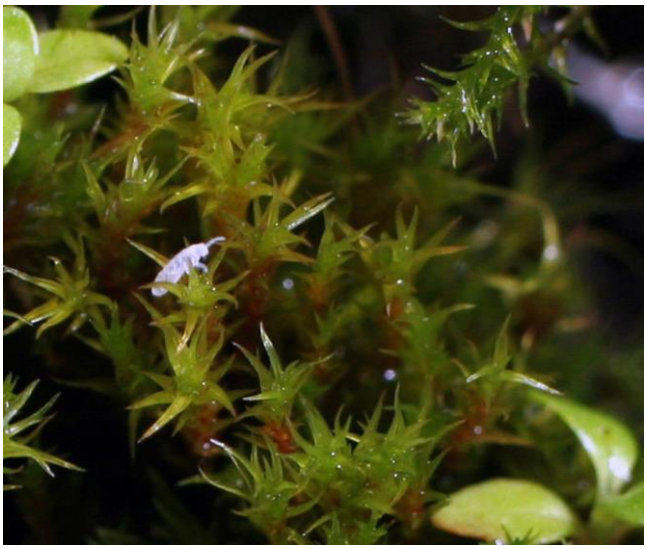

Figure 22. ***Folsomia candida*** (**Collembola)** on ***Ceratodon purpureus*** in fertilization study. Photo courtesy of Erin Shortlidge.

Dispersal

Dispersal can limit the species that reach inselbergs because the surrounding vegetation is of a completely different type (Burke 2002a). Frahm and Porembski (1994) considered the inselbergs of western Africa to be refugia for dry-adapted bryophyte species. Burke (2002a) investigated the role of inselbergs in Namibia as refugia for tracheophyte species. These inselbergs are considered to have a high recolonization potential and a high diversity relative to the landscape. Burke found that gene flow and nutrient flow occur from the inselbergs to the surrounding lowlands. The granite inselbergs support longer-lived species of stable communities, whereas the dolerite inselbergs support transient communities of short-lived species. Regional differences relate to climate, with differences in climate and geology contributing. Altitude is likewise an important variable. Species of granite inselbergs are more closely allied to the surrounding habitats than are those of dolerite inselbergs. Burke concluded that conserving groups of inselbergs is more important to conserving their unique species than conserving isolated mountains. "Stepping stone" inselbergs have greater potential for conserving those species with short dispersal ranges.

These principles should likewise apply to bryophytes, but most likely at a greater distance scale. One way that bryophyte dispersal is facilitated to boulders and inselbergs is having a large number of propagule sources nearby. This can be other boulders and inselbergs, but for many species, it is the ability to grow on other types of substrates. Pócs (1982) demonstrated that many of the tropical species of **Meteoriaceae** (Figure 69-Figure 70), **Neckeraceae** (Figure 23-Figure 24), **Pterobryaceae** (Figure 25), ***Plagiochila*** (Figure 26), and **Lejeuneaceae** (Figure 37) that are typically corticolous (growing on bark) may also be abundant on rocks.

Figure 23. ***Neckera*** on rock. Photo by Michael Lüth, with permission.

Figure 24. ***Neckera urnigera*** from the Neotropics. Photo by Michael Lüth, with permission.

Figure 25. ***Calyptothecium duplicatum*** (**Pterobryaceae**) from the Neotropics. Photo by Michael Lüth, with permission.

Figure 26. ***Plagiochila*** sp. from the Neotropics. Photo by Michael Lüth, with permission.

Desiccation Recovery

One area of adaptations that was usually ignored in early studies was physiological adaptations. Lüttge *et al*. (2008) reported strong quenching of chlorophyll fluorescence in the three desiccated bryophytes in their study of three poikilohydric, homiochlorophyllous moss species from sun-exposed rocks of a Brazilian tropical inselberg. Using ***Campylopus savannarum*** (Figure 27-Figure 28), ***Rhacocarpus fontinaloides*** (see Figure 29), and ***Ptychomitrium vaginatum*** (see Figure 30), they concluded that these species have photo-oxidative protection that permits them to live on exposed rocks that experience high light intensity. They achieve this by a reduction of the base chlorophyll fluorescence to nearly zero. Upon rewetting there is a rapid recovery to higher values in the first 5 minutes, requiring more than 80 minutes to reach equilibrium. These adaptations help to define their niches, with ***C. savannarum*** forming an inner belt and ***R. fontinaloides*** forming an outer belt around the vegetation. ***Ptychomitrium vaginatum***, on the other hand, lives in small cushions on bare rock. Nevertheless, these three species differ little in their reduction of fluorescence or rewetting recovery and have only slight differences in photosynthetic capacity. The researchers suggest that CO_2 acquisition is a greater problem in ***P. vaginatum*** than in the other two species, with water films causing limitations in CO_2 uptake.

Figure 27. ***Campylopus savannarum*** and ***C. pilifer*** in fissure of rock outcrop in Brazil. Photo by courtesy of Tatiany Oliveira da Silva.

Figure 28. ***Campylopus savannarum***, a species that has photo-oxidative protection that helps to adapt it to living in exposed rock habitats. Missouri Botanical Garden, through Creative Commons.

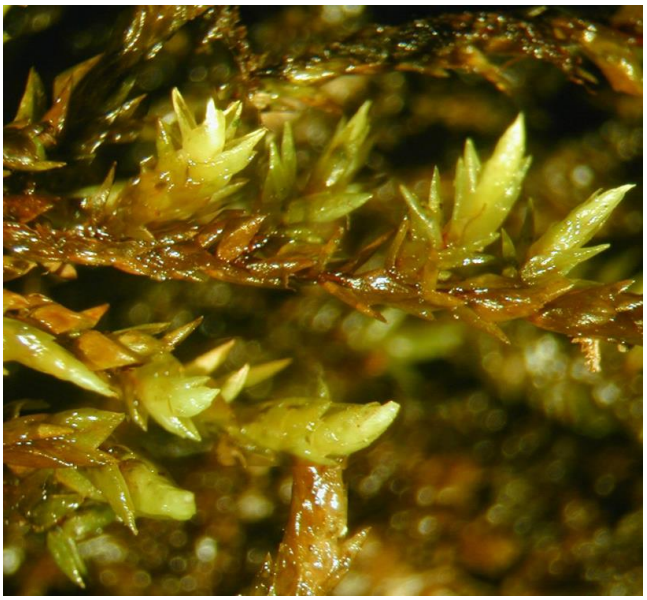

Figure 29. ***Rhacocarpus inermis*** from the Neotropics; ***Rhacocarpus fontinaloides*** has photo-oxidative protection that permits it to live on exposed rock surfaces. Photo by Michael Lüth, with permission.

Figure 30. ***Ptychomitrium*** sp. with capsules; ***Ptychomitrium vaginatum*** has photo-oxidative properties that help to permit it to live on exposed rocks. Photo by Paul Wilson, with permission.

Figure 31. ***Cyanotis lanata***, a species that seems to improve the rock outcrop environment for the moss ***Archidium acanthophyllum***. Photo by Anya Quinn, through Creative Commons.

Figure 32. ***Archidium ohioense***; in southwestern Nigeria, ***Archidium acanthophyllum*** occurs on rock outcrops. Photo by Li Zhang, with permission.

Interactions with Other Plants

As noted by During and van Tooren (1990) as a general principle, bryophyte habitats can be defined by not only the physical environment, but also the tracheophyte vegetation associated with it. Nevertheless, at that time few studies had analyzed the functionality of these interactions.

Tracheophytes on boulders and inselbergs collect soil, provide shade, and retain moisture for longer times than unvegetated areas. Protection by the monocot ***Cyanotis lanata*** (Figure 31) permits ***Archidium*** (see Figure 32) to survive on savannah rock outcrops in southwestern Nigeria (Egunyomi 1984; Oluwole & Adetunji 2010). [The naming of this ***Archidium*** has been problematic, with Egunyomi naming it ***Archidium ohioense***, then Frahm and Porembski (1994) determining it to be ***Archidium globiferum*** in West Africa. However, currently it seems to be considered to be ***Archidium acanthophyllum***.] During the rainy season, the annual mosses ***Bryum argenteum*** (Figure 20) and ***Pelekium gratum*** (Figure 33) may also appear in this association (Egunyomi 1984).

Figure 33. ***Pelekium*** *cf.* ***gratum***, a species that often accompanies ***Archidium acanthophyllum*** on rock outcrops in southwest Nigeria. Photo by Shyamma L., through Creative Commons.

On these southwestern Nigerian inselbergs, there is a three-member association that illustrates relationships among the moss ***Archidium acanthophyllum*** (see Figure 32), tracheophyte ***Cyanotis lanata*** (Figure 31), and lichen ***Diploicia canescens*** (Figure 34) (Oyesiku & Amusa 2010). Oyesiku and Egunyomi (2004) found a frequency of 50% of occurrences of ***Archidium acanthophyllum*** with ***Cyanotis lanata***, whereas only 20% grew alone and 30% grew with other plants, suggesting some benefit from its association with ***C. lanata***. But these two species grow best in somewhat different optima. For ***C. lanata***, the optimum *p*H is 6.7, whereas it is 7.7 for ***A. acanthophyllum***. ***Cyanotis lanata*** density increases and ***Archidium acanthophyllum*** decreases from March to September, whereas both the ***A. acanthophyllum*** and ***C. lanata*** decrease from September to December (Figure 35). This is likely due to the strong increase in temperature of the substrate to 39.6ºC in December. Both plants are harmed at temperatures above 50ºC. In June and September, the relative humidity above the vegetation increases significantly, with a mean of 79% during the study. Data indicate that ***C. lanata*** and ***A. acanthophyllum*** facilitate each other. As noted in other ecosystems (*e.g.* Richardson 1958; Edward & Miller 1977), thick bryophyte growths can serve as insulation to buffer the temperature of the underlying substrate. Richardson (1958) also noted that bryophytes could reduce evaporation. Both of these properties provide a more favorable environment for the roots of tracheophytes. Oyesiku and Egunyomi (2004) verified that these relationships are true for bryophytes on inselbergs.

Figure 34. ***Diploicia canescens***, a lichen that occurs on rock outcrops in southwestern Nigeria. Photo by Jymm, through public domain.

On these inselbergs in southwestern Nigeria, the lichen ***Diploicia canescens*** (Figure 34) maintains a consistent density throughout the year (Oyesiku & Amusa 2010). On the other hand, the monocot ***Cyanotis lanata*** (Figure 31) and the moss ***Archidium acanthophyllum*** (see Figure 32) coexist, but in this relationship, the density of ***A. acanthophyllum*** decreases as that of ***Cyanotis lanata*** increases from March to September (Figure 35). From September to December, both species decrease (Figure 35). Whereas the moss and monocot seem to facilitate each other, the lichen is inhibited by growth of these two species.

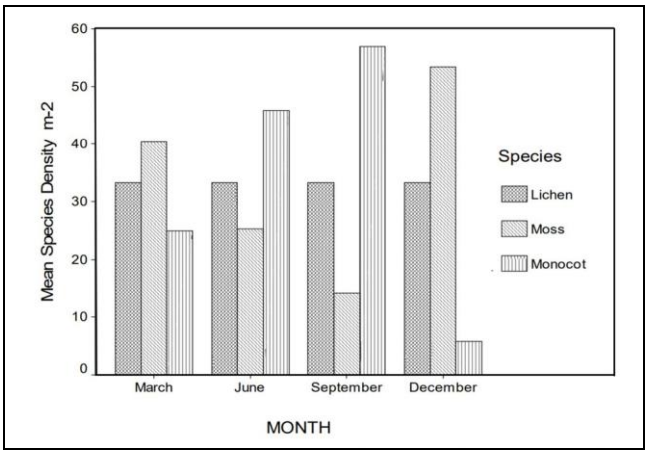

Figure 35. Quarterly density dominance of three interacting plants and lichens on the Baasi Inselberg, Nigeria. Modified from Oyesiku and Egunyomi 2004.

The bryophytes and tracheophytes can also have nutrient cooperation. Bryophytes collect dust and runoff that contain nutrients. These can later be transferred to the tracheophytes. Oyesiku (2018 in press) investigated these relationships between ***Archidium acanthophyllum*** (see Figure 32) and ***Cyanotis lanata*** (Figure 31).

Lava Flows

Tropical lava flows provide unique rock habitats. Ah-Peng *et al*. (2007) investigated the altitudinal differences on a recent lava flow (19 years old) on Réunion Island. Because of the uniformity of the lava flow, it is easier than in most habitats to isolate variables such as altitudinal effects. They surveyed bryophyte communities from 250 to 850 m asl using the three substrates of ground and rachises of two fern species. As in many other altitudinal studies, bryophyte diversity increased with altitude. They identified 70 species of bryophytes in the study, with diversity related to microhabitats. The lava flows support a high number of pioneer organisms that are able to colonize remnant lowland rainforest.

Richness and Diversity

Rocky outcrops and inselbergs form islands amid the surrounding soil vegetation (Silva *et al*. 2014a, b), although Silva and coworkers did not compare the flora of the inselbergs with the surrounding vegetation. If they are correct, the species that arrive there must often come from a distance and must rely on **stochasticity** (unpredictable events). Silva and coworkers demonstrated that such processes are the major factors determining species clustering at a regional scale. Such a relationship was not clear at the local level.

Later, Sarthou *et al*. (2017) provided us with evidence that the surrounding forest, regional climate, and inselberg features including altitude, shape, habitats, summit vegetation, epiphytism, and fire events contribute to shifts in the distribution of species and functional traits. These factors determine the floristic patterns on inselbergs in French Guiana and demonstrate that the surrounding forest

can contribute to the inselberg vegetation. This is probably even more likely for bryophytes.

Ribeiro *et al*. (2007) often found xerophytes and hydrophytes (of the tracheophytes) side-by-side on the boulders due to the small scale environmental heterogeneity. Such conditions also support the great variety of bryophytes on these rocks.

Africa

The inselbergs of West Africa are geologically old and typically dome-shaped monoliths (Porembski & Barthlott 1996). The vegetation differs starkly from that of the surrounding vegetation. The inselbergs provide a severe climate with extreme temperatures and light intensity. Nevertheless, ~600 tracheophyte species occur among these inselbergs, predominately in the grasses (Poaceae), sedges (Cyperaceae), and legumes (Fabaceae). The rocks provide such habitats as cryptogamic crusts, rock pools, monocotyledonous mats, and ephemeral flush vegetation that can be distinguished based on physiognomy (Porembski *et al*. 1997). The ephemeral flush vegetation is the richest in species (Porembski & Barthlott 1996). Moss **cushions**, particularly those of ***Bryum arachnoideum*** (Figure 10), can establish where seepage water is sufficient (Frahm & Porembski 1994).

The tracheophytes on Ivory Coast inselbergs exhibit low **beta diversity** – that is, the flora is relatively uniform across the country (Porembski & Barthlott 1996). Higher beta diversity occurs in the small habitats like rock pools, presumably due to stochasticity. Diversity decreases from savannahs toward the rainforest zone. In the drier areas in the northern part of the Ivory Coast, the growing conditions are less favorable, permitting weak competitors to have a better chance.

On the tropical inselbergs of the Ivory Coast (Côte d'Ivoire) (Figure 36) and Zimbabwe, Frahm and coworkers found that the number of bryophyte species does not correlate with either size of inselberg or elevation (Frahm 1996; Frahm *et al.* 1996). In the Ivory Coast, species richness is greater when the inselberg is in the savannah compared to those in rainforest regions. In the Ivory Coast, they found total species richness of inselbergs to be 31, whereas in Zimbabwe it was only 25. Only 3 families are represented. These researchers found that inselberg bryophytes have larger distribution areas and no endemic species compared to tracheophytes on them. Eight species are common to both. One interesting feature is that these bryophytes typically lack sexual reproduction, but have "conspicuous" vegetative reproduction.

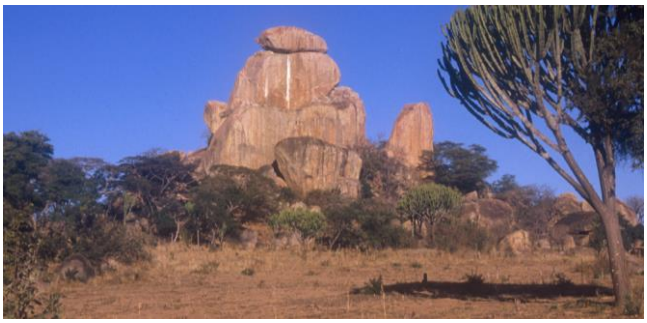

Figure 36. Inselberg (kopje) in Marada Hills, Zimbabwe. Photo by Kevin Walsh, through Creative Commons.

The highest number of bryophyte species from African inselbergs was in the Côte d'Ivoire with 31 species, contrasting with the lowest number of 16 in the Seychelles. This can probably be explained by the location of Côte d'Ivore in the rainforest as well as in the savanna belt, widening the surrounding vegetation types. Most of the species of bryophytes are acrocarpous mosses, with only ***Sematophyllum fulvifolium*** and ***Erythrodontium squarrosum*** representing the pleurocarpous mosses.

Frahm and Porembski (1997) visited the small tropical African country of Benin. They identified 8 liverworts and 10 mosses from inselbergs. Of these, 5 liverworts ([***Acrolejeunea emergens*** (Figure 37), ***Riccia atropurpurea*** (Figure 38, ***R. congoana*** (Figure 39), ***R. discolor***, ***R. moenkemeyeri***] and all of the mosses [***Archidium ohioense*** (possibly ***A. acanthophyllum***; Figure 32), ***Brachymenium acuminatum*** (Figure 40), ***B. exile*** (Figure 41), ***Bryum arachnoideum*** (Figure 10), ***B. argenteum*** (Figure 20), ***Bryum depressum***, ***Garckea moenkemeyeri*** (see Figure 42), ***Hyophila involuta*** (Figure 43-Figure 44), ***Philonotis mniobryoides*** (see Figure 58) and ***Weissia cf. edentula*** (Figure 45)] proved to be new records for the country. This may relate more to lack of studies than to uniqueness of the inselbergs.

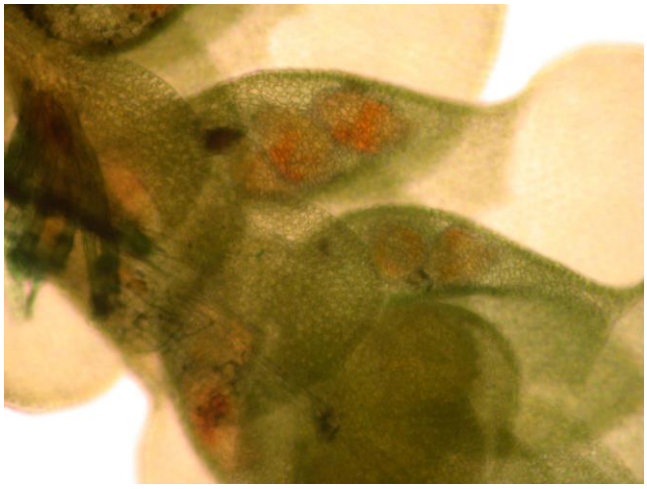

Figure 37. ***Acrolejeunea emergens*** (**Lejeuneaceae**) with rotifers (reddish). Photo courtesy of Claudine Ah-Peng.

Figure 38. ***Riccia atropurpurea***, a liverwort that occurs on inselbergs in Benin, Africa. Photo from Missouri Botanical Garden, through Creative Commons.

Figure 39. ***Riccia congoana***, a liverwort that occurs on inselbergs in Benin, Africa. Photo from Missouri Botanical Garden, through Creative Commons.

Figure 40. ***Brachymenium acuminatum***, a moss that occurs on inselbergs in Benin, Africa. Photo by Jan-Peter Frahm, with permission.

Figure 41. ***Brachymenium exile***, a moss that occurs on inselbergs in Benin, Africa. Photo by Show Ryu, through Creative Commons.

Figure 42. ***Garckea flexuosa***; ***Garckea moenkemeyeri*** is a moss that occurs on inselbergs in Benin, Africa. Photo by Manju C. Nair, through Creative Commons.

Figure 43. ***Hyophila involuta*** habitat in India. Photo by Michael Lüth, with permission.

Figure 44. ***Hyophila involuta***, a moss that occurs on inselbergs in Benin, Africa. Photo by Michael Lüth, with permission.

Figure 45. ***Weissia edentula*** with capsules, a moss that occurs on inselbergs in Benin, Africa. Photo by Louis Thouvenot, with permission.

Burke (2002b) found that in Namibia, soil properties do not seem to have an important role in the arid environments. Furthermore, parameters such as slope aspect and angle play a minor role. The grassland and shrubland plant communities relate primarily to general habitat, elevation, size of inselberg, and geology. The inselbergs are able to harbor plant species from neighboring higher rainfall areas, thus providing a propagule source for recolonization.

Burke (2003) found that granite inselbergs in Namibia are more closely related to mountain habitats than are the dolerite ridges. And as expected, higher inselbergs are more closely related to mountain habitats than are lower inselbergs. Many species, especially those with broad habitat requirements, are common to both inselbergs and mountain habitats. On the other hand, the short-lived transient species are more similar between the dolerite ridges and the "mainland." Thus, the granite inselbergs can be important sources of remnant populations from a wetter past, whereas the dolerite ridges can form species pools for the rangeland.

Kürschner (2003) extended our knowledge of rock outcrops in the Jabal Arays area of Yemen. Here they found communities of ***Riccia jovet-astiae*** (see Figure 38-Figure 39) and ***Riccia argenteolimbatae*** on the thin soils overlying volcanic rock outcrops in monsoon areas where woodlands are characterized by *Sterculia africana* (Figure 46). These are typically accompanied by ***Mannia androgyna*** (Figure 47) and ***Barbula unguiculata*** (Figure 48-Figure 49). The shallow soils generally have large numbers of riccioid and marchantioid liverworts, with ***Riccia atromarginata***, ***R. albolimbata*** (Figure 50-Figure 51), and ***R. argenteolimbata*** characterizing the association.

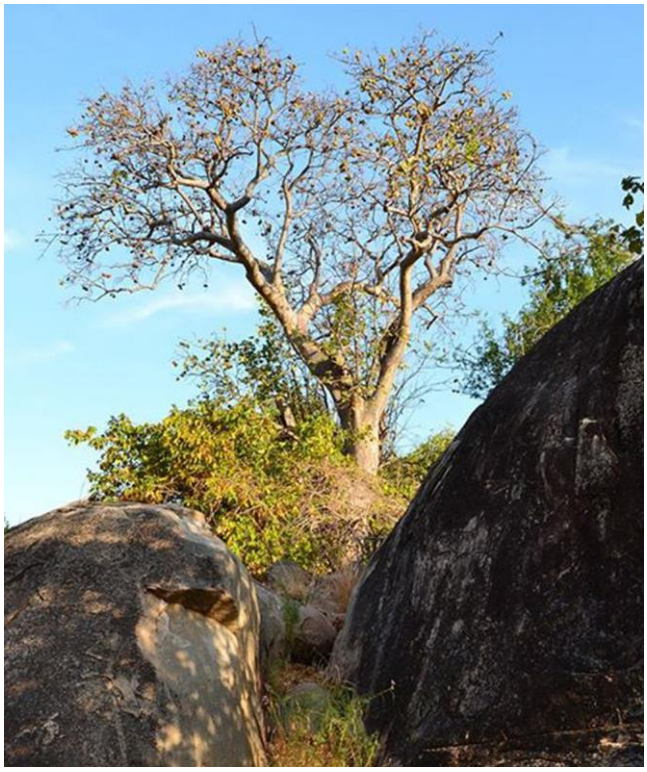

Figure 46. ***Sterculia africana*** in Malawi. Photo by Jinge Norvall Andrews, through Creative Commons.

Figure 47. ***Mannia androgyna***, a species of rock outcrops in the Jabal Arays area of Yemen. Photo by Valter Jacinto, through Creative Commons.

Figure 48. ***Barbula unguiculata*** (dry), a species of rock outcrops in the Jabal Arays area of Yemen. Photo by Bob Klips, with permission.

Figure 49. ***Barbula unguiculata*** with capsules (wet), a species of rock outcrops in the Jabal Arays area of Yemen. Photo by Michael Lüth, with permission.

Figure 50. ***Riccia albolimbata*** (dry), a species of rock outcrops in the Jabal Arays area of Yemen. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

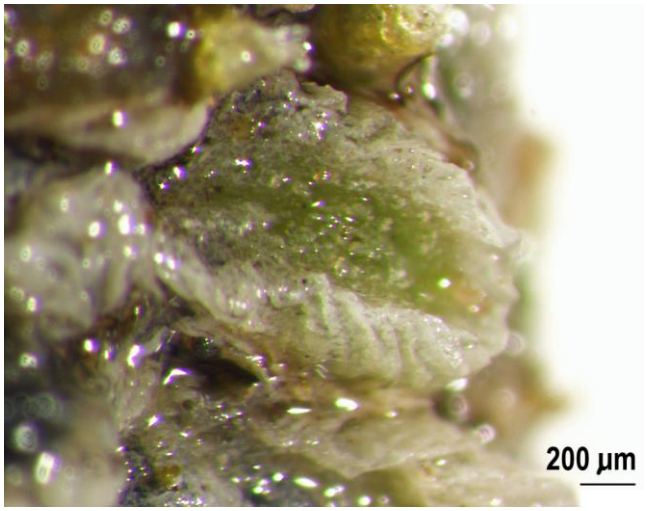

Figure 51. ***Riccia albolimbata*** (wet), a species of rock outcrops in the Jabal Arays area of Yemen. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

In the Drakensberg area of South Africa, Hodgetts *et al*. (1999) found that lowland sandstones support common and widespread species that can survive long drought periods. More species are present where there is more moisture, as in ravines, rock crevices, and on stream banks. A different suite of species occur on shaded sandstone cliffs and rocks. A third type of community occurs in flushes. Exposed rocks generally have few species, with ***Grimmia pulvinata*** (Figure 52) and ***Ptychomitrium cucullatifolium*** (Figure 53) being common here. On the basalt rocks, at about 3,000 m asl, most species are restricted to crevices, on boulders, and in the turf below the cliffs. ***Quathlamba debilicostata*** (in narrow cracks) and ***Orthotrichum oreophilum*** (in cushions on inner vertical and overhanging surfaces of wider cracks; Figure 54) seem to occur only in vertical cracks in the basalt cliffs.

Figure 52. ***Grimmia pulvinata*** with capsules, a species of exposed rocks in tropical South Africa. Photo by Michael Becker, through Creative Commons.

Figure 53. ***Ptychomitrium polyphyllum*** with capsules; ***Ptychomitrium cucullatifolium*** is a species of exposed rocks in tropical South Africa. Photo by David T. Holyoak, with permission.

Figure 54. ***Orthotrichum*** sp. on vertical rock; ***Orthotrichum oreophilum*** occurs on the inner vertical surfaces of wide cracks of inselbergs. Photo by Algirdas, through public domain.

Neotropics

Porembski *et al*. (1998; Porembski 2007) defined **inselbergs** as "mostly" dome-shaped rock outcrops in all climatic and vegetational zones of the tropics." In Brazil, these consist of Precambrian granites and gneiss that form ancient and stable landscape elements. Because of their exposure, they create harsh conditions of microclimate. These strikingly different conditions result in strikingly different vegetation. One of the most characteristic communities is one of monocotyledonous mats. These can provide cover and retain moisture that permits some bryophytes to survive there. Porembski and coworkers, studying tracheophytes, found that the alpha diversity (community diversity) of the mats differed little among the six outcrops studied. However, beta diversity (regional) differed greatly between sites. The Brazilian rock outcrops demonstrate a higher diversity compared to those of West African inselbergs, with the appearance of more endemics in the Brazilian communities. However, some species considered endemics at that time may have proved to be synonyms of more widespread species since then. Nevertheless, the diversity is high, perhaps due to the large species pool.

Silva (2012) studied the rock communities in the state of Pernambuco, Brazil. She divided the microhabitats on the outcrops into exposed rock, fissure, soil island, and **cacimba** (rock pool pit in wet or marshy ground, collecting water present in soil that accumulates in it by condensation). Substrates also differed: rock, live trunk, dead trunk, and soil. She identified 49 species in 36 genera and 20 families. Of these, 34 were mosses, 15 were liverworts. The most species-rich families were the leafy liverworts **Lejeuneaceae** (Figure 37) (7 spp) and **Frullaniaceae** (Figure 55) (4 spp), and the moss families **Bryaceae** (Figure 20) (6 spp), **Dicranaceae** (Figure 27-Figure 28, Figure 56) (4 spp), and **Pottiaceae** (Figure 14) (4 spp), comprising 53% of the species. The liverwort genus ***Frullania*** (Figure 55) and moss genus ***Campylopus*** (Figure 56) had the highest species richness. The most common species were the mosses ***Brachymenium exile*** (Figure 57), ***Bryum argenteum*** (Figure 20), ***Campylopus pilifer*** (Figure 56), ***C. savannarum*** (Figure 27-Figure 28), ***Philonotis hastata*** (Figure 58), and ***Syrrhopodon gaudichaudii*** (Figure 59-Figure 60), and the liverworts ***Frullania kunzei*** (Figure 55) and ***Riccia vitalii*** (Figure 61); frequencies are in Table 1. Two of the less common species, ***Atractylocarpus brasiliensis*** (see Figure 62) and ***Riccia taeniiformis*** (Figure 63), are endemic to Brazil. **Turf** comprised 74% of the life forms. The most species richness (37spp., 89%) occurred on soil islands that were 1.0 and 4.9 cm deep, whereas only 12 species occurred on rock. Approximately half the species had a wide distribution pattern. Similarity among sites was less than 50%.

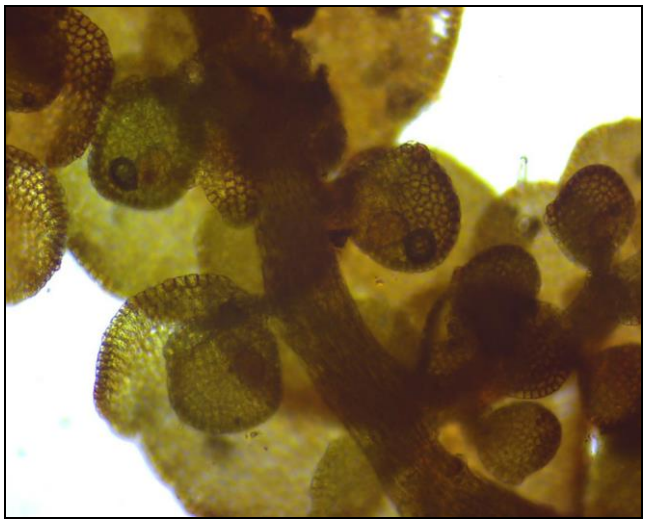

Figure 55. ***Frullania kunzei***, a frequent rock outcrop species in Brazil. Photo by Y. Inturias, through Creative Commons.

Figure 56. ***Campylopus pilifer*** on rock outcrop in Brazil. Photo courtesy of Tatiany Oliveira da Silva.

Figure 57. ***Brachymenium exile***, one of the most common species on rock outcrops in Brazil. Photo by Show Ryu, through Creative Commons.

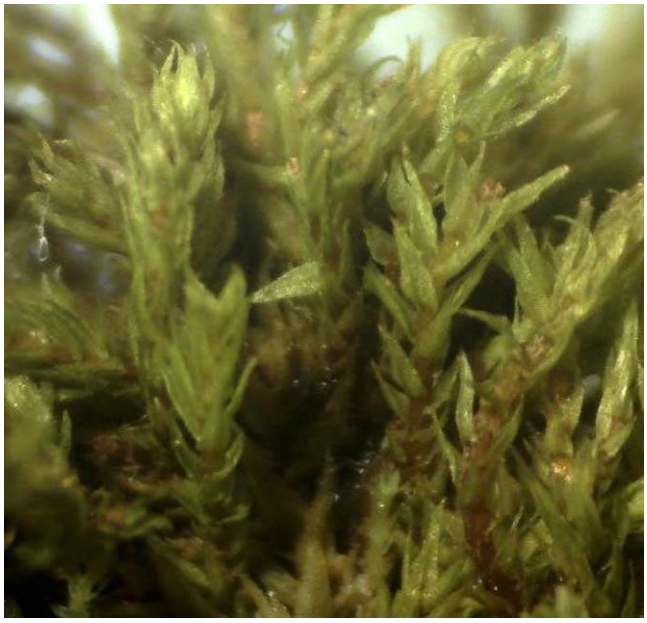

Figure 58. ***Philonotis hastata***, a common species on rock outcrops in Brazil. Photo by Y. Inturias, through Creative Commons.

Figure 59. ***Syrrhopodon gaudichaudii***, on a rock outcrop in Brazil. Photo courtesy of Tatiany Oliveira da Silva.

Figure 60. ***Syrrhopodon gaudichaudii*** demonstrating the leaf curling that helps it conserve water on exposed rocks. Photo by Juan David Parra, Creative Commons.

Figure 61. ***Riccia vitalii***, a common liverwort on rock outcrops in Brazil. Photo courtesy of Tatiany Oliveira da Silva.

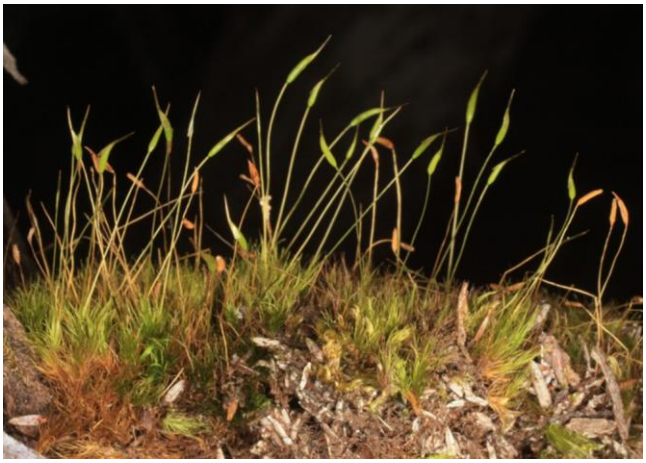

Figure 62. ***Atractylocarpus madagascariensis***; ***Atractylocarpus brasiliensis*** occurs on rock outcrops in Brazil, where it is endemic. Photo by Jan-Peter Frahm, with permission.

Figure 63. ***Riccia taeniiformis*** on rock outcrop in Brazil. Photo courtesy of Tatiany Oliveira da Silva.

Table 1. The most common bryophyte species on rock outcrops in Brazil (Silva 2012).

Species	Frequency
Campylopus savannarum (Figure 27-Figure 28)	97
Campylopus pilifer (Figure 56)	52
Bryum argenteum (Figure 20)	30
Frullania kunzei (Figure 55)	15
Philonotis hastata (Figure 58)	14
Syrrhopodon gaudichaudii (Figure 59-Figure 60)	14
Barbula indica (Figure 64-Figure 65)	13
Brachymenium exile (Figure 57)	13
Riccia vitalii (Figure 61)	12
Octoblepharum albidum (Figure 66)	10

Figure 64. ***Barbula indica*** on rock in Bareilly India. Photo by Michael Lüth, with permission.

Figure 65. ***Barbula indica***, a common species on rock outcrops in Brazil. Photo by Jan-Peter Frahm, with permission.

Figure 66. ***Octoblepharum albidum***, a common species on rock outcrops in Brazil. Photo courtesy of Tatiany Oliveira da Silva.

Like Silva (2012), when studying Brazilian ironstone outcrops Peñaloza-Bojacá *et al*. (2018a) found the greatest bryophyte diversity on soil, but also on the rocks. They identified 108 species of bryophytes (42 liverworts and 66 mosses). In Cangas sites, Peñaloza-Bojacá *et al*. (2018b) reported 96 bryophyte species from Brazilian ironstone outcrops. These were comprised of 56 mosses and 40 liverworts, with 68 of the species associated with tree microhabitats and 67 species with bark substrates. The ironstone sites seem to harbor more species that other types of rock outcrops in the country.

Silva and Germano (2013) studied rock outcrops in the caatinga biome in the state of Paraiba, Brazil, from February 2010 to May 2011 and identified 21 bryophyte species, 6 liverworts and 15 mosses. They were able to identify three species clusters. These were **generalist** species that required high light. Their leaf structures generally permitted them to withstand drying environmental conditions.

In their study of the campos rupestres of Chapada Diamantina, Bahia, Brazil, Bastos *et al*. (2000) identified 65 taxa (41 moss species, 24 liverwort species) comprising a total of 20 families. Most of these taxa seem to be restricted to the Chapada Diamantina and are not known from other parts of the state.

Sarthou *et al*. (2009) examined the factors that have a role in the seral stages on the inselbergs in French Guiana. The environment is harsh, with violent storms, intense runoff, and lightning strikes, destroying vegetation cover and organic matter. They considered the vegetational changes to be truly successional, not conditioned by slope. The vegetation experienced cyclic changes that were reinitiated by fire (lightning), wood-destroying fungi, and termites that destroyed the vegetation.

In her inselberg succession studies, Sarthou and coworkers (2009, 2017) found that where the aerial parts of ***Clusia minor*** (Figure 67) have been destroyed, the ground frequently is covered with mosses and lichens. Their rhizoids capture and retain soil particles, preventing them from being flushed away by water.

Figure 67. ***Clusia minor***, an inselberg species that is replaced by mosses and lichens when it is destroyed by fire or other disturbance. Photo by David J. Stang, through Creative Commons.

Sarthou *et al*. (2017) compared 22 inselbergs in French Guiana. They found that the spatially dictated environmental gradient was a primary driver in the floristic composition on these inselbergs. Southward communities have more drought-adapted plants. The northern group has high endemism. The north-south gradient is driven by regional climate (annual rainfall), forest matrix (canopy openness), and inselberg features (altitude, shape, habitats, summit forest, degree of epiphytism, fire events).

Breen (1953) studied bryophytes in subtropical Florida, USA. She found that a number of tropical species occurred exclusively on limestone in subtropical Florida (and in many cases other southern states). Tropical ***Jaegerinopsis*** (Pterobryaceae), ***Vesicularia*** (Hypnaceae; Figure 68), ***Meteoriopsis*** (Figure 69), ***Papillaria*** (Figure 70), and ***Syrrhopodon*** (Figure 59-Figure 60) are restricted mostly to hammocks, usually on bark of 1-2 species of hardwoods. In swamps, ***Cyclodictyon*** (Figure 71) and some tropical ***Fissidens*** (Figure 72) occur. But the limestone regions hold the most bryologically interesting species. Most of the coastal land in the Caribbean and in the West Indies is of limestone origin. She found 11 Neotropical species that in Florida are restricted to limestone. ***Luisierella barbula*** is a tiny species easily overlooked, but is relatively widespread in Central America and Brazil. ***Hyophiladelphus agraria*** (see Figure 73) is widespread in both the Neotropics and subtropics. ***Weissia jamaicensis*** (Figure 74) occurs in some Central American countries as well as Florida; it is sterile in Florida. This species typically occurs there with ***Marchantia paleacea*** (Figure 75). ***Hypopterygium tamarisci*** (Figure 76) is a tropical relic in Florida, also known from both Central and South American tropics. ***Leptodictyum riparium*** (Figure 77), also a Floridian limestone dweller, is more widespread in aquatic habitats, but is known from Mexican tropics. ***Gymnostomiella vernicosa*** (Figure 78-Figure 79) is also in Jamaica, Haiti, and Mexico. ***Plaubelia sprengelii*** (Figure 80) also occurs in the West Indies, Mexico, and Central America, whereas ***Syrrhopodon prolifer*** (Figure 81) occurs in these locations plus South America, typically on thin layers of soil over limestone in protected pockets. ***Taxiphyllum cuspidatum*** (see Figure 82) occurs on boulders. ***Hyophila involuta*** (Figure 43-Figure 44) is a common tropical rock dweller, but is again restricted to limestone in Florida. ***Fissidens hallianus*** (see Figure 72) is restricted in the USA to Florida. The other species Breen found on the Floridian limestone are not tropical.

Figure 68. ***Vesicularia vesicularis*** var ***vesicularis*** from the Neotropics. ***Vescicularia*** occurs on limestone rocks in Florida, USA. Photo by Michael Lüth, with permission.

Figure 69. ***Meteoriopsis squarrosa***; the genus ***Meteoriopsis*** is restricted mostly to bark in hammocks in Florida. Photo by Manju Nair, through Creative Commons.

Figure 70. ***Papillaria crocea***; ***Papillaria*** is restricted mostly to bark in hammocks in Florida. Photo by Peter Woodard, through public domain.

Figure 71. ***Cyclodictyon albicans*** with capsules, in a tropical genus that also occurs in Florida, USA. Photo by Claudio Delgadillo Moya, with permission.

Figure 72. ***Fissidens asplenioides*** from the Neotropics, in a genus found in swamps in Florida. Photo by Michael Lüth, with permission.

Figure 73. ***Hyophiladelphus*** sp. with capsules; ***H. agraria*** is a Neotropical species that in Florida is restricted to limestone. Photo by Fred Essig, with permission.

Figure 74. ***Weissia jamaicensis*** on limestone rock bands, Uige Province, Angola, a species that also occurs on limestone rocks in Florida, USA, and the Neotropics. Photo by T. Lautenschläger, through Creative Commons.

Figure 75. ***Marchantia paleacea***, a species that occurs on limestone rocks in Florida, USA, and the Neotropics. Photo by David Long, with permission.

Figure 76. ***Hypopterygium tamarisci***, a species that occurs on limestone rocks in Florida, USA, and the Neotropics. Photo by Peter Woodard, through Creative Commons.

Figure 77. ***Leptodictyum riparium***, a species that occurs on limestone rocks in Florida, USA, and the Neotropics. Photo by Michael Lüth, with permission.

Figure 78. ***Gymnostomiella vernicosa tenerum***, a species that occurs on limestone rocks in Florida, USA, and in the Neotropics. Photo by Sean Edwards, with permission.

Figure 79. ***Gymnostomiella vernicosa tenerum*** gemma, a species that occurs on limestone rocks in Florida, USA, and in the Neotropics. Photo by Sean Edwards, with permission.

Figure 80. ***Plaubelia sprengelii***, a species that occurs on limestone rocks in Florida, USA, and the in Neotropics. Photo by Jan-Peter Frahm, with permission.

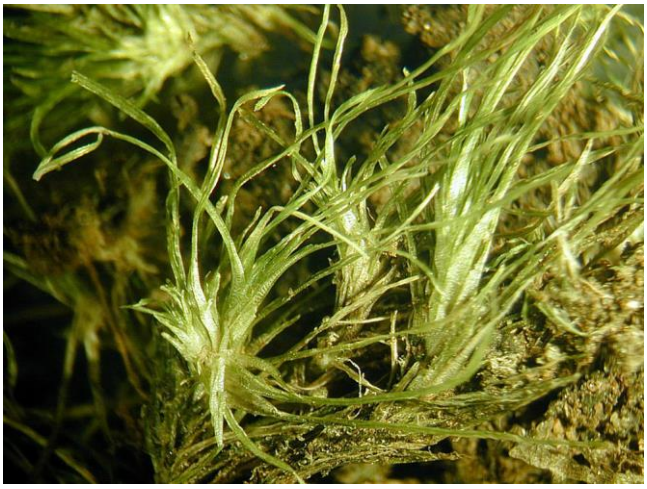

Figure 81. ***Syrrhopodon prolifer*** var. ***scaber*** from the Neotropics, a species that occurs on limestone rocks in Florida, USA, and in the Neotropics. Photo by Michael Lüth, with permission.

Figure 82. ***Taxiphyllum taxirameum*** with capsule; ***Taxiphyllum cuspidatum*** occurs on limestone rocks in Florida, USA, and in the Neotropics. Photo by Bob Klips, with permission.

Conceição and Pirani (2005) noted the lack of quantitative studies in tropical cave habitats. They compared outcropping, intertidal, and trench habitats, and found that when different types of habitats are contiguous, there is greater heterogeneity of both strata and life forms in a restricted area, supporting more species. Their study was not based on bryophytes, but it would be interesting to test this hypothesis on the bryophytes.

Summary

Inselbergs (abrupt rock outcrops) and other rock formations are typically xeric and have unique vegetation surrounded by vegetation of a different type, often isolating them like an island. Temperatures and water availability can vary widely, and exposure to high light intensity is common. The bryophytes, and even the tracheophytes, are typically **poikilochlorophyllous mats**). Differing niches are created by fissures and crevices, pockets where water collects, tracheophyte shade, and vertical faces that are shaded or exposed. Limited competition permits **stochastic** processes to determine communities. Surprisingly, inselberg vegetation units of South America and Africa are similar.

Moss **cushions** are common. Adaptations such as hyaline tips and awns protect against UV light during dry periods. Leaves often twist when dry, have infolded leaf margins, thickened cell walls, small cells, and papillae to protect against UV damage and to retain water longer. Lobules help to store water in some leafy liverworts. Mosses such as ***Leucobryum*** have hyaline cells that store water and protect the chlorophyll. Sexual reproduction is infrequent. Photo-oxidative protection protects chlorophyll from UV light when dry. ***Riccia*** species on thin soil produce large spores with short-range dispersal and storage in diaspore banks, permitting them to be **shuttle** species. Other bryophytes are drought-tolerant **cushions**, **short turf**-forming **perennial shuttle species**, **perennial stayers**, and **pauciennial colonists**. Mosses are more likely to have asexual reproduction, whereas liverworts mostly exhibit sexual reproduction. ***Bryum argenteum*** is a common rock resident that frequently has sporophytes, perhaps due to sperm dispersal by springtails and mites. It is important to conserve groups of inselbergs to facilitate stepping stone dispersal. For others (*e.g.* **Meteoriaceae**, **Neckeraceae**, **Pterobryaceae**, ***Plagiochila***, and **Lejeuneaceae)**, having other suitable substrates increases dispersal potential.

In some cases the bryophytes retain moisture and collected nutrients that provide for the tracheophyte roots, whereas the tracheophyte provides shade that cools the bryophytes and protects from UV damage, as seen in the moss ***Archidium globiferum*** and the shrub ***Cyanotis lanata***.

In Africa, inselbergs surrounded by savannah have a higher species richness than when forests surround them. Inselbergs can harbor recolonization sources for surrounding disturbed dry habitats. Asexual reproduction predominates. Leafy liverworts seem to be more common on the Neotropical rock outcrops than on the African inselbergs. ***Riccia*** species are common on thin soils in both areas. Having trees and shrubs to provide shade can greatly increase the diversity. Limestone areas in subtropical Florida, USA, provide similar habitats and harbor a number of tropical species.

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TROPICS: INTERACTIONS AND ROLES

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CHAPTER 8-13
TROPICS: INTERACTIONS AND ROLES

Figure 1. ***Craugastor bransfordii*** on mosses in the tropics. Note the moss stuck to its skin (**arrow**). Photo by Jason Folt, with permission.

Role

Although we have discussed the role of bryophytes in retaining water earlier, its role in water relations in the tropics cannot be overemphasized. Romero (1999) suggested that bryophyte sensitivity to moisture could be an indicator of the health of the forests where the bryophytes abound. In one submontane forest in Tanzania, epiphytes (including bryophytes, lichens, and tracheophytes) comprised 2,130 kg ha^{-1}, intercepting about 15,000 L of rainfall water per hectare (Pócs 1980). In the elfin (cloud) forest, at only 2,120 m, a biomass of 14,000 kg ha^{-1} intercepts nearly 50,000 L ha^{-1}. Thus, the impact of bryophytes on the water and nutrient regime of the cloud forest is surely significant.

In montane forests, bryophytes make considerable contribution to both biomass and litter. Growth of epiphytic bryophytes in Monteverde, Costa Rica, was approximately 39-49.9% per year, providing a net productivity of 122-203 g m^{-2} yr^{-1} (Clark *et al*. 1998). Nitrogen accumulation in these bryophytes was also significant at 1.8-3.0 g N m^{-2} yr^{-1}. Most of the decomposition seems to occur the first year, with loss from litterbags in the canopy of 17±2% and 19±2% by the end of the second year. On the ground, losses were quite different, with 29±2% the first year and 45±3% after two years. One advantage to the ecosystem was that approximately 30% of the initial N mass was released rapidly both on the ground and from canopy litter. Furthermore, green shoots on the ground lost about 47% of their initial N content within the first three months. Although these were significant rapid releases from these sources, providing a steady supply of N to the soil, the remaining N content was recalcitrant, creating an N sink within the bryophytes. What may be more important is their role in transforming N from mobile forms reaching the canopy as atmospheric deposits to highly immobile forms. This maintenance of low N levels despite atmospheric deposition may help to maintain these low-nutrient bryophyte habitats and prevent the conversion to graminoids more typical of fertilized soil conditions.

Even in lowland floodplain forests, bryophyte biomass can be significant in the accumulation of nutrient elements. With an accumulation of only 210-1,400 kg ha^{-1} ash-free dry weight biomass on 10-year-old stakes in a floodplain, Frangi and Lugo (1992) still considered that the bryophytes in these floodplains served as biotic filters of flood waters that could retain nutrients in the terrestrial system.

In Guadeloupe and other tropical locations, nutrients in the canopy, particularly in the upper canopy of the montane rainforest, are released from bryophytes in pulses (Coxson 1991). These pulses result from rewetted bryophytes that have suffered membrane damage during desiccation. The ions are normally those of intracellular pools that were not otherwise available to the throughfall. During rewetting experiments, concentrations reached 11.8 kg ha^{-1} yr^{-1} for N, 1.4 kg ha^{-1} yr^{-1} for P, and 80.1 kg ha^{-1} yr^{-1} for K.

Bryophytes provide a substrate for tracheophyte epiphytes to become established. In a study of the palm ***Socratea exorrhiza*** (Figure 2), Zotz and Vollrath (2003) found that tracheophytic epiphytes on these trunks are associated with bryophyte patches to a much greater extent than dictated by chance, suggesting a higher success rate, but none seem to require bryophytes for establishment. In the lowland rainforest of Guyana the bryophyte mats and their accumulated debris support different tracheophyte epiphytes in the lower canopy than can be found in the middle and upper canopy branches (ter Steege & Cornelissen 1988).

Figure 2. ***Socratea exorrhiza***, a palm on which tracheophytic epiphytes are more frequently associated with bryophytes. Photo by A. Araujo, through Creative Commons.

Bryophytes also moderate the microclimate. Stuntz *et al*. (2002) reported the importance of epiphytes in moderating the climate of the crowns in the rainforest, creating a natural air conditioning. In this case, they were discussing members of the pineapple family, finding that water loss through evaporative drying at microsites adjacent to them is nearly 20% lower than at exposed microsites. They create a habitat that is significantly lower in temperature than sites with no epiphytes in the same tree crown. Hence, these tracheophytic epiphytes create a habitat more hospitable to bryophytes, but it is likely that the bryophytes also contribute to evaporative cooling, thus helping to lower the temperature. These cooler microsites with greater moisture provide suitable habitats for small arthropods.

Tropical ferns are often associated with bryophyte-covered substrates. Carvalho *et al*. (2012) noted that ***Cochlidium connellii*** (see Figure 4), a fern in the **Polypodiaceae**, grows among mosses in rocky crevices. ***Trichomanes robustum*** (**Hymenophyllaceae**; Figure 3) and ***Terpsichore taxifolia*** (**Polypodiaceae**; Figure 5) occur on moss-covered trunks in the upper montane forest in Brazil and other locations in the tropics.

Figure 3. ***Trichomanes boschianum***; ***Trichomanes robustum*** grows among mosses in rock crevices in the tropics. Photo by Robert Klips, with permission.

Figure 4. ***Cochlidium serrulatum***; ***Cochlidium connellii*** grows among mosses in rock crevices in the tropics. Photo by Photo by Robbin Moran, with permission.

Figure 5. ***Terpsichore asplenifolia***; ***Terpsichore taxifolia*** grows among mosses in rock crevices in the tropics. Photo by Daniel Tejero, with permission from Robbin Moran.

Effect on Tree Seedlings

One might think that bryophytes would benefit tree seedlings by maintaining moisture, but often they are a detriment. The shade tents in the experiments at the alpine treeline in northern Ecuador did indeed have a greater growth of mosses, indicating greater moisture (Bader *et al*. 2007). But thick mats of mosses can be detrimental. Bader and coworkers found that seedlings of forest trees in the tropics often appeared to have negative growth because the bryophytes, especially mosses, grew up around them. This growth often deprived the seedling leaves of light. Bader and coworkers concluded that the seedlings grew in the mosses because no other substrate was available in the forest and did not appear to be benefitted by them.

Bryophyte and Fauna Relationships

In an Ecuadorian cloud forest (Figure 7), Zitani *et al*. (2018) found annelids, molluscs, crustaceans, millipedes, centipedes, arachnids, and hexapods (and others) among the bryophytes. And of course many birds use bryophytes for making nests, especially the pendent and mat-forming species (Cao & Caihua 1991) (see also Chapter 16). And some rodents occur only in mossy forests (see Chapter 17).

When the new species ***Herbertus sendtneri*** (Figure 6) was discovered, it displayed swollen tips resembling gynoecia (Gradstein *et al*. 2018). These proved instead to be small, whitish colonies of protozoans that resemble gnathifers, but remain to be identified. These infected shoot tips failed to develop normally and instead produced branch innovations (1-2) below the swollen tips.

Figure 6. ***Herbertus sendtneri***. Photo by Paulo Henrique Silva <siaram.azores.gov.pt>, with online permission.

Zitani *et al*. discovered an arboreal **Onychophoran** (velvet worm; Figure 8), along with a **Lepidopteran** (butterfly or moth) mimic, among the epiphytic bryophyte mats that are up to 10 cm deep in an Ecuadorian cloud forest (Figure 7). **Onychophorans** are highly susceptible to desiccation, so the bryosphere most likely maintains their moisture at a safe level.

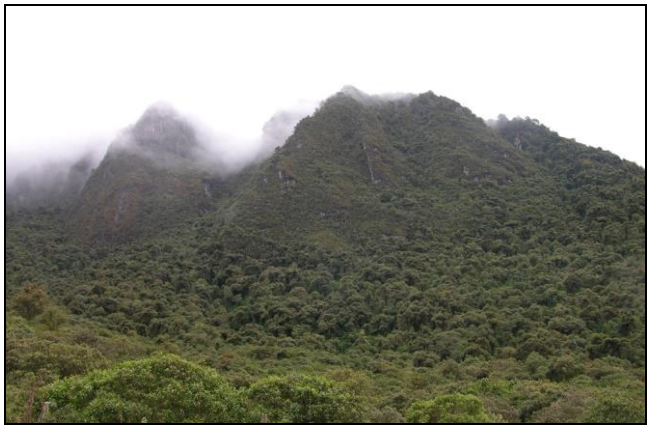

Figure 7. Ecuadorian cloud forest. Photo by Arthur Anker, with permission.

Figure 8. **Onychophoran**, a moss inhabitant in the tropics. Photo through Creative Commons.

Insects abound in tropical forests, including those in bryophyte mats (Nadkarni & Longino 1990). Epiphytes can contribute antifeedants that help protect the host. Frahm and Kirchhoff (2002) tested alcoholic extracts from the moss ***Neckera crispa*** (Figure 9) and the liverwort ***Porella obtusata*** (Figure 10) on feeding by the slug ***Arion lusitanicus*** (Figure 11). ***Neckera crispa*** had only low antifeedant properties at 0.5% or more dry weight. ***Porella obtusata***, on the other hand, was moderately effective at concentrations of 0.05%, with total effectiveness at 0.25% of dry weight.

Figure 9. ***Neckera crispa***, a moss with weak antifeedant activity on the slug ***Arion lusitanicus***. Photo by Jan-Peter Frahm, with permission.

Figure 10. ***Porella obtusata***, a moss with antifeedant activity against the slug ***Arion lusitanicus***. Photo by Jan-Peter Frahm, with permission.

Figure 11. ***Arion lusitanicus***, a slug that is deterred by extracts from ***Porella obtusata***. Photo by Håkan Svensson, through Creative Commons.

Most of the animal interactions are discussed in the chapters on interactions in volume 2, but some deserve repetition here for those who want a quick view of their roles in the tropics. In addition to the many bryophytes in the tropics and the many more waiting to be discovered, there are likely many unusual or intimate relationships with insects to be discovered.

Arthropods

Many arthropods live among the epiphytic bryophytes. Yanoviak *et al*. (2004) compared the arthropod assemblages in the vegetative portions vs the humic portions of Neotropical cloud forest epiphyte mats. Many types of arthropods occur among the bryophytes of the Neotropical cloud forests. Bryophytes at different elevations and tree levels provide different conditions for these arthropods and thus increase their diversity in the tropics. Furthermore, the green and brown portions of the bryophytes support different communities, with the green portion containing twice as many individuals and species per gram dry mass compared to the brown portion.

Some species of invertebrates seem to be associated exclusively with bryophytic epiphytes. ***Bryospilus repens*** (**Branchiopoda**) has been considered a strictly epiphytic moss inhabitant (Cammaerts & Mertens 1999).

The rainforest brings new meaning to letting moss grow on your feet – or head or back. In the cloud forests of Papua New Guinea, at 2,000-3,000 m asl, one can find mosses (***Daltonia angustifolia***; Figure 12) and liverworts [***Cololejeunea*** (Figure 13), ***Microlejeunea*** (Figure 14), and ***Metzgeria*** (Figure 15)] on the back of a beetle, a small weevil (**Curculionidae**) in the genus ***Gymnopholus*** (Figure 12) (Gressitt *et al*. 1965; Gradstein *et al*. 1984; Gradstein & Equihua 1995). ***Daltonia*** is not restricted to this weevil, but rather grows on bark and small branches of the montane rainforest where it is able to subsist when it is not being transported around the canopy. Gradstein and coworkers (1984) attribute the ability of ***Daltonia*** to inhabit the beetle to the ability of this moss to mature quickly and grow where the beetle lives. It is likely that the moss affords camouflage to the beetle. Could it also make the beetle distasteful?

Figure 12. ***Daltonia angustifolia*** on weevil, ***Gymnopholus*** sp., in the montane mossy forest of New Guinea. Photo by Robbert Gradstein, with permission.

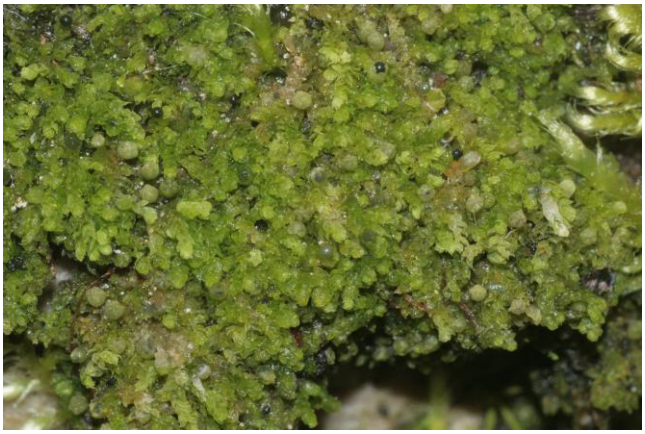

Figure 13. ***Cololejeunea calcarea***; members of this genus can inhabit the backs of the weevil ***Gymnopholus*** sp.. Photo by Hermann Schachner, through Creative Commons.

Figure 14. ***Microlejeunea ulicina***; members of this genus can inhabit the backs of the weevil ***Gymnopholus*** sp. Photo by Malcolm Storey <www.discoverlife.org>, with online permission.

Figure 15. ***Metzgeria claviflora*** from the Neotropics; members of this genus can inhabit the backs of the weevil ***Gymnopholus*** sp. Photo by Michael Lüth, with permission.

Epizoic bryophytes occur on a variety of insects in the tropics. Epiphyllous liverworts sometimes extend their substrate to the forewings and pronotum of the Costa Rican shield mantids [***Choeradodis rhombicollis*** (Figure 16) and ***C. rhomboidea*** (Figure 17)] (Lücking *et al*. 2010). These insects can become home to five species of liverworts. In their collection of 84 individuals, the researchers found 60 with epiphylls. They colonized more females than males and more of ***C. rhombicollis*** than ***C. rhomboidea***. This is likely due to the longer lifespan of females and suggests that the same should be true for host leaves. The bryophytes may provide camouflage for the insects.

Figure 16. ***Choeradodis rhombicollis***, a mantid whose wings can be colonized by epiphyllous liverworts. Photo by Benjamint444, through GNU free documentation license.

Figure 17. ***Choeradodis rhomboidea***, a mantid whose wings can be colonized by epiphyllous liverworts. Photo by Andreas Kay, through Creative Commons.

Several mantids and walking sticks are mimics of mosses or liverworts. In other cases, insect larvae may use epiphyllous bryophytes as host plants in the tropics (DeVries 1988).

Callaghan (1992) described the behavior of 16 **Lycaenidae** butterflies in Nigeria. The larvae of all these species grazed on epiphylls "such as lichens and fungi." Mimicry is much more common in the tropics than elsewhere. Occasionally epiphyllous bryophytes, especially liverworts, are able to contribute to this mimicry.

Insects and other animals associated with your bryophyte collections can cause immigration control to quarantine your specimens for months and may result in your never seeing them again. Heating/drying methods beforehand can drive these inhabitants out or kill them, increasing your chances of getting your samples through customs.

Vertebrates

Reptiles and Amphibians

Many tropical amphibians (see, for example, Allison & Kraus 2000) and some snakes and lizards are associated with bryophytes. Many tropical epiphytes provide nesting sites and cover for animals such as salamanders (Bruce 1999). Some amphibians use them as calling sites, with the bryophytes modifying the types of sounds they make. Others use them for egg-laying sites. See Chapters 14 (Amphibians) and 15 (Reptiles) in Volume 2 (Bryological Interaction) for details.

In a study in the montane cloud forest of Cameroon, Böhme and Fischer (2000) found lizards with a greenish coloration. This ground chameleon, ***Rhampholeon spectrum*** (Figure 18), was sporting an overgrowth of four species of typically epiphyllous liverworts from the family **Lejeuneaceae**. The species included ***Cololejeunea jovetastiana*** (see Figure 19) and ***Colura digitalis*** (Figure 20) as the most abundant; only a few plants of ***Cololejeunea*** sp. were present; ***Lejeunea*** (Figure 21) was present in only two samples.

Figure 18. ***Rhampholeon spectrum*** in Cameroon, a species that can be inhabited by several species of liverworts in the **Lejeuneaceae**. Photo by Bernard DuPont, through Creative Commons.

Figure 19. ***Cololejeunea minutissima***; ***Cololejeunea jovetastiana*** is one of the leafy liverworts known to live on the lizard ***Rhampholeon spectrum***. Photo by David T. Holyoak, with permission.

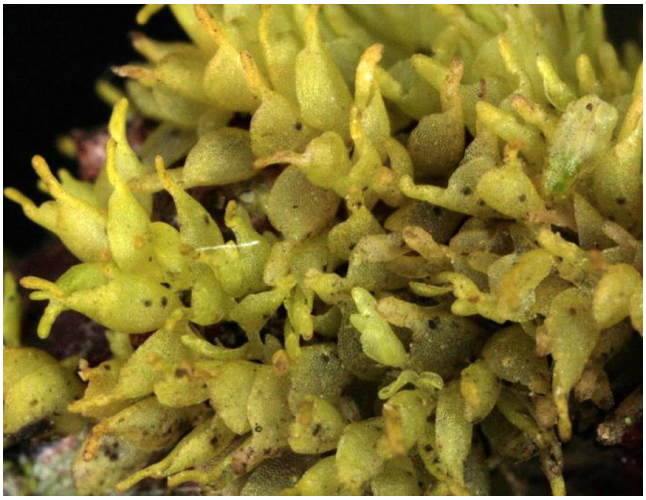

Figure 20. ***Colura digitalis***, one of the leafy liverworts known to live on the lizard ***Rhampholeon spectrum***. Photo by Jan-Peter Frahm, with permission.

Figure 21. ***Lejeunea anisophylla***; ***Lejeunea*** is one of the genera of leafy liverworts known to live on the lizard ***Rhampholeon spectrum***. Photo by Lionel Courmont, through Creative Commons.

But a stranger vision might be that of a lizard with a head dress! In the Mexican rainforest, ***Corythophanes cristatus*** (Figure 22-Figure 23), a lizard of the lowland rainforest of the Chiapas, sports a crown of filamentous algae including *Cladophora* (dominant; Figure 24), and Chaetophorales (Figure 25), with the tiny leafy liverwort ***Taxilejeunea obtusangula*** (Figure 26) living among them (Gradstein & Equihua 1995). This liverwort species is normally a common bark inhabitant, but also occurs on rocks (Evans 1911).

Figure 22. ***Corythophanes cristatus***, a lizard species that uses its head as a shovel and sometimes carries a mantle of bryophytes there. Photo by Simon J. Tonge, through Creative Commons.

Figure 23. Head of ***Corythophanes cristatus*** showing colonization by bryophytes. Photo by Twan Leenders, with permission.

Figure 24. ***Cladophora*** sp., a green alga that lives on the heads of ***Corythophanes cristatus***. Photo by Kristian Peters, through Creative Commons.

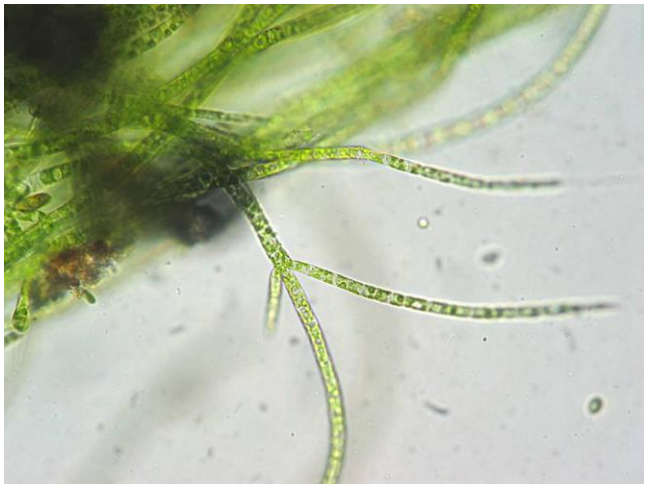

Figure 25. ***Stigeoclonium*** sp., an alga in the **Chaetophorales** – an order of green algae known to live on the heads of ***Corythophanes cristatus***. Photo by Kristian Peters, through Creative Commons.

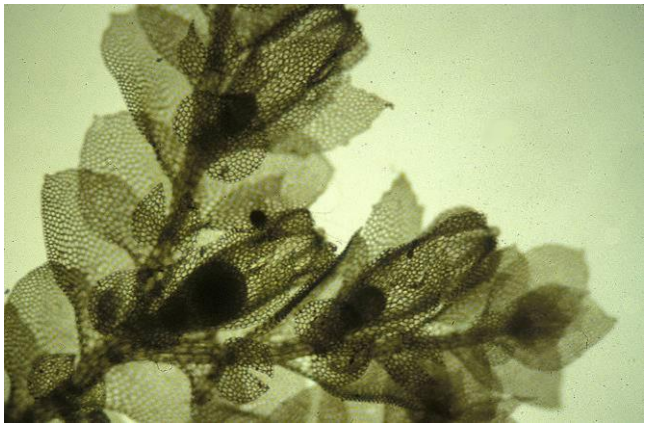

Figure 26. ***Taxilejeunea obtusangula***, one of the inhabitants on some crested lizards, ***Corythophanes cristatus***. Photo by Elena Reiner-Drehwald, with permission.

Rodents

Even mice (moss mice) live among bryophytes in the tropics. In Sulawesi, Indonesia, moss mice live and nest among the bryophytes (Helgen & Helgen 2009).

Bryophytes on Fungi

A surprising number of bryophytes are able to grow on the sporocarps of **Basidiomycota** fungi. Vital *et al*. (2000) identified 26 moss and 35 liverwort species growing on these substrates. None was exclusive to the fungi, all occurring on dead trunks where fungi occurred as well. Could it be that the fungus provides some chemical that is needed for the bryophyte life cycle to be completed?

Summary

Bryophytes can play major roles in water and nutrient cycling in tropical forests. In particular, they provide suitable habitat for nitrogen-fixing Cyanobacteria, as well as trapping nutrients from rainwater and the atmosphere. These nutrients can be

released in pulses, often at important times for forest growth.

Bryophytes in trees provide suitable substrate for many species of flowering and fern epiphytes, but their exact role is poorly known. On the other hand, many organisms use the mosses as homes or for nesting materials. Inhabitants include insects and other arthropods, velvet worms, annelids, molluscs, frogs, snakes, and rodents. On the other hand, bryophytes can inhibit the growth of bacteria and fungi and discourage herbivory by insects and other herbivores. Some of these organisms are known exclusively from bryophytes. Rodents and birds use bryophytes as nesting materials. Some bryophytes grow on insects or lizards and may provide camouflage. And a surprisingly large number of bryophytes are able to grow on fruiting parts of fungi.

Acknowledgments

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CHAPTER 8-14
TROPICS: DISTURBANCE AND CONSERVATION

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CHAPTER 8-14
TROPICS: DISTURBANCE AND CONSERVATION

Figure 1. Deforestation in Indonesia, a common scene throughout the tropics. Photo from Rainforest Action Network, through Creative Commons.

From a northern perspective, most of what we hear about the tropics is about massive disturbance. Hence, it would be irresponsible to discuss this region without at least a glimpse of the impact of disturbance on the bryophyte flora. Unfortunately, we have no before-and-after data for the vast areas that have been converted from tropical rainforest into short-lived agricultural land and that are now experiencing the jungle of plants tolerant of low nutrients, shallow soil, and exposure. However, some recent comparative studies may help us understand what we have lost.

Natural Disturbance

Nature has her own form of devastating disturbances. These include events such as hurricanes, tornadoes, and other high winds, animal activities, volcanoes, fire, and extreme drought.

El Niño and Hurricanes

Despite the frequency of hurricanes in some tropical areas, it appears that few studies have addressed the effects on bryophyte communities. Weber (1985) seems to be one of the earliest. He assessed the effects on both bryophytes and lichens resulting from the El Niño in the Galápagos Islands.

Hurricanes can have severe impacts on the epiphytic bryophytes in the tropics (Loope *et al*. 1994). Hurricanes can be very powerful forces that destroy nearly everything in their paths. In Puerto Rico, Hurricane Hugo created mass destruction in 1989. Recovery in the cool cloud forest has been slow compared to that of the lowland. Bryophytes were stripped from the trees by the high-powered winds and rain. Fortunately, the return frequency of hurricanes to any given area is low, usually occurring after years or decades (Lodge & McDowell 1991). But at the same time, the life span of a canopy tree or a forest ecosystem is longer than that interval.

Considering the number of hurricanes in the tropics, and the considerable damage I have witnessed to epiphytic bryophyte communities following Hurricane Hugo (see Weaver 1999) in Puerto Rico, I am surprised at how few

studies have addressed the damaging effects of hurricanes on these communities.

Nutrient Relationships

Nutrient levels can affect the damage to trees and their adhering bryophytes. Herbert *et al*. (1999) found that large trees sustained damage at twice the frequency of smaller trees. Thus, trees that had a richer phosphorus environment were more susceptible to damage due to greater growth.

Hurricanes alter the nutrient cycling in tropical forests (Lodge *et al*. 1991). Hurricane Hugo (Figure 2), in September 1989, struck Puerto Rico, severely damaging wet forest sites. This, and other hurricanes since, have caused a massive increase in fine litter as leaves (Figure 3), small twigs, and other miscellaneous debris were ripped from the trees and deposited on the forest floor. Concentrations of N and P increased as much as 1.5 times for N and 3.3 for P compared to normal litter fall. This raises the question of effects on competition and the success of bryophytes under these conditions.

Figure 2. Hurricane Hugo forest damage in Puerto Rico. Photo by Matthew C. Larsen and Angel J. Torres Sánchez, USGS, through public domain.

Figure 3. El Yunque forest after Hurricane Irma, showing extensive leaf litter and branches brought down by the hurricane. Photo by Joel S. Olivencia, USDA, through public domain.

Walker *et al*. (1996) mentioned bryophytes in their study comparing altitudinal responses by hurricane-damaged forests in Puerto Rico. Nutrient treatments initiated 1-6 months after the hurricane decreased the bryophytes threefold while causing graminoids to increase 10-fold in the cloud forest.

The cloud forest understory is dominated by bryophytes; epiphytes are common. Walker *et al*. (1996) tested the effects of fertilization on the vegetation following hurricane damage. Fertilization increased biomass of the graminoids (grasses, sedges) in the elfin cloud forest by a factor of 10, whereas bryophytes decreased 3-fold. The same differences were absent in the lowland forest. Cover of ferns did not respond to differences in treatment or time. At the high elevations, bryophyte biomass is most likely sustained by the constant high humidity. It is likely that the bryophytes were negatively affected by the fertilizer salts. They could also have been out-competed by the graminoids. Recovery of the bryophytes was most likely facilitated by their ability to spread. As I have observed in Puerto Rico after Hurricane Hugo (Figure 2), the bryophytes are removed from the trees in patches, leaving behind the source for new growth. This removal is due to high winds and driving rain.

Recovery

Some bryophytes escape damage by living in protected locations. The rare liverwort species ***Lejeunea paucidentata*** (**Lejeuneaceae**; Figure 4) occurs in the rainforests of Dominica (Figure 5) (Schäfer-Verwimp 1999). Fortunately, it escapes hurricane damage because it lives on small fern fronds in the undergrowth and benefits from similar conditions in humid secondary vegetation or in heavily damaged old growth rainforest. On the other hand, Schäfer-Verwimp considers that the disappearance of ***Phycolepidozia exigua*** (Figure 6) is possibly due to hurricane damage to bark. This species most commonly grows on the bark of old trees, but old trees tend to be more susceptible to hurricane damage than the more pliable young trees.

Figure 4. ***Lejeunea paucidentata*** with perianths and young sporophytes. Photo by Elena Reiner-Drehwald, with permission.

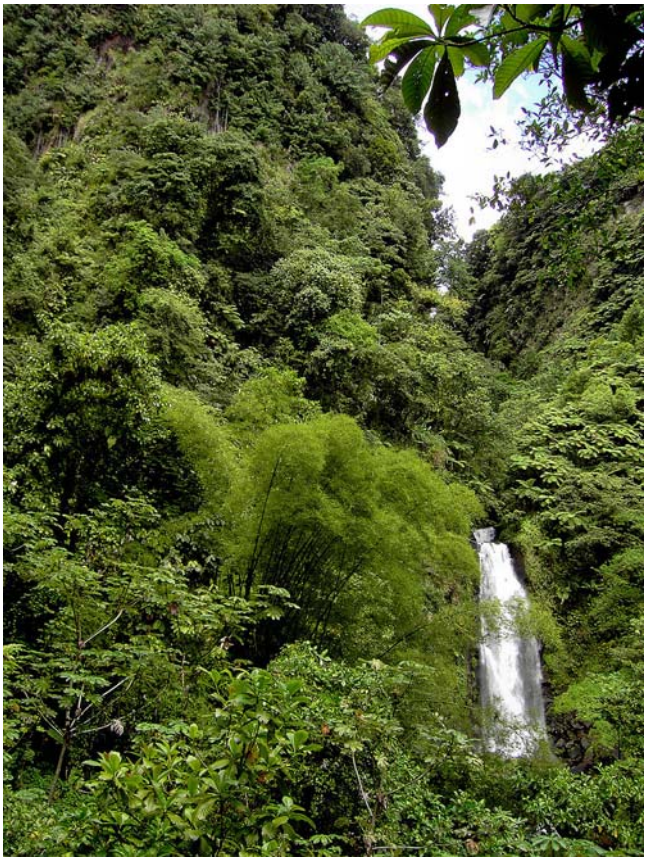

Figure 5. Rainforest at Trafalgar Falls, Dominica. Photo by Hans Hillewaert, through Creative Commons.

Figure 6. ***Phycolepidozia indica***, a species that seems to have disappeared due to hurricanes. Photo by Uwe Schwarz, courtesy of Robbert Gradstein.

Many have tried to determine what limits the species that become established on a given tree. Yeaton and Gladstone (1982) tried to determine what determines the structure of the epiphytic tracheophyte community on the calabash tree (***Crescentia alata***; Figure 7-Figure 8). As a result of their data analysis, they hypothesized that the colonization pattern is the result of the quantity of propagules produced by each species. It is possible that this is an important factor for bryophytes as well.

Figure 7. ***Crescentia alata*** with epiphytes in the Guanacaste dry forest. Photo by Daniel H. Janzen, through Creative Commons.

Figure 8. ***Crescentia alata*** in the Guanacaste dry forest. Photo by Daniel H. Janzen, through Creative Commons.

Nadkarni (2000) found a 30% reduction in bryophyte cover at severely impacted sites. She demonstrated, by experimental branch stripping, that epiphyte colonization occurs upwards from the **abaxial** (in this case, lower) branch surface. She considered that the shading by the branch permitted these abaxial sites to retain more water, increasing the time that the surface provided a suitable microclimate.

Bryophyte Loss Effect on Tracheophytes

Batke and Kelly (2015) documented the effects of a hurricane on the epiphytic bryophytes in the Cusuco National Park, northwest Honduras (Figure 9). They considered the epiphytes to be mechanically dependent plants and examined how hurricanes affected these dependents (Figure 10). Although the effect on bryophytes was not discussed directly, the researchers found that differences in life forms and families of tracheophytes among the tree branches resulted from branch surface area and bryophyte cover. Hence, the destruction of bryophyte mats led to reduced communities of tracheophytic epiphytes. They found that branches on trees that were more severely impacted had significantly lower cover. They considered that branches that were stripped of bryophytes and their dependent (Figure 10) plants during the severe gusts are less likely to experience early recolonization.

Figure 9. Cusuco National Park, Honduras. Photo by Anjelkaido, through public domain.

Figure 10. Montaña de Yoro forest in Honduras, showing the numerous epiphytes. Photo by Josiah Townsend, with permission.

Damage to the bryophyte communities can affect other epiphytes as well. Tremblay (2008) assessed the relationships of a rare epiphytic orchid after Hurricane Georges. At first he could find no correlation with the percent cover of mosses on standing trees. But a non-parametric density contour map revealed that the moss density does seem to affect the population size of the orchids. Using this technique, Tremblay demonstrated that the orchids are present more frequently when there is a 40-90% moss cover.

Fire

Many forests around the world are subject to fire. In the tropical cloud forests, the bryophytes may actually reduce fire damage. They not only reduce the likelihood of fire because of the moisture they hold, they also facilitate growth of additional epiphytes through their moisture-absorbing and moisture-holding capacity (Proctor 1982; Frahm & Gradstein 1991). This moisture-holding capacity reduces the flammability of the forest (Bruijnzeel & Proctor 1995).

Nepstad *et al*. (2008) noted that forest degradation and dieback and subsequent drought increase the susceptibility to forest fires. And fires increase drought, further increasing the susceptibility to bryophyte loss. Furthermore, deforestation and smoke can inhibit rainfall, further increasing fire risk. These researchers predicted that in the next 20 years following 2008 approximately 55% of the Amazon forests will be cleared, logged, damaged by drought, or burned.

Diaspore banks can facilitate recovery of bryophytes after a fire. In a diaspore bank, Zander and During (1999) found the moss ***Neophoenix matoposensis*** (**Pottiaceae**) in Zimbabwe as a new species. They recommended the "forced diaspore bank analysis" as a means to find small species with short life cycles, giving them only limited above-ground exposure. In this case the method was used to uncover species in experimental fire plots. Two additional species were uncovered as new to Zimbabwe and new to Africa. One of these was previously known only from Brazil and Australia.

Volcanoes

Air pollution is not always of human origin. Volcanic activity (Figure 11, Figure 15) can be a major contributor. Baudoin (1985) reported that epiphyllous bryophytes can be used satisfactorily as indicators of volcanic air pollution.

Figure 11. Pāhoehoe lava flows, Hawaii. Picture from Brocken Inaglory, through Creative Commons.

Volcanoes offer opportunities for observing effects of elevation with fewer environmental variables than most substrates. However, when they erupt, they create severe disturbances. These severe habitats, following cooling, create bare rock substrate that differs drastically from the surrounding area. Smith (1981) compared the bryophyte and lichen communities of these severe substrates with those of the surrounding ecosystems at the Puhima Geothermal Area in the Hawaii Volcanoes National park. He found very few of the species from surrounding areas to be present on the volcano ground in geothermal areas. The center of the geothermal area is nearly lacking in any vegetation. Only small communities of vegetation, dominated by the endemic moss ***Campylopus praemorsus*** (see Figure 12) are scattered here. The mosses seem to provide a safe haven for the lichen ***Cladonia oceanica*** (see Figure 13), where it grows epiphytically on the mosses in areas lacking the high temperatures. Outside that central zone, where temperatures are lower, the grass ***Andropogon*** (Figure 14) dominates. Here, both ***Campylopus praemorsus*** and ***Cladonia oceanica*** commonly produce reproductive structures.

Figure 12. ***Campylopus holomitrium*** in a geothermal area; ***Campylopus praemorsus*** occurs in volcanic and geothermal areas of Hawaii. Photo by Janice Glime.

Figure 13. ***Cladonia*** sp.; ***Cladonia oceanica*** is a geothermal lichen that grows epiphytically on the mosses. Photo by Tigerente, through Creative Commons.

Figure 14. *Andropogon leucostachyus*; the genus *Andropogon* dominates outside that central zone of a geothermal vent, where root temperatures are lower. Photo by João Medeiros, through Creative Commons.

In Costa Rica, Griffin (1974) suggested that sulfur gasses downwind from a volcano might account for the paucity of mosses there. Both species composition and cover of mosses are diminished on the downwind side of the Poas Volcano (Figure 15).

Figure 15. Poas Volcano, Costa Rica, showing downwind plume of steam. Photo by Franz Xaver, through Creative Commons.

Ah-Peng *et al*. (2007) found 70 species of bryophytes on a 19-year-old lava flow. They suggested that the high diversity is promoted by the host substrate and the bryophyte adaptations to colonize this new substrate. Hence, the disturbance by the volcano brought new space there to house a wide diversity of pioneer organisms.

Animal Activity

Forest animals can likewise be very destructive to bryophytes (Nadkarni 2000). Howler monkeys (***Alouatta*** spp.; Figure 16) and tayras (***Eira barbara***; Figure 17) knock clumps of moss and other epiphytes from the branches as they climb and jump about. White-faced capuchins (***Cebus capucinus***; Figure 18) remove them to look for invertebrates in the bromeliads. Most literature indicates that such disturbances are easily and quickly healed with recolonization coming primarily through encroachment from the sides of the plots, thus having the same species. But in the detailed study at Monteverde, Costa Rica, mimicking effects of animal activity, Nadkarni found something quite different when she removed 75 cm strips of epiphytes from canopy branches. Despite the presence of neighboring plants, recolonization was extremely slow, with no colonization during the first five years after stripping. When it did occur, the communities were quite different. Crustose and foliose lichens began the colonization, two groups that were totally absent originally. And rather than encroaching from the sides, colonization extended from the bottoms of the branches. By the sixth year, there were some algae and bryophytes on the undersides of branches. It was not until the eighth year that some of the bryophytes from the underside had joined on the top side. Small seedlings began to appear in the tenth year.

Figure 16. ***Alouatta palliata*** (Howler Monkey), an animal whose activities in the trees can dislodge clumps of bryophytes. Photo by Hans Hillewaert, through Creative Commons.

Figure 17. Tayra (***Eira barbara***), an animal whose activities in the trees can dislodge clumps of bryophytes. Photo by Greg Hume, through Creative Commons.

Figure 18. White-faced Capuchin (***Cebus capucinus***) in Costa Rica, a species that removes mosses in search of invertebrates. Photo by Cephas, through Creative Commons.

Rare and Threatened Species

By their very nature, severe habitats often have rare and endangered species. That is because bryophytes must have special adaptations to survive in these extreme habitats. Perhaps they sacrifice competitive ability to achieve this physiological adaptation.

Gradstein (1992a) noted that loss of tropical species may vary considerably in deforested areas, depending on the size of the area affected and degree of habitat change. This damage is greatest for shade epiphytes, with an estimated 10% of rainforest species under threat by 1992. Gradstein listed 19 endangered species and 27 rare ones that are disappearing from the rainforests. Costa Rica and Panama have been particularly vulnerable, along with the Greater Antilles, the Chocó, southeastern Brazil, and parts of Amazonia.

Koponen (1992) considered the bryophytes in the tropical (and temperate) regions to have much more danger of becoming rare or extinct than those of the boreal and Arctic regions. The richest tropical floras are in the rainforests and montane forests, and deforestation creates disjunct patterns. Deforestation is particularly problematic in China, where nearly all the forests have been cut for agriculture. Very few bryophyte species from virgin tropical forests are able to survive in manmade habitats.

On the other hand, some disturbed habitats, created by agroforestry, can provide the conditions needed for some of the rare species. For example, Gradstein (1999) rediscovered the endangered leafy liverwort ***Spruceanthus theobromae*** (**Lejeuneaceae**; Figure 19) on cacao trees (***Theobroma cacao***; Figure 20) in western Ecuador.

Figure 19. ***Spruceanthus theobromae***, a species endemic to cacao plantations. Photo by Robbert Gradstein, with permission.

Figure 20. ***Theobroma cacao*** with bryophytes; this species supports some forest bryophytes in plantations in the tropics. Photo by Fpalli, through Creative Commons.

The real loss of tropical rare and endangered species is difficult to assess. Many areas were destroyed before any bryophyte assessment occurred. And many species considered rare or endemic have proven to be synonyms of species in a neighboring country or mountain.

Pollution and Disturbance

Managing for bryophytes often does not coincide with the best management plan for the forest. Andersson and Gradstein (2005) studied the biodiversity of bryophyte and lichen epiphytes in cacao plantations (Figure 21) in western Ecuador. They found 51 bryophyte and 61 lichen species. The managed cacao plantation epiphyte assemblages resembled those of natural tropical rainforests, but with lower species richness. Species also were typically found lower on the trunks. The species on cacao were typically widespread Neotropical or pantropical species. But ***Spruceanthus theobromae*** (Figure 19) is endemic to cacao plantations in western Ecuador. Management involving manual removal of epiphytes in the plantations significantly impacted the epiphyte species diversity. High management intensity particularly affected diversity of liverworts and lichens, but not mosses. As one might expect, plantations with low management had the highest percent cover of bryophytes. Plantations with low and moderate management serve as reserves for some ecological specialists, making these plantations important in the conservation of epiphytes.

Figure 21. ***Theobroma cacao*** plantation in Dominican Republic, home for a number of bryophytes, some of which would normally be in local forests. Photo by C. T. Cooper, through public domain.

Working in tropical rainforests of the Pacific, Pócs and Tóthmérész (1997) found that the average species richness in the most diverse epiphyll communities was 8-9 per leaf. Degraded habitats exhibited as few as 3-4 species. At the habitat level, the number of species could reach 24-25 species. The number of species per habitat does not typically decrease as a result of habitat degradation because **beta diversity** (differences in species composition among sites; regional diversity) tends to increase while the number of species per leaf decreases. The study emphasizes the importance of the scale of the study in order to assess the impacts of disturbance.

Some of our understanding of microhabitat differences can be derived from studies on the effects of disturbance. For example, Werner and Gradstein (2009) compared various degrees of disturbance in closed-canopy mixed acacia forest (old secondary), pure acacia forest (old secondary), forest edge, young semi-closed secondary woodland, and isolated trees in grassland. They found that density of bryophytic epiphytes on 100 trees of ***Acacia macracantha*** (Figure 22) in northern Ecuador at 2,300 m asl is significantly lower in edge habitat and on isolated trees than in closed forest. Forest edge is more

impoverished than semi-closed woodland and has similar floristic affinity to isolated trees and to closed forest types. The microhabitats among these habitat types vary, contributing to the diversity. As they point out, "Assemblages were significantly nested; habitat types with major disturbance held only subsets of the closed forest assemblages, indicating a gradual reduction in niche availability." They found no diversity effect from distance to the forest for epiphytes on isolated trees. Species density is closely correlated with crown closure. They concluded that microclimate, not dispersal constraints, determine most of the epiphyte assemblages. The researchers also concluded that the bryophytic epiphytes are sensitive indicators of changes in microclimate and human disturbance in the montane dry forests. A major treatise on the canopy community is that of Lowman *et al.* (2013).

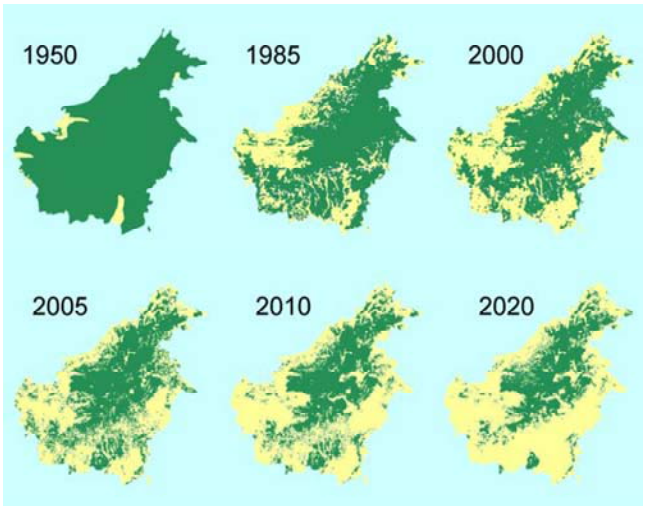

Figure 23. 70 years of Borneo deforestation. Photo courtesy of Robbert Gradstein.

Figure 22. ***Acacia macracantha***, a species where density of bryophytic epiphytes in northern Ecuador at 2300 m asl is significantly lower in edge habitat and on isolated trees than in closed forest. Photo by Vladeq, through Creative Commons.

Deforestation

Deforestation has become a major factor impacting diversity and biomass in the tropics (Figure 23). "Between 1990 and 1997, 5.8 ± 1.4 million hectares of humid tropical forest were lost each year, with a further 2.3 ± 0.7 million hectares of forest visibly degraded." (Achard *et al*. 2002) although the rate has slowed in recent years, deforestation continues, increasing the total impact.

Scatena *et al.* (2010) noted that the cloudy, wet, difficult terrain of the tropical montane cloud forests had afforded the bryophytes some protection from deforestation. However, in the late 1970's and early 1980's, even these forests were being torn down or fragmented. By the 1990's they became one of the most threatened ecosystems in the world, with a loss rate exceeding that of the lowland tropical forests (1.1% y^{-1} vs. 0.8% y^{-1}).

Deforestation (Figure 1, Figure 24) has greatly reduced diversity of bryophytes, as one might expect. The loss of high canopy has forced species that typically occupy the canopy to appear as low as the base of the tree (Gradstein 2002). This change in position correlates with the microclimate of the canopy in the mature forest, with the microclimate in the fallows matching closely the humidity and air temperature of the mature canopy. Such is not the case with the microclimate of the tree bases under the mature canopy.

Figure 24. Deforestation in the Amazon forest. Photo by Matt Zimmerman, through Creative Commons.

Pócs (1989) reported that epiphytes are much rarer in disturbed forests than they are in undisturbed forests in submontane rainforests in the East Usambara Mountains of East Africa. Rather, the species in the disturbed forests are sun species and occur on the lower parts of trunks of ***Maesopsis*** (umbrella tree; Figure 25). In the undisturbed

forests, these same species occur in the canopy. Pócs has also found a decline in epiphytes in the "undisturbed forest." He attributed this to the drying climate.

Henderson *et al*. (1991) reported that approximately 90% of the South American tropical mountain forests had been converted into pastureland or other non-forest use. Bryophyte losses are greater among mosses than among liverworts (Jácome *et al*. 2011). Shade species are more affected than drought-tolerant canopy species. The latter species are able to grow in lower positions on the remaining trees. A dense canopy is important in maintaining high diversity (Steffan-Dewenter *et al*. 2007; Sporn *et al*. 2009). Despite the negative impact, in Costa Rica the secondary forests may have up to 40% of their epiphytic species exclusively in the secondary forest.

Alvarenga *et al*. (2009, 2010) likewise reported a highly significant loss of richness as a result of habitat loss in a Brazilian Atlantic forest. The most conserved fragments have more than 10 times the species richness of the least conserved fragment. In non-conserved fragments, the epiphytes do not colonize the lower trunks (2.1-10 m) or higher zones. Instead, they are restricted to the lowest 2 m at the tree base and clearly exhibit an altered floristic composition. Specialists of sun or shade are impacted more than generalists. The generalists decrease in richness in non-conserved habitats, but their proportion increases due to the loss of specialists. The habitats that retain their rich epiphyte flora are greater than 300 ha in size – an uncommonly large size in the Brazilian Atlantic rainforest.

Figure 25. ***Maesopsis eminii*** (umbrella tree) providing shade for a coffee plantation. Photo by Aniruddha Dhamorikar, through Creative Commons.

In upper montane ***Quercus copeyensis*** forests (Figure 26) of Costa Rica, Holz and Gradstein (2005) found that total species richness of bryophytes and lichens differs little between primary and early or late secondary forests. The high richness in the secondary forest is most likely due to the high humidity under the closed canopy. Nevertheless, species composition differs markedly. After 40 years of recovery, 46 (one-third) of the species still had not become re-established. Of all recorded species, 40% (68 species) occur exclusively in the secondary forests.

Figure 26. ***Quercus copeyensis*** forest wherein species richness differs little between primary and secondary forest, but the kinds of species differ. Photo through Creative Commons.

When epiphytes were transplanted to lower elevations in the Bolivian Andes, the cover became more even and dominance of individual species decreased (Jácome *et al*. 2011). The researchers concluded that as climate changes, individual species responses will differ, resulting in new community relationships. They warn that short-term responses might not be indicative of long-term responses.

Costa (1999) compared epiphytic bryophyte diversity in primary and secondary lowland rainforests of southeastern Brazil. The highest species richness occurs in mature secondary hillside rainforest (43 species). The lowest is in a highly degraded hillside rainforest (6 species) and a hillside secondary rainforest (5 species). As seen elsewhere, the important families are **Lejeuneaceae** (Figure 4; 23 species, 30%) and **Sematophyllaceae** (Figure 27; 7 species, 10%). And as in other studies, the canopy

has the highest number of exclusive species (45% of canopy species). The shade epiphytes are the most affected by deforestation and many do not return 20-45 years after the destruction. However, after 80 years the species composition is similar to that of the primary forest.

Figure 27. ***Sematophyllum*** (**Sematophyllaceae**); **Sematophyllaceae** is among the important moss families from the lowland rainforests of southwestern Brazil. Photo by Michael Lüth, with permission.

In a different location in southeastern Brazil, Costa (1998) found the highest species richness in the mature secondary hillside rainforest (43 species). The lowest is again the highly degraded hillside rainforest (6 species).

Nöske *et al*. (2008) compared the epiphyte diversity of mature and recovering forest and that in open vegetation in the montane zone of Ecuador. They were unable to discern any pattern of change in species richness among different taxonomic groups (lichens, bryophytes, tracheophytes, and moths) with increasing disturbance. However, richness of epiphytic bryophytes decreased significantly from mature forest through the cline to open vegetation. For some of the taxa, the modified habitats serve to increase overall biodiversity in the Andes.

Hyvönen *et al*. (1987), however, found that many mosses can find suitable niches even in disturbed areas, unless destruction of the habitat is complete. Nevertheless, some are eliminated by current practices of land use. In their study on the Huon Peninsula of Papua New Guinea, they used 18,000 specimens to determine effects of disturbance on the bryophytes. Of 43 species, 14 were restricted to undisturbed habitats, 16 occurred about equally in both, and 23 were preferentially in disturbed areas. Primeval habitats were dominated by terrestrial and epiphytic mosses; weedy species occurred in disturbed habitats. The sensitive epiphytic species that decreased with disturbance include ***Meteorium buchananii*** (Figure 28), ***Trachypus bicolor*** (Figure 29), ***T. humilis*** (Figure 30), ***Pseudotrachypus wallichii***, ***Cryptopapillaria fuscescens***, and ***Pelekium contortulum*** (Figure 31). In addition, ***Campylopus clemensiae*** (see Figure 42) and ***Leptocladiella flagellaris*** grow on living trees as well as rotten wood. Soil species that are sensitive include ***Dawsonia grandis***, ***D. papuana*** (see Figure 32), ***Rhodobryum giganteum*** (Figure 33), with less substrate-discriminating ***Macrothamnium hylocomioides*** (see Figure 34), ***Thuidium cymbifolium*** (Figure 35), and ***T. glaucinum*** (Figure 36). Persistent species include ***Bryum apiculatum*** (Figure 37) and ***Plagiomnium integrum*** (see Figure 38), although they decrease in altered habitats. On the other hand, the outer crown epiphyte ***Leptostomum intermedium*** (see Figure 39) seems to increase with human influence, but that could be an artifact due to the difficulty of sampling it. The species that clearly increase with disturbance include ***Brachymenium nepalense*** (Figure 40), ***Bryum billarderii*** (Figure 41), ***Campylopus exasperatus***, ***C. umbellatus*** (Figure 42), ***Elmeriobryum philippinense***, and ***Orthomnion elimbatum*** (Figure 43). Species that were clearly present only following disturbance include ***Bryum argenteum*** (Figure 44) and ***Gemmabryum subapiculatum*** (syn.= ***Bryum microerythrocarpum***; Figure 45).

Figure 28. ***Meteorium buchananii***, a sensitive moss species that decreases with disturbance. Photo by Li Zhang, with permission.

Figure 29. ***Trachypus bicolor***, a sensitive moss species that decreases with disturbance. Photo through Creative Commons.

Figure 30. ***Trachypus humilis*** with capsules, a sensitive moss species that decreases with disturbance. Photo through Creative Commons.

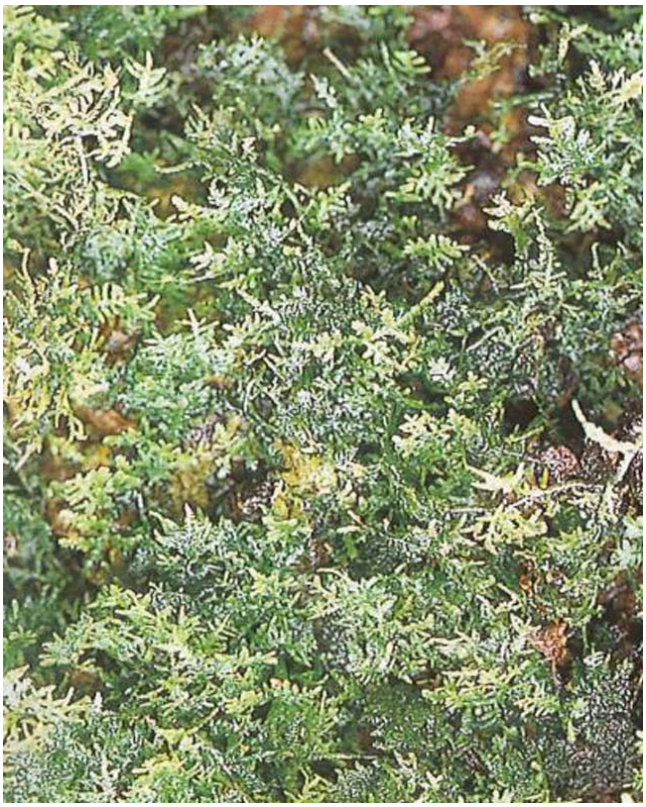

Figure 31. ***Pelekium contortulum***, a sensitive moss species that decreases with disturbance. Photo through Creative Commons.

Figure 32. ***Dawsonia superba***; ***Dawsonia grandis*** and ***D. papuana*** are soil species that are sensitive to disturbance. Photo by Phil Bendle, with permission from John Grehan.

Figure 33. ***Rhodobryum giganteum***, a sensitive moss species that decreases with disturbance. Photo by Leonardo L. Co, with online permission.

Figure 34. ***Macrothamnium submacrocarpum*** from Doi Inthanon, Thailand; ***Macrothamnium hylocomioides*** is a sensitive soil species that decreases when faced with disturbance. Photo courtesy of Hiroyuki Akiyama.

Figure 35. ***Thuidium cymbifolium*** with capsules, a sensitive species of soil and other substrates that decreases when faced with disturbance. Photo by Li Zhang, with permission.

Figure 36. ***Thuidium glaucinum***, a sensitive species of soil and other substrates that decreases when faced with disturbance. Photo through Creative Commons.

Figure 37. ***Bryum apiculatum*** with capsules, a persistent tropical soil species that is less negatively affected by disturbance. Photo by David T. Holyoak, with permission.

Figure 38. ***Plagiomnium affine***; ***Plagiomnium integrum*** is a persistent tropical soil species that is less negatively affected by disturbance. Photo by Michael Lüth, with permission.

Figure 39. ***Leptostomum inclinans*** with capsules; ***Leptostomum intermedium*** is an outer crown species that actually increases with human disturbance. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 40. ***Brachymenium nepalense***, a species that becomes more abundant with disturbance. Photo by Li Zhang, with permission.

Figure 41. ***Bryum billarderii***, a species that becomes more abundant with disturbance. Photo by Bramadi Arya, through Creative Commons.

Figure 42. ***Campylopus umbellatus*** with capsules, a species that becomes more abundant with disturbance. Photo by Li Zhang, with permission.

Figure 43. ***Orthomnion elimbatum***, a species that becomes more abundant with disturbance. Photo by Andrew Franks, with permission.

Figure 44. ***Bryum argenteum***, a species that becomes more abundant with disturbance. Photo by Michael Becker, through Creative Commons.

Figure 45. ***Gemmabryum subapiculatum***, a species that becomes more abundant with disturbance. Photo by Michael Lüth, with permission.

Evidence shows that logging does not have to be totally destructive. The main effect of such disturbance in tropical forests is increased desiccation due to greater wind movement and insolation, causing a reduction in biomass of epiphytic bryophytes (Norris 1990). This, in turn, decreases the water and mineral retention of the remaining bryophytes and interferes with their ability to trap and release water and mineral nutrients. In Papua New Guinea, Norris found that logging and agricultural practices may alter bryophyte species frequency, but with careful attention to logging management, there is no evidence of a significant loss of species.

When Romero (1999) compared bryophytes in logged and non-logged plots in a tropical montane forest in Costa Rica, he found that pendent epiphytes were more abundant on branches less than 1 cm in diameter. The highest biomass was that of branches supporting shade-tolerant species, *i.e.*, non-logged plots.

A comparison of fallow land (4-15 years) vs submontane rainforest in Bolivia reveals considerably less diversity of both bryophyte families and species in the fallows (Acebey *et al*. 2003). Surprisingly, there is little difference in liverwort diversity between them except in the

very young (4-year-old) fallows. Life forms differ, with significantly more smooth mats (72%) in the fallows. Nevertheless, in just 10-15 years, approximately half of the bryophyte taxa of the rainforest are re-established among the trees of the fallows. Most of these arrivals are ecological generalists and sun-loving epiphytes, with ecological specialists and shade species arriving and establishing more slowly. The highest diversity of the fallows is in the understory, contrasting with the highest richness in the canopy of the uncut rainforest. The shift to lower parts of the trees in the fallows corresponds with the greater air humidity there and most likely also with lower temperatures and reduced light intensity.

The Neotropics are not the only tropical area experiencing serious species loss. Turner *et al*. (1994) reported extinction of 594 of the 2,277 tracheophyte species in the Republic of Singapore. Epiphytic species have suffered 62% loss. These losses are due to deforestation (99.8% of primary forest) and disturbance, with the mangrove epiphytic flora disappearing completely. These losses will necessarily impact the losses of bryophytes through loss of substrate, shade, and sufficient humidity.

Much of the land in the tropics has been lost to agriculture before we have even assessed what bryophyte species live there. Sulawesi, Indonesia (Figure 46), is characterized by steep slopes that are often difficult for bryologists to navigate, but logging has nevertheless altered the environment. Ariyanti *et al*. (2008) investigated the bryophytes on tree trunk bases in the natural forest, selectively logged forest, and cacao plantation (Figure 21) shaded by remnants of the natural forest there. They found that species richness differs little among these forest types. But on close inspection, one finds that the moss richness is lowest in the cacao plantations, but the liverwort richness differs little among the forests. By contrast, the moss cover differs little among the forests, but liverwort cover is significantly less in the disturbed forest. Species composition likewise differs markedly in the cacao plantations compared to the natural forests and selectively logged forests. Drought-sensitive species are notably rare or absent in the cacao plantation, with drought-tolerant species replacing them. Large vs small trees have little effect on bryophyte species composition except in the cacao plantation; the latter phenomenon the researchers attribute to changes in stemflow of precipitation water.

Figure 46. Tangkoko National Park, North Sulawesi, Indonesia. Photo by Lip Kee Yap, through Creative Commons.

Gradstein and Sporn (2010) compared epiphytic bryophytes from different land use types in several countries of the Neotropics and Indonesia (Sulawesi), including natural rainforests, secondary rainforests, fallows, isolated pasture trees (Figure 20), and cacao agroforests (Figure 21). They found changes in species richness between these disturbed habitats and the various disturbances to vary by 0-10% species loss in the old secondary forest and up to 65-80% loss in young fallows and cacao agroforests. The cacao agroforests lost 75% of their species. In contrast, the remnant forest trees in pastures provide a rich habitat where bryophytes can be conserved. In submontane forests, there were considerable changes in life forms, but these changed little in the montane zones. Sun epiphytes replace shade epiphytes in the deforested areas. The study demonstrates the importance of canopy cover in preserving the rainforest bryophyte vegetation.

Benítez *et al*. (2015) likewise noted the decline of bryophyte and lichen epiphytes in moist tropical montane forests, due to deforestation and habitat loss. Benítez and coworkers investigated 240 trees in primary and secondary forests of southern Ecuador and found that diversity is higher in primary forests and lower in monospecific secondary forest stands. Habitat loss and reduction of canopy cover negatively affect total diversity. This, in turn, modifies the water balance and nutrient cycling of these forests, further complicating the loss of bryophytes and lichens. Shade epiphytes are replaced by sun epiphytes, and species richness diminishes.

In the fragmented Afromontane forests, Malombe *et al*. (2016) found the diversity of epiphyllous bryophytes exhibits no direct correlation with the distance from forest edge. However, they are affected by microenvironmental variables. These variables include tree species composition, sunlight exposure, and canopy structure, all factors that are typically affected by deforestation, even just thinning.

Cloud forests (Figure 47) are unique ecosystems with high bryological diversity and cover in the northern Andes (Benavides & Gutierrez 2011). But this ecosystem is also one of the most endangered ecosystems in the tropics. Agricultural techniques using slash and burn leave behind isolated individual palms in the middle of newly created grasslands or agricultural fields. This isolates the rare canopy bryophyte species. In Colombia, 72 liverwort species and 21 moss species comprised these epiphytic communities. The researchers found a decrease in the number of species from the forest to the grassland. The diversity likewise decreases from base to canopy of palms, with the more common species appearing an average of 4 m lower on the palms in the grassland when compared to those in the forest. The species remaining tend to be drought-tolerant forest species and species that commonly occur in disturbed sites. Hence, these isolated palms do not serve as suitable refugia for the rarer cloud forest species.

Cordova and del Castillo (2001) conducted a chronosequence study exclusively on tree bases in a tropical montane cloud forest in Mexico (Figure 48). The trees examined were in stands of 15, 45, 75, >90 years old, and a primary forest, and had originally been tropical montane cloud forests. They sampled the trees at 1 dm intervals using a sampling grid, up to 160 cm. Total

epiphyte cover increases with forest age, following an S-shaped curve. The highest rate of increase is between 15 and 45 years. Whereas moss and liverwort cover increases with stand age, macro- and microlichen cover appear to be independent of age. Cover of microlichens decreases as cover of mosses and tracheophytes increases. Total epiphyte cover per unit area shows some decrease as the diameter of the tree increases.

Figure 47. Cloud forest, Monteverde, Costa Rica. Photo by R. K. Booth, through Creative Commons.

Figure 48. Cloud forest, Bosque Comaltepec, Mexico. Photo by Prsjl, through Creative Commons.

In an assessment of bryophytic epiphytic diversity in Columbian (Figure 49) forest patches, Orrego (2005) suggested that there is a direct relationship between bryophyte species diversity and the structural heterogeneity of forest fragments. He cautioned that a single index is not adequate to assess the epiphytic bryophyte diversity.

Figure 49. Mangrove forest and lowland forest, Ensenada de Utría, Chocó, Colombia. Photo by Philipp Weigell, through Creative Commons.

Gradstein (2008) noted that drought-intolerant species suffer more than drought-tolerant ones under the loss of cover due to deforestation. In the South American tropics, disturbance causes high species turnover and the return to the original epiphytic bryophyte flora is slow. Even after 50 years of forest recovery, the bryophyte flora is still very different from the undisturbed flora. Gradstein and Sporn (2010) documented the tropical diversity of epiphytic bryophytes with land use gradients.

Gradstein and Sporn (2010) summarize the effects of deforestation on the bryophyte communities of the tropics:

1. Deforestation has a significant impact on the bryophyte diversity in what was once forested land. Old secondary forests still experience 0-10% loss, whereas young fallows and cacao agroforest can have 65-80% loss. Epiphytic bryophytes are more strongly affected than are lichens (Gradstein 1992b), with a 4X turnover of bryophytes compared to lichens (Nöske *et al*. 2008). In the arid regions, bryophytes are more sensitive to land use changes than are the tracheophytes (Werner & Gradstein 2009).
2. Life form proportions change in the submontane forests, but not in the montane forests. **Mats** increase in submontane fallows and **tufts** increase in cacao agroforests; this change is accompanied by a loss of **fans**, **pendants**, and **tails**.
3. Shade epiphytes disappear as more exposure is created, and these are replaced by sun epiphytes. Epiphyte heights on the trees experience a shift to lower locations. The canopies become almost devoid of epiphytes.
4. Canopy closure, microclimate, and host tree characteristics serve as drivers of the epiphytic bryophyte diversity under different land-use types, indicating that canopy cover is necessary to maintain the rainforest diversity (Steffan-Dewenter *et al.* 2007). As a result, it may take more than 100 years for the bryophyte diversity to fully recover in second-growth forests.

5. Remnant trees in the pastures can provide a rich habitat where bryophyte species can be conserved. However, some agroforests, such as the cacao agroforest, are unable to provide this role (Andersson & Gradstein 2005).
6. Some bryophyte species can serve as indicators of land-use change at the local and regional scales, but not at larger scales. Qualitative and quantitative study of life forms and ecological groups of epiphytic bryophytes promise to provide bioindication of land-use change and rainforest disturbance in the tropics.

Fragmentation Effects

Deforestation is creating forest fragments in many areas of the tropics (Figure 1). Zartman (2003) discussed the effects of this habitat fragmentation on epiphyllous bryophyte communities in central Amazonia. He found that regionally common taxa are often reduced in epiphyll diversity in small fragments. On the other hand, rare taxa are often more abundant in fragments than in continuous forest habitat. Larger fragments (100 ha) exhibit higher species richness, abundance, and among site variation than do the smaller fragments (1 & 10 ha).

Silva and Pôrto (2009) assessed effects of fragmentation on bryophytes of decaying logs in the Atlantic Forest remnants in northeastern Brazil. They identified 99 bryophyte species (52 liverworts, 47 mosses). They determined that fragment size is important in determining the community structure on decaying logs. They did not find a correlation between distance from forest edge and bryophyte richness or cover, suggesting that the relationship is non-linear.

Zartman and Shaw (2006) consider the demographic mechanisms causing species loss in the tropics to be greatly under-explored. To contribute to the understanding of the impact of fragmentation, they chose the epiphyllic leafy liverworts ***Radula flaccida*** (Figure 50) and ***Cololejeunea surinamensis*** (see Figure 51). They transplanted these two species to study sites with areas ranging 1, 10, 100, up to 110,000 ha. All the transplants exhibited significantly positive local growth with a nearly constant per-generation extinction probability of 15%. In reserves of 100 ha or greater, the colonization rate nearly doubled (to 48%) compared to small reserves (27%). They considered this an indication that epiphyll loss in small fragments was due to reduced colonization.

Figure 50. ***Radula flaccida*** habit with gemmae. Photo by Michaela Sonnleitner, with permission.

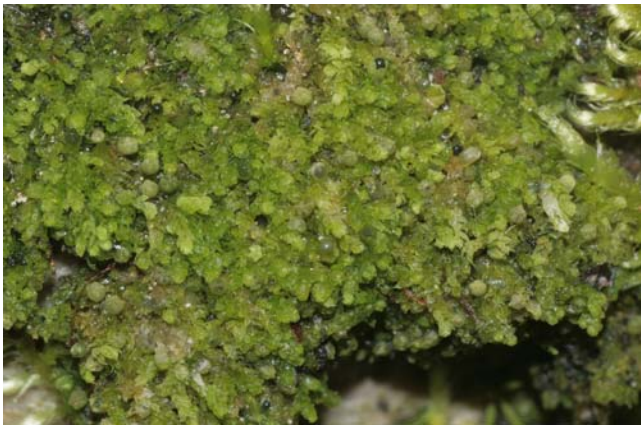

Figure 51. ***Cololejeunea calcarea***; ***Cololejeunea surinamensis*** reproduces more frequently by fragments in larger forest fragments. Photo by Hermann Schachner, through Creative Commons.

Bryophytes have relatively fast colonization and extinction rates, making them ideal study organisms for the effects of forest fragmentation (Pharo & Zartman 2007). Nevertheless, they are limited by dispersal, and this somewhat random process helps to explain their observed recolonization patterns.

Nevertheless, edge effects have an impact on community structure, especially where these create abrupt differences in microclimate. Establishment experiments repeatedly indicate dispersal limitation to explain the absence of typical forest species in fragmented habitats (Zartman & Nascimento 2006; Gunnarsson & Söderström 2007).

Younger fragments (<25 yrs), in particular, have lower richness and different species composition than adjacent mature forests (Pharo *et al*. 2004). Similarly, Snäll *et al.* (2003) found that age of the trees is more important than size for the moss ***Orthotrichum*** (Figure 52) on aspen (***Populus***; Figure 53) trees. Older trees support larger colonies.

Figure 52. ***Orthotrichum*** sp. on bark; on aspen trees, age of tree is more important than tree size. Photo by Algirdas, through public domain.

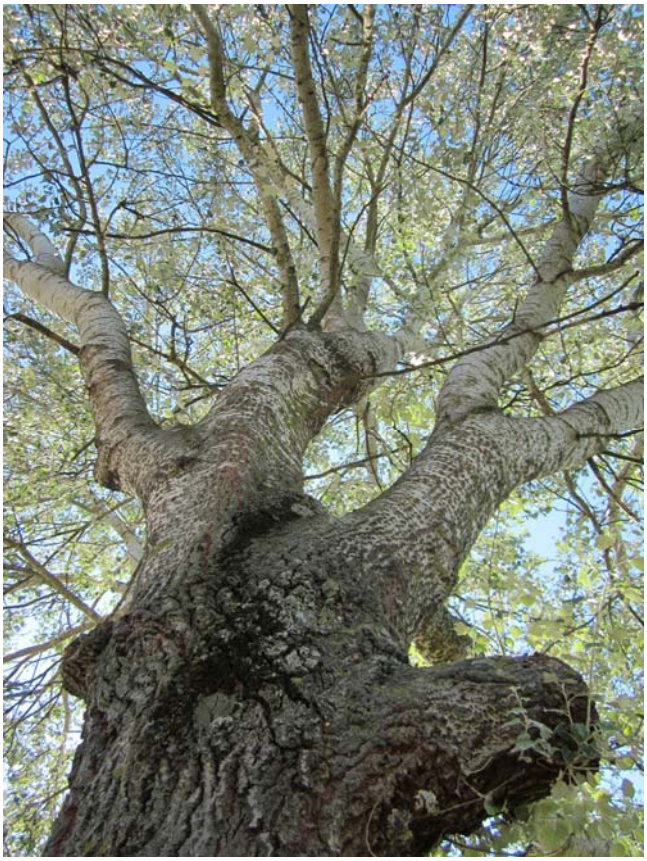

Figure 53. ***Populus*** bark showing old and young parts of the tree. Photo through public domain.

In southern Veracruz, Mexico, the number of epiphytic tracheophyte species per tree and total estimated biomass correlate most with tree size, measured as diameter at breast height (Hietz-Seifert *et al*. (1996). When considering this relationship, the number of epiphytes on remnant trees is similar to that in the forest plots. However, the forest plots still differ significantly from each other, a response Heitz-Seifert and coworkers considered might be due to differences in humidity. The number of epiphytes on isolated forest tree species exhibit a negative correlation with distance from the forest border. The researchers also considered that some of the differences exhibited by the remnant trees, which included many figs, may have been due to the attraction of birds and bats that could contribute to seed dispersal. Although the importance of various environmental variables differ between bryophytes and tracheophytes, some of these same variables may affect both, and destruction of bryophytic epiphytes can affect the success of tracheophytic epiphytes and *vice versa*.

In open, disturbed areas in the Amazonian Andes of northern Peru, contrasting with the larger life forms of the forests, the disturbed and exposed areas comprising secondary forests are characterized by **short turf**-forming acrocarpous mosses that have a **colonist life strategy**, a life form not typically found within the developed forests (Kürschner & Parolly 1998; Kürschner *et al*. 1999).

Visnadi (2018) examined fragmented vegetation in Brazil by assessing the bryophytes in seven urban parks in São Paulo. As we might expect, those parks with different types of environments had greater species richness. More densely wooded neighborhoods with colder termpratures supported the richest bryoflora. Even one vulnerable species, ***Metzgeria hegewaldii***, and two endemic species (***Fissidens pseudoplurisetus*** - Figure 54 and ***Pterogoniopsis paulista***) occurred in some of these fragments.

Figure 54. ***Fissidens pseudoplurisetus***, a species endemic to Brazil and found in environmental fragments such as parks. Photo by Juçara Bordin, with permission.

Harvesting

Deforestation isn't the only human danger. Harvesting of bryophytes for commercial use likewise can endanger the bryophytes (Peralta & Wolf 2001). In addition to many Neotropical areas, in India, Japan, and China mats of mosses are peeled from their substrates for use in the horticulture industry (Wuethrich 1993; Peck 2006; Peck & Moyle Studlar 2008). These can greatly reduce cover on the reachable branches and logs.

In the monarch butterfly biosphere reserve, Sierra Chincua, Michoacan, Mexico, mats of bryophytes are harvested, packed, and sold in Mexico City for ornamental use. One family alone (about 10 members) harvested 50 tons (fresh weight) of bryophytes in one collecting season. This created a mosaic of gaps of bare soil in the mossy layer, with an average gap size of 0.48 m^2. This moss removal consequently caused the removal of 11,000 ***Abies*** (fir) seedlings that were growing with the mosses.

In the montane tropical oak-bamboo forests in Costa Rica, pendent bryophytes are a locally valuable resource subject to commercial harvesting (Romero 1999). Thus, logging that destroys the habitat of these taxa is of local concern. These harvestable bryophytes include the mosses ***Pilotrichella flexilis*** (Figure 55-Figure 56), ***Phyllogonium viscosum*** (Figure 57), ***Zelometeorium*** sp. (Figure 58), and ***Squamidium leucotrichum*** (Figure 59) and the leafy liverworts ***Frullania convoluta*** (Figure 60) and other ***Frullania*** species. These pendent life forms are important in water interception and thus might be expected to have an important effect on the hydrological balance in these forests. However, nine years after careful selective logging in a montane oak-bamboo forest, there were no detectable negative impacts on the biomass of these bryophytes at commercially available heights (1-3 m). Unfortunately, there is no comparable study in Costa Rica to show the

impact of bryophyte harvesting on their successful return. In Africa, Jacobsen (1978) found that epiphytes require a minimum of 7-10 years to regenerate after harvesting from the forest.

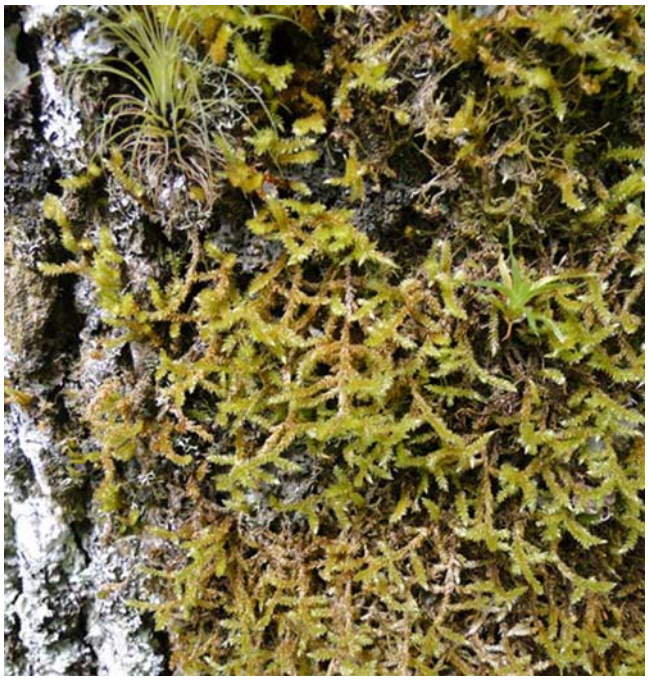

Figure 55. ***Pilotrichella flexilis nudiramulosa***, a pendent bryophyte that is used locally in Costa Rica as a forest product. Photo by Claudio Delgadillo Moya, with permission.

Figure 56. Close view of ***Pilotrichella flexilis***, a pendent bryophyte that is used locally in Costa Rica as a forest product. Photo by Claudio Delgadillo Moya, with permission.

Figure 57. ***Phyllogonium viscosum***, a pendent bryophyte that is used locally in Costa Rica as a forest product. Photo by Jan-Peter Frahm, with permission.

Figure 58. ***Zelometeorium patulum*** from the Neotropics, a pendent bryophyte in a genus that is used locally in Costa Rica as a forest product. Photo by Michael Lüth, with permission.

Figure 59. ***Squamidium leucotrichum*** from the Neotropics, a pendent bryophyte that is used locally in Costa Rica as a forest product. Photo by Michael Lüth, with permission.

Figure 60. ***Frullania convoluta***, a pendent bryophyte that is used locally in Costa Rica as a forest product. Photo by Jan-Peter Frahm, with permission.

Industrialization and Air Pollution

In addition to habitat loss, pollutants can destroy canopy bryophytes. Bryophytes are scavengers of atmospheric nitrogen as they collect the dust from the atmosphere. In this way, they are able to serve as bio-indicators of nitrogen pollution. Shi *et al*. (2017) examined epiphytic bryophytes from a subtropical montane cloud forest in southwest China. The critical load of nitrogen deposition there was estimated at 18 kg N ha^{-1} yr^{-1}. The bryophytes become nutrient pools in these circumstances. These high levels are detrimental to the bryophytes, with a significant decrease in cover when the nitrogen input is only 7.4 kg ha^{-1} yr^{-1}. The study site had a nitrogen deposition rate of 10.5 kg ha^{-1} yr^{-1}. The researchers suggested that the high N levels not only did direct damage, but caused the leakage of magnesium and potassium, both essential nutrients for cellular metabolism.

Escocia Ariza (1998) reported losses of epiphyllous and epiphytic bryophyte species in the 20th century. The industrial district in particular has lower coverage, sexual reproduction, diversity, and a lower index of community vigor. **Chlorosis** (loss of green color of chlorophyll) indicates stress. ***Lejeunea trinitensis*** (Figure 61) emerged as a stress-tolerant species, whereas ***Leptolejeunea exocellata*** (Figure 62) is a sensitive species that disappears from the industrialized area. The species present in the polluted area are **colonists**, particularly on rocks. The colonization is a slow process. Species with both sexual and asexual reproduction are more successful at establishment.

Figure 61. ***Lejeunea trinitensis***, a stress-tolerant species. Photo by Scott Zona, through Creative Commons.

Figure 62. ***Leptolejeunea elliptica***; ***L. exocellata*** is a stress-intolerant species. Photo by Yang Jia-dong through Creative Commons.

Figure 63. ***Usnea*** from Cumbre Vieja, Canary Islands, a genus used locally in Costa Rica as a forest product. Photo by Fährtenleser, through Creative Commons.

Figure 64. *Usnea barbata*, a fruticose lichen with higher accumulations of Cd, Cu, Pb, and Zn levels than surrounding tracheophytes. Photo from MO Observers, through Creative Commons.

Figure 65. *Huperzia selago*, a tracheophyte with less accumulation of Cd, Cu, Pb, and Zn than the associated moss and lichen tested. Photo by Malcolm Storey, DiscoverLife, with online permission.

Vareschi (1953) was one of the earliest researchers on tropical air pollution in Venezuela. These studies were actually the reverse of most, looking at the influence of the forests and parks on the air quality of the city of Caracas. Rebelo *et al*. (1995) reported on the epiphytic bryophyte communities under the effects of air pollution in Brazil.

In 1992, Durán *et al*. used the Index of Air Purity (IAP) to evaluate the responses of epiphytic mosses to air pollution in Mexico City, Mexico. They were able to demonstrate a significant negative correlation ($p<0.5$) between these IAP values and SO_2, NO_2, NO_x, and Pb (lead). On the other hand, there were significant positive correlations with ozone. This relationship is manifest in the gradual decrease in frequency and cover of epiphytic mosses in Mexico City.

Bryophytes in temperate zones are well known for their ability to accumulate heavy metals (*e.g.* Faus-Kessler *et al*. 2001). But the behaviors of tropical bryophytes are less well known. Based on many temperate studies showing that bryophytes were good accumulators of heavy metals, Lisboa and Borges (1995) examined the potential use of bryophyte diversity as an indicator of pollution in Belém, in the lower Amazon region of Brazil.

Jayasekera and Rossbach (1996) conducted one of the few tropical species to address this issue. They examined background levels of heavy metals and their differences in plants of different taxonomic groups, including bryophytes, in a montane rainforest in Sri Lanka. They found that when a lichen (*Usnea barbata*; Figure 63-Figure 64), an epiphytic club moss (*Huperzia selago*; Figure 65), an epiphytic fern (*Pleopeltis lanceolata*; Figure 66), an epiphytic orchid (*Bulbophyllum elliae* (see Figure 67), a large dicotyledonous tree (*Actinodaphne ambigua*; see Figure 68), and a moss [***Pogonatum*** sp. (Figure 69)] were compared for their heavy metal content, the levels were essentially homogeneous for Cd, Cu, Pb, and Zn. The moss ***Pogonatum*** had the highest degree of homogeneity for lead. The primitive taxa, the lichen *Usnea* and moss ***Pogonatum***, seem to have higher accumulation levels of As, Cd, Co, and Pb than do the tracheophytes.

Figure 66. ***Pleopeltis lanceolata***, a tracheophyte with less accumulation of Cd, Cu, Pb, and Zn than the associated moss and lichen tested. Photo by Robbin Moran, with permission.

Figure 67. *Bulbophyllum guadense*; *Bulbophyllum elliae* is a tracheophyte with less accumulation of Cd, Cu, Pb, and Zn than the associated moss and lichen tested. Photo by USDA & GPEPP, through Creative Commons.

Faus-Kessler *et al*. (2001) used biannual collections of epiphytic ***Hypnum cupressiforme*** (Figure 70) to determine changes in accumulations of trace metals.

Figure 68. *Actinodaphne angustifolia*; *Actinodaphne ambigua* is a tracheophyte with less accumulation of Cd, Cu, Pb, and Zn than the associated moss and lichen tested. Photo by Dinesh Balke, through Creative Commons.

Figure 69. ***Pogonatum urnigerum***, a species that has a high degree of homogeneity for absorbing lead. Photo by David Holyoak, with permission.

Figure 70. ***Hypnum cupressiforme***, a species used for determining accumulations of trace metals. Photo by Aconcagua, through Creative Commons.

On the other hand, bryophytes have been used to help clean the air and remove pollutants (Vareschi 1953). Bryophytes greatly expand the available surface area for trapping and immobilizing both water and ions from the atmosphere (Coxson 1991).

Radiation

Although the studies on radiation effects on tropical bryophytes are limited, the extensive study at El Verde, Puerto Rico (Figure 71), did include bryophytes (Odum *et al*. 1970). High levels of radiation fallout retention were present in the epiphytic mosses in the mossy forest (Figure 72) of the Luquillo Mountains in 1962. The algae-moss-liverwort encrustations had the highest levels of radiation, with massive moss colonies being second. Bromeliads and rooted plants had less. Radioactivity in tree leaves was in proportion to the epiphyllous growths on them, and that growth was related to leaf age.

Figure 71. Rainforest of El Yunque, Puerto Rico, where the El Verde radiation study site is located. Photo by Alessandro Cai, through public domain.

Figure 72. Elfin forest at the Luquillo Mountains, Puerto Rico. Photo by Janice Glime.

Man-made Habitats

Many forested areas have been replaced by man-made habitats. These provide greater variety in available habitats. In the tropics, one can find ***Diplophyllum obtusatum*** (Figure 73), ***Solenostoma sphaerocarpum*** (Figure 74), and ***Schistochilopsis incisa*** (Figure 75) in man-made habitats (Gradstein & Vána 1987). It appears that these Laurasian species have spread relatively recently through human activities.

Figure 73. ***Diplophyllum obtusatum***, a species that thrives in man-made habitats. Photo by Paul Davison, with permission.

Figure 74. ***Solenostoma sphaerocarpum***, a species that thrives in man-made habitats. Photo by Michael Lüth, with permission.

Figure 75. ***Schistochilopsis incisa***, a species that thrives in man-made habitats. Photo by Michael Lüth, with permission.

In Alto Beni, Bolivia, corticolous bryophytes on trees in the primary rainforest decreased significantly in the

fallows as measured after 4-15 years (Cabby *et al*. 2003). But liverwort diversity barely changed except in the 4-year-old forest. **Smooth mats** had a significantly higher percentage (72%) in the fallows, perhaps due to the warmer, drier microclimate. But even in the 10-15-year-old fallows, only about half the species had returned, mostly generalists and sun epiphytes. Whereas species richness is highest in the undisturbed canopy, in the fallows it is highest in the understory, with **rough mats**, **fans**, and **tails** shifting to lower heights on the trees, most likely due to changes in air temperature an air humidity.

If sufficient natural forest is retained, artificial forests can increase the diversity by providing new niches. Petit and Symons (1974) reported 28 bryophyte species from 17 artificial woodlands planted with *Cupressus* (Figure 76-Figure 77) and *Acacia* (Figure 22) in Burundi, Africa. In these woods, the litter layer is covered with bryophytes and the flowering plants are almost absent.

Figure 76. ***Cupressus lusitanica*** (=***Hesperocyparis lusitanica***) cones; this species is the most commonly harvested *Cupressus* species in Burundi. Photo from Wikimedia, through Creative Commons.

Figure 77. ***Cupressus lusitanica*** (=***Hesperocyparis lusitanica***) being harvested in Uganda. Photo by J. D. Ward, USDA Forest Service, <Bugwood.org>, through Creative Commons.

Sillett *et al*. (1995) compared bryophyte diversity in ***Ficus*** tree crowns from the cloud forest and a pasture in Costa Rica. In the lower montane wet forest, they found 127 bryophyte species (50 mosses, 76 liverworts, 1 hornwort) in the inner crowns of only six ***Ficus tuerckheimmi*** trees. Of these, 52 were found only in the intact forest, whereas only 18 species occurred exclusively in the isolated trees of the pasture. One of the factors contributing to the differences was a moisture gradient that diminished away from the intact forest.

In the northern Andes, roadside habitats in humid locations can be invaded by canopy liverworts from the montane forest (Gradstein 1992b). These include such liverwort species as ***Dicranolejeunea axillaris***, ***Frullania brasiliensis*** (Figure 78), ***Frullania convoluta*** (Figure 60), ***Frullanoides densifolia*** (Figure 79), ***Herbertus acanthelius*** (see Figure 80), ***Jamesoniella rubricaulis*** (Figure 81), ***Omphalanthus filiformis*** (Figure 82), and ***Taxilejeunea pterigonia*** (see Figure 83). In such locations these liverworts behave as pioneers.

Figure 78. ***Frullania brasiliensis***, a species that inhabits wet roadside habitats in the northern Andes. Photo by Germaine A. Parada, through Creative Commons.

Figure 79. ***Frullanoides densifolia***, a species that inhabits wet roadside habitats in the northern Andes. Photo by Jan-Peter Frahm, with permission.

Figure 80. ***Herbertus*** sp., Oahu, Hawaii; ***Herbertus acanthelius*** inhabits wet roadside habitats in the northern Andes. Photo by David Eickhoff, with online permission.

Figure 81. ***Jamesoniella rubricaulis***, a species that inhabits wet roadside habitats in the northern Andes. Photo by Jan-Peter Frahm, with permission.

Figure 82. ***Omphalanthus filiformis***, a species that inhabits wet roadside habitats in the northern Andes. Photo by Michael Lüth, with permission.

Figure 83. ***Taxilejeunea*** sp. from the Neotropics; ***Taxilejeunea pterigonia*** inhabits wet roadside habitats in the northern Andes. Photo by Michael Lüth, with permission.

Climate Change

Benzing, in 1998, stressed the vulnerabilities of tropical forests to climate change, and even more so to that of their bryophytic inhabitants. Noting the complexity of these systems, he pointed to the narrow set of circumstances that define the habitats for these bryophytes. This raises the concern of their often underestimated role in both hydrology and mineral cycling, added to their ability to support a wide diversity of smaller organisms such as salamanders, arthropods, fungi, and micro-organisms, making them major contributors to the ecosystem. Yet their vulnerability in tropical forests under climate change is great.

Many bryophytes in the tropics are approaching their limits of tolerance to the high temperatures that increase their rate of respiration (see Microclimate above). Hence, as considered by Zotz and Bader (2009), "rising temperatures could have disastrous effects." Moving farther away from the equator may provide a refuge for some species, but the authors suggest that epiphytes may be "particularly threatened" because the cloud forest habitats are likely to be the most seriously affected. And these are species-rich habitats where "exceptional" species occur. They furthermore are often isolated, requiring long-distance dispersal to reach a suitable climate.

Durán *et al*. (1992) used the IAP values to demonstrate that higher rainfall and relative humidity helped to account for higher bryophyte diversity values. Climate changes can affect these parameters, making some areas drier. Furthermore, bryophyte IAP values exhibit a negative correlation with temperature.

Climate change studies in the tropics are of utmost importance in a region where many species are already limited by temperature. Jácome *et al*. (2011) summarized what we know about the effects on the epiphytic bryophyte communities of simulated climate change in the tropics. Based on a translocation experiment in the upper montane forest in Bolivia they showed that exposure to air temperature increases of 1.5-2.5ºC had a measurable effect on the structure of epiphytic bryophyte communities of the tropical montane forest within two years. The results confirm the sensitivity of non-tracheophytic epiphytes to

atmospheric changes and predict that changes in the climatic regimes of tropical montane forests will rapidly affect the rich non-tracheophytic epiphyte communities.

Epiphytes seem to be particularly vulnerable to climate change because they must survive "at the interface of vegetation and atmosphere" (Zotz & Bader 2009). Furthermore, land use exacerbates the problem by decreasing the suitability of the environment. On the other hand, some drought-resistant species may benefit. They projected that new assemblages would form among bryophytes and lichens. But rising temperatures can be very destructive for both bryophytes and lichens. This will most likely be most detrimental to the habitats in the tropics with exceptional species richness, in particular, the cloud forests.

Sometimes human interference resulting in local climate change actually helps bryophytes. Kautz and Gradstein (2001) found that the critically endangered ***Spruceanthus theobromae*** (**Lejeuneaceae**; Figure 19) grows on the trunk bases of ***Theobroma cacao*** (Figure 20-Figure 21) in 12 plantations that had minimal management. In fact, the researchers felt that it should instead be considered as a near-threatened species and removed from the World Red List.

Recovery

Hallingbäck and Tan (1996) bemoaned the loss of species worldwide, citing reduction, fragmentation, and isolation of their habitats, in addition to damaging pollution. They noted the value of designating certain bryophytes as key species to protect because of the associated plants and animals that would also be protected. But if areas already impacted are allowed to recover, what can we expect?

Return of bryophytes to remnant forests after logging is slow. In subtropical rainforests of Australia, few bryophytes had returned even 25 years after the disturbance (Chapman & King 1983). The same was true in southeastern Brazil (Costa 1999). In Costa Rica, isolated remnant trees (*e.g.* Figure 84), lacking the dense canopy of the undisturbed forest, had bryophyte diversity reduced by 50% compared to the remaining intact forest.

Figure 84. Tropical montane meadow with remnant tree; undisturbed forest is on the far side of the river in back, San Francisco Reserve, Ecuador, 2000 m asl. Photo courtesy of Robbert Gradstein.

Gradstein and Sporn (2010) found that canopy closure, microclimate, and host tree characteristics are important in determining epiphytic bryophyte diversity. Preservation of the canopy, therefore, is important in maintaining this diversity. Recovery of bryophyte communities after clear-cutting is very slow and may take more than 100 years.

Recovery following deforestation requires the presence of viable plant parts or reproductive units. Olarinmoye (1986), working in Nigeria, examined survival strategies in three species during re-establishment after a period of drought. ***Hyophila involuta*** (Figure 85-Figure 86) is able to re-establish through spores, with its sporophyte production appearing to give it a competitive advantage compared to ***Barbula indica*** (Figure 87) and ***Fissidens asplenioides*** (Figure 88). The latter two species were similarly wide-spread, using vegetative regrowth from rhizoids, shoot bases, apices, or the main stem, with rhizoids contributing the most regrowth.

Figure 85. ***Hyophila involuta***, a species that can recolonize disturbed areas. Photo by Shyamal L., through Creative Commons.

Figure 86. ***Hyophila involuta***, a species that can colonize by spores after disturbance. Photo by M. C. Nair, K. P. Rajesh, and Madhusoodanan, through Creative Commons.

Figure 87. ***Barbula indica***, a species that can colonize deforested areas by vegetative means. Photo by Michael Lüth, with permission.

Figure 88. ***Fissidens asplenioides***, a species that can colonize deforested areas by vegetative means. Photo by David Tng, with permission.

Liu *et al*. (2007) elaborated the species on the forest floor and on the tree trunks in the forest of Heishiding Nature Reserve, Guandong, China. They found that species composition of the mature forest was similar to that of the mixed pine and broad-leaved forest, and to young secondary forest, but community structure of the mature forest was quite different from that of the secondary forest. Most of the bryophytes occurred on the tree trunks (40 species), with only 24 species on the forest floor. Bryophyte cover was low on both substrata. Species richness of forest floor bryophytes in 2,500 m^2 quadrats ranged 8 to 13 with 0.59% to 1.12% cover. Slope and microenvironment were the primary determinants of species distribution and richness on the forest floor. Epiphytes, on the other hand, exhibited 12 to 20 species with a mean cover of 0.63 to 1.63% in these plots. The researchers concluded that bryophytes in 30-year-old secondary broad-leaved forest had returned to the level of the mature broad-leaved forest.

Corrales *et al*. (2010) recorded 151 terrestrial bryophyte species in secondary and planted montane forests in the northern portion of the Central Cordillera of Colombia. Secondary montane forests have a higher weighted species richness than do the pine plantations. Weighted species richness is higher in secondary montane forests and cypress plantations than in pine plantations. Cypress plantations have the highest bryophyte abundances, although Detrended Correspondence Analysis indicates a high floristic similarity among the various forest types. Differences seem to relate to soil *p*H, slope, and light availability. Regional patterns depend on continuous dispersal of propagules.

Serrano (1996) found 37 species of mosses in 25 genera in disturbed areas in the municipality of Bayamon, Puerto Rico. ***Fissidens*** is the most species-rich genus. The most frequent of all species is ***Fissidens zollingeri*** (see Figure 88), occurring at all study sites. It is an indicator of disturbed areas. Urbanization further reduces the number of species present. One mechanism accounting for the spread of the species is spore production. Of the 37 species, 18 were observed with capsules and these species tended to occur more frequently when their sporophytes were more frequent. Only 7 species exhibited special vegetative reproductive structures. Among the pleurocarpous species, those with the greatest frequency in collections were those colonizing the greatest number of substrates.

Conservation Issues

Gradstein (1992a, b) and Pócs (1996) emphasized that conservation of epiphytes "can only be achieved through the rigorous protection of the forests."

Hallingbäck and Hodgetts (2000) contend that the negative impact of habitat loss has already gone too far in the tropical lowlands. Forested land has been cleared continuously for the expansion of the human population and the agriculture to support it (Hyvönen *et al*. 1987).

Hodgetts *et al*. (2016) raised concern about the very diverse tropical Atewa Forest in the Eastern Region of Ghana. This area is highly threatened by human activities, including illegal mining, farming, and hunting, as well as thread from industrial bauxite mining. Little is known of its bryophyte flora, and it could be lost before it can be explored adequately. A single survey in March 2014 revealed 164 species, with 58 new to Ghana and 1 new to science.

Costa and Faria (2008) noted conservation priorities for bryophytes in the state of Rio de Janeiro, Brazil. Recognizing the high degree of biological diversity, with an estimated 1,040 species of bryophytes, they cautioned that most of the inventories have focussed on the montane rainforest and coastal region. Among those bryophytes that have been recorded, 14% are considered vulnerable or threatened in the region. They considered the old-growth Atlantic forests (Figure 89) to be among most important habitats needing conservation, citing reduction, fragmentation, and isolation as causes for concern. Although 13% of the land area of the state is protected,

these protected areas are mostly montane and upper montane Atlantic rainforests.

Figure 89. Atlantic Forest, Antonina Bay, Brazil. Photo by Deyvid Setti and Eloy Olindo Setti, through Creative Commons.

As already noted, Jacobsen (1978) found that epiphytes require a minimum of 7-10 years to regenerate after harvesting of the forest. In any case, deforestation leads to local extinction of species (Gradstein 1992b). Shade epiphytes are the most easily affected by disturbance.

The International Association of Bryologists has representation on the IUCN (International Union for Conservation of Nature). To quote Söderström *et al*. (1992), "The conservation process involves recognizing and listing rare and decreasing species, recording their distribution, biology and specific threats, proposing conservation programmes, and executing these programmes." But they point out that the large gaps remaining in our knowledge about bryophytes complicate conservation practices. They list areas needing further study, including taxonomy, bryogeography, habitat demands, natural dynamics, dispersal ability, population structure, and genetics. They stress the importance of focussing on conservation of habitats and sites where species can survive on their own.

In this regard, Villaseñor *et al*. (2006) gathered data on the rich moss and *Senecio* (Figure 90) flora in the Trans-Mexican volcanic belt. They were able to identify 11 hotspots that are beneficial to the rich species composition of both groups. They conclude that 18 "cells" in this range would conserve the total diversity of both mosses and *Senecio* species in these species-rich hotspots. It is important that we identify such hotspots and find ways to conserve them.

Figure 90. ***Senecio toluccanus***, a common species of the Trans-Mexican volcanic belt. Photo by Juan Carlos Pérez Magaña, through Creative Commons.

Twenty years ago, our knowledge of tropical bryology was quite meager, making conservation efforts problematic. Sastre de Jesus and Tan (1995) noted the problems in Puerto Rico and the Philippines. As noted by Streimann (1994) for Australia, conservation programs must be preceded by a good knowledge of the bryophytes. In absence of those data, he recommended that at least for those areas that are poorly known for bryophytes, those areas conserved for vascular plants, including national parks and forest reserves, would in most cases be adequate to conserve bryophytes as well.

The bryophyte flora of Mexico was somewhat better known, with more than 900 species, including 98 endemic taxa (Delgadillo 1996). Even so, many areas still need to be explored. Meanwhile, habitat destruction may be destroying some taxa forever. Delgadillo bemoaned the fact that there still was no legislation to protect the habitats of any Mexican mosses.

As in Mexico, moss diversity in the tropical Andes is extensive, with 2,058 species known in 1995. Although this number is probably inflated due to the same species being named multiple times in different locations, the presence of 343 genera and 75 families is still an indicator of the high diversity. Churchill *et al*. (1995a) estimate the

actual number to be 1,500-1,700 species. They contended that the tropical Andes are eight times as rich in moss species as the Amazon basin. Churchill (1996) summarized the status of our knowledge of moss diversity and conservation in the Andes, noting the needs to prepare for the future. But one of the problems with conserving bryophytes in Neotropical cloud forests (Figure 47) is that they are typically surrounded by xeric habitats unsuitable for their survival (Churchill *et al*. 1995b).

Holz and Gradstein (2005) considered that genera and species of bryophytes and macrolichens that are exclusive to the primary (uncut) forests could be used as indicator taxa and that these species and their forests should be conserved.

In French Guiana, water availability affects the bryophyte life forms. When Pardow *et al*. (2012) compared the life forms of the lowland cloud forests with those of the other lowland forests, they concluded that life forms could indicate lowland cloud forests that are appropriate for conservation. This would permit conservation of a rich bryophyte flora with higher biomass and cover.

With 1,000 epiphyllous liverworts worldwide, these tiny plants represent a group that is also endangered worldwide (Pócs 1996). Of these, 504 are in Asia and 375 in the Americas. They are by far the most species rich in the tropical and subtropical rainforests, but as these forests disappear, so do the epiphylls.

Climate change studies in the tropics are of utmost importance in a region where many species are already limited by temperature. Jácome *et al*. (2011) summarized what we know about the effects on the epiphytic bryophyte communities to simulated climate change in the tropics.

Newer tools may help us to process the data in meaningful ways to understand environmental impacts. In summarizing the symposium and priorities for future research, presented at the first IAB and IAL Symposium on Foliicolous Cryptogams, Gradstein and Lücking (1997) noted that multivariate statistical methods were useful in analyzing the foliicolous community data.

With the inevitability of global climate change, bryophytes living in tropical mountain habitats are clearly in danger. Zhang (2001) found a linear increase in number of species per forest plot with an increase in altitude. As those areas become warmer, those species may not have the time needed for significant dispersal to distant areas with a similar cool climate.

Gradstein and Pócs (1992a) advised that protection of as much as possible of the remaining natural tropical rainforest area seems the best approach to the conservation of the tropical bryophyte flora. This seems to be working in the Wet Tropics of northern Queensland, Australia.

Current Status

In 1982, Schultze-Motel referred to the crisis in tropical bryology. Part of this crisis is the loss of habitats and species before we have even explored to determine what is there to be lost. Even worse, we know little of their role in these sensitive, disappearing ecosystems, even today.

In 1992, Motito *et al.* recognized the need for bryological study in Cuba (Figure 91). At that time 383 infrageneric bryophyte taxa were known, and studies had begun on phytochemistry and antibiosis. However, it seems that little progress has been made since then on protection of species or of understanding their ecology.

Figure 91. Montane moist forest, Pico Turquino, Cuba. Photo by Male Gringo, through Creative Commons.

In Brazil, biological diversity is high, particularly in the state of Rio de Janeiro (Figure 92). In this area, there are many bryophyte endemics with a total species number estimated at ~1,040 species. Of these, 150 species are classified as vulnerable or threatened. Unfortunately, many of the 1,040 species are in the "data deficient" category, so their abundance is not known, nor do we know what conditions are needed to maintain them. Fortunately, almost 13% of Rio de Janeiro is protected land, but it is mostly in the montane and upper montane Atlantic rainforests. The remaining old-growth Atlantic rainforests are in need of greater conservation.

It appears that the Wet Tropics of Australia may be among the best protected areas with rare and endemic species (Streimann 2000). Most of these areas are in national parks, national estates, world heritage sites, and flora reserves. Evenso, they are impacted by tourism.

Figure 92. Rio de Janeiro Tijuca Forest, Brazil. Photo by Pierre André, through Creative Commons.

Summary

Natural disturbances such as El Niño, hurricanes, fire, volcanoes, and animal activity can dislodge bryophytes or provide conditions unsuitable to their continued growth. Some rare and threatened species thrive in these altered conditions, but in general these are potential sources of species losses.

Disturbance is a major cause of loss of species and populations in the tropics. Approximately half of the bryophyte taxa lost on fallow land can become re-established in 10-15 years; most of these are ecological generalists and sun-loving epiphytes. For others it can take 100 years. Sufficient fragment size is important in maintenance and re-establishment of species.

The highest diversity of the fallows is in the understory, contrasting with the highest richness in the canopy of the uncut rainforest. This difference is the result of light penetration, and in some cases moisture.

Human harvesting of bryophytes for horticulture and other human uses not only reduces the bryophyte cover, but also removes habitat for numerous invertebrates and many amphibians.

Industrialization can raise nitrogen levels beyond the limits of tolerance. Heavy metals accumulate in the bryophytes and an reach lethal levels. On the other hand, the bryophytes can serve as filters to remove these pollutants from the air, in some cases after the bryophytes die.

Man-made habitats displace natural habitats, but they do increase the number of niches. Some species thrive in these new niches. For example, the leafy liverwort ***Spruceanthus theobromae*** is currently known from the bark of cacao on plantations.

Many bryophytes have narrow temperature, light, and moisture requirements. Changing climate can not only destroy the forests where they live, but change the microclimate so that it is no longer suitable for them.

Bryophyte recovery can take a long time. In particular, those species living on mountain tops may not have any suitable propagule source without intervening unsuitable habitats. Even in restored lowland rainforests, recovery of bryophyte diversity can require more than 100 years.

The most pressing issues seem to be massive losses of habitat due to agriculture and forestry management for trees only. But climate change is likely to be a close second in the loss of tropical bryophytes in the tropics.

Current practices are beginning to recognize that some species can be conserved by maintaining larger fragments, keeping more trees where trees are cut, and designating more land to conservation.

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CHAPTER 18-1
CAVES – THE ENVIRONMENT

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CHAPTER 18-1
CAVES – THE ENVIRONMENT

Figure 1. Stalactite, stalagmite, and column formations in Avshalom Cave, Israel. Photo by Sir Joseph, through Creative Commons.

Caves

Traditional definitions of caves note such characteristics as perpetual darkness, environmental stability, and oligotrophy, characters that apply to large cavities (**macrocaverns**) in rocks (Moseley 2009a). Moseley attempted to provide an ecological definition of a cave. But he did this from an animal perspective, and thus light mattered less than for bryophytes. By definition, macrocaverns, mesocaverns, and microcaverns differ from each other only in magnitude (*i.e.* scale). Because these caves differ in more characteristics than size, particularly in view of the habitat needs of the inhabitants, we should more properly refer to subterranean habitats.

Schuster (1958) noted that bryophytes are able to survive in small niches or "pockets" because of their small size, causing them to be limited by their microenvironment rather than the macroenvironment. Thus, we can find unique communities in caves, no matter how small the cave may be (see Schade 1917; Clausen 1952).

Terminology

Caves bring with them a set of terminology that is unfamiliar in other contexts. Some are necessary to understand the relevant literature.

Caves themselves, typically known as underground or subterranean habitats, have a number of other names, including **alcove**, **antre**, **cavern**, **cavity**, **chamber**, **den**, **dugout**, **gallery**, **grotto**, **hollow**, **pothole**, **recess**, **rock shelter**, **subterrane**, and **tunnel**. As a synonym of sinkhole (Figure 2), **doline** (Figure 3) or **dolina** refers to shallow, usually funnel-shaped depression of ground surface formed by solution in limestone regions.

Figure 2. Sinkhole with bryophytes in Wilson County, Tennessee, USA. Photo by Brian Stansberry, through Creative Commons.

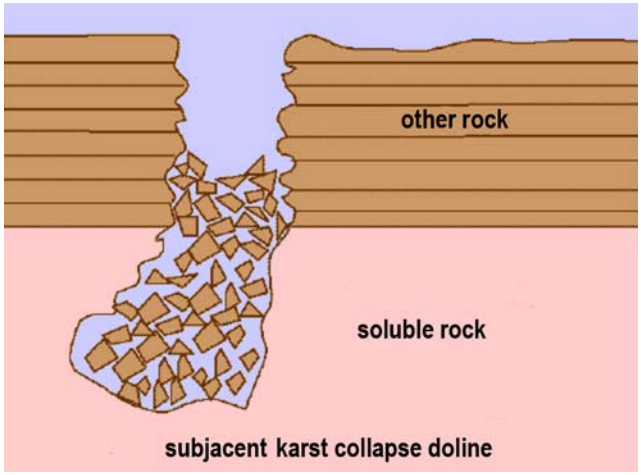

Figure 3. Doline diagram by B.Z. Saylor, MIT, <oeit.mit.edu>.

Terms Used to Describe Caves

algific: cold producing

algific cave: subterranean cave that vents cold air; Figure 4

Figure 4. Algific talus slope with vent northeastern Iowa. Photo courtesy of Beth Lynch.

column: formed by union of stalagmite and stalactite; Figure 5, Figure 6

Figure 5. Travertine dripstone columns, San Salvador Island, Bahamas. Photo by James St. John, through Creative Commons.

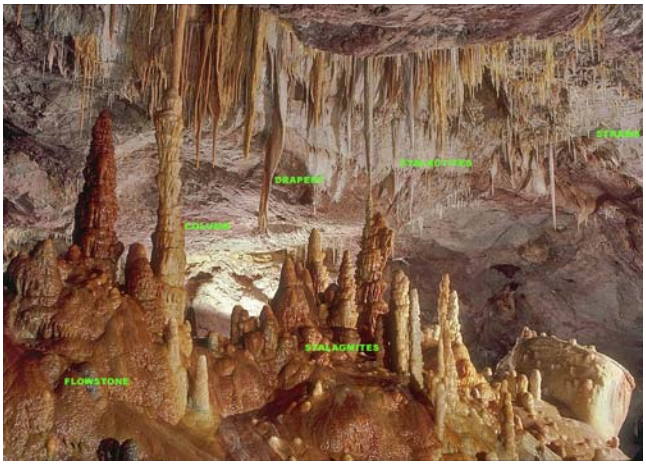

Figure 6. Labelled speleothems. Photo by Dave Bunnell, through Creative Commons.

flowstone: rock deposited as thin sheet by precipitation from flowing water; Figure 6, Figure 7

Figure 7. Travertine flowstone and draperies, Diamond Caverns, Kentucky. Photo by James St. John, through Creative Commons.

helictite: distorted form of stalactite, typically resembling twig; usually made of needle-form calcite and aragonite; Figure 8-Figure 9

Figure 8. Helictites at Treak Cavern, Derbyshire, UK. Photo by Bill Lion, through Creative Commons.

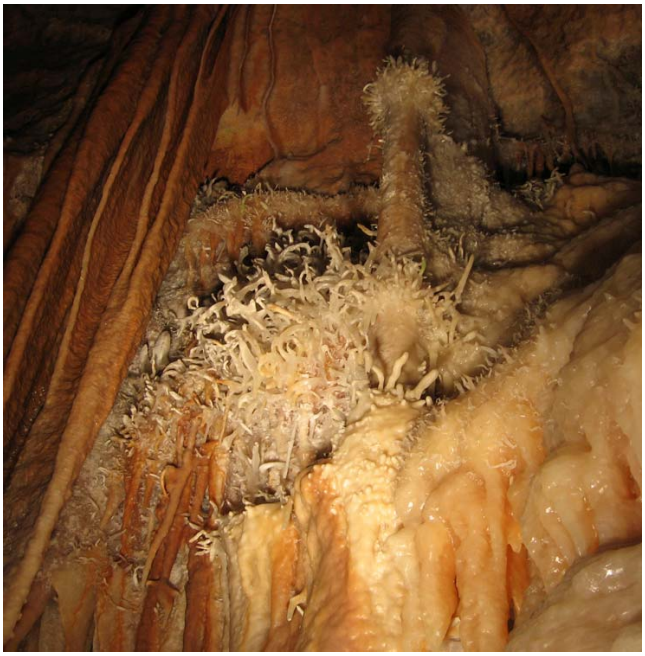

Figure 9. **Helictites** at Jenolan Caves, Australia. Photo by Jason 7825, through Creative Commons.

soda straws: speleothem in form of hollow mineral cylindrical tube; tubular stalactites; Figure 6, Figure 10

Figure 10. Travertine soda straw stalactites in dolostone, Crystal Cave, Wisconsin, USA. Photo by James St. John, through Creative Commons.

speleothem: structure formed in cave by deposition of minerals from water, *e.g.* stalactite or stalagmite; Figure 6

stalactite: type of cave structure, hanging from cave **c**eiling, formed by deposition of minerals from water (stala**c**tites have to hang on tight; they form on the **c**eiling); Figure 1, Figure 6

stalagmite: type of cave structure, projecting from cave floor, formed by deposition of minerals from water dripping from ceiling (**stalagmites** are little mites; they form on the **g**round); Figure 1, Figure 6

talus: broken rock; Figure 11

Figure 11. **Talus slope** at Ruby Mountains. Photo from USGS, through public domain.

Moseley (2009a) defined cave dwellers, based on animals that live in caves. Various authors have used the same terms to describe bryophyte cave dwellers.

1. **Troglobites:** Obligate cavernicoles: species that can survive only in caves.
2. **Troglophiles:** Facultative cavernicoles: species which survive and are able to complete their life-cycle in caves, but also survive and complete their life-cycle in other habitats.

3. **Trogloxenes:** Species found in caves which cannot complete their life-cycles there: a. **Habitual trogloxenes** – Species which habitually frequent caves and thus, whilst not completing their life-cycle there, form a part of the cave community (also called 'regular trogloxenes'). b. **Accidentals** – Surface (**epigean**) species introduced accidentally, *e.g.* by floods, or by straying in.

Moseley (2009a, b) contended that this grouping "lends support to the proposal, recently made elsewhere, that caves can be seen as transitional environments (ecotones) between adjacent hypogean, epigean and/or endogean communities. It also appears to eliminate a number of longstanding conceptual and terminological difficulties, and might offer a rich framework for new understanding of subterranean ecology."

Ecotones

I have seen an analogy that **ecotones** are like a membrane, occupying relatively little space between two constituents. Cave openings have been compared to these ecotones, providing a rapid transition between environmental conditions, *i.e.* between hypogean, epigean, and endogean communities (Moseley 2009a).

Moseley (2009b) considers all caves to be ecotones because they have a "steep environmental gradient between adjacent ecological communities or ecosystems." Within the cave, the ecotonal changes include light levels (Figure 12), temperature (Figure 12), relative humidity (Figure 12), CO_2 concentration, and physical scale. These parameters apply well to large caves and caverns, but would not seem to apply as well to the very small caves between boulders or under ledges. Nevertheless, even these small spaces can have light and moisture gradients. Moseley argues that considering caves as ecotones can change the way we understand the communities we find there. He raises the question of what role "these transitional habitats play in the initial colonization of the subterranean milieu; and in persistence, adaptation and speciation of hypogean organisms." Although Prous *et al*. (2004) and Moseley examine the notion of caves as ecotones using an animal perspective, the ecotone perspective should apply to plant communities as well, particularly the bryophyte communities that respond to varying levels of light (*e.g.* Pentecost & Zhang 2001).

Prous *et al*. (2004) suggested a methodology using a similarity matrix. Prous *et al*. (2015) further elaborated on cave entrances as ecotones, noting that bryophytes were present as far as 30 m into the cave. The depth of light penetration is very much dependent on the size of the opening, the inclination, and the surrounding vegetation and rock formations that can block light entrance to the cave. Prous and coworkers reported "considerable light penetration even at 30 m."

Cave Conditions

Caves typically serve as islands, providing habitats that are isolated from similar conditions outside the cave (Culver 1970). Hence, they can maintain isolated populations of bryophytes that continue to reproduce, mostly asexually. Under this isolation, bryophytes can develop unique genotypes and even cryptic species, as noted already for animals (Moseley 2009a). In fact, Culver (1971) even considered caves to be like archipelagoes. But Culver (1970) pointed out that caves differ from islands by a lack of area effect. Nevertheless, both are subject to effects of time and stochastic processes.

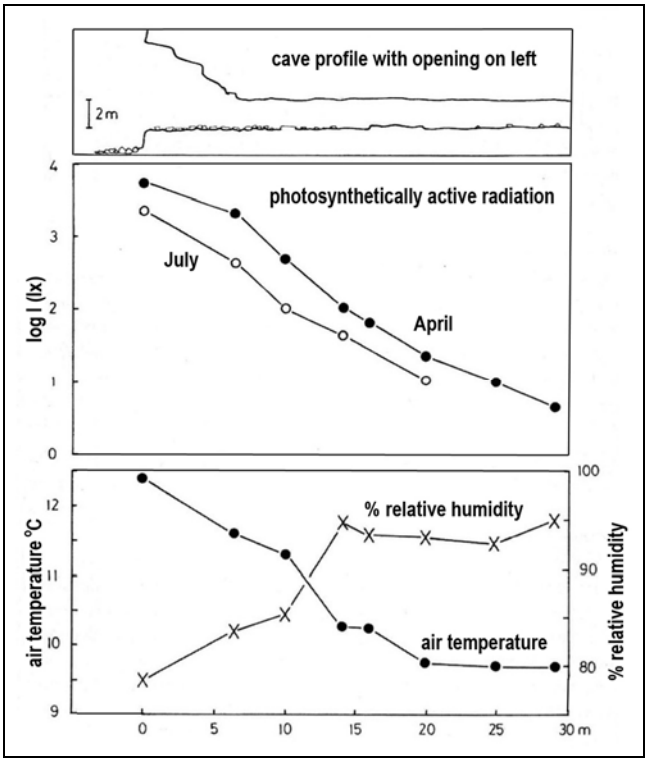

Figure 12. Cave parameters. Modified from Pentecost & Zhang 2001.

Caves provide natural laboratories for assessing the effects of gradients on species compositions (Poulson & White 1969). As islands, they can also help us to understand the effect of isolation on rate of genetic change and natural selection. And caves are simple systems with few tracheophytes to affect either competition or microclimate.

Tuttle and Stevenson (1978) have summarized the variation to be found in one cave environment and its impact on biological populations. They point out that many researchers have assumed a constancy in the cave environment, particularly that of temperature, assuming that it approximates the mean annual surface temperature. Researchers also often assume that humidity is near saturation and essentially unvarying. It is true that the cave environment varies less than that of the surrounding area, but it can indeed vary, at least in some caves, and this can impact the cave fauna (Jegla & Poulson 1970; Juberthie & Delay 1973; Delay 1974; Juberthie 1975; Poulson 1975; Tuttle 1975, 1976; Wilson 1975; Peck 1976), and presumably also the flora.

Substrate

Working in Eastern Australia, Downing (1992) noted that bryophytes were more abundant, exhibiting greater percent cover and a greater number of species, on limestone substrates than on nonlimestone substrates. Such preference may contribute to the diversity found in caves.

Fraser *et al*. (2014) suggested that in glacial regions organisms could have survived in geothermal areas in sub-ice caves. Such refugia could have permitted bryophytes to survive in these glacial areas until the ice receded. However, the ice itself is not a very good substrate.

Light

Like most studies, Mason-Williams and Benson-Evans (1967) identified two important ecological factors in Welsh caves: substrate and penetration of light. But they noted that aspect was also important, with north-facing walls having abundant growth and the south-facing walls having scanty, often atypical, growth. Bryophytes in higher light intensities had relatively typical life forms, but as light diminished the dendroid forms and smooth mats became less frequent and rough mats, thalloid mats, and wefts predominated. Spores of bryophytes were common throughout the sampled areas of the cave.

Similarly, Jedrejko and Ziober (1992) investigated bryophytes in caves on the Krackòw-Wieluñ Upland. They identified 10 liverworts, 59 mosses, and 3 unidentified mosses. Of these, 50% occur only where they get at least some time in full light. As expected, the number of species decreased with distance from light sources of cave inlets. Only 25% of the species occurred in continuously dry places.

Our constant attempts to classify things, even when they represent a continuum, have resulted in identification of the cave as the twilight zone **near** the entrance, a **middle** zone of complete darkness, and a zone of complete darkness and constant temperature **deep** in the cave (Poulson & White 1969). Among the fauna, the middle zone has several very common species which may go in and out of the cave.

Temperature and Humidity

Light, moisture, and temperature are variables in the cave environment and are not as constant as once thought. Buecher (1999), in a study of Kartchner Caverns in Arizona, USA, found that the cave could become drier due to increased airflow. This was caused by air entering from a second entrance and also by climate change. The relative humidity in the cave was 99.4% (pretty damp!) but had the potential of dropping to only 98.7%. At this only slightly lower humidity, the moisture loss from the cave surfaces would double! This would initiate the drying of the cave interior. Outside moisture is always less than that in the cave except during rain events. But since movement of air into the cave in summer is reduced, this does little to replenish lost humidity.

De Freitas and Littlejohn (1987) illustrate the seasonal changes in Glowworm Cave in New Zealand. They found that the external air temperature and humidity can be determinants of the spatial and temporal distribution of air temperature and humidity within the cave. The external conditions are also important in determining direction of airflow. In winter, these forces result in strong drying and cooling of the cave interior. External air enters the cave and is warmed. In summer the humidity levels of the cave rise substantially, resulting in condensation throughout the cave as it warms.

Gamble *et al*. (2000) demonstrated that tropical flank margin caves in the Bahamas and Puerto Rico presented different temperature regimes from those in temperate regions. These caves tend to be warmer than outside the cave in winter and cooler in summer. They also lacked diurnal temperature fluctuations. One cause for these differences is that these marginal caves tend to have a width greater than the length. Tidal water can also serve as a buffer to temperature conditions. These differences could be reflected in the bryophyte flora.

Cao and Yuan (1999) examined the water-holding capacity of the various groups of photosynthetic organisms and their effects on the carbon cycle on the rock surface. They found that the loss vs of absorption of water for algae was 18.8 and 1.6 times respectively, for lichens 2.9 and 19.1 times, and for mosses 81.2 and 8.1 times, compared to rocks with none of these growths. The organisms permit the rocks to hold onto water longer, increasing the rates of carbonate rock corrosion beneath them. Nutrients accumulate in these colonized areas and the biological cycle is accelerated.

CO_2

Asencio and Aboal (2011) noted that cave CO_2 concentrations were high (0.8% in cave compared to 0.45% in atmosphere). Oxygen was slightly lower (18.5%) than that of the atmosphere (~21%). The temperature ranged 27-43ºC – much more variation than many people seem to expect in caves. The humidity (100%) is quite favorable for algal species.

Some caves have changing airflow patterns between summer and winter (Spotl *et al*. 2005). This results in changes in CO_2 levels within the cave. Spotl and coworkers document the predictable changes from high $\boldsymbol{pCO_2}$ (partial pressure of dissolved CO_2; gas phase pressure of carbon dioxide in air above waterway which would be in equilibrium with dissolved carbon dioxide) in summer and low pCO_2 in winter in the Obir Cave in Austria. Winter flushing by relatively CO_2-poor air enhances degassing of CO_2 in the cave and leads to a high degree of supersaturation of calcite in dripwater (see also Whitaker *et al*. 2009).

Frisia *et al*. (2011) recorded a similar phenomenon in Grotta di Ernesto cave (NE Italy). Air advection causes the winter pCO_2 to drop in the cave air to ~500 ppm from a summer peak of ~1500 ppm, with a rate of air exchange between cave and free atmosphere of approximately 0.4 days. The process of cave ventilation forces degassing of CO_2 from dripwater before calcite precipitation onto stalagmites.

When investigating the Scoska Cave in the UK, Whitaker *et al*. (2009) suggested that bryophytes could act as CO_2 sinks, but that decomposition of bryophytes would release CO_2. They concluded that most of the CO_2 in the photic zone of the cave came from advection and diffusion of air from deeper in the cave.

Mazina and Popkova (2020a) examined the effects of high CO_2 levels on the photosynthetic organisms in the photic zone of the Anyashka Cave in the Caucasus. The dominant photosynthesizers were **Cyanobacteria**. Nevertheless, the highest gross primary productivity (**GPP**) occurred in communities dominated by pteridophyte and bryophyte species on water-splashed clay. Such communities on limestone or clay on limestone exhibited lower GPP. The GPP of these various communities varied from -0.1503 g C m^{-2} h^{-1} to -0.0109 g C m^{-2} h^{-1}. They also

found that some of these communities served as CO_2 sinks, but others were actually CO_2 sources.

In the seven caves studied in Montenegro, Mazina *et al*. (2020) found that all communities on various substrates were carbon sinks, in both summer and winter. Maximal dry mass production occurred when acrocarpous mosses and case-forming **Cyanobacteria** dominated, both being maximal for both phototrophic respiration and gross primary production.

In the Balcarka Cave and adjacent soils in the Czech Republic, Faimon *et al*. (2012) determined that human visitors and **epikarstic** (uppermost weathered zone of carbonate rocks with substantially enhanced and more homogeneously distributed porosity and permeability) sources contribute to the CO_2 levels in the caves. The epikarstic source seems to control the dripwater chemistry and maximum CO_2 in the cave. In show caves such as this one, breathing by visitors and door openings create fluctuations in the levels.

In the Císařská Cave (Moravian Karst, Czech Republic), Faimon *et al*. (2006) compared the chamber CO_2 levels with that of the drip chemistry. They found that the peak levels of CO_2 during visitor presence did not reach the theoretical values at which the dripwater carbonates and air CO_2 would be at equilibrium. However, visitation only resulted in 2.85 hours of human contribution. Increasing that to 4 hours could exceed the dripwater contribution. Nevertheless, achieving the threshold values at which water would damage the calcite would require extreme conditions, *e.g.*, simultaneous presence of 100 persons in the cave chamber for 14 h.

Howarth and Stone (1990) found that in May and June the CO_2 levels in the deeper passages in Bayliss Cave, Australia, reached up to 200X the ambient CO_2 in the atmosphere. This environment supported the largest diversity of obligate cave fauna known in its bad air zone. Such levels should be beneficial for photosynthetic organisms, provided there is sufficient light, and can permit growth even in low light (Lovalo *et al*. 2010). Artificial illumination in such conditions should create an interesting environment for bryophytes and algae. Photosynthetic studies are needed across the CO_2 and light gradients, coupled with laboratory experiments to sort out the individual effects.

Liu *et al*. (2017) examined the **carbonic anhydrase** activity of six epilithic mosses on soil in the Puding karst area, Guizhou Province, China. Carbonic anhydrase **catalyzes** the bidirectional conversion of carbon dioxide (CO_2) and water (H_2O) into bicarbonate (HCO_3^-) and protons (H^+). These reactions are important in the photosynthetic pathway but are also important in the CO_2 equilibrium of the habitat.

Huang *et al*. (2015) found that external carbonic anhydrase activity differed among the bacteria, fungi, and **Actinomycota**. This activity in bacteria and fungi was promoted by Zn and Co, whereas it was promoted most by Ca in **Actinomycota**. See also Li *et al*. 2005 for more cation and anion effects. The role of these reactions in facilitating bryophyte photosynthesis remains unknown.

Suitability for Flora and Fauna

Culver and Pipan (2009) note that the more superficial subterranean habitats such as small drainages that emerge as seeps, small cavities in the uppermost part of karstified rock, talus slopes, and cracks and shallow tubes in lava share only two important characters with caves. They are **aphotic** (having too little light for photosynthesis) and they harbor fauna suited for subterranean life. For bryophytes, only the often very limited photic portion is of relevance. They consider that these aphotic habitats may have given rise to species of animals adapted for the deepest parts of caves. For bryophytes, the openings of such small "caves" could serve the same role, providing stepping stones between caves or serving as refugia where suitable cave habitats may have been destroyed by human activity.

Radiation

Damaging radiation in caves can be much greater than outside. Buecher (1999) concluded that in Kartchner Caverns this was not enough to be of concern for cave visitors, but they could be for long-term employees. Measurements at the cave entrance are not representative of the deeper parts of the cave.

Algific Caves

The **algific caves** (Figure 13-Figure 18) result from cold air drainage in places like the driftless area of northeastern Iowa and southwestern Wisconsin, USA. These serve as refugia for boreal bryophyte species (Andrews 2003; Dale Vitt, pers. comm. 4 August 2021).

Figure 13. Algific cave in Fillmore County, Minnesota, USA. Photo by S. C. Zager, MN DNR, through public domain.

Figure 14. Algific caves in Wisconsin, USA. Photo by Ryan O'Connor, Wisconsin DNR through public domain.

Figure 15. Algific talus slope with mossy vent obscured by vegetation in northeastern Iowa. Photo courtesy of Beth Lynch.

Figure 16. Algific talus slope with vent in northeastern Iowa with researcher collecting soil. Photo courtesy of Beth Lynch.

Figure 17. Algific talus slope with vents in northeastern Iowa. Photo courtesy of Beth Lynch.

Figure 18. Algific talus slope with mossy vent, northeastern Iowa. Photo courtesy of Beth Lynch.

Andrews (2003) described the windhole caves at Ice Mountain, West Virginia, USA (Figure 19). He concluded that bedrock benches in the subsurface of the slope provides surfaces where cooler air and water become trapped. This results in frost and ice accumulation. Surface benches at the bottom of the slope are continuously cooled by the heavier down-slope winds. Although the airflow cycles and structural makeup of the algific caves differs among North American locations, they typically sustain an unusually cold environment. These environments are able to support species that otherwise occur in more northern or higher altitude sites.

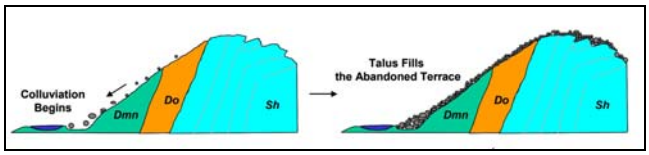

Figure 19. Algific slope cave formation, Ice Mountain, West Virginia, USA. The three colors are three different types of bedrock. Modified from Andrews 2003.

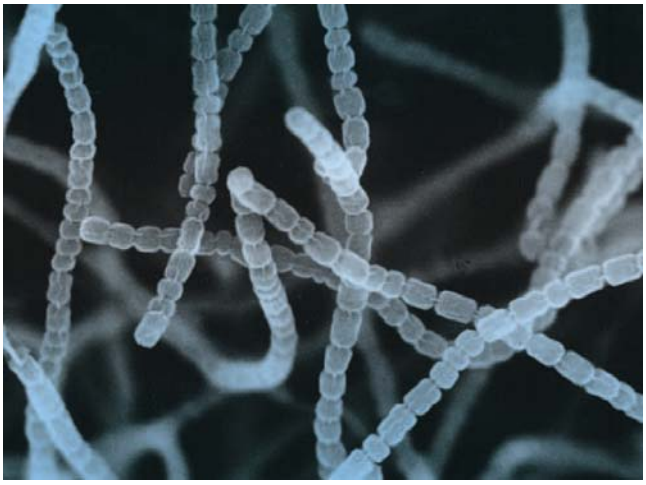

Figure 20. ***Streptomyces*** sp. Photo by Doc Warhol, through Creative Commons.

Non-Bryophyte Flora

The changes in the flora of caves are very dependent on light intensity. Whereas the entrance of the cave may have tracheophytes, including seed plants, further in the cave the **Cyanobacteria**, algae, bryophytes, and ferns are the only photosynthetic organisms able to grow in the limited light (Gurnee 1994; Lamprinou *et al*. 2014; Turchinskaia *et al*. 2019). Less commonly they may have liverworts or lichens; fungi and bacteria comprise non-photosynthetic organisms (Czerwik-Marcinkowska *et al*. 2019).

Roldán and Hernández-Mariné (2009) summarized some of the important factors determining phototrophic biofilm communities in three caves in Spain. They found that these films consisted of **Cyanobacteria**, green microalgae, diatoms, mosses, and lichens, and that these communities differed among sampling sites. Light-related stress and low humidity both result in thinner biofilms and lower species diversity. Similarly, the duration of light exposure reduces both thickness and diversity.

Microbes

In addition to photosynthetic organisms, caves provide suitable habitat for microbes and fungi (Laiz *et al*. 1999). Water communities are mainly composed of gram-negative rods and cocci (**Enterobacteriaceae** and **Vibrionaceae**), while those of ceiling rocks are mainly ***Streptomyces*** spp. (Figure 20). The conditions include high humidity, relatively low and stable temperature, water *p*H close to neutrality, and varying mixes of organic matter. These conditions seem to favor colonization and long-term growth of **Actinomycota** over other heterotrophic bacteria on ceiling rocks in the Altamira cave, Spain.

Cyanobacteria and Algae

Algal and cyanobacterial communities have been described in a number of caves around the world. These communities typically form a zone dependent on the light intensity. For example, Selvi and Altuner (2007) have described the algal flora in Ballica Cave in Turkey. Buczkó and Rajczy (1989) reported 49 algal taxa, but only 17 bryophyte taxa in three caves in Hungary.

In caves of Bashkirskiyi Ural Biosphere Reserve (southern Urals, Bashkortostan Republic, Russia), Gainutdinov *et al.* (2017) found 42 taxa of **Cyanobacteria** (42.9%), 31 taxa of **Bacillariophyta** (31.6%), 20 taxa of **Chlorophyta** (20.4%), 3 taxa of **Charophyta** (3.06%), and 2 taxa of **Ochrophyta** (2.04). ***Leptolyngbya boryana*** (**Cyanobacteria**; Figure 21-Figure 22), ***Mychonastes homosphaera*** (**Chlorophyta**; Figure 23), and ***Eolimna minutissima*** (**Bacillariophyta**; Figure 24) were present in all caves examined. The authors found that the diatoms ***Humidophila contenta*** (Figure 25), ***Hantzschia amphioxys*** (Figure 26), and ***Orthoseira roeseana*** (Figure 27), present in these caves, were those most commonly mentioned in other publications on caves. Others mentioned from other caves were ***Pinnularia borealis*** (**Bacillariophyta**; Figure 28), ***Stichococcus bacillaris*** (**Chlorophyta**; Figure 29), and ***Klebsormidium flaccidum*** (**Charophyta**; Figure 30-Figure 31). These species occurred in the highly illuminated areas on cave walls and on mosses at the cave entrance. Dominant algae in well-illuminated zones include the diatoms ***Orthoseira roeseana***, ***Humidophila contenta***, and ***Hantzschia amphioxys***, and ***Oscillatoria rupicola*** (**Cyanobacteria**; Figure 32), using substrates of damp walls and mosses. They concluded that the similarity of algae on the wall surfaces and on mosses was because the moss samples were usually collected from the walls. The mosses at the cave entrances usually exist in moist conditions with adequate lighting, favoring the growth of algae.

Figure 21. ***Leptolyngbya*** sp., a **Cyanobacteria** genus found in all caves examined by Gainutdinov *et al.* (2017) in the southern Urals. Photo by Philippe Bourjon, through Creative Commons.

Figure 22. ***Leptolyngbya boryanum***, a **Cyanobacteria** species found in all caves examined by Gainutdinov *et al.* (2017) in the southern Urals**.** Photo from UTEX, through Creative Commons.

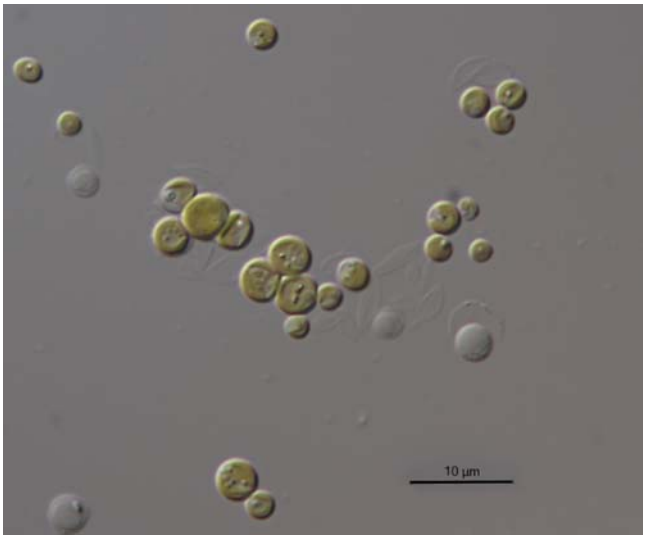

Figure 23. ***Mychonastes homosphaera***, a **Chlorophyta** species found in all caves examined by Gainutdinov *et al.* (2017) in the southern Urals**.** Photo by T. Darienko, through Creative Commons.

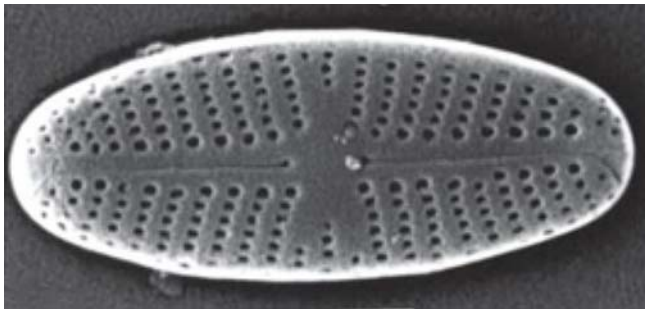

Figure 24. ***Eolimna*** sp. ***Eolimna minutissima*** is a diatom species found in all caves examined by Gainutdinov *et al.* (2017) in the southern Urals**.** Photo from Sala *et al*. 2003, through Creative Commons.

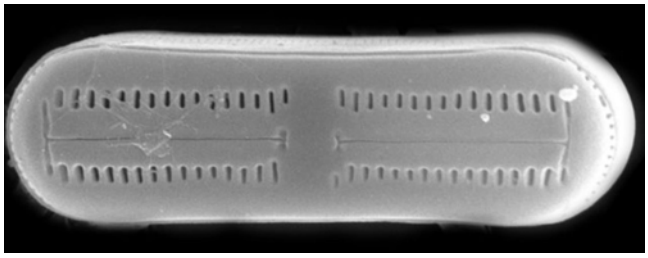

Figure 25. ***Humidophila contenta***, a species of diatom that is among the most common in caves. Photo by Rex Lowe from <diatoms.org>, with permission.

Figure 26. ***Hantzschia amphioxys***, a species of diatom that is among the most common in caves. Photo by Yuuji Tsukii, with permission.

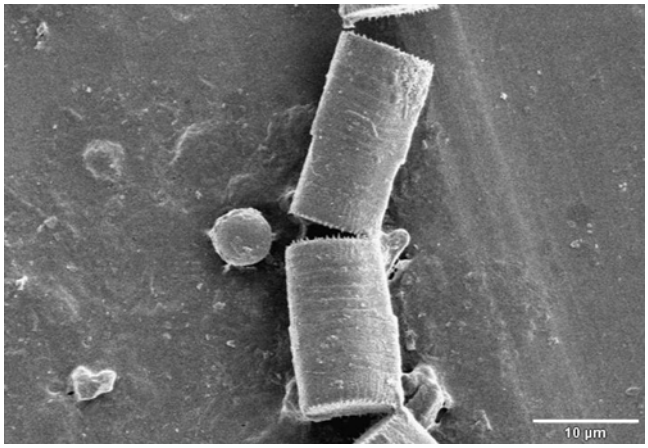

Figure 27. ***Orthoseira roeseana***, a species of diatom that is among the most common in caves. Photo by Birger Skjelbred, Nordic Microalgae <www.nordicmicroalgae.org>, with online permission.

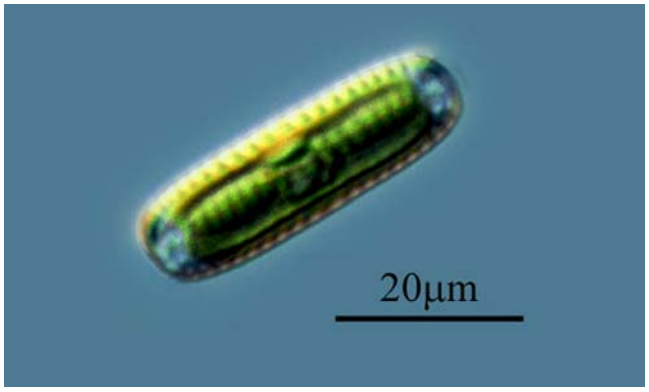

Figure 28. ***Pinnularia borealis***, a diatom species that has been found in multiple cave studies. Photo from Proyecto Agua Water Project, through Creative Commons.

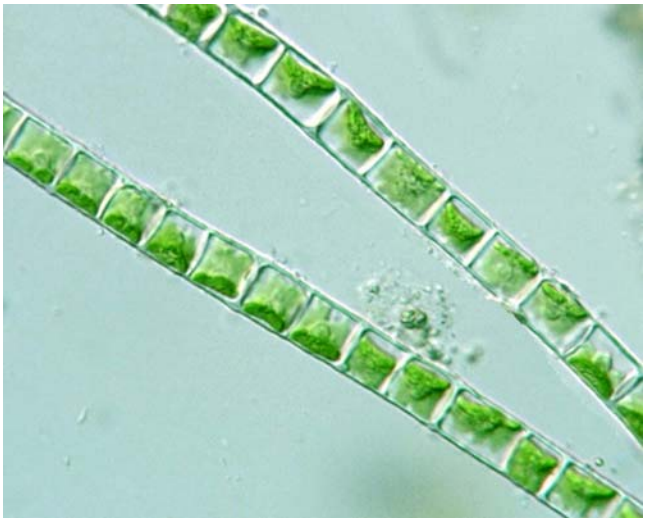

Figure 31. ***Klebsormidium flaccidum***, a **Charophyta** species that has been found in multiple cave studies. Photo Yuuji Tsukii, with permission.

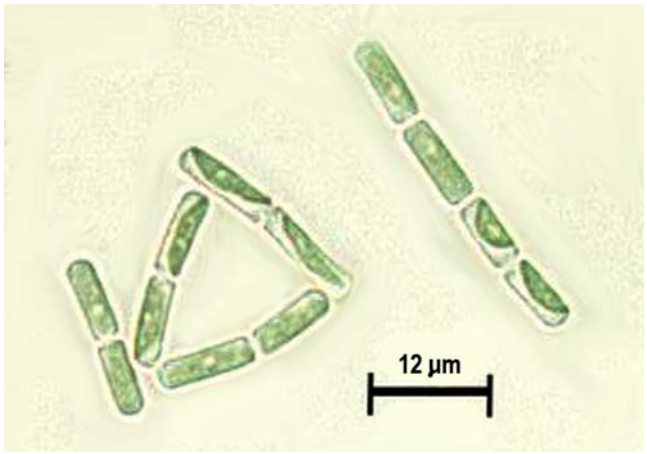

Figure 29. ***Stichococcus bacillaris***, a **Chlorophyta** species that has been found in multiple cave studies. Photo from UTEX, through Creative Commons.

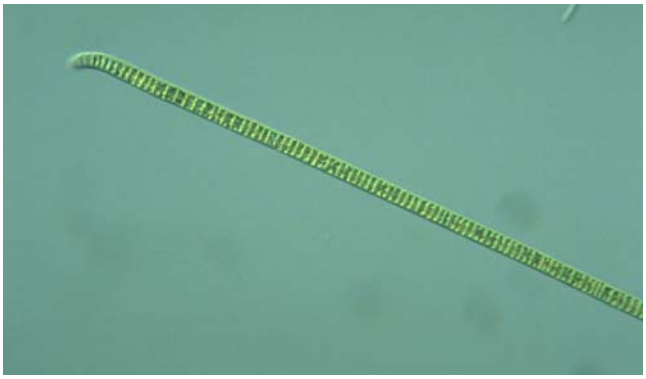

Figure 32. ***Oscillatoria*** filament; ***O. rupicola*** is a **Cyanobacteria** species that is common near cave lights in . Photo Yuuji Tsukii, with permission.

Figure 30. ***Klebsormidium*** sp. growing epiphytically. Photo by Des Callaghan, with permission.

Lowe *et al*. (2013) discovered two new species of diatoms in the genus ***Orthoseira*** (see Figure 27) from lava tubes in Hawai'i and Île Amsterdam (subAntarctic). The bottoms of these caves have a cover of mosses and liverworts surrounding a puddle.

Mulec and Kosi (2009) note the invasion of algae and **Cyanobacteria** deep into the caves where artificial illumination has been added so that visitors can see the cave interior. The caves are usually naturally humid, and the illumination makes them suitable for these growths. The authors consider the invading phototrophic organisms to be inappropriate aesthetically, but they note that the organisms also cause degradation of the cave substrata they colonize. These are especially problematic in caves with prehistoric art (Figure 33). It is advisable, for the preservation of the cave walls and art, to eliminate these Cyanobacteria and algae early because they play the most important role in early stages. Mosses and ferns typically colonize later. These photosynthetic organisms have acquired the name of **lampenflora**.

Figure 33. Rock art from 7000 BP, Cave of Beasts, Libyan desert; such paintings are easily damaged by algae and other growths and by methods used to remove those growths. Photo by Clemens Schmillen, through Creative Commons.

Distribution and species of **Cyanobacteria** and algae in caves are typically limited by the same parameters that influence bryophytes in cave habitats – reduced light intensity, low nutrients, and absence of seasonality (Dayner & Johansen 1991; Pedersen 2000; Popović *et al.* 2015). To these defining habitat characters, Mulec *et al*. (2008) added temperature, humidity, and flowing water as important in delimiting the aerial habitats.

Popović *et al*. (2015) noted that the biofilm on cave walls in Božana Cave (Serbia) included **Cyanobacteria**, algae, and microfungi. Popović *et al*. (2016) found a new coccoid member of the **Cyanobacteria**, ***Nephrococcus serbicus***, from the Božana Cave, Serbia. Popović *et al*. (2015) found that chlorophyll content of the biofilm was not proportional to the light intensity, but was instead proportional to the biomass of the film. Coccoid **Cyanobacteria** were the most abundant at the lowest light intensities, whereas **Nostocales** occurred in the highest light. ***Desmococcus olivaceus*** (Figure 35-Figure 36) and ***Trentepohlia aurea*** (Figure 37-Figure 38) were the only green algae on the walls, whereas ***Gloeocapsa*** (Figure 39), ***Scytonema*** (Figure 40), ***Aphanocapsa*** (Figure 41), and ***Chroococcus*** (Figure 42) were the most common **Cyanobacteria**, with 21 taxa of ***Chroococcus*** alone.

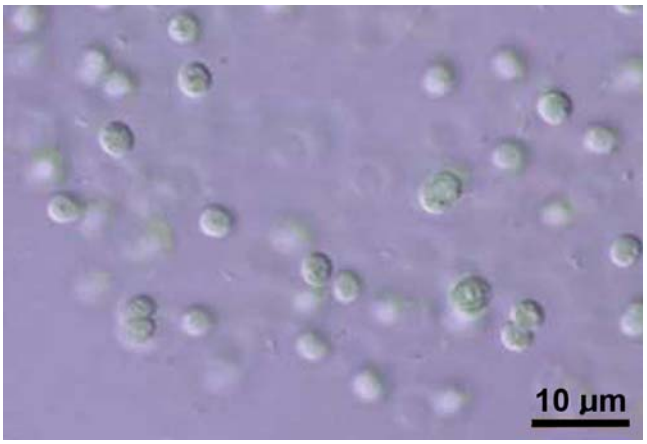

Figure 34. ***Nephrococcus*** sp.; ***Nephrococcus serbicus*** (**Cyanobacteria**) was found as a new species in the Božana Cave, Serbia. Photo modified from Linda Amaral Zettler and David Patterson, through Creative Commons.

Figure 35. ***Desmococcus olivaceus*** growing on a log, a terrestrial member of **Chlorophyta** that also occurs on cave walls. Photo by Bob O'Kennon, through Creative Commons.

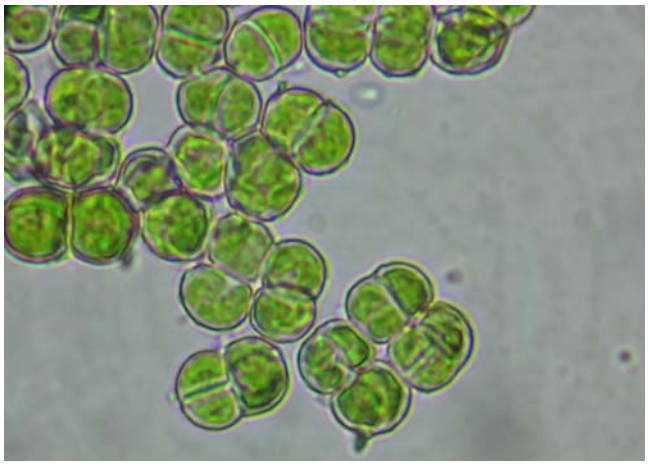

Figure 36. ***Desmococcus olivaceus***, one of only two green algae found on cave walls in Božana Cave (Serbia). Photo by Alejandra Huereca, through Creative Commons.

Figure 37. ***Trentepohlia aurea***, a terrestrial member of **Chlorophyta** that also occurs on cave walls. Photo by Malcolm Storey (DiscoverLife.com), with online permission.

Figure 38. ***Trentepohlia aurea***, one of only two green algae found on cave walls in Božana Cave (Serbia). Photo by Alan J. Silverside, with permission.

Figure 39. ***Gloeocapsa***, a genus common on cave walls in Serbia and elsewhere. Photo by Yuuji Tsukii, with permission.

Figure 40. ***Scytonema*** sp., a genus common on cave walls in Serbia and elsewhere. Photo from UTEX, through Creative Commons.

Figure 41. ***Aphanocapsa*** sp., a genus common on cave walls in Serbia and elsewhere. Photo by Jason Oyadomari, with permission.

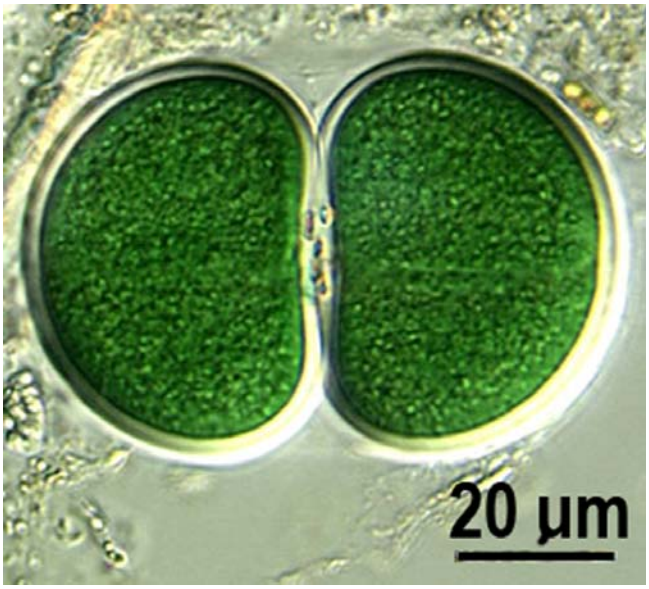

Figure 42. ***Chroococcus*** sp., a genus common on cave walls in Serbia and elsewhere. Photo by Jason Oyadomari, with permission.

Mulec *et al*. (2008) reported on the **aerophytic** (designates living in air in terrestrial habitats, on rocks, stones, sediments, trees, needing water only from atmosphere) algal community from a cave entrance in contrast to the lampenflora. They found the entrance community to be almost entirely **Cyanobacteria**, whereas at the lights green algae (**Chlorophyta**) became more dominant. They concluded, based on lack of correlation of chlorophyll *a* concentration per surface unit with photon flux density, that microhabitat substrate characteristics were important in influencing algal growth. The chlorophyll *a* concentration is lower in algae at the cave entrance than it is among the lampenflora. The low temperatures of the cave result in a low light saturation point. At 9ºC, the production of accessory photosynthetic pigments is elevated considerably in the **Cyanobacterium *Chroococcus minutus*** (Figure 43) and green alga ***Chlorella*** sp. (Figure 44).

Figure 43. ***Chroococcus minutus***, a species for which accessory photosynthetic pigments increase when the temperature is lowered to 9ºC. Photo from Nordic Microalgae <nordicmicroalgae.org>, through Creative Commons.

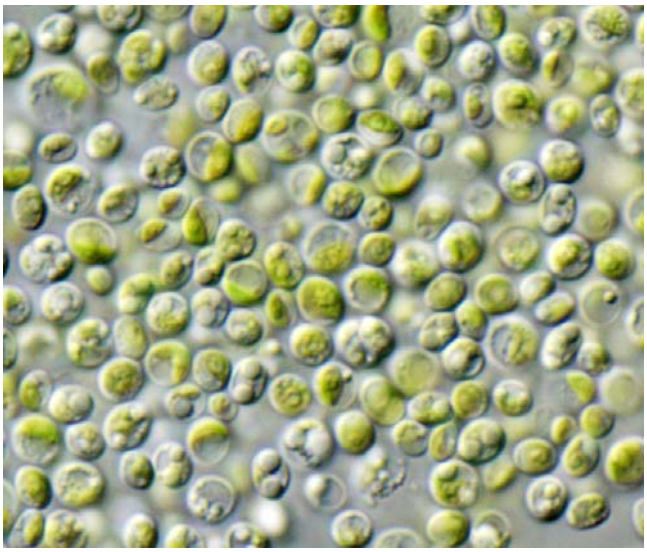

Figure 44. ***Chlorella vulgaris***. A cave member of ***Chlorella*** increases its accessory photosynthetic pigments when the temperature is lowered to 9ºC. Photo by Neon, through Creative Commons.

Popović *et al*. (2017) found that the greatest number of phototrophic microorganisms in three Siberian caves were **Cyanobacteria**, with ***Gloeocapsa*** (Figure 39, Figure 50, Figure 55, Figure 56) being the most diverse genus. They found that relative humidity is important in accounting for differences among the three microbial communities in the three caves. **Cyanobacteria** mostly occurred in locations with lower relative humidity, whereas **Chlorophyta** (green algae) and **Bacillariophyta** (diatoms) occurred where there was higher humidity.

Some of the biofilm taxa can be recognized by their colors (Popović *et al*. 2020). Coccoid cyanobacterial forms create gelatinous, olive to dark-green biofilms. ***Gloeobacter*** (Figure 45) appears purple; ***Gloeocapsa*** (Figure 46) is yellow, and ***Chroococcidiopsis*** (Figure 47) forms a black film. The heterocystic biofilms are primarily ***Nostoc*** (Figure 48-Figure 49) and are brown to dark in color.

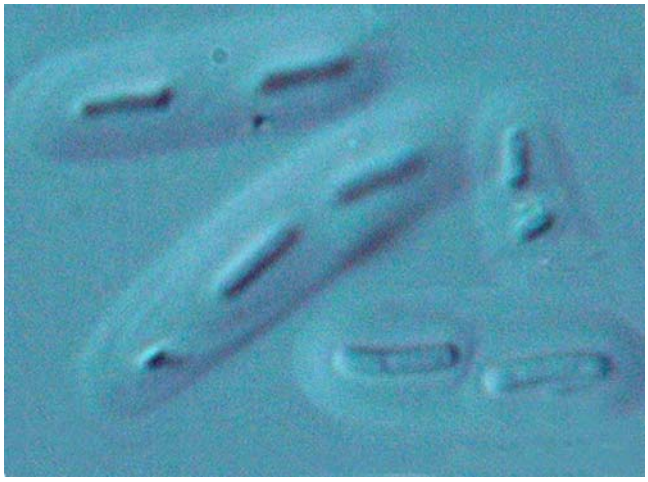

Figure 45. ***Gloeobacter*** sp., a genus that appears purple in cave biofilms. Photo by Burn12121212, through Creative Commons.

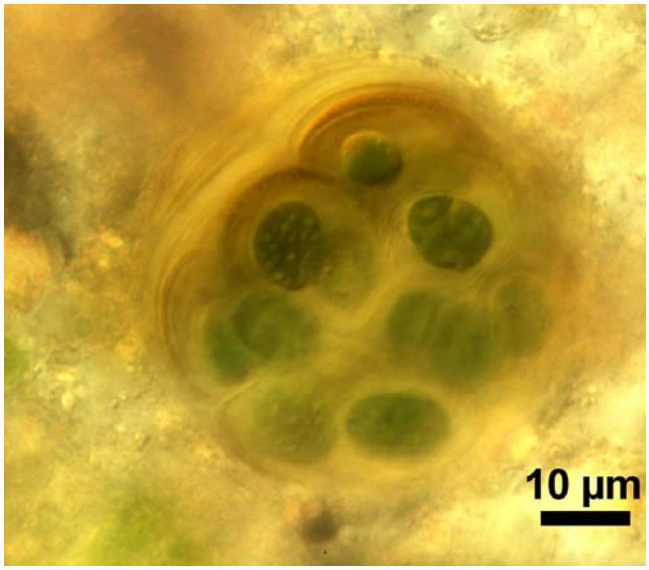

Figure 46. ***Gloeocapsa rupestris*** showing yellow color typical of its occurrence in cave biofilms. Photo by Cyanpro, through Creative Commons.

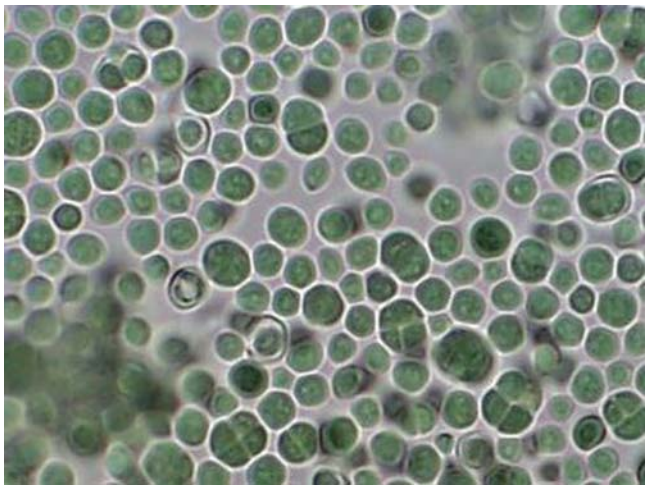

Figure 47. ***Chroococcidiopsis*** sp., a genus that appears black in cave biofilms. Photo by Burn12121212, through Creative Commons.

Figure 48. ***Nostoc commune***, a common cave-dwelling member of **Cyanobacteria**, on soil with mosses. Photo by Yamamaya, through Creative Commons.

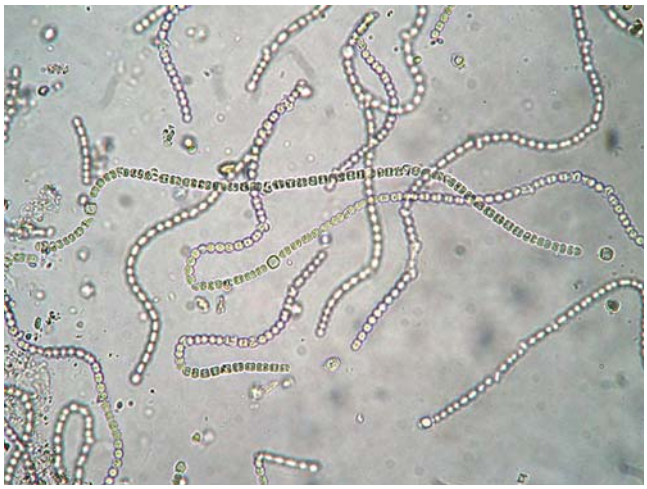

Figure 49. ***Nostoc commune***, a common cave dweller. Photo by Kristian Peters, through Creative Commons.

Czerwik-Marcinkowska (2013) studied the **Cyanobacteria** and algae in ten caves in the Ojców National Park, Poland. The author identified 35 **Cyanobacteria**, 30 **Chlorophyta**, and 20 from other groups of algae. These were dominated by aerophytic **Cyanobacteria** (see also Komáromy *et al*. 1985). The **Cyanobacteria**/algae ***Gloeocapsa alpina*** (Figure 50), ***Nostoc commune*** (Figure 48-Figure 49), ***Chlorella vulgaris*** (Figure 44), ***Dilabifilum arthropyreniae***, ***Klebsormidium flaccidum*** (Figure 51), ***Muriella decolor***, ***Neocystis subglobosa***, and ***Orthoseira roseana*** (Figure 27) were the most abundant taxa in all ten caves. The **Cyanobacteria** are typically the only phototrophs in the deepest parts of the caves, but around the entrance and electric lights they must compete for light with the other algae, bryophytes, and even ferns (Round 1981). Czerwik-Marcinkowska (2013) suggested that it was the nearly constant conditions that were so favorable to these algae.

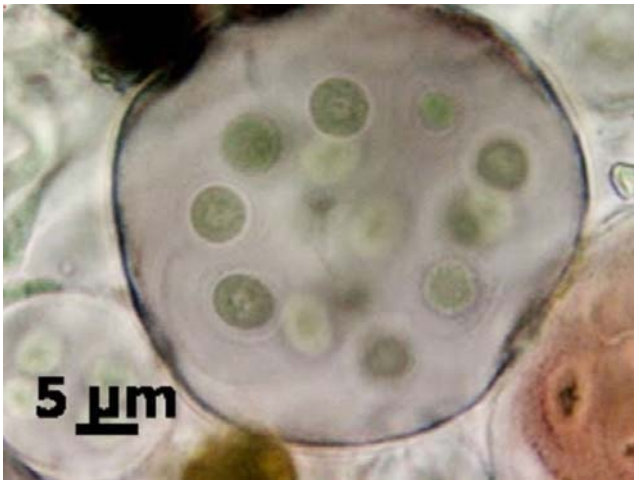

Figure 50. ***Gloeocapsa alpina***, one of the most abundant **Cyanobacteria** in ten caves in the Ojców National Park, Poland. Photo from AlgaeBase, through Creative Commons.

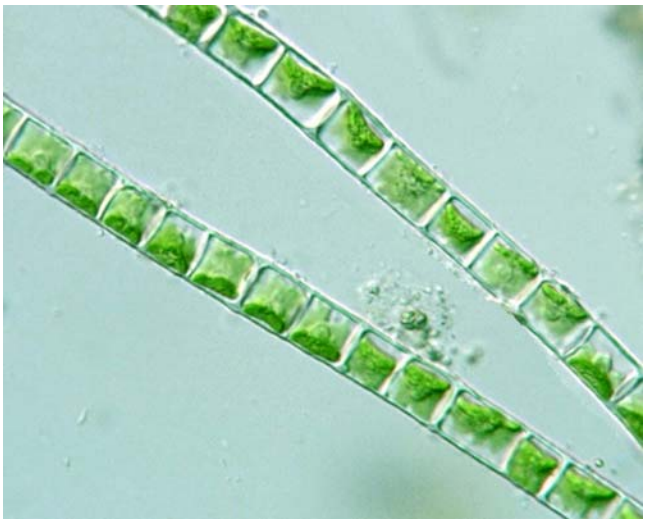

Figure 51. ***Klebsormidium flaccidum***, a common green alga in ten caves in the Ojców National Park, Poland. Photo by Yuuji Tsukii, with permission.

In Seneca Cavern, Ohio, USA, Dayner and Johansen (1991) found 25 algal taxa in subaerial habitats. These were mostly aerophilic species, with the most abundant being ***Chlorella miniata***, ***Pleurochloris commutata*** (**Ochrophyta**; see Figure 52), ***Navicula tantula*** (Figure 53), and ***Navicula contenta*** f. ***biceps***. They considered the dim light in this earth crack cave and lack of running water to be the reason for the smaller than typical number of species.

Mazina and Popkova (2020b) found ***Chroococcus minutus*** (Figure 43) and ***Chlorella vulgaris*** (Figure 44) to be the most frequent phototrophs in all the studied caves in Ukraine, Italy, and Hungary.

When lights are present in caves, the phototrophs can penetrate to a much greater distance. Komáromy *et al*. (1985) used cluster analysis to clarify relationships of the photosynthetic organisms in the cave. These researchers found 42 algal taxa in a single Hungarian show cave. (This number apparently included the **Cyanobacteria** as they were considered by the authors to be blue-green algae). They noted that the **Cyanobacteria** were species with

small cell sizes and that both lichens and liverworts are extremely rare in the habitats surrounding lamps. They delineated the algae by using scrapings that were then cultured on liquid Bold medium.

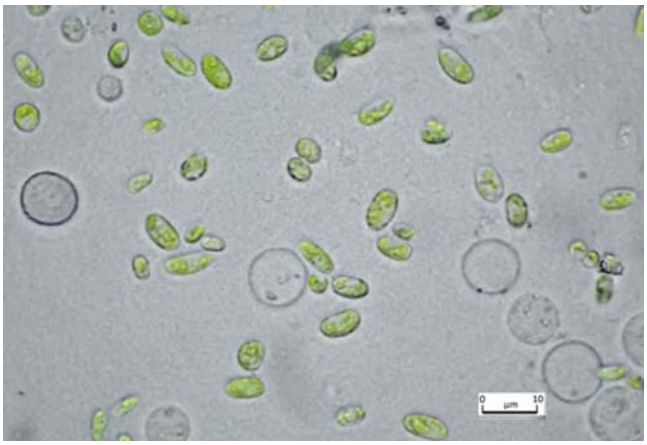

Figure 52. ***Pleurochloris pyrenoidosa***; ***P. commutata*** is among the most abundant algae in Seneca Cavern, Ohio, USA. Photo by Pierre Noel, through Creative Commons.

Figure 53. ***Navicula tantula***, a species that is among the most abundant algae in Seneca Cavern, Ohio, USA. Photo from UTEX, through Creative Commons.

Czerwik-Marcinkowska *et al*. (2019) similarly cultured scrapings of the algae and **Cyanobacteria** from walls of a cave in the Tatra Mountains of Poland. Ten of the species were **Cyanobacteria**; ***Gloeocapsa*** (Figure 39) was the most diverse genus. Four were diatom taxa. Diversity did not relate to temperature or humidity.

Czerwik-Marcinkowska *et al*. (2019) explored the relationship between brown bears (***Ursus arctos***; Figure 54) in caves and the diversity of airborne algae and **Cyanobacteria** in the Glowoniowa Nyża Cave, Tatra Mountains, Poland. Like Popović *et al*. (2017), they found the cyanobacterial genus ***Gloeocapsa*** (Figure 39, Figure 50, Figure 55, Figure 56) to be the most diverse. The highest number of species were in **Cyanobacteria** (10), but they also found 10 algae and four diatom species. The algal diversity did not correlate with temperature or humidity. The aerophytic organisms in the wall flora were apparently brought by wind, whereas the ones on twigs may have been brought by wind and bears. The bears in the cave use mosses, among other materials, to line their dens, creating another means of dispersal into the cave.

Figure 54. ***Ursus arctos*** (brown bear), a potential disperser of **Cyanobacteria** and algae into some caves. Photo by Magnus Johansson, through Creative Commons.

Nostoc commune (Figure 48-Figure 49) forms thick mats along with other airborne algae in the Glowoniowa Nyża Cave, Tartra Mountains, Poland (Czerwik-Marcinkowska *et al*. 2019). ***Gloeocapsa atrata*** (Figure 55) occurs in the cave and among mosses, especially on wet rocks (John *et al*. 2011). ***Gloeothece palea*** (Figure 56) occasionally grows among mosses (Czerwik-Marcinkowska *et al*. 2019).

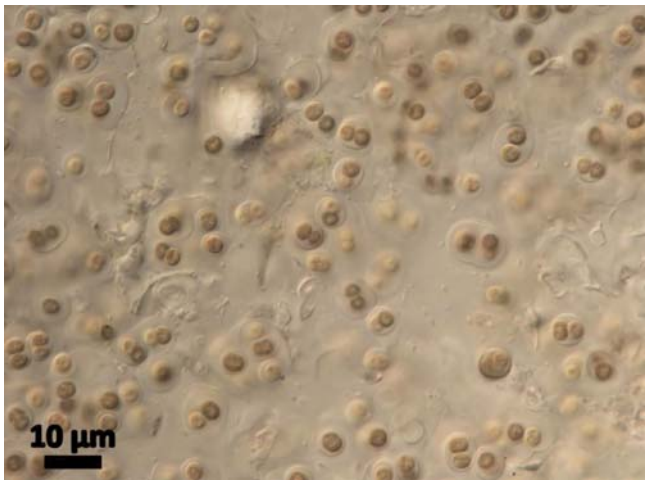

Figure 55. ***Gloeocapsa atrata***, a species that occurs among mosses on wet cave rocks. Photo from AlgaeBase, through Creative Commons.

Figure 56. ***Gloeothece palea***, a species that occurs among mosses on wet cave rocks. Photo Davydov D., through Creative Commons.

Like many other researchers, Czerwik-Marcinkowska *et al*. (2015) found that aerophytic **Cyanobacteria** were the most important members of the cave photosynthetic microflora. The most frequent were ***Aphanocapsa*** (Figure 41), ***Chroococcus*** (Figure 42, Figure 43), ***Gloeocapsa*** (Figure 50, Figure 55-Figure 56), ***Leptolyngbya*** (Figure 21-Figure 22), and ***Synechocystis*** (Figure 57). The predominant green algae were ***Apatococcus*** (Figure 58), ***Klebsormidium*** (Figure 31), ***Chlorella*** (Figure 44), ***Muriella***, and ***Neocystis***. Diatoms were dominated by ***Orthoseira*** (Figure 27) and ***Pinnularia*** (Figure 28). The algae were mostly cosmopolitan and ubiquitous, with simple nutrient requirements and wide ecological tolerance.

Figure 57. ***Synechocystis*** sp., a member of **Cyanobacteria**, one of the most important members of the cave photosynthetic microflora. Photo by Yuuji Tsukii, with permission.

Figure 58. ***Apatococcus*** sp., a member of **Chlorophyta**, one of the most important members of the cave photosynthetic microflora. Photo by Yuuji Tsukii, with permission.

Popović *et al*. (2017) likewise found that most of the taxa in cave biofilms in Serbia belonged to the **Cyanobacteria**. **Chroococcales** were dominant, and ***Gloeocapsa*** (Figure 50, Figure 55-Figure 56) was the most diverse genus. They found that **Cyanobacteria** were able to dominate where humidity was lower; **Chlorophyta** and **Bacillariophyta** occurred in locations with higher humidity. The chlorophyll *a* content was highest on horizontal surfaces, corresponding with the highest content of organic and inorganic matter as well. The highest water content was maintained in biofilms that contained many **Cyanobacteria**.

Poulíčková and Hašler (2007) reported aerophytic diatoms from caves in central Moravia in the Czech Republic. Rushforth *et al*. (1984) explored the subaerial diatom flora in the Thurston lava tube in Hawaii, USA. These occurred on wet mucilage and bryophytes on the walls. Falasco *et al*. (2015) described a new species of diatom (***Nupela troglophila***) from the Bossea Cave in Italy. They also noted that Rushforth *et al*. (1984) had found ***Nupela thurstonensis*** on the wet walls and bryophytes of the Thurston lava tube in Hawai'i. Both species occurred near the entrance and the artificial lighting.

Falasco *et al*. (2014) reported that the cave flora produces polysaccharides, proteins, lipids, and nucleic acids. This matrix is anionic, and facilitates the adsorption of cations and dissolved organic molecules from the cave formations. These exchanges can contribute to the corrosion of the cave walls. Diatoms, in particular, typically colonize these areas when there is sufficient light. Falasco and coworkers reported 363 species of diatoms listed in the literature as occupying subterranean habitats. The most frequent cave diatom species, in order from most frequent, are ***Hantzschia amphioxys*** (Figure 26), ***Humidophila contenta*** (Figure 25), ***Orthoseira roseana*** (Figure 27), ***Luticola nivalis*** (see Figure 59), ***Pinnularia borealis*** (Figure 28), ***Diadesmis contenta*** var. ***biceps*** (see Figure 60), and ***Luticola mutica*** (Figure 61). They also noted that it is not uncommon to find new species in these habitats.

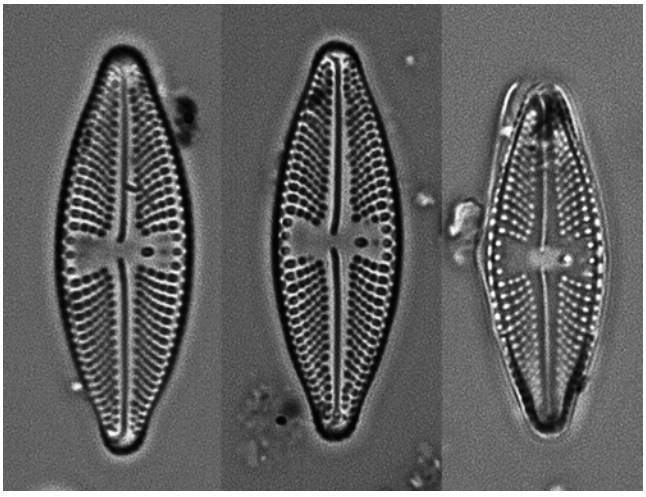

Figure 59. ***Luticola*** sp.; ***Luticola nivalis*** is one of the most frequent diatoms in caves. Photo by A. E. Drahos, through Creative Commons.

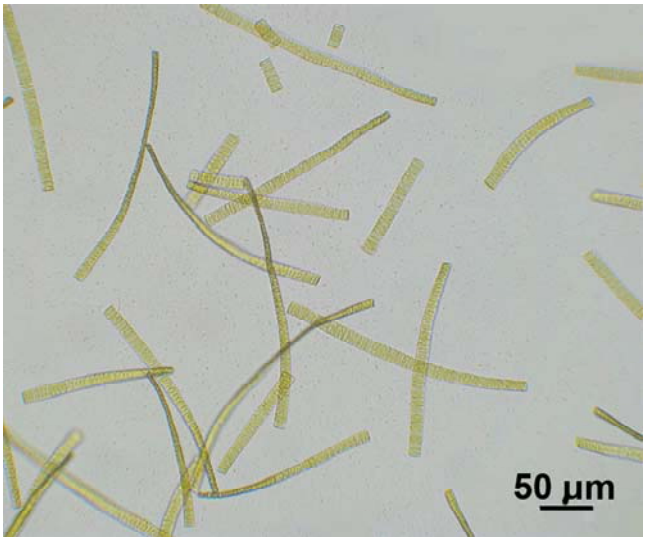

Figure 60. ***Diadesmis** cf. **gallica**; **Diadesmis contenta** var. **biceps** is one of the frequent diatoms in caves. Photo modified from ©BELSPO, with online permission.

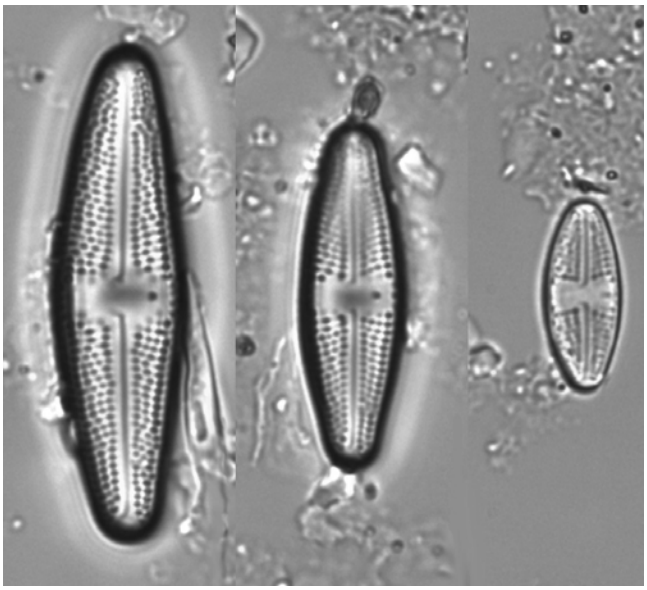

Figure 61. ***Luticola mutica***, one of most common species of diatoms in caves. Photo by Lane Allen, through Creative Commons.

Hantzschia amphioxys (Figure 26) is aerophilous (Germain 1981) and one of the most frequently recorded taxa on submerged bryophytes (Reichardt 1985; van de Vijver & Beyens 1997). ***Humidophila contenta*** (Figure 25) occurs on both wet walls and on bryophytes (Rushforth *et al*. 1984; Roldán & Hernández-Mariné 2009). ***Diadesmis contenta*** var. ***biceps*** (see Figure 60) occurs on wet walls and bryophytes (Dayner & Johansen 1991; Falasco *et al*. 2014). ***Luticola mutica*** (Figure 61) is one of the most frequent taxa on submerged bryophytes (Reichardt 1985; van de Vijver & Beyens 1997); it is resistant to moderately high conductivity levels (Poulíčková & Hašler 2007). This tolerance seems to account for its common occurrence also in lowland rivers (van Dam *et al*. 1994; Czerwik-Marcinkowska & Mrozińska 2011).

Pinnularia borealis (Figure 28) is one of the most frequent diatoms on submerged bryophytes (Reichardt 1985; Van de Vijver & Beyens 1997; Falasco *et al*. 2014). Nevertheless, Vande Vijver and Beyens (1997) found it to be in an assemblage on very dry mosses in South Georgia. ***Pinnularia borealis*** (Figure 28), common in the Glowoniowa Nyża Cave, is aerophilous, but frequently occurs on submerged bryophytes and in wild caves near the main entrance on very wet walls (Garbacki *et al*. 1999). Van de Vijver and Beyens (1997) found that ***Pinnularia borealis*** size drops with the increasing dryness of the moss habitat.

Borrego-Ramos *et al*. (2018) reported on the diatoms from the Valporquero Cave in Spain. They found that moss-dwelling diatom associations differed from those in other parts of the cave. They found ***Mayamaea cavernicola*** (incorrectly identified as *Navicula seminulum* var. *hustedtii*; Figure 62), a species already known from a lava tube cave on the Hawai'ian Islands (Rushforth *et al*. 1984). A different sample from the Spanish cave was almost entirely made up of ***Humidophila gallica*** (see Figure 25).

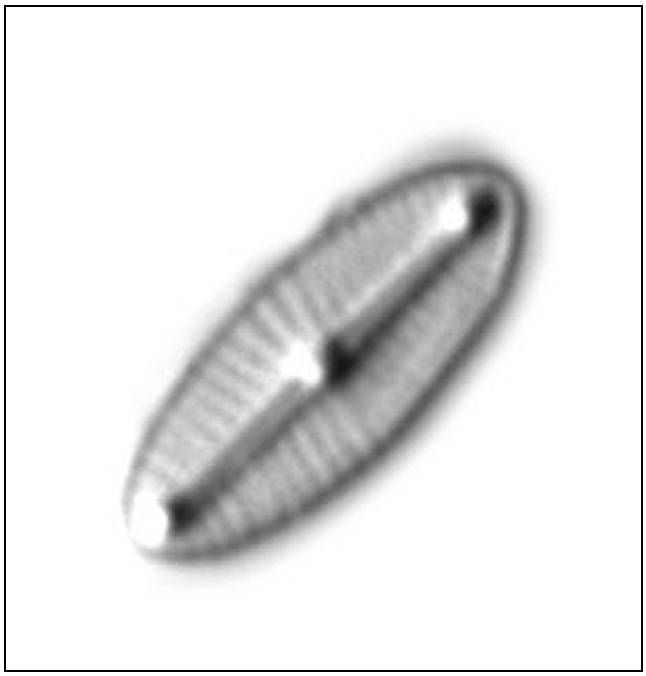

Figure 62. ***Mayamaea atomus***; ***M. cavernicola*** is a species known from lava tubes and caves. From Sarah Spaulding and Mark Edlund, <diatoms.org>, with permission.

Lauriol *et al*. (2006) found that 80% of the diatoms in ice caves (Figure 63) of the Yukon Territory were of local origin from subaerial habitats near the cave entrances. These include the sub-aerial diatoms ***Orthoseira dendroteres*** (a common bryophyte dweller; Figure 64) and ***O. roseana*** (Figure 27). Larger caves tended to have more species, presumably due to the greater air circulation in these caves. The **grus** (accumulation of angular, coarse-grained fragments resulting from granular disintegration of crystalline rocks), ice plugs, and ice stalagmites have the greatest relative abundance of diatoms, but the lowest diversity. Can these principles serve as models for bryophytes? It appears that they do.

Figure 63. Ice cave in natural glacier, often a home for diatom species in the genus ***Orthoseira***. Photo by Serge J. F., through Creative Commons.

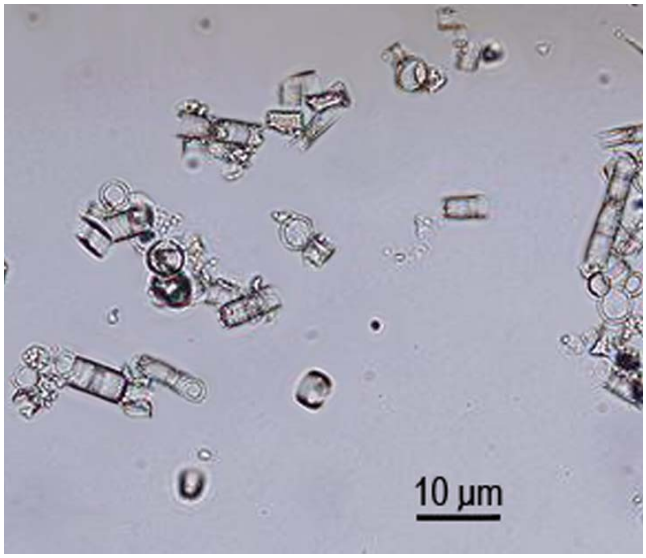

Figure 64. ***Orthoseira dendroteres***, a subaerial diatom that occurs in ice caves in the Yukon Territory. Photo by UTEX, through Creative Commons.

When light enters the cave, particularly at the entrances, **Cyanobacteria** contribute to the growth of **stalactites** (tapering structures hanging like icicles from roof of cave, formed of calcium salts deposited by dripping water; "stalactites must hang on tight;" think **c** for ceiling; Figure 1, Figure 6) and **stalagmites** (mound or tapering columns rising from floor of cave, formed of calcium salts deposited by dripping water and often uniting with stalactite to form column; "stala**g**mites are little mites;" think **g** for ground; Figure 1, Figure 6) (Mulec *et al*. 2007).

The **Cyanobacteria** contribute to making the layers of stromatolitic stalagmites. Mulec *et al*. (2007) found 35 taxa associated with them at the cave entrance of Škocjanske jame, Slovenia. These had a low portion of coccoid **Cyanobacteria** and other **Cyanobacteria** such as ***Calothrix*** sp. (Figure 65), ***Homeothrix*** sp. (Figure 66), and ***Schizothrix*** sp. (Figure 67).

Figure 65. ***Calothrix parietina***, a cave dweller in a genus that contributes to making layers of stalagmites. Photo from AlgaeBase, through Creative Commons.

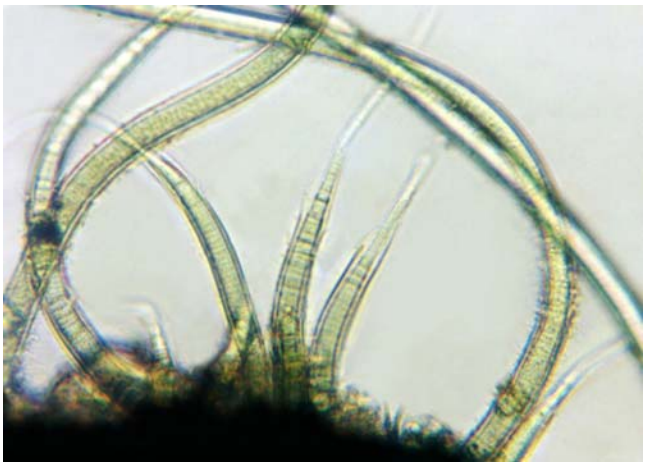

Figure 66. ***Homeothrix*** sp., in a genus that contributes to making layers of stalagmites. Photo from Manaaki Whenua – Landcare Research, with online permission.

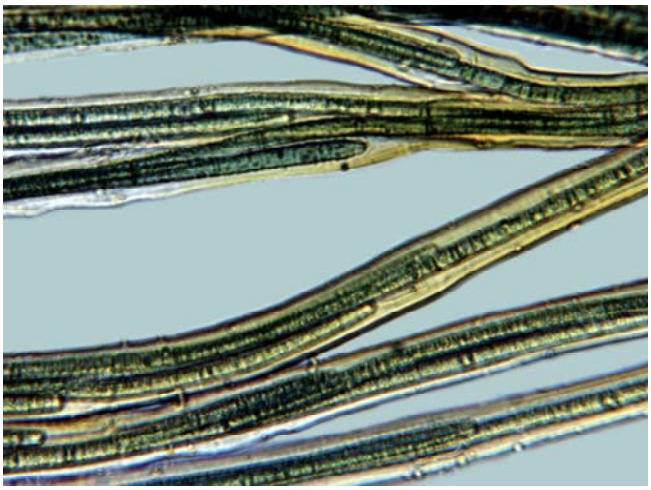

Figure 67. ***Schizothrix*** sp., in a genus that contributes to making layers of stalagmites. Photo from Manaaki Whenua – Landcare Research, with online permission.

One bryophyte that seems to occur in multiple caves is ***Eucladium verticillatum*** (Figure 68-Figure 69) (Dalby 1966a). It actually helps to build the stalactites by

collecting the dripping lime water. The stalactite surrounds the moss, and green leaves are visible only at the tips. It is notable that this species does not become etiolated even in the lowest illumination where it grows. Dalby found that it did not even become etiolated when kept in a polyethylene bag in total darkness for two months, but with no light I wouldn't have expected it to grow at all.

Figure 68. ***Eucladium verticillatum*** with mineral deposits on leaf tips. Photo by Armand Turpel, through Creative Commons.

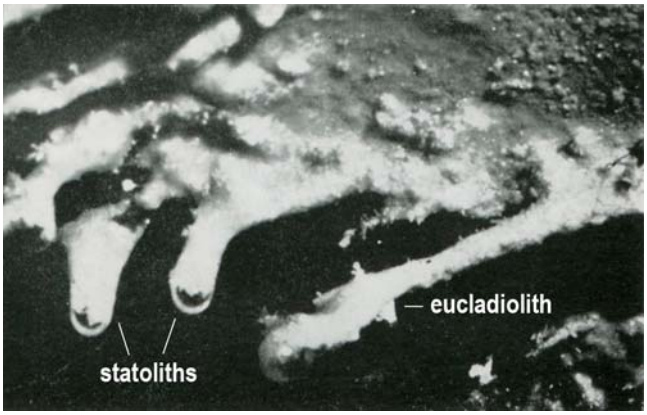

Figure 69. ***Eucladium verticillatum*** forming stalactite (eucladiotite) in mine in Dorset, UK. Note the nearly horizontal development of the eucladiolith. Photo from Dalby 1966b.

In the carbonate depositions on the lighted side of the stalactites, there were 14 species of **Cyanobacteria**, mainly coccoid forms (Mulec *et al*. 2007). Their growth and biolithogenic activity are especially associated with the moss ***Eucladium verticillatum*** (Figure 68-Figure 69). This results in formations known as **eucladioliths** (Figure 69) (Dalby 1966b).

Czerwik-Marcinkowska and Mrozińska (2011) reported 82 species of aerophytic **Cyanobacteria** and algae from 25 caves in the Polish Jura. Of these, 33 species were **Cyanobacteria** with the **Chlorophyta** represented by 30 species. There were even 2 species of **Dinophyta**. They found a number of rare species, some of them specific to these caves. **Cyanobacteria** at the entrance and around lights included predominantly ***Calothrix parietina*** (Figure 65), ***Gloeocapsopsis magma*** (Figure 70-Figure 71), ***Nostoc commune*** (Figure 48-Figure 49), ***Oscillatoria brevis*** (Figure 72), and ***Tolypothrix tenuis*** (Figure 73). These **Cyanobacteria** competed with algae, especially the **Chlorophyta** ***Chlamydomonas*** sp. (Figure 74), ***Muriella decolor***, and ***Klebsormidium flaccidum*** (Figure 31), as well as with mosses and pteridophytes. The moss ***Cratoneuron*** (Figure 75) was accompanied by aerophilic diatoms [***Humidophila contenta*** (Figure 25), ***Gomphonema italicum*** (Figure 76-Figure 77)] and **Chlorophyta** [***Chlorella vulgaris*** (Figure 44), ***Trentepohlia aurea*** (Figure 37-Figure 38), ***Stichococcus bacillaris*** (Figure 29)].

Figure 70. ***Gloeocapsopsis magma*** on rock, a common species at cave entrances and near lights. Photo by Randal, through Creative Commons.

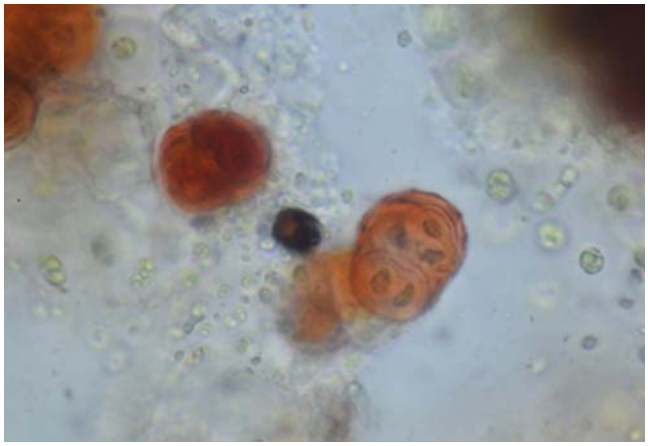

Figure 71. ***Gloeocapsopsis magma***, a common cave species. Photo by Randal, through public domain.

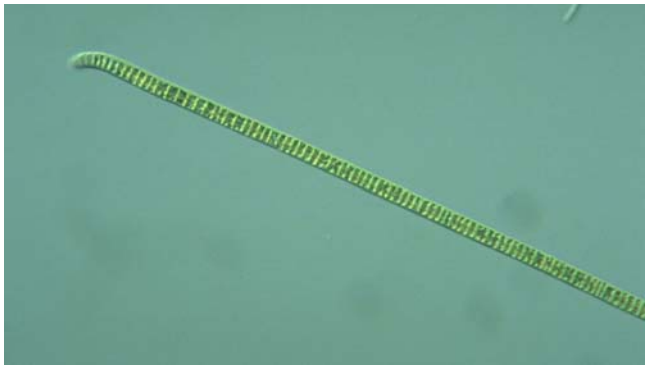

Figure 72. ***Oscillatoria brevis***, a common cave entrance and lampenflora species. Photo by Yuuji Tsukii, with permission.

Figure 73. ***Tolypothrix tenuis***, a common cave entrance and lampenflora species. Photo by Yuuji Tsukii, with permission.

Figure 74. ***Chlamydomonas globosa***, a common cave entrance and lampenflora species. Photo by Picturepest, through Creative Commons.

Figure 75. ***Cratoneuron filicinum***, a species that provides substrate for several species of diatoms in caves. Photo by Hermann Schachner, through Creative Commons.

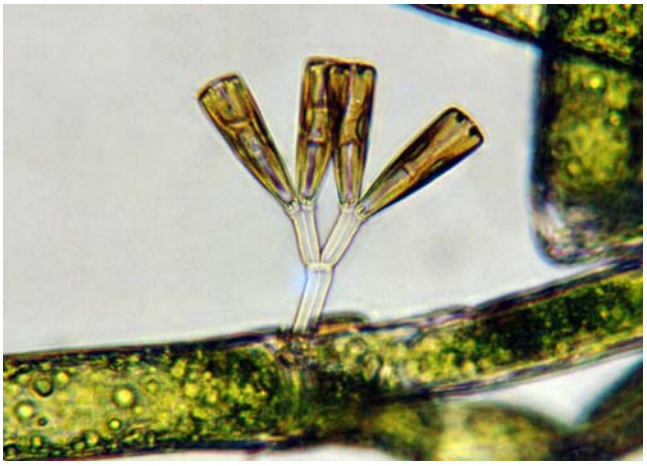

Figure 76. ***Gomphonema*** sp., member of a cave-dwelling diatom genus, attached to ***Cladophora***. Photo from Manaaki Whenua – Landcare Research, with online permission.

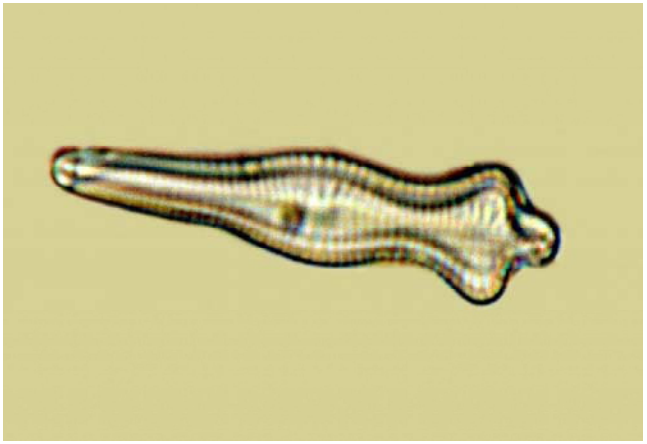

Figure 77. ***Gomphonema*** sp. Photo from Manaaki Whenua – Landcare Research, with online permission.

Sciuto *et al*. (2017) described the new genus ***Timaviella*** (**Leptolyngbyaceae** in **Cyanobacteria**) from the Giant Cave lampenflora in Italy. There were actually two species described for it in that cave (***Timaviella circinata*** and ***Timaviella karstica***).

Koch (1976) suggested that bryophytes create runoff that might affect the other organisms living with them. One such possibility is indicated between bryophytes and the green alga ***Protococcus vestitus*** (Figure 78). Data also suggested that bryophytes might be important in colonization by ***Trochiscia ohioensis*** (see Figure 79). It was closely associated with bryophytes at Ash Cave Cliff in Ohio, USA. But whereas ***Trochiscia ohioensis*** occurred in 51 collections, bryophytes occurred in only 6 of these. Nevertheless, both ***Protococcus vestitus*** and ***Trochiscia ohioensis*** had high correlations with bryophytes. They were present in 18 of the 20 stands in which ***Trochiscia ohioensis*** occurred. (Unfortunately, I was unable to match either of these algal species names to any in AlgaeBase; all records of the rare ***Protococcus vestitus*** other than this one are 19th century.) Koch suggested that the bryophytes, especially thallose liverworts, could retain enough moisture to make the habitat suitable for the algae. The frequently abundant chroococcalean **Cyanobacteria** are only present with the bryophytes when there is abundant moisture present.

Figure 78. ***Apatococcus lobata*** (syn. = *Protococcus viridis*); ***Protococcus vestita*** had a high correlation with bryophytes in Ash Cave Cliff in Ohio, USA. Photo by Yuuji Tsukii, with permission.

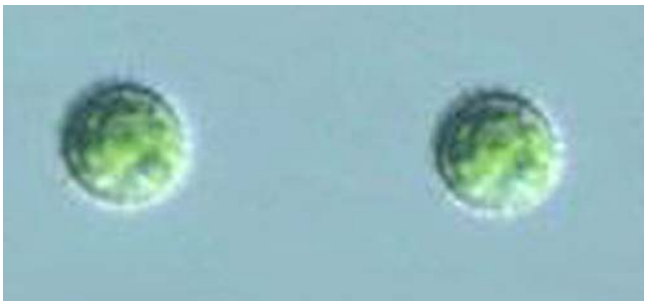

Figure 79. ***Trochiscia aspera***; ***T. ohioensis*** has a high correlation with bryophytes on Ash Cave Cliff in Ohio, USA. Photo by Yuuji Tsukii, with permission.

Cyanobacteria with **heterocysts** (Figure 80) can fix atmospheric N_2 into usable forms (Lamprinou *et al.* 2012) that prepare the environment for colonization of other **Cyanobacteria**, algae, and mosses (Ortega-Calvo *et al.* 1995). **Cyanobacteria** are important in many ecosystems for their ability to transform atmospheric nitrogen into usable forms. Asencio and Aboal (2011) found that ***Scytonema julianum*** (see Figure 40) contributed to this activity in Vapor Cave in Spain.

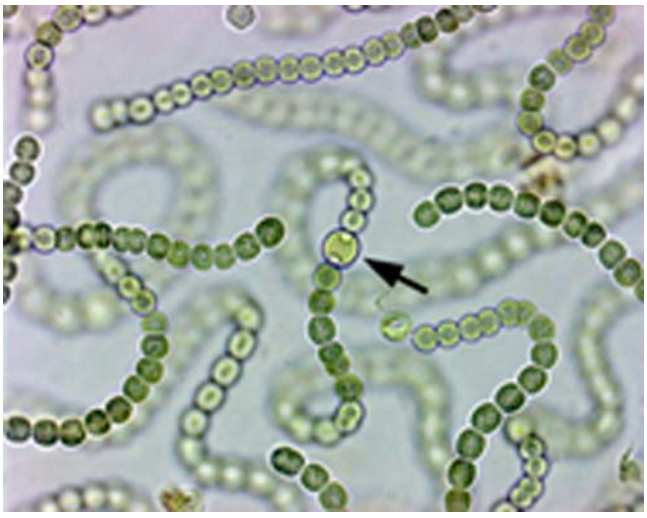

Figure 80. ***Nostoc*** sp. 1 showing heterocyst <vle.du.ac.in>, through Creative Commons.

Fungi

Vanderwolf *et al.* (2013) documented 1029 species of fungi, slime molds, and yeasts, based on 225 publications on caves and mines. They found the **Ascomycota** to be the dominant group among these. The cave fungi communities are typically those requiring few nutrients (**oligotrophic**) and tolerating year-round low temperatures (**psychrotolerant**).

Fungi in three Serbian caves were primarily **Ascomycota** or **Zygomycota** (Popović *et al.* 2017). Popović *et al.* (2015, 2017) found that **Ascomycota** were common [*e.g.* ***Alternaria*** (Figure 81-Figure 82), ***Aspergillus*** (Figure 83), ***Cladosporium*** (Figure 84), ***Epicoccum*** (Figure 85-Figure 86), ***Penicillium*** (Figure 87-Figure 88), and ***Trichoderma*** (Figure 89-Figure 90)], while **Zygomycota** and **Oomycota** were less frequent in Božana Cave, Serbia. The only member of **Basidiomycota** was one of ***Rhizoctonia*** *s.l.* (Figure 91-Figure 92) (Popović *et al.* 2017).

Figure 81. ***Alternaria alternata*** on tobacco leaf. Photo from the Bugwood Network, through Creative Commons.

Figure 82. ***Alternaria alternata***, a common **Ascomycota** fungus in three Serbian caves. Photo by Abdulghafour, through Creative Commons.

Figure 83. ***Aspergillus oryzae***, a common **Ascomycota** fungus in three Serbian caves. Photo by Yulianna, through Creative Commons.

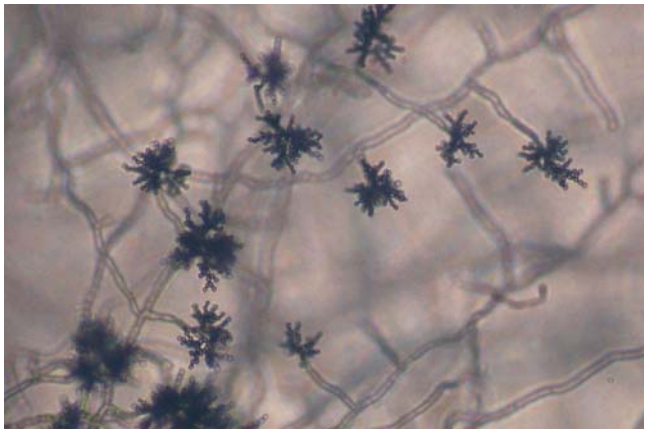

Figure 84. ***Cladosporium*** sp. conidia, a common **Ascomycota** fungus in three Serbian caves. Photo by Keisotyo, through Creative Commons.

Figure 85. ***Epicoccum nigrum*** infection on mushroom. Photo by Walt Sturgeon, through Creative Commons.

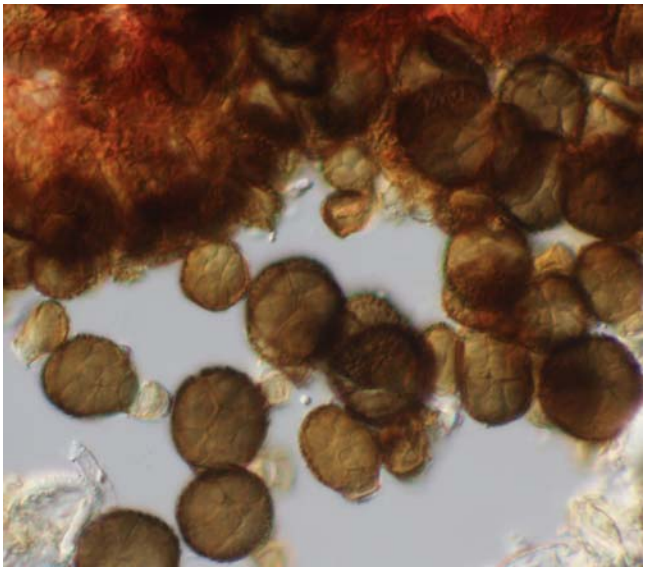

Figure 86. ***Epicoccum nigrum***; the genus ***Epicoccum*** is a common **Ascomycota** fungus in three Serbian caves. Photo by Paul Cannon, through Creative Commons.

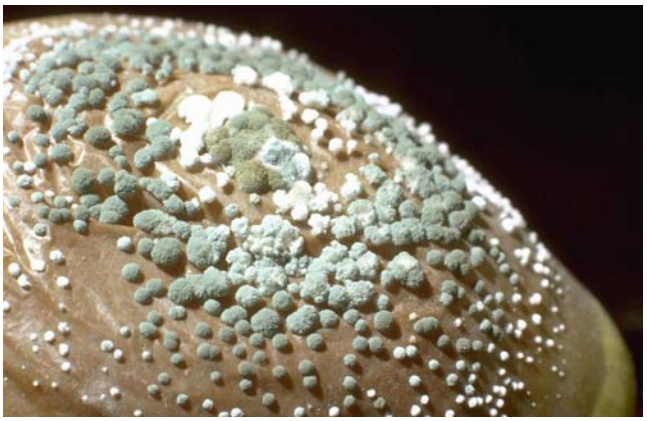

Figure 87. ***Penicillium expansum*** on pear. Photo by H. J. Larsen, through Creative Commons.

Figure 88. ***Penicillium spinulosum***; the genus ***Penicillium*** is a common **Ascomycota** fungus in three Serbian caves. Photo by Medmyco, through Creative Commons.

Figure 89. ***Trichoderma*** sp. on decaying wood in Japan. Photo by Keisotyo, through Creative Commons.

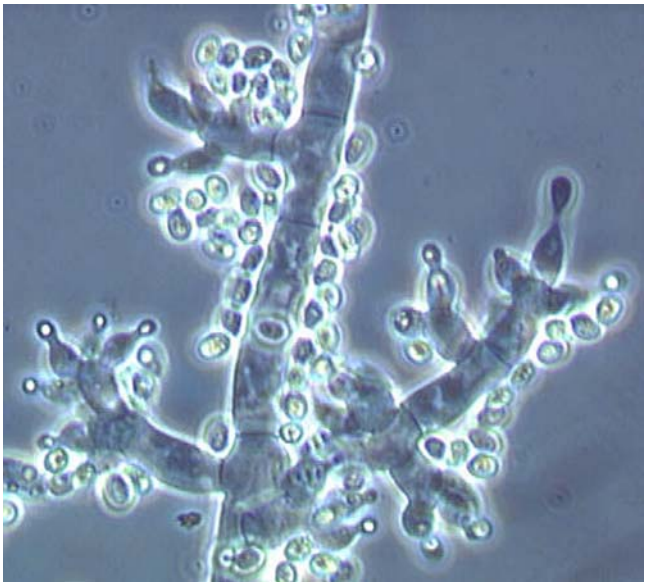

Figure 90. ***Trichoderma fertile***; the genus ***Trichoderma*** is a common **Ascomycota** fungus in three Serbian caves. Photo through public domain.

Figure 91. ***Rhizoctonia solani*** on sugar beet root, a genus found in three Serbian caves. Photo through Creative Commons.

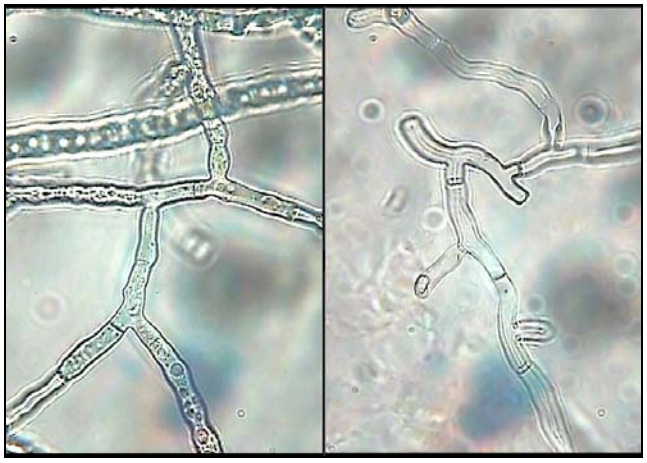

Figure 92. ***Rhizoctonia solani***; ***Rhizoctonia*** *s.1.* is the only member of **Basidiomycota** found in three Serbian caves. Photo by Tashkoskip, through Creative Commons.

Air currents in the cave are likely to contribute to dispersal of fungal spores, but Jurado *et al*. (2009) suggested that insects within the cave might play a role in spore dispersal as well. This possibility is further supported by the fact that most of the fungi proved to be **entomopathogens** (micro-organisms capable of infecting insects). In European caves with rock-art paintings (Figure 33), a test area was sterilized and after two months the rock tablets placed there were heavily colonized by fungi.

Nováková (2009) reported on the microscopic fungi isolated from the Domica Cave system in Slovakia. The frequent species included ***Penicillium glandicola*** (Figure 93), ***Trichoderma polysporum*** (see Figure 89-Figure 90), ***Oidiodendron cerealis***, ***Mucor*** spp. (Figure 94-Figure 95), ***Talaromyces flavus*** (Figure 96-Figure 97), and species of the genus ***Doratomyces*** (Figure 98).

Figure 93. ***Penicillium glandicola***, a frequent species in the Domica Cave system in Slovakia. Photo by Y. V. Sagar, through Creative Commons.

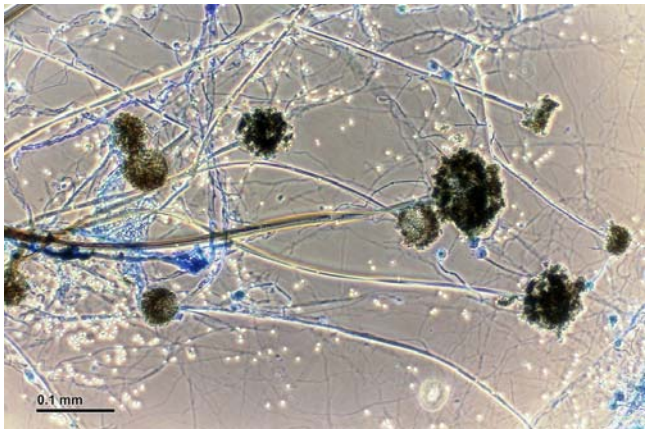

Figure 94. ***Mucor*** sp., a frequent genus in the Domica Cave system in Slovakia. Photo by Josef Reischig, through Creative Commons.

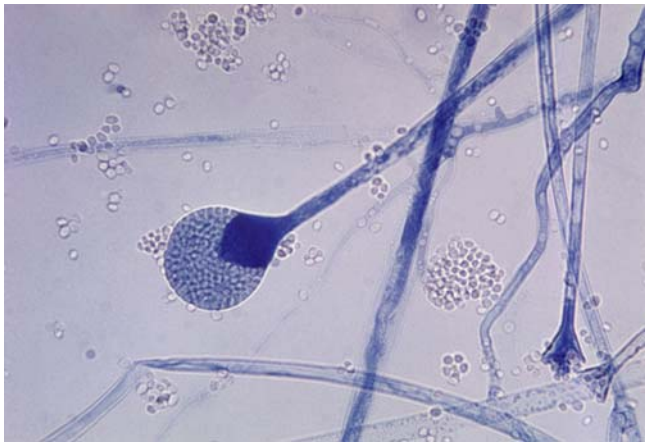

Figure 95. ***Mucor*** mature sporangium, a frequent genus in the Domica Cave system in Slovakia. Photo by Lucille K. Georg, CDC, through public domain.

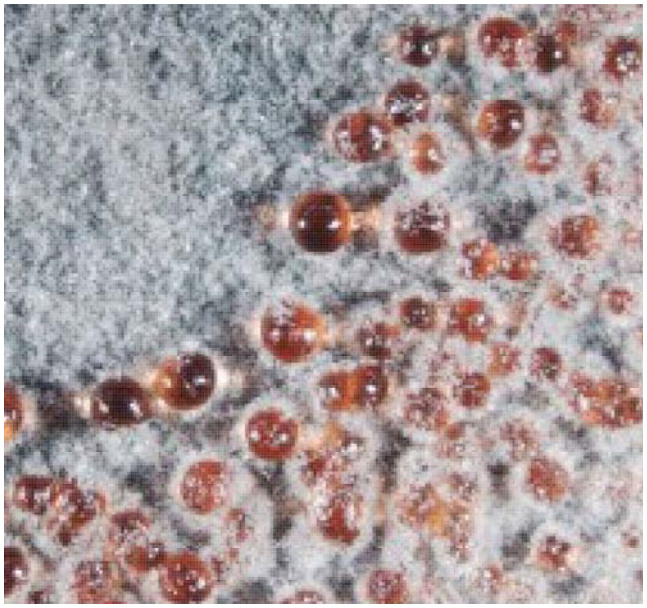

Figure 96. ***Talaromyces atroroseus*** colony. Photo by Jens C. Frisvad, Neriman Yilmaz, Ulf Thrane, Kasper Bøwig Rasmussen, Jos Houbraken, and Robert A. Samson, through Creative Commons.

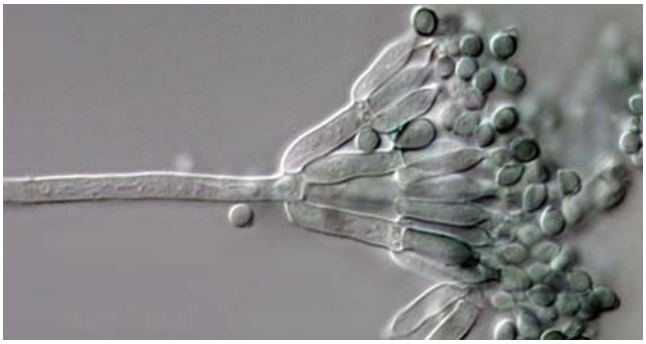

Figure 97. ***Talaromyces atroroseus***; ***Talaromyces flavus*** is frequent in the Domica Cave system in Slovakia. Photo by Jens C. Frisvad, Neriman Yilmaz, Ulf Thrane, Kasper Bøwig Rasmussen, Jos Houbraken, and Robert A. Samson, through Creative Commons.

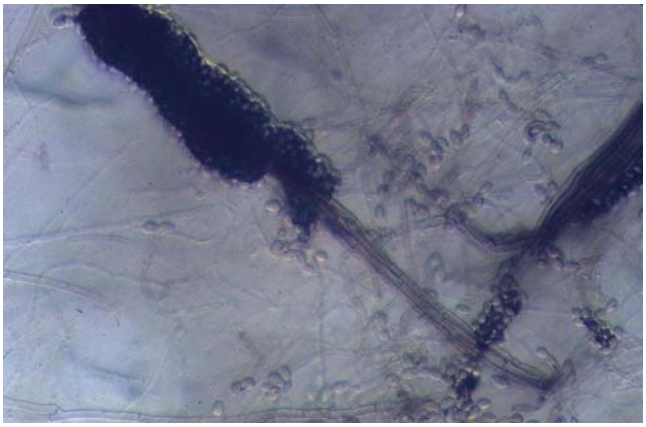

Figure 98. ***Doratomyces stemonitis***; ***Doratomyces*** is a frequent genus in the Domica Cave system in Slovakia. Photo by Gerald Holmes, through Creative Commons.

Summary

Caves are interesting ecotones of light and temperature gradients. They are further differentiated on type of substrate, *p*H, aspect, and air exchange. CO_2 levels can be higher than outside the cave, promoting greater photosynthesis in the limited light. Although conditions do fluctuate, they are more constant than outside the cave, being cooler in summer and warmer in winter. Because of these conditions, caves are often refugia, permitting the growth of species that do not grow elsewhere in the area.

A wide variety of caves exist, both large and small. Some are created in crevices, some among the rocks of talus slopes, and some in volcanic tubes, with a variety of other cave-like conditions as well. These can harbor rare species.

In addition to an array of bryophytes in the photic zone at the entrance of caves, others penetrate into the twilight zone. **Cyanobacteria**, algae, and fungi join the bryophytes, but usually penetrate farther into the darkness. ***Streptomyces*** (**Eubacteria**) species dominate the rock microbes. Among the **Cyanobacteria** ***Gloeocapsa*** often has the most species in a cave, but in others it is ***Chroococcus*** that has the most species.

Species like ***Scytonema julianum*** with heterocysts are able to fix atmospheric nitrogen gas into ammonia and ultimately amino acids.

Humidophila contenta, ***Hantzschia amphioxys***, and ***Orthoseira roeseana*** are among the most frequent diatoms in caves, although ***Pinnularia borealis*** is common in some areas. Frequent **Chlorophyta** include ***Stichococcus bacillaris*** and ***Klebsormidium flaccidum***. Fungi are most likely to be **Ascomycota** or **Zygomycota**, with **Basidiomycota** being relatively rare.

Rare and new species often occur in caves in the unusual conditions. Competition from tracheophytes is limited, further encouraging the growth algae and bryophytes.

Acknowledgments

Many Bryonetters responded to my call for images for this chapter. Wolfgang Hofbauer provided me with a paper that gave me a good list of current references on wind holes. Thank you to our Chinese colleagues (Wen Ye, Xinlei Guo, Yang Liu, Xiaoming Shao, and Wang Zhe) who responded to my request for the English translation of the abstract of a Chinese study.

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CHAPTER 18-2
CAVES – OVERALL BRYOPHYTE FLORA

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CHAPTER 18-2
CAVES – OVERALL BRYOPHYTE FLORA

Figure 1. Mammoth Cave entrance showing ferns and other plants at entrance and the rapid entrance into darkness. Photo through Creative Commons.

Bryophyte Flora

Overall

Lämmermayer (1912) described the bryophyte flora in 48 caves in Austria. He reported 72 bryophyte species. ***Eurhynchium*** *s.l.* was the most frequent genus and was represented by 6 species. ***Eurhynchium praelongum*** (Figure 2-Figure 3) occurred at only 200 lux. Thompson (1945) was among the early explorers of cave mosses. Rajczy (1978) explored the cave environment and its effect on mosses. Barr (1964) noted that the occurrence of numerous species of animal troglobites in any major limestone region is common and highly probable. But is that true of bryophytes?

Figure 2. ***Eurhynchium praelongum*** in England, member of the most common bryophyte genus in Austrian caves. Photo by Janice Glime.

Figure 3. ***Eurhynchium praelongum***, a species that occurred at 200 lux light intensity in an Austrian cave. Photo by Michael Lüth, with permission.

Hajdu (1977) opined that there are no true troglobites among the bryophytes because of their light limitations. Mosses (**Bryophyta**) form the bulk of the plant biomass in the caves studied in Hungary, and this seems to be the most likely case for most caves. Tracheophytes are more limited by light, and the algae and **Cyanobacteria** (Figure 4) form only thin crusts, thus contributing less to biomass.

Figure 4. **Cyanobacteria** and algae on rock formations in Lost River Caverns, Pennsylvania, USA. Photo by Janice Glime.

Studied Caves

I was surprised when I began this chapter to find how many studies there have been on cave bryophytes. Studies included the Azores (Figure 5) and Canary Islands (González-Mancebo *et al*. 1989, 1991, 1992); Jennings (2009) wrote a Master's thesis on bryophyte diversity in Azorean caves. Other studies include Isle of May (Watson 1953), Jura Souabe, Swabian Alps, Germany (Dobat (1970), Saarland, Germany (Weber 1989), grottos in Italy, karst caves in the Ercole cave area, and Carso Triestino of Italy (Lo Giudice & Privitera 1984; Polli & Sguazzin 2002; Castello 2011), Polish caves (Ziober 1980, 1981), sea caves on the Isle of Capri in Italy (Sguazzin 2005), Cave Baradla (Figure 6) in Hungary (Hajdu & Orban 1981), other caves in Hungary (Rajczy 1982, 1989, 1990), Cave Perama in Greece (Rajczy 1979), caves in Romania (Stefureac 1985), moss and algal development in an urbanized cave in Bulgaria (Stoyneva *et al*. 2002), and karst caves in England (Zhang & Pentecost 2002).

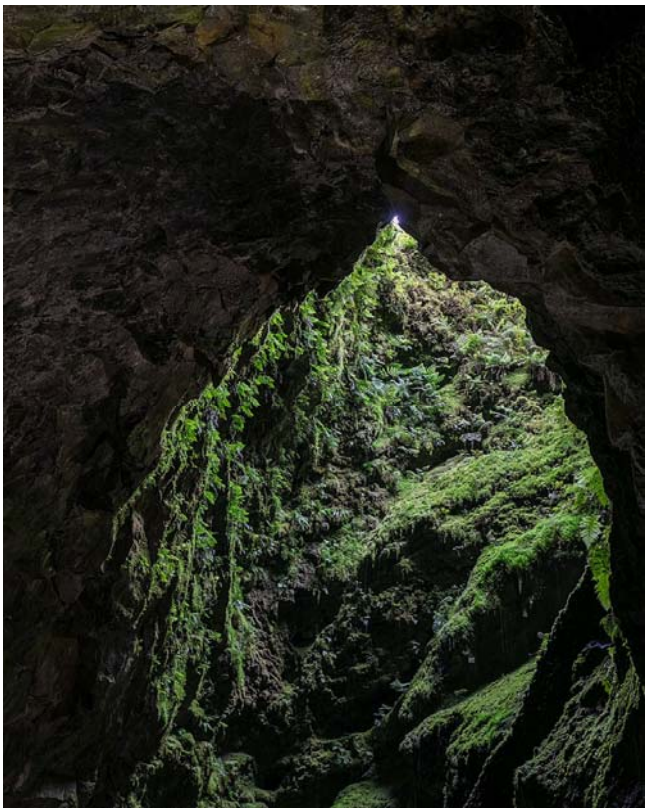

Figure 5. Cave in the Azores. Photo by Diego Delso, through Creative Commons.

Figure 6. Giant's Hall Baradla Cave, Hungary. Photo by Hanc Tomasz, through Creative Commons.

Cros and Rosselló (1984) relocated the mosses ***Palustriella commutata*** (Figure 7-Figure 8) and ***Eucladium verticillatum*** (Figure 9-Figure 10) reported by Maheu (1912) in caves of the Pityusic Islands in the Mediterranean Sea, but no bryophytes were mentioned in the early studies by Maheu (1912) in the coastal caves.

Figure 7. ***Palustriella commutata***, a long-time resident of caves in the Pityusic Islands, small islands in the Mediterranean Sea. Photo by Hermann Schachner, through Creative Commons.

Figure 8. Early spring or low light growth form that one might find of ***Palustriella commutata*** or ***P. decipiens***. Photo by Michael Becker, through Creative Commons.

Figure 9. ***Eucladium verticillatum*** in lime seep, a bryophyte that prefers limestone substrate. Photo by Resso Taelspeus, through Creative Commons.

Downing (1992) compared substrate preferences of bryophytes at three locations in southeastern Australia, including the Jenolan Caves (Figure 11). Limestone substrates had more abundant bryophytes, exhibiting more species and greater percent ground cover, than did nonlimestone substrates. Many of the species from limestone sites were typical of arid and semiarid habitats in Australia. Downing *et al*. (1995) listed the bryophytes of Wombeyan Caves (Figure 12) in New South Wales. Downing *et al*. (1997) revisited the Yarrangobilly Caves (Figure 13) in New South Wales, Australia, and reported that most of the mosses collected by Watts in 1906 were still present. Martin (2003) reported on the flora of a volcanic collapse pit on the lower slopes of Onehunga, Auckland.

Figure 10. ***Eucladium verticillatum***, a common bryophyte in limestone caves. Photo by Christian Berg, through Creative Commons.

Figure 11. Interior of Jenolan Caves, Australia. Photo by Janice Glime.

Figure 12. Wombeyan karst cave, Fig Tree Cave Interior, New South Wales, Australia. Photo by XLerate, through Creative Commons.

Figure 13. Yarrangobilly Caves, Australia. Photo by Colin Henein, through Creative Commons.

In China, Zhang (1993) described moss communities of the Maolan karst caves. Zhang and Wang (2002) studied them at the Flying-Dragon Cave. Wang and Zhang (2002) explored the bryophytes in karst caves in Guangxi Province, China. Zhang *et al*. (2005) studied karst caves in the Guilin area (Figure 14). Li *et al*. (2015, 2019) studied the karstification processes and bryophyte diversity in various locations in China. Cong *et al*. (2017) studied epilithic mosses on rock in the Puding karst area.

Figure 14. Cave in Guilin area, China. Photo by Michael Gunther, through Creative Commons.

Shiomi (1991) described the ecological distribution of bryophytes and other plants based on cave effects on the Akiyoshi-dai Plateau in Japan.

Ren *et al*. (2021) characterized the cave bryophyte flora as having a poor but unique diversity. They found that it was related to the vegetation and microhabitat. When comparing six karst caves with varying degrees and types of disturbance in southern China (Figure 15), they found a total of 43 angiosperm species, 20 lycophyte and fern species, and 20 species of bryophytes. The highest disturbance coincided with the lowest species richness, number of individuals, and Shannon-Wiener diversity index, but had the highest Simpson's dominance index. Less disturbance was the opposite, corresponding with the highest species numbers, numbers of individuals, and Shannon-Wiener diversity index, and lowest Simpson's dominance index. Diversity also was affected by habitat heterogeneity, light intensity, water status, and nutrient availability. Liverworts were more common in low-light conditions; mosses were more common in strong light and were more drought tolerant. Diversity of bryophytes and tracheophytes diminished from the entrance to the intermediate plots to the distant plots (Figure 16). The bryophytes form crusts around the lights, facilitating colonization by other plants.

Figure 15. Furong Cave, a karst cave in southern China. Photo by Brookchi, through Creative Commons.

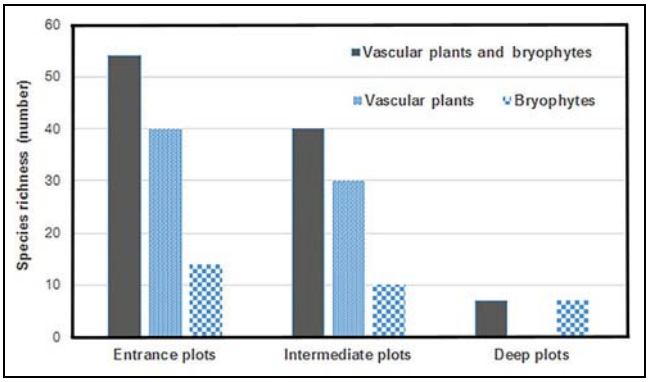

Figure 16. Cave species vs distance from entrance. Modified from Ren *et al*. 2021.

Pentecost (2010) found a total of 59 species, including 4 algae, 3 lichens, 47 bryophytes, 4 ferns, and only 1 angiosperm in Scoska Cave, UK (Figure 17). This is the most bryologically rich cave in Britain. Most (all but 9) of the species were recorded from other caves in Europe. Species richness declines rather irregularly from the entrance to 34 m depth, with relative irradiance decreasing from 12% of that in open sky to 0.004% at 34 m into the cave. Bryophytes occurred from 0-16 m into the cave, with relative irradiance decreasing to 0.2%. Only algae were able to grow at 34 m from the entrance. Whereas light decline represented a continuum, substratum characteristics and surface moisture were more irregular and accounted for various differences in the bryophyte flora.

Figure 17. Scoska Cave, UK. Photo by Bob Jenkins, through Creative Commons.

Moisture can also play a major role in determining the bryophyte flora. In one relatively dry cave on the Juan Fernandez Islands (Figure 18), Skottsberg (1935) found only the liverwort ***Balantiopsis purpurata*** (see Figure 19), although it was fairly well developed there. In another, ***Symphyogyna hochstetteri*** (see Figure 20) occurred in the illuminated edges of shallow pits, whereas ***Fissidens maschalanthus*** (see Figure 41-Figure 42) formed a closed carpet. In another cave Skottsberg found ***Balantiopsis purpurata***, ***Lepidozia*** sp. (Figure 21), ***Riccardia brevirarnosa*** (see Figure 98), ***Riccardia insularis*** (see Figure 98), and ***Symphyogyna hochstetteri***, and the mosses ***Distichophyllum subelimbatum*** (see Figure 22), ***Fissidens maschalanthus***, and several small areas of ***Philonotis krausei*** (see Figure 23). It is somewhat unusual to find more liverworts than mosses in a cave. On the Juan Fernandez Islands ***Riccardia insularis*** is not known outside the caves.

Figure 18. Juan Fernandez Islands, where dry caves have some unusual bryophyte species. Photo by Serpentus, through Creative Commons.

Figure 19. ***Balantiopsis*** sp.; ***Balantiopsis purpurata*** was the only liverwort found in a cave on the Juan Fernandez Islands off the coast of Chile. Photo by Felipe Osorio-Zúñiga, with permission.

Figure 20. ***Symphyogyna circinata***; ***Symphogyna hochstetteri*** occurs in the illuminated edges of shallow pits on the Juan Fernandez Islands. Photo by Jan-Peter Frahm, with permission.

Figure 21. ***Lepidozia reptans***; a species of ***Lepidozia*** occurs in at least one cave on the Juan Fernandez Islands. Photo by J. C. Schou, with permission.

Figure 22. ***Distichophyllum carinatum*** habitat in Allgau; ***Distihophyllum subelimbatum*** occurs in a cave on the Juan Fernandez Islands. Photo by Michael Lüth, with permission.

Figure 23. ***Philonotis fontana***; ***Philonotis krausei*** occurs in a cave on the Juan Fernandez Islands. Photo by Malcolm Storey, DiscoverLife.com, with online permission.

Bryophytes seem to be less diverse than algae in caves. Buczkó and Rajczy (1989) found 17 bryophyte taxa, compared to 49 algal taxa, in three caves in Hungary. The most characteristic moss was ***Amblystegium serpens*** (Figure 24-Figure 25).

Figure 24. ***Amblystegium serpens*** on rock ledge. Photo by Claire Halpin, with permission.

Figure 25. ***Amblystegium serpens*** leafy stem. Photo by Hermann Schachner, through Creative Commons.

Refugia

Caves often serve as refugia for rare species of more northern bryophytes, as observed in the Red River Gorge (Figure 26) of Kentucky, USA (Studlar & Snider 1989). Likewise, Christy and Meyer (1991) found that the **algific** (cold-producing) talus slopes in Wisconsin, USA, provided suitable microclimates for disjunct or relict plant and invertebrate populations. One third of the 39 species of bryophytes were restricted to the cold air vents there.

Figure 26. Red River Gorge, Kentucky, USA, showing caves in cliff. Photo by Jarek Tuszyński, through Creative Commons.

Puglisi *et al*. (2019) found boreo-arctic-montane species in some of the high mountain caves in Sicily; Fiol (1995) found that cavities in Mallorca (Figure 27) served as refugia. Alegro *et al*. (2015) found the circumpolar boreo-arctic montane ***Isopterygiopsis pulchella*** (Figure 28-Figure 29) and ***Platydictya jungermannioides*** (Figure 30-Figure 31) in rock crevices and caves as well as scattered in higher mountain areas of Croatia.

Figure 27. Cave at Porto Cristo, Mallorca. Photo by Lolagt, through Creative Commons.

Figure 28. ***Isopterygiopsis pulchella***, a species known from the low-light habitats of rock crevices and caves in Croatia. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Gabriel *et al.* (2006, 2011) considered the caves in the Azores (Figure 5) to serve as a refuge for bryophytes. Mulec (2018) likewise considered the dimly lit cave conditions to be refugia for some plants.

Figure 29. ***Isopterygiopsis pulchella***, a species of low-light locations. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

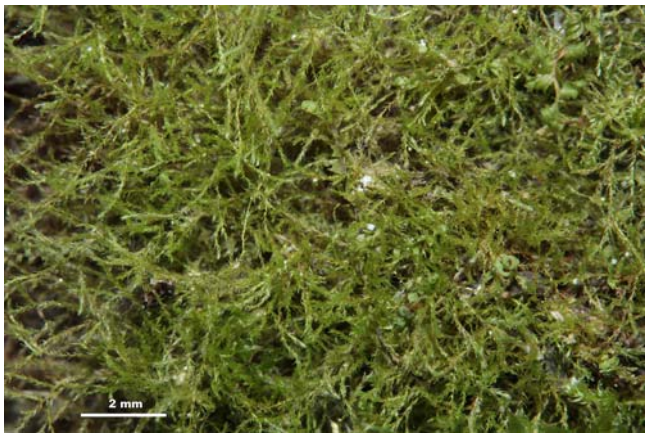

Figure 30. ***Platydictya jungermannioides***. Photo by Hermann Schachner, through Creative Commons.

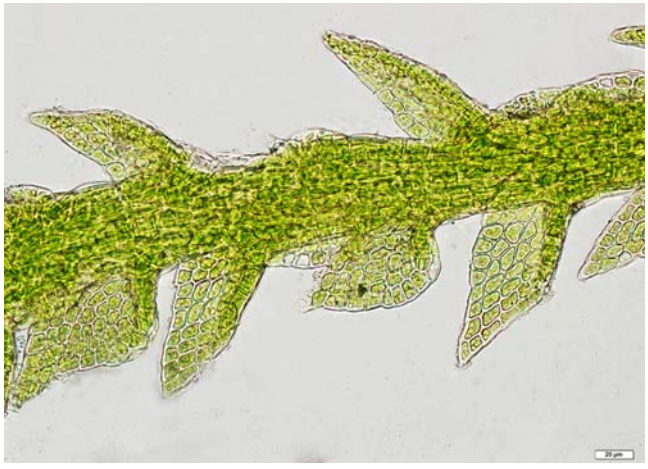

Figure 31. ***Platydictya jungermannioides*** branch. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

On the Socompa Volcano, Andes, Halloy (1991) found that at 6000 m asl communities of bryophytes, algae, fungi, lichens and animals formed at cave entrances where warm vapor (9-37ºC) was emitted. These warmer conditions at such high elevations permitted the development of communities, including bryophytes, up to 200 m².

Distance

In an artificial cave in the Iwato-jinjya area of Japan, Nakanishi (2002) found that bryophyte communities only extended 13 m into the cave, stopping 6 m short of the end of the cave (Table 1). The composition of the epigeous bryophyte communities changed more rapidly (ATR=5.97) (**ATR** = average turnover rate of species; Itow 1991) than did those of the other communities along the environmental gradients.

Table 1. Bryophytes on soil of Iwato-linjya, Minamitakaki, Nagasaki, Japan, showing position in the cave, up to 15 m. From Nakanishi 2002, with updated nomenclature.

Stand No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Cover degree (%)	40	60	60	80	80	70	80	80	90	80	100	90	100	100
Number of species	6	8	10	9	8	12	14	13	15	13	14	15	17	15
Distance from St. 1. (m)	0	1	2	3	4	5	6	7	8	9	10	11	12	13
Plagiomnium maximoviczii	12	22	22	22	33	22	22	22	12	12	12	+	+	+
Heteroscyphus planus	22	22	22	22	22	12	12	12	12	12	12	+	+	+
Eurhynchium savatieri	12	12	12	22	22	22	22	+2	22	+	+	+	+	+
Thuidium cymbifolium	+2	+2	+2	12	22	+2	·	·	·	·	·	·	·	·
Lophocolea minor	+	+2	+2	+2	+2	+2	·	·	·	·	·	·	·	·
Pellia endiviifolia	+	22	22	·	·	·	·	·	·	·	·	·	·	·
Heteroscyphus coalitus	·	12	12	12	·	·	·	·	·	·	·	·	·	·
Dumortiera hirsuta	·	11	11	12	·	22	33	33	33	·	·	·	·	·
Makinoa crispata	·	·	12	12	22	12	12	12	·	·	·	·	·	·
Ctenidium capillifolium	·	·	·	·	·	+	12	+2	33	·	·	·	·	·
Marchantia emarginata subsp. *tosana*	·	·	·	·	·	+	+	·	·	·	·	·	·	·
Taxiphyllum taxirameum	·	·	·	·	·	+	+	+	+	·	·	·	·	·
Mnium laevinerve	·	·	·	·	·	·	+	12	12	·	·	·	·	·
Conocephallum japonicum	·	·	·	·	·	·	12	12	12	33	33	33	+	+
Fissidens tosaensis	·	·	·	·	·	·	+	+	+	+2	12	12	·	+
Radula japonica	·	·	·	·	·	·	·	·	+	+2	+2	+2	+2	·
Bryum capillare	·	·	·	·	·	·	·	·	+	22	22	22	+2	+2
Fissidens crispulus	·	·	·	·	·	·	·	·	+	12	12	·	·	·
Brachythecium plumosum	·	·	·	·	·	·	·	·	·	·	22	22	22	33
Haplocladium microphyllum	·	·	·	·	·	·	·	·	·	·	12	12	22	22
Thamnobryum subseriatum	·	·	·	·	·	·	·	·	·	·	·	12	12	12
Isothecium subdiversiforme	·	·	·	·	·	·	·	·	·	·	·	12	12	+2
Thuidium pristocalyx	·	·	·	·	·	·	·	·	·	·	·	·	22	22
Bazzania tridens	·	·	·	·	·	·	·	·	·	·	·	·	+2	·

Lowe *et al*. (2013) found that the bottom of a lava tube cave (Figure 32) in Hawai'i was covered by bryophytes surrounding a puddle.

Prior (1961) provided a short review of cave bryophyte studies. He noted that the bryophytes from the Luray Caverns (Figure 33) in Virginia, USA, were all known from nearby areas in Virginia. Furthermore, the same genera were known from caves in Europe. These Luray Cavern species included ***Amblystegium serpens*** (Figure 24-Figure 25) (only 1 location, but with capsules), ***Anomodon rostratus*** (Figure 34), ***Ptychostomum pseudotriquetrum*** var. ***bimum*** (= ***Bryum pseudotriquetrum*** var. **bimum**; dense mats on moist limestone; see Figure 35-Figure 36), ***Campylium hispidulum*** (with sporophytes at 3 of 8 locations; on moist limestone and silt; Figure 37), ***Tortula obtusifolia*** (1 large mat on wet limestone with 2 capsules; Figure 38-Figure 39), ***Eurhynchium hians*** (on wet limestone, abundant, 3 of 19 collections with abundant sporophytes; Figure 40), ***Fissidens bryoides*** (moist limestone at cave entrance; Figure 41-Figure 42), ***Funaria hygrometrica*** (with numerous capsules; Figure 43), ***Leptobryum pyriforme*** (with numerous capsules at 10 of its 18 sites; Figure 44-Figure 45), ***Leskea polycarpa*** (on wet limestone, at edge of underground lake; Figure 46-Figure 47).

Figure 32. Lava tube, Maui, Hawai'i. Photo by Dronepicr, through Creative Commons.

Figure 33. Luray Cavern, Virginia, USA. Photo by Alejocrux, through public domain.

Figure 34. ***Anomodon rostratus*** dry, with capsules, a species known from caves in several locations, including Luray Caverns. Photo by Bob Klips, with permission.

Figure 35. ***Ptychostomum pseudotriquetrum***, a species forming dense mats on limestone in the Luray Cavern. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 36. ***Ptychostomum pseudotriquetrum*** stem showing rhizoids and decurrent leaf bases. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

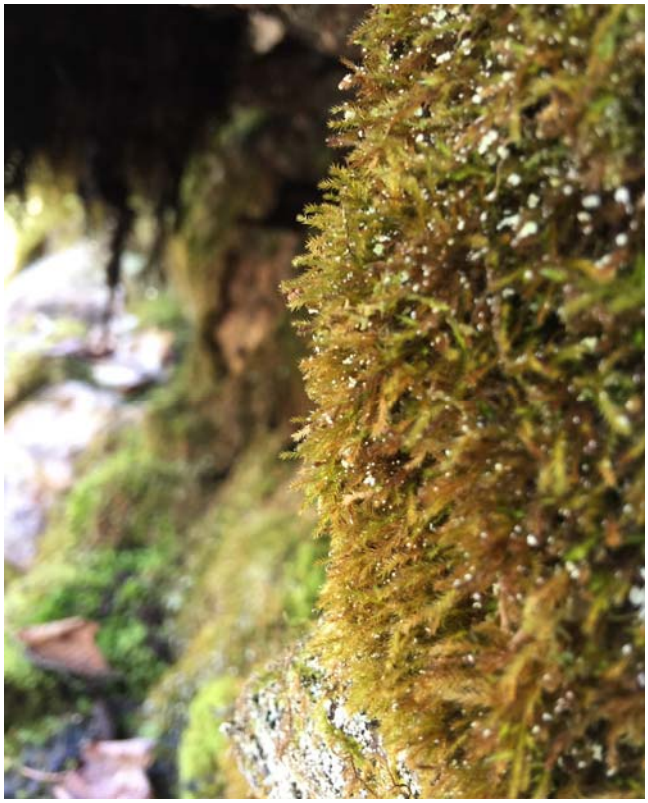

Figure 37. ***Campylium hispidulum*** on a vertical limestone wall, a species that occurs in Luray Caverns. Photo by Tom Neily, through Creative Commons.

Figure 38. ***Tortula obtusifolia*** on rock, a species that occurs in the Luray Caverns. Photo by Bob Klips, with permission.

Figure 39. ***Tortula obtusifolia*** on rock. Photo by Paul Wilson, with permission.

Figure 40. ***Eurhynchium hians***, a species that occurs in Luray Caverns. Photo by Bob Klips, with permission.

Figure 41. ***Fissidens bryoides*** with capsules, a species that occurs in the Luray Caverns. Photo courtesy of Donna Bennett.

Figure 42. ***Fissidens bryoides*** with retained protonemata. Photo by Dick Haaksma, with permission.

Figure 43. ***Funaria hygrometrica***, a species of low-competition habitats, usually exposed, that is known from Luray Caverns. Photo by Janice Glime.

Figure 44. ***Leptobryum pyriforme*** with capsules on rock, a species that occurs in Luray Caverns. Photo by Michael Lüth, with permission.

Figure 45. ***Leptobryum pyriforme*** stems. Photo by Štěpán Koval, with permission.

Figure 46. ***Leskea polycarpa*** in Denmark, a species that is known from Luray Caverns. Photo by Weblar, through Creative Commons.

Figure 47. ***Leskea polycarpa***. Photo from Snappy Goat, through public domain.

Numbers of Species

Sguazzin and Polli (2011) reported 7 liverworts and 25 mosses from a cave on Mount Saint Michael off the coast of Cornwall. Zhang and Pentecost (2002) found 65 bryophyte taxa in 41 genera and 20 families in various karst caves in England (from 1998 to 2000) and Pentecost and Zhang (2001) found 4 algae, 3 lichens, 47 bryophytes, 4 ferns, and 1 angiosperm in just the Scoska Cave (Figure 17), North Yorkshire, UK, the most species-rich cave known in Britain to date. All but nine of these species were known from other European caves. Castello and Strazzaboschi (2013) reported 9 liverworts and 33 mosses from Della Grotta Dell'orso (Figure 48) in Italy. In Sicily, Puglisi *et al*. (2019) identified 20 liverworts, 3 hornworts, and 113 mosses in 28 caves. Rajczy (1979) found only 2 liverworts and 14 mosses at the upper entrance of Cave Perama (Figure 49) in Greece, but only 7 mosses were found within the cave. Rajczy *et al*. (1986) reported 11 algae and 7 bryophyte taxa in one cave and 38 alga, 12 moss, 1 fern, and 1 angiosperm in another in the Bükk Mountains of Hungary (Figure 50).

Figure 48. Cave Grotta Dell'orso, Italy, a karst cave. Photo by Tiesse, through Creative Commons.

Figure 49. Cave interior, Perama Cave, Greece. Photo from <7toucans.com>, through Creative Commons.

Figure 50. Cave entrance, Balla-barlang Cave, Bükk Mountains, Hungary. Photo by Czina Tivadar, through Creative Commons.

Jedrejko and Ziober (1992) found 72 bryophyte species, including 10 liverworts, 59 mosses, and 3 mosses that remained unidentified in the Krackòw-Wieluñ Upland caves of Poland. Of these, 50% developed only in full access of light, with numbers of species diminishing with distance from the entrance.

In China, Zhang *et al*. (1996a, b) reported 59 bryophyte species in 43 genera from the karst caves of Huangguoshu. Zhang *et al*. (2005) found 28 species in only 18 genera in karst caves of the Guilin area, China (Figure 14).

Ammons (1933) found 46 moss and 44 liverwort species at the entrance of McKinney's Cave, West Virginia, USA. She noted the absence of ***Reboulia*** (Figure 51) and ***Eucladium*** (Figure 9-Figure 10). Within the cave she reported 31 liverwort species and 34 moss species, including 3 ***Sphagnum*** (Figure 69) species.

Figure 51. ***Reboulia hemispherica***, a cave dweller that was absent in McKinney's Cave, West Virginia, USA. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman and Karen Blisard.

Species

Mason-Williams and Benson-Evans (1967) described some of the ecological requirements of cave bryophytes in South Wales. Most of the caves visited had mesophilous forms with a *p*H tolerance of 4.8-7.0. These included ***Amblystegium serpens*** (Figure 24-Figure 25), ***Bryoerythrophyllum recurvirostrum*** (Figure 52-Figure 53), ***Thamnobryum alopecurum*** (Figure 54-Figure 55), ***Fissidens bryoides*** (Figure 41-Figure 42), ***F. taxifolius*** (Figure 56-Figure 57), ***Ctenidium molluscum*** (Figure 58), ***Rhizomnium punctatum*** (Figure 59). Few acid-tolerant forms occurred: ***Polytrichum juniperinum*** (Figure 60-Figure 61), ***Pseudotaxiphyllum elegans*** (Figure 62-Figure 64), ***Hypnum cupressiforme*** (Figure 65-Figure 66), ***Blindia acuta*** (Figure 67-Figure 68), ***Sphagnum subnitens*** (Figure 69). The mesophilic liverworts ***Pellia epiphylla*** (Figure 70-Figure 71) and ***Plagiochila asplenioides*** (Figure 72) were also present at most sites. Surprisingly, to me at least, ***Pellia endiviifolia*** (Figure 73) and ***Conocephalum conicum*** (Figure 74-Figure 75) were found less frequently. Mason-Williams and Benson-Evans (1958) considered ***Pseudotaxiphyllum elegans*** to be one of the most shade-tolerant mosses in acid sites.

Figure 52. ***Bryoerythrophyllum recurvirostrum*** on rock wall. Photo by Calum McLennan, through Creative Commons.

Figure 53. ***Bryoerythrophyllum recurvirostrum*** showing red bases. Photo by Christian Berg, through Creative Commons.

Figure 54. ***Thamnobryum alopecurum*** in limestone cave at Traeth Glaslyn Nature Reserve, Wales. Photo by Janice Glime.

Figure 55. ***Thamnobryum alopecurum***. Photo by David T. Holyoak, with permission.

Figure 56. ***Fissidens taxifolius***, a species that occurs in caves in South Wales. Photo by David T. Holyoak, with permission.

Figure 57. ***Fissidens taxifolius***. Photo by Hermann Schachner, through Creative Commons.

Figure 58. ***Ctenidium molluscum***, a mesophilous species from South Wales caves. Photo by Hermann Schachner, through Creative Commons.

Figure 59. ***Rhizomnium punctatum***, a mesophilous species from South Wales caves. Photo by Bob Klips, with permission.

Figure 60. ***Polytrichum juniperinum*** on rock, a mesophilous species in South Wales caves. Photo by Robbie Hannawacker, through public domain.

Figure 61. ***Polytrichum juniperinum*** showing leaves with edges rolled over (**arrow**) and calyptra over young sporophyte. Photo from Botany Website, UBC, with permission.

Figure 62. ***Pseudotaxiphyllum elegans*** on wall, a species that grows in South Wales caves. Photo by Hermann Schachner, through Creative Commons.

Figure 63. ***Pseudotaxiphyllum elegans*** showing growth form. Photo from Botany Website, UBC, with permission.

Figure 64. ***Pseudotaxiphyllum elegans*** asexual propagules produced in winter, a typical means of propagation in caves. Photo from Botany Website, UBC, with permission.

Figure 65. ***Hypnum cupressiforme*** on rock in a minicave. Photo by Fabio Clanferoni, through Creative Commons.

Figure 66. ***Hypnum cupressiforme*** with capsules. Photo by Aconcagua, through Creative Commons.

Figure 67. ***Blindia acuta*** on rock, a species that occurs in caves in South Wales. Photo by David T. Holyoak, with permission.

Figure 68. ***Blindia acuta*** with capsules, on rock. Photo by David T. Holyoak, with permission.

Figure 69. ***Sphagnum subnitens*** with capsules, a species that can occur in caves in South Wales. Photo by David T. Holyoak, with permission.

Figure 70. ***Pellia epiphylla***, a species that occurs in caves in South Wales. Photo by Frank Vincentz, through Creative Commons.

Figure 71. ***Pellia epiphylla*** with capsules. Photo by Hermann Schachner, through Creative Commons.

Figure 72. ***Plagiochila asplenioides***, a species that occurs in caves in South Wales. Photo by J. C. Schou, with permission.

Figure 73. ***Pellia endiviifolia*** with capsules, a species that occurs in caves in South Wales. Photo by Hermann Schachner, through Creative Commons.

Figure 74. ***Conocephalum conicum*** on cave roof. Photo by Allen Norcross, with permission.

Figure 75. ***Conocephalum conicum***, a species that occurs in caves in South Wales. Photo by Lairich Rig, through Creative Commons.

In North America, Maheu (1926) explored Mammoth Cave (Figure 76) and two others in Kentucky, USA. The bryophytes in all three caves were identical: the mosses ***Anomodon attenuatus*** (Figure 77-Figure 78), ***A. rostratus*** (Figure 34), ***Brachythecium rivulare*** (Figure 79), ***Eurhynchium praelongum*** (Figure 2-Figure 3), ***Gymnostomum calcareum*** (Figure 80-Figure 81), and ***Plagiomnium rostratum*** (Figure 82), and the thallose liverwort ***Marchantia polymorpha*** (Figure 83). Maheu described the plants as etiolated, and lacking sporophytes. ***Marchantia polymorpha*** occurred in the least light but did not exhibit the morphological changes seen in the other species.

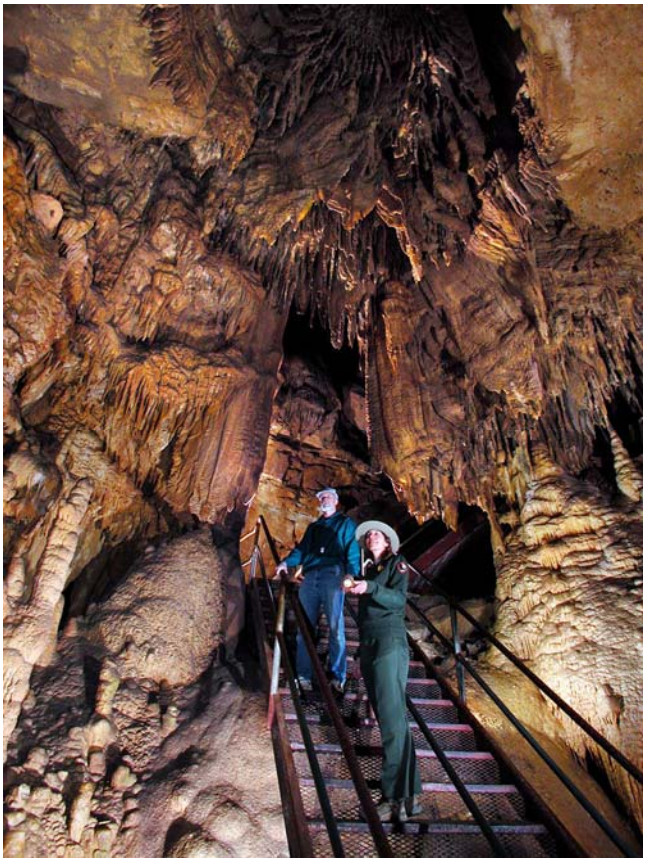

Figure 76. Mammoth Cave National Park. Photo through public domain.

Figure 77. ***Anomodon attenuatus***, a species that occurs in Mammoth Cave. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 78. ***Anomodon attenuatus*** wet. Photo by Hermann Schachner, through Creative Commons.

Figure 79. ***Brachythecium rivulare***, a species that occurs in Mammoth Cave, Kentucky. Photo by Hugues Tinguy, with permission.

Figure 80. ***Gymnostomum calcareum*** on rock, a species that occurs in Mammoth Cave. Photo by L. Jensen, University of Auckland, with online permission.

Figure 81. ***Gymnostomum calcareum***. Photo by L. Jensen, University of Auckland, with online permission.

Figure 82. ***Plagiomnium rostratum***, a species that occurs in Mammoth Cave. Photo by Hermann Schachner, through Creative Commons.

Figure 83. ***Marchantia polymorpha***, a species that occurs in Mammoth Cave. The cups contain gemmae that are a primary means of dispersal in caves. Photo by Jan-Peter Frahm, with permission.

Puglisi *et al.* (2019) found the mosses ***Amphidium mougeotii*** (Figure 84-Figure 85), ***Isopterygiopsis pulchella*** (Figure 28), ***Rhynchostegiella tenella*** (Figure 86-Figure 87), and ***Thamnobryum alopecurum*** (Figure 54-Figure 55), to be well adapted to the cave environment.

Figure 84. ***Amphidium mougeotii*** on rock, a species that is well adapted to cave life.. Photo by Hugues Tinguy, with permission.

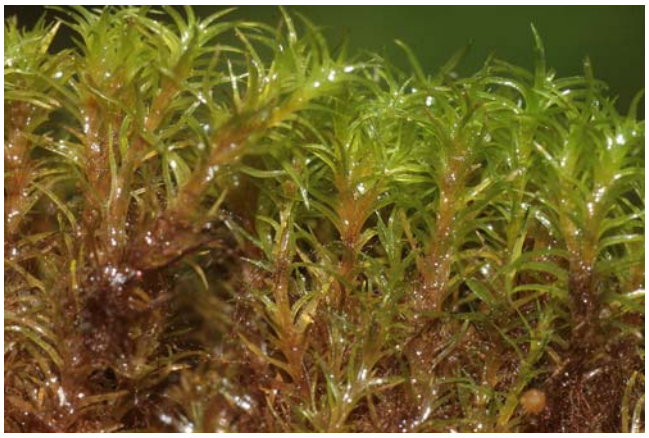

Figure 85. ***Amphidium mougeotii***, Photo by Hermann Schachner, through Creative Commons.

Figure 86. ***Rhynchostegiella tenella*** on a rock ceiling. Photo by Andy Hodgson, with permission.

Figure 87. ***Rhynchostegiella tenella*** with many sporophytes, on rock. Photo by Michael Lüth, with permission.

Among the 17 bryophyte species in three Hungarian caves (*e.g.* Figure 6), the most common included ***Pellia endiviifolia*** (Figure 73), ***Amblystegium serpens*** (Figure 24-Figure 25), ***Bryum*** sp. (see Figure 88), ***Encalypta vulgaris*** (Figure 89), ***Eucladium verticillatum*** (Figure 9-Figure 10), ***Eurhynchium schleicheri*** (Figure 90), ***Fissidens taxifolius*** (Figure 56-Figure 57), ***Plagiomnium cuspidatum*** (Figure 91), ***Rhynchostegiella tenella*** (Figure 86-Figure 87), and ***Rhynchostegium murale*** (Figure 92) (Buczkó & Rajczy 1989).

Figure 88. ***Bryum capillare***; a species of ***Bryum*** is common in some Hungarian caves. Photo by Andy Hodgson, with permission.

Figure 89. ***Encalypta vulgaris*** with capsules, on rock, a species known from Hungarian caves. Photo by Kai Vellak, through Creative Commons.

Figure 90. ***Eurhynchium schleicheri***, a species known from Hungarian caves. Photo by Hugues Tinguy, with permission.

Figure 91. ***Plagiomnium cuspidatum***, a species known from Hungarian caves. Photo by Bob Klips, with permission.

Figure 92. ***Rhynchostegium murale***, a species known from Hungarian caves. Photo by Michael Lüth, with permission.

The flora of a very wet rock cave in Corsica, France, however, had a different array of species (Sotiaux *et al*. 2007). These included ***Aneura maxima*** (Figure 93-Figure 95), ***Lophocolea fragrans*** (Figure 96-Figure 97), and ***Riccardia multifida*** (Figure 98) near a stream in the cave; ***Plagiothecium cavifolium*** (Figure 99) occurred in a rock cave along a stream. ***Neckera menziesii*** (Figure 100) occurred in microcaves in schist rocks. ***Gymnostomum aeruginosum*** (Figure 101-Figure 102) was more typical of caves, occurring in a rock cave.

Figure 93. ***Aneura maxima*** habitat in ravine in Norway, a habitat shaded by a deep cut in the rock. Photo by Jan-Peter Frahm, with permission.

Figure 94. ***Aneura maxima***, a species known from near a stream in a rock cave in Corsica. Photo by Jan-Peter Frahm, with permission.

Figure 95. ***Aneura maxima*** branch of thallus. Photo by Hugues Tinguy, with permission.

Figure 96. ***Lophocolea fragrans***, a species known from near a stream in a rock cave in Corsica. Photo by David T. Holyoak, with permission.

Figure 97. ***Lophocolea fragrans*** branch. Photo by George G., through Creative Commons.

Figure 98. ***Riccardia multifida***, a species known from near a stream in a rock cave in Corsica. Photo by Hermann Schachner, through Creative Commons.

Figure 99. ***Plagiothecium cavifolium***, a species that occurs in a rock cave along a stream in Corsica. Photo by Hermann Schachner, through Creative Commons.

Figure 100. ***Neckera menziesii***, a species that occurs in a rock cave along a stream in Corsica. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 101. ***Gymnostomum aeruginosum*** on limestone rock. Photo by Bob Klips, with permission.

Figure 102. ***Gymnostomum aeruginosum*** with capsules and ***Nostoc***, a species that occurs in a rock cave along a stream in Corsica. Photo by Hermann Schachner, through Creative Commons.

Rajczy *et al*. (1986) were unable to relocate four cave species in a Hungarian cave. One of these was a typical cave dweller, ***Eucladium verticillatum*** (Figure 9-Figure 10), which may have been destroyed by excavations. ***Rhynchostegiella tenella*** (Figure 86-Figure 87), a typical cave moss, was found as new.

Tanaka *et al*. (2001) discussed the mosses of a limestone cave in Kyushi, Japan.

Zonation

The steepest and most evident zonation pattern in caves is related to light intensity. Pentecost and Zhang (2001) found that species richness exhibited an irregular decline from the entrance (12% relative irradiance compared to open sky) to 0.004% relative irradiance at 34 m depth. Bryophytes occurred at 0-16 m in light that declined to 0.2% relative irradiance. Differences in substrate characters and surface moisture caused the irregularities in bryophyte decline with distance.

Zhang *et al*. (1996b) identified 68 communities of bryophytes in 7 karst caves in the Huangguoshu area of China. They classified the ecological distribution of the bryophytes as limestone and dolomite, limestone soil, and cave tufa.

Hajdu (1977) considered the zones to be cave entrances, area around lights, and darkness. Hajdu considered the cave-dwelling plants to have extremely low ecological requirements. Nevertheless, there seems to be no species that is restricted to cave environments.

More commonly, caves are divided into three major zones based on light intensity. These are **entrance** (Figure 1), **twilight**, and **dark** zone (World Atlas 2021). But perhaps this is not the most appropriate classification for photosynthetic organisms since they are unable to occupy the third zone.

Hajdu (1977) described the vegetation changes within the cave from the most harsh habitat to the most favorable. In that order, they progressed from blue-green bacteria to green algae and diatoms to mosses and finally in the best conditions to ferns. But he noted that the larger plants will eventually outgrow the smaller ones, thus causing mosses to replace the algae. Fiol (1995) examined bryophytes at cavity entrances in Mallorca (Figure 27) and described different regions, especially in shafts.

Uniyal *et al*. (2007) described the zonation seen in an array of caves as a result of decreasing light. They found that the liverworts ***Plagiochasma appendiculatum*** (Figure 103-Figure 104), ***Plagiochasma pterospermum***, ***Plagiochila chinensis*** (Figure 105), ***Porella densifolia*** (see Figure 106), and ***Targionia hypophylla*** (Figure 107-Figure 108), and mosses ***Anomodon rugelii*** (Figure 109-Figure 110), ***Plagiothecium neckeroideum*** (Figure 111-Figure 112), and ***Pelekium versicolor*** (Figure 113) occur at the twilight zone near the cave entrance. ***Funaria*** (Figure 43) and ***Cyathodium*** (Figure 115) invade the bare substrate further into the cave. ***Cryptomitrium himalayense*** (see Figure 114), ***Cyathodium tuberosum*** (Figure 115), ***Lejeunea*** (Figure 116), ***Fissidens*** (Figure 56-Figure 57), ***Isopterygium albescens*** (see Figure 117), and ***Plagiothecium neckeroideum*** occur on rock ledges in the cave interior. Even further from the entrance light one might find ***Cryptomitrium***. ***Stephensoniella brevipedunculata*** (Figure 118) and ***Hymenostylium recurvirostrum*** (Figure 119-Figure 120) may grow together in deep-shaded caves (Tewari *et al*. 1994).

Figure 103. ***Plagiochasma appendiculatum***, a species of the twilight zone, but near the cave entrance. Photo by Michael Lüth, with permission.

Figure 104. ***Plagiochasma appendiculatum*** with archegoniophores. Photo by Michael Lüth, with permission.

Figure 105. ***Plagiochila chinensis***, a species of the twilight zone, but near the cave entrance. Photo by Yang Jia-Dong, through Creative Commons.

Figure 106. ***Porella obtusata***; ***Porella densifolia*** is a species of the twilight zone, but near the cave entrance. Photo by Michael Lüth, with permission.

Figure 107. ***Targionia hypophylla*** on rock, a species of the twilight zone, but near the cave entrance. Photo by Malcolm Storey, DiscoverLife.com, with online permission.

Figure 108. ***Targionia hypophylla*** showing purplish pouches beneath thallus. Photo by Ken Ichi Ueda, through Creative Commons.

Figure 109. ***Anomodon rugelii*** dry, a species of the cave twilight zone, but near the cave entrance. Photo by Hugues Tinguy, with permission.

Figure 110. ***Anomodon rugelii*** wet. Photo by Hermann Schachner, through Creative Commons.

Figure 111. ***Plagiothecium neckeroideum***, a species of rock ledges in the cave interior. Photo by Taiwan Life Encyclopedia, through Creative Commons.

Figure 112. ***Plagiothecium neckeroideum***. Photo by David Long, with permission.

Figure 113. ***Pelekium versicolor***, a species able to live in the twilight zone. Photo by John C. Brinda, through Creative Commons.

Figure 114. ***Cryptomitrium tenerum***; ***Cryptomitrium teneriffae*** is a species able to live in the twilight zone of caves. Photo by Sachacari, through Creative Commons.

Figure 115. ***Cyathodium tuberosum***, a species of the twilight zone, but near the cave entrance. Photo by Silvia Pressel and Jeff Duckett, with permission.

Figure 116. ***Lejeunea lamacerina***; a species of ***Lejeunea*** occurs on rock ledges in the cave interior. Photo by Andrew Hodgson, with permission.

Figure 117. ***Isopterygium tenerum***, a species of rock ledges in the cave interior. Photo from Biopix, through Creative Commons.

Figure 118. ***Stephensoniella brevipedunculata***, a species able to grow in the deeper shade of caves. Photo by Anil Sharma, permission pending.

Figure 119. ***Hymenostylium recurvirostrum*** on cliff face, a species able to grow in the deeper shade of caves. Photo by Bob Klips, with permission.

Figure 120. ***Hymenostylium recurvirostrum*** with capsules. Photo by Paul Wilson, with permission.

Some mosses don't seem to be as sensitive to the diminishing light. Ren *et al*. (2021) reported that among 20 bryophyte species in six karst caves in southern China, ***Eurhynchium hians*** (Figure 40), ***Fissidens teysmannianus*** (Figure 121), and ***Taxiphyllum taxirameum*** (Figure 122-Figure 123) occur in entrance plots, intermediate plots, and deep plots, the latter two having different degrees of light in the twilight zone.

Figure 121. ***Fissidens teysmannianus*** on rock ledge, a species that occurs in entrance, intermediate, and deep locations in Chinese caves. Photo by Wuchan Kwan, permission pending.

Figure 122. ***Taxiphyllum taxirameum*** in Ohio, a species that occurs in entrance, intermediate, and deep locations in Chinese caves. Photo by Bob Klips, with permission.

Figure 123. ***Taxiphyllum taxirameum*** with capsule. Photo by Bob Klips, with permission.

Li *et al*. (2019) identified three zones for liverworts in four caves in the Guizhou Province, China: middle-depth cave, mainly of ***Cyathodium smaragdinum*** (Figure 124) + ***Pellia endiviifolia*** (Figure 73) + ***Riccia fluitans*** (Figure 125); lower-middle-depth cave, mainly of ***Cyathodium smaragdinum*** + ***Riccia fluitans***; bottom cave, mainly including ***Pellia endiviifolia*** + ***Conocephalum japonicum*** (Figure 126) + ***Dumortiera hirsuta*** (Figure 127). These caves tended to have 1-2 dominant liverwort species. The diversity in both vertical and horizontal distances from the entrance were affected by the gradient variation of temperature, humidity, and illumination.

Figure 124. ***Cyathodium smaragdinum*** on rock, a species that occurs at a middle depth in caves of Guizhou Province, China. Photo through Creative Commons.

Figure 125. ***Riccia fluitans***, a species that occurs at a middle depth in caves of Guizhou Province, China. Photo by Ralf Wagner, with permission.

Figure 126. ***Conocephalum japonicum***, a species that occurs at the bottom of caves of Guizhou Province, China. Photo by David Long, with permission.

Figure 127. ***Dumortiera hirsuta***, a species that occurs at the bottom of caves of Guizhou Province, China. Photo by Michael Lüth, with permission.

Summary

Among the cave bryophyte flora, ***Eurhynchium*** often is represented by the most species, often occurring in very low light (200 lux). But light limitation limits the number of bryophyte species able to grow at any distance into the cave, creating zones known as **entrance**, **twilight**, and **dark**. Algae and **Cyanobacteria** typically comprise more species than do bryophytes; liverworts are usually few in species number. Light conditions create a zonation pattern of ferns in the best conditions, to moss, to algae, and in the most distant photic zone, the **Cyanobacteria**. Disturbance further limits the species richness. And as one might expect, richness decreases with distance from the cave entrance. Nevertheless, the cave bryophyte flora tends to be unique, with some species known only from caves in some regions. Caves serve as refugia in many geographic regions.

There are many studies on the cave flora in Europe and Asia, but studies occur on all the continents. ***Eucladium verticillatum*** occurs frequently on both sides of the Atlantic and may contribute to the formation of stalactites in limestone caves. Likewise, ***Amblystegium serpens*** is common is a wide range of caves and locations. The Australian cave species tend to be species from arid and semiarid habitats.

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CHAPTER 18-3
CAVES – ZONES OF BRYOPHYTE FLORA

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CHAPTER 18-3
CAVES – ZONES OF BRYOPHYTE FLORA

Figure 1. View of the twilight zone and entrance light at Son Doong Cave, Vietnam. Photo by Doug Knuth, through Creative Commons.

Habitat Differences

Cave Mouth Area

The area near the opening of the cave (Figure 1) can often have its own flora, different from the surrounding area and different from the cave entrance. These floral differences result from exposed rock of the cave, cool air emitted from the cave, and differing moisture conditions. Depending on the site, it might be drier due to exposure, but it can also be moister from air emitted by the cave. This is particularly true of caves with additional openings elsewhere among the rocks.

Conard (1938) found ***Pohlia elongata*** (Figure 2) with capsules and ***Pohlia proligera*** (Figure 3) with propagules around a cave mouth near Au Train, Michigan, USA. Capsules are typically uncommon within caves, but conditions of light and moisture, coupled with seasonal changes, can support the production of sporophytes near the entrance.

Figure 2. ***Pohlia elongata*** capsules, a species found with capsules around a cave mouth in Michigan, USA. Photo by David T. Holyoak, with permission.

Figure 3. ***Pohlia proligera*** with numerous propagules among the leaves, a species that occurs around a cave mouth in Michigan, USA. Photo by Hermann Schachner, through Creative Commons.

Areas near entrances can even support species unique in the area. For example, Aziz (2011) reported ***Tortula truncata*** (Figure 4) in rock fissures and at the mouth of Baston cave, a new species for Iraq.

Figure 4. ***Tortula truncata*** with numerous capsules, a species found for the first time in Iraq around a cave entrance. Photo from Botany Website, UBC, with permission.

Salamah *et al*. (2019) found six bryophyte species in the area near the Selarong Cave, Indonesia. These were ***Hyophila involuta*** (Figure 5-Figure 6), ***Barbula consanguinea*** (see Figure 7), ***Bryum erythropus*** (see Figure 123), ***Weissia controversa*** (Figure 8-Figure 9), ***Preissia*** sp. (Figure 10-Figure 11), and ***Vesicularia dubyana*** (Figure 12).

Figure 5. ***Hyophila involuta*** dry, a species that occurs in the area near a cave in Indonesia. Photo by Wayne Lampa, through Creative Commons.

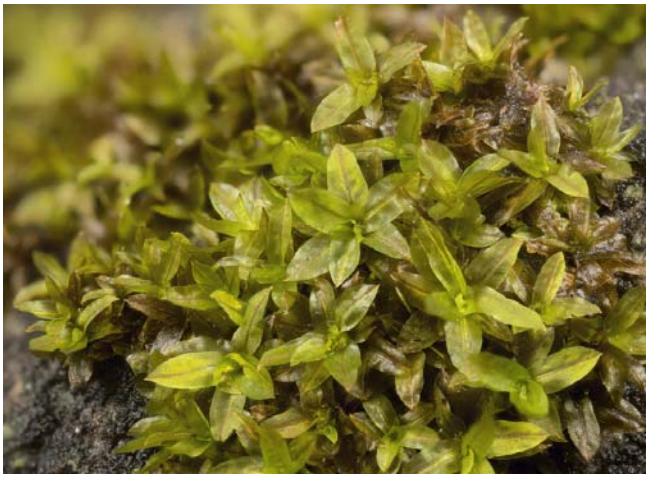

Figure 6. ***Hyophila involuta*** wet. Photo by Bob Klips, with permission.

Figure 7. ***Barbula unguiculata*** with capsules on wall, a species that occurs in the area near a cave in Indonesia. Photo by Susan Marley, through Creative Commons.

Figure 8. ***Weissia controversa*** on rock, a species that occurs in the area near a cave in Indonesia. Photo by Andrew Hodgson, with permission.

Figure 9. ***Weissia controversa*** with capsules. Photo by Hermann Schachner, through Commons.

Figure 10. ***Preissia quadrata***, in a genus that occurs in the area near a cave in Indonesia. Photo by Hermann Schachner, through Creative Commons.

Figure 11. ***Preissia quadrata*** with mature archegoniophores and dying thallus. Photo by Jiří Kameníček (BioLib, Obázek), with permission.

Figure 12. ***Vesicularia dubyana***, a species that occurs in the area near a cave in Indonesia. Photo by Tan Sze Wei, Aquamoss website <www.aquamoss.net>, with permission.

Castello and Strazzaboschi (2013) noted that the cave entrance of Grotta dell'Orso (Figure 13), a cave of the karst area of Trieste, Italy, is more bryologically rich than the area near the cave mouth despite the smooth, rocky walls and poor light in the entrance. Outside the cave most of the plants are concentrated in the first 50 cm above the ground where they experience higher humidity, particularly in small cornices, ravines, and rock irregularities. ***Conocephalum conicum*** (Figure 14) forms large colonies on the ground near the entrance.

Figure 13. Grotta dell'orso, Italy, cave mouth. Photo by Tiesse, through Creative Commons.

Figure 14. ***Conocephalum conicum*** males, a species that forms large colonies in the area near the entrance of Grotta dell'orso, Italy. Photo by Janice Glime.

Castello and Strazzaboschi (2013) described the exterior of the Della Grotta Dell'orso Cave (Figure 13). The exterior near the entrance had a northern exposure with intense dripping. They found that these conditions permitted growth of numerous bryophytes that are typical of the cave interiors, particularly from the shady, damp walls at the entrance. However, in the darker interior, few species are present, and only develop to about 10 m into the cave.

Puglisi *et al*. (2018) recognized a number of communities in the entrance and twilight area of Sicilian caves. In the lava caves, these included the liverwort species of ***Plagiochasma rupestre*** (Figure 15-Figure 16), ***Riccia glauca*** (Figure 17-Figure 18), and ***Targionia hypophylla*** (Figure 19); hornwort ***Anthoceros crispatus*** (see Figure 20); and moss species of ***Amphidium mougeotii*** (Figure 21-Figure 22), ***Bartramia ithyphylla*** (Figure 23), ***Brachythecium velutinum*** (Figure 24-Figure 25), ***Pohlia annotina*** (Figure 26-Figure 27), ***Pohlia cruda*** (Figure 28), ***Rhabdoweisia fugax*** (Figure 29), ***Rhynchostegiella tenella*** (Figure 30), and ***Timmia bavarica*** (Figure 31). In the karst caves they found ***Eucladium verticillatum*** (Figure 32-Figure 33), ***Thamnobryum alopecurum*** (Figure 34), ***Timmiella barbuloides*** (see Figure 35), and ***Weissia controversa*** (Figure 8-Figure 9).

Figure 15. ***Plagiochasma rupestre*** on rock, a species that occurs in lava caves. Photo by Rory Hodd, with permission.

Figure 16. ***Plagiochasma rupestre*** with archegoniophores. Photo by Valter Jacinto, through Creative Commons.

Figure 17. ***Riccia glauca*** on soil, a species that occurs in lava caves. Photo by Bernd Haynold, through Creative Commons.

Figure 18. ***Riccia glauca***. Photo by Štěpán Koval, with permission.

Figure 19. ***Targionia hypophylla***, a species that occurs in lava caves in Sicily. Photo by Luis Fernández García, through Creative Commons.

Figure 20. ***Anthoceros*** sp.; ***Anthoceros crispatus*** occurs in the entrance and twilight area of Sicilian lava caves. Photo from USFWS, through Creative Commons.

Figure 21. ***Amphidium mougeotii*** on rock wall with snow, a species that occurs in the entrance and twilight area of Sicilian lava caves. Photo by Tuomo Kuitunen <luopioistenkasvisto.fi.>, with permission.

Figure 22. ***Amphidium mougeotii***. Photo from Northern Forest Atlas, with permission through Jerry Jenkins.

Figure 23. ***Bartramia ithyphylla*** with capsules on rock, a species that occurs in lava caves. Photo by Štěpán Koval, with permission.

Figure 24. ***Brachythecium velutinum*** among rocks, a species that occurs in lava caves. Photo by Michael Lüth, with permission.

Figure 25. ***Brachythecium velutinum***. Photo by Michael Lüth, with permission.

Figure 26. ***Pohlia annotina*** among rocks, a species that occurs in lava caves. Photo by Hermann Schachner, through Creative Commons.

Figure 27. ***Pohlia annotina*** with bulbils, a common means of reproduction in caves. Photo by Hermann Schachner, through Creative Commons.

Figure 28. ***Pohlia cruda*** on rock, a species that occurs in lava caves. Photo by Štěpán Koval, with permission.

Figure 29. ***Rhabdoweisia crispata*** shaded at rock base, a species that occurs in lava caves. Photo by Tuomo Kuitunen <luopioistenkasvisto.fi.>, with permission.

Figure 30. ***Rhynchostegiella tenella*** with capsules, a species that occurs in the entrance and twilight area of Sicilian lava caves. Photo by Michael Lüth, with permission.

Figure 31. ***Timmia bavarica***, a species that occurs in lava caves. Photo by Štěpán Koval, with permission.

Figure 32. ***Eucladium verticillatum*** habitat or rock cliff face, a species that occurs in the karst caves of Sicily. Photo by Dick Haaksma, with permission.

Figure 33. ***Eucladium verticillatum*** with mite. Photo by Barry Stewart, with permission.

Figure 34. ***Thamnobryum alopecurum***, a species that occurs in the karst caves of Sicily. Photo by Michael Lüth, with permission.

Figure 35. ***Timmiella*** sp.; ***Timmiella barbuloides*** occurs in the karst caves of Sicily. Photo by Ken-Ichi Ueda, through Creative Commons.

The cave mouth can influence the vegetation near the entrance due to moist and cool air drafts emanating from the cave. Dalton (1995) found ***Seligeria cardotii*** (see Figure 36) as a new record for Tasmania on a moist calcareous rock face that was overhanging the entrance to a small cave. The moist conditions of the habitat were attributed to the limestone cave entrance and supported a lush bryophyte and fern flora there.

Figure 36. ***Seligeria*** sp.; ***Seligeria cardotii*** occurs in Tasmania on a moist calcareous rock face overhanging the entrance to a small cave. Photo by Bob Klips, with permission.

Gabriel *et al*. (2011) reported a number of bryophyte species that occurred both in the cave entrances and in the native forest in the Azores (Figure 37): ***Cyclodictyon laetevirens*** (Figure 38), ***Plagiochila longispina*** (Figure 39), ***Plagiothecium nemorale*** (Figure 40), ***Tetrastichium virens*** (Figure 41), and others.

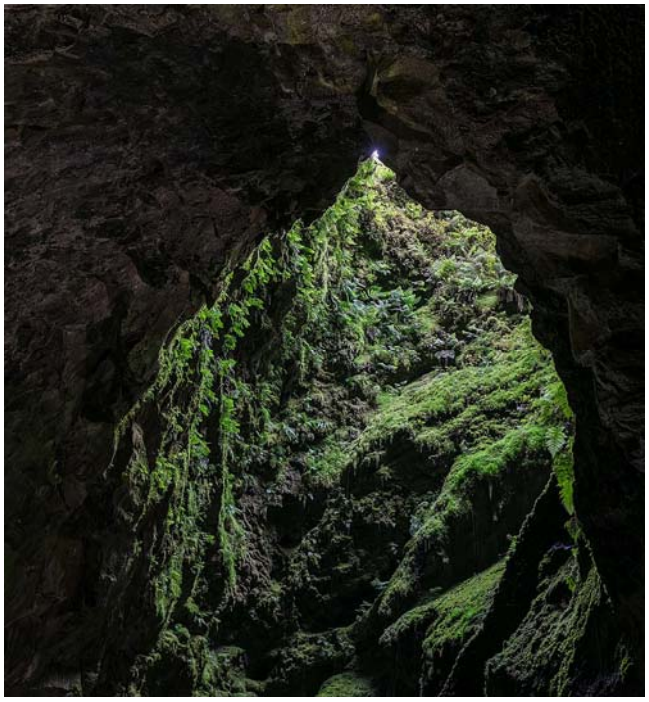

Figure 37. Cave entrance in the Azores. Photo by Diego Delso, through Creative Commons.

Figure 38. ***Cyclodictyon laetevirens***, a species that occurs in both cave entrances and in the native forest in the Azores. Photo by Sean Edwards, with permission.

Figure 39. ***Plagiochila longispina***, a species that occurs in both cave entrances and in the native forest in the Azores. Photo by Jan-Peter Frahm, with permission.

Figure 40. ***Plagiothecium nemorale***, a species that occurs in both cave entrances and in the native forest in the Azores. Photo by Hermann Schachner, through Creative Commons.

Figure 41. ***Tetrastichium virens*** with capsule, a species that occurs in both cave entrances and in the native forest in the Azores. Photo by Michael Lüth, with permission.

What seems to be lacking is a widespread comparison of abundance and frequency of each species of bryophyte within vs around the caves, particularly on similar substrata. Some studies imply that bryophyte cover is richer inside the cave due to the more constant conditions and available moisture. In other cases, the exterior is more favorable due to greater light intensity.

Entrance

"The entrance zone refers to the entry point of a cave, which usually receives adequate sunlight. This part of the cave opens to the outside environment and experiences varied temperatures, as it adjusts to the external environment and climate. The entrance zone can be either naturally formed or created by humans. Green plants grow in this zone because it has sunlight, which is needed for photosynthesis. The entrance zone of a cave can be inhabited by various forms of life, including beetles, small rodents, spiders, snakes, salamanders, earthworms, millipedes, owls, and snails. Additionally, certain terrestrial animals, such as raccoons and bears, may take refuge in the entrance zone to sleep, eat, and nest." (World Atlas 2021). These animals may influence the kinds of plants that arrive and survive there.

The cave entrance often provides protection not available further away. This can be shade and greater

moisture, thus protecting it from bright sun, high temperatures, and drought. For example, Aziz (2011) reported ***Tortula viridifolia*** (Figure 42) at the entrance of a cave as new for Iraq.

Figure 42. ***Tortula viridifolia*** with capsules, on rock, was reported as a new species for Iraq from a cave entrance. Photo by George G., through Creative Commons.

Grebe (1918) observed bryophytes from 5-10 meters from the mouths of several caves in Germany. The light was very dim and was reflected in from the cave surface. He reported thick mats of ***Amblystegium serpens*** (Figure 43-Figure 44) around electric lights in Dunkel der Deckenhohle at Iserlohn. Fiol (1995) explored the flora of cavity entrances of more than 40 cavities in Mallorca (Figure 45). He was able to report relict species and frequent species in the shafts. The moss ***Homalia lusitanica*** (Figure 46) occurs between 40 and 200 lux, whereas **Cyanobacteria** can survive 1/2000 of the surface light. The access region of the caves tend to support xerophytes, including the liverworts ***Plagiochila asplenioides*** (Figure 47) and ***Porella arboris-vitae*** (Figure 48), and mosses ***Anomodon viticulosus*** (Figure 49), ***Ctenidium molluscum*** (Figure 50-Figure 51), and ***Scorpiurium circinatum*** (Figure 52-Figure 53). In the entrance he found the liverworts ***Conocephalum conicum*** (Figure 14), ***Mesoptychia turbinata*** (Figure 54), and ***Pellia endiviifolia*** (Figure 55), and the mosses ***Neckera crispa*** (Figure 56) and ***Rhynchostegiella tenella*** (Figure 30), as well as a few of the access region species.

Figure 43. ***Amblystegium serpens*** with capsules on rocks, a species that occurs in thick mats around electric lights in Dunkel der Deckenhohle at Iserlohn, Germany.

Figure 44. ***Amblystegium serpens***. Photo by Michael Lüth, with permission.

Figure 45. Interior of cave at Porto Cristo, Mallorca. Photo by Lolagt, through Creative Commons.

Figure 46. ***Homalia lusitanica***, a species that can live at 40 and 200 lux in Mallorcan caves. Photo by Hugues Tinguy, with permission.

Figure 47. ***Plagiochila asplenioides***, a species found in the cave access region of Mallorcan caves. Photo by Malcolm Storey, <DiscoverLife.com>, with online permission.

Figure 50. ***Ctenidium molluscum*** in rock canyon, a species that occurs in the access region of Mallorcan caves. Photo by Michael Lüth, with permission.

Figure 48. ***Porella arboris-vitae***, a species that occurs in the access region of Mallorcan caves. Photo by Abalg, through Creative Commons.

Figure 51. ***Ctenidium molluscum***. Photo by Michael Lüth, with permission.

Figure 49. ***Anomodon viticulosus***, a xerophytic species that occurs in the access region of Mallorcan caves. Photo by Aimon Niklasson, with permission.

Figure 52. ***Scorpiurium circinatum*** habitat on a rock wall, a xerophytic species that occurs in the access region of Mallorcan caves. Photo by Hugues Tinguy, with permission.

Figure 53. ***Scorpiurium circinatum*** dry. Photo by David T. Holyoak, with permission.

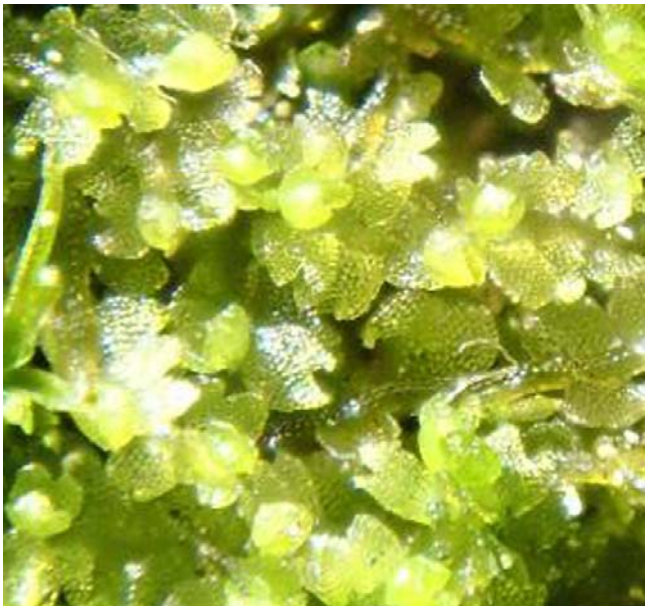

Figure 54. ***Mesoptychia turbinata***, a species of the entrance zone in Mallorcan caves. Photo by Hugues Tinguy, with permission.

Figure 55. ***Pellia endiviifolia*** with red antheridia, a species of the entrance zone in Mallorcan caves. Photo by Hermann Schachner, through Creative Commons.

Figure 56. ***Neckera crispa***, a species of the entrance zone in Mallorcan caves. Photo by Hermann Schachner, through Creative Commons.

Rushin (1973) reported that mostly bryophytes grow on the upper ledges near the cave entrance and where light reaches the floor of the Natural Trap Cave (Figure 57) in the Bighorn Mountains of Wyoming, USA. The cool, moist environment is ideal for the bryophytes. But farther into the cave where it is dark, only bacteria and fungi survive.

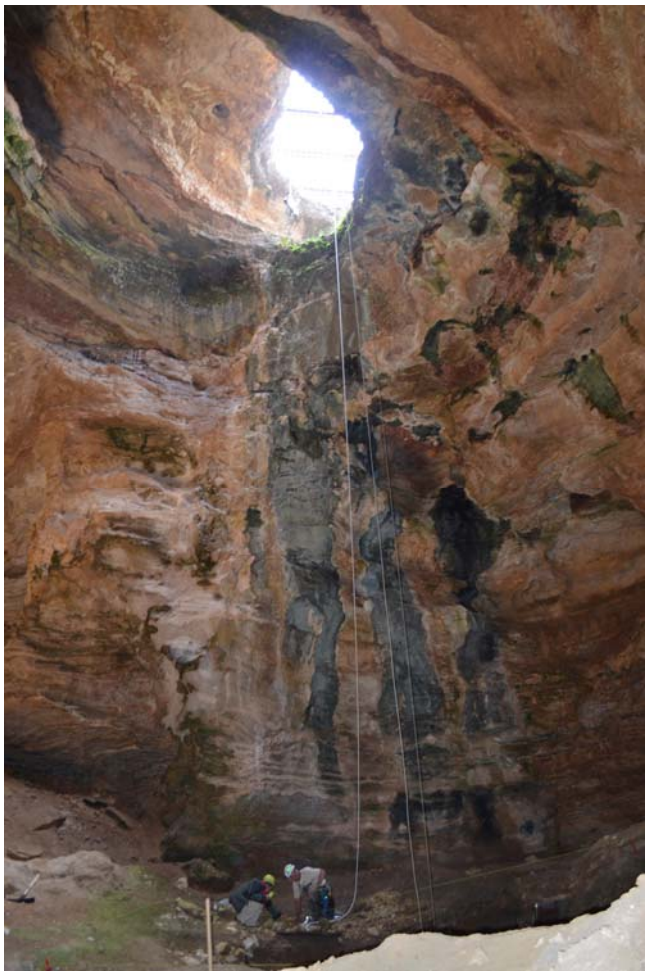

Figure 57. Natural Trap Cave, Wyoming. Photo from Bureau of Land Management, through public domain.

Borges *et al*. (2008) indicated a twofold importance of cave entrances for both bryophytes and arthropods in the Azores (Figure 37). They are sheltered and humic, supporting good diversity of bryophytes representing 25% of the Azorean bryophyte flora; many of the species found there are rare or endemic. They argued that these serve as hotspots for species that permit us to answer ecological questions.

In Montenegro, Kozlova *et al*. (2019) found 64 species of algae and Cyanobacteria and 21 species of bryophytes in the entrance zone of 7 caves (Figure 58). They found that the morphology of the cave entrance was more important than the proximity to the opening in determining the composition of the phototrophic community.

Figure 58. Cave entrance in Montenegra. Photo through Creative Commons.

Buczkó and Rajczy (1989) reported the troglophil ***Eucladium verticillatum*** (Figure 32-Figure 33) "in great mass" on rock at the entrance of a Hungarian cave.

Natcheva (2008) reported ***Conocephalum conicum*** (Figure 14, Figure 59-Figure 61) from the Zandana (Biserna) cave in Bulgaria. My own experience supports this as a suitable habitat for the species. I have seen it on canyon walls at Hocking Hills, Ohio, USA (Figure 59-Figure 60), behind Hungarian Falls (Figure 61) in Houghton County, Michigan, USA, and near the entrance in a cave in Wales.

Figure 59. ***Conocephalum conicum*** on canyon walls, Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 60. Ash Cave at Hocking Hills, Ohio, USA. Photo courtesy of Kim Barton.

Figure 61. Crest of Hungarian Falls, Tamarack City, Michigan, USA. ***Conocephalum conicum*** grows behind the waterfall on the rock. Photo by Janice Glime.

Pentecost and Zhang (2006) found ***Eucladium verticillatum*** (Figure 32-Figure 33), ***Gymnostomum aeruginosum*** (Figure 62-Figure 63), and ***Palustriella commutata*** (Figure 64-Figure 65) at cave entrances in European travertines, but these species failed to penetrate into the twilight zone. Pentecost and Zhang (2001) found that these three species were common at 0-4 m from the entrance with 10% relative irradiation (RI) in Scoska Cave (Figure 66) in the UK.

Figure 62. ***Gymnostomum aeruginosum***, a species that occurs at cave entrances in European travertines, but it fails to penetrate into the twilight zone. Photo by Michael Lüth, with permission.

Figure 63. ***Gymnostomum aeruginosum*** with capsules. Photo by Michael Lüth, with permission.

Figure 64. ***Palustriella commutata*** habitat in Scotland, a species that occurs at cave entrances in European travertines, but it fails to penetrate into the twilight zone. Photo by Michael Lüth, with permission.

Figure 65. ***Palustriella commutata***. Photo by Michael Lüth, with permission.

Figure 66. Entrance of Scoska Cave, Littondale, UK. Photo by Bob Jenkins, through Creative Commons.

Zhang *et al*. (2004a) studied the bryophytes in the entrance zone of a karst cave in Kunming, China. Ren *et al*. (2021) found a similar restriction to that in the UK found by Pentecost and Zhang (2001, 2006) for the mosses ***Ectropothecium zollingeri*** (Figure 67), ***Hypopterygium tamarisci*** (Figure 68), ***Plagiomnium vesicatum*** (Figure 69), and ***Racopilum cuspidigerum*** (Figure 70-Figure 71), and the liverwort ***Lejeunea sordida*** (see Figure 75-Figure 76) to the entrance area of karst caves in southern China.

Figure 67. ***Ectropothecium zollingeri***, a species that is unable to penetrate beyond the entrances of karst caves in China. Photo by Jan-Peter Frahm, with permission.

Figure 68. ***Hypopterygium tamarisci*** with capsules, a species that is unable to penetrate beyond the entrances of karst caves in China. Photo by George Shepherd, through Creative Commons.

Figure 69. ***Plagiomnium vesicatum***, a species that is unable to penetrate beyond the entrances of karst caves in China. Photo from Digital Museum, Hiroshima University, with permission.

Figure 70. ***Racopilum cuspidigerum***, a species that is unable to penetrate beyond the entrances of karst caves in China. Photo by John Game, through Creative Commons.

Figure 71. ***Racopilum cuspidigerum*** branch. Photo by Peter Woodward, through Creative Commons.

Gabriel *et al*. (2008) noted that cave entrances in the Azores (Figure 37) were particularly humid. Gabriel (2006) found that ~25% of the Azorean bryoflora can be found in this habitat. He noted that 19 vulnerable and 13 rare bryophytes on the European Red List can be found there. Gabriel *et al*. (2008) used both published records and their own field sampling to evaluate the species diversity and rarity of bryophytes at the entrances of all known Azorean lava tubes and volcanic pits (Gabriel *et al*. 2008). They found the frequent liverworts to include ***Calypogeia arguta*** (Figure 72), ***Jubula hutchinsiae*** (Figure 73-Figure 74), and ***Lejeunea lamacerina*** (Figure 75-Figure 76). Frequent mosses included ***Epipterygium tozeri*** (Figure 77-Figure 78), ***Eurhynchium praelongum*** (Figure 79), ***Fissidens serrulatus*** (Figure 80), ***Pseudotaxiphyllum elegans*** (Figure 81), ***Tetrastichium virens*** (Figure 41), and ***Tetrastichium fontanum*** (Figure 82). Even some rare Azorean species appeared at the entrances: ***Archidium alternifolium*** (Figure 83-Figure 84), ***Asterella africana*** (Figure 85), and ***Plagiochila longispina*** (Figure 39). Gabriel *et al*. (2018) found ***Radula holtii*** (Figure 86) at cave entrances in the Azores (Figure 37) and expressed concern that climate change and other factors of anthropogenic origin could threaten it. Gabriel *et al*. (2011) consider ***Asterella africana*** to be a specialist of cave entrances.

Figure 72. ***Calypogeia arguta***, a species that occurs at the entrances of all known Azorean lava tubes and volcanic pits. Photo by Claire Halpin, with permission.

Figure 73. ***Jubula hutchinsiae*** beside a waterfall, a species that occurs at the entrances of all known Azorean lava tubes and volcanic pits. Photo by Michael Lüth, with permission.

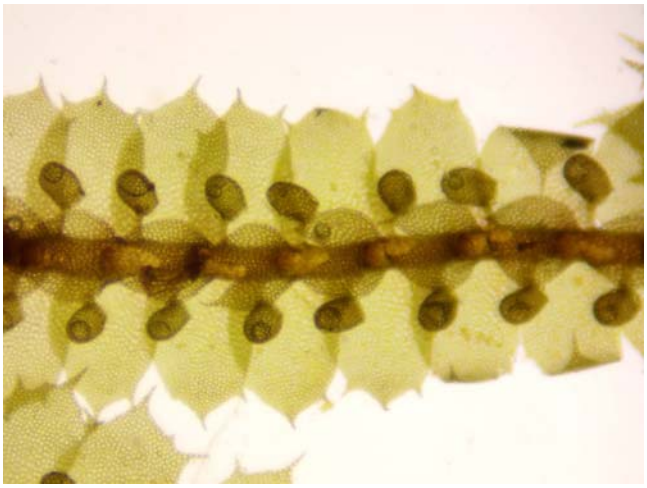

Figure 74. ***Jubula hutchinsiae*** branch. Photo by Rory Hodd, with permission.

Figure 75. ***Lejeunea lamacerina*** habitat, a species that occurs at the entrances of all known Azorean lava tubes and volcanic pits. Photo by Michael Lüth, with permission.

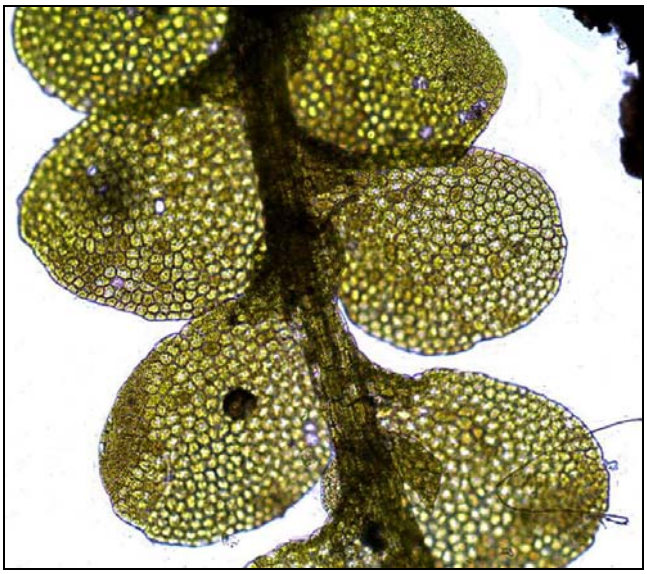

Figure 76. ***Lejeunea lamacerina*** branch. Photo by Hugues Tinguy, with permission.

Figure 77. ***Epipterygium tozeri*** showing water on waxy surface; this species is frequent in Azorean lava tubes and volcanic pits. Photo by Michael Lüth, with permission.

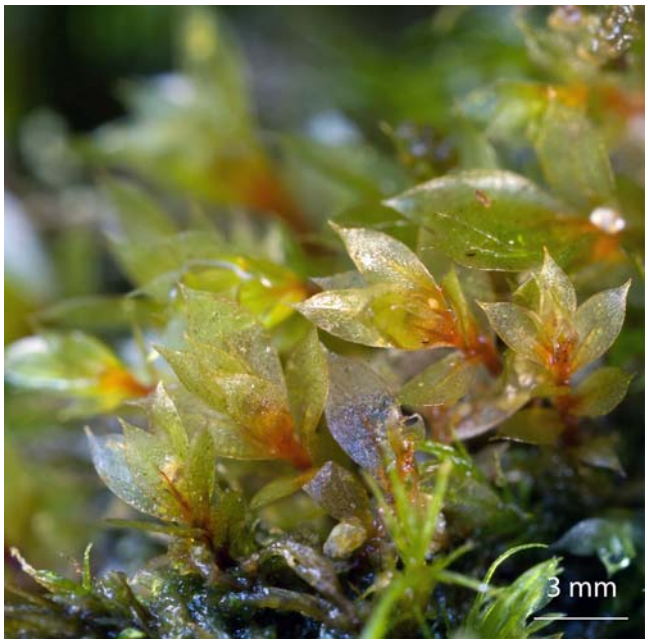

Figure 78. ***Epipterygium tozeri***. Photo by Felipe Gutiérrez Pérez, through Creative Commons.

Figure 79. ***Eurhynchium praelongum***, a frequent moss at entrances of Azorean lava tubes and volcanic pits. Photo by David T. Holyoak, with permission.

Figure 80. ***Fissidens serrulatus***, a species that occurs at the entrances of all known Azorean lava tubes and volcanic pits. Photo by Artdivcan, with permission.

Figure 81. ***Pseudotaxiphyllum elegans*** with capsule, a species that occurs at the entrances of all known Azorean lava tubes and volcanic pits. Photo by Matt Goff, with permission.

Figure 82. ***Tetrastichium fontanum***, a species that is frequent in Azorean lava tubes and volcanic pits. Photo by Michael Lüth, with permission.

Figure 83. ***Archidium alternifolium***, a rare species in the Azores, but that occurs at cave entrances. Photo by George G., through Creative Commons.

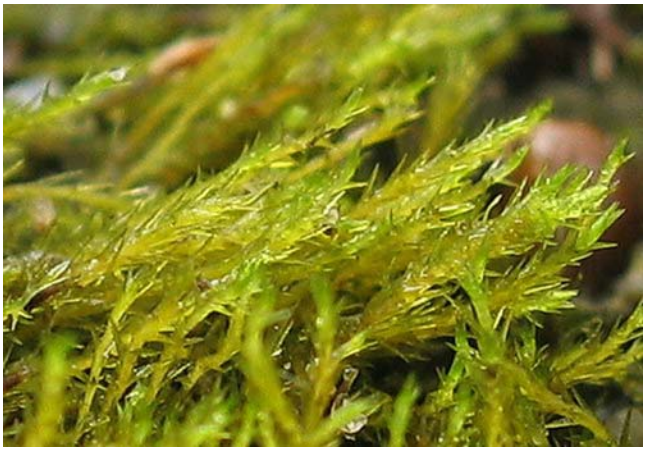

Figure 84. ***Archidium alternifolium***. Photo by Andrew Spink, with permission.

Figure 85. ***Asterella africana*** with archegoniophores, a rare species in the Azores, but that occurs at cave entrances. Photo by Paulo A. V. Borges, with permission.

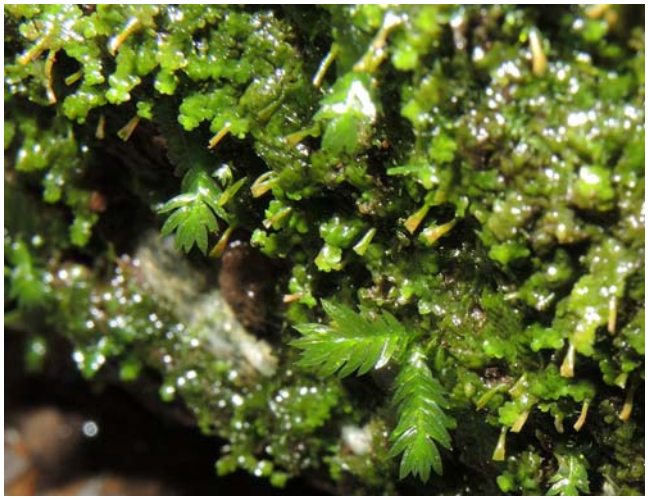

Figure 86. ***Radula holtii*** with perianths, a species in the Azores that occurs at cave entrances, but that could disappear due to climate change. Photo by Rory Hodd, with permission.

Ros *et al*. (2000) found ***Schistidium cinclidodonteum*** (Figure 87) on rocks with soil in a protected and dark cave in Morocco (Figure 88). Its more typical habitat is on acid rocks that are periodically flooded or in stream beds.

Figure 87. ***Schistidium cinclidodonteum***, a species that occurs on rocks with soil in a dark cave in Morocco. Photo by Scot Loring, through Creative Commons.

Figure 88. Interior of Morocco cave. Photo by Diego Delso, through Creative Commons.

Pilkington (2003) found the flora of the cave entrance of a cave in Ireland (Figure 89) to contrast sharply with that of the nearby surface vegetation. The entrance had 23 species of tracheophytes and 17 species of bryophytes in 20 quadrats: ***Ctenidium molluscum*** (Figure 50-Figure 51), ***Eurhynchium praelongum*** (freq=14; Figure 79), ***Fissidens taxifolius*** (Figure 90), ***Thuidium tamariscinum*** (Figure 91-Figure 92), ***Palustriella commutata*** (wet places; Figure 64-Figure 65), ***Rhizomnium punctatum*** (Figure 93), ***Pellia endiviifolia*** (Figure 55), ***Thamnobryum alopecurum*** (freq=20; Figure 34), ***Plagiochila asplenioides*** (Figure 47), ***Plagiomnium undulatum*** (freq=15; Figure 94-Figure 95), ***Plagiomnium affine*** (Figure 96), ***Calliergonella cuspidata*** (Figure 97), ***Plagiochila spinulosa*** (Figure 98-Figure 99), ***Brachythecium rutabulum*** (Figure 100), ***Hookeria lucens*** (wet places; Figure 101), ***Isothecium myosuroides*** (Figure 102), and ***Dichodontium pellucidum*** (Figure 103). Note that only ***Pellia endiviifolia***, ***Plagiochila asplenioides***, and ***Plagiochila spinulosa*** are liverworts.

Figure 89. Entrance of a Keshcorran Cave, Ireland. Photo by Jon Sullivan, through public domain.

Figure 90. ***Fissidens taxifolius***, a species that occurs at the cave entrance of a cave in Ireland. Photo by David Holyoak, with permission.

Figure 91. ***Thuidium tamariscinum***, a species to be found at a cave entrance in Ireland. Photo by Hermann Schachner, through Creative Commons.

Figure 92. ***Thuidium tamariscinum*** branch. Photo by Hugues Tinguy, with permission.

Figure 93. ***Rhizomnium punctatum*** on canyon wall, a species to be found at a cave entrance in Ireland. Photo by Janice Glime.

Figure 94. ***Plagiomnium undulatum***, a species that occurs at the entrance of a cave in Ireland. Photo by Hermann Schachner, through Creative Commons.

Figure 95. ***Plagiomnium undulatum*** branch showing undulations. Photo by James K. Lindsey, through Creative Commons.

Figure 96. ***Plagiomnium affine***, a species that occurs at the entrance of a cave in Ireland. Photo by Michael Becker, through Creative Commons.

Figure 97. ***Calliergonella cuspidata***, a common wetland species that occurs at the entrance of a cave in Ireland. Photo by Hermann Schachner, through Creative Commons.

Figure 98. ***Plagiochila spinulosa***, a species that occurs at the entrance of a cave in Ireland. Photo by David T. Holyoak, with permission.

Figure 99. ***Plagiochila spinulosa***. Photo by David Rycroft, with permission.

Figure 100. ***Brachythecium rutabulum*** with capsules, a species that occurs at the entrance of a cave in Ireland. Photo by J. C. Schou, through Creative Commons.

Figure 101. ***Hookeria lucens***, a species that occurs at the entrance of a cave in Ireland. Photo by Malcolm Storey, <DiscoverLife.com>, with online permission.

Figure 102. ***Isothecium myosuroides***, a species that occurs at the entrance of a cave in Ireland. Photo by Claire Halpin, with permission.

Figure 103. ***Dichodontium pellucidum*** on rock ledge, but restricted to clay soil in Scoska Cave, North Yorkshire, UK. Photo by Claire Halpin, with permission.

Gabriel *et al*. (2006) found relatively rare species at cave entrances in the Azores (Figure 37), including the non-threatened ***Frullania azorica*** (Figure 104-Figure 105), ***Frullania microphylla*** (Figure 106), ***Homalia webbiana*** (Figure 107), ***Marchesinia mackaii*** (Figure 108-Figure 109), ***Myurium hochstetteri*** (Figure 110), ***Fissidens luiserii*** (name of unknown status; Figure 111), and the rare ***Tetrastichium fontanum*** (Figure 82), ***Fissidens coacervatus*** (Figure 112), and ***Tetrastichium virens*** (Figure 41). ***Radula wichurae*** (see Figure 86) is vulnerable. Other more common species were also present at cave entrances: the hornwort ***Anthoceros punctatus*** (Figure 113); liverworts ***Calypogeia arguta*** (Figure 114), ***Lophocolea coadunata*** (Figure 115), ***Conocephalum conicum*** (Figure 14, Figure 59-Figure 61), ***Fossombronia casepitiformis*** (Figure 116), ***Frullania tamarisci*** (Figure 117), ***Lejeunea lamacerina*** (Figure 76), ***Lunularia cruciata*** (Figure 118), ***Plagiochila bifaria*** (Figure 119), ***Porella obtusata*** (Figure 120), ***Radula lindenbergiana*** (Figure 121), ***Riccardia latifrons*** (Figure 122); mosses ***Bryum canariense*** (Figure 123), ***Campylopus pilifer*** (Figure 124-Figure 125), ***Epipterygium tozeri*** (Figure 77-Figure 78), ***Heterocladium wulfsbergii*** (Figure 126-Figure 127), ***Hypnum cupressiforme*** (Figure 128-Figure 129), ***Leucobryum juniperoideum*** (Figure 130), ***Plagiothecium nemorale*** (Figure 40), ***Perigonium gracile*** (Figure 131), ***Scorpiurium circinatum*** (Figure 132-Figure 133), ***Thamnobryum maderense*** (Figure 134). This is an unusually large number of liverworts for cave habitats.

Figure 104. ***Frullania azorica*** on rock, a relatively rare species that occurs at cave entrances in the Azores. Photo by Rosalina Gabriel, with permission.

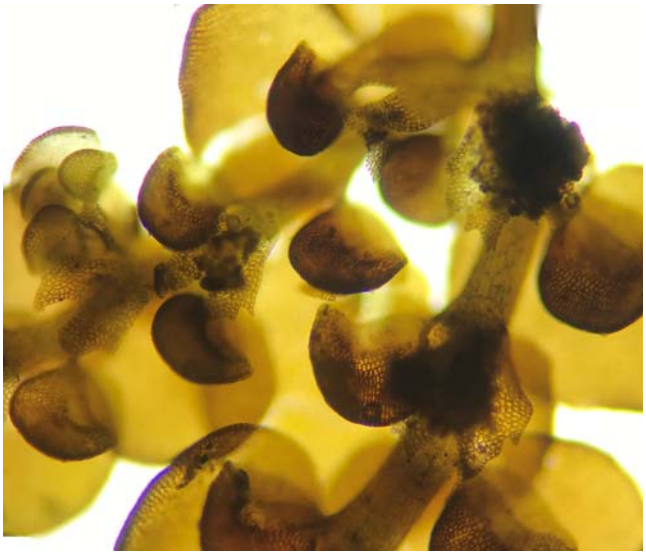

Figure 105. ***Frullania azorica***. Photo courtesy of Tatiana Oliveira da Silva.

Figure 106. ***Frullania microphylla*** on rock, with enlarged inset. This is a relatively rare species that occurs at cave entrances in the Azores. Photo by Michael Lüth, with permission.

Figure 107. ***Homalia webbiana***, a relatively rare species that occurs at cave entrances in the Azores. Photo from <Earth.com>, with permission.

Figure 108. ***Marchesinia mackaii*** habitat on limestone boulder, England; this is a relatively rare species that occurs at cave entrances in the Azores. Photo by Richtid, through Creative Commons.

Figure 109. ***Marchesinia mackaii***. Photo by Malcolm Storey <DiscoverLife.com>, with online permission.

Figure 110. ***Myurium hochstetteri***, a relatively rare species that occurs at cave entrances in the Azores. Photo by Michael Lüth, with permission.

Figure 111. ***Fissidens luisieri*** with capsules, from Madeira off Africa, a relatively rare species that occurs at cave entrances in the Azores. Photo by Michael Lüth, with permission.

Figure 112. ***Fissidens coacervatus*** with capsules, Madeira, a relatively rare species that occurs at cave entrances in the Azores. Photo by Michael Lüth, with permission.

Figure 113. ***Anthoceros punctatus***, a more common species that occurs at cave entrances in the Azores. Photo by Malcolm Storey <DiscoverLife.com>, with online permission.

Figure 114. ***Calypogeia arguta***, a more common species that occurs at cave entrances in the Azores. Photo by Claire Halpin, with permission.

Figure 115. ***Lophocolea coadunata***, a more common species that occurs at cave entrances in the Azores. Photo by J. C. Schou, with permission.

Figure 116. ***Fossombronia casepitiformis*** with capsules, a more common species that occurs at cave entrances in the Azores. Photo by Michael Lüth, with permission.

Figure 117. ***Frullania tamarisci***, a more common species that occurs at cave entrances in the Azores. Photo by David T. Holyoak, with permission.

Figure 118. ***Lunularia cruciata***, a more common species that occurs at cave entrances in the Azores. Photo by Hermann Schachner, through Creative Commons.

Figure 119. ***Plagiochila bifaria***, a more common species that occurs at cave entrances in the Azores. Photo by Paulo Borges, with permission.

Figure 120. ***Porella obtusata***, a more common species that occurs at cave entrances in the Azores. Photo by Kristian Hassel, through Creative Commons.

Figure 121. ***Radula lindenbergiana***, a more common species that occurs at cave entrances in the Azores. Photo by Hermann Schachner, through Creative Commons.

Figure 122. ***Riccardia latifrons***, a more common species that occurs at cave entrances in the Azores. Photo from Botany Website, UBC, with permission.

Figure 123. ***Bryum canariense***, a more common species that occurs at cave entrances in the Azores. Photo by Claire Halpin, with permission.

Figure 124. ***Campylopus pilifer***, a more common species that occurs at cave entrances in the Azores. Photo by Blanka Aguero, with permission.

Figure 125. ***Campylopus pilifer***. Photo by Des Callaghan, with permission.

Figure 126. ***Heterocladium wulfsbergii*** on vertical rock, a more common species that occurs at cave entrances in the Azores. Photo by Claire Halpin, with permission.

Figure 127. ***Heterocladium wulfsbergii***. Photo by Claire Halpin, with permission.

Figure 128. ***Hypnum cupressiforme*** on rock wall, a more common species that occurs at cave entrances in the Azores. Photo by Allen Norcross, with permission.

Figure 129. ***Hypnum cupressiforme***. Photo by Michael Lüth, with permission.

Figure 130. ***Leucobryum juniperoideum***, a more common species that occurs at cave entrances in the Azores. Photo by David T. Holyoak, with permission.

Figure 131. ***Pterogonium gracile*** wet, a more common species that occurs at cave entrances in the Azores. Photo by David T. Holyoak, with permission.

Figure 132. ***Scorpiurium circinatum***, a more common species that occurs at cave entrances in the Azores. Photo by Hugues Tinguy, with permission.

Figure 133. ***Scorpiurium circinatum*** dry. Photo by David T. Holyoak, with permission.

Figure 134. ***Thamnobryum maderense***, a more common species that occurs at cave entrances in the Azores. Photo by Kristian Peters, with permission.

Even small caves can provide unique local habitats. In the Flume (Figure 135) at Franconia Notch, New Hampshire, USA, ***Campylium chrysophyllum*** (Figure 136) was only found on the floor of a small cave above the falls (Glime 1982).

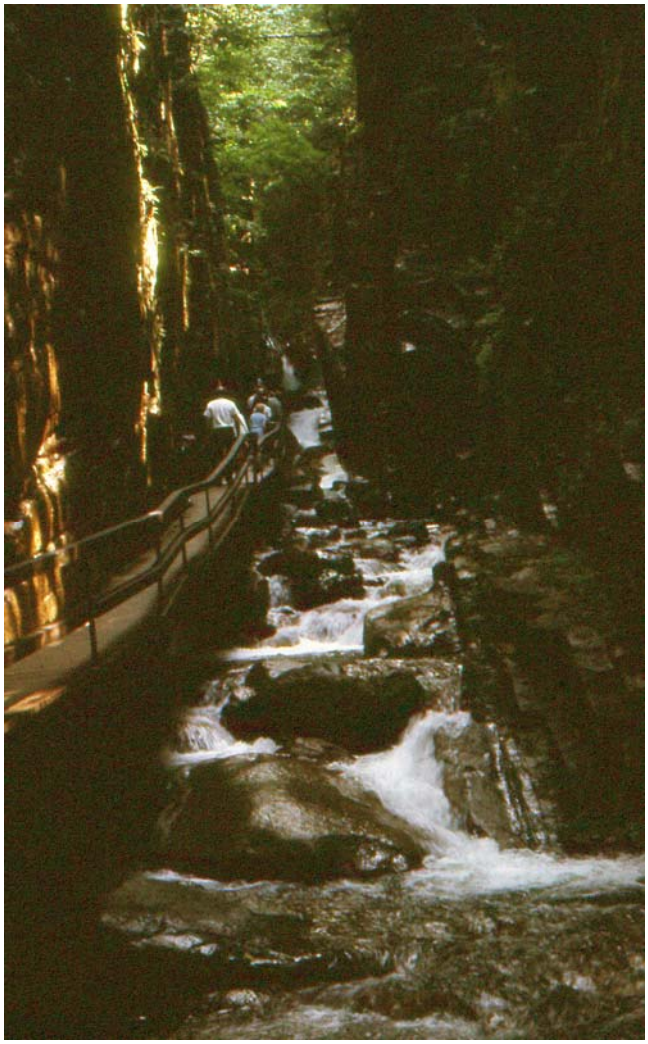

Figure 135. Flume, Franconia Notch, New Hampshire, USA, where small caves can have ***Campylium chrysophyllum***. Photo by Janice Glime.

Figure 136. ***Campylium chrysophyllum***, a species that occurs in a very shallow cave in the Flume at Franconia Notch, New Hampshire, USA. Photo by Bob Klips, with permission.

Twilight Zone

The **twilight zone** (Figure 137) is the part of a cave that receives a small amount of sunlight since it is not too far from the entrance. This seems to coincide with the **threshold** part of the cave, where light penetrates to some degree. This zone is cool and damp, and its temperature is usually relatively constant. The twilight zone is shared by both outside organisms and cave dwellers.

Figure 137. Twilight zone of Rawhiti Cave, South Island, New Zealand. Photo by Pseudopanax, through public domain.

Pleurocarpous mosses such as ***Amblystegium serpens*** var. ***juratzkanum*** (Figure 138) predominate among bryophytes in areas with less light (down to 232 lux) in the three Hungarian caves studied by Buczkó and Rajczy (1989), although the acrocarpous moss ***Bryoerythrophyllum recurvirostrum*** (Figure 139) also occurs in deeper parts.

Figure 138. ***Amblystegium serpens*** var. ***juratzkanum*** with capsules, on rock. Pleurocarpous mosses such as this one predominate in areas with less light. Photo by Štěpán Koval, with permission.

Figure 139. ***Bryoerythrophyllum recurvirostrum*** showing red base, an acrocarpous moss that grows in deep parts of caves. Photo by Janice Glime.

In Mallorcan caves (Figure 45), Fiol (1995) described the "transition zone," which presumably corresponds with the **twilight zone**. The bryophytes in this zone seem to include the most cavernicolous of the entrance species, including ***Eucladium verticillatum*** (Figure 32-Figure 33), ***Fissidens dubius*** (Figure 140), ***Homalia lusitanica*** (Figure 46), ***Mnium*** sp. (Figure 152-Figure 153), and ***Thamnobryum alopecurum*** (Figure 34). ***Thamnobryum alopecurum*** and ***Homalia lusitanica*** mark the light extinction limit of bryophytes into the next zone. Relicts include the liverwort ***Jungermannia atrovirens*** (Figure 141), and the mosses ***Taxiphyllum wissgrillii*** (Figure 142), ***Orthothecium intricatum*** (Figure 143), and ***Rhizomnium punctatum*** (Figure 62), all of which were known in Mallorca only from these caves.

Figure 140. ***Fissidens dubius*** on rock ledge, a species that occurred deepest within Scoska Cave, North Yorkshire, UK. Photo by Hermann Schachner, through Creative Commons.

Figure 141. ***Jungermannia atrovirens*** with perianths, a relict species known in Mallorca only from caves. Photo by Hugues Tinguy, with permission.

Figure 142. ***Taxiphyllum wissgrillii***, a species that occurs on a boulder at the deepest position of bryophyte presence in the Della Grotta Dell'orso, Italy. It is a relict species known in Mallorca only from caves. Photo by Hugues Tinguy, with permission.

Figure 143. ***Orthothecium intricatum***, a relict species known in Mallorca only from caves. Photo by Hermann Schachner, through Creative Commons.

In the Azores (Figure 37), Frahm (2005) found bryophytes in a small crater with a cave at the bottom. Ferns are common where there is enough light, but bryophytes extend farther into the dark interior. These are primarily ***Riccardia chamedryfolia*** (Figure 144-Figure 145) and ***Thamnobryum*** sp. (Figure 34), with smaller quantities of ***Cyclodictyon laetevirens*** (Figure 38) and ***Fissidens serrulatus*** (Figure 80). He describes the ***Thamnobryum*** as conspicuous because of its large, lax plants with long, flagelliform branches.

Figure 144. ***Riccardia chamedryfolia***, a species that occurs in a cave at the bottom of a crater in the Azores. Photo by Bernd Haynard, through Creative Commons.

Figure 145. ***Riccardia chamedryfolia***. Photo by Hugues Tinguy, with permission.

In the Della Grotta Dell'orso, Italy (Figure 146-Figure 147), Castello and Strazzaboschi (2013) found ***Oxyrrhynchium speciosum*** (Figure 148) and ***Taxiphyllum wissgrillii*** (Figure 142) on a large boulder 10 m from the entrance, marking the deepest position of bryophytes in the cave. Bryophyte growth in the twilight zone was more reduced than at the entrance, with species exhibiting stunted growth in small patches. Other species in the twilight zone included ***Fissidens crispus*** (Figure 149), ***Isopterygiopsis pulchella*** (Figure 150-Figure 151), ***Mnium stellare*** (Figure 152-Figure 153), ***Neckera complanata*** (Figure 154-Figure 155), and ***Rhynchostegiella tenella*** (Figure 30).

Figure 146. Outside of entrance to Grotta dell'orso, Italy. Photo by Tiesse, through Creative Commons.

Figure 147. Grotta dell'orso, Italy, inside entrance, entering the twilight zone. Photo by Tiesse, through Creative Commons.

Figure 148. ***Oxyrrhynchium speciosum***, a species that occurs on a boulder at the deepest position of bryophyte presence in the Della Grotta Dell'orso, Italy. Photo by Hugues Tinguy, with permission.

Figure 149. ***Fissidens crispus***, a species of the twilight zone in the Della Grotta Dell'orso, Italy. Photo by D. B. Tucker, through Creative Commons.

Figure 150. ***Isopterygiopsis pulchella***, a species of the twilight zone in the Della Grotta Dell'orso, Italy. Photo by Michael Lüth, with permission.

Figure 151. ***Isopterygiopsis pulchella*** on a rock wall. Photo by Michael Lüth, with permission.

Figure 152. ***Mnium stellare*** with capsules, on rock, a species of the twilight zone in the Della Grotta Dell'orso, Italy. Photo by Michael Lüth, with permission.

Figure 153. ***Mnium stellare***. Photo by Hermann Schachner, through Creative Commons.

Figure 154. ***Neckera complanata*** on a vertical substrate, a species of the twilight zone in the Della Grotta Dell'orso, Italy. Photo by Gerd Höhenberger, through Creative Commons.

Figure 155. ***Neckera complanata*** on rock. Photo by Andy Hodgson, with permission.

Pentecost and Zhang (2001, 2006) found that ***Eurhynchium pumilum*** (Figure 156), ***Fissidens adianthoides*** (Figure 157-Figure 158), and ***Pseudotaxiphyllum elegans*** (Figure 81) were frequent bryophytes in the region 6-10 m with relative illumination (RI) 1-2% in Scoska Cave (Figure 66), North Yorkshire, UK. ***Amblystegium serpens*** (Figure 44), ***Fissidens dubius*** (Figure 140), and ***Thamnobryum alopecurum*** (Figure 34) penetrated the furthest. ***Thamnobryum alopecurum*** was the most frequently encountered bryophyte in the cave. Further into the cave they found ***Orthothecium intricatum*** (Figure 143), ***Pseudotaxiphyllum elegans***, ***Rhynchostegiella teneriffae*** (Figure 159), and ***Platydictya confervoides*** (Figure 160-Figure 161) (l5.9 m, RI 0.23%). ***Dichodontium pellucidum*** (Figure 103) was restricted by substrate to clay soil.

Figure 156. ***Eurhynchium pumilum***, a species frequent in the region 6-10 m with RI of 1-2% in Scoska Cave, North Yorkshire, UK. Photo by Hugues Tinguy, with permission.

Figure 157. ***Fissidens adianthoides*** with capsules on rock, a species frequent in the region 6-10 m with RI of 1-2% in Scoska Cave, North Yorkshire, UK. Photo by Michael Lüth, with permission.

Figure 158. ***Fissidens adianthoides***. Photo by Hermann Schachner, through Creative Commons.

Figure 159. ***Rhynchostegiella teneriffae***, among the species that occurred deepest within Scoska Cave, North Yorkshire, UK. Photo by Hermann Schachner, through Creative Commons.

Figure 160. ***Platydictya confervoides*** habitat on boulder, a species that occurs deepest within Scoska Cave, North Yorkshire, UK. Photo by Bob Klips, with permission.

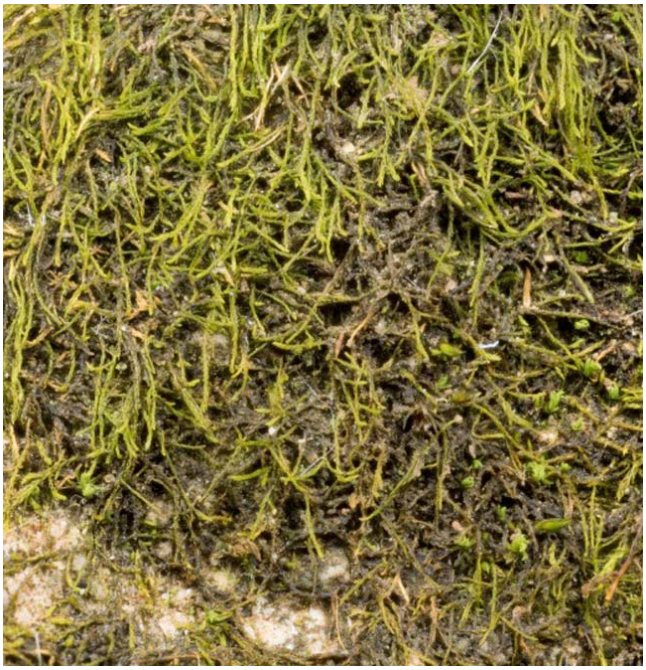

Figure 161. ***Platydictya confervoides***. Photo by Bob Klips, with permission.

Ren *et al*. (2021) found that some species were restricted to the twilight zone of six karst caves in southern China. ***Fissidens taxifolius*** (Figure 90) and ***Hyophila javanica*** (see Figure 162) occurred only in intermediate light. ***Radula kojana*** (Figure 163-Figure 164) was found only in deep plots. This led them to conclude that liverworts were better adapted to low light conditions, but this needs a much wider sampling effort in a wide range of caves. Furthermore, they found that the mosses were in locations that indicate they are more drought tolerant, which could account for the absence of liverworts in areas closer to the opening.

Figure 162. ***Hyophila involuta*** with capsules among rocks; ***Hyophila javanica*** occurs only in intermediate light in karst caves in southern China. Photo by Wayne Lampa, through Creative Commons.

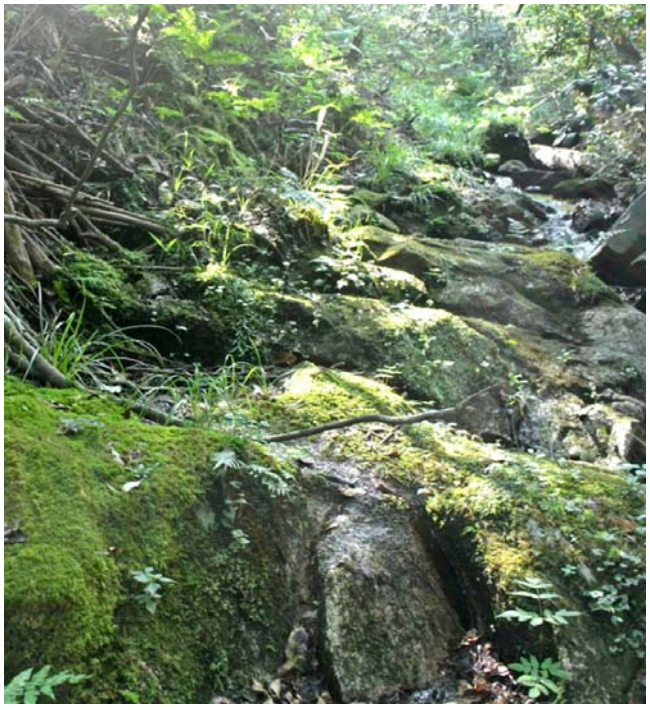

Figure 163. ***Radula kojana*** habitat on rock, a species that occurs only in deep locations in karst caves in southern China. Photo by Kochibi, through Creative Commons.

Pentecost and Zhang (2001) found that in Scoska Cave (Figure 66), UK, ***Hypnum resupinatum*** (Figure 165), ***Orthothecium intricatum*** (Figure 143), and ***Weissia*** cf. ***perssonii*** (Figure 166) penetrated the farthest, to regions where the RI fell to about 0.4%. Liverworts were unable to penetrate very far, an absence that the researchers attributed to the dry conditions of the cave. Only ***Conocephalum conicum*** (Figure 14, Figure 59-Figure 61) and ***Metzgeria conjugata*** (Figure 167) were able to penetrate to 12 m.

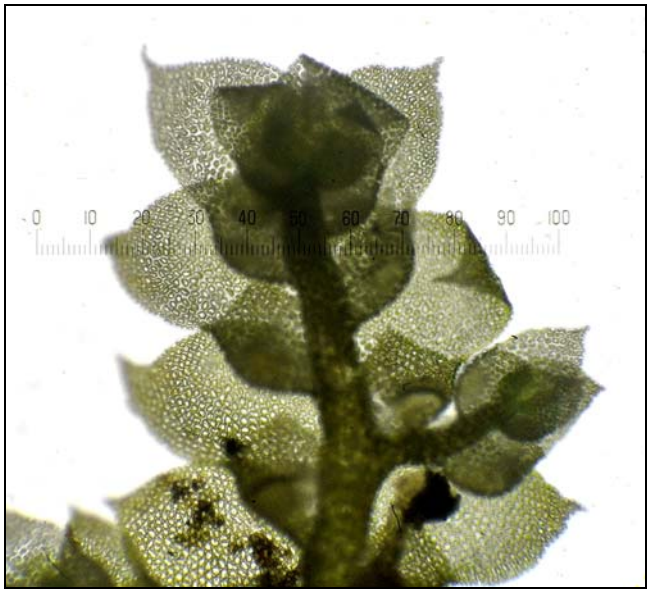

Figure 164. ***Radula kojana*** branch. Photo by Kochibi, through Creative Commons.

Figure 165. ***Hypnum resupinatum*** on rock, among the species that penetrate the farthest into the Scoska Cave, UK. Photo by George G., through Creative Commons.

Figure 166. ***Weissia perssonii*** with capsules, among the species that penetrate the farthest into the Scoska Cave, UK. Photo by Barry Stewart, with permission.

Figure 167. ***Metzgeria conjugata*** on rock, the species that penetrated the farthest (12 m) into Scoska Cave, UK. Photo by Barry Stewart, with permission.

Wang *et al*. (1998) examined the biokarst formations in the twilight zone of Chinese caves.

In a study of 17 Guilin caves (*e.g.* Figure 168), Zhang *et al*. (2005) found ***Gymnostomum calcareum*** (Figure 169-Figure 170), ***Hymenostylium recurvirostrum*** (Figure 171-Figure 172), and ***Philonotis turneriana*** (Figure 173) associated with travertine deposits in the twilight zone of karst caves in the Guilin area of China. Guo *et al*. (2018) examined the communities of dolomite cave twilight zones in Shuidong Cave in Guizhou Province, China.

Figure 168. Cave at Guilin (Li River), Crown Cave, China. Photo by Dan Lundberg, through Creative Commons.

Figure 169. ***Gymnostomum calcareum*** on vertical rock, a species associated with travertine deposits in the twilight zone of karst caves in the Guilin area of China. Photo by Michael Lüth, with permission.

Figure 170. ***Gymnostomum calcareum***. Photo by Larry Jensen, with permission.

Figure 171. ***Hymenostylium recurvirostrum*** on shaded wall in India, a species associated with travertine deposits in the twilight zone of karst caves in the Guilin area of China. Photo by Michael Lüth, with permission.

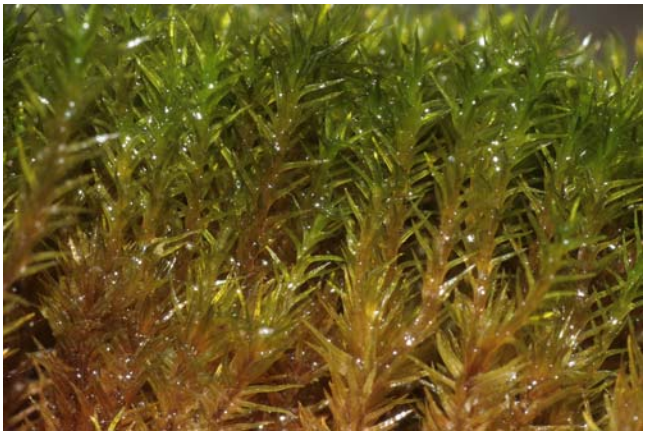

Figure 172. ***Hymenostylium recurvirostrum***. Photo by Hermann Schachner, through Creative Commons.

Figure 173. ***Philonotis turneriana***, a species associated with travertine deposits in the twilight zone of karst caves in the Guilin area of China. Photo by Kochibi, through Creative Commons.

Stalactites and Stalagmites

In addition to growing on cave walls, some bryophytes are able to grow in the stalactite or stalagmites where there is enough moisture dripping down. In Yunnan Province, P. R. China, Zhang *et al*. (2004b) found ***Gymnostomum aurantiacum*** (see Figure 169-Figure 170) and ***Hymenostylium recurvirostrum*** (Figure 171-Figure 172). These can contribute to the formation of the stalactites. ***Eucladium verticillatum*** (Figure 32-Figure 33) and ***Didymodon*** (Figure 174) are also important in forming stalactites. For a description of this process, see Chapter 18-1 of this volume. Bryophytes seem to be rare on the surfaces of these formations, perhaps in part due to the changing nature of the formations.

Figure 174. ***Didymodon brachyphyllus*** on rock; ***Didymodon*** is an important genus for forming stalactites. Photo by Michael Lüth, with permission.

Vertical Shafts

Not all cave inclines progress slowly away from the entrance. Moseley *et al*. (2013) describe a cave in Nova Scotia, Canada, that has vertical shafts as entrances (Figure 175). The fern zone is missing, and three pleurocarpous mosses are dominant: ***Loeskeobryum brevirostre*** (Figure 176), ***Isopterygiopsis muellerianum*** (Figure 177-Figure 178) (1st dominant), and ***Heterocladium dimorphum*** (Figure 179), along with two liverwort species: ***Calypogeia*** (Figure 72; Figure 114) and ***Lophocolea*** (Figure 115). The crustose lichen ***Lepraria*** sp. also occurs on the shaft walls. ***Isopterygiopsis muellerianum*** is the most prominent bryophyte and extends to the deepest location of photosynthetic organisms. ***Loeskeobryum brevirostre*** is present only in the uppermost part of the shaft where it is able to receive sufficient light.

Figure 175. Wisqoq Cave from surface, showing shaft entrance, Nova Scotia, Canada. Photo modified from Moseley 2017, through Creative Commons.

Figure 176. ***Loeskeobryum brevirostre***, one of the dominant bryophytes in a cave in Nova Scotia, Canada. Photo by Bob Klips, with permission.

Figure 177. ***Isopterygiopsis muellerianum*** on rock, one of the dominant bryophytes in a cave in Nova Scotia, Canada. Photo from <Earth.com>, with permission.

Figure 178. ***Isopterygiopsis muellerianum*** branch. Photo by Wayne Lampa, through Creative Commons.

Figure 179. ***Heterocladium dimorphum***, one of the dominant bryophytes in a cave in Nova Scotia, Canada. Photo by Štěpán Koval, with permission.

Summary

The cave bryophyte flora is generally divided into that of the **entrance**, **twilight zone**, and **dark zone**. A further zone of note is the cave mouth area on the outside of the cave. The penetration of light suitable for photosynthesis is the limiting factor for these bryophyte distributions.

Because of the influence of cave temperatures on the **mouth** area, this area can have species that are unique within the region. There tend to be more liverworts there, and mosses such as propaguliferous ***Pohlia*** spp. and ***Tortula truncata*** may be present.

The **entrance** provides only a short distance with sufficient light for a number of species, with morphology of the opening being more important than distance in determining light penetration. One of the most common bryophytes here is ***Amblystegium serpens***. The cave moss ***Eucladium verticillatum*** is often in this zone, especially on the eastern side of the Atlantic. This area can harbor rare species, and species composition often contrasts sharply with that outside the cave.

The **twilight zone** has a more buffered climate than the entrance, but due to low light it has fewer species. Both ***Amblystegium serpens*** and ***Eucladium verticillatum*** extend into this zone, often being abundant. Its often moist conditions and suitable substrate can create refugia for bryophytes not occurring elsewhere in the region. Several species of ***Fissidens*** are among those surviving in this low light.

Stalactites and stalagmites are seldom colonized by bryophytes, but ***Eucladium verticillatum*** and several other bryophytes can contribute to their formation. **Vertical shafts** differ in flora and light intensity from horizontal cave entrances.

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CHAPTER 18-4
CAVES – BRYOPHYTE STRATEGIES

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CHAPTER 18-4
CAVES – BRYOPHYTE STRATEGIES

Figure 1. ***Cyathodium cavernarum*** on a dark ledge. Photo by Cédric de Foucault, through Creative Commons.

Rare Species and New Finds

I have tried throughout the book not to reveal the exact location of rare species. Bryologists and other collectors have been known to contribute to the disappearance of species from some locations through their collections.

Unique habitats always draw our attention in anticipation of finding something new, as already reported in Chapters 18-1 for the **Cyanobacteria** and algae in caves. Some of the rare bryophytes have been mentioned in Chapters 18-2 to 18-3. Likewise, the various caves and cave-like habitats often don't disappoint us for new bryophytes, particularly if they have not previously been explored by a bryologist. For example, Aziz (2011) reported 17 new species records for Iraq, and four of these were associated with caves. These included ***Tortula viridifolia*** (Figure 2) cited as ***Pottia wilsonii*** var. ***crinata*** and ***Tortula truncata*** (Figure 3-Figure 4).

Figure 2. ***Tortula viridifolia*** with capsules, a species Aziz found in caves as new to Iraq. Photo by Michael Lüth, with permission.

Figure 3. ***Tortula truncata***, a species Aziz found in caves as new to Iraq. Photo from Botany Website, UBC, with permission.

Figure 4. ***Tortula truncata*** with capsules. Photo by Claire Halpin, with permission.

Vitt and Belland (1997) found that 25% of the mosses in Alberta, Canada, are rare. This study allows us to asses the characteristics of rare species. In their study, the found that pleurocarpous species, long-lived perennials, and competitive strategists were less likely to be among the rare species. Members of **Bryales**, **Dicranales**, and **Funariales** are more likely to be represented, whereas **Hypnales**, **Orthotrichales**, and **Sphagnales** are underrepresented. Of interest in cave bryology is that 42% of the rare species have boreal distributions, 57% occur on soil, and 34% occur on rock. These attributes make caves suitable places for finding disjunct and rare species.

Since caves create unique conditions within an ecosystem or region, it is not surprising to find that they harbor species that are rare for that area. In the Red River Gorge of Kentucky, USA, Studler and Snider (1989) found rare mosses and liverworts were "favored by the numerous caves and ravines." In the caves they found such rare species as ***Bryoxiphium norvegicum*** (Figure 5), ***Hookeria acutifolia*** (Figure 6), ***Brothera leana*** (Figure 7), ***Diphyscium mucronifolium*** (Figure 8), ***Rhabdoweisia crispata*** (Figure 9), ***Syrrhopodon texanus*** (Figure 10), ***Trichostomum tenuirostre*** (Figure 11-Figure 13), and ***Plagiochila sullivantii*** (Figure 14) representing relict or disjunctive taxa.

Figure 5. ***Bryoxiphium norvegicum***, a rare taxon that can be abundant in caves. Photo by Amelia Merced, through Creative Commons.

Figure 6. ***Hookeria acutifolia***, a rare taxon that can be abundant in caves. Photo by John Game, through Creative Commons.

Figure 7. ***Brothera leana***, a rare taxon that can be abundant in caves. Photo by Wayne Lampa, through Creative Commons.

Figure 8. ***Diphyscium mucronifolium***, a rare taxon that can be abundant in caves. Photo by Blanka Aguero, with permission.

Figure 9. ***Rhabdoweisia crispata*** shaded at rock base, a rare taxon that can be abundant in caves. Photo by Tuomo Kuitunen <luopioistenkasvisto.fi.>, with permission.

Figure 10. ***Syrrhopodon texanus*** with gemmae, a rare taxon that can be abundant in caves. Photo by Bob Klips, through Creative Commons.

Figure 11. ***Trichostomum tenuirostre*** sandstone cliff habitat in Ohio, USA. Photo by Bob Klips, with permission.

Figure 12. ***Trichostomum tenuirostre*** sandstone cliff habitat, a rare taxon that can be abundant in caves. Photo by Bob Klips, with permission.

Figure 13. ***Trichostomum tenuirostre***. Photo by Bob Klips, with permission.

Figure 14. ***Plagiochila sullivantii***, a rare taxon that can be abundant in caves. Photo by probably Paul Davison, University of North Alabama.

Evans and Nichols (1935) reported that the original specimens of ***Mesoptychia gillmanii*** (as *Jungermannia gillmanii*; Figure 15) came from a cave in a cliff of Potsdam sandstone on an island in Lake Superior. This was collected in 1867 by Henry Gillman and seems to be the first liverwort collected in Michigan. However, Stephani concluded that it was in fact ***Lophozia inflata***. Observations of the paroicous inflorescences later placed it in the genus ***Leiocolea***, but its current status in Söderström *et al*. (2016) places it back in ***Mesoptychia gillmanii***.

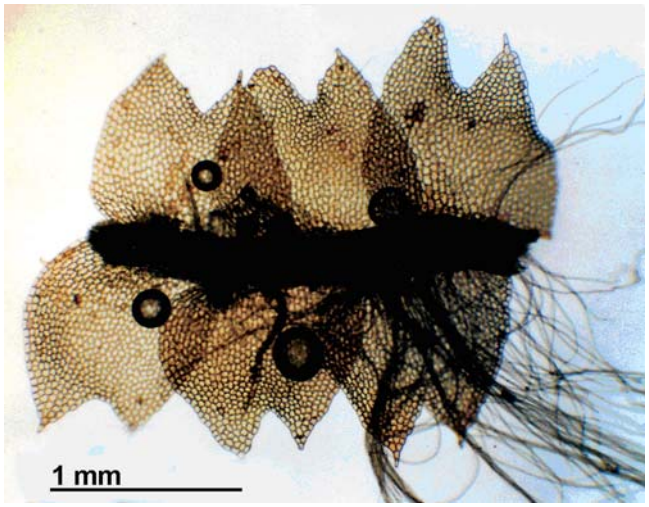

Figure 15. ***Mesoptychia gillmanii***, a species first reported in Michigan, USA, from a cave in a cliff of Potsdam sandstone on an island in Lake Superior. Photo by David Wagner, with permission.

Hermann (1964) added ***Aneura pinguis*** (Figure 16) to the known flora of Mt. Katahdin, Maine, USA, from a collection on the peaty floor of a cave between huge boulders.

Sguazzin and Polli (2011) found ***Ptychostomum moravicum*** (= *B. laevipilum*; Figure 17-Figure 18) from a cave on Mount Saint Michael off the coast of Cornwall. Puglisi *et al*. (2019) found species that are rare in Sicily: ***Brachytheciastrum collinum*** (Figure 19), ***Grimmia torquata*** (Figure 20), ***Ptychostomum cernuum*** (Figure 21-Figure 22), ***Rhabdoweisia fugax*** (Figure 23), and ***Tortula bolanderi*** (Figure 24) in Italian caves. Castello and Strazzaboschi (2013) reported the liverwort ***Cololejeunea rossettiana*** (Figure 25) from Della Grotta Dell'orso karst cave as new to the Friuli Venezia Giulia region of Italy.

Figure 16. ***Aneura pinguis***, a species that added to the known Maine, USA, flora from a collection on the floor of a cave. Photo by Hermann Schachner, through Creative Commons.

Figure 17. ***Ptychostomum moravicum***, a relatively rare species from a cave on Mount Saint Michael off the coast of Cornwall. Photo by Hugues Tinguy, with permission.

Figure 18. ***Ptychostomum moravicum***, Photo by jonnyecology, through Creative Commons.

Figure 19. ***Brachytheciastrum collinum*** on rock, a rare species found in caves in Italy. Photo by Andy Hodgson, with permission.

Figure 20. ***Grimmia torquata***, a rare species found in caves in Italy. Photo by Des Callaghan, with permission.

Figure 21. ***Ptychostomum cernuum*** with capsules, on rock, a rare species found in caves in Italy. Photo by Tom Neily, through Creative Commons.

Figure 22. ***Ptychostomum cernuum***. Photo by Wayne Lampa, through Creative Commons.

Figure 23. ***Rhabdoweisia fugax*** with capsules, on rock ledge, a rare species found in caves in Italy. Photo by Michael Lüth, with permission.

Figure 24. ***Tortula bolanderi*** with capsules, a rare species found in caves in Italy. Photo by Randal, through Creative Commons.

Figure 25. ***Cololejeunea rossettiana***, a rare species found in caves in Italy. Photo by George G., through Creative Commons.

In the Azores, Gabriel *et al*. (2006) found 119 bryophyte species in lava tubes and volcanic pits from Graciosa Island. However, there were no endemic plants from the Azores present. On the other hand, six European and four Macaronesian endemic species occurred in the entrances of these cave formations. One of these was a Vulnerable species and three were Rare. These cave entrances are important sites for harboring rare and endemic species.

Singh and Singh (2007) reported new records for Doon Valley, India, citing ***Mesoptychia gillmanii*** (Figure 15) in or near caves, ***Asterella wallichiana*** (Figure 26), ***Plagiochasma appendiculatum*** (Figure 27), ***Marchantia paleacea*** (Figure 28), and ***Riccia cruciata*** (see Figure 29) from a cave.

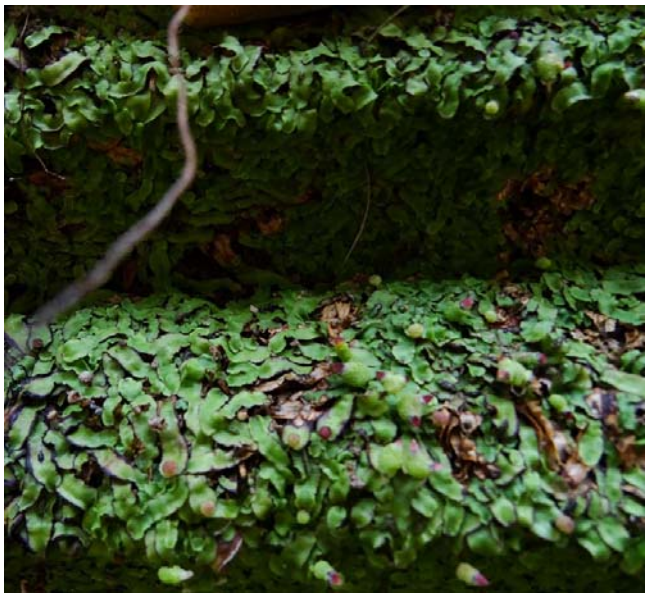

Figure 26. ***Asterella wallichiana*** on ledge, a species that was collected in or near a cave in India, adding to the known Indian bryophyte flora. Photo by Forest Owlet, through Creative Commons.

Figure 27. ***Plagiochasma appendiculatum*** in India, a species that was collected in or near a cave in India, adding to the known Indian bryophyte flora. Photo by Michael Lüth, with permission.

Figure 28. ***Marchantia palacea*** with gemmae, a species that was collected in or near a cave in India, adding to the known Indian bryophyte flora. Photo by Earth.com, with permission.

Figure 29. ***Riccia huebeneriana***; ***Riccia cruciata*** occurs on or near a cave in India, adding to the known Indian bryophyte flora. Photo by Show Ryu, through Creative Commons.

Puglisi and Privetera (2018) reported ***Tortula bolanderi*** (Figure 24) at the entrance of a grotto on Mt.

Etna in Sicily, a species that is rare in the Mediterranean area. Ursavaş and Çetin (2014) described the new species ***Cinclidotus asumaniae*** (see Figure 30) from a cave in southern Turkey, where it was on submerged and emergent rocks.

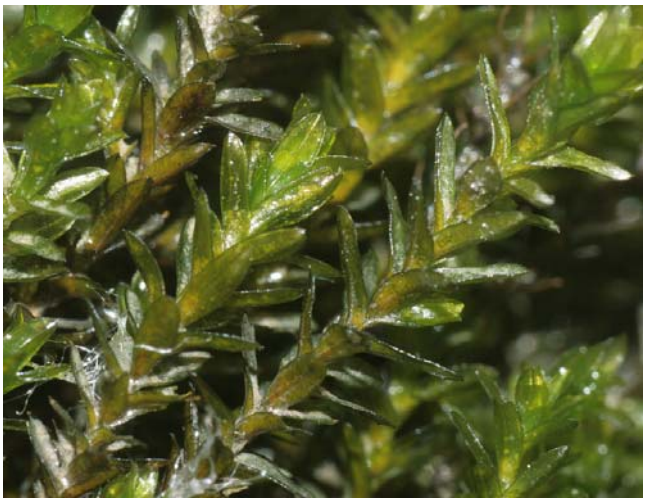

Figure 30. ***Cinclidotus riparius***; ***Cinclidotus asumaniae*** was described as a new species from a cave in southern Turkey. Photo by Hermann Schachner, through Creative Commons.

In the Azores, Gabriel *et al*. (2006) reported interesting species in the lava tubes and volcanic pits. They were able to find six European and four Macaronesian endemic species in the entrances of these volcanic formations, including one vulnerable species and three rare species. Rare species at these entrances include ***Fissidens coacervatus*** (Figure 31), ***Tetrastichium fontanum*** (Figure 32), and ***Tetrastichium virens*** (Figure 33); the liverwort ***Radula wichurae*** (Figure 34) is considered vulnerable.

Figure 31. ***Fissidens coacervatus*** with capsules, endemic, Madeira, a rare species that occurs in the entrances of lava tubes and volcanic pits in the Azores. Photo by Michael Lüth, with permission.

Figure 32. ***Tetrastichium fontanum***, a rare species that occurs in the entrances of lava tubes and volcanic pits in the Azores. Photo by Michael Lüth, with permission.

Figure 33. ***Tetrastichium virens***, a rare species that occurs in the entrances of lava tubes and volcanic pits in the Azores. Photo by Michael Lüth, with permission.

Figure 34. ***Radula kojana*** branch; ***Radula wichurae*** is a vulnerable species that occurs at cave entrances. Photo by Kochibi, through Creative Commons.

In the Neotropics of Fernando de Noronha, Brazil, Vital *et al*. (1991) found ***Fissidens cf. elegans*** (Figure 35) to be common at the entrance of a small cave.

Figure 35. ***Fissidens elegans*** on rock, a species common at the entrance of a small cave in Brazil. Photo by Wayne Lampa, through Creative Commons.

On Isle Royale, in Lake Superior, Thorpe and Povah (1935) reported ***Atrichum tenellum*** (Figure 36) from a cave in Rock Harbor, but the misidentification of ***Mnium thomsonii*** (Figure 37) as ***M. orthorrhynchum*** in the USA (Crum 1983) means this could be in error, and now ***M. orthorrhynchum*** is considered a synonym of ***Atrichum tenellum***.

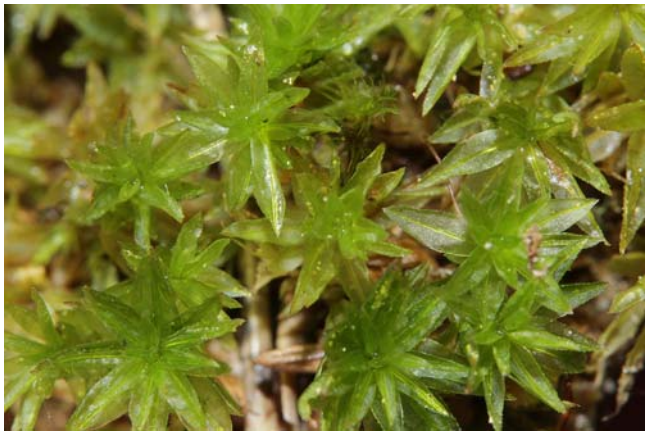

Figure 36. ***Atrichum tenellum***, a species known from a cave on Isle Royale, Michigan, USA. Photo by Hermann Schachner, through Creative Commons.

Figure 37. ***Mnium thomsonii***, possibly the species found in a cave on Isle Royale. Photo by Hermann Schachner, through Creative Commons.

I cite several examples here, but there certainly must be more that were not immediately obvious to me.

Liverworts

Cyathodium cavernarum (Figure 1, Figure 38-Figure 39)

Cyathodium cavernarum (Figure 1, Figure 38-Figure 39) earned its name as a cave liverwort, but it is not restricted to caves. It has been described as **iridescent** (showing luminous colors that seem to change when seen from different angles; Figure 39) (Reeb *et al*. 2018) and **luminous** (Zhang *et al*. 2004b). Zhang *et al*. 2004b) attributed this to a "peculiar light-reflecting power which produces a kind of starry effect, so that the plants seem to flood the dark caves where they grow with a luminous, golden-green light."

Figure 38. ***Cyathodium cavernarum*** on rock. Photo by Hermann Schachner, through Creative Commons.

Figure 39. ***Cyathodium cavernarum*** on rock where it is dark enough for its iridescence to show. Photo by Jan-Peter Frahm, with permission.

Cyathodium cavernarum (Figure 1, Figure 38-Figure 39) is frequently found within 1-12 m into the karst caves of Guangxi province, P. R. China, whereas ***C. smaragdinum*** (Figure 40) occurs within 0.5-22 m (Zhang *et al*. 2004a). The latter species lacks luminescence. Zhang *et al*. (2004b) similarly reported ***Cyathodium cavernarum*** from karst caves in Yunnan Province, P. R. China, but there it was found at 6~24 m into the cave.

Differences in depth permissible for growth can result from greater light penetration into the cave, influenced by the size of the opening and shading outside the cave.

Figure 40. ***Cyathodium smaragdinum*** on rock. Photo through Creative Commons.

On Réunion Island, Ah-Peng *et al*. (2010) found ***Cyathodium cavernarum*** (Figure 1, Figure 38-Figure 39) on the walls of a lava cave. In Birds'-Nest Cave in Sarawak, Holttum (1938) found it with the fern ***Tectaria dissecta*** (Figure 41) in low light, forming an association at the furthest photosynthetic location from the mouth of the cave.

Figure 41. ***Tectaria dissecta*** on cave wall, one of the ferns living in low light in caves. Photo by Gildas Gâteblé, through Creative Commons.

Cyathodium cavernarum (Figure 1, Figure 38-Figure 39) is a widely distributed pantropical species (Duckett & Ligrone 2006), primarily of low altitudes (Nair *et al*. 2005). Duckett and Ligrone (2006) expanded its distribution with a find in southern Italy. Surprisingly, Glenny (2002) reported it from Australia. It is found in both urban areas and shaded disturbed areas. For example, Pócs and Arnstein Lye (1999) found it on overhanging, dripping or sprayed rocks as well as on temporarily inundated, muddy riverine forest floors. In Gujarat, India, it is one of the most widely distributed species of liverworts (Shah & Gujar 2016).

Scott *et al.* (1997) described ***Cyathodium cavernarum*** (Figure 1, Figure 38-Figure 39) from a collection in Australia: "The glistening golden-green plates of this very pretty thallose species, ~c. .5-1 cm across have an almost iridescent lustre accentuated by the darkness of the habitat. It seems to be confined to the floor of a single small cleft in south-facing cliffs of the Napier Range in the Kimberley region of Western Australia." Glenny (2002) notes that the plants die off in late spring, regrowing from spores at the end of each wet season. This assumes that it is an annual with a very precarious survival in any location. One might expect this strategy to eventually be lost in cave populations that lack the usual seasonal fluctuations.

Mosses

Bartramia ithyphylla (Figure 42-Figure 43)

De Leeuw *et al*. (1998) describe the Antarctic ***Bartramia ithyphylla*** (Figure 42-Figure 43) from Cuverville Island, Antarctica. It grows in cushions in shallow caves and crevices, sometimes upright and sometimes upside down on the ceiling of the cave. It produced sporophytes in the crevices, but not elsewhere. Could it be that the caves and crevices, in this case, permit them to live in the otherwise hostile environment of Antarctica? Nevertheless, it is not restricted to these habitats elsewhere in the Antarctic region (Bergstrom *et al*. 2002; Matteri & Schiavone 2004). But on the South Sandwich Islands, this species occurs only on the heated soil of geothermal areas (Convey & Lewis Smith 2006).

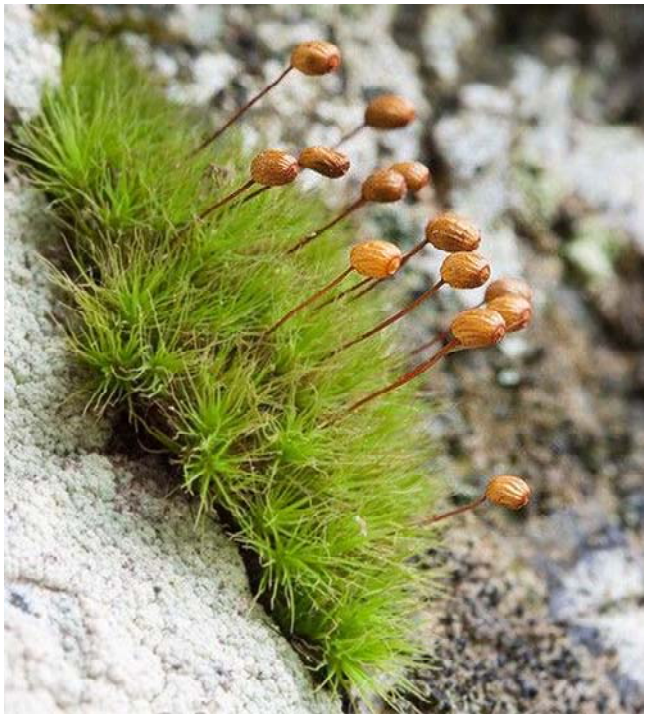

Figure 42. ***Bartramia ithyphylla*** with capsules, on rock. Photo by Štěpán Koval, with permission.

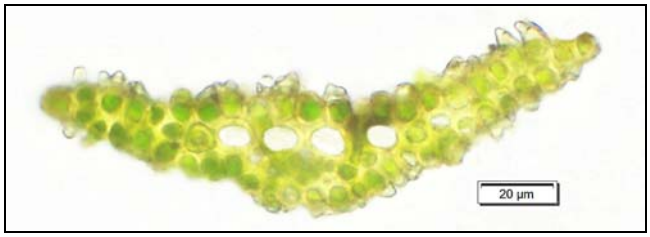

Figure 43. ***Bartramia ithyphylla*** leaf cs showing papillae and internal layering of leaf. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Cyclodictyon laetevirens (Figure 44)

Porley (2013) tells the story of the discovery of the moss ***Cyclodictyon laetevirens*** (Figure 44) in a Cornish sea cave. This resulted in its eradication by "a well-meaning but seriously misguided vicar keen to stop anyone else finding it." Porley was pleased to report that it was subsequently found in another cave nearby.

Figure 44. ***Cyclodictyon laetevirens***, a moss that can live in sea caves. Sean Edwards, with permission.

Cyclodictyon laetevirens (Figure 44) is a rare moss in Britain and Ireland. It tolerates both acid and mildly basic substrata on deeply-shaded wet rocks in ravines, caves, and crevices near waterfalls (Smith 1978; Hill *et al*. 1994). ***Cyclodictyon laetevirens*** is unable to survive either dehydration or freezing (Burch 2003), perhaps explaining its existence in caves where the conditions are less variable.

Didymodon glaucus (Figure 45-Figure 46)

Porley (2007) reported another threatened bryophyte, ***Didymodon glaucus*** (Figure 45-Figure 46), from caves in Europe. The species occurs deep in caves, near the entrance or surrounding artificial lights. Such localities are known in Hungary and Germany. In Luxembourg it occurs under rocky overhangs of calcareous sandstone, with similar habitats in Norway. Despite its somewhat wide occurrence in caves and shaded rock overhangs, it must reproduce completely by vegetative means; only female plants are known. Apparently ***Didymodon verbanus***, a species with only males known, is actually the male of this species (Kučera 2002; TROPICOS 2021).

Figure 45. ***Didymodon glaucus***, a threatened species that succeeds in caves in Europe. Photo by Tomas Hallingbäck, with permission.

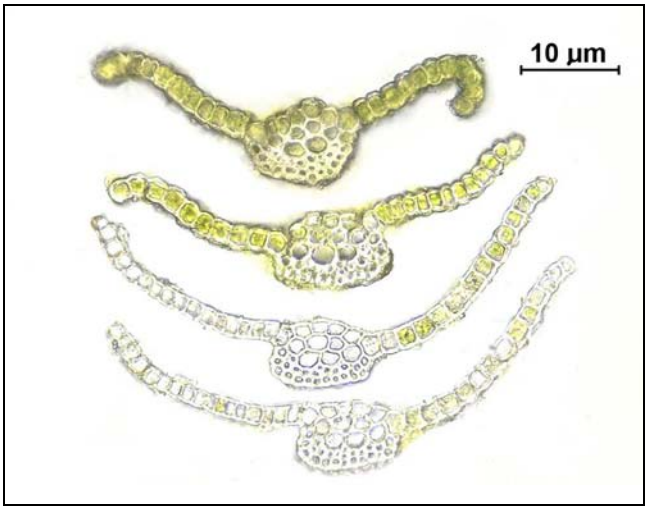

Figure 46. ***Didymodon glaucus*** leaf cs showing strong costa. Photo by Hugues Tinguy, with permission.

Didymodon glaucus (Figure 45-Figure 46) produces protonemal gemmae (Figure 47), both chains and single gemmae from modified axillary rhizoids (Porley 2004). In some locations, protonemal gemmae of ***Eucladium verticillatum*** (Figure 52-Figure 53) occur mixed with this species in the deep shade of clefts. On the other hand, ***D. glaucus*** does not tolerate excessive shading and the leafy plant disappears; however, the protonema often persists. ***Amblystegium serpens*** (Figure 48), when growing intermixed with ***D. glaucus*** (Figure 45-Figure 46), is able to increase as ***D. glaucus*** declines. Within 5 years, only a few moribund gemmae-bearing leafy shoots remain. Nevertheless, ***D. glaucus*** is able to penetrate deep into the cave, where it is able to grow in the light of the artificial cave lights.

Figure 47. ***Didymodon glaucus*** spores and tuber (protonemal gemmae). Photo by Hugues Tinguy and F. Bick, with permission.

Figure 48. ***Amblystegium serpens*** on rock ledge, a species that can outcompete ***Didymodon glaucus*** in low light. Photo by Claire Halpin, with permission.

Didymodon glaucus (Figure 45-Figure 46) is also known from calcareous walls of caves in the French Alps (Skrzypczak 2004) and inside cave entrances in Germany (Frahm 2005). In Sussex it grows in crevices and hollows.

The life strategy (During 1979, 1992) of ***Didymodon glaucus*** (Figure 45-Figure 46) has been considered a short-lived shuttle colonist by Hodgetts (1996) and a stress-tolerant perennial by Hallingbäck (1998). Despite its lack of spores, it is able to colonize quickly. Porley (2005) observed that it colonized a freshly exposed section of chalk between February 2003 and May 2004 at a location several meters from the nearest location. Dispersal outside of caves can be by rabbits that run along the cliff face ledges. In locations unsuitable for rabbits, it may benefit from snails such as ***Trochulus striolatus*** (Figure 49) and ***Cochlodina laminata*** (Figure 50) that have been observed crossing the moss.

Figure 49. ***Trochulus striolatus***, a snail that might disperse ***Didymodon glaucus*** propagules. Photo by Roy Anderson, through Creative Commons.

Figure 50. ***Cochlodina laminata*** on rock with moss, a snail that might disperse ***Didymodon glaucus*** propagules. Photo by O. Gargominy, through Creative Commons.

Epipterygium koelzii (see Figure 51)

Robinson (1968) found ***Epipterygium koelzii*** (see Figure 51) in a damp cave in the Himalayas. It remains an endemic there with apparently no further reports outside that area (Hanusch *et al*. 2020).

Figure 51. ***Epipterygium tozeri***; ***Epipterygium koelzii*** occurs in a damp cave in the Himalayas. Photo by Ken-Ichi Ueda, through Creative Commons

Eucladium verticillatum (Figure 52-Figure 53)

As I read the many studies on caves, I got the impression that ***Eucladium verticillatum*** (Figure 52-Figure 53) was perhaps the most likely bryophyte to find in a cave.

Figure 52. ***Eucladium verticillatum***, a limestone species that builds tufa and statoliths in streams and caves, respectively. Photo by Christian Berg, through Creative Commons.

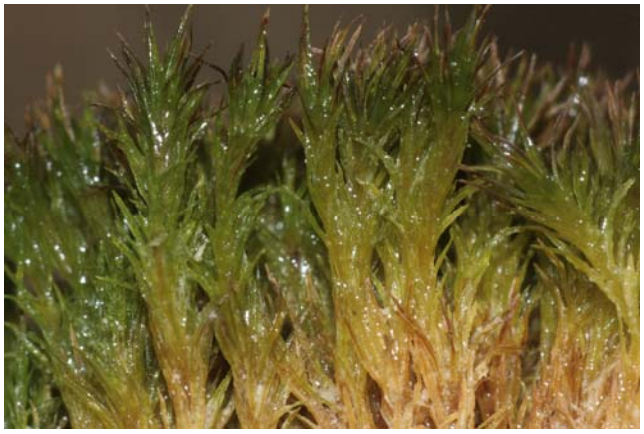

Figure 53. ***Eucladium verticillatum***. Photo by Hermann Schachner, through Creative Commons.

Eucladium verticillatum (Figure 52-Figure 53) was found for the first time in Indiana, USA, in a wet, cave-like depression (Miller & Thomson 1959). Shirzadian and Gholami (2001) treated it as the first moss report from the Alisadr Cave in Iran. Aboutabl *et al*. (1999) widened the types of caves with their report of the species on exposed rocks or fragments in protected habitats, including "small" caves and wet crevices. Its growth formed carpets that covered wide areas on the vertical rock of a cave. It became inundated by rainwater and its surface exhibited a dense cover of the ***Nostoc*** (**Cyanobacteria**; Figure 54) balls. They found a higher concentration of metals in plants from a wadi-bed than from those in the cave.

Figure 54. ***Nostoc commune*** on soil with mosses. Photo by Yamamaya, through Creative Commons.

Popkova *et al*. (2019) found that ***Eucladium verticillatum*** (Figure 52-Figure 53) and several algae and **Cyanobacteria** (Figure 54) dominate the photosynthetic communities near the entrance and around lights in the Ahshtyrskaya Cave in Russia.

Osada (1958) described the habitats (Figure 55-Figure 63) of ***Eucladium verticillatum*** (Figure 52-Figure 53). It is rare, despite being widespread geographically. Gradstein (1972) reported ***Eucladium verticillatum*** (Figure 52-Figure 53) from the entrance of a cave on the Maltese Islands, growing on moist limestone. It also had non-cave habitats on a moist perpendicular wall below an irrigation gully where it was whitish and lime-encrusted. A similar form is found in the Mediterranean area on constantly moist limestone rocks near springs and rivulets.

Figure 55. ***Eucladium verticillatum*** with accumulated minerals on the leaves. Photo by Martina Peoltl, through Creative Commons.

Figure 56. ***Eucladium verticillatum*** at cave entrance. Photo by Hermann Schachner, through Creative Commons.

Figure 57. ***Eucladium verticillatum*** in lime seep. Photo by Resso Taelspeus, through Creative Commons.

Figure 58. ***Eucladium verticillatum*** on rock. Photo by Hermann Schachner, through Creative Commons.

Figure 59. ***Eucladium verticillatum*** on rock wall. Photo by Paul Bowyer, through Creative Commons.

Figure 60. ***Eucladium verticillatum*** on rock wall. Photo by Paul Wilson, with permission.

Figure 61. ***Eucladium verticillatum*** with calcium deposits. Photo by Christian Berg, through Creative Commons.

Figure 62. ***Eucladium verticillatum*** with mineral deposits. Photo by Martina Peoltl, through Creative Commons.

Figure 63. ***Eucladium verticillatum*** with mineral deposits on leaf tips. Photo by Armand Turpel, through Creative Commons.

Wigginton (2001) notes that ***Eucladium verticillatum*** (Figure 52-Figure 53) growing under an overhang in a deep gully was encrusted with tufa (Figure 61-Figure 63). The leaves were atypical, lacking the recurved, basal marginal teeth (Figure 64) and having sparse papillae, sometimes lacking the papillae entirely (Figure 65).

Figure 64. ***Eucladium verticillatum*** leaf. Photo by Armand Turpel, through Creative Commons.

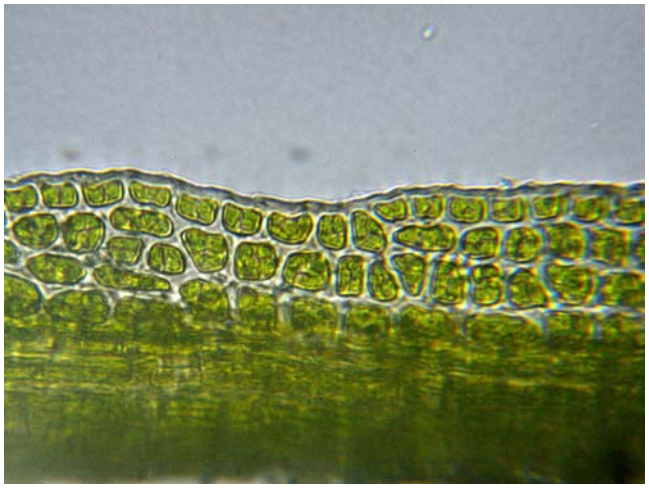

Figure 65. ***Eucladium verticillatum*** leaf margin showing sparse papillae, as one might fid in a cave. Photo by Armand Turpel, through Creative Commons

Little is known of the reproduction of ***Eucladium verticillatum*** (Figure 52-Figure 53). It is **dioicous** and sporophytes seem to be rare in caves, although Dalby (1966a) reported seeing shrivelled archegonia. Instead, it appears that gemmae are the primary means of reproduction. These structures are attached to rhizoid branches among the lowermost leaves.

Dalby (1966a) provided a detailed description of the plants and the cave conditions where they occurred in a cave in Dorset, UK. The plants occurred in a mine cave of a sea cliff, where they occupied the floor, walls, and ceiling, penetrating to 14.6 m from the opening. Their light limit seemed to be at about 100 lux. Prior (1961) reported that growth stopped at about 400-500 lux in Luray Cavern. Mulec and Kubešová (2010), in Slovenian show caves, found that ***Eucladium verticillatum*** had the widest range of acceptable light levels (1.4 to 530.0 µmol photons m^{-2} s^{-2}) for photosynthesis.

Dalby (1966a) reported that the plants remained alive in a polyethylene bag in total darkness for two months. It did not become etiolated, but Dalby did not indicate if it grew. Etiolation would require growth. It is possible that such long periods of darkness in the cave could be compensated by periods when the sun is low in the sky and light penetrates farther into the cave. These plants developed wider leaf laminae in poor light. ***Eucladium verticillatum*** (Figure 52-Figure 53) forms **eucladioliths** (Figure 66) by accretions around several stems. They ultimately leave the eucladiolith hollow. These structures are affected by growth of the moss toward light and downward pull of gravity. They are prone to breaking away from the ceiling, and when that happens, more ***Eucladium verticillatum*** will often colonize the bare spot.

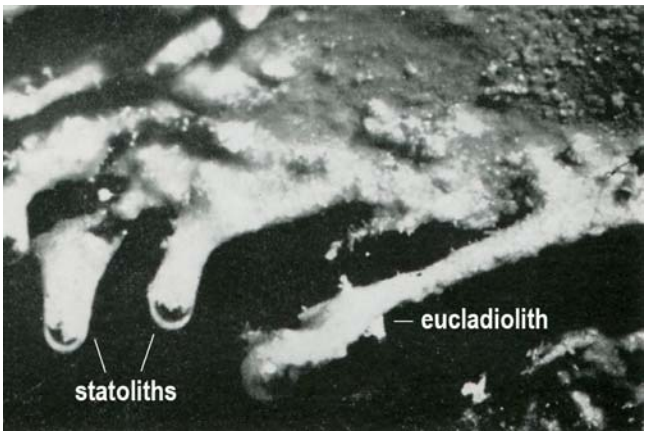

Figure 66. ***Eucladium verticillatum*** forming stalactite (eucladiotite; eucladiolith) in mine in Dorset, UK. Photo modified from Dalby 1966b.

Pentecost (1996) further described the formation of eucladioliths. The formation involves deposition of calcium carbonate through photosynthesis, evaporation, and CO_2 escape. Pentecost estimated that 6-12% of the carbonate was deposited through photosynthesis, 10-20% through evaporation, and the remaining 70-80% through gas escape.

Despite its rarity, El-Saadawi *et al.* (1997) were able to assess the variation in the chemical constituents of ***Eucladium verticillatum*** (Figure 52-Figure 53).

Eurhynchium hians (Figure 67-Figure 69)

Reports on ***Eurhynchium hians*** (Figure 67-Figure 69) seem to be few. Papp *et al.* (2008) reported that it occurs on limestone rock in a cave in Montenegro. Prior (1961) reported it from the Luray Cavern in Virginia, USA. Achoual *et al.* (2021) found it associated with ***Oxyrrhynchium speciosum*** (Figure 70-Figure 71) stream under the waterfall of Pigeon Cave in Morocco. Wareham (1941) reported ***Eurhynchium hians*** from Hocking County, Ohio, USA, where many caves and canyons exist, but he did not mention its habitat there. It is also able to grow around lamps in show caves (Kubešová 2001), where it was frequent in the Moravian Karst of the Czech Republic.

Figure 67. ***Eurhynchium hians***, a species that occurs in caves in limited locations in Europe, including around cave lamps. Photo by Bob Klips, with permission.

Figure 68. ***Eurhynchium hians***. Photo by Bob Klips, with permission.

Figure 69. ***Eurhynchium hians*** branch. Photo by Tuomo Kuitunen, with permission.

Figure 70. ***Oxyrrhynchium speciosum***, a species that has been found in association with ***Eurhynchium hians*** in caves. Photo by Hugues Tinguy, with permission.

Figure 71. ***Oxyrrhynchium speciosum***. Photo by George G., through Creative Commons.

Homalia webbiana (see Figure 72-Figure 74)

In the Azores, Gabriel *et al*. (2006) reported ***Homalia webbiana*** (see Figure 72-Figure 74) in the lava tubes and volcanic pits. ***Homalia webbiana*** is endemic to Europe and is known from only 10 localities in the Azorean archipelago. Sjögren (2003) found that it prefers *p*H above 5.5, permitting it to occur on lava boulders of stone fences and on cement. It can occur in strongly exposed habitats and is highly drought tolerant and is highly dominant on tree trunks, but it also occurs on cement and on coastal lava boulders in stone fences where it is greatly exposed.

Figure 72. ***Homalia trichomanoides***; ***Homalia webbiana*** occurs in lava tubes and volcanic pits in the Azores. Photo by Janice Glime.

Figure 73. ***Homalia trichomanoides***. Photo by Andrew Spink, with permission.

Figure 74. ***Homalia trichomanoides***, on a canyon wall, Jacob's Creek, Keweenaw Co., Michigan, USA. Photo by Janice Glime.

There have been numerous taxonomic and systematic publications on ***Homalia webbiana***, but ecological information is not very frequent. In part because of the confusion in the identity of the species, Ros *et al*. (2013) consider ***Homalia webbiana*** (see Figure 72-Figure 74) to be restricted to Macaronesia.

Mittenia plumula (Figure 75-Figure 77)

Mittenia plumula (Figure 75-Figure 77) has lots of similarities to ***Schistostega pennata*** (Figure 75-Figure 77), including persistent, highly refractive protonemata, protonemal gemmae, and pennate leaves (Stone 1961a, b, 1986; Frahm 2012). It also seems to prefer similar habitats. Stone (1961a) describes the protonema (Figure 78-Figure 79) as highly refractive and lenticular.

Figure 75. ***Mittenia plumula*** growing on a vertical wall. Photo by David Tng, with permission.

Figure 76. ***Mittenia plumula*** mature gametophyte. Photo by David Tng, with permission.

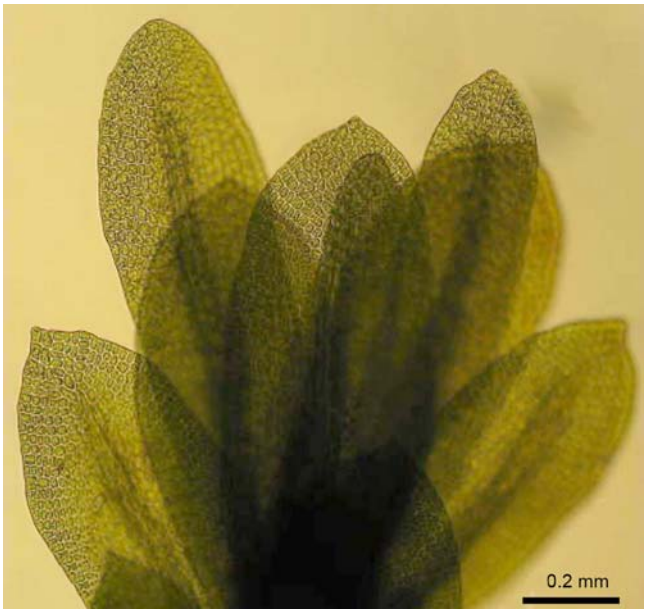

Figure 77. ***Mittenia plumula*** showing leaf structure. Photo by Tom Thekathyil, with permission.

Figure 78. ***Mittenia plumula*** protonema in New Zealand. Photo courtesy of David Glenny.

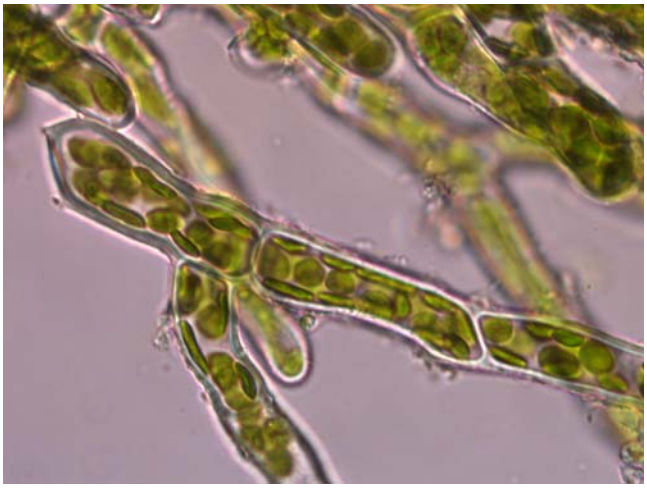

Figure 79. ***Mittenia plumula*** protonema from New Zealand. Photo courtesy of David Glenny.

I first learned about ***Mittenia plumula*** (Figure 75-Figure 77) in Australia when we found it at the entrance of a wombat hole (Figure 80-Figure 82). Fife and Shaw (1990) describe it as a species that grows only in microhabitats where it is deeply shaded. For example, it occurred 20 cm further beneath an overhang than did other bryophytes.

Figure 80. ***Mittenia plumula*** in wombat hole, showing iridescent look. Photo by Tony Markham; permission pending.

Figure 81. ***Mittenia plumula***, Mt Wilson, Blue Mountains, NSW, Australia, in opening of wombat hole. Photo by Janice Glime.

Figure 82. ***Mittenia plumula*** growing on soil at wombat hole entrance, Mt. Wilson, NSW, Australia. Photo by Janice Glime.

Fife (1984) reported ***Mittenia plumula*** (Figure 75-Figure 77) from New Zealand. Its habitats include silt soil beneath a sandstone overhang in a roadcut, clay soil in a crevice beneath roots, and mesic humus beneath a granite boulder. It seems to prefer soil (Figure 83) to rock and occurs mostly in small cavities. Similarly, Beever and Brownsey (1993) found it under soil overhangs in New Zealand. But its habitats there also include rock walls of caves (Figure 84).

Figure 83. ***Mittenia plumula*** on soil in New Zealand. Photo by Janice Glime.

Figure 84. ***Mittenia plumula*** on cave wall, Okere Falls, NZ. Photo by Janice Glime.

Schistostega pennata (Figure 85-Figure 118)

I first saw ***Schistostega pennata*** (Figure 85-Figure 118) on a field trip in New York, USA. It was in a small cave in a bank (Figure 87) where one had to look carefully to avoid shading it completely. It has earned its names of cave moss, goblin gold, or Dragon's gold (Berqvist 1991). In a cave in Alger County, Michigan (Figure 88-Figure 90), ***Schistostega pennata*** occurs on the ceiling of the cave, visible in the dim light due to its unique way of rotating its protonemal chloroplasts (Figure 91-Figure 102) to reflect (and absorb) maximum light intensity (Crum 1983). Conard (1938) refers to its presence in a tiny cave near Au Train, perhaps referring to the same location as that of Crum. He noted that ***Schistostega pennata*** "disappears" when you block the light so that it is unable to reflect (as in Figure 87).

Figure 85. ***Schistostega pennata*** leafy gametophytes on rock, a moss of low light such as that in caves. Photo by Hermann Schachner, through Creative Commons.

Figure 86. ***Schistostega pennata*** leafy gametophytes. Photo from Northern Forest Atlas, with permission through Jerry Jenkins.

Figure 87. Nancy Slack exploring a small cave with ***Schistostega pennata***, my first view of the species. Photo by Janice Glime.

Figure 88. Cave entrance, Alger County, Michigan, home of ***Schistostega pennata***. Photo by Janice Glime.

Figure 89. View from entrance of cave in Alger County, Michigan. There are protonemata overhead, but the lighting is wrong to see the luminescence. Photo by Janice Glime.

Figure 90. ***Schistostega pennata***, on a ledge near Scott's Cave, Munising, MI. Photo by Janice Glime.

Figure 91. ***Schistostega pennata*** leafy plant with protonemata. Photo by Des Callaghan, with permission.

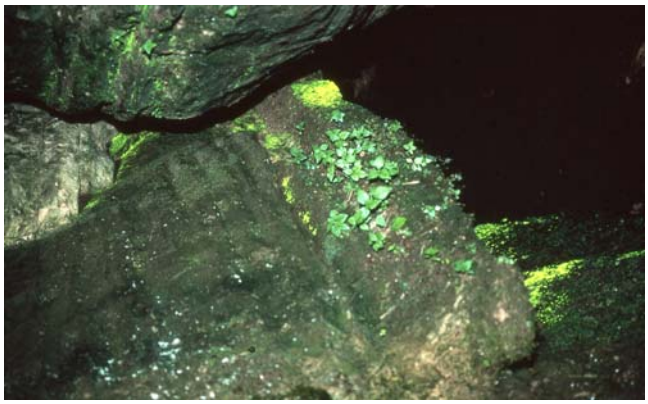

Figure 92. ***Schistostega pennata*** showing luminescence. Photo Courtesy of John Christy.

Figure 93. ***Schistostega pennata*** luminescent protonemata. Photo courtesy of Martine Lapointe.

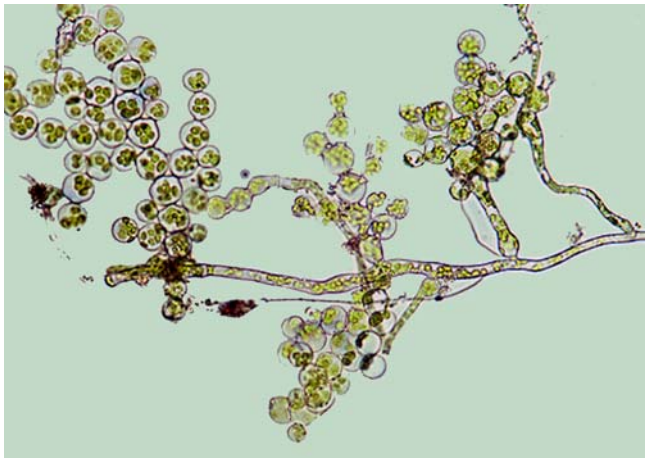

Figure 94. ***Schistostega pennata*** protonema with gemmae. Photo courtesy of Irene Bisang.

Figure 95. ***Schistostega pennata*** with protonemata and leafy gametophytes on soil. Photo courtesy of Martine Lapointe.

Figure 96. ***Schistostega pennata*** leafy plant with protonemata at base. Exposure to light suppresses the luminescence. Photo by Bob Klips, with permission.

Figure 97. ***Schistostega pennata*** carpet with both leafy gametophytes and luminescent protonemata. Photo by Alpsdake, through Creative Commons.

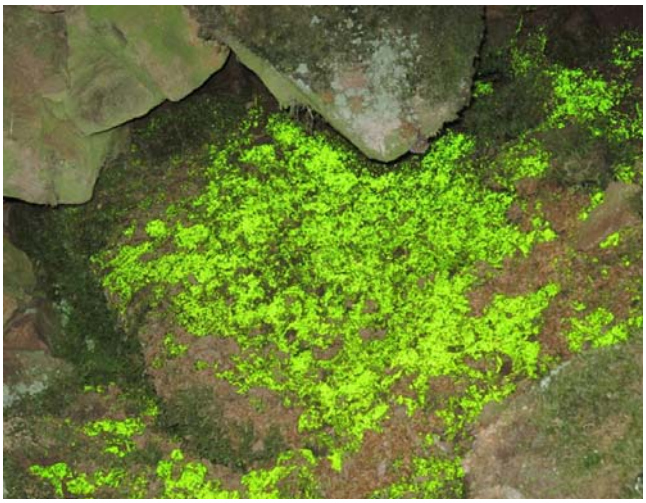

Figure 98. ***Schistostega pennata*** protonemata showing luminescence in cave. Photo by Hugues Tinguy, with permission.

Figure 99. ***Schistostega pennata*** showing luminescent protonemata and a few leafy plants. Photo by Bob Klips, with permission.

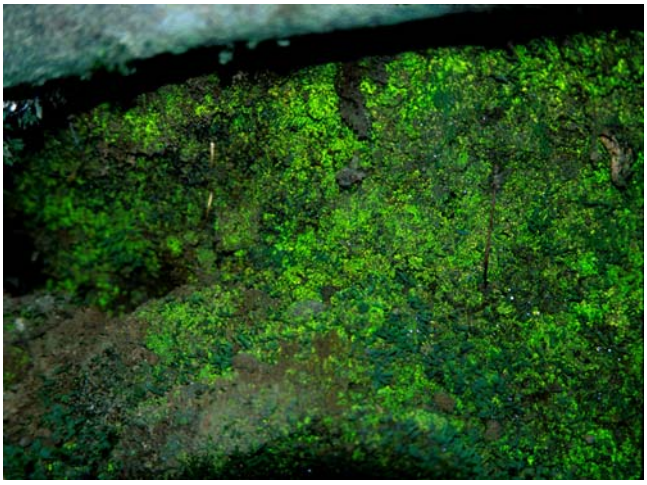

Figure 100. ***Schistostega pennata*** luminescence. Photo by Martin Hutten, with permission.

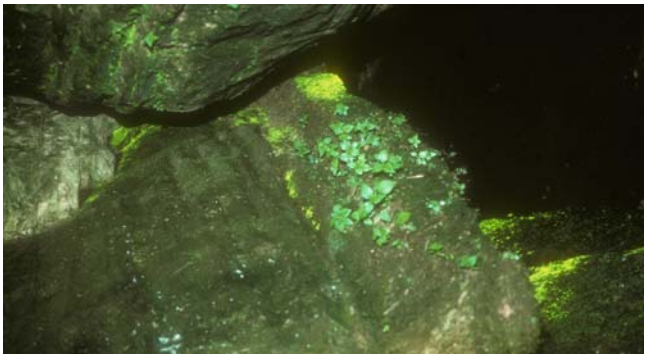

Figure 101. ***Schistostega pennata*** protonemata. Photo by courtesy of John Christy.

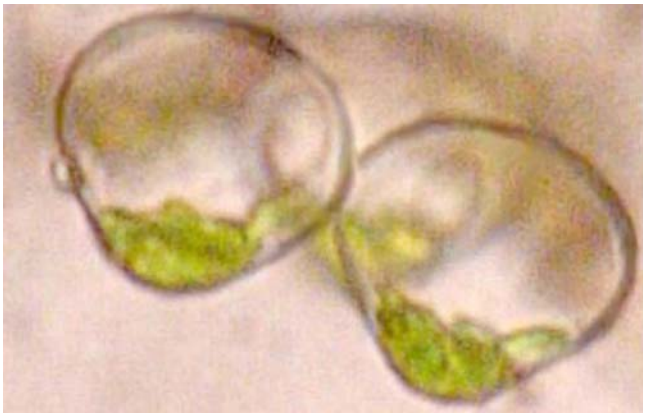

Figure 102. ***Schistostega pennata*** showing lens-shaped protonema cells. Photo by Misha Ignatov, with permission.

In Japan, there is a national monument (Figure 103-Figure 104) to the cave where ***Schistostega pennata*** (Figure 85-Figure 118) grows (Glime & Iwatsuki 1987). It inspired an opera that told the lore of a group of stranded sailors who spent the winter in the cave. They had no source of food and no way to travel in the dead of winter, so they resorted to cannibalism. When the last two men remained, one of these sailors was saved from death because his would-be killer saw the glow of the moss behind the poor sailor's head and changed his mind about murdering his companion for food. Kanda (1988) reviewed the status of the colony in the cave.

Figure 103. ***Schistostega pennata*** Monument in Japan. Photo by Janice Glime.

Figure 104. ***Schistostega pennata*** monument, Japan, with view into cave where the moss grows. Photo by Janice Glime.

Schistostega pennata (Figure 85-Figure 118) grows in a variety of low-light habitats (Figure 105-Figure 110). I have seen ***Schistostega pennata*** in Germany at the base of a boulder on soil that was protected by the overhang of the boulder. The most prolific growth I have seen was on the roof of a cave behind a waterfall in the Upper Peninsula of Michigan, USA (Figure 88). In Iraq, Aziz (2011) reported it from a Shanadar cave (also spelled Shanidar; Figure 111), noting its rarity in Iraq.

Figure 105. ***Schistostega pennata*** protonemata showing luminescence in cave. Photo by César Garcia, with permission.

Figure 106. ***Schistostega pennata*** on rock in a crevice, showing protonemal luminescence. Photo courtesy of Martine Lapointe.

Figure 107. ***Schistostega pennata*** in a rock crevice with luminescent protonemata showing deeper in. Photo by Michael Lüth, with permission.

Figure 108. ***Schistostega pennata*** protonemata in cave. Photo by Hugues Tinguy, with permission.

Figure 109. ***Schistostega pennata*** habitat. Photo courtesy of Martine Lapointe.

Figure 110. ***Schistostega pennata*** growing on a darkened soil bank. Photo courtesy of Martine Lapointe.

Figure 111. Shanadar cave, Iraqi Kurdistan, a cave where one can find ***Schistostega pennata***, a rare species in Iraq. Photo by Osama Shukir Muhammed Amin, through Creative Commons.

Kanda (1971) described cave localities for ***Schistostega pennata*** (Figure 85-Figure 118) in Hokkaido, Japan. Its substrate rocks included granite, andesite, and the base of a fallen tree. The mean *p*H of its substrates was 4.7, but it was found once at 6.8. Matsuda (1963) noted that it also occurs in artificial caves.

Reinoso Franco *et al*. (1994) reported on its ecology in the Iberian Peninsula. The cave was very humid, only 50 m above the sea, and the substrate had a *p*H of 5.7. Werner (2011) reported it as occurring in caves in Luxembourg.

Schistostega pennata (Figure 85-Figure 118) is listed as rare in Latvia, with only 21 published records from 1924 until 2010 (Mežaka *et al*. 2011). Of these, 18 records were from protected areas. Its most common habitat there is on ***Picea abies*** (Figure 112) root mass rather than on sandstone. This demonstrates that even small "caves" such as those created by roots provide suitable habitat. It also occurs in the minicaves made by roots in calcareous areas (Crum 1983).

Figure 112. ***Picea abies*** that can form a habitat for ***Schistostega pennata*** among exposed roots. Photo from European Environment Agency, through Creative Commons.

Schistostega pennata (Figure 85-Figure 118) has sticky spores (Figure 113-Figure 116) much like those of the **Splachnaceae** (Ignatov & Ignatova 2001). This suggests that it may be dispersed by animals, perhaps insects. Its rapid expansion upon arrival at a new location in Russia supports this, and Ignatov and Ignatova suggest it could be dispersed by birds, mammals, insects, or spiders.

Figure 113. ***Schistostega pennata*** leafy plants with sporophytes. Photo courtesy of Martine Lapointe.

Figure 114. ***Schistostega pennata***, with capsules. Photo by Martin Hutten, with permission.

Figure 115. ***Schistostega pennata*** capsule with sticky spores. Photo by Misha Ignatov.

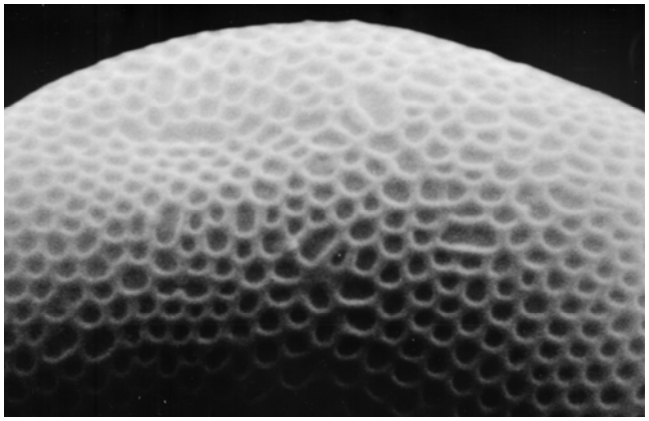

Figure 116. ***Schistostega pennata*** SEM of spore surface. Photo by Misha Ignatov.

Edwards (1978) described protonemal gemmae (Figure 117-Figure 118) from a British ***Schistostega pennata*** (Figure 85-Figure 118). In particular, he noted the similarity to those of ***Mittenia plumula*** (Figure 75-Figure 77). This is a common means of propagation in cave bryophytes.

Figure 117. ***Schistostega pennata*** protonemata with gemmae branches. Photo courtesy of Misha Ignatov.

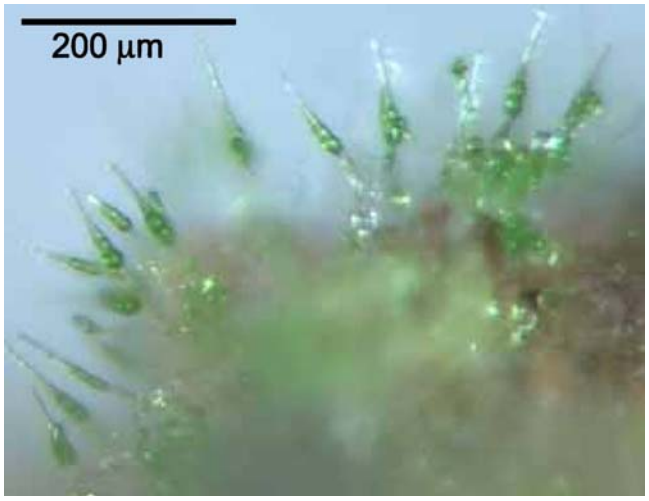

Figure 118. ***Schistostega pennata*** protonemal gemmae. Photo modified from Ignatov *et al.* 2012, with permission.

Takakia lepidozioides (Figure 119-Figure 122)

Takakia (Figure 119-Figure 122) has been reported from distant places around the world. It is so unusual that for a long time bryologists were unable to put it into a phylum with certainty. Phycologists wouldn't claim it as an alga. In the absence of sporangia or antheridia, it was originally classified as a liverwort, but Mizutani (1967) considered the stalked archegonia to be a moss character. Finally, sporophytes were found in ***Takakia ceratophylloides*** (Figure 123) and it has capsules with spiral sutures that split much like those of ***Andreaeobryum*** (Figure 124). It is now classified as a moss (Murray 1988; Smith & Davison 1993).

Figure 119. ***Takakia lepidozioides***, a species sometimes found in caves or cave-like situations. Photo by Quentin Cronk, through Creative Commons.

Figure 120. ***Takakia lepidozioides***. Photo by Rafael Medina, with permission.

Figure 121. ***Takakia lepidozioides***. Photo by Rafael Medina, with permission.

Figure 122. ***Takakia lepidozioides***. Photo by Stu Crawford, through Creative Commons.

Figure 123. ***Takakia ceratophylla*** with dehisced capsules. Photo by Karen Renzaglia, with permission.

Figure 124. ***Andreaeobryum macrosporum*** with capsules. Photo by Botany Website, UBC, with permission.

In the Kinabalu National Park, Sabah, Malaysia, Akiyama *et al*. (2001) found ***Takakia lepidozioides*** (Figure 119-Figure 122) at Paca Cave. Unfortunately, it is unclear if it is inside or near the cave. Caves are certainly not its typical habitat. Persson (1958) found it on soil partly covering non-calcareous rocks. Higuchi and Lin (2005) reported it from Taiwan. Other records from the Himalayas likewise are in cool locations, but not caves. It seems to prefer places that are constantly moist.

Tetrodontium brownianum (Figure 125-Figure 130)

In Michigan, USA, ***Tetrodontium brownianum*** (Figure 125-Figure 130) occurs under over-hanging ledges of calcareous sandstone near Munising (Steere 1942). These ledges are associated with waterfalls. Sporophytes were present only on plants attached to the ceiling of an open cave, but not on plants adhering to vertical rock walls.

A number of the rare bryophytes that are known from caves seem to have unusual protonemata. ***Tetrodontium brownianum*** (Figure 125-Figure 130) instead has a rather unusual stem (Hodgetts 1915). It is nearly stemless with the vegetative part consisting of a tuft of narrowly clavate frondiform leaves (Figure 125). These may even be somewhat palmately branched at the apex where the capsule (Figure 126) is produced.

Figure 125. ***Tetrodontium brownianum*** plant showing the short stem and branching. Photo by Hugues Tinguy, with permission.

Figure 126. ***Tetrodontium brownianum*** with capsules. Photo by Andy Hodgson, with permission.

Figure 127. ***Tetrodontium brownianum*** with capsules. Photo by Hugues Tinguy, with permission.

Slack and Horton (2010) explored the bryophytes of the Bering Glacier Region. There one can find small caves formed by the rocks of the tundra. They found the rare ***Tetrodontium brownianum*** (Figure 125-Figure 130) in such a small cave there. Other records indicate that it lives on the underside of overhanging rock. Müller (2004) found it inverted on a sandstone overhang in Saxony. Grout (1899) reported it from stones in Devil's Den in New Hampshire, USA, where it grew upright on moist stones near the top of the cave.

Figure 128. ***Tetrodontium brownianum*** upside down or boulder, showing setae and capsules. Photo by Stefan Gey, through Creative Commons.

Figure 129. ***Tetrodontium brownianum*** upside down or boulder. Photo by Stefan Gey, through Creative Commons.

Gauthier (2011) described the genus ***Tetradontium*** from Québec, Canada, to grow exclusively in the shade on both acidic and limestone rocks. It occurs suspended from the ceiling of rock shelters (caves?), in rock wall crevices (Figure 130), and even at the bottom of caves in constant high humidity but not oozing rocks. Williams (1968) reported it as new to Ontario, Canada, occurring in moist crevices of shaded granite cliffs.

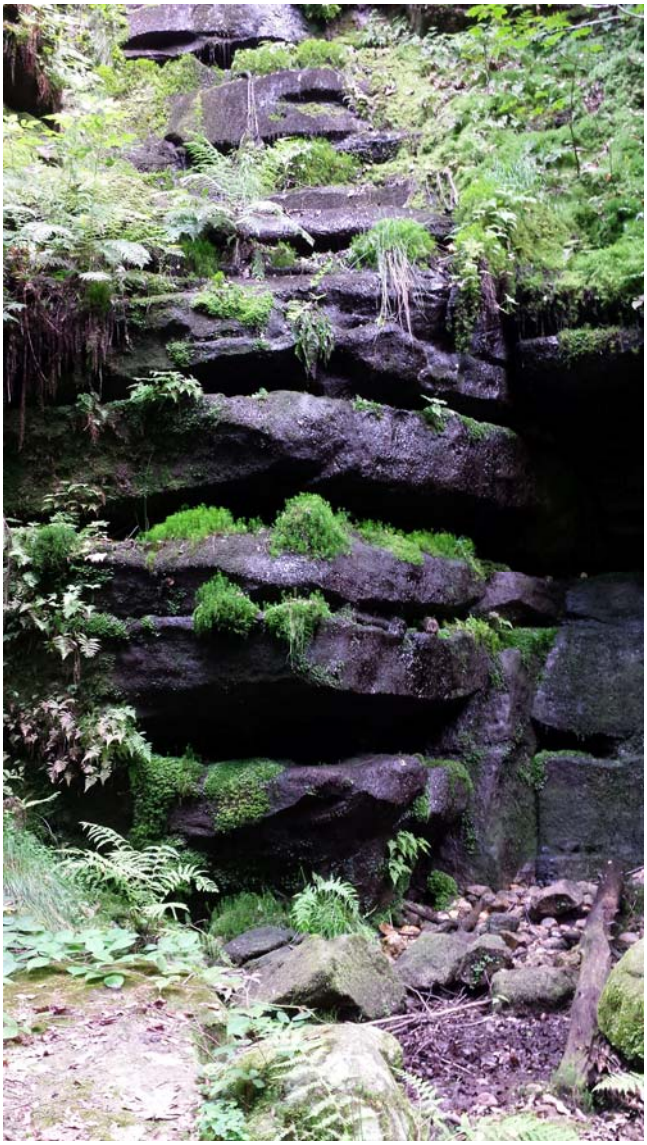

Figure 130. ***Tetrodontium brownianum*** habitat in rock wall crevices. Photo by Stefan Gey, through Creative Commons.

Pentecost and Rose (1985) reported ***Tetrodontium brownianum*** (Figure 125-Figure 130) as common under rock overhangs at the Wealden sandrocks in the UK. Pursell (2006) found it in a similar Saxon habitat on the underside of a sandstone overhang.

In North America, Lawton and Ireland (1963) reported it from under a rock ledge in Washington state. Taylor (1967) found it British Columbia on a boulder face in the forest, presumably receiving enough shade from the forest. Snider and He (1992) referred to ***Tetrodontium brownianum*** (Figure 125-Figure 130) as a rare cave moss in Ohio, USA.

Timmia norvegica/*Timmia sibirica* (Figure 131-Figure 132)

Vitt and Horton (1979) found what they considered might be ***Timmia norvegica*** (Figure 131-Figure 132) on rock in the spray zone in a small limestone cave in Banff National Park in Alberta, Canada. Although the species is somewhat common in more northern locations, it is critically imperiled in Alberta and represented a new record for the province at the time. The authors suggested that it might actually be a previously undescribed species. However, later investigations caused Horton (1981) to place it in ***T. sibirica***, a species that is also critically endangered in Alberta, having a predominantly High Arctic distribution. The typical habitat of ***T. sibirica*** is on strongly calcareous substrates adjacent to waterfalls, along streams, or in low-lying tundra (Horton 1981). Based on nuclear and chloroplast sequence data, Budke and Goffinet (2006) considered this to be a morphotype of ***T. norvegica*** with the presence of multipapillose cells in ***T. sibirica*** being a homoplastic trait. Hedenäs (2011) further evaluated the ***norvegica*** group and concluded, based on the 26S differences and morphological evidence, that ***T. sibirica*** is a valid separate species.

Figure 131. ***Timmia norvegica***, a species that sometimes grows in small caves in limestone areas. Photo by Hermann Schachner, through Creative Commons.

Figure 132. ***Timmia norvegica***, a species that sometimes grows in small caves in limestone areas. Photo by Hermann Schachner, through Creative Commons.

Timmia sibirica is a relatively rare species, occurring mostly on wet or moist calcareous sites (FNA 2021). It is often near small streams or on seepage slopes, near snowmelt areas, or in open tundra depressions. Its distribution is throughout the Arctic tundra, but at low elevations. Fedosov *et al.* (2018) reported ***T. sibirica*** on a gentle foothill slope and moist hollow on gravelly ground on the Russian Arctic Severny Island, demonstrating its lack of necessity for a cave-like environment.

Brassard (1979) noted the rarity of sporophytes in the genus ***Timmia***, with only three populations known with sporophytes for ***T. norvegica*** (Figure 131-Figure 132) and only immature spores known from ***T. sibirica***.

Bryophyte Adaptations

Zhang *et al*. (1996a, b) reported that of eight bryophyte life forms found in the karst caves of Huangguoshu, Guizhou, China, the predominate forms were **mats**, **short turfs**, **tall turfs**, and **wefts**. In the karst caves in England, Zhang and Pentecost (2002) found **fans** (4.08%), **mats** (4.08%), **short turfs** (20%), **tall turfs** (9.22%), and **wefts** (61.5%)

The *p*H seems to matter. Mason-Williams and Benson-Evans (1958) found that there is a richer bryophyte flora on limestone than on acid rocks. In water, high *p*H prevents most bryophytes from getting enough CO_2 for photosynthesis. So what is the value of the high *p*H to bryophytes in many caves?

Many of the cave bryophytes grow on the ceiling of the cave. This means adherence is important, particularly where the ceiling is dripping. Hughes (1982) found that the rhizoids of ***Tortula muralis*** (Figure 133) become well cemented in the oolitic limestone. We might expect similar attachment in cave bryophytes.

Figure 133. ***Tortula muralis*** on rock, a species that produces protonemal gemmae in caves. Photo by Bjorn S., through Creative Commons.

Rajczy (1978; 1978-1979) found that ***Atrichum undulatum*** (Figure 134) could live more than two years in cave conditions. The humidity ranged 95-100%.

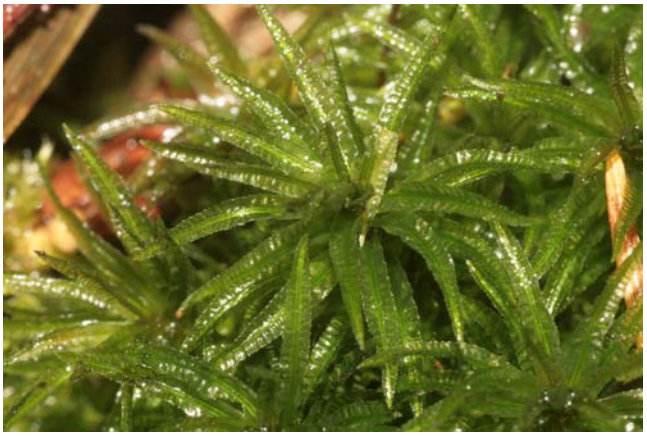

Figure 134. ***Atrichum undulatum***, a species that can live more than two years in cave conditions. Photo by Hermann Schachner, through Creative Commons.

Responses to Low Light

Puglisi *et al*. (2018) demonstrated a relationship between lighting conditions and bryophyte life form in Sicilian caves. Davison *et al*. (1995) reported "interesting" morphotypes in two liverworts from Cave Spring, Mississippi, USA.

Marschall and Proctor (2004) reported that bryophytes, especially liverworts, typically grow in light conditions at <10% relative illumination. But in a single limestone cave, Pentecost and Zhang (2001) reported that 14 species of mosses and liverworts grew at light levels below 0.5% relative illumination. ***Fissidens dubius*** and ***Thamnobryum alopecurum*** occurred at levels as low as 0.2% relative illumination. For the cave moss ***Schistostega pennata***, survival at even lower levels (0.005-0.2% relative illumination) is possible (Toda 1918).

Lang (1905) described the morphology of ***Cyathodium*** (Figure 1, Figure 38-Figure 39). It has retained the layer of air chambers with pores (Figure 135), but the basal portion of the thallus is mostly only a single layer of cells. It lacks assimilation filaments in the air chambers and instead assimilation occurs in the epidermis (Figure 135). This could be a photosynthetic advantage by reducing light blockage by the plant itself.

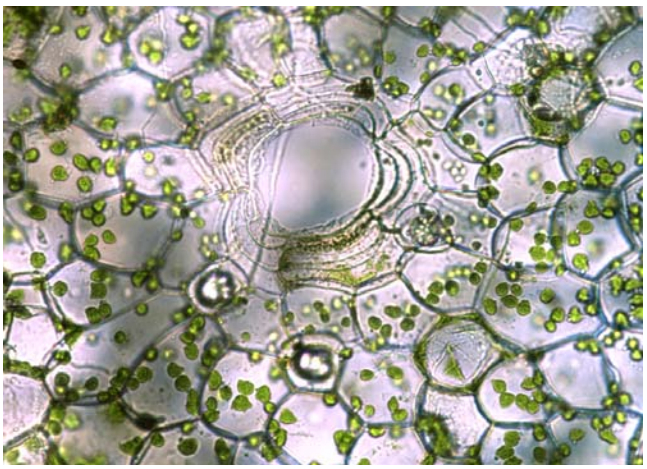

Figure 135. ***Cyathodium cavarnarum*** thallus pore and photosynthetic epidermis. Photo courtesy of Noris Salazar Allen.

Dunham and Lowe (1927) described the unusual growth of bryophytes in such habitats as caves. He discovered early in his career that bryophytes, like tracheophytes, "reach out" to the light, at times exceeding their normal height in low light conditions. He describes the leaves of ***Leptobryum pyriforme*** (Figure 136) from a specimen that had grown in the basement of an old iron foundry – the stems were 5 cm long compared to 1 cm in the light. A similar elongated growth occurred in ***Ceratodon purpureus*** (Figure 137) from the dark pocket of a ledge. I have experienced the same etiolated appearance of mosses growing in my terrarium, making the habitus unrecognizable.

Figure 136. ***Leptobryum pyriforme*** showing internodal areas that elongate in low light. Photo by Štěpán Koval, with permission.

Figure 137. ***Ceratodon purpureus*** with capsules, a species that responds to low light by stem elongation. Photo by Štěpán Koval, with permission.

Etiolation is a common response of mosses to low light (Mulec 2018). Dalby (1966b) reported that ***Pohlia nutans*** (Figure 138) becomes etiolated when buried under leaves. In a cave, ***Eurhynchium*** sp. (see Figure 67-Figure 69) has elongated branches with small, widely spaced leaves. I have found that mosses in plastic bags continue to grow in the lower light of the lab, becoming very etiolated.

Figure 138. ***Pohlia nutans*** with capsules, on rock, a species that elongates when buried by leaves. Photo by J. C. Schou, with permission.

In caves of South Wales, Mason-Williams and Benson-Evans (1967) found that dominant bryophyte growth forms changed with light intensity. As the light decreased, **dendroids** and **smooth mats** decreased in abundance, whereas **rough** or **thalloid mats** and **wefts** increased.

Dalby (1966b) reported on various responses to reduced light in caves. In ***Rhizomnium punctatum*** (Figure 139) and ***Cyrtomnium*** (Figure 140), the leaves grew perpendicular to the light, which in a cave comes from a low position that would normally strike the side of any plant growing away from gravity**.** In ***Eurhynchium hians*** (Figure 67-Figure 69), it is the flattened branches that grow perpendicular to light. ***Eucladium verticillatum*** (Figure 52-Figure 53) leaves become broader in shade (Figure 141) and Dalby noted that this response is uncommon in mosses. The liverwort ***Conocephalum conicum*** (Figure 142-Figure 143), on the other hand, is smaller in the shade; even the areolae are 1/3 as wide. By contrast, ***Eucladium verticillatum*** growing near a lamp died when the lamp was replaced with a brighter bulb. I have seen the same thing happen to house plants that are placed outside when the weather gets warm. But in this case, Dalby considered the heat and resulting desiccation to be the cause of the ***E. verticillatum*** death.

Figure 139. ***Rhizomnium punctatum***, a species whose leaves can change positions to become perpendicular to the light. Photo by Hermann Schachner, through Creative Commons.

Figure 140. ***Cyrtomnium hymenophylloides***, a species whose leaves can change positions to become perpendicular to the light. Photo by Hermann Schachner, through Creative Commons.

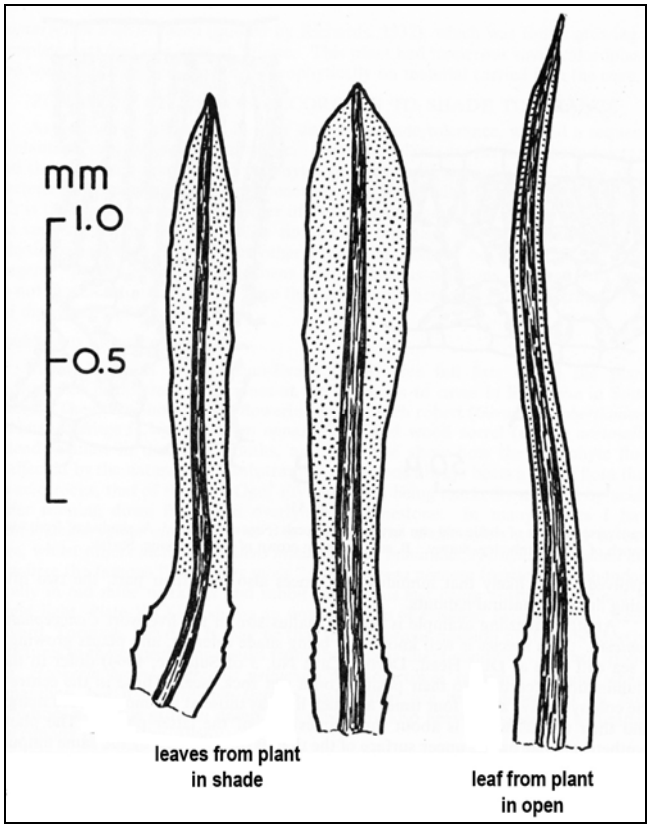

Figure 141. ***Eucladium verticillatum*** deep shade and open leaves. Diagram modified from Dalby 1966b.

Figure 142. ***Conocephalum conicum*** showing pores and areolae. Both the thallus and areolae are smaller in the shade. Photo by Hermann Schachner, through Creative Commons.

Figure 143. ***Conocephalum conicum*** cs of thallus where photosynthesis occurs. Photo by Ralf Wagner, with permission.

Richards (1932) found that ***Isopterygiopsis muellerianum*** (Figure 144) in complete darkness in a cave had numerous small chloroplasts. Richards assumed it was growing saprophytically, but it is also possible that in some seasons, probably winter, it received enough light to grow. At other times it could be dormant. Even protonemata can remain dormant for an inordinate period of time. Bristol (1916) found that protonemata that had remained sealed for 50 years began to grow when given water and light, demonstrating the incredible dormancy capability of some bryophytes.

Uniyal *et al*. (2007) noted that bryophytes are able to acclimate to low light. Watkins (2002) examined the adaptations of ***Megaceros pellucidus*** (Figure 145) to extremely low light conditions. The light conditions of 0.5-7 µmol photons m^{-2} s^{-1} where it grows in the wet, cool temperate rainforest are similar. Unlike cave bryophytes, this species has the opportunity to use the burst of light in sunflecks. But its ability to use reflected light from water (or rocks in caves) could be similar to opportunities for cave bryophytes. The chloroplast position of this hornwort in its rainforest habitat is an expanded form that is situated on the periclinal cell wall closest to the light source. Thallus sections revealed that when the thallus is irradiated with blue light of more than 3 µmols photons m^{-2} s^{-1} the

chloroplasts shrank "dramatically" and moved to a position on anticlinal walls. Red (662 nm) light of <130 µmol photons m^{-2} s^{-1} or darkness did not elicit any response in the chloroplast position except in those cells that had been exposed to blue light. In the latter case, the chloroplast expanded and resumed the position closest to the light source. Specimens were obtained from the Apiti Glow Worm Caves where sunlight is reflected off the river surface, reaching considerable distance into the cave. As seen in Figure 146, the light penetration changes as the sun arches across the sky during the day.

Figure 144. ***Isopterygiopsis muellerianum*** branch, a species that develops many small chloroplasts when in complete darkness. Photo by Wayne Lampa, through Creative Commons.

Uniyal *et al*. (2007) noted that bryophytes are able to acclimate to low light. Watkins (2002) examined the adaptations of ***Megaceros pellucidus*** (Figure 145) to extremely low light conditions. The light conditions of 0.5-7 µmol photons m^{-2} s^{-1} where it grows in the wet, cool temperate rainforest are similar. Unlike cave bryophytes, this species has the opportunity to use the burst of light in sunflecks. But its ability to use reflected light from water (or rocks in caves) could be similar to opportunities for cave bryophytes. The chloroplast position of this hornwort in its rainforest habitat is an expanded form that is situated on the periclinal cell wall closest to the light source. Thallus sections revealed that when the thallus is irradiated with blue light of more than 3 µmols photons m^{-2} s^{-1} the chloroplasts shrank "dramatically" and moved to a position on anticlinal walls. Red (662 nm) light of <130 µmol photons m^{-2} s^{-1} or darkness did not elicit any response in the chloroplast position except in those cells that had been exposed to blue light. In the latter case, the chloroplast expanded and resumed the position closest to the light source. Specimens were obtained from the Apiti Glow Worm Caves where sunlight is reflected off the river surface, reaching considerable distance into the cave. As seen in Figure 146, the light penetration changes as the sun arches across the sky during the day.

Figure 145. ***Megaceros pellucidus***, a species whose chloroplasts are next to the walls closest to the light source in low light. Photo by Ashley M. Bradford, through Creative Commons.

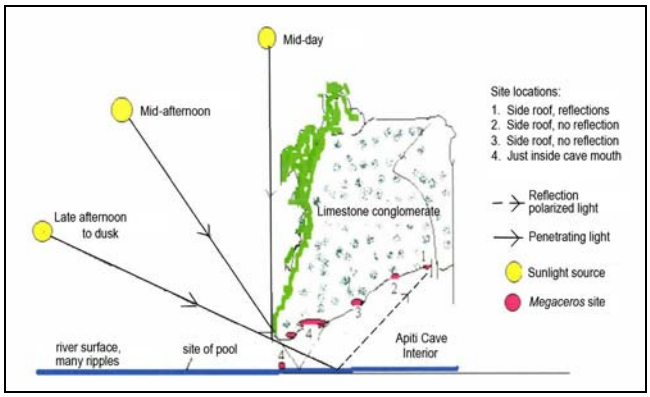

Figure 146. Sunlight paths at various times of the day in a cave at Apiti. Note the reflections onto the cave roof from 14:00-17:00 hours, thus illuminating colonies of ***Megaceros pellucidus*** for part of the day. Modified from Watkins 2002.

Gabriel and Bates (2003) studied the photosynthetic responses of bryophytes and the effects of light intensity on these responses of bryophytes from the Azores. They found photosynthetic saturation at 30 µmol m^{-2} s^{-1}. The lowest rate was in ***Andoa berthelotíana*** (Figure 147) (20 µmol m^{-2} s^{-1}) and the highest in ***Myurium hochstetteri*** (Figure 148) (68 µmol m-2 s-1). The dark respiration rate is critical for tolerating shade; it was highest in the species with the highest Pmax. The extremely low light compensation point of 7 µmol photons m^{-2} s^{-1} in ***Fissidens serrulatus*** (Figure 149) is adaptive in its deep shade and cave habitats. ***Myurium hochstetteri***, on the other hand, is restricted to habitats with good illumination; it has the highest light compensation point.

Figure 147. ***Andoa berthelotiana***, a species with a low light saturation point for photosynthesis. Photo by Pedro Cardoso, with permission through Azoresbioportal.

Figure 148. ***Myurium hochstetteri*** on exposed rock, a species with a high light saturation point for photosynthesis, and thus restricted to high light sites. Photo by Michael Lüth, with permission.

Figure 149. ***Fissidens serrulatus***, a species with an extremely low compensation point that permits it to live in such dark places as caves. Photo by David T. Holyoak, with permission.

One adaptation that may be helpful to cave bryophytes is the ability to synthesize chlorophyll in the dark. The data on this topic is scant indeed, and it seems to be assumed to be a bryophyte character even though it appears that it has only been demonstrated in ***Marchantia*** (Figure 150-Figure 151) (Takio *et al*. 1988; Ueda *et al*. 2014). Takio and coworkers demonstrated that cultured cells of ***Marchantia paleacea*** subsp. ***diptera*** (Figure 150) had a doubling time of 1.2 days when grown in the light and 1.5 days when grown in the dark. Chlorophyll concentrations were high (6-15 μg mg^{-1} dry weight) in both types of cultures. But this is not conclusive evidence that whole plants growing deep in caves are able to sustain such ability. The cultures were maintained at least 16 days before these measurements, but they had glucose in the medium, so we need evidence that the glucose did not provide the energy needed for the dark production of chlorophyll.

Figure 150. ***Marchantia palacea*** subsp. ***diptera*** females with capsules, a subspecies whose cultured cells produce chlorophyll in the dark. Photo by Janice Glime.

Another study on ***Marchantia polymorpha*** (Figure 151) indicates that it has the genes for light-independent Pchlide reductase (Ueda *et al*. 2014). But in flowering plants, these genes (for DPOR) that occur in the chloroplast seem to be lost. This means that ***M. polymorpha*** has the enzyme needed to produce chlorophyll in the dark.

Figure 151. ***Marchantia polymorpha*** gemmae cups, growing among rocks. This species has genes for producing chlorophyll in the dark. Photo by Rudolf Macek, with permission.

But what about other bryophytes? Ueda and coworkers noted that we do not understand why the DPOR genes have been lost from the chloroplast in some land plants, while persisting in others. Nor do we understand what environmental factors might have played a role in this loss in some and not in others. I cannot accept one record of these genes in a single liverwort as proof of their general presence in bryophytes. Nevertheless, their presence in ***Marchantia polymorpha*** (Figure 151), and their implied presence in ***Marchantia paleacea*** var. ***diptera*** (Figure 150), suggest that at least some cave bryophytes might be able to produce chlorophyll in the dark. This would make living in the limited light of caves, and particularly near the artificial lighting, an opportunity to take advantage of these genes for DPOR.

Jack Brunkard (Bryonet 17 August 2021) explained the two enzymes (LPOR and DPOR) that can catalyze the same reaction of reducing protochlorophyllide to chlorophyllide *a* (the immediate precursor of chlorophyll). LPOR is light dependent and DPOR is not. DPOR is strongly and irreversibly inhibited by oxygen. Brunkard suggested that many bryophytes that live in low light and moist environments that become hypoxic could gain an advantage from having DPOR in these environments. On the other hand, for plants that live in well-oxygenated habitats, DPOR would be inhibited by the oxygen. Furthermore, red light is most effective in production of LPOR, but many bryophytes live in forests that transmit predominantly green light through the canopy. This means that bryophytes with DPOR (that does not need red light) would have an advantage in these conditions. In some caves green light transmission predominates through the surrounding canopy and into the cave. But for the lampenflora, in most cases the light source emits predominantly red waves. Clearly we need further studies on the presence of DPOR throughout bryophytes and how it relates to their habitats.

Figure 152. ***Didymodon luridus***, a cave moss that produces protonemal gemmae. Photo by Hermann Schachner, through Creative Commons.

Figure 153. ***Gyroweisia tenuis*** on rock, a cave-dwelling species that produces protonemal gemmae. Photo by Michael Lüth, with permission.

Reproduction

Komáromy *et al*. (1985) found that the mosses occupying lamp-lit areas in the Anna-Barlang cave of Hungary were mostly **colonists** and **perennials**, each represented by five species. Colonists were the most frequent, most likely as a function of good dispersal ability. The cave bryophytes must be able to establish quickly or remain for a long time. Mason-Williams and Benson-Evans (1967) reported that spores were common and widespread in caves in South Wales, were commonly found around the threshold areas, and were widespread in soil samples throughout the caves. Nevertheless, protonemal gemmae seem to be important in the reproduction of cave mosses. Whitehouse (1980) found these on ***Didymodon luridus*** (Figure 47, Figure 152), ***Gyroweisia tenuis*** (Figure 153-Figure 154), ***Eucladium verticillatum*** (Figure 52-Figure 53), and ***Schistostega pennata*** (Figure 85-Figure 118). He considered them to be an adaptation for survival and propagation at low light intensities.

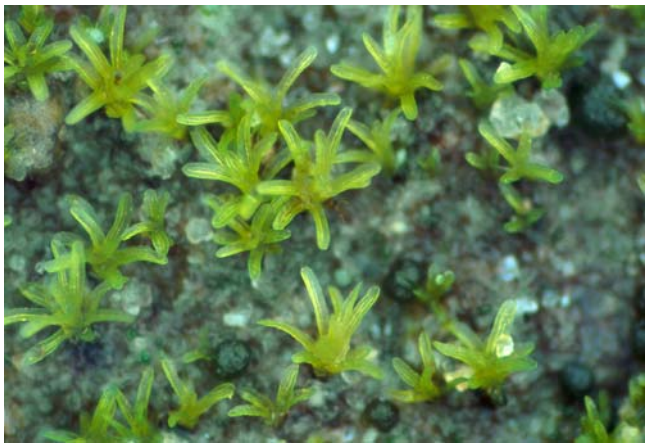

Figure 154. ***Gyroweisia tenuis***. Photo by Tomas Hallingbäck, with permission.

Allen and Korpelainen (2006) found ***Cyathodium*** (Figure 1, Figure 38-Figure 39) species to be **r-selected** (have high reproductive capacity). The **dioicous** species

that produce abundant sporophytes also produce tubers. As already noted, ***Cyathodium cavernarum*** (Figure 1, Figure 38-Figure 39) dies off in late spring and regrows from spores at the end of the wet season (Glenny 2002).

Summary

Caves are among those environments that often have rare, relict, or even unique species. Some of these are specialized cave or low light species, not to be found outside such habitats. Others are widespread species with a broad ecological range.

Cyclodictyon cavernarum is the only liverwort that is primarily a cave dweller, exhibiting a "luminescence" similar to that seen in ***Schistostega pennata***. A number of mosses are either rare or occur predominantly in low light.

Rhizoids are important for "cementing" bryophytes to the cave ceilings. *p*H can be important in creating a favorable CO_2 environment.

Thallose liverworts such as ***Cyathodium*** compensate for low light by reducing plant interference, in this case by having photosynthesis in the epidermis. **Etiolation** is common in mosses in low light. Dominant growth forms change from **dendroids** and **smooth mats** to **rough** or **thalloid mats** and **wefts** as light decreases. Growth tends to form perpendicular to light. Chloroplasts can be more numerous in low light. ***Marchantia*** can synthesize chlorophyll in the dark, but this has not been explored in other taxa; DPOR may facilitate this when oxygen levels are low, *i.e.,* light is too low for photosynthesis. Both protonemata and gametophores can remain dormant for long periods of time.

Colonists and **perennials** seem to be most successful. Spores can be common throughout the caves, but protonemal gemmae are more common than in species assemblages in most other habitats. The **r-selected** species may have an advantage, but this needs to be explored for cave species.

Acknowledgments

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CAVES – CAVERNS

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CHAPTER 18-5
CAVES – CAVERNS

Figure 1. Luray Cavern, Virginia, USA – a popular tourist cavern shown here illuminated with electric lights. Alejocrux, through public domain.

Caverns

Caverns are both natural and artificial. They are made by natural processes, but those places we typically call caverns are extensive networks of tunnels with interesting rock formations that attract the attention of tourists. To this end, enterprising companies installed lights that extend the distance into the cavern where the bryophytes, algae, and ferns are able to live.

Prior (1961) described the mosses in the well-known Luray Caverns, Virginia, USA (Figure 1). He found ***Amblystegium serpens*** (Figure 2) forming a loose mat with sporophytes in only one location on wet limestone. ***Amblystegium serpens*** is also common in European caves (*e.g.* Mulec & Kubešová 2010), but it is widespread and common outside caves, frequently presenting sporophytes. ***Anomodon rostratus*** (Figure 3) likewise occurred on moist limestone, along with ***Leptobryum pyriforme*** (Figure 4), but also occurred on silt of the cavern (Prior 1961). ***Bryum pseudotriquetrum*** (Figure 5) formed fairly "dense mats" on moist limestone, along with ***Leptobryum pyriforme***. ***Campylium hispidulum*** (Figure 6), sometimes with capsules, was scattered among 8 locations on moist limestone, either alone or with ***Leptobryum pyriforme*** and/or ***Eurhynchium hians*** (Figure 7). The latter species was abundant, occurring at 19 of the 33 study plots, either

in pure stands or mixed with other bryophytes. Only 3 populations of this species had sporophytes, but these were abundant. ***Tortula obtusifolia*** (Figure 8-Figure 9) formed a large, dense mat on wet limestone with just 2 sporophytes. ***Fissidens bryoides*** (Figure 10-Figure 11), a tiny rock-dwelling species, occurred only once, near the entrance. ***Funaria hygrometrica*** (Figure 12-Figure 13), a widespread species typically in exposed locations, occurred only once, with abundant sporophytes, contrasting sharply with ***Leptobryum pyriforme***, a species lacking sporophytes in the cavern despite being present at 18 locations. ***Leskea polycarpa*** (Figure 14) occurred only once, on wet limestone at the edge of an underground lake.

Figure 2. ***Amblystegium serpens***, a species common in European and some North American caves. Photo by Claire Halpin, with permission.

Figure 3. ***Anomodon rostratus***, a species that occurs on moist limestone and silt in Luray Caverns, Virginia, USA. Photo by Hermann Schachner, through Creative Commons.

Figure 4. ***Leptobryum pyriforme***, a species that occurs on moist limestone in Luray Caverns, Virginia, USA. Photo by Robin Bovey, with permission through Dale Vitt.

Figure 5. ***Bryum pseudotriquetrum***, a species that grows in dense mats on moist limestone. Photo by J. C. Schou, with permission.

Figure 6. ***Campylium hispidulum***, a species found in 8 of the Luray Caverns, on moist limestone. Photo by Zihao Wang, through Creative Commons.

Figure 7. ***Eurhynchium hians***, a moss that occurs on moist limestone in the Luray Caverns, Virginia, USA. Photo by Wayne Lampa, through Creative Commons.

Figure 8. ***Tortula obtusifolia*** on rock, a species that forms large, dense mats on moist limestone in Luray Caverns. Photo by Bob Klips, with permission.

Figure 9. ***Tortula obtusifolia*** on rock, a species that can withstand drought. Photo by Bob Klips, with permission.

Figure 10. ***Fissidens bryoides*** on rock, a tiny moss that was found only once at the Luray Caverns, near the entrance. Photo by Zihao Wang, through Creative Commons.

Figure 11. ***Fissidens bryoides*** protonemata with new stems, a form that can be seen in some caverns. Photo by Bob Klips, with permission.

Figure 12. ***Funaria hygrometrica*** in rock crevice, a species that occurred only once in the Luray Caverns, but that had abundant sporophytes like the population shown here. Photo by Bob Klips, with permission.

Figure 13. ***Funaria hygrometrica*** showing basal leaves and young sporophytes before capsule development. Photo by Bob Klips, with permission.

Figure 14. ***Leskea polycarpa***, a species that occurred at the edge of an underground lake in the Luray Caverns. Photo by Hugues Tinguy, with permission.

Contrasting to the Northern Hemisphere Luray Caverns, de Lange and Stockley (1987) found only one of the same genera in the Lost World Cavern at Waitomo, New Zealand, where the light levels are low and the humidity is high. Documented species there include the liverworts ***Lobatiriccardia alterniloba*** (Figure 15), ***Heteroscyphus triacanthus*** (Figure 16), ***Frullania nicholsonii*** (Figure 17-Figure 18), ***Monoclea forsteri*** (Figure 19-Figure 20), ***Radula buccinifera*** (Figure 21-Figure 22), and ***Symphyogyna tenuinervis*** (Figure 23), and mosses ***Achrophyllum dentatum*** (Figure 24), ***Beeveria distichophylloides*** (Figure 25), ***Camptochaete arbuscula*** (Figure 26-Figure 27), ***Cyathophorum bulbosum*** (Figure 28), ***Distichophyllum microcarpon*** (see Figure 29), ***Echinodium hispidum*** (Figure 30), ***Fissidens leptocladus*** (Figure 31), ***Gymnostomum calcareum*** (Figure 32-Figure 33), ***Hypnodendron arcuatum*** (Figure 34-Figure 35) (Smart 1978), ***Hypopterygium filiculaeforme*** (Figure 36), ***Leucobryum candidum*** (Figure 37) (Smart 1978), ***Lopidium concinnum*** (Figure 38) (Smart 1978), ***Papillaria crocea*** (Figure 39-Figure 40), ***Pseudotaxiphyllum falcifolium*** (Figure 41), ***Racopilum convolutaceum*** (Figure 42), ***Thamnobryum pandum*** (Figure 43), ***Thuidium laeviusculum*** (Figure 44-Figure 45) (Smart 1978), and ***Weymouthia mollis*** (Figure 46), with ***Achrophyllum dentatum***, ***Echinodium hispidum***, and ***Thamnobryum pandum*** being the most important and common around the cave entrance. These species also occur in the low-light flora near the cave.

Figure 15. ***Lobatiriccardia alterniloba***, a liverwort in the Lost World Cavern at Waitomo, New Zealand. Photo by Joe Dillon, through Creative Commons.

Figure 16. ***Heteroscyphus triacanthus***, a leafy liverwort in the Lost World Cavern at Waitomo, New Zealand. Photo by John Steel, through Creative Commons.

Figure 17. ***Frullania nicholsonii***, a leafy liverwort in the Lost World Cavern at Waitomo, New Zealand. Photo by Shirley Kerr, with permission.

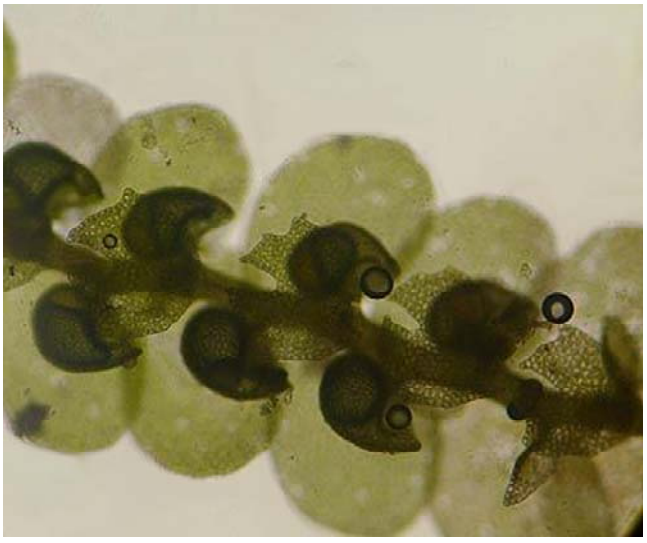

Figure 18. ***Frullania nicholsonii*** showing lobules and underleaves. Photo by Shirley Kerr, with permission.

Figure 19. ***Monoclea forsteri***, a thallose liverwort in the Lost World Cavern at Waitomo, New Zealand. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Figure 20. ***Monoclea forsteri*** with sporophytes. Photo by John Braggins, with permission.

Figure 21. ***Radula buccinifera***, a leafy liverwort in the Lost World Cavern at Waitomo, New Zealand. Photo by John Walter, through Creative Commons.

Figure 22. ***Radula buccinifera*** showing underleaf. Photo by John Walter, through Creative Commons.

Figure 23. ***Symphyogyna tenuinervis***, a liverwort in the Lost World Cavern at Waitomo, New Zealand. Photo by Shirley Kerr, with permission.

Figure 24. ***Achrophyllum dentatum***, a moss in the Lost World Cavern at Waitomo, New Zealand, where it is most common at the entrance. Photo by Des Callaghan, through Creative Commons.

Figure 25. ***Beeveria distichophylloides***, a moss in the Lost World Cavern at Waitomo, New Zealand, where it is most common at the entrance. Photo by Bill and Nancy Malcolm, with permission.

Figure 26. ***Camptochaete arbuscula***, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Peter de Lange, through Creative Commons.

Figure 27. ***Camptochaete arbuscula***. Photo by Alan Melville, through Creative Commons.

Figure 28. ***Cyathophorum bulbosum***, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Peter Woodard, through Creative Commons.

Figure 29. ***Distichophyllum procumbens***; ***Distichophyllum microcarpon*** occurs in Lost World Cavern at Waitomo, New Zealand. Photo courtesy of Olubukunola O. Oyesiku.

Figure 30. ***Echinodium hispidum***, a moss in the Lost World Cavern at Waitomo, New Zealand, where it is most common at the entrance. Photo by John Steel, through Creative Commons.

Figure 31. ***Fissidens leptocladus***, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Heino Lepp, Australian National Botanic Gardens, with online permission for educational use.

Figure 32. ***Gymnostomum calcareum***, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Andy Hodgson, with permission.

Figure 33. ***Gymnostomum calcareum***. Photo by John Game, through Creative Commons.

Figure 36. ***Hypopterygium filiculaeforme***, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Sara Smerdon, through Creative Commons.

Figure 34. ***Hypnodendron arcuatum*** with capsules, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo from Te Papa, through Creative Commons.

Figure 37. ***Leucobryum candidum***, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by David Tng, with permission.

Figure 35. ***Hypnodendron arcuatum*** with capsules. Photo from Te Papa, through Creative Commons.

Figure 38. ***Lopidium concinnum*** with capsules, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Te Papa, through Creative Commons.

Figure 39. ***Papillaria crocea*** on a vertical wall, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Daniel Ohlsen, through Creative Commons.

Figure 40. ***Papillaria crocea***. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Figure 41. ***Pseudotaxiphyllum falcifolium***, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo from Te Papa, NZ, through Creative Commons.

Figure 42. ***Racopilum convolutaceum*** with capsules, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Figure 43. ***Thamnobryum pandum***, a moss in the Lost World Cavern at Waitomo, New Zealand, where it is most common at the entrance. Photo from Te Papa, through Creative Commons.

Figure 44. ***Thuidium laeviusculum***, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Peter de Lange, through Creative Commons.

Figure 45. ***Thuidium laeviusculum***. Photo by Bill Malcolm, with permission.

Figure 46. ***Weymouthia mollis***, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Visitors increase the exposure of the caverns to fluctuating temperatures, moisture fluctuations, drafts, propagules, light, exhaled CO_2, trampling, and other factors that alter the ability of bryophytes to reach and succeed in the interior of the caverns. Rakovec (2020) modelled the effect of visitor number and cave size on visitor impact. He found that the direct human sources of heat and CO_2 cause linear responses. But the exchange between the walls and the exterior have exponential consequences dependent on time. Thus, visitors have both direct and indirect effects on the flora in the display caverns.

Cave Lamp Communities (Lampenflora)

The flora associated with lights in caverns (**lampenflora**) has fascinated many researchers (*e.g.* Lundegårdh 1931; Maheu & Guérin 1935; Shiomi 1973; Rajczy 1979, 1989; Rajczy *et al*. 1985; Padisák *et al*. 1985; Végh 1985; Rajczy *et al*. 1986; Rajczy & Buczkó 1989; Olson 2002; Zhang & Wang 2002; Mazina & Maximov 2011; Cigna 2012; Mazina 2016a, b). Mulec (2012) noted that permanent electric lights are used in show caves to highlight cave formations for visitors. But these also create new ecological conditions that permit the colonization by lampenflora. Although the community is relatively complex, it is also limited in diversity, comprised usually of **Cyanobacteria** outermost from the light, to algae, bryophytes, and ferns (closest to the light) (Boros 1964; Castello 2014; D'Agostino *et al*. 2015; Mazina 2015; Kurniawan *et al*. 2018; Mulec 2018; Kozlova & Mazina 2020; Pfendler *et al*. 2021). Flowering plants are usually unable to live in these sites, although Mazina (2015) found two species of flowering plants near lamps in the Nomoafonskaya Cave, Abkhazia, in the South Caucasus.

Naturally illuminated caves provide sufficient light at the entrance and a short distance into the twilight zone (Figure 47) for some bryophytes to reach extensive development (Mulec 2018). Beyond that, in the dark zone, plants, including bryophytes, are only able to live near artificial lighting. Mazina (2016a) noted that the bryophyte diversity is higher in caves with artificial lighting. Popkova *et al*. (2019) noted that the lampenflora tends to be similar to that of the entrance zone. Thatcher (1949) found that the lampenflora extended 8-61 cm from the lamps, with light intensities ranging 250-800 lux. Verdoorn (1932) offers the opinion that the very dim light conditions may be offset by the higher carbon dioxide content of the limestone.

In New York, USA, Haring (1930) described the flora of the Howe Caverns. The lights were turned on and the caverns opened to the public in 1929. Within 2.5 months plant life began to appear. After 8 months, she identified 7 species of bryophytes from the two clumps given to her, although nearly 50 lights had bryophyte colonies. She listed the liverwort ***Marchantia polymorpha*** (Figure 48) and the mosses ***Amblystegium serpens*** (Figure 2), ***Amphidium mougeotii*** (Figure 49-Figure 50), ***Brachythecium rutabulum*** (Figure 51), ***Bryoerythrophyllum recurvirostrum*** (Figure 52), ***Bryum caespiticium*** (Figure 53-Figure 54), ***Leptobryum pyriforme*** (Figure 4), and ***Rosulabryum capillare*** (Figure 55).

Figure 47. Entrance light at Son Doong Cave, showing penetration of photosynthetic organisms. Photo by Doug Knuth, through Creative Commons.

Figure 48. ***Marchantia polymorpha*** with gemmae cups, a liverwort found in the lampenflora of Mammoth Cave, Kentucky, USA, and in Howe Caverns, New York, USA. Photo by Hermann Schachner, through Creative Commons.

Figure 49. ***Amphidium mougeotii***, a moss found near lamps in Howe Caverns, New York, USA. Photo by Michael Lüth, with permission.

Figure 50. ***Amphidium mougeotii***. Photo by Hugues Tinguy, with permission.

Figure 51. ***Brachythecium rutabulum***, found in the lampenflora of Howe Caverns, New York, USA. Photo by Des Callaghan, with permission.

Figure 52. ***Bryoerythrophyllum recurvirostrum***, a species found in Crystal Cave, Wisconsin, USA. Photo by Hermann Schachner, through Creative Commons.

Figure 53. ***Bryum caespiticium*** with capsules, a species found in Crystal Cave, Wisconsin, USA. Photo by Bob Klips, with permission.

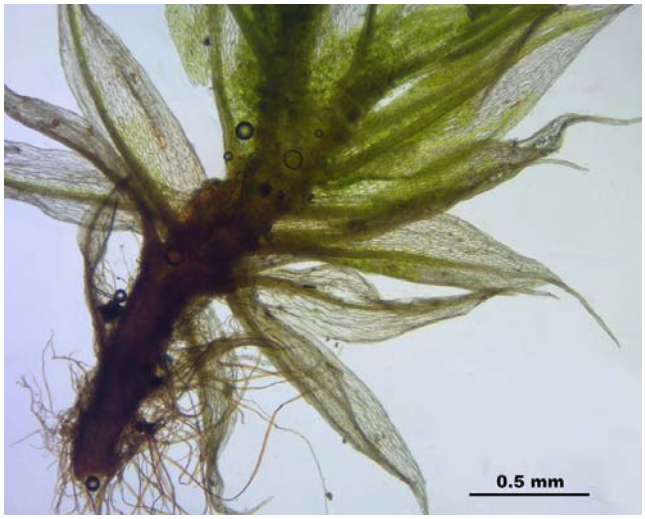

Figure 54. ***Bryum caespiticium*** showing numerous rhizoids. Photo by Hermann Schachner, through Creative Commons.

Figure 55. ***Rosulabryum capillare*** with capsules, on rock, found in the lampenflora of Howe Caverns, New York, USA. Photo through Creative Commons.

Kozlova and Mazina (2020) concluded that macrogroups dominated by bryophytes had well-defined boundaries, whereas the microgroups dominated by green algae were often located between these macrogroups, thus forming distinct but small communities and transitions.

Succession

Algae and **Cyanobacteria** typically are the first of the lampenflora to arrive (Hajdu 1977; Mulec & Kosi 2009; Cigna 2012). Following that are the bryophytes, ferns, and less frequently, seed plants. But Hajdu (1977) contends that the mosses will eventually outgrow and suppress the algae (presumably including the Cyanobacteria).

Hazslinsky (2002) noted that the lampenflora can spread "rather quickly." In Baradla Cave, Hungary, it doubled in seven years. Thomas (1897) reported that ***Rhynchostegiella tenella*** var. ***cavernarum*** (Figure 56) appeared around cave lights in about one year after their installation. The species ***Rhynchostegiella tenella*** has been found in underground rooms of the Roman Coliseum, suggesting that it is also a long-time stayer. Pfendler *et al*. (2021) conducted a quantitative study on bryophyte colonization on illuminated limestone blocks in caves. Some of the blocks similarly had dense colonization within a year.

Figure 56. ***Rhynchostegiella tenella***, a species that has appeared around cave lights within a year of their installation. Photo by Michael Lüth, with permission.

Popkova *et al*. (2019) found that the greatest similarity between the lampenflora and the entrance occurred under the greatest light intensity, supporting the role of light in determining the community structure. ***Eucladium verticillatum*** (Figure 57-Figure 58) was the predominant bryophyte in these photic zones, accompanied by the **Cyanobacteria** ***Microcystis pulverea*** (Figure 59) and ***Scytonema drilosiphon*** (see Figure 60) and the airborne and widespread green alga ***Chlorella vulgaris*** (Figure 61).

Figure 57. ***Eucladium verticillatum*** in lime seep, a common species around cavern lights. Photo by Resso Taelspeus, through Creative Commons.

Figure 58. ***Eucladium verticillatum***. Photo by Christian Berg, through Creative Commons.

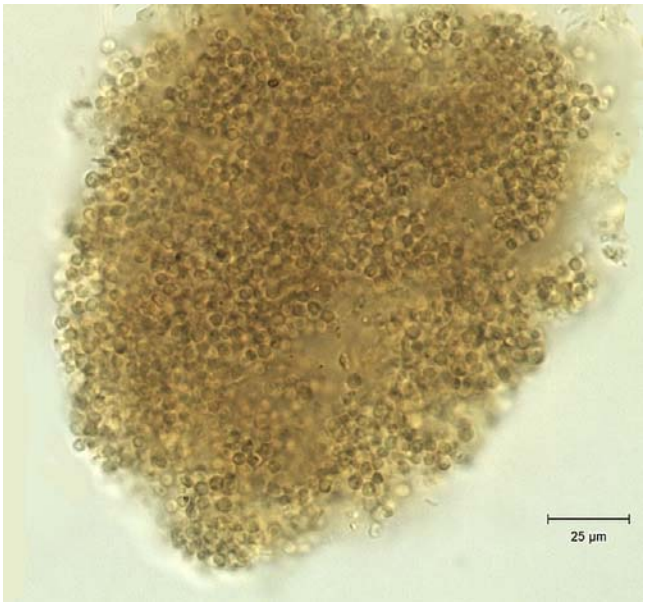

Figure 59. ***Microcystis pulverea***, a common member of **Cyanobacteria** found near lights in caverns. Photo by Chris Carter, with permission, AlgaeBase.

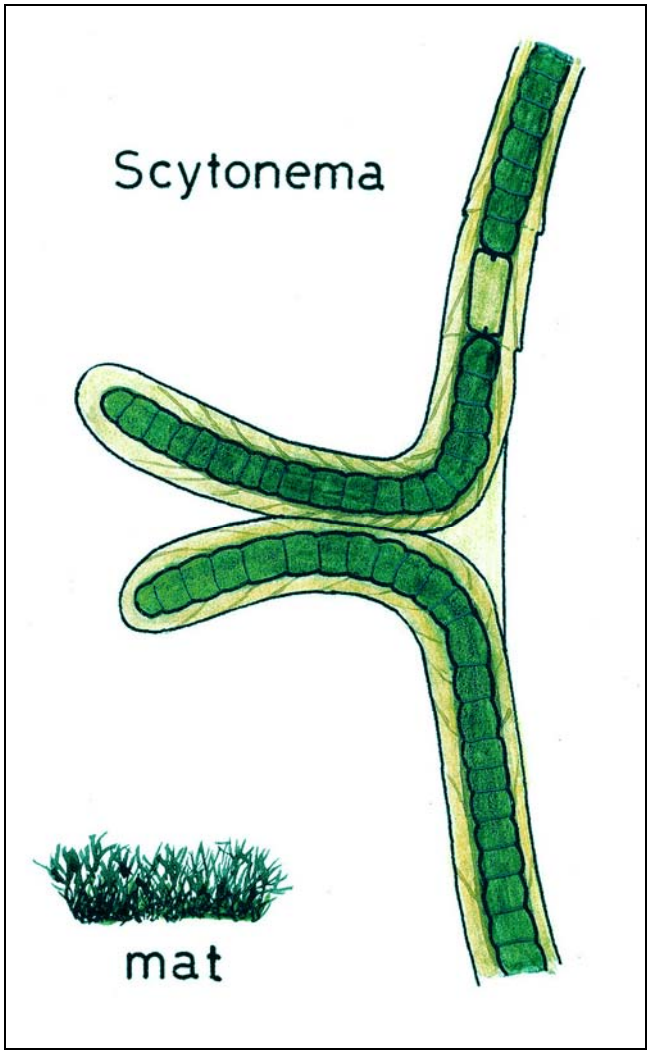

Figure 60. ***Scytonema***; ***Scytonema drilosiphon*** is one of the **Cyanobacteria** that grows near the lights in caverns. Drawing by Allen Pentecost, through Creative Commons.

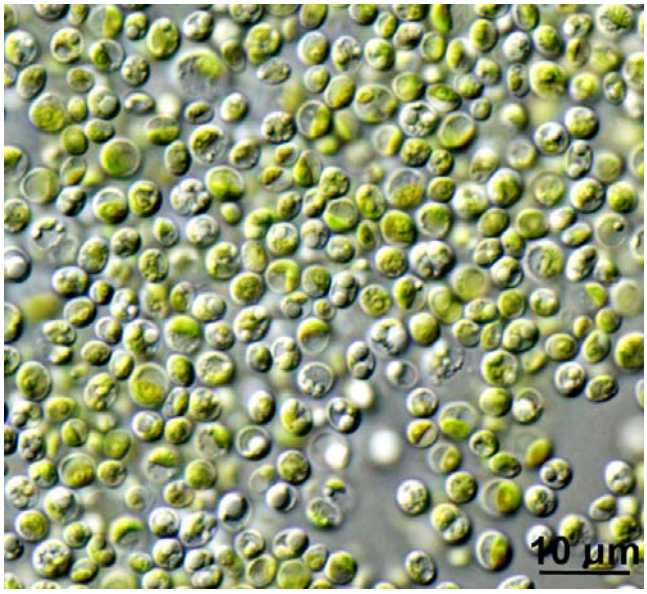

Figure 61. ***Chlorella vulgaris***, a widespread, airborne green alga that grows near lights in caverns. Photo by Neon, through Creative Commons.

Species Numbers

As an example of the distribution among photosynthetic groups near lamps, in addition to 2 flowering plants, Mazina (2015) found 34 species of **Cyanobacteria**, 5 **Chlorophyta**, 2 **Ochrophyta** (planktonic and benthic algae), 9 **Bacillariophyta** (diatoms), 22 **Bryophyta**, and 6 **Polypodiophyta** (ferns etc.) in Vorontsovskaya Cave, Russia. Komáromy *et al*. (1985) found 42 alga taxa (including **Cyanobacteria**), 10 moss taxa, and 1 fern taxon in the lamp-lit areas of the cave Anna-Barlang near Lillafuered, Hungary. In Italy, Castello (2012, 2014) found 16 moss species and 2 ferns (algae were not assessed) in the lampenflora. Castello found that some of the mosses were typical of cave entrances in the Italian Karst, but others were typical of disturbed and open habitats. Lundegårdh (1931) described the zonation as ferns nearest to the lamp, mosses farther away, and algae at the farthest locations from the light.

Mazina and Maximov (2011) reported 14 **Cyanobacteria**, 4 **Chlorophyta**, 4 **Bacillariophyta**, 11 **Bryophyta**, and 5 **Polypodiophyta** among the lampenflora of an excursion cave in Russia. The ferns were juveniles and the only moss with sporophytes was ***Isopterygiopsis pulchella*** (Figure 62). Moss protonemata (Figure 63) were subdominants on the limestone and **argillaceous veneers** (coverings containing clay).

Figure 62. ***Isopterygiopsis pulchella*** with capsule, the only species with a capsule in a Russian excursion cave. Photo by Michael Lüth, with permission.

Figure 63. Protonemata of the moss ***Physcomitrium pyriforme***, a typical sight in cave lampenflora Photo by Bob Klips, with permission.

In an exhibition cave in the Czech Republic, Faimon *et al*. (2003) found 12 taxa of algae and **Cyanobacteria** (Figure 59-Figure 60) and 19 moss taxa.

Dominant Species

Pentecost (2011) described the lampenflora of tourist caves in northern England. The **Cyanobacteria** (Figure 59-Figure 60) numbered 18 species, supporting the conclusion that it is the most species-rich group in the lamp communities. He also found 6 diatoms, 4 bryophytes, 1 coccoid green alga, and 1 fern species. The **Cyanobacteria** were the predominant organisms and grew at light levels of 0.06-2.08 µmol m^{-2} s^{-1}. ***Eucladium verticillatum*** (Figure 57-Figure 58) was the most common moss, surviving in light levels of 0.55-2.08 µmol m^{-2} s^{-1}

Mulec and Kubešová (2010) reported species from 8 Slovenian show caves. Once again, ***Eucladium verticillatum*** (Figure 57-Figure 58) was among the most frequent mosses, along with ***Amblystegium serpens*** (Figure 2), ***Brachythecium*** sp. (Figure 66), and ***Fissidens taxifolius*** (Figure 64). Bryophytes and ferns together comprised 37 taxa. Not surprisingly, ***Eucladium verticillatum*** had the widest range of photosynthetic photon flux density (1.4-530.0 µmol photons m^{-2} s^{-1}). ***Cratoneuron filicinum*** (Figure 65) even developed sporophytes at 2.1 and 2.4 µmol photons m^{-2} s^{-1}. ***Brachythecium salebrosum*** (Figure 66) developed sporophytes at 4.7 µmol photons m^{-2} s^{-1}.

Figure 64. ***Fissidens taxifolius*** with young capsules, a species known from Slovenian excursion caverns. Photo by Bob Klips, with permission.

Figure 65. ***Cratoneuron filicinum***, a species that can develop sporophytes at 2.1 and 2.4 µmol photons m^{-2} s^{-1}. Photo by J. C. Schou, with permission.

Figure 66. ***Brachythecium salebrosum***, a species that can develop sporophytes at 4.7 µmol photons m^{-2} s^{-1}. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Maheu (1926) recorded 6 moss species [***Anomodon attenuatus*** (Figure 67), ***A. rostratus*** (Figure 3), ***Brachythecium rivulare*** (Figure 68), ***Eurhynchium praelongum*** (Figure 69), ***Gymnostomum calcareum*** (Figure 32-Figure 33), and ***Plagiomnium rostratum*** (Figure 70)], and the liverwort ***Marchantia polymorpha*** (Figure 48) from the twilight zone, including lamp areas, of Mammoth Cave, Kentucky, USA. These bryophytes were etiolated and lacked sporophytes. Barr (1968) later reported 200 species of animals, 67 species of algae, 27 species of fungi, and 7 species of twilight-zone bryophytes in the Mammoth Cave system.

Figure 67. ***Anomodon attenuatus***, found in the lampenflora of Mammoth Cave, Kentucky, USA. Photo by Dendrofil, through Creative Commons.

Figure 68. ***Brachythecium rivulare***, found in the lampenflora of Mammoth Cave, Kentucky, USA. Photo by Hermann Schachner, through Creative Commons.

Figure 69. ***Eurhynchium praelongum***, found in the lampenflora of Mammoth Cave, Kentucky, USA. Photo by Peter Woodard, through Creative Commons.

Figure 70. ***Plagiomnium rostratum***, found in the lampenflora of Mammoth Cave, Kentucky, USA. Photo by Hermann Schachner, through Creative Commons.

Like many other studies, D'Agostino *et al*. (2015) found that the bryophytes in the Zinzulusa Show Cave (South Italy) mainly consisted of unidentified protonemata Figure 63) and the mosses ***Rhynchostegiella tenella***

(Figure 56) and ***Eucladium verticillatum*** (Figure 57-Figure 58). The latter species is instrumental in the formation of concretions that grow from water that drips from the ceilings, but are oriented toward the outside of the cave due to the phototropic growth of the moss (Figure 117).

In a cave in Hungary, Komáromy *et al*. (1985) found the mosses ***Brachythecium velutinum*** (Figure 71), ***Campylium chrysophyllum*** (Figure 72), ***Eucladium verticillatum*** (Figure 57-Figure 58), ***Fissidens dubius*** (Figure 73), ***F. pusillus*** (Figure 74), ***Gymnostomum calcareum*** (Figure 32-Figure 33), ***Hypnum cupressiforme*** (Figure 75), ***Pseudoscleropodium purum*** (Figure 76), ***Rhynchostegium megapolitanum*** (Figure 77), and ***Tortella tortuosa*** (Figure 78) near lights. These were all common species outside the caves. Note the absence of liverworts.

Figure 71. ***Brachythecium velutinum***, a common moss species that is also frequent around lights in caverns in Hungary. Photo by James K. Lindsey, through Creative Commons.

Figure 72. ***Campylium chrysophyllum***, a common moss species that is also frequent around lights in caverns in Hungary. Photo by Hermann Schachner, through Creative Commons.

Figure 73. ***Fissidens dubius*** on vertical substrate, a moss species that is frequent around lights in caverns in Hungary. Photo by Hermann Schachner, through Creative Commons.

Figure 74. ***Fissidens pusillus*** with capsules on rock on vertical substrate, a moss species that is frequent around lights in caverns in Hungary. Photo by David T. Holyoak, with permission.

Figure 75. ***Hypnum cupressiforme***, a moss species that is frequent around lights in caverns in Hungary. Photo by Fabio Cianferoni, through Creative Commons.

Figure 76. ***Pseudoscleropodium purum***, a common moss species that is also frequent around lights in caverns in Hungary. Photo by Emilie Bernard, through Creative Commons.

Figure 77. ***Rhynchostegium megapolitanum***, a moss species that is also frequent around lights in caverns in Hungary. Photo by David T. Holyoak, with permission.

Figure 78. ***Tortella tortuosa*** on rock, a common moss species that is also frequent around lights in caverns in Hungary. Photo by Bernd Haynold, through Creative Commons.

Verdoorn (1927) reported ***Brachythecium velutinum*** (Figure 71), ***Rhynchostegium murale*** (Figure 79), and ***Rosulabryum capillare*** (Figure 80) around the dim lights of 2 German caves. These exhibited small, etiolated, and crumpled leaves.

Figure 79. ***Rhynchostegium murale*** with capsules on rock – a species that occurs around dim lights in some German caves. Photo by Hugues Tinguy, with permission.

Figure 80. ***Rosulabryum capillare*** with capsules, on rock, a species that occurs around dim lights in some German caves. Photo by 3 through Creative Commons.

Kubešová (2001) reported 46 species of bryophytes in the lampenflora in public caves in the Moravian Karst (Czech Republic) in the 1960s to 1970s, but only 34 were located in 1999-2000. Of these, 2 liverworts and 10 moss species could not be relocated, but 2 new moss species were found. The bryophytes present all occur on the soil and rocks outside the caves (Rajczy 1989; Šmarda 1970). The mosses ***Amblystegium serpens*** (Figure 2), ***Eurhynchium hians*** (Figure 7), ***Leptobryum pyriforme*** (Figure 4), and ***Rhynchostegium murale*** (Figure 79) were frequent in the 1970s and in the later study (Kubešová 2001). The liverworts ***Fossombronia wondraczekii*** (Figure 81) and ***Pellia epiphylla*** (Figure 82) and the mosses ***Aulacomnium androgynum*** (Figure 83), ***Dichodontium pellucidum*** (Figure 84), ***Eurhynchium angustirete*** (Figure 85), ***Mnium marginatum*** (Figure 86), ***Plagiomnium affine*** (Figure 87), ***Plagiomnium rostratum*** (Figure 88), ***Rhizomnium punctatum*** (Figure 89), ***Timmia bavarica***

(Figure 90), ***Tortella tortuosa*** (Figure 78), and ***Trichostomum tenuirostre*** (Figure 91-Figure 92), were not relocated. The mosses ***Ditrichum flexicaule*** (Figure 93-Figure 94), ***Rhodobryum ontariense*** (Figure 95), and ***Thamnobryum alopecurum*** (Figure 96) were new in the present study. The mosses ***Brachythecium velutinum*** (Figure 71), ***Ceratodon purpureus*** (Figure 97-Figure 98), ***Dichodontium pellucidum*** (Figure 84), ***Funaria hygrometrica*** (Figure 12-Figure 13), ***Leptobryum pyriforme*** (Figure 4), ***Physcomitrium pyriforme*** (Figure 63, Figure 99), ***Rhynchostegium murale*** (Figure 79), and ***Tortula subulata*** (Figure 100-Figure 101) had at least some fertile populations in the 1970s, but only ***Funaria hygrometrica*** (Figure 12-Figure 13) was fertile in the later study. Hajdu (1977) noted that sporophytes were rare in cave bryophyte populations. Were these changes due to competition by later arrivals, or to changing conditions due to human presence?

Figure 81. ***Fossombronia wondraczekii*** with capsules, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Michael Lüth, with permission.

Figure 82. ***Pellia epiphylla*** with capsules, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Hermann Schachner, through Creative Commons.

Figure 83. ***Aulacomnium androgynum*** with gemmae, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Hugues Tinguy, with permission.

Figure 84. ***Dichodontium pellucidum***, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Claire Halpin, with permission.

Figure 85. ***Eurhynchium angustirete***, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Hermann Schachner, through Creative Commons.

Figure 86. ***Mnium marginatum***, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Hermann Schachner, through Creative Commons.

Figure 87. ***Plagiomnium affine*** branches, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Hermann Schachner, through Creative Commons.

Figure 88. ***Plagiomnium rostratum***, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Hermann Schachner, through Creative Commons.

Figure 89. ***Rhizomnium punctatum***, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Jean Faubert, with permission.

Figure 90. ***Timmia bavarica***, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Hugues Tinguy, through Creative Commons.

Figure 91. ***Trichostomum tenuirostre*** habitat, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Bob Klips, with permission.

Figure 92. ***Trichostomum tenuirostre***. Photo by Bob Klips, with permission.

Figure 93. ***Ditrichum flexicaule***, a species found in Moravian Karst (Czech Republic) in 1999-2000, but not in the 1960s to 1970s. Photo by Hermann Schachner, through Creative Commons.

Figure 94. ***Ditrichum flexicaule*** among rocks. Photo by Hermann Schachner, through Creative Commons.

Figure 95. ***Rhodobryum ontariense***, a species found in Moravian Karst (Czech Republic) in 1999-2000, but not in the 1960s to 1970s. Photo by Hugues Tinguy, with permission.

Figure 96. ***Thamnobryum alopecurum*** on vertical surface, a species found in Moravian Karst (Czech Republic) in 1999-2000, but not in the 1960s to 1970s. Photo by Hugues Tinguy, with permission.

Figure 97. ***Ceratodon purpureus*** on rock, a species that was fertile in the 1970's, but not in 1999-2000 in the Moravian Karst. Photo by Aleksandr Levon, through Creative Commons.

Figure 98. ***Ceratodon purpureus*** with capsules. Photo by Bob Klips, with permission.

Figure 99. ***Physcomitrium pyriforme*** with capsules, a species that has capsules in early lampenflora, but not 30 years later, in the Moravian Karst. Photo by Lee Elliot, through Creative Commons.

Figure 100. ***Tortula subulata***, a species that was fertile in the 1970's, but not in 1999-2000 in the Moravian Karst. Photo by Hermann Schachner, through Creative Commons.

Figure 101. ***Tortula subulata*** with immature capsules, on rock. Photo by Hugues Tinguy, with permission.

Kubešová (2013) reported ***Amblystegium serpens*** (Figure 2), ***Brachytheciastrum velutinum*** (Figure 102), ***Cratoneuron*** spp. (Figure 65), and ***Fissidens taxifolius*** (Figure 64) as frequent species around lights in 14 caves in the Czech Republic, all common outside caves as well. In total, he found 62 moss species, but no liverworts, with 0-24 species in a single cave. Overall, 45% of the bryophyte flora remains the same as in the past (1960s-70s). In the 1988-1990 period, 26% of the species were newly recorded. Only nine of the 1960-70's species of mosses were relocated in 1988-1990.

Figure 102. ***Brachytheciastrum velutinum***, a frequent species around lights in 14 caves in the Czech Republic. Photo by Claire Halpin, with permission.

When Kubešová (2005, 2006) reviewed the bryophytes in public caves in the Czech Republic, he found that the mosses ***Amblystegium serpens*** (Figure 2), ***Brachythecium velutinum*** (Figure 71), ***Fissidens taxifolius*** (Figure 64) and ***Leptobryum pyriforme*** (Figure 4) were the ones most frequently present in both early studies in the 1960s-70s and in 2004.

But in North America, the composition differs. Thatcher (1949) noted the absence of both ***Reboulia*** (Figure 103) and ***Eucladium*** (Figure 57-Figure 58) in Crystal Cave in Wisconsin, USA, a tourist cavern. Only ***Ceratodon purpureus*** (Figure 97-Figure 98), ***Fissidens***

taxifolius (Figure 64), ***Leptobryum pyriforme*** (Figure 4), and ***Rosulabryum capillare*** (Figure 80) were found in both the Crystal Cave, Wisconsin, and the Czech caverns. Instead, Thatcher reported the thallose liverwort ***Marchantia polymorpha*** (Figure 48) and the mosses ***Barbula unguiculata*** (Figure 104), ***Brachythecium populeum*** (Figure 105-Figure 106), ***Brachythecium salebrosum*** (Figure 66), ***Bryoerythrophyllum recurvirostrum*** (Figure 52), ***Bryum caespiticium*** (Figure 53-Figure 54), ***Leptodictyum riparium*** (Figure 107-Figure 108), ***Plagiomnium cuspidatum*** (Figure 109), and ***Warnstorfia fluitans*** (Figure 110) from Crystal Cave. A small amount of the fern ***Cryptogramma stelleri*** (Figure 111) was the only fern present, and in only a small amount, but with prothalli, growing among moss protonemata (Figure 63). ***Bryum caespiticium*** was the only moss to display a sporophyte – a single sporophyte for the entire study.

Figure 103. ***Reboulia hemispherica*** with archegoniophores; ***Reboulia*** is found in some European caverns, but was absent in Crystal Cave, Wisconsin, USA. Photo by Bob Klips, with permission.

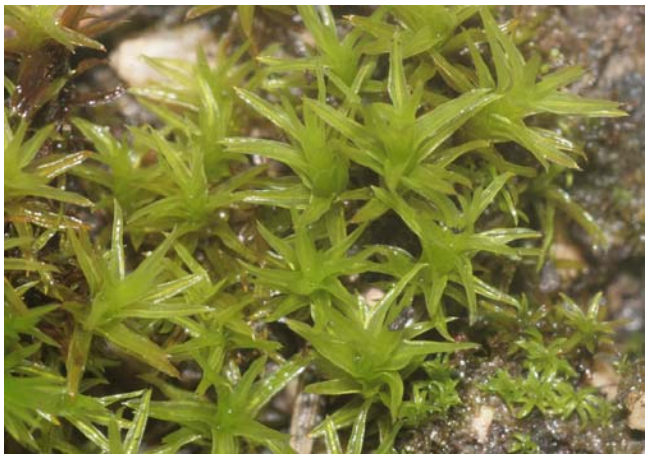

Figure 104. ***Barbula unguiculata***, a species found in Crystal Cave, Wisconsin, USA – a tourist cavern. Photo by Hermann Schachner, through Creative Commons.

Figure 105. ***Brachythecium populeum*** on rock, a species that occurs in Crystal Cave, Wisconsin, USA. Photo by Michael Lüth, with permission.

Figure 106. ***Brachythecium populeum*** with capsules. Photo by Hermann Schachner, through Creative Commons.

Figure 107. ***Leptodictyum riparium*** on rock at edge of stream, a species found in Crystal Cave, Wisconsin, USA. Photo by Hermann Schachner, through Creative Commons.

Figure 108. ***Leptodictyum riparium***. Photo by J. C. Schou, with permission.

Figure 109. ***Plagiomnium cuspidatum*** branches, a species found in Crystal Cave, Wisconsin, USA. Photo by Hermann Schachner, through Creative Commons.

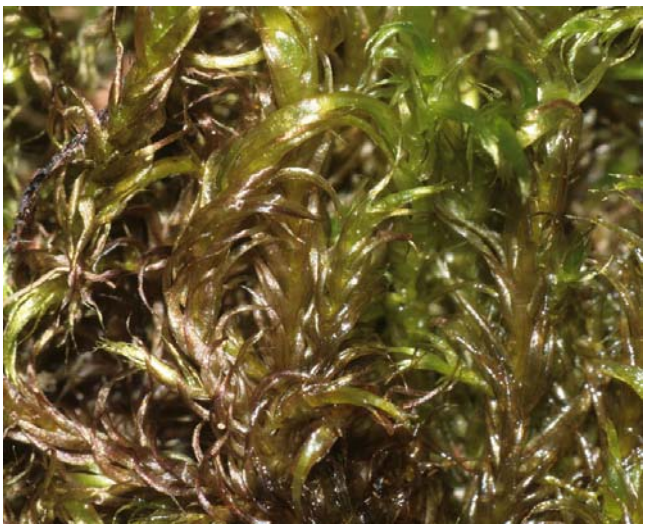

Figure 110. ***Warnstorfia fluitans***, a species found in Crystal Cave, Wisconsin, USA. Photo by Hermann Schachner, through Creative Commons.

Figure 111. ***Cryptogramma stelleri*** in rock crevice, a species found in Crystal Cave, Wisconsin, USA. Photo by Rob Routledge, through Creative Commons.

Castello (2014) found 16 moss species and 2 ferns in 26 sites near artificial lights of various kinds in the Trieste Karst in NE Italy. The most common of these were the mosses ***Eucladium verticillatum*** (Figure 57-Figure 58), ***Fissidens bryoides*** (Figure 10-Figure 11), ***Oxyrrhynchium schleicheri*** (Figure 112-Figure 113), and ***Rhynchostegiella tenella*** (Figure 56) and the fern ***Asplenium trichomanes*** (Figure 114-Figure 115). Of these, ***Eucladium verticillatum*** was the most common, exhibiting a wide amplitude for light intensity and substrate type (see also Dalby 1966a; Popkova *et al*. 2019). The most important factors determining the species present were light intensity, water availability, type of substrate, morphological features of surfaces, and presence of clay. To these factors, Mazina (2016a) added the connection of the location with the surface.

Figure 112. ***Oxyrrhynchium schleicheri***, one of the most common mosses near cavern lights at the Trieste Karst in NE Italy. Photo by Hugues Tinguy, with permission.

Figure 113. ***Oxyrrhynchium schleicheri*** branch. Photo by Hermann Schachner, through Creative Commons.

Figure 115. ***Asplenium trichomanes*** on rock wall. Photo by Ori Fragman-Sapir, through Creative Commons.

Modifications of Cave Dwellers

Piano *et al*. (2015) found that increased illumination was the primary factor influencing both increased presence and increased productivity of **Cyanobacteria** (Figure 59-Figure 60), **diatoms** (Figure 116), and **green algae** (Figure 61). The presence of seeping water on the substrate and the distance from the cave entrance are important in determining patterns of colonization. Differences in light likewise influences the bryophyte flora, its appearance, its physiological acclimation, and its productivity.

Figure 114. ***Asplenium trichomanes*** on rock wall, one of the most common plants near cavern lights at the Trieste Karst in NE Italy. Photo by Egon Krogsgaard, through Creative Commons.

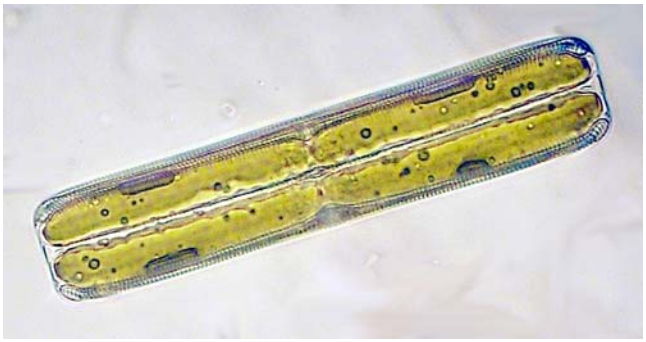

Figure 116. ***Pinnularia*** sp. a diatom in a genus that occurs on cave bryophytes. Photo by Denis Barthel, through Creative Commons.

The lampenflora organisms are usually ubiquitous in nature, having the ability to survive in new conditions through a wide ecological tolerance (Mulec 2012; Mazina 2016a). Nevertheless, lampenflora bryophytes are often etiolated (Mulec 2018). Conard (1932) remarked on the ***Fissidens taxifolius*** (Figure 64) that he found within 20 cm of a light in Crystal Cave, Virginia, USA. The leaves were more widely spaced than in typical specimens outside caves. Prior (1961) found that the leaves of cave-dwelling mosses are often much more crisp than those outside the cave. Prior also found that the number of chloroplasts seems to be unaffected by the light intensities; nevertheless, the mosses are typically pale, resulting from a reduction in chlorophyll content.

Maheu (1926) summarized the reported modifications of cave and sink hole bryophytes. These included sterility, elongation of leaves, increased spacing of leaves along the stem, elongation of cells, and disappearance or attenuation of the costa or rib. The liverworts present the least

modification, despite penetrating the greatest distance into the cave.

The phototropic response is quite evident among acrocarpous mosses, with some inclined as much as 75º from vertical at the deepest location of mosses in the cave (Prior 1961). When the nearest lamp is on the ground, this response is evident throughout the growth; such responses cause some statoliths to develop horizontally (Figure 117). For example, sporophytes on ***Leptobryum pyriforme*** (Figure 4) are inclined in the same way as the stem of the gametophyte.

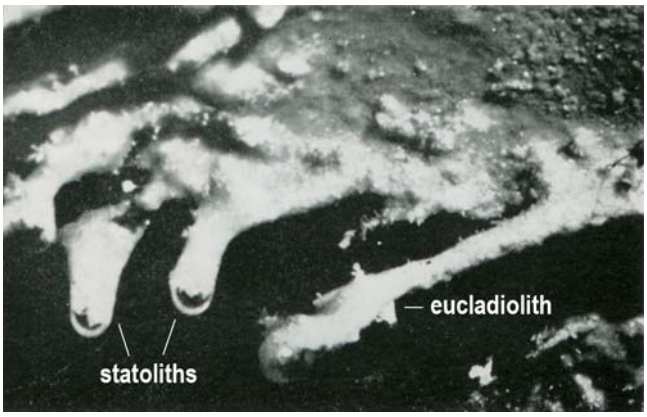

Figure 117. ***Eucladium verticillatum*** forming stalactite (eucladiotite) in mine in Dorset, showing horizontal growth of the statolith (eucladiolith in this case). Photo from Dalby 1966b.

Life Strategies

In a Hungarian cave, Komáromy *et al*. (1985) found that moss species in lamp-lit areas were **colonists** and **perennials** (5 species each). Similarly, in the Czech Republic Kubešová (2006, 2013) found the most frequent life strategies to be **colonists** and **perennials**, but also included fugitives, with the most common growth forms being **short turf** and **rough mat**.

Sporophytes are generally scarce among bryophytes in caves. Prior (1961) seems to have found more than most bryologists, with 50% of the moss species in Luray Cavern Kentucky, USA, having sporophytes. As noted earlier, he found ***Amblystegium serpens*** (Figure 2), ***Campylium hispidulum*** (Figure 6), ***Tortula obtusifolia*** (Figure 8-Figure 9), ***Eurhynchium hians*** (Figure 7), ***Funaria hygrometrica*** (numerous; Figure 12-Figure 13), and ***Leptobryum pyriforme*** (Figure 4) with sporophytes in at least some locations. He noted that plants farthest from the lights often did not have capsules, but conceded that these could simply be too young.

Propagation and Survival

Mazina and Kozlova (2018) attempted to determine dominant propagation means occurring in the Lipska Cave in Montenegro. They used soil and water samples from the unlighted zone and cultured them to understand the propagules that were able to enter through airflows. Among these, they identified 17 species of algae and **Cyanobacteria**, and 12 bryophyte species. The mosses ***Fissidens taxifolius*** (Figure 64) and ***Brachythecium tommasinii*** (Figure 118-Figure 119) dominated the lampenflora communities, while ***Entodon schleicheri*** (Figure 120) and ***Tortella*** sp. (Figure 78) had the highest abundance in the natural entrance zone.

Figure 118. ***Brachythecium tommasinii***, a species that occurs in Lipska Cave in Montenegro. Photo by Hermann Schachner, through Creative Commons.

Figure 119. ***Brachythecium tommasinii***. Photo by Hermann Schachner, through Creative Commons.

Figure 120. ***Entodon schleicheri*** with capsules. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

In Russia and the Crimea, Mazina (2016a) found the highest species diversity of bryophytes and ferns in caves where the lampenflora had not been removed. In seeming

contrast, Burgoyne *et al*. (2021), using DNA identification, found that bacterial communities of unlit nearby caves had a greater diversity than did the excursion caves with lights (Lehman Caves, Great Basin National Park, Nevada, USA). There was little overlap among the communities of the Lehman Caves. Could it be that the lampenflora out-competed the bacteria? But this would not be true away from the lights.

In Virginia, USA, caves, Lang (1941) found the colors of the lampenflora to add a "pleasing variation" to the natural colors of the rock formations. These same organisms are absent within the caves where there are no lights. Lang noted that during the tourist season, the organisms may experience a lighted period as long as that in nature outside the cave. However, in winter they are seldom illuminated and usually turn yellowish or brown and die. On the other hand, many such caves around the world continue to serve the public throughout the year, permitting the continued growth of the lampenflora.

Lang (1943) collected mosses from the Luray Caverns, Virginia, USA, and kept them between blotters, dry and dark for one year. Under these conditions, the mosses remained as green as when first collected. This is consistent with their ability to dry in nature and remain alive, whereas those that were kept moist by the cave, but without light, most likely used up their energy through respiration and were therefore unable to manufacture new chlorophyll while remaining physiologically active.

Conservation and Control Measures

Although the lampenflora is considered by some to be unsightly, the greater concern is its ability to deteriorate the substratum. **Cyanobacteria** (Figure 59-Figure 60), in particular, are common in these dimly lit conditions (Mulec 2012).

Conservation in the caves can have conflicting goals. On the one hand, to maintain the original conditions of the natural cave, it is desirable to prevent or remove the growth around cave lights needed to provide safety to tourists (Kim 2008). On the other hand, these can be points of interest to both scientists and tourists, illustrating the differences in light requirements among the algae, bryophytes, and ferns. Furthermore, lights are necessary for safety in show caves.

In Pacitan, Indonesia, the extensive karst topography creates a large number of caves, several of which serve as show caves (Kurniawan *et al*. 2017). The show caves provide many jobs in the area, both in the caves and in the community through tourism, and they are of essential economic importance to the local area. This use is more sustainable of the caves than is mining, but the tourism creates problems that are often in conflict with management for profit.

Many impacts of cave visitation are more subtle, noticed only by those conducting intensive study on the cave. This is particularly true for the non-photosynthetic cave dwellers. Elliott (2006) noted that typical cave dwellers such as some insects, salamanders, bats, and other animals have long life spans, slow rates of reproduction, and ability to survive in low food conditions. Some of the cave dwellers (*e.g.* moths, raccoons, bears) are seasonal, surviving there in winter and other unfavorable weather conditions. These organisms often avoid humans and can disappear without the average visitor ever noticing.

Human Impacts

Kurniawan and coworkers (2017) cited various dangers to the natural beauty of the caves: cement walkways, lights of various colors, big fans, added perfumes, weak regulation of visitor numbers, breakage and other damage of the rock formations, and application of dangerous substances to lessen the odor of guano and repel the cave fauna. Not only do the lights permit growth of lampenflora, but visitors introduce dust that covers the formations and alters their colors, leave garbage, vandalize, alter the microclimate, and cause decline in the numbers of biota. Similar impacts have been documented in other studies (Gillieson 2011; Mulec 2019).

Most cave formations of interest for tourists occur in limestone formations. The presence of lampenflora introduces organic acids that can corrode the limestone substrate (Aley 2004; Cigna 2012).

Russell and MacLean (2008) also noted the addition of concrete and steel structures, change in the air movement regime, and alteration of temperature through the movement of warm bodies through the cave. Human presence in the cave can also alter the available CO_2 (Russell & MacLean 2008; Lamprinou *et al*. 2014). This becomes more apparent when ventilation is limited (Russell & MacLean 2008; Lang *et al*. 2015). And the addition of entrances or blockage of entrances changes airflow patterns within the cave, with the entrance of visitors disturbing the relatively limited variation in temperature and humidity.

Visitors to caves can be a major source of propagules, especially on shoes and boots (Mulec 2014). Mulec estimated that more than 10,000 colony-forming units arrive per 100 cm² in such caves.

Many researchers have pointed out the destructive nature of cave lamps and human presence to the natural formations (Rajczy *et al*. 1997; Kubešová 2001; Cigna 2011; Gillieson 2011; Parise 2011; Mulec 2012; Šebela & Turk 2014; Mazina 2015; Piano *et al*. 2015; Meyer *et al*. 2017; Mulec 2019; Pfendler *et al*. 2021). Mulec (2012) considered the lampenflora to be unsightly, as well as having detrimental effects on the underlying substrata. But, unfortunately, the chemicals available to remove the lampenflora are not specifically targeted to these organisms, but can also be detrimental to the cave fauna. Furthermore, they can corrode the very substrate that is in need of protection. New lighting technology and better practices seem to be a better means of control.

In public caves in the Czech Republic, Kubešová (2006) found that the species richness was highest in the caves where the visitors' tour was long and the caves experienced the highest number of visitors. Hence, it is likely that humans are strong dispersal agents.

Treatments - Chemical

In Crystal Cave, Sequoia National Park, California, USA, Meyer *et al*. (2017) found that 1.0 and 0.5% sodium hypochlorite (Clorox) effectively eliminate lampenflora in 11 and 21 days, respectively, greatly outperforming 15.0% hydrogen peroxide. The springtail ***Tomocerus celsus*** (see Figure 121) had a similar diet both when living among the lampenflora and away from it. Nevertheless, ***T. celsus*** experiences a negative response to 1.0% sodium hypochlorite, and its presence was inversely related to the effectiveness of each treatment.

Figure 121. *Tomocerus vulgaris*; ***Tomocerus celsus*** lives among the lampenflora in Crystal Cave, Sequoia National Park, California, USA. Photo by Andy Murray, through Creative Commons.

Because chlorine and other compounds used to remove lampenflora are deleterious to the cave substrate, Faimon *et al*. (2003) tested hydrogen peroxide as an alternative in a cave in the Moravian Karst, Czech Republic. They found that a 15% by volume solution was an adequate strength to destroy the lampenflora. But limestone and speleothem dissolution rates were 1 order of magnitude higher than that by the karst water. To alleviate this problem, they found that there was little damage if a few limestone fragments were added to the solution at least 10 hours prior to application.

Mulec (2018) elaborated on the types of changes that lampenflora can make in caves. Plant thalli can calcify, and tuffaceous stalactites and stromatolitic stalagmites add variety to the cave formations. But these are natural processes, at times increased by access of the phototrophs deeper into the cave by the presence of artificial light.

In prehistoric caves, serious damage may occur to wall paintings, as observed in the Lascaux cave in France (Ruspoli 1986). In historic caves where cave art is of interest, alteration of the artwork is of concern (Mulec 2018). The hygroscopic nature of the **Cyanobacteria** (Figure 59-Figure 60) and algae (Figure 61) and can make them especially harmful to artwork (Roldán *et al.* 2006). The lampenflora creates a greenish cast to the artwork and the photosynthetic organisms promote the growth of bacteria and fungi that "weather" the underlying art. Mulec (2018) contended that altering the spectra of the lights did not help in preventing lampenflora. Instead, he recommended removing the lampenflora and restricting the use of the lamps.

Kim (2008) noted that even though the lights may be shut down for periods of time, these **Chlorophyta** (Figure 61) and **Bryophyta** that have disappeared grow again "immediately" when suitable growth conditions return. Kim (2008) recommended the "necessity" of keeping the illumination distance over 2 m and using indirect light. This researcher warned against unintentional dispersal by moist pieces of cloth or sponge when removing the lampenflora and noted the importance of removing them at an early stage of development. Heat created by the lighting can also be a problem.

Sea caves (Figure 122) require special management (Gurnee 1994) that involves innovative techniques to protect them from the intrusion of visitors and exposure to the destructive sea air. These are sometimes protected by glass enclosures, use of boats and vehicles that keep visitors from especially sensitive areas, and lighting and cleaning techniques that minimize lampenflora.

Figure 122. View from inside of sea cave at Cape Greco National Park, Cyprus. Photo by Kallerno, through Creative Commons.

De Freitas (2010) emphasized the importance of managing the microclimate in the caves. These are easily altered by changes in entrance conditions, changing both spatial and temporal patterns of the climates within the cave. And changing air patterns will necessarily change patterns of dispersal of propagules. This means that management techniques must be appropriate to a particular cave condition or needed environmental condition.

Treatments – Alternative Lighting Regimes

Kim (2008) reported that the cave green algae and bryophytes disappeared by shutting down the lights and maintaining the natural low temperatures in caves. But this is not an option in show caves.

Whereas daylight spectrum lighting and red-enriched tungsten lighting promote the growth of **Cyanobacteria**, algae, and plants, UV light has antibiotic properties and is even used in hospitals and microbiology labs to control pathogens and contaminants. UV lights have been used to control the lampenflora in some caves (Mulec & Kosi 2009). In Grotta Gigante, Trieste, Italy, new germicidal lamps earned the cave the 2008 Green certificate (Fabbricatore 2009). These were considered environmentally friendly and kept the lampenflora under control. For safety purposes, these are on timers that turn them on when no other lights are on in the cave. They can be detrimental to human eyes and skin, so their use should be avoided when humans are in the cave. But what about the fauna of the cave?

Pfendler *et al*. (2021) experimented with the growth of bryophytes on block samples with several pigments such as one might find in the prehistoric art. Several blocks in the study sustained dense bryophyte propagation. Nevertheless, the success of growth rate correlated with the chemical composition of the pigments. Such elements as As, Cr, Ti, and Co reduced bryophyte growth. UV-C light proved to be highly efficient *in situ*, although in the laboratory such treatments experienced fast recolonization. The researchers suggested that the recolonization was due

to the high density of the bryophyte growth that protected the lower parts from the UV-C light penetration.

Perhaps a better solution is the use of green light (Roldán *et al*. 2006). Changes is the light spectrum can include pigment changes in the **Cyanobacteria** and algae. In fact, green light affects pigment composition (Tandeau de Marsac *et al*. 1988; Albertano 1991). But it also retards growth (Hauschild *et al*. 1991) and causes vacuolation in the chlorophyll thylakoid system (Albertano 1991). An added bonus is that it provides the maximum absorbance in human vision.

Using the cyanobacterian ***Gloeothece membranacea*** (Figure 123) and chlorophytan ***Chlorella sorokiniana*** (Figure 124), Roldán *et al*. were able to demonstrate that green light could prevent the growth of photosynthetic organisms, except for those capable of modifying accessory pigments. Even so, the very light-adaptable ***Gloeothece membranacea*** exhibited lower photosynthetic pigment biovolume, smaller thylakoid regions, and a weaker mean fluorescence intensity.

Figure 123. ***Gloeothece membranacea***, a member of **Cyanobacteria** that is damaged by green light. Photo by Chris Carter, with permission.

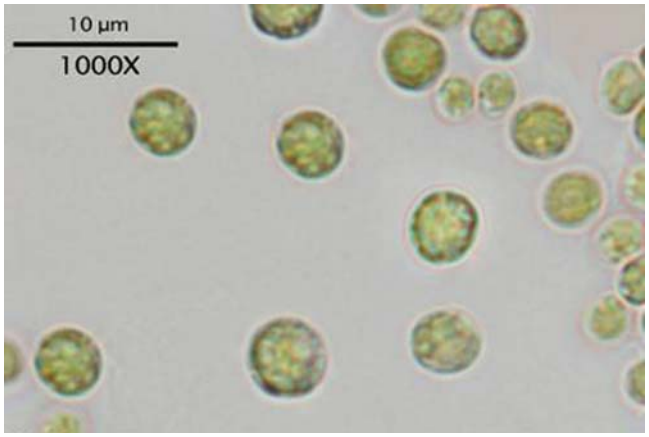

Figure 124. ***Chlorella sorokiniana***, a member of **Chlorophyta** in which growth is prevented by green light. Photo by UTEX, through Creative Commons.

Pollution and Role of Bryophytes

In the Zhijin Cave in China, heavy metal pollution was introduced by the development of the karst caves for show purposes. Liu *et al*. (2018) sought to determine the effect of the bryophytes on the cave pollution. The cave had 12 liverwort and 37 moss taxa, dominated by **Pottiaceae**, **Fissidentaceae**, and **Mniaceae**. Mercury levels were especially elevated and represented the most serious pollutant in the cave. The bryophyte community diminished as the heavy metal levels increased. Furthermore, the bryophytes served as accumulators that could be used to indicate the level of pollution in the cave. The liverwort ***Conocephalum conicum*** (Figure 125), in particular, is affected by substrate Hg content and can be used as a biomonitor in caves.

Figure 125. ***Conocephalum conicum***, a species that can be used to monitor mercury in caves. Photo by Claire Halpin, with permission.

One consequence of the lampenflora is the production of **aragonite** (mineral consisting of calcium carbonate, typically occurring in white seashells, including pearls, and as colorless prisms in deposits in hot springs) instead of **calcite** (more common form of calcium carbonate in limestone caves) (Forti 1980). This is accomplished by the different arrangement of atoms. Such modifications can be minimized by use of special lamps that do not support the range of maximum absorption for photosynthesis (Gurnee 1994; Olson 2002; Roldán *et al.* 2006; Mulec & Kosi 2009; Lamprinou *et al*. 2014).

Summary

Succession of **lampenflora** usually begins with **Cyanobacteria**, then algae, then bryophytes, and finally ferns (and possibly flowering plants). The **Cyanobacteria** and algae are forced farther and farther from the light by the increasingly larger bryophytes and ferns. The caves with lamps typically have greater species diversity of bryophytes and other cave flora.

Dominant bryophyte species, and those with widespread occurrence, include ***Amblystegium serpens***, ***Eucladium verticillatum***, ***Fissidens bryoides***, and ***Fissidens taxifolius***, but dominant species differ regionally. Liverworts are few or absent. ***Rhynchostegiella tenella*** can arrive and establish within one year.

Bryophytes in the low light of caves, whether in the twilight zone or around lights, frequently have diminished chlorophyll content (pale), leaves more widely spaced, leaves elongated, cell elongation, reduction of costa, and reduction or lack of sexual structures. They are often positively phototropic.

The lampenflora are typically **colonists** and **perennials** with a **rough mat** or **short turf** life form. The sporophyte generation is poorly represented, and the plants seem to rely on asexual propagules and fragmentation for spreading within the cave. Those with sporophytes typically produce them frequently outside the caves, but the converse is less likely.

The lampenflora is typically considered a nuisance in caverns. It changes the colors, increases the decomposition of the cave, and can damage prehistoric artwork. Efforts to remove or prevent the lampenflora include peroxide, scraping, and reducing the time lights are on. But new treatments with green light or use of UV light when humans are not present offer promise.

Although bryophytes are susceptible to damage by pollutants, they can also be accumulators that help to remove heavy metals and other pollutants introduced by human activity.

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CHAPTER 18-6
CAVES – SIMILAR SECLUDED HABITATS

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CHAPTER 18-6
CAVES – SIMILAR SECLUDED HABITATS

Figure 1. Zen Iwatsuki photographing fissure in lava, with bryophytes, Grjotagja, Myvatn, Iceland, 1985. Photo by Janice Glime.

Artificial "Caves"

Mine Shafts

Mines and mine shafts, in many ways, act like caves. Their cold air typically comes from lower levels rather than through channels above. They are dark, and they are usually damp. These habitats can have their own unique bryophyte flora, often influenced by the types of minerals being mined. Strip mines can in some cases resemble sink holes, but often have a much shorter history and much less moisture. But I have to wonder why I was unable to find many studies on these human-made habitats.

In Ireland, Holyoak and Lockhart (2009) found ***Cephaloziella massalongi*** (Figure 2) at the top of a copper mine shaft on rock where it was lightly shaded (Figure 3). Although it seems to always be associated with copper in Britain, ***Cephaloziella massalongi*** only occurs on acidic sites (Figure 4), and is not known from limestone sites. Cornish sites typically have *p*H levels of 5.1-5.4 and are often associated with moderate levels of both lead and zinc as well as copper. Callaghan (2011) studied the ecology of this species and found that it typically grows in shaded conditions (Figure 4) with less than 10% relative light, a level that characterizes many of the liverworts (Marschall & Proctor 2004). In an old mine adit of Wales, it grew at 2.5 lux (0.2% relative light). Callaghan suggested that ***Cephaloziella massalongi*** may be confined to such shaded conditions because of its need for moisture and inability to successfully compete elsewhere.

Figure 2. ***Cephaloziella massalongi***, a copper-tolerant liverwort. Photo by Des Callaghan, with permission.

Figure 3. ***Cephaloziella massalongi*** habitat in old metal mine. Photo by Des Callaghan, with permission.

Figure 4. ***Cephaloziella massalongi*** in Hermon Copper Bog under overhanging sod that provides it with shade. Photo by Des Callaghan, with permission.

The number of taxa in the Tongshankou Copper Mine in China is much greater than in many caves (Pen & Zhang 2005). So far 29 moss taxa, representing 7 families and 20 genera, have been identified. Pan *et al*. (2011) found a similar number of species (30 taxa) in four abandoned mercury mines in China. Bryophytes occurred within the first 10 m into the mine. The life forms were 60% short turfs, 33% wefts, and 7% mats. Among these was the luminous thallose liverwort ***Cyathodium smaragdinum*** (Figure 5).

Figure 5. ***Cyathodium smaragdinum***, a luminous thallose liverwort that is known from a copper mine in China. Photo by 楊玉鳳, through Creative Commons.

Koponen (1977) reported the mosses ***Pohlia nutans*** (Figure 6) and ***Ceratodon purpureus*** (Figure 7-Figure 10) at a depth of 176 m in a mine in Finland. But this mine was continuously illuminated by electric lights. The mosses covered an area of ~0.5 m² in this mine under a constant ~8ºC and high humidity. The mine was rich in zinc, lead, and copper. ***Ceratodon purpureus*** is a moss of a wide range of habitats, from dry roadsides to submerged in Antarctic ditches and resplendent on its boulders (Figure 9). It is not unusual to see it growing on stone ledges (Figure 10).

Figure 6. ***Pohlia nutans*** with capsules on rock, a widespread species that occurs at a depth of 176 m in a mine in Finland. Photo by J. C. Schou, with permission.

Figure 7. ***Ceratodon purpureus***, a moss that can grow at 176 m depth in a continuously illuminated mine. Photo by Michael Lüth, with permission.

Figure 8. ***Ceratodon purpureus*** with immature capsules, showing how abundant the capsules can be. Photo courtesy of Dale Sievert.

Figure 9. ***Ceratodon purpureus*** on boulders in the Antarctic. Photo courtesy of Rod Seppelt.

Figure 10. ***Ceratodon purpureus*** on a shaded ledge in Dollar Bay, Michigan, USA. Photo by Janice Glime.

Mine entrances seem to be overlooked habitats where one might find unusual species in areas where similar cave habitats are absent. On the other hand, the surface around mines is typically rich in ore and often has rare species (*e.g.* Callaghan 2018), but these areas are not similar to caves and will be discussed elsewhere.

Subways

Subways are manmade caves, but are typically illuminated and are open at both ends. They are likely to suffer from the pollution created by trains.

The granitic subway in Stockholm has lighting throughout. Established in 1970, the tunnel has a flora including **Cyanobacteria**, fungi, bacteria, diatoms, and the moss ***Eucladium verticillatum*** (Figure 11), a species not known elsewhere in Stockholm. Its occurrence on granite is unusual – it usually occurs on limestone. The subway also is home to a spider that is unknown elsewhere in Sweden.

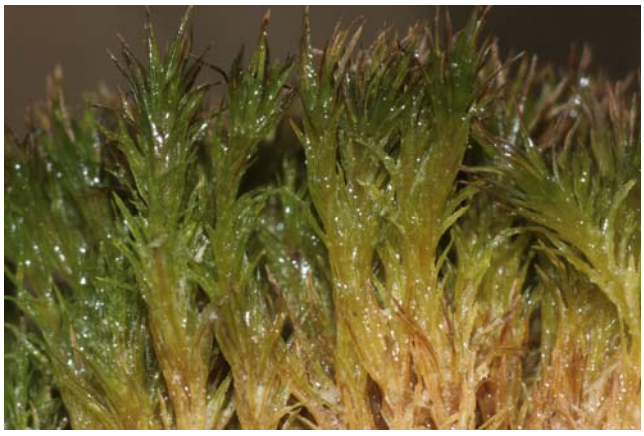

Figure 11. ***Eucladium verticillatum***, a moss that grows in a granitic subway in Stockholm. Photo by Hermann Schachner, through Creative Commons.

Small Caves and Fissures

Various fissures and cracks in rocks (Figure 1, Figure 12-Figure 13), including lava, make tiny caves and cave-like habitats that are suitable refuges for bryophytes. While

in Iceland, Yojiro Iwatsuki uncovered ***Saelania glaucescens*** (Figure 14) growing completely hidden under cracked rocks in a lava field (Figure 15-Figure 17).

Figure 12. Fissures in hard lava rock, Myvatn, Iceland, making cave-like environments. Photo by Janice Glime.

Figure 13. Fissures with hot springs at bottom and bryophytes growing on the warm, humid rocks, Myvatn, Iceland. Photo by Janice Glime.

Figure 14. ***Saelania glaucescens***, a species that grows in protected areas on cliffs or even completely under rocks in volcanic areas. Photo by Janice Glime.

Figure 15. Cracked lava that hides ***Saelania glaucescens*** north of Reykjahlid, Iceland. Photo by Janice Glime.

Figure 16. ***Saelania glaucescens*** revealed as layers of rock are removed, north of Reykjahlid, Iceland. Photo by Janice Glime.

Figure 17. ***Saelania glaucescens*** with capsules revealed from under lava crack N of Reykjahlid, Iceland. Photo by Janice Glime.

Krukowski and Świerkosz (2005) found the fern ***Vandenboschia radicans*** (Figure 18) in its easternmost locality in Europe. Its gametophytes grew in horizontal rock fissures with sparse growths of the mosses ***Schistostega pennata*** (Figure 19) and ***Distichium inclinatum*** (Figure 20). I observed the same phenomenon with ***Asplenium scolopendrium*** gametophytes growing among mosses on the vertical sides of boulders in the Upper Peninsula of Michigan, USA.

Figure 18. ***Vandenboschia radicans***, a fern species whose prothalli grow in rock crevices with mosses in Europe. Photo through Creative Commons.

Figure 19. ***Schistostega pennata*** carpet; dark green plants are upright gametophytes; yellow-green color indicates presence of the protonemata; this mat of mosses can provide suitable habitat in crevices for the fern ***Vandenboschia radicans*** in Europe. Photo by Alpsdake, through Creative Commons.

Figure 20. ***Distichium inclinatum***; this mat of mosses can provide suitable habitat in crevices for the fern ***Vandenboschia radicans*** in Europe. Photo by Hermann Schachner, through Creative Commons.

Scree

Screes (slopes covered with small loose stones; **talus**; Figure 21-Figure 22) create numerous minicaves that can act as refugia for more northern boreal and Arctic bryophyte, pteridophyte, and arthropod species (Růžička *et al*. 2012). These can even have year-round ice.

Figure 21. Scree in Switzerland, creating tiny darkened caves where bryophytes enjoy protection. Photo by Urs Kormann, through Creative Commons.

Figure 22. Talus slope at Ruby Mountains, Nevada, USA. Photo from USGS, through public domain.

In the Czech Republic, 92 bryophyte and 10 pteridophyte species were encountered among the scree. The liverworts ***Sphenolobus saxicola*** (Figure 23), ***Diplophyllum taxifolium*** (Figure 24), ***Gymnomitrion***

concinnatum (Figure 25), ***Gymnomitrion corallioides*** (Figure 26-Figure 27), and ***Barbilophozia sudetica*** (Figure 28), and mosses ***Andreaea rupestris*** (Figure 29), ***Polytrichastrum alpinum*** (Figure 30), ***Racomitrium fasciculare*** (Figure 31) and ***Racomitrium lanuginosum*** (Figure 32) have isolated populations in the Kamenec Hill of the Czech Republic, and the populations of the fern ***Cryptogramma crispa*** (Figure 33) and liverworts ***Gymnomitrion*** spp. (Figure 25-Figure 27) represent the lowest known elevational limits for the Czech Republic and Central Europe. Some species occur only near ice plots, including the liverworts ***Diplophyllum taxifolium***, ***Gymnomitrion corallioides***, and ***Lophozia sudetica*** and the mosses ***Andreaea rupestris*** and ***Polytrichastrum alpinum***. On the other hand, the liverworts ***Sphenolobus saxicola*** and ***Gymnomitrion concinnatum*** and mosses ***Racomitrium fasciculare*** and ***Racomitrium lanuginosum*** never occurred near ice.

Figure 23. ***Sphenolobus saxicola***, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo through Creative Commons.

Figure 24. ***Diplophyllum taxifolium***, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Hermann Schachner, through Creative Commons.

Figure 25. ***Gymnomitrion concinnatum***, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Štěpán Koval, with permission.

Figure 26. ***Gymnomitrion corallioides***, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Rory Hodd, with permission.

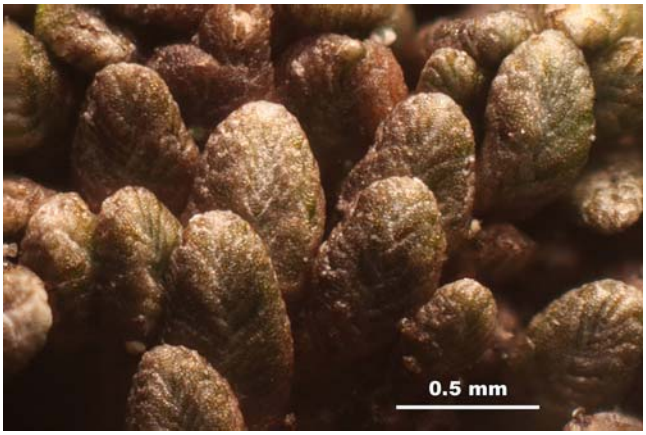

Figure 27. ***Gymnomitrion corallioides***. Photo by Hermann Schachner, through Creative Commons.

Figure 28. ***Barbilophozia sudetica***, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Hugues Tinguy, with permission.

Figure 29. ***Andreaea rupestris***, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by J. C. Schou, with permission.

Figure 30. ***Polytrichastrum alpinum***, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by David T. Holyoak, with permission.

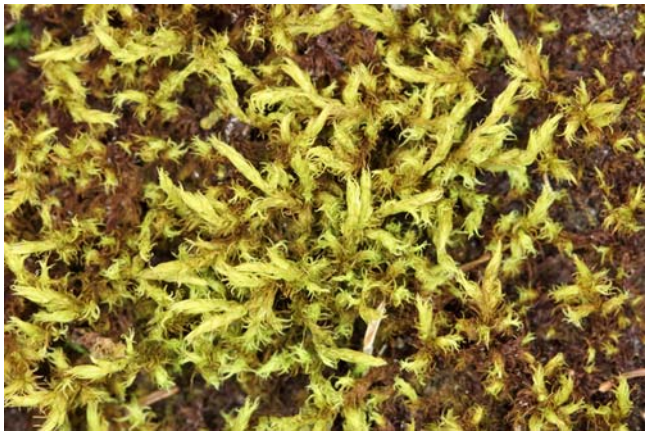

Figure 31. ***Racomitrium fasciculare***, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Jean Faubert, with permission.

Figure 32. ***Racomitrium lanuginosum***, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Hermann Schachner, through Creative Commons.

Figure 33. ***Cryptogramma crispa***, a species that reaches its lowest elevation in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Joan Simon, through Creative Commons.

These scree habits likewise provide a deep labyrinth where arthropods and other organisms find refuge (Růžička *et al*. 2010). In NE Bohemia, Czech Republic, deep vertical spaces among the scree provide microhabitats for montane bryophyte species such as the liverwort ***Diplophyllum taxifolium*** (Figure 24), and the mosses ***Dicranum elongatum*** (Figure 34) and ***Pohlia drummondii*** (Figure 35) occur. Living among these are numerous arthropods, with spiders and beetles being the most numerous. A total of 304 species of arthropods were identified in the study.

Figure 34. ***Dicranum elongatum*** with capsules, a species that lives in deep cavities among the scree in NE Bohemia, Czech Republic. Photo by Jean Faubert, with permission.

Figure 35. ***Pohlia drummondii***, a species that lives in deep cavities among the scree in NE Bohemia, Czech Republic. Photo by David T. Holyoak, with permission.

In Iceland, the mosses ***Distichium capillaceum*** (Figure 36-Figure 37), ***Mnium marginatum*** (Figure 38), and ***Pohlia cruda*** (Figure 39), and the fern ***Cystopteris fragilis*** (Figure 40), grow over the **loess** (silt-sized sediment formed by accumulation of wind-blown dust) deposits inside the scree cavities, surviving with reduced light but buffered microclimate (Blažková 1973). Similar associations also occur in crevices on loess in the Czech Republic (Hesselbo 1918; Šmarda 1947).

Figure 36. ***Distichium capillaceum*** with capsules, under grass cave; this species grows over the loess deposits inside in karst cavities and at the bottom of the deep karstic Macocha Chasm in the Czech Republic. Notice the lines of reddish brown capsules. Photo by Michael Lüth, with permission.

Figure 37. ***Distichium capillaceum***. Photo by Hermann Schachner, through Creative Commons.

Figure 38. ***Mnium marginatum***, a species that grows over the loess deposits in karst cavities. Photo by Hermann Schachner, through Creative Commons.

Figure 39. ***Pohlia cruda***, a species that grows over the loess deposits in karst cavities. Photo by Hermann Schachner, through Creative Commons.

Figure 40. ***Cystopteris fragilis*** among mosses on rock, a species that grows over the loess deposits in karst cavities. Photo by Bryant Olson, through Creative Commons.

Similar cavities occur in lava fields (Figure 41). Blažková (1973) described these from northern Iceland. Aeolian sediments accumulate on the bottom of these cavities. Light intensity is greatly reduced and the microclimate is buffered from the extremes at the surface. Blažková reported 12 bryophyte species from these. In very dark parts of the cavities mainly liverworts occur, including ***Blepharostoma trichophyllum*** (Figure 42), ***Mesoptychia collaris*** (Figure 43-Figure 44), and ***Sauteria alpina*** (Figure 45-Figure 46). Close to the openings where it is well illuminated, one can find ***Polytrichum juniperinum*** (Figure 47-Figure 48) and especially ***Timmia austriaca*** (Figure 49).

Figure 41. Sheep near lava rock at Myvatn, northern Iceland, showing the tumbled arrangement of rocks that creates minicaves. Photo by Janice Glime.

Figure 42. ***Blepharostoma trichophyllum***, a species that can occur in dark cavities of lava fields in northern Iceland. Photo by Hermann Schachner, through Creative Commons.

Figure 43. ***Mesoptychia collaris***, a species that can occur in dark cavities of lava fields in northern Iceland. Photo by Hermann Schachner, through Creative Commons.

Figure 44. ***Mesoptychia collaris*** with capsules. Photo by Hermann Schachner, through Creative Commons.

Figure 45. ***Sauteria alpina***, a species that can occur in dark cavities of lava fields in northern Iceland. Photo by Michael Lüth, with permission.

Figure 46. ***Sauteria alpina*** with archegoniophores. Photo by Hermann Schachner, through Creative Commons.

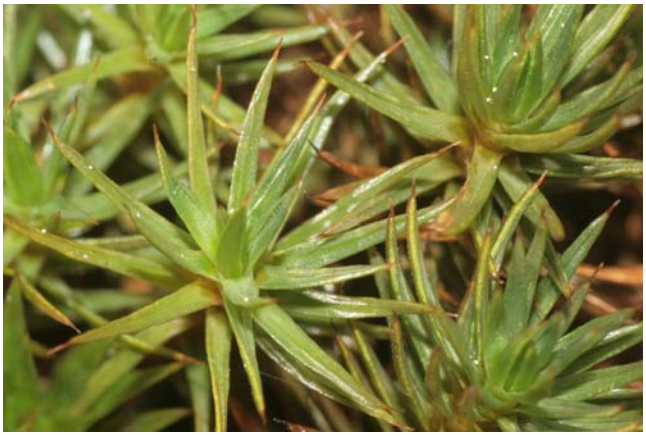

Figure 47. ***Polytrichum juniperinum***, a species that grows close to the openings of cavities among lava stones where it is well illuminated. Photo by Hermann Schachner, through Creative Commons.

Figure 48. ***Polytrichum juniperinum*** with male splash cups. Photo by Ian Sutton, through Creative Commons.

Figure 49. ***Timmia austriaca***, a species that grows close to the openings of cavities among lava stones where it is well illuminated. Photo by Jean Faubert, with permission.

Bjarnason (1991) considered every cavity around a boulder at Hekla (Figure 50), southern Iceland, to be

different, thus making all the holes different in ecological character. The moss ***Racomitrium lanuginosum*** (Figure 32) frequently grows on these rocks and covers the cavity (Figure 51-Figure 52), making the area somewhat dangerous for walking. The very deep, narrow lava clefts (Figure 53-Figure 54) support vegetation similar to that of the holes, with ***Conostomum tetragonum*** (Figure 55), ***Pohlia drummondii*** (Figure 35), ***Pohlia wahlenbergii*** (Figure 56), and ***Polytrichastrum sexangulare*** (Figure 57-Figure 58). The vegetation in these narrow lava cavities at Hekla has a very different flora from those in northern Iceland (Figure 41). Some species prefer the holes in the Hekla area, but are not restricted to them: the liverworts ***Blepharostoma trichophyllum*** (Figure 42) and ***Nardia geoscyphus*** (Figure 59) and the mosses ***Isopterygiopsis pulchella*** (Figure 60), ***Mnium stellare*** (Figure 61), ***Oligotrichum hercynicum*** (Figure 62), and ***Pohlia cruda*** (Figure 39). Many species also occupy the crags, including the liverworts ***Diplophyllum albicans*** (Figure 63) and ***Mesoptychia gillmanii*** (Figure 64) and the mosses ***Encalypta ciliata*** (Figure 65) and ***Plagiothecium cavifolium*** (Figure 66-Figure 67). Others occur in small ruptures in the main surface (Figure 54), including the liverwort ***Cephaloziella divaricata*** (Figure 68-Figure 69) and mosses ***Dicranoweisia crispula*** (Figure 70), ***Diphyscium foliosum*** (Figure 71), and ***Pohlia drummondii***. As in northern Iceland, ***Racomitrium lanuginosum*** (Figure 32, Figure 51-Figure 52) is common near the openings of the holes, infrequently accompanied by ***Andreaea rupestris*** (Figure 29) and ***Schistidium apocarpum*** (Figure 72) (Bjarnason 1991). As in northern Iceland, the moist, sandy bottom (40-60 cm) supports small patches of liverworts; mixed with larger bryophytes such as the moss ***Bartramia ithyphylla*** (Figure 73) and liverwort ***Plagiochila porelloides*** (Figure 74). In wide, shallow holes the number of species is greater at this sandy bottom, including ***Brachythecium albicans*** (Figure 75), ***Polytrichum juniperinum*** (Figure 47-Figure 48), ***Rhytidiadelphus squarrosus*** (Figure 76), and ***Timmia austriaca*** (Figure 49).

Figure 51. ***Racomitrium*** mounds, Iceland. Photo by Janice Glime.

Figure 52. Lava beds of Nass Valley, British Columbia, with ***Racomitrium***, illustrating the cavities and multiple formations created. Photo by Darren Kirby, through Creative Commons.

Figure 50. Hekla, Iceland, cairns and various rock sizes. Photo by cogdogblog, through Creative Commons.

Figure 53. Fissure in hard lava rock, with the lichen ***Cetraria*** and bryophytes, Myvatn, Iceland. Photo by Janice Glime.

Figure 54. Fissure with mosses in its small rupture, N. Myvatn, Iceland. Photo by Janice Glime.

Figure 55. ***Conostomum tetragonum*** with capsules, a species that occurs in very deep, narrow lava clefts in Iceland. Photo by Hermann Schachner, through Creative Commons.

Figure 56. ***Pohlia wahlenbergii***, a species that occurs in very deep, narrow lava clefts in Iceland. Photo by Hermann Schachner, through Creative Commons.

Figure 57. ***Polytrichastrum sexangulare***, a species that occurs in very deep, narrow lava clefts in Iceland. Photo by Tomas Hallingbäck, with permission.

Figure 58. ***Polytrichastrum sexangulare***. Photo by Hermann Schachner, through Creative Commons.

Figure 59. ***Nardia geoscyphus***, a species that prefers the holes in the Hekla area of Iceland, but is not restricted to them. Photo by Rayna Natcheva, with permission.

Figure 60. ***Isopterygiopsis pulchella*** with capsule, a species that prefers the holes in the Hekla area of Iceland, but is not restricted to them. Photo by Michael Lüth, with permission.

Figure 61. ***Mnium stellare***, a species that prefers the holes in the Hekla area of Iceland, but is not restricted to them. Photo by Hermann Schachner, through Creative Commons.

Figure 62. ***Oligotrichum hercynicum***, a species that prefers the holes in the Hekla area of Iceland, but is not restricted to them. Photo by Štěpán Koval, with permission.

Figure 63. ***Diplophyllum albicans***, a species that occupies the crags in the Hekla area of Iceland. Photo by David T. Holyoak, with permission.

Figure 64. ***Mesoptychia gillmanii***, a species that occupies the crags in the Hekla area of Iceland. Photo by Tomas Hallingbäck, with permission.

Figure 65. ***Encalypta ciliata*** with capsules, among rocks, a species that occupies the crags in the Hekla area of Iceland. Photo by Tony Frates, through Creative Commons.

Figure 66. ***Plagiothecium cavifolium*** on shale, a species that occupies the crags in the Hekla area of Iceland. Photo by Bob Klips, with permission.

Figure 67. ***Plagiothecium cavifolium***. Photo by Christian Berg, through Creative Commons.

Figure 68. ***Cephaloziella divaricata***, a species that occupies the crags in the Hekla area of Iceland. Photo by Hermann Schachner, through Creative Commons.

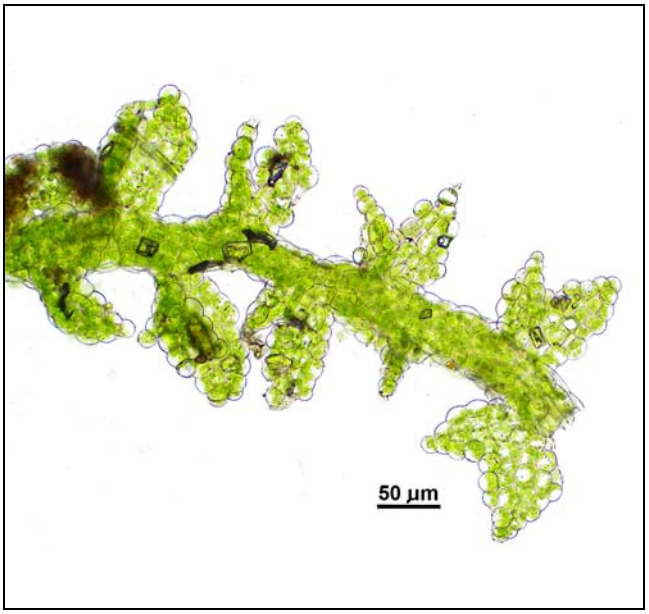

Figure 69. ***Cephaloziella divaricata*** branch. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 70. ***Dicranoweisia crispula*** with capsules, on rock, a species that occupies the crags in the Hekla area of Iceland. Photo by Hermann Schachner, through Creative Commons.

Figure 71. ***Diphyscium foliosum*** capsules, a species that occupies the crags in the Hekla area of Iceland. Photo by Hermann Schachner, through Creative Commons.

Figure 72. ***Schistidium apocarpum*** with capsules, a species that occurs near the opening of an ice cave in Iceland. Photo by Hermann Schachner, through Creative Commons.

Figure 73. ***Bartramia ithyphylla*** with capsules on vertical rock, a species that occurs on the moist, sandy bottoms (40-60 cm) of small caves in Iceland. Photo by Štěpán Koval, with permission.

Figure 74. ***Plagiochila porelloides*** on vertical bank, a species that occurs on the moist, sandy bottoms (40-60 cm) of small caves in Iceland. Photo from Botany Website, UBC, with permission.

Figure 75. ***Brachythecium albicans***, a species that occurs in the shallow bottom of wide, sandy holes in Iceland. Photo by Kristian Peters, through Creative Commons.

Figure 76. ***Rhytidiadelphus squarrosus***, a species that occurs in the shallow bottom of wide, sandy holes in Iceland. Photo by Johan N, through Creative Commons.

Ice Caves

Bryophytes in ice caves (Figure 77) are much more uncommon. Jakab (2000) found ***Heterocladium heteropterum*** (Figure 78-Figure 79) and ***Cyrtomnium hymenophylloides*** (Figure 80) in ice caves in Romania. But outside, the caves can cause a **temperature inversion** (reversal of normal decrease of air temperature with altitude). Other bryophytes seem to benefit from the conditions emanating from these caves, permitting more Arctic species to survive here.

Figure 77. Ice cave in natural glacier. Photo by Serge J. F., through Creative Commons.

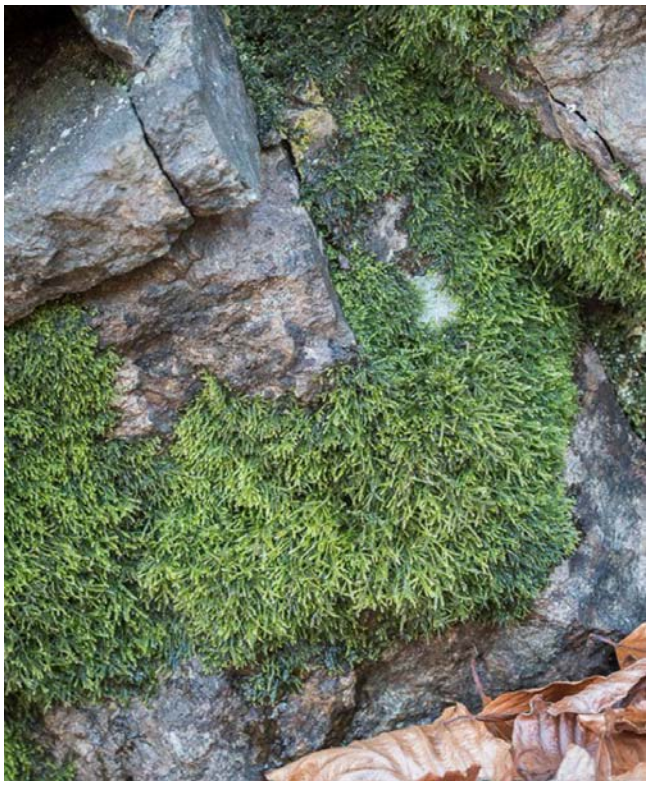

Figure 78. ***Heterocladium heteropterum*** on rock, a species that occurs in an ice cave in Romania. Photo by Štěpán Koval, with permission.

Figure 79. ***Heterocladium heteropterum*** branch showing large stem leaves and smaller branch leaves. Photo by Štěpán Koval, with permission.

Figure 80. ***Cyrtomnium hymenophylloides***, a species that occurs in an ice cave in Romania. Photo by Michael Lüth, with permission.

Windholes

Windholes (Figure 81-Figure 83, Figure 88) are also known as **Kaltluftlöcher**, **Kondenswassermoore**, and **ventaroles (**Wolfgang Karl Hofbauer, pers. comm. 26 July 2021). Natural windholes are made by the wind in sandstone formations as a result of centuries of wind and weather, making the rock formations pock-marked with windholes and caves. In summer, these cool the surrounding area with cool air that blows out, but during winter the air from the windholes is milder than that of the surrounding area (Kong *et al* 2011). These can be categorized as talus (Figure 84), cave (Figure 81-Figure 83), and sink types of windholes. Like caves, these can provide refugia for plants that normally occur at higher elevations or closer to the poles (Kong *et al*. 2012).

Figure 81. Algific talus slope with windholes in northeastern Iowa, USA. photo courtesy of Beth Lynch.

Figure 82. Algific talus slope with windholes obscured by mosses and other vegetation, northeastern Iowa, USA. Photo courtesy of Beth Lynch.

Figure 83. Algific cave opening (windhole) in Fillmore County, Minnesota, USA. Photo by S. C. Zager, MN DNR, through public domain.

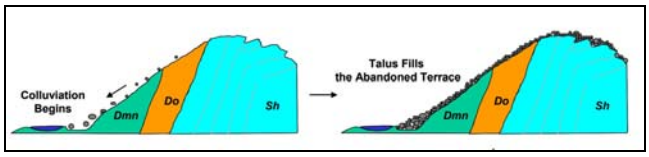

Figure 84. Algific slope cave formation, Ice Mountain, West Virginia, USA. Modified from Kevin M. Andrews, MS thesis 2003.

Harald Zechmeister (pers. comm. 26 July 2021) described the windholes in Austria. These have channels that are over 100 m long. This permits them to reach interior temperatures that are just slightly above 0ºC, often creating ice cores at the openings that persist through the summer. This favors the growth of Arctic-alpine liverworts like ***Protochilopsis*** (=***Schistochilopsis***) ***grandiretis*** (Figure 85), ***Odontoschisma macounii*** (Figure 86), or ***Tritomaria scitula*** (Figure 87) at low altitudes. He reports more than 100 bryophyte species associated with the surroundings of approximately 20 windholes.

Figure 85. ***Protochilopsis grandiretis***, an Arctic species that grows in windholes in Austria. Photo by Vadim Bakalin, with permission.

Figure 86. ***Odontoschisma macounii***, an Arctic species that grows in windholes in Austria. Photo from Earth.com, with permission.

Figure 87. ***Tritomaria scitula***, an Arctic species that grows in windholes in Austria. Photo by Tomas Hallingbäck, with permission.

Bakalin *et al*. (2017) describe these as formations in East Manchuria of Russia as places where the wind enters large holes tens of meters above, then goes underground, where it passes among wet stones and cliffs in areas with much lower temperatures due to evaporation of water from the stones. Therefore, at the exit hole, the air temperature may be about 10ºC below that of the surrounding environment.

In the Wisconsin Driftless Area, USA, Christy and Meyer (1991) similarly reported disjunct species that are restricted to the "refrigerated" windholes (Figure 88). Among these, the tiny moss ***Seligeria donniana*** (Figure 89) was new to Wisconsin. Among the 39 species of bryophytes identified from four of the largest algific slopes, one third were restricted to these cold air vents. These included the liverworts ***Marchantia polymorpha*** (Figure 90), ***Porella platyphylla*** (Figure 91), and ***Preissia quadrata*** (Figure 92), and the mosses ***Abietinella abietinum*** (Figure 93)**,** ***Anomodon attenuatus*** (Figure 94), ***Anomodon rostratus*** (Figure 95), ***Bartramia pomiformis*** (Figure 96), ***Brachythecium oxycladon*** (Figure 97), ***Koponeniella graminicolor*** (Figure 98), ***Bryoerythrophyllum recurvirostrum*** (Figure 99), ***Campylium chrysophyllum*** (Figure 100), ***Ceratodon purpureus*** (Figure 7-Figure 10), ***Climacium americanum*** (Figure 101), ***Didymodon fallax*** (Figure 102), ***Entodon seductrix*** (Figure 103), ***Eurhynchium hians*** (Figure 104), ***Hylocomiadelphus triquetrus*** (Figure 105), ***Mnium marginatum*** (Figure 38), ***Mnium stellare*** (Figure 61), ***Plagiomnium cuspidatum*** (Figure 106), ***Plagiomnium medium*** (Figure 107), ***Pohlia wahlenbergii*** (Figure 56), ***Rhodobryum ontariense*** (as ***Rhodobryum roseum***; Figure 108), ***Seligeria campylopoda*** (Figure 109), ***Seligeria donniana***, ***Thuidium delicatulum*** (Figure 110), and ***Thuidium recognitum*** (Figure 111).

Figure 88. Algific caves (windholes) in Wisconsin, USA. Photo by Ryan O'Connor, Wisconsin DNR, through public domain.

Figure 89. ***Seligeria donniana*** with capsules, a species that occurs in windholes in the algific slopes of the Driftless Area of Wisconsin, USA. Photo by Tom Neily, with permission.

Figure 90. ***Marchantia polymorpha***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Brenda Dobbs, through Creative Commons.

Figure 91. ***Porella platyphylla***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.

Figure 92. ***Preissia quadrata***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.

Figure 93. ***Abietinella abietinum*** on rock, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.

Figure 94. ***Anomodon attenuatus***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Dendrofil, through Creative Commons.

Figure 95. ***Anomodon rostratus***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.

Figure 96. ***Bartramia pomiformis*** with capsules, on rock ledge, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by David T. Holyoak with permission.

Figure 99. ***Bryoerythrophyllum recurvirostrum*** with capsules, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.

Figure 97. ***Brachythecium oxycladon***, on rock ledge, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Bob Klips, with permission.

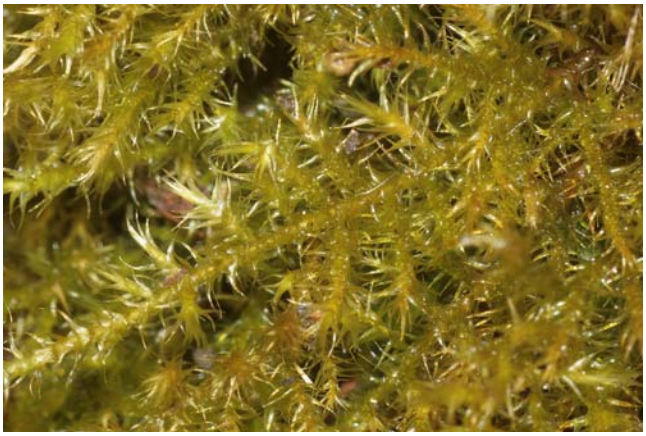

Figure 100. ***Campylium chrysophyllum***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.

Figure 98. ***Koponeniella graminicolor***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Bob Klips, with permission.

Figure 101. ***Climacium americanum***, a common species in moist habitats, occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Rafael Medina, through Creative Commons.

Figure 102. ***Didymodon fallax***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Jean Faubert, with permission.

Figure 103. ***Entodon seductrix***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Bob Klips, with permission.

Figure 104. ***Eurhynchium hians***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Wayne Lampa, through Creative Commons.

Figure 105. ***Hylocomiadelphus triquetrus***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by J. C. Schou, with permission.

Figure 106. ***Plagiomnium cuspidatum*** branch, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Bob Klips, with permission.

Figure 107. ***Plagiomnium medium*** with capsules, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Bob Klips, with permission.

Figure 108. ***Rhodobryum ontariense***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.

Figure 109. ***Seligeria campylopoda*** with capsules showing tropism, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo from Earth.com, with permission.

Figure 110. ***Thuidium delicatulum*** with capsules, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.

Figure 111. ***Thuidium recognitum***, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Sture Hermansson, with online permission.

Beth Lynch (pers. comm. 29 July 2021) finds a few bryophyte species that are common around the windhole vents of northeastern Iowa, USA (Figure 81-Figure 82), but are very infrequent or absent in the surrounding areas. Presumably due to these microclimatic conditions, ***Hylocomium splendens*** (Figure 112) and ***Hylocomiadelphus triquetrus*** (Figure 105) can be relatively common on the algific slopes, but are absent in other cool, moist microsites in the area. It is interesting that, like most caverns, these areas seem to be devoid of leafy liverworts.

Figure 112. ***Hylocomium splendens***, a northern species that can be found around windhole vents in Iowa, USA. Photo by Hugues Tinguy, with permission.

Higuchi (1991) reported that the montane mosses ***Dicranum elongatum*** (Figure 34) and ***Pohlia drummondii*** (Figure 35) and liverwort ***Diplophyllum taxifolium*** (Figure 24) occur in windhole areas of the Senpoku-gun in Japan.

The unusual microclimate near the windholes can bring surprises for curious bryologists (Choi *et al*. 2020). Choi *et al*. (2020) found ***Mannia fragrans*** (Figure 113) and ***Mannia androgyna*** (Figure 114) in windholes near the Donggang River, the first find of these species in Korea. Borovichev and Bakalin (2016) similarly reported ***Mannia triandra*** (Figure 115) from the windhole area of Magadan Province and the Korean Peninsula.

Figure 113. ***Mannia fragrans***, a species that occurs in windholes in Korea. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 114. ***Mannia androgyna***, a species that occurs in windholes in Korea. Photo from Earth.com, with permission.

Figure 115. ***Mannia triandra*** with archegoniophores among rocks, a species that occurs in windholes in Korea. Photo by Oliver Dürhammer, through Creative Commons.

Shirasaki (1990) investigated the ecological distribution of bryophytes in the windhole areas of Mt. Naeba, Niigata and Nagano Prefectures, Japan. Shirasaki (1998) found that the moss ***Trachycystis flagellaris*** (Figure 116) sometimes grows on the ground under shrubs where there are cool sites maintained by windholes that provide a temperature below 10ºC and a high air humidity in warmer seasons.

Figure 116. ***Trachycystis flagellaris***, a species that grows on the ground under shrubs where there are cool sites maintained by windholes in Japan. Photo by Misha Ignatov, with permission.

Hitoshi and Masaji (2003) found that in the windhole area of Niigata Prefecture, Japan, one could find ***Pogonatum urnigerum*** (Figure 117) and ***Polytrichastrum formosum*** (Figure 118) growing together. Elsewhere, ***Pogonatum urnigerum*** is able to grow at higher elevations than those of ***Polytrichastrum formosum***, whereas their distribution on a flat map is similar. ***Pogonatum urnigerum*** often has caducous leaves, as known in the Arctic (Long 1988) and in northern New York, USA (McDaniel & Miller 2000).

Figure 117. ***Pogonatum urnigerum*** with capsules, among rocks, a species that grows in windhole areas of Japan. Photo by Claire Halpin, with permission.

Figure 118. ***Polytrichastrum formosum***, a species that grows in windhole areas of Japan. Photo by Leonhard Lenz, through Creative Commons.

At the Bixby State Park and Preserve in Iowa, USA, Kleinman and Blisard (2018) reported 68 bryophyte species from the algific talus slopes near cold air vents. Of these, 16 moss species and 1 liverwort species are uncommon elsewhere in the Bixby park.

Sinkholes

Sinkholes (cenote, sink, sink-hole, sink hole, swallet, swallow hole, or doline; Figure 119-Figure 121) are large depressions in the ground due to collapse of the underlying substrate. This collapse is often caused by karstic processes that dissolve underlying carbonate rocks.

Figure 119. Sinkhole along Rio Camuy, Puerto Rico, aerial view. Photo from US Geological Survey, through Creative Commons.

Figure 120. Looking out of deep sinkhole at Gouffre-v-hdr in France, showing vegetation at the bottom. Photo through Creative Commons.

Figure 121. Sinkhole with bryophytes in Wilson County, Tennessee, USA. Photo by Brian Stansberry, through Creative Commons.

Linares *et al*. (2017) demonstrated the correlation between drought and the formation of sinkholes. This has occurred repeatedly in the karst of the fluvial valley of northeastern Spain (Figure 122), and it has been widely visible in Florida, USA (Figure 123), due to the emptying of aquifers by water usage and periods of drought.

Figure 122. Sinkhole Chinchón dolina c, collapse sinkhole in Spain. Photo through Creative Commons.

Figure 123. Sinkhole, Dover, Florida, USA, collapsed during a winter freeze event. Photo by Ann Tihansky, USGS, through public domain.

Sinkholes encompass some of the same characteristics as caves, especially high humidity and reduced light intensity (Maheu 1926). Because they are sunken, they tend to be more moist than the surrounding forest, with humidity increasing toward the base (Maheu 1926; Li *et al*. 2020b). The additional moisture is at least a contributor to lower temperatures. Maheu noted that the same dominant genera of mosses occurred in the sinkholes as in caves: ***Anomodon*** (Figure 94-Figure 95), ***Eurhynchium*** (Figure 104), ***Mnium*** (Figure 38, Figure 61). Perhaps this is in part due to their ease of starting protonemata from stems and leaves of these mosses. Maheu also considered that the protonemata of the mosses could enter in symbiosis with fungi. The modifications in these conditions are likewise similar to those of cave bryophytes: sterility, leaf elongation, longer internodes, elongation of cells, and disappearance or attenuation of the rib or costa.

The sinkhole often has greater bryophyte diversity than does the surrounding surface forest, but it also can increase the diversity of the adjoining forest. Li *et al*. (2020a) reported 71 taxa of bryophytes from a sinkhole forest in southeastern China, whereas the forest at the surface had only 29, and farther from the sinkhole only 22 taxa were present (Figure 124). Furthermore, the sinkholes were more favorable to liverworts, with 22 taxa compared to only 2 in the adjoining surface forest. In this study, 93% of the sinkhole bryophytes were absent from the surface forest. Li and coworkers found that in the sinkholes the dominant families were **Brachytheciaceae** (Figure 75, Figure 104), **Fissidentaceae** (Figure 128), **Plagiochilaceae** (Figure 74), and **Hypopterygiaceae** (Figure 125). The sinkhole bryophytes, by importance, were ***Conocephalum conicum*** (Figure 126), ***Homaliodendron montagneanum*** (see Figure 127), ***Fissidens cristatus*** (Figure 128), ***Leucobryum glaucum*** (Figure 129-Figure 130), ***Makinoa crispata*** (Figure 131), ***Plagiomnium rhynchophorum*** (Figure 132), ***Claopodium aciculum*** (see Figure 133), ***Eurhynchium laxirete*** (see Figure 104), ***Claopodium gracillimum*** (see Figure 133), and ***Fissidens hyalinus*** (Figure 134). The surface families were completely different, with the exception of **Brachytheciaceae**.

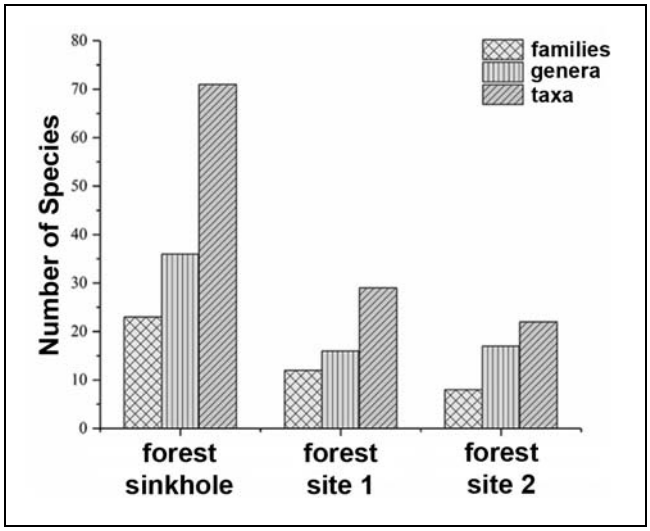

Figure 124. Sinkhole diversity vs forest diversity at 2 distances from sinkhole. Modified from Li *et al*. 2020a.

Figure 125. ***Hypopterygium filiculaeforme***, a member of the family **Hypopterygiaceae**, a family that is among the dominant families occurring in sinkholes in China. Photo by Sara Smerdon, through Creative Commons.

Figure 128. ***Fissidens cristatus***, one of the most important bryophytes associated with sinkholes in a sinkhole forest in southeastern China. Photo by Brad von Blon, through Creative Commons.

Figure 126. ***Conocephalum conicum*** with archegoniophores, most important bryophyte associated with sinkholes in sinkhole forest in southeastern China. Photo by Claire Halpin, with permission.

Figure 129. ***Leucobryum glaucum*** habitat on cliff, Canyon Falls, Michigan, USA, one of the most important bryophytes associated with sinkholes in a sinkhole forest in southeastern China. Photo by Janice Glime.

Figure 127. ***Homaliodendron flabellatum***; ***Homaliodendron montagneanum*** is among most important bryophytes associated with sinkholes in forest in southeastern China. Photo by Chris Alice Kratzer, through Creative Commons.

Figure 130. ***Leucobryum glaucum***. Photo by Janice Glime.

Figure 131. ***Makinoa crispata*** with capsules, one of the most important bryophytes associated with sinkholes in a sinkhole forest in southeastern China. Photo by 楊玉鳳, through Creative Commons.

Figure 132. ***Plagiomnium rhynchophorum***, one of the most important bryophytes associated with sinkholes in a sinkhole forest in southeastern China. Photo by Paul Davison, with permission.

Figure 133. ***Claopodium*** sp.; ***Claopodium aciculum*** and ***C. gracillimum***, both among the most important bryophytes associated with sinkholes in a sinkhole forest in southeastern China. Photo by John Game, with permission.

Figure 134. ***Fissidens hyalinus*** (whitish green), one of the most important bryophytes associated with sinkholes in a sinkhole forest in southeastern China. Photo by Ivanov, with permission.

In the Guda Sinkhole in China, Li *et al*. (2020b) found 75 species of bryophytes. They recorded the highest bryophyte diversity and abundance in the middle and upper sections, with the lowest in the top section and in the base. Furthermore, the most rapid turnover of species occurred in the two middle sections, presumably in response to a rapidly changing gradient of conditions of light and moisture. On the other hand, Váňa *et al*. (2014) found the liverworts ***Riccardia insularis*** (see Figure 135) and ***Calypogeia fissa*** (Figure 136) on both the floor and wall of a sink-hole cave on Ile Amsterdam in the South Indian Ocean.

Figure 135. ***Riccardia multifida***; ***Riccardia insularis*** occurs in a sink-hole cave on Ile Amsterdam in the South Indian Ocean. Photo by Hermann Schachner, through Creative Commons.

Figure 136. ***Calypogeia fissa***, a liverwort that occurs on both the floor and walls of a sink-hole cave on Ile Amsterdam in the South Indian Ocean. Photo by Claire Halpin, with permission.

In the large (280 m deep, 300 m diameter) Monkey-Ear sinkhole in China, Li *et al*. (2018) found 71 species of bryophytes. The greatest diversity was on tree trunks (41 species), followed by forest land > stone surfaces > carrion > leaf surfaces. There are 10 different life forms, 88% of which are typical of dark, humid habitats, whereas only 12% are adapted to bright light and dry conditions. The dissimilarity with surface bryophyte communities is high. Light, humidity, and temperature all influence the distribution of species, but light had the most influence.

In their study of Karst Mountain Sinkhole of Southeastern China, Li *et al*. (2020a) found that the number of life forms diminished from the sink hole to the first forest site and diminished more to the second (farthest) forest site (Figure 137).

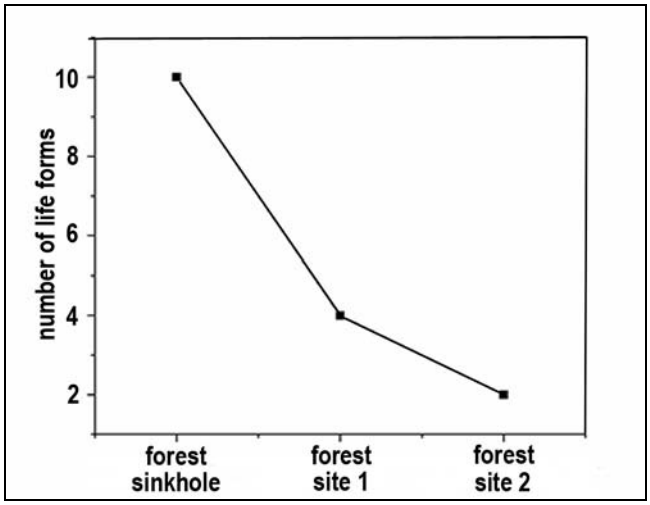

Figure 137. Sinkhole vs forest life forms in Karst Mountain Sinkhole of Southeastern China. Modified from Li *et al*. 2020a.

Thus, like caves, sinkholes provide refugia for species that are unable to live in that geographic region outside the sinkhole (Li *et al*. 2020a). Enclosing cliffs reduce the rate of water loss, thus increasing the humidity within the sinkhole. And these same cliffs can contribute to shading that reduces the temperature as well as the light levels. Furthermore, at least in the sinkhole studies in southeastern China, the nutrients are in greater supply in the sinks (Figure 138), although one would think this would be more beneficial to tracheophytes than to bryophytes.

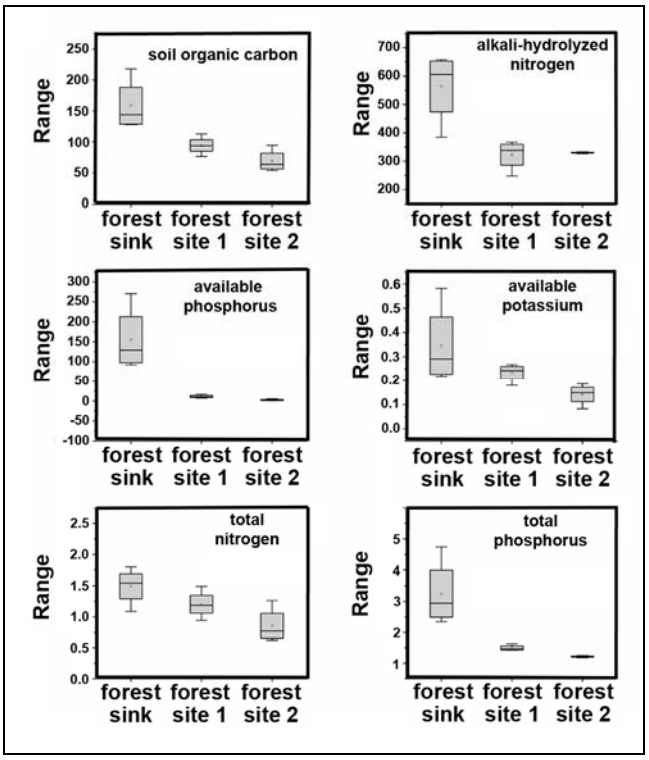

Figure 138. Soil nutrients in sinkhole forest and two surface forests. Bottom and top sections of the box plots indicate the inner quartile ranges. Horizontal bar within the box represents median. Whiskers indicate spread. Modified from Li *et al*. 2020a.

Rosseló and Ginés (1980), referring to them as potholes, reported 36 species of bryophytes in 23 sinkholes of Mallórca. They considered ***Eucladium verticillatum*** (Figure 11), ***Fissidens cristatus*** (Figure 128), ***Homalia lusitanica*** (Figure 139), ***Mnium*** sp. (Figure 38, Figure 61), and ***Thamnobryum alopecurum*** (Figure 140) to be "regular inhabitants." These species are likewise known from caves.

Figure 139. ***Homalia lusitanica***, a common species in sinkholes of Mallórca. Photo by Hugues Tinguy, with permission.

Figure 140. ***Thamnobryum alopecurum*** with capsules, a common species of sinkholes of Mallórca. Photo by David T. Holyoak, with permission.

Fergusen and Knobloch (1998) likewise found a high plant diversity in the Pliocene sinkhole of Willerhausen, Germany. Herrero-Borgonon and Puche (1987) found 26 moss species in the sinkholes of the Valencia region, Spain. In the Apuseni Mountains of Romania, Sass-Gyarmati *et al*. (2009) identified 21 liverwort and 59 moss species in sinkholes, compared to 43 species of **Cyanobacteria** and 50 of lichens.

Sinkholes can often present interesting species that are not found in other habitats of the area and, like caves, may provide conditions suitable for species of more polar or higher elevation habitats (Luo & Zhang 2017). Li *et al*. (2020c) explored the third largest sinkhole in the world – Haolong sinkhole in China. They identified 183 species, of which 26 are endemic to China.

Reyes-Colón and Sastre-D.J. (2000) reported 50 bryophyte species two sinkholes in the north-central karst region of Puerto Rico. They found that the bryophyte flora of the sinkholes was very different from that of the Puerto Rican forests and considered them to be centers for diversity in the area. Pérez and Jesús (2009) reported new bryophyte species from sinkholes in old-growth forest fragments in Puerto Rico. Allred (1998) rediscovered the tiny moss ***Fissidens littlei*** (Figure 141) in a sinkhole in New Mexico, USA.

Figure 141. ***Fissidens littlei***, a rare, tiny moss found in a sinkhole in New Mexico, USA. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Other rare surprises may delight the explorer. In the Alpena, Michigan, USA, limestone sinks, Robinson and Wells (1956) found ***Mannia sibirica*** (see Figure 113-Figure 115), ***Seligeria calcarea*** (Figure 142-Figure 143), and ***Tritomaria scitula*** (Figure 87), all new for Michigan. In all, there were 110 species of bryophytes in six sinks. Later Miller and Vitt (1970) found ***Orthotrichum pallens*** (Figure 144) in sinkholes in Alpena County – a new species for the eastern part of North America. Priwer (1979) reported that bryophytes were dominant in number of species in these sinks, and that she did not find rare species of tracheophytes.

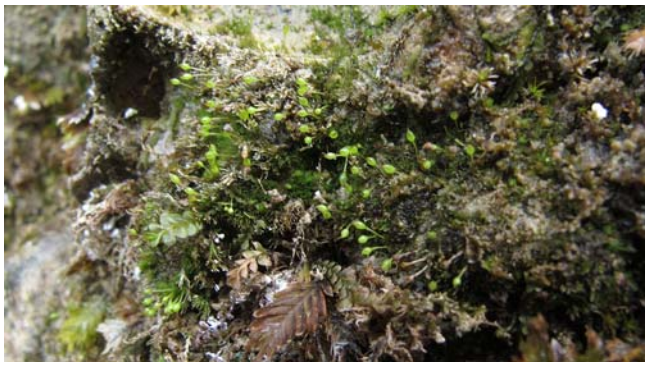

Figure 142. ***Seligeria calcarea*** with capsules, a species that occurs in the Alpena limestone sinks, Michigan, USA. Photo by Michael Lüth, with permission.

Figure 143. ***Seligeria calcarea*** with capsules, on stone. Photo by Brian Eversham, with permission.

Figure 144. ***Orthotrichum pallens*** with capsules; its occurrence in sinkholes in Alpena County, Michigan, USA, represented a new species for the eastern part of North America. Photo by Hermann Schachner, through Creative Commons.

In New Zealand, ***Timmia norvegica*** (Figure 145) occupies sinkholes on rock where there is seepage and calcareous detritus over marble (Horton & Bartlett 1983). This species is one of the bipolar species whose distributions are hard to explain.

Figure 145. ***Timmia norvegica***, a species that occurs on seepage rocks in calcareous sinkholes in New Zealand. Photo by Hermann Schachner, through Creative Commons.

Cao *et al*. (2020) described the relationship of the bryophytes to the microbial communities of sinks in the Guizhou Province, China. They found 145 species of bryophytes in the sinks, five of which were highly drought tolerant, including ***Eurohypnum leptothallum***, ***Hyophila involuta*** (Figure 146-Figure 147), and ***Racopilum cuspidigerum*** (Figure 148). They found that both moss species and the karst rocky desertification types affect the microbial communities, but that the moss species had the much stronger effect on the microbial diversity. Bacteria species composition changed strongly between mosses and drought resistance factors. Hence, bryophytes play a strong role in these communities.

Figure 146. ***Hyophila involuta*** wet, a highly drought-tolerant moss found in karst sinks in Guizhou Province, China. Photo by Bob Klips, with permission.

Figure 147. ***Hyophila involuta*** dry, a drought-tolerant species that survives on dry vertical rock surfaces. Photo by Bob Klips, with permission.

Figure 148. ***Racopilum cuspidigerum***, a highly drought-tolerant moss found in karst sinks in Guizhou Province, China. Photo by Andrew Thornhill, through Creative Commons.

Like so many of the richest bryophyte sites, sinkholes are subject to human disturbance (Liu *et al*. 2019). As refugia, the sinkholes play a crucial role in retaining many rare species, at least at the local level. As you might expect, the number of species in undisturbed sinkholes was considerably higher than in those affected by tourism or farming. Others, sadly, are used as garbage dumps.

Karstification

Karst (type of topography formed from dissolution of soluble rocks such as limestone, dolomite, and gypsum; characterized by underground drainage systems with sinkholes and caves) topography provides a variety of cave-like small and large spaces where bryophyte can live.

Šmarda (1947) recorded the presence of ***Distichium capillaceum*** (Figure 36-Figure 37) and ***Timmia bavarica*** (Figure 149) at the bottom of the deep karstic Macocha Chasm in the Czech Republic, thriving in little light but a moist environment with basic soil.

Figure 149. ***Timmia bavarica***, a species that grows at the bottom of the deep karstic Macocha Chasm in the Czech Republic. Photo by Hugues Tinguy, through Creative Commons.

Jia *et al*. (2014) explored the role of karst bryophytes and their local occupancy. They found 33 bryophytes in their study area in a Guizhou mountain area of China. In particular, they found that bryophytes were important in storing water, becoming saturated at 849-1474% of dry weight. Soil absorption ranged 464-1025%. Furthermore, they absorbed the heavy metals Pb, Zn, and Cd, with concentrations 2.25, 3.98, and 2.49 times that in their substrates, respectively. The concentrations in the bryophytes were not significantly correlated with that in their substrate. The researchers concluded that bryophytes had an important role both in providing a water reserve and in absorbing heavy metals from automotive exhaust. The water absorption helps to stabilize the road slopes in the karst area. Wu *et al*. (2019) described the vertical distribution of the **Hypopterygiaceae** and the environmental factors influencing that distribution in a karst sinkhole in China.

Bryokarst

That's right. Bryophytes contribute to karstification (Meng *et al*. 2019). Meng and coworkers explained that bryophytes can act as physical forces, including expansion, curling, freezing, and thawing (Figure 150-Figure 151). These are most evident under alternating wet and dry conditions and can destroy rock. They also can destroy rocks through metabolic secretions and the H_2CO_3 formed using the CO_2 expelled in respiration.

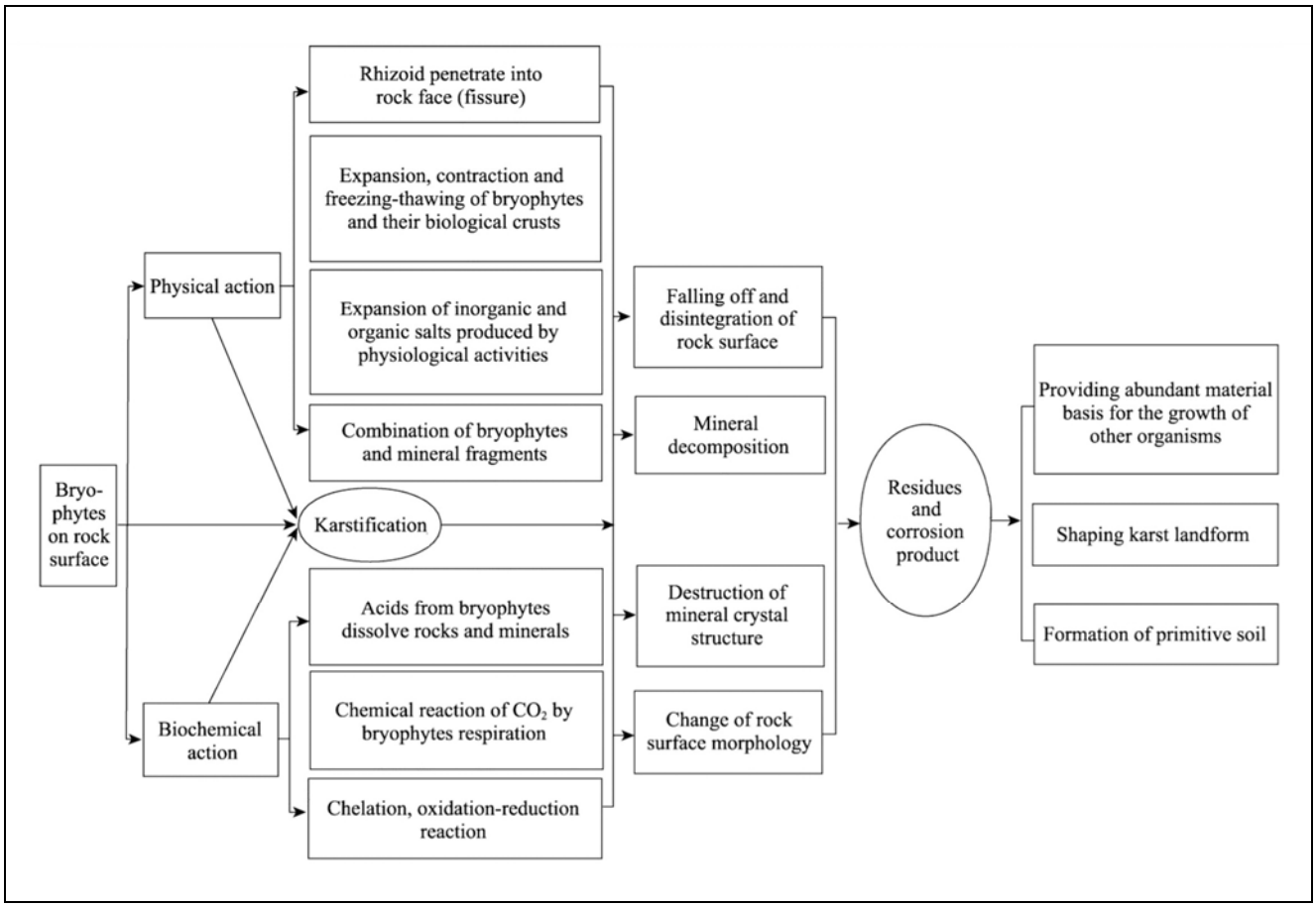

Figure 150. Flowchart showing bryophyte role in karstification. Mosses on the rock surface use physical and biochemical action to destroy and corrode the rock, change the rock surface morphology, and form the karst microtopography. The dissolved products are deposited to form the original soil. Modified from Meng *et al*. 2019.

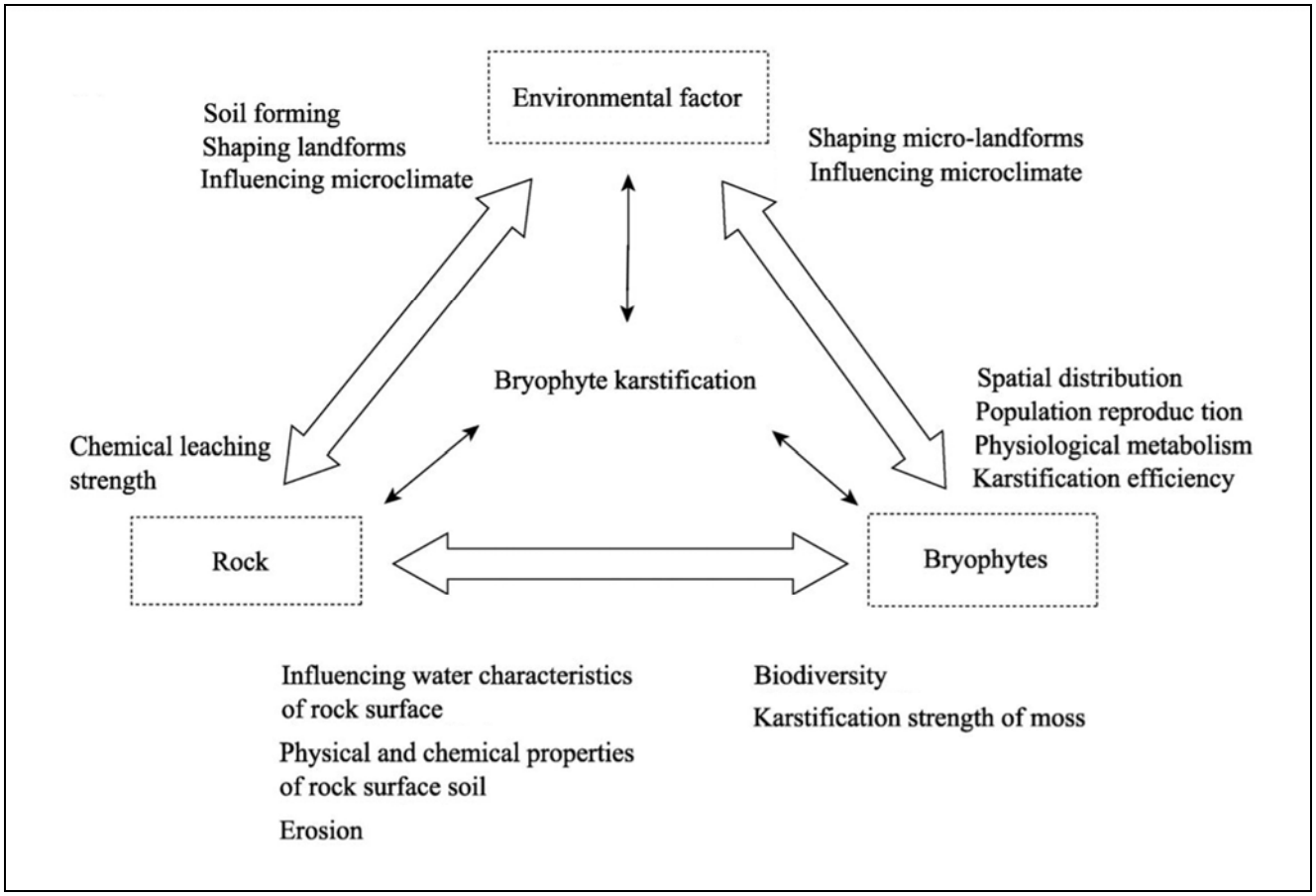

Figure 151. Three-way circulation interaction modified from Meng *et al*. (2019). The bryophytes, environmental factors, and rock promote and restrain each other in the karstification process. The environmental factors and rock affect the karstification process and its efficiency by controlling the community characteristics, morphology, physiological processes, genes, and other bryophyte factors. The resulting lithology, composition, occurrence of rock, and the improvement of the bryophytes on the rock surface microhabitat (temperature, humidity, light, soil fertility, microbes) are closely related to the rate of karstification.

Zhang *et al*. (1996) described four types of **bryokarst** deposition from caves (drop bryophytes-tufa, waterfall bryophyte-tufa, seasonal river bryophyte-tufa, and phototropism bryophytes-scale) in the Huangguoshu area of China, based on light, water availability, and bryophyte growth. They also identified four forms of bryophyte corrosions: corrosional hole, corrosional spot, corrosional block, and corrosional filament. These caves had 59 species of bryophytes in 43 genera.

Pentecost (1987) enumerated the annual growth rates of some mosses associated with tufa formation: ***Palustriella commutata*** (Figure 152), 1-4 mm; ***Eucladium verticillatum*** (Figure 11), 2-3 mm; ***Hymenostylium recurvirostrum*** (Figure 153-Figure 155), 1-3 mm; ***Platyhypnidium riparioides*** (Figure 156), *ca.* 30 mm. Pentecost (1996) followed this study with one on the role of photosynthesis vs other factors in the karstification process. ***Palustriella commutata*** and ***Eucladium verticillatum*** both deposited 6-12% of the carbonate through photosynthesis. In addition, 10-20% was deposited through evaporation and 70-80% through gas evasion.

Figure 152. ***Palustriella commutata***, a moss that grows 1-4 mm per year in tufa formation. Photo by J. C. Schou, with permission.

Figure 153. ***Hymenostylium recurvirostrum*** habit, a moss associated with tufa formation. Photo by Hermann Shachner, through Creative Commons.

Figure 154. ***Hymenostylium recurvirostrum*** on side of cliff, with icicles. Photo by Bob Klips, with permission.

Figure 155. ***Hymenostylium recurvirostrum*** showing color of lower portions and three growth regions distinguishable by color changes. This species grows 1-3 mm per year in tufa formations. Photo by Hermann Schachner, through Creative Commons.

Figure 156. ***Platyhypnidium riparioides***, a moss that grows ~30 mm per year in tufa formation. Photo by Hermann Schachner, through Creative Commons.

Lyons and Kelly (2020) pointed out the paucity of knowledge regarding deposition rate of tufa or the growth rates of involved bryophytes living in petrifying springs. Using fixed bar markers, they measured the heights of bryophytes at six petrifying springs in Ireland. They found that tufa deposits increased 20.5 ± 1.1 mm yr^{-1}. The moss ***Palustriella commutata*** (Figure 152) worked together with the surface water to increase the annual deposition of tufa by 5.7 ± 1.9 mm. Unvegetated tufa achieved a growth of only 16.5 ± 3.0 mm yr^{-1}. Thus, with an annual growth of 27.6 ± 1.9 mm, ***Palustriella commutata*** outgrows the unvegetated tufa growth. The smaller mosses ***Didymodon tophaceus*** (Figure 157-Figure 158) and ***Eucladium verticillatum*** (Figure 11) grew only 9.1 ± 1.6 mm yr^{-1} and 9.5 ± 1.3 mm yr^{-1}, respectively, thus being less important in tufa formation; they were typically displaced by ***Palustriella commutata*** through competition.

Figure 157. ***Didymodon tophaceus*** habitat at cliff base. Photo by Jean Faubert, with permission.

Figure 158. ***Didymodon tophaceus***, a tufa moss that grows at a mean of 9.1 ± 1.6 mm yr^{-1}. Photo by David T. Holyoak, with permission.

Waterfall Caves

Waterfalls often fall over ledges, creating a curtain in front of shallow caves. These caves are typically shaded and moist, with rock surfaces (Figure 159).

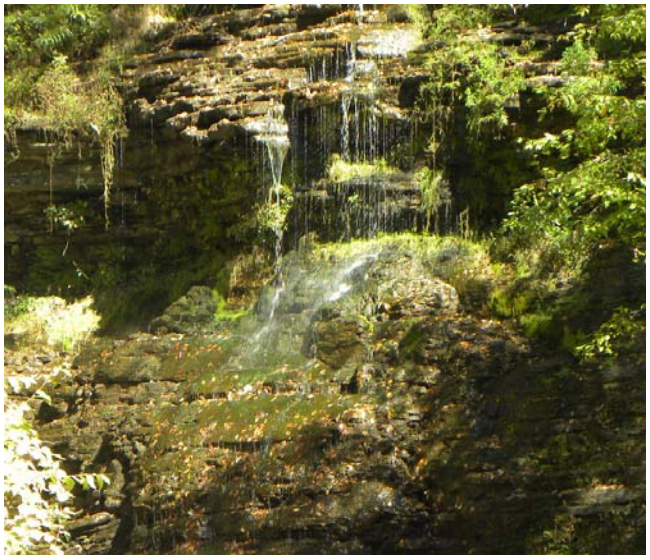

Figure 159. Waterfall in West Virginia, USA, with bryophytes and ferns growing on the ledges behind the water. Photo by Eileen Dumire, with permission.

I have seen ***Conocephalum*** (Figure 126, Figure 160-Figure 161) species several times in the shallow caves behinds waterfalls (Figure 162). Although these were usually named as ***Conocephalum conicum*** (Figure 126) in North America, we have recently realized that these are really ***Conocephalum salebrosum*** (Figure 160-Figure 161), a species with much larger thalli than those of the former. This habitat occurs in the Keweenaw Peninsula of Michigan, USA, and at Hocking Hills, Ohio, USA. The latter also has a number of small caves where the species is abundant.

Figure 160. ***Conocephalum salebrosum*** under overhanging rocks, a common liverwort in rock canyons and behind waterfalls. Photo by Claire Halpin, with permission.

Figure 161. ***Conocephalum salebrosum***, a common species in cool, shaded, damp places in the US. Photo by Claire Halpin, with permission.

Figure 162. Scot Falls, Michigan, USA, with cave behind waterfalls. Bryophytes occur on the ceiling of the cave. Photo by Janice Glime.

Higuchi *et al*. (2020) reported ***Fissidens geminiflorus***, ***F. nobilis*** (Figure 163), and ***Timmiella anomala*** (Figure 164) on wet stones in a cave behind a waterfall in Cambodia.

Figure 163. ***Fissidens nobilis***, a moss that lives on wet stones behind a waterfall in Cambodia. Photo by Janice Glime.

Figure 164. ***Timmiella anomala***, a moss that lives on wet stones behind a waterfall in Cambodia. Photo from Earth.com, with permission.

Natalie Cleavitt found ***Haplodontium macrocarpum*** (Figure 165) in Mountain Park, Alberta, Canada, where it occurs on the underside of overhangs associated with ephemeral waterfalls (Dale Vitt, pers. comm. 4 August 2021).

Figure 165. ***Haplodontium macrocarpum*** on cave wall, a species that also occurs under overhangs of ephemeral waterfalls. Photo by René J. Belland, with permission.

Townsend (2006) reported ***Epipterygium tozeri*** (Figure 166) from Kenya in a cave behind a waterfall.

Figure 166. ***Epipterygium tozeri***, a species that grows in a cave behind a waterfall in Kenya. Photo by Hugues Tinguy, with permission.

Other Bryophyte Roles

Building and destroying cave formations are not the only roles of bryophytes in caves. They increase the diversity of stalactites and stalagmites (Mulec 2018). They can be diversity hotspots. Bryophytes increase the loss of water by 81.2 times and absorption by 8.1 times, the highest compared to the algae (18.8 and 1.6) and lichens 2.9 and 19.1) (Cao & Yuan 1999). Bryophytes also prolong the period of water loss by 610%, but do not extend the period of absorption. This improves the water holding by 57.2 times! This increases the activity of the carbon cycle on the rock surface, affection rates of corrosion under the growths.

Pentecost (1999) notes the importance of bryophytes, along with algae, in stabilizing ephemeral sand ripples on steep rock surfaces in the UK. Fu and Zhang (2010) identified four types of bryophyte erosions on limestone: erosional fusion, erosional plaques, erosional bands, and erosional blocks.

Ren *et al*. (2010) found that the rare and endangered flowering plant ***Primulina tabacum*** (Figure 167) is found

only at cave entrances of a small number of karst caves in southern China. The researchers transplanted small plants of this species to several new cave entrances. The only seedlings that survived were associated with the moss ***Gymnostomiella longinervis*** (Figure 168), performing well under the cover of the moss. It appears that the moss nurse plant is necessary for the success of ***P. tabacum***.

Figure 167. ***Primulina linearifolia*** × ***Primulina tabacum***; ***Primula tabacum*** seems to require the moss ***Gymnostomiella longinervis*** to be successful in karst cave entrances. Photo by Kenpei, through Creative Commons.

Figure 168. ***Gymnostomiella longinervis*** on bark, a moss that helps ***Primulina tabacum*** succeed in entrances of karst caves in southern China. Photo through Creative Commons.

Submerged cave bryophytes can serve as substrate for the diatom ***Pinnularia borealis*** (Figure 169) (Czerwik-Marcinkowska *et al*. 2019). The cyanobacterial ***Gloeocapsa atrata*** (Figure 170) occurs frequently on mosses on wet cave wall rocks in the Glowoniowa Nyża Cave. The latter species can contribute to nitrogen fixation, thus increasing the levels of usable nitrogen in the cave.

Figure 169. ***Pinnularia borealis***, a diatom that often uses bryophytes as a substrate in caves. Photo from BELSPO, with online permission.

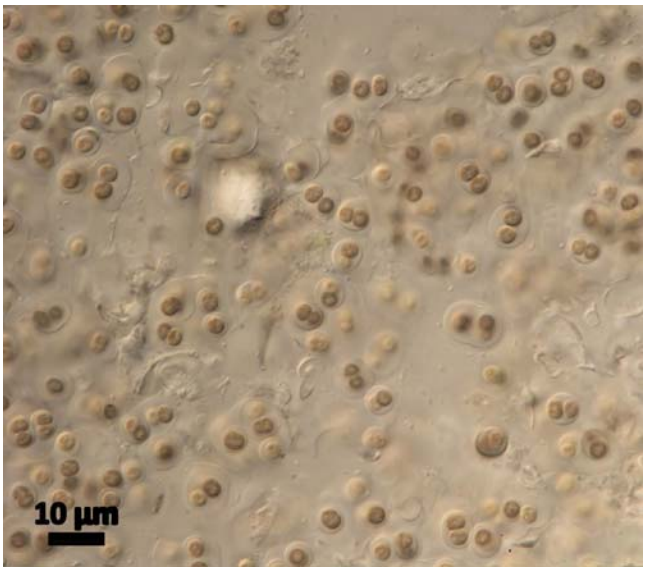

Figure 170. ***Gloeocapsa atrata***, a member of **Cyanobacteria** that fixes nitrogen and can occur on mosses in caves. Photo by Sergei Shalygin, through Creative Commons.

Cave Fauna Interactions with Bryophytes

Galas *et al*. (1996) found that the decay rates of two seed plants and of moss were all slow in a mountain cave in the Tatra Mts., Poland. They attributed this slowness to the absense of large shredders in the cave. The energy released through respiration by microorganisms on the moss was higher than that released from microorganisms on sorb and alder litter.

Cao and Yuan (1999) reported that the water holding by evaporation of carbonate rock increases 81.3 times and water absorption by 8.1 times for mosses compared to relative fresh rock samples. The amount of water holding by the rock improves 57.2 times with mosses on them.

Copepods

In Japan, Iwatsuki and Ueno (1959) found the fern ***Cyrtomium fortunei*** (Figure 171) and moss ***Fissidens geminiflorus*** (see Figure 128, Figure 134, Figure 141, Figure 163) to be dominant, sometimes obtaining a "full growth." They also found cave fauna that associated with the mosses, including the harpacticoid copepod ***Bryocamptus zschokkei*** (Figure 172), the latter occurring in a carpet of ***Fissidens geminiflorus***.

Figure 171. ***Cyrtomium fortunei***, a dominant fern in some Japanese caves. Photo by Bing Liu, Kew Plants of the World, through Creative Commons.

Figure 172. ***Bryocamptus zschokkei***, a harpacticoid copepod associated with mosses in caves in Japan. Photo by Joe Connolly, through Creative Commons.

Stoch (2000) reviewed the aquatic fauna of caves in northern Italy, including some that are part of the bryophyte fauna. Watiroyram *et al*. (2012) found 11 species of the copepod ***Bryocyclops*** (Figure 173) from wet mosses in caves.

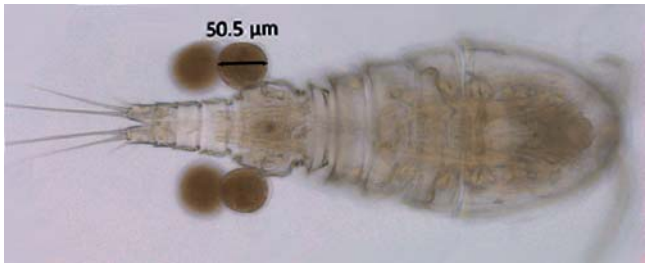

Figure 173. ***Bryocyclops*** sp.; 11 species in this genus occur among mosses caves in Italy. Photo by Watiroyram, S., through Creative Commons.

Tardigrades

One of the best places to look for tardigrades is nestled among the leaves of bryophytes. Cave-dwelling tardigrades are no exception to that (Bartels & Nelson 2007). This affinity for bryophytes, particularly mosses, includes a special adaptation for feeding on the mosses [Tardigrada (Water Bears) 2005]. Members of **Echiniscidae** are adapted to this mode of living by having a long stylet that can penetrate the moss cell wall and suck out the cell contents. In addition to eating moss cell contents, the bryophyte dwellers might eat epiphytic diatoms and bacteria from the moss surface.

Insects

In addition to the copepod, Iwatsuki and Ueno (1959) found the troglophilous fly ***Exechia*** sp. (fungus fly; Figure 174) associated with the mosses in a cave in Japan.

Figure 174. ***Exechia fusca*** adult, a fungus fly similar to those that occur with mosses in a Japanese cave. Photo by Jostein Kjaerandsen, through Creative Commons.

Even in Death Valley. California, USA, caves can serve as a refuge for insects. Hungerford (1917) reported the true bug ***Mesovelia mulsanti*** (Figure 175) from among mosses in a hot spring cave. Later, Polhemus and

Chapman (1979) reported ***Mesovelia amoena*** (Figure 176) on moss-covered rocks in hot spring caves, also in Death Valley. This species is parthenogenetic in Hawaii, a trait that might make reproduction easier in caves. Kamp (1970) reported cave grasshoppers that were associated with bryophytes in caves in the western United States.

Figure 175. ***Mesovelia mulsanti***, a true bug that occurs among mosses in a hot spring cave in Death Valley, California, USA. Photo by Matt Bertone, through Creative Commons.

Figure 176. ***Mesovelia amoena*** wingless female, a species that lives on moss-covered rocks in hot spring caves in Death Valley, California, USA. Photo by Claudia Moreno-R., Wendy Molina-J., Juliana Barbosa, and Filipe Moreira, through Creative Commons.

In icefields, ice bugs (**Grylloblattodea**) lay their eggs in the soil or mosses (Ramel 2015). They hide under stones during the ay and prefer low temperatures. These also occur in caves in Korea. These insects are extremophiles. In the Oregon Caves in the Klamath Mountains of Oregon and California, USA, Schoville (2012) found three new species of **Grylloblattodea**: ***Grylloblatta oregonensis*** (Figure 177), ***G. siskiyouensis***, and ***G. marmoreus***. This species occupies the dark zone and twilight zone of caves. Their relationships to the bryophytes in the caves is not known, but they may have the same uses for egg laying as members of the genus found in Korea.

Figure 177. ***Grylloblatta oregonensis***, a new species discovered in Oregon caves in the twilight and dark zones. Other members of the genus use mosses for egg laying, but egg laying has not been described in this species. Photo through Creative Commons.

There are two tiphiid wasp species (***Tiphia andersoni*** and ***T. nona*** – see Figure 178) that are able to hibernate beneath rocks surrounded by mosses in caves (Wynne 2013). Moss gardens in lava tubes have the most developed bryophyte communities (Lindsey 1951) and present a biologically unique bryophyte community (Lightfoot *et al.* 1994; Wynne 2013). This includes a high arthropod biological diversity (Wynne 2013).

Figure 178. ***Tiphia*** sp. Several species in the genus hibernate beneath rocks surrounded by mosses in caves. Photo by XPDA, through Creative Commons.

Other Arthropods

Importantly, this habitat has been identified as supporting at least two presumed relict species (Lightfoot *et al*. 1994, this paper) and high arthropod biological diversity (Wynne 2013).

Benedict (1979) found that the pseudoscorpion ***Apochthonius forbesi*** (see Figure 179) benefits from the mossy litter layer in sinks in Oregon, USA. This species was described as a new species based on populations in a lava tube sink where it lived at the cold air trap that

retained permanent ice but a mossy litter layer. ***Syarinus*** (Figure 180) was an accompanying species in this habitat.

Figure 179. ***Apochthonius diabolus***; ***Apochthonius forbesi*** lives in lava tube sinks with permanent ice and a mossy litter layer. Photo by Steve Taylor and Mike Slay, through Creative Commons.

Figure 180. ***Syarinus*** sp.; a species in this genus of pseudoscorpion accompanies ***Apochthonius forbesi*** in lava tube sinks with permanent ice and a mossy litter layer. Photo by P. M. Brousseau, through Creative Commons.

Wynne and Shear (2016) found a new millipede species, ***Austrotyla awishoshola*** in "cave moss gardens" in New Mexico, USA. The millipedes need mesic conditions, and these are limited in these caves to locations with mosses. As is the case for mosses, the caves serve as refugia for insects and other fauna that found refuge here following the end of the more moist Pleistocene. Such refugia are known in other parts of the world where mosses have become the restricted environment for relict species (Benedict 1979; Wynne *et al.* 2014).

For the invertebrate cave fauna, the bryophytes provide opportunities for a high diversity. They are also home to the relict spider ***Lepthyphantes turbatrix*** (Figure 181) (Wynne 2013).

Figure 181. ***Lepthyphantes turbatrix***, a spider that uses cave mosses as a home. Photo by Tom Murray, through Creative Commons.

Salamanders

Some salamanders are especially adapted to cave living. Others benefit from the cooler, more moist conditions. Gorman and Camp (1953) found the new species ***Hydromantes shastae*** (Figure 182-Figure 183) under a mossy log at a cave entrance in California, USA. The salamander ***Aneides aeneus*** (Figure 184) is known to eat mosses (Lee & Norden 1973), although it may just be the result of foraging there for ants and spiders. This salamander has occurred in Bat Cave in Rutherford County, North Carolina, USA, and is also known from Cooper's Rock, West Virginia, where small caves or cave-like habitats can occur among the rocks.

Figure 182. ***Hydromantes shastae***, a species that includes mossy logs at a cave entrance as a hiding place. Photo by James Bettaso, USFWS, through public domain.

Figure 183. ***Hydromantes shastae*** showing a color form that is well adapted to a mossy habitat. Photo by John Clare, through Creative Commons.

Figure 184. ***Aneides aeneus***, a species known to eat mosses and hangs out among boulders and in caves. Photo by Alan Cressler, through public domain.

Frogs

In the borderland between Venezuela and Brazil, Myers and Donnelly (1997) found the frog ***Eleutherodactylus cavernibardus*** (*cavernibardus* means cave singer; see Figure 185) calling during the day in local caves formed by granite boulders or on mosses. It is likely that the frogs use both of these habitats.

Figure 185. *Eleutherodactylus planirostris*; ***Eleutherodactylus cavernibardus*** calls from mosses in caves. Photo by Todd Pierson <www.discoverlife.org>, with permission.

Angulo *et al*. (2003) reported ***Stefania riae*** in a sinkhole at Sarisariñama tepui in Peru. The habitat lacked either flowing or standing water, but the walls of rocks, crevices, and caves were moist and mossy, presumably providing moisture for the frogs, as suggested by Barrio-Amorós and Fuentes (2003).

Reptiles

Little seems to be known about the role of bryophytes for cave reptiles. Storey (2006) reported that reptiles seek refuge in winter in locations such as caves, burrows, grass, or moss hummocks. It might be worthwhile to look for some of the smaller reptiles among the cave mosses in winter. If nothing else, the mosses might be a source of invertebrate food. I wonder if lizards and snakes find the older sinkholes in Florida suitable.

Birds

Even birds can benefit from bryophytes in caves. In Brazil the White-collard Swift [***Streptoprocne zonaris*** (Figure 186)] typically breeds in wet caves next to waterfalls (Figure 187) (Biancalana 2014). Nests are made mostly of bryophytes (Figure 188). The birds returned to the same nest sites in subsequent years.

Figure 186. ***Streptoprocne zonaris*** on rock wall. Photo by Amesac, through Creative Commons.

Figure 187. ***Streptoprocne zonaris*** behind waterfall, where it typically builds nests mostly of mosses. Photo by Donald Hobern, through Creative Commons.

Figure 188. ***Streptoprocne zonaris*** on nest made of mosses. Photo by Sesernam, through Creative Commons.

On the young island of Surtsey, Iceland, a Herring Gull-Glaucous Gull hybrid pair [***Larus argentatus*** (Figure 189) - ***Larus hyperboreus*** (Figure 190)] nested in a small collapsed cave, using primarily the moss ***Racomitrium*** (Figure 31-Figure 32) as nesting material (Olafsson 1982). When a Berlese funnel was used to search the nest for arthropods, only a single specimen, that of an **acarid** (mites & ticks) was revealed.

Figure 189. ***Larus argentatus***; a hybrid of this species uses ***Racomitrium*** as nesting material in the volcanic island of Surtsey, Iceland, in a collapsed cave. Photo by Kulac, through Creative Commons.

Figure 190. ***Larus hyperboreus*** and offspring; a hybrid of this species uses ***Racomitrium*** as nesting material in the volcanic island of Surtsey, Iceland, in a collapsed cave. Photo by A. Weith, through Creative Commons.

The Biscutate Swift (***Streptoprocne biscutata***; Figure 191) has been studied at its home in a cave in the Paraná State, southern Brazil (Pichorim 2002). The birds use bryophytes, among other plants and lichens, to build its nests. When the birds are nesting in the cave, the cave floor has abundant moss and lichen fragments. The birds collect these materials for nesting and at times even pull pieces of bryophytes from the vertical wall. The unusual observation was that they appeared to chew the fragments soon afterwards. Observations of a viscous substance in the moss fragments in the nests suggest that the chewing was practiced to add the saliva. Fragments in the nests included the liverworts ***Frullania brasiliensis*** (Figure 192) (most common – 14 of 23 nests), ***Herbertus*** sp. (Figure 193), ***Lejeunea flava*** (Figure 194), ***Omphalanthus filiformis*** (Figure 195), ***Plagiochila*** sp. (see Figure 74), and ***Plagiochila rutilans*** (see Figure 74), and the mosses ***Campylopus*** sp. (see Figure 196), ***Campylopus aemulans*** (Figure 196), ***Leucobryum crispum*** (Figure 197), ***Leucoloma*** sp. (Figure 198), ***Macromitrium punctatum*** (Figure 199), ***Phyllogonium viride*** (Figure 200), ***Polytrichum juniperinum*** (Figure 47-Figure 48), ***Porotrichum longirostre*** (see Figure 201), ***Rhacocarpus*** sp. (Figure 202), ***Schlotheimia rugifolia*** (Figure 203), ***Schlotheimia tecta*** (Figure 204), ***Sematophyllum subpinnatum*** (see Figure 205), ***Squamidium leucotrichum*** (Figure 206), ***Syrrhopodon prolifer*** (Figure 207), and ***Zelometeorium recurvifolium*** (Figure 208).

Figure 191. ***Streptoprocne biscutata***; when this species nests in caves in Brazil, it uses mosses available from the cave floor as nesting material. Image by Joseph Wolf and J. W. Wood, through public domain.

Figure 192. ***Frullania brasiliensis***, a liverwort used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Jan-Peter Frahm, with permission.

Figure 193. ***Herbertus aduncus*** subsp. ***hutchinsiae***; a species of ***Herbertus*** is used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by J. Barry Stewart, with permission.

Figure 194. ***Lejeunea flava***, a liverwort used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Rory Hodd, with permission.

Figure 195. ***Omphalanthus filiformis***, a liverwort used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Michael Lüth, with permission.

Figure 196. ***Campylopus aemulans***, a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Michael Lüth, with permission.

Figure 197. ***Leucobryum crispum***, a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Claudio Delgadillo-Moya, with permission.

Figure 198. ***Leucoloma*** sp., a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Shyamal L., through Creative Commons.

Figure 199. ***Macromitrium punctatum***, a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Maarta Luz Uribe, through Creative Commons.

Figure 200. ***Phyllogonium viride*** with capsules, a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by George Shepherd, with online permission.

Figure 201. ***Porotrichum bigelowii*** branch; ***Porotrichum longirostre*** is a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Brian Starzomski, through Creative Commons.

Figure 202. ***Rhacocarpus purpurascens***; a species of ***Rhacocarpus*** is used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Jan-Peter Frahm, with permission.

Figure 203. ***Schlotheimia rugifolia***,a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Juan David Parra, through Creative Commons.

Figure 204. ***Schlotheimia tecta***, a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Michael Lüth, with permission.

Figure 205. ***Sematophyllum*** sp.; ***Sematophyllum subpinnatum*** is used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Michael Lüth, with permission.

Figure 206. ***Squamidium leucotrichum***, a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Michael Lüth, with permission.

Figure 207. ***Syrrhopodon prolifer*** var. ***scaber***, a moss species used in the nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Michael Lüth, with permission.

Figure 208. ***Zelometeorium patulum***; ***Zelometeorium recurvifolium*** is used in nests of the Biscutate Swift (***Streptoprocne biscutata***) in Brazilian caves. Photo by Michael Lüth, with permission.

Mammals

Several mammals use caves as their dens. The bear has perhaps the most influence on the bryophytes. The brown bear (***Ursus arctos***; Figure 209) includes mosses to line its den (Czerwik-Marcinkowska *et al*. 2019). This can bring moss spores and fragments into the cave for possible establishment and growth there.

Figure 209. ***Ursus arctos*** (brown bear) running, a species that uses mosses to line its den in caves. Photo by Malene Thyssen, through Creative Commons.

Sampling Methods

Bryophyte sampling methods have varied among researchers. Many researchers sought only to document the flora, with no attempt to quantify species. Li *et al*. (2020a) used 8 plots, 10 x 10 m, in each section of a sinkhole, totalling 80 plots. In addition to assessing the bryophyte flora, they measured depth, *p*H, light level, humidity, temperature, and slope, making it possible to find correlations.

Although caves have more constant conditions than those found outside the cave, conditions nevertheless vary between caves and within the caves. Poulson and Culver (1969) measured evaporative rate, substrate moisture, substrate organic content, predictability and stability of food and microclimate, substrate diversity, and intensity of flooding in Mammoth Cave, Kentucky, USA. They found that arthropod diversity exhibited significant correlations with substrate diversity, substrate organic content, and intensity of flooding. To this list, light intensity must be added for photosynthetic organisms, and even for some cave animals. Thus it is instructive to measure these conditions.

Nakanishi (2002) established 14 quadrats in a light intensity gradient. The quadrats were 20 x 20 cm and restricted to clayey soils; they assessed the bryophytes using the Braun-Blanquet method.

Pakeman *et al*. (2019) used Attribute values based on the Ellenberg values (see Schaffers & Sýkora 2000) to describe the nitrogen, light, and moisture in bryophyte habitats in Scotland. These have been used in some cave studies for similar purposes.

Summary

Cave-like conditions are present in a variety of landforms. Among these are mine shafts, subways, fissures, minicaves among rocks and at the base of boulders, among scree, ice caves, windholes, sinkholes, behind water falls, and in animal burrows. These differ in available light, substrate, moisture, nutrients, *p*H, and toxic substances such as pollutants.

Mine shafts are often vertical structures with light diminishing with depth. The exposure of the substrate to the ore being mined can be a toxic factor. There are few published records of bryophytes in mines, but the presence of the ubiquitous ***Ceratodon purpureus*** is a not surprising find.

Subways are typically well lit and may have some of the same species as caves. Because the subway age is known, it can provide a suitable laboratory for studying colonization rates.

Small fissures often support surface bryophytes due to their collection of nutrients and soil and a greater moisture-holding ability than the rock surface. Larger fissures as found in lava fields, geothermal areas, and some large rock formations may support bryophytes for a short distance into the fissure, again dependent on light, moisture, and substrate type. Such fissures offer protection from direct sun, reducing sun bleaching, photoinhibition, and drying.

Among the lava rocks and fissures one can find ***Saelania glaucescens***, ***Distichium inclinatum***, and ***Schistostega pennata***, but much more study is needed to relate the bryophyte species to the cave-like locations vs the surface locations. The scree presents a similar problem, although there are more studies that list species found there. Despite the shallowness of its caves, they can provide cool refugia in otherwise hot, dry, exposed fields of rock.

Ice caves typically do not support bryophytes, but ***Heterocladium heteropterum*** and ***Cyrtomnium hymenophylloides*** are known in ice caves. On the other hand, the cool air from these caves, especially in summer, can alter the climate and bryophyte composition outside the cave. Windholes have similar effects, providing a cool cave, but also cooling the area near the cave. These cool refugia permit Arctic species to live at much lower latitudes, occurring there as disjuncts.

Sinkholes have much in common with caves, including low light and usually greater moisture. However, they experience seasonal changes much like the surrounding forest. They have many species on their walls that coincide with those in caves. Their responses to these conditions are similar to those of bryophytes in caves: sterility, leaf elongation, longer internodes, elongation of cells, and disappearance or attenuation of the rib or costa. The protection provided by the sinkhole can result in a greater species diversity than that found in the surrounding forest.

Karstification is a process of dissolution of soluble rocks, characterized by underground drainage systems with sinkholes and caves. Bryophytes can play a role in the process, creating stalactites and stalagmites by the accumulation of $CaCO_3$ around some bryophyte

species, particularly accomplished by ***Eucladium verticillatum***. The bryophytes can also destroy rock formations by exuding organic acids or holding water that makes breakdown of the rock easier.

Waterfall caves maintain a moist habitat while reducing light intensity. They seem to be an especially suitable habitat for some ***Conocephalum*** species. There are probably many records for this habitat, but they are often embedded in studies of the larger area without specific separation of the cave area.

Bryophytes in caves can serve various roles for the cave fauna. For copepods, tardigrades, insects, and other arthropods, they provide cover and moisture and sometimes food. Salamanders may forage there or sometimes use the bryophytes for cover and moisture conservation. Frogs can use them as calling locations and sources of moisture. Reptiles can occasionally be found there. Birds use them for nesting material, as do some mammals, especially bears.

Cave sampling is useful to determine gradient effects on species composition. This sampling typically uses quadrats (plots) of 10 x 10 cm or larger. A distance transect is useful for assessing gradient effects. It is useful to measure both physical and chemical parameters along these transects.

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CHAPTER 1

HOUSEHOLD AND PERSONAL USES

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CHAPTER 1
HOUSEHOLD AND PERSONAL USES

Figure 1. Mosses being sold along with fruits and vegetables in a marketplace in China. Photo courtesy of Eric Harris.

Household Uses

I think every bryologist must have been asked "what good are they?" The small size, difficult taxonomy, and inconspicuous position in the ecosystem of bryophytes have caused most people to ignore bryophytes. Nevertheless, the rate at which bryophytes are being harvested from some of our national forests in North America and elsewhere suggests they are useful for something. In the high mountains of Malaysia, simply collecting mosses as a novel pillow filler (Kuen 2002) has caused vast areas of bryophyte destruction in a pristine forest. In New Zealand the small number of peatlands is diminishing from horticultural usage. In the southeastern United States, sheet mosses are removed by the truckload, and in the Pacific Northwest epiphytes are disappearing from old growth forests.

Although ***Sphagnum*** (Figure 3) seems to be the most commonly used bryophyte, it is not the only moss with endearing, and enduring, qualities. Including all the known uses of bryophytes, Harris (2008) found that the most commonly mentioned uses of bryophytes are those of ***Marchantia*** (Figure 2), ***Sphagnum*** (Figure 3), and ***Polytrichum*** (Figure 10). Other genera used in more than two countries are ***Conocephalum*** (Figure 4), ***Climacium*** (Figure 64), ***Hylocomium*** (Figure 16), ***Hypnum*** (Figure 5), ***Rhytidiadelphus*** (Figure 17, Figure 118), ***Thuidium*** (Figure 22, Figure 42), ***Antitrichia*** (Figure 104, Figure 111)***, Bryum*** (Figure 6)***, Dicranum*** (Figure 13)***, Fontinalis*** (Figure 75)***, Funaria*** (Figure 89), ***Philonotis*** (Figure 7), ***Pleurozium*** (Figure 45-Figure 46), and ***Rhizomnium*** (Figure 8).

Durability and elasticity may have contributed to the Japanese use of ***Hypnum*** (Figure 5) to stuff balls and dolls (Pant & Tewari 1990). Others have used them for stuffing upholstery and hassocks (Thomas & Jackson 1985).

Figure 2. ***Marchantia polymorpha***, a species put into wine where it soaks up the wine and makes a tasty treat. Photo by Michael Lüth, with permission.

Figure 3. ***Sphagnum capillifolium***, on of many members of the genus with various human uses. Photo by Michael Lüth, with permission.

Figure 4. ***Conocephalum conicum***, a liverwort used in more than one country. Photo by Robert Klips, with permission.

Figure 5. ***Hypnum cupressiforme***, a commonly used moss around the world. Photo by Dick Haaksma, with permission.

Figure 6. ***Bryum argenteum***, member of a genus that is used in more than two countries. Photo by Michael Lüth, with permission.

Figure 7. ***Philonotis fontana***, member of a genus that is used in more than two countries. Photo by Michael Lüth, with permission.

Figure 8. ***Rhizomnium magnifolium***, a moss in a genus used in more than two countries. Photo by Janice Glime.

Robin Stevenson (pers. comm.) shared his surprise at finding a reference to moss use in the "Rough Guide to Moscow. "One of the main roads in central Moscow, which runs parallel to the Kremlin Gardens, separating them from the Lenin Library and the Arbat district, is Mokhovaya ulitsa or Moss Street. So named, apparently, because this is where moss (mokh) was formerly sold. This

moss was used as a caulking material for filling in chinks in wooden buildings, a use which is pretty well documented. However, it was also sold to put between the panes of glass in double-glazed windows."

Clearly, the use of mosses is not just a tale from the past (Welch 1948; Ando 1957, 1972). In the USA today, there are about 200 "mossers" (moss growers) (Epstein 1988), a testimony that the industry has not outlived its usefulness. The Chinese continue their tradition of using mosses and other herbals in medicines and food (Figure 1).

Furnishings

Imagine yourself in a remote village where there are no grocery stores and the nearest mall is 100 miles away by horseback. Villagers carry water on their heads, cushioned by a sirona, and bags of fruits wrapped in native moss. In your hut, you protect a fragile souvenir in a gentle bed of moss. Your mattress and pillow are stuffed with mosses. Mosses collect urine from pigs in the stall. And your child plays with a hand-made doll stuffed with moss. In these conditions, mosses take on an important role in your daily life.

In fact, mosses seem to be useful in maintaining structural integrity in a variety of materials. Siberian Eskimos roll up skins and freeze them into the shape of a sled runner (Figure 9), which they cover with a moss/water mix to protect the skins, smoothing them as they shape them onto the runners (R. Seppelt, pers. comm., based on "Man on the Rim" documentary; Wikipedia 2017). This makes a smoother ride.

Figure 9. Qamutiik with moss and ice on runners. Photo by Adolphus Greely, through public domain.

In India, mosses are used for door covers and smoke filters (Pant 1989) and the pharki – a door mat (Glime & Saxena 1991). In Sweden, ***Polytrichum commune*** (Figure 10) has likewise been used as a doormat (Hedenäs 1991). Their use as kindling is surely still valuable to campers (Thomas & Jackson 1985). Both ***Neckera crispa*** (Figure 11) and ***N. complanata*** (Figure 12) have been used as bedding in Europe (Dickson 2000).

Figure 10. ***Polytrichum commune***, a large moss used in making doormats, brooms, clothing, and other items. Photo by David T. Holyoak, with permission.

Figure 11. ***Neckera crispa***, a species that has been used in bedding in Europe. Photo by Malcolm Storey, through DiscoverLife.

Figure 12. ***Neckera complanata***, a species that has been used in bedding in Europe. Photo by Michael Lüth, with permission.

In some places, the past mixes in strange ways with the present. Among the Inuit at Pangnirtung in the Canadian North, electrical lines run to summer tents to power electric guitars while the tent is heated by ancient kudliks that burn

with a wick of moss (Crowe 1974). A number of mosses make ideal lamp wicks: ***Dicranum elongatum*** (Figure 13) by the Cree Indians, ***Racomitrium lanuginosum*** (Figure 14) by Labrador Eskimos (Bland 1971), and, of course, ***Sphagnum*** (Figure 3) (Crum 1988).

Figure 13. ***Dicranum elongatum***, a moss used as a wick by the Cree Indians. Photo by Michael Lüth, with permission.

Figure 14. ***Racomitrium lanuginosum***, a species used by the Cree Indians as a lamp wick. Photo by Janice Glime.

A rather unique new use is to create tables using mosses as photovoltaic cells (Figure 15) (Chandler 2012). Bio-Photo-Voltaic (BPV) technology strives to make use of biological materials to trap light energy and convert it to a usable form. The table has a futuristic look with more than 100 round cells with growing mosses in them and a lamp at the edge. The moss is not yet able to power the lamp, but it can power a small clock. Currently it can produce about 520 Joules (J) of energy per day – enough to power a laptop for 20 seconds!

Figure 15. Moss pots as photovoltaic cells. Photo from The hidden power of moss, through Creative Commons.

To create the power in the table, the mosses convert carbon dioxide, using sunlight, to create organic compounds (Biophotovoltaics 2015). Some of these compounds are released into the soil where bacteria break them down and free by-products, including electrons. Conductive fibers inside the moss table capture these electrons and can use them, generating a potential of 0.4-0.6 volts (V) and a current of 5-10 microamps (μA).

Padding and Absorption

The absorbent properties and abundance of ***Sphagnum*** (Figure 3) make it the most used taxon among the bryophytes (Densmore 1928). The Chippewa Indians in North America used it as an absorbent. It serves as an insulator, as pillow, mattress, and furniture stuffing, to keep milk warm or cool, to stuff into foot mats for cleaning shoes, to weave welcome mats, and in Lapland to line baby cradles, keeping the infant clean, dry, and warm (Stark 1860).

Mosses were sold on Moss Street in Moscow to put between the panes of glass in double-glazed windows, to absorb condensation (Robin Stevenson, pers. comm.). A colleague of mine used lichens (*Cladina*) similarly between the inner window and the storm window for the same purpose.

And Anders Hagborg (Bryonet 11 June 2016) shared his experience with that very use. He remembers in his childhood in Sweden it was common practice to put mosses between the storm window and inside window to absorb the moisture from condensation on the cold glass in winter. He thinks this moss may have been ***Sphagnum*** (Figure 3).

In Germany, ***Sphagnum*** (Figure 3) has been used in hospitals as neck and head rests, to support hips and backs, and to elevate the legs of wounded people (Hotson 1921). On the farm it is particularly good for absorbing urine from livestock and pets, a function shared with ***Hylocomium splendens*** (Figure 16), absorbing up to 55%, ***Rhytidiadelphus squarrosus*** (Figure 17) 33%, and ***Pseudoscleropodium purum*** (Figure 18) 6%. And even the Romans used it for toilet paper (Birks 1982)! In the laboratory ***Sphagnum*** prevents red-leg in frogs, in part by absorbing the urine. In the Philippines, the crocodile breeding station uses peat moss as a cushion or layering material for incubation of crocodile eggs (Tan 2003).

Figure 16. ***Hylocomium splendens***, a species used to absorb farm urine in Europe. Photo by Michael Lüth, with permission.

Figure 17. ***Rhytidiadelphus squarrosus***, a species used to absorb farm urine in Europe. Photo by Michael Lüth, with permission.

Figure 18. ***Pseudoscleropodium purum***, a species used to absorb farm urine in Europe. Photo by Michael Lüth, with permission.

Mattresses

Mosses have been used for sleeping for a long time. Dickson (2000) reported that mosses, especially ***Neckera crispa*** (Figure 11), were used for mattresses during the Bronze Age.

The Potawatomi Indians in North America used ***Sphagnum*** (Figure 3) species as fibers for rugs, mats, and bedding (Smith 1933). In the North Central States, USA, the Ojibwe Indians have used dried ***Sphagnum dusenii*** to make mattresses (Smith 1932).

In parts of the Malay Peninsula, ***Leucobryum*** (Figure 19) is used together with ***Campylopus*** (Figure 20) to stuff cushions and mattresses (B. C. Tan, pers. comm.). Burkill (1966) likewise reported that ***Calymperes*** (Figure 21), ***Campylopus*** (Figure 20), and ***Sphagnum*** (Figure 3) are used for stuffing mattresses in Malaysia.

Earlier uses of mosses to stuff mattresses are known from Carlisle, UK, where Woodward (1996) reported that 86 horseloads of moss were delivered to Council in 1584. One of the uses was for bedding as a form of down. Woodward contends that harvesting of mosses and other natural materials was more important in early modern society than we typically realize, providing significant employment for the poor of the land. A load of mosses brought 4 [old] pence.

Figure 19. ***Leucobryum sanctum***, a Malayan species in a genus used to stuff mattresses there. Photo by Niels Klazenga, with permission.

Figure 20. ***Campylopus introflexus***, a genus that has been used to stuff pillows. Photo by Michael Lüth, with permission.

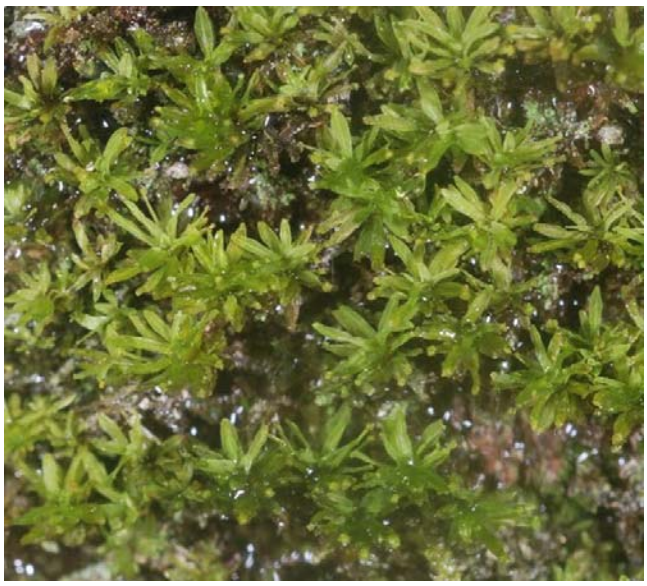

Figure 21. ***Calymperes*** sp, a genus used for stuffing mattresses in Malaysia. Photo by Niels Klazenga, with permission.

Table 1. Comparison of weight gain measured as wet weight to dry weight ratio of selected bryophytes (Horikawa 1952).

Atrichum	6.9
Barbula	8.3
Bazzania pompeana	4.0
Haplomitrium mnioides	12.0
Hylocomium cavifolium	9.8
Plagiomnium maximoviczii	6.7
Rhodobryum	10.0
Sphagnum	12.4
Trachycystis microphylla	3.2

In the Azores, ***Thuidium tamariscinum*** (Figure 22), ***Pseudoscleropodium purum*** (Figure 18), and ***Hypnum cupressiforme*** (Figure 5) were used to stuff pillows and mattresses (Allorge 1937). In fact, ***Hypnum*** was so popular as a pillow stuffing that Dillenius (1741) chose ***Hypnum*** as its name because of its association with sleep (sleep, from Greek *hypnos*). And Linnaeus copied the bears that sleep among mosses, choosing ***Polytrichum commune*** (Figure 10) for bedding (Crum 1973), stating that if a quilt could be made of it, nothing could be more comfortable (Black 1979). Both humans and domestic animals have enjoyed the comfort of a moss bed, with the absorptive ability serving an additional function for the animals (Ando & Matsuo 1984). And for all, mosses such as ***Brachythecium*** (Figure 23), ***Dicranum*** (Figure 13), ***Hypnum*** (Figure 5), ***Neckera*** (Figure 11-Figure 12), ***Papillaria*** (Figure 24), and ***Thuidium***, add the advantages of being insect-repellent and resistant to mold (Pant & Tewari 1989).

Figure 22. ***Thuidium tamariscinum*** with capsules, an insect-repellant moss used to stuff mattresses and pillows. Photo by Michael Lüth, with permission.

In 1868, Albert G. Morey applied for a patent for an "improved mattress." "Be it known that I, ALBERT G. MOREY, of Chicago, in the county of Cook, in the State of Illinois, have invented a new and useful Improvement in the Construction of Elastic Mattresses or Cushions…" The improvement appears to be the use of layers, with the bottom layer being moss, the middle layer of woody fiber or excelsior, and the top layer of elastic sponge. This sponge was not the synthetic sponge we know today, but the real animal, dead of course. "The object of my invention is to furnish an elastic mattress for beds, or cushion for seats, which, while possessing the peculiar qualities of the sponge mattress or cushion, shall yet be afforded at a less cost."

Figure 23. ***Brachythecium rutabulum***, in a genus of insect-repellant mosses used in bedding. Photo by Michael Lüth, with permission.

Figure 24. ***Papillaria nigrescens***, a suitable moss for packing fragile objects or making a bed. Photo by Michael Lüth, with permission.

Shower Mat

A modern use of mosses for absorption is that of Swiss artist/designer La Chanh Nguyen (Nguyen 2014; Telegraph.Co.UK 2009). She used 70 pieces of forest and island moss in cushions 6 cm in diameter to make a bath mat. Each piece is placed in a foam frame to prevent the moss from spreading. She reveres its softness underfoot and lack of unpleasant odor, claiming that it is relaxing and requires little care. Now she is looking for financial backing so she can mass produce it at less than the £220 it cost her to make her own.

But all may not be rosy with this special mat. Bryonetters (Bryonet-L@mtu.edu) quickly expressed their concern about conservation issues and the unlikelihood that the moss would survive indoors in low light. They suggested that most likely it looks alive, when it is really dead.

Such concerns aside, Winter (2014) shares her advice in **making a moss shower mat**. It is her perspective that these mats help you to make the transition from "insanely comfortable shower time" to "everything else you absolutely have to do with your life" by embracing the comfortable feel of a moss mat. Although these mats are available commercially, they are expensive, so she suggests making your own:

Materials needed:

- Substrate for the moss, such as high density foam, about 2.54 cm (1 inch) thick
- Sharp utility knife
- Silicone sealer, like caulk or cement
- Posterboard or cardstock for creating stencils
- Marker or grease pencil
- Spray bottle filled with water
- Moss (many kinds of moss can be used, just choose yours based on the amount of sunlight and average temperature of your bathroom)

How to do it:

- Choose the **size** of your mat. This can be as large or small as you need it to be, given the size of your bathroom. If using foam, be sure that you have enough to make two layers. Bamboo or wood trays will not work quite as well, given their tendency to produce mold and mildew under the conditions required to keep the moss alive.
- Choose the **shape** of your mat. You will need to create several cutouts for your moss. The shape of the cutouts and the edge of the mat are entirely up to you! Any shaping of the edges will need to be done to both pieces of foam, but the cutouts for the moss will only be on the top layer. Use the marker or grease pencil to trace the shapes onto the foam and use the utility knife to cut through the entire thickness. Use as many as you need to cover the mat with moss. Keeping small sections (as opposed to filling a tray with moss) will prevent it from growing excessively.
- **Seal the mat**. An adhesive like silicone caulk is recommended, because it will create a water-tight environment for the moss. Using a product like hot glue or certain other adhesives may melt the foam. Apply the adhesive to the underside of the top layer with the cutouts, making sure each section and the edge of the mat will be properly sealed. Press the top layer to the bottom layer, cleaning up any excess that may have squeezed out the sides. Use books or something heavy to weigh down the mat until the adhesive has dried.
- Prep the mat. Once the mat is ready for the moss, it will need to be properly prepped to ensure its survival. Use the spray bottle to mist the surface of the mat. Keep the spray bottle handy in the bathroom while the moss gets established.
- Plant the moss. Insert the moss into each cutout, until the mat is covered.
- Depending on what species of moss you have used, you might need to water it more than just the drips from your shower once a day. Use the spray bottle to mist the moss for the first couple of months while it gets established. This will keep it moist without over-saturating it.

Urinal Absorption

It seemed unlikely that the desert moss ***Syntrichia caninervis*** (Figure 25) would have any commercial potential. But it is great at absorbing water. Hence, Williams (2016) suggested its potential use to make bathroom urinals "less disgusting." It is able to take water from fog, dew, snow, and of course rain, very efficiently (Pan *et al.* 2016). Having this moss in the urinal would seem a good way to prevent the splashback, according to Tadd Truscott, Assistant Professor of Mechanical Engineering at Utah State and one of the study's authors (Hurd *et al.* 2015). But being the technology-oriented society we are, it is likely that the moss will only be a model, with an artificial moss serving the function. Good luck!

Figure 25. ***Syntrichia caninervis***, a highly absorbent moss with the potential to prevent backsplash in urinals. Photo by John Game, through Creative Commons.

Cleaning

The absorptive property, and often crunchy texture when dry, makes mosses useful for cleaning pots when camping (Gould, pers. comm.), while the remaining mosses can be used to keep the fishing worms alive. In India villagers use mosses mixed with burned ashes to clean household utensils (Pant 1989).

Brushes and Brooms

Polytrichum, with its long, stiff stems, makes good brooms for dusting curtains and carpets (Crum 1973) and apparently ***P. commune*** (Figure 10) is still in use for brushes in southern Sweden today (Hedenäs 1991). Stems are stripped of their leaves to make a broom 30-45 cm long (Thieret 1954).

Robin Stevenson (pers. comm.) reminded me that mosses have been used to make brushes.

Oily Humans

Imagine yourself all greasy and dirty, far from any source of soap or hot water. Your clothes are dirty and your hands are encrusted with grime. Fridtjof Nansen (1897) recounts an experience that is best told in the original language: "Fancy being able to throw away all the heavy, oily rags we had to live in, glued as they were to our bodies. Our legs suffered most; for there our trousers stuck fast to our knees, so that when we moved they abraded and tore the skin inside our thighs till it was all raw and

bleeding. I had the greatest difficulty in keeping these sores from becoming altogether too ingrained with fat and dirt, and had to be perpetually washing them with moss, or a rag from one of the bandages (Figure 26) in our medicine-bag, and a little water, which I warmed in a cup over a lamp. I have never before understood what a magnificent invention soap really is. We made all sorts of attempts to wash the worst of the dirt away; but they were all equally unsuccessful. Water had no effect upon all this grease; it was better to scour oneself with **moss** and sand. We could find plenty of sand in the walls of the hut, when we hacked the ice off them. The best method, however, was to get our hands thoroughly lubricated with warm bears' blood and train-oil, and then scrub it off again with moss. They thus became as white and soft as the hands of the most delicate lady, and we could scarcely believe that they belonged to our own bodies. When there was none of this toilet preparation to hand, we found the next best plan was to scrape our skin with a knife." (Contribution from Robin Stevenson, pers. comm.)

Figure 26. ***Sphagnum*** for surgical dressings. Photo by National Museum of American History, with online permission.

Soaps

Stevenson (2012) recalls his recent visit to an antique shop. There he was surprised to find a new use for ***Sphagnum*** (Figure 3) – Sphagnol Soap – produced by a British company called Peat Products (Sphagnol) Limited (Figure 27-Figure 28) (see also Richardson 1981; The Science Museum 2012). A search on the web produced several useful references to this company and its various products. Each bar contains 15% pure Sphagnol, which is said to consist of 'Emollient Vegetable Tars and Oils.' The 'active ingredient,' Sphagnol, appears to have been a distillate of peat, prepared by the calcination of the peat itself. Details of the chemistry of this mysterious distillate are not available, leading one to the suspicion that a certain amount of scientific mumbo-jumbo may have been involved. The product was, however, said to be 'delightful in use'. The company was in existence at least as early as 1899, since a testimonial of that date from Dr. Carl Peters, wrapped around each bar, states that it not only helped prevent prickly heat on his expedition to the Zambesi district, but also cured one member of the expedition of piles! (Carl Peters was a German explorer and journalist).

Figure 27. Sphagnol soap ad. Photo courtesy of Robin Stevenson.

Figure 28. Sphagnol soap on display in an antique shop. Photo courtesy of Robin Stevenson.

Kai (1919), in a New Zealand nursing journal advertisement, lists Sphagnol soap, but also ointment, suppositories, and shaving soap made with ***Sphagnum*** (Figure 3). The claim was that all these products were awarded a "certificate of purity, quality and merit by the Institute of Hygiene."

Pools and Spas

If you are guessing that ***Sphagnum*** (Figure 3) might be the moss of choice here, you are right. But Dick Andrus warns that not all ***Sphagnum*** species are created equal. Ecology is important. The "aquatic" species like ***S. cuspidatum*** (Figure 29), ***S. torreyanum*** (Figure 30), ***S. majus*** (Figure 31), and ***S. macrophyllum*** (Figure 32) appear to have little or no cation exchange capacity. Rather, hummock species like ***S. fuscum*** Figure 33), ***S. capillifolium*** (Figure 3), and ***S. rubellum*** (Figure 34) should work well.

Figure 29. ***Sphagnum cuspidatum***, an aquatic species with little cation exchange capacity. Photo by Michael Lüth, with permission.

Figure 30. ***Sphagnum torreyanum***, an aquatic species with little cation exchange capacity. Photo by Janice Glime.

Figure 31. ***Sphagnum majus***, an aquatic species with little cation exchange capacity. Photo by Michael Lüth, with permission.

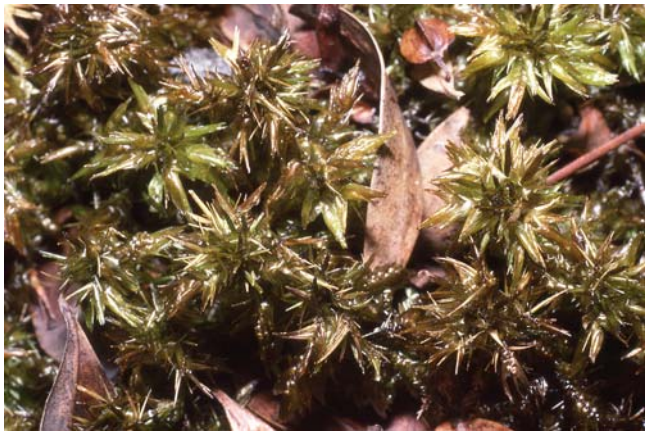

Figure 32. ***Sphagnum macrophyllum***, an aquatic species with little cation exchange capacity. Photo by Janice Glime.

Figure 33. ***Sphagnum fuscum***, a species with good cation exchange capacity. Photo by Jutta Kapfer, with permission.

Figure 34. ***Sphagnum rubellum***, a species with good cation exchange capacity. Photo by Michael Lüth, with permission.

For those of you who are new to the wonders of ***Sphagnum*** (Figure 3), it has two huge advantages as an absorbent of such things as heavy metals and other contaminants. It has large hyaline cells (Figure 35), especially in dryer habitats, that permit it to absorb large quantities of water. And it is able to exchange hydrogen ions (Figure 36) on its cell walls for other ions with a positive charge, hence removing them from the surrounding water.

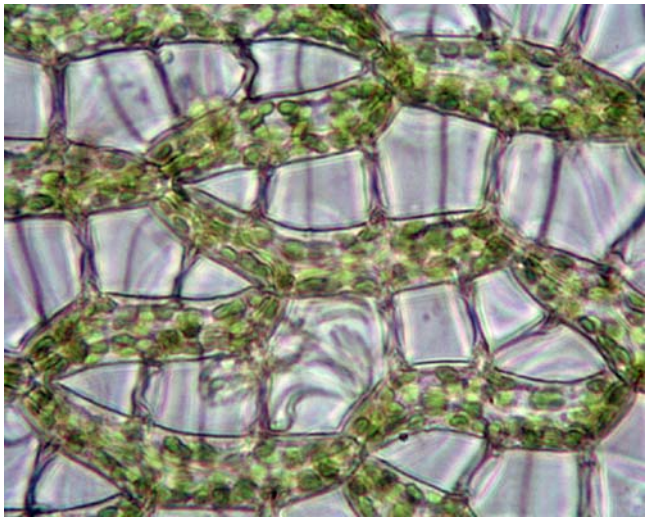

Figure 35. ***Sphagnum palustre*** leaf cells showing green photosynthetic cells and hyaline cells with bars. Photo by Malcolm Storey, through Creative Commons.

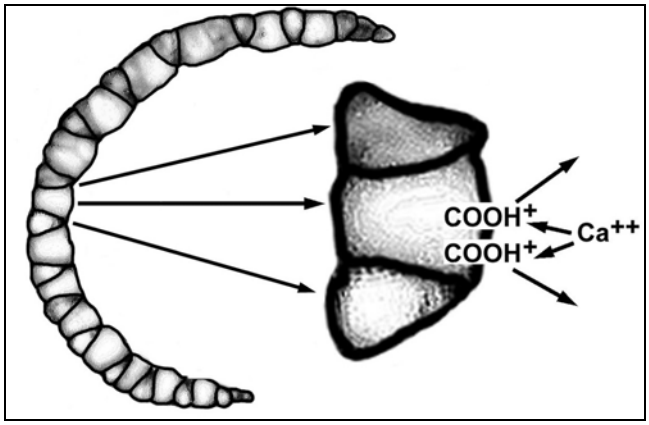

Figure 36. View of leaf cross section of ***Sphagnum*** (**left**) with two enlarged chlorophyllous cells and hyaline cell on **right**. Enlargement shows **carboxyl groups** ($COOH^+$) of the **polyuronic acid** and one Ca^{++} that will exchange for two H^+ ions in cation exchange. Drawing by Janice Glime.

The folks at Creative Water Solutions have been very helpful in telling me about their use of ***Sphagnum*** (Figure 3, an aquatic species with little cation exchange capacity. Photo by) absorbents. They were concerned with removing biofilms in various water systems (including pools). Research shows that the chemicals typically used actually bind to the biofilms, making the chemicals less effective. Furthermore, the biofilm itself provides an environment that is protective of the bacteria. They can only be attacked by the chemicals when they are freed from the biofilm, causing managers to add more and more chemicals to the water. Enter ***Sphagnum***. This moss has permitted them to reduce the need for chemicals by as much as 90%.

Toiletries and Toilets

I have learned from Susana Rams Sánchez that mosses are sold, mixed with a variety of other plant items (Figure 37), and sold in Morocco for washing one's hair. I have to wonder what their role is – antibiotic perhaps? Other items in the mix include fresh flowers, presumably for their sweet odors.

Figure 37. **Upper:** Market place in Azrou, Morocco, where bags of herbals comprise the ingredients for washing hair. **Lower:** Bag of herbals mixed and ready for sale for washing hair. Photos by Susana Rams Sánchez, with permission.

Dillenius (in Crum 1973) stated that ladies of his time used an oil extract of ***Polytrichum*** (Figure 10) for their hair, applying the Doctrine of Signatures because of the hairs on the calyptra.

One use that will probably remain forever among field personnel is that of toilet "paper" (Open-Air 2007). ***Sphagnum*** (Figure 29-Figure 34) is particularly suitable, both for its absorptive properties and its antibiotic properties. Use as toilet paper is most likely ancient. Rösch (1988) reported the use of ***Neckera*** (Figure 11-Figure 12) species for toilet paper. Dickson (2000) reported eleven species of forest mosses mixed with human excrement, indicating their use for toilet paper. Among these, species of ***Neckera*** were prominent.

The German peat closet is one step further in toilet use. This is a toilet in which peat is used instead of water (Turner 1993). The peat was thus mixed with the human excreta (both feces and urine) and the mix was disposed into a mobile cart.

Pesticides

We have known about the ability of bryophytes to discourage insect pests for centuries. Whereas tracheophyte herbaria require ill-smelling moth balls to protect them from destruction by tiny beetles, bryophytes store safely with no such protection. Such safety suggests

that bryophytes may contain some sort of natural pesticide (Yepsen 1984), or simply be unpalatable. In nature, it is not unusual for capsules to be grazed by slugs – not a common organism in a dry herbarium, but the leafy portion of the same plant is often ignored.

Davidson and coworkers (1989) isolated the antifeedants ferulic and possibly m- or p-coumaric acid from a wall-bound fraction of the leafy shoots of ***Brachythecium rutabulum*** (Figure 38) and ***Mnium hornum*** (Figure 39), parts ignored by slugs that readily grazed the capsules. Asakawa has devoted his life to finding a wide variety of phenolic and other ill-tasting or lethal compounds in liverworts. For example, the liverwort ***Plagiochila*** (Figure 40) contains the sesquiterpene hemiacetyl plagiochiline A (Asakawa et al. 1980b) that inhibits the feeding of an African army worm (Asakawa *et al.* 1980a) and is an extremely potent poison to mice (Matsuo *et al.* 1983, unpublished data).

Figure 38. ***Brachythecium rutabulum***, a large pleurocarpous moss that produces antifeedants such as ferulic acid. Photo by Michael Lüth, with permission.

Figure 39. ***Mnium hornum***, a species that is endowed with antifeedants such as ferulic acid. Photo by Michael Lüth, with permission.

Clearly not all bryophytes are so inhospitable to hungry herbivores. My students and I have found that pillbugs (***Porcellio*** spp.; Figure 41) will readily consume ***Thuidium delicatulum*** (Figure 42) plants and ***Polytrichum juniperinum*** (Figure 43) leaves while preferring starvation or paper towels to ***Polytrichum*** stems, ***Dicranum polysetum*** (Figure 44), or ***Pleurozium schreberi*** (Figure 45-Figure 46). However, this avoidance is not always the case, suggesting that seasonal differences may occur (Hribljan 2009).

Figure 40. ***Plagiochila sciophila***, in a liverwort genus that contains the sesquiterpene hemiacetyl plagiochiline A. Photo by Yang Jia-dong, through Creative Commons.

Figure 41. ***Porcellio scaber*** on bryophytes, a species that consumes mosses. Photo by Bernard Dupont, through Creative Commons.

Figure 42. ***Thuidium delicatulum***, a species eaten by pillbugs (***Porcellio*** spp.). Photo by Janice Glime.

Figure 43. ***Polytrichum juniperinum***, a species for which leaves, but not stems, are eaten by pillbugs in the genus ***Porcellio***. Photo by Paul Slichter, with permission.

Figure 44. ***Dicranum polysetum***, a species not eaten by pillbugs (***Porcellio*** spp.). Photo by Janice Glime.

Figure 45. ***Pleurozium schreberi***, a species sometimes eaten by pillbugs (***Porcellio*** spp.) and sometimes avoided. Photo by Janice Glime.

Figure 46. ***Pleurozium schreberi*** eaten in its forest home by ***Porcellio scaber*** (see upper left). Photo by courtesy of John Hribljan.

L. Russell found that one insect readily devours ***Porella navicularis*** (Figure 47) until it eats a species of ***Porella*** that has a peppery taste (D. H. Wagner, pers. comm.). After eating the peppery species for a few minutes, it stops eating it and henceforth refuses to eat either ***Porella*** species. (How is it these creatures are such good taxonomists!?)

Figure 47. ***Porella navicularis***, in a genus with some edible species and some with an unpalatable peppery taste. Photo by Kent Brothers, Botany Website, UBC, with permission.

It appears that exploration of antiherbivory compounds in bryophytes could prove quite profitable for moving genes to crop plants. But I must ask, if insects don't eat them, what is the reason? Doesn't that mean that the ones that ate them didn't pass on their genes? And do I really want the lethal products of those bryophyte genes in **my** food? Certainly a long regime of testing stands between us and widespread use for this purpose, I hope!

Fortunately, so far moss genes are only being considered for a commercial level of transplantation into tobacco (Comis 1992) – a step that has already been accomplished. Oliver and colleagues, working at the United States Department of Agriculture in Lubbock, Texas, have isolated (Scott & Oliver 1994) and transplanted (Oliver *et al.* 2000) several genes from ***Syntrichia*** (formerly in ***Tortula***; Figure 48) that are specific for recovery from desiccation. Antiherbivory genes are being considered as well. But will tracheophytes

be able to express these genes in meaningful ways? And what will they do to the safety of our food?

Figure 48. ***Syntrichia ruralis***, a moss being studied for possible transfer of genes for drought tolerance and antiherbivory into tobacco. Photo by Michael Lüth, with permission.

Kenneth Adams (pers. comm. 1 November 2013) reports that ***Pseudoscleropodium purum*** (Figure 18) has been used in tobacco tins for cleaning up maggots for fishing.

Clothing

Can you imagine wearing mosses? In some parts of Germany, wool was woven with ***Sphagnum*** (Figure 29-Figure 34) to make a good, cheap cloth (Hotson 1921), whereas in Mexico, the dark-colored extract of a rock-inhabiting moss is used to color it (Delgadillo, pers. comm.).

In the Philippines, the tall moss ***Spiridens reinwardtii*** (Figure 49) is used by some of the natives to decorate head gear and clothing (B. C. Tan, pers. comm.). Likewise, in the area around Mount Wilhelm in Papua New Guinea ***Dawsonia*** (Figure 50) is used together with other bryophytes to decorate head gear and body wear (Dickson 2000; Tan 2003). In Malaysia, the large mosses ***Dawsonia***, ***Pogonatum*** (Figure 51), and ***Spiridens*** are used for body decoration and to ward off evil spirits.

Figure 49. ***Spiridens reinwardtii***, a moss used to decorate head gear in the Philippines. Photo by Daniel Nickrent, with online permission.

Figure 50. ***Dawsonia superba***, a moss used to decorate head gear and clothing in New Guinea. Photo by Jan-Peter Frahm, with permission.

Figure 51. ***Pogonatum cirratum***, member of this genus in Malaysia where ***Pogonatum*** is used for body decoration and to ward off evil spirits. Photo by Li Zhang, with permission.

Several cultures have used ***Sphagnum*** (Figure 29-Figure 34) (Bland 1971; Carrier Linguistic Committee 1973; Turner 1983; Compton 1993; Smith 1997; Moerman 1998; Marles *et al*. 2000) and ***Dicranum scoparium*** (Figure 52) for lining diapers (Adelson 2002; Kimmerer 2003), and even modern diapers from Johnson & Johnson in the U.S. and Canada can have ***Sphagnum*** liners (Johnson Gottesfeld & Vitt 1996). ***Sphagnum*** is also used for diapers by the Maori of New Zealand (Macdonald 1974; Harris 2008). Alaskan Native Peoples have used blades of grass, rubbed together until soft, mixed with peat moss and squirrels' nests to line a cradle as a diaper (Kari 1985).

Figure 52. ***Dicranum scoparium***, a moss used by several Canadian cultures for diapers. Photo by Michael Lüth, with permission.

John Steel provided me with an image of a fashion statement that appeared in the Otago Daily Times, New Zealand, 30 March 2012. It shows a sweater coat with mosses used to create the design.

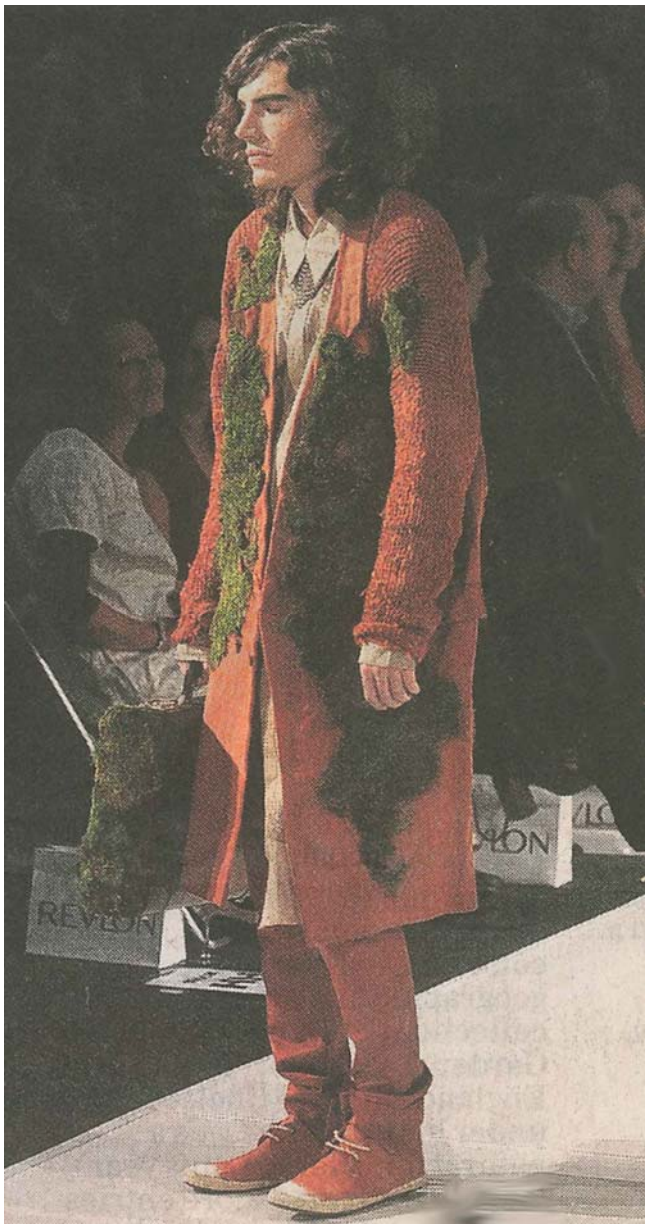

Figure 53. Moss used as design on clothing, modified fom Otago Daily Times, 30 March 2012, p 18 1b. Photo courtesy of John Steel.

Doug Elliott describes the benefits of using *Sphagnum* diapers in his Adventures website (Elliott 2012). The moss wicks the water away from the skin, acting much like talcum powder, and preventing diaper rash. This may be due to its acidity and antibiotic properties. One of its endearing qualities is that the baby's feces become covered with the ***Sphagnum*** (Figure 29-Figure 34) and are easy to remove and are kept away from the baby's skin. The soiled moss is easily discarded into compost or buried in the soil, even when hiking. Elliott prefers ***Sphagnum*** to other products for diapers, and he has tried a number of them. In Cree, the word for ***Sphagnum*** is *otaow*, and would translate to mean "protectively holds" or "embraces."

Elliott warns that the moss should be dried immediately for safe keeping. I would add that any discolored moss should be avoided because it could contain the fungus ***Sporothrix schenckii*** (Figure 54) that causes **sporotrichosis**. Elliott claims that the fungus can be avoided by gathering the moss in a tarp and spreading it so it dries quickly. That is probably sufficient to protect from adhering spores, but I wouldn't trust it against infected plants (Figure 55-Figure 57). When gathering the moss, care should be taken to minimize impact, gathering small clumps and moving around to avoid creating gaping holes.

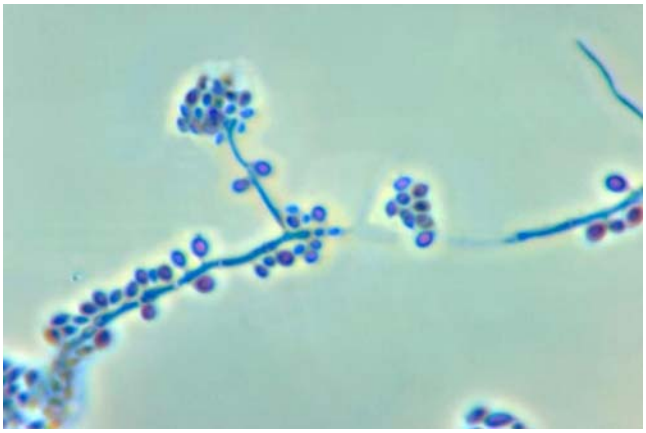

Figure 54. ***Sporothrix schenckii*** conidia, a fungus that inhabits ***Sphagnum***. Photo by USDHHS, through public domain.

Figure 55. ***Sphagnum*** with fungi causing the moss to lose color (left). Photo by Janice Glime.

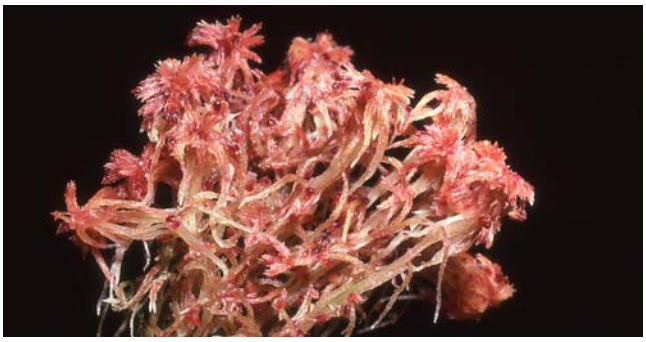

Figure 56. ***Sphagnum*** infected with fungi. Photo by Janice Glime.

Figure 57. ***Sphagnum*** being used for diaper. Photo courtesy of Doug Elliott.

Elliott describes the diapering process: "Though some of our friends lay the ***Sphagnum*** (Figure 29-Figure 34) moss on a cotton diaper, we find that a moss-filled nylon diaper cover works best for us. To prepare for diapering, open the diaper cover and place it on a flat surface. Place a couple handfuls of the moss in the diaper cover and arrange it 'strategically' (more in front for boys). Examine the moss carefully to be sure it is free of leaves, pine needles and other potentially uncomfortable debris. (I press the moss into place with the back of my hand to be sure it is soft and free of projections.) Sometimes we use different 'grades' of moss. The softest moss is reserved for the inner layer and the rest is used as the 'backfill.' Sometimes we place a few sheets of toilet paper on top to cover the moss. Then we set the babe down onto the moss and fasten the diaper up as gracefully as possible. Since managing a squirmy baby on an easily scatterable pile of moss is not always easy, having an extra person helping usually makes it easier. (We call it 'tag team diapering.')"

Michigan's Chippewa Indians used ***Sphagnum*** for this purpose to keep the babies clean and warm (Crum 1973). In fact, Johnson Gottesfeld and Vitt (1996) learned that certain species were preferred and some avoided by the indigenous people of North America. The long, pink (not red) plants of ***Sphagnum divinum*** (Figure 58) were preferred, whereas short, yellow-green, and red plants (Figure 59) were considered unsuitable. Red ***Sphagnum nemoreum*** (Figure 60) caused irritation.

The New Zealand Maori have used ***Lembophyllum clandestinum*** (Figure 61) for diapers as well as for baby bedding (Cooper & Cambie 1991) – just think, a dual purpose moss! ***Sphagnum*** is even used in the modern world in mattress pads for infants (Turner 1993). In California, there is no ***Lembophyllum***, but ***Alsia*** (Figure 62) served the Native Americans for baby bedding (Thieret 1956).

Figure 58. ***Sphagnum divinum*** that is pink and suitable for diapers. Photo by David T. Holyoak, with permission.

Figure 59. ***Sphagnum divinum***, a species that is no longer suitable for diapers when it reaches this deep red stage. Photo by Michael Lüth, with permission.

Figure 60. ***Sphagnum*** (***capillifolium***) ***nemoreum*** illustrating the red colors that seem to be associated with diaper rash when used for baby diapers. Photo by Jan-Peter Frahm, with permission.

Figure 61. ***Lembophyllum clandestinum***, a moss used by the Maori in New Zealand for diapers and bedding. Photo by Tom Thekathyil, with permission.

Figure 62. ***Alsia californica*** in California, USA, a moss used by Native Americans for baby bedding. Photo by Michael Lüth, with permission.

In Germany and Nordic countries, ***Sphagnum*** (Figure 29-Figure 34)) has become popular to line hiking boots (Figure 63; Hedenäs 1991), not only cushioning the feet, but absorbing moisture and odors while discouraging bacteria. Thanks to Gillis Een, I have been enjoying the boot liners and can attest to their comfort.

Natives of the Philippines use mosses to decorate headwear and clothing (B. Tan, pers. comm.). In New Guinea, ***Dawsonia grandis*** (see Figure 50) is worn by natives in bracelets and hair (Van Zanten 1973) and to decorate ceremonial masks (Richardson 1981). The British in England used the moss ***Climacium dendroides*** (Figure 64), artificially colored (Clarke 1902), to decorate a lady's hat (Tripp 1888). And in Boston, the early cultural center of the United States, braids of ***Pseudoscleropodium purum*** (Figure 18) and cords of ***Neckera crispa*** (Figure 11) and bits of ***Dicranum*** (Figure 52) decorated ladies' hats and bonnets (Clarke 1902). These were woven into bands and sold for $0.10 per yard. In the villages of Kumaun, India, women stuff such mosses as ***Hylocomium*** (Figure 16), ***Hypnum*** (Figure 5), and ***Trachypodopsis*** (Figure 66) into cloth sacks to make the **sirona**, a head cushion, that both cushions the vessel carried on the head and absorbs water that splashes from it (Pant & Tewari 1989).

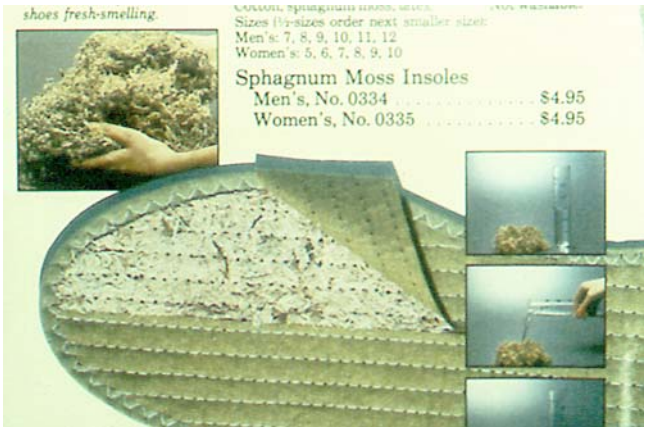

Figure 63. Advertisement for shoe lining made from ***Sphagnum***. Photo by Janice Glime.

Figure 64. ***Climacium dendroides***, a moss dyed and used to decorate ladies' hats in Great Britain. Photo by Michael Lüth, with permission.

The large size of ***Dawsonia grandis*** (see Figure 65) affords it more utility than most mosses. In New Guinea, it is stripped of its leaves, dried over a glowing fire, stripped of its outer layers, split in two, then plaited into a red rope to decorate net bags and other objects (Van Zanten 1973). In New Zealand, it was other members of the **Polytrichaceae** that proved useful. The shoots and leaves of ***Polytrichum commune*** (Figure 10) and ***Polytrichadelphus magellanicus*** (Figure 67) were used in making Maori cloaks, with alternating brown and black serving as decoration (Beever & Gresson 1995). The numerous air spaces, serving the moss for capillary movement and water retention, most likely provided an insulating warmth to the wearer.

Figure 65. ***Dawsonia superba***; ***Dawsonia grandis*** stems are used to decorate net bags in New Zealand. Photo by Velela, through Creative Commons.

Figure 66. ***Trachypodopsis serrulata***. Members of this genus are stuffed into sacks to make a sirona used to cushion water vessels carried on the head in India. Photo by Michael Lüth, with permission.

Figure 67. ***Polytrichadelphus magellanicus***, a moss used to make Maori cloaks. Photo by Phil Bendle, with permission.

Even buttons (Figure 68) can be made from bryophytes. In Europe, peat is pressed into disks and a design stamped into it to make an attractive button for clothing.

Figure 68. Button made of pressed peat. Photo by Janice Glime.

Archaeological evidence tells us that soft mosses such as ***Loeskeobryum brevirostre*** (Figure 69) were used to pad Mesolithic flint blades, protecting the user's hand (Dickson 1973; Figure 70).

Figure 69. ***Loeskeobryum brevirostre***, a moss used to pad Mesolithic flint blades to protect the hand. Photo by Bob Klips, with permission.

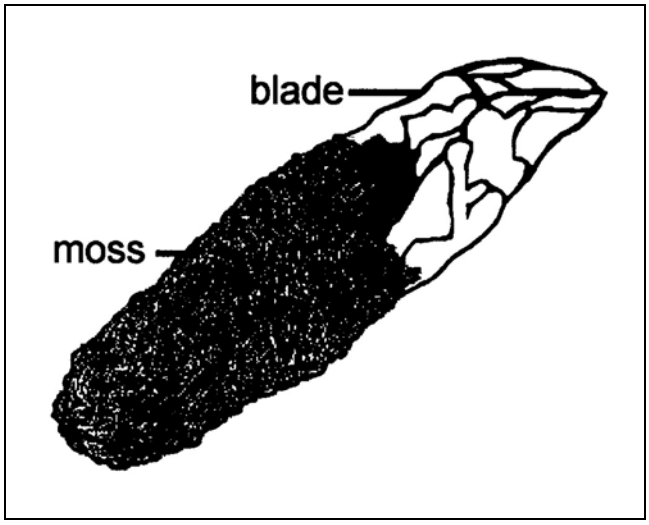

Figure 70. Mesolithic knife handles in Europe were sometimes wrapped with moss. Drawing based on photograph by Dickson 1981.

Tyrolean Iceman's clothes exhibit 30 species of bryophytes (Dickson *et al*. 1996), most likely as involuntary passengers. Nine of these would have been unable to grow at the high altitude where the Iceman was found. Two particularly notable mosses were the low altitude woodland species ***Neckera complanata*** (Figure 12) and ***N. crispa*** (Figure 11), indicating Iceman came from the south (now Italy) and not north (Austria). Most common in 30 samples were ***Polytrichum piliferum*** (Figure 71), ***Pohlia*** spp. (Figure 72), ***Andreaea*** spp. (Figure 73), ***Racomitrium lanuginosum*** (Figure 14), and ***Polytrichastrum sexangulare*** (Figure 74).

Figure 71. ***Polytrichum piliferum***, one of the common mosses on the clothes of the Iceman. Photo by Michael Lüth, with permission.

Figure 72. ***Pohlia nutans*** with capsules, member of a genus of the common mosses on the clothes of the Iceman. Photo by Malcolm Storey <www.discoverlife.org>, with online permission.

Figure 73. ***Andreaea rupestris*** with capsules, member of a genus of the common mosses on the clothes of the Iceman. Photo by J. C. Schou, with permission.

Figure 74. ***Polytrichastrum sexangulare***, one of the common mosses on the clothes of the Iceman. Photo by Hermann Schachner, through Creative Commons.

The Iceman had multiple uses for bryophytes (Dickson 2000). Among these was the use of ***Neckera complanata*** (Figure 12) for leggings and upper body clothing. ***Neckera crispa*** (Figure 105) was used in upper body clothing, leggings, aprons, twisted thongs, and hair decorations. In fact, ***N. crispa*** was the most abundantly used bryophyte in that part of the world. Ochsner (1975) reported its use by prehistoric Swiss.

Jewelry

A creative entrepreneur in Iceland is selling jewelry with a moss garden as the main attraction (HAF 2010). These items include a necklace with a small cup of mosses, a ring, and a knuckle garden that bridges four fingers. The included prices were 150€ for the ring and 180€ for the necklace.

Food Source

If even most insects won't eat the bryophytes, it is no wonder that they seldom have been used for human food. The Chinese consider mosses to be a famine food (Bland 1971). Their low caloric value (Forman 1968) and often abominable taste are efficient deterrents to herbivores of all sizes. Mizutani (1961) complained that it was necessary to gargle to get rid of the bitter liverwort taste, no doubt a result of the numerous phenolic compounds in a single species. Thus it is not surprising that the only country where any bryophyte seems to be a significant component of food is in the peat-rich Lapland where ***Sphagnum*** (Figure 29-Figure 34) was reportedly once used as an ingredient in bread (Bland 1971). However, Jim Dickson (Bryonet 20 February 2015) consulted a Swedish colleague who is an expert on the historic making and composition of bread and she has never heard of such a recipe including ***Sphagnum***. Even Linnaeus did not mention any use of ***Sphagnum*** in making 18th century bread [but then, Linnaeus put the aquatic flowering plant *Potamogeton* in the moss genus ***Fontinalis*** (Figure 75), so his understanding of mosses appears to be minimal]. John Lindley (1849) says ***Sphagnum palustre*** (Figure 76) is a "wretched food in barbarous countries." Native Americans used *Camassia quamash*, simmered in blood with moss, to make a soup (Hart 1992).

Figure 75. ***Fontinalis antipyretica***, a large aquatic moss. Photo by Michael Lüth, with permission.

Figure 76. ***Sphagnum palustre***, a "wretched food." Photo by Michael Lüth, with permission.

Weyrich *et al*. (2017) used DNA in dental calculus to infer the presence of bryophytes (***Physcomitrella patens***; Figure 77) in the diet of Neanderthals from El Sidrón cave, Spain. But Dickson *et al*. (2017) have taken exception to this as evidence of the use of bryophytes as food. They argue that bryophytes are neither palatable nor nutritious and that there is no conclusive evidence that people eat or have eaten mosses. They do not consider the presence of "forest moss" in the dental calculus on one Neanderthal to be an adequate basis to claim it as a dietary component.

Figure 77. ***Physcomitrella patens*** with capsules, a moss whose DNA was found in the calculus of the teeth of one Neanderthal man in Spain. Photo by Bob Klips, with permission.

Dickson *et al*. (2017) argue that fragments of DNA from a taxonomic group (bryophytes) that is under-represented in sequencing studies is a major limitation in interpreting diet. In the case of ***Physcomitrella patens***, it is not a forest moss as claimed, but lives on pool and river margins. It is furthermore so small that it is unlikely to be of interest for food.

On the other hand, Villarroel *et al*. (2007) described the use of ***Sphagnum*** in making cakes in Latin America. The recipe called for resistant starch, ***Sphagnum divinum*** (as ***S. magellanicum***; Figure 58-Figure 59), and defatted hazel nut flour (*Gevuina avellana*, Mol). The starch, HI Maize, and moss provided rich sources of dietary fiber (8.7%). With these ingredients, the product could be stored at refrigerated temperatures but not at 20ºC.

Mummified bodies give us clues into past uses of bryophytes for food. There is evidence that suggests the Iceman consumed bryophytes. ***Neckera intermedia***

(Figure 78) occurred in the eviscerated abdomen of a Guanche (aboriginal Berber inhabitant) "mummy" from the Canary Islands. And ***Sphagnum*** (Figure 29-Figure 34) is known from intestines of Danish and English bog bodies (Dickson 2000).

Figure 78. ***Neckera intermedia***, a species found in the eviscerated abdomen of a Guanche "mummy." Photo by Jan-Peter Frahm, with permission.

Scientists retrieved fragments of six moss species from the alimentary tract of the Tyrolean Iceman (5200 years BP) from the eastern Alps, including ***Anomodon viticulosus*** (Figure 79), ***Hymenostylium recurvirostrum*** (Figure 80), ***Neckera complanata*** (Figure 81), and ***Sphagnum imbricatum*** (Figure 82) (Dickson *et al*. 2009). The reason for having these in his gut remains unknown. Did he use the mosses to stop the bleeding of his wounded hand, then unintentionally ingest them along with his food? Or did they come with the drinking water? Were some of them used to wrap food, then get ingested with it? Or did these people use the mosses like the monkeys (Lamon *et al*. 2017), dipping them in water and squeezing the water into their mouths?

Figure 79. ***Anomodon viticulosus***, a moss that occurred in the alimentary tract of the Tyrolean Iceman. Photo by Hermann Schachner, through Creative Commons.

In British Columbia, Canada, an ancient human body, 17-20 years of age, from a glacier likewise displayed bryophytes in the gut (Dickson *et al*. 2004, 2009; Mudie *et al*. 2005). At least twelve species of mosses were in the gut from the duodenum to the rectum. One of these was a member of the ***Acutifolia*** (Figure 83) section of ***Sphagnum***. But this circumstantial evidence does not tell us the reason for the ingestion.

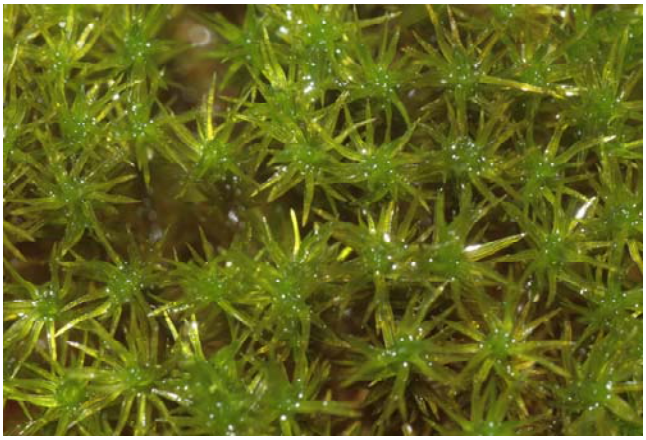

Figure 80. ***Hymenostylium recurvirostrum***, a moss that occurred in the alimentary tract of the Tyrolean Iceman. Photo by Hermann Schachner, through Creative Commons.

Figure 81. ***Neckera complanata***, a moss that occurred in the alimentary tract of the Tyrolean Iceman. Photo by Michael Lüth, with permission.

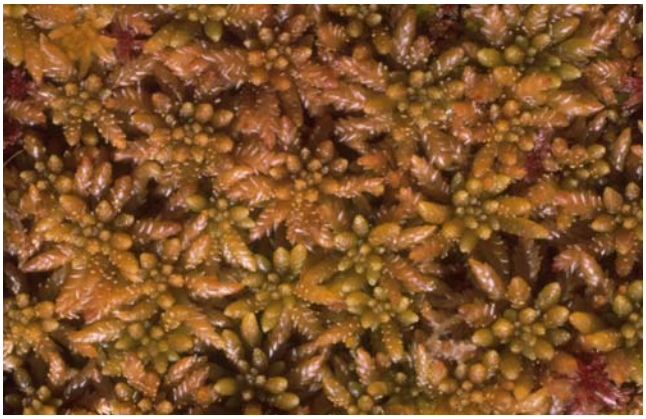

Figure 82. ***Sphagnum imbricatum***, a moss that occurred in the alimentary tract of the Tyrolean Iceman. Photo by Jan-Peter Frahm, with permission.

Figure 83. ***Sphagnum fimbriatum***, a member of the ***Acutifolia*** section of ***Sphagnum***. Photo by David Holyoak, with permission.

There is an interesting report of bryophytes being eaten by Neanderthal man, based on DNA evidence (Weyrich *et al*. 2017). In this treatise, pine nuts (*Pinus koraiensis*), a mushroom (*Schizophyllum commune*), and the moss ***Physcomitrella patens***, identified as "forest moss." Dickson *et al*. (2017) has published the same problems with this interpretation as I have. First, this moss does not grow in forests, but rather in mud flats in the open. Second, it is a tiny moss only a few mm tall, usually in small patches. And finally, this is the moss with its entire genome mapped; many mosses are not even in the database and those that are have been identified by only a small number of genes. On top of these factors making the consumption of this species unlikely, we don't know the reason for finding moss genetic material in the calculus on the teeth of this Neanderthal. Any number of reasons could be considered – perhaps mosses were a primitive tooth brush!

One historic note is that in the second edition of the Dictionary of Dates (Joseph Haydn, London, 1854), Peter, the Wild Boy, is described (C. R. Stevenson, Bryonet 27 November 2006). Peter was a savage creature who lived in the forest of Hertswold, electorate of Hanover, Great Britain. Peter walked on his hands and feet, climbed trees like a squirrel, and was found eating grass and moss in November of 1725. But even this recorded history of human consumption is in question because moss has many meanings to a lay person, and we cannot be sure it was truly a bryophyte being described.

A lot of drinks, especially teas, are made from a variety of odd plant substances with antibiotic properties. Some Native Americans have used ***Sphagnum*** (Figure 29-Figure 34) leaves to make tea (Carrier Linguistic Committee 1973).

Vitamins

Although bryophytes do not seem to be good candidates for food, some bryophytes may provide specific needs for animals both in the wild and on farms. For example, ***Neodicladiella pendula*** has a high content of vitamin B_{12} and causes no noticeable side effects when fed to puppies and chickens (Sugawa 1960). ***Sphagnum*** (Figure 29-Figure 34), as milled peat, provides a binder for iron and vitamins used to supplement the diet of anemic piglets.

Masanobu Higuchi (Bryonet 20 November 2006) reports being served a soup in southwestern Yunnan, China, ordered by his friend. He found something tough and hard to chew in the soup. On close examination, he identified it to be the moss ***Rhodobryum giganteum*** (Figure 84). He speculated that the chef may be including it as a medicinal herb.

Figure 84. ***Rhodobryum giganteum***, a medicinal herb and soup ingredient in China. Photo by David Long, with permission.

Flavoring

Mosses have, however, been used for flavoring, though not commonly. ***Sphagnum*** (Figure 29-Figure 34, Figure 85) contributes to the flavor of Scotch whisky. Scotch whiskies that contain peat include Ardbeg TEN, Highland Park, Octomore, Laphroaig, and Talisker <Whiskey.com>. First, the grains are steeped in water from a ***Sphagnum*** peatland during the malting stage, but this does not contribute to the smoky flavor (Miller 1981; <Whisky.com>). Drying the malt over a peat fire adds the smoke flavor to the barley grains <Whisky.com>. The degree of smokiness in the flavor depends on the length of time the barley grain is dried over the peat fire. Damp malt usually requires about 30 hours of drying.

Figure 85. Mined peat bog in Ireland. Peat like this is used in the fires used to dry the malt for making whisky. Photo by Amos, through Creative Commons.

In Germany one can buy "drinkable peatbog (Trinkmoor)" as a diet addition (Wolfgang Hofbauer, Bryonet 20 February 2015). This is a suspension made not from fresh ***Sphagnum*** (Figure 29-Figure 34), but from peat (Figure 85). ***Lunularia*** (Figure 86) and ***Plagiochasma*** (Figure 87) are used in preparation of maize beer (Franquemont *et al.* 1990).

Figure 86. ***Lunularia cruciata***, a liverwort used in making maize beer. Photo by Michael Lüth, with permission.

Figure 87. ***Plagiochasma appendiculatum***, a liverwort used in making maize beer. Photo by Michael Lüth, with permission.

In a drink of wine, ***Marchantia polymorpha*** (Figure 2) soaks up the wine and makes a tasty, crunchy treat with your drink. Hmm... are our favorite organisms only consumed with alcohol?

Vassilios Sarafis (Bryonet, 19 November 2006) reports having tried capsules of ***Polytrichum commune*** (Figure 10, Figure 88), finding them tasty. Amanda Hardman (Bryonet, 19 November 2006) claims to fancy eating ***Funaria hygrometrica*** capsules (Figure 89), but states that you must catch them at just the right ripeness. To her, they can taste "as good as yummy sweet peas." Nevertheless, Rod Seppelt (Bryonet, 19 November 2006) compares preparing bryophytes as a food to that of the recommended way to cook a Galah (otherwise known as a Rose-breasted Cockatoo) in Australia. You put a stone and water in the pot with the Galah, bring to a boil, and when the stone is soft, throw away the Galah and eat the stone! In the case of bryophytes, it is the phenolic compounds that make them unpalatable and of questionable safety for consumption.

Figure 88. ***Polytrichum commune*** immature capsules, a stage some might consider edible. Photo by Michael Lüth, with permission.

There have certainly been experimental uses of mosses for food flavoring. Stefan Rensing (Bryonet, 21 November 2006) reports that a group of ~50 botanists at a party sampled a newly created drink called "Psycho Physco." This drink contained a teaspoonful of protonemata from a bioreactor liquid culture of the prominent research moss ***Physcomitrella patens*** (Figure 90). Rensing reports that the taste was "quite interesting (not unpleasant)" and all 50 persons survived unharmed.

Figure 89. ***Funaria hygrometrica*** with capsules that apparently are suitable as human food. Photo by Hermann Schachner, through Creative Commons.

Figure 90. ***Physcomitrella patens***, the lab rat of bryophytes for which the protonema was tested for "taste" in a drink by a group of European botanists. Photo by Michael Lüth, with permission.

A well-known chef in Europe is looking for bryophytes to flavor his dishes, giving them a unique taste (Marta Infante & Patxi Heras, Bryonet, 18 November 2006). He plans to enter them in a gastronomical contest. So far he has tried ***Pseudoscleropodium purum*** (Figure 91) in tempura and made an infusion with ***Boletus edulis*** (Figure 92). But there are concerns about possible side effects and bryophytes to avoid.

Figure 91. ***Pseudoscleropodium purum***, a large moss being explored for taste contributions to food and still being used in shipping plants and fragile objects. Photo by Michael Lüth, with permission.

Figure 92. ***Boletus edulis*** with moss, a mushroom cooked with ***Pseudoscleropodium purum*** by a European chef. Photo by H. Krisp, through Creative Commons.

Chinese Gallnuts

Perhaps the most important use of mosses in the food industry is indirect. Several mosses, especially species of ***Plagiomnium*** (Figure 93), are winter hosts to the Chinese gallnut aphid (*Schlechtendalia chinensis*), the insect that provides those gallnuts (Figure 94-Figure 96) that are both a delicacy and important medicine in China (Horikawa 1947; Wu 1982; Ando 1983). The gallnuts, formed on the leaves of *Rhus javanica* (Figure 94-Figure 96) are used as pain killers, antiseptic and antidiarrheal agents, and as expectorants, astringents, and preservatives (Min & Longton 1993), and in industry as a source of tannic acid.

Figure 93. ***Plagiomnium undulatum***, one of the overwintering host mosses for the Chinese gallnut aphid. Photo by Michael Lüth, with permission.

Figure 94. Leaves of the summer gallnut host, *Rhus javanica*. These plants must be near suitable mosses for the gallnut aphid to survive the winter. Photo by Kenpei, through Creative Commons.

Figure 95. These gallnuts of the aphid *Schlechtendalia chinensis* occur on the branch of the sumac, *Rhus javanica*. Photo by Yingdi Liu, with permission.

Figure 96. These harvested gallnuts are used for eating and medicinal purposes in China. Photo by Yingdi Liu, with permission.

The gallnuts were so important that Takagi (1937) proposed the culture of suitable mosses in order to increase gallnut (Figure 96) production. In China, the aphids are now reared agriculturally on mosses (Tang 1976). In Yunnan the host tree and the most common host mosses (species of ***Plagiomnium***, Figure 93) do not have large overlapping distributions, making establishment of the gall aphids difficult. The aphids lay their eggs on the moss and the young nymphs survive during winter using the moss as food. In some areas, mosses are reared in bowls that are placed under the trees for several weeks during autumn until the aphids locate them (Min & Longton 1993). Then the bowls are moved into sheds for the winter. In April the moss is removed from the bowls and placed back under the trees. The bowls are supplied with fresh soil and kept in a more suitable place where the remaining moss fragments regenerate. By October these mosses are sufficiently large to use the same bowls to gather the next winter's crop of aphids.

Food Improvement

There seems to be little interest in cultivating bryophytes themselves for agricultural purposes. However, they do contribute peripherally to our food. They are used as a carrying medium for the nitrogen-fixing *Rhizobium* (Figure 97) inoculants for legume production (Turner 1993). And currently there is research to try to encourage the **Cyanobacterium *Nostoc*** (Figure 98) to grow on roots and stems of plants. This photosynthetic bacterium, once known as a blue-green alga, is able to convert atmospheric nitrogen into ammonia, making is usable for plants. But what has this to do with bryophytes? Well, there has to be a source of the ***Nostoc***, and this should be a species adapted to living in association with a plant. A number of liverwort taxa are known for cyanobacterial partners. In this case, it is ***Anthoceros*** (Figure 99) that has contributed the ***Nostoc***, which Gantar and coworkers (1995) are trying to persuade to live and fix nitrogen on, of all things, wheat roots! That would go a long way toward solving fertilizer problems! And Rao and Burns (1990a, b) have suggested the use of ***Anthoceros*** as a living agricultural fertilizer because of its ***Nostoc*** partners. That might even work, since ***Anthoceros*** likes disturbed areas.

Figure 97. ***Rhizobium*** nodules on the roots of a legume. Photo by Terraprima, through Creative Commons.

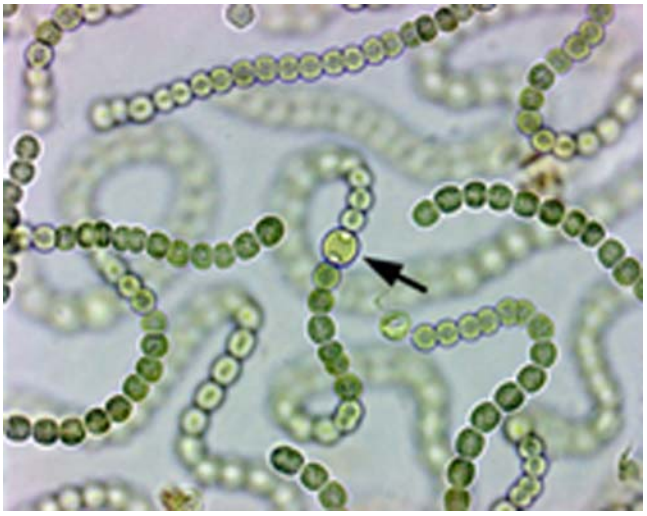

Figure 98. ***Nostoc*** sp., a nitrogen fixer that is often found on mosses, especially ***Sphagnum***. Photo from <vle.du.ac.in>, through Creative Commons.

Figure 99. ***Anthoceros agrestis***, a hornwort with Cyanobacterial partners that fix atmospheric nitrogen. Photo by Michael Lüth, with permission.

Use of peat mosses for culturing certain foods is common. One environmentally friendly use is the combination of extracts from fisheries by-products with peat compost (Martin 1992). This is especially true in coastal areas where the more usual by-products are limited in availability. Products of this fermentation process can be used successfully to feed, of all things, more fish! Then there are the agricultural uses – growing mushrooms, salad greens, and other specialty crops (Turner 1993) that will be discussed in the sub-chapter on commercial uses.

Peat water is typically brown and looks unfit to drink, but for sailors going on a long journey, it has provided a safer alternative (Dente 1997). It stays free of algae longer than well or spring water.

Extracts from the leafy liverwort ***Porella platyphylla*** are able to inhibit "radice" (root) seedling growth (Beike *et al*. 2010). On the other hand, extracts of the moss ***Brachythecium rutabulum*** promote their growth, demonstrating the individuality of the bryophytes.

A major threat to crop plants in many parts of the world is drought. Many kinds of bryophytes are very tolerant of drought, so enterprising scientists endeavored to identify the genes in bryophytes that endowed them with their unique ability to recover from drought. Among these, the model system created with the moss ***Physcomitrella patens*** (Figure 90) had a high tolerance to such abiotic stresses as salt and osmotic stress (Frank *et al*. 2005b).

Physcomitrella patens (Figure 90) is an ideal laboratory culture organism. Hence, Frank *et al*. (2005a) have developed molecular tools to identify its genes and their roles. Reski and Frank (2005) have identified the genes it uses for drought protection and other stress response genes. Not only does it produce plant metabolites, but it also produces animal, fungal, and algal metabolites, suggesting they might be useful for therapeutic and diagnostic purposes.

One important use of the bryophytes has been to identify the genes involved in drought tolerance and apply this knowledge to other organisms. At the University of Freiburg, 40 scientists and technicians collaborated on identifying genes from ***Physcomitrella patens*** (Figure 90) that could potentially be used to improve crop plants (Schiermeier 1999). The complete genome was enumerated in 2007 (Anonymous 2007; Rensing *et al*. 2008).

Following this elucidation, Richardt *et al*. (2010) were able to recognize the vegetative osmotic stress tolerance genes in the moss ***Physcomitrella patens*** (Figure 90) that were identical to those in maize. Na^+ pumps existed in such early land plants as ***P. patens***, but these seem to have been lost as the tracheophytes evolved (Benito & Rodríquez-Navarro 2003; Horie & Schroeder 2004). This discovery led to studies on feasibility of moving stress tolerance genes from ***P. patens*** into crop plants (Reski & Frank 2005). In 2007, the sequencing of the complete genome of ***P. patens*** was completed (BIOPRO 2011).

A group of Spanish researchers have identified a Na^+ pump in ***Physcomitrella patens*** (Figure 90) and Australians have transferred it into maize to make those plants more salt tolerant (Ralf Reski, pers. comm. 14 August 2017).

By now, moss genes have found their way into our food (Ralf Reski, pers. comm. 14 August 2017). The patent <http://patents.com/us-8835715.html> for creating unsaturated fatty acids has just been approved:

"Abstract: The present invention relates to an improved process for the preparation of unsaturated fatty acids and to a process for the preparation of triglycerides with an increased content of unsaturated fatty acids. The invention relates to the generation of transgenic organism, preferably of a transgenic plant or of a transgenic microorganism, with an increased content of fatty acids, oils or lipids with .DELTA.6 double bonds owing to the expression of a **moss** .DELTA.-6-desaturase [sic]. The invention furthermore relates to transgenic organisms comprising a .DELTA.6-desaturase gene, and to the use of the unsaturated fatty acids or of the triglycerides with an increased content of unsaturated fatty acids prepared in the process."

"The genomic .DELTA.6-acyllipid desaturase from ***Physcomitrella patens*** was modified, isolated and used in the process according to the invention on the basis of the published sequence (Girke *et al*., Plant J., 15, 1998: 39-48) using a polymerase chain reaction and cloning. To this end, a desaturase fragment was first isolated by means of polymerase chain reaction using two gene-specific primers, and inserted into the desaturase gene described in Girke *et al*. (see above)." Permission was granted for "A process of preparing an unsaturated fatty acid, which comprises introducing, into an organism being a yeast or a monocot or dicot plant, at least one nucleic acid sequence encoding a polypeptide having .DELTA.6-desaturase activity…" This patent application was submitted 16 September 2014 and has just been approved (September 2017), added on to a patenting history starting in 1987.

Food Preservation

Modern methods of packing food have actually increased the incidence of botulism more than 12-fold among Alaskan natives since 1966 (Segal 1992). Traditionally, the natives processed fish and sea mammals on the ground where the animals easily made contact with bacteria from the soil or animal viscera. The food was then placed in a shallow pit lined with wood, animal skins, or leaves. These buried animals were then covered with moss or leaves and left to ferment for one or two months. However, the natives switched to modern technology and

used plastic bags to line the pits and enclose the food, eliminating the use of moss and other plant matter. The anaerobic conditions created by this method promoted the growth of *Clostridium botulinum* (Figure 100-Figure 101), permitting the production of the botulism toxin. The natives do not trust the advice of outsiders, so the Health Department feels the best plan to reduce the spread of the disease is to encourage them to return to their traditional use of mosses. The mosses permit aeration and may even have antibiotic effects.

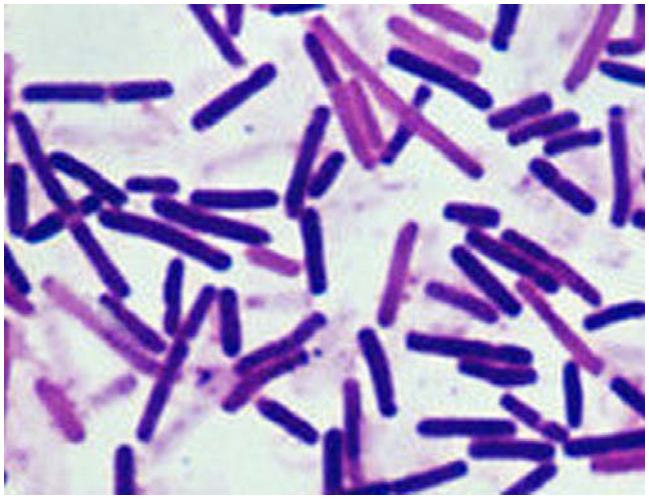

Figure 100. ***Clostridium botulinum***, a source of food poisoning that can be prevented by storing food with mosses. Photo by Science Photo Library, through Creative Commons.

Figure 101. ***Clostridium botulinum*** SEM. Photo by Christine Schramm, through Creative Commons.

Mark Smits (Bryonet 20 February 2015) reports that ***Sphagnum*** bogs (Figure 102) were used to preserve food, including butter (Figure 103). Reade (2013) noted the use of "bog butter," especially in Scotland and Ireland. This is butter that has been buried in a peat bog. The earliest known use of this method is from the Middle Iron Age (400-350 BC). Reade reports on the experiment of Daniel C. Fisher that found bacterial counts in meat after one year in a peat bog was comparable to that which had been in a freezer for the same length of time.

Figure 102. Raised bog with ***Sphagnum fimbriatum*** surrounded by ***Sphagnum magellanicum***, a suitable site for making bog butter. Photo from Tuberas de Chile, through Creative Commons.

Figure 103. Bog butter found near Enniskillen, County Fermanagh, Ireland. Photo by Bazonka, through Creative Commons.

It appears that the potential use of ***Sphagnum*** for preservation is still alive. Børsheim *et al.* (2001) experimented with fish preservation in ***Sphagnum***, peat, and holocellulose. Salmon (*Salmo salar*) skin and whole zebra fish (*Brachydanio rerio*) were preserved for many weeks in ***Sphagnum palustre*** and compared to those in peat that came mostly from ***Sphagnum*** mosses, acetone-extracted moss, and chlorite holocellulose of the moss. Interestingly, the chlorite holocellulose performed as well or better than the other products. The watersoluble sphagnan in this holocellulose portion produced the same results as the other treatments. Similarly, mackerel (*Scomber scombrus*) skin became brown and completely bio-resistant after repeated immersion in aqueous (3% w/v) sphagnan (with intermittent drying). This process achieved the same effect as smoking the fish. However, the process does not work on filleted fish muscle because the soluble protein diffuses out too quickly and neutralizes the carbonyl groups in the sphagnan.

It appears we should give more consideration to bryophytes for our modern food storage. Not so long ago, before refrigerators were invented, people built root cellars to preserve vegetables through the winter. But today, we can still use mosses for this purpose. Dorothy Allard (12 August 2017) shared with me her use of ***Sphagnum*** to keep her carrots for several months in a root cellar at 4-16ºC. She washed the carrots, cut off their tops, and layered them in a 5-gallon (19-liter) plastic bucket so that the carrots were not touching each other. The carrots did not rot, but they did develop a few small root hairs and eventually developed a "peat mossy" taste. It was easier to clean them than carrots packed in sand.

Cookery and Pottery

The use of peat as a fuel in northern parts of Europe is common, and this includes its use for heat for cooking. The pendant ***Antitrichia curtipendula*** (Figure 104) was also used by Native Americans in earthen ovens for cooking (Compton 1993).

Figure 104. ***Antitrichia curtipendula***, a species used in ovens by Native Americans. Photo by Hermann Schachner, through Creative Commons.

Early uses of mosses in pottery can be traced as far back as the Stone-age people, who apparently used the moss ***Neckera crispa*** (Figure 105) (Grosse-Brauckmann 1979) in a region now settled by Germany. In the French Stone Age, ***Neckera crispa***, ***Tortula*** (Figure 107), and other mosses were used as we now use sand, apparently to make the pottery less "fat," improving the quality of the pottery (H. J. During pers. comm.; Figure 106). Analysis of ancient pottery demonstrates presence of animal parts, and the defatting agents help in defatting their fats. In both France and Belgium, mixtures of moss containing ***Neckera crispa***, in particular, were used to temper pottery (Constantin & Kuijper 2002). Is it possible that the mosses kept the pottery safe after it was used for cooking or serving animal foods, discouraging the multiplication of bacteria and fungi?

In France and Belgium the Epi-Rössen and Michelsberg cultures have used mosses, primarily ***Neckera crispa*** (Figure 105), as a temper (degreasant = defatter) in making pottery (Figure 108) (Constantin & Kuijper 2002; Jan & Savary 2011; Jan 2016). The mosses were used for tempering the ceramics during the Mid-Neolithic (~4700-3500 BC) (Denis Jan, pers. comm. 14 December 2015). Some of the mosses resemble ***Rhytidiadelphus squarrosus*** (Figure 17). Other studies have revealed the use of ***Neckera crispa*** and ***Fissidens dubius*** (Figure 109). When mosses are used as a temper they reinforce the clay of vases like a wattle for mud. Combustion of the ceramic causes the plant parts to disintegrate and create a high porosity. This serves two purposes – it makes the vase lighter and absorbs shock waves that would otherwise cause the vase to break.

Figure 105. ***Neckera crispa***, a large, pleurocarpous moss of tree trunks that has been used as a mordant in pottery. Photo by Michael Lüth, with permission.

Figure 106. A piece of ancient pottery with the impression of ***Neckera crispa*** that has been used as a mordant. Photo courtesy of Heinjo During of Universiteit Utrecht and Wim Kuijper from Archeological Centre of Leiden University.

Figure 107. ***Tortula calcicolens***, a moss used as a defatter in making pottery. Photo by Michael Lüth, with permission.

Figure 108. Ceramic with moss inclusions, before firing. Photo courtesy of Dennis Jan.

Figure 109. ***Fissidens dubius*** with capsules, a moss used as a defatter in making pottery. Photo by Hermann Schachner, through Creative Commons.

Packing

One wouldn't expect a plant that harbors a wide range of insects to be a suitable insect repellent, but the Himalayans dried mosses, made them into a coarse powder, and sprinkled them over grains and other containerized goods to repel insects (Pant & Tewari 1989). They covered the top of the container with a plug of mosses. When they were ready to use the grain, they simply blew off the light-weight mosses from the grain. Just consider the safety of this natural way of repelling the insects while protecting the human consumer. In the Pacific Northwest, mosses are collected to pack mushrooms and keep them safe (Cleavitt 1996).

Taxidermy usually requires the use of arsenic to keep hungry beetles from consuming our treasures. But at the British Museum, it was mosses that served this role. Curators stuffed the skins with mosses to ward off the dermestid beetles and at the same time keep the skins plump and natural (Harrington 1985).

Packing materials vary with what is available locally and can even be used to determine the region and habitat of origin. In the western USA, A. J. Grout (in a comment to Clarke 1902) cited the use of ***Dendroalsia abietina*** (Figure 110) and ***Antitrichia californica*** (Figure 111) to pack vegetables that were shipped from California to Seattle. These reportedly came from Boulder's Island. Epiphytic mosses such as ***Antitrichia californica***, ***Dendroalsia abietina***, and ***Metaneckera menziesii*** (Figure 112) provided suitable packing material for vegetables by helping to retain moisture (Frye 1920), whereas today similar bryophyte species are used to pack mushrooms (C. W. Smith, pers. comm.).

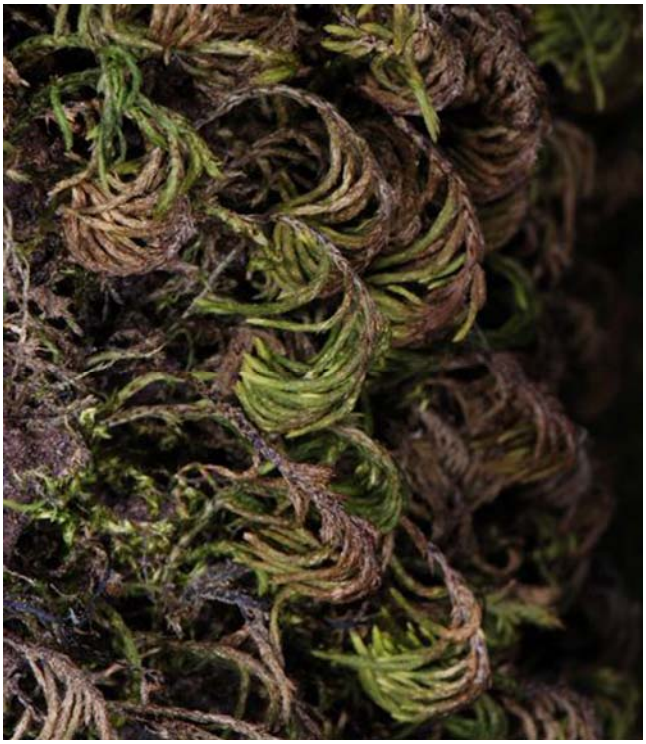

Figure 110. ***Dendroalsia abietina***, a moss used in the Pacific states of the USA as packing material for fresh vegetables. Photo by Paul Wilson, with permission.

Figure 111. ***Antitrichia californica***, a moss used in the Pacific states of the USA as packing material for fresh vegetables. Photo by Michael Lüth, with permission.

Figure 112. ***Metaneckera menziesii***, a moss used in the Pacific states of the USA as packing material for fresh vegetables. Photo by Michael Lüth, with permission.

The Himalayans still use both soil and epiphytic mosses such as ***Brachythecium salebrosum*** (Figure 113), ***Cryptoleptodon flexuosus***, ***Hypnum cupressiforme*** (Figure 5), ***Macrothamnium submacrocarpum*** (Figure 114), ***Taiwanobryum crenulata***, ***Trachypodopsis serrulata*** var. ***crispatula***, ***Thuidium tamariscellum***, and ***Sphagnum*** (Figure 29-Figure 34) to pack apples and plums (Pant & Tewari 1989). But in the tropics, it is the leafy liverworts that play this role because of their abundance (Bland 1971). Large and abundant mosses like ***Pseudoscleropodium purum*** (Figure 91) (Dickson 1967; Figure 115), ***Hylocomium splendens*** (Figure 16), and ***Rhytidiadelphus squarrosus*** (Figure 17) have been dispersed and grow around the world due to their widespread use as packing materials (Seaward & Williams 1976). Allen and Crosby (1987) refer to these worldwide expansions of ***Pseudoscleropodium purum*** as legendary – even today, it is used for packing young trees destined for Tristan da Cuñha, where its establishment is imminent. It seems to have arrived on the West Coast of North America by the late 1800's (Miller & Trigoboff 2001).

Figure 113. ***Brachythecium salebrosum***, a moss used in the Himalayas to pack apples and plums. Photo by Hermann Schachner, through Creative Commons.

Figure 114. ***Macrothamnium submacrocarpum***, a moss used for packing apples and plums in the Himalayas. Photo courtesy of Hiroyuki Akiyama.

Figure 115. ***Pseudoscleropodium purum***, a moss commonly used in packing. Photo by Michael Lüth, with permission.

In some Asian countries, bryophytes are used for packaging gifts and displays during the Christmas Season (Tan 2003).

Large mosses make good cushions for fragile objects. In Japan, boxes packed with large pendant mosses such as ***Aerobryopsis subdivergens*** (Figure 116), ***Barbella determesii***, and ***Meteorium helminthocladulum*** (Figure 117) guarded ancient silk clothes, providing a clean and soft packing (Noguchi 1952). Where dirty soil was of less concern, soil mosses such as ***Rhytidiadelphus triquetrus*** (Figure 118) protected fragile China (Dickson 1973), and Espie (1997) claims it is "most valuable for packing material for porcelain" in New Zealand; it was pre-shredded for packing to protect other delicate objects (Kenneth Adams, pers. comm. 1 November 2013). Other mosses are used for packing fragile items in the Philippines (B. C. Tan, pers. comm.). ***Hypnum*** (Figure 5), ***Plagiomnium undulatum*** (Figure 93), and ***Sphagnum*** (Figure 29-Figure 34) guarded the blades of daggers and scrapers (Dickson 1967). Even the Department of Defense used mosses (***Sphagnum***) to pack fragile bomb sights during World War II (K. Parejko, pers. comm.).

Figure 116. ***Aerobryopsis subdivergens***, a moss used for packing in Japan. Photo by Digital Museum, University of Hiroshima, with permission.

Figure 117. ***Meteorium helminthocladulum***, a moss used for packing material in Japan. Photo from Digital Museum, University of Hiroshima, with permission.

Figure 118. ***Rhytidiadelphus triquetrus***, a moss used for packing material in Japan. Photo by Malcolm Storey, through Creative Commons.

The Open-Air Natural History Museum states that ***Sphagnum*** (Figure 29-Figure 34) is good for winter storage of carrots to keep them fresh (Open-Air 2007).

The antibiotic properties of ***Sphagnum*** (Figure 29-Figure 34) make it ideal for shipping small amphibians such as salamanders and frogs from biological supply houses (Figure 119). It keeps the animals moist and helps prevent diseases like red leg by absorbing the urine and reducing bacterial growth.

Figure 119. ***Rana pipiens***, sitting on ***Sphagnum***, protected from red leg by the ***Sphagnum*** substrate in the terrarium. Photo by Janice Glime.

In New Zealand, where ***Sphagnum*** (Figure 29-Figure 34) has never been common, new commercial uses are surfacing (SFF Project Summary 2006). In a project titled "Economically sustainable novel Sphagnum moss products," three new commercial uses are proposed. These include packaging due to the absorbent and antibiotic properties that would reduce fruit spoilage. They likewise suggest using ***Sphagnum*** for animals, but on the larger scale of veterinarian services, reducing odors and providing absorption. Their third suggestion, already done in several large wars, is to use the moss for bandages, especially those that are particularly "weepy" and thus more prone to infection. In their early experiments, however, they failed to show that ***Sphagnum*** protects apricots or avocados from post-harvest infections. They are currently looking for a sponsor to research the effects of using ***Sphagnum*** bandages on burn victims.

In his accountig of mosses and liverworts W. H. Burrell observed that ***Thamnobryum alopecurum*** (as *Porotrichum*) is 'used by the gamekeeper as a packing for eggs' (Nicholson 1914). What a nice cushion before the modern-day egg cartons.

Burial Wreath

In Nairobi, Kenya, mosses are used to make wreaths for burial ceremonies (Itombo Malombe, pers. comm. 15 August 2017). These are mostly pendent mosses, including ***Neckera*** (Figure 11-Figure 12) and ***Pilotrichella*** (Figure 120). A sack of mosses for this purpose is sold for 10,000 ksh (~$100 US) and more than ten sacks are used.

Figure 120. ***Pilotrichella***, a moss used in burial wreaths in Nairobi. Photo from iNaturalist, through Creative Commons.

Summary

Mosses are used for carrying water, stuffing mattresses, pillows, and dolls, collecting urine from farm animals, making bandages, cushioning fruits, making soap, and packing fragile articles. They even provide vitamin supplements to animal feed. In northern areas they are used for heating, making wicks, and in Morocco they are used to wash hair.

Recently, one of the more important uses is for physiological studies and genetic studies linking genes to processes. This investigation is leading to the possibility of transplanting genes for traits like drought tolerance and antiherbivory into agricultural plants.

Despite the unpleasant taste of most bryophytes, ***Sphagnum*** has been used in Scotch whisky, ***Marchantia polymorpha*** has been added to wine, and one European chef is experimenting with new recipes using bryophytes. Capsules may be more tasty if collected at the right stage. Some mosses serve indirectly by providing the overwintering home for gall aphids. The galls made by these insects are used for food and medicine. More commonly, mosses are used for culturing a variety of food plants.

Mosses have been used for making and decorating clothing and pressed buttons. Most importantly, they have been used for diapers and other absorbent roles like lining boots.

Pottery makers in the used bryophytes to temper the pottery.

The soft and flexible texture of mosses makes them ideal for packing a variety of items, leading to the spread of some species around the world. Their antibiotic properties make them ideal for shipping amphibians.

Acknowledgments

I am grateful to Robin Stevenson who has sent me several of the stories covered by this chapter. Patxi Heras Pérez and Marta Infante Sánchez alerted me to the use of mosses to temper pottery. John Steel alerted me to the publication on bread and provided me with a copy of the chapter by John Lindley. Jim Dickson has been an invaluable resource in providing anecdotes and references. Denis Jan has provided me with helpful discussion and an unpublished copy of his manuscript. Ralf Reski was very helpful in documentation of bryophyte genes being transferred to crop plants.

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CHAPTER 2-1

MEDICAL USES: MEDICAL CONDITIONS

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MEDICAL USES: MEDICAL CONDITIONS

Figure 1. Bryophytes and other herbs on sale in a Yunnan, China, market. The newspaper has the contents of a prescription that is under preparation, including ***Rhodobryum***. Photo courtesy of Eric Harris.

New Medical Sources

One of the reasons for exploring biological compounds in bryophytes is the potential for medical use. It's a scary thought, but substances we know as pesticides and fungicides that discourage insect feeding and bacterial or fungal attack are likely to have antibiotic properties that could prove useful in treating human disease. We know bryophytes contain numerous potentially useful compounds, including oligosaccharides, polysaccharides, sugar alcohols, amino acids, fatty acids, aliphatic compounds, phenylquinones, and aromatic and phenolic substances, but much work remains to link medical effects with specific bryophyte species or compounds (Pant & Tewari 1990). For this reason, traditional uses named here should be viewed with caution because we don't know the dosage needed, side effects, or other precautions that need to be taken. We do know that traditional medicines that may be safe for one race of people may not be for others. After all, those alive today are descendents of survivors. And diet may affect the ways that some of these compounds work, causing geographic differences.

Hansen (1994) suggested that fatty acids produced by members of **Hypnaceae** (Figure 70) and **Brachytheciaceae** (Figure 2) produce high levels of arachidonic acid and EPA and might be used for "producing unique and highly priced compounds for pharmaceutical industry." Mosses contain both n-3 (EPA, 18:3) and n-6 (arachidonic acid, DHGLA, 18:2) fatty acids. Gellerman *et al*. found that ***Mnium*** (Figure 3), ***Polytrichum*** (Figure 4), and ***Marchantia*** (Figure 5) have highly unsaturated lipids. Thus, the potential is real – we need to explore it.

Figure 2. ***Eurhynchium striatum***, a member of the **Brachytheciaceae** with a high content of arachidonic acid. Photo by Michael Lüth, with permission.

Figure 3. ***Mnium stellare***. The genus ***Mnium*** is known to have highly unsaturated lipids. Photo by Michael Lüth, with permission.

Figure 4. ***Polytrichum commune*** is used in China to reduce inflammation and fever, as well as to treat the common cold and kidney and gallstones. Photo by Michael Lüth, with permission.

Asakawa has spent his career studying the secondary compounds of liverworts. In this time he has found that some of them produce a number of terpenoids, aromatic compounds, and acetogenins, several of which show interesting biological activity (Asakawa 2008; Asakawa *et al*. 2013). Among these are agents that cause allergenic contact dermatitis, insecticides, insect antifeedants, cytotoxins, piscicides, muscle relaxants, plant growth regulators, anti-HIV agents, DNA polymerase β inhibitory compounds, anti-obesity compounds, neurotrophic agents, NO production inhibitors, antimicrobial agents, and antifungal agents. However, few of these have reached application by the medical practitioners.

Figure 5. ***Marchantia polymorpha*** thallus illustrating the surface that the Chinese considered to resemble the cross section of the liver. Photo by Michael Lüth, with permission.

Bryophytes can be cultured to produce medical compounds. Using knockout genes, we cannot only sequence the genome of bryophytes, but also determine the function of individual genes. It is also easier to transplant genes into the bryophyte genome than into tracheophytes. This is possible because the bryophyte spends an extended period of time as a leafy plant with only one set of chromosomes. The model system ***Physcomitrella patens*** (Figure 6, Figure 7) is superior to the traditional mammalian production hosts and cultures can even be stored frozen for ten years, then begin producing again when thawed and cultured (Beike *et al*. 2010).

Figure 6. ***Physcomitrella patens*** growing in the wild. Photo by Michael Lüth, with permission.

Figure 7. ***Physcomitrella patens*** growing on agar plates. Photo by Sabisteb, through Creative Commons.

Herbal Medicines

Not surprisingly, herbal medicines of China (Figure 1), India, and Native Americans include bryophytes (Harris 2008). In China, 63 species are known to have medicinal uses. In India, 22 species are known to have medicinal use, but only in the Himalayas. Ayurvedic (holistic medicine of India, over 3000 years old) texts report little or no use. Native Americans have used bryophytes for drugs, fibers, and clothing (University of Michigan, Dearborn, 2003). The mosses ***Calymperes*** (Figure 8), ***Campylopus*** (Figure 9), and ***Sphagnum*** (Figure 10) have been used for medicinal purposes in Malaysia (Burkill 1966; Tan 2003). ***Timmiella*** (Figure 11) has been used medicinally in Egypt (Harris 2008).

Figure 8. ***Calymperes erosum***, considered a medicinal plant in Malaysia. Photo by Li Zhang, with permission.

Figure 9. ***Campylopus introflexus***, considered a medicinal plant in Malaysia. Photo by Michael Lüth, with permission.

Native Americans have long traditions of using bryophytes for medical purposes. The languages of the natives of the central coast of British Columbia include words for ***Plagiomnium insigne*** (Figure 12) that mean tiny, tiny little trees in Oweekeno; this moss is important to them for medicinal use (Turner 1973; Compton 1993; Harris 2008). The users recognize two different forms of the species (Compton 1993; Harris 2008). Those that grow under Douglas fir (*Pseudotsuga menziesii*; Figure 13) are less effective medically than those that grow under spruce (*Picea*; Figure 14).

Figure 10. ***Sphagnum centrale***, considered a medicinal plant in Malaysia. Photo courtesy of Betsy St. Pierre.

Figure 11. ***Timmiella barbuloides*** with capsules. A species of ***Timmiella*** is used for medicine in Egypt. Photo by Michael Lüth, with permission.

Figure 12. ***Plagiomnium insigne*** with capsules, a species used by natives in British Columbia, Canada. Photo from Botany Website, UBC, with permission.

Figure 13. ***Pseudotsuga menziesii*** forest in snow, habitat for ***Plagiomnium insigne***. Photo by Dave Powell, USDA, through Creative Commons.

Figure 14. ***Picea sitchensis*** forest floor. ***Plagiomnium insigne*** produces more potent medicine in western spruce forests compared to those of Douglas fir. Photo by Henry Hartley, through Creative Commons.

The Doctrine of Signatures (based on the concept that God provided visual cues through the characteristics of the plants), highly developed during the European Renaissance, has dictated the use of a variety of bryophytes, especially liverworts, in herbal medicine. For example, liverworts resemble the liver, so they have been used to treat liver ailments.

Asakawa (2015) names ***Bryum argenteum*** (Figure 47) as an antibacterial moss.

Not only do a number of bryophytes serve as medicinal herbs, but ***Sphagnum*** (Figure 10) has been used to deliver the medicine by using it to make a suppository (Stevenson 2012).

Medicinal Teas

Johannes Enroth (Bryonet 28 January 2009) visited the Yucatan, Mexico, and discovered mosses in use there. The local guide was a "coba-maya" who was familiar with uses of plants. He reported a medical tea made from a moss growing on tree trunks. Enroth collected a bit and identified the moss as ***Sematophyllum adnatum*** (Figure 15).

Figure 15. ***Sematophyllum adnatum***, a moss used to make a medicinal tea in the Yucatan of Mexico. Photo by Bob Klips, with permission.

The moss ***Rhodobryum*** (Figure 1) is used to make a medicinal tea (Franquemont *et al.* 1990; Harris 2008), and as you will see below, it has tested medicinal properties useful for several medical conditions. ***Polytrichum commune*** (Figure 4) has been boiled to make a tea for treating colds (Gulabani 1974; Beike *et al*. 2010).

Liver Ailments

The most widely known use of bryophytes determined by its appearance is that of ***Marchantia polymorpha*** (Figure 5) to treat liver and other ailments; the surface suggests the cross section of liver (Miller & Miller 1979). In China, it is still used to treat the jaundice of hepatitis and as an external cure to reduce inflammation (Hu 1987) and has gained the reputation of cooling and cleansing the liver (Bland 1971). But it has also been used for liver problems in Europe (Thieret 1956) and South America (Garcia Barriga 1992; Roig y Mesa 1945).

Based on the Doctrine of Signatures, it is not surprising that ***Marchantia polymorpha*** (Figure 5) is not the only species in that genus to be used to treat liver ailments. In India, ***M. convoluta*** is also used (Rao 2009; Chandra *et al*. 2017). And ***Marchantia palacea*** (Figure 16**)** is used to treat hepatitis (Sabovljević *et al*. 2011; Chandra *et al*. 2017).

Figure 16. ***Marchantia paleacea***, a liverwort used to treat hepatitis in India. Photo by Jan-Peter Frahm, with permission.

Perhaps there is more wisdom in these ancient remedies than at first appears. Asakawa (2012) found that some of the isolated terpenoids from liverworts had anti-HIV inhibitory properties. ***Fissidens nobilis*** (Figure 48) is useful for jaundice (Asakawa 2015).

Stones

In the western Himalayans, native people use ***Wiesnerella denudata*** (Figure 17) to treat gall stones (Kumar *et al*. 2007). In China, ***Polytrichum commune*** (Figure 4) is boiled to make a tea that reputedly helps to dissolve stones of the kidney and gall bladder (Gulabani 1974; Chandra *et al*. 2017). Asakawa (2015) reported that ***Conocephalum conicum*** (Figure 18) is useful in treating gallstones.

Figure 17. ***Wiesnerella denudata***, a liverwort used to treat gall stones in the western Himalayas. Photo by Jan-Peter Frahm, with permission.

Figure 18. Thallose liverwort, ***Conocephalum conicum***, one of the thallose liverworts used to treat gallstones, bites, boils, burns, cuts, eczema, and wounds. Photo by Janice Glime.

Ringworm

Riccia spp. (Figure 19) were ground to a paste and used in the Himalayas to treat ringworm (*Tinea* spp., a fungus; Figure 20) because of the resemblance of the growth habit of those liverworts to the rings made by the fungus (Shirsat 2008; Chandra *et al*. 2017). Recent tests on ***Riccia fluitans*** (Figure 21) from Florida indicated no ability to inhibit growth of bacteria [*Pseudomonas aeruginosa* (Figure 22), *Staphylococcus aureus* (Figure 23)] or yeast (*Candida albicans*; Figure 24) (Pates & Madsen 1955). Might ***Riccia*** species do any better with ringworm?

Figure 19. Circular formations of ***Riccia*** species, such as this ***Riccia austinii***, suggested their use for curing ringworm, according to the Doctrine of Signatures. Photo by Janice Glime.

Figure 20. ***Tinea*** (ringworm) on arm. Photo by Grook Da Oger, through Creative Commons.

Figure 21. ***Riccia fluitans***, a floating aquatic liverwort that seems to lack antibiotic properties. Photo by Jan-Peter Frahm, with permission.

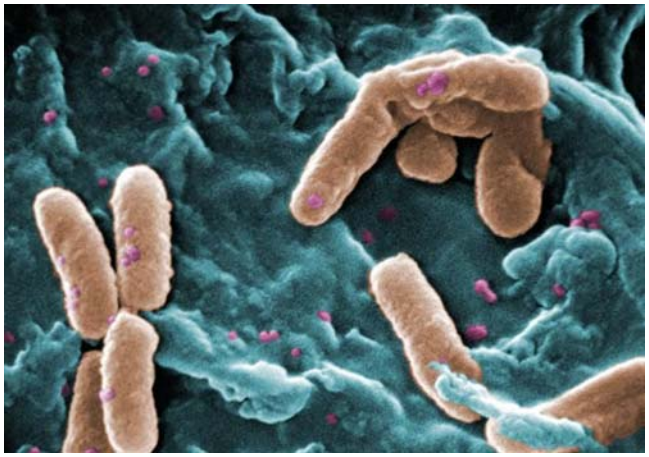

Figure 22. SEM of ***Pseudomonas aeruginosa***, a bacterial species that is not inhibited by ***Riccia fluitans***. Photo by Janice Haney Carr, through Creative Commons.

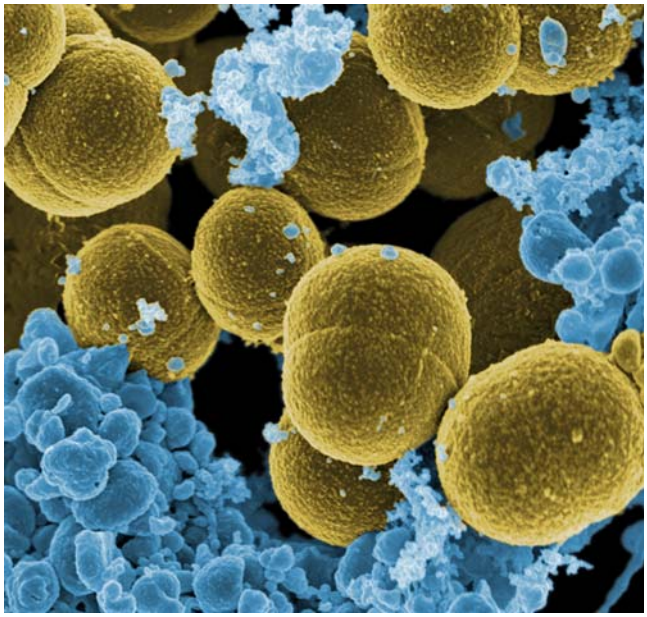

Figure 23. SEM of *Staphylococcus aureus*, a bacterium that is not inhibited by ***Riccia fluitans***. Photo by NIAID, through Creative Commons.

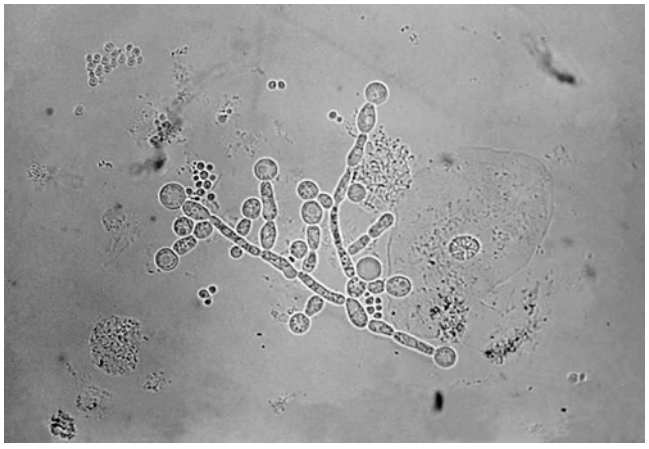

Figure 24. *Candida albicans*, a yeast species that is inhibited by extracts of the liverworts ***Conocephalum conicum***, ***Marchantia polymorpha***, and ***Plagiochasma appendiculatum***, but not ***Riccia fluitans***. Photo from Public Health Image Library, through public domain.

Heart, Blood, and Cardiovascular Medicine

In China, 30-40 species of bryophytes may be found on the shelves of the local pharmacist (Ding 1982). Among the more common ones are ***Rhodobryum giganteum*** (Figure 25, Figure 30) and ***R. roseum*** (Figure 26), used to treat nervous prostration and cardio-vascular diseases, the latter being a use that may have scientific merit (Wu 1982). Among these uses is the treatment of hypertension (high blood pressure) with ***R. giganteum*** (Wu 1977; Pant 1998; Asakawa 2007b, 2015; Chandra *et al*. 2017).

Figure 25. ***Rhodobryum giganteum***, a species widely used medicinally in Yunnan, China. Photo by David Long, with permission.

Figure 26. ***Rhodobryum roseum***, a species that is used to treat nervous prostration and cardio-vascular diseases in China. Photo by Michael Lüth, with permission.

In 1977, Wu reported the use of ***Rhodobryum giganteum*** (Figure 25, Figure 30) to cure cardiovascular disease in China. Chinese scientists have attempted to demonstrate the basis for the healing powers of some of the mosses, including ***Rhodobryum giganteum***, used in ancient treatments in China (Ding 1982). Going directly to the peasants in east Szechuan, the staff of the Laboratory of the Fourth Medical School in China learned about mosses used by the peasants (Wu 1982). Through clinical research, they successfully demonstrated that an ether extract of ***Rhodobryum giganteum***, used by these peasants to cure angina, contains volatile oils, lactones, and amino acids; when given to white mice, the extract actually reduced the

oxygen resistance by increasing the rate of flow in the aorta by over 30%. Is it time to replace ACE inhibitors, calcium channel blockers, and beta blockers and their side effects?

The term *Hui Xin Cao* in Yunnan refers to the medical effect of ***Rhodobryum*** species, meaning "return-the-heart-herb" (Harris 2008). The Chinese use ***R. roseum*** (Figure 26), ***R. giganteum*** (Figure 25, Figure 30), and ***R. ontariense*** (Figure 27). Unfortunately, the term *Hui Xin Cao* refers to other plants as well (remember that the name refers to its use, not its morphology), including the moss ***Pogonatum cirratum*** (Figure 28) and the shrub *Ledum* (Figure 29). Members of the genus ***Rhodobryum*** are used in Yunnan for minor heart problems (Harris & Yang 2009). Usage depends on location, not on gender, occupation, or ethnicity. And its use also occurs in both rural areas and in traditional Chinese medicine hospitals and medical colleges.

Figure 27. ***Rhodobryum ontariense***, a species used in China to treat the heart. Photo by Janice Glime.

Figure 28. ***Pogonatum cirratum***, a species used in China to treat the heart. Photo by Li Zhang, with permission.

These reports of traditional usage were supported by a number of studies on ***Rhodobryum. giganteum*** (Figure 25, Figure 30) that demonstrated its usefulness in treating cardiovascular problems and illustrating the physiological mechanisms involved (Yu & Ma 1993; Yu *et al*. 1994, 1995; Yan *et al*. 1998; Lei *et al*. 2001a, b; Gao *et al*. 2004; Zhou *et al*. 2004; Wang *et al*. 2005; Dai *et al*. 2006; Hu *et al*. 2009). Pejin *et al*. (2011a, 2012c) reported on the antihypertensive effect of ***R. ontariense*** (Figure 27) *in vivo* and attempted to find the mechanism used by ***R. ontariense*** in controlling hypertension (Pejin *et al*. 2012e). They were able to eliminate any effect on human erythrocyte membrane fluidity, there was no reservoir of nitric oxide in the blood, and there was only low ABTS cation scavenging activity and little content of phenolic contents. The actual mechanism remains elusive.

Figure 29. ***Ledum*** sp., a shrub with the same Chinese name as ***Pogonatum cirratum*** and several species of ***Rhodobryum*** because they are all used to treat heart problems. Photo by Meggar, through Creative Commons.

Masanobu Higuchi (Bryonet, 20 November 2006) reports that when he stayed in Zhong Dian, northwestern Yunnan, China, in 1994, he saw local people selling herbal medicines by the roadside. Among these was the moss ***Rhodobryum giganteum*** (Figure 25, Figure 30) in dry condition, a traditional Tibetan medicine for heart trouble. It was selling for US $0.50 per 10g. The same species is used in the Himalayas as a neurologial and cardiac activant (Kumar *et al*. 2007).

As already noted, their use as medical plants has made ***Rhodobryum*** species the subject of a number of biochemical studies, revealing a variety of biochemical constituents in ***R. ontariense*** (Figure 27) [fatty acids 9,12,15-octadecatrien-6-ynoic and α-linolenic acid, having known heart protective activity (Pejin *et al.* 2012a); 1-kestose, a "health promoter" (Pejin *et al*. 2012b); short-chain fructooligosaccharides, well known as prebiotics (Pejin *et al*. 2012e). Thirteen essential oils have been identified in ***R. ontariense*** (Pejin *et al*. 2011b), but their roles in efficacy of Chinese medicine still remain to be determined.

But wait! Mosses are known accumulators of heavy metals, and we know that high amounts of these are dangerous to human health. Pejin *et al*. (2012d) tested ***Rhodobryum ontariense*** (Figure 27) for its heavy metal content. Fortunately, they found that the concentrations of arsenic, cadmium, chromium, copper, iron, lead, mercury, nickel, manganese, and zinc in these mosses used in tea were at safe levels for a typical daily intake of the tea. They suggested that manganese was one of the important components in treating hypertension. Nevertheless, these results do not mean that the Chinese populations and

species are safe as the heavy metal concentrations vary by locations and distance from pollution source.

Lisu women in Yunnan Province, China, hike to fens in the alpine area above the Salween River Valley (Nu Jiang) to collect large amounts of ***Sphagnum*** (Figure 10), which they subsequently dry (James Shevock, Bryonet, 16 January 2007). Despite about 27 species of ***Sphagnum*** reported in Yunnan, these Lisu women (one of several minority peoples in Yunnan Province) seem able to recognize a particular species in the field; they claim that it is only this species that is used for medicinal purposes. This species of ***Sphagnum*** is used as a heart tonic, probably brewed like a tea. Once dried and packaged, the moss was to be exported to Canada! (Surely Canada has more ***Sphagnum*** than Yunnan?)

Figure 30. Dried ***Rhodobryum giganteum*** (left container) at a shop in Yunnan, China. Photo by David Long, with permission.

In India, bryophytes have also been used to treat heart disease. One such treatment is with ***Cratoneuron filicinum*** (Figure 31) (Pant 1998; Asakawa 2015; Chandra *et al*. 2017).

Figure 31. ***Cratoneuron filicinum***, a species used in India to treat the heart. Photo by Barry Stewart, with permission.

The Indians have also used several bryophytes to stop bleeding. These include the thallose liverwort ***Reboulia hemisphaerica*** (Figure 32) and the mosses ***Funaria hygrometrica*** (Figure 33), ***Plagiomnium cuspidatum*** (Figure 34), ***Polytrichum commune*** (Figure 4), ***Pogonatum cirratum*** (Figure 28), and ***Taxiphyllum taxirameum*** (Figure 35) (Gulabani 1974; Ding 1982; Pant 1998; Asakawa 2007b, 2015; Azuelo *et al*. 2011; Alam 2012; Shirsat 2008; Chandra *et al*. 2017).

Figure 32. ***Reboulia hemisphaerica***, a species used in India to stop bleeding. Photo by Jan-Peter Frahm, with permission.

Figure 33. ***Funaria hygrometrica***, a species used in India to stop bleeding. Photo by Michael Lüth, with permission.

Figure 34. ***Plagiomnium cuspidatum***, a species used in India to stop bleeding. Photo by Hermann Schachner, through Creative Commons.

Figure 35. ***Taxiphyllum taxirameum***, a species used in India to stop bleeding. Photo by Michael Lüth, with permission.

Nosebleeds

One odd choice is the use in Cambridge of ***Homalothecium sericeum*** (Figure 36) from skulls used to treat nosebleeds, with recorded records as early as 1537 (Belcher & Swale 1998). The skulls were placed in damp places to cultivate this moss. But other researchers concluded that the tale was concocted and that no medicinal value was present (Scott 1988). On the other hand, Robert Boyle used it effectively on his own nosebleeds. Perhaps it is just a good absorbent.

Figure 36. ***Homalothecium sericeum*** from skulls is used to treat nosebleeds in Cambridge. Photo by Michael Lüth, with permission.

In another context, ***Plagiomnium cuspidatum*** (Figure 34) has been used to treat nosebleeds in India (Pant 1998; Asakawa 2007a, 2015). This casts suspicion on my suggestion of absorbency as this species does not rehydrate easily. On the other hand, as already noted, Asakawa (2015) reported that the mosses ***Funaria hygrometrica*** (Figure 33), ***Oreas martiana*** (Figure 38), ***Polytrichum commune*** (Figure 4), and ***Taxiphyllum taxirameum*** (Figure 35) and the liverwort ***Reboulia hemisphaerica*** (Figure 32) stop bleeding.

Neurological Conditions

Few bryophytes seem to be used for neurological conditions. Nevertheless, in Cambridge, England, the moss ***Homalothecium sericeum*** (Figure 36) from skulls has been used in the treatment of epilepsy (Belcher & Swale 1998). In China, liverworts have been used to treat convulsions, neurasthenia (emotional disturbance typically involving lassitude, fatigue, headache, and irritability), and other nerve conditions (Asakawa 2012). ***Rhodobryum roseum*** is useful for treating neurasthenia (Asakawa 2015).

Several bryophytes have been used to treat pain. For ***Leucobryum bowringii*** (Figure 37), a paste is made of leaf tips mixed in a cup of *Phoenix sylvestris* (silver date palm) to treat pain (Lubaina *et al*. 2014; Chandra *et al*. 2017). ***Oreas martiana*** (Figure 38) is used as an anodyne for treating pain (Asakawa 2007b, 2015; Chandra *et al*. 2017). These authors also reported the use of ***Oreas martiana*** to treat nervosism and nervous exhaustion as well as epilepsy. ***Ditrichum pallidum*** (Figure 39) has been used in India to treat convulsions, especially in infants (Pant 1998; Asakawa 2007b, 2015; Chandra *et al*. 2017).

Figure 37. ***Leucobryum bowringii***, a species used to treat pain. Photo through Creative Commons.

Figure 38. ***Oreas martiana***, a species used to treat pain. Photo by Michael Lüth, with permission.

Figure 39. ***Ditrichum pallidum*** on the forest floor. This species has been used in India to treat convulsions in infants. Photo by Janice Glime.

Figure 41. ***Bryum capillare*** with capsules, a moss used by Seminole native people in North America to treat body aches and fever. Photo by Michael Lüth, with permission.

Inflammation and Fever

Today we have freezers and use cold packs to soothe inflammation and reduce fevers, but not so long ago those conveniences were not available. Instead, ***Polytrichum commune*** (Figure 4) has been used in China to reduce inflammation and fever (Ding 1982; Chandra *et al*. 2017), and the Seminole native people in North America used the small mosses ***Barbula unguiculata*** (Figure 40) and ***Bryum capillare*** (Figure 41), as well as larger mosses like ***Octoblepharum albidum*** (Figure 42), as external applications for fever and body aches (Sturtevant 1954; Chandra *et al*. 2017). ***Barbula indica*** (Figure 43) and ***Weissia controversa*** (Figure 44) have also been used in the Western Ghats to treat intermittent fever (Lubaina *et al*. 2014). ***Taxiphyllum taxirameum*** (Figure 35) is an anti-inflammitory (Asakawa 2015).

Figure 42. ***Octoblepharum albidum***, a moss used by Seminole native people in North America to treat body aches and fever. Photo by Niels Klazenga, with permission.

Figure 40. ***Barbula unguiculata***, a moss used by Seminole native people in North America to treat body aches and fever. Photo by Bob Klips, with permission.

Figure 43. ***Barbula indica***, a moss used in the Western Ghats to treat fever. Photo by Li Zhang, with permission.

Figure 44. ***Weissia controversa***, a moss used in the Western Ghats to treat fever. Photo by Michael Lüth, with permission.

Fontinalis antipyretica (Figure 45) reputedly got its specific name from its ability to work against fever, as recorded in the journal of Linnaeus (Nils Cronberg, pers. comm.). Drobnik and Stebel (2014) found that its use against fever is reported in pre-Linnaean bryophyte floras of central Europe. However, many people have interpreted the name to be derived from its use to insulate chimneys against fire, where in actuality it seems to have little value. On the other hand, it may reduce the heat penetrating into the house. But does it reduce fever? Perhaps it can serve as a cool poultice.

Figure 45. ***Fontinalis antipyretica***, reported by Linnaeus as being used to treat fever. Photo by Michael Lüth, with permission.

Sabovljević *et al*. (2011) reported the use of ***Marchantia palacea*** (Figure 16) to reduce swelling and bring down fever. ***Leptodictyum riparium*** (Figure 46), an aquatic moss, ***Philonotis fontana*** (Figure 62), a wetland moss, and the cosmopolitan moss ***Bryum argenteum*** (Figure 47) are used to treat fever in India (Pant 1998; Asakawa 2007b, 2015; Chandra *et al*. 2017). ***Octoblepharum albidum*** (Figure 42) was considered in India to have similar ability to reduce fever (Singh 2011; Chandra *et al*. 2017). The mosses ***Haplocladium capillatum*** (see Figure 52) and ***Leptodictyum riparium***, ***Polytrichum commune*** (Figure 4), ***Rhodobryum giganteum*** (Figure 25, Figure 30), and ***Weissia controversa*** (Figure 44) and the thallose liverworts ***Conocephalum conicum*** (Figure 18) and ***Marchantia polymorpha*** (Figure 5) are likewise antifever agents.

Figure 46. ***Leptodictyum riparium***, a moss used to treat fever in India. Photo by David T. Holyoak, with permission.

Figure 47. ***Bryum argenteum***, a moss used to treat fever in India. Photo by Tushar Wankhede, through Creative Commons.

Urinary and Bowel Treatments

The Chinese also use ***Polytrichum commune*** (Figure 4) as a detergent diuretic, laxative, and hemostatic agent (Ding 1982; Ando & Matsuo 1984; Hu 1987; Fan *et al*. 2004; Harris 2008). In India, ***Fissidens nobilis*** (Figure 48) and ***Dawsonia longifolia*** (Figure 49) are used as diuretics (Pant 1998; Azuelo *et al* 2011; Chandra *et al*. 2017), and Asakawa (2015) reports ***Marchantia polymorpha*** (Figure 5) for the same purpose. ***Pogonatum cirratum*** (Figure 28) has been used as a laxative in India (Azuelo *et al*. 2011; Alam 2012; Chandra *et al*. 2017). Asakawa (2015) reports ***Fissidens nobilis*** (Figure 48) as a diuretic and ***Haplocladium capillatum*** (see Figure 52) for treatig cystitis and uropathy. ***Leptodictyum riparium*** (Figure 46) and ***Rhodobryum giganteum*** (Figure 25, Figure 30) likewise are used to treat **uropathy** (restricted urine flow) (Asakawa 2015).

Figure 48. ***Fissidens nobilis***, a species that is used as a diuretic in India. Photo by Jan-Peter Frahm, with permission.

Figure 49. ***Dawsonia longifolia***, a species used as a diuretic in India. Photo by Jan-Peter Frahm, with permission.

I was surprised to find ***Polytrichum juniperinum*** (Figure 50) listed in Materia Medica as a treatment for painful urination of the elderly, obstruction or suppression, and dropsy (Available Materia Medicas 2011). The medicine is made by boiling two ounces of the moss in a liter of water until it boils down to only half that – a pint, making a "tincture." One dose (4 ozs, 113 g) should be taken every 8 hours.

Figure 50. ***Polytrichum juniperinum***, a hairy cap moss, is used in China to treat urinary and prostate problems. It can be recognized by the brown tips on the leaves and the rolled over leaf edges that cover the lamellae. Photo by Michael Lüth, with permission.

The leafy liverwort ***Herbertus*** sp. (Figure 51) is used in India as an antiseptic, antidiarrheal agent, expectorant, and astringent (Azuelo *et al*. 2011; Alam 2012; Chandra *et al*. 2017). In both China and India, **cystitis** (inflammation of the bladder) has been treated with the moss ***Haplocladium microphyllum*** (Figure 52) (Ding 1982; Pant 1998).

Figure 51. The leafy liverwort ***Herbertus sendtneri***. Some members of the genus ***Herbertus*** are used in India as a filter for smoking. Photo by Michael Lüth, with permission.

Figure 52. ***Haplocladium microphyllum***, a species that is used to treat bladder infections in China and India. Photo by Robin Bovey, with permission through Dale Vitt.

Gynecology

The absorbent properties that make ***Sphagnum*** (Figure 10) an excellent bandage also make it suitable for diapers and sanitary napkins, a product currently sold by Johnson and Johnson Company (D. H. Vitt, pers. comm.).

Figure 53. ***Sphagnum*** Sanitary napkin. Photo from National Museum of American History, with online permission.

Sphagnum (Figure 10) has also been used, along with grass, sponge, and other plant fiber, as a contraceptive to block the entry of sperm (Stanley 1995). By contrast, following successful pregnancies, the Nitinaht peoples of Vancouver Island, Canada, used ***Polytrichum commune*** (Figure 4) as a gynecological aid (Turner *et al*. 1983; Chandra *et al*. 2017). Women in labor chewed the moss to speed up the labor process.

In China, ***Polytrichum*** (Figure 4, Figure 50) has been used to stop bleeding and night sweats, presumably associated with menopause (EBCHSATCM 1999; Cheng *et al*. 2008; Fu *et al*. 2009). It has also been used to treat **uterine prolapse** (the uterus sags due to weakening of muscles or ligaments that support it).

The moss ***Oreas martiana*** (Figure 38) is used to treat **menorrhagia** (prolonged bleeding with menstrual period) (Asakawa 2007b; Chandra *et al*. 2017). ***Barbula indica*** (Figure 43) has been used in the Western Ghats to treat menstrual pain (Lubaina *et al*. 2014; Chandra *et al*. 2017).

Disinfectant and Infections

The Native American Nitinahts also used ***Sphagnum*** (Figure 10) as a disinfectant (Turner *et al*. 1983). ***Fissidens*** (Figure 54) is used in China as an antibacterial agent for swollen throats and other symptoms of bacterial infection, and in Bolivia it likewise has medicinal uses. Judith Sullivan (Bryonet, 16 January 2007) reported seeing labels on Chinese medicines that included ***Grimmia*** (Figure 55), ***Atrichum*** (Figure 56), ***Polytrichum*** (Figure 4, Figure 50), and ***Thuidium*** (Figure 57), primarily as anti-bacterial and anti-inflammatory agents. ***Polytrichum juniperinum*** (Figure 50) is used there for some prostate and urinary difficulties.

Figure 54. ***Fissidens osmundoides***, a moss in one genus used as an antibacterial agent to treat sore throats in Bolivia and several Asian countries. Photo by Michael Lüth, with permission.

Figure 55. ***Grimmia pilifera***, a Chinese species. Some members of this genus are used in medicines in China. Photo by Henk Greven, with permission.

Figure 56. ***Atrichum undulatum***. Some members of this genus are used in medicines in China. Photo by Michael Lüth, with permission.

Figure 57. ***Thuidium recognitum***. Some members of ***Thuidium*** are used as anti-bacterial and anti-inflammatory agents in China. Photo by Jan-Peter Frahm, with permission.

Dried ***Sphagnum*** (Figure 58) is sold to treat hemorrhages (Bland 1971), and ***S. teres*** (Figure 58) is used to treat eye diseases and hemorrhoids (Ding 1982). ***Haplocladium microphyllum*** (Figure 52) is sold to treat bronchitis, tonsillitis, and tympanitis, as well as cystitis (Ding 1982).

Figure 58. ***Sphagnum teres*** is used to treat eye diseases in Asia. Photo by Michael Lüth, with permission.

As noted in Chapter 1 of this volume, the soap **Sphagnol** is a ***Sphagnum*** (Figure 10; Figure 58) product used to treat skin problems such as acne, eczema, chilblains (painful inflammation of small blood vessels in the skin), dandruff, insect bites, and ringworm (a fungus) (The Science Museum 2012). This product was used during both World Wars by the British Red Cross to treat facial wounds and is believed to have antibiotic properties.

Kumar *et al*. (2007) reported on antibacterial species used in India, as discussed in Chapter 2-2 on Biologically Active Substances. ***Oreas martiana*** (Figure 38) and ***Taxiphyllum taxirameum*** (Figure 35) likewise are used to treat wounds (Asakawa 2015), perhaps having antibiotic properties. the leafy liverwort ***Frullania tamarisci*** has known antiseptic properties (Asakawa 2015).

Nose and Throat

In both India and North America, the moss ***Philonotis fontana*** (Figure 62) has been used to treat **adenopharyngitis**, an inflammation of the pharynx and tonsils (Flowers 1957; Pant 1998; Asakawa 2007b; Chandra *et al*. 2017). ***Haplocladium capillatum*** (see Figure 52) and ***Philonotis fontana*** likewise can be used to treat adenopharyngitis (Asakawa 2015). ***Bryum argenteum*** (Figure 47) and ***Weissia controversa*** (Figure 44) have chemical properties used to treat **rhinitis** (inflammation of the mucous membrane of the nose) (Asakawa 2015).

Lung Diseases

Funaria hygrometrica (Figure 33) has been used in India to treat pulmonary tuberculosis (Pant 1998; Chandra *et al*. 2017), and Asakawa (2015) indicates it has compounds useful for that purpose, as does ***Polytrichum commune*** (Figure 4). The similarity of ***Marchantia polymorpha*** (Figure 5) thalli to the texture of lung tissue caused Europeans to use that liverwort to treat pulmonary tuberculosis (Bland 1971). It is likely that this Doctrine of Signatures was also responsible for the Chinese use of liverworts to treat pulmonary tuberculosis (Asakawa 2012). It is interesting that its thallus has been interpreted as resembling both liver tissue and lung tissue.

In Cambridge, England, the moss ***Homalothecium sericeum*** (Figure 36) was used to treat whooping cough (Belcher & Swale 1998). In the Himalayas the moss ***Haplocladium microphyllum*** (Figure 52) is used to treat bronchitis (Kumar *et al*. 2007). ***Haplocladium microphyllum*** has also been used to treat tonsillitis and pneumonia (Ding 1982; Pant 1998; Chandra *et al*. 2017); ***H. capillatum*** (see Figure 52) is known for its use in treating in pneumonia (Asakawa 2015).

Treatments of colds, not surprisingly, has made use of bryophytes. ***Hyophila involuta*** (Figure 59) has been used for the symptoms of a cold, cough, and sore throat. This treatment is a leaf decoction with a pinch of ground pepper, used daily (Lubaina *et al*. 2014; Chandra *et al*. 2017). Also in India, natives in the Western Ghats have used ***Weissia controversa*** (Figure 44) to treat colds.

Figure 59. ***Hyophila involuta*** drying. This species has been used to treat cold, cough, and sore throat. Photo by Bob Klips, with permission.

The other side of the coin is the ability of some mosses, especially ***Sphagnum*** (Figure 58), to harbor fungi that cause lung disease. ***Sphagnum*** was once thought to harbor *Mycobacteria* (Figure 60), the genus in which the tuberculosis bacterium resides, but now it seems that it is not the reservoir for this genus it was thought to be (Deriu *et al*. 1995). On the other hand, the fungus *Sporothrix schenckii* (Figure 61), common on ***Sphagnum***, does cause pulmonary **sporotrichosis**, an infection of the lung resulting from breathing the fungi (McCain & Buell 1968).

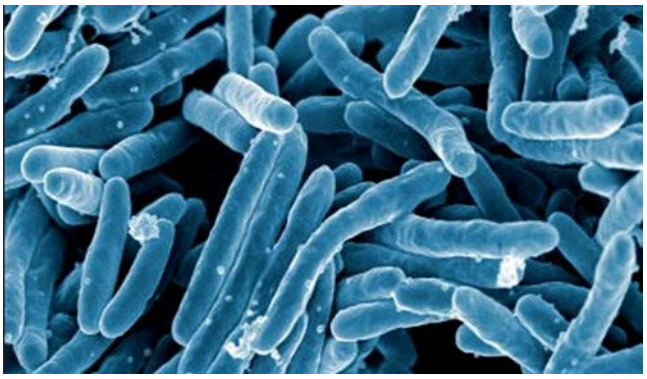

Figure 60. ***Mycobacterium tuberculosis*** SEM, member of a pathogenic genus once thought to live among ***Sphagnum***. Photo from NIAID, through Creative Commons.

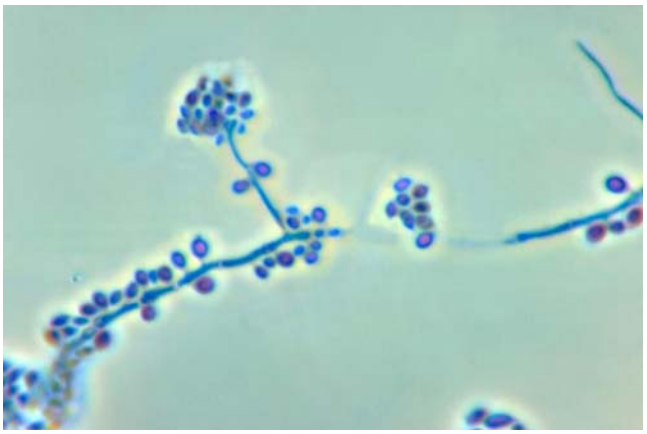

Figure 61. ***Sporothrix schenckii*** conidia, a species that grows among ***Sphagnum*** and causes **sporotrichosis**. Photo from USDHHS, through public domain.

Skin Ailments and Burns

The antibiotic properties of many bryophytes suggest that they should promote healing of skin infections. The thallose liverwort ***Reboulia hemisphaerica*** (Figure 32) is used to treat skin blotches, external wounds, and bruises and ***Oreas martiana*** (Figure 38) is used to treat external wounds (Asakawa 2007b, 2015; Chandra *et al*. 2017). ***Fissidens nobilis***, ***Conocephalum conicum*** (Figure 18), and ***Marchantia polymorpha*** (Figure 5) have compounds that help in the healing of burns (Asakawa 2015). ***Funaria hygrometrica*** (Figure 33) is useful in treating bruises and Athlete's foot. ***Rhodobryum giganteum*** (Figure 25, Figure 30), ***Conocephalum conicum***, and ***Marchantia polymorpha*** can be used to treat cuts (Asakawa 2015).

Himalayan Indians use a mixture of moss ashes with fat and honey to soothe and heal cuts, burns, and wounds (Pant *et al*. 1986; Pant 1998; Chandra *et al*. 2017), claiming that these ashes heal wounds more quickly (Pant & Tewari 1989). ***Taxiphyllum taxirameum*** (Figure 35) is among those mosses used to treat surface wounds (Pant 1998; Asakawa 2007b; Chandra *et al*. 2017). In the Himalayas, the Gaddi tribe uses ***Philonotis fontana*** (Figure 62) and ***Plagiochasma appendiculatum*** (Figure 63) to treat burns and skin diseases (Flowers 1957; Pant 1998; Asakawa 2007b; Kumar *et al*. 2007; Shirsat 2008; Alam 2012; Chandra *et al*. 2017). ***Bryum thomsonii*** is used in the Northwest Himalayas for healing wounds (Kumar *et al*. 2007). Himalayan Indians have used ***Marchantia polymorpha*** (Figure 5; Figure 64) or ***M. palmata*** to treat boils and abscesses because the young archegoniophore resembles a boil as it emerges from the thallus (Pant & Tewari 1989).

Figure 62. ***Philonotis fontana*** is a wetland moss used by Gosuite native people to relieve pain of burns. Photo by Michael Lüth, with permission.

In India, the pendent moss ***Aerobryum lanosum*** is used to treat burns. The whole plant is boiled in goat urine and applied externally (Lubaina *et al*. 2014; Chandra *et al*. 2017). Species of ***Mnium*** (*sensu lato*?) (Figure 3) have been used in a poultice to reduce pain from bruises, wounds, and burns (Azuelo *et al*. 2011; Chandra *et al*. 2017). Similarly, these authors found that ***Plagiomnium*** (Figure 12, Figure 34) has been used for treating infections and swellings.

Also in India, the thallose liverwort ***Targionia hypophylla*** (Figure 65) is used, mixed with leaves of the flowering plant *Actiniopteris radiata*, and ground into a paste, then mixed with two tablespoons of coconut oil. This paste is smeared over the body of the children affected by itching skin, scabies, and other skin diseases (Remesh & Manju 2009; Chandra *et al*. 2017).

Figure 63. ***Plagiochasma appendiculatum*** with archegoniophores, a species used in the Himalayas to treat burns and skin diseases. Photo by Michael Lüth, with permission.

Figure 64. Young archegoniophores of ***Marchantia polymorpha***, somewhat resembling a boil. Photo by Rudolf Macek, with permission.

Figure 65. ***Targionia hypophylla***, a species used in India to treat skin diseases. Photo by Martin Hutten, with permission.

Marchantia palmata is made into a fleshy leaf paste and applied directly to acute inflammation caused by heat (burns) (Tag *et al*. 2007; Chandra *et al*. 2017).

Another skin-related use in India is that of the cosmopolitan moss ***Funaria hygrometrica*** (Figure 33) to treat bruises and skin infections (Pant 1998; Chandra *et al*. 2017).

Among the Native Americans, the Cheyenne in Montana use ***Polytrichum juniperinum*** (Figure 50) in medicines (Hart 1981). In Utah, USA, the Gosuite native peoples used ***Bryum*** (Figure 41, Figure 47), ***Mnium*** (Figure 3), ***Philonotis*** (Figure 62), and various matted hypnaceous forms crushed into a paste applied to reduce the pain of burns, bruises, and wounds (Flowers 1957). ***Sphagnum*** (Figure 10) was used by Native Americans as a carrier for berries that were rubbed on children's sores (Carrier Linguistic Committee 1973).

As one might expect, the Chinese have used liverworts in the treatment of skin ailments, including cuts, burns, and bruises (Asakawa 2012). A mixture of the thallose liverworts ***Conocephalum conicum*** (Figure 18) and ***Marchantia polymorpha*** (Figure 5) with vegetable oils is used in China on bites, boils, burns, cuts, eczema, and wounds (Wu 1977; Ding 1982; Ando 1983; Yan *et al.* 1999).

In China and India, ***Conocephalum conicum*** (Figure 18) has a number of medical uses. Its antimicrobial, antifungal, antipyretic, and antidotal activities contribute to its usefulness to treat cuts, swollen tissue, scalds, burns, fractures, and poisonous snake bites (Ding 1982; Alam 2012; Chandra *et al*. 2017). Likewise, ***Marchantia polymorpha*** (Figure 5) has been used to treat snake bites (Hu 1987; Shirsat 2008; Azuelo *et al*. 2011; Asakawa 2015; Chandra *et al*. 2017). ***Bryum argenteum*** (Figure 47), ***Polytrichum commune*** (Figure 4), and one or more species of ***Philonotis*** (Figure 62) have been used as antidotes (Asakawa 2007b, 2015; Chandra *et al*. 2017).

Alaskan native peoples have used ***Sphagnum*** (Figure 10), mixed with fat, to make a salve (Schofield 1969; Miller & Miller 1979). In Britain ***Sphagnum*** was used to treat boils (Bland 1971), its derivative **sphagnol** to relieve the itch of a mosquito bite (Crum 1988), and for medicinal baths (Crum 1973; Weber & Ploetner 1976; Turner 1993), although the small amounts of active substances put into an average bath are not likely to have any effect.

Nevertheless, Mitchell and Rook (1979) caution us about the possible allergenic effects of ***Sphagnum*** (Figure 10), especially because of its ability to harbor the fungus causing **sporotrichosis** (Adams *et al*. 1982). It is a known danger to nursery workers and harvesters who are in constant contact with the ***Sphagnum*** (D'Alessio *et al.* 1965; McCain & Buell 1968; Tamblyn 1981; Keller 1988; Padhye & Ajello 1990; Coles *et al*. 1992), even affecting areas like the abdomen (Frankel & Frankel 1982). In 1988, sporotrichosis reached sufficient proportions that "*Sphagnum* the culprit" made its debut in the *Milwaukee Journal* (Rosenberg 1988). In 1995, nine of the 65 workers involved in making topiary art at a Florida nursery became infected with lymphocutaneous sporotrichosis (Hajjeh *et al* 1997). Even forestry workers who don't handle the moss directly can contract the disease from working in peatlands (Powell *et al.* 1978). The threat is sufficient to cause the American Orchid Society to warn its members of this occupational hazard (Padhye & Ajello 1990). The Macauley Institute in Aberdeen, England, is investigating the use of hydroponics to produce ***Sphagnum*** that is free of microorganisms and other contaminants. Wearing gloves helps to protect against the lymphocutaneous sporotrichosis (Hajjeh *et al*. 1997), but longer exposures can still lead to pulmonary infections.

Eye Problems and Diseases

In the northwest Himalayas, ***Sphagnum teres*** (Figure 58) is used to treat ophthalmic diseases (Kumar *et al*. 2007). There seems to be medical evidence that at least some of the bryophytes can be used effectively to treat age-related blindness (age-related macular degeneration) (Albert-Ludwigs-Universität Freiburg 2010). Factor H is necessary to maintain healthy eyes (Coffey 2007). The Freiburg research lab has produced a protein in a bioreactor using factor H from mosses. Factor H is otherwise known only from blood and is important for the immune system. 50 million people suffer blindness due to lack of this protein, especially in industrial countries.

Büttner-Mainik *et al*. (2011) developed a protocol to produce Factor H using ***Physcomitrella patens*** (Figure 6, Figure 7). Factor H is a protein that is difficult to produce in animal lines, but these researchers successfully produced it in transgenic ***P. patens***.

Flatbergium sericeum (Figure 66), a relative of ***Sphagnum***, has been used to treat eye diseases (Azuelo *et al*. 2011; Chandra *et al*. 2017). Similarly, ***Sphagnum teres*** (Figure 58) has been used for this purpose in China (Ding 1982).

Figure 66. ***Flatbergium sericeum***, a species that has been used to treat eye diseases. Photo courtesy of Jon Shaw.

Ear Ache and Hearing Problems

Entodon flavescens is used by the Kani tribes in the Western Ghats for treating ear ache (Lubaina *et al*. 2014; Chandra *et al*. 2017). They use a leaf juice as ear drops, especially in cold weather. ***Haplocladium capillatum*** (see

Figure 52) has been used to treat tinnitis, but recent news reports suggest this is not really related to the ears.

Hair Treatments

Soothing a wound of a different sort (human pride), the Chinese use ***Fissidens*** (Figure 54; Figure 79), burned, to put on their heads to encourage hair growth! (Harris 2002). In India, ***Fissidens nobilis*** (Figure 48) has likewise been used to grow hair (Pant 1998; Azuelo *et al*. 2011). And Asakawa (2015) found compounds in ***Fissidens nobilis*** (Figure 48) that should promote hair growth

Most likely following the Doctrine of Signatures, Himalayan natives use ***Polytrichum commune*** (Figure 4) to promote hair growth (Kumar *et al*. 2007). The Doctrine of Signatures is a theory that the plant tells us what it is useful for by its morphology or other properties. Since ***Polytrichum commune*** has a hairy calyptra (Figure 67), that would suggest it is good for growing hair. Similarly, the hairs on the calyptra most likely account for the use of ***Dawsonia longifolia*** (Figure 69) to grow hair (Azuelo *et al*. 2011; Chandra *et al*. 2017).

Figure 67. ***Polytrichum commune*** capsules with hairy calyptrae (and one with calyptra removed). This species is used to help grow hair. Photo by Michael Lüth, with permission.

Frullania ericoides (Figure 68) is used to treat the hair and scalp in India (Remesh & Manju 2009; Chandra *et al*. 2017). It purportedly gets rid of head lice and nourishes the hair.

Figure 68. ***Frullania ericoides***, a species used in India to treat the hair and scalp. Photo by Paul Davison, with permission.

Figure 69. ***Dawsonia longifolia*** with capsule, showing long hairs on the calyptra. Photo by Vita Plasek, with permission.

Sedatives

The use of bryophytes as sedatives seems to be uncommon. The moss ***Hypnum*** (Figure 70) was named for sleep, but that is because it was used to stuff pillows, not for any known sedative effect (Dillenius 1741). However, ***Plagiopus oederianus*** (Figure 71) has been used in India as a sedative, as well as for treating epilepsy (Pant 1998; Asakawa 2015; Chandra *et al*. 2017). And the widely used ***Rhodobryum roseum*** and ***R. giganteum*** (Figure 26) likewise have been used as sedatives (Wu 1977; Pant 1998; Asakawa 2007b, 2015; Chandra *et al*. 2017).

Figure 70. ***Hypnum cupressiforme***, a moss that filters substances out of items for smoking and is used to stuff pillows. Photo by Michael Lüth, with permission.

Figure 71. ***Plagiopus oederianus***, a species used in India as a sedative and to treat epilepsy. Photo by Michael Lüth, with permission.

Antidotes

The mosses ***Bryum argenteum*** (Figure 47), ***Haplocladium capillatum*** (see Figure 52). ***Philonotis fontana*** (Figure 62), ***Polytrichum commune*** (Figure 4), and ***Weissia controversa*** (Figure 44) can be used as an antidote, as well as ***Conocephalum conicum*** (Figure 18) and ***Marchantia polymorpha*** (Figure 5). But Asakawa does not state what things these will treat (Asakawa 2015). For ***Conocephalum conicum***, Asakawa reports that it can be used to treat snake bites.

Filters

Kumaun Indians (also Kumaon) of the Himalayas use slender bryophytes such as ***Herbertus*** (Figure 51), ***Anomodon*** (Figure 72), ***Entodon*** (Figure 76), ***Hypnum*** (Figure 70), ***Meteoriopsis*** (Figure 73), and ***Scapania*** (Figure 74), wrapped in a cone of *Rhododendron campanulatum* (Figure 75) leaves, to serve as a filter for smoking (Pant & Tewari 1989). One must wonder if any of those heated phenolic compounds in bryophytes might be as harmful as the substances they filter out!

Figure 72. ***Anomodon rugelii***, a moss of vertical surfaces, filters substances out of items for smoking. Photo by Michael Lüth, with permission.

Figure 73. ***Meteoriopsis squarrosa***, a pendent species in the Western Ghats. The genus ***Meteoriopsis*** is used as a smoking filter in the Himalayas. Photo by M. C. Nair, K. P. Rajesh, and P. V. Madhusoodanan, through Creative Commons.

Figure 74. ***Scapania gracilis***. Members of this genus are used as smoking filters in the Himalayas. Photo by Michael Lüth, with permission.

Figure 75. ***Rhododendron campanulatum***. Leaves of this species are used to wrap bryophytes to serve as smoking filters. Photo by Kurt Stüber, through Creative Commons.

One peat product has actually entered modern medicine as a means to cleanse the body of pollutants: humic acids. HUMET-R syrup entered medicine as a transporter of trace elements, reducing excess trace elements that are bombarding the human body from pollutants and other sources (Kleb *et al*. 1999). The active substance is humin acid.

Figure 76. The pleurocarpous moss ***Entodon concinnus*** is used as a smoking filter. Photo by Michael Lüth, with permission.

Surgical and Larger Wounds

Bryophytes have been used both in treating and in cushioning wounds. In Utah, the Gosuite native people used poultices of ***Bryum*** (Figure 41, Figure 47), ***Mnium*** (Figure 3), ***Philonotis*** (Figure 62), and various matted hypnaceous forms as padding under splints to set broken bones.

But it is ***Sphagnum*** (Figure 10) that has gained fame for its use as a bandage (Figure 77) (Painter 2003). It appears that even before the First World War, ***Sphagnum*** was used to bandage the wounded in the Russo-Japanese War (1904-05). In the First World War, the Americans (USA) and Canadians used ***Sphagnum*** (peat moss) to make bandages, conserving the valuable cotton for making and packing gunpowder (Porter 1917; Hotson 1918, 1919, 1921; Nichols 1918a, b, c, d, 1920). The wounds apparently healed better than those with sterile surgical bandages, benefitting from the moisture and fewer infections. The British Army used about 1,000,000 pounds (453590 kg) of dressing per month (Nichols 1918c, 1920), saving about US $200,000 (Bland 1971), the Canadian Red Cross about 200,000 pounds (90720 kg) per month, and the United States about 500,000 pounds (226800 kg) during the last six months of war (Bland 1971). After the war, these countries returned to traditional gauze bandages, but the Chinese have continued to use ***Sphagnum*** for this purpose (Ding 1982).

The superiority of ***Sphagnum*** (Figure 10) bandages is attributed in part to its ability to absorb 3-4 times as much liquid as a cotton bandage at a rate three times as fast (Porter 1917). This is due to the interlaced hyaline cells that are dead and possess pores (Figure 78). These cells retain water and readily absorb water when dry. Hence, the bandage retains liquids longer and more uniformly, necessitating less frequent change. It is more comfortable for the user because it is cooler, softer, less irritating, and retards bacterial growth (Banerjee 1974). In fact, tests indicate that the amount of wound area covered by new epidermis doubles with use of ***Sphagnum*** dressing compared to no dressing (Varley & Barnett 1987).

Figure 77. ***Sphagnum*** for surgical dressings. Photo from National Museum of American History, with online permission.

This news article appeared on page 4 of *The Seattle Star* (Washington, USA), 3 April 1918:

"U" STUDENTS TO MAKE 50,000 MOSS DRESSINGS

Fifty thousand sphagnum dressings, for use in France, will be made at the University of Washington before June 15. The dressings will follow a new design and will be submitted for experiment. If successful, it is expected that a call will come for 50,000 each week.

Between 800 and 900 freshman and sophomore girls are now registered for work on sphagnum moss dressings.

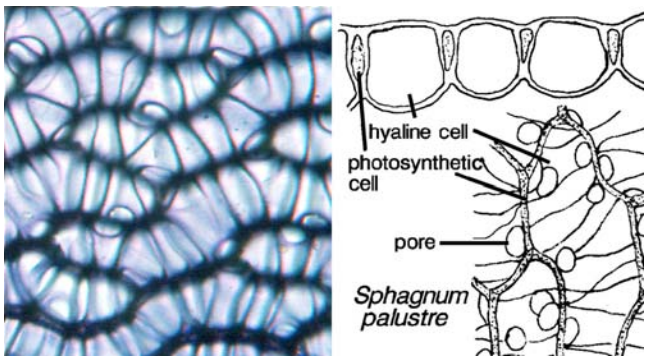

Figure 78. Stained cells of ***Sphagnum*** showing large hyaline cells with pores and small photosynthetic cells. Photo and drawings by Janice Glime.

The pectin complex in the ***Sphagnum*** (Figure 78) cell wall is similar structurally to immunostimulatory pectin from tracheophytes that has traditionally been used for healing wounds (Painter 2003).

Sphagnum (Figure 10) is not the only moss that has been used for bandages. The Nitinaht native people of Vancouver Island, Canada, used a moss known as maidenhair moss (***Fissidens adianthoides***; Figure 79) to bandage wounds. The Anglo-Saxons gave it the name of maidenhair moss because to them it resembled a maiden's pubic hair.

Figure 79. ***Fissidens adianthoides*** is the maidenhair moss used by the Nitinaht native people for bandages. Photo by Michael Lüth, with permission.

Perhaps one of the more unusual uses of liverworts is the Chinese use to promote healing of fractures (Asakawa 2012); he reports ***Conocephalum conicum*** (Figure 18) and ***Marchantia polymorpha*** (Figure 5) to be useful for this (Asakawa 2015). Lubaina *et al*. (2014) reported the use of the leafy liverwort ***Plagiochila beddomei*** (see Figure 80) for healing wounds in the Western Ghats.

Figure 80. ***Plagiochila*** sp. ***Plagiochila beddomei*** is used in the Western Ghats for healing wounds. Photo by Lin Kyan, with permission.

The use of ***Sphagnum*** (Figure 10) as a bandage is not without its hazards, as mentioned earlier. Perhaps other mosses may serve an absorptive function as well or better than ***Sphagnum*** and impose fewer hazards. Horikawa (1952) compared a number of mosses and their ability to absorb water. He found several that could rival ***Sphagnum*** in absorptive ability (Table 1).

Table 1. Weight gain measured as wet weight to dry weight ratio of selected bryophytes (Horikawa 1952).

Atrichum	6.9	Figure 56
Barbula	8.3	Figure 40, Figure 43
Bazzania pompeana	4.0	*cf*. Figure 81
Haplomitrium mnioides	12.0	Figure 82
Loeskeobryum cavifolium	9.8	*cf*. Figure 83
Plagiomnium maximoviczii	6.7	Figure 84
Rhodobryum	10.0	Figure 25
Sphagnum	12.4	Figure 58
Trachycystis microphylla	3.2	Figure 85

Figure 81. ***Bazzania trilobata***. ***Bazzania pompeana*** gains water up to 4 time its dry weight. Photo by Janice Glime.

Figure 82. ***Haplomitrium mnioides***, a species that gains water up to 12 times its dry weight. Photo by Yang, Jia-Dong, through Creative Commons.

Figure 83. ***Loeskeobryum brevirostre***. ***Loeskeobryum cavifolium*** gains water up to 9.8 times its dry weight. Photo by Bob Klips, with permission.

Figure 84. ***Plagiomnium maximoviczii***, a species that gains water up to 6.7 times its dry weight. Photo through Creative Commons.

Figure 85. ***Trachycystis microphylla***, a species that gains water up to 3.2 times its dry weight. Photo by Li Zhang, with permission.

Covid Masks

Professor Hazem Kalaji (2022), from Warsaw University of Life Sciences, filed for a patent with the Japanese Patent Office for a moss anti-virus half mask. The project was in collaboration with the virologist Dr. Seiya Sato, president of Green's Green Ltd., Niigata, Japan. In this half mask, mosses (apparently ***Hypnum plumaeforme***, Figure 86) are placed in a thin layer of transparent material, thus enabling them to photosynthesize. The wearer provides the mosses with CO_2 and moisture while breathing, and the mosses provide oxygen. The virus is adsorbed in the mask due to differences in electrical charge. Viruses have a negative charge and the mosses a positive one. The capsids (envelopes) of the viral proteins are broken and the harmless interior leaks out and disintegrates, leaving non-infectious RNA.

Figure 86. ***Hypnum plumaeforme*** moist, from Kogen Spa, Japan. Photo by Janice Glime.

Breaking News

After "completing" the revision of this chapter, I received an email announcing the completion of a safety study for the pharmaceutical use of a bryophyte-produced compound, Moss-aGal (Kirstein 2017). Six patients were monitored for 28 days following a single dose of the pharmaceutical and showed no negative effects. This is only phase 1 of the study, but it provides promise in relieving symptoms in patients suffering from Fabry disease. This is the first moss-based clinical product to be tested in humans. The research has been done at Greenovation, a privately-owned biopharmaceutical company based in Heilbronn, Germany. It was founded in 1999 by Prof. Dr. Ralf Reski and Prof. Dr. Gunter Neuhaus.

Fabry disease is a rare genetic disease causing a deficiency of the enzyme **alpha-galactosidase A** (a-Gal A), hence the name Moss-aGal for the moss compound to treat it. This disease causes a buildup of a type of fat called **globotriaosylceramide** (Gb3, or GL-3) in the body. Fabry disease is classified as a type of lysosomal storage disorder. There is no known cure, only treatments of the deficiency.

Summary

Bryophytes have been traditionally used for their medicinal properties in China, India, and among Native Americans. Their use in Europe became more widespread following the development of the Doctrine of Signatures. Among the most commonly used, ***Marchantia polymorpha*** was used for liver ailments and is still used in some places, but is also used for boils and abscesses. ***Rhodobryum giganteum*** is used for cardiovascular problems, a use supported by clinical tests.

Traditional uses of bryophytes include treatment for liver ailments, ringworm, heart problems, inflammation, fever, urinary and digestive problems, female problems, infections, lung disease, skin problems, and as filters and cleansing agents against pollutants.

The ability of ***Sphagnum*** to promote healing of flesh wounds is well documented. **Sphagnol** is used to treat boils and mosquito bites, and ***Sphagnum*** in diapers prevents diaper rash.

Acknowledgments

I appreciate the continued support of Robin Stevenson in providing me with interesting articles such as the one on the medical use of mosses growing on skulls. Eric Harris generously shared his papers and images of medicinal bryophytes.

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CHAPTER 2-2

MEDICAL USES: BIOLOGICALLY ACTIVE SUBSTANCES

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CHAPTER 2-2
MEDICAL USES: BIOLOGICALLY ACTIVE SUBSTANCES

Figure 1. Bryophytes and other herbs on sale in a Yunnan, China, market. ***Rhodobryum giganteum*** (upper bag) and ***Leucobryum*** (lower bag), both called Hui Xin Cao. Photo by courtesy of Eric Harris.

Antibiotics and Other Biologically Active Substances

Bryophyte species actually produce broad-range antibiotics (Asakawa 2007a, b, 2008; Asakawa *et al*. 2013). Their usage in surgical dressings, diapers, and other human medicinal applications is well known. And their use has not been confined to Asia (Frahm 2004), but is known in Brazil (Pinheiro da Silva *et al*. 1989), England (Wren 1956), North America (Pejin *et al*. 2011a, b), and Germany (Frahm 2004), as well as in China (Ding 1982; Wu 1982) and India (Watts 1891). Frahm (2007) has reviewed the literature on bryophytes and their antibiotic activity.

Bryophytes discourage the feeding by a variety of organisms, as discussed in the chapters on terrestrial insects, arthropods, and other interaction chapters. Frahm and Kirchhoff (2002) showed that extracts of the epiphytic

moss ***Neckera crispa*** (Figure 2) and leafy liverwort ***Porella obtusata*** (Figure 3) both discouraged feeding by the Portuguese slug ***Arion lusitanicus*** (Figure 4).

Figure 2. ***Neckera crispa***, a species that discourages the Portuguese slug from eating it. Photo by Jan-Peter Frahm, with permission.

Figure 3. ***Porella obtusata***, a species that discourages the Portuguese slug from eating it. Photo by Michael Lüth, with permission.

Figure 4. ***Arion lusitanicus***, a slug that avoids eating extracts of the moss ***Neckera crispa*** and leafy liverwort ***Porella obtusata***. Photo by Ondřej Zicha, through Creative Commons.

One indication of the presence of unique and potentially important pharmaceutically and anti-feedant chemicals in bryophytes is the presence of unique odors. This is especially true for liverworts, with more than several hundred new compounds identified among them (Asakawa 2012). In addition, more than 40 new carbon skeletal acetogenins, phenolic compounds, and terpenoids were identified. Testing of these compounds has led to the commercial development of a natural pesticide (Frahm 2004).

Leptolejeunea (Figure 5) and ***Moerckia*** (Figure 6) are distinctly aromatic (Schuster 1966), ***Lophozia bicrenata*** (Figure 7) has a pleasant odor, species of ***Solenostoma*** (Figure 8) smell like carrots, ***Geocalyx graveolens*** (Figure 9) has a turpentine-like odor, and ***Conocephalum conicum*** (Figure 10) smells like mushrooms. The tropical ***Plagiochila rutilans*** (Figure 11) smells like peppermint, caused by several menthane monoterpenoids (Heinrichs *et al*. 2001).

Figure 5. ***Leptolejeunea elliptica***, a species with a distinct odor. Photo by Yan Jia-dang, through Creative Commons.

Figure 6. ***Moerckia flotoviana*** female, a species with a distinct odor. Photo by Michael Lüth, with permission.

Figure 7. The leafy liverwort ***Lophozia bicrenata***. Photo by Michael Lüth.

Figure 8. ***Solenostoma hyalina***, a species that smells like carrots. Photo by Janice Glime.

Figure 9. The leafy liverwort ***Geocalyx graveolens***. Underleaf is indicated by the red star. Photo by Michael Lüth.

Figure 10. ***Conocephalum conicum***, a species that smells like mushrooms. Photo by Hermann Schachner, through Creative Commons.

But can you imagine using mosses to lower your cholesterol? Yes, mosses contain polyunsaturated fatty acids that are already known to have important potentials in human medicine, such as preventing atherosclerosis and cardiovascular disease, reducing collagen-induced thrombocyte aggregation, and lowering triacylglycerols and cholesterol in plasma (Radwan 1991).

Figure 11. ***Plagiochila*** sp. ***Plagiochila rutilans*** smells like peppermint. Photo by Lin Kyan, with permission.

It appears that these unique odors result from a combination of many compounds, including monoterpene hydrocarbons such as α-pinene, ß-pinene, camphene, sabinene, myrcene, alpha-terpinene, limonene, fatty acids, and methyl esters of low molecular weight (Hayashi *et al.* 1977). For example, ***Isotachis japonica*** (Figure 12) has at least three aromatic esters: benzyl benzoate, benzyl cinnamate, and B-phenylethyl cinnamate (Matsuo *et al.* 1971).

Figure 12. ***Isotachis*** sp. ***Isotachis japonica*** has at least three aromatic esters. Photo by George Shepherd, through Creative Commons.

But progress in purifying and identifying bryophyte biochemical components and demonstrating their antibiotic effects has been slow. As early as 1952, Madsen and Pates found inhibition of microorganisms in products of bryophytes, including ***Sphagnum portoricense*** (Figure 13), ***S. strictum*** (Figure 14), ***Conocephalum conicum*** (Figure 10), and ***Dumortiera hirsuta*** (Figure 15) (see also Sabovljević *et al*. 2011; Chandra *et al*. 2017). Pavletic and Stilinovic (1963) found that ***Dicranum scoparium*** (Figure 16) strongly inhibited all bacteria tested but Gram-negative *Escherichia coli* (Figure 17). McCleary and Walkington (1966) considered that non-ionized organic acids and polyphenolic compounds might contribute to the antibiotic properties of bryophytes and found eighteen mosses that strongly inhibited one or both of Gram-positive and Gram-negative bacteria, the most active being ***Atrichum*** (Figure

20), ***Dicranum*** (Figure 16), ***Mnium*** (Figure 18), ***Polytrichum*** (Figure 19), and ***Sphagnum***. Reminiscent of ***Dicranum scoparium*** (Figure 16), ***Atrichum undulatum*** (Figure 20) was effective on everything tested except *Enterobacter aerogenes* (drug resistant and infectious to people with weak immune systems; Figure 21) and *E. coli*.

Figure 13. ***Sphagnum portoricense***, a species that inhibits microorganisms. Photo by Blanka Shaw, with permission.

Figure 14. ***Sphagnum strictum***, a species that inhibits microorganisms. Photo by Jan-Peter Frahm, with permission.

Figure 15. ***Dumortiera hirsuta,*** a species that inhibits microorganisms. Photo by Michael Lüth, with permission.

Figure 16. ***Dicranum scoparium***, a species that inhibited all bacteria tested but Gram-negative *Escherichia coli*. Photo by Janice Glime.

Figure 17. *Escherichia coli*, a species that is inhibited by acetone-soluble extracts of several thallose liverwort species. Photo by NIAID, through Creative Commons.

Figure 18. ***Mnium spinulosum***. Members of the genus ***Mnium*** are among the most active against one or both of Gram-positive and Gram-negative bacteria. Photo by Michael Lüth, with permission.

Figure 19. ***Polytrichum commune***. Members of the genus ***Polytrichum*** are among the most active against one or both of Gram-positive and Gram-negative bacteria. Photo by Michael Lüth, with permission.

Figure 20. ***Atrichum undulatum*** is a moss that is very effective against a wide range of bacteria. Photo by Michael Lüth.

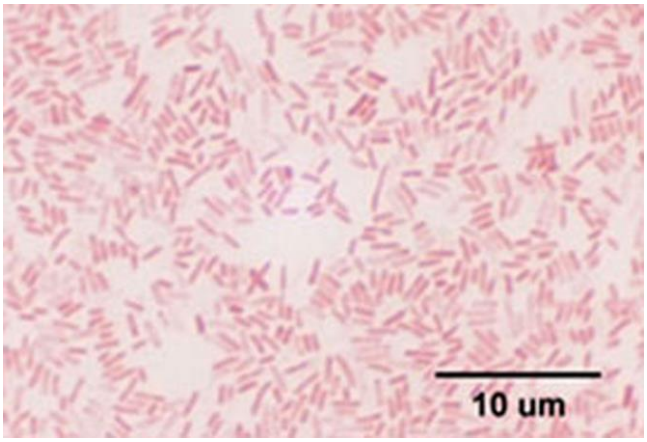

Figure 21. *Enterobacter aerogenes*, a bacterium that seems to be resistant to extracts of 18 moss species that negatively affect other bacteria. Photo by Alexa Rakusin Muna, through Creative Commons.

Gupta and Singh (1971) found high occurrence of antibacterial activity in extracts of ***Barbula*** species (Figure 22), reaching as high as 36.2%, whereas it was only half that in ***Timmiella*** species (Figure 23) (18.8%). In 1982, Asakawa *et al.* (1982) isolated three prenyl bibenzyls from ***Radula*** spp. (Figure 24) and demonstrated that these bibenzyls could inhibit growth of *Staphylococcus aureus* (Figure 25) at concentrations of 20.3 µg ml^{-1}. Out of more than 80 species tested, Ichikawa (1982) and coworkers (1983) found antimicrobial activity in nearly all. Acyclic acetylenic fatty acid and cyclophentenonyl fatty acid extracts from the mosses completely inhibited the growth of the rice blast fungus *Magnaporthe grisea* (Figure 26). Belcik and Wiegner (1980) reported antimicrobial activity in extracts of the liverworts ***Pallavicinia*** (Figure 27) and ***Reboulia*** (Figure 28), and Isoe (1983) reported it from ***Porella*** (Figure 29).

Figure 22. ***Barbula convoluta***, member of a genus with high antibacterial activity. Photo by Michael Lüth, with permission.

Figure 23. ***Timmiella*** sp., a genus with high antibacterial activity. Photo by Ken-ichi Ueda through Creative Commons.

Figure 24. ***Radula complanata***, a species with bibenzyls that could inhibit growth of *Staphylococcus aureus*. Photo by Michael Lüth, with permission.

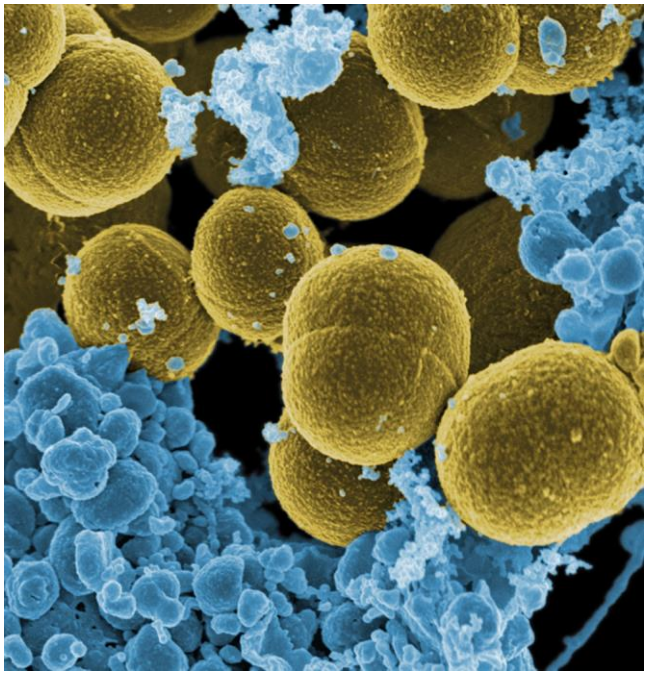

Figure 25. *Staphylococcus aureus*, a bacterium that is not inhibited by the thallose liverwort ***Riccia fluitans***. Photo by NIAID, through Creative Commons.

Figure 26. *Magnaporthe grisea*, a plant pest that is inhibited by several liverworts. Photo by IRRI Photos, through Creative Commons.

Figure 27. ***Pallavicinia lyellii***, member of a genus with reported antimicrobial activity. Photo by Jan-Peter Frahm, with permission.

Figure 28. ***Reboulia hemisphaerica***, member of a genus with reported antimicrobial activity. Photo by Malcolm Storey <www.discoverlife.org>, with online permission.

Figure 29. ***Porella platyphylla***, member of a genus with reported antimicrobial activity. Photo by Tim Waters through Creative Commons.

Another three species of mosses [***Anomodon rostratus*** (Figure 30), ***Plagiomnium cuspidatum*** (Figure 31), ***Orthotrichum rupestre*** (Figure 32)] produce substances that inhibit bacteria and fungi, but these inhibitors seem to be unstable products that vary considerably among species and possibly also among seasons (McCleary *et al*. 1960). Indeed, it would appear that some of these antibiotic compounds are the very ones that bryophytes produce in response to stress. However useful they may be, it seems that these discoveries have not yet found their way into medical practice.

Figure 30. ***Anomodon rostratus***, a species that inhibits bacteria and fungi. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 31. ***Plagiomnium cuspidatum***, a species that inhibits bacteria and fungi. Photo by Štěpán Koval, with permission.

Figure 32. ***Orthotrichum rupestre***, a species that inhibits bacteria and fungi. Photo by Michael Lüth, with permission.

Scientists have found innumerable kinds of biological activity in compounds from bryophytes. Even in a single species, one might find multiple kinds of activity. For example, the liverworts ***Plagiochasma japonica*** and ***Marchantia emarginata*** subsp. ***tosana*** (Figure 33) exhibit antitumor activity, antifungal and antimicrobial activity, inhibition of superoxide release, inhibition of thrombin activity, and muscle relaxation (Lahlou *et al.* 2000). As is often the case with herbal medicine, the effect of the total extract is better than that of the isolated compounds, perhaps due to a synergistic effect (Frahm 2004).

Figure 33. ***Marchantia emarginata*** subsp. ***tosana***, a subspecies with a wide range of medicinal properties. Photo by Taiwan Mosses, through Creative Commons.

On the other hand, some researchers claim that antibiotic properties of some mosses, including ***Sphagnum*** (Figure 13, Figure 14), may actually be the work of associated microorganisms. In some cases, *e.g.* ***Sphagnum***, it may be *Penicillium* sp. (Figure 34) effecting this antibiotic ability (Lewington 1990). Or is it the closely associated **Cyanobacteria**, such as ***Nostoc*** (Figure 35) (Spjut *et al*. 1988; Solheim & Zielke 2002)?

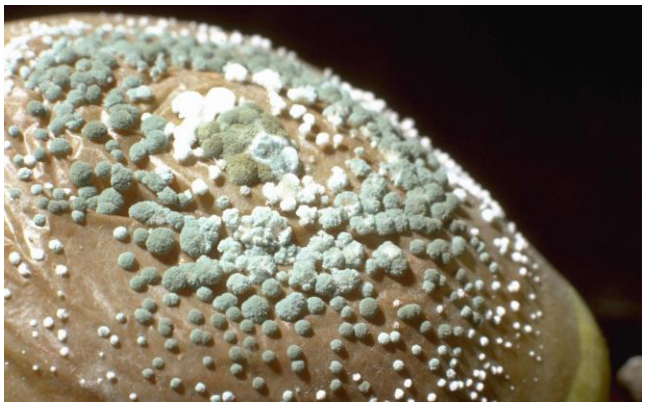

Figure 34. ***Penicillium expansum*** on pear, in a genus that can grow on ***Sphagnum*** and may contribute to its antibiotic effects. Photo by H. J. Larsen, through Creative Commons.

Figure 35. ***Nostoc pruniforme***, in a genus with close associations with ***Sphagnum*** and other bryophytes and could contribute to antibiotic properties. Photo by Lairich Rig, through Creative Commons.

Painter (2003) notes that ***Sphagnum*** (Figure 13, Figure 14) can be 3-4 times as absorbent as cotton equivalents. But its call to fame seems to be its ability to react chemically with all sorts of proteins. ***Sphagnum*** species have the potential to immobilize whole bacterial cells, enzymes, exotoxins, and lysins that are secreted by most of the invasive pathogens. Once these are immobilized, they are inactivated by a **Maillard reaction**.

The **Maillard reaction** makes this story complex. It is known to suppress the virulence gene expression operon in the bacterium *Listeria monocytogenes* (Figure 36) (Sheikh-Zeinoddin *et al*. 2000), so that is a good thing. On the other hand, a variety of foods form potential cancer-causing acrylamides, especially fried foods (Stadler *et al*. 2002). Such acrylamides can be released by thermally treating certain amino acids such as asparagine, especially in combination with reducing sugars through the Maillard

reaction. The early Maillard reaction products are N-glycosides. Painter (1998) found that the Maillard reaction inhibits microbial growth in animal products preserved in bogs by sequestering ammonia, amino acids, and peptides, whereas the polymeric end-products (melanoidins) inhibit their growth by cross-linking the polypeptide chains and sequestering essential multivalent metal cations. In short, the Maillard reaction appears to be an important component of the ***Sphagnum*** (Figure 13, Figure 14) antibiotic activity. Furthermore, its preservative ability correlates with α-keto-carboxylate groups in a glycuronoglycan (**sphagnan**) that comprises ~60% of the holocellulose in the ***Sphagnum*** hyaline cell walls.

Figure 36. *Listeria monocytogenes*, a bacteria species that is inhibited by extracts of the leafy liverwort ***Porella cordaeana***. Photo from CDC, through public domain.

Harris (2009) considered phylogenetic, elevational, and latitudinal relationships of the production of flavonoids in medicinal mosses. He was unable to show any significant correlation between phylogenetic independent contrasts of total phenolic content, number of flavonoids, or percent luteolin derivatives. He furthermore found no correlation with elevation or latitude. He could not rule out the possible correlation with fine-scale ecological features, and he considered flavonoid variation to reflect recent evolution.

Labbé *et al*. (2007) tested the thallose liverwort ***Riccardia polyclada*** for potential pesticidal properties. They identified four compounds that contributed to lethality in the brine shrimp (*Artemia salina*; Figure 37). Two of the compounds had moderate activity as an antifeedant for the African cotton leafworm (*Spodoptera littoralis*; Figure 38). They also inhibited culture growth of the fungal plant pathogen *Cladosporium herbarum* (Figure 39).

Figure 37. ***Artemia salina***, a species that is killed by extracts from the liverwort ***Riccardia polyclada***. Photo by Hans Hillewaert, through Creative Commons.

Figure 38. ***Spodoptera littoralis***, a species that is discouraged from eating the liverwort ***Riccardia polyclada*** by its chemical compounds. Photo from Forestry Images, through Creative Commons.

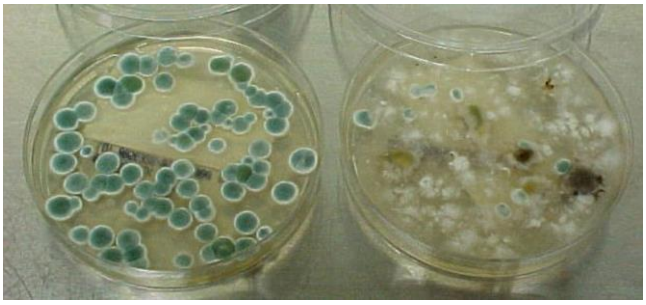

Figure 39. ***Cladosporium*** spp., fungal pathogens that are inhibited by extracts from the liverwort ***Riccardia polyclada***. Photo from Mold Treatment Centers of America, through Creative Commons.

Antimicrobial Activity

Our knowledge of antimicrobial activity of bryophytes is mostly based on ***Sphagnum*** (Figure 13, Figure 14). However other bryophytes are now known to have antibiotic properties. Some of these may just be folklore as they have not been tested experimentally. For example, Cheng *et al*. (2008) reported the folk use of ***Polytrichum*** to treat pneumonia. And we have already seen that ***Polytrichum commune*** (Figure 19) is used in a tea for treating colds (Gulabani 1974; Beike *et al*. 2010).

Nevertheless, antibiotic properties have been demonstrated in the laboratory. Moss activity against Gram-positive and Gram-negative bacteria have been demonstrated (Basile *et al.* 1999; Merkuria *et al.* 2005; Zhu *et al.* 2006). Asakawa (2007a, b) has demonstrated many effects of liverworts.

Kumar *et al*. (2007), in their review of classical ethnobotanical Indian uses, reported the antibacterial value of the mosses ***Anomodon rostratus*** (Figure 30), ***Atrichum angustatum*** (Figure 40), ***A. undulatum*** (Figure 41), and ***Hyophila involuta*** (Figure 42) and the thallose liverworts ***Conocephalum conicum*** (Figure 10) and ***Dumortiera hirsuta*** (Figure 15). These bryophytes reportedly produce antibiotics. The leafy liverwort ***Radula complanata*** (Figure 24) similarly has antimicrobial properties. To these we can add the antiseptic properties of ***Frullania tamarisci*** (Figure 43) (Asakawa 2007b; Chandra *et al*. 2017) and antimicrobial activity of ***Pallavicinia*** sp. (Figure 27) (Azuelo *et al*. 2011; Chandra *et al*. 2017).

Figure 40. ***Atrichum angustatum***, a species with antibacterial properties. Photo by Janice Glime.

Figure 41. ***Atrichum undulatum***, a species with antibacterial properties. Photo by Brian Eversham, with permission.

Figure 42. ***Hyophila involuta***, a species with antibacterial properties. Photo by Michael Lüth, with permission.

Figure 43. ***Frullania tamarisci***, an epiphytic species with antiseptic properties, having both allergenic and medicinal properties. Photo by Michael Lüth, with permission.

Recent tests on the floating thallose liverwort ***Riccia fluitans*** (Figure 44) from Florida indicated no ability to inhibit growth of the tested bacteria [*Pseudomonas aeruginosa* (Figure 45), *Staphylococcus aureus* (Figure 25)] or yeast (*Candida albicans*; Figure 46) (Pates & Madsen 1955). Vashistha *et al*. (2007) determined the antimicrobial activity of three other thallose liverworts. They found that water soluble extracts from ***Conocephalum conicum*** (Figure 10), ***Marchantia polymorpha*** (Figure 47), and ***Plagiochasma appendiculatum*** (Figure 48) had no effect on any of the pathogens tested [Gram-negative bacteria *Escherichia coli* (Figure 17) and *Salmonella typhi* (a variant of *S. enterica*; Figure 49)] and fungi *Aspergillus niger* (Figure 50) and yeast *Candida albicans* (Figure 46). However, acetone-soluble extracts of all three bryophyte species were inhibitory against the pathogens. They were more effective against the growth of *S. typhi* than against *E. coli*. ***Plagiochasma appendiculatum*** had a strong inhibitory effect against *A. niger* and ***Conocephalum conicum*** was strongly inhibitory to *Candida albicans*.

Figure 44. ***Riccia fluitans***, a species that was unable to inhibit the growth of several tested bacteria. Photo by Štěpán Koval, with permission.

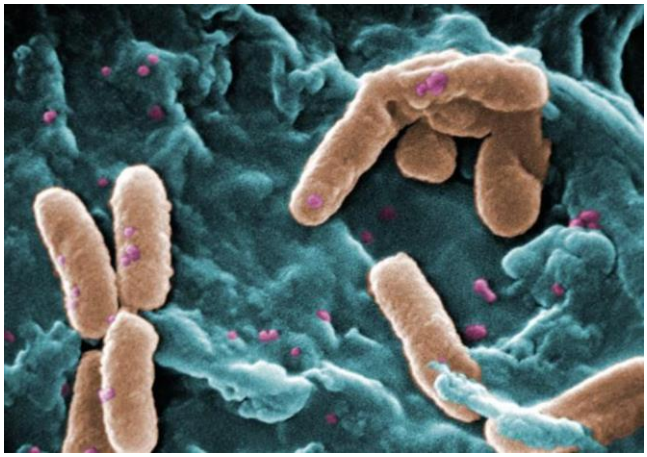

Figure 45. ***Pseudomonas aeruginosa***, a species that is not inhibited by ***Riccia fluitans***. Photo by Janice Haney Carr, through Creative Commons.

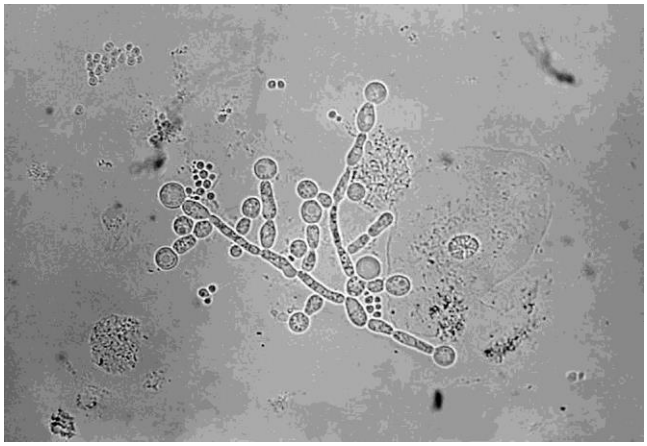

Figure 46. *Candida albicans*, a yeast species that is inhibited by extracts of the liverworts ***Conocephalum conicum***, ***Marchantia polymorpha***, and ***Plagiochasma appendiculatum***, but not ***Riccia fluitans***. Photo from Public Health Image Library, through public domain.

Figure 47. ***Marchantia polymorpha*** subsp. ***ruderalis***. This species had no effect on the fungi or Gram negative bacteria tested by Vashistha *et al*. Photo by Malcolm Storey, through Creative Commons

Figure 48. ***Plagiochasma appendiculatum***, a species that is effective against some pathogens. Photo by Ying Jia-dong, through Creative Commons.

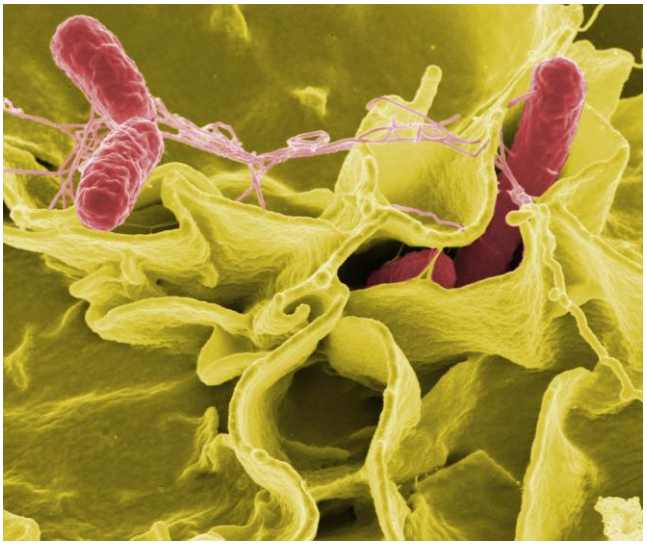

Figure 49. ***Salmonella enterica*** invading human cells. Photo by NIAID, through public domain.

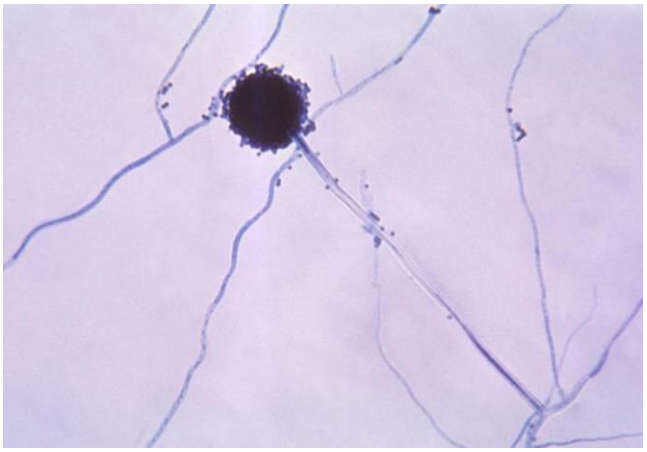

Figure 50. *Aspergillus niger*, a fungal species that is inhibited by extracts of the liverworts ***Conocephalum conicum***, ***Marchantia polymorpha***, and ***Plagiochasma appendiculatum***. Photo from Public Health Image Library, through public domain.

Bukvicki *et al*. (2012), using solid-phase microextraction-gas chromatography mass spectrometry, explored the volatile components of the leafy liverwort ***Porella cordaeana*** (Figure 51). Using methanol, ethanol, and ethyl acetate to extract terpenoids, they were able to identify sesquiterpene hydrocarbons and monoterpene

hydrocarbons. These same hydrocarbons were active against the eleven food microorganisms tested, but at different concentrations among the microorganisms. The fungi among these will be discussed blow. Affected bacterial strains were *Salmonella enteritidis* (food poisoning that causes diarrhea, fever, and abdominal cramps; Figure 52), *Escherichia coli* (commonly found in lower intestine of warm-blooded organisms with some strains causing food poisoning; Figure 17), and *Listeria monocytogenes* (very virulent food pathogen that causes the infection listeriosis; Figure 36). Methanol extracts showed the best activity.

Figure 51. ***Porella cordaeana***, a species that is able to inhibit a variety of yeasts and bacteria. Photo by J. C. Schou, with permission.

Figure 52. *Salmonella enteritidis*, a bacteria species that is inhibited by extracts of ***Porella cordaeana***. Photo through OGL (public domain).

It appears that differences in bryophyte extract activity among various pathogens may be common. Extracts of the liverworts ***Marchantia polymorpha*** (Figure 47), ***Porella platyphylla*** (Figure 29), and the moss ***Dicranum scoparium*** (Figure 16) showed antimicrobial effects on the Gram-positive bacteria *Bacillus subtilis* (Figure 53), *Staphylococcus aureus* (Figure 25), and *Micrococcus luteus* (Figure 54) (Pavletic & Stilinovic 1963; Frahm 2004). These same bryophytes exhibited no activity against Gram-negative *Escherichia coli* (Figure 17).

Figure 53. SEM of ***Bacillus subtilis***, a species that is inhibited by extracts of several bryophyte species. Photo by Davehwng, through Creative Commons.

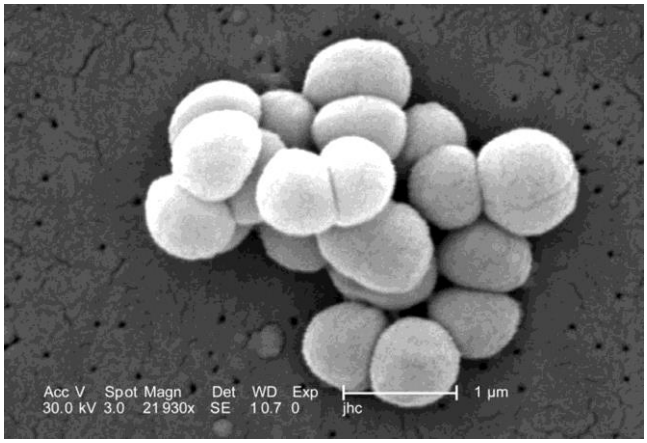

Figure 54. *Micrococcus luteus*, a bacteria species that is inhibited by extracts of several bryophyte species. Photo by Janice Carr, through public domain.

Basile *et al*. (1999) isolated seven pure flavonoids from five species of mosses. Some of these exhibited strong antibacterial effects against the bacteria *Enterobacter cloaceae* (Figure 55), *E. aerogenes* (Figure 56), and *Pseudomonas aeruginosa* (Figure 45). They were mainly active against Gram-negative bacteria that caused severe opportunistic infections and were at the same time resistant to commonly used antibacterial therapy. This means that the bryophyte products could become important tools in treating some bacterial infections.

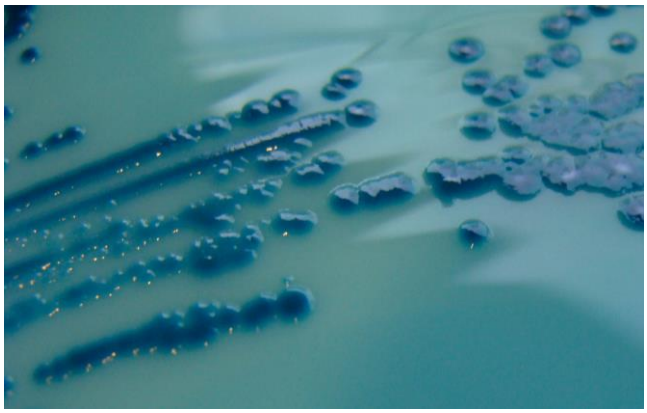

Figure 55. ***Enterobacter cloaceae***, a species that is active against Gram-negative bacteria. Photo by Nathan Reading, through Creative Commons.

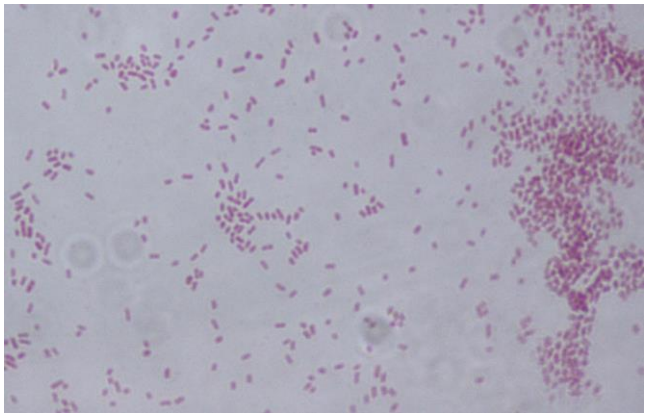

Figure 56. ***Enterobacter aerogenes***, a species that is active against Gram-negative bacteria. Photo by Riraq25, through Creative Commons.

Ariyo *et al*. (2011) compared the efficacy of extracts from the Nigerian thallose liverwort ***Riccia nigerica*** as antimicrobial agents. These extracts were tested against the bacteria *Bacillus subtilis* (Figure 53), *Pseudomonas aeruginosa* (Figure 45), *Shigella dysenteriae* (Figure 57), and *Staphylococcus aureus* (Figure 25) and fungi *Rhizopus* spp. (Figure 58), *Aspergillus flavus* (Figure 59), *A. niger* (Figure 50), *Penicillium* spp. (Figure 34), and and demonstrated strong significant antibacterial and antifungal activity.

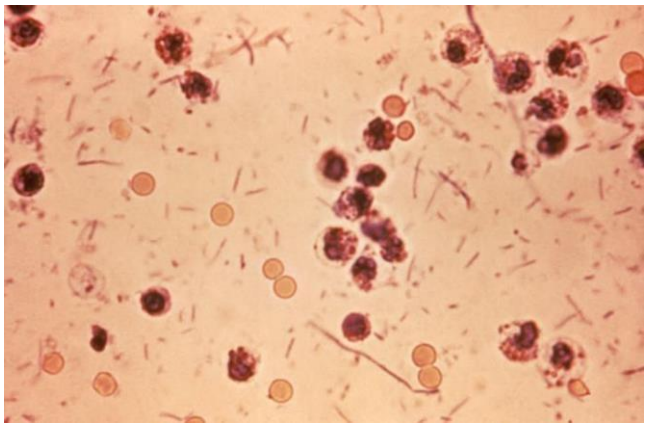

Figure 57. *Shigella dysenteriae*, a bacterial species that is inhibited by extracts of ***Riccia nigerica***. Photo by Public Health Image Library, through public domain.

Figure 58. ***Rhizopus*** on yam, a fungal species that is inhibited by extracts of ***Riccia nigerica***. Photo by Charles Averre, through Creative Commons.

Figure 59. ***Aspergillus flavus***, a fungal species that is inhibited by extracts of ***Riccia nigerica***. Photo by Medmyco, through Creative Commons.

The leafy liverwort ***Ptilidium pulcherrimum*** (Figure 60) exhibits antimocrobial activity against both Gram + bacteria and Gram negative bacteria, but the effect is greater on the Gram positive bacteria (Veljić *et al*. 2010).

Figure 60. ***Ptilidium pulcherrimum***, a species that is effective against both Gram positive and Gram negative bacteria. Photo by Hermann Schachner, through Creative Commons

Antifungal Activity

Although mosses are known to harbor fungi and will quickly become infected if kept moist in a plastic bag, some fungi are inhibited by many species of bryophytes, including many that cause skin infections. Jennings (1926) reported moss immunity to molds as early as 1926, but the possibility of using them as a source of antifungal activity seems to have been largely overlooked. Among these, the cosmopolitan moss ***Hypnum cupressiforme*** (Figure 61) has remarkable antibacterial and antifungal effects. Ven Hoof *et al*. (1981) demonstrated strong antibacterial and antifungal effects by extracts of ***Hypnum cupressiforme***.

Figure 61. ***Hypnum cupressiforme***, a species that is effective against fungi that cause skin infections. Photo by Michael Lüth.

Kumar *et al*. (2007) report antifungal properties for the widespread leafy liverwort ***Porella platyphylla*** (Figure 29). Ando and Matsuo (1984) demonstrated antifungal effects of bryophytes on human pathogenic fungi, but they warned that while the bryophyte extracts have fungicidal and antifeedant effects, they also may cause allergic reactions and dermatitis for some humans.

Bukvicki *et al*. (2012), using solid-phase microextraction-gas chromatography mass spectrometry, explored the volatile components of the related liverwort ***Porella cordaeana*** (Figure 51). Using methanol, ethanol, and ethyl acetate to extract terpenoids, they were able to identify sesquiterpene hydrocarbons and monoterpene hydrocarbons. These same hydrocarbons were active against the eleven food microorganisms tested, but at different concentrations among the microorganisms. These included the yeasts *Saccharomyces cerevisiae* (yeast used in wine making, baking, and brewing, but antibodies against *S. cerevisiae* are found in 60-70% of patients with Crohn's disease; Figure 62), *Zygosaccharomyces bailii* (species causing significant spoilage in the food industry; Figure 63), *Aureobasidium pullulans* (an inhabitant of humidifiers or air conditioners that can lead to hypersensitivity pneumonitis; Figure 64), *Pichia membranifaciens* (species causing grey mold of fruits; Figure 65) (2 strains), *Pichia anomala* (used in winemaking) (2 strains), and *Yarrowia lipolytica* (used in industrial microbiology for production of specialty lipids). Methanol extracts showed the best activity.

Figure 62. *Saccharomyces cerevisiae* SEM, a yeast species that is inhibited by extracts of the leafy liverwort ***Porella cordaeana***. Photo by Mogana Das Murtey and Patchamuthu Ramasamy, through Creative Commons.

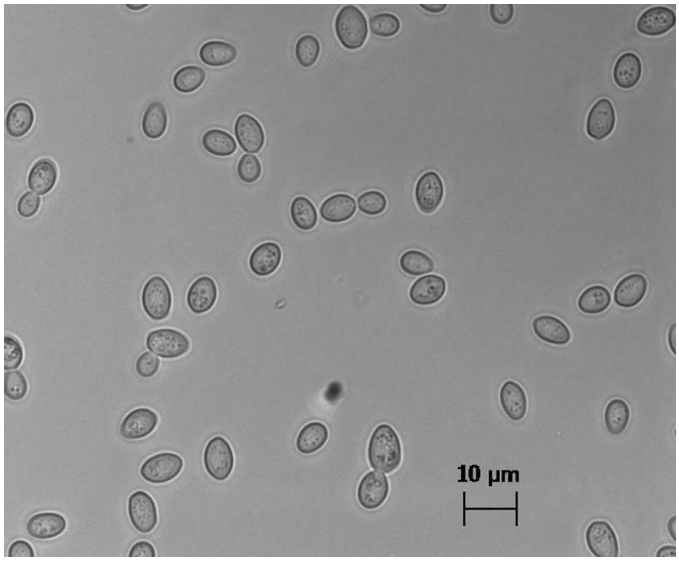

Figure 63. *Zygosaccharomyces bailii*, a yeast species that is inhibited by extracts of ***Porella cordaeana***. Photo by DTDT, through Creative Commons.

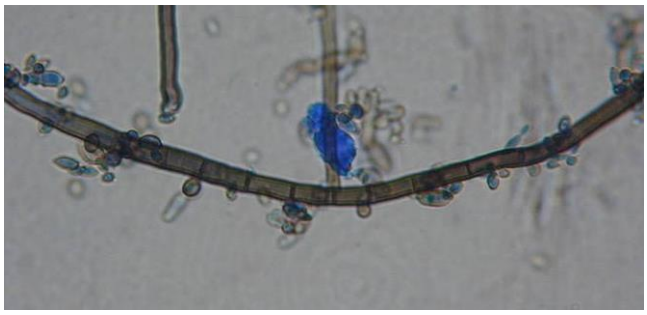

Figure 64. *Aureobasidium pullulans*, a yeast species that is inhibited by extracts of the leafy liverwort ***Porella cordaeana***. Photo by Tom Volk, through Creative Commons.

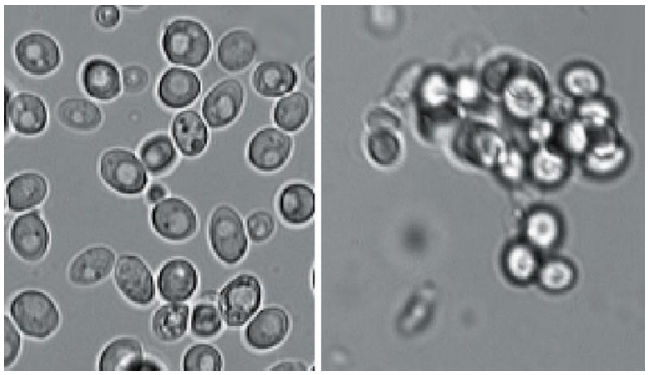

Figure 65. *Pichia membranaefaciens*, a yeast species that is inhibited by extracts of ***Porella cordaeana***. Photo by Luciana Francisco Fleuri & Hélia Harumi Sato, through Creative Commons.

The leafy liverwort ***Ptilidium pulcherrimum*** (Figure 60) is not only effective against bacteria, but also against fungi (Veljić *et al*. 2010). Its best antifungal activity was against *Trichoderma viride* (Figure 66), compared to the activity of the synthetic bifonazol.

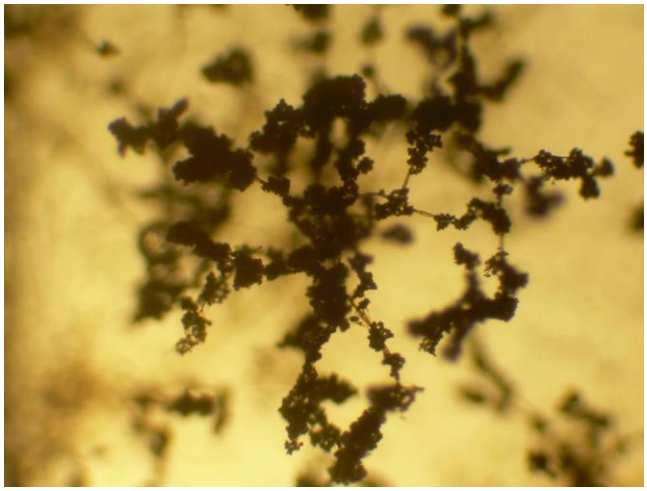

Figure 66. ***Trichoderma viride*** conidiophores, a fungal species that is inhibited by ***Atrichum undulatum***, ***Physcomitrella patens***, and ***Marchantia polymorpha***. Photo by Ninjatacoshell, through Creative Commons.

The absence of fungal diseases in liverworts led Pryce (1972) to suggest that **lunularic acid**, a hormone that affects aging in liverworts but not in mosses, might be responsible for liverwort antifungal activity. Banerjee and Sen (1979; Bannerjee 1974) found that the degree of antibiotic activity in a given species may depend on the age of the gametophyte; Matsuo *et al*. (1982a, 1982b, 1983) supported this conclusion by demonstrating that antifungal activity against *Botrytis cinerea* (Figure 67), *Pythium debaryanum* (Figure 68), and *Rhizoctonia solani* (Figure 69) by the liverwort ***Herbertus aduncus*** (Figure 70) was age-dependent. They subsequently isolated three aging substances from it: (-)-alpha-herbertenol; (-)-Beta-herbertenol, and (-)-alpha-formylherbertenol.

Figure 67. ***Botrytis cinerea*** on grapes. The liverwort ***Herbertus aduncus*** can exercise antifungal activity against this fungus, but activity is age-dependent. Photo by Alexandre Dulaunoy, through Creative Commons.

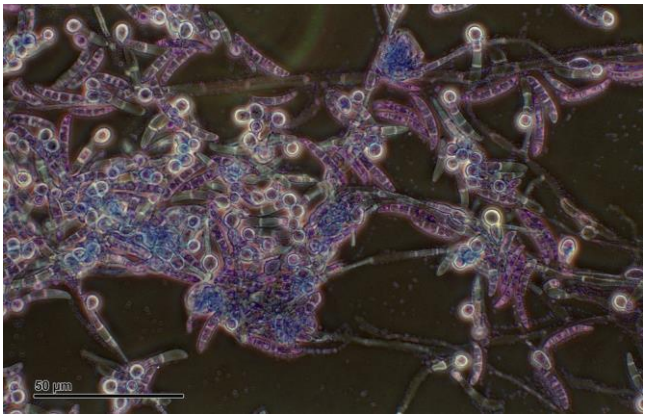

Figure 68. ***Pythium*** sp. The liverwort ***Herbertus aduncus*** can exercise antifungal activity against this fungus, but activity is age-dependent. Photo by Josef Reischig, through Creative Commons.

Figure 69. ***Rhizoctonia solani*** infecting leaves. The liverwort ***Herbertus aduncus*** can exercise antifungal activity against this fungus, but activity is age-dependent. Photo by Howard F. Schwartz, through Creative Commons.

Figure 70. ***Herbertus aduncus***, a leafy liverwort that can exercise antifungal activity against several fungi, but activity is age-dependent. Photo by Martin Hutten, with permission.

Vashistha *et al*. (2007) determined the antimicrobial activity for the thallose liverworts ***Plagiochasma appendiculatum*** (Figure 48), ***Marchantia polymorpha*** (Figure 47), and ***Conocephalum conicum*** (Figure 10). Acetone-soluble extracts of all three bryophyte species

were inhibitory against the fungal pathogens tested. ***Plagiochasma appendiculatum*** had a strong inhibitory effect against *Aspergillus. niger* and ***C. conicum*** was strongly inhibitory to *Candida albicans*. When Niu *et al*. (2006) tested ***Marchantia polymorpha*** (Figure 47) for antifungal activities against the yeast *Candida albicans* (Figure 46), they found **plagiochin** E, 13,13'-O-isoproylidenericcardin D, and neomarchantin A were active against the yeast. The other identified compounds had only weak effects.

Sabovljević *et al*. (2011) used DMSO extracts of both cultured and wild grown mosses ***Atrichum undulatum*** (Figure 20) and ***Physcomitrella patens*** (Figure 71-Figure 72) and thallose liverwort ***Marchantia polymorpha*** ssp. ***ruderalis*** (Figure 47) to test for antifungal activity. Using *Aspergillus versicolor* (Figure 73), *Aspergillus fumigatus* (Figure 74), *Penicillium funiculosum* (see Figure 34), *Penicillium ochrochloron*, and *Trichoderma viride* (Figure 66), these researchers demonstrated antifungal activity by all three bryophytes against all five fungal species. Most of the bryophytes grown in culture had greater antibiotic activity than the wild-grown ones.

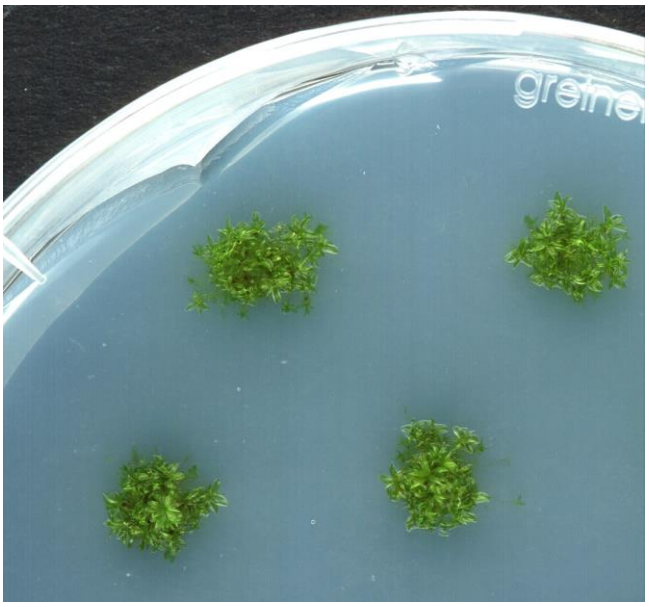

Figure 71. ***Physcomitrella patens*** growing on agar plates. Photo by Sabisteb, through Creative Commons.

Figure 72. ***Physcomitrella patens***, a source of human proteins and blood-clotting factor IX. Photo by Michael Lüth.

Figure 73. ***Aspergillus versicolor***, a fungal species that is inhibited by ***Atrichum undulatum***, ***Physcomitrella patens***, and ***Marchantia polymorpha***. Photo by James Scott, through Creative Commons.

Figure 74. ***Aspergillus fumigatus***, a fungal species that is inhibited by ***Atrichum undulatum***, ***Physcomitrella patens***, and ***Marchantia polymorpha***. Photo through Creative Commons.

Alcoholic extracts of all twenty bryophytes tested at Bonn University had antifungal activity on infected crops (Frahm 2004), as demonstrated in a Petri dish (Figure 75). Frahm reports curing a fungal infection of the skin with a bryophyte extract. The success was reported in a TV magazine and a published book, causing a number of people to use the extract for fungal infections, mostly with favorable results. However, Frahm warns that the biologically active substances are terpenoids, and these may cause allergic effects to some people (Ando & Matsuo 1984). One reputedly can cure athlete's foot by walking through a peat bog, presumably because of these same terpenoids (Frahm 2004).

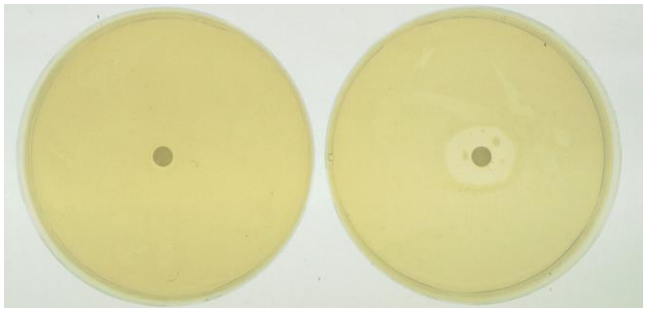

Figure 75. Bryophytes are known to inhibit growth of some kinds of bacteria and fungi. **Left:** Microbes grow uninhibited around a disk with only extraction fluid. **Right:** A zone of inhibition occurs around the disk with bryophyte extract. Photo by Jan-Peter Frahm.

One extract has actually been patented to cure fungal infections of horses (Frahm 2004). An industrious horse owner was inspired by what he read about the Bonn experiments and made a paste of ***Ceratodon purpureus*** (Figure 76) and ***Bryum argenteum*** (Figure 77). The fungus disappeared from the horse in 24 hours! This same extract is also sold as a human foot cream to refresh and fight odor. Unfortunately, the use for curing fungal infections cannot be mentioned in advertising because then it would require the extensive testing necessary to meet medical approval, which might be difficult because it can cause allergies and dermatitis in some people. It also works as an antifeedant against slugs. Unfortunately, to date it must be extracted from field-collected material, creating conservation concerns.

Figure 76. ***Ceratodon purpureus***, a species was used with ***Bryum argenteum*** and killed a fungal infection on a horse. Photo by Janice Glime.

It appears that some bryophytes may contribute to antifungal compounds by hosting a fungus that manufactures both antifungal and antitumor compounds (Guo *et al*. 2008). The leafy liverwort ***Scapania verrucosa*** hosts the fungus ***Chaetomium fusiforme*** (Figure 78). Not only does the latter produce both antifungal and antitumor compounds, but the liverwort itself likewise produces them. However, the fungus compounds provide superior properties and the liverwort might contribute to the medicinal field through this fungal **endophyte** (organisms growing within cells of plant, ranging from symbiotic to parasitic).

Figure 77. ***Bryum argenteum***, a species that was used in a paste with ***Ceratodon purpureus*** and killed a fungal infection on a horse. Photo by Martin Hutten, with permission.

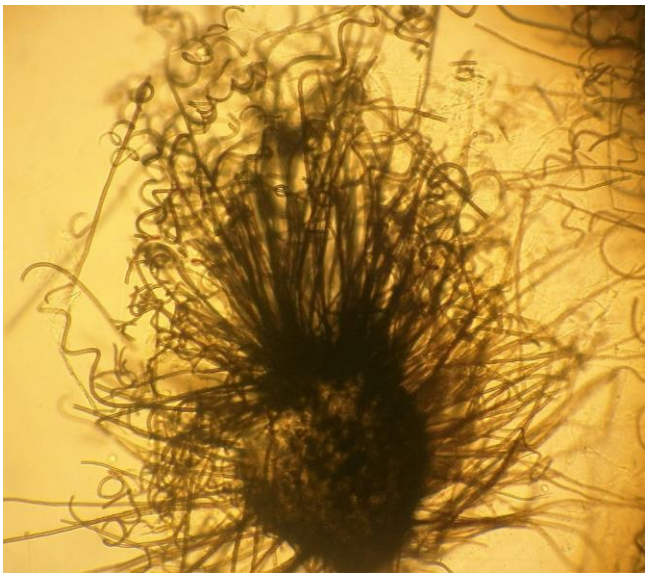

Figure 78. ***Chaetomium globosum***. The fungus ***Chaetomium fusiforme*** occurs on ***Scapania verrucosa*** and produces both antifungal and antitumor compounds. Photo by Ulitca, through Creative Commons.

Antiviral Activity

Even viruses may some day be cured by extracts of mosses, but we cannot simply identify them as "moss" as many of our ecologist friends have been wanton to do in reporting the ground cover. The Maoris of New Zealand have used bryophytes to treat venereal disease by packing wet plants on the infected organs (Frahm 2004). Nevertheless, van Hoof and coworkers (1981) found no effect of 20 species of moss extracts on the herpes virus, but earlier Klöcking *et al.* (1976) found that at least some peat humic acids possess antiviral activity against herpes simplex virus types 1 and 2, interfering primarily with the adsorption of viruses to host cells.

Sphagnum (Figure 13, Figure 14) produces several antivirally active humic acids, and ***Camptothecium*** (Figure 79) extracts can inhibit growth of the poliovirus (Witthauer *et al.* 1976; van Hoof *et al*. 1981). Nevertheless, actual usage of bryophytic extracts has not developed outside of Asia.

Figure 79. ***Camptothecium lutescens***, in a genus that can inhibit growth of the poliovirus. Photo by David T. Holyoak, with permission.

Cancer and Anti-tumor Properties

In the same year as the Madsen and Pates (1952) report of antibiotics in bryophytes, Belkin *et al*. (1952-53) reported anticancer activity against Sarcoma 37 in mice, using extracts of ***Polytrichum juniperinum*** (Figure 80). But application of the antitumor activity fared no better and was apparently not rediscovered in bryophytes until the next century. Finally, Anterola *et al*. (2009) considered the anticancer drug precursors in mosses to be so important that they titled their presentation on them "Turning precursors into gold: Production of anticancer drug precursors in moss."

Figure 80. ***Polytrichum juniperinum*** with antheridial splash cups, a species that produces anticancer compounds. Photo by Paul Slichter, with permission.

Fu *et al*. (2009) attempted to show anti-cancer capabilities of the moss ***Polytrichum commune*** (Figure 19). To this end, they isolated two "unusual" flavones and other compounds from this moss. However, when tested against a small panel of cancer cell lines, they failed to find any activity.

Kumar *et al*. (2007) found that Indians have used ***Polytrichum juniperinum*** (Figure 80) to treat cancer. The anti-tumor use of bryophytes in India included ***Chiloscyphus polyanthos*** (Figure 81), ***Diplophyllum albicans*** (Figure 82), ***D. taxifolium*** (Figure 85), ***Marchantia palmata***, and ***M. polymorpha*** (Figure 47). ***Frullania tamarisci*** (Figure 43) is used as an antileukemic agent. To this list, others added ***Riccardia*** sp. (Figure 84) (Azuelo *et al*. 2011; Alam 2012; Chandra *et al*. 2017) and ***Plagiochila*** sp. (Figure 11) (Asakawa 2007; Alam 2012; Chandra *et al*. 2017).

Figure 81. ***Chiloscyphus polyanthos***, a species that may cause allergic reactions. Photo by Barry Stewart, with permission.

Figure 82. ***Diplophyllum albicans***, used as an anti-tumor treatment in India and as an agent against epidermoid carcinoma. Photo by Michael Lüth, with permission.

Asakawa (1981) has shown that several compounds from leafy liverworts exhibit antileukemic activity. From the thallose species, Marchantin A from ***Marchantia palacea*** (Figure 83), ***M. polymorpha*** (Figure 47), and ***M. emarginata*** subsp. ***tosana*** (Figure 33), riccardin from ***Riccardia multifida*** (Figure 84), and perrottetin E from ***Radula perrottetii*** all show cytotoxicity against the leukemic KB cells (Asakawa *et al*. 1982).

Figure 83. ***Marchantia paleacea***, a thallose liverwort known for its antileukemic activity. Photo by Jan-Peter Frahm, with permission.

Figure 84. ***Riccardia multifida***, a thallose liverwort known for its antileukemic activity. Photo by Michael Lüth, with permission.

In 1976, Adamek reported that peat preparations hold some promise against some types of human cancer. In 1977, Ohta and coworkers (1977) reported that diplophyllin, isolated from the liverworts ***Diplophyllum albicans*** (Figure 82) and ***D. taxifolium*** (Figure 85), shows significant activity (ED50 4-16 μg/ml) against human epidermoid carcinoma (KB cell culture).

Figure 85. ***Diplophyllum taxifolium***, a species that produces diplophyllin, a compound that is active against human epidermoid carcinoma. Photo by Hermann Schachner, through Creative Commons.

Hughes and Anterola (2010) attempted to transplant genes for producing **Taxol** (a potent anticancer agent) into the moss ***Physcomitrella patens*** (Figure 71, Figure 72). They found evidence of small amounts of the anticancer precursors in the moss. If the moss can be taught (genetically) to produce Taxol, it could become a laboratory means to manufacture this important anti-cancer drug without destroying the diminishing number of *Taxus* (Figure 86) shrubs that produce it naturally. Bryophytes are ideal organisms for such gene transplants because of their dominant state with a single set of chromosomes and the relative ease with which genes can be put into them.

Figure 86. ***Taxus baccata***, member of the genus that produces the anticancer agent Taxol. Photo through Creative Commons.

When Asakawa (1981, 1982) entered the arena, he isolated the sesquiterpenoids costunolide and tulipinolide from ***Conocephalum supradecompositum***, ***Frullania monocera***, ***F. tamarisci*** (Figure 43), ***Marchantia polymorpha*** (Figure 47), ***Wiesnerella denudata*** (Figure 87) and ***Porella japonica*** (Figure 88). To this list, Matsuo and coworkers (1980, 1981a, b, c, 1984) added ***Lepidozia vitrea*** (Figure 89) and ***Plagiochila semidecurrens*** (Figure 90). These substances, already known from higher plants, have activity to combat carcinoma of the nasopharynx, at least in cell culture.

Figure 87. ***Wiesnerella denudata***, a species that produces sesquiterpenoids that are likely to have antibiotic properties. Photo by Ying Jia-dong, through Creative Commons.

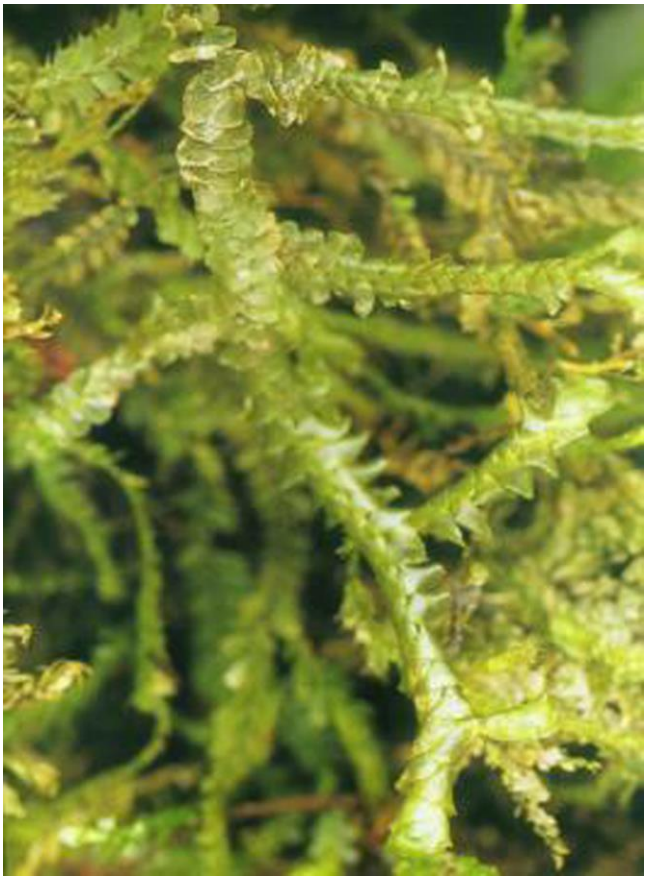

Figure 88. ***Porella japonica***, a species that produces compounds that combat carcinoma of the nasopharynx. Photo from Taiwan mosses color illustrations, through Creative Commons.

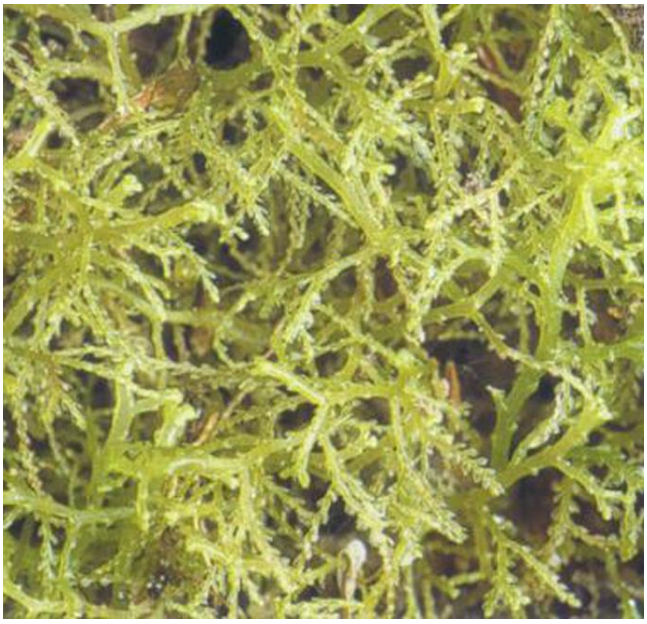

Figure 89. ***Lepidozia vitrea***, a species that produces compounds that combat carcinoma of the nasopharynx. Photo by Lin Shanxiong, through Creative Commons.

Figure 90. ***Plagiochila semidecurrens***, a species that produces compounds that combat carcinoma of the nasopharynx. Photo by Martin Hutten, with permission.

When the National Cancer Institute became interested, Spjut and his coworkers (1986) tested 184 species of mosses and 23 species of liverworts for antitumor activity. Of these, 43 species contained active substances, while those of 75 species were toxic to tested mice. The most activity was found in **Brachytheciaceae** (Figure 91), **Dicranaceae** (Figure 16), **Grimmiaceae** (Figure 92), **Hypnaceae** (Figure 61), **Mniaceae** (Figure 18, Figure 31), **Neckeraceae** (Figure 2), **Polytrichaceae** (Figure 19, Figure 80), and **Thuidiaceae** (Figure 93). However, in 1988, doubt was cast on the role of the moss when this team reported that the antitumor activity of the moss ***Claopodium crispifolium*** (Figure 94) was greatest in samples contaminated with the Cyanobacterium ***Nostoc*** cf. ***microscopicum*** (Figure 95), suggesting that ***Nostoc*** could be the direct source of the activity or a necessary partner for interaction between the species (Spjut *et al.* 1988). Interaction could result from the transfer of a precursor from the ***Nostoc*** to the moss, which could then transform it into an active substance. Alternatively, the moss might produce the substance as an allelopathic response to the ***Nostoc***. In any event, this raises important and intriguing questions, both medically and ecologically.

Figure 91. ***Brachythecium salebrosum*** (**Brachytheciaceae**). Some members of this family exhibit high antitumor activity. Photo by Hermann Schachner, through Creative Commons.

Figure 92. ***Grimmia nutans*** (**Grimmiaceae**). Some members of this family exhibit high antitumor activity. Photo by Michael Lüth, with permission.

Figure 93. ***Thuidium tamariscinum*** (**Thuidiaceae**). Some members of this family exhibit high antitumor activity. Photo by Malcolm Storey (DiscoverLife.com), with online permission.

Figure 94. ***Claopodium crispifolium***, a moss that provides habitat for ***Nostoc***, which in turn has anti-tumor properties. Photo from Botany Website, UBC, with permission.

Figure 95. ***Nostoc*** sp., a moss contaminant that can increase anti-tumor activity. Photo from Retina, through Creative Commons.

For some reason, much of the biochemical work has concentrated on the liverworts. Similar studies on activities of moss compounds are sparse and there may be good reason to presume a greater medical treasure chest among the liverworts. Since these compounds generally benefit the bryophytes by discouraging their would-be herbivores, it is the tiny, slow-growing liverworts that stand to benefit most. Where other, larger plants have spent their evolutionary history developing a diversity of structure, it would seem that small size has afforded these plants only the benefits of diversity of biochemistry as a means of combating the hungry herbivores.

Burgess *et al*. (2000) found that the leafy liverwort ***Bazzania novae-zelandiae*** (Figure 96) produces a sesquiterpene caffeate that has selective activity against certain human tumor cells. The active compound has been identified as the new compound naviculyl caffeate.

Figure 96. ***Bazzania novae-zealandiae***, a species that is active against human tumor cells. Photo by Shirley Kerr, with permission.

Even breast cancer sufferers might benefit from bryophytes. Huang *et al*. (2010) found that **marchantin A** produced by ***Marchantia emarginata*** subsp. ***tosana*** (Figure 33) induced apoptosis in MCF-7 breast cancer

cells. This compound demonstrates strong antioxidant activity, scavenging free radicals.

The leafy liverwort ***Scapania verrucosa*** and its endophytic fungal inhabitant ***Chaetomium fusiforme*** (see Figure 78) produce several compounds that act as antitumor agents (Guo *et al*. 2008).

The thallose liverwort ***Dumortiera hirsuta*** (Figure 15) produces **riccardin D**, a macrocyclic bisbibenzyl compound that induces apoptosis of human leukemia cells (Xue *et al*. 2012). Xue and coworkers verified anticancer activity by riccardin D against human non-small cell lung cancer. In mice it produced a 44.5% inhibition of cancer growth with no apparent toxicity.

Pharmaceutical Production

Welcome to Greenovation! Moss for a healthy future. So began the website <http://www.greenovation.com/> of an upstart company that is growing the tiny ***Physcomitrella patens*** (Figure 71, Figure 72) for medicinal purposes. Yes, bryophytes have indeed finally penetrated the forefront of modern medicine!

Physcomitrella patens (Figure 71, Figure 72) is able to accept transferred human genes and express them to produce human antibodies in a liquid culture, making the antibodies easy to harvest (ETH Zurich 2009). So far, this is not possible when the genes are transplanted into "higher' organisms. One advantage of ***Physcomitrella patens*** is its ability to grow in a "bioreactor" (Figure 97; Decker & Reski 2004), a fermenter in which only water and minerals are needed to nourish the moss, of course in the presence of light and CO_2 (Greenovation). These tiny plants are actually superior (and cheaper) production systems for many complex recombinant pharmaceuticals (Bauer *et al*. 2005; Decker & Reski 2007, 2012; Gitzinger *et al*. 2009). Contrary to many mammalian systems that have been used to produce pharmaceuticals but that cause serious immune responses, those produced by ***Physcomitrella patens*** are non-immunogenic, a huge advantage for the patient, and making them superior to currently used mammalian cell lines for producing antibodies.

Among its many assets, ***Physcomitrella patens*** (Figure 71, Figure 72) is able to produce human proteins (Hohe *et al*. 2002; Decker *et al*. 2003) and is the only plant being used to produce the blood-clotting factor IX for pharmaceutical use. This discovery, patented by Prof. Reski of the Institute of Biotechnology of Plants at the University of Freiburg in Germany, led to the founding of the Greenovation Company in 1999. By 2002, the company was already employing 30 people to produce this valuable blood factor (Frahm, Bryonet discussion 2002).

Bryophytes offer the researchers, and the company, a number of advantages over "higher" plants. They can be grown without antibiotics, hence avoiding the danger of contamination of the final product. The moss is quite small and thus is cultured only in the lab with little danger of the transgenic plants escaping into the environment. But the real advantage comes from the dominant gametophytic generation of mosses as opposed to the dominant sporophyte of the tracheophytes. As a result, mosses are the only plants known to have a high frequency of homologous recombination. The result – stable integration of inserted genes into the genome. Furthermore, the highly complex moss system, compared to bacteria and fungi, permits a much wider array of expression than is possible in those systems. Thus, mosses are extremely useful as production systems for targeted substances that can be produced through gene manipulation.

Figure 97. This type of bioreactor is used to grow ***Physcomitrella patens*** for human proteins and human blood-clotting factor IX. Photo by Ralf Reski.

Unfortunately, most biologically active substances so far obtained have not proved economical for use, at least in part due to the slow-growing nature and difficulty of culturing bryophytes. And, while their pharmaceutical use seems promising, we lack any understanding of their potential harmful side effects.

In the words of Ma *et al*. (2003), "Imagine a world in which any protein, either naturally occurring or designed by man, could be produced safely, inexpensively and in almost unlimited quantities using only simple nutrients, water and sunlight. This could one day become reality as we learn to harness the power of plants for the production of recombinant proteins on an agricultural scale. Molecular farming in plants has already proven to be a successful way of producing a range of technical proteins. The first plant-derived recombinant pharmaceutical proteins are now approaching commercial approval, and many more are expected to follow."

Medical Dangers

Caution is in order in exercising any medicinal use of bryophytes, particularly liverworts, because of their potential for causing allergic reactions (Mitchell *et al.* 1969, 1970; Benezra *et al*. 1985, Asakawa 2012). Often the very compounds that have these medical potentials can cause allergic reactions. For example, it is a sesquiterpene lactone (Asakawa 1981) that gives the common epiphyte ***Frullania*** (Figure 98-Figure 99) its ability to cause contact dermatitis, especially to forest workers (Mitchell *et al.* 1969). Now there is a patch test with a sesquiterpene lactone mix to determine sensitivity to ***Frullania*** (Quirce *et al*. 1994).

Yet sesquiterpene lactones are well known for their antimicrobial activity. In southern Europe, ***Frullania tamarisci*** (Figure 43, Figure 98) imparts an allergic reaction to olive pickers, yet is listed as one of the medicinal species (J. Curnow, pers. comm.). D. H. Wagner (pers. comm.) reports an allergy to ***Chiloscyphus polyanthos*** (Figure 81), especially when he squeezes it to remove excess water. By 1981, 24 liverwort species were known to have potential allergenic sesquiterpene lactones (Asakawa 1981). These compounds undoubtedly endow the same advantage to bryophytes that they do to flowering plants – discouraging consumption by hungry herbivores.

Figure 98. ***Frullania tamarisci***, showing underside of branch with lobules by which the genus may be determined. Photo by Michael Lüth, with permission.

Frullania tamarisci (Figure 43, Figure 98) grows on trees and can cause skin irritations for loggers and even for their wives who handle their clothes. Allergic reactions to ***Frullania nisquallensis*** (Figure 99) occurred in patch tests on seven forest workers who had contact dermatitis (Mitchell *et al*. 1969). These forest workers exhibited the dermatitis only when they were working on forest areas. The problem was worse in wet weather and appeared within 1-2 days of starting work. The condition persisted for 2-4 weeks after leaving work in forested areas where the liverwort grew. The condition is often known locally in British Columbia, Canada, as cedar poisoning, but in fact it is caused by the liverworts that commonly grow on the cedars (*Thuja*; Figure 100).

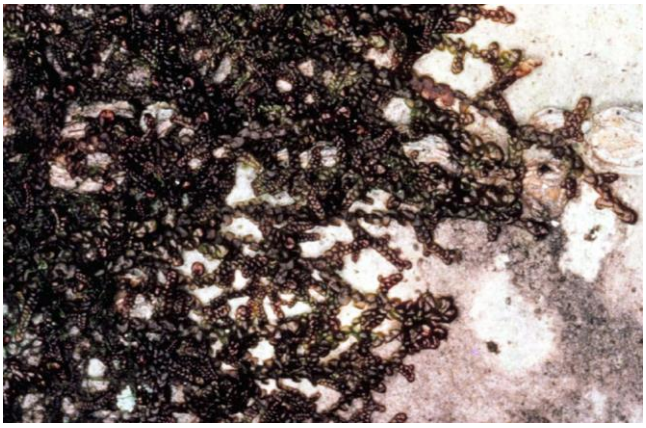

Figure 99. ***Frullania nisquallensis***, a leafy liverwort epiphyte that causes allergic reactions among forest workers. Photo by Dale Vitt, with permission.

Figure 100. ***Thuja plicata***, host plant for ***Frullania*** species. Photo from <www.nwplants.com>, through Creative Commons.

Summary

Bryophytes, especially liverworts, often have distinct odors, suggesting aromatic compounds such as phenols. However, few bryophytes have been linked to actual curative properties and identifiable associated compounds.

One danger in using bryophytes is that the same compounds that may have antibiotic properties may also be toxic or allergenic, or be associated with such compounds. Furthermore, peatland mosses may have associated fungi that cause **sporotrichosis**.

Many antibiotics have been isolated from bryophytes, but few have been developed for medical use, despite their demonstrated effectiveness. In Germany, ***Ceratodon purpureus*** and ***Bryum argenteum*** are used to cure fungal infections of horses. Several medical uses seem promising, such as antileukemic properties and anticancer agents.

The most promising uses of bryophytes in medicine seem to lie in genetic engineering. Bryophytes are being used already to produce human blood-clotting proteins, while others are known to reduce thrombin activity.

Acknowledgments

I appreciate the continued support of Robin Stevenson in providing me with interesting articles such as the one on the medical use of mosses growing on skulls. Eric Harris generously shared his papers and images of medicinal bryophytes.

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CHAPTER 3-1
FINE ARTS: DECORATIVE

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CHAPTER 3-1
FINE ARTS: DECORATIVE

Figure 1. Mosses used in a shop window to display trolls. Photo courtesy of Irene Bisang.

Decoration

Sheet mosses [large strips of pleurocarpous moss mats such as ***Hypnum*** (Figure 2), ***Thuidium*** (Figure 3), and ***Ptilium crista-castrensis*** (Figure 4) are still quite popular for decoration in store windows and displays (Figure 1), floral arrangements, Christmas tree and train yards, and Christmas ornaments (Miller in Crum 1973).

Figure 2. ***Hypnum imponens***, a popular mat-forming moss used in displays. Photo by Janice Glime.

Figure 3. ***Thuidium delicatulum***, a mat-forming moss that is often used in displays. Photo by Janice Glime.

Figure 4. ***Ptilium crista-castrensis***, a common decorative moss. Photo by Janice Glime.

Nativity

I still have the manger scene that belonged to my parents. Among its figures is a crèche, with baby Jesus nestled in a cradle filled with moss. How much nicer that would have been for the real Jesus instead of a bed of straw. In Mexico (and many other places), mosses are used to simulate vegetation in nativity scenes (Figure 5) (Delgadillo & Cárdenas 1990; Tan 2003) or to cover the roof of the nativity. These commonly include ***Hypnum*** (Figure 2), ***Thuidium*** (Figure 3), ***Campylopus*** (Figure 6), ***Leptodontium*** (Figure 7), and ***Polytrichum*** (Figure 8).

Figure 5. A nativity scene in Spain, using mosses for the vegetation. Photo courtesy of Francisco Lara.

Figure 6. ***Campylopus pyriformis***, member of a genus that is used to simulate grass or cover the roof of the nativity. Photo by Michael Lüth, with permission.

Figure 7. ***Leptodontium styriacum***, member of a genus commonly used to simulate grass in nativity scenes. Photo by Michael Lüth, with permission.

Figure 8. ***Polytrichum strictum***, member of a genus commonly used to cover nativity roofs or to simulate grass. Photo by Michael Lüth, with permission.

Lara *et al*. (2006) reported on the bryophytes used in nativity sets in Spain. They found that 66 bryophytes, 3 ferns, and 37 flowering plants were in use there. Most of the moss species seemed to be collected accidentally among the four favorite mosses and are similar to those used in Mexico: ***Thuidium tamariscinum*** (Figure 11), ***Eurhynchium striatum*** (Figure 12), ***Hypnum cupressiforme*** (Figure 13), and ***Pseudoscleropodium purum*** (Figure 14). Rees (1976) lists ***Campylopus*** sp., ***Dendropogonella rufescens***, ***Dicranum*** sp. (Figure 15), ***Hypnum*** sp., and ***Leptodontium*** sp. (Figure 7) as the bryophytes being sold in the markets in Oaxaca city, Mexico, at Christmas.

Figure 9. Village scenes use mosses for vegetation in Spain. Such scenes are often used in miniature train yards. Photo courtesy of Francisco Lara.

Figure 10. Nativity and village scenes in Spain use mosses for vegetation. Such scenes are often used in Christmas tree yards and miniature train yards. Photos courtesy of Francisco Lara.

Figure 11. ***Thuidium tamariscinum***, a species commonly used in nativity scenes in Spain. Photo by Michael Lüth, with permission.

Figure 12. ***Eurhynchium striatum***, a species commonly used in nativity scenes in Spain. Photo by Michael Lüth, with permission.

Figure 13. ***Hypnum cupressiforme*** var. ***cupressiforme***, a species commonly used in nativity scenes in Spain. Photo by David Holyoak, with permission.

Figure 14. ***Pseudoscleropodium purum***, a species commonly used in nativity scenes in Spain. Photo by Michael Lüth, with permission.

Figure 15. ***Dicranum***, a genus that is sold for decoration at Christmastime in Mexico. Photo by Janice Glime.

Salazar Allen (2001) reported the use of mosses for nativity in Panama, including ***Thuidium delicatulum*** (Figure 3), ***Hypnum*** sp. (Figure 2), ***Leptodontium*** sp. (Figure 7), ***Breutelia tomentosa*** (see Figure 16),

Rhacocarpus purpurascens (Figure 17), ***Sematophyllum cuspidiferum*** (see Figure 18), and the liverworts ***Frullania*** (Figure 19) and ***Lepidozia*** (Figure 20). Similar packages of sheet mosses are sold in the USA (Figure 21).

Figure 16. ***Breutelia subtomentosa***. ***Breutelia tomentosa*** is used in Panama in nativity scenes. Photo by Michael Lüth, with permission.

Figure 17. ***Rhacocarpus purpurascens***, a species that is used in Panama in nativity scenes. Photo courtesy of Jeff Duckett and Silvia Pressel.

Figure 18. ***Sematophyllum demissum***. ***Sematophyllum cuspidiferum*** is used in nativity scenes in Panama. Photo by Michael Lüth, with permission.

Figure 19. ***Frullania***, a genus that is used in Panama in nativity scenes. Photo by George Shepherd, through Creative Commons.

Figure 20. ***Lepidozia glaucophylla***, member of a genus that is used in nativity scenes in Panama. Photo by Jeff Duckett and Silvia Pressel.

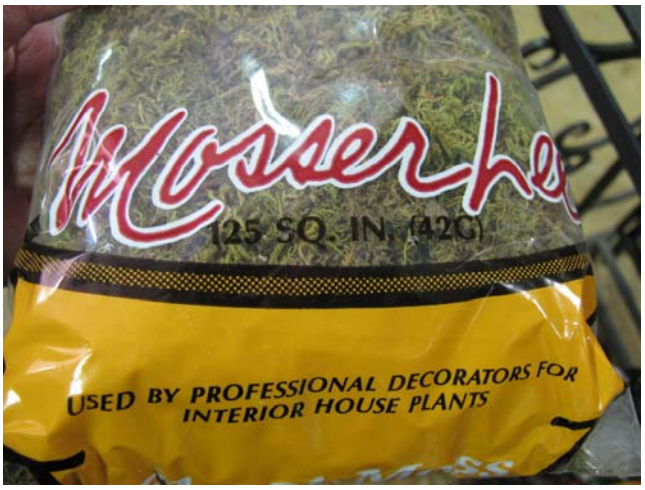

Figure 21. This bag of sheet moss is ***Thuidium*** sp., for sale in a gardening shop in Columbus, Ohio, USA. Photo by Janice Glime.

Christmas Decorations

Other Christmas-related uses also have emerged. There are wreaths made with mosses (Figure 22-Figure 23). And mosses provide a nice covering at the tree base (Figure 24), perhaps helping to reduce evaporation and to cover

bare soil for live trees. Others have created a variety of uses in making decorations and ornaments (Figure 25-Figure 27). Tan (2003) reports the use of mosses at Christmas for window dressing, showcasing gift displays, and packaging.

Figure 22. Moss in wreath in garden shop, Columbus, Ohio, USA. Photo by Janice Glime.

Figure 23. This twig wreath, decorated with mosses, was available at Christmastime at Michael's Hobby Shop in Reynoldsburg, Ohio, USA. Photo by Janice Glime.

Figure 24. Moss covering soil in pot with Christmas tree in garden shop in Columbus, Ohio, USA. Photo by Janice Glime.

Figure 25. Moss reindeer in garden shop in Columbus, Ohio, USA. Photo by Janice Glime.

Figure 26. Moss bird's nest (human-made), a potential tree decoration, at Michael's Hobby Shop in Reynoldsburg, Ohio, USA. Photo by Janice Glime.

Figure 27. Moss bird house, a potential tree decoration, at Michael's Hobby Shop in Reynoldsburg, Ohio, USA. Photo by Janice Glime.

Household Decorations

I have seen a moss table runner (Figure 28). I debated putting it in the chapter on household uses, but I consider it

more decorative than practical, so I have included it here. The distributor must expect it to be popular since the label is printed in three languages (Figure 29).

Figure 28. Moss table runner at Michael's Hobby Shop in Reynoldsburg, Ohio, USA. Photo by Janice Glime.

Figure 29. Moss table runner for sale at Michael's Hobby Shop in Reynoldsburg, Ohio, USA. Photo by Janice Glime.

If you want "matching" accessories, there are vine and moss baskets where you can store your fruit (Figure 30). Other entrepreneurial Americans have created a number of decorative pieces (Figure 31-Figure 35).

Figure 30. Moss basket at Michael's Hobby Shop in Reynoldsburg, Ohio, USA. Photo by Janice Glime.

Figure 31. Moss snail at Michael's Hobby Shop in Reynoldsburg, Ohio, USA. Photo by Janice Glime.

Figure 32. Moss rabbits and owl at Michael's Hobby Shop in Reynoldsburg, Ohio, USA. Photo by Janice Glime.

Figure 33. Moss mouse at Michael's Hobby Shop in Reynoldsburg, Ohio, USA. Photo by Janice Glime.

Figure 34. Frog made of moss, Denoyer's Nursery, Columbus, Ohio, USA. Photo by Janice Glime.

Figure 35. Moss balls, useful in floral arrangements and Christmas decorations, at Michael's Hobby Shop in Reynoldsburg, Ohio, USA. Photo by Janice Glime.

Moss Walls

Some moss walls are art in their own right, with elaborate designs using different species with various shades of green, red, and brown. But some are simply green walls, as seen in Figure 36-Figure 37. I have seen pictures of similar green walls flanking one side of a bath tub. What a relaxing background for a bath!

Figure 36. Gaia moss wall in Singapore. Photo courtesy of Ben Tan.

Figure 37. Ben Tan and Etzel at the Gaia moss wall in Singapore. Photo courtesy of Ben Tan.

In Japan, you can buy a kit for making your own moss wall (Figure 38). Thanks to Hironori Deguchi, we can enjoy this vicariously (Figure 39-Figure 42).

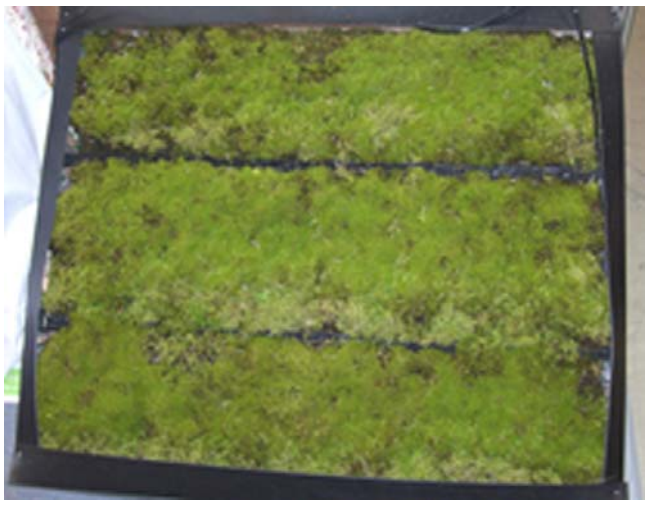

Figure 38. ***Sphagnum*** Greening Unit for Green Wall Kit. Photo courtesy of Hironori Deguchi.

Figure 39. ***Sphagnum*** Wall Kit final product on display in Japan. Photo courtesy of Hironori Deguchi.

Figure 40. ***Sphagnum*** Green Wall Kit by Takeda. Photo courtesy of Hironori Deguchi.

The Mayo Clinic in Rochester, Minnesota, USA, has used mosses and ferns to create a relaxing atmosphere in the clinic. These can be found on walls along stairways and in lobbies around the facility. They are billed as being maintainance-free – the mosses are preserved.

Figure 41. Moss wall in Mayo Cllinic, Rochester, Minnesota, USA. Photo courtesy of Janet Marr.

Shop Windows and Displays

From ***Leucobryum glaucum*** (Figure 43, Figure 57) in a tailor's window to ***Rhytidiadelphus*** (Figure 44) in a craft display, to ***Hypnum cupressiforme*** (Figure 13), ***Isothecium myosuroides*** (Figure 45), ***Pleurozium schreberi*** (Figure 46), and ***Pseudoscleropodium purum*** (Figure 14) in a shop window (Ando 1972), mosses will probably remain popular adornments to add a fresh look to displays (Figure 47). In Japan, even the sporophytes are used to make decorative arrangements (Manzoku 1963).

Figure 42. A variation on the ***Sphagnum*** Green Wall from the kit. Photo courtesy of Hironori Deguchi.

Figure 43. ***Leucobryum glaucum***, a species commonly used in floral and shop window arrangements. Photo by Janice Glime.

Figure 44. ***Rhytidiadelphus triquetrus***, in a genus commonly used in floral and shop window arrangements. Photo courtesy of John Hribljan.

Figure 45. ***Isothecium myosuroides***, a species commonly used in shop window displays in Europe. Photo by Janice Glime.

Figure 46. ***Pleurozium schreberi***, a species commonly used in shop window displays. Photo by Janice Glime.

Figure 47. Shop display in USA with purse on mosses. Photo courtesy of J. Paul Moore.

Like flowers, mosses are used in floral arrangements to create aesthetic appeal or create a relaxing atmosphere (Figure 49-Figure 48).

Figure 48. Moss in bulb pot, in a cafe in Helsingborg, Sweden. Photo courtesy of Irene Bisang.

Figure 49. ***Leucobryum glaucum*** in floral arrangement in shop window in Vienna, Austria. Photo courtesy of James Dickson.

Figure 50. ***Climacium americanum***, a species used in North America to make wreaths and crosses. Photo by Janice Glime.

Figure 51. ***Climacium japonicum***, a species used in Japan to make ornamental water flowers. Photo by Li Zhang, with permission.

Floral Industry

Tan (2003) considered horticulture to be the largest market for moss products. Some of these are for gardening, but others are decorative in pots and displays.

Use of bryophytes in the floral industry spans the globe, from ***Climacium americanum*** (Figure 50) in North America to make wreaths and crosses to ***Climacium japonicum*** (Figure 51) in Japan to make ornamental water flowers (Mizutani 1963). ***Hylocomium splendens*** (Figure 52) has been used similarly in North America to make moss roses, but it is also a preferred species in floral arrangements (Welch 1948; Thieret 1956). ***Bryum argenteum*** (Figure 53) is used in Missouri, USA, for floral arrangements. More commonly, ***Dicranum scoparium*** (Figure 54), ***Hylocomium splendens***, ***Rhytidiadelphus loreus*** (Figure 55), and ***R. triquetrus*** (Figure 44) are popular for floral exhibitions because they form large carpets of green (Welch 1948; Thieret 1956).

Figure 52. ***Hylocomium splendens***, used here in a shop window display. Photo courtesy of Irene Bisang.

Figure 53. ***Bryum argenteum***, a species used in Missouri, USA, in floral arrangements. Photo by Tushar Wankhede, through Creative Commons.

Figure 54. ***Dicranum scoparium***, a popular species for floral arrangements. Photo by Janice Glime.

Figure 55. ***Rhytidiadelphus loreus***, a popular species for floral arrangements. Photo by Malcolm Storey <www.discoverlife.org>, with online permission.

The role of mosses in decorations pervades hotels, shop windows (Figure 52, Figure 57-Figure 58), optometry displays (Figure 59), tea houses (Figure 60) (Tan 2003; Irene Bisang & Lars Hedenäs, pers. comm.), and even displays in the Ford automobile showroom (Kenneth Adams, pers. comm. 1 November 2013). They can enhance the flowers that often serve to greet those entering a building (Figure 61).

Figure 56. A variety of mosses adorn this shop display. Photo courtesy of Irene Bisang.

Figure 57. ***Leucobryum*** ball in a shop window display at Paradeplatz in Europe. Photo courtesy of Irene Bisang.

Figure 58. Closer view of the variety of mosses adorning this shop display. Photo courtesy of Irene Bisang.

Figure 59. Large pleurocarpous mosses are used here to adorn a display of an optometrist. Photo courtesy of Irene Bisang.

Figure 60. Mosses add to the display of a tea shop window. Photo courtesy of Irene Bisang.

Figure 61. Floral display in Göteborg showing ***Leucobryum***. Photo courtesy of Lars Hedenäs and Irene Bisang.

Mosses are ideal for nursery and floral shop displays (Figure 62-Figure 63). Denoyer's Nursery in Columbus, Ohio, USA, uses some of the same sheet mosses they sell to make displays of their garden decorations (Figure 64-Figure 67).

Figure 62. Mosses are used here to enhance a floral display. Photo courtesy of Irene Bisang.

Figure 63. Mosses adding to the decorations in a Paradeplatz florist shop window. This combination of mosses and flowers is reminiscent of the Japanese "kokedama," plant decoration with moss-ball and associated phanerogams. Photo courtesy of Irene Bisang.

Figure 64. Moss base for decorative dolls in garden shop in Columbus, Ohio, USA. Photo by Janice Glime.

Figure 65. Garden furnishings displayed with moss, Denoyer's Nursery, Columbus, Ohio, USA. Photo by Janice Glime.

Figure 66. Garden furnishings displayed with moss, Denoyer's Nursery, Columbus, Ohio, USA. Photo by Janice Glime.

Figure 67. ***Leucobryum glaucum*** memorial cross. Photo courtesy of Roy Perry.

Moss Rocks

Mosses conjure up a peaceful experience, as recognized so clearly in the Japanese moss gardens. Some entrepreneurs have capitalized on this feeling by creating indoor miniature gardens that are stylized versions of a moss and rock habitat (Figure 68). such are the creations at Moss & Stone Gardens (Spain 2012). The rocks in Figure 68 show these stylized rocks. Prices range from US $14.99 for the smallest (6 cm) to $39.99 for the largest (16.5 cm).

Figure 68. Three sizes of moss rocks available from the Moss & Stone Gardens, Raleigh, NC, USA. Photo by Moss & Stone Gardens.

Flower Pots

The use of mosses to encase flower pots seems to be popular. The mosses are attractive and look natural without detracting from the flower as the center of attention (Figure 69-Figure 75). For clay pots they can reduce evaporation and absorb spills. If they are outside, they may even provide insulation.

Figure 69. Moss flower pots at Michael's Hobby Shop in Reynoldsburg, Ohio, USA. Photo by Janice Glime.

Figure 70. Moss flower pot, showing plastic liner, at Michael's Hobby Shop in Reynoldsburg, Ohio, USA. Photo by Janice Glime.

Figure 71. Moss and vine flower pot at Michael's Hobby Shop in Reynoldsburg, Ohio, USA. Photo by Janice Glime.

Figure 72. Planter decorated with moss-covered twigs in a gardening shop near Columbus, Ohio, USA. Photo by Janice Glime.

Figure 73. Vase decorated with moss-covered twigs in gardening shop near Columbus, Ohio, USA. Photo by Janice Glime.

Figure 74. Moss decorating planter in garden shop, Columbus, Ohio, USA. Photo by Janie Glime.

Figure 75. Mat of twigs with epiphytic mosses, presumably to put under a flower pot. Are there enough mosses to absorb spills? Photo by Janice Glime.

Jewelry

Mosses imbedded in glass or clear plastic have been around for some time. But some enterprising artists have endeavored to create jewelry with living mosses. One example of this is a ring (Figure 76), maintained long enough to produce sporophytes (Figure 77). Mariaela creates jewelry with living mosses in the necklace pendant (Figure 78).

Figure 76. Moss ring with live ***Ditrichum pallidum***. Photo by Brandon Holschuh.

Figure 77. Moss ring with living mosses (***Ditrichum pallidum***), including capsules! Photo by Brandon Holschuh.

Figure 78. Moss necklace from Mariaela at <www.etsy.com>.

Collection Dangers

Bryologists in Venezuela are concerned that moss harvesting in the Andes during the Christmas season for use in nativity scenes is endangering the fragile cloud forest and páramos ecosystems (León & Ussher 2005). Similar harvesting occurs in the Pacific Northwest of the USA (Figure 79).

Figure 79. Branch showing removal of bryophytes harvested for use as sheet moss. Photo courtesy of JeriLynn Peck.

Sheet moss (*e.g.* Figure 4) can be collected at any time, but preferably in summer (I know not why – perhaps because it is dry and light weight then), with a single wholesaler supplying about 14,000 pounds of dry moss per year (Nelson & Carpenter 1965).

These mosses may be packaged and sold for individuals to use in flower pots, tree yards, or other displays (Figure 80-Figure 82). The ones pictured here range US $6.95-$9.95 (Figure 80). But some of the "Supermoss" packages contain other things with the common name of "moss" (Figure 80-Figure 82).

Figure 80. Moss bags for decorations at Michael's Hobby Shop in Reynoldsburg, Ohio, USA. Photo by Janice Glime.

Figure 81. Supermoss package of real moss, Denoyer's Nursery, near Columbus, Ohio, USA. Photo by Janice Glime.

Figure 82. Supermoss Reindeer Moss, a lichen in the genus ***Cladina***, Denoyer's Nursery, near Columbus, Ohio, USA. Photo by Janice Glime.

Moss Celebration Day

Khoroshyy Petro announced to Bryonet that 22 January was Moss Celebration Day in a short-lived calendar created following the French Revolution, in the French Republican calendar (Khoroshyy Petro, Bryonet 21 January 2021 EST). This calendar, designed to celebrate the arts and nature, lasted only a decade because the church objected. The calendar did not include the traditional recognition of important dates.

Summary

Sheet mosses such as ***Hypnum*** spp. have been common in decorations, especially nativity scenes, shop windows, and floral arrangements. Some are used for wreaths and crosses and even jewelry. Gathering of bryophytes for Christmas decorations in some countries can lead to conservation concerns due to over collecting and collection of rare species lurking among the common ones being collected.

Acknowledgments

Many Bryonetters have contributed to this and other chapters through Bryonet discussions, pictures, and help in finding references. Thank you to Bob and Janet Marr for taking pictures for me at the Mayo Clinic moss walls.

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CHAPTER 3-2
FINE ARTS: ART

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CHAPTER 3-2
FINE ARTS: ART

Figure 1. Floats made of foam present artistic figures with mosses for hair and other accents. Artwork and photograph courtesy of Minoru Takeda.

In Artwork

Mosses would seem to be a natural for art work (Saito 1973), but they are actually rather difficult to portray. I once helped run a workshop using mosses for water color subjects and tools. The seemingly delicate moss leaves and branches, pressed into water color paints, then onto paper, did little more than make a smudge at the hands of these beginning artists. And painting their delicate structure is no less of a challenge.

Beatrix Potter, of Peter Rabbit fame, rendered mosses in her beautiful watercolors (Edwards 1993).

Most recently, I have seen an advertisement for moss graffiti. The "artist" is experimenting with a formula for painting moss parts onto a building, wall, or even a coffee pot (!) instead of paint to serve as decoration. The creator provides a recipe involving a blend of mosses, beer, and sugar that are then applied with a paintbrush. The promoter advises to visit your handiwork over the next few weeks to be sure it has ample water. The pictures provided, however, are an artist's rendition with real paint, as the moss artist is still perfecting the moss paint formula.

One Finnish artist, Barbro Eriksson, is creating a sculpture in which mosses will be used to fill in the design on a slab of rock, thus providing the relief (Figure 2).

Other artwork includes picture frames, decorations of bookmarks (Figure 3), and even wall hangings. Pressed, dried bryophytes are often used in framed artwork (Saito 1973), and I was privileged to receive a poem about mosses, framed in the same, from one of my students.

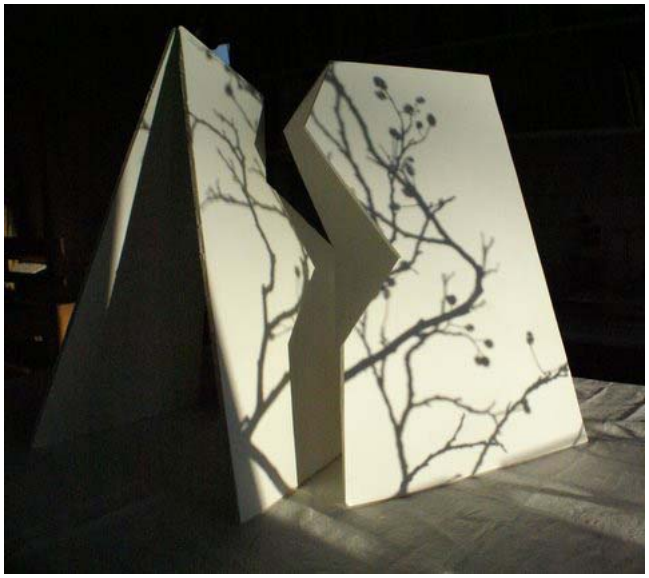

Figure 2. Model of sculpture that will become a living sculpture of mosses growing in the crevices that create the design. Artwork and photo courtesy of Barbro Eriksson.

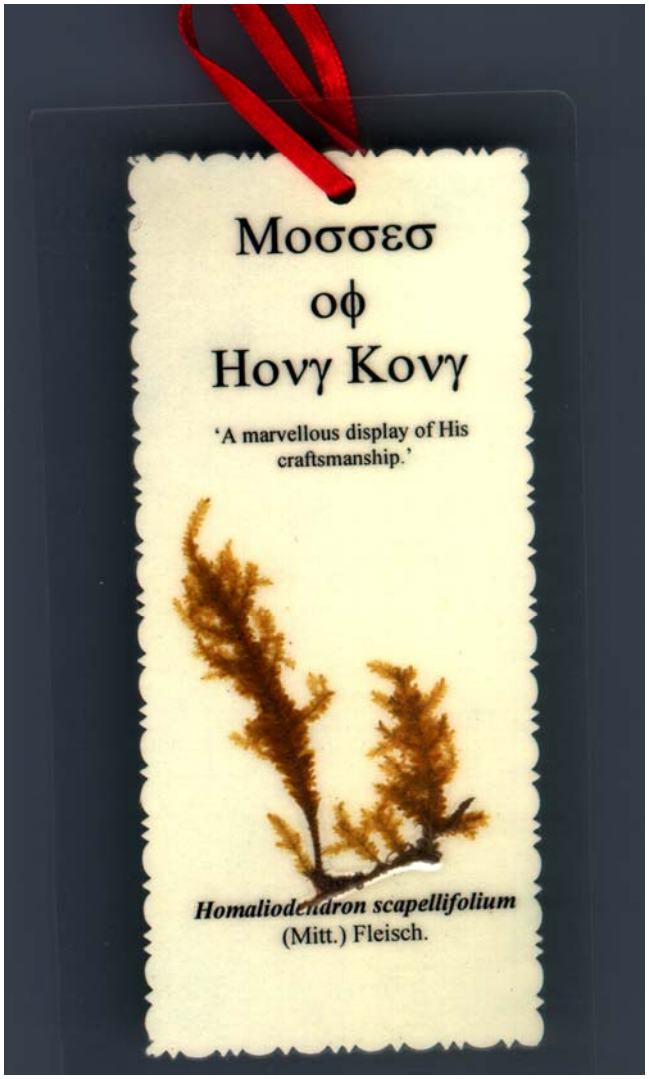

Figure 3. The moss ***Homaliodendron scapellifolium*** is used here to make a bookmark. Photo by Janice Glime.

Rarely does a moss receive such a place of honor as a coin, but in 1990, a species of ***Polytrichum*** decorated one side of the Finnish 50 penny coin, with the national animal, a brown bear (*Ursus arctos*), on the other (Hyvönen 1990; Figure 4). It would be nice to think the intention was to honor the moss, but in fact, it was the bear that was "honored" and the moss inclusion was really a product of language. In several Scandinavian languages, the word moss is affiliated with the word for bear, *e.g.* björnmossa, bjørnemose, and karhunsammal. Hyvönen speculated that the name of the bear may have been associated with the moss because bears sometimes bury their food under carpets of ***Polytrichum commune*** (Figure 5) in wet forests. Linnaeus reported that bears gather ***Polytrichum*** to line their winter holes. However, it seems that bears now are not so discriminate, using the more common ***Pleurozium schreberi*** (Figure 6) and ***Hylocomium splendens*** (Figure 7).

Figure 4. The Finnish 50 cent coin exhibits a bear on one side and the moss ***Polytrichum*** on the other. Photo courtesy of Jaakko Hyvönen.

Figure 5. ***Polytrichum commune***, a model for the image on the 50 cent Finnish coin. Photo by Christopher Tracey through Creative Commons.

Figure 6. ***Pleurozium schreberi***, a moss used by bears to line their beds. Photo by Janice Glime.

Figure 7. ***Hylocomium splendens*** on spruce forest floor, a moss used by bears to line their beds. Photo by Janice Glime.

Foam Novelties

Not surprisingly, the Japanese use bryophytes in their artwork. Minoru Takeda is a master at growing art pieces with bryophytes (Deguchi 2007; Figure 1, Figure 8). He has kindly contributed the many photographs that follow. Among these are foam figures that float on ponds (Figure 9 - Figure 11) or in glass dishes to decorate a table (Figure 12).

Figure 8. Floats and mascots with moss highlights, usually forming hair. Artwork and photo courtesy of Minoru Takeda.

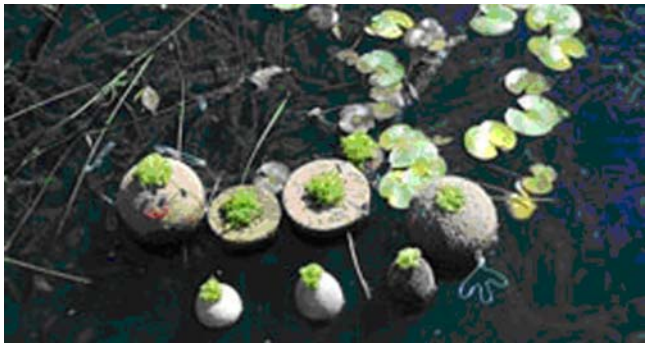

Figure 9. Moss floats on a pond in Japan. Artwork and photo courtesy of Minoru Takeda.

Figure 10. Moss floats on a pond in Japan. Artwork and photo courtesy of Minoru Takeda.

Figure 11. Moss floats on a pond in Japan. Artwork and photo courtesy of Minoru Takeda.

Figure 12. Japanese moss float decoration. Artwork and photo courtesy of Minoru Takeda.

The use of bryophytes in artwork, particularly moss pots and ceramic designs (Figure 13 - Figure 15), is popular enough that there are classes where students of all ages learn the art (Figure 16 - Figure 18). Even streets may be decorated with this unusual form of art (Figure 19).

Figure 13. Float with moss as hair. Artwork and photo courtesy of Minoru Takeda.

Figure 14. Float with moss. Artwork and photo courtesy of Minoru Takeda.

Figure 15. Japanese mascot with ***Sphagnum*** as hair. Artwork and photo courtesy of Minoru Takeda.

Figure 16. Students of all ages learning how to create moss art in Japan. Photo courtesy of Minoru Takeda.

Figure 17. A moss art teacher demonstrates how to make moss pots. Photo courtesy of Minoru Takeda.

Figure 18. Students complete their moss pots with ***Sphagnum*** as a bed. Photo courtesy of Minoru Takeda.

Figure 19. Mascot with moss as hair. Artwork and photo courtesy of Minoru Takeda.

Figure 20. Mascot ***Racomitrium japonicum*** "hair." Photo courtesy of Hironori Deguchi.

Figure 21. Mascot ***Racomitrium japonicum*** art. Photo courtesy of Hironori Deguchi.

Glass Bryophytes

For teaching purposes, various museums and other institutions have engaged artists to make glass bryophytes. These endeavor to illustrate the special structures on a scale that can easily be seen without a handlens and in three dimensions (Figure 23-Figure 30).

Figure 22. Workshop students in China learning how to make molds for creating bryophytes. Photo courtesy of Zhang Li.

Figure 23. ***Bryum capillare*** model in Chinese educational display. Photo courtesy of Zhang Li.

Figure 24. ***Haplomitrium mnoides*** model in Chinese educational display. Photo courtesy of Zhang Li.

Figure 25. ***Marchantia emarginata*** model in Chinese educational display. Photo courtesy of Zhang Li.

Figure 26. ***Phaeoceros laevis*** model in Chinese educational display. Photo courtesy of Zhang Li.

Figure 27. ***Physcomitrium eurystomum*** model in Chinese educational display. Photo courtesy of Zhang Li.

Figure 28. ***Pogonatum subfuscatum*** model in Chinese educational display. Photo courtesy of Zhang Li.

Figure 29. Show table of models in Chinese educational display. Photo courtesy of Zhang Li.

Figure 30. ***Funaria*** model in USA educational display. Photo courtesy of David Wagner.

Corpus Christi Festival

In Béjar, Salamanca, Spain, mosses are a major part of the Corpus Christi celebration (Martínez Abaigar & Núñez Olivera 2001). The border between the Moslem and Christian kingdoms had been under siege for more than 300 years. According to the legend of the Moss Men, Christians were hidden in the mountains at El Castañar, 3 km from the present town of Béjar. On the day of the feast of St. Marina of Bitinia, the Christians gathered to celebrate mass at La Centenna. After the ceremony, they covered their clothes and weapons with mosses from nearby stones. So camouflaged, they went to the Moslem fortress and lay on the walls and rocks. When the gates opened at dawn, they were able to enter and surprise the watchtowers. In a day-long struggle, the Christians took the streets one-by-one. Thus, on the ninth Sunday after Easter each year the event is celebrated with Moss Men as part of the Corpus Christi festival. Six Moss Men volunteers from the region of Béjar each year use more than 200 m^2 of moss made into moss plates, including such common ones as ***Hypnum cupressiforme*** (Figure 31), ***Antitrichia californica*** (Figure 32), ***A. curtipendula*** (Figure 33), and ***Homalothecium sericeum*** (Figure 34). They use these plates to dress

themselves in commemoration of this historic event (Figure 35 - Figure 40). Fortunately, these moss plates are kept at the Convent of San Francisco, and only damaged parts need be replaced by new mosses each year.

Figure 31. ***Hypnum cupressiforme***, one of the mosses used in commemorative dress in the Corpus Christi festivity. Photo by Michael Lüth, with permission.

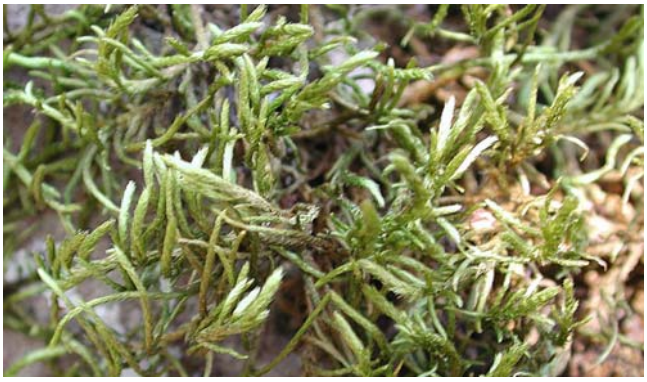

Figure 32. ***Antitrichia californica***, one of the mosses used in commemorative dress in the Corpus Christi festivity. Photo by Michael Lüth, with permission.

Figure 33. ***Antitrichia curtipendula***, one of the mosses used in commemorative dress in the Corpus Christi festivity. Photo by Michael Luth, with permission.

Figure 34. ***Homalothecium sericeum***, one of the mosses used in commemorative dress in the Corpus Christi festivity. Photo by Proyecto Musgo through Creative Commons.

Figure 35. Men being dressed in mosses for the Corpus Christi Festival. Photo by Eloy Diaz-Redondo.

Figure 36. Parade of Moss Men in the Corpus Christi celebration. Photo by Eloy Diaz-Redondo.

Figure 37. Participants of the Corpus Christi Festival clothed in mosses. Photo by Eloy Diaz-Redondo.

Figure 38. Corpus Christi celebrators surround the "monstrance," a sacred vessel in which the consecrated host is displayed. Photo by Eloy Diaz-Redondo.

Figure 39. Moss Men with one of the dignitaries during the Corpus Christi celebration. Photo by Eloy Diaz-Redondo.

Figure 40. Close view of one of the Moss Men in the Corpus Christi celebration. Photo by Eloy Diaz-Redondo.

Figure 41. Moss costumes in Papua New Guinea. Photo by Deb Jordan through Robin Stevenson.

Figure 42. Moss costumes in Papua New Guinea. Photo by Deb Jordan, provided by Robin Stevenson.

In what is apparently a different ceremonial use of bryophytes in New Guinea, the villagers of Payakona Village hold a singing ceremony (Laman 2012). They are not covered with bryophytes, but rather wear what appear to be mosses in strategic positions to create beards, hair, and decorative pieces on the head or over the chest. In what appears to be a reverse of the usual confusion, the decorations labelled lichens and Spanish moss appear to be real mosses.

Body Art

In The Philippines, ***Dawsonia*** (Figure 43), ***Pogonatum*** (Figure 44), and ***Spiridens*** (Figure 45) are used both as body decoration and to ward off evil spirits.

Figure 43. ***Dawsonia polytrichoides***, in a genus used as body decoration in the Philippines. Photo by Niels Klazenga, with permission.

Figure 44. ***Pogonatum aloides*** males, in a genus used as body decoration in the Philippines. Photo by David Holyoak, with permission.

Figure 45. ***Spiridens flagellosus***, in a genus used as body decoration in the Philippines. Photo by John Game Flickr Creative Commons.

Statues or Topiary?

Bryophytes can be fashioned into various forms with the help of wires and some sort of central core – or just moss. These are sometimes stained so they remain green, but they also can remain alive for a period of time, the duration depending on the suitability of conditions. Such statues (are these really topiary, since they are planted that way instead of cut to make the shapes?) are used to decorate gardens and lawns or used in displays indoors.

Atproot (2009) reports that mosses and lichens can have a different relationship to statues and outdoor art. They may be introduced with stones used in outdoor art. And rock carvings may be damaged by the invasion of bryophytes and lichens, as witnessed at Tennes in Balsfjord, Troms, Norway (Bjerke 2000).

Figure 46. Decorative moss turtle on display at Denoyer's Nursery, Columbus, Ohio, USA. Photo by Janice Glime.

Figure 47. Decorative moss frog on display at Denoyer's Nursery, Columbus, Ohio, USA. Photo by Janice Glime.

Figure 48. Labramoss topiary at Gray Summit, Franklin County, Missouri. Photo courtesy of Marshall Crosby.

Figure 49. Close view of labramoss topiary. Photo courtesy of Marshall Crosby.

Figure 50. Moss dog moodle topiary. Photo courtesy of Marshall Crosby.

Figure 51. Close view of moss topiary of dog moodle. Photo courtesy of Marshall Crosby.

Figure 52. Toad topiary in Europe. Photo courtesy of David Long.

Figure 53. Swan moss topiary in Europe. Photo courtesy of David Long.

Figure 54. Moss topiary dragonfly in Europe. Photo courtesy of David Long.

Film-making

To make a film of King Kong, film makers had to actually miniaturize the mosses (Simpson 2006). Real mosses posed two problems – they were at the wrong scale for the landscape, shrubs, logs, and trees created for the set, and they dried too repidly under the studio lights. They used a material called flocking that they attached to dacron with adhesive. But in Lord of Rings trilogy, the scene when a member of the Fellowhsip of Rings dies on a bed of pleurocarpous mosses used real mosses. Moss Man in Masters of Universe also had real moss. However the toy made in his image used green flock.

Figure 55. Moss monkey in garden shop in Columbus, Ohio, USA. Photo by Janice Glime

Summary

Artists have used bryophytes in framing, accenting relief in sculptures, and providing texture. Even a Finnish coin sports a moss. The Japanese use them to simulate hair and other adornments on foam statues and floats.

The Corpus Christi Festival in Béjar, Salamanca, Spain celebrates the capture of the Moslem fortress by donning sheets of moss and parading through town.

Mosses have been used in movies and in others miniature artificial mosses were used. For educational purposes, some museums and other teaching organizations have ade model mosses of glass or ceramics.

Moss topiary can be made into almost any shape.

Acknowledgments

Inkeri Ahonen helped me obtain the picture and information from the sculptor, Barbro Eriksson.

Hironori Deguchi provided me with the pictures of artwork from Minoru Takeda.

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CHAPTER 3-3
FINE ARTS: LITERATURE

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CHAPTER 3-3
FINE ARTS: LITERATURE

Figure 1. Rugged shorelines such as this with a bank of moss (***Grimmia maritima***) inspire poems that relate the ruggedness of the moss. Photo by Michael Lüth, with permission.

Stories and Verse

For some, mosses inspire poetic thoughts. Allan Fife (bryonet, 26 June 2008) has provided us with "a more or less contemporary thought on the study of mosses" by Thomas Taylor, a botanist in the British Isles, apparently written in the year he died, and published in the *London Journal of Botany* in 1848:

"They who consider attention paid to such minute objects a trifling with time, should recollect, that a moss is as much a species as a man, and the work of the same divine Creator; also, that the attentive study of the little leads to the discovery of general laws applicable to the great; and the knowledge of such laws arms the mind and the hand with power convertible to the highest purposes of life."

I began my search for mention of mosses in the Haiku poetry book I found at a used book sale, but alas, not a single poem mentioned a moss. However, a less likely occurrence is the theme of a Japanese opera developed around a moss! In Volume 1, Chapter 9-5 on light I have described this story, which is developed around the luminous properties of the cave moss, ***Schistostega pennata*** (Figure 2-Figure 3). According to legend, the luminescence of the moss (protonemata) saved the life of the man in its foreground.

Figure 2. ***Schistostega pennata*** mature gametophytes. Photo courtesy of Martine Lapointe.

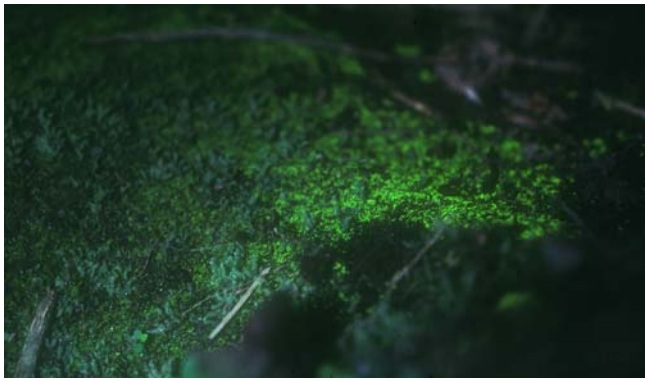


Figure 3. ***Schistostega pennata*** protonemata reflecting light. Photo from Rausu, Japan, by Janice Glime.

Philip Stanley, in his message to Bryonet on 13 July 2008, tells us of an unusual 203-page novel written by the Reverend W. R. Megaw of Belfast, who was also a bryologist. The novel was published in 1934 by The Quota Press of Belfast. In this novel, "***Ulota*** is a story, ***Ulota*** is a moss, and again ***Ulota*** is an Irish cottage (Figure 4). How the story, the moss, and the cottage are blended into one... this is the secret charm of the book" – the comment on the dustcover of the book.

Figure 4. ***Ulota phyllantha*** at Traeth Gaslyn Nature Reserve, Wales. Photo by Janice Glime.

One famous quote, permeating many cultures, includes a moss: "The rolling stone gathereth no moss." Although old, this quote is still used to remind us that we need to keep busy, that accomplishments require our energy. It is too bad that it treats the moss as a symbol of laziness. I prefer to think of it as enduring, settled, or peaceful.

Hawthorne (1996) uses mosses to describe a scene in "The Old Manse, Preface to Mosses:" "Looking down into the river, I once discovered some heavy fragments of the timbers, all green with half-a-century's growth of water-moss; for during that length of time, the tramp of horses and human footsteps have ceased, along this ancient highway." This theme of representing the passage of time is a common use of mosses in poetry.

John Ruskin discovered mosses late in life, stating "It is mortifying enough to write, - but I think thus much ought to be written, - concerning myself as the author of Modern Painters. In three months I shall be fifty years old; and I don't at this hour – ten o'clock in the morning of the two hundred and sixty-eighth day of my forty-ninth year – know what 'moss' is. He did indeed get introduced to moss, examining the "emerald green velvet" of a brick, and later wrote, "No words that I know of will say what these mosses are. None are delicate enough, none perfect enough, none rich enough." Kendall (1926) says of him, "To Ruskin, mosses were no mere botanical pigeonhole – they were a fresh pasture for his thought. With the bright thread of his fancy he wove them into the very texture of life."

Ruskin sees mosses as having particular roles in the natural world, with the adornment of rock as their principal role. Like many other poets, he refers to them as "soft mosses." And like so many others, he compares them to death, stating, "No other plants have so endless variety on so similar a structure as the mosses; and none teach us so well the Humility of Death. As for the death of our bodies, we have learned, wisely, or unwisely, to look the fact of that in the face."

Mosses often represent the passing of time, as will be seen in several of the poems here. Judson Crews, in his book, *The Clock of Moss*, writes about native peoples, farmers, and Penitentes in the Southwest, picturing the changing of the Southwest and the difficult journeys of the these people.

Shakespeare seems not to appreciate mosses as objects of beauty, but like so many poets considers them as signs of age.

In *Comedy of Errors*, Act II, Sc. 2:

"It is dross, usurping ivy, brier, or idle moss."

In *Titus Andronicus*, Act II, Sc. 3:

A barren, detested vale . . .
The trees, though summer, yet forlorn
Oercome with moss, and baleful mistletoe.

Occasionally an entire poem or story may be dedicated to moss, although it is more likely that mosses are used in the imagery. Some of these attempt to describe bryophytes in ways to rest the soul, but others tell stories from the perspective of the moss. Such is the poetic prose by the Indian writer Uma Narayan (*The Adirondack Review*):

Gathering Moss

Surely the stone would not suddenly find itself encased in a velvet muff of moss if it merely stopped rolling; after all, it might come to a standstill in a spot that lacked the moist good moss requires. Piles of sedentary stone have stood in sandy deserts, bleached by sun, unspeckled by moss. There was no moss on indolent moon rocks; lunar vegetation would have made the headlines, provoked thoughtful interviews with Carl Sagan. Evidently, many stationary stones manage to miss out on moss. There is more to moss than mere halting – unplanned fluke, serendipity. Knowing that, it may make more sense to accept the loss of moss, and enjoy the rough adventures of rolling, despite the implications of downward mobility. You wake up in a different place each day and never grow bored or outstay your welcome. You travel without a passport, see the world without paying for transport. You careen down mountains scaring hikers, go rafting in unruly waters, surrender to slope, to gravity. Moss requires tradeoffs, and one of them is staying put in a damp spot. Some stones may find real satisfaction in settled tranquility,

in providing space for green growth. Other pebbles have precipitate souls, value exuberance, cultivate the arts of falling fluently, and embrace the spry delights of a mossless life. In this matter of moss, as in many others, there are pluralities of possibility, a rich variety of ways to be stone.

Gathering Moss is also the title of a popular book by Robin Wall Kimmerer (2003). It is the Winner of the 2005 John Burroughs Medal Award for Natural History Writing. Its description in the online advertisement:

Living at the limits of our ordinary perception, mosses are a common but largely unnoticed element of the natural world. *Gathering Moss* is a beautifully written mix of science and personal reflection that invites readers to explore and learn from the elegantly simple lives of mosses. Robin Wall Kimmerer's book is not an identification guide, nor is it a scientific treatise. Rather, it is a series of linked personal essays that will lead general readers and scientists alike to an understanding of how mosses live and how their lives are intertwined with the lives of countless other beings, from salmon and hummingbirds to redwoods and rednecks. Kimmerer clearly and artfully explains the biology of mosses, while at the same time reflecting on what these fascinating organisms have to teach us. Drawing on her diverse experiences as a scientist, mother, teacher, and writer of Native American heritage, Kimmerer explains the stories of mosses in scientific terms as well as in the framework of indigenous ways of knowing. In her book, the natural history and cultural relationships of mosses become a powerful metaphor for ways of living in the world. *Gathering Moss* appeals to a wide range of readers, from bryologists to those interested in natural history and the environment, Native Americans, and contemporary nature and science writing.

Elizabeth Gilbert (2013) has contributed *The Signature of All Things*. This fictional book is not much about mosses themselves, although some are mentioned specifically. What it does include is the story of a girl, then a woman, who became a botanist and met some of the great personalities in bryology.

Edwards (1992) has analyzed the role of mosses in literature. He suggests that they moved from the maligned, being associated with death, to the benign, representing the accumulation of time. They also have represented stagnation and barrenness, but likewise may represent the "spark of green, or optimism in an otherwise bleak place." They can represent solitude, but they also represent haunting, which Edwards suggests may be due to their habit of growing on tombstones.

Ando (1990) summarizes similar associations with "koke," the Japanese word for moss. These comprise four groups: 1) old age, antiquity, solemnity, 2) Beauty, quiet, elegance, 3) seclusion, simplicity, loneliness, and 4) desolation, retrospection, mutability, death.

Fillers

The editors of *The Bryologist* from 1966 to 1975 found a great use of bryological literature. These were placed to fill empty spaces at the ends of articles, especially near the ends of issues. Since these contributions are not cited in the regular indices of *The Bryologist*, Reese (1994) published the references in *Evansia*. These numbered 79, including both bryophytes and lichens.

Poetry

The poets seem to think of mosses in two extremes, one as the delicate beings on the forest floor, requiring moisture and refuge from the sun (Figure 5), and the other as rugged and enduring, living where nothing else can (Figure 1). This short verse by Willis Boyd Allen describes the delicate nature of woodland mosses:

Children of lowly birth,
Pitifully weak;
Humblest creatures of the wood
To your peaceful brotherhood
Sweet the promise that was given
Like the dew from heaven:
'Blessed are the meek,
They shall inherit the earth'
Thus are the words fulfilled:
Over all the earth
Mosses find a home secure.
On the desolate mountain crest,
Avalanche-ploughed and tempest-tilled,
The sweet **mosses** rest;
On shadowy banks of streamlets pure,
Kissed by the cataracts shifting spray,
For the bird's small foot a soft highway
For the many and one distressed.
Little sermon of peace.

Figure 5. "On shadowy banks of streamlets pure, Kissed by the cataracts shifting spray." Here ***Platyhypnidium riparioides*** fulfills the poet's verse. Photo by Michael Lüth, with permission.

A. Muriel Saunders wrote "***Sphagnum* Moss** (Figure 6)," describing the virtues of using peatmosses for bandages:

The doctors and the nurses
Look North with eager eyes,
And call on us to send them
The dressing that they prize,
No other is its equal –
In modest bulk it goes,
Until it meets the gaping wound
Where the red life blood flows,
Then spreading, swelling in its might,
It checks the fatal loss,

And kills the germ, and heals the hurt –
The kindly ***Sphagnum*** Moss (Figure 6).

Figure 6. ***Sphagnum*** in a poor fen. Photo by Janice Glime.

Marshall (1907) includes a varied collection of poetry and prose where mosses help to describe the nature of things. When he discusses using moss for chinking and filling cracks, he compares this to uses by birds in building their nests (Figure 7) by quoting a poem by Claire, **The Thrush's Nest**:

Within a thick and spreading hawthorn bush
That overhung a molehill large and round,
I heard from morn to morn a merry thrush
Sing hymns of rapture, while I drank the
Sound with joy – and oft an unintruding guest,
I watched her secret toils from day to day;
How true she warped the **moss** to form her nest,
And modell'd it within with wood and clay.

Figure 7. "How true she warped the **moss** to form her nest," this bird's nest is constructed of dead plant material with living **mosses** woven among it. Photo courtesy of Jeri Peck.

Marshall (1907) begins his chapter entitled "**Leafy Mosses**" with this poem (Figure 8):

The tiny **moss**, whose silken verdure clothes
The time-worn rock, and whose bright capsules rise,
Like fairy urns, on stalks of golden sheen,
Demand our admiration and our praise,
As much as cedar, kissing the blue sky,
Or Krubul's giant flower. God made them all,
And what He deigns to make should ne'er be deemed
Unworthy of our study and our love.

Figure 8. "The time-worn rock, and whose bright capsules rise, Like fairy urns, on stalks of golden sheen," aptly describes this ***Ortrhotrichum pulchellum***, although this species grows on bark of trees. Photo by Michael Lüth, with permission.

Humble Moss

The delicate and peaceful nature of mosses has inspired poets. Smallness and closeness to the ground have labelled bryophytes as humble in many literary treatments. Thus begins the poem of Richard Henry Dana, Sr. (1787-1879), a lecturer, lawyer, and journalist, but also a poet, from Massachusetts. He found the moss a worthy literary subject in his poem, **The Moss Supplicateth for the Poet**. (Figure 9):

Though I am humble, slight me not,
But love me for the Poet's sake;
Forget me not till he's forgot,
For care of slight with him I take.

For oft he passed the blossoms by
And turned to me with kindly look;
Left flaunting flowers and open sky,
And wooed me by the shady brook.

They said the world he fain would shun,
And seek the still and twilight wood, -
His spirit, weary of the sun,
In humblest things found chiefest good;

That I was of a lowly frame,
And far more constant than the flower,
Which, vain with many a boastful name,
But fluttered out its idle hour;

That I was kind to old decay,
And wrapped it softly round in green, -
On naked root, and trunk of gray,
Spread out a garniture and screen.

He praised my varied hues, - the green,
The silver hoar, the golden, brown;
Said, lovelier hues were never seen;
Then gently pressed my tender down.

And where I sent up little shoots,
He called them trees, in fond conceit:
Like silly lovers in their suits
He talked, his care awhile to cheat.

I said, I'd deck me in the dews,
Could I but chase away his care,
And clothe me in a thousand hues,
To bring him joys that I might share.

He answered, earth no blessing had
To cure his lone and aching heart;
That I was one, when he was sad,
Oft stole him from his pain, in part.

But e'en from thee, he said, I go,
To meet the world, its care and strife,
No more to watch this little flow,
Or spend with thee a gentle life.

That I was of a lowly frame,
And far more constant than the flower,
Which, vain with many a boastful name,
But fluttered out its idle hour;

That I was kind to old decay,
And wrapped it softly round in green,
On naked root, and trunk of gray,
Spread out a garniture and screen.

They said, that he was withering fast,
Without a sheltering friend like me;
That on his manhood fell a blast,
And left him bare, like yonder tree;

That spring would clothe his boughs no more,
Nor ring his boughs with song of bird, -
Sounds like the melancholy shore
Alone were through his branches heard.

Methought, as then he stood to trace
The withered stems, there stole a tear, -
That I could read in his sad face,
Brothers, our sorrows make us near.

And then he stretched him all along,
And laid his head upon my breast,
Listening the water's peaceful song: -
How glad was I to tend his rest!

Then happier grew his soothed soul;
He turned and watched the sunlight play
Upon my face, as in it stole.
Whispering, Above is brighter day!

He praised my varied hues, - the green,
The silver hoar, the golden, brown;
Said, Lovelier hues were never seen;
Then gently pressed my tender down.

And where I sent up little shoots,
He called them trees, in fond conceit:
Like silly lovers in their suits
He talked, his care awhile to cheat.

I said, I'd deck me in the dews,
Could I but chase away his care,
And clothe me in a thousand hues,
To bring him joys that I might share.

He answered, earth no blessing had
To cure his lone and aching heart;
That I was one, when he was sad,
Oft stole him from his pain, in part.

But e'ven from thee, he said, I go,
To meet the world, its care and strife,
No more to watch this little flow,
Or spend with thee a gentle life.

And yet the brook is gliding on,
And I, without a care, at rest,
While he to toiling life is gone;
Nor finds his head a faithful breast.

Deal gently with him, world, I pray;
Ye cares, like softened shadows come;
His spirit, well nigh worn away,
Asks with ye but awhile a home.

O, may I live, and when he dies
Be at his feet a humble sod;
O, may I lay me where he lies,
To die when he awakes in God!

Figure 9. ***Grimmia elongata*** demonstrates "He praised my varied hues, - the green, the silver hoar, the golden, brown." Photo by Michael Lüth, with permission.

Carol Reed-Jones tells how she develops a list poem, in this case first listing all the things she sees in the woods. Then she must think how they relate to each other and how she can use the senses to describe them. Thus, she adds moisture and texture to the green color of the moss to make the image come alive (Figure 10):

In the Woods

In the woods, scraps of fog
  drape themselves
  like gray scarves on the trees.
In the woods,
  frogs sing and crows squawk,
  and one heron flaps past on silent wings.
In the woods, blooming plants
  exhale a sweet perfume,
  and the taste of green growing things
  is in the air.
In the woods, each tree
  wears soft, moist green **moss**
  over its rough, dry bark.

Figure 10. Here every tree "wears the soft, green moss" ***Eurhynchium praelongum***. Photo by Michael Lüth, with permission.

One reference that seems common in the use of mosses in literature is that they are "soft underfoot," as Edwards (1993a) points out. He found fifteen occurrences of such a reference.

From Twenty Lessons on British Mosses (1846)

by William Gardiner (1808-1852)

O! Let us love the silken **moss**
That clothes the time-worn wall
For great its Mighty Author is,
Although the plant be small.

The God who made the glorious sun
That shines so clear and bright,
And silver moon, and sparkling stars,
That gem the brow of night-

Did also give the sweet green **moss**
Its little form so fair;
And, though so tiny in all its parts,
Is not beneath His care.

When wandering in the fragrant wood,
Where pale primroses grow
To hear the tender ring-dove coo,
And happy small birds sing,

We tread a fresh and downy floor,
By soft green **mosses** made ;
And, when we rest by woodland stream,
Our couch with them is spread.

In valley deep, on mountain high-
The **mosses** still are there :
The dear delightful little things-
We meet them everywhere!

And when we mark them in our walks,
So beautiful, though small,
Our grateful hearts should glow with love
To Him who made them all.

The American poet Amy Clampitt begins her poem, **Cloudberry Summer**, part of her collection 'What the Light Was Like,' as follows:

Cloudberry Summer
First ventured into
in mid-July, the bog's sodden hollow
muffled the uproar of the shore
it hunkered in the lee of. Wrung residues
of ***Sphagnum*** **moss** steeped in self-
manufactured acids stained the habitat's
suffusing waters brown...

Rugged Mosses

It seems it is often the smallness that is stressed, and seldom the ruggedness, but these poems show that the tenacity of such a small plant gives hope that we too can survive adversity. This wonderful little poem, Ode to ***Grimmia***, Anonymous, p. 433, describing ***Grimmia*** (Figure 11) as only a bryologist could, obviously had an author, but I had only a photocopy and a page number, with no indication of where it came from. A year after my plea for help in identifying the author (first edition of this chapter), Andi Cairns found a scrap of paper with the poem and the author Peter Albert, but no source. Fortunately, I misread her email as a name familiar to me, Peter Alpert. I was able to track him down and contact him. Peter responded that this was the first and last poem he ever wrote, a contribution to his doctoral thesis (Alpert 1982).

Ode to ***Grimmia*** – by Peter Alpert

The most casual talker, if he be a walker,
is surely acquainted with moss;
He will say it's a thing that to grow needs a spring,
leafy shade, and a log to emboss.
But he's wrong three times over; he's yet to discover
there's a moss which is doughty and tough;
One he's likely to see, and dismiss thoughtlessly
as dead, brown, old fungus-like stuff.
Bravely crowning a rock, this is pure mossy stock,
air, it's dry, yes, but far from inert;
Give one drop of rain – it will turn green again!
And resume making moss leaves, unhurt.
It can manage drought slyly, knowing poikilohydry,
like its kin in the genus of ***Grimmia***,,
Which from bare alpine col to the seer chaparral
make hard boulders seem soft and familiar.

Figure 11. ***Grimmia arenaria*** demonstrates the brown-black moss as described in **Ode to *Grimmia***. Photo by Michael Lüth, with permission.

Thomas James Allen seems also to find moss in those dreary places in his four poem parts called "Moss Upon the Brick." But in the end, the endurance of the moss gives him hope:

Moss Upon The Brick - Part 1

In an older part of town,
Covered far and green and thick,
An ancient house, an antique home,
With **moss** upon the brick.

A window's broken, boards are split,
The clocks inside have stopped,
The pictures hung upon the walls
Have bent their nails and dropped.

A fence outside surrounds the house,
The gate squeaks with the breeze,
The yard is filled from left to right
With dying grass and trees.

The road untravelled past the house
Is muddy, brown and slick,
And the sidewalk from the house
Has **moss** upon the brick.

Moss Upon The Brick - Part 2

The children discover the ancient house
That townsfolk pass by quick,
A haunted place with summer weeds,
And **moss** upon the brick.

They sneak inside through an open door
That leads into a hall,
An empty spiderweb above
Is stretched from wall to wall.

They wander past the dining room,
That's lit through broken panes,
The rug on the floor below the chairs
Is soiled by coffee stains.

The kitchen with its well-worn tiles
Is empty, dark and cold;
A hardened breadcrumb on the floor
Is covered with blue mold.

The children wander past the stairs,
They're walking hand in hand;
They're frightened by an old umbrella,
Discarded in a corner stand.

All at once the wind blows hard
And slams a door upstairs;
The children race back through the rooms,
Disturbing rugs and chairs.

Back home they run with screaming cries,
For Nature's played a trick;
They'll never come to play in the house
With **moss** upon the brick.

Moss Upon The Brick - Part 3

A November walk down an old rutted road
Through a fog, though misty and thick,
I've ventured to see that old rustic house,
With **moss** upon the brick.

The sun has been swallowed behind the dark clouds,
The air is bitter and chilled,
The winds change from North to East to South-
South-West, but never are stilled.

The weeds growing thick by the edge of the house,
Live now, while others cannot,
They thrive in the cold with the wind and the snow,
Instead of the summertime hot.

The apple trees dropped their fruits in the yard
When nobody came to call,
The red and the yellow lie mixed with the brown
Of the leaves that were dropped in the Fall.

A November day in the life of the house,
Like others of future or past,
Does little to change the brick and the wood,
Or the darkened shadows cast.

An early Fall snow still clings to the roof,
And ice makes the sidewalk slick,
But the wind and the cold can never remove
The **moss** upon the brick.

Moss Upon The Brick - Part 4

Now I have grown old, my hair has turned gray,
The passage of time was so quick;
I wonder if years have weathered the house
With **moss** upon the brick?

I remember the house as it was in my youth,
I'm drawn down the muddy lane;
The trees, the walk, the peeling paint,
The broken window pane.

Why, even in my day, the boards on the porch,
From lying so long were sore,
They'd bent their necks and arched their backs,
Pulling their nails from the floor.

I wonder if years have caved in the roof?
If the weeds are growing thick?
If wind and rain have even left
A brick upon a brick?

I'm nearing the house, I'm afraid to look,
I laugh, my fearing is odd;
I'd always supposed the house would stand strong,
Like mountains, or faith in a god.

But mountains with time have melted away,
And I've had my faith in God shaken,
And someday the earth will not turn 'round the sun,
Oh what is this risk that I've taken?

If I shatter a memory by returning to see
Whether my childhood world is the same,
And finding that things are not as I left them,
I've only myself to blame.

My hand on the gate, I look up the walk,
My heart turns the clock back a tick;
My faith, my life saved! - for there stands the house,
With **moss** upon the brick.

Among the more famous bryological poems (at least among bryologists) is the one by Mungo Park, written

about his African travels when he thought he would surely die in the desert, with no compass and no food, but who gained the hope he needed upon seeing a lowly moss, a small ***Fissidens*** (Figure 12), green and growing (Crum 1973). Park wrote in his journal, "Can that Being (thought I), who planted, watered, and brought to perfection in this obscure part of the world a thing which appears of so small importance, look with unconcern upon the situation and sufferings of creatures formed after his own image? Surely not! Reflections like these would not allow me despair. I started up, and disregarding both hunger and fatigue, travelled forward, assured that relief was at hand." He did indeed survive to reach hospitable land:

Sad, faint and weary, on the sand
Our traveller sat him down; his hand
Cover'd his burning head.
Above, beneath, behind, around,
No resting for the eye he found;
All nature seemed as dead.

One tiny tuft of **moss** alone,
Mantling with freshest green a stone,
Fix'd his delighted gaze;
Through bursting tears of joy he smiled,
And while he raised the tendril wild,
His lips o'erflowed with praise.

Oh! shall not He who keeps thee green,
Here in the waste, unknown, unseen,
Thy fellow-exile save?
He who commands the dew to feed
Thy gentle flower, can surely lead
Me from a scorching grave.

Thy tender stalks, and fibres fine,
Here find a shelter from the storm;
Perhaps no human eye but mine
Ere gazed upon thy lovely form.

He that form'd thee, little plant,
And bade thee flourish in this place,
Who sees and knows my every want,
Can still support me with His grace.

Figure 12. ***Fissidens bryoides***, identified by W. J. Hooker, surviving in the desert soil, brought hope to Mungo Park as he was about to give up all hope. Photo by Michael Lüth, with permission.

Winter seems to inspire mention of mosses, when all else is dark and grey, as in this verse by George Crabbe called **Tales of the Hall**:

All green was banished save of pine and yew,
That still displayed their melancholy hue;
Save the green holly with its berries red,
And the green **moss** that o'er the gravel spread.

But Whittier, in **Mogg Megone**, Pt. III, speaks of spring, when other plants overtake the mosses:

'Tis spring-time on the eastern hills!
Like torrents gush the summer rills,
Through winter's **moss** and dry dead leaves
The bladed grass revives and lives,
Pushes the mouldering waste away,
And glimpses to the April day.

The freshness of rainfall likewise makes the mosses stand out, inspiring the poet, as Alfred Tennyson writes in **The Lotos Eaters: Choric song**:

Here are cool **mosses** deep,
And thro' the **moss** the ivies creep.

One anonymous poem appeared in the Bryological Times 96 in 1998 as lyrics of a song sung by the students in a peatlands bryophyte course in Finland in 1997:

Ten Keen Bryologists

Ten keen bryologists
Were learning bryophytes,
one of them got stuck in those,
but nine spent all their nights!

Nine freak bryologists
went out into a mire,
one of them got grilled in there,
but eight survived the fire!

Eight smart bryologists went out into a bog,
one found too much ***Sphagnum*** there,
the rest got through the fog!

Seven dumb bryologists went out into a fen,
one discovered two bears there,
the others passed the den!

Six sane bryologists collected more mass samples,
one mistook it all for spinach
five needed no example!

Five lax bryologists
took a break with sauna,
one got broiled like a fish,
the rest remained living fauna!

Four wise bryologists,
jumped into a river,
one of them jumped down the rapids,
three cared not a shiver!

Three sure bryologists
identified Mniaceae,
one took ***Mnium*** (Figure 13) for a ***Bryum*** (Figure 14),
two were like Timo so crazy!

Two brave bryologists
were walking near the border,
one saw a Russian endemic,
the other returned in order!

One lone bryologist
liked bryophytes, so then
he looked for nine more bryophiles
and started again as ten!

Figure 13. ***Mnium hornum*** with capsules. Photo by Jan-Peter Frahm, with permission.

Figure 14. ***Bryum capillare*** with capsules. Photo through Creative Commons.

Some poetry is just for fun and expresses the author's state of mind. This anonymous 1996 poem, published in Bull. Brit. Bryol. Soc. 67: 45, perhaps by a frustrated student, expresses the trials and tribulations of dealing with bryophyte systematics (Figure 15 - Figure 18):

Modern studies in ***Drepanocladus***
Lars Hedenäs of Sweden,
By the Nine Gods he swore,
The genus ***Drepanocladus***
Should trouble us no more.

The concept was old-fashioned
Just taxonomic tedium,
So he split it into several parts,
And one of them's ***Scorpidium*** (Figure 16).

Perplexed and puzzled by the rest,
He paused to scratch his ear,
And after labours long and hard,
Arrived at ***Warnstorfia*** (Figure 17).

Axillary hairs he laboured o'er,
And peristomial matters,
And other trivial details which
Will drive us mad as hatters.

At last he faced the final rump
'Now what on earth'll I call this?'
Then final inspiration struck –
And gave us ***Hamatocaulis*** (Figure 18).

Now sound his reasons may well be,
For splitting, and not lumping,
But as I struggle with new names,
I'm half inclined to thump him.

Figure 15. The traditional genus ***Drepanocladus*** has few remaining species, now including this ***D. sendtneri***, as Hedenäs has attempted to "trouble us no more." Photo by Michael Lüth, with permission.

Figure 16. Hedenäs concluded that this member of ***Drepanocladus*** should be moved to ***Scorpidium*** as ***S. revolvens***. Others, such as Blockeel (2000) still include it in ***Drepanocladus***. Photo by Michael Lüth, with permission.

Figure 17. Once called ***Drepanocladus exannulatus***, Hedenäs has renamed this one ***Warnstorfia exannulatus***. Photo by Michael Lüth, with permission.

Figure 18. And another once named ***Drepanocladus vernicosus***, this one is now ***Hamatocaulis vernicosus***. It seems that Hedenäs has solved the problems of *Drepanocladus* by removing most of its species! This seems to have resulted in no less consternation by his student, as lamented in the poem, **Modern Studies in *Drepanocladus***. Photo by Michael Lüth, with permission.

There are many translations of a poem by the Chinese poet Wang Wei, where in the end it is the moss that is given importance (Figure 19). I prefer this one by W. J. B. Fletcher in 1919:

> So Lone seem the hills; there is no one in sight there.
> But whence is the echo of voices I hear?
> The rays of the sunset pierce slanting the forest,
> And in their reflection green **mosses** appear.

Figure 19. ***Hypnodendron menziesii***, showing "The rays of the sunset pierce slanting the forest, And in their reflection green mosses appear." Photo by Jan-Peter Frahm, with permission.

In a discussion on Bryonet in June 2008, Dan Paquette was more a realist in this contribution:

> Dirty Little Moss
> By Dan Paquette
>
> Dirty little **moss**
> on the cottonwood trunk,
> my spray bottle
> washes away the debris.
>
> Your stem snuggles close
> to your siblings, green
> unbrushed curls
> of sun-loving leaves.
>
> Your generation lies
> criss-crossed above
>
> tired wet scaffolding
> twisted remnants
> of your first borne branches
> and some great, great
> uncles and aunts
> in mucous, brown
>
> intertwined stems, leaves—
> limp banners
> of whom
> they once were—
>
> **mosses**.
> One day, your skin
> will be coal pudding
> for some thermal bacteria
>
> long after you and I

It is seldom that mosses figure in such touching dramas and struggles as seen in the works of Walt Whitman in his twelve-poem sequence, "Live Oak, with Moss." In 1858 or 1859, Whitman described one man's love for another, the happiness they shared, and the aftermath of that relationship (Parker 1996). But that sequence, in its original form and presentation of honest struggles, was never published. Rather, a revised version, missing the comma, was ultimately published as "Live Oak with Moss" within a forty-five poem "Calamus" section of the 1860 *Leaves of Grass.* The original "Live Oak, with Moss," finally published by Bowers in 1953 (see Parker 1996), gives an honest rendition of the struggle and feelings of a man's love for a man while living in a world of homophobia.

In contrast to the usual imagery and friendly moss names, it seems that in recent works in Great Britain, scientific names of mosses may appear in literary works. For example, in Dulcie Domum's "Bad Housekeeping" (*The Guardian*, 8 February 1992), she writes "Gertrude was seated on a mat of ***Grimmia pulvinata*** (Figure 20) gazing thoughtfully out across glittering Rough Dike reservoir." (Edwards 1993a; Figure 20). Even less recently, Dutton, in "The Craggie" (1976) wrote "Remarkable woman," mused the Doctor, turning again to the wall. "Had an entire liverwort subspecies named after her – ***Dicranodontium uncinatum*** McHattii (Figure 21); should have been a genus – *Agenesia*." It is too bad that ***Dicranodontium*** is a moss, not a liverwort (Figure 21).

Figure 20. This ***Grimmia pulvinata*** hardly gives the image of "Gertrude was seated on a mat of ***Grimmia pulvinata*** gazing thoughtfully out across glittering Rough Dike reservoir," but it can form extensive mats, and those spiny looking hair tips are actually quite soft. Photo by Michael Lüth, with permission.

Figure 21. This moss, ***Dicranodontium uncinatum***, is clearly not the liverwort as referenced in the words of Dutton. Perhaps it is best that poets stick to common names. They cannot be easily challenged and are usually more poetic. Photo by Michael Lüth, with permission.

Perhaps more commonly, mosses are used as a means of describing something else. In her poem describing the habit of burying daughters live with their dead fathers in Arabia, Anne Sexton (1981) again uses mosses as a means of showing the passing of time, writing:

The **Moss** of his Skin
It was only important
to smile and hold still,
to lie down beside him
and to rest awhile,
to be folded up together
as if we were silk,
to sink from the eyes of mother
and not to talk.
The black room took us
like a cave or a mouth
or an indoor belly.
I held my breath
and daddy was there,
his thumbs, his fat skull,
his teeth, his hair growing
like a field or a shawl.
I lay by the **moss**
of his skin until
it grew strange. My sisters
will never know that I fall
out of myself and pretend
that Allah will not see
how I hold my daddy
like an old stone tree.

Even in poetry, mosses are often associated with death and decay. John Greenleaf Whittier wrote, in **A Dream of Summer**:

The Night is Mother of the Day,
The Winter of the Spring,
And ever upon old Decay,
The greenest **mosses** cling.

And John Masefield wrote in **Vagabond**:

Dunno about Life – it's jest a tramp alone
From wakin'-time to doss,
Dunno about Death – it's jest a quiet stone
All over-grey wi' **moss**.

Emily Dickinson often wrote of death, so it is not surprising that mosses entered into her imagery. In "**I died for Beauty – but was scarce**," she uses it as her final image, signifying the passage of time as the moss covers our names (on the tombstone):

Adjusted in the Tomb
When one who died for Truth, was lain
In an adjoining Room –
He questioned softly "Why I failed"?
"For Beauty", I replied –
"And I – for Truth – Themself are One –
We Brethren, are," He said –
And so, as Kinsmen, met a Night –
We talked between the Rooms –
Until the **Moss** had reached our lips –
And covered up – our names

A pleasant contrast to these morbid references to mosses is "The Thorn" by William Wordsworth (Everything2 2005). In this poem, of 22 stanzas, he starts by describing the thorn tree as sad, aging, and decrepit with lichens. Later, however, he describes the heap of earth the size of a child's grave by that same tree as more beautiful than any he has seen because the **moss** growing there shines with all kinds of colors – olive green and scarlet bright. The **moss** looks like a skillfully woven patchwork with beautiful colors of green, red, and pearly white. Here, the **moss** seems to symbolize that life goes on despite death around it.

Johann Greilhuber on Bryonet 15 July 2008, "The nice mossy poem by Siegfried von Vegesack, posted by Goda Sporn on June 30, 2008, was probably incomprehensible to those, who had no training in German language. Therefore I tried a free paraphrasing translation (I hope, with not too many errors) as follows:"

Moss

Have you already **mosses** seen?
Have you already down there been,
looking not just from above,
not being close enough –

no – kneeling down, so that you look
at them as if you read the letters in a book?
O wizard fonts! O wondersigns!
A matchless jungle grows, where branch to branch aligns,
and thrives and sprouts abundantly
in forest dawn.

Throughout the year you see
the curled fringes, peaked cones,
the silverhelmets, bells, pompones,
the tangled branchlets, crossed shafts
with petticoats of laced tufts.

This lowly grows on soil and stones --
just **mossy** stuff.
And huge above
the forest thrones.

But now and then a slender deer
walks below the bushes here,
bows under the leafy roof,
stamps into the **moss** its hoof.

And a guileless leveret might
bleed under the foxes bite.
Crawling over liverworts
a paunchy hedgehog lightly snorts,
and in endless caravans
march here legions of ants.

A weasel jumps and rips the prey,
while cool and impressively may
a snake find through the **moss** its way.
What happens here in brushweed deep
on **mossy** stones
nobody learns, the **mosses** secrets keep.
And huge above the forest thrones.

Have you already down there been?
Have you already **mosses** seen?

The original by Siegfried von Vegesack:

Moos

Hast du schon jemals **Moos** gesehen?
Nicht bloss so im Voruebergehen,
so nebenbei, von oben her,
so ungefaehr -
nein, dicht vor Augen, hingekniet,
wie man sich eine Schrift besieht?

Oh Wunderschrift! Oh Zauberzeichen!
Da waechst ein Urwald ohnegleichen,
und wuchert wild und wunderbar
im Tannendunkel, Jahr fuer Jahr,
mit krausen Fransen, spitzen Huetchen,
mit silbernen Trompetentuetchen,
mit wirren Zweigen, krummen Stoeckchen,
mit Sammethaerchen, Bluetengloeckchen,
und waechst so klein und ungesehen -
ein Huempel **Moos**.

Und riesengross
die Baeume stehen.

Doch manchmal kommt es wohl auch vor,
dass sich ein Reh hierher verlor,
sich unter diese Zweige bueckt,
ins **Moos** die spitzen Fuesse drueckt
und dass ein Has, vom Fuchs gehetzt,
dies **Moos** mit seinem Blute netzt...

Und schnaufend kriecht vielleicht hier auch
ein sammetweicher Igelbauch,
indes der Ameis' Karawanen
sich unentwegt durchs Dickicht bahnen.

Ein Wiesel pfeift, ein Sprung und Stoss...
und kalt und gross
gleitet die Schlange durchs **Moos**...
Wer weiss, was alles hier geschieht,
was nur das **Moos** im Dunkeln sieht:
Kein Wort verraet das **Moos**.
Und riesengross die Baeume stehen.
Hast du schon jemals **Moos** gesehen?

Sir Orfeo (translated by J.R.R. Tolkien 1975) written by a medieval poet whose name is unknown:

He once had ermine worn and vair,
on bed had purple linen fair,
now on the heather hard doth lie,
in leaves is wrapped and grasses dry.
He once had castles owned and towers,
water and wild, and woods, and flowers,
now though it turn to frost or snow,
this king with **moss** his bed must strow.

In the *Bible*

Old names and changes in language make it difficult to determine if any bryophytes are truly mentioned in the **Bible**. Most references to them seem shaky at best. Sean Edwards (1993b) has demonstrated this difficulty with several examples.

In the *Bible*, hyssop has dubious meaning. In Exodus 12:22, Leviticus 14:4, 6, 49-52, Numbers 19:6,18, and Hebrews 9:19, hyssop refers to use in procedures involving dipping it into blood or water and sprinkling it about. Again in Psalms 41:7 it was used to purge or cleanse, and in John 19:29 it was used as a sponge for vinegar. Scholars think different plants may have been used in these different examples, and there is no clear evidence any was a moss.

However, in I Kings 4:33, the "hyssop that springeth out of the wall" narrows the habitat enough to encourage the suggestion of a moss. Other possibilities include small wall ferns, and even species today known as hyssop are possible. However, Linnaeus, who was not known for his understanding of mosses, identified this text to refer to the moss ***Bryum truncatulum***, later known as ***Pottia truncata***, and now known as ***Hennediella truncata*** (Figure 22), stating that "The houses and walls of Jerusalem are clothed at their base with green moss, the smallest of all;

Hasselquist sent me some and it is ***Bryum truncatulum***. He similarly concludes that the other references to hyssop refer to moss, using the argument that all mosses absorb liquids and can be used as absorbents. The argument is, however, hardly proof.

Figure 22. ***Hennediella truncata***, once known as ***Pottia truncata***, and before that as ***Bryum truncatulum***, was the guess of Linnaeus for the "hyssop that springeth out of the wall" (I Kings 4:33). Photo by Michael Lüth, with permission.

The saga does not end there, however, as Mr. Dickson subsequently identified what appears to be the same moss, collected from the location described in the *Bible*, as ***Bryum pyriforme***, figured by Hedwig as ***Gymnostomum fasciculare***, and now named as ***Entosthodon fascicularis*** (Figure 23) (Edwards 1999).

Figure 23. This possible "hyssop that springeth out of the wall" is possibly ***Entosthodon fascicularis***, a moss. However, it is possible that the plant in question in the Bible was not a moss at all, but a tracheophyte, perhaps even a fern. Photo by Michael Lüth, with permission.

On the other hand, I (Janice Glime) just loaded searchable pdf files of the old and new testaments. Then I did a search for "moss." Zero records were found. So if moss is named in the King James *Bible*, the reference must be indirect.

Literature References from Bryonetters

In April 2016, Bryonetters opened a discussion on proverbs and folk sayings regarding mosses. These included introductory comments by Robin Stevenson, Bryonet 4 April 2016:

Proverbs, and similar folk sayings, are a way of preserving fundamental truths or pieces of advice. In English the only moss-related example which springs to mind is: '**Rolling stones gather no moss**.'

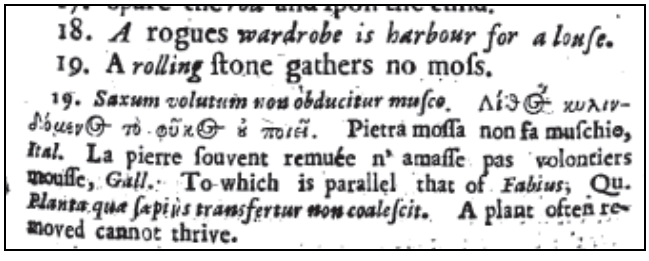
A non-proverbial observation which verges on a 'Law' is that 'Leaning trees gather most moss', whilst an undoubted element of name-magic frequently surfaces in the course of field meetings; someone will say 'Has anybody seen *Bryum elixir-vitae* yet?' and it is usually found very soon afterwards.

Javier Martínez-Abaigar, Bryonet 4 April 2016, reported that "in Spanish we have a similar saying as that reported by Robin ("**rolling stones gather no moss**"): "piedra movediza nunca moho la cobija." Curiously, this saying is mentioned in the act XV of the "Tragicomedy of Calisto and Melibea," know in Spain as "La Celestina," published in 1499. Also curiously, the term "moho" (English "mould") mentioned in that saying was used in ancient Spanish with the meaning of "musgo" (English "moss"). This use was maintained until probably the XVIII century, when the meaning of these two words (moho-musgo) was clearly different (mould-moss).

Pierre Morisset, Bryonet 4 April 2016, reported that "the same saying is used in French: "Pierre qui roule n'amasse pas mousse." As mentioned in <http://www.expressio.fr/expressions/pierre-qui-roule-n-amasse-pas-mousse.php>, it also occurs in German, Italian, Portuguese, Dutch, Walloon... and Latin.

Norbert Stapper, pers. comm. 4 April 2016, agreed that "Pierre is right, but I actually never heard someone using this nice phrase in Germany. Hasty research reveals that it is not necessarily meant in a negative way (*i.e.* that 'people who don't shave get a beard,' or "that someone gets rusty bones due to being lazy"). Instead, it can also be used to indicate that a restless and constantly moving person lacks the requisite for a successful life and the ability to take permanent responsibility."

Chris Preston added that as Pierre says, 'A rolling stone...' is known in several languages and in his pioneer 'A collection of English proverbs' (1670) the naturalist John Ray included Italian, French, Latin, and Greek versions:



18. *A* rogues *wardrobe is harbour for a louſe.*
19. A *rolling* ſtone gathers no moſs.

19. *Saxum volutum non obducitur muſco.* Λίθος κυλινδόμενος τὸ φῦκος οὐ ποιεῖ. Pietra moſſa non fa muſchio, *Ital.* La pierre ſouvent remuée n' amaſſe pas volontiers mouſſe, *Gall.* To which is parallel that of *Fabius*; Qu. *Planta quæ ſæpius transfertur non coaleſcit.* A plant often removed cannot thrive.

Chris Preston contributed several occurrences of "moss" in literature:

Ray also includes Scottish proverbs including 'Better wooe over middling nor over **moss'** - I assume that moss here is equivalent to bog, as in Guy's proverb, and that middling is a midden or rubbish heap, but the proverb still seems rather obscure. Maybe Gordon could assist here? Some of the Scottish proverbs are more direct, such as 'Better sit idle than work for nought.'

Ray's third moss proverb – which may only be in the second edition (1678) – is 'I took him napping, as **Moss** took his mare' but as Ray comments, 'Who this **Moss** was is not very materiall to know.'

Two quotes from Shakespeare were recalled by Ann Gordon, Bryonet 4 April 2016:

•in As You Like It: "Under an old oak, whose boughs were **mossed** with age..."

•in The Comedy of Errors: "Usurping ivy, brier, or idle **moss**..."

Moss in Music

In his tribute to Wilf Schofield, Adolf Ceska reports that mosses are only seldom mentioned in classical music. One mention, however, is in Richard Wagner's Parsifal. Kundry describes to Parsifal the way his mother cared for him as a child:

Gebettet sanft auf weichen **Moosen**
den hold geschlafert sie mit Kosen.
or
Gently bedded in soft **moss**
she lulls carressingly her darling boy.

The Czech composer Bedrich Smetana was a follower of Wagner and as such had a similar moss theme. In his opera "Hubicka (Kiss)," the smugglers walk through a forest and sing (quite loudly) a nice chorus:

"Quiet, quiet, [step] on **moss** ..."

Uses of the Word Moss

The word moss is used by many ecologists to mean bryophyte, but an even broader use is to mean any small plant. It is also used to refer to bogs and fens, to moss heaths, or other mossy habitats.

Johannes Enroth, Bryonet 4 April 2016, contributed this Finnish use of the word for moss:

Well, in Finnish colloquial speech moss translates to "sammal," from which stems the verb "sammaltaa," meaning speaking in a very unclear manner, especially when one is heavily drunk. You speak as if you had your mouth full of moss or something like that.

From Norway, Hans K. Stenøien, Bryonet 4 April 2016, contributed this:

In Norwegian one might say that there are "owls in the moss" ("ugler i mosen"), meaning that something is not right, suspicious.

(Note, the burrowing owl uses mosses in its nest – JG)

Later, Stenøien added:

My literate friends Hans Blom and Gustaf Granath have pointed out to me that "ugler i mosen" (Norwegian) and "ugglor i mossen" (Swedish) is actually derived from Danish: "ulve i mosen," and that "ugler" ("owls") is a complicated way of saying "uller," which is dialect for "ulver" or wolves.

The original Danish (medieval?) saying would therefore be "wolves in the mire" rather than "owls in the moss," with the meaning being the same: something fishy (suspicious).

Stefan Schneckenburger, Bryonet 4 April 2016, offered some German things:

- Moos haben – to have moss – to have money, to be rich
- ein bemoostes Haupt haben/sein: to have/to be a mossy head: to be old
- das Moss der Maennlichkeit – the moss of maleness: beard
- Ohne Moss nix los: Nothing happens without moss. Here Moos means money

To the last German statement, Norbert Stapper (Bryonet 4 April 2016) added:

A second meaning of moss ("Moos") in colloquial German means money, and the phrase "ohne Moos nix los" (= life is dull without money or, similar, in French: "sans pognon pas de trognon") is used frequently. This use of Moos goes back to the Yiddish language.

With regard to the word moss in German everyday use Stapper contributed "I would like to add that moss (Moos) is widely accepted, as long as it grows in the woods or in a similar natural habitat. People then talk about *e.g.* "Moosteppich" (moss carpet), positive connotation. But as soon as you enter the direct human environment, the words "bemoost" (=covered by moss) or "übermoost" (totally covered by mosses) are often linked to dirt or deterioration. Then they are used to illustrate the transition from a well-maintained building to a ruin with wet walls *etc.* If something is grown by mosses, it is in a bad state.

This brings us to one of the reasons to get rid of mosses on *e.g.* cobblestones or on the small houses of litter bins. Principle: Keep the wild out! Moss symbolizes the wild. There seems to be a difference between the European countries in tolerance to mosses in human/urban environment, maybe it is linked to recent history, the fact to have rebuilt the country after the war?

In parallel to the differing interpretations of the proverb with the word moss (see my mail from the afternoon), the use and the connotation of the word Moos itself appears to be conflicting – at least in the language of the people in the part of Deutschland where I live.

As a followup to the comments by Stapper, Stefan Schneckenburger, Bryonet 4 April 2016, commented that Shakespeare didn't really discriminate between mosses and lichens. "At the moment I am studying the Bard's plants when curating an exhibition in the German Botanic Gardens: <http://www.verband-botanischer-gaerten.de/pages/bg_woche.html>. "

Possibly he owed Gerads "Herball" from 1597 (as Peter Ackroyd pointed out in his biography). Here you can

find *Lycopodium* species, mosses, and lichens under "Mosses" – even a specific moss on human sculls (the German text relies on the borrowing of German woodcuts by the British publisher and printer). Even algae are listed under "sea mosses." Hepatics are treated separately; including *Cetraria e.g.* Here you can find the "Herball" from 1597; the mosses are treated on p. 1369-ff.

Very impressive is a scene in bloody "Titus Andronicus": A forest is first described as sunny, warm, and sexually stimuling (Tamora is waiting for her lover). 80 verses later, the same forest is the location of murder and rape (act II, sc. 3):

My louely Aaron,
Wherefore look'st thou sad,
When euerything doth make a Gleefull boast?
The Birds chaunt melody on euery bush,
The Snake lies rolled in the chearefull Sunne,
The greene leaues quiuer.with the cooling winde,
And make a cheker'd shadow on the ground:
Vnder their sweete shade, Aaron let vs sit,
And whil'st the babling Eccho mock's the Hounds,
Replying shrilly to the well tun'd-Hornes,
As if a double hunt were heard at once,
Let vs sit downe, and marke their yelping noyse:
And after conflict, such as was suppos'd.
The wandring Prince and Dido once enioy'd,

Haue I not reason thinke you to looke pale.
These two haue tic'd me hither to this place,
A barren, detested vale you see it is.
The Trees though Sommer, yet forlorne and leane,
Ore-come with **Mosse**, and balefull Misselto.
Heere neuer shines the Sunne, heere nothing breeds,
Vnlesse the nightly Owle, or fatall Rauen:
And when they shew'd me this abhorred pit,
They told me heere at dead time of the night.

Schneckenburger added, "If you will visit Germany during June or later – please inform you beforehand, in which Botanic Garden you can see my exhibition on Shakespeare's plants! I add "bonus material," prepared for of my exhibition, dealing with mosses. Even if you are not able to read German, you will find two plates from Gerard's Herball."

To the word usage of "moss," Mark Seaward (Bryonet 5 April 2016) added "Stefan is right: it should be remembered, when reading any old texts and correspondence, certainly in Britain, that in the past "growths" on trees, rocks, and indeed skeletons did not differentiate between mosses and lichens, and mostly referred to both. Furthermore, common names for lichens are named "Moss" even to this day, such as:

Iceland Moss – *Cetraria islandica*
Reindeer Moss – *Cladonia* subgenus *Cladina*

And Norbert Stapper (Bryonet 5 April 2016) added Eichenmoos (Oak moss) = *Evernia prunastri*.

This is one of the few German lichen names that, like "Gelbflechte" (*X. parietina*), seems to be part of common language (if there is anything "common" with lichens at all). As you will know for sure, some people, among them Volker, have created a list of German names of lichens. I hope I will never be compelled to use 'em in textwork…

Ambroise Baker, Bryonet 5 April 2016, reflected on similar usage in Switzerland. "We have sweets called Mousse d'Islande (Islaendisch Moos, Muschio Islandese), which I read from the ingredients contain 0.17% of 'Iceland lichen extract.' How to tell which moss lores refer to moss proper? Most people won't tell moss from lichen apart. – I'll ponder over it sucking on my Swiss sweets..."

Adolf Ceska, Bryonet 4 April 2016, reported that the "national anthem of Japan is a song entitled 'Kimigayo.' It was formally designated the national anthem in 1893, during the reign of the Meiji Emperor. The song was composed by an Imperial Court Musician of the Meiji era. The lyrics are from a poem that was written over 1000 years ago. The words mean 'May your reign continue for a thousand, nay, eight thousand generations and for the eternity that it takes for small pebbles to grow into a great rock and become covered with **moss**.'"

Masaki Shimamura, Bryonet 5 April 2016, clarified the words in the national anthem of Japan:

Many people might think the phrase "small pebbles to grow into a great rock" is unscientific. This is the problem with translation. In here, a Japanese term "Sazare-Ishi" have been simply translated in "small pebbles." Strictly speaking, "Sazare-Ishi" means "conglomerate rock" (small pebbles cemented by calcium carbonate or Iron oxide-hydroxide) and "Sazare-Ishi no Iwao" means "a giant conglomerate rock" (may be calcareous). In this poem, the giant and mossy conglomerate rock represents the eternity.

In honor of bryologist Wilf Schofield, Adolf Ceska (1997) <http://bomi.ou.edu/ben/ben168.html> reminded us of Schofield's love of music and poetry. Ceska cited the anthology "A Book of Luminous Things" (edited by Czeslaw Milozs) as having a poem "Moss-Gathering" by Theodore Roethke (1944). The poem describes techniques of moss collecting. This technique is exactly the same as that applied by Dr. Wilf Schofield (see also Peck 2006):

To loosen with all ten fingers held wide and limber
And lift up a patch, dark-green, the kind for lining
cemetery baskets,
Thick and cushiony, like an old-fashioned doormat,
The crumbling small hollow sticks on the underside mixed
with roots,
And wintergreen berries and leaves still stuck to the top,-
That was **moss**-gathering.

[Roethke feels remorse for gathering so much moss:]

But something always went out of me when I dug those
loose carpets
Of green, or plunged my elbows in the spongy yellowish
moss of the marshes:
And afterwards I always felt mean, jogging back over the
logging road,
As if I had broken the natural order of things
in that swampland;
Disturbed some rhythm, old and of vast importance.
By pulling off flesh from the living planet (Figure 24);
As if I had committed, against the whole scheme of life,
a desecration.

Figure 24. Jeri Peck would agree with Roethke as he writes, "Disturbed some rhythm, old and of vast importance, By pulling off flesh from the living planet." Here she records data on the impact of harvesting in the Pacific Northwest, USA, while examining a patch that has been loosened "with all ten fingers held wide and limber" and lifted up. Photo courtesy of Jeri Peck.

From North America, Guy Brassard, Bryonet 4 April 2016, contributed this:

There is an interesting old one from Newfoundland (Canada): **moss child**: an illegitimate child; presumably originating because such children were often conceived on the fens or bogs.

Also from North America, Annie Martin (Bryonet 5 April 2016) added colloquial uses of the word moss:

Most people in my moss world are moss lovers, not scientists. As I share my interest in moss gardening with others, I use scientific terminology to describe the botany of bryophytes and advocate proper nomenclature instead of common names. However, I have my own moss "slang" words – nouns, verbs and adjectives:

Mosser: Any person who engages in the enjoyment of mosses; collects/harvests/rescues mosses; creates moss landscapes

Mossin': The act of enjoying, collecting, harvesting, rescuing, creating with mosses.

Moss-scape: A landscape that features mosses.

Moss-some: Exceptional moss landscapes; exclamation of joy or admiration synonymous with awesome.

"I am a **mosser** who goes **mossin'** on a daily basis. My greatest pleasure is to create **moss-scapes** that are **moss-some**."

When I was writing my book, *The Magical World of Moss Gardening,* I used the reference – "Mossy Smile." The publisher discouraged this usage. In my mind, it meant a beaming face with a big smile because the person's spirit was happy over mosses. Well, "mossy smile" means grungy, green teeth in several cultures. So I resisted using this term to avoid any negative connotation.

The Urban Dictionary offers quite a few interpretations of the word "moss" used in recent years. **Mainly, moss means to chill out or relax.** However, there are other very different meanings, including several references for un-sportsman-like behavior. I've cited a few "new" meanings for moss and related moss words. Some uses of the word "moss" were not fit for polite company and therefore are not mentioned. To review all comments, visit: Urban Dictionary <http://www.urbandictionary.com/>.

When someone is funny in an awkward and charming way.

"That boy was so **Moss** when he tripped in front of the girl he likes and blushed to make her laugh."

Describes one's hair.

"Dennis Eckersly had some serious moss in the 80's."

Someone who is a know it all, but when challenged on a topic they profess to be a genius about, they can't front up – just like moss they have no depth / roots

"He's moss."

moss ayre: Arabic familiar expression used by friends to greet each other

Mossbird: Looking at things from a higher perspective. Eating the seeds of knowledge and using it to accomplish goals.

"Just look at it from a Mossbird's perspective."

To jump up and catch a football over a defender.

"He jumped up and mossed him to score the touchdown."

Originally used in football, it is now being used to indicate that you have destroyed someone in a verbal, or physical manner. Bad-sportsmanship-like behavior.

The act of puking, usually associated with the flu or heavy drinking.

"Dude, that guy just mossed all over the place"

A super secret slang word for marijuana. Getting mossed equates to getting high.

"Hey man... you got any moss over there?"

Translations to other languages can introduce confusion. Masaki Shimamura, Bryonet 6 April 2016, tells us that "in eastern Asia, the notations of Chinese character corresponding to liverworts and mosses vary depending on the region. In Japan, '苔' means 'bryophytes' (without distinctly differentiating mosses and liverworts) as informal term. In the academic field, '苔' means 'liverworts' and '蘚' means 'mosses,' '角苔' means 'hornworts.' However, in Taiwan that is completely the opposite to Japanese usage. In Taiwan, '苔' means 'mosses' and '蘚' means 'liverworts.' Maybe, the usage in Taiwan is correct with respect to the original meaning of Chinese characters (The researchers of Taiwan strongly insisted so). Although the detailed reason is not known, in the process of establishing the modern Botany in Japan, Japanese old botanists may have mistook the original meaning of the Chinese character. If this

opinion is right, as far as I know, the usage originated from the misunderstanding of Japanese also has been spread widely in Mainland China."

Zhang Li, Bryonet 7 April 2016, contributed this on the Chinese characters: "The confirmed earliest Chinese character relevant to bryophytes is 蒚 (liverworts, pronounced tai, equivent to 苔 later) which occurred in a poem written by Ms Ban Jueyu (born 48 BC, died 2 AD) who is the Hancheng Empire's princess. Originally, 蒚 indicates all small plants in moist and shady habitats. Most of them are bryophytes of course. I don't believe the ancient people can differ liverworts from mosses correctly, including lichens and small ferns.

Interestingly, the term 苔 (liverworts) is quite popular in ancient poems from the Tang Dynasty (618-907 AD) and afterwords. Dr PAN Fujun, a colleague in Taiwan, investigated the plants occurring in poems written in the Tang Dynasty. There are totally 398 plant species mentioned in 53,000 pieces of poems, and the top five plants are willow, bamboo, pine, lotus and peach, and 苔 (liverworts) ranks the sixth, occurring in 1,248 pieces of poems.

Ann Gordon, Bryonet 6 April 2016, Contributed this personal story. "When our first grandchild was about to be born, my daughter asked me what I wanted to be called for my 'grandmother' name. I said that the first grandchild might pick the best, but if they needed a 'choice' from me, I would pick MOSSY, because learning about and experiencing mosses is such a passion of mine."

"Things went along fine until...! my older son, who lives in China, suggested I doublecheck The Urban Dictionary for current 'meanings' before I really got comfortable with Mossy as my name. So I did, and to my dismay, I discovered that 'mossy' and therefore moss, was being given a really bad rap!!! I think at that time there were 6 definitions for mossy and EACH was derogatory to the -nth degree in MY book! I was furious! I either had to give in to cultural norms, give up my name, and let moss have a bad rap, OR submit my OWN definition! So I DID. And they accepted it. It has now moved to #1 definition. Here it is as I submitted it:
(Check out Urban Dictionary under 'mossy' and see some terrible definitions. Thumbs up votes for my definition will help us keep moss in the realm of meanings it deserves!"
mossy: n.

1. a person of great integrity; resilience, sustainability; true blue, forever, dependable.
2. a bearer of enthusiasm, delight; a supporter of new life on the earth.
3. in ancient times, it has been said to be used as a name for a loving grandmother, always there to support the earth's little ones.

adj.: like, similar to the moss of the earth, resilient, bringing forth new seeds of life, able to survive even when other living forms can't.

n. She was called Mossy, the one who delighted in all the young offspring. Mossy nurtured their bodies, their souls, and their dreams in a way that only a good grandmother could do!

adj. The mossy bank was always there. It held the moisture from the air even when all else was drying and dying off from the drought. Seeds blew to the mossy beds to grow their roots and start new life.

Literature and Bryophyte Names

Literature often plays a role in the naming of organisms. Sometimes it is because the organism reminds someone of a character or story. Sometimes the story dictates the behavior of the author. Such was the naming of ***Buxbaumia*** (Figure 25) (Crum 1973). Johann Christian Buxbaum discovered the genus in 1712 and described it in 1728. He chose to name it after his father, but he recalled the story of the fox who was derided for asking for grapes, not for himself, of course, but for his sick mother. The modest Buxbaum left the moss unnamed. It was 1744 when Haller finally named the moss ***Buxbaumia***.

Figure 25. ***Buxbaumia aphylla***, named for its discoverer Johann Christian Buxbaum. Photo by Štěpán Koval, with permission.

The Greek term for bryophytes is *Bruon*, but its meaning in the time of Aristotle is much wider than that (Scott 1987). Furthermore, this term does not seem to appear in the botanical literature of that period. It was not until about the first century B.C. that the Latin term *Muscus* was introduced into general use, particularly by poets.

Summary

Bryophytes have been mentioned in literature to create imagery. Often they are used to create images of passing time, death, or other indications of aging. In some cases they are used to create an image of serenity. They sometimes appears in titles when they have no part in the actual story.

In older literature, and in common usage today, the word moss has multiple meanings. It is commonly used to mean any small plant. And in the vernacular, it has been use to create mental images in rather creative ways.

The Bible seems to overlook them, with only a few references that use the word hyssop, which has multiple interpretations.

Acknowldegments

Thank you to Brent Mishler for his contribution to Bryonet of the poem by William Gardiner, to Robin Stevenson for the verse from "Cloudberry Summer" by Amy Clampitt, and to Lee Ellis for completing the poem "The Moss Supplicateth the Poet" by Richard Henry Dana, Sr. Thank you Andi Cairns for helping me track down the author to "Ode to *Grimmia*" and to Peter Alpert for completing the story. And thank you to many Bryonetters for their contributions.

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CHAPTER 4
AQUARIA

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CHAPTER 4
AQUARIA

Figure 1. The dangling moss ***Fontinalis antipyretica*** (willow moss) adds interest and hiding places in aquaria. Photo by Li Zhang, with permission.

Aquarium Bryophytes

In aquaria, mosses not only are decorative, but provide oxygen, hiding places, and egg-laying substrates (Benl 1958). Fish such as danios and killies will lay their eggs in the moss (Tinkerfish). Many taxa can be used, provided the water is not too warm and copper content is low, including common taxa: ***Bryum pseudotriquetrum*** (Figure 2), ***Fontinalis antipyretica*** (Figure 1), ***Leptodictyum riparium*** (Figure 3), ***Platyhypnidium riparioides*** (Figure 6), ***Riccia fluitans*** (Figure 7), ***Ricciocarpos natans*** (Figure 8), ***Taxiphyllum barbieri*** (Figure 9-Figure 10), and ***Vesicularia dubyana*** (Figure 11) (Benl 1958; Cook *et al*. 1974; Takaki *et al*. 1982; Gradstein *et al*. 2003; Tan 2003; Tan *et al*. 2004).

One should be aware that scientific names provided by aquarium stores are often wrong. I have seen ***Leptodictyum riparium*** (Figure 3) labelled ***Fontinalis*** (Figure 1) and ***Taxiphyllum barbieri*** (Figure 9-Figure 10) is often misnamed as ***Vesicularia dubyana*** (Figure 11).

Figure 2. ***Bryum pseudotriquetrum*** grows in marshes and in shallow water at lake and stream edges. It can make an interesting small forest on the bottom of an aquarium. Photo by Michael Lüth, with permission.

Figure 3. ***Leptodictyum riparium*** (stringy moss) adorning an unusual aquarium. Photo by Sze Wei Tan <www.aquamoss.net>, with permission.

Figure 4. ***Leptodictyum riparium*** showing its growth habit in an aquarium. Photo by Tan Sze Wei <www.aquamoss.net>, with permission.

Figure 5. ***Leptodictyum riparium*** leaves showing the rib and leaf arrangement. Photo by Tan Sze Wei <www.aquamoss.net>, with permission.

Figure 6. ***Platyhypnidium riparioides*** (also known as ***Rhynchostegium riparioides*** and ***Eurhynchium riparioides***) is a stream moss that grows in dense clumps. However, some people have succeeded in keeping it as an aquarium moss. Photo by Michael Lüth, with permission.

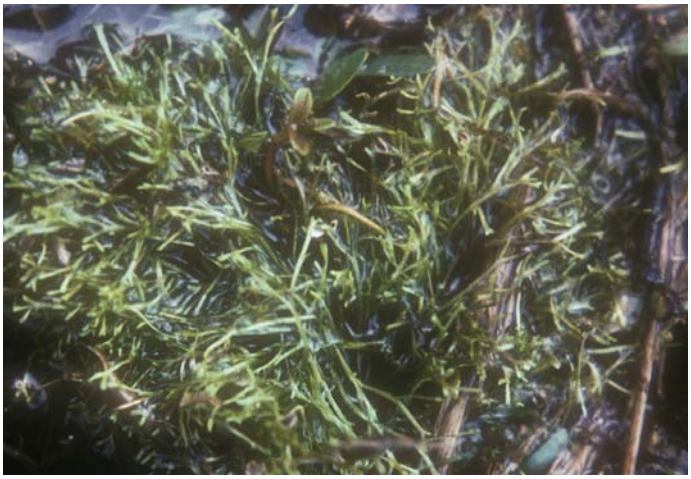

Figure 7. ***Riccia fluitans*** can be grown floating or in balls at the bottom of the aquarium in medium soft to hard water, *p*H 6-8, 15-30ºC (Aquatic Community). Photo by Janice Glime

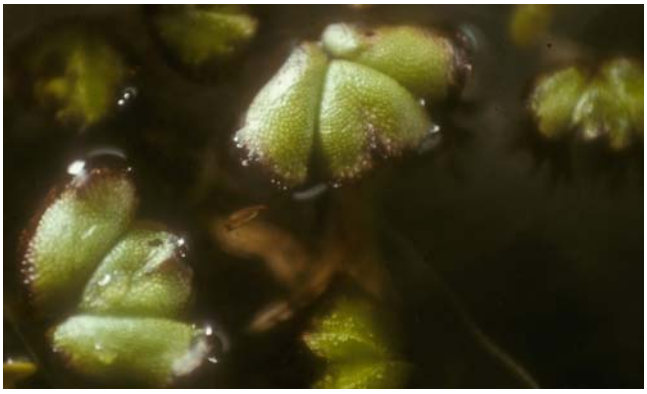

Figure 8. ***Ricciocarpos natans***, a thallose liverwort sometimes used in aquaria. Photo by Janice Glime.

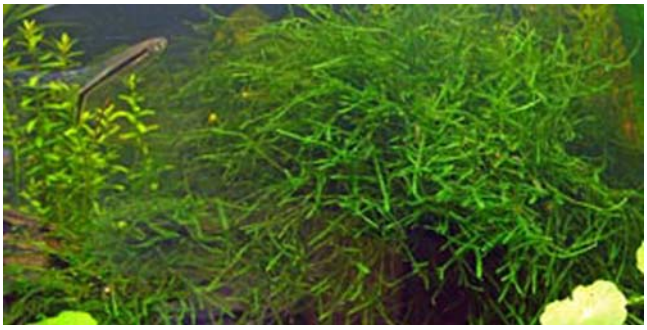

Figure 9. ***Taxiphyllum barbieri*** (Java moss) provides dimension to the aquarium and permits little fish to hide from larger aggressive fish. Photo by Sze Wei Tan <www.aquamoss.net>, with permission.

Java moss [often incorrectly identified as ***Vesicularia dubyana*** (Figure 11), Iwatsuki 1970; Tan *et al.* 2004] is a popular tropical moss that is highly tolerant of a wide array of water chemistries and temperatures and may even help to absorb the ammonia derived from the fish. Singh (in Tan 2006a) describes growing conditions as with or without fertilizer, with or without added CO_2, with or without added light, temperatures to 30ºC, and tap water. It grows rapidly and will fill the tank in short order, but is easily removed. Compared to the wild mosses I have tried to grow, this is much easier.

Unfortunately, the name Java moss has been applied to a variety of aquatic mosses sold for aquaria (Tan *et al.* 2004; Akiyama 2009). "Java moss" most likely was originally applied to ***Vesicularia dubyana*** (Figure 11), but the faster-growing ***Taxiphyllum barbieri*** (Figure 9-Figure 10) was later used in its place (Stephan Mifsud, pers. comm. 14 December 2007). The current Java moss (***Taxiphyllum barbieri***; Figure 9-Figure 10) has flattened, oval-oblong leaves arranged on two sides of the stem and branches, and possesses two short costae (Figure 10). Its narrowly oblong leaf cells differ from the shorter ones of ***Vesicularia*** spp. (Figure 11).

The true Java moss is the easiest to grow of all aquatic mosses (Tan 2006; Tan & Leong 2007). It thrives not only in cool water, but in low light at tropical temperatures of 28-30ºC, temperatures that would soon result in death of the common temperate moss ***Fontinalis antipyretica*** (willow moss; Figure 1). In my aquarium, I need to remove vast quantities of Java moss approximately every month. It adheres to driftwood, stones, or rests on the bottom. As an aquarium plant, it provides a nice green, filmy look and provides good hiding places for small fish and fish eggs (Takaki *et al.* 1982). On the other hand, I have had spiny fish get caught in it and die struggling to get free.

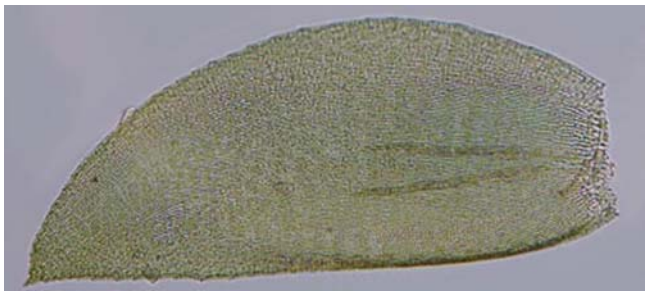

Figure 10. The leaf of ***Taxiphyllum barbieri***, the true Java moss, has two short costae and narrowly oblong leaf cells. Photo by Sze Wei Tan <www.aquamoss.net>, with permission.

Figure 11. The moss often mistakenly called Java moss is ***Vesicularia dubyana*** (Singapore moss) and has shorter cells. Photo by Sze Wei Tan <www.aquamoss.net>, with permission.

Cliff Townsend sent me a short note (22 Nov 2004) that attests to the aggressive nature of this group of "Java mosses," given the right conditions:

> "A slant on British 'Java Moss' is given by C. R. Stevenson & E. W. Jones in Journal of Bryology 15: 624-626 (1989). The material of ***Vesicularia reticulata***, mentioned by them as having been distributed by me through the B.B.S. exchange in 1962 as ***V. dubyana***, was collected from the former orchid pits at Kew (since demolished), where this moss grew in great quantity and fruiting very freely. It still occurs in other greenhouses at Kew, and I was informed by P. J. Edwards of the pteridophyte department in the Kew Herbarium that both this and ***Racopilum cuspidigerum*** (Schwaegr.) Aongstr. (det. B. O. Zanten from a gathering of mine) are quite valuable for water retention."
>
> "Fairly recently, this ***Vesicularia*** was sent to me for opinion by the late Theo Arts, who had collected it in the *Victoria amazonica* house at the Nationale Plantentuin van Belgie, Domein non Bouchout, Meise, Belgium in 1987. I have also received material from the same greenhouse collected by H. Stieperaere in 1996. It is of interest that I recorded the species from a bank by a millstream near Mogul Gardens, Wah, Pakistan in 1973 in Journal of Bryology 17: 677 (1993). Unfortunately, this and other mosses from the same spot (which included an ***Entodon*** as yet unidentified) were grubbed up in a hurry and not named until I got home, so there is no means of knowing if the moss was native there (the place is within its area) or was an escape from the gardens, having been introduced to them with phanerogams."

"Gangulee (Mosses of eastern India: 2001) reports ***Vesicularia montagnei*** as occurring 'on the floors of nurseries in Calcutta and in Howrah National Botanic Garden.' In the description, he cites it as 'forming thin but very extensive mat covering whole nursery floor and brick edging...'. The leaf-shape depicted by Gangulee looks very like that of ***V. reticulata***, whereas that given of ***reticulata*** itself shows the leaves much too narrow. One cannot but wonder if the Calcutta nursery plant is in fact ***reticulata***, perhaps even the source from which it has reached other botanic gardens."

"It would no doubt take more time than it is worth to trace the source from which ***V. reticulata*** entered the aquarium trade, but it seems very likely that it has been propagated from material occurring as a weed in some nursery or botanic garden."

The Christmas moss (***Vesicularia montagnei***, Figure 12-Figure 13) is often used to provide a backdrop to aquaria (Tan & Leong 2007). It is semi-aquatic and grows on shaded, wet banks. In an aquarium, it becomes distinctly pinnate to subpinnate, giving a miniature fernlike appearance. Unlike the hanging habit of ***Vesicularia montagnei***, the habit of ***Vesicularia reticulata*** (erect moss; Figure 14) is upright, giving it a different role when tied to driftwood or other substrate under water (Tan & Leong 2007). The true ***Vesicularia dubyana*** (Figure 16), now dubbed Singapore moss, looks like a smaller version of Christmas moss.

Figure 12. ***Vesicularia montagnei***, the Christmas moss, serving as an aquarium backdrop. Photo by Tan Sze Wei <www.aquamoss.net>, with permission.

Figure 13. ***Vesicularia montagnei*** (Christmas moss) is a hanging moss. Photo by Sze Wei Tan <www.aquamoss.net>, with permission.

Figure 14. ***Vesicularia reticulata*** (erect moss) works well when tied to driftwood or other substrate. Photo by Sze Wei Tan <www.aquamoss.net>, with permission.

Figure 15. ***Vesicularia dubyana*** (Singapore moss), the original Java moss and a species suitable for aquaria. Photo by Sze Wei Tan <www.aquamoss.net>, with permission.

Figure 16. ***Vesicularia dubyana*** (Singapore moss). Photo by Sze Wei Tan, with permission <www.aquamoss.net>.

Taxiphyllum cf. alternans (Figure 17) is a beautiful, soft moss that is sought after by hobbyists, but is more expensive (Tan *et al*. 2004). Its true identity remains uncertain because no capsules have been available to permit certain affiliation.

Figure 17. ***Taxiphyllum alternans*** (Taiwan moss) is a pinnately divided moss often sold for aquaria. Photo by Sze Wei Tan <www.aquamoss.net>, with permission.

Many mosses can be grown successfully in an aquarium. The limits may depend on the water quality, whether it is acid or alkaline, on the temperature, and on your ability to keep algae from taking over. Table 1 includes the more common ones available in North America, Europe, and Asian areas. Nevertheless, aquarium stores in other parts of the world sell some of these, and local aquatic mosses may be added to them.

Several liverworts are suitable, including the rare ***Monosolenium tenerum*** (Figure 18), originally from Asia (Wikipedia). While this species is hard to find in the wild and should be protected, it seems to do well in aquaria and can be easily grown from a small clump of plants. You may find it sold as ***Pellia*** because it was originally misidentified as ***Pellia endiviifolia*** (Figure 19) (Stephan Mifsud, pers. comm. 14 December 2007).

Figure 18. ***Monosolenium tenerum*** growing on soil in its natural habitat. Photo by Li Zhang, with permission.

Figure 19. ***Pellia endiviifolia***, the real species, and not usually a submersed species. Photo by Hermann Schachner, through Creative Commons.

Table 1. Mosses suitable for aquarium culture (Benl 1958; Cook *et al*. 1974; Takaki *et al*. 1982; Gradstein *et al*. 2003; Tan *et al*. 2004; Tan 2006a).

Amblystegium serpens	nano moss	Figure 20
Bryum pseudotriquetrum	marsh bryum	Figure 21
Chiloscyphus polyanthos	square leaved liverwort	Figure 22
Ectropothecium zollingeri	Bogor's moss	Figure 23
Fissidens crassipes		Figure 24
Fissidens fontanus	Phoenix moss	Figure 25
Fissidens grandifrons	Christmas tree moss	Figure 26
Fissidens nobilis	doormat moss	Figure 27
Fissidens rivularis	river pocket moss	Figure 28
Fissidens splachnobryoides	doormat moss	
Fissidens taxifolius	common pocket moss	Figure 29
Fissidens zippelianus	zipper moss	
Fontinalis antipyretica	willow moss	Figure 1
Hyophila involuta	cement moss	Figure 30
Isopterygium sp.	mini Taiwan moss	Figure 31
Leptodictyum riparium	stringy moss	Figure 5
Monosolenium tenerum	giant riccia	Figure 18
Plagiomnium acutum		Figure 32
Platyhypnidium riparioides	beaked water moss	Figure 6
Rhacopilum aristatum		
Riccardia chamedryfolia	mini pellia	Figure 33
Riccia fluitans	floating crystalwort	Figure 7
Ricciocarpos natans	water star	Figure 8
Taxiphyllum alternans	Taiwan moss	Figure 17
Taxiphyllum barbieri	Java moss	Figure 9
Taxiphyllum sp.	flame moss	Figure 34
Taxiphyllum sp.	giant moss	Figure 35
Taxiphyllum sp.	green sock moss	Figure 36
Taxiphyllum sp.	peacock moss	Figure 37
Taxiphyllum sp.	spiky moss	Figure 38
Taxiphyllum sp.	string moss	Figure 39
Vesicularia dubyana	Singapore moss	Figure 15
Vesicularia ferriei	weeping moss	Figure 40
Vesicularia montagnei	Christmas moss	Figure 12
Vesicularia reticulata	erect moss	Figure 14
Vesicularia sp.	creeping moss	Figure 41

Figure 20. ***Amblystegium serpens***, a terrestrial moss that can be used in aquaria. Photo by Andrew Spink, with permission.

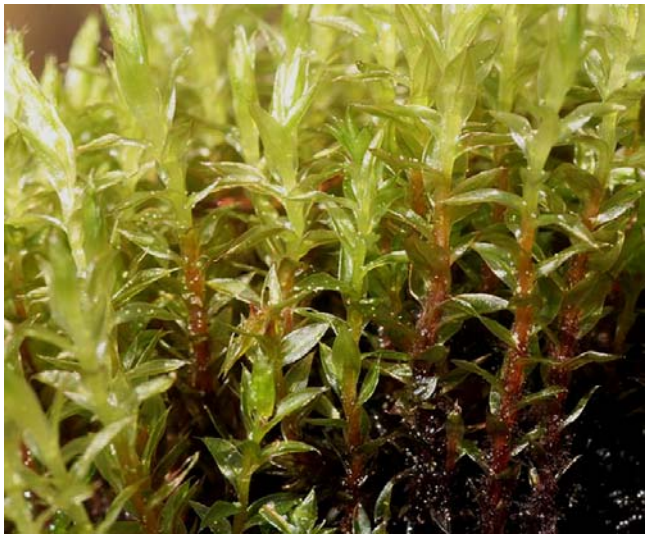

Figure 21. ***Bryum pseudotriquetrum***, a moss of wetlands that can survive under water. Hermann Schachner, through Creative Commons.

Figure 22. ***Chiloscyphus polyanthos***, an aquatic liverwort. Photo by Hermann Schachner, through Creative Commons.

Figure 23. ***Ectoprothecium zollingeri***, a moss previously listed as ***Glossadelphus zollingeri***. Photo by Jan-Peter Frahm, with permission.

Figure 24. ***Fissidens crassipes***, a species of on limestone or siliceous rocks, avoiding very acid situations, submerged or on stream banks. Photo by Michael Luth, with permission.

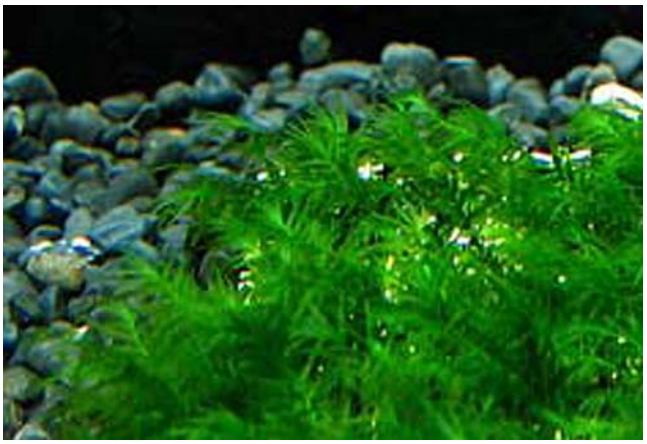

Figure 25. ***Fissidens fontanus***, a true aquatic ***Fissidens***. Photo by Tan Sze Wei <www.aquamoss.net>, with permission.

Figure 26. ***Fissidens grandifrons***, largest species of ***Fissidens***, living in limestome and alkaline areas that are either cold water or turbulent water with lots of CO_2. Photo by Michael Lüth, with permission.

Figure 27. ***Fissidens nobilis*** comes from Asia and nearby islands. Photo by Jan-Peter Frahm, with permission.

Figure 28. ***Fissidens rivularis*** grows on shaded, moist or submerged, rocks in lowland neutral to acidic streams, rivers, and by lakes. Photo by Jan-Peter Frahm, with permission.

Figure 29. ***Fissidens taxifolius***, worldwide species from damp, shaded soil and rocks. Photo by David Holyoak, with permission.

Figure 30. ***Hyophila involuta***, a species that has been spread on calcareous walls of locks (Ireland & Shchepanek 1993) and therefore should not be dumped from aquaria because it could become invasive, although it is naturally rare. Photo by Li Zhang, with permission.

Figure 31. ***Isopterygium*** sp., a genus that has some aquatic species suitable for aquaria. Photo by Tan Sze Wei <www.aquamoss.net>, with permission.

Figure 32. ***Plagiomnium acutum***, a species known to many aquarists by its synonym ***Plagiomnium trichomannes***. Photo by Harum Koh through Creative Commons.

Figure 33. ***Riccardia chamedryfolia***, a thallose liverwort that is a slow-growing species that is easily overtaken by algae or mosses. Photo by David T. Holyoak, with permission.

Figure 34. ***Taxiphyllum*** sp., known in the aquarium world as flame moss. Photo by Tan Sze Wei <www.aquamoss.net>, with permission.

Figure 35. ***Taxiphyllum***, giant moss, commonly sold as an aquarium moss. Photo by Tan Sze Wei <www.aquamoss.net>, with permission.

Figure 36. ***Taxophyllum***, green sock moss, a common aquarium moss. Photo by Tan Sze Wei <www.aquamoss.net>, with permission.

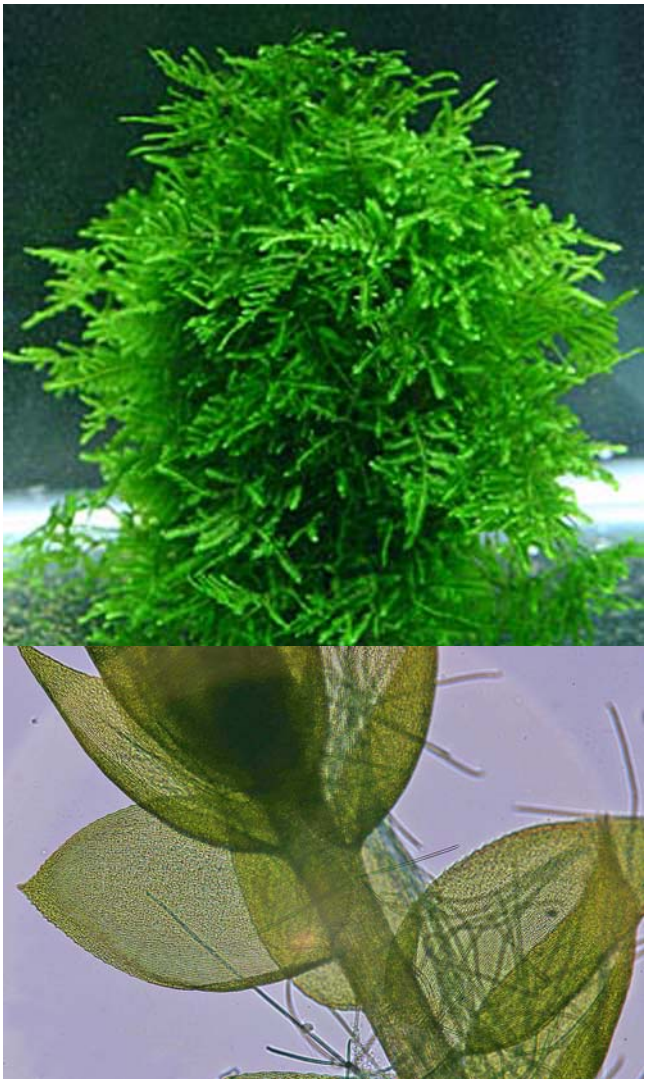

Figure 37. ***Taxiphyllum***, peacock moss, a common aquarium moss. Photo by Tan Sze Wei <www.aquamoss.net>, with permission.

Figure 38. ***Taxiphyllum***, spiky moss, a common aquarium moss. Photo by Tan Sze Wei <www.aquamoss.net>, with permission.

Figure 39. ***Taxiphyllum***, string moss, a common aquarium moss. Photo by Tan Sze Wei <www.aquamoss.net>, with permission.

Figure 40. ***Vesicularia ferriei***, weeping moss, a common aquarium moss in Asia. Photo by Tan Sze Wei <www.aquamoss.net>, with permission.

Figure 41. ***Vesicularia***, creeping moss, a common aquarium moss. Photo by Tan Sze Wei <www.aquamoss.net>, with permisssion.

Mifsud (pers. comm. 7 December 2007) found that ***Hyophila involuta*** (cememt moss) is sold on ebay, often mislabelled as star moss (***Tortula ruralis***). He has successfully grown ***Barbula***, probably ***Barbula bolleana***. Others that grow well but lack an attractive form are ***Rhynchostegiella curviseta***, ***Didymodon tophaceus***, ***Pohlia melanodon***, and ***Leptodictyum humile***. These species are either too small or become stringy (probably due to low lght). In addition to the ***Vesicularia*** mix up, ***Monosolenium tenerum*** is often sold as ***Pellia*** due to its original misidentification as ***Pellia endiviifolia***.

This list of mosses may not match the names being used in aquarium shops. We cannot expect these shop owners to keep up with changes in bryoogical nomenclature. That is not their area of expertise. For example, ***Glossadelphus zollingeri*** is now under the name ***Ectoprothecium zollingeri*** (see www.tropicos.org).

Preparing a Moss Wall

One aquarium website describes a method to make a wall of mosses in the aquarium (Tan 2006b). A plastic mesh of 7 -10 mm, preferably black or other neutral color, is used as the foundation (Figure 42). The author suggests cutting the mesh to twice the size of the aquarium, folding it, and putting the moss in between taco style (like a sandwich; Figure 43). The wall can be affixed with suction cups or rocks at the bottom with clamps at the top (Figure 44). The sandwich can be tied together where needed with fishing line so that fish cannot enter and get stuck. Mosses will grow through the mesh and soon fill in the spaces (Figure 45; Figure 46). Mosses can be grown on the bottom in a similar manner, again making sure fish cannot get under the layers of mesh (Figure 47).

To add interest, you might want to add some wood (without bark) where your mosses can grow. The best is wood that has soaked in a lake, then been sun-baked. More fresh wood must be soaked several days to remove the tannins (Sheng 2007). Moss can be tied to the wood with fishing line. Wait a week or so before introducing fauna to give the mosses a chance to attach. Sheng (2007) suggests setting the light at 9 watts to slow the growth of the moss (and algae).

Figure 42. To make a moss wall for an aquarium, one needs scissors, moss, screening, something to sew the screening together, and something to affix the moss wall to the aquarium wall. Photo by Sze Wei Tan <www.aquamoss.net>, with permission.

Figure 43. Mosses are woven into or sandwiched into the mat. Photo by Sze Wei Tan <www.aquamoss.net>, with permission.

Figure 44. The two halves of the mat are folded over and sewn together to prevent fish from entering. Suction cups or other means are used to attach the moss wall to the wall of the aquarium. Photo by Sze Wei Tan <www.aquamoss.net>, with permission.

Figure 45. As time passes, mosses grow through the mesh to cover the wall of the aquarium. Photo by Sze Wei Tan <www.aquamoss.net>, with permission.

Figure 46. An established moss wall can extend into the aquarium and provide hiding places for fish and nesting sites for eggs. Photo by Sze Wei Tan <www.aquamoss.net>, with permission.

Figure 47. A modification of the wall idea can be used to anchor mosses such as this ***Fissidens fontanus*** (Phoenix moss) to the floor of the aquarium. Photo by Sze Wei Tan <www.aquamoss.net>, with permission.

Maintenance

Most mosses are not as easy to cultivate as Java moss. If you are successful, the mosses often will grow long and fill a tank, collecting lots of organic matter from the fish. One trick to give them a fluffier look is to keep them trimmed (Jelsoft Enterprises Ltd. 2007).

Moss and other aquatic plant growth is usually enhanced by additional CO_2, up to 15-30 ppm (Stephan Mifsud, pers. comm. 14 December 2007). Light needs vary, so pay attention to the field light conditions for any wild mosses you use. ***Vesicularia reticulata*** (erect moss; Figure 14), for example, requires a brighter light than other species. Most of the aquarium mosses cannot tolerate temperatures greater than 26-28°C and stream mosses usually do better at temperatures closer to 15°C.

The mosses will typically collect detritus from fish feces and algae. Some of the small shrimp discussed below can help to clean these up, but check to be sure they aren't eating the mosses.

Dangers from other Organisms

Tan (2006a) warns against including the Siamese algae eater (***Crossocheilus siamensis***) in a tank with aquatic mosses (Figure 48). They will devour the moss and leave only a stubble of plants. Another moss scavenger, when the algae and other plants are scarce, is the Yamato shrimp (Yamato numa-ebi in Japanese), also known as Amano shrimp, Algae shrimp, or Japanese marsh shrimp (***Caridina multidentata***; Figure 49). When there is ample food, these shrimp will keep the mosses clean from algae without eating the mosses (Stephan Mifsud, pers. comm. 14 December 2007). Crystal red shrimps (***Caridina cantonensis*** sp. Crystal Red; Figure 50-Figure 51) and red cherry shrimps (***Neocaridina davidi***; Figure 52) are a nice color contrast in small aquaria with mosses. I would suggest also being careful about including snails, especially with ***Fissidens***, as they can likewise consume the mosses, although they seem to avoid ***Fontinalis*** (Figure 1) (Lohammar 1956).

Figure 48. Siamese algae eater (***Crossocheilus siamensis***) eating ***Taxiphyllum alternans*** (Taiwan moss). Photo by Sze Wei Tan <www.aquamoss.net>, with permission.

Figure 49. The Yamato shrimp (***Caridina multidentata***) will eat mosses when algae and other plants become scarce. Photo by Richard Bartz through Creative Commons.

Figure 50. ***Caridina cf cantonensis***, a species that helps to keep aquarium mosses clean. Photo by D. Tng through Public Domain.

Figure 51. ***Caridina cf. cantonensis*** (crystal red shrimp) in an aquarium with mosses and other aquatic plants. Photo by Sean Murray through Creative Commons.

Figure 52. ***Neocaridina heteropoda*** (red cherry shrimp) in an aquarium – a species that can help keep mosses clean. Photo by Joseph Hoetzl through Creative Commons.

Algae Problems

Maintaining the moss is not difficult once you have established the right water conditions. However, eliminating the algae that can overgrow the moss is another story indeed. My own Java moss soon became so covered with algae that it no longer looked like a moss (Figure 53). Tan (2006a) recommends using a 5% solution of bleach. The alga-covered moss is placed into the solution and stirred in the solution for about two minutes. When the algae begin to turn white, the moss should be removed and placed into a rinse bucket. It should be rinsed several times in fresh water to remove all the bleach. This method is too harsh for some mosses, and in much less than two minutes. It was the moss ***Fontinalis antipyretica*** (Figure 1) that I found to be white; the algae, fungi, and bacteria seemed to survive quite well! Be sure to bleach the aquarium also to reduce new infections, and replace the water in the aquarium with clean water. The same goes for any rocks collected from outside or from an aquarium with algal growths. Let these sit for a while to let the chlorine escape before introducing fish, or use one of the agents for removing chlorine.

In my own research, I have found that high nutrient levels encourage algae at the expense of the mosses. These soon cover the mosses and rob them of CO_2 and light.

Mosses are usually low nutrient plants and will probably do best in the water they came from. However that water may carry disease organisms for which your fish have no immunity, so it might help to boil the water first for about 20 minutes. **Cyanobacteria**, those smelly blue-green things, can be especially problematic and take over your aquarium. Filter feeders can have problems because the gelatinous matrix around them can clog their feeding mechanisms and in some cases can clog gills.

Sheng (2007) cautions against putting your aquarium where it will receive direct sunlight, as that encourages the growth of algae. However, some mosses will need more light than is available to the typical indoor aquarium and may benefit from the addition of LED or other higher intensity light.

Figure 53. ***Taxiphyllum barbieri*** (Java moss) is soon densely covered with algae in an aquarium. Photo by Janice Glime.

Some organisms are browsers on the algae and will eat them without harming the moss. The small shrimp have already been mentioned as cleaners. In addition, some snails will keep the mosses clean. The Ramshorn snail, ***Planorbis*** sp. (Figure 54), will not eat mosses, but it will eat both **Cyanobacteria** (Figure 55) and **diatoms** (Stephan Misud, pers. comm. 14 December 2007). The shrimp are best for the filamentous algae. Mifsud finds that high CO_2 (15-30 ppm) will lower the *p*H enough to make it unsuitable for most of the invading algae.

Figure 54. ***Planorbis corneus/rubrum***, a snail that can be used to keep aquarium mosses clean. Photo by Adilson Borszcz, through Creative Commons.

Figure 55. ***Oscillatoria***, a common genus of **Cyanobacteria** that can overtake aquarium mosses. Photo by Janice Glime.

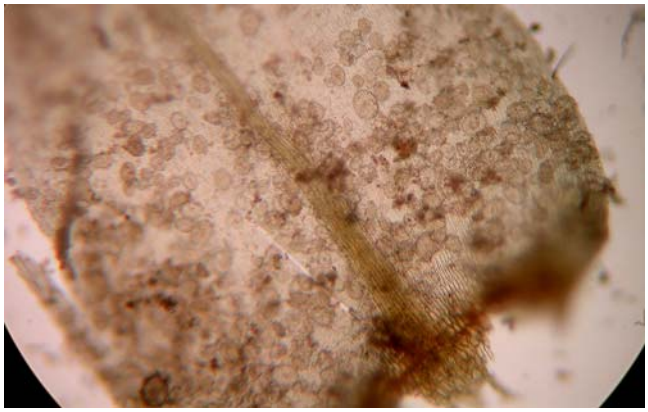

Figure 56. Diatoms (***Cocconeis***) on ***Platyhypnidium riparioides***. These are easily introduced into the aquarium from mosses collected from the wild. Photo by Daniel Spitale, with permission

Commercial Fisheries

Little has been published on use of bryophytes for the commercial rearing of fish or use in fish hatcheries. However, persons interested in spawning fish for such purposes might learn something from the aquarium industry. In one of the few studies in the laboratory, Bohlen (1999) describes breeding the spined loach, ***Cobitis taenia*** (Figure 57). He used thick tufts of moss on top of gauze-covered plastic boxes as spawning sites. Those eggs that were nonadhesive fell through the gauze into the box. The oviposition occurred in the most dense areas of moss and produced numerous young.

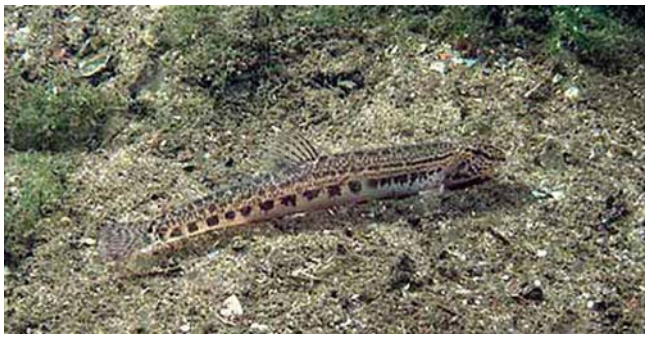

Figure 57. ***Cobitis taenia***, a fish that benefits from breeding in a bed of aquarium mosses. Photo by Ron Offermans, through Creative Commons.

Summary

Mosses in aquaria help to decorate while providing oxygen and hiding places, especially for laying eggs. They can be used to make walls, attached to logs and rocks, or grown from the sand on the floor of the aquarium. Most aquatic bryophytes prefer cool temperatures, low nutrients, and medium light; more light encourages algal growth. A mesh wall can hold the mosses or they can be allowed to grow free.

Some animals (fish, snails, algae shrimp) may eat the mosses. Others can be used to keep the mosses clean. Algae can be removed with a weak bleach solution.

Use of mosses as spawning grounds for commercial rearing of fish warrants further exploration.

Acknowledgments

Tan Sze Wei kindly allowed me to use any pictures I wished from his Aquamoss website. Stephan Mifsud wrote to me to add many bryophyte species to the list, updated nomenclature, provided advice on cleaner shrimp, and suggested growing conditions. I rarely get suggestions on my chapters, so his comments were greatly appreciated and have strengthened this chapter.

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CHAPTER 5
CONSTRUCTION

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CHAPTER 5
CONSTRUCTION

Figure 1. A log cabin in Norway illustrates the use of bryophytes for chinking between the logs, and more recently for the construction of green roofs. Photo by Michael Lüth, with permission.

Construction

One would hardly expect the non-lignified mosses to be useful in construction (Figure 1), but in fact, they can be quite utilitarian, especially in polar climates and remote areas. In the Antarctic, Granite House at Granite Harbour, Cape Geology, still has remnants of mosses placed there (Figure 5) by Scott's last Antarctic Expedition when they built the house in 1911. Stuffed into the cracks in the walls are ***Bryum argenteum*** (Figure 2), ***B. pseudotriquetrum*** (Figure 3), and ***Hennediella heimii*** (Figure 4) (Rod Seppelt, pers. comm.). The Inuktitut Indians in western Canada used ***Sphagnum*** (Figure 6) for chinking (Wilson 1978). The Shuswap Indians in British Columbia, Canada, use the mosses ***Aulacomnium*** (Figure 7) and ***Dicranum*** (Figure 8) for chinking by mixing it with clay (Palmer 1975). And, they were used by early settlers on Isle Royale, Michigan, USA, as chinking (Figure 9).

Figure 2. ***Bryum argenteum***, one of the mosses stuffed in cracks in the walls of the Granite House on Antarctica. Photo by Michael Becker, through Creative Commons.

Figure 3. ***Bryum pseudotriquetrum***, a moss used in chinking in Granite House, Antarctica. Photo by Michael Lüth, with permission.

Figure 4. ***Hennediella heimii***, a tiny moss used in chinking in Granite House, Antarctica. Photo by Michael Lüth, with permission.

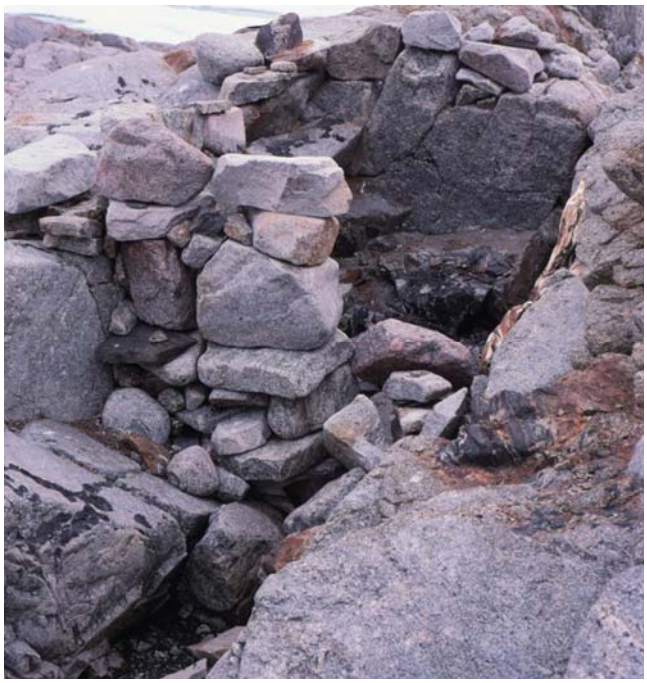

Figure 5. Remains of Granite House, with moss chinking, at Cape Geology, Antarctica. Photo by Rod Seppelt, with permission.

Figure 6. ***Sphagnum capillifolium***. Species of ***Sphagnum*** were used by the Inuktitut Indians in British Columbia, Canada, for chinking. Photo by Li Zhang, with permission.

Figure 7. ***Aulacomnium palustre***, a moss used by the Shuswap Indians in British Columbia, Canada, for chinking. Photo by Janice Glime.

Figure 8. ***Dicranum scoparium*** on forest floor, in a genus of mosses used by the Shuswap Indians in British Columbia, Canada, for chinking. Photo by Janice Glime.

Figure 9. Moss chinking with a variety of species in a fishery hut on the dock near the Rock Harbor Light House, Isle Royale National Park, Michigan, USA. Photo courtesy of Diane Lucas.

The use of mosses in caulking (chinking) is ancient. Dickson (2000) reports it from the Bronze Age by Iceman (also known as Ötzi; ~3,300 BC). ***Neckera crispa*** (Figure 10) was the most abundantly used, but ***N. complanata*** (Figure 11) was also used in **wattle walls** (woven wall daubed with sticky material; Figure 12) for construction. Could mosses have served as the first rebar? Von Ochsner (1975) also reported the use of ***Neckera crispa*** in construction of lake dwellings in Switzerland and wondered why this moss had been chosen over other bryophytes.

Figure 10. ***Neckera crispa***, a rock-dwelling moss species used for chinking during the Bronze Age. Photo by Des Callaghan, with permission.

Figure 11. ***Neckera complanata***, a rock-dwelling moss species used for chinking in the Bronze Age. Photo by Michael Lüth, with permission.

Figure 12. Wattle and daub construction, with sometimes uses mosses in the mud daub. Photo by Pany Goff, through Creative Commons.

In northern Europe some houses still have chinking of ***Homalothecium sericeum*** (Figure 13), ***Isothecium myosuroides*** (Figure 14), and ***Pleurozium schreberi*** (Figure 15) (Richardson 1981) or ***Fontinalis antipyretica*** (Figure 16) as fire insulation between the chimney and walls, hence its name (Thieret 1956). But even in our modern technological times, Philippine construction still uses them as fillers between wooden posts of walls and roof shingles (B. Tan, pers. comm.), Alaskans still use ***Hylocomium splendens*** (Figure 17), ***Racomitrium canescens*** (Figure 18), ***Rhytidiadelphus loreus*** (Figure 19), and ***Sphagnum*** (Figure 6) as chinking (Lewis 1981), and shepherds in the Himalayan highlands use local species for chinking in temporary summer homes (Pant & Tewari 1989). In the more recent habitation of Isle Royale, Michigan, where there are no cars or commercial enterprises, mosses have been used for chinking in a fishery hut (Figure 9, Diane Lucas, pers. comm.).

Figure 13. ***Homalothecium sericeum***, a species still found in chinking in older houses in Northern Europe. Photo by Janice Glime.

Figure 14. ***Isothecium myosuroides***, a species still found in chinking in older houses in Northern Europe. Photo by Michael Lüth, with permission.

Figure 15. ***Pleurozium schreberi***, a species still found in chinking of older houses in Northern Europe. Photo by Sture Hermansson, with online permission.

Figure 16. ***Fontinalis antipyretica***, an aquatic moss that was used for insulation between the heat of the chimney and the house. Photo by Štěpán Koval, with permission.

Figure 17. ***Hylocomium splendens***, a moss still used in Alaska as chinking. Photo by Michael Lüth, with permission.

Figure 18. ***Racomitrium canescens***, a moss still used in Alaska as chinking. Photo by Michael Lüth, with permission.

Figure 19. ***Rhytidiadelphus loreus***, a moss still used in Alaska as chinking. Photo by Tim Waters, through Creative Commons.

Jan (2016) indicates that mosses can be used as additives to "building earth," as seen on the site of Chalain 3 (see Bailly 1997). In the Philippines, one of the "tallest" mosses known, ***Spiridens reinwardtii*** (Figure 20), is still used as a binding material (B. C. Tan, pers. comm.). It also serves as a filler between wooden posts and shingles in building the local huts (Tan 2003).

Figure 20. ***Spiridens reinwardtii***, an epiphytic moss used as binding material and a filler in the Philippines. Photo by Daniel Nickrent, with online permission.

Li Zhang, on Bryonet 6 January 2017, reported that the local Tuvan people, Xinjiang Province, NW China, use ***Climacium dendroides*** (Figure 21), ***Hylocomium splendens*** (Figure 17, Figure 22), and ***Pleurozium schreberi*** (Figure 15) in the caulking of houses (Figure 9) (See Zhang *et al*. 2015).

Figure 21. ***Climacium dendroides***, a moss used in chinking. Photo by Li Zhang, with permission.

Figure 22. A log house that has caulking (chinking) with ***Hylocomium splendens*** in China. Photo courtesy of Li Zhang.

For chinking, mosses are pressed between the logs with the fingers or an instrument and left to dry, where they remain compressed and still green. Use of peat for construction will be further described in the Uses: Technological & Commercial chapter.

Robin Stevenson provided me with this church reference and an interesting reference to use of mosses in their slate roofs (Figure 23). Churches sometimes laid a bed of mosses on which to lay slate of roofs (**mosseying**) (Friar 2003). The addition of mosses provided protection against melting snow, but they had to be renewed periodically, often replaced with hay or straw.

Figure 23. St. Fagans Tannery, Wales, slate roof with mosses that have arrived after construction, along with many crustose lichens. It appears that this one might be laid on a bed of mosses beneath the slate. Photo by Zureks, through Creative Commons.

Modern Building Construction

In Japan, mosses are used on walls, embankments, and roofs for both aesthetic purposes and practical ones (Deguchi, personal communication 2005). Deguchi has actually published in the Green Architecture Tribune 22: 8, a newsletter among the building industries in Japan, encouraging the use of bryophytes. Mosses not only give the building an "old" and quiet appearance, but they also reduce heat loss in winter and air conditioning needs in summer. Typical mosses for these purposes are ***Hypnum plumaeforme*** (Figure 24) and ***Racomitrium japonicum*** (Figure 25).

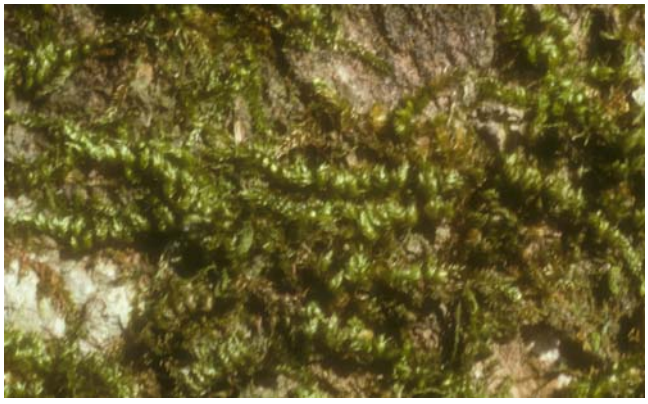

Figure 24. An epiphyte, ***Hypnum plumaeforme***, is a moss among those used to repair a log dam in Japan and is also used on living walls there to give a cooling effect. Photo by Janice Glime.

Figure 25. ***Racomitrium japonicum***, a moss used for insulation in Green Architecture. Photo from Digital Museum, Hiroshima University, with permission.

Custom Stone Handlers, Squirrel Mountain Stone, in Tennessee, will provide choices of boulders with intact moss. It appears that most of these are intended for gardens, but they could be used in construction as well. A die-hard bryologist might even choose them for fireplace construction. This could work well outside, but indoors they would require frequent misting with rainwater.

Insulation

I have had inqueries from people interested in using bryophytes for insulation. This has raised questions of longevity, renewable harvesting, and conservation issues. Rod Seppelt (Bryonet 12 January 2010) expressed concern over the widespread mining of living ***Sphagnum*** (Figure 6) in some areas and suggested instead that crop waste could be used. For example, in Australia mashed up leaf and stem waste from sugar cane are being used as garden mulch. But could they serve as insulation without creating a greater fire hazard or insect infestation?

Proof that mosses are still used for insulation comes from a web article by Stephanie (2017). She cautions that one encounters several problems – birds removing the mosses, the problem of uneven stacking of logs, and the need to replace the mosses (***Sphagnum***; Figure 6) periodically as they are lost. Furthermore, the mosses become brittle and also shrink, likewise requiring replacement or additional mosses. On the other hand, the moss does not rot, thus protecting the wood, and provides good ventilation.

Travertine Rock

In calcareous waters, certain mosses are tufa formers (Crum 1973). The species ***Didymodon tophaceous*** (Figure 26-Figure 27) makes such deposits, forming **didymodontoliths**! The tufa is formed by $CaCO_3$ deposits on the moss surface as photosynthesis removes the CO_2 from the water. These deposits result in a soft limestone that hardens into a porous brownish stone known as **travertine (**Figure 28-Figure 29**)**. This elegant-appearing travertine was once a common flooring material in many public buildings, especially banks. But its use was not just modern; the Roman Coliseum was built of travertine. This travertine rock, formed by the mosses, is not to be confused with the volcanic tufa that was a fragile rock also used by the Romans (Michel Chiaffredo, personal communication 2007).

Figure 26. ***Didymodon tophaceus***. Note the $CaCO_3$ on the leaf tips as the tufa begins to build. Photo by Martin Hutten, with permission.

Figure 27. ***Didymodon tophaceus***, building a **didymodontolith** with the $CaCO_3$ deposits at the base. Photo by Michael Lüth, with permission.

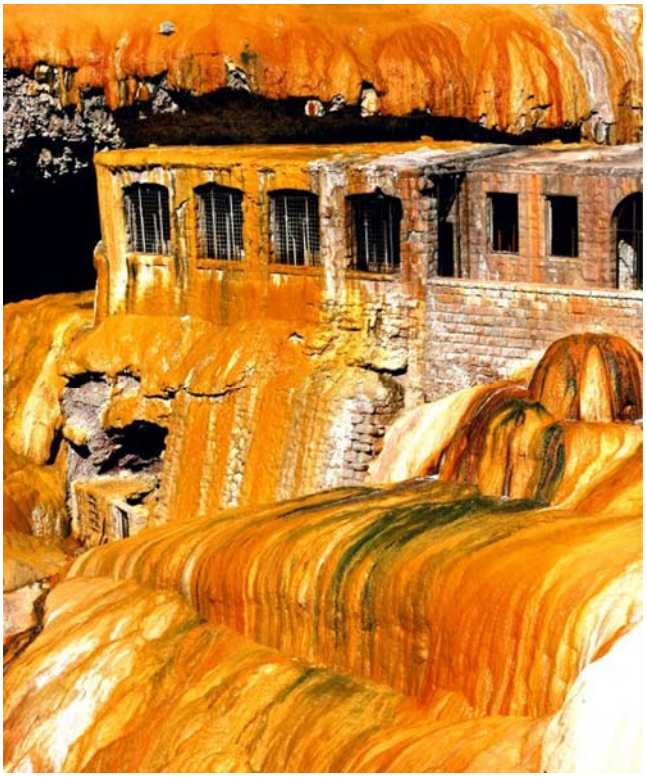

Figure 28. Travertine formation at Puente del Inca hot springs, Argentinian Andes. Photo by Oliver Gallannd, through Creative Commons.

Figure 29. Travertine facade sample for wall. Photo by Julian Herzog, through Creative Commons.

Problems in Construction

But mosses are not always welcome in construction. Not only are they considered a problem on roofs, but their moisture and organic acids contribute to the degradation of statues, tombstones, and walls (Perry 1987). On my own campus, student workers were instructed to spray them with herbicides in the cracks in the sidewalks because they made the walks look "unsightly." Fortunately, from my biased point of view, the mosses usually survive the herbicide treatments. And to my eyes, the mosses looked much better than the anthills that appeared in their absence! But, alas, this year they are being dug out. Obviously, our maintenance folks do not agree with Vivian (1996), or me!

Moss Walls

Planted walls, or living walls, have been gaining popularity in recent years (Figure 30-Figure 31). In addition to their aesthetic contributions, they help to insulate and to remove pollutants, including CO_2, from the atmosphere. And bryophytes have entered into this trend. For example, the City Hall in Iceland is decorated with mosses (Figure 32).

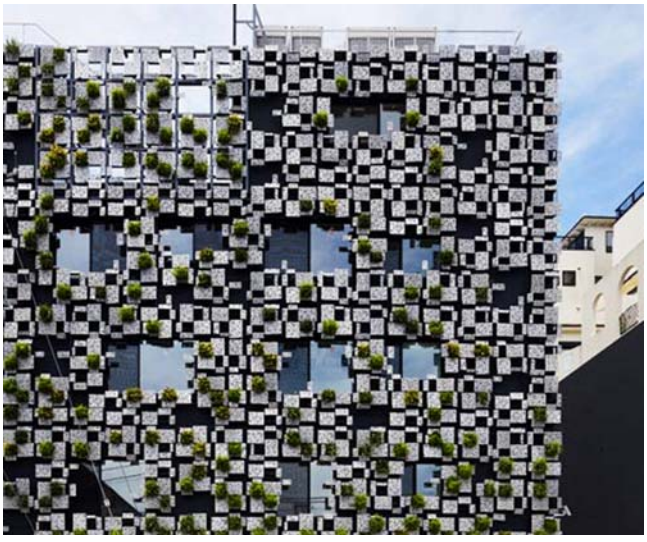

Figure 30. Living wall, dezeen Green Cast by Kengo Kuma. Photo courtesy of Sandra Manso Blanco.

Figure 31. Closer view of living wall, dezeen Green Cast by Kengo Kuma. Photo courtesy of Sandra Manso Blanco.

Figure 32. Moss wall decorating the Reykjavik City Hall in Iceland. Photo courtesy of Steffi Wilberscheid.

Vertical exterior walls of vegetation (Figure 33) became popular as a means to improve air quality and improve the aesthetic appeal of cityscapes. They also help to control runoff from roofs, reducing street flooding and blockage of storm sewers.

Mosses are common volunteers, and on older walls they can be quite extensive and charming (Figure 34). But the modern moss walls are often intended vertical walls, indoors or out, covered with mosses. Many have been inspired by rocks in nature (Figure 35).

Figure 33. Green walls of Dezeen House in Travessa do Patrocinio by Luis Rebelo de Andrade. Photo courtesy of Sandra Manso Blanco.

Figure 34. Mossy wall in Kusel, Germany. Photo courtesy of Kristi Bevard.

Figure 35. Natural model of mosses and lichens inspiring moss wall designs. Photo by Sandra Manso Blanco, with permission.

Elizabeth Brown began a discussion on Bryonet (8 March 2010) when she became allied with an architectural firm wishing to build a moss wall. Originally it was going to be a project to beautify an alley wall in the city, but the local city council couldn't cope with anything more problematic than a colorful mural. But the determination of the firm to build a moss wall was undaunted, so they decided to build a 2 X 2 m moss wall in their office.

The first hurdle was that the commercial firms who build living walls in Australia have no experience doing so with bryophytes. This brought questions about the substrate, water, lighting, and nutrient requirements to run such a wall long term.

In 2012, Sandra Manso Blanco, a Ph. D. student at Barcelona Tech, was struggling with a similar problem and contacted me for any advice. By 2013, she had made some progress in achieving colonization of her investigated substrate material. This material was a new type of concrete that could capture water and support the growth of bryophytes (Manso Blanco 2013). These "moss walls" (Figure 36-Figure 37) have a waterproof layer that separates the bryophytes (and other colonizers) from the inner structural part of the concrete (Manso *et al*. 2014a). The outer layer allows the rain water to enter it and holds it there. This layer is made with magnesium phosphate cement that has a slightly acidic *p*H (Manso *et al*. 2014b). This outer mix also absorbs carbon dioxide from the atmosphere and acts as an insulating material and a thermal regulator.

Figure 36. Centro Cultural Aeronáutico, Barcelona, showing biological concrete. Photo from Escofet 1886, S.A., courtesy of Sandra Manso Blanco.

The desire for these walls was rapid colonization (less than a year) and a changing face (Manso *et al*. 2014a). Color changes with seasons and natural succession of species could achieve the latter. And it is so constructed that rooted plants that could damage the structure are disfavored. Field tests indicated that the response was different from that in the laboratory (Manso *et al*. 2015). What these researchers learned was that the environment and the interactions between organisms were the most important determinants of success.

Roberto Vallejo Díez, Bryonet 4 March 2013, also a student in Spain, reported a similar project to develop a vertical garden system and was seeking advice on an appropriate substrate.

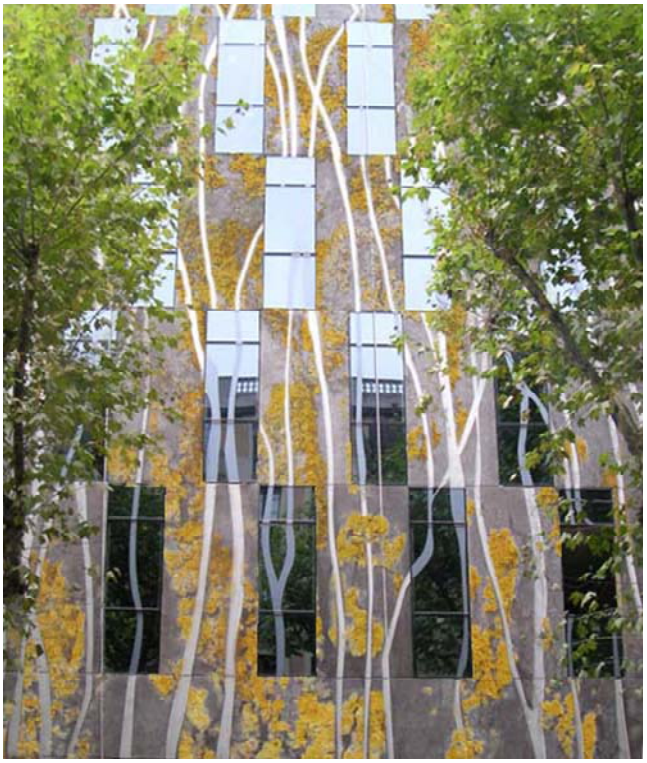

Figure 37. Simulation of a vegetated facade at the Ako-Suites Aparthotel in Barcelona, Spain. Photo from Escofet 1886, S.A., courtesy of Sandra Manso Blanco.

One method that has been used to encourage moss growth on rocks, and more recently may have been applied to vertical walls, is to paint the substrate with a mix of buttermilk and bryophyte fragments. But users have gotten mixed results. Annie Martin (Bryonet 9 March 2010) related the experiences of some of her moss-loving friends. One used the technique successfully on a small plastic waterfall feature. But another friend reported that when he coated his rocks with buttermilk moss, all he got was "biscuits." When I used a recommended egg white mix, the mosses looked for several weeks. Then one day they mat had holes in it. I lifted it and dozens of pillbugs (***Porcellio*** sp.; Figure 38) fell off. Yet another neighbor painted only buttermilk on boulders and six years later the huge rocks were covered with a variety of bryophytes. Moss Acres in Honesdale, PA, USA actually sells a Moss Milkshake.

Figure 38. ***Porcellio scaber***, known as a woodlouse or pillbug, on bryophytes. Photo by Bernard Dupont, through Creative Commons.

David Long (Bryonet 9 March 2010) describes his own sandstone and basalt moss wall, bound together with lime mortar, and most likely colonized completely naturally over the past 200 years. It sports at least 30 different species of bryophytes in its southern Scotland home. Its inhabitants include species like ***Hypnum cupressiforme*** (Figure 39), ***Mnium hornum*** (Figure 40), and ***Polytrichastrum formosum*** (Figure 41) growing on top. The mortar is highly calcareous, supporting many calcicoles such as ***Anomodon viticulosus*** (Figure 42), ***Bryum capillare*** (Figure 43), ***Ctenidium molluscum*** (Figure 44), ***Encalypta streptocarpa*** (Figure 45), ***Thamnobryum alopecurum*** (Figure 46), and ***Zygodon viridissimus*** (Figure 47). "The combination of acidic stone and calcareous mortar works really well. Some parts of the wall are heavily shaded by trees, others more open, but humidity is important."

Figure 39. ***Hypnum cupressiforme*** var. ***cupressiforme***, a colonizer of stone walls. Photo by David T. Holyoak, with permission.

Figure 40. ***Mnium hornum***, a colonizer of stone walls. Photo by Michael Lüth, with permission.

Figure 41. ***Polytrichastrum formosum*** with capsules, a moss that is able to grow on stone walls. Photo by Michael Lüth, with permission.

Figure 42. ***Anomodon viticulosus***, a moss that grows on the alkaline mortar of walls. Photo by Janice Glime.

Figure 43. ***Bryum capillare***, a moss that grows on the alkaline mortar of walls. Photo by Michael Lüth, with permission.

Figure 44. ***Ctenidium molluscum***, a moss that grows on the alkaline mortar of walls. Photo by Tim Waters, through Creative Commons.

Figure 45. ***Encalypta streptocarpa***, a moss that grows on the alkaline mortar of walls. Photo by Michael Lüth, with permission.

Figure 46. ***Thamnobryum alopecurum***, a moss that grows on the shaded alkaline mortar of walls. Photo by Michael Lüth, with permission.

Figure 47. ***Zygodon viridissimus***, a moss that grows on the alkaline mortar of walls. Photo by Michael Lüth, with permission.

Unfortunately, mosses used on the sides of buildings do not always meet the aesthetic goal we would hope for. In Munich, Germany, a huge tufa stone wall of an insurance building was covered with mosses (Figure 49) (J.-P. Frahm, pers. comm.). However, eventually the mosses, so carefully cultivated on the rock (Figure 49), were washed off. The contractor, Michel Chiaffredo, blamed this on the heavy metal pollution and especially the copper that mosses accumulated before dying (Michel Chiaffredo, personal communication 2007). The water used for the irrigation was the water retrieved from roofs, then stored in a tank. The quantity of copper and other heavy metals in these mosses, indicated by the analysis conducted by the Pasteur Institute, killed the ***Aloina ambigua*** (Figure 50) used for the green wall (Figure 48). Unfortunately, nobody wanted to assume the responsibility for the copper sulfate and other metals. ***Aloina ambigua*** is well adapted to a calcareous tufa, but it is not a copper moss. A new gardener tried to replace the lost mosses with ***Brachythecium rutabulum*** (Figure 51), installing an expensive system to wet the stone, but this water dissolved the carbonates of the tufa rock, which then crystallized on the mosses and killed them (J.-P. Frahm, pers. comm. 2007). It appears that the new gardener did not understand the ecology of the moss – or the rock.

Figure 48. ***Aloina ambigua*** shown growing here on tufa rock such as that used for the insurance building in Munich. Photo courtesy of Michel Chiaffredo.

Figure 49. These mosses are being cultured on tufa to be used in building construction. Photo courtesy of Michel Chiaffredo.

Figure 50. ***Aloina ambigua***, one of the mosses cultured on tufa for exterior construction. Photo by Michael Lüth, with permission.

Figure 51. ***Brachythecium rutabulum***, a moss that was used to replace lost ***Aloina***, but that was killed by the dissolving carbonates from the tufa. Photo by Michael Lüth, with permission.

Roads and Paths

Most of us have seen bryophytes growing along roads or between the stones (Figure 52) and along the edges of paths. Older patios and walkways around buildings were often constructed of bricks. Mosses eventually filled in the spaces between the bricks, adding a rustic and restful look (Figure 53). Vivian (1996) proclaims the need for such walkways, criticizing the sterile, formal appearance of straight concrete or blacktop. Such mosses seem to be a frequent subject for poets. See the subchapter on Uses: Literature.

Figure 52. ***Bryum argenteum*** between pavement bricks. Photo from South African National Biodiversity Institute, South Africa, with online permission.

Figure 53. ***Bryum***, ***Barbula***, and other small plants and seedlings in crack between concrete bricks in patio. Photo by Janice Glime.

Mosses had invaded the cracks between sections of concrete in the walks on my campus and I noted that where there were no mosses, ant hills prevailed. How much nicer the mosses looked!

Erosion and Ecocity

Use of mosses to control erosion (Conard 1935; Figure 54), muffle traffic noise, and retain cooling moisture forms the basis of a modern philosophy that may be labelled "**ecocity**." It follows the premise that mosses form a natural part of the ecosystem and that they have an important role in that ecosystem that can make life more pleasant for the human species, as well as maintaining a healthier ecosystem.

Figure 54. Soil bank where mosses such as ***Polytrichum*** help to maintain stability. Photo by Janice Glime.

At Ilsong (Ilsong 2004), in Korea, mosses are being touted for their ability to stabilize and beautify the environment in an environmentally friendly way. The Codra system starts with a soil embankment, such as one would find along a highway, and covers it with a layer of concrete formed like a rock outcrop, *i.e.*, not flat, but with undulations like rocks. To this, mosses are added and eventually make a soothing green mat that catches water and helps to stabilize the bank. Presumably, even if the concrete develops cracks, the mosses will be able to fill in and maintain the stability. Mosses such as ***Hyophila*** (Figure 55) readily grow on such concrete coverings in Japan and presumably elsewhere that this moss occurs naturally. The moss catch system consists of blocks forming vertical walls that are covered with mosses. These systems require early maintenance that assures sufficient water until the moss system becomes established.

Figure 55. The drought-tolerant, calciphilic moss, ***Hyophila involuta***, grows easily on concrete. Photo by Michael Lüth, with permission.

Among her many projects, Annie Martin (Mountain Moss Enterprise, Brevard, NC, USA) set out to stabilize a vertical cut in a clay bank (Figure 56-Figure 57), of course using bryophytes. She followed the natural contours first, then created depressions to establish a somewhat uniform cover (Figure 58-Figure 59). Mosses were then added in

that remaining space (Figure 60). The mosses were affixed with slanted toothpicks (Figure 61-Figure 62). Mosses in the completed wall (Figure 63-Figure 65) will spread to hold the soil even in heavy rainfall.

Figure 56. This recently cut clay bank is begging for erosion protection. The stone wall at the bottom will only catch the clay after it has been washed down. Photo from MountainMoss, courtesy of Annie Martin.

Figure 57. Clay bank showing natural depressions before adding bryophytes. Photo courtesy of Annie Martin.

Figure 58. A coworker prepares the crevices for the addition of bryophytes by making them more suitable for attaching the bryophytes. Note the sled that holds the mosses. Photo courtesy of Annie Martin.

Figure 59. Annie Martin inserting mosses in cracks. Photo courtesy of Annie Martin.

Figure 60. Coworker inserting mosses in depressions made for the moss. Photo courtesy of Annie Martin.

Figure 61. Mosses are held in place with slanted toothpicks. Photo courtesy of Annie Martin.

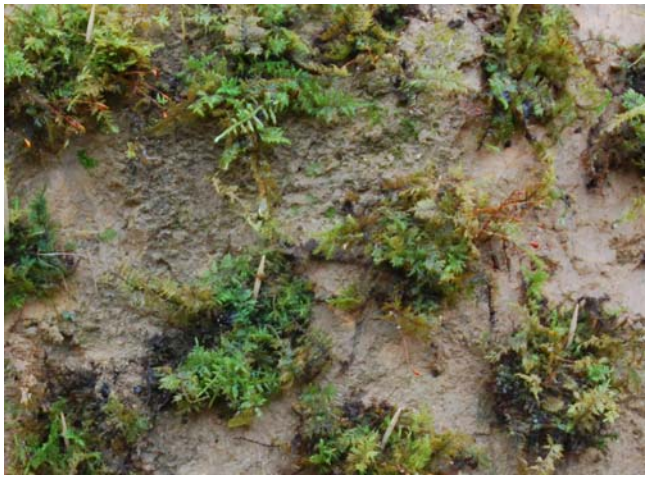

Figure 62. ***Thuidium*** held in place with toothpicks. Photo by courtesy of Annie Martin.

Figure 63. A completed portion of the clay wall. Photo courtesy of Annie Martin.

Figure 64. A completed portion. Photo courtesy of Annie Martin.

Figure 65. The natural creases break the monotony of a continuous design. Photo courtesy of Annie Martin.

Green Roofs

In 1584, Carlisle, UK, 86 horseloads of mosses, costing 4 pence (old currency) per load, were delivered to the Council for use as weather-proofing of roof slates, among other purposes (Woodward 1996). This early use of mosses is experiencing somewhat of a comeback in the form of "green roofs."

Annika Jaagerbrand, Bryonet 9 September 1999, relayed a story from Raymond Clarysse. He was curious because in northern countries there is a moss that grows on the roofs. People do not remove it because they consider it to be protection against the cold. Even some modern constructions are now cultivating mosses on roofs. Des Callaghan provides a diagram of a workable substrate for a moss culture on the roof (Figure 66).

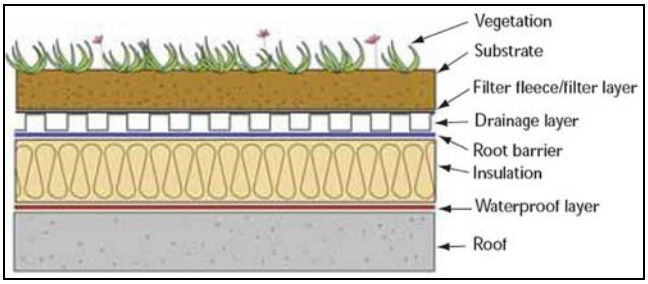

Figure 66. Green Roof diagram. Image courtesy of Des Callaghan.

Not all mosses are welcome. On wooden shingles, roof invaders can hold water, increasing the possibility of rotting. In western Washington, USA, these include ***Dicranoweisia cirrhata*** (Figure 67) among the first, with ***Ceratodon purpureus*** (Figure 75), ***Racomitrium ericoides*** (Figure 68), ***Bryum argenteum*** (Figure 2, Figure 52) arriving somewhat later (Frye 1920).

I am a little disappointed when I know of someone risking life or limb on the roof, trying to remove mosses from the shingles. Although mosses have traditionally been considered a nuisance on roofs, with people spending hundreds of dollars to remove them, more recently they have made a new debut in Germany, the United States, and other places. Their new acclaim offers the advantage of cleaning the atmosphere of pollution while buffering the temperature, fireproofing, reducing roof runoff, and creating a sound barrier. For more southern locations

where slate roofs are common, they offer a lighter and cheaper alternative to the slate (Posth 1993).

Figure 67. ***Dicranoweisia cirrata***, a moss that can hold water, causing damage to wooden roof shingles. Photo by Michael Luth, with permission.

Figure 68. ***Racomitrium ericoides***, a moss that can hold water, causing damage to wooden roof shingles. Photo by David Holyoak, with permission.

Moss green roofs are now being produced commercially in Germany (Behrens Systemtechnik) (Frahm 2004; Figure 69). Interestingly, it is this German company that is installing moss roofs in Michigan, USA. However, most people still consider mosses on roofs a nuisance because they add weight and increase the growth of fungi, and many consider the roof to look dirty.

Figure 69. Jan-Peter Frahm demonstrates a sheet of moss that is ready to be used in "green roof" construction. Photo courtesy of Jan-Peter Frahm.

Michel Chiaffredo and Franck-Olivier Denayer (2004) treat the mosses as both aesthetically beautiful and ecologically sound additions to urban roofs (Figure 70; Figure 71). And they are getting customers in the "green roof revolution" who agree with them (Chiaffredo 2004). To quote them, "It is thus possible to set up on roofs, in one go, a combination of all the living elements that nature would introduce spontaneously over a far longer period of time: veil of micro-organisms associated with mosses, and wild seeds of dependent xerophilous plants. The natural environment thus reconstituted will evolve very slowly according to the ecological conditions of the site, requiring neither maintenance nor the introduction of fertilizers. This innovative phytoecological engineering makes it truly possible to maintain biodiversity, unlike all the agronomic or horticultural processes, even within the very heart of towns and cities." (Chiaffredo & Denayer 2004; Figure 72).

Figure 70. This modern building has a green moss roof. Photo courtesy of Michel Chiaffredo.

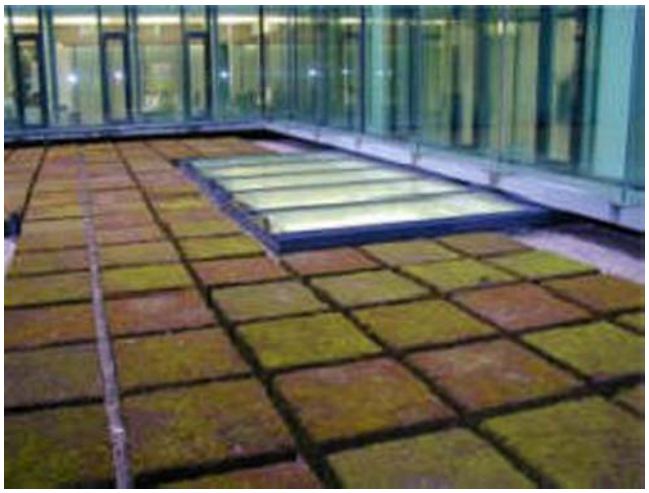

Figure 71. This green roof has bryophytes with skylights. Photo courtesy of Michel Chiaffredo.

Figure 72. This bryophyte plantation prepares bryophytes for green roof construction. Photo by Jan-Peter Frahm, with permission.

Chiaffredo and Denayer point out the advantages of using such vegetation on one's roof:

- *Regulate rainwater*: Collection of water by rooftop vegetation, especially bryophytes, will prevent the movement of water from large surfaces onto a small area of ground below and permit the return of water slowly to the atmosphere by evapotranspiration.
- *Increase biodiversity*: Opportunities for diversity in urban areas is limited, and rooftops add an opportunity for additional flora and fauna.
- *Decrease the greenhouse effect*: Bryophytes are heat sinks that will cool by evapotranspiration on the one hand and retain heat by insulation in winter on the other, reducing the heat flux in and out of the building.
- *Improve air quality*: Bryophytes produce oxygen, use CO_2, and trap dust particles, thus helping to clean the atmosphere.
- *Reduce sound pollution*: Roofs can serve as sounding boards to bounce sounds, whereas the rough surface of a bryophyte mat absorbs sound, thus reducing the sound pollution of traffic or noisy equipment.

When the roof is flat, the moss garden can be aesthetically pleasing as well (Figure 73). Mosses for green roof gardening can be grown in plantations (Figure 72) where natural diversity develops (Figure 74). The area then provides green space for relaxation and can be enhanced with stone benches and statuary.

In 2004, Bryonetters contributed their ideas regarding the species of mosses suitable for roofs. John Christy suggested that ***Ceratodon purpureus*** (Figure 75) was a good candidate because of its ability to form sods on concrete, gravel, asphalt, and wood. It tolerates nitrogen, so air pollution and bird droppings would be less of a problem than for some mosses. Use of zinc-plated metal around roof vents, chimneys, skylights, and other objects must be avoided because they will kill the mosses. Spreading mosses by fragments will accelerate their establishment. Other weedy species such as the acrocarpous ***Bryum argenteum*** (Figure 2), ***Tortula***/***Syntrichia*** (Figure 76), and ***Racomitrium*** (Figure 78) will colonize the more exposed areas, whereas horizontally growing or pleurocarpous taxa such as **Mniaceae** (Figure 40) and ***Brachythecium*** (Figure 51) will colonize shadier sites.

Figure 73. This completed green roof has a formal design, but many are more casual. Photo by Jan-Peter Frahm, with permission.

Figure 74. This mat of mixed mosses is ready for transplantation to make a "green roof." Photo courtesy of Jan-Peter Frahm.

Figure 75. ***Ceratodon purpureus***, a good choice for green roofs because of its wide tolerance. Photo by Janice Glime.

David Wagner has captured the effect of zinc on the mosses growing on a roof for ~25 years. On an office building at the Andrews Experimental Forest in Oregon,

USA, the galvanized zinc plates were used with guy wires to steady the chimney and prevented moss growth down-roof from them (Figure 77). This moss mat is dominated by ***Racomitrium elongatum*** (Figure 78) and ***Dicranoweisia cirrata*** (Figure 79) (David Wagner, Bryonet 29 June 2017).

Figure 76. ***Syntrichia ruralis***. ***Syntrichia*** and ***Tortula*** are suitable for green roofs because of their drought tolerance and are able to colonize the exposed portions. Photo by Michael Lüth, with permission.

Figure 77. Moss roof and zinc plates that prevented moss growth down-roof. Photo by David Wagner, with permission.

Figure 78. ***Racomitrium elongatum***. ***Racomitrium*** species are suitable for green roofs because of their drought tolerance and they are able to colonize the exposed portions. Photo by Paul Slichter, with permission.

Figure 79. ***Dicranoweisia cirrata***, one of the mosses in the mat on the roof above (Figure 77). Photo by Michael Lüth, with permission.

Henk Greven suggested that ***Polytrichastrum formosum*** (Figure 41) is easily transplanted and he would expect it to do well on roofs. Michel Chiaffredo has shown this to be the case (Figure 80-Figure 81).

Controversies have arisen regarding the best upkeep for the green roof. Ideally, these roofs are low or no maintenance ecosystems. Thus, we would anticipate no need for fertilizers, which generally seem detrimental to bryophytes anyway. However, many of the roof gardens that have been in existence seem to be deteriorating (Koehler 2003), leading the roof gardeners to promoting fertilization. Chiaffredo and Denayer (2004) disagree with this approach, concluding that it is "contrary to the very definition of extensive vegetalization." The International Green Roof Association lists the moss-sedum-herbs and grasses community as a low maintenance, low cost green-roof plant community (IGRA).

Figure 80. These large mats of ***Polytrichum*** are ready for transplantation to a "green roof" site. Photo by Jan-Peter Frahm, with permission.

Figure 81. A ***Polytrichum*** species displays a marvelous collection of capsules with hairy caps in the background and numerous male splash cups in the foreground. Photo by Jan-Peter Frahm, with permission.

The principle of the green roof for some companies relies on the well-known ability of mosses to colonize such a substrate with no help from us (Figure 82). At this stage, they are pioneers and require no watering or fertilizer (Figure 83). Diversity develops normally, hence providing stability (Figure 84). Their development can be compared to that of the cryptogamic crust (Figure 85) that is so important in anchoring and nurturing the soil of prairies and semideserts in the North American Southwest, Israel, and parts of China and Australia. These crusts remove CO_2 (Johansen 1993) from the atmosphere, convert atmospheric N to ammonia and nitrates (Verrecchia *et al*. 1995), and generally improve the quality of the habitat for invading organisms (Evans & Lange 2001), while improving the air quality for humans.

Figure 82. Buildings in Norway with natural green roofs. Photo by Michael Lüth, with permission.

Figure 83. Seashore damaged by tourists shows damaged bare sand area and restored area beyond the rope. Photo by Michel Chiaffredo, with permission.

Figure 84. This restored area shows colonization by pioneer plants, including the bryophytes. Photos by Michel Chiaffredo, with permission.

Figure 85. Cryptogamic crust with mosses and lichens in southern Australia. Photo by Thomas Hunt, through Creative Commons.

Using the studies on bryophytes as pioneers in these natural habitats as models, green roof landscapers have conducted studies on the best substrates for the roofs. The most popular and successful roofing material is a mineral one of volcanic origin, having a granulometric variation of 1-16 mm. Fentiman Consulting advocates a thin layer of concrete as a substrate for moss establishment (Grant 2006).

In London, England, the CUE Building of the Morniman Museum did not begin with bryophytes on its green roof (Grant 2006). However, successful establishment of tracheophytes led to natural succession and invasion of native species, including bryophytes. Mosses became frequent in the more open areas, including ***Bryum capillare*** (Figure 43), ***Ceratodon purpureus*** (Figure 75), ***Hypnum cupressiforme*** (Figure 39), ***Pseudoscleropodium purum*** (Figure 86), and ***Brachythecium rutabulum*** (Figure 51). The wetter north-facing section sported, in addition to a number of grasses, a luxuriant growth of mosses made up of ***Brachythecium albicans*** (Figure 87), ***B. rutabulum***, ***Calliergonella***

cuspidata (Figure 88), ***Eurhynchium praelongum*** (Figure 89), and ***Rhytidiadelphus squarrosus*** (Figure 90).

Figure 86. ***Pseudoscleropodium purum***, a species that colonizes open areas of roofs. Photo by Phil Bendle, with permission.

Figure 87. ***Brachythecium albicans***, a moss that grows on the wetter north-facing portions of roofs. Photo by Janice Glime.

Figure 88. ***Calliergonella cuspidata***, a moss that grows on the wetter north-facing portions of roofs. Photo by Janice Glime.

Figure 89. ***Eurhynchium praelongum***, a moss that grows on the wetter north-facing portions of roofs. Photo by Janice Glime.

Figure 90. ***Rhytidiadelphus squarrosus***, a moss that grows on the wetter north-facing portions of roofs. Photo by Michael Lüth, with permission.

Hironori Deguchi shared the experience of construction of a ***Sphagnum*** (Figure 6) bog on a roof in Japan (Figure 91). As you might guess, this required some maintenance to insure both a restful appearance and its survival (Figure 92-Figure 93).

Figure 91. ***Sphagnum*** bog on roof in Japan. Photo courtesy of Hironori Deguchi.

Figure 92. Maintaining ***Sphagnum*** bog for roof. Photo courtesy of Hironori Deguchi.

Figure 93. ***Sphagnum*** being grown for bog on roof in Japan. Photo courtesy of Hironori Deguchi.

Annie Martin shows the process of making a moss roof in the North Carolina Botanical Garden (Figure 94). First the metal roof is covered with a planting cloth (Figure 95-Figure 96). The mosses have already been planted in flats (Figure 97) and are ready for placement. They are organized by colors and textures to make the roof design easier (Figure 98-Figure 101).

Figure 94. Experimental moss roof before application of mosses, North Carolina Arboretum in Asheville, NC, USA. Note the rain barrels already collecting rainwater for watering the mosses when they are planted. This building and its rainwater collection system is a demonstration experiment for the botanical garden. Photo by Annie Martin, with permission.

Figure 95. Moss roofing, preparing the substrate. Photo by Annie Martin, with permission.

Figure 96. Laying the substrate on the metal roof. Photo by Annie Martin, with permission.

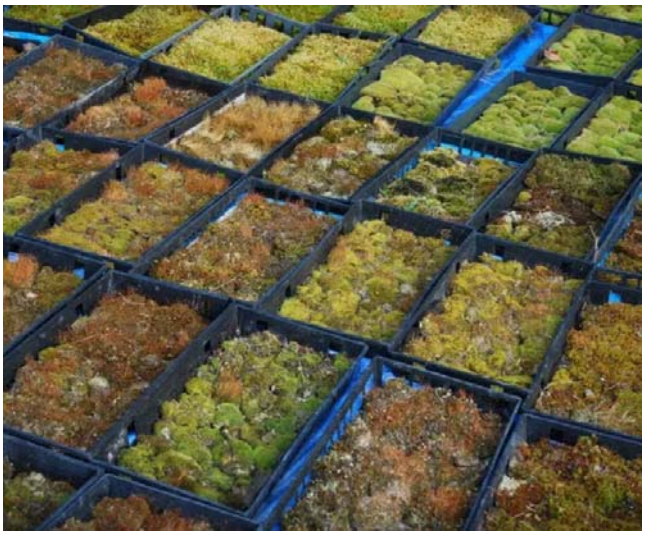

Figure 97. Moss roofing flats ready for planting. Photo by Annie Martin, with permission.

Figure 98. Moss roofing completed. Photo by Annie Martin, with permission.

Figure 99. Moss roofing completed showing variety of colors and patterns. Photo by Annie Martin, with permission.

Figure 100. Moss roofing, with stones adding texture and anchors. Photo by Annie Martin, with permission.

Figure 101. Moss roofing showing other ways to vary the landscape. Photo by Annie Martin, with permission.

Utilizing bryophytes (mosses) that like direct sun exposure [***Polytrichum*** (Figure 80-Figure 81), ***Atrichum*** (Figure 102), ***Climacium*** (Figure 21), ***Entodon*** (Figure 108-Figure 109), ***Hedwigia*** (Figure 109), ***Leucobryum*** (Figure 139), ***Ceratodon*** (Figure 75), and ***Ditrichum*** (Figure 129)], Mountain Moss has transformed a glaringly bright tin roof into a verdant expanse of moss art. With various shades of green and textures, the mosses will provide additional delight with brilliant reds, golds and bronzes when in sporophytic reproductive stage. When other garden plants are dormant or dead, the mosses will keep on giving joy, even in winter months.

Figure 102. ***Atrichum undulatum***, a sun-tolerant moss suitable for roofs. Photo by Michael Luth, with permission.

There is a Ford Green Roof Project at Michigan State University. Bryophytes were not planted originally, but they have introduced themselves since the project began. Annie Martin credits Michigan State, along with NC State and Penn State Universities as leading the way in green roof research in the United States.

Dr. Brad Rowe heads up the Michigan State (MSU) research team. He elaborates on the advantages of the green roof. These include:

- greatly aiding storm water management by absorbing rainwater that would normally run off buildings and create flooding in the streets in

urban areas. They can reduce total runoff by 60% and detain 85% of short showers or initial rainfall
- retention of pollutants from rainwater, roofing materials, and atmospheric deposition
- reduction of urban heat island effect
- improving air quality by capturing pollutants, filtering noxious gases, and reducing the ambient temperature
- increasing energy efficiency
- reducing waste by prolonging life of waterproofing membranes, using recycled materials, and prolonging the service life of HVAC systems through decreased use
- blocking electromagnetic radiation
- reducing noise
- retarding fire
- increasing space for growing vegetables or relaxing
- aesthetic improvement

The number of deaths in Europe that can be attributed to airborne micro-particles approaches 300,000 each year (Colbond 2009). This is a particular problem for the elderly and weak. Wolfgang Behrens and Jan-Peter Frahm (pers. comm.) were researching green roofs with the potential to partially cleanse the air of these dangerous particulates.

Grant (2006) sums up the green roof concept, stating "Green roofs are arguably the best example of multifunctional urban design, whereby elements on, in, and around the built environment serve several purposes. A roof (or external wall) can and should be more than just a weather-proof surface or structural element – it can be part of a living, cooling, cleansing skin that not only helps reduce flooding, urban heat-island effects, and air and noise pollution, but also provides wildlife habitat and tranquility." As proof of this utility, we have learned that at the Michigan Ford Rouge auto manufacturing plant, the green roof reduces power needs (Cesere 2006) through its function as a heat sink and evaporative cooling ability (Roofscapes 2004)!

Sadly, it seems that using mosses for green roof construction has not become a common practice in the USA. Rather, xerophytic tracheophytes dominate greenroof landscaping there. But the idea has been planted, and ecologically minded green-roofers are considering the advantages in heat control vs. the disadvantages in introduction of pests, added weight, and moisture damage to roofing shingles.

The Downside?

But alas, mosses on roofs have gotten a bad reputation among urbanites. If the neighbors aren't complaining that the mosses make the house look unclean and therefore devalue their property, then the house owner is concerned that they are destroying the roof. But is this really the case? It might depend on where you are. I used to delight when I could view the roof over the entryway of the building where I taught because it was covered with a multi-colored carpet of mosses that I could view as I descended the stairs. I'm pretty certain that the flat roof never leaked, and the building is 50 years old.

Annie Martin, Bryonet 19 November 2009, rescues unwanted mosses from roofs (Figure 103, Figure 105) and has seen no evidence that mosses deteriorate the surface of shingles (Figure 104, Figure 107). Rather, they add insulation and even evaporative cooling. One roofer even admitted to her that he did not see any problem until the moss was removed; it was then that the roof started to leak. Martin has seen slight, but not significant, deterioration of concrete. The mosses seem to occur where there is partial shade on the roof. And some of them are species one might find on logs (***Entodon***; Figure 108-Figure 109) or rocks (***Hedwigia ciliata***; Figure 109).

Figure 103. A rescue operation is about to begin here to remove these mosses and plant them somewhere that they are wanted. Photo by Annie Martin, with permission.

Figure 104. Mosses growing on an asphalt tile roof. Photo by Annie Martin, with permission.

Figure 105. A moss rescue operation where Annie Martin is gleefully pulling up thick carpets of mosses for transplanting. Photo courtesy of Annie Martin.

Figure 106. Rescue of mosses from asphalt roof shingles. Photo courtesy of Annie Martin <www.mountainmoss.com>.

Figure 107. Moss shingle spot where mosses were removed. Photo courtesy of Annie Martin, <www.mountainmoss.com>.

Figure 108. ***Entodon***, growing as a volunteer on this roof. The owner wanted it removed and Annie Martin rescued it for planting elsewhere. Photo courtesy of Annie Martin, <www.mountainmoss.com>

Figure 109. Mosses ***Hedwigia ciliata*** and ***Entodon*** looking healthy on a roof. Photo by Annie Martin, with permission.

Suitable Species

Studlar and Peck (2009) reviewed some of the green roof literature. They found that bryophyte roofs are more common in Europe than in the USA. The bryophytes are usually mixed with *Sedum* (Figure 110), a succulent flowering plant. They also examined natural (volunteer) roof moss communities near Terra Alta, West Virginia, USA. There they found ten moss and one liverwort species on four partly shaded roofs. These roofs had been relatively undisturbed for more than 40 years. They found the most frequent and abundant taxa to be ***Brachythecium laetum*** (Figure 111), ***Hedwigia ciliata*** (Figure 112), ***Plagiomnium cuspidatum*** (Figure 113), and ***Platygyrium repens*** (Figure 114), but each roof had a different dominant species among these. They recommended ***Hedwigia ciliata*** for further investigation for making extensive green roofs, suggesting that its growth form and drought tolerance were similar to that of ***Racomitrium*** (Figure 18, Figure 25), which is used for green roofs in Japan.

Figure 110. Living roof of ***Sedums***, Treasury Building, Athens, Greece. Bryophytes move in among these plants. Photo by Andrew Michael Clements, through Creative Commons.

Figure 111. ***Brachythecium laetum***, a species that grows on partly shaded roofs in West Virginia, USA. Photo by Michael Lüth, with permission.

Figure 112. ***Hedwigia ciliata*** with capsules, drying, a species tolerant of sun exposure and high temperatures on exposed roofs. Photo by Janice Glime.

Figure 113. ***Plagiomnium cuspidatum*** with young capsules, a species tolerant of sun exposure and high temperatures on exposed roofs. Photo by Michael Lüth, with permission.

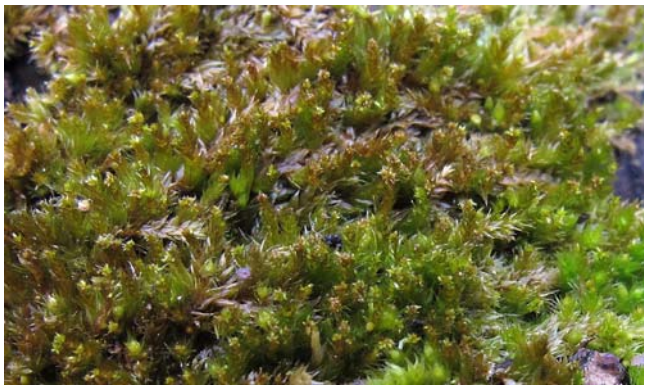

Figure 114. ***Platygyrium repens*** with bulbils, a species tolerant of sun exposure and high temperatures on exposed roofs. Photo by Michael Lüth, with permission.

Bill McKnight, Bryonet 28 June 2017, added ***Funaria hygrometrica*** (Figure 115) as being common on roofs in Indiana, USA. Graduate student Jillian Simpson (Bryonet 10 March 2010) also recommended studying ***Funaria hygrometrica*** for the potential of its use in green roofs. Her reasoning was that it is easy to grow, completes its life cycle in only 4 months with leafy gametophytes on the protonema in three weeks, is drought tolerant, and adds nitrogen through its epiphytes of ***Anabaena*** (Figure 116) and ***Nostoc*** (Figure 117). It prefers low-nutrient substrate and an alkaline *p*H. The biggest drawback may be that it is an annual, suggesting it is not suitable for vertical walls.

Figure 115. ***Funaria hygrometrica***, a species requiring low nutrients and that is suitable for roofs. Photo by Brian Eversham, with permission.

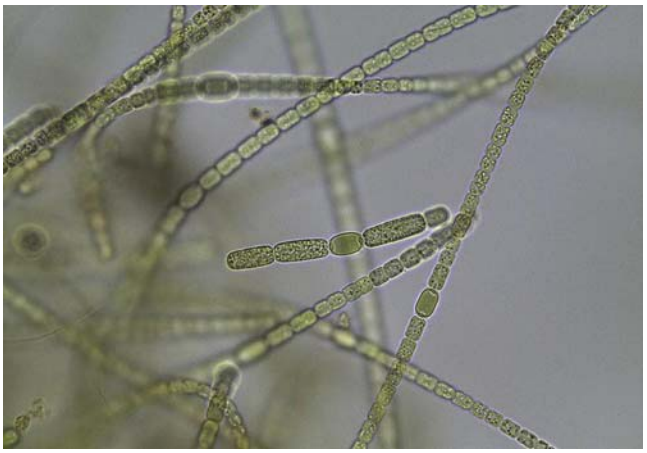

Figure 116. ***Anabaena subcylindrica***, member of a genus that is a common nitrogen fixer on mosses. Photo by Aimar Rakko, Nordic Microalgae <www.nordicmicroalgae.org>, through Creative Commons.

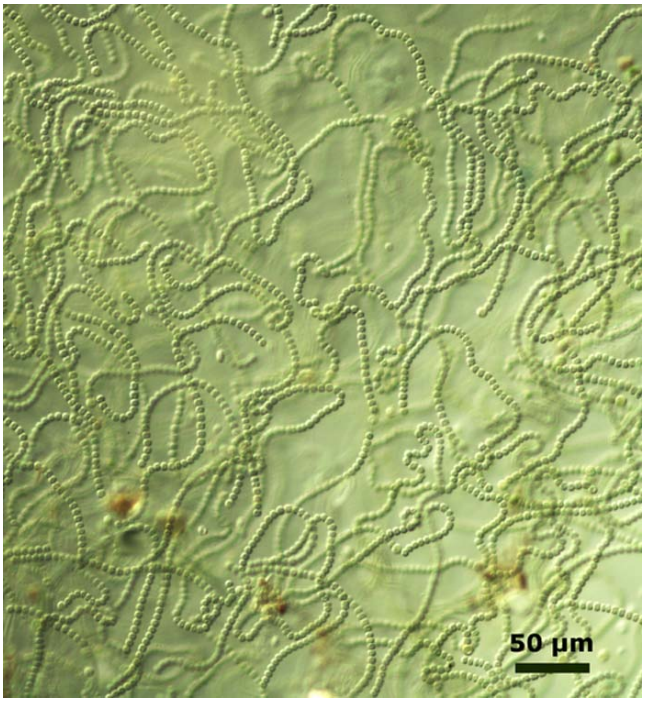

Figure 117. ***Nostoc commune***, member of a genus that is a common nitrogen fixer on mosses. Photo by Sergei Shalygin, through Creative Commons.

Annie Martin, Bryonet 28 June 2017) is very familiar with the roof mosses in her area of North Carolina, USA. "Tolerant of high heat index and sun exposures, most often I find ***Bryum argenteum*** (Figure 2), ***Ceratodon purpureus*** (Figure 75), ***Entodon seductrix*** (Figure 118), ***Grimmia*** sp. (Figure 124), ***Hedwigia ciliata*** (Figure 112), ***Platygyrium repens*** (Figure 114), and a few others. On roofs that are located under the shade of a tree canopy, I find ***Plagiomnium*** (Figure 113), ***Thuidium*** (Figure 119), and ***Mnium*** (Figure 40) species." These two lists are similar to those found by Studlar and Peck (2009) in West Virginia.

Figure 118. ***Entodon seductrix*** with capsules, a species tolerant of sun exposure and high temperatures on exposed roofs. Photo by Janice Glime.

Figure 119. ***Thuidium delicatulum***, a species that grows on shaded roofs. Photo by Hermann Schachner, through Creative Commons.

On the other side of the Atlantic, Sean O'Leary, Bryonet 28 June 2017, considered his home region in Buckinghamshire, UK, to be rather dull with regard to roof mosses. Instead, the mosses ***Grimmia trichophylla*** (Figure 120), ***Racomitrium fasciculare*** (Figure 121), and ***R. heterostichum*** (Figure 122) seem to be confined to roof tiles in old churches. He found ***Grimmia decipiens*** (Figure 123) only once on a roof.

Figure 120. ***Grimmia trichophylla*** with capsules, a species on roof tiles of old churches in the UK. Photo by John Game, through Creative Commons.

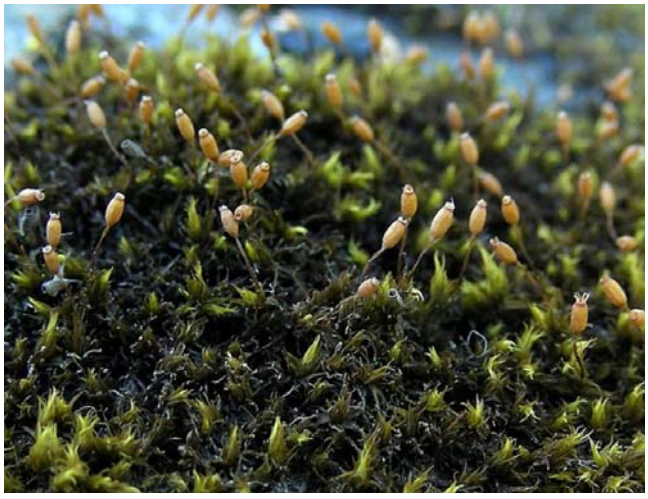

Figure 121. ***Racomitrium fasciculare***, a species that lives on roof tiles of old churches in the UK. Photo by Michael Lüth, with permission.

Figure 122. ***Racomitrium heterostichum***, a species on roof tiles of old churches in the UK. Photo by Sture Hermansson, with online permission.

Figure 123. ***Grimmia decipiens*** with capsules, a species that rarely occurs on roof tiles of old churches in the UK. Photo by Henk Grevens, with permission.

Michael Lüth finds roof tiles to be interesting habitats for mosses. ***Grimmia laevigata*** (Figure 124) and ***G. ovalis*** (Figure 125) grow on hand-made clay roof tiles around Freiburg, Germany, appearing only on the southern exposure of steep roofs. But outside the roof tile habitat, these two species are rare in the area, growing in just a few steep, sunny rocks in the Black Forest. The tiles are more than 100 years old and are chemically more suitable than the newer ones. On the other hand, lichens also grow on the tiles, but they destroy the tile surface. Nevertheless, even roofs more than 200 years old are still okay. Similar substrates, measured in geological time scales, do indeed show wear due to the bryophytes (and lichens) (Lenton *et al*. 2012).

Figure 124. ***Grimmia laevigata*** on 150-year-old roof tiles. Photo Michael Lüth, with permission.

Figure 125. ***Grimmia ovalis*** with capsules, a species that grows on hand-made clay roof tiles in Germany. Photo by Henk Greven, with permission.

The most extensive list I have found is from Sweden (Table 1).

Table 1. Mosses that Occur on Roofs (Green Roofs) in Sweden. Green Roof accessed on 12 January at <http://www.greenroof.se/default.asp?pid=51&sub=20>.

Latin name	Figures
Abietinella abietina	Figure 126
Barbula unguiculata	Figure 127
Brachythecium albicans	Figure 87
Bryum argenteum	Figure 2
Ceratodon purpureus	Figure 75
Ctenidium molluscum	Figure 128
Ditrichum flexicaule	Figure 129
Encalypta streptocarpa	Figure 45
Funaria hygrometrica	Figure 115
Homalothecium lutescens	Figure 13
Pohlia nutans	Figure 130
Polytrichum juniperinum	Figure 131
Polytrichum piliferum	Figure 132
Ptilidium cilare (liverwort)	Figure 133
Racomitrium lanuginosum	Figure 134
Rhytidiadelphus squarrosus	Figure 90
Rhytidiadelphus triquetrus	Figure 154
Rhytidium rugosum	Figure 135
Syntrichia ruralis	Figure 76
Tortella tortuosa	Figure 136

Figure 126. ***Abietinella abietina***, a roof dweller in Sweden. Photo by Janice Glime.

Figure 127. ***Barbula unguiculata***, a roof dweller in Sweden. Photo by Michael Lüth, with permission.

Figure 128. ***Ctenidium molluscum***, a roof dweller in Sweden. Photo by Tim Waters, through Creative Commons.

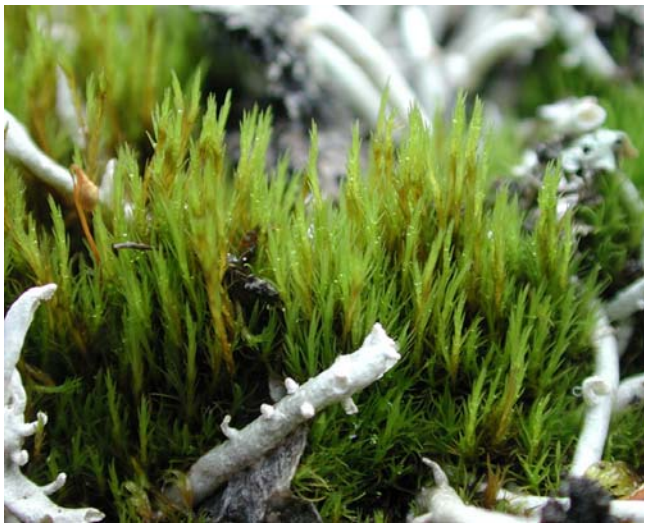

Figure 129. ***Ditrichum flexicaule***, a roof dweller in Sweden. Photo by Michael Lüth, with permission.

Figure 130. ***Pohlia nutans***, a cosmopolitan moss that is a roof dweller in Sweden. Photo by Michael Lüth, with permission.

Figure 131. ***Polytrichum juniperinum***, a widespread moss species and a roof dweller in Sweden. Photo by Janice Glime.

Figure 132. ***Polytrichum piliferum*** with capsules, a widespread species and a roof dweller in Sweden. Photo by Michael Lüth, with permission.

Figure 133. ***Ptilidium ciliare***, a leafy liverwort and a roof dweller in Sweden. Photo by Janice Glime.

Figure 134. ***Racomitrium lanuginosum***, a species that survives extremes and is a roof dweller in Sweden. Photo by Janice Glime.

Figure 135. ***Rhytidium rugosum***, a roof dweller in Sweden. Photo by Michael Lüth, with permission.

Figure 136. ***Tortella tortuosa***, a roof dweller in Sweden. Photo by Michael Lüth, with permission.

Eliminating Moss

Unfortunately, not everyone shares the perception of the aesthetic appeal of mosses and liverworts. When they occur on roofs, and even in the cracks in the sidewalks, some people will declare war. I have been asked how to eliminate them on a roof, and my answer is "Why do you want to?" Of course on roofs they add weight, especially when wet, and can get in the way when shovelling heavy snow off during six months of winter, but still!

Bryonetters seem to be in agreement that the bryophytes do no harm on roofs (*e.g.* Rod Seppelt, 4 October 2010; Bill McKnight, 28 June 2017; Michael Richardson, 28 June 2017). Annie Martin (Bryonet 28 June 2017), who spends lots of time crawling around on roofs to rescue mosses, reports that "Ironically, rather than damaging the roof, I have observed that shingles underneath moss colonies are not degraded or in a state of deterioration. Instead, the shingles are almost pristinely new. The surrounding asphalt shingles show evidence of degradation due to UV, wind, rain, snow, *etc*. It is my opinion that mosses protect the shingles. Tiny rhizoids hold tightly to the surface but do not compromise the integrity of the roof."

But roofers and urbanites like to convince us otherwise. And even a Bryonetter explains reasons why bryophytes might need to be removed (Mark Smits, Bryonet 28 June 2017). Smits explains that at one part of his house he has to remove bryophytes because they block the water flow, causing the roof to leak. Ken Kellman (Bryonet 28 June 2017) agreed; damming can force water under the tiles. And bryophytes can build up enough soil that tracheophytes can take root. Johannes Enroth (Bryonet 28 June 2017) added his experience to this. On a roof with tiles made of concrete, the mosses get wet, freeze, and thaw repeatedly. This causes damage to the tiles, especially in eroding the tile edges. Vinegar (50%) eliminated the mosses, but the lichens remained unharmed.

For those anti-bryophyte folks, there are a few solutions. Shunda Lee, Bryonet 19 April 2001, reports that Clorox works successfully in Singapore. So if you must get rid of the mosses, we have already seen that zinc works, and now we know that bleach works. Today's Homeowner <www.todayshomeowner.com> recommends a 50:50% water:bleach mix. To keep mosses off, they recommend a copper or zinc strip across the peak of the roof. They also recommend removing any branches that shade the roof.

Several bryocides seem to be successful. The one most familiar to me is lime ($CaCO_3$), partly because most bryophytes prefer more acid conditions, but perhaps even more important are the desiccating properties of lime. Bogdanov (1963) describes liming to eliminate mosses in forest stands (!) of drained swamps.

Several people and web sites advocate zinc or copper strips placed near the peak of the roof. Rainwater dissolves enough zinc to form zinc carbonate, which washes down the roof, killing the mosses. Of course, it accumulates on the ground below and will ultimately get into the water supply, so the solution can be a deadly one if many people begin this practice.

Rod Seppelt, Bryonet 4 October 2010, points out that bryophytes will only grow on the roof if it is moist and shaded. If the mosses must be removed, he recommends experimenting with non-herbicides. Try fertilizer or detergent. Aerate the substrate. If you need to remove them from a lawn, avoid mowing so they don't get enough light. Raise the *p*H – add lime, or add calcium. Use an iron sulfate spray. Johannes Enroth, Bryonet 5 October 2010, reports that a 1:1 vinegar:water solution is a fast, easy way to kill mosses.

One web site advocates using a standard scrub brush on a long handle to remove the moss. I cannot help but wonder if the brush doesn't do more damage to the asphalt than the moss does. And how practical is it for a steep roof like the one in Figure 137?

Figure 137. This house in Bretagne has mosses invading the roof. Photo by Michael Lüth, with permission.

But while we are discussing green roofs, some folks don't want mosses on their property in any form! Terry McIntosh, Bryonet 9 March 2010, lamented the difficulty of persuading these people to appreciate mosses. He cited a website where someone described how to get rid of the moss on the oak trees:

"Oak trees are functional as well as attractive. Their leafy green foliage provides shade and color to the natural environment. Sometimes the presence of ball moss causes the tree to appear less than attractive. Getting rid of this unsightly moss is something that can be done in a relatively short time with the right tools and equipment." (Meason 2017). To each his own!

Golf Courses

In September 2006, Bryonet subscribers were asked to recommend the ideal moss for a golf course. Susan Moyle-Studlar (Bryonet, 14 September 2006) contributed several suggestions. She suggested ***Polytrichum*** (Figure 41) species because they tolerate the high light levels of a golf course and are trampling resistant, being firmly anchored to the substrate. In fact, the trampling can help to propagate them by creating fragments that can produce new plants. They are common plants along trails and railroad tracks. However, she cautioned that they are a bit tall and will require frequent watering. I wonder how they would respond to being mowed – perhaps make a shorter, denser turf?

A shorter and softer turf, relatively trampling resistant, is formed by ***Dicranella heteromalla*** (Figure 138) along forest trails, but she cautions that it is not well-anchored, possibly leading to a "choppy turf" following the activity of golfers. But, like ***Polytrichum*** (Figure 41) species, these would also need watering and additionally would need shade.

Figure 138. ***Dicranella heteromalla***, known as green thread moss, grows here on a vertical bank. Photo by Michael Lüth, with permission.

Leucobryum (Figure 139) can tolerate trampling, as exhibited by its proliferation near a picnic shelter in West Virginia, USA. Moyle-Studlar considers this a possible candidate because of its tolerance of greater aridity than the former two, its retention of its attractiveness when dry, and its ability to reproduce from broken leaves. Nevertheless, the chopping effect of golf clubs would most likely be quite destructive; hopefully winter would give it a chance to recover in areas where golfing is not a winter sport.

Figure 139. ***Leucobryum glaucum***, a species that is often successful on golf courses because it can tolerate trampling. Photo by Janice Glime.

Pleurocarpous mosses such as ***Hypnum imponens*** (Figure 140) and ***Thuidium delicatulum*** (Figure 119) likewise seem to return from trampling damage, but they also pose the same problems of the above mosses and lack a secure anchoring system.

Figure 140. ***Hypnum imponens*** appears here with ***H. jutlandica*** in the background. Photo by Michael Lüth, with permission.

John Christy (Bryonet, 15 September 2006) reported seeing ***Bryum argenteum*** (Figure 2) forming tightly-packed, extensive turfs growing among the closely clipped grass on golf greens on the west coast of North America. The moss seemed to grow well on the hard but well-drained surface. Diana Horton (Bryonet, 15 September 2006) reported the same species from a golf course in Arizona, where it formed a "beautiful, short and dense sod." Only this time the manager wanted advice on how to eliminate it!

Researchers are looking for ways to reduce moss cover in putting greens without damaging the desired bentgrass (Nus 2009). To this end, the Chicago District Golf Association has tried baking soda, a herbicide (carfentrazone-ethyl; Quicksilver). and a fungicide (chlorothalonil; Daconil Ultrex). So far the researchers have concluded that there are multiple strategies available to suppress the mosses, but that none of them eliminate the mosses. They have advised that treatments should be in spring and fall when the mosses have active growth; summer treatment is probably unnecessary. They also found that baking soda need be applied only twice in spring to suppress moss growth all season, but unfortunately, it is toxic to the bentgrass and requires spot application onto the moss patches, making it more labor intensive. Chlorothalonil alone or in combination with fungicides requires at least three applications at 2-week intervals to suppress growth for that year. Applications of Quicksilver (6 oz per acre) in spring and fall (4 total) is also effective at suppressing the mosses without harming the bentgrass. But it appears that ***Bryum argenteum*** (Figure 2) is more tolerant, with no single product being effective in controlling it in the tested golf greens in Illinois, USA (Settle *et al*. 2009). This moss is problematic throughout the country because it interrupts surface aesthetics and smoothness.

A recent ad on the internet, however, seems to me a slightly better solution, if you must. This is a product called Moss Aside™, an herbicidal soap (Gardens Alive 2017). It will let you grow thicker lawns!

Roman Wells

In ruins near Abingdon, Great Britain, mosses were tucked between and behind the stones of a Roman well. Dickson (1981) concluded that the mosses were placed there deliberately because they were not the ones that one would expect there naturally. Hence, he suggested they might have been used to filter the water. One might expect them to help hold the rocks together as well.

Herman Stieperaere (pers. comm.) reported his involvement in the analysis of extensive carpets of bryophytes surrounding a late Roman well (5th century AD; Figure 141-Figure 146). This bryophyte surrounding is a filter to prevent pollution of the central well. In fact, in a prior occupation period of the Roman fort, the area was heavily polluted by iron forges. The moss and sand layer acted as a barrier/filter against infiltrating polluted water.

Dickson (2000) identified the mosses in one Roman well near Stuttgart, Germany, as ***Neckera crispa*** (Figure 10). He found other Roman wells in England that used ***Neckera complanata*** (Figure 11).

Figure 141. Moss in Roman well. Photo from Flemish Heritage Institute (VIOE), courtesy of Herman Stieperaere.

Figure 142. Moss in Roman well. Photo from Flemish Heritage Institute (VIOE), courtesy of Herman Stieperaere.

Figure 143. Moss in Roman well. Photo from Flemish Heritage Institute (VIOE), courtesy of Herman Stieperaere.

Figure 144. Moss in Roman well. Photo from Flemish Heritage Institute (VIOE), courtesy of Herman Stieperaere.

Figure 145. Moss in Roman well. Photo from Flemish Heritage Institute (VIOE), courtesy of Herman Stieperaere.

Figure 146. Moss in Roman well. Photo from Flemish Heritage Institute (VIOE), courtesy of Herman Stieperaere.

Log Dams

Bryophytes can have advantages in emergencies because of their absorptive ability and small size. For example, when a temporary log dam developed a leak during a timber harvest in Japan, the resourceful workers used ***Hypnum plumaeforme*** (Figure 24), ***Loeskeobryum brevirostre*** (Figure 147), ***Rhytidiadelphus japonicus*** (Figure 148), and ***Thuidium kanedae*** (Figure 149) to stop the leak (Ando 1957). And forest workers in Pennsylvania, USA, deliberately use rocks with ***Fontinalis*** (Figure 16) on them to help stabilize newly constructed weirs. The mosses quickly spread to other rocks, effectively gluing them together.

Figure 147. ***Loeskeobryum brevirostre***, one of the species used to stop a leak in a log dam. Photo by Blanka Shaw, with permission.

Figure 148. ***Rhytidiadelphus japonicus***, one of the species used to stop a leak in a log dam. Photo from Digital Museum, Hiroshima University, with permission.

Figure 149. ***Thuidium kanedae***, one of the species used to stop a leak in a log dam. Photo from Red Book of the Sakhalin Oblast, through Creative Commons.

It appears that the use of mosses in weirs was not new in the past century. Woodward (1996) reported that in 1555, a "gang" of 68 women and 13 children spent nearly 10 weeks gathering mosses to pack the cracks between the boulders of a new weir.

Boat Construction

Use of mosses in boat construction is well documented (*e.g.* Dickson & Ransom 1968). In the Scottish Highlands, mosses were prepared by steeping in tar, then used for caulk (Crum 1973; Figure 150). As in those used for houses, they were usually relatively large, pleurocarpous mosses such as ***Eurhynchium striatum*** (Figure 151) and ***Neckera complanata*** (Figure 11) (Pant & Tewari 1990). Saatkamp *et al*. (2011) reported on 15 boats, conserved as wrecks, in the upper French Rhône and Saône (Eastern France) from the 3rd to the 20th century. Among these, the use of ***Neckera crispa*** (Figure 10) as caulking to make boats tight was common. While the use of ***N. crispa*** in much of Europe has strongly decreased as a caulking material from the 14th century onwards, this was not the case in their study area. This was most likely because suitable forests remained in the Jura mountains.

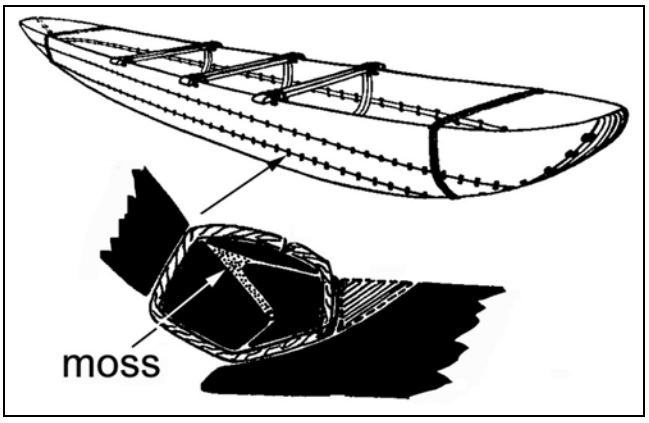

Figure 150. In this boat, mosses were used as rope caulk. Redrawn by Janice Glime from Dickson 1973.

Figure 151. ***Eurhynchium striatum***, one of the large, pleurocarpous mosses used in boat construction. Photo by Michael Lüth, with permission.

Dickson (2000) found that sewn boats in the Bronze Age (3300 BC – 1200 BC) were caulked with essentially pure ***Neckera complanata*** (Figure 11) in all the seams. And ***Polytrichum commune*** (Figure 152) served for making the ropes (Figure 153) (Dickson 1973, 2000).

Mosses were even imported into Holland from Belgium after the 16th Century for caulking the carvel-built boats (Dickson 1973). The online Deutsches Schiffahrtsmuseum, accessed on 20 March 2013 at <www.dsm.de/MA/schlachte.htm> displayed a rope made of this moss and carbon-dated to 1770.

Figure 152. ***Polytrichum commune***, a moss that has been used in making rope caulk. Photo by Christopher Tracey through Creative Commons.

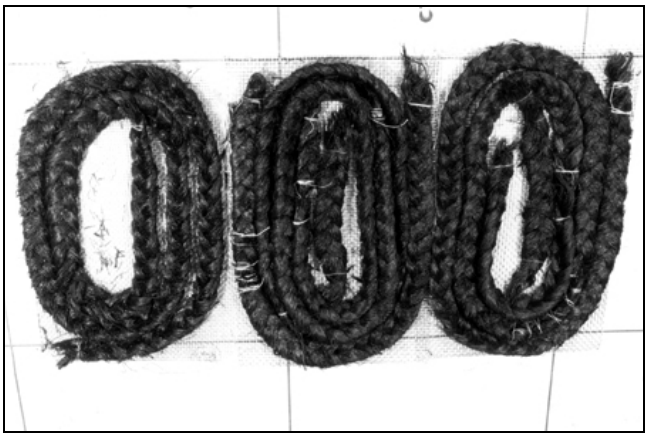

Figure 153. ***Polytrichum*** was used as rope caulk. Photo by Per Hoffmann.

The native Yaghan people in Chile used mosses to build their canoes in quite a different way (Metzner Productions 2006). They buried tree bark in peat for a season, allowing the acidity to preserve the bark while the moisture made it flexible. They could then form it into a canoe.

Dickson *et al*. (2013) described a dug-out boat made of an alder (*Alnus*) trunk about 4,000 years ago. The space between the stern transom board and the slot cut into the hull was caulked with mosses comprised primarily of ***Anomodon viticulosus*** (Figure 42), but 13 other mosses and 1 liverwort were also present.

In Northern Spain, Heras-Pérez *et al*. (2009) examined two wooden pieces from the hull of a 15th Century iron transport vessel. The was the first evidence of the use of mosses in boats in Spain and revealed fragments of eight different moss species: ***Eurhynchium praelongum*** (Figure 89), ***E. striatum*** (Figure 151), ***Hylocomium splendens*** (Figure 17), ***Hypnum cupressiforme*** var. ***cupressiforme*** (Figure 39), ***Neckera complanata*** (Figure 11), ***Pseudoscleropodium purum*** (Figure 86), ***Rhytidiadelphus triquetrus*** (Figure 154), and ***Thuidium tamariscinum*** (Figure 155).

Figure 154. ***Rhytidiadelphus triquetrus***, a moss used in the construction of boats in Spain in the 15th Century. Photo by Malcolm Storey, through Creative Commons.

Figure 155. ***Thuidium tamariscinum***, a moss used in the construction of boats in Spain in the 15th Century. Photo by Malcolm Storey <DiscoverLife.com>, with online permission.

Summary

In construction, mosses can provide chinking and even building material, as well as ameliorating the climate. They have been mixed with mud in building and chinking, much like using rebar. Green Roof technology uses the process of natural succession to vegetate roofs and disturbed areas. Caution must be exercised in choosing bryophytes that are adapted to the type of substrate being used, climatic conditions, and microclimate. Shaded roofs often develop moss mats without human help, and in urban areas these are often considered unsightly. They can be discouraged by using a strip of zinc across the peak of the roof or removed with Clorox or vinegar.

Green roofs meet with the same restrictions as roofs. They can be arranged in artistic patterns, and both green roofs and living walls can remove air pollution, insulate the interior, reduce CO_2, and reduce runoff to the street.

On golf courses, bryophytes require no mowing and withstand at least some trampling, but they can make the surface uneven. Bryophyte ropes have been used to construct boats.

Roman wells and log and rock dams and weirs may be packed with mosses that help to hold the rocks in place. In the wells they may function to purify the water that seeps in from the sides.

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CHAPTER 6
TECHNOLOGICAL AND COMMERCIAL

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CHAPTER 6
TECHNOLOGICAL AND COMMERCIAL

Figure 1. Commercial cranberry farm near Black River Falls, Wisconsin, USA. ***Sphagnum*** peatlands are necessary to protect the cranberries and maintain sufficient water for their growth. Photo by Janice Glime.

Sphagnum Peatlands

First, a definition of peat and peatlands is in order. **Peat** is comprised of partly decomposed vegetable matter containing a variety of plants (Figure 2) that may or may not include ***Sphagnum*** (Figure 3). Peat is brown and soil-like and is derived from boggy, acidic ground (Figure 1). **Peat mosses**, on the other hand, are species of ***Sphagnum*** (Figure 3). **Peatlands** are lands consisting largely of peat or peat bogs (Figure 4). They may be dominated by ***Sphagnum*** (Figure 3), but there are also peatlands that have no ***Sphagnum***.

Figure 2. Harvesting peat in Saterland, Germany. Photo by Pyt, through public domain.

Figure 3. ***Sphagnum magellanicum***, one of many species of ***Sphagnum*** from ***Sphagnum*** peatlands and in widespread usage in horticulture, fuel, and other applications. Photo by James K. Lindsey, with permission.

Certainly the best-known and widespread uses for mosses in both modern and ancient times are the uses of ***Sphagnum*** (Figure 3). This is not surprising since it occupies 3% of the Earth's surface, mostly in the northern hemisphere (Clymo 1987). Its abundance, longevity, cation exchange (Clymo 1963; Fischer et al. 1968), and ability to hold water make it ideal for commercial exploitation. Its largest usage in North America is for horticulture and cranberry culture (Figure 1; Figure 5), but in Europe, fuel is an important use as well (Clarke 2008).

Figure 4. Peatlands in Manitoba, Canada. Photo by subarcticmike, MSG Family, Mukhrino FS, through Creative Commons.

Figure 5. Cranberries (*Vaccinium macrocarpon*) growing among ***Sphagnum*** and ***Polytrichum***. Photo by Janice Glime.

Turner (1993) reviewed the human uses of peat. In addition to 100 million tons a year used as fuel in Ireland, peat provides a source of waxes and resins. The by-products provide oily materials for dyes, varnish, and leather treatments. More recent uses include making biofilters.

In the UK, ***Sphagnum*** (Figure 3) has been recommended as a litter for milking cows. Peltola (1986) reported that compared to straw and sawdust, peat provides better absorption of urine and binding of ammonia than the other litters. The spent litter is good for growing plants because it contains more than the average amounts of nitrogen and magnesium in a form readily used by plants.

In Japan, the Technical Academy of Sphagnum and the Marsh Bowz Factory illustrate uses, including peat grown on clay shapes, a restful boardwalk through the green moss (Figure 6), a cover for an aquarium that presumably reduces water loss while still permitting the entry of fresh air, and a peat roof garden with stepping-stones.

Figure 6. Boardwalk on the Fort River Birding and Nature Trail, Hadley, Massachusetts, USA, a restful walk with protection of peatlands and other delicate plants. Photo from USFWS, through public domain.

Heavy Metal Detection and Cleanup

Cleaning up heavy metals from waterways is one of the most important environmental problems facing Americans (and others) today (Trujillo *et al*. 1991). Such methods as chemical precipitation, ion exchange, reverse osmosis, and solvent extract have been widely used, but are less than desirable. Their metal removal is incomplete, they require large quantities of reagents or high amounts of energy, and they generate toxic sludge and waste products that require expensive and dangerous disposal. The U.S. Bureau of Mines is using ***Sphagnum*** (Figure 3) that has been immobilized in porous polysulfone beads. These are able to remove zinc, cadmium, and other metals selectively from zinc mine wastewater, reducing the concentrations to well below the national drinking water standards. Furthermore, the adsorptive capacity of the beads appeared to increase after the first few cycles.

The cation exchange ability of ***Sphagnum*** (Figure 3), with its walls packed with polyuronic acids, gives it unique properties unmatched by its tracheophyte counterparts, and often even by the connivances of humans. It serves well in an electrode for the detection of lead, offering a detectability level of 2 ng ml^{-1} (Ramos *et al*. 1993). The 10% moss electrode is easily regenerated by immersion in 0.05 M perchloric acid for only 60 seconds.

Now that the lead has been detected, one can remove it and other heavy metals with the biomass beads made of dried, ground ***Sphagnum*** (Figure 3) in a porous polysulfone matrix (Spinti *et al*. 1995). However, they seem to have lower capacity than other commercially available ion exchange resins.

Filtration

The ability of peat mosses to bind heavy metals and other substances on their cation exchange sites makes them ideal organisms for cleaning up a variety of heavy metals and organic compounds in liquids. I have used peat mosses to clean up creosote in a very small pond. The peat removed the toxicity and took the toxic substance with the peat when I removed the mosses. Before I used the mosses, the fish all died, even when fresh water sat in the pond for a month. After subsequently letting the mosses soak in the pond water for a month, the new fish survived.

Farmers may use both inorganic and organic (including ***Sphagnum***; Figure 3) amendments to reduce the loss of ammonia from liquid hog manure and to keep the hog pens fresh by controlling odors (Al-Kanani *et al*. 1992a, b)

Other forms of wastewater benefit from peat filtration. A counter-current system is used to purify water, with peat serving to both absorb and adsorb contaminants (Asplund *et al*. 1976; Brown & Farnham 1976; Coupal & Lalancette 1976). Even organic waste such as pentachlorophenol can be removed by using peat as a filter (Viraraghavan & Tanjore 1994). Peat us used to filter out heavy metals, microbes, pesticides, organic acids, oils, and odors (Turner 1993).

Oil Cleanup

Mele, in his book *Polluting for Pleasure* (1993), claims that 420 million gallons of oil from pleasure boating enter our waterways in America each year. This staggering number is equivalent to 40 Exxon Valdez disasters! Peat mosses are among the very best absorbents of the oil and can even be used to rescue birds (Figure 7) and other animals covered in oil. As early as 1972, D'Hennezel and Coupal recognized their utility for cleanup. They are readily available, and bales could be stored near a harbor, ready for small spills. Today, there are also commercial peat moss "fences" available from several sources, especially in Canada, to contain oil spills.

Figure 7. Sea bird covered in oil from Black Sea oil spill. Photo by Pauk, through Creative Commons.

One supplier advertises that Hydro-Weed (Figure 8), made from a blonde ***Sphagnum*** (Figure 3) peat from Newfoundland, is a lightweight, natural hydrocarbon absorbent (Hydro-Weed 2007). The processing sterilizes the plants and kills the insects. Hydro-Weed is currently used by all branches of the United States Navy, Army, National Guard, Marines, and Air Force.

Figure 8. This pile of Hydro-Weed, made with ***Sphagnum***, is a good absorbent of oil while repelling water. Photo from Hydro-Weed 2007.

Hydro-Weed is extremely effective at absorbing oil and other hydrocarbons. One pound will absorb 8-12 times its weight in medium weight oil, fifteen times more than clay absorbers! But it won't absorb water! Anyone knowing the ecology of ***Sphagnum*** (Figure 3) would immediately become skeptical, and I can only conjecture on this water-repelling shift. We know that oil and water don't mix. IF the oil is absorbed preferentially, then the oil would undoubtedly contribute to the loss of water absorption by actually repelling it. Furthermore, if dry peat is used, it would float, and so would the oil, so the oil would be contacted first and make the plants as repellent as a duck's back.

A further advantage of Hydro-Weed is that it will not release the oil. The company suggests putting it along a fencerow where microbes will break down the oil or other absorbed chemical, leaving the peat moss to benefit the soil. And a bird landing on the floating or discarded Hydro-Weed will leave without "a single drop of oil on its feathers."

The saturated Hydro-Weed can be put to even more valuable uses. It can be incinerated as fuel, contributing 7,200 BTU's per pound during incineration (excluding hydrocarbons). It is clean, generating only 0.42% of ash residual per pound after incineration. This makes it a good fuel for cement kilns and coal-generating fossil fuel plants.

Marcus (2002), in a science fair project, compared several materials [Sea Sweep, Spill Magic, saw dust, Enviro-Bond (a polymer that bonds to hydrocarbons), and peat moss] at two temperatures to determine which took the greatest weight of crude oil in salt water. When compared by weight of sorbent, at 6.6ºC the Enviro-Bond worked best, but at 21ºC the peat moss absorbed the most. Most of the sorbents worked best at 6.6ºC.

While this was just a science fair project, use of peat mosses has a sound basis in practice. Hunt (1995-2007, 2000, 2002-2007) reported the use of ***Sphagnum*** (Figure 3) from SpillSorb Canada Inc. to clean up an oil spill at the Dassen and Robben Islands off the coast of South Africa where 41% of the African penguins reside. First, the penguins themselves were dusted with peat dust, rendering them dry and safe to return to the water (Ark Enterprises Inc. 2004). Next, peat-based absorbents were used to clear oil from rocks (Crawford *et al*. 2000). Although the spill occurred on 23 June 2000, the shore was clean by 5 July that year (Hunt 1995-2007, 2000, 2002-2007). The hyaline cells of the ***Sphagnum*** leaves readily absorb the oil, up to

10 or even 20X the oven-dry weight of the moss. The ***Sphagnum*** also aids in the conversion of the oil to safe products. Rich in humic acids, it becomes a natural catalyst to aid in breaking down the hydrocarbon molecules of the oil; with the help of some microbes, it can aid the conversion of the oil to fatty acids, CO_2, and water. Peat Sorb is one such ***Sphagnum*** product (SANCCOB 2006).

Oclansorb Plus from Canada (Hi Point Industries 1991) is an oil-absorbent peat moss designed for application to surface oil and fuel spills in fresh and salt water marshes, wetlands, and any open water environment which cannot be efficiently cleaned by manual techniques. It blends a time-release system of peat moss that begins soaking up the oil within seconds, non-pathogenic bacteria bred specifically to metabolize petroleum hydrocarbons, N, P, trace nutrients, and pH buffers to enhance efficiency of bacterial degradation, and non-toxic gelling agents that facilitate adhesion of Oclansorb Plus to exposed tree roots, aquatic plants, and shoreline rocks.

In New Hampshire, the Department of Environmental Services made a novel use of peat moss. They rehearsed their response to an oil spill in Portsmouth's Great Bay Estuary (Dillon 2003), using peat moss and oranges to simulate the spread of the oil! The peat moss spread across the water like thin oil and the oranges simulated the bobbing tar balls, both without harming the environment.

The terrestrial environment is not immune to oil problems. A diesel oil spill in an Alaskan subalpine meadow had poor recovery after nine years, but the moss ***Racomitrium sudeticum*** (Figure 9) was one of the three species that survived (Belsky 1982). The moss was one of the few plants making the area green.

Figure 9. ***Racomitrium sudeticum***, a species that is able to survive an oil spill. Photo by Hermann Schachner, through Creative Commons.

Leaking crude oil production wells can create contaminated soils that must be cleaned up. For example, in McKean County, Pennsylvania, the use of fertilizers and leaf detritus or peat moss boosts the nitrogen content of the soils. This, combined with aeration by rototilling has been very successful in reducing total petroleum hydrocarbons (TPH) in soils. "Healing" is evident in a few weeks and the area can be replanted with grass seed the same season. The Maryland Department of the Environment (2004) suggests peat moss, among other things, for heating-oil cleanup. In New Zealand, Enviropeat™ is sold for cleanup of service stations, driveways, forecourts, maintenance areas, parking areas, refuelling areas, vehicle repair shops, ports & marinas, shoreline, and open sea oil spills (Enviropeat 2004). Unfortunately, using ***Sphagnum*** (Figure 3) to clean up large oil spills is not practical. Thus, spills like those in the gulf require other methods.

Fuel

The use of mosses for fuel is not just ancient history. Nearly half the world's peat production (Figure 10) is used for fuel (Figure 11-Figure 12), particularly in Scotland (Figure 13) and Ireland, providing the equivalent of 100-200 million tons of oil (UNERG report 1984). In Canada the peat deposits store more energy than do the forests and natural gas reserves combined (Taylor & Smith 1980). Nevertheless, the use of peat as fuel is down in Scotland, from 70,000 tonnes in 1955 to 20,000 tonnes in 1999 (Macleod 2006).

Figure 10. Peat extraction in East Frisia, Germany. Photo by Christian Fischer, through Creative Commons.

Figure 11. Peat mine with peat bricks for fuel. Photo by Paciana, through Creative Commons.

Figure 12. Peat fire. Photo by Cqui, through public domain.

Figure 13. Peat harvested in Lewis, Scotland. Photo by Wojsyl, through Creative Commons.

We might cringe that Ireland burns over 100 million tons of peat each year to generate power (Turner 1993), requiring large peatlands (Figure 14). What a scourge on the landscape! And it certainly does not renew at that rate, if ever. It is also used for waxes, resins, and oily materials for dyes and varnish and in treatment of leather.

Figure 14. Large peatlands like this one at Farwell, Michigan, USA, are rapidly disappearing due to development. Photo by Janice Glime.

At least it doesn't further pollute the environment. For example, in Minnesota it is used to remove chromium from power station wastes (Turner 1993), and it has been important in rescuing penguins in South Africa by cleaning up oil spills (Hunt 2004).

Peat is a promising replacement for our dwindling oil supplies, packing more than 8,000 BTU per dry pound, and is renewable when harvested carefully. It is such a clean-burning fuel that some have attributed the lovely complexions of Irish and Swedish women to use of peat as fuel (Drlica 1982). Its attractive feature as a fuel is that it is low in sulfur content, cleaner burning, and superior in heating value compared to wood, similar to lignite.

No longer restrained in use to the developing countries, liverworts and mosses are important sources of fuel in northern Europe, especially in Finland, Germany, Ireland, Poland, Russia, and Sweden. In Ireland, 25% of the fuel source is mosses (Richardson 1981). It serves not only to produce heat, but also electricity, with the former Soviet Union burning ~70 million tons and Ireland 3.5 million tons of mosses for that purpose in 1975 (Boffey 1975). If Hinrichsen (1981) was correct, the world should have been using peat in the equivalent of 60-70 million tons of oil by the year 2000.

Although peat is often considered to be a clean fuel, such is not the case with CO_2 emissions. Peat burning emits 106 g CO_2 MJ^{-1} whereas coal emits only 94.6 and natural gas only 56.1 g CO_2 MJ^{-1} (VTT 2004).

Peat is currently considered a slow renewable resource. Although peat is renewable, little of it has been harvested with a renewal plan in mind. Hence, many scientific studies are currently focusing on regeneration of various ***Sphagnum*** (Figure 3) species in the hope of restoring some of our lost peatlands. Unfortunately, little of it regenerates at the rate it is being used.

Hence, we need improved methods for harvesting, drying, and conversion to a burnable fuel (Lindstrom 1980). Although harvesting is easy, compared to that for coal, forests, and hunting for oil, we need to find ways that do not destroy the wetlands and convert them to non-peat-producing vegetation.

The Finns, in their attempt to become 40-50% self sufficient (Miller 1981) and provide a cleaner fuel (Johansson & Sipilae 1991), have suggested that placement of processing stations on the peatlands will reduce transport cost (Taylor & Smith 1980). They have introduced a de-watering process that produces dry pellets of partly carbonized peat (Taylor & Smith 1980). Finland is also exporting pulverized peat to northern Sweden, where it is used in industry and municipal heating, power generation, and oil burners of pulp and paper companies (Summerton 1981). However, for heating houses alone, replacement of light fuel oil with peat will require up to 6.2 million tons of peat pellets per year (Kinnunen *et al*. 1982). If this is reduced to only a 5% replacement of fuel oil, that consumption could be reduced to 310,000 tons per yr.

It took a coal miners' strike in 1903 to interest Americans to use peat as a fuel, but the cheaper availability of other fuels has prevented its widespread use (Thieret 1956). Nevertheless, planning for the future, the U. S. Geological Survey and other organizations have mapped North American peat deposits and estimated their extent (Miller 1981). This time it was an energy crisis with the possibility of diminished oil trade that fueled interest in peat fuel in the 1970's. In 1975, First Colony Farm in North Carolina began peat harvest to make methane and to

generate electricity; their land has an estimated 400 million tons of peat, enough to fuel a 400 megawatt power plant for 40 years (Carter 1978). The Minnesota Gas Company planned for its use of methane by applying for a long-term lease on 200,000 acres of peatland (Boffey 1975). Use of peats for production of methane eliminates the chopping that is required for other plants, and peat products can be used to produce ethylene, hydrogen, methanol, synthetic or natural gas, and low and intermediate BTU gas.

Ralf Pope (pers. comm. 12 July 2012) told me that there in an 860-acre peat mining operation in Deblois, Maine, USA (Figure 15-Figure 16). The Worcester Peat Company harvested peat there until ~2002 and used it to run a 22.8 megawatt peat-fired power plant. When the plant re-opens, they plan to use a mix of peat and septic sludge, billing it as green renewable power.

Figure 15. 860-acre peat mining operation of The Worcester Peat Company in Deblois, Maine, USA. Photo courtesy of Ralph Pope.

Figure 16. 860-acre peat mining operation by The Worcester Peat Company in Deblois, Maine, USA. Note the wood treads that minimize damage to the peatland by distributing the weight. Photo courtesy of Ralph Pope.

Peat in Construction

Whereas other mosses have played minor roles in construction, mostly for chinking, ***Sphagnum*** (Figure 17) has the potential to enter the arena big time (conservation issues aside). As early as 1903, the Swedes ground peat with asphalt to make a durable street pavement (Drlica 1982). Peat Crete, a mixture of peat with light concrete that is hydraulically pressed with Portland cement and water, provides a low-cost material that boasts easy sawing, nailing, casting, and molding, does not need to dry, is inflammable, and of low density (0.7 to 1.2 sp. gr.; 45-70 lb/ft^3) (Ruel *et al*. 1977). Its only negative quality is its low mechanical strength, but this seems more than balanced by its light weight for use in places where transportation is a problem. In dry places, flammability could be a problem.

Figure 17. ***Sphagnum magellanicum*** is a large moss that can be used in making various construction products. Photo by Janice Glime.

In June, 1972, Andrew Gilchrist, Chair of the Highlands and Islands Development Board at Bridge House, Bank Street, Inverness, Scotland, presented to the Right Honourable Gordon T. C. Campbell, Her Majesty's Secretary of State for Scotland, a report in which he referred to the possibility of production of Peat Crete as a means of improving the economy, stating: "We continue to watch over prospects for possible uses of peat, including the Building Research Centre's work on 'peatcrete.'" Unfortunately, or perhaps fortunately, a Google search does not indicate any commercial sources of this commodity.

In 1920, peat-based pasteboard and wrapping paper appeared in Michigan, USA, near Capac (Miller 1981). Peat boards have been used in chicken houses to help insulate them (Moore & Bellamy 1974).

Like many other mosses, ***Sphagnum*** (Figure 3) was used in chinking in log cabins (Lewis 1981), and the northern Europeans, living where peat is abundant to this day, stuffed it between the timbers of their houses to deaden sound (Thieret 1954). To this purpose, the Russians added slabs that they heated and pressed for insulation of refrigerators, and of course their houses (Sukhanov 1972; Ruel *et al*. 1977).

Peat then made its debut in place of particle board, as peatwood (Ruel *et al*. 1977). Dried ***Sphagnum*** (Figure 3) is blended with a phenolic resin and pressed into a heating mold; it offers quick hardening, attractive texture, good strength, easily nailed, screwed, and glued, and light weight (40-60 lb ft^{-3}). Other construction materials include the ultra-light peatfoam (peat moss and foamed resin) and

peatcork (made from the coarse fraction of peat (Ruel *et al*. 1977).

Harvesting Peat and Peatland Destruction

In 1991, a survey of Finnish peatlands revealed that only 26% of the peatlands remained in natural condition (Eurola *et al.* 1991). The majority are drier, less productive, and more forested than just 30 years ago. Most of the loss of peatlands is due to forestry (Finland) and agriculture (France) (Francez & Vasander (1995), although peat harvesting for fuel is a growing concern in northern Europe. In North America, most of the harvest is for horticulture (Ferland & Rochefort 1997). This horticultural loss began early in the 20th century, with the practice of leaving the peatlands to regenerate in their own way when the mining operation was over (Lavoie & Rochefort 1996). Upon examining a typical "regenerating" peatland in Quebec, Lavoie and Rochefort found that although the block-cut trenches had more than 50% cover and were occupied by typical peatland species, ***Sphagnum*** (Figure 17-Figure 19) was much more common in the natural conditions than in the cutover peatland. They concluded that this location was not returning to a functional peatland ecosystem.

Loss of peatlands affects the forestry species that were growing there. For example, in the New Jersey pinelands, *Chamaecyparis* swamps may suffer from loss of ***Sphagnum*** (Figure 3) cover because the tops of hummocks become more prone to drought, making them less suitable for seedling regeneration (Ehrenfeld 1995).

Even large browsers like caribou depend on refuge in peatlands (Dyer *et al*. 2001), but these losses have ramifications far beyond the simple loss of peatlands. Their loss is a contributor to global warming. Reduction in peatlands means that less carbon will be tied up in that carbon sink, instead going to rapidly cycling grasses. Furthermore, it leads to greater decomposition of accumulated peat, releasing yet more greenhouse gases. Ohlson and Økland (1998) found that it can take 40 years of peat accumulation before any significant amounts are lost through decay, resulting in a net carbon sink. In hummocks of ***Sphagnum fuscum*** (Figure 18) and ***S. rubellum*** (Figure 19), carbon accumulation exceeded 2 g dm^{-2} yr^{1} during a 50-year growth period.

Figure 18. ***Sphagnum fuscum***, a hummock species that takes 40 years to recover from harvesting. Photo by Oscar Gran, through Creative Commons.

Figure 19. ***Sphagnum rubellum***, a hummock species that takes 40 years to recover from harvesting. Photo by B. Gliwa, through Creative Commons.

"Harvest" is usually a misnomer for what is more accurately called peatland mining. With a vertical accumulation rate of 10-40 cm per thousand years in Finnish peatlands, repeatable harvests must be discussed in geologic time scales (Crum 1988). Consequently, peatlands the world over are diminishing. Knight (1991) bemoaned the dwindling number of peat bogs in Britain due to exploitation for horticulture.

Others have more encouraging numbers, considering peat formation of ~1-2 mm per year (note, that is not rate of growth). Using this estimate, they consider that harvested (not mined) peat can be replaced in ~20 years. In Ireland, 1 million m^3 of peat is used for horticulture and another 7-9 million pounds are exported yearly (Richardson 1981), not to mention the use for fuel that seriously threatens that country's 3 million acres of peatland (Drlica 1982). Yet 90% of the world's marketed peat comes from Wisconsin, USA, primarily from Jackson and Monroe Counties (Epstein 1988). The series of pictures below shows one company's attempt to maintain a sustainable crop that can be harvested again in about ten years (Figure 20-Figure 27). But this is a labor intensive method that most "miners" would shun.

Figure 20. At this peat harvesting operation in Wisconsin, USA, peat can be reharvested in about a 10-year cycle. The rake being used is wooden and pulls both ***Sphagnum*** and accompanying sedges. Photo by Janice Glime.

Figure 21. A tractor with a wooden tread pulls the wagon on which peat is loaded, minimizing damage to the peatland. Photo by Janice Glime.

Figure 22. A full wagon of peat is ready to be spread for drying. Photo by Janice Glime.

Figure 23. Freshly harvested peat is spread to dry. Photo by Janice Glime.

Figure 24. Spent tires will be used to anchor the mosses. As mosses dry, they become light-weight and can blow away. Photo by Janice Glime.

Figure 25. This packaging equipment is used for bagging the dry mosses ready for sale without need for a building or power. Photo by Janice Glime.

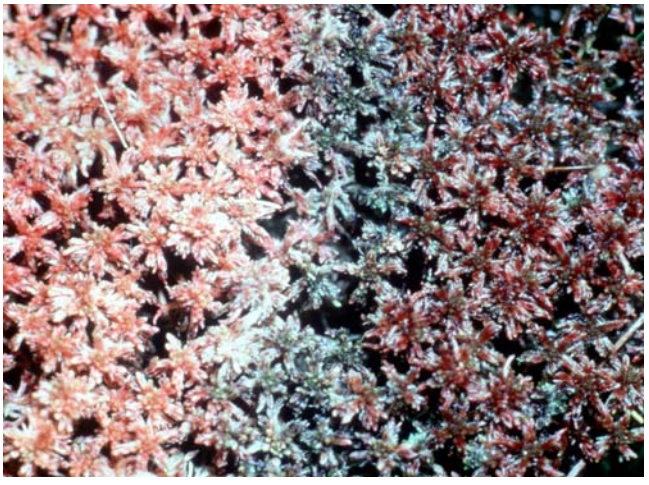


Figure 26. This ***Sphagnum*** is infected with fungus and could cause sporotrichosis. Photo by Janice Glime.

Figure 27. This mined peatland in Maryland, USA, exposes the peat profile. Photo by Janice Glime.

Climate Reconstruction

Peatlands are history books, recording for us what has occurred long before humans considered maintaining a written record (Grosse-Brauckmann 1979; Janssens 1988; Klinger *et al*. 1990). While this often has only heuristic value, it can be invaluable in attempting to interpret our tempestuous climatic variation in the present decades. Whereas fossil and other paleoecological records are scanty and difficult to interpret in other habitats, buried peat can provide us with clear chronosequences of vegetation, giving us indications of alternating dry and wet periods and even of warming and cooling. The pattern of cores can easily be calibrated between locations (Ellis & Tallis 2000). The peat stratigraphy of a blanket mire in Scotland, coupled with radiocarbon dating, indicates eight wet shifts that began about 3250, 2550, 2150, 1400, 1150, 875, 600, and 325 years ago. Seven of these correlate closely with similar indications from peat in Britain and Ireland.

Likewise, in the coastal region of Maine, USA, bryophytes, along with pollen, diatoms, and other plant fossils, have been useful in reconstructing past conditions (Tolonen & Tolonen 1984). In this case, the bryoflora support the other taxa to indicate that the flora is predominately that restricted to calcareous habitats.

Jonsgard and Birks (1995) were able to reconstruct the climate (moisture, temperature, light availability, and *p*H) from partially decomposed fossil mosses at Krakenes, western Norway, by comparing the taxa with bryophyte communities at various present-day altitudes. They found that mosses are able to colonize new habitats as rapidly as their tracheophyte counterparts. The advantage to using mosses for this purpose is that they provide evidence for microhabitats that cannot be obtained from tracheophyte fossils.

Jonsgard and Birks (1995; Birks 1982) also used fossil mosses to characterize late-glacial climate, *p*H, light availability, and continentality of Norway, using the mosses as ecological indicators.

Glaciers are often the site of modern dispersal of moss fragments. This wide, smooth surface also permitted ease of travel of fragments that became fossils in the frozen water, preserving the communities surrounding them. Thus, ice cores serve as historic records of the surrounding communities, much as peatlands do in other areas (Lindskog & Eriksen 1995).

While studying the Quelccaya ice cap in Peru, Ohio State University glaciologist Lonnie Thompson found mosses that had appeared out of ice laid down 5200 years earlier (Rozell 2005). This date of preserving a green moss coincides with the age of the Ice Man found recently in a melting ice field in the Austrian Alps. Thompson used the moss example to demonstrate the rapid response of a sensitive environment. When he returned to the site, he found more of the exposed mosses. Upon sending them to Woods Hole Oceanographic Institute for dating, he learned that one of them was 50,000 years old! In disbelief, Thompson sent the moss to Lawrence Livermore National Laboratory in California. Results were the same. Thompson reasoned that the only way these 5200-year-old mosses and the 50,000-year-old ones could appear together is that the ice field has not been smaller than it is today in the last 50,000 years and that it had to be colder than it is today for the past 50,000 years! Indications are that the ice cap is melting 40 times faster than it was in 1963.

Graves, Burial, and Preservation

Tombstones more than 100 years old typically are encrusted with lichens and mosses (Figure 28). In a recent bryonet discussion, Sean Edwards (Bryonet on 20 April 2005) sought a way to expedite this process (2005). In an old churchyard, strips of marble on a tomb had been replaced and no longer matched the weathered and lichen/moss-covered older marble. He was seeking ways to encourage the mosses and lichens to grow to age the stone.

Figure 28. Moss ***Schistidium apocarpum*** and lichens on cemetery marker, with the moss mostly established in the indentations. Photo by Janice Glime.

Burial ceremonies seem to have been a part of human culture for a long time. Hence, it might be expected that the resourceful human found mosses to be a suitable way to preserve the bodies of loved ones. In the Canary Islands, the Guanche mummy (1380 ± 80 years B.P.) was preserved with the epiphyte ***Neckera intermedia*** (Figure 29) in its abdominal cavity (Horne & Ireland 1991). However, an earlier report of a frozen Eskimo woman with moss in her lungs seems instead to have been the result of inhalation of the moss as she was being accidentally buried alive (Zimmerman & Smith 1975; Horne & Ireland 1991).

Figure 29. ***Neckera intermedia***, the moss used in the abdominal cavity to preserve the Guanche mummy. Photo by Jan-Peter Frahm, with permission.

In one case, a strange coincidence got a man to confess to the murder of his wife (Dente 1997). Police in Macclesfield, England, had investigated reports that Peter Reyn-Bardt had boasted of murdering his wife 23 years earlier and buried her dismembered body in his backyard. But the police could find no such evidence. However, the backyard bordered a peat excavation site where only a short time later an excavation uncovered a well preserved skull of a 30-50-year-old female. After the man confessed to the murder of his wife, the Oxford University Research Laboratory for Archaeology determined that the skull was actually 1660-1820 years old!

More recently, it appears that mosses have been used to clothe the last resting place. In Siberia 2,500 years ago, large mosses like ***Pleurozium schreberi*** (Figure 30), ***Ptilium crista-castrensis*** (Figure 31), and ***Rhytidium rugosum*** (Figure 32) were used with sheets of bark to line the roofs of tombs (Rudenko 1970). In Alaska and Japan, they have provided a burial bed (Bland 1971; Ando & Matsuo 1984) with larger mosses such as the pendant ***Aerobryopsis subdivergens*** (Figure 33) (Iwatsuki & Inoue 1971).

Figure 30. ***Pleurozium schreberi***, a moss once used in Siberia with sheets of bark to line the roofs of tombs. Photo by Janice Glime.

Figure 31. ***Ptilium crista-castrensis***, a moss once used in Siberia with sheets of bark to line the roofs of tombs. Photo by Janice Glime.

Figure 32. ***Rhytidium rugosum*** is a pleurocarpous moss that has been used to line the last resting place of humans in Siberia. Photo by Michael Lüth, with permission.

Figure 33. ***Aerobryopsis subdivergens***, one of the large mosses that has been used as a burial bed in Japan. Photo through Creative Commons.

The expansive peatlands of northern Europe seem to have provided a grave for hundreds of men, taking us back to the days of Roman rule – The Iron Age (Glob 1969). At first, these men were assumed to be peat cutters who had in recent years been trapped in the muck (Robinson 2002). But with 1500 bodies (Robinson 2002), speculation about the reasons for the early demise of these "bogmen" soon abounded (Painter 1991). Sanders (2002) relates that the Nazis used them as propaganda, claiming that two men found together in a Dutch peatland had been executed for their crime of homosexuality, whereas Heinrich Himmler was more cautious in a 1937 speech, stating that the deaths had been "not a punishment, but simply the termination of such an abnormal life."

In 1835, a well preserved woman in a Danish moor was identified as Queen Gunhild, a monarch in a Norse legend (Sanders 2002). When the Danish King, Frederick VI, learned of this find, he prepared her for a royal burial beside Danish royalty in a churchyard. However, carbon dating belies the royalty theory, placing the lady in a much earlier time.

In Tollund Fen in Bjaeldskor Dale in Denmark, two brothers (peat cutters) were surprised in 1952 by a body that surely was a recent victim of an onerous crime (The Discovery of Tollund Man). On closer inspection, the man had a twisted leather noose about his neck, but his face bespoke peace, as if death was his salvation (Figure 34-Figure 35). Police work turned to archaeologists who determined the "crime" to be 2000 years old. That look and the grains in his stomach have led many to conclude that he was a holy man sacrificed and preserved in the peat.

Figure 34. Tollund Man who lived in the 4th century BC. This "bogman" was perfectly preserved for centuries by the tannic acid in the peatland. Photo by Seamus Heaney, through Creative Commons.

Figure 35. Tollund Man head with rope around his neck. Photo by Seamus Heaney, through Creative Commons.

The Tollund Man

Seamus Heaney

I

Some day I will go to Aarhus
To see his peat-brown head,
The mild pods of his eye-lids,
His pointed skin cap.

In the flat country near by
Where they dug him out,
His last gruel of winter seeds
Caked in his stomach,

Naked except for
The cap, noose and girdle,
I will stand a long time.
Bridegroom to the goddess,

She tightened her torc on him
And opened her fen,
Those dark juices working
Him to a saint's kept body,

Trove of the turfcutters'
Honeycombed workings.
Now his stained face
Reposes at Aarhus.

II

I could risk blasphemy,
Consecrate the cauldron bog
Our holy ground and pray
Him to make germinate

The scattered, ambushed
Flesh of labourers,
Stockinged corpses
Laid out in the farmyards,

Tell-tale skin and teeth
Flecking the sleepers
Of four young brothers, trailed
For miles along the lines.

III

Something of his sad freedom
As he rode the tumbril
Should come to me, driving,
Saying the names

Tollund, Grauballe, Nebelgard,
Watching the pointing hands
Of country people,
Not knowing their tongue.

Out here in Jutland
In the old man-killing parishes
I will feel lost,
Unhappy and at home.

Copyright

In the same year, 1952, Grauballe Man (Figure 36) was found in a similar manner by peat cutters (Grauballe Man 2002). His body was dated to about 210-410 AD. His stomach was full of porridge of 63 different grains, but no fruits or leafy green material, no meats, suggesting a winter meal or a poor harvest? A gruel with that recipe tastes horrible (Lienhard 1988). Unlike the Tollund Man, his face expressed terror and pain (Grauballe Man 2002). His throat had been cut and his skull was fractured. Later, in 1984, Lindow Man was found under similar circumstances in England (Lindow Man 2002). Like the Grauballe Man, his skin betrayed a man of high rank, not one who labored. He was at least 2000 years old, yet preserved well by the peat. He had died a violent death, with two blows to the head, his throat cut, and a thong for hanging. Was he a human sacrifice, or victim of a brutal murder?

Figure 36. Grauballe Man as he was discovered. Photo through public domain.

As history unfolds and great minds conjecture, it seems that Druid priests, important in the Celtic tribes, may have died in this manner, chosen as a sacrifice to the Earth Goddess (Robinson 2002). The Lindow Man had a last meal consisting only of a small cake containing bits of charred flour that would have required 400°C – much hotter than one would ever consider for baking. Archaeologists Ann Ross and Don Robbins speculate that this cake was used in a lottery to determine who should be sacrificed – perhaps explaining the look of pain and terror! Parts of such a ceremony still existed in England in the 20th century, but without the ultimate sacrifice.

Peatlands have a number of qualities that make them ideal preservation sites (Robinson 2002). Although the low oxygen and high acidity discourage most bacteria, it is the peat itself that imparts the preservation. The **Sphagnan** resulting from phenolic breakdown binds the sparse minerals in the water. Lacking their essential minerals, bacteria are unable to grow. Much like the tanning of cowhide to leather, the body is turned to leather by the tannins from the ***Sphagnum*** (Figure 3), preserving wool and leather garments along with the skin. The calcified bone, however, loses its calcium in the acid water, becoming rubbery and crumpled under the weight of the peat. And linen, faring less well than wool, disappears due to decay, accounting for the Tollund Man wearing nothing but his leather belt and hat when he re-appeared in the 20th century.

Sphagnum (Figure 3) even has a modern use in commemoration of the dead. In Wisconsin, USA, thousands of cemetery wreaths are made. These usually have various decorations and flowers attached to them, with the ***Sphagnum*** peat retaining water to keep them fresh.

Anthropology and Archaeology

An archaeologist investigating Paleolithic settlements reported finding animal and human bones in cave sediments (Patxi Heras & Marta Infante, Bryonet, 5 April 2006). These are often eroded with shallow depressions and holes. The zoologist she consulted disclaimed the marks, suggesting they were created by plant growth. Since there is typically abundant moss growth in the cave entrances, the archaeologist considered that they could make the marks. While no one could confirm that mosses make such marks on bones, we do know that mosses in the **Splachnaceae** (Figure 37), among others, can grow on bones.

Figure 37. ***Tetraplodon angustatus*** on caribou skull, Jasper, Canada. Photo by Janice Glime.

Peat mosses (***Sphagnum*** species; Figure 3) are well known for their ability to preserve the dead (Folger 1992). When a giant mastodon (Figure 38) was found in Ohio, USA, it likewise had been preserved in ***Sphagnum*** for 11,000 years. It was so well preserved that its last meal remained.

Figure 38. Burning Tree Mastodon excavation, Heath, east-central Ohio, USA, where that animal was preserved in peat. Photo by James St. John, through Creative Commons.

Hawes *et al*. (2002) attempted to use bryophyte growth markers to hindcast ice melt patterns in Arctic lakes, but they were unable to establish any correlation, concluding that the relationship was more complex.

Forensics

I have always loved mystery books, but I never dreamed I could be part of a criminal investigation, especially not a likely murder. But one day I opened my email and found a plea for help from a detective from one of the Michigan police departments. He introduced me to the case in which a father had left with his baby daughter and she had never been seen again. He had been convicted for unlawful imprisonment, but the police were seeking evidence that would help them find the child and convict him of murder. His missing daughter was believed to be discarded in a swamp. This belief was based on items adhering to the shoes of the father. These included the sedge *Carex*, a 2-needle pine, a fern, and moss, all of which are known from a wet conifer environment. I wasn't able to participate in the search, but I referred them to Matt von Konrat, who was able to identify ***Sphagnum affine*** (Figure 39), ***Warnstorfia fluitans*** (Figure 40), and ***Plagiomnium rostratum*** (Figure 41) from the clothing. This enabled the botanists to narrow the search to one location. A search, including von Konrat on the team, ensued in wetlands that matched the known plants from the shoes, but the baby was never found.

Figure 39. ***Sphagnum affine***, a moss that provided forensic evidence in the case of a missing child. Photo by Michael Lüth, with permission.

Figure 40. ***Warnstorfia fluitans***, a moss that provided forensic evidence in the case of a missing child. Photo by Michael Lüth, with permission.

Figure 41. ***Plagiomnium rostratum***, a moss that provided forensic evidence in the case of a missing child. Photo by Michael Lüth, with permission.

In Finland, a man disappeared and his body was later found in a woodland (Korpelainen & Virtanen 2003b). Three suspects were arrested, but there was no direct evidence to connect them. However, the bryophytes ***Brachythecium albicans*** (Figure 42), ***Calliergonella lindbergii*** (Figure 43), and ***Ceratodon purpureus*** (Figure 68, Figure 95) were identified from their shoes, clothes, and also in their car. Using DNA fingerprinting analyses on the two pleurocarpous species (***B. albicans***, ***C. lindbergii***) that primarily reproduce clonally, they were able to determine that these two species were likely to have originated from populations of the same two species found near the body (Korpelainen & Virtanen 2003a, b). Based largely on the moss evidence, the three suspects were convicted.

Figure 42. ***Brachythecium albicans***. This moss species adhered to clothing of three murderers and helped to convict them. Photo by Janice Glime.

Figure 43. ***Calliergonella lindbergii***. This moss species adhered to clothing of three murderers and helped to convict them. Photo by Bob Klips, with permission.

Figure 45. ***Climacium dendroides*** from Beppo Japan, a species tested for its genetic variability among locations. Photo by Janice Glime.

Following that court case, Virtanen and Korpelainen were able to obtain a grant to design species-specific microsatellite markers for a group of bryophytes that are globally common so that they can be used in forensic applications (Virtanen *et al*. 2004). They selected 12 species for which they obtained 20 specimens to represent the entire distribution area of each species, thus representing the range of genetic variation. The selected species were the mosses ***Aulacomnium palustre*** (Figure 44), ***Brachythecium albicans*** (Figure 42), ***Climacium dendroides*** (Figure 45), ***Dicranum polysetum*** (Figure 46), ***Hylocomium splendens*** (Figure 47), ***Plagiomnium cuspidatum*** (Figure 48), ***Pleurozium schreberi*** (Figure 30), ***Racomitrium microcarpon*** (Figure 49), ***Rhytidiadelphus squarrosus*** (Figure 50), and ***Sphagnum fuscum*** (Figure 18), and the leafy liverworts ***Plagiochila asplenioides*** (Figure 51) and ***Ptilidium ciliare*** (Figure 52).

Figure 46. ***Dicranum polysetum*** from Michigan, USA, a species tested for its genetic variability among locations. Photo by Janice Glime.

Figure 44. ***Aulacomnium palustre***, a species tested for its genetic variability among locations. Photo by Tim Waters, through Creative Commons.

Figure 47. ***Hylocomium splendens*** from Michigan, USA, a species tested for its genetic variability among locations. Photo by Janice Glime.

Figure 48. ***Plagiomnium cuspidatum*** from Europe, a species tested for its genetic variability among locations. Photo by Michael Lüth, with permission.

Figure 49. ***Racomitrium microcarpum*** with capsules, from Europe, a species tested for its genetic variability among locations. Photo by Michael Lüth, with permission.

Figure 50. ***Rhytidiadelphus squarrosus*** near Swallow Falls, Wales, a species tested for its genetic variability among locations. Photo by Janice Glime.

Figure 51. ***Plagiochila asplenioides***, a leafy liverwort species tested for its genetic variability among locations. Photo by Tim Waters, through Creative Commons.

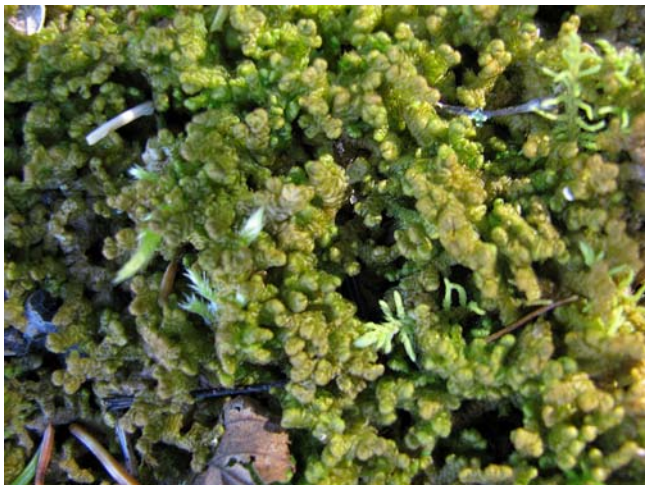
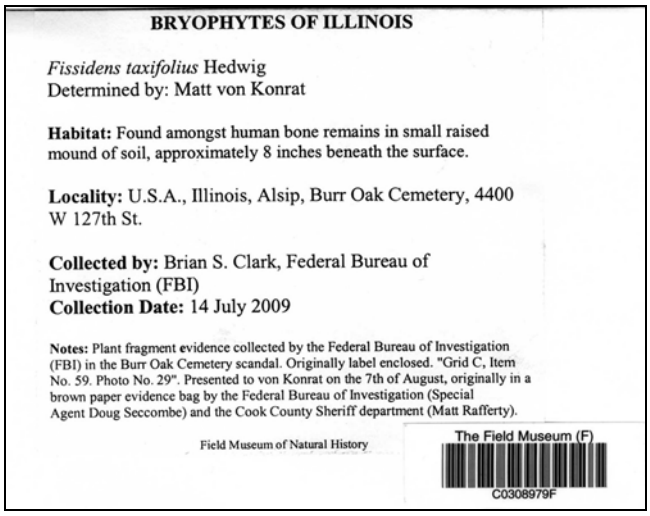


Figure 52. ***Ptilidium ciliare*** from Michigan, USA, a species tested for its genetic variability among locations. Photo by Janice Glime.

In another case, the FBI was interested in bryophytes in the soil covering a number of bodies that had been relocated from their graves. More than 200 bodies were discovered in shallow graves outside the cemetery. The FBI alleged that the cemetery workers had dug up the bodies and relocated the remains so that they could resell the graves at an historic African-American cemetery. However, some of the defendants claimed that the bodies had been moved before they began working there. Thus, it was important to determine when the relocation occurred. The anthropologist Anne Grauer discovered something green on some of the bodies ~20 cm beneath the surface and determined it to be a moss. The FBI then delivered the moss to bryologist Matt von Konrat at the Chicago Field Museum (Figure 53). He was able to identify it as ***Fissidens taxifolius*** (compare Figure 54 to Figure 55), but the important question was how long the buried mosses had been there. How long does a buried moss stay green? With the help of a physiologist, von Konrat experimented with the moss and also compared it to herbarium specimens of various ages (Figure 56). Ultimately he determined the moss to have been buried alive between six months and two years earlier, refuting the claim that the bodies had been moved after employment began for the accused.

Furthermore, no ***Fissidens taxifolius*** could be found growing near the bodies, but it did grow in the main cemetery. Matt von Konrat (Figure 56) was declared an expert witness by the court and the moss evidence led to convictions.


BRYOPHYTES OF ILLINOIS

Fissidens taxifolius Hedwig
Determined by: Matt von Konrat

Habitat: Found amongst human bone remains in small raised mound of soil, approximately 8 inches beneath the surface.

Locality: U.S.A., Illinois, Alsip, Burr Oak Cemetery, 4400 W 127th St.

Collected by: Brian S. Clark, Federal Bureau of Investigation (FBI)
Collection Date: 14 July 2009

Notes: Plant fragment evidence collected by the Federal Bureau of Investigation (FBI) in the Burr Oak Cemetery scandal. Originally label enclosed. "Grid C, Item No. 59. Photo No. 29". Presented to von Konrat on the 7th of August, originally in a brown paper evidence bag by the Federal Bureau of Investigation (Special Agent Doug Seccombe) and the Cook County Sheriff department (Matt Rafferty).

Field Museum of Natural History

The Field Museum (F)
C0308979F

Figure 53. ***Fissidens taxifolius*** forensic label in material delivered by FBI to the Field Museum. Photo courtesy of Matt von Konrat.

Figure 54. ***Fissidens taxifolius*** found with buried bodies that had been illegally relocated from the cemetery. Photo courtesy of Matt von Konrat.

Figure 55. ***Fissidens taxifolius*** in fresh condition such at that found in the cemetery. Photo by David Holyoak, with permission.

Figure 56. Matt von Konrat looking for comparison specimens of ***Fissidens taxifolius*** in the Herbarium at the Chicago Field Museum. Photo courtesy of Matt von Konrat.

One of the uses of plants in forensics is to establish the "post mortem interval (PMI)." Cardoso *et al*. (2009) found bryophytes to be useful in determining the time of death of an adult male in Portugal in an advanced state of skeletonization. The skeleton had green algae, bryophytes, and shrub roots in, around, and through the remains. The bryophytes and shrub roots were aged at three years, making the remains at least three years old. Time to colonization and state of decomposition of the remains put death at six years earlier, coinciding with the time the person went missing.

In another case, the aquatic moss ***Leptodictyum riparium*** (Figure 57) was used to estimate the PMI of skeletal remains in a wooded area in Central Italy (Lancia *et al*. 2013). Lacking specific growth rates for ***L. riparium***, the authors used the known rate for ***Hypnum cupressiforme*** (Figure 58), a moss with similar structure and growth habit. By counting the annual segments of the stem, they determined the moss to be 24-30 months old, narrowing the search for missing person records to those known to be missing for at least 2.5 years.

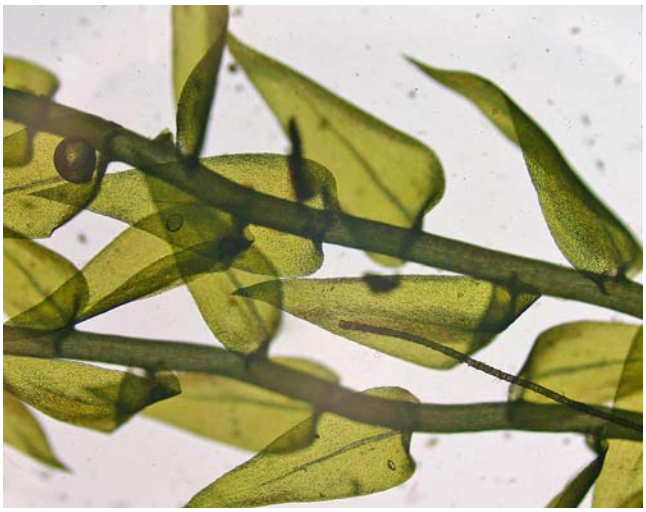


Figure 57. ***Leptodictyum riparium***, a moss used to help identify the body of a missing person. Photo by Tan Sze Wei, Aquamoss website <www.aquamoss.net>.

Figure 58. ***Hypnum cupressiforme*** var. cupressiforme, a moss with a growth rate assumed to be similar to that of ***Leptodictyum riparium***. Photo by David Holyoak, with permission.

Bryophytes can accomplish their own form of DNA fingerprinting (Korpelainen & Virtanen 2003a). Mosses can be used in much the same way as tracheophytes in crime investigation. Virtanen and coworkers (2004) are developing protocol for linking patches of bryophytes from the crime scene with fragments found on a suspect. Their approach is to find specific microsatellites to identify globally common bryophytes. Many species fragment easily and stick to clothing, making DNA analysis possible long after the event of fragmentation. Such evidence can tie the suspect to the scene of a crime.

Bryophytes could be useful forensic tools, but do we know enough about them, or is there still much work to do? Ann Mills (Bryonet 17 August 2011) reports identifying ***Brachythecium rutabulum*** (Figure 59) growing "in profusion" around an area where a human skeleton was discovered. To be useful forensically, we need to know how fast this moss might grow over the skeleton in this red spruce (*Picea rubens*) forest. In this case, Furness and Grime (1982) give us some information on growth rate of ***B. rutabulum***. Rod Seppelt (Bryonet 17 August 2011) adds that this species is an opportunist that propagates easily from fragments. To this, Steve Newmaster (Bryonet 18 August 2011) added observations from the long-term biodiversity research plot in Ontario, Canada. There ***Brachythecium rutabulum*** colonizes disturbed areas on organic soil, remaining there for several years. The mean increase per year is ~15% in southern Ontario (285 plots).

If we are to use bryophytes as a regular forensic tool, we need to determine how well they adhere to clothing, especially footwear, and how long the DNA can remain before breakdown destroys it. Virtanen *et al*. (2007) set out to contribute to answering these questions. Sixteen persons walked outdoors wearing rubber boots or hiking boots to determine what would adhere to the footwear. All plant fragments were collected after 24 hours of wear. In a second experiment, fresh bryophyte material from nine species was stored in a shed in adverse conditions for 18 months, and then DNA was extracted and subjected to genotyping. Both experiments supported the usability of bryophytes for forensics. Footwear did indeed collect bryophytes, and the bryophytes remained despite the wearer walking on dry ground and roads after walking on the bryophytes. And the DNA was still in good condition after 18 months of unfavorable storage conditions.

Figure 59. ***Brachythecium rutabulum***, a moss used to determine how long a corpse had been at that location. Photo by Michael Lüth, with permission.

Fuselier *et al*. (2011) used a forensic theme to make an investigative lab for Fuselier's students. The students had to pose the question, evaluate the evidence, and report the results. She based the study on Virtanen *et al*. (2007) and Korpelainen and Virtanen (2003a). The students learned how to use bryophytes in forensics and developed proficiency in DNA isolation, polymerase chain reaction, gel electrophoresis, capillary electrophoresis, and genotyping. The students paid more attention to accuracy in their methods than in standard labs. The researchers found that the students who participated in the bryophyte forensic lab performed well on content-based assessment (Figure 60) and exhibited positive attitudes toward the experience, indicative of engaged learning.

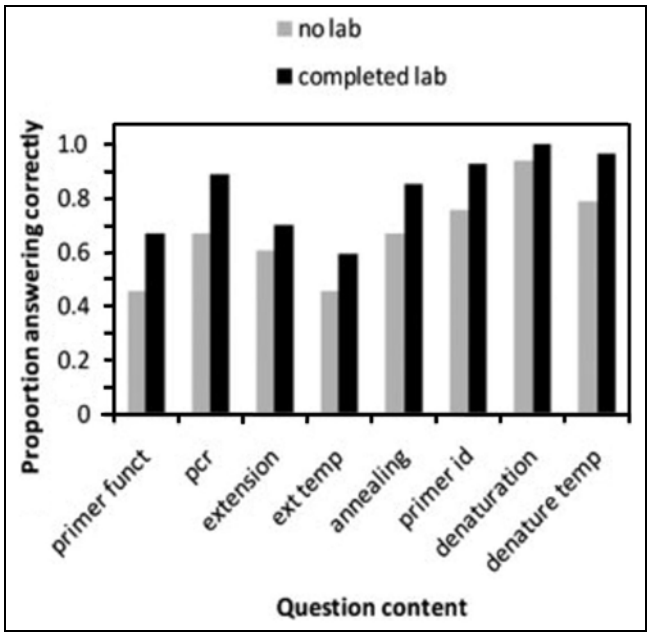


Figure 60. Student performance after bryophyte forensic lab, compared to performance of students who did not have the lab. Modified from Fuselier *et al*. 2011.

Archaeological Preservation

A recent recommendation for the use of ***Sphagnum*** (Figure 3) extracts is in the preservation of artwork (Zaitseva 2009). Extracts of polysaccharides (**Sphagnan**) were tested first on 17 fungal species and several bacteria species that could be found on ethnographic museum objects and archaeological objects from Arctic excavations. The bacteria ***Escherichia coli*** (Figure 61) and ***Pseudomonas aeruginosa*** (Figure 62) were negatively affected, whereas ***Staphylococcus aureus*** (Figure 63) was unaffected.

Twelve of the fungal species were inhibited (Zaitseva 2009). In one experiment, 1 ml of the nutritious broth with 40µl of 3% solution of polysaccharides in water killed 10,000 fungal spores in 6 hours. The Sphagnan was then added to conservation waxes as a preservative. With three weeks of exposure, the wax alone experienced a 44% consumption by the fungus *Aspergillus* (Figure 64). But when ~0.1% Sphagnan was included in the wax mix, the weight loss from the wax was only 4%. Zaitseva recommended using Sphagnan in art conservation. Additional discussion on the antibiotic properties of bryophytes are in the Chapter on Medicine in this volume.

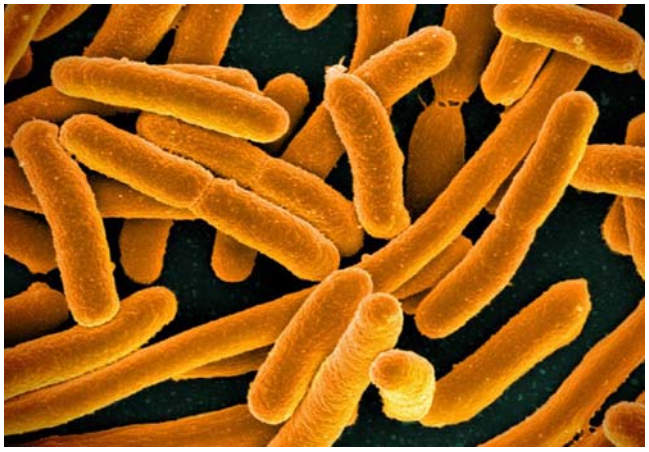


Figure 61. ***Escherichia coli***, a bacterium that is negatively affected by ***Sphagnum*** extracts, thus permitting preservation of archaeological artifacts with these extracts. Photo by NIAID, through Creative Commons.

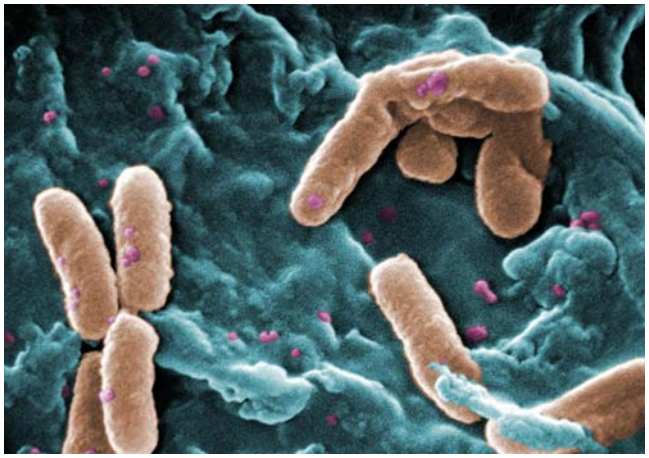


Figure 62. ***Pseudomonas aeruginosa***, a bacterium that is negatively affected by ***Sphagnum*** extracts, thus permitting preservation of archaeological artifacts with these extracts. Photo by Janice Haney Carr, through public domain.

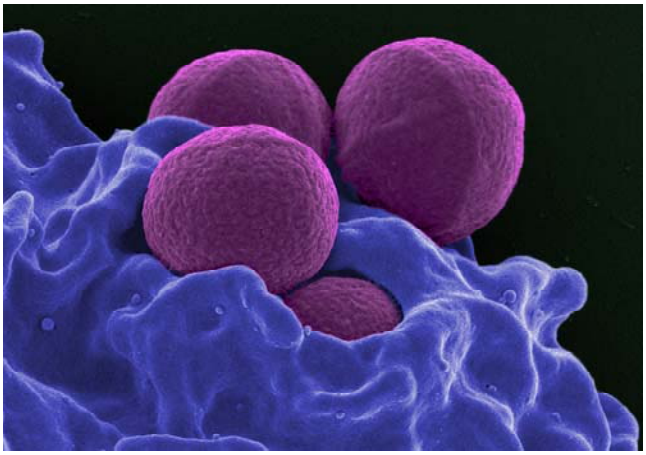


Figure 63. ***Staphylococcus aureus***, a bacterium that is not affected by peat extracts. Photo by NIAID, through Creative Commons.

Figure 64. ***Aspergillus fumigatus***. The genus ***Aspergillus*** was inhibited by Sphagnan and helps to preserve the waxes in art conservation. Photo through Creative Commons.

Erosion Control

The role of bryophytes in erosion control is well known (Figure 65), and several people have considered their commercial use along roadsides and other steep slopes through transplantation or propagation from fragments.

Figure 65. Erosion control on steep streamsides is an important use for bryophytes, both naturally, and on manmade slopes along canals or roads. Here, naturally occurring ***Polytrichum*** does the job. Photo by Janice Glime.

On dunes, seaside bluffs, and other areas where tourists often disturb the clinging vegetation, few plants, commercial or natural, survive the unstable conditions. Nevertheless, certain mosses may cling there when most other plants have been destroyed. Michel Chiaffredo and coworkers have a patent for Procédé BRYOTEC (BRYOTEC Process) that uses bryophytes instead of tracheophytes to stabilize such fragile sites (Chiaffredo 2007). The company MCK Environnement, using the BRYOTEC Process, has managed to restore, in only five years, the indigenous vegetation of a cliff top in a maritime setting in the Vendée region of France (Figure 66), where the tourist trampling had completely eradicated the original vegetation. This restoration involved the introduction of bryophytes with a small number of seeds from the native vegetation.

Figure 66. Restoration of a trampled cliff using a mix of bryophytes and other naturally occurring plants. Photo courtesy of Michel Chiaffredo.

The association ***Ceratodonto-Polytrichetea piliferi*** (Figure 67-Figure 68) (Dierßen 2001) is one that has proved particularly successful in helping to restore lost vegetation on a disturbed site.

Figure 67. Dry ***Ceratodon purpureus*** with ***Polytrichum piliferum*** (mostly at lower left), an association that has helped to restore vegetation on a disturbed site. Photo by Janice Glime.

Figure 68. Wet ***Ceratodon purpureus*** with capsules at left and ***Polytrichum piliferum*** at middle right. Photo by Michael Lüth, with permission.

In France, one may observe granitic embankments along a highway with the grass *Festuca ovina duriuscula* enduring the summer sun, but only in crevasses where mosses share the space. Perhaps the moss is necessary to provide sufficient moisture for seed germination of the grass (see Figure 69).

Figure 69. *Festuca ovina guestfalica* established in a crevice. The subspecies *Festuca ovina duriuscula* invades crevices in granitic embankments where it shares space with mosses. Photo by Andrea Moro, through Creative Commons.

One approach to rehabilitation has been to accelerate the establishment and growth of mosses by introducing mosses to the damaged area. However, the technique has used fragmented or chopped mosses and has met only limited success, despite the humid climate (rain on 80% of days). Furthermore, it has required collection of great quantities of samples from nature, which is contrary to the objectives of such a project. The BRYOTEC Process, on the other hand, produces large quantities of pioneer mosses from small samples of several cm^2. It therefore enjoys the status of a non-destructive biotechnology.

In addition to controlling erosion, mosses may help to stabilize and build soil on mine spoil. Peat mosses have been used for recultivation of ash dumps from brown and hard coal, a difficult substrate to colonize (Biernacka 1976).

Revegetation

Occasionally mosses are used to revegetate mining spoils. In a discussion on Bryonet in August 2007, several people suggested ***Polytrichum*** species (Figure 70), measuring some degree of success in the United States and Canada, as pointed out by Jean Faubert. Justin Wynns reports that in Boone, NC, USA, large carpets of ***Polytrichum*** have been planted in full sun, covered with large pieces of cloth to stabilize and retain moisture. Steve Timme suggested that naturally appearing mosses on mine tailings of one South Kansas site included ***Ceratodon purpureus*** (Figure 68), ***Bryum argenteum*** (Figure 71), and ***Bryum pseudotriquetrum*** (Figure 72), making those good choices to start. Shana Gross has found that she can get ***Ceratodon purpureus*** and ***Bryum argenteum*** to grow easily from fragments in the greenhouse, but they do not easily form thick mats. It is even more difficult to get such mats in the field.

Figure 70. ***Polytrichum piliferum***, a species tolerant of full sun and drying habitats such as mine tailings. Photo by Thomas Brown, through Creative Commons.

Figure 71. ***Bryum argenteum***, a cosmopolitan species tolerant of full sun and drying habitats such as mine tailings. Photo by Janice Glime.

Figure 72. ***Bryum pseudotriquetrum***, a species that colonizes mine tailings. Photo by Michael Lüth, with permission.

Road cuts, construction, and other forms of "progress" often leave huge scars on the landscape that do not quickly heal and soon become unstable detractants from the landscape around them. Thus, it is desirable to solve both the technical stabilization problem and to create an attractive replacement for the former vegetation. To this end, the Bryotec Corporation has introduced mosses as a solution to both problems. They have found that such bare terrain can be stabilized in a few months with a bed of bryophytes combined with other vegetation to form a pre-sod. The mat is both stable and attractive and helps to prepare the landscape for larger plant species (Michel Chiaffredo, Bryotec Corp., Pers. Comm.)

Recreation

Bryophyte forays have been part of many cultures for a long time (Glime 1982). These have been organized groups that included beginners through top experts who gathered to catalog bryophytes in an area, to learn new species, and to share interests with fellow bryologists.

But in Japan, a new trend has begun. These are excursions, led by an expert, for recreation of non-bryologists, and usually many non-bryologists (Pfanner 2015). In 2013, the Hoshino Resorts Oirase Keiryu Hotel in Aomori Prefecture initiated a one-night stay that included a moss tour on a riverside in the forest region (Matsumoto 2015). Most of the participants are women who find the tours a relaxing way to escape the normal stresses and competition of daily life. But they are shy about sharing their interest in mosses to friends and family.

It is not surprising to me that this interest in mosses by non-biologists has arisen in Japan. Japan is the land of famous moss gardens. It is the land where women traditionally have learned the finer things in life. And as pointed out by Nozu and Thompson (2015), it is a culture that values age and history. And mosses themselves are a thing of beauty with vibrant colors that vary from brown to bright green to red. And mosses make a soft and inviting surface. The slow growth and longevity give the mosses an inherent virtue. There is even a moss reserve around lake Shirakoma that has been designated by the Bryological Society of Japan and is known as a "precious moss-covered forest."

Pesticides and Antifeedants

Frahm (2004) extolled the virtues of bryophytes as anti-snail and anti-fungal sources. He reported that bryophyte extracts only spoil the appetite of the slug ***Arion lusitanicus*** (Figure 73) without killing it (Figure 74). The tested extracts came from the rock-dwelling moss ***Neckera crispa*** (Figure 75) and the leafy liverwort ***Porella obtusata*** (Figure 76) (Frahm & Kirchhoff 2002).

Figure 73. ***Arion lusitanicus*** mating, a species that is discouraged from consuming lettuce that has extracts from the moss ***Neckera crispa*** or leafy liverwort ***Porella obtusata***. Photo from Biopix, through Creative Commons.

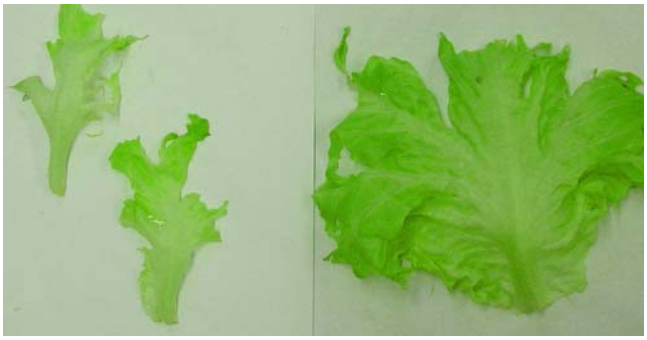


Figure 74. Slugs (***Arion lusitanicus***) can devour garden vegetables, especially soft tissues such as those of lettuce. Here the untreated control on the **left** has been almost completely eaten whereas the liverwort-treated leaf on the **right** remains unharmed. Photos by Jan-Peter Frahm, with permission.

Figure 75. ***Neckera crispa***, the source of a slug antifeedant. Photo by David T. Holyoak, with permission.

Figure 76. ***Porella obtusata***, a leafy liverwort source of a slug antifeedant. Photo by Kristian Hassel, through Creative Commons.

When fungal spores fall on bryophyte leaves, the bryophyte releases phenolic compounds when the surface becomes wet, inhibiting spore germination. To support the anti-fungal use, Frahm encouraged the head of the Department of Phytopathology at the University of Bonn to test their properties in greenhouse experiments. Crop plants such as green peppers, tomatoes, and wheat were infected with such fungal plant pathogens as *Phytophthora infestans* (Figure 77, Figure 78), *Botrytis cinerea* (Figure 79), and *Blumeria graminis* (Figure 80). These infected plants were treated with alcoholic extracts from 20 European species of bryophytes (*e.g.* Figure 78). The extracts had various effects, with liverworts (Figure 76) being most effective (Figure 81), followed by ***Sphagnum*** (Figure 3), then other mosses (Tadesse 2002). Two of the liverworts caused systemic effects. Plants that were sprayed prior to their inoculation were not affected at all by the fungi; the leaves that developed after the application of the extract were resistant, suggesting that the antibiotic substance was translocated within the plant. The ability of moss extracts to inhibit fungal growth is easily demonstrated by saturated disks on inoculated Petri plates (Figure 82).

Figure 77. *Phytophthora infestans* blight on tomatoes. Photo by Scot Nelson, through Creative Commons.

Figure 78. Extracts of 20 species of bryophytes inhibit the growth of fungal pathogens on vegetable crops such as these tomatoes. The plant on the **left** is the control and is infected with the fungus *Phytophthora infestans*. The other two have been treated with two concentrations of alcohol extract from bryophytes. Photo by Jan-Peter Frahm, with permission.

Figure 81. The healthy tomato plant on the **left** has been treated with liverwort extract, whereas the untreated plant on the **right** is infected with *Phytophthora infestans*. Photo by Jan-Peter Frahm, with permission.

Figure 79. *Botrytis cinerea* on grapes. Photo by John Yesberg, through public domain.

Figure 80. *Blumeria graminis* on Kentucky bluegrass, *Poa pratensis*. Photo by Rasbak, through Creative Commons.

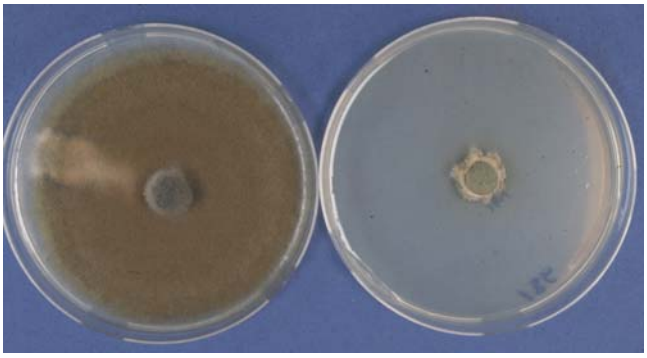


Figure 82. Rampant fungal growth occurs on the plate lacking bryophyte extract (**left**) while growth is inhibited on a plate with a bryophyte extract disk (**right**). Photo by Jan-Peter Frahm.

Once the news of this antifungal activity was distributed to the news media, there was a huge response, indicating a great need for such an alternative product. The moss extracts are a safer alternative to the copper sulfate and other heavy metal salts currently being used. The heavy metals accumulate in the soil, whereas the bryophyte extracts quickly degrade in the soil. Furthermore, it is easy to produce and farmers in third world countries could even produce it themselves. Are these anti-herbivore compounds safe for our consumption?

A private German development company, Red de Accio´n en Alternativas al uso de Agroquı´micos (RAAA) persuaded the Universidad Nacional de San Martin in Peru to test extracts of local bryophytes on coffee and tomatoes as protection against tropical plant diseases in the field. Unfortunately, they tried only mosses and not the more potent liverworts, but they still achieved positive results. Sadly, the high cost of the alcohol prevented wide-scale use in Peru.

In Bolivia, the Unidad de Investigacio´n y Desarollo FAN made extracts of ***Frullania brasiliensis*** (Figure 83) and ***Sphagnum*** sp. (Figure 3) and applied them to tomatoes and potatoes. While controls were infected, the treated plants exhibited no visible bacterial or fungal infections (Figure 78; Figure 81).

Figure 83. ***Frullania brasiliensis***, a species that prevented infections on tomatoes and potatoes. Photo by Jan-Peter Frahm, with permission.

Frahm, failing to persuade any German company to produce the product, took the product to a company that produces herb liquors. It was sold by a chain of drugstores(!) as an alternative to fungicides. Finally, a new commercial company received permission from Biologische Bundesanstalt to produce the product commercially. Several thousand liters of bryophyte extract were sold during the first 8 months. This product is diluted 1:100 for use. A major limitation is obtaining enough plant material in the field. Although the moss used is abundant in silvicultural fir forests, the quantities needed for agriculture is enormous.

Frahm's group is conducting further testing to produce the moss horticulturally and hopefully to find clones with higher biological activity. Such commercial production would also eliminate the need for cleaning, reducing costs and time.

Rearing Fish

The Nashua National Salmon Hatchery has considered using the aquatic moss ***Fontinalis*** (Figure 84) in the salmon raceways (Abigail Walker, Intern, Nashua National Fish Hatchery, 19 April 2005). It grows there on the cement and they hope to use it as both a nutrient sink and a natural cover for young fry in the rearing tank.

Figure 84. ***Fontinalis antipyretica*** is a moss used in fish hatcheries today, but formerly used for chimney chinking with the belief it would insulate against fire or heat. Photo by Michael Lüth.

As described in the Aquarium subchapter, Bohlen (1999) reported the use of aquaria equipped with a thick moss tuft for spawning of the spined loach *Cobitis taenia* (Figure 85). The moss was placed on top of a gauze-covered plastic box. The fish laid their eggs in the most dense vegetation available. The dead eggs fell through the gauze and collected in the box.

Figure 85. ***Cobitis taenia***, a species that benefits from mosses in aquaria for spawning. Photo by Ron Offermans, through Creative Commons.

The bryophytes may well be protected from herbivory by the fish at the same time. Asakawa *et al*. (1985) has shown that at least one liverwort (***Riccardia lobata*** var. ***yakushimensis***), although not itself aquatic, has piscicidal secondary compounds (diterpenedial).

Toxicity Testing

Numerous studies have used bryophytes as indicators of pollution, with symptoms indicating, in many cases, the type of pollution. These are so numerous as to warrant several chapters, if not an entire volume. It is almost predictable that one of the organisms that has been studied for this potential is the bryological lab rat, ***Physcomitrella patens*** (Figure 86). Morgan *et al*. (1990) used cultures of this moss to examine effects of various salt solutions (aluminium sulfate, barium chloride, boric acid, cadmium chloride, cobalt chloride, as well as lead nitrate, mineralized-acidic leachate, and coal combustion fly ash leachate) on various life cycle stages (Figure 86). Aberrations such as altered morphology, loss of regeneration ability, reduced dry weight, and altered chlorophyll contents indicated damage by the salts. Surprisingly, the spore and gametophore cultures differed little in their responses. Cadmium chloride and aluminum sulfate caused the greatest reduction in chlorophyll concentration and dry weight, whereas boric acid and barium chloride were least toxic. Fly ash likewise seemed to cause no harm to the plants.

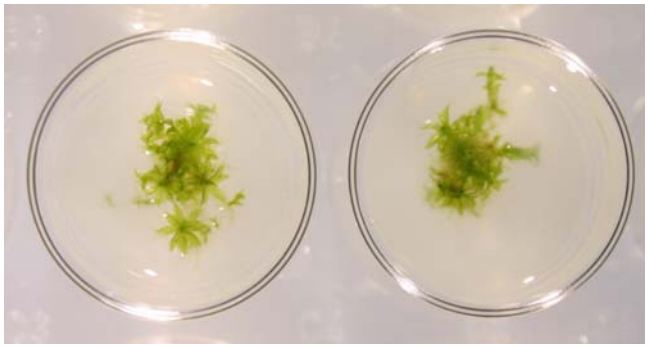


Figure 86. Mosses such as ***Physcomitrella patens*** can be used to test effects of salt concentrations, acidic leachates, heavy metals, and fly ash on morphological alterations and changes in chlorophyll concentrations. Photo by Ralf Reski, with permission.

Kenneth Adams (pers. comm. 1 November 2013) used balls of acid-washed ***Sphagnum*** (Figure 3) in bun hair nets in the 1970's to accumulate airborne heavy metals in locations of interest. These were placed in concentric survey locations around smelters in the U. K. and assayed with flame photometry. This was used routinely to assay for petrol lead levels along roadsides. He even found a zinc source from burned car tires in east London.

There is considerable literature on the use of bryophytes for biomonitoring, including moss bags and *in situ* assessment in concentric rings or distances along a transect starting from a pollution source. These have been useful in both aquatic and terrestrial studies. Several reviews and books (*e.g.* Leblanc & Rao 1974; Nash & Wirth 1988; Tyler 1990; Bates & Farmer 1992; Greven 1992; Onianwa 2001; Zechmeister *et al*. 2003; Tuba *et al*. 2011; Harmens *et al*. 2013) have been written on these studies, so I will not elaborate here. Hopefully I will write a volume on this after other volumes are completed.

Filters

Copper is toxic to plants except in small quantities. Itouga *et al*. (2006) tested the copper mosses ***Scopelophila cataractae*** (Figure 87) and ***S. ligulata*** (Figure 88) for their effect in removing the copper toxicity in copper-polluted water used for growing rice. Using bryophyte columns packed with each of these two species, the researchers determined that ***S. cataractae*** was superior at copper toxicity removal. Furthermore, ***S. cataractae*** filtrate was no longer toxic to the rice. We still need to know the practicality of this method – how much moss would be required and how long would the column be effective. Nevertheless, this could be a practical solution for small applications such as home aquaria and pools.

Many studies exist on the sorption of metal ions by mosses. These have been reviewed in several books on bryophytes and pollution. However, their use as filters has received much less attention. Al-Asheh and Duvnjak (1997) discussed the adsorption of metal ions by mosses. Such publications led to the exploration of bryophytes as filters against metal ions. Abdel-Jabbar *et al*. (2001) successfully modelled the copper adsorption of a moss-packed bed. This model accounted for differences such as axial dispersion, external film, and within-particle diffusion. In a different study, Ho and McKay (2000) developed a sorption model for copper using ***Sphagnum*** (Figure 3). They determined that sorption through chemical bonding might be rate limiting. Nevertheless, they were able to develop a model that could predict the sorption capacity of metal ions sorbed.

Figure 87. ***Scopelophila cataractae***, a moss that successfully removes copper from water used in rice culture and that is superior for this purpose compared to ***S. ligulata***. Photo by Blanka Shaw, with permission.

Figure 88. ***Scopelophila ligulata***, a copper moss that is less effective than ***S. cataractae*** in removing copper toxicity from water used to culture rice. Photo by Michael Lüth, with permission.

Electricity

Using mosses to produce electricity might be a pipe dream, but it has at least limited possibilities. Mosses are able to produce enough energy through photosynthesis to power a clock, but the same amount would only keep a laptop alive for about 20 seconds (Chandler 2012).

In another example, mosses have been placed in a glasstop table (University of Cambridge 2011). They are able to power the lamp through photosynthesis (Inhabitat 2017). Mosses photosynthesize and release organic compounds into their substrate. Bacteria in that soil break down these organic compounds, liberating by-products, including electrons. The table is designed to capture these electrons and use them to produce an electrical current. This research is led jointly by Dr. Adrian Fisher, Professor Christopher Howe, and Professor Alison Smith at Cambridge, and Dr. Petra Cameron at Bath.

Scientific Use

Today, bryophytes are receiving considerable attention from the scientific world. ***Marchantia polymorpha*** (Figure 89) has long been a subject of physiological studies. ***Funaria hygrometrica*** (Figure 90) and ***Physcomitrella patens*** (Figure 91) are everyday names to the plant physiologists. And ***Syntrichia*** (syn.=***Tortula***; Figure 92) is being studied by the Department of Agriculture (Comis 1992; Hoffman 1992)! What is it that has caused this sudden agricultural interest in bryophytes?

Figure 89. ***Marchantia polymorpha***, a common liverwort, is used for teaching and scientific research. Photo by Michael Lüth, with permission.

Figure 90. ***Funaria hygrometrica***, a moss that has often been used in plant physiological studies. Photo by Michael Lüth, with permission.

Figure 91. ***Physcomitrella patens***, a moss with a fully mapped genome and that has often been used in plant physiological studies. Photo by Michael Lüth, with permission.

Figure 92. ***Syntrichia ruralis***, a desiccation-tolerant moss that has been used in many physiological studies. Photo by Michael Lüth, with permission.

The ability to grow bryophytes from spores and fragments has made some kinds of physiological studies easy. Much of what we know about tropisms has been learned from studies on moss protonemata, which respond to gravity and demonstrate what occurs inside the cell. With only one cell in thickness, and an easily observable and measurable linear structure, the moss protonema provides an ideal study organism for this purpose. But agriculture? It seems that mosses have characteristics that are desirable for crop plants. They tolerate desiccation better than almost any crop plant and can withstand freezing while still in a state of hydration, yet recover almost instantly (Rütten & Santarius 1992). Furthermore, they seem seldom to be eaten, especially by insects. With our new tools for moving genes around almost anywhere we want with the help of bacteria and bryophytes, the genes of mosses suddenly became an attractive commodity.

The bryophytes, and especially ***Physcomitrella patens*** (Figure 91), and to a lesser extent ***Ceratodon purpureus*** (Figure 68), have been a true boon to unravelling the genetic control of physiology and development by identifying which genes control which actions (Cove & Cuming 2014). With only one set of chromosomes, inserting a new gene so that it is expressed is a much simpler task in bryophytes than doing the same thing in a flowering plant with two sets of chromosomes. Furthermore, it is easy to grow large quantities of these mosses in culture. And both species experience a high frequency in gene targetting, permitting researchers to knock out a gene to determine its function (*e.g.* Brücher *et al*. 2005). ***Physcomitrella patens*** has been completely sequenced and much of the genome of ***C. purpureus*** is likewise known (Cove & Cuming 2014).

Model Systems

It seems fitting, yet ironic, that these plants of ancient use may reach the forefront of technology. But this time, their uses are much less obvious and much more sophisticated.

In the early part of the last century, bryophytes led the arena of genetic research (Wettstein 1932). Mutagenic effects of X-rays [on ***Sphaerocarpos donnellii*** (Figure 93; Knapp 1935, Schieder 1973); on ***Marchantia polymorpha***

(Figure 89; Miller *et al*. 1962a, b); on ***Physcomitrium pyriforme*** (Figure 94; Barthelmess 1941a); and on ***Physcomitrella patens*** (Figure 91; Engel 1968)], α particles on ***Physcomitrium pyriforme*** (Barthelmess 1938), and γ-rays on ***Brachythecium rutabulum*** (Figure 59; Moutschen 1954), and chemical mutagenesis on ***Physcomitrium pyriforme***, and ***Physcomitrella patens***, among others, Barthelmess 1941a, b, 1953) were more easily studied on these haploid organisms, and their multi-year life exposed to the atmosphere made them ideal for integrating effects over time. Both morphological and physiological effects were manifest (Cove 1983).

Figure 93. ***Sphaerocarpos donnellii***, a species used to determine mutagenic effects of X-rays. Photo by Belinda Lo, through Creative Commons.

Figure 94. ***Physcomitrium pyriforme***, a moss used to test the mutagenic effects of α particles. Photo by Janice Glime.

Although bryophytes seldom reach the headlines, they have served as model systems in many branches of biology for a long time. The first sex chromosomes in plants were described from a liverwort, then the continuity of chromosomes during mitosis, then the discovery of non-Mendelian inheritance (Reski 1998). Mutagenesis, using UV, was first demonstrated in mosses (Reski 2005).

Many aspects of plant physiology have been elucidated using mosses as model systems. It seems that photorespiration was first recognized in ***Fontinalis*** (Figure 84) (Buch 1945), although Buch is not given credit in modern literature. And it is much easier to study tropisms, amyloplasts, and statoliths in the one-cell-wide protonema (Walker & Sack 1990; Young & Sack 1992; Sack 1993; Chaban *et al*. 1998; Kern *et al*. 2001). This system likewise is ideal for trying to understand the early developmental pathways and their hormonal controls (Bopp 1974). The moss provides a simple plant system in which to understand mechanisms of Ca regulation and signal transduction in plants (Schumaker & Gizinski 1995).

Thus, in recent years bryophytes have become established as model plants for the study of many physiological aspects of plants, especially in linking genes to function, including developmental processes [cell polarity and plastid development (Jenkins & Cove 1983)], homologous recombination, and cellular (calcium signaling) processes. Expression of characters in the haploid state makes it much easier to understand gene expression (*e.g.* Wood *et al*. 2004 on GAPN enzyme effects), and isolation of mutants has facilitated the breakdown of developmental and biochemical pathways. Now, the ability to transplant genes or target knockout genes in mosses, especially in ***Physcomitrella patens*** (Figure 91), permits us to understand gene/pathway/phenotypic response relationships through the use of reverse genetics (Reski 2005).

Sineshchekov *et al*. (2000) transplanted the moss ***Ceratodon purpureus*** (Figure 95) CP2 gene to the yeast *Saccharomyces cerevisiae* (Figure 96) to reconstitute **phycocyanobilin**. This permitted examination of emission spectra of the pigment in isolation from the influence of other pigments. Studies such as this are being used to understand a variety of gene functions in plants, with bryophytes expressing transplanted genes more easily than do other plants. Hence, they have been invaluable in advancing our understanding of plant functions.

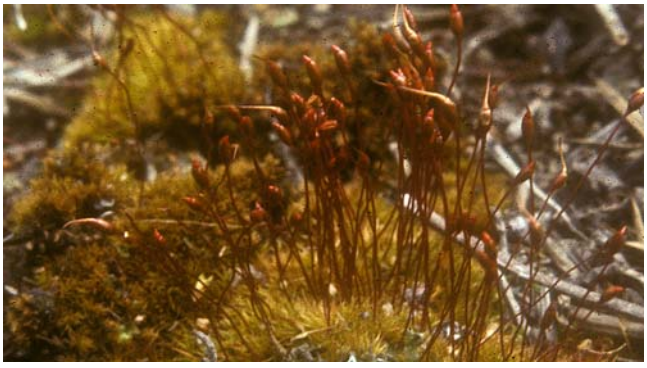


Figure 95. The moss ***Ceratodon purpureus***, used for transplanting genes to yeast in order to identify pigment emission spectra. Photo by Janice Glime.

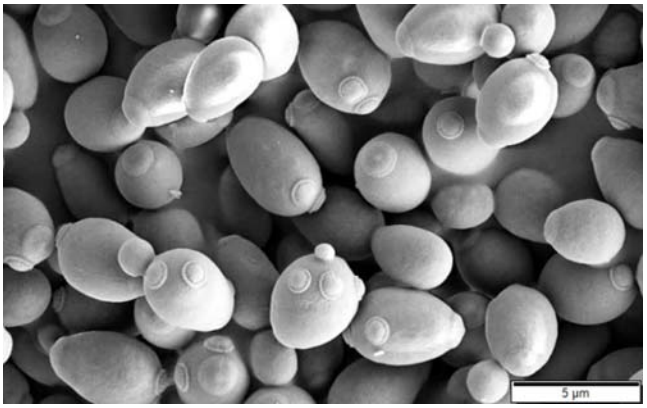


Figure 96. *Saccharomyces cerevisiae* SEM, a yeast that received genes for phycocyanobilin from the moss ***Ceratodon purpureus*** so that the emission spectrum could be isolated and analyzed. Photo by Mogana Das Murtey and Patchamuthu Ramasamy, through Creative Commons.

Genetic Engineering

While genetic engineers are making the headlines with marketable fruits, vegetables, and even modified animals, the genetic engineers of bryophytes remain quietly in the background figuring out "what makes things tick." Although few people have any interest in how a moss functions, the ability of using mosses to figure out how a tracheophyte, especially a crop plant, goes about its daily life is of enormous importance to the agriculture industry.

Cove and coworkers (1997) have suggested that mosses "hold many attractions" as model organisms, arguing that position as the simplest of land plants permitted them to shed light on the development of terrestrial plants from formerly aquatic ancestors. But this simple evolutionary approach soon blossomed into a new and strategic use of bryophytes in understanding not only evolution, but in understanding the functioning of plants in general (Reski & Frank 2005).

To quote Reski (1998), "due to the simplicity of the plants, development can be pinpointed to the differentiation of a single cell and be analyzed in living tissues, making mosses ideal candidates for analysis of development in an integrated approach of cell and molecular biology." In fact, it is the humble moss ***Physcomitrella patens*** (Figure 91) that is proving to be an appropriate model for studying the molecular development of not just mosses, but plants in general. The nuclear genes of this moss can be targeted for homologous recombination, making reverse genetics a viable tool for plant physiologists.

In the past, we have studied gene function by identifying the gene product, then trying to identify the gene involved. With reverse genetics, we instead identify the gene on the basis of its position. We can then remove it or insert it in another organism to determine the effect that gene has on phenotypic expression. As haploid organisms, mosses are ideal for this approach because the gene is not masked by a second allele that may alter or prevent its expression. It is as easy in this moss to target nuclear genes for recombination as it is in yeast, providing a powerful tool for understanding plant gene function (Reski & Frank 2005). Using ***Physcomitrella patens*** (Figure 91) to confirm the transgene in chloroplast transformation, Cho and coworkers (1999) were able to demonstrate the applicability of this moss as a model system for basic biological research.

The model moss ***Physcomitrella patens*** (Figure 91) not only is useful for expressing genes transferred from other plants, but it also has genes of its own to contribute. Its high tolerance against drought, osmotic stress, and salt (Frank *et al*. 2005) suggest that it has genes that could be useful in other plants. Because it is easier to identify specific genes and link them to their functions in haploid plants, it could serve as a source for genes that could be moved into crop plants to endow them with these desirable traits.

One advantage of using mosses to understand physiology is their ability to exhibit conditional lethal genes (King 1986). Such mutants permit physiologists to understand processes because the gene is lethal until the problem is corrected.

Beike *et al*. (2010) discussed the use of bryophytes in biotechnology, known as bryotechnology. Many of these uses have been discussed earlier in this chapter or in the chapter on medicine. Beike noted some of the potential uses in agriculture. For example, the leafy liverwort ***Porella platyphylla*** (Figure 97) inhibits the growth of radish seedlings, whereas an extract from the moss ***Brachythecium rutabulum*** (Figure 59) promotes the growth. Stress tolerance is more common among bryophytes and genes effecting that ability have potential for introduction into flowering plants, including food plants. But there are tradeoffs we must not ignore. If a plant puts its energy into making the products of those new genes, what other aspects of the plant might be sacrificed? Will the plant still be safe to eat? Will it still have the same nutritional value? Will it become allergenic?

Figure 97. ***Porella platyphylla***, a species that can inhibit the growth of radish seedlings. Photo by Janice Glime.

One such stress-responsive gene is ALDH21A1 from ***Syntrichia ruralis*** (Figure 92) (Chen *et al*. 2002). This appears to be a unique stress tolerance gene not present in tracheophytes. It is important in the detoxification of aldehydes that are created in response to desiccation and salinity stress.

Modification of non-food crop plants poses fewer risks. Yang *et al*. (2012, 2016) have isolated the ScALDH21 gene from the very drought-tolerant ***Syntrichia caninervis*** (Figure 98) that grows in deserts of Central Asia and North America. This gene was effectively transplanted into cotton (*Gossypium hirsutum*; Figure 99). Testing indicated that the gene was expressed, and under drought stress the cotton with the new gene accumulated ~11.8-304% more of the amino acid proline than did the unmodified cotton. It furthermore produced a lower concentration of lipid peroxidation-derived reactive aldehydes than untreated plants, and it had a higher peroxidase activity under oxidative stress. These modified plants exhibited greater plant height, larger bolls, and greater cotton fiber yield, while losing nothing in fiber quality.

Figure 98. ***Syntrichia caninervis***, a drought-tolerant species whose genes have been successfully transplanted into cotton and expressed. Photo by John Game, through Creative Commons.

Figure 99. Cotton (*Gossypium hirsutum*), a species that benefits from drought tolerance genes from ***Syntrichia caninervis***. Photo by Forest & Kim Starr, through Creative Commons.

Manufacturing Human Protein

Most recently, the mosses, and especially ***Physcomitrella patens*** (Figure 91), are being used to culture needed human proteins because they are much easier systems than tracheophytes for gene manipulation (Figure 100) (Reski 1998; Baur *et al*. 2005). And mosses are much cheaper and easier to culture than human cell systems.

Reski and Frank (2005) have identified three public demands in modern plant biotechnology:

1. More people in the population require more food, but they also reduce the area of arable land, constraining the food production.
2. The mean age of the population is increasing, requiring a higher quality of food to prevent typical "diseases of civilization" such as cardiovascular diseases and cancer.
3. Medical science is experiencing a paradigm shift from broad-based treatments to very patient-specific treatments, requiring safe and cost-effective production of complex pharmaceuticals.

Reski and Frank (2005) suggest that ***Physcomitrella patens*** (Figure 91) can contribute in all three of these needs. "Virtually every gene can be knocked out by targeted ... approaches in attempts to establish saturated mutant collections." And the phenotypes can be screened within weeks! Gene targeting in this moss is about five orders of magnitude more efficient than in any seed plant and about two orders of magnitude more than in embryonic mice stem cells.

Figure 100. ***Physcomitrella patens*** is cultured for gene manipulation and proteomics. Photo courtesy of Ralf Reski.

It appears that there are already over 200,000 expressed sequence tags in ***Physcomitrella patens*** (Figure 91) (Reski & Frank 2005). There are about 6000 protein-encoding genes which are not identifiable in the public databases, most likely representing novel genes, out of the 30,000 protein-encoding genes present in the moss. It is interesting that about 100 genes in this moss can be matched only to non-plant organisms, including humans!

One advantage to working with a moss such as ***Physcomitrella patens*** (Figure 91) is the ability to culture it in a bioreactor (Figure 101), thus eliminating the problems of contamination from soil or other growth media (Reski & Frank 2005). This makes the study of proteomics (examination of the protein complement of a genome) much easier.

Figure 101. Moss bioreactors provide sterile cultures of ***Physcomitrella patens***, avoiding the contamination problem prevalent with soil-grown plants. Photo by Ralf Reski, with permission.

Mosses may help us to address needs in the human diet that are not available from other plants. For example, eicosapentaenoic acid (EPA) and arachidonic acid (AA) are only produced by non-seed plants, including bryophytes. Yet these acids play a role in human eicosanoid metabolism. Furthermore, polyunsaturated acids are most abundant in non-seed plants, including mosses, and likewise are beneficial for human growth and continued good health. As our fish (also large sources of polyunsaturated acids) dwindle and become contaminated with metal pollutants, these plants may become an essential source of these important fatty acids. Genes from ***Physcomitrella patens*** (Figure 91), identified to have this function of producing polyunsaturated fatty acids, have already been planted and expressed in tobacco (*Nicotiana tabacum*; Figure 102) and linseed (*Linum usitatissimum*; Figure 103) (Abbadi *et al.* 2004).

One problem with many plant cell culture systems is genetic instability (Reski & Frank 2005). The ***Physcomitrella patens*** (Figure 91) bioreactor, on the other hand, maintains well-differentiated and genetically stable cell types. The culture conditions are much simpler than those required for mammalian cells.

Figure 102. Tobacco, *Nicotiana tabacum*, a species that is able to express genes for producing polyunsaturated fatty acids, transplanted from the moss ***Physcomitrella patens***. Photo by Magnus Manske, through Creative Commons.

Figure 103. *Linum usitatissimum*, a species that is able to express genes for producing polyunsaturated fatty acids, transplanted from the moss ***Physcomitrella patens***. Photo through Creative Commons.

Targetted gene removal or transfer can render the moss products safe for humans, avoiding production of allergenic products that are unsafe for humans (Reski & Frank 2005). For example, xylose and fucose form allergenic residues of plant glycoproteins in most plants, but in the mosses, a targetted double knockout provides moss plants with no fucose or xylose residues attached to their proteins. This modified moss was still able to produce the same level of recombinant human growth factor, serving as a living reservoir for this purpose.

Model for Pipettes

Plants have been used as models in engineering, but use of a bryophyte for this purpose is unusual. Nakamura *et al*. (2018) used ***Marchantia polymorpha*** (Figure 104) to understand the mechanism of fertilization in its archegonial head. This study not only challenges some of our traditional concepts about fertilization in this species, but also provides a model for a very effective small pipette.

Figure 104. ***Marchantia polymorpha*** archegoniophores at the stage used in experiments by Nakamura and coworkers. Photo by Janice Glime.

This liverwort has an archegoniophore shaped like a parasol, but with finger-like apppendages radiating from its head (Nakamura *et al*. 2018). When it is young, the fingers of the archegonial head tend to hang downward and provide an ideal water-trapping device through the cohesive and adhesive properties of water. This collection of water droplets provides a suitable medium for sperm to swim to the archegonia on the lower surfaces of the fingers. Nakamura and coworkers developed a similar parasol-like object to grab, transport, and release water droplets up to about 1 cm in diameter. Their simulated "archegoniophore," like the plant that serves as its model, is "largely insensitive" to such properties of water as surface tension and viscosity. This permits bubble-free capture and drop of liquids that is useful in laboratories and in soft robotics.

Goodyear Tires

Thank you to my alert former graduate student, Geert Raeymaekers, I am reporting to you on the use of "moss" in Goodyear tires (Figure 105). The "mosses" are packed into the sidewalls of the tires, where they can photosynthesize, absorb CO_2, and put O_2 into the atmosphere (Leary 2018). The tires are made of recycled tires and can't go flat, thus requiring fewer needs for new tires. Goodyear estimates that in a city about the size of Paris, the tires could absorb more than 4,000 tons of CO_2 and release ~3,000 tons of O_2 per year.

Figure 105. Goodyear Oxygene tire, showing "moss in sidewall. Photo from Goodyear, through Creative Commons at Futurism.

I have several concerns about this innovation. First, they look more like an ***Evernia***-type lichen, or perhaps reindeer "moss" – also a lichen. But more importantly, whether a true moss or a lichen, to work they must be alive. I would think that the heat created in a tire, the salt on winter roads, mud puddles, and rapid drying on a revolving wheel would make an unsuitable habitat for either.

Summary

Sphagnum is the most widely used moss, including uses for bandages, diapers, boot liners, sanitary napkins, horticultural soil mixes, cranberry farms, orchid and mushroom culture, green roofs, flower arrangements, fuel, peatwood, peatcrete, litter for animals, lead detection electrodes, filtration, and oil spill cleanup. Products such as Hydro-Weed, SpillSorb, Oclansorb Plus, and Peat Sorb are peat products designed for hydrocarbon cleanup projects. These properties also make it an effective filter for removing heavy metals and other pollutants. Sphagnan makes a good preservative and is probably responsible for the preservation of the Tollund man.

Peat is a renewable fuel and horticultural source, but it must be harvested with sustainability in mind. Hand raking and light-weight wagons travelling on restricted paths can leave sufficient live plant material that harvesting may be repeated in 10-20 years. Lack of care about renewability has caused mass destruction of peatlands, along with destruction caused by development of industry, business, and housing land.

In addition to burning the peat, peatlands can be used to generate methane for fuel. Peat has been used in construction to make asphalt, peatcrete (light concrete), peatfoam, peatcork, and peatwood. Their natural role to control erosion has recently been copied in road construction.

Peatlands harbor a rich history and because of their antiquity can be used for aging and determining past vegetation and climate. And bryophytes on Ötzi and other icemen can tell us about their origins and suggest some of their uses of bryophytes.

The Japanese have capitalized on the beauty of bryophytes to lead excursions for people who have become interested in the natural world.

Bryophytes produce a wide range of antibiotics that have been used against fungi, slugs, and other invertebrate herbivores. The antibiotic and absorbent capabilities make bryophytes good agents of preservation, as seen in ancient tombs, stuffed mummies, and the preservation of bogmen. Photosynthesis of bryophytes has been used indirectly to power small users such as lights and clocks.

Because of their 1*n* state, bryophytes are useful in unravelling the roles of individual genes in plant physiology. And subsequently, adaptive genes are being moved into crop plants to increase drought tolerance (cotton) or lower targeted fatty acids. In other cases, genes are moved into bryophytes to make them create a needed human protein without causing an immune response in the human recipient.

Modern science is now using bryophytes in forensics to put suspects at the scene of a crime, using the techniques of DNA fingerprinting to match fragments on

clothing to a particular location. They can also help to determine the post mortem interval.

Bryophytes are good organisms for testing the toxicity of various substances, using the bryological "lab rat" ***Physcomitrella patens***. Other scientific uses include unravelling the mysteries of gene function and plant physiology by studies with knock-out genes and gene transplants. Mosses are ideal for this because of their dominant 1*n* generation. This same advantage permits us to put genes for producing human substances such as blood protein into a moss and produce it in culture, avoiding any animal rights violations.

Marchantia polymorpha archegoniophores serve as a good model for a laboratory pipette. Goodyear is experimenting with using "mosses" in the sidewalls of tires to clean the air of CO_2 and replenish it with O_2.

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I appreciate the contributions of Michel Chiaffredo, Jan-Peter Frahm, and Ralf Reski in making this chapter timely and for their contributions of photographs. If anyone can provide me with the original source of the photograph of the bogman, I would greatly appreciate it so that I can gain permission and give proper credit. I appreciate Andrew Wood's efforts to bring me up to date on GMO's using bryophytes. Geert Raeymaekers sent me the link to the Goodyear tire story. Claudio Delgadillo Moya sent me the link to the story about the ***Marchantia*** model for a pipette.

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CHAPTER 7-1
GARDENING: HORTICULTURAL USES

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CHAPTER 7-1
GARDENING: HORTICULTURAL USES

Figure 1. ***Sphagnum*** species such as this ***S. russowii*** are commonly used in horticulture as bedding material. Photo by Michael Lüth.

Horticultural Uses

I was surprised that in my search for moss uses in horticulture I stumbled on a patent for culturing "moss seedlings" (Hiraoka 1995). The patent was to culture mosses that could henceforth be transplanted and grown in a nursery. Hiraoka presented this as a means of reducing the necessity of collecting wild mosses and creating undesirable forest conditions due to drying soils and erosion. This consideration should serve as a warning for all who desire to use bryophytes for any commercial purpose, and even on a small personal scale, collection can produce local damage.

"People have probably used organic materials as an aid for plant culture since the eve of human history, but documentation is scarce" (Raviv *et al*. 1986). Use of organic materials, including mosses, may not have started that early, but if monkeys can discover the advantage of mosses for getting water to drink, why not? At the beginning of the 18th Century, we find reference to using peat moss as an amendment for clay soils, whereas animal dung was used for sandy soils (Raviv *et al*. 1986). Since then, the need to keep plants alive during transfer made bryophytes a desirable medium because of their ability to retain moisture.

It is surprising how difficult it is today to find literature on the use of bryophytes in plant cultivation, despite the widespread sale of peat mosses for gardening, potting, air layering, and other uses. Rather, the use of mosses, especially peat moss, seems to be assumed and publications concentrate on finding substitutions for it (*e.g.* Tripepi *et al*. 1996) or creating the right mix of moss and amendments (*e.g.* Chong & Lumis 2000; Shujun *et al*. 2004).

Horticulture is the largest market for moss products in Asia (Tan 2003), and probably in most North American countries (Muir *et al*. 2006). In horticulture, mosses find a niche unparalleled in any other living bryophyte industry (Nelson & Carpenter 1965; Tan 2003). In some parts of

the world, they are routinely mined (Clarke 2008). Bryophytes, especially peat mosses (Figure 1), have played a major role in horticulture for centuries (Perin 1962; Arzeni 1963; Adderley 1964, 1965). Although their use as part of the landscape in gardens has traditionally been mostly an Asian practice, they have commonly been used as soil additives and bedding for greenhouse crops, potted ornamental plants, and seedling beds (Cox & Westing 1963; Sjors 1980). They are stuffed into wire frames to make totem poles to support climbing plants (at the Mossers Lee Plant), topiary (Figure 2), moss-filled wreaths, or baskets (Thomason 1994), or for covering the soil in floral arrangements. One company advertises a birch bark pedestal topped by a moss globe.

Figure 2. A swan topiary exhibited in a pedestrian area of Minneapolis, Minnesota, USA. Photo courtesy of David Long.

Overuse of mosses is concerning in several countries. Thus, some horticulturists seek substitutes. The use of rice hulls may provide a more renewable alternative to ***Sphagnum*** (Figure 1) peat for horticulture usage (Sambo *et al*. 2008). Peat has more total pore space and a lower air-filled pore space compared to rice hulls, coinciding with a higher water-holding capacity and the highest water content at container capacity. Nevertheless, peat had a lower available water content than the rice hulls, while releasing its water more slowly.

Shipping and Protecting

Sphagnum (Figure 1) is almost indispensable for shipping live plants, keeping them moist, yet free from mold. In countries where peat is abundant, the damp peat is burned to produce a smoke screen against frost, hence protecting the plants (Thieret 1954). This is one of its uses in Asian countries as well (Tan 2003).

Soil Conditioning

The Shuswap Indians of North America use ***Aulacomnium*** (Figure 3) and ***Dicranum*** (Figure 4) mixed with dirt to make plants healthier (Palmer 1975). As a soil conditioner, coarse-textured mosses increase water storage capacity; fine-textured mosses provide air spaces (Ishikawa 1974; Bernier 1992; Bernier *et al*. 1995). Although supporting experiments seem to be lacking, we assume that mosses improve the nutrient condition of outdoor soils by holding nutrients, especially from dust and rainfall, then releasing them slowly over a much longer period than normal nutrient residency near the soil surface (Stewart 1977; Rieley *et al.* 1979; Scafone unpubl. data).

Figure 3. ***Aulacomnium palustre***. Species of ***Dicranum*** used by the Shuswap Indians of North America to condition the soil for plant growth. Photo by Michael Lüth, with permission.

Figure 4. ***Dicranum scoparium***. Species of ***Dicranum*** used by the Shuswap Indians of North America to condition the soil for plant growth. Photo by Janice Glime.

Their ability to sequester nutrients varies with species and type of nutrient. For most taxa, they do not compete for soil nutrients like phosphorus, but can accumulate from rainfall the potassium, magnesium, and calcium (Timmer 1970). When the mosses later dehydrate, their membranes are damaged, making them leaky. When they rehydrate, nutrients can be dissolved and washed into the soil. It takes a few hours to a day to repair the damaged membranes, giving the roots beneath a chance to retrieve the nutrients that are slowly being washed down from the dusty, leaky mosses. This is dependent also on the force of the rain, with light rains more likely to remain on the mosses long enough for them to absorb the nutrients. This seems to be especially important for potassium, the most soluble and most easily leached nutrient. (See Nutrient chapter in Volume 1 for details.)

Peat, in particular, offers a number of properties important to the growth of plants. To be suitable for most root growth, the peat needs to have about equal proportions of air and water retention. The Peat Research Institute determined that the inclusion of shrubs and cotton grass

from the field site could make the peat inconsistent and alter the water-holding capacity and aeration needed for good plant growth. Therefore, they recommended that the proportion of subshrub residues not exceed 3% wet weight, that the proportion of cotton grass and sedge residues not exceed 6%, and that the proportion of ***Sphagnum*** (Figure 1) residues be at least 90% (Puustjarvi 1982).

In remote places, including national parks, remote villages, and other places where sewage systems are not in place, peat may be mixed with human waste to form compost (Wikipedia 2017). The extra aeration provided by the spaces among the peat plants helps the process of breaking down the sewage. Nevertheless, human pathogens can be a problem, with the greatest of these being *Ascaris* eggs (a nematode parasite; Figure 5-Figure 6) (Hill 2013). A long time or high temperatures are needed to destroy these pathogens. Berger (2011) claims that the compost should be free of live pathogens after at least two weeks at 55ºC or one week at 60ºC.

Figure 5. ***Ascaris*** larva hatched on microscope slide, a genus of parasitic worms of concern in human feces. Photo by SuSanA Secretariat, through Creative Commons.

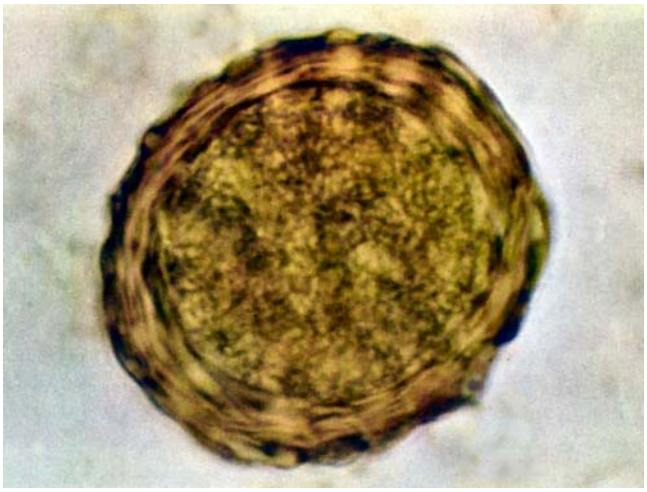

Figure 6. ***Ascaris lumbricoides*** fertilized egg. Presence of these in human feces is of concern when the feces are mixed with peat as a plant growth medium. Photo by Graham Colm, through Creative Commons

In England, the Wye College, University of London, and Southern Water have cooperated to develop a compost that takes advantage of sewage, mixed with peat mosses, providing a valuable soil conditioner and slow-release fertilizer that can be used for container-grown plants (Lopez-Real *et al.* 1989).

One use for the nasty-smelling fish offal takes advantage of the absorptive properties of ***Sphagnum*** (Figure 1) to create a superior compost (Martin & Chintalapati 1990), a real boon for getting rid of fish waste. And, when mixed with fish processing wastes, peat mosses are superior to sawdust and wood shavings in conserving nitrogen, but are a bit more expensive (Liao *et al*. 1995).

Martin (1992) considered that it should be an easy and inexpensive process to use fish by-products (fish offal) with ***Sphagnum*** (Figure 1) peat as a substrate to grow microorganisms for submerged fermentation. Martin conducted experiments on growing fungi and yeast as potential sources of microbial biomass protein for feeding animals. These products, which the fish were willing to include in their diet, served successfully as proteinaceous food for feeding farmed fish.

One of the microorganisms tested was the acid-tolerant fungus ***Scytalidium acidophilum*** (Figure 7) (Martin & Chintalapati 1989). Martin and Chintalapati found that the culture did not produce any better concentration of the fungus dry weight than when they used a diluted ***Sphagnum*** (Figure 1) peat hydrolysate as the substrate source. Martin and Chintalapati (1990) considered that the higher production of nutrients such as nitrogen in the fish offal mixed with peat made this a "promising" source of protein produced by ***Scytalidium acidophilum***.

Figure 7. ***Scytalidium*** sp. ***Scytalidium acidophilum*** is a promising source of protein when grown in fish offal with peat. Photo by Gerardo Garcia-Aguirre, Virginia Vanzinni-Zago, Hugo Quiroz-Mercado, through Creative Commons.

Johnson *et al*. (1992) similarly worked with people from the Wisconsin Sea Grant Inst to find a suitable use for fish by-products to provide a useful compost. They found that the wide range of values for the C:N ratios and other properties related mostly to the initial C:N ratio and the time the mix of peat and fish by-products had been allowed to cure. The ***Sphagnum*** (Figure 1) peat fish by-product composts, especially those with higher C:N ratios, compared well with commercial fertilized mixes.

As with human waste, destruction of pathogens is important for the fish waste, but Liao and coworkers (Liao 1997; Liao *et al*. 1997) found that the rise in temperature during composting, plus the ammonia and volatile fatty acids produced, were sufficient to destroy the pathogens. Addition of fir (*Abies*) or alder (*Alnus*) chips (Figure 8) caused the compost to stabilize sooner.

Figure 8. Wood chips like those used to stabilize the fish offal/***Sphagnum*** compost and destroy pathogens. Photo through Creative Commons.

The addition of ***Sphagnum fuscum*** (Figure 9) peat to hog manure reduced the volatile loss of ammonia, a primary source of nitrogen, by 75%, mainly due to lowered *p*H, making it a more suitable fertilizer (Al-Kanani *et al*. 1992a). It offers the added advantage of preventing release of offensive odors caused by 1,2-ethanediamine, methyl hydrazine, N-methyl methanamine, 3-methyl 2-butanamine, ethanethioic acid, and methanethiol (Al-Kanani *et al*. 1992b).

Figure 9. ***Sphagnum fuscum*** combined with hog manure makes a suitable fertilizer high in nitrogen. Photo by Michael Lüth, with permission.

Rao and Burns (1990) found yet another way of providing nitrogen in the culture of oil-seed rape. They provide **Cyanobacteria** (nitrogen fixers; Figure 10) and bryophytes in the growing medium. Bryophytes are well known for their ability to harbor **Cyanobacteria**.

Miller (1981) found that bryophytes can even increase the buffering capacity of the soil, surprisingly even against the abrupt changes resulting from fertilizer. And as a mulch, the slow decomposition of peat mosses makes them much more long-lasting than leaf litter and compost.

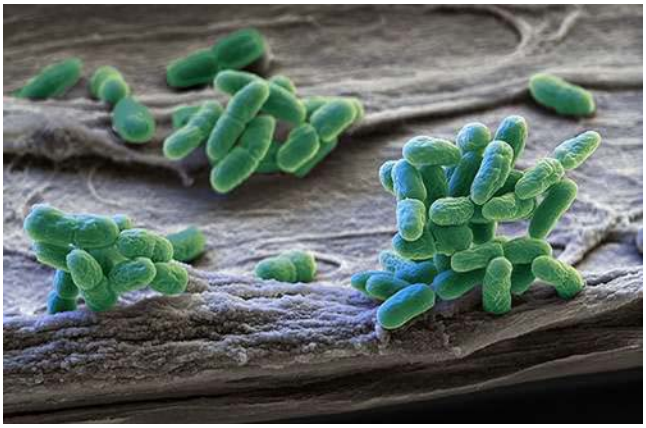

Figure 10. SEM image of ***Synechocystis*** (***Cyanobacteria***) on substrate. Photo from BASF, through Creative Commons.

Mosses such as ***Sphagnum*** (Figure 1) retain moisture and prevent weed growth, while at the same time discouraging damping-off fungi (Miller & Miller 1979).

Culturing

Some mosses, for example the epiphytic ***Octoblepharum albidum*** (Figure 11), are especially suitable for growing hard-to-grow epiphytic ferns (Arzeni 1963). In the Philippines, ***Leucophanes octoblepharioides*** (see Figure 12) and other members of the family are used by gardeners and plant growers instead of peat moss in potting new plants (Ben C. Tan, pers. comm.). ***Leucobryum*** (Figure 13) is a suitable medium for inducing good root sprouts on orchid cuttings, sold at U.S. $0.50 per kilo (in 1963), increased to US $1 in 1986 (Tan 2003). The most popular moss medium for growing orchids, most of which are likewise epiphytes, is ***Sphagnum*** (Figure 1), but mosses like ***Homalothecium arenarium*** (Figure 14), ***Hypnum imponens*** (Figure 15-Figure 16), ***Leucobryum*** spp. (Figure 13), ***Rhytidiopsis robusta*** (Figure 17), and ***Thuidium delicatulum*** (Figure 18) are also useful (Perin 1962; Adderley 1964, 1965). Chen and Chang (2000a, b) had almost 100% survival success when growing the orchid *Oncidium* (Figure 19) from callus explants on ***Sphagnum*** peat. Whereas most of their culture media produced abnormal shoots, both embryo-and shoot-bud-derived regenerants developed into healthy plantlets when potted in ***Sphagnum*** and acclimatized in the greenhouse.

Figure 11. ***Octoblepharum albidum***, a moss suitable for growing hard-to-grow epiphytic ferns. Photo by Niels Klazenga, with permission.

Figure 12. ***Leucophanes*** sp. ***Leucophanes octoblepharioides*** is used instead of peat moss in the Philippines for planting new plants. Photo by Niels Klazenga, with permission.

Figure 13. This epiphytic species of ***Leucobryum*** demonstrates its suitability for supporting root growth by hosting an epiphytic fern. Photo by Janice Glime.

Figure 14. ***Homalothecium aureum*** may be used as a substitute for peat in potting young plants. Photo by Jan-Peter Frahm, with permission.

Figure 15. ***Hypnum imponens*** growing in a sheet on a log. Photo by Janice Glime.

Figure 16. ***Hypnum imponens***, a moss that may be used as a substitute for peat in potting young plants. Photo by Janice Glime.

Figure 17. ***Rhytidiopsis robusta***, a moss that may be used as a substitute for peat in potting young plants. Photo by Blanka Shaw, with permission.

Figure 18. ***Thuidium delicatulum***, a moss that may be used as a substitute for peat in potting young plants. Photo by Janice Glime.

Figure 19. New ***Oncidium*** hybrid pseudobulb that must form a mycorrhizal connection. Photo by Consuelo Tugnoli, through Creative Commons.

But one consideration is that orchids are **mycorrhizal** (see Figure 20). That means they require an appropriate fungal partner in order to successfully form plants from seeds or cuttings. Kreier (2003) reasoned that a fungus that was mycorrhizal to bryophytes might be a good place to find a proper associate for the orchids. Several members of the liverwort family **Aneuraceae** (Figure 21) are mycorrhizal in association with the fungal genus ***Tulasnella*** (Figure 21-Figure 22). Kreier reasoned that if the orchids have the same mycorrhizal fungi, then it should be possible to use those liverwort associations to inoculate the orchids with mycorrhizae from the liverworts. Oberwinkler *et al*. (2017) reported ***Tulasnella*** species are worldwide and likewise are associated with orchids on a global scale. The possibilities look good.

Figure 20. Mycorrhizal root tips of an ***Amanita*** mushroom, partnering with a tree. Photo by Ellen Larsson, R. Henrik Nilsson, Erik Kristiansson, Martin Ryberg, and Karl-Henrik Larsson, through Creative Commons.

Figure 21. ***Cryptothallus*** (white; in **Aneuraceae**) and ***Pinus pinaster-Tulasnella*** ectomycorrhizae. Photo courtesy of Martin Bidartondo.

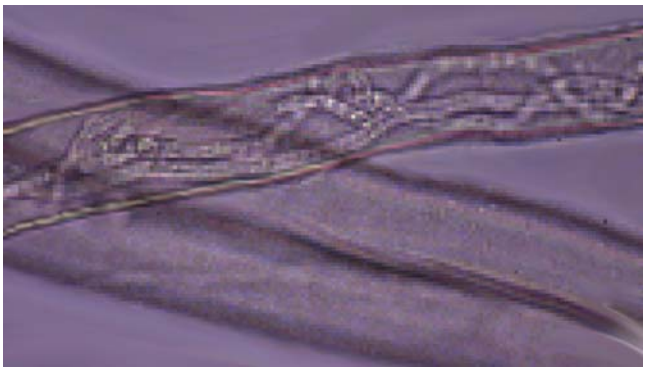

Figure 22. ***Cryptothallus*** rhizoids colonized by ***Tulasnella*** hyphae in a microcosm. Photo courtesy of Martin Bidartondo.

Air Layering

Horticulturists may have learned some lessons from nature. Mosses in nature provide suitable media for air layering of plants like the heath shrub *Calluna* (Figure 23) (Scandrett & Gimingham 1991; MacDonald *et al*. 1995) and even some tropical trees. MacDonald and coworkers (1995) demonstrated that layering was actually associated with the absence or low abundance of the mosses ***Hypnum cupressiforme*** (Figure 24) and ***H. jutlandicum*** (Figure 25) and *Cladonia* lichens (*e.g*. Figure 26). On the other hand, there seems to be a weak connection with layering in ***Sphagnum*** spp. (Figure 1), ***Leucobryum glaucum*** (Figure 27), and pleurocarpous mosses other than ***Hypnum***.

Figure 23. *Calluna vulgaris*, a species that undergoes air layering in mosses in nature. Photo by Willow, through Creative Commons.

Figure 24. ***Hypnum cupressiforme***, a moss that is negatively associated with air layering of *Calluna* in nature. Photo by Michael Lüth, with permission.

Figure 25. ***Hypnum jutlandicum***, a moss that is negatively associated with air layering of *Calluna* in nature. Photo by Janice Glime.

Figure 26. ***Cladonia fimbriata***, a moss that is negatively associated with air layering of *Calluna* in nature. Photo by Paul Cannon, through Creative Commons.

Figure 27. ***Leucobryum glaucum***, a moss that can contribute to air layering of *Calluna*. Photo by Janice Glime.

Despite these somewhat weak connections for ***Calluna*** (Figure 23), mosses, especially ***Sphagnum*** (Figure 1), are used almost exclusively for air layering as a means of propagation of plants. The moss is wrapped (Figure 28) around the area where roots (Figure 29) are to be encouraged, often held in place with cloth mesh, wire, or dark plastic (Figure 30). The moss provides a continuous supply of moisture and encourages the development of adventitious roots while discouraging fungi. Once the roots have formed, the stem can be cut below that point and the explant grown into a new individual (Figure 31). Pant (1989) reports similar use for grafting fruit trees.

Figure 28. Wrapping the tree with ***Sphagnum*** for air layering to make a bonsai. Photo from Bonsai Eejit, through Creative Commons.

Figure 29. Removal of part of the air layer, exposing roots and new branches of a bonsai. Photo from Bonsai Eejit, through Creative Commons.

Figure 30. Bonsai showing air layering with ***Sphagnum***. Photo from Bonsai Eejit, through Creative Commons.

Figure 31. Air layer of oak using moss to make bonsai. Photo from Bonsai Eejit, through Creative Commons.

In addition to its ability to promote root sprouts in orchid cuttings, ***Sphagnum*** (Figure 1) is suitable for air layering of a number of kinds of plants, including trees for bonsai (Tan 2003). The moisture and antimicrobial properties are beneficial in the development of new shoots and roots.

It appears that preparing a tree for bonsai often involves air layering with mosses (Morrow 2001; Hasegawa 2002; Relf 2009). In their book on bonsai, Yoshimura and Halford (1957) provide instructions for making a bonsai. Mosses, usually ***Sphagnum*** (Figure 1), are wrapped around the stem, including a location with young buds, and covered with a material like plastic to retain the moisture. If the plastic is transparent, you can see when the new roots and branches have formed. The lower part of the old stem is then cut off and the layering removed. The bonsai is ready for planting.

Pot Culture

Mosses can also encourage growth of potted plants. Pant (1989) reports that *Begonia* (Figure 32) and *Fuchsia* (Figure 33) bud and flower more profusely in pots where mosses are used to separate the humus-rich top soil from the bottom soil. Members of the Ericaceae, in particular, benefit from the acid of peat mosses. But in Japan, ***Hypnum plumaeforme*** (Figure 34), ***Leucobryum bowringii*** (Figure 35), ***L. neilgherrense***, and occasionally ***L. scabrum*** (Figure 36) fragments are used, mixed with sand or soil, to cultivate *Rhododendron* (Figure 37) shrubs (Ando 1957). Could it be that these mosses also acidify the soil?

Figure 33. Potted *Fuchsias*, a genus whose growth is encouraged by potting with mosses in the mix. Photo by pxhere, through Creative Commons.

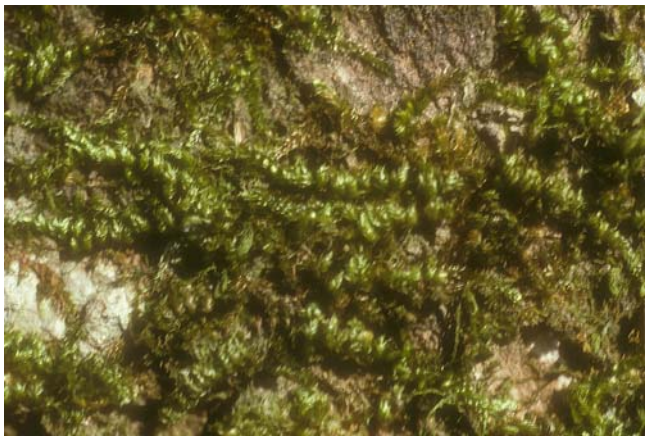

Figure 34. ***Hypnum plumaeforme***, a species used in Japan with sand or soil to cultivate *Rhododendron* shrubs. Photo by Janice Glime.

Figure 32. Potted begonias, a genus whose growth is encouraged by potting with mosses in the mix. Photo by Pixabay, through Creative Commons.

Figure 35. ***Leucobryum bowringii***, a species used in Japan with sand or soil to cultivate *Rhododendron* shrubs. Photo through Creative Commons.

Figure 36. ***Leucobryum scabrum***, a species used in Japan with sand or soil to cultivate *Rhododendron* shrubs. Photo Taiwan Encyclopedia of Life, through Creative Commons.

Figure 37. *Rhododendron*, a genus that benefits from having mosses in the potting mix. Photo by Pete Bobb, through Creative Commons.

The forestry industry likewise finds peat invaluable for culturing young seedlings (see also Reforestation below). Heiskanen and Rikala (2000) found ***Sphagnum*** (Figure 1) peat to be superior to fine sand or peat with perlite, the latter resulting in more weakened seedlings as a consequence of the lower water retention of the medium. However, peat is not always readily available. Israeli researchers found that composted cattle manure mixed with grape marc were good substitutes for peat in that country where peat must be imported; the substitutes were likewise effective at suppressing plant pathogens (Chen *et al*. 1992).

In other cases, the pots themselves (Figure 38) are made of mosses. These are good for starting seedlings and can be planted without removing the plants. Roots will eventually penetrate the pot and grow into the soil.

Figure 38. 3-Inch Jiffy pot of peat moss fibers from Second Sun Garden Supply. Photo from Second Sun Garden Supply, modified by Janice Glime.

Potting Medium

In parts of Asia, horticultural mosses include ***Vesicularia*** (Figure 39), ***Bazzania*** (Figure 40), ***Heteroscyphus*** (Figure 41), and ***Pallavicinia*** (Figure 42) (Tan 2003). Orchid growers in particular use ***Leucobryum*** (Figure 35-Figure 36, Figure 43) and ***Sphagnum*** (Figure 1, Figure 44), especially for their ability to store large amounts of water in their **hyaline cells (**Figure 43-Figure 44).

Figure 39. ***Vesicularia vesicularis*** var. ***vesicularis***. The genus ***Vesicularia*** is among the horticultural mosses in Japan. Photo by Michael Lüth, with permission.

Figure 40. ***Bazzania trilobata***, a leafy liverwort. The genus ***Bazzania*** is among the horticultural bryophytes used in Japan. Photo by Ondřej Zicha (Discover Life), through Creative Commons.

Figure 41. ***Heteroscyphus fissistipus***, a leafy liverwort. The genus ***Heteroscyphus*** is among the horticultural bryophytes used in Japan. Photo by David Francis, through Creative Commons.

Figure 42. ***Pallavicinia lyellii***, a thallose liverwort. The genus ***Pallavicinia*** is among the horticultural bryophytes used in Japan. Photo by Des Callaghan, with permission.

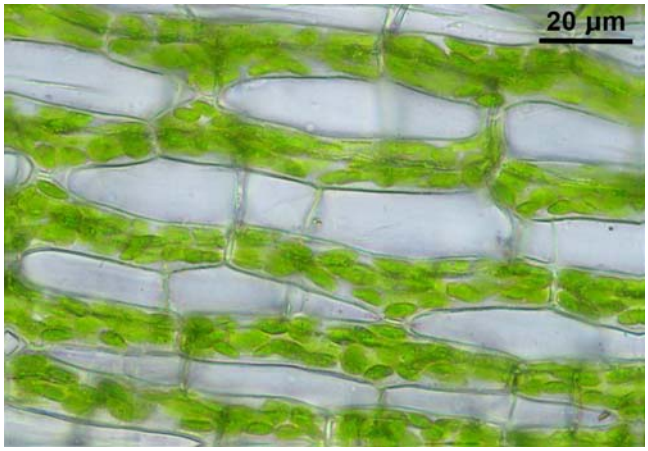

Figure 43. ***Leucobryum glaucum*** leaf cells showing alternating hyaline and photosynthetic cells. Photo by Ralf Wagner <www.drralf-waner.de>, with permission.

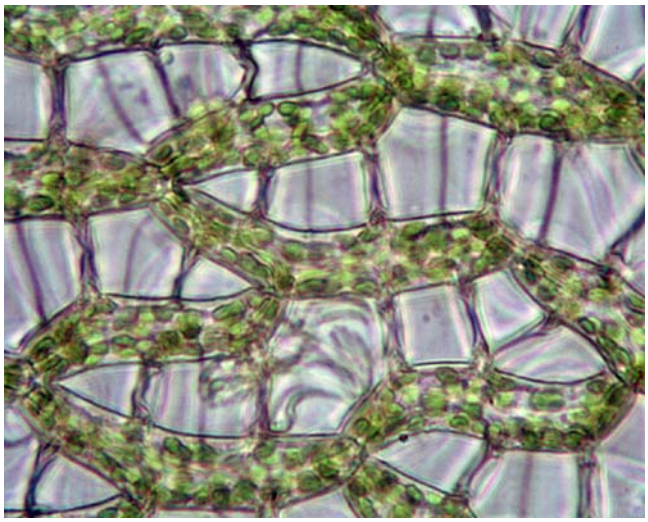

Figure 44. ***Sphagnum palustre*** photosynthetic (green) and hyaline cells. Note that the hyaline cells are not short cells, but are elongate cells with bars across them. Photo by Malcolm Storey through Creative Commons.

Sphagnum (Figure 1) and ***Leucobryum*** (Figure 35-Figure 36) seem to be particularly preferred as a potting medium for orchids (Tan 2003). Tan reported the use of ***Leucobryum*** as a substitute for peat moss to grow orchid cuttings in Asia. The mosses, especially ***Sphagnum***, were good as a potting medium for a variety of seeds.

But in North America, diversity of mosses as a potting medium seems to be absent. I searched with Google for "potting medium moss" and stopped after the 20th hit. All 20 of the mosses were named as peat moss or ***Sphagnum*** (Figure 1).

Dangers of Peat Culturing

There are drawbacks to using mosses in culturing of some plants. We have seen that ***Sphagnum*** (Figure 1) can be dangerous because of its cohabiting fungus that causes **sporotrichosis** (Chapter 1 of this volume). In containers of conifer seedlings, they can choke young seedlings, compete for nutrients, and repel water (Haglund *et al*. 1981). But they can also pose serious dangers. But causing fires? As Michael Richardson shared with Bryonet on 20 June 2013,

peat, including shrubs and other debris along with the mosses, is good potting material, but it can be flammable under the wrong circumstances. The oxygen available in the pot can permit decay to occur, causing heat that is amplified if the pot is in the sun. An article in the *Northumberland News* reported a house fire in June 2013 that was attributed to a pot with peat mosses on a second floor balcony. The deputy chief of the fire department said that the dry peat can easily ignite and can, after being in direct sunlight long enough, ignite by itself. This was not his first experience with flower beds on fire. His advice is to use non-combustible flower pots (not plastic), such as concrete or metal.

Covering Pot Soil

Sheet mosses are frequently used to cover the soil in pots housing flowering plants (Nelson & Carpenter 1965). This is especially true when they are sold by florists. Species of ***Leucobryum*** (not a sheet moss; Figure 35-Figure 36) can be used for this purpose, providing a pale green color contrast to the green of most tracheophyte leaves. In some cases, the strong anti-microbial properties of bryophytes might reduce invasions of bacteria and fungi.

Mat-forming mosses are typically sold as sheet mosses (Figure 45) (Peck *et al*. 2001). These are pleurocarpous mosses that grow horizontally, often on logs. Collectors strip the logs, and sometimes low branches, of their mats. In the eastern USA, one of the mosses used is ***Thuidium*** (Figure 46).

Figure 45. A package of sheet moss being sold in a gardening shop in Ohio, USA. Photo by Janice Glime.

Figure 46. ***Thuidium*** sheet moss, sold at a gardening shop in Ohio, USA. Photo by Janice Glime.

Culturing Mushrooms and Other Fungi

Sphagnum (Figure 1) peat is the substrate of choice as casing medium for cultivating the common grocery store mushroom, *Agaricus bisporus* (Figure 47) (Eicker & van Greuning 1989; Reddy & Patrick 1990; Jarial *et al*. 2005). (Casing is the process in which a non-nutritious layer, in this case peat, is applied over the colonized substrate so that the mycelium has access to more moisture, thereby increasing the size and number of growths.) Sungrow had a multi-million-dollar contract from Campbell (of Campbell soup fame) to improve mushroom culturing using a ***Sphagnum*** mix (Vitt, pers. comm.; Miller 1981). However, in places such as South Africa, where there is no peat, substitutes are necessary. The need for peat substitutes led Eicker and van Greuning (1989) to test other substrata and compare, but peat still gave the highest yields compared to eight other materials, with only weathered, spent compost offering similar results. Other types of mushrooms are grown in peat as well, such as *Pleurotus ostreatus* (Figure 48) (Manu-Tawiah & Martin 1986).

Figure 47. *Agaricus bisporus*, a species commonly grown in ***Sphagnum***. Photo by I. G. Safonov, through Creative Commons.

Figure 48. ***Pleurotus ostreatus*** on a mossy tree trunk. This species can be cultivated in peat. Photo from Charl de Mille-Isles.

In an attempt to make further improvements in mushroom success, Beyer (1997) sought ways to reduce the effect of accumulated substances on late mushroom crops. Surprisingly, he found that the addition of ***Hypnum*** (Figure 15-Figure 16, Figure 24-Figure 25) peat to the compost improved later break yield, but the addition of ***Sphagnum*** (Figure 1) did not. One of the concerns is that the peat becomes infested with nematodes (Figure 49) and may carry *Pseudomonas tolaasii* (see Figure 50), the cause of bacterial blotch, both of which cause serious diseases to the mushrooms (Nikandrow *et al*. 1982).

Figure 49. Soil nematode, a common pest in ***Sphagnum*** that may carry the bacterium ***Pseudomonas tolaasii***. Photo by Christina Menta, through Creative Commons.

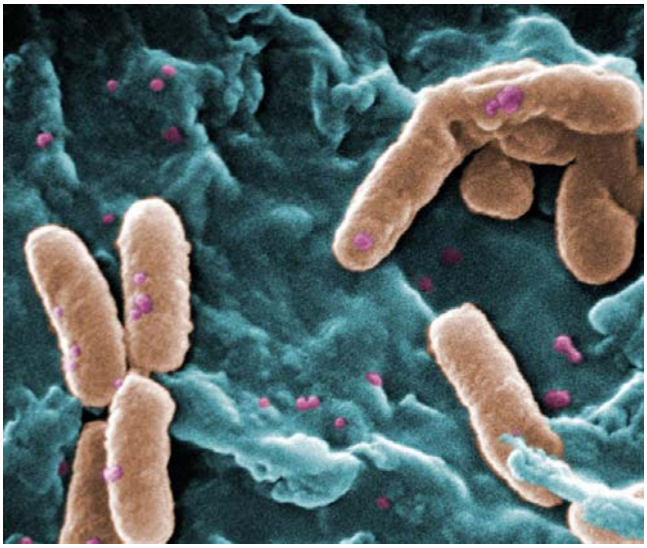

Figure 50. *Pseudomonas*, a bacterium carried by soil nematodes. Photo by Janice Carr, through public domain.

Martin and Bailey (1983) succeeded in using peat as a fermentation medium in which acclimated fungi could be grown. They were more successful with the common mushroom *Agaricus campestris* (Figure 51) than with the morel *Morchella esculenta* (Figure 52) (Martin 1982). Martin and Bailey considered that growth inhibitors might be present in peat. Using sulfuric acid hydrolysates with autoclaved peat released a liquid that, when supplemented with nutrients, would enhance growth and crude protein content of these two edible fungi. Nutrient-supplemented peat hydrolysates enhance growth and crude protein content of fungal biomass.

Figure 51. ***Agaricus campestris***, a species that grows well in a peat fermentation medium. Photo by Andreas Kunze, through Creative Commons.

Figure 52. *Morchella esculenta*, the common morel, can be cultured in a bed of peat. Photo by Janice Glime.

A mixture of ***Sphagnum*** (Figure 1) with fish offal promises to be a suitable substrate for culturing the acid-tolerant fungus *Scytalidium acidophilum* (see Figure 7), which is considered to be a promising source of microbial protein (Martin & Chintalapati 1990). However, not all fungal cultures seem to benefit from peat mixtures. In one commercial operation, the yield of mushrooms improved when the peat was omitted from the cultivation medium (Smith 1983).

Reforestation

The genus ***Tulasnella*** (Figure 21-Figure 22) is a mycorrhizal partner with several members of the thallose liverwort family **Aneuraceae** (Figure 21). If this fungus is likewise a partner with trees, then it should be possible to use those liverworts to help the trees to become established (Kreier 2003). In fact, ***Cryptothallus*** (Figure 21), a member of the **Aneuraceae**, shares its fungal partner with at least some members of the birch (*Betula*; Figure 53) and pine (*Pinus*; Figure 54) genera. Kreier found that both liverworts ***Riccardia palmata*** (Figure 55) and ***R. latifrons*** (Figure 56) grew on rotten wood and were well infected by

mycorrhizal fungi. Kreier also figured it would be relatively easy to disperse these liverworts on the forest floor, and that they would spread easily, preparing the soil with mycorrhizae that could partner with the trees. At that time, the fungi had been grown in culture but not the field. However, the discovery of rhizoidal bridges in tropical ***Aneura*** (**Aneuraceae;** Figure 57) provided a hopeful twist. In 2017, Oberwinkler *et al*. noted that ***Tulasnella*** species are worldwide in distribution and that they may occur in many forest ecosystems in association with wood. And we have already noted that they form mycorrhizal associations with orchids.

Figure 53. *Betula pendula*. Some members of the genus *Betula* share their fungal partner with the thallose liverwort ***Cryptothallus***. Photo by Percita, through Creative Commons.

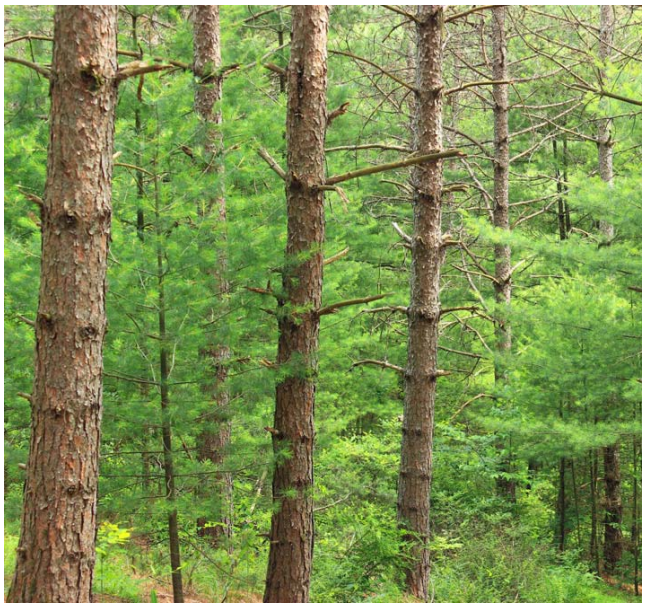

Figure 54. *Pinus strobus*. Some members of the genus *Pinus* share their fungal partner with the thallose liverwort ***Cryptothallus***. Photo through Creative Commons.

Figure 55. ***Riccardia palmata***, a species that grows on rotten wood and is infected by mycorrhizal fungi. Photo by Bernd Haynold, through Creative Commons.

Figure 56. ***Riccardia latifrons***, a species that grows on rotten wood and is infected by mycorrhizal fungi. Photo by Bernd Haynold, through Creative Commons.

Figure 57. ***Aneura pinguis***, a species that might be associated with ***Tulasnella*** on wood. Photo by Li Zhang, with permission.

Container Gardens

Mosses are commonly used in container gardens with **bonsai** (dwarfed ornamental tree; Figure 58) and **bonkei** (tray landscape; Figure 59), where they help to stabilize the soil and retain moisture for the shallow roots.

Figure 58. Bonsai at Dawes Arboretum, Ohio, USA, showing dwarfed tree and mosses at base. Photo by Janice Glime.

Figure 59. Outdoor bonkei in a Japanese private garden. *Selaginella*, a relative of club mosses and not a true moss, is used to represent a tree, with mosses growing on the rocks that form the basin for a small "lake." Photo by Janice Glime.

Designers select the species of mosses to serve particular functions in the container landscapes. Large, upright mosses such as ***Atrichum*** (Figure 60), ***Climacium*** (Figure 61), ***Dicranum*** (Figure 4), ***Polytrichum*** (Figure 62), and ***Rhodobryum*** (Figure 63) simulate forests. ***Bryum argenteum*** (Figure 64) has a silvery, compact look that can simulate grasslands, and ***Leucobryum*** (Figure 27) usually has the role of a mountain. For snow-capped mountains, ***Racomitrium canescens*** (Figure 65) provides a frosted look. ***Physcomitrium*** (Figure 66-Figure 67), often a volunteer in greenhouse flower pots, is so miniature as to appear like a moss, or maybe a grass, in a landscape of ***Leucobryum*** mountains. ***Barbula unguiculata*** (Figure 68), ***Funaria hygrometrica*** (Figure 69), and ***Weissia controversa*** (Figure 70) can contribute to needs of intermediate size. In Mexico, some mosses are even used for fake bonsai: ***Campylopus*** (Figure 71), ***Dendropogonella rufescens***, ***Hypnum*** (Figure 15-Figure 16, Figure 24-Figure 25, Figure 34), and ***Thuidium*** (Figure 18) (C. Delgadillo, pers. comm.). In the Pacific Northwest of North America, ***Leptobryum pyriforme*** (Figure 72), known as Kyoto moss, is sold for bonsai trays (J. Christy, pers. comm.). I would expect ***Climacium*** and ***Polytrichum*** to serve well as trees in miniature landscapes as well.

Figure 60. ***Atrichum angustatum***, in a genus used to simulate forests in tray gardens. Photo by Keith Bowman, with permission.

Figure 61. ***Climacium dendroides***, simulating trees in a dish garden. Photo by Keith Bowman, with permission.

Figure 62. ***Polytrichum juniperinum***, in a genus used to simulate forests in tray gardens. Photo by Janice Glime.

Figure 63. ***Rhodobryum roseum***, in a genus used to simulate forests in tray gardens. Photo by Michael Lüth, with permission.

Figure 64. ***Bryum argenteum***, a species used to simulate grasslands or mountains in tray gardens. Photo by Tushar Wankhede, with permission.

Figure 65. ***Racomitrium canescens***, a moss that is used to simulate snow on mountains. Photo by Michael Lüth, with permission.

Figure 66. ***Physcomitrium pyriforme*** in a dish garden. Photo by Michael Lüth, with permission.

Figure 67. ***Physcomitrium pyriforme*** with capsules, a common volunteer in flower pots. Photo by Janice Glime.

Figure 68. ***Barbula unguiculata***, a moss of intermediate size to fill in as grass or other intermediate needs. Photo by Michael Lüth, with permission.

Figure 69. ***Funaria hygrometrica***, a moss of intermediate size to fill in as grass or other intermediate needs. Photo by Michael Lüth, with permission.

Figure 70. ***Weissia controversa***, a moss of intermediate size to fill in as grass or other intermediate needs. Photo by Michael Lüth, with permission.

Figure 71. ***Campylopus introflexus***; the genus ***Campylopus*** is used in Mexico for fake bonsai. Photo by Michael Lüth, with permission.

Figure 72. ***Leptobryum pyriforme***, a species that is used in the Pacific Northwest, USA, in bonsai trays. Photo by Michael Lüth, with permission.

Bonkei

Miniature tray landscapes [bonkei or **saikei** (art of creating tray landscapes that combine miniature living trees with soil, rocks, water, and related vegetation); Figure 73-Figure 76] in Japan use mosses to provide appropriate texture and color with little danger of damage due to drying (Kawamoto 1980; Oishi 1981). Such trays can delight the bed-ridden. Gerritson (1928) arranged sixteen species of mosses in various stages of maturity to provide a changing landscape for a hospitalized friend: "Each day the mosses had changed appearance; so each day added a new joy. The nurses came from time to time to see and admire. Other patients shared its freshness and beauty. Visitors, too were invited to see the charm of a 'platter of mosses.'"

Figure 73. Bonkei with its miniature landscape containing mosses to simulate mountains. Photo courtesy of Hironori Deguchi.

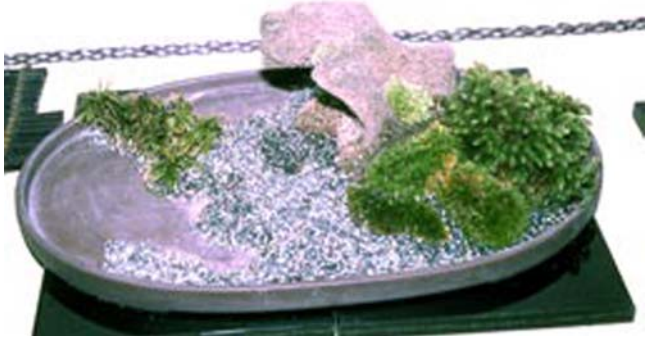

Figure 74. Bonkei with mosses simulating trees with a rocky crag. Photo courtesy of Hironori Deguchi.

Figure 75. Bonkei simulating a volcano and surrounding mountains and forests. Photo courtesy of Hironori Deguchi.

Figure 76. *Selaginella* (a club moss relative) and moss bonsai, Kyushu, Japan. Photo by Janice Glime.

For making these miniature landscapes, Schenk (1997) recommends the usual potting mix of humus, including peat moss, ground-up tree bark, or rotted sawdust. He cautions that sand, vermiculite, or perlite can be used, but that they must be kept moist because they tend to have larger spaces and dry quickly near the surface, leaving the moss with no source of moisture.

Even in this seemingly harmless occupation, one must use caution against allergens. Tray gardens and other forms of bonsai and dish gardens may use ***Sphagnum*** (Figure 1) peat as a medium or even as the plants of interest (Figure 77). This moss is well known for its ability to harbor the fungus that causes sporotrichosis (Dong *et al*. 1995).

Figure 77. ***Sphagnum*** moss pot in Japan, a potential source of allergens. Photo courtesy of Hironori Deguchi.

Dish Gardens

Dish gardens (Figure 78) are a scaled down version of bonkei. The size may not be scaled down, but they typically do not represent a landscape and may have only one bryophyte species (Figure 78), sometimes as ground cover for flowering plants like spring bulbs (Figure 79).

Figure 78. Dish garden of moss. Photo courtesy of J. Paul Moore.

Figure 79. Dish garden for spring bulbs in cafe in Helsingborg, Sweden. Photo courtesy of Irene Bisang.

Figure 80. A cross between a bonsai arrangement and a dish garden. Photo courtesy of Lars Hedenas and Irene Bisang.

Annie Martin, a prize-winning gardener and landscaper (Figure 81), runs classes for both adults and children in which she teaches them how to make dish gardens and terraria (Figure 82-Figure 83).

Figure 81. The award-winning creator (Annie Martin) of dish gardens, terrariums, and moss gardens is shown here framed by her own artistic bryophyte creation. Photo courtesy of Annie Martin.

Figure 82. Children creating their first dish garden, under the tutelage of Annie Martin, MountainMoss. Photo courtesy of Annie Martin.

Figure 83. The proud owner of a new dish garden that she created. Photo courtesy of Annie Martin.

Similar to the dish gardens, moss rocks (Figure 84-Figure 85) have become popular in some places. These typically have a species of moss growing in a depression or on the surface of a rock.

Figure 84. ***Dicranodontium denudatum*** stone pots in shop in Hakone, Japan. These are a variation on the dish garden, but the mosses are grown on the surface or in a depression of a natural rock and typically have only one moss species. Photo courtesy of Hironori Deguchi.

Figure 85. Moss-Rocks-logo at Moss and Stone Gardens, Pennsylvania, USA, showing a more formal American version. Photo with permission from David Smith.

Bonsai

The term **bonsai** (Figure 86) refers to a dwarfed ornamental tree or shrub grown in a pot and prevented from reaching its normal size. Inoue (1972) pointed out that moss bonsai and moss bonkei (tray landscapes) are popular in Japan by both amateurs and professional horticulturists. But even bonsai trees are potted in wide pots and the soil is typically covered with mosses (Figure 86-Figure 89).

Figure 86. Bonsai at Dawes Arboretum, Ohio, USA, showing the dwarfed tree and mosses at its base. Photo by Janice Glime.

Figure 87. This bonsai arrangement incorporates features of bonkei with rocks and mosses giving it the look of a miniature forest. Photo by Janice Glime.

Figure 88. Bonsai at Dawes Arboretum, Ohio, USA. This bonsai uses a deciduous tree, and bryophytes can warn its owner to water it before the leaves begin to drop or become crispy. Photo by Janice Glime.

Figure 89. Bonsai using the fern ***Osmunda lancea***. Courtesy of Hironori Deguchi.

The mosses can contribute to the success of the bonsai. When the mosses appear dry, you can be sure your bonsai needs water (Figure 90-Figure 91). However, mosses are not always the friends of the bonsai. The continuous moisture of the mosses can inhibit root growth and promote sudden fungal attacks. The experts advise removing the mosses each autumn to reduce fungal damage (Bland 1971).

Figure 90. Bonsai in Dawes Arboretum, Ohio, USA. Mosses on the roots are a good indicator when the soil is becoming dry and the tree needs water. Photo by Janice Glime.

Figure 91. Bonsai on wood, increasing the need for bryophytes to maintain root moisture and warn when it is time to water it. Photo courtesy of Annie Martin, MountainMoss.

In India, bonsai is included in horticultural texts. Dhanda (1984) suggests that the bonsai may be finished off with a layer of moss on top (Figure 92). Yoshimura and Halford (1957) likewise consider the mosses growing around the bonsai to be important. The mosses provide several advantages. They add aesthetic appeal, creating a more natural looking landscape. And they make watering easier, permitting a raised base on the tree while catching the water and protecting the furniture.

Figure 92. Bonsai at Dawes Arboretum, Ohio, USA, illustrating mosses covering the pot and signalling when the tree roots need more water. Photo by Janice Glime.

In Malaysia, bonsai makers typically use the acrocarpous mosses ***Bryum*** (Figure 93) and ***Philonotis*** (Figure 94), and sometimes the pleurocarpous mosses ***Isopterygium/Pseudotaxiphyllum*** (Figure 95) and ***Vesicularia*** (Figure 39) and the thallose liverwort ***Riccia*** (Figure 96) (Tan 2003). In Singapore, the moss ***Ochrobryum kurzianum*** is imported from Thailand for ornamental use in bonsai arrangements. In Japan, ***Leucobryum*** (Figure 27) is common in bonsai landscape design.

Figure 93. ***Bryum capillare*** with capsules, in a genus used in bonsai in Malaysia. Photo by Michael Lüth with permission.

Figure 94. ***Philonotis fontana***, in a genus used in bonsai in Malaysia. Photo by Michael Lüth, with permission.

Figure 95. ***Pseudotaxiphyllum elegans***, in a genus used in bonsai in Malaysia. Photo by J. C. Schou, with permission.

Figure 96. ***Riccia sorocarpa***, in a genus used in bonsai in Malaysia. Photo by <www.aphotofauna.com>, with permission.

Hanging Baskets

Mosses are often used in the construction of hanging baskets for flowers (Smith 1996). In California, USA, meter-long "strips" 8-10 cm wide are used to make hundreds of baskets per week!

In Asia, species of ***Sphagnum*** (Figure 1) are used to line hanging baskets (Tan 2003). Its ability to hold water and its antimicrobial activity make this a good substrate for the roots of flowering plants.

A wire frame is used to give the basket support, with mosses wound among the wires or laid within to provide the structure. Not only do they make an attractive, natural-looking basket, but they reduce the need for frequent watering (Lohr & Pearson-Mims 2001). Species of ***Hypnum*** (Figure 15-Figure 16, Figure 24-Figure 25, Figure 34) and ***Sphagnum*** (Figure 1) are commonly used for this purpose.

The long, stiff stems of ***Polytrichum*** (Figure 62) permitted the early Romans to weave it into baskets (Bland 1971), but these most likely did not have a horticultural purpose.

Terraria

The **terrarium**, a drier plant version of the aquarium, is often arranged like an enclosed garden (Figure 97), a miniature garden like the container gardens. Because of its small size, bryophytes are often used to give the look of mountains (Figure 98); dry brooks made of pebbles ramble between clumps of various hues of green. But bryophytes are not easy to grow in such conditions. If the container is fully open (Figure 98, Figure 99), mosses soon dry out and become crispy. If it is sealed (Figure 97, Figure 100-Figure 103), as many terraria are, fungi can easily grow. The best choice is to leave the top partially open to permit air circulation.

Figure 97. Closed terrarium from MountainMoss, showing miniature garden. Photo courtesy of Annie Martin.

Figure 98. Open terrarium from MountainMoss. Note the mound of ***Leucobryum*** which is sometimes used to simulate mountains. Photo courtesy of Annie Martin.

Figure 99. Open terrarium with moss. Photo courtesy of J. Paul Moore, with permission.

Figure 100. In some covered terraria, small holes with plugs, similar to the green ones seen here, can be opened and even kept open to maintain at least some air movement and reduce condensation. Photo courtesy of Annie Martin of MountainMoss.

Figure 101. Tiered terrarium from MountainMoss. Photo courtesy of Annie Martin.

Figure 102. Terrarium with lid. Note the tiny figure that turns the tall mosses into "trees." Photo by Erin, through Creative Commons.

Figure 103. Tall moss terrarium that not only permits taller plants like ferns, but also provides more air space, reducing fungal takeover. Photo by Ken Gergle, through David Spain.

It seems appropriate to cite the first terrarium, known as the **Wardian case** (Figure 104), invented by Nathaniel Bagshaw Ward (1791-1868) (Hershey 1996). He had fallen in love with plants on a trip to Jamaica and despite ultimately pursuing a profession as a physician, he pursued plants through his attempts at gardening. But, sadly, his attempts at a moss and fern garden failed, due severe air pollution in the outskirts of London. It was this failure that led him to invent the Wardian case, or terrarium. He had placed a "chrysalis" (actually a moth pupa) in a bottle and observed it daily. Then, to his surprise, a "seedling" fern and a grass appeared. He considered the conditions and noted the need for "a moist atmosphere free from soot or other extraneous particles; light; heat; moisture; periods of rest; and change of air." He moved the bottle to the outside of a northern window and there the plants thrived for four years with no additional attention!

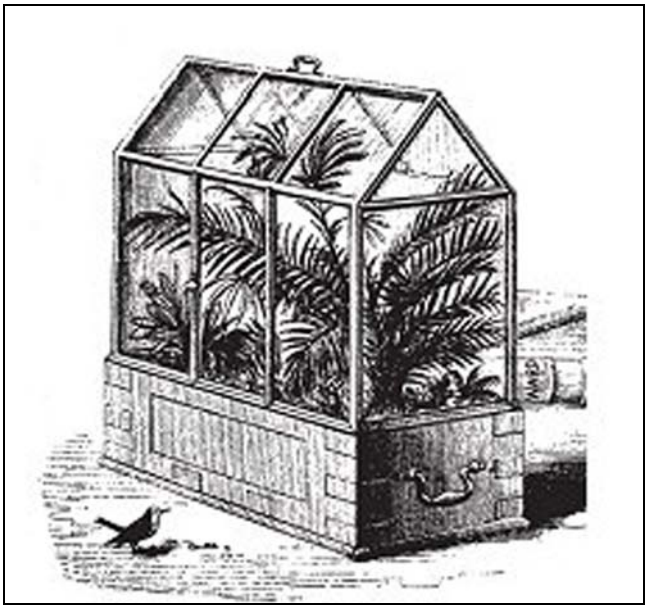

Figure 104. Wardian Case, similar to the first terrarium by Nathaniel Bagshaw Ward. Image through public domain.

Choice of mosses depends in part on how moist you intend to keep it and in part on the effect you want to achieve. ***Polytrichum*** (Figure 62) can survive in a somewhat dry terrarium but will easily be covered with mold when it is too damp. Likewise, ***Leucobryum*** (Figure 27) likes it airy with good circulation. ***Ceratodon purpureus*** (Figure 105) is sometimes successful, again requiring at least some air circulation. Schenk (1997) states, "I must tell the whole truth by identifying the great enemy of terrarium gardening with native woodlanders, for there is one: mold." He admonishes that most terraria have a short life due to this problem. My own experience certainly agrees.

Figure 105. ***Ceratodon purpureus***, a species used in bonsai in Malaysia. Photo by Michael Lüth, with permission.

Funaria hygrometrica (Figure 69) can be encouraged in more moist conditions, but it still needs circulation. With a little luck it will even produce capsules. We successfully maintained ***F. hygrometrica*** in an uncovered aquarium in our university greenhouse. These lasted for several years, but we avoided getting tap water on them and only used misting from distilled water or tap water that had been allowed to sit to allow the chlorine to escape.

Schenk (1997) suggests that a container the size of an aquarium (Figure 106) is best, smaller ones being more subject to mold. Air space is of the essence, and it needs to circulate. He considers a potting mix to be suitable, whereas it does not tend to work well in open-air gardens. On the other hand, if the bryophytes have their own deep brown portions (Figure 107), no substrate is necessary. Charcoal may be added to the substrate to absorb excessive acidity and gases produced by decay. Little water is needed as it will recycle (Figure 108) within the nearly sealed container. Adding flowering plants can add color (Figure 109). Mosses that are collected wet generally do not need additional water and may even need to be dried by leaving the terrarium open wide for a day or two. Slightly dry mosses can be moistened with 30-35 ml (2-3 tablespoons) of water; totally dry ones may require up to 70 ml (1/4 cup) (Schenk 1997).

Figure 106. Kitchen terrarium in an aquarium. Photo by Janice Glime.

Figure 107. ***Campylopus flexuosus*** with brown base, needing no substrate. Photo by Michael Lüth, with permission.

Figure 108. Condensation on wall of kitchen terrarium, endangering a mold outbreak. Photo by Janice Glime.

Figure 109. Mix of a variety of plants with color (red-leafed *Begonias*, pale *Tillandsias*) and rocks in kitchen terrarium built in an aquarium. Photo by Janice Glime.

Maintenance for the first few days after planting is essential to avoid an immediate mold attack. Schenk (1997) advises that if a heavy dew (Figure 108, Figure 110) appears on the walls of the container, open it and dry the walls. This should be repeated daily until morning brings only a light condensation on the upper half of the walls of the container. When you discover, probably in a few weeks, that there is no longer any morning dew, it is time to add water, but not much.

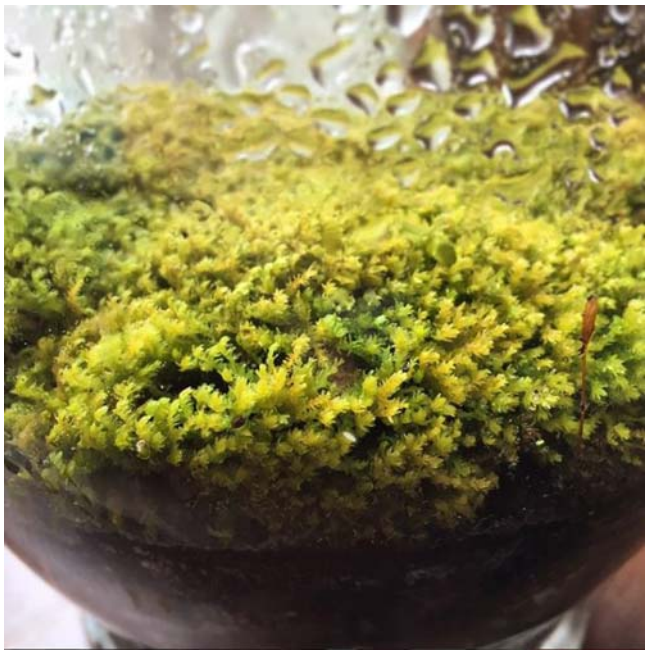

Figure 110. Terrarium with moss, showing severe condensation that must be removed by drying the walls or keeping the container open until it is gone. Photo by J. Paul Moore, with permission.

After all this care, Schenk (1997) warns that the terrarium will most likely last only three weeks! (I have had better success than that with larger aquaria.) That can be extended by providing fluorescent lights to avoid the etiolated growth so noticeable in low light. Nevertheless, a mold garden is most likely to ensue within this short time,

and great care and luck are needed to find the right wetting and drying cycle.

Within those first few weeks, a moss garden terrarium can be full of surprises, with mushrooms appearing, capsules extending, and the somewhat rapid but unnatural elongation of the moss stems in low light.

One of the contributors to the demise of the moss terrarium indoors is the warm temperatures night and day indoors. If there is a cool location for the terrarium, it might survive a longer display, and surely in the refrigerator it would last, but would be of little use, not to mention suffering from lack of light.

One last caution I would insert is that lichens are to be avoided if one wishes to maintain a moss terrarium for any length of time. In the moist conditions of confinement, they will soon spread their fungi broadly and overtake the moss, albeit no longer as lichens, but nevertheless encroaching rapidly upon the surfaces of green. If lichens are to be enjoyed in this terrarium, it must by all means be kept open and the mosses provided with water occasionally as needed, perhaps with dry periods, but not too frequently.

I was relieved to read this moss gardener's treatment of the terrarium. If such an expert as Schenk was able to maintain such a terrarium garden for only three weeks, I felt elated that I, too, had succeeded on occasion to maintain one for so long! In short, if you wish to maintain a terrarium of bryophytes for a lengthy period of time, my best advice to you is Good Luck!

Echoing the comments above, David Wagner (Bryonet 23 June 2013) suggested that the problem with terraria is that they are usually closed containers. He has observed mosses doing well for several years in an open water table where water flowed across the water table. This depends on water that is low in dissolved minerals and may require a filtering system on tap water. One danger in closed terraria, especially small ones, is that the enclosed humidity and lack of air movement encourages the growth of fungi and soon they take over.

Alison Downing (Bryonet 23 June 2013) reported success in growing bryophytes for display by using fish tanks for the mesic species. She attributed the success to using water from a garden pond, citing high levels of chlorine in tap water as a possible source of bryophyte collapse. Nevertheless, these bryophytes in the aquaria also have a limited life.

Ben Tan (Bryonet 23 June 2013) found that bryophytes transplanted to a closed terrarium usually survived from 6-18 months. Even on moss walls, the bryophytes needed complete replacement every two years to maintain aesthetic appeal. This is with no fertilizer, watered with tap water, in a fully air-conditioned room. Even ***Bryum*** (Figure 93) and ***Hyophila*** (Figure 111) last only about one year in a self-contained environment indoors with proper light and high humidity.

Alison Dibble (Bryonet June 2013) reports better success. She grows bryophytes on the windowsill all winter in small bonsai dishes. Others are in clear plastic boxes or a clear glass container with a loose-fitting lid. If the container is open, Dibble soaks the mosses in the sink once a week. In the summer she puts them outside under the overhang of a north-facing boulder and lets nature do the watering, but if there is a dry spell she waters them. Using this method, she has kept one bottle of mosses, including ***Sphagnum*** (Figure 1), for more than three years. And even in a terrarium there is competition. Her ***Saelania glaucescens*** (Figure 112) had been growing well for five years, but ***Mnium*** (Figure 113) began to overtake it.

Figure 111, ***Hyophila involuta***, in a genus that lasts about one year in a terrarium. Photo by Michael Lüth, with permission.

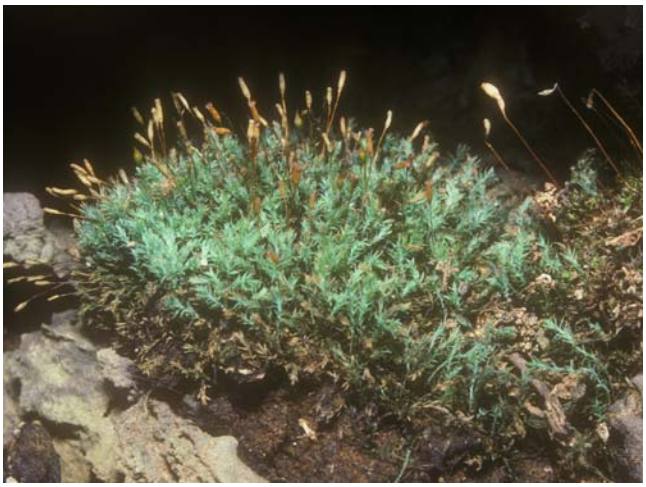

Figure 112. ***Saelania glaucescens***, a moss that has survived a terrarium for five years, but that is being overtaken by ***Mnium***. Photo by Janice Glime.

Figure 113. ***Mnium marginatum*** overgrowing other mosses, a problem it can cause in a terrarium. Photo by Jan-Peter Frahm, with permission.

Appropriate moisture levels are clearly a problem. Yoest (2011) suggests that if mosses and flowering plants or other tracheophytes are to co-exist, one must periodically remove the covering to water the tracheophytes. Keep the cover off for a day or two to allow excess water to escape. When you return the lid, check for condensation and vent the container until you achieve the right balance. In a dish garden or terrarium, proper drainage is needed, so putting pebbles on the bottom can help. Contrary to what most people might expect, the humidity level must be kept low. This condition can often be achieved by using a cover with a small opening at the top.

As an alternative, David Spain (in Yoest 2011) suggests removing the cover in the daytime and covering it at night. He has created a terrarium with a tall cover over a dish, using this routine. The terrarium has the fern ebony spleenwort (*Asplenium platyneuron*; Figure 114) and the mosses ***Dicranum scoparium*** (Figure 4), ***Leucobryum glaucum*** (Figure 27), ***Hypnum imponens*** (Figure 15-Figure 16), and ***Campylopus introflexus*** (Figure 71). (Be careful with the latter – it is an invasive species, so don't just throw it outside when you no longer want it.) Another of Spain's favorites is the moss ***Climacium americanum*** (Figure 115). Spain concludes that "mosses do not make ideal terrarium plants."

Figure 114. ***Asplenium platyneuron***, a fern that survives in a terrarium that is opened daily and closed at night. Photo by F. B. Matos, through Creative Commons.

Figure 115. ***Climacium americanum*** with capsules in moss garden, a species that looks good in a terrarium. Photo by Janice Glime.

I have a large (40-gallon) terrarium with begonias, ferns, *Tillandsia*, and a few mosses (Figure 106). Like Spain and Yoest, when I water it, I leave the cover partially open for a few days until the excess water evaporates. Then I cover it and it will last about six months before it needs to be watered again. I have limited success with the mosses because they seem to produce weak stems and to become infected with fungi. Extra aeration helps to avoid fungi, but then more frequent watering is needed, at least for the tracheophytes.

Bryophytes as Pests

Sadly, bryophytes can even be considered to be pests in gardens and flower pots (*e.g.* Newby *et al*. 2007). Greenhouse managers are often dismayed at having the invasion of ***Marchantia polymorpha*** (Figure 116) in many of their flower pots. But it is their method of watering that distributes this liverwort everywhere. The heavy force of water from a hose propels the gemmae out of their cups and onto bare soil nearby. These liverworts often arrive in the greenhouse initially as free-loading passengers in flower pots of new flowers or ferns, either as plants or as gemmae. And the greenhouse satisfies their growing needs.

Figure 116. ***Marchantia polymorpha*** with gemmae cups. Gemmae are splashed about in greenhouses when plants are watered. Photo by David T. Holyoak, with permission.

Another species known throughout most of North America only in greenhouses is the thallose liverwort ***Lunularia cruciata*** (Figure 117). Like species of ***Marchantia*** (Figure 116), it produces gemma in cups, in this case crescent-shaped cups, and these likewise are easily dispersed by typical greenhouse watering methods.

Figure 117. ***Lunularia cruciata*** with gemmae cups and gemmae that are distributed with rain or watering in a greenhouse. Photo by Des Callaghan, with permission.

Other volunteers that I have observed include ***Bryum*** spp. (Figure 64, Figure 93), ***Leptobryum pyriforme*** (Figure 72), and ***Ceratodon purpureus*** (Figure 105). These are all mosses, with the latter two frequently producing numerous capsules and thus most likely spreading by spores. ***Bryum argenteum*** (Figure 64) has detachable terminal buds that will grow new plants. It is likely that it benefits in the same way as the gemmae of the two liverwort species.

A final caution is appropriate. Some bryophytes are invasive, although much less so than their flowering plant counterparts. Nevertheless, they can disrupt ecosystems, changing the success of seed germination, affecting the invertebrates that live there, and changing the hydrology. In addition to the ones that like to travel among flower pots, the most invasive and widespread of these are ***Campylopus introflexus*** (Figure 71), ***Eurhynchium praelongum*** (Figure 118), ***Lunularia cruciata*** (Figure 117), ***Orthodontium lineare*** (Figure 119), ***Pseudoscleropodium purum*** (Figure 120), and ***Lophocolea semiteres*** (Figure 121) (Essl *et al*. 2013; Mateo *et al*. 2015). Some of these have spread due to their use as packing material, especially for shipping plants in the horticultural industry.

Figure 118. ***Eurhynchium praelongum***, a widespread moss species that often travels in flower pots. Photo by Janice Glime.

Figure 119. ***Orthodontium lineare***, a widespread moss species that often travels in flower pots. Photo by Michael Lüth, with permission.

Figure 120. ***Pseudoscleropodium purum***, a widespread moss species that often travels in flower pots and also is used for packing. Photo by Phil Bendle, with permission.

Figure 121. ***Lophocolea semiteres***, a widespread leafy liverwort species that often travels in flower pots. Photo by David Long, with permission.

Summary

Peat mosses have been widely used in horticulture as soil additives, and for bedding, as well as forming the foundation for topiary, wreaths, and hanging baskets. Their ability to add moisture makes them ideal as a shipping medium for plants.

Peat mosses are used as soil conditioners, providing a holding medium for nutrients, releasing them slowly following drying. They provide good compost, especially when mixed with such waste products as fish offal or sewage. Some peat mosses provide additional fixed nitrogen through their **Cyanobacteria** flora. Their antibiotic properties discourage damping-off fungal growth while maintaining moisture. These same properties make them good for air layering. All of these properties make peat mosses good culture media and potting mixes, but other relatively dense mosses work well also.

Peat mosses have been used in forestry to culture young seedlings and in the food industry to culture mushrooms and morels.

Small mosses work well in container gardens such as bonsai and bonkei, where various species are used to simulate different aspects of miniature landscapes. Terraria are more difficult, with mold being a frequent problem. Aeration is important, as is the choice of mosses.

Some species are pests in greenhouses, sometimes being dispersed as gemmae. The watering techniques make gemmae and other detachable parts airborne.

Acknowledgments

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CHAPTER 7-2
GARDENING: JAPANESE MOSS GARDENS

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CHAPTER 7-2
GARDENING: JAPANESE MOSS GARDENS

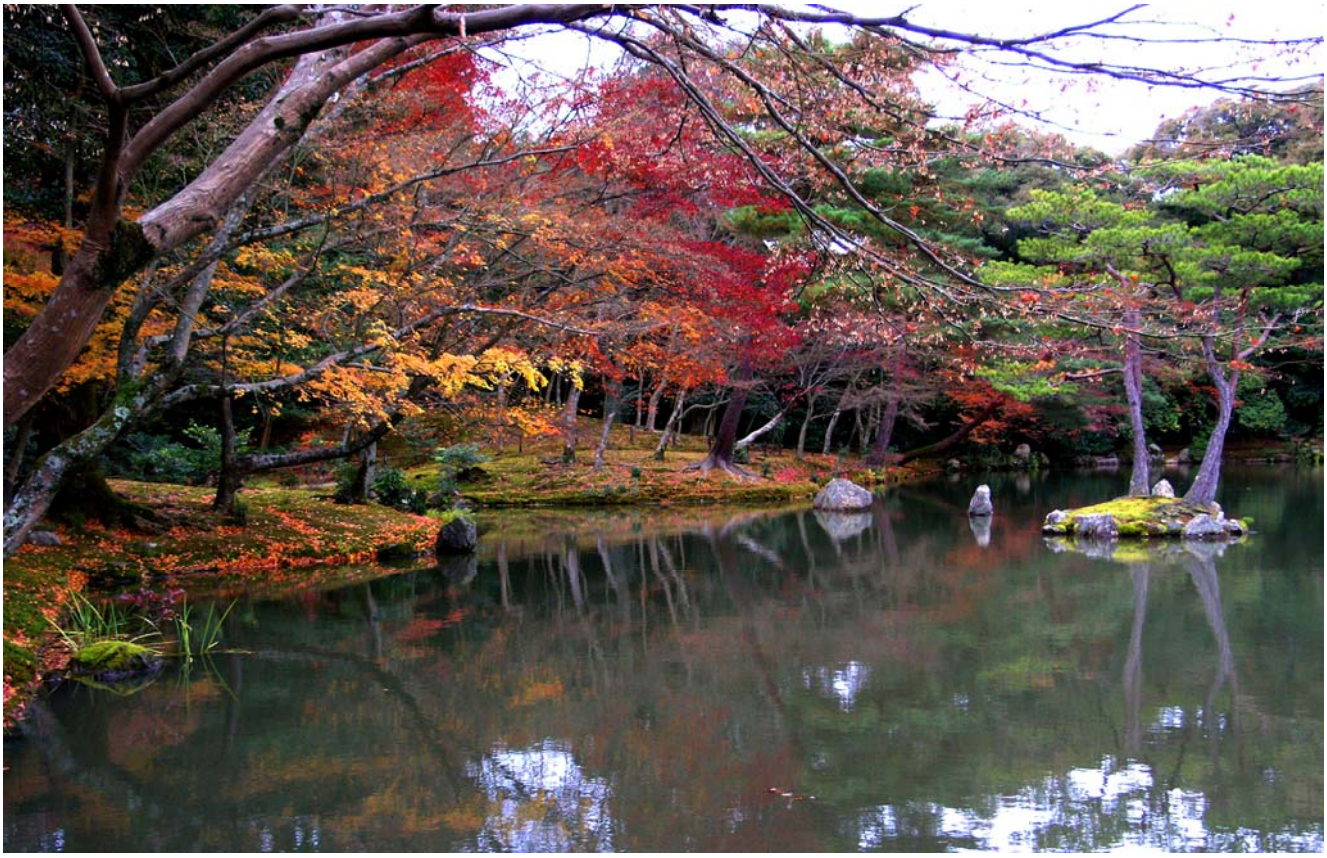

Figure 1. Kyoto Gold Temple moss garden in fall. Photo courtesy of Leng Yang.

Moss Gardens

It is the end of a hectic week and your mind is racing between projects nagging to be finished before another set entreats you. The afternoon hour is late and Friday traffic winds about you in the fury to be somewhere else. Children shout and horns warn of impending danger, or just impatience. You turn the corner and park in the only remaining spot next to the shrouded garden. The Japanese have taught us how to construct a fence that deflects the city's clamor, creating a refuge from the turmoil that bombards our daily lives. But within that fence, in the midst of the city, is a garden – a moss garden. Barely 50 meters on a side, the garden is a far away and peaceful world. Here all seems to melt away as the soft mountains in the distance, created by gentle hills of moss, blend into the quiet fields of green before us. At last we can relax. In such a setting, we can reflect on all that is beautiful and calm.

For the caretaker of this garden, be it large or small, it certainly requires an understanding of mosses in all their ecological and physiological glory. Although the Japanese have been successful for centuries, moss gardening is no small challenge.

Japanese Moss Gardens

Perhaps originating in their present usage during Japan's feudal era (12th-19th centuries), mosses have become a part of Japanese tradition (Schenk 1997). In Japanese, ***koke*** means moss and ***dera*** means temple, hence the name of the moss temple *kokedera* (Figure 1). However, as far back as a thousand years ago the Zen Buddhist monks wrote of the mosses in their temple gardens. Yet the rest of the world is just beginning to understand and copy the tranquility of the moss garden.

Bryophytes have always been greatly appreciated as a precious attribute in Japanese gardens (Figure 1). Some of the Japanese gardens are known from as early as the 7th

century A.D. (Seike *et al*. 1980). The earliest of these were based on the T'ang China gardens, but they soon developed their own character, resembling the Japanese landscape. The theme generally reflects the Japanese religion of Shinto, wherein the world is viewed as "infused with the primeval forces of creation" (Seike *et al*. 1980).

By the fifteenth and sixteenth centuries, the scale of the gardens was smaller, opening the way for miniature plants such as bryophytes to provide the feeling of expanse. Natural features such as ponds and waterfalls were represented by stone and gravel (Figure 2). Unlike gardens throughout most of the world, the Japanese garden is ruled by simplicity. Following this theme of tranquility, the garden must not appear manicured, but rather must maintain a natural look, as in Figure 3. For this reason, as the gardens became the setting for the tea ceremony, they also continued this tradition of a natural look. To avoid the austerity of too much care, the Tea Masters considered the most appropriate caretakers to be old men (Figure 4) and boys who would not be too painstaking in their care to sweep and clean the garden. Having leaves tucked among the rocks or at the bases of trees provides interest (A. L. Sadler in Seike *et al*. 1980).

Figure 2. This moss is interrupted by a sand garden at Ginkakuji, Kyoto, Japan. This sand resembles a river and the rock an island. Photo by Janice Glime.

Figure 3. Ginkakuji Silver Temple Moss Garden with ***Polytrichum*** in Kyoto, Japan. Stones give the sense of boulders, giving the feeling of mountain crags, adding focus and depth. Photo by Janice Glime.

Public gardens often have a gate at the entrance. Even these offer serenity and often have bryophytes growing on the roof of the gate (Figure 5). The gate gives one the impression of shutting out the world of work, noise, and traffic.

Figure 4. Ginkakuji moss gardener using a broom to clean leaves from the moss garden. Photo by Janice Glime.

Figure 5. Kyoto gold temple with mosses growing on the entrance gate. Photo courtesy of Leng Yang.

Courtyard gardens (Figure 6-Figure 7) are small and provide a relaxing view from a window or doorway. Generally only a few plants provide highlights to an arrangement of gravel and rocks. Mosses may be used here to make a green layer on the ground, or may be islands in a bed of gravel (Figure 8) that simulates the sea or a pond (Seike *et al*. 1980). In even larger courtyards and many moss gardens, the pond may be real, with koi swimming about (Figure 9).

Figure 6. Courtyard with moss garden outside window of Kanazawa Historical Pharmacist (merchant) residence in Japan. Photo courtesy of Elin LeClaire.

Figure 7. Courtyard garden at Tofukuji Reiunin, Japan. Photo from Wikimedia Commons.

Figure 8. Zuihō-in garden, the Garden of the Blissful Mountain, in Kyoto, Japan. Rocks and raked sand in wave formation simulate the ocean, with mosses to simulate islands. Photo from Wikimedia Commons.

Figure 9. Shrine and pond with koi in Kyoto, Japan. Photo by Janice Glime.

Sand is used in many of the gardens. It is always well kept, often raked with the ridges of raking forming various designs (Figure 10-Figure 12). Some of these simulate a lake with islands and mountains (Figure 10). In other cases, the mosses surround a gravel bed shaped to resemble a lake (Figure 11). The mosses are not arranged in rectangular plots so common to western gardens, but rather typically follow a circular theme. Species of ***Polytrichum*** (Figure 12) are often used for these islands to break up the bright appearance of the sand (Saito 1980).

Figure 10. Tofukuji Garden bordered with mosses. The raked sand and moss islands give the illusion of a lake with mountains. Photo from Wikimedia Commons.

Figure 11. Rosan-ji garden, Kyoto, Japan, showing gravel with islands of mosses. Photo from Wikimedia Commons.

Figure 12. Toufuku-ji hojyo, a sand garden surrounded with ***Polytrichum***. Photo from Wikimedia Commons.

A path of stones may meander (Figure 13) through the gravel or across the moss bed and is often not straight or even direct. Even the straight paths give a sense of meander by mixing large and small stones (Figure 14) or making sure 4 corners never meet (Seike *et al*. 1980). Small stone or wooden bridges (Figure 15) may cross the gravel bed in somewhat larger courtyards, and generally a stone or iron lamp such as the one seen in Figure 16-Figure 17 provides the soft light of a candle or merely a point of interest. Other common objects in the moss and temple gardens are a small pagoda, often made of stone (Figure

18) or a basin for washing one's hands (Figure 19-Figure 20). A small garden, such as most courtyard gardens, will typically have a single plant or one of the above objects as its point of focus.

Figure 13. Stone path in moss garden. Photo by Szabolcs Arany, through Creative Commons.

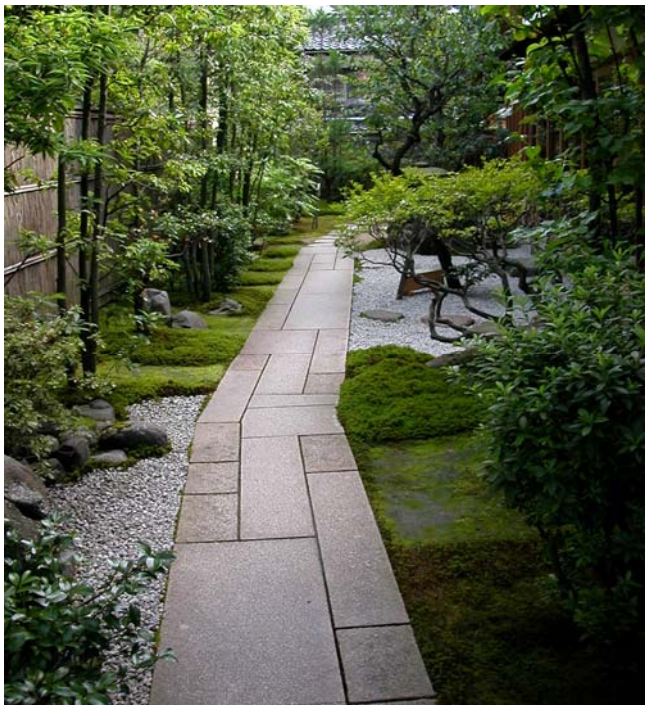

Figure 14. Kanazawa, Japan – Nagamachi samurai district, house garden walk, demonstrating a straight path with multiple sizes of stones, giving a sense of meandering. Photo courtesy of Elin LeClaire.

Figure 15. A rock bridge retains a natural look in this moss garden and pond at Ginkakuji, Kyoto, Japan. Photo by Janice Glime.

Figure 16. Shrine and pond with stone lamp (foreground), Kyoto, Japan. Photo by Janice Glime.

Figure 17. Nagoya Private Moss Garden with stone lantern as a point of focus. Photo by Janice Glime.

Figure 18. Kanazawa Kenroku-en Garden in Japan showing stone pagoda. Photo by Elin LeClaire.

Figure 19. Kanazawa, Japan – Nagamachi samurai district, house garden with small basin for washing hands. Photo courtesy of Elin LeClaire.

Figure 20. Kenroku-en garden stone water basin in a moss garden in Japan. Note the natural appearance of the basin. It is likely that the leaf was added as a touch of nature and to add a spot of color. Photo from Wikimedia Commons.

Among the larger gardens, one may see, instead of mosses mimicking the mountains, that shrubs mimic the mosses (Figure 21). In these gardens, the shrubs are cut into rounded forms that look like moss-covered rocks, cascading down a hillside, and sometimes with a small stream or waterfall in their midst. Waterfalls are common in the larger gardens, but occasionally even in very small ones (Figure 22-Figure 24).

Figure 21. Saihouji-kokedera. In this moss garden, the shrubs are cut to look like moss cushions. Photo from Wikimedia Commons.

Figure 22. This small waterfall in Ginkakuji moss garden in Japan retains the natural look using rocks and ferns with the mosses. Photo by Janice Glime.

Figure 23. Nanzen-in – Nanzenji, Kyoto, Japan, showing a natural waterfall in a mossy part of this garden. Photo from Wikimedia Commons.

Figure 24. Even this tiny restaurant garden in Nagoya, Japan has a waterfall. This is a restful view outside your window while you eat. Photo by Janice Glime.

Many attractive moss gardens are seen in Kyoto, the ancient capital city of Japan, where the surrounding mountains ensure constant humidity, and prolonged summer rainy seasons favor growth and survival of the mosses. Perhaps the most popular Kokedera, or Moss Temple, is the Koinzan Saihoji Temple (Figure 21) located at the foot of Mt. Koinzan in the west of Kyoto City. There are 92 different species there, each with its own required environmental conditions (Figure 25).

Figure 25. Hill and pond garden in Koinzan Saihoji Temple garden in Kyoto, Japan, with ***Polytrichum*** in the foreground and several other bryophyte species. Photo by Janice Glime.

Types of Japanese Moss Gardens

Generally there are three types of Japanese moss gardens: the flat garden (Figure 26) "for contemplation and meditation," the Tea Ceremony garden (Figure 27-Figure 28) that must convey the feeling of simplicity and seclusion, and both the oldest and most widely appreciated – the hill and pond garden (Figure 29-Figure 31). A roofed courtyard or indoor garden may provide a tea table and cushions for a tea ceremony. The hill and pond gardens resemble the natural landscapes of Japan in simplified form (Avery 1966). They may have bridges, often not straight (Figure 32), forcing the visitor to walk slowly and enjoy the garden. The use of rocks to portray mountains or add a focus point (Figure 33), ponds as oceans or lakes (Figure 25), and bryophytes as the foliage are the essence of traditional Japanese gardens where flowers, *per se*, are of lesser importance; a green garden, unlike ephemeral flowers, symbolizes long life and offers a place for relaxation and contemplation. In sharp contrast to the myriad of colors and shapes in a traditional American or European garden, the moss garden allures with its subtle shades of green, accented here and there with a rock or group of rocks (Figure 34), a bamboo fountain (Figure 35), a lamp (Figure 36), or an occasional small flowering shrub (Figure 37).

Figure 26. Ryoanji Temple garden in Kyoto, Japan, representing the flat garden. Photo by Janice Glime.

Figure 27. Japanese Tea Garden in San Francisco, CA, USA. Photo by Redhairedflip, through Creative Commons.

Figure 28. The same Japanese Tea Garden, San Francisco, CA, USA, as in Figure 27, but with the azaleas in full bloom. Photo by Caroline Culler, through Creative Commons.

Figure 29. Kanazawa Kenroku-en Garden in Japan, an example of a hill and pond garden. Note the lamp that adds a point of focus. Photo courtesy of Elin LeClaire.

Figure 30. Kyoto Nijo Castle, Shogun's palace garden, illustrating the hill and pond garden with mosses and stones. Photo by Elin LeClaire.

Figure 31. Kokedera Pond in Kyoto, Japan, an example of a hill and pond garden. Photo by Janice Glime.

Figure 32. Kanazawa Kenroku-en Garden in Japan, showing a meandering bridge that forces the visitor to slow down. Photo courtesy of Elin LeClaire.

Figure 33. Boulders add interest to this moss garden at the Saihoji Kokedera in Kyoto, Japan. Photo by Janice Glime.

Figure 34. Kyoto Nijo Castle garden with rocks, Shogun's residence. Photo by Elin LeClaire.

Figure 35. Bamboo fountain in moss garden, a point of interest and focus. Photo by Jeff Kramer, through Creative Commons.

Figure 36. Kanazawa - Nagamachi samurai district, house garden with lamp. Stone lamps are common in Japanese gardens. Photo by courtesy of Elin LeClaire.

Figure 37. Kokedera moss garden in Kyoto, Japan, with ***Leucobryum*** and two flowering shrubs as highlights and points of focus. Photo by Janice Glime.

Imagine yourself sitting alone in a Japanese spa perched near the top of a mountainside overlooking a green valley untouched by habitation. On every side of the valley are mountains and boulders – as far as you can see. All is peaceful and you are able to relax your eyes and your body. Thousands of Japanese seek just such retreats every year to take them away from the stresses of daily life. Among the most ancient uses of mosses that has persisted into modern life is the design of moss gardens to create that same feeling of distance, lack of commercial clutter, and tranquility of spirit. By using rocks and tiny plants such as mosses, the Japanese create in miniature those scenes that they crave in nature. Even in the space of a few feet in a dooryard or window garden in a city, they often create such an illusion of distant mountains, dry stream beds, and green forests (Figure 38). The Japanese Zen scholars have philosophical ideas about landscapes, and about simplicity and repose, which they try to express in their traditional gardens (Fletcher 1991). While the space in the gardens is usually small, they may try to create an atmosphere of being deep within the mountains and provide a feeling of tranquility. Japanese gardening is not a mere imitation of nature; perhaps "borrowed scenery" is a more appropriate description (Avery 1966) for the attempt to alleviate the drabness of city life. Contemporary Zen scholars contend that many such gardens represent the best in abstract art (Avery 1966).

Figure 38. This tiny moss garden with a waterfall can be seen through a guest window in a restaurant in Nagoya, Japan. ***Platyhypnidium riparioides*** is in the water and ***Philonotis falcata*** is at the edge. Photo by Janice Glime.

Even bowls (Figure 39) and other objects in the gardens are likely to be covered in mosses, softening the lines and giving a quiet, cool appearance.

Figure 39. This moss-bearing basin is in a city park in Nagoya, Japan. Photo by Janice Glime.

Dangers to Gardens

These ancient gardens suffer new dangers in our modern society. Kyoto is the city of moss gardens (Figure 40-Figure 56), especially temple gardens. But even restaurants and private residences share in the serenity with their own small gardens. Aside from the effects of trampling from the ever-increasing population of visitors, the fumes of cars and busses have taken their toll. The pollution from these visitor vehicles has forced the closing of Saihoji in Kyoto to the casual visitor, requiring reservations in advance and forcing visitors to park at the bottom of the hill and walk up to avoid further damage from air pollution.

Figure 40. This moss garden in Kyoto, Japan, has a single species to emphasize its tranquility. Photo by Janice Glime.

Figure 41. This pond in the moss garden at the Saihoji Kokedera (moss temple) in Kyoto, Japan, gives a natural look and one of distance. Photo by Janice Glime.

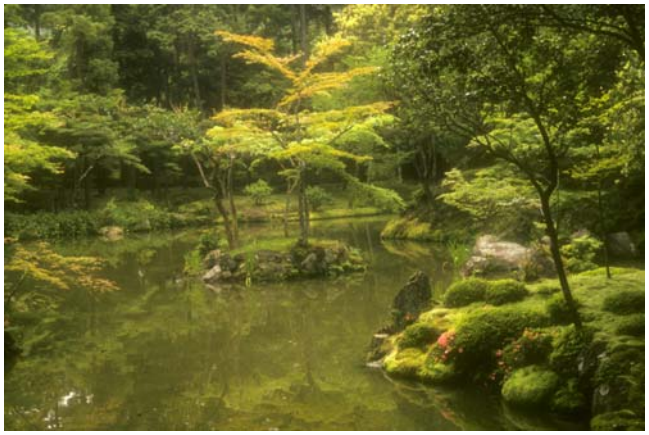

Figure 42. This pond with a small island and surrounded with mosses at the Saihoji Kokedera in Kyoto, Japan, gives the illusion of a lake. Photo by Janice Glime.

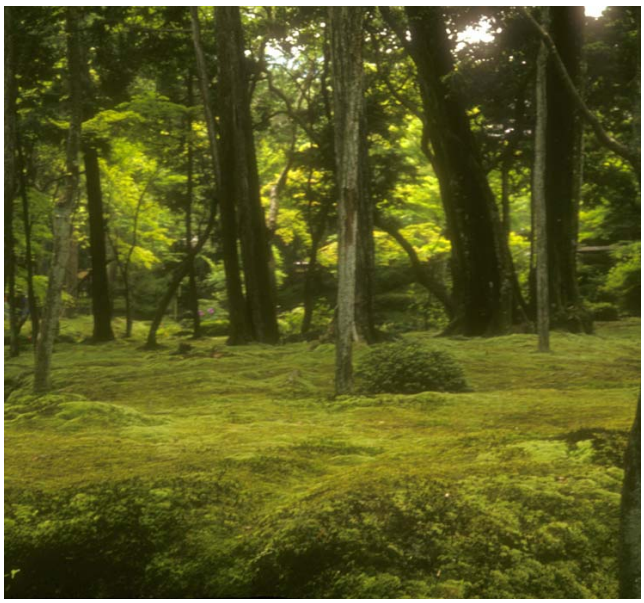

Figure 43. Several mosses provide subtle color differences in this moss garden at Saihoji Kokedera in Kyoto, Japan. Photo by Janice Glime.

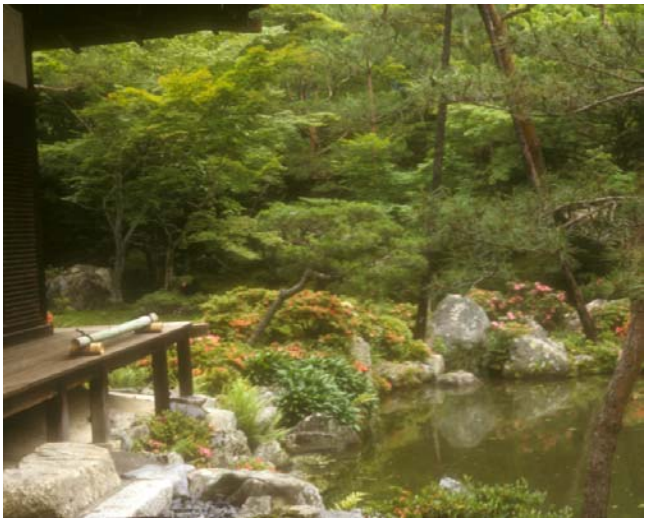

Figure 44. This Ginkakuji Temple (Silver Temple) overlooks moss gardens in Kyoto, Japan. Photo by Janice Glime.

Figure 45. A small river provides a natural setting in this moss garden at Ginkakuji in Kyoto, Japan. Photo by Janice Glime.

Figure 46. Here sand forms a volcano (mid right) and mosses miniaturize the landscape at the Ginkakuji shrine in Kyoto, Japan. Photo by Janice Glime.

Figure 47. This path through the moss garden at Ginkakuji Temple in Kyoto, Japan, retains a natural appearance. Photo by Janice Glime.

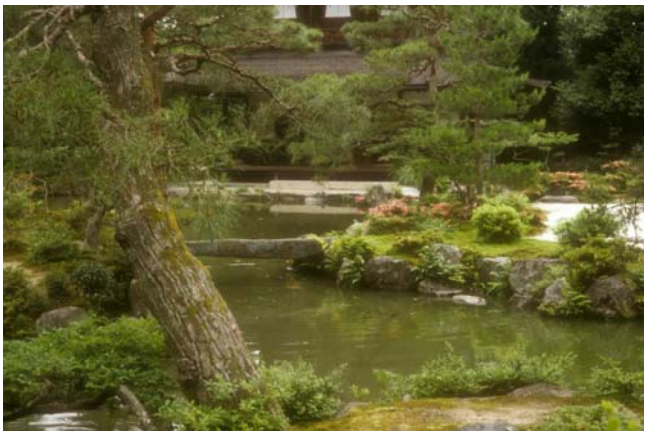

Figure 48. This moss garden at Ginkakuji Temple in Kyoto, Japan, has depth provided by the pond. Photo by Janice Glime.

Figure 49. Sand is used for dry stream beds and unused paths in moss gardens such as this one at Ginkakuji Temple in Kyoto, Japan. Photo by Janice Glime.

Figure 50. This moss garden at Ginkakuji (Silver Temple) garden in Kyoto, Japan, maintains a natural look. Photo by Janice Glime.

Educational Gardens

One unusual feature at the Ginkakuji (Silver Temple) garden in Kyoto is that it attempts to teach the public about the mosses. In Japan, each species has a Japanese name, and like birds and flowering plants, mosses are known by these names. However, the bryologists know both the scientific names and Japanese names of the mosses. The displays of mosses provide an explanation of their utility to the gardens, showing the most important species (Figure 51, Figure 52). The "interrupter" mosses are "undesirable" mosses that must be weeded out (Figure 53). Among these are non-weedy things, but nevertheless undesirable ones, often for aesthetic reasons. To our surprise, this included ***Andreaea*** (Figure 54) because of its nearly black (and undesirable) color. Heinjo During, with the help of his students, attempted to interpret the Japanese names into their proper Latin ones, giving us a list of important temple garden species (Figure 55).

Figure 51. This educational display is labelled VIP mosses. Each is labelled with its Japanese name. These VIP mosses are among the most important ones in the moss garden at the Ginkakuji Temple in Kyoto. Photo courtesy of Onno Muller.

Figure 52. These mosses, also on educational display at the Ginkakuji Temple, are normal inhabitants of the Ginkakuji garden. Photo courtesy of Onno Muller.

Figure 53. This educational display is labelled "the Interrupter Mosses." These are weedy mosses that must be pulled from the gardens to permit the others to survive. Apparently they "interrupt" the tranquility. Photo courtesy of Onno Muller.

Figure 54. ***Andreaea rupestris rupestris***. ***Andreaea rupestris*** var. ***fauriei*** is among the mosses considered undesirable in the Ginkakuji (Silver Temple) garden in Kyoto because of its black color. Photo by Des Callaghan, with permission.

【銀閣寺の大切な苔】	**Very Important Mosses**
オオスギゴケ、	*Polytrichum formosum*
コスギゴケ、	*Pogonatum inflexum*
スギゴケ、	*Polytrichum juniperinum*
ウマスギゴケ、	*Polytrichum commune*
ミヤマスギゴケ	*Polytrichastrum alpinum*
ホウライスギゴケ	*Pogonatum cirratum*
ビロードゴケ	??
アラハシラガゴケ	*Leucobryum bowringii*
チャボスギゴケ、	*Pogonatum otaruense*
イトラッキョウゴケ、	*Anoectangium thomsonii*
ヤマゴケ、	*Oreas martiana*
カモジゴケ、	*Dicranum scoparium*
イワダレゴケ、	*Hylocomium splendens*
コキンシゴケ、	??
ネジクチゴケ、	*Barbula unguiculata*
ホソバシラガゴケ、	??
ヒノキゴケ、	*Rhizogonium dozyanum*
ヒロハヒノキゴケ、	*Pyrrhobryum spiniforme* var. *budakense*
イノウエネジクチゴケ、	??
コツクシサワゴケ、	*Philonotis thwaitesii*
アラハシラガゴケ、	*Leucobryum bowringii*
オオホウオウゴケ、	??
ハマキゴケ、	??
キャラハラッコゴケ。	*Taxiphyllum taxirameum*?
【ちょっと邪魔な苔】	**The inhabitants of Ginkaku-ji**
ヒロハツヤゴケ、	*Entodon challengeri*
タチハイゴケ、	*Pleurozium schreberi*
ハイゴケ、	*Hypnum plumaeforme*
タニゴケ、	??
コツボゴケ、	*Plagiomnium acutum*
コバノチョウチンゴケ、	*Trachycystis microphylla*
ハネヒツジゴケ、	*Brachythecium plumosum*
オオサナダゴケ、	*Plagiothecium neckeroideum*
サナダゴケ、	??
ススキゴケ、	*Dicranella heteromalla*
エダツヤゴケ、	*Entodon flavescens*
ミズシダゴケ。	??
【とても邪魔な苔】	**Moss the Interrupter**
ゼニゴケ、	*Marchantia polymorpha*
ヒメジャゴケ、	*Conocephalum japonicum*
ジャゴケ、	*Conocephalum conicum*
ホソバミズゼニゴケ、	*Pellia endiviifolia*
アズマゼニゴケ、	*Wiesnerella denudata*
ミズゼニゴケ、	*Pellia epiphylla*
コバノエゾシノブゴケ、	*Thuidium recognitum* var. *delicatulum*
アオシノブゴケ、	*Thuidium pristocalyx*
トヤマシノブゴケ、	*Thuidium kanedae*
タカネカモジゴケ、	*Dicranum viride* var. *hakkodense*
クロゴケ、	*Andreaea rupestris* var. *fauriei*
センニチゴケ。	??

Figure 55. Japanese moss names and Latin names for those in the educational collection in Kyoto. From Heinjo During.

Figure 56. This moss is growing on the tile of a temple garden roof in Kyoto, Japan. Photo by Janice Glime.

Variations

We must not forget that the Japanese are also creative. While they appreciate the calm of a garden, they do not restrict themselves to the purity of the three garden types mentioned above. The following images illustrate some of that diversity (Figure 57-Figure 63).

Figure 57. Tōfuku-ji, Kyoto, Japan. This formal pattern looks like a mix of western and Japanese design. Photo from Wikimedia Commons.

Figure 58. Here the meandering path takes on a different form in the Rhododendron garden with mosses playing a minor role. Photo by Monty Monsees, through Creative Commons.

Figure 59. Ankokuji garden in Hiroshima, Japan, giving a natural appearance but with rocks providing the major feature. Photo from Wikimedia Commons.

Figure 60. Kanazawa Kenroku-en Garden showing the famous koto-fret stone lantern. The bamboo fence is also a common feature in Japanese gardens. Photo courtesy of Elin LeClaire.

Figure 61. Courtyard garden of a former geisha house in Kanazawa, Ishikawa, Japan – straw protects trees from snow. But even that protection is artistic, natural, and restful. Photo from Wikimedia Commons.

Figure 62. Ginkakuji Moss Garden pool in Kyoto, Japan, with coins, a practice that may have originated in western countries. Photo by Janice Glime.

Figure 63. The mosses in this Japanese garden near Columbus, Ohio, USA, do not quite reach the restful landscape achieved in most of the Japanese gardens. This may be partly due to the lack of a rainy season and the land-bound location. Photo by Janice Glime.

Charcoal Gardens

Nancy Church provided me with images of the charcoal gardens (Figure 64-Figure 66) in which moss gardeners used charcoal, providing highlights. The small black pieces with lines are charcoal, a feature that Nancy considered to be beautiful and amazing.

Figure 64. Japanese charcoal and moss garden. Photo by Amy Laudenslager through Nancy Church.

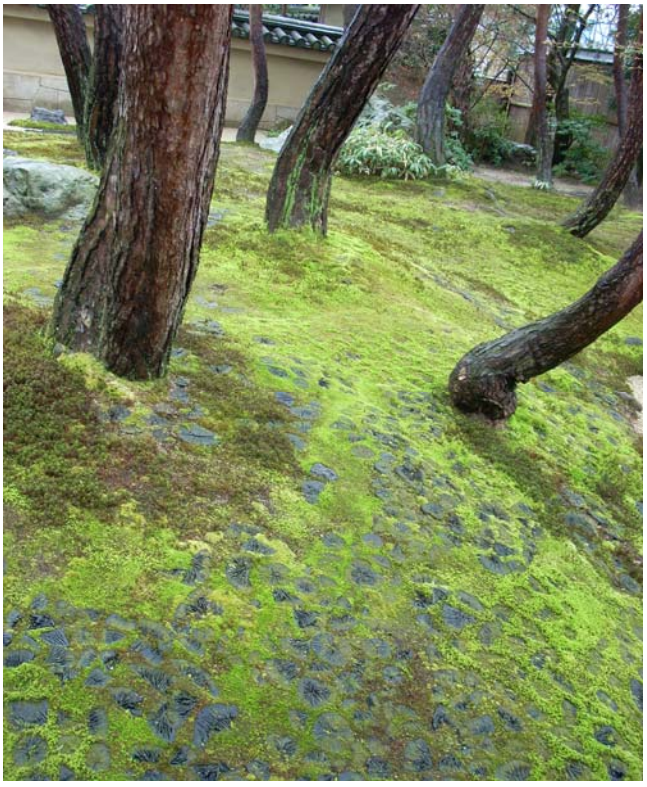

Figure 65. Japanese charcoal and moss garden. Photo by Amy Laudenslager, through Nancy Church.

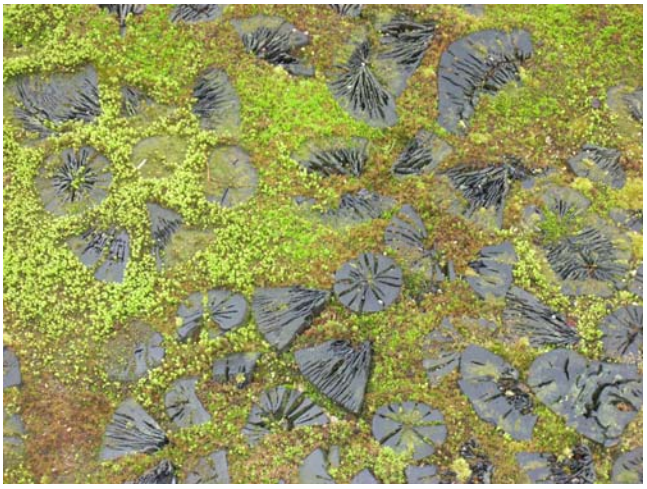

Figure 66. Japanese charcoal and moss gardens. Photo by Amy Laudenslager, through Nancy Church.

Dominant Species

Although many species are used, a few dominate the gardens, especially the private gardens. One of the most common is ***Polytrichum*** (Figure 67-Figure 71). This is most likely because it does well in the conditions of the garden and is easier to transplant than most (personal experience). ***Leucobryum*** (Figure 72-Figure 74) is used frequently, despite its narrower requirements (it seems to be a problem to cultivate in the USA according to my friends and my own experience). Perhaps the Japanese species are easier to grow than ours. But its endearing quality is its beautiful, pale cushions. It creates a restful landscape.

Figure 67. Ginkakuji Moss Garden, Kyoto, with a carpet of ***Polytrichum***. Photo by Janice Glime.

Figure 68. Kanazawa Kenroku-en Garden in Japan with lawn of ***Polytrichum***. Photo courtesy of Elin LeClaire.

Figure 69. Kanazawa Kenroku-en Garden with **Polytrichaceae**. Photo courtesy of Elin LeClaire.

Figure 70. Kanazawa Kenroku-en Garden in Japan, with a ***Polytrichum*** lawn and stone lantern. Photo courtesy of Elin LeClaire.

Figure 71. ***Polytrichum commune*** in a small garden at the entrance to the Japanese Cake Shop in Hiroshima, Japan. Photo courtesy of Hironori Deguchi.

Figure 72. ***Leucobryum*** spills down a slope in a moss garden at the Saihoji Kokedera (moss temple) in Kyoto, Japan. Photo by Janice Glime.

Figure 73. ***Leucobryum juniperoideum*** at moss temple in Kyoto, Japan. Photo courtesy of Zen Iwatsuki.

Figure 74. ***Leucobryum*** in a temple garden in Japan. Photo by Janice Glime.

At a plantation preparing for the sale of bryophytes for gardens, the thallose liverwort ***Riccia*** (Figure 75) was cultured. It has the advantage of being able to withstand dry conditions for long periods, then wake up during the rainy season. But I must admit to finding none of it in the gardens I saw. It does not give the restful look of the two mosses mentioned above.

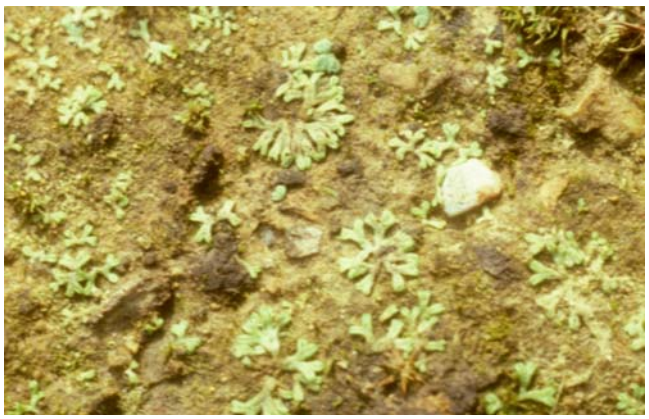

Figure 75. Nagoya bryophyte plantation with ***Riccia***, a thallose liverwort that is able to dry up and then rejuvenate during the rainy season. Photo by Janice Glime.

Summary

Moss gardens are known for their serenity, emphasizing simple shades of green with only occasional color from shrubs or other flowers. Mosses are used to miniaturize the landscape, giving the feeling of distance. They have been a part of Japanese tradition since the feudal era.

There are three basic types of Japanese moss gardens: flat gardens, Tea Ceremony gardens, and pool and mountain gardens. In addition, sand gardens are often combined with moss gardens, often simulating lakes or streams. A number of variants exist, including the charcoal garden.

Even private homes, restaurants, and other shopkeepers maintain small moss gardens, especially where they can be viewed from within the building. The greatest number of moss gardens is in the city of Kyoto. The primary mosses used are species of ***Polytrichum*** and ***Leucobryum***, but some gardens have nearly 100 species.

Acknowledgments

Heinjo During kindly sent me the pictures and gained the permission for me to use the educational pictures taken by his student, Onno Muller, illustrating the educational displays at the gardens at Ginkakuji, Kyoto, Japan. He and his students translated the Japanese names into the Latin names.

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CHAPTER 7-3
GARDENING: PRIVATE MOSS GARDENS

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CHAPTER 7-3
GARDENING: PRIVATE MOSS GARDENS

Figure 1. This is a large private moss garden in Nagoya, Japan, using boulders to add interest. Photo by Janice Glime.

Private Gardens

Private gardens are gaining popularity in the USA (Dunn 2008; Martin 2008; Cullina 2009). You know moss gardens are coming of age when an article appears in the *New York Times* (see Tortorella 2014). Garden journals give advice on establishment and care of moss gardens. But what works in one part of the world may not work in another, and that is true within countries as well. Watering instructions and species choice must be in tune with local climate, light, available bryophytes, and competing species.

In Japan, even tiny spaces a meter wide by three meters long are used for a garden. It may be a vegetable garden, but often it is a moss garden with a few tracheophyte highlights (Figure 1). Such private gardens give their owners a sense of space and tranquility (Figure 2). Mosses are particularly enjoyed because they miniaturize the landscape and give a feeling of looking into the distance (Figure 3-Figure 9). Cushions of ***Leucobryum*** (Figure 10) can resemble distant mountains. ***Polytrichum*** (Figure 11) can simulate a forest. ***Hypnum imponens*** (Figure 12), a common "sheet moss" sold for decorative purposes, is used to "fill nooks and crannies" (Cullina 2008). Small mosses in the foreground provide the open fields. Pebbles become boulders.

Figure 2. This peaceful scene is a private moss garden in Kyoto, Japan. Photo by Janice Glime.

Figure 3. This lamp adds interest in a private moss garden at a home near Nagoya, Japan. Photo by Janice Glime.

Figure 4. These rocks form a path through ***Polytrichum*** in a private moss garden in Nagoya, Japan. Picture by Janice Glime.

Figure 5. Fukushima-san sweeping his private moss garden in Nagoya, Japan. Photo by Janice Glime.

Figure 6. This path leads through ***Polytrichum*** in a private garden in Nagoya, Japan. Photo by Janice Glime.

Figure 7. ***Entodon*** and ***Polytrichum*** grow in a private moss garden in Nagoya, Japan. Typically, the ***Polytrichum*** will outgrow the pleurocarpous mosses such as ***Entodon***. Photo by Janice Glime.

Figure 8. This portion of a private moss garden in Nagoya, Japan, has texture created by different species of mosses. Photo by Janice Glime.

Figure 9. This private moss garden in Nagoya, Japan, has a dry "stream" and bridge. Photo by Janice Glime.

Figure 10. ***Leucobryum glaucum*** growing naturally around a tree at Coopers Rock, West Virginia, USA. Species of ***Leucobryum*** are used to simulate mountains in moss gardens. Photo by Janice Glime.

Figure 11. ***Polytrichum piliferum*** showing white leaf tips. Species of ***Polytrichum*** are used to simulate mountains in moss gardens. Photo by David Holyoak, with permission.

Figure 12. ***Hypnum imponens***, a common species in private gardens, available as sheet moss. Photo by Janice Glime.

Smith *et al.* (2010) summarized the role of residential gardens in preserving biodiversity in urban areas. But bryophytes are typically neglected in such studies. In their studies of 61 domestic gardens in Sheffield, UK, they found 67 bryophyte taxa and 77 lichen taxa. The individual gardens supported growth of 3 to 24 bryophyte species each, with a mean richness of 11.3 species. Of these, 14 species occurred in lawns. About one quarter of the species occurred in only one garden. Only 10% of the species occurred in more than half the gardens. The richness of species correlated with garden area (correlated with substrate richness) and altitude. Species present in 20 or more of the 61 gardens were ***Amblystegium serpens*** (Figure 13; 31 spp), ***Barbula convoluta*** (Figure 14; 30 spp), ***Barbula unguiculata*** (Figure 63; 22), ***Brachythecium rutabulum*** (Figure 15; 55 spp), ***Bryum argenteum*** (Figure 16; 21 spp), ***Ceratodon purpureus*** (Figure 45-Figure 46; 42 spp), ***Didymodon insulanus*** (Figure 17; 27 spp), ***Funaria hygrometrica*** (Figure 18; 23 spp), ***Kindbergia praelonga*** (Figure 19; 56 spp), ***Ptychostomum capillare*** (Figure 20; 37 spp), ***Rhynchostegium confertum*** (Figure 21; 32 spp), ***Rhytidiadelphus squarrosus*** (Figure 22; 23 spp), and ***Tortula muralis*** (Figure 23; 35 spp).

Figure 13. ***Amblystegium serpens***, a species that occurred in more than 50% of the gardens studied in Sheffield, UK. Photo by Michael Lüth, with permission.

Figure 14. ***Barbula convoluta***, a species that occurred in more than 30% of the gardens studied in Sheffield, UK. Photo by Ivanov, with permission.

Figure 15. ***Brachythecium rutabulum*** capsule, a species that occurred in more than 50% of the gardens studied in Sheffield, UK. Photo by Wesley, with permission from BBS webmaster.

Figure 16. ***Bryum argenteum***, a species that occurred in more than 30% of the gardens studied in Sheffield, UK. Photo by Michael Lüth, with permission.

Figure 17. ***Didymodon insulanus***, a species that occurred in more than 30% of the gardens studied in Sheffield, UK. Photo by David T. Holyoak, with permission.

Figure 18. ***Funaria hygrometrica***, a species that occurred in more than 30% of the gardens studied in Sheffield, UK. Photo by Michael Lüth, with permission.

Figure 19. ***Kindbergia praelonga***, a species that occurred in more than 50% of the gardens studied in Sheffield, UK. Photo by Michael Lüth, with permission.

Figure 20. ***Ptychostomum capillare*** with capsules, a species that occurred in more than 50% of the gardens studied in Sheffield, UK. Photo by through Creative Commons.

Figure 21. ***Rhynchostegium confertum*** with capsules, a species that occurred in more than 50% of the gardens studied in Sheffield, UK. Photo by Michael Lüth, with permission.

Figure 22. ***Rhytidiadelphus squarrosus***, a species that occurred in more than 30% of the gardens studied in Sheffield, UK. This species often occurs in lawns in Europe. Photo by Michael Lüth, with permission.

Figure 23. ***Tortula muralis*** and water drops in Dunblane Scotland, a species that occurred in more than 50% of the gardens studied in Sheffield, UK. Photo courtesy of Peggy Edwards.

Making Your Garden

Private moss gardens are common in Japan (Pullar 1966/1967; Inoue 1980), but elsewhere they are rare. In Chatsworth, Great Britain, there is a moss and lichen garden of 33 moss and 4 liverwort species, including such common taxa as ***Dicranella heteromalla*** (Figure 24-Figure 25), ***Dicranum scoparium*** (Figure 26), ***Hylocomium splendens*** (Figure 27), ***Neckera crispa*** (Figure 28), ***Plagiomnium undulatum*** (Figure 29), ***Polytrichum commune*** (Figure 30), ***P. piliferum*** (Figure 31-Figure 32), ***Rhizomnium punctatum*** (Figure 33-Figure 34), and ***Thamnobryum alopecurum*** (Figure 35) (Ando 1972). And where else but at the home of a poet – we find cushions of ***Polytrichum commune*** adorning the gardens of Poet Laureate W. Wordsworth.

Figure 24. ***Dicranella heteromalla*** on soil bank, a common species in this habitat. Photo by Janice Glime.

Figure 25. ***Dicranella heteromalla*** with capsules, showing the hair-like leaves. Photo by Michael Lüth, with permission.

Figure 26. ***Dicranum scoparium***, a common species that is used in moss gardens in Europe and the USA. Photo by Janice Glime.

Figure 27. ***Hylocomium splendens***, a common northern moss used in European and American moss gardens. Photo by Michael Lüth, with permission.

Figure 28. ***Neckera crispa***, a common species in Europe, where it is used in moss gardens. Photo by Michael Lüth, with permission.

Figure 29. ***Plagiomnium undulatum***, a common species in Europe, where it is used in moss gardens. Photo by Michael Lüth, with permission.

Figure 30. ***Polytrichum commune***, a common species that is used in moss gardens in Europe and the USA. Photo by David Holyoak, with permission.

Figure 31. ***Polytrichum piliferum*** antheridial splash cups. These add color to moss gardens in the spring. Photo by Janice Glime.

Figure 32. ***Polytrichum piliferum*** with calyptrae, demonstrating colorful calyptrae in late summer. Photo through GNU Free Documentation License.

Figure 33. ***Rhizomnium punctatum*** exhibiting its typical growth form on a rock wall; compare to the soil form in Figure 34. Photo by Michael Lüth, with permission.

Figure 34. ***Rhizomnium punctatum*** exhibiting its growth form on soil. This species is common and often used in moss gardens in Europe. Photo by Michael Lüth, with permission.

Figure 35. ***Thamnobryum alopecurum*** with capsules, a common species that is used in moss gardens in Europe. Photo by Michael Lüth, with permission.

In the Netherlands, a Japanese garden at the estate of Clingendael has become a moss garden. It sports several locally rare species [the leafy liverworts ***Odontoschisma denudatum*** (Figure 36) and ***Plagiochila asplenioides*** (Figure 37)] among its 57 taxa. Schoenmakers (1985) speculates that several of the species that are restricted to paths are the inadvertent contributions of visitors.

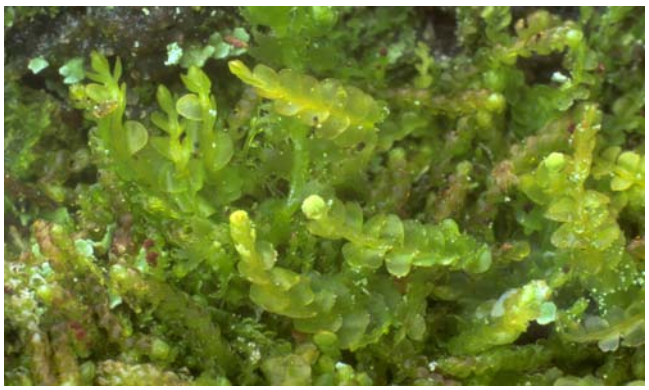

Figure 36. ***Odontoschisma denudatum***, one of 57 taxa in a moss garden in The Netherlands. Photo by Jan-Peter Frahm, with permission.

Figure 37. ***Plagiochila asplenioides***, one of 57 taxa in a moss garden in The Netherlands. Photo by Michael Lüth, with permission.

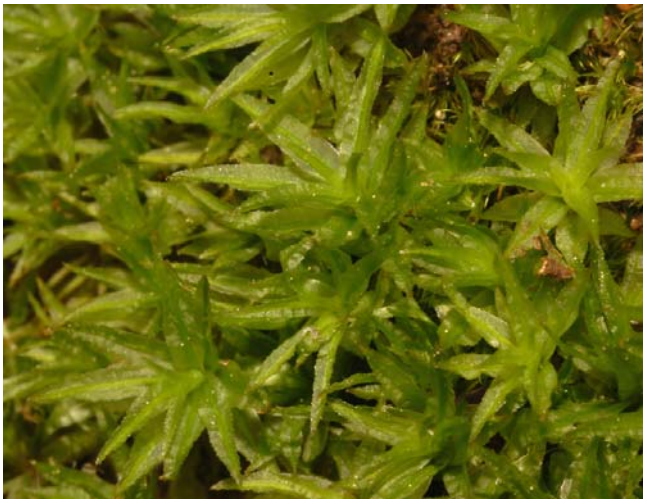

Figure 38. ***Atrichum altecristatum***, a rapid invader of newly opened forest edges and a suitable moss garden species. Photo courtesy of Eric Schneider.

Mossery

In the 19th Century, a number of British and Americans joined the fad of moss collecting (Wikipedia 2017). This interest led to the establishment of mosseries in a number of both British and American gardens. Mosseries are typically made with slatted wood, with a flat roof. They are open to the north, permitting the entrance of light while maintaining shade. Moss samples were installed in the cracks between the wooden slats. Regular moistening of the entire structure helped to maintain growth.

Garden Variety

In the United States, mosses are being used as a means of exploring new garden themes (Massie 1996). A number of web sites give instructions for planting moss gardens, often supplying pictures of very small ones to the large ones of Japan. Even in the highly settled New Jersey, one anthropologist maintains an entire acre of moss (Whiteside 1987). And the prestigious journal *Horticulture* sports one article titled "Even a rolling stone could get some moss here" (Atkinson 1990).

In spite of the presence of moss gardens in the United States at least as early as the 1930's (at Cutting Estate, Great River, Long Island, N.Y.; Grout 1931), few suppliers provide a selection of mosses. Atkinson (1990) complained that when inquiring of the editor of a horticulture magazine where one could obtain mosses for gardens he was referred to Carolina Biological Supply! Nevertheless, more recently a quick search on the web revealed several sources for ***Atrichum*** (Figure 38), ***Callicladium*** (Figure 39), ***Dicranum scoparium*** (Figure 26), ***Campylopus*** (Figure 40), ***Hypnum imponens*** (Figure 12), ***Thuidium delicatulum*** (Figure 41), ***Leucobryum*** (Figure 10), ***Climacium dendroides*** (Figure 42), ***Dicranella heteromalla*** (Figure 24-Figure 25), and ***Plagiomnium cuspidatum*** (Figure 43). One site sold sheet moss that had been cleaned, spread on a backing, glued down, and dyed green! No, thank you! Another source offers a complete garden, including 400 sq feet of moss, for $US 399.99.

Figure 39. ***Callicladium haldanianum***, a shade-loving moss available for purchase for moss gardens in the USA. Photo by Janice Glime.

Figure 40. ***Campylopus pilifer***; the genus ***Campylopus*** can be purchased in the USA for use in moss gardens. Photo by Michael Lüth, with permission.

Figure 41. ***Thuidium delicatulum***, a moss that does well in American moss gardens. Photo by Janice Glime.

Figure 42. ***Climacium dendroides***, a moss often used in American moss gardens. Photo by Janice Glime.

Figure 43. ***Plagiomnium cuspidatum***, a common species in American moss gardens, often as a volunteer. Photo by Janice Glime.

Seasons

To maintain variations in color through the growing season, one needs to pay attention to the phenological changes among the mosses, just as in planting a flower garden. This can provide highlights in different places as the garden changes through the growing season.

Mosses have life cycles that change their appearance. Spring is a typical season for the production of antheridial splash cups. In some species these are reddish (Figure 31); in others, especially splash platforms, they are green, but look like green flowers (Figure 44). Others have colorful setae (Figure 45, Figure 47) and capsules (Figure 46-Figure 48), and these can appear throughout the summer and autumn, depending on the species.

Figure 44. ***Rhizomnium punctatum*** males showing splash platforms that look like green flowers. Photo by Michael Lüth, with permission.

Figure 45. ***Ceratodon purpureus*** showing red-tipped setae in early spring. Photo by Hermann Schachner, through Creative Commons.

Figure 46. ***Ceratodon purpureus***, showing red capsules in early summer. Photo by Michael Lüth, with permission.

Figure 47. Moss with ice on capsules, showing colorful setae even in early winter. Photo by J. Paul Moore, with permission.

Figure 48. ***Pottia lanceolata*** with contrasting capsule color. Photo by Michael Lüth, with permission.

Water Gardens

Many bryophytes like a damp habitat (Figure 49). And some of these habitats are very poor in nutrients. Hence, the bryophytes are naturals for water gardens (Figure 50-Figure 51) (Freiland 2017).

Among the many aquatic species, one of the best for a garden is ***Philonotis fontana*** (Figure 52). It has a fresh, pale green color and tolerates partial submersion or soggy ground.

Figure 49. Water garden and moss where a pipe has been repurposed for creating a garden. Photo from pxhere, through Creative Commons.

Figure 50. Water garden with mosses and waterfall. Photo by David Spain, with permission.

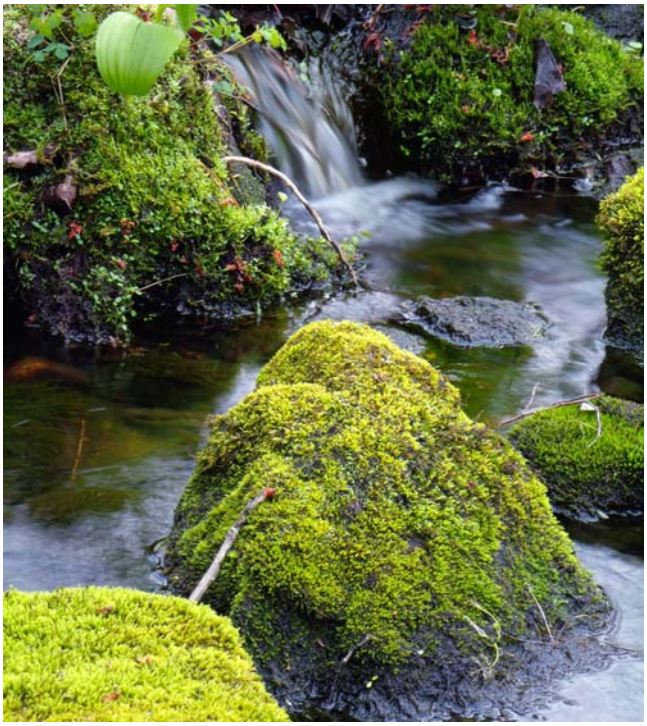

Figure 51. Water garden with mosses on rocks. Photo from pxhere, through Creative Commons.

Figure 52. ***Philonotis fontana*** with capsules, a suitable moss for water gardens. Photo by Michael Lüth, with permission.

Bog Garden

Gardeners such as Case (1994) have found ***Sphagnum*** (Figure 53) bog gardens to be a viable alternative in the Great Lakes area, avoiding high maintenance problems of woodland species unsuited for residential living. These require special conditions devoid of limestone rock and chlorine.

The RaisingRarities website <http://raisingrarities.com/bog-garden/> provides instructions for preparing a bog garden. The pond is excavated and a pond liner is used to cover the shape (Figure 54). It can have a pool attached, as in the diagram, but will require a shallow section for the bog (Figure 55). The lining at the lip of the bog area keeps sand from entering the deeper pool and should go up the bog side of the stones and under them (Figure 56). The bog shelf should be filled 2.5-5 cm deep with pure silica sand. Plant ***Sphagnum*** (Figure 53) on the bog shelf and fill the entire shelf with it. Pitcher plants and sundews can be added for interest, planted among the ***Sphagnum***. Collect rainwater and use it to keep the pond and bog at a constant level.

Figure 53. Colorful ***Sphagnum*** that could be used in a bog garden. Photo by Janice Glime.

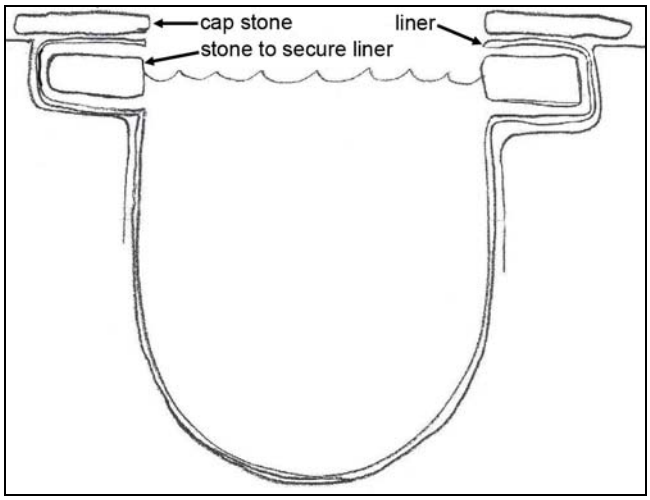

Figure 54. Bog basin and liner in cross section. Redrawn from RaisingRarities.

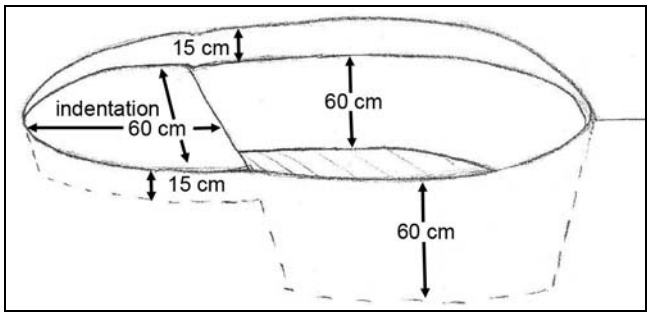

Figure 55. Bog basin and liner showing important dimensions. Redrawn from RaisingRarities.

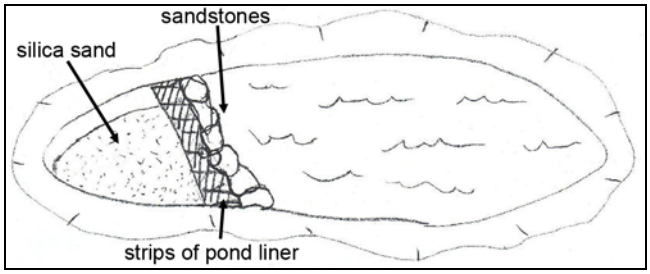

Figure 56. Bog basin shape showing retaining rocks. ***Sphagnum*** will be located on top of the sand. Redrawn from RaisingRarities.

My Personal Garden

For my own moss garden, I managed to rescue ***Marchantia polymorpha*** (Figure 57; with gemmae cups) that was being overtaken by lawn grass on the university campus. It started as a small clump, but one day only a few weeks later I found tiny grey-green specks all over my bare soil (I was just starting the garden). On closer inspection, I found these to be germinating gemmae – the liverwort had spread all over the bare surface and was invading my dying ***Leucobryum*** (Figure 10) cushion as well. By the second year, I had several forests of archegoniophores (Figure 58), but it seems I didn't get any males.

Figure 57. My moss garden initially had a small patch of ***Marchantia polymorpha***, about 10 cm in diameter. Within a month, it spread by gemmae, extending about a half meter in each direction. Photo by Michael Lüth, with permission.

Figure 58. The second year these ***Marchantia*** plants produced archegoniophores in abundance. After a few years, I had to remove some of the ***Marchantia*** to provide space for mosses. Photo by Janice Glime.

Added to that were ***Fissidens*** (Figure 59), ***Brachythecium*** (Figure 60), ***Climacium dendroides*** (Figure 42), ***Dicranum scoparium*** (Figure 26)), ***Leucobryum glaucum*** (Figure 10), ***Plagiomnium cuspidatum*** (Figure 43), ***Polytrichum juniperinum*** (Figure 61), ***Rhytidiadelphus triquetris*** (Figure 62), ***Barbula*** (Figure 63), ***Thuidium delicatulum*** (Figure 41), and ***Ceratodon purpureus*** (Figure 45-Figure 46) that I was able to collect locally, mostly in places where they were doomed to be overgrown or destroyed by traffic. Of these, ***Fissidens***, ***Plagiomnium cuspidatum***, and ***Thuidium delicatulum*** (Figure 41) were the most successful.

Figure 59. ***Fissidens taxifolius*** with capsules; some species of ***Fissidens*** grow easily in moss gardens in North America. Photo by Keith Bowman, with permission.

Figure 60. ***Brachythecium salebrosum***, a species that can occur in large mats usable for moss gardens. Photo by Michael Lüth, with permission.

Figure 61. ***Polytrichum juniperinum*** with capsules in moss garden in Michigan, USA. Photo by Janice Glime.

Figure 62. ***Rhytidiadelphus triquetrus***, a species that often grows well in moss gardens in North America. Photo by Janice Glime.

Figure 63. ***Barbula unguiculata***, a hardy species that adds a contrasting color in the moss garden, preferring a sunny site. Photo by Michael Lüth, with permission.

The ***Leucobryum glaucum*** (Figure 10) was a gift from a friend, and it fared well the first year. It looked bad when winter ended and stains of tannic acid from leaf litter discolored it. It survived, but not well, so the next year I made sure it was not covered with litter for the winter, but it did not make it. I replaced it with a really nice hummock of ***L. glaucum***. This time I put it on a bed of pine needles, a substrate it often has in nature. But it wasn't long before the chipmunks decided that made a nice entrance to their tunnel.

Some night-active animal also tore up all the ***Dicranum scoparium*** (Figure 26) and ***Thuidium delicatulum*** (Figure 41) the first night, and once dismembered from their normal growth habit, both failed to thrive. However, later introductions have survived winter and both have produced new growth, so there is hope. Some rodent decided that the ***Thuidium*** patch was the best place to enter its underground passage, but I seem to have thwarted that hole by stepping on it and filling it in. Alas, now there is a hole in the ***Polytrichum*** patch.

Most of the ***Polytrichum juniperinum*** (Figure 61) is doing fine (Figure 64). It is only the large patch that didn't have good structural integrity that looks like a fallen forest. But even there a few die-hards are putting up new shoots.

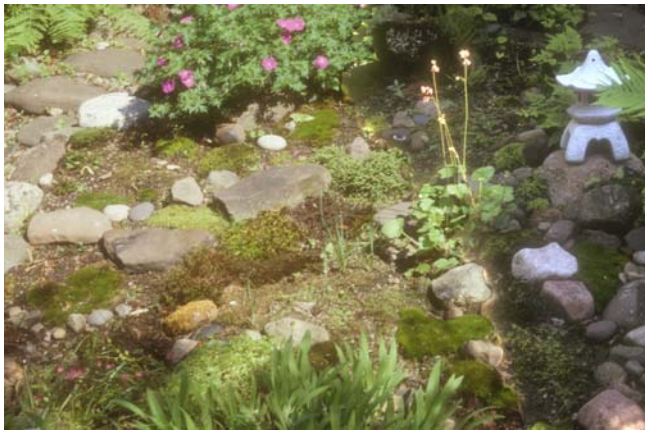

Figure 64. My personal moss garden, when it was about three years old, in Houghton, Michigan, USA. Photo by Janice Glime.

The real winners [***Marchantia*** (Figure 57-Figure 58) aside] are ***Fissidens*** (Figure 59) and ***Plagiomnium cuspidatum*** (Figure 43), with the latter looking a luscious bright green. To my surprise, the ***Rhytidiadelphus triquetrus*** (Figure 62) did well, whereas ***Hylocomium splendens*** (Figure 27) didn't like its transplant at all. One patch of ***Climacium dendroides*** (Figure 42) had mostly brown plants with a few new green shoots arising, but the second patch eventually sprang to life, producing a solid cushion of plants of a most vital green. The old, weedy ***Ceratodon purpureus*** (Figure 45) seems not to like my gardens much and disappears rather rapidly.

A new patch of the liverwort ***Conocephalum conicum*** (Figure 65) seems to be doing well. It, and ***Fissidens*** (Figure 59), also fared well in my indoor garden. That is, they fared well until the birds ate the ***Conocephalum***. I found it with triangular cuts around the edge. Each day it grew smaller until it disappeared. The ***Fissidens*** diminished and ultimately disappeared after the box turtle died. Apparently the turtle had been an effective dispersal agent for both species because they kept appearing in new places until after the turtle died.

Figure 65. ***Conocephalum conicum***, a rock and soil dweller that adds interesting texture to a moss garden. Photo by Robert Klips, with permission.

I attribute my success, after several failures, to the installation of a sprinkling system. It comes on about 4 am for 20 minutes each night. (We usually don't get much rain in spring or summer.) That makes it hydrated and ready to

take advantage of the cool morning sun. It seems to have made all the difference.

I have learned that leaf litter apparently creates more problems than just deprivation of light during the growing season. The tannic acid seems detrimental to several species, because even when I remove the litter the day the snow retreats from its surface, the mosses that were covered with it seem to have suffered. When I removed most of the leaves before winter, the mosses seemed to fare much better.

Mountain Moss Enterprises

The Mountain Moss Enterprises is located near Revard, North Carolina, USA, and is owned by Annie Martin. Known as Mossin' Annie, this entrepreneur has dedicated her life to rescuing bryophytes that are in the path of destruction due to construction or other human activities. These mosses she either plants in one of her many projects, both public and private, or in her own garden where she cares for them until they meet their destiny in a moss garden somewhere.

One of the frequent sources of her bryophytes is from overgrown blacktop. This seemingly unlikely habitat can be a good source for large patches of bryophytes that come in large sheets. Others come from roofs where the owners are convinced they are harmful.

Martin lives in an area of the Appalachians that receives 150-200 cm rainfall per year (Tortorella 2014). Nevertheless, she waters her moss gardens three times each day. She claims that with 3-4 minutes of supplemental water per day the mosses will grow year-round in "nearly any temperature." (I can't imagine that watering when they are under snow is helpful. It would most likely create ice that could actually dry them out more.)

Mosses can dry out or freeze, and easily survive, green up when once again getting wet, but during that dry period they don't look nice. This ability to dry makes them easy to ship, so the distance to a moss supplier is not a real problem. But obtaining mosses from elsewhere does present ecological problems. In addition to the raping of the landscape by some moss collectors, it introduces non-native species.

Martin makes a variety of designs in her gardens, sometimes using differences in colors of leaves to create designs (Figure 66). In other cases, she may use colorful lichens (Figure 67) or furniture to create highlights (Figure 68).

Figure 66. Moss garden at Mountain Moss Enterprises, Pisgah Forest, North Carolina, USA, August 2009. Photo by Annie Martin.

Figure 67. MountainMoss Enterprises moss arrangement with red cap lichens, ***Cladonia*** sp. Photo courtesy of Annie Martin.

Figure 68. Mossin' Annie garden in snow, showing the green of the mosses, even in winter. Photo courtesy of Annie Martin.

Annie Martin (pers. comm. 31 January 2010) received a grant to explore the cultivation of mosses as a cash crop to replace declining tobacco farms. This study involved a partnership of NC Cooperative Extension, Rural Advancement foundation International-USA, and the NC Tobacco Trust Fund Commission which provided the funding. Martin was able to explore various propagation techniques.

Martin points out that moss cultivation requires far less time, labor, and equipment for both maintenance and harvesting compared to tobacco farming. Start-up money is likewise far less for establishing mosses. Maintenance costs are limited to labor and watering, requiring no chemicals, no fertilizers, no pesticides, and no herbicides. This eliminates the pollution of groundwater that is typical of agriculture. On the other hand, the mosses in the Southeast can be harvested any time of year, with their productivity measured in square feet.

Moss and Stone Gardens

David Spain is the owner of Moss and Stone Gardens in Raleigh, North Carolina, USA (Tortorella 2014). Spain presented moss gardening on the Martha Stewart Show, reporting that "she was a big moss fanatic." Spain recounts his early attempts to grow mosses, bemoaning the lack of teachers or sources appropriate for the area. One of these early attempts, following online advice, was to make a mix of mosses in a blender with buttermilk. This slurry was

painted onto rocks or soil. Instead of a moss garden, he got a mold garden. His garden designs tend to mimic nature (Figure 96-Figure 98).

Figure 69. ***Thuidium delicatulum*** in Moss and Stone Garden, showing a fern highlight and a small stream with a stone bridge. Photo from Moss and Stone Garden, with permission from David Spain.

Dale Sievert's Garden

Dale Sievert is a landscape gardener in Wisconsin. He became enamored with mosses and now his property is adorned with 60 species of bryophytes. Some of these species arrived by themselves. Among the more common ones in the garden are ***Bryum caespiticium*** (a widespread species; Figure 70), ***Thuidium delicatulum*** (a species that spreads rapidly; Figure 71), ***Rhodobryum ontariense*** (an interesting species that resembles miniature palm trees; Figure 72), ***Plagiomnium cuspidatum*** (a species that commonly volunteers; Figure 73), ***Leucobryum glaucum*** (a cushion moss that prefers acidic soil; Figure 75), and ***Anomodon rostratus*** (a very common species locally and in his garden; Figure 87).

Figure 70. ***Bryum caespiticium*** forming intriguing hummocks among the rocks. Photo courtesy of Dale Sievert.

Figure 71. ***Thuidium delicatulum***, a moss that spreads easily and usually survives well in the Sievert and other gardens. Photo courtesy of Dale Sievert.

Figure 72. ***Rhodobryum ontariense***, a moss shaped like a palm tree that adds interest to any garden. Photo courtesy of Dale Sievert.

Figure 73. ***Plagiomnium cuspidatum*** in snow. This is a common volunteer in Dale Sievert's garden and in mine, where it doesn't mind being buried in snow. Photo courtesy of Dale Sievert.

Sometimes Sievert lets the mosses determine their own successional pathway. As is typical, pleurocarpous mosses often overrun the acrocarpous mosses (Figure 74). But acrocarpous mosses can invade tight acrocarpous moss cushions as well, as is a common event in which ***Polytrichum*** invades a ***Leucobryum*** cushion (Figure 75). A series of pictures demonstrates some of the changes through time, 2011-2015 (Figure 76-Figure 78).

Figure 74. Nature has her own ideas about what belongs where. Here ***Atrichum*** is being invaded by pleurocarpous mosses. Photo courtesy of Dale Sievert.

Figure 75. ***Leucobryum glaucum*** with invading ***Polytrichum***. Photo courtesy of Dale Sievert.

Figure 76. Moss and cat statues in 2011 showing well-established but still thin mat of mosses. Photo courtesy of Dale Sievert.

Figure 77. Moss and cat statues in 2013 showing thick mat and capsules. Photo courtesy of Dale Sievert.

Figure 78. Moss and cat statues in 2015. The original moss has been replaced with ***Thuidium delicatulum*** dominating the scene. Photo courtesy of Dale Sievert.

Sievert has a number of special features to highlight the various areas of his garden. A bamboo fountain pours into a small pool surrounded by mosses (Figure 79). A bird bath is adorned by colorful rocks and moss-covered rocks (Figure 80). As in many gardens, including my own, a Japanese lantern adds interest (Figure 81). Small to large boulders can add diversity to the scene and may add their own beauty (Figure 82-Figure 83). Stumps provide flat platforms for miniature gardens (Figure 84-Figure 85) or depressions that have their own interest and are great bryophyte substrates (Figure 86). Statuary peers at the visitors or poses playfully among mosses (Figure 85-Figure 86). Ferns provide changes in texture (Figure 87). Pools can attract frogs (Figure 88).

Figure 79. Bamboo fountain in mossy garden, creating a refreshing pool that raises the humidity for the nearby mosses. Photo courtesy of Dale Sievert.

Figure 80. Birdbath garden in Dale Sievert's moss garden. Photo courtesy of Dale Sievert.

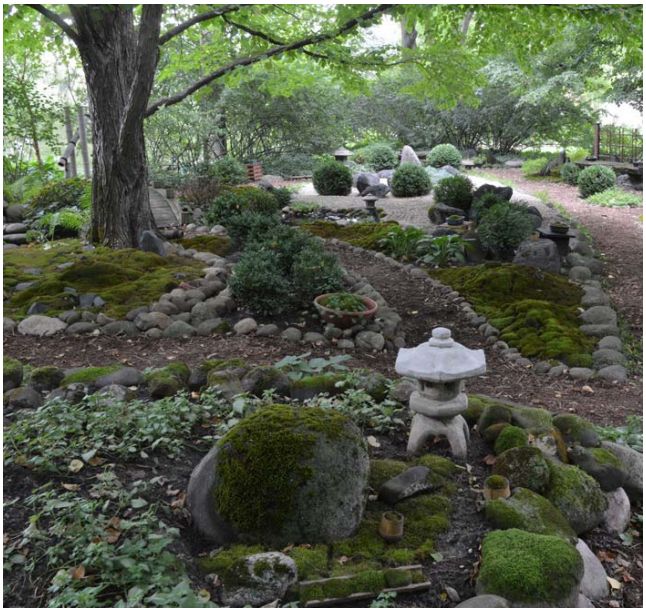

Figure 81. Dale Sievert's moss garden, adorned by a Japanese lamp. Photo courtesy of Dale Sievert.

Figure 82. Rocks and a bit of wood enhance this scene with mostly ***Anomodon rostratus***, a common mss in Dale Sievert's garden. Photo courtesy of Dale Sievert.

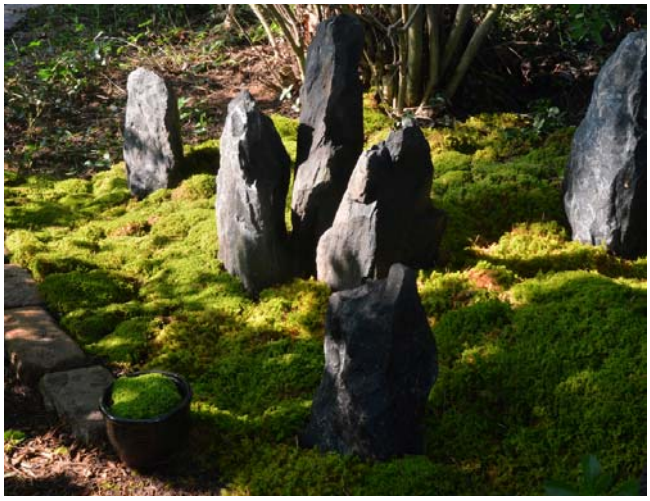

Figure 83. ***Thuidium delicatulum*** and rocks in Dale Sievert's moss garden. Photo courtesy of Dale Sievert.

Figure 84. Here a miniature garden grows on a stump in Dale Sievert's moss garden. Photo courtesy of Dale Sievert.

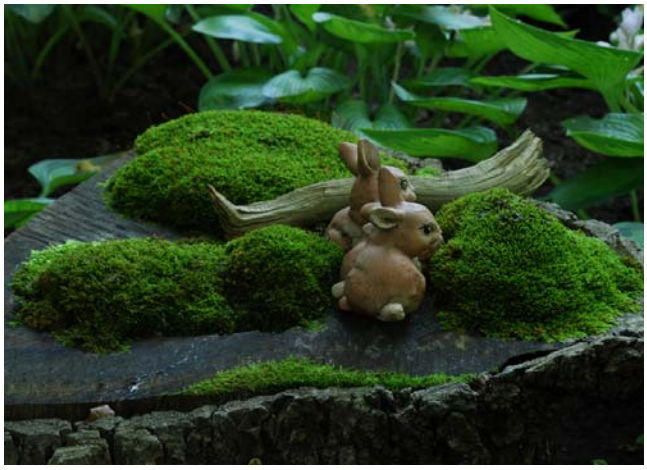

Figure 85. Statuary can add interest or even bring a laugh. Here ***Anomodon rostratus*** grows with bunnies on a stump. Photo courtesy of Dale Sievert.

Figure 86. Raccoon statues in tree stump bring a smile in the moss garden. Photo courtesy of Dale Sievert.

Figure 87. Even a fern can provide a highlight, seen here hovering over ***Anomodon rostratus***. Photo courtesy of Dale Sievert.

Figure 88. Pools can provide habitat and a welcome drink for wildlife. Here the Green Frog ***Rana clamitans*** sits on a mossy rock. Photo courtesy of Dale Sievert.

Fungi (Figure 89-Figure 90) are willing participants in Dale Sievert's garden. The mosses help to keep the soil moist longer, permitting the fungal threads to thrive. In the right conditions, the fruiting bodies emerge, adding color to the garden.

Figure 89. The pore fungus *Boletus* sp. and moss. Photo courtesy of Dale Sievert.

Figure 90. ***Coprinus*** with the moss ***Anomodon rostratus***. Photo courtesy of Dale Sievert.

Dale has been fortunate to have some of his mosses exhibit prolific "fruiting." The setae and capsules often add brilliant colors to the landscape.

Figure 91. ***Ceratodon purpureus*** with numerous red setae. Later red capsules will develop. Photo courtesy of Dale Sievert.

Figure 92. ***Amblystegium varium*** with capsules, a colorful addition in a rock garden. Photo courtesy of Dale Sievert.

Figure 93. This patch of mixed mosses will soon have capsules to change the color scheme. Photo courtesy of Dale Sievert.

Figure 94. ***Plagiomnium cuspidatum*** with capsules, adding a fresh shade of green to the scene. Photo courtesy of Dale Sievert.

The beauty of a Japanese garden captures the admiration of many moss gardeners. And Dale Sievert's garden has its own Japanese garden section. It is complete with a small pond, bridge, and Japanese lantern (Figure 95).

Figure 95. In the Japanese garden portion, a pool, moss, rocks, and raked sand give the feel of a Japanese garden. Photo courtesy of Dale Sievert.

New Methods in Moss Gardening

Rick Smith (2009) has written one of the North American guides to moss gardening, *New Methods in Moss Gardening*. Smith provides his personal experiences around the world where he has created moss gardens or been a consultant. He provides instructions for growing twelve of the most common mosses, accompanied by pictures (Figure 96-Figure 98).

Figure 96. Moss garden designed by Rick Smith. Photo courtesy of Rick Smith.

Figure 97. Moss garden designed by Rick Smith at Illinois Central College. Note the ***Polytrichum*** in the foreground. Photo by Rick Smith, with permission.

Figure 98. Moss garden designed by Rick Smith. Photo courtesy of Rick Smith.

Indoor Moss Garden

As my aging body prevents me from maintaining my outdoor moss garden, I am now attempting an indoor moss garden. So far, I am able to do the required bending, but at least once planted it is essentially maintenance-free – no weeds! I was pleased to have a supplier who rescues the bryophytes she sells by removing them from roofs or construction sites where they are slated for destruction, then cultivates them. Several other suppliers state that they grow their own mosses. I avoid the "grab bags" after trying one and concluding they were ravaged from the forest.

My previous attempts at introducing mosses inside were unsuccessful, with the town's water quality being incompatible despite a filter on the garden room watering system. I was successful with ***Conocephalum*** *cf.* ***salebrosum***. And it also appeared that my turtle was successful in dispersing it.

My new adventure in the indoor moss garden is still quite young, but I do have some success stories. My first introduction was again ***Conocephalum*** *cf.* ***salebrosum*** (Figure 99-Figure 104), and it has been highly successful. The ***Conocephalum*** *cf.* ***salebrosum*** is doing especially well at the base of the waterfall and the stream margins (Figure 99-Figure 101). My ***Marchantia polymorpha*** got dried out, but it is trying to come back, perhaps from gemmae.

Figure 99. Newly planted ***Conocephalum salebrosum*** along stream, with some bare fake rock at edge. on 16 December 2022. Photo by Janice Glime.

Figure 100. ***Conocephalum salebrosum*** growing successfully at the very moist base of the waterfall on 19 February 2023. The green rock and its surrounding liverworts can be seen at the middle left of Figure 99 from two months earlier. Photo by Janice Glime.

Figure 101. ***Conocephalum salebrosum*** growing on wet soil beside the stream in the garden room, 16 December 2022. Photo by Janice Glime.

Figure 102. ***Conocephalum salebrosum*** invading soil on the rock, extending by fragments from the clump above in Figure 101, two months after being planted. Photo by Janice Glime.

Figure 103. ***Conocephalum salebrosum*** colonizing a ledge in the garden room waterfall. Photo by Janice Glime.

Figure 104. ***Conocephalum salebrosum*** showing the bright green of new branches on the thallus after two months in the garden room. Photo by Janice Glime.

My next adventure was a small patch of ***Thuidium delicatulum*** (Figure 105). To my surprise, this was also quite successful (Figure 106). Both of these bryophytes have produced new branches and have a wonderful, fresh color.

Figure 105. ***Thuidium delicatulum*** in garden room on 19 Feb 2023. Photo by Janice Glime.

Figure 106. ***Thuidium delicatulum*** in garden room on 19 Feb 2023; it was planted ~25 November 2022. Photo by Janice Glime.

Two other bryophytes seem to be doing very well – ***Rhytidiadelphus squarrosus*** and ***Rhytidiadelphus triquetris***. I wasn't surprised at the latter because it had also been successful in my outdoor garden. ***Leucobryum glaucum*** is surviving, appears healthy, but so far no expansion. Of course it is winter here, so the room is cool, but not freezing. It gets watered at least 3 times a week and has a small, two-meter high waterfall to maintain moisture.

Figure 107. ***Rhytidiadelphus squarrosus*** in garden room 19 Feb 2023 after nearly three months. Photo by Janice Glime.

Figure 108. ***Rhytidiadelphus triquetrus*** in garden room 19 Feb 2023 after nearly three months there. Photo by Janice Glime.

Figure 109. ***Leucobryum glaucum*** in garden room 19 Feb 2023 after ~3 months. The color is darker than normal and many apical pieces are scattered loose on it. Photo by Janice Glime.

Sun-loving mosses usually die within the same growing season. Likewise, xerophytes don't do well in the high level of moisture.

After 45 years, there are at last volunteers in the garden. These are mostly on pumice that I put there just for that purpose. The mosses are thin and I don't recognize them, but they are healthy.

Figure 110. Volunteer moss on pumice beside the garden room waterfall – after more than 40 years of opportunity! Photo by Janice Glime.

Harvesting Ban

In 2006, a moratorium was declared on moss harvesting in the national forests around Asheville, North Carolina, USA (Tortorella 2014). This ban was based on a study of the moss trade. Local collectors would sell sheet moss for as little as $.50 per pound to members of the floral trade. But stripping a log of all its moss requires 20 years for a new crop, despite all the local rainfall. Gary Kauffman, an ecologist and researcher on the study, determined that if a third of the moss was left on the log, the mosses would grow back in ten years. One of the dangers of collecting the mosses is what fishermen call "bycatch." Unintended species come along with the desired ones, and some of these are rare and endangered. Including these bycatch species, studies indicate that more than 70 species are harvested in the Appalachian moss industry.

Because of these conservation concerns, it is best to do as Annie Martin has done – rescue mosses and liverworts that are scheduled for destruction. In many of these locations, the moss "invaders" are hardy species and ones likely to survive in a garden.

Summary

Private moss gardens tend to serve the same purpose as the larger moss gardens. Rocks, pebble paths, lamps, and other items add interest, and the limited color gives them a peaceful appeal. Outside of Japan, fewer moss gardens exist, in part because the climate is often not suitable. Another difference seems to be the love of color in other parts of the world.

Mosseries are an older form of growing mosses. The moss gardens themselves have a wide variety, using artistic designs, Japanese styles, natural styles, and mixed with flowering plants. They vary by season, changing colors when producing reproductive structures and between wet and dry states. Water gardens require different species, but running water can add sound to the landscape. Bog gardens can be used to grow insectivorous plants and other bog plants.

Worldwide, mosses such as ***Polytrichum*** and ***Leucobryum*** seem to be popular choices for these gardens. Species like ***Thuidium delicatulum***, ***Fissidens*** sp., and ***Plagiomnium cuspidatum*** spread easily and may overtake acrocarpous mosses nearby. ***Plagiomnium cuspidatum*** can often arrive by itself.

Conocephalum salebrosum, ***Thuidium delicatulum***, ***Rhytidiadelphus triquetrus***, and ***R. squarrosus*** do well in indoor gardens.

Harvesting mosses should only be done on your own property or other private property where you have permission. The best way to get plants is to rescue them where they are scheduled for destruction.

Acknowledgments

I appreciate the email discussions with Nancy Church, Annie Martin, Rick Smith, and David Spain. Most recently, I spent an afternoon discussing mosses and moss gardening with Dale Sievert, leading me to include additional topics in an attempt to answer his questions.

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GARDENING: MOSS GARDEN DEVELOPMENT AND MAINTENANCE

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CHAPTER 7-4
GARDENING: MOSS GARDEN DEVELOPMENT AND MAINTENANCE

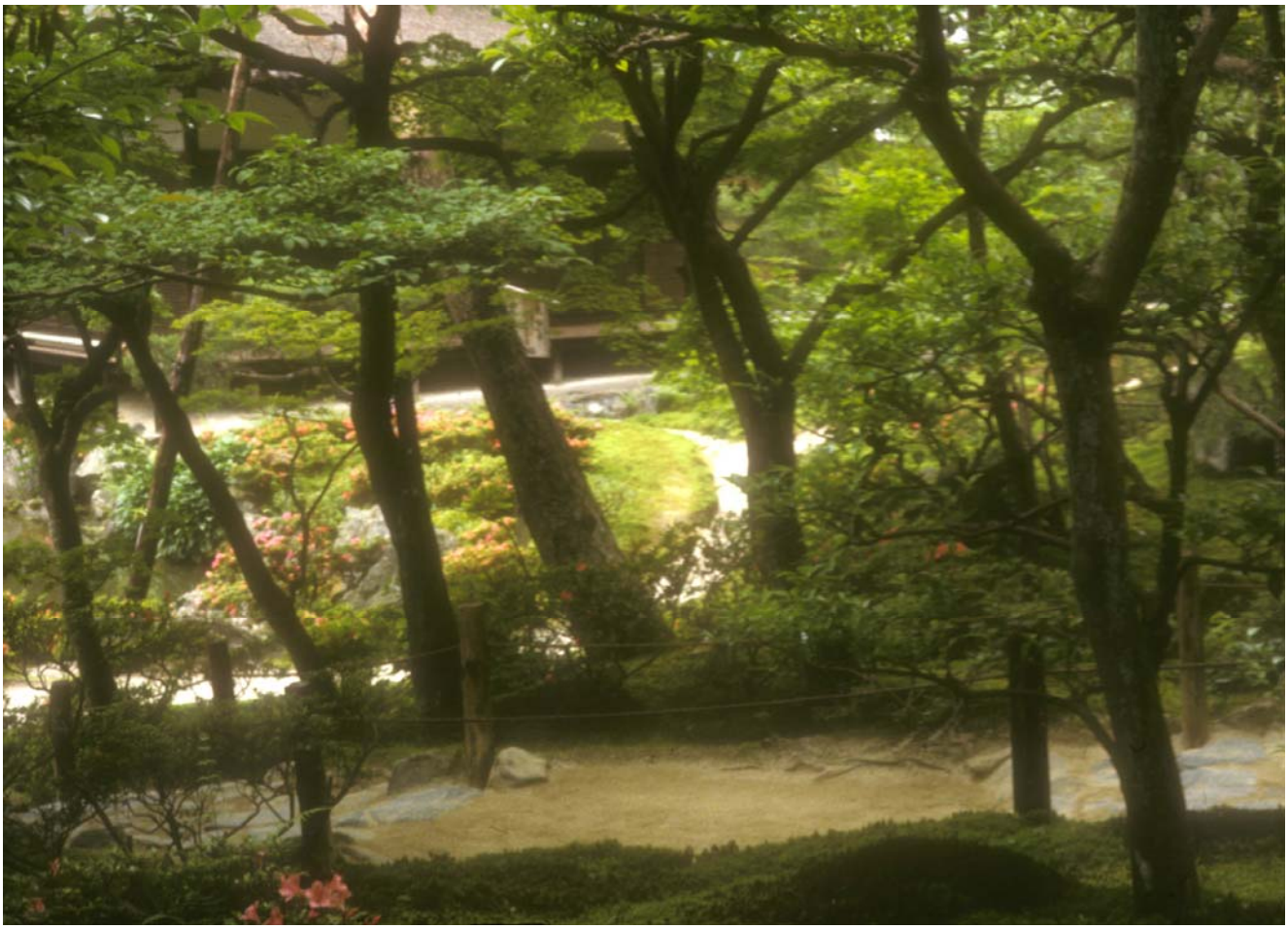

Figure 1. This moss garden in Kyoto, Japan, takes advantage of a stream to add to its peaceful nature. Photo by Janice Glime.

Choice of Bryophytes

Careful selection of bryophytes will greatly increase the chances for success. These plants often have niches that are not provided by the typical garden spot, so care should be taken to select species with habitat requirements similar to that available in the garden.

When you collect different species of mosses and then plant them together, the needs of the different species may differ. There are many species and it's often difficult to discern differences without using a hand lens or consulting a bryologist. If requirements differ, the one most suited can more easily overgrow the other. I suggest that you learn to distinguish the acrocarpous from pleurocarpous species and keep these two separated. The horizontal growth form of pleurocarpous species easily overtakes the upright acrocarpous species.

Most acrocarpous mosses do not like constant moisture whereas most pleurocarpous ones do. One way to deal with this is to maintain a regular watering schedule and allow the mosses that are flourishing to take over the ones that are not. Dead or dying mosses of one species can make a welcoming surface for other mosses to invade or provide suitable substrate for spores to germinate. You can speed up the process by fragmenting some of the flourishing mosses directly on top of the ones that are failing.

In some cases large areas might be transplanted with a moss that is not appropriate for the new conditions and all of the new transplants die. If the area continues to be watered as if the moss is still alive, after several months the spores of another species might germinate on top of the decaying moss and a more appropriate species will develop.

This bed of dead moss retains moisture, controls erosion, and reduces weed invasion. It permits spores of other mosses to have places to land and establish without blowing away. Developing a moss area will eventually lead to some of the species performing better than others and the faster-growing species will subsequently dominate the area.

Spain (2012a) advises that you can "let mother nature decide what species to introduce by clearing the area down to bare earth and then begin watering just as though there was moss already present… If you build it, they will come!"

One might learn from the mosses that are often considered weeds. Charlie Campbell (Bryonet 17 April 2014) found that his parents' lawn in northern England had ***Rhytidiadelphus squarrosus*** (Figure 2) as a co-dominant with the grass. ***Atrichum undulatum*** (Figure 3) and ***Plagiomnium undulatum*** (Figure 4) also occurred in small patches. In Berkshire, his flats were surrounded by grasslands and were on dry, sandy, open lawn. On the shady side of the flats the ***Rhytidiadelphus squarrosus*** grew, but on the sunny areas two different communities developed. On the west-facing slope the community was rich in bryophytes, including ***Riccia glauca*** (Figure 5), ***Sphaerocarpos*** sp. (Figure 6), ***Didymodon vinealis*** (Figure 7), and others. On the east-facing side, an abundant ***Polytrichum juniperinum*** (Figure 8) cover developed. After several days of rain, ***Lophocolea bidentata*** (Figure 9) became extremely frequent on both sunny sites.

Figure 2. ***Rhytidiadelphus squarrosus***, a common moss in lawns in parts of Europe. Photo by Michael Lüth, with permission.

Figure 3. ***Atrichum undulatum***, a moss that sometimes invades lawns. Photo by Janice Glime.

Figure 4. ***Plagiomnium undulatum*** with ice, a moss that sometimes invades lawns in Europe. Photo by Tim Waters through Creative Commons.

Figure 5. ***Riccia glauca***, a thallose liverwort that survives on west-facing slopes. Photo by Bernd Haynold, through Creative Commons.

Figure 6. ***Sphaerocarpos*** sp., a liverwort that survives on west-facing slopes. Photo by David T. Holyoak, with permission.

Figure 7. The moss ***Didymodon vinealis*** is often found on rooftops, concrete, and rock walls. Photo by Michael Lüth, with permission.

Figure 8. ***Polytrichum juniperinum***, a moss that does well on west-facing slopes. Photo by Jan-Peter Frahm, with permission.

Figure 9. ***Lophocolea bidentata***, a moss that seems to suddenly appear in sunny spots after a rainfall. Photo by Michael Lüth, with permission.

Few published studies have taken an experimental approach to moss gardening, although I'm sure many gardeners have used trial and error to determine the best bryophytes for their gardens. Radu *et al*. (2016), however, were interested in bryophytes for a variety of applications and set out to determine the most suitable species. They used six species of mosses in hydroponic experiments: ***Syntrichia ruralis*** (Figure 10), ***Homalothecium sericeum*** (Figure 11), ***Ceratodon purpureus*** (Figure 12), ***Grimmia pulvinata*** (Figure 13), ***Racomitrium aciculare*** (Figure 14), and ***Bryum capillare*** (Figure 15). These species were tested at different light intensities and water dosing regimes. The researchers concluded that ***Grimmia pulvinata*** and ***Ceratodon purpureus*** adapted the best to the controlled environment. They thus considered them to be suitable for use in landscape design. But lab conditions are not field conditions, and constant conditions are quite different from constantly varying conditions. The chapter on Phenology in Volume 1 can suggest a few.

Figure 10. ***Syntrichia ruralis***, a species tolerant of bright sun and desiccation. Photo by Janice Glime.

Figure 11. ***Homalothecium sericeum***, a common species in Europe. Photo by Janice Glime.

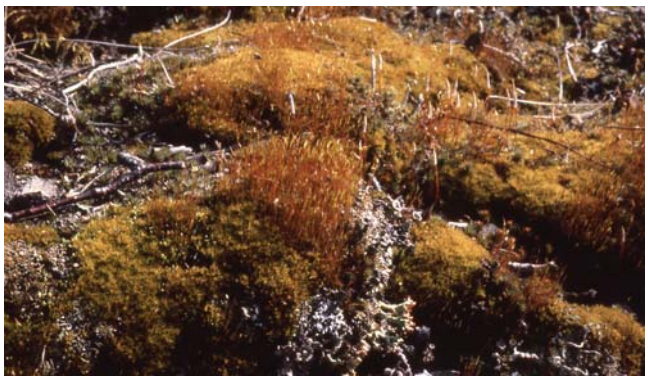

Figure 12. ***Ceratodon purpureus***, a widespread and sun-tolerant species that adapts well to a controlled environment. Photo by Janice Glime.

Figure 13. ***Grimmia pulvinata*** on wall, a moss that is widespread and common on walls and rock. It also grows well in controlled environments. Photo from Botany Department Website, UBC, Canada, with permission.

Figure 14. ***Racomitrium aciculare***, a rock-dwelling moss. Photo by Michael Lüth, with permission.

Figure 15. ***Bryum capillare***, a common moss with a wide distribution. Photo by Des Callaghan, with permission.

Thallose Liverworts

One seldom thinks of liverworts in the context of a "moss" garden, but several thallose liverworts are suitable for "moss" gardens. These can be pressed into soft soil so that they have good contact with the substrate (Fletcher 1991). Among the known successful ones are ***Marchantia polymorpha*** (Figure 16) and ***Lunularia cruciata*** (Figure 17) on garden paths and damp soil, ***Conocephalum conicum*** (moist soil; Figure 18), and ***Riccia sorocarpa*** (Figure 19) and ***Riccia glauca*** (Figure 5) in damp fields and garden beds (but small and easily overgrown).

Figure 16. ***Marchantia polymorpha*** with its umbrella-like **archegoniophores**, a species that spreads easily on disturbed soil. Photo by Janice Glime.

Figure 17. ***Lunularia cruciata***, a species that is common in greenhouses in the USA, but can be grown in moss gardens. Photo by Des Callaghan, with permission.

Figure 18. ***Conocephalum conicum***, a thallose liverwort that multiplies rapidly and can be dispersed by turtles and other fauna. Photo by Janice Glime.

Figure 19. ***Riccia sorocarpa***, a common thallose liverwort. Photo by Michael Lüth, with permission.

Sphagnum – peat mosses

Most ***Sphagnum*** (Figure 20) taxa require a wet, acidic habitat, and most have a somewhat narrow range for both of these. Their habitat should be mimicked, and that means that they need to be supplied water from below (Fletcher 1991). This can be accomplished by placing them in flower pots in a shallow tray of standing water. ***Sphagnum*** is well constructed to soak up and transport the water externally through all the capillary spaces surrounding its stem. The proper *p*H can be maintained by growing the plants on their own peat. Tap water can easily kill them. If it has many minerals in it, they will accumulate on the surface and eventually kill them. Calcium is particularly lethal to ***Sphagnum***. To solve this dilemma, distilled water or rainwater is the best watering medium. No fertilizer is needed, and in fact should be avoided.

Figure 20. ***Sphagnum fuscum***, a species that lives on tops of hummocks. Photo by Michael Lüth, with permission.

Sphagnum comes in a wide range of colors (Figure 21), and a bouquet of colors and hues can be arranged in the same garden by using some care in choices of species. Some of these may be maintained by placing them at greater distance from the water source, such as ***Sphagnum fuscum*** (Figure 20) (Fletcher 1991).

Figure 21. ***Sphagnum magellanicum*** and other species of ***Sphagnum*** showing some of the range of colors that occur together naturally. Photo by Janice Glime.

Although many ***Sphagnum*** (Figure 20) species are sun-loving, too much can fry them. Fletcher (1991) reports losing many of his plants during a hot summer when he forgot to move the plants into the shade. The problem is that sun will quickly dry out the plants, and most of the taxa are not drought tolerant. Furthermore, most lack protection against bright sun that can destroy the chlorophyll.

Birds can be a problem in a moss garden. The conditions that favor growth of ***Sphagnum*** (Figure 20-Figure 21) also favor the presence of a number of invertebrates. Hungry birds, especially early in spring, can be quite disruptive as they rummage for dinner. And nesting can be an even bigger problem, especially if your garden provides lots of mosses in a city area where few other mosses exist. In my indoor garden, mosses and zebra finches simply cannot co-exist. The birds win every time, carrying off every bit of moss for nesting material. Fletcher (1991) suggests covering the mosses with netting to minimize the disturbance. Wire netting must be avoided because it is likely to release zinc or other metal that is toxic to the bryophytes.

Fletcher (1991) suggests ***Sphagnum quinquefarium*** (Figure 22) for well-drained slopes in wet woods. ***Sphagnum cuspidatum*** (Figure 23) does well in pools, where it looks like a wet kitten. Fletcher has even kept it in a jam jar for a year. On a bed of peat, ***Sphagnum compactum*** (Figure 24) can tolerate drying, prefers shade, and does not like being water-logged.

Figure 22. ***Sphagnum quinquefarium***, a moss of well-drained slopes in forests. Photo by Michael Lüth, with permission.

Figure 23. ***Sphagnum cuspidatum***, an emergent species for pools. Photo by Jan-Peter Frahm, with permission.

Figure 24. ***Sphagnum compactum***, a species that grows on wet sand or rocks in shaded areas where it tolerates drying. Photo by Michael Lüth, with permission.

Polytrichum – hairy cap mosses

The most common of the mosses in Japanese gardens (Figure 1) of all kinds is the common hairy cap moss, ***Polytrichum*** (Figure 25). This group of mosses is common in both temple gardens and private gardens. ***Polytrichum*** is difficult to transplant because the clump easily becomes disturbed in the process. For that reason, smaller, young clumps work best. But don't despair if those larger clumps collapse and turn brown. I have learned to trust the resilience of moss stems, and ***Polytrichum*** stems are a good example to support this trust. I transplanted one year after they had collapsed from their original orientation. They looked pretty bad when they went into the garden, and they didn't improve much. The next spring I was nearly ready to remove them, but didn't get the energy to do it. Then small green tips began to appear. Most of the sprawling clump still looks rather sad. They might have come back, but a chipmunk decided to occupy that part of the garden, building an entrance to its underground runway, Nevertheless, life is there, and perhaps with time the clump will fill in through stems.

Figure 25. ***Polytrichum commune*** var ***commune***, a common species used in moss gardens. Photo by David Holyoak, with permission.

Members of the genus ***Polytrichum*** can resist disturbance by the broom or bamboo rake used to remove fallen leaves and other debris (Ando 1987), and they are unusual among mosses for their resistance to drought and ability to withstand direct sunlight as well as shade (Steere 1968). ***Polytrichum juniperinum*** (Figure 8) and ***P. piliferum*** (Figure 26-Figure 27) do well if the clump integrity is maintained, again making small, young clumps easier to transplant.

Figure 26. ***Polytrichum piliferum*** males, adding a bit of color to moss gardens in spring. Photo from Proyecto Musgo, through Creative Commons.

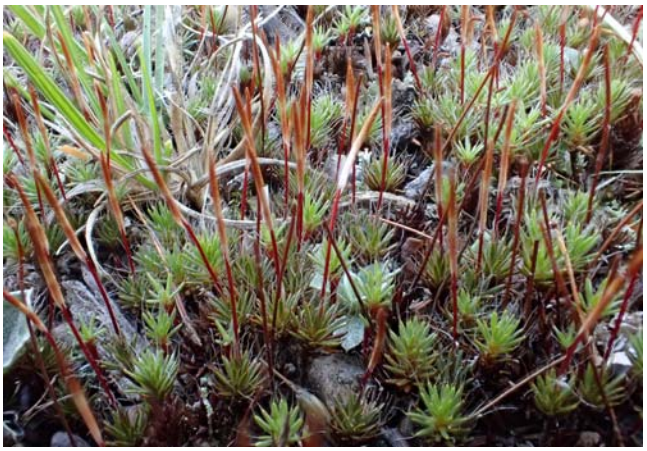

Figure 27. ***Polytrichum piliferum*** with young sporophytes. Photo by Janice Glime.

As with ***Sphagnum*** (Figure 22-Figure 24), lime in some tap water can form crusts on the leaves (Fletcher 1991). One reason for this is that water for ***Sphagnum*** in nature must generally come from above. Although many mosses have good capillary action to move water externally, ***Polytrichum*** (Figure 25-Figure 27) species have large, waxy leaves that tend to repel water and do not move it well externally. Although they have one of the best developed internal conducting systems, they still take in most, if not all, of their water through the tip of the plant. Thus, water must be supplied from above and needs to be almost completely free from minerals. Even so, dust splashing from the soil can easily reach the leaves and contribute to their mineral accumulation.

Fletcher (1991) contends that the most easily grown mosses are those that have strong rhizoids, because they are least damaged by lime. For the remaining majority, one can use peat as a substrate, but that is often too moist. Another alternative is to use a sand substrate or in some cases organic soil free of lime, and water only with distilled water. Rain water is also a good choice, but may be contaminated with lime in areas with alkaline soil or limestone rocks. Nevertheless, as Fletcher points out, the impact of rainfall helps to wash off the minerals. A good spraying system is essential in areas where rainfall is infrequent. Fletcher advises to wash the mosses off with a spray of rainwater when they have accumulated minerals on their leaves.

Fletcher has succeeded in keeping ***Polytrichum*** (Figure 8) alive for 20 years, but he finds it necessary to transplant them every 1-2 years onto fresh peat. Once done, this permits old, dying shoots to produce new sprouts that emerge from the peat. On the other hand, I have had a bed of ***Polytrichum juniperinum*** (Figure 8) for seven years without disturbing it, and it is still doing well. It looks awful in the spring, but it recovers.

Polytrichum commune (Figure 25) and ***P. strictum*** (Figure 28) grow mostly in bogs and fens. ***Polytrichum strictum*** is aided in its quest for water by a white tomentum on the lower part of the stem.

Figure 28. ***Polytrichum strictum*** with capsules, a bog/fen species that is suitable for moss gardens. Photo by Michael Lüth, with permission.

Atrichum

Atrichum (Figure 3) is a relative in the same family as ***Polytrichum*** (Figure 25-Figure 27). But its needs are somewhat different. Whereas ***Polytrichum*** has stiff, waxy leaves with lamellae across most of the surface, ***Atrichum*** has thin leaves (Figure 29) with lamellae only in the middle over the more narrow costa (Figure 30). This genus does best on soil, not peat (Fletcher 1991). Some species can be an invasive moss along paths (Figure 31) and can easily regrow from fragments. These provide a nice yellowish green.

Figure 29. ***Atrichum altecristatum*** leaf portion showing lamellae over costa down center. Photo by Bob Klips, with permission.

Figure 30. ***Atrichum altecristatum*** showing lamellae over costa in leaf cross section. Photo by Bob Klips, with permission.

Figure 31. ***Atrichum altecristatum*** along a path in the forest in Houghton, Michigan, USA. Photo by Janice Glime.

When ***Atrichum*** dries, the leaves curl (Figure 32) and often turn brown (Figure 33). In this form it is not very attractive. It will look nice in a well-watered or humid garden.

Figure 32. ***Atrichum altecristatum*** drying and curling. Photo courtesy of Eric Schneider.

Figure 33. ***Atrichum angustatum*** with dry, brown leaves and capsules. Photo by Janice Glime.

Leucobryum

Leucobryum glaucum (Figure 34) was a favorite moss of many of my students. A common moss, it is easily recognizable by its whitish color and pincushion appearance. Its whiteness is emphasized in its name, with *bryum* meaning moss, *leuco* meaning white, and *glaucum* meaning whitish like wax. It goes by the common names of cushion, pincushion, or white moss. It likes acid soil, frequently occurring in conifer forests. Although it typically occurs in the shade, it can tolerate sun exposures. And the genus is common on many continents.

Leucobryum (Figure 34) is an **acrocarpous** moss, or upright type, producing stalks and capsules at the tips of the upright stems. Its mound form (Figure 34) makes a striking element in garden designs and borders, providing both a break in the topography and a striking contrast in color. This color contrast is due to hyaline cells that mask the green color of the leaves. As the moss dries, the hyaline cells lose water, the optics change, and the moss appears whiter.

Figure 34. ***Leucobryum glaucum*** at tree base, a common species in moss gardens. Photo by Janice Glime.

The texture of ***Leucobryum*** (Figure 34) cushions is somewhat coarse, due to the leaves that are more than one cell thick and relatively large. Cushion size can become quite large (Figure 35), and these will be very compact.

Figure 35. ***Leucobryum glaucum*** demonstrating the large cushions in an undisturbed forest In Copper Harbor, Michigan, USA. Photo by Janice Glime.

Annie Martin (Mountain Moss Newsletter winter 2010) relayed her experience relocating ***Leucobryum glaucum*** (Figure 34) from a gravel road where it was growing in full sun. It was dehydrated and white. She placed it among other ***Leucobryum*** plants in her garden and watered it three different times that evening. By morning it looked as fresh and alive as the established ***Leucobryum*** plants.

I have attempted cultivating ***Leucobryum glaucum*** (Figure 34) several times with only short-lived success. This moss seems especially susceptible to destruction by the leachates of leaf litter, even if the litter is cleared as soon as the snow melts.

Another habit of this plant might lead to dismay if one isn't familiar with its behavior. When it is reproducing

asexually, the leaves at the tip break off, providing a white covering of fragments on the colony (Martin 2010). This gives it a "cruddy" appearance for a while, but the plants are fine – just reproducing and dispersing. You can sweep these off with a soft brush to improve the appearance and at the same time disperse your ***Leucobryum*** (Figure 34) to additional locations in your garden.

If your ***Leucobryum glaucum*** (Figure 34) turns black, you do have a problem. This indicates that it is being kept too wet (Martin 2010). Perhaps this explains its sickly look in my garden when it emerged from the snow in spring. The slow melt in spring may have kept it too wet too long with little light and no opportunity to get dry. This discoloration can also be caused by fungal attack – an event further promoted by moisture. Martin advises to let the moss dry out for a while to see if it will recover.

On the other side of the coin, ***Leucobryum*** (Figure 34) has some remarkable recovery techniques. If it gets turned upside down, it will begin growing from the exposed side (Martin 2010), sometimes making a ball!

Martin (2010) finds this moss to be easy to pick up. The pincushion sits on the soil surface and grows on its own dead base (Figure 36). There is usually no soil attached. I have been advised to plant it on a bed of pine needles, but my one attempt at that was undone by a chipmunk that chose it for making the entrance to a burrow. It seems to like sandy soil and to avoid rich soil. As always, Martin warns us not to take bryophytes from parks or forests and to ask permission before collecting on private land.

Figure 36. ***Leucobryum glaucum*** showing dead lower parts that sit on the soil surface. Photo courtesy of Diane Lucas.

Leucobryum bowringii (Figure 37), ***L. juniperoideum*** (Figure 38) grow in mounds or cushions, creating a gentle, rolling landscape resembling miniature hills (like Figure 36). ***Leucobryum*** (Figure 39) is abundant and highly praised for its huge whitish cushions that provide beautiful contrast.

Figure 37. ***Leucobryum bowringii***, a species used in Japanese moss gardens. Photo through Creative Commons.

Figure 38. ***Leucobryum juniperoideum***, a species used in Japanese moss gardens. Photo by Jan-Peter Frahm, with permission.

Figure 39. ***Leucobryum*** "spills" down the hill in a moss garden in Kyoto, Japan. Photo by Janice Glime.

Dicranum

Dicranum is an acrocarpous genus that prefers shade. The most widespread and common species, ***Dicranum scoparium*** (Figure 40), forms cushions. The leaves curve and typically they all curve in one direction (Figure 41), creating the temptation to pet it. It provides a dark green contrast to ***Leucobryum*** (Figure 34) species and is found in

many parts of the world, permitting its use in the moss gardens of Japan.

Figure 40. ***Dicranum scoparium*** on forest floor, a common moss of forests that adds a dark green to the garden. Photo by Janice Glime.

Figure 41. ***Dicranum scoparium*** showing leaves curved in one direction. Photo by Janice Glime.

Mniaceae

Mniaceae can be similarly propagated, preferring damp, shaded places. ***Plagiomnium cuspidatum*** (Figure 42) has been quite successful in my garden and thrived as an invader among the shrubs around the campus library. Several members of **Mniaceae** are known and used for their big, lush leaves (Figure 42).

Figure 42. ***Plagiomnium cuspidatum*** is easily grown if it can be transplanted without disturbing its connections to the soil and each other. Photo by Michael Lüth, with permission.

I have found this species as a well-developed moss among my flagstones on a path, where it was totally a volunteer.

Thuidium delicatulum

Thuidium delicatulum (Figure 43) is one of the fast-growing mosses (Martin 2010) and can take over a moss garden (Dale Sievert, pers. Comm. 13 October 2017). Despite the disturbances by chipmunks, I have found it to be persistent in my garden, showing up in new locations.

Figure 43. ***Thuidium delicatulum*** when it is wet and fresh. Photo by Jan-Peter Frahm, with permission.

Martin (2010) finds this moss to be a strong grower in winter in North Carolina – in her words, growing "by leaps and bounds during the winter months." She found that it quickly spread over mosses like ***Leucobryum*** (Figure 34) and ***Dicranum*** (Figure 40), invading and sometimes covering these mounds.

Thuidium is papillose (Figure 44), crunchy when dry (Figure 45), but soft when wet (Figure 43). It looks like a miniature fern and is often known as "fern moss." It will grow in open areas among grasses, but its need for some shade makes it a more likely candidate for shady portions of a garden.

Figure 44. ***Thuidium delicatulum*** branch showing the projecting papillae on the leaves. Photo by Bob Klips, with permission.

Figure 45. ***Thuidium delicatulum*** dry (and crunchy). Photo by Janice Glime.

Pseudoscleropodium purum

Pseudoscleropodium purum (Figure 46) is a large, pleurocarpous moss that tends to grow on acidic soil. It seems to like acidic grasslands, roadsides, and maintained lawns. It has attractive branches that look rope-like due to the concave leaves that end in a sudden, short, narrow tip. Like ***Thuidium*** (Figure 43), it is a rapidly growing species (Martin 2010). But be careful – it is also an invasive species, sometimes getting introduced when it is used as a packing material.

Figure 46. ***Pseudoscleropodium purum***, a common moss in Europe, but invasive in parts of the USA. Photo by Janice Glime.

Rhodobryum

Rhodobryum (Figure 47) is a special genus that has very attractive individual plants. The leaves are crowded at the tips of the stems, making these look like a colony of miniature palm trees. The genus can grow in deep shade and seems to like it somewhat damp. Hilty (2017) describes its habitats in Illinois as moist ground in woodlands, wooded hillsides, ground at the base of trees in woods, swampy woodlands, shaded clay banks of ravines, moist decaying logs, limestone rocks along streams, moist limestone cliffs, shaded limestone ledges, limestone blocks in woods, thin soil over sandstone rocks in wooded areas, shaded ground in hanging fens, and sandy clay banks along creeks. Although it is a relatively uncommon moss, this presents a wide range of habitats where you can grow them.

Figure 47. ***Rhodobryum ontariense***, an attractive moss for gardens. It prefers alkaline habitats but also grows over sandstone rocks. Photo by Janice Glime.

The ***Fissidens*** (Figure 48) in my moss garden has spread to other gardens in my yard. It can be aggressive, as seen in Figure 49 where it is overgrowing ***Marchantia polymorpha***.

Fissidens

Fissidens (Figure 48) is not often mentioned as a genus for moss gardens. However, my experience with it is that it is an excellent choice. It holds up well and stays green when it is dry. But the best news is that it grows well when propagated and spreads by itself, perhaps with the help of the chipmunks.

Figure 48. ***Fissidens adianthoides*** is a moss easily cultivated by transplant or fragments. Photo by Michael Lüth, with permission.

Figure 49. ***Fissidens*** in my moss garden in Houghton, Michigan, USA, on 15 April 2010 soon after snow melt. Here it is taking over ***Marchantia polymorpha***. Photo by Janice Glime.

Others

In the shade in Japan, common species include ***Pyrrhobryum dozyanum*** (Figure 50), and ***Trachycystis microphylla*** (Figure 51). Like ***Leucobryum***, these latter taxa grow in mounds or cushions, creating a gentle, rolling landscape resembling miniature hills. ***Hypnum*** (Figure 52) and ***Racomitrium*** (Figure 53) are common in drier places and ***Fissidens*** (Figure 48) and ***Atrichum*** (Figure 3) in wet places (Steere 1968). Both ***Hypnum plumaeforme*** (Figure 54) and ***Racomitrium canescens*** (Figure 53) are able to grow without deep shade, but require frequent watering and weeding (Ueta & Deguchi 1980). In his webpage, Svenson (2000) recommended ***Racomitrium canescens*** as a moss for both sun and shade. It is quite drought tolerant, and it can form large, thick mats that have a broad tolerance, even to trampling. Other mosses suitable for gardens include ***Eurhynchium praelongum*** (Figure 55), ***Rhynchostegium confertum*** (Figure 56), ***Brachythecium rutabulum*** (Figure 57), and ***Rhytidiadelphus squarrosus*** (Figure 2) (Fletcher 1991).

Figure 52. ***Hypnum imponens***, a widespread species suitable for moss gardens. Photo by Janice Glime.

Figure 50. ***Pyrrhobryum dozyanum***, a large moss that does well in shady sites in Japanese gardens. Photo by Janice Glime.

Figure 53. ***Racomitrium canescens***, a moss suitable for a sunny garden that might get dry frequently. Photo by Michael Lüth, with permission.

Figure 51. ***Trachycystis microphylla*** with capsules, a moss that does well in shady sites in Japanese gardens. Photo from Digital Museum, Hiroshima University, with permission.

Figure 54. ***Hypnum plumaeforme***, an epiphyte in Japan. When planted in moss gardens, it requires frequent watering and weeding. Photo by Janice Glime.

Figure 55. ***Eurhynchium praelongum***, a beautiful plumose moss suitable for gardens. Photo by Blanka Shaw, with permission.

Figure 56. ***Rhynchostegium confertum*** with capsules, a species suitable for moss gardens. Photo by Michael Lüth, with permission.

Figure 57. ***Brachythecium rutabulum*** with capsules, a common moss that will grow in gardens. Photo by Michael Lüth, with permission.

Some mosses are especially adept at being transplanted and seem to survive despite drought or rainy season. Among these, I have been most successful with the medium-sized species of ***Fissidens*** such as ***F. adianthoides*** (Figure 48). It helps considerably if the shape of the original colony can be maintained, preventing exposure of longer stems by maintaining the shorter outer members of the cushion. This is especially true for cushion-formers like ***Leucobryum*** (Figure 39) and ***Dicranum*** (Figure 40). If this is not possible, pushing a rock against the exposed broken parts of the cushion helps to maintain the moisture there.

Hylocomium splendens (Figure 58) and ***Pleurozium schreberi*** (Figure 59) likewise do not transplant well. I have to wonder if a symbiotic fungus is involved. I was surprised that ***Rhytidiadelphus triquetris*** (Figure 60), a species in the same family as ***Pleurozium*** and ***Hylocomium***, does well. ***Thuidium delicatulum*** (Figure 43-Figure 45) is somewhat successful, but mine was disturbed badly by a chipmunk that seemed to think that was the best place to enter its burrow. Followed by a very dry summer, ***T. delicatulum*** did not seem to be doing well. Nevertheless, it now occupies spots shaded by flowering plants and rocks, having dispersed there without my help.

Figure 58. ***Hylocomium splendens***, a species that does not transplant well. Michael Lüth, with permission.

Figure 59. ***Pleurozium schreberi***, a species that does not transplant well. Photo by Sture Hermansson, with online permission.

Figure 60. ***Rhytidiadelphus triquetrus***, a species that transplants well. Photo by Janice Glime.

Moss gardening is a growing industry, even in the United States and other parts of the world outside Japan. However, not all plants touted as mosses are truly mosses. Spanish moss (***Tillandsia usneoides***; Figure 61), a bromeliad, hence a flowering plant, is included among the types available from at least one moss seller. Rock mosses (*Selaginella*; Figure 62) and club mosses (Figure 63) (both Lycopodiaceae) are both cryptogamic tracheophytes, not bryophytes. Sheet moss, ***Sphagnum*** (Figure 20-Figure 24), and "bun" moss (growing in clumps) are other types listed and are true mosses. Sheet mosses include such mosses as ***Hypnum*** (Figure 52) and ***Thuidium*** (Figure 43-Figure 45) (Nelson & Carpenter 1965).

Figure 61. ***Tillandsia usneoides***, Spanish moss, but not a real moss. Photo by George Shepherd, through Creative Commons.

Figure 62. ***Selaginella rupestris***, a rock moss that resembles a moss when it lacks the strobili shown here. Photo by Nancy Leonard, with permission.

Figure 63. ***Lycopodium annotinum***, a club moss, but not a true moss. Photo by Janice Glime.

Annie Martin has ***Climacium americanum*** in her moss garden (Figure 64). This attractive moss looks like miniature trees. It is especially interesting when it produces capsules because it looks like a miniature Christmas tree with candles (Figure 66). This same moss grows in abundance along the path to the Frank Lloyd Wright house, Falling Waters, Pennsylvania, USA (Figure 65).

Figure 64. ***Climacium americanum*** in MountainMoss Enterprises garden. Photo by Annie Martin <www.mountainmoss.com>, with permission.

Figure 65. ***Climacium americanum*** bordering the path at Falling Waters, Pennsylvania, USA. Photo by Janice Glime.

Figure 66. ***Climacium americanum*** with capsules in moss garden. Photo by Janice Glime.

Sources

Few sellers are available for purchasing live mosses. And even where these sources are available, the mosses are usually expensive. Even when people have the sources and the money for purchase, gathering one's own is always a temptation. There are advantages to the latter – it shows the gatherer how and where the moss grows in nature and makes it easier to create the right microclimate for it.

BUT good stewardship is of paramount importance. And good stewardship precludes removing mosses from nature, whether it is a national forest or private land. Annie Martin, in response to criticism from Bryonetters, explained her method of developing moss mats for sale. She obtains her mosses in two ways – rescuing those that are about to be destroyed by development or because they are presumed to be a nuisance (roofs, parking lots, cracks in the sidewalk) or by obtaining permission from owners on private land. Judicious harvesting on private land can permit the mosses to grow back. On her own property, she cultivates these for sale. Martin expressed dismay that she could not get a permit to remove mosses in an area to be logged. Logging permits are permitted, but saving mosses beforehand is prohibited! They can't even be rescued to prevent destruction by trucks fighting fires. On the other hand, Martin has had good experience with private owners and business owners who give her permission to remove mosses. People in the area know her and call her before destroying unwanted mosses.

It also helps to know the relative growth rates of mosses. Annie Martin suggests that log mosses tend to fall in the faster growing category. I can add ***Plagiomnium cuspidatum*** (Figure 42), ***Fissidens adianthoides*** (Figure 48), and ***Marchantia polymorpha*** (Figure 16) as species that spread quickly.

Lawns

One typical push lawn mower running for one hour equals 43 new automobiles running for the same time (Martin 2010)! Go green with moss!

David Benner developed a moss lawn so he would never have to mow again (Dunn 2008). He hasn't watered or mowed his lawn since the Kennedy Administration, and it's doing just fine, reports Jancee Dundee (2008) in her "In the Garden" column. Benner, a retired professor of horticulture, is a long-time moss lawn advocate. He is delighted that this approach is gaining momentum. But to visitors of his mossy lawn, he forbids high heels. (I wonder if it isn't more dangerous for the wearer than it is for the moss!)

Tim Currier, owner of Sticks and Stones Farm, Newtown, CT, USA, had been selling mosses for gardening for ten years, but in 2007 his sales increased by 30% (Dunn 2008). Celeste Kennedy, owner of Rolling Hill Farm in Green Bay, VA, USA, reports a 40% increase in the same time frame. Both homeowners and businesses have contributed to this rise in sales.

Dunn (2008) touts the advantages of mosses, including erosion prevention, density that repels weeds, no need for fertilizer, lack of herbivory by deer, and tolerates at least some trampling (*e.g.* Figure 67). It thrives in poor soil and only requires shade and occasional water.

Figure 67. Moss lawn near Minisink Lake, Bushkill, PA, USA. Photo by Janice Glime.

The American Society of Landscape Architects predicted that native drought-resistant plants such as mosses would be a trendy change in 2008, providing a sustainable substitute for grass in lawns (Dunn 2008). Nancy Somerville, the executive vice president, states that the organization is seeing more creative plantings, with moss being "a great one." It satisfies needs for both better environmentalism and concerns about water. The EPA estimates that nearly one third of residential water use is for landscaping, a condition our diminishing water supply cannot sustain. The condition will only get worse with global warming, although in some areas more rain will fall.

Christine Cook, owner of Mossaics in Easton, CT, USA, contends that a moss lawn needs only one percent or less of the amount of water needed to maintain a suburban grass lawn (Dunn 2008). Benner's philosophy (Dunn 2008) is even better – he doesn't water; "things have to tough it out."

In 1962, when Benner first began his moss lawn, the only book he could find on the subject was written in Japanese (Dunn 2008). But he knew that moss thrives in acidic soil, whereas some people spread lime on a grassy lawn to eliminate moss. Therefore, he covered his lawn with a mix of sulfur powder and aluminum sulfate to acidify it. Three months later he removed the dead leaves, exposing the soil. Winter was the wait and see period, but in the spring mosses began to sprout everywhere. "It was like magic" he remembers. He didn't even have to plant – he just waited for spores to blow in. He now has 25 different kinds, and he didn't plant any of them! He has found fern moss (***Thuidium*** sp.; Figure 43-Figure 45), hair cap moss (***Polytrichum***; Figure 8, Figure 25-Figure 28), rock cap moss (***Dicranum***; Figure 40), and cushion moss (***Leucobryum***; Figure 34, Figure 37-Figure 39) to be the easiest to grow. These four taxa are now sold by his son, Al Benner, through Moss Acres, a commercial establishment in the Poconos of Pennsylvania, USA. This business has actually increased about 30% each year, with such customers as the New York Times' headquarters for its atrium garden.

Benner senior claims that "some sort of magical invigorating energy goes through you when you stand on a thick patch of wet moss" (Dunn 2008).

It seems that moss enthusiasts are lurking everywhere. T. J. Turgeon, an executive vice president of a private bank for wealthy people, began his moss growing in 2004 (Dunn 2008). He says, "I'm having an absolute blast with it. I'm great at a dinner party, because I can talk about moss and no one's ever heard it before. People at work think I'm out of my mind. I don't know if other people do this, but wherever I go, I take moss."

Sallie Baldwin is a graphic designer from Greenwich, CT, USA, who has been turning her front yard into a moss lawn for 18 years (Dunn 2008). She sometimes amuses her neighbors by swapping a bit of "weedy" grass in her lawn for the "weedy" moss in theirs.

Special Use Species

You may choose to place some of your bryophytes in special locations that are more restrictive. These could include boulders, rock or concrete walls, or even paths. Some mosses are suitable for transplanting to these special situations.

If it is not too dry, ***Marchantia polymorpha*** (Figure 16) does well on disturbed soil. My ***Marchantia polymorpha*** (Figure 16) sported a bevy of children in a 25-cm circle around the parent plants, products of gemmae (Figure 68) splashed by the rain or the sprinkler system, and the parents had only been in the garden about three weeks! These young thalli were not only on the bare ground, but had become established on the cushions of ***Leucobryum*** (Figure 34) within reach. The following year the original clump was a forest of **archegoniophores** (structure where female gametes and ultimately capsules are produced; Figure 16).

My ***Marchantia polymorpha*** (Figure 16) sported a bevy of children in a 25-cm circle around the parent plants, products of gemmae splashed by the rain or the sprinkler system, and the parents had only been in the garden about three weeks! These young thalli were not only on the bare ground, but had become established on the cushions of ***Leucobryum*** (Figure 34) within reach.

Figure 68. ***Marchantia polymorpha*** gemmae cups with gemmae. Photo by Dick Haaksma, with permission.

Lawn Species

For substitute lawns and gardens, ***Eurhynchium praelongum*** (Figure 55), ***Calliergonella cuspidata*** (Figure 69), and ***Polytrichum juniperinum*** (Figure 8) serve well, although I doubt the North American populations of ***C. cuspidata*** would do so well in most terrestrial areas. In Europe this moss is found on dry hillsides, but in North America it behaves as an aquatic, at least anywhere I have seen it.

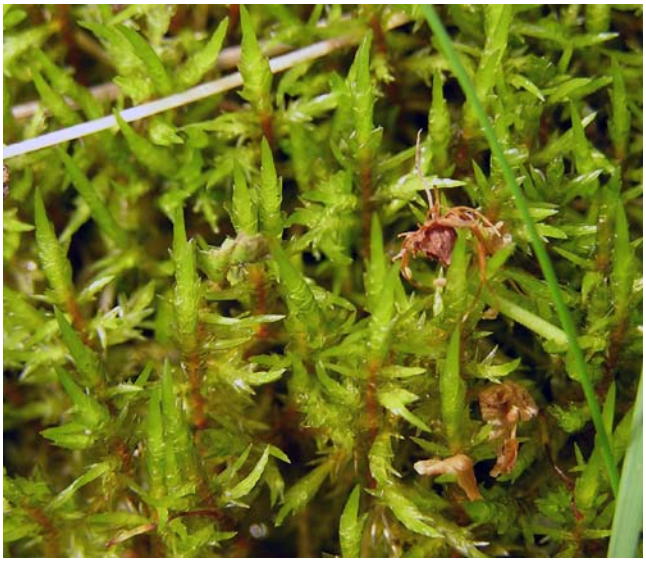

Figure 69. ***Calliergonella cuspidata***, a species that does well in lawns and gardens in Europe, but not in North America. Photo by Michael Becker through creative Commons.

One of the most common lawn mosses is the pleurocarpous species ***Brachythecium rutabulum*** (Figure 57) (Fletcher 1991). It is among the largest of the ***Brachythecium*** species, has the typical plicate leaves, and can be distinguished from the others by its papillose seta (Figure 70-Figure 71). Its ability to grow in more sunny areas makes it also a good candidate for gardens as well as paths. It has invaded between the stones of the path along the side of my house. The moss ***Eurhynchium***

praelongum (Figure 55) will grow in similar areas, but is a smaller plant.

Figure 70. ***Brachythecium rutabulum*** showing setae that support the capsules. Photo by David Holyoak, with permission.

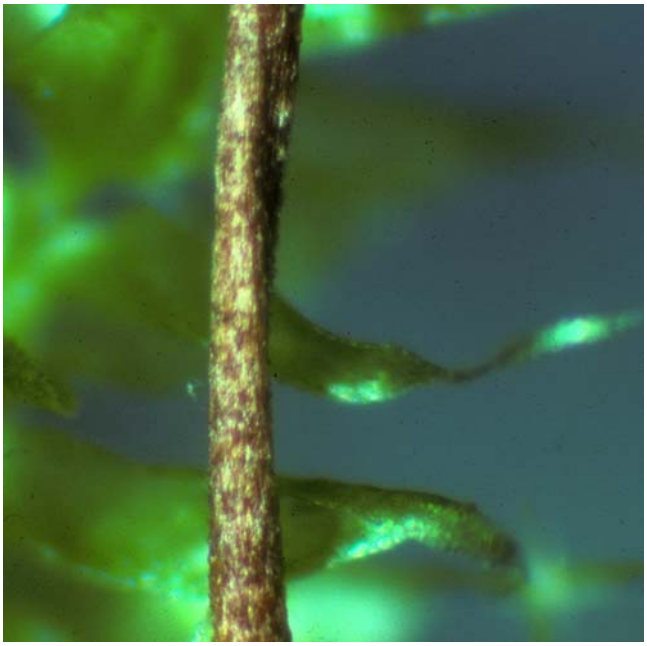

Figure 71. ***Brachythecium rutabulum*** papillose seta. The papillae are best seen along the lower sides of the seta in this picture. Photo by Janice Glime.

Another lawn species in Europe is ***Rhytidiadelphus squarrosus*** (Figure 2). Well manicured and fertilized lawns are deprived of this species, but grassy meadows mowed by livestock may have it abundantly (Fletcher 1991).

Since mosses barely penetrate the soil with their rhizoids, only shallow soil of 1-2 cm is needed. Texture determines ability to attach but also determines moisture retention. Thus species that typically grow on sand are not likely to do well on humus or clay. Fletcher (1991) suggests bringing back a small plastic bag of soil that can be placed on top of a peat substrate. He contends that the soil type is more important for small moss plants than for large ones. Large plants most likely provide their own substrate after a few years of growth (Figure 72).

Figure 72. ***Campylopus flexuosus*** showing senesced lower parts of plants upon which the active parts are able to grow. Photo by Michael Lüth, with permission.

Sun Species

Bryum argenteum (Figure 73) and ***Ceratodon purpureus*** (Figure 12) are good sun species. ***Bryum argenteum*** changes little in appearance between wet and dry. It reproduces largely by fragmentation of the tips and typically does well in locations where there is a fair amount of foot traffic.

Figure 73. ***Bryum argenteum***, a common lawn species that propagates from fragments from the tips. Photo by Michael Lüth, with permission.

Ceratodon purpureus (Figure 12; Figure 74-Figure 84) is the moss my students nicknamed "tricky moss." It can take on many forms, depending on its microclimatic conditions. In spring, it is usually well hydrated and bright green (Figure 74-Figure 75). In summer, and often in autumn, it is usually dry and becomes crispy, brittle, and dark green or brownish (Figure 80-Figure 82). Its carpets can be somewhat loose (Figure 75) or quite tight (Figure 77). It is an early invader of roofs, areas on the ground receiving roof runoff, rock ledges, road sides, parking lots, and sparsely vegetated fields. In even grows in Antarctic pools (Figure 84). Nevertheless, it often does not respond well to transplantation.

Figure 74. ***Ceratodon purpureus*** in its fresh, green form. Photo by Michael Lüth, with permission.

Figure 75. ***Ceratodon purpureus*** with an uncommon loose form. Photo by Michael Lüth, with permission.

Figure 76. ***Ceratodon purpureus***, with lush, green color after a wet summer and autumn. Setae are formed for next spring's capsules. Photo by Janice Glime.

Figure 77. ***Ceratodon purpureus*** with red setae and young capsules. Photo by Annie Martin <www.mountainmoss.com>, with permission.

Figure 78. ***Ceratodon purpureus*** in moss garden at Mountain Moss Enterprises, showing spring growth and mature capsules. Photo by Annie Martin <www.mountainmoss.com>, with permission.

Figure 79. ***Ceratodon purpureus*** showing dry portion (upper left) and moist portion. Photo by Janice Glime.

Figure 80. ***Ceratodon purpureus*** showing dry plants in autumn. Photo by Janice Glime.

Figure 81. ***Ceratodon purpureus*** dry with immature capsules. Photo by Bob Klips, with permission.

Figure 82. ***Ceratodon purpureus*** in brown state after a dry summer. Photo by Janice Glime.

Figure 83. ***Ceratodon purpureus*** with mature capsules and dry leaves. Photo by Michael Lüth, with permission.

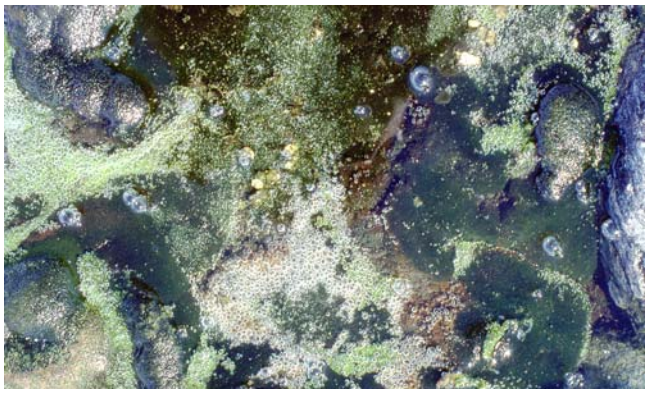

Figure 84. ***Ceratodon purpureus*** submersed with air bubbles at Casey Station, Antarctica. Photo courtesy of Rod Seppelt.

Wall Species

The common European moss ***Tortula muralis*** (Figure 85) easily establishes itself on cement, bricks, or other walls (Fletcher 1991). Although it may be found on soil, this is not its best habitat. For rooftops (the clay tile kind), concrete, and rock walls, Svenson (2000) recommends ***Tortula muralis*** and ***Didymodon vinealis*** (Figure 7).

Figure 85. The moss ***Tortula muralis*** is often found on rooftops, concrete, and rock walls; *muralis* means "of the wall." Photo by Michael Lüth, with permission.

Path Species

The most famous of the species growing on paths is ***Bryum argenteum*** (Figure 73), silver moss. It is easily dispersed by its deciduous tips whenever something walks across it. Hence, it is common in cemeteries and other soil areas with light foot traffic.

In addition to the ubiquitous silver moss, ***Barbula*** [***B. unguiculata*** (Figure 86), ***B. convoluta*** (Figure 87), ***B. cylindrica*** (Figure 88), and ***B. fallax*** (Figure 89) is common, especially between bricks or stones (Figure 90) (Fletcher 1991). Species of ***Barbula*** add a fresh green color to the garden (Figure 91).

Figure 86. ***Barbula unguiculata***, a common species between bricks and stones. Photo by Michael Lüth, with permission.

Figure 87. ***Barbula convoluta***, a common species between bricks and stones. Photo by Janice Glime.

Figure 88. ***Barbula cylindrica***, a common species between bricks and stones. Photo by Des Callaghan, with permission.

Figure 89. ***Barbula fallax***, a common species between bricks and stones. Photo by Kristian Peters, with permission.

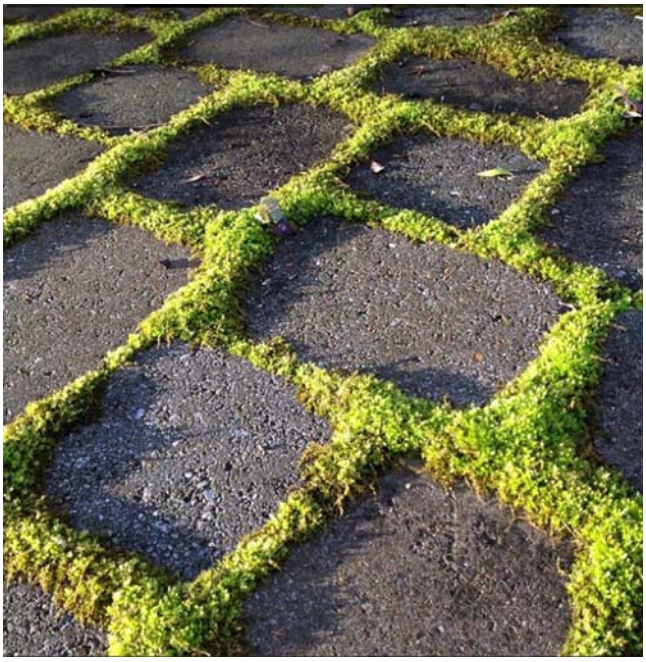

Figure 90. Mosses in pavement. Photo by J. Paul Moore, with permission.

Figure 91. ***Barbula unguiculata*** in the center, flanked by ***Conocephalum conicum*** at the top right, and ***Polytrichum juniperinum*** below it. Photo by Janice Glime.

Based on invasion of a newly cut ski trail, I would recommend ***Atrichum altecristatum*** (Figure 92). This moss invaded quickly about 10 years ago and is still present today. The plants provide a yellow-green color when fresh. However, when they dry out they are not nice to look out. If a watering system is present, they will benefit.

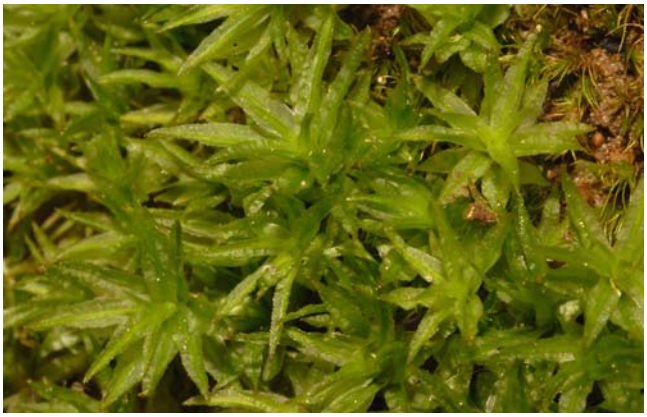

Figure 92. ***Atrichum altecristatum*** drying, a species tolerant of living on paths. Photo courtesy of Eric Schneider.

Annie Martin includes ***Ceratodon purpureus*** (Figure 93-Figure 94) among her plantings between stones of paths. If you are willing to wait, this species will probably arrive by itself.

Figure 93. Stone path planting, showing Annie Martin pushing mosses, including ***Ceratodon purpureus***, into cracks between the stones. Photo courtesy of Annie Martin <www.mountainmoss.com>.

Figure 94. ***Ceratodon purpureus*** with capsules in stone path in March 2017. These were planted here in December 2016. Photo courtesy of Annie Martin <www.mountainmoss.com>.

I was surprised to find ***Hedwigia ciliata*** (Figure 95) covering paths in our local cemetery (Figure 96). The paths were covered in gravel and could be identified by the yellow-green color of the wet moss. The moss all but disappeared from a distance when it dried and became whitened. I would not ordinarily think of this as a path moss, but it was certainly doing well in parts of the cemetery.

Figure 95. ***Hedwigia ciliata*** drying, a moss that grows on pebbles and rocks. Photo by Janice Glime.

Figure 96. ***Hedwigia ciliata*** wet, on pebbles, in the Houghton cemetery path. Photo by Janice Glime.

Erosion Control

The use of mosses to control erosion has probably been known for many centuries. Shana Gross (Bryonet 23 January 2009) reported her experiments on establishing moss growths for this purpose. She examined effects of fragment size, substrate, fragment location along the shoot, watering methods, hormone application, and nutrient application on ***Bryum argenteum*** (Figure 73), ***Ceratodon purpureus*** (Figure 12; Figure 74-Figure 84), and ***Polytrichum juniperinum*** (Figure 8). The responses depended on the species. She strongly supports the use of mosses for erosion control, but this adventure is not without its problems. The mosses grew well in the greenhouse, but responded poorly in the field. Fragments planted in the field required some means to affix them until

they became established. Transplanting clumps from field populations was more successful, but that is not feasible for larger areas. She suggested using methodology from cryptogamic crusts (see Belnap 1993), where inoculum of the species improved colonization over letting nature do the propagating.

Shaw (1986) developed experimental propagation methods. He was successful in propagation when he dried the gametophytes (leafy plants), ground them into a fine powder, and sowed them on native soil. His purpose was to develop a laboratory protocol for evolutionary studies, but it could be applied to getting starter biomass for stopping erosion. He found that the plants presented normal morphology.

Cultivation

Fletcher (1991) has found that mosses can be grown in a variety of containers, including Perspex sandwich boxes, Tupperware, plastic ice cream boxes, glass jars, and aquaria. However, bryophytes kept in this way typically do not survive for more than a few months. He replaced this method with a seed tray, covered with a sheet of glass or sheet of acrylic plastic. These must be kept in cool, open air and shaded. But even this improved method does not work as one might hope; bryophytes fare well for only a few weeks to months. Fletcher even tried peat beds or other means to maintain moisture, but this made matters worse. Clearly there was a need for a better method.

Johannes Enroth related to Bryonet (5 March 2010) his experience growing ***Racomitrium canescens*** (Figure 53) experimentally in a cemetery. The study group took advantage of the fragmentation growth capabilities of mosses and cut the shoots into small pieces (see also Figure 97). They spread these on sand and kept them moist until they became established. "The moss grew fast and formed a dense, beautiful cover that changed color along with changing air moisture" (Figure 105). This moss is a good suggestion for sunny areas.

Figure 97. ***Climacium americanum*** clipping to propagate. Photo by J. Paul Moore, with permission.

In Australia, Alison Downing (Bryonet 23 January 2009) and her coworkers experimented with calcareous and acid soils to look for the success of dormant propagules. They collected soil in the field and carried it back to the lab in cotton bags to prevent mold in the humidity of plastic bags. They collected only the top 10 mm of soil, avoiding the collection of plants. In the lab, they sieved the soil in a clean environment. The sand foundation was steam-sterilized to avoid contamination from the sand. Dry heat is not effective for the resistant bryophytes unless it is at extremely high temperatures. Using the sterilized sand, they filled a 10-cm-diameter plastic horticultural pot to about 1 cm below the top. The collected soil was placed in a 5 mm layer on top of the sand. The soil propagules were cultured in a greenhouse, watered carefully with demineralized water, and the pots covered with sheets of glass to prevent contamination. The pots were checked daily and kept moist by misting with demineralized water when needed. After 8 weeks the calcareous and arid soils exhibited 100% bryophyte cover. The propagules in the non-calcareous soil required a few more weeks. Even rare species can show up using this method.

Annie Martin (Bryonet 6 August 2010) prepares the ground to prevent the invasion of rooted plants. She has used five different substrates (Figure 98-Figure 99) in her gardens, including 0.3 cm synthetic felt, 0.6 cm felt with adhesive plastic backing (used for installing carpets), basic landscape fabric (paper thin), black landscape fabric 0.5 cm thick (perforated and similar to felt; Figure 98), and coco fiber mat (to control erosion; Figure 98-Figure 99). For ***Bryum*** (Figure 73), ***Ceratodon*** (Figure 12; Figure 74-Figure 84), and ***Hedwigia*** (Figure 95), she uses asphalt shingles for a substrate.

Figure 98. Mats for planting mosses. The black layer is a synthetic felt with adhesive plastic backing. Photo by Annie Martin <www.mountainmoss.com>, with permission.

Figure 99. Close view of coco fiber mat and black felt for planting mosses. Photo by Annie Martin <www.mountainmoss.com>, with permission.

These substrates are not eco-friendly or natural. When installing a moss garden for her clients, Martin (Bryonet 6 August 2010) plants the mosses directly on the ground. In the nursery, the felt substrates help in retaining moisture and make it easier to lift the mosses into flats or boxes for shipping.

As Annie Martin (Bryonet 8 March 2012) gained experience, experimenting with various substrates, she developed a preference for Geo-Tex fabric as the primary substrate for field production. This retains moisture and provides a weed barrier. Martin (Bryonet 8 March 2012) plants large areas by transplanting hand-sized colonies and spreading fragments in between (Figure 100). Watering for the next few weeks is critical, but make it gentle.

Figure 100. Planting of bryophytes on mat of coco fibers. Annie Martin disperses fragments between the clumps. Photo by Annie Martin <www.mountainmoss.com>, with permission.

Katherine Frego (pers. comm. to Nancy Church 6 April 2010) reported on her success in growing ***Pleurozium schreberi*** (Figure 59), ***Dicranum polysetum*** (Figure 101), ***D. scoparium*** (Figure 40), ***Ptilium crista-castrensis*** (Figure 102), and ***Ptilidium ciliare*** (Figure 103). She found she could collect them at any time. She then dried them in the shade and chopped them with scissors. These fragments were stored in paper bags for months. When she was ready to culture them, she put them on a humus-y soil and covered them with a hairnet to keep them in place. She sprayed them thoroughly to wet them and they sprouted new shoots very soon afterwards. Fragments about 1 cm long formed new shoots directly. Smaller shoots formed protonemata first, and these were more fragile and vulnerable.

Figure 101. ***Dicranum polysetum*** with capsules, a moss successfully grown from dry fragments. Photo by Janice Glime.

Figure 102. ***Ptilium crista-castrensis***, a moss successfully grown from dry fragments. Photo by Janice Glime.

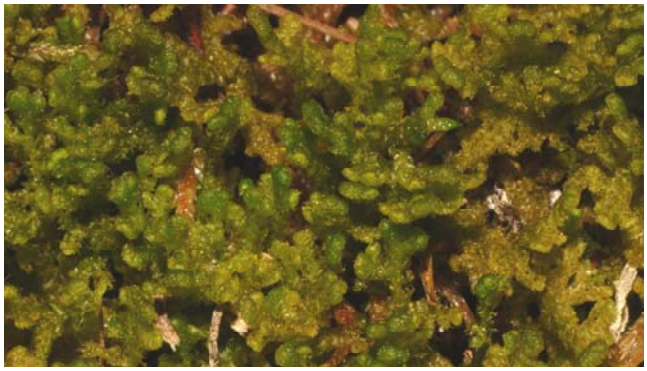

Figure 103. ***Ptilidium ciliare***, a moss successfully grown from dry fragments. Photo courtesy of Eric Schneider.

Johannes Enroth (Bryonet 6 August 2010) became the curator of a stone and moss garden in the courtyard of the Ministry of Education in downtown Helsinki, Finland. The original garden, planted by Timo Koponen in the 1980's, had only three species: ***Racomitrium canescens*** (Figure 104-Figure 105), ***Plagiomnium cuspidatum*** (Figure 42), and ***Climacium dendroides*** (Figure 106). In 2007, the number of species had expanded to 15, dominated by ***Encalypta streptocarpa*** (Figure 107). The latter forms a pure mat of several square meters on the sand in the middle of the yard.

Figure 104. ***Racomitrium canescens*** exhibiting dry appearance. The tips look frosted and add interesting contrast to other shades of green in the garden. Photo by Michael Lüth, with permission.

Figure 105. ***Racomitrium canescens*** in its wet appearance. The pale green color adds a fresh look. Photo by Michael Lüth, with permission.

Figure 106. ***Climacium dendroides***, an attractive moss for moss gardens. Photo by Janice Glime.

Figure 107. ***Encalypta streptocarpa*** with capsules, a species that arrived in a Finnish moss garden by itself. Photo by Michael Lüth, with permission.

I have experimented in my own garden, using various substrates and cultivation methods. One of my early attempts was to use burlap (Figure 108-Figure 109), placing it on top of visqueen plastic to prevent seeds in the soil from germinating and penetrating into the moss carpet (Figure 109). It also meant that seeds germinating on top would be unable to drive their roots into soil. Netting over the mosses helped to hold them in place when chipmunks and squirrels ran over them (Figure 110). But apparently the soil helps in the retention of moisture because these mosses dried out more quickly than those directly on soil.

Figure 108. ***Bryum*** sp. on burlap. Photo by Janice Glime.

Figure 109. ***Ceratodon purpureus*** and ***Bryum*** sp. on burlap. Photo by Janice Glime.

Figure 110. ***Ceratodon purpureus*** and ***Bryum*** sp. with partial netting on burlap. Photo by Janice Glime.

Next I tried cutting the bryophytes into fragments (Figure 111) and spreading them on brown felt (Figure

112-Figure 113). This met with similar problems. The felt dried quickly, became stiff, and the moss fragments likewise dried out.

Figure 111. Fragments of bryophytes on cutting board, ready to plant. Photo by Janice Glime.

Figure 112. Fragments that have been scattered on wet brown felt. Photo by Janice Glime.

Figure 113. Planting fragments of ***Polytrichum juniperinum*** on felt, underlain with visqueen. Photo by Janice Glime.

To understand the best way to keep bryophytes, we must understand how they normally grow. Rather than being the moisture-loving plants portrayed in most popular literature, they actually prefer places with good air circulation and only a small percentage of species grow in the damp, enclosed places most people think of. Rather, many taxa grow on dry rocks, sand, or in open sun. Some prefer acid rocks and some prefer limestone. Most cannot grow where leaf litter will cover them in the fall and remain there for the winter. Some do well in pine forests where they can grow over or between the needle litter.

Johannes Enroth, Bryonet 9 March 2010, recalls covering a surface with ***Racomitrium canescens*** (Figure 104-Figure 105) shoot fragments. Within a matter of months, the moss formed a "nice mat." Two ***Polytrichum*** (Figure 8, Figure 25-Figure 28) species from spores and individual shoots planted in the soil were not very successful. Growth was slow and the planted shoots often died. ***Plagiomnium*** sp. (Figure 42) was more successful.

Nancy Church (pers. comm. 27 July 2010), formerly from Moss Acres, told me that they used a product called Terra Blend70/30 with Ultra Grow. The 70/30 ratio refers to the wood fiber/paper fiber content. The Moss Acre folks believe the "Ultra Grow," the ingredients of which are kept a close secret of the manufacturer, is part of what makes this so effective with mosses. Keith Bowman, one of Dr. Kimmerer's graduate students, worked with Moss Acres on experiments with the Ultra Grow cellulose, and Church was curious to see if the fertilizer helped the vascular plants (weeds) or the moss more. It has certainly helped the moss in all of the "amateur" experiments they've done at Moss Acres.

Sandrine Hogue-Hugron (Bryonet 31 May 2011) experimented with growing bryophytes to restore sand pits. Although there was colonization on the bare sand, colonization was optimal when the sand was mixed with peat. Peat is also a good substrate for making a bog garden. Industrial peat is a good choice because it is usually free of propagules. The peat can be further sterilized by heating to 60ºC for an hour and a half.

Winter Culture

Martin (2010) finds that winter is a good time to harvest and plant mosses in western North Carolina, USA. But if you live in the Keweenaw Peninsula of Michigan, USA, the mosses are under a meter or more of snow. In Japan, the best time to plant is just before the rainy season, reducing the need for frequent watering. Martin reports that her mosses emerge from short snowfall events looking green, whereas when mine emerge after 4-5 months of snow burial, they often look brown, becoming green when new growth appears.

Freezing doesn't harm the mosses (Figure 114), with some photosynthesizing at temperatures below 0ºC (Liu *et al*. 2001). Snow insulates them, and I am guessing that some photosynthesis is able to occur in the light filtering through shallow snow in spring and fall. Martin (2010) has been successful in planting mosses on frozen ground, but the moss itself should be thawed first. She warns that on warmer days when the temperatures are above freezing, the garden should be watered, especially during the first few weeks after planting. (And don't forget to empty the hose so it won't freeze and burst.)

Figure 114. ***Hylocomium splendens*** in snow. Photo by Michael Lüth, with permission.

When there is no snow cover, winter is a season of growth, along with spring and autumn when the air is cool. Bryophytes tend to be dormant in the heat of summer, especially if they are dry.

Moss Plantations

When visiting a commercial moss plantation in Japan near Nagoya, I found the ground planted in several species of ***Polytrichum*** (Figure 8, Figure 25-Figure 28) and its relatives ***Pogonatum*** (Figure 115) and ***Atrichum*** (Figure 3, Figure 92). The landscape was dotted with small pine and fig trees, providing light shade for the mosses beneath (Figure 116). Other growers cover the mosses with straw or bamboo screens to provide shade. The proprietor proceeded to show me, with hand motions and occasional translations by N. Takaki (for whom ***Takakia*** is named), how the mosses were dried, then pulverized between the hands, and sown like grass seed in wooden flats. These flats were kept well watered in full shade until the mosses were well established. Then they were transplanted outside under the shade of the pines and figs until they formed a carpet (Figure 116).

Figure 115. ***Pogonatum japonicum***, a moss in a genus used in moss gardens in Japan. Photo from Digital Museum, Hiroshima University, with permission.

Figure 116. This plantation in Nagoya, Japan, uses pine trees to provide shade for growing mosses. Photo by Janice Glime.

When they were harvested for a buyer, they were removed in squares about 20x20 cm and stacked to dry (Figure 117). Their new owner would then plant them, checkerboard fashion, in a dooryard garden or along a small backyard path, trampling them into the ground and once again breaking off small fragments of moss. A small board can be used to press and spread the mosses instead of trampling, but pressing them into the ground is important. It is the ability of mosses to regenerate from fragments that makes this process work so well. The fragments and new growth eventually fill in the empty squares of the checkerboard, providing a continuous carpet for the moss garden, although Schenk (1997) advises us that it can take 2-3 years for a ***Polytrichum*** (Figure 8, Figure 25-Figure 28) carpet to fill the gap. Mosses such as ***Brachythecium*** (Figure 57), with their horizontal growth form, may fill the gap within a year.

Figure 117. Stacks of ***Polytrichum*** are ready for delivery to a private garden near Nagoya, Japan. Photo by Janice Glime.

This ancient art of planting mosses by pulverizing them has been adopted by the American Horticulturist Society. In their Fact Sheet for Moss Gardening, they recommend grinding dried moss and spreading it as powder, cautioning the gardener never to buy moss from a grower unless you are certain that the moss has been propagated by the seller and not taken from the wild – good conservation advice.

Experimental studies support this pulverizing method as well. Miles and Longton (1990) found that fragmentation was superior to spores in the development of upright shoots in such common garden mosses as ***Atrichum***

undulatum (Figure 3) and ***Bryum argenteum*** (Figure 73). In fact, Shaw (1986) contends that whether in an industrial setting or in the laboratory, starting cultures from spores is impractical for many species. He found, using the pulverizing method, that within a month, new gametophores were evident in most species, and within three months regenerated plants filled his pots. He had the best results when the plants were misted for six seconds every thirty minutes. Svenson (2000), on his moss gardening website, recommended filling in the bare spots between patches of moss by using the pulverizing method. This can be done by putting pieces of moss in a blender with a small quantity of water for two minutes, then spreading them between the transplanted mosses.

A mixture of 50% coarse sand, 30% vermiculite, and 20% peat provides a good substrate, and the optimum growth temperature for temperate zone mosses is believed to be around 10°C (Iwatsuki 1979). In the laboratory, Petri plates with layers of filter paper saturated in tap water have been successfully used to regenerate ***Atrichum undulatum*** (Figure 3) leaf fragments (Gemmell 1953); in nature, the soil will do just fine if kept moist. [Note that not all tap water is created equal; it may kill some species and be worse in some areas.]

My students at Michigan Technological University successfully grew protonemata from fragments of five North American taxa in genera commonly used in moss gardens [***Atrichum oerstedianum*** (Figure 118), ***Dicranum scoparium*** (Figure 40), ***Fissidens adianthoides*** (Figure 48), ***Leucobryum glaucum*** (Figure 34), ***Plagiomnium affine*** (Figure 119)] in a dish garden, using this method and a modified version with a strip of cheesecloth over the fragments to retain moisture (Plante *et al*. unpublished data 1993; pers. obs.). Protonemata developed in 2-3 weeks. Fragments placed on sand alone failed to produce any growth during the experiment. In addition to the fragments, whole plants were planted, and at least a few plants of ***Atrichum oerstedianum***, ***Fissidens adianthoides***, and ***Plagiomnium affine*** produced new branches, although the original branches became brown and wilted. Subdued light (900 lux for 8 hr d^{-1}) and moderate temperatures (ca. 20°C) seemed more favorable than a higher light intensity and temperatures of 38°C.

Figure 118. ***Atrichum oerstedianum***, a species that can be grown from fragments. Photo by Karen Renzaglia, with permission.

Figure 119. ***Plagiomnium affine***, a species that can be grown from fragments. Photo by Janice Glime.

It is during the critical early establishment stage that moisture is very important, and the Japanese often time their planting to coincide with the rainy season so that the mosses get natural watering daily. Yet, the entire first year and often the second require careful attention to water requirements. As discussed in the chapter on "Water Relations: Rehydration and Repair," frequent wetting and drying is quite detrimental to a moss because each time it is dried and rewet it must repair damaged membranes, often requiring a full day before there is any net energy gain. Transplanting brings with it its own share of damage and adjustment that makes the mosses less tolerant of natural stresses.

It is interesting that Schenk (1997), with his long-time experience as a moss gardener, reports that few mosses will grow successfully from fragments. He touts ***Leucobryum*** (Figure 34; Figure 120-Figure 121), ***Racomitrium*** (Figure 53), and ***Dicranoweisia*** (Figure 122) with this ability, but finds others to be reticent to yield to the gardener's wishes. Nevertheless, as he acknowledges, all mosses share this ability to regenerate from fragments, and I have observed in nature young shoots of ***Scapania undulata*** (Figure 123) (Glime 1970) and ***Atrichum*** (Figure 3, Figure 92) (Glime 1982) developing from leaf fragments to which they were still attached. ***Fissidens*** (Figure 48) species are especially adept at this, and I soon found new colonies all over my garden room, presumably transported about as fragments by my box turtle – they had never produced any capsules. In the lab, Plante *et al*. (unpub. data 1993) were successful with both whole plants and fragments of ***Fissidens***.

Figure 120. ***Leucobryum glaucum*** apical rhizoids, ready to grow if they get broken off. Photo courtesy of Sean Edwards.

Figure 121. ***Leucobryum*** sp. showing protonemata growing from leaf fragments. Photo courtesy of Andi Cairns.

Figure 122. ***Dicranoweisia crispula***, a moss that is easily grown from fragments. Photo by Michael Lüth, with permission.

Figure 123. ***Scapania undulata***, a leafy liverwort species that regenerates from leaf fragments. Photo by David T. Holyoak, with permission.

One of the most luxurious growths of moss I have seen outside of nature was on a discarded piece of carpet that was able to soak up and maintain moisture over long periods of time (see, for example, Figure 124). This is reminiscent of the technique of using cheesecloth on flats to grow mosses that are to be draped over rocks or uneven landscapes. The cheesecloth method takes advantage of fragments, although spores can be used as well (McDowell 1968). Partially dried moss fragments must be spread over cheesecloth that overlies a sand-peat moss or sawdust mix in a flat. The *p*H can be lowered by soaking the mix in a solution of 1 part skim milk or prepared powdered milk to 7 parts water (McDowell 1972). These are covered with a second piece of cheesecloth and kept moist by misting.

Figure 124. This rug has a luxurious growth of ***Ceratodon purpureus***. Photo by Michael Lüth, with permission.

When the plants are well established (about 4 ½ months), it is easy to transplant them by lifting the soil/cheesecloth layer. The cheesecloth can be cut to shape as needed. Some gardeners have been successful in growing rock-dwelling taxa this way as well. The cheesecloth can easily be draped over rocks. The mosses grow through the cheesecloth, and eventually the cloth will rot away. If the white color of the cheesecloth is bothersome, coffee (soak in 3 teaspoons instant coffee per cup boiling water for 10 minutes) can be used to stain the cloth (McDowell 1972). Crum (1973) has found that ***Brachythecium salebrosum*** (Figure 125) and ***Plagiomnium cuspidatum*** (Figure 42) are relatively easy to grow in this way, emphasizing that regeneration works better than transplantation.

Figure 125. ***Brachythecium salebrosum*** with capsules, a moss that will develop well on cheesecloth. Photo by Michael Lüth, with permission.

Even when mosses are transplanted or sewn directly on the garden soil, it is often necessary to spread a cover of cheesecloth to prevent damage from birds that would destroy the tender plants before they could gain sufficient establishment. If the moss is to be transplanted, the cheesecloth serves the double purpose of keeping the moss from breaking apart as it is handled.

Planting on rocks can be a challenge, as the moss may buckle up on the dry substrate, or simply get blown away. One solution to this is to glue them there with a good epoxy such as Araldite, a very strong two component epoxy resin (Paul King, pers. comm.).

Transplanting

For those preferring the transplant method, the best place to gather moss is rich woodland areas (Pullar 1966/1967) and the best time of year to collect is from autumn into the winter months (Iwatsuki 1979), depending on where you live. But mosses should not be gathered without permission of the owner, and on public lands a collecting permit is usually required (and should only be done if the area is scheduled for destruction). Furthermore, bryophytes should not be imported from other countries for one's personal gardens, and when such importation is necessary for an institution, proper permission must be gained from both the country of origin and the one of import.

Mosses can be transported in a variety of ways fitting your own convenience. Annie Martin uses plastic sleds (Figure 126) and plastic flats (Figure 127). Paul More uses cardboard boxes (Figure 128). I have used deeper boxes, putting layers of newspaper between the layers of mosses to separate them. The newspaper can be omitted, but it is easier to separate the mosses later when the layers are distinct. I have also used ice cream buckets on short excursions when I had no transportation (Figure 129).

Figure 126. Sleds of mosses, in this case being transported for planting. Photo by Annie Martin <www.mountainmoss.com>, with permission.

Figure 127. Raleigh Project, loading moss in plastic flats into truck. Photo courtesy of Annie Martin <www.mountainmoss.com>.

Figure 128. Paul Moore planting mosses directly on the ground, using boxes to transport them. Photo courtesy of Paul Moore.

Figure 129. Janice Glime gathering moss for her garden. Photo courtesy of Eileen Dumire.

Although bryophytes lack roots, their rhizoids are often connected to symbiotic fungi (*e.g.* Davey & Currah 2006; Renzaglia *et al*. 2007; Pressel *et al*. 2010). Therefore, they should not simply be plucked from their substrate. It is preferable to bring the top layer of soil with them. This is important for several reasons. It will help to maintain fungal connections and provide an inoculum for new associations to establish; it will help hold cushion growth forms together; and it will retain the suitable nutrient and *p*H conditions of its original substrate, at least initially.

For some species, removal from their forest habitat might mean removal from a necessary host plant. Some bryophytes, in particular ***Cryptothallus mirabilis*** (Figure 130), require a photosynthetic partner to provide carbohydrates. This partnership can be mediated by the mycelial threads of a fungus that is also linked to a shrub or tree that reaches closer to the canopy. Or it might be linked to decaying leaves or logs. This is a recent area of research, so we know little about these partnerships, but they may explain the failure of some transplants.

Figure 130. ***Cryptothallus mirabilis***, a thallose liverwort that requires a fungal partner to obtain carbohydrates. Photo by David Holyoak, with permission.

Pinning the bryophytes to the substrate with wooden toothpicks angled through the mat (Figure 131), a technique I learned from Jon Shaw, helps to maintain contact with the substrate during dry periods, and of course keeps them where you put them. Special moss clips (Figure 132) are available for anchoring the mosses, but toothpicks work and are less conspicuous.

Figure 131. Toothpicks holding transplanted mosses onto a clay bank. Photo courtesy of Annie Martin <www.mountainmoss.com>.

Figure 132. Moss pins from Moss and Stone Garden. Photo with permission from David Spain.

In this regard, Schenk (1997) advises maintaining as much soil depth as possible when gathering the clump of moss, whereas Bland (1971) advises one to remove as much as possible to prevent curling up at the edges (Figure 133), turning the moss upside down and washing away the soil to prevent shrinkage. I recommend the former because it causes the least disruption of rhizoids and one doesn't have to worry about destroying possible mycorrhizal connections, which may be more common than we realize. It does require keeping the moss and soil wet until the soil has blended with the underlying substrate.

Figure 133. ***Bryum*** sp. in moss garden. These mosses were touching tightly together when they were planted, but when they dried they shrank, creating spaces around the edges. Photo by Janice Glime.

Signs of death occur rapidly in transplants, but those clumps that remain green will become stabilized within a few weeks. Once they do, Ando (1971) suggests that regular watering can be discontinued. Seike *et al*. (1980), on the other hand, recommend daily watering.

Maintenance of the integrity of the clump is of utmost importance. If it is necessary to expose the lower part of the stems around the edge of the clump (Figure 134) due to using only part of a clump or other disruption, these lower parts should be protected either by building up soil around them or pressing a rock next to them (Figure 135). If some of the stems are taller than the other stems, they can be cut to avoid having them dry out. For many bryophytes, a new branch will form and continue growing.

Figure 134. ***Bryum*** sp. with exposed edge in the forefront. The moss will dry out here and die back from the edge. Rocks placed against such edges, or other moss clumps, will reduce the drying, but frequent watering after transplanting is important. Photo by Janice Glime.

Figure 135. ***Ceratodon purpureus*** and ***Bryum*** sp. with stones to protect edges. Photo by Janice Glime.

If you are trying to establish a lawn, you might be able to purchase a ready-to-go mat (Figure 136). These can be rolled up much as the sod purchased for grass lawns. With a landscaping mat under them, they are easy to handle (Figure 137) and to cut to fit any area (Figure 138-Figure 140).

Figure 136. Pre-vegetated mat from MountainMoss. Photo courtesy of Annie Martin <www.mountainmoss.com>.

Figure 137. Raleigh Project laying down sheet of moss. Photo courtesy of Annie Martin <www.mountainmoss.com>.

Figure 138. Cutting shape of the moss mat. Photo courtesy of Annie Martin <www.mountainmoss.com>.

Weeding of the imported moss is important so that competition is not planted with the mosses. Leaf, stick, and seed litter should be removed, but caution must be used to prevent disruption of the clump.

Some gardeners recommend making a depression, laying a bed of gravel, then putting the mosses on top, but still within the depression. Exposure of the lower parts of the moss seems to be a prescription for disaster due to excessive drying.

Figure 139. Removing cut portion from the moss sheet. Photo courtesy of Annie Martin <www.mountainmoss.com>.

Figure 140. Moss mat after it has been positioned and cut to allow for planting flowers. Photo courtesy of Annie Martin <www.mountainmoss.com>.

It is to our benefit in gardening that the mosses respond quickly to the stresses of sun, showing bleaching or browning of leaves in only a day (Schenk 1997). This quick forewarning tells us to try a different location, a different moss, or provide more care and maintenance.

Substrate Conditioning

Successful moss gardening requires at least a modicum of knowledge of the ecology of mosses, and a student of their ecology has much to learn from the successful moss gardener. Aside from the expectation that they will require a moist, shaded habitat, most non-bryologists have little understanding of bryophyte requirements. Most mosses seem to prefer a *p*H of about 5.5, attainable by spreading powdered sulfur over the soil (about 1.1 kg per 9 m^2) (Schenk 1997). Alternatives include powdered skimmed milk, aluminum sulfate, or rhododendron fertilizer. A light misting from the sprinkler will help to affix these to the ground. However, Alison Downing reminded us on Bryonet (20 April 2005) to be careful using milk (or any lime) on sandstone because the calcium in milk can completely change the nature of a sandstone habitat. Instead of ***Campylopus*** (Figure 141), ***Lophocolea*** (Figure 9), ***Sclerodontium*** (Figure 142), and other typical sandstone taxa, you will find instead introduced or cosmopolitan taxa such as ***Funaria*** (Figure 143) or ***Bryum*** (Figure 73).

Figure 141. ***Campylopus introflexus***, an invasive species that will be discouraged by milk applied to sandstone due to the calcium. Photo by Michael Lüth, with permission.

Figure 142. ***Sclerodontium pallidum***, a species that will be discouraged by milk applied to sandstone due to the calcium. Photo by Niels Klazenga, with permission.

Figure 143. ***Funaria hygrometrica***, a species tolerant of charcoal and calcium. Photo by Michael Lüth, with permission.

Maintenance

Martin (2016) advises using the three W's in caring for a moss garden: Water, Walk, Weed. Although mosses will survive extended drought, they won't look nice. And when you are first propagating them, whether by spores, fragments, or transplants, they need constant hydration, often requiring watering. Walking on more mature plants helps to spread them through fragmentation (Figure 144). Weeding needs no explanation – the tracheophytes can quickly outgrow them.

Figure 144. Annie Martin demonstrates walking on mosses to help in fragmentation and dispersal. Photo by Annie Martin, with permission <www.mountainmoss.com>.

No Fertilizers?

Fertilizers must be applied to mosses with great caution. An "elixir" of manure seems to be a suitable supplement (Schenk 1997). Svenson's (2000) website suggested steeping cow manure in a burlap or cheesecloth bag in a bucket of water for 3 weeks (outside, I hope!) before applying it. An alternative is using 1 part of skim milk or buttermilk to 7 parts of water and applying twice per day for two weeks in spring to acidify the soil. Most other fertilizers, especially if applied dry, can kill the moss.

David H. Wagner (Bryonet 8 May 1998) told us that the egg albumen mixed with buttermilk would polymerize and act as a protein binder, creating an adhesive. As the mosses grow and become established, the mix becomes a source of nitrogen for them.

Iwatsuki and Kodama (1961) caution that fertilizer should never be used for mosses. Contrasting to the powdered sulfur acidifier recommendation of Schenk (1997), Stubbs (1973) recommends the use of fertilizer based on iron sulfate as a means of killing moss fast. In fact, fertilizer is a commonly suggested means for getting rid of unwanted mosses. On these one-cell-thick leaves, the dry powder soon goes into solution when water becomes available, greatly altering the osmotic relationship between outside and in and introducing the potential of membrane damage. Furthermore, dry fertilizers tend to be hygroscopic and draw water from the delicate and unprotected moss leaves. The effect is much like the desiccation seen among the mosses on Mount Rainier shortly after the eruption of nearby Mt. St. Helen's (Figure 145). However, if applied in liquid form followed by frequent watering, fertilizer can benefit the moss. Lime fertilizers, however, should be avoided due to their alteration of the *p*H. The seeming contradiction to the advice of Schenk is that he suggests applying the acidifiers to the soil and wetting them down **before** the moss is planted there.

Horticultural magazines and texts extol the advantages of a wide variety of human foods as starters for mosses. Gillis (1991) describes making moss beds by mixing a handful of moss, a can of beer, and a half teaspoon of sugar in a blender, then spreading the mix 5 mm thick on the ground. She found that the mosses grew within five weeks. In addition to beer, egg whites, and buttermilk, others have successfully used rice water, carrot water, potato water, and just water as the medium. Ellis (1992) claims that such mixtures, even the water, are particularly helpful in adhering the moss fragments to rocks. My own experience is that these food additions serve best to feed fungi and pillbugs, thus being detrimental to the mosses.

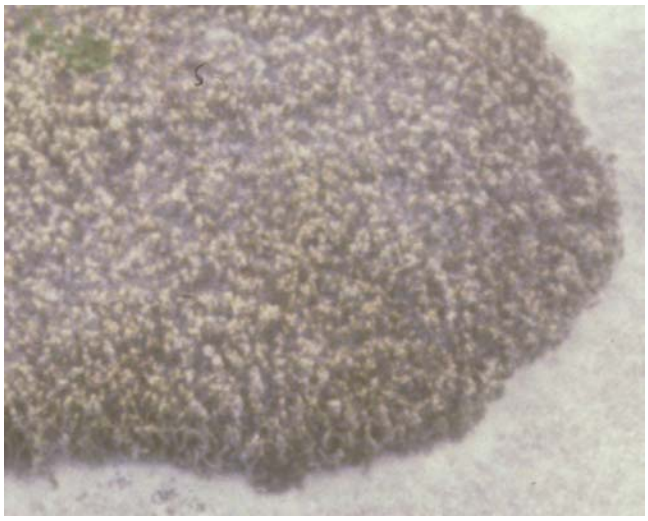

Figure 145. This ***Grimmia*** on Mt. Rainier, Washington, USA, is covered with ash from the eruption of nearby Mt. St. Helen's. The moss is badly desiccated by the ash that is like some fertilizers. Photo by Janice Glime.

Annie Martin (Bryonet 22 June 2013) raised the issue of fertilizing the mosses. First, fertilizers should be applied in very dilute watering additions. Fertilizers on dry mosses can further desiccate them. As in all other issues regarding bryophytes, bryophyte species differ in their responses. Annie Martin (Bryonet 22 June 2013) reported that in her early days of moss gardening experimentation, she watered with Miracle-Gro acid mix. However, when she learned of the dangers of fertilizers she switched to straight tap water only.

One additional problem with applying fertilizers is that flowering plants will benefit more than the mosses, thus introducing a greater weed problem.

Watering

The subject of watering is an interesting one. Some people are adamant that only distilled, demineralized, or rainwater can be used. Others have no problem using tap water (Figure 146). This argument does not surprise me. Tap water can differ greatly between locations. I was amazed to find ***Fontinalis*** (Figure 147) growing happily for years in a tap water aquarium in Japan. But when I tried to grow several species in tap water in New Hampshire, USA, the copper in the water from the pipes turned the plants yellow overnight. After that failure, we used only stream water.

Figure 146. Sprinkling system used by Paul Moore on his moss lawn. Photo courtesy of J. Paul Moore.

Figure 147. ***Fontinalis antipyretica***, an aquatic moss that is sensitive to heat. Photo by Bernd Haynold, through Wikimedia Commons.

City water is much more likely to kill bryophytes than spring water. City water usually has chlorine added and suffers from the solution of metals from water pipes. It also matters if the tap water is the exclusive source of water. Minerals can accumulate on the surface on the bryophytes; intermittent rainfall can remove some of that accumulation. *p*H can make a difference because it is less likely to carry calcium that forms crusts on the mosses. Annie Martin (Bryonet 22 June 2013) has had no problems using tap water (Figure 148) for at least 10 years, but her water is acidic. Martin considers adequate watering to be the most important factor in moss garden success.

For my own garden, I used collected distilled water or rainwater for several years (Figure 149). Other years I used only misting with a sprinkling system that used tap water (Figure 150). However, that tap water went through a filtering system that removed some of the minerals, and spraying it in the air helped to dissipate the chlorine.

Figure 148. Furman-Moss-Watering at Mountain Moss. Photo courtesy of Annie Martin <www.mountainmoss.com>.

Figure 149. Distilled water and collected rainwater are both good sources of water if your tap water is detrimental to your bryophyte garden. Since the garden is outdoors, the bryophytes collect dust and get their nutrients from that dust when they are watered. Photo by Janice Glime.

Figure 150. Sprinkler in my own moss garden. When the water comes on, the sprinkler head rises to about 15 cm and sends water in all direction.

One gardener in Raleigh, NC, USA, has been very successful growing **Mniaceae**, including ***Plagiomnium*** (Figure 42) (reported by Annie Martin, Bryonet 6 August

2010). He, like Martin, uses three layers of felt with plastic underneath and netting on top. Martin believes his success is due to watering six times each day for 4 minutes per watering session. He uses creek water in his misting system. Watering in unplanted areas also resulted in a carpet of thriving ***Plagiomnium*** that arrived by itself.

Annie Martin (Bryonet 6 August 2010) warns that not all mosses have the same nutrient or watering requirements. She finds that ***Bryum*** species (Figure 73) need to dry out sometimes; likewise, ***Dicranum scoparium*** (Figure 40) will not tolerate being wet all the time.

I have never tested it because my own garden is too small to replicate, but I have assumed that watering the mosses on a sunny, hot afternoon is not wise. They can't close guard cells like flowering plants, and they are C_3 plants that respire more than they photosynthesize at higher temperatures, often starting above 20ºC. I have assumed that it is best to let them shut down on hot, sunny afternoons. I do know that ***Fontinalis*** species (Figure 147) cannot sustain vitality if kept in water at 20ºC for more than 3 weeks (Glime 1987), presumably due to the high respiratory ratio. In my own moss garden, I have an automatic sprinkling system that comes on at 6 am, giving the plants sufficient moisture to photosynthesize in the cool hours of the morning. This regime seemed to work well. In hotter locations, an earlier watering time might be preferable.

One dealer recommends daily misting as opposed to intermittent watering to avoid drying or water logging. But one must exercise caution here. Bryophytes that suffer frequent wetting and drying (to the point of damage) will not have sufficient time for repair during the intermittent moist periods. Consider a sprinkling system to keep things moist, preferably on a timer to water at night, permitting the bryophytes to photosynthesize in the cool morning.

I have found that advice I get on moss gardening from another part of the country often does not work for me, and I end up going back to my original methods. Alkaline soils or clay soils will require different watering regimes from those of humus, and ease of transplanting and growing will be much better in humid or rainy climates. For example, I found that mosses stay wet longer for me if I do NOT put them on layers of felt, but can understand that downstate where Rick Smith gardens, limestone soils may serve as a desiccant and dry the mosses more quickly and the felt would protect against that. The felt and plastic do help reduce weed invasion.

Weeding

Mashuri Waite (Bryonet 2 February 2011) expressed his surprise when visiting the Cibodas Botanical Garden in West Java, Indonesia. He found that a species of ***Marchantia*** (Figure 16) was a problem weed in that garden. This was in contrast to his experience in Hawaii. This is yet another example of differences in the success of a species of bryophyte under different growing conditions.

Weeds are also a matter of personal choice. To one person it is a weed; to another it is a cherished plant to be encouraged.

Weeding bryophyte gardens requires different methodology from gardens of flowers and ferns. The surface-growing bryophytes are easily dislodged as the weeds are pulled up. It is best to pull the weeds, especially tracheophytes, as soon as they appear and before they grow large roots. This will create the least disruption. When pulling them, especially if they have penetrated the ground very far, hold the plant to be pulled close to the ground and place the middle and index fingers of the opposite hand so that one is on each side of the base of the stem to hold the bryophyte in place as the rooted plant is pulled. Weeding should be done as often as necessary to keep the garden weed free.

Weeding is not as big a job as it may seem if it is done frequently. Young plants are easy to pull. And usually kneeling or stepping on the bryophytes does not harm the bryophytes and may even help to propagate them.

Herbicides

There actually are a number of publications on the effects of herbicides on bryophytes (*e.g.* Stjernquist 1981; Balcerkiewicz & Rusinska 1987).

Of course mosses are slow growing and soon succumb to the encroachment of tracheophytes, so it is no wonder that herbicide applications can result in luxurious moss carpets. Schenk (1997) has witnessed the ready success of ***Polytrichum*** (Figure 8, Figure 25-Figure 28), ***Pohlia*** (Figure 151), and ***Atrichum*** (Figure 3, Figure 92) following such applications, and Ella Campbell, at a bryological meeting, once commented that the hornworts were ready colonizers following herbicide applications. Likewise, Balcerkiewicz and Rusinska (1987) found that bryophytes expanded on areas treated with herbicides.

Figure 151. ***Pohlia nutans***, a species that seems to benefit from herbicide applications. Photo by Michael Lüth, with permission.

Herbicides such as Paraquat, Simazine (Bond 1976), 2, 4-D, Atrazine (D. H. Wagner, pers. comm.), and Roundup (Schenk 1997) will encourage moss growth by eliminating invading tracheophytes (Bond 1976). Weeding is of course a safer option, but be sure to hold the mosses down as you pull each weed to avoid disrupting the rhizoids too badly.

Ben Tan (Bryonet 15 April 2014) reported that experiments using herbicides and pesticides, conducted by his students, did not result in an easy kill of the mosses except at very high concentrations. He cautioned that if one does eliminate the mosses, aggressive flowering plants (weeds) will readily establish themselves.

But this is not the experience of all researchers. Rowntree *et al*. (2003) found that the herbicide Asulox inhibits moss growth. When they cut plants to a standard length and expose them to Asulox for 24 hours, they found

that all 18 species tested exhibited reduced elongation. The amount varied among species and at different concentrations. The effective concentrations were the same as those effective on fern gametophytes. Rowntree and coworkers suggested that the ability to produce secondary branches might confer tolerance to single exposures of Asulox in some species.

In a different study, Rowntree *et al*. (2005) exposed cultures of ***Bryum rubens*** (Figure 152-Figure 153), ***Campylopus introflexus*** (Figure 141), and ***Polytrichastrum formosum*** (Figure 154) to Asulam in the culture medium. This study used protonemata that were exposed for 24 hours to Asulam, then transferred to herbicide-free media. A second trial maintained the protonemata on the herbicide medium for three weeks. In this case, the 24-hour exposure at concentrations of 0.001 g active ingredient L^{-1} had no effect on growth or development of the mosses. However, all three species experienced reduced growth and developmental anomalies in continuous of exposure at 0.01 g L^{-1}. ***Campylopus introflexus*** was the least sensitive; ***Polytrichastrum formosum*** was the most sensitive, with a 10-fold difference in response.

Figure 152. ***Bryum rubens***, a species for which development is affected by the herbicide Asulam. Photo by Michael Lüth, with permission.

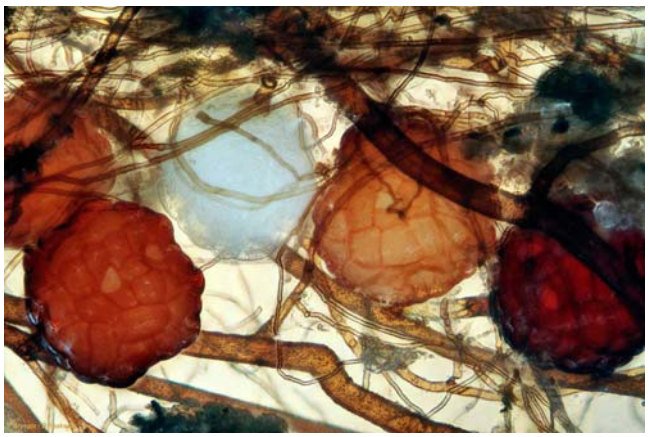

Figure 153. ***Bryum rubens*** tubers that help the plants survive unfavorable conditions and produce new plants. Photo by Dick Haaksma, with permission.

Figure 154. ***Polytrichastrum formosum***, a species for which development is affected by the herbicide Asulam. Photo by Michael Lüth, with permission.

Karunen *et al*. (1976) exposed germinating ***Polytrichum commune*** (Figure 25) spores to S-ethyl dipropylthiocarbamate. Surprisingly, at low concentrations (2 ppm by weight), the herbicide actually stimulated the growth of the young protonemata compared to the controls. They had a higher chloroplast pigment content as well. When the concentration was increased to 100 ppm, however, the development was slowed and there was a 30% reduction of chlorophylls and carotenoids. Nevertheless, the dry weight did not differ significantly from that of the controls. At 200 ppm, the spores either did not germinate, stopped germinating at an early stage, or formed deformed sporelings with few tightly-packed short cells. A number of unusual morphological changes occurred. A concentration of 300 ppm the spores rarely germinated.

Dichlorophen (2, 2′-methylene-bis(4 chlorophenol)) is a commercial product used to eliminate bryophytes (Brown *et al*. 1986). Brown and coworkers experimented with the pleurocarpous moss ***Rhytidiadelphus squarrosus*** (Figure 2) and the thallose liverwort ***Marchantia polymorpha*** (Figure 16). Dichlorophen induces loss of intracellular potassium and magnesium, inhibits photosynthesis, and depending on concentrations either stimulates or depresses CO_2 production in the dark. These symptoms suggest membrane damage. Tissue age affects the sensitivity, but light does not.

Rod Seppelt (Bryonet 17 April 2011) reported that an Australian student had studied the effects of herbicides on mosses. The student concluded that it was the surfactants in some herbicides that provided the damaging factor. But he concluded that bryophyte response to herbicides was complex.

Using 115 plots in a randomized design, Newmaster *et al*. (1999) compared the effects of two silvicultural herbicides (Vision®, Release®) on bryophytes and lichens in a harvested boreal mixed woodland. Concentration gradients of 0.71-6.72 kg active ingredient ha^{-1} caused a decrease in species richness and abundance in both groups. Only a few species of colonizers remained. Bryophytes and lichens could be sorted into herbicide-tolerant colonizers, semi tolerant long-term stayers from dry open forest, and sensitive forest mesophytes.

Bryophyte "Predators"

Bryophytes are not without their share of enemies – playing roles with impacts that few ecologists have begun to imagine. I couldn't keep mosses in my garden room – even when I brought in vast quantities; my finches soon spread them about the room in their efforts to carry them to their nests, but even the dispersed mosses were soon removed by the birds. Newly established protonemata are soon disrupted and destroyed by birds gathering new plants or scratching for grit. In my terrarium, the pillbugs (***Porcellio scaber***; Figure 155) eradicated them from the rocks completely in just a few weeks, and the beautiful carpet I draped on a rock outside was transformed literally overnight into the look of Swiss cheese. Picking up the moss carpet to understand the problem resulted in hundreds of pillbugs falling to the ground! As mentioned earlier, those wanting to use moss they collect are often encouraged to spray a 50% mix of buttermilk and water on the desired surface and then presumably spread a moss carpet over it, but I tried a similar recommendation of raw eggs to little avail. It was that patch of moss that became devoured by pillbugs and I suspect the egg helped make it so.

Figure 155. ***Porcellio*** *cf.* ***scaber*** on ***Marchantia polymorpha***, a common herbivore on bryophytes. Photo by Walter Obermayer, with permission.

To keep your bryophyte garden healthy and green, Mizutani (1975, 1976) and Fukushima (1979a, b, 1980) advise eliminating potential destroyers such as moles (Figure 156), slugs (Figure 157), crickets (Figure 158), and ants (Figure 159). Good luck!

Figure 156. Mole, sometimes a pest in moss gardens. Photo by Michael David Hill, through Creative Commons.

Figure 157. Slug on ***Fissidens*** sp. Photo by Janice Glime.

Figure 158. ***Gryllus rubens***, southeastern field cricket. Crickets can be a pest in moss gardens. Photo by Jeffrey Reed, through Creative Commons.

Figure 159. Ant on moss, sometimes a pest in moss gardens. Photo through Creative Commons.

A second concern may be introducing pests from other locations, especially outside the country. Bryonetters discussed this several years ago, but many of the reports covered what didn't work. Among these, Eva Krab (Bryonet 3 February 2012) reported using 100% CO_2 for 12 hours in a closed chamber, then leaving the cores of moss out at room temperature for 24 hours to allow eggs to hatch, then freezing them at -20ºC. After three rounds of those treatments, she had no success with ***Sphagnum fuscum*** (Figure 20) and only limited success with ***Hylocomium splendens*** (Figure 58).

Other Pests

Rick Smith, on Bryonet 9 February 2011, claimed that "birds have so much time on their hands they relentlessly attack moss gardens and unless the botanic garden has lots of moss then the birds concentrate their damage on the small poor moss garden." My own experience is that chipmunks can be just as destructive. They need only run across the bryophytes and their feet kick them up. And they seem to have a special attraction for ***Thuidium delicatulum*** (Figure 43-Figure 45) as the entrance to their tunnels. Mine never lasted for more than a few days before it had a bare spot and a tunnel entrance in the middle of it! I'm fairly certain that was a chipmunk, but some of those torn up patches may have been the work of birds instead of chipmunks. The fresh patches of mosses seem to attract the most attention. Perhaps it is due to birds looking for food among the fauna. Rick Smith also warned that "other obstacles are rodent damage (vole, squirrel, raccoon) and leaf removal."

Rick Smith has written a small book, *New Methods in Moss Gardening*. In that book he explains using an invisible mat system to reduce the unwanted interaction. He places felt (Figure 162) on the bottom – 2-3 layers, to block the competing vascular plants from emerging and to keep the soil from wicking the water away. On that he grows the mosses with a net on top to keep the birds and rodents from tearing it up. I have not had much success with the felt, but I think the problem is that I start with clumps of moss and Rick starts with tiny pieces that he broadcasts on the felt, then grows them in controlled conditions until they are large enough to put in the garden. I did try that once, but mine dried out too quickly. His method is much like grabbing that discarded carpet that has accumulated bits of soil and a healthy growth of mosses. But for thicker mats where tree seeds can lodge, seeds still germinate and succeed.

Overwatering can have some interesting invertebrate consequences. Too much water encourages earthworms to live closer to the surface, resulting in castings (Spain 2012b). If this is a moss garden with thin mats, the castings are deposited on the moss (Figure 160). When these are numerous, as they can be, they become unsightly. The prevention is to decrease the watering.

Figure 160. Earthworm castings on a moss mat. Photo by Ken Gergle for Moss and Stone Gardens.

Earthworm castings can be removed by letting them dry and removing them with a knife or crumbling them (Spain 2012b). The remaining hard portion can be removed by using a pump sprayer to soften them and gently wash them away. Using a hose or other high-power sprayer should be avoided because it will make the moss and soil wet again, once again encouraging movement of the worms to near the surface.

Netting

The netting is another story. One recommendation is to use a fine net with a mesh of about 0.8 mm such as a bridal veil, a material known as **tulle**, to keep rodents and birds from disrupting the bryophytes. But bridal veil is unsightly. Instead, I started with a fine mesh like one might find on a wedding veil, but instead of the soft cloth of wedding veils, I chose nylon window screening because it was not so conspicuous. That protected the mosses from rodents and birds, but for some of the mosses it kept them from getting wet unless it was a downpour. The water would bead up on top of the screen (Figure 161-Figure 162) and its cohesion kept it from penetrating. Sometimes cohesion and adhesion work to disadvantage!

Figure 161. ***Bryum*** sp. on burlap with wet net in lower half of image. Upper mosses in image have no netting. Photo by Janice Glime.

Figure 162. Wet netting on ***Polytrichum commune*** that is planted on brown felt, showing the water beading on the net and not penetrating to the moss. Photo by Janice Glime.

Polytrichum (Figure 8) had particular problems with the nylon window screening. It often bent over instead of growing through the mesh (Figure 163-Figure 165), and the water beaded up on top of the net. In the morning when dew was on the net, the mosses were invisible. The next growing season some of the narrower young shoots grew through the net, but setae formed the previous autumn were trapped under the net (Figure 166). Finally, all the growing tips were above the netting that spring (Figure 167). But even then, water movement was not normal because of the constricting threads at the point where the moss penetrated the net. And if the mosses grow through the net, the netting can never be removed. Now, seven years later, the net is hidden and the mosses appear to be normal (Figure 168).

Figure 163. ***Polytrichum juniperinum*** under netting, showing how they have grown sideways due to the restriction of the netting. Photo by Janice Glime.

Figure 164. ***Polytrichum*** and fragments on felt under nylon window screening. Rocks hold the edges of the screening in place. Photo by Janice Glime.

Figure 165. ***Polytrichum juniperinum*** under netting after stems became more upright. Photo by Janice Glime.

Figure 166. ***Polytrichum juniperinum*** emergence through netting with sporophytes produced the previous growing season trapped beneath the netting. Photo by Janice Glime.

Figure 167. ***Polytrichum juniperinum*** emergence through netting after several years of growth. Note how it keeps the plants separated, reducing their ability to help each other transport and retain water. Photo by Janice Glime.

Figure 168. ***Polytrichum juniperinum*** in moss garden, November 2017. They are continuing growth above the netting, with netting completely hidden. Photo by Janice Glime.

Rick Smith (Bryonet 30 August 2010) solved the constriction problem by placing the net over moss fragments so that they grew through it while they were still small and thin. Young (small) plants will grow through the bird netting, but so do some young weeds, and they are pretty impossible to pull out by the roots and to get out of the netting.

One solution to this problem is to put bird mist netting over the bryophytes instead. Susan Moyle Studlar (Bryonet 6 February 2012) considers netting to be essential to keep birds out. In her West Virginia, USA, garden, the birds toss the mosses about "with abandon" in search of the invertebrates beneath them. She found that the Berlin Botanic Garden used bird netting to protect the bryophytes from birds (Figure 169).

Figure 169. Moss garden in Berlin Botanic Garden, showing bird netting. Photo courtesy of Susan Moyle Studlar.

I finally solved the problem by ordering bird mist netting. It has a mesh about 5-6 mm and is made of fine black plastic. I hold it in place and help it conform to the uneven surface be pinning it down with bobbi pins. Once it is firmly attached, it is invisible unless you are looking for it or are up close. This type of netting is less conspicuous and doesn't interfere with growth (Figure 170-Figure 171). It must be firmly attached at its edges or the mosses will still be susceptible to disturbance and the netting can come off. Some birds may even try to remove it for nesting material.

Figure 170. ***Leucobryum glaucum*** moss garden with bird netting. Note the clumps that have been broken up – damage done before the netting was applied. Photo by Janice Glime.

Figure 171. ***Leucobryum glaucum*** with bird netting in moss garden. Photo by Janice Glime.

Removing Autumn Leaves

Most of the bryophytes will need partial shade. But in a relatively small space, the best shade is likely to come from one or two deciduous trees. And these dump enough leaves in the fall to bury the bryophytes. The leaves do not decay rapidly enough to expose the bryophytes the next spring, and some seem to suffer from the tannic acids during the winter under the snow. Hence, removal is necessary.

Famous gardens such as Saihoji in Kyoto require constant maintenance to encourage the mosses against the competing tracheophytes. Leaf litter and weeds must be removed lest the mosses be crowded out, but care must be taken to maintain the natural, unmanicured look. Wire or bamboo rakes or soft brooms (Figure 172) are used for such maintenance; brooms should be firm but not harsh to reduce damage to the delicate moss leaves. There is a Japanese saying that only old men and little boys can tend the moss gardens because anyone else would be too careful and the gardens would lose their natural look (Takaki, pers. comm.; Figure 173).

Figure 172. This broom is used for tending a private moss garden in Japan. Photo by Janice Glime.

Figure 173. This "old man" tends moss in Ginkakuji temple garden in Kyoto, Japan. Photo by Janice Glime.

Benner avoids raking leaves by covering the mosses with netting (Dunn 2008). He then collects the leaves and puts them in his compost heap.

Modern technology offers other solutions. One can vacuum the leaves or blow them onto a pile or onto flower gardens where they serve as a mulch (Figure 174). Annie Martin <https://www.youtube.com/watch?v=nh9S1IDfXzE&t=3s> suggests watering the moss garden first when blowing them. The mosses will stay put, but the leaves will still blow. Use an up and down jerky motion to dislodge the leaves.

Figure 174. Blowing leaves off the mosses. Photo by Annie Martin, with permission.

The modern methods of vacuuming the leaves have their limitations. Vacuuming is best done when the leaves are dry, and in some areas there are few dry days at that time of year or in some years. One must be careful not to blow or suck up dry mosses that are not well-connected yet. But then, even raking or brushing the leaves away is best done with dry leaves to protect the bryophytes from being removed.

Overwintering

Generally the predominantly perennial mosses will come through winter just fine. And in most cases, they will look bright green as soon as the snow recedes, being the earliest of the green plants to appear (Figure 175).

Figure 175. ***Dicranella heteromalla*** and ***Atrichum*** sp. demonstrate the fresh condition exhibited by many kinds of mosses that have just been uncovered from winter snow. Photo by Michael Lüth, with permission.

But don't despair if your moss garden comes out from under the snow the next spring looking like soon-to-be fossils. With a few warm (not hot) days and plenty of water, new shoots arise above the pathetic remnants of last year. My ***Leucobryum*** (Figure 34), ***Polytrichum*** (Figure 8, Figure 176), and ***Fissidens*** (Figure 48) did just that. The ***Racomitrium*** (Figure 53) remained brown and dead-looking for a long time, and I was ready to replace it with something more friendly when tiny green tips began to appear. There is nothing like a personal garden to teach you about the trials and tribulations of the bryophytes and their ways of solving these problems. And ***Marchantia polymorpha*** thalli are green and healthy when the snow recedes in the spring. It will be interesting to see how the competition plays out. I think ***Marchantia*** (Figure 16) is going to win.

Figure 176. ***Polytrichum*** sp. in snow. Photo by Annie Martin <www.mountainmoss.com>, with permission.

Arranging the Garden

Give some thought to the arrangement of the mosses and other plants. For the mosses to offer their peaceful appeal, flowering plants must be kept at a minimum. One long-blooming highlight is enough for a garden of $4m^2$, and it should be set off to the side or back to avoid detracting from the mosses (Figure 177). Be sure the plant won't crowd the ground, lie on top of the moss, or prevent light and/or water from reaching the moss. And avoid things that lose lots of leaves, requiring raking. As an alternative, lamps or statues can serve as highlights (Figure 178).

Figure 177. Moss garden with geranium accent. In early spring the irises on the right will bloom and be the accent. Photo by Janice Glime.

Figure 178. A small painted clay lantern provides a highlight in this garden when the flowers have stopped blooming. Netting over some of the mosses has water beads on the netting. Photo by Janice Glime.

Most mosses will need light shade, especially in the afternoon. A small tree, large shrub, building, or fence can provide this (Figure 179).

Figure 179. A neighbor's garage, a cedar fence, lilac bushes, and a Japanese maple tree provide shade for this moss garden in the morning, with the garage and my house shading it in the afternoon. Photo by Janice Glime.

The benefit of mosses in the garden can extend beyond their aesthetic value to that of enhancing the quality of other garden plants. Schenk (1997) reports that his friend, Gordon Emerson of Ohio, finds that bulbs, tubers, and corms increase more readily under moss cover than when planted in bare ground. Presumably the increased moisture permits them to produce and store more energy.

Environmental Benefits

I have already noted the decrease in water usage need by a moss garden vs a grass lawn. The bryophytes can often provide other solutions to environmental issues, such as collecting and preventing water run-off from storms. They also require no pesticides, herbicides, or fertilizers, therefore avoiding the contamination of the water that filters through them.

Figure 180. ***Fontinalis antipyretica***, an aquatic moss that is sensitive to heat. Photo by Bernd Haynold, through Wikimedia Commons.

Summary

Among the most common "moss" garden plants are thallose liverworts, especially ***Marchantia polymorpha***, peat mosses (***Sphagnum***), ***Polytrichum***, ***Atrichum***, members of the **Mniaceae**, ***Leucobryum*** (but it is somewhat difficult), ***Rhizogonium*** in Asia, ***Rhytidiadelphus triquetris***, ***Eurhynchium*** (*sensu lato*), and ***Bryum argenteum***. *Fissidens* species seem to be particularly easy to grow in temperate North America.

Special habitats may support only a few species, including ***Rhytidiadelphus squarrosus*** and ***Brachythecium rutabulum*** for lawns, ***Bryum argenteum*** and ***Barbula*** for paths, and ***Tortula muralis*** for walls.

Mosses cultivated in containers will need plenty of ventilation. Flats are good starter containers, with the mosses later transplanted to a "plantation" with light shade. Both can be planted by pulverizing the plants and spreading them like grass seed. A sprinkling system may be needed in a climate without a rainy season, and one should take advantage of the rainy season, where it exists, by planting just before it so the young plants or transplanted ones get plenty of water.

When transplanting mosses from the wild, the integrity of the clump or mat must be maintained. Of course one must have permission, and care should be taken not to decimate the population.

The substrate may be amended with a variety of substances to lower the *p*H, but liming and fertilizers are detrimental to bryophyte health. Herbicides may eliminate tracheophyte competition, but hand care by pulling weeds and clearing away litter is most likely a safer choice. Avoid giving the garden a manicured look and use only a light broom or wooden rake to clear away litter. Winter care need be no more than removing deciduous litter.

Once established, the bryophytes will require less water than a lawn or flower garden, require no fertilizers or pesticides, and prevent erosion. They are more environmentally friendly than most kinds of gardens.

Acknowledgments

I must acknowledge many Japanese friends for their tours of Japanese gardens and explanations of the establishment and care. In particular, Zen Iwatsuki and Norio Takaki gave me wonderful tours of both public and private gardens, indoors and out, and explained to me in English what the Japanese gardeners were telling us about the care of the gardens and plantation.

Thank you Ken Kellmann and Steve Soldan for calling our attention to the delightful New York Times article on moss lawns.

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CHAPTER 7-5
GARDENING: PUBLIC GARDENS

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CHAPTER 7-5
GARDENING: PUBLIC GARDENS

Figure 1. Jassy moss house. This unusual garden transports you into another world. Photo courtesy of Ben Tan.

Botanical Gardens

Botanical gardens often have a bryophyte section, sometimes mimicking a Japanese garden. Some use mosses around indoor or outdoor waterfalls. And some actually label the bryophytes for teaching purposes. As you might guess, Japan is one of the places to see this latter practice.

Bryophyte gardening has been somewhat limited in North America, but there are notable exceptions. Annie Martin rescues bryophytes that are slated for destruction in North Carolina, USA.

Rick Smith teaches moss gardening by offering workshops. As a result of his workshops, Smith was invited to establish a moss garden at the Luthy Botanic Garden in Peoria, Illinois, USA, and a second at the Illinois Central College Arboretum in East Peoria. Both of these gardens have ***Dicranum scoparium*** (a dark green moss forming cushions; Figure 2), ***Polytrichum commune*** (Figure 3), ***Bryoandersonia illecebra*** (Figure 4), ***Leucobryum glaucum*** (Figure 5), ***Hypnum*** spp. (Figure 6), ***Thuidium delicatulum*** (a species that spreads easily; Figure 7), ***Anomodon attenuatus*** (Figure 8), and ***Plagiomnium cuspidatum*** (Figure 9).

Figure 2. ***Dicranum scoparium*** with capsules, a common species in moss gardens, public or private. Photo by Janice Glime.

Figure 3. ***Polytrichum commune***, a moss frequently occurring in moss gardens. Photo by Alan J. Silverside, with permission.

Figure 4. ***Bryoandersonia illecebra***, a moss from the southeastern USA and used by Rick Smith in moss gardens. Photo by Bob Klips, with permission.

Figure 5. ***Leucobryum glaucum***; this genus is used in moss gardens all over the world. Photo by Janice Glime.

Figure 6. ***Hypnum imponens***, a common sheet moss that appears in moss gardens. Photo by Janice Glime.

Figure 7. Fern moss, ***Thuidium delicatulum***, a suitable moss for moss gardens. Photo courtesy of Rick Smith.

Figure 8. ***Anomodon attenuatus*** on trees, a common species in somewhat alkaline areas. Photo by Janice Glime.

Figure 9. ***Plagiomnium cuspidatum***, a frequent volunteer in moss gardens. Photo by Hermann Schachner, through Creative Commons.

Rick Smith (Bryonet) reports that he uses the mat system in both his own private garden and in public gardens. He uses a thin synthetic mat that stores rainwater similar to the storage by a sponge. As the moisture evaporates from the mosses, they draw more water from the underlying mat. He does not water his gardens, but in many climates watering is necessary, especially when the bryophytes are first getting established. He recommends only rainwater if watering is necessary, but occasional watering with other sources such as distilled water usually won't harm the garden if it is interspersed with frequent natural watering.

George Schenk has moss gardens in Seattle, Washington, USA, New Zealand, and the Philippines, all areas that receive considerable annual rainfall. His book on *Moss Gardening* received the 1997 Horticultural Society of America's book of the Year Award. Amazon says of the book "A delightful book that encourages gardeners to pay closer attention to the subtle beauty of miniature landscapes and introduces one of the glories of Japanese gardens into American designs. The author writes entertainingly of mosses on rocks and walls, in containers, and as a lush ground cover, and he presents a gallery of his favorite moss species."

Problems in Public Gardens

Rick Smith (Bryonet 9 February 2010) admonished that the challenge in most public gardens is growing bryophytes in urban areas vs. their natural woodland setting. Traditional moss gardens require a staff to weed the garden of the tracheophyte seedlings.

In public gardens, the gardeners are also the problems. They want to treat the bryophytes like "small vascular plants" that need to be watered and fertilized, but these are just what one must avoid. Care is primarily that of removing unwanted plants and leaf litter.

One additional problem in public gardens is human traffic. Although Annie Martin frequently points out that you should walk on your bryophytes to help in their dispersal, they are not equipped to withstand the parade of an army of people or small children playing tag. This presents the need for paths. These can be presented in a variety of ways, as you will see in the images in this chapter. Sand paths are common, but stone paths can be works of art themselves, with bryophytes filling the spaces between the stones. Wooden steps, including logs, provide niches for additional bryophytes. Care must be taken that there is no smooth wood that might invite algae, hence becoming slippery and a safety hazard.

Moss Gardens of the World

Dale Sievert has visited many gardens, large and small, and has kindly contributed his images for this chapter. This is but a small sampling of moss gardens in the world.

Bloedel Reserve, Washington, USA

The Bloedel Reserve is a 60.7-hectare (150-acre) forest garden on Bainbridge Island in the state of Washington, USA, first opened to the public in 1988. There one can find beautiful mossy landscapes. It includes a Japanese garden with a sand, moss, and rock garden, but many of the bryophyte landscapes in the reserve have a more natural look (Figure 10-Figure 11).

Figure 10. A large moss lawn at Bloedel Reserve, Washington, USA. Photo courtesy of Dale Sievert.

Figure 11. Interesting mossy topography at Bloedel Reserve, Washington, USA. Photo courtesy of Dale Sievert.

Seattle Japanese Garden, Seattle, Washington, USA

The Seattle Japanese Garden occupies 1.4 hectares (3.5 acres) in the Madison Park neighborhood of Seattle. It was designed under the supervision of the Japanese gardener Juki Iida in 1960. It features pools, streams, bridges, lamps, and the beautiful autumn color of Japanese maples, along with bryophytes (Figure 12-Figure 13).

Figure 12. Mosses offset by fall colors of Japanese maples in the Seattle Japanese Garden, Seattle, Washington, USA. Photo courtesy of Dale Sievert.

Figure 13. Moss-covered lantern in Seattle Japanese Garden. Photo courtesy of Dale Sievert.

Portland Japanese Garden, Portland, Oregon, USA

This garden is considered to be the most authentic Japanese garden outside of Japan. It occupies 2.2 hectares (5.5 acres) in the scenic west hills of Portland. The garden was designed by Professor Takuma Tono. One can see crooked paths, waterfalls, arched bridges, moss-covered lanterns, pools with koi, and other features often found in the gardens in Japan. Bryophytes are a prominent feature (Figure 14-Figure 16).

Figure 14. Sand and moss garden at the Portland Japanese Garden, Portland, Oregon, USA. Photo courtesy of Dale Sievert.

Figure 15. Moss lawn at the Portland Japanese Garden, Portland, Oregon, USA. Photo courtesy of Dale Sievert.

Figure 16. Path through the Portland Japanese Garden, Portland, Oregon, USA. Photo courtesy of Dale Sievert.

Anderson Japanese Garden, Rockford, IL, USA

These gardens are considered to be premiere among American Japanese gardens (Figure 17-Figure 19). They were established in 1978 when John Anderson, a Rockford businessman, was inspired by his visit to the Portland Japanese Garden. The design was assisted by Hoichi Kurisu, using the Anderson's swampy backyard. With 12 acres of gardens and koi-filled pools, this setting is often used for both peaceful reprise and weddings.

Figure 17. A blend or rocks, moss, and sand in the Anderson Japanese Garden, Rockford, IL, USA. Photo courtesy of Dale Sievert.

Figure 18. A mixture of round and rectangular steps at the Anderson Japanese Garden, Rockford, IL, USA. Photo courtesy of Dale Sievert.

Figure 19. Water feature with a large, moss-covered rock at the Anderson Japanese Garden, Rockford, IL, USA. Photo courtesy of Dale Sievert.

Golden Gate Park, San Francisco, California, USA

Starting with sand dunes, William Hammond Hall (a park engineer) and master gardener John McLaren created a restful place to escape the bustle of the city. The Golden Gate Park is a large urban park of 411.6 hectares (1,017 acres). In addition to its conservatory of flowers, it presents a Japanese tea garden, an oak forest, a botanical garden that began in 1890, and two Dutch windmills that pump the water to irrigate the garden (Figure 20-Figure 21). More than 8000 varieties of plants occupy the gardens.

Figure 20. Mosses and trees in garden of Golden Gate Park, San Francisco, California, USA. Photo by courtesy of Dale Sievert.

Figure 21. Golden Gate Park, San Francisco, California, USA showing a walking path and a moss lawn. Photo courtesy of Dale Sievert.

Zion National Park, Utah, USA

Zion National Park covers 593 km² (229.1 mi²) and is characterized by rivers in deep canyons, colorful stone cliffs, waterfalls, and fantastic views. Despite the xeric nature of most of the park, one can still find bryophytes there (Figure 22). In 1909, the area was established as a National Monument by President William Henry Taft. But its name of Mukuntuweap National Monument drew criticism because it was difficult to pronounce. In 1918 it was renamed to Zion, the name that had been used by the Mormons who settled there. In 1919 it was established by The United States Congress as a national park.

Figure 22. Moss along walk in Zion National Park, Utah. Photo courtesy of Dale Sievert.

Missouri Botanical Garden, St. Louis, Missouri, USA

The Missouri Botanical Garden was founded in 1859 and is the oldest botanical garden in the USA. The garden is comprised of 32 hectares (79 acres) and includes a Japanese strolling garden (Seiwa-en) of 5.7 hectares (14 acres). Designed by Koichi Kawana, this is the largest Japanese garden in North America (Figure 23).

Figure 23. Moss lawn in the Missouri Botanic Garden, St. Louis, Missouri. Photo courtesy of Dale Sievert.

Rotary Botanical Garden, Janesville, Wisconsin, USA

The Rotary Botanical Garden in Janesville is an 81 hectare (20-acre) reprise. Bryophytes can be seen along some of the paths and in the Japanese garden, and some have managed to establish themselves between the stones of the paths (Figure 24). Of interest to the bryologists is the fern and moss garden.

Figure 24. Path and balls of mosses at the Rotary Botanic Garden, Janesville, Wisconsin, USA. Photo courtesy of Dale Sievert.

Sarah Duke Gardens, Durham, North Carolina, USA

The Sarah Duke Gardens comprise approximately 22 hectares (55 acres) of landscaped and wooded areas at Duke University. There are 5 miles of allées, walks, and pathways throughout the gardens. The official beginning of the gardens was 1934, when Dr. Frederick Moir Hanes, a faculty member at the Duke Medical School, persuaded Sarah P. Duke to provide $20,000 toward planting flowers in a debris-filled ravine. But alas, the gardens were destroyed in 1935 by a flood. Sarah Duke's daughter provided funds to rebuild the gardens above the flooding zone as a memorial to her mother, who died in 1936. In parts of the gardens, the ground is covered by a restful green mat of bryophytes (Figure 25).

Figure 25. Path in moss and shrub garden at Sarah Duke Gardens, Durham, NC, USA. Photo courtesy of Dale Sievert.

Limahuli Gardens, Kauai, Hawaii, USA

The Limahuli Gardens are part of the Limahuli Preserve and occupy 6.9 hectares (17 acres) among the 399 hectares (985 acres) of the preserve. The gardens were built to "honor the connection between nature and humanity." This is in one of the last easily-accessible valleys where native forest, pristine streams, and archaeological complexes remain. The descendants of its original inhabitants are its caretakers. In 1967, after Hawaii became a state, Juliet Rice Wichman, a member of the Hui, was assigned to develop the new park. She immediately began to plan and plant. She bequeathed the gardens to one of her grandsons. Since its beginnings it has been awarded "Best Natural Botanical Garden" from the American Horticultural Society for demonstrating the "best environmental practices of water, soil, and rare plant conservation in an overall garden design" and the Koa Award for dedication to the perpetuation of the Hawaiian culture. Bryophytes contribute to the luscious natural landscape (Figure 26).

Figure 26. Mosses and tropical vegetation in the Limahuli Gardens, Kauai, Hawaii, USA. Photo courtesy of Dale Sievert.

Sikkum, India

In Sikkum, one can find many walls with mounds of mosses growing on the sides and tops. Waterfalls are green with bryophytes. And bryophytes adorn the forest floor and branches (Figure 27-Figure 28).

Figure 27. Moss epiphytes in Sikkum, India. Photo courtesy of Dale Sievert.

Figure 28. Mosses at Sikkum, India. Photo courtesy of Dale Sievert.

Floriade, Venlo, Holland

This garden at Floriade represents modern architecture that utilizes bryophytes in the design (Figure 29).

Figure 29. Moss garden at Floriade, Venlo, Holland. Photo courtesy of Dale Sievert.

Villa d'Este, Tivoli, Italy

The Villa d'Este is near Rome, Italy. It is adorned with numerous fountains, some of which are covered with bryophytes (Figure 30).

Figure 30. Villa d'Este fountain with mosses. Photo courtesy of Dale Sievert.

Herculaneum, Italy

Herculaneum rests in the shadow of Mount Vesuvius. It was an ancient Roman town destroyed in 79 AD by volcanic pyroclastic flows. Only ruins remain of the ancient town, and ruins often provide suitable substrates for bryophytes (Figure 31). But more recent statues may be covered with bryophytes (Figure 32).

Figure 31. Herculaneum, Italy, ruins with mossy surfaces. Photo by Xtreambar, through Creative Commons.

Figure 32. Mossy statuary fountain at Herculaneum, Italy. Photo courtesy of Dale Sievert.

Cibodas Botanical Garden, Java, Indonesia

Gradstein (2006) reported that personnel created a small river and pond to grow ***Plagiomnium*** (Figure 9) in the Cibodas Botanical Garden, Java, Indonesia (Figure 77). The area was sprayed with water, particularly during the dry season. This permitted successful cultivation of ***Marchantia*** (Figure 34), ***Dumortiera*** (Figure 35), ***Trichocolea tomentella*** (Figure 36), and ***Plagiochila tjibodensis***. Other bryophytes that did not require special treatment were ***Hypopterygium*** (Figure 37), ***Pyrrhobryum*** (Figure 38), ***Fissidens*** (Figure 39), ***Thuidium*** (Figure 7), ***Leucobryum*** (Figure 5), and ***Hypnodendron*** (Figure 40). ***Pogonatum*** (Figure 41) grew on sand and ***Rhodobryum*** (Figure 42) grew on a mix of sand and humus. The garden was successful in growing epiphytes on soil covered with bark chips.

Figure 33. Cibodas Botanical Garden, Indonesia, where water sources were added to encourage the success of a moss garden. Photo by Hullie, through Public Domain.

Figure 34. ***Marchantia polymorpha*** with antheridiophores and archegoniophores; ***Marchantia*** may need added water in dry areas until it becomes established. Photo by Robert Klips, with permission.

Figure 35. ***Dumortiera hirsuta***, in a genus that may need added water in dry areas until it becomes established. Photo by Michael Lüth, with permission.

Figure 36. ***Trichocolea tomentella***, a species that may need added water in dry areas until it becomes established. Photo by Michael Lüth, with permission.

Figure 37. ***Hypopterygium didictyon***; ***Hypopterygium*** requires no special treatment when cultivated during a dry season. Photo by Juan Larrain, with permission.

Figure 38. ***Pyrrhobryum spiniforme***, in a genus that requires no special treatment when cultivated during a dry season. Photo by David Long, with permission.

Figure 39. ***Fissidens taxifolius*** (Common Pocket-moss), in a genus that requires no special treatment when cultivated during a dry season. Photo by Barry Stewart, with permission.

Figure 40. ***Hypnodendron comosum***, in a genus that can be grown on sand. Photo by Mezy Moo, through Creative Commons.

Figure 41. ***Pogonatum perichaetiale***, in a genus that can be grown on sand. Photo by Li Zhang, with permission.

Figure 42. ***Rhodobryum giganteum***, in a species from Java that can be grown on mix of sand and humus. Photo by David Long, with permission.

Bryophytes Occurring in Public Gardens

This chapter has only a small sampling of public gardens and parks with mosses, including some that have attempted to mimic the Japanese gardens. Some are natural and others are planted with horticultural varieties, but the non-"moss gardens" included here have bryophytes that have arrived and survived without deliberate human intervention.

Chris Preston (Bryonet 2 February 2022) reported 97 moss species and 14 liverwort species from the Cambridge University Botanic Garden (Figure 43) in the winter/spring season. These were volunteer species, not planted ones. Preston was unable to relocate at least 25 of the species that had been recorded there by past bryologists.

Figure 43. Cambridge Botanic Garden lake, illustrating the variety of habitats that support 97 moss and 14 liverwort species. Photo by C. M. Glee, through Creative Commons.

Morgan *et al*. (2008) reported 52 species of mosses and 15 of liverworts at the 31-hectare Bartlett Arboretum Forest (Figure 44) in Stamford, Connecticut, USA. This multiuse forest provides multiple opportunities for species to arrive on shoes and boots and perhaps even clothing.

Figure 44. Bartlett, Arboretum, Stamford, Connecticut , where 52 moss and 15 liverworts are reported. Photo through Creative Commons.

Eckstein and Burghardt (2008) found 139 bryophyte species in the Old Botanical Garden in Göttingen (Figure 45), Germany. These were comprised of 123 mosses and 16 liverworts, making it one of the richest botanical gardens investigated in Germany and the one with the greatest density of bryophytes. One of these is ***Didymodon umbrosus*** (Figure 46), a rare introduced species. Furthermore, 23 of these species are on the Lower Saxony Red List.

Figure 45. Old Botanical Garden, Universität Göttingen, Germany, home to 123 mosses and 16 liverworts. Photo by Valérie Chansigaud, through Creative Commons.

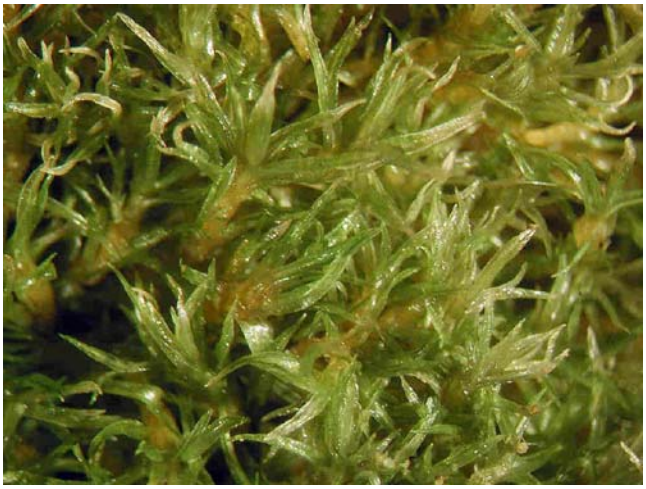

Figure 46. ***Didymodon umbrosus***, an introduced species in the Old Botanical Garden in Göttingen, Germany. Photo by Michael Lüth, with permission.

Odgaard (Bryonet 5 February 2022) has investigated the mosses in the botanical garden of Aarhus, Denmark (Figure 47). In the 1970's, only ***Dicranoweisia cirrata*** (Figure 48) grew there as an epiphyte. In 2022 he reported that the epiphyte flora had expanded considerably, including the new inhabitants ***Orthotrichum affine*** (Figure 49), ***O. diaphanum*** (Figure 50), ***O. lyellii*** (Figure 51-Figure 52), ***O. pulchellum*** (Figure 53), ***Ulota phyllantha*** (Figure 54), ***Syntrichia laevipila*** (Figure 55-Figure 56), ***S. latifolia*** (Figure 57-Figure 59), and ***Zygodon conoideus*** (Figure 60-Figure 62). He attributed this increase in diversity to the improved air quality, especially the reduction of sulfur. Like many researchers, he noted the importance of bryophytes in botanical gardens as a means of monitoring changes in air quality.

Figure 47. Botanical garden of Aarhus, Denmark, where epiphytic bryophytes have increased since the air pollution has decreased. Photo by Andreas Jensen, through Creative Commons.

Figure 48. ***Dicranoweisia cirrata*** with capsules, the only epiphytic species in the botanical garden of Aarhus, Denmark, in the 1970's. Photo by Sharon Pilkington, with permission.

Figure 49. ***Orthotrichum affine*** with capsules, on bark, a species that is a recent arrival in the botanical garden of Aarhus, Denmark and occurs in 5 or more of 14 plots at the Botanic Garden Rombergpark, Germany. Photo by Malcolm Storey, EOL, through Creative Commons.

Figure 50. ***Orthotrichum diaphanum*** with capsules, a species that is a recent arrival in the botanical garden of Aarhus, Denmark. Photo by Hermann Schachner, through Creative Commons.

Figure 51. ***Orthotrichum lyellii***, an epiphytic species that is a recent arrival in the botanical garden of Aarhus, Denmark. Photo by J. C. Schou, with permission.

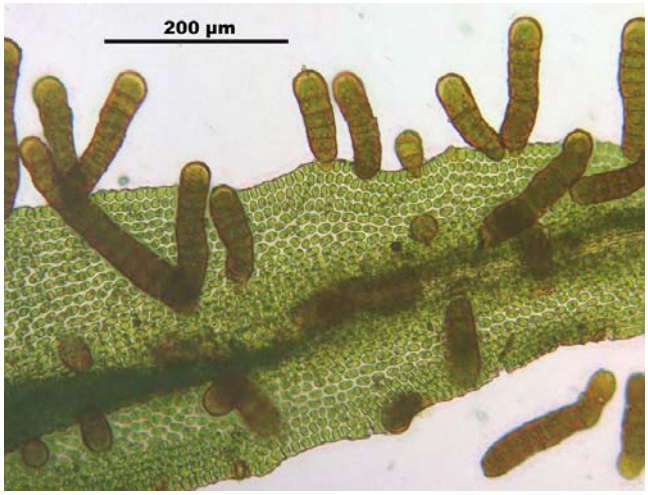

Figure 52. ***Orthotrichum lyellii*** leaf with gemmae, a possible means for its arrival in the botanical garden of Aarhus, Denmark. Photo by Hermann Schachner, through Creative Commons.

Figure 53. ***Orthotrichum pulchellum*** with capsules, an epiphytic species that is a recent arrival in the botanical garden of Aarhus, Denmark. Photo by Biopix, through Creative Commons.

Figure 54. ***Ulota phyllantha*** on a branch, a species that is a recent arrival in the botanical garden of Aarhus, Denmark. Photo by David T. Holyoak, with permission.

Figure 55. ***Syntrichia laevipila*** with gemmae, an epiphytic species that is a recent arrival in the botanical garden of Aarhus, Denmark. Photo by Hugues Tinguy, with permission.

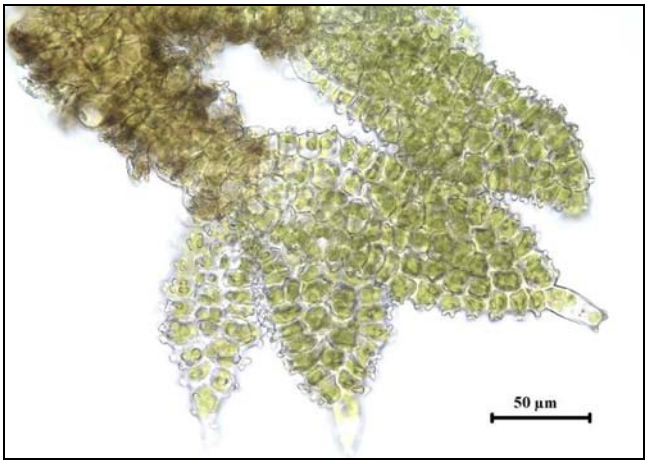

Figure 56. ***Syntrichia laevipila*** gemmae, a possible means for arrival of this species in the botanical garden of Aarhus, Denmark. Photo by Hugues Tinguy, with permission.

Figure 57. ***Syntrichia latifolia*** on tree trunk, an epiphytic species that is a recent arrival in the botanical garden of Aarhus, Denmark. Photo by Sharon Pilkington, with permission.

Figure 58. ***Syntrichia latifolia*** with leaf gemmae, possible propagules to arrive in the botanical garden at Aarhus. Photo by Claire Halpin, with permission.

Figure 59. ***Syntrichia latifolia*** leaf with gemmae, showing how numerous they are. Photo by Claire Halpin, with permission.

Figure 60. ***Zygodon conoideus*** on large branch, an epiphytic species that is a recent arrival in the botanical garden of Aarhus, Denmark. Photo by Sharon Pilkington, with permission.

Figure 61. ***Zygodon conoideus*** with capsules. Photo by Claire Halpin, with permission.

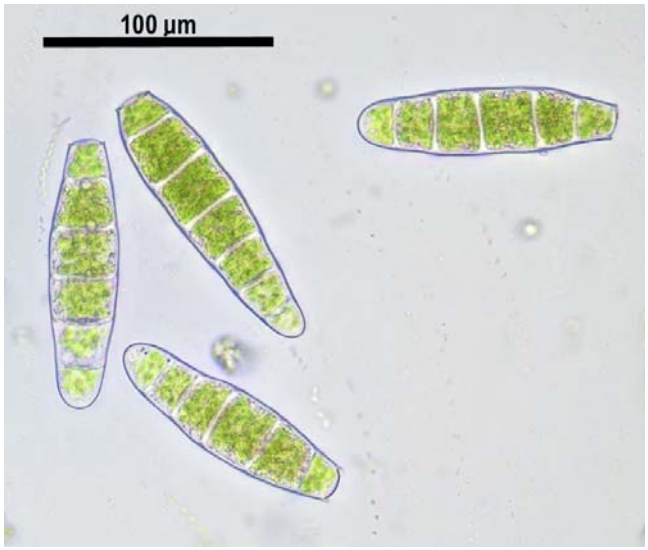

Figure 62. ***Zygodon conoideus*** gemmae, possible dispersal units to reach the botanical garden at Aarhus, Denmark. Photo by Claire Halpin, with permission.

Visnadi (2019) identified 63 species of bryophytes in 158 ha of parkland in the Ibirapuera Park, São Paulo, Brazil (Figure 63). She concluded that city parks serve as refuges for bryophytes, particularly those with heterogeneous forests, streams, and lakes, providing dispersal jumping areas between areas where buildings predominate. Even endemic species have been found there.

Figure 63. Ibirapuera Park, São Paulo, Brazil, showing some of the heterogeneity that supports 63 species of bryophytes. Photo by Sérgio Valle Duarte, through Creative Commons.

Müller (2013) was able to report the first record of epiphytic ***Ulota phyllantha*** (Figure 54) in Brandenburg, eastern Germany, from a population in a botanical garden in Potsdam (Figure 64).

Figure 64. Potsdam botanical garden, Brandenburg, eastern Germany, site of the first record of the epiphyte ***Ulota phyllantha*** (Figure 54) in Brandenburg. Photo by Wolfgang Pehlemann, through Creative Commons.

Common Species in Public Places

Fukarek (2006) notes that the bryophyte survey of the Botanic Garden Rombergpark (Figure 65) in Dortmund, Germany, is the first survey of bryophytes in that area. The bryophytes that occurred in 5 or more of the 14 sampling plots are ***Amblystegium serpens*** (Figure 66), ***Atrichum undulatum*** (Figure 67), ***Brachythecium rutabulum*** (Figure 68), ***Ceratodon purpureus*** (Figure 69-Figure 70), ***Eurhynchium praelongum*** (Figure 71), ***Grimmia pulvinata*** (Figure 72), ***Hypnum cupressiforme*** (Figure 73), ***Orthotrichum affine*** (Figure 49), ***Rhynchostegium confertum*** (Figure 74), and ***Tortula muralis*** (Figure 75). Smith *et al*. (2010) examined bryophyte species in 61 domestic gardens in the city of Sheffield, UK. They similarly found that only 10% of the bryophyte species occurred in more than half of the gardens. In the Bartlett Arboretum Forest (Figure 44) in Stamford, Connecticut, the mix of bryophytes was different, but there was no quantification in the study (Morgan *et al*. 2008). Only ***Atrichum undulatum*** (Figure 67), ***Brachythecium rutabulum*** (Figure 68), and ***Ceratodon purpureus*** (Figure 69-Figure 70) occurred here in common with those in 5 or more plots at the Botanic Garden Rombergpark.

Figure 65. Botanic Garden Rombergpark in Dortmund, Germany, where 10 species of bryophytes occurred in 5 or more of the 14 plots. Photo by Frank Vincentz, through Creative Commons.

Figure 66. ***Amblystegium serpens*** with capsules, a species that occurs in 5 or more of 14 plots at the Botanic Garden Rombergpark, Germany. Photo by Hugues Tinguy, with permission.

Figure 67. ***Atrichum undulatum***, a species that occurs in both the Bartlett Arboreum Forest in Connecticut, USA, and at the Botanic Garden Rombergpark, Germany. Photo by Hermann Schachner, through Creative Commons.

Figure 68. ***Brachythecium rutabulum*** with capsules, a species that occurs in both the Bartlett Arboreum Forest in Connecticut, USA, and at the Botanic Garden Rombergpark, Germany. Photo by Sharon Pilkington, with permission.

Figure 69. ***Ceratodon purpureus***, a species that occurs in both the Bartlett Arboreum Forest in Connecticut, USA, and at the Botanic Garden Rombergpark, Germany. Photo by Claire Halpin, with permission.

Figure 70. ***Ceratodon purpureus*** with capsules and dry leaves, a ubiquitous species, including in parks. Photo by Michael Lüth, with permission.

Figure 71. ***Eurhynchium praelongum*** with capsules, a species that occurs in 5 or more of 14 plots at the Botanic Garden Rombergpark, Germany. Photo by Andrew Spink, with permission.

Figure 72. ***Grimmia pulvinata*** with capsules, a rock-dwelling species that occurs in 5 or more of 14 plots at the Botanic Garden Rombergpark, Germany. Photo by Claire Halpin, with permission.

Figure 73. ***Hypnum cupressiforme***, a species that occurs in 5 or more of 14 plots at the Botanic Garden Rombergpark, Germany. Photo by Claire Halpin, with permission.

Figure 74. ***Rhynchostegium confertum*** with capsules, a species that occurs in 5 or more of 14 plots at the Botanic Garden Rombergpark, Germany. Photo by Claire Halpin, with permission.

Figure 75. ***Tortula muralis*** with capsules, on rock, a species that occurs in 5 or more of 14 plots at the Botanic Garden Rombergpark, Germany. Photo by David T. Holyoak, with permission.

Lunularia cruciata (Figure 76) is the only liverwort to appear in as many as 5 plots at the Botanic Garden Rombergpark, Germany (Figure 65). Interestingly, ***Lunularia cruciata*** is the only one of these species listed by Essl and Lambdon (2009) as alien species in Europe.

Figure 76. ***Lunularia cruciata***, the only liverwort appearing in five or more plots at the Botanic Garden Rombergpark, Germany. Its gemmae spread from rain and sprinklers. Photo by Hermann Schachner, through Creative Commons.

Among the 90 species of bryophytes in the tropical Cibodas Botanical Garden, Indonesia (Figure 77) (Nadhifah *et al*. 2018), there were no species in common with temperate Bartlett Arboretum Forest (Figure 44) in Stamford, Connecticut (Morgan *et al*. 2008) or the Botanic Garden Rombergpark, Germany (Figure 65) (Fukarek 2006), but several genera seem to be common in such gardens in widespread regions, boreal to tropical and both hemispheres. These include the thallose liverworts ***Marchantia*** (Figure 34) and ***Riccia*** (Figure 78), the leafy liverwort ***Frullania*** (Figure 79), and the mosses ***Barbula*** (Figure 80), ***Bryum*** (Figure 81), ***Campylopus*** (Figure 82), ***Fissidens*** (Figure 83), ***Leucobryum*** (Figure 5), ***Plagiomnium*** (Figure 9), and ***Sphagnum*** (Figure 84).

Figure 77. Cibodas Botanical Garden, Indonesia, a tropical garden with very different bryophytes from those in the temperate zone. Photo by Hullie, through public domain.

Figure 78. ***Riccia sorocarpa***; the genus ***Riccia*** is frequent in parks throughout the world. Photo by Claire Halpin, with permission.

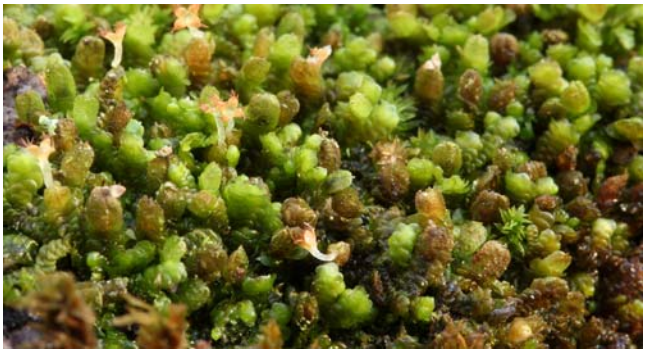

Figure 79. ***Frullania dilatata*** with capsules dehiscing; the genus ***Frullania*** is frequent in parks throughout the world. Photo by Claire Halpin, with permission.

Figure 80. ***Barbula unguiculata*** with capsules, a species that occurs in multiple botanical gardens in Hungary, representing a common genus in parks throughout the world. Photo by Claire Halpin, with permission.

Figure 81. ***Bryum argenteum***, a species that occurs in multiple botanical gardens in Hungary, representing a common genus in parks throughout the world. Photo by Claire Halpin, with permission.

Figure 82. ***Campylopus introflexus***, an invasive species; the genus ***Campylopus***, including this species, is frequent in parks throughout the world. Photo by WildWind, through Creative Commons.

Figure 83. ***Fissidens taxifolius*** with immature capsules, member of a genus that occurs in multiple gardens worldwide, including the tropical Cibodas Botanical Garden in Indonesia. Photo by Bob Klips, with permission.

Figure 84. ***Sphagnum fallax***, member of a genus that occurs in multiple gardens worldwide, including the tropical Cibodas Botanical Garden in Indonesia. Photo by Bob Klips, with permission.

Fastanti and Wulanasari (2021) found 30 species (27 moss species, 3 liverwort species) of bryophytes in the 189 ha of Cibinong Science Center-Botanical Garden, Indonesia. There were no hornworts. In sharp contrast, the 4.3 ha of the Szent István University Gödöllő Botanical Garden in Hungary had 69 bryophyte species with 3 liverwort and 66 moss species (Fintha *et al*. 2021). Most of these were common in Hungary and many also occur in other Hungarian botanical gardens, including ***Amblystegium serpens*** (Figure 66), ***Barbula unguiculata*** (Figure 80), ***Brachythecium rutabulum*** (Figure 68), ***Brachythecium salebrosum*** (Figure 1), ***Bryum argenteum*** (Figure 81), ***Calliergonella cuspidata*** (Figure 86), ***Ceratodon purpureus*** (Figure 69-Figure 70), ***Fissidens taxifolius*** (Figure 83), ***Grimmia pulvinata*** (Figure 72), ***Homalothecium lutescens*** (Figure 87), ***Homalothecium sericeum*** (Figure 88), ***Hypnum cupressiforme*** (Figure 73), ***Leskea polycarpa*** (Figure 89), ***Orthotrichum affine*** (Figure 49), ***Orthotrichum diaphanum*** (Figure 50), ***Eurhynchium hians*** (=***Oxyrrhynchium hians***; Figure 90), ***Plagiomnium cuspidatum*** (Figure 9), ***Syntrichia ruralis*** (Figure 91), ***Tortula muralis*** (Figure 92).

Figure 85. ***Brachythecium salebrosum***, a species that occurs in multiple botanical gardens in Hungary. Photo by Michael Lüth, with permission.

Figure 86. ***Calliergonella cuspidata***, a species that occurs in multiple botanical gardens in Hungary. Photo by Claire Halpin, with permission.

Figure 87. ***Homalothecium lutescens***, a species that occurs in multiple botanical gardens in Hungary. Photo by Claire Halpin, with permission.

Figure 88. ***Homalothecium sericeum***, a species that occurs in multiple botanical gardens in Hungary and elsewhere. Photo by Kristian Peters, through Creative Commons.

Figure 89. ***Leskea polycarpa*** with capsules, a species that occurs in multiple botanical gardens in Hungary and elsewhere. Photo by David T. Holyoak, with permission.

Figure 90. ***Eurhynchium hians*** (=***Oxyrrhynchium hians***), a species that occurs in multiple botanical gardens in Hungary and elsewhere. Photo by David T. Holyoak, with permission.

Figure 91. ***Syntrichia ruralis*** in rock crevice, a species that occurs in multiple botanical gardens in Hungary and elsewhere. Photo by Darkone, through Creative Commons.

Figure 92. ***Tortula muralis*** with capsules, a species that occurs in multiple botanical gardens in Hungary and elsewhere. Photo by David T. Holyoak, with permission.

On the other hand, five species [***Brachythecium glareosum*** (Figure 93), ***Dicranella varia*** (as *Dicranella howei*; Figure 94), ***Didymodon insulanus*** (Figure 95, ***Fissidens bryoides*** (as *Fissidens viridulus*; Figure 96), ***Orthotrichum obtusifolium*** (as *Nyholmiella obtusifolia*; Figure 97)] were listed as near threatened on the Hungarian Red Data List (Fintha *et al*. 2021). However, since three have been reclassified into widely distributed species, it is possible they were not legitimately red-listed.

Figure 93. ***Brachythecium glareosum***, a near threatened species found at the Szent István University Gödöllő Botanical Garden in Hungary. Photo by Sharon Pilkington, with permission.

Figure 94. ***Dicranella varia*** with capsules, a near threatened species found at the Szent István University Gödöllő Botanical Garden in Hungary. Photo by David T. Holyoak, with permission.

Figure 95. ***Didymodon insulanus***, a near threatened species found at the Szent István University Gödöllő Botanical Garden in Hungary. Photo by Claire Halpin, with permission.

Figure 96. ***Fissidens bryoides*** with capsules, a tiny moss that often occurs on wet rocks, and among the mosses found at the Szent István University Gödöllő Botanical Garden in Hungary. Photo by Janice Glime.

Figure 97. ***Orthotrichum obtusifolium*** with capsules, a near threatened species found at the Szent István University Gödöllő Botanical Garden in Hungary. Photo by Hermann Schachner, through Creative Commons.

In the preparation of this chapter, I compiled a total species list for 30 studies of bryophytes in parks, cemeteries, and botanical gardens to provide an estimate of the most frequent species. This is a crude list because of the huge variation in size and the worldwide distribution of the gardens. Nevertheless, some species seem to be everywhere.

Hornworts are notably absent in most gardens, with only ***Anthoceros agrestis*** (Figure 99) present in as many as three. Liverworts varied widely in number of species with some gardens lacking them entirely [*e.g.* 1500 ha forest park at Hôrka, Slovakia (Figure 98) (Mišíková *et al.* 2007)] and others having numbers of liverwort species exceeding those of the mosses [*e.g.* 1480 ha in restinga in Setiba State Park, Espírito Santo State, Brazil, has 25 liverworts and 9 mosses (Visnadi & Vital 1995)].

Figure 98. Forest path above the tunnel, Malkovská Hórka location, Prešov forest park, Slovakia, a park devoid of liverworts. Photo by Jozef Kotu, through Creative Commons.

In Serra da Canastra National Park (Figure 100), Minas Gerais, Brazil, with more than 71,000 hectares, Marchi do Carmo and Peralta (2016) found the hornwort ***Phaeoceros laevis*** (Figure 101). Among the liverworts, there were 53 species of the **Lejeuneaceae** (Figure 102). The park supported 289 species of bryophytes, most of which are widely distributed in Brazil.

Figure 99. ***Anthoceros agrestis***, the only hornwort present in as many as three parks out of 30 published species lists. Photo by Hermann Schachner, through Creative Commons.

Figure 100. Serra da Canastra National Park, Minas Gerais, Brazil - Rasga Canga Falls, a park with more liverworts than mosses. Photo by Halley Pacheco de Oliveir, through Creative Commons.

Figure 101. ***Phaeoceros laevis*** with sporophytes, the only hornwort found in Serra da Canastra National Park, Minas Gerais, Brazil in more than 71,000 ha. Photo by David T. Holyoak, with permission.

Figure 102. **Lejeuneaceae**, a leafy liverwort family with 53 species in Serra da Canastra National Park, Minas Gerais, Brazil. Photo by George Shepherd, through Creative Commons.

In the park of Mátrai Gyógyintézet Sanatorium, NE Hungary, Szűcs *et al*. (2018) found 65 bryophytes, of which only 3 were liverworts. Red-listed species for the territory, but found in the park, included ***Brachythecium glareosum*** (Figure 93), ***Cirriphyllum piliferum*** (Figure 103), ***Orthotrichum pumilum*** (Figure 104), ***Rhynchostegiella tenella*** (Figure 105), and ***Syntrichia latifolia*** (Figure 57-Figure 59).

Figure 103. ***Cirriphyllum piliferum***, a red-listed species found in the park of Mátrai Gyógyintézet Sanatorium, NE Hungary. Photo by Claire Halpin, with permission.

Figure 104. ***Orthotrichum pumilum*** with capsules, a red-listed species found in the park of Mátrai Gyógyintézet Sanatorium, NE Hungary. Photo by Hugues Tinguy, with permission.

Figure 105. ***Rhynchostegiella tenella*** with capsules, a red-listed species found in the park of Mátrai Gyógyintézet Sanatorium, NE Hungary. Photo by Hugues Tinguy, with permission.

Szűcs and Fintha (2019) reported 54 bryophyte species from the Erdőtelek Arboretum in Hungary. It is interesting that among these were the red-listed ***Brachythecium glareosum*** (Figure 93), ***Cirriphyllum piliferum*** (Figure 103), and ***Orthotrichum obtusifolium*** (Figure 97), also present in the park of Mátrai Gyógyintézet Sanatorium, NE Hungary (Szűcs *et al*. 2018) or Szent István University Gödöllő Botanical Garden in Hungary (Fintha *et al*. 2021). Based on this and other studies, the common species in these parks and botanical gardens are ***Amblystegium serpens*** (Figure 66), ***Barbula unguiculata*** (Figure 80), ***Brachythecium rutabulum*** (Figure 68), ***Bryum argenteum*** (Figure 81), ***Ceratodon purpureus*** (Figure 69-Figure 70), ***Hypnum cupressiforme*** (Figure 73), ***Leskea polycarpa*** (Figure 89), ***Orthotrichum anomalum*** (Figure 106), ***Orthotrichum diaphanum*** (Figure 50), ***Eurhynchium hians*** (=***Oxyrrhynchium hians***; Figure 90), ***Radula complanata*** (Figure 107), ***Syntrichia ruralis*** (Figure 91), and ***Tortula muralis*** (Figure 75).

Figure 106. ***Orthotrichum anomalum*** with capsules, one of the common species in Hungarian parks and botanical gardens. Photo by Claire Halpin, with permission.

Figure 107. ***Radula complanata*** on bark, one of the common species in Hungarian parks and botanical gardens. Photo by Jutta Kapfer, with permission.

Europe

Numbers of species vary widely among the parks in Europe. Nevertheless, they provide a glimpse of the abundance of mosses vs liverworts vs hornworts, the substrate distribution, and the effects of urban vs suburban vs natural habitats.

In the Azorean parks and gardens of the Reserva Florestal de Recreio do Pinhal da Paz on São Miguel Island (Figure 108), an Island of Portugal, Polaino-Martin *et al*. (2020) identified 43 bryophyte species, of which 19 were liverworts and 1 hornwort. These represented 17 sites about 100 m apart on rocks, soil, and tree bark, but concentrated on the "most striking" species. Three of these are endemic to Macaronesia. Others are endemic to Europe. This compares with 279 taxa known from the Serra de Sintra in Portugal (Figure 109) (Cacciatori *et al*. 2015).

Figure 108. Pinhal da Paz, Ponta Delgada, São Miguel, Açores, site of 43 bryophyte species. Photo by José Luís Ávila Silveira & Pedro Noronha e Costa through public domain.

Figure 109. Serra de Sintra, Portugal, home of 279 bryophyte taxa. Photo by Vitor Oliveira, through Creative Commons.

Segarra Moragues *et al*. (2021) investigated the bryophytes in 94 sampling sites in the city of Valencia, Spain. They identified 96 moss and 6 liverwort species. The greatest taxon richness occurred in locations with a variety of natural and relatively undisturbed substrates such as those found at the Botanical Garden (Figure 110), Viveros Garden (Figure 111), and the Turia River Garden (Figure 112).

Figure 110. Valencia Botanical Garden, Spain, where natural substrates favor bryophyte richness. Photo by Pablo Enzo, through Creative Commons.

Figure 111. Viveros Garden Entrance, Valencia, Spain, where natural, undisturbed substrates favor bryophyte richness. Photo by Thelma Datter, through Creative Commons.

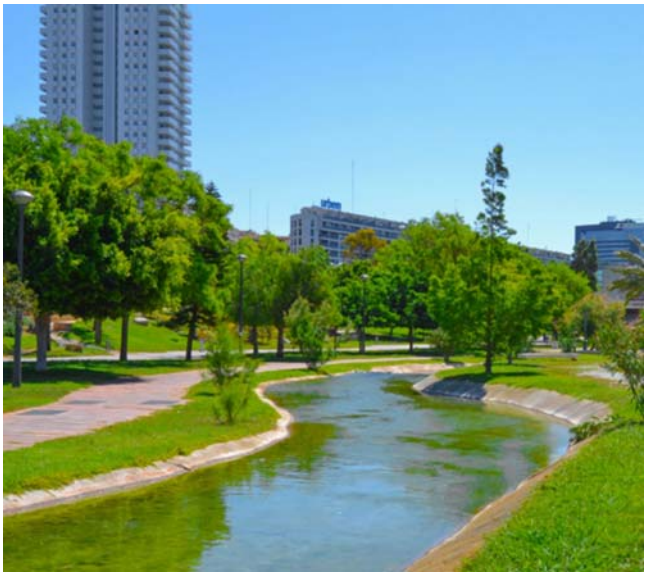

Figure 112. Turia River Garden, a park with a variety of natural substrates that support bryophytes. Photo by through Creative Commons 1 Stefan Majewski, through Creative Commons.

In Germany, Stech (1996) found 80 species (9 liverworts, 80 mosses) in the outdoor area of the Botanical Gardens of the University of Bonn (Figure 113). The greenhouses (Figure 114) had 11 liverworts and 41 mosses. In the UNESCO Heritage Park Sanssouci in Potsdam, Germany (Figure 115), Müller (2014) found 118 species of bryophytes. Of these, 25 were red-listed as threatened. This was in part due to a large re-colonization of epiphytes following the reduced air pollution. (See also Müller 2015).

Giordano *et al*. (2004) examined the biodiversity of epiphytic bryophytes in urban and nearby sites in southern Italy. Their interest was in the use of these as indicators through their bioaccumulations. As indicated by Segarra Moragues *et al*. (2021) they showed clearly that the number of species was lower in more urban areas. They also found that acrocarpous mosses and vegetative reproduction occur more frequently in more urban areas.

Figure 113. Botanical Garden, University of Bonn, Germany, home of 9 liverwort and 80 moss species. Photo by Carson DeLake, through Creative Commons.

Figure 114. Botanical Gardens of the University of Bonn greenhouses, home of 11 liverwort and 41 moss species. Photo by Elekes Andor, through Creative Commons.

Figure 115. UNESCO Heritage Park Sanssouci in Potsdam, Germany, home of 118 species of bryophytes, including 25 red-listed species. Photo by Wolfgang Pehlemann, through Creative Commons.

In Wroclaw, Poland, Fudali (2001, 2005) found only 81 bryophyte species in 22 town parks and 6 cemeteries. These were more specialized in their substrates, with more

than 40% occurring on only one type. Epiphytes were rare, but did seem to occur at the bases and first 30 cm of the tree trunks. Only the outer locations had forest species. In cemeteries, a higher number of species correlated with the age of monuments and dimensions of the object areas. In a wider study, Fudali (2006) found 125 species on 145 sites in 94 parks and 51 cemeteries in Poland. These were comprised of 11 liverwort and 114 moss taxa. The number of taxa was not significantly correlated with area of the study site, emphasizing the importance of even small parks in maintaining diversity of bryophytes. Parks on the outskirts typically had more diversity than did those in the city center. Frequent mosses were similar to those found in other studies of parks, including ***Amblystegium serpens*** (Figure 66), ***Bryum argenteum*** (Figure 81), ***B. caespiticium*** (Figure 116), ***Ceratodon purpureus*** (Figure 69-Figure 70), and ***Funaria hygrometrica*** (Figure 117). As in many other locations, epilithic species included ***Barbula unguiculata*** (Figure 80), ***Grimmia pulvinata*** (Figure 72), ***Orthotrichum diaphanum*** (Figure 50), ***Ptychostomum capillare*** (=***Bryum capillare***; Figure 118), ***Schistidium apocarpum*** (Figure 119), and ***Tortula muralis*** (Figure 75); frequent terrestrial species included ***Barbula convoluta*** (=*Streblotrichum convolutum*; Figure 120), ***Brachythecium rutabulum*** (Figure 68), and ***Eurhynchium hians*** (=***Oxyrrhynchium hians*** Figure 90). ***Marchantia polymorpha*** (Figure 34) was the only liverwort found in the city interiors. Fudali *et al*. (2015) reported 171 bryophyte taxa from the 8483 ha Roztocze National Park in Poland (Figure 121). These included 43 species protected by law in Poland, 20 of which are strictly protected and 13 as threatened in Poland. Furthermore, 36 species were new for the region.

Figure 117. ***Funaria hygrometrica*** with capsules, a species common in parks and cemeteries of six cities in Poland. Photo by Hugues Tinguy, with permission.

Figure 118. ***Ptychostomum capillare*** with capsules, an epilithic species common in parks and cemeteries of six cities in Poland. Photo by Wouter Van Landuyt, through Creative Commons.

Figure 116. ***Bryum caespiticium*** with capsules, a species common in parks and cemeteries of six cities in Poland. Photo by Bob Klips, with permission.

Figure 119. ***Schistidium apocarpum*** with capsules, an epilithic species common in parks and cemeteries of six cities in Poland. Photo by Christophe Quintin, through Creative Commons.

Figure 120. ***Barbula convoluta*** with capsules, a terrestrial species common in parks and cemeteries of six cities in Poland. Photo by David T. Holyoak, with permission.

Figure 121. Roztocze National Park in Poland, home of 171 bryophyte taxa. Photo by Rysy, through Creative Commons.

In an experimental and teaching garden at the University of Lodz, Poland, Wolski *et al*. (2012) found 41 species of mosses and only 1 liverwort. These represented the epigeic, epilithic, epiphytic, epixylic, and aquatic habitats. The epigeic (soil) habitat had the most species (34), whereas the aquatic habitat had the least (1). These urban parks, nevertheless, exhibit a large diversity of species of bryophytes, especially species not found elsewhere in the city.

In Slovakia, Godovičová *et al*. (2020) found 12 liverwort and 92 moss species in 14 historical parks and gardens. Among these, ***Amblystegium serpens*** (Figure 66), ***Brachythecium rutabulum*** (Figure 68), ***Bryum argenteum*** (Figure 81) and ***Tortula muralis*** (Figure 75) were present in all 14 study sites. Small urban parks had fewer bryophyte species than did rural areas, with the most species on soil and least on wood. As in some other studies, a rare species (***Ptychostomum bornholmensis*** – see Figure 122) used the parks as a refuge.

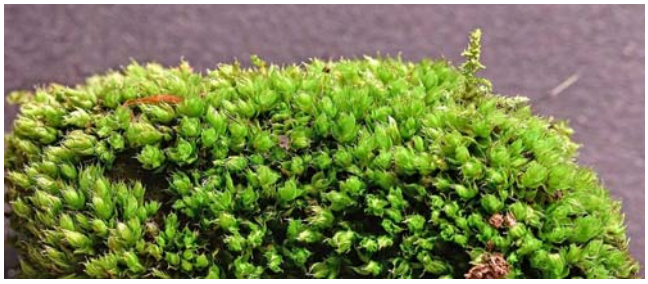

Figure 122. ***Ptychostomum creberrimum***; ***Ptychostomum bornholmensis*** is a rare species occurring in historical parks and gardens in Slovakia. Photo by Wayne Lampa, through Creative Commons.

In the forest park of Hôrka (Figure 98), located in the center of the town Veľký Krtíš, Slovakia, Mišíková *et al*. (2007) found 37 bryophyte species, but no liverworts or hornworts. In a broader study, Mišíková *et al*. (2015) found 81 bryophyte species in ten villages in Slovakia. These were not parks, where the bryophytes are afforded some degree of protection. Nevertheless, with the 81 species in total, species richness of individual localities ranged 17 to 57 species. They suggested that the cooler, more humid climate in the northern part of central Slovakia favored a greater species richness there. They also found that cemeteries and parks contributed to higher diversity. The highest numbers of species occurred on bare damp soil or on concrete and stony walls.

Godovičová (2019) explored the bryophytes in the Horský Park protected area (Figure 123) in the urban Bratislava, Slovakia. This forest park had 57 bryophytes, with 6 liverworts and no hornworts. Two red-listed species [***Fissidens exilis*** (Figure 124) and ***Rhynchostegium rotundifolium*** (Figure 125)] occurred there. As in many other studies, the greatest number of species (19) occurred on exposed soil and the least along streams (6).

Figure 123. Bratislava Horský Park, a forested park with 57 bryophyte species, including 6 liverworts. Photo by Peter Zelizňák, through Creative Commons.

Figure 124. ***Fissidens exilis*** with capsules, a red-listed species that occurs in the Horský park, Slovakia. Photo by Hugues Tinguy, with permission.

Figure 125. ***Rhynchostegium confertum*** with capsules, a red-listed species that occurs in the Horský park, Slovakia. Photo by Claire Halpin, with permission.

In the Central Park Archbishop's Garden in Eger, Hungary (Figure 126), Szűcs *et al*. (2020) found 55 moss and 4 liverwort taxa. Of these, 49% were from only three families (**Orthotrichaceae**, **Pottiaceae**, and **Brachytheciaceae**). The species composition and life strategies of bryophytes in this park differed remarkably from that of other Central and Eastern European parks.

Figure 126. Central Park Archbishop's Garden in Eger, Hungary, home to 55 moss and 4 liverwort species, with nearly half in only three families. Photo by Zolchew, through Creative Commons.

In eastern Serbia, Sabovljević (2006) found 82 bryophyte species, including 11 liverworts, in the Djerdap National Park (Figure 127). Although this seems like a large number, the park occupies 63,786 ha with a wide range of habitats.

Figure 127. Djerdap National Park on the Danube. Photo by Milan Paunović, with permission.

In the Vrana Park (<40 ha), Sofia city, Bulgaria, Gospodinov *et al*. (2018) found 68 bryophyte species, four of which are of conservation importance. In Loven Park, in the same city, only 31 species of mosses and 5 of liverworts were found, despite the larger size (243 ha) of the park (Natcheva & Gospodinov 2020). The researchers considered the lack of habitat diversity and microrelief, a dense understory of shrubs and saplings, and invasion of ivy (*Hedera helix*) on soil and tree trunks to be the reasons for the low diversity.

In 2018, Mamchur *et al*. found 143 moss species in the Pohulyanka forest park, Ukraine (Figure 128). They compared the bryophytes in this study to earlier records in the last 50-100 years and found that 34 species could no longer be located. On the other hand, 72 species in this study were not found in those earlier studies. Among the current species, 25 are rare for the **nemoral** (pertaining to groves or woodlands) and forest steppe zones. The number of epiphytic species has increased, a fact that the researchers attribute to anthropogenic activity.

Figure 128. Pohulyanka forest park, Ukraine, home to 143 moss species, with 72 that were not present 50 years earlier. Photo by M. Sha, through public domain.

Asia

Lu and Jing (2019) reported on the ground bryophytes of 11 parks in Nanjing, China. They found only 51 bryophyte species, with 35% of them in only three families (**Pottiaceae**, **Bryaceae**, **Brachytheciaceae**). The most common ones were ***Barbula unguiculata*** (Figure 80), ***Brachythecium rutabulum*** (Figure 68), ***Haplocladium angustifolium*** (Figure 129), ***Haplocladium microphyllum*** (Figure 130), ***Physcomitrium sphaericum*** (Figure 131), and ***Taxiphyllum taxirameum*** (Figure 132). The first two of these are widespread and common in various parks and gardens. The number of species per park ranged from 3 to 20, with turfs as the main life form. They found an interesting correlation of environmental factors with diversity. Humidity, human disturbance, canopy density, and distance to main roads were the important factors. The latter variable is one that seems not to be considered in most studies.

Figure 129. ***Haplocladium angustifolium***, among the most common species in 11 parks in Nanjing, China. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 130. ***Haplocladium microphyllum***, among the most common species in 11 parks in Nanjing, China. Photo by Bob Klips, with permission.

Figure 131. ***Physcomitrium sphaericum*** with capsules, among the most common species in 11 parks in Nanjing, China. Photo by Štěpán Koval, with permission.

Figure 132. ***Taxiphyllum taxirameum*** with capsule, among the most common species in 11 parks in Nanjing, China. Photo by Bob Klips, with permission.

Liu *et al*. (2015) found 83 species in saxicolous communities in urban habitats in Chongqing, China. Soil communities supported only 46 species, contrasting with European studies cited above. Surprisingly to me, diversity indices of both of these communities were higher on campuses than in parks, natural scenic resorts, or the Jinyunshan National Nature Reserve (Figure 133). The environmental parameters differed in importance, with canopy density being most important for saxicolous communities in parks and campuses. In natural science scenic resorts and the nature reserve, altitude, relative humidity, and human disturbance were most important. In the soil communities, *p*H, canopy density, and human disturbance were of major importance in parks and campuses. In the natural scenic resorts and nature reserve, altitude, relative humidity and water content of the soil were the most important determinants of the soil bryophyte communities.

Figure 133. Jinyunshan Nature Reserve with karst topography in Chongqing, China, an area with lower bryophyte diversity than urban areas in the province. Photo by Bernt Rostad, through Creative Commons.

The Japanese are famous for their moss gardens, which are discussed elsewhere in this chapter. Nakamura and Suga (1997) instead studied the bryophytes in various urban and natural environments, including a nature park, agricultural area, urban park, street residential district, housing complex district, commercial district, and industrial district. These study sites had 83 bryophyte species in 1975, but in 1995, only 78 were located (Figure 134). Nevertheless, the number of species at individual sites increased for most sites. Only the agricultural site experienced a decrease in species. **Erect** forms increased at all sites, whereas **prostrate** forms decreased in both the nature park and the agricultural district. On the other hand, **thalloid** forms increased in the nature park site. In the industrial site, **erect** forms were the only remaining type. Like several sites in Europe, soil was the most common substrate, followed by tree trunks and then concrete. The number of bryophyte species was positively correlated with the woody vegetation cover, indicating a dependence on shade and perhaps moisture.

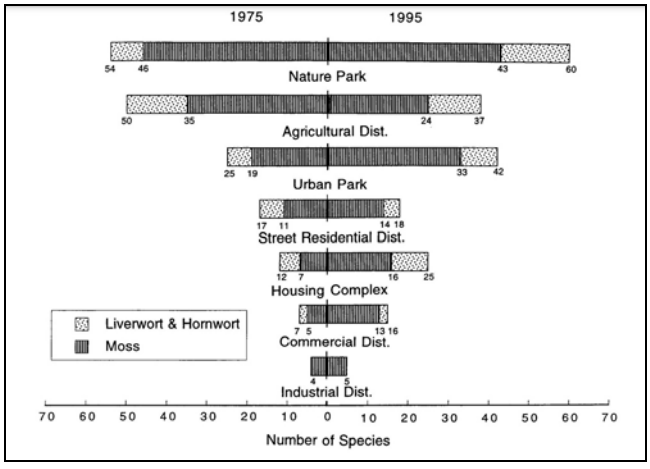

Figure 134. Changes in moss, liverwort, and hornwort species from 1975 to 1995 in Chiba City and Yotsukaidou City, Japan. Image slightly modified from Nakamura & Suga 1997.

Tropics

In the Chapada Diamantina National Park, Brazil (Figure 135), Bastos *et al*. (1998) found only 27 species of mosses and 4 species of liverworts. Most of these species were restricted to this high altitude complex. Later, Sierra *et al.* (2018) studied the bryophyte flora of the Jaú National Park (Figure 136) in Brazil. In their extensive collecting of 712 collections, they found 150 species. Of these, 20 were rarely collected Amazonian endemics.

Figure 135. Chapada Diamantina National Park, Brazil, home to 27 species of mosses and 4 species of liverworts. Photo by Roney, through Creative Commons.

Figure 136. Jaú National Park, Brazil, home to 150 bryophyte species, 20 of which are rare Amazonian endemics. Photo by Dalia McGill, through Creative Commons.

In the more tropical Panama, Gradstein and Salazar Allen (1992) sampled the bryophytes along an elevational gradient in the Dárien National Park (Figure 137). The inundated lowland, hillside-lowland, submontane, and montane elfin forest had distinctly different species assemblages. They found the largest number of exclusive species as well as the greatest bryophyte biomass in the montane forest. The submontane forest, however, has the greatest overall species richness. The lowland forest had the lowest diversity. Forty liverwort taxa in the park were reported as new to Panama.

Figure 137. Dárien National Park, where the montane forest has the most exclusive bryophyte species and greatest bryophyte biomass among the five elevational zones. Photo by Harvey Barrison, through Creative Commons.

North America

In the Taum Sauk Mountain State Park, Missouri, USA (Figure 138), Holmberg and Atwood (2014) documented 123 bryophytes, with 103 mosses, 18 liverworts, and 2 hornworts in 3035 ha.

Figure 138. Taum Sauk Mountain State Park, Slippery Rock, Missouri, a temperate park with 103 mosses, 18 liverworts, and 2 hornworts. Photo by Yinan Chen, through Creative Commons.

Australia

In Mungo National Park in arid Australia (Figure 139), Downing and Selkirk (1993) found that the number of species did not differ significantly between sites representing differences in soils, topography, and tracheophytes. Bryophytes were well represented in soil crusts. Ephemerals were censused by soil cultures. Factors influencing the bryophyte vegetation included soil texture, *p*H, conductivity, nutrient status, vascular plant vegetation, light level, leaf litter, and fire frequency. The species are typical of calcareous substrates throughout the desert area.

Ramsay *et al*. (1990) found more than 90 species in the Mount Tomah Botanic Garden in Australia (Figure 140), a 30 ha park. In the Royal Botanic Gardens, Sydney (Figure 141), Ramsay *et al*. (1993) found 70 moss, 24 liverwort, and 1 hornwort species. These included many species and genera noted in other parks and gardens around the world, including ***Amblystegium serpens*** (Figure 66), ***Barbula*** (2 spp.; Figure 80), ***Brachythecium rutabulum*** (Figure 68), ***Bryum argenteum*** (+ 9 other ***Bryum*** spp., Figure 81), ***Campylopus*** (6 species; Figure 82), ***Ceratodon purpureus*** (Figure 69-Figure 70), ***Eurhynchium praelongum*** (Figure 71), ***Fissidens*** (8 spp.; Figure 83), ***Leucobryum*** (1 sp.; Figure 5), ***Ptychostomum capillare*** (=***Bryum capillare***; Figure 118), ***Syntrichia laevipila***, (+ 1 other ***Syntrichia*** sp.; Figure 55-Figure 56). ***Tortula muralis*** (Figure 75), and the liverworts ***Frullania*** (3 spp.; Figure 79), ***Lunularia cruciata*** (Figure 76), ***Marchantia polymorpha*** (Figure 34), and ***Riccia*** (4 spp.; Figure 78). Some of these species may have arrived from other parts of the world.

Figure 139. Mungo National Park, Lake Mungo, Australia, a site with soil crusts where bryophytes were well represented. Photo by Dhum Dhum, through Creative Commons.

Figure 140. Mt. Tomah Botanical Gardens, Australia, home to 70 moss, 24 liverwort, and 1 hornwort species. Photo by L. Walsh84, through Creative Commons.

Figure 141. Pond in Royal Botanic Gardens, Sydney, Australia, a park with 70 moss, 24 liverwort, and 1 hornwort species known. Photo by J. Bar, through Creative Commons.

Other botanical garden investigations include those of Nohl (1977), Menzel (1984), Al Araj and Klotz (1989), Ziegler (1996), Kiessling & Stetzka (1997), De Bruyn & Homm (2009), and Teutsch (2021).

Value

Public gardens cover a wide range of purposes. This translates into a variety of sources for any bryophytes found there. Bryophytes can serve as aesthetic enhancement, but they can also provide protected places where experimentation is possible. Since gardens are likely to be encouraged by use of fertilizers, response of bryophytes can be studied by providing invisible (hidden) markers and following the responses of the bryophytes to the fertilizers. This might be complicated, however, when one tries to create a suitable control.

Among the 90 species of bryophytes in the Cibodas Botanical Garden, Indonesia (Figure 77), Nadhifah *et al*. (2018) found 42 species with potential use and 42 species with potential use in medicine, ornamental purposes, agriculture, and environmental services.

Perhaps one of the most valuable uses would be to track dispersal and its mechanisms. Plants in botanical gardens often come from all over the world, or at least from some place else. Hence, these gardens can have species that arrived as hitchhikers with the tracheophytes that were planted there. This provides an opportunity to see what survives in both the short and long term. But, of course, these hitchhikers are a problem beyond the confines of the garden. They can become invasive species, as seen for ***Pseudoscleropodium purum*** (Figure 142) and others.

Figure 142. ***Pseudoscleropodium purum***, an invasive species. Photo by Claire Halpin, with permission.

Bryophyte Volunteers in Personal Gardens

Smith *et al*. (2010) studied the bryophytes in 61 domestic gardens in Sheffield, UK. They recorded 67 bryophytes, with individual gardens having 3-24 species. The mean richness was 11.3. Slightly over 20% of the bryophyte species occurred in grass lawns, and these species were the most widespread compared to those of other habitats. Only 10% occurred in more than half the gardens. Area, substrate richness, and altitude explained 39.1% of the bryophyte richness.

Dick Lister (Bryonet 5 February 2022) provided us with a species list from the Royal Horticultural Society's garden tour at Wisley, Surrey, England. Of the 8 categories of gardens, the most common bryophyte taxa, occurring in at least 4 of the 8 are ***Brachythecium rutabulum*** (Figure 68), ***Bryum dichotomum*** (Figure 143), ***Campylopus introflexus*** (Figure 82), ***Ceratodon purpureus*** (Figure 69-Figure 70), ***Cratoneuron filicinum*** (Figure 144), ***Eurhynchium praelongum*** (as ***Kindbergia praelonga***; Figure 71), ***Funaria hygrometrica*** (Figure 117), ***Hypnum cupressiforme*** (Figure 73), ***Zygodon viridissimus*** (Figure 145). Of these, all are common elsewhere in gardens except ***Cratoneuron filicinum*** and ***Zygodon viridissimus***. In addition to these frequent species, these gardens had many additional species and genera that are frequent in the public parks and gardens elsewhere, including the liverworts ***Lunularia cruciata*** (Figure 76), ***Marchantia polymorpha*** (Figure 34), and ***Riccia sorocarpa*** (Figure 78), the hornwort ***Anthoceros*** (Figure 99), and the mosses ***Amblystegium serpens*** (Figure 66), ***Atrichum undulatum*** (Figure 67), ***Barbula convoluta*** (Figure 120), ***Barbula unguiculata*** (Figure 80), ***Bryum argenteum*** (Figure 81), ***Ptychostomum capillare*** (as ***Bryum capillare***; Figure 118), ***Eurhynchium hians*** (as ***Oxyrrhynchium hians***; Figure 90), ***Fissidens*** (Figure 83), ***Grimmia pulvinata*** (Figure 72), ***Homalothecium sericeum*** (Figure 88), ***Orthotrichum affine*** (Figure 49), ***Orthotrichum anomalum*** (Figure 106), ***Orthotrichum diaphanum*** (Figure 50), ***Orthotrichum lyellii*** (Figure 51-Figure 52), ***Rhynchostegium confertum*** (Figure 74), ***Syntrichia laevipila*** (Figure 55-Figure 56), ***Syntrichia latifolia*** (Figure 57-Figure 59), ***Syntrichia ruralis*** (Figure 91), ***Tortula muralis*** (Figure 75), and ***Ulota phyllantha*** (Figure 54).

Figure 143. ***Bryum dichotomum***, a species that is frequent in private gardens in Wisley, Surrey, England, but not in gardens and parks elsewhere. Photo by Claire Halpin, with permission.

Figure 144. ***Cratoneuron filicinum***, a species that is frequent in private gardens in Wisley, Surrey, England, but not in gardens and parks elsewhere. Photo by Claire Halpin, with permission.

Figure 145. ***Zygodon viridissimus*** with capsules, a species that is frequent in private gardens in Wisley, Surrey, England, but not in gardens and parks elsewhere. Photo by David T. Holyoak, with permission.

Alien Species

It would appear that bryophytes should be able to invade new areas such as gardens more easily than most tracheophytes (Essl & Lambdon 2009). Their dispersal by spores is easier than that by seeds, making colonization easier. On the other hand, their very limited cultivation use results in few deliberate introductions. Their impacts, due to their small size, are small. Nevertheless, we have almost no understanding of the long-term effects of invasive bryophytes.

Essl and Lambdon (2009) noted that we have little information regarding the invasion history of bryophytes. Their spore dispersal is efficient, giving them a greater colonizing ability than that of tracheophytes. Deliberate introductions are rare because they are seldom used in gardens. Because of their small size, we assume that they have little measurable impact on the ecosystems they invade. This is an area that needs to be considered by the scientific community, particularly as their use in green technology and gardening is increasing and their availability through internet orders is increasing.

In Europe, Essl and Lambdon (2009) identified 45 species that seem to be alien in at least parts of Europe (Table 1). These include at least 21 mosses and 11 liverworts, but no hornworts. Of these, ***Campylopus introflexus*** (Figure 82) and ***Orthodontium lineare*** (Figure 146) have become widespread mosses and the Mediterranean liverwort ***Lunularia cruciata*** (Figure 76) has exhibited great northward expansion. A number of tropical species were present only in glasshouses, including ***Marchantia pappeana*** (Figure 147), ***Vesicularia reticulata*** (Figure 148), and ***Zoopsis liukiuensis*** (Figure 149). Glasshouses seem to be the only places outside California to find ***Lunularia cruciata*** in North America (Schuster 1992).

Table 1. Alien bryophytes in Europe, ranked by decreasing number of invaded countries/regions. Only species invading >3 countries/regions are shown. From Essl and Lambdon 2009.

Campylopus introflexus	21
Orthodontium lineare	15
Didymodon australasiae	11
Ricciocarpos natans	8
Leptophascum leptophyllum	6
Hennediella stanfordensis	4
Tortula bolanderi	4
Lunularia cruciata	12
Riccia rhenana	12
Scopelophila cataractae	7
Dicranoweisia cirrata	4

Figure 146. ***Orthodontium lineare*** with capsules, on soil bank, an invasive species in parts of Europe. Photo by Claire Halpin, with permission.

Figure 147. ***Marchantia pappeana***, a species that has invaded glass houses in Europe. Photo by Rob Palmer, through Creative Commons.

Figure 148. ***Vesicularia reticulata***, a species that has invaded glass houses in Europe, most likely arriving in the aquarium trade. Photo by Tan Sze Wei, with permission.

Figure 149. ***Zoopsis leitgebiana***; ***Zoopsis liukiuensis*** has invaded glass houses in Europe. Photo from Auckland Museum, through Creative Commons.

Although most of the alien bryophytes remain rare in their new locations, several have become rather widespread and have the potential to impact their ecosystems (Essl & Lambdon 2009). At present, these are ***Campylopus introflexus*** (Figure 82) and ***Orthodontium lineare*** (Figure 146). The thallose liverwort ***Lunularia cruciata*** (Figure 76) continues to spread, but it seems to be rather restricted in its habitat, mostly surviving in glass houses outside its normal range. Essl and Lambdon concluded that the alien bryophyte species in Europe tend to occur in disturbed habitats where humans have played a major role, including gardens, roadsides, and walls.

We must first ask ourselves what impacts invasive bryophyte species **might** have. Essl and Lambdon (2009) suggest that they could compete with native bryophytes and lichens or even with germinating seedlings by blocking light, sequestering nutrients, or occupying space. It appears that the only documented strong impact by an invasive bryophyte is that of ***Campylopus introflexus*** (Figure 82). Its dense mats significantly reduce the diversity of both bryophytes and lichens (Hahn 2006). In other cases, this species has colonized thatched roofs in southern England

where they could replace the diminishing populations of ***Leptodontium gemmascens*** (pers. comm. by Ron Porley, in Essl & Lambdon 2009).

As interest has grown regarding invasive species, Essl *et al*. (2013) have provided us with a glimpse of the forces behind invasive bryophytes. Of the 139 bryophytes considered to be alien in Europe, they consider 34 to be hitch-hikers (34 species) or companions (27 species) with ornamental plants, constituting the most important means of introduction. Fortunately, most of these seem to be successful only in habitats created by humans and seem unable to become established in natural ecosystems.

Impacts of alien bryophytes on biodiversity and socio-economy are a recent phenomenon, with >85 % of impacts on biodiversity, and 80 % of impacts on socio-economy recorded since 1990 (Essl *et al*. 2014). On average, 40 years (impacts on biodiversity) and 25 years (impacts on socio-economy) elapsed between the year a bryophyte species was first recorded as alien in a region and the year impacts were first recorded. They found that since the first reported invasion occurred, the number of records has increased rapidly. Based on this trend, they concluded that the impacts of these invaders will continue to increase.

Essl *et al*. (2015) began to explore the macroecology of bryophyte invasions. Most naturalizations occurred in complementary regions of the opposite hemisphere (Essl *et al*. 2015). And the Southern Hemisphere has experienced more invasions with naturalizations than has the Northern Hemisphere. Hence, naturalizations are most likely to occur in biogeographically separated regions that exhibit climates similar to that of the location of origin.

Bryophytes in Glass Houses

France (2019) interviewed the horticultural staff at the Ferns and Fossils House at the Royal Botanic Garden Edinburgh (Figure 150). He recommended raising the status of bryophytes in botanic gardens and increasing the diversity of living collections.

Figure 150. Greenhouse, Royal Botanic Garden of Edinburgh, an opportunity to include more bryophytes in a public place. Photo by Eldubhe, through Creative Commons.

Botanical gardens and greenhouses often import and cultivate non-native species. Essl and Lambdon (2009) assessed the reasons for studying bryophyte invasions. They considered them to be poorly recorded and thus provide little information upon which to assess their invasion history. They have efficient dispersal by spores and have a greater ability to naturalize than other major taxonomic groups. They are seldom cultivated, so deliberate introductions are few. Their small size makes their impact on the environment small. On the other hand, the possibility that these invasions have long-term effects has never been explored.

For whatever reason, ***Lunularia cruciata*** (Figure 76) is particularly common in glass houses (Sabovljević & Marka 2009), often in parts of the world where it is unknown outside these structures.

Educational Displays

A number of gardens serve educational needs. This may be the entire garden, or only small portions. This education is usually accomplished by signs. Some gardens include a feel garden, especially pitched toward the blind, but can also be attractive to children. Mosses offer a wide range of textures that can be a delight to those meeting them for the first time. Additional information can be provided in Braille.

The Moss House (Figure 151-Figure 152) in India is designed for teaching. The bryophytes are planted and the species patch is outlined with white rocks (Figure 153-Figure 154). A label is placed on a stake in the patch. A simpler design without the feel of a garden is to plant bryophytes in pots and provide them with a label (Figure 155).

Indoor gardens like the Moss House require watering. This is best done with an automatic misting system (Figure 156), but care must be taken to create the appropriate regime. A filtering system might be needed to remove chlorine and unwanted minerals from the water. A fan may be needed to prevent mold.

Figure 151. Moss house where mosses are inside a shaded greenhouse. Photo courtesy of Virendra Nath.

Figure 152. Moss greenhouse in preparation, showing a fountain that will help to maintain moisture. Photo courtesy of Virendra Nath.

Figure 155. Labelled pots with species name, family, common name, and location of origin. Photo courtesy of Virendra Nath.

Figure 153. Labelled bryophytes in the Moss House, showing the white rock and label system used to identify the species. Photo courtesy of Virendra Nath.

Figure 156. Misting indoor moss garden in India. Photo courtesy of Virendra Nath.

Figure 154. ***Plagiochasma appendiculatum*** showing white rocks and labelling. Photo courtesy of Virendra Nath.

Labelling

In an arboretum labels (Figure 153-Figure 155) help us to learn the names of the trees. Few gardens exist where a similar education is available for bryophytes. I quickly learned one of the problems of providing such labels for bryophytes. I learned that the field trip I had been asked to lead would have 60 participants. I went armed with a stack of pink computer cards. At each bryophyte, I placed a card with the name of the species. But the bryophytes were small and the cards were large. Many of the cards touched several species. That is only part of the problem in a bryophyte garden. As time passes, the species that is labelled can expand or get overgrown by other bryophytes. Furthermore, to most people, all bryophytes look pretty much the same. One Botanical Garden has attempted to solve the problem by locating a large patch of the bryophyte and attaching a label, then posting information explaining the characters used to identify the bryophyte and providing other useful information about it (Figure 157).

Figure 157. Labelling of the leafy liverwort ***Frullania dilatata*** in a Botanical Garden. Photo courtesy of Stefan Schneckenburger.

Summary

Public gardens occur all over the world, and many have sections with bryophytes, especially in Japanese gardens. These bryophytes require caretakers who understand the differences in the needs of bryophytes, avoiding fertilizers and maintaining boundaries between species. Watering may also be necessary.

Moss gardens are best known from Japan, but a number have mimicked the Japanese style of moss gardens in other countries.

Local species can be preserved in parks that serve as refuges in city landscapes. The number of species depends on the size of the park, the number of habitat types, and degree of human disturbance. Climate affects the parks in the same way it does non-park areas.

Bryophytes may enter the country or local area in pots of other plants that become a part of these gardens, whether public or private. These tend to be more successful in the human disturbance areas like parks and gardens than they do in nature. These aliens are most likely to arrive from the opposite hemisphere from areas with similar climates. ***Campylopus introflexus*** and ***Orthodontium lineare***, in particular, have become well established in many areas as invasive species. Glass houses may have bryophytes that arrive in pots from all over the world. ***Lunularia cruciata*** exists in many locations only in glass houses.

Teaching gardens are often enhanced for learning by having labels. These need to be carefully monitored to be sure the same species remains with its label.

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